The History of Life on the Net

A Reference Work on Evolution and the Vacuum.Net

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How to read this book

This book tells the history of life, from the chemistry before the first cell to the net that humans have laid over the Earth, and one step beyond. It tells it with the measured cases: the dates, the sizes, the times and the counts.

Through the whole history runs one set of forms, the forms of the Vacuum.Net. What closes stays, and a living strand has one direction. The form lasts while its carriers are replaced.

The residue of one depth becomes the alphabet of the next. A closure is never loaded twice. A new kind of union opens once and is then filled many times.

Reading keeps the relations and drops the rest.

Where a form shows in the history, the text names it in a sentence or two, and the history goes on. The forms are read in the history. They are described beside it, not as its cause.

Chapter 1 gives the few basics of the net where the history first needs them. Every later chapter refers back to them.

The ladder. Every size and every time in the book has a position on one scale. The position of a length is log base 3 of the length over 4.558816×10^{-8} m. The position of a time is log base 3 of the time over 1.520655×10^{-16} s.

One year is 3.15576×10^{7} s. An age of A million years is placed as the time from then to now. The day sits at 43.50, the year at 48.87.

Chapter 24 sets the lengths, durations and ages of the catalogue in order on one ladder: 2,702 positions.

Self-contained. Every number stands in the text with its unit, and every calculation is shown. The numbers in square brackets point to the list of sources at the end of the book. The reader needs nothing else to follow the text.

The catalogue. Every case told in the book is also a row in the catalogue: 8,761 cases with their values, positions, forms and sources. The catalogue is held in the MAZE.

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1. Before the Cell

The history of life begins before life. It begins with the first solid grains of the solar system, 4,567.30 ± 0.16 million years ago [1]. Within 267 million years the young Earth carried liquid water at its surface.

This chapter follows that stretch in order. It dates the Earth, its oldest crystal and its first water, and the later bombardment in its two readings.

It then follows the chemistry that makes the parts of life without life: amino acids from sparks, sugars from formaldehyde, nucleotides from cyanide and sulfide, carbon chains on vent minerals. It ends with catalytic RNA, the genetic code and membranes that grow and divide.

The net appears here for the first time. Its basics are named once, where the history first shows them.

The ladder comes with the first dates, the trit and the window with the first crystal, ring, depth and edge with the first membranes. Later chapters refer back to them.

The first solids and the young Earth

The oldest solids of the solar system are small inclusions rich in calcium and aluminium. They are found in meteorites. Dated by uranium and lead, they formed 4,567.30 ± 0.16 million years ago (Ma) [1].

The process that formed them lasted about 3 million years. The round grains called chondrules formed between 4,567.32 ± 0.42 and 4,564.71 ± 0.30 Ma [1]. The Earth itself formed at about 4,550 Ma [2].

Every size and every time in this book has a position on one ladder. The position is the logarithm, base 3, of a size over 4.558816×10^{-8} m, or of a time over 1.520655×10^{-16} s. One step up the ladder is a factor of three.

On this ladder the day sits at 43.50 and the year at 48.87. An age of A million years is $A \times 10^{6} \times 3.15576 \times 10^{7}$ s. The first solids are $4{,}567.30 \times 10^{6} \times 3.15576 \times 10^{7}$ s = 1.4413×10^{17} s old, position 69.12.

The Earth at 4,550 Ma stands at 69.11. The positions are coordinates, given to two decimals. The whole history of this book lies between them and the present.

Soon after its formation the Earth melted. A zircon examined atom by atom fixes the end of that melt. Its age is consistent with a magma ocean about 4.5 billion years ago, formed by the impact that made the Moon [3].

The oldest crystal and the first water

The oldest parts of the Acasta Gneiss are 4,030 million years old [2].

The record of that time lies in single mineral grains, the zircons, held in later sediments. In the Jack Hills of the Yilgarn Craton, Western Australia, one detrital zircon is 4,404 ± 8 million years old, position 69.08 [2].

That grain is about 130 million years older than any earth material known before it. Earlier Yilgarn zircons reached about 4,276 million years [2]. The grain formed 146 million years after the Earth and 163 million years after the first solids.

Its oxygen records how it grew. The ratio of heavy to light oxygen, $\delta^{18}O$, is zoned from 7.4 ‰ to 5.0 ‰ across the grain [2]. The granite melt it grew from carried 8.5 to 9.5 ‰.

On these values the grain is read as the earliest evidence for continental crust and oceans on the Earth [2].

A second study analysed Jack Hills zircons aged 3,910 to 4,280 million years. They are held in a quartzite of the Murchison District that is itself 3 billion years old [4]. Their $\delta^{18}O$ ranges from 5.4 ± 0.6 ‰ to 15.0 ± 0.4 ‰.

These values are consistent with a body of water interacting with the crust by 4,300 million years ago, position 69.06 [4]. The oldest exposed crust, by contrast, is granitoid gneiss and supracrustal rock of 3,800 to 4,000 million years [4].

A 4.4-billion-year age was checked inside a Hadean zircon at the scale of atoms. Atom-probe tomography found isolated clusters rich in lead, about 10 nm across and spaced 10 to 50 nm apart [3]. These clusters stand at position −1.38; their spacing at −1.38 to 0.08.

The grain carries a rim grown at high temperature, about 1 billion years after its core [3]. Any mixing of the silicate Earth must have ended before 4.4 billion years ago.

From 4,404 to 4,300 Ma is 104 million years. The first solids to the first recorded water is 4,567.30 − 4,300 = 267 million years. Liquid water stood on the Earth within the first 6 per cent of its history.

The trit and the window

The zircon is a crystal, and with it the net appears in the history. The net is a strand.

Every crossing of the strand holds one of three values: +1, 0 or −1. Such a value is a trit.

Three trits in a row form a window. A window is closed when its three values add to zero, counted in threes. Of the 3 × 3 × 3 = 27 possible windows, 9 are closed.

Three of the nine hold one value three times: +1 +1 +1, 0 0 0 and −1 −1 −1. That is the form of a crystal. The other six hold all three values once, in the six possible orders.

In those six the content changes while the window stays closed. That is the form of metabolism.

An open window carries tension. Only what closes, stays.

The zircon shows the first kind of closure. Its order repeats through the grain. The Jack Hills grain has held its record of water for 4,404 million years.

The bombardment: two readings

The Moon carries the record of impacts. Argon ages of lunar rocks peak near 3.9 billion years [5]. One reading takes this as a spike of impacts across the inner solar system at that time [6].

A model of the giant planets places the spike about 700 million years after the planets formed [7]. In that model the spike follows a rapid migration of the giant planets after a long quiet period. From the first solids that gives 4,567.3 − 700 = 3,867 Ma, position 68.96.

A model of the Earth's crust under that bombardment set the window at about 4.1 to 3.8 billion years ago. That is 300 million years, between positions 69.02 and 68.95 [6]. Thermal metamorphic ages lie around 3.9 billion years and do not exceed it.

The same model asked whether the bombardment could sterilise the Earth. Its answer: "there is no plausible situation in which the habitable zone was fully sterilized on Earth" [6].

In the extreme case the surface stood at 50 °C and the crust warmed by 48 °C per km. It delivered 100 times the mass, in impactors larger than 10 km [6]. The crust then stayed habitable to a depth of 4 km.

The second reading denies the spike. Argon ages of lunar rocks can be partly reset by later heating. Partial loss of argon biases the dates toward younger values [5].

Modelled argon loss in Apollo samples turns a steadily declining history of impacts into an apparent peak near 3.9 billion years [5]. On this reading the impacts fell off smoothly from the start.

The oldest zircon (4,404 Ma) and the first recorded water (4,300 Ma) are 400 to 500 million years older than the claimed spike. The zircon to the spike at 3.9 billion years is 504 million years.

The material

Life is built from a short list of atoms. Of the 94 elements that occur in nature, 57 are found in a measured amount in a human body. Nineteen of them have a known function [8].

Four elements make 96.9 per cent of that body by weight: oxygen, carbon, hydrogen and nitrogen [8]. By count of atoms, hydrogen alone makes 62 of every 100. Four kinds of atom together make 99.4 per cent of the count.

The body does not copy the rock beneath it or the Sun above it. The table sets the main elements side by side.

Element	Body, by weight [8]	Earth's crust [9]	Sun, by mass [10]
Oxygen	61.4 %	46.6 %	0.80 %
Carbon	22.9 %	within 1.5 % of "others"	0.20 %
Hydrogen	10.0 %	within "others"	73.4 %

Nitrogen	2.6 %	within “others”	0.09 %
Calcium	1.43 %	3.6 %	—
Iron	0.006 %	5.0 %	0.14 %
Silicon	0.0014 %	27.7 %	0.09 %

Silicon is the second element of the crust and nearly absent from life: 27.7 ÷ 0.0014 = 19,786, about 20,000 times less. Carbon, hydrogen and nitrogen are less than 1.5 per cent of the crust and 22.9 + 10.0 + 2.6 = 35.5 per cent of the body. Life is built from what moves: carbon and nitrogen from the air, hydrogen and oxygen from water.

Atoms and bonds

An atom is about 10^{-10} m across, position −5.57 [11]. Its nucleus is about 10^{-15} m, 100,000 times smaller. The covalent bonds that hold life’s molecules run from 74.1 pm (H–H) to 203.8 pm (S–S), positions −5.85 to −4.92 [12].

All of them lie within one step of three. A C–C bond is 153.6 pm, position −5.18. A C–H bond is 109.1 pm, position −5.49.

Two kinds of contact hold molecules. The covalent bond holds atoms within a molecule. Its energy is 215 to 741 kJ/mol, 83 to 287 times the thermal energy of 2.58 kJ/mol at 37 °C [13].

The hydrogen bond holds molecules to each other. Its energy is 6 to 30 kJ/mol, only 2.3 to 11.6 times the thermal energy [14]. A peptide bond in water, without a catalyst, lasts close to 1,000 years, position 55.16 [15].

A hydrogen bond in liquid water is exchanged every 3.2 to 3.8 ps, positions 9.06 to 9.22 [16]. The lifetimes of the two kinds of contact stand 46 steps apart on the ladder. The covalent frame holds; the weak contacts form and break without help.

Water

Water is one oxygen atom holding two hydrogen atoms. The O–H bond is 0.958 Å long and the angle between the two bonds is 104.48° [17]. The molecule is 275 to 282 pm across, position −4.65 to −4.63 [18].

In the liquid each molecule is held by its neighbours through hydrogen bonds of 1.74 Å, position −5.07 [19]. In ice every molecule has four such bonds; in the liquid between 3 and 4. Breaking one takes about 23 kJ/mol as heat, but the free-energy difference at 25 °C is only about 2 kJ/mol.

The molecule lasts. It splits into ions once in about 11 hours at 25 °C, position 42.79 [20]. A hydrogen bond lasts about 1 ps near 0 °C, position 8.00 [19].

A broken hydrogen bond re-forms with the same partner in more than 97 cases of 100 [19]. A proton hops from oxygen to oxygen in 1.7 ps, position 8.49 [21]. No molecule travels; the charge is handed on.

Here the form of the net is form and carrier. The molecule is the closed form and lasts 39,600 s ÷ 10^{-12} s = 4×10^{16} times as long as its bond to a neighbour. The hydrogen bond is the unclosed carrier: it lasts briefly and hands tension from one molecule to the next.

Water weakens the pull between electric charges about 78-fold at 25 °C [22]. Salts fall apart into ions in it. Water is densest at 3.98 °C, so lakes freeze from the top and stay liquid below [22].

In the visible range pure water absorbs least at 418 nm [23]. Light reaches tens of metres into the sea. Today the ocean holds 1,370 million km³, 97.1 per cent of all water, and keeps a molecule for 3,100 years on average, position 56.19 [24].

Carbon

A carbon atom forms up to four bonds [25]. Carbon atoms link to each other into chains, branched chains and rings. A single C–C bond is 1.536 Å and can rotate; a double bond is 1.339 Å and holds its neighbours in one plane [26].

The number of possible molecules below a mass of 500 Da is estimated at about 10^{60} [27]. The Human Metabolome Database lists 3,444 compounds detected and quantified in the human body and 20,924 detected without a quantity [28]. Together that is 24,368: one found in every $10^{60} \div 24{,}368 = 4 \times 10^{55}$ possible.

The parts life uses

Six kinds of small carbon molecule make the parts of every cell. Each is named here with its measured size and count.

Part	What it is	Measured	Position	Source
Amino acid	central carbon with amino group, acid group, hydrogen, side chain	0.4 to 1 nm; 20 kinds in proteins	−4.31 to −3.48	[29], [30]
Sugar	carbon chain with a hydroxyl on nearly every carbon; C : H : O = 1 : 2 : 1	glucose about 1 nm long	−3.48	[29], [31]
Base	flat ring of carbon and nitrogen; A, G, C, T, U	step along DNA 0.34 nm	−4.46	[32]
Nucleotide	base, five-carbon sugar and phosphate	about 300 Da	—	[29]
Fatty acid	carbon chain with a carboxyl at one end	usually 14 to 24 carbons; 0.126 nm per carbon	C16 chain 2.02 nm, −2.84	[33], [34]
ATP	adenine nucleotide with three phosphates	1.4 nm; about 500 Da	−3.17	[29]

Glucose closes into a ring of six atoms; fructose and ribose into rings of five [31]. A sugar of six carbons with an end carbonyl has four inner carbons that can each stand two ways: $2^4 = 16$ forms, 8 D and 8 L. The fuel of life is one of the sixteen, D-glucose.

The bases come in two kinds. Adenine and guanine are purines with two rings; cytosine,

thymine and uracil are pyrimidines with one [32]. In DNA a purine always faces a pyrimidine, so every pair has the same width.

Adenine pairs with thymine by two hydrogen bonds; guanine with cytosine by three [32]. One turn of the double helix is 3.4 nm and holds 10 pairs; a second textbook gives 10.4 pairs per turn [32], [35]. The helix is 2 nm across, position −2.85.

A strand of nucleotides has a direction. One end carries a free hydroxyl at carbon 3′, the other a phosphate at carbon 5′ [36]. The two strands of DNA run in opposite directions [35].

Fatty acids in living systems have an even number of carbons, usually 14 to 24, most often 16 or 18 [33]. The chain does not mix with water; the carboxyl end does. A cis double bond kinks the chain: stearic acid with no double bond melts at 69.6 °C, oleic acid with one at 13.4 °C.

ATP carries energy in its third phosphate. Under standard conditions its split releases 28 to 34 kJ/mol [37]. In a growing bacterium the value is 47 kJ/mol, because the cell keeps ATP far from balance with its products.

A chain of 100 amino acids from 20 kinds has 20^{100} possible orders. Since $100 \times \log_{10} 20 = 130.1$, that is about 10^{130} [30]. The sections that follow show how far chemistry without a cell reaches toward each of these parts.

Sparks: amino acids from a gas

The first chemistry of life’s parts in the laboratory was a spark in a flask. In 1953 Stanley Miller passed electric discharges through a gas of methane, ammonia, hydrogen and water [38]. Amino acids formed.

The classic apparatus held 200 torr of methane, 200 torr of ammonia and 100 torr of hydrogen in a flask of 500 cm^3. It was sparked for one week, position 45.27 [39]. Glycine could be detected “after only two days of sparking”, position 44.13 [40].

A small number of compounds formed in high yields [40]. Miller ran a second, volcanic apparatus in 1953–54 and a silent-discharge apparatus at about 97 W. From the volcanic one he identified five amino acids and several unknowns [39].

Miller died on 20 May 2007. Shortly afterwards his archived vials were found [38]. Eleven vials of the volcanic run were analysed again with a detection limit below 10^{-12} M [39].

They held 22 amino acids and 5 amines [39]. The volcanic apparatus gave more kinds and higher yields than the classic one. The silent discharge gave a lower diversity.

A run of 1958 added hydrogen sulfide to methane, ammonia and carbon dioxide. Re-analysed, it held 23 amino acids and 4 amines, with 7 compounds of sulfur: 6 sulfur amino acids and 1 sulfur amine [41]. Its yield of amino acids not found in proteins was at least 100 times that of the original, volcanic and silent runs together [38].

The main amino acids of the 1958 run were racemic: both mirror forms in equal parts [41]. Sparks give both hands.

The surroundings set the yield. Miller’s runs stood near pH 8; runs with ammonia alone at pH 8 to 10.8 [38].

A mixture of carbon dioxide and nitrogen, buffered at pH 7 with calcium carbonate, gave about half the amino acid yield of methane and ammonia. Unbuffered runs fell to about pH 3.

Run	Gas	Amino acids found	Amines	Source
Volcanic, 1953–54, read by Miller	CH_4, NH_3, H_2, H_2O	5 and several unknowns	—	[39]
Volcanic, same vials, re-read 2008	CH_4, NH_3, H_2, H_2O	22	5	[39]
Sulfide run, 1958, re-read 2011	CH_4, NH_3, H_2S, CO_2	23	4	[41]

The same vials, read 55 years apart, gave 5 and 22 amino acids. The spark had made more than its first reader could see.

Sugars, cyanide and sulfide

Sugars form from formaldehyde in alkaline water. This is the formose reaction. Ribose appears in it, at a yield “unlikely to be greater than 1%”, in reactions with formaldehyde at 0.15 M or more [42].

The sugar mixture of the formose reaction is destroyed rapidly under the conditions that make it [42]. A study of 2020 followed the reaction in full. Formaldehyde at 1.0 M (100 mmol) started at pH 12.5 and fell to about 8; it was held at 120 °C and 200 kPa for 1 hour [43].

Of the formaldehyde, 63.1 mol% became organic acids: lactic 41.0, formic 7.4, glycolic 7.4 and acetic 7.3 mol%. Low alcohols took 35.6 mol% [43]. Non-sugars to sugars stood at “about 99+% to 1−%”.

Only about 8×10^{-5} per cent of the moles of formaldehyde remained as sugars [43]. Without catalyst at 80 °C the sugars were glucose 79.3, xylose 14.5 and mannose 6.25 mol%. Calcium raised the sugar yield about tenfold, still below 1 per cent.

In a reactor built like a vent, 0.5 M formaldehyde at starting pH 12 and 60 °C for 5 hours gave about 0.06 per cent ribose [44]. The formose reaction makes sugars and destroys them in the same pot.

Cyanide is the second feedstock. Hydrogen cyanide joins into chains in water only above 0.01 M, and works best at pH 8 to 10 [45].

Its trimer and tetramer are intermediates. Broken down in water, the cyanide polymers give amino acids and hydantoins.

The surroundings set how long cyanide lasts. In black smokers above 250 °C it lasts seconds [38]. In white smokers at 60 to 90 °C and pH above 9, its half-life at 75 °C and pH 10 is under a day.

In 2009 a route reached nucleotides without passing through free ribose or free bases.

Five starting materials, cyanamide, cyanoacetylene, glycolaldehyde, glyceraldehyde and inorganic phosphate, gave an activated pyrimidine ribonucleotide [46]. The path ran through 2-amino-oxazole and an arabinose amino-oxazoline to an anhydronucleoside.

Phosphate had to be present from the start. Its “presence from the start is essential as it controls three reactions in the earlier stages” [46].

In 2015 the same laboratory widened the route. Hydrogen cyanide, reduced step by step with hydrogen sulfide under ultraviolet light, gave the precursors of ribonucleotides, amino acids and lipids [47]. Copper cycling between its two charges sped the reactions.

In 2019 drying and wetting alone gave the pyrimidine nucleosides from small molecules and ribose. With phosphate minerals, their 5′-mono- and diphosphates formed in one pot [48]. The route works beside the purine route, so that all four bases of RNA form together.

Carbon on vent minerals

Carbon dioxide and hydrogen react on the minerals of vents. At 100 °C, in alkaline water, on greigite (Fe_3S_4), magnetite (Fe_3O_4) and awaruite (Ni_3Fe), they gave formate up to 200 mM [49].

The same runs gave acetate up to 100 µM, pyruvate up to 10 µM and methanol up to 100 µM. Methane reached 0.04 mM from carbon monoxide on greigite [49]. The gas stood at 25 bar for 16 hours, position 43.13.

The products fall off steeply with size: formate exceeds acetate 200 mM ÷ 100 µM = 2,000-fold, and acetate exceeds pyruvate 10-fold. The surroundings set the yield again. Formate reached 8 mM at pH 5 and 100 mM at pH 8 [49].

At the Lost City vent field the rock makes hydrocarbons itself. Its hydrocarbons of one to four carbons show an isotope trend of abiotic synthesis [50]. Radiocarbon excludes the carbonate of seawater as their source.

Each of the three routes starts from one-carbon or few-carbon molecules: formaldehyde, cyanide, carbon dioxide with hydrogen. Each gives a broad spread with little of any one product. The cyanide and sulfide route reaches nucleotides in a short sequence.

The vents

Hot springs on the sea floor were first explored in 1979, on the Galápagos Rift, with the submersible *Alvin* [51]. Their animal communities live on bacteria that oxidise sulfur. Up to two-thirds of the heat lost from new ocean floor in its first million years may vent through such springs.

Two kinds of vent are measured. Black smokers vent above 250 °C [38]. White smokers vent at 60 to 90 °C, with pH above 9.

The alkaline kind was found in 2001 at 30° N near the Mid-Atlantic Ridge. The Lost City field lies on crust 1.5 million years old, position 61.81, nearly 15 km from the spreading

axis [52]. Its fluids are “relatively cool (40–75 °C) and alkaline (pH 9.0–9.8)”.

Seawater reacts there with the rock of the upper mantle. The reaction gives fluids rich in methane and hydrogen, at temperatures from below 40 °C to 90 °C and pH 9 to 11 [53]. The fluids build chimneys of carbonate 30 to 60 m tall, positions 18.48 to 19.11.

In the laboratory a reactor rebuilt the setting. Its vessel was 100 mm by 100 mm, position 13.29 [44]. Alkaline fluid of about pH 11 at about 70 °C met an acidic “ocean” of about pH 5 at about 20 °C.

The temperature fell by up to about 50 °C across the vessel, at 0.5 °C per mm or less. The pH stepped by 5 or 6 units across micrometres, at the thin mineral walls between the two fluids [44]. The reactor made formate at about 50 µM and formaldehyde at about 100 nM.

Membranes form in the same window. Mixed fatty acids of 10 to 15 carbons, with alcohols of the same chains, form vesicles most readily at about 70 °C [54].

They form from about pH 6.5 to above 12. Alkaline vents typically run at 50 to 90 °C.

Here the form of the net is the edge. Where an alkaline fluid meets an acidic one across a thin wall, the largest step lies at the wall: 5 to 6 pH units across micrometres. Inside each fluid the values are uniform.

Drying and wetting on land

On land the cycle is drying and rewetting. Mononucleotides, adenosine and uridine monophosphate, were mixed with lipid and dried and wetted at 60 to 90 °C [55]. The yield was highest at 90 °C.

One to seven cycles were run. The yield rose until the fifth cycle and then held [55]. The starting pH of 6.8 fell to 2.2 after seven cycles.

The products were strands mostly 25 to 75 nucleotides long, with a smaller fraction near 100 [55]. Nucleotide to lipid ran from 2 : 1 to 8 : 1. The total product was 24 to 155 µg, at most about 6 per cent of the input by weight.

Here the form of the net is rest and discharge. Each cycle loads the mixture by drying, holds it, and discharges it by wetting. Five such cycles fill the yield; further cycles add nothing.

A hypothesis of 2020 places the start of life in volcanic hot-spring pools on land [56]. Their water rises and falls. Lipid-wrapped polymers form there through repeated wetting and drying.

Organic molecules from the Murchison meteorite form membrane-like boundaries in water [57]. The matter of the meteorite, older than the Earth’s oldest rock, holds parts that close into a skin.

One hand

A carbon atom that holds four different groups can be built in two ways. The two forms

are mirror images, like a left and a right hand [58].

They are called L and D for amino acids and sugars. A mixture of equal parts is racemic.

Life uses one hand of each pair. Only L amino acids are built into proteins; glycine, with two hydrogens on its central carbon, has no hand [30].

Most sugars in nature are D, among them ribose and glucose [58]. Almost all helices in proteins turn to the right [59].

Chemistry without a catalyst of one hand gives both hands in equal parts. The Miller products were racemic [41]. A single hand also does not stay single: the molecules flip one by one toward the mixture.

In living tooth enamel at about 37 °C, the share of D-aspartic acid rises by about 0.1 per cent per year, position 48.87 [60]. The drug thalidomide turns from one hand into the mixture with a half-life of about 1 hour in serum and about 12 hours in buffer, positions 40.61 and 42.87 [61]. The surroundings set the rate of the flip.

Excesses in meteorites

Matter older than life already holds an excess of one hand. In the Murchison meteorite the L form of an α-methyl amino acid is in excess by 7.0 and 9.1 per cent, in its two pairs of mirror forms [62]. Isovaline and α-methylnorvaline show the same.

The α-H analogues of the same rocks, α-amino-n-butyric acid and norvaline, are racemic [62]. These meteorites formed about 4.5 billion years ago, position 69.10.

A later study found L-isovaline in excess by 18.5 ± 2.6 per cent in Murchison, of class CM2 [63]. It was the largest excess measured for this compound. In Orgueil, of class CI1, the excess was 15.2 ± 4.0 per cent; in the CR meteorites EET 92042 and QUE 99177 there was none.

Murchison gives 7.0 to 9.1 per cent for the pairs of one α-methyl amino acid and 18.5 per cent for isovaline. The second is 2.0 to 2.6 times the first. Glavin and Dworkin read the excess as a small asymmetry amplified while water altered the parent bodies [63].

The amino acids of Murchison are enriched in heavy nitrogen, ^{15}N, relative to those of the Earth [64]. Their D and L forms of alanine were measured apart. Engel and Macko read the non-racemic amino acids as extraterrestrial.

Sugar acids of several carbonaceous meteorites, rare and common, carry significant excesses of one hand [65]. Comparable sugar alcohols in the same rocks are racemic.

How an excess grows

Three laboratory steps raise a small excess. In 1986 Kagan and co-workers found that a partly pure catalyst can give a product purer than itself [66]. A left and a right catalyst bind each other and drop out of the work.

In 1995 Soai and co-workers reported a reaction whose product catalyses its own formation and passes on its hand [67]. A starting excess of 2 per cent was enhanced in the product. In 2003 the same group started at about 0.00005 per cent excess [68].

Three rounds in a row gave an excess above 99.5 per cent. The main hand multiplied about 630,000-fold, the other less than 1,000-fold [68]. Since $\log_2 630{,}000 = 19.26$, the main hand doubled about 19 times; the excess rose $99.5 \div 0.00005 = 1.99 \times 10^6$-fold, or 126-fold per round.

In 2023 the RNA precursor of the cyanide and sulfide route was crystallised on magnetite. Racemic ribo-aminooxazoline first gave crystals of “about 60%” excess, then, on further crystallisation, crystals of “100% ee” [69]. The proposed setting is magnetite-bearing sediment in shallow lakes.

Electrons also sort by hand. Films of chiral molecules scatter polarised electrons unequally [70].

Electrons passed through double-stranded DNA on gold emerge with a spin polarisation exceeding 60 per cent at room temperature [71]. The effect grows with the length of the DNA.

The form of one direction

Here the form of the net is one direction. A living strand has one direction or it does not exist.

The rule is symmetric: which direction wins, it does not say. It keeps the direction of what was laid down first. The meteorites show a small L excess laid down before life, and the laboratory shows how a small excess grows to one hand only.

Catalytic RNA

A cell builds its proteins on the ribosome. The ribosome is two-thirds RNA and one-third protein, with more than 50 proteins and a mass of several million daltons [72]. In bacteria it adds about 20 amino acids per second, in eukaryotes about 2.

Its working centre is RNA. In the structure of 2000 no protein side-chain atom lies closer than about 18 Å to the peptide bond being made [73]. That distance, 1.8 nm, stands at position -2.94.

The active site is formed by conserved 23S RNA, in its domain V. One base, A2486 (A2451 in *Escherichia coli*), acts as the general base [73]. Proteins line the exit tunnel and ring it from outside.

The ribosome reads with about 1 error per 10,000 amino acids [72]. The enzymes that load the transfer RNAs make about 1 error in 40,000. The machine that makes every protein has an RNA core.

Small RNAs cut RNA. In 1987 a fragment of 19 nucleotides was shown to cleave a fragment of 24 nucleotides, fast and with high specificity, again and again [74]. This is the hammerhead.

RNA catalysts can be found by selection from random sequences. In 1993 a ligase was isolated from a large random pool. It joins RNA by the 3′-OH attack on a 5′-triphosphate, forming the same 3′,5′ bond as protein polymerases, “7 million times faster” than without catalyst [75].

In 1995 seven families of ligase in three classes were described [76]. The minimal catalytic domain was 93 nucleotides.

The rate constant exceeded one per second, with multiple turnover. One turnover per second stands at position 33.15.

RNA that copies RNA

From the ligase came polymerases: RNAs that extend an RNA primer along an RNA template. Their record products grew year by year.

Year	Ribozyme	Longest product or result	Fidelity	Source
2001	class I ligase-derived polymerase	up to 14 nucleotides, more than one turn of an RNA helix	1,088 of 1,100 matched (98.9 %)	[77]
2011	engineered polymerase	RNAs up to 95 nucleotides; copied an active hammerhead	—	[78]
2013	tC19Z, evolved in ice	up to 206 nucleotides, longer than itself; active down to −19 °C	—	[79]
2016	24-3 polymerase	aptamers, ribozymes and tRNA; short templates amplified more than 10,000-fold	—	[80]
2018	t5+1 heterodimer, triplet building blocks	52-nucleotide aptamer; its own catalytic subunit from five segments	97.4 % per position	[81]
2020	class I polymerase	made its own ancestor, a ligase of three strands	—	[82]
2024	polymerase in two lineages	the low-fidelity lineage lost function; the high-fidelity one evolved fitter hammerheads	—	[83]

Product length rose from 14 to 95 to 206 nucleotides, by factors 6.8 and 2.2. The 2013 product is longer than the ribozyme that made it.

The 2018 polymerase is a pair of subunits of 135 and 153 nucleotides, 288 in all [81]. It took building blocks three nucleotides long, all 64 triplets at 5 mM each. It joined them at 78 per cent per junction in copying itself, and 74 per cent on an open template.

Those reactions ran in ice at −7 °C for 9 to 38 days, positions 45.50 to 46.81 [81]. The starting library held 1.5×10^{15} variants. Fidelity was 97.4 per cent per position overall, 98.8 per cent for defined triplets against 96.7 per cent for random ones.

In 2009 two RNA enzymes were made that each build the other from four smaller RNAs [84]. “Amplification occurs with a doubling time of about 1 hour and can be continued indefinitely”, position 40.61. Recombinant replicators arose and took over.

Here the form of the net is the pair. Two closures together build each other: each is the template and the product of the other. The pair doubles every hour.

In the 2024 lineages evolution held only where copying was accurate [83]. Copy errors of the polymerases run from 1.1 to 2.6 per 100 positions; the ribosome reads with 1 error per 10,000.

The difference is large over a whole strand. At 97.4 per cent per position a strand of 100 nucleotides is copied without error in 0.974^{100} = 7 per cent of copies. At 1 error in 10,000 the share is 0.9999^{100} = 99 per cent.

Catalytic RNA appears at every size measured: 19 nucleotides in the hammerhead, 93 in the ligase core, 2,904 in the 23S RNA of the bacterial ribosome [85]. The same catalysis by RNA stands at the size of a fragment and of the cell’s largest machine. Here the form of the net is the same winding at every depth.

The code of three

The ribosome reads a messenger RNA “consecutively in groups of three” [72]. Four kinds of nucleotide in groups of three give 4 × 4 × 4 = 64 codons. Of these, 61 name one of 20 amino acids and 3, UAA, UAG and UGA, mean stop.

That is 61 ÷ 20 = 3.05 codons per amino acid on average. Through loose pairing at the third letter, bacteria fit the 20 amino acids to their 61 codons with as few as 31 kinds of transfer RNA [72]. That is 61 ÷ 31 = 1.97 codons per transfer RNA.

The human genome holds 497 transfer RNA genes with only 48 different anticodons, 10.4 genes per anticodon [72]. In 1961 cell-free extracts of *E. coli* were shown to make protein only when given natural or synthetic RNA [86].

The code is nearly universal. The NCBI lists 27 translation tables, numbered 1 to 33, each a small departure from the standard code [87]. The standard code allows a start at UUG and CUG as well as at AUG.

The code buffers errors. Against random codes of the same structure, single-base changes in the natural code have a smaller effect on the polarity of the amino acid than in all but 0.02 per cent of them [88]. Weighted for the errors that occur most often, only 1 in every million random codes does better [89].

The natural code beats 99.98 per cent of random codes (1991) and, weighted for common errors, 99.9999 per cent (1998). The second letter of the codon limits errors about a thousand times less well than the first and third [89].

Here the form of the net is the window. The code reads its letters three at a time, and each reading of three names one amino acid. The nucleotide, itself a closed small molecule, has become a letter.

Here the form of the net is also the residue that becomes the alphabet. The closed forms of the first chemistry, the nucleotides and the amino acids, are the letters of the next

closure. A protein is a word of 50 to 2,000 letters from an alphabet of 20 [15].

Membranes that grow and divide

Fatty acids close into skins of their own accord. Mixed with water above a threshold, they form micelles about 3 nm across, position −2.48 [90]. Micelles become vesicles: hollow spheres bounded by a double layer.

Clay speeds the change. In 2003 montmorillonite clay was shown to speed the turning of micelles into vesicles [91].

The clay was taken inside, with RNA bound to it. The vesicles grew by taking up micelles and divided when pressed through small pores, without loss of contents.

In 2005 vesicles of myristoleic acid and its glycerol ester were pressed to 100 nm, position 0.72 [90]. With a ribozyme inside, their mean diameter was 65 nm, position 0.32. Half an equivalent of added micelles grew their surface by about 50 per cent, with a rate constant of 1.5 per minute.

They held more than 95 per cent of a dye for at least 3 hours, position 41.61 [90]. They lost no RNA over 19 hours in 4 mM magnesium, position 43.29. Magnesium crossed the membrane at 2×10^{-7} cm/s.

The surroundings set the limits. Pure myristoleic acid vesicles stood 0.5 mM magnesium chloride; the 2 : 1 mixture with the glycerol ester stood 4 mM [90]. Decanoic acid clumped below 1.5 mM.

In 2004 vesicles with RNA inside were shown to swell by osmotic tension [92]. The swollen vesicles took membrane from relaxed neighbours, which shrank. That is competition between protocells.

In 2008 such membranes were shown to let charged molecules such as nucleotides pass [93]. A genetic polymer was copied on a template inside a model protocell.

In 2009 large vesicles fed with micelles grew from spheres into long threads [94]. Modest shear split them into many daughters without loss of contents. The RNA inside was shared among the daughters.

In 2011 a small amount of phospholipid in a fatty-acid membrane slowed the loss of fatty acid [95]. Such vesicles grew at the expense of their neighbours.

In 2019 mixed chains of 10 to 15 carbons, with alcohols, formed bilayers at about 1.3 mM, 225 µM of each acid [54]. Decanoic acid alone needs 39 mM: a 30-fold difference. The mixed vesicles stood 100 to 600 mM sodium chloride, 10 to 50 mM magnesium chloride and 1 to 10 mM calcium chloride at pH about 12.

At the salt of seawater, 600 mM NaCl, 50 mM Mg^{2+} and 10 mM Ca^{2+}, they formed only when isoprenoids were added [54]. At 600 µM total they stayed below 200 nm, position 1.35. They came apart only below about pH 6.5.

From micelle to vesicle the size rises from 3 nm to 65 to 100 nm, a factor of 22 to 33. On the ladder that is from −2.48 to 0.32 to 0.72, about three steps.

Ring, depth and edge

Here the net shows its next basics. A ring of trits can close with all three values only at lengths 3, 6, 9 and onward. At depth 3 the first ring appears that stays closed while all its values change: the first living form.

At depth 6 that ring can divide into two closed rings of three. Both halves keep the parent’s direction: the form of a single cell. The vesicles of 2009 show this form in chemistry: they grow, split into daughters, and each daughter keeps a share of the contents.

Where the living ring touches uniform surroundings, the windows stand open. There is tension at the edge and rest inside. “The correspondence is the cell membrane, where the largest potential step of the cell is found.”

The fatty-acid vesicle is that edge in its first form. Inside it RNA builds osmotic tension, and the swollen vesicle takes membrane from its neighbours. At the vent the same edge stands at the mineral wall, with 5 to 6 pH units across micrometres.

Toward the first cell

The parts of life formed in many places at once. Sparks gave 22 to 23 amino acids.

The formose reaction gave sugars at about 1 per cent. Cyanide and sulfide under light gave nucleotides, amino acid and lipid precursors from one network.

Vent minerals turned carbon dioxide and hydrogen into formate at 200 mM. Drying and wetting joined nucleotides into strands of 25 to 100. RNA catalysed its own joining, copied strands of 206 nucleotides and built its own ancestor.

Fatty acids closed into vesicles of 65 to 200 nm that grow, compete and divide. Meteorites carried an excess of L amino acids of up to 18.5 per cent, and laboratory steps raised such excesses to one hand only.

The record of the Earth sets the time. Water stood at the surface by 4,300 Ma.

One Jack Hills zircon of 4.10 ± 0.01 billion years, among more than 10,000, holds graphite with $\delta^{13}C$ of −24 ± 5 ‰, “potentially biogenic” [96]. That is 304 million years after the oldest grain, position 69.02.

The molecular estimate for the last universal common ancestor lies at 4.09 to 4.33 billion years, with a composite range of 3.94 to 4.52 [97]. That ancestor, the first cell and the record of its descendants are the subject of chapter 2.

Order	Age	Event	Position	Source
1	4,567.30 ± 0.16 Ma	first solids of the solar system	69.12	[1]
2	about 4,550 Ma	Earth formed	69.11	[2]
3	about 4,500 Ma	magma ocean, Moon-forming impact	69.10	[3]
4	4,404 ± 8 Ma	oldest zircon: crust	69.08	[2]

		and oceans		
5	by 4,300 Ma	water interacting with crust	69.06	[4]
6	4.09–4.33 Ga	last universal common ancestor, molecular estimate	69.02–69.07	[97]
7	4.10 ± 0.01 Ga	graphite in zircon, potentially biogenic	69.02	[96]
8	4.1–3.8 Ga	claimed bombardment window	69.02–68.95	[6]
9	about 3.9 Ga	claimed impact spike; read also as an argon artefact	68.97	[7], [5]
10	3,800–4,000 Ma	oldest exposed crust	68.95–69.00	[4]

What this part of the history shows

The ladder places the whole stretch. The first solids stand at 69.12, the oldest zircon at 69.08, the first recorded water at 69.06 and the graphite in a zircon at 69.02.

The first closure is the crystal: one value three times. The Jack Hills zircon has kept its record of water for 4,404 million years.

Form and carrier stand in the first molecules. The water molecule lasts about 11 hours before it splits (42.79); its hydrogen bond lasts about 1 ps (8.00). The covalent frame of a peptide lasts about 1,000 years in water (55.16); its weak contacts are exchanged every 3.2 to 3.8 ps.

What closes, stays. Of about 10^{60} possible small molecules, 24,368 are found in a human body. In the formose pot 99 per cent of the products are not sugars, and the sugars that form are destroyed again.

One direction shows in the hands of life’s molecules. Proteins use L amino acids only; ribose and glucose are D. Meteorites carry an L excess of 7.0 to 18.5 per cent from before life, and autocatalysis raised 0.00005 per cent to 99.5 per cent in three rounds.

The surroundings set the values of the same rule. Cyanide lasts seconds above 250 °C and under a day at 75 °C. Formate on vent minerals rose from 8 mM at pH 5 to 100 mM at pH 8.

The edge appears where two surroundings meet. At the wall of a vent the pH steps by 5 to 6 units across micrometres. At the skin of a vesicle RNA builds osmotic tension, and the swollen vesicle takes membrane from its neighbours.

Rest and discharge show in drying and wetting: each cycle loads, holds and discharges, and the yield rose until the fifth cycle. The pair shows in RNA. Two RNA enzymes, each building the other, double every hour.

The residue becomes the alphabet. Nucleotides and amino acids, closed small

molecules, become the letters of strands. The code reads them three at a time: 64 codons, 61 for 20 amino acids and 3 for stop.

The same winding stands at every depth. Catalysis by RNA works in 19 nucleotides, in 93, and in the 2,904 of the ribosome’s core.

2. The First Cell

Chapter 1 ended with the parts: amino acids, sugars, nucleotides, catalytic RNA and fatty-acid skins that grow and divide. This chapter follows the first cells built from them. It reads their traces in the oldest rocks and their common ancestor in the genomes of living cells.

The first cell is known in two ways. The rocks hold its products: carbon of light isotopes, mineral filaments, layered mats and the gases and sulfides of its metabolism. The genomes of all living cells hold its descent: one last universal common ancestor, dated by molecular clocks and reconstructed gene by gene.

The chapter then follows what every cell measured still holds: a membrane of two layers of lipid, 4 nm thick, with a voltage across it, negative inside. It holds channels and pumps, a ring of DNA copied before division, and a division into two that each keep a full copy.

The net shows here in the forms named in chapter 1. The cell is the first ring that stays closed while all its content changes.

Its membrane is the edge, where the largest step of the cell is found. Its division is the ring of six that parts into two rings of three, both keeping the parent’s direction.

The oldest traces

The record of the first cells has two tiers. The older tier, 3.7 to 4.28 billion years, consists of single signals in rocks that were later heated and deformed. The younger tier, 3.40 to 3.48 billion years, lies in the Pilbara of Western Australia and carries several independent signals within about 80 million years.

The older tier

One zircon from the Jack Hills, Western Australia, was the only grain older than 3.8 billion years among more than 10,000 [96]. Its concordant age is 4.10 ± 0.01 billion years (Ga), position 69.02. Its inclusions of graphite have $\delta^{13}C$ of −24 ± 5 ‰, consistent with a biogenic origin.

If the zircon graphite is biogenic, it places a biosphere on Earth about 300 million years earlier than proposed before, position 66.64.

The Nuvvuagittuq belt in Quebec holds putative microfossils “at least 3,770 million and possibly 4,280 million years old” [98]. Their positions are 68.94 and 69.06; the range of 510 million years stands at 67.12. They lie in precipitates of hydrothermal vents.

The filaments average 8.3 µm across (standard deviation 2.8, n = 23), position 4.74 [98]. The tubes average 24.9 µm (standard deviation 6.3, n = 40), position 5.74. In the younger jasper of Løkken-Høydal, Norway, the same structures measure 9.1 µm and 19.5 µm, positions 4.82 and 5.51.

At Isua, West Greenland, a banded iron formation of about 3,800 million years holds carbon inclusions of light isotopes, position 68.95 [99]. A similar formation on Akilia island is possibly older than 3,850 million years, position 68.96.

Isua sediments older than 3,700 million years hold globules of graphite 2 to 5 µm across, positions 3.44 to 4.28 [100]. Their $\delta^{13}C$ is −19 ‰. They are read as biogenic detritus, possibly plankton.

Nanoscale graphite depleted in ^{13}C, in polygonal and tube-like grains, was deposited in the Isua belt at least 3.7 billion years ago [101]. From the zircon graphite at 4.10 Ga to the Isua graphite at 3.70 Ga is 0.40 billion years, position 66.90.

Isua also yielded cones 1 to 4 cm high in rocks of 3,700 million years, positions 11.19 to 12.46 [102]. They were read as stromatolites. That placed them 220 million years before the best-supported evidence of the time, in the 3,480-million-year Dresser Formation.

A reassessment reads the same cones as deformation structures of “non-biological, post-depositional origin” [103].

The younger tier

At about 3.48 Ga, position 68.87, the Dresser Formation of the Pilbara holds deposits of hot springs on land [104]. Geyserite, sinter terraces, pool and vent remnants carry stromatolites, palisade fabric and gas bubbles in inferred exopolymeric substance.

These deposits extend the record of inhabited hot springs on land by about 3 billion years, position 68.73 [104]. They place life on land about 580 million years earlier than previously thought, position 67.24.

Barites of about 3.47 billion years at North Pole, Australia, record microbial sulfate reduction [105]. The sulfide is lighter than the sulfate by at most 21.1 ‰ and on average about 11.6 ‰. The record of this metabolism moves back by more than 750 million years, from about 2.7 Ga.

Fluid inclusions of about 3.5 billion years in Pilbara vent precipitates hold methane with $\delta^{13}C$ below −56 ‰ [106]. Microbes that make methane are therefore older than 3.46 billion years, position 68.86.

The Apex chert, about 3,465 million years old, holds microbial fossils of five species [107]. The carbon isotopes of 11 fossils were measured one by one. Two species are read as photosynthesizers, one as a methane-producing archaeon, others as methane consumers.

At Strelley Pool a reef of about 3,430 million years shows seven forms of stromatolite along an outcrop of 10 km, position 23.77 [108]. In the 3.4-billion-year-old Strelley Pool Formation, micrometre-sized pyrite is read as a by-product of sulfate reduction and sulfur disproportionation [109]. Its microstructures are read as microfossils of sulfur-metabolising cells.

Biological fixation of nitrogen has an isotopic minimum age of 3.2 billion years, position 68.79 [110]. The $\delta^{15}N$ is 0.0 ± 1.2 ‰ in rocks 3.2 to 2.75 billion years old.

Age	Signal	Place	Position	Source
4.10 ± 0.01 Ga	graphite, $\delta^{13}C$ −24	Jack Hills	69.02	[96]

	‰, in one zircon of >10,000			
≥3.77, possibly 4.28 Ga	filaments 8.3 µm, tubes 24.9 µm	Nuvvuagittuq	68.94 (69.06)	[98]
>3.85 Ga, possible	light carbon	Akilia	68.96	[99]
about 3.80 Ga	light carbon	Isua	68.95	[99]
>3.70 Ga	graphite globules 2–5 µm, $\delta^{13}C$ −19 ‰	Isua	68.92	[100], [101]
3.70 Ga	cones 1–4 cm, two readings	Isua	68.92	[102], [103]
ca. 3.48 Ga	hot springs on land with stromatolites	Dresser Formation	68.87	[104]
about 3.47 Ga	sulfate reduction, 21.1 ‰	North Pole	68.87	[105]
>3.46 Ga	methanogenesis, below −56 ‰	Pilbara	68.86	[106]
about 3.465 Ga	five species of microfossil	Apex chert	68.86	[107]
about 3.43 Ga	reef of seven stromatolite forms, 10 km	Strelley Pool	68.86	[108]
3.4 Ga	sulfur-metabolising cells	Strelley Pool	68.85	[109]
3.2 Ga	nitrogen fixation	—	68.79	[110]

From the Isua carbon at 3.80 Ga to the Apex fossils at 3.465 Ga is 0.335 billion years, position 66.74. By about 3.46 Ga the rocks record four metabolisms: sulfate reduction, methane production, methane consumption and, inferred, photosynthesis.

Here the form of the net is what closes, stays. Each signal of the younger tier is the residue of a metabolism, a flow of carbon or sulfur through a cell that kept its form. The cells are gone; the products of their flow remain in rock 3.4 to 3.5 billion years old.

The last universal common ancestor

All cells now living descend from one ancestor, the last universal common ancestor, LUCA. Molecular clocks date it from the genomes of its descendants, and three dates are published.

The most recent places LUCA at about 4.2 Ga, position 69.04 [97]. Its interval under one clock model is 4.09 to 4.33 Ga, positions 69.02 to 69.07; under a second model 4.18 to 4.33 Ga. A composite estimate runs from 3.94 to 4.52 Ga, positions 68.98 to 69.11.

An earlier study gives LUCA more than 3.9 Ga, position 68.97 [111]. It places the crown groups of Bacteria and of Archaea below 3.4 Ga, position 68.85, and crown eukaryotes below 1.84 Ga. A third study gives about 3.5 to 3.8 Ga [112].

The central values spread by $4.2 - 3.65 = 0.55$ billion years. The most recent estimate is the oldest. From LUCA to the crown groups of Bacteria and Archaea is at least $3.9 - 3.4 = 0.5$ billion years, position 67.10.

The 4.2-Ga date lies before the oldest zircon graphite and close to the first recorded water of 4.3 Ga (chapter 1). From LUCA at 4.2 Ga to the Pilbara tier at 3.48 Ga is 0.72 billion years, position 67.43.

Its genes

Two reconstructions give LUCA's gene set. The first screened 6.1 million protein-coding genes from sequenced prokaryotes, grouped into 286,514 protein clusters [113]. It traced 355 protein families to LUCA: 355 ÷ 286,514 = 0.124 per cent of the clusters.

It describes LUCA as "anaerobic, CO2-fixing, H2-dependent with a Wood–Ljungdahl pathway", thermophilic and fixing nitrogen [113]. Chapter 1 described carbon dioxide and hydrogen turning into formate and acetate on vent minerals.

The second reconstruction, of 2024, gives a genome of 2.75 Mb (2.49 to 2.99 Mb) encoding 2,657 proteins (2,451 to 2,855) [97]. A conservative subset holds 399 gene families found in both prokaryotic domains. It includes 19 families of class 1 CRISPR–Cas effectors.

The two counts differ by 2,657 ÷ 355 = 7.5. One method counts only families that meet a strict criterion in both domains [113]. The other reconciles gene trees with species trees by probability [97].

One reconstruction infers that LUCA fixed nitrogen [113]. Another finds the enzyme nitrogenase absent from LUCA and dates its origin at roughly 1.5 to 2.2 Ga, positions 68.10 to 68.45 [112].

Here the form of the net is opened once, filled many times. One ancestral cell opened the depth of the cell. Every cell since, from 3.4 Ga to the present, fills that depth again.

The smallest cell and its standard

A bacterium is a single cell without a nucleus. Its DNA lies free in the cell, gathered in a region called the nucleoid [114]. It is the smallest form that lives and divides on its own.

The measured standard is *Escherichia coli*, a rod from the gut. The cell is about 1 µm by 2 µm, positions 2.81 and 3.44, with a volume of about 1 µm³ and a mass of about 1 pg [115]. About 70 per cent of that is water.

Dry mass runs from 148 fg in cells that divide every 100 minutes to 865 fg in cells that divide every 24 minutes [115]. Protein is about 55 per cent of the dry mass [116].

What	Number in one *E. coli*	Source
Base pairs of DNA	4,639,221	[117]
Protein-coding genes	4,288	[117]
Protein molecules	2 to 4 million	[116]
Ribosomes, at a division time of 24 min	72,000	[118]

At that speed the ribosomes are more than a third of the dry mass [118]. One textbook count gives about 20,000 ribosomes [119]. The bacterial ribosome holds RNAs of 1,542, 2,904 and 120 nucleotides and 21 + 34 = 55 proteins, 2.7 million daltons in all [85],

[118].

The DNA is one closed ring. Its length is 4,639,221 × 0.34 nm = 1.58 mm, position 9.51 [117].

The cell is 2 µm long, so the thread is 790 times longer than the cell. Many bacteria also carry plasmids, small rings of DNA, often hundreds per cell [114].

The smallest genomes

Mycoplasma genitalium has a genome of about 580,000 base pairs with 470 predicted genes [120]. At its publication it was the smallest known genome of any free-living organism. That is 580 ÷ 4,639 = 12.5 per cent of the genome of *E. coli*.

Mycoplasma pneumoniae is 300 nm wide and 700 nm long, positions 1.72 and 2.49 [121].

A built cell goes lower. JCVI-syn3.0 has a designed and chemically made genome of 531,000 base pairs with 473 genes [122].

Of these, 149 have no known function. It grows and divides; its genes are 473 ÷ 4,288 = 11 per cent of those of *E. coli*.

Smaller cells live in groundwater. Bacteria of the Candidate Phyla Radiation measure 0.009 ± 0.002 µm³, with median axes of 322.6, 242.5 and 189.7 nm, positions 1.78, 1.52 and 1.30 [123].

Each holds 42 ± 9.5 ribosomes, typically 34 to 59. Their genomes are 0.878 Mb and 0.694 Mb.

The marine bacterium SAR11 has a volume of about 0.01 µm³ [124]. *E. coli*, at about 1 µm³, is 100 times larger; the groundwater cells are 111 times smaller. The archaeon *Nanoarchaeum equitans*, about 400 nm across, position 1.98, has a genome of 0.5 Mb, the smallest archaeal genome known at the time [125].

Cell	Genome	Genes	Source
LUCA, reconstructed	2.75 Mb (2.49–2.99)	2,657 proteins	[97]
E. coli	4.64 Mb	4,288 protein genes	[117]
M. genitalium	0.58 Mb	470	[120]
JCVI-syn3.0	0.531 Mb	473 (149 unknown)	[122]
groundwater bacterium WWE3	0.878 Mb	—	[123]
groundwater bacterium OD1	0.694 Mb	—	[123]
Nanoarchaeum equitans	0.5 Mb	—	[125]

The smallest built genome that grows and divides holds 473 genes. The reconstructed ancestor held about 2,657 proteins, between that minimum and the 4,288 genes of *E. coli*.

The membrane

Every cell is closed by a membrane: a sheet of lipid two molecules thick, with proteins

set in it. The phospholipid molecule has a head that mixes with water and two tails of 10 to 20 carbons that do not [34], [126]. Each carbon adds 0.126 nm to the tail.

In water the tails turn to each other and the heads turn outward. The sheet forms by itself and closes into a bag. Chapter 1 followed the same closure in fatty-acid vesicles of 65 to 200 nm.

What	Size	Position	Source
Phospholipid, head to tail	2 nm	−2.85	[34]
Water-free core of the bilayer	3 nm	−2.48	[34]
Bilayer, thickness	4 nm (3.56 to 4.25 nm)	−2.21	[34]
Membrane with its proteins and sugars	4 to 10 nm	−2.21 to −1.38	[34]
Lactose carrier in the membrane	6 nm by 3 nm	−1.85 by −2.48	[127]

A bacterium of 2 µm has a membrane 2,000 ÷ 4 = 500 times thinner than its width [34]. One square micrometre of bilayer holds about 5×10^6 lipid molecules [128]. That gives 10^6 nm² × 2 sides ÷ 5×10^6 = 0.4 nm² per molecule; the direct measurement gives 0.25 to 0.5 nm² [126].

About half of the area of a cell membrane is protein [34]. A protein chain that crosses the sheet once does so with 20 to 25 amino acids; some proteins cross 12 times [129].

A liquid in two dimensions

A lipid changes place with its neighbour every 10^{-7} s, position 18.48 [128]. Its sideways diffusion coefficient is about 10^{-8} cm² per second. A lipid crosses a bacterium of 2 µm in about 1 s, position 33.15.

A lipid flips to the other side of the sheet unaided only after more than a month, position above 46.60 [128]. Sideways exchange is 30 × 86,400 s ÷ 10^{-7} s = 2.6×10^{13} times more frequent than a flip. The sheet is a liquid in two dimensions, and its two sides stay different.

A membrane protein in cultured rat liver cells has a half-life of 17 to 100 hours, positions 43.19 to 44.80 [130]. In that time each lipid changes neighbours 6.1×10^{11} to 3.6×10^{12} times. The sheet stays closed.

Here the form of the net is the six closed windows that hold all three values. The content of the membrane changes ten million times a second, and the closure holds.

What passes

Oxygen, carbon dioxide, alcohol and fats pass straight through the sheet. Water passes slowly. Ions do not pass, whatever their size, and neither do glucose and amino acids [131].

Carbon dioxide passes at 0.01 to 1 cm/s, glycerol at 10 to 100 nm/s [132]. That is 10^3 to 10^6 times slower for glycerol. From the fastest to the slowest substance the range is

10^{10}.

Because ions do not pass, the membrane can keep them apart. It stores charge like a capacitor of 1 µF per cm² [133]. The cell's largest electric step therefore lies across these 4 nm.

The voltage across the edge

Every cell measured carries a voltage across its membrane, negative inside [134], [135], [136].

E. coli holds a membrane potential of about −140 mV during aerobic growth on glycerol and about −105 mV during fermentation of glucose [134]. "A typical bacterial membrane potential is around 150 mV, corresponding to Cin/Cex ≈ 350" [135].

The proton-motive force of respiring *E. coli* is 230 ± 15 mV, in *Staphylococcus aureus* 211 ± 15 mV, each from six determinations at external pH about 6.5 [137].

For eukaryotic cells resting potentials between −40 and −95 mV are typical [136]. The bacterial range, −105 to −150 mV, lies beyond it in magnitude. A bacterial cell has a surface of about 6 µm², a mammalian cell about 1,600 µm², 267 times more [138].

Few ions set the voltage. At −150 mV a membrane of 1 µF per cm², 0.01 F per m², holds $0.01 \times 0.15 = 1.5 \times 10^{-3}$ C per m². Divided by the charge of one ion, 1.602×10^{-19} C, that is about 9,400 ions per square micrometre.

Across 4 nm the field is $0.15 \text{ V} \div 4 \times 10^{-9} \text{ m} = 3.75 \times 10^{7}$ V per m.

Here the form of the net is the edge. Where the living ring touches uniform surroundings, the windows stand open: tension at the edge, rest inside. The largest step of the cell, −105 to −150 mV in bacteria, stands across its 4-nm membrane.

The voltage moves. *E. coli* cells imaged with a voltage-sensitive protein spiked "at up to 1 hertz", one cycle per second, position 33.15 [139]. Each spike coincided with a rapid efflux of a small dye molecule.

Channels and pumps

The lipid sheet stops ions and sugars; proteins set in it let them through [140]. A channel is a pore through which ions run down their gradient.

A carrier binds one molecule, changes shape and releases it on the other side. A pump is a carrier that uses energy to move its load against the gradient.

Channels for potassium stand in both prokaryotic domains. The bacterial channel KcsA is built of four identical subunits of two membrane-crossing segments each [141]. Its selectivity filter is 12 Å long, position −3.31, and holds two K^+ ions about 7.5 Å apart, position −3.74.

The KcsA pore is 45 Å long, position −2.11, with a water-filled cavity of about 10 Å [141]. It passes up to 10^8 ions per second, 10 ns per ion, position 16.39. K^+ is "at least 10,000 times more permeant than Na^+".

Oxygen atoms line the filter, spaced as the water around a K^+ ion in solution [142]. The K^+ ion leaves its water and fits. The smaller Na^+ ion does not fit between the oxygens and stays in the water.

The archaeon *Aeropyrum pernix* carries KvAP, a K^+ channel opened by voltage [143]. Its structure was solved at 3.2 Å for the full channel and 1.9 Å for the isolated voltage sensor. Positively charged “voltage-sensor paddles” sit on its outer perimeter.

The archaeon *Methanobacterium thermoautotrophicum* carries MthK, a K^+ channel opened by calcium [144]. Eight RCK domains form a gating ring on its inner side.

Bacteria also carry sodium channels opened by voltage. NaChBac, from *Bacillus halodurans*, is encoded by one gene of six membrane-crossing segments [145].

It forms “four identical subunits, each of which contains six transmembrane segments” [146]. The NavAb pore of *Arcobacter butzleri* has a water-filled filter about 4.6 Å wide, position −4.18, with four acidic side chains at its narrowest point [147].

The eukaryotic Na^+ and Ca^{2+} channels are one chain of four repeated domains of six segments [145], [148]. Both builds give $4 \times 6 = 24$ membrane-crossing segments around a fourfold pore. A genome survey found “two sodium channels and one calcium channel in prokaryota”, the sodium channels in alkaliphilic bacteria [149].

NaChBac opens and closes in fractions of a millisecond. Its gating currents appear at −90 mV from a holding potential of −150 mV, and the gating charge saturates at −10 mV [150]. Each channel moves about 16 elementary charges; a shift of 533 µs, position 26.29, follows a change of prepulse from −160 to −80 mV.

In cultured HEK cells NaChBac half-activates at -35.0 ± 1.3 mV and half-inactivates at -52.3 ± 1.3 mV [146]. The bacterial channel works in the range of voltages that its own membrane holds.

The pump that makes ATP

ATP synthase runs a pump backwards. Protons flow through a wheel in the membrane; the wheel turns an axle inside a head of six subunits, and the head makes ATP [151]. The whole weighs more than 500,000 Da.

Each full turn gives three ATP [152]. The turning was seen directly in 1997: a fluorescent rod fixed to the axle turned one way for more than 100 revolutions [153]. More than 100 ATP per second gives one ATP in less than 10 ms, position below 28.96, and one turn in less than 30 ms.

A sugar carrier moves about 100 molecules per second, 30 to 300 [127]. One cycle lasts about 10 ms, position 28.96. A K^+ channel moves 10^8 ions per second: a million times more.

Here the form of the net is form and carrier. The channel and the pump are closed forms: each returns to its starting shape after every cycle, and membrane proteins last 17 to 100 hours [130]. The ion current through them is the carrier: one ion crosses in 10 ns and is gone.

The pump and the channel also show one direction. The rod on the axle of ATP synthase turned one way for more than 100 revolutions [153]. The machine that makes the cell’s

ATP turns in one sense only.

Copying and dividing

A cell makes two cells by copying its thread and then dividing. The copying enzyme of a bacterium adds 500 units per second at each fork, 2 ms per unit, position 27.50 [154]. A fork in a cell with a nucleus moves one tenth as fast.

Direct copying leaves about one error in 10^7 units [155]. A second system checks the new strand against the old and lowers this a further 100-fold, to about one error in 10^9 [154]. For the 4,639,221 pairs of *E. coli* that is 4.6×10^{-3} errors per copy: one error in about 220 divisions.

One copy of the *E. coli* genome takes at least 2,500 s, position 40.27 [156]. The fastest cells divide in 20 minutes, position 39.61 [157]. Copying takes longer than dividing.

The cell therefore starts a new round of copying before the last has ended. A fast cell holds more than 6 starting points and over 10 copying forks at once [156]. Copying runs in both directions along the ring until the end point.

A protein named FtsZ forms a ring on the inside of the membrane and marks the plane of division [157]. Each daughter cell receives a full copy of the chromosome and a share of the cell content.

Each new double helix holds one strand of the parent and one new strand, running in the direction of the parent [158]. The two strands of DNA run in opposite directions, and the helix is right-handed along its length [159].

A cell with a nucleus runs the same round in four phases [158]. It grows (G1, about 11 h), copies its DNA (S, about 8 h), prepares (G2, about 4 h) and divides (M, about 1 h). The sum is 11 + 8 + 4 + 1 = 24 h, position 43.50, against 20 minutes for the fastest bacterium.

In both, the whole genome is copied before the cell divides: 2n becomes 4n, and each daughter receives 2n [158]. The bacterium does it in one ring; the cell with a nucleus in many chromosomes.

Doubling

One cell that divides every 20 minutes makes 72 doublings in 24 hours. That would give $2^{72} = 4.7 \times 10^{21}$ cells. At 1 pg each they would weigh 4.7×10^9 g, or 4,700 tonnes.

The Earth’s stock holds near 4 to 6×10^{30} prokaryotic cells, with 1.7×10^{30} new cells per year [160]. The whole stock is replaced once in $4 \div 1.7 = 2.4$ to $6 \div 1.7 = 3.5$ years.

The form of the single cell

Here the form of the net is the ring of six that divides into two rings of three. Both halves keep the parent’s direction. The bacterium copies its ring of DNA, grows, and parts into two, each with a full copy.

Both daughters hold the same right-handed helix and build their proteins from the same

hand of amino acids. The direction laid down in the parent passes to both.

Here the form of the net is also memory with reach two. Each daughter helix holds one strand of the parent. The parent’s own strands reach its two daughters directly; beyond them the line continues only by chaining, copy after copy, at one error in 10^9 units.

The first cell in the line of the history

The traces and the clocks place the first cells in one stretch. Water stood at the surface by 4.3 Ga. The ancestor of all living cells is dated 4.09 to 4.33 Ga, and the zircon graphite at 4.10 Ga.

The single signals of 3.7 to 4.28 Ga follow, then the four metabolisms of the Pilbara at 3.40 to 3.48 Ga. The crown groups of Bacteria and Archaea follow below 3.4 Ga, and nitrogen fixation by 3.2 Ga.

Order	Age	Event	Position	Source
1	4.52–3.94 Ga	LUCA, composite estimate	69.11–68.98	[97]
2	4.33–4.09 Ga, central 4.2 Ga	LUCA, clock model	69.07–69.02	[97]
3	4.10 ± 0.01 Ga	graphite in zircon	69.02	[96]
4	>3.9 Ga	LUCA, earlier study	68.97	[111]
5	3.8–3.5 Ga	LUCA, third study	68.95–68.87	[112]
6	≥3.77, possibly 4.28 Ga	Nuvvuagittuq filaments and tubes	68.94	[98]
7	≥3.70 Ga	Isua graphite; Isua cones, two readings	68.92	[100], [102]
8	3.48–3.40 Ga	Pilbara: hot springs, sulfate reduction, methane, microfossils, reef	68.87–68.85	[104], [105], [106], [107], [108], [109]
9	<3.4 Ga	crown Bacteria and crown Archaea	68.85	[111]
10	3.2 Ga	nitrogen fixation, isotopic minimum	68.79	[110]
11	2.2–1.5 Ga	nitrogenase by molecular clock	68.45–68.10	[112]
12	<1.84 Ga	crown eukaryotes	68.29	[111]

From 4.2 Ga to 1.84 Ga is 2.36 billion years, position 68.52. Prokaryotes alone filled that time: 56 per cent of the history since LUCA by the 4.2-Ga date. Chapter 3 follows them.

What this part of the history shows

The cell is the first ring that stays closed while all its content changes. A lipid changes neighbours every 10^{-7} s, a membrane protein lasts 17 to 100 hours, and the sheet stays closed. The cells of the Pilbara are gone; the residues of their flow of carbon and sulfur remain after 3.4 to 3.5 billion years.

The edge carries the largest step. Bacteria hold −105 to −150 mV across a membrane of 4 nm, a field of 3.75×10^{7} V per m, set by about 9,400 ions per square micrometre.

The proton-motive force reaches 211 to 230 mV. Eukaryotic cells hold −40 to −95 mV.

Form and carrier stand in the membrane. Channels and pumps return to their shape after each cycle, and membrane proteins last 17 to 100 hours. One K^{+} ion crosses KcsA in 10 ns; a sugar carrier cycles in 10 ms; ATP synthase turns in under 30 ms and gives three ATP per turn.

One direction holds in every part. The DNA strands run 5′ to 3′ in opposite senses, the helix is right-handed, the proteins are of L amino acids, and ATP synthase turns one way for more than 100 revolutions. Each daughter keeps the direction of the parent.

The ring of six divides into two rings of three. *E. coli* copies its 4,639,221 pairs in at least 2,500 s, divides in 20 minutes, and gives each daughter a full copy. The cell with a nucleus runs the same round in 24 hours.

Memory reaches two. Each new helix holds one strand of the parent and one new strand. Further than the two daughters the line runs by chaining, at about one error in 10^{9} units copied.

One depth opened once and has been filled since. One ancestor, dated 4.09 to 4.33 Ga, with some 355 to 2,657 genes, stands at the root of every cell. The smallest built cell that grows and divides holds 473 genes.

3. Bacteria and Archaea

Chapter 2 ended below 3.4 billion years ago, where the crown groups of Bacteria and Archaea begin. From the last universal common ancestor to the first cells with a nucleus, prokaryotes alone held the Earth for about 2.36 billion years. They hold most of its cells still.

This chapter follows the two prokaryotic domains. It tells how they were told apart, how many kinds and cells there are, and how small, large, fast and slow they are. It follows the genes they pass sideways, the walls and signals of their communities, and the metabolisms by which they carry the cycles of carbon, nitrogen, sulfur and oxygen.

The net shows here in the forms of chapter 1. The two domains are two long branches of one address.

Their genes pass between branches, so that a community is a shared prefix. Their metabolisms are closures through which whole elements flow.

Two lines from one ancestor

The grouping began with ribosomal RNA. A 1977 comparison found “three aboriginal lines of descent”: eubacteria, archaebacteria with the methanogens, and “urkaryotes” [161]. The urkaryote line is the cytoplasm of eukaryotic cells.

In 1990 the rank of domain was proposed above the kingdom, with three domains: Archaea, Bacteria and Eucarya [162]. The Archaea were split into two kingdoms, Euryarchaeota and Crenarchaeota. From 1977 to 1990 is 13 years, position 51.21.

In 2013 newer methods placed the core genes of eukaryotes within the Archaea [163]. The authors wrote that “the three-domains tree may be incorrect” and that the results “support … only two primary domains of life”. From 1977 to 2013 is 36 years, position 52.13.

A tree of ribosomal proteins from 3,083 genomes, 1,011 of them newly reconstructed, used 16 proteins joined end to end [164]. It holds 92 named bacterial phyla, 26 archaeal phyla and all five eukaryotic supergroups. The Candidate Phyla Radiation, with other lineages that have no cultured member, “clearly comprises the majority of life’s current diversity”.

The crown groups of both prokaryotic domains are younger than 3.4 billion years, position 68.85 [111]. Their common ancestor is older than 3.9 billion years in the same study. At least 0.5 billion years separate the root from the two crowns.

The count of kinds

The Genome Taxonomy Database, release R226 of 16 April 2025, holds 732,475 genomes [165]. Its species clusters number 136,646 for Bacteria and 6,968 for Archaea, 143,614 in all. Its phyla number 169 and 20.

Archaea are 4.85 per cent of the species clusters; Bacteria outnumber them 19.6 to 1. The list of validly published names holds 22,681 species in 4,007 genera and 48 phyla, at its refresh of 18 September 2026 [166]. Named species are 22,681 ÷ 143,614 = 15.8 per cent of the genome clusters.

Phyla are thus counted three ways: 92 + 26 [164], 169 + 20 [165] and 48 [166]. A scaling model, fitted to about 35,000 sites and 5.6 million catalogued species, gives upward of 10^{12} microbial species on Earth [167].

The archaea nearest the eukaryotes

The first genome of the Asgard archaea, of the Lokiarchaeota, is a composite of 5.1 Mbp, 92 per cent complete, with 5,381 protein-coding genes [168]. The closest matches of its proteins were eukaryotes for 3.3 per cent (175 proteins), bacteria for 29, archaea for 26 and none for 32.

Small GTPases make up nearly 2 per cent of that proteome [168]. The lineage forms one group with the eukaryotes. The core came from sediment under 3,283 m of water, 75 cm below the sea floor, about 15 km from the Loki's Castle vents.

In 2017 four clades, Loki-, Thor-, Odin- and Heimdallarchaeota, were grouped as the superphylum Asgard [169]. Eight genome bins came from seven sites; Odinarchaeota came only from hot springs. All lineages were enriched in proteins that are otherwise signatures of eukaryotes.

Eukaryotes fell inside Asgard with posterior probability 1 on ribosomal proteins, 0.95 on conserved markers and bootstrap 91 on rRNA [169]. Heimdallarchaeota were nearest in most analyses, at posterior probability 0.77.

In 2023, 63 new Asgard genomes from 11 sites were added; one data set held 175 Asgard representatives [170]. The analysis covered 17,200 protein families in 181 archaeal genomes. Eukaryotes were "placed, with high confidence, as a well-nested clade within Asgard archaea", sister to the Hodarchaeales.

The ancestral proteome is 3,134 proteins for the last Asgard common ancestor and 4,053 for the Hodarchaeales ancestor [170]. The ratio is 1.29. The Asgard ancestor was "probably a thermophilic chemolithotroph"; the Hodarchaeales have a median predicted optimal growth temperature of 36.7 °C.

The first cultured Asgard cell, *Prometheoarchaeum syntrophicum* MK-D1, came from sediment under 2,533 m of water [171]. It was incubated at 20 °C. Its cells measure 300 to 750 nm, mean 550 nm (n = 15), position 2.27, with protrusions 80 to 100 nm wide.

It doubles in "approximately 14–25 days", positions 45.90 to 46.43 [171]. It grew first with *Halodesulfovibrio* (85 per cent of the culture) and *Methanogenium* (2 per cent), later in a pure co-culture with *Methanogenium*. Cultivation took 12 years by the preprint and was "decade-long" by the published summary.

Nanoarchaeum equitans grows attached to another archaeon, *Ignicoccus* [125]. Its spherical cells are about 400 nm across, position 1.98. Its genome of 0.5 Mb was the smallest archaeal genome known at the time.

Here the form of the net is community as shared prefix. The eukaryotes sit as a branch

inside the Asgard archaea, and the Asgard archaea inside the Archaea: an address inside a longer address. MK-D1 grows with partners, and *Nanoarchaeum* attached to *Ignicoccus*.

Small, large, fast and slow

Prokaryotic cells range from 0.1 to 5 µm in diameter, positions 0.72 to 4.28 [172]. Most bacterial cells are about 2 µm long, position 3.44 [173]. The extremes reach far beyond.

What	Size	Position	Source
MK-D1 protrusions, width	80–100 nm	0.51–0.72	[171]
groundwater bacteria of the CPR, median axes	189.7 / 242.5 / 322.6 nm	1.30 / 1.52 / 1.78	[123]
Nanoarchaeum equitans, diameter	about 400 nm	1.98	[125]
MK-D1 cell	300–750 nm; mean 550 nm	1.72–2.55; 2.27	[171]
Pyrococcus furiosus, width	0.8–2.5 µm	2.61–3.64	[174]
most bacterial cells, length	about 2 µm	3.44	[173]
largest bacterium before 2022	750 µm	8.84	[173]
Ca. Thiomargarita magnifica, cell with measured cytoplasm	4.27 mm	10.42	[173]
T. magnifica, mean length	9.72 ± 4.25 mm	11.17	[173]
T. magnifica, maximum length	20.00 mm	11.83	[173]

The groundwater cells measure 0.009 ± 0.002 µm³ and hold 42 ± 9.5 ribosomes [123]. SAR11 measures about 0.01 µm³ [124]. A 400-nm sphere is 0.034 µm³ and a 550-nm sphere 0.087 µm³.

Thiomargarita magnifica lives on sunken leaves of the red mangrove in Guadeloupe [173]. It is about 50-fold larger than other giant bacteria. Its cytoplasm in a cell of 4.27 mm is 5.91×10^{-12} m³, or 5.91×10^{6} µm³: about 5.9 million cells of *E. coli*.

A central vacuole fills 73.2 ± 7.5 per cent of its volume [173]. Its genome is 11.5 to 12.2 Mb with 11,788 genes. It holds 36,880 ± 7,956 genome copies per mm, and 737,598 ± 159,115 copies in a cell of 2 cm.

The maximum length is 20,000 ÷ 2 = 10,000 times a cell of 2 µm and 26.7 times the 750-µm record. From the shortest axis of the groundwater cells to 20 mm is a factor of 1.05×10^{5}, positions 1.30 to 11.83.

Here the form of the net is opened once, filled many times. The depth of the prokaryotic cell opened once; it has filled from 0.009 µm³ to 5.9×10^{6} µm³ of cytoplasm, nine orders of magnitude of volume, without a nucleus.

Heat and cold

Microbes grow from −15 °C, the lower end given for cold-loving species, to 122 °C [175], [176]. The upper value was measured for the archaeon *Methanopyrus kandleri* under 20 MPa of pressure. That is a span of 137 K.

Pyrococcus furiosus grows from 70 to 103 °C, best at 100 °C, and doubles there in 37 minutes, position 40.17 [174]. Some archaea grow at 105 °C and survive autoclaving [175].

Here the form of the net is context. The same rule of closure takes other values in other surroundings. A cell that doubles in 37 minutes at 100 °C, and a cell that grows at 122 °C only under 20 MPa, hold the same closed form at other temperatures and pressures.

Division and turnover

What	Duration	Position	Source
Vibrio (*Pseudomonas*) *natriegens*, generation	9.8 min	38.96	[177]
E. coli, shortest division in the laboratory	20 min	39.61	[157]
Pyrococcus furiosus, doubling at 100 °C	37 min	40.17	[174]
Vibrio cholerae, wild doubling	1.1 h	40.69	[178]
Pseudomonas aeruginosa, wild doubling	2.3 h (other estimate 1.9–2.4 h)	41.36	[178]
median laboratory doubling	3 h	41.61	[178]
median wild doubling	7.4 h (95 % CI 3.1–19 h)	42.43	[178]
rhizosphere bacteria, turnover	12–19 h	42.87–43.29	[179]
E. coli, wild doubling	15 h	43.07	[178]
Mycobacterium tuberculosis, division	15–20 h	43.07–43.33	[157]
Salmonella enterica, wild doubling	25 h	43.54	[178]
soil bacteria at about 20 °C, turnover	2.3–33 d, mean 9.3 d	44.26–46.68	[179]
prokaryotes, upper 200 m of open ocean	6–25 d	45.13–46.43	[160]
Mycobacterium leprae, division	14 d	45.90	[157]
anammox planctomycete, division	about 2 weeks	45.90	[180]
MK-D1, doubling	14–25 d	45.90–46.43	[171]
prokaryotes, ocean below 200 m	0.8 yr	48.67	[160]
prokaryotes, soil	2.5 yr	49.70	[160]

cyanobacterial akinetes, dormancy	up to 60 yr	52.60	[181]
prokaryotes, subsurface	1,000–2,000 yr	55.16–55.79	[160]

In culture, division times run from 9.8 minutes to 25 days. The fastest to MK-D1 is a factor of 2,057 to 3,673. The fastest to the turnover of the subsurface is a factor of 5.4×10^{7} to 1.1×10^{8}.

The wild median, 7.4 h, is longer than the laboratory median, 3 h [178]. *E. coli* doubles in 15 hours in the wild against 20 minutes at best in the laboratory, 45 times slower. Soil bacteria grow fifteen times faster at 20 °C than at 0 °C and about five times slower at pH 4.0 than at pH 8.3 [179].

Here the form of the net is context again. The same cell divides at another rate in another place. The positions run from 38.96 in a broth to 55.79 in rock, 17 steps of three.

The line of cells has persisted since the Strelley Pool stromatolites of 3.43 billion years, position 68.86 [108]. At the fastest rate the line outlasts the single cell by $3.43 \times 10^{9} \times 525{,}960 \div 20 = 9 \times 10^{13}$ divisions. Here the form of the net is form and carrier: the line is the form, each cell a carrier that divides or is taken apart.

Wall, signal and film

Outside its membrane a bacterium carries a wall of peptidoglycan: sugar chains tied by short peptides [114]. Bacteria with a thick wall have many sheets of it: 30 to 100 nm together, positions −0.38 to 0.72, in one source, and 20 to 80 nm, positions −0.75 to 0.51, in another [182]. Bacteria with a thin wall have a sheet of no more than about 4 nm and a second membrane outside it.

The peptides of the wall hold D amino acids: D-isoglutamic acid and D-alanine, next to L-alanine [182]. The hand that proteins never use is built into the bacterial wall.

Bacteria signal to each other with small molecules, the autoinducers [157]. Thin-walled bacteria mainly use N-acylated homoserine lactones; thick-walled bacteria mostly use small peptides.

Bacteria on a surface build a shared coat. This matrix is 50 to 90 per cent of the dry mass of the film [157], [183]. Of all bacterial and archaeal cells, 40 to 80 per cent live in such biofilms, about 80 per cent in surface habitats other than the ocean [184].

Here the form of the net is form and carrier. The cell is the closed form; its line persists through each division. The signal molecule between cells is the unclosed carrier: it leaves one cell and is read by another.

Electric waves in a film

In biofilms of *Bacillus subtilis*, long-range electrical signals travel as waves of potassium outside the cells [185]. The K^{+} leaves through the channel YugO, gated by an internal TrkA domain. Deletion of the gene for YugO removed the release.

Inside the cells K^{+} is about 300 mM, “nearly 40 times” the medium [185]. The medium

then holds about 300 ÷ 40 = 7.5 mM. More than 75 biofilms were analysed, each holding “billions of densely packed cells”.

The signal was followed over a profile of about 1.5 mm, position 9.47 [185]. Its spread has a log-log slope of 1.1 (R^2 = 0.96) against 0.5 expected for diffusion. The diffusion coefficient of K^+, 19.7 × 10^{-6} cm^2 per second in water, was taken as 13.8 × 10^{-6} in the film, 70 per cent.

The oscillations of these films are metabolic [186]. Growth halts periodically, which raises the supply of nutrients to the cells inside. The period increases slightly over time.

The waves begin when the film holds “over one million cells” [187]. Motile *B. subtilis* cells nearby peak 26 ± 9 minutes after the electrical peak of the film, position 39.85, over 44 pulses. Cells of another species, *Pseudomonas aeruginosa*, peak 22 ± 13 minutes after, position 39.69, over 30 pulses.

The mean interval between peaks for *P. aeruginosa* is 2.1 hours, position 41.28 [187]. A film lacking TrkA gives a signal 75 ± 4 per cent lower. Motile cells lacking KtrA are 57 ± 6 per cent more polarised and 239 ± 25 per cent more attracted.

Here the form of the net is rest and discharge. The film loads, holds and discharges potassium in waves with a period of hours. A second species nearby joins the same rhythm.

Here the form of the net is also community as shared prefix. Two species answer one signal, 22 to 26 minutes after the peak. The community is the signal they share.

Genes that move sideways

Genes pass from parent to daughter. Among Bacteria and Archaea they also pass sideways, between lineages, and the share is large.

In *E. coli* strain MG1655, 755 of 4,288 genes, 547.8 kb, entered by at least 234 transfer events [188]. This happened since its divergence from *Salmonella* about 100 million years ago, position 65.64. That is 755 ÷ 4,288 = 17.6 per cent of the genes; the source gives about 18 per cent of the chromosome.

The introduced genes have a mean age of 14.4 million years, position 63.87, and arrive at 16 kb per million years per lineage [188]. Retained sequence is 547.8 kb ÷ 100 = 5.5 kb per million years. About 34 per cent of the inflow is kept, if the rate held over the full 100 million years.

In 181 prokaryotic genomes with 539,723 genes, “at least 81 +/- 15%” of each genome’s genes took part in transfer at some point [189]. The range is 66 to 96 per cent. The mean genome holds 539,723 ÷ 181 = 2,982 genes.

In 329 proteobacterial genomes with 1,207,272 proteins, at least 75 per cent of protein families showed at least one transfer [190]. Events ran at about one per family at the level of species and class. They doubled to about two per family at the level of phylum.

In 110 genomes, 3,190 protein families entered the main analysis [191]. “Between 88% and 98%” of the expansions of families came from transfer; with a single criterion the share was 65 per cent. Transferred copies were introduced on average twice as long

ago as duplicated copies.

Twenty strains of *E. coli* share a pan-genome of 17,838 gene families and a core of 1,976 [192]. The average genome holds about 4,721 genes. The core is 41.9 per cent of one genome and 11.1 per cent of the pan-genome.

Between the domains

In 134 archaeal genomes, the origins of 13 higher groups correspond to 2,264 gene acquisitions from bacteria [193]. That is 2,264 ÷ 13 = 174 per origin. Transfers from bacteria to archaea were “more than fivefold more frequent” than the reverse.

Of 25,762 gene clusters, 16,983 were found only in archaea and 3,315 were imports [193]. The shares are 65.9 and 12.9 per cent.

Tree and net

A tree of 31 proteins present in each of 191 genomes “represents only about 1% of an average prokaryotic proteome” [194]. Against about 3,000 genes, 31 ÷ 3,000 = 1.03 per cent. For a large eukaryotic proteome the share is “only 0.1%”.

A forest of 6,901 trees for 100 prokaryotes, 41 archaea and 59 bacteria, holds 102 nearly universal trees [195]. Their inconsistency is 1.4 to 4.3 per cent, and 14 of them are strict one-to-one families of ribosomal proteins. The nearly universal trees are 1.48 per cent of all trees.

Within the nearly universal trees a quartet analysis showed “a dominant tree-like signal” [196]. In 5,218 trees of 4 to 25 species the tree-like signal “becomes virtually undetectable”. The trees outside the universal set number 6,799, or 98.5 per cent.

In 35 groups of closely related genomes, genes are lost at about three times the rate at which they are gained [197]. Gain and loss run about ten times above the expansion and reduction of families. Change amounts to “typically tens of thousands” of genome events per nucleotide substitution per site.

In prokaryotes the tree of descent holds in about 1 per cent of genes, and the rest of the genome is a net of transfers.

Here the form of the net is also community as shared prefix. A gene shared by transfer makes two lineages share a stretch of address. The 17,838 families of the *E. coli* pan-genome are such a shared store, of which each strain carries 4,721 ÷ 17,838 = 26 per cent.

Into the eukaryotes

Genes also passed from bacteria into eukaryotes. One model holds this transfer episodic, at the origins of the mitochondrion and the chloroplast, with later loss in different lineages [198]. A review instead gives transfer “an important role” with a “highly variable impact … in different lineages” [199].

About 4,500 protein-coding genes of the plant *Arabidopsis*, about 18 per cent, are of cyanobacterial origin [200]. The study compared 24,990 proteins; earlier estimates were 800 to 2,000.

The red alga *Galdieria sulphuraria* has a genome of 13.7 Mb and grows on more than 50 carbon sources [201]. “At least 5%” of its protein-coding genes probably came from bacteria and archaea. They include genes for removing heavy metals and for taking up glycerol.

In bdelloid rotifers, 2,792 of 28,922 matched transcripts (9.7 per cent) were foreign; the true rate is at least 8 to 9 per cent [202]. The sources were about 59 per cent bacterial, 23 per cent fungal, 6 per cent algal or plant and 1 per cent archaeal. About 80 per cent of the expressed foreign genes code for enzymes.

Wolbachia insertions occur in the genomes of four insect and nematode species [203]. They run from under 500 bp to “nearly the entire Wolbachia genome (>1 megabase)”, and the inserted genes are transcribed. Three more insect genomes show potential transfers.

A screen of 26 animal species and 14 vertebrates found 145 foreign genes of its class C in humans, 110 of class B and 39 of class A [204]. A re-examination of 17 human genes from 2001 and 28 top claims of that screen kept 7 genes, from four events [205].

The metabolisms that carry the cycles

The oldest dated step of any element cycle is microbial sulfate reduction, in barites of about 3.47 billion years (chapter 2) [105]. Each later cycle also began with a step that only bacteria or archaea carry.

Nitrogen

Nitrogen fixation is the reduction of the nitrogen of the air by the enzyme nitrogenase, found only in bacteria and archaea [112]. In archaea they are limited to methanogens of three orders: Methanococcales, Methanobacteriales and Methanosarcinales.

In bacteria the genes occur in cyanobacteria, Firmicutes, Chloroflexi, Chlorobi, Bacteroidetes, Actinobacteria, Proteobacteria and Aquificales [112]. Of 44 sequenced cyanobacterial genomes, 21 carry them.

Nitrogenase occurs in three forms: with molybdenum (nif), with vanadium (vnf) and with iron only (anf) [112]. The two alternatives are nested within the molybdenum lineage, so the molybdenum form came first. An active molybdenum enzyme needs at least six genes, nifHDKENB.

Sedimentary rocks 3.2 to 2.75 billion years old carry a mean $\delta^{15}N$ of 0.0 ± 1.2 ‰, read as fixation, most probably by the molybdenum enzyme [110]. The minimum age is 3.2 billion years, position 68.79.

A molecular clock places the origin of nitrogenase at roughly 1.5 to 2.2 billion years, positions 68.10 to 68.45 [112]. The isotope minimum and the clock differ by 1.0 to 1.7 billion years.

Here the form of the net is the residue that becomes the alphabet. Fixed nitrogen made by prokaryotes is the letter that every amino acid and every nucleotide carries. Eukaryotes never acquired the enzyme; they take the letter from the prokaryotes that make it.

The cyanobacterium *Trichodesmium* lives in colonies in the open sea. It fixes nitrogen while it produces oxygen, with fixation confined to daylight [206]. In poor tropical waters it can be much of the plant biomass.

About 15 per cent of the cells in a *Trichodesmium* filament are fixing cells [207]. They lie in zones of 2 to 30 cells, one or two zones per filament, up to four; a filament holds 10 to 20 such cells. Its fixation was first estimated at about 5 Tg N per year; the current estimate is about 60 to 80 Tg N per year.

Of a marine total of 100 to 200 Tg N per year, that is 60 ÷ 200 = 30 per cent to 80 ÷ 100 = 80 per cent [207]. The estimate rose 12- to 16-fold between the first and the current reading.

The unicellular cyanobacterium UCYN-A lives in mutual symbiosis with a single-celled alga [208]. The alga receives fixed nitrogen; the cyanobacterium receives fixed carbon. Its genome is reduced to 1.44 Mb and lacks the oxygen-producing photosystem II and the citric acid cycle [209].

In 2024 UCYN-A was described as a nitrogen-fixing organelle of a marine alga [210]. Its genome is 1.44 ÷ 1.66 = 87 per cent of the 1.66-Mb genome of *Prochlorococcus* MED4 [211].

Plants house fixers in their roots. Nodulating plants fall in about 10 of about 380 families of flowering plants, all in one clade [212]. A single origin of the predisposition to nodules lies slightly over 100 million years ago, position 65.64; nodulation then arose about 8 times and was lost about 10 times [213].

Legumes number over 19,500 species; their rhizobia fall in 13 genera of Alphaproteobacteria and 2 of Betaproteobacteria [214], [215]. Actinorhizal plants, 8 families, 24 genera and over 220 species, house *Frankia* [216].

Cycads, 382 species, house the cyanobacterium *Nostoc* [217]. Chapter 12 follows these partners.

Archaea also oxidise ammonia. In 12 soils the archaeal gene *amoA* was up to 3,000-fold more abundant than its bacterial form [218].

In a shortgrass prairie, bacteria release 4.5 g N per m² per year from organic matter, soil animals 2.9 and fungi 0.3 [219]. The total is 7.7 g, or 77 kg N per hectare per year. The shares are 58 per cent bacteria, 38 per cent animals and 4 per cent fungi.

Bacteria also return nitrogen to the air by two routes. The anammox organism is an autotrophic planctomycete that divides only once every two weeks [180]. It oxidises ammonia without oxygen.

In the oxygen-free water of Golfo Dulce, Costa Rica, a coastal bay 200 m deep, anammox gives 19 to 35 per cent of the nitrogen gas formed [220]. In sediments of the continental shelf it gives 24 and 67 per cent at two sites [221].

Natural fixation on land is 58 Tg N per year (range 40 to 100) in one compilation and 128 in another [222], [223]. At sea it is 140 Tg N per year in one source and 120 (100 to 200) in another [224], [223]. Lightning adds 5 Tg N per year.

Today the Haber–Bosch process fixes about 120 Tg N per year [223]. That is 120 ÷ 58 =

2.07 times the natural rate on land and 24 times lightning. Of 413 Tg of reactive nitrogen made each year, about 210 Tg come from human activity [224].

Oxygen

Free oxygen came from prokaryotes. One record places lasting oxygen in the air at about 2.33 billion years, position 68.50, with the change completed within roughly 1 to 10 million years [225]. A second places the onset at 2,460 to 2,426 million years, positions 68.55 to 68.54 [226].

The interval from the nitrogen-fixation minimum to the oxidation is $3.2 - 2.33 = 0.87$ billion years or $3.2 - 2.46 = 0.74$ billion years. The oxidation significantly predates the modern cyanobacteria [111].

Free oxygen began to build up roughly 2.5 billion years ago, from biological production [227]; cyanobacteria were the producers [183]. Organic matter in a soil of South Africa dated 2.6 to 2.7 billion years is read as microbial mats on the land surface, positions 68.60 to 68.64 [228].

Today the cyanobacterium *Prochlorococcus* numbers about $2.9 \pm 0.1 \times 10^{27}$ cells and *Synechococcus* $7.0 \pm 0.3 \times 10^{26}$ [229]. The counts come from models fitted to more than 35,000 observations. The ratio is 4.1.

Roughly half of the oxygen produced on Earth each year comes from the ocean, up to 20 per cent of it from *Prochlorococcus* [230]. Marine life consumes about as much oxygen as the ocean produces.

Here the form of the net is what closes, stays. The oxygen stock of the air is the residue of a flow through cells: produced and consumed, it built up over geological time while each cell lasted hours to days.

Carbon and sulfur

Bacteria in the sea use about 10 to 50 per cent of the carbon fixed by photosynthesis [231]. Free-living bacteria are grazed by flagellates, which are eaten by small zooplankton. The named steps run from dissolved organic matter to bacteria, flagellates, small zooplankton and the classical food chain.

Those steps pass four domains or kingdoms: algae, bacteria, protists and animals [231]. Here the form of the net is metabolism at the scale of the sea: carbon flows from one closure to the next while each keeps its form.

In coastal sediments, sulfate-reducing bacteria oxidise as much organic matter to carbon dioxide as all oxygen-using organisms together [232]. Their share falls threefold across the shelf, from the shore to 200 m depth.

Global marine sulfate reduction is 11.3 Tmol of sulfate per year, from a model trained on 199 profiles [233]. In mass that is $11.3 \times 32.06 = 362$ Tg S per year. It accounts for 12 to 29 per cent of the organic carbon reaching the sea floor.

Only certain bacteria and one archaeon make vitamin B12; plants do not [234]. Ruminants obtain it from the bacteria in their stomachs, fish and shellfish through plankton and bacteria in the water.

Where they live and how many

A 1998 estimate gives 4 to 6 × 10^{30} prokaryotic cells on Earth, holding 350 to 550 Pg of carbon, 85 to 130 Pg of nitrogen and 9 to 14 Pg of phosphorus [160]. The oceanic subsurface holds 3.5 × 10^{30} cells, the land subsurface 0.25 to 2.5 × 10^{30}, soil 2.6 × 10^{29} and the open ocean 1.2 × 10^{29}.

A 2019 revision gives 1.2 × 10^{30} cells [184]. The deep oceanic subsurface holds 4 × 10^{29}, the deep continental subsurface and soil 3 × 10^{29} each, the oceans 1 × 10^{29} and the upper sediment of the ocean 5 × 10^{28}. The two totals differ by a factor of 3.3 to 5.

In the 2019 count the subsurface holds 7 × 10^{29} of 1.2 × 10^{30} cells, 58 per cent: more than soil and ocean together. Production is 1.7 × 10^{30} cells per year [160]. The whole stock is replaced in 0.7 years against the 2019 total and in 2.4 to 3.5 years against the 1998 total.

By carbon, bacteria hold about 70 Gt and archaea about 7 Gt, against 450 Gt in plants and 2 Gt in animals, of about 550 Gt in all [235]. Bacteria to archaea is 10 to 1, and prokaryotes hold 77 ÷ 550 = 14 per cent of the carbon of life. About 88 per cent of the microbial carbon lies in the deep subsurface.

The marine group SAR11 makes up 26 per cent of all rRNA genes identified in seawater [124]. A human body carries about 3.8 × 10^{13} bacteria, about 0.2 kg, against 3.0 × 10^{13} of its own cells [236].

In soil

A gram of soil holds up to 10^{10} bacterial cells; a modelled bulk density is 10^{8} cells per gram [237]. At 10^{8} cells per gram and 1.3 g per cm^3 that is 1.3 × 10^{8} cells per cm^3. Species per gram are estimated at 4 × 10^{3} to 5 × 10^{4}.

The mean distance between bacterial cells in soil is 12.46 µm, position 5.11 [237]. It is 10.38 µm near the surface, more than 18 µm at depth and 29 µm below 60 cm, positions 4.94, above 5.44 and 5.88.

DNA reassociation gives about 4,000 distinct genomes in the bacterial fraction of one soil [238]. Across 237 sites on six continents, about 2 per cent of bacterial types, about 500, make up nearly half of soil communities [239]. The implied total is 500 ÷ 0.02 = 25,000 types.

Place	Cells, 1998 [160]	Cells, 2019 [184]
Oceanic subsurface	3.5 × 10^{30}	4 × 10^{29}
Continental subsurface	0.25–2.5 × 10^{30}	3 × 10^{29}
Soil	2.6 × 10^{29}	3 × 10^{29}
Open ocean	1.2 × 10^{29}	1 × 10^{29}
Upper ocean sediment	—	5 × 10^{28}
Total	4–6 × 10^{30}	1.2 × 10^{30}

Here the form of the net is opened once, filled many times. The prokaryotic depth, opened before 3.4 billion years, is filled by 10^{30} cells in about 143,614 genome species,

from the deep subsurface to the open sea.

The order of events

Order	Age	Event	Position	Source
1	>3.9 Ga	last universal common ancestor	68.97	[111]
2	about 3.47 Ga	sulfate reduction, North Pole	68.87	[105]
3	about 3.43 Ga	Strelley Pool stromatolite reef	68.86	[108]
4	<3.4 Ga	crown Bacteria and crown Archaea	68.85	[111]
5	3.2 Ga	nitrogen fixation, isotopic minimum	68.79	[110]
6	2.6–2.7 Ga	microbial mats on a soil	68.60–68.64	[228]
7	2,460–2,426 Ma	onset of oxygen in the air	68.55–68.54	[226]
8	about 2.33 Ga	lasting oxygen in the air	68.50	[225]
9	2.2–1.5 Ga	nitrogenase, molecular clock	68.45–68.10	[112]
10	<1.84 Ga	crown eukaryotes, nested in Asgard archaea	68.29	[111], [170]
11	slightly over 100 Ma	predisposition to root nodules	65.64	[213]
12	about 100 Ma	*E. coli* and *Salmonella* diverge	65.64	[188]
13	14.4 Ma	mean age of genes introduced into *E. coli*	63.87	[188]
14	present	1.2×10^{30} or 4–6 × 10^{30} cells	—	[184], [160]

From LUCA to the crown eukaryotes is 2.36 billion years. Prokaryotes alone filled 56 per cent of the time since LUCA by the 4.2-Ga date. Chapter 4 follows the viruses that run through them.

What this part of the history shows

Two branches of one address hold most of life’s cells. Bacteria and Archaea, told apart in 1977 and named as domains in 1990, count 136,646 and 6,968 genome species. The eukaryotes sit inside the Asgard archaea, sister to the Hodarchaeales: an address inside a longer address.

One depth opened once and filled many times. Prokaryotic cells run from 0.009 μm^3 with 42 ribosomes to a cell of 20 mm with 737,598 genome copies, positions 1.30 to

11.83. The Earth holds 1.2×10^{30} to 6×10^{30} of them, with 77 Gt of carbon and 58 per cent of the cells below the surface.

The surroundings set the values. Growth runs from −15 °C to 122 °C under 20 MPa, and doubling from 9.8 minutes in a broth to a wild median of 7.4 hours. *E. coli* doubles 45 times more slowly in the wild than in the laboratory.

Form and carrier stand between line and cell. The line has persisted 3.43 billion years, 9×10^{13} divisions at the fastest rate. Each cell, and each signal molecule between cells, is a carrier that ends.

Genes move sideways: the tree of descent holds in about 1 per cent of prokaryotic genes. In 181 genomes 81 ± 15 per cent of genes took part in transfer, in 329 genomes 75 per cent of families, and 88 to 98 per cent of family expansions came from transfer.

Community is a shared prefix. Twenty strains of *E. coli* share 17,838 gene families, each carrying 26 per cent. Two species in one film answer one potassium wave within 22 to 26 minutes.

Rest and discharge show in the film. A biofilm of more than a million cells loads and releases potassium in waves with a period of hours, and its growth halts and resumes in the same rhythm.

What closes, stays: the cycles flow through closed cells. Nitrogenase, only in prokaryotes, fixed nitrogen by 3.2 Ga; oxygen in the air had its onset at 2,460 to 2,426 Ma [226], and lasting oxygen stood at about 2.33 Ga [225]. Bacteria in the sea use 10 to 50 per cent of the carbon fixed by photosynthesis.

The residue becomes the alphabet. The fixed nitrogen of prokaryotes is the letter in every amino acid and nucleotide of every other life. Plants never acquired the enzyme; they house the organisms that make it, in about 10 of 380 families of flowering plants.

4. Viruses

The first cells and the two domains of chapters 2 and 3 never lived alone. Beside them, and inside them, ran strands that copy themselves only in a cell. These are the viruses and their smaller and larger relatives: viroids, giant viruses and the virus of a virus.

Their history starts before the last universal common ancestor and runs to the present day. It is read in four records: the genes that viruses share, the fossils they left in host genomes, the defences that cells keep, and the particles that live today.

A virus particle is a strand of DNA or RNA in a coat of protein. It is not a cell. Outside a cell it does not multiply [240].

In the terms of chapter 1 the particle is a window that holds one value: uniform, closed and still. It turns only as part of a cell that turns.

Before the cells: the oldest virus genes

Some genes are shared by many groups of viruses and have only distant relatives in cells. They are called virus hallmark genes: “Genes shared by many diverse groups of viruses, with only distant homologs in cellular organisms” [241]. Named among them are the jelly-roll capsid protein, a helicase of superfamily 3, a packaging ATPase, an archaeo-eukaryotic primase and a rolling-circle replication endonuclease [241].

From these genes the same study reads the order of events. “Virus-like entities are older than typical, modern-type cells” [241].

Agents like modern viruses existed before the first cells closed by a membrane. A flow of genes through selfish elements runs from that stage to the present day [241].

A later study gives the origin in two parts. “Different types of primordial, selfish replicons gave rise to viruses” [242].

Each virus joins a module for copying with a module for building the particle [242]. New groups of viruses “have repeatedly emerged at all stages of the evolution of life” [242].

Five of the seven Baltimore classes descend from one ancestor [243]. Three RNA classes and two reverse-transcribing classes share an RNA-directed RNA polymerase or a reverse transcriptase as their root gene [243].

That is 5 / 7 = 71 % of the classes. Viral genomes are modular, and their relations form a network, not a tree [243].

The viruses of the last universal ancestor

The last universal common ancestor, LUCA, is dated about 4.2 Ga, with a range of 4.09–4.33 Ga and a composite range of 3.94–4.52 Ga [97]. The time position of 4.2 Ga is 69.04. Its genome is reconstructed at 2.75 Mb (2.49–2.99 Mb), coding 2,657 proteins

(2,451–2,855) [97].

That ancestor already had viruses. Its virome “already included the main groups of extant viruses of bacteria and archaea” [244].

The same study finds “extensive virus evolution antedating the LUCA” [244]. The bacterial and archaeal virus lineages are therefore at least 4.09–4.33 Gyr old.

LUCA also carried a defence. Nineteen class 1 CRISPR–Cas effector protein families are inferred in its genome [97]. A complex virome and a CRISPR-type defence thus stand together in one ancestor.

Two older studies give other dates: older than 3.9 Ga [111] and about 3.5–3.8 Ga [112]. Their time positions are 68.97 and 68.87–68.95. The largest viral genomes known today, 2.5–2.8 Mb, are close to the 2.75 Mb reconstructed for LUCA [97, 245, 267].

The smallest replicators: viroids

The smallest known strands that copy themselves in a cell are the viroids. They are rings of RNA that code for no protein and have no coat. They fall into two families that differ in where they copy.

The Pospiviroidae have “circular RNA of 246–375 nt”, folded into a rod or near-rod with a central conserved region [246]. They copy in the nucleus and are not translated. The family holds 5 genera with 40 species: *Apscaviroid*, *Cocadviroid*, *Coleviroid*, *Hostuviroid* and *Pospiviroid* [246].

The Avsunviroidae have genomes “ranging in size from 246 to 434 nt” [247]. They carry hammerhead ribozymes in strands of both polarities and copy in plastids, mostly chloroplasts. The family holds 3 genera, *Avsunviroid*, *Pelamoviroid* and *Elaviroid*, with 5 species in all [247].

Both families share the lower limit of 246 nt. Together they hold 40 + 5 = 45 species in 8 genera. The largest viroid, 434 nt, is 434 / 1,759 = 25 % of the smallest circovirus genome; the smallest, 246 nt, is 14 % [247, 248].

The step from viroid to virus is short in length. The porcine circovirus genome, 1,759 nt, is 7.2 times the smallest viroid and codes for two proteins, Rep and Cap [248].

A viroid ring is a closed form with nothing outside it. The virus adds a coat.

The particle: size and coat

A single particle is a virion. Most viruses infect the cells of only one or a few species [240]. The particles span more than four steps of the ladder, from 15 nm to 1.5 µm.

Particle	Size	Position	Source
Circoviridae, diameter	15–25 nm	−1.01 to −0.55	[249]
Porcine circovirus, diameter	17 nm	−0.90	[250]
Nanoviridae, diameter	18–19 nm	−0.85 to −0.80	[251]

Tobamovirus rod, diameter	about 18 nm	−0.85	[252]
Geminate particle of maize streak virus	22 × 38 nm	−0.66; −0.17	[253]
Parvoviruses	23–28 nm	−0.62 to −0.44	[254]
Bromoviridae (cucumber mosaic virus)	26–35 nm	−0.51 to −0.24	[255]
Picornaviruses, with poliovirus	30–32 nm	−0.38 to −0.32	[256]
Hepatitis B and its family	42–50 nm	−0.07 to 0.08	[257]
Sputnik virophage	50 nm	0.08	[258]
Phage HK97, empty mature capsid	66 nm	0.34	[259]
Phage PRD1	about 70 nm	0.39	[260]
Retroviruses, with HIV	80–100 nm	0.51 to 0.72	[261]
Influenza and its family	80–120 nm	0.51 to 0.88	[262]
Coronaviruses, with SARS-CoV-2	80–160 nm	0.51 to 1.14	[263]
PBCV-1, chlorella virus	190 nm	1.30	[264]
Tobamovirus rod, length	300–310 nm	1.72 to 1.74	[252]
Mimivirus particle	400 nm	1.98	[265]
Mimivirus capsid	500 nm	2.18	[266]
Megaviridae, largest	up to 0.7 µm	2.49	[267]
Mimivirus with its fibres	750 nm	2.55	[266]
Pandoravirus, length	about 1 µm	2.81	[245, 267]
Pithovirus sibericum, length	1.5 µm	3.18	[267]
Closteroviridae filament, length	650–2,200 nm	2.42 to 3.53	[268]

From porcine circovirus to *Pithovirus* the size grows 1,500 / 17 = 88-fold. That is 3.18 − (−0.90) = 4.08 steps of three. With the longest closterovirus filament it is 4.43 steps.

The middle of the range sits at the unit of size. The hepatitis B family, 42–50 nm, runs from position −0.07 to 0.08. The particles from the circoviruses to influenza, −1.01 to 0.88, lie within about one step on either side of 0.

The coat of twenty faces

Most compact capsids are icosahedra. Their build follows one rule: the triangulation number $T = h^2 + hk + k^2$, with h and k whole numbers [269]. The rule permits “capsid layouts with 60T CPs, organised into 12 pentamers and 10(T-1) hexamers” [269].

The first allowed values are T = 1, 3, 4 and 7, with 60, 180, 240 and 420 coat proteins [269]. Hexamers lie everywhere except at the 12 vertices [270]. Some values are mirror-symmetric (T = 3, 16, 25 …); others are handed (T = 7, 13, 21 …) [270].

(h, k)	T	Coat proteins, 60T	Pentamers	Hexamers, 10(T − 1)
(1, 0)	1	60	12	0

(1, 0)	1	60	12	0
(1, 1)	3	180	12	20
(2, 0)	4	240	12	30
(2, 1)	7	420	12	60
(3, 0)	9	540	12	80
(4, 0)	16	960	12	150

Measured coats follow the series. Circoviruses are T = 1 [249].

A picornavirus coat has 60 identical units, 60 × 1 [256]. Phage MS2 is T = 3, with 180 proteins [269].

The core of most hepatitis B particles has 240 units, 60 × 4 [257]. Phage λ is classed T(2,1) = 7, as are HSTV-2 and phage P22; herpes simplex virus 1 is T(4,0) = 16 [269]. The thermophilic phage P23-45 has a “supersized T=7” coat [269].

Phage HK97 shows the T = 7 coat as chainmail. Its 420 subunits form 12 pentameric and 60 hexameric rings [259].

They are joined by 420 isopeptide bonds between lysine 169 and asparagine 356 into topologically linked rings [259]. The count fits the rule: 420 / 60 = 7, and 10 × (7 − 1) = 60 hexamers.

The large coats keep the same twelve corners. PBCV-1 has “T = 169d”, a right-handed skew lattice with h = 7 and k = 8 [271]. Check: $7^2 + 7 \times 8 + 8^2 = 169$.

Its coat holds 1,680 hexavalent capsomers, each a trimer of VP54, and 12 pentavalent capsomers [271]. They are arranged as 12 pentasymmetrons of 31 capsomers and 20 trisymmetrons of 66 trimers [271]. Check: 10 × (169 − 1) = 1,680, and 12 × 30 + 20 × 66 = 360 + 1,320 = 1,680.

The Mimivirus coat has “972 ≤ T ≤ 1200”, from h = k = 19 ± 1 [266]. Its depressions lie 140 Å apart and its capsomer centres 81 Å apart [266]. For h = k = 18, 19 and 20, T is 972, 1,083 and 1,200; at T = 1,083 the hexamers number 10 × 1,082 = 10,820.

One vertex of the Mimivirus coat is different. It carries a “starfish-like” structure with arms about 400 Å thick and 500 Å wide, reaching about 2,000 Å [266]. The coat is covered by “a dense layer of 1,250-Å-long fibers” [266].

Across the series the pentamers stay at 12 while the hexamers rise from 0 to 1,680 and about 10,820. The closed shell keeps its twelve corners; only the faces fill. Several coats fall outside the classical series: the 120-protein inner shell of phage φ6 and the picobirnavirus with a “forbidden T=2” [269].

Tobacco ringspot virus has a pseudo T = 3 coat, and Bacillus phage Basilisk is T(3,0) = 9 in the classical scheme; SIO-2 is T = 12 [269]. The same study proposes other tilings for these: Basilisk T = 12, herpes simplex virus 1 T = 64/3 and phage λ T = 28/3 [269].

Rods

Other viruses build a helix instead of a shell. Tobacco mosaic virus is a rigid rod about 18 nm wide and 300–310 nm long [252]. It is 310 / 18 = 17 times longer than wide.

The Virgaviridae, the family of these rods, are “about 20 nm in diameter” and “up to

300 nm long” [272]. The helix pitch is 2.3–2.5 nm around an axial canal, built from one coat protein of about 17–24 kDa [272].

A 300 nm rod therefore makes 300 / 2.5 = 120 to 300 / 2.3 = 130 turns. The family holds 7 genera with 59 species [272]. The structure of the rod was solved by X-ray fibre diffraction at 3.6 Å; its assembly starts from a short helix of “about two turns” [273].

The closteroviruses make the longest particles. Their filaments are about 12 nm wide and 650–2,200 nm long [268]. The longest is 2,200 / 12 = 183 times longer than wide, and 2,200 / 18 = 122 tobamovirus diameters long.

Packing and the crystal

In a bacteriophage the strand can fill up to about 50 % of the space in the coat [260]. Some viruses carry an envelope of membrane around the coat; retroviruses and coronaviruses are of this kind [261, 263].

In 1935 Stanley isolated tobacco mosaic virus as a crystalline protein that kept the properties of the virus [274]. A thing that multiplies in a cell had been crystallised like a salt. In the terms of chapter 1 the particle has the form of the crystal: one value repeated, a closed window that does not turn.

The strand: from 1.7 kb to 2.8 Mb

The genomes of viruses span three orders of magnitude. The smallest, of the circoviruses, are rings of single-stranded DNA of about 1.7–2.1 kb [249]. The porcine circovirus PCV1 has 1,759 nt; PCV2 has 1,767–1,777 nt, “approximately 1,770”; PCV4 has 1,770 nt [248].

The porcine circovirus was first described in 1982 from the pig cell line PK-15. Its particle was 17 nm wide, and its closed circular single strand weighed 0.58×10^6 daltons; the main coat protein weighed about 36,000 [250]. Its two main reading frames, Rep and Cap, lie in opposite orientation [248].

The circovirus family has two genera: *Circovirus* with 70 species and *Cyclovirus* with 90 [249]. The hosts of *Circovirus* are only vertebrates: mammals, birds and fish [249].

Virus	Strand	Length	What it codes for	Source
Circoviridae	DNA, single, ring	1.7–2.1 kb	2 main reading frames	[248, 249]
Nanoviridae	DNA, single, 6–8 rings	about 1 kb each	—	[251]
Geminiviridae	DNA, single, ring	2.5–3.0 kb, or 4.8–5.6 kb in two parts	—	[253]
Duck hepatitis B virus	DNA, ring	3,024 bp	—	[275]
Hepatitis B family	DNA, partly double	3.0–3.4 kb	3 or 4 reading frames	[257]
Tobamovirus	RNA, single, one piece	6.3–6.5 kb	—	[252]
Picornaviruses	RNA	6.7–10.1 kb	one long protein	[256]

Picornaviruses	RNA	6.7–10.1 kb	one long protein, cut into parts	[256]
Retroviruses	RNA, two copies	7–13 kb each	coat, core and three enzymes	[261]
Cucumber mosaic virus	RNA, three pieces	3,357 + 3,050 + 2,216 = 8,623 nt	—	[255]
Virgaviridae	RNA	about 6.3–13 kb	—	[272]
Influenza A	RNA, 8 pieces	13.5 kb	11 proteins	[262]
Closteroviridae	RNA	13–19.3 kb	—	[268]
Sputnik virophage	DNA, double, ring	18,343 bp	21 genes	[258]
Coronaviruses	RNA	22–36 kb	4 building and 14–16 working proteins	[263]
PBCV-1	DNA, linear	330,740 bp	—	[271]
Pithovirus sibericum	DNA	600 kb	—	[267]
Mimivirus	DNA	1,181,404 bp	1,262 reading frames	[265]
Megaviridae	DNA	up to 1.25 Mb	about a thousand proteins	[267]
Pandoraviruses	DNA	at least 2.5 Mb; up to 2.8 Mb	up to 2,500 proteins	[245, 267]

The largest virus genome, 2.8 Mb, is 2.8×10^6 / 1,759 = 1,592 times the smallest. Against the smallest viroid, 246 nt, it is 11,382 times. The pandoraviruses hold at least 2.5 Mb in the first two isolates and up to 2.8 Mb in a later set [245, 267].

Genome length and particle size do not rise together in the giants. *Pithovirus* has the largest particle, 1.5 µm, and a “surprisingly smaller 600 kb” genome [267]. The Mimivirus genome, 1,181 kb, is 1,181 / 600 = 2.0 times longer, in a particle 3 to 3.75 times shorter.

The Mimivirus genome holds 1,262 reading frames in 1,181.404 kb, 1.07 per kb [265]. About 10 % of its predicted genes match proteins of known function [265]. It carries many genes for protein translation, DNA repair and topoisomerases [265].

The giants and the virus of a virus

The first giant virus was found after an outbreak of pneumonia in 1992. It was isolated “from the water of a cooling tower in Bradford, England” [276]. It grew in amoebae and resembled a small Gram-positive coccus; the description appeared in 2003 [276].

Its genome followed in 2004: 1,181,404 base pairs [265]. Its discovery pushed back the assumed limits of a virus. Giant viruses reach a “particle size (>0.7 micrometers)” and more than 1,000 genes, comparable to parasitic bacteria [245].

Two families of giant amoeba viruses are known. The Megaviridae have pseudo-icosahedral particles up to 0.7 µm, AT-rich genomes up to 1.25 Mb and virion factories in the cytoplasm [267]. The pandoraviruses have amphora-shaped particles about 1 µm long and copy with the help of the host nucleus [267].

The first two pandoraviruses came from the coast of central Chile and from a freshwater pond near Melbourne, Australia [245]. Neither resembles a known family in shape or genome [245]. Their DNA genomes are “at least 2.5 and 1.9 megabases” [245].

Pithovirus sibericum came from Siberian permafrost, from “a >30,000-y-old radiocarbon-dated sample” [267]. It was revived in amoebae. Its age, 30,000 years, lies at time position 58.25.

Pithovirus joins a pandoravirus-like particle, 1.5 µm long, to a gene content like that of the iridoviruses and Marseillevirus [267]. A virus can rest more than 30,000 years and still enter a cell. Here the form of rest and discharge shows: a particle holds, unloaded, until a cell reads it.

A giant virus can itself be a host. The Sputnik virophage is a particle of 50 nm with a ring genome of 18,343 bp [258]. Of its 21 predicted genes, eight have detectable relatives elsewhere: 8 / 21 = 38 % [258].

Sputnik “cannot multiply in Acanthamoeba castellanii” on its own. It “grows rapidly” in the virus factory of amoebae infected with the mimivirus APMV [258]. Its copying “results in the production of abortive forms and abnormal capsid assembly of the host virus” [258].

The Sputnik genome is 18,343 / 1,181,404 = 1.6 % of the Mimivirus genome. Its particle is 50 / 400–500 = 0.10–0.13 of the host-virus diameter. The amoeba holds the giant virus, and the giant virus holds the virophage.

The partner with its own genome sits two deep here. The net has the same form: a closure cannot load twice in succession, and partners with their own genome sit at most two deep inside a cell.

Inside the cell: entry, burst and rest

A virus multiplies only inside a cell. There the cell’s own machines copy the strand, read it and build the parts of new particles [240, 277]. The cell is the mixed window of chapter 1, the form that turns; the particle turns only as part of it.

Entry starts at the edge of the cell, where it is read. HIV enters only where it meets the protein CD4 together with CCR5 or CXCR4 [261]. Phages bind specific receptors on the bacterium [277].

Three outcomes follow at the edge. The particle fits and enters; or the defence meets it and takes it apart; or no receptor meets it, and nothing happens. The last is the common case, since most viruses infect one or a few species [240].

What	Duration	Position	Source
Phage T4 in *E. coli*, entry to burst, shortest	20 min	39.61	[278]
Phage λ in *E. coli*, entry to burst, shortest	50 min	40.44	[278]
Influenza A, infection of a cell to first release	about 6 h	42.24	[279]
Influenza A, release by	about 5 h	42.07	[279]

one cell			
Influenza A, life of an infected cell	11.4 h (8.8–14.7 h)	42.82 (42.59–43.05)	[279]

The influenza values come from a model fitted to measurements in infected people [279]. The phage cycle in *E. coli* takes 20–50 min, positions 39.61–40.44. The influenza cell lives about half a day, below the day at 43.50.

One bacterium infected by a T phage releases 120 to 300 new particles [280]. A burst of about 200 fills about 2 % of the volume of the bacterium [281]. One cell infected with influenza A releases 1,000 to 10,000 particles [282].

A T cell infected with SIV, a relative of HIV, releases about 50,000 particles, about 5 % of its volume [281]. The burst is a discharge: the cell is loaded with particles and then opens.

Some viruses do not burst. They stay in the cell as a ring of DNA beside the chromosomes and give no signs for years [277].

Others write their strand into the chromosome of the host. A retrovirus writes its strand into the DNA of the cell it enters [261].

In bacteria the written-in phage is a prophage. A survey found 2,246 prophages in complete bacterial genomes [283]. “Nearly half” of the sequenced bacteria are lysogens, carrying at least one [283].

Lysogens are more common among pathogens and among bacteria with small genomes and short doubling times [283]. The effect of genome size holds only below about 6 Mb [283]. Prophages are rarer where CRISPR spacers are many and where type III systems occur, and more frequent with types I and II [283].

The two ways show the form of rest and discharge. The burst is loading followed by discharge. The prophage is holding: the strand stays inside the cell.

The sea and the Earth: how many

Viruses are the most numerous particles of life. Earth holds about 10^{31} of them [284]. The figure traces to Hendrix and co-workers in 1999 [284, 285].

The ocean holds about 10^{30} viruses [286]. That is $10^{30} / 10^{31} = 10$ % of the Earth total. Sea water typically holds ten billion viruses per litre, 10^{10} L^{-1} = 10^{7} per mL [287].

A survey of 5,508 paired counts of microbial cells and viruses from 22 marine surveys relates the two by power laws [288]. Upper virus counts exceed 10^{8} per mL, and the exponents are typically below 1 [288].

Counts in samples from soil and sea give about 10 viruses per bacterium and about 10^{7} particles per mL [260]. The Earth holds about 4–6 × 10^{30} prokaryotes, and the viruses weigh about 5 % of their mass [260]. Against 10^{31} particles that is $10^{31} / 6 \times 10^{30} = 1.7$ to $10^{31} / 4 \times 10^{30} = 2.5$ particles per prokaryote.

Samples give about 10 particles per prokaryote; the global totals give 1.7–2.5.

In the census of all biomass, viruses hold 0.2 Gt of carbon of about 550 Gt, with an

uncertainty of 20-fold [235]. That is 0.04 % of the living carbon.

The particles turn over fast. About 10^{23} viral infections take place in the ocean every second, and viruses kill about 20 % of oceanic microbial biomass each day [286]. Per day that is $10^{23} \times 86{,}400 = 8.6 \times 10^{27}$ infections.

Spread over 10^{30} particles, 10^{23} infections per second give 10^{-7} per particle per second. One particle thus succeeds about once in 10^{7} s, or 116 days, time position 47.82. If each infection releases about 200 particles, as a T-phage burst does, daily production is about 1.7×10^{30}, the size of the standing stock.

Viruses are “abundant and dynamic members of marine systems”, with roles in the cycling of nutrients and carbon [289]. Between cells the particle reads as the unclosed class, which carries tension from one closure to the next.

A human body carries about 10^{13} virus particles [290]. The body has 3.0×10^{13} cells of its own [236]. That is $10^{13} / 3.0 \times 10^{13} = 0.33$, about one particle for every three cells.

Part of these particles are bacteriophages [277]. In the gut they meet the bacteria that live there [291].

The cell’s record of infection: CRISPR

Cells keep a defence against viruses in their own strand. CRISPR–Cas systems are viral defence systems [292]. Their arrays hold short spacers between repeats, and a survey of 16,990 complete prokaryote genomes counts them [293].

That survey holds 16,650 bacteria from 2,973 species and 340 archaea from 300 species [293]. CRISPR–Cas systems occur in 36 % of bacterial and 75 % (75.3 %) of archaeal strains [293]. The arrays hold 211,397 spacers [293].

“More than 50% of archaeal genomes have a total of 100 or more spacers” [293]. For bacteria “the majority of genomes have a total of 50 spacers or less” [293]. The longest array has 587 spacers, in the bacterium *Haliangium ochraceum* DSM 14365 [293].

The repeats are 23–50 bp long and fall into three classes, of 24–25, 28–30 and 36–37 bp [293]. Another count, in 2,740 complete genomes, gives “an incidence rate of 40.6% for bacterial genomes and 79.4% for archaeal genomes” [292]. Earlier reports had given 40 % and 81 % [292].

Archaea carry CRISPR about twice as often as bacteria: 79.4 / 40.6 = 2.0, and 75 / 36 = 2.1. Uncultured lineages carry far fewer. In 1,724 genomes from groundwater the systems were “present in only 10%” (10.4 % of bacteria and 10.1 % of archaea after correction) [292].

In the Candidate Phyla Radiation and related lineages they were “found in only 1.4% of over 354 high quality draft genomes” [292]. The classification of the systems grew fast. It counts “2 classes, 6 types and 33 subtypes, compared with 5 types and 16 subtypes in 2015” [294].

Class 2 now holds 3 types and 17 subtypes [294]. The subtypes doubled in five years: 33 / 16 = 2.1. Nineteen class 1 effector families are already inferred in LUCA [97].

The array is a record of the outside kept inside the cell’s own strand. It has the form of reading: a homomorphic image that keeps the relations and drops the rest.

Genes on the move

Viruses carry genes between cells. Phage genomes are mosaics with access to a large common pool of genes [285]. DNA and protein similarities connect the lambdoid phages of *E. coli*, φC31 of *Streptomyces*, a cryptic prophage of *Haemophilus influenzae* and two prophage-like elements of *Mycobacterium tuberculosis* [285].

In the sea, phages carry genes of photosynthesis. Three phage genomes of two families, Myoviridae and Podoviridae, infect the cyanobacterium *Prochlorococcus* [295]. All three carry *psbA*, the D1 protein of photosystem II, and *hli*; one myovirus also carries *psbD* (D2), the other *petE* and *petF* [295].

The phage genes cluster with *Prochlorococcus* genes across several clades. The source reads this as several transfers from host to phage [295]. A phage-driven expansion of the *hli* family is proposed [295].

Phages also move bacterial genes from cell to cell, by transduction. In marine bacterial isolates the frequencies were “1.33 x 10(-7) to 5.13 x 10(-9) transductants/PFU” [296]. In natural mixed communities they were “1.58 x 10(-8) to 3.7 x 10(-8)” [296].

Putative transductants appeared in two of six community experiments [296]. A model gives “up to 1.3 x 10(14)” transduction events per year in the Tampa Bay Estuary [296]. That is $1.3 \times 10^{14} / 3.156 \times 10^{7}$ s = 4.1×10^{6} events per second in one estuary.

A gene of the host becomes a gene of the virus, and a gene of the virus a gene of the host. The closed form of one depth becomes a letter of the next. Here the residue becomes the alphabet.

Fossils in the genome: 450 Ma to the present

Viruses leave no bones. Their deep history is read in the copies they left in the genomes of their hosts, the endogenous viral elements. Each date is a minimum age, set by the host lineage that carries the copy.

Retroviruses in the Ordovician sea. Foamy-like endogenous retroviruses occur in 36 lineages of basal amphibians and fish [297]. In ray-finned fish they largely split together with their hosts [297].

Retroviruses arose with “jawed vertebrate hosts >450 million years ago in the Ordovician period” [297]. The position of 450 Ma is 67.01.

Viruses in the first vascular plants. The caulimovirids, the pararetroviruses of plants, left reverse-transcriptase copies in nearly all vascular plants screened [298]. The survey covered 72 genome assemblies (4 green algae, 1 moss, 1 clubmoss, 4 gymnosperms, 62 angiosperms) and 6 fern genomes [298]. It found 14,895 high-confidence loci in 17 operational taxonomic units, 9 of them new [298].

The family arose “at latest during the Devonian, about 320 million years ago” [298]. The

position of 320 Ma is 66.70. Vascular plants are older, at 452 Ma: 452 − 320 = 132 Myr separate the two [298, 299].

Florendoviruses sit in 46 of 62 seed plants, about 5,000 copies, and petuviruses in 27 of 62, about 1,900 [298]. Densities reach 2.3 copies per Mb in *Citrus sinensis*, with a mean of 0.2 per Mb [298]. *Zea mays* and *Arabidopsis thaliana* carry none [298].

A second survey screened 20 genomes of gymnosperms, ferns and early-branching plants [300]. It found 17,574 endogenous pararetroviruses in gymnosperms, 18–6,194 per species, and 289 in ferns: 17,863 in all [300]. The earlier-branching moss, liverwort, lycophyte and charophyte carried none [300].

The copies form seven groups, five in gymnosperms and two in ferns, and angiosperm caulimovirids arose at least three times [300]. In *Pinus taeda* four bursts of insertion are dated 119.3–183.6, 122–187.8, 108–166.1 and 151.4–232.9 Ma [300]. The positions run from 65.71 to 66.41.

Shared insertions are at least 75 Ma old in *Pinus* and at least 16.9 Ma in *Picea*, positions 65.38 and 64.02 [300]. These ages are lower bounds, and the authors read the copies as passed across species [300]. One survey dates the family at about 320 Ma [298]; its bursts in *Pinus* fall at 108–233 Ma [300].

The syncytins of the placenta. Marsupials and eutherian mammals split about 190 Ma, position 66.22 [301]. In the South American opossum an envelope gene of a retrovirus, syncytin-Opo1, makes cells fuse [301]. It is expressed in the placenta at the fused layer between foetus and mother and is conserved across *Monodelphis* species [301].

A second, non-fusing envelope gene has been conserved “for >80 My of evolution” among marsupials, the tammar wallaby included, position 65.43 [301]. In humans, syncytin-1 was found in 2000 in the placenta, in the sheet of fused cells that covers the villi [302, 303]. The syncytins are made almost only in the placenta and make cells fuse [303].

Syncytins were captured “on multiple occasions and independently” in diverse mammals, some replacing earlier ones [304]. The capture of an envelope gene for the placenta took place more than once: in the eutherians and, separately, in the opossum [301, 304]. A gene of a virus became a gene of the placenta.

Viruses other than retroviruses. Animal genomes also hold copies of viruses that are not retroviruses [305]. Bornavirus elements occur in 16 mammalian genomes, at least 93 million years old, “at least the late Mesozoic Era (~93 million years ago)” [305]. Circovirus elements are at least 68 Myr old, and filovirus and parvovirus elements at least 30 Myr [305].

The same screen found 58 elements in 17 species that matched *Dependovirus* and 41 in 5 species that matched *Parvovirus* [305]. The zebra finch holds 7 hepadnavirus loci on 7 chromosomes [305]. The screen covered 2 bird, 3 mosquito, 1 tick and 44 mammal genomes [305].

The positions are 65.57 for 93 Ma, 65.29 for 68 Ma and 64.54 for 30 Ma. Bornaviruses, filoviruses, parvoviruses, circoviruses and hepadnaviruses all left copies [305]. Five families beside the retroviruses left copies in animal lines.

Hepatitis B viruses in birds. In birds, hepadnaviruses entered the germ line “from >82 to <12.1 million years ago” [275]. Six elements are of Oligocene or Eocene age, among them eZHBV_O1–O5 at 26.6–34.2 Ma [275]. The oldest relic covers about 99 % of a hepatitis B genome and is shared across the Neoaves [275].

The family is thus “>63 million years older than previously known” [275]. The extant duck hepatitis B virus has a circular genome of 3,024 bp [275]. The positions run from 65.46 (82 Ma) to 63.72 (12.1 Ma).

Primates. In the human line one retrovirus family, HERV-K(HML2), kept an infectious pool for the past 30 Myr, position 64.54 [306]. All its genes, *env* included, are under continuous purifying selection, and it spread almost entirely by reinfection [306]. The *env* genes of eight other HERV families point to reinfection as the common route [306].

The human genome contains about 8 % of sequences of retroviral origin [303, 307].

About half of the human genome derives from transposable elements [309]. The retroviral copies are passed on from parent to child [303].

Dated virus record	Age	Time position	Source
Virome of LUCA	4.09–4.33 Ga	69.02–69.07	[97, 244]
Retroviruses with jawed vertebrates	>450 Ma	67.01	[297]
Caulimoviridae	about 320 Ma	66.70	[298]
Pararetrovirus bursts in *Pinus taeda*	108–233 Ma	65.71–66.41	[300]
Marsupial–eutherian split	about 190 Ma	66.22	[301]
Bornavirus elements	≥93 Ma	65.57	[305]
Hepadnavirus elements in Neoaves	>82 Ma	65.46	[275]
Marsupial envelope gene conserved	>80 Myr	65.43	[301]
Shared pararetrovirus copies in *Pinus*	≥75 Ma	65.38	[300]
Circovirus elements	≥68 Ma	65.29	[305]
Hepadnavirus elements, Oligocene and Eocene	26.6–34.2 Ma	64.43–64.66	[275]
HERV-K(HML2) pool; filovirus and parvovirus elements	30 Myr	64.54	[305, 306]
Shared pararetrovirus copies in *Picea*	≥16.9 Ma	64.02	[300]
Youngest dated hepadnavirus element	<12.1 Ma	63.72	[275]
Pithovirus in permafrost	>30,000 years	58.25	[267]
Potyvirus radiation	about 6,600 years	56.88	[310]

The genome fossils reach back 450 Ma at most. That is 450 / 4,200 = 11 % of the time since LUCA. The record becomes dense after 100 Ma.

Plant viruses and the plant’s answer

How many. The plant viruses are counted in three lists. The 2021 list of the international committee held 2,134 species of plant and fungal viruses, viroids and satellites, in 46 families and 193 genera [311]. That is 2,134 / 16,215 = 13.2 % of the 2025 total of all virus species.

A public database integrates 3,206 plant virus species from 46 families, on 2,231 plant species in 92 orders, with 9,604 virus–plant interactions [312]. Of these, 1,739 species (54 %) are RNA viruses and 1,465 (46 %) DNA viruses [312]. The older DPVweb holds 1,503 species and 3,706 interactions [312].

Screening of plant transcriptomes found 270 virus species from 29 families in 335 plant species, in 1,344 data sets from 1,173 plant species [312]. Japan alone records 407 viruses, 303 species and 104 unclassified, in 24 families and 75 genera [311].

In 2012 the committee recognised 92 plant virus genera, 82 of them in 21 families [313]. Most plant viruses infect few plant species, and most plants host few viruses [312]. The 9,604 links give 9,604 / 3,206 = 3.0 hosts per virus and 9,604 / 2,231 = 4.3 viruses per plant species.

How they travel. “About 80 % of plant viruses are transmitted by specific insect vectors” [314]. Most described plant viruses travel in hemipteroid insects: aphids, whiteflies, leafhoppers, planthoppers and thrips [315]. More than 200 viruses persist inside their vectors [315].

The closteroviruses travel semi-persistently: *Closterovirus* in aphids, *Ampelovirus* in mealybugs and soft scales, *Crinivirus* in whiteflies [268]. Geminiviruses travel in insects and nanoviruses in aphids [251, 253]. Cucumber mosaic virus is carried non-persistently by insects and has an “extremely broad” host range [255].

The youngest radiation. The potyviruses are about 15 % of named plant virus species and are carried by aphids [310]. Their tree was built from partial coat-protein genes of 50 potyviruses [310]. It was calibrated on dated events: the plum pox epidemic in 20th-century Europe, entries into Australia after European farming, and the transport of cowpea aphid-borne mosaic virus in the 16th century [310].

Their rate is about 1.15×10^{-4} substitutions per site per year [310]. Their first radiation was about 6,600 years ago, “during the dawn of agriculture”, position 56.88 [310]. The host plant changes at 1.43–2.2 $\times 10^{-9}$ per site per year [300].

The virus thus changes $1.15 \times 10^{-4} / 2.2 \times 10^{-9} = 5.2 \times 10^{4}$ to $1.15 \times 10^{-4} / 1.43 \times 10^{-9} = 8.0 \times 10^{4}$ times faster than its host. The radiation falls in the window of the first farming. One radiation opened, and the group then filled with species, about 15 % of all named plant viruses.

Small RNAs. The plant answers a virus with small RNAs that match it. In 1999 small antisense RNAs of uniform length, estimated at 25 nt, were found in four kinds of silencing, one of them induced by a virus [317]. They needed sense transcription or the copying of an RNA virus [317].

Arabidopsis has four DICER-LIKE proteins [318]. All four cut DNA-virus RNA into pieces of 21, 22 and 24 nt: DCL1 some of 21 nt, DCL2 22 nt, DCL3 24 nt and DCL4 21 nt [318].

The RNA tobamovirus is cut mainly by DCL4 [318].

DCL4 gives antiviral defence, and a viral protein that blocks DCL4 exposes a backup role for DCL2 [319]. Removing both DCL2 and DCL4 is “necessary and sufficient” to restore systemic infection by a virus without a suppressor [319].

Viruses answer back. Cauliflower mosaic virus impairs the processing of RDR6-made double strands; oilseed rape mosaic virus blocks the methylation step by HEN1 [318]. One review names 10 distinct viral suppressors of silencing [320].

They are P0 of polerovirus, P25 of potato virus X, 2b of cucumber mosaic virus and P6 of cauliflower mosaic virus. Then come protein 6 of rice yellow stunt rhabdovirus and V2 of tomato yellow leaf curl virus [320].

They also include p19 of tomato bushy stunt virus, a GW-repeat protein, a viral RNase III and a tobamovirus replicase [320]. Suppressors of silencing occur in plant-pathogenic bacteria and oomycetes as well, and 21-nt rather than 22-nt viral small RNAs direct strong defence [320].

The small RNAs are made from the virus and match its strand [317, 318]. Their 21–24 letters keep the order of the viral strand and drop the rest. The defence again has the form of reading.

Resistance genes. About 200 resistance genes against plant viruses are known, about half of them inherited as recessive [313]. At least 5 dominant RTM genes act against potyviruses [313]. After a hypersensitive response to tobacco mosaic virus, the plant stays protected for up to 3 weeks, position 46.27 [313].

A mild virus against a severe one. Cross-protection was observed “almost a century ago”, in work of 1929–1938 [321]. A citrus tristeza isolate, IAC, protected Pera sweet orange in São Paulo but not Hamlin or Valencia [321].

A mild pepino mosaic virus strain, CH2 isolate 1906, was cleared by the European Food Safety Authority in 2015 [321]. It is licensed in 14 European countries and protected more than 4,500 ha of tomatoes; a second strain, VX1, was assessed in 2017 [321].

The plant keeps the strain that came first. Here the form of one direction shows: the net keeps the direction of what was laid down first.

Viruses that help. A virus in the endophytic fungus of a tropical panic grass is required for growth in hot soil [322]. Fungal isolates cured of the virus cannot give heat tolerance; it returns when the virus is put back [322]. The infected fungus gives tolerance to a monocot and to a eudicot host [322].

Beneficial viruses are recorded in bacteria, insects, plants, fungi and animals [323]. Among them are acute plant viruses that raise drought tolerance and a white clover cryptic virus whose coat protein suppresses nodules in *Lotus japonicus* [323]. Others are beet cryptic virus, endogenous pararetroviruses in banana and tomato, hypoviruses of chestnut blight, killer viruses of yeasts and polydnaviruses of parasitoid wasps [323].

A virus in a fungus in a plant forms three closures nested inside one another. As with Sputnik, the partner with its own genome sits two deep inside the host.

Epidemics in crops

The plant viruses of the human era are counted in trees, tonnes and money. Plant virus pandemics and epidemics cost more than US$30 billion per year, in a 2014 estimate [324]. Of the pathogens behind emerging and re-emerging plant epidemics, 47 % are viruses [324]; another review gives “about half” [313].

Citrus tristeza has killed more than 100 million trees: more than 26 million in Argentina, 40 million in Spain, 6 million in Brazil, 6 million in Venezuela and 3 million in the USA [324]. In 1959 it killed 75 % of the orange trees of São Paulo, about 6 million [324]. Cacao swollen shoot led to more than 200 million trees being removed in Togo, Ghana and Nigeria [313].

Rice tungro costs US$1.5 billion per year, with 70–90 % loss in susceptible cultivars infected early [324]. Wheat streak mosaic takes 80–100 % of an early-infected crop, and potato virus Y up to 80 % of the tubers [324]. Faba bean necrotic yellows occurs in 17 countries, with up to 90 % seed loss [324].

Tomato brown rugose fruit virus, first reported in Jordan in 2014, takes 30–70 % of marketable fruit in Florida, US$262 million per year [324]. Maize lethal necrosis spread around 2010 to eight countries of sub-Saharan Africa, about 1.2 million km², where maize feeds more than 300 million people [324]. Cassava mosaic takes more than 25 million tonnes per year, and more than 500 million people depend on cassava [313].

Potato leafroll costs US$100 million per year in the USA and £30–50 million in the UK; barley yellow dwarf about £10 million per year in the UK [313]. The management of sharka has cost more than €10 billion since the 1970s, and rice viruses more than US$1.5 billion in South-East Asia [313].

The dated outbreaks run in order. Rice tungro was known in Indonesia in 1869, banana bunchy top in Fiji in 1889, plum pox in Bulgaria in 1915 [324]. Wheat streak mosaic followed in the USA in 1922, wheat yellow dwarf in California in 1951, rice tungro epidemics from 1963 and maize lethal necrosis in the USA in 1977 [324].

Across all crops, pathogens and pests together take 21.5 % of wheat, 30.0 % of rice, 22.5 % of maize, 17.2 % of potato and 21.4 % of soybean [325]. The estimate covers 137 pathogens and pests [325]. Its ranges are 10.1–28.1 %, 24.6–40.9 %, 19.5–41.1 %, 8.1–21.0 % and 11.0–32.4 % [325].

Rates of change

Viruses change fast. From more than 40 studies, mutation rates per nucleotide per cell infection are about 10^{-8}–10^{-6} in DNA viruses and 10^{-6}–10^{-4} in RNA viruses [326]. The lowest RNA estimate, 1.6×10^{-6}, lies close to the highest DNA estimate, 1.1×10^{-6} [326].

Substitutions are about four times as frequent as insertions and deletions [326]. Tobacco mosaic virus mutates at 8.7×10^{-6} (another estimate 1.2×10^{-5}), tobacco etch virus at 4.8×10^{-6} (to 3.0×10^{-5}) [326]. Phage φX174 mutates at 1.0–1.3 $\times 10^{-6}$ and phage M13 at 7.9×10^{-7} [326].

Across all viruses the mutation rates “range from 10−8 to 10−3 substitutions per nucleotide site per cell infection” [327]. Evolution rates “range from 10−6 to 10−2 substitutions per nucleotide site per year” [327].

The mutation span is $10^{-3} / 10^{-8} = 10^{5}$, five orders [327, 328]. Substitution rates span four orders in one review and six in the other [327, 328].

Per genome per infection, single-stranded positive RNA viruses make 0.663 ± 0.417 mutations, negative-strand RNA viruses 0.372 ± 0.124 and reverse-transcribing viruses 0.445 ± 0.116 [327]. At 0.66 mutations per genome, a share $e^{-0.663} = 0.52$ of offspring genomes carries no change. About half the offspring differ from the parent.

Single-stranded RNA and reverse-transcribing viruses evolve fastest, then double-stranded RNA and single-stranded DNA viruses, and double-stranded DNA viruses slowest [327]. Single-stranded DNA viruses behave like RNA viruses, and smaller viruses mutate faster [328]. “A threefold increase in the mutation rate of ss(+)RNA viruses would produce a 48-fold evolutionary slowdown” [327].

In 19 DNA viruses the evolution rate falls with genome size: partial r = −0.707 (P = 0.001), slope −0.906 ± 0.216 [327]. In RNA viruses the partial r is −0.267 (P = 0.038) [327]. HPV-16 evolves faster than its genome size predicts [327].

A slope near −1 means that the rate per site falls about as the genome grows. The number of changes per genome per year then stays nearly constant. The same rule takes other values in other genomes: the rate per site is a value of the genome it sits in.

Viruses and people today

The young, the old and those with weak defences are hit hardest. An estimated 95,000 people died of measles in 2024, mostly children under five [329]. Influenza brings about a billion cases a year, 3 to 5 million of them severe, and 290,000 to 650,000 deaths [330].

Of the deaths of children under five from influenza-related lung infection, 99 % are in developing countries [330]. Measles vaccination averted nearly 59 million deaths between 2000 and 2024 [329]. That is 59 million / 25 years = 2.4 million a year.

In 2025, 84 % of children received a first dose of measles vaccine and 77 % both doses; 13.5 million children received no vaccine at all [329, 331]. The antibody response to chickenpox virus has a half-life of 50 years, time position 52.43 [332].

How the viruses were found

Human knowledge of viruses began with a disease of tobacco. Dutch growers reported a new disease in 1857; Mayer named it in 1879 and published its spread by sap in 1886 [333]. In 1892 Ivanovsky in the Crimea showed that the agent passed a porcelain filter [333].

In 1898 Beijerinck described a “contagium vivum fluidum” [333]. Tobacco mosaic virus is counted as the first virus described, in 1898 [323]. Losses to the disease were 20–80 % in the early 1900s [333].

In 1935 the virus was crystallised [274]. In 1938 Holmes published the work on the N gene of resistance [333]. In 1982 the porcine circovirus showed a particle of 17 nm [250].

The giants came later: the Bradford virus described in 2003 and sequenced in 2004, Sputnik in 2008, the pandoraviruses in 2013 and *Pithovirus* in 2014 [245, 258, 265, 267, 276]. From 1898 to 2026 is 128 years, time position 53.29. Discovery ran from large to small and back to large.

The international committee named 16,215 species in its list of 2025 [334]. They fall in 7 realms, 11 kingdoms, 22 phyla, 49 classes, 93 orders, 368 families and 3,769 genera [334]. The list was posted on 3 March 2025.

That year 1,563 new species, 243 new genera, 55 new families and 11 new orders were ratified; 112 of 115 proposals were accepted [335]. Each rank holds a few of the next: 16,215 / 3,769 = 4.3 species per genus, 3,769 / 368 = 10.2 genera per family and 368 / 93 = 4.0 families per order.

Against 10^{30} particles in the ocean the named set is small. The ocean holds 10^{30} / 16,215 = 6×10^{25} particles per named species.

What this part of the history shows

The virus particle has the form of the crystal: one value repeated in a closed shell. Tobacco mosaic virus crystallises like a salt, and a picornavirus coat is 60 identical units [256, 274]. The particle turns only inside a cell, the mixed form, and in the sea it succeeds in a cell about once in 116 days.

The closed shell keeps a fixed frame while its faces fill. Every icosahedral coat has 12 pentamers, from T = 1 with 60 proteins to Mimivirus at T = 972–1,200 [266, 269]. The hexamers fill from 0 to 1,680 in PBCV-1 and about 10,820 in Mimivirus [271].

Between cells the virus reads as the unclosed class, which carries tension from one closure to the next. In the ocean 10^{23} infections per second kill about a fifth of the microbial mass each day [286]. Phages carry photosystem genes between cyanobacteria, and one estuary is modelled at 4 million transduction events per second [295, 296].

“The residue of depth n is the alphabet of depth n+1.” An envelope gene of a retrovirus became the fusing gene of the placenta in eutherians and, separately, in the opossum [301, 304]. A second, non-fusing envelope gene has been held more than 80 Myr in marsupials [301].

A new kind opens once and then fills many times. Five of seven Baltimore classes share one polymerase root [243]. The potyviruses radiated once, about 6,600 years ago, and now hold about 15 % of named plant virus species [310].

Partners with their own genome sit at most two deep. The Sputnik virophage copies inside the factory of the mimivirus, inside the amoeba [258]. In the panic grass a virus sits in a fungus that sits in the plant, and the three together allow life in hot soil [322].

The defence has the form of reading. CRISPR arrays keep a record of the outside in the

cell’s own strand, up to 587 spacers in one array, in 36–41 % of bacteria and 75–79 % of archaea [292, 293]. Plant small RNAs of 21–24 nt are cut from the virus and keep the order of its strand [318].

Rest and discharge show in the life of the particle. A phage bursts after 20–50 min with 120–300 particles, and a prophage holds in nearly half of sequenced bacteria [278, 280, 283]. *Pithovirus* held more than 30,000 years in frozen soil and then entered a cell again [267].

The rates of change show one rule taking other values in other genomes. Mutation rates run from 10^{-8} to 10^{-3} per site per infection [327]. In DNA viruses the rate per site falls about as the genome grows, slope -0.91, so the changes per genome stay nearly constant [327].

The record runs from before the cell to the present. The virome of LUCA, 4.09–4.33 Ga at positions 69.02–69.07, already held the main groups of bacterial and archaeal viruses beside 19 CRISPR effector families [97, 244]. Fossils in genomes follow from 450 Ma, position 67.01, to the potyvirus radiation 6,600 years ago, position 56.88 [297, 310].

5. The Cell That Took In a Cell

The cells of chapters 2 and 3 copied, divided and traded genes, and the viruses of chapter 4 entered them. Then one cell took another inside and kept it. The kept cell divided with its host and lost most of its genes, and some of those genes moved to the host’s nucleus.

The mitochondrion and the primary plastid arose this way. Both “arose from a single endosymbiotic event” [336]. Plastids then passed from one eukaryote to another at second and third hand.

At second hand some hosts kept the nucleus of the eaten alga as a reduced organelle, the nucleomorph [337]. Younger cases stand at earlier stages: the *Paulinella* chromatophore, the nitrogen-fixing UCYN-A and the cyanobacterium of the water fern *Azolla*. In insects a bacterium lives inside another bacterium, and some sea slugs keep only the stolen plastid, without the alga [338, 339].

In the terms of chapter 1 a single cell is a ring of depth 6 that divides into two closed halves with the parent’s direction. Here a ring is taken whole into another ring, and both go on dividing.

The host and the guest

The host lineage lies among the Asgard archaea. Eukaryotes nest within them as sister to the Hodarchaeales of the Heimdallarchaeia [170]. The last Asgard common ancestor was “probably a thermophilic chemolithotroph” [170].

The lineage leading to eukaryotes “adapted to mesophilic conditions” [170]. Its median predicted optimal growth temperature is 36.7 °C [170].

The cultured Asgard archaeon *Prometheoarchaeum syntrophicum* MK-D1 has cells of 300–750 nm, mean 550 nm, position 2.27 [171]. It doubles in 14–25 days, positions 45.90–46.43 [171]. It grows only with partners, the bacterium *Halodesulfovibrio* and the archaeon *Methanogenium* [171].

The nearest measured cell to the host is MK-D1. A sphere of 550 nm has a volume of 0.087 µm³.

The guest of the mitochondrion came from a proteobacterial lineage that branched before all sampled Alphaproteobacteria [340]. The analysis that placed it added twelve divergent alphaproteobacterial clades and one sister clade [340].

Among living bacteria, *Rickettsia prowazekii* is “more closely related to mitochondria than is any other microbe studied so far” [341]. Its genome is 1,111,523 bp with 834 protein-coding genes [341]. Of its length 75.4 % codes for protein, 24 % does not, and pseudogenes take 0.9 % [341].

The mitochondrion

When. The mitochondrial symbiosis is dated 2.053–1.21 Ga, positions 68.39–67.91 [111]. The window is 2.053 − 1.21 = 0.843 Gyr wide. Crown eukaryotes are younger than 1.84 Ga, position 68.29 [111].

A later clock places the last eukaryotic common ancestor, LECA, at 2,386–1,958 Ma, positions 68.53–68.35 [342]. It used 733 taxa and 320 nuclear protein-coding genes [342]. The two clocks thus place the eukaryotic crown below 1.84 Ga and at 2,386–1,958 Ma.

Fossils held to be of cells with a nucleus are about 2 billion years old [343]. The mitochondrion has thus lived in its host about 2 billion years, time position 68.36. The account of its origin as one cell taking up a bacterium was set out by Lynn Sagan in 1967 [344]; its core is now widely accepted [343].

The evidence. The mitochondrion has two membranes, the inner one of bacterial nature and the outer one of the host's [343]. It has its own circular chromosome fixed to the inner membrane and its own ribosomes, which resemble those of prokaryotes [343]. It divides by itself, in a way like the splitting of a bacterium, and its genome is strikingly similar to that of *Rickettsia* [343, 345].

The human mitochondrial ribosome has 80 proteins, 36 of them found only in mitochondria, and three RNA molecules [346]. It makes 13 proteins, all parts of the machinery that burns food with oxygen [346].

What it kept. Human mitochondrial DNA is a ring of 16,569 bp [347]. It holds 2 rRNA, 22 tRNA and 13 protein-coding genes, 37 genes in all, with few or no non-coding bases between them [347]. Stretched, the ring is 16,569 × 0.34 nm = 5.63 µm long, position 4.38.

Arabidopsis mtDNA has 366,924 nt with 57 identified genes, which cover only 10 % of the genome [348]. Integrated plastid sequences make up 1 % and retrotransposon remnants of nuclear origin 4 % [348].

The jakobid *Reclinomonas americana* has 69,034 bp of mtDNA with 97 genes, "the largest collection of genes (97) so far identified in any mtDNA" [349]. They include at least 18 proteins not known before to be coded in mitochondria, and four genes of a bacterial-type RNA polymerase of several subunits [349].

A later survey counts "as many as 96 assigned genes" for *Reclinomonas* [350]. It finds exactly 100 mitochondrial genes in *Andalucia godoyi*, the largest set of any eukaryote examined [350]. Jakobid mtDNAs measure 65–100 kbp [350].

The largest mtDNA read is that of *Silene conica*: 11.3 Mb in 128 circular-mapping chromosomes [351]. *S. noctiflora* has 59 chromosomes, *S. vulgaris* 4, and *S. latifolia* has 0.25 Mb [351]. Intergenic sequence makes up 99 % of the extra size, and mutation rates in *Silene* mtDNA vary about 100-fold [351].

Genome	Length	Genes	Kept, against 834 *Rickettsia* protein genes	Source
Rickettsia prowazekii	1,111,523 bp	834 protein	—	[341]
Silene conica mtDNA	11.3 Mb, 128 chromosomes	—	—	[351]

mtDNA	chromosomes			
Arabidopsis mtDNA	366,924 nt	57	≤6.8 %	[348]
Andalucia godoyi mtDNA	65–100 kbp (jakobids)	100	≤12.0 %	[350]
Reclinomonas americana mtDNA	69,034 bp	97 (96)	≤11.6 %	[349, 350]
Human mtDNA	16,569 bp	13 protein, 22 tRNA, 2 rRNA	1.6 %	[347]

The last two jakobid shares include RNA genes and are upper bounds. Human mtDNA is 16,569 / 1,111,523 = 1.5 % of the *Rickettsia* genome by length. *Silene conica* mtDNA is 10.2 times the *Rickettsia* genome and 682 times human mtDNA, with fewer genes.

Gene number falls from bacterium to organelle; genome length moves both ways. The kept ring holds what the host's nucleus does not supply. Here the residue becomes the alphabet: the closed form of one depth is kept as a letter of the next.

What moved. MitoCarta3.0 lists 1,136 human and 1,140 mouse mitochondrial genes, in 149 pathways [352]. The 13 proteins coded in human mtDNA are 13 / 1,136 = 1.1 % of the list. More than 95 % of the proteins of a mitochondrion are coded in the nucleus, made in the cell fluid and brought in [345].

One model holds the transfer of bacterial genes to eukaryotes episodic: at the origins of mitochondria and chloroplasts, with later differential loss [198]. In that model continuous transfer in single lineages "does not contribute to long-term gene content evolution" [198]. A review instead gives transfer "an important role" with a "highly variable impact … in different lineages" [199].

Through the mother. Almost all mitochondria of a fertilised egg come from the egg cell and not from the sperm [345]. Mitochondrial DNA is therefore passed on through the mother [345]. The line keeps one direction: the direction of what was laid down first.

The primary plastid

When. One clock places the branching of the chloroplast lineage within the cyanobacterial tree at about 2.1 Ga, position 68.41 [353]. Establishment took another 200 Myr, a span at position 66.27 [353]. The ancestral habitat reconstructs as low in salt [353].

Another clock gives the plastid of the Archaeplastida 2,137–1,807 Ma, positions 68.42–68.27 [342]. The window is 330 Myr wide, position 66.72. Crown red algae fall at 1,984–1,732 Ma, positions 68.36–68.23 [342].

A review gives the chloroplast symbiosis "more than 1.5 billion years ago", position 68.10 [354]. The fossil record gives two later dates.

In the Tirohan Dolomite of central India, probable crown-group red algae are dated 1,650 ± 89 Ma by Pb–Pb isochron, position 68.19 (68.24–68.14) [355]. They are about 400 Myr older than the oldest red alga accepted before them, a span at position 66.90 [355].

Rafatazmia chitrakootensis forms filaments 58–175 µm wide with compartments 30–165 µm long and central rhomboidal disks of 50–60 µm [355]. *Denaricion mendax* filaments are 130–275 µm, of uncertain affinity [355]. *Ramathallus lobatus* thalli run from about 0.5 to more than 3 mm, with cells of 5–15 µm [355].

Bangiomorpha pubescens, from Baffin Island, first appears at 1.047 +0.013/−0.017 Ga by Re–Os, position 67.78 (67.79–67.76) [356]. This is about 150 Myr younger than the earlier 1.2 Ga constraint [356]. It is the only recognised crown-group eukaryote older than about 0.8 Ga, position 67.53 [356].

Clocks calibrated on *Bangiomorpha* place eukaryotic photosynthesis at about 1.25 Ga, position 67.94 [356]. The same study puts eukaryote origins between 1.9 and 1.4 Ga in the rock record, positions 68.32–68.04 [356].

The plastid or the first plastid-bearing cell is thus dated about 2.1 Ga, 2.14–1.81 Ga, more than 1.5 Ga, 1.65 Ga and about 1.25 Ga. The central values spread by 2.1 − 1.25 = 0.85 Gyr, a span at position 67.59.

The guest. Plastids “evolved from endosymbiotic cyanobacteria on a single occasion” [357]. The plastids of glaucophytes, red algae and green algae derive from one ancestor [336].

The free-living cyanobacterium *Synechocystis* PCC 6803 has 3,573,470 bp and “a total of 3,168 potential protein genes” [358]. *Prochlorococcus* MED4 has 1,657,990 bp and 1,716 genes; MIT9313 has 2,410,873 bp and 2,275 genes [211].

What it kept. The *Arabidopsis* chloroplast genome is 154,478 bp [359]. It carries 87 protein-coding genes (8 of them duplicated), 4 rRNA and 37 tRNA genes, with inverted repeats of 26,264 bp each [359].

The plastid keeps 87 / 3,168 = 2.7 % of the protein genes of *Synechocystis*. Against the small *Prochlorococcus* it keeps 87 / 1,716 = 5.1 %. By length the plastid genome is 4.3 % of *Synechocystis* and 9.3 % of *Prochlorococcus* MED4.

What moved. About 4,500 *Arabidopsis* protein-coding genes, about 18 % of the total, are of cyanobacterial origin [200]. The study compared 24,990 proteins; 9,368 were conserved and 866 had cyanobacterial homologues [200]. Earlier estimates were 800 to 2,000 [200].

Genes of plastid origin in the nucleus outnumber those kept in the plastid by about 4,500 / 87 = 52 to 1. The plastid keeps a short list, and the nucleus holds the long one.

Plastids that shrink further. In plants that no longer photosynthesise the plastid genome shrinks again. *Polytoma uvella* keeps 25 genes, the largest non-photosynthetic plastid genome noted [357]. *Pilostyles* keeps five or six genes, and in *Rafflesia* no plastid genome was detected [357].

One of each. The smallest red alga, *Cyanidioschyzon merolae*, is a cell of 2 µm, position 3.44, with one nucleus, one mitochondrion and one plastid [360]. It lives in hot springs at pH 1.5 and 45 °C [360]. Its genome has 20 chromosomes, 16,520,305 bp and 5,331 genes [360].

Plastids at second and third hand

A eukaryote with a plastid could itself be taken in. Green algal plastids were taken up by euglenids and by chlorarachniophytes, on two separate occasions [336, 357]. Plastid loss “happened at least once” [336].

One review has red algae taken up once [336]. A later review gives models with tertiary and quaternary steps, “cryptophyte first” [357].

A serial model proposes three transfers [361]. A red alga passed to the cryptophytes, a cryptophyte to the ancestor of the ochrophytes, and an ochrophyte to the ancestor of the haptophytes [361]. The model used 50 organisms in 14 eukaryotic lineages and 5,818 amino-acid positions [361].

The 2021 clock also favours serial secondary uptakes of red plastids [342]. The lineages with plastids from second or later hand are the euglenids, chlorarachniophytes, cryptophytes, haptophytes and ochrophytes, which include diatoms, brown and golden algae [357]. They also include the dinoflagellates, the apicomplexans with their remnant apicoplast, and *Lepidodinium* [357].

Lineage or event	Dated window (95 % range)	Width	Positions	Source
Red-algal plastid donor, stem Rhodophytina	1,675–1,281 Ma	394 Myr	68.20–67.96	[342]
Cryptophytes	1,658–440 Ma	1,218 Myr	68.19–66.99	[342]
Haptophytes	1,943–579 Ma	1,364 Myr	68.34–67.24	[342]
Myzozoans (dinoflagellates, apicomplexans and kin)	1,520–696 Ma	824 Myr	68.11–67.40	[342]
Ochrophytes	1,298–622 Ma	676 Myr	67.97–67.30	[342]
Serial secondary uptakes of red plastids	1,079–650 Ma	429 Myr	67.80–67.34	[342]
Tertiary plastid in a stem ochrophyte	≤819 Ma (633–1,017)	—	67.55 (67.32–67.75)	[342]

The serial red window, 1,079–650 Ma, follows the red donor stem at 1,675–1,281 Ma. Each further hand lies later than the one before. The secondary uptake of a red alga into a heterotrophic host, the source of the heterokont plastid, is placed at about 1,000 Ma, position 67.73 [362].

Diatoms have “plastids acquired by secondary endosymbiosis” [363]. *Thalassiosira pseudonana* has a 129 kb plastid genome and a 44 kb mitochondrial genome beside a draft nuclear genome of 34 Mb [363]. Diatoms perform about 20 % of global carbon fixation [363].

Haptophytes are “a lineage possessing secondary plastids” [364]. Brown algae are “chlorophyll-c containing algae” with a plastid from a red algal endosymbiont [365].

Dinoflagellates. Dinoflagellates hold the most plastids from later hands. Outside the dinotoms they carry two permanent replacements: a haptophyte-derived plastid in the

Kareniaceae and a green-alga-derived one in *Lepidodinium* [357]. The dinotoms carry diatom-derived plastids from at least 11 diatom species [357].

The *Lepidodinium chlorophorum* plastid genome is a ring of 66,223 bp with 63 ORFs, 60 of them with a putative function, 27 tRNA and 2 rRNA genes [366]. It derives from an endosymbiotic pedinophyte, nearest to the sampled *Pedinomonas minor* [366]. It is 43 % of the *Arabidopsis* plastid by length and 72 % by the count of reading frames.

The count. The events named are: primary 1, green secondary 2, red 1 or 3, green replacement 1, tertiary in dinoflagellates 2, and the stem ochrophyte 1 [336, 342, 357, 361]. The minimum is 1 + 2 + 1 + 1 + 2 + 1 = 8, with the dinotoms counted once. With three red steps the total is 1 + 2 + 3 + 1 + 2 + 1 = 10.

The primary plastid opened once. Its form was then passed from hand to hand: 8 − 1 = 7 times at least, and 10 − 1 = 9 times with three red steps. A new kind of union opened once, and the depth it opened was then filled again and again.

The serial red series runs red alga → cryptophyte → ochrophyte → haptophyte [361]. Each step hands on a plastid that the giver itself received. Here the form of memory with reach two shows: each hand inherits from the one before, and the series reaches further only as a chain.

Nucleomorphs: the nucleus of the eaten alga

In two lineages the host kept more than the plastid of the alga it took in. It kept a small remnant of the alga’s nucleus, the nucleomorph [337]. These lineages are the cryptophytes, with a red-algal endosymbiont, and the chlorarachniophytes, with a green-algal one [337].

Both genomes were reduced, independently, to under 1 Mbp with a similar layout of three chromosomes [337].

The *Guillardia theta* nucleomorph is 551 kb on 3 chromosomes, at one gene per 977 bp [367]. It keeps “hundreds of genetic-housekeeping genes” and only 30 for proteins that work in the chloroplast [367]. A later table gives 550.5 kbp and 487 protein-coding genes [368].

The *Bigelowiella* paper gives *G. theta* 531 genes in all and 17 introns [369].

The *Hemiselmis andersenii* nucleomorph is 0.572 Mbp (571.4 kbp) on 3 chromosomes, with no spliceosomal introns at all [337]. It carries 472 protein-coding genes [368].

The nucleomorph of the non-photosynthetic *Cryptomonas paramecium* is 486 kbp [368]. It has 518 predicted genes, 466 of them protein-coding, and still 18 genes for plastid proteins [368]. The three cryptophytes share 217 of 230 conserved reading frames, 94.3 % [368].

The *Bigelowiella natans* nucleomorph is 372,870 bp on chromosomes of 140.5, 134.1 and 98.1 kb [369]. It carries 331 protein-coding genes, 18 rRNA, 20 tRNA and 4 snRNA genes, and 5 DnaK pseudogenes [369]. It has 0.88 genes per kb and 22.4 % non-coding sequence [369].

It holds 17 genes for plastid proteins and 852 introns in 240 genes, all of 18–21 nt, most

often 19 nt [369]. That is 852 / 372.87 kb = 2.3 introns per kb.

Nucleomorph (host lineage)	Size	Chromosomes	Protein genes	Plastid-protein genes	Introns	Source
Hemiselmis andersenii (cryptophyte)	571.4 kbp	3	472	—	0	[337, 368]
Guillardia theta (cryptophyte)	551 kb (550.5 kbp)	3	487 (531 genes in all)	30	17	[367, 368, 369]
Cryptomonas paramecium (cryptophyte, non-photosynthetic)	485.9 kbp	—	466	18	—	[368]
Bigelowiella natans (chlorarachniophyte)	372,870 bp	3	331	17	852	[369]

Plastid-protein genes form 30 / 487 = 6.2 % of the *G. theta* protein genes, 17 / 331 = 5.1 % of *Bigelowiella* and 18 / 466 = 3.9 % of *Cryptomonas*. The green-derived nucleomorph is 373 / 551 = 68 % of *G. theta* in length, and *Cryptomonas* 88 %. *Bigelowiella* averages 372,870 / 331 = 1,126 bp per protein gene.

A red-derived and a green-derived nucleomorph came to the same build: three chromosomes and 373–572 kb. Inside the host cell sits the remnant alga, and inside it the plastid with its own genome. The partner with its own genome sits two deep, the same depth as the virophage of chapter 4.

Bacteria in insects: the smallest cellular genomes

From at least 260 Ma insects that feed on plant sap have held bacteria in their cells. *Sulcia* was acquired by the ancestor of the Auchenorrhyncha at least 260 Ma, position 66.51 [370]. The cicada, spittlebug and sharpshooter lineages split at least 200 Ma, position 66.27 [370].

Sulcia and *Nasuia* have been partners since the leafhopper–spittlebug split more than 200 Ma; the pairing began before 260 Ma [371]. The *Buchnera* symbiosis of aphids was established “200–250 Myr ago”, positions 66.27–66.47 [372].

Buchnera sp. APS of the pea aphid has a chromosome of 640,681 bp and two plasmids, pLeu of 7,786 bp and pTrp of 7,258 bp [372].

It has 583 predicted reading frames: about 500 with an assigned function, 79 hypothetical and 4 unique [372]. It carries 55 genes for making amino acids [372].

Buchnera holds more than 100 copies of its genome per cell [372]. Aphids carry “60–80 huge cells called bacteriocytes” [372]. Its 583 reading frames are 583 / 4,288 = 13.6 % of those of *E. coli* MG1655 [188].

Symbiont genomes of 139–250 kb code for 121–227 proteins [373]. The smallest, *Ca.* Tremblaya princeps, has “a genome of only 139 kb” [373].

Before 2006 the smallest known cellular genomes were about 500 kb, with about 500

genes [373].

Carsonella ruddii of the psyllids has a circular chromosome of 159,662 bp, 16.5 % GC, with 97 % of its length coding [374]. A minimal genome had been proposed at roughly 400 kb [374].

Hodgkinia cicadicola of the cicadas has 143,795 bp at 58.4 % GC [375]. It reads the codon UGA as tryptophan instead of stop [375]. Its partner *Sulcia* has 22.6 % GC [375].

In the leafhopper *Macrosteles quadrilineatus*, *Nasuia deltocephalinicola* has 112 kb and *Sulcia muelleri* 190 kb [371]. Together they make 10 essential amino acids [371]. Both lost the genes for making ATP by oxidative phosphorylation [371].

Sulcia-CARI of the spittlebug *Clastoptera arizonana* has 276,511 nt and 246 protein-coding genes [370]. Its partner *Zinderia insecticola* has 208,564 nt and 202 protein-coding genes [370]. The genes kept are completely colinear across three *Sulcia* genomes [370].

The two symbionts of one insect divide the work. Two closures stand together and make what neither makes alone: the form of the pair.

A bacterium inside a bacterium. In the mealybug *Planococcus citri* each *Tremblaya princeps* cell holds several gammaproteobacterial cells [338]. The *T. princeps* genome is 138.9 kb and that of the inner *Moranella endobia* 538.2 kb [338]. *Tremblaya phenacola* PAVE, in a host lineage without the inner symbiont, has 171.5 kb [338].

The inner genome is 538.2 / 138.9 = 3.9 times that of its container. *Tremblaya* with an inner symbiont is 81 % the size of *Tremblaya* without one. An insect cell holds a bacterium that holds a bacterium: the inner partner with its own genome sits two deep.

Symbiont (host)	Genome	Protein genes	Age of association	Source
Nasuia deltocephalinicola (leafhopper)	112 kb	—	>200 Ma	[371]
Tremblaya princeps (mealybug)	138.9 kb	group range 121–227	—	[338, 373]
Hodgkinia cicadicola (cicada)	143,795 bp	—	—	[375]
Carsonella ruddii (psyllid)	159,662 bp	—	—	[374]
Tremblaya phenacola (mealybug)	171.5 kb	—	—	[338]
Sulcia muelleri (leafhopper)	190 kb	—	≥260 Ma	[371]
Zinderia insecticola (spittlebug)	208,564 nt	202	—	[370]
Sulcia-CARI (spittlebug)	276,511 nt	246	≥260 Ma	[370]
Moranella endobia (inside *Tremblaya*)	538.2 kb	—	—	[338]

Buchnera APS (aphid)	640,681 bp	583 reading frames	200–250 Myr	[372]

The protein-gene counts span 121–583, which is 121 / 4,288 = 2.8 % to 13.6 % of *E. coli*. All but *Buchnera* lie below the about 500 genes of the smallest cellular genomes known before 2006.

Young partners: three cyanobacteria taken in late

Three cyanobacteria entered eukaryotes long after the plastid. Their genomes stand at different stages of reduction.

The *Paulinella* chromatophore. The amoeba *Paulinella* holds a cyanobacterium related to the *Prochlorococcus*/*Synechococcus* clade [376]. *Paulinella* split from its heterotrophic relatives about 90–140 Myr ago, positions 65.54–65.94 [376]. This is a maximum age for the chromatophore [376].

The main scheme gives 93.6 Myr (38.1–138.2), position 65.58 (64.76–65.93) [376]. An alternative scheme gives 141.4 Myr (48.7–210.4), position 65.95 (64.98–66.31), and two others give 55.8 and 47.9 Myr, positions 65.11 and 64.97 [376]. An earlier figure of 60 Myr, position 65.17, was derived from the loss of pseudogenes in *Buchnera* [376].

The chromatophores of strains FK01 and M0880/a carry 841 and 867 protein-coding genes; the free-living *Synechococcus* WH5701 carries 2,917 [376]. They keep 841 / 2,917 = 28.8 % and 867 / 2,917 = 29.7 %. The chromatophore genome is 1.02 Mb against about 3 Mb in WH5701, “about a quarter” of its coding capacity [357].

About 65 % of the protein-coding genes were lost in the common ancestor of the species studied [357]. By length the chromatophore is 1.02 / 3 = 34 % of its free relative. The nucleus codes for 433 proteins sent to the chromatophore, 17 of them of α-cyanobacterial origin and 26 from other bacteria [357].

UCYN-A, the nitroplast. *Ca.* Atelocyanobacterium thalassa, UCYN-A, has a genome of 1.44 Mb [209]. It lacks the oxygen-evolving photosystem II, the genes for fixing carbon and the tricarboxylic acid cycle [209].

It has inverted repeats of rRNA operons, as many chloroplasts do [209].

Its genome is 1.44 / 3.57 = 40 % of the *Synechocystis* genome. The partner is a single-celled prymnesiophyte alga [208]. “The prymnesiophyte receives fixed N in exchange for transferring fixed carbon to UCYN-A” [208].

The sublineages UCYN-A1 and UCYN-A2 split about 91 Myr ago, in the late Cretaceous, position 65.55 [377]. The host of UCYN-A2, *Braarudosphaera bigelowii*, is 7–10 µm, positions 4.58–4.91; the host of UCYN-A1 is 1–3 µm, positions 2.81–3.81 [377]. One UCYN-A1 cell lives in each host cell, and each *B. bigelowii* cell holds about 3–10 UCYN-A2 cells [377].

UCYN-A is “tightly integrated into algal cell architecture” and into the division of its organelles [210]. It “imports proteins encoded by the genome” of the host [210]. It is proposed as an early-stage organelle, the “nitroplast” [210].

The cyanobacterium of *Azolla*. *Nostoc azollae* 0708 has a genome of 5,486,145 bp

with 5,357 predicted coding sequences [378]. Of these, 31.2 % are pseudogenes, and 3,668 reading frames are intact [378]. The free-living *Anabaena*/*Nostoc* PCC 7120 has 6,413,771 bp and 5,368 potential protein genes [379].

The intact share is 3,668 / 5,368 = 68.3 %. Other plant-symbiotic *Nostoc* genomes are 7.1–10.4 Mb, “among the largest Nostocales genomes” [380]. “*N. azollae* is the only clear example of a plant symbiotic cyanobacteria genome that underwent genome streamlining” [380].

The relationship is dated three ways. It is “potentially extending back for as long as 140 million years”, position 65.94 [378]. Fossils give about 100 Myr, position 65.64 [381], and a review “more than 60 my”, position 65.17 [354].

Cyanobacterial symbioses with plants “emerged multiple times independently” [354]. In symbiosis the share of heterocysts rises from 4–10 % of cells to 30–50 % [382]. The cyanobiont grows 5–10 times slower and keeps as little as 20 % of the nitrogen it fixes [382].

In the coralloid roots of cycads the heterocyst share rises up to 80 % [181]. The cyanobiont genomes there are 5.4–9.0 Mbp [181].

The three young partners stand at three stages. *Paulinella* keeps 29 % of its genes and imports 433 proteins; *N. azollae* keeps 68 % intact beside 31 % pseudogenes; UCYN-A keeps 1.44 Mb without photosystem II and imports host proteins. Each stands at its own stage of the step that the plastid took about 2 Gyr before.

Stolen plastids: kleptoplasty

Some animals and protists keep the plastid of an alga they eat, without the rest of the alga. Photosynthetic yields were measured in 29 species of sacoglossan sea slugs, 186 specimens [339]. Three derived species among them kept yields above 0.4 after 20 days, position 46.23 [339].

They are *Elysia crispata*, *E. timida* and *Plakobranchus ocellatus*, 3 / 29 = 10 % of the species measured [339]. *E. chlorotica* is a fourth long-term species, taken from the literature and not among the 29 [339].

Short-term keepers, among them *Thuridilla*, *Bosellia mimetica* and several *Elysia*, start above 0.5 for 1–2 days, positions 43.50–44.13 [339]. Their yield falls within 7–14 days, positions 45.27–45.90 [339]. The Oxynoacea and most Limapontioidea keep no working plastids, with yields below 0.2 on the first day [339].

Elysia timida kept a yield above 0.52 after 35 days, position 46.74 [339]. In *Plakobranchus ocellatus* the mean yield fell from 0.78 to 0.59 over 74 days, position 47.42 [339]. That is 76 % of the starting yield.

P. ocellatus was starved 47 days and *E. timida* 28 days before sequencing, positions 47.00 and 46.53 [383]. Their transcripts gave 77,648 and 24,200 contigs, of which 6,088 and 2,227 had database hits [383]. Algal or plant-like hits were 79 (1.3 %) and 16 (0.7 %), mostly plastid-coded or widespread genes [383].

Thuridilla hopei keeps plastids up to 15 days, position 45.96 [383]. The authors

conclude that “the slugs maintain their long-lived plastids without the help of algal nuclear genes” [383].

Another study reports the algal nuclear gene *psbO*, from the prey *Vaucheria litorea*, expressed in *Elysia chlorotica* [384]. The gene sits in the slug germ line and is identical to the prey sequence [384]. The slug plastid depends on the nucleus for “>90%” of its proteins, and the slugs photosynthesise “for months” [384].

Kleptoplasty also occurs outside the slugs.

Flatworms keep plastids about two weeks, position 45.90 [357]. The ciliate *Mesodinium rubrum* keeps them up to a month, position 46.61 [357]. The dinotom *Durinskia capensis* keeps its diatom about 2 months, position 47.24, and an Antarctic dinoflagellate of the Ross Sea keeps haptophyte plastids at least 30 months, position 49.70 [357].

Keeper	Duration	Position	Source
Short-term sea slugs, yield above 0.5	1–2 d	43.50–44.13	[339]
Short-term sea slugs, fall	within 7–14 d	45.27–45.90	[339]
Flatworms	about 2 weeks	45.90	[357]
Thuridilla hopei	up to 15 d	45.96	[383]
Long-term threshold, yield above 0.4	20 d	46.23	[339]
Mesodinium rubrum	up to a month (30.44 d)	46.61	[357]
Elysia timida, yield above 0.52	35 d	46.74	[339]
Durinskia capensis, diatom kept	about 2 months (60.88 d)	47.24	[357]
Plakobranchus ocellatus, yield 0.78 → 0.59	74 d	47.42	[339]
Ross Sea dinoflagellate	at least 30 months (913.2 d)	49.70	[357]

A stolen plastid works from 15 days to at least 30 months, positions 45.96 to 49.70. It is a carrier without the form that made it. The closed class persists and holds form; the unclosed class lasts a while and carries.

The guest at work today

Size and number. A mitochondrion has the size of a bacterium. Its diameter is 0.5–1 µm, positions 2.18–2.81, against about 1 µm for *E. coli* [151, 385]. Its textbook length is about 2 µm, position 3.44, and its range 1 to 10 µm or more, positions 2.81–4.91 [343, 385].

In many cells the mitochondria join into a branched net that spreads over tens of micrometres [385]. A mammalian cell holds 1,000 to 10,000 of them [385]. A liver cell holds 1,000 to 2,000, about one fifth of its volume, and their inner membrane is about

one third of all its membrane [151].

In the mouse heart muscle cell mitochondria take 30.7 % of the volume [386]. The heart mitochondrion carries three times more cristae than that of the liver [151].

Two membranes. The outer membrane lets through all molecules of 5,000 daltons or less [151]. The inner membrane is tight and folded into ridges, the cristae, around the matrix [151]. In the liver 67 % of mitochondrial protein is in the matrix, 21 % in the inner membrane, and 6 % each in the outer membrane and the space between [151].

The gradient. More than 15 electron carriers pass electrons from food to oxygen and pump protons out of the matrix [151]. The protons flow back through ATP synthase, a turning machine of more than 500,000 daltons [151]. Across the inner membrane stand about 140 mV and a pH difference of about 1 unit, worth about 60 mV: 140 + 60 = 200 mV of proton-motive force [151].

The voltage stands across a bilayer of 4 nm, position −2.21. The field in it is 0.14 V / 4 × 10^{-9} m = 3.5 × 10^{7} V/m. Here the edge of chapter 1 shows: the largest step of tension stands at the boundary, with rest inside.

The yield. Complete burning of one glucose gives a net of about 30 ATP; without mitochondria the cell gets 2 [151]. That is 30 / 2 = 15 times more. Three or four protons pass per ATP, and one synthase makes more than 100 ATP per second [151].

What	Duration	Position	Source
ATP synthase, one ATP	less than 10 ms	below 28.96	[151]
One ATP molecule, used and remade	less than 1 min	below 36.88	[151]
Mitochondrion in mouse liver on a restricted diet, half-life	1.16 days	43.63	[387]
Mitochondrion in mouse liver, half-life	1.83 days	44.05	[387]
Mitochondrion in a liver cell, lifetime	about 10 days	45.60	[388]
The mitochondrion in its host	about 2 billion years	68.36	[343]

The mouse liver replaces half its mitochondria in 1.83 days; three months of a restricted diet shorten this to 1.16 days, 1.6 times faster [387]. The kind has lasted about 2 billion years while each mitochondrion lasts days: 1.83 × 86,400 s / 60 s = 2,635, so more than 2,635 ATP lifetimes pass in one mitochondrial half-life.

The form lasts and its carriers are replaced. The mitochondrion, closed, holds its form for 2 Gyr; ATP, unclosed, is used and remade within a minute. More than 300 protons cross one synthase per second, at 3 protons per ATP and more than 100 ATP per second.

Power. An adult at rest uses 250 mL of oxygen per minute, and about 20 kJ is released per litre of oxygen, whatever the food [389]. The power is 0.250 L/min × 20 kJ/L = 5.0 kJ/min = 83 W; the measured table gives 85 W [389]. Per day that is 360 L of oxygen and 7.2 MJ.

Organ at rest	Power	Oxygen	Share
Liver and spleen	23 W	67 mL/min	27 %
Brain	16 W	47 mL/min	19 %
Skeletal muscle	15 W	45 mL/min	18 %
Kidney	9 W	26 mL/min	10 %
Heart	6 W	17 mL/min	7 %
Other	16 W	48 mL/min	19 %
Total	85 W	250 mL/min	100 %

All values are from one table [389]. A man of 76 kg uses 0.24 L of oxygen per minute asleep, 0.80 L walking at 5 km/h and 2.12 L running cross-country [389]. Running takes 2.12 / 0.24 = 8.8 times the oxygen of sleep.

In the nerve cell, neocortical presynaptic terminals hold 0.3–1.4 mitochondria each, and dendrites about one per 7 µm, position 4.58 [390]. About 80 % of these mitochondria are stationary [390]. They supply about 93 % of the ATP and glycolysis about 7 %, with oxygen and glucose used in a ratio near 6:1 [390].

More with training. A review of 353 studies with 5,650 participants measured the mitochondrial content of human muscle before and after training [391]. It rose 22.7 ± 4.6 % with endurance training, 27.0 ± 5.1 % with high-intensity intervals and 27.0 ± 6.7 % with sprint intervals [391]. The untrained gained most; age and sex did not change the gain [391].

Per hour of training, sprint intervals gave about 2.3 times more than high-intensity intervals and about 3.9 times more than endurance training [391]. In the mouse heart, voluntary running raised the mitochondrial share of the muscle cell from 30.7 to 38.7 %, a rise of 8.0 points [386].

When it fails. Changes in mitochondrial DNA cause disease in the tissues that use most energy [345]. Leber’s hereditary optic neuropathy leads to blindness; it follows from changes in mitochondrial genes for parts of the respiratory chain and is passed on by the mother [345].

The other rooms of the cell

The cell that took in a cell is also divided inside by its own membranes. The membrane of the endoplasmic reticulum is about half of all membrane in the cell [392]. In a liver cell its area is 25 times that of the outer membrane; in a cell of the pancreas, 12 times [392].

Not every room came from a guest. The peroxisome has one membrane, no DNA and no ribosomes; all its proteins come from the cytosol, and new peroxisomes arise from old ones by growth and splitting [393]. Its diameter is 0.1–0.2 µm, positions 0.72–1.35 [394].

The proteasome, the cell’s cutter of tagged proteins, is a barrel of four stacked rings of seven subunits [395]. In the archaeon *Thermoplasma* it has two kinds of subunit, 14 of each, and a mass of 673,000 daltons [395]. In HeLa cells its core, of about 720,000 daltons, is about 0.6 % of all protein, which gives about 1.5×10^6 proteasomes per cell

[396, 397].

Room	Size	Position	Number per cell	Source
Synaptic vesicle	about 50 nm	0.08	—	[398]
Peroxisome	0.1–0.2 µm	0.72–1.35	—	[394]
Centriole, diameter	200–220 nm	1.35–1.43	2	[399]
Centriole, length	500 nm	2.18	—	[399]
Lysosome, median diameter	0.5 µm	2.18	50–1,000	[400, 401]
Cilium or flagellum, shaft	10–200 µm	4.91–7.63	200–300 on a ciliated cell	[399, 402]

A Golgi stack usually has four to six flat sacs, with at least three compartments of different tasks [403]. A lysosome holds about 40 to 50 kinds of digesting enzymes that work at about pH 5 and hardly at pH 7.2 [388, 404].

The 2.2 units are a factor of $10^{2.2} = 158$ in hydrogen ions; one textbook gives “about a hundredfold” [404]. A centriole wall has nine triplets of microtubules, and the shaft of a cilium nine doublets around a central pair [399, 402].

The median protein in mouse cells has a half-life of 46 h, position 44.09 [405]. A liver mitochondrion lasts about 10 days, position 45.60, and a vesicle carried 10 µm at 1 µm/s takes 10 s, position 35.25 [388, 406]. The organelle holds 10 × 86,400 / 10 = 86,400 times as long as the vesicle that carries between membranes.

Order of events

Event	Age	Position	Source
LECA	2,386–1,958 Ma	68.53–68.35	[342]
Primary plastid	2,137–1,807 Ma; about 2.1 Ga plus about 200 Myr	68.42–68.27; 68.41	[342, 353]
Mitochondrial symbiosis	2,053–1,210 Ma	68.39–67.91	[111]
Fossils of cells with a nucleus	about 2,000 Ma	68.36	[343]
Crown red algae	1,984–1,732 Ma	68.36–68.23	[342]
Eukaryote origins in the rock record	1.9–1.4 Ga	68.32–68.04	[356]
Crown eukaryotes	<1.84 Ga	68.29	[111]
Red-algal plastid donor stem	1,675–1,281 Ma	68.20–67.96	[342]
Probable crown red algae, Chitrakoot	1,650 ± 89 Ma	68.19	[355]
Chloroplast symbiosis	>1.5 Ga	68.10	[354]
Eukaryotic photosynthesis, calibrated clock	about 1.25 Ga	67.94	[356]
Serial secondary	1,079–650 Ma	67.80–67.34	[342]

uptakes of red plastids			
Bangiomorpha	1.047 Ga	67.78	[356]
Secondary uptake behind the heterokont plastid	about 1,000 Ma	67.73	[362]
Tertiary plastid in a stem ochrophyte	≤819 Ma (633–1,017)	67.55	[342]
Sulcia in the auchenorrhynchan ancestor	≥260 Ma	66.51	[370, 371]
Buchnera in aphids	250–200 Ma	66.47–66.27	[372]
Sulcia and *Nasuia*; cicada, spittlebug and sharpshooter split	>200 Ma	66.27	[370, 371]
Azolla cyanobiont	≤140 Ma; about 100 Ma; >60 Ma	65.94; 65.64; 65.17	[354, 378, 381]
Paulinella chromatophore, maximum	140–90 Ma	65.94–65.54	[376]
UCYN-A1 and UCYN-A2 split	about 91 Ma	65.55	[377]
Kleptoplasty in slugs, flatworms, ciliates, dinoflagellates	present	—	[339, 357]

From the primary plastid, near 2.0 Ga, to the serial red window, near 0.86 Ga, about 1.1 Gyr pass. From there to *Sulcia* at 0.26 Ga about 0.6 Gyr pass, and from *Sulcia* to the three young cyanobacterial partners at 0.09–0.14 Ga about 0.12–0.17 Gyr. Four primary uptakes are counted in more than 2 Gyr: the mitochondrion, the plastid, the *Paulinella* chromatophore and UCYN-A, with organelle status proposed for the last [210].

What this part of the history shows

One closed ring was taken whole into another, and both went on dividing. The mitochondrion has lived in its host about 2 Gyr, time position 68.36, and still keeps its own ring of 16,569 bp in humans [343, 347]. Two closed forms persist, one inside the other.

The kept genome becomes a letter of the host. *Rickettsia* has 834 protein genes; mitochondria keep 13 to about 100 genes, and more than 95 % of their proteins come from the nucleus [341, 345, 347, 350]. *Synechocystis* has 3,168 protein genes; the *Arabidopsis* plastid keeps 87, and about 4,500 of the same origin sit in the nucleus, 52 for each one kept [200, 358, 359].

“The residue of depth n is the alphabet of depth n+1.” The kept ring holds what the nucleus does not supply. In plants that no longer photosynthesise the list shrinks to 25, then 5–6 genes, then none [357].

The plastid opened once and filled many times. Plastids “evolved from endosymbiotic cyanobacteria on a single occasion”, and that one form was then passed on at least 7 times, and 9 times with three red steps [357]. Green plastids were taken up twice at

second hand, red plastids once or in a chain of three, and dinoflagellates took plastids from haptophytes, green algae and at least 11 diatom species [336, 357, 361].

Partners with their own genome sit at most two deep inside a cell. In the cryptophytes the host holds the remnant alga with its nucleomorph, and the remnant holds the plastid [337, 367]. In the mealybug the insect cell holds *Tremblaya*, which holds *Moranella* with a genome 3.9 times its own [338].

The serial transfer of red plastids has the form of memory with reach two. A red alga passed its plastid to a cryptophyte, a cryptophyte to an ochrophyte and an ochrophyte to a haptophyte, between 1,079 and 650 Ma [342, 361]. Each hand reaches the next only by chaining.

Two closures together make the pair. *Sulcia* and *Nasuia* together make 10 essential amino acids in one leafhopper, and UCYN-A gives fixed nitrogen to its alga for fixed carbon [208, 371]. Neither partner makes the whole alone.

The form lasts while its carriers are replaced. A mouse liver replaces half its mitochondria in 1.83 days, and ATP is used and remade within a minute [151, 387]. A stolen plastid, cut off from the nucleus that made it, still works for 15 days to at least 30 months [357, 383].

The edge carries the tension. Across the 4 nm inner membrane of the mitochondrion stand about 140 mV, a field of 3.5×10^7 V/m, and protons flow back through the synthase as long as the chain pumps [151]. The line keeps one direction: almost all mitochondria come from the egg, so the kept ring passes through the mother [345].

6. Becoming Many

The cells of chapters 2 to 5 lived one by one, or one inside another. This chapter follows the step from single cells to bodies of many cells. The step was taken separately in bacteria, in several eukaryotic supergroups, and in each kingdom that later became interwoven: animals, fungi, land plants, and red and brown algae.

In the terms of chapter 1 the single cell is a ring of depth 6 that divides into two closed halves, each with the parent's direction. A body of many cells is what forms when the halves stay together. The form of the cell is then repeated, and the repeat itself becomes a closure.

Two cases involve a second kingdom directly. A bacterium sets off the colonial stage of the closest living relative of animals [407]. Single-celled predators of another supergroup select for colonies in green algae, in the laboratory [408, 409].

Two ways to become many

Multicellularity "has arisen more than 25 times across the eukaryotic tree of life" [410]. A later review calls a count of 25 "very likely a serious underestimate" [411]. The counts are lower bounds.

Two modes are distinguished. In aggregation, separate cells come together. In the clonal or divisional mode, the cells of one body stay together after division from a single founder.

Aggregative multicellularity "arose independently in at least seven eukaryotic lineages" [410]. They are *Fonticula*, *Copromyxa*, the dictyostelids, the acrasids, *Sorogena*, *Sorodiplophrys* and *Guttulinopsis* [410]. They occur in all major eukaryotic clades except the Archaeplastida, the red and green line [410].

Divisional multicellularity has "numerous origins in both red and green algae, and once at the base of the brown algae" [410]. Within the Amorphea, which hold animals, fungi and Amoebozoa, there are three further origins besides the animal one [410]. Within the Amoebozoa there are two aggregative origins, the dictyostelids and *Copromyxa* [410].

On the bacterial side the multicellular groups are cyanobacteria, myxobacteria and actinomycetes [410]. On the eukaryote side they are the Amorphea (animals, fungi, Amoebozoa, *Fonticula*) and the Archaeplastida (red algae, green algae and land plants). Then come the stramenopiles (brown algae, *Sorodiplophrys*), the alveolates (*Sorogena*) and the Excavata or Discoba (acrasids) [410].

Counts at lower ranks repeat the pattern. In one class of green algae, the Zygnematophyceae, filamentous growth arose "at least five" times [412]. That count rests on 46 taxa and 326 nuclear loci [412].

Complex multicellularity is the form with many cell types and tissues. A "long apparent lag" separates the first simple multicellularity in eukaryotes from the radiation of groups with complex build [413]. Brown algae are "among a small number of eukaryotic

lineages” with complex multicellularity, and the same source counts five groups that reached it [414].

Bacteria first: the cyanobacteria

The oldest multicellular state is bacterial. “The majority of extant cyanobacteria descend from multicellular ancestors” [415]. Fossil comparison supports an origin “possibly as early as” the Great Oxygenation Event, 2.45–2.22 Ga, positions 68.55–68.46 [415].

A follow-up dates the origin “before 2.4 billion years ago”, position 68.53 [416]. It places the Great Oxidation Event at 2.45–2.32 Ga, positions 68.55–68.50, and finds that the origin of multicellularity came with a rise in the rate of diversification [416].

The oxygen rise itself is dated in two ways. Sulfur isotopes in pyrite of three drill cores in South Africa place the transition to permanent oxygen at about 2.33 Ga, position 68.50, “within roughly 10 Myr” [225]. A U–Pb age puts the first global glaciation and the onset at about 2.460–2.426 Ga, positions 68.55–68.54, with oscillations for about 200 Myr until 2.250–2.240 Ga [226].

The oldest conclusive fossils of all five cyanobacterial sections are about 2.15 Ga old, position 68.43 [415]. Fossil akinetes, differentiated resting cells, date to about 2.00 Ga, position 68.36 [415]. A filamentous microfossil candidate from the Panorama Formation is 3.45 Ga old, position 68.86 [415].

Within the cyanobacteria the state was lost and found again. Reversals to single cells occurred “at least 5 times” [415].

Multicellularity was “established again at least once within a single-celled clade”, in *Spirulina* sp. PCC 6313 [415].

The study used 1,254 16S rDNA sequences from 2,065 downloaded, 58 taxa in the reconstruction subset and 10,000 sampled trees [415]. “Many cyanobacteria are multicellular” [417]. In filaments with heterocysts three differentiated cell types stand beside the vegetative cell: the heterocyst for fixing nitrogen, the akinete for resistance and the hormogonium for dispersal [417].

That makes four cell types in one filament. Heterocysts stand “at semi-regular intervals” along the filament [417]. The akinete shows the form of rest inside the filament: one cell holds while the others work.

In the Francevillian B Formation of Gabon, black shales 2.1 Gyr old hold structures “up to 12 cm in size” [418]. They are large colonial organisms with coordinated growth, position 68.41 in time and 13.46 in size [418]. “Geochemical analyses suggest that the sediments were deposited under an oxygenated water column” [418].

The fossils lie “after the 2.45–2.32-Gyr increase in atmospheric oxygen concentration” [418]. The interval from the oxygen rise to the Gabon fossils is $2.33 - 2.1 = 0.23$ Gyr, or $2.46 - 2.1 = 0.36$ Gyr.

Red algae: the oldest named many-celled eukaryote

Bangiomorpha pubescens, from the Hunting Formation of Somerset Island, Arctic Canada, is a bangiacean red alga [419]. It has a differentiated holdfast and spores or gametes [419]. Its Re–Os age is 1.047 +0.013/−0.017 Ga, that is 1.030–1.060 Ga, positions 67.76–67.79 with the centre at 67.78 [356].

An older claim comes from the Tirohan Dolomite of India, at about 1.6 Ga, position 68.16 [355]. *Rafatazmia chitrakootensis* and *Ramathallus lobatus* are there called “probable crown-group red algae” [355]. They show pit connections, apical growth and pyrenoid-like bodies [355].

The red line is thus dated 1.6 Ga, probable, and 1.047 Ga, the accepted bangiacean. Clocks place crown red algae at 1,984–1,732 Ma, positions 68.36–68.23, and the primary plastid at 2,137–1,807 Ma, positions 68.42–68.27 [342]. A clock cross-calibrated on *Bangiomorpha* places eukaryotic photosynthesis at about 1.25 Ga, position 67.94 [356].

The interval from the crown-red-algae clock to *Bangiomorpha* is 1,732 − 1,047 = 685 Myr at the least and 1,984 − 1,047 = 937 Myr at the most. Their positions are 67.39 and 67.67.

Later red algal lines are dated by clock. The root of the Plantae lies at about 1,694 Ma, position 68.21 [420]. The Bangiophyceae and Florideophyceae split at 943 Ma (817–1,049), position 67.68; the Hildenbrandiophycidae follow at 781 Ma, the Nemaliophycidae at 661 Ma and the Corallinophycidae at 579 Ma (543–617) [420].

The smallest red alga, *Cyanidioschyzon merolae*, is a single cell of 2 µm, position 3.44 [360]. It has 20 chromosomes, 16,520,305 bp and 5,331 genes [360]. The red line thus runs from a 2 µm cell to thalli of millimetres in the fossils of 1.6 Ga.

Green seaweeds

Proterocladus antiquus, from the Nanfen Formation of North China, is about 1,000 Ma old, position 67.73 [421]. It is a millimetre-sized, multicellular, branched siphonocladalean chlorophyte [421]. A millimetre lies at position 9.10.

Core Chlorophyta date to about 1,000–700 Ma, positions 67.73–67.41 [422]. The main Ulvophyceae lineages radiated just before or during the Cryogenian, and Bryopsidales and Dasycladales fossils come from the Cambro-Ordovician [422]. The title of that study records “multiple transitions to macroscopic growth in green seaweeds” [422].

Green bodies take many forms. *Chlamydomonas* is a single flagellate cell, *Volvox* a sphere of cells, *Ulva* a sheet, *Acetabularia* a giant cell with one nucleus and *Caulerpa* a giant cell with many [423, 424, 425, 426, 427]. *Proterocladus* is a branched filament [421].

Ulva has three cell types: rhizoid, stem and blade [425]. It becomes able to form gametes after 3–5 weeks, positions 46.27–46.74 [425].

One coenocytic cell of *Caulerpa taxifolia* bears stolons “upwards of 1 m”, position 15.39, and fronds of 15–30 cm, positions 13.66–14.29 [427]. A single cell here reaches the size of a body. The same form stands at the size of a cell and of an organism.

The charophyte *Palaeonitella cranii* of the Rhynie chert is a small multicellular alga with furcating branchlets [428]. Its gyrogonites are built of 6 spiral cells [428].

Fungi: hyphae once, fruiting bodies many times

Fungus-like mycelial filaments occur in vesicular basalt 2.4 Ga old, position 68.53 [429]. The oldest unambiguous fungus, *Ourasphaira giraldae*, is 1,010–890 Ma old, positions 67.74–67.63, from Arctic Canada [430].

A six-gene clock on 199 fungi places crown Fungi at about 1,020 Ma, position 67.75 [299]. The flagellum was lost about 720 Ma, position 67.43 [299]. The same clock gives the Glomeromycota about 659 Ma (715–606), the Dikarya 649 Ma and crown Agaricomycetes 299 Ma (351–252), positions 67.35, 67.34 and 66.63 [299].

A study of 72 genomes compared 4 single-celled fungi, 41 hyphal fungi, 13 yeast-like fungi and 14 relatives outside the fungi [431]. It found 362 gene families of hyphal growth with 651 genes, and 414 gene families that track the evolution of hyphae [431]. Of these, 114 arose at the three candidate nodes that split the Blastocladiomycota, Chytridiomycota and Zoopagomycota [431].

Hyphae “evolved early in fungal evolution”, at one of these nodes or gradually across all three [431]. No expansion of kinases came with the step [431]. The hyphae of 31 soil strains are 2.7–6.5 µm wide, positions 3.72–4.51 [432].

Glomalean hyphae and spores occur in the Ordovician of Wisconsin, about 460 Ma, position 67.03 [433]. *Tortotubus protuberans* is a cord-forming mycelium with septal perforations and a double wall, from the earliest Silurian [434]. The base of the Silurian is 443.8 Ma, position 66.99 [435].

Devonian *Prototaxites* trunks reach 8 m, position 17.28 [436]. The oldest fossil mushroom is from the Lower Cretaceous Crato Formation of Brazil [437]. It is the first from Gondwana and the only one not preserved in amber [437].

The complex form of fungi, the fruiting body, “appears 8–11 times in distinct fungal lineages” [438]. The preprint of the same work gives 8 to 12 origins [438]. Fungi are the only lineage in which complex multicellularity shows signs of convergence [438].

One body of a fungus can cover a forest. A genet of *Armillaria ostoyae* in Oregon covers about 965 ha, with isolates up to about 3,810 m apart, position 22.89 [439]. The side of a square of 965 ha is $\sqrt{(965 \times 10^4\ \text{m}^2)} = 3{,}106$ m, position 22.71.

Against a hyphal width of 5 µm the genet spans $3{,}810 / (5 \times 10^{-6}) = 7.6 \times 10^8$ widths. The thread of one cell and the body of one fungus are the same form at two depths. The hypha arose once, and the fruiting body filled the opened depth 8 to 12 times.

Social amoebae: bodies by aggregation

The dictyostelids form bodies by aggregation. The three sequenced social amoebae split from their last common ancestor “at least 0.6 billion years ago”, position 67.27 [440]. Only about half of their protein-coding genes form an identifiable set of orthologues [440].

The Amoebozoa “diverged from the animal–fungal lineage after the plant–animal split” [441]. The last common ancestor of dictyostelids and animals lived more than one billion years ago, position 67.73 [410].

Dictyostelium discoideum has a genome of 34,042,810 bp in six chromosomes, 77.57 % A+T, with about 12,500 predicted proteins [441]. Its body comes from cells that meet, not from one founder. Aggregation recurs in every major eukaryotic clade except the red and green line [410].

The closest relatives of animals

The choanoflagellates are the single-celled sister group of animals. *Monosiga brevicollis* has a genome of about 41.6 Mb with about 9,200 intron-rich genes, 9,196 gene models [442]. It carries about 6.6 introns per gene, against 7.7 in humans [442].

It holds 78 protein domains found only in choanoflagellates and animals, and at least 23 genes with cadherin domains [442]. It carries about 120 tyrosine kinase domains, about 30 tyrosine phosphatase domains and about 80 SH2 domains [442].

Salpingoeca rosetta has a genome of about 55 Mb with 11,629 genes; the same paper also gives 11,628 [443]. It has at least five differentiated cell types: thecate cells, slow swimmers, fast swimmers, chain colonies and rosette colonies [443]. Rosettes develop by incomplete division, with neighbouring cells joined by bridges [443].

A bacterium sets the switch. The prey bacterium *Algoriphagus machipongonensis*, of the Bacteroidetes, and its relatives induce rosettes in *S. rosetta* [407]. The inducing molecule, RIF-1, is a sulfonolipid [407]. It works at femtomolar concentrations, 10^{-15} M, and *S. rosetta* responds to it over nine orders of magnitude [407].

Rosettes form from a single founding cell, as animals do from a zygote [444]. The mutant *rosetteless* maps to a predicted C-type lectin, a protein that forms an outer coating joining the basal poles of the rosette cells [444].

Chains of cells form “in the absence of RIFs” [445]. Rosettes induced by outer-membrane vesicles of *A. machipongonensis* most often have 8 cells and reach as many as 25 [445]. At steady state 90 % hold 4–12 cells, and 51 % hold 6–8 [445].

A rosette cell has a volume of 105.9 ± 8.8 µm³ when untreated [445]. Its equivalent sphere has a diameter of (6 × 105.9 / π)^(1/3) = 5.87 µm, position 4.42. Mean cell volume drops between the 4- and 5-cell stage and then stays constant; rosette cells divide slightly faster than chain cells (P = 0.03) [445].

The colony keeps the direction of its one founder. It responds to a molecule from a bacterium that the cell eats, at 10^{-15} M, and switches to the colonial form.

Animals

First reading: sponge sterols before 635 Ma. The steranes 24-isopropylcholestane, 24-ipc, are abundant in all formations of the Huqf Supergroup in the South Oman Salt Basin [446]. They lie beneath the Marinoan cap carbonate, older than about 635 Ma, position 67.32 [446]. That study reads them as demosponges before the end of the

Marinoan glaciation [446].

A second sterane, 26-methylstigmastane, 26-mes, occurs with 24-ipc in rocks and oils of the same basin, in a sequence “around 100 Myr long”, position 65.64 [447]. That study calls 26-mes “the first animal-specific sterane” and extends demosponges “at least back to the Cryogenian” [447].

Second reading: the sterane is algal. A later study states that 24-ipc “is not diagnostic for sponges” [448]. Heating algal C29 sterols under simulated burial produced 24-ipc and 24-n-propylcholestane [448]. On that reading the oldest evidence for animals moves to the latest Ediacaran, with the earliest animal-like fossils at about 571 Ma, position 67.22 [448].

In the same window the ocean took in oxygen again. Black shales of the basal Doushantuo Formation of South China, about 635–630 Ma, record “a widely oxygenated ocean” right after the Marinoan glaciation [449].

From the oxygen rise of 2,330 Ma to that second oxygenation, 2,330 − 635 = 1,695 Myr pass, a span at position 68.21 [225, 449].

Bodies. The oldest architecturally complex Ediacaran macrofossils are 574.17 ± 0.66 Ma old, position 67.23, from the upper Drook Formation at Mistaken Point, Newfoundland [450]. The “Brasier” Surface is 567.63 ± 0.66 Ma and the “E” Surface 565.00 ± 0.64 Ma; the youngest rangeomorphs there are no younger than 564.13 ± 0.65 Ma [450]. The section has 76 fossil-bearing horizons, and rangeomorphs with one growing tip appear several Myr before those with many [450].

Dickinsonia is an animal by its sterols, at 558 Ma, position 67.20 [451]. In its largest specimen the sterols are 93 % cholesteroids, 1.8 % ergosteroids and 5.2 % stigmasteroids [451]. Across specimens the cholesteroids run 84.8–93.0 %, rising with size [451].

Host sediment holds 10.6 % cholesteroids in clay and 11.9 % in sandstone, and a microbial mat with *Andiva* 18.7 % [451]. That study calls *Dickinsonia* among “the oldest confirmed macroscopic animals” and gives the Ediacara biota a span of 571–541 Ma, positions 67.22–67.17 [451].

The *Dickinsonia* specimens are 1.0–6.0 cm wide, positions 11.19–12.83, and dickinsoniids reach 1.4 m, position 15.69 [451]. The base of the Cambrian is 538.8 ± 0.2 Ma, position 67.17 [435]. The Chengjiang biota has a maximum depositional age of 518.03 ± 0.69/0.71 Ma, position 67.13, from U–Pb on the youngest detrital zircon in the Maotianshan Shale [452].

The Cambrian explosion as a whole “lasted more than 22 million years”, position 64.26 [452]. The steps are spaced by tens of millions of years.

Marinoan steranes to Ediacaran bodies take 635 − 574 = 61 Myr, Ediacaran bodies to the Cambrian base 574 − 538.8 = 35.2 Myr. The Cambrian base to Chengjiang takes 538.8 − 518.0 = 20.8 Myr; the three spans lie at positions 65.19, 64.69 and 64.21.

A living sponge, *Spongilla lacustris*, without nerves or muscles, has 18 distinct cell types by single-cell RNA sequencing of the whole body [453]. The human reference man, 20–30 years old, 70 kg and 1.70 m, holds 3.0×10^{13} human cells, with 2 % calculated uncertainty and 14 % CV [236]. Of these, red blood cells number 2.5×10^{13}, or 84 %,

and nucleated cells about 0.3×10^{13} [236].

His mean mass per cell is 70 kg / 3.0×10^{13} = 2.3 ng, extracellular mass included.

Land plants

The oldest cryptospores, spores of the first land plants, are Dapingian, about 473–471 Ma, position 67.05, from Argentina [454]. The previous oldest were about 463–461 Ma, position 67.03 [454].

Clocks give three values for crown embryophytes: 515.1–470.0 Ma [455], 515–493 Ma with 68 fossil calibrations [456], and 482 Ma (485–473) [299]. Their positions are 67.13–67.05, 67.13–67.09 and 67.07.

Cooksonia cf. *pertoni* gives a minimum age for crown tracheophytes of 426.9 Ma, position 66.96; a second minimum is 420.7 Ma, position 66.95 [455]. *Baragwanathia longifolia*, the earliest club moss, is Gorstian, in the Ludlow of the Silurian [457].

The Rhynie chert has a U–Pb age of 411.5 ± 1.3 Ma, position 66.93 [458]. A second study places *Asteroxylon mackiei* from the same chert at “407 Ma”, position 66.92 [459].

Land plants then grew tall. The tallest moss, *Dawsonia superba*, has stems of 65 cm, position 14.99 [460]. Carboniferous arborescent lycopsids reached about 45 m, position 18.85, with trunks of 2 m, position 16.02 [461].

The tallest tree measured is a *Sequoia sempervirens* of 112.7 m, position 19.69 [462]. The mechanical limit to tree height is 122–130 m, positions 19.76–19.82 [462].

One clone can form a forest. The aspen *Pando* covers 43–43.6 ha with about 47,000 ramets [463]. The side of a square of that area is 656–660 m, positions 21.29–21.30.

Brown algae: one late origin, the largest seaweeds

The accepted brown-algal fossils are Cretaceous and younger [365]. The oldest calibration fossil is *Padina* of the Dictyotales, at a minimum of 100 Ma, position 65.64 [365]. The 550 Ma *Miaohephyton* is not counted as a brown alga [365].

The clock origin of brown algae is 449.41 Ma (333.85–572.02), position 67.01 (66.73–67.23) [365]. Uncorrelated clocks give 435–455 Ma and autocorrelated ones 595–600 Ma, positions 66.98–67.02 and 67.26–67.27 [365].

Crown Laminariales is 83.44 or 231.51 Ma, positions 65.47 or 66.40, under the two clock models [365]. Crown Fucales is 65.81 or 134.28 Ma, positions 65.26 or 65.91 [365]. Brown algae reached divisional multicellularity once, at the base of the group [410].

Ectocarpus siliculosus has a genome of 214 Mbp with 16,256 protein-coding genes [414]. Its receptor kinases form a clade apart from those of animals and green plants [414]. Receptor-kinase evolution is read as key to complex multicellularity in “at least three of the five” groups that reached it [414].

The giant kelp *Macrocystis pyrifera* “may become more than 60 meters long”, position 19.11 [365]. It emerged about 6 Ma, position 63.08, and has a genome of 537 Mb with 25,919 genes [464]. Its fronds grow 12.8–23.3 cm per day, positions 13.52–14.06 [465].

Its mass rises 3.5 % per day [464]. The doubling time is ln 2 / ln 1.035 = 20.1 days, position 46.23. Brown algae number 2,125 species, 46 % of 4,619 non-diatom heterokonts in AlgaeBase [365].

Volvocine algae: becoming many in steps

The volvocine origin is dated four ways. One study gives an ancestor of *Volvox* and *Chlamydomonas* at about 50 ± 20 Ma, position 65.01 (64.54–65.31) [466]. Another gives “around 250 MY”, position 66.47 [424].

A third gives “about 230 million years ago”, position 66.40 [467]. A fourth dates the split of the multicellular volvocine lineage to “at least 200 million years ago”, position 66.27, against earlier estimates of 50–75 Ma, positions 65.01–65.38 [468].

Chlamydomonas reinhardtii is a single cell of 10 µm, position 4.91 [423]. Its genome is 121 Mb with 15,143 protein-coding genes [423]. *Gonium* colonies hold 8 or 16 cells, and the *Gonium pectorale* genome has 120.9 genes per Mb [467].

Volvox carteri holds about 2,000 somatic cells and 12–16 gonidia, in two cell types, with a new generation every 48 h, position 44.13 [424]. Its spheroid is “several hundred microns” across, and its two cell types make a “germ-soma division of labor” [424, 466]. Its genome is 138 Mb with about 14,500 predicted proteins [469].

A body of 2,000 cells thus has 14,500 / 15,143 = 0.958, 4 % fewer, predicted proteins than its single-celled relative.

Expressing the *Gonium* retinoblastoma gene in single-celled *Chlamydomonas* gave colonies of 2–16 cells [467]. The volvocine step is modelled as at least 12 steps in three phases: cell-cycle control to form groups, increase in size, and division into germ and soma [467]. Five of the steps concern forming groups of cells [467].

Becoming many in the laboratory

The green alga *Chlorella vulgaris* had been single-celled for thousands of generations in culture [408]. It was exposed to the phagotrophic flagellate *Ochromonas vallescia*, a stramenopile [408]. Globose clusters of tens to hundreds of cells appeared first [408].

Eight-celled colonies predominated after about 10–20 generations with the predator [408]. A multicellular form dominated “within less than 100 generations” [408]. The eight-celled colonies were nearly immune to the predator while each cell still touched the medium, and the form persisted in continuous culture and on agar [408].

Chlamydomonas reinhardtii was placed under predation by the ciliate *Paramecium tetraurelia*, an alveolate [409]. Five selected populations and three unselected controls ran for about 750 asexual generations: 50 weekly transfers, about 350 days, position 48.83 [409].

Two of the five selected populations evolved multicellular structures absent from the controls [409]. Their propagules were nearly all 4, 8 or 16 cells, some up to 64 [409]. Median cluster size at maximum growth was 1–6.2 cells [409].

Snowflake yeast, *Saccharomyces cerevisiae*, went through 600 rounds of selection for size, 600 days at one transfer a day, position 49.32 [470]. The anaerobic line grew about 20,000-fold in size, to millimetre scale, and about 10,000-fold in toughness [470]. The low-oxygen line stayed microscopic, at about 6-fold; about 3 % of cells survive each daily transfer [470].

The same selection gave two outcomes in two surroundings: the same rule takes other values in other surroundings. Under predators the colonies came to the same counts: 4, 8, 16 and up to 64 cells.

The size of life

The maximum size of life rose about 16 orders of magnitude over more than 3.5 Gyr [471]. Most of the rise came in two steps of about equal size, about 16 / 2 = 8 orders each [471]. The first step fell at about 1.9 Ga, position 68.32, after the eukaryotic cell; the second at 0.6–0.45 Ga, positions 67.27–67.01, after multicellularity [471].

Both steps coincide with or slightly follow rises in atmospheric oxygen [471]. The bodies measured in this chapter span 2 µm to more than 3 km.

Body	Size	Position	Source
Cyanidioschyzon merolae, single red alga	2 µm	3.44	[360]
Fungal hypha, narrowest of 31 strains	2.7 µm	3.72	[432]
S. rosetta cell, equivalent sphere	5.87 µm	4.42	[445]
Fungal hypha, widest of 31 strains	6.5 µm	4.51	[432]
Chlamydomonas reinhardtii	10 µm	4.91	[423]
Proterocladus antiquus	about 1 mm	9.10	[421]
Evolved snowflake yeast cluster	about 1 mm	9.10	[470]
Dickinsonia, narrowest and widest	1.0–6.0 cm	11.19–12.83	[451]
Gabon colonial fossils	up to 12 cm	13.46	[418]
Macrocystis frond growth per day	12.8–23.3 cm	13.52–14.06	[465]
Caulerpa taxifolia frond	15–30 cm	13.66–14.29	[427]
Dawsonia superba stem	65 cm	14.99	[460]
Caulerpa taxifolia stolon, one cell	1 m	15.39	[427]
Dickinsoniids, largest	1.4 m	15.69	[451]

Human reference man, height	1.70 m	15.87	[236]
Carboniferous lycopsid trunk, width	2 m	16.02	[461]
Prototaxites trunk	8 m	17.28	[436]
Carboniferous lycopsid, height	45 m	18.85	[461]
Macrocystis pyrifera, length	>60 m	19.11	[365]
Sequoia sempervirens, tallest tree	112.7 m	19.69	[462]
Tree height, mechanical limit	122–130 m	19.76–19.82	[462]
Pando clone, side of a square of its area	656–660 m	21.29–21.30	[463]
Armillaria ostoyae genet, side of a square of its area	3,106 m	22.71	[439]
Armillaria ostoyae genet, greatest distance between isolates	3,810 m	22.89	[439]

From the 2 µm red alga to the 3,810 m fungus the ladder runs from position 3.44 to 22.89, about 19.45 steps of three. The cell itself spans part of this range: one cell of *Caulerpa* reaches 1 m.

Body	Cells	Cell types	Source
Chlamydomonas; *Cyanidioschyzon*	1	1	[360, 423]
Chlamydomonas with RB gene of *Gonium*	2–16	1	[467]
Chlamydomonas under ciliate predation	4, 8, 16, up to 64	1	[409]
Chlorella under flagellate predation	8	1	[408]
S. rosetta rosette	4–25, mostly 8	at least 5 in the life cycle	[443, 445]
Gonium pectorale	8 or 16	1	[467]
Volvox carteri	about 2,000 + 12–16	2	[424]
Heterocystous cyanobacterial filament	many	4	[417]
Ulva	many	3	[425]
Spongilla lacustris	—	18	[453]
Human reference man	3.0×10^{13}	—	[236]

Order of events

Event	Age	Position	Source
Filamentous microfossil	3.45 Ga	68.86	[415]

candidate, Panorama Formation			
Oxygen rise, onset	2.460–2.426 Ga	68.55–68.54	[226]
Multicellular cyanobacteria	2.45–2.22 Ga; before 2.4 Ga	68.55–68.46; 68.53	[415, 416]
Fungus-like filaments in basalt	2.4 Ga	68.53	[429]
Permanent atmospheric oxygen	about 2.33 Ga	68.50	[225]
Conclusive fossils of all five cyanobacterial sections	about 2.15 Ga	68.43	[415]
Primary plastid, clock	2,137–1,807 Ma	68.42–68.27	[342]
Gabon colonial organisms	2.1 Ga	68.41	[418]
Fossil akinetes	about 2.00 Ga	68.36	[415]
Crown red algae, clock	1,984–1,732 Ma	68.36–68.23	[342]
First step in maximum size	about 1.9 Ga	68.32	[471]
Root of Plantae, clock	about 1,694 Ma	68.21	[420]
Probable crown red algae, India	about 1.6 Ga	68.16	[355]
Eukaryotic photosynthesis, calibrated clock	about 1.25 Ga	67.94	[356]
Bangiomorpha pubescens	1.047 Ga	67.78	[356]
Crown Fungi, clock; *Ourasphaira*	about 1,020 Ma; 1,010–890 Ma	67.75; 67.74–67.63	[299, 430]
Ancestor of dictyostelids and animals	>1,000 Ma	67.73	[410]
Proterocladus	about 1,000 Ma	67.73	[421]
Core Chlorophyta	1,000–700 Ma	67.73–67.41	[422]
Bangiophyceae–Florideophyceae split	943 Ma (817–1,049)	67.68 (67.55–67.78)	[420]
Hildenbrandiophycidae	781 Ma	67.51	[420]
Flagellum lost in fungi	about 720 Ma	67.43	[299]
Nemaliophycidae; Glomeromycota; Dikarya	661; 659; 649 Ma	67.36; 67.35; 67.34	[299, 420]
24-ipc and 26-mes steranes	>635 Ma	67.32	[446, 447, 448]
Second oxygenation, Doushantuo	635–630 Ma	67.32–67.31	[449]
Dictyostelid lineages split	≥0.6 Ga	67.27	[440]
Corallinophycidae	579 Ma (543–617)	67.24 (67.18–67.29)	[420]
First complex Ediacaran macrofossils	574.17 Ma	67.23	[450]

Start of the Ediacara biota	571 Ma	67.22	[448, 451]
Dickinsonia with animal sterols	558 Ma	67.20	[451]
Base of the Cambrian	538.8 Ma	67.17	[435]
Chengjiang biota	≤518.03 Ma	67.13	[452]
Crown embryophytes, clocks	515–470 Ma	67.13–67.05	[299, 455, 456]
Oldest cryptospores	473–471 Ma	67.05	[454]
Glomalean hyphae and spores	about 460 Ma	67.03	[433]
Brown algae, clock	449.41 Ma	67.01	[365]
Tortotubus cords, after the Silurian base	<443.8 Ma	66.99	[434, 435]
Crown-tracheophyte minima	426.9 and 420.7 Ma	66.96; 66.95	[455]
Rhynie chert plants and charophytes	411.5 or 407 Ma	66.93; 66.92	[428, 458, 459]
Crown Agaricomycetes, clock	299 Ma	66.63	[299]
Volvocine colonies	about 250, 230, ≥200 or 50 Ma	66.47; 66.40; 66.27; 65.01	[424, 466, 467, 468]
Padina, oldest brown-alga calibration fossil	≥100 Ma	65.64	[365]
Macrocystis emerged	about 6 Ma	63.08	[464]

What this part of the history shows

A ring that divides into two closed halves becomes a body when the halves stay together. At the threshold the colonies hold 2–16 cells with the *Gonium* gene, up to 64 under a ciliate, and mostly 8 in rosettes and *Chlorella* [408, 409, 445, 467]. *Volvox* reaches about 2,000 somatic cells and a human 3.0×10^{13} cells [236, 424].

The clonal body has one direction: “A living strand has one direction or it does not exist.” Rosettes grow from one founding cell, as animals do from a zygote [444]. A body made by aggregation comes instead from many cells that meet, and it is absent from the red and green line [410].

Becoming many opened once, in the cyanobacteria, and the opened depth was then filled many times. More than 25 origins are counted across eukaryotes, at least 7 by aggregation and at least 5 for filaments in one green class [410, 412]. In fungi the hypha arose early and once, and the fruiting body then filled that depth 8–11 or 8–12 times [431, 438].

Brown algae reached the many-celled form once, at the base of the group, and now number 2,125 species [365, 410]. The red line holds the oldest named many-celled eukaryote, *Bangiomorpha* at 1.047 Ga [356]. Cyanobacteria were many-celled first, at 2.45–2.22 Ga, lost the state at least 5 times and found it again at least once [415].

The same form stands at several depths. One cell of *Caulerpa* bears stolons of 1 m and fronds of 15–30 cm, the size of a body [427]. One genet of *Armillaria* spans 3,810 m, 7.6 × 10^{8} hyphal widths, and one aspen clone holds about 47,000 ramets [439, 463].

The same rule takes other values in other surroundings. Selected for size, snowflake yeast grew 20,000-fold in the anaerobic line and 6-fold in the low-oxygen line [470]. Both steps in the maximum size of life coincide with or slightly follow rises in oxygen, and the 12 cm colonies of Gabon lay under an oxygenated water column [418, 471].

Other organisms set the switch. A sulfonolipid of a prey bacterium switches *S. rosetta* to rosettes from 10^{-15} M, over nine orders of magnitude [407]. A predator of another supergroup turns single green cells into eight-celled colonies within 10–20 generations [408].

Rest stands inside the body. In heterocystous filaments the akinete holds as a resting cell beside the working cells, and fossil akinetes are about 2.00 Ga old [415, 417]. In *Volvox* 12–16 gonidia carry the next generation while about 2,000 somatic cells carry the body [424].

The bodies spread over 19 steps of the ladder, from a 2 µm cell at position 3.44 to a 3,810 m fungus at 22.89 [360, 439]. The maximum size of life rose 16 orders of magnitude in two steps, at about 1.9 Ga and 0.6–0.45 Ga [471].

7. The First Animals

Chapter 6 followed the step from one cell to many cells. Several lineages took it. One of them built bodies that pump water, move, eat other bodies and carry nerve cells: the animals.

This chapter tells their early history. It runs from the single-celled sister of animals, through the first split of the animal tree and the Ediacaran bodies, to the phyla of the Cambrian. It then follows the groups that keep a simple body plan to the present day.

Four kinds of evidence carry the story: molecules in rocks, molecular clocks, fossils and living animals. Each gives its own dates. Every age is placed on the ladder of chapter 1 as a duration, an age of A million years being $A \times 10^6 \times 3.15576 \times 10^7$ s.

The parts before the animal

Animals and their unicellular relatives diverged “more than 800 million years ago”, position 67.53, by a clock [472]. No fossil records the split. The stem from that split to the crown animals lasted about 150–200 million years, positions 66.01–66.27 [473].

That stem carried about 28 % of the substitutions between humans and choanoflagellates [473]. On it 235 animal-specific protein domains and 769 animal-specific domain combinations arose [473]. Of 4,670 gene families shared across animals, 1,286 are found only in animals; 1,286 / 4,670 = 27.5 % [473].

Many parts of the later nerve cell were already present before the animal. The post-synaptic scaffold proteins Shank, Homer and DLG and some of their partners “were acquired in a unicellular ancestor” of choanoflagellates and animals [474]. That scaffold emerged in a single cell and was probably not involved in signalling between cells [474].

The choanoflagellate *Monosiga brevicollis* carries Shank, Homer, DLG, CaMKII, Citron, Cortactin, the Ephrin receptor, IP_3R, PKCαβγ and Shaker K^+ channels [474]. Three DLG partners, CRIPT, Shaker and PMCA, have clear orthologues in it [474]. The mammalian post-synaptic density, for comparison, holds about one thousand proteins [474].

The Munc18/syntaxin-1 complex was once known only from nerve tissue [475]. It is present in *Monosiga* and is “structurally and functionally very similar” to the vertebrate complex [475]. This secretion machinery of the common ancestor was later taken up for synaptic work [475].

All voltage-gated channel families are present in choanoflagellates [148]. *Monosiga* has one low-voltage (T-type) and one high-voltage calcium channel, putative Kv channels and a Nav-like channel [148]. The selectivity filter of its sodium-channel homologue lies between those of calcium and sodium channels [476].

The *Monosiga* genome is about 41.6 Mb, with about 9,200 genes in 9,196 gene models [442]. It holds 78 protein domains otherwise found only in animals, at least 23 cadherin genes, about 120 tyrosine kinase domains and about 80 SH2 domains [442]. It has 58 PDZ-domain genes against 66 in the sea anemone *Nematostella*; 15 are orthologous

between the two, 7 with the same full domain architecture [477].

At least 54 PDZ genes are inferred for the ancestor of the eumetazoans [477]. Immunoglobulin-like proteins number 5 in *Monosiga* and 218 in the sponge *Amphimedon*, 218 / 5 = 44 times more [473].

The colonial choanoflagellate *Salpingoeca rosetta* has a cell volume of 105.9 ± 8.8 µm³ [445]. A sphere of that volume has a diameter of (6 × 105.9 / π)^(1/3) = 5.87 µm, position 4.42. Its rosettes hold 4–25 cells, mostly 8, and its genome is about 55 Mb with 11,629 genes [445][443].

The chromosomes keep an older order. The 2023 linkage study counts 31 ancestral animal synteny groups of 5–29 genes each, holding 291 of 2,474 orthology groups, which is 12 % [472]. Of the 31 groups, 29 are shared with *Capsaspora*, 20 with *Salpingoeca* and 8 with *Creolimax* [472].

Haploid chromosome numbers are 36 in *Salpingoeca*, 16 in *Capsaspora* and 26 in *Creolimax* [472]. About 1 % of genes move to another chromosome every 40 million years, position 64.80 [472].

Here the form is that of the residue becoming the alphabet: what closed in the single cell becomes a letter of the next closure. Scaffold, secretion complex and channels were whole before any nerve cell; the animal body uses them as its alphabet.

The first split of the animal tree

Which living group branched first is read in two ways. Four publications place the comb jellies (ctenophores) as sister to all other animals [478][479][480][472]. Three place the sponges there: a review of 2015 and studies of 2017 and 2021 [481][482][483].

The comb-jelly reading rests on the *Mnemiopsis* genome, the *Pleurobrachia* genome and 27 new transcriptomes [478][479][480]. A fourth study found seven derived chromosome fusions shared by sponges, cnidarians and bilaterians but not by comb jellies; 4 of them are fusions with mixing, and the posterior for comb-jelly-first is 1.0 [472]. It names the clade of all other animals Myriazoa [472].

The sponge reading rests on 1,719 genes under a site-heterogeneous model, which “strongly” supports sponges first and comb jellies second [482]. Partitioned analyses with recoding recover sponges first with 95 % and 99 % support in two datasets, and placozoans first weakly, at 52 %, in a third; each test set held 133–146 genes [483]. The 2015 review finds a single origin of nerve cells “compatible” with shared traits and states that the data “do not strongly challenge” sponges first [481].

Placozoans move between positions. In the 2008 genome analysis they group with cnidarians and bilaterians, with sponges earliest [484]. Moving them around the eumetazoan node “has a profound impact on the estimated age of the root” [485].

One clock study gives intervals for the main nodes [485]. Each interval is wide.

node	interval	positions	width	width position
crown Metazoa	833.5–649.8 Ma	67.57–67.34	184 Myr	66.19
crown Eumetazoa	746.2–625.9 Ma	67.47–67.31	120 Myr	65.81

crown Bilateria	688.3–595.7 Ma	67.39–67.26	93 Myr	65.57
crown Deuterostomia	662.3–587.2 Ma	67.36–67.25	75 Myr	65.38
crown Protostomia	653.1–578.1 Ma	67.35–67.23	75 Myr	65.38
crown Cnidaria	641.8–531.5 Ma	67.33–67.16	110 Myr	65.73

The widths are 833.5 − 649.8 = 183.7, 746.2 − 625.9 = 120.3, 688.3 − 595.7 = 92.6, 662.3 − 587.2 = 75.1, 653.1 − 578.1 = 75.0 and 641.8 − 531.5 = 110.3 Myr. In the same work crown animals arise in the Cryogenian, and most bilaterian phyla diversify in the Ediacaran [485]. Bilaterian phyla diverged more than 100 million years before the Cambrian, so before 538.8 + 100 = 638.8 Ma, position 67.33 [485][435].

A second clock, built on sponges, gives crown Metazoa at 781 Ma, with a 95 % interval of 718–838 Ma, position 67.51 [486]. The two clock readings for the crown animals, 833.5–649.8 Ma and 718–838 Ma, overlap between 718 and 833.5 Ma.

Sponges

Traces in the rock

Sponges (Porifera) are animals without nerve cells and without muscles [453]. They filter water through choanocyte chambers, groups of collared cells [487]. Their record begins as molecules.

The sterane 24-isopropylcholestane (24-ipc) is abundant in all formations of the Huqf Supergroup, South Oman Salt Basin [446]. These strata lie below the Marinoan cap carbonate and are older than about 635 Ma, position 67.32. The authors read them as demosponges before the end of the Marinoan glaciation [446].

A second sterane, 26-methylstigmastane (26-mes), occurs with 24-ipc in rocks and oils of the same basin [447]. The sequence spans “around 100 Myr”, position 65.64. 26-mes is called “the first animal-specific sterane”, and demosponges are taken back “at least to the Cryogenian” [447].

A second reading gives these molecules to algae. Simulated diagenesis of algal C29 sterols produced 24-ipc and 24-n-propylcholestane, so 24-ipc “is not diagnostic for sponges” [448]. On this reading the oldest animal evidence moves to the latest Ediacaran, with the earliest animal-like fossils at about 571 Ma, position 67.22 [448].

Body fossils of claimed sponges come in a series. At about 890 Ma, position 67.63, millimetre-to-centimetre “possible poriferan body fossils” occur in the Little Dal reefs, Stone Knife Formation, Northwest Territories, Canada [488]. If accepted, they are about 350 Myr older than the next undisputed sponge body fossils, which are Cambrian; 350 Myr has position 66.78 [488].

At about 760 Ma, position 67.48, sponge-like fossils named *Otavia* occur in Namibian rocks dated between about 760 and 550 Ma [489]. The authors move the origin of animals “some 100 to 150 million years earlier” than the 600–650 Ma held before [489]. At about 600 Ma, position 67.27, *Eocyathispongia qiania* from the Doushantuo Formation, South China, is one three-dimensional specimen of hundreds to thousands of cells [490].

Eocyathispongia has three hollow tubes on a common base. Its surface carries flat, tile-like cells like the pinacocytes of living sponges, and it is “probably poriferan” [490]. It is slightly over 1.2 mm wide, position 9.26, and 1.1 mm high, position 9.19 [490].

Precambrian spicules are claimed from the Doushantuo Formation of China, the Kuibis Formation of Namibia and the Tsagaan Oloom Formation of Mongolia [486]. Each is a single occurrence or of questioned veracity [486]. The first uncontested spicules are Lower Cambrian, about 520 Ma, position 67.14 [486].

The first accepted crown-group sponge is *Helicolocellus cantori* from the Dengying Formation, South China, about 551–539 Ma, positions 67.19–67.17 [491]. It has a goblet-shaped body more than 0.4 m high, position 14.55. Its body wall is a nested grid of at least three orders [491].

The claimed first appearances fall at 890, 760, 600, 551 and 520 Ma. The steps between them are 890 − 760 = 130, 760 − 600 = 160, 600 − 551 = 49 and 551 − 520 = 31 Myr. Their positions are 65.88, 66.07, 64.99 and 64.57.

Sponge clocks

One clock study gives node ages with 95 % intervals under a soft bound [486]. Metazoa is 781 (718–838) Ma, Silicea 759 (698–832) Ma, Demospongiae 699 (660–749) Ma and Calcarea + Epitheliozoa 754 (695–820) Ma. Calcarea is 487 (433–539) Ma, given as 488 Ma in the discussion, and Hexactinellida 418 (291–515) Ma [486].

Under a hard maximum of 713 Ma the same study gives Silicea 740 (683–789) Ma and Demospongiae 692 (650–711) Ma [486]. Hexactinellida becomes 440 (326–543) Ma and Calcarea 475 (382–564) Ma [486].

node	soft bound	position	hard bound	position
Metazoa	781 (718–838) Ma	67.51	—	—
Silicea	759 (698–832) Ma	67.48	740 (683–789) Ma	67.46
Calcarea + Epitheliozoa	754 (695–820) Ma	67.48	—	—
Demospongiae	699 (660–749) Ma	67.41	692 (650–711) Ma	67.40
Calcarea	487 (433–539) Ma	67.08	475 (382–564) Ma	67.06
Hexactinellida	418 (291–515) Ma	66.94	440 (326–543) Ma	66.99

The study names a gap between the origin of siliceous spicules and their first unequivocal fossils: about 240 Myr in the text, position 66.43, and 200 Myr in the title, position 66.27 [486]. Without the glass sponges about 140 Myr remains, position 65.94; the Mongolian or Namibian spicules would shorten it by only about 30 Myr, position 64.54 [486]. From the Silicea node at 759 Ma to the first uncontested spicules at 520 Ma is 759 − 520 = 239 Myr, position 66.43.

Carnivorous cladorhizid and freshwater spongillid demosponges diverged about 450 Ma, position 67.01, by the linkage clock [472]. Sponges “diverged from other animals more than 600 million years ago”, position 67.27 [473].

The living sponge

Four classes are recognised: Demospongiae, Hexactinellida (glass sponges), Calcarea

and Homoscleromorpha [492]. The sizes run over five orders of magnitude.

what	size	position
choanocyte chamber, *Cliona delitrix*	16.0 µm	5.33
choanocyte chamber, *Callyspongia vaginalis*	19.7 µm	5.52
choanocyte chamber, *Tethya californiana*	21.1 µm	5.59
choanocyte chamber, *Neopetrosia problematica*	23.3 µm	5.68
choanocyte chamber, *Haliclona mollis*	28.5 µm	5.86
choanocyte chamber, *Haliclona permollis*	30 µm	5.91
choanocyte chamber, *Aphrocallistes vastus*	56 µm	6.47
homoscleromorph spicules, usually	100 µm or less	7.00
ordinary spicules, all classes	0.01–1 mm	4.91–9.10
Eocyathispongia qiania (fossil), height	1.1 mm	9.19
Monorhaphis chuni giant spicule, diameter	up to 10 mm	11.19
Sycon ciliatum, diameter	0.03 m	12.19
Helicolocellus cantori (fossil), height	more than 0.4 m	14.55
Sycon ciliatum, largest calcareous sponge, length	over 0.50 m	14.76
Xestospongia muta, largest of 12 transects, diameter	0.98 m	15.37
Xestospongia muta, same sponge, height	1.23 m	15.57
Monorhaphis chuni giant spicule, length	up to 3 m	16.39

[487][492][490][493][494][491][495]

Most calcareous sponges measure millimetres to a few centimetres [492]. The longest spicule is 3 m / 10 µm = 3×10^5 times the smallest ordinary spicule. From the 1.1 mm fossil to the 1.23 m barrel sponge, length spans a factor of 1.23 / 0.0011 = 1,118.

The barrel sponges of the transects had volumes of 24.05 to 80,281.67 cm³, that is 2.4×10^{-5} to 8.0×10^{-2} m³ [495]. The deepest recorded sponge is a carnivorous species at 8,840 m below the surface, position 23.66 [492].

The filter unit repeats. Seven species have counted chambers, collars and microvilli [487].

species	chamber diameter	chambers per mm³	collars per chamber	microvilli per collar
Haliclona permollis	30 µm	12,000	95	28

Aphrocallistes vastus	56 µm	1,876	260	38
Neopetrosia problematica	23.3 µm	9,792	80	40
Haliclona mollis	28.5 µm	2,684	139	40
Tethya californiana	21.1 µm	14,403	99	39
Callyspongia vaginalis	19.7 µm	14,358	93	33
Cliona delitrix	16.0 µm	35,175	50	33

Collars per chamber range 50–260, a factor 260 / 50 = 5.2. Microvilli per collar range 28–40, a factor 40 / 28 = 1.4. Chamber density ranges 1,876–35,175 per mm³, a factor 35,175 / 1,876 = 18.8: the smallest chambers stand densest and the largest sparsest [487].

Sponges “can filter up to 900 times their body volume of water per hour” [487].

Excurrent jets run at 11.04 ± 0.54 cm s^{-1} in *Cliona delitrix*, 5.93 ± 0.67 in *Callyspongia vaginalis* and 3.04 ± 0.30 in *Haliclona mollis* [487]. They run at 1.95 ± 0.30 in *Tethya californiana* and 1.37 ± 0.25 cm s^{-1} in *Neopetrosia problematica*. The fastest is 11.04 / 1.37 = 8.1 times the slowest.

Volume flow per sponge volume runs from 0.09 ± 0.007 L h^{-1} mL^{-1} in *T. californiana* to 1.13 ± 0.18 L h^{-1} mL^{-1} in *C. vaginalis* [487]. The upper value is 1.13 L = 1,130 mL per mL per hour, 1,130 body volumes per hour, beside the 900 of the abstract. At 150 m below the surface, position 19.95, the glass sponge *Aphrocallistes vastus* filtered two-thirds of the water during short bursts of high ambient current, with excurrent flow following ambient current ($r > 0.75$) [496].

Whole-sponge respiration and pumping power were measured in five species [487]. Pumping cost is given under two models.

species	respiration	pumping power (two models)	cost, % of respiration (two models)
Neopetrosia problematica	87 µW	3 µW	3.70 / 3.99
Haliclona mollis	790 µW	15 / 8 µW	1.89 / 1.01
Tethya californiana	1,396 µW	11 µW	0.80 / 0.74
Callyspongia vaginalis	14,218 µW	504 / 766 µW	3.54 / 5.38
Cliona delitrix	42,102 µW	6,377 / 5,038 µW	15.15 / 11.97

Respiration rises from 87 to 42,102 µW, a factor 42,102 / 87 = 484. The text gives 1–15 % (or 1–12 %) of respiration for pumping, earlier estimates give below 1 %, and at modest rates pumping requires at least 28 % [487][496]. Oxygen removal runs from 0.71 ± 0.12 to 49.72 ± 15.87 µmol O_2 h^{-1} g^{-1} dry mass [487].

Per volume it runs from 0.23 ± 0.04 to 3.12 ± 0.99 µmol O_2 h^{-1} mL^{-1}. Filtration per oxygen is 0.42 ± 0.03 L $µmol^{-1}$ in *C. vaginalis* and 0.40 ± 0.18 L $µmol^{-1}$ in *C. delitrix* [487].

The water passes; the chamber stays. Here the form is that of metabolism in chapter 1: the content flows through a thousand body volumes an hour while the filter holds its

shape.

The freshwater sponge *Spongilla lacustris* has 18 cell types by whole-body single-cell sequencing [453]. They include contractile pinacocytes sensitive to nitric oxide, amoeboid phagocytes and secretory “neuroid” cells beside the digestive choanocytes [453]. The neuroid cells hold secretory vesicles and send projections that wrap the microvilli and cilia of the choanocytes [453].

The demosponge *Amphimedon queenslandica* has a “nearly complete set of post-synaptic protein homologs” among 36 gene families analysed [477]. Present are dlg, Shank, Homer, GRIP, CRIPT, GKAP, PICK1 and several metabotropic glutamate receptors [477]. Absent are the whole ionotropic glutamate receptor family, Shaker-type Kv channels and neuroligin [477].

The 13 ligand-binding residues of the dlg PDZ domains are 100 % the same in sponge and human [477]. Within the domain about 88.5 % is conserved across four animals, against about 68 % for the rest; rat and sponge PDZ3 are about 50 % identical [477]. Five scaffold genes, DLG, HOMER, GRIP, CRIPT and GKAP, are expressed together in larval flask cells and in no other larval cell [477].

Amphimedon has 705 kinases, more than 150 of them receptor tyrosine kinases, and more than 200 G-protein-coupled receptors [473]. It has 3 Wnt, 2 Frizzled, 8 TGF-β ligands, 5 TGF-β receptors, 1 Notch and 5 Delta genes [473]. Its genome is about 167 Mb with about 30,000 predicted loci, a number its authors call an overestimate; 18,693 loci, 63 %, have Swiss-Prot homologues [473].

It has homologues of proneural proteins, metabotropic glutamate, dopamine and serotonin receptors, and an ephrin receptor without its ligand [473]. It has only two-transmembrane Kir potassium channels, no Kv and no Nav homologue [148]. Bilaterian peptide hormones were not detected [473].

Amphimedon has eight NK-like homeobox genes; six lie within 71 kb in a bilaterian-like order [497]. A commentary counts seven NK genes [498]. The sponge has no Hox, ParaHox or EHGbox genes, and 32 homeodomain genes in all [497][479].

The NK cluster of the sponge–cnidarian–bilaterian ancestor held at least five genes [497]. The calcisponge *Sycon raphanus* has a single NK2 gene and a possible Hmx orthologue [498]. Glass sponges keep relicts of 10 of the 29 bilaterian–cnidarian–sponge linkage groups [472].

The glass sponge *Rhabdocalyptus dawsoni* conducts all-or-none impulses through a syncytial trabecular tissue at 0.27 ± 0.1 cm s^{-1} at 10 °C [499]. After an impulse it cannot fire again for 29 s, position 36.22, the absolute refractory period [499]. A relative refractory period follows to 95–100 s, positions 37.30–37.34.

The refractory period has the form of a closure that cannot load twice in succession. A second impulse waits until the first has discharged.

Sponges live long. The giant basal spicule of *Monorhaphis chuni* records a lifespan of 11,000 ± 3,000 years, position 57.34, from oxygen-isotope and Mg/Ca temperature trends since the Last Glacial Maximum [494]. A conference abstract on the same spicules gives “several thousand years” and a warming of about 3 °C over the lifespan [493].

AnAge lists *Scolymastra joubini* at 15,000 years, position 57.62, with quality "questionable" [500]. One 2 m specimen in the Ross Sea, position 16.02, was estimated at 23,000 years, position 58.01, and is held unlikely to exceed 15,000 years because of Ross Sea level history [500].

In the Florida Keys, 104 tagged *Xestospongia muta* were followed for 4.5 years, position 50.24, from 1997; 33 were measured at 6-month intervals [495]. Mean specific growth was 0.52 ± 0.65 yr^{-1}, range 0.02–4.04 yr^{-1}, a factor 4.04 / 0.02 = 202 [495].

The largest sponge of the transects, 1.23 m, is estimated at 127 years, position 53.28 [495]. Barrel sponges "may exceed 2,300 years", position 55.92. Giant ones are given as "2,000 years or more", position 55.79 [492].

Amphimedon larvae swim "after several hours in the water column" before they settle [501]. The NK homeobox cluster has been kept in sponges and bilaterians for more than 550 Myr, position 67.19 [497].

The water passes through the sponge in hours; the sponge itself stands for thousands of years. Here the form of carrier and form shows at the scale of a whole animal: the cells and the water are replaced, the body holds.

Counting sponges

The World Porifera Database held 8,553 valid Recent species on 31 August 2011 [492]. Demospongiae held 83 %, Hexactinellida about 600, Calcarea about 680 (Calcinea 166, Calcaronea 515) and Homoscleromorpha 87 [492]. The census counted 25 orders, 128 families and 680 genera among about 20,000 names [492].

In 2026 the database lists 9,837 valid species [502]. The rise since 2011 is 9,837 − 8,553 = 1,284 species in about 15 years, about 1,284 / 15 = 86 per year; the 2012 paper gives 35–87 new taxa per year [492]. The total may be "as many as twice" the valid number, about 17,000, and at least 12,000 are expected to be known by the end of this century [492].

A 2013 census of 1.66 million described animals in 40 phyla gives Porifera about 10,900 species [503]. That is 10,900 / 1,660,000 = 0.66 % of described animals; with the 2026 count it is 9,837 / 1,660,000 = 0.59 %.

Freshwater sponges (Spongillina) hold roughly 200–250 accepted species; the database search gave 257 and another overview 219, in six families and an unplaced group [492]. Carnivorous sponges numbered 90 species in Cladorhizidae (3 genera) at the end of the 20th century and 119 species in 3 families and 8 genera in 2012 [492].

The phylum opened once, and its depth has filled since: one body plan, four classes, nearly ten thousand species. This is the form of a union opened once and filled many times.

Comb jellies and placozoans

Comb jellies

Comb jellies (ctenophores) are marine carnivores that swim with rows of ciliary comb plates [504][480]. Their ancestor reconstructs as pelagic, tentacled, bioluminescent and hermaphroditic [480]. Benthic life arose from it at least twice [480].

The Ediacaran *Eoandromeda octobrachiata* has eight arms spiralling along a tall conical body [505]. Its transverse bands may match comb plates, and one study reads it as an early stem comb jelly, octoradial rather than biradial [505]. A second study finds it "unlikely to be a ctenophore" and proposes the latest-Ediacaran *Namacalathus* as a possible stem member [506].

The oldest unequivocal comb jellies are early Cambrian, from Chengjiang, and middle Cambrian, from the Burgess Shale [506]. Chengjiang is not older than 518.03 ± 0.69/0.71 Ma, position 67.13 [452]. Its stem comb jellies include *Daihua sanqiong* (3 specimens), *Xianguangia sinica* and the scleroctenophore *Galeactena hemispherica* (1 specimen) [506].

Five Chengjiang scleroctenophore genera are named: *Galeactena*, *Maotianoascus*, *Thaumactena*, *Batofasciculus* and *Trigoides* [506]. Six armoured early Cambrian comb jellies with eight-fold symmetry and eight pairs of comb rows form the class Scleroctenophora [507]. Burgess Shale genera are *Fasciculus*, *Ctenorhabdotus* and *Xanioascus*, of the Wuliuan [506].

Chengjiang forms have an organic skeleton; Burgess Shale forms lack it and lack paired tentacles [506]. The skeleton was "lost twice independently". Paired tentacles like those of living forms appear first in Devonian comb jellies [506].

The comb rows of the fossils come in fixed counts. The scleroctenophores have 8 pairs, 16 rows [507][506]. *Ctenorhabdotus* and *Xanioascus* have 24 each, and *Fasciculus* has about 64 and about 16 on its two lobe sets, about 80 in all [506].

The stem fossils carry tentacles in fixed counts too. *Xianguangia*, *Daihua* and *Dinomischus* have 18 tentacles each; *Dinomischus* was first estimated at 20 [506]. Eighteen mesenteries are inferred in *Xianguangia* and *Dinomischus*, more than 12 and possibly 18 [506].

Siphusauctum has 6 tentacles and 6 aboral openings and is hexaradial [506]. *Daihua* carries more than 30 paired pinnule sets per tentacle surface and three oral domes, triradial [506]. The flexible tip is about 20 % of tentacle length in *Daihua* and 15 % in *Dinomischus* [506].

fossil part	size	position
Daihua, cilia-like structures, width	19–25 µm	5.49–5.74
Xianguangia, macrocilia, thickness	19–23 µm	5.49–5.66
Daihua, pinnule width	60–120 µm	6.54–7.17
Daihua, cilia-like structures, length	175–200 µm	7.51–7.63
Xianguangia, macrocilia, length	up to 600 µm	8.63
Daihua, oral opening	about 2.4 × 1.6 mm	9.90 × 9.53
Daihua, pinnule length	over 5 mm	10.56

[506]

A clock dates living comb-jelly diversity to 350 ± 88 Ma, range 262–438 Ma, position

66.78 [480]. An earlier hypothesis gave about 65 Ma, position 65.25 [480]. *Euplokamis dunlapae* is sister to the other living comb jellies [480].

Lobate and cydippid comb jellies diverged 160–260 Ma, positions 66.07–66.51, by the linkage clock [472]. From Chengjiang to the crown estimate is 518.03 − 350 = 168 Myr, position 66.11. From the crown to the lobate–cydippid split is 350 − 260 = 90 to 350 − 160 = 190 Myr, positions 65.54–66.22.

Comb rows are present in the earliest fossils [505][506]. Statoliths, tentacles, polar fields and biradial symmetry are traits of the crown, absent in *Eoandromeda* [505].

The living animals span millimetres to near a metre. Oceanic comb jellies “approach a meter”, coastal ones run from a few millimetres to several centimetres, and cydippids are usually less than 3 cm across, position 12.19 [508].

what	size	position
Mnemiopsis synaptic vesicle, median (n = 56)	51 nm	0.10
Mnemiopsis dense-core vesicle, median (n = 66)	202 nm	1.36
Pleurobrachia pileus, spacing of plate bases (n = 40)	0.46 ± 0.06 mm	8.39
P. pileus, comb-plate length	0.79 ± 0.13 mm	8.88
P. pileus, cilium length	about 800 µm	8.90
living comb-jelly cilia	up to 2 mm	9.73
Mnemiopsis leidyi, cydippids at 3–5 days	3–5 mm	10.10–10.56
P. pileus, body (n = 25)	8.0 ± 1.4 mm	10.99
M. leidyi, Florida study animals (median 38 mm)	12–70 mm	11.36–12.97

[509][504][506][510]

The dense-core vesicle is 202 / 51 = 4.0 times the synaptic vesicle. A *Pleurobrachia* plate carries about 100,000 cilia [504]. Plate length is 0.79 / 8.0 = 0.099 of body length and plate spacing 0.46 / 8.0 = 0.058.

The *Pleurobrachia* plates beat at 2–28 Hz when driven at 20 °C and 2–14 Hz at 10 °C; spontaneously active animals reached 20 Hz [504]. The maximum regularly driven rate was 14.7 Hz at 10 °C and 31.1 Hz at 25 °C, a ratio of 31.1 / 14.7 = 2.1 over 15 °C [504]. Plate tips moved at about 20–75 mm s^{-1}, and the metachronal wave ran at 56 ± 14 mm s^{-1} at 5 Hz and 95 ± 23 mm s^{-1} at 25 Hz [504].

Maximum water flow was 60–90 mm s^{-1} at 20 Hz [504]. The number of plates per wave fell from 23 ± 3 at 5 Hz to 7 ± 2 at 25 Hz at 20 °C, a factor 23 / 7 = 3.3 [504]. At 10 Hz it rose from 10.2 ± 0.8 at 10 °C to 16.4 ± 1.3 at 20 °C, a factor 16.4 / 10.2 = 1.6 [504].

A momentum-jet estimate gives about 10^{-10} W per wave at about 20 mm s^{-1} tip speed and about 10^{-8} W at about 75 mm s^{-1} [504]. Power rises about 100-fold for a 75 / 20 = 3.75-fold rise in tip speed. The table range is 0.6 × 10^{-10} to 630 × 10^{-10} W, a factor 630 / 0.6 = 1,050; each axoneme delivers about 1.7 fJ per stroke at 20 Hz [504].

Mnemiopsis develops fast. Development to juveniles takes about 24 h at 18–20 °C,

position 43.50, and eggs hatch 22–26 h after spawning, positions 43.42–43.57 [510] [509]. Egg to reproductive adult can take as few as 13 days, position 45.83 [510].

Adults can produce thousands of eggs a day [510]. Thirty spawning animals produced 25 to 3,934 eggs, median 484 [510]. Spawning depends on size: below 26 mm 1 of 22 spawned (4.5 %), at 26–30 mm 6 of 16 (37.5 %), and above 30 mm 77 of 80 (96.3 %) [510].

Earlier size thresholds were 10 and 15 mm in the Caspian and Baltic, positions 11.19 and 11.56, and up to 32 mm in the native range, position 12.25 [510]. Spawning occurred under all light regimes: constant light 20 of 21, 11 h : 4 h 15 of 15, 7 h : 8 h 12 of 12, constant dark 17 of 18 [510]. The light periods of 11, 4, 7 and 8 h sit at positions 42.79, 41.87, 42.38 and 42.50.

Respiration per unit carbon is about 9 times higher at 20 °C than at 3 °C, with a Q10 of 3.67 over 3.5–20.5 °C [511]. From basal metabolism the animals survive without food about 80 days at 3 °C, position 47.49, and about 9 days at 20 °C, position 45.50 [511]. *Mnemiopsis* can revert from the mature lobate form to an early cydippid form when fed after stress [512].

Before that report, *Turritopsis dohrnii* was the only species known to reverse development after sexual maturity [512]. The adult returns to an earlier form of its own body and goes on from there.

The comb-jelly nervous system stands apart. The *Pleurobrachia* authors “strongly suggest” that comb jellies do not use serotonin, acetylcholine, dopamine, noradrenaline, adrenaline, octopamine, histamine or glycine as messengers between cells [479]. L-glutamate is a candidate neuromuscular transmitter, active at about 10^{-7} M; other classical transmitters were ineffective up to 5 mM [479].

“Many bilaterian neuron-specific genes and genes of ‘classical’ neurotransmitter pathways either are absent or, if present, are not expressed in neurons” [479]. Neurons appear about 2 days after muscle in development, position 44.13 [479]. The authors conclude that neural systems in comb jellies “evolved independently from those in other animals” [479].

The *Mnemiopsis* genome reads differently. Its neural gene set resembles that of sponges, which the abstract reads as a possible loss of a nervous system in comb jellies [478]. The 2015 review favours “an independent complexification of nervous systems from a simple precursor state” and notes complete loss of a nervous system in only two animals, both parasites [481].

In a 1-day-old *Mnemiopsis* cydippid, position 43.50, volume electron microscopy reconstructed 5 nerve-net neurons, 6 mesogleal neurons and 22 sensory cells in five types [513]. The neurites of the five net cells form “an anastomosed continuous network” with one continuous plasma membrane, a syncytium [513]. No electrical or chemical synapses were found between the net cells, while the net does synapse onto polster cells [513].

The source leaves one question open: do the net neurons divide and stay connected, or do neurites from separate cells fuse [513]. A reconstructed net neuron sends five neurites from its cell body [509]. Of nine synthetic *Mnemiopsis* peptides tested, four raised swimming speed [509].

Mnemiopsis has 129 putative neuropeptide precursors: 67 linear, 27 meeting all four models, 30 enriched in metacells and at least 42 mature peptides found [509]. An earlier genome search had found one [509]. It has 35 Kv homologues, 2 Nav and 2 innexins [509].

Pleurobrachia has 72 novel prohormones, more than 100 orphan neuropeptide-like receptors, 12 pannexins/innexins, 29 ASIC-type sodium-channel genes and 8 glutaminases [479]. Its homeodomain genes number 92, against 76 in *Mnemiopsis* and 32 in *Amphimedon* [479]. Hox genes, Drosha and Pasha are absent [479].

The *Pleurobrachia bachei* draft genome is 156,146,497 bp, estimated at 160–180 Mb, with 19,523 genes [479]. Of these, 44 % have orthologues in other animals: 0.44 × 19,523 = 8,590 genes [479]. The haploid chromosome number of comb jellies is 13 [472].

The *Mnemiopsis* statocyst carries four clusters of ciliated balancer cells bearing the statolith, and 1,011 cells were reconstructed in it [514]. Some neurons synapse onto balancer cells, with reciprocal connections to bridge cells [514].

The Mills list of valid species, updated 12 June 2017, tallies 198 comb jellies [515]. A 2017 paper gives about 200 and the main Mills page “about 100–150” [480][508].

order	valid species
Cydippida	71
Platyctenida	49
Lobata	42
Beroida	26
Cestida	2
Ganeshida	2
Cryptolobiferida	2
Lobata incertae	2
Cambojiida	1
Thalassocalycida	1

[515]

The orders sum to 198, and the three largest hold 71 + 49 + 42 = 162. The share of described animals is 198 / 1,660,000 = 0.012 % [503].

Placozoans

Placozoans are flat, ciliated sheets about 20 µm thick, position 5.54, and about 1 mm across, position 9.10 [516]. Thickness to width is 20 µm / 1 mm = 1 : 50. Two genera are named in the genome literature, *Trichoplax* and *Hoilungia* [516].

No placozoan fossil is known from a primary source. They have no nervous system but keep sodium-channel homologues, all with the DEEA filter, and putative Kv channels [476][148].

what	size	position
Trichoplax secretory granules	300–500 nm	1.72–2.18

T. adhaerens, spacing of secretory cells	about 5 µm	4.28
algae eaten by *T. adhaerens*	9 × 6 µm	4.81 × 4.44
T. adhaerens, cilia	about 10 µm	4.91
placozoan body, thickness	about 20 µm	5.54
Trichoplax, reach of a pausing animal	up to about 200 µm	7.63
Trichoplax with about 1,500 secretory cells	500 µm	8.47
T. adhaerens, diameter	0.3–1.5 mm	8.00–9.47

[517][516]

A 500 µm *Trichoplax* is 500 / 5 = 100 secretory-cell spacings across. Secretory cells make up 4 % of all cells [517]. Ciliated epithelial cells form about 70 % of the ventral epithelium [517].

There are no gap junctions, and fibre cells “do not form chemical synapses” [517]. The count of cell types was four, possibly five, in 2008 and six in 2017 [484][517]. Whole-organism single-cell sequencing finds several types of peptidergic cells, and comb jellies show more cell-type diversity than placozoans and sponges [518].

Six peptidergic cell populations have distinct distributions, each secreting one peptide: SIFGamide, TrIns3, SITFamide, YYamide, RWamide or FFNPamide [519]. Under some peptides the animals flatten to up to 5 times their default size [519]. Peptides were tested at 200 nM–50 µM, 20 µM for detail [519].

Twelve peptides were tested in feeding: 3 commercial and 9 custom amidated [517]. The threshold is 100 nmol l^{-1}; YPFFamide acted in 3 of 6 animals and YPWFamide in 3 of 3, and full pausing occurs above 200 nmol l^{-1} [517]. As few as 10 algae suffice for a pause, and a pausing animal affects others up to about 200 µm away [517].

behaviour	duration	position
onset of pause after a peptide pulse	about 30 s	36.25
single feeding pause (n = 64)	2.97 ± 0.96 min	37.87
group pause	4.13 min	38.17
repeat of pause under peptide (n = 33)	9.11 ± 4.22 min	38.89
effect of the peptide PWN	about 10 min	38.98
group pause cycle (n = 38)	12.9 ± 2.0 min	39.21

[517][519]

A single pause lasts 2.97 / 12.9 = 23 % of a group cycle. The behavioural units run from 30 s to 13 min, positions 36.25 to 39.21.

A neuropeptide precursor of the large connected peptide network occurs in *Trichoplax*, “an animal without neurons” [520]. The genome “contains most post-synaptic genes but lacks some of them”: Shank, GRIP, the ErbB receptor, mGluR and SynGAP are missing [474]. The 2014 reconstruction predicts a loss of 4,952 genes on the placozoan branch [479].

Trichoplax has the homeobox genes Not, Mnx, Dll, Hmx and the ParaHox gene Gsx [498]. It lacks Msx, NK2, NK6, Tlx, Hex and the two Bar genes of demosponges [498]. Its Hox count is 0 and its ParaHox count 1.

The *Hoilungia hongkongensis* genome is 87,194,036 bp in 669 contigs, with 12,010 gene models and 1.6 % heterozygosity [516]. *T. adhaerens* is about 7 Mb larger, about 94 Mb, with about 12,521 gene models reannotated and 11,520 in the 2008 annotation [516]. The 2008 genome paper gives about 98 Mb and 11,514 genes [484].

There are 19 genetic lineages, 16S haplotypes H1–H19, in clades I–VII; *Trichoplax* holds clades I and II and *Hoilungia* III–VII [516]. Protein distances across 6,554 orthologues range 0.9–80.1 %, mean 28.3 % [516]. Between the two genera 2,101 genes, about 25 %, are inverted or translocated; 97 % of orthologues are under strong purifying selection and 3 under positive selection [516].

Hoilungia hongkongensis, of 2018, is “the second described placozoan species” [516]. A 2022 taxonomy erects 2 classes, 4 orders, 3 families and 1 new genus and species [521].

T. adhaerens of the H1 Grell strain was kept in clonal culture at 24 °C from January 2014 to December 2024, 11 years, position 51.05 [522]. The animals divided about once every 1–2 days, positions 43.50–44.13, with no sign of sexual reproduction [522]. Median counts per dish were 52 (IQR 23–112) in the control line and 95 (30–220) in the ampicillin line, from 9,203 and 4,419 observations [522].

At one division per 1–2 days, 11 years hold 11 × 365.25 / 2 = 2,009 to 11 × 365.25 / 1 = 4,018 generations. They were fed *Tetraselmis marina*, 1–2 mL added weekly [522]. The flat sheet was carried through two to four thousand generations of cells and animals, and it stayed the same sheet: the form lasts, the carriers are replaced.

The Ediacaran bodies

The oldest architecturally complex Ediacaran macrofossils are 574.17 ± 0.66 Ma old, position 67.23 [450]. They come from the upper Drook Formation at Mistaken Point, Newfoundland. The “Brasier” Surface there is 567.63 ± 0.66 Ma and the “E” Surface 565.00 ± 0.64 Ma, positions 67.22 and 67.21 [450].

The youngest rangeomorphs at Mistaken Point are no younger than 564.13 ± 0.65 Ma, position 67.21 [450]. The Ediacara biota as a whole spans 571–541 Ma, positions 67.22–67.17, which is 571 − 541 = 30 Myr, position 64.54 [451].

Dickinsonia is an animal by its sterols, at 558 Ma, position 67.20 [451]. The study calls it among “the oldest confirmed macroscopic animals” [451]. In the largest specimen the sterols are 93 % cholesteroids, 1.8 % ergosteroids and 5.2 % stigmasteroids [451].

Across specimens the cholesteroids range 84.8–93.0 %, rising with size [451]. Host sediment holds 10.6 % in clay and 11.9 % in sandstone, and a microbial mat with *Andiva* holds 18.7 % [451]. The specimens are 1.0–6.0 cm wide, positions 11.19–12.83, and dickinsoniids reach 1.4 m, position 15.69 [451].

The animal sterol rises as the body grows, from 84.8 % to 93.0 %. The surroundings hold 10.6–18.7 %. The animal keeps its own composition against that of the mat it lies on.

Haootia quadriformis, from Newfoundland at about 560 Ma, position 67.21, shows twisted fibrous bundles in a square pattern [523]. Four bifurcating branches leave its corners. It is compared with the muscles of living staurozoans and proposed as the

earliest body fossil of animal muscle [523].

Auroralumina attenboroughii comes from Bed B of the Bradgate Formation, Maplewell Group, Charnwood Forest, UK, at 557–562 Ma, positions 67.20–67.21 [524]. It is one specimen, with the holotype left in the rock. It has two equal bifurcating polyps in goblet-shaped sheaths, with at least 30 tentacles on the better cup [524].

***Auroralumina* part**	**size**	**position**
tentacle length	about 2.75 cm	12.12
cup length, and width up to	about 6 cm	12.83
stalk	about 12 cm	13.46
total length	about 20 cm	13.92

[524]

Auroralumina extends the crown-group cnidarian record by about 25 Myr, position 64.38 [524]. Its polyp is at least ten times as wide as those of living staurozoans, cubozoans and scyphozoans [524]. The authors know no wider medusozoan polyp [524].

Muscle enters the fossil record before any nerve. *Haootia* is 574.17 − 560 = 14.17 Myr younger than the first complex macrofossils, position 63.86. Their nerve tissue is inferred [523].

The moulting animals (Ecdysozoa) are dated by a clock into the Ediacaran [525]. The clock origin lies at least 23 Myr, position 64.30, before the earliest potential ecdysozoan trace fossils, which are latest Ediacaran and younger than 556 Ma, position 67.20 [525]. The origin therefore lies at 556 + 23 = 579 Ma or earlier, position 67.24.

The oldest recorded attack on an animal is a hole in a tube of *Cloudina*. *Cloudina* is the earliest known animal with a mineralised skeleton, from the late Precambrian of Shaanxi Province, China [526]. Of more than 500 tubes, 2.7 % carry rounded holes 40 to 400 µm across, positions 6.17–8.26 [526].

That is at least 0.027 × 500 = 13.5, so 14 bored tubes. Hole size follows the width of the bored tube, which the authors read as predation selective for size [526]. The holes span a factor 400 / 40 = 10.

A second study of uppermost Neoproterozoic *Cloudina* from China finds borings 15–85 µm wide, positions 5.28–6.85, in nearly one-fifth of almost one hundred tubes [527]. That is about 0.2 × 100 = 20 tubes. In the same beds no shell of *Sinotubulites* is bored [527].

The borings sit at a fairly uniform distance from the aperture, and their size varies [527]. The prey was attacked throughout its growth after a minimum size [527]. The two studies give 2.7 % with holes of 40–400 µm and about 20 % with holes of 15–85 µm.

The base of the Cambrian is 538.8 ± 0.2 Ma, position 67.17 [435]. The steps between the dated Ediacaran events are short on the scale of the clocks.

step	**duration**	**position**
Marinoan steranes (635 Ma) to first complex macrofossils (574 Ma)	61 Myr	65.19

first complex macrofossils to *Haootia* (574.17 − 560)	14.17 Myr	63.86
first complex macrofossils to *Dickinsonia* (574.17 − 558)	16.17 Myr	63.98
Dickinsonia to the Cambrian base (558 − 538.8)	19.2 Myr	64.14
first complex macrofossils to the Cambrian base (574 − 538.8)	35.2 Myr	64.69

The clock intervals are 75–184 Myr wide; the fossil steps are 14–61 Myr. Within some 35 million years after the first complex fossils, bodies with muscle, tentacles, skeletons and holes bored by other animals had all appeared.

Cnidarians: the first nerve nets

Origins

Cnidarians are the corals, sea anemones, jellyfish and hydrozoans, together with the parasitic Myxozoa [528][529]. All carry cnidae, the stinging capsules, and no loss of cnidae is documented [528]. The main living groups are Anthozoa, with hexacorals and octocorals, and the medusozoans [528].

A mitochondrial clock places the cnidarian origin at 741 Ma, with a 95 % credible region of 686–819 Ma, position 67.46 [530]. The same study places the diversification of the major cnidarian taxa before the Cambrian, at 543 Ma in its abstract, position 67.18 [530]. The second clock gives crown Cnidaria at 641.8–531.5 Ma [485].

The two clock readings, 686–819 Ma and 641.8–531.5 Ma, do not overlap; between them lie 686 − 641.8 = 44.2 Myr, position 64.89. From the 741 Ma clock age to *Auroralumina* at about 560 Ma is 741 − 560 = 181 Myr, position 66.18. From the clock age to the first complex macrofossils is 741 − 574.17 = 166.83 Myr, position 66.10.

Cnidarian sodium-selective channels diverged from calcium-conducting homologues more than 540 Ma, position 67.17 [148]. Cnidarian Cav genes are conserved for at least 500 Myr, position 67.10 [148]. Sodium selectivity arose once in cnidarians and once in bilaterians [476][531].

The oldest free-swimming medusa is *Burgessomedusa phasmiformis* from the middle Cambrian Burgess Shale [532]. It is known from 182 specimens, with a cuboidal umbrella up to 20 cm high, position 13.92, and more than 90 short tentacles [532].

The oldest scleractinian corals are mid-Triassic, about 240 Ma, position 66.43 [528]. Isotopes in about 212 Ma Late Triassic coral skeletons from Antalya record photosymbiosis, position 66.32 [533]. The coral algae (Symbiodiniaceae) first diversified about 160 Ma, position 66.07, in the Jurassic by clock; seven genera are described [534].

The coral order runs skeleton (240 Ma), photosymbiosis (212 Ma), symbiont clock (160 Ma). The steps are 240 − 212 = 28 Myr, position 64.48, and 212 − 160 = 52 Myr, position 65.04. Coral symbionts double in about 7 days, range 3–74 days, positions 45.27 and 44.50–47.42 [535].

Sizes and genomes

what	size	position
Hydra nerve cell body, length	about 10 µm	4.91
Aglantha digitale giant axon, diameter	22–40 µm	5.62–6.17
Hydra nerve cell bodies, spacing	50–100 µm	6.37–7.00
small *Hydra* (imaging work)	about 0.3 mm	8.00
Parantipathinae polyps	2–3 mm	9.73–10.10
small *Nematostella*	2.5–5 mm	9.93–10.56
Schizopathinae polyps	over 3 mm	10.10
Tripedalia cystophora, bell	7–9 mm	10.87–11.10
large *Hydra* (imaging work); antipatharian polyps, up to	about 1 cm	11.19
Aurelia aurita, animals studied	about 5 and 7.6 cm	12.66, 13.04
Auroralumina, total length	about 20 cm	13.92
Burgessomedusa, umbrella height	up to 20 cm	13.92
deep-sea black corals and zoanthids, below the surface	about 300–3,000 m	20.58–22.67

[536][537][538][528][539][540][541][524][532][542]

From the smallest *Hydra*, 0.3 mm, to a 20 cm fossil medusa, length spans a factor 0.20 / 0.0003 = 667. The myxozoans lie below this range, with life stages of “just a few cells” [529].

Genome sizes span the phylum [529]. The myxozoan *Kudoa iwatai* has 22.5 Mb (a second estimate 23.5 Mb), 5,533 protein-coding genes and a mean intron of 82 bp; the myxozoan *Thelohanellus kitauei* has 188.5 Mb [529]. *Polypodium hydriforme* has 561 Mb and 17,440 genes, *Nematostella vectensis* 450 Mb and 18,000 genes, and *Hydra magnipapillata* 1,005 Mb and 16,839 genes [529].

The *Velella velella* nuclear genome is estimated at 3.16 Gb [543]. The range is 22.5 Mb to 3.16 Gb, a factor 3,160 / 22.5 = 140; the smallest genome belongs to a parasite of a few cells.

Radial bodies

Octocorals have eight tentacles and eight mesenteries, without exception [528]. They are colonial, with one documented solitary exception, *Taiaroa tauhou* [528]. Most hexacorals are six-part; eight- or ten-part symmetry is “not uncommon” [528].

Antipatharians have six simple tentacles, six primary mesenteries and 0, 4 or 6 secondary mesenteries [528]. Among sea anemones, Andresiidae and Iosactiidae have 24 pairs of perfect mesenteries and 24 tentacles, and Oractiidae 10 pairs of mesenteries and 8 macrocnemes [528]. In *Nematostella* the gene anthox6a is expressed in 6 of 8 presumptive mesenteries [544].

Box-jellyfish swim pacemakers sit in four rhopalia, sense organs at the bell margin

[545]. Each rhopalium carries two lensed eyes, two pit ocelli and two slit ocelli, six eyes of four types; a medusa has 6 × 4 = 24 eyes [545][540]. A nerve ring connects the four rhopalia and the four tentacle bases, and in *Tripedalia* it holds two or three tracts of small fibres [545].

“Most scyphozoans have eight or more rhopalia, typically with species-specific numbers that are multiples of four” [545]. Whole *Aurelia aurita* and *Dactylometra quinquecirrha* had eight marginal ganglia, and some *Aurelia* had only five or three [541]. Eight rhopalia occur “usually” in *Aurelia* [546].

Haootia shows a four-fold pattern [523]. *Auroralumina* carries at least 30 tentacles per cup and *Burgessomedusa* more than 90 [524][532]. The tentacle number of *Nematostella* neurons is “not stereotyped” between tentacles or animals, and small animals carry 20–40 longitudinal neurons [539].

Nematostella has 18 Hox-related genes in 7 genomic clusters [544]. Of these, 7 are putative Hox genes: about 5 of anterior type (anthox6, 6a, 7, 8a, 8b) and about 2 of posterior type (anthox1, 1a) [544]. There are 2 ParaHox genes, anthox2 (Gsx-like) and NVHD065 (Cdx/Xlox-like, placement ambiguous) [544].

The largest cluster holds 7 genes, the Mox cluster 4 genes over about 23.2 kb, and the ParaHox pair lies about 13 kb apart [544]. Five Hox genes and one ParaHox gene are expressed in nested domains along the secondary, directive axis [544]. The expression work counts 20 ANTP-class genes and a figure caption gives 30; the cluster count is 18 [544].

Cnidarian PaxB shares 75 % identity with mouse Pax6 in the paired domain and 55 % in the homeodomain [547]. *Nematostella* has 44 Kv and 5 Nav2 channels, *Hydra magnipapillata* 35 Kv, and anemones and corals 6 Cav [148].

Handedness in a floating colony

The by-the-wind sailor *Velella velella* comes in two mirror forms, left-sailing and right-sailing [543]. The asymmetry begins in early development and is fixed for life [543]. The shares come from 6,421 iNaturalist observations with a sail direction, to 9 May 2024, and from samples at sea and on shore [543].

sample	left	right	minority share
Northern Hemisphere (iNaturalist)	5,000	438	8.1 % right
Southern Hemisphere (iNaturalist)	443	540	45.1 % left
North Pacific Subtropical Gyre, 27 stations	43	133	24.4 % left
western Portugal strandings, 281 reports	208	73	26.0 % right
Portugal, under northerly winds	116	4	3.3 % right
Portugal, under south-westerly winds	29	59	33.0 % left

[543]

The two iNaturalist totals sum to 5,438 + 983 = 6,421. The northern sample is 5,000 / 5,438 = 91.9 % left and the southern 540 / 983 = 54.9 % right. The gyre samples are from June–August 2019 and June–July 2022 [543].

Left and right Atlantic animals do not differ genetically: Fst is effectively zero, from 24

left and 24 right animals sequenced [543]. Atlantic against Pacific animals give Fst 0.140–0.141 [543]. The Portuguese man-of-war, *Physalia physalis*, also has two mirror-image forms [548].

Each colony keeps one direction for life, and the same genome carries either direction. This is the form of one direction in its symmetric variant. “The rule is symmetric … which direction wins, the rule does not say.”

In the north one direction holds 92 %, in the south the other holds 55 %.

The *Hydra* nerve net

A nerve net is a nervous system without a central organ. In *Hydra* there are two separate nets, one in the ectoderm and one in the endoderm, and they do not mix [536]. The endoderm of the tentacles holds no nerve cells, and endodermal sensory cells make up more than 50 % of all endodermal nerve cells [536].

Ectodermal cell bodies are about 10 µm long and usually 50–100 µm apart [536]. In the ectoderm only about 20 % of cross-sectioned nerve tracks are single neurites, the rest bundles [536]. In the endoderm about half are single and half bundles of two, and no endodermal bundle holds more than two [536].

The bundle counts rest on 130 ectodermal and 47 endodermal tracks from four sections spanning 40 µm, position 6.17 [536]. A serial block-face block of 2,000 planes at 30 nm steps, position -0.38, with a lateral resolution of 20 × 20 nm², position -0.75, gave the contact geometry [536]. The block measured 40 × 13 × 56 µm³, sides at positions 6.17, 5.15 and 6.47.

In the block two reconstructed cell bodies lay about 50 µm apart, position 6.37 [536]. At one contact the terminal neurite fingers overlapped over about 8 µm, position 4.70, and a second contact spanned about 4 µm, position 4.07 [536]. The nerve-cell antibody PNab stained 684 of 684 NeonGreen cells, 149 of 149 Hym176B cells and 51 of 51 nGreen cells [536].

The ratio of nerve cells to epithelial cells is 0.12 by two methods [536]. By region it is 0.10–0.19 in body-column endoderm and 0.15–0.22 in the ectoderm of gastric region and peduncle [536]. Samples held 80–400 nerve cells per body-column or peduncle sample and 20–30 per hypostome sample [536].

Tissue bands covering about 4 % of the body column held 133 nerve cells, 57 ectodermal and 76 endodermal [536]. Scaled up, 133 / 0.04 = 3,325 nerve cells per body column. In *Hydra oligactis* a nerve ring around the hypostome holds 20–30 nerve cells, with at least four neuron subsets [536][549].

One account gives three sensory and five ganglion populations, 8 in all; one ganglion population lies in the endoderm and two in the ectoderm [536]. A single-cell atlas sequenced 24,985 *Hydra* cells and found 12 neuronal subtypes from 15 clusters, 3 of them progenitors [550]. In the same atlas 46 % of all cells are nematoblasts or nematocytes [550].

The net renewed

The *Hydra* nerve net depends on a stem-cell pool. Interstitial stem cells cycle every 24

h, position 43.50; a later account gives about 24–30 h, positions 43.50–43.70 [551][552]. The pool holds 3,000–6,000 cells per animal, and about 4 % of all cells of a whole *Hydra* are stem cells [551][553].

Per generation about 60 % of stem-cell daughters stay stem cells and about 40 % differentiate [551]. About 900 nerve cells and about 1,760 nematocyte nests are made per day per animal, 1,760 / 900 = 1.96 nests per nerve cell [551]. The nematocyte to nerve ratio is 3 : 1 over the whole animal and about 7 : 1 in the gastric region [551].

Nerve differentiation takes about 10 % of stem cells, and the stem population doubles with the epithelium in about 3–4 days, positions 44.50–44.76 [552]. Commitment to nerve fate falls in S phase: “Committed cells completed the cell cycle, divided, and daughter cells differentiated to nerve cells” [552]. Hydroxyurea lowers interstitial cells to 1–2 % of normal [552].

About 1.2 % of input cells formed clones, scored after 1–2 weeks, positions 45.27–45.90; nine clones held both nerve cells and nematocytes [553]. In the peduncle of *Hydra oligactis* about 50 % of interstitial cells grow rapidly and the rest sit in G1 as committed nerve precursors [554]. In *Hydra attenuata* “nerves and nematocytes have 2n postmitotic nuclear DNA content” [551].

step	duration	position
labelling to nematoblast	12 h	42.87
labelling to visible nerve cell	about 18 h	43.24
nerve differentiation from stem cells	about 1 day	43.50
neurite extension along the net in grafts	by days 2 and 3	44.13–44.50
labelling to nematocyte	72–96 h	44.50–44.76
renewal of tentacle tissue	4–5 days	44.76–44.96
nematocyte differentiation	5–7 days	44.96–45.27
renewal of all tissues, nerve net included	2–3 weeks	45.90–46.27

[551][536]

“All *Hydra* tissues, including the nerve net, are newly formed every 2–3 weeks in well-fed animals” [536]. Every epithelial cell is displaced, carrying neurons toward head or foot; the ectoderm around the hypostome nerve ring is a stationary zone [549]. New nerve cells are added alongside the existing ones, and the divisions recorded are those of stem cells and committed precursors [536][552].

About 2,256 *Hydra* polyps of two closely related species were followed in 12 cohorts, more than 3.9 million individual-days, position 57.31 [555]. Cohorts reached ages up to 41 years, position 52.25. Mortality and fertility stayed constant over age, and the non-senescent lifespan is “at least several decades” [555].

The net is rebuilt every few weeks, and the animal does not age over four decades. Here the form of form and carrier is plain: the closed class persists and holds form while all its carriers are replaced. *Hydra* also shows a sleep-like state with a 4 h ultradian rhythm, position 41.87, and 212 sleep-dependent genes [556].

Conduction

The nerve cell adds nothing new to the cell. It is a cell whose edge tension travels along its length. The speeds of that travel differ over two orders of magnitude.

tissue	speed	source
Calliactis SS2 slow system, 11–14 °C	3.0–5.3 cm s^{-1}	[557]
Calliactis SS1 slow system (oral disc mean 12.3, column 5.2)	4.4–14.6 cm s^{-1}	[557]
Pennatula slow system	about 6 cm s^{-1}	[558]
Pennatula nerve net, 10 °C	7.5 cm s^{-1}	[558]
Virgularia nerve net, about 16 °C	40–60 cm s^{-1}	[558]
Aglantha myoepithelium	0.22–0.29 m s^{-1}	[537]
Aglantha tentacle axons	0.4–0.8 m s^{-1}	[537]
Aurelia motor nerve net	0.45–1 m s^{-1}	[546]
Aglantha ring giant axon, 15 ± 1 °C	1–2.6 m s^{-1}	[537]
Aglantha motor giant axons	1–4 m s^{-1}	[537]

Across these tissues the speeds span 3.0 cm s^{-1} to 4 m s^{-1}, a factor 400 / 3.0 = 133. Within one *Aglantha* the speed rises with axon diameter [537]. In *Virgularia* velocity rises with repeated stimulation [558].

***Aglantha* axon**	**diameter**	**position**
tentacle axon	3.6–7.8 µm	3.98–4.68
ring giant axon, one 10 mm animal	5–24 µm	4.28–5.70
motor giant axon, one animal	7.5–32 µm	4.64–5.97
ring giant axon	22–35 µm	5.62–6.05
motor giant axon	up to 40 µm	6.17

[537]

The ring giant spike of *Aglantha* reaches up to 68 mV, and an escape burst holds 2–6 impulses [537]. The *Hydra* imaging work states that action potentials “likely propagate through gap junctions” [538]. The *Aurelia* motor nerve net holds of the order of 10,000 neurons in a jellyfish about 4 cm across, position 12.46, by a model [546].

Refractory periods and pacemakers

event	duration	position
chronaxie, *Virgularia* nerve net	0.6–1 ms	26.40–26.87
chronaxie, *Pennatula* nerve net	about 0.8 ms	26.66
motor giant spike at half amplitude, *Aglantha*	1.2–1.4 ms	27.03–27.17
ring giant spike; synaptic delay motor giant to muscle	about 1.6 ms	27.29
synaptic delay ring giant to motor giant	1.6–1.8 ms	27.29–27.40

escape-burst impulse	2–3 ms	27.50–27.87
minimum repeat interval, ring giant	3.5 ms	28.01
myoepithelial impulse	15–70 ms	29.33–30.73
absolute refractory period, *Pennatula* nerve net	40–50 ms	30.22–30.43
time to peak of escape contraction, shortest	40.5 ms	30.23
half relaxation of escape contraction	94 ms	31.00
escape contraction complete	about 100 ms	31.06
facilitation peak, paired interval, *Pennatula*	about 250 ms	31.89
SS1 absolute refractory period, *Calliactis*	about 300 ms	32.06
second facilitation peak, *Pennatula*	about 600 ms	32.69
absolute refractory period, *Aurelia*	0.7 s	32.83
SS1 relative refractory period	about 1,400 ms	33.46
SS1 fails above one shock per	3 s	34.15

[558][537][557][541]

In SS1 the relative refractory period is 1,400 / 300 = 4.67 times the absolute one. Each conducting system has its own interval within which it cannot fire again. A closure cannot load twice in succession without first discharging: the refractory period is that form, in times from 3.5 ms to 3 s.

Medusae beat in rhythm. *Aurelia* at 16–18 °C beats at intervals as short as about 0.25 s in the smallest animals and 0.75 s in larger ones, positions 31.89 and 32.89, a ratio 0.75 / 0.25 = 3 [541]. *Dactylometra* at 12–13 °C commonly beats at intervals as short as 0.4 s, position 32.32 [541].

The source gives the *Aurelia* sizes as about 2 and 3 inches, 2 × 2.54 = 5.08 and 3 × 2.54 = 7.62 cm, positions 12.67 and 13.04 [541]. The beat intervals of 0.25–0.75 s give 1 / 0.75 = 1.3 to 1 / 0.25 = 4 Hz.

The *Tripedalia* pacemaker at 28 ± 0.5 °C runs “close to 1Hz” in darkness, period about 1 s, position 33.15 [540]. Over 10 s intervals it ranges 0.5–1.6 Hz, periods 2 s and 1 / 1.6 = 0.625 s, positions 33.78 and 32.73 [540]. The first 7 min, position 38.65, average about 1.25 Hz and the last 7 min about 0.9 Hz [540].

Light-off after lower-lens-eye stimulation overshoots to 2.4 Hz in the first 10 s, period 1 / 2.4 = 0.42 s, position 32.36 [540]. Light-on via the upper lens eye gives more than 1.8 Hz, then about 1.5 Hz; pit eyes give 1.7–1.9 Hz at light-on and 0.3–0.6 Hz at light-off [540]. Slit eyes give at most 1.7 Hz, about 1.3 Hz in light, and the full range under light steps is 0.3–2.4 Hz, a factor 2.4 / 0.3 = 8 [540].

A regenerating *Tripedalia* rhopalium runs its pacemaker at about 0.03 Hz on day 6 and about 0.2 Hz on day 8 [559]. The periods are 1 / 0.03 = 33 s and 1 / 0.2 = 5 s, positions 36.34 and 34.62; days 6 and 8 sit at positions 45.13 and 45.39. The rate rises by 0.2 /

0.03 = 6.7 in two days, and most rhopalial neural elements regrow within 2 weeks, position 45.90 [559].

In the regenerating rhopalium the FMRFamide-positive giant neurons rose from 7 to 14 in about a week, position 45.27 [559]. RFamide-positive neurons rose from 8 on day 8 to 16 on day 14 [559]. Both counts double: 14 / 7 = 2 and 16 / 8 = 2.

The *Tripedalia* central nervous system holds “several thousand nerve cells” [540].

Nematostella grows and shrinks

Fed *Nematostella* grew 75.9 ± 20.8 % in 3 weeks, position 46.27, then shrank 38.6 ± 9.1 % in 11 weeks of starvation, position 47.45 [539]. Starved-then-fed animals shrank 26.1 ± 7.4 % in 7 weeks, position 47.04, then grew 164 ± 34.9 % [539]. Resting length varies 14 ± 3 % over 5 days, position 44.96 [539].

In 146 adults the counts of longitudinal neurons (r = 0.854) and tripolar neurons (r = 0.791) rise with body length, and both fall as animals shrink [539]. Oral regeneration was complete by 7 days in 82 of 83 animals, position 45.27 [539]. Regenerates are smaller than before and show 4–5 peristaltic waves per 5 min, position 38.34 [539].

Cell death peaks 1.5–12 h after amputation, positions 40.98–42.87, and the first proliferation comes at 12 h [539].

In *Nematostella* NvSoxB(2) is expressed in neural progenitors “before mitosis”, and S phase to mitosis at the gastrula takes about 2–4 h, positions 41.24–41.87 [560]. Of NvSoxB(2)-positive cells 10 % (mid-planula) to 25 % (early blastula) take up EdU by the figure legend, and 30 % by the text [560]. In 97 % of two-cell clusters only one cell is labelled.

Peptides

As of 2018, “neuropeptides that act as ligands for GPCRs have yet to be identified in any of the four non-bilaterian phyla” [561]. Homologues of most bilaterian neuropeptides and their receptors have not been found outside the bilaterians [561]. About a quarter of animal peptide families form one large, loosely connected similarity network [520].

Nematostella precursors carry 12 C-terminal motifs, none orthologous to bilaterian neuropeptides: RIamides, RPamides, RWamides, LWamides, ITamide, MTamide, VRamide, RRamide, PGamides, RGamides, PVamides and LVamide [561]. A family of 13 ENaC-type channels are receptors for *Hydra* RFamide peptides [561]. In *Pleurobrachia* none of 72 putative precursors is orthologous to those of other animals, except glycoprotein-, bursicon- and insulin-type hormones [561].

Two peptide families, GRFamide and X1PRX2amide, are present in all cnidarian classes studied [562]. Medusozoa and Octocorallia hold 66 preprohormones; 3 scyphozoan species have 6 preprohormone genes and 5 staurozoan species 3 [562]. Five cubozoan species had 6 families in an earlier study and 7 octocoral species have 5 [562].

A cnidarian precursor carries up to 32 copies of its peptide [562]. GPRRamide copies number 22 in *Briareum*, 15 in *Xenia*, 8 in *Eleutherobia*, 5 in *Clavularia* and 4 in *Heliopora*; RPRSamide copies number 3–16 in staurozoans [562]. At least 30 neuropeptide systems trace to the common ancestor of protostomes and deuterostomes,

against counts of 29 and 27 from 2013 [561].

Long lives, heat and counts

The black coral *Leiopathes* reaches about 4,265 years, position 56.48, and the zoanthid *Gerardia* about 2,742 years, position 56.08 [542]. They grow radially at 4–35 µm a year [542]. The two ages are 4,265 / 2,742 = 1.56 apart.

AnAge lists *Hydra* and *Turritopsis nutricula* without a maximum longevity [563]. After size standardisation jellyfish excrete about 10 times slower than other pelagic animals and grow about 2 times faster, at Reynolds numbers about 10 times greater [564].

Coral bleaching begins at 1 °C above the maximum monthly mean [565]. Reef-wide bleaching occurs at 4 °C-weeks and death of sensitive corals at 8 °C-weeks or more [565]. Severe bleaching now returns at a median interval of 6 years, position 50.50 [566].

A 2013 census gives about 16,400 cnidarian species, 16,400 / 1,660,000 = 0.99 % of described animals [503]. Anthozoa hold about 7,500 living species: Hexacorallia about 4,300 and Octocorallia about 3,000, together 7,300 [528]. Actiniaria hold about 1,200 species in 46 families and Ceriantharia about 100 [528].

Scleractinia hold about 1,300 living species, 656 reef builders and 669 others, together 1,325 [528]. Antipatharia hold 235 species in 40 genera and 7 families, about 50 of them described since 1990 [528]. The Myxozoa number “over 2,000” by the abstract and “over 2,180” by the introduction; 2,180 / 16,400 = 13 % of cnidarians [529].

The crystalline aragonite skeleton of *Heliopora* and the Scleractinia arose twice [528]. Cnidarians hold 0.1 Gt C of the 2 Gt C of all animals, 0.1 / 2 = 5 % [235].

The Cambrian opening

The Cambrian begins at 538.8 ± 0.2 Ma, position 67.17 [435]. Its explosion of body plans “lasted more than 22 million years”, position 64.26 [452]. Most of the phyla that follow appear in its first twenty million years.

The oldest armoured scalidophoran, a moulting animal, is *Eokinorhynchus rarus*, about 535 Ma, position 67.16, from the Fortunian Xinli Member of the Dengying Formation in Sichuan [567]. Four specimens were described, and three more of two unnamed forms come from the Kuanchuanpu Formation in Shaanxi [567]. They are the first dated body fossils with cuticle sclerites [567].

The oldest proposed stem echinoderm is *Yanjiahella biscarpa*, from Bed III of the Yanjiahe Formation, Hubei, early Cambrian (Fortunian) [568]. It rests on 35 specimens, and no stereom was seen [568]. Echinoderms otherwise first appear “during Cambrian Stage 3 (about 520 Ma ago)”, position 67.14, and *Yanjiahella* is “several million years” older [568].

The oldest brachiopods of South Australia are *Askepasma saproconcha*, pre-trilobitic, Terreneuvian (Cambrian Stage 2) [569]. They come from the basal Wilkawillina and Wirrapowie limestones; *A. toddense* follows mainly in the *Abadiella huoi* Zone of Stage 3 [569]. The shell structure of *Askepasma* lies near the base of the brachiopod stem, close

to the tommotiids [569].

A second study places the first brachiopods in the Tommotian of Siberia and Mongolia, with stem tommotiids in the older Fortunian [570]. Most Palaeozoic brachiopod classes are present by Cambrian Series 3 [570]. One Cambrian formation, the Forteau, holds at least 13 brachiopod species, 11 with organophosphatic shells; the abstract gives 11 species and the text 13 [570].

The oldest bryozoan has three readings. In 2021 *Protomelission gatehousei* was described from Cambrian Stage 3, from the lower Wirrealpa Limestone of Australia and the Dengying Formation of South China [571]. That claim moved the first bryozoan back by about 35 Myr, position 64.68, from *Prophyllodictya* at the base of the Ordovician [571].

In 2023 *Protomelission* was read as “the earliest dasycladalean green alga”, with “no unequivocal Cambrian bryozoans” known [572]. In 2026 a reply described 38 modular fossils of *P. gatehousei* and *Dayingomelission hexaclitia* from the Terreneuvian Xiannüdong Formation, southern Shaanxi [573]. They show styles, annular muscles, membranous sacs 10 µm apart, position 4.91, and ring septa, and are placed in crown-group stenolaemates [573].

The 2026 colonies are 1–2 mm wide, positions 9.10–9.73, and up to 3 mm high, position 10.10 [573]. The 2021 zooids average 174 µm wide and 220 µm long, positions 7.51 and 7.72 [571]. A gap of about 44 Myr, position 64.89, separates the unequivocal Tremadocian record from clock origins in the Terreneuvian [571].

The oldest durophagy, shell crushing, is damage on *Mobergella holsti* from Sweden [574]. Most Cambrian drill and puncture holes are on brachiopods, and the drillers are largely unknown [574].

The Chengjiang biota is not older than 518.03 ± 0.69/0.71 Ma, position 67.13, by U–Pb dating of the youngest detrital zircon in the Maotianshan Shale [452]. From the Cambrian base to Chengjiang is 538.8 − 518.03 = 20.77 Myr, position 64.21. Its comb jellies are described above.

The oldest recorded parasitism is from the Lower Cambrian (Stage 4) Wulongqing Formation, Guanshan biota, eastern Yunnan [575]. Tube-dwelling organisms encrust the brachiopod *Neobolus wulongqingensis* in a one-species assemblage [575]. Of 429 specimens, 205 are encrusted and 224 free, 205 / 429 = 47.8 % [575].

Encrustation gives a 26.08 % reduction in fitness, from ash-free dry weight estimated from shell size [575]. Tube orientation was measured on 146 individuals, 31 of them with a single tube [575]. The tubes align with the host’s feeding currents, and the authors read the interaction as kleptoparasitism [575].

The oldest exceptionally preserved ecdysozoan body fossils are about 520–508 Ma, positions 67.14–67.12 [525]. Bilateral plated stem echinoderms, *Ctenoimbricata* from the Murero Formation of NE Spain and *Courtessolea moncereti* from the Coulouma Formation of the Montagne Noire, are of Stage 5, about 510 Ma, position 67.12 [576]. They are bilateral, with a mouth in front and an anus behind [576].

Ctenoimbricata has a body of 20 mm, position 11.83, with an aperture of about 4 mm, position 10.36 [576]. The earliest radiate forms (helicoplacoids, stromatocystitids,

gogiids) carry two to five primary ambulacral rays [576]. *Yanjiahella* is 20–50 mm high, positions 11.83–12.66, with plates up to 2.5 mm and feeding appendages up to 43 mm, positions 9.93 and 12.52 [568].

The acorn worm *Spartobranchus tenuis* comes from the middle Cambrian Burgess Shale (Series 3, Stage 5) [577]. Its fibrous, sometimes branched tube is read as a forerunner of the pterobranch sheath [577]. Graptolite-type pterobranchs are “diverse by the mid-Cambrian”, and a pterobranch zooid from China places the phylum in the early Cambrian [578].

Anomalocaris canadensis of the Burgess Shale (Wuliuan) is one of the largest Cambrian animals [579]. Large specimens have body-lobe widths of 60–70 mm, positions 12.83–12.97 [579]. Flow simulations use swimming speeds of 0.4, 0.7 and 0.9 m s^{-1}, and its raptorial appendages are built for soft prey, not for crushing trilobites [579].

One specimen of *Anomalocaris* carries a putative injury [579]. A redescription from all known specimens records stalked eyes, a three-part oral cone and a tail fan with a central blade and three pairs of lateral blades [580].

The Burgess Shale also holds the medusa *Burgessomedusa* and the comb jellies *Fasciculus*, *Ctenorhabdotus* and *Xanioascus* [532][506]. Drill holes in the Palaeozoic are recorded in brachiopods and sessile echinoderms [581]. From the Ediacaran to the Silurian the maximum drilling frequency per species is 10–20 % [582].

The Ordovician begins at around 490 Ma by one source, position 67.08 [583]. *Aegirocassis benmoulae* of the Early Ordovician Fezouata Biota, Morocco, is an anomalocaridid filter-feeder more than 2 m long, position 16.02 [583]. The frequency of predation traces rises notably by the Ordovician [584].

The median drill hole of the Ordovician is 0.35 mm across, position 8.14 [585]. Six of the eight bryozoan orders are present by the Early Ordovician [573]. Asterozoans first appear in “a comparatively brief interval of the Early Ordovician” [586].

event	age	position
base of the Cambrian	538.8 ± 0.2 Ma	67.17
Eokinorhynchus rarus, Fortunian	about 535 Ma	67.16
first echinoderms with stereom, Stage 3	about 520 Ma	67.14
first uncontested sponge spicules	about 520 Ma	67.14
ecdysozoan body fossils	about 520–508 Ma	67.14–67.12
Chengjiang biota, not older than	518.03 Ma	67.13
bilateral plated stem echinoderms, Stage 5	about 510 Ma	67.12
beginning of the Ordovician	around 490 Ma	67.08

[435][567][568][486][525][452][576][583]

The phyla appear in this interval of some 30 Myr. A new kind of body opens once; from then on the opened depth fills, phylum by phylum, with species.

Flatworms and small spiralians

Five spiralian groups keep small or simple bodies: flatworms (Platyhelminthes), rotifers, bryozoans, brachiopods and nemerteans. Zhang's 2013 classification lists 29,488 described flatworm species, 2,049 rotifers, 11,474 bryozoans, 7,390 brachiopods and 1,358 nemerteans, fossils included [587]. A second count gives "over 30000 described extant species" of flatworms [588].

The flatworm record

The oldest free-living flatworm record is a set of marine trails from the Vauréal Formation, Katian, Canada [588]. Their minimum age is 444.0 Ma in the table and "at least as old as 445.2 ± 0.9 Ma" in the text, positions 66.99 and 67.00 [588]. Freshwater trails of Tricladida date from 274.4 Ma, position 66.56, in the Pizzo del Diavolo Formation, Kungurian, Italy [588].

The oldest parasitic flatworms are Monopisthocotylea, known as circlets of up to 16 hooks from the Lode Formation, Givetian, Latvia [588]. The table gives 377.7 Ma and the text 378.9 ± 1.2 Ma, positions 66.85 and 66.85 [588]. "Over 69 circlets of hooks" are known, and at least 29 are still attached to placoderm and acanthodian fishes [588].

Cestodes first appear as an egg at 304.8 Ma, position 66.65, in the Stark Shale Member, Kasimovian, USA [588]. Eucestoda follow at 259.1 Ma, position 66.50, as eggs inside proglottids from the Rio do Rasto Formation, Brazil [588]. A cestode tentacle in Myanmar amber "at least 98.79 ± 0.62 Ma old", position 65.63, has an uncertain assignment [588].

Trematodes first appear as an operculate egg at 120.2 Ma, position 65.81, from the La Huérguina Formation, Barremian, Spain [588]. The family Gymnophallidae appears at 75.22 Ma as an igloo-shaped trace and at 52.93 Ma in the London Clay, positions 65.38 and 65.06 [588]. A Precambrian putative flatworm, the Precambrian–Cambrian *Curvolithus* trails and an Eocene amber species are set aside by the same review [588].

record	age	position
free-living marine trails, Katian	444.0–445.2 Ma	66.99–67.00
monopisthocotylean hooks, Givetian	377.7–378.9 Ma	66.85–66.85
first cestode egg, Kasimovian	304.8 Ma	66.65
freshwater triclad trails, Kungurian	274.4 Ma	66.56
Eucestoda, eggs in proglottids	259.1 Ma	66.50
first trematode egg, Barremian	120.2 Ma	65.81
cestode tentacle in amber	at least 98.79 Ma	65.63
Gymnophallidae trace	75.22 Ma	65.38
Gymnophallidae, London Clay	52.93 Ma	65.06

[588]

The record runs from free life (445 Ma) to parasites on fishes (378 Ma), then to tapeworm eggs (305 Ma) and fluke eggs (120 Ma). The free form came first; each parasitic depth opened later and filled.

Bodies of one species over a wide range

The planarian *Schmidtea mediterranea* spans more than 40-fold in body length, from about 0.5 mm to 20 mm, positions 8.47–11.83 [589]. Its dry mass spans more than 9,000-fold and its cell number more than 800-fold, on an axis from about 10^4 to 10^7 cells [589]. Adults change size reversibly over 2 orders of magnitude, “life history-independent” [589].

Metabolic rate, by microcalorimetry at 20 °C, ranges from about 0.02 to 10 mW, a factor 10 / 0.02 = 500 [589]. The number of animals per vial ran from 2 for the largest to 130 for the smallest [589].

relation	exponent
metabolic rate with wet mass	0.75 ± 0.01
metabolic rate with cell number	0.96 ± 0.02
metabolic rate per cell with cell number	0.05 ± 0.02
wet mass with dry mass	1.03 ± 0.01
cell number with wet mass	0.72 ± 0.01
cell number with dry mass	0.74 ± 0.01
energy content per cell with cell number	0.38 ± 0.03
energy influx per cell with cell number	0.00 ± 0.03

[589]

Triglycerides per cell are 88-fold higher in large animals, and glycogen per cell more than 8-fold [589]. The influx per cell stays the same at every size, while the store per cell grows.

In flatworms “Differentiated somatic cells do not divide” [590]. “The only somatic cells capable of mitosis are neoblasts”, and BrdU entered only neoblasts and appeared in differentiated cells later [590]. Planarian neoblasts have a median G2 of about 6 h, position 42.24, with no large slow-cycling population in intact animals [591].

Planarian memory is kept for at least 14 days, position 45.90, and it is kept through head regeneration [592]. One pool of dividing cells supplies the whole body, and the body keeps what it learned while its head is replaced. The form lasts; its carriers are replaced.

Schmidtea mediterranea has 13 Hox genes, “not organized in a genomic cluster”, covering all major anterior–posterior categories [593]. Parasitic flatworms have 7; before this count no single planarian study had described more than 7, and 10 Hox genes had been cloned across 6 planarian species [593]. *Macrostomum lignano* has Cdx homologues absent in polyclads, cestodes, trematodes and triclads [593].

Across the phylum PG-5, *Antp*, *Lox2* and *Post-1* are absent, the Hox cluster is broken, and PG-2 is absent in Cestoda [594].

Rotifers, nemerteans, brachiopods, bryozoans

A bdelloid rotifer of the genus *Adineta* (strain SCL-15-7) was revived from Siberian permafrost [595]. The sample lay 3.5 m below the surface, position 16.53, at the Alazeya River, north-eastern Siberia [595]. Its calibrated radiocarbon age is 23,960–24,485 years, positions 58.05–58.07 [595].

The clonal culture reproduced by obligate parthenogenesis [595]. In a test 144 individuals were frozen at −15 °C for a week, position 45.27, and their freeze tolerance did not differ from that of modern *Adineta* (p = 0.25) [595]. Earlier reports gave 6–10 years frozen, positions 50.50–50.97; the permafrost record is longer by 23,960 / 10 = 2,396 to 24,485 / 6 = 4,081 times.

The rotifer held its closed form through twenty-four thousand years without exchange and then took up life again. Here the form is rest and discharge: loading, holding, release, with a holding phase of any length.

In bdelloid rotifers 2,792 of 28,922 matched transcripts are foreign, 2,792 / 28,922 = 9.7 % [202]. About 59 % of the foreign sources are bacterial and 23 % fungal [202]. The rotifer *Adineta vaga* lacks PG-3, *Lox2* and the posterior Hox genes and has its other Hox genes in several copies; *Philodina roseola* has two central genes [594].

In the nemertean *Micrura alaskensis* nine Hox genes were analysed, and *Lox2* and *Post-1* were not recovered in three nemerteans [594]. In the brachiopod *Lingula anatina* *Lox4* and *Lox2* are identified [594]. Nemerteans have ventral nerve cords, and ventral nerve cords evolved convergently “many times” among bilaterians [596].

Gigantoproductid brachiopods of the Visean of Derbyshire “reach over 30 cm in width and over 1 cm in shell thickness”, positions 14.29 and 11.19 [597]. The mean shell area of *Gigantoproductus* species is 11,393 mm², against 679 mm² in associated genera, 11,393 / 679 = 16.8 [597]. A large *G. okensis* lived 20 years by its growth bands, position 51.60, and its growth rates “were high, especially at the juvenile stages” [597].

The span of sizes runs from 174 µm bryozoan zooids, modules of a colony, to brachiopod shells over 30 cm wide: 0.30 / 174 × 10⁻⁶ = 1,724. The smallest whole animal among them is the 0.5 mm planarian, 0.30 / 0.0005 = 600 times smaller than the largest shell.

Counting the small spiralians

group	described species	of which fossil
Platyhelminthes	29,488	1
Gastrotricha	794	0
Rotifera	2,049	0
Acanthocephala	1,199	2
Gnathostomulida	97	—
Micrognathozoa	1	—
Cycliophora	2	—
Nemertea	1,358	0
Phoronida	16	—
Bryozoa	11,474	5,466
Brachiopoda	7,390	6,998
Entoprocta	172	1
All Animalia	1,659,420	133,692

[587]

Living bryozoans number 11,474 − 5,466 = 6,008; fossils are 5,466 / 11,474 = 47.6 % of

described bryozoans. Living brachiopods number 7,390 − 6,998 = 392, 392 / 7,390 = 5.3 % of the phylum; fossils are 94.7 %.

The five groups sum to 29,488 + 2,049 + 11,474 + 7,390 + 1,358 = 51,759 species, 51,759 / 1,659,420 = 3.1 % of described animals. With the seven other small phyla of the table the sum is 54,040, 3.3 %. Flatworms alone are 29,488 / 51,759 = 57.0 % of the five-group sum.

The brachiopods opened in the early Cambrian and reached their fullest in the Palaeozoic; nineteen in twenty of their known species are fossils. The form held while its carriers came and went.

Nematodes and small moulting animals

The moulting animals, Ecdysozoa, are defined by a moulting cuticle [567]. Seven of their eight phyla keep small bodies: Nematoda, Nematomorpha, Tardigrada, Onychophora, Priapulida, Kinorhyncha and Loricifera. The eighth, the arthropods, shows the least conflict between clock and fossil ages [525].

The record

The armoured *Eokinorhynchus* of 535 Ma has a trunk of at least 20 annuli, A1 to A20, each with about 20–40 small plates [567]. The trunk carries 5 bilateral pairs and 1 midventral large sclerite, and 2 pairs of caudal spines [567]. Its longest trunk annulus is about 110 µm, position 7.09, and its largest sclerites up to about 290 µm, position 7.97 [567].

The introvert of *Eokinorhynchus* carries 7 circlets of scalids, with 25 scalids in each of the first two [567]. The neck has 5 circlets of 10, 11, 11, 13 and 12 scalids, 10 + 11 + 11 + 13 + 12 = 57 in all [567].

The oldest unequivocal nematodes come from the Rhynie chert of Scotland, Early Devonian, Pragian, 410.8–407.6 Ma, positions 66.92–66.92 [598]. They may carry the earliest evidence of plant parasitism [598].

Before 2021 only two definite crown-group tardigrades had been described, plus one possible Cambrian stem form [599]. *Paradoryphoribius chronocaribbeus*, from Dominican amber at La Cumbre, about 16 Ma old, position 63.97, raised the count of confident fossils to three [599]. It is 559 µm long, position 8.57, and is the first unambiguous fossil of the Isohypsibioidea [599].

Later work redescribed *Beorn leggi* and described *Aerobius dactylus* from Canadian Cretaceous amber [600]. It lists *Milnesium swolenskyi* (Late Cretaceous) and *Paradoryphoribius* (Miocene) as the earlier resolved fossils [600]. Its clock gives an early Palaeozoic diversification of crown tardigrades and a split from the other panarthropods before the Cambrian [600].

The same analysis places the move to land of eutardigrades and heterotardigrades around the end of the Carboniferous and in the Lower Jurassic [600]. Four Hox genes ancestral for the Panarthropoda, *pb*, *Scr*, *Antp* and *Ubx/abd-A*, were lost in the tardigrade line [601]. The tardigrade body consists of “just a head and four leg-bearing

segments”, five body units [601].

Caenorhabditis elegans

The adult *C. elegans* hermaphrodite has 959 cells and 302 neurons; neurons are 302 / 959 = 31.5 % of its cells [602]. The 302 neurons fall into 118 classes [603]. They form about 5,000 chemical synapses, 2,000 neuromuscular junctions and 600 gap junctions, about 7,600 connections [603].

stage	duration	position
age at maturity	3 d	44.50
MY6, minimum generation time	67.3 h	44.44
N2, minimum generation time	73.0 h	44.51
MY6, mean generation time	84 h	44.64
N2, mean generation time, 20 °C	90 h	44.70
MY6, lifespan	14.7 d	45.95
N2, lifespan	16.7 d	46.06
maximum longevity in captivity, 0.16 yr	58 d	47.20

[604][605]

The life-cycle values were measured at 20 °C with 5 × 10^9 *E. coli* per ml [604]. Strain N2 (n = 69) reached an intrinsic growth rate of 1.375 d^{-1}, a net reproductive rate of 291 and peak egg-laying above 140 eggs a day [604]. AnAge gives 0.16 years, 0.16 × 365 = 58 days; higher temperatures shorten life and lower ones extend it [605].

The worm passes through 4 moults, and before each it enters lethargus, a sleep-like state [606]. Six Hox genes lie as three pairs in one region of chromosome III: *ceh-13*, *lin-39*, *mab-5*, *egl-5*, *php-3* and *nob-1* [607][608]. They keep 4 orthology classes (labial, Scr, Antp, posterior) in 6 genes.

The tardigrade *Hypsibius dujardini* has orthologues of five Hox genes, *lab*, *Hox3*, *Dfd*, *ftz* and *Abd-B*; *Abd-B* has three paralogues, so the total is eight [601]. *Milnesium tardigradum* has the same five with one *Abd-B* [601]. The authors call the loss “an unprecedented degree of loss in Panarthropoda”; the *H. dujardini* assembly is 212.3 Mb [601].

The *C. elegans* embryo has a fixed left–right handedness [609]. Reversing it by micromanipulation at the 6-cell stage gave “healthy, fertile animals with all the usual left–right asymmetries reversed” [609]. Left–right asymmetry is set by a series of inductive events in the embryo, and mutants that lose it completely are known only in this worm [610].

The direction is laid down at six cells and kept by the whole body after. Either direction makes a whole, fertile worm; the body keeps the one it was given first.

Long rest

suspended life	duration	position
Acutuncus antarcticus (tardigrade), frozen in moss	about 30.5 yr	51.98

Panagrolaimus kolymaensis (nematode), in permafrost	about 46,000 yr	58.64

[611][612]

The tardigrade *Acutuncus antarcticus* was recovered from Antarctic moss kept at −20 °C for about 30.5 years [611]. Two eggs from separate samples developed and one hatched, and a revived animal reproduced again and again [611].

Panagrolaimus kolymaensis was revived from Siberian permafrost after about 46,000 years, dated by radiocarbon to the late Pleistocene [612]. Its toolkit for suspended life is partly shared with the dauer larva of *C. elegans* [612]. The permafrost record is 46,000 / 0.16 = 287,500, about 290,000, times the active life of *C. elegans*.

Velvet worms

Velvet worms (Onychophora) give the within-species counts of this group. A 2018 study counted leg pairs in six *Epiperipatus* species [613].

species	males (leg pairs)	females (leg pairs)
E. titanicus	36–38 (abstract: 38)	36–39 (abstract: 39)
E. lucerna	27–29	29–31 (diagnosis: 29–30)
E. hyperbolicus	23 (holotype)	24 and 25 (diagnosis: 23–25)
E. beckeri	unknown	28–30, juveniles included; holotype 30
E. marajoara	27	31 (one female)
E. edwardsii	30 (one male)	—

[613]

Within one species the counts step by 1: *E. titanicus* shows 36, 37, 38 and 39 pairs, *E. hyperbolicus* 23, 24 and 25 [613]. Females carry 1–4 more pairs than males, or 1–2 without *E. marajoara*, where one female has 31 − 27 = 4 more.

species	length	position
E. lucerna, males	13–29 mm	11.43–12.16
E. titanicus, females	16–76 mm	11.62–13.04
E. hyperbolicus, females	22–33 mm	11.91–12.28
E. lucerna, females	23–44 mm	11.95–12.54
E. hyperbolicus, male	26 mm	12.06
E. titanicus, males	29–41 mm	12.16–12.48
E. beckeri	35–53 mm	12.33–12.71

[613]

In *E. titanicus* the female range contains the male range; in *E. lucerna* the female range lies above it [613].

Nematodes in the soil

Soil nematodes fall into five feeding guilds: bacterivores, fungivores, herbivores,

omnivores and predators [614]. Bacterivores are the most abundant and predators the least [614]. The median density is 859 per 100 g of dry soil, the mean 2,671 and the maximum above 20,000; the mean is 2,671 / 859 = 3.1 times the median [614].

Biome medians run from 2,695 per 100 g in tundra to 44 in hot desert [614]. The global soil stock is 4.4 ± 0.64 × 10^{20} individuals, with about 0.3 Gt biomass [615]. One soil nematode has a mean fresh mass of 0.3 × 10^{15} g / 4.4 × 10^{20} = 0.68 µg.

Of all soil nematodes, 38 % live in sub-Arctic soils, 24 % in temperate and 21 % in tropical soils, 83 % together [615]. In carbon, nematodes hold 0.02 Gt C, against 0.2 Gt C for terrestrial arthropods and 1 Gt C for marine arthropods [235].

About 4,100 nematode species are plant parasites, about 25 % of about 16,000 terrestrial species; 4,100 / 16,000 = 25.6 % [616]. Plant parasitism evolved independently in 4 major clades and several times within them, and losses to plant-parasitic nematodes are estimated at about €110 billion a year [616]. In root-knot nematodes the first eggs appear 28–42 days after infection, positions 46.53–46.90 [617].

Counting the small moulting animals

The 2022 nematode census lists 28,537 valid species named to the end of 2019, in 3,030 genera, 276 families, 32 orders and 3 classes [618]. The estimated true total is 0.5–10 million species [618]. A census of 2011 gives 24,783 nematodes, 10 of them fossil, 28,537 − 24,783 = 3,754 fewer [619].

phylum	species (2011)
Nematoda	24,783 (10 fossil)
Nematomorpha	351
Tardigrada	1,157
Onychophora	182 (3 fossil)
Priapulida	19
Kinorhyncha	179
Loricifera	30
Animalia	1,552,319 (24,659 fossil)

[619]

The seven phyla total 24,783 + 351 + 1,157 + 182 + 19 + 179 + 30 = 26,701 species, 26,701 / 1,552,319 = 1.7 % of described animals [619]. Nematodes alone are 1.6 %, and the same census places about 80 % of animal species in the arthropods [619]. The tardigrade checklist of 2019 lists 1,508 species in 164 genera and 35 families, against 1,157 in 2011 [620][619].

Echinoderms and hemichordates

Echinoderms and hemichordates together form the Ambulacraria. Echinoderms carry a calcite skeleton, a water-vascular system and “usually five-part radial symmetry” [621]. Hemichordates are the acorn worms (Enteropneusta) and the colonial pterobranchs [578].

After the Cambrian

Asterozoans first appear in the Early Ordovician, and living sea stars have a Triassic first occurrence [586]. A second source places the origin of Asteroidea in the Late Ordovician, and sea stars break or drill shells by then [622]. Sea stars live from the intertidal zone down to about 6,000 m, position 23.30 [586].

A clock on 1,346 loci and 22 fossil calibrations places crown Eleutherozoa before the end of the Cambrian, with a youngest median of 492.1 Ma, position 67.09 [623]. Crown Echinodermata estimates are often older than the stereom calibration, some “even predating the origin of the Ediacaran biota” [623]. Crown sea urchins fall between the Pennsylvanian and the Cisuralian, with posterior 30.2 % for the late Carboniferous and 69.1 % for the early Permian [623].

Euechinoidea span the Permian–Triassic boundary [623]. Sand dollars (Scutelloida) originate before the K–Pg boundary with posterior 1.00, and clypeasteroids with 0.97 [623]. That lies at least 40–50 Myr, positions 64.80–65.01, and possibly 65 Myr, position 65.25, before their first fossils [623].

The five-part body

Echinoderm larvae are bilateral at first [576]. They pass through an asymmetric phase and give rise to a five-part adult [576]. Among fossil forms cinctans and stylophorans are asymmetric and derived ctenocystoids weakly so [576].

Some sea cucumbers lack calcite in the body wall [621]. Many sea stars have more than five arms, “about 50 in some cases”, with a bilateral pattern on top of the radial one [621]. Sea stars carry “five to 50 rays” and brisingids “six to 20 elongate arms” [586].

Coscinasterias acutispina typically has 7–10 arms and 2–5 madreporites; laboratory juveniles had six equal arms and one madreporite at 12 months after metamorphosis, position 48.87 [624]. Two of three then split; the third split four months later, position 47.87 [624]. Each split divided a six-armed animal into two halves of 3 arms [624].

Each half regrew 4 or 5 arms within 30 days, position 46.60, to 3 + 4 = 7 or 3 + 5 = 8, with 2 or 4 madreporites [624]. A second fission followed 1–3 months later, positions 46.61–47.61, in four or five of six [624]. The three founders became 12 individuals, with gonads fully developed 1–3 months after the second fission [624].

A body of six divides into two bodies of three, and each half grows on. This is the same form as the ring of chapter 1 that divides at depth 6 into two closed rings of three: here it shows at the size of an animal, 12 months old.

Allostichaster capensis was collected at Kaiser Bay, Golfo Nuevo, Argentina, at 10 m in November 2001, the peak of fission [625]. Of 15 parents 1 had 4 arms, 5 had 5 and 9 had 6, shares of 6.7 %, 33.3 % and 60.0 % [625]. Fourteen of the 15 split into two or more animals [625].

Offspring carried 1–4 arms; most splits gave two animals of 2 or 3 arms [625]. One five-armed parent gave three pieces of 2, 2 and 1 arms [625].

Pentaceraster cumingi in Bahía Chamela, Mexican Pacific, was sampled in one cold and one warm season each year from June 2016 to October 2019 [626]. Of 849 animals, 28

were abnormal, 3.29 % by the sum of three classes and 28 / 849 = 3.30 % by quotient [626]. Four arms occurred in 0.82 %, six arms in 1.06 % and five arms with one forked arm in 1.41 %, which is 7, 9 and 12 animals [626].

Most abnormal animals occurred in October 2016, then in February 2017 and October 2019 [626]. Both minority forms occurred in more than one year. The animals were 123.8 ± 15.2 mm long, position 13.48, and weighed 326.0 ± 62.4 g [626].

At 16 sites in Barkley Sound, British Columbia, atypical arm numbers occurred in 5 of 9 five-armed species [627]. Site means ran 0.8–14.6 % and species means 0–10 %; the bat star *Patiria miniata* was highest, with 0–25 % per site [627].

In *Acanthaster planci* identification codes are built from the number and arrangement of arms, and natural injuries changed the code in about 20–40 % of animals [628]. Gross deformities reached 43 % on Guam and 17 % in Panamá [628]. In the Philippines about 60 % carried sublethal arm injuries, most of them at 11–20 cm, positions 13.38–13.92 [629].

species	arm counts	shares or frequencies
Asteroidea (class)	5–50	—
brisingids	6–20	—
earliest radiate forms	2–5 primary rays	—
Coscinasterias acutispina	7–10 typical; 6 juvenile; 3 per half; 7 or 8 after regrowth	3 founders → 12 animals
Allostichaster capensis, parents (n = 15)	4 / 5 / 6	1 / 5 / 9 (6.7 / 33.3 / 60.0 %)
A. capensis, offspring	1–4	most 2 or 3
Pentaceraster cumingi (n = 849)	4 / 5 forked / 6	0.82 / 1.41 / 1.06 %; 3.29 % abnormal
Barkley Sound, 5 of 9 species	atypical	0.8–14.6 % per site; *Patiria* 0–25 %

[586][576][624][625][626][627]

The sea urchin *Strongylocentrotus purpuratus* holds the first intact deuterostome Hox cluster, in an unusual order [630]. From 5′ to 3′ it runs Hox1, Hox2, Hox3, 11/13c, 11/13b, 11/13a, 9/10, Hox8, Hox7, Hox6, Hox5, 11 genes with the anterior genes nearest the posterior ones [630].

The acorn worms *Saccoglossus kowalevskii* and *Ptychodera flava* carry Hox and ParaHox clusters in ordered micro-synteny [631]. The assemblies are about 758 Mb and about 1,229 Mb, with at least 19,270 and 18,556 genes with detectable orthologues [631]. A six-gene gill-slit cluster, *nkx2.1*, *nkx2.2*, *pax1/9*, *foxA*, *slc25A21* and *mipol1*, is intact in *Saccoglossus* in the vertebrate order over about 0.5 Mb [631].

The 3-day pluteus larva of *S. purpuratus*, position 44.50, yielded 19,699 cells that passed quality checks, of 29,130 estimated [632]. They form 21 clusters, 20 mapped to larval domains, and the larva holds 12 neuronal cell types [632]. In sea-urchin eggs the fast block to polyspermy acts “within a few seconds” of sperm entry, by depolarisation of the egg membrane [633].

Sizes, eggs and ages

what	size	position
Meioglossus psammophilus, adult	0.6 mm	8.63
Allostichaster palmula, disk-to-arm radius	2–10 mm	9.73–11.19
Ptychodera flava	more than 5 cm	12.66
Acanthaster planci, disk diameter	7–36 cm (mean 18.23 cm)	12.97–14.46 (13.84)
red urchin test at jaw 2.0 cm	11.9 cm	13.45
red urchin test at jaw 2.7 cm, printed	17.9 cm	13.82
largest reported red urchins	more than 19 cm	13.87
Evasterias echinosoma, *Pisaster brevispinus*, arm tip to arm tip	nearly 90 cm	15.29
Balanoglossus gigas	up to 2.5 m	16.22

[578][586][634][635]

The enteropneust range is 2.5 m / 0.6 mm = 4,167, and deeper pterobranch colonies reach “up to several centimeters” [578]. In the red sea urchin *Strongylocentrotus franciscanus*, test diameter follows jaw length J as D = 4.8951 J^1.2817 [635]. For a 2.0 cm jaw it gives 4.8951 × 2.0^1.2817 = 11.9 cm; for 2.7 cm it gives 17.5 cm, against 17.9 cm printed.

The 389 *Acanthaster planci* of the southern Gulf of California were measured from February 2008 to March 2009 [634]. More than 90 % of large animals fed on *Pocillopora*, and small ones more on *Porites panamensis*, coralline algae and turf, from 298 feeding observations [634]. In New Caledonia a 40 cm *A. planci* “can produce up to sixty million oocytes per spawning season”, up to sixty times more than one of 25 cm [636].

Eggs were compiled for 596 echinoderm species: holothuroids 184, ophiuroids 132, asteroids 149 and echinoids 131 [637]. Egg diameter runs from 50 µm to 4,400 µm, a factor 88 in diameter and $88^3 = 6.8 \times 10^5$ in volume [637]. The log-transformed distributions are bimodal in three of four classes [637].

eggs	diameter	position
smallest (*Synaptula reciprocans*, *Ophiactis kroeyeri*)	50 µm	6.37
ophiuroid planktotrophs	80–185 µm	6.80–7.56
ophiuroid brooders	100–1,000 µm	7.00–9.10
ophiuroid abbreviated development	150–350 µm	7.37–8.14
holothuroid lecithotrophs	150–950 µm	7.37–9.05
ophiuroid maximum (*Astrospartus mediterraneus*)	1,500 µm	9.47
largest (*Psychropotes longicauda*)	4,400 µm	10.45
asteroid modes	162, 475, 1,008, 2,472 µm	7.44, 8.42, 9.11, 9.92

echinoid modes	102, 317, 1,157, 2,000 µm	7.02, 8.05, 9.23, 9.73
holothuroid modes	194, 421, 1,024, 2,603 µm	7.61, 8.31, 9.12, 9.97
ophiuroid modes	165, 450, 1,528 µm	7.46, 8.37, 9.48

[637]

Large red sea urchins “are old and may have ages of 100 years or more”, position 53.06 [635]. The largest British Columbia animals, with jaws of about 2.8 cm, are estimated at around 200 years, position 53.69, from tetracycline tagging and bomb-^{14}C in jaw samples of seven urchins [635]. AnAge gives the red urchin 200 years in the wild and maturity at 550 days, position 49.24, with data quality acceptable [638].

AnAge gives the purple urchin *S. purpuratus* 50 years from growth rates, position 52.43, possibly an underestimate, and maturity at 730 days, position 49.50 [638]. The two maxima differ by 200 / 50 = 4.

In situ oxygen use of four abyssal brittle-star and sea-cucumber species was measured in chambers set down by ROV at 2,200–3,600 m, positions 22.39–22.84 [639]. The data were joined with those of 84 echinoderm species from all five classes [639]. The scaling of metabolic rate with mass differs among classes, and it shows no trend from shallow to deep water [639].

Counting

Echinodermata number 20,550 described species, 13,000 of them fossil, which leaves 20,550 − 13,000 = 7,550 living [587]. A second source gives about 7,000 living and 13,000 fossil species [621]. Echinoderms are 20,550 / 1,659,420 = 1.24 % of all described animals, fossils included.

Sea stars number 1,890 living species in about 370 genera and 36 families [586]. Valvatacea hold 1,224, Forcipulatacea 393, Velatida 145 and Spinulosida/Echinasteridae 135 species, 1,897 in sum [586].

Hemichordates hold 130 living species: Enteropneusta 108 (83 %) and Pterobranchia 22 (17 %), in 24 genera [578]. Ptychoderidae hold 41 species and Harrimaniidae 40; *Balanoglossus* holds 20 species, *Saccoglossus* 18 and *Cephalodiscus* 18 [578]. A second total gives 126, 23 of them fossil [587].

What this part of the history shows

The residue becomes the alphabet: the post-synaptic scaffold, the Munc18/syntaxin secretion complex and every family of voltage-gated channels were complete in a single cell more than 800 Ma. The sponge keeps five scaffold genes switched on together in one larval cell type, and its NK cluster stood before any Hox gene. What closed at one depth became a letter of the next.

What closes, stays: a sponge passes 900 to 1,130 body volumes of water an hour through chambers of 16–56 µm that keep their shape. *Hydra* renews every tissue, nerve net included, in 2–3 weeks, and its form holds. The content flows; the closure stays.

The form lasts; its carriers are replaced. *Hydra* makes about 900 nerve cells a day and

shows no ageing over 41 years of cohorts. *Trichoplax* divided through some 2,000–4,000 generations in 11 years and stayed the same sheet.

The same form shows in long single lives. A *Monorhaphis* spicule holds 11,000 ± 3,000 years and a black coral 4,265 years. Planarians keep a memory of 14 days through the replacement of the head, and only their neoblasts divide.

The nerve cell is a cell whose edge tension travels along its length. In cnidarian tissues the travel runs at 3.0 cm s^{-1} to 4 m s^{-1}, a factor 133. The first comb-jelly net is five fused cells without synapses; the *Hydra* net holds 0.12 nerve cells per epithelial cell.

A closure cannot load twice in succession without first discharging. Every conducting tissue shows it as a refractory period. It lasts 3.5 ms in the *Aglantha* giant axon, 40–50 ms in a sea-pen nerve net, about 300 ms in an anemone slow system and 29 s in a glass sponge.

A living strand has one direction. *Velella* colonies sail left or right for life, without genetic difference between the forms; the north holds 91.9 % left and the south 54.9 % right. A *C. elegans* embryo reversed at six cells grows into a whole, fertile worm with every asymmetry reversed.

The same winding shows at every depth. A six-armed *Coscinasterias* divides into two halves of three arms, as the ring of six divides into two closed rings of three. Each half regrows to seven or eight arms and divides again.

Loading, holding, discharge. A bdelloid rotifer held for 23,960–24,485 years and a nematode for about 46,000 years, then fed and reproduced. *Trichoplax* pauses for 3 min within cycles of 13 min, and box jellyfish pacemakers beat near 1 Hz.

A new kind of body opens once; then the opened depth fills many times. The phyla appear within about 30 Myr of the Cambrian base. Then they fill: about 9,837 sponges, 16,400 cnidarians, 29,488 flatworms and 28,537 nematodes, with 0.5–10 million nematodes estimated in all.

8. Plants Take the Light

Chapter 3 followed the bacteria and archaea; chapter 5 followed the cell that took in a cell. One bacterial line learnt to split water with light, and one eukaryote took such a bacterium in and kept it. From that pair come the red algae, the green algae and every plant on land.

This chapter tells that history in fifteen parts. It runs from the cyanobacteria through the algae of red, green and brown, onto land with the bryophytes, up into trees with the lycophytes, ferns and seed plants, and into the flowers. It ends with the extremes of size and age and with the green cover of the present Earth.

Each group is given by its first appearance, its sizes, its times, its build, its light, and its count. Every size and time stands with its position on the ladder of chapter 1.

The light that is taken

Plant pigments take up light between 400 and 700 nm, positions 1.98 and 2.49 [640]. Chlorophyll a absorbs blue and red and passes green; carotenoids take up blue and reflect yellow, orange and red [640]. A photon above 700 nm does not excite chlorophyll, and more than half of the Sun's photons at the ground lie there [641].

The Sun delivers 1,360.8 ± 0.5 W m^{-2} at the top of the atmosphere, measured at the solar minimum of 2008; the NASA fact sheet gives 1,361.0 [642][643]. Spread over the turning sphere this is 1,360.8 / 4 = 340.2 W m^{-2}. Of it 29 % returns to space, 23 % is taken up in the air and 48 % reaches land and ocean, 0.48 × 340 = 163 W m^{-2} [644].

One mole of photons at 700 nm carries $6.626 \times 10^{-34} \times 2.998 \times 10^{8} / 7.00 \times 10^{-7} \times 6.022 \times 10^{23}$ = 171 kJ; at 400 nm it carries 299 kJ. The excess of the blue photon over the red is given off at once as heat [641].

The lowest measured requirement is 9.7 photons absorbed per molecule of oxygen, in the green alga *Chlorella vulgaris* under weak light [645]. One glucose needs six oxygen, so 6 × 9.7 = 58.2 photons and 58.2 × 171 = 9,950 kJ per mole of glucose. Glucose gives back 2,800 kJ per mole when burnt, so 2,800 / 9,950 = 28 % of the red light is kept; a table of the same reckoning gives 27 % [646][647].

Under the full spectrum of sunlight the kept share falls to 5 % [647]. Light-saturated leaves, the plant's own respiration and the growing season bring a well-tended field to about 1 % of the light that falls on it [641]. About half the sugar made is burnt by the plant itself [641].

The light is the carrier that does not stay; the sugar is the closed form that does. Fifty-eight photons, each gone the moment it is absorbed, leave one molecule that holds 2,800 kJ per mole for years in dry grain.

Cyanobacteria: water split by light

The oldest stromatolites with a biogenic shape lie in the Strelley Pool Chert, Pilbara, Australia, at 3,430 Ma, position 68.86 [108]. The earliest undisputed cyanobacterial body fossil is *Eoentophysalis belcherensis* from silicified stromatolites of the Belcher Group, 2,018–1,854 Ma, positions 68.37–68.30 [648]. The oldest fossil thylakoids lie in *Navifusa majensis* of the McDermott Formation, Australia, 1,780–1,730 Ma, positions 68.26–68.23 [648].

The same structure appears in the Grassy Bay Formation, Canada, at 1,010–900 Ma, positions 67.74–67.64 [648]. A clock places crown cyanobacteria in the Archean, and the living diversity of the ocean picocyanobacteria *Prochlorococcus* and *Synechococcus* after the Cryogenian [649].

Free oxygen in the air is dated to about 2.33 Ga from sulfur isotopes in three drill cores of the Transvaal Supergroup, a change that took roughly 10 Myr, position 63.54 [225]. A U–Pb age of 2.426 ± 0.003 Ga for Ongeluk magmatism puts the onset between 2.460 and 2.426 Ga, with oscillation for about 200 Myr to 2.250–2.240 Ga [226]. The positions are 68.50 and 68.55; another summary gives roughly 2.5 Ga, position 68.57 [227].

Oxygen reached near-modern levels in sea and air about two billion years after it first rose [227]. Black shales of the basal Doushantuo Formation, 635–630 Ma, position 67.32, record a widely oxygenated ocean right after the Marinoan glaciation [449]. The gap from 2.33 Ga is 2,330 − 635 = 1,695 Myr, position 68.21.

The smallest cyanobacterium is *Prochlorococcus*, 0.5–0.7 µm across, positions 2.18–2.49, “the smallest-known oxygen-evolving autotroph” [650]. In the deep sunlit zone it exceeds 10^5 cells per ml [651]. It “typically divides once a day”, and in the equatorial Pacific at 30 m it reached about one doubling a day, position 43.50 [650][652].

DNA replication falls in the afternoon and division at night, in phase with the daily light [652]. In strain MED4 under 14 h light and 10 h dark, 80 % of genes cycle over 24 h, position 43.50 [653]. Growth falls in the light, division in the dark, and all cells have divided by sunrise.

A single cell ends at fission; its life is its generation.

Prochlorococcus carries divinyl chlorophyll a and b with α-carotene and zeaxanthin [651][650]. It has replaced the large phycobilisomes of other cyanobacteria by a light-harvesting protein induced under iron stress, and some strains keep a little phycoerythrin [650]. Chlorophyll f, a fifth chlorophyll isolated from Western Australian cyanobacteria, absorbs at 706 nm and fluoresces at 722 nm, positions 2.49 and 2.51 [654].

Chlorophyll d is “a major pigment” in one cyanobacterium [655]. Thylakoids are unstacked, in fascicular, radial or parallel sheets [656]. Rubisco “is confined to multiple capsid-like carboxysomes” [657].

Many cyanobacteria are multicellular [417]. In heterocystous filaments three differentiated cell types stand beside the vegetative cell: the heterocyst for nitrogen fixation, the akinete for resistance and the hormogonium for dispersal, 4 in all [417]. Heterocysts stand “at semi-regular intervals” along the filament [417].

Trichodesmium has two cell states, diazocyte and vegetative, and no heterocysts [207]. Its nitrogen-fixing zones hold about 2–30 cells, with 1–2 zones per filament and about 15

% of cells [207]. Its genome is 7.75 Mbp [207].

Prochlorococcus marinus MED4 has 1,657,990 bp and 1,716 genes, “the smallest genome of any known oxygenic phototroph” [211]. Strain MIT9313 has 2,410,873 bp and 2,275 genes; the two share 1,350 genes, and differ by 752,883 bp and 559 genes [211]. The ocean makes about half of each year’s oxygen, and *Prochlorococcus* up to 20 % of it [230].

Algae in all number about 72,500 estimated and about 44,000 named, with 33,248 processed in AlgaeBase by June 2012 [658][659].

The cell that splits water keeps one rhythm with the light: replication by afternoon, division by night, all cells divided by sunrise. Here the form is metabolism held in a day: the content passes and the cell holds its closed form through one turn of the Earth.

Red algae: the first plastid in a multicellular body

Bangiomorpha pubescens from the Hunting Formation, Somerset Island, Arctic Canada, is a bangiacean red alga with a differentiated holdfast and spores or gametes [419]. Re–Os dating of the Bylot Supergroup gives it 1.047 +0.013/−0.017 Ga, position 67.78 [356]. A clock in the same study puts eukaryotic photosynthesis at about 1.25 Ga, position 67.94 [356].

An older claim rests on *Rafatazmia chitrakootensis* and *Ramathallus lobatus* from the Tirohan Dolomite, India, about 1.6 Ga, position 68.16, “probable crown-group red algae” [355]. *Ramathallus* shows apical growth; *Rafatazmia* has pit connections and a rhomboidal body read as a pyrenoid [355].

Clocks put crown red algae at 1,984–1,732 Ma and the primary plastid at 2,137–1,807 Ma [342]. The root of red plus green, Plantae, is 1,694 Ma (95 % HPD 1,484–1,925), position 68.21 [420]. The Bangiophyceae–Florideophyceae split is 943 Ma (817–1,049), and the subclasses follow: Hildenbrandiophycidae 781, Nemaliophycidae 661, Corallinophycidae 579 (543–617) and Ahnfeltiophycidae/Rhodymeniophycidae 508 Ma [420].

event	age	position
primary plastid, clock	2,137–1,807 Ma	68.42–68.27
crown red algae, clock	1,984–1,732 Ma	68.36–68.23
root of Plantae, clock	1,694 Ma	68.21
Tirohan Dolomite red algae	about 1,600 Ma	68.16
eukaryotic photosynthesis, clock	about 1,250 Ma	67.94
Bangiomorpha, Re–Os	1,047 Ma	67.78
Bangiophyceae–Florideophyceae	943 Ma	67.68
Hildenbrandiophycidae	781 Ma	67.51
Nemaliophycidae	661 Ma	67.36
Corallinophycidae	579 Ma	67.24
Ahnfeltiophycidae/Rhodymeniophycidae	508 Ma	67.12

[342][420][355][356]

The smallest red alga is *Cyanidioschyzon merolae*, 2 µm across, position 3.44 [360]. It has one nucleus, one mitochondrion and one plastid, no rigid wall, and lives in hot springs at pH 1.5 and 45 °C [360]. Its cell cycle is “highly synchronized by a 12-h light/12-h dark cycle”, with binary fission in the dark at 42 °C: one division in each 24 h, position 43.50 [660].

The circadian control of its cell cycle does not need translation [660]. Its 10D genome has 16,520,305 bp on 20 chromosomes, 5,331 genes, at least 86.3 % of them expressed, 26 genes with introns and 3 rDNA copies; a later paper gives 16.7 Mb [360][660].

The red-algal body runs from one cell (*Cyanidioschyzon*) through filaments (*Bangiomorpha*) to many-celled thalli [360][419]. Florideophyceae have a carposporophyte stage and are “the most abundant and diverse class of Rhodophyta” [420]. Red algae keep phycobilisomes, bilin-based light harvesting, and “do not exhibit thylakoid stacking” [360][661][656].

The red-algal plastid is “surrounded by a double membrane”, two membranes, as in glaucophytes and green plants [661]. *C. merolae* has no pyrenoid and no carbon-concentrating mechanism [657].

The cyanobacterium inside the eukaryote has two membranes, one closure inside another. Here the form is the residue becoming the alphabet: a whole free-living closure becomes one letter, the plastid, of the next.

Green algae

Proterocladus antiquus from the Nanfen Formation, North China, about 1,000 Ma, position 67.73, is a millimetre-sized, multicellular chlorophyte with lateral branches [421]. Clocks put core Chlorophyta at about 1,000–700 Ma, and the main Ulvophyceae lines radiated just before or during the Cryogenian [422]. Bryopsidales and Dasycladales fossils occur from the Cambro-Ordovician [422].

For the volvocine algae two values are published: the common ancestor of *Volvox* and *Chlamydomonas* at about 50 ± 20 Ma, position 65.01, and at “around 250 MY”, position 66.47 [466][424].

what	size or time	position
Chlamydomonas reinhardtii, cell	about 10 µm	4.91
Caulerpa taxifolia, frond	15–30 cm	13.66–14.29
Caulerpa taxifolia, stolon	more than 1 m	15.39
Acetabularia, circadian period	about 27 h	43.61
Volvox carteri, generation	48 h	44.13
Ulva mutabilis, growth to gametogenesis	3–5 weeks	46.27–46.74

[423][427][662][424][425]

Volvox carteri is a sphere of “several hundred microns diameter” with about 2,000 somatic cells and 12–16 gonidia, and “a new generation every 48 h” [424]. It has 2 cell types, sterile somatic and germ, a “germ-soma division of labor” [466][424]. Somatic cells carry 2 flagella and gonidia none; it is haploid in the vegetative phase with only the

zygote diploid [424].

Caulerpa taxifolia is one coenocytic cell with stolons “upwards of 1 m in length” and fronds of 15–30 cm, “debatably the largest single-celled organism in the world” [427]. Its pinnate fronds sit on a stolon with frond, rachis, pinnule, stolon and holdfast [427]. *Acetabularia* is one uninucleate cell “centimeters tall at maturity” that grows at an apical tip [426].

In a single *Acetabularia* cell the oxygen balance cycles with a period of “about 27 hours” [662]. Period and phase of the photosynthetic rhythm are unaffected by actinomycin D, puromycin and chloramphenicol [663].

Ulva has 3 cell types, rhizoid, stem and blade, and shows “alternation of isomorphic generations”, 2 phases [425]. Its gametes carry 2 flagella, as does *Chlamydomonas* [425][423]. *Proterocladus* has lateral branches [421].

Green algae have no phycobilisomes: green plants “retained bilin biosynthesis in the absence of phycobiliproteins” [661]. Their thylakoids have “clearly differentiated stacked and unstacked regions” without the many-disc grana of land plants [656]. The *Chlamydomonas* pyrenoid is near-spherical, 1.5–2 µm across, positions 3.18–3.44; pyrenoids are “often absent in seaweeds” [657].

The *Chlamydomonas reinhardtii* genome is a 121 Mb draft with 15,143 protein-coding gene predictions and 17 linkage groups [423]. *Volvox carteri* has 138 Mb and about 14,500 predicted proteins, 17 Mb more [469].

One cell of *Caulerpa* reaches a metre; a sphere of *Volvox* holds two thousand cells of two kinds. The same closed cell at the base carries both: one nucleus-filled body, or many bodies with one division of labour.

Charophytes: the algae nearest the land plants

The stoneworts (Charales) are present as *Palaeonitella cranii* in the Rhynie chert, Early Devonian [428]. It has furcating branchlets, antheridia on a pedicel, and gyrogonites of 6 sinistrally spiralling cells with a coronula [428]. The Rhynie chert has a U–Pb age of 411.5 ± 1.3 Ma, position 66.93 [458].

Older charophyte gyrogonites belong to the Palaeozoic Sycidiales and Moellerinaceae [664]. The origin of the land plants is Cambrian by clock [455]. A phylogenomic study of the Zygnematophyceae, the sister of land plants, covers 46 taxa and 326 nuclear loci, defines five orders and finds at least 5 independent origins of filamentous growth [412].

Six cells, all wound one way, close the gyrogonite. Here the form is a closed ring of six with one direction.

Chara internodal cells reach “up to diameter of 1 mm and up to half meter long in some species”, and axial internodes “up to 30 cm” [665]. The positions are 9.10, 14.76 and 14.29. The extreme cell is 0.5 / 0.001 = 500 times as long as wide.

Cytoplasmic streaming in characean cells “can reach 100 µm/sec” [665]. At that speed a 30 cm internode is crossed in 0.30 / (100 × 10^{-6}) = 3,000 s, position 40.44.

The Zygnematophyceae are unicellular (*Mesotaenium*) or unbranched filaments

(*Spirogyra*, *Zygnema*), and hold “>4,000” species [412]. The Charales, with nodes, internodes and whorled branchlets, have “the most complex body plans” among charophytes, and their zygote stores proteins [666][665]. *Spirogyra* runs a carbon-concentrating mechanism with a pyrenoid [657].

Charophyte thylakoids are stacked; some authors call the stacks of Coleochaetales and Charales “grana”, and others do not [656]. The plastid has 2 membranes [661].

genome	size	genes
Chara braunii S276	1,751,211,849 bp (flow cytometry 1.89–1.96 Gbp; k-mer 2.35 Gbp)	34,718
Mesotaenium endlicherianum SAG 12.97	173.77 Mbp	10,300
Spirogloea muscicola CCAC 0214	171.14 Mbp	24,093

[666][667]

The *Chara* assembly is 1,751.2 / 173.77 = 10.1 times the *Mesotaenium* assembly.

Brown algae, diatoms and the plastid taken twice

The secondary endosymbiosis of a red alga into a heterotrophic host, the source of the heterokont plastid, is about 1 billion years old, position 67.73 [362]. Brown algae are “chlorophyll-c containing algae” with a plastid from a red-algal endosymbiont [365]. Diatoms have “plastids acquired by secondary endosymbiosis”, and haptophytes are “a lineage possessing secondary plastids” [363][364].

A cyanobacterium inside a red alga, inside a third cell: the plastid now sits two deep. Partners with their own genome sit at most two deep inside a cell, and here the plastid stands at that second depth.

Brown algae (Phaeophyceae) have no accepted fossil older than the Cretaceous [365]. The oldest calibration fossil is *Padina*, minimum 100 Ma, position 65.64; *Julescraneia* and *Paleocystophora*/*Paleohalidrys* give a minimum of 13 Ma [365]. The 550 Ma *Miaohephyton* was tested and rejected as a brown alga [365].

The clock origin of the brown algae is 449.41 Ma (95 % HPD 333.85–572.02 Ma), Ordovician, position 67.01 [365]. Uncorrelated clocks give 435–455 Ma and the autocorrelated clock 595–600 Ma [365].

order crown	uncorrelated clock	autocorrelated clock
Laminariales	83.44 Ma (65.47)	231.51 Ma (66.40)
Fucales	65.81 Ma (65.26)	134.28 Ma (65.91)
Ectocarpales	54.08 Ma (65.08)	135.60 Ma (65.91)

[365]

The giant kelp *Macrocystis* emerged about 6 Ma, position 63.08 [464]. It “may become more than 60 meters long”, position 19.11 [365]. The smallest brown algae are “small filaments” [365].

Macrocystis fronds at Bahía Tortugas, Baja California, grew 12.8 cm a day in summer to 20.8 cm a day in winter in an unharvested bed [465]. In a harvested bed they grew 14.7 cm a day in spring to 23.3 cm a day in winter [465]. Mass increases 3.5 % a day in favourable places, a doubling time of ln 2 / ln 1.035 = 20.1 days, position 46.23 [464].

Macrocystis has a large diploid sporophyte alternating with a microscopic haploid gametophyte [464]. *Ectocarpus* alternates sporophyte and gametophyte too; its genome was sequenced from a haploid male [414].

The purported Lower Jurassic diatom *Pyxidicula*, about 182 Ma, and Middle Jurassic forms of 174–163 Ma are calcareous nannofossils and a testate amoeba [668]. The oldest accepted diatom assemblages are Lower Cretaceous, from Australia (37 species, 13 genera) and the Weddell Sea (47 species, 20 genera) [668]. The clock origin lies near the Triassic–Jurassic boundary, about 200 Ma, position 66.27; crown 190 and stem 199 Ma, with estimates of 250–183 Ma [668][669].

The oldest raphe-bearing diatoms are 82 Ma, early Campanian, from the Wombat locality, Canada, position 65.46; the Battle Formation gives 66.88–67.20 Ma [669]. *Thalassiosira* and *Phaeodactylum* diverged about 90 Myr ago, position 65.54 [362]. Coccolithophores have acted on climate “for over 200 million years” [364].

The diatom *Thalassiosira pseudonana* has a valve of 3.7 ± 0.62 µm in the wild type by SEM, position 4.00; across evolution experiments 3.66–4.97 µm, and Coulter means 3.98–5.93 µm [670]. Its exponential growth rate was 1.71 ± 0.42 and 1.79 ± 0.2 as slope of ln cell number [670]. Diatom cell volume spans “more than nine orders of magnitude” [670].

Diatoms harvest light with “fucoxanthin chlorophyll a/c-binding proteins” and perform about 20 % of global carbon fixation [671][363]. *Thalassiosira* has 24 diploid chromosomes [363].

Brown algae number 2,125 species, 46 % of the 4,619 non-diatom heterokonts in AlgaeBase; 2,125 / 4,619 = 46.0 % [365]. Some estimates give more than 200,000 diatom species [658].

genome	size	genes
Ectocarpus siliculosus	214 Mbp	16,256
Thalassiosira pseudonana	34 Mb draft (reannotation 32.4 Mb); plastid 129 kb, mitochondrion 44 kb	11,776
Phaeodactylum tricornutum	27.4 Mb	10,402
Macrocystis pyrifera	537 Mb (k-mer 513–542 Mb), 35 scaffolds	25,919
Emiliania huxleyi	141.7 Mb haploid (other isolates 99–133 Mb)	30,569

[414][363][362][464][364]

Onto land: the bryophytes

The oldest trace of land plants is cryptospores from the Dapingian, early Middle

Ordovician, Argentina, about 473–471 Ma, position 67.05 [454]. The record before stood at the late Darriwilian, about 463–461 Ma [454]. The oldest credible bryophyte body fossil is *Riccardiothallus devonicus*, Pragian, Early Devonian [455].

Plants colonised land from about 470 Ma, position 67.05 [672]. Carbonate $\delta^{13}C$ rose by a sustained 2 ‰ by about 445 Ma, deep-ocean oxygenation followed at 435–392 Ma, and charcoal shows oxygen above 15–17 % by 420–400 Ma [672]. A model gives about 2–11 % oxygen from the Cambrian to the mid-Ordovician and a low of about 14.5 % at about 393 Ma [673].

The Ordovician glaciation set in before 444 Ma, after non-vascular plants had spread [674]. Charcoal is present in sediments younger than 419 Ma and bounds oxygen to roughly 13–35 % since then [673][675].

Two clock studies date the land plants. One gives crown embryophytes 515.1–470.0 Ma, crown bryophytes 506.4–460.3 Ma, crown liverworts 443.6–405.3 Ma and crown mosses 448.6–344.3 Ma [455]. The other, with 68 fossil calibrations, gives crown embryophytes 515–493 Ma, crown bryophytes 500–473 Ma and mosses plus liverworts against hornworts 479–450 Ma [456].

The second study gives crown mosses 420–364 Ma, crown liverworts 440–412 Ma and crown hornworts 294–214 Ma, with alternatives of 258–419 and 331–445 Ma [456]. The first gives the first and second bryophyte divergences at 496.5–456.2 and 478.7–438.0 Ma [455].

event	age	position
crown embryophytes	515.1–470.0 Ma; 515–493 Ma	67.13–67.05
crown bryophytes	506.4–460.3 Ma; 500–473 Ma	67.11–67.03
oldest cryptospores	473–471 Ma	67.05–67.05
crown mosses	448.6–344.3 Ma; 420–364 Ma	67.00–66.76
crown liverworts	443.6–405.3 Ma; 440–412 Ma	66.99–66.91
crown hornworts	294–214 Ma	66.62–66.33
Sphagnum reference species	about 16 Ma	63.97
Physcomitrella within Funariaceae	about 10 Ma	63.54

[455][456][454][676][677]

Hornworts diverged from the other land plants more than 400 Ma ago, and the bryophyte–tracheophyte ancestor lived “some 500 million years ago” [678][679]. *Physcomitrella* separated from flowering plants “more than 400 million years” ago [680]. *Sphagnum* diversified in the Miocene, 7–20 Ma, with whole-genome duplications at 189–247 and 102–122 Ma [676].

The tallest moss is *Dawsonia superba* var. *superba*, with stems of 65 cm, position 14.99 [460]. The variety *pulchra* is 6–25 cm, leafy part to 15 cm; *D. polytrichoides* is 3–10 (–20) cm and *D. longiseta* 0.5–3.0 (–5.0) cm, in a genus of 9 species [460].

Polytrichaceae are “the tallest bryophyte family” [681].

what	duration	position
Marchantia, sporeling apical cell specified	7–10 days	45.27–45.60

Marchantia, three sporophyte tissues after fertilisation	2 weeks	45.90
Marchantia, gemma to new gemma cups	about 3 weeks	46.27
Marchantia, sporangia after fertilisation	about 4 weeks	46.53
Physcomitrella, full life cycle in a dish	about 4 months	47.87
Physcomitrella, annual life	1 year	48.87

[682][683][684][677]

In *Physcomitrella* the apical cell turns to caulonema “several days after germination” [677]. New *Marchantia* gemmae form 2–3 weeks after germination [683]. *Sphagnum* in culture grows +0.88 mm² a day at control pH and −0.08 mm² a day at low pH [676].

Sphagnum length growth in Karelia ran from 28 ± 7.0 mm a year (*S. majus*) to 77 ± 18.5 mm a year (*S. riparium*) in 2014 [685]. In 2015 it ran from 16 ± 7.5 (*S. papillosum*) to 266 ± 39.7 mm a year (*S. riparium*) [685]. In Kolkheti, Georgia, length growth reached 30.3 cm a year, position 14.30, and productivity 269–548 g m⁻² a year in *S. papillosum* and 387–788 in *S. palustre* [686].

The moss shoot grows from a “tetrahedral shaped apical cell, which subsequently cleaves spirally to produce a leafy shoot” [687]. The protonema grows by “uniplanar division of single apical stem cells”, and moss leaves are “spirally inserted” [687][677]. The *Marchantia* thallus has “a single wedge-shaped apical cell that resides in an apical notch”, dividing “in four planes” and branching by bifurcation [687].

The *Marchantia* prothallus has “an apical cell with two cutting faces”, shifting to four at the step from two to three dimensions [682]. Hornwort apical cells are “wedge-shaped” and “divide in four planes” [687]. Liverwort elaters have “helical wall thickenings”, about 32 : 1 relative to spore mother cells [682].

The *Physcomitrella* capsule has stomata “defined by a single guard cell” in its lower part, and its stem has “a central strand of thin-walled cells” [677]. Stomata are more than 400 Myr old [688]. Hornwort stomata were lost twice in derived taxa, and their guard cells resemble 400-Myr-old fossils [689].

In *Polytrichum commune* the water-conducting hydroids refill after embolism [681]. Most hornworts have a single chloroplast per cell and are “the only land plants with a pyrenoid-based CCM” [678]. Their pyrenoids were “lost at least five times during the last 100 million years” [678].

Chromosome numbers are 9 in *Marchantia*, 27 pseudochromosomes in *Physcomitrella* and 6 pairs in *Anthoceros agrestis* [682][677][678]. *Sphagnum* has 20 pseudochromosomes, with a small sex chromosome of about 4.7–5.4 Mb; cytology shows 19 bivalents plus usually two smaller M chromosomes [676]. In all bryophytes the haploid gametophyte dominates.

Mosses number 12,700 species, liverworts about 9,000 and hornworts about 225, together 21,925 [659]. Marchantiopsida hold 350–430 species in about 34 genera and Jungermanniopsida 4,000–7,000 [682]. The *Sphagnum* panel holds 17 species [676].

genome	size	genes
Marchantia polymorpha	about 220 Mb, 9 chromosomes	about 20,000
Physcomitrella patens v3.3	about 500 Mbp, 27 pseudochromosomes	32,458 gene models; 86,669 transcripts
Anthoceros spp.	117–133 Mb	24,700–25,800
Sphagnum divinum	439 Mb	25,227
S. angustifolium	395 Mb	25,100

[682][677][678][676]

The land plants form one crown group. From that one opening the depth filled: about twenty-two thousand bryophytes, and after them every vascular plant.

Lycophytes: the first vascular trees

Baragwanathia longifolia is the earliest club moss, of Gorstian (Ludlow, Silurian) age on graptolite evidence; its flora persisted into the Early Devonian [457]. *Asteroxylon mackiei* comes from the Rhynie chert, 407 Ma, position 66.92 [459]. The crown-tracheophyte minimum age is 420.7 Ma (Ludlow), and *Cooksonia* cf. *pertoni* gives 426.9 Ma (Wenlock) [455].

Vascular plants evolved in the Middle to Late Silurian, about 420 Ma, position 66.94 [690]. Clocks give crown lycophytes at 432.5–392.8 Ma and at 431–411 Ma [455][456]. Crown tracheophytes are 472.2–419.3 Ma across all analyses, 450.8–431.2 Ma with monophyletic bryophytes, and 452–447 Ma in the second study [455][456].

Isoetes has a fossil record back to “at least the late Devonian” and diverged from other CAM lineages more than 300 Ma ago [691].

Carboniferous scale trees (*Lepidodendron* and allies) reached “statures up to c. 45 m” with “trunk diameters up to 2 m”, positions 18.85 and 16.02 [461]. Height to trunk diameter is 45 / 2 = 22.5. Another source gives 10–50 m and 0.1 to more than 2 m [692].

The life of these trees is read in three ways.

An earlier estimate gave “no greater than 10–15 years”, positions 50.97–51.34 [461]. A life of about 10 years would need growth “twenty times higher than modern angiosperm trees” and “at least 60 times higher than modern lycopsids” [692]. Lifespans are “most likely measured in centuries”, position 53.06.

A third estimate gives about 400 years for a 40 m tree, range 200–800, position 54.32, with height growth of about 0.10 m a year [692]. The *Lepidodendron* stand of the Herrin coal, Illinois, had 1,769 stems per ha, basal diameters of 95 cm (34–144 cm), position 15.34, and a basal area of 992 m² per ha [693].

living lycophyte part	size	position
Selaginella apoda, lateral leaf length	1.35–2.25 mm	9.37–9.84
Selaginella selaginoides, leaf	2–4 mm	9.73–10.36
Selaginella rupestris, leaf length	2.5–4 (–4.5) mm	9.93–10.36
Lycopodium clavatum, leaf	3–5 mm	10.10–10.56
Huperzia lucidula, largest leaves	7–11 mm	10.87–11.28

Huperzia lucidula, largest leaves	7–11 mm	10.87–11.28
Isoetes lacustris, megaspore	0.55–0.75 mm	8.55–8.84
L. clavatum, upright shoot diameter	0.6–1.2 cm	10.73–11.36
S. apoda, strobili	1–2 cm	11.19–11.83
L. clavatum, strobili	15–25 × 3–6 mm	11.56–12.03
S. selaginoides, stem	3–15 cm	12.19–13.66
L. clavatum, peduncle	3.5–12.5 cm	12.33–13.49
I. lacustris, leaf	80–200 (–450) mm; up to 250 mm	13.09–13.92
H. lucidula, shoot	14–20 (–100) cm	13.60–13.92
L. clavatum, creeping stem	30–100 cm	14.29–15.39

[694][695][696][697]

From a *Selaginella apoda* leaf of 1.35 mm to a 45 m scale tree the span is 45 / 0.00135 = 33,333-fold. *Selaginella rupestris* leaves stand in pseudowhorls of 6 on the main stem and 4 on branches [696]. *S. apoda* leaves are 0.75–1.35 mm wide and *S. rupestris* leaves 0.45–0.6 mm [696].

Asteroxylon has three axis types: leafy shoots, root-bearing axes and rooting axes, the last formed “through anisotomous dichotomy” [698]. Its rooting meristems “lacked root caps”, and roots with caps are “a relatively late origin in lycophytes” [459]. *Selaginella* has “one or two transiently acting apical initials”, while the meristems of Isoëtaceae and Lycopodiaceae “contain multiple apical initials” [687].

The scale trees “produced secondary phloem”, limited bark and “relatively complex” wood [699]. The sporophyte dominates. *Isoetes taiwanensis* has 2n = 22 and a genome of 1.66 Gb (k-mer 1.65 Gb, flow cytometry 1.55 Gb) with 39,461 high-confidence genes [691].

Isoetes performs CAM under water: leaf acidity rises through the night, peaks in the morning and falls in daylight when the plant is submerged, a 24 h rhythm [691]. Lycopods number 1,290 species and *Isoetes* about 250, 250 / 1,290 = 19.4 % [659] [691].

The quillwort takes up carbon by night under water and by day in air. The same fixation runs to other hours in other surroundings: here the form is that of context.

Ferns and horsetails

Crown monilophytes date to 411.5–384.9 Ma and crown euphyllophytes to 437.6–402.2 Ma by one clock and 432–414 Ma by another [455][456]. The fern–seed plant divergence is about 400 Ma, position 66.90 [700]. The horsetail line reaches “back to the Upper Devonian” [701].

The *Equisetum* crown is mid-Paleogene by molecules; fossils with possible shared traits occur in the Triassic, and Equisetaceae and calamitaceans have been separate since the Carboniferous [702]. *Azolla* fossils occur from the Maastrichtian–Paleocene on [381].

The fern *Azolla* grew and reproduced in the Arctic Ocean about 50 Ma, position 65.01, for about 800,000 years, position 61.24 [703][381]. The *Azolla* phase stored 0.9–3.5 ×

10^{18} g C and drew CO_2 down by 55–470 ppm [704]. The *Azolla–Nostoc* partnership spans about 100 Myr, position 65.64 [381].

Azolla carries the obligate nitrogen-fixing cyanobacterium *Nostoc azollae* in leaf cavities and passes it on to its offspring [381]. Its doubling time is “as low as 2 days in their exponential growth phase” without fertiliser, position 44.13 [705]. *A. filiculoides* yields 9.72 g dry weight m^{-2} a day, 9.72 × 365.25 = 3,550 g m^{-2} = 35.5 t ha^{-1} a year, with mats of 2–3 kg fresh weight m^{-2} [705].

A plant with a bacterium in its leaves, the bacterium passed on with the plant: two addresses sharing one prefix. Here the form is community as shared prefix, held for about a hundred million years.

what	size	position
Equisetum spore	about 50 µm	6.37
Azolla caroliniana, stem	0.5–1 cm	10.56–11.19
Azolla mat thickness	up to 4 cm	12.46
E. telmateia subsp. *braunii*, fertile stem	17–45 cm	13.77–14.66
E. telmateia subsp. *braunii*, vegetative stem	30–100 (–200) cm	14.29–15.39
Pteridium aquilinum, leaf	30–180 (–500) cm	14.29–15.92
E. hyemale, height	up to 150 cm	15.76
E. hyemale subsp. *affine*, aerial stem	18–220 cm	13.83–16.10
E. giganteum, stem	more than 5 m	16.85
tree ferns, measured individuals	up to 6 m	17.02

[706][707][708][709][710][711][712]

Tested *E. hyemale* stems were 476–767 mm [710]. Giant horsetails “represent the largest living Sphenophyta” [701]. From an *Azolla* stem of 0.5 cm to a 6 m tree-fern trunk is a span of 1,200.

Dicksonia antarctica trunks grow 3.3 ± 1.3 cm a year, rising about 0.6 cm a year per metre of height; *Cyathea australis* trunks grow 7.3 ± 2.2 cm a year [712]. These were measured over 5 years after the 2009 fire in south-east Australia [712]. At 3.3 cm a year a 6 m trunk takes 6 / 0.033 = 182 years, position 53.61.

Shoots of *Nephrolepis exaltata* and *Ceratopteris richardii* “develop from a single tetrahedral AC”, with three cutting faces [700]. Ferns mostly have single apical cells, and *Ceratopteris* usually one apical initial [687]. *Equisetum* spores “have four elaters” that walk and jump as they fold with humidity [706].

Equisetum leaves are reduced to sheath teeth in whorls: 14–50 per whorl in *E. hyemale* subsp. *affine* and 14–30 (–36) in *E. telmateia* subsp. *braunii* [708].

Salvinia and *Pilularia* are heterosporous, and *Azolla* has nearly twice the chromosome number of other heterosporous ferns [381]. *Ceratopteris* has n = 39 [713].

Ferns number 10,560 species, “over 10,500 extant species”, the second richest vascular-plant clade [659][713]. Leptosporangiate ferns are about 80 % of non-flowering

vascular-plant species [700]. *Equisetum* has 15 living species [701][702].

genome	size	genes
Azolla filiculoides	0.75 Gb	20,201
Salvinia cucullata	0.26 Gb, “smallest fern genome reported to date”	19,914
Ceratopteris richardii	7.46 Gb assembled (k-mer 9.6 Gb), 39 chromosomes	36,857; 38,397 alternative transcripts

[381][713]

The *Ceratopteris* assembly is 7.46 / 0.26 = 28.7 times the *Salvinia* genome.

The first forests and the first seeds

The oldest known forest of standing trees lies in the Eifelian Hangman Sandstone Formation of Somerset and Devon [714]. Its trees are cladoxylopsids, mostly *Calamophyton*, on a river plain [714]. The Eifelian spans 393.3–387.7 Ma, positions 66.88–66.87 [435].

At Gilboa, New York, *Wattieza*/*Eospermatopteris* stumps belong to a cladoxylopsid tree “tall (at least 8 m)”, position 17.28, “about 385 million years old”, Givetian [715]. The oldest forest with *Archaeopteris* root systems is the Cairo quarry, New York, “early mid Givetian (ca. 385 Ma)”, position 66.86 [716]. Cairo is “approximately 2–3 Ma” older than Gilboa Riverside, and the same study defines the Mid-Devonian as 393–383 Ma [716].

From the Eifelian base to Cairo is 393.3 − 385 = 8.3 Myr, and from its top 387.7 − 385 = 2.7 Myr. The Hangman forest is placed before Cairo, which its own paper calls the oldest forest [714][716].

At Cairo the *Archaeopteris* root systems have “radial dimensions as much as 11 m across the paleosol surface”, position 17.57 [716]. Primary roots are “6–16 cm in diameter”, positions 12.83–13.72, with “as many as 10–15 primary roots” per tree [716]. Eighteen root systems were mapped in about 3,000 m², one per 3,000 / 18 = 167 m² [716].

The *Archaeopteris* roots reach 1.2–1.6 m deep, positions 15.55–15.81, and their 18 trees have trunk bases of 8–45 cm [716]. Heights estimated from root-system size are about 11–32 m, positions 17.57–18.54 [716]. A possible lycopsid left a root mound 1.9 m across [716].

The Cairo *Eospermatopteris* bases are “bowl-shaped depressions 20–50 cm in diameter”, positions 13.92–14.76 [716]. Their roots, “0.7–1 cm in diameter”, positions 10.87–11.19, reach 1–2 m from the centre and about 30 cm deep, position 14.29 [716]. Heights step by 32 / 8 = 4 from the Gilboa minimum to the Cairo estimate.

Archaeopteris branches laterally, not by dichotomy, a “lateral branching syndrome” of the modern tree with four traits of modernisation [717]. Its wood shows “strategies that minimize the mechanical stresses caused by perennial branch growth” [717]. Its root system is “essentially comparable to modern seed plants”, and it had “greatly expanded energy and resource use” [716].

Anatomically preserved *Archaeopteris* trunks occur in Famennian marine beds of south-east Morocco as “370-million-year-old plants”, position 66.83 [717]. The genus went extinct “around the Devonian/Carboniferous boundary” [717]. The Famennian begins at 372.2 ± 1.6 Ma and the Carboniferous at 358.9 ± 0.4 Ma, positions 66.83 and 66.80 [435].

The seed precursor *Runcaria heinzelinii* from Belgium is “middle Givetian (385 million years ago)” and predates “the earliest seeds by about 20 million years” [718]. The earliest seeds then fall at about 385 − 20 = 365 Ma, position 66.82. Seed plants “originated at least before 300 Ma (in the Carboniferous)”, position 66.64 [719].

Runcaria has a “radially symmetrical, integumented megasporangium surrounded by a cupule”, with a “multilobed integument” [718]. It is one lobed integument plus a cupule, and it is “anemophilous”, wind-pollinated [718]. The seed habit is present from the Famennian [718].

Medullosa shows “anomalous vascular cambium growth and many leaf traces entering each petiole base” [720]. Its tracheids are very large, with “volume flow rates closer to angiosperm vessels than to typical … coniferophyte tracheids”, and the plants may have been vines [720]. These are “tracheid-based stem plants” without vessels, at “significant risk of embolism and implosion” [720].

On the plant side five stages are distinguished over 485–298.9 Ma: non-vascular plants, vascular plants with lignified tissue, shallow roots, trees with deep complex roots, and seed plants [721]. Rooted plants appeared 400–360 Ma with a drop in CO_2 [722]. Tree plots raise calcium weathering about tenfold over bare plots at Hubbard Brook and 5–10 times in Iceland [722].

A compilation of 1,241 proxy estimates gives about 2,000 ppm CO_2 at about 400 Ma and values near 278 ppm at about 300 Ma [723]. The fall is (2,000 − 278) / 100 = 17 ppm per Myr over 100 Myr. Positions are 66.90, 66.80 and 66.64.

Coal forests spread across the palaeotropics in the Serpukhovian, expanded greatly in the late Bashkirian, contracted by about half in the Kasimovian and briefly re-expanded in the Early Permian [724]. The stage bases are Serpukhovian 330.9, Bashkirian 323.2, Moscovian 315.2, Kasimovian 307.0, Gzhelian 303.7 and Permian 298.9 Ma [435]. The forests lasted 330.9 − 307.0 = 23.9 to 330.9 − 303.7 = 27.2 Myr, positions 64.33–64.45.

Above the Mahoning coal more than 800 upright stumps stand in a peat body of about 60 km² [725]. After the earliest Kasimovian, about 305 Ma, tetrapod extinction peaked [726]. Oxygen stood above 26 % at the Carboniferous–Permian maximum by charcoal in mires, and insect wingspans then reached about 70 cm, position 15.06 [727][728].

Cycads and *Ginkgo*

The least equivocal early cycad is *Crossozamia* from the Shihhotse Formation, China, of Roadian–Wordian age, 265.1–272.3 Ma, positions 66.52–66.55 [729]. One source puts the cycad crown in the Permian and the split from *Ginkgo* in the Carboniferous; a nuclear-gene clock dates the crown to the Middle Jurassic, 158.1 Ma, position 66.05 [729][719].

Living cycad species are “not much older than ~12 million years”, position 63.71, from a near-synchronous worldwide rediversification beginning in the late Miocene [730]. Living genera show “rapid radiations ranging from 11 to 20 Myr ago”, positions 63.63–64.17 [731].

Ginkgo is “known to have existed early in the Jurassic period 170 million years (Myr) ago”, position 66.12 [732]. Yixian Formation *Ginkgo* with modern-type ovulate organs is “over 121 Myr old”, position 65.81 [732]. Its form is “essentially unchanged … for more than 200 million years”, “at least 200 million years” in a second source [733][734].

what	size	position
Ginkgo seed	20–30 × 16–24 mm	11.83–12.19
Lepidozamia hopei, stem diameter	50 cm	14.76
Encephalartos transvenosus, stem diameter	0.4–0.45 m	14.55–14.66
Macrozamia moorei, stem diameter	50–80 cm	14.76–15.18
Encephalartos woodii, trunk base	up to 900 mm	15.29
Ginkgo, stem diameter in cultivated Chinese trees	1–4 m	15.39–16.65
L. hopei, leaf	200–300 cm	16.02–16.39
Cycas media, stem	up to 3 (–6) m	16.39
Cycas angulata, stem	up to 5 (–12) m	16.85
M. moorei, stem	2–7 m	16.02–17.16
E. woodii, trunk	up to 6 m	17.02
E. transvenosus, stem	12–13 m	17.65–17.72
L. hopei, stem	up to 20 m	18.11
Ginkgo, typical tree	20–40 m	18.11–18.74
Ginkgo, reported maximum	64 m	19.17

[735][736][737][738]

Lepidozamia hopei carries up to 100 leaves in its crown, and *Cycas media* leaves carry 160–300 pinnae [735]. The tallest cycad stem is 20 / 0.5 = 40 times its diameter. One Korean *Ginkgo* is reported at 64 m with a girth of 14 m [738].

A cambial study covered *Ginkgo* trees “ranging from 15 to 667 years old”, position 54.79 [739]. Ring width drops sharply over the first 100–200 years while basal-area increment keeps rising, and there is no whole-plant senescence [739]. “The oldest known ginkgo trees in China were estimated to be approximately 1000–3000 years old”, positions 55.16–56.16 [734].

Ginkgo reaches sexual maturity at 20–30 years, positions 51.60–51.97, and grafted cultivars at about 5 years, position 50.34 [738]. Pollination falls in early April to late May and fertilisation in late August to late September, about 4–5 months later, positions 47.87–48.07; the ovules fall about 1 month after, position 46.61 [738]. The seed-to-seed generation is about 20–30 years plus 5–6 months.

Pollen germination takes “several days or more among cycads”, position 44.50 for three

days [740]. Gymnosperm pollen tubes grow at “<~20 µm/h”; at 20 µm an hour a tube covers 1 mm in 50 h, position 44.17 [741].

Cycad and *Ginkgo* sperm are multiflagellate; the structure “bears numerous flagella” [742]. Pollen has “four cells in pine and ginkgo”: two prothallial cells, a generative cell and a tube cell [743]. Both groups are dioecious, and the *Cycas* male-specific Y region is 45.5 Mb with 624 putative genes [731].

“Cycads are the only early seed plants that have evolved a specialized root to host endophytic bacteria that fix nitrogen” [744]. *Nostoc* is prevalent in these coralloid roots, with *Calothrix*; six cyanobacterial draft genomes were obtained from them [744].

Ginkgo has a vascular cambium [739]. Gymnosperms “cannot form structures that are homologous to angiosperm vessels”, and end-walls account for 56–64 % of xylem resistance in both tracheids and vessels [745][746].

Gymnosperms number 1,079 species [659]. The World List of Cycads gives 10 genera and 382 accepted species, 396 names with 14 infraspecific [747].

cycad genus	**species**
Cycas	124
Zamia	90
Encephalartos	71
Ceratozamia	45
Macrozamia	41
Dioon	19
Bowenia	2
Lepidozamia	2
Microcycas	1
Stangeria	1

[747]

The genera sum to 396; the list’s own accepted total is 382. Other counts give “about 360 extant species in 10 genera” and “~300 species” [731][730]. Cycads are 382 / 1,079 = 35.4 % of gymnosperms, and *Ginkgo* is one species.

genome	**size**	**genes**
Ginkgo biloba, draft	10.61 Gb, with 493 Mb of gaps	41,840
Ginkgo biloba, near-complete	9.87 Gb	27,832
Cycas panzhihuaensis	10.5 Gb, 76.14 % repeats, n = 11	32,353

[733][748][731]

The mean *Cycas* intron is about 30.8 kb and the longest about 1.5 Mb [731]. The *Ginkgo* form has stood for more than 200 million years; single trees hold it for 667 years without senescence, and the species as one form for longer. The form lasts; its carriers are replaced.

Conifers and gnetophytes

The conifer fossil record spans “more than 300 million years”, position 66.64 [749]. The last common ancestor of Pinaceae is 198.4 Ma, position 66.26; the Cupressaceae–Taxaceae split is Late Triassic to Early Jurassic; the Gnetales crown is calibrated at at least 125 Ma, position 65.84 [719]. Most conifer species diverged in the Neogene and the clades in the Mesozoic [750].

Welwitschia and *Gnetum* diverged “over 110 million years ago”, position 65.72, and the *Welwitschia* whole-genome duplication is about 86 Ma (78–96), position 65.50 [751]. The major seed-plant lineages diverged about 300 Ma [745].

what	size	position
Pinus sylvestris, average height	23–27 m	18.24–18.39
P. sylvestris, New York plantation, tallest at 74–77 years	29.0 m	18.45
P. sylvestris, maximum	more than 40 m	18.74
Picea abies	50–60 m (30–60 m at maturity)	18.95–19.11
Sequoia sempervirens, common height	60–84 m	19.11–19.42
Sequoia, champion	101 m	19.59
Sequoia, tallest in Silvics (1964)	112.1 m	19.68
Sequoia, tallest measured	112.7 m	19.69
height limit, estimate	122–130 m	19.76–19.82

[752][753][754][755][756][757][462]

Welwitschia has “just two leaves”, two ever-growing leaves on an unbranched stem [751]. It “can live for several thousand years”, and its leaves “grow continuously throughout the plant’s life” at 0.37 mm a day on average, varying 22-fold within individuals [751][758]. Its sex ratio is male-biased and the males are larger [758].

what	duration	position
Gnetales pollen germination	1–72 h	40.61–44.50
conifer pollen germination in vivo	0.5–9 months	45.98–48.61
pollination to fertilisation, *Pinus*	up to a year	48.87
needle life, low-elevation pines	2–4 yr	49.50–50.13
first seed, *Sequoia*	5–15 yr	50.34–51.34
first flowers, *P. sylvestris*, Michigan	5–8 yr (average 10–15)	50.34–50.76
first flowers, *P. abies*	20–30 (–40) yr	51.60–51.97
minimum seed bearing, *P. abies*	40–60 yr	52.23–52.60
needle life, *Pinus longaeva*	up to about 45 yr	52.34
lifespan, *P. abies*	200–300 yr	53.69–54.06
seed viability, *Sequoia*	more than 250 yr	53.90
lifespan, *P. sylvestris*	400+ yr; one tree over 750 yr	54.32; 54.90
oldest *Sequoia* by ring count	nearly 2,200 yr	55.88
Pinus longaeva, Wheeler Peak	4,900 yr	56.60

[740][743][759][757][756][753][754][755][752][760]

Pollination to fertilisation takes “up to a year (*Pinus* and some Araucariaceae)”, with pine pollen dormant from mid-summer to the next spring, and “from several weeks” in other Pinaceae and most Cupressaceae [743]. *Picea abies* pollen tubes grow at about 20 µm an hour against 300–1,500 µm an hour in flowering plants, a ratio of 15 to 75 [743].

Pinus sylvestris bears viable seed to at least age 200 [753]. *Picea abies* first flowers at 20–30 years by one source, while the other gives a minimum seed-bearing age of 40–60 years [754][755]. *Sequoia* lives 2,000+ years and seeds at 5–15 years [756].

A *Pinus longaeva* on Wheeler Peak, Nevada, was a “4,900-year-old” tree [760]. Its needles last “up to about 45 years”, a record among conifers [759]. The tree stood for 4,900 years while its needles turned over about a hundred times: 4,900 / 45 = 109.

Cone scales are set in spirals. The prevalent parastichy pair is 8/13 in *Pinus nigra*, 5,838 of 6,000 cones from one tree, and 5/8 in *Larix decidua*, 1,181 of 1,506 cones [761]. The shares are 5,838 / 6,000 = 97.3 % and 1,181 / 1,506 = 78.4 %.

The quotients are 8 / 13 = 0.615 and 5 / 8 = 0.625, close to 0.618 [761]. Nine rarer aberrant Fibonacci-type patterns occur, and their frequency falls as the parastichy quotient departs from 0.618; all lie within two of a convergent pair [761].

Pollen holds 4 cells in *Pinus*, 2 in *Sequoia* and 1 in *Juniperus* [743]. In *Ephedra nevadensis* the sperm are non-motile and double fertilisation occurs: the second sperm nucleus fuses with the ventral canal nucleus [762]. Conifer wood is homoxylous tracheid wood without vessels [746].

Gnetum has vessels, but “vessels in the two groups are convergent characters”, and gymnosperms lack the VND clades [745]. Vessels are about an order of magnitude longer than tracheids of the same diameter but not necessarily more efficient, through torus–margo pits [746]. All conifers are wind-pollinated, as *Runcaria* already was [718].

All are C3 except *Welwitschia*. Its night CO_2 uptake is “never exceeding 4 % of total 24-hour CO_2 uptake”, with a peak of at most 0.2 µmol m^{-2} s^{-1} and only in December–January; it is classed as CAM [763]. *Welwitschia* is 1 species [751].

genome	size	genes
Picea abies	“20-gigabase genome”, 19.6 Gb estimate	28,354 of 70,968 loci
Pinus taeda	about 22 Gb; assembly 20.1 Gb, 82 % repeats	50,172
Welwitschia mirabilis	6.8 Gb per 1C	26,990
Gnetum montanum	4.07 Gb (flow cytometry about 4.2 Gb)	27,491

[764][765][751][745]

The longest intron is 68 kb in *Picea abies* and 318 kb in *Pinus taeda* [764][765]. The *Pinus taeda* genome is 22 / 4.07 = 5.4 times that of *Gnetum*.

The first flowers: basal angiosperms and magnoliids

The oldest confirmed fossil flowers are “no older than about 130 million years”, position

65.88 [766]. The crown-angiosperm calibration is 136–139.35 Ma, and the last common ancestor “likely existed ~140–250 million years ago” [766]. *Archaefructus liaoningensis* and *A. sinensis* from the Yixian Formation, Liaoning, are “at least 124.6 million years old”, herbaceous water plants, position 65.84 [767].

Montsechia vidalii, Barremian, Spanish Pyrenees, is known from about 1,000 specimens, a submerged water plant and possible sister to *Ceratophyllum* [768]. *Archaefructus* has no petals or sepals, and its stamens stand in pairs below folded carpels [767].

event	age	position
crown angiosperms, clock	234–263 Ma	66.41–66.52
monocot–eudicot split, clock	171–203 Ma	66.13–66.28
Nymphaeaceae–Cabombaceae, clock	147–185 Ma	65.99–66.20
Magnoliidae crown	178.78–126.82 Ma	66.17–65.85
crown-angiosperm calibration	136–139.35 Ma	65.92–65.94
oldest confirmed flowers	no older than about 130 Ma	65.88
Archaefructus	at least 124.6 Ma	65.84
Magnoliaceae–Lauraceae split	113–128 Ma	65.75–65.86
Liriodendron whole-genome duplication	about 116 Ma	65.77

[769][770][766][767][771]

Crown angiosperms are “Upper Triassic” from 2,881 plastomes and 62 calibrations [772]. The fossil floor of about 130 Ma and the clock range of 234–263 Ma differ by 234 − 130 = 104 to 263 − 130 = 133 Myr.

The ancestral flower, reconstructed from 792 species in 63 orders, is bisexual and radially symmetric [766]. It has “more than two whorls of three separate perianth organs each (undifferentiated tepals)”, and “more than two whorls of three separate stamens each” [766]. It has “more than five spirally arranged separate carpels”; perianth and stamens stand in whorls, carpels in a spiral [766].

An independent reconstruction gives more than 2 whorls or series of tepals and stamens, free carpels closed by secretion and at least 1 pendent ovule [773]. It leaves bisexual against unisexual and whorled against spiral open [773].

The first flower is built of whorls of three. Here the ring of three of chapter 1 shows at the size of a flower: closed rounds of three organs, stacked.

what	size	position
Amborella trichopoda, seed	4.19 ± 0.99 × 1.57 ± 0.37 mm	10.40
Amborella, drupe without flesh	5.98 ± 0.24 × 3.49 ± 0.11 mm	10.73
Victoria amazonica, seed	7–8 × 9–10 mm	10.87–11.19
V. cruziana, seed	8–9 × 9–10 mm	10.99–11.19
V. boliviana, seed	12–13 × 16–17 mm	11.36–11.68
V. amazonica, ovary	8–12 cm	13.09–13.46
V. amazonica, fruit	10–15 cm	13.29–13.66
V. amazonica, flower at second-night anthesis	up to 28 cm	14.23

Liriodendron tulipifera, mature trunk	0.6–1.5 m	14.92–15.76
V. amazonica, leaf breadth	up to 2.3 m	16.14
L. tulipifera, old-growth d.b.h.	2.4–3.7 m	16.18–16.58
Victoria, growth depth	up to 5.25 m	16.90
L. tulipifera, mature height	30.5–45.7 m	18.50–18.87
L. tulipifera, old growth	about 61 m	19.13

[774][775][776]

The *Victoria* leaf rim is 4–7 % of leaf length in *V. amazonica*, 5–7 % in *V. boliviana* and 8–10 % in *V. cruziana* [775]. *Amborella* is a “dioecious shrub, endemic to the understorey of humid tropical forests” [774]. A seed-size analysis of 12,987 species finds the split of angiosperms from gymnosperms the largest single contributor to the present spread [777].

The progamic phase, pollination to fertilisation, spans “15 min to 13 months” across 131 angiosperm species, positions 39.34–48.94 [740]. The span is 13 × 30.44 × 24 × 60 / 15 = 38,000-fold. In *Austrobaileya scandens* it is 18 h, position 43.24, and germination takes 8.3 % of it [740].

Pollen tubes of *Amborella*, *Nuphar* and *Austrobaileya* grow at about 80–600 µm an hour, against less than about 20 in gymnosperms [741]. Nymphaeales tubes run 2–10 times faster than those of *Amborella* and *Austrobaileya* [740].

Amborella seeds need warm stratification of at least about 90 days; the radicle emerges about 17 days later and the cotyledons 24 days after that [774]. The sum is 90 + 17 + 24 = 131 days, position 47.94. *Liriodendron tulipifera* flowers first at 15–20 years, positions 51.34–51.60, and dies at about 200–250 years, some trees reaching 300, positions 53.69–54.06 [776].

The *Amborella* female gametophyte is 8-celled and 9-nucleate, with 3 synergids plus the egg, a “four-celled egg apparatus” [778][779]. Nymphaeales, including Hydatellaceae, and Austrobaileyales are 4-celled and 4-nucleate; the common Polygonum type is 7-celled and 8-nucleate; the 4-celled state is inferred ancestral [778]. *Nuphar polysepalum* has “diploid biparental endosperm” from a “four-celled/four-nucleate” gametophyte [780].

Double fertilisation is universal in flowering plants and occurs in *Ephedra* too [762]. *Nymphaea colorata* has 2n = 28, and *Liriodendron* 19 chromosomes [769][771]. Early angiosperm evolution “may have required a phase of mechanical and hydraulic instability” [746].

Flowering plants number 295,383 species: monocots 74,273, eudicots 210,008 and the rest 295,383 − 74,273 − 210,008 = 11,102 [659]. Vascular plants number 308,312 and all plants about 374,000 [659]. Magnoliidae hold about 10,000 species in 20 families [770].

genome	size	genes
Nymphaea colorata	409 Mb, 14 pseudochromosomes	31,580
Liriodendron chinense	1.74 Gb (k-mer 1.75 Gb, flow cytometry about 1.8 Gb), 19	35,269

	pseudomolecules	

[769][771]

Monocots

The oldest monocot pollen is *Mayoa portugallica* (Araceae), Barremian–Aptian, Portugal, in floras of “roughly 110–120 million years ago” [781][782]. Monocots, magnoliids and eudicots diversified “135–130 Ma” by clock [783].

The earliest grass fossils are silicified epidermis and phytoliths in the teeth of a hadrosauroid from Gansu, Albian, “113–101 Ma” [784]. Phytoliths in dinosaur coprolites of the Lameta Formation, India, “67–65 Ma”, include rice-tribe types [785]. The root of the grasses is dated 128 Ma, with estimates “from 107 Ma (new fossils excluded) to 129 Ma” [785].

The oldest unequivocal palm fossils are “early to mid Late Cretaceous”, and the palm crown is “about 100 Ma (95% HPD 108–92 Ma)” [786][782]. The oldest orchid fossil is *Meliorchis caribea*, a pollinarium on a bee in amber, “15–20 Ma”; the orchid ancestor is “76–84 Ma” by one clock and about 112 Ma by another [787][788].

event	age	position
monocot diversification, clock	135–130 Ma	65.91–65.88
root of Poaceae, clock	128 Ma (107–129)	65.86
Mayoa pollen floras	about 110–120 Ma	65.72–65.80
orchid crown, second clock	about 112 Ma	65.74
earliest grass fossils	113–101 Ma	65.75–65.65
palm crown	about 100 Ma (108–92)	65.64
Bambusoideae–PACMAD split	86 / 72 Ma	65.50 / 65.34
orchid ancestor	76–84 Ma	65.39–65.48
Ehrhartoideae, with fossils	72 Ma	65.34
Lameta coprolite phytoliths	67–65 Ma	65.27–65.25
Oryzeae, with / without fossils	63 / 28 Ma	65.22 / 64.48
oldest orchid fossil	15–20 Ma	63.91–64.17

[783][785][781][788][784][782][787]

The smallest seeds are orchid seeds: from “0.31 µg” to 24 µg, length “c. 0.05 to 6.0 mm”, positions 6.37–10.73, and from 20–50 to “about 4,000,000” seeds per capsule [789]. *Lodoicea maldivica* bears “the world’s largest seed”: fruit up to 45 kg and 50 cm long, position 14.76, seed up to 25 kg [790][791]. The seed is up to 25 / 45 = 56 % of the fruit mass, and a warden-collected sample gave fresh seeds of 1–18 kg [792].

Palms hold “record features in leaf and seed size, inflorescence size, and leaf complexity” [793]. The *Amorphophallus titanum* inflorescence reaches “up to about 3 m”, position 16.39, and its spadix surface exceeds 36 °C against 27 °C around it [794]. *Wolffia australiana* is rootless [795].

The fastest doubling in a flowering plant is *Wolffia microscopica* clone 2005 at “29.3 h”,

position 43.68, “the fastest growing flowering plant known till date” [796]. Twenty-five clones of all 11 *Wolffia* species were measured [796].

Moso bamboo, *Phyllostachys edulis*, grows up to “114.5 cm/day”, 114.5 / 24 = 4.77 cm an hour, and its culms are “>20-m tall within 45–60 days”, positions 18.11 and 46.96–47.23 [797]. Internode 18 grows at most “~11.8 cm/day” and completes its rapid growth at 29 cm in 23 days, position 46.35 [797]. About 570 million cells are added a day in one internode; cells lengthen from 13.9–33.1 µm to 127.4 µm at 5.6–6.8 µm an hour [797].

The largest sampled culm stage was 11.04 m, position 17.57 [797]. A second study finds the maximum growth rate reached at about 20 days and full height at about 40 days, positions 46.23 and 46.86, with an asymptotic height of 10.46–15.66 m [798].

Bamboo flowering intervals run “some as long as 120 years” [799]. *Bambusa bambos* flowers every 32 years, *Phyllostachys nigra* f. *henonis* every 60 and *P. bambusoides* every 120 [799].

Their positions are 52.02, 52.60 and 53.23.

Phyllostachys species share a base interval of 15 years (15, 30, 60, 120), and *Chusquea* species a base of 8 years (16, 23 [predicted 24], 32) [799]. The measured intervals lie significantly closer to numbers built only of the primes 2, 3 and 5 (P = 0.0041) [799]. A stand holds its load for decades, and then all its culms flower and discharge at once: loading, holding, discharge.

The largest clone is the seagrass *Posidonia oceanica*, with genets “up to 15 km” across, position 24.14 [800]. Clones 1–15 km across, at 4 cm a year, are “about 10,000 to several tens of thousands of years” old, at least about 12,500 years, position 57.46 [800]. Shared genets 15 km apart give “a minimum age estimate between 80,000 and 200,000 years” at the upper growth bound of 6 cm a year, positions 59.15–59.98 [800].

Lodoicea takes about 25 years to reproductive age, position 51.80, about 10 months to enlarge its fruit, position 48.70, and about 5 (7) years to ripen it, position 50.34 [791]. It reaches full size in about 100 years, position 53.06, and may live 350 years, position 54.20 [791].

The monocot flower has a “typical trimerous-pentacyclic groundplan”: 5 whorls of 3, that is 3 + 3 tepals, 3 + 3 stamens and 3 carpels, 15 organs [801]. The first flowering plants had “monosulcate pollen” [802]. Palms build tall trees “entirely through primary growth” [793].

Anomalous secondary growth runs through a “secondary thickening meristem (STM) or monocot cambium”, recorded in 22 genera of Asparagales [803]. In double fertilisation one sperm fertilises the egg and “the other sperm fertilizes the central cell”; the endosperm is usually triploid, with a 2 : 1 ratio of maternal to paternal genomes [804]. The seagrass *Zostera marina* lacks the “entire repertoire of stomatal-differentiation genes” [805].

Two sperm, two unions in one flower: the egg and the central cell. Here the form is the pair, two closures made together.

C4 photosynthesis arose in 62 recognisable lineages: 18 in grasses within 26 monocot lineages, 6 in sedges and 36 in eudicots, with C3–C4 intermediates in 21 lineages and origins placed for 47 [806]. The C4 lineages hold about 7,500 species in 19 families

[806]. C4 vegetation covers 18.8 million km² and makes about 35.3 Pg C a year of gross production against about 115 for C3, so 35.3 / 150.3 = 23.5 % [807].

C4 plants became abundant worldwide 8–6 Ma, position 63.34, and C4 grasslands spread 8–3 Ma [808][809]. CAM occurs in “close to 6% of vascular plant species across at least 35 families”, strongly in orchids, and adds “from values of <1% to 100%” of carbon gain [810][811].

Monocots number 74,273 accepted species, 74,273 / 295,383 = 25.1 % of flowering plants; about 2,000 species of plants are described each year [659]. Grasses number 11,506 species, orchids “over 25,000” in 736 genera, palms “roughly 2,400”, *Wolffia* 11 and *Ceroxylon* 12 [812][788][813][782][796][814].

genome	size	genes
Oryza sativa ssp. *japonica* Nipponbare	389 Mb estimated; 370 Mb finished	37,544 non-TE protein-coding
Triticum aestivum Chinese Spring	about 16 Gb; 14.5 Gb assembly	107,891 high-confidence
Wolffia australiana	357 Mb	about 15,000
Zostera marina	202.3 Mb	20,450
Paris japonica	1C = 152.23 pg = 148.9 Gb	—

[815][816][795][805][817]

Wheat is allohexaploid [816]. In *Wolffia australiana* 13 % of genes show time-of-day expression against about 40 % in model plants [795]. *Paris japonica* holds the largest eukaryotic genome known, and angiosperm genomes span about 2,400-fold; at 0.978 Gb per pg its 152.23 pg are 148.9 Gb [817].

Eudicots

“The earliest eudicot fossil records, based on pollen, are 127 to 125 million years old”, positions 65.86–65.84 [818]. The oldest eudicot macrofossil is *Leefructus mirus*, Yixian Formation, north-east China, “122.6–125.8 Ma” (editorial summary 124.4–122.9 Ma) [818]. Its leaves are whorled, its reproductive axis carries five carpels, and it belongs near the Ranunculaceae [818].

The γ whole-genome triplication is restricted to core eudicots, after the Ranunculales diverged [819]. Duplications cluster “around 117 million years ago”, and about 75 % of angiosperm species descend from lines that diversified at or soon after γ [819]. An *Arabidopsis* duplication lies “roughly 112 million years ago”, the Asteraceae crown is “about 83 million years ago”, and the sunflower’s second whole-genome duplication is about 29 Ma [820][821][822].

event	age	position
eudicot crown, clock	135–130 Ma	65.91–65.88
oldest tricolpate pollen	127–125 Ma	65.86–65.84
Leefructus mirus	122.6–125.8 Ma	65.82–65.85
γ triplication	about 117 Ma	65.78
Arabidopsis paleopolyploidy	about 112 Ma	65.74

Asteraceae crown	about 83 Ma	65.47
sunflower WGD-2	about 29 Ma	64.51

[783][818][819][820][821][822]

The genome tripled once, about 117 Ma, and three in four flowering-plant species descend from that line [819].

“Tree species exceeding 70 m in height are rare globally”; the tallest flowering plants are the eucalypts of south-east Australia [823]. *Eucalyptus regnans* has been measured “up to 100 m tall”, position 19.58 [824]. It “grows fast, dies relatively young”; the oldest climbed tree had 651 years of heartwood, position 54.77 [825].

what	size	position
Rafflesia lagascae, flower	15–20 cm	13.66–13.92
Rafflesiaceae, flower diameters	about 11–100 cm (*R. keithii* ≥80, *R. pricei* ≥25 cm)	13.38–15.39
Rafflesia arnoldii, flower	nearly 1 m	15.39
Quercus robur, typical diameter	up to 1 m (3–4 m maximum)	15.39 (16.39–16.65)
baobab Platland, height	18.9 m	18.06
Fagus sylvatica, mature height	20–30 m (up to 50 m)	18.11–18.48 (18.95)
Q. robur, height	30–40 m (34 m at maturity)	18.48–18.74
baobab Platland, girth	34.11 m	18.60
rare tree height	more than 70 m	19.25
Eucalyptus regnans	up to 100 m	19.58

[826][827][828][829][830][831][832][823][824]

Rafflesiaceae “produce the largest flowers of any angiosperm”; they are endoparasites without leaves, stems or roots [833]. The largest baobab, Platland, holds 501 m³ of wood [830].

The Venus flytrap closes its “leaf in about 100 ms”, position 31.06, by a snap-buckling instability of its 2 lobes [834]. The *Utricularia* suction trap moves its door in “less than a millisecond”, position 26.87, “among the fastest plant movements known” [835]. Its traps fire on their own every 5–20 h, positions 42.07–43.33 [835].

The trap loads over hours, holds, and discharges in a millisecond. Here the form is rest and discharge, in the times of an animal’s movement.

what	duration	position
Arabidopsis, life cycle on soil	about 2 months	47.24
Q. robur, seed crops every	2–4 yr	49.50–50.13
Q. robur, minimum seed-bearing age	20 yr	51.60
F. sylvatica, first seed in open	40–50 yr	52.23–52.43
F. sylvatica, first seed in stands	60–80 yr	52.60–52.86
oak reference tree	about 100 yr	53.06
F. sylvatica, lifespan	150–300 yr	53.43–54.06
Q. robur, lifespan in some cases	over 1,000 yr	55.16

baobab Platland	about 1,100 yr	55.24
baobab Chapman	about 1,400 yr	55.46
baobab Grootboom	1,500 (Table 1) or 1,600 (supplement) yr	55.53–55.59
baobab Holboom	about 1,800 yr	55.69
baobab Glencoe	+2,000 yr	55.79
baobab Dorslandboom	about 2,100 yr	55.83
baobab Panke, calibrated	2,450 (+45/−40) cal yr; calculated +2,500	55.97; 55.99
Jurupa Oak clone	more than 13,000 yr	57.49
Lomatia tasmanica clone	at least 43,600 yr	58.59

[836][829][831][832][837][828][830][838][839]

Arabidopsis plants on soil are grown “for a period of ~2 months” through the full cycle [836]. *Quercus robur* has a “lifespan of several hundred years” and lives “over 1000 years in some cases” [837][828]. *Fagus sylvatica* reproduces “very late (40–50 years old)” and lives typically 150–300 years [831].

Of 46 somatic mutations in the branches of one oak, 9 of 19 tested were recovered in 116 acorns [837]. Among African baobabs, “9 of the 13 oldest and 5 of the 6 largest individuals have died” over the past 12 years, by radiocarbon dating [830]. The oldest, Panke in Zimbabwe, was 2,450 years as of 2011 [830].

The Jurupa Oak, *Quercus palmeri*, is one clone “>13,000 years old”, a Pleistocene relict that resprouts after fire [838]. *Lomatia tasmanica* is a clone at least 43,600 years old [839].

Pollen of the first flowering plants was monosulcate [802]. “Pentamerous flowers in eudicots” are named as a possible key innovation, and *Leefructus* has five carpels [840] [818]. The eudicot vascular cambium is continuous, unlike the monocot cambium, which is “not continuous … storied” [803].

Parasitism arose independently 12 times in flowering plants: 292 genera, about 4,750 species, of which Santalales hold 2,428 and Orobanchaceae more than 2,100 [841]. Of the 62 C4 lineages, 36 are eudicots, which the paper gives as 60 % and which is 36 / 62 = 58.1 % [806]. Fifty Aizoaceae species were screened for facultative CAM [811].

Eudicots number 210,008 species, 210,008 / 295,383 = 71.1 % of flowering plants [659]. Asteraceae are “10% of all flowering plant species” [821].

genome	**size**	**genes**
Arabidopsis thaliana	about 125 Mb; 115,409,949 bp sequenced; 5 chromosomes	25,498 predicted
Helianthus annuus	about 3.6 Gb; 3 Gb assembly; transposable elements 74.7 %	52,232
Quercus robur	about 740 Mb by flow cytometry; 736 Mb k-mer; 716.6 Mb anchored	25,808
Eucalyptus grandis	640 Mb; 605 Mb in 11 pseudomolecules	36,376

[820][842][822][837][843]

In *Arabidopsis* 24 duplicated segments of at least 100 kb cover 65.6 Mb, 58 %, and 1,528 tandem arrays hold 4,140 genes, 17 %; Araport11 added 635 protein-coding genes [820][842]. In *Eucalyptus* 34 % of genes lie in tandem duplications [843].

Spirals in leaves and cones

Leaves, scales and florets are laid down one after another at the growing tip. Each new one stands where the earlier ones leave room, never on top of the last. The spirals they form are counted as parastichy pairs.

In 657 sunflower heads 768 reliable parastichy counts were obtained, and 565 of them are Fibonacci numbers: 565 / 768 = 73.6 % [844]. A further 67 show a Fibonacci-type structure, 82.3 % with them [844]. Parastichy numbers one less than a Fibonacci number are significantly more frequent than one more [844].

In cones the dominant pair is 8/13 in 97.3 % of 6,000 *Pinus nigra* cones and 5/8 in 78.4 % of 1,506 *Larix decidua* cones [761].

case	pair or count	share
Pinus nigra cones, one tree (n = 6,000)	8/13 in 5,838	97.3 %
Larix decidua cones (n = 1,506)	5/8 in 1,181	78.4 %
sunflower heads (n = 657), reliable counts (n = 768)	Fibonacci in 565	73.6 %
same, with Fibonacci-type structures	565 + 67 = 632	82.3 %

[761][844]

The same Fibonacci order arises in a laboratory experiment and simulation in which each new element is placed where the earlier ones leave most room [845]. It is explained there as the avoidance of rational, periodic arrangements, which leads the system toward the golden mean [845].

The convergents of 1/φ are 1/1, 1/2, 2/3, 3/5, 5/8, 8/13; the two cone pairs are the fifth and sixth. The quotient 8/13 = 0.6154 lies 0.618 − 0.6154 = 0.0026 from 1/φ = 0.6180. The convergents of $1/\varphi^2 = 0.381966$ are 1/2, 1/3, 2/5, 3/8, 5/13, 8/21, and the angle $360° / \varphi^2 = 137.508°$ follows from them.

A new leaf cannot stand on the last one: no closure loads twice in succession. That constraint gives $x^2 = x + 1$ and its root φ = 1.618, the ratio the spirals approach. “φ is the law of tension; growth in time.”

Records of size and age

A clone has no fossil first appearance; its age is bounded by growth rate and extent, or by radiocarbon on its own tissue. The oldest bound is for *Posidonia oceanica*, 80,000–200,000 years [800]. Pando, a clone of *Populus tremuloides*, is “not older than 14,000

years”, post-glacial, and “likely thousands of years old”, position 57.56 [463].

Fossil leaves of *Lomatia tasmanica* are dated at least 43,600 years, so the clone may be at least that old [839]. It is one population over about 1.2 km, position 21.84, with several hundred stems, no diversity at 16 isozyme loci in 78 plants, and is triploid and sterile [839].

Pando is one genet that matches its outline, about 43.6 ha, from 209 stems sampled on a 50 m grid with 7 microsatellite loci; about 40 further genotypes stand next to it [846]. It covers 43 ha with an estimated 47,000 identical ramets, “putatively the largest known organism on earth in terms of dry-weight mass” [463]. A square of 43.6 ha has a side of √436,000 = 660 m, position 21.30.

Pando was followed in 65 plots over a 72-year series of aerial photographs [463]. Standing dead basal area is 24–37 %, and self-replacement has declined for 30–40 years under mule-deer browsing [463]. *Posidonia* genets reach “up to 15 km”, from 1,544 sampling units at 40 locations, with very large clones at 3.5–8.9 % prevalence [800].

Clones persist by ramets from roots or rhizomes: Pando by aspen root suckers, seagrass rhizomes at 4–6 cm a year, *Quercus palmeri* by resprouting after fire [846][463][800] [838]. Maximum clone age and size are “typically limited by the scale of sampling” [800].

organism	size	position
Prochlorococcus, smallest photosynthetic organism	0.5–0.7 µm	2.18–2.49
orchid seed, smallest seed	0.05 mm; 0.31 µg	6.37
Lodoicea fruit, largest seed (seed up to 25 kg)	up to 50 cm	14.76
Rafflesia arnoldii, largest flower	nearly 1 m	15.39
Macrocystis pyrifera, longest alga	more than 60 m	19.11
Eucalyptus regnans, tallest flowering plant	up to 100 m	19.58
Sequoia sempervirens, tallest tree	112.7 m	19.69
Pando, largest clone by area (side of equal square)	43–43.6 ha	21.30
Posidonia oceanica, largest clone by extent	15 km	24.14

[650][789][791][827][365][824][462][846][463][800]

From 0.5 µm to 15 km is 15,000 / (0.5 × 10^{-6}) = 3 × 10^{10}-fold, or 24.14 − 2.18 = 21.96 positions. For a single body, 0.5 µm to 112.7 m is 2.3 × 10^{8}-fold, or 19.69 − 2.18 = 17.51 positions. The *Ostreococcus tauri* nuclear genome is 12.56 Mb on 20 chromosomes, and it carries one copy of each organelle [847][848].

what	duration	position
Utricularia door	less than 1 ms	26.87
Prochlorococcus generation	about 1 day	43.50
Wolffia doubling	29.3 h	43.68

baobab Panke, radiocarbon	2,450 cal yr	55.97
Sequoia, ring count	about 2,200 yr	55.88
bristlecone pine, ring count	4,900 yr	56.60
Jurupa Oak clone	more than 13,000 yr	57.49
Pando, upper bound	up to 14,000 yr	57.56
Lomatia clone	at least 43,600 yr	58.59
Posidonia shared genet	80,000–200,000 yr	59.15–59.98

[835][650][796][830][757][760][838][463][839][800]

The span of times, from the 1 ms trap door to the 200,000-year bound, is 59.98 − 26.87 = 33.11 positions. Genomes run from 1,657,990 bp in *Prochlorococcus* MED4 to 148.9 Gb in *Paris japonica*, 148.9 × 10^9 / 1,657,990 = 89,800-fold; the eukaryote span as a whole is about 66,000-fold [211][817].

The clone stands for tens of thousands of years while every ramet in it is replaced. The form lasts; its carriers are replaced, at the largest extent any closure on Earth has reached.

The green cover today

Plants hold about 450 Gt C of the 550 Gt C of all life, 450 / 550 = 82 % [849]. About two-thirds of plant carbon is wood, and animals hold 2 / 450 = 0.4 % of the plant carbon that feeds them [849]. Plants hold about 320 Gt C above ground and about 130 Gt C in roots [849].

The living world fixes about 104.9 Pg C a year as net primary production, in roughly equal shares on land and in the ocean [850]. Terrestrial gross production is about 150 Pg C a year by one estimate and 129 ± 32 Gt C by another [807][851]. Plant matter turns over in 2–6 days in the ocean, positions 44.13–45.13, and in 19 years on land, position 51.55 [850].

The oldest crossdated tree, the bristlecone pine Methuselah, is 4,850 years old in the tree-ring list, position 56.60, against 4,900 years for the Wheeler Peak tree [852][760]. The oldest tree has stood through 4,850 / 19 = 255 turnovers of the land’s plant matter.

The land’s plant matter is renewed every nineteen years while single trees stand for nearly five thousand. Here metabolism shows at the scale of the biosphere: the content passes through, the forest form holds.

what	size	position
cellulose microfibril, onion cell wall	8–15 nm	-1.58–-1.01
plant cell, diameter	10–100 µm	4.91–7.00
leaf thickness, thale cress	240 µm	7.80
leaf thickness, C3 leaf in general	0.3 mm	8.00
tallest measured tree, a redwood	112.7 m	19.69
predicted limit of tree height	122–130 m	19.76–19.82

[853][172][854][462]

The wall fibril and the tallest tree are 19.69 − (−1.58) = 21.3 positions apart. A 240 µm leaf holds 240 / 10 = 24 cells of 10 µm across its thickness. In spruce wood the fibril is built of 24 chains with a rectangular cross-section [853].

Stomata number 5 to 1,000 per mm² across plants [855]. The living parenchyma is 7.6 ± 2.6 % of the wood in conifers, 21.1 ± 7.9 % in temperate broad-leaved trees and 36.2 ± 13.4 % in tropical ones [856]. In a pine about 100 − 7.6 = 92 % of the trunk is dead and still carries the tree.

Most of the trunk is dead wood, and the tree lives on it. The closed form outlasts the cells that built it.

Stomata follow the air: herbarium leaves of eight tree species show a drop in stomatal density of about 40 % over about 200 years, for a CO_2 rise of about 60 µmol mol^{-1} [857]. Growth at 280 → 340 µmol mol^{-1} cut density by 67 % in some species [857]. *Pinus flexilis* needles lost about 17 % during the deglaciation 15,000–12,000 years ago, with about 30 % more CO_2 [858].

The same leaf builds fewer pores in a richer air. The rule is the same; its value is set by the surroundings: the form of context.

Dry air is 78.08 % N_2, 20.95 % O_2, 9,340 ppm argon and 420 ppm CO_2 by volume [643]. In September 2026 the Mauna Loa monthly mean was 426.07 ppm, 426.07 / 278 = 1.53 times the value of 1750 [859]. The atmosphere–ocean oxygen reservoir is 3.78 × 10^{19} mol with a source of 1.8 × 10^{13} mol a year, a residence of 3.78 × 10^{19} / 1.8 × 10^{13} = 2.1 Myr, position 62.12 [860].

what	value
leaf area index, global mean	4.5–5.2 m² m^{-2}
leaf area index, deserts; plantations; maximum	1.3 ± 0.9; 8.7 ± 4.3; 18 m² m^{-2}
global transpiration	62,000 ± 8,000 km³ a year, 80–90 % of land evapotranspiration
biogenic volatile emission	about 1 Pg a year (isoprene about 50 %, 41 monoterpenes about 15 %)
organic carbon burial, land; sea	350; 200 × 10^{12} g C a year
forests	42 million km², about 45 % of land carbon, about 50 % of land NPP

[861][851][862][863][864]

The seasonal CO_2 swing is 15–20 ppm in the far north and about 3 ppm near the Equator [865]. It has grown about 20 % at Hawaii and 40 % in the Arctic since the early 1960s.

One turn of the seasons, position 48.87, is one breath of the northern forests. Over 1982–2009, 25–50 % of the vegetated area greened in growing-season leaf area and less than 4 % browned [866].

The world’s forests covered 4.06 billion ha in 2020, nearly a third of the land [867]. Net loss was 7.8 million ha a year in 1990–2000, 5.2 million in 2000–2010 and 4.7 million in 2010–2020, and deforestation alone ran at 10 million ha a year in 2015–2020 [867]. Since 1990 about 420 million ha were deforested, a net loss of 178 million ha, 4.2 % of the 1990 area [867].

Primary forest is at least 1.11 billion ha, five countries hold 54 % of all forest, and there is 0.52 ha of forest per person [867]. People took 15.6 Pg C a year from the land in 2000, 23.8 % of the production the vegetation would have had without them [868]. From 1910 to 2005 that share rose from 13 to 25 %, from 6.9 to 14.8 Pg C a year [869].

The forests hold about 3.04 trillion trees: 1.30 trillion tropical, 0.74 boreal and 0.66 temperate [870]. More than 15 billion are cut each year, and the number has fallen by about 46 % since civilisation began, from about 5.6 trillion [870]. That is 749 trees per ha of forest.

Of about 73,300 tree species about 9,000 are undescribed; South America holds 43 %, Eurasia 22 % and Africa 16 % [871]. Amazonia alone has about 16,000 tree species in about 3.9×10^{11} trees [872], 12.8 % of all trees (computed). There 227 species, 1.4 %, make half of all stems, and the rarest 5,800, about 36 %, have fewer than 1,000 individuals each [872].

forest carbon	value
total	861 ± 66 Pg C
tropical; boreal; temperate	471 ± 93 (55 %); 272 ± 23 (32 %); 119 ± 6 (13 %) Pg C
density: tropical; boreal; temperate	242; 239; 155 Mg C ha^{-1}
sink: gross; net	4.05 ± 0.67; 1.11 ± 0.82 Pg C a year

[873]

Trees compete for light. Under a closed canopy the daily photon flux is about 1 % of a clearing, 9 % in a 200 m^2 gap and 20–35 % in a 400 m^2 gap [874]. Diffuse light is about 2 % at 1 m and over 10 % at 9 m above the floor [875].

On Barro Colorado Island the 50 ha plot holds more than 300,000 stems of 314 species, and over 13 years more than 1,200 gaps of 25–1,150 m^2 opened [876]. Of 229 species analysed 47 are pioneers, 7.1 % of stems in the smallest gaps and 26.3 % in the largest [876]. Gaps form at 0.45–6.5 % of the area a year, a full turnover in 1 / 0.065 = 15 to 1 / 0.0045 = 222 years, positions 51.34–53.79 [877].

Amazon stems die at 1.3–2.8 % a year, a residence of 36–77 years, positions 52.13–52.82 [878]. Neotropical regrowth reaches 90 % of old-growth biomass in a median 66 years, position 52.68 [879]. Lidar gap fraction is 1.41 % in old growth, with a gap-size power-law exponent of 2.01–2.11 [880].

The 1963 self-thinning rule set mean plant mass in proportion to density to the power −3/2 [881]. Of 63 published thinning lines, 19 showed no significant slope and 20 of the other 44 differed from −3/2 [881]. Across worldwide data the number of individuals falls as the −2 power of stem diameter, and branch cross-section is conserved across branching nodes [882][883].

roots	value	position
half of root mass, globally	within 20 cm	13.92
half of root mass, trees (60 %)	within 30 cm	14.29
maximum rooting depth, global mean	4.6 ± 0.5 m	16.78
maximum rooting depth, trees	7.0 ± 1.2 m	17.16

deepest, *Boscia albitrunca*	68 m	19.23

[884][885]

Root/shoot ratios are 0.1–0.5 in forests and 4–7 in tundra, grassland and cold desert [884]. Hydraulic lift was shown in 27 species, and neighbours of a sugar maple took 3–60 % of their water from its night-time lift, within 2.5–5 m [886][887]. Carbon moves both ways between *Betula papyrifera* and *Pseudotsuga menziesii*, a net gain to Douglas-fir of 6 % of its fixed isotope, while claims of widespread networks are judged insufficiently supported [888][889].

Branches keep their cross-section at every fork, and trees from seedling to giant fall in number as the square of their diameter. The same rule holds at each scale of the stand.

What this part of the history shows

The residue becomes the alphabet. A free cyanobacterium became the plastid of the red and green line, kept inside two membranes; clocks place that union at 2,137–1,807 Ma. About a billion years ago a red alga became in turn the plastid of the brown algae and diatoms, two deep inside its host.

What closes, stays. Fifty-eight photons leave one glucose that holds 2,800 kJ per mole, 28 % of the red light taken in. The land’s plant matter turns over in 19 years and the ocean’s in 2–6 days, while 104.9 Pg C a year pass through a cover of 450 Gt C.

The form lasts; its carriers are replaced. A pine trunk is 92 % dead wood and still carries the tree. A bristlecone pine stood 4,850–4,900 years while its needles lasted up to 45; *Ginkgo* trees of 667 years show no senescence; a *Posidonia* clone holds for 80,000–200,000 years across 15 km.

Growth in time follows φ. A new leaf or scale is never laid on the last one. The spirals come out as 8/13 in 97.3 % of 6,000 pine cones, 5/8 in 78.4 % of 1,506 larch cones and Fibonacci numbers in 73.6 % of 768 sunflower counts, approaching $1/\varphi = 0.618$.

A new kind of union opens once; then the opened depth fills. The land plants form one crown, with spores from about 473 Ma; the seed plants another, by about 365 Ma; the flowering plants a third, by about 130 Ma. The depths filled: 21,925 bryophytes, 10,560 ferns, 1,079 gymnosperms and 295,383 flowering plants.

The ring of three shows at the size of a flower and a fruit. The ancestral flower stands in whorls of three, the monocot flower in 5 whorls of 3, and the gyrogonite of *Palaeonitella* closes 6 cells wound in one direction. A *Selaginella* stem carries leaves in pseudowhorls of 6.

Partners share a prefix. *Azolla* has carried *Nostoc azollae* in its leaves for about 100 Myr and passes it to every offspring. Cycads alone among early seed plants house nitrogen-fixing cyanobacteria in special roots.

The same rule takes other values in other surroundings. *Isoetes* fixes carbon by night under water. Stomatal density falls with each rise of CO_2: by 17 % at the end of the last glaciation, by 40 % over two centuries, by 67 % in a growth chamber.

Loading, holding, discharge. Bamboo stands hold for 32, 60 or 120 years and then

flower together. A *Utricularia* trap loads for 5–20 h and fires in less than a millisecond; a flytrap snaps in 100 ms.

9. Fungi

Chapter 7 followed the animals and chapter 8 the plants. The fungi stand between them. They are the sister kingdom of the animals, and for most of their history they have lived inside, beside and beneath the plants.

This chapter tells their history from the split with the animals to the present soil. It follows the first fungi in the rock, the hypha that is their unit, and their unions with roots and algae. It then follows their opening of wood, their farms in the nests of insects, the diseases they bring, and the largest single bodies on land.

A fungus is a mesh of tubes. Each size and time of that mesh stands below with its position on the ladder of chapter 1.

The split from the animals

Fungi and animals together form the Opisthokonta. A multigene clock dates their node to 1,389–1,240 Ma with all calibration constraints, positions 68.03–67.93 [890]. Across the full set of analyses the node falls at 1,240–1,481 Ma, positions 67.93–68.09 [890].

The same study dates the last eukaryotic common ancestor to 1,866–1,679 Ma, with a mean of 1,774 Ma (95 % HPD 1,632–1,911 Ma) from 109 taxa, position 68.26 [890]. A second clock places that ancestor at 2,386–1,958 Ma and puts the origin of the fungi “even before (1759 to 1078 Ma)” [342]. A third, a six-gene clock on 199 fungi, dates crown Fungi to about 1,020 Ma, position 67.75 [299].

Crown Fungi at 1,020 Ma lies 1,240 − 1,020 = 220 to 1,389 − 1,020 = 369 Myr after the opisthokont node, positions 66.36–66.83. The range 1,759–1,078 Ma overlaps the node. Crown animals arose in the Cryogenian by a further clock, and the Cryogenian base stands at about 720 Ma; crown Fungi is 1,020 − 720 = 300 Myr older, position 66.64 [485][435].

The third clock places the loss of the fungal flagellum, read as the move of fungi onto land, at about 720 Ma, position 67.43 [299]. It dates Glomeromycota to about 659 (715–606) Ma and Dikarya to 649 Ma, positions 67.35 and 67.34 [299].

The first fungi in the rock

Fungus-like mycelial filaments occur in vesicular basalt of the Ongeluk Formation, South Africa, at 2.4 Ga, position 68.53 [429]. Their home is the rock, not a land surface. They lie before every clock date for the fungi.

Ourasphaira giraldae comes from the Grassy Bay Formation, Arctic Canada, at about 1,010–890 Ma, positions 67.74–67.63 [430]. It is “more than half a billion years older than previously reported unambiguous fungi” [430]. The opisthokont node, at its younger bound of 1,240 Ma, precedes it by at least 1,240 − 1,010 = 230 Myr, position 66.40.

Glomalean hyphae and spores occur in the Ordovician of Wisconsin at about 460 Ma, position 67.03 [433]. From *Ourasphaira* to these spores is 1,010 − 460 = 550 Myr, position 67.19.

Tortotubus protuberans is a cord-forming mycelium from the earliest Silurian, with septal perforations, a bilayered wall and affinity to the Dikarya [434]. The Silurian begins at 443.8 Ma, position 66.99 [435]. *Prototaxites* of the Lower Devonian stands with trunks “as long as 8 m”, position 17.28, read as a heterotroph consistent with a fungus [436].

event	age	position
fungus-like filaments in basalt	2,400 Ma	68.53
last eukaryotic common ancestor, second clock	2,386–1,958 Ma	68.53–68.35
last eukaryotic common ancestor, first clock	1,866–1,679 Ma	68.30–68.21
fungal origin, second clock	1,759–1,078 Ma	68.25–67.80
opisthokont node	1,481–1,240 Ma	68.09–67.93
crown Fungi	about 1,020 Ma	67.75
Ourasphaira giraldae	about 1,010–890 Ma	67.74–67.63
fungal flagellum lost	about 720 Ma	67.43
Glomeromycota	about 659 (715–606) Ma	67.35
Dikarya	649 Ma	67.34
glomalean hyphae and spores	about 460 Ma	67.03
Tortotubus, after the Silurian base	443.8 Ma	66.99

[429][342][890][299][430][433][434][435]

The hypha

The unit of a fungus is the hypha, a tube. Across 31 soil-fungus strains its diameter is 2.7–6.5 µm, positions 3.72–4.51 [432]. The widest is 6.5 / 2.7 = 2.4 times the narrowest.

A hypha extends at its tip. At 25 °C the mean extension per tip is 33 µm an hour in *Aspergillus nidulans* and 48 in *Geotrichum candidum*; it is 125 in *Mucor hiemalis* and 21 in *Neurospora crassa* [891].

The fastest branch reaches 325 µm an hour and the fastest colony 377 µm an hour [891]. In µm per minute the means are 0.35–2.1, the fastest branch 5.4 and the fastest colony 377 / 60 = 6.3.

The tube grows only at its open end, where it meets ground not yet taken; behind the tip the wall stands closed. Here the form is that of the edge in chapter 1: tension where the closure meets uniform surroundings, rest inside.

Onto land with the plants

The clock that dates crown Fungi also dates the arbuscular mycorrhizal symbiosis to about 480 Ma, position 67.07 [299]. Glomeromycota begin to diversify at 484 (529–437) Ma and crown land plants date to 482 (485–473) Ma in the same study [299]. The Leotiomyceta radiation falls at about 446 Ma (467–425 Ma), position 67.00 [299].

From crown Fungi to the arbuscular symbiosis is 1,020 − 480 = 540 Myr. The fungal clock age, 1,020 Ma, is about twice the plant clock age, 482 Ma.

The plant side of the union is older than the land plants. Symbiosis signalling genes, CCaMK among them, are present in green algae: 259 algal transcriptomes and 10 basal land-plant genomes were searched [892]. The genes the plant uses for the union were closed before the union existed.

The first fossil arbuscules sit in *Aglaophyton major* in the Rhynie chert, older than 400 Ma, and they are “morphologically identical” to living arbuscules [893]. The chert has a U–Pb age of 411.5 ± 1.3 Ma, position 66.93; the age c. 407 Ma is also used, position 66.92 [458][894]. From the arbuscular clock origin to Rhynie is 480 − 407 = 73 Myr.

Of vascular plants, 72 % form arbuscular mycorrhiza, 2.0 % ectomycorrhiza, 1.5 % ericoid and 10 % orchid mycorrhiza [895]. Mycorrhiza arose in three waves, the second in the Cretaceous [895]. About 85 % of living plants are mycorrhizal by one review; a survey of 3,617 species in 263 families finds 80 % of species and 92 % of families [896] [897].

With 308,312 vascular plant species, the arbuscular hosts number 0.72 × 308,312 = 221,985 [659]. Glomeromycota hold about 360 described species in 49 genera, 17 families, 6 orders and 3 classes [898]. The Neotropics hold 221 species, given as 69 % of the phylum, which implies 221 / 0.69 = 320 [899].

Each arbuscular fungus then serves 221,985 / 360 = 617 to 221,985 / 320 = 694 plant species. Of 1,014 root samples worldwide, 93 % of arbuscular taxa occur on more than one continent and 34 % on all six sampled [900].

One fungal phylum of a few hundred species joins with seven in ten plant species. Here the form is the residue becoming the alphabet: a union closed once, 480 Ma, now a letter in the roots of two hundred thousand species.

Ectomycorrhiza is the reverse arrangement, the fungus sheathing the root. On the fungal side it arose independently at least 66 times, with 162 proven genera, and by a later count in 78–82 lineages and 251–256 genera [901][902]. On the plant side it occurs in 30 lineages, 2 in gymnosperms and 28 in angiosperms, with 335 genera and about 8,500 species [903].

The plants able to form ectomycorrhiza are estimated at 6,000–7,000 species, 1.7–2.4 % of land plants, and the habit has been present “since the Early Jurassic” [903]. The Pinaceae crown dates to 183 Ma (233–150 Ma) and the Agaricomycetidae to 154 Ma, positions 66.19 and 66.03 [299]. Known ectomycorrhizal fungi number 7,750, with 20,000–25,000 likely [904].

Per ectomycorrhizal plant species that is 20,000 / 6,000 = 3.3 to 25,000 / 7,000 = 3.6 fungal species. Against about 8,500 plant species it is 20,000 / 8,500 = 2.4 to 25,000 / 8,500 = 2.9.

The arbuscular union opened once. The ectomycorrhizal union opened at its first origin;

its later origins, in at least 66 fungal lines and 30 plant lines, fill that depth.

Plants pass carbon to mycorrhizal mycelium at 13.12 Gt CO_2e a year, 2001–2021: arbuscular 3.93, ectomycorrhizal 9.07 and ericoid 0.12 Gt CO_2e [905]. In carbon that is 13.12 × 12.011 / 44.009 = 3.58 Gt C a year, split 1.07, 2.47 and 0.03 Gt C [905]. As shares of net primary production the transfer is 6.2 % for arbuscular, 13.1 % for ectomycorrhizal, 3.5 % for ericoid and 1.0 % for orchid mycorrhiza, from 194 datasets [905].

Vegetation cover is 57.4 % arbuscular, 25.7 % ectomycorrhizal, 2.6 % ericoid and 14.3 % non-mycorrhizal; arbuscular vegetation holds 241 Gt C of plant biomass and ectomycorrhizal vegetation 100 Gt C [905]. Arbuscular hyphae exceed 100 m per cm^3 of prairie soil, about 0.5 mg dry hyphae per g, and ectomycorrhizal mycelium reaches 2,000 m per cm^3, 2 × 10^9 m per m^3 [905].

Three and a half gigatonnes of carbon a year pass from the plants into the fungal mesh and on into the soil. The carbon flows through; the union holds. Here the form is that of metabolism: what closes, stays.

The arbuscular spore of *Rhizophagus intraradices* measures 40–140 µm, mean 93.3 µm (n = 170), positions 6.17–7.31 and 6.94; its subtending hypha is 11–18 µm wide [906]. The largest spore is 140 / 2.7 = 52 times the thinnest hypha.

Lichens

Stratified lichens appear in the Welsh Borderland at 415 Myr, position 66.93 [907]. *Cyanolichenomycites devonicus* carries a cyanobacterial partner and *Chlorolichenomycites salopensis* a green-algal one [907]. A clock places the ascolichens at 467–410 Ma, positions 67.04–66.92 [299].

The Rhynie lichen *Winfrenatia reticulata* dates to about 400 Ma, position 66.90 [908]. Its thallus bands are 1–2 mm wide with mesh openings of about 25 µm; its hyphae are 1–4 µm wide and its photobiont cells 15 µm, with up to 32 daughter cells per sheath [908].

***Winfrenatia* part**	**size**	**position**
hyphae	1–4 µm	2.81–4.07
photobiont cell	15 µm	5.28
mesh opening	about 25 µm	5.74
thallus band	1–2 mm	9.10–9.73

[908]

Lichenised fungi number 19,387 species in 995 genera; 172 of them, 0.9 %, are Basidiomycota [909]. Lichenisation arose 20–30 times: 14–23 times in Ascomycota and 6–7 in Basidiomycota [909]. Of 155,000 named fungi, 19,387 / 155,000 = 12.5 % are lichenised [910].

Rhizocarpon geographicum grows radially at 0.23–1.47 mm a year, and thalli reach 120 mm in Norway, position 13.46 [911]. The slowest recorded, *R. superficiale*, grows 0.006 mm a year over 16 years [912]. Reported thallus ages reach at least 4,500 years and

about 9,000 years, positions 56.53 and 57.16, and the largest recorded thallus, of *R. alpicola*, is 480 mm, position 14.72 [912].

A fungus with an alga or a cyanobacterium inside its thallus is two addresses sharing one prefix. Here the form is community: the partners nested, the shared body growing a few hundredths of a millimetre a year for thousands of years.

Wood opened

Lignin-degrading class II peroxidases expanded in the line leading to the ancestor of the Agaricomycetes, which reconstructs as a white-rot fungus [913]. They contracted in parallel in brown-rot and mycorrhizal lines [913]. The analysis used 31 fungal genomes, 12 of them new [913].

Clocks place the origin of lignin degradation “around the end of the Carboniferous”, at the time of a sharp fall in organic carbon burial [913].

A study of 62 genomes finds the first class II peroxidases in the common ancestor of the Auriculariales and the other Agaricomycetes [914]. It dates them to “about 300 Ma, roughly at the end of the Carboniferous”, position 66.64. The Carboniferous ends at 298.9 Ma, position 66.63 [435].

The Agaricomycetes crown dates to 299 (351–252) Ma and the diversification of the AA2 enzymes to 350–295 Ma, positions 66.63 and 66.78–66.62 [299]. AA2 genes rise from 3 ancestral copies to 16 in the ancestor of the Auriculariales and 21 in the ancestor of the Trechisporales and later orders [914]. The Dacrymycetes lack AA2, and brown-rot and ectomycorrhizal lines lost both AA2 and the sets of genes for cellulose [914].

Resurrected Polyporales peroxidases date their ancestor to 399 ± 140 Ma and the clade D ancestor to 259 ± 94 Ma [915]. The first versatile peroxidase dates to 194 ± 70 Ma and the first lignin peroxidase to 178 ± 64 Ma [915]. The surface tryptophan that attacks non-phenolic lignin arose independently in two lines [916].

peroxidase step	age	position
Polyporales peroxidase ancestor	399 ± 140 Ma	66.90
AA2 diversification	350–295 Ma	66.78–66.62
class II peroxidases in the Agaricomycete ancestor	about 300 Ma	66.64
Agaricomycetes crown	299 (351–252) Ma	66.63
clade D (manganese peroxidase) ancestor	259 ± 94 Ma	66.50
first versatile peroxidase	194 ± 70 Ma	66.24
first lignin peroxidase	178 ± 64 Ma	66.16

[915][299][914]

The lignin peroxidase of *Phanerochaete chrysosporium* has 343 residues, 37.3 kDa per chain [917]. Brown-rot fungi open cellulose by a non-enzymatic Fenton reaction and do not much degrade lignin [914]. Brown rot arose at least four times [918].

Of 1,157 wood-decay species in 14 orders, 126 are brown rot and 1,031 white rot, a white-rot share of 1,031 / 1,157 = 89 % [918]. They comprise 205 gymnosperm specialists, 565 angiosperm specialists and 387 generalists, and brown rot goes with conifer wood [918][919].

The enzyme to open lignin closed once, in one ancestor about 300 Ma; it was lost again in at least four brown-rot lines and in the mycorrhizal fungi. A new kind of closure opened once, and its depth filled with about a thousand white-rot species.

Two readings of the coal stand side by side. One links lignin decay to the drop in carbon burial at the end of the Carboniferous [913]. The other rejects a fungal cause of the Carboniferous coal peak and points to everwet tropics and wide depositional basins during the assembly of Pangaea [920].

In the Early Pennsylvanian tree lycopods made 60 to more than 80 % of peat contributors, and their periderm 20–45 % of peat biomass, with no more aromatic content than other tissues [921]. Organic-carbon burial roughly doubled over the Carboniferous and returned slowly to near-modern values in the Permian [921]. Modern peat reaches 15 m and the thickest coal beds 61 m, positions 17.85 and 19.13 [922].

The end-Permian fungal spike

At the end of the Permian, fungal remains make up 30–80 % of land-derived palynomorphs through the Changxing Formation of South China, at about 30 localities [923]. *Reduviasporonites stoschianus* is more than 90 % of the basal Tesero assemblage, with cells 10–90 µm long, positions 4.91–6.91 [924]. The proliferation lasted less than 1 Myr, position 61.45 [923][924].

The first reading was saprotrophic fungi on dead wood; the second, by the same authors in 2011, a *Rhizoctonia*-like soil pathogen of plants [923][924]. The spike falls at 254–252 Ma, positions 66.49–66.48 [923][924].

Decay today

World forests hold 861 ± 66 Pg C [873]. Soil to 1 m holds 383 ± 30 (44 %), live biomass 363 ± 28 (42 %), dead wood 73 ± 6 (8 %) and litter 43 ± 3 (5 %). Dead wood and litter together hold 73 + 43 = 116 Pg C, 13.5 % [873].

Coarse woody detritus is produced at about 12 Pg dry matter a year, its pool is about 150 Pg and it turns over in about 13 years, position 51.21 [925]. Fine litter turns over in about 5 years in forests and 1.4–3.4 years on global mean, positions 50.34 and 49.18–49.98 [925]. Global litter production is 90–110 Pg dry matter a year including below-ground [925].

Downed coarse wood decays at rates k that vary at least 244-fold worldwide and up to 76-fold among species at one site [926]. The fastest is 0.975 a year in *Heliocarpus appendiculatus* and the slowest 0.004 a year in *Eucalyptus camaldulensis*; 95 % of the mass is lost in about 3–750 years, positions 49.87–54.90 [926]. The constant rises about 2.6 times per 10 °C from a base of 0.058–0.061 a year at 10 °C, from 295 constants, 78 sources and 114 species [926].

wood decay constant k	half-life ln 2 / k	position
0.975 a year (*Heliocarpus appendiculatus*)	0.71 yr	48.56
0.058 a year (base at 10 °C)	12.0 yr	51.13
0.004 a year (*Eucalyptus camaldulensis*)	173 yr	53.56

[926]

Leaf litter has a median k of 0.300 a year, 0.300 / 0.058 = 5.2 times the wood base [927]. Litter decomposes about 8 % faster under its own plant species than under another [928]. Fresh plant carbon added deep in the soil led microbes to mineralise soil carbon 2,567 ± 226 years old, position 56.02 [929].

Termites take 58–64 % of dead-wood mass loss in a Bornean suppression experiment, against 10–20 % commonly attributed to invertebrates [930][931]. Where termites find the wood, decay has a Q10 of 6.85 (4.73–9.92) against 1.73 (1.44–2.09) for microbes, from 8,922 *Pinus radiata* blocks at 133 sites, a ratio of 6.85 / 1.73 = 4.0 [932]. Termites find more than 50 % of wood above 21.33 °C, over 30.2 % of the land surface [932].

Across 20 studies, 207 sites and 1,427 paired observations, invertebrates raise wood decomposition by ln RR 0.339 globally, 0.560 in the tropics, 0.798 in arid lands, 0.12 in temperate and 0.020 in continental climates [933]. That is +40 %, +75 %, +122 %, +13 % and +2 %.

Of about 500 soil and 500 litter bacterial isolates from one forest, about 12 % of colonies were cellulolytic [934]. Their 42 OTUs made 17.6 % of sequences in litter and 3.7 % in soil.

Herbivores remove about 17 % of land production, so 83 % is not eaten alive and falls to the decomposers [935]. Global net primary production is 104.9 Pg C a year [850]. Wood turns over in decades to centuries while the forest stands; the carbon passes through the fungi, the forest form holds.

Farmers

Ants

The ancestral fungus-farming ant population dates to about 66.65 ± 13.28 Ma, rounded to about 66 Ma, position 65.27 [936]. Higher agriculture follows at about 27 Ma, position 64.45 [936]. Fungus-farming ants diversified into 247 living, largely Neotropical species, 52 of them leaf-cutters [936].

The chronograms hold 276 ants, 208 of them fungus farmers, and 475 fungi, 288 of them ant cultivars [936]. A clade of 30 *Apterostigma pilosum*-group species farms coral fungi of the Pterulaceae [936]. The *Myrmecopterula* ancestor dates to about 48 Ma and the yeast-cultivar origin to about 32 Ma, positions 64.97 and 64.60 [936].

An earlier estimate dates lower fungus farming to between 61 Ma (52–70) and 57 Ma (48–66), and the tribe Attini in the wide sense to 66 Ma (56–76) [937]. Higher agriculture then arose between 31 Ma (26–37) and 27 Ma (22–33), and leaf-cutters (*Atta* + *Acromyrmex*) between 19 Ma (15–24) and 18 Ma (14–22) [937]. The earlier study counts about 250 described attine species against 247 in the later one [937][936].

From farming to higher agriculture is 66.65 − 27 = 39.65 Myr, position 64.80, or 57 − 27 = 30 to 61 − 27 = 34 Myr, positions 64.54–64.66. From higher agriculture to leaf-cutting is 27 − 19 = 8 to 31 − 18 = 13 Myr, positions 63.34–63.78.

Termites

Fungus growing in termites (Macrotermitinae) had a single origin, in Africa, with no reversal to free-living fungi [938]. Horizontal transmission is ancestral; clonal vertical transmission arose twice, in *Microtermes* through females and in *Macrotermes bellicosus* through males [938].

An earlier molecular estimate dates termite fungus farming to about 31 Ma (19–49) [939]. The recalibrated age is 31.41 Ma (95 % CI 25.82–39.53), position 64.58, with alternatives of 27–36 Ma [939]. The oldest fossil fungus gardens, from the Rukwa Rift, Tanzania, are about 25 Ma (24.8–24.5 Ma), position 64.37 [939].

fossil nest part, 25 Ma	size	position
peloid	about 1 mm	9.10
comb cell	about 10 mm	11.19
comb height	3–6 cm	12.19–12.83
comb width	6–9 cm	12.83–13.19
nest chamber height, maximum	8 cm	13.09
nest chamber diameter	4–13 cm	12.46–13.53

[939]

Macrotermitinae number about 330 species in 11 genera, against about 50 *Termitomyces* species, a ratio of 330 / 50 = 6.6 [940]. Colonies last up to several decades, and primary reproductives live up to about 20 years, position 51.60 [940]. Mounds reach 10 m high and more than 15 m across, positions 17.48 and 17.85, with ages of about 700 and at least 2,200 years, positions 54.83 and 55.88 [940].

Termitomyces fruits every year with the rains, position 48.87 [940]. New workers appear 1.5–3 months after swarming, positions 46.98–47.61 [940]. A 10 m mound is 10 / (6.5 × 10^{-6}) = 1.5 × 10^{6} times the width of the widest hypha.

The termite crown dates to 149 (136–170) Ma, the oldest termite fossils to 135 Ma and the Termitidae to 54 (46–66) Ma, positions 66.00, 65.91 and 65.08 [941]. From the termite crown to fungus farming is 149 − 31.41 = 117.6 Myr, position 65.79. Termites emit 19.7 ± 1.5 Mt CH_4 and 3,500 ± 700 Mt CO_2 a year, and their mounds oxidise about half of the methane made [942][943].

Beetles

Bark and ambrosia beetles (Scolytinae) number more than 6,000 species, about 10 % of weevils, and originated at 100–120 Ma, positions 65.64–65.80 [944]. Fungus farming evolved among them at least ten times; reconstructions give 10 or 11 origins [944]. The oldest dates to about 50 Ma, the Xyleborini to about 21 Ma, and crown ages run 8–48 Ma, positions 65.01, 64.22 and 63.34–64.97 [944].

Each new origin of the symbiosis evolved a mycangium, an organ that carries the spores

[945]. “Over 95%” of the beetle–fungus pairs are economically harmless, and pest damage comes in three types [945].

The ant carries its fungus in its nest, the termite in its mound, the beetle in an organ of its own body. Here the form is community as shared prefix: a fungus inside an insect’s house, the house inside a forest, each address within a longer one.

Fungi that take

Amphibians

Chytridiomycosis has contributed to the decline of at least 501 amphibian species, 6.5 % of described amphibians [946]. Of these, 90 (18 %) are confirmed or presumed extinct in the wild, and a further 124 (25 %) show a more than 90 % fall in abundance [946]. The implied number of described amphibians is 501 / 0.065 ≈ 7,700, so the extinctions are 90 / 7,700 = 1.2 %.

Declines peaked worldwide in the 1980s, before the disease was found in 1998, with a smaller peak in the early 2000s in western South America [946]. Of 292 surviving species with known trends, 60 (20 %) show initial recovery and 197 continue to decline, 197 / 292 = 67 % [946]. The chance of recovery after a more than 90 % decline is “less than one in ten” [946].

All declines but one are attributed to *Batrachochytrium dendrobatidis*; the exception, *Salamandra salamandra*, declined from *B. salamandrivorans* [946]. *B. dendrobatidis* traces to the Korean peninsula, lineage BdASIA-1, with emergence “to the early 20th century”, and its spread is linked to the trade in amphibians [947]. From emergence to the peak of decline is roughly 60–80 years, positions 52.60–52.86.

B. salamandrivorans was checked in more than 5,000 amphibians from four continents [948]. It infects only salamanders and newts and is highly pathogenic to them; it came from Asian hosts to naïve European populations [948].

Bats, ants and humans

White-nose syndrome is caused by *Pseudogymnoascus destructans* [949]. Winter counts cover 200 sites in 27 US states and 2 Canadian provinces over 1995–2018, 23 years, position 51.72 [949]. Three bat species declined by more than 90 %, two others less severely [949].

Fossil death-grip leaf scars from Messel, Germany, at 48 Ma, position 64.97, are the first fossil record of fungus-steered ant behaviour [950]. Fifteen new *Ophiocordyceps* species with hirsutella-like asexual forms infect ants only [951].

Invasive fungal infections of humans number 6.5 million a year (6,548,000), with 3.8 million crude deaths (3,752,000) [952]. About 2.5 million deaths, 68 % (range 35–90 %), are directly attributable [952]. Invasive aspergillosis brings about 2,113,000 cases and 1,801,000 deaths, *Candida* about 1,565,000 and 995,000, and cryptococcal meningitis 194,000 and 147,000 [952].

Plants

An “unprecedented number of fungal and fungal-like diseases” has recently caused some of the most severe die-offs in wild animals and plants [953]. Dutch elm disease came in two pandemics, from about 1910 and from the 1940s, and killed about 30 million elms in the UK [954]. The first pandemic took 10–40 % of elms in most European countries [954].

Chestnut blight was first noticed in 1904, at the New York Zoological Park [955]. It reached Trenton and Poughkeepsie by August 1907 and changed the face of the eastern forests within 50 years [955]. The span from 1904 to now is 122 years, position 53.24.

Of 1,090 fungal species with genomes sequenced by October 2016, 35.5 % are pathogens, and 191 species are plant pathogens, 61.3 % of them on food crops [956]. The oomycete *Phytophthora*, not a fungus, has 142 described and 43 provisional species [957]. The plant answers with 149 NBS-LRR immune genes in *Arabidopsis thaliana* [958].

Fungi living inside leaves without harm, the endophytes, were sampled as 1,403 strains from the Canadian Arctic to lowland Panama [959]. Their incidence, diversity and host breadth rise toward the tropics [959].

The largest bodies on land

Armillaria bulbosa, now *A. gallica*, in Michigan “occupies a minimum of 15 hectares” and “weighs in excess of 10,000kg” [960]. It has been genetically stable “for more than 1,500 years”, position 55.53 [960]. Its mass per area is more than 10,000 / 15 = 667 kg per ha.

Re-sampling with 248 collections found one genet over about 75 ha, with a minimum age of 2,500 years, position 55.99 [961]. Its genome is about 90 Mb with an “extremely low” somatic mutation rate [961].

Armillaria ostoyae in the Blue Mountains, Oregon, forms a genet of about 965 ha within about 16,100 ha of mixed-conifer forest [439]. Its isolates lie up to about 3,810 m apart, position 22.89; other genets cover about 20, 95, 195 and 260 ha [439]. The genet is 1,900–8,650 years old by three spread rates, positions 55.74–57.12 [439].

genet	area	side of equal square	position
Michigan, 1992 minimum	15 ha	387.3 m	20.81
Michigan, 2018	about 75 ha	866.0 m	21.54
Oregon	about 965 ha	3,106.4 m	22.71
Oregon forest	about 16,100 ha	12,688.6 m	23.99

[960][961][439]

The sides are √(area × 10^4 m^2 per ha). The Oregon genet is 965 / 75 = 12.9 times the Michigan genet of 2018 and 64 times its 1992 minimum. Its radial spread of 3,810 / 2 = 1,905 m in 8,650–1,900 years is 0.22–1.0 m a year, 0.42–1.9 µm a minute.

The 3,810 m genet is 3,810 / 4 × 10^{-6} = 9.5 × 10^8 times the width of a 4 µm hypha. Its

hyphae are made and lost at their tips while the genet stays one genome with an extremely low mutation rate for 2,500 years and more. The form lasts; its carriers are replaced.

How many fungi

Accepted fungal species number 120,000, with an estimated total of 2.2–3.8 million [962]. About 1,300 new species were named a year over 40 years and about 1,800 a year since 2010, and the ratio of fungal to plant species is 9.8 : 1 [962]. A later count states that “only 155,000 have been formally named to science”, with 2.5 million in all and about 2,500 named a year [910].

The named share is 155,000 / 2.5 × 10^6 = 6.2 %. At 2,500 a year the rest would take (2.5 × 10^6 − 155,000) / 2,500 = 938 years to name, position 55.10. At 1,300 a year, 40 years of naming, position 52.23, added 52,000.

More than 250 million ITS2 sequences from more than 200 studies to 2019 resolve 1.08 million non-singleton taxa at 97 % similarity: 56.8 % Ascomycota and 36.7 % Basidiomycota [963]. The Chao-1 estimate of the total is 6.28 million taxa, “a conservative estimate” [963]. Per 5,000 sequences the habitat Chao-1 is 1,219 in soil, 569 in litter, 392 in air, 228 in plant shoots, 215 in roots and 140 in deadwood [963].

The named share thus runs from 120,000 / 6.28 × 10^6 = 1.9 % to 155,000 / 2.2 × 10^6 = 7.0 %. Against about 374,000 plant species the fungal ratio is 2.5 million / 374,000 = 6.7 : 1, and 16.8 : 1 at 6.28 million [659].

The fungal kingdom opened once, about a billion years ago. Its depth fills still: 1.9 to 7.0 per cent named, and from 2.2 to 6.28 million estimated.

The fungal share of the present Earth

Topsoil fungal biomass, 0–30 cm, holds 12.6 (6.6–16.4) Pg C against 4.3 (0.5–10.3) Pg C of bacteria, from 1,323 measurement points across 11 biomes [964]. The fungal share of topsoil microbial carbon is 12.6 / (12.6 + 4.3) = 75 % [964]. The fungal-to-bacterial ratio runs from 1.8 (1.6–2.1) in savanna to 8.6 (6.7–11.0) in tundra [964].

Tundra soil holds 3,684 mg fungal carbon per kg against 428 bacterial; desert soil 16.92 against 6.83 [964]. The tundra-to-desert fungal ratio is 3,684 / 16.92 = 218. The mycorrhizal flux of 3.58 Gt C a year is 3.58 / 12.6 = 0.28 of the topsoil fungal stock a year, a stock of about 3.5 years of flux.

Fungi send about 50 Tg of spores a year into the air, about 17 Tg of them basidiospores, against about 47 Tg a year of human primary organic aerosol [965]. All life holds about 550 Gt C: plants about 450, bacteria about 70, archaea about 7 and animals about 2 [235].

The mean date of mushroom fruiting in 83 species shifted by 13.3 ± 1.2 days over 1940–2006, position 45.85 [966]. Fruit bodies stand “a few days each year” [966]. The fungal mesh under the ground lasts; the mushroom is its brief discharge.

What this part of the history shows

The residue becomes the alphabet. The genes a plant uses for its fungal union were closed in green algae before any plant reached land. A union closed once, about 480 Ma, now joins one phylum of 320–360 species with 72 % of 308,312 vascular plants.

What closes, stays. Plants pass 3.58 Gt C a year, 6.2–13.1 % of their production, into the mycorrhizal mesh. Wood and litter, 116 Pg C, turn over in 1.4 to 750 years while forest and fungal mesh hold their form.

A hypha of 2.7–6.5 µm grows only at its tip, at 21–125 µm an hour. The tube behind the tip does not extend.

The form lasts; its carriers are replaced. An *Armillaria* genet of 965 ha has held one genome for 1,900–8,650 years. A lichen thallus grows 0.006 mm a year and stands for 9,000.

Partners share a prefix. Lichens hold an alga or a cyanobacterium in the fungal body, and lichenisation arose 20–30 times. Ants, termites and beetles keep fungi in nest, mound and mycangium; ant farming began about 66 Ma, termite farming about 31 Ma, beetle farming at least ten times from about 50 Ma.

A new kind of union opens once; then the depth fills. White rot opened once, about 300 Ma, and filled with 1,031 species; brown rot is its loss in at least four lines. The ectomycorrhizal union opened at its first origin and filled through at least 66, by a later count 78–82, origins in fungi and 30 in plants.

Loading, holding, discharge. A fungal mesh holds through the year and fruits for a few days; lichen and genet hold for thousands of years. At the end of the Permian, within less than a million years, fungal remains rose to 30–80 % of land palynomorphs in South China and one taxon to more than 90 % at Tesero.

10. Ashore Together

Life began in water, and for most of its history the land stood bare. The move ashore was not one event. Microbes, fungi, plants, arthropods and vertebrates arrived in a sequence that spans more than three billion years.

Each arrival came with partners. The first land plants carried fungi in their cells.

The first land animals ate spores and fungi. The first forests stood on soils that microbes, fungi and roots had built together.

This chapter tells that history from the first mats on river gravels to the coal forests. Stage boundaries follow the chart of the International Commission on Stratigraphy, v2023/09 [435]. On that chart the Ordovician begins at 485.4 Ma, the Silurian at 443.8, the Carboniferous at 358.9 and the Triassic at 251.902 Ma [435].

Every age of A million years is placed on the ladder of chapter 1 as a duration of $A \times 10^6 \times 3.15576 \times 10^7$ s. An age of 400 Ma sits at 66.90; an age of 3,220 Ma at 68.80. The year sits at 48.87.

Microbes on the bare land

The oldest life on land is a set of microbial mats in the Moodies Group, South Africa, at 3,220 Ma (68.80) [967]. The mats drape fluvial conglomerates and gravelly sandstones [967]. Their organic carbon has $\delta^{13}C$ in a narrow range centred on −21 ‰, against marine mats as low as −34 ‰ (measured [967]).

Their bulk $\delta^{15}N$ is 2–5 ‰, against 0–3 ‰ in marine mats [967]. The source attributes the difference to denitrification on land, possibly of atmospheric nitrate [967]. A nitrogen cycle thus ran on land long before any plant.

Palaeosols of Mpumalanga, South Africa, dated 2.6–2.7 Gyr (68.60–68.64), hold organic matter read as the remains of microbial mats on the soil surface [228]. One section at Schagen is 17 m thick (17.97) [228]. The source places terrestrial biomass “more than 1.4 billion years earlier” than the 1.2 Gyr Arizona microfossils [228].

The non-marine Torridonian sequence of NW Scotland dates to 1.2–1.0 Gyr (67.90–67.73) [968]. Its microfossils were first described in 1907 [968].

Some are “approaching one millimetre in diameter” (9.10) [968]. Eukaryotes appear to have dominated non-marine settings by 1 Gyr ago [968].

Ediacaran palaeosols of South Australia carry fossils on their uppermost surfaces in growth position [969]. They are interpreted as lichens and microbial soil crusts [969]. The age is 635–542 Ma (67.32–67.18) in the abstract and 625–542 Ma in the editorial summary [969].

The gaps between these records are long. With mid-ranges, 3,220 − 2,650 = 570 Myr (67.22) separate the river mats from the soil mats. Then 2,650 − 1,100 = 1,550 Myr (68.13) pass to the Torridonian, and 1,100 − 473 = 627 Myr (67.31) to the first land-

plant spores (computed).

Microbial life on land precedes land plants by 3,220 − 473 = 2,747 Myr (68.65) (computed). For more than two and a half billion years the land carried thin living films and nothing taller than a millimetre.

Here the form of the edge from chapter 1 shows at the scale of a continent. A thin living layer lies on bare mineral ground, and its chemistry differs measurably from that of the sea.

Fungi before plants

Fungus-like mycelial filaments occur in 2.4 Ga basalt (68.53) [429]. That habitat lies below the surface. The unambiguous fungus *Ourasphaira* dates to 1,010–890 Ma (67.74–67.63) [430].

A molecular clock places the loss of the fungal flagellum, taken as the move to land, at ca. 720 Ma (67.43) [299]. The same clock gives Glomeromycota, the arbuscular mycorrhizal fungi, at 659 (715–606) Ma (67.35) [299]. It gives the arbuscular mycorrhizal symbiosis itself at ca. 480 Ma (67.07) [299].

Glomalean hyphae and spores occur in the Ordovician of Wisconsin at ~460 Ma (67.03) [433]. *Tortotubus protuberans* is a cord-forming mycelium of the earliest Silurian [434].

Prototaxites, of the Lower Devonian, had trunks up to 8 m (17.28) [436]. Its isotopes read it as a heterotroph consistent with a fungus [436]. It was the tallest living thing on land before trees.

By clock, the fungal partner of the plants is older than the plants. Glomeromycota at 659 Ma precede crown land plants at 482 Ma by 177 Myr (computed from [299]). Here the form of the residue that becomes the alphabet shows: a fungus already on the ground becomes a letter of the plant that follows.

The first plants and the first fire

The oldest cryptospores, the spores of land plants, come from Argentina, Dapingian, about 473–471 Ma (67.05) [454]. The previous oldest were late Darriwilian, about 463–461 Ma (67.03) [454].

Three clocks date the crown of the land plants. One gives 515.1–470.0 Ma (67.13–67.05) and crown vascular plants at 472.2–419.3 Ma (67.05–66.94) [455].

A second, with 68 fossil calibrations, gives 515–493 Ma (67.13–67.09) [456]. The third gives 482 (485–473) Ma (67.07) [299].

The fossil minima are 426.9 Ma (66.96), Wenlock, for *Cooksonia* cf. *pertoni*, and 420.7 Ma (66.95), Ludlow, for crown vascular plants [455]. From the first spores to *Cooksonia* is 473 − 426.9 = 46 Myr (64.93) (computed). *Baragwanathia longifolia*, the earliest club moss, is Gorstian, in the Ludlow of the Silurian [457].

A model puts the cover of non-vascular plants at about 30 % of today’s terrestrial net

primary production by about 445 Ma (modelled [672]). In that model early plant material has a molar C:P of about 2,000, against about 100 in marine biomass (modelled [672]). The model gives a sustained +2 ‰ rise in carbonate $\delta^{13}C$ by about 445 Ma and O_2 near the present level by 420–400 Ma (modelled [672]).

Non-vascular plants are proposed to have triggered the Late Ordovician glaciation by weathering [674]. That glaciation ended about 444 Ma (66.99) [674].

The earliest wildfire is recorded as charcoalified rhyniophytoid plants at Ludford Lane, in the Welsh Borders [970]. The level is basal Přídolí, 423.0 ± 2.3 Ma (66.95) [970]. Fire follows the *Cooksonia* minimum by 426.9 − 423.0 = 3.9 Myr (62.68) (computed).

The land plants hold one direction once they are laid down. The order of their stages, non-vascular, vascular, shallow roots, deep roots, seeds, is fixed over 485–298.9 Ma [721]. The net keeps the direction of what was laid down first, and the land-plant line has the same form.

Arthropods walk out

Arthropods left tracks on land before they left bodies. Trackways occur in basal terrestrial deposits of the Cambrian–Ordovician Nepean Formation, near Kingston, Ontario [971]. They lie in an eolian dune field and are mainly undertracks of large amphibious arthropods, possibly euthycarcinoids [971].

These tracks extend the record of the first arthropod landfall back “by as much as 40 m.y.” (64.80) [971]. The Cambrian–Ordovician boundary lies at 485.4 Ma (67.08) [435].

Burrows occur in Late Ordovician palaeosols of the Juniata Formation, Pennsylvania [972, 973]. They are *Scoyenia beerboweri*, of Ashgill age, older than 443.8 Ma (66.99) [972, 973]. They formed with the soil, and their size distribution shows discontinuous, arthropod-like growth [972, 973].

Faecal pellets in the burrows show that the makers ate sediment [973]. The makers were most likely millipedes [973]. The vegetation is unknown, but liverwort spores are widespread in the same beds [973].

The oldest scorpion yet reported dates to ca. 437.5–436.5 Ma (66.98), Llandovery, Telychian [974]. Two substantially complete specimens come from the Waukesha Biota, Wisconsin [974].

The myriapod clock gives ~500 Ma (67.10), against earliest confirmed fossils at ~425 Ma (66.95) [975]. The gap is 75 Myr (65.38) [975]. Uranium–lead ages place Kerrera, with kampecarid millipedes, at ~425 Ma [975].

The Ludlow, ~420 Ma (66.94), brings the first trigonotarbids with book lungs and millipedes with spiracles [975]. Cowie Harbour follows at ~414 Ma (66.93) and Rhynie at ~407 Ma (66.92) [975]. Forest-grade arthropod communities exist by ~385 Ma (66.86) [975].

In the Upper Silurian of Shropshire, ~414 Ma (66.93), lie the earliest land animals with direct evidence: at least two centipedes and one trigonotarbid [976]. The centipede fossil record spans 420 million years (66.94) [977].

Pneumodesmus newmani, the oldest millipede with spiracles, comes from Cowie Harbour, Stonehaven [978]. Spores dated it ~427 Ma (66.96); fish and arthropods suggest Přídolí, 423–419 Ma [978]. Zircon gives maximum depositional ages of 413.7 ± 4.4 Ma and 414.3 ± 7.1 Ma, lowermost Devonian [978].

The redating moves the oldest air-breathing land animal by 427 − 414 = 13 Myr (63.78) (computed).

A molecular clock on 1,478 genes dates insects to ~479 Ma (67.06) [979]. It dates flight to ~406 Ma (66.91) and the major living lineages to ~345 Ma (66.76) [979].

The oldest winged-insect fossil, *Delitzschala bitterfeldensis*, is Arnsbergian, in the Serpukhovian, 330.9–323.2 Ma (66.73–66.71) [980]. From clock flight to that fossil is 406 − 330.9 = 75.1 Myr (65.38) (computed).

Rhyniognatha hirsti of the Rhynie chert was described in 2004 as the oldest true insect, with mandibles shared with winged insects [981]. A reinterpretation finds new remains that “do not support an interpretation as an insect” [982].

It reads the animal as a myriapod, “possibly as a centipede” [982].

From the insect clock age to the Rhynie hexapods is 479 − 411.5 = 67.5 Myr (65.28) to 479 − 407 = 72 Myr (65.34) (computed). In insects and myriapods the clock age leads the first fossil by 67.5–75 Myr.

Tracks before burrows, burrows before bodies, clocks before fossils: in the arthropod record, traces and molecular dates come before preserved bodies.

The Rhynie chert: a whole community at once

The Rhynie chert of Aberdeenshire preserves one Early Devonian land community in place. Its uranium–lead age is 411.5 ± 1.3 Ma (66.93) (measured [458]).

Other printed ages are “about 396–407 million years ago” [981], “c. 390 million years old” [983], “400 million year old” and “410 million years ago” [984]. Together they span 411.5–390 Ma (66.93–66.88).

The site is c. 3.2 m (16.45) of chert, mudstone and sandstone, formed from hot siliceous solutions [983]. “The 22 species of plant fossil (including fungi) are unique to this locality” [983]. The list in the same text holds 25 names [983].

“Six different types of sporophytes and three gametophytes have been described” [985]. The vascular plants “were small, ca. 10 to 40 cm high” (13.29–14.55) [985]. Two species lived entirely above ground, *Rhynia gwynne-vaughanii* and *Aglaophyton major* [985].

Asteroxylon mackiei had roots penetrating the soil [985]. Roots arose stepwise and independently in lycophytes and euphyllophytes; *Asteroxylon* is dated 407 Ma (66.92) [459].

The inventory holds 6 cyanobacteria, 3 algae, 1 lichen (*Winfrenatia reticulata*) and 2 nematophytes [985]. It holds about 10 named fungal taxa, plus “several Chytridiomycetes”, ascomycetes and other undescribed fungi [985].

Arbuscules sit inside the cells of *Aglaophyton* [893]. These are the tree-like branchings

of a mycorrhizal fungus within a plant cell, 400 million years old [893]. The lichen *Winfrenatia* has hyphae 1–4 µm wide (2.81–4.07) [908].

The fauna holds the oldest unequivocal nematodes, possibly the earliest plant parasites [598]. It holds trigonotarbid arachnids with book lungs, and mites, including fungus-eaters [598]. A harvestman shows the earliest preserved tracheae and genitalia [598].

There are a scutigeromorph centipede and a putative millipede [598]. Springtails are likely fungus-eaters [598]. A hexapod has plant debris in its gut, and the source records the earliest true insects with chewing mandibles [598].

The springtail *Rhyniella praecursor* is “between 1-2mm in length” (9.10–9.73), with a head of 300–400 µm (8.00–8.26) (measured [984]). It has antennae of four segments and six abdominal segments [984]. It was first described from four head specimens in 1926 [984].

The trigonotarbids *Palaeocharinus rhyniensis* and *P. hornei* reach “up to 4 mm” (10.36) [984]. *P. tuberculatus* reaches at least 6 mm (10.73) [984]. Larger unnamed specimens reach 14–20 mm (11.50–11.83) [984].

Of five trigonotarbid species described in 1923, “only two valid species are probably present” [984]. With *P. tuberculatus* the count is three (computed from [984]).

Mites are 290–450 µm long (7.97–8.37) (measured [984]). Five species are named, one in 1923 and four in 1962 (computed from [984]). Seven arthropod groups are listed: trigonotarbids, harvestmen, mites, myriapods, springtails, crustaceans and euthycarcinoids [984].

Across the community the sizes step up in ratios. Mite 0.29 mm to trigonotarbid 20 mm is a factor 69; trigonotarbid to plant 400 mm is a factor 20 (computed). The whole span from mite to plant is 400 / 0.29 = 1,380 (computed).

From a 1–4 µm lichen hypha to a 40 cm plant the ratio is 10^5 (computed). On the ladder that is 2.81 to 14.55, nearly twelve steps of three within one hot-spring meadow.

The Rhynie community is the first land community seen whole. Plants hold fungi in their cells; a fungus holds an alga in the lichen; mites and springtails eat fungi; a hexapod eats plants.

Here the form of community as shared prefix shows: “Community is topological, not chosen: shared prefix.” The partners sit inside one another, as addresses inside longer addresses.

The lichen and the arbuscule show the depth of that nesting. A fungus lives in the plant cell; an alga lives in the fungal body.

Each partner carries its own genome one level inside its host. Here the form of never loaded twice shows in its plain count: partners with their own genome sit at most two deep.

Roots and the first deep soils

Drepanophycus-like rhizomes run through Pragian palaeosols, about 411–408 Ma

(66.92), of the Xujiachong Formation, Yunnan [986]. Their density is 800–1,300 m per m³ of sediment (measured [986]). They fill 6.9–11.3 % of the sediment volume (measured [986]).

The trace widths run 5.9–18 mm (10.71–11.73), mean 10.5 mm (11.24) [986]. The thickest exposed palaeosol is 15.5 m (17.88), originally 17.0–19.4 m (17.97–18.09) [986]. Others are 9.0, 7.8 and 4.4 m thick (17.39, 17.26, 16.73) [986].

The density 800–1,300 m m^{-3} equals 0.0008–0.0013 m cm^{-3} (computed). Modern arbuscular mycorrhizal hyphae exceed 100 m cm^{-3} in soil [905]. The Devonian rhizome network is thus about 10^5 times sparser in length than a modern fungal network (computed).

Plants built soils with stems and roots of a centimetre. Fungi now fill the same soils with threads of micrometres, at a hundred thousand times the length.

The same form of a branching network stands at two sizes, a factor of about 100,000 apart. This is the same winding at another depth.

Eating the land plants

Land plants were eaten from the start, but each tissue was eaten on its own schedule. Phase 1 of herbivory on land runs from the latest Silurian to the Early Devonian, 417–403 Ma (66.94–66.91) [987].

Phase 1 includes the eating of spores. Coprolites such as *Lancifaex simplex* at Rhynie hold plant and fungal spores together [987].

It includes a probable bored stem and a piercing by a stylet in *Rhynia gwynne-vaughanii*, and borings in *Prototaxites* [987]. In phase 1 each tissue is eaten 0–20 Myr (up to 64.17) after its origin [987].

A mid-Palaeozoic hiatus of 65 Myr (65.25) follows [987]. Phase 2 runs 327–309 Ma (66.72–66.66) [987]. Feeding on leaf margins of *Triphyllopteris austrina* begins at 326 Ma (66.71), in the Serpukhovian, 76 Myr (65.39) after leaves arose [987].

Seed predation, as holes in *Trigonocarpus*, appears in the Early–Middle Pennsylvanian, 54 Myr (65.08) after seeds [987]. Wood boring in *Trivenia* appears in the mid-Namurian, 63 Myr (65.22) after wood [987]. Root feeding appears in the early Late Pennsylvanian, after a lag of 98 Myr (65.62) [987].

The first wood borings are Late Devonian, ~383–359 Ma (66.86–66.80) [988]. Pennsylvanian borings in tree ferns have diameters “approaching a tenfold increase” over those of oribatid mites [988].

The oldest insect gall, ~302 Ma (66.64), is a petiole gall in the tree fern *Psaronius* [989]. A holometabolan larva made it [989].

Herbivory came in two pulses: one in the Early Devonian, one from the Mississippian–Pennsylvanian boundary [990]. About 12 ordinal-level insect lineages first appear in the second [990]. There are seven functional feeding groups [990].

The order of eating is spores and stems, then wood, then leaves, then seeds and roots,

then galls. The first eaters at Rhynie took plant and fungal spores in one meal.

Herbivory as a kind of union opened once, at 417 Ma; then the same opening filled tissue after tissue. Here the form of opened once, filled many times shows.

Vertebrates come ashore

Tetrapod trackways occur at Zachełmie, Poland, in the Eifelian, early Middle Devonian, 393.3–387.7 Ma (66.88–66.87) [435, 991]. They are “approximately 18 million years older than the earliest tetrapod body fossils” (64.08) [991].

They are “10 million years earlier than the oldest elpistostegids” (63.54) [991]. The earliest body fossils are thus implied at 393.3 − 18 = 375.3 to 387.7 − 18 = 369.7 Ma (66.84–66.83) (computed). The oldest elpistostegids are implied at 383.3–377.7 Ma (66.86–66.85) (computed).

Tiktaalik roseae is a tetrapod-like fish from the Late Devonian of Arctic Canada [992]. Its describers write that the fish–tetrapod transition “occurred over 370 million years ago” (66.83) [992]. The footprints are older than this fish.

The Joggins Fossil Cliffs, Nova Scotia, expose Pennsylvanian strata of 318–303 Ma (66.69–66.65) [993]. They hold 148 fossil species and 20 footprint groups in 96 genera [993]. They record “the first reptiles in Earth history” [993].

The site has 14.7 km (24.12) of sea cliffs within 689 ha [993]. A square of equal area has a side of $\sqrt{(689 \times 10^4\ \text{m}^2)} = 2{,}624.9$ m (22.55) (computed).

The listing gives the Carboniferous as “354 to 290 million years ago” (66.79–66.61) [993]; the chart gives 358.9–298.9 Ma [435].

The oldest known synapsid herbivore, *Melanedaphodon hovaneci*, comes from Linton, Ohio, Moscovian, about 307 Ma (66.66) [994]. Diadectids, captorhinids, bolosaurids, caseids and edaphosaurids took up herbivory by the early Permian [994].

Tetrapod herbivory arose “at least five times” in the Late Carboniferous–Early Permian [995]. Herbivores stayed rare until the Late Permian [995].

From the first arthropod herbivory, 417 Ma, to the first vertebrate herbivory, 307 Ma, is 110 Myr (65.72) (computed). From the first footprints, about 390 Ma, to the first tetrapod herbivore is about 83 Myr (65.47) (computed). The Joggins reptiles and the first herbivore overlap in time.

Here the vertebrates repeat what the arthropods did. Traces precede bodies by 18 Myr, as arthropod tracks preceded arthropod bodies. Plant-eating opens once in arthropods; its origins in vertebrates, at least five in one interval, fill the opened depth.

The first forests

The oldest fossil forest of standing trees lies in the Eifelian Hangman Sandstone Formation of Somerset and Devon, SW England [714]. The Eifelian spans 393.3–387.7 Ma (66.88–66.87) [714].

The trees are cladoxylopsids, mostly *Calamophyton*, on a large distributive river system with seasonal disturbance [714]. The rock records structures made by vegetation, rooting features and accumulations of plant debris [714].

At Gilboa, New York, stand the stumps of *Wattieza*/*Eospermatopteris*, Givetian, “about 385 million years old” (66.86) [715]. The trees were “at least 8 m” tall (17.28) [715].

At Cairo quarry, New York, lies a forest with *Archaeopteris* root systems, “early mid Givetian (ca. 385 Ma)” [716]. It is “approximately 2–3 Ma” older than Gilboa (62.08–62.45) [716].

Its describers call it “the oldest forest (mid Givetian) yet identified worldwide” [716]; the Hangman forest is placed earlier, in the Eifelian [714].

About 3,000 m² of palaeosol were uncovered at Cairo, and three kinds of root system appear [716]. *Eospermatopteris* roots of 0.7–1 cm (10.87–11.19) reach 1–2 m (15.39–16.02) from the base and penetrate about 30 cm (14.29) [716]. Its bases are 20–50 cm (13.92–14.76) [716].

Archaeopteris root systems spread “as much as 11 m across the paleosol surface” (17.57) [716]. Their traces reach 1.2–1.6 m deep (15.55–15.81) [716]. Primary roots are 6–16 cm in diameter (12.83–13.72), 10–15 per tree (measured [716]).

Eighteen root systems were mapped in about 3,000 m², one per 3,000 / 18 = 167 m² (computed). Their trunk bases are 8–45 cm (13.09–14.66) [716]. Tree heights are estimated at 11–32 m (17.57–18.54) from base diameter, and at about 18–27 m (18.02–18.39) by regression (modelled [716]).

A possible lycopsid root mound at Cairo is 1.9 m across (15.97) [716]. The source finds the *Archaeopteris* root system “essentially comparable to modern seed plants” [716].

Archaeopteris trunks occur in Famennian marine beds of SE Morocco, “370-million-year-old” (66.83) [717]. They show lateral branching of the modern-tree type [717]. *Archaeopteris* went extinct around the Devonian/Carboniferous boundary, 358.9 Ma (66.80) [435, 717].

From the first plant spores to the first forests is 473 − 385 = 88 Myr (65.52) (computed). Forest-grade arthropod communities appear at the same ~385 Ma [975].

At Gilboa, oribatid mites occur as 14 fossils, 2 species, 2 new genera and 2 new families [996]. They “roughly double the known age of the group” [996].

The forest is the Rhynie meadow at a larger size. The plant rises from 40 cm to 8–32 m, the root from a centimetre to 11 m across, and the mites come along. The same community form stands three to four steps higher on the ladder, from 14.55 to 17.28–18.54.

Weathering, carbon dioxide and the soil makers

Rooted plants spread at 400–360 Ma (66.90–66.80) [722]. Carbon dioxide dropped as deep-rooted vascular plants reached the uplands [722].

Tree plots at Hubbard Brook show roughly tenfold calcium weathering over bare plots

[722]. In Iceland the factor is 5–10 for calcium and magnesium [722].

A set of 1,241 CO_2 proxy estimates from 112 studies gives about 2,000 ppm at ~400 Ma [723]. CO_2 is close to the pre-industrial 278 ppm through much of the Carboniferous, ~300 Ma [723]. The long-term decline is ~3.4 ppm per Myr over 420 Myr (66.94) [723].

From 400 to 300 Ma the fall is (2,000 − 278) / 100 = 17 ppm per Myr (computed). The 100 Myr of that fall sit at 65.64.

Trees and seeds are linked to faster weathering, nutrient delivery to shallow seas, algal blooms, anoxia, carbon burial, lower CO_2 and a brief Late Devonian glaciation [997]. Five land-plant stages follow one another over 485–298.9 Ma: non-vascular, vascular, shallow roots, trees with deep roots, and seed plants [721].

Mycorrhizal mycelium weathers minerals, and forested ecosystems diversified more than 350 Ma (66.78) [998]. Angiosperm hosts released calcium from basalt at twice the rate of gymnosperm hosts [999].

The worms joined the soil later. The clitellates had a freshwater common ancestor in the Devonian, roughly 419–359 Ma (66.94–66.80), on a tree of 74 taxa [1000]. The earthworm crown lies at the Carboniferous–Permian boundary, 298.9 Ma (66.63) [1001].

Carbon is taken from the atmosphere into rock and soil over 100 Myr, and the gas falls from 2,000 to 278 ppm. Plants, fungi and soil animals take part in one movement.

Coal forests, oxygen and giants

The coal forests spread across the palaeotropics in the Serpukhovian, from 330.9 Ma (66.73) [724]. They expanded greatly in the late Bashkirian, 323.2–315.2 Ma (66.71–66.68) [724].

They contracted by about one-half in the Kasimovian, and briefly re-expanded in the Early Permian [724]. The lost carbon sink is estimated to have raised CO_2 by about 2–5 ppm per year (modelled [724]).

From the Serpukhovian base to the Kasimovian base is 330.9 − 307.0 = 23.9 Myr (64.33) (computed). To the Gzhelian base it is 330.9 − 303.7 = 27.2 Myr (64.45) (computed). The Pennsylvanian itself lasts 323.2 − 298.9 = 24.3 Myr (64.35) (computed).

Arborescent lycopsids of the late Carboniferous coal swamps reached “statures up to c. 45 m” (18.85) and “trunk diameters up to 2 m” (16.02) [461]. Another study gives maximum heights of 10–50 m by taxon (17.48–18.95) [692]. Trunks over 30 m are “rarely reported”, and diameters run from a decimetre to more than 2 m [692].

An earlier estimate gave these trees lifespans of 10–15 yr (50.97–51.34) [692]. That would require 3–4 m of height growth a year, about 20 times modern angiosperm trees and 60 times modern lycopsids [692].

The revised estimate is about 400 yr (54.32) for a 40 m tree, within 200–800 yr (53.69–54.95) [692]. The growth is then 40 / 400 = 0.10 m per year (computed).

The lycopsids formed “a volumetric majority of the biomass” in many wetlands [692]. In the Early Pennsylvanian of Euramerica tree lycopods made 60 to more than 80 % of the peat contributors [921]. Their bark formed 20–45 % of peat biomass, and it was suberin-like rather than lignin-like [921].

A *Lepidodendron* stand in the Herrin (No. 6) Coal of Illinois holds 39 stumps, 33 within a grid of 130 m² [693]. The square side of that grid is 11.40 m (17.60) (computed). The stand density is 1,769 stems per ha [693].

Basal diameters average 95 cm (15.34), within 34–144 cm (14.40–15.72) [693]. The basal area is 992 m² per ha, about 10 % of the ground, possibly inflated by up to 30 % [693]. The nearest-neighbour ratio is R = 1.27, slightly uniform [693].

Fifty-one fallen trunks in the stand average 46.2 cm (14.68), within 20–101 cm (13.92–15.40) [693]. The stand is read as even-aged opportunists with little competition among them [693]. Its density is 1,769 / 565 = 3.1 times the median stem density of Amazonia today (computed from [693, 872]).

A drowned lycopsid forest above the Mahoning coal, Ohio, holds more than 800 upright stump casts [725]. The peat body covers about 60 km², a square of 7,746 m side (23.54) (computed).

The stumps reach 1.2 m basal diameter (15.55) and taper to no less than 0.3 m (14.29) [725]. They are randomly distributed along 2,585 m (22.54) of transects [725].

Organic-carbon burial roughly doubled over the Carboniferous [921]. Enzymatic lignin decay originated “around the end of the Carboniferous” in the ancestor of the Agaricomycetes [913]. Another study rejects this as the cause of the coal peak [920].

It attributes the peak to everwet tropics and extensive depositional settings during the assembly of Pangaea [920].

From the first forests, 385 Ma, to white-rot decay, about 300 Ma, is about 85 Myr (65.49) (computed). Coal beds run from a few inches to, rarely, 200 ft (61 m, 19.13) [1002]. Modern peat reaches 50 ft (15 m, 17.85) [1002].

The late Paleozoic ice age ran 340–260 Ma (66.75–66.51) with CO_2 below 500 ppm [1003]. CO_2 swung on a timescale of ~10^5 yr (59.35) over a 16-Myr (63.97) record [1004]. Tropical forests were restructured again and again in those swings [1004].

After the earliest Kasimovian, about 305 Ma (66.65), the rainforests collapsed [726]. Tetrapod diversity had risen from the Visean to the Moscovian [726]. After the collapse extinction peaked, diversity fell and endemism developed; amphibians were hit hardest and amniotes less [726].

Oxygen rose and fell with these forests. A revised GEOCARBSULF model shows no drop below 15 % O_2 at any time (modelled [863]). Its largest excursion above present lies in the Permo-Carboniferous, 300–260 Ma (66.64–66.51) (modelled [863]).

In that model present terrestrial organic-carbon burial is ~350 × 10^{12} g C per year and marine burial ~200 × 10^{12} [863]. An earlier model gives O_2 of roughly 15–30 % over 550 Myr (67.19) (modelled [1005]). A maximum of “about 35 %” around 300 Ma is disputed [1006].

Charcoal in mires puts pO_2 “continuously above 26 %” through the Carboniferous and Permian [727]. A sharp drop follows near the Permian–Triassic boundary, 251.902 Ma (66.48) [435, 727].

The GEOCARBSULFOR model gives O_2 of 2–11 % from the Cambrian to the mid-Ordovician, and near-modern values in the Devonian (modelled [673]). It has a mid-Devonian low of ~14.5 % at ~393 Ma (66.88) and more than 25 % in the early Mississippian (modelled [673]). A dip to ~20 % follows at ~323 Ma (66.70) (modelled [673]).

Charcoal is present after 419 Ma (66.94), but scarce at ~400–360 Ma [673]. Fire is suppressed below 18.5 % O_2 and off below 16 %, and it rises fast between 19 and 22 % [1007]. Flammability was high in the Carboniferous, 350–300 Ma (66.78–66.64) [1007].

The oxygen reservoir of the air is 3.78×10^{19} mol, and its source 1.8×10^{13} mol per year [1008]. The residence time is $3.78 \times 10^{19} / 1.8 \times 10^{13} = 2.1 \times 10^{6}$ yr, ~2.1 Myr (62.12) (computed from [1008]). With Berner’s burial fluxes it is 0.8 Myr (61.24) (computed from [1008]).

The gas of the air flows through in two million years, while the composition holds for hundreds of millions. This is the form of what closes, stays, at the scale of the planet: the content changes, the form holds. The fire window adds the form of context: the same burning takes other values at other oxygen levels, off below 16 %, fast above 19 %.

Animals grew large in this air. *Arthropleura* partial remains measure 76 × 36 cm (15.14; 14.46) (measured [1009]).

The animal was ~55 cm wide (14.84), up to 2.63 m long (16.27) and ~50 kg [1009]. It is Serpukhovian, from the Stainmore Formation, Northumberland [1009].

Carboniferous–Permian insect wingspans reach about 70 cm (15.06), from more than 10,500 fossil wing lengths [728]. Maximum insect size tracks pO_2 until the end of the Jurassic, then decouples as birds radiate [728].

The size steps run from Rhynie mite 0.29 mm to trigonotarbid 20 mm to *Arthropleura* 2,630 mm. The ratios are 69 and 132; the total is 9,070 over ~80 Myr (65.43), from 411 to 331 Ma (computed). On the ladder the land arthropods climb from 7.97 to 16.27, more than eight steps of three.

Here the form of context shows in the body. The same arthropod plan reaches 2.63 m and 70 cm wings in an air above 26 % oxygen. The rule of growth is the same; its value is set by the surroundings.

The land today

The land that held no plant before 473 Ma now holds most of the living carbon. Global biomass is ≈550 Gt C [235]. Plants hold ≈450, bacteria ≈70, fungi ≈12, archaea ≈7 and animals ≈2 Gt C [235].

Plants thus hold 450 / 550 = 82 % of biomass carbon, and fungi 12 / 550 = 2.2 % (computed). Terrestrial biomass exceeds marine biomass by about two orders of

magnitude [235].

Global net primary production is 104.9 Pg C per year, with land and ocean roughly equal [850]. The world's forests hold 861 ± 66 Pg C [873]. Of this, soil holds 383, live biomass 363, dead wood 73 and litter 43 Pg C [873].

Plants pass 3.58 Gt C per year to their mycorrhizal fungi [905]. The partnership seen in the cells of *Aglaophyton* at Rhynie now moves that much carbon every year.

Dry air holds 20.95 % O_2 and 420 ppm CO_2 [1010]. At Mauna Loa the monthly mean of September 2026 was 426.07 ppm [1011].

The two arthropod groups first seen together at Rhynie have filled the land since. Springtails count 9,186 species in the 2024 checklist [1012]. More than 12,000 millipede species are described [1013].

What this part of the history shows

Life came ashore in one order, and every later arrival kept it. Microbial mats stand on land at 3,220 Ma (68.80), fungi by clock at ~720 Ma (67.43), plant spores at 473–471 Ma (67.05), vascular plants at 426.9 Ma (66.96), footprints of vertebrates at 393.3–387.7 Ma (66.88–66.87). The net keeps the direction of what was laid down first, and the history of the land has the same form.

The partner comes before the host it serves. Glomeromycota are dated 659 Ma by clock, 177 Myr before the crown land plants at 482 Ma; at Rhynie, 411.5 Ma, arbuscules sit inside *Aglaophyton*. Here the residue becomes the alphabet: a closed form already present becomes a letter of the next one.

At Rhynie six sporophytes and three gametophytes, 6 cyanobacteria, 3 algae, 1 lichen, about 10 named fungi, nematodes and seven arthropod groups of 0.29–20 mm share one hot-spring meadow. Fungi live in plants, an alga lives in a fungus, mites and springtails eat fungi. This is community as shared prefix: partners nested inside partners, as addresses inside longer addresses.

Traces come before bodies. Arthropod tracks lie at the Cambrian–Ordovician boundary, burrows before 443.8 Ma, body fossils from ~425 Ma; vertebrate footprints precede vertebrate bodies by 18 Myr. Clocks lead fossils by 67.5–75 Myr in insects and myriapods.

Herbivory opened once, at 417 Ma, and then filled tissue after tissue. Spores and stems are eaten at 417–403 Ma, wood in the Late Devonian, leaves at 326 Ma, seeds and roots in the Pennsylvanian, galls at 302 Ma. Vertebrate herbivory arises from ~307 Ma, at least five times, and these repeated origins fill the same depth.

The same form stands at several sizes. A rhizome network of 800–1,300 m per m^3 in Devonian soil and a modern fungal network of more than 100 m per cm^3 differ by a factor of about 10^5 in length. Land arthropods climb from 0.29 mm (7.97) to 2.63 m (16.27): the same winding at another depth.

Carbon is loaded into soil, peat and coal. Organic-carbon burial doubles over the Carboniferous; white-rot decay appears near its end; fire is frequent at 350–300 Ma.

Loading, holding and discharge stand in the record in that order.

The air also shows what closes, stays. Its oxygen turns over in 0.8–2.1 Myr, yet charcoal records pO_2 above 26 % through the Carboniferous and Permian. The content flows through while the form holds.

The same rule takes other values in other surroundings. Fire is off below 16 % O_2 and rises fast between 19 and 22 %. Insect size tracks pO_2 to the end of the Jurassic, with 70 cm wings and a 2.63 m *Arthropleura* in air above 26 %: constants are state functions of the local vacuum.

Today the land holds 450 of 550 Gt C of living carbon, and plants pass 3.58 Gt C per year to fungi. The springtails and millipedes of Rhynie count 9,186 and more than 12,000 species. The union opened ashore at the start of the Devonian is still being filled.

11. Earth and Life Together

The Earth and its life have one history. Microbes changed the sea, the air and the rocks long before any animal existed.

Plants and fungi then built soils and drew carbon from the air. Animals now carry elements from the deep sea to the inland forest.

This chapter follows the elements through that history: sulphur, nitrogen, oxygen, carbon, phosphorus and water. It goes in time order, from the first isotope traces at 3.47 Ga to the measured flows of the present. Each step is carried by one kind of organism and passed on to another.

Ages are placed on the ladder of chapter 1 as durations: an age of A million years is $A \times 10^6 \times 3.15576 \times 10^7$ s. The year sits at 48.87, the day at 43.50. An age of 1 Ga sits at 67.73, an age of 100 Ma at 65.64.

The first cycles: sulphur and nitrogen

Sulphate reduction is the oldest dated step of an element cycle. Barites about 3.47 Gyr old (68.87) from North Pole, Australia, give a maximum $\Delta^{34}S$ of 21.1 ‰ and a mean of about 11.6 ‰ (measured [105]).

At sulphate above 1 mM, sulphides are typically fractionated by 10–40 ‰ [105]. The authors read the barites as microbial sulphate reduction and extend its record back by more than 750 Myr [105].

Biological nitrogen fixation follows. Sedimentary rocks 3.2–2.75 Gyr old (68.79–68.65) carry a mean $\delta^{15}N$ of 0.0 ± 1.2 ‰ (measured [110]). This is read as fixation, most probably by the molybdenum nitrogenase, with a minimum age of 3.2 Gyr [110].

A molecular clock gives roughly 1.5–2.2 Ga (68.10–68.45) for the nitrogenase [112]. In the same study the last universal common ancestor, about 3.5–3.8 Ga (68.87–68.95), lacks the enzyme [112]. The molybdenum form came first; the vanadium and iron-only forms nest within it [112].

The isotope minimum and the clock differ by 1.0–1.7 Gyr (67.73–68.22) (computed).

At least six genes, *nifHDKENB*, are needed for an active molybdenum enzyme [112]. Of 44 sequenced cyanobacterial genomes, 21 carry *nif* [112]. In archaea only methanogens of the Methanococcales, Methanobacteriales and Methanosarcinales carry the genes, and no eukaryote carries them [112].

From sulphate reduction at 3.47 Ga to fixation at 3.2 Ga is 0.27 Gyr (66.54) (computed). From sulphate reduction to free oxygen at 2.46–2.33 Ga is 1.01–1.14 Gyr (67.74–67.85) (computed). From fixation to free oxygen is 0.74–0.87 Gyr (67.46–67.61) (computed).

The fixing of nitrogen opened once, in prokaryotes, and stayed there. Every later plant and animal that uses fixed nitrogen houses a fixer or eats one. Here the form of the residue that becomes the alphabet shows: a closure made once in bacteria becomes a

letter that every later body takes in and does not make.

Oxygen in three steps

Permanent oxygen in the atmosphere is dated to about 2.33 Ga (68.50) [225]. The date comes from multiple sulphur isotopes in diagenetic pyrite of three coeval drill cores of the Transvaal Supergroup, South Africa [225]. The change took roughly 10 Myr, within 1–10 Myr (61.45–63.54) [225].

A second record dates Ongeluk magmatism at 2.426 ± 0.003 Ga by uranium–lead [226]. It places the onset of oxygenation between 2.460 and 2.426 Ga (68.55–68.54) [226].

The rise oscillated for about 200 Myr (66.27), to 2.250–2.240 Ga (68.47) [226]. The Lomagundi carbon-isotope excursion ends about 2.060 Ga (68.39) [226].

A palaeosol-based reading puts the rise between roughly 2.4 and 2.2 Ga, “about 2.3 Ga” [860]. Free oxygen was “a scarce commodity” in the atmosphere until about 2 Ga (68.36) [1014]. All dates stand side by side.

The Great Oxidation Event significantly predates the modern cyanobacteria [1015]. The mitochondrion arose at 2.053–1.21 Ga (68.39–67.91), and crown eukaryotes are younger than 1.84 Ga (68.29) [1015].

The second step is oceanic. Black shales of the basal Doushantuo Formation, South China, about 635–630 Ma (67.32–67.31), lie directly after the Marinoan glaciation [449]. They are enriched in molybdenum and vanadium, with pyrite $\Delta^{34}S$ of at least 65 ‰ [449].

They are read as “a widely oxygenated ocean” [449]. That is more than 50 Myr (65.01) earlier than previous estimates of 580–550 Ma (67.24–67.19) [449]. From the step at 2.33 Ga to this one is 2,330 − 635 = 1,695 Myr (68.21) (computed).

The third step comes with the land plants. Plants colonised the land from about 470 Ma (67.05) [672]. Carbonate $\delta^{13}C$ rose by a sustained 2 ‰ by about 445 Ma (67.00) [672].

Redox proxies place the oxygenation of the deep ocean at 435–392 Ma (66.98–66.88) [672]. Fossil charcoal shows O_2 above 15–17 % by 420–400 Ma [672]. A model gives present levels, about 21 %, by 420–400 Ma, with fire holding the high level in place (modelled [672]).

After the third step the record holds. Charcoal is continuous in sediments younger than 419 Ma [673], and its presence bounds O_2 to roughly 13–35 % since then [675]. This is the form of what closes, stays: once the window is closed, the content flows through it while the form holds.

Soil becomes a living layer

Soil appears in the record as a product of life. Palaeosols of Mpumalanga, South Africa, dated 2.6–2.7 Gyr (68.60–68.64), hold organic matter read as microbial mats on the soil surface [228]. One section at Schagen is 17 m thick (17.97) [228].

Ediacaran palaeosols of the Ediacara Member, South Australia, are dated 635–542 Ma (67.32–67.18) [969]. On their uppermost surfaces lie *Charniodiscus*, *Dickinsonia* and *Tribrachidium* in growth position [969].

They are read as lichens and microbial soil crusts [969]. The 2023 chart places the Ediacaran base at about 635 Ma [435].

Animals burrowed in soil before any rooted plant. Burrows in buried soils of the Late Ordovician Juniata Formation, Pennsylvania, are the oldest reported non-marine trace fossils [972]. They are most concentrated near the top of the palaeosols [972].

Named *Scoyenia beerboweri*, they cut and are cut by pedogenic carbonate nodules [973]. Backfill banding and faecal pellets indicate a bilaterally symmetrical sediment-eater with discontinuous growth, most likely a millipede [973]. The Ordovician ends at 443.8 Ma, so the burrows are older than that, at 66.99 [435].

The first soil fauna preserved in place lies in the Rhynie and Windyfield cherts, Pragian, 410.8–407.6 Ma (66.92) [435]. It holds the oldest unequivocal nematodes, trigonotarbids, fungus-eating mites, a harvestman, a centipede and a putative millipede [598].

It also holds springtails, the earliest true insects with chewing mandibles, and coprolites [598]. The printed age of the chert in one source is “about 396–407 million years ago” [981].

Fourteen oribatid mite fossils from the Devonian near Gilboa, New York, fall in two described species, *Protochthonius gilboa* and *Devonacarus sellnicki* [996]. They form two new genera and two new families [996]. They “roughly double the known age of the group” [996].

The Devonian brought trees, deeper roots and seeds [997]. Soils became thicker and more widespread, and chemical weathering intensified [997]. *Archaeopteris* roots reached 1.2–1.6 m deep (15.55–15.81) at about 385 Ma [716].

Arbuscular mycorrhizal fungi coincided with the colonisation of land [998]. Ectomycorrhizal fungi rose in the Cenozoic with gymnosperm and angiosperm trees [998]. Mycelial networks acidify soil and release chelators that weather minerals [998].

In field experiments the hyphae preferentially colonised silicate basalt [999]. Weathering increased from arbuscular to ectomycorrhizal hosts, and from gymnosperm to angiosperm hosts [999]. Angiosperms released calcium from basalt at twice the rate of gymnosperms [999].

The clitellate annelids have a freshwater common ancestor in the Devonian, roughly 419–359 Ma (66.94–66.80), from 74 transcriptomes [1000]. Their living lineages arose over the following ~150 Myr (66.01) [1000]. An earlier analysis of 175 annelid sequences also finds the ancestor most likely in freshwater [1016].

The earthworm crown group dates to the Carboniferous–Permian boundary, 298.9 Ma (66.63) [435, 1001]. The gap from the clitellate ancestor to the earthworm crown is 60–120 Myr (65.17–65.80) (computed).

Earthworms arose on Pangaea. Splits between their northern and southern families are dated 161–186 Ma (66.07–66.20), with the break-up of Pangaea given as about 200–185

Ma [1017]. A leech cocoon of 201 Ma serves as a calibration, and clitellate body fossils are Permian [1017].

The Carboniferous coal is attributed to everwet tropics and extensive depositional systems on Pangaea [920]. Decay was pervasive wherever conditions allowed, and many coals are dominated by unlignified lycopsid bark [920].

The order is fixed: microbial mats, then crusts, then sediment-eating animals, then fungus-eating arthropods and nematodes, then rooted trees, then earthworms. Each later group stands on what the earlier ones left: dead mats, dung and litter are the ground on which the next soil animal lives.

The Paleozoic air: carbon down, oxygen up

Chapter 10 told how the land plants, their fungi and the coal forests came ashore. Over the same 200 Myr the air changed with them.

About 1,500 proxy estimates of CO_2 from 112 studies, 1,241 of them retained, span the last 420 Myr (66.94) [723]. CO_2 stood highest, about 2,000 ppm, in the Devonian at ~400 Ma (66.90) [723]. It was close to the pre-industrial 278 ppm through much of the Carboniferous, ~300 Ma (66.64) [723].

The fall from 2,000 to 278 ppm over 100 Myr is 17 ppm per Myr (computed). Over the whole 420 Myr the long-term average declined by about 3.4 ppm per Myr [723].

Over the same span solar irradiance rose about 50 W m^{-2}, a radiative forcing of about +9 W m^{-2} [723]. The CO_2 decline largely offset it, and the source attributes the decline to silicate weathering and the expansion of the land biosphere [723]. Net forcing varied by up to about 10 W m^{-2}, with 95 % of values within ±7 W m^{-2} [723].

A second set of 372 observations shows CO_2 below 500 ppm during long, widespread continental glaciations and above 1,000 ppm in warm periods [1018]. A review gives CO_2 above 2,000 ppm through much of the early Paleozoic, falling to present-like levels near the end of the Devonian [1003].

The threshold for growing ice sheets under a Sun about 4 % fainter is likely 2,000–4,000 ppm [1003]. Models require at most 1,500 ppm for the end-Ordovician glaciation [1003].

The spread of non-vascular plants is proposed to have triggered that glaciation, which ended about 444 Ma (66.99) [674]. Rooted plants then appeared at 400–360 Ma (66.90–66.80), with a CO_2 drop as deep-rooted plants reached the uplands [722]. Tree plots raise calcium weathering about tenfold over bare plots at Hubbard Brook and 5–10 times in Iceland [722].

Five land-plant stages follow over 485–298.9 Ma: non-vascular, vascular with lignified tissue, shallow roots, trees with deep complex roots, and seed plants [721]. Plants raised O_2 and lowered CO_2 by burying decay-resistant matter and by changing weathering [721]. Short pulses of phosphorus, at most 1 Myr (61.45), are linked to marine anoxia [721].

The late Paleozoic ice age is the longest and most severe icehouse of the past 500 Myr

[1004]. It is the only recorded passage from icehouse to greenhouse in the Phanerozoic [1019]. Its glaciation ran 340–260 Ma (66.75–66.51) with CO_2 below 500 ppm [1003].

A 16-Myr record (63.97) of soil carbonate and fossil leaves shows CO_2 swinging on a ~10^5-yr timescale (59.35) [1004]. The swings track sea level and ice volume, and the tropical forests of Euramerica were restructured again and again [1004].

Oxygen moved the other way. A rebuilt model gives O_2 of about 2–11 % from the Cambrian to the mid-Ordovician (modelled [673]).

It rises to near-modern values in the Devonian, with a low of about 14.5 % at ~393 Ma (66.88) (modelled [673]). It exceeds 25 % in the early Mississippian and dips to about 20 % at ~323 Ma (66.70) (modelled [673]).

In the charcoal record used there, charcoal is scarce from the mid-Emsian to the end of the Famennian, about 400–360 Ma [673]. Charcoal shows O_2 rising from about 13 % toward about 30 % from the Late Devonian to the Late Permian [675]. Fires were widespread by the Early Mississippian; the first upland fires come in the Pennsylvanian, and fire was very important in Permian mires [675].

Charcoal in mires puts pO_2 “continuously above 26 %” through the Carboniferous and Permian [727]. The GEOCARBSULF model shows no appreciable drop below 15 % at any time, with its largest excursion in the Permo-Carboniferous, 300–260 Ma (66.64–66.51) (modelled [863]). An earlier model gives roughly 15–30 % over 550 Myr (67.19) (modelled [1005]).

A model gives a maximum of “about 35 %” near 300 Ma, when CO_2 stood near 0.03 % [1006]. Plants grown at 35 % O_2 fractionate carbon 2.4–2.6 ‰ more than at 21 %; growth at 15 % lowers it by about 2.1 ‰ [1006].

Fossil plant $\delta^{13}C$ rose about 5.0 ‰ from the Devonian to the end of the Permian [1006]. A review describes Carboniferous O_2 as “a large positive excursion above 30 %” [1003].

Fire is greatly suppressed below 18.5 % O_2, off below 16 %, and rises fast between 19 and 22 % [1007]. Flammability was high in the Carboniferous, 350–300 Ma (66.78–66.64), and in the Cretaceous, 145–65 Ma (65.98–65.25) [1007]. It was intermediate in the Permian, Late Triassic and Jurassic, and low to absent in the Early–Middle Triassic, 250–240 Ma (66.47–66.43) [1007].

More than 10,500 fossil insect wing lengths show maximum size tracking O_2 until the end of the Jurassic [728]. Wingspans reach about 70 cm (15.06) in the Carboniferous and Permian [728]. After the Jurassic maximum size stays roughly constant, and the decoupling coincides with the early radiation of birds [728].

Most insects grow smaller in low O_2, some grow larger in high O_2, and insects invest less in tracheae in high O_2 [1020]. Larger insects invest more in tracheae [1020].

The fire window and the insect wing show the form of context. The same burning and the same tracheal body take other values in another air: fire off below 16 %, wings of 70 cm above 26 %. Constants are state functions of the surroundings.

From the Great Dying to the age of grasses

The end-Permian extinction began at 251.941 ± 0.037 Ma and ended at 251.880 ± 0.031 Ma (66.48) [1021]. It lasted 60 ± 48 kyr (58.88) [1021]. A short negative carbonate $\delta^{13}C$ spike of about 3 ‰ marks it, and the carbon cycle stayed volatile for about 500 kyr (60.81) before returning near its earlier values [1021].

It is the most severe extinction of the last 542 Myr [1021]. Charcoal O_2 drops sharply near it [727]. Flammability was low to absent at 250–240 Ma [1007].

CO_2 rose again to about 2,000 ppm in the Triassic, 220–200 Ma (66.36–66.27) [723]. The single highest estimate is about 3,700 ± 1,600 ppm at 215 Ma (66.33) [723].

Across the Triassic–Jurassic boundary leaf stomata record a fourfold CO_2 rise and about 3–4 °C of warming [1022]. Species turnover in the megaflora exceeded 95 % [1022].

Charcoal shows Triassic and Jurassic O_2 cycles with amplitudes up to 10 % and periods of 20–30 Myr (64.17–64.54) [727]. A stomatal-index record from four *Ginkgo*-related genera over 300 Myr gives the Mesozoic, about 65–250 Ma, at 1,000–2,000 ppmv, with brief excursions above 2,000 [1023]. The same record has two low intervals below 1,000 ppmv: the Neogene, about 1–8 Ma (61.45–63.34), and the early Permian, about 275–290 Ma (66.56–66.61) [1023].

In the sea, new carbon carriers appeared. Calcifying algae arose in the Late Triassic, 237–201 Ma (66.42–66.27) [1024].

The first calcifiers were probably small calcareous dinoflagellates, about 233 Ma (66.41) [1024]. Coccolithophores followed in the middle–late Norian, about 215–210 Ma (66.33–66.31) [1024].

Molecular clocks place the diatom origin near the Triassic–Jurassic boundary, about 200 Ma (66.27) [668]. Lower Jurassic *Pyxidicula*, about 182 Ma (66.18), is reinterpreted as most likely calcareous nannofossils [668]. The Middle Jurassic species, 174–163 Ma (66.14–66.08), are reassigned to the Lower Cretaceous as a likely testate amoeba [668].

The next diatom records are Aptian, 125–115 Ma (65.84–65.76), from eastern Australia, and 113–110 Ma (65.75–65.72) from the Weddell Sea [668]. Without *Pyxidicula* the gap from origin to the oldest abundant record is 75 Myr (65.38) [668]. That record lies at 200 − 75 = 125 Ma (computed).

The order is calcareous dinoflagellates, then coccolithophores, then diatoms by clock, then abundant diatom fossils. From coccolithophores to the diatom clock origin is 10–15 Myr (63.54–63.91); to abundant diatoms 85–90 Myr (65.49–65.54) (computed).

On land a phylogeny places a single origin of the predisposition to root nodules slightly over 100 Ma (65.64) [213]. After it come about 8 origins and 10 losses of nodulation in the Fabales, Rosales, Cucurbitales and Fagales [213].

An earlier chloroplast-gene study also finds a single origin of the predisposition [212]. Here the form of opened once, filled many times shows: one opening, then eight fillings.

The Cretaceous stood at about 1,000 ppm CO_2, with a steady decline afterwards [1003]. The late Cretaceous, ~80 Ma (65.43), was close to the pre-industrial 278 ppm [723].

The Paleocene–Eocene Thermal Maximum, about 56 Ma (65.11), lasted about 170 kyr (59.83) by an orbital chronology [1025]. Sedimentation in the cores ran 1–3 cm per kyr

[1025].

About 50 Ma (65.01) the floating fern *Azolla* grew and reproduced in the Arctic Ocean [703]. Freshwater microfossils show the surface diluted episodically over about 800,000 years (61.24) [703]. Local sea-surface temperature rose from about 10 °C to 13 °C at the end of the phase [703].

A second study dates the bloom to about 48.5 Ma (64.98) [704]. Its carbon and nitrogen isotopes indicate nitrogen fixation [704]. The interval stored 0.9–3.5 × 10^{18} g C, and the estimated drawdown is roughly 55–470 ppm CO_2 (modelled [704]).

That is 900–3,500 Pg C; over 800 kyr it is 1.1–4.4 Tg C per year (computed). A floating fern left that carbon in the sediments of one ocean over most of a million years.

C4 plants became much more abundant worldwide between about 8 and 6 Ma (63.34–63.08), from carbon isotopes in fossil tooth enamel [808]. The shift came earlier at lower latitudes [808]. C4 grasslands spread across warm regions at 8–3 Ma (63.34–62.45) [809].

C4 photosynthesis is counted in 62 lineages, at least 18 in the grasses and 26 in the monocots overall [806]. About 7,500 species in 19 families use it [806].

C4 vegetation now covers 18.8 million km² and contributes about 35.3 Pg C per year of gross production, against about 115 for C3 [807]. The C4 share is 35.3 / 150.3 = 23.5 % (computed).

The first of the 62 C4 origins opened a new way of closing carbon after CO_2 fell; the other 61 fill it. This is the same form as the nodules.

The ice ages and the breathing of the land

The last few million years have the rhythm of the orbit. Southern Ocean sediments spanning 450,000 years (60.72) show spectral peaks at roughly 23,000, 42,000 and 100,000 years (58.01, 58.56, 59.35) [1026].

These carry about 10 %, 25 % and 50 % of the variance [1026]. The 42-kyr part is in phase with obliquity, and the 100-kyr part is close to eccentricity [1026].

A stack of 57 benthic $\delta^{18}O$ records covers 5.3 Myr (62.96) and is coherent with obliquity, 41 kyr (58.54), throughout [1027]. The obliquity lag is about 3.4 kyr (56.27) before 3 Ma and rises to about 6.8 kyr (56.90) in the Pleistocene [1027].

The 88–120 kyr band holds about 45 % of late-Pleistocene variance, over 0–780 ka [1027]. The precession phase jumps abruptly at about 1.6 Ma (61.87) [1027].

Between about 1,250 and 700 ka (61.65–61.12) the dominant cycle changed from about 41 kyr to about 100 kyr [1028]. The orbital forcing did not change substantially [1028]. Antarctic ice volume increased abruptly at about 900 ka (61.35) [1028].

The Vostok core holds four glacial–interglacial cycles over 420,000 years (60.66) [1029]. In it CO_2 and methane track Antarctic temperature, and present levels exceed anything in the record [1029].

The EPICA Dome C core holds eight glacial cycles over about 740,000 years (61.17)

[1030]. Between about 740 and 430 ka interglacial warmth was weaker, but warm conditions filled a larger share of each cycle [1030]. The interglacial after Termination V, at about 430 ka, lasted about 28,000 years (58.19); the present one has lasted about 12,000 years (57.42) so far [1030].

Over 800 kyr the pre-industrial CO_2 ranged 172–300 ppmv [1031]. In Marine Isotope Stage 16 it stayed below 180 ppmv for about 3,000 years (56.16) [1031].

The ice sheets grew to their maximum between about 33.0 and 26.5 ka (58.34–58.14), from 5,704 radiocarbon, beryllium and helium ages [1032]. Nearly all stood at their maximum positions at 19–20 ka (57.84–57.88) [1032].

At the glacial maximum tundra and steppe were extensive and the northern forest zones lay further south [1033]. Boreal and temperate deciduous forests were fragmented, and the European and East Asian steppes expanded [1033]. Tropical moist forest contracted, and open conifer woodland replaced the desert of south-western North America [1033].

At 6,000 radiocarbon years before present the Arctic forest limit lay further north in some sectors [1033]. Monsoon forest extended in China, and the Sahara and Sahel shrank [1033].

Leaves recorded the change. Needles of *Pinus flexilis* in packrat middens lost about 17 % of their stomatal density, and $\delta^{13}C$ fell about 1.5 ‰, during deglaciation [858]. That was about 15,000–12,000 years ago (57.62–57.42), with about 30 % more CO_2, in a record of 30,000 years (58.25) [858].

In the early Holocene CO_2 fell about 5 ppmv, read as uptake of about 290 Gt C by the land biosphere [1034]. It then rose about 20 ppmv, read mainly as carbonate compensation and coral-reef growth with a small land loss [1034]. The record covers 11,000 years (57.34) [1034].

The Taylor Dome core shows that the carbon cycle was not in equilibrium over the past 11,000 years [1035]. Millennial CO_2 swings are attributed to land biomass and sea-surface temperature [1035].

Herbarium leaves of eight tree species show stomatal density falling about 40 % over about 200 years (53.69), while CO_2 rose by about 60 µmol mol^{-1} [857]. Growth from 280 to 340 µmol mol^{-1} reduced it by 67 % in some species [857].

Small, densely packed stomata are the only way to reach high conductance under low CO_2 [1036]. That fits density cycles in the Permo-Carboniferous and Cenozoic glaciations over 400 Myr [1036].

Every record read shows the same inverse relation: −17 % for +30 % CO_2, −40 % for +60 ppm, −67 % for 280 → 340 ppm. The rule of the leaf is one; its value follows the air. This is again the form of context.

The ice ages show the form of rest and discharge. Ice loads over 41 kyr or 100 kyr and discharges at each termination; CO_2 swings between 172 and 300 ppmv with it. No closure is exact, and each leaves a remainder: the Holocene carbon cycle, out of equilibrium for 11,000 years, is one such rest.

The carbon cycle today

Global net primary production is 104.9 Pg C per year, with land and ocean roughly equal (measured [850]). Global biomass is about 550 Gt C: plants about 450, bacteria about 70, archaea about 7, animals about 2, and marine biota about 6 [235]. Terrestrial biomass lies about two orders of magnitude above marine biomass [235].

Plant biomass against marine biota, 450 against 6 Gt C, is 75-fold (computed). Production is split nearly evenly, while the standing stock sits almost wholly on land.

On land the producers are plants. Terrestrial gross primary production is about 150 Pg C per year, with C3 plants about 115 and C4 plants 35.3 [807].

A second estimate, from transpiration and water-use efficiency, gives 129 ± 32 Gt C per year [851].

At sea the producers are algae and cyanobacteria. Bacteria use about 10–50 % of the carbon fixed by photosynthesis [231]. Free-living bacteria are grazed by heterotrophic nanoflagellates, which are eaten by microzooplankton [231].

Flagellates and microzooplankton overlap in size with phytoplankton, so energy returns from this “microbial loop” to the classical food chain [231]. The steps run: dissolved organic matter → bacteria → heterotrophic nanoflagellates → microzooplankton → classical food chain [231].

The microbial loop has the form of community as shared prefix. One carbon atom passes from dissolved organic matter to bacteria, nanoflagellates and microzooplankton, each a step on the same path.

Diatoms account for about 40 % of marine primary production and the same share of particulate carbon exported downward [1037]. Tara Oceans sampling gave about 12 million ribotypes from 293 communities at 46 sites, and 4,748 diatom OTUs [1038]. *Chaetoceros* is the most abundant and diverse genus, then *Fragilariopsis*, *Thalassiosira* and *Corethron* [1038].

Biogenic silica production is 200–280 Tmol Si per year, a mean of 0.6–0.8 mol Si m^{-2} yr^{-1} [1039]. At least 50 % of it dissolves in the upper 100 m, and 100–140 Tmol Si per year is exported to depth [1039]. Coastal rates are 3–12 times the global mean; oligotrophic gyres are 2–4 times lower [1039].

Waters over diatomaceous sediments, about 10–12 % of the ocean surface, supply 10–25 % of production and bury 15–25 % of their silica [1039]. Elsewhere virtually none accumulates, and global burial over production is about 3 % [1039]. Each buried silicon atom passes on average through 1 / 0.03 = 33 frustules (computed).

The silicon passes through 33 diatom shells for each atom that stays. This is the form of form and carrier: the frustule form persists, while the silicon that carries it is used and dissolved again and again.

Coccolithophores carry carbonate. In the North Pacific their calcite is about 90 % of total pelagic $CaCO_3$ production, with foraminifera and pteropods secondary [1040]. A large, unquantified portion is remineralised within the photic zone [1040].

Organic carbon leaves the surface as marine snow. Larger flocculent aggregates of 4–5

mm (10.36–10.56) sink about 1 m per day [1041].

Smaller compact aggregates of 1–2.5 mm (9.10–9.93) sink about 36 m per day [1041]. All particles at Station Papa settle at 175 m per day, at concentrations of about 1 to more than 500 mm^3 per litre [1041].

In situ, 80 aggregates had a median excess density of 0.00014 g cm^{-3}, spanning four orders of magnitude [1042]. Field sinking was up to four times slower than in the laboratory [1042].

To sink 1,000 m (21.67) takes 1,000 days (49.79) at 1 m per day, 28 days (46.53) at 36 m per day and 5.7 days (45.09) at 175 m per day (computed). The fastest is 175 times the slowest (computed).

Export of organic carbon from the sunlit layer is about 9 Pg C per year, from a model that assimilates satellite and tracer data (modelled [1043]). Earlier estimates span about 4 to 12 Pg C per year [1043]. A model ensemble gives a sinking flux of 6.08 ± 1.17 Pg C per year at 100 m (19.58) (modelled [1044]).

The export ratio, sinking flux over production, is 0.154 ± 0.026 (modelled [1044]). The flux at 1,000 m is 0.65 ± 0.24 Pg C per year, a transfer efficiency of 0.122 ± 0.041 (modelled [1044]). The two export figures, about 9 and 6.08, differ by a factor 1.48 (computed).

Marine organic-carbon burial is about 200 × 10^{12} g C per year, 0.2 Pg; terrestrial burial about 350 × 10^{12} (modelled [863]). Burial is 0.2 / 9 = 2.2 % to 0.2 / 6.08 = 3.3 % of export (computed). As shares of global production, export is 5.8–8.6 %, the 1,000 m flux 0.62 %, and marine burial 0.19 % (computed).

On land herbivores take part. They remove 51 % of production in water and about one third of that on land [935]. On land this is 51 / 3 = 17 %, so 83 % of land production is not eaten alive (computed).

Decomposers take the rest. Litter decay constants from 293 values run from 0.006 to 4.993 yr^{-1}, mean 0.581 and median 0.300 [927]. Rain forest decays at 1.3 and tundra at 0.18 yr^{-1}, more than 7 times slower [927].

Half-lives are 0.53 yr (48.29) in rain forest, 2.3 yr (49.63) at the median and 3.9 yr (50.11) in tundra (computed from [927]). The times to 95 % loss, 3 / k, are 2.3, 10.0 and 16.7 yr (49.63, 50.97, 51.43) (computed). The vegetation order runs rain forest, swamp, broadleaf forest, mixed forest, grassland, shrubland, coniferous forest, tundra [927].

Decay follows temperature: $k = 0.0376 \times MAT + 0.0819$, with $R^2 = 0.29$, and $k = -0.0169 \times \text{latitude} + 1.212$, with $R^2 = 0.15$ [927]. Total nutrients and C:N explain 70.2 % of the variation; with latitude and temperature added, 87.54 % [927]. Here the form of context shows: one rule of decay, with its rate set by the warmth of the place.

Soil organic carbon is 684–724 Pg to 30 cm, 1,462–1,548 Pg to 1 m and 2,376–2,456 Pg to 2 m, from 4,353 profiles [1045]. Carbonate carbon is 695–748 Pg to 1 m, and total soil carbon to 1 m is 2,157–2,293 Pg [1045]. Soil nitrogen is 133–140 Pg to 1 m, with C:N from 9.9 in Yermosols to 25.8 in Histosols [1045].

A later estimate gives 2,270–2,770 Pg C to 2–3 m, possibly 700 Pg smaller, with more than 500 Pg below 3 m [1046]. Soil organic matter holds more carbon than plants and

atmosphere together [1046]. Root inputs are about five times more likely than leaf litter to be stabilised, and below about 30 cm binding to minerals dominates [1046].

Global soil respiration was 98 ± 12 Pg C in 2008, rising 0.1 Pg C per year over 1989–2008, with Q_{10} of 1.5 [1047]. The stock to 1 m over the flux is 1,462–1,548 / 98 = 14.9–15.8 yr (51.33–51.38) (computed). To 2 m it is 2,270 / 98 = 23 yr (51.72) (computed).

The radiocarbon mean age of soil carbon to 1 m is 4,830 ± 1,730 yr (56.59), from 789 profiles [1048]. Depth is the primary driver, and mean annual temperature a major control at the surface [1048]. The age exceeds the stock-to-flux time by 4,830 / 15 ≈ 320 (computed).

A small fast pool carries the flux, and a large slow pool carries the age. The soil turns over its carbon in fifteen years and keeps it for five thousand. This is the form of form and carrier: the closed class persists, the open class carries.

The nitrogen cycle today

The air is 78.08 % nitrogen by volume [1049]. None of it can be used by a plant or an animal as it is.

The two atoms of N_2 are held by a triple bond of 946 kJ/mol, against 160 for a single N–N bond and 498 for the double bond of O_2 [1050]. The ratio 946 / 160 is 5.9 (computed).

Nitrogen enters the living world through certain microorganisms only: free-living bacteria such as *Azotobacter* and cyanobacteria, and symbiotic bacteria such as *Rhizobium* in legume roots [1051, 1052]. Since 1908 it also enters through a factory, by the Haber–Bosch process [1053].

Trichodesmium is a colonial marine fixer. It fixes N_2 while producing O_2, with fixation confined to daylight [206]. Its colonies host diverse associated organisms, and in oligotrophic tropical waters it can be much of the plant biomass [206].

About 15 % of its trichome cells are less-granulated diazocytes, in zones of about 2–30 cells, 1–2 zones per trichome and up to four in long ones [207]. About 10–20 cells per filament are diazocytes [207].

Its fixation was first estimated at about 5 Tg N per year; the current estimate is about 60–80 Tg N per year [207]. The estimate rose 12–16-fold (computed). Of a marine total of 100–200 Tg N per year [207], that is 60 / 200 = 30 % to 80 / 100 = 80 % (computed).

UCYN-A is a unicellular fixer living in mutualistic symbiosis with a unicellular prymnesiophyte alga [208]. The alga receives fixed nitrogen; the cyanobacterium receives fixed carbon [208]. Its genome is reduced to 1.44 Mb and lacks the O_2-producing photosystem II and the tricarboxylic acid cycle [209].

In 2024 it was described as a nitrogen-fixing organelle of a marine alga [210]. The UCYN-A genome is 1.44 / 1.66 = 87 % of the 1.66 Mb genome of *Prochlorococcus* MED4 (computed from [211]). The *Arabidopsis* chloroplast genome of 154,478 bp is 10.7 % of 1.44 Mb (computed from [359]).

The housing of the fixer runs in three stages: colonies with associates, an outside symbiont, and an organelle. Here the residue becomes the alphabet: a free cell becomes

a letter inside another cell. It sits one level inside its host, the depth at which a partner with its own genome holds.

On land plants house fixers in root nodules. Legumes count over 19,500 species, with nodules usually in the Papilionoideae, about 14,000, and variably in the Caesalpinioideae, about 4,400 [214]. Nodulation occurs in about 10 of about 380 angiosperm families [212].

Actinorhizal plants with *Frankia* number 8 families, 24 genera and over 220 species [216]. In the World List of Cycads, 382 species host *Nostoc* [217]. A soybean nodule reaches 5 mm in diameter (10.56) by day 45 (46.96) [1054].

Ammonia is oxidised by archaea and bacteria. Archaeal *amoA* genes are up to 3,000-fold more abundant than bacterial ones in 12 soils [218].

Across 100 studies, gross nitrification rises log-linearly with gross mineralisation and shows no relation to pH [1055]. Gross mineralisation rises with microbial biomass carbon [1055].

In a shortgrass prairie detrital food web, bacteria mineralise 4.5 g N m^{-2} yr^{-1}, fauna 2.9 and fungi 0.3 [219]. Bacterial-feeding amoebae and nematodes supply over 83 % of faunal mineralisation [219]. The total is 7.7 g N m^{-2} yr^{-1}, or 77 kg N ha^{-1} yr^{-1}, with shares of 58 % bacteria, 38 % fauna and 4 % fungi (computed).

The return to N_2 runs through bacteria. The anammox organism is an autotrophic planctomycete that divides only once every two weeks, 1.21×10^{6} s (45.90) [180]. Until then, bacteria able to oxidise ammonia without oxygen had not been found [180].

In the anoxic water of Golfo Dulce, Costa Rica, a 200 m deep (20.21) coastal bay, anammox gives 19–35 % of N_2 formation [220]. In continental-shelf sediments it gives 24 % and 67 % at two typical sites [221].

One table sets four ocean budgets side by side, in Tg N per year [1056]:

term	Gruber & Sarmiento 2002	Galloway 2004	Codispoti et al. 2001	Codispoti 2007
water-column denitrification	80 ± 20	50 ± 20	150	150+
benthic denitrification	95 ± 20	180 ± 50	300	300+
N fixation	132 ± 41	135 ± 51	132	135+
atmospheric input	30 ± 5	50	86	30
riverine input	76–80 ± 14			
balance	+34 ± 53	+5 ± 78	−188	−234

Oceanic denitrification is unlikely to be less than 400 Tg N per year [1056]. The deficit is about 200 Tg N per year against present fixation estimates, while NO_3^-/PO_4^{3-} stays near the Redfield value of 16 [1056]. The two sinks sum to 450 Tg N per year in the 2007 column and to 175 in the 2002 column, a factor 2.6 (computed).

The four columns leave balances from +34 to −234 Tg, while the ratio of nitrate to phosphate holds near 16.

Each year 413 Tg of reactive nitrogen is fixed on land and sea, about half of it, 210 Tg, by people [224]. Marine biological fixation is about 140 Tg; nitrate leaching 40–70; ammonia and nitrogen oxide emissions 100 [224]. The remainder, 413 − 210 − 140 = 63 Tg, is natural fixation on land (computed).

A second account gives Haber–Bosch about 120 Tg N, lightning 5, marine fixation 120 (100–200) and natural land fixation 128 Tg N per year [223]. Anthropogenic reactive nitrogen was 220 Tg N in 2010 [223].

Pre-industrial land fixation from ^{15}N data is 58 (40–100) Tg N per year, or 44 with conservative rock nitrogen [222]. Two land figures stand: 58 and 128.

Agricultural fixation is 50–70 Tg N per year [1057]. Soybean alone fixes 16.4 Tg, 77 % of the crop-legume total; pulses fix 2.95, rice fields 5 [1057]. Haber–Bosch is 120 / 58 = 2.07 times the pre-industrial land fixation and 24 times lightning (computed).

Fixation gives ammonia. Ammonification releases ammonium from dead matter, nitrification turns it into nitrite and nitrate, and denitrification returns N_2 to the air [1052]. A side product, N_2O, warms 273 times as much as the same mass of CO_2 over 100 years and stays in the air more than 100 years (above 53.06) [1058].

Reactive nitrogen stays a few weeks in the atmosphere, about 2 weeks (45.90) [224]. It stays a few decades in land ecosystems, about 30 years (51.97), and 100–1,000 years in peatlands (53.06–55.16) [224].

N_2 is the closed form: its triple bond holds through every season, and it forms four fifths of the air. Ammonium and nitrate are the carriers, gone from the soil in weeks to decades. This is the form of form and carrier: the closed class persists and holds the form, the open class carries.

The phosphorus cycle today

Phosphorus occurs in nature as the phosphate ion and has no significant gas phase [1052]. It enters water when rock weathers, runs to the sea, settles in sediment and returns to land only when the sea floor is lifted [1052]. The average phosphate ion stays in the ocean between 20,000 and 100,000 years (57.88–59.35) [1052].

On a Hawaiian chronosequence of 300 yr to 4.1 Myr (54.06–62.73), mineral phosphorus falls from 82 % to 1 % of soil phosphorus between 300 and 20,000 yr (54.06–57.88) [1059]. Organic phosphorus reaches its maximum at about 150,000 yr (59.72) [1059].

Plants reach the phosphorus mainly through fungi. Arbuscular mycorrhizal fungi form symbioses with the roots of about 80 % of vascular plants [1060]. They “can provide the dominant route for plant P supply, even when overall growth or P uptake remains unaffected” [1060].

Of 3,617 surveyed species 80 % are mycorrhizal, and so are 92 % of 263 families [897]. Among vascular plants 72 % are arbuscular mycorrhizal [895]; about 85 % of living plants are mycorrhizal [896].

Plants allocate 13.12 Gt CO_2-equivalent per year to mycorrhizal mycelium, as the mean of 2001–2021 [905]. The split is arbuscular 3.93, ectomycorrhizal 9.07 and ericoid 0.12;

in carbon the total is 3.58 Gt C per year [905]. That is 3.4 % of the 104.9 Pg fixed on land and sea each year (computed).

The shares of production allocated are 6.2 % for arbuscular, 13.1 % for ectomycorrhizal, 3.5 % for ericoid and 1.0 % for orchid mycorrhiza, from 194 datasets [905]. Vegetation cover is 57.4 % arbuscular, 25.7 % ectomycorrhizal, 2.6 % ericoid and 14.3 % non-mycorrhizal [905].

Seabirds carry phosphorus from sea to land. Breeding colonies of 320 species, at more than 3,000 sites, excrete 591 Gg N and 99 Gg P per year [1061].

The readily soluble fractions are 72.5 Gg N and 21.8 Gg P [1061]. The breeding population is about 804 million birds, or 1,045 million with non-breeders [1061].

The Antarctic and Southern Ocean give 80 % of the nitrogen and phosphorus, 470 Gg N and 79 Gg P, from about 26 % of the birds, 213 million [1061]. Penguins give 307 Gg N and 51 Gg P per year, 52 % of each (computed). With non-breeders and full seasons the flows are 3,800 Gg N and 631 Gg P, about 6.4 times more [1061].

The colony flows are of the same order as lightning, 5.0×10^{3} Gg N per year, and rice-field fixation, 5.0×10^{3} [1061]. Per area they are 500 to more than 1,100 times annual farm nitrogen inputs of about 65–80 kg N ha^{-1} yr^{-1} [1061]. Ammonia from seabird excrement is estimated at 97–442 Gg NH_3 per year [1061].

In the body the same element turns far faster. The ATP pool of a mammalian cell turns over 1.5 times a minute, once in 40 s (36.51) [1062], while the phosphate ion stays in the ocean 20,000–100,000 years.

Between them lie 21 to 23 steps of three (computed: 57.88 − 36.51 = 21.37; 59.35 − 36.51 = 22.84). One element carries the same form from the cell to the sea floor.

The sulphur cycle today

Sulphate reduction remains bacterial. In coastal sediments sulphate-reducing bacteria oxidised as much organic matter to CO_2 as all aerobic organisms together [232]. Their share fell threefold across the shelf, from the shore to 200 m (20.21) [232].

Global marine sulphate reduction is 11.3 Tmol SO_4^{2-} per year, from a neural network trained on 199 profiles, about 15 % above earlier estimates (modelled [233]). In mass this is 11.3 × 32.06 = 362 Tg S per year (computed). It accounts for 12–29 % of the organic carbon reaching the sea floor (modelled [233]).

Prokaryote cell numbers are about one order of magnitude higher in sulphate-depleted margin sediments [233]. In coastal sediments the share is about one half, against 12–29 % globally.

The upward route is algal. Phytoplankton release dimethylsulphide, typically at 1–7 nM in surface water and higher at high latitudes [1063]. The database grew threefold in a decade, from 15,000 to over 47,000 measurements [1063].

The sea-to-air flux is 28.1 (17.6–34.4) Tg S per year, 17 % above the calculation with the previous climatology [1063]. That is 0.88 Tmol S per year, 7.8 % of the sea-floor reduction flux (computed).

Dimethylsulphide appears to be the major source of cloud-condensation nuclei over the oceans [1064]. Cloud albedo is sensitive to their density, and an approximate doubling of them would be needed to counteract the warming from doubled CO_2 [1064].

Oxygen today

Modern O_2 is about 21 % [1014], or 20.95 % of dry air by volume [1049]. The atmosphere–ocean reservoir is 3.78×10^{19} mol, with a source flux of 1.8×10^{13} mol O_2 per year [860]. The residence time is $3.78 \times 10^{19} / 1.8 \times 10^{13} = 2.1 \times 10^{6}$ yr, about 2.1 Myr (62.12) (computed).

With total organic burial of 550 Tg C per year, 4.58×10^{13} mol, the residence is 0.82 Myr (61.27) (computed from [860, 863]). Since the mid-Cretaceous, charcoal shows a steady decline to about 21 % [727].

Marine cyanobacteria are counted directly. Annual global means are $2.9 \pm 0.1 \times 10^{27}$ *Prochlorococcus* cells and $7.0 \pm 0.3 \times 10^{26}$ *Synechococcus* cells (modelled [229]).

They come from niche models on more than 35,000 observations [229]. The ratio is 4.1, and the projected end-of-century increases are 29 % and 14 % (modelled [229]).

The oxygen of the air turns over in about one to two million years. Charcoal records 13 to 35 % over 419 Myr; at a turnover of 1–2 Myr that is 419 / 2 = 210 to 419 / 1 = 419 turnovers (computed). The content flows through while the form holds.

Water and air

The Earth holds about 1,386 million km³ of water [1065]. The oceans hold 1,338 million km³, 96.54 % [1065]. Ice caps, glaciers and permanent snow hold 24.06 million km³, 68.7 % of the fresh water; fresh groundwater holds 10.53 million km³, 30.1 % of it [1065].

Fresh lakes hold 91,000 km³, soil moisture 16,500 km³, the atmosphere 12,900 km³, rivers 2,120 km³, and all living things 1,120 km³ [1065]. Life holds less water than the rivers and less than a tenth of the air’s.

Each year 372,800 km³ of rain and snow falls on the ocean and 112,600 km³ on land, 485,400 km³ together (computed); the source gives the total as 486,900 km³ [1066]. From the land 72,600 km³ returns to the air by evaporation and through plants, and 40,000 km³ runs to the sea in rivers [1066]. About 0.36 of what falls on land runs off; the rest returns to the air (computed).

The FAO gives almost 110,000 km³ of precipitation on land and 43,000 km³ per year of renewable fresh water [1067].

Transpiration is 80–90 % of terrestrial evapotranspiration, and global transpiration is 62,000 ± 8,000 km³ per year [851]. Earlier model estimates gave 20–65 %, 14,000–41,000 km³ per year [851]. A 2014 comment holds the share overestimated [851].

Water stays 8 days (45.39) in the atmosphere, or 8.2 days (45.41) in a second text [24, 1068]. It stays 12–20 days (45.76–46.23) in rivers and 280 days (48.63) as soil moisture

[24]. It stays about 300 years (54.06) as groundwater, 3,100 years (56.19) in the ocean and 16,000 years (57.68) in glaciers [24].

Two checks from the stores and flows: the atmosphere gives 12,900 / 486,900 = 0.0265 yr = 9.7 days (45.57), and the ocean 1,338,000,000 / 413,000 = 3,240 years (56.23) (computed). The residence times of water span 57.68 − 45.39 = 12.29 positions, from 8 days to 16,000 years.

Ice is the closed form, in which every molecule holds four hydrogen bonds. Vapour and liquid are the carrier.

A glacier holds its water 16,000 years and the air passes its own on in 8 days, a ratio of 16,000 × 365.25 / 8 = 730,000 (computed). This is the form of form and carrier.

Dry air is 78.08 % nitrogen and 20.95 % oxygen by volume; argon is 9,340 ppm, CO_2 about 420 ppm and methane 1.94 ppm [1049]. Water vapour varies and is typically about 1 % [1049]. The atmosphere weighs 5.1×10^{18} kg, presses at the surface with 101.4 kPa and has a density of 1.217 kg m^{-3} [1049].

Its scale height, the rise over which pressure falls by a factor e, is 8.5 km (23.62) [1049]. The troposphere reaches 6 km (23.30) at the poles and 18–20 km (24.30–24.40) at the equator [1069]. The stratosphere tops out at 50 km (25.23), the thermosphere at 600 km (27.50), and the exosphere reaches 10,000 km (30.06) [1069].

Ninety per cent of the ozone lies in the stratosphere, at 10–50 km (23.77–25.23) [1070]. Temperature falls from about 17 °C at the surface to −51 °C at the tropopause and rises again through the stratosphere, where ozone forms [1069].

Of the present greenhouse effect, water vapour accounts for about 50 %, clouds for 25 % and CO_2 for 20 % [1071]. Global surface temperature was 1.09 °C higher in 2011–2020 than in 1850–1900, likely range 0.95–1.20 °C [1072].

Ozone-depleting substances have continued to fall since 2018 [1073]. Total column ozone is expected to return to its 1980 values around 2066 over the Antarctic, 2045 over the Arctic and 2040 elsewhere [1073].

The living soil today

Soil is the thin living skin on the rock of the Earth. Mineral soils, most of the cultivated land of the world, hold from a trace to 30 % organic matter; soils above 30 % are called organic soils [1074]. The top metre holds about 2×10^9 prokaryotic cells per gram, and 1–8 m down about 10^8 per gram [1075].

The grains have fixed limits. Fine clay ends at 0.2 µm (1.35), clay at 2 µm (3.44), silt at 50 µm (6.37) and sand at 2 mm (9.73) [1076]. From the clay limit to the sand limit is a factor 1,000, or 9.73 − 3.44 = 6.29 steps of three (computed).

Within soil organic matter an active fraction, including the microbes, forms 10–40 %; a resistant fraction that decomposes very slowly forms 40–60 % [1074]. In 19 days (46.18) after tillage a field lost 860 kg of organic matter per hectare under direct seeding and 4,300 kg under a mouldboard plough and two passes of a disc harrow [1074]. That is five times more (computed).

The mineral grain is the closed form; it passes through a soil unchanged. The organic matter is the carrier; it passes carbon and nitrogen from dead plant to living root. Here the edge of chapter 1 shows: below about 30 cm the carbon is held longest by binding to mineral surfaces [1046], where the crystal meets the living matter.

Soil holds 59 ± 15 % of Earth's species, about twice earlier estimates [1077]. The share living in soil is 98.6 % for Enchytraeidae, 90 % for fungi, 85.5 % for Plantae and 84.2 % for Isoptera [1077].

Soil protists reach tens of thousands of individuals per gram, with dormant banks of 10^4–10^7 per gram [1078]. Their length spans at least six orders of magnitude, from a few µm (*Mycamoeba*, about 3.81 for 3 µm) to more than 1 mm (*Darbyshirella*, above 9.10) [1078]. The largest testate amoebae, *Bullinularia*, *Centropyxis* and *Distomatopyxis*, reach about 150 µm (7.37) [1078].

Protist division times are often "a few hours", about 41.61 for 3 h [1078]. Bacterivory by protists is a major cause of bacterial death [1078]. Almost 15 % of known protists live symbiotically, and about 100 protist species infect humans [1078].

Soil bacteria turn over in days to weeks near 20 °C: 2.3–33 days (44.26–46.68), mean 9.3 days (45.53), and at least 30 days (46.60) by one count [179]. In the rhizosphere they turn over in 12–19 h (42.87–43.29), with generation times as short as 7.5–9.1 h (42.44–42.62) [179]. Doubling takes 24 h (43.50) on young roots and more than 100 h (44.80) on old roots [179].

Soil fungi turn over in 20–40 days (46.23–46.86) with straw or alfalfa, 130–150 days (47.93–48.06) unamended, and 170 days (48.17) at 15 °C [179]. Their turnover is up to one order of magnitude longer than that of bacteria [179].

Soil nematodes number $4.4 \pm 0.64 \times 10^{20}$ in surface soils, with a biomass of about 0.3 Gt, from 6,759 samples [615]. Of the individuals, 38 % live in sub-Arctic regions, 24 % in temperate and 21 % in tropical ones [615]. The mean fresh mass is 0.3×10^{15} g / $4.4 \times 10^{20} = 0.68$ µg (computed).

A database of 6,825 samples from the top 15 cm (13.66) gives a median of 859 and a mean of 2,671 nematodes per 100 g of dry soil, with a maximum above 20,000 [614]. Biome medians are 2,695 in tundra, 2,119 in temperate broadleaf forest, 2,016 in boreal forest, 124 in flooded grassland, 89 in Antarctica and 44 in hot desert [614].

At a bulk density of 1.3 g cm^{-3}, the top 15 cm of one m^2, 0.15 m^3, weighs 195,000 g, that is 1,950 × 100 g. The median and mean are then $859 \times 1{,}950 = 1.7 \times 10^6$ and $2{,}671 \times 1{,}950 = 5.2 \times 10^6$ per m^2 (computed).

Nematodes fill five feeding guilds: bacterivores, fungivores, herbivores, omnivores and predators, with bacterivores most abundant and predators least [614]. *Caenorhabditis elegans* at 20 °C has a mean generation of 90 h (44.70), a minimum of 73.0 h (44.51) and a lifespan of 16.7 days (46.06) [604]. Its strain MY6 has 84 h and 14.7 days (45.95), and peak egg-laying exceeds 140 eggs a day [604].

Valid nematode species number 28,537 in 3,030 genera, 276 families and 32 orders [618]. Estimates of the total run from half a million to 10 million [618].

Oribatid mites count about 9,000 valid species and subspecies to 2002, in 1,204 genera and 169 families [1079]. By region about 3,200 are Palaearctic, 1,500 Ethiopian, 1,500

Neotropical, 1,400 Oriental, 1,200 Nearctic, 1,000 Australian and 100 Antarctic [1079]. The Oppiidae alone hold 13 subfamilies, 166 genera and subgenera and about 1,000 species [1079].

Aquatic oribatids are about 90 species in 10 genera, under 1 % of the group [1080]. The alpine oribatid *Oromurcia sudetica* needs 2–4 years from egg to adult (49.50–50.13) and lives 1–2 years as an adult (48.87–49.50) [1081].

Springtails count 9,186 species in 2024, or 9,270 species and 686 genera in a fuller count [1012, 1082]. Tardigrades count 1,508 species in 164 genera and 35 families [620]. Clitellata number more than 5,000 species [1016].

Earthworms count about 5,738 valid species and subspecies: 5,406 species and 332 subspecies, in 23 families and 382 genera [1083]. Of these, 1,201 taxa were described since 2000, and the total is estimated at well over 8,000 [1083]. The largest families are Megascolecidae with 2,208 species, Acanthodrilidae 746, Lumbricidae 615, Rhinodrilidae 376 and Benhamiidae 351 [1083].

The companion dataset, to the end of 2022, holds 5,420 species and 333 subspecies, 5,753 taxa [1084]. An earlier database counts about 6,000 names since *Lumbricus terrestris* of 1758, of which about 3,000–3,500 are valid [1085].

Across 6,928 earthworm sites in 57 countries, local richness and abundance peak at higher latitudes, the opposite of above-ground life [1086]. Climate shapes the communities more than soil or habitat [1086]. The same pattern runs the other way above and below the ground: the form of context.

A preprint of the same study predicts 1–4 species per site, mean 1.98, and 5–150 individuals per m², mean 57.0 [1087]. It gives biomass of 1–150 g m⁻², an optimum of 12–20 °C, and dispersal of about 10 m per year against about 600 m for an average land organism [1087].

In six weeks (46.90) in repacked soil, *Lumbricus terrestris* dug 9.2 m (17.41) of burrows, 14.5 burrows with 12.2 branches per m, 7.78 mm (10.97) wide [1088]. *Aporrectodea nocturna* dug 21.2 m (18.17), 23.5 burrows with 20.2 branches per m, 5.16 mm (10.59) wide; *A. icterica* dug 15.7 m (17.89) [1088]. The rates are 0.22 and 0.50 m per day (computed).

At 15 °C *L. terrestris* lays 15.1–32.2 cocoons a year [1089]. They hatch 132–731 days (47.94–49.50) after laying, in two peaks about 12 months apart, with 88–94 % viability [1089]. Earlier laboratory values were 90–280 days (47.60–48.63) [1089].

Darwin measured worms directly. Leaves were dragged into burrows to a depth of 1–3 inches, 2.5–7.6 cm (12.04–13.04) [1090].

A worm buried itself in loose mould in 2–3 minutes (37.51–37.88); a large worm took 25 h 40 min (43.56) in compact sand, by swallowing it [1090]. Gardens held about twice as many worms as cornfields [1090].

The shortgrass prairie food web holds 13 functional groups [219]. They are bacteria, fungi, root-feeding nematodes, springtails, fungus-feeding mites, fungus-feeding nematodes, flagellates, bacterium-feeding nematodes, amoebae, omnivorous nematodes, predatory nematodes, nematode-feeding mites and predatory mites [219]. In real soil food webs strong top-down effects at low levels pair with strong bottom-up

effects at high levels, and this pattern holds the webs stable [1091].

Fine roots turn over at 53 % a year in grasslands, 55 % in wetlands and 56 % in forests; shrubland roots at 34 % and whole tree root systems at 10 % [1092]. The data come from 190 studies, with Q_{10} of 1.4–1.9 [1092]. At 56 % a year the mean fine-root life is 1 / 0.56 = 1.8 yr (49.41) (computed).

Glomalin, a glycoprotein of arbuscular mycorrhizal hyphae, predicts aggregate stability across 37 soils: AS = 42.7 + 61.3 × $\log_{10}$ IREEG, r^2 = 0.86 [1093]. Macro-aggregates above 250 µm (7.84) are held by roots and hyphae; micro-aggregates depend on persistent organic agents [1094].

Soil forms at 0.023–0.064 mm per year in the UK, with a global median of about 0.026 mm per year from 252 rates [1095]. At the median, a centimetre forms in 385 yr (54.29) and a metre in 38,500 yr (58.48) (computed). Soil production declines exponentially with soil depth [1096].

At the UK arable site erosion runs at 1.19 mm per year, and the 30 cm A horizon would be gone in 256–263 yr (53.92–53.94) [1095]. The time to bedrock is 394–1,325 yr (54.31–55.41) [1095].

Under conventional ploughing erosion averages 1–2 orders of magnitude above soil production, about 1 mm per year [1097]. The ratio at the median production rate is 1 / 0.026 = 38 (computed).

The FAO counts 33 % of the world’s soils as moderately to highly degraded [1098]. At 0.01–0.1 mm per year a centimetre of soil forms in 100–1,000 years (53.06–55.16) (computed from [1097]).

Ploughing can take 4,300 kg of organic matter per hectare in 19 days [1074]. The soil is a slow store that lends to a fast one.

Animals as carriers

Animals move elements against the downhill run of water. Zooplankton migrate daily between the surface and the depths.

A model gives export from the base of the sunlit layer of 6.5 Pg C per year, 14 % higher than without the daily migration (modelled [1099]). The migration carries 0.16 ± 0.04 of total carbon export, 0.16 × 6.5 = 1.04 Pg C per year (modelled [1099]; computed).

Southern Ocean sperm whales defecate an estimated 50 t of iron per year into the photic zone [1100]. This exports about 4 × 10^5 t C per year against about 2 × 10^5 t C respired.

About 12,000 whales thus act as a net sink of about 2 × 10^5 t C per year [1100]. Per whale that is 33 t of carbon exported and 4.2 kg of iron per year; against a global export of about 9 Pg C it is 0.004 % (computed).

Whales and seals may return 2.3 × 10^4 t N per year to the sunlit zone of the Gulf of Maine, more than all its rivers combined [1101]. Before commercial hunting the recycling was likely more than three times the atmospheric nitrogen input [1101]. Cetaceans give about 77 % of the nutrients that mammals and birds release to the gulf

[1101].

Large whales stand at about 10 % of their historical numbers in Massachusetts Bay and about 45 % in the Bay of Fundy; small cetaceans at about 50 % [1101]. Salmon carry nitrogen inland. Trees and shrubs near spawning streams take about 22–24 % of their leaf nitrogen from salmon, by isotope analysis [1102].

Serengeti wildebeest carry it into a river. Mass drownings of more than 100 animals occur in at least 13 of 15 years in the Mara River [1103]. On average 6,250 carcasses and 1,100 t of biomass enter the river each year, a mean of 176 kg per carcass (computed from [1103]).

Soft tissue decays in 2–10 weeks (45.90–47.37), bone in about 7 years (50.64) [1103]. Carcasses supply 34–50 % of the assimilated diet of fish while present, and 7–24 % through bone biofilm afterwards [1103]. Bone lasts 36–182 times as long as soft tissue (computed).

Seabirds, at 99 Gg P per year, close the chain from sea to land (see the phosphorus section) [1061]. Marine mammals, seabirds, migrating fish and land animals once formed a linked system from the deep ocean to the continental interiors [1104].

That capacity is now about 8 % of its value before the extinctions on land and about 5 % in the oceans (modelled [1104]). Upward phosphorus transport by marine mammals is about 23 % of a former 340 × 10^6 kg per year, a loss of 262 × 10^6 kg (modelled [1104]; computed). Seabirds and migrating fish once moved about 150 × 10^6 kg P per year from sea to land; now it is less than 4 %, below 6 × 10^6 kg [1104].

Two seabird figures stand: 99 Gg P excreted at colonies [1061], much of it at the coast, and below 6 Gg P moved inland by birds and fish together [1104]. The carriers run from zooplankton of millimetres to whales of tens of metres, and the same carrying recurs at each size. This is the same winding at every depth: one transport, from the plankton to the herd.

Plants, forests and the climate now

Forests cover about 42 million km², roughly 30 % of the land surface [864]. They store about 45 % of terrestrial carbon and supply about 50 % of terrestrial production [864]. The FAO gives 4.06 billion ha in 2020, 40.6 million km², with a net loss of 4.7 Mha per year in 2010–2020 [1105].

Deforestation ran about 10 Mha per year in 2015–2020 and 12 Mha in 2010–2015 [1105]. Primary forest is at least 1.11 billion ha, down 81 Mha since 1990, and total loss since 1990 is about 178 Mha [1105]. That is 4.2 % of the 1990 area in 30 years (51.97) (computed).

Forests have lower albedo than croplands and grasslands [864]. Boreal forests have the greatest biophysical effect of any biome on annual global temperature; tropical forests cool partly by evaporation [864]. A burn three years old in Alaska had 31 % less annual net radiation than an 80-year-old black spruce forest [864].

In many boreal areas the warming from lower albedo after forestation can offset the cooling from carbon uptake [1106]. A model of complete deforestation gives albedo

forcing of −0.96 W m⁻², boreal −0.51 and tropical −0.18 (modelled [1107]). CO_2 forcing after 100 years (53.06) is +2.22 W m⁻², and short-lived forcers add +0.12 (modelled [1107]).

The total is +1.38 W m⁻² and about 0.8 K of warming (modelled [1107]). Isoprene emission falls 87 %, monoterpenes 94 % and biogenic secondary aerosol 91 % (modelled [1107]). Tropical removal warms about 0.6 K; boreal removal cools about 0.3 K (modelled [1107]).

Plants emit about 1 Pg of volatile organic compounds per year, in a model [862]. Isoprene is about 50 %, 41 monoterpenes about 15 %, 32 sesquiterpenes about 3 % [862].

Leaf area averages 5.2 m² per m² over all biomes before outlier removal and 4.5 after, from more than 1,000 estimates at about 400 sites [861]. Deserts reach 1.3 ± 0.9, tree plantations 8.7 ± 4.3, and the maximum reported is 18 [861].

Over non-forested land, precipitation falls exponentially with distance from the ocean over a few hundred kilometres [1108]. Over the Amazon, the Yenisey basin and equatorial Africa it shows no clear dependence over thousands of kilometres [1108]. The authors propose an “evaporative force” drawing air toward strong evaporation [1108].

A comment holds that this force lacks grounding in basic physics [1109]. The proposed vertical velocities reach 50 m s⁻¹, while the characteristic velocity of 5.6 mm s⁻¹ is four orders of magnitude smaller [1109].

The critics accept that links between vegetation and moisture transport matter [1109].

Between 1982 and 2009, 25–50 % of the vegetated area greened and less than 4 % browned [866]. The attribution is 70 % CO_2 fertilisation, 9 % nitrogen deposition, 8 % climate and 4 % land-cover change [866].

The land breathes once a year. The seasonal CO_2 swing is 15–20 ppm in the far north and about 3 ppm near the Equator [865]. Since the early 1960s it has grown about 20 % at Hawaii and about 40 % in the Arctic, and the falling phase has moved about 7 days (45.27) earlier [865].

The Mauna Loa peak-to-trough is about 6.5 ppm [1110]. At some latitudes the amplitude has grown more than 50 % in about 50 years (52.43), attributed to changed structure and composition of northern ecosystems [1111]. The far north swings 15 / 6.5 = 2.3 to 20 / 6.5 = 3.1 times Mauna Loa (computed).

The seasonal swing is the form of rest and discharge on the scale of a year (48.87). The northern forests load carbon each summer and release it each winter, and the air records both.

Pre-industrial CO_2 was about 278 ppm in 1750; the 2022 annual mean was 417.1 ± 0.1 ppm [1112]. That is 50.0 % above 278 (computed). One ppm equals 2.124 Gt C, so the air holds 417.1 × 2.124 = 886 Gt C (computed from [1112]).

At Mauna Loa the monthly mean was 426.07 ppm in September 2026, against 424.37 in September 2025 [859]. That is 1.53 times the 1750 value (computed).

Annual global growth was 2.83 ppm in 2016, 2.14 in 2017, 2.39 in 2018, 2.50 in 2019 and 2.32 in 2020. It was 2.38 in 2021, 2.24 in 2022, 2.69 in 2023, 3.76 in 2024 and 2.06 in 2025 [859].

The land sink was 3.3 ± 0.8 Gt C per year for 2013–2022, 31 % of emissions; the ocean sink 2.9 ± 0.4, 26 % [1112]. Fossil emissions were 9.9 ± 0.5 Gt C in 2022, and land-use change 1.2 ± 0.7 [1112]. Deforestation released about 1.9 Gt C per year and re- and afforestation took up 1.3 over 2013–2022; the air gained 5.2 Gt C per year [1112].

The air's 886 Gt C exchanges with land production of 129–150 Gt C per year in 5.9–6.9 yr (50.49–50.63) (computed). A fossil pulse equilibrates among air, ocean and land in 2–20 centuries (53.69–55.79), after which 20–35 % stays airborne [1113]. Carbonate neutralisation draws it down further over 3–7 kyr (56.16–56.93) [1113].

People in the cycles

People now move the elements at the scale of the planet. Synthetic nitrogen fed 44 % of the world population in 2000 and 48 % in 2008 (measured [1053, 1114]). Haber–Bosch adds about 120 Tg N per year, as much as all marine fixation [223].

Inorganic phosphorus fertiliser is about 15 Mt P per year, and human mobilisation by 2000 was about three times the natural flows [1115]. Phosphorus stored in land and freshwater ecosystems rose by at least 75 % over pre-industrial levels [1116]. Human activity has roughly doubled the natural phosphorus load of rivers, with a lasting effect of several thousand years (about 56.16 for 3,000 years) [1117].

Seabird colonies deliver 591 Gg N per year, 11.8 % of lightning nitrogen; their 99 Gg P is 0.66 % of fertiliser phosphorus (computed from [1061, 1115]). Commercial fishing moves 3.7×10^3 Gg N and 0.32×10^3 Gg P per year [1061].

Human appropriation of fresh water now equals about half of the discharge of all rivers [1118]. Groundwater depletion rose from 126 ± 32 km^3 per year in 1960 to 283 ± 40 km^3 in 2000, 39 % of all pumping, adding 0.8 mm a year to sea-level rise [1119]. Drained peat emits about 3 % of all human greenhouse gases; each 10 cm of raised water table cuts at least 3 t CO_2 per hectare per year, down to 30 cm [1120].

What this part of the history shows

The cycles appear one after another and each stays once it has opened. Sulphate reduction is dated at 3.47 Ga (68.87), nitrogen fixation at 3.2 Ga (68.79), free oxygen at 2.46–2.33 Ga (68.55–68.50), an oxygenated ocean at 635–630 Ma (67.32–67.31), and the Paleozoic oxygen step at 445–400 Ma. Charcoal is continuous from 419 Ma, and oxygen stays within 13–35 %: what closes, stays.

The fixing of nitrogen opened in prokaryotes, and no eukaryote carries its genes. The housing of fixers runs from colonies of *Trichodesmium*, to UCYN-A beside an alga, to UCYN-A as an organelle with a genome of 1.44 Mb. Here the residue becomes the alphabet: a closed cell becomes a letter inside the next.

New ways of closing carbon opened once and then filled many times. The predisposition

to root nodules arose once, slightly over 100 Ma; nodulation then arose about 8 times and was lost 10 times. The first C4 origin opened a new way after CO_2 fell; the later origins, 62 lineages and about 7,500 species in all, fill it.

Every cycle has a closed form and a carrier. N_2, with its 946 kJ/mol triple bond, holds four fifths of the air; ammonium and nitrate pass on in weeks to decades. Glaciers hold water 16,000 years; the air passes it on in 8 days.

The same rule takes other values in other surroundings: the form of context. Fire is off below 16 % O_2, and insect wings reach 70 cm above 26 %. Litter decays seven times faster in rain forest than in tundra, and earthworm richness peaks at high latitudes, the opposite of life above ground.

Loading and discharge stand in every record. CO_2 falls from about 2,000 to about 278 ppm over 400–300 Ma; rises to about 2,000 ppm at 220–200 Ma; falls below 1,000 ppmv by 8 Ma. The ice loads and discharges on cycles of 41 and 100 kyr, with CO_2 between 172 and 300 ppmv.

Community appears as shared prefix. One carbon atom passes from dissolved organic matter to bacteria, to nanoflagellates and to microzooplankton in the microbial loop. The prairie soil holds 13 functional groups on one nitrogen path, with bacteria, fauna and fungi mineralising 58, 38 and 4 %.

The same carrying recurs at every size. Migrating zooplankton carry 1.04 Pg C per year downward, and 12,000 sperm whales export 4×10^5 t C through 50 t of iron. Salmon give streamside trees 22–24 % of their nitrogen; 6,250 drowned wildebeest add 1,100 t to one river a year.

The cell turns its phosphate in 40 s (36.51), and the ocean in 20,000–100,000 years (57.88–59.35). This is the same winding at another depth.

Today the land holds about 450 of 550 Gt C of living carbon, and production of 104.9 Pg C per year is split evenly between land and sea. People now fix 210 of 413 Tg N per year, mobilise three times the natural phosphorus, and have raised CO_2 by 53 % to 426.07 ppm. The animals that carried elements uphill now carry 5–8 % of what they once did.

12. Partners

No plant or animal lives alone. Roots hold fungi, legume nodules hold bacteria, insect cells hold bacteria with the smallest genomes known, and a human colon holds as many bacterial cells as the body holds human cells. These partners came in at dated points of the history, and many stayed for hundreds of millions of years.

This chapter follows the partnerships in time order. It starts with the fungi in the first land plants, goes on to the bacteria in insect cells, corals, termites and ruminants, and ends with the partners counted today. Chapter 5 told how one cell took in another and kept it as an organelle; here the partners keep their own cells.

Ages are placed on the ladder of chapter 1 as durations, an age of A Ma being $A \times 10^6 \times 3.15576 \times 10^7$ s. An age of 400 Ma sits at 66.90 and one of 100 Ma at 65.64. The day sits at 43.50 and the year at 48.87.

Partners from the first land plants

The genes the plant uses for its fungal partner are older than the land plants. The signalling pathway, with the kinase CCaMK, is present in green algae [892]. The algal ancestor of land plants was thus prepared for symbiosis before it came ashore [892].

A six-gene clock on 199 fungi places crown Fungi at about 1,020 Ma (67.75) and the loss of the flagellum at about 720 Ma (67.43) [299]. The same clock places Glomeromycota, the arbuscular mycorrhizal fungi, at about 659 Ma (67.35), within 715–606 Ma [299]. Dikarya diverge at 649 Ma (67.34) [299].

Crown land plants follow at 482 Ma (67.07), within 485–473 Ma, and the diversification of Glomeromycota begins at about 484 Ma, within 529–437 Ma [299]. The arbuscular mycorrhizal symbiosis itself is placed at about 480 Ma (67.07) [299]. The gap from crown Fungi to that symbiosis is 540 Myr (67.17) (computed).

The partnership is first seen in rock at about 460 Ma (67.03). Hyphae and spores resembling modern Glomales occur in the Ordovician of Wisconsin [433]. Complex mycelia, *Tortotubus protuberans*, with septal pores and a double wall, follow in the earliest Silurian, after 443.8 Ma (66.99) [434].

Arbuscules morphologically identical to living ones sit in the cells of *Aglaophyton major*, more than 400 Ma old [893]. Their host rock, the Rhynie chert, has a uranium–lead age of 411.5 ± 1.3 Ma (66.93) [458]. From the clock origin of the symbiosis to Rhynie is 480 − 411.5 = 68.5 Myr (65.29) (computed from [299][458]).

Lichens stand at the same time. Internally stratified lichens with cyanobacterial and green-algal partners occur in rocks 415 Myr old (66.93) of the Welsh Borderland [907].

They are *Cyanolichenomycites devonicus*, with a cyanobacterium and a pycnidium of asexual spores, and *Chlorolichenomycites salopensis*, with a single-celled, presumably green alga [907]. Later records follow at 325 Myr (66.71) and about 195 Myr (66.25) [907].

The clock places the ascolichens at 467–410 Ma (67.04–66.92), and the oldest lichen fossil gives a minimum of 415 Ma [299]. The Rhynie lichen *Winfrenatia reticulata*, about 400 Ma, has thallus bands 1–2 mm thick (9.10–9.73) [907, 908].

Its mesh openings average about 25 µm (5.74), its hyphae are 1–4 µm (2.81–4.07), and a solitary partner cell is 15 µm (5.28) [908]. Up to 32 daughter cells sit in one sheath [908].

The partner was laid down before the plant that holds it. The algal signalling genes, the fungus at 659 Ma and the spores at 460 Ma all come before the arbuscule at 411.5 Ma. Here the residue of one depth is the alphabet of the next: a closure already made becomes a letter the next closure uses.

The lichen and the arbuscule nest one partner inside another. A fungus lives in the plant cell; an alga lives inside the fungal body. This is community as shared prefix: “Community is topological, not chosen: shared prefix.”

Animals and microbes at the vents

The oldest known vent community with animals is the Yaman Kasy deposit of the southern Urals, about 440 Ma (66.99) [1121]. Its age is poorly constrained, from the late Ordovician to the early Silurian [1121]. Microbial filaments lie on and around the tubes of the tubeworms *Eoalvinellodes annulatus* and *Yamankasia rifeia* [1121].

The *Eoalvinellodes* tubes are 0.2–3 mm across (7.63–10.10) and the *Yamankasia* tubes 3–39 mm (10.10–12.43) [1121]. The filaments are read as an association on the surface, not a proven symbiosis [1121]. The 3.24 Ga Sulphur Springs deposit (68.80) holds filaments of questioned biological origin [1121].

Chemosynthetic symbioses were discovered at the Galápagos Rift vents, described in 2008 as “30 years ago”, about 1978, 48 years before 2026 (52.39) [1122]. “At least seven animal phyla are known to host these symbionts” [1122]. The associations evolved “on multiple occasions” by convergence, and more than two endosymbionts can live in one host [1122].

The giant tubeworm *Riftia pachyptila* takes its symbiont from the water [1123]. The symbiont is “facultative” and is taken up by the metatrochophore larva in each generation [1123]. Its tube “can reach up to three metres in length and five centimetres in diameter”, 3 m (16.39) and 5 cm (12.66) [1123].

The host genome is 560.7 Mb haploid, with 25,984 protein-coding genes and 8,629 lineage-specific genes [1123]. It has 1,897 contracted and 734 expanded gene families [1123]. The same paper puts *Riftia*’s genome about 168 Mb below the ~688 Mb of *Lamellibrachia*, which gives 520 Mb (computed).

Insects take bacteria into their cells

From the Permian onward some insects carry bacteria inside special cells. *Sulcia* was acquired by the ancestor of the Auchenorrhyncha at least 260 Ma (66.51) (modelled [370]). The cicada, spittlebug and sharpshooter lineages split at least 200 Ma (66.27)

(modelled [370]).

Sulcia and *Nasuia* have been partners since the leafhopper–spittlebug split, more than 200 Ma, and the pairing began before 260 Ma (modelled [371]). The *Buchnera* symbiosis of aphids was established “200–250 Myr ago” (66.27–66.47) (modelled [372]).

Buchnera sp. APS of the pea aphid has a chromosome of 640,681 bp and two plasmids, pLeu of 7,786 bp and pTrp of 7,258 bp [372]. It has 583 predicted ORFs, about 500 with assigned function, and 55 genes for amino-acid synthesis [372]. That is 583 / 4,288 = 13.6 % of the ORFs of *Escherichia coli* MG1655 (computed from [188]).

Buchnera holds more than 100 genome copies per cell, and an aphid carries 60–80 bacteriocytes [372].

Symbiont genomes of 139–250 kb encode 121–227 proteins [373]. Before 2006 the smallest known cellular genomes were about 500 kb, with about 500 genes [373]. *Carsonella ruddii* of psyllids has a circular chromosome of 159,662 bp, 16.5 % GC and 97 % coding density; a minimal genome had been proposed at about 400 kb [374].

Hodgkinia cicadicola of cicadas has 143,795 bp at 58.4 % GC [375]. It reads the codon UGA as tryptophan instead of stop [375]. Its partner *Sulcia* has 22.6 % GC [375].

In the leafhopper *Macrosteles quadrilineatus*, *Nasuia deltocephalinicola* has 112 kb and *Sulcia muelleri* 190 kb [371]. Together they make the 10 essential amino acids [371]. Both have lost the genes for ATP synthesis by oxidative phosphorylation [371].

Sulcia-CARI of the spittlebug *Clastoptera arizonana* has 276,511 nt and 246 protein-coding genes; its partner *Zinderia insecticola* has 208,564 nt and 202 [370]. The genes kept are completely colinear across three *Sulcia* genomes [370]. Insect symbiont protein genes span 121–583, 2.8–13.6 % of *E. coli* (computed from [188]).

Two bacteria together supply the ten amino acids that the insect cannot make. This has the form of the pair: two closures together, which jointly make what the host needs.

In the mealybug *Planococcus citri* each cell of *Tremblaya princeps* holds several gammaproteobacterial cells [338]. The *T. princeps* genome is 138.9 kb, the inner *Moranella endobia* 538.2 kb [338]. *Tremblaya phenacola* PAVE, in a lineage without the inner partner, has 171.5 kb [338].

The inner genome is 538.2 / 138.9 = 3.9 times its container’s (computed). *Tremblaya* with an inner partner has 81 % of the genome of *Tremblaya* without one (computed).

Here the nesting reaches its limit. Host cell, *Tremblaya*, *Moranella*: two partners with their own genome, one inside the other. This is the form of never loaded twice: partners with their own genome sit at most two deep inside a cell.

The insect symbionts keep only what the host does not supply. *Buchnera* keeps 13.6 % of the genes of a free bacterium, *Tremblaya* a fraction of that, and *Hodgkinia* has changed its code. The letter keeps what the word does not supply: this is the residue that becomes the alphabet.

Supergroups A and B of *Wolbachia*, a bacterium of arthropod cells, are about 200 Myr old (66.27), “considerably older than previously appreciated” (modelled [1124]). Four strains co-diverged with their host lineage for about 2 Myr (62.08) (modelled [1124]). A

biotin-synthesis operon was acquired by recent lateral transfer [1124].

Mesozoic partners: corals, termites, trees and light

Scleractinian corals expanded and diversified about 240 Ma (66.43) [533]. Late Triassic coral skeletons from Antalya, Turkey, about 212 Ma (66.32), record the coral–dinoflagellate symbiosis [533]. The evidence is skeletal microstructure, carbonate $^{13}C/^{12}C$ and $^{18}O/^{16}O$, and skeletal organic $^{15}N/^{14}N$ [533].

The symbiotic signal appears also in species with growth forms thought to lack it, and the Tethys habitat of those corals was poor in nutrients [533]. From the coral expansion to the recorded symbiosis is 240 − 212 = 28 Myr (64.48) (computed).

The coral partners form the family Symbiodiniaceae [534]. In a revision the former *Symbiodinium* “clades” became genera, seven of them described [534]. A recalibrated clock puts the earliest diversification of the family at about 160 Ma (66.07), in the Jurassic, with the radiation of modern shallow-water corals (modelled [534]).

The fossil isotopic date is 212 − 160 = 52 Myr (65.04) older than the clock date of the living symbiont family (computed).

Termites split from the wood roach *Cryptocercus* about 170 Ma (66.12), within 153–196 Ma (66.02–66.25) (modelled [941]). The termite crown is 149 Ma (66.00), within 136–170 (65.92–66.12) (modelled [941]). The first undisputed termite fossils are Early Cretaceous, 110–135 Ma (65.72–65.91) [941].

From the split to the crown is 170 − 149 = 21 Myr (64.22) (computed). Primitive termites digest wood with cellulose-digesting gut protists [1125]. Protists in termites were first recorded by Leidy in 1877, 149 years before 2026 (53.43) [1126].

The ectomycorrhizal habit, a fungal sheath around tree roots, is present since the Early Jurassic [903]. The crown of the Pinaceae dates to 183 Ma (66.19), within 233–150 Ma, and the Agaricomycetidae to 154 Ma (66.03) [299]. A second wave of mycorrhizal lineages came in the Cretaceous, and a recent wave continues [895].

The earliest bioluminescence in ray-finned fishes is Early Cretaceous, about 150 Ma (66.01), in the Stomiiformes (modelled [1127]). Light made by bacteria evolved at least 17 times in that group [1127].

On land, a phylogeny of 32,223 species places a single origin of the predisposition to root nodules slightly over 100 Ma (65.64), within the Fabidae [213]. A second source gives legumes at about 60 Ma (65.17) and nodulation at about 58 Ma (65.14) [1128]. The difference is 100 − 58 = 42 Myr (64.85) (computed).

The oldest unequivocal legume fossil is 65.35 Ma (65.25) [1129]. Crown legumes are Maastrichtian or early Paleocene, with a stem calibration of 63.5 Ma (65.22) and the Cretaceous–Paleogene boundary at 66 Ma (65.26) [1129]. Stem fossils of the subfamilies are about 58 Ma for Caesalpinioideae and about 56 Ma for Papilionoideae (65.14, 65.11) [1129].

The water fern *Azolla* carries a nitrogen-fixing cyanobacterium. The relationship is “potentially extending back for as long as 140 million years” (65.94) [378].

Fossils give about 100 Myr (65.64), back to the mid-Cretaceous [381]; a review gives “more than 60 my” (65.17) [354].

The UCYN-A sublineages A1 and A2, nitrogen-fixing cyanobacteria inside single-celled algae, diverged around 91 Ma (65.55), in the late Cretaceous (modelled [377]). The host of UCYN-A2, *Braarudosphaera bigelowii*, is 7–10 µm (4.58–4.91) and holds about 3–10 partner cells; the host of UCYN-A1 is 1–3 µm (2.81–3.81) and holds one [377].

UCYN-A has a genome of 1.44 Mb and lacks the oxygen-evolving photosystem II, carbon fixation and the tricarboxylic acid cycle [209]. “The prymnesiophyte receives fixed N in exchange for transferring fixed carbon to UCYN-A” [208]. In 2024 it was described as an early-stage nitrogen-fixing organelle, the “nitroplast”, which imports proteins encoded by the host genome [210].

Cenozoic partners: farms, forestomachs and apes

The termite family Termitidae dates to 54 Ma (65.08), within 46–66 Ma (64.93–65.26) (modelled [941]). It has an entirely prokaryotic gut microbiota and has lost the protists of the lower termites [1125]. From the termite crown to Termitidae is 149 − 54 = 95 Myr (65.59) (computed).

Fungus farming by the Macrotermitinae with *Termitomyces* had a single origin in Africa [938]. It is dated about 31.4 Ma (64.58), within 25.82–39.53 Ma (64.41–64.79) (modelled [939]). Fossil fungus gardens are 24.8–24.5 Ma old (64.37–64.36) [939].

A study of 44 newly sequenced ruminant genomes, 36 genera and all six families, dates crown Ruminantia to 39.1–32.3 Ma (64.78–64.61) (modelled [1130]). The paper prints this as “late Oligocene” [1130]. Pecora date to 23.3–20.8 Ma (64.31–64.21) (modelled [1130]).

The rumen, reticulum and omasum have expression profiles closest to the oesophagus, which suggests an oesophageal origin of the forestomach [1130]. From the termite crown to the ruminant crown is 109.9–116.7 Myr (65.72–65.78) (computed).

Several dominant gut bacteria cospeciated with hominids over the past ~15 Myr (63.91): humans, chimpanzees, bonobos and gorillas [1131]. Bacterial divergence times match those of the hosts [1131]. Clades of Bacteroidaceae and Bifidobacteriaceae were kept within single host lineages over “hundreds of thousands of generations” [1131].

The partnerships open and then fill. Termites take protists, then one family drops them for bacteria alone, then one subfamily adds a fungus.

Ruminants open a fermentation chamber in front of the stomach, and the apes carry several gut lines along their branches. This is opened once, filled many times.

The partners of plants today

Of vascular plant species, 72 % form arbuscular mycorrhiza, 2.0 % ectomycorrhiza, 1.5 % ericoid and 10 % orchid mycorrhiza [895]. Eight per cent are completely non-mycorrhizal and 7 % inconsistent [895].

Of 3,617 surveyed species in 263 families, 80 % of species and 92 % of families are mycorrhizal [897]; about 85 % of living plants are mycorrhizal [896].

Vascular plants number about 308,312 species [659]. The arbuscular host count is 0.72 × 308,312 = 221,985 (computed).

Glomeromycota hold about 360 described species in 49 genera, 17 families, 6 orders and 3 classes [898]. The same source estimates 7,247 species from environmental sequences and about 4.6 new species a year; the first two were described in 1844 [898].

The Neotropics hold 221 species, given as 69 % of the phylum, which implies 221 / 0.69 = 320 (computed from [899]). The ratio of host species to fungal species is 221,985 / 360 = 617 to 221,985 / 320 = 694 (computed).

Of 1,014 root samples worldwide, 93 % of arbuscular fungal taxa occur on more than one continent and 34 % on all six sampled [900]. A spore of *Rhizophagus intraradices* is 40–140 µm (6.17–7.31), mean 93.3 µm (6.94), on a hypha of 11–18 µm (4.99–5.44), from 170 spores [1132].

The hyphae of 31 soil fungi are 2.7–6.5 µm wide (3.72–4.51) [432]. The largest arbuscular spore is 140 / 2.7 = 52 times the thinnest hypha (computed). Arbuscular hyphae exceed 100 m per cm^3 of prairie soil, and ectomycorrhizal mycelium reaches up to 2,000 m per cm^3 [905].

One fungal phylum of a few hundred species serves more than two hundred thousand plant species. Here the form of opened once, filled many times shows in plain numbers: one union, about 617–694 hosts per fungus.

Ectomycorrhiza has the reverse arrangement. On the fungal side it arose independently and persisted at least 66 times in Basidiomycota, Ascomycota and Zygomycota, in 162 proven genera [901].

An update gives 78–82 lineages and 251–256 genera [902].

On the plant side the habit occurs in 30 lineages, 335 genera and about 8,500 species; it evolved twice in gymnosperms and 28 times in angiosperms [903]. Plants able to form it are estimated at 6,000–7,000 species, 1.7–2.4 % of land plants [903].

The fungal species number 7,750 from the literature and likely 20,000–25,000 [904]. The ratio of fungi to plants is 20,000 / 6,000 = 3.3 to 25,000 / 7,000 = 3.6 (computed). The first ectomycorrhizal origin opened the union; the later origins, at least 66 and by the update 78–82 in fungi, fill it.

Plants allocate 13.12 Gt CO_2-equivalent per year to mycorrhizal mycelium, the mean of 2001–2021 [905]. The split is arbuscular 3.93, ectomycorrhizal 9.07 and ericoid 0.12 [905]. In carbon this is 13.12 × 12.011 / 44.009 = 3.58 Gt C, split 1.07, 2.47 and 0.03 Gt C [905].

The shares of net primary production allocated are 6.2 % (arbuscular), 13.1 % (ectomycorrhizal), 3.5 % (ericoid) and 1.0 % (orchid), from 194 datasets [905]. Vegetation cover is 57.4 % arbuscular, 25.7 % ectomycorrhizal, 2.6 % ericoid and 14.3 % non-mycorrhizal [905]. Plant biomass is 241 Gt C in arbuscular vegetation and 100 Gt C in ectomycorrhizal vegetation [905].

Lichenisation arose 20–30 times: 14–23 in Ascomycota and 6–7 in Basidiomycota [909]. Lichenised fungi count 19,387 species in 995 genera, 115 families, 39 orders and 8 classes; 172 of them, 0.9 %, are Basidiomycota in 15 genera [909].

Thalli of *Rhizocarpon geographicum* reach 120 mm (13.46) in Norway, and the largest recorded thallus, of *R. alpicola*, is 480 mm (14.72) [911, 912]. *R. geographicum* grows 0.23–1.39 mm a year in Iceland, mean 0.64–0.65; 0.34 in Labrador; 0–0.35 in Alaska; 0.1–0.2 in Greenland; 0.26–0.41 in British Columbia; 1.47 on Welsh gravestones; about 0.1 in the Cascades [911].

The slowest recorded, *R. superficiale* in Colorado, grows 0.006 mm a year over 16 years (51.39) [912]. Some thalli in West Greenland are “at least 4500 years old” (56.53) [912].

In Alaska *R. alpicola* grows 3.4 mm per 100 years (53.06); a 15.5 cm (13.69) thallus is about 3,700 years (56.35) and the 480 mm thallus about 9,000 years (57.16) [912]. Colonisation lags 5–18 years (50.34–51.50) and mortality runs 2–3 % a year [912].

A lichen of a fungus and an alga lasts for thousands of years while its cells turn over. This is the form of form and carrier: the joined form persists; its carriers are replaced.

Nitrogen-fixing partners are bacteria only. Nitrogenase occurs in three forms, molybdenum, vanadium and iron-only; the alternatives nest within the molybdenum line, so molybdenum came first [112]. In bacteria the genes occur in cyanobacteria, Firmicutes, Chloroflexi, Chlorobi, Bacteroidetes, Actinobacteria, Proteobacteria and Aquificales; no eukaryote carries them [112].

Nodulating plants fall in about 10 of about 380 angiosperm families, all in one clade [212]. In that clade of Fabales, Rosales, Cucurbitales and Fagales nodulation originated about 8 ± 2.47 times and was lost about 10 ± 2.80 times [213].

The precursor was lost 16.7 ± 3.21 times, and stable fixers arose 24.5 ± 4.79 times [213]. The study analysed 3,467 species against a database of 9,156 nitrogen-fixing angiosperms [213].

Genomes of 37 species show the gene *NIN* lost in 10 of 13 non-nodulating species, in at least eight independent losses [1133]. *RPG* is missing from 12 non-nodulating species and from the nodulating *Arachis ipaensis* [1133]. The nodules of *Parasponia andersonii*, a non-legume, and of *Medicago truncatula* may share a single origin, with parallel gene loss in non-nodulating relatives [1134].

Legumes count over 19,500 species in 765 genera and six subfamilies [214]. Papilionoideae hold 503 genera and about 14,000 species; Caesalpinioideae 148 and about 4,400; Detarioideae 84 and about 760; Cercidoideae 12 and about 335; Dialioideae 17 and about 85; Duparquetioideae 1 and 1 [214]. Nodules are usually present in Papilionoideae, variable in Caesalpinioideae and absent in the other four [214].

The two nodulating subfamilies hold 14,000 + 4,400 = 18,400 species, 94.4 % of 19,500, as an upper bound (computed). The four without nodules hold 1,181 species, 6.1 % (computed). An infection route without infection threads persists in 25 % of legumes [1128].

Rhizobia occur in Alphaproteobacteria and Betaproteobacteria; 13 alphaproteobacterial and 2 betaproteobacterial genera are named [215]. Rhizobial species per crop are 14

for common bean, 11 for soybean, 6 for cowpea, 5 for chickpea, 5 for peanut, 4 for lentil, 3 for faba bean and 2 for pea [1135]. In 1990 they were 1, 1 and 2 for bean, faba bean and soybean [1135].

One tree, *Vachellia karroo*, yielded 88 nodule isolates in 7 genera and 26 putative species: 67 Alphaproteobacteria and 21 Betaproteobacteria [1136]. In soybean, root-hair curling peaks at day 8 (45.39), nodules swell by day 15 (45.96), and a nodule reaches 5 mm (10.56) by day 45 (46.96) [1054].

Actinorhizal plants with *Frankia* number 8 families, 24 genera and over 220 species [216]; a second count gives 25 genera [1137]. *Frankia* falls in three clades with genomes of 5.43, 7.50 and 9.04 Mbp, a range of 1.66 times (computed from [1138]).

Cyanobacteria partner with plants in 13 hornwort genera and in 4 of more than 340 liverwort genera [382]. In the World List of Cycads, 382 species in 10 genera host *Nostoc* [217]. *Azolla* is a host, and *Gunnera* is the only angiosperm host [354].

In symbiosis the same cyanobacterium takes other values. Heterocysts, the fixing cells, are 4–10 % of cells in free-living *Nostoc* and 30–50 % in symbiosis [382].

The partner keeps as little as 20 % of the nitrogen it fixes and grows 5–10 times slower than when free [382]. In cycad roots heterocyst frequency rises up to 80 %, and akinetes stay dormant up to 60 years (52.60) [181].

That is the form of context: one cell, one rule, other values in other surroundings. The *Nostoc* hormogonia move at 0.7–1.7 µm per s, with pili 7–10 nm wide (−1.71 to −1.38) and up to 10 µm long (4.91) [382]. Cyanobiont genomes are 5.4–9.0 Mbp [181].

Nostoc azollae 0708 has a genome of 5,486,145 bp with 5,357 predicted coding sequences; 31.2 % are pseudogenes and 3,668 ORFs are intact [378]. The free-living *Anabaena*/*Nostoc* PCC 7120 has 6,413,771 bp and 5,368 protein genes [379]. The intact share is 3,668 / 5,368 = 68.3 % (computed).

Other plant-symbiotic *Nostoc* genomes are 7.1–10.4 Mb, “among the largest Nostocales genomes” [380]. “*N. azollae* is the only clear example of a plant symbiotic cyanobacteria genome that underwent genome streamlining” [380]. It is passed down within the fern, and it keeps two thirds of its genes.

Arbuscular mycorrhiza is formed by the roots of 70–90 % of land plant species [1139]. Seven plant genes are required for signalling in both arbuscular mycorrhiza and the root-nodule symbiosis [1139]. The nodule uses the letters of the older fungal partnership.

Around the roots live free bacteria. A gram of soil can hold up to 10^{10} bacterial cells, from thin-section densities of 1.09×10^{7} to 1.16×10^{10} per gram [237]. Species per gram are estimated at 4×10^{3} to 5×10^{4} [237].

The mean distance between bacterial cells is 12.46 µm (5.11), 10.38 µm (4.94) near the surface, more than 18 µm (above 5.44) at depth and 29 µm (5.88) below 60 cm [237]. Within 20 µm (5.54) of a cell lie about 12 cells at 10^{8} per gram, 120 at 10^{9} and 555 at 10^{10} [237]. They belong to about 11, 97 and 284 species [237].

DNA reassociation of one soil bacterial fraction gives about 4,000 distinct genomes [238]. Across 237 sites on six continents, about 2 % of phylotypes, about 500, make up

nearly half of soil bacterial communities [239]. The implied total is 500 / 0.02 = 25,000 phylotypes (computed).

In *Arabidopsis thaliana* grown in natural soils, Proteobacteria, Bacteroidetes and Actinobacteria colonise the roots preferentially [1140]. Cell-wall features of other plant species assemble about 40 % of the root microbiota [1140]. Across more than 600 plants in two soils, root endophytes are enriched in Actinobacteria and some Proteobacteria families [1141].

Grasses allocate 33 % of assimilated carbon below ground and annual crops 21 %, from 281 data sets [1142]. Shoots retain 45 % in crops and 34 % in grasses [1142]. Crops allocate most below ground in their first 1–2 months (46.61–47.24), grasses after 2–4 months (47.24–47.87) [1142].

Rhizosphere bacteria turn over in 12–19 h (42.87–43.29), against 2.3–33 days (44.26–46.68) in bulk soil [179]. In humus of a forest bacterial production is 30–60 g C m^{-2} yr^{-1}, against a plant carbon input of 200 g C m^{-2} yr^{-1} [179].

The partners of animals today

The human count is the reference. A reference man of 20–30 years (51.60–51.97), 70 kg and 170 cm (15.87) carries 3.8×10^{13} bacteria, ±25 % [236].

He has 3.0×10^{13} human cells, with 2 % calculated uncertainty and 14 % variation [236]. The ratio is 1.3, and 1.3–2.3 across population groups [236].

Red blood cells number 2.5×10^{13}, 84 % of human cells [236]. Against the nucleated human cells, about 0.3×10^{13}, the ratio is about 10 to 1 [236].

Almost all the bacteria sit in the colon, whose content is 0.4 L, about 0.4 kg [236]. A cube of that volume has an edge of 7.37 cm (13.01) (computed). Earlier values were 340 mL and, by MRI, 430 mL [236].

The colon holds about 0.9×10^{11} bacteria per g of wet stool [236]. Check: 0.4 kg × 0.9×10^{11} per g × 1,000 g per kg = 3.6×10^{13}, close to the published 3.8×10^{13} (computed). Skin holds about 10^{12} bacteria, and the stomach and upper small intestine 10^{3}–10^{4} per mL [236].

The mouth holds less than 1 % of the colon bacteria, and all sites outside the colon together at most about 10^{12} [236]. The mean gut bacterium weighs about 5 pg wet, 1–2 pg dry [236]. The bacterial mass is about 0.2 kg wet, 50–100 g dry, about 0.3 % of body mass [236].

The old figure of 10 to 1 came from Luckey in 1972, who multiplied about 10^{11} bacteria per g by 1 L of gut volume [236]. That gave about 10^{14}, 2.6 times the revised count (computed). Each defecation removes “a quarter to a third” of the colon content [236].

The colon population is replaced in part every day while its numbers hold. The partnership has the form of what closes, stays: the content flows through, the form of the community holds.

A catalogue of 204,938 non-redundant gut genomes, from 286,997, represents 4,644 prokaryote species: 4,616 bacterial and 28 archaeal [1143]. Of these species 71 % have

no cultured representative [1143]. The genomes come from 31 countries on six continents [1143].

The catalogue holds 170,602,708 protein sequences at 100 % identity; the Methods give 625,255,473 full-length sequences [1143].

Volatile fatty acids from microbial fermentation supply about 70 % of the energy requirement of ruminants such as sheep and cattle [1144]. They supply about 10 % in humans and about 20–30 % in several other omnivores and herbivores [1144]. Acetate:propionate:butyrate ratios range from 75:15:10 to 40:40:20 [1144].

There are at least 200 living ruminant species, Bovidae at least 143 [1130]. The Hungate1000 project sequenced 410 cultured rumen bacteria and archaea, in a catalogue of 501 genomes: 480 bacteria and 21 archaea [1145]. About 75 % of rumen genus-level taxa are represented, 73 of 88 described genera, or 83 % [1145].

The genomes code 32,755 carbohydrate-active degradative enzymes: 31,569 glycoside hydrolases and 1,186 polysaccharide lyases, about 2.2 % of all ORFs [1145]. At least 47 isolates may make vitamin B12 from scratch, and 140 more carry salvage pathways [1145]. Of the rumen organisms, 134 also occur in human gut datasets [1145].

In the honey-bee worker, seven species at 97 % 16S identity make up more than 90 % of the gut community on average [1146]. Density is highest in the hindgut; the ileum holds mostly Proteobacteria, the rectum mostly Lactobacilli and Bifidobacteria [1146].

A reconstituted community reached “approximately 10^9 bacterial cells per gut after 10 d of colonization”, 10 days at 45.60 [1146]. Bees without it held fewer than 10^6 cells per gut [1146].

A second study counts “8–10 core bacterial species”, and its 17 isolates resolved into 11 phylotypes at 97 % identity and 17 at 98 % [1147].

In *Drosophila melanogaster*, *Lactobacillus* and *Acetobacter* make up 94 % of the community [1148]. Culturable bacteria per fly span about 10^2 to 10^6 colony-forming units, with a detection limit of 25 [1148].

At 1 h (40.61) after emergence 9 of 10 flies had no detectable bacteria; within 24 h (43.50) 6 of 10 had them [1148]. Without repeated access to bacteria in food the two genera fall 10- to 1,000-fold in older flies, detectably within 6 h (42.24) [1148].

The fly keeps its partners only by eating them again and again. The form of the community holds; its carriers come in from the food and pass out.

Termites number 3,106 living and fossil species in nine living families, with a fossil record of 135 Myr (65.91) [1149]. Of these, 363 are significant pests [1149]. Termitidae hold more than 75 % of living species by one count and 84 % by another [941, 1150].

Lower termites carry “a few to a dozen” protist species each, and “roughly 500 termite-associated protist species have been described” [1126]. The protists in turn carry bacterial endosymbionts of four phyla [1126]. The hindgut is described as a “one-microliter environment”, a cube of 1 mm edge (9.10) (computed from [1126]).

Cloning studies found 222–1,318 bacterial ribotypes [1126]. *Reticulitermes flavipes* holds more than 4,761 species-level phylotypes, over 99 % of them bacteria;

Coptotermes gestroi holds an estimated 1,460 bacterial species [1126].

Bacteria in protists in a termite gut: partners nested inside partners. Here community shows as shared prefix, addresses inside longer addresses.

Global termite emission is 19.7 ± 1.5 Mt CH_4 and 3,500 ± 700 Mt CO_2 per year, about 4 % and 2 % of global emissions [942]. Termite mounds oxidise about half of termite methane before it escapes [943].

The royal pair of a termite colony lives at most about 20 years (51.60), while colonies last decades [940]. Mounds last about 700 years (54.83), and those of fungus-growers up to 2,200 years (55.88) [940].

The bobtail squid *Euprymna scolopes* takes up *Vibrio fischeri* from seawater [1151]. Within 12 h (42.87) of hatching, bacteria gathered in mucus migrate to the pores and enter the crypts [1151]. The light organ has three pairs of crypts, six in all, and its population grows to about 10^6 cells [1151].

Each dawn the squid expels most crypt contents, “including 90–95% of the bacterial population” [1151]. That releases 0.9–0.95 × 10^6 symbionts to the sea per squid per day (computed). The rest regrow in 4–6 h (41.87–42.24) [1151].

Regrowth from 5–10 % to 100 % needs $\log_2(100 / 10) = 3.3$ to $\log_2(100 / 5) = 4.3$ doublings (computed). In 4–6 h that is a doubling time of 0.93–1.8 h (40.54–41.14) (computed).

The squid holds a light organ for life and empties it each day. This is form and carrier in a daily cycle (43.50): the form persists; its carriers are replaced every dawn.

Sponge microbial communities “can constitute up to 35% of the sponge biomass” [1152]. They include members of about 30 bacterial phyla and several archaeal lineages [1152]. The review calls sponges “the most ancient of the metazoan animals” [1152].

High-microbial-abundance sponges hold 10^8–10^{10} bacteria per g wet weight, “exceeding seawater concentrations by 2–4 orders of magnitude” [1153]. Low-microbial-abundance sponges hold 10^5–10^6 per g, within the seawater range [1153].

In *Hydra*, *Curvibacter* forms about 76 % of the stable community, described as “three main families” [1154]. One polyp holds at most about 2 × 10^5 *Curvibacter* cells, reached within 24–72 h (43.50–44.50) [1154]. The stable maximum was seen at 168 h (45.27), with at most 23 % variation between replicates [1154].

Final capacities in three experiments were 207,309, 202,242 and 214,222 cells [1154]. A second colonist arriving 24, 48 or 72 h later made up about 60 %, 30 % and 10 % of the final population [1154]. What came first holds the space.

In corals the partners are dinoflagellates of the Symbiodiniaceae, with seven described genera, living inside the coral animal [533, 534]. The bleaching threshold is 1 °C above the maximum monthly mean, the highest summer mean temperature [565]. Degree Heating Weeks add up excesses of at least 1 °C over the past 12 weeks (47.53) [565].

At 4 °C-weeks reef-wide bleaching is expected; at 8 °C-weeks or more, bleaching with death of heat-sensitive corals [565]. Alert Levels 3–5 were added in December 2023 [565].

Records from 100 reef locations, 1980–2016 (36 years, 52.13), show the median return time of severe bleaching falling steadily to 6 years (50.50) [566]. Tropical sea temperatures in present La Niña conditions exceed those of El Niño events three decades earlier [566].

The coral partnership holds below a fixed line and breaks above it. The same pair takes other values in other water: the form of context.

Wolbachia infects a large share of arthropod species. Within a species infection is "most-or-few", typically more than 90 % or fewer than 10 % of individuals [1155]. A statistical analysis gives 66 % of species infected, from 20 screenings of more than 900 species [1155, 1156].

A second analysis gives about 40 % of terrestrial arthropod species, an incidence of 0.406, from 136 species, 2,052 individuals and 15 orders [1156]. The plain ratio of infected to tested is 22.8 % [1156]. The same analysis gives more than 1 million infected species, and *Spiroplasma* incidences of 0.032–0.221 (modelled [1156]).

A third analysis covers more than 3,600 arthropod species and about 150,000 individuals [1157]. It gives *Wolbachia* 52 % of species (95 % CI 48–57), *Rickettsia* 24 % (20–42) and *Cardinium* 13 % (13–55) (modelled [1157]). Incidence is weakly and inconsistently higher in species-rich clades [1157].

Wolbachia wMel, from *D. melanogaster*, has a circular genome of 1,267,782 bp at 35.2 % GC [1158]. Repeats longer than 200 bp make 14.2 % of it, in 19 families, 15 of them likely mobile elements; it carries three prophages [1158]. The host genome is about 180 Mb, $180 \times 10^6 / 1.268 \times 10^6 = 142$ times larger (computed); the paper says about 100 times [1158].

Ray-finned fishes show 27 independent origins of bioluminescence, all in marine lines [1127]. Light made by bacteria evolved at least 17 times and intrinsic light 8 times; 25 of 27 are assigned (computed) [1127]. The origins fall in 14 major clades, sixteen in the figure caption [1127].

About 725 of about 1,510 luminous fish species, 48 %, make light with bacteria, and about 785 make their own [1127]. Six orders hold 57 % of luminous species, about 814 [1127]. Light production "has evolved many times, from bacteria to fish" [1159].

What this part of the history shows

The partner is laid down before the host that uses it. The signalling genes for the fungal partner sit already in green algae; Glomeromycota date to 659 Ma by clock, the land-plant crown to 482 Ma, the first arbuscules to 411.5 Ma. Seven plant genes serve both the fungal partnership and the younger nodule, and the residue of one depth becomes the alphabet of the next.

Partners with their own genome nest, and the nesting stops at two. Fungus in plant cell, alga in fungal body, bacteria in termite protists, *Moranella* of 538.2 kb inside *Tremblaya* of 138.9 kb inside a mealybug cell. Partners with their own genome sit at most two deep inside a cell: the form of never loaded twice.

The partner keeps only what the host lacks. *Buchnera* holds 583 genes, 13.6 % of *E.*

coli; *Sulcia* and *Nasuia*, 190 kb and 112 kb, together make the 10 essential amino acids and have lost their own ATP synthesis. *N. azollae* keeps 68.3 % of its genes intact, UCYN-A 1.44 Mb without photosystem II: the letter keeps what the word does not supply.

Each kind of union opens once; its later origins fill the opened depth. Ectomycorrhiza arose at least 66 times in fungi, 78–82 by a later count, and 30 times in plants; lichenisation arose 20–30 times. Nodulation arose about 8 times after one predisposition slightly over 100 Ma, and bacterial light at least 17 times in fishes.

Community is a shared prefix. The holobiont is one address with many partners inside: 3.8×10^{13} bacteria in 4,644 species with 3.0×10^{13} human cells. Seven species make more than 90 % of a bee gut, and more than 4,761 phylotypes live in one termite.

The partnership holds while its carriers are replaced. A squid vents 90–95 % of 10^{6} bacteria each dawn and regrows them in 4–6 h; a colon loses a quarter to a third at each emptying. A lichen thallus lives about 3,700 to 9,000 years on cells that turn over.

The same partner takes other values in other surroundings: the form of context. Heterocysts rise from 4–10 % of cells free to 30–50 % in symbiosis and up to 80 % in cycad roots; the partner grows 5–10 times slower. Corals bleach above 1 °C over the summer maximum, reef-wide at 4 °C-weeks.

What arrives first holds. In *Hydra* a second colonist arriving 24, 48 or 72 h late takes 60, 30 and 10 % of a population capped near 2×10^{5} cells. The net keeps the direction of what was laid down first, and the first colonist keeps the polyp.

Partnerships last far longer than their partners, which turn over in hours to days. Hominid gut clades have held for about 15 Myr, the rumen for 32–39 Myr, the coral algae for about 160 Myr, *Sulcia* for more than 260 Myr and arbuscular mycorrhiza for more than 400 Myr. The earliest fish bioluminescence is about 150 Ma, and *Wolbachia* supergroups A and B are about 200 Myr old.

13. Eating and Being Eaten

The first cells fed on what their surroundings held. Once there were bodies, a body became food for another body. This chapter follows that line from the oldest bored shell to the present weight of living carbon.

Four kinds of eating run through it. A predator kills and eats its prey, and a herbivore eats living plant tissue. A parasite lives on or in a host and takes from it; a parasitoid is a parasite that ends by killing its host.

Each kind left a record: holes in shells, scars on leaves, tubes on brachiopods, viral sequences in plant genomes. Each was answered by the eaten: thicker shells, toxins, spines, receptors. The chapter gives the dates, sizes and counts of both sides, then the measured shape of the present food web.

Positions on the ladder are those of chapter 1. An age of A million years is placed as a duration of $A \times 10^{6} \times 3.15576 \times 10^{7}$ s. Every size and time carries its coordinate.

The first holes

The oldest recorded attack on an animal is a hole in a *Cloudina* tube. *Cloudina* is the earliest known animal with a mineralised exoskeleton, from the late Precambrian of Shaanxi Province, China [526]. Of more than 500 tubes, 2.7 % carry rounded holes 40 to 400 µm in diameter [526].

That is at least 14 bored tubes: 0.027 × 500 = 13.5, rounded up. Hole size relates to the width of the bored tube, which the authors record as size-selective predation [526]. The source calls it “the oldest case of predation in the fossil record” [526].

A second study of uppermost Neoproterozoic *Cloudina* from China gives another frequency. Nearly one-fifth of almost one hundred tubes carry predatory borings 15–85 µm wide [527]; 0.2 × 100 = 20 tubes. No *Sinotubulites* shell from the same beds is bored [527].

The borings sit at a fairly uniform distance from the aperture, and their size varies [527]. The authors record attack throughout prey growth after a minimum size [527]. The two studies disagree: 2.7 % of more than 500 tubes with holes of 40–400 µm [526], against about 20 % of about 100 tubes with borings of 15–85 µm [527].

On the ladder the holes of the first study run from 4×10^{-5} m (position 6.17) to 4×10^{-4} m (8.26), a factor of 10. Those of the second run from 1.5×10^{-5} m (5.28) to 8.5×10^{-5} m (6.85), a factor of 85 / 15 = 5.7. The first predation trace thus sits between positions 5.28 and 8.26.

A review of Cambrian, and possibly Ediacaran, crushing, drilling and puncturing finds predation on shelled prey other than trilobites rarely documented [574]. The oldest shell crushing, durophagy, is damage on *Mobergella holsti* from Sweden [574]. Most Cambrian drill and puncture holes are on brachiopods, and the drillers are largely unknown [574].

The first parasites

The oldest recorded parasitism is from the Lower Cambrian, Stage 4, Wulongqing Formation of the Guanshan Konservat-Lagerstätte, eastern Yunnan [575]. Tube-dwelling organisms encrust the brachiopod *Neobolus wulongqingensis* in a monospecific assemblage [575].

Of 429 specimens, 205 are infested and 224 uninfested [575]; the infested share is 205 / 429 = 47.8 %. Encrustation gives a 26.08 % reduction in overall fitness, from ash-free dry weight estimated from shell size [575].

Tube orientation was measured on 146 individuals, 31 of them with a single tube [575]. The tubes align with the host's feeding currents, and the authors record the interaction as kleptoparasitism: the parasite takes food from the host's own stream [575].

A pentastomid from 425-million-year-old Silurian marine rocks (position 66.95) is attached externally to an ostracod, near the host's eggs [1160]. It is the only fossil pentastomid associated with a host [1160].

Living pentastomids number about 140 species, all but four parasitic on vertebrates [1160]; 136 / 140 = 97 %. The host line has changed since the Silurian; the parasitic form has held.

Hunters of the Cambrian and Ordovician seas

Anomalocaris canadensis of the Burgess Shale (Cambrian, Miaolingian, Wuliuan) is one of the largest Cambrian animals [579]. Large specimens have body-lobe widths of 60–70 mm, positions 12.83–12.97 [579].

Flow simulations use swimming speeds of 0.4, 0.7 and 0.9 m s^{-1}, taken from earlier calculations for lobe widths of 60–70 mm [579]. The raptorial appendages are built for soft prey, not for crushing trilobites [579]. One specimen carries a putative injury [579].

A redescription from all known specimens records an oval head carapace, stalked eyes, a triradial oral cone and a gut with paired midgut glands [580]. The tail fan has a central blade and three pairs of lateral blades [580].

Aegirocassis benmoulae of the Early Ordovician Fezouata Biota, Morocco, is an anomalocaridid more than 2 m long, position 16.02 [583]. It fed by filtering. The source places the beginning of the Ordovician at around 490 million years ago, position 67.08 [583].

The same lineage thus holds a soft-prey hunter with lobes of 60–70 mm and a filter-feeder longer than 2 m. From 12.83 to 16.02 is a step of 3.19 positions, a factor of 3^3.19 = 33 in size.

Drilling and crushing through the Phanerozoic

Drilling, the boring of a hole through a shell to reach the animal inside, falls into three phases [581]. In the Palaeozoic, latest Precambrian to Carboniferous, it is rare to

moderately frequent, on brachiopods and sessile echinoderms [581].

In the Mesozoic, Permian to Early Cretaceous, drilling is very rare or facultative [581]. A gap of 120 million years (position 65.80) separates the Late Triassic from the Early Cretaceous, with drilled Jurassic shells from Hungary, India and four other localities [581]. In the Cenozoic, Late Cretaceous to Holocene, gastropods drill molluscs frequently [581].

A species-level database of drillings and repair scars covers the Ediacaran to the Holocene, a span of 550 million years (position 67.19) [582]. It holds 196 papers and 2,291 species occurrences [582]. The frequency of predation traces rises notably by the Ordovician, not in the mid-Palaeozoic [584].

Predation intensity and global marine animal diversity correlate throughout the Phanerozoic, regardless of corrections [584]. The maximum drilling frequency per species runs as follows [582]:

Interval	Maximum drilling frequency per species
Ediacaran–Silurian	10–20 %
Devonian–Mississippian	30–50 %
Permian–Triassic	species-level data scarce
Jurassic	about 30 %
Quaternary	100 %

From the Jurassic the maximum rises steadily to 100 % in the Quaternary, while the minimum frequencies do not rise [582]. The ceiling climbs; the floor stays where it was.

Single counts come from the older record. Fewer than 3 % of Silurian *Dicaelosia* brachiopods carry borings, and 19 % of juvenile *Nautilus pompilius* carry repaired injuries [622].

The holes grow wider. The median drill-hole diameter rises from 0.35 mm in the Ordovician (position 8.14) to 3.25 mm in the Quaternary (10.17) [585], a factor of 3.25 / 0.35 = 9.3. Over the same interval predator–prey size ratios rise 67-fold, while drilled prey size shows no Phanerozoic trend [585].

Since the Permian, drilling frequencies are higher on molluscs than on co-occurring brachiopods [585]. Drill holes made by a predator in a shell of its own family, predator on predator, increase in the Mesozoic and Cenozoic [585].

The Mesozoic marine revolution

The shells answer. Open coiling, planispiral coiling and umbilici weaken a shell; they are commoner in Palaeozoic and early Mesozoic gastropods [622]. Strong sculpture, narrow apertures and apertural teeth resist crushing; they occur mainly in post-Jurassic groups [622].

In Palaeozoic and early Mesozoic Pleurotomariacea about 74 % of genera are umbilicate, against 58–60 % in Mesozoic and Cenozoic Trochacea [622]. Open-coiled genera number about 18–20 in the Palaeozoic and 2 in the Triassic [622].

Today open coiling is rare. Fifteen Recent open-coiled species are known, 8 marine, 3

freshwater and 4 terrestrial: about 1 in 2,200 marine, 1 in 1,000 freshwater and 1 in 3,750 terrestrial species [622].

Shell sturdiness rises from the Early Cretaceous; the changes begin in the Jurassic and accelerate in the Cretaceous [622]. The shell-breaking and drilling groups are listed with their origin and the onset of breaking or drilling [622]:

Predator group	Origin	Onset of shell-breaking or drilling
Asteroidea	Late Ordovician	by then
Dipnoi	Devonian	Devonian
Heterodontidae	Jurassic	Jurassic
Batoidea	Jurassic	Cretaceous
Stomatopoda	Jurassic	possibly Late Cretaceous
Palinuridae / Nephropidae	Jurassic	date uncertain
Cymatiidae	Late Cretaceous	Late Cretaceous
Brachyura	Jurassic	latest Cretaceous or Paleocene
Aves	Late Jurassic	Late Eocene
Naticacea	Triassic	drilling by Campanian
Muricacea	Albian	drilling by Campanian
Other Neogastropoda	Early Cretaceous	Late Cretaceous
Teleostei	Triassic	late Cretaceous or earliest Tertiary

Thirteen groups are listed. Eleven of them, all but Asteroidea and Dipnoi, arise in the Triassic to Cretaceous. The Jurassic opens at 201.4 Ma (66.27), the Cretaceous at 145.0 Ma (65.98) and the Campanian at 83.6 Ma (65.47) [435].

The record of drilling has the form of loading and discharge. Drilling rises through the Palaeozoic, falls to near nothing for 120 million years, and returns from the Late Cretaceous with a higher ceiling each interval.

Plants are eaten on land

On land, arthropods are the first eaters of plants. The first phase of herbivory runs from the latest Silurian to the Early Devonian, 417 to 403 Ma (positions 66.94–66.91) [987]. It consists of spore feeding, with spores in coprolites such as *Lancifaex simplex* of the Rhynie chert, a probable bored stem, a styletal piercing in *Rhynia gwynne-vaughanii* and borings in *Prototaxites* [987].

In this first phase each tissue is eaten 0 to 20 million years after it arises; 20 Myr sits at position 64.17 [987]. A mid-Palaeozoic hiatus of 65 Myr (65.25) follows [987].

The second phase runs from 327 to 309 Ma (66.72–66.66) [987]. The earliest margin feeding on a leaf, on *Triphyllopteris austrina*, is 326 Ma (66.71), 76 Myr after the origin of leaves (65.39) [987].

Seed predation, circular holes in *Trigonocarpus*, follows the origin of seeds by 54 Myr (65.08). Wood boring in *Trivenia* follows the origin of wood by 63 Myr (65.22), and root feeding follows roots by 98 Myr (65.62) [987]. About 12 ordinal-level insect lineages first appear in this second pulse [990].

The oldest insect gall is about 302 Ma (66.64): petiole galls in the tree fern *Psaronius*, made by a holometabolan larva [989]. The authors note that most estimates had placed such interactions about 175 Myr later [989].

Seven functional feeding groups are used for fossil damage: external foliage feeding, piercing and sucking, oviposition, leaf mining, galling, seed predation and wood boring [990]. Oviposition dominates the Early–Middle Permian Karoo floras [990].

Insect herbivores and their numbers

Across 31 insect orders herbivory relates positively to diversification and accounts for 25–35 % of the variation in diversification rate and about 25 % of the variation in richness [1161]. The share of herbivorous species is about 100 % in Lepidoptera, about 94 % in Orthoptera, about 80 % in Hemiptera, about 26 % in Coleoptera and about 7 % in Hymenoptera [1161]. In all five sister pairs the more herbivorous clade is the richer [1161].

Among beetles, the Jurassic basal lineages of the Phytophaga still feed on conifers and cycads [1162]. Angiosperm-feeding lineages arose repeatedly with raised diversification, and these radiations hold nearly half of Coleoptera [1162].

Gall-inducing insects were once estimated at 13,000 species; new estimates give 21,000 to 211,000, with a mean of 132,930, from 10 studies and 422,000 seed plant species [1163]. Seed beetles, Bruchinae, count about 1,700 species, about 84 % of them strictly on legume seeds [1164].

The seed-beetle subfamily originates about 78–81 Ma (65.41–65.45). Its Convolvulaceae-feeding *Spermophagus* clade is about 57 Ma (65.13) and its Malvoideae-feeding clade about 42 Ma (64.85) [1164].

Insect herbivores are counted at more than 1 million species against more than 300,000 flowering plants [1165]; the ratio is 1,000,000 / 300,000 = 3.3. Among more than 7,500 insect herbivore species with site-specific host records, specialists predominate, and their share rises toward the tropics [1166].

Vertebrates take up plants

The oldest known synapsid herbivore is *Melanedaphodon hovaneci* from Linton, Ohio [994]. It is Moscovian, about 307 Ma (66.66), Middle Pennsylvanian; the Moscovian spans 315.2–307.0 Ma (66.68–66.66) [435, 994]. It bears large bulbous cusped marginal teeth and a palatal tooth battery, and is read as an omnivore to low-fibre herbivore [994].

From the first arthropod herbivory to the first vertebrate herbivore is 417 − 307 = 110 Myr (65.72); from the younger end it is 403 − 307 = 96 Myr (65.60). Herbivory arose in tetrapods at least five times in the Late Carboniferous to Early Permian: in diadectids, bolosaurids, captorhinids, edaphosaurids and caseids [995].

Diadectids, edaphosaurids and captorhinids have Late Carboniferous origins and diversify in the early Permian; the oldest caseid is from the Late Pennsylvanian of Kansas [994]. Herbivores stay rare until the Late Permian, when they become abundant and diverse [995]. The Permian begins at 298.9 Ma (66.63) and the Kungurian at 283.5

Ma (66.59) [435].

Large dinosaurs fed on plants older than the flowering plants. In vitro fermentation shows that horsetails and certain conifers and ferns have energy content comparable to living browse [1167]. *Equisetum*, *Araucaria*, *Ginkgo* and *Angiopteris* were likely major sauropod foods; cycads, tree ferns and podocarp conifers are poor energy sources, and *Araucaria* is energy-rich but slow to ferment [1167].

Latest Cretaceous coprolites from India, attributed to titanosaurs, contain phytoliths of at least five extant grass subclades, with dicotyledons, conifers and palms [1168]. The Maastrichtian spans 72.1–66.0 Ma (65.34–65.26) [435]. Gondwanatherian mammals with high-crowned cheek teeth from the same setting are read as grazers [1168].

Grass, teeth and spines

Grasses, Poaceae, number about 11,000 species [1169]. They are present in northern South America, northern Africa and India in the latest Cretaceous and Paleocene [1169].

In North America pooid and PACMAD phytoliths are present by 42–38 Ma (64.85–64.76) [1169]. Grasslands occupy drier habitats by about 20 Ma (64.17), and C4 grasslands stand by 7–6 Ma (63.22–63.08); horse enamel is mainly C4 by 6.6 Ma (63.16) [1169].

In Africa, grass pollen in the Niger Delta rises from 2 % in the Early Miocene to more than 50 % after 8.2 Ma (63.36); C4 grasses dominate after 5 Ma (62.91) [1169]. Southern Africa holds open, fire-prone grasslands by 5–4 Ma (62.91–62.71) [1169].

In South Asia grass pollen exceeds 90 % between 8.5 and 6.5 Ma (63.39–63.15); in Australia the earliest grassland evidence is Pliocene [1169]. C4 photosynthesis evolved at least 9 and perhaps up to 20 times within PACMAD [1169]. C4 grasses originated by the Early Oligocene, at least 25 Myr (64.38) before their Late Miocene–Pliocene dominance [1169].

High-crowned teeth, hypsodonty, follow the grass. In North America and western Eurasia hypsodonty evolved or became common several million years after open-habitat grasses expanded [1169]. In South America hypsodont notoungulates appear in the latest Paleocene–Early Eocene and dominate at the Eocene–Oligocene boundary [1169].

Habitats dominated by C3 grasses were established in the Central Great Plains by at least 21.9 Ma (64.26), and hypsodont Equinae emerged at least 4 Myr (62.71) later [1170]. The latest date for hypsodont Equinae from these numbers is $21.9 - 4 = 17.9$ Ma (64.07). The study rests on 99 phytolith assemblages from the middle Eocene to the late Miocene, and the mesodont *Parahippus* overlapped the earliest savanna woodlands [1170].

Horse tooth wear has been surveyed over the past 55 million years (65.09) [1171]. Grasslands hold a high silica reservoir, and silica-rich grasses and dust wear herbivore teeth [1169].

In southern Africa, 1,852 of about 2,200 woody species were analysed; 213 are spiny, in 29 families [1172]. That is $213 / 1{,}852 = 11.5$ %. Spines are hard sharp structures of at least 5 mm (position 10.56), from the epidermis, the stipules or the stem apex [1172].

Spinescence evolved at least 55 times, the great majority of spiny clades within the last 17 Ma (64.02), with a mid-Miocene radiation [1172]. Horned bovids arrived in Africa by 16 Ma (63.97) [1172]. Spiny plant diversification comes long after proboscideans and hyracoids but matches bovid diversification [1172].

Africa has 92 large herbivore species in five functional types; megaherbivores weigh more than 1,000 kg and mesobrowsers 4–450 kg [1172]. C4 grasses emerged in the late Oligocene, about 30 Ma (64.54), and fire-maintained savannas became a major biome in the late Miocene, more than 20 Myr later [1172].

Herbivory through the great dyings and the warm peaks

Herbivory collapsed at the Permian–Triassic boundary, about 252 Ma (66.48), and recovered by about 228 Ma (66.39), 24 Myr later (64.34) [990]. After the K–Pg boundary it recovered from 65.5 to 55.8 Ma (65.25–65.11), about 10 Myr (63.54) [990]. Herbivory is elevated in the Early Eocene Climatic Optimum, 53–51 Ma (65.06–65.02) [990].

In the Bighorn Basin, 5,062 fossil leaves from five sites record the damage across the Paleocene–Eocene Thermal Maximum [1173]:

Age	Position	Mean annual temperature	Leaves damaged
58.9 Ma	65.16	10.5 °C	34.5 %
57.5 Ma	65.13	10.5 °C	14.9 %
55.9 Ma	65.11	15.7 °C	37.8 %
55.8 Ma (PETM)	65.11	20.1 °C	57.3 %
55.2 Ma	65.10	16.4 °C	33.0 %

At the thermal maximum specialised damage reaches 21.6 % and damage per species 45–94 % [1173]. Leaves with four or more damage types are 7.3 %, against 0.4–2.6 % before; 50 damage morphotypes fall into seven feeding groups [1173].

The rise from 55.9 to 55.8 Ma is 57.3 − 37.8 = 19.5 percentage points, for a warming of 20.1 − 15.7 = 4.4 °C.

Global warming at the event is at least 5 °C over about 10,000 years (position 57.25), and CO_2 roughly tripled [1173]. The share then falls back to 33.0 %.

Plants answer: chemistry, structure and signal

The chemical store

Plants hold more than 100,000 known secondary metabolites [1174]. The described structures by class are these [1174]:

Class	Described structures
Alkaloids	27,000
Monoterpenes	3,000
Sesquiterpenes	5,000
Diterpenes	2,500
Triterpenes, steroids, saponins	5,000

Tetraterpenes	500
Phenylpropanoids, coumarins, lignans	2,000
Flavonoids, anthocyanins, tannins	4,000
Polyketides	800
Glucosinolates	150
Cyanogenic glucosides	60

The terpene classes sum to 3,000 + 5,000 + 2,500 + 5,000 + 500 = 16,000. A second count gives about 12,000 alkaloids [1175]; the two alkaloid counts differ by 27,000 / 12,000 = 2.25.

Every terpene is built from one five-carbon unit, isoprene, C_5H_8, of molar mass 68.117 g mol^{-1} [1176]. Here the form is that of a residue becoming an alphabet: one closed small molecule is the letter, and 16,000 described terpenes are its words.

The genes behind them grow in number up the plant line. Terpene synthase genes number 1 in the moss *Physcomitrella patens*, 18 in the lycophyte *Selaginella moellendorffii* and 40–152 in angiosperm and gymnosperm genomes, in seven clades [1177].

The molar masses of the defence molecules run from isoprene at 68.117 through nicotine at 162.23, caffeine at 194.19 and xanthotoxin at 216.19 to the cardenolide digitoxin at 764.94 g mol^{-1} [1176]. The span is 764.94 / 68.117 = 11.2.

Toxins and their answers

Leaf damage raises alkaloid levels in the undamaged leaves of field-grown wild tobacco [1178]. The ability to respond returns 6 days (45.13) after plants are released from pots [1178]. *Manduca sexta* larvae on high-alkaloid foliage eat and gain weight at 57.2 % and 45.7 % of controls; on artificially induced leaves they gain 38.5 % [1178].

Caffeine has evolved multiple times among plants; in *Coffea canephora* the caffeine N-methyltransferase genes expanded by tandem duplication, with similar independent expansions in tea and cacao [1179]. Caffeine arose independently in the cacao, citrus, guaraná, coffee and tea lineages, by different pathways [1180]. The resurrected ancestral enzymes were already suited to caffeine synthesis [1180].

The Pieridae butterflies carry a nitrile-specifier protein that detoxifies the glucosinolates of their host plants [1181]. Five temporal estimates place its origin within about 10 Myr (63.54) of the appearance of the host order Brassicales [1181]. The glucosinolate-feeding Pierinae then hold significantly more species than related clades [1181].

Cardenolides inhibit the animal Na^+/K^+-ATPase. They occur sporadically in 12 botanical families, dominant in Apocynaceae, and most insects that feed on them are highly specialised [1182].

The Na,K-ATPase α-subunit was sequenced in 18 cardenolide-feeding insects from 15 genera and four orders [1183]. The substitution N122H, known from the monarch and *Chrysochus* beetles, recurs in *Oncopeltus fasciatus*, *Lygaeus kalmii*, *Labidomera clivicollis* and *Liriomyza asclepiadis* [1183]. Specialists on these plants occur in six

insect orders [1183].

Q111 and N122 together give more than 12-fold resistance over the wild type and more than 2-fold over either alone [1183]. The same change recurs across 300 Myr (66.64) of insect divergence [1183].

Latex, a sticky emulsion that flows from canals on damage, has no known primary metabolic function [1184]. It occurs in about 10 % of flowering plant species [1184]. Herbivores avoid it by cutting the canals or feeding between them, and convergent evolution is common on both sides [1184].

Silica and tough leaves

Grasses from more heavily grazed Serengeti grassland carry more leaf-blade silica than those from less grazed sites, and defoliation raises it [1185]. Four populations of three species were studied [1185].

Silicon content accounts for more than 70 % of the variation in leaf abrasiveness across 18 grass species [1186]. Damage raises silicon in the damaged leaves but not in undamaged leaves of the same plant, and only after repeated damage above a threshold; the regime was weekly damage over 10 weeks (47.37) [1186].

High-silica diets lower the efficiency with which *Spodoptera exempta* larvae turn food into body mass and absorb nitrogen [1187]. Mandible wear appears within a single larval instar, and that wear accounts for up to a third of the residual effect after transfer to a silica-free diet [1187].

The leaf economics spectrum rests on 2,548 species at 175 sites: one axis from fast to slow return on nutrients and dry mass, across growth forms and biomes [1188]. In 280 species leaf lifespan runs from 2.5 ± 0.6 to 66.2 ± 10.6 months (47.44–50.42) [1189].

In the same set specific leaf area runs from 35 to 267 $cm^2\ g^{-1}$, leaf nitrogen from 8.7 to 40.9 $mg\ g^{-1}$ and mass-based photosynthetic capacity from 21 to 289 $nmol\ g^{-1}\ s^{-1}$ [1189]. The lifespan ratio is 66.2 / 2.5 = 26.5. The scaling of mass-based capacity with leaf lifespan is -0.74 ± 0.05 [1189].

Signals and recruited defenders

The plant signal that answers wounding is older than vascular plants. The jasmonate receptor COI1 is functionally conserved between the liverwort *Marchantia polymorpha* and *Arabidopsis* across about 450 Myr (67.01) of independent evolution [1190].

Bryophytes carry all signalling components but no JA-Ile; their ligand is dinor-OPDA, and one amino-acid change switches ligand specificity [1190]. JA-Ile and its receptor form emerged in vascular plants [1190].

Jasmonic acid rises within 2–5 min (120–300 s; positions 37.51–38.34) of wounding in *Arabidopsis* [1191]. The stimulus that leads to its accumulation in distal leaves travels at 3 $cm\ min^{-1}$ or faster [1191].

Maize seedlings fed on by caterpillars release large amounts of terpenoid volatiles [1192]. Artificially damaged seedlings release none unless caterpillar oral secretion is applied, and undamaged leaves release none [1192]. Females of the parasitic wasp

Cotesia marginiventris learn to use these volatiles to find their hosts [1192].

In maize sampled every 0.5 h for 12 h after simulated herbivory, green-leaf volatiles are emitted at once [1193]. Several induced compounds follow within 2 h (41.24) and sesquiterpenoids after 4 h (41.87) [1193].

Here the form is that of reading: the wasp takes the plant’s answer to the caterpillar as a sign of the caterpillar. The reading keeps the relation and drops the rest.

Extrafloral nectaries, which feed ants that guard the plant, are reported in 3,941 species, 745 genera and 108 families [1194]. They occur in 33 of 65 angiosperm orders, in about 1–2 % of vascular plant species and in 4 of 36 fern families [1194]. They arose in at least 457 lineages on a phylogeny of more than 55,000 species [1194].

Ant domatia, cavities that house ants, occur in 681 vascular plant species in 159 genera and 50 families; the true number may approach 1,140 [1195]. There are at least 158 origins and 43 losses within 19 Myr (64.13) on a 1,181-species tree [1195]. Australasian and Neotropical ant-plant symbioses are early Miocene, African ones later than the late Miocene [1195].

Species per origin fall from nectaries to domatia to spines: 3,941 / 457 = 8.6, 681 / 158 = 4.3 and 213 / 55 = 3.9.

Pathogens of plants

A pathogen is a virus, bacterium, oomycete, fungus, nematode or parasitic plant that grows in or on a living plant at the plant’s cost. The plant answers with an immune system of surface receptors, intracellular receptors and small RNAs [1196].

Viruses written into plant genomes

Plant viruses leave no body fossils. Their age is read from viral sequences inserted in plant genomes. Endogenous caulimovirid reverse-transcriptase loci occur in nearly all vascular plants screened: 14,895 high-confidence loci in 72 genome assemblies and 6 fern genomes [298].

Florendoviruses occur in 46 of 62 seed plants, with about 5,000 copies, and petuviruses in 27 of 62, with about 1,900 [298]. Densities reach 2.3 loci per Mb in *Citrus sinensis*, with a mean of 0.2 per Mb, and there are none in *Zea mays* or *Arabidopsis thaliana* [298]. The family’s origin is placed “at latest during the Devonian, about 320 million years ago” (66.70) [298].

A second screen of 20 genomes found 17,574 endogenous pararetroviruses in 10 gymnosperms, from 18 to 6,194 per species, and 289 in 6 ferns [300]. None were found in a moss, a liverwort, a lycophyte or a charophyte [300]. Angiosperm caulimovirids have at least three independent origins [316].

Insertion bursts in *Pinus taeda* date to 119.3–183.6, 122–187.8, 108–166.1 and 151.4–232.9 Ma (positions 65.71–66.41) [316]. Orthologous insertions are at least 75 Ma (65.38) in *Pinus* and 16.9 Ma (64.02) in *Picea* [300]. These are lower bounds at host substitution rates of 1.43–2.2 × 10^{-9} per site per year [316].

On the plant side, tracheophytes are 452 Ma (67.01) and the angiosperm crown 151 Ma (66.01) [299]. Vascular plants are thus 452 − 320 = 132 Myr older than the oldest dated viral insertion, and angiosperms are younger than the caulimovirids. The angiosperm radiation is given as roughly 140–180 Ma (65.94–66.17) [1196].

The potyviruses, about 15 % of named plant virus species, radiated about 6,600 years ago (56.88), “during the dawn of agriculture” [310]. Their rate is about 1.15×10^{-4} substitutions per site per year [310]. The virus rate exceeds the host rate by $1.15 \times 10^{-4} / 2.2 \times 10^{-9} = 5.2 \times 10^{4}$ to $1.15 \times 10^{-4} / 1.43 \times 10^{-9} = 8.0 \times 10^{4}$.

Viral mutation rates per nucleotide per cell infection, from more than 40 studies, are about 10^{-8} to 10^{-6} for DNA viruses and 10^{-6} to 10^{-4} for RNA viruses [326]. Tobacco mosaic virus mutates at 8.7×10^{-6} and tobacco etch virus at 4.8×10^{-6} [326]. Across viruses mutation rates vary over five orders of magnitude and substitution rates over six; smaller viruses mutate faster [328].

Human recognition

Tobacco mosaic disease was reported by Dutch growers in 1857 [333]. Mayer named it in 1879 and published its transmission by sap in 1886 [333].

Ivanovsky showed in 1892 that the agent passed a porcelain filter, and Beijerinck described a “contagium vivum fluidum” in 1898 [333]. Stanley crystallised the virus in 1935 [333]. From 1898 to 2026 is 128 years (53.29).

Particles

Particle	Size	Position	Source
Closterovirid filament, diameter	about 12 nm	−1.21	[268]
Tobamovirus rod, diameter	about 18 nm	−0.85	[252]
Nanovirus particle	18–19 nm	−0.85 to −0.80	[251]
Geminate particle (maize streak virus)	22 × 38 nm	−0.66; −0.17	[253]
Bromovirid virion	26–35 nm	−0.51 to −0.24	[255]
Phytoplasma cell	80–800 nm	0.51 to 2.61	[1197]
Tobamovirus rod, length	300–310 nm	1.72 to 1.74	[252]
Closterovirid filament, length	650–2,200 nm	2.42 to 3.53	[268]

The tobamovirus aspect ratio is 310 / 18 = 17, and the longest closterovirid filament is 2,200 / 18 = 122 tobamovirus diameters. Genomes run from 2.5–3.0 kb (monopartite) or 4.8–5.6 kb (bipartite) in geminiviruses, through 6–8 segments of about 1 kb in nanoviruses and 6.3–6.5 kb in tobamoviruses, to 13–19.3 kb in closterovirids [251, 252, 253, 268].

The three RNAs of cucumber mosaic virus are 3,357, 3,050 and 2,216 nt, together 8,623 nt [255]. Phytoplasma chromosomes are 600–880 kb, with a GC content of 21–28 % [1197].

Counts of viruses and other pathogens

The ICTV list of 2025 holds 16,215 virus species in 3,769 genera, 368 families and 93 orders [334]. In that year 1,563 species, 243 genera, 55 families and 11 orders were added [335].

Plant and fungal viruses, viroids and satellites numbered 2,134 species in 46 families and 193 genera in the 2021 list [311]; 2,134 / 16,215 = 13.2 %, across different release years. A public database holds 3,206 plant virus species from 46 families on 2,231 plant species, with 9,604 interactions, 54 % RNA and 46 % DNA viruses [312]. The older DPVweb list has 1,503 species [312].

In 2012 the ICTV recognised 92 plant virus genera, 82 of them in 21 families [313]. Most viruses infect few plant species, and most plants host few viruses [312].

About 80 % of plant viruses are carried by specific insect vectors [314]. The majority are carried by hemipteroid insects, aphids, whiteflies, leafhoppers, planthoppers and thrips, and more than 200 persist inside their vectors [315].

Other pathogen groups are counted as follows:

Group	Measured count	Source
Pseudomonas syringae: pathovars; phylogroups	more than 60; 13	[1198]
Bacterial effectors delivered per strain	15–30	[1196]
Xylella fastidiosa: host species; families; subspecies	696; 88; 5	[1199]
Phytoplasmas: host plant species	more than 700	[1197]
Agrobacterium T-DNA: sweet potato cultigens; sequenced dicots	291 of 291; 23 of 275	[1200, 1201]
Phytophthora infestans: RXLR effectors; CRN genes; protein-coding genes	563 (earlier 425); 196; 17,797	[1202, 1203]
Puccinia graminis f. sp. *tritici*: haploid chromosomes	18	[1204]
Coffee leaf rust: physiological races	more than 50	[1205]
Barley powdery mildew: gene models; core candidate effectors	7,118–7,239; 190	[1206]
Plant-parasitic nematodes: species; independent origins	about 4,100; 4 clades	[616]
Striga: obligate root-parasitic species	about 30	[1207]

T-DNA sits in 23 / 275 = 8.4 % of sequenced dicots. The *P. infestans* genome is about 240 Mb, about 74 % repeats, and RXLR effectors are 563 / 17,797 = 3.2 % of its genes [1202]. The Ug99 stem rust lineage arose by somatic hybridisation, sharing one haploid nucleus with the African race 21 lineage [1204].

The plant’s receptors

Arabidopsis has at least 610 receptor-like kinases, nearly 2.5 % of its protein-coding genes; the family was near its present size before land-plant lineages diversified [1208]. The implied gene count is 610 / 0.025 = 24,400.

Col-0 has over 200 LRR-kinases, 28 of them induced within 30 min (39.98) of the flagellin peptide flg22 [1196]. It has 56 receptor-like proteins and about 125 NB-LRR genes; flg22 is 22 amino acids long and induces at least 1,100 genes [1196]. Another count gives 159 NB-LRR genes [1209].

NLR genes per genome, as cited, run from 54 in papaya to 992 in apple; tomato has 267, potato 443 and pepper 755 intact genes [1209]. The range is 992 / 54 = 18.4-fold. Across 100 chromosome-level genomes there are 68,452 NLRs, from 28 in *Coriandrum sativum* to 3,428 in *Medicago sativa*, with a mean of about 685 [1210]; that range is 3,428 / 28 = 122-fold.

The ancestral angiosperm had 7 TNL, 14 CNL and 2 RNL immune-receptor lineages, 23 in all [1211]. CNLs expanded gradually over the first about 100 Myr (65.64) of angiosperm evolution [1211]. Both TNL and CNL expansion intensified from the Cretaceous–Paleogene boundary, 66 Ma (65.26) [1211].

The *Arabidopsis* pan-NLRome saturates at about 40 wild strains, with about half present in most accessions [1212]. About 200 resistance genes against viruses are known, about half of them recessive [313]. Solvent-exposed LRR residues evolve fast, with common polymorphism within species [1213].

Small RNAs

Antisense RNAs of about 25 nt were found in silencing systems in 1999 [317]. *Arabidopsis* has four DICER-LIKE proteins that produce virus-derived small RNAs of 21, 22 and 24 nt: DCL4 21 nt, DCL2 22 nt, DCL3 24 nt [318]. Inactivating both DCL2 and DCL4 is necessary and sufficient to restore systemic infection by a virus that lacks its suppressor [319].

One review names 10 distinct viral suppressors of silencing; such suppressors also occur in pathogenic bacteria and oomycetes [320]. A small RNA of 21–24 nt is a short complementary copy of the viral strand. It has the form of a reading: it keeps the sequence relation and drops the rest of the virus.

Durations of resistance

Defence and attack run on very different clocks. Root-knot nematodes lay their first eggs 4–6 weeks (46.53–46.90) after infection [617]; if continuous, that is 365 / 42 = 8.7 to 365 / 28 = 13 generations a year.

Systemic protection after a tobacco mosaic hypersensitive response lasts up to 3 weeks (46.27) [313]. In *Daphnia*, a parasite readapts to its host within a few years [1214].

The wheat gene *Sr31* controlled stem rust from its wide deployment in the 1970s until Ug99 overcame it in 1998 [1204, 1215], 28 years (51.90). *Lr34* has given resistance to leaf rust, stripe rust and powdery mildew for more than 50 years (above 52.43) [1216].

At *Rpm1* in *Arabidopsis*, resistance and susceptibility alleles have coexisted for millions of years [1217]. The data fit balanced polymorphism rather than a succession of sweeps;

RPM1 carries a large fitness cost in the field [1217, 1218]. In wild flax and its rust, allele frequencies at recognition loci fluctuate asynchronously among populations and track disease prevalence [1219].

Epidemics

Late blight reached the United States in 1843 and Belgium and Ireland in 1845 [1220]. The FAM-1 lineage was sampled from 1845 to 1987, 144 years (53.39) [1220].

The Irish famine of 1845–1850 caused about 1 million deaths, emigrants excluded [1221]. Another account gives about two million lives, families or homes lost, with about 3 million people depending on a single potato variety [1222]. Both figures stand.

Ug99 was detected in Uganda in 1998 and had seven races by 2011; about 90 % of wheat varieties grown worldwide were susceptible [1223]. By 2014 the group held two further races virulent on *SrTmp*, in Kenya, Uganda, Rwanda and Egypt [1224].

Citrus tristeza has killed over 100 million trees; rice tungro costs US$1.5 billion a year; 47 % of the pathogens behind emerging plant epidemics are viruses [324]. Another review gives “about half”, and more than 200 million cacao trees eradicated for swollen shoot [313].

Cavendish is 99 % of banana exports, and spores of the TR4 wilt survive more than 20 years (51.60) in soil [1225]. TR4 was reported on Cavendish in 1990, in Australia in 1997, Mozambique in 2013, and Pakistan and Queensland in 2015 [1225].

Wind-borne fungal spores carry crop diseases between continents, and epidemics require one susceptible genotype grown over large areas [1226]. From 1843 to 2014 fifteen named pandemics or resistance breakdowns are listed, one every (2014 − 1843) / 15 = 11.4 years (51.09).

Measured losses to pathogens and pests are 21.5 % of wheat, 30.0 % of rice, 22.5 % of maize, 17.2 % of potato and 21.4 % of soybean, from 137 pathogens and pests [325]. Plant virus losses exceed US$30 billion a year [324].

A virus that is required

A mild pepino mosaic virus strain, licensed in 14 European countries, protects more than 4,500 ha of tomatoes against severe strains [321]. Cross-protection of this kind was first observed in 1929–1938 [321].

A fungal virus is required for the endophyte of a tropical panic grass to give the grass heat tolerance [322]. Isolates cured of the virus fail, and reintroducing it restores tolerance; the infected fungus confers it on a monocot and a eudicot host [322].

Here a virus sits inside a fungus that sits inside a plant. The form is that of community as shared prefix: partners nested inside partners, as addresses inside longer addresses.

Parasites through the tree

Parasitism evolved independently at least 223 times in 15 animal phyla [1227], on average 223 / 15 = 14.9 origins per phylum. Most origins lie in Arthropoda or below

family level, and parasitism is almost absent from deuterostomes [1227].

Parasitic groups do not differ from their free-living relatives in speciation rate [1227]. The 10 largest parasitic clades hold about 90 % of described parasite species and perhaps 40 % of all animal species [1227].

The pattern is that of a form opened once and filled many times. Parasitism opens once with its first trace; its at least 223 later origins fill the opened depth, and the ten largest clades hold nine-tenths of the parasite species known.

In flowering plants haustorial parasitism, a root or stem that taps another plant, evolved 12 times independently [841]. It covers 292 genera and about 4,750 species [841]. On a base of 295,383 accepted angiosperm species [659], parasitic plants are 4,750 / 295,383 = 1.6 %.

Santalales hold 179 genera and 2,428 species: 149 hemiparasitic genera with 2,312 species, 17 holoparasitic genera with 45 species and 13 autotrophic genera with 71 species [841]. The parts sum to 2,428. Orobanchaceae hold 102 genera and more than 2,100 species [841].

Holoparasitism, the loss of all photosynthesis, occurs in every parasitic clade except *Cassytha* and *Krameria* [841]. About 25 of the 292 genera are crop or forestry pathogens [841]. *Striga* holds about 30 obligate root-parasitic species, most on grasses, and costs about US$1 billion a year [1207].

Plant-parasitic nematodes number about 4,100 species, about 25 % of about 16,000 terrestrial nematodes, in 4 independent clades [616]. Slightly more than a dozen species cause most losses, about €110 billion a year [616].

Helminths parasitising vertebrates number 75,000–300,000 species [1228]. There is no credible way to estimate the numbers of protozoan, fungal, bacterial or viral parasites [1228]. Linnaeus catalogued about 20,000 species; the best recent total for all life is about 6 million [1228].

A re-estimate that counts cryptic arthropods and their host-associated mites, nematodes, protists, fungi and bacteria gives at least about 6 billion species, 70–90 % of them bacteria [1229]. Described species are about 1.5 million; earlier projections ran from 2 million to about 1 trillion [1229].

About 75 % of food-web links involve parasitic species [1228]. Parasites raise species richness, link number and food-chain length in food webs, and after correction of a calculation error they increase connectance, sometimes sharply [1230]. Mid-trophic levels are the most exposed to natural enemies, and parasitism is recorded as the most common animal lifestyle [1230].

Parasites also weigh. In three Pacific estuaries, Carpinteria Salt Marsh in California and Bahía San Quintín and Estero de Punta Banda in Baja California, trematode biomass exceeds winter bird biomass threefold to ninefold [1231]. Mean bird mass is 4.1 kg ha^{-1} in winter and 0.89 kg ha^{-1} in summer [1231].

Parasites are 1.2 %, 0.9 % and 0.2 % of total animal biomass, and total animal biomass is 925, 2,240 and 2,594 kg ha^{-1} [1231]. The annual production of trematode larvae, cercariae, is about three times the standing biomass of the trematode stages in snails, and three to ten times winter bird biomass [1231].

Of helminths, 3–5 % are threatened with extinction within 50–100 years (52.43–53.06) [1228]. Of 457 parasite species modelled from 53,133 occurrences in eight major clades, 5–10 % are committed to extinction by 2070 from climate-driven habitat loss alone [1232]. Up to 30 % of parasitic worms are committed when host coextinction is included [1232].

Who eats whom: sizes, chains and transfer

Body size of eater and eaten

A global food-web database holds 16,863 consumer–resource links [1233]. Body mass is measured directly in 13,085 of them and estimated from length in 3,778 [1233]; 13,085 + 3,778 = 16,863.

After excluding parasites, unknown habitats and 53 outliers, 6,519 links were analysed [1233]. They are 5,156 predatory, 215 parasitoid, 930 herbivorous and 218 detritivorous links; by habitat, 2,245 terrestrial, 1,214 lake, 736 stream and 2,324 marine [1233]. Both sets sum to 6,519.

The ratios are given as $\log_{10}$ of consumer mass over resource mass, as geometric means ± SE [1233]:

Consumer class	$\log_{10}$ ratio	n	Ratio
All predators	1.62 ± 0.03	5,156	10^1.62 = 42
Aquatic predators	1.82 ± 0.04	3,126	10^1.82 = 66
Parasitoids	−0.12 ± 0.03	215	10^−0.12 = 0.76
Aquatic herbivores	8.99 ± 0.15	930	10^8.99 = 9.8×10^8
Aquatic detritivores	13.41 ± 0.18	218	10^13.41 = 2.6×10^{13}

About 80 % of predators are larger than their prey [1233]. By predator type and habitat the $\log_{10}$ ratios are these [1233]:

Predator type	Terrestrial	Lake	Stream	Marine
Invertebrates	0.60 (n = 1,263)	0.96 (728)	0.91 (165)	0.37 (759)
Ectotherm vertebrates	2.08 (375)	4.15 (130)	3.82 (175)	2.57 (783)
Endotherm vertebrates	2.91 (392)	—	—	2.86 (333)

As ratios, invertebrate predators span 10^0.37 = 2.3 to 10^0.96 = 9.1. Ectotherm vertebrates span 10^2.08 = 120 to 10^4.15 = 1.4×10^4, and endotherm vertebrates 10^2.86 = 720 to 10^2.91 = 810.

Biomass of eater and eaten

Predator biomass was set against prey biomass across 2,260 communities from 1,512 locations, drawn from more than 1,000 studies of large mammals, invertebrates, plants and plankton [1234]. The exponents lie near ¾ [1234]:

Relation	Exponent k	n

African savanna predator vs prey biomass (y = 0.094 x^0.73, R^2 = 0.92)	0.73	46 ecosystem periods in 23 protected areas
Top carnivore vs herbivore biomass	0.74	184
Zooplankton vs algae	0.71	667
Validation, 25 datasets	mean 0.72	2,950 ecosystems
Plant production vs foliage biomass	0.67	1,153
Aquatic community production vs biomass	0.76	256
Fish	1.09	—
Mean carnivore and herbivore body mass vs biomass	0.03	—
Individual maximum production vs body mass (y = 3.5 x^0.75, R^2 = 0.98)	0.75	1,635 estimates, 1,098 species

The savanna data cover five carnivores and about 27 prey species of 5–500 kg [1234]. From the Kalahari to Ngorongoro there are three times fewer predators per unit of prey [1234].

The exponent of a single body's production against its mass, 0.75, recurs in a whole community's predators against its prey, 0.71–0.74. The same winding is found at the depth of an organism and at the depth of a community.

Length of food chains

The 25 north-temperate lakes of one study range from 3.8×10^5 to 1.7×10^{12} m^3 [1235]. Maximum trophic position is about 3.5 in the smallest and about 5 in the Laurentian Great Lakes [1235].

The fit is MTP = 2.51 + 0.2 $\log_{10}$ volume (r^2 = 0.80, $P < 0.001$) [1235]. With $\log_{10}$ volumes of 5.58 and 12.23 it gives 2.51 + 0.2 × 5.58 = 3.63 and 2.51 + 0.2 × 12.23 = 4.96. The volumes span 12.23 − 5.58 = 6.65 orders of magnitude.

Total phosphorus of 2.6–230 µg l^{-1}, an 88-fold range, is not a significant predictor (t = 0.59, P = 0.56), and volume and phosphorus are uncorrelated (r = −0.21) [1235].

Across 219 lake, stream and marine ecosystems, food-chain length from nitrogen isotopes is about 3.5 trophic levels in streams and about 4.0 in lakes [1236]. Marine mammals lengthen marine chains by ⅔ of a level, and estimates span two full levels within each ecosystem type [1236].

The isotope estimates have similar means to food webs built from connections, with less variance [1236]. At global scale they show weak or no relationship with ecosystem size, air temperature or latitude [1236]. The two studies differ by scale: size sets chain length across 25 lakes [1235], and the relation is weak or absent across 219 systems [1236].

Transfer between levels

World fisheries for 1988–1991, 4 years (50.13), had a mean reported catch of 94.3

million t in 39 species groups, plus 27 million t of discarded bycatch [1237]. Their fractional trophic levels run from 1.0 for edible algae to 4.2 for tunas, from 48 published trophic models of six aquatic ecosystem types [1237].

The mean transfer efficiency between trophic levels is 10 %, re-estimated rather than assumed [1237]. Catches required 8.0 % of global aquatic primary production, nearly four times the previous estimate: 2 % in the open ocean and 24–35 % in freshwater, upwelling and shelf systems [1237]. Catch and bycatch together are 94.3 + 27 = 121.3 million t a year.

A review of marine transfer efficiency gives biome ranges as low, mean and high [1238]:

Biome	Low	Mean	High
Polar / subarctic-boreal	3.5 %	12.0 %	25.5 %
Temperate	1.9 %	9.6 %	34.4 %
Tropical / subtropical	0.8 %	8.6 %	52.0 %
Upwelling	0.3 %	8.0 %	27.1 %

One compilation in the review gives 13 % (11–17 %) for trophic level 1 → 2 and 10 % (7–12 %) for 2 → 3 [1238]. Another gives 5 % for upwelling, 10 % for temperate and 15 % for tropical systems; a third gives 14 % on average, with tropical values at 74 % of temperate ones [1238]. The second and third disagree on the regional order; both stand.

At 10 % per step, the energy reaching trophic level n is 0.1^(n−1) of primary production. Tuna at level 4.2 receive $0.1^{3.2} = 6.3 \times 10^{-4}$ of it; at 8 % and 14 % per step the shares are $0.08^{3.2} = 3.1 \times 10^{-4}$ and $0.14^{3.2} = 1.9 \times 10^{-3}$.

Ninety parts in a hundred leave at every step; the trophic level remains. Here the form is that of metabolism: what closes, stays, while the content flows through.

The rate of burning

Tested on 13 groups of animals, from steers and humans to hens, pigeons, rats and a ring dove, metabolism per unit surface is higher in larger animals [1239]. The unit of body size proposed for comparing metabolism is body weight to the ¾ power, W^3/4 [1239].

A model of space-filling fractal branching networks with size-invariant terminal units yields the ¾ power for metabolic rate [1240].

For mammalian basal metabolic rate, 619 species in 19 orders cover five orders of magnitude of body mass [1241]. Corrected for body temperature, digestive state and phylogeny, the rate scales as M^2/3, with no support for ¾ [1241]. The two exponents disagree; both stand.

Across the major transitions, metabolic scaling is superlinear in prokaryotes, linear in protists and sublinear in animals; the ¾ law is not universal [1242]. Maximum population growth rate scales positively in prokaryotes and negatively in protists and animals, and production efficiency declines across the three [1242].

An earlier version gives exponents of 1.79 for prokaryotes, 0.92 for eukaryotic unicells

and 0.99 for all unicells ($R^2 = 0.94$), over ten orders of magnitude of mass [1243]. The same rule of burning takes other exponents in other grades of organisation: the form of context.

How much is eaten today

Across vascular plants, 5.3 % of the leaf tissue produced each year is eaten, over 1,058 species and 2,085 populations [1244]. Earlier estimates were up to 3.8 times higher, that is 5.3 × 3.8 = 20.1 % [1244]. Woody species have 64 % higher leaf herbivory than non-woody ones [1244].

The companion dataset covers 1,145 species, 2,641 population estimates and 189 studies [1245]. Across 44 aquatic sites, herbivores remove on average 51 % of annual primary production, three times more than on land [935]; the terrestrial share is 51 / 3 = 17 %.

Herbivore biomass and herbivory rates rise with primary productivity at similar rates in water and on land [935]. At a given productivity herbivore biomass is similar, and herbivory per unit of herbivore mass is higher in water [935].

In the Serengeti in 1974–1979, 6 years (50.50), herbivores consumed on average 0.66 of annual aboveground production, with a range of 0.15–0.94 across sites [1246]. Grazing stimulated productivity at most sites, most at intermediate intensity, by keeping the vegetation in “an immature, rapidly growing state” [1246].

Plant communities with higher nutrient concentrations lose more production to herbivores [1247]. They channel less to detritus, decompose faster and store less carbon [1247].

Wolves returned to Yellowstone in 1995–1996. Browsing on young aspen fell from about 90 % in 1997–1998 to 37–63 % by 2012, over 14–15 years (51.27–51.34) [1248].

The weight of the living

The living biomass of Earth totals about 550 Gt C [235]. The kingdoms divide it as follows, each with the uncertainty of its estimate [235]:

Group	Gt C	Uncertainty	Share of 550
Plants	450	1.2-fold	81.8 %
Bacteria	70	10-fold	12.7 %
Fungi	12	3-fold	2.2 %
Archaea	7	13-fold	1.3 %
Protists	4	4-fold	0.7 %
Animals	2	5-fold	0.36 %
Viruses	0.2	20-fold	0.04 %

Plants outweigh animals 450 / 2 = 225 to 1. Plants hold about 320 Gt C above ground and about 130 Gt C in roots; about 70 % of plant biomass is stems and trunks [235]. About 90 % of bacterial biomass lies in the deep subsurface [235].

Among animals the census gives, in Gt C [235]:

Animal group	Gt C
Marine arthropods	1
Fish	0.7
Terrestrial arthropods	0.2
Annelids	0.2
Molluscs	0.2
Cnidarians	0.1
Livestock	0.1
Humans	0.06
Nematodes	0.02
Wild mammals	0.007
Wild birds	0.002

Humans outweigh wild mammals 0.06 / 0.007 = 8.6-fold, and livestock outweigh them 0.1 / 0.007 = 14-fold. Humans and livestock together, 0.16 Gt C, are 0.16 / 0.167 = 96 % of all mammal biomass.

Land holds about 470 Gt C and the ocean about 6 Gt C, double a previous marine estimate [235]. In the ocean about 1 Gt C of producers carries about 5 Gt C of consumers, an inverted standing pyramid [235]. The consumers outweigh the producers 5 to 1.

Plant biomass is about twofold below its value before civilisation [235]. Wild mammal biomass has fallen by a factor of about 6, about 7-fold on land and about 5-fold at sea [235].

In the ocean, across body sizes from bacteria to whales, the biomass in most order-of-magnitude size classes is nearly constant at about 1 Gt wet weight, 10^{15} g [1249]. Bacteria lie well above that value and whales well below, and human activity has truncated the upper third of the spectrum [1249].

If length goes as the cube root of mass, an order of magnitude of mass is a factor of 10^(1/3) = 2.15 in length, or 0.70 of a position on the ladder of sizes. Every 0.70 positions, from bacteria to whales, the sea held about the same weight of life: the same form at every depth.

What this part of the history shows

Eating opens early and fills late. The first predation trace is a hole in the first mineralised tube, on 2.7 % of more than 500 *Cloudina* tubes or about 20 % of about 100. The maximum drilling frequency per species then climbs from 10–20 % in the Ediacaran–Silurian to 100 % in the Quaternary.

Parasitism has the form of a union opened once and filled many times. Its first trace is Lower Cambrian; it then arose at least 223 times in 15 animal phyla, 12 times in flowering plants and 4 times in plant-feeding nematodes. The ten largest parasitic clades hold about 90 % of described parasite species and perhaps 40 % of all animals.

The defences of plants fill in the same way. Spines arose at least 55 times, the great majority of spiny clades within the last 17 Ma (64.02); domatia arose at least 158 times within 19 Myr (64.13). Extrafloral nectaries arose in at least 457 lineages, caffeine in five plant lineages and the cardenolide-resistant pump substitution in six insects of four orders.

The record has the form of rest and discharge. Drilling rises through the Palaeozoic, falls almost silent for 120 Myr (65.80) and returns with a higher ceiling. Herbivory collapses at 252 Ma and needs 24 Myr (64.34) to recover; after 66 Ma it needs about 10 Myr (63.54).

Form and carrier separate. Caulimovirid insertions have held in plant genomes since about 320 Ma (66.70), and *Rpm1* alleles for millions of years, while a *Daphnia* parasite readapts within a few years. Pentastomids moved from Silurian ostracods to vertebrates, and the parasitic form held: “The closed class persists and holds form.”

A residue becomes an alphabet. Isoprene, one closed molecule of 68.117 g mol^{-1}, is the letter of 16,000 described terpenes. The genes that write them grow from 1 in a moss to 18 in a lycophyte and 40–152 in seed plants.

The flow through the levels has the form of metabolism. About 10 % passes each step and about 90 % leaves; tuna at level 4.2 receive 6.3×10^{-4} of primary production. The levels stay while their content is replaced, and the chains stay 3.5 to 5 levels long.

The same winding appears at two depths. A single body’s maximum production scales with its mass at 0.75, and a community’s predators scale with its prey at 0.71–0.74. In the sea, before the truncation of its upper third, each order of magnitude of body mass held about 1 Gt of life.

Context sets the values. Transfer efficiency runs from 0.3 % to 52 % between single systems, and herbivores take 51 % of production in water and 17 % on land. Metabolic exponents run 1.79 in prokaryotes, 0.92 in eukaryotic unicells and ⅔ to ¾ in animals: one rule, other surroundings, other constants.

Partners nest as addresses: a virus inside a fungus inside a grass gives the grass its heat tolerance. Parasites sit on about 75 % of all food-web links, and trematodes outweigh the birds of three estuaries threefold to ninefold. Community is a shared prefix: the eater lives inside the address of the eaten.

14. Flowers and Their Animals

Plants stay where they grow, so their pollen and their seeds must be carried. Animals carry them: pollen from flower to flower, seeds away from the parent plant. In return the plant gives food, nectar, pollen or flesh.

This chapter follows those two unions from their first traces to the present. The insects come first, long before any flower.

Pollination begins on gymnosperms, then passes to the flowering plants. Fleshy seeds come before any clear animal carrier, and the carriers come later: birds, bats, primates, ants.

The chapter ends with the shape of the present web of plants and animals and with the measured effects of losing partners. Eating plants is treated in chapter 13; here the animal is a carrier, not an eater.

Positions are those of chapter 1: an age of A million years is placed as a duration of $A \times 10^6 \times 3.15576 \times 10^7$ s. Every size and every time carries its coordinate on the ladder.

Insects before flowers

The oldest fossil described as an insect is *Rhyniognatha hirsti* from the Rhynie chert, Scotland [981]. The paper gives its Pragian age as about 396–407 Ma (66.89–66.92); on the 2023 chart the Pragian spans 410.8–407.6 Ma (66.92) [435, 981]. A reinterpretation of new remains reads it as a myriapod, “possibly as a centipede” [982].

A molecular clock on 1,478 protein-coding genes places the origin of insects in the Early Ordovician, about 479 Ma (67.06) [979]. It places the origin of insect flight in the Early Devonian, about 406 Ma (66.91), and the main living lineages in the Mississippian, about 345 Ma (66.76) [979].

The oldest winged insect fossil, *Delitzschala bitterfeldensis*, is Arnsbergian, from Bitterfeld and Delitzsch in Germany [980]. That interval lies within the Serpukhovian, 330.9–323.2 Ma (66.73–66.71) [435]. The gap between the molecular age of flight and the oldest winged fossil is $406 - 330.9 = 75.1$ Myr (65.38).

The butterflies and moths, Lepidoptera, have a crown in the Late Carboniferous, about 300 Ma (66.64) [1250]. Their tube-like proboscis dates to the Middle Triassic, about 241 Ma (66.44), and day-flying butterflies to about 98 Ma (65.62) [1250]. That study uses 186 species and 2,098 genes [1250].

Wing scales of proboscis-bearing Lepidoptera, Glossata, occur in latest Triassic to earliest Jurassic sediments of northern Germany [1251]. The Triassic–Jurassic boundary is 201.4 Ma (66.27) [435]. These scales extend the minimum age of Glossata by about 70 Myr (65.31) and predate the flowering plants [1251].

From the oldest insect fossil to the main angiosperm clades, 135–130 Ma, is $410.8 - 135 = 275.8$ to $407.6 - 130 = 277.6$ Myr (66.56–66.57). From the molecular origin of

insects it is 479 − 135 = 344 Myr.

Pollination before flowers

The interaction is first recorded on gymnosperms. The oldest definitive pollinating insects carry siphonate proboscides and date to the late Middle Jurassic, about 165 Ma (66.09) [990]. The long-proboscid mode is documented from about 165 to about 100 Ma (65.64), with at least 85 described species of long-proboscid and related insects in the Eurasian mid-Mesozoic [990].

Long-proboscid scorpionflies, 11 species in three extinct families, fed on the ovular secretions of gymnosperms over a 62-million-year interval (65.20) [1252]. Their five co-occurring hosts are a seed fern, a conifer, a ginkgoopsid, a pentoxylalean and a gnetalean [1252]. All three families became extinct in the Early Cretaceous [1252].

The first beetle pollinator, *Darwinylus marcosi*, a false blister beetle from Peñacerrada I amber in Spain, is about 105 Ma (65.68) [1253]. It carries 126 associated pollen grains, 5 still attached, of the form-genus *Monosulcites*, from Ginkgoales, Cycadales or Bennettitales [1253].

The same authors count four gymnosperm pollination modes before angiosperm pollination and four cohorts of insect pollinators between 125 and 90 Ma (65.84–65.54) [1253]. Seven direct-evidence cases of insect pollination are known, four of them from Spanish amber [1253].

A boganiid beetle, *Cretoparacucujus cycadophilus*, in Burmese amber of about 99 Ma (65.63), carries cycad pollen of *Cycadopites* [1254]. Twenty-one grains were measured: polar axis 20.65 µm (5.57), from 20.07 to 21.04 µm, equatorial diameter 14.30 µm (5.23), in clumps of 3–14 grains [1254].

The oldest boganiid fossil, *Palaeoboganium jurassicum*, is Middle Jurassic, about 165 Ma (66.09) [1254]. Molecular ages of crown cycads run from about 200 Ma (66.27) to 274.5 Ma (66.56) [1254].

Long-proboscid flies, Zhangsolvidae, in amber from Spain (about 105 Ma) and Myanmar (100 Ma), carry clumped *Exesipollenites* pollen of a gymnosperm, most likely a bennettitalean [1255]. Angiosperm clades replaced the gymnosperm pollination modes between 120 and 100 Ma (65.80–65.64) [990].

The union of pollen and insect is thus opened on gymnosperms and only later filled with flowers. A new kind of union opens once; then the opened depth fills many times.

The flowers arrive

The angiosperm crown is Early Cretaceous [783]. Magnoliids, monocots and eudicots diversified 135–130 Ma (65.91–65.88) [783]. Pentapetalae follow at 126–121 Ma (65.85–65.81), Rosidae at 123–115 Ma (65.83–65.76) and Asteridae at 119–110 Ma (65.80–65.72) [783].

That time-tree rests on 137 calibrated nodes and 87 % of families [783]. No unequivocal pre-Cretaceous angiosperm fossil is known [1256].

The bees, crown Anthophila, date to about 123 Ma (65.83), with a range of 113–132 Ma (65.75–65.89), from seven genes and 14 fossil calibrations [1257]. The same study gives eudicots as 75 % of angiosperm species [1257].

The oldest bee, *Melittosphex burmensis* in Burmese amber, is approximately 100 Ma (65.64) [1258]. It gives a minimum date for bee pollination [1258].

The oldest direct evidence of insect pollination of a eudicot is the tumbling flower beetle *Angimordella burmitina*, 99 Ma (65.63), carrying tricolpate pollen [1259]. It extends the record of insect pollination of angiosperms by at least 50 Myr (65.01) [1259].

Obligate pairs

Some unions close into obligate pairs. At least five such pairs are dated.

Figs and fig wasps. *Ficus* holds about 750 species, with more than 750 interacting pairs of fig and wasp species [1260]. About 200 pairs were sampled with 850 new sequences; nearly half of the fig and pollinator lineages diverged at the same time, and the origin is Eurasian [1260]. A second count gives 874 *Ficus* species [1261].

Ten pairs of interacting fig and wasp lineages have co-diverged over at least 60 Myr (65.17) [1262]. Wasp and seed development inside the fig takes 15 to 100 days (45.96–47.69) [1261]. Pollinating females usually live 24–48 h (43.50–44.13) [1261].

Insect life inside the fig is thus 15 d / 2 d = 7.5 to 100 d / 1 d = 100 times shorter than the fig cycle. The wasp develops inside the fig whose flowers it pollinates.

Yuccas and yucca moths. Moths colonised yuccas 41.5 ± 9.8 Ma, that is 31.7–51.3 Ma (64.59–65.03) [1263]. Pollinator behaviour arose 0–6 Myr after colonisation, a diversification burst followed at 3.2 ± 1.8 Ma (62.50), and non-pollinating cheaters at 1.26 ± 0.96 Ma (61.66) [1263].

The *Tegeticula yuccasella* complex holds 13 described species, 11 of them pollinators, and *Parategeticula* holds 4 [1264]. Cheating arose twice independently [1264]. A female carries up to nearly 10,000 pollen grains, about 10 % of her body weight [1264].

Perfume orchids and orchid bees. The orchid bees, Euglossini, share a most recent common ancestor at 34–38 Ma (64.66–64.76) [1265]. Their perfume-orchid lineages are younger: Catasetinae 18–27 Ma (64.08–64.45), Zygopetalinae 20–25 Ma and Stanhopeinae 21–26 Ma [1265].

The orchids arose at least three times independently after the bees [1265]. There are more than 200 euglossine species and more than 600 orchid species, about 10 % of Neotropical Orchidaceae; the bees collect 585 volatile compounds [1265].

Darwin’s orchid and its hawkmoth. *Angraecum sesquipedale* has a nectar spur of 33 cm (14.38) [1266]. Madagascar has about 30 long-spurred orchids and 7 long-tongued hawkmoths; 62 of 144 Madagascan *Angraecum* were sampled [1266].

The Madagascan moth split from the African *morgani* 7.4 ± 2.8 Ma (63.27), and *A. sesquipedale* from *A. sororium* 7.5 ± 5.2 Ma (63.28) [1266]. The two splits stand 0.1 Myr apart.

Ants and their fungi. Fungus-farming ants arose as lower fungus farmers at the end of the Palaeocene, between 61 Ma (52–70) and 57 Ma (48–66), positions 65.19–65.13 [937]. The tribe Attini in the wide sense is 66 Ma (56–76) [937].

Higher agriculture arose between 31 Ma (26–37) and 27 Ma (22–33), positions 64.57–64.45 [937]. Leaf-cutter ants, *Atta* with *Acromyrmex*, arose in the Miocene between 19 Ma (15–24) and 18 Ma (14–22), positions 64.13–64.08 [937]. From first farming to leaf-cutting is 61 − 19 = 42 Myr (64.85); about 250 New World attine species are described [937].

Each pair is between about 7.5 and at least 60 Myr old. In each, the insect side is dated first or together with the plant. Here the form is that of the pair: two closures that hold only together.

Seeds before their carriers

Seeds first appeared in the late Middle or Late Devonian [1267]. The Givetian begins at 387.7 Ma and the Famennian ends at 358.9 Ma (66.87–66.80) [435].

By the Pennsylvanian, 323.2–298.9 Ma (66.71–66.63), “large, flesh-covered seeds had evolved in both seed ferns and cordaitaleans” [435, 1267]. Medullosan seed-fern seeds averaged 20,000–50,000 mm³, and one species exceeded 300,000 mm³ [1267]. Cordaitalean seeds ran from 122 to more than 12,000 mm³ [1267].

As spheres of equal volume, 20,000–50,000 mm³ is a diameter of 33.7–45.7 mm (12.30–12.58), and 300,000 mm³ is 83.1 mm (13.12). The cordaitalean seeds are 6.2–28.4 mm across (10.75–12.14).

The plants had the structures needed for animal dispersal by the Pennsylvanian, “but possibly in the absence of clear vertebrate dispersal agents” [1267]. Plant-eating vertebrates first diversified in the Permian, 298.9–251.902 Ma (66.63–66.48) [435, 1267]. The author now doubts that the Mississippian and Pennsylvanian fleshy seeds evolved for animal dispersal [1267].

The oldest seed ingestion is Late Permian. Nearly 60 seeds of the wind-dispersed conifer *Pseudovoltzia* lie in the gut of the reptile *Protorosaurus* from Germany, and a second specimen holds similar seeds [1267]. A Permian seed with fleshy appendages may have attracted an arthropod or a vertebrate, or served pollination [1267].

Fruit eating by fishes may date to the Palaeozoic [1268]. Fishes “were probably the first vertebrate seed dispersers” [1269].

In the Mesozoic large plant-eating dinosaurs may have dispersed seeds across whole plants [1267]. Small vertebrates, lizards and later birds and mammals, may have formed more specific associations, but the evidence is thin, and reported dinosaur gut contents “have been questioned” [1267].

An Early Cretaceous ankylosaur about 1.4 m long (15.69) held “three 4.5 mm long fruits and several 0.3 mm diameter seeds”, with fern sporangia and leaves [1267]. The fruits sit at position 10.47 and the seeds at 8.00. An Early Cretaceous bird about 60 cm long (14.92) has plant remains in its stomach region [1267].

Mesozoic cycad and *Ginkgo* seeds generally lack preserved flesh; their fleshiness is inferred from living relatives [1267]. In an Early Cretaceous Portuguese flora of 106 taxa, “nearly 25% of the species were fleshy” [1267].

A Campanian coprolite, probably from a turtle, holds “nearly 200 achenes of early Ranunculaceae” [1267]. The Campanian spans 83.6–72.1 Ma (65.47–65.34) [435]. Maastrichtian dicot fruits are associated with coprolites [1267].

Late Cretaceous marsupials and multituberculates may have been omnivores or occasional dispersers; *Glasbius intricatus* is the only species named as a possible early frugivore [1267]. “No compelling evidence presently exists for obligate fruit or seed dispersal by mammals” in the Mesozoic [1267].

Fleshy fruits and angiosperm seed-size diversification “commenced around 80 million years ago” (65.43) [1270]. The diversity of seed sizes, fruit sizes and fruit types peaked in the Eocene, 55–50 Ma (65.09–65.01) [1270].

In 25 angiosperm floras from about 124 Ma (65.83) to about 2 Ma (62.08), seed and fruit sizes are small through most of the Cretaceous [1271]. The increase begins before the Cretaceous–Tertiary boundary; sizes fall in the late Eocene and Oligocene and stay low [1271].

Animal dispersal was fairly common in the Cretaceous, rose sharply in the Early Tertiary and then declined with seed and fruit size [1271]. Wind dispersal is bimodal, high in the Late Cretaceous and in the Oligocene–Miocene [1271]. An earlier view held Cretaceous angiosperms to be dominated by abiotic dispersal [1267]; both readings stand.

From the Pennsylvanian fleshy seeds to the onset of angiosperm fleshy-fruit diversification is at least $298.9 - 80 = 218.9$ Myr (66.35). The fleshy seed is laid down first; the radiation of fleshy fruit and its carriers follows more than two hundred million years later.

The carriers radiate

The main disperser groups follow the fruit. Palaeognathae and Neognathae split “about 100 Ma in the Late Cretaceous” (65.64), and Neognathae split into Galloanseres and Neoaves about 88 Ma (65.52) [1272]. Palaeognathae split about 84 Ma (65.48), and basal Neoaves divergences fall before the K–Pg boundary, at 67–69 Ma (65.27–65.30) [1272].

Thirty-six Neoaves lineages arose within 10–15 Myr (63.54–63.91) after the K–Pg boundary at 66 Ma (65.26) [1272]. Nearly all ordinal divergences were complete by 50 Ma (65.01), and the basal split of Passeriformes is around 39 Ma (64.78) [1272]. The study rests on 48 genomes [1272].

The Tertiary radiation of birds involved many frugivorous and seed-eating birds, especially passerines [1267]. The oldest known primate skeleton, a basal tarsiiform haplorhine from the early Eocene of China, is about 55 Ma (65.09), “about the size of the modern pygmy mouse lemur” [1273]. Primates and rodents were likely important frugivores in the latter part of the first phase of fruit evolution [1270].

The oldest bat, *Onychonycteris finneyi* of the Green River Formation, Wyoming, is Early Eocene; it could fly and probably could not echolocate [1274]. The Early Eocene spans 56.0–47.8 Ma (65.11–64.97) [435].

Old World fruit bats, Pteropodidae, have been distinct from other bats since at least the early Eocene; their crown divergence is 31–20 Ma (64.57–64.17) [1275]. They hold 186 species in 46 genera, and their first three splits fall within about 0.5 Myr (60.81) when 26 Myr is used for the radiation [1275]. The oldest frugivorous bat fossil is a middle Oligocene megachiropteran [1267].

Flying frugivores, birds and bats, evolved mainly in a second phase in the Oligocene and Miocene [1270]. The climate shift at the Eocene–Oligocene boundary, “around 34 Mya” (64.66), favoured bat and passerine frugivory [1270].

Scatter-hoarding of nuts by rodents and corvids may date to the Paleocene, about 60 Ma (65.17) [1276]. It covers 10 nut genera, among them *Juglans*, *Quercus*, *Fagus* and *Corylus*, and most nut plants descend from wind-dispersed ancestors [1276]. Corvids disperse *Pinus* and *Quercus* [1277].

Seed dispersal by ants, myrmecochory, is “more frequent in families with crown group ages under 80 million years than in older families” [1278].

The fruit and its carriers have the form of form and carrier. The fleshy seed is the closed form that persists; the carrier changes, from Permian reptiles to Cretaceous turtles, to birds, primates and bats.

Who pollinates today

Accepted angiosperms number 295,383 species, 74,273 of them monocots and 210,008 eudicots; gymnosperms number 1,079 [659]. All plants number about 374,000, and about 2,000 new species are named each year [659].

Two estimates of the animal-pollinated share disagree. The first gives 87.5 %, or 308,006 of about 352,000 species, with community means of 78 % in temperate and 94 % in tropical sites [1279]. Earlier literature values ran from 67 % to 96 % [1279].

The second gives about 90 % [1280]. On the GBIF list 33,623 of 332,341 species are abiotically pollinated and 296 both; on the WFO list 32,129 of 339,876 are abiotic and 267 both [1280]. The animal-pollinated share is (332,341 − 33,623) / 332,341 = 89.9 % on GBIF and (339,876 − 32,129) / 339,876 = 90.5 % on WFO.

Recalculated with weighting by sample size and latitude, the first estimate rises from 87.5 % to 89.5 % [1280]. About 88 % of genera are exclusively animal-pollinated: GBIF counts 14,437 genera with 1,573 abiotic and 88 mixed, WFO 13,772 with 1,548 and 90 [1280]. For families the share is 67 % on GBIF, with 105 of 465 abiotic, and 64 % on WFO, with 103 of 414 [1280].

Known pollinator species total 349,368, about 350,000 [1281]. By group they are these [1281]:

Pollinator group	Species
Lepidoptera (moths 123,100; butterflies 18,500)	141,600

Beetles	77,300
Hymenoptera, all	70,000
Flies (hoverflies 6,000; bee flies 4,500)	55,000
Bees	17,000
Thrips	1,500
Birds (hummingbirds 365)	1,089
Mammals (bats 236)	344
Lizards	37

The author calls the insect figures “certainly too low” [1281]. Known pollinators per angiosperm species are 349,368 / 295,383 = 1.18.

Vertebrate pollinators number 1,089 + 344 + 37 = 1,470, which is 0.42 % of 349,368. A review of nectar feeding gives about 360 hummingbird species [1282]; the two hummingbird counts agree within 1.4 %.

About 528 angiosperm species in 67 families and 28 orders are bat-pollinated [1283]. Bat pollination arose independently many times, from insect, bird and non-flying-mammal pollination, and bats carry large pollen loads over long distances [1283].

Bat-pollinated species are 528 / 295,383 = 0.18 % of angiosperms, and there are 528 / 236 = 2.2 bat-pollinated plant species per pollinating bat species.

The insects in numbers

About 1 million insect species are named and about 5.5 million are estimated; beetles alone are estimated at 1.5 million [1284]. Terrestrial arthropods number about 7 million, about 80 % of insect species are undescribed, and 1–2 % of species in well-studied faunas are cryptic [1284].

Insects hold about 62 % of about 1.6 million described living species [1161]. Lepidoptera count 157,424 species in 15,578 genera [1285]; Coleoptera 386,500 species in 29,500 genera and 176 families [1286]; Hymenoptera 153,088 described species [1287].

Bees count 20,446 living species [1288] or 17,000 [1281]; both counts stand. Bees are 20,446 / 153,088 = 13.4 % of Hymenoptera. The three largest orders together hold 386,500 + 157,424 + 153,088 = 697,012 named species.

Who carries seeds today

Among angiosperms, 30 % of families are biotically dispersed, with a further 22 % both biotic and abiotic; by species 14 % are biotic and a further 42 % both [1267]. Among gymnosperms, 64 % of families and 46 % of species are biotically dispersed, with a further 39 % of species both [1267]. Palms are “almost entirely animal dispersed” [1267].

At least 11,000 plant species are ant-dispersed, about 4.5 % of angiosperms, in 334 genera (2.5 % of genera) and 77 families (17 % of families) [1278]. Ant dispersal has at least 101 independent origins, possibly up to 147; 13 families hold three or more origins

[1278].

An earlier count by the same group gives a conservative 11,532 species and 101 lineages, perhaps 140 or more, from 241 genera in 55 families [1289]. Most origins lie in Asteraceae (10), Euphorbiaceae (8), Fabaceae (6), Ranunculaceae (5), Lamiaceae (4) and Liliaceae (3) [1289].

Ant-dispersed lineages hold more species than their sister group in 68 of 101 comparisons, about 2.24 times as many [1289]. Regionally, Australia holds 134 ant-dispersed genera and at least 1,500 species, and the South African fynbos about 1,200 species, 20 % of its flora [1289]. Ant dispersal covers 30–40 % of the herbs of eastern North American forests and 40–50 % of those of eastern European deciduous forests [1289].

The implied angiosperm total is 11,000 / 0.045 = 244,444. Ant dispersal arose at least 101 times; each origin holds on average about 109 species.

Birds number 11,063 extant species in 2,389 genera, 251 families and 44 orders, with 164 extinct [1290]. Of 8,918 terrestrial bird species, 1,230 are frugivores: 365 obligate and 865 partial, with a further 1,659 opportunistic fruit eaters and 6,029 non-fruit-eaters [1291].

Frugivores are 1,230 / 8,918 = 13.8 % of terrestrial birds, and obligate frugivores 365 / 8,918 = 4.1 %. Passeriformes supply 618 frugivores, 50 % of the total and 11 % of 5,841 passerines [1291].

Columbiformes supply 179 (58 % of the order), Psittaciformes 141 (40 %), Piciformes 112 (32 %) and Musophagiformes 23, the whole order [1291]. Frugivore richness peaks in the Neotropics; actual evapotranspiration alone accounts for 71–73 % of its variation, and with realm for 80–85 % [1291].

Mammals number 6,495 recognised species, 6,399 of them extant, in 1,314 genera and 167 families; about 25 new species are described each year [1292]. Birds outnumber mammals 11,063 / 6,399 = 1.73 to 1.

More than 275 fish species are frugivorous, mainly Characiformes and Siluriformes [1268]. In serrasalmids frugivory evolved from omnivory, with powerful jaws and specialised teeth, and no fruit traits are specific to fish dispersal [1269].

A Mediterranean scrub community of 41 bird species holds 14 seed dispersers, 4 seed predators, 8 pulp predators and 15 non-frugivores [1293]. A global seed-ingestion dataset holds 13,135 animal × seed interactions across fishes, amphibians, reptiles, birds and mammals [1294].

Ingested seed size falls with body mass overall, a result driven by ungulates eating small dry seeds, and rises when ungulates or dry fruits are excluded [1294]. Larger animals eat larger maximum and smaller minimum seeds and more seed species [1294].

At Sarapiquí, Costa Rica, 200 of 240 canopy tree species, 83.5 %, are animal-dispersed [1295]. In regrowth 11–45 years old, animal-dispersed stems exceed 75 % after about 17 years for seedlings, 20 years for saplings and about 35 years for trees of 10 cm diameter or more [1295].

In a Panama forest, 200 seed traps caught 386,027 seeds over 4 years, and 13,068

seedlings were recruited [1296]. That is 386,027 / 800 = 482.5 seeds per trap-year and 13,068 / 386,027 = 3.39 % seedlings per seed. Seedling diversity was higher than seed diversity [1296].

In Brazil 103 of 1,361 sampled species carry the megafaunal-fruit syndrome, in 22 families and 46 genera; 83.3 % are trees [1297]. The share is 30 % of 147 fleshy-fruited species in the Pantanal and 13 % of 246 in the Atlantic forest [1297].

At the end of the Pleistocene the Neotropics held at least 6 families and 13 genera of animals above 1,000 kg, none surviving; Africa keeps 5 such genera and Asia 2 [1297]. More than 15 genera of Central American large herbivores became extinct roughly 10,000 years ago (57.25) [1298].

Sizes and times of the partners

Bodies, mouths and spurs

What	Size	Position	Source
Smallest adult insect, male *Dicopomorpha echmepterygis*	139–240 µm	7.30–7.80	[1299]
Pollen, *Cycadopites* on the 99 Ma beetle, equatorial	14.30 µm	5.23	[1254]
Pollen, *Cycadopites*, polar axis	20.65 µm	5.57	[1254]
Pollen, *Myosotis sylvatica* (class)	below 10 µm	below 4.91	[1300]
Pollen, *Cucurbita pepo* (class)	above 100 µm	above 7.00	[1300]
Butterfly proboscis diameter, *Eurybia lycisca*	0.26 mm	7.87	[1301]
Honey bee worker reach into a corolla	7 mm	10.87	[1302]
Butterfly proboscis, *Eurybia lycisca*, mean	36.5 mm	12.37	[1301]
Butterfly proboscis, *Eurybia lycisca*, maximum	45.6 mm	12.58	[1301]
Orchid spur, *Angraecum sesquipedale*	33 cm	14.38	[1266]
Longest insect, *Phobaeticus chani* female, body	357 mm	14.45	[1303]
Longest insect, *Phobaeticus chani* female, overall	567 mm	14.87	[1303]

The males of *Dicopomorpha* are wingless and eyeless, 0.4 times the female length, with 1–3 males per host egg [1299]. Insect body length spans 567 / 0.139 = 4,079, or 7.30 to

14.87 on the ladder. The *Eurybia* proboscis, from 20 butterflies, is about twice the body length [1301].

Seeds and fruits

What	Size	Position	Source
Seed in the ankylosaur gut	0.3 mm	8.00	[1267]
Fruit in the ankylosaur gut	4.5 mm	10.47	[1267]
Largest seed dispersed reliably	about 2.5 cm	12.03	[1297]
Largest seed of African cephalophine dispersers	about 2.8 cm	12.13	[1297]
Largest seed of extant Neotropical frugivores	about 3.5–4.0 cm	12.33–12.46	[1297]
Megafaunal fruit, Type I diameter	4–10 cm	12.46–13.29	[1297]
Megafaunal fruit, Type II diameter	above 10 cm	above 13.29	[1297]
Jackfruit seed	2–4 cm	11.83–12.46	[1304]
Jackfruit, width	15–50 cm	13.66–14.76	[1304]
Jackfruit, length	20–90 cm	13.92–15.29	[1304]

Type I megafaunal fruits are fleshy with up to 5 large seeds above 2.0 cm; Type II are fleshy with more than 100 small seeds [1297]. They weigh about 50–1,000 g, with a seed load of up to 140 g per fruit [1297]. Seed mass is 0.2–97.4 % of fruit mass in megafaunal fruits against 0.1–8.9 % in others [1297].

Megafaunal seeds of *Astrocaryum* and *Syagrus* exceed 15 g against below 10 g in other species, and those of *Licania* exceed 10 g against below 2.0 g [1297]. Jackfruit reaches up to 50 kg, with 100–500 seeds per fruit [1304]. A single nut holds 5.7–153.5 kJ, 10 to 1,000 times most wind-dispersed seeds [1276].

Across 12,987 species the split between angiosperms and gymnosperms is the largest single contributor to the present spread of seed mass [777]. Seed-mass shifts track growth form more than dispersal syndrome or climate [1305].

Lives and cycles

What	Duration	Position	Source
Flower handling, *Eurybia lycisca*	54.5 ± 28.5 s	36.79	[1301]
Flower longevity, shortest	below 1 d	below 43.50	[1306]
Adult pollinating fig wasp	24–48 h	43.50–44.13	[1261]
Fig cycle inside the syconium	15–100 d	45.96–47.69	[1261]
Honey bee worker,	2–6 weeks	45.90–46.90	[1307]

normal lifespan			
Honey bee worker, caged	23–42 d	46.35–46.90	[1307]
Honey bee drone, maximum	20–40 d	46.23–46.86	[1307]
Caged workers, USA, median, now	17.7 d	46.12	[1308]
Caged workers, USA, median, 1970s	34.3 d	46.72	[1308]
Honey bee queen, maximum	8 yr	50.76	[1307]
Periodical cicadas, juvenile period	13 yr; 17 yr	51.21; 51.45	[1309]

Flowers last from less than a day in morning glory to several weeks in orchids [1306]. The queen-to-worker lifespan ratio is 8 yr / 42 d = 70 to 8 yr / 14 d = 209. Caged workers now live half as long as 50 years ago [1308].

Periodical cicadas, *Magicicada*, hold 7 species: 4 of 13 years and 3 of 17 years, in 12 broods of 17 years and 3 of 13 years [1309]. The life cycles diverged 200,000–100,000 years ago (59.98–59.35), and the species groups split 3.9–2.5 Ma (62.68–62.28) [1309].

Gut passage and distance

Mediterranean passerines pass seeds mostly within 5–30 min (38.34–39.98) of eating them [1293]. Seasonal means per species run from 22.9 ± 15.7 min (39.73) to 69.4 ± 32.7 min (40.74), over 30 species with passage data from 1978 to 1982 [1293].

An 80 g disperser has a gut-passage time like a 9 g non-disperser; at about 15 g the non-dispersers' passage time is about 2.5 times that of dispersers [1293]. Fruit density nears 10^6 fruits per hectare at some Mediterranean scrub sites [1293].

Forest elephants in Gabon have a mean gut passage of 39.5 h (43.95), with a field range of 16.6–113.7 h (43.16–44.92) [1310]. Adult females take 42.2 h (44.01), juveniles 34.8 h (43.84), and *Tin* seeds 65.6 h (44.41) [1310]. The elephant mean is 39.5 h / 17.5 min = 135 times the passerine mid-range.

Dispersal distance grows with the carrier:

Carrier	Distance	Position	Source
Ants, shortest	0.01 m	11.19	[1289]
Ants, typical	about 1 m	15.39	[1289]
Small passerines, half the seeds within	51 m	18.97	[1311]
Ants, longest	77 m	19.34	[1289]
Medium-sized birds, half the seeds beyond	110 m	19.66	[1311]
Carnivorous mammals, half the seeds beyond	495 m	21.03	[1311]
Forest elephants, median	5.3 km	23.19	[1310]

Forest elephants, mean	6.5 km	23.38	[1310]
Forest elephants, 10 % of seeds beyond	14.1 km	24.08	[1310]
Forest elephants, 95 % quantile	16.4 km	24.22	[1310]
Forest elephants, average maximum over 96 animals	40.1 km	25.03	[1310]
Forest elephants, longest simulated (male; female)	87.4 km; 101 km	25.74; 25.87	[1310]

For *Prunus mahaleb* in Spain, mammals carry about two-thirds of the immigrant seeds and birds one-third [1311]. Of the elephants' seeds, 89 % travel more than 1 km (21.67) [1310]. Extinct megafauna dispersed seeds over 10^3–10^4 m (21.67–23.77), extant dispersers over 10^1–10^3 m (17.48–21.67) [1297].

Long-distance dispersal is more common in open landscapes and is "often associated with unusual behavior of the standard vector" [1312]. From the typical ant distance to the elephant median is a factor of 5,300 / 1 = 5,300, or 7.80 positions.

Seeds that wait

A date-palm seed from Masada, radiocarbon-dated to the first century CE, germinated; its age is about 2,000 years (55.79) [1313]. Its seedling grew over 26 months like modern seedlings and carries more genetic variation than modern elite cultivars [1313].

Immature fruits of *Silene stenophylla* from fossil squirrel burrows 38 m deep (18.70) in north-eastern Siberia are dated to 31,800 ± 300 radiocarbon years (58.31) [1314]. Whole fertile plants were regenerated from their placental tissue; the result is tissue regeneration, not germination [1314].

Mast years

Many trees fruit together in some years and hardly at all in others. A survey of 570 masting datasets finds wind-pollinated species more variable than animal-pollinated ones, and frugivore-dispersed species less variable than predator-dispersed ones [1315]. Variability peaks at mid-latitudes and in the Southern Hemisphere [1315].

Quercus species that take two years to ripen acorns show negative autocorrelation at a lag of 2 years; other trees at a lag of 1 [1316]. Seed production and ring growth are negatively correlated at sites up to 1,000 km apart, a synchrony over areas "almost the size of a continent" [1317].

European beech holds 337 time series with 5,774 yearly observations from 1760 to 2015 [1318]. Fifteen years lie above the 95th percentile of the masting index: 1773, 1811, 1846, 1858, 1869, 1888, 1900, 1909, 1918, 1926, 1948, 1958, 1995, 2006 and 2011 [1318].

Their mean spacing is (2011 − 1773) / 14 = 17.0 years (51.45). Beech and spruce share eight events, in 1974, 1990, 1992, 1995, 2000, 2004, 2006 and 2011, with a mean spacing of 37 / 7 = 5.3 years (50.39) [1318]. The wavelet band runs from 7 to 16 years

(50.64–51.39) [1318].

In England, 139 beech trees at 12 sites over 1980–2018 show that warming raised seed production but lowered its variability and synchrony [1319]. A mast year has the form of loading and discharge: years of holding, then one year of release across a continent.

Generations of the carriers

Bird generation length runs from 1.42 to 27.87 years (49.19–51.90), with a median of 2.99 years (49.87) [1320]. Sixty-one per cent of bird species have generations under 3.33 years (49.97) [1320]. Generation-length records exist for 5,427 extant mammals [1321], 5,427 / 6,399 = 84.8 %.

Hunter-gatherers began to move away from foraging some 11,000–10,000 years ago (57.34–57.25) [1322]. Domestication is the latest form of carriage: the human carries the seed.

Nut trees shifted their ranges over the last 16,000 years (57.68) after the glaciers retreated, likely carried by squirrels, jays and their relatives [1276].

The web of flowers, fruit and animals

Nested networks

One study compares 52 mutualistic networks, 27 of seed dispersal and 25 of pollination, with 14 bipartite food webs [1323]. Each matrix was tested against 50 random networks under two null models; 6 of the 52 change status between the models [1323].

Set	Size (plant + animal species)	Nestedness N	Mean N ± SE	Significantly nested
Seed dispersal	9–317	0.565–0.999	0.844 ± 0.043	19 of 27
Pollination	22–446	0.594–0.975	0.853 ± 0.047	20 of 25
Food webs	12–104	0.507–0.942	0.694 ± 0.077	—

Values from [1323]. The nested shares are 19 / 27 = 70.4 %, 20 / 25 = 80.0 % and 39 / 52 = 75.0 %. Every seed-dispersal network with at least 28 species and every pollination network with at least 50 species is nested [1323].

In a nested network, specialists interact with subsets of the partners of generalists, and together they form a cohesive core [1323]. The networks are neither random nor compartmentalised [1323].

The specialist’s partners lie inside the generalist’s partners, as a short address lies inside a longer one. Here the form is that of community as shared prefix.

Degrees, connectance and modules

Of 29 plant–pollinator and 24 plant–frugivore networks, 53 in all, 65.6 % have degree distributions that follow a truncated or broad-scale power law [1324]. Another 22.2 % are scale-invariant, following a pure power law [1324]. The deviations are attributed to morphological mismatch and to partners active at different times, termed forbidden

links [1324].

In 29 complete plant–pollinator networks from arctic to tropical sites, connectance falls exponentially with richness [1325]. The fit is C = 13.83 exp[−0.003 (A + P)], with A animal and P plant species [1325].

Taking C in per cent, a network of 100 species has 13.83 × e^−0.3 = 10.2 % connectance, one of 500 species 3.1 % and one of 1,000 species 0.69 %. Highland networks above 1,500 m (22.04) have lower connectance than lowland ones [1325]. Oceanic islands are poorer in pollinators and more specialised, and tropical plants are not more specialised [1325].

Fifty-one pollination networks with about 10,000 species and about 20,000 links were analysed by simulated annealing [1326]. That is 10,000 / 51 = 196 species and 20,000 / 51 = 392 links per network on average.

All networks with more than 150 plant and pollinator species are modular, and networks with fewer than 50 species are never modular [1326]. Module number and size rise with network size, and each module holds one or a few convergent trait sets [1326]. “Only 15% of all species were structurally important to their network”, as hubs, connectors or both [1326].

The same nested form appears in every network above 28–50 species, and modules appear in every network above 150. The form holds at every size of web; only the number of its parts grows.

In models, highly connected nested architectures favour stability in mutualistic networks [1327]. Compartmentalised, weakly connected architectures favour stability in trophic networks, and a meta-analysis of large pollination and herbivory networks supports the split [1327].

Two large networks

Two well-sampled pollination networks give these counts [1328]:

Network	Plants	Animals	Links
Robertson, Illinois	456	1,428 (1,430 in results)	15,265
Clements & Long, Colorado	97	275	918

In Robertson, animals outnumber plants 1,428 / 456 = 3.13 to 1, links per species are 15,265 / 1,884 = 8.1, and connectance is 15,265 / (456 × 1,428) = 2.3 %. In Clements & Long the ratio is 275 / 97 = 2.84, links per species 918 / 372 = 2.5, and connectance 918 / (97 × 275) = 3.4 %. The source gives pollinators outnumbering plants by about 3 to 1 [1328].

In Robertson 11 % and in Clements & Long 18 % of plant species have a single visitor species [1328].

Losing partners

Removals in models

Simulated removals were run on the two networks [1328]. With pollinators removed at random, plant species are lost only after 70–80 % of the pollinators are gone [1328].

With the most-linked pollinators removed first, plant loss is roughly linear, “no worse than linear” [1328]. In Robertson the plants are nearly unaffected until the last ten most generalised pollinators, fewer than 1 % of animal species, are removed [1328]. Removing species of both sets by linkage collapses the networks after the top 22 % (Robertson) and 21 % (Clements & Long) of species [1328].

Measured dependence

A meta-analysis covers 126 exclusion experiments in 69 articles on 90 plant species [1329]. Excluding vertebrate pollinators reduces fruit or seed production by 63 % on average [1329].

The loss is 84 % with bats in the abstract and 83 % in the results, and 46 % with birds [1329]. It is 71 % in the tropics and 45 % at higher latitudes [1329].

Pollinating birds and mammals show a deteriorating Red List Index, with more species moving toward extinction than away [1330]. On average 2.5 species a year moved one Red List category toward extinction in recent decades [1330].

Coextinction

A probabilistic model covers 20 affiliate–host systems, among them fig wasps and figs, parasites and hosts, and butterflies and host plants [1331]. It gives 6,300 affiliate species coendangered with hosts listed as critically endangered, endangered or vulnerable [1331].

At least 200 affiliate species are historically extinct with their hosts in the groups studied [1331]. The army ant *Eciton burchelli* hosts at least 100 affiliate species, and the nomographic and probabilistic models agree, with Rc ≈ 0.99 [1331].

Coextinction may be the most common form of biodiversity loss in models, yet few historical or current cases are known [1332]. Of 457 parasite species modelled from 53,133 occurrences in eight clades, 5–10 % are committed to extinction by 2070 from climate alone [1232]. Up to 30 % of parasitic worms are committed when host coextinction is included [1232].

On virtual Earths driven to total extinction by heating or cooling, ecological dependencies amplify the direct environmental effects on the collapse of diversity “by up to ten times” [1333].

The loss of the great carriers

Megafauna extinction falls at 10–15 kyr before present (57.25–57.62), about 10,500 years ago (57.30) in the discussion of the same study [1297]. In simulation, extinct large frugivores often moved large seeds over a thousand metres, smaller frugivores a few hundred metres, and their long-distance events were up to ten times longer [1334].

Long-distance seed dispersal “contracted by at least two thirds” in South American Pleistocene assemblages [1334]. Introduced horses and cattle may have restored the

ranges of *Crescentia alata* and *Enterolobium cyclocarpum* [1298].

The capacity of animals to move nutrients away from concentration patches has fallen to about 8 % of its former value on land and about 5 % in the oceans [1104]. Marine mammals now move upward about 23 % of a former 340 × 10^6 kg of phosphorus a year [1104]. Seabirds and anadromous fish formerly moved about 150 × 10^6 kg of phosphorus a year from sea to land, now given as “less than 4 %” of that [1104].

Models built on more than 400 seed-dispersal interaction networks show that past defaunation cut by more than half the seeds dispersed far enough to track climate change [1335]. The fruit stays; its carriers go.

What this part of the history shows

Insects stand at 410.8–407.6 Ma (66.92) and the main flowering-plant clades at 135–130 Ma (65.91–65.88), about 276 Myr later. The proboscis of moths, about 241 Ma (66.44), is older than those clades. The bees, about 123 Ma (65.83), are 7–12 Myr younger.

Pollination opens once and fills many times. It is recorded first on gymnosperms, from about 165 Ma (66.09), in four modes, and passes to the angiosperms from 100–99 Ma. Today 87.5 % of about 352,000 angiosperm species are animal-pollinated, 89.5 % when recalculated, by 349,368 known pollinator species.

Ant dispersal has the same form at a smaller scale. It arose at least 101 times, the filling of one opened depth, and holds at least 11,000 species, about 109 per origin. These lineages hold 2.24 times the species of their sisters in 68 of 101 comparisons.

Some unions close as pairs. Figs and fig wasps, yuccas and yucca moths, perfume orchids and orchid bees, Darwin’s orchid and its hawkmoth, and ants and their fungi each hold for about 7.5 to at least 60 Myr. Here the form is that of the pair: two closures that hold only together.

Form and carrier separate. The fleshy seed appears in the Pennsylvanian, more than 218.9 Myr before the radiation of fleshy fruit. Its carriers change: a Permian reptile with nearly 60 seeds, a Cretaceous turtle with nearly 200 achenes, then birds, primates, bats, elephants and humans.

The megafaunal fruit outlasts its carriers. In Brazil 103 of 1,361 species still carry the syndrome, while all 13 Neotropical genera of animals above 1,000 kg are gone. The fruit stays closed; the dispersal it waits for, over 10^3–10^4 m, is reduced by at least two-thirds.

The networks have the form of a shared prefix. Three-quarters of 52 mutualistic networks are nested, with mean nestedness 0.84–0.85 against 0.69 in food webs. The specialist’s partners lie inside the generalist’s partners, as addresses inside longer addresses.

The same form holds at every size of web. Every seed-dispersal network above 28 species and every pollination network above 50 is nested, and every network above 150 species is modular. The largest network, 1,884 species, keeps a connectance of 2.3 %.

Context sets the values. Animal pollination covers 78 % of species in temperate and 94 % in tropical communities. Excluding vertebrate pollinators costs plants 71 % of their

seed in the tropics and 45 % elsewhere, and highland networks above 1,500 m (22.04) are less connected.

Reproduction itself loads and discharges. European beech holds its seed for years and releases it together across a continent, on average every 17.0 years (51.45) for the extreme years since 1773. Periodical cicadas hold underground for 13 or 17 years (51.21; 51.45) and emerge together.

15. Animals Spread Out

The first animals of chapter 7 lived in the sea as sponges, comb jellies, cnidarians, flatworms and worms in the mud. From the late Ediacaran and the Cambrian on, the bilateral body spread into every water and onto the land. This chapter follows nine groups along that spread: molluscs, annelids, chelicerates and myriapods, fishes and early chordates, crustaceans, insects, amphibians and reptiles, mammals and birds.

For each group it gives the first dated traces, the sizes and times of its members, its body plan, its energy and its numbers. Two kinds of measure run through all nine. The first is the count of repeated units within one species: plates, segments, legs, vertebrae.

The second is handedness: whether a body coils, crosses or turns to the right or to the left, and in what share of a population. Each such count is given as the record holds it, species by species.

Positions are those of chapter 1: an age of A million years is placed as a duration of $A \times 10^6 \times 3.15576 \times 10^7$ s. The basics of the strand, its trits, windows and rings, are those set out there.

Molluscs

Molluscs are the gastropods, bivalves, cephalopods, chitons and their allies. Zhang’s 2013 classification lists 118,061 described species, of which 33,084 are fossil [587]. The living species number 84,977, which is 5.1 % of all 1,659,420 described animals.

A separate review gives 70,000–76,000 described Recent molluscs; both counts stand [1336]. Cephalopods number “around 750 species” [1337].

First traces

Kimberella is known from “over thirty-five specimens” on the White Sea coast, with further finds from South Australia [1338]. It is reconstructed as a bilaterally symmetrical animal on the sea floor with a non-mineralised single shell, “mollusc-like” [1338]. One reading places it with the molluscs; another places it outside them [1338].

The White Sea beds are dated “558 ± 1 to 555.3 ± 0.3” Ma (positions 67.20 and 67.20), with “Numerous locomotion traces of *Kimberella*” [1339]. Scratch traces, *Kimberichnus teruzzii*, are attributed to *Kimberella quadrata*, “a large mollusc-grade bilaterian” [1340].

A molecular clock places crown Aculifera at “488 Ma (credibility interval: 517–453 Ma)”, positions 67.08, 67.13 and 67.01 [1341]. Crown chitons, Polyplacophora, are placed at 357 Ma (408–298; positions 66.80, 66.92, 66.63) and Chitonida at 272 Ma (336–201; positions 66.55, 66.74, 66.27) [1341]. Aculifera split from Conchifera in the Early Cambrian [1341].

The clock uses 11 fossil calibrations [1341]. The bivalve–gastropod calibration has a

minimum of 530 Ma (67.16), set by the stem gastropods *Pelagiella* and *Aldanella*, and a maximum of 543 Ma (67.18) [1341]. Crown Mollusca has a calibration maximum of 549 Ma (67.19) from the Nama Group; the root prior is 600 + 100 Ma (600 Ma at 67.27) [1341].

A possible earliest cephalopod is known from four specimens from the uppermost Bonavista Formation at Bacon Cove, Newfoundland, about 522 Ma (67.14), upper Terreneuvian [1342]. The paper calls it “potential”; the earlier oldest cephalopod, *Plectronoceras cambria*, is “middle late Cambrian” [1342].

Crown coleoids were dated with 180 genes in 26 species [1343]. The vampire squid and dumbo octopus lineages are placed at 242 ± 38 Ma (66.44), and the ten-armed squids diversified in the Jurassic [1343].

The largest-known ammonite lineage, *Parapuzosia*, reaches about 1 m in diameter in the early Santonian and 1.5–1.8 m in the middle early Campanian [1344].

Sizes

What	Size	Position	Source
Angustopila psammion, shell height	0.46–0.57 mm	8.39–8.59	[1345]
A. psammion, shell width	0.6–0.68 mm	8.63–8.75	[1345]
Squid giant axon, diameter (August–May)	383–506 µm	8.23–8.48	[1346]
Possible Cambrian cephalopod, width; largest visible height	about 3 mm; about 14 mm	10.10; 11.50	[1342]
Graneledone egg capsule at laying	about 1.5 × 0.5 cm	11.56 × 10.56	[1347]
Graneledone egg capsule before hatching	3.3 × 1.6 cm	12.28 × 11.62	[1347]
Colossal squid, lower rostral beak	42.5 mm	12.51	[1348]
Graneledone boreopacifica, mantle length	21.2 cm	13.97	[1347]
Parapuzosia, early Santonian; early Campanian	about 1 m; 1.5–1.8 m	15.39; 15.76–15.92	[1344]
P. seppenradensis, Seppenrade specimen (1895)	1.74 m	15.89	[1344]
Colossal squid, mantle length; total length	2.5 m; 4.2 m	16.22; 16.69	[1348]
Colossal squid, first estimates of total length	8–10 m	17.28–17.48	[1348]

Angustopila psammion from northern Laos is “the new global record-holder of the tiniest land snail title” [1345]. The largest living mollusc in the record is the colossal

squid at Te Papa, 495 kg [1348]. Its total length is 4.2 / 0.00046 = 9,130 times the smallest shell height, a span from 8.39 to 16.69 on the ladder.

Times

What	Duration	Position	Source
Octopus vulgaris heartbeat at rest (50–40 beats min⁻¹)	1.2–1.5 s	33.32–33.52	[1349]
Octopus active-sleep bout; quiet-sleep bout; interval between active bouts	75 ± 28 s; 50.5 ± 16.43 min; about 60 min	37.08; 40.45; 40.61	[1350]
Euprymna symbiont regrowth after dawn; entry after hatching	4–6 h; within 12 h	41.87–42.24; 42.87	[1151]
Aplysia long-term habituation retained, minimum	3 weeks	46.27	[1351]
Colossal squid frozen; earlier octopus brooding record	14 months	49.01	[1347, 1348]
Bivalve maxima: *Tivela*, *Argopecten*; *Mytilus californianus*; *Thyasira*; *Corbicula*, *Yoldia*	2; 3; 3.2; 4 years	49.50; 49.87; 49.93; 50.13	[1352]
Graneledone boreopacifica, egg brooding	53 months	50.22	[1347]
Arctica islandica, maturity (female; male)	4,562; 4,780 days	51.17; 51.21	[1352]
Mesodesma, *Geukensia*, *Mytilus edulis*; *Architeuthis dux*	24; 35 years	51.76; 52.11	[1352]
Cyrtodaria siliqua; *Panopea generosa*	105; 168 years	53.11; 53.53	[1352]
Arctica islandica “Ming”, maximum lifespan	507 years	54.54	[1352]
Clausiliid coiling reversals, one per	3.2–4.6 Myr	62.50–62.83	[1353]
Period holding at least 14 clausiliid reversals	more than 65 Myr	65.25	[1353]

Graneledone boreopacifica brooded its eggs from May 2007 to September 2011, the longest egg-brooding of any animal, 1,397 m below the sea surface (21.98) at 2.8–3.4 °C [1347]. The clutch held 155–165 eggs; the previous record, *Bathypolypus arcticus*, is 53 / 14 = 3.8 times shorter [1347].

The octopus heart beats about 40–50 times a minute at rest near 22 °C, with a Q10 of about 3 [1349]. Squid giant axons conduct at 9.56 m s⁻¹ at 5 °C and 18.94 m s⁻¹ at 20 °C [1346]. Octopuses have 10 ± 3.5 active-sleep and 12 ± 3 quiet-sleep bouts per 24 h

[1350].

Repeated units

A normal chiton has 8 shell plates. Abnormal shares in four Chilean chitons are low [1354]:

Species	Abnormal / examined	Share	Plates in the abnormal case
Tonicia fremblyana	1 / 290	0.34 %	five or six
Chiton magnificus	1 / 750	0.13 %	—
Plaxiphora mercatoris	1 / 165	0.61 %	seven
Chiton granosus	1 / 1,108	0.09 %	seven

Worldwide, six-plate chitons number “merely around 40 cases” and seven-plate chitons “several hundred” [1354]. The eight-plate body holds in 164 / 165 = 99.39 % to 1,107 / 1,108 = 99.91 % of each sample (computed); the variants carry one to three plates fewer.

The arm cord of *Octopus bimaculoides* holds about 7.5 nerve segments per sucker: 7.64 in arm 1 and 7.88 in arm 2 [1355]. The squid *Doryteuthis pealeii* has about 4.5 [1355].

Handedness

A snail shell coils to the right, dextral, or to the left, sinistral. Regional land-snail faunas give these shares [1353]:

Region	Species	Dextral	Sinistral	Sinistral without Clausiliidae	Reversals
Europe	331	84.0 %	16.0 %	1.1 % of 281	4
Turkey	541	75.2 %	24.8 %	5.3 % of 430	14
North America north of Mexico	689	99.4 %	0.6 %	—	2
Japan	861	82.0 %	18.0 %	0.8 % of 712	3

The reversals fall by family: in Europe Clausiliidae 1, Vertiginidae 2 and Enidae 1; in Turkey Clausiliidae 1, Orculidae 2, Vertiginidae 2 and Enidae 9 [1353]. In North America they lie in Gastrocoptidae and Pupillidae, and in Japan in Clausiliidae and Camaenidae [1353].

Sinistral species per family are, in Europe, Vertiginidae 2 of 22 and Enidae 1 of 5 [1353]. In Turkey they are Vertiginidae 2 of 10, Orculidae 4 of 38 and Enidae 17 of 92 [1353]. In North America they are Gastrocoptidae 1 of 25 and Pupillidae 3 of 11, and in Japan Camaenidae 6 of 196 [1353].

Clausiliid reversals come one per 3.2–4.6 Myr (62.50–62.83), at least 14 of them within more than 65 Myr (65.25) [1353]. Of 838 genera, 33 hold both dextral and sinistral species, 33 / 838 = 3.9 % [1356]. Sinistrals are “much less than 10%” of snail species, and “Over 90% are dextral” [1357, 1358].

Sinistral coiling is uncommon, especially in marine snails, while fossil cephalopods are roughly evenly split [1359]. In *Satsuma*, 75 species, the sinistral species lie in three

clades of independent origin [1356].

Against the snail-eating snake *Pareas iwasakii*, 87.5 % of sinistral snails survived and no dextral snail did [1356]. The snake has about six more teeth on its right mandible than on its left [1356].

Amphidromus. On Pulau Kapas, Malaysia (2.3 × 1.0 km; positions 22.43 × 21.67), 56 sites of 25 m radius (18.32) were sampled in 2013 [1360]. Of 1,392 *Amphidromus inversus*, 914 were sinistral: a pooled share of 0.65, and 478 / 1,392 = 0.343 dextral [1360].

Per-site sinistral shares run 0.30–0.85 in the abstract and 0.36–0.83 for samples above 9 in the results [1360]. Two earlier sites were “stable at 65 % sinistrals” [1360]. Coiling follows “delayed, single-gene inheritance and full dominance”, and the subgenus holds “circa 35 species”, “almost all chirally dimorphic” [1360].

A Malaysian *A. inversus* population is 36 % dextral; of almost 700 marked snails, almost two-thirds had moved a year later [1361]. The marking period was 7 days (45.27) and the recapture interval 1 year (48.87) [1361]. In *Amphidromus* the two forms occur “in roughly equal numbers”, and opposite pairs mate more often than chance [1362].

At Nam Yuen, Thailand, *A. inversus annamiticus* in October 2010 gave 21 dextral and 14 sinistral living snails, plus 2 and 2 empty shells [1363]. The living sinistral share is 14 / 35 = 40 %. Earlier, more than 2,200 specimens from 16 Thai localities were all dextral [1363].

In *A. martensi* on Borneo the two forms show no consistent clustering [1364].

Partula. *Partula suturalis* on Moorea gave 906 sinistral and 621 dextral snails from 32 populations, 906 / 1,527 = 59.3 % sinistral [1357]. Populations 121, 124 and 125 are 97.9 %, 97.3 % and 97.2 % sinistral [1357]. Clines about 0.5–1 km wide (21.04–21.67) separate purely sinistral from purely dextral populations [1357].

Opposite-coil pairs copulate about 20 % as often as same-coil pairs [1357]. Hatching is 50.4 ± 2.8 % in dextral against 47.3 ± 2.2 % in sinistral snails, not a significant difference [1357]. At locus H the sinistral allele is dominant to the dextral one, with maternal expression delayed one generation [1365].

Lymnaea. A pond at Neustadt an der Donau, 112.8 m² and at most 1.1 m deep (15.47), gave these counts of the pond snail *Lymnaea stagnalis* [1366]:

Year	Sinistral	Dextral	Phenotypic frequency	Sinistral allele frequency
1991	3	not given	—	—
2000	7	about 1,884 (estimated)	0.0037	0.061
2001	5	201	0.024	0.156
2002	0	349	0	—
2007	no *L. stagnalis* found	—	—	—

The frequencies check as 7 / 1,891 = 0.0037 and 5 / 206 = 0.024. Near Aerschot, Belgium, a pond under 100 m² held 7 sinistrals and 23 dextrals in 1871, 7 / 30 = 23 %,

and 20 sinistrals in 1872 [1366]. In *Lymnaea* the dextral allele is dominant, with maternal single-locus inheritance [1366].

Offspring of sinistral snails are about 62 % viable in the first generation against 96 % from dextral stock; in the second, hatching is 43 % against 88 % [1357]. Sinistrals in *L. peregra* and *L. stagnalis* are “extremely rare in nature” [1353].

In *Lymnaea stagnalis* handedness is set by the mother before or during early cleavage [1367]. It is prepared from the 1-cell stage and fully fixed only at the third cleavage, the 4- to 8-cell stage [1367].

The mRNA of the gene *Lsdia1* is 40.4 times higher in dextral than in sinistral 1-cell embryos [1367]. The sinistral strain carries c.del184C in exon 3 of that gene, a frameshift after amino acid 62 [1367].

Quaternary and modern Europe. Reversed coiling is generally “extremely low (zero to <1%)” [1358]:

Species or site	Sinistral / total	Share
Aegopinella nitidula	1 / 6,814	0.01 %
Acicula fusca (four samples)	1 / 227; 1 / 37 (7650 ± 80 ^{14}C BP); 2 / 270; 3 / 597	0.4 %; 2.7 %; 0.74 %; 0.5 %
Lauria cylindracea	1 / 76	1.3 %
Discus rotundatus	1 / 849	0.1 %
Nesovitrea hammonis	1 / 1,127	0.08 %
Clausilia bidentata	1 / 24	4.1 %
Trochulus hispida	2 / 1,694	0.1 %
Cochlicopa, Krasniy Yar, Siberia (more than 6000 ^{14}C BP)	38 / 385; highest sample 13 / 52	9.8 %; 25 %
Cochlicopa, Basovo; Burdukovo	0 / 1,923; 0 / 2,116	0
Cepaea nemoralis, Nottingham 1976, living	13 / 20	65 %
Cepaea nitens, Teguldet, modern	6 / 10	60 %

Values above about 1 % are “essentially statistical artefacts” in the source’s reading; Krasniy Yar holds 12 samples, eight of them above 10 % [1358]. Four Turkish species and *Alopia* are dimorphic without shares given [1353].

Here the form is that of one direction. Every shell has one direction, and the rule is symmetric: it does not say which direction wins. The faunas are 75.2–99.4 % dextral by region, yet one *Partula* population is 97.9 % sinistral.

The net keeps the direction of what was laid down first. In the record, majorities hold: two *Amphidromus* sites stay at 65 % sinistral, and pure sinistral and pure dextral *Partula* populations meet only in clines 0.5–1 km wide.

The coil is set by the mother. A snail’s coil is written by its mother’s genes, not its own, so that each shell carries the order of the generation before it.

Genes, energy and numbers

Pinctada fucata has “all 11 Hox genes” on three scaffolds, and *Octopus bimaculoides*

eight of 11 identified, on eight [594]. *Crassostrea gigas* lacks *Antp*, with Hox genes on four scaffolds; the *Lottia gigantea* cluster is “intact” [594]. The octopus genome shows expanded protocadherins and C2H2 zinc-finger genes, and coleoids edit RNA at “tens of thousands” of sites [1368, 1369].

Cephalopod oxygen consumption, standardised to 5 °C with Q10 2.5, scales as follows; whole-animal exponents are 1 + b [1370]:

Taxon	b (mass-specific)	N	1 + b
All Cephalopoda	−0.20 ± 0.038 (r^2 = 0.13)	218	0.80
Loliginidae	−0.084 ± 0.010	51	0.92
Ommastrephidae	−0.077 ± 0.015	20	0.92
Gonatidae	−0.02 (n.s.)	24	0.98
Octopodidae	−0.27 ± 0.054	15	0.73
Histioteuthidae; Cranchiidae; Bolitaenidae; Vampyroteuthidae	−0.24; −0.19; −0.25; −0.23	—	0.76; 0.81; 0.75; 0.77
Loligo forbesi; *Dosidicus gigas*	−0.09; −0.06	—	0.91; 0.94
Octopus vulgaris	−0.10 and −0.28	—	0.90 and 0.72

The constants at 1 g run from 8.20 (Loliginidae) to 0.14 µmol O_2 g^{-1} h^{-1} (Vampyroteuthidae), 8.20 / 0.14 = 59-fold [1370]. The source gives “more than 200-fold variation in metabolic rates independent of body mass and temperature” [1370].

Resting *Octopus vulgaris* at 21 ± 2 °C uses 0.06–0.11 ml O_2 g^{-1} h^{-1}, in nine animals of 220–710 g [1349]. A 500 g animal at 22 °C uses about 0.08 ml O_2 g^{-1} h^{-1}, or 80 ml kg^{-1} h^{-1} [1349]. Molluscs hold 0.2 Gt C of biomass, equal to annelids and terrestrial arthropods [235].

Fossil species are 33,084 / 118,061 = 28.0 % of Zhang’s molluscs, and the total is 7.1 % of all described animals [587]. The review gives 43,600 ± 900 marine species, published estimates of 34,000–120,000, and about 200,000 often cited with undescribed species [1336].

Terrestrial gastropods number 28,895 ± 630 accepted species at the end of 2021, a minimum estimate [1371]. MolluscaBase listed 27,050 on 27 July 2021 and 24,202 on 11 August 2020 [1371]. Cephalopods, at about 750, are 0.9 % of the living molluscs.

Annelids

Annelids are the segmented worms: polychaetes, the clitellates (earthworms and leeches) and their allies. Zhang’s 2013 classification lists 17,426 described species, of which 38 are fossil [587]. Polychaetes number 11,456 valid Recent species, and Clitellata “more than 5000 species” [1016, 1372].

First traces

Phragmochaeta canicularis is known from about 40 specimens from the Sirius Passet Lagerstätte, Peary Land, North Greenland [1373]. Its age is “likely lower to middle Atdabanian”, and it is described as “the oldest known polychaete” [1373]. It has about 20 chaetigers, each with notochaetae and neurochaetae [1373].

At that time the Chengjiang Lagerstätte had “no reliable annelid records” [1373]. *Dannychaeta tucolus* from the early Cambrian Canglangpu Formation of South China lived in organic tubes and had a spade-shaped head with palps and biramous parapodia [1374]. It resembles living Magelonidae and is “the oldest polychaete that clearly belongs to crown annelids” [1374].

A phylogenomic study of earthworms used a minimum of 520 Ma (67.14) for crown Annelida [1017]. It used a leech cocoon fossil of 201 Ma (66.27) and 67–97 Ma (65.27–65.61) for Hormogastridae [1017]. It dates earthworm clade splits to 161–186 Ma (66.07–66.20) and to 165 ± 22 Ma (66.09) [1017].

A study of 74 taxa places the most recent common ancestor of clitellates in fresh water in the Devonian, roughly 419–359 Ma (66.94–66.80) [1000]. A later analysis with 15 fossil calibrations, a conference abstract, places the earthworm crown at the Carboniferous–Permian boundary, 298.9 Ma (66.63) [1001].

Websteroprion armstrongi comes from the Lower–Middle Devonian Kwataboahegan Formation of Ontario, “about 400 million years ago” (66.90) [1375]. Its maxillae exceed 1 cm, “the largest polychaete jaws known from the fossil record”, and its body length is estimated at over 1 m [1375].

Myelin arose independently in polychaetes and in oligochaetes, as in vertebrates and crustaceans [1376]. Earthworm myelin has “60 to 200” layers [1376].

Sizes

What	Size	Position	Source
Usual fossil scolecodonts (jaws), lower end	0.1 mm	7.00	[1375]
Diurodrilus minimus, body length	ca. 250–450 µm	7.84–8.37	[1377]
Platynereis dumerilii, three-segmented larva	about 300 µm	8.00	[1378]
Helobdella fertilised egg, diameter	about 400 µm	8.26	[1379]
Usual fossil scolecodonts, upper end	2 mm	9.73	[1375]
Aporrectodea caliginosa, adult width	2–5 mm	9.73–10.56	[1380]
Octodrilus complanatus cocoon	6.9 × 4.8 mm	10.86 × 10.53	[1381]
Websteroprion maxillae	over 1 cm	11.19	[1375]
Amynthas srinan, length	35–47 mm	12.33–12.60	[1382]
Aporrectodea caliginosa, adult length	36–83 mm	12.36–13.12	[1380]

(58 adults)			
Amynthas tontong, length	39–53 mm	12.43–12.71	[1382]
Amynthas borealis, length	42–54 mm	12.50–12.73	[1382]
Saccocirrus major (largest interstitial annelid)	up to 70 mm	12.97	[1377]
Amynthas phatubensis, length	80–148 mm	13.09–13.65	[1382]
Websteroprion armstrongi, estimated body length	over 1 m	15.39	[1375]
Burrow length per core after 6 weeks, *Lumbricus terrestris*	9.2 m	17.41	[1088]
Burrow length per core after 6 weeks, *Aporrectodea nocturna*	21.2 m	18.17	[1088]

The estimated fossil length of over 1 m is 1 / 0.00025 = 4,000 times the 250 µm *D. minimus*; the 148 mm *Amynthas* is 592 times that length. *Octodrilus complanatus* is mature at 6.1 ± 0.2 g and reaches 8.2 ± 0.2 g; hatchlings weigh 82 ± 3 mg and cocoons 92 ± 4 mg [1381].

Times

What	Duration	Position	Source
Platynereis at 18 °C: hatching; plankton phase; on the sea floor; first feeding	24 h; about 2 days; about 3 days; 6 days	43.50; 44.13; 44.50; 45.13	[1378]
Platynereis posterior segment addition begins	about 2 weeks	45.90	[1378]
Octodrilus cocoon production after mating	34 ± 3 days	46.71	[1381]
Burrowing experiment	6 weeks	46.90	[1088]
Octodrilus cocoon incubation (range)	66 ± 2 days (50–70)	47.31 (47.06–47.37)	[1381]
Platynereis juveniles feed and grow, at least	2 months	47.24	[1378]
Platynereis egg to egg, shortest; regularly	11 weeks; 3 months or longer	47.45; 47.61	[1378]
Lumbricus terrestris hatching after deposition	132–731 days	47.94–49.50	[1089]
Octodrilus sexual maturity at 20 °C	150 days	48.06	[1381]
Octodrilus stationary growth from	day 210	48.37	[1381]
L. terrestris hatching	about 12 months	48.87	[1089]

peaks, apart			
Escarpia laminata, regular age	100–200 years	53.06–53.69	[1383]
Lamellibrachia luymesi, longevity	250 years	53.90	[1384]
Escarpia laminata, *Seepiophila jonesi*, longevity	300 years	54.06	[1384]

At 6 days the *Platynereis* larva has “no more than 12,000 cells comprising hundreds of cell types” [1378]. Cephalic metamorphosis comes with the 6th segment; gonial clusters appear at 35–40 segments, gamete growth at about 50 and maturation at about 70 [1378]. Egg to egg takes “as short as 11 weeks” and “regularly takes 3 months or longer”, and the animal breeds once and dies [1378].

Octodrilus complanatus grows 43.9 ± 1.8 mg a day before maturity and 27.6 ± 2.8 mg after; hatchability is 55 %, with one hatchling per cocoon [1381]. Cocoon output is 52 per worm per year in the abstract and 0.82 ± 0.14 per week in the results, that is 42.6 per year; both stand [1381].

Lumbricus terrestris at 15 °C produces 15.1–32.2 cocoons per individual per year, with a viability of 88–94 % [1089]. The cold-seep tubeworm *Escarpia laminata* “regularly reaches 100–200 years”, some individuals exceed 300 years, and the populations’ mortality rate is 0.67 % [1383].

Repeated units

In leeches “the posterior growth zone invariably generates exactly 32 segments” [1379]. Each midbody segment has one ganglion, and rostral ganglia R1–R4 and caudal ganglia C1–C7 fuse into head and tail brains [1379]. The within-species range of segment number in leeches is zero: 32.

The growth zone holds five bilateral pairs of teloblasts, 10 in all [1379]. The M and O/P teloblasts make one blast cell per segment, N and Q two [1379].

The fossil *Phragmochaeta* has about 20 chaetigers [1373]. *Platynereis dumerilii* has 3 segments in the young larva and about 70 at maturation, a rise of 70 / 3 = 23 times [1378]. A 72-hour larva (44.50) has three chaetigerous segments, a cryptic anterior segment and a pygidium [1385].

In the peregrine earthworm *Aporrectodea caliginosa*, segment counts were read for all 58 adults of three genetic lineages [1380]:

Lineage	n	Segment counts	Mean
1	7	92, 106, 108, 111, 114, 120, 121	110.3
2	21	111–177	152.7
3	30	114–166	137.0
All	58	92–177	139.5

A single *A. trapezoides* specimen has 165 segments [1380]. The 58 counts hold 43 distinct values; 130 and 131 occur three times each, and 133, 147, 155 and 167 twice each [1380]. The smallest step between two observed counts is 1 in every lineage, and

the full range spans 177 − 92 = 85 segments.

Four Thai *Amynthas* species give these counts, holotype plus paratypes [1382]:

Species	n	Segments	Holotype	Span
A. phatubensis	22	85–114	108	29
A. tontong	4	71–80 (paratypes 71–74)	80	9
A. borealis	9	77–89 (paratypes 77–87)	89	12
A. srinan	29	52–78	77	26

The same segmental unit repeats along the worm in both groups. In leeches the number of units is closed at 32; in earthworms it runs over a range within the species, from 9 to 85 segments wide.

Capitella sp. I has 11 Hox genes in 11 paralog groups, at least 8 of them in one cluster transcribed in the same orientation [1386]. Three, *lab*, *pb* and *Hox3*, are expressed before segments form [1386]. The leech *Helobdella* has 19 Hox genes; the ancestor of Sedentaria and Errantia is inferred with all 11 [594, 1379].

The 72-hour *Platynereis* larva has 8,852 cells with a soma; one count gives 892 neurons in 180 types and 2,905 non-neuronal cells in 90 types [1387]. Another gives “over 9000” cells, 202 neuronal and 92 non-neuronal types; both stand [1385]. Ventral nerve cords “likely evolved convergently” [596].

Handedness

Spirorbin worms build coiled tubes. “Direction of coiling seems to be constant for each species in the Australian material” [1388]. *Janua (Dexiospira) steueri* “occurs with both dextral and sinistral coiling in certain Red Sea locations” [1388].

A serpulid tube worm is cited as the first annelid known to cleave sinistrally [1357]. In annelids the direction is held at the level of the species, with one species that holds both.

Energy and numbers

The standard metabolic rate of the ragworm *Hediste diversicolor* was measured in 108 worms of 4–94 mg dry mass at 11, 17, 22 and 27 °C [1389]. It scales with dry mass at 0.80 ± 0.06 (R^2 0.80) and with wet mass at 0.78 ± 0.06 [1389]. It scales with segment number at 1.16 ± 0.20 (R^2 0.46) and with total length at 1.30 ± 0.13 [1389].

The mass-specific rate is 6.85, 10.41, 12.91 and 20.90 µmol O_2 g^{-1} dry mass h^{-1} at the four temperatures, with a reference value of 12.33 at 20 °C [1389]. From 11 to 27 °C the rate rises 20.90 / 6.85 = 3.05-fold; Q10 is 2.00–2.01 in the results and 1.9 in the discussion [1389].

Using the paper’s own conversion of 0.439 J per µmol, the reference rate is 12.33 × 0.439 = 5.41 J g^{-1} h^{-1}, about 1.5 W kg^{-1} dry mass [1389]. The earthworm *Dendrobaena mrazeki* respires below 70 µl O_2 g^{-1} h^{-1} over 5–35 °C, “lower than in other earthworm species”, with Q10 about 1.2–1.7 [1390].

After 6 weeks *Aporrectodea nocturna* had made 21.2 / 9.2 = 2.30 times the burrow

length of *L. terrestris* [1088]. Annelids hold 0.2 Gt C [235].

Annelids are 17,426 / 1,659,420 = 1.05 % of described animals. Polychaetes, in 1,417 genera and 85 families, were described by 835 first authors, with a peak in the 1960s; they are forecast at 14,100 species by 2050 and about 16,700 by 2100 [1372].

Earthworms number about 5,738 valid species and subspecies, 5,406 species and 332 subspecies, in 23 families and 382 genera; total richness is “well over 8,000” [1083]. Megascolecidae hold 2,208 species, Acanthodrilidae 746 and Lumbricidae 615 [1083]. A 2012 count gives about 6,000 names, of which 3,000–3,500 are valid [1085].

Self-fertilisation among clitellates is documented only in three *Helobdella* species [1379].

Chelicerates and myriapods

The chelicerates are the horseshoe crabs, the extinct sea scorpions, the arachnids and the sea spiders [1391]. The myriapods are the centipedes, millipedes, pauropods and symphylans [1391]. In the 2013 census Arthropoda hold 1,302,809 species, Chelicerata 115,992 (8.9 % of arthropods) and Myriapoda 12,010 (0.92 %) [1391].

First traces

Stem chelicerates occur in the middle Cambrian Burgess Shale; *Habelia optata* and *Sanctacaris uncata* form the order Habeliida [1392]. The great-appendage arthropod *Alalcomenaeus* from Chengjiang, about 520 Ma (67.14), shows a “chelicerate neural ground pattern” [1393]. It has one optic neuropil, four head ganglia and eight further ganglia in an eleven-segment trunk [1393].

The oldest horseshoe crab, *Lunataspis aurora*, Upper Ordovician, about 445 Ma (67.00), comes from Manitoba and carries lateral compound eyes [1394]. The oldest scorpion yet reported is about 437.5–436.5 Ma (66.98), Llandovery, Telychian, from two substantially complete specimens of the Waukesha Biota, Wisconsin [974].

The first land arachnids with book lungs are trigonotarbids of the Ludlow, about 420 Ma (66.94) [975]. The earliest land animals with direct evidence come from the Upper Silurian of Shropshire, about 414 Ma (66.93): at least two centipedes and one trigonotarbid [976]. Acariform mites, including fungus feeders, and a harvestman with the earliest preserved tracheae occur in the Rhynie chert, 410.8–407.6 Ma (66.92) [598].

Oribatid mites at Gilboa, New York, are Devonian: 14 fossils and 2 described species, which “roughly double the known age of the group” [996]. Spiders and scorpions descend from a polyploid ancestor that lived more than 450 Ma (67.01); the conservative floor for that whole-genome duplication is 430 Ma (66.97) [1395].

The molecular clock places the myriapods at about 500 Ma (67.10), in the late Cambrian; the earliest confirmed fossils are about 425 Ma (66.95) [975]. The gap is 500 − 425 = 75 Myr (65.38). Uranium–lead ages place Kerrera, with kampecarid millipedes, at about 425 Ma, Cowie Harbour at about 414 Ma (66.93) and Rhynie at about 407 Ma (66.92) [975].

Pneumodesmus newmani is the oldest millipede with spiracles [978]. Spores gave it an age of about 427 Ma (66.96); uranium–lead maximum depositional ages give 413.7 ± 4.4 and 414.3 ± 7.1 Ma (66.93), in the lowermost Devonian [978]. The two ages differ by about 13 Myr (63.78); both stand.

Burrows of *Scoyenia beerboweri* in Late Ordovician soils older than 443.8 Ma (66.99) are “most likely millipedes” [973]. The centipede fossil record spans 420 million years (66.94), and a scutigeromorph centipede occurs at Rhynie [598, 977].

Sizes

What	Size	Position	Source
Rhynie chert mites, 5 species	0.29–0.45 mm	7.97–8.37	[1396]
Eumillipes persephone, width, male; female	0.92 mm; 0.95 mm	9.02; 9.05	[1397]
Palaeocharinus rhyniensis, *P. hornei* (trigonotarbids)	up to 4 mm	10.36	[1396]
Palaeocharinus tuberculatus	at least 6 mm	10.73	[1396]
Larger unnamed Rhynie trigonotarbids	14–20 mm	11.50–11.83	[1396]
Scolopendropsis duplicata, 39-segmented	31–74 mm	12.22–13.02	[1398]
Scolopendropsis duplicata, 43-segmented	53–78 mm	12.71–13.06	[1398]
Eumillipes persephone, length, male; female	54.7 mm; 95.7 mm	12.74; 13.25	[1397]
Arthropleura, partial remains	76 × 36 cm	15.14 × 14.46	[1009]
Arthropleura, body width	about 55 cm	14.84	[1009]
Jaekelopterus rhenaniae, chelicera	46 cm	14.68	[1399]
Jaekelopterus rhenaniae, estimated body length	about 2.5 m	16.22	[1399]
Arthropleura, estimated body length	up to 2.63 m	16.27	[1009]

Two claims to the largest arthropod stand. A 46 cm chelicera of the Early Devonian sea scorpion *Jaekelopterus rhenaniae* gives an estimated body length of about 2.5 m [1399]. The Carboniferous millipede *Arthropleura* is estimated at up to 2.63 m and about 50 kg; its Serpukhovian remains from Northumberland carry 12–14 anterior tergites [1009].

Eumillipes persephone was collected 15–60 m below ground in Western Australia [1397]. The female’s length is 95.7 / 0.95 = 101 times its width.

Times

What	Duration	Position	Source
Damon annulatipes, laboratory period with falling rate	2 weeks	45.90	[1400]
Oromurcia sudetica, adult lifespan	1–2 yr	48.87–49.50	[1081]
Oromurcia sudetica, egg to adult	2–4 yr	49.50–50.13	[1081]
Gaius villosus, oldest recorded spider	43 yr	52.29	[1401]

The longest-lived spider is a female *Gaius villosus* that died aged 43 years, from an annually monitored population near Tammin, south-western Australia [1401]. The alpine oribatid mite *Oromurcia sudetica* takes at least two and up to four years from egg to adult, and its adults live one to two years [1081].

Repeated units

Stem chelicerates have three tagmata and a prosoma of 7 segments, with 5 pairs of large gnathobasic basipods [1392]. In *Lunataspis* the abdominal tergites are fused into two sclerites; the mesosoma has six or seven fused segments and the metasoma three reduced ones [1394].

The house spider *Parasteatoda tepidariorum* has all ten arthropod Hox classes in two clusters, and “The only Hox gene not found in duplicate is ftz” [1395]. That gives $10 \times 2 - 1 = 19$ Hox genes. Scorpions likewise carry nearly all Hox genes in two copies, while the tick has one copy of each; the spider genome assembly is 1,443.9 Mb with 27,990 genes [1395].

Centipedes carry 15 to 191 leg pairs, with “invariably odd leg-bearing segments” [977]. Scutigeromorpha, Lithobiomorpha and Craterostigmomorpha have 15 leg pairs, Scolopendromorpha 21 or 23 and Geophilomorpha 27 to 191 [1402].

All families of Geophilomorpha show variation in segment number within species, whereas most arthropod classes and orders contain species with none [1403]. Across arthropods segment number varies “more than 20-fold” [1403]. In *Strigamia maritima* a warmer embryo gives more segments; embryos at 18 °C and 10 °C differ by about 1.5 segments in the mean [1402, 1403].

The centipede counts within species are these:

Species	Counts observed	Sample	Source
Strigamia maritima, adults (UK)	43–53 leg-bearing segments; Brora modal male 47, female 49; means male 46.7 (n = 72), female 48.9 (n = 72); cultured adults all male 47, all female 49 (n = 14)	Brora, Scotland	[1404]
S. maritima, embryos	41–47 visible segments, odd and even; male modal 43, female modal 45 (57 embryos: 29	13 clutches	[1404]

	male, 28 female); means 42.7 (n = 34) and 44.8 (n = 37)		
Geophilus flavus (Sognefjord)	female 53, 55, 57; male 49, 51, 53, 55; site means female 54.33–55.45, male 51.79–53.12	421 adults (189 female, 232 male), 8 sites, 2009	[1402]
Scolopendropsis duplicata	39 or 43; at least 13 specimens with 39, at least 8 with 43, 3 unresolved (24 in all)	Brazil, museum lots	[1398]
Scolopendropsis bahiensis	21 or 23 (type material 23; most of the range 21)	—	[1398]

In *S. maritima* embryos at stage 6.1 in culture, males show 42–43 and females 44–45 segments [1404]. Adult counts in *S. maritima* and *G. flavus* differ by 2, odd numbers only; embryonic counts differ by 1. “Females of any given population typically have a modal number of segments that is two higher than males” [1404].

In *S. maritima* the female mean exceeds the male mean by 48.9 − 46.7 = 2.2 segments. In *G. flavus* the site means differ by about 1.5 segments over about 1.4 °C [1402].

S. duplicata counts differ by 4 and *S. bahiensis* counts by 2. *S. duplicata* has double the segment number of its relatives and of all other known Scolopendromorpha, which number “700+” species [1405]. Doubling of segment number in Scolopendromorpha is known from this one case [1398, 1405].

Millipedes grow by anamorphosis, adding rings at moults; hatchlings usually have three leg pairs, rarely four, exceptionally more [1406]. Growth either stops at a final number or continues “indefinitely until the millipede dies” [1406].

In Polydesmida the last ring with legs added in stadia I to VIII is 4, 6, 8, 11, 14, 16, 17, 18, in steps of 2, 2, 3, 3, 2, 1, 1 [1406]. Most species end with 18 legged rings plus 1 legless ring [1406].

The julidan *Ussuriiulus pilifer* has a largest female of 51 legged + 2 legless rings; the holotype male has 47 rings, and stadium X has 39 + 2 [1406]. Inferred stadia run 4+2, 6+3, 9+3, 12+4, 16+5, 21+5, 26+5, 31+5, 36+3, with outliers 37 + 5/6 and 27 + 3 [1406]. The legged steps between these stadia are 2, 3, 3, 4, 5, 5, 5, 5.

Stadium II is 6 + 4 or 6 + 5 in all other studied Julida, and 6 + 3 in *Nemasoma varicorne*, *Nopoiulus kochii* and 0.03 % of *Choneiulus palmatus* [1406]. *Koiulus interruptus* reaches 46 + 3 at most, and adult Spirostreptidae normally have 53 + 0 rings, as in *Sagmatostreptus strongylopygus* [1406].

Eumillipes persephone holds the record for legs [1397]:

Specimen	Sex	Segments	Legs
T147124	female	330	1,306
T146684	female	253	998
T147100	male	208	818
T147101 (holotype)	male	198	778

The four segment counts span 330 − 198 = 132. Super-elongation, above 180 segments, evolved repeatedly in millipedes [1397]. The previous record holder, *Illacme plenipes*, has 192 segments and 750 legs; its 17 specimens come from 3 localities within 4.5 km² [1397, 1407].

A homeotic *Ommatoiulus moreleti* male at stadium 10 had 46 legged rings plus the telson [1408]. It carried six extra pairs of gonopods on rings 8, 15 and 16, repeating “after exactly 16 leg positions” [1408]. The authors propose a module of 16 leg pairs from 4 rounds of binary splitting of a primary segment, $2^4 = 16$ [1408].

A primary segment splits, its halves split again, and the module repeats down the trunk; in the centipedes the count steps by 2 in adults and by 1 in embryos.

Energy and numbers

Centipedes are predators, and their first trunk leg pair is a venom-delivering organ [977]. The whip-spider *Damon annulatipes*, 640 ± 66 mg, measured at 21 °C, produces 30.22 ± 2.87 µl CO_2 h^{-1}, about 229.6 ± 21.8 µW, with RQ 0.72 [1400]. The mass-specific rate is 229.6 µW / 0.640 g = 0.36 W kg^{-1}.

Within the species the rate scales as µW = 342 M^0.857, with M in g; at 0.64 g this gives 342 × 0.64^0.857 = 233 µW against 229.6 µW measured [1400]. Over two weeks in the laboratory the rate fell by 16–33 % without change in mass [1400]. It is lower than in most spiders and insects of the same size, higher than in ticks and similar to scorpions [1400].

The 2013 census gives these counts [1391]:

Taxon	Species	Fossil
Arthropoda	1,302,809	45,769
Chelicerata	115,992	2,219
Arachnida	114,275	1,833
Araneae	44,863	1,185
Acari (six orders)	55,214	—
Opilioacarida / Holothyrida / Ixodida	37 / 27 / 897	2 / 0 / 5
Mesostigmata / Trombidiformes / Sarcoptiformes	more than 11,424 / 25,821 / 16,412	5 / 55 / 239
Scorpiones	2,109	121
Opiliones	6,571	37
Pseudoscorpiones	3,574	41
Pycnogonida	1,346	11
Xiphosura	103	—
Eurypterida	249	249 (all fossil)
Myriapoda	12,010	11
Chilopoda	3,118	6
Diplopoda	7,842	5
Pauropoda	846	0

Symphyla	204	0

Mites are 55,214 / 114,275 = 48.3 % of arachnid species and spiders 39.3 %; millipedes are 65.3 % of myriapods and centipedes 26.0 %. The 2011 census gives Arachnida 112,201 and Myriapoda 11,885 [619]. Of 1,552,319 described animals, arachnids are 7.2 % and myriapods 0.77 %.

Oribatid mites number about 9,000 species and subspecies described from 1758 to 2002, in 1,204 genera and 169 families [1079]. Millipedes have 12,116 nominal species, of which 7,753 are listed as valid, in about 3,000 genera, with an estimated total of 15,000–20,000 [1013]. Between 0 and 300 species are described a year [1013].

Fishes and early chordates

This group holds the tunicates, the lancelets, the jawless fishes, the sharks and rays and the bony fishes. “Fishes” number 35,644 described species, 32,834 extant and 2,810 fossil; Tunicata number 2,804 and Cephalochordata 33 [587]. Craniates number 85,432 species, including 19,974 fossil, so fishes hold 35,644 / 85,432 = 41.7 % of craniates and 2.15 % of all described animals [587].

First traces

The oldest accepted vertebrates are *Myllokunmingia fengjiaoa* and *Haikouichthys ercaicunensis* from the Lower Cambrian Chengjiang Lagerstätte, Yunnan [1409]. *Myllokunmingia* is lamprey-like, and *Haikouichthys* stands closer to hagfish [1409]. Zircon dating places Chengjiang at 518.03 Ma or younger (67.13); the same abstract suggests that chordates may have arisen in the Ediacaran, about 555 Ma (67.20) [1409].

The split between cyclostomes and jawed vertebrates is dated “more than 500 million years ago” (67.10) in one study and “around 560 million years ago” (67.21) in another [1410, 1411]. The second date exceeds the Chengjiang limit by 560 − 518.03 = 41.97 Myr (64.85).

The oldest complete jawed vertebrates come from the Chongqing Lagerstätte, South China: *Xiushanosteus mirabilis*, a jawed stem gnathostome, and *Shenacanthus vermiformis*, a chondrichthyan [1412]. Their age is early Silurian, “Telychian age, around 436 Ma” (66.98) [1412]. Earlier complete jawed fishes were late Silurian, “about 425 Ma” (66.95), and molecular studies place jawed vertebrates “no later than the Late Ordovician period (around 450 million years ago)” (67.01) [1412].

Myelin is “thought to have arisen around the time of hinged jaws”; lamprey axons are not myelinated [1413]. A molecular clock on 63 taxa, 18 of them tunicates, splits the appendicularians from all other tunicates at 447 ± 20 Ma (67.00), credibility interval 484–411 Ma [1414].

Stolidobranchs split from the other ascidians and thaliaceans at 389 ± 32 Ma (66.87), interval 449–333 Ma [1414]. The calibration for Olfactores runs from 519 Ma (67.14) to 581 Ma (67.24), and congeneric splits in *Ciona* and *Molgula* exceed 100 Myr (65.64) [1414]. The tunicate fossil record is “deceptively scarce and controversial” [1414].

Sizes

What	Size	Position	Source
Ciona intestinalis tadpole larva	about 1 mm	9.10	[1415]
Paedocypris progenetica, mature female	7.9 mm	10.98	[1416]
Greenland shark, smallest measured female	81 cm	15.19	[1417]
Greenland sharks carrying the bomb pulse	up to 220 cm	16.10	[1417]
Ocean sunfish, record length	3.3 m	16.47	[1418]
Greenland shark, largest measured female	502 cm	16.85	[1417]
Greenland shark, maximum in survey	6.4 m	17.08	[1418]
Giant manta, disc width	at least 7 m	17.16	[1418]
Great white shark, dataset maximum	7.13 m	17.17	[1418]
Oarfish, dataset maximum; maximum	7.72 m; just under 8 m	17.25; 17.28	[1418]
Basking shark, record	12.27 m	17.67	[1418]
Whale shark, largest accepted	18.8 m	18.06	[1418]
Whale shark, discounted claim	about 20 m	18.11	[1418]

The smallest vertebrate in this record is *Paedocypris progenetica*, a mature female of 7.9 mm from the blackwater peat swamps of Southeast Asia [1416]. The largest accepted whale shark, 18.8 m, is from the Arabian Sea; claims of about 20 m and 34 t are discounted [1418]. Masses reach 2,721 kg in the giant manta and 2,300 kg in the ocean sunfish [1418].

The length range of living fishes is 18.8 m / 7.9 mm = 2,380, from 10.98 to 18.06 on the ladder. The *Ciona* tadpole has “a mere ~2600 cells”, and its central nervous system about 330 cells, 177 of them neurons [1415].

Times

What	Duration	Position	Source
Nothobranchius furzeri, sexual maturity	28 d	46.53	[1419]
N. furzeri, laboratory strain	32 weeks	48.43	[1419]
Lag between the two *Perissodus* species	nearly 1 yr	48.87	[1420]
N. furzeri, maximum longevity	1.1 yr	48.96	[1419]
Perissodus oscillation	3.9 yr; 4.1 yr	50.11; 50.15	[1420]

periods			
Perissodus period in the introduction	5 yr	50.34	[1420]
Perissodus census series	31 yr	52.00	[1420]
Kandalaksha flounder samples apart	40 yr	52.23	[1421]
Greenland shark maturity	156 ± 22 yr	53.47 (53.33–53.59)	[1417]
Greenland shark, minimum age	272 yr	53.97	[1417]
Greenland shark, 502 cm animal	392 ± 120 yr	54.31 (53.97–54.55)	[1417]

The longest-lived vertebrate is the Greenland shark: eye-lens radiocarbon of 28 females gives at least 272 years [1417]. The turquoise killifish lives at most 1.1 years in captivity; the shark exceeds it 392 / 1.1 = 356 times [1419].

Repeated units

Vertebral number varies within species. In Atlantic cod *Gadus morhua* from the southern Grand Bank, 239 fish in three samples were counted on 12–15 May 1965 [1422]:

Sample	Vertebrae	n
All, 1965	51–58, mean 54.04, variance 1.77	239
11–30 cm	51–57	50
31–50 cm	51–58	92
51–70 cm	52–57	27
71–90 cm	51–56	34
91–120 cm	52–55	36
One sample	52 (7), 53 (17), 54 (21), 55 (20), 56 (5)	70

The length groups span 11–120 cm (13.38–15.55). Means fall from 54.38 in the smallest fish to 53.36 in the largest, by 1.02 vertebrae [1422]. The single sample of 70 has a mean of 53.99 and a printed variance of 1.23; its smallest step between counts is 1 [1422].

The record covers 416 samples from 1947–71, most of 70–120 columns [1422]. On Flemish Cap, 21 cod year-classes of 1940–66 were compared: 17 with homogeneous variances have means of 54.37–54.78, not significantly different, while the means of all 21 differ significantly [1423].

In 90 wild-derived medaka stocks, *Oryzias latipes* complex, with six adults per stock, median abdominal vertebrae run from 11 (*O. sinensis*, Kunming) to 13 (*Oryzias* sp., Sokcho) [1424]. The abdominal count rises with latitude of origin, partial R^2 0.191 [1424].

Rearing at 22, 24, 26 and 28 °C did not change abdominal or total counts, and caudal counts were lower at 26 °C only [1424]. One SNP on chromosome 10 is associated with total count. The variance attributed to SNPs is 0.16 ± 0.28 for abdominal, 0.24 ± 0.16

for caudal and 0.29 ± 0.21 for total counts [1424].

Amphioxus holds one uninterrupted cluster of 15 Hox genes and one *Evx*; the ancestral chordate cluster held “up to 14 Hox genes plus one Evx gene” [1425]. Lampreys carry at least three or four Hox clusters; in the horn shark the A, B and D clusters match the jawed-vertebrate ancestor except *Hoxa14*, a pseudogene [1425].

Zebrafish carry seven *hox* clusters, mammals four and invertebrate chordates one [1426]. The duplication falls after the split of ray-finned and lobe-finned fishes and before the teleost radiation [1426].

Handedness

Flatfish lie on one side, with both eyes on the other, so that each body has a side.

Polymorphism for that direction is “limited to seven of c. 715” flatfish species [1427, 1428]. The share is 7 / 715 = 0.98 %; eye side is fixed in 708 species.

In the starry flounder *Platichthys stellatus*, historical and recent shares of sinistral fish were compared, the recent samples from 1999–2004 [1427]. No locality differed between the periods [1427]:

Locality	Historical n, % sinistral	Recent n, % sinistral
Columbia River, Washington	225, 60.4 % (1942)	54, 61.1 %
Puget Sound	8,972, 51.6 % (1942)	20, 55.0 %
British Columbia	7,671, 66.4 % (1969)	148, 62.8 %
Alaska	5,129, 68.0 % (1942)	94, 63.8 %
Japan (recent: Russia just north)	476, 100 % (1942)	39, 97.4 %

Twelve recent sites gave sinistral frequencies of 0.45–1.00, with 12–59 fish per site, 355 in total [1427]. The frequency falls with distance from Japan at $r^2 = 0.56$; without the two Russian samples r^2 is 0.06 [1427]. At Denman Island, British Columbia, a figure legend gives 27 sinistral and 28 dextral adults; the text gives 40 [1428].

In the European flounder *Platichthys flesus* the White Sea holds long series [1421]. At Onega Bay, 2002–2019, n = 4,716, the left-sided share ran 13–26 % a year, mean 21 ± 3.1 % [1421]. At Dvina Bay, 2005–2019, n = 4,717, it ran 2–7 %, mean 5 ± 1.3 % [1421].

At Mezen Bay, 2010–2016, n = 2,267, the share ran 1–7 %, mean 4 ± 1.8 % [1421]. No trend with year was found, and Kandalaksha samples 40 years apart do not differ [1421]. Across the range the shares are these [1429]:

Locality (year)	n	% left-sided
Chupa Inlet (2014–2021)	584	28.4
Onega Bay (2014–2021)	4,527	20.6
Dvina delta (2014–2021)	5,007	5.2
Mezen (2014–2021)	2,272	3.3
Kuz Inlet (published 1949)	187	31.3
Kolezhma (1958)	358	28.5
Velikaya Salma (1964/2009)	957	37.1
Barents Sea, Murman coast (1930)	475	44.5

Barents Sea, Murman coast (1930)	475	44.5
Kiel/Eckernförde (1905)	3,331	42.7
Pudisoo (1958)	1,271	33.1
Öland (2002)	1,673	21.1
Den Helder (1915)	75	48
Elbe mouth (1900)	225	23.6
Skagerrak, Lysekil (2002)	653	27
Plymouth (1900)	1,120	5.4
Plymouth (1982)	40	7.5
Dublin Bay (2012)	590	5.6

The overall range runs from 3.1 % at Mezen to 48 % at Den Helder [1429]. In four White Sea populations the share of reversed fish does not differ among size or age classes or between the sexes [1430].

The scale-eating cichlids *Perissodus microlepis* and *P. straeleni* of Lake Tanganyika open their mouths to one side, a second handedness [1420]. Both were sampled at Kasenga Point, Zambia, each September–November of 1988–2018 except 1989 and 1991, with 10–200 fish per sample and means of 132 and 57 [1420].

The righty frequency was “almost always maintained within a range of 0.4 to 0.6” [1420]. It oscillated with a period of 3.9 years in *P. microlepis* and 4.1 years in *P. straeleni*, the first lagging the second by nearly a year [1420]. *P. microlepis* occurs at 8.4 times the density of *P. straeleni* [1420].

Righties attack left flanks and lefties right flanks [1420]:

Attacker	Victims R	Victims L	Odds ratio
P. microlepis, righty	3	19	26.4
P. microlepis, lefty	25	6	(same)
P. straeleni, righty	4	21	28.88
P. straeleni, lefty	22	4	(same)

The odds ratios follow as (19 × 25) / (3 × 6) = 26.4 and (21 × 22) / (4 × 4) = 28.875. The original report states that mouth direction follows “simple genetics” [1431].

Narrow-sense heritability of mouth asymmetry is 0.22 ± 0.06 in the field and 0.18 ± 0.05 in the laboratory [1432]. Offspring frequencies did not fit a single-locus two-allele model, which could not be rejected with confidence either; a later paper gives “a relatively large environmental component (around 80%)” [1432, 1433].

In one wild brood of 141 larvae, 93 were scored; inheritance at marker UNH2101 on linkage group 10 fit a lefty × lefty model with a dominant allele lethal when homozygous [1434]. Larval asymmetry was unimodal, and adults are described as bimodal [1434].

Other work reports mouth asymmetry as “a continuous unimodal distribution” in 266 adults from seven sites [1435]. Over 155,000 ddRAD and 3,900,000 PoolSeq SNPs gave 1 differentiated SNP and 38 or 378 differentiated windows [1435]. The record holds both a discrete dimorphism with simple inheritance and a continuous trait with a heritability of 0.18–0.22.

The *Ciona* larva shows sidedness in its peripheral nervous system: of 28 neurons, 8 lie left, 6 in the centre and 14 right [1415].

The flounders show the form of one direction held by place. Each fish has one side, and the share of each side holds in its population for decades. It runs 51.6 % to 55.0 % in Puget Sound since 1942 and 13–26 % at Onega Bay over 18 years.

The scale-eaters show the same form in motion. Their two directions swing about one half with a period of 3.9–4.1 years (50.11–50.15). Here the form is loading and discharge between the two directions of one species.

Energy and numbers

Resting metabolism was compiled from 138 studies of 69 teleost species over a span of about 40 °C [1436]. The mean scaling exponent within species is 0.79 (SE 0.11), and the all-fish equation is ln Rb = 0.80 ln M − 5.43, with Rb in mmol O_2 h^{-1} and M in g [1436].

A 50 g tropical fish at 30 °C needs about six times the metabolism of a polar fish at 0 °C [1436]. Q10 across species is 1.83 over 0–30 °C, and the median acclimation Q10 within species is 2.40 (n = 14) [1436].

The 2,810 fossil fish species divide as hagfishes 1, lampreys and their relatives 5, sharks and rays 1,186, chimaeras 162, ray-finned fishes 1,235 and lobe-finned fishes 221 [587]. Electroreception occurs in lampreys, chondrichthyans, lungfishes, coelacanths and several ray-finned fishes, and “evolved independently at least twice within teleosts” [1437]. It was lost in frogs, amniotes and neopterygians [1437].

Crustaceans

Crustaceans are the branchiopods, copepods, barnacles, ostracods and the malacostracans: decapods, krill, isopods, amphipods and mantis shrimps [1438]. Recent Crustacea number approximately 66,914 species in 1,003 families and 9,522 genera, 4.3 % of described animals [619, 1438]. Antarctic krill alone hold a standing stock of 379 million tonnes, and marine arthropods as a whole hold 1 Gt C [235, 1439].

First traces

A crown-group crustacean comes from an Orsten-type deposit in the Lower Cambrian of China, holding “at least three new arthropod species” [1440]. Its limb outgrowths, epipodites, “occur in a set of three, derive from setae and are a ground-pattern feature of Eucrustacea” [1440]. Eucrustaceans are “common in the fossil record of the past 500 million years” (67.10) [1440].

The mandibulate body plan is shown by *Tokummia katalepsis*, “a large bivalved arthropod from the 508 million-year-old Marble Canyon fossil deposit” of the Burgess Shale (67.12) [1441]. The oldest lobster-like decapod is *Palaeopalaemon newberryi*, probably a bottom dweller [1442].

The earliest continental decapods are *Tealliocaris walloniensis*, Famennian, Late Devonian, from floodplain and temporary-pond deposits in Belgium [1443]. Decapods have lived in continental ecosystems “at least since the Late Devonian”, while

Palaeopalaemon and *Aciculopoda*, the earliest undoubted decapods, are offshore marine [1443]. Crustaceans are among the 7 arthropod groups of the Early Devonian Rhynie chert [1396].

Shell-breaking began later than the lineages themselves [622]. Mantis shrimps and lobsters arose in the Jurassic, the first possibly breaking shells from the Late Cretaceous; true crabs arose in the Jurassic and broke shells from the latest Cretaceous or Paleocene [622].

Myelin is present in copepods and in penaeid shrimp [1444]. Among calanoid copepods, 3 younger superfamilies have myelin and 2 older ones lack it, in a survey of 20 calanoids [1444]. That gives two crustacean origins of myelin among at least four in animals [1376].

Sizes

What	Size	Position	Source
Penaeid shrimp, myelinated fibre diameter	120 µm	7.17	[1376]
Uca lactea, carapace width above which all males are asymmetric	5.3 mm	10.62	[1445]
Uca lactea, young crabs examined	below 7.0 mm	10.87	[1445]
Euphausia superba, maximum length	6.4 cm	12.88	[1446]
Macrocheira kaempferi, female carapace width; length (Taiwan)	0.184 m; 0.242 m	13.85; 14.09	[1418]
Bathynomus giganteus, maximum carapace length; total length	45 cm; 50 cm	14.66; 14.76	[1418]
Macrocheira kaempferi, leg span (Scheveningen)	3.7 m	16.58	[1418]
Macrocheira kaempferi, unconfirmed claims	3.8 m; 4 m	16.60; 16.65	[1418]

The 3.7 m span belongs to a Japanese spider crab of more than 13.6 kg; claims of 4 m and 3.8 m “cannot be confirmed” [1418]. Copepod dry mass runs from 0.0038 mg in *Paracalanus parvus* to 34.5 mg in *Bathycalanus bradyi*, a 9,100-fold range [1447]. For krill, 379 Mt over 8×10^{14} post-larvae gives 0.47 g per animal [1439].

Times

What	Duration	Position	Source
Odontodactylus scyllarus, interval between strike force peaks	390–480 µs	26.01–26.20	[1448]
Undinula vulgaris, minimum escape	1.5 ms	27.23	[1444]

reaction (myelinated)			
Neocalanus gracilis, minimum escape reaction (myelinated)	1.6 ms	27.29	[1444]
Labidocera madurae, minimum escape reaction (non-myelinated)	3.1 ms	27.90	[1444]
Acartia, escape response	within 4 ms	28.13	[1444]
Pleuromamma xiphias, minimum escape reaction (non-myelinated)	6.6 ms	28.58	[1444]
Acartia, stroke and recovery	about 7 ms	28.64	[1444]
Alpheus armillatus, time after limb loss: reversal about 50 %; 67 %; 100 %	33 h; 40 h; 72 h	43.79; 43.96; 44.50	[1449]
Uca lactea, interval for one-third left-handed; 17 of 21; 28 of 29	under 96 h; 144 h; 192 h	44.76; 45.13; 45.39	[1445]
Parhyale hawaiensis, embryogenesis at 26 °C	about 10 d	45.60	[1450]
Parhyale hawaiensis, life cycle at 26 °C	about 2 months	47.24	[1450]
Uca lactea, juvenile survey 1971–1975; adult survey 1969–1975	5 yr; 7 yr	50.34; 50.64	[1445]
Antarctic krill, period of the mean biomass (1926–2004)	78 yr	52.84	[1439]
Homarus americanus, maximum longevity (wild)	100 yr	53.06	[1451]

The peacock mantis shrimp strikes with two force peaks 390–480 µs apart: the limb impact, then the collapse of a cavitation bubble [1448]. Impact peaks reach 400–1,501 N and cavitation peaks up to 504 N; cavitation gives on average about 50 % of the force, up to 280 % of the impact [1448].

Among copepod escapes the slowest is 6.6 / 1.5 = 4.4 times the fastest. *Acartia* often exceeds 500 mm s^{-1} and 100 m s^{-2} [1444].

Copepods escape at up to 200 body lengths a second, and penaeid myelinated fibres conduct at “over 200 m s^{-1}”, “the fastest speeds known” [1376, 1452]. Fenestration nodes occur in at least six *Penaeus* species [1453].

Repeated units and genes

Eucrustacean epipodites occur in sets of three [1440]. *Parhyale hawaiensis* has “a complement of 9 canonical Hox genes that exhibit both spatial and temporal

colinearity”: *lab*, *pb*, *Dfd*, *Scr*, *Antp*, *Ubx*, *abd-A* and *Abd-B*, with *Hox3* unconfirmed in the cluster [1450]. Its genome is estimated at 3.6 Gb, with an assembly of 4.02 Gb, 28,155 gene models and 28,666 proteins [1450].

Handedness

Fiddler crab males carry one large claw. In *Uca lactea* of Japan, 8,088 adult males were counted in eight local populations from Amakusa (Kyushu) to Ishigaki-jima (Ryukyu Islands), 1969–1975 [1445]. Of them 4,071 were right-handed and 4,017 left-handed: 50.3 % and 49.7 % [1445].

No population differed significantly from 1 : 1, and no significant annual change was found [1445]. In 1971–1975, 13,913 young crabs under 7.0 mm were examined: 318 lacked the right claw, 293 the left, and 300 had two large claws [1445]. All males above 5.3 mm carapace width were asymmetric [1445].

The experiments on *U. lactea* gave these results [1445]:

Treatment	Outcome
One claw removed from megalopae or first crabs with two small claws	left-handed males on the other side: 33 of 33; 193 of 193; 163 of 165
Large claw removed from asymmetric young males	124 of 126 survivors kept the same handedness
Both claws removed	106 survivors exactly as before
Interval effect	under 96 h about one-third left-handed; 17 of 21 at 144 h; 28 of 29 at 192 h

“Once the handedness was established in a male, it could not be reversed by the subsequent removal of one or both chelipeds” [1445]. The kept share is 124 / 126 = 98.4 %.

In *U. marionis*, 554 of 567 adult males were right-handed, 97.7 % right and 2.3 % left [1445]. Its handedness was described as “controlled not accidentally but genetically”, without a test [1445].

In the swimming crab *Portunus trituberculatus*, over 300 mature crabs were 75 % right crusher with left cutter and 25 % the reverse [1454]. A wild sample held 19 right-handed of 31, a minority of 12 / 31 = 39 % [1454].

Offspring of right-handed females were 75 of 77 megalopae (97 %) and 29 of 30 first crabs (97 %) right-handed [1454]. Offspring of the other female group were 98 % of 88 megalopae and 100 % of 42 crabs right-handed; “Right-handedness could be inheritable across generations” [1454]. After the right claw was shed “all crabs were left-handed thereafter”, and “Right-handedness never reappeared” [1454].

In early juvenile lobsters the two claws and their closer muscles are identical [1455]. The claw with greater reflex activity becomes the crusher, with slow fibres; the other becomes the cutter, with fast fibres, and substrate and exercise during rearing set the side [1455].

Reared lobsters showed “approximately equal distribution of the crusher on the right or left side”, and “In no case did a crusher develop on both sides” [1456]. Without substrate and with a claw removed, “all but one lobster failed to develop a crusher

claw” [1456]. Claw type is set in juvenile stages 4–5 and assessed at stage 8 or 9; a survey of 2,433 wild lobsters found no paired crushers [1456].

The cutter closer muscle has about 90 % fast fibres, the contralateral muscle 10–90 % and the crusher 10–30 % [1457]. “Once claw type is determined during the critical period, it is fixed for life” [1457].

In the snapping shrimp *Alpheus heterochelis* the snapping claw “appears with equal probability on the right or left side” [1449]. After removal of the pincer and then the snapper, reversal reached “100% … at stage 3-5 limb buds”, in a series of 36 animals of which 24 regenerated [1449].

Simultaneous removal (27 animals, 16 regenerated) and snapper-first removal (52 animals, 38 regenerated) kept the configuration “in all cases” [1449]. In *Alpheus armillatus* reversal was about 50 % at 33 h, 67 % at 40 h and 100 % at 72 h [1449].

The minority shares in natural populations are 49.7 % in *U. lactea* over 7 years and 8 populations (n = 8,088) and 2.3 % in *U. marionis* (n = 567). In *Portunus* they are 25 % (n > 300) and 39 % (n = 31).

Here the form of one direction is laid down within a few days of life. Once the large claw is set it holds for life in *Uca* and in lobsters; one species keeps the two directions at 50.3 % and 49.7 %, another holds 97.7 % to one side.

In *Portunus* the direction passes from mother to young, 97–100 % right-handed. The direction of what was laid down first is kept across the generation.

Energy and numbers

Antarctic krill have a summer range of about 19 × 10^{6} km² and a mean abundance of 8 × 10^{14} post-larvae; their biomass is 379 million tonnes as the mean over 1926–2004 [1439]. The 2000 survey area held 28 % of the stock, about 133 Mt in January–February 2000, and the Scotia Sea acoustic estimate was 37.3 Mt [1439].

Gross post-larval production is 342–536 Mt a year by three methods, and predators consume 128–470 Mt a year [1439]. Production over biomass is 342 / 379 = 0.90 to 536 / 379 = 1.41 a year.

Copepod respiration was compiled from 253 data sets, 65 from the upper ocean and 188 from the deep sea, covering 108 species, 51 genera and 21 families [1447]. Upper-ocean temperatures ran from −1.7 to 28.5 °C and the deep zones were at 1.5–3 °C [1447].

The model $R = R_0 \cdot M^{(3/4)} \cdot e^{(-E/kT)}$, with the mass exponent fixed at 0.75, reaches R^2 = 0.76; empirical four-variable models reach 0.72–0.80 [1447]. In those models depth enters with a negative sign and oxygen saturation with a positive one [1447].

In 19–24 krill species from the upper to the deep ocean, body mass, temperature and depth account for 71–89 % of the variance in respiration and 69–81 % in ammonia excretion [1458]. The atomic O:N ratio is 11–90, median 27 [1458].

The small classes, summed over their families, hold Remipedia 18, Cephalocarida 13, Mystacocarida 13, Tantulocarida 36, Euphausiacea 87, Pentastomida 130 and Branchiura 168 species [1438]. The 2013 census gives Crustacea 73,141 species, including 5,406 fossil, a Recent count of 67,735; both the 2011 and 2013 counts stand

[1391].

Woodlice number 3,710 species in 527 genera and 37 families, to April 2014, which is 3,710 / 66,914 = 5.5 % of Recent crustaceans [1459].

Insects

Insects number 1,070,781 described species, 1,070,781 / 1,302,809 = 82.2 % of all arthropods and 64.5 % of all 1,659,420 described animals [587, 1391]. A second count gives insects about 62 % of about 1.6 million described living species [1161]. Their earliest traces, flight and the first pollinators are set out in chapter 14.

First traces

The oldest insect claimed, *Rhyniognatha hirsti*, is Pragian, “about 396–407 million years ago” in the paper and 410.8–407.6 Ma (66.92) on the 2023 chart [981, 1460]. A second reading of new remains takes it as a myriapod, “possibly a centipede” [982].

A clock on 1,478 genes dates insects to about 479 Ma (67.06), flight to about 406 Ma (66.91) and the main living lineages to about 345 Ma (66.76) [979]. The oldest winged fossil, *Delitzschala bitterfeldensis*, lies within the Serpukhovian, 330.9–323.2 Ma (66.73–66.71) [980]. The clock age of flight exceeds it by 75.1 Myr (65.38).

The oldest insect gall, the first record of a larva of the insects with complete metamorphosis, sits in petioles of the tree fern *Psaronius*, about 302 Ma (66.64) [989]. The oldest pupation chamber in wood is a U-shaped boring from the Late Triassic Chinle Formation, Utah, backfilled with digested xylem; cupedid beetles are the most plausible makers [1461].

Termites have a crown age of 149 Ma (136–170; 66.00, 65.92–66.12), oldest fossils at 135 Ma (65.91) and Termitidae at 54 Ma (46–66; 65.08) [941]. Fungus farming dates to 31.41 Ma (25.82–39.53; 64.58) in termites by the clock, about 25 Ma (64.38) in fossil gardens and about 50 Ma (65.01) in ambrosia beetles [938, 939, 944].

A leafhopper’s obligate symbionts *Nasuia* and *Sulcia*, with genomes of 112 kb and 190 kb, together make 10 essential amino acids [371]. The partners have been associated for more than 200 Myr (66.27) [371].

Sizes

What	Size	Position	Source
Platygaster vernalis egg, about 7×10^{-7} mm³; cube edge	8.88 µm	4.80	[1462]
Megaphragma mymaripenne, adult nervous system, 52,200 µm³; cube edge	37.4 µm	6.11	[1463]
M. mymaripenne, pupal nervous system, 93,600 µm³; cube edge	45.4 µm	6.28	[1463]

Dicopomorpha echmepterygis male, body length	139–240 µm	7.30–7.80	[1299]
Megaphragma caribea, body length	170 µm	7.49	[1463]
M. mymaripenne, body length	200 µm	7.63	[1463]
Honeybee brain, about 1 mm^3; cube edge	1 mm	9.10	[1464]
Bolboleaus hiaticollis egg, about 5×10^2 mm^3; cube edge	7.94 mm	10.98	[1462]
Phobaeticus chani female, body; overall with legs	357 mm; 567 mm	14.45; 14.87	[1303]
Largest fossil wingspan, Carboniferous–Permian	about 70 cm	15.06	[728]

The smallest free-living winged insects are *Megaphragma caribea* and *M. mymaripenne*; the adult nervous system holds 52,200 / 93,600 = 55.8 % of the pupal volume [1463]. Living insect length spans 567 / 0.139 = 4,079, from 7.30 to 14.87 on the ladder.

The largest fossil insects reach wingspans of “about 70 cm”, a figure that rests on more than 10,500 fossil wing lengths [728]. Maximum insect size tracks atmospheric oxygen until the end of the Jurassic and is decoupled from it in the Cretaceous and Cenozoic [728].

Egg size is compiled from 10,449 descriptions of 6,706 species in 526 families; eggs span more than eight orders of magnitude in volume, $5 \times 10^2 / 7 \times 10^{-7} = 7.1 \times 10^8$ [1462]. A honeybee brain is about 1 mm^3 with about 960,000 neurons; another source gives “a brain as small as 1 µL containing 950,000 neurons” [1464, 1465].

Times

What	Duration	Position	Source
Drosophila pupariation after larval hatching	about 96 h	44.76	[1466]
Megaphragma mymaripenne adult, 25 °C; 15 °C	5 d; 8.8 d	44.96; 45.48	[1463]
Drosophila egg to adult, 28 °C; age at maturity	7 d	45.27	[1466, 1467]
Termite new workers after swarming	1.5–3 months	46.98–47.61	[940]
Honeybee non-foraging workers	0.2–0.4 yr	47.41–48.04	[1467]
Nala earwig, interval between penis switches per male	64–143 d	47.28–48.02	[1468]
Drosophila maximum longevity	0.3 yr	47.77	[1467]
Honeybee winter	0.9 yr	48.77	[1467]

workers			
Lasius niger workers	1–2 yr	48.87–49.50	[1467]
Honeybee queen maximum	8 yr	50.76	[1467]
Magicicada juvenile period	13 yr; 17 yr	51.21; 51.45	[1309]
Termite primary reproductives, maximum	about 20 yr	51.60	[940]
Lasius niger queen maximum	28 yr	51.90	[1467]
Macrotermes mound	about 700 yr; at least 2,200 yr	54.83; 55.88	[940]

A comparison of 87 solitary insect species in eight orders with 61 eusocial species links eusociality with a “100-fold increase in insect lifespan” [1469]. The *Lasius niger* queen at 28 years and the adult *M. mymaripenne* at 5 days differ 2,045-fold. Fungus-growing termite colonies live up to several decades [940].

Repeated units

Within insect species the units counted with a range are small ones: the facets of the eye and the cells of the brain.

The eye of *Drosophila melanogaster* holds 700–800 ommatidia in one entry and 483 ± 7 in a second, tied to a growth-mutant study [1466]. Kenyon cells per mushroom body number 2,597 on the right and 2,580 on the left in one brain (FlyWire), a difference of 17 cells, and 1,917 in another dataset (hemibrain) [1470].

The ancestral arthropod Hox set has 10 genes: *labial*, *proboscipedia*, *Hox3*, *Deformed*, *Sex combs reduced*, *fushi tarazu*, *Antennapedia*, *Ultrabithorax*, *abdominal-A* and *Abdominal-B* [1471]. In *D. melanogaster* the cluster is split into two complexes “separated … by 9.6 Mb”, and in the silkworm *labial* lies about 12 Mb from the rest [1471]. Arthropod Hox clusters range from 0.3 to 13.6 Mb; *Daphnia pulex*, at 0.34 Mb, has the tightest [1471].

The adult *Drosophila* single-nucleus atlas holds more than 580,000 cells in 15 tissues, with 251 cell types in the stringent and 264 in the relaxed dataset [1472]. The median is 15 types per tissue; the head holds 81 types and the testis 25 [1472].

Handedness

Males of the earwig *Labidura riparia* carry two penises side by side and use one per copulation [1473]. Across 10 populations from 2.23° to 43.3° N, the right penis was used in 88.6 % of copulations and the left in 11.4 % [1473]. About 23 % of left-handed males had a damaged penis [1473].

Males made to use the right penis outperformed left-handed males, with odds ratios of 3.50 for coupling within 1 h (40.61) and 2.94 for sperm transfer [1473]. The female sperm-storage organ is coiled, with a right-facing opening [1473].

In the earwigs *Nala lividipes* of Ishigaki Island and *N. nepalensis* of Taiwan, males used the right and left penis about equally often, in multiple populations and broods [1468].

Each male almost consistently used one penis, switching at intervals of 64–143 days [1468].

In wild-type *D. melanogaster* the male genitalia loop to the right [1474]. Mutations in the myosin gene *Myo31DF* reverse the looping, and the same gene directs the right-handed looping of the gut [1474].

Across animals, 140 inferred transitions among symmetry, antisymmetry, dextral and sinistral states come from 11 classes in five phyla; antisymmetry is mainly a state after the larva [1475].

Each *Nala* male keeps one direction while the population holds both at about equal shares. In *Labidura* the population holds the right side at 88.6 %, a direction that matches the right-facing opening of the female organ.

Energy and numbers

Across 31 insect orders herbivory is associated with 25–35 % of the variation in diversification rate [1161]. Lower termites digest wood with gut protists; in Termitidae the gut holds prokaryotes only [1125].

Across 391 insect species metabolic rate scales with mass at 0.82 before and 0.75 after phylogenetic correction [1476]. Within species, size-polymorphic workers of eight ant species give exponents of 0.67–1.0; where the exponent is 1.0, body size varies through cell number only [1476].

Tethered *Drosophila* flight muscles produce nearly 80 W kg^{-1} muscle at 24 °C, enough for forces of about 150 % of body weight [1477]. Muscle efficiency rises with force by at most 10 %, and in hovering it is 9 % [1466, 1477]. Honeybee oxygen uptake in flight is 580 times the resting rate at 18 °C and 1,100 times at 11 °C [1466].

Beetles are 392,415 / 1,070,781 = 36.6 % of insect species [1391]. About 1 million insects are named and about 5.5 million estimated, beetles at about 1.5 million, with about 80 % undescribed [1284]. Termites number 3,106 living and fossil species in nine families; Termitidae hold 84 % of them in one count and more than 75 % in another [941, 1478, 1479].

Insect flight has one origin, at about 406 Ma [979]. Fungus farming arose once in termites, once in attine ants and at least 10 times in bark and ambrosia beetles, at least 12 times in all [937, 938, 944]. Clonal transmission of the fungus arose twice in termites [938].

Flight is the form of an opening made once and filled many times. One origin, about 406 Ma, holds 1,070,781 described species and an estimated 5.5 million.

Amphibians and reptiles

Amphibians and reptiles are the four-limbed vertebrates other than birds and mammals. AmphibiaWeb counted 9,022 amphibian species on 29 April 2026, in three orders: frogs, salamanders and caecilians [1480]. The Reptile Database counted 12,650 reptile species in June 2026: lizards with amphisbaenians, snakes, turtles, crocodiles and the tuatara [1481].

First traces

The oldest tetrapod traces are trackways at Zachełmie, Poland, from the Eifelian stage of the early Middle Devonian, 393.3–387.7 Ma (66.88–66.87) [991]. They are "approximately 18 million years older than the earliest tetrapod body fossils" and "10 million years earlier than the oldest elpistostegids" [991]. The implied earliest body fossils are 375.3–369.7 Ma (66.84–66.83); the 18 Myr lie at 64.08.

Tiktaalik roseae comes from the Late Devonian of Arctic Canada; its describers place the fish–tetrapod transition at "over 370 million years ago" (66.83) [992]. The Joggins Fossil Cliffs of Nova Scotia expose Pennsylvanian strata of 318–303 Ma (66.69–66.65) with "the first reptiles in Earth history" [1482]. The site yields 148 fossil species and 20 footprint groups in 96 genera [1482].

Triadobatrachus massinoti from the Early Triassic of Madagascar is "the earliest known lissamphibian" [1483]. *Megachirella wachtleri* from the Middle Triassic of the Dolomites is "75 million years older than the previously known oldest squamate fossils" (65.38), in an analysis of 129 lizard and snake taxa [1484].

Odontochelys semitestacea, from the Late Triassic of Guizhou, China, is about 220 Ma (66.36) and "somewhat older than *Proganochelys*", from marine deposits [1485]. Its plastron is fully developed; its carapace consists of neural plates only, with expanded dorsal ribs and no osteoderms [1485].

The oldest snake is *Eophis underwoodi*, Bathonian, about 167 Ma (66.10), from Kirtlington, Oxfordshire [1486]. *Portugalophis lignites* and *Diablophis gilmorei* are Kimmeridgian, about 155 Ma (66.04), and *Parviraptor estesi* from Dorset is about 150–140 Ma (66.01–65.94) [1486]. Before these finds the oldest snake was about 100 Ma (65.64); the record moved back by about 70 Myr (65.31) [1486].

The giant boa *Titanoboa* comes from the Cerrejón Formation of north-eastern Colombia, about 58–60 Ma (65.14–65.17) [1487]. The oldest synapsid herbivore, *Melanedaphodon hovaneci*, is about 307 Ma (66.66), and tetrapod herbivory arose "at least five times" in the Late Carboniferous–Early Permian [994, 995].

Sizes

What	Size	Position	Source
Paedophryne amauensis, adult male snout–vent length	7.0–8.0 mm; mean 7.7 mm	10.87–10.99; 10.96	[1488]
Paedocypris progenetica (fish), adult	7.9–10.3 mm	10.98–11.22	[1488]
P. swiftorum, male	8.25–8.90 mm	11.02–11.09	[1488]
P. kathismaphlox	10.1–10.9 mm	11.20–11.27	[1488]
P. oyatabu	11.3 mm	11.31	[1488]
29 smallest frogs, maximum male length below	13 mm	11.43	[1488]
Sphaerodactylus ariasae (gecko), mean	16.3 mm	11.64	[1488]

Thorius arboreus (salamander), mean	17.0 mm	11.68	[1488]
Titanoboa, length	about 13 m	17.72	[1487]
Blue whale, mean adult (comparison)	25.8 m	18.34	[1488]

Paedophryne amauensis of Papua New Guinea, with a type series of 7, is “the smallest known vertebrate species” [1488]. Living vertebrate sizes span “about 3,000-fold”; the exact quotient is 25.8 m / 7.7 mm = 3,351 [1488]. *Titanoboa* weighed about 1,135 kg [1487].

Adult masses in AnAge are 420 kg in the leatherback turtle, 200 kg in the saltwater crocodile and 117.2 kg in the Aldabra giant tortoise [1489]. They are 430 g in the tuatara, 17 g in the olm and about 8.73 g in Labord’s chameleon [1489]. Among living reptiles with a recorded mass the range is 420,000 / 8.73 = 4.8×10^4.

Times

Species	Maximum longevity	Position	Female maturity	Position
Aldabra giant tortoise	152 years	53.44	9,131 days (25.0 years, both sexes)	51.80
Olm	102 years (wild estimate); captive 58 years	53.08; 52.57	4,124 days (11.3 years)	51.08
Tuatara	90 years	52.97	4,380 days (12.0 years)	51.13
Saltwater crocodile	57 years	52.55	3,652 days (10.0 years); male 5,844 days (16.0 years)	50.97; 51.39
Leatherback turtle	30 years	51.97	4,748 days (13.0 years)	51.20
Chinese giant salamander	captive 19.9 years	51.59	—	—
Labord’s chameleon	1.3 years	49.11	about 60 days	47.23

Values from [1489]. The tortoise value is from captivity; a caught adult was “probably around 180” [1489]. In the olm, maturity takes an extra 14 years at 10 °C (51.27) [1489].

In Labord’s chameleon the eggs incubate about 260 days (48.56); the animals mature in about 2 months and die within 2–3 months, an “annual lifecycle” [1489]. The phases add to 260 + 60 + 60 to 90 = 380–410 days (48.91–48.98). The leatherback egg incubates 60 days (47.23) [1489].

Maximum lifespans span 1.3 to 152 years, a factor of 117, and female maturity about 60 to 9,131 days, a factor of 152. In seven lizard species at 20–27 °C an infraslow sleep rhythm runs with a period of 84–134.5 s (37.19–37.61), mean 113.2 ± 6.8 s [1490].

In the bearded dragon *Pogona vitticeps*, slow-wave and REM sleep alternate every 80 s (37.14), for 6–10 h (42.24–42.70) [1491].

Repeated units

Micro-CT of *Triadobatrachus* shows a presacral region of 15 vertebrae with a unique atlas–axis complex; an earlier reading gave 14 [1483].

In hynobiid salamanders trunk vertebrae were counted within species [1492]:

Species	n	Mean	Range	Frequencies (%)
Onychodactylus fischeri	33	20.2	19–21	19: 9; 20: 67; 21: 24
Onychodactylus japonicus	5	17.8	17–18	17: 20; 18: 80
Ranodon sibiricus	77	15.1	14–16	14: 1; 15: 89; 16: 10
Salamandrella keyserlingii	504	16.9	15–19	—
Batrachuperus mustersi	6	17.3	17–18	—
Hynobius naevis	3	16.7	16–17	16: 33; 17: 67
Batrachuperus pinchonii	2	15.5	15–16	15: 50; 16: 50

In most species the range is two or fewer; in *S. keyserlingii* it is four, and within its single populations at most three [1492]. The coefficient of variation is 2.2–3.0 % in *S. keyserlingii*, *R. sibiricus* and *O. fischeri*, and 0–4.3 % within populations across salamander families [1492].

Geographic variation occurs only in *S. keyserlingii*: south-eastern samples average 16.2–16.4, others 16.9–17.4 [1492]. In the Tekeli sample of *R. sibiricus*, 20 males and 11 females have nearly equal counts [1492].

The occurring counts are consecutive integers in every species with frequencies; the smallest step is 1. In the two species with 33 or more animals the mode holds 67 % (*O. fischeri*) and 89 % (*R. sibiricus*) of individuals [1492].

In the newts *Lissotriton*, 118 adult males of seven species and two subspecies were examined, 7–25 per taxon [1493]. “The number of trunk vertebrae in the genus is 12, exceptionally 13”: all taxa have 12 except *L. v. vulgaris*, with 13 [1493].

In crested newts *Triturus*, rib-bearing presacral vertebrae number 14 in *T. karelinii*, 15 in *T. carnifex* and *T. macedonicus*, 16 in *T. cristatus* and 17 or 18 in *T. dobrogicus* [1494].

Snake vertebrae are counted as trunk + cloacal + caudal [1495]:

Species (family)	Trunk	Cloacal	Caudal
Epictia albipuncta (Leptotyphlopidae)	205–228	2–5	22–23
Epictia rioignis	231–248	3–5	14–21
Habrophallos collaris	132–144	3–4	14–17
Leptotyphlops conjunctus	191–223 (with cloacal)		21–26

Mitophis leptepileptus	354–391	6	19–21
Mitophis calypso	350–352	—	—
Myriopholis phillipsi	335–343 (with cloacal)		41–49
Siagonodon exiguum, males	239–263	3–4	18–20
Siagonodon exiguum, females	248–260	4–5	18
Tetracheilostoma bilineatum	152–160	3	16
Trilepida salgueiroi, males	203–228	3–5	21–28
Trilepida salgueiroi, females	211–231	3–5	17–27
Afrotyphlops angolensis (Typhlopidae), total	209–236 male; 213–236 female		
Rhinoleptus koniagui, total	546		

A second source gives *A. angolensis* a total of 206–246, and the highest count in a living snake is 546 in *R. koniagui* [1495]. Trunk range widths within species are 23, 17, 12, 37 and 2 in *E. albipuncta*, *E. rioignis*, *H. collaris*, *M. leptepileptus* and *M. calypso*. They are 24 in male *S. exiguum*, 20 in female *T. salgueiroi* and 8 in *T. bilineatum*: 2 / 350 = 0.6 % to 8 / 152 = 5.3 % of the minimum.

In Asian anilioid snakes, 48 specimens of 24 species carry 4 to 8 scales on the midline of the chin in front of the neck joint, varying within a species by up to 2 [1496].

The vertebra is one unit repeated along the body, 12 to 18 times in the trunk of newts and up to 546 times in a blind snake. Within a species its number steps by 1 around a mode.

Handedness

Snail-eating snakes of the genus *Pareas* carry more teeth on the right lower jaw [1497]. In *P. atayal* (n = 38) the left side has 13.6 ± 1.0 teeth and the right 20.1 ± 1.1; in *P. formosensis* (n = 13) 15.8 ± 1.0 and 19.1 ± 1.1 [1497].

Right exceeds left in both ($p < 0.01$), by 6.5 and 3.3 teeth, with median asymmetry indices of 20.0 and 8.6 [1497]. Most pareids have more right teeth; *Asthenodipsas malaccanus* has symmetric teeth [1497]. Yet *P. formosensis* completely avoided the snail *Acusta despecta* and preferred slugs [1497].

The snakes’ right-sided jaw meets the dextral shells of the molluscs above. One direction stands in the prey and one in the eater: against *Pareas iwasakii*, 87.5 % of sinistral snails survived and no dextral snail did [1356].

Brains, energy and numbers

Reptile neuron numbers average “over 20 times lower” than in birds and mammals of similar body size [1498]. The smallest amniote brain in the record, of the Algerian sand gecko, has just under 2 million neurons, and the Sumatran flying dragon barely over 5

million [1499]. Reptiles hold 1.4 ± 0.6 neurons in the telencephalon per neuron in the rest of the brain [1499].

The tuatara has a resting metabolic rate of 0.0605 W at 430 g, that is 0.0605 / 430 = 0.000141 W g^{-1} or 0.141 W kg^{-1}, at 22.4 °C [1489]. The standard metabolic rate of 938 vertebrate species spans six orders of magnitude of body mass [1500]. The scaling exponents of fish, amphibians, reptiles, birds and mammals differ significantly, and there is “no universal metabolic allometry” [1500].

For a snake the size of *Titanoboa*, about 13 m and 1,135 kg, the minimum mean annual temperature is estimated at 30–34 °C [1487].

Group	Species	Share of class
Frogs (Anura)	7,961	88.2 %
Salamanders (Caudata)	830	9.2 %
Caecilians (Gymnophiona)	231	2.6 %
All amphibians, 29 April 2026	9,022	
Lizards, with 204 amphisbaenians	8,003	63.3 %
Snakes	4,249	33.6 %
Turtles	370	2.9 %
Crocodiles	27	0.21 %
Tuatara	1	
All reptiles, June 2026	12,650	

Counts from [1480, 1481]. The reptiles fall into 1,258 genera and 94 families [1481]. A 2013 count gave 7,171 amphibian species, 1,851 fewer than in 2026, and 15,507 reptiles including fossils [587].

On the 2013 living total of 1,525,728 described animals, amphibians are 0.59 % and reptiles 0.83 % [587]. Chytridiomycosis contributed to the decline of at least 501 amphibian species, 6.5 % of described amphibians [946]. Ninety of them are presumed extinct in the wild and 124 lost more than 90 % of their abundance [946].

Mammals

Mammals are the amniotes that feed their young on milk. The Mammal Diversity Database of 28 July 2026 lists 6,904 species: 6,791 extant (6,774 wild and 17 domestic) and 113 extinct since 1500, in 1,363 genera, 169 families and 27 orders [1501]. The extant species are 0.45 % of described living animals.

First traces

Juramaia sinensis, from the Jurassic of China, about 160 Ma (66.07), is the oldest eutherian [1502]. It extends the first appearance of the eutherian–placental line by about 35 Myr (64.68), from 125 Ma (65.84), and places the split of placentals and marsupials at about 160 Ma [1502].

Sizes

The Etruscan shrew *Suncus etruscus* weighs 2.4 ± 0.3 g as an adult (n = 7); field-caught animals range 1.6–2.4 g, mean about 2 g [1503]. AnAge gives 2.1 g; both values stand [1504].

The blue whale *Balaenoptera musculus* averages 25.8 m as an adult (18.34), “the largest extant vertebrate” [1488]. The bowhead whale *Balaena mysticetus* weighs 100 t as an adult and 900 kg at birth [1504]. Mass runs from 2.1 g to 100 t, a factor of 4.8 × 10^7.

The human adult weighs 62,035 g in AnAge, with an entry body mass of 70,000 g, and 3,313 g at birth [1504]. The newborn is 3,313 / 62,035 = 5.3 % of adult mass in the human and 900 / 100,000 = 0.9 % in the bowhead.

The human egg cell is about 120 µm across (7.17) [1505]. A girl is born with 1–2 million egg cells, and about 400,000 remain at puberty [1505].

A 70 kg reference man holds 3.0 × 10^{13} cells, 2.5 × 10^{13} of them red cells and about 3 × 10^{12} nucleated [236]. A second census gives 36 × 10^{12} for a man of 70 kg, 28 × 10^{12} for a woman of 60 kg and 17 × 10^{12} for a child of 32 kg [1506]. The two counts for the man differ by a factor of 1.2.

Times

Species	Maximum longevity	Position	Female maturity	Position	Gestation	Position
Bowhead whale	211 years (wild)	53.74	8,212 days (22.5 years)	51.70	396 days	48.94
Human	122.5 years	53.25	4,745 days (13.0 years); male 5,110 days (14.0 years)	51.20; 51.27	280 days	48.63
Naked mole-rat	31 years (captivity)	52.00	228 days	48.44	70 days	47.37
Etruscan shrew	3.2 years (captivity)	49.93	365 days	48.87	27 days	46.50

Values from [1504]. The bowhead’s maturity is “probably 20–25” years; the shrew value is “questionable” and “may still be considerably underestimated” [1504]. The naked mole-rat record is an animal caught wild in 1980 that died in 2010, 31 years at 35 g, 9.7 times the shrew’s span [1504].

Maximum lifespans span 3.2 to 211 years, a factor of 66. Human life expectancy at birth is 73.3 years worldwide (52.78) [1507]. Fusion of the human vertebrae begins after age 20 (51.60) [1508].

The resting Etruscan shrew at 22 °C has a heart rate of 835 ± 107 a minute and breathes 661 ± 93 times a minute [1503]. After stimulation the heart reaches 1,093 ± 235, with a highest single value of 1,511; breathing reaches 758 ± 109, highest 894, at a body temperature of 34–37.5 °C [1503].

A blue whale tagged with an ECG dived to 184 m (20.13) for 16.5 min (39.43) [1509]. Its heart rate was typically 4–8 a minute during dives, as low as 2, and 25–37 at the surface

after dives, with a rise of about 2.5-fold during the lunge ascent [1509].

Heartbeat	Duration	Position	Source
Shrew at 1,511 min⁻¹	0.040 s	30.22	[1503]
Shrew at rest, 835 min⁻¹	0.072 s	30.76	[1503]
Human at 60–100 min⁻¹	1.0–0.6 s	33.15–32.69	[1505]
Blue whale at 4–8 min⁻¹	15–7.5 s	35.62–34.99	[1509]
Blue whale at 2 min⁻¹	30 s	36.25	[1509]

The shrew maximum over the whale minimum is 1,511 / 2 = 756; within the whale the range is 37 / 2 = 18.5-fold and within the shrew 1,511 / 835 = 1.8-fold. The human sinus node fires 80–100 times a minute; the lower pacemakers fire more slowly, the atrioventricular node 40–60, its bundle 30–40, the bundle branches 20–30 and the Purkinje fibres 15–20 [1505].

Repeated units

The human column has 7 cervical, 12 thoracic and 5 lumbar vertebrae, 24 separate [1508]. The sacrum consists of 5 fused vertebrae and the coccyx of 4, and the column “originally develops as a series of 33 vertebrae” [1508]. The adult skeleton has 206 bones, 80 axial and 126 appendicular [1505].

The cervical count is “almost fixed at 7” [1510]. Thoracolumbar vertebrae “tend to number 19 in many mammalian groups”, also in monotremes and marsupials, so that 7 cervical and 19 thoracolumbar are presumed primitive; Carnivora have 20 thoracolumbar [1510].

Xenarthrans, sirenians and hyraxes were counted specimen by specimen [1511]:

Species	n	4C	5C	6C	7C	8C	With rudimentary ribs
Choloepus hoffmanni	3	0	3	0	0	0	3
Choloepus didactylus	16 (13 counted)	0	5	8	0	0	13
Bradypus tridactylus	11	0	0	0	2	9	9
Trichechus spp. (two species)	18	2	13	3	0	0	16
Dugong dugon	11	0	0	6	5	0	7
Tamandua tetradactyla	8	0	0	1	7	0	3
Dasypus novemcinctus	9	0	0	0	9	0	0
Euphractus sexcinctus	12	0	0	0	12	0	0
Other armadillos (5	6	0	0	0	6	0	2

species)							
Hyraxes (*Dendrohyrax*, *Procavia*)	17 (16 counted)	0	0	2	14	0	3

The minority shares are 5 / 13 = 38 % with 5 cervicals in *C. didactylus* and 2 / 11 = 18 % with 7 in *B. tridactylus*. They are 5 / 18 = 28 % other than 5 in *Trichechus* and 5 / 11 = 45 % with 7 in the dugong. *Tamandua* and the hyraxes have 6 cervicals in 1 / 8 and 2 / 16 = 12.5 % each; the armadillos, 27 specimens, all have 7.

In each variable species the smallest step between two occurring counts is 1. Abnormalities were “always found in conspecifics with an abnormal vertebral number” and in “many” dugongs [1511]. Swans have 22–25 cervicals and giraffes 7; mice with Hox6 mutations can have 8 cervicals, and mice overexpressing *Cdx1* go from 25 to 23 presacral vertebrae [1511].

Changes in cervical number occur in about 7.5 % of human conceptions, and “virtually all” affected die before reproductive age; childhood cancer is roughly 120-fold higher with cervical ribs [1511].

Of 598 deceased human fetuses and infants radiographed in 1992–1999, 30 were excluded for poor ossification and 44 as hard to read [1512]. Cervical ribs occurred in 54.8 % (95 % CI 50.5–59.0) [1512]. In adults the frequency is 0.04–1.07 % across radiographic studies, the largest sample holding 4,333,200 people; the highest-incidence adult study gives 1.1 % (0.3–2.0) [1512].

Healthy children show 0.5 % (25,949 girls), diseased children and adults about 1–6 % [1512]. A model estimates cervical ribs in 9.7 % of recognised pregnancies and absent or rudimentary twelfth ribs in 3.1 % [1512]. At least 78 % of those with a cervical rib die before birth and 83 % before age one, against 9 % without [1512].

Relative survival to age one with a cervical rib is at most 19 %, or 21 % if difficult cases lack one [1512]. For absent or rudimentary twelfth ribs the figures are at most 38 % before birth, 40 % before age one and a relative survival of 73 % [1512]. Cervical ribs are one-sided in 22.8 % of cases, and a shift of all thoracic vertebrae accompanies 26.4 % [1512].

Two figures for conceptions stand: 7.5 % [1511] and 9.7 % [1512]. Dead fetuses and infants carry cervical ribs 54.8 / 1.1 = 50 to 54.8 / 0.04 = 1,370 times as often as adults.

The seven-unit neck is the closed number of the mammal. It holds in all 27 armadillos. In the human model of cervical ribs, at least 78 % of the bodies that depart from it die before birth.

Handedness

Human laterality defects occur in about 1.1 per 10,000 live births (95 % CI 1.0–1.2) [1513]. Of 517 non-syndromic cases in 1998–2007, 378 (73.1 %) were heterotaxy and 139 (26.9 %) situs inversus totalis, the full mirror image of the organs [1513]. Situs inversus totalis is then 0.269 × 1.1 = 0.30 per 10,000 births, about 1 in 34,000.

In primary ciliary dyskinesia, situs inversus totalis occurs in 40–50 % and situs ambiguus or heterotaxy in about 9–12 % [1514]. The disorder is usually autosomal

recessive; FOXJ1- and TUBB4B-related forms are dominant and DNAAF6-, OFD1- and RPGR-related forms X-linked [1514].

A meta-analysis of hand preference covers 200 studies, 262 datasets and 2,396,170 individuals [1515]. Left-handedness is 10.60 % (95 % CI 9.71–11.50) and non-right-handedness 18.10 % (13.90–22.30) [1515].

By definition, forced-choice left-handedness is 10.20 %, stringent 9.34 % and mixed 9.33 %; by instrument it runs from 9.24 % by self-classification to 15.11 % by observation [1515]. Men are 11.62 % left-handed and women 9.53 %, and a roughly 1 : 10 ratio holds across regions [1515].

The human body has one direction in its organs: the mirror image comes in about 1 in 34,000 births. In primary ciliary dyskinesia the mirror image comes in 40–50 % of cases, close to one half.

Brains, energy and numbers

The African elephant brain has 257 billion neurons, the largest amniote brain in the dataset [1499]. Mammals hold about 4 cerebellar neurons per cortical neuron, the elephant 44.8 [1499, 1516]. The cerebellum holds almost 70 % of the neurons in the rat, 80 % in the human and 97.5 % in the elephant [1516, 1517, 1518].

The human brain has 86 billion neurons [1518]. Brain mass scales with body mass to the 0.75 by ordinary least squares over 1,552 species (95 % CI 0.742–0.758), and to 0.57 by phylogenetic least squares [1519]. More than 70 % of extant mammals lack brain-size data [1519].

Species	Body mass	Basal rate	W kg⁻¹	Body temperature
Etruscan shrew	2.4 g	0.0630 W	26.3	36.0 °C
Naked mole-rat	35.3 g	0.1280 W	3.63	32.1 °C
Human	70,000 g	82.78 W	1.18	37.0 °C

Values from [1504]. The two-point exponent from shrew to human is log(82.78 / 0.063) / log(70,000 / 2.4) = 0.698, and from mole-rat to human 0.852.

The resting shrew at 22 °C uses 267 mL O_2 kg^{-1} min^{-1}, “about 67 times that of resting humans” [1503]. At 35 °C it uses 100 mL and at most about 1,000 mL; its aerobic scope is 7–10, its relative heart mass about three times the human, its stroke volume 8.3 µL [1503].

A resting human uses 250 mL O_2 min^{-1}, releasing about 20 kJ per litre of oxygen, a measured resting power of 85 W [389]. Liver and spleen take 23 W, the brain 16 W, skeletal muscle 15 W, the kidneys 9 W, the heart 6 W and the rest 16 W [389]. Liver and spleen are 23 / 85 = 27 % and the brain 16 / 85 = 19 %.

A 76 kg man uses 0.24 L O_2 min^{-1} asleep, 0.80 walking at 5 km/h and 2.12 running cross-country [389]. Kleiber used body weight to the ¾ power as the unit for comparing metabolism across 13 groups [1239]. Mammal basal rate in 619 species of 19 orders, corrected for temperature, digestive state and phylogeny, scales as M^2/3 [1241].

About 150 species spanning three to four orders of magnitude suffice to estimate the mammal exponent; the dataset then held about 600 species over five orders [1520]. A ¾

exponent follows from space-filling fractal branching networks [1240]. The measured values ¾ and ⅔ both stand.

A 2005 paper gives 4,600 extant mammal species, and the 2013 count 16,014 including fossils [587, 1520]. White-nose syndrome cut three bat species by more than 90 % at 200 sites over 1995–2018 [949].

Birds

Birds are the living descendants of a dinosaur lineage. The IOC World Bird List of 13 April 2026 holds 11,227 species, 164 of them extinct, in 44 orders, 251 families and 2,389 genera [1521]. The 11,063 living species are 0.73 % of described living animals, and about 50 billion individual birds live today [1522].

Birds are bipedal amniotes with the forelimbs as wings [1523]. A 2019 paper gives “about 10,000 extant bird species”, and a 2013 count 11,087 [587, 1523].

First traces

Nyasasaurus parringtoni, from the Middle Triassic of Tanzania, is “either the earliest known member of Dinosauria or the sister taxon” to it [1524]. The first dinosaur radiation possibly began 15 Myr (63.91) earlier than thought [1524].

The eleventh *Archaeopteryx* skeleton known since 1861 has pennaceous feathers over the whole body, with long symmetrical feathers on the shank [1525]. *Asteriornis maastrichtensis*, from the Maastrichtian of Belgium, 66.8–66.7 Ma (65.27), is one of the only well-supported Mesozoic crown birds and the first with a well-represented skull [1526]. It weighed about 394 g [1526].

A study of 363 species in 218 families, 92 % of families, used 63,430 intergenic loci [1527]. Neoaves “experienced rapid radiation at or near the Cretaceous–Palaeogene boundary”, dated 66.043 ± 0.011 Ma (65.26), and only two Neoaves divergences predate it [1527].

Split (crown age)	Age, Ma (95 % CI)	Position
Mirandornithes	67.4 (66.2–68.9)	65.28 (65.26–65.30)
Columbaves	66.5 (65.2–67.9)	65.27 (65.25–65.29)
Passeriformes crown	50.7 (48.3–53.0)	65.02 (64.98–65.06)
Tyranni–Passeri	47.3 (45.1–49.8)	64.96 (64.91–65.00)
Corvides	25.7 (23.8–27.7)	64.40 (64.33–64.47)
Passerides subclade	22.4 (20.6–24.2)	64.28 (64.20–64.35)

Values from [1527]. An earlier study used 198 species and 259 nuclear loci, more than 390,000 bases per species, and placed a major radiation of crown birds “in the wake of” the K–Pg extinction [1528].

From *Asteriornis* to the boundary is 0.66–0.76 Myr (61.07–61.20). From the boundary to the passerine crown is 66.04 − 50.7 = 15.3 Myr (63.93), and from the passerine crown to Corvides 25.0 Myr (64.38).

Sizes

The smallest bird is the bee hummingbird *Mellisuga helenae*, 5–6 cm long (12.66–12.83) [1529]. Adult males weigh 1.74 ± 0.06 g (n = 8) and females 2.2 g [1529].

The ruby-throated hummingbird weighs 3.1 g as an adult and 0.62 g at hatching, 20 % of adult mass [1530]. The Laysan albatross weighs 3,150 g as an adult and 167.2 g at hatching, 5.3 % [1530].

The largest bird known is the extinct elephant bird *Vorombe titan* of Madagascar, with a mean body mass of “almost 650 kg” [1531]. The largest living bird in AnAge is the ostrich, 111,000 g [1530]. Living adult mass runs from 1.74 to 111,000 g, a factor of 6.4 × 10^{4}, and with *Vorombe* 3.7 × 10^{5}.

Times

Species	Maximum longevity	Position	Maturity	Position	Incubation	Position	Clutch
Major Mitchell’s cockatoo	83 years (captivity)	52.89	breeding from about 5 years	50.34	—	—	—
Laysan albatross	70 years (wild)	52.74	female 3,141 days (8.6 years); male 3,068 days (8.4 years)	50.83; 50.81	64 days	47.28	1
Ostrich	50 years (captivity)	52.43	female 1,000 days (2.7 years)	49.79	—	—	—
Ruby-throated hummingbird	9.1 years (wild)	50.88	365 days	48.87	13 days	45.83	2

Values from [1530]. The cockatoo record is “Cookie”, who died at Brookfield Zoo in 2016 [1530]. Maximum lifespans span 9.1 to 83 years, a factor of 9.1.

Two hummingbirds were measured in the laboratory [1532]:

Species (mean mass)	State	Heart rate (min⁻¹)	Ambient
Lampornis clemenciae (7.9 g)	resting minimum	480–510	35 °C
	maximum	1,200–1,260	35 °C
	torpid	140; 36	24 °C; 15 °C
Eugenes fulgens (6.6 g)	resting minimum	420	34 °C
	maximum	1,200	34 °C
	torpid	120; 107; 55	22.6; 20.5; 15 °C

The maximum is about 20–21 beats a second in both species [1532]. A beat at 1,260 a minute lasts 0.048 s (30.38) and in torpor at 36 a minute 1.67 s (33.62); within one species the range is 1,260 / 36 = 35-fold. The pigeon’s infraslow sleep rhythm has a

period of 49 s (36.70) [1490].

Repeated units

Birds are bilateral and bipedal, with a rigid trunk, a short fused tail, three-segmented legs and digitigrade feet [1523]. The neck lengthens with body size, unlike in mammals, and scales isometrically with total leg length; cervical count tracks phylogeny, with only a few specialist groups unusually high [1523]. Swans have 22–25 cervical vertebrae [1511].

Sixty-six penguin specimens of six species were counted [1533]. The modal formula is 13 cervical + 2 cervicothoracic + 6 thoracic + 13–14 synsacral + 6–7 caudal + pygostyle, total 41–42 [1533].

Aptenodytes forsteri and *Eudyptes chrysocome* have 13 synsacral and 7 caudal, total 42; the three *Pygoscelis* species 14 and 6, total 42; *Spheniscus magellanicus* 13 and 6, total 41 [1533]. All six species have 13 cervical vertebrae, with “no intraspecific variation”; earlier reports range from 13 to 15 [1533].

Species (n)	Variants within species
Pygoscelis adeliae (20)	2 homeotic (T7, S13); 3 extra caudal (total 43); 1 missing thoracic (T5, total 41)
Pygoscelis papua (9)	1 extra caudal (43); 1 missing synsacral (41); 2 missing caudal (41)
Aptenodytes forsteri (3)	1 extra thoracic (T7, total 43)
Spheniscus magellanicus (32)	1 homeotic (T7, Ca5); 8 extra synsacral in the table, 11 in the text; 2 or 3 extra caudal; 2 with five thoracics (text only)

Values from [1533].

Totals within *P. adeliae* and *P. papua* are 41, 42 and 43, steps of 1. Specimens off the modal total are 4 / 20 = 20 % in *P. adeliae*, 4 / 9 = 44 % in *P. papua* and 1 / 3 = 33 % in *A. forsteri*. Off the modal formula are 6 / 20 = 30 % of *P. adeliae*, 2 of them homeotic.

The neck holds 13 units without exception; the trunk and tail vary by one unit around their totals.

Handedness

In white-winged crossbills *Loxia leucoptera* the lower mandible crosses to the left in a minority [1534]:

Sample	Left / total	Share left
Northern Ontario, wild-caught, 1987	43 / 145	29.7 %
Riding Mountain NP, Manitoba, wild-caught	11 / 49	22.4 %
National Museum of Canada (since the late 1800s)	88 / 309	28.5 %
American Museum of Natural History	39 / 141	27.7 %
Museum of Vertebrate Zoology	37 / 140	26.4 %
Pooled	218 / 784	27.8 %
Females	90 / 288	31.2 %

Males	100 / 411	24.3 %

No sample differs from 3 : 1, while females are more left-crossed than 3 : 1 [1534]. In two families in 1987, all 4 adults and 7 offspring crossed to the right [1534].

In red crossbills *L. curvirostra*, 1,895 of 3,647 North American specimens are left-crossed, 52.0 % [1535]. Males are 1,182 of 2,256 left (52.4 %) and females 713 of 1,391 (51.3 %) [1535]. In a small-billed subset with lower mandible width of 9.0 mm or less, 411 are left and 403 right of 814 [1535].

Two left-billed captive parents gave 7 offspring in three broods, 2 of them right-billed [1535]. Under a left-dominant model the allele frequencies are 0.307 left and 0.693 right [1535]. The pooled white-winged sample was recomputed as $\chi^2 = 3.29$, and the females as $\chi^2 = 6.0$, against 4.50 in the original [1534, 1535].

Females of “most bird species” develop only the left ovary [1536]. The white-browed coucal has the larger left testis, the general avian pattern; five coucal species have a larger right testis, and two have no left testis [1536].

The crossbill bill has one direction in each bird, and the two species hold different shares: 27.8 % left in one, 52.0 % in the other. The ovary has one direction in almost all birds: the left.

Brains, energy and numbers

Parrots and songbirds have on average twice the neurons of primates of the same brain mass [1537]. Birds hold 4.5 cerebellar neurons per hindbrain neuron, and most bird clades about 3 pallial neurons per neuron in the rest of the brain; owls hold 12 [1499].

Flight metabolism in two hummingbirds is “nearly ten-fold” resting [1532]. Their resting rate is 2.3 and 2.7 $cm^3\ O_2\ g^{-1}\ h^{-1}$, and in torpor 0.10–1.18 $cm^3\ O_2\ g^{-1}\ h^{-1}$ at 14.9–26.9 °C, 0.04–0.51 of rest [1532].

Species	Body mass	Basal rate	W kg^{-1}
Ruby-throated hummingbird	3.2 g	0.0783 W	24.5
Laysan albatross	2,522 g	7.462 W	2.96
Ostrich	100,000 g	69.63 W	0.696

Values from [1530]. Over a 31,000-fold rise in mass the mass-specific rate falls 35-fold. The two-point exponent from hummingbird to ostrich is log(69.63 / 0.0783) / log(100,000 / 3.2) = 0.656, and from albatross to ostrich 0.607.

Of 248 species, 67 met the data criteria for avian basal-rate allometry; they give log BMR = −1.461 + 0.669 log Mb, 10–12 % lower than the earlier analysis [1538]. Passerines and other birds do not differ once phylogeny is included [1538].

With the rate in W and the mass in g, the equation predicts 0.0753 W at 3.2 g, 6.53 W at 2,522 g and 76.6 W at 100 kg. The AnAge values are 1.04, 1.14 and 0.91 times these.

Bird abundance estimates cover about 9,700 species, about 92 % of extant species, with a strongly skewed distribution: many rare species and few common ones [1522]. The mean is 5×10^{10} / 9,700 = 5.2 million individuals per species.

What this part of the history shows

Every body in this chapter has one direction, and the populations differ in which one: “The rule is symmetric … which direction wins, the rule does not say.” Land-snail faunas are 75.2–99.4 % dextral, while one *Partula* population is 97.9 % sinistral. *Uca lactea* holds 50.3 % right against 49.7 % left over 8,088 males.

The variants of the form are measured species by species. A species may hold one direction almost alone, as *U. marionis* at 97.7 % right, the *Lymnaea* pond at 0.37–2.4 % sinistral or 708 of about 715 flatfish species with a fixed eye side. It may hold both, as *Partula suturalis* at 59.3 % sinistral, *Amphidromus inversus* at 0.65, *Platichthys stellatus* at 0.45–1.00 by site and *Loxia curvirostra* at 52.0 % left.

Where both directions are held, each body still has one. A crab’s large claw, once set within its first 96–192 h (44.76–45.39), is not reversed; a *Nala* earwig keeps one penis for 64–143 days (47.28–48.02); a crossbill keeps one crossing. Here each body is a strand with one direction.

The direction passes through the mother. In *Lymnaea* it is set before or during the first cleavages by the mother’s genes, and in *Partula* maternal expression is delayed one generation. In *Amphidromus* inheritance is delayed and single-gene, and *Portunus* mothers give young that are 97–100 % right-handed.

The direction can swing. The scale-eating *Perissodus* keep their righty share within 0.4–0.6 and swing about one half every 3.9–4.1 years (50.11–50.15). The form is loading and discharge between the two sides of one species.

The body repeats one unit, and within a species the count steps by one. Cod vertebrae run 51–58, *Aporrectodea* segments 92–177 with 43 distinct values, hynobiid trunk vertebrae around modes of 67 % and 89 %, penguin totals 41–43. In adult geophilomorph centipedes the step is 2, always odd, and in their embryos 1.

Some counts are closed. Leeches have exactly 32 segments; all six penguin species have 13 cervicals; mammals have 7; chitons have 8 plates in 99.39–99.91 % of each sample (computed). Others are open: 198–330 segments in *Eumillipes*, 354–391 trunk vertebrae in *Mitophis leptepileptus*.

A millipede repeats a module of 16 leg pairs, a snake one vertebra up to 546 times, and an octopus arm about 7.5 nerve segments per sucker. Sets of three show in the epipodites of the first crustaceans and in the three tagmata of the stem chelicerates.

Context sets the counts: a *Strigamia* embryo at 18 °C has about 1.5 more segments than one at 10 °C. Medaka abdominal vertebrae rise from 11 to 13 with latitude, and the starry flounder’s sinistral share falls with distance from Japan. Metabolic exponents run 0.73–0.98 in cephalopods, 0.669 in birds and ⅔ to ¾ in mammals, and across 938 vertebrates no single allometry holds.

Insect flight opens once, at about 406 Ma (66.91), and fills 1,070,781 described species of an estimated 5.5 million. The molluscs fill 118,061 described species, the crustaceans 66,914, the fishes 35,644 and the birds 11,063. The bodies run from a 139 µm wasp (7.30) to a 25.8 m whale (18.34), and their lives from 5 days (44.96) to 507 years (54.54).

16. The Great Dyings and the Refilling

Animals had spread into every sea and onto the land (chapter 15). The record of their spread is not a smooth rise.

Five times in the last 540 million years the Earth lost more than three-quarters of its species in a geologically short interval [1543]. Each time the emptied places filled again.

This chapter follows the dyings in time order. It begins with the rise of oxygen, near 2.4 Ga, and the first animal extinction at the end of the Ediacaran.

It then takes the five great events: end-Ordovician, Late Devonian, end-Permian, end-Triassic and end-Cretaceous. For each it gives the date, the losses, the duration and the measured times of refilling.

After the five, the chapter compares them, places them on the long curve of diversity and gives the background rate between them. It ends with the rate of loss measured today.

Every age carries its position on the ladder of chapter 1. A time of A million years sits at $\log_3$ of $A \times 10^6 \times 3.15576 \times 10^7$ s over 1.520655×10^{-16} s.

The clock of the dyings

The dates come from the International Chronostratigraphic Chart of 2023 [435]. The five boundaries used here are the base of the Hirnantian, the base of the Famennian, the base of the Triassic, the base of the Jurassic and the base of the Paleogene.

Boundary	Age	Position	Source
Base of the Hirnantian (end-Ordovician)	445.2 ± 1.4 Ma	67.00	[435]
Base of the Silurian (Rhuddanian)	443.8 ± 1.5 Ma	66.99	[435]
Base of the Frasnian	382.7 ± 1.6 Ma	66.86	[435]
Base of the Famennian (Late Devonian, Kellwasser)	372.2 ± 1.6 Ma	66.83	[435]
Base of the Carboniferous (Hangenberg)	358.9 ± 0.4 Ma	66.80	[435]
Base of the Capitanian	264.28 ± 0.16 Ma	66.52	[435]
Base of the Wuchiapingian	259.51 ± 0.21 Ma	66.51	[435]
Base of the Triassic (end-Permian)	251.902 ± 0.024 Ma	66.48	[435]
Base of the Olenekian	251.2 Ma	66.48	[435]
Base of the Anisian	247.2 Ma	66.46	[435]

(Middle Triassic)			
Base of the Carnian	about 237 Ma	66.42	[435]
Base of the Norian	about 227 Ma	66.38	[435]
Base of the Jurassic (end-Triassic)	201.4 ± 0.2 Ma	66.27	[435]
Base of the Paleogene (end-Cretaceous)	66.0 Ma	65.26	[435]
Base of the Selandian	61.6 Ma	65.20	[435]
Base of the Eocene	56.0 Ma	65.11	[435]

The gaps between the five events are 445.2 − 372.2 = 73.0 Myr, 372.2 − 251.902 = 120.3 Myr, 251.902 − 201.4 = 50.5 Myr and 201.4 − 66.0 = 135.4 Myr (computed). Their positions are 65.35, 65.81, 65.02 and 65.91. From the first event to the last is 445.2 − 66.0 = 379.2 Myr, position 66.85 (computed).

The uncertainty on the ages shrinks with time. It is ±1.4 to ±1.6 Myr at the Palaeozoic boundaries, ±0.2 Myr at the base of the Jurassic and ±0.024 Myr at the base of the Triassic [435]. The Early Triassic, from the base of the Induan to the base of the Anisian, lasts 251.902 − 247.2 = 4.7 Myr (computed), position 62.85.

The Cambrian begins at 538.8 ± 0.2 Ma, position 67.17, and the Ediacaran at about 635 Ma, position 67.32 [435].

Oxygen and the first turnover

The first great change in the surroundings of life was the rise of free oxygen. Multiple sulfur isotopes in pyrite from three coeval drill cores in South Africa place the transition to permanent atmospheric oxygen at about 2.33 Ga, position 68.50 [225]. The change there was rapid, “within roughly 10 Myr”, and a slower rise of ocean sulfate followed [225].

A second record dates the first global glaciation and the onset of oxygenation between about 2.460 and 2.426 Ga, positions 68.55–68.54 [226]. It rests on a U–Pb age of 2.426 ± 0.003 Ga for magmatism of the Ongeluk Formation [226]. In this record oxygen oscillated for about 200 Myr, until about 2.250–2.240 Ga, and the Lomagundi carbon excursion ended near 2.060 Ga, position 68.39 [226].

The two onsets, 2.33 Ga [225] and 2.46–2.43 Ga [226], differ by 2.46 − 2.33 = 0.13 Gyr, position 65.88 (computed). Free oxygen stayed “a scarce commodity” until about 2 Ga [1014]. Today the air holds about 21 % O_2 [1014].

The record of this time is a sequence of first appearances. Most living cyanobacteria descend from multicellular ancestors, and reversals to single cells occurred “at least 5 times” [415].

Their multicellularity arose “possibly as early as” the oxidation, 2.45–2.22 Ga, positions 68.55–68.46 [415]. A second study places it “before 2.4 billion years ago”, together with a rise in diversification rate, and gives the oxidation as 2.45–2.32 Ga [416].

The oldest conclusive cyanobacterial fossils of all five sections date to about 2.15 Ga, position 68.43, and fossil resting cells (akinetes) to about 2.00 Ga, position 68.36 [415].

In black shales of the Francevillian B Formation, Gabon, 2.1 Gyr old (position 68.41), large colonial organisms reach “up to 12 cm in size” [418]. A 12 cm body has size position 13.46 (computed).

The Gabon sediments were laid down “under an oxygenated water column” [418]. They follow the oxygen rise by 2.33 − 2.1 = 0.23 Gyr or 2.46 − 2.1 = 0.36 Gyr, positions 66.40 and 66.80 (computed).

The cell that took in a cell came next (chapter 5). The mitochondrial symbiosis is dated 2.053–1.21 Ga, and crown eukaryotes younger than 1.84 Ga [111].

A clock on 733 taxa and 320 nuclear genes places the last eukaryotic common ancestor at 2,386–1,958 Ma, positions 68.53–68.35 [342].

Probable crown red algae from the Tirohan Dolomite, central India, date to 1,650 ± 89 Ma, position 68.19 [355]. Their filaments are 58–175 µm wide, size positions 6.51–7.51 [355]. *Bangiomorpha pubescens* first appears at 1.047 +0.013/−0.017 Ga, position 67.78, and eukaryotic photosynthesis is placed near 1.25 Ga, position 67.94 [356].

A second oxygenation follows the Marinoan glaciation. Basal black shales of the Doushantuo Formation, South China, about 635–630 Ma (positions 67.32–67.31), record “a widely oxygenated ocean” [449]. From the first oxygen rise to this second step is 2,330 − 635 = 1,695 Myr, position 68.21 (computed).

The end of the Ediacara biota

The first animal extinction comes at the close of the Ediacaran. The Ediacara biota forms three assemblages that follow one another in time [1539]. The Avalon assemblage spans about 575–560 Ma, the White Sea about 560–550 Ma and the Nama about 550–539 Ma [1539].

Assemblage	Span	Duration	Positions	Source
Avalon	575–560 Ma	15 Myr	67.23–67.21	[1539]
White Sea	560–550 Ma	10 Myr	67.21–67.19	[1539]
Nama	550–539 Ma	11 Myr	67.19–67.17	[1539]

The durations are computed from the spans: 15 Myr has position 63.91, 10 Myr 63.54 and 11 Myr 63.63. The oldest architecturally complex Ediacaran fossils, at Mistaken Point, Newfoundland, date to 574.17 ± 0.66 Ma, position 67.23 [450].

Across the White Sea–Nama transition “~80% of taxa are absent” [1539]. The authors set this loss beside the mass extinctions of the Phanerozoic. The ecological traits they examined show “minimal differences between these two assemblages” [1539].

In the youngest Ediacaran strata of southern Namibia, the Farm Swartpunt assemblage “has significantly lower genus richness than older assemblages” after correction for sampling [1540]. Its geochemistry shows “an oxygenated non-restricted palaeoenvironment” [1540]. The authors read this as “first quantitative support for the biotic replacement model” [1540].

One reading ties the end to oxygen and the surroundings [1539]. The other reads it as replacement by Cambrian-type ecosystem engineers in oxygenated water [1540].

The end of the Nama interval, about 539 Ma, lies 539 − 538.8 = 0.2 Myr before the base of the Cambrian (computed), position 59.98. From the oldest complex fossils to the Cambrian base is 574.17 − 538.8 = 35.4 Myr, position 64.69 (computed).

The first measured animal extinction thus falls about 11 Myr before the Cambrian. It falls 2,330 − 550 = 1,780 Myr or 2,460 − 550 = 1,910 Myr after the first oxygen rise (computed), positions 68.26 and 68.32.

The end-Ordovician dying

The end-Ordovician event is the “first of the five big Phanerozoic extinction events” [1541]. It is also the first to strike communities built of animals [1541]. It sits at the base of the Hirnantian, 445.2 ± 1.4 Ma, position 67.00, 1.4 Myr before the base of the Silurian (computed), position 61.75 [435].

It came in two phases, both tied to a brief and intense glaciation centred on the South Pole [1541]. The first phase falls at or just below the *Normalograptus extraordinarius* graptolite biozone. It struck swimming, floating and shallow-shelf species [1541].

The second phase falls within the *N. persculptus* biozone. It was less selective and reached all water depths [1541]. It is tied to widespread anoxia during a late Hirnantian rise of sea level [1541].

Three primary sources give the loss. Harper and colleagues write that “about 85% of marine species were removed” [1541]. Sheehan gives “about 85% of marine species died” [1542], and a table of the five events gives about 86 % of species, with an end near 443 Ma [1543].

The same table gives a duration of 3.3 to 1.9 Myr, positions 62.53–62.03 [1543]. It names the cause as the “Onset of alternating glacial and interglacial episodes” [1543]. Models of CO_2 require no more than 1,500 ppm for this glaciation [1003].

Recovery “took several million years” [1542]. The second extinction “marked the end of a long interval of ecologic stasis” [1542].

In a study of origination and extinction across the Phanerozoic, the end-Ordovician intensity “appear[s] as outliers” against neighbouring stages [1544]. That outlier is “generated exclusively by elevated extinction” [1544].

The Late Devonian crisis

The Late Devonian crisis has two dated steps. The Kellwasser event sits at the base of the Famennian, 372.2 ± 1.6 Ma, position 66.83.

The Hangenberg event sits at the base of the Carboniferous, 358.9 ± 0.4 Ma, position 66.80 [435]. The two are 372.2 − 358.9 = 13.3 Myr apart, position 63.80 (computed).

Stigall dates the Frasnian–Famennian crisis to about 375 Ma, position 66.84 [1545]. That date and the chart’s 372.2 Ma [435] differ by 2.8 Myr, position 62.38 (computed).

Here the loss came more from a fall in the birth of species than from a rise in deaths.

“The primary cause of biodiversity decline was reduced speciation during the crisis interval” [1545]. Of all identified invasion events, “68% … occurred in the Frasnian”, and “65% of Frasnian invasion events correlate with transgressive events” [1545].

Speciation by splitting of ranges (vicariance) made up “only 12% to 50%” of quantifiable speciation events per clade [1545]. Over all clades it was 28 % against 72 % by dispersal [1545]. Bambach and colleagues class the late Frasnian as a “mass depletion”: “Low origination contributed more than high extinction” [1544].

The reef was the largest single loss. The crisis brought “a fundamental collapse of the reef ecosystem” [1545].

The extent of the Middle Devonian reef ecosystem “was reduced by a factor of 5000” [1545]. That leaves 1 / 5,000 = 0.02 % of the former extent (computed).

Brachiopods record three pulses [1546]. “The transgressive/hypoxic Lower Kellwasser Event” had “only a regional destructive effect” [1546].

The atrypids ended with the Upper Kellwasser Event, and the Frasnian–Famennian event followed a “catastrophic eustatic fall during the late *Palmatolepis linguiformis* Zone” [1546]. The overall pattern is a “moderate diversity and stepdown but irregular extinction pattern” [1546].

Entomozoacean ostracods in the Holy Cross Mountains of Poland give a local count [1547]. The background assemblage was “moderately diverse (10 species)” [1547]. Extinction came “in two closely spaced steps within the *Palmatolepis linguiformis* conodont Zone”, and the first step left “only two *Entomoprimitia* species” [1547].

The loss from 10 to 2 species is 80 % (computed). In the recovery “Some 13 species have been identified and assigned to seven genera” [1547]. That is 13 / 10 = 1.3 times the count before the event (computed).

The table of five events gives the Devonian about 75 % of species, a duration of 29 to 2 Myr (positions 64.51–62.08) and an end near 359 Ma [1543]. It names “Global cooling (followed by global warming)” [1543]. Two plant innovations of the Devonian stand beside the crisis: trees with deep roots and the seed habit [997].

They are linked to faster weathering, nutrients carried to shallow seas, algal blooms, anoxia and burial of organic carbon [997]. Lower CO_2 and cooling followed, with a brief Late Devonian glaciation [997]. Plants on land and life in the sea thus changed together (chapter 11).

The end-Permian dying

Before the largest dying came two smaller ones. Sahney and Benton date two Guadalupian events to about 270 and 260 Ma, positions 66.54 and 66.51, before the end-Permian event at 251 Ma [1548].

The timing. Five volcanic ash beds at the boundary section of Meishan, China, were dated by U–Pb on zircon [1021]. They place the extinction “between 251.941 ± 0.037” and “251.880 ± 0.031 Mya”, “an interval of 60 ± 48 ka” [1021]. The span is 251.941 − 251.880 = 0.061 Myr, or 61 kyr (computed), position 58.90.

The end of that interval lies 251.902 − 251.880 = 0.022 Myr after the chart's base of the Triassic (computed), position 57.97. Carbon in limestone shows a "sharp (3‰), short-lived negative spike" [1021]. The carbon cycle stayed unsettled and "persists for ~500 ka" before it returned near its earlier values, position 60.81 [1021].

The authors call it the most severe loss of life in "the last 542 My" [1021]. The table of five events gives a duration of 2.8 Myr to 160 kyr, positions 62.38–59.78, and names "Siberian volcanism" [1543].

The loss. Raup wrote in 1979 that "as many as 96 percent of all marine species may have died out" [1549]. The table of five events also gives about 96 % [1543]. Chen and Benton give ">90% species globally" [1551].

Stanley gives about 81 % of marine species against the often quoted 90–96 % [1550]. In his count at least 90 orders and 220 families of marine animals survived [1550]. "Life did not nearly disappear at the end of the Permian, as has often been claimed" [1550].

Four species-level values thus stand for one event: 96 % [1549], 96 % [1543], more than 90 % [1551] and about 81 % [1550]. A genus curve corrected for sampling gives a "78% end-Permian extinction" [1552]. In the same curve "Early Triassic standing diversity is only 32% lower than Late Permian standing diversity" [1552].

The end-Permian intensity is an outlier "generated exclusively by elevated extinction" [1544]. The event "permanently reduced" the diversity of groups that had dominated before, such as brachiopods and crinoids [1553].

On land. Fungal remains make up 30–80 % of land-derived pollen and spores through the Changxing Formation of South China, at about 30 localities [924]. *Reduviasporonites stoschianus* forms more than 90 % of the basal Tesero assemblage [924]. Its cells are 10–90 µm long, size positions 4.91–6.91 [924].

The fungal spike took less than 1 Myr, position 61.45 [924]. In 1996 it was read as saprotrophs on dead wood [923].

In 2011 the same group read it as a *Rhizoctonia*-like soil pathogen [924].

Charcoal in mires puts atmospheric oxygen "continuously above 26 %" through the Carboniferous and Permian, with a sharp drop near the extinction [727]. Flammability was low to absent in the Early and Middle Triassic, 250–240 Ma, positions 66.47–66.43 [1007]. Insect feeding on plants collapsed at about 252 Ma and recovered by about 228 Ma, a span of 24 Myr, position 64.34 [990].

The refilling. Shocks to the surroundings "were repeated over the next 5–6 Myr" [1551]. The positions of 5 and 6 Myr are 62.91 and 63.08. Yet "Ammonoids and some other groups diversified rapidly, within 1–3 Myr", positions 61.45–62.45 [1551].

Reefs of "various sponges and serpulids associated with microbialites" formed in the western United States "only 1.5 million years after the extinction", position 61.81 [1554]. Recovery had been assumed to span "the full 5 million years of the Early Triassic" [1554]. Ecosystems were rebuilt in steps, from low to high levels of the food chain, through the Early to Middle Triassic [1551].

"A stable, complex ecosystem did not re-emerge until the beginning of the Middle Triassic, 8–9 Myr after the crisis" [1551]. The positions of 8 and 9 Myr are 63.34 and

63.45.

On the chart of 2023 the base of the Anisian lies 4.7 Myr after the base of the Triassic, position 62.85 [435]. The two spans, 8–9 Myr [1551] and 4.7 Myr [435], rest on different time scales.

New groups arose in the recovery. They include marine reptiles, decapod crustaceans and new tetrapods on land, and in time the dinosaurs [1551].

Reef-building scleractinian corals have their oldest fossils in the mid-Triassic, about 240 Ma, position 66.43 [528]. That is 251.9 − 240 = 11.9 Myr after the extinction (computed), position 63.70.

Sea urchins carry the line through the boundary. A clock places crown Echinoidea between the Pennsylvanian and the Cisuralian, with posterior probability 30.2 % for the late Carboniferous and 69.1 % for the early Permian [623]. The Euechinoidea span the Permian–Triassic boundary [623].

The end-Triassic dying and the dinosaurs

The rise before the boundary. The dinosaurs spread before the end-Triassic event, not after it. *Nyasasaurus parringtoni*, from the Middle Triassic of Tanzania, is “either the earliest known member of Dinosauria or the sister taxon” [1524]. By that find the first dinosaur radiation may have begun 15 Myr earlier than thought, position 63.91 [1524].

The Carnian Pluvial Episode, “234–232 Ma” (positions 66.41–66.40), brought humid pulses of “about 1.6/1.7 myr” [1558]. Footprints in the Dolomites track the change [1558].

Interval	Dinosaur tracks	Other tracks	Source
Before the episode (Julian)	0 %	crurotarsans 80–100 %	[1558]
Early Tuvalian	“40% of specimens”	non-dinosaurian dinosauromorphs 10 %; crurotarsans 50 %	[1558]
Late Tuvalian–Norian	more than 90 %	—	[1558]

The shift took “a relatively brief interval of about 3-4 myr”, positions 62.45–62.71 [1558]. Earlier counts of skeletons give a rise in the share of dinosaurs “from 5–10% to 70–90%” [1558]. The Late Triassic as a whole is “over 35 myr long”, position 64.68 [1558].

The dinosaur radiation spans “from 230 to 200 million years ago”, positions 66.40–66.27 [1557]. Early dinosaurs “exhibited lower disparity and indistinguishable rate of character evolution” against their crurotarsan competitors [1557]. The authors favour “historical contingency” over superiority or long competition [1557].

From the end-Permian, 251.9 Ma, to the Carnian Pluvial Episode is 17.9–19.9 Myr, positions 64.07–64.17 (computed). From the episode to the end-Triassic, 201.4 Ma, is 30.6–32.6 Myr, positions 64.56–64.62 (computed). The radiation of 230–200 Ma lasts 30 Myr, position 64.54, and ends within 1.4 Myr of the base of the Jurassic (computed).

The event. Zircon U–Pb dates link the end-Triassic extinction with the Central Atlantic Magmatic Province [1555]. Its magma came “in four pulses over about 600,000 years”, position 60.98 [1555]. Two marine sections place the boundary and the biological crisis within less than 150 kyr of the onset of the flood basalts, position 59.72 [1556].

The last Triassic negative carbon spike lies within less than 290 kyr of the boundary, position 60.32 [1556]. The correlation of crisis and volcanism was narrowed “by an order of magnitude” [1556].

The table of five events gives about 80 % of species, a duration of 8.3 Myr to 600 kyr (positions 63.37–60.98) and an end near 200 Ma [1543]. It names “Activity in the Central Atlantic Magmatic Province” [1543].

The corrected genus curve gives a “63% end-Triassic extinction” [1552]. The event is a “mass depletion”: “Low origination contributed more than high extinction” [1544].

The refilling. After 201.4 Ma the dinosaurs went on to “dominate Earth for the next 136 million years”, position 65.92 [1555]. 201.4 − 136 = 65.4 Ma, position 65.25 (computed). That lies within 0.6 Myr of the base of the Paleogene at 66.0 Ma.

Corals again built reefs. Isotopes in Late Triassic coral skeletons of about 212 Ma, position 66.32, show partnership with algae (photosymbiosis) [533]. From the oldest scleractinians, about 240 Ma, to this is 240 − 212 = 28 Myr, position 64.48 (computed).

The end-Cretaceous dying

The date and the impact. The extinction “occurred around 66 million years ago” [1559]. The impact “occurred within 33,000 years of the mass extinction”, position 58.34 [1559]. The atmospheric carbon cycle was “severely disrupted” for “less than 5000 years”, position 56.62 [1559].

A 41-author review ties the Chicxulub impact to the extinction at “approximately 65.5 million years ago”, position 65.25 [1560]. It names the event one of the three largest mass extinctions “in the past 500 million years” [1560]. The ages given are 65.5 Ma [1560], about 66 Ma [1559], 66.043 ± 0.011 Ma [1527] and 66.0 Ma [435], all at position 65.25–65.26.

The loss. The mass extinction “eradicated 76% of species on Earth” [1561]. The table of five events also gives about 76 %, with a duration of 2.5 Myr to “under a year” (positions 62.28 to below 48.87) [1543]. It names “A bolide impact in the Yucatán” [1543].

In the corrected genus curve “the 55% Cretaceous-Tertiary mass extinction does not register as a visible net change” [1552]. “There is little net change from the mid-Cretaceous through the Paleogene” [1552]. The end-Cretaceous is an outlier “generated exclusively by elevated extinction” [1544].

Who was lost. In western North America, of “59 species, four survived” among mammals [1563]. That is a “93% species extinction” and loss of “86% genera” [1563]. The check is 55 / 59 = 93.2 % (computed).

Among lizards and snakes “Species-level extinction was 83%” [1564]. Their diversity

“did not approach Cretaceous levels until 10 My after the change in faunal composition”, position 63.54 [1564].

The refilling at the crater. A core from the peak ring of the Chicxulub crater, Expedition 364, records the return [1561]. “Life reappeared in the basin just years after the impact” [1561]. “A high-productivity ecosystem was established within 30 kyr”, position 58.25 [1561].

The record covers about the first 200 kyr of the Palaeocene, position 59.98 [1561]. Elsewhere, in the Gulf of Mexico and the North Atlantic–western Tethys, export production took “300 thousand years (kyr) to return to levels similar to those of the Late Cretaceous”, position 60.35 [1561].

Nearness to the impact did not delay recovery [1561]. The ratio of the two times is 300 / 30 = 10 (computed).

The refilling on land. At Corral Bluffs in the Denver Basin, the record runs in steps: “Within ~100 thousand years”, “at ~300 ka” and “by ~700 ka” after the event [1562]. The positions are 59.35, 60.35 and 61.12. Within “the first million years” “mammalian taxonomic richness doubled” and there was “A threefold increase in dietary niche specialization” [1562].

There “body-mass shifts coincide with warming intervals” [1562]. In western North America local mammal diversity recovered “Within 300 000 years”, and regional diversity “rose to twice Cretaceous levels” [1563]. Insect feeding on plants recovered from 65.5 to 55.8 Ma, 65.5 − 55.8 = 9.7 Myr, position 63.51 (computed) [990].

The maximum body size of land mammals rose after the boundary and “leveled off 40 million years ago”, position 64.80 [1565]. It then “remained approximately constant” [1565]. The rise took 66.0 − 40 = 26 Myr, position 64.41 (computed).

Groups present before, filling after. A study scored “4541 phenomic characters de novo for 86 species” of mammals [1566]. It found that “crown clade Placentalia orders originated after the K-Pg boundary” [1566].

The crown bird *Asteriornis maastrichtensis*, from the Maastrichtian of Belgium, lived 66.8–66.7 Ma (position 65.27) and weighed about 394 g [1526]. It lies 0.66–0.76 Myr before the boundary at 66.043 Ma (computed), positions 61.07–61.20. Only two divergences within Neoaves predate the boundary [1527].

Neoaves “experienced rapid radiation at or near the Cretaceous–Palaeogene boundary” [1527]. Thirty-six lineages arose within 10–15 Myr after 66 Ma, positions 63.54–63.91, and nearly all ordinal splits were done by 50 Ma, position 65.01 [1272].

The crown of the passerines dates to 50.7 Ma, 66.04 − 50.7 = 15.3 Myr after the boundary (computed), position 63.93 [1527]. A further study places a major radiation of crown birds “in the wake of” the extinction [1528].

Plants and sea urchins show the same timing. The oldest unequivocal legume fossil dates to 65.35 Ma, position 65.25 [1129]. That is 66.0 − 65.35 = 0.65 Myr after the boundary (computed), position 61.05.

Sand dollars (Scutelloida) originate before the boundary with posterior probability 1.00, and clypeasteroids with 0.97 [623]. That lies at least 40–50 Myr, possibly 65 Myr, before

their first fossils, positions 64.80–65.01 and 65.25 [623].

Among seed plants, the rise in seed size was already under way before the boundary [1271]. Seed and fruit sizes then fell at the Eocene–Oligocene shift, about 34 Ma (position 64.66), and stayed low [1271].

The five compared

Raup and Sepkoski compiled marine families in 1982. They found that “four mass extinctions in the marine realm are statistically distinct from background extinction levels”: the Ordovician, Permian, Triassic and Cretaceous events [1567]. A fifth, the Devonian, stands out but does not reach significance in those data [1567].

With Sepkoski’s genus compendium only three events stand out as a separate class after the Early Ordovician [1568]. In that record “18 intervals during the Phanerozoic have peaks of both magnitude and rate of extinction” [1568]. No consensus exists on the kill mechanism of any marine mass extinction [1568].

Bambach, Knoll and Wang divide the Phanerozoic into “six stratigraphically coherent intervals of alternating high and low intensity” [1544]. End-Ordovician, end-Permian and end-Cretaceous are outliers of raised extinction [1544]. The late Frasnian and the end-Triassic are mass depletions with low origination, and each of the three mass extinctions “has a unique pattern of extinction” [1544].

Barnosky and colleagues define a mass extinction as a time when the Earth “loses more than three-quarters of its species in a geologically short interval” [1543]. This “has happened only five times in the past 540 million years or so” [1543]. The span of 540 Myr has position 67.17.

Event	Boundary age	Position	Species lost	Marine genera lost (corrected)	Duration	Class
End-Ordovician	445.2 ± 1.4 Ma [435]	67.00	about 85 % [1541] [1542]; about 86 % [1543]	—	3.3–1.9 Myr [1543]; two phases [1541]	extinction [1544]
Late Devonian	372.2 ± 1.6 Ma; 358.9 Ma [435]	66.83; 66.80	about 75 % [1543]	—	29–2 Myr [1543]	depletion (Frasnian) [1544]
End-Permian	251.902 ± 0.024 Ma [435]	66.48	96 % [1543] [1549]; >90 % [1551]; about 81 % [1550]	78 % [1552]	60 ± 48 kyr [1021]; 160 kyr–2.8 Myr [1543]	extinction [1544]
End-Triassic	201.4 ± 0.2 Ma [435]	66.27	about 80 % [1543]	63 % [1552]	8.3 Myr–600 kyr [1543]; four pulses over about 600 kyr [1555]	depletion [1544]
End-	66.0 Ma	65.26	76 % [1543]	55 % [1552]	2.5 Myr–	extinction

Cretaceous	[435]		[1561]		under 1 yr [1543]; impact within 33 kyr [1559]	[1544]

The mean of the five species values of one table is (86 + 75 + 96 + 80 + 76) / 5 = 413 / 5 = 82.6 % (computed). Their range is 75–96 %. The corrected genus losses of the last three events fall in time order, 78 → 63 → 55 % (computed from [1552]).

The long curve of diversity

Sepkoski's compendium holds "36380 marine genera" [1569]. After removal of genera of uncertain age and genera known from one occurrence, "the 17797 genera that remain" were used [1569]. That keeps 17,797 / 36,380 = 48.9 % (computed).

Of these, 13,682 short-lived genera, lasting 45 Myr or less, make up on average 44 % of diversity at any time [1569]. They carry 86 % of the amplitude of a cycle of 62 ± 3 Myr, position 65.20 [1569]. That cycle, 0.016 cycles per Myr, holds 35 % of the variance and is called "clearly significant" [1569].

A second cycle of 140 ± 15 Myr, position 65.94, 0.007 cycles per Myr, "can plausibly result from purely random processes" [1569]. Diversity "drops to a nadir near the Permian-Triassic boundary (251 Ma)" and then rises to the present [1569]. The record spans 0–542 Ma, position 67.18 [1569].

The Paleobiology Database gives a second curve [1552]. It holds 284,816 fossil occurrences of 18,702 genera in 44,446 collections, from 5,384 literature sources and about 3.5 million specimens [1552]. The data fall in 48 time bins of about 11 Myr each, position 63.63 [1552].

Corrected for sampling, diversity is "less than twice as high in the Neogene as in the mid-Paleozoic" [1552]. The last point is "a factor of 1.74 higher than the median Paleozoic point" [1552].

Raw counts give 3.74-fold between the late Neogene and the median Ordovician–Devonian interval, and 3.54-fold in Sepkoski's compendium [1552].

The corrected curve shows "a large mid-Devonian drop with no clear recovery until the Permian" [1552]. The radiation after the Palaeozoic is "largely confined to the Jurassic and Early Cretaceous" [1552].

Each major group has "a consistent net rate of diversification" and a limit [1553]. The limits change after radiations or extinctions, at different times in different taxa [1553].

A newer summary resolves Cambrian to Early Triassic marine invertebrates at "time intervals of ~26,000 years", position 58.12 [1570]. Against the bins of about 11 Myr that is 11 Myr / 26 kyr = 423 times finer (computed).

The pace between the dyings

The background. An older benchmark gives a background rate of "1 per million

species per year (E/MSY)” [1571]. Fossil data suggest “0.01 genera per million genera per year” [1571]. Median estimates for land plants and animals “ranged from 0.023 to 0.135 E/MSY”, and the background “may be closer to 0.1 E/MSY” [1571].

New species arise at “0.05-0.2 new species per million species per year” [1571]. That is the same order as the background loss of 0.1 E/MSY. The mean fossil background for mammals is “about 1.8 E/MSY” [1543].

Ceballos and colleagues take 2 mammal extinctions per 10,000 species per 100 years, which is 2 E/MSY, “about twice common estimates” [1572]. The values 0.1 [1571], 1 [1571], 1.8 [1543] and 2 E/MSY [1572] span 2 / 0.1 = 20-fold (computed). Background rates “appear to have declined since the Cambrian” [1567].

The lag of refilling. Across the whole marine record, extinction rates correlate with origination rates “roughly 10 million years later”, position 63.54 [1574]. They do not correlate with origination at the same time [1574]. The lag remains when the five great events are removed, so refilling after mass and background extinctions takes similar times [1574].

After	Group or measure	Lag	Position	Source
End-Cretaceous	life in the crater	years	—	[1561]
End-Cretaceous	high-productivity ecosystem at the crater	30 kyr	58.25	[1561]
End-Cretaceous	export production elsewhere	300 kyr	60.35	[1561]
End-Cretaceous	local mammal diversity	300 kyr	60.35	[1563]
End-Cretaceous	oldest legume	0.65 Myr	61.05	[1129] (computed)
End-Cretaceous	mammal richness doubled; threefold dietary specialisation	within 1 Myr	61.45	[1562]
End-Permian	ammonoids diversify	1–3 Myr	61.45–62.45	[1551]
End-Permian	sponge–serpulid–microbialite reefs	1.5 Myr	61.81	[1554]
End-Ordovician	recovery	“several million years”	—	[1542]
End-Permian	stable complex ecosystem	8–9 Myr; 4.7 Myr to the Anisian base	63.34–63.45; 62.85	[1551]; [435] (computed)
End-Cretaceous	insect herbivory	9.7 Myr	63.51	[990] (computed)
End-Cretaceous	lizards and snakes near Cretaceous levels	10 Myr	63.54	[1564]
End-Cretaceous	Neoaves, 36 lineages	10–15 Myr	63.54–63.91	[1272]
End-Permian	scleractinian corals	11.9 Myr	63.70	[528] (computed)
End-Cretaceous	passerine crown	15.3 Myr	63.93	[1527] (computed)

End-Permian	Carnian Pluvial Episode; dinosaur tracks rise	17.9–19.9 Myr	64.07–64.17	[1558] (computed)
End-Permian	insect herbivory	24 Myr	64.34	[990]
End-Cretaceous	maximum mammal body size levels off	26 Myr	64.41	[1565] (computed)
End-Triassic	dinosaur dominance	136 Myr from the boundary	65.92	[1555]

The lags fall in three bands. The first runs from years to 300 kyr, at the crater and in local mammals. The second runs 0.65–3 Myr, for legumes, ammonoids, reefs and mammal richness, and the third 8–26 Myr, for stable ecosystems, corals, birds, lizards and body size.

The reefs. Reef taxa show “greater turnover rates in reef taxa than in nonreef taxa” [1575]. The Phanerozoic reef record has a “boom and bust pattern” [1575]. “Threshold effects appear to be involved not only in crises”, and biological factors of competition for space are “probably more important” than geological controls [1575].

The reef record gives three measured steps. Reef extent fell 5,000-fold in the Late Devonian [1545]. Metazoan reefs returned 1.5 Myr after the end-Permian [1554], and the scleractinians appeared 11.9 Myr after it [528] and lived with algae by 212 Ma [533].

Today about 1,300 scleractinian species live, 656 of them reef builders and 669 not [528]. Severe bleaching of reefs now returns every 6 years, position 50.50, as the median over 100 reefs from 1980 to 2016 [566].

The present rate

“Current rates of extinction are about 1000 times the background rate of extinction” [1573]. “These are higher than previously estimated and likely still underestimated” [1573]. Against a background of 0.1 E/MSY that is 1,000 × 0.1 = 100 E/MSY (computed).

Vertebrate losses over the last century run up to 100 times the background of 2 E/MSY [1572]. At the background rate those losses would have taken 800 to 10,000 years, positions 54.95–57.25 [1572]. Current rates are commonly stated as “100-1000 times pre-human or background levels”, and future rates are “likely to be 10,000 times higher” [1571].

For mammals the recent average rates are “over 5” E/MSY in bins under 50 years, rising to 23 [1543]. Since 1,000 years ago the maximum reaches “E/MSY < 693 in 1-year bins” [1543]. The record holds “80 extinct of 5,570 species living in 500 years”, which is 80 / 5,570 = 1.44 % (computed) over 500 years, position 54.53 [1543].

Historic extinction runs “zero to 1%” across the groups assessed [1543]. Threatened species make up “20–43% of their species” for corals, amphibians, birds and mammals [1543]. If all threatened species were lost within a century and the rate went on, 75 % of species would be gone in about 240–540 years [1543].

The times are 241.7 years for amphibians, 334.4 for mammals and 536.6 for birds,

positions 53.87, 54.16 and 54.59 [1543]. The threshold of the five great dyings could thus be reached “in as little as three centuries” [1543].

What this part of the history shows

Long holding, short discharge. The dyings have the form of rest and discharge. The intervals between the five events are 73.0, 120.3, 50.5 and 135.4 Myr, positions 65.02–65.91. The discharges are short: the end-Permian loss took 60 ± 48 kyr, and the end-Cretaceous impact fell within 33 kyr of the extinction, positions 58.90 and 58.34.

Two ways to fall. The end-Ordovician, end-Permian and end-Cretaceous events are outliers of raised extinction [1544]. The late Frasnian and the end-Triassic are depletions in which new species failed to form [1544][1545]. In the first kind the closures discharge; in the second the loading stops.

The form outlasts its carriers. At the end of the Permian about 81 % to 96 % of marine species were lost, yet at least 90 orders and 220 families of marine animals survived [1549][1550][1543]. Standing diversity of genera fell only 32 % [1552]. The species are the carriers; the orders and families are the forms that hold.

What closes, stays. The curve of diversity has the form of a closure whose content flows through: corrected marine diversity rose only 1.74-fold from the median Palaeozoic to the last point [1552]. Brachiopods and crinoids never regained their share after the Permian–Triassic trough [1553]; the place they held was filled by others.

Opened once, filled many times. The refilling shows the form that evolution “is not selection on frequency … but the filling of depths until the next is forced”. Dinosaur tracks rose from 0 % to 40 % to more than 90 % between 234 and about 227 Ma [1558]. That is more than 25 Myr before the end-Triassic, after which dinosaurs held the land for 136 Myr [1555].

At the end of the Cretaceous some groups were present before the boundary and others arose after it. The crown bird *Asteriornis* lived 0.66–0.76 Myr before the boundary [1526], two Neoaves splits predate it [1527], and sand dollars had arisen before it [623]. Thirty-six bird lineages arose within 10–15 Myr after it [1272], placental orders arose after it [1566] and the first legume follows it by 0.65 Myr [1129].

The same winding at every depth. The refilling runs in the same order at three scales. At the crater life returned within years and a productive ecosystem within 30 kyr, elsewhere within 300 kyr [1561]; mammal richness doubled within 1 Myr [1562]. The full set of new groups filled over 8–26 Myr [1551][1272][1565].

After the Permian the order was the same: ecosystems rebuilt from the lowest levels of the food chain to the highest [1551]. Kirchner and Weil measure a lag of about 10 Myr, position 63.54, that is the same after mass and after background extinctions [1574].

The background. The background never falls to zero. It is given as 0.1, 1, 1.8 and 2 E/MSY, and new species arise at 0.05–0.2 per million species per year [1571][1543] [1572].

The same rule in other surroundings. The pace of loss is itself a value of its surroundings: background rates declined since the Cambrian [1567]. Today the rate

stands near 1,000 times the background, about 100 E/MSY [1573], with 20–43 % of species threatened in four groups [1543]. If all threatened species were lost within a century and the rate went on, 75 % of species would be gone in about 240–540 years, positions 53.86–54.60 [1543].

17. The Excitable Cell Becomes a Nerve

Every cell measured carries a voltage across its membrane, negative inside [136][134]. That voltage sits at the edge of the cell, where the living ring of chapter 1 meets uniform surroundings and its windows stand open. An excitable cell lets that voltage jump and return in a pulse.

This chapter follows the pulse from bacteria to brains. It begins with the voltage of the first cells and the channels that carry ions through the membrane. It then follows electrical signals in bacterial communities, protists, algae and plants, and the parts of the synapse that existed before any neuron.

The animals come next: the first nerve cells, the nerve nets of cnidarians and ctenophores, and the gathering of nerve cells into cords and brains. The chapter then gives the speed of the pulse, its cost in energy, the number of neurons in brains and the fate of the neuron as a cell that no longer divides. It ends with the human nervous system as it stands today.

The voltage at the edge of the first cells

No fossil dates the membrane potential. Clocks date the last universal common ancestor (LUCA), the ancestor of all cells now living. One clock places LUCA at about 4.2 Ga, position 69.04, within 4.09–4.33 Ga, positions 69.02–69.07 [97].

A composite range in the same study runs 3.94–4.52 Ga, positions 68.98–69.11 [97]. The first interval is 240 Myr wide, position 66.43, the composite 580 Myr, position 67.24 (computed). A second study places LUCA before 3.9 Ga, position 68.97, and crown Bacteria and crown Archaea after 3.4 Ga, position 68.85 [111].

All bacteria and archaea in the sources carry a membrane potential, negative inside. *Escherichia coli* holds about −140 mV during aerobic growth on glycerol and about −105 mV during fermentation of glucose [134]. “A typical bacterial membrane potential is around 150 mV, corresponding to Cin/Cex ≈ 350” [135].

The proton-motive force of respiring *E. coli* is 230 ± 15 mV, and of *Staphylococcus aureus* 211 ± 15 mV, from six determinations each at external pH about 6.5 [137]. For eukaryotic cells, resting potentials “between −40 and −95 mV are typical” [136]. The bacterial range, −105 to −150 mV, lies beyond it in magnitude (computed).

A bacterial cell has a surface of about 6 µm², a mammalian cell about 1,600 µm² [138]. The ratio is 1,600 / 6 = 267 (computed).

Single *E. coli* cells imaged with the voltage-sensitive protein PROPS spiked “at up to 1 hertz”, one spike per second, position 33.15 [139]. The spiking came with a rapid efflux of a small fluorescent molecule [139].

The channels

Proteins set in the membrane let ions through. A channel is a pore; a pump uses energy to move its load against the gradient [140]. The potassium channel KcsA is built of four identical subunits around one pore [141].

Its selectivity filter is 12 Å long, position −3.31, and holds two K^+ ions about 7.5 Å apart, position −3.74 [141]. The water-filled cavity is about 10 Å, position −3.48, and the whole pore 45 Å long, position −2.11 [141]. K^+ is "at least 10,000 times more permeant than Na^+" [141], and one Na^+ passes for every 10,000 K^+ [1576].

KcsA passes up to 10^8 ions per second, one ion each 10 ns, position 16.39 (computed) [141]. A typical open channel passes about 10^7 ions per second, about 0.1 µs per ion, position 18.48 [1577]. The sodium-potassium pump moves three Na^+ out and two K^+ in for each ATP [140][1578].

The pump runs about 450 cycles per second, one cycle in 2.2 ms, position 27.59 [1579]. It moves 5 × 450 = 2,250 ions per second, so the K^+ channel is 10^8 / 2,250 = 44,000 times faster (computed). K^+ is 10 to 20 times higher inside the cell than outside, and Na^+ the reverse [140].

The pump adds no more than 10 % of the resting voltage directly [140]. At rest the sodium-potassium pump uses a third of all ATP that is made [1578][152]. In the brain the estimates run from 20–40 % of all energy [1580] to three quarters of the energy of grey matter [1581].

Bacteria hold the same channel forms. The voltage-gated sodium channel NaChBac of *Bacillus halodurans* forms "four identical subunits, each of which contains six transmembrane segments" [146].

Its pore resembles that of voltage-gated Ca^{2+} channels and is blocked by Ca^{2+}-channel blockers [145]. The canonical eukaryotic Na^+ and Ca^{2+} channels carry four repeated six-segment domains in one chain; both forms give 4 × 6 = 24 transmembrane segments (computed) [145][148].

NaChBac moves about 16 elementary charges per channel when it opens [150]. Its gating currents appear at −90 mV from a holding potential of −150 mV and saturate at −10 mV [150]. A Cole–Moore shift of 533 µs, position 26.29, was found for a prepulse change from −160 to −80 mV [150].

In human cells NaChBac half-activates at −35.0 ± 1.3 mV and half-inactivates at −52.3 ± 1.3 mV [146]. The bacterial channel NavAb of *Arcobacter butzleri* has a water-filled filter about 4.6 Å wide, position −4.18, with four acidic side chains at its narrowest point [147]. The archaeal K^+ channel KvAP of *Aeropyrum pernix* carries positively charged "voltage-sensor paddles" on its outer edge [143].

Channel structure	Size	Position	Source
KvAP isolated voltage sensor, resolution	1.9 Å	−4.99	[143]
NavAb structure, resolution	2.7 Å	−4.67	[147]
KcsA structure, resolution	3.2 Å	−4.51	[141]
KvAP full channel, resolution	3.2 Å	−4.51	[143]
NavAb selectivity filter, width	about 4.6 Å	−4.18	[147]
KcsA, distance between two K^+ ions	about 7.5 Å	−3.74	[141]
KcsA water-filled cavity	about 10 Å	−3.48	[141]

KcsA selectivity filter, length	12 Å	−3.31	[141]
KcsA pore, length	45 Å	−2.11	[141]

The archaeal Ca^{2+}-gated K^+ channel MthK of *Methanobacterium thermoautotrophicum* carries eight RCK domains on its inner side [144]. A genome survey found “two sodium channels and one calcium channel in prokaryota” [149]. The Na^+ channels come from alkaliphilic bacteria, the Ca^{2+} channel from *Paracoccus* [149].

Waves in a bacterial community

In biofilms of *Bacillus subtilis* NCIB 3610, long-range electrical signals travel as waves of extracellular potassium [185]. The K^+ leaves through the channel YugO, gated by an inner TrkA domain, “the only experimentally characterized K^+ channel” of the species [185]. Deletion of *yugO* removed the release [185].

Inside, K^+ is about 300 mM, “nearly 40 times” the medium, which then holds about 300 / 40 = 7.5 mM (computed) [185]. No extracellular Na^+ oscillation was found [185]. More than 75 biofilms were analysed, each with “billions of densely packed cells” [185].

The signal was followed over a profile of about 1.5 mm, position 9.47 [185]. Its spread has a log-log slope of 1.1 (R^2 = 0.96), against 0.5 for diffusion [185]. K^+ diffusion, 19.7 × 10^{-6} cm^2 s^{-1} in water, was taken as 13.8 × 10^{-6} in the biofilm, 70 % (computed) [185].

The oscillations are metabolic [186]. Growth halts at intervals, which raises the supply of nutrients to cells deep inside [186]. The period “slightly increases over time”, and biofilm periods were imaged at one frame per 10 min, position 38.98 [186].

A model gives a period “on the order of hours” that grows with biofilm size, with onset only above a critical size [1582]. Oscillations begin when the biofilm holds “over one million cells” [187]. Other cells are drawn in [187].

Motile *B. subtilis* cells peak 26 ± 9 min after the biofilm’s electrical peak, position 39.85, over 44 pulses [187]. *Pseudomonas aeruginosa* cells peak 22 ± 13 min after it, position 39.69, over 30 pulses, with a mean interval of 2.1 h between peaks, position 41.28 [187]. A Δ*trkA* biofilm gives a signal 75 ± 4 % lower, and Δ*ktrA* motile cells are 57 ± 6 % more polarised and 239 ± 25 % more attracted [187].

The pulse in single eukaryotic cells

The channel families. Genes of the Na^+-channel type occur in the apusozoan *Thecamonas* and the choanoflagellate *Monosiga* [148]. “NaV-like channels emerged before nervous systems or even multicellularity evolved”, “more than a billion years ago”, position 67.73 [148]. Ca^{2+}-conducting Nav2 channels appeared before fungi and animals split, and Cav channels occur in green algae, which places Cav in the common ancestor of plants and animals [148].

NALCN diverged before Cav and Nav diversified [148]. The four-domain Nav arose by two rounds of duplication from a single-domain gene [148]. “All voltage-gated channel families are present in choanoflagellates” [148].

The choanoflagellate Na^+-channel homologue has a filter between that of Ca^{2+} and Na^+ channels [476]. In the same source, sodium channels “are believed to have evolved from calcium channels at the origin of the nervous system” [476]. The fast Na^+/Ca^{2+} action potential arose “in ancestral unicellular eukaryotes” and was kept in opisthokonts and stramenopiles [1583].

Four-domain Na^+/Ca^{2+} channels are “widespread” in eukaryotes; land plants and fungi have lost them [1584]. Single-domain channels of a new kind, EukCats in three classes, are “broadly distributed across major phytoplankton lineages” [1584].

Ciliates. In *Paramecium caudatum* depolarisation reverses the ciliary beat [1585]. The cell rests at about −62, −55.5, −44.7 and −30.3 mV at 0.1, 0.3, 1.1 and 5.1 mM external Ca^{2+} [1586]. Across 0.44–3.2 mM K^+ it rests at −38 to −43 mV, single cells range from −56 to −69 mV, and membrane resistance is 45–90 MΩ [1586].

The Ca^{2+} response overshoots by +5 to +15 mV and rises at up to about 7 V s^{-1} [1587]. The overshoot rises 22–25 mV per tenfold external Ca^{2+}, against a Nernst slope of 29 mV [1587]. That is 22 / 29 = 76 % to 25 / 29 = 86 % of the Nernst slope (computed).

The overshoot stays at least 100 mV short of the Ca^{2+} equilibrium potential, +64 to +133 mV for 0.016–4 mM, at 18 °C [1587]. Ba^{2+} and Sr^{2+} turn the graded response into an all-or-none one [1587]. Before stimulation the cilia beat at 13–27 Hz, one beat in 37–77 ms, positions 30.15–30.82 (computed) [1586].

Ciliary reversal lasts from 50 ms to 2.4 s, positions 30.43–33.95, longer with stronger stimuli, 2.4 / 0.05 = 48 times from shortest to longest (computed) [1585]. Reversal is suppressed at +70 mV and above [1585].

Paramecium tetraurelia holds about 40,000 genes and is “one of the gene-richest organisms” [1588]. It has 34 Ca^{2+}-release channel genes in 6 groups, diversified by whole-genome duplication [1589]. Its K^+ channels Pak1 and Pak2 are distantly related to animal Kv channels, with a conserved pore [1590].

By 1994 “over 50” K^+ channel sequences were known; all but two, both from plants, came from triploblast animals [1591].

***Paramecium* event**	**Duration**	**Position**	**Source**
“Off” latency	2–4 ms	27.50–28.13	[1585]
Reversal latency	30 to ≤4 ms	29.96–28.13	[1585]
Regenerative component absent below	30 ms	29.96	[1587]
Electrotonic time constant	40–50 ms	30.22–30.43	[1587]
Regenerative component reduced >75 % at	80 ms	30.85	[1587]
Refractoriness, up to	200 ms	31.69	[1587]

Green algae. *Chlamydomonas reinhardtii* has two light-regulated inward currents, one at the eyespot and one in the region of the flagella [1592]. Both depend on Ca^{2+} and are blocked by verapamil and pimozide [1592]. A photoreceptor current and a fast, action-potential-like flagellar current come before the light-avoiding (photophobic) response [1593].

During the flagellar current the flagella switch from forward to backward beating [1593]. The cell body has a radius of 4.4 ± 0.3 µm, position 4.16, and a flagellum of 13.5

± 0.8 µm, position 5.18 [1594]. It swims at about 75 µm s^{-1} on average, with peaks near 300 µm s^{-1} [1594].

The flagellum beats at 43.2 ± 8.0 Hz, one beat in 23 ms, position 29.73 (computed) [1594]. The body rotates at 1.67 ± 0.35 Hz, one turn in 0.60 s, position 32.69 (computed) [1594]. The product of rotation frequency and adaptation time is 1.27 ± 0.41; the check 1.67 × 0.764 = 1.28 agrees (computed) [1594].

***Chlamydomonas* event**	**Duration**	**Position**	**Source**
Response time τr	0.018 ± 0.009 s	29.50	[1594]
Phototransduction delay	28 ± 11 ms; 38 ± 5 ms	29.90; 30.18	[1594]
Time to peak	97 ± 18 ms	31.03	[1594]
Adaptation time τa	0.764 ± 0.190 s	32.91	[1594]
Reorientation	0.96 ± 0.36 s	33.12	[1594]
Recovery of flagellar asymmetry	about 1–2 s	33.15–33.78	[1594]

The same product is 1.20 ± 0.44 in *Volvox* and 0.95 ± 0.50 in *Gonium* [1594].

Diatoms and dinoflagellates. The diatom *Odontella sinensis* fires a fast Na^+/Ca^{2+}-based action potential, close in its properties to invertebrate and vertebrate muscle [1583]. The source calls it the “first demonstration” of voltage-activated Na^+ channels and Na^+-based action potentials in a single-celled photosynthetic organism [1583].

Its peak inward current is −19.7 ± 2.6 nA; activation is half-maximal at −58.5 ± 1.0 mV and inactivation at −69.4 ± 0.5 mV [1595]. The delayed outward current is 13.1 ± 1.1 nA [1595]. The action potential lasts 50–100 ms, positions 30.43–31.06, and recovery from inactivation has τ = 5.1 ± 0.4 ms, position 28.35 [1595].

In *Phaeodactylum tricornutum* single-domain EukCatA channels carry voltage-activated Ca^{2+} signals [1584]. They pass Na^+ and Ca^{2+} with fast kinetics like animal four-domain channels, and mutants glide poorly [1584].

Organism	**Channel count**	**Source**
Thalassiosira pseudonana (diatom)	1 putative four-domain Na^+/Ca^{2+} channel + single-domain channels	[1595]
Phaeodactylum tricornutum (diatom)	0 four-domain channels; EukCatA single-domain	[1595][1584]
Karenia brevis (dinoflagellate)	7 four-domain channels (transcriptome)	[1595]

Most diatom channel sequences are single-domain channels closest to NaChBac; only *T. pseudonana* has both kinds [1595].

The pulse in plants

Characean algae, the closest algal relatives of land plants, fire action potentials, as do flowering plants [1596]. A healthy *Chara* cell rests “around −200 mV”, “up to −250 mV”; one cell rested at −170 mV [1596]. Peaks reach near 0 mV, an amplitude of about 140 mV in a second cell [1596].

The Nernst potentials in *Chara* are E_K −177, E_Na −99, E_Ca +58 and E_Cl +100 mV [1596]. Cytoplasmic streaming stops within 1 s after the spike and recovers in about 250 s, position 38.18 [1596]. The half-amplitude duration is about 2–3 s, positions 33.78–34.15 [1596].

The absolute refractory period is 2–10 s and the relative one up to 90 s, positions 33.78–35.25 and 37.25 [1596]. In *Chara corallina* the action potential lengthens 30 times between 40 °C and 3.5 °C, from about 1 s to about 30 s, positions 33.15 and 36.25 [1597]. The activation enthalpy is about 7 kJ mol⁻¹ above 20 °C and about 350 kJ mol⁻¹ below 7 °C, while the peak amplitude is almost independent of temperature [1597].

The Venus flytrap. In *Dionaea muscipula* action potentials close the trap and switch on digestion [1598]. Three trigger hairs stand on each lobe, and about 37,000 glands line the inner surface [1599][1598]. Gland cells rest at −116 ± 19 mV and at −122 ± 14 mV when activated [1598].

The flytrap action potential lasts 2 s, position 33.78, and is 1.6-fold higher at 40 °C than at 10 °C [1599]. It induces a magnetic signal of up to 0.5 pT [1599]. Half-depolarisation takes 0.13 ± 0.02 s at 30 °C and 0.29 ± 0.08 s at 10 °C, 2.2 times faster when warm (computed), positions 31.30 and 32.03 [1599].

The trap closes after two action potentials, in 15–20 s by the Results and “within about 30 s” by the Discussion, positions 35.62–35.88 and 36.25 [1598]. Struggling prey elicit 63 ± 13 action potentials in the first hour, position 40.61, n = 5, and more than 100 within 6 h, position 42.24 [1598]. Heat-induced firing reaches 50 % at 33.8 °C, and at 46 °C the trap fires a steady 3.8 action potentials per minute [1599].

The plant counts its pulses. More than three action potentials are needed to induce hydrolase genes, and five for strong expression [1598]. DmJAZ1 rises 5.5-fold after two [1598].

The Na^+ transporter DmHKT1 stays at 147 molecules per 10,000 actin, 1.5 % (computed), up to three action potentials [1598]. After 5–60 action potentials it rises up to 60-fold, with a maximum 4 h after stimulation, position 41.87 [1598]. Its Km is 10 mM [1598].

The sensitive plant. In *Mimosa pudica* the Ca^{2+} rise precedes leaflet movement by up to 0.15 s, position 31.43 [1600]. *Mimosa* shows three signal classes: the action potential (“steep spike-like waveform”), the slower variation potential and a faster “rapid unknown signal” [1601].

***Mimosa* signal**	**Speed**	**Source**
Touch-induced action potential, rachilla	5.52 ± 0.43 mm s⁻¹	[1600]
Wound-induced action potential	4.27 ± 0.41 mm s⁻¹	[1600]
Ca^{2+} wave, leaflet vein (n = 6)	1.31 ± 0.17 mm s⁻¹	[1600]
Ca^{2+} wave, rachilla, first peak	2.65–3.11 mm s⁻¹	[1600]
Ca^{2+} wave after touch	5.87 ± 0.75 mm s⁻¹	[1600]
Ca^{2+} wave after wounding	4.13 ± 0.45 mm s⁻¹	[1600]

A general plant range is 0.01–0.04 m s⁻¹, against 0.4–200 m s⁻¹ in animals [1596]. The flytrap action potential is cited at “around 10 m/s” [1599]. The *Mimosa* action potential

at 5.52 mm s⁻¹ is slower than the general plant range by 1.8 to 7.2 times (computed).

About 5 % of the *Arabidopsis thaliana* genome encodes membrane transport proteins [1602]. It holds 9 Shaker-type and 6 KCO K^+ channels, 20 cyclic-nucleotide-gated channels and about 880 transporters in 46 families [1602].

The synapse before the neuron

The dates of the early animal nodes. Animals and their single-celled relatives diverged “more than 800 million years ago”, position 67.53 [472]. The stem from that split to crown animals lasted “about 150–200 million years”, positions 66.01–66.27 [473]. It carried about 28 % of the substitutions between humans and choanoflagellates [473].

Node	Interval	Positions	Width	Source
Crown Metazoa	833.5–649.8 Ma	67.57–67.34	184 Myr	[485]
Crown Eumetazoa	746.2–625.9 Ma	67.47–67.31	120 Myr	[485]
Crown Bilateria	688.3–595.7 Ma	67.39–67.26	93 Myr	[485]
Crown Deuterostomia	662.3–587.2 Ma	67.36–67.25	75 Myr	[485]
Crown Protostomia	653.1–578.1 Ma	67.35–67.23	75 Myr	[485]
Crown Cnidaria	641.8–531.5 Ma	67.33–67.16	110 Myr	[485]

The widths are computed from the intervals. Their positions are 66.19, 65.81, 65.57, 65.38, 65.38 and 65.73.

The choanoflagellate. The scaffold proteins of the post-synaptic density, Shank, Homer and DLG, “were acquired in a unicellular ancestor” of choanoflagellates and animals [474]. The scaffold “emerged in a unicellular context and was probably not involved in cell-cell communication” [474]. Most post-synaptic proteins did not arise together with synapses or neural-like cells [474].

Monosiga brevicollis carries Shank, Homer, DLG, CaMKII, Citron, Cortactin, the Ephrin receptor, IP_3R, PKCαβγ and Shaker K^+ channels [474]. Three DLG partners, CRIPT, Shaker and PMCA, have clear orthologues [474]. The mammalian post-synaptic density holds “about one thousand proteins” [474].

The Munc18/syntaxin-1 complex was once known only from nerve tissue [475]. In *Monosiga* it is “structurally and functionally very similar” to the vertebrate complex [475]. That secretion machinery of the common ancestor was later taken up for synaptic roles [475].

Monosiga has one T-type and one high-voltage Cav channel, putative Kv channels and a Nav-like channel [148]. Its genome of about 41.6 Mb holds about 9,200 genes (9,196 models) and 78 protein domains otherwise found only in animals [442]. It has at least 23 cadherin genes, about 120 tyrosine kinase domains and about 80 SH2 domains [442].

It has 58 PDZ-domain genes against 66 in *Nematostella*, 15 of them orthologous between the two [477]. *Salpingoeca rosetta* has a genome of about 55 Mb with 11,629 genes and a cell volume of 105.9 ± 8.8 µm³ [443]. A sphere of that volume has a diameter of (6 × 105.9 / π)^(1/3) = 5.87 µm, position 4.42 (computed); its rosettes hold

4–25 cells, mostly 8 [443].

The sponge. Sponges “diverged from other animals more than 600 million years ago”, position 67.27 [473]. Sponge sterane biomarkers are older than about 635 Ma, position 67.32 [446][447]. A second reading gives the same molecule an algal origin [448].

The demosponge *Amphimedon queenslandica* has a “nearly complete set of post-synaptic protein homologs” among 36 gene families [477]. Present are dlg, Shank, Homer, GRIP, CRIPT, GKAP, PICK1 and several metabotropic glutamate receptors [477]. Absent are the ionotropic glutamate receptors, Shaker-type Kv channels and neuroligin [477].

The 13 ligand-binding residues of the dlg PDZ domains are 100 % the same in sponge and human [477]. Five genes, DLG, HOMER, GRIP, CRIPT and GKAP, are expressed together in larval flask cells and in no other larval cell type [477]. *Amphimedon* has only two-segment Kir K^+ channels, no Kv and no Nav homologue [148].

The *Amphimedon* genome of about 167 Mb holds about 30,000 loci, 18,693 of them (63 %) with known homologues [473]. It has 705 kinases, more than 150 receptor tyrosine kinases and more than 200 G-protein-coupled receptors [473]. Of 4,670 pan-metazoan gene families, 1,286 (27 %) are found only in animals [473].

The freshwater sponge *Spongilla lacustris* has no nerves or muscles [453]. Single-cell RNA sequencing of the whole body found 18 cell types [453]. Among them are secretory “neuroid” cells whose projections wrap the microvilli and cilia of the feeding cells [453].

The glass sponge *Rhabdocalyptus dawsoni* has no neurons, yet it conducts all-or-none impulses [499]. They run in a syncytial tissue “that penetrates all parts of the body” at 0.27 ± 0.1 cm s^{-1} at 10 °C, which is 2.7 mm s^{-1} [499]. The absolute refractory period is 29 s, position 36.22, and the relative one 95–100 s, positions 37.30–37.34 [499].

The placozoan. *Trichoplax adhaerens* has “just six identified cell types” [517]. In 2008 it was known to have four, possibly five [484]. It has no gap junctions, and its fibre cells “do not form chemical synapses” [517].

Secretory cells make up 4 % of the total, about 1,500 around a 500 µm animal, spaced about 5 µm apart [517]. A 500 µm animal is 500 / 5 = 100 secretory-cell spacings across (computed). Six peptide-secreting cell populations each secrete one peptide: SIFGamide, TrIns3, SITFamide, YYamide, RWamide or FFNPamide [519].

Twelve peptides were tested in feeding; the threshold is 100 nmol l^{-1} and full pausing comes above 200 nmol l^{-1} [517]. As few as 10 algae suffice for a pause, and a pausing animal affects others up to about 200 µm away, position 7.63 [517]. Under some peptides animals flatten to up to 5 times their default size [519].

***Trichoplax* behaviour**	**Duration**	**Position**	**Source**
Onset of pause after a peptide pulse	about 30 s	36.25	[517]
Single feeding pause (n = 64)	2.97 ± 0.96 min	37.87	[517]
Group pause	4.13 min	38.17	[517]
Repeat of pause under peptide (n = 33)	9.11 ± 4.22 min	38.89	[517]

Effect of PWN peptide	about 10 min	38.98	[519]
Group pause cycle (n = 38)	12.9 ± 2.0 min	39.21	[517]

A single pause lasts 2.97 / 12.9 = 23 % of a group cycle (computed). The *Trichoplax* genome of about 98 Mb holds 11,514 genes [484]. A reconstruction of gains and losses predicts a loss of 4,952 genes on the placozoan branch [479].

An egg. In the sea-urchin egg the fast block to a second sperm acts “within a few seconds” of sperm entry [633]. It comes from depolarisation of the egg membrane [633].

The first nerve cells

Nerve cells “appear restricted to eumetazoans sensu stricto” [473]. Where they first arose depends on where the comb jellies, the ctenophores, branch from the animal tree [479][481]. The positions in the record alternate.

The genome of *Mnemiopsis leidyi* placed ctenophores, not sponges, as sister to all other animals [478]. Its neural gene set resembles that of sponges, which the abstract reads as a possible loss of a nervous system in ctenophores [478]. The *Pleurobrachia bachei* genome also placed ctenophores first, and its authors concluded that neural systems “evolved independently from those in other animals” [479].

They called a single origin “a less parsimonious scenario” [479]. A 2015 review found a single origin “compatible” with shared traits and favoured “an independent complexification of nervous systems from a simple precursor state” [481]. The same review notes complete loss of a nervous system in only “two examples” of animals, both parasites [481].

Twenty-seven new ctenophore transcriptomes placed Ctenophora as “sister group to all other animals” [480]. A dataset of 1,719 genes with a site-heterogeneous model “strongly” supports sponges as sister to all others, ctenophores second [482]. Partitioned analyses found that support for ctenophores first declines as model fit improves, with sponges first at 95 % and 99 % in two datasets of 133–146 genes [483].

Chromosome-scale genomes of 1 ctenophore, 2 sponges and 3 single-celled relatives were compared in 2023 [472]. Seven derived fusions are shared by sponges, bilaterians and cnidarians to the exclusion of ctenophores, 4 of them fusion-with-mixing [472]. The posterior for ctenophores first is 1.0, and the clade of all other animals is named Myriazoa [472].

Four publications place ctenophores first (2013, 2014, 2017, 2023) and three place sponges first (2015, 2017, 2021) [478][479][480][472][481][482][483]. There are 31 ancestral animal synteny groups of 5–29 genes, together 291 of 2,474 orthology groups, 12 % [472]. Glass sponges keep relics of 10 of the 29 ancient bilaterian–cnidarian–sponge linkage groups [472].

The ctenophore nerve. In ctenophores “many bilaterian neuron-specific genes and genes of ‘classical’ neurotransmitter pathways either are absent or, if present, are not expressed in neurons” [479]. The *Pleurobrachia* authors “strongly suggest” that

serotonin, acetylcholine, dopamine, noradrenaline, adrenaline, octopamine, histamine and glycine are not used as messengers [479]. L-glutamate is a candidate transmitter to muscle, active at about 10^{-7} M, while other classical transmitters had no effect up to 5 mM [479].

The *Pleurobrachia* draft genome holds 156,146,497 bp (estimated 160–180 Mb) and 19,523 genes, 44 % of them with orthologues in other animals [479]. That is 0.44 × 19,523 = 8,590 genes (computed). It has 72 novel prohormones, more than 100 orphan neuropeptide-like receptors, 12 pannexins or innexins, 29 ASIC-type Na^+ channel genes and 92 homeodomain genes [479].

In a 1-day-old *Mnemiopsis* cydippid, electron microscopy in serial blocks reconstructed 5 nerve-net neurons under the skin [513]. It also found 6 mesogleal neurons and 22 putative sensory cells in five morphological groups [513]. The neurites of the five net cells form “an anastomosed continuous network” with one continuous plasma membrane, a syncytium [513].

“Neither electrical nor chemical synapses were detected between the cells” of the net [513]. Chemical synapses run from the net to polster cells [513]. Whether the neurons “divide, but remain connected” or whether neurites of separate cells “reach out and fuse” is left open [513].

Mnemiopsis has 129 predicted neuropeptide precursors, at least 42 mature peptides, 35 Kv homologues, 2 Nav and 2 innexins [1603]. Its synaptic vesicles have a median diameter of 51 nm, position 0.10, and its dense-core vesicles 202 nm, position 1.36, four times wider (computed) [1603]. Of nine synthetic peptides tested, four raised swimming speed [1603].

Ctenophore neurons appear about 2 days after muscle in development, position 44.13 [479]. *Mnemiopsis* eggs hatch 22–26 h after spawning, positions 43.42–43.57, and cydippids of 3–5 days are 3–5 mm long, positions 10.10–10.56 [1603]. The statocyst connectome holds 1,011 cells, with four clusters of ciliated balancer cells bearing the statolith [514].

Six armoured comb jellies with eight-fold symmetry and eight pairs of comb rows come from the early Cambrian [507]. Living ctenophore diversity arose about 350 ± 88 Ma, position 66.78, range 66.51–66.98 [480]. About 200 species are described [480].

Sodium and peptides. Sodium selectivity arose twice, once in cnidarians and once in Bilateria, both from older channels that also passed Ca^{2+} [531]. The cnidarian Na^+-selective group split from Ca^{2+}-conducting relatives “more than 540 million years ago”, position 67.17 [531]. Nav1, Na^+-selective with a DEKA filter, occurs only in Bilateria and appeared in the urbilaterian [148].

Cnidarian-specific Cav genes have been kept “at least 500 million years”, position 67.10 [148]. Placozoans and ctenophores carry Nav channels with the DEEA filter [148].

As of 2018 “neuropeptides that act as ligands for GPCRs have yet to be identified in any of the four non-bilaterian phyla” [561]. At least 30 neuropeptide signalling systems trace to the common ancestor of protostomes and deuterostomes; Mirabeau and Joly counted 29 and Jékely 27 [561]. About one quarter of animal peptide families form one large, loosely connected similarity network [520].

Nematostella vectensis has precursors with 12 C-terminal motifs, none orthologous to bilaterian neuropeptides, and 13 ENaC-type channels serve as receptors for *Hydra* RFamide peptides [561]. Two peptide families, GRFamide and X1PRX2amide, occur in all cnidarian classes studied [562]. A cnidarian precursor carries up to 32 copies of its peptide [562].

Non-bilaterian animals have about 5–15 cell types, invertebrate bilaterians about 50–100 and vertebrates about 225 [473].

Nerve nets

A nerve net is a nervous system without a central organ. In *Hydra* there are two separate nets, one in the ectoderm and one in the endoderm, and they do not mix [536]. The tentacle endoderm holds no nerve cells, and sensory cells are more than 50 % of the endodermal nerve cells [536].

Ectodermal cell bodies are about 10 µm long, position 4.91, usually 50–100 µm apart, positions 6.37–7.00 [536]. In the ectoderm only about 20 % of nerve tracks are single neurites; in the endoderm about half are single and half bundles of two [536]. The counts rest on 130 ectodermal and 47 endodermal tracks [536].

At one contact the terminal neurite fingers overlap over about 8 µm, position 4.70, and at another about 4 µm, position 4.07 [536]. Nerve cells number 0.12 per epithelial cell by two methods [536]. Tissue bands of about 4 % of the body column held 133 nerve cells, 57 ectodermal and 76 endodermal [536].

In *Hydra oligactis* a nerve ring around the mouth cone holds 20–30 nerve cells [536]. That ring has at least four neuron subsets [549]. One account gives three sensory and five ganglion populations [536]; a single-cell atlas of 24,985 cells gives 12 neuronal subtypes, and 46 % of all cells are stinging-cell lineages [550].

The supply of nerve cells. A *Hydra* nerve net depends on a pool of stem cells. The interstitial stem cells cycle every 24 h, position 43.50, or “about 24–30 hours”, positions 43.50–43.70 [551][552]. The pool holds 3,000–6,000 cells per animal, and about 60 % of daughters stay stem cells while 40 % differentiate [551].

About 900 nerve cells and 1,760 stinging-cell nests are made per day per animal [551]. Commitment to the nerve fate comes in S phase of a precursor: “Committed cells completed the cell cycle, divided, and daughter cells differentiated to nerve cells” [552]. In *Hydra attenuata* “nerves and nematocytes have 2n postmitotic nuclear DNA content” [551].

“All *Hydra* tissues, including the nerve net, are newly formed every 2–3 weeks in well-fed animals”, positions 45.90–46.27 [536]. Nine clones held both nerve cells and stinging cells, which share one origin [553]. The divisions observed are of stem cells and committed precursors [552].

***Hydra* supply**	**Duration**	**Position**	**Source**
Labelling to nematoblast	12 h	42.87	[551]
Labelling to visible nerve cell	about 18 h	43.24	[551]
Stem-cell cycle	24 h; 24–30 h	43.50; 43.50–43.70	[551]; [552]

Stem-cell cycle	24 h, 24–30 h	43.50, 43.50–43.70	[551], [552]
Neurite extension in grafts	by days 2 and 3	44.13–44.50	[536]
Doubling of stem-cell population	3–4 days	44.50–44.76	[552]
Tentacle tissue renewal	4–5 days	44.76–44.96	[536]
Whole-tissue renewal, nerve net included	2–3 weeks	45.90–46.27	[536]

In *Nematostella* NvSoxB(2) is expressed in neural progenitors “before mitosis”, and in 97 % of two-cell clusters only one cell is labelled as dividing [560]. In 146 adult *Nematostella* the counts of longitudinal and tripolar neurons rise with body length (r = 0.854 and 0.791) [539]. Small animals of 2.5–5 mm carry 20–40 longitudinal neurons, positions 9.93–10.56 [539].

In planarians “differentiated somatic cells do not divide”, and “the only somatic cells capable of mitosis are neoblasts” [590]. Planarian neoblasts have a median G2 phase of about 6 h, position 42.24 [591].

Conduction in nets. The sea anemone *Calliactis parasitica* carries two slow systems beside its nerve net [557]. SS1 runs at 4.4–14.6 cm s^{-1} at 11–14 °C, SS2 at 3.0–5.3 cm s^{-1} [557]. SS1 has an absolute refractory period of about 300 ms and a relative one of about 1,400 ms, positions 32.06 and 33.46 [557].

The sea pen *Pennatula phosphorea* conducts through its net at a mean 7.5 cm s^{-1} at 10 °C; *Virgularia* conducts at 40–60 cm s^{-1} at about 16 °C [558]. Chronaxie is about 0.8 ms in *Pennatula*, position 26.66, and 0.6–1 ms in *Virgularia*, positions 26.40–26.87 [558]. The *Pennatula* net has an absolute refractory period of 40–50 ms, positions 30.22–30.43 [558].

Giant axons in a medusa. The hydromedusa *Aglantha digitale* carries a ring giant axon, motor giant axons and thin tentacle axons [537]. At 15 ± 1 °C the ring giant conducts at 1–2.6 m s^{-1}, the motor giants at 1–4 m s^{-1} and the tentacle axons at 0.4–0.8 m s^{-1} [537]. Speed rises with axon diameter, from 3.6–7.8 µm in tentacle axons to up to 40 µm in motor giants, positions 3.98–6.17 [537].

The ring giant spike reaches up to 68 mV and lasts about 1.6 ms, position 27.29 [537]. An escape burst holds 2–6 impulses of 2–3 ms each, and the ring giant repeats at intervals of at least 3.5 ms, position 28.01 [537]. The synaptic delay from motor giant to muscle sheet is about 1.6 ms, and the escape contraction is complete in about 100 ms, position 31.06 [537].

Across these cnidarian tissues the speeds span 3.0 cm s^{-1} to 4 m s^{-1}, a factor of 133 (computed).

Rhopalia and pacemakers. Box jellyfish and scyphozoans carry rhopalia, sense organs at the bell margin with swim pacemakers [545]. A cubozoan rhopalium carries two lensed eyes, two pit ocelli and two slit ocelli, and a nerve ring joins the four rhopalia and four tentacle bases [545]. “Most scyphozoans have eight or more rhopalia, typically with species-specific numbers that are multiples of four” [545].

In *Tripedalia cystophora* each rhopalium holds six eyes, 24 per medusa, and the rhopalial nervous system holds “several thousand nerve cells” [540]. In darkness the

swim pacemaker runs “close to 1Hz”, 0.5–1.6 Hz over 10 s windows [540]. Under light steps it ranges 0.3–2.4 Hz, a factor of 8 (computed) [540].

A regenerating rhopalium paces at about 0.03 Hz on day 6 and 0.2 Hz on day 8, periods of 33 s and 5 s, positions 36.34 and 34.62 [559]. Its FMRFamide-positive giant neurons rise from 7 to 14 in about one week [559]. *Aurelia aurita* and *Dactylometra quinquecirrha* have eight marginal ganglia, and some *Aurelia* only five or three [541].

Aurelia beat intervals run from about 0.25 s in the smallest animals to 0.75 s in larger ones, positions 31.89 and 32.89 [541]. A model gives “of the order of 10000 neurons” in the motor net of a jellyfish about 4 cm across [546].

Fossils. No fossil nerve net is known; the nerve net is dated by the animals that carry it. A mitochondrial clock places the cnidarian node at 741 Ma, position 67.46, with a 95 % region of 686–819 Ma, positions 67.39–67.55 [530]. Major cnidarian groups had diversified before the Cambrian, given as 543 Ma in that study, position 67.18 [530].

Haootia quadriformis, from Newfoundland at about 560 Ma, position 67.21, is an impression of twisted fibrous bundles proposed as the earliest body fossil of animal muscle [523]. It is 574.17 − 560 = 14.17 Myr younger than the first complex Ediacaran fossils (computed), position 63.86 [450]. The oldest free-swimming medusa, *Burgessomedusa phasmiformis* of the middle Cambrian Burgess Shale, is known from 182 specimens with umbrellas up to 20 cm high, position 13.92, and more than 90 tentacles [532].

Cords and brains

Two accounts. Centralisation is the gathering of nerve cells into cords, cross-links (commissures) and brains. One account starts from a nerve net with two centres at opposite ends, an “apical nervous system” for body physiology and a “blastoporal nervous system” for feeding and movement [1604]. Their growth, joining and fusion gave the bilaterian nerve cord and brain, by this account [1604].

A second account rests on gene expression in the nerve cords of five clades: Xenacoelomorpha, Rotifera, Nemertea, Brachiopoda and Annelida [596]. No species studied shows a conserved molecular pattern along the back-to-belly axis of its cords [596]. The authors conclude that ventral nerve cords likely arose convergently, “many times” [596].

Nerve cords also differ in place: nemertodermatids have cords on the back and nemerteans on the belly [596]. The xenacoelomorph *Nemertoderma westbladi* has a ring-like commissure in front and a pair of condensations on the belly [596]. In the annelid *Owenia fusiformis* a medially condensed trunk cord resembles those of vertebrates and flies [596].

The first bilaterian. One study places Xenacoelomorpha as sister to all other Bilateria, the Nephrozoa [1605]. By that placement the last common bilaterian ancestor “was probably a benthic, ciliated acoelomate worm” with one gut opening [1605]. Nerve cords, excretory organs and body cavities then arose after the xenacoelomorphs split off [1605].

That study used 11 new transcriptomes and matrices of up to 881 genes × 77 taxa, 337,954 amino acids, 62 % complete [1605]. A second study corrects for systematic error and concludes: “the Xenacoelomorpha are simplified relatives of the Ambulacraria” [1606].

Most crown-bilaterian phyla diversified in the Ediacaran, more than 100 Myr before the Cambrian, which places them before 638.8 Ma, position 67.33 (computed) [485]. *Ikaria wariootia*, from the Ediacaran of South Australia, is presented as one of the oldest bilaterians and as matching a small, simple last common bilaterian ancestor [1607]. The Ediacara biota spans about 571–539 Ma, positions 67.22–67.17, about 32 Myr, position 64.60 [1607].

A brain at small size. A juvenile acoel, *Symsagittifera roscoffensis*, averages 200 µm long and 100 µm wide, positions 7.63 and 7.00 [1608]. Its brain of “approximately 700 cells” fills the front third of the body [1608]. A second paper calls it “a centralized anterior brain made up of about 700 neurons” [1609].

Three commissures link its neuropil, seven (c1–c7) in the whole-body model, and three pairs of nerve cords run along the body [1608]. The front cords carry about 50–100 neurites, the rear cords about 15–30 [1608]. The statocyst has three cells, and there are eight ocellar cells, three sensory and one pigment cell per ocellus [1608].

The acoel regrows its brain. Of 50 acoels without heads, 42 (84 %) began head regeneration [1609]. About 70 % had a brain neuropil “virtually indistinguishable” from intact animals by 50 days, position 47.06 [1609].

Before decapitation acoels took 8.6 s on average for geotaxis, position 35.11, N = 69 [1609]. Phototaxis carried them 2.59 cm, position 12.06, and was not restored at 5 days [1609]. Speed was 1.63 mm s^{-1} in controls and 1.37 mm s^{-1} one day after decapitation, 84 % (computed) [1609].

Segments and ganglia. In leeches “the posterior growth zone invariably generates exactly 32 segments”, and each midbody segment has one ganglion [1379]. Rostral ganglia R1–R4 and caudal ganglia C1–C7 fuse into head and tail brains [1379]. In cephalopods the arm cord is segmented: *Octopus bimaculoides* holds 7.64 segments per sucker in arm 1 and 7.88 in arm 2, the squid *Doryteuthis pealeii* about 4.5 [1355].

Fossil brains. Fossil brains appear in Cambrian Stage 3, whose base is about 521 Ma, position 67.14 [435]. *Kerygmachela kierkegaardi*, from Sirius Passet in North Greenland, has a “unipartite” brain, a small protocerebrum serving eyes and frontal appendages [1610]. It is described from 15 specimens with 11 pairs of trunk flaps [1610].

Fuxianhuia protensa from Chengjiang has “a tripartite pre-stomodeal brain” with “traces of three nested optic centres serving forward-viewing eyes” [1611]. The great-appendage arthropod *Alalcomenaeus* has one optic neuropil, four head ganglia and eight further ganglia in an eleven-segment trunk [1393]. The radiodont *Lyrarapax unguispinus* has paired ganglia in front of the protocerebrum at the base of its frontal appendages [1612].

The sources give the Chengjiang brains an age of 520 Ma, position 67.14 [1611][1393]. The youngest detrital zircon gives Chengjiang a maximum depositional age of 518.03 ± 0.69/0.71 Ma, position 67.13 [452]. Fossil brains follow the Cambrian base by 18.8 Myr

at 520 Ma, or by at least 20.77 Myr at 518.03 Ma, positions 64.12 and 64.21 (computed).

One reading takes these structures as brains [1611][1393][1612]. The other, from "numerous articulated individuals" of *Fuxianhuia*, reads them as microbial biofilms formed as tissues decayed [1613].

The first vertebrates. *Myllokunmingia fengjiaoa*, lamprey-like, and *Haikouichthys ercaicunensis*, closer to hagfish, come from the Lower Cambrian at Chengjiang [1409]. Their source gives the Cambrian as 545–490 Ma and suggests chordates arose near 555 Ma, position 67.20 [1409]. Cyclostomes and jawed vertebrates diverged more than 500 Ma, position 67.10 [1614], or around 560 Ma, position 67.21 [1411].

The hagfish *Eptatretus burgeri* develops domains equal to the medial ganglionic eminence and the rhombic lip [1614]. "Brain regionalization as seen in crown gnathostomes is not an evolutionary innovation of this group" [1614]. The lamprey pallium has a separate visual area with a map of the retina and an area for head and trunk touch, both relayed through the thalamus [1411].

By the 560 Ma estimate the sensorimotor plan and the thalamocortical relay "had already evolved" in the common ancestor [1411]. The arthropod central complex and the vertebrate basal ganglia both arise from forebrain lineages under a conserved genetic programme and both use inhibitory and dopamine circuits for choosing actions [1615]. The authors propose "deep homology"; against it stand the readings of tripartite brains as "convergent adaptations" [1610] and of nerve cords as convergent "many times" [596].

Counted nervous systems

System	Neurons	Other counts	Source
Ciona intestinalis tadpole larva, CNS	177 with axons and synapses (of about 330 CNS cells)	about 2,600 cells; ≥25 types, 52 subtypes	[1415]
Caenorhabditis elegans hermaphrodite	302 in 118 classes	959 cells; about 5,000 chemical synapses, 2,000 neuromuscular junctions, 600 gap junctions	[603][602]
Strongylocentrotus purpuratus pluteus, 3 days	12 neuronal cell types	19,699 cells sequenced of 29,130 estimated; 21 clusters	[632]
Platynereis dumerilii larva, 72 h	892 classified, in 180 types	8,852 cells with a soma; 25,509 synapses	[1387]
Drosophila larva, brain	3,016	about 548,000 synapses	[1616]
Adult *Drosophila* hemibrain	about 25,000	about 20 million chemical synapses	[1617]
Adult *Drosophila* male nerve cord	about 23,000	10 million T-bars, 74 million PSDs	[1618]
Adult *Drosophila* brain (FlyWire)	139,255	about 5×10^7 (54.5 million) synapses	[1619]

In *C. elegans* neurons are 302 / 959 = 31.5 % of all cells (computed) [602]. In *Ciona* CNS neurons are 177 / 2,600 = 6.8 % (computed), and the 28 peripheral neurons sit 8 left, 6 centre and 14 right [1415]. The *Ciona* synapse total is 6,618 in the abstract, 8,768 in the Results and 8,617 in Table 1 [1415].

In *Platynereis*, classified neurons are 892 / 8,852 = 10.1 % of cells with a soma (computed), beside 2,905 non-neuronal cells in 90 types [1387]. The later version gives “over 9000” cells, 202 neuronal and 92 non-neuronal types [1385]. The grouped graph holds 45 sensory, 61 interneuron and 35 motor neuron types, 141 in all (computed) [1387].

Full brains of eight *C. elegans* individuals were reconstructed from birth to adulthood [1620]. “The overall geometry of the brain is preserved from birth to adulthood”, and with age the brain becomes “progressively more feedforward and discernibly modular” [1620].

The FlyWire brain holds 2,700,513 connections of at least five synapses among 134,181 identified neurons in 78 neuropils [1619]. Of 118,501 intrinsic neurons, 77,536 (65.4 %) lie in the optic lobes and 32,388 (27.3 %) wholly in the central brain (computed) [1619]. Its total path length is about 149 m, position 19.94, a mean of 1.07 mm per neuron, position 9.16 (computed) [1619].

The annotation lists 8,453 cell types, 59 % of them singletons [1621]. It counts 5,512 sensory neurons into the central brain, 1,303 descending and 2,362 ascending neurons [1621]. Kenyon cells number 2,597 on the right and 2,580 on the left, against 1,917 in the hemibrain [1621].

About one type in six differs in count between hemispheres and one in three between brains [1621]. Left and right central brains differ by 27 intrinsic neurons, 0.1 % [1621]. The male nerve cord carries 44 m of neuronal cable, position 18.83 [1618].

Brain plus nerve cord give 139,255 + 23,000 = 162,255 neurons in the adult fly central nervous system (computed), from different animals. The hemibrain paper gives the whole fly brain as “approximately 100,000 neurons” [1617]; FlyWire gives 139,255 [1619].

Synapses per neuron run 16.6 in the worm and 28.6 in *Platynereis* (computed) [603] [1387]. They run 182 in the fly larva, 391 in the FlyWire brain and 800 in the hemibrain (computed) [1616][1619][1617]. A mouse somatosensory cortex neuron has about 8,200 synapses [1415].

From 302 neurons in the worm to 139,255 in the fly brain is a factor of 461 (computed). Light-sheet imaging records “more than 80% of all neurons at single-cell resolution” in the larval zebrafish brain, one volume each 1.25 s, position 33.36 [1622].

The speed of the pulse

Speed in an axon rises with its width or with insulation. In bare axons the axial resistance “drops as the square of diameter”, and speed rises “in proportion to the square root of the interior diameter” [1376]. A tenfold gain by width alone needs axons “100 times larger”, since √100 = 10 (computed) [1376].

Giant axons. Giant axons “evolved in invertebrates such as squid” [1623]. The squid *Loligo pealei* giant axon measured 506 µm across in May and 383 µm in August, positions 8.48 and 8.23, in waters of about 10–12 °C and 20 °C [1346]. It conducted 9.56 m s⁻¹ at 5 °C, 12.45 m s⁻¹ at 10 °C and 18.94 m s⁻¹ at 20 °C [1346].

The ratio over 15 °C is 18.94 / 9.56 = 1.98, an implied Q10 of 1.98^(10/15) = 1.58 (computed). Giant axons are “several times larger” than other large axons in the same animals [1376].

Myelin. A myelin sheath is a wrapping of membrane layers around an axon, broken at nodes. In myelinated fibres speed shows “a first power (rather than square root) dependence on diameter over a substantial range” [1376]. For fibres of a few µm or more, myelin speeds conduction “by a factor of ten or more” [1376]; another source gives “more than 20-fold” [1413].

Myelin appears in “each of the major bilaterian lineages”: gnathostomes among deuterostomes, polychaetes and oligochaetes among lophotrochozoans, copepods and malacostracans among ecdysozoans [1376]. It “seems to have arisen independently in evolution several times in vertebrates, annelids and crustacea” [1376]. Molluscs and insects lack it, and “lamprey axons are not ensheathed by myelin” [1376][1413].

The first myelinated vertebrate “was likely to have been a placoderm” [1376]. Myelin is thought to have arisen near the time of hinged jaws, and placoderms are “the most ancient group of jawed vertebrates” [1413]. A lamprey protein segment is “86% identical over 22 amino acids” to a fragment of myelin basic protein, which Werner reads as homologous to GOLLI instead [1413].

Several myelin proteins are older than the sheath. CNP, PMP22, MAL and PLP are “evolutionarily older than vertebrates” [1413]. The paranodal proteins Caspr and neurexin IV have been kept “over 750 million years of evolution”, position 67.47 [1376].

In a survey of 20 calanoid copepod species, two of the older superfamilies lack myelin, and it is “present in the species from three more recently evolved superfamilies” [1624]. Copepod sheaths reach “up to 60 layers” [1624], and earthworm myelin has “60 to 200 such layers” [1376]. Copepod sheaths are compared to “those that give a tenfold boost” in vertebrates [1452].

Copepod	Sheath	Minimum reaction time	Position	Source
Undinula vulgaris	myelinated	1.5 ms	27.23	[1624]
Neocalanus gracilis	myelinated	1.6 ms	27.29	[1624]
Labidocera madurae	none	3.1 ms	27.90	[1624]
Pleuromamma xiphias	none	6.6 ms	28.58	[1624]

The ratios are 6.6 / 1.5 = 4.4 and 3.1 / 1.6 = 1.9 (computed). Spike heights in the two species without myelin are 1–4 mV, about ten times those in the two with it [1624]. *Acartia* often reaches more than 500 mm s⁻¹, with acceleration usually above 100 m s⁻² and turning at about 30° per ms, and kicks follow each other at 5 ms, position 28.33 [1624].

Escape accelerates copepods “to 200 body lengths per second” “within milliseconds” [1452]. Penaeid shrimp, in “at least six species of Penaeus shrimp”, carry myelinated fibres with a “fenestration node”, a compact sheath and a wide space under the sheath

[1453]. Their fibres of 120 µm, position 7.17, conduct “over 200 m s^{-1}”, “the fastest speeds known” [1376][1453].

The fastest myelinated vertebrate axons reach about 100 m s^{-1} [1376]. A textbook gives 0.5–10 m s^{-1} for bare axons and up to 150 m s^{-1} for myelinated ones [1623].

The shrimp exceeds them by 2.0 or 1.33 times (computed). It exceeds the warm squid axon by 200 / 18.94 = 10.6 times at a width 4.2 times smaller (computed).

Rushton’s “critical diameter” of 1 µm, position 2.81, is the width below which myelin gives no gain [1625]. Waxman and Bennett report that “myelinated fibres considerably smaller than 1 µm” conduct faster than bare fibres of the same size [1625].

Node length spans a 4.4-fold range in rat optic nerve and 8.7-fold in cortex, with far less variation along one axon [1626]. It is modelled to shift speed by about 20 % [1626]. Random sealing of over half an axon’s surface by glia is also predicted to raise speed by about 20 % [1376].

The heart. In the human heart conduction runs at about 0.5 m s^{-1} in the atria and about 0.05 m s^{-1} in the atrioventricular node [1627][1628]. It runs at about 2 m s^{-1} in the bundle branches and about 4 m s^{-1} in the Purkinje fibres [1627][1628]. Unaided, the sinus node fires 80–100 per minute, the AV node 40–60, the bundle 30–40 and the branches 20–30 [1627][1628].

Heart event	Duration	Position	Source
AV delay	100 ms	31.06	[1627]
Sinus node to last ventricular cell	225 ms	31.80	[1627]
Ventricular action potential	250–300 ms	31.89–32.06	[1627]
Sinus node interval (80–100 min^{-1})	0.60–0.75 s	32.69–32.89	(computed)

The AV delay is 100 / 225 = 44 % of the conduction time (computed). Heart muscle cells renew by 1 % per year at age 25 and 0.45 % at 75, and fewer than half are replaced in a lifetime [1629].

The full span. Conduction speeds read run from 2.7 mm s^{-1} in the glass sponge to 200 m s^{-1} in shrimp nerve, a factor of 200 / 0.0027 = 74,000 (computed) [499][1376]. Within nerve alone they run 0.5 to more than 200 m s^{-1}, a factor of 400 (computed). The slowest wave read is the *Mimosa* Ca^{2+} wave, 1.31 mm s^{-1} [1600].

The cost of the pulse

Per spike. The Na^+ entry needed for one action potential, quadrupled to allow for overlap of Na^+ and K^+ currents, gives 11.5 × 10^8 Na^+ per spike and 3.84 × 10^8 ATP [1630]. Rodent signalling at 4 Hz costs 4 × (3.84 × 10^8 + 3.28 × 10^8) = 2.85 × 10^9 ATP per neuron per second (computed) [1630]. With the resting potential the total is 3.29 × 10^9, of which rest takes (3.29 − 2.85) / 3.29 = 13 % (computed) [1630].

That budget splits into action potentials 47 %, postsynaptic glutamate effects 34 %, resting potential 13 % and glutamate recycling 3 % [1630]. One extra spike per cortical

neuron per second raises oxygen use by 145 mL per 100 g grey matter per hour [1630]. Measurement in rat hippocampal mossy fibres gives Na^+ entry "only 1.3 times the theoretical minimum", "in contrast to the factor of 4" [1631].

A second budget gives postsynaptic receptors 50 %, action potentials 22 %, resting potential 20 %, glutamate recycling 4 % and presynaptic Ca^{2+} 4 % [390]. One vesicle released costs 1.64×10^5 ATP, and one bit about 24,000 ATP [390].

One spike with its downstream events costs 4.5×10^8 ATP per 2.5 ms, position 27.70, against 3×10^6 for rest and upkeep, 150 times less [390]. White matter uses 3-fold less energy than grey matter, and its synapse density is 80-fold lower [390]. The fly retina uses 10 % of the fly's resting ATP [390].

Neuron (model)	Na^+ load	Efficiency	Source
Squid giant axon, 6.3 °C	1,098 nC/cm²	about 9 %	[1632]
Squid giant axon, 18 °C	331 nC/cm²	about 24 %	[1632]
Honeybee Kenyon cell	186 nC/cm²	33 %	[1632]
Mouse fast-spiking interneuron	315 nC/cm²	41 %	[1632]
Crab motor neuron	364 nC/cm²	29 %	[1632]
Rat hippocampal interneuron	76 nC/cm²	74 %	[1632]
Rat granule cell	72 nC/cm²	about 100 %	[1632]
Mouse thalamocortical relay neuron	65 nC/cm²	about 100 %	[1632]

The squid load over the thalamocortical load is 1,098 / 65 = 16.9, "about 17×" [1632]. Spike heights run 55.5 to 129 mV, and resting use is below 1.5 % of spike use [1632]. Myelin gives "a several hundred-fold improvement in metabolic efficiency" [1376].

Neocortical presynaptic terminals hold 0.3–1.4 mitochondria each, and dendrites about one per 7 µm, position 4.58 [390]. About 80 % of mitochondria stay in place [390]. Mitochondria supply about 93 % of ATP and glycolysis about 7 %, with oxygen and glucose used near 6:1 [390].

Per brain. The human brain is "only 2% of the body's mass" and uses "~20% of the O_2 consumed by the resting body" [390]. The nervous system takes 20 % of the resting energy budget by a second source [1376]. The share is ten times the mass share (computed).

At birth brain glucose use is 52.5 % of resting metabolic rate in boys and 59.8 % in girls [1633]. The childhood peak is 66.3 % and 65.0 % of resting rate, and 43.3 % and 43.8 % of daily energy use [1633]. Body growth runs opposite to the brain's demand [1633].

Across six species (mouse, rat, squirrel, macaque, baboon, human), glucose use per neuron varies by only 40 % [1634]. The whole-brain average is 5.79×10^{-9} µmol glucose per minute per neuron [1634]. A human brain of 86×10^9 neurons then uses $86 \times 10^9 \times 5.79 \times 10^{-9} = 498$ µmol glucose per minute (computed).

Cerebral cortex neurons use 1.50×10^{-8} and cerebellar neurons 0.87×10^{-9} µmol per minute each, a ratio of 17.2 (computed) [1634]. The source states "nearly 20×" in its Results and "at least 10×" in its abstract [1634]. Glucose use scales with brain mass at

exponent 0.873 and with neuron number at 0.988 [1634].

The number of neurons

Rat and human. The adult rat brain holds about 330 million cells and 200.13 ± 21.17 million neurons, 61 % (computed) [1517]. Its cortex holds about 30 million neurons among 80 million cells, and its cerebellum, with more than 80 % neurons, holds almost 70 % of all the rat's neurons [1517].

The human brain holds 86 billion neurons and 85 billion other cells [1518]. The cerebral cortex holds 16 billion neurons in 1,233 g, 82 % of brain mass; the cerebellum 69 billion in 154 g, 69 / 86 = 80 % of neurons (computed) [1518]. The rest holds 86 − 16 − 69 = 1 billion (computed) [1635].

The often repeated ratio of ten glial cells to one neuron holds only in a few deep nuclei [1635]. A second count gives the human cortex 16.3 billion neurons, 21,450 per mg of grey matter and 80,064 per mm² of cortex [1516]. Hippocampus and amygdala hold about 250 million [1516].

Elephant. The African elephant brain holds 257.0 billion neurons in 4,618.6 g without the olfactory bulb [1516]. Its cerebellum holds 250.7 billion, 97.5 %, and its cortex 5.6 billion, 0.34 times the human count (computed) [1516]. That is 44.8 cerebellar neurons per cortical neuron [1516].

Elephant cortical grey matter holds 3,661 neurons per mg and 10,752 per mm², against 21,450 and 80,064 in the human, ratios of 5.9 and 7.4 (computed) [1516]. The table of the source prints "3.661" against the text value 3,661 [1516].

Mammals. Data on 41 species in 6 mammalian clades show about 2 cortical and 8 cerebellar neurons added per neuron added to the rest of the brain [1636]. The cortex runs from 9.8 million neurons in the smoky shrew to 16 billion in the human, 1,630-fold (computed) [1636]. The cerebellum runs from 21 million to 69 billion, 3,290-fold (computed), and the rest of the brain from 6 million to 690 million [1636].

In primates cortical mass scales with neuron number at exponent 1.087 ± 0.074, in other clades at 1.688 ± 0.051 [1636]. Doubling cortical neurons thus multiplies cortical mass by 2^1.087 = 2.12 in primates and 2^1.688 = 3.22 in other mammals (computed). In mammals more neurons go with lower neuron density and little change in glial density [1636].

The cerebellum scales at 0.976 ± 0.036 in primates, 1.028 ± 0.084 in eulipotyphlans and 1.296 ± 0.043 in other clades [1636]. The human olfactory bulb holds 15–16 million neurons and the mouse lemur's 7.6 million [1636]. In six rodent species larger structures hold more and larger neurons and many more non-neuronal cells of roughly constant size [1637].

Birds and reptiles. Parrots and songbirds have on average twice the neurons of primates of the same brain mass [1537]. Large-brained parrots and corvids have as many forebrain neurons as primates with much larger brains, or more [1537]. In 111 bird species, the number of pallial neurons rises with the tendency to innovate [1638].

Reptile neuron numbers are "over 20 times lower" than in birds and mammals of similar

body size [1498]. Amniote brains run from just under 2 million neurons in the Algerian sand gecko to 257 billion in the African elephant, 1.3 × 10^5-fold (computed) [1499]. The Sumatran flying dragon has barely more than 5 million [1499].

Mammals hold about 4 cerebellar per cortical neuron, birds 4.5 cerebellar per hindbrain neuron and reptiles 1.4 ± 0.6 telencephalic per rest-of-brain neuron [1499]. Most bird clades hold about 3 pallial per rest-of-brain neuron, owls 12, and primates can exceed 20 [1499]. Non-neuronal density stays at 50,000–120,000 cells per mg in all three classes, a 2.4-fold span (computed) [1499].

Four major shifts in neuron–brain scaling occurred over 300 Myr of amniote history, position 66.64 [1498].

Brain and body. In 1,552 mammal species from 28 orders, ordinary least squares gives log brain mass = −1.26 + 0.75 log body mass, slope 95 % CI 0.742–0.758 [1519]. A phylogenetic fit gives log brain mass = −0.83 + 0.57 log body mass [1519]. Per-order slopes run from 0.24 (Peramelemorphia) to 0.81 (Chiroptera), median 0.64, and more than 70 % of living mammals lack brain data [1519].

A larger dataset of 20,213 specimens of 4,587 jawed-vertebrate species finds brain–body slopes among species constant across classes [1639]. Birds and mammals extend fetal brain growth relative to fishes [1639]. A critique holds that the static slopes of indeterminate growers cannot be compared with those of birds and mammals [1640], and brain size may follow maternal metabolic turnover [1641].

The neuron stops dividing

The nerve cells of cnidarians and flatworms come from dividing precursors, and the nerve cells themselves are not seen to divide [552][590]. In planarians “BrdU was incorporated only into neoblasts and appeared in differentiated cells later” [590]. In *Hydra* 900 nerve cells differentiate per day from stem cells [551].

Neurons of the human cerebral cortex date from around birth by carbon-14 [1642]. They are not made in adulthood at detectable levels, while non-neuronal cortical cells are replaced [1642]. A review states: “Adult CNS neurons are typically described as permanently postmitotic, but there is probably nothing permanent about the neuronal cell cycle arrest” [1643].

Neurons that re-enter the cycle “will re-enter a cell cycle that they will not be able to complete” [1643]. In Alzheimer’s disease “Nearly 4% of the at-risk neurons are in a polyploid state” in the hippocampus, with a mean of 0.037 ± 0.028 over 6 patient and 4 control cases [1644]. “Because mitosis is not initiated, the cells remain tetraploid”, and “No neuron has ever been observed in M phase” [1644].

Such neurons survive “hundreds of days” or “many months” before dying [1644]. In the normal human brain about 10 % of neurons hold more than the diploid DNA content and fewer than 1 % are tetraploid [1645]. Tetrasomic neurons rise six-fold in early Alzheimer’s disease to 2.4 ± 0.7 %, an implied baseline of 0.4 % (computed) [1645].

When re-entry is forced in cultured mouse cortical neurons, about 70 % become hyperploid; some exceed 4C, replication without division [1646]. Viability holds for 3

days, position 44.50, and death follows through day 7, position 45.27 [1646]. Division with neuronal identity kept is recorded only after loss of the Rb-family genes or added DNA damage [1647].

Rb-triple-knockout cortical neurons were 13.9 ± 1.2 % EdU-positive and 2.02 ± 0.06 % in mitosis at 4 days, and “the daughter cells were both Satb2 positive” [1647]. Of their cells in G2/M, 14.21 ± 5.36 % carried a marker of dying cells [1647].

One study reports about 700 new neurons per day in each hippocampus, a turnover of 1.75 % a year [1648].

Another found no young neurons in 17 brains after death and 12 surgical samples, ages 18–77, and only a few at 7 and 13 years [1649]. At 1.75 % a year the turnover time is 57 years, position 52.55 (computed) [1648].

The human nervous system

Size. The adult brain weighed 1,407 g in men (range 1,070–1,767) and 1,233 g in women (range 1,000–1,618) in autopsy series [1650][1651]. One hemisphere has 973 cm² of cortex, both 1,946 cm² or 0.19 m² (computed), divided into about 150–200 areas that differ in size more than 100-fold [1652]. The cortex is 2.69 mm thick, position 10.00, so its volume is 1,946 × 0.269 = 523 cm³ (computed) [1653].

Part	Size	Position	Source
Synaptic vesicle, diameter (from 10^{-5} µm³)	26.7 nm	−0.49	[1654]
Synaptic cleft	20–40 nm	−0.75 to −0.12	[1654]
Synapse, edge of its box	about 1 µm	2.81	[1654]
Cerebral cortex, thickness	2.69 mm	10.00	[1653]
Spinal cord, width at T8	8.3 mm	11.02	[1655]
Spinal cord, width at C5	13.3 mm	11.45	[1655]
Spinal cord, length	43–45 cm	14.62–14.66	[1656]

Contacts. One cubic millimetre of cortex holds about 10^9 synapses [1654]. For 523 cm³ that gives 523,000 mm³ × 10^9 = 5.2 × 10^{14} synapses, about 33,000 per cortical neuron (computed). Estimates for the whole brain run from 10^{13} to 10^{15}, and a vesicle releases about 1,000 transmitter molecules that cross in less than 1 ms [1654].

The cord gives off 31 pairs of nerves: 8 + 12 + 5 + 5 + 1 = 31 (computed) [1657]. Twelve pairs leave the brain itself, the tenth, the vagus, running to the heart and gut [1657]. More than 400 human genes encode ion channels, at least 232 of them pore-forming parts of surface channels [1658][1659].

The human voltage-gated-like channel superfamily has 143 members in eight families, the third largest group of signalling proteins [1660]. Human Kv genes number 27 [148] or 35 [149], and 10 Nav genes (Nav1.1–1.9 and Nax) [148]. In the worm *C. elegans* a 1996 count gives 38 K^+ channel subunits [1661] and a 1998 count at least 80, with no voltage-gated Na^+ channel [1662].

Organism	Kv genes	Nav genes	Source
Amphimedon (sponge)	0	0	[148]
Nematostella vectensis	44	5 Nav2	[148]
Hydra magnipapillata	35	—	[148]
Drosophila melanogaster	5	1 Nav1 + 1 Nav2	[148]
Homo sapiens	27 (or 35)	10	[148][149]

The pulse. At rest the inside stands at −70 mV; at −55 mV the Na^+ channels open, the voltage rises to +30 mV and falls back, all in about 2 ms, position 27.50 [1663]. Every impulse reaches the same peak, and the Na^+ channel closes within a fraction of a millisecond [1663]. Sodium is about ten times more concentrated outside the neuron than inside [1663].

Event	Duration	Position	Source
Synaptic delay, frog, 20 °C	0.4–0.75 ms	26.03–26.60	[1664]
Impulse at one point	2 ms	27.50	[1663]
One metre of the fastest fibre, 150 m s^{-1}	6.7 ms	28.59	(computed)
Detecting a signal on a screen	131 ms	31.30	[1665]
Simple reaction time, 1,469 adults	213 ms	31.75	[1665]
One metre of the slowest fibre, 0.5 m s^{-1}	2 s	33.78	(computed)

Reaction time grows by 0.55 ms per year of age, 26 ms between 18 and 65 (computed), while detection stays at 131 ms [1665].

Growth and pruning. Synapses form from before the 27th week of pregnancy [1666]. Their density peaks at 3 months in the hearing cortex, position 47.61, and after 15 months in the frontal cortex, above position 49.07 [1666]. Net removal then follows and ends by 12 years in the hearing cortex, position 51.13 [1666].

White matter holds 176,000 km of myelinated fibre at 20 in men and 149,000 km in women [1667]. At 80 the lengths are 97,200 and 82,000 km, a loss of 44.8 % and 45.0 % (computed) [1667].

What this part of the history shows

The edge before the nerve. The voltage at the edge of the cell is older than any nerve. Bacteria hold −105 to −150 mV [134][135], *Chara* −170 to −250 mV [1596], *Paramecium* −30 to −69 mV [1586] and the neuron −70 mV [1663]. Single bacteria spike at up to 1 Hz [139], and ciliates, algae, diatoms, plants and a glass sponge without neurons all fire pulses [1587][1583][1598][499].

The nerve adds nothing new. The nerve cell has the form named in chapter 1: “It is a cell whose edge tension travels along its length.” The voltage, the channel families of choanoflagellates [148], the post-synaptic scaffold and the secretion complex all occur in single cells [474][475]. What changes is the length the pulse travels, from a cell of a

few µm to a fibre whose fastest metre takes 6.7 ms [1623].

The residue becomes the alphabet. The parts made at one depth serve as letters at the next. The scaffold arose in single cells [474], and in the sponge five of its genes are expressed together in one larval cell type [477]. The secretion machinery of the single-celled ancestor was later taken up for the synapse [475], and myelin proteins are older than myelin [1413].

Rest, loading and discharge. The pulse has the form of rest and discharge. The neuron rests at −70 mV, loads to −55 mV and discharges to +30 mV in about 2 ms [1663]. The flytrap counts its discharges: two close the trap, more than three start digestion genes and five give strong expression [1598].

Never loaded twice. After each discharge the cell cannot fire again until it has recovered: the form that a closure cannot load twice in succession. The ring giant axon of a medusa repeats at intervals of at least 3.5 ms [537]. The refractory period is 40–50 ms in a sea-pen net [558], up to 200 ms in *Paramecium* [1587], 2–10 s in *Chara* [1596] and 29 s in the glass sponge [499].

The form outlasts its carriers. The pulse is the carrier; the cell and its net are the form. One ion crosses a channel in 10 ns, position 16.39 [141], and the impulse ends after 2 ms, position 27.50 [1663]. The *Hydra* nerve net is renewed every 2–3 weeks while it keeps its shape [536], and human cortical neurons last from birth [1642].

Opened once, filled many times. The origin of the nerve has two readings. With ctenophores first, in four publications, neural systems evolved independently [479]; with sponges first, in three, the nerve has one origin [482][483]. After the first nerve the opened depth fills many times: neurons run 177, 302, 892, 3,016, 139,255, 86 billion and 257 billion [1415][603][1387][1616][1619][1518][1516].

The same rule in other surroundings. The same pulse takes other values in other surroundings. The *Chara* action potential lengthens 30-fold from 40 °C to 3.5 °C [1597], and the flytrap pulse is 1.6-fold higher at 40 °C than at 10 °C [1599]. The squid axon is wider in cool May than in warm August and doubles its speed over 15 °C [1346].

The same winding at every depth. The pulse appears at the size of a channel, a cell, a plant and a community. A biofilm of more than a million cells carries a K^+ wave over 1.5 mm with a period of hours [185][187][1582]. Electrical events run from 533 µs in a bacterial channel [150] and 2 ms in the neuron to 50–100 ms in a diatom, 2 s in the flytrap and hours in the biofilm, positions 26.29 to above 40.

18. Senses, Rhythms, Memory

The nerve carried the pulse along its length (chapter 17). Three further capacities rest on it. A sense cell turns one kind of change outside into an electrical signal.

A clock keeps a period of its own. A memory keeps a change made by the past.

This chapter follows all three in the order of their record. It begins with the molecules that take up light, the eyes built from them, and the senses of smell, taste, touch, hearing and electric fields. It then turns to the clocks of cells and bodies, the rhythms of the brain and sleep.

It ends with learning and memory, from a single cell that stops responding to a repeated touch to synapses that hold a change for a year. Every size and every time carries its position on the ladder of chapter 1.

Light

The first light receptors. Microbes take up light with the type 1, or microbial, rhodopsins [1668]. Bacteriorhodopsin is 4.3 ± 0.5 nm across, position −2.15 [1669]. It has a quantum efficiency of about 60 % and moves 188 H^+ per molecule per minute [1669].

Purple membrane holds more than 100,000 proton-pumping rhodopsins per cell [1669]. A SAR86 bacterial cell holds 24,000 proteorhodopsin molecules [1668]. The oceans hold an estimated 10^{28} bacteria that make proteorhodopsin [1669].

The rhodopsins of microbes fall into two bands of time. Transport rhodopsins have photocycles “typically <20 ms”, position below 29.59, and the proteorhodopsin cycle is 15 ms, position 29.33 [1668]. Sensory rhodopsins have cycles of at least 300 ms, position 32.06, at least 300 / 20 = 15 times the pump band (computed) [1668].

Channelrhodopsin-2 (ChR2) is “a directly light-switched cation-selective ion channel” of the green alga *Chlamydomonas reinhardtii* [1670]. It is expressed mainly under low light, and in continuous light it settles to a smaller steady conductance [1670]. Its single-channel conductance at −60 mV is 42 ± 7 fS with Na^+ and 61 ± 18 fS with Li^+, up to 129 ± 9 fS, at 226 active channels per μm^2 [1671].

ChR2 drives spikes “with millisecond precision”, but many cells cannot follow trains above about 40 Hz [1672]. The engineered variant ChETA allows trains up to at least 200 Hz [1672]. The C128 mutation extends the open state “vastly”, so that channels respond at far lower light [1673].

Opsins. Animal light reception rests on opsins, membrane proteins of 30–50 kDa that bind retinal [1674]. Retinal is bound at lysine K296 on helix VII; the counterion is E113 in vertebrate opsins and E181 in others [1674]. The first step of vision is the 11-cis to all-trans turn of retinal, on a femtosecond time scale [1675].

Opsins share a common ancestor with melatonin receptors, and placozoans have them

[1676]. The first opsin arose by gene duplication in a eumetazoan ancestor and “may not have been light-sensitive” [1676]. Two further duplications gave the progenitors of the ciliary, rhabdomeric and Go/RGR subfamilies, into which all known neuralian opsins fall [1676].

A phylogeny on sequences of 14 animal phyla finds at least four opsins in the last common ancestor of Cnidaria and Bilateria [1677]. The bilaterian ancestor had at least nine [1677]. Opsins were duplicated and lost many times [1677].

More than a thousand opsins have been identified, in seven subfamilies [1674]. Similarity is below about 25 % between subfamilies and above about 40 % within them [1674]. Other counts give 3 major neuralian subfamilies [1676] and at least 9 bilaterian paralogs [1677].

Genome	Opsin genes	Source
Homo sapiens	9, in 6 of the 7 subfamilies	[1674]
Drosophila melanogaster	7, all Gq-coupled, melanopsin subfamily	[1674]
Amphioxus	at least 6, from 4 subfamilies	[1674]
Caenorhabditis elegans	0	[1674]

Gene duplication “produced all of the different kinds of cone pigments before the evolution of rod pigments” [1678]. Cone-like cells “first appear among cnidarians” [1678].

One activated rhodopsin activates the G protein transducin at about 1,000 molecules per second [1675]. Each activated enzyme breaks about 4,000 cGMP per second, so one photon changes more than 10^5 molecules [1675]. Bovine rhodopsin was sequenced as protein in 1982 and as cDNA in 1983 [1674].

Eyes

How many origins. Salvini-Plawen and Mayr concluded that “at least 40 different lines of photoreceptor differentiation must be postulated”, as Land reports [1679]. Gehring gives their count as “at least 40 but possibly up to 65 or more phyletic lines” [547]. He argues from Pax6 for a single origin of eyes [547].

Of the Precambrian lines “only about [a] quarter” gave rise to resolving eyes, which is 10 of 40 (computed) [1679]. The rest are small pigmented pits under 100 µm, position 7.00 [1679]. Three phyla have “good” eyes: molluscs, arthropods and chordates, and eight optical types are known [1679].

One gene. Drosophila *eyeless* carries a paired domain and a homeodomain and is homologous to mouse *Small eye* (*Pax-6*) and human *Aniridia* [1680]. Targeted expression of *eyeless* produced extra eyes on wings, legs and antennae, with differentiated ommatidia and a full set of photoreceptors [1680]. Mouse Pax6 also induced extra compound eyes in *Drosophila* [547].

The *eyeless* mutation was identified by Hoge in 1915, and the fly gene was isolated about 80 years later [547]. The cnidarian relative PaxB is identical to mouse Pax2 at 82 % and Pax6 at 75 % in the paired domain [547]. In the homeodomain the identity is 60

% with Pax3/7 and 55 % with Pax6 [547].

How fast an eye can arise. Optical theory gives a light-sensitive patch becoming a focused lens eye in “only a few hundred thousand years” [1681]. The assumptions are deliberately pessimistic [1681]. Land restates the figure as “less than half a million generations”, about 5×10^5 years at one generation a year, position 60.81 [1679].

The first dated eyes. The earliest dated eyes are Early Cambrian fossils from the Emu Bay Shale, South Australia, at about 515 Ma, position 67.13 [1682][1683]. Arthropod compound eyes there carry “over 3,000 large ommatidial lenses” [1683]. *Anomalocaris* eyes, 2–3 cm long (positions 11.83–12.19), carry “at least 16,000 hexagonally packed ommatidial lenses” [1682].

The two lens counts differ by at least 16,000 / 3,000 = 5.3 times (computed). Compound eyes evolved before a hardened exoskeleton [1682]. Soft eyes of similar complexity do not appear again in the record for about 85 Myr, position 65.49, until about 515 − 85 = 430 Ma, position 66.97 (computed) [1683].

The Cambrian radiation “may have lasted for as little as 25 million years”, position 64.38 [1679]. The oldest horseshoe crab, *Lunataspis aurora*, from the Upper Ordovician of Manitoba at about 445 Ma (position 67.00), carries lateral compound eyes [1394]. Ordovician jawless fishes date to 450 Ma, position 67.01 [1679].

Resolution. Acceptance angles reach 90° in pigment-pit eyes, and about 5° is a likely threshold for tasks after the Cambrian [1679]. At 5° a 1 cm object, position 11.19, is detectable at 11 cm, position 13.38 [1679]. Many insects resolve about 1°, none better than about 0.25°, and the human fovea about 1 arc minute, “60 times better than a typical insect” [1679].

The span from pit eye to fovea is 90 × 60 = 5,400-fold, and the best insect is 15 times coarser than the fovea (computed). The bee lens is 25 µm across, position 5.74, with blur of about 0.02 rad or 1.15° [1679]. The human pupil of about 2.5 mm, position 9.93, is “a hundred times the diameter of a bee lens” [1679].

A compound eye with human resolution would be about 12 m across, position 17.65, and about 1 m with reduced resolution at the edge, position 15.39 [1679]. Fish lenses have a focal length of about 2.5 lens radii against about 4 for a uniform lens [1679]. Their refractive index rises from about 1.38 in the lens cortex to about 1.52 at the centre, in sea water of 1.34 [1679].

Eye	Count	Source
Insect ommatidium	typically 8 or 9 receptors	[1679]
Tiger beetle larval ocellus	about 6,300 receptors, 1.8° apart	[1679]
Drosophila melanogaster	700–800 ommatidia per eye; 483 ± 7 in a second count	[1466]
Scallop	about 100 eyes of about 1 mm	[1679]
Nautilus	perhaps a million receptors	[1679]
Box jellyfish *Tripedalia*	6 eyes per rhopalium, 24 per medusa	[540]

Decapod facets are about 50 µm, position 6.37, and a scallop eye about 1 mm, position 9.10 [1679]. *Nautilus* is described as having had “half a billion years” to improve its eye

[1679].

Photoreceptor timing. A fly compound-eye microvillus is about 1 µm long and 55 nm wide, positions 2.81 and 0.17, and holds about 1,000 rhodopsin molecules [1684]. Fly photoreceptors respond to a flash with a slow graded depolarisation “typically hundreds of milliseconds long” [1685]. In *Drosophila* at 25 °C, information capacity “starts to saturate at ~200 bits/s” with light adaptation [1686].

Rising temperature speeds the cascade, and the effective Q10 for information capacity is 6.5 [1687]. The fly retina uses 10 % of the fly’s resting ATP [390].

Vertebrate photoreceptor event	Duration	Position	Source
Human cone inactivation, fast	about 3 ms	27.87	[1688]
Human cone inactivation, slow	about 10 ms	28.96	[1688]
Macaque green cone integration	19 ± 9.8 ms	29.55	[1689]
Human cone dim-flash time to peak	about 20 ms	29.59	[1688]
Macaque red cone integration	28 ± 14 ms	29.90	[1689]
Mouse activated-rhodopsin lifetime	40–45 ms	30.22–30.33	[1678]
Macaque cone time to peak, within 1 mm of fovea	47 ± 14 ms	30.37	[1689]
Macaque green cone time to peak	51 ± 13 ms	30.44	[1689]
Macaque red cone time to peak	55 ± 18 ms	30.51	[1689]
Mouse GNAT2C rod decay	122 ms	31.24	[1678]
Mouse wild-type rod decay	258 ms	31.92	[1678]
Vertebrate cascade as a whole	about 1 s	33.15	[1675]

The cone time to peak is about 20 ms in human [1688] and 47–55 ms in macaque at 37 °C [1689]; the macaque value is 2.4–2.75 times the human (computed). The macaque single-photon response is about 30 fA: 33 fA from dim-flash sensitivity in 26 cells and 17.7 ± 8.7 fA from noise in 5 cones [1689]. Amplification is “at least 2–3 times larger in rods than in cones”, 20.5 s^{-2} in wild-type mouse rods against 10.2 s^{-2} in GNAT2C rods [1678].

The human eye. The retina holds 91 million rods and about 4.5 million cones, 20 rods to one cone (computed) [1690]. A rod answers one photon; a cone needs more than 100 photons for a comparable answer [1690]. Cone density rises almost 200-fold toward the centre of the fovea, and six degrees away sharpness has dropped by 75 % [1690].

Human eye	Size	Position	Source
Light the Sun puts on the eye	430	3.02	[1691]

Light the S cone takes up best	420 nm	2.02	[1691]
Light the rod takes up best	498 nm	2.18	[1691]
Light the M cone takes up best	534 nm	2.24	[1691]
Light the L cone takes up best	564 nm	2.29	[1691]
Cone in the centre of the fovea	1.5 µm	3.18	[1692]
Rod inner segment	2 µm	3.44	[1692]
Cone at the edge of the retina	6 µm	4.44	[1692]
Foveola, the zone without rods	300 µm	8.00	[1690]
Retina, thickness	0.5 mm	8.47	[1692]
Fovea, diameter	1.2 mm	9.26	[1690]
Retina spread flat	30–40 mm	12.19–12.46	[1692]

The macaque cone references are 430, 530 and 560 nm, positions 2.04, 2.23 and 2.28 [1689]. Human melanopsin takes up light best near 480 nm, position 2.14 [1675]. The eye reads sunlight between about 380 and 720 nm, positions 1.93–2.51 [1691].

Up to 50 photoreceptors feed one ganglion cell of the optic nerve [1691]. The proteins of the lens core are laid down around birth and keep their carbon for life [1693]. A cone recovers from a bright flash in about 200 ms, position 31.69, and a rod more than four times slower [1690].

Smell and taste

Mammals. Thirteen placental mammals hold more than 10,000 intact olfactory receptor genes in all, a mean of more than 769 per species (computed) [1694]. They fall into 781 orthologous gene groups, and “only three OGGs” show one-to-one orthology across the 13 species without gains or losses [1694]. African elephants have “~2000” functional OR genes in enlarged clusters [1694].

Species	OR genes	Pseudogene share	Source
Human	about 800	about 50 %	[1695]
Mouse	about 1,400	20–25 %	[1695]
Rat	1,493	19.5 %	[1695]
Dog	1,094	20.3 %	[1695]
Cow	nearly 1,000 functional	nearly as many pseudogenes	[1695]
Opossum	—	below 20 %	[1695]
Platypus	fewer than 400 functional	about 50 %	[1695]
Macaque	fewer than 400 functional	—	[1695]
African elephant	about 2,000 functional	—	[1694]

Species other than platypus and primates have “800–1,200 functional OR genes” [1695]. The human–mouse ancestor had about 690 genes, or about 750 by another method [1695]. The elephant repertoire is about 2,000 / 400 = 5 times that of primates and platypus (computed).

Gains and losses are large. The opossum lineage gained more than 750 genes, the cetartiodactyl and rodent lineages more than 400 each, and each branch to the

placental orders lost more than 170 [1695]. Total gains and losses are 4,968 or 5,134, depending on the tree [1695].

The human nose. The human genome holds 339 intact and 297 broken OR genes at 51 places on 21 chromosomes [1696]. A second count gives 400 working genes [1697]. Of the 636 genes of the first count, 339 / 636 = 53 % are intact (computed).

Each receptor neuron carries one type of receptor [1698]. The receptor field covers about 5 cm^2 and holds 6–20 million receptor neurons, each with 5–20 cilia [1698][1699]. They report to a little under 2,000 collecting points in the brain [1699].

The 339 types spread over 6–20 million neurons give 6×10^6 / 339 = 18,000 to 20×10^6 / 339 = 59,000 neurons per type (computed). An olfactory neuron lives 30 days to 1 year, positions 46.60–48.87 [1699].

Insects. *Drosophila melanogaster* has 62 odorant receptors and *Anopheles gambiae* 79 [1700]. The honey bee has 170 annotated, 7 of them pseudogenes; one subfamily is expanded to 157 genes, and one tandem array holds 60 [1700]. The number of bee Ors roughly equals the number of glomeruli in the antennal lobe, about 160–170 [1700].

Gustatory receptors number 10 in the bee, 68 in *D. melanogaster* and 76 in *A. gambiae* [1700]. The bee ratio of intact odorant to gustatory receptors is 163 / 10 = 16, the fly ratio 62 / 68 = 0.9 (computed).

Taste. Five qualities are read: sweet, sour, bitter, salty and umami [1698]. An adult has 2,000–4,000 taste buds, each with 10–50 sensory cells [1701]. A taste bud is 30–60 µm across, position 6.22 at the geometric mean of 42.4 µm [1702].

A taste cell is renewed after 7 days by one source and after 10–14 days by another, positions 45.27 and 45.60–45.90 [1698][1701].

Touch and hearing

Channels that read force. Mechanosensitive channels occur in bacteria, fungi, plants and animals [1703]. Channels purified from bacteria “sense forces from the lipid bilayer in the absence of other proteins” [1703]. The *E. coli* large-conductance channel MscL is encoded by *mscL* alone, a protein of 136 amino acids [1704].

Piezo1 and Piezo2 are multipass membrane proteins needed for mechanically activated cation currents [1705]. Piezo2 carries the rapidly adapting currents of dorsal root ganglion neurons [1705]. Piezo homologues occur in invertebrates, plants and protozoa [1705].

The hair cell. The vertebrate hair-cell receptor current is carried in the living animal by K^+ [1706]. The channel passes Li^+, Na^+, K^+, Rb^+, Cs^+, Ca^{2+} and at least one small organic cation [1706]. A hair bundle holds 30 to a few hundred stereocilia; fine threads join their tips, and bending the bundle stretches the threads and opens channels [1690].

The bundle reads deflections of 0.3 nm, position −4.57, and forms its receptor potential in about 10 µs, position 22.67 [1690]. The cochlea is 10 mm wide and 35 mm long uncoiled, positions 11.19 and 12.33 [1690]. The smallest movement read and the organ that reads it differ by 35 mm / 0.3 nm = 1.2×10^8, which is 12.33 + 4.57 = 16.90

positions (computed).

Each human ear holds about 3,500 inner hair cells in one row and about 12,000 outer hair cells, 15,500 in all (computed) [1698]. About 90 % of the auditory nerve fibres come from the inner hair cells [1698]. The ear reads 20–20,000 Hz, a 1,000-fold range (computed), low tones at the tip of the cochlea and high tones at its base [1691].

Balance and the body. The utricle holds about 30,000 hair cells and the saccule about 16,000, 46,000 in all (computed) [1698]. Crystals of calcium carbonate weigh down the membrane above them, and three semicircular canals read turning of the head [1691]. Muscle spindles read the stretch of a muscle, Golgi tendon organs that of a tendon, and osmoreceptors the concentration of body fluids [1691].

Skin. The Merkel disc tells points 0.5 mm apart, position 8.47, and reads slow vibration of 5–15 Hz [1699][1691]. The Meissner corpuscle, 10 × 20 µm (positions 4.91 and 5.54), reads vibration below 50 Hz [1698][1691]. The Pacinian corpuscle, 1.4 mm (position 9.40), reads vibration near 250 Hz [1698][1691].

Free nerve endings read pain, temperature and deformation, and the channel that capsaicin opens also opens above 37 °C [1691]. One study turned a field of the Earth’s strength, about 35 µT, around 36 seated adults [1707]. Brain waves of 8–13 Hz dropped after some rotations, only when the field pointed down [1707].

The electric sense

Lateral-line electroreception is present in lampreys and in jawed fishes [1437]. It was lost in frogs, amniotes and neopterygian fishes, later also in Asian notopterids and characiforms [1437]. It “evolved independently at least twice within teleosts”, with ampullary receptors arising separately in Osteoglossomorpha and Ostariophysi [1437].

Electroreceptive groups include lampreys, sharks, rays and holocephalans, lungfishes, coelacanths, salamanders and caecilians, and bichirs, paddlefishes and sturgeons [1437]. Among teleosts they include mormyriforms, gymnotiforms and catfishes [1437]. Monotremes sense fields by trigeminal endings, apart from the lateral line [1437].

The count is at least 2 teleost origins, 1 ancestral vertebrate system and 1 monotreme system, at least 4 in all, against 3 losses plus 2 later ones (computed from [1437]). Lamprey end buds hold up to 30 receptor cells, each with 80–90 microvilli [1437].

About 16 % of fish species sense fields passively, and about 1.5 % have electric organs, a ratio of 10.7 (computed) [1708]. Passive prey detection uses fields in the microvolt range [1708]. Weak discharges stay below 1 V in electrolocating taxa and below 10 V in other weak groups; strong discharges exceed 50 V [1708].

From 1 µV to 50 V is 5×10^{7}, more than seven orders of magnitude (computed). The electric organ “has evolved six times in fishes” [1709]. Three lineages compared share transcription factors and developmental pathways [1709].

The human senses today

Event	Duration	Position	Source

Hair cell: bundle movement to signal	10 µs	22.67	[1690]
Sound to the brain	8–10 ms	28.76–28.96	[1710]
Light to the brain	20–40 ms	29.59–30.22	[1710]
Reaction to sound	140–160 ms	31.36–31.48	[1710]
Reaction to touch	155 ms	31.46	[1710]
Reaction to light	180–200 ms	31.59–31.69	[1710]
Cone recovers after a bright flash	about 200 ms	31.69	[1690]
Taste cell renewed	7 days; 10–14 days	45.27; 45.60–45.90	[1698][1701]
Olfactory neuron, lifespan	30 days to 1 year	46.60–48.87	[1699]

The smallest difference that is noticed is a constant fraction of the stimulus, Weber's law [1711]. The WHO table of sounds runs from breathing at 10 dB to a jackhammer at 130 dB [1712]. The 120 dB difference is a ratio of sound intensity of 10^(120 / 10) = 10^{12} (computed).

More than 25 % of people over 60 have disabling hearing loss [1713]. About 430 million people need care for it, 34 million of them children, and over 1 billion young adults are at risk through loud listening [1713]. At least 2.2 billion people have impaired vision, for at least 1 billion of them preventable or untreated, with cataract at 94 million and uncorrected refractive error at 88.4 million [1714].

In Guangzhou 39.5 % of six-year-olds became short-sighted within three years [1715]. In 12 schools that added one 40-minute outdoor class each school day the share was 30.4 %, 9.1 points or 23 % fewer (computed) [1715].

Clocks

The oldest clock. The oldest clock in the record is a loop of three proteins in cyanobacteria. Of its genes "kaiC is evolutionarily the oldest, and kaiA is the youngest and likely evolved only in cyanobacteria" [1716]. The order was drawn from "≈70 complete prokaryotic genomes", and homologues "occur in Archaea and Proteobacteria as well" [1716].

The oscillation was rebuilt in a test tube "by incubating KaiC with KaiA, KaiB, and adenosine triphosphate" [1717]. The cycle "persists even without transcription or translation", and its period "was stable despite temperature change (temperature compensation)" [1717]. The KaiC phosphorylation cycle lasts 24 h, position 43.50, and *Synechococcus elongatus* glows in a cycle of 25.6 ± 0.1 h at 30 °C, position 43.56 [1718].

KaiC consumes "15 ATPs" "per day per KaiC subunit", 15 / 24 = 0.63 ATP per hour (computed) [1718]. A null mutant is "reported to consume 27 ATP molecules per day", 1.8 times the normal rate (computed) [1718]. *Synechocystis* sp. PCC 6803 carries two further Kai systems whose KaiC1 and KaiC3 "exhibit phase-locked free-running phosphorylation rhythms"; both systems are needed for the rhythm of about 24 h [1719].

The animal clock. The *period* gene of the fly was cloned in the mid-1980s [1720]. Its protein PER suppresses its own messenger RNA; TIM binds PER and governs its entry into the nucleus, and DBT phosphorylates PER and speeds its breakdown [1720]. Most peripheral organs and tissues can keep circadian oscillations in isolation [1720].

In mammals the suprachiasmatic nucleus of the hypothalamus is the primary pacemaker [1721]. Its single neurons, grown apart, each keep their own rhythm; in the intact nucleus their connections hold them in step, sharpen their precision and let light shift their phase [1721]. In the mouse, feeding at a fixed time of day shifts the phase of peripheral tissues by up to 12 h, position 42.87, while the nucleus stays unchanged [1722].

The liver resets fastest; kidney, heart and pancreas follow, and after a week of daytime feeding (position 45.27) all share the shifted phase [1722]. Light sets the central clock; food sets the clock of the liver [1722].

The intrinsic period of the human pacemaker, measured in healthy young and older people under controlled light, is 24.18 h, position 43.51, in both age groups [1723]. The day itself sits at position 43.50 (computed). The clock runs 0.18 × 60 = 10.8 minutes slow each day and is reset by light (computed).

The clock is present before birth [1724]. Rhythms of sleep and hormone release become pronounced after about two months of age, position 47.24 [1724]. Cycled light hastens the alignment of rest and activity with the 24-hour day [1724].

The rhythms of the body. The body does nothing at a constant rate. Its rhythms run from the brain waves to the year.

Rhythm	Period	Position	Source
Heartbeat, 75 per minute at rest (60–100)	0.8 s (0.6–1.0 s)	32.95 (32.69–33.15)	[1725]
Breath, 12–18 per minute	3.3–5 s	34.43	[1726]
Mayer waves of blood pressure, about 0.1 Hz	about 10 s	35.25	[1727]
Sleep cycle, non-REM and REM	90–110 min	41.07	[1728]
Migrating motor complex of the gut	90–120 min	41.11	[1729]
The day	24 h	43.50	(computed)
Intrinsic circadian period	24.18 h	43.51	[1723]
Menstrual cycle, median of 600,000 cycles	29.3 days	46.57	[1730]
Winter excess of deaths, Europe	1 year	48.87	[1731]

Kleitman proposed a basic rest-activity cycle that appears in sleep as the alternation of non-REM and REM and goes on in a similar form by day [1732]. The median menstrual cycle has a follicular phase of 16.9 days and a luteal phase of 12.4 [1730]. The winter excess of deaths, 1988–1997, was 28 % in Portugal and 21 % in Spain and in Ireland [1731].

The heart follows the breath. When a choir sings a slow chant breathed in ten-second cycles, the heart rate of every singer rises and falls with that breath, and the singers' heart rates move together [1733]. This coupling is respiratory sinus arrhythmia [1734].

A healthy heart rhythm varies. In 736 people of mean age 72, one standard deviation less heart rate variability raised the hazard of death over four years by 1.70 (1.37–2.09) [1735]. In 4,414 adults followed ten years, variability fell with age in both sexes, apart from disease or medication [1736].

The day rhythm holds its period of 24.18 h for life [1723]. Cortisol, one of the hormones that carry it, has a half-life of 66 minutes, position 40.69 [1737]. The ratio is 24.18 × 60 / 66 = 22 (computed).

88,905 adults wore a light sensor for one week [1738]. Over eight years the brightest tenth of nights carried a hazard of death of 1.21–1.34 against the darkest half, and the brightest days 0.66–0.83 [1738]. Night shift work is classed as probably carcinogenic to humans, Group 2A, with limited evidence in humans and sufficient evidence in animals [1739].

Brain rhythms

Networks of neurons in the mammalian forebrain oscillate in bands "from approximately 0.05 Hz to 500 Hz" [1740][1741]. Their mean frequencies "form a linear progression on a natural logarithmic scale" [1740]. The classes were defined by Penttonen and Buzsáki in 2003, whose centre frequencies and ranges "form an arithmetic progression on the natural logarithmic scale" [1742].

A 2012 review prints ten classes in its figure "Oscillatory classes in the cortex" [1741]. Each class centre below is the geometric mean of its printed limits (computed).

Class as printed	Limits (Hz)	Period	Positions	Geometric centre (Hz)
"15-40 s, slow 4"	0.025–0.0667	15–40 s	35.62–36.51	0.0408
"5-15 s, slow 3"	0.0667–0.200	5–15 s	34.62–35.62	0.1155
"2-5 s, slow 2"	0.200–0.500	2–5 s	33.78–34.62	0.3162
"0.7-2 s, slow 1"	0.500–1.429	0.7–2 s	32.83–33.78	0.8452
"1.5-4 Hz, delta"	1.5–4	0.25–0.667 s	31.89–32.78	2.4495
"4-10 Hz, theta"	4–10	0.1–0.25 s	31.06–31.89	6.3246
"10-30 Hz, beta"	10–30	33.3–100 ms	30.06–31.06	17.3205
"30-80 Hz, gamma"	30–80	12.5–33.3 ms	29.16–30.06	48.9898
"80-200 Hz, fast"	80–200	5–12.5 ms	28.33–29.16	126.4911
"200-600 Hz, ultra fast"	200–600	1.67–5 ms	27.33–28.33	346.4102

The legend reads: "Note the linear progression of the frequency classes" "on the natural log scale" [1741]. Neighbouring bands "tend to have constant ratios" [1741]. The axis is ticked at 0.05, 0.37, 2.72, 20.09 and 148.41 Hz, which equal e^−3, e^−1, e^1, e^3 and e^5 (computed).

Adjacent centres differ by factors of 2.58 to 2.90, with a geometric mean of (346.41 / 0.0408)^(1/9) = 2.73 (computed). Each class spans a factor of 2.50–3.00, which is 0.83–1.00 positions on the ladder ($\log_3 2.50 = 0.83$; $\log_3 3.00 = 1.00$, computed). The whole figure spans 1.67 ms to 40 s, positions 27.33–36.51, a factor of 24,000 (computed).

Other lists differ. One gives "<0.5 Hz (ultra-slow oscillations), 0.5–1 Hz (slow oscillations), 1–3.5 Hz (delta), 3.5–8 Hz (theta)", then alpha, beta, gamma and ">80 Hz" [1743]. The text of the 2012 review gives theta as "4 to 9 Hz" and gamma as "30 to 90 Hz", against 4–10 and 30–80 Hz in its figure [1741].

Named rhythm	Period	Position	Source
Hippocampal ripples, 140–200 Hz	5–7.14 ms	28.33–28.65	[1741]
Mouse hippocampal gamma, 40–100 Hz	10–25 ms	28.96–29.80	[1744]
Membrane time constant	10–30 ms	28.96–29.96	[1741]
Spindles, "12 to 18 Hz"	55.6–83.3 ms	30.52–30.89	[1741]
Alpha, "8 to 12 Hz"	83.3–125 ms	30.89–31.26	[1740]
Sharp-wave ripple event	80–150 ms	30.85–31.43	[1741]
Rodent theta, 6–12 Hz	83.3–167 ms	30.89–31.52	[1741]
Mouse hippocampal theta, 6–9 Hz	111–167 ms	31.15–31.52	[1744]
Carnivore theta, 4–6 Hz	167–250 ms	31.52–31.89	[1741]
Human theta, 1–4 Hz	0.25–1 s	31.89–33.15	[1741]
Neocortical slow oscillation, 0.5–1.5 Hz	0.667–2 s	32.78–33.78	[1741]
Ultra-slow rhythm, 0.1 Hz	10 s	35.25	[1741]

On the scalp of the waking adult, beta (13–30 Hz) is the most common rhythm, and alpha (8–12 Hz) marks rest with closed eyes [1745]. Theta (4–7 Hz) comes with drowsiness and delta (0.5–4 Hz) with deep sleep [1745].

Within mammals the classes are "largely preserved throughout the mammalian evolution" [1740]. "All known oscillations in humans are present in all other mammals investigated to date" [1741]. "Brain rhythms vary little across species (30% to 100%), brain size increases hundreds- to thousands-fold" [1741].

Gamma keeps "the same frequency range (30 to 90 Hz)" across the species discussed, and spindles "the same frequency (12 to 18 Hz)" [1741]. The twin correlation of gamma is "r = 0.9" [1741]. The sleep spectrum in the 8–16 Hz band allows ">90% correct discrimination among individuals" [1741].

Correlated firing. In awake cortex, pairs of neurons recorded together share little trial-to-trial variation in spike counts. Thirteen measured values run from −0.02 to 0.20, nine of them below 0.1 [1746][1747][1748][1749][1750]. The MT values weighted by pairs give (57 × 0.20 + 12 × −0.02 + 34 × 0.06) / 103 = 0.128 (computed) [1747].

Area	Value	State	Source
Monkey	0.12	awake	[1746]

Macaque MT, similar preferred directions (n = 57)	0.20 (SD 0.15)	awake task	[1747]
Macaque MT, opposite preferred directions (n = 12)	−0.02 (SD 0.09)	awake task	[1747]
Macaque MT, non-directional cell (n = 34)	0.06 (SD 0.15)	awake task	[1747]
Macaque V4, 3,240 pairs	0.058 ± 0.001	evoked	[1748]
Macaque V4, 1,122 pairs	0.110 ± 0.003	spontaneous	[1748]
Macaque V4	around 0.08	desynchronized	[1749]
Macaque V1, 1 s window, three layers	0.10 ± 0.02; 0.09 ± 0.02; 0.08 ± 0.02	awake	[1750]
Macaque V1, 200 ms window, three layers	0.05 ± 0.01; 0.01 ± 0.01; 0.05 ± 0.01	awake	[1750]

Nearby, similarly tuned neurons in V1 show “virtually no correlated variability” [1751], and rodent neocortex shows “Near-zero” mean correlation [1752]. Attention gains over 80 % from lower correlation in V4 [1753], and attention “can either increase or decrease spike count correlations” [1754].

Under anaesthesia median noise correlations are 0.020, 0.015 and 0.007 in macaque IT, V4 and V1, over 1,291, 759 and 1,014 pairs [1755]. Correlations are “uniformly higher in synchronized states” [1756] and lower in awake than anaesthetised rats [1757].

Seizures. In rat brain slices treated with 4AP, cross-correlation fell during seizure-like events in 27 of 30 pairs, and mutual information and phase correlation in 28 of 30 [1758]. “Unexpectedly, seizure-like events in 4AP were desynchronous events” [1758]. Human single neurons are “not hypersynchronous” at onset and “nearly homogenous” at the end [1759].

Human intracranial recordings show synchrony rising at the smallest and largest scales [1760]. In 88 seizures of 21 patients, network flexibility fell from 0.665 ± 0.205 to 0.274 ± 0.165, a factor of 2.43 (computed) [1761]. The balance of excitation and inhibition is “disrupted” during seizures [1762].

Sleep

Without a brain. Sleep-like states occur in Cnidaria, “an earlier-branching metazoan lineage” [1763]. In *Hydra vulgaris* the sleep-like state is regulated by homeostasis and needed for cell proliferation [556]. Its ultradian rhythm has a period of 4 h, position 41.87 [556].

Sleep deprivation in *Hydra* changed expression of “212 genes, including cGMP-dependent protein kinase 1 (PRKG1) and ornithine aminotransferase” [556]. Melatonin, GABA and PRKG1 promoted sleep, and dopamine induced it [556].

Worms and flies. In *C. elegans* lethargus, a sleep-like state, “occurs before each of the four moults” [606]. In *Drosophila* rest is “characterized by an increased arousal

threshold” and “is homeostatically regulated independently of the circadian clock” [1764]. Flies lacking arylalkylamine N-acetyltransferase “show increased rest after rest deprivation” [1764].

Homeostatic regulation of rest depends on *timeless*, not on *period* [1765]. The longest immobility of a fly lasts up to 157 min, position 41.48 [1765].

The octopus. Octopus sleep shows “wake-like skin patterning” [1350]. Active sleep shows prominent 30 Hz oscillations; quiet sleep shows events of 12–18 Hz, up to 1 s long, in the superior frontal lobe [1350]. The 12–18 Hz range is the range printed for mammalian spindles [1741].

Octopus sleep	Duration	Position	Source
Active-sleep bout	75 ± 28 s	37.08	[1350]
Quiet-sleep bout	50.5 ± 16.43 min	40.45	[1350]
Interval between active bouts	about 60 min	40.61	[1350]
Quiet sleep per 24 h (12 × 50.5 min)	about 10.1 h	42.71	(computed)

An octopus has 10 ± 3.5 active and 12 ± 3 quiet bouts per 24 h [1350].

Fishes. In zebrafish, “common neural signatures of sleep may have emerged in the vertebrate brain over 450 million years ago”, position 67.01 [1766]. The larvae were recorded at 7 days after fertilisation, position 45.27 [1766]. They show “at least two major sleep signatures”, “slow bursting sleep” and “propagating wave sleep” [1766].

Reptiles. In the lizard *Pogona vitticeps*, slow-wave and REM sleep alternate every 80 s, position 37.14, for 6–10 h a night, positions 42.24–42.70 [1491]. A night thus holds 6 h / 80 s = 270 to 10 h / 80 s = 450 cycles (computed). These dynamics reach back “at least to the emergence of amniotes” [1491].

An infraslow rhythm of sleep is “conserved across amniotes” [1490]. In all seven lizard species tested heart rate followed the phase of the beta rhythm, and breathing and muscle tone followed in five [1490]. In the bearded dragon the rhythm of cerebral blood volume was strong only in sleep [1490].

Infraslow sleep rhythm	Period	Position	Source
Lizards, beta power, range across individuals	84–134.5 s	37.19–37.61	[1490]
Lizards, mean across seven species	113.2 ± 6.8 s	37.46	[1490]
Human, N2	51 s	36.73	[1490]
Rat, NREM	47 s	36.66	[1490]
Pigeon, NREM	49 s	36.70	[1490]
Mouse, cerebral blood volume	50 s	36.71	[1490]
Bearded dragon, cerebral blood volume	100 s	37.34	[1490]
Panther chameleon, skin brightness	175.7 ± 18.3 s	37.86	[1490]

Human, rat and pigeon periods are “roughly half” those of lizards; the lizard mean over the pigeon is 113.2 / 49 = 2.31 (computed) [1490]. Across species the period follows body temperature, $R^2 = 0.88$ [1490]. The study recorded 7 lizard species at 20–27 °C, 5 rats, 11 pigeons and 8 humans, with ultrasound in 4 bearded dragons and 4 mice [1490].

Birds. Birds sleep in flight [1767]. In flight they slept 0.69 h a day, position 40.27, which is 7.4 % of their sleep on land [1767]. Time asleep was 2.89 ± 0.58 % in flight against 53.28 ± 4.82 % on land, N = 14 and 9 [1767].

Slow-wave episodes lasted 10.89 ± 0.81 s in flight and 28.25 ± 1.75 s on land, positions 35.33 and 36.19 [1767]. Half the brain slept at a time in 47.27 ± 5.30 % of asymmetric slow-wave sleep in flight against 24.96 ± 2.26 % on land [1767]. The longest flight lasted 10.02 days, position 45.60 [1767].

Mammals. Daily sleep runs from 18–20 h in bats and opossums to 3–4 h in elephant and giraffe [1768].

Mammal	Sleep	Position	Source
Bats and opossums, daily	18–20 h	43.24–43.33	[1768]
Platypus, adult REM	8 h	42.50	[1768]
Bushtail possum, REM	6.6 h	42.32	[1768]
African elephant (captive), sleep / REM	3.9 h / 1.8 h	41.85 / 41.14	[1768]
Elephant and giraffe, daily	3–4 h	41.61–41.87	[1768]
Wild elephant matriarchs, daily	2.3 and 1.8 h	41.36 and 41.14	[1769]
Guinea pig, REM	1 h	40.61	[1768]
Sleep cycle, Asiatic elephant	1.8 h	41.14	[1768]
Sleep cycle, short-tailed shrew	about 8 min	38.77	[1768]

The sleep cycle of the elephant is 108 / 8 = 13.5 times that of the shrew (computed). Across 71 mammals, log body weight against sleep amount gives $R = -0.5$, about 25 % of the variance [1768]. Brain weight and encephalisation “correlate poorly and negatively” with NREM and REM amounts [1768].

The two wild elephant matriarchs were recorded 35 days each, a combined 2.0 h of sleep a day [1769]. Lying-down sleep came on 10 of 35 days, and they went up to 46 h without sleep, position 44.09, on 4 days by the results and 5 by the discussion [1769]. Captive elephants are reported at 3.10–6.90 h and an earlier wild study at 3.17–3.36 h [1769].

The all-mammal regression is $TST = 17.946 \times Mb^{-0.076}$ ($r^2 = 0.25$), which predicts 5.46–5.87 h for elephants [1769]. The same paper cites the horse at 2 h 53 min, the captive giraffe at about 4.6 h and the Amazonian manatee at 6.75 h [1769].

The human night. A night holds 4–6 cycles of 90–110 min, positions 40.98–41.16

[1728]. Light sleep (N1) takes 5 % of the night, N2 45 %, deep sleep with delta waves (N3) 25 % and REM 25 % [1728]. The first REM period lasts about 10 min, the last up to an hour, positions 38.98 and 40.61 [1728].

In mice the space between brain cells widened by 60 % during sleep and under anaesthesia, and waste left the brain faster [1770].

Synchrony in sleep. In cat neocortex the correlation length of field potentials is 3.7 ± 0.4 mm awake, position 10.29 [1771]. It is 13.0 ± 1.2 mm in slow-wave sleep and 3.1 ± 0.5 mm in REM, positions 11.43 and 10.13 [1771].

The ratio of slow-wave sleep to waking is 13.0 / 3.7 = 3.5 (computed). Joint silence and firing of units reach 7 mm in slow-wave sleep, position 10.87 [1771].

In rat cortex in NREM sleep, population ON periods last 815.5 ± 119.9 ms and OFF periods 85.8 ± 5.9 ms, positions 32.97 and 30.92 [1772]. Synchrony at ON–OFF transitions “decreased by 18% from early to late sleep”, and by 24 % at OFF–ON transitions [1772]. NREM shows “a several fold increase in long ISIs (>100 ms)” against waking and REM [1772].

In 13 patients with 600 recorded units, firing at EEG positivity was 39 ± 1 % of the mean NREM rate, at negativity 198 ± 11 % [1773]. “85% ± 0.7% of slow waves were detected in less than half of the recording sites”, with a mean involvement of 27.1 ± 0.4 % of regions [1773]. Spindles of 10–16 Hz occupied less than half the regions in 75.8 ± 0.9 % of cases [1773].

Zero-lag correlation of excitatory and inhibitory ensembles in human cortex is 0.726 awake, 0.47 in slow-wave sleep and 0.503 in REM [1762]. In rat cortex 10.8 ± 6.3 % of 14,343 pairs had a significant peak of synchrony in NREM and 3.6 ± 3.4 % a trough [1774]. Synchrony among hippocampal principal cells is “lowest during θ oscillations and highest during slow-wave sleep” [1741].

Learning without a nerve

No fossil or clock dates learning. Its record consists of living species, and it begins in single cells and in plants.

A ciliate. The single cell *Stentor coeruleus* habituates to repeated touch [1775]. Habituation used 30 stimuli at 1-min intervals, position 36.88, in 31 and 44 cells; a 2.5-min interval used 43 cells, position 37.71 [1775]. “Within 15 minutes, 90% of habituated cells became fully responsive again”, position 39.34 [1775].

A slime mould. In the plasmodium of *Physarum polycephalum* habituation was tested “with chemotaxis as the behavioural output and quinine or caffeine as the stimulus” [1776]. The organism “learnt to ignore the stimuli when they were repeated, but responded again when the stimulus was withheld” [1776]. It met the criteria of “responsiveness decline and spontaneous recovery”, plus “stimulus specificity” [1776].

The studies used 410 of 416 plasmodia: 140 with quinine at 4 mM, 70 with caffeine at 1 mM and 200 controls [1776]. In tests at 1–4 mM, caffeine was crossed only below 2 mM [1776].

The habituation phase lasted 5 days and the whole experiment 9, positions 44.96 and 45.50 [1776]. On day 1 trained plasmodia crossed the bridge in 4 h against about 1 h for controls, and later they “crossed the bridge twice as fast” [1776]. The stimulus was withheld for 2 days before recovery, position 44.13 [1776].

A learned response passes by fusion. Transfer occurred “when fusion was lengthened to 3 h”, position 41.61; 1 h was not enough [1777]. “Veins between the two slime moulds are apparent after 2 h”, and “A minimum of habituated individuals is required” [1777].

The habituation index rose with the share of habituated plasmodia up to about 0.4 and then levelled [1777].

A plant. In *Mimosa pudica*, leaf folding “exhibits clear habituation” [1778]. Habituation was “more pronounced and persistent for plants growing in energetically costly environments” [1778]. The learned response was kept “even when left undisturbed in a more favourable environment for a month”, position 46.60 [1778].

A 2016 review states that “it is critical that the Gagliano et al. (2014) results be repeated by an independent laboratory” [1779]. It adds that without data across intertrial intervals “it is difficult to separate sensory adaptation from habituation” [1779].

In pea seedlings, learning by association was reported in 2016 [1780]. With fan and light on the same arm 62 % grew towards the fan; on opposite arms 69 % grew away from it [1780]. Training in the subjective day, in light–dark and in dark gave 61 %, 47 % and 20 % in 83 seedlings, and “learning was successful only when it occurred during the subjective day” [1780].

A replication in 2020 counted 61 plants against 60 controls and 42 against 40 [1781]. Its p values were 0.335 and 0.387, against 0.0027 and 0.0017 in the original with 13 + 10 and 13 + 9 plants [1781].

Learning with a nerve

Worms. A planarian keeps a familiarisation memory for at least 14 days, position 45.90, and keeps it through regeneration of the head [592]. *C. elegans*, with “302 neurons” among “959 cells” and “about 5000 chemical synapses”, habituates to taps [602].

Tap habituation plateaus “after about seven taps at a 10-sec ISI”, position 35.25 [602]. Long-term memory followed “four blocks (each separated by 1 h) of 20 taps at a 60-sec ISI”, and worms “massed trained with 80 taps” kept nothing at 24 h [602]. A heat-shock block of protein synthesis during training “blocked consolidation” [602].

Salt aversion reversed “within 10 min” if salt came with food [602]. The temperature thresholds of the AFD neuron were 15, 17 and 21 °C for worms grown at 15, 20 and 25 °C [602]. A tap made the worm reverse by around 1 mm, position 9.10 [602].

The sea hare. In *Aplysia* the gill-withdrawal reflex habituates to repeated touch, recovers after rest and returns after a strong stimulus elsewhere [1782]. Long-term habituation took “Five” daily ten-trial sessions and lasted at least 3 weeks, position 46.27; spaced sessions lasted longer than massed training [1351].

A rapid protocol of “Four ten-trial training sessions”, “only 40 patterned stimuli”, 1.5 h apart over 5 h, gave habituation lasting more than a week [1783]. A synaptic decrement was found in the isolated ganglion 24 h later, position 43.50 [1783].

After long-term sensitisation the sensory-to-motor connections were “significantly larger (2.2x)” than in controls [1784]. Blocks of protein and RNA synthesis “blocked long-term facilitation without interferring with short-term facilitation” [1784].

The octopus. *Octopus vulgaris* learns by watching another, and makes the correct choice without further conditioning for 5 days, position 44.96 [1785].

Insects. In *Drosophila* about 150 flies per chamber received twelve shock pulses with one odour, and “Typically, 95% of trained flies avoided the shock-associated odor” [1786]. Wild-type memory decayed gradually over the first 7 h and was present at 24 h [1786]. The mutants *amnesiac*, *rutabaga* and *dunce* lost memory fast in the first 30 min, yet it stayed measurable for at least 3 h [1786].

The honeybee has “a brain as small as 1 µL containing 950,000 neurons”, 3,146 times the worm’s 302 (computed) [1465]. A second count gives about 960,000 neurons in about 1 mm³ [1464]. “Three learning trials produce a stable long-term memory” [1465].

The early long-term memory of the bee lasts 1–2 days and needs no protein synthesis; the late one lasts at least 3 days and needs it [1465]. Spaced trials came 10 min apart and massed trials 30 s apart [1465]. The reinforcing neuron VUMmx1 is one of 15 ventral unpaired median neurons of the suboesophageal ganglion [1465].

“A life-long memory of a colour signal is already established after 3 operant learning trials” [1787]. Colour memory dips to a minimum after roughly 2–3 min and rises again over 10–20 min [1787]. Hungry bees respond to an odour on their own at “a few percent up to 30%” [1787].

Memory in the synapse

The timing window. In cultured rat hippocampal neurons, a postsynaptic spike “within a time window of 20 msec after presynaptic activation resulted in long-term potentiation” [1788]. A spike within 20 ms before it led to depression [1788]. The mean changes were +48.4 ± 9.9 % and −18.0 ± 3.2 %, and the window has position 29.59 [1788].

Early and late. Long-term potentiation has an early and a late phase. The early phase lasts “less than three hours”, and “The synaptic tag decays in less than three hours”, position 41.61 [1789]. The late phase needs transcription and translation [1789].

Months in a living rat. Trains of “400 Hz, 25 msec” (position 29.80) induced potentiation in the hippocampus of living rats [1790].

Protocol	Animals with stable LTP	Decay time constant	Position	Source
5 trains	0 of 6	0.7 d	43.17	[1790]
20 trains	1 of 6	1.0 d	43.50	[1790]
4 × 5 trains	3 of 6	3.3 d	44.59	[1790]
50 trains, long	8 of 12	—	—	[1790]

50 trains, long baseline	8 of 12			[1790]
50 trains, short baseline	1 of 9	32 d	46.65	[1790]
Lateral perforant path	3 of 4	42 d	46.90	[1790]
One animal, 369 days	—	127 d	47.91	[1790]

The stable group held an asymptote of 21 ± 3 % against 0.4 ± 1 % in the decremental group [1790]. The stable animals were recorded over 42–119 days, mean 68, positions 46.90–47.85 [1790]. The longest record lasted 369 days, position 48.88, and kept 13 % on the 119-day fit and 10 % on the 369-day fit [1790].

The decay constants span 127 / 0.7 = 181-fold (computed).

Spines. About 50 % of spines in mouse barrel cortex persist for at least a month, and the rest last “a few days or less” [1791]. Another study finds ~73 % stable over a month in young cortex and ~96 % in adult cortex, with an adult half-life “greater than 13 months”, position 48.94 [1792].

In mouse CA1 the mean spine lifetime is about 1–2 weeks, positions 45.27–45.90, and full turnover “~2–3 times this interval” [1793]. CA1 turnover “differed sharply” from neocortex [1793]. New spines formed by a novel experience are kept in “a small fraction” “throughout the entire life” [1794].

Engrams. Richard Semon introduced the term “engram” in 1904 for the neural substrate of a memory [1795]. An experience activates a subset of cells that undergo lasting change; their reactivation brings retrieval [1795]. In mice, light stimulation of dentate-gyrus cells labelled during fear conditioning recalled the fear: “The mice showed increased freezing only upon light stimulation”, over 3 min of light, position 37.88 [1796].

Hippocampus and sleep. In rats conditioned to tone and context, hippocampal lesions at 1 day after training abolished contextual fear; lesions at 7, 14 or 28 days spared it, and tone fear was unaffected [1797]. In humans, memories of everyday life “depend initially on the medial temporal lobe system, including the hippocampus” [1798]. Damage there disrupts recent memories more than older ones [1798].

Place cells active together during a task were more likely to fire together in the following slow-wave sleep, in three rats, and the tendency declined over each sleep session [1799]. Sharp-wave ripple events “last 80-150 ms” and carry ripples of 140–200 Hz [1741]. The number of cell assemblies that can nest in one theta period is “7 to 9” [1741].

Human forgetting. A replication of Ebbinghaus used lists of 104 nonsense syllables, 8 rows of 13, tested after 20 min, 1 h, 9 h, 1 day, 2 days, 6 days and 31 days [1800]. Those intervals have positions 39.61, 40.61, 42.61, 43.50, 44.13, 45.13 and 46.63. Savings at 31 days were 0.0410, 0.137 corrected, and the curve shows “a jump upwards starting at the 24 hour data point” [1800].

School Spanish was tested in 733 people over 50 years, position 52.43 [1801]. Retention fell exponentially for the first 3–6 years, positions 49.87–50.50, then held roughly unchanged up to 30 years, position 51.97, before a final decline [1801]. Responses fell

into two groups with life spans of 0–6 years and 6–25 years, the “permastore”, positions up to 50.50 and 50.50–51.80 [1801].

The memory durations read run from the 20 ms window to 50 years, positions 29.59 to 52.43, a span of 10.90 decades (computed).

What this part of the history shows

Reading. A sense has the form of reading, “a homomorphic image: it keeps the relations and drops the rest”. The smallest difference noticed is a constant fraction of the stimulus [1711], and the decibel scale counts ratios of 10^{12} [1712]. The ear reads 20–20,000 Hz and the eye 380–720 nm, and what lies outside passes unread [1691].

The reading keeps relations at every scale. A hair bundle reads 0.3 nm in an organ 35 mm long, 16.90 positions apart [1690]. One photon changes more than 10^5 molecules [1675], and 339 receptor types spread over 6–20 million neurons, 18,000–59,000 per type [1696][1699].

Opened once, filled many times. Light reception opened once and then filled many forms. The first opsin arose by one duplication in a eumetazoan ancestor [1676]; more than a thousand opsins followed in seven subfamilies [1674]. Eyes arose in at least 40, possibly 65 or more lines, with one Pax6 gene able to start an eye in a fly [1679][547] [1680].

The same holds for smell and the electric sense. Olfactory receptor genes run from fewer than 400 to about 2,000 per mammal, with about 5,000 gains and losses [1695] [1694]. Electroreception has at least 4 origins, and the electric organ arose six times [1437][1709].

The same winding at every depth. The daily clock keeps nearly the same period from a protein loop to a whole body. KaiC cycles in 24 h in a test tube without transcription [1717][1718], single neurons of the suprachiasmatic nucleus keep their own rhythm [1721], and the human pacemaker runs at 24.18 h [1723]. The positions are 43.50 and 43.51.

The brain rhythms show one form across brains of very different size: frequencies vary 30–100 % across mammals while brain size varies hundreds- to thousands-fold [1741]. Spindles keep 12–18 Hz in mammals, and octopus quiet sleep carries events of the same 12–18 Hz [1741][1350]. The centres of the ten classes of cortical rhythm step by a mean factor of 2.73, over positions 27.33–36.51 (computed from [1741]).

The same rule in other surroundings. The rhythm takes the value of its surroundings. The infraslow sleep period follows body temperature with $R^2 = 0.88$, 113.2 s in lizards and 47–51 s in endotherms [1490]. The fly photoreceptor’s information capacity rises with temperature at a Q10 of 6.5 [1687]; habituation in *Mimosa* is stronger in costly surroundings [1778]; birds sleep 7.4 % as much in flight as on land [1767].

Rest and discharge. Sleep has the form of rest and discharge. Cortex in NREM alternates ON periods of 815.5 ms with OFF periods of 85.8 ms [1772], and in slow-wave sleep synchrony reaches 13.0 mm against 3.7 mm awake [1771]. Habituation

follows the same form: the response falls with repetition and returns after rest, in 90 % of *Stentor* cells within 15 min [1775][1776][1782].

The form outlasts its carriers. The senses hold while their cells are replaced: taste cells are renewed in 7–14 days and olfactory neurons in 30 days to 1 year [1698][1701] [1699]. The clock holds its period for life while cortisol is cleared 22 times within one turn [1723][1737]. CA1 spines live 1–2 weeks while potentiation lasts a year [1793] [1790].

Two phases of memory. Memory has an early and a late phase. Early potentiation lasts less than 3 h and needs no new protein, while the late phase needs transcription and translation [1789]; the bee and *Aplysia* separate the two phases the same way [1465][1784]. School Spanish falls for 3–6 years and then holds for up to 30 years in a “permastore” [1801].

19. Many Minds

The nerve cell and the brain arose once in the animal line (chapter 17). Senses, rhythms and memory followed in many bodies (chapter 18). This chapter follows what happened next: complex brains and measured capacities appeared again and again, in lineages that share no complex-brained ancestor.

Seven groups carry such brains: insects, octopuses, teleost fishes, corvid and parrot birds, whales, elephants and primates [1802]. They sit in three great bilaterian lineages: ecdysozoans, lophotrochozoans and vertebrates [1802]. Each group pairs its capacities with its own multimodal brain centre: the mushroom bodies of insects, the vertical lobe of octopuses, the pallium of birds and the cerebral cortex of primates [1802].

The chapter runs from the Cambrian origin of the vertebrates, before 520 Ma, to the dated declarations on animal consciousness of 2012 to 2024. The capacities recorded are counting, self-control, planning, tool making, social learning, play and self-recognition in a mirror. The positions on consciousness are given as positions of the authors who hold them, with their dates.

The primate and human brain follows in chapter 20. Language, song and the record of culture follow in chapter 21.

Cephalopods: the octopus line

A possible earliest cephalopod comes from four specimens of the uppermost Bonavista Formation, Bacon Cove, Newfoundland [1342]. They date to about 522 Ma, at position 67.14, in the upper Terreneuvian [1342]. The title of the study calls the find “potential”; the earlier oldest cephalopod, *Plectronoceras cambria*, is middle to late Cambrian [1342].

The living coleoids, squid, cuttlefish and octopus, were dated with a molecular clock of 180 genes, about 36,000 amino acids and 26 species [1343]. The crown divergence falls in the Silurian–Devonian [1343]. The vampire squid and dumbo octopus lineages date to 242 ± 38 Ma, from 280 to 204 Ma, at positions 66.57 to 66.29 [1343].

Squid and cuttlefish diversified in the Jurassic [1343]. The authors note that the timing coincides with the Mesozoic Marine Revolution [1343]. About 750 cephalopod species live today [1337].

The genome. The genome of *Octopus bimaculoides*, the California two-spot octopus, has a core gene set like that of other invertebrate bilaterians [1368]. Two families “formerly thought” to be vertebrate-specific are expanded: the protocadherins and the C2H2 zinc-finger transcription factors [1368]. The genome also shows extensive RNA editing and hundreds of cephalopod-specific genes [1368].

Coleoid cephalopods carry “tens of thousands of evolutionarily conserved sites” of RNA editing [1369]. The sites are enriched in the nervous system, in molecules for excitability and for the shape of neurons [1369]. The genome flanking these sites is

itself highly conserved [1369].

This has the form of form and carrier (chapter 1). The edited message changes while the stretch of genome that holds it stays fixed.

The developing brain. In *Octopus vulgaris* embryos the neural progenitors lie outside the central brain cords [1803]. They sit near the lateral lips beside the eyes [1803]. New postmitotic neurons migrate from there into the cords over long distances, and the place of origin on the lip sets the lobe supplied [1803].

New neurons come from progenitors, not from the division of differentiated neurons [1803].

The arm. The axial nerve cord of the octopus arm is divided into segments [1355]. In *O. bimaculoides* the number of segments per sucker stays constant along the arm, at about 7.5: 7.64 in arm 1 and 7.88 in arm 2, with two animals per condition [1355]. The squid *Doryteuthis pealeii* has about 4.5 segments per sucker, in three animals [1355].

Each octopus arm also carries four smaller intramuscular nerve cords and “hundreds of chemotactile suckers” [1355]. The oral roots of the cord cover about 65 % of the sucker [1355]. The adults studied were at least 6 months old (position 48.24) and the juveniles 6 weeks (position 46.90) [1355].

The connections. A preprint maps 32 cortical and subcortical regions of the octopus brain, with 249 directed edges between them [1804]. Its abstract gives “more than 350 main neural connections” and its discussion 439 [1804]. The methods report 2,178 literature hits, and the authors call the 249 edges an underestimate [1804].

What the octopus does. Untrained *O. vulgaris* watched demonstrators choose between two objects that differed only in colour [1785]. The watchers then chose the same object, whichever object the demonstrators had taken [1785]. They performed the task “without significant errors and further conditioning for 5 days”, position 44.96 [1785].

Self-control in the cuttlefish. Cuttlefish waited for a preferred food over delays “up to 50-130 s” (positions 36.71 to 37.58) [1805]. Animals that waited longer learned a reversal task better [1805]. The authors give “several seconds” for other species and “up to several minutes” for large-brained vertebrates [1805].

Fishes: pain, tools and the mirror

Vertebrates arose in the Cambrian, before 520 Ma, at position 67.14, in the dating used by Feinberg and Mallatt (2013) [1806]. All living vertebrates carry several levels of maps of the body surface in the brain [1806].

Receptors for harm. Trigeminal receptors in the rainbow trout respond to mechanical pressure, to temperatures “more than 40 degrees C” and to 1 % acetic acid [1807]. Noxious stimulation raised the rate of opercular beating [1807]. It also lengthened the time the fish took to resume feeding “over a prolonged period of time” [1807].

Tool-using brains. At least three different brain organisations support higher-order cognition: in mammals, in birds and in teleost fishes [1808]. The tool-using wrasses

Choerodon anchorago and *Thalassoma hardwicke* have enlarged ventral forebrain and midbrain regions [1808]. The enlargement is built from fibre bundles linking the pallium to the inferior lobe, not from larger cells [1808].

The inferior lobe is a midbrain structure absent in amniotes [1808]. In the fishes the higher capacities run through a part of the brain that birds and mammals do not have.

The study covered 11 species: 3 wrasses, 4 cichlids and 4 outgroup species [1808]:

group	brain mass	total brain cells (not neurons)	[n]
wrasses	34.62–338.8 mg	45.7–185.08 million; one large *C. anchorago* 301.9 million	[1808]
cichlids	42.43–96.94 mg	37.54–61.78 million	[1808]
outgroup species	8.38–354.73 mg	6.66–100.84 million	[1808]

Teleosts hold more brain cells than rodent brains of similar body mass, and fewer than birds and primates [1808].

The mark test. Ten cleaner wrasses, *Labroides dimidiatus*, 51–68 mm long (positions 12.68 to 12.94), were given a mirror of 45 × 30 cm (positions 14.66 and 14.29) [1809]. Seven attacked the mirror at first [1809]. Mouth fighting at the mirror fell to zero by day 7 (position 45.27) [1809].

Atypical behaviour directed at the mirror peaked on days 3–5, at about 36 acts per hour on days 3–4 in seven fish [1809]. It had nearly ended by day 10 (position 45.60) [1809]. Four fish were then marked on the throat [1809].

Three of the four scraped the mark while they could see the mirror [1809]. None scraped in control, sham-mark or no-mirror periods [1809]. The scrapes numbered 37 in total, 15, 16 and 6, with Friedman $\chi^2 = 9.0$, df = 3, P = 0.029 [1809].

After passing the mark test the wrasses stopped attacking still photographs of their own faces [1810]. They kept attacking photographs of unfamiliar fish [1810].

Insects: the smallest brains

The honeybee brain. The honeybee brain holds about 960,000 neurons in a volume of about 1 mm³ [1464, 1811]. A cube of that volume has an edge of 1 mm, at position 9.10. A second source gives “a brain as small as 1 µL containing 950,000 neurons” [1465].

The mushroom bodies are the multimodal centre of the insect brain [1802]. In stage 1 honeybee larvae there are about 40 neuroblasts per brain hemisphere in the protocerebrum, each about 20 µm across, at position 5.54 [1812]. Kenyon cell precursors form clusters of about 20 cells at larval stage 2 [1812].

Bees, wasps and ants. Brain cell numbers were estimated for 32 species of Hymenoptera in seven subfamilies [1813]. The estimates match the whole-brain counts available for two species [1813]. Ants have smaller brains than bees and wasps, by mass and by cell number [1813].

Smaller Hymenoptera have denser brains [1813]. The same holds in most vertebrates,

and not in primates [1813].

The smallest insects. The smallest insects measured are 170 µm long (*Megaphragma caribea*, position 7.49) and 200 µm long (*M. mymaripenne*, position 7.63) [1463]. The central nervous system of *M. mymaripenne* has a volume of 93,600 µm³ in the pupa and 52,200 µm³ in the adult [1463]. As cubes these are 45.4 µm and 37.4 µm on edge, at positions 6.28 and 6.11; the adult volume is 0.56 of the pupal volume (computed: 52,200 / 93,600).

The pupal nervous system holds 7,199–7,593 cells (mean 7,396, two animals) [1463]. The adult holds 339–372 nuclei (mean 361, three animals), of which 179–253 (mean 215) lie in the brain [1463]. The adult carries “about 7000 anucleate cells”: nuclei and cell bodies lyse “in over 95% of the neurons” [1463].

The adult mean of nuclei is 4.9 % of the pupal mean of cells (computed: 361 / 7,396 = 0.049). So 95.1 % of the cells lose their nucleus (computed). The adult lives 5 days at 25 °C and 8.8 days at 15 °C, at positions 44.96 and 45.48 [1463].

Counting. Honeybees “can count up to four objects, when they are encountered sequentially during flight” [1814]. They also count objects they have not seen before [1814]. Individual honeybees trained on “greater than” and “less than”, with one to six elements, placed the empty set at the low end of the number line [1815].

Same and different. Honeybees form concepts of “sameness” and “difference” in delayed matching and non-matching tasks [1816]. They carry the concepts over to new stimuli, also from one sense to another [1816]. The reading keeps the relation and drops the stimulus: the form of reading of chapter 1.

String pulling. Bumblebees, *Bombus terrestris*, were trained step by step to pull a string [1817]. Training took 309 ± 18 min per bee on average, position 42.10, and 23 of 40 bees learned (57.5 %, computed) [1817]. Naïve attempts lasted 5 min (position 38.34) [1817].

condition	solved	[n]
naïve bees from eight colonies, first 5-min attempt	0 of 291	[1817]
second 5-min session	2 of 25, “about 1 %” of the 291 (computed 0.69 %)	[1817]
control bees over 5 days (position 44.96)	0 further solvers among 165	[1817]
observers of a trained demonstrator, first test	15 of 25 (60 %)	[1817]
observers of a “ghost” flower moved by the experimenter	0 of 15	[1817]
colourless flower, at first; after 48 h practice (position 44.13)	2 of 15; 11 of 15	[1817]
coiled string, observers; experienced bees	0 of 27; 3 of 8	[1817]

Three colonies were then seeded with trained bees [1817]. After 150 paired foraging bouts 25 of 47, 17 of 29 and 12 of 28 foragers pulled strings (53 %, 59 % and 43 %, computed) [1817]. Later 34 of 47 and 18 of 28 did so (72 % and 64 %, computed); in

three control colonies 0 of 51, 0 of 58 and 0 of 57 [1817].

The skill passed from forager to forager in the seeded colonies and appeared in none of the controls.

Ball rolling. In a second study 45 tagged bumblebees from one colony rolled balls 910 times, 20 times per bee on average (computed: 910 / 45) [1818]. The experiment ran 3 h a day for 18 days, at positions 41.61 and 46.13 [1818]. Rolls per bee ranged from 1 to 117 over the experiment, up to 44 on one day [1818].

Younger bees, 3–7 days from emergence (positions 44.50 to 45.27), rolled more [1818].

Of three-day-old bees 11 of 13 rolled (85 %, computed), with 11 ± 3.7 actions [1818]. Of bees older than 10 days (position 45.60) 14 of 33 rolled (42 %, computed), with 4 ± 1.4 actions [1818]. The difference gave Wilcoxon Z = 2.30, P = 0.02 [1818].

Forty-two female bees from four colonies, in two groups of 21, preferred the colour of the chamber where they had rolled balls [1818]. The test gave a GLM estimate of 1.696, SE 0.761, Z = 2.228, P = 0.026 [1818]. The authors state five behavioural criteria for play as fulfilled [1818].

Insect societies: one colony, many bodies

Dates. Termites have a crown age of 149 Ma (136–170 Ma), at position 66.00 (65.92 to 66.12) [941]. The oldest termite fossils are 135 Ma old (position 65.91), and the Termitidae date to 54 Ma (46–66 Ma), position 65.08 [941]. Crown bees date to 123 Ma (113–132 Ma), position 65.83, and the oldest bee fossil to about 100 Ma, position 65.64 [1257].

A molecular tree of the ants used 4.5 kb of six gene regions, 139 of 288 living genera and 19 of 20 subfamilies, calibrated with 43 fossils [1819]. Most subfamilies arose earlier than proposed before [1819]. Ant diversification took off in the Late Cretaceous to Early Eocene, with the rise of the flowering plants [1819].

In the Hymenoptera the elaboration of the mushroom bodies “preceded the evolution of eusociality” [1820].

Single mating at the start. A comparison of 267 species of eusocial bees, wasps and ants found single mating ancestral in all eight independent lineages of eusociality examined [1821]. Multiple mating is always derived [1821]. High polyandry, more than two effective mates, occurs only where workers had lost the ability to reproduce [1821].

Single mating means that the workers of each first colony shared one mother and one father. Community here has the form of shared prefix (chapter 1): it is given by common descent, not chosen. The first of these origins opened the colony as a union; the later origins filled that opened depth, each among bodies of one shared descent.

The colony outlives its members. Across 87 solitary insect species in eight orders and 61 eusocial species, eusociality goes with a “100-fold increase in insect lifespan” [1469]. Ant lifespans are associated with extrinsic mortality [1469]. The lifespans read are these:

what	duration	position	[n]

termite new workers after swarming	1.5–3 months	46.98–47.61	[940]
honeybee workers prevented from foraging	0.2–0.4 y	47.41–48.04	[1822]
honeybee winter workers, up to	0.9 y	48.77	[1822]
Lasius niger workers, typically	1–2 y	48.87–49.50	[1823]
honeybee queen, maximum	8 y	50.76	[1822]
termite primary reproductives, at most	about 20 y	51.60	[940]
Lasius niger queen, maximum	28 y	51.90	[1823]
Macrotermes mound	about 700 y	54.83	[940]
Macrotermes mound	at least 2,200 y	55.88	[940]

Fungus-growing termite colonies last up to several decades [940]. The *Lasius* queen lives 14 to 28 times as long as her workers (computed: 28 / 2; 28 / 1). The oldest mound is 110 times the longest termite reproductive life (computed: 2,200 / 20).

This is form and carrier: the closed form persists while its carriers are replaced. The workers are replaced many times over while the colony, and then the mound, persists.

The largest unit. In southern Europe the Argentine ant, *Linepithema humile*, forms two supercolonies [1824]. The main one extends over 6,000 km, at position 29.59, from Italy to the Spanish Atlantic coast [1824]. Within a supercolony there is no aggression across large distances; between the two there is consistent aggression [1824].

The authors describe the main supercolony as the largest cooperative unit ever recorded [1824]. Here the shared prefix runs over 6,000 km. Ants of one prefix treat each other as one; the boundary between the two prefixes holds.

Ants on Earth. Almost 20×10^{15} ants live on Earth, $19.8 \pm 5 \times 10^{15}$, with over 3×10^{15} dwelling on the ground [1825]. Their dry biomass is about 12 Mt of carbon, 12.3 ± 3.1 Mt C, more than wild birds and mammals combined and about 20 % of human dry biomass [1825]. The estimate rests on 489 studies in the abstract and 465 studies at 1,306 sampling locations in the results [1825].

Named ant species and subspecies number “more than 15,700” [1825]. Known ant species rose from “roughly 5,000–6,000 circa 1,940” to more than 14,000 today, and subfamilies from 6 to about 20 [1820].

Colony size and brain size. Workers of species with larger colonies have larger brains [1820]. In monomorphic fungus-growing ants, larger colonies go with smaller brains [1820].

Amniotes and birds: dense forebrains

Three hundred million years of scaling. Neuron numbers were compared across reptiles, birds and mammals [1498]. The high counts of warm-blooded land vertebrates

are reached through “as few as four major changes in neuron-brain scaling over 300 million years”, a span at position 66.64 [1498]. Mammals and birds have “dramatically increased neuron numbers in the telencephalon and cerebellum” compared with reptiles [1498].

Reptile neuron numbers average “over 20 times lower” than those of birds and mammals of similar body size [1498]. A preprint dataset of amniotes runs from the Algerian sand gecko, with just under 2 million neurons, to the African elephant, with 257 billion [1499]. The range is $257 \times 10^9 / 2 \times 10^6 = 1.3 \times 10^5$-fold (computed); the Sumatran flying dragon has barely more than 5 million neurons [1499].

The same preprint gives signature proportions between brain parts [1499]:

group	neurons in one part per neuron in another	[n]
mammals	about 4 cerebellar per cortical	[1499]
birds	4.5 cerebellar per hindbrain	[1499]
reptiles	1.4 ± 0.6 telencephalic per rest of brain	[1499]
most bird clades	about 3 pallial per rest of brain	[1499]
owls	12 pallial per rest of brain	[1499]
primates	can exceed 20	[1499]

The preprint covers 107 or 108 reptile species, 68 to 75 mammal species and 65 bird species [1499].

The bird line. *Asteriornis maastrichtensis*, from the Maastrichtian of Belgium, is 66.8–66.7 Ma old, position 65.27 [1526]. It is one of the few well-supported crown birds of the Mesozoic [1526]. A genome study of 363 species in 218 families dates the passerine crown to 50.7 Ma (48.3–53.0 Ma) and the Corvides, the crow line, to 25.7 Ma (23.8–27.7 Ma) [1527].

These sit at positions 65.02 (64.98 to 65.06) and 64.40 (64.33 to 64.47). From the passerine crown to the Corvides is $50.7 - 25.7 = 25.0$ Myr (computed) [1527].

Primate numbers in bird brains. Parrots and songbirds hold on average twice as many neurons as primate brains of the same mass [1537]. Corvids and parrots hold much higher proportions of their neurons in the pallium [1537]. Large-brained parrots and corvids reach forebrain counts equal to or greater than those of primates with much larger brains [1537].

In 111 bird species the number of pallial neurons goes with the propensity to innovate [1638]. Pallial counts are higher in brains large in absolute and in relative terms, and with longer development after hatching [1638].

Corvid counts. Four brains of each of three corvid species were counted per hemisphere and set beside the ostrich [1826]:

species	telencephalon mass	telencephalic neurons	pallial neurons	mesopallium	nidopallium	[n]
hooded crow	2,666 mg	352.7 million	301.8 million	81.1 million	156.9 million	[1826]
carrion crow	2,512 mg	409.9 million	336.1 million	89.4 million	182.7 million	[1826]

rook	2,401 mg	483.0 million	408.7 million	116.0 million	214.2 million	[1826]
ostrich	8,168 mg	228.3 million	208.1 million	41 million	—	[1826]

The text of the same paper gives 282 million telencephalic neurons for the ostrich [1826]. Rooks hold 1.37 times the telencephalic neurons of hooded crows (computed: 483.0 / 352.7). The rook brain is the lightest of the three and holds the most.

Telencephalic neurons per milligram are 132,000 in the hooded crow, 163,000 in the carrion crow, 201,000 in the rook and 28,000 in the ostrich (computed from the table). The pallium holds 86 %, 82 % and 85 % of the telencephalic neurons in the three corvids, and 91 % in the ostrich (computed). With the text figure of 282 million the ostrich share is 74 % (computed).

The paper names primate comparators: 68 million neurons in one hemisphere of rhesus prefrontal cortex and 115 million in one hemisphere of baboon prefrontal cortex [1826]. A corvid pallium of one hemisphere holds 2.6 to 6.0 times these counts (computed: 301.8 / 115 = 2.6; 408.7 / 68 = 6.0).

Planning. Ravens tolerated delays “up to 17 hours” in planning for tool use and for bartering, at position 43.19 [1827]. The authors report that this matches the great apes [1827]. The raven delay is 471 times the upper cuttlefish delay (computed: 61,200 s / 130 s).

Compound tools. Four of 8 naïve New Caledonian crows combined separate elements into working compound tools [1828]. They built their first compound tools “within only 4-6 min of engaging with the tool elements”, at positions 38.14 to 38.51 [1828]. One bird built tools of 3 and of 4 pieces [1828].

Zero in the crow. Two male carrion crows, *Corvus corone corone*, aged 6 and 5 years (positions 50.50 and 50.34), judged numerosities 0 to 4 [1829]. A 500 ms sample followed a 500 ms baseline, and a 1,000 ms delay followed the sample, at positions 32.52 and 33.15 [1829]. Neurons of the nidopallium caudolaterale (NCL) answered with an average visual latency of 144 ms, position 31.39 [1829].

Of 501 NCL neurons recorded (233 and 268), 27 % (134 of 501) were selective for numerosity in the sample period and 31 % (153 of 501) in the delay [1829]. Of the selective neurons, 35.8 % (n = 34) preferred zero in the sample period and 41.8 % (n = 38) in the delay [1829].

Report in the crow. Single pallial neurons in crows tracked reported perception in a visual detection task [1830]. The response came in two stages: the first followed mainly the strength of the stimulus, the later one the crow’s report [1830]. The pallium of birds has no layered cortex [1830].

Elephants and whales: the largest counts

The elephant. The brain of the African elephant weighs 4,618.6 g without the olfactory bulb, about three times the human brain [1516]. It holds 257 billion neurons [1516]. Of these, 251 billion (97.5 %) lie in the cerebellum and 5.6 billion in the cerebral cortex [1516].

There are 44.8 cerebellar neurons per cortical neuron (computed: 250.7 / 5.6) [1516]. The elephant cortex holds about one third of the human cortex figure of 16.3 billion cited in the same paper (computed: 5.6 / 16.3 = 0.34) [1516]. The elephant brain as a whole holds 3.0 times the 86 billion neurons of the human brain (computed: 257 / 86).

The packing differs as much as the totals. Human cortical grey matter holds 21,450 neurons per mg, elephant cortical grey matter 3,661 per mg, a ratio of 5.9 (computed) [1516].

Per mm^2 of cortex the human value is 80,064 neurons and the elephant value 10,752, a ratio of 7.4 (computed) [1516]. Human hippocampus and amygdala together hold about 250 million neurons [1516].

The pilot whale. Ten long-finned pilot whales from the Faroe Islands had total brain weights of 3,062–4,618 g [1831]. The neocortex held about 37.2×10^9 neurons, range $29.1–46.3 \times 10^9$, “almost twice as many as humans” [1831]. It held 127×10^9 glial cells, range $99.9–183 \times 10^9$, or 3.4 glial cells per neuron (computed: 127 / 37.2) [1831].

The pilot whale neocortex holds 2.3 times the human cortical count of 16.3 billion (computed: 37.2 / 16.3). The neocortical counts run 5.6 billion (elephant), 16.3 billion (human) and 37.2 billion (pilot whale).

The largest whole brain and the largest cortex in this record belong to two different animals, and neither is human. Each lineage fills its brain in its own proportions: the elephant in the cerebellum, the whale in the neocortex.

Positions on consciousness, 2012–2024

Beside the measured cases stand dated statements on which animals are conscious. Each statement is the position of the authors named, at its date. In order of date they widen step by step.

7 July 2012: the Cambridge Declaration. The declaration was proclaimed at the Francis Crick Memorial Conference on Consciousness in Human and non-Human Animals, Churchill College, University of Cambridge [1832]. It was written by Philip Low and signed by participants that evening “in the presence of Stephen Hawking” [1832]. Its position: “all mammals and birds, and many other creatures, including octopuses” possess the neurological substrates of consciousness [1832].

2013: Feinberg and Mallatt. Feinberg and Mallatt propose several levels of isomorphic maps of the body surface as a marker of sensory consciousness [1806]. All living vertebrates have such maps, so they date sensory consciousness to the origin of the vertebrates in the Cambrian, before 520 Ma (position 67.14) [1806]. They propose that the lamprey has the basic requirements for the simplest qualia [1806].

Their minimal brain for qualia has forebrain, midbrain and hindbrain, with widespread activity of the reticular formation [1806]. They propose two steps: the optic tectum as the first centre of multisensory perception, in fish and amphibians, then the dorsal pallium, in mammals, reptiles and birds [1806]. They propose vision as the first conscious sense [1806].

2016: Barron and Klein. Barron and Klein propose that “at least one invertebrate

clade", the insects, has the capacity for subjective experience [1833]. They base this on insect brain structures that perform functions like those of integrated vertebrate midbrain structures [1833]. They state that the origins of consciousness "can be traced to the Cambrian" [1833].

2020: Birch, Schnell and Clayton. Birch, Schnell and Clayton propose five dimensions of animal consciousness [1834]. These are perceptual richness, evaluative richness, integration at a time, integration across time, and self-consciousness [1834]. On their position each species has its own "consciousness profile", and "no single scale" ranks species [1834].

2020: Nieder, Wagener and Rinnert. The authors read the two-stage response of crow pallial neurons as a correlate of sensory consciousness [1830]. They conclude that its neural basis may have arisen before birds and mammals diverged, or independently in birds [1830]. In both readings it arose without a layered cortex [1830].

November 2021: the LSE review. Birch, Burn, Schnell, Browning and Crump reviewed the evidence for sentience in cephalopods and decapod crustaceans for the UK government department DEFRA [1337]. They drew on "over 300 scientific studies" and used eight criteria [1337].

As summarised from the report, the criteria are nociceptors, integrative brain regions, and connections between the two [1337]. The others are responses altered by anaesthetics or analgesics, motivational trade-offs, flexible self-protection, associative learning, and valuing analgesics when injured [1337].

The review states for each group how many criteria are met with high or very high confidence [1337]:

group	criteria met with high or very high confidence (of 8)	[n]
octopods	7 (medium for the 8th)	[1337]
true crabs	5	[1337]
squid and cuttlefish	4	[1337]
anomuran crabs	3	[1337]
astacid lobsters and crayfish	3	[1337]
spiny lobsters	2	[1337]
caridean shrimps	2	[1337]
penaeid shrimps	1	[1337]

The review recommends that all cephalopods and all decapods be regarded as sentient for UK animal welfare law [1337]. It counts about 750 living cephalopod species and about 15,000 decapod species [1337].

28 April 2022: the UK Act. Section 5(1) of the Animal Welfare (Sentience) Act 2022 defines "animal" as any vertebrate other than *Homo sapiens*, any cephalopod mollusc and any decapod crustacean [1835]. With the species counts of the review, the Act covers all non-human vertebrates, about 750 cephalopod species and about 15,000 decapod species [1337, 1835].

19 April 2024: the New York Declaration. The New York Declaration on Animal Consciousness makes three statements [1836]. There is "strong scientific support" for

conscious experience in other mammals and in birds [1836]. There is “at least a realistic possibility” of conscious experience in all vertebrates, reptiles, amphibians and fishes, and in many invertebrates, “at minimum, cephalopod mollusks, decapod crustaceans, and insects” [1836].

The third statement holds that ignoring a realistic possibility in decisions that affect an animal is “irresponsible” [1836]. The declaration page showed 611 signatures on 14 October 2026 [1836].

The widening. In 2012 the named groups are mammals, birds and octopuses. In 2016 insects are added; in 2021 and 2022 all cephalopods and decapods; in 2024 all vertebrates and, at minimum, cephalopods, decapods and insects as a realistic possibility. Two proposed origins, for vertebrates and for insects, both lie in the Cambrian.

What this part of the history shows

Many origins, many centres. Complex brains appear in seven groups across three bilaterian lineages [1802]. Each pairs its capacities with its own centre: mushroom body, vertical lobe, pallium, cortex, and in the tool-using wrasses a pallium joined to an inferior lobe that amniotes lack [1802, 1808]. Mammals, birds and teleost fishes reach higher cognition with three different brain organisations [1808].

Reading. Honeybees carry “same” and “different” from one sense to another, and place the empty set below one [1815, 1816]. In the crow, 27–31 % of 501 NCL neurons are tuned to number, and 35.8–41.8 % of those prefer zero [1829]. Each case keeps a relation and drops the stimulus, which is the form of reading.

Reading that counts itself. Three of four marked cleaner wrasses scraped the mark only with the mirror in view, and the fish then left their own photographs alone [1809, 1810]. In crows a later stage of the neuronal response follows the report, not the stimulus [1830]. These cases have the form that chapter 1 names consciousness: representation that counts itself.

Form and carrier. Coleoids edit tens of thousands of RNA sites while the genome around them stays conserved [1369]. A *Lasius* queen of 28 years outlives workers of 1–2 years, and a *Macrotermes* mound lasts at least 2,200 years [940, 1823].

Shared prefix. Eusociality began from single mating in all eight lineages examined, so each first colony was one line of descent [1821]. The Argentine ant supercolony holds one prefix over 6,000 km, with aggression only at the border with the second [1824].

Learning from others. Spontaneous string pulling was solved by 2 of 291 bumblebees; 15 of 25 solved it after watching one demonstrator [1817]. In seeded colonies the skill reached 34 of 47 foragers, and none in 166 control foragers (computed: 51 + 58 + 57) [1817]. Octopuses copied a demonstrator’s choice and held it for 5 days [1785].

Holding before discharge. Cuttlefish hold back for 50–130 s, ravens plan across 17 h, large-brained vertebrates “up to several minutes” [1805, 1827]. Each is a loading held before its release: the form of rest and discharge, here at positions 36.71 to 43.19.

The widening. The positions on consciousness widen by date from mammals, birds and

octopuses (2012) to all vertebrates and, at minimum, cephalopods, decapods and insects (2024) [1832, 1836]. Two proposed origins of consciousness, for vertebrates and for insects, both lie in the Cambrian [1806, 1833].

On the ladder. The minds of this chapter run from a nervous system 37.4 µm on edge (position 6.11) to a cooperative unit of 6,000 km (position 29.59). Their measured times run from a neuronal latency of 144 ms (position 31.39) to a plan held 17 h (43.19) and a mound of 2,200 years (55.88).

20. The Human

The many minds of chapter 19 arose in seven groups. One of them, the primates, carries the line that ends in the human. This chapter follows that line from the split with the chimpanzee to the first farmers.

The history is told in fossils, stone, fire and genomes. Brain volume rises from about 450 cc to about 1,300–1,460 cc. The body changes on its own schedule, and the population passes through a narrow neck before it spreads over every continent.

The chapter closes with the human brain and the human life in numbers, and with the census from 10,000 BCE. Language, art and writing follow in chapter 21; the networks of the farming world follow in chapter 22.

The split from the chimpanzee

Three clock values are given for the split of the human and chimpanzee lines. Molecular studies cited in 2001 placed it about 6.5–5.5 Ma, in the Late Miocene, at positions 63.15 to 63.00 [1837]. Generation times measured in wild chimpanzees and mountain gorillas, with a per-generation mutation rate, give at least 7–8 Ma, positions 63.22 to 63.34 [1838].

Transitions at CpG sites “behaved like a clock” in 10 primate genomes [1839]. They give 12.1 Ma for the human–chimpanzee split and 15.1 Ma for the human–gorilla split, at positions 63.72 and 63.92 [1839]. The spread of the three values runs from 5.5 to 12.1 Ma, a factor of 2.2 (computed).

The clock itself runs at different speeds in different branches [1839]. Substitution rates are up to 64 % higher on the branch to the common ancestor of hominoids and New World monkeys than in apes [1839]. Within the apes they are about 2 % higher in chimpanzees and about 7 % higher in gorillas than in humans [1839].

Fossils of 6–7 Ma are attributed to the human line [1838]. The generation-time study places the population split of Neanderthals and modern humans at about 400,000–800,000 years ago [1838].

The two genomes. The chimpanzee and human genomes differ by about 35 million single-nucleotide changes and 5 million insertion or deletion events [1840]. The genome-wide nucleotide divergence is 1.23 % over about 2.4 Gb of aligned high-quality sequence [1840]. That gives $0.0123 \times 2.4 \times 10^9 = 2.95 \times 10^7$ differences in the aligned part, against 3.5×10^7 single-nucleotide changes counted over the whole (computed).

Partners that split with the host. Several dominant gut bacterial lines cospeciated with the hominids over the past 15 Myr, position 63.91 [1131]. The hosts are humans, chimpanzees, bonobos and gorillas [1131]. The divergence times of the bacteria match those of their hosts [1131].

Partners nest inside partners as addresses inside longer addresses: community as shared prefix (chapter 1). Each split of the host line is carried into its gut partners at

the same date.

The first hominins, 7.2–4.4 Ma

Toumaï, *Sahelanthropus*. Six hominid specimens of *Sahelanthropus tchadensis*, Toumaï, come from the Djurab Desert of Chad [1841]. The associated fauna “suggest the fossils are between 6 and 7 million years old” [1841]. The site lies 2,500 km from the East African Rift Valley, position 28.80 [1841].

Authigenic $^{10}Be/^{9}Be$ dating of the fossil-bearing unit at locality TM 266 brackets the Toumaï level between 6.8 and 7.2 Ma, positions 63.19 to 63.24 [1842]. Biochronology gives about 7 Ma [1842].

The genera *Orrorin* and *Ardipithecus*. *Orrorin tugenensis*, from Kenya, is dated to about 6 Myr, position 63.08 [1837]. *Ardipithecus* specimens from the Middle Awash, Ethiopia, later named *Ar. kadabba*, date to 5.2–5.8 Myr, positions 62.95 to 63.05 [1837]. They lived in a wooded setting [1837].

They share derived dental characters only with younger hominids, and keep primitive dental and postcranial characters [1837]. The author calls them “the earliest definitive evidence of the hominid clade” [1837].

The species *Ardipithecus ramidus*. More than 110 specimens come from 4.4-million-year-old sediments in the Afar Rift, Ethiopia, position 62.79 [1843]. They include a partial skeleton and much of the skull, hands, feet, limbs and pelvis [1843]. The animal combined tree climbing with a bipedal walk more primitive than that of *Australopithecus* [1843].

Its canine–premolar complex is reduced, its diet was mainly C3 plants, and its habitat was woodland [1843]. *Sahelanthropus*, *Ardipithecus* and chimpanzees have brains about 20 % smaller than *Australopithecus* [1820]. With *Australopithecus* at about 450 cc, that gives $450 \times 0.8 = 360$ cc (computed).

Upright walking: *Australopithecus* and the footprints

The species *A. anamensis*. Twenty-one specimens, nine of them from Kanapoi, come from Kanapoi and Allia Bay, Kenya [1844]. They date “between about 3.9 million and 4.2 million years ago”, positions 62.68 to 62.75 [1844]. A tibia “establishes that hominids were bipedal at least half a million years” before the earlier evidence [1844].

The Laetoli footprints. Excavation of the tuffs of the Laetolil Beds, northern Tanzania, revealed “a large variety of footprints” [1845]. Many correlate with Pliocene animals found as fossils in the same area [1845]. The hominin prints, found in 1978, date to 3.66 Ma (position 62.63) and are attributed to *A. afarensis* [1846].

New tracks at Site S were left by two bipedal individuals walking in the same direction as the three hominins of Site G [1846]. Five individuals thus stand on one time level (computed: 2 + 3). The stature of S1 exceeds earlier reconstructions of *A. afarensis* from skeletons and prints, and body size varied widely within one species [1846].

Chad, and the flat brain. *Australopithecus bahrelghazali*, Abel, from locality KT 12 in

Chad, is dated to 3.58 ± 0.27 Ma (position 62.61), contemporary with *A. afarensis* [1842]. The *Australopithecus* brain was "~450 cc", roughly unchanged from 3.5 to 2.0 Ma, positions 62.59 to 62.08 [1820].

The flat stretch lasts 1.5 Myr (computed: 3.5 − 2.0). Upright walking is recorded in bone at 4.4 and 4.2–3.9 Ma, before the footprints at 3.66 Ma.

Stone tools before *Homo*

Lomekwi. Stone tools at Lomekwi 3, West Turkana, Kenya, are 3.3 million years old, position 62.53 [1847]. They predate the Oldowan by 700,000 years, a span at position 61.12 [1847]. Before them the earliest sharp-edged tools were about 2.6 million years old, in Ethiopia [1847].

The Oldowan. Oldowan tools at Bokol Dora 1, Ledi-Geraru, Ethiopia, are "bracketed between 2.61 and 2.58 Ma", positions 62.32 to 62.31 [1848]. The authors place them about 250,000 years before the Oldowan at Gona [1848]. Gona itself is "securely dated between 2.6–2.5 Myr" by radio-isotopic ages and magnetic polarity stratigraphy, positions 62.32 to 62.28 [1849].

From the two age brackets the gap between Bokol Dora and Gona is 0–0.11 Myr (computed), against the 250,000 years stated by Braun and co-authors [1848, 1849].

The Acheulean. The Acheulean first appears at Kokiselei 4, Nachukui Formation, West Turkana, 1.76 Myr ago, position 61.96 [1850]. This is "350,000 years older" than the previous earliest record, which was therefore about 1.41 Myr (computed: 1.76 − 0.35), position 61.76 [1850].

Each first date was pushed back by a later find: by 700,000, about 250,000 and 350,000 years. The tool record begins 0.5 Myr before the first *Homo* jaw (computed: 3.3 − 2.8).

Early *Homo* and the first leaving of Africa

The first jaw. The partial mandible LD 350-1, from Ledi-Geraru in the Afar, dates to 2.80–2.75 Ma, positions 62.38 to 62.37 [1851]. It combines primitive traits of early *Australopithecus* with derived traits of later *Homo* [1851]. The record of eastern Africa between 3.0 and 2.0 Ma is sparse [1851].

The species *Homo habilis*. The type specimen OH 7, from Olduvai Gorge, Tanzania, is 1.8 million years old, position 61.98 [1852]. Its reconstructed endocranial volume of 729–824 ml is "larger than any previously published value" [1852]. The *H. habilis* lineage "originated before 2.3 million years ago" (position 62.20), and the A.L. 666-1 maxilla is 500,000 years older than OH 7 [1852].

Three genera side by side. At Drimolen, South Africa, *H. erectus* (DNH 134) and *Paranthropus robustus* date to 2.04–1.95 Ma, positions 62.09 to 62.05 [1853]. These are the oldest definitive specimens of both species [1853]. *Australopithecus*, *Paranthropus* and early *H. erectus* overlapped in the South African karst about 2 million years ago [1853].

China. At Shangchen, on the Chinese Loess Plateau, 17 artefact layers run from

palaeosol S15, about 1.26 Ma, to loess L28, “about 2.12 Ma” [1854]. These sit at positions 61.66 and 62.13. Hominins “had left Africa by at least 2.1 million years ago” [1854].

Dmanisi. In the Georgian Caucasus the first occupations at Dmanisi came shortly after 1.85 Ma [1855]. The site was used again and again across most of the Olduvai subchron, 1.85–1.78 Ma, positions 62.01 to 61.97 [1855]. Its fossils, dated before to about 1.77 Ma, belong to a small-brained population with primitive and derived traits [1855].

The authors infer that *H. erectus* probably reached Eurasia before it appears in the East African fossil record [1855]. Within 700,000 years of the first *Homo* jaw, hominins and their tools stand in China (computed: 2.80 − 2.12 = 0.68 Myr).

A new kind of body opened once and then filled many places: the form of opened once, filled many times (chapter 1). Its first known places lie 2.80 Ma in the Afar and 2.12 Ma on the Loess Plateau.

The brain grows

Change points. A change-point analysis used 981 cranial capacity estimates from the last 10 Myr, without the small-brained Pleistocene *Homo* [1820]. Before the first change point the rate of increase was 0.03 ± 0.01 $\log_{10}$ cc per Myr [1820]. The change points are these [1820]:

change point	date	position	rate after ($\log_{10}$ cc per Myr)	[n]
first	2.10 ± 0.07 Ma	62.12	0.35 ± 0.05	[1820]
second	1.49 ± 0.14 Ma	61.81	0.19 ± 0.01	[1820]
third	0.003 ± 0.001 Ma	56.16	−17.16 ± 6.69	[1820]
first, small-brained *Homo* included (985 estimates)	2.10 ± 0.05 Ma	62.12	0.72 ± 0.51	[1820]
second, small-brained *Homo* included	1.97 ± 0.12 Ma	62.06	0.20 ± 0.01	[1820]
third, small-brained *Homo* included	0.003 ± 0.001 Ma	56.16	−16.74 ± 7.55	[1820]

The rate after the first change point is 11.7 times the rate before it (computed: 0.35 / 0.03). The third change point is taken up with the Holocene below.

Within the lineages. Across the hominin clade endocranial volume rose gradually [1856]. Change within lineages accounts for 64 % of the rise with a finer taxonomy, or 88 % with a less speciose one [1856]. The rest comes from the appearance of larger-brained *Homo* and the loss of smaller-brained *Australopithecus* and *Paranthropus* [1856].

The change within lineages fits episodes of directional selection with stasis and/or drift [1856]. A long hold, then a step: the form of rest and discharge (chapter 1). The *Australopithecus* brain holds at about 450 cc for 1.5 Myr, and the rate steps up 11.7-fold

at 2.10 Ma.

Volumes. The endocranial volumes are these, with each volume placed as the edge of a cube of equal volume:

taxon	volume	cube edge	position	[n]
Sahelanthropus, *Ardipithecus*, chimpanzee	about 360 cc (computed)	7.11 cm	12.98	[1820]
H. floresiensis LB1, micro-CT	426 cc	7.52 cm	13.03	[1857]
Australopithecus, 3.5–2.0 Ma	about 450 cc	7.66 cm	13.05	[1820]
H. naledi DH3	460 mL	7.72 cm	13.05	[1858]
H. habilis, lower	500 mL	7.94 cm	13.08	[1858]
H. erectus, lower	550 mL	8.19 cm	13.11	[1858]
H. naledi DH1	555 mL	8.22 cm	13.11	[1858]
H. habilis, upper	more than 700 mL	8.88 cm	13.18	[1858]
OH 7, *H. habilis* type	729–824 ml	9.00–9.38 cm	13.19–13.23	[1852]
H. erectus, upper	more than 1,200 mL	10.63 cm	13.35	[1858]
modern mean, DeSilva dataset	1,297 cc	10.91 cm	13.37	[1859]
modern, other estimates	1,340–1,460 cc	11.02–11.34 cm	13.38–13.41	[1859]

The *H. erectus* range includes Dmanisi and Ngandong [1858]. Earlier virtual composites of *H. naledi* gave 560 mL (DH1/DH2) and 465 mL (DH3/DH4) [1858]. For LB1 published estimates run 380–430 cc, with 400 cc the value commonly cited before; the study took human brain–body scaling from 20 modern populations [1857].

H. naledi and *H. floresiensis* fall “within or just above the range of *Australopithecus*” [1858]. The Dinaledi fossils of *H. naledi* date “between 236,000 and 335,000 y ago”, positions 60.13 to 60.45; the significance statement of the same paper gives 226,000 [1858]. Small-brained *Homo* thus lived beside large-brained *Homo* late in the history.

The modern mean in the DeSilva dataset is 2.9 times the *Australopithecus* value (computed: 1,297 / 450). With the other estimates the factor is 3.0–3.2 (computed: 1,340 / 450; 1,460 / 450).

Genes copied on the human line. SRGAP2 was duplicated three times only in humans [1860]. The promoter and first nine exons of SRGAP2A, at 1q32.1, were copied to 1q21.1 as SRGAP2B about 3.4 million years ago, position 62.56 [1860]. Larger copies of SRGAP2B went to 1p12 as SRGAP2C about 2.4 mya (position 62.24), and to proximal 1q21.1 as SRGAP2D about 1 mya (position 61.45) [1860].

The authors propose that the new function arose “at birth” 2–3 mya, at the transition from *Australopithecus* to *Homo* and the start of neocortex expansion [1860]. That window contains the first change point in brain size at 2.10 Ma (computed comparison of [1860] and [1820]).

ARHGAP11B arose by partial duplication of *ARHGAP11A*, a Rho GTPase-activating protein gene, “on the human lineage after separation from the chimpanzee lineage” [1861]. A screen found 56 genes preferentially expressed in human apical radial glia that lack mouse orthologs, and *ARHGAP11B* showed the highest radial-glia specificity [1861]. Expressed in embryonic mouse neocortex, it increased basal progenitors and their self-renewal, enlarged the cortical plate and induced folding [1861].

A later study states that “a single nucleotide substitution” underlies its properties [1862]. A second screen found 35 hominid-specific duplicated genes with dynamic expression during human cortical neurogenesis [1863]. NOTCH2NL promotes the maintenance and clonal expansion of progenitors by inhibiting cis Delta/Notch interactions [1863].

Three NOTCH2NL paralogs are highly expressed in radial glia [1864]. The NOTCH2NL genes form the breakpoints of the 1q21.1 distal deletion and duplication syndrome [1864]. Duplications go with macrocephaly and autism; deletions go with microcephaly and schizophrenia [1864].

Fire

Wonderwerk. In Wonderwerk Cave, Northern Cape, South Africa, burned bone, ashed plant remains and burning inside the cave come from an early Acheulean occupation of about 1.0 Ma, position 61.45 [1865]. The evidence comes from micromorphology and FTIR microspectroscopy [1865]. The authors call it “the earliest secure evidence” of fire in an archaeological context [1865].

Gesher Benot Ya’aqov. At this Acheulian site in Israel, burned seeds, wood and flint are “suggestive of control of fire by humans nearly 790,000 years ago”, position 61.23 [1866]. Small burned flint fragments are concentrated in spots, possibly hearths [1866]. Burned wood comes from six taxa, at least three of them edible, including wild barley and grape [1866].

Fire inside a living site thus stands at about 1.0 Ma in South Africa and at 790 ka in the Levant, both with Acheulean tools.

Body and brain on different schedules

Body size. One study gathered 254 body-mass and 204 stature estimates from 311 hominin specimens, from 4.4 Ma to the Holocene [1867]. It found long phases of relative stasis interrupted by rapid increases [1867]. Early *Homo* was on average significantly heavier than the australopithecines but still diverse, including small sizes [1867].

Modern human stature is maintained from about 1.6 Ma, position 61.87 [1867]. Consistently higher body masses come only from the Middle Pleistocene, about 0.5–0.4 Ma, positions 60.81 to 60.61 [1867]. After 1.4 Ma (position 61.75) individuals under 40 kg and under 140 cm are selected against [1867].

H. naledi, at about 0.3 Ma, and *H. floresiensis*, at about 100–60 ka (positions 59.35 to 58.88), are small-bodied exceptions [1867]. Late Holocene *H. sapiens* declines in body size on average [1867].

What tracks what. Over the last one million years temperature is the main predictor of body size within *Homo* [1868]. Net primary productivity and long-term variability of rainfall correlate with brain size but explain little of its variation [1868]. Most predictors of body size do not predict brain size [1868].

Stature becomes modern at about 1.6 Ma and body mass at 0.5–0.4 Ma. The brain steps up at 2.10 and 1.49 Ma, on dates of its own. Long stasis broken by rapid increase is the form of rest and discharge, here in body and brain at different dates.

The narrow neck

Effective size. Genetic variation at most loci gives an effective population size of about 10^4 over the past 1 Myr [1869]. The population probably never shrank to a few individuals, even for one generation, and models with few founders through the late Pleistocene are rejected [1869]. Polymorphism at the Mhc, traced over a lineage history of 35 Myr, gives an effective size of about 10^5 for the line leading to humans [1869].

The bottleneck. The FitCoal method, applied to 3,154 present-day human genomes, finds a severe bottleneck of "about 1,280 breeding individuals" [1870]. It lasted from about 930,000 to 813,000 years ago, positions 61.38 to 61.26, about 117,000 years (position 59.49) [1870]. It brought human ancestors close to extinction and coincides with a gap in the African and Eurasian fossil record [1870].

The long-term effective size of 10^4 is 7.8 times the 1,280 breeders of the bottleneck (computed: 10,000 / 1,280) [1869, 1870]. All genomes, modern and archaic, also show a reduction in population size before 1.0 Ma [1871].

All living humans descend through this neck. On the net the whole later population is one long address with one short prefix; the form is shared prefix.

Three lineages that met again

The splits. The modern line split from the line of Neanderthals and Denisovans 553,000–589,000 years ago by one method (PSMC) and 550,000–765,000 years ago by allele sharing [1871]. Neanderthals and Denisovans split 381,000 years ago (PSMC) or 445,000–473,000 years ago (allele sharing) [1871]. These spans sit at positions 60.90 to 61.20 and 60.57 to 60.76.

The genomes. A draft Neanderthal genome from three individuals, more than 4 billion nucleotides, was compared with five present-day humans [1872]. Neanderthals share more variants with present-day Eurasians than with sub-Saharan Africans, and gene flow came before the Eurasian groups diverged [1872]. Neanderthals lived across much of Europe and western Asia until about 30,000 years ago, as stated in 2010 [1872].

A Denisovan genome was sequenced from a finger bone to about 1.9-fold coverage [1873]. The Denisovans "contributed 4–6% of its genetic material to the genomes of present-day Melanesians" [1873].

The Altai Neanderthal genome reached 52-fold coverage, from a layer at least 50,000 years old (position 58.72) [1871]. It holds 1.7–1.8 heterozygous sites per 10,000 bp, or

2.1–2.2 after removing long runs of homozygosity [1871]. The parents of this individual were related at the level of half-siblings [1871].

The Vindija 33.19 genome, from a female Neandertal about 50,000 years old in Croatia, reached about 30-fold coverage [1874]. It shows “1.6 differences per 10,000 base pairs” between its two copies, fewer than in present-day humans [1874]. She is closer than the Altai individual to the Neandertals who mixed with non-Africans, and with her genome 10–20 % more Neandertal DNA is found in present-day humans [1874].

The shares. Neanderthal-derived DNA makes up 1.5–2.1 % of the genomes of people outside Africa [1871]. Per haploid genome of 3.055×10^9 bp that is 46–64 Mb (computed). The Denisovan share is about 0.2 % in mainland Asians and Native Americans, about 25 times smaller than in Papua New Guinea and Australia [1871].

That gives about 0.2 % × 25 = 5 % Denisovan DNA in Papua New Guinea and Australia (computed), beside 4–6 % in Melanesians [1873]. The 2014 study analysed 25 present-day genomes and found several gene-flow events among Neanderthals, Denisovans and early modern humans [1871].

What all humans share. The catalogue of changes found in all present-day humans analysed, and in no archaic genome, holds 31,389 single-nucleotide substitutions and 4,113 short insertions and deletions [1871]. It “contains only 96 fixed amino acid substitutions in a total of 87 proteins” [1871]. That is 35,502 changes in all, and 1.10 amino-acid changes per affected protein (computed).

The range of the Denisovans. The Xiahe mandible from the Tibetan Plateau is Denisovan and “at least 160 thousand years old” (position 59.78), by U-series dating of carbonate on the bone [1875].

The end of the Neanderthals. Forty key Mousterian and Neanderthal sites from Russia to Spain were dated again [1876]. “The Mousterian ended by 41,030–39,260 calibrated years bp (at 95.4% probability)”, positions 58.54 to 58.50 [1876]. Neanderthals and modern humans overlapped for 2,600–5,400 years, positions 56.03 to 56.69 [1876].

Two ends are thus on record: about 30,000 years ago (2010) and 41,030–39,260 cal BP (2014) [1872, 1876]. Three lineages split twice and met again. Each later genome carries a part of the other two: lines nested as addresses within addresses, the form of shared prefix.

Homo sapiens across Africa and beyond

Jebel Irhoud. New fossils from Jebel Irhoud, Morocco, carry “an age of 315 ± 34 thousand years (as determined by thermoluminescence dating)”, position 60.39 [1877]. The weighted average age of the Middle Stone Age artefacts and fossils is the same, 315 ± 34 ka [1878]. A recalculated U-series and ESR date of a tooth from the mandible gives 286 ± 32 ka, position 60.31 [1878].

The previous oldest *H. sapiens* fossil, from eastern Africa, was about 195 thousand years old [1878]. The question posed was whether modern morphology “rapidly emerged approximately 200 thousand years ago” or “evolved gradually over the last 400

thousand years” [1877].

Omo. The fossils Omo I from Kibish, Ethiopia, have a new minimum age of 233 ± 22 kyr, position 60.12, from the deposits of the eruption that overlies them [1879]. The earlier estimate was about 197 kyr [1879]. The oldest *H. sapiens* fossils thus lie in the north and the east of Africa, 315 and at least 233 ka old.

Out of Africa. A left upper jaw with a nearly complete set of teeth from Misliya, Mount Carmel, Israel, lay with hearths, a stone industry and animal remains [1880]. It is “at least 177,000 years” old, position 59.87, the oldest member of the *H. sapiens* clade outside Africa [1880]. That is more than 55,000 years earlier than the exits of about 120,000 years proposed before [1880].

The genome record. European and Chinese populations had very similar histories of population size before 10–20 kyr ago [1881]. “Both populations experienced a severe bottleneck 10–60 kyr ago”, positions 57.25 to 58.88, while African populations had a milder one with earlier recovery [1881]. All three had an elevated effective size between 60 and 250 kyr ago [1881].

Differentiation may have begun around 100–120 kyr ago, positions 59.35 to 59.52, with “considerable genetic exchanges” until 20–40 kyr ago [1881].

Australia. At Madjedbebe, northern Australia, “Human occupation began around 65,000 years ago”, position 58.96 [1882].

Europe and the shared admixture. Modern humans were in Europe more than 45,000 years ago [1883]. The remains from Ranis (Ilsenhöhle, Germany) are about 45,000 years old, and the Zlatý kůň individual about 47–48 ka, with large uncertainty [1883].

Their genomes show “a single admixture event shared with all non-Africans” [1883]. It is dated to about 45,000–49,000 years ago, positions 58.62 to 58.70 [1883].

The Ranis and Zlatý kůň individuals lived 56–98 generations after the admixture, about 80 in a model over several generations [1883]. At 25–30 years per generation, 80 generations span 2,000–2,400 years (computed).

From one shared admixture the non-African population filled Europe, Asia, Australia and the Americas. A new kind of union opened once and the opened depth filled many times.

The human genome

One complete human genome, T2T-CHM13, holds 3.055×10^9 base pairs [1884]. A body cell carries two copies in 46 chromosomes, 23 from each parent [1885]. The mitochondrial genome holds 16,569 bp, coding for 13 proteins, 2 rRNAs and 22 tRNAs [347].

Protein-coding genes number 19,442 in one count, with 35,885 long non-coding RNA genes and 78,733 genes in all [1886]. A second count gives 20,090 protein-coding genes, of which 8,839 (44 %) are detected in all tissues [1887]. The coding sequence is about 34 million bp, 1.2 % of the sequence finished in 2004 [1888].

New mutations arise at 1.20×10^{-8} per base per generation, measured in 78 Icelandic families [1889].

That is about 73 new changes per child (computed: $1.20 \times 10^{-8} \times 2 \times 3.055 \times 10^{9}$) [1889]. Each year of the father's age adds about two more; the mean age of the fathers was 29.7 years [1889]. About 8 % of the genome sequence is of retroviral origin [307].

The genome is the form; each child is a new carrier with about 73 changes. Form and carrier: the closed form persists while its carriers are replaced.

The human brain in numbers

Neurons. The human brain holds 86.1 ± 8.1 billion neurons and 84.6 ± 9.8 billion non-neuronal cells, in adult male brains [1518]. The ratio is 1.02 to one (computed: 86.1 / 84.6). Its proportions match those of other primates, and the authors call it "an isometrically scaled-up primate brain" [1518].

The cerebral cortex holds 19 % of all neurons in 82 % of brain mass [1518]. The cortex holds 16 billion neurons and the cerebellum 69 billion, leaving about 1 billion for the rest (computed) [1635]. The cerebellum holds 80 % of the neurons (computed: 69 / 86) in 154 g; the ratio of ten glia to one neuron holds only in a few deep nuclei [1635].

The brain of the men studied weighed about 1.5 kg, with the cerebral cortex at 1,233 g [1635]. At autopsy men's brains weigh 1,407 g (range 1,070–1,767) and women's 1,233 g (range 1,000–1,618) [1890].

Synapses and surface. The surface of the cerebral cortex is 973 cm^2 per hemisphere, the area of a square 31.2 cm on edge, position 14.33 [1652]. Both hemispheres hold $2 \times 973 = 1{,}946$ cm^2; at a thickness of 2.69 mm the sheet holds $1{,}946 \times 0.269 = 523$ cm^3 (computed) [1653].

The cortex holds about 10^9 synapses per mm^3, and estimates for the whole brain run from 10^{13} to 10^{15} [1891]. In the cortex that is 523,000 $mm^3 \times 10^9 = 5.2 \times 10^{14}$ synapses (computed). Over 16 billion cortical neurons this is about 33,000 synapses per neuron (computed: $5.23 \times 10^{14} / 1.6 \times 10^{10} = 32{,}700$) [1635].

Energy. The brain is about 2 % of body mass and "consumes about 20% of the whole body energy budget" [1634]. The adult brain uses 20 % of resting metabolism [1892].

It uses 3.5 mL O_2 per 100 g per min [1892]. A brain of about 1,400 g uses about 49 mL O_2 per min, close to one fifth of the basal oxygen use of a healthy young adult [1892].

Over a day this is $49 \times 1{,}440 = 70.6$ L O_2 (computed). A resting human uses 250 mL O_2 per min, and the measured resting power is 85 W, of which the brain takes 16 W, or 19 % (computed: 16 / 85) [389].

Glucose use per neuron is near constant across six species of rodents and primates, including humans [1634]. It varies about 0.4-fold while neuron numbers vary about 1,000-fold, given as 1,213-fold in the paper [1634]. The measured rates are these [1634]:

part	glucose use per neuron	[n]
cerebral cortex	$1.50 \times 10^{-8} \pm 0.49 \times 10^{-8}$ µmol	[1634]

	per min	
cerebellum	$0.87 \times 10^{-9} \pm 0.36 \times 10^{-9}$ µmol per min	[1634]
whole-brain average	$5.79 \times 10^{-9} \pm 0.76 \times 10^{-9}$ µmol per min	[1634]

Cortical neurons use “nearly 20×” (results) or “at least 10×” (abstract) more than cerebellar neurons; the ratio of the two means is 17 (computed: $1.50 \times 10^{-8} / 0.87 \times 10^{-9} = 17.2$) [1634]. For 86 billion neurons the use is $86 \times 10^{9} \times 5.79 \times 10^{-9} = 498$ µmol glucose per min (computed). Over a day this is 498 × 1,440 = 717,000 µmol, or 0.717 mol × 180.16 g/mol = 129 g of glucose (computed).

Each day about 129 g of glucose and 70.6 L of oxygen flow through a brain that holds its form for life. The content flows through while the form holds: what closes, stays.

The human life against the chimpanzee

The life histories of the two species, as given in AnAge, are these [1893, 1894]:

variable	human	position	chimpanzee	position	ratio human / chimpanzee (computed)	[n]
gestation	280 d	48.63	229 d	48.45	1.22	[1893, 1894]
weaning	not reported	—	1,111 d (3.04 y)	49.88	—	[1894]
sexual maturity, female	4,745 d (12.99 y)	51.20	3,376 d (9.24 y)	50.89	1.41	[1893, 1894]
sexual maturity, male	5,110 d (13.99 y)	51.27	2,920 d (7.99 y)	50.76	1.75	[1893, 1894]
interval between births	639 d (1.75 y)	49.38	840 d (2.30 y)	49.63	0.76	[1893, 1894]
litters per year	0.3	—	0.2	—	1.5	[1893, 1894]
birth weight	3,313 g	—	1,821 g	—	1.82	[1893, 1894]
adult weight	62,035 g	—	44,984 g	—	1.38	[1893, 1894]
birth weight / adult weight	5.3 %	—	4.0 %	—	—	[1893, 1894]
maximum longevity	122.5 y	53.25	68 y in captivity; 55 y wild, one female	52.71; 52.52	1.80	[1893, 1894]

The human runs longer in every phase but one. The interval between births runs the other way, 639 against 840 days.

On the human page, mortality rises exponentially after about age 30 and doubles about every 8 years [1893]. World life expectancy is 73 years there, and hunter-gatherer life

expectancy about 30 years [1893]. The chimpanzee page notes “considerable controversy” over menopause in chimpanzees and that the onset of ageing “appears to occur at earlier ages in chimpanzees” [1894].

Weaning. In 39 Holocene skeletal populations worldwide, nitrogen isotopes give a weaning age of 2.80 ± 1.32 years, position 49.81 [1895]. It does not differ from ethnographic weaning ages, nor between ways of subsistence [1895]. Breastfeeding in early Holocene humans was already shorter than in living great apes [1895].

A slower life. Human life history is slower than that of all great apes, with reduced adult mortality since the split from the chimpanzee line, short intervals between births and early weaning [1896]. No fossil taxon matches one “primitive” hominin pattern [1896]. Mortality profiles of hunter-gatherer and horticultural populations give an adaptive lifespan of “68–78 years”, positions 52.71 to 52.84 [1897].

Menopause in two species. In wild chimpanzees at Ngogo, Kibale, Uganda, the post-reproductive representation is 0.195 [1898]. A female who reaches adulthood spends about one fifth of adult life past reproduction, about half the share in human hunter-gatherers; gonadotropins rise sharply after age 50 [1898]. The human hunter-gatherer share is then about 2 × 0.195 = 0.39 (computed).

In women menopause comes between 45 and 55 years, positions 52.34 to 52.52 [1899].

The growing brain

Before birth. Synapse formation in the human cerebral cortex begins before the 27th week of pregnancy, position 48.27 [1666].

The first 90 days. One study scanned 87 infants 211 times between the ages of 2 and 90 days, positions 44.13 and 47.60 [1900]. At birth whole-brain volume is about one third of elderly brain volume [1900]. Growth runs about 1 % per day and slows to 0.4 % per day by 3 months, when the volume is just over half of adult [1900].

Total growth in 90 days is 64 %; the cerebellum more than doubles and the hippocampus grows by 47 % [1900]. A birth one week earlier gives a brain 5 % smaller, still 2 % smaller at 90 days [1900].

Peaks across the lifespan. Brain charts were built from 123,984 MRI scans of 101,457 people in more than 100 studies, from 115 days after conception (position 47.82) to 100 years (position 53.06) [1901]. The peak ages, with 95 % bootstrap intervals, are these [1901]:

measure	peak age	95 % interval	position of peak	[n]
cortical thickness	1.7 y	1.3–2.1 y	49.35	[1901]
grey matter volume	5.9 y	5.8–6.1 y	50.49	[1901]
total cerebrum volume	12.5 y	12.14–12.89 y	51.17	[1901]
subcortical grey matter	14.4 y	14.0–14.7 y	51.30	[1901]
white matter volume	28.7 y	28.1–29.2 y	51.93	[1901]

Cerebrospinal fluid volume rises to age 2 and then holds level to age 30, positions 49.50 and 51.97 [1901].

Synapses and spines. Synapse density peaks near 3 months after birth in auditory cortex (position 47.61) and after 15 months in frontal cortex (position 49.07) [1666]. Net elimination of synapses has ended by 12 years in auditory cortex, position 51.13 [1666].

Dendritic spines were counted on prefrontal pyramidal neurons of layers IIIC and V, from newborn to 91 years (position 52.98) [1902]. Childhood spine density is two- to threefold the adult value, and the decline begins at puberty [1902]. Overproduction and remodelling continue “into the third decade of life” [1902].

Myelin. Myelinated axon fibre density and myelin-protein expression were measured across postnatal life in four cortical regions [1903]. Chimpanzees (N = 20) reach adult-like levels around sexual maturity [1903]. In humans (N = 33) maturation extends “past late adolescence” [1903].

The total length of myelinated fibre is 176,000 km in men and 149,000 km in women at age 20, at positions 32.67 and 32.52 [1667]. At age 80 it is 97,200 km and 82,000 km, positions 32.13 and 31.97 [1667]. The loss is 45 %, about 10 % per decade, in a sample of 36 people [1667].

Energy in childhood. At birth the brain uses 52.5 % (boys) and 59.8 % (girls) of resting metabolism, and 35.4 % and 38.7 % of daily energy [1633]. At the childhood peak it uses 66.3 % and 65.0 % of resting metabolism, and 43.3 % and 43.8 % of daily energy [1633]. The peak lies in childhood, not at birth, and the rate of body growth is inversely related to brain glucose use until puberty [1633].

New neurons in the adult: two records. Carbon-14 dating of DNA gives about 700 new neurons per day in each adult hippocampus, a turnover of 1.75 % per year [1648]. At that rate the renewing population turns over in 57 years, position 52.55 (computed: 1 / 0.0175). In 17 post-mortem brains and 12 surgical samples aged 18–77 years, no young neurons were found in adults, only a few at 7 and 13 years [1649].

In both records new neurons come from progenitor cells, not from the division of differentiated neurons [1648, 1649]. No cortical neurons are added after birth [1642].

The brain is built fast, held long and released slowly: synapses overproduced, then pruned; white matter rising to 28.7 years, then falling 45 % by 80. Loading, holding and discharge is the form of rest and discharge, here across one life.

The course of a life

From one cell. A human life runs from one cell to about 3×10^{13} cells [236]. The egg is a cell about 120 µm across, position 7.17 [1891]. Taken as a sphere of the density of water, its mass is $4/3 \times \pi \times (60 \times 10^{-6})^3 \times 1{,}000 = 9.0 \times 10^{-10}$ kg (computed).

An adult of 70 kg is 7.7×10^{10} times heavier: 36.2 doublings of mass (computed: $\log_2 7.7 \times 10^{10}$) [236]. In cells, 1 to 3×10^{13} is 44.8 doublings (computed: $\log_2 3 \times 10^{13}$). The newborn of 3.3 kg has 4.4 doublings left (computed: $\log_2(70 / 3.3)$) [1904].

The build. From ovulation to birth the median is 268 days, position 48.59, with a natural range of 37 days among pregnancies with a known ovulation date [1905]. That is 38.3 weeks (computed). AnAge gives 280 days, counted the conventional way [1893].

The median newborn weighs 3.3 kg (boys) or 3.2 kg (girls); two standard deviations below is 2.5 and 2.4 kg, two above 4.4 and 4.2 kg [1904]. The median newborn is 49.9 cm long (boys, position 14.75) and 49.1 cm (girls, position 14.74) [1904]. In the womb, 49.9 cm in 268 days is 68 cm per year (computed).

Boys grow 75.7 − 49.9 = 25.8 cm in the first year and girls 24.9 cm; in the second year 12.1 and 12.4 cm (computed from [1904]). Growth halves from the first year to the second.

The spurt. From the reference medians, girls grow 6.4 cm between 10 and 11 years and boys 7.2 cm between 13 and 14 (computed from [1906]). Girls stand at 162.5 cm at 16 and 163.2 cm at 19 (position 15.83): 99.6 % of final height at 16 (computed) [1906]. Boys stand at 172.9 cm at 16, 176.1 cm at 18 and 176.5 cm at 19 (position 15.90): 98.0 % at 16 and 99.8 % at 18 (computed) [1906].

Puberty. In 17,077 American girls, breast development began at a mean age of 9.96 years in white girls and 8.87 years in African American girls, positions 50.96 and 50.86 [1907]. Menarche came at 12.88 and 12.16 years, positions 51.20 and 51.14 [1907]. Across 30 studies from 1977 to 2013 the age at breast development fell by 0.24 years per decade (−0.44 to −0.04) [1908].

The hold. Total body calcium rises from 26–30 g at birth to about 1,200 g in women and 1,400 g in men by adulthood [1909]. After menopause women lose about 1 % of bone mineral density a year [1909].

The release. The measured rates of decline are these:

function	rate	[n]
peak oxygen uptake, 810 adults aged 21–87	3–6 % per decade in the twenties and thirties; more than 20 % per decade in the seventies and beyond; larger in men from the forties on	[1910]
muscle mass, cross-sectional	0.47 % per year in men, 0.37 % in women; 0.64–0.98 % per year at 75	[1911]
muscle strength at 75	3–4 % per year in men, 2.5–3 % in women; 2 to 5 times faster than mass	[1911]
creatinine clearance, 254 healthy adults followed	0.75 mL/min per year; one third showed no decline	[1912]
working glomeruli per kidney, 1,638 donors	about 990,661 at 18–29 years; about 520,410 at 70–75 years	[1913]
hearing	more than 25 % of people over 60 have disabling hearing loss	[1713]
near vision	1.8 billion people, 25 % of the world, had presbyopia in 2015	[1914]

The nephron loss is 47 % (computed: (990,661 − 520,410) / 990,661), and the remaining nephrons take over [1913].

The length of life. World life expectancy at birth was 73.3 years in 2023, position 52.78, and healthy life expectancy 62.8 years, position 52.64 [1507]. The difference is

10.5 years, 14 % of the whole (computed). In 2021 the highest life expectancy was 88 years, in Hong Kong, and Nigeria's was thirty years below Japan's [1915].

The longest verified life, Jeanne Calment's, ran from 21 February 1875 to 4 August 1997: 122 years and 164 days, position 53.25 [1916]. In 1980 Fries observed that life expectancy had risen from about 47 to 73 years in a century while the maximum lifespan had not moved [1917]. He estimated an ideal average lifespan of about 85 years, position 52.91 [1917].

Inheritance of lifespan. In 2,872 Danish twin pairs born 1870 to 1900 the heritability of lifespan was 0.26 for men and 0.23 for women [1918]. Family trees of hundreds of millions of people gave nominal estimates of 15–30 %, but the same correlation among in-laws, who share no genes [1919]. Corrected for like marrying like, the heritability was well below 10 % [1919].

On the ladder. The times of a life run from the day at 43.50 to the longest life at 53.25. A life of 73.3 years holds 26,773 days (computed: 73.3 × 365.25). A generation of 25–30 years sits at positions 51.80 to 51.97.

The Holocene brain and the first farmers

Two records of the last 3,000 years. DeSilva and co-authors report a decrease in brain size from about 3,000 years ago, position 56.16 [1820]. They give its rate as "50 times greater" than the Pleistocene increase [1820]. A fall of 5 kg in body size would account for only 22 mL of the reduction, and the reported reduction is "more than 5x greater" [1820].

A reanalysis of the same dataset, 987 specimens, finds human brain size stable over the last 300 ka, with no change point near 3 ka [1859].

Domestication. Plants and animals were domesticated over the past 11,500 years, position 57.38 [1920]. In the Eastern Mediterranean the first domestication of plants and animals dates to the 12th millennium cal BP [1921]. Herd management and crop cultivation appear at least 1,000 years before the changes of form used to recognise domestication [1921].

Different species were domesticated in different parts of the Fertile Crescent, with several domestic lines per species [1921]. In 11 domesticated plants from 60 archaeological sites, non-shattering and larger grain evolved slowly [1922]. The dates per species in the Near East are these [1923]:

species or process	date (cal BP)	position	[n]
cultivation of wild einkorn and rye, Abu Hureyra and Mureybit	13,000–12,000	57.49–57.42	[1923]
several plant species under cultivation	at least 11,500	57.38	[1923]
cattle, Euphrates valley	11,000–10,000	57.34–57.25	[1923]
sheep, herd management complete at Nevali Çori	about 10,500	57.30	[1923]
emmer and einkorn	about 10,500–10,200	57.30–57.27	[1923]

einkorn and einkorn, earliest secure domestic grain	about 10,500–10,200	57.30–57.27	[1923]
pig, Cafer Höyük	about 10,300	57.28	[1923]
managed goat, Nevali Çori; herding at Ganj Dareh	about 10,200; 9,900	57.27; 57.24	[1923]
barley, Middle PPNB	about 10,000	57.25	[1923]

Maize was present by 8,700 cal BP at Xihuatoxtla, Central Balsas, Mexico, position 57.13 [1924]. Rice was domesticated in the Lower Yangtze 6,900–6,600 years ago, positions 56.92 to 56.88 [1925]. Over that span non-shattering spikelet bases rose from 27 % to 39 %, and rice from 8 % to 24 % of plant remains [1925].

The dog was the first domesticated animal [1926]. East Asian and Western Eurasian dogs diverged about 14,000–6,400 years ago, positions 57.56 to 56.85 [1927]. Domestication opened once, and the opened depth then filled many times: the dog first, then cereals, cattle, sheep, pig and goat in the Near East, maize in Mexico and rice on the Yangtze.

The census. World population from 10,000 BCE, from HYDE v3.3 before 1800, is this [1980]:

year	world population	factor over the previous row (computed)	[n]
10,000 BCE	4,501,152	—	[1980]
9,000 BCE	5,687,125	1.26	[1980]
8,000 BCE	7,314,623	1.29	[1980]
7,000 BCE	9,651,703	1.32	[1980]
6,000 BCE	13,278,309	1.38	[1980]
5,000 BCE	19,155,698	1.44	[1980]
4,000 BCE	28,859,174	1.51	[1980]
3,000 BCE	44,577,880	1.54	[1980]
2,000 BCE	72,685,064	1.63	[1980]
1,000 BCE	110,530,464	1.52	[1980]
year 0	232,268,832	2.10	[1980]
1800	983,104,755	4.23	[1980]
1900	1,627,273,655	1.66	[1980]
2000	6,171,702,992	3.79	[1980]
2023	8,091,734,933	1.31	[1980]

From 10,000 BCE to year 0 the population grew by a factor of 51.6, a mean doubling time of 1,758 years (computed). The factor per millennium rises from 1.26 to 2.10, with one dip, 1.52 in 2000–1000 BCE (computed). From 1900 to 2000 the factor is 3.79 in one century (computed).

The line that passed through about 1,280 breeding individuals between 930 and 813 ka holds 4.5 million people at 10,000 BCE and 8.09 billion in 2023. The networks of that population follow in chapter 22.

What this part of the history shows

Rest and discharge in the brain. The *Australopithecus* brain holds at about 450 cc from 3.5 to 2.0 Ma [1820]. At 2.10 Ma the rate of increase steps from 0.03 to 0.35 $\log_{10}$ cc per Myr, 11.7-fold, and changes again at 1.49 or 1.97 Ma [1820]. A long hold, then a step: the form of rest and discharge, at positions 62.59 to 62.08 and then 62.12.

Rest and discharge in the body. Body size shows long phases of stasis interrupted by rapid increases [1867]. Stature becomes modern at about 1.6 Ma and body mass at 0.5–0.4 Ma, on a schedule of its own [1867, 1868]. One life repeats the form: a build to white-matter peak at 28.7 years, a hold, and a release of 45 % of myelinated fibre by 80 [1667, 1901].

What closes, stays. Each day about 129 g of glucose and 70.6 L of oxygen pass through the adult brain (computed from [1634, 1892]). The brain takes 20 % of resting energy at 2 % of body mass, and up to 66.3 % of resting metabolism in childhood [1633, 1634]. The content flows through while the form holds.

Form and carrier. The genome of 3.055×10^9 bp is the form, and each child carries about 73 new changes into it [1884, 1889]. “The closed class persists and holds form”: the genome holds while every life that carries it ends.

Shared prefix. Gut bacteria split with their hominid hosts over 15 Myr, partner nested in partner [1131]. All living humans pass through a neck of about 1,280 breeding individuals at 930–813 ka [1870]. All share 35,502 fixed changes, 96 of them in proteins, and non-Africans share one admixture with the Neanderthals at 49–45 ka [1871, 1883].

Opened once, filled many times. *Homo* appears at 2.80–2.75 Ma and stands in China by 2.12 Ma and in the Caucasus by 1.85 Ma [1851, 1854, 1855]. *H. sapiens* stands in Morocco at 315 ka, in the Levant by 177 ka, in Australia by 65 ka and in Europe by 45 ka [1877, 1880, 1882, 1883]. Domestication, first of the dog, filled the Near East with cereals, cattle, sheep, pig and goat at 13,000–10,000 cal BP [1923, 1926].

On the ladder. The dated history of this chapter runs from the CpG split at 12.1 Ma (position 63.72) to the Holocene at 3 ka (56.16). The brains run from cube edges of 7.11 cm (12.98) to 11.34 cm (13.41). The narrowest neck and the steepest rise lie on the same line: 1,280 breeders, then a factor of 3.79 in the twentieth century [1870, 1980].

21. Language and Culture

The human line of chapter 20 ends with 8.09 billion people. Before that number, and beside it, runs a second history: of signals passed from body to body, of songs and skills learned from others, and of marks made to last.

Codes and traditions are older than the human. A bee dance codes a distance, a monkey call a predator, a whale song an ocean basin. Songbirds, whales and chimpanzees carry traditions that pass from one generation to the next.

In the human record pigment, beads and engraved marks come first, then images on rock and flutes, then writing, the alphabet, printing and mass literacy. The chapter follows that order, with every dated case in the record, and places each date on the ladder.

Codes in other animals

The waggle dance. The honeybee dancer “generates a specific, coded message that describes the direction and distance from the hive of a new food source” [1928]. Karl von Frisch concluded that recruits use the information in the dance [1928]. Riley and co-authors recorded the actual flight paths of recruited bees with harmonic radar [1928].

One study decoded 5,097 waggle dances: 2,351 from August 2009 to July 2010 and 2,746 from August 2010 to July 2011 [1929]. Duration was converted to distance with a linear calibration built for the local population and landscape [1929]. The mean communicated foraging distances by season are these [1929]:

season	mean distance	position	foraging area	[n]
spring	493 m	21.03	0.8 km²	[1929]
summer	2,156 m	22.37	15.2 km²	[1929]
autumn	1,275 m	21.90	—	[1929]

From spring to summer the distance rose by a factor of 4.37 and the area by a factor of 19.0 (computed: 2,156 / 493; 15.2 / 0.8).

The dance is learned from other bees. Bees with no chance to follow dancers danced in disorder, with larger divergence in angle and wrongly coded distances [1930]. The angle error improved with experience, but the distance error persisted for life; bees that had followed dancers showed neither error [1930].

The dance keeps two relations, direction and distance, and drops everything else about the flower. That is the form of reading: an image that keeps the relations and drops the rest.

Alarm calls. Vervet monkeys give acoustically different alarm calls to different predators [1931]. Played back with no predator present, each call produces its own escape: into the trees for the leopard alarm, looking up for the eagle alarm, looking

down for the snake alarm [1931]. Adults give the calls mainly to leopards, martial eagles and pythons: three calls for three classes [1931].

Infants also give alarms to other mammals, to many birds and to objects that look like snakes [1931]. “Predator classification improves with age and experience” [1931]. The mapping from sound to class narrows as the young monkey grows.

Learned song

The vocal learners. Besides humans, three groups of birds learn to produce their sounds: passerine songbirds, parrots and hummingbirds [1932]. Among mammals the learners are some bats, the pinnipeds, the cetaceans and the elephants [1932]. That is 3 bird groups and 5 mammal groups with the human (computed count of named groups) [1932].

The list “has recently expanded to include elephants” [1932].

Songbirds “must hear the sounds of adults during a sensitive period” [1933]. Songbirds and humans both learn complex sounds early in life, depend on hearing adults and on practice, and pass through a mainly perceptual phase that later guides production [1934]. Both show a critical period [1934].

A song culture from isolates. Zebra finches “tend to learn one song type as juveniles” [1932]. Isolate zebra finches, raised without singing males, sing abnormal song [1935]. Their pupils imitated them but changed some features; the changes accumulated, and “songs evolved towards the wild-type in three to four generations” [1935].

Each learner copied its tutor with a small change. Over three to four generations the changes ran toward the wild-type song [1935].

Whale song. Humpback whales produce long, patterned sequences of sound, called songs, that last from 7 to 30 minutes, positions 38.65 to 39.98, and are repeated with great precision [1936]. A singing session can last hours [1936]. Songs are built of themes repeated in sequence; the number of phrases per theme varies, and one individual keeps to its song type [1936].

Populations in different ocean basins normally sing distinct songs [1937]. Along the east coast of Australia, between 1995 and 1998, the song was “replaced rapidly and completely by the song of the Australian west coast population from the Indian Ocean” [1937]. This followed the arrival of a small number of foreign singers [1937].

Across the South Pacific “multiple song types spread rapidly and repeatedly in a unidirectional manner” [1938]. They moved eastward through the populations of the western and central South Pacific “over an 11-year period”, position 51.05 [1938].

Traditions in apes

Cultures in chimpanzees. A synthesis of the seven longest-term field studies, with 151 years of chimpanzee observation in all, found “39 different behaviour patterns, including tool usage, grooming and courtship behaviours” [1939]. Each is customary or habitual in some communities and absent in others, where ecological explanations are

excluded [1939]. The mean observation per study is 151 / 7 = 21.6 years, position 51.67 (computed).

A chimpanzee Stone Age. Chimpanzee sites in Côte d'Ivoire hold stones modified by use, with starch residues, dated to about 4,300 years ago, position 56.49 [1940]. The authors describe a "Chimpanzee Stone Age" that predates the settled farming villages of the region [1940].

Traditions lost. Human disturbance reduces the behavioural and cultural diversity of chimpanzees, also where populations persist: "human-mediated disturbance is reducing these complex traits" [1941]. The traditions are carried by the members of a community and are lost with them. The tradition is the form and the animals are its carriers; where the carriers are disturbed, the form goes before the animals do.

A tradition of bumblebees has the same form: string pulling spread from trained bees to 34 of 47 foragers of one colony and to none of 166 in control colonies (chapter 19).

The speaking body

FOXP2. In the three-generation KE family a severe speech and language disorder "is transmitted as an autosomal-dominant monogenic trait" [1942]. The locus maps "to a 5.6-cM interval of region 7q31" on chromosome 7 [1942]. Affected members carry a point mutation that changes an invariant amino acid in the forkhead domain of FOXP2 [1942].

"Two functional copies of FOXP2 seem to be required for acquisition of normal spoken language" [1943]. A reanalysis of hundreds of genomes from around the world finds no evidence of recent positive or balancing selection at FOXP2, and attributes the earlier signal to sample composition [1944]. The two amino-acid substitutions of the human form are present in archaic hominins [1944].

The same reanalysis finds an intronic region of FOXP2 enriched for highly conserved sites that are polymorphic in humans [1944]. The region is compatible with loss of function and is lowly expressed in human prefrontal cortex [1944].

The hyoid. A well-preserved human hyoid bone from Middle Palaeolithic layers of Kebara Cave, Mount Carmel, Israel, dates to "about 60,000 years BP", position 58.88 [1945]. It is "almost identical in size and shape to the hyoid of present-day populations" [1945]. The authors infer that the morphological basis for speech "appears to have been fully developed during the Middle Palaeolithic" [1945].

The Kebara 2 Neanderthal "dates from approximately 60 ka and is part of a near-complete adult male skeleton unearthed in 1983" [1946]. Its hyoid was described in 1989, six years after excavation (computed) [1945, 1946]. A second, partial Neanderthal hyoid, SDR-034 from El Sidrón Cave, Asturias, Spain, is "dated to ~43 ka", position 58.58 [1946].

The bone that holds the tongue and larynx keeps its present form for at least 60,000 years.

Pigment, ornament and the first marks

Eagle talons at Krapina. The Neandertal site of Krapina, Croatia, holds “eight, mostly complete white-tailed eagle” talons with modifications, *Haliaeetus albicilla*, “dating to approximately 130 kyrs ago”, position 59.59 [1947]. That is more talons than in the entire European Mousterian [1947].

Shell beads at Skhul. Perforated marine gastropod shells come from Skhul in western Asia and Oued Djebbana in North Africa [1948]. A *Nassarius gibbosulus* bead from Skhul lies in a layer with 10 human fossils dated to 100,000–135,000 years ago, positions 59.35 to 59.62 [1948]. That is about 25,000 years earlier than the earlier evidence for personal decoration in South Africa [1948].

The ochre workshop at Blombos. About 100,000 years ago (position 59.35), at Blombos Cave, South Africa, an ochre-rich liquid was made and stored in two abalone shells, *Haliotis midae* [1949]. Ochre, bone, charcoal, grindstones and hammerstones formed one composite toolkit [1949]. The workshop was excavated in 2008 [1949].

Beads at Taforalt. Perforated *Nassarius gibbosulus* shells from the Grotte des Pigeons, Taforalt, Morocco, date by luminescence and U-series “to approximately 82,000 years ago”, position 59.17 [1950]. Their wear shows that some were hung on a cord, and they are covered in red ochre [1950]. “The shells are of the same genus as shell beads from slightly younger levels at Blombos Cave in South Africa” [1950].

Bead-making in North Africa and southwest Asia began “at least 40 millennia before the appearance of similar cultural manifestations in Europe” [1950]. One genus of shell, *Nassarius*, is pierced and worn from Morocco to Israel and South Africa.

Engraved ochre. Two pieces of red ochre from Middle Stone Age layers at Blombos carry abstract engravings [1951]. Thermoluminescence on burnt stone gives “a mean date of 77,000 years” (position 59.11), and luminescence on an overlying dune gives “70,000 years” (position 59.03) [1951]. The authors set the engravings “at least 35,000 years before the start of the Upper Paleolithic”, where such images appear about 35,000 years ago [1951].

The first drawing. An abstract drawing at Blombos comes from Middle Stone Age levels about 73,000 years old, position 59.06 [1952]. It is at least 30,000 years older than other abstract and figurative drawings, which date after 40,000 years ago (position 58.52) [1952].

Images on rock

Sulawesi, 2014. Fourteen images in seven caves of the Maros karst, South Sulawesi, were dated by U-series: “12 human hand stencils and two figurative animal depictions” [1953]. The oldest hand stencil has a minimum age of 39.9 kyr, position 58.51, “the oldest known hand stencil in the world” at that date [1953]. A painting of a babirusa is at least 35.4 kyr old, position 58.40 [1953].

Sulawesi, 2024. Narrative cave art at Leang Karampuang, Maros-Pangkep, was painted at least 51,200 years ago, position 58.74 [1954]. The minimum age for the scene is 53.5 ± 2.3 ka, position 58.78 [1954]. The hunting scene at Leang Bulu’ Sipong

4, dated before to 43.9 ka (position 58.60), was re-dated to at least 50.2 ± 2.2 ka (position 58.72) [1954].

The dates come from laser-ablation U-series imaging [1954].

Muna, 2026. A hand stencil at Liang Metanduno, Muna Island, southeast Sulawesi, lies under calcite that "yielded a U-series date of 71.6 ± 3.8 thousand years ago (ka)", position 59.05 [1955]. The minimum age for the motif is 67.8 ka, position 59.00 [1955]. It "exceeds the published minimum for rock art in Maros-Pangkep by 16.6 thousand years" [1955].

That places the Maros-Pangkep minimum at 67.8 − 16.6 = 51.2 ka, the date of 2024 (computed). The stencil is also 1.1 kyr older than the published minimum of 66.7 ka (position 58.98) for a hand stencil in Spain attributed to Neanderthals [1955]. All the rock-art ages are minima [1955].

The oldest dated Sulawesi image moved from 39.9 ka (2014) to 51.2 ka (2024) to 67.8 ka (2026). Hand stencils come first both in Sulawesi and in Spain; figurative animals and narrative scenes follow.

Music

Flutes. Bone and ivory flutes from the early Aurignacian of southwestern Germany, at Hohle Fels and Vogelherd, document a musical tradition already established when modern humans settled Europe [1956]. They date to "more than 35,000 calendar years ago", position 58.39 [1956]. A five-hole flute of bird bone comes from Hohle Fels, and other early evidence of music in France and Austria "post-date 30,000 years ago" (position 58.25) [1956].

Hearts under one breath. Fifteen of eighteen singers took part, and eleven were analysed [1733].

They hummed, sang a hymn with free breathing, and sang a slow chant breathed only between phrases, in ten-second cycles (position 35.25) [1733]. In the chant the heart-rate variability and breathing of every singer were dominated by 0.1 Hz, and the singers' heart rates rose and fell together [1733]. In the hymn the coupling was weaker and spread over 0.05, 0.1 and 0.2 Hz; humming gave regular variation that differed from singer to singer [1733].

The languages of today

The count. Glottolog 5.3 counts 7,674 spoken first languages "Currently 2026-03-02" [1957]. It groups them in 246 families and lists 183 isolates, counted as families of one member in the same classification [1957]. With the 183 isolates counted among the 246 families, 63 families have more than one member (computed: 246 − 183); the mean is 7,674 / 246 = 31.2 languages per family (computed).

Ethnologue, of SIL International, covers "over 7,000 living languages", counted as languages "still used by at least one person as their first language" [1958]. The two counts differ by less than 674 languages (computed: 7,674 − 7,000) [1957, 1958].

Four families each hold more than 500 languages: Atlantic-Congo, Austronesian, Indo-European and Sino-Tibetan [1957]. Together they hold more than 2,000 languages, more than 26 % of 7,674 (computed: 4 × 500). Many lines hold one language, a few hold hundreds.

A family is a shared prefix: every language in it carries the address of the common root. The form is community as shared prefix (chapter 1), here among languages.

Click languages. Hadza and Sandawe are two click-speaking peoples of Tanzania, and the Sandawe live within 150 km of the Hadza, position 26.23 [1959]. They share rare mtDNA and Y-chromosome haplogroups [1959]. Divergence estimates exceed 35,000 years for one split and 15,000 years for the common ancestry of Hadza and Sandawe, positions 58.39 and 57.62 [1959].

The two groups were already isolated when farming and herding spread [1959]. Hadza (Glottocode hadz1240, ISO 639-3 hts) is listed as “shifting”, and in Brenzinger 2011 as “Threatened (40 percent certain, based on the evidence available)” [1957]. In southern Africa Glottolog lists three separate families with click languages: Khoe-Kwadi, Tuu and Kx’a [1957].

Fewer sounds with distance. Across 504 languages the phoneme inventory declines with distance from Africa [1960]. The decline matches a model of expansion by serial founders and is not accounted for by recent history, regional clustering or family membership [1960]. The address grows longer with each founding step, and each step carries fewer sounds onward.

Turn-taking. In ten languages speakers avoid overlap and minimise silence between turns [1961]. The mean gaps differ between languages, but all fall within 250 ms of the cross-language mean, a spread at position 31.89 [1961]. The ten languages keep one timing of the turn, within a quarter of a second.

Brain with brain. Nine pairs of adults imitated each other’s hand movements while two EEG sets recorded [1962]. The rhythms of the two brains synchronised in the alpha-mu band, most strongly between the right centro-parietal regions, and also in the beta and gamma bands [1962].

When one romantic partner received pain, holding hands increased the coupling of the two brains in the alpha-mu band, 8 to 12 Hz [1964]. The coupling was strongest in central regions and the right hemisphere of the observer [1964]. It went with the size of the pain relief and with the observer’s empathic accuracy [1964].

Writing

Uruk. The Uruk phases run “Uruk V, ca. 3500-3350 BCE; Uruk IV, ca. 3350-3200 BCE; Uruk III, ca. 3200–3000 BCE” [1965]. Proto-cuneiform is attested in the later half of the Uruk period, about 3200–3000 BC [1965]. Counted from 2026 with no year zero, 3500 BCE lies 5,525 years back (position 56.71), 3200 BCE 5,225 years (56.66) and 3000 BCE 5,025 years (56.63) (computed).

Excavation at Uruk from 1928 to 1976 yielded “nearly 5000 tablets and fragments” [1965]. The corpus holds nearly 4,900 texts of the Uruk III period, Jemdet Nasr

included: “Of these texts, 703 are lexical texts and 4167 are administrative” [1965]. The administrative share is 4,167 / 4,870 = 85.6 %, and the lexical share 14.4 % (computed).

“There are a total of 1246 signs and sign variants attested in administrative texts and 802 in lexical texts” [1965]. Traditionally about 800 separate signs are counted, and the 200 most common signs cover 84 % of attestations in administrative texts [1965]. The Unicode proposal encodes 200 signs and 64 numeric characters, 264 in all [1965].

Writing begins as record-keeping, with numbers and lists. Six of every seven early texts are administrative (computed: 85.6 %).

Egypt. Ivory labels from tomb U-j at Abydos, excavated under Günter Dreyer, “bear evidence of writing dating back to ca. 3000 BC”, 5,025 years back (position 56.63) [1966]. The find is of “special importance” for understanding the origin of writing [1966].

China. Radiocarbon dating of late Shang oracle bones gives King Wu Ding a reign “during 1254 BC to 1197 BC” [1967]. “The Shang Dynasty terminated around 1041 BC” [1967]. About 100 samples were collected and 50 placed in the Bayesian model, with an uncertainty of about 10 years per phase [1967].

Wu Ding reigned 57 years (computed: 1254 − 1197). From the start of his reign to the end of the Shang is 213 years (computed: 1254 − 1041). The year 1254 BC lies 3,279 years back, position 56.24 (computed).

Mesoamerica. “A block with a hitherto unknown system of writing has been found in the Olmec heartland of Veracruz, Mexico” [1968]. The Cascajal block dates to the early first millennium BCE on stylistic and other evidence, the oldest writing in the New World [1968]. At San Bartolo, Guatemala, Maya hieroglyphs on painted walls and plaster fragments of the structure Las Pinturas come with carbonised wood dated 300 BC to AD 200 [1969].

That is 2,325 to 1,826 years back, positions 55.93 to 55.71 (computed). Writing thus appears in Mesopotamia, Egypt, China and Mesoamerica, from about 3200 BCE at Uruk to the early first millennium BCE in Veracruz.

The alphabet

Egypt and Sinai. Two early alphabetic inscriptions from Wadi el-Hol, Egypt, found in 1998, are tentatively dated to the late Middle Kingdom: “late Twelfth to early Thirteenth Dynasties; late nineteenth/early eighteenth century BC” [1970]. The Proto-Sinaitic inscriptions of Serabit el-Khadim were first dated to “the Twelfth Dynasty (early second millennium BC)” by Gardiner in 1916 [1970]. Later proposals put them “after 1500 BC (in the Eighteenth Dynasty), or even later”, or in the 14th or early 13th century BC [1970].

The earliest Sinai and Egyptian evidence is “dated to the nineteenth century BC”, 1900–1801 BC, which lies 3,925 to 3,826 years back, positions 56.40 to 56.38 (computed) [1970].

Lachish. An early alphabetic sherd from Tel Lachish lies in a burnt lens whose two barley grains fall in the fifteenth century BC [1970]. Its stratum is constrained to “1460–

1430 BC, 1σ; 1485–1425 BC, 2σ”, 3,510 to 3,450 years back, positions 56.30 to 56.29 (computed) [1970]. The early alphabet spread to the southern Levant and became the Phoenician alphabet, from which the Greek alphabet derived [1970].

Phoenician. “The twenty-two letters in the Phoenician block” encode a script that “evolved over the period from about the 12th century BCE” and “came into its own from the 9th century BCE” [1971]. It is the forerunner of the Etruscan, Latin, Greek, Arabic, Hebrew and Syriac scripts [1971]. The 12th century BCE begins 3,225 years back, position 56.22 (computed).

From 800 signs to 22 letters. Proto-cuneiform has about 800 signs in the traditional count; Phoenician has 22 letters, a ratio of 800 / 22 = 36 (computed from [1965, 1971]). From the first proto-cuneiform, about 3200 BCE, to the alphabetic inscriptions of the 19th century BC is about 1,300 years (position 55.40) (computed). To the Phoenician script of about 1200 BCE it is about 2,000 years (position 55.79) (computed).

Each letter is the residue of a sign: a closed form of the earlier script, kept as a unit of the next. The form is the one of chapter 1: “The residue of depth n is the alphabet of depth n+1.” One alphabet opened once and filled six scripts and their languages.

Manuscripts and printing

The manuscript centuries. Over thirteen centuries book production in Western Europe grew at an average of about 1 % per year [1972]. Monasteries mattered most early, universities in the early modern period, and lay demand dominated in the later Middle Ages [1972]. Manuscript production per century, by region, is this [1972, 1973]:

region	6th c.	9th c.	12th c.	13th c.	14th c.	15th c.	[n]
Italy	10,194	20,307	95,207	253,013	879,364	1,423,668	[1973]
France	1,682	74,190	197,831	510,828	564,624	1,195,783	[1973]
Germany	0	59,771	166,876	270,392	293,814	515,116	[1973]
Belgium	0	3,029	43,219	119,588	106,148	572,124	[1973]
Iberia	1,594	21,693	114,422	237,818	344,284	390,478	[1973]
Central Europe	0	0	27,530	120,987	301,833	376,650	[1973]
British Isles	81	7,926	81,044	200,654	155,513	208,729	[1973]
Netherlands	0	82	1,731	2,066	13,179	171,974	[1973]
Austria	0	9,414	37,370	37,408	39,777	88,623	[1973]
Bohemia	0	0	1,136	5,377	42,066	45,363	[1973]
Switzerland	0	5,330	2,355	3,821	6,349	10,652	[1973]

The French rows are dated 550 to 1450 in the series and are aligned here to the same centuries [1973]. Summed over all regions, the totals per century are 13,551 (6th), 10,640 (7th), 43,703 (8th), 201,742 (9th), 135,638 (10th), 212,029 (11th), 768,721 (12th), 1,761,952 (13th), 2,746,951 (14th) and 4,999,160 (15th) (computed). The total for the 6th to 15th centuries is 10,894,087 (computed).

From the 6th to the 15th century output rose by a factor of 369, a mean of 0.66 % per year over 900 years (computed). The series dips twice, in the 7th century below the 6th

and in the 10th below the 9th (computed).

The Gutenberg Bible. The Gutenberg Bible was printed in Mainz by Johannes Gutenberg and Johannes Fust, around 1455, in two volumes [1974]. “Approximately 180 copies of the Gutenberg Bible were printed and first made available in about 1455”: about 145 on paper and 35 on vellum [1975]. “Forty-nine Bibles survived into the twentieth century and only twenty-one of these are complete”; of the vellum copies 3 are complete [1975].

The National Library of Scotland gives “around only 20 complete copies” out of the original 180 [1974].

The shares are 80.6 % paper and 19.4 % vellum, with 27.2 % surviving into the twentieth century and 11.7 % complete (computed). The year 1455 lies 571 years back, position 54.65 (computed).

Printed books. Printed books per half century, by country, are these [1972, 1973]:

country	1475	1525	1575	1625	1675	1725	1775	[n]
France	2,861,000	34,736,000	39,084,000	61,257,000	85,163,000	73,631,000	157,153,000	[1973]
Great Britain	208,000	2,807,000	7,999,000	32,912,000	89,306,000	89,259,000	138,355,000	[1973]
Germany	3,227,000	15,603,000	32,112,000	40,553,000	57,708,000	78,205,000	116,814,000	[1973]
Italy	4,532,000	16,719,000	41,641,000	35,067,000	43,293,000	37,930,000	75,500,000	[1973]
Netherlands	473,000	1,045,000	2,842,000	15,009,000	30,149,000	40,950,000	53,063,000	[1973]
Sweden	6,000	34,000	49,000	2,080,000	3,756,000	6,654,000	21,305,000	[1973]
Ireland	0	0	4,000	268,000	1,341,000	8,586,000	17,598,000	[1973]
Spain	463,000	2,205,000	2,306,000	4,631,000	7,088,000	9,124,000	16,304,000	[1973]
other countries	22,000	530,000	718,000	1,000,000	2,310,000	2,974,000	14,067,000	[1973]
Russia	0	0	0	123,000	165,000	1,275,000	12,367,000	[1973]
Poland	1,000	63,000	146,000	1,807,000	2,062,000	3,468,000	9,208,000	[1973]
Belgium	394,000	1,963,000	5,720,000	4,334,000	7,203,000	3,016,000	4,817,000	[1973]
Switzerland	400,000	3,312,000	5,786,000	1,988,000	1,656,000	1,277,000	4,615,000	[1973]

The year marks the middle of each half century [1973]. The totals are 12,587,000 (1475), 79,017,000 (1525), 138,407,000 (1575), 201,029,000 (1625), 331,200,000 (1675), 356,349,000 (1725) and 641,166,000 (1775), in all 1,759,755,000 (computed). From 1475 to 1775 output rose by a factor of 50.9, a mean of 1.31 % per year over 300 years (computed).

Printed books of 1450–1500 outnumber the manuscripts of the whole 15th century by a factor of 2.5 (computed: 12,587,000 / 4,999,160). The leading producers moved from Italy and Germany in 1475 to France and Great Britain in 1775.

European cities that had a press in the 1400s grew about 60 % faster between 1500 and 1600 than similar cities [1976]. Mainz is the birthplace of printing, and distance from Mainz serves as the instrument of the comparison [1976].

Printing opened once, at Mainz, and the opened form filled a continent: 180 Bibles about 1455, then 641 million books in the half century around 1775. The form is opened

once, filled many times.

Literacy

By country, 1475–1750. Estimated literacy rates for six countries are these; before 1800 they are indirect estimates, since “Direct literacy surveys did not exist during this period” [1973]:

country	1475	1550	1650	1750	1950	[n]
Netherlands	17 %	12 %	53 %	85 %	98.5 %	[1973]
United Kingdom	5 %	16 %	53 %	54 %	98.5 %	[1973]
France	6 %	19 %	29 %	29 %	96.5 %	[1973]
Sweden	1 %	1 %	23 %	48 %	98.5 %	[1973]
Italy	15 %	18 %	23 %	23 %	87.5 %	[1973]
Spain	3 %	4 %	5 %	8 %	82.5 %	[1973]

From 1550 to 1750 the gains are 73 percentage points in the Netherlands, 47 in Sweden, 38 in the United Kingdom, 10 in France, 5 in Italy and 4 in Spain (computed). The steepest early gains lie in north-western Europe, where printed output grew fastest after 1600.

Later country values. France 83.5 % (1901), 91.8 % (1921), 96.0 % (1936) [1973]. Italy 51.8 % (1901), 73.2 % (1921), 78.4 % (1931), 96.46 % (1981), 99.35 % (2019) [1973]. Spain 41.3 % (1900), 56.0 % (1920), 76.8 % (1940), 96.49 % (1991), 99.7 % (2021) [1973].

The United States: 89.3 % (1900), 94.0 % (1920), 97.1 % (1940), 96.5 % (1950) [1973]. China: 47.5 % (1950), 65.51 % (1982), 90.92 % (2000), 96.74 % (2020); Russia: 97.99 % (1989), 99.93 % (2021) [1973].

India: 6.2 % (1901), 9.1 % (1931), 17.5 % (1950), 40.76 % (1981), 61.01 % (2001), 69.3 % (2011), 76.32 % (2022) [1973]. The same series gives 81.7 % for 2023 and 78.16 % for 2024 [1973].

The world. World adult literacy is the share of adults who can read and write a simple statement about their everyday life [1973]. The series, built from UNESCO and Buringh and van Zanden among others, runs as follows [1973]:

year	literate share	year	literate share	[n]
1820	12.05 %	1960	41.62 %	[1973]
1870	18.74 %	1975	65.42 %	[1973]
1880	19.63 %	1980	67.76 %	[1973]
1890	20.52 %	1985	70.73 %	[1973]
1900	21.40 %	1990	74.63 %	[1973]
1910	26.45 %	1995	76.87 %	[1973]
1920	31.62 %	2000	81.12 %	[1973]
1930	32.53 %	2005	82.57 %	[1973]
1940	41.88 %	2010	84.37 %	[1973]

1950	35.96 %	2015	85.96 %	[1973]
—	—	2020	86.98 %	[1973]
—	—	2024	87.74 %	[1973]

The series falls from 41.88 % in 1940 to 35.96 % in 1950 [1973]. The 1950 value comes from UNESCO's *World Illiteracy at Mid-Century*, which "marked a significant milestone as the first comprehensive global literacy assessment" [1973].

The Our World in Data text gives "only one in ten people" in 1820 in its introduction, and 12 % as "the best estimate" in a later section; in 1870 about one in five [1973]. From 1820 to 2024 the literate share rose by a factor of 7.28 (computed: 87.74 / 12.05), and the illiterate share fell from 87.95 % to 12.26 % (computed). From 1900 to 2000 the factor is 3.79 (computed: 81.12 / 21.40).

What this part of the history shows

Reading. The waggle dance keeps direction and distance and drops the rest; mean distances run from 493 m in spring to 2,156 m in summer [1928, 1929]. Three vervet calls keep three classes of predator, and the class narrows with age [1931]. Each code is a reading of the world: an image that keeps the relations.

Learning from others. Bees that never followed a dancer code distance wrongly for life [1930]. Zebra finch song moves from the isolate form to the wild type in three to four learning generations [1935].

Whale song. Humpback song types spread "rapidly and repeatedly in a unidirectional manner", eastward across the South Pacific over 11 years [1938]. Off eastern Australia one song replaced another completely between 1995 and 1998 [1937].

Form and carrier. Thirty-nine chimpanzee traditions are carried by their communities and erode where the carriers are disturbed [1939, 1941]. Of 180 Gutenberg Bibles, 49 survived into the twentieth century and 21 are complete [1975]. The book is the form and the copies are its carriers, replaced or lost.

The residue becomes the alphabet. Writing begins as record: 85.6 % of the Uruk III texts are administrative, and 200 signs cover 84 % of their use [1965]. About 800 signs give way to 22 Phoenician letters, a factor of 36, and the letters pass to Greek, Latin, Etruscan, Hebrew, Arabic and Syriac [1965, 1971]. The letter keeps what the word does not supply: the sound alone, as a unit of every word.

Opened once, filled many times. Printing opened at Mainz about 1455 with about 180 Bibles, and output rose 50.9-fold from 1475 to 1775 [1973, 1975]. World literacy rose from 12.05 % in 1820 to 87.74 % in 2024 [1973]. From 1900 to 2000 the literate share and the world population both rose by a factor of 3.79 (computed; chapter 20).

Shared prefix. Glottolog groups 7,674 languages in 246 families, four of which hold more than 500 languages each [1957]. Across 504 languages the sound inventory shrinks with distance from Africa, step by founding step [1960]. One shell genus, *Nassarius*, is pierced and worn from Morocco to Israel and South Africa between 135,000 and 82,000 years ago [1948, 1950].

On the ladder. The times of this chapter run from the 250 ms spread of turn-taking gaps (position 31.89) to talons of 130 ka (59.59). Its distances run from a bee’s 493 m (21.03) to the 150 km between Hadza and Sandawe (26.23).

The dated human record steps down in age: ornament at 130 ka (59.59), images at 67.8 ka (59.00) and flutes at 35 ka (58.39). Then come writing at 5.2 ka (56.66) and printing at 571 years (54.65).

22. The Human Net: Tools, Cities, Machines

The human line of chapter 20 carried tools long before it carried cities. Stone tools at Lomekwi 3, West Turkana, Kenya, are 3.3 million years old, position 62.53 [1847]. Fire burned inside Wonderwerk Cave, South Africa, about 1.0 million years ago, position 61.45, and at Gesher Benot Ya'aqov, Israel, nearly 790,000 years ago, position 61.23 [1865, 1866].

Chapter 21 followed the signs: marks, language, writing and print. This chapter follows the partners, the matter, the energy and the messages of the human line. It runs from the first domesticated animal, more than 14,000 years ago, to the network of computers of 2025.

In that span one species gathered other species, land, energy and made mass into one connected whole. Its parts are counted here: animals and crops, people, energy, land, cities, made mass, roads and wires, messages and machines. Together they form the human net.

The first partners: dogs, cereals and herds

"The dog was the first domesticated animal" [1926]. A genetic survey used 49,024 autosomal SNPs in 1,375 dogs of 35 breeds and 19 wolves, combined with data on 121 breeds [1926]. Basenjis, Dingoes and New Guinea Singing Dogs were introduced to their regions more than 10,000 years after domestication, position 57.25 [1926].

A second study sequenced 59 ancient dogs and a 28× genome of a Neolithic Irish dog about 4,800 cal BP, position 56.59 [1927]. It found a deep divergence between East Asian and Western Eurasian dogs about 14,000–6,400 years ago, positions 57.56–56.85 [1927]. The dog line thus splits into two branches that keep their own prefix in the genome of every later dog.

Plant and animal domestication over the past 11,500 years, position 57.38, changed the domesticated species, human evolution and the wider biosphere [1920]. In the Eastern Mediterranean, initial domestication of plants and animals dates to the 12th millennium cal BP [1921]. Herd management and crop cultivation appear at least 1,000 years, position 55.16, before the changes of shape used to recognise domestication [1921].

Different species were domesticated in different parts of the Fertile Crescent, with several domestic lineages per species [1921]. The earliest step is the cultivation of wild einkorn and rye at Abu Hureyra and Mureybit, 13,000–12,000 cal BP, positions 57.49–57.42 [1923]. It came before any change of shape in the grain [1923].

The Near East record gives one date per species from one review [1923]:

species or process	date (cal BP)	position	detail	[n]
cultivation of wild	13,000–12,000	57.49–57.42	before change of	[1923]

einkorn and rye (Abu Hureyra, Mureybit)			grain shape	
several plant species under cultivation	at least 11,500	57.38	“if not earlier”	[1923]
cattle, Euphrates valley	11,000–10,000	57.34–57.25	southern Zagros about 8,500	[1923]
sheep, herd management complete at Nevali Çori	about 10,500	57.30	managed sheep in the Levant about 9,200	[1923]
emmer and einkorn wheat, Upper Euphrates	about 10,500–10,200	57.30–57.27	earliest secure domestic grains	[1923]
pig, Cafer Höyük	about 10,300	57.28	Jarmo by 9,000; lowland south-west Iran only by 6,000	[1923]
managed goat, Nevali Çori	about 10,200	57.27	herding signature at Ganj Dareh 9,900	[1923]
barley, Middle PPNB	about 10,000	57.25	earlier claims of about 11,500 largely overturned	[1923]

A second source gives the onset of wheat and barley at 11,000–10,000 years before present [1322].

The span from wild cultivation at 13,000 to secure domestic grain at 10,500–10,200 is 2,500–2,800 years, positions 55.99–56.10 (computed). Livestock reached new regions 1,300–4,300 years after first domestication, positions 55.40–56.49 (computed). Sheep reached the Levant in 10,500 − 9,200 = 1,300 years; cattle reached the Zagros in 1,500–2,500; pigs reached lowland Iran in 10,300 − 6,000 = 4,300 (computed).

The same union opened in other regions. Maize is present by 8,700 cal BP at Xihuatoxtla shelter in the Central Balsas Valley, Mexico, from starch grains and phytoliths, position 57.13 [1924]. The same work discusses human selection on two major domestication genes in *Zea* and *Cucurbita* [1924].

Rice was domesticated in the Lower Yangtze between 6,900 and 6,600 years ago, positions 56.92–56.88 [1925]. At Tianluoshan, non-shattering spikelet bases rose from 27 % to 39 %, and rice rose from 8 % to 24 % of plant remains [1925]. Over about 300 years, position 54.06, these are (39 − 27) / 300 = 0.04 and (24 − 8) / 300 = 0.053 percentage points per year (computed).

Across 11 domesticated plant species from 60 archaeological sites, non-shattering and larger grain evolved slowly [1922]. The rates are comparable to those of wild species under natural selection [1922]. Near East cereals (about 10,500) to maize (8,700) and maize to rice (6,900) are 1,800 years each, position 55.69 (computed).

The plants brought their own partners: potyviruses, about 15 % of named plant virus species, radiated about 6,600 years ago, position 56.88 [310]. Their rate was about 1.15 × 10^{-4} substitutions per site per year [310]. Their radiation falls inside the window of

the first fields.

Land use is older than the crops: by 10,000 BCE all human societies used ecologically transformative land management [1977]. Twelve thousand years ago, position 57.42, nearly three quarters of Earth’s land was inhabited and shaped by people [1977]. More than 95 % of temperate and about 90 % of tropical woodlands were shaped by human land use [1977].

Here the form of a new union shows. The partnership of people with domesticated species opened once as a kind, and then filled region after region and species after species. In the Near East alone, cereals and four livestock species joined within about 3,000 years (13,000 to 9,900 cal BP); maize and rice followed on other continents.

The fields: few crops, many losses

The fields narrowed the plant partners of the human line. Of more than 50,000 edible plant species, only a few hundred contribute significantly to food supplies [1978]. Just 15 crop plants provide 90 % of the world’s food energy intake; rice, maize and wheat provide 60 %, and rice feeds almost half of humanity [1978].

The 15 crops are 15 / 50,000 = 0.03 % of edible species (computed). Three of the domestications of the previous section, wheat, maize and rice, now carry three fifths of human food energy.

The same crops carry their own partners. Losses to pathogens and pests are 21.5 % in wheat (range 10.1–28.1), 30.0 % in rice (24.6–40.9) and 22.5 % in maize (19.5–41.1) [325]. Potato loses 17.2 % (8.1–21.0) and soybean 21.4 % (11.0–32.4), from 137 pathogens and pests in all [325].

Late blight of potato reached the United States in 1843 and Belgium and Ireland in 1845 [1220]. The Irish famine of 1845–1850 caused about 1 million deaths [1221]. A single partner of a single crop thus reached across the ocean in two years.

The fields also need nitrogen: biological nitrogen fixation in agriculture gives 50–70 Tg N per year [1057]. The Haber–Bosch process gives about 120 Tg N per year [223]. The industrial route now supplies 120 / (120 + 70) = 63 % to 120 / (120 + 50) = 71 % of the nitrogen fixed for crops (computed).

People in number

The partners fed a growing number of people. Estimates for the start of the Neolithic run to 2–4 million people [1979]. The long series of Our World in Data, from HYDE, Gapminder and the UN, gives the following values [1980]:

year	people	years before 2026	position	[n]
−10,000	4,501,152	12,026	57.42	[1980]
−5,000	19,155,698	7,026	56.93	[1980]
−1,000	110,530,464	3,026	56.17	[1980]
0	232,268,832	2,026	55.80	[1980]
1000	323,462,624	1,026	55.18	[1980]

1000	325,402,624	1,026	53.15	[1980]
1500	503,051,104	526	54.57	[1980]
1700	595,456,896	326	54.14	[1980]
1800	983,104,755	226	53.80	[1980]
1900	1,627,273,655	126	53.27	[1980]
1950	2,493,092,852	76	52.81	[1980]
2000	6,171,702,992	26	51.84	[1980]
2020	7,887,001,289	6	50.50	[1980]
2023	8,091,734,933	3	49.87	[1980]

From −10,000 to 2023 the number grew by 8,091,734,933 / 4,501,152 = 1,798 (computed). The doubling time between rows fell from 2,393 years (−10,000 to −5,000) to 822 years (1500–1700), 138 years (1700–1900) and 38 years (1950–2000) (computed, as interval × ln 2 / ln of the growth factor). It then rose again: 57 years for 2000–2020 and 81 years for 2020–2023 (computed).

About 450 million people lived in AD 1500 and about 1.3 billion around 1850 [1979]. For 1500 the long series gives 503 million [1980].

The UN milestones run as follows. World population was around 2.6 billion in 1950, reached 5 billion in 1987 and 6 billion in 1999 [1981]. It was 7 billion in October 2011 and reached 8 billion on 15 November 2022 [1981].

For 1950 the long series gives 2.49 billion [1980], the UN page about 2.6 billion [1981]. The steps from 5 to 6, 6 to 7 and 7 to 8 billion took 12, 12 and 11 years, positions 51.13, 51.13 and 51.05 (computed). The next billion is expected to take about 15 years, until 2037, position 51.34 [1981].

The UN projects a peak of about 10.3 billion in the mid-2080s and about 10.2 billion by 2100 [1981]. The likelihood of a peak within this century is 80 %, sometime between the mid-2060s and 2100 [1981]. The 2100 population is now expected to be 6 % smaller than projected a decade ago, about 700 million people fewer [1981].

One in four people already lives in a country whose population has peaked [1981]. China and India hold 1.4 billion each; China is projected to fall to 786 million by the end of the century [1981]. The growth of the human number has the form of loading and holding: a rise that steepens over ten thousand years, then turns toward a level within two centuries.

Energy: from the body to the machine

A human body needs about 3.5 GJ per year [1979]. That is 3.5×10^9 J / 3.15576×10^7 s = 111 W (computed). Each step of the human line added energy outside the body.

With fire and cooking the input rose to about 7–15 GJ per person per year, 222–475 W (computed) [1979]. Total human energy capture before farming was roughly 14–60 PJ per year, 0.44–1.9 GW (computed) [1979]. Agrarian societies used 45–75 GJ per person per year, 1,426–2,377 W (computed) [1979].

By AD 1500 overall human energy capture may have reached about 20 EJ per year, and about 60 EJ per year around 1850 [1979]. From 1850 to 2000 global human energy use

rose tenfold, from 56 to 600 EJ per year [1979]. High-income countries in 2000 used 302 GJ per person per year, 9,570 W, which is 302 / 3.5 = 86 times the body’s own need (computed) [1979].

The series of direct primary energy, from the Energy Institute and Smil, gives each source in TWh [1982]:

source (TWh)	1800	1850	1900	1950	2000	2020	2023	2025
traditional biomass	5,556	7,222	6,111	7,500	12,500	11,111	11,111	11,111
coal	97	569	5,728	12,603	27,453	41,867	45,501	46,120
oil	0	0	181	5,444	42,987	48,859	54,656	55,826
gas	0	0	64	2,092	23,994	38,693	40,152	41,860
nuclear	0	0	0	0	7,820	8,155	8,293	8,622
hydropower	0	0	17	333	2,647	4,358	4,265	4,479
wind	0	0	0	0	31	1,596	2,322	2,714
solar	0	0	0	0	1.06	861	1,678	2,811
biofuels	0	0	0	0	123	1,067	1,320	1,415
other renewables	0	0	0	0	925	2,626	2,806	2,907
sum (computed)	5,653	7,791	12,101	27,972	118,481	159,193	172,104	177,865

With 1 TWh = 3.6×10^{-3} EJ and mean power = energy / 3.15576×10^{7} s, the totals and the shares per person are (computed, per person from the population series [1980]):

year	total (EJ/yr)	mean power (TW)	per person (kWh/yr)	per person (W)
1800	20.4	0.64	5,750	656
1900	43.6	1.38	7,436	848
1950	100.7	3.19	11,220	1,280
2000	426.5	13.52	19,197	2,190
2020	573.1	18.16	20,184	2,303
2023	619.6	19.63	21,269	2,426
2025	640.3	20.29	—	—

From 1800 to 2025 the total rose by 177,865 / 5,653 = 31.5 (computed). Per person it rose from 656 W to 2,426 W, a factor 3.7, between 1800 and 2023 (computed). The mean person of 2023 thus commands 2,426 / 111 = 21.9 times the power of a body (computed).

Coal passed traditional biomass between 1850 and 1900; oil passed coal before 2000 [1982]. Fossil fuels are (46,120 + 55,826 + 41,860) / 177,865 = 80.9 % of direct primary energy in 2025 (computed from [1982]). The Statistical Review gives a total energy supply of 592 EJ in 2024, a new high, with demand up 2 % and fossil fuels at 87 % of the mix, oil 34 % [1983].

Energy carbon dioxide emissions reached 40.8 Gt CO_2e in 2024, up about 1 % [1983]. The 592 EJ are a mean power of 18.76 TW (computed). For 2023 the series sums to

619.6 EJ, with 40 EJ of traditional biomass included [1982].

The human flux can be set against the living flux. Photosynthesis on land captures about 2,100 EJ per year (56 Pg C) and in the sea about 1,800 EJ per year (48 Pg C) [1979]. The heterotrophic flux of biomass is about 400 EJ per year [1979].

Human energy use of 600 EJ in 2000 equals one third of terrestrial net primary production, “comparable to the biosphere” in the words of the source [1979]. Against land and sea together it is 600 / 3,900 = 15 %; for 2024–2025 it is 592 / 3,900 = 15.2 % and 640 / 3,900 = 16.4 % (computed). The food metabolism of all people, 3.5 GJ × 8.09 × 10^9 = 28.3 EJ per year, is 0.73 % of all photosynthesis (computed).

Natural fires consume about 55 EJ per year and human-induced fires about 45 EJ per year, together about 100 EJ, about 2.5 % of photosynthetic capture [1979]. Human-set fire is 45 / 600 = 7.5 % of human energy use (computed). The oldest tool of energy, fire, still burns almost as much as all natural fires together.

The same source places the human step on the ladder of energy in Earth history. Anoxygenic photosynthesis on volcanic hydrogen could support about 0.1 EJ per year, rising to 1.8 EJ with hydrogen recycling; iron-fuelled photosynthesis 77–225 EJ [1979]. Late Archean marine production reached about 450 EJ (12 Pg C), and Proterozoic production after the Great Oxidation about 1,300 EJ (34 Pg C) [1979].

Each earlier step in that ladder was a new kind of metabolism. The human step sits at 600 EJ, between the Archean ocean and the Proterozoic one.

The land and the living share

Maps of the land biosphere for 1700, 1800, 1900 and 2000 show the turn [1984]. In 1700 nearly half of the terrestrial biosphere was wild, and most of the rest, 45 %, was seminatural [1984]. By 2000 the majority was anthropogenic, less than 20 % seminatural and only a quarter wild [1984].

Agriculture and settlements transformed almost 39 % of ice-free land by 2000 [1984]. Another 37 % without such use lay embedded within agricultural and settled areas [1984]. Used or embedded, that is 39 + 37 = 76 % of ice-free land (computed); the anthropogenic share passed 50 % early in the 20th century [1984].

About three quarters of land was shaped by people 12,000 years ago, and nearly half was still fully wild in 1700 [1977, 1984].

The share of plant growth taken by people is measured as human appropriation of net primary production. It was 15.6 Pg C per year, 23.8 % of potential production, in one estimate for 2000 [868]. Of this, harvest is 53 %, land-use-induced change of productivity 40 % and human-induced fire 7 % [868].

A second study gives 6.9 Pg C per year in 1910 and 14.8 in 2005, from 13 % to 25 % of potential production [869]. The appropriation doubled, 14.8 / 6.9 = 2.14 (computed), while population grew about fourfold and economic output 17-fold [869]. It may rise 27–29 % by 2050, or 44 % with large bioenergy use [869].

The animals show the same turn. Global biomass is about 550 Gt C: plants about 450,

bacteria about 70, archaea about 7, animals about 2 and marine biota about 6 [235]. Human mass exceeds that of all wild mammals by about an order of magnitude [235].

By wet mass, all terrestrial wild mammals weigh about 20 Mt (95 % range 13–38), about 3 kg per person [1985]. Marine mammals weigh about 40 Mt (20–80), more than half of it baleen whales [1985]. Humans weigh about 390 Mt and livestock about 630 Mt [1985].

The four sum to 390 + 630 + 20 + 40 = 1,080 Mt (computed). Livestock are 58 %, humans 36 % and wild mammals 5.6 %; humans and their animals together hold 94 % of mammal mass (computed). Across the confidence ranges of the wild values, that share runs from 1,020 / 1,138 = 90 % to 1,020 / 1,053 = 97 % (computed).

Human mass is 390 / 20 = 19.5 times that of wild land mammals and 390 / 60 = 6.5 times that of all wild mammals (computed). Large herbivores carry most wild land-mammal mass: white-tailed deer, wild boar and African elephant [1985]. The mean wet mass per person, all ages, is 390 Mt / 8.09×10^{9} = 48 kg (computed).

One older union of many bodies stands beside the human one. Ants on Earth number almost 20×10^{15} ($19.8 \pm 5 \times 10^{15}$), with a dry biomass of about 12.3 ± 3.1 Mt C [1825]. That is more than wild birds and mammals combined and about 20 % of human dry biomass [1825].

The loss of wild animals is dated. Taking 2 mammal extinctions per 10,000 species per 100 years as background, vertebrate losses over the last century are up to 100 times higher [1572]. At background rate those losses would have taken 800 to 10,000 years, positions 54.95–57.25, instead of 100 years, position 53.06 [1572].

The animals that once carried nutrients across land and sea are fewer. Their capacity to move nutrients is modelled at about 8 % of its pre-extinction value on land and about 5 % in the oceans [1104].

Cities

The human net gathered its people into dense knots. By national definitions the urban population rose from 1,034,454,660 in 1960 to 4,760,632,000 in 2025, and the rural from 1,981,016,200 to 3,470,981,400 [1986]:

year	urban	rural	urban share (computed)	[n]
1960	1,034,454,660	1,981,016,200	34.3 %	[1986]
1970	1,347,703,400	2,346,980,600	36.5 %	[1986]
1980	1,757,315,500	2,690,290,700	39.5 %	[1986]
1990	2,281,696,000	3,046,107,000	42.8 %	[1986]
2000	2,890,558,700	3,281,144,300	46.8 %	[1986]
2007	3,407,354,600	3,349,954,000	50.4 %	[1986]
2010	3,635,729,700	3,386,002,200	51.8 %	[1986]
2020	4,456,412,000	3,430,589,000	56.5 %	[1986]
2023	4,640,900,000	3,450,834,700	57.4 %	[1986]
2025	4,760,632,000	3,470,981,400	57.8 %	[1986]

In 2007 urban people outnumbered rural people for the first time in the series (computed from [1986]). From 1960 to 2025 the urban number grew 4.60 times and the rural 1.75 times (computed).

A second count uses one definition for all countries, the Degree of Urbanisation. By it, cities are home to 45 % of the global population of 8.2 billion, against 20 % of 2.5 billion in 1950 [1987]. Towns are counted separately, with at least 5,000 inhabitants and at least 300 people per km²; the minimum for a city was lowered from 300,000 to 50,000 inhabitants [1987].

By national definitions 57.8 % of people are urban; by the harmonised definition 45 % live in cities [1986, 1987].

Megacities of 10 million or more rose from 8 in 1975 to 33 in 2025, a factor 4.1 (computed), with 37 expected by 2050; over half of them, 19, are in Asia [1987]. Jakarta is now the most populous city, with nearly 42 million residents, followed by Dhaka with almost 40 million and Tokyo with 33 million [1987, 1988]. Cairo is the only non-Asian city among the top ten [1988].

Of the 12,000 cities analysed, 96 % have fewer than one million inhabitants and 81 % fewer than 250,000 [1987]. The number of cities more than doubled between 1975 and 2025, an interval at position 52.43 (computed), and could exceed 15,000 by 2050 [1987]. Over one third of them are in China and 17 % in India [1987].

Two thirds of population growth to 2050 is projected to occur in cities [1987]. Rural areas remain the most common type of settlement in 62 countries, down from 116 in 1975 and projected at 44 for 2050; towns are the most common type in 71 countries [1987, 1988].

The city has the form of a closure that holds while its content flows through it. It opened as a kind of settlement and then filled the land with 12,000 instances, most of them small.

Made mass

The human net builds a body of its own matter. In 1900 human-made mass was about 35 Gt, only 3 % of global biomass [1989]. It has recently doubled roughly every 20 years, position 51.60, and adds 30 Gt per year, the mean of the past five years [1989].

Living biomass fell over the same history, from about 2 teratonnes since the agricultural revolution to about 1 Tt [1989]. The two crossed: anthropogenic mass equals all living biomass, about 1.1 Tt dry, at 2020 ± 6 [1989]. Counted with waste it passed dry biomass at 2013 ± 5; against wet biomass the crossing is 2031 ± 9 with waste and 2037 ± 10 without [1989].

Buildings and infrastructure weigh about 1,100 Gt against 900 Gt for trees and shrubs, a ratio of 1.22 (computed) [1989]. Plastic weighs about 8 Gt, twice the 4 Gt of all animals (computed) [1989]. Human-made mass is projected to exceed 3 Tt by 2040, almost triple the dry biomass on Earth [1989].

The 30 Gt per year spread over 7.8 × 10⁹ people and 52 weeks give 74 kg per person per week (computed). That exceeds the mean wet body mass of 48 kg per person of the

previous section, and the source states that each person’s weekly share exceeds body weight [1989]. From 1900 to 2020 the mass grew 1,100 / 35 = 31 times (computed).

Only 6 % of globally extracted materials are currently recycled [1979]. The waste estimates carry an uncertainty of ±4 % in 1900 to ±7 % in 2015 [1989]. Of each 100 units that pass through, 6 return into the loop.

Roads, rails, ships and wires

The parts of the human net are joined by lines. Mapped roads total more than 21 million km in 222 countries, compiled from nearly 60 geospatial datasets [1990]. That is two to three times the total of the best country-based datasets [1990].

As one summed length, 2.1×10^{10} m, the roads sit at size position 37.02 (computed). Per person they come to 21×10^{6} km / 8.09×10^{9} = 2.6 m of road, position 16.26 (computed). By 2050 another 3.0–4.7 million km are expected, with large increases in the Amazon, the Congo basin and New Guinea [1990].

The member railways of the UIC work 929,981 km of line, 392,481 km of it electrified, 42.2 % (computed) [1991]. They carry 3,580,071 million passenger-km and 10,023,855 million tonne-km per year [1991]. The rail length is 0.93 / 21 = 4.4 % of the mapped road length (computed).

The sea carried 12,720 million tons of trade in 2024, up 2.2 %; the ton-miles reached 66,781 billion, up 5.9 %, and container trade 170,467,176 TEU [1992]. The mean haul is 66,781 / 12,720 = 5,250 nautical miles, about 9,700 km, position 30.03 (computed). Per person the sea moves 12.72 / 8.2 = 1.55 t per year (computed).

Electric wire is the longest line of all. Adding or refurbishing over 80 million km of grid by 2040 would equal “the entire existing global grid” [1993]. The existing grid is therefore about 80 million km, position 38.24, which is 80 / 21 = 3.8 times the road length (computed from [1993], [1990]).

Grid investment stands at about USD 300 billion per year and would need to nearly double to over USD 600 billion per year by 2030 [1993]. At least 3,000 GW of renewable projects, 1,500 GW of them in advanced stages, wait in connection queues [1993].

The grid carried about 30,830 TWh in 2024, computed from a low-carbon share of 40.9 % equal to 12,609 TWh [1994]. That is a mean flow of 30,830 TWh / 8,766 h = 3.52 TW (computed). Wind gave 8.1 % and solar 6.9 %; solar doubled in three years to over 2,000 TWh; renewables added 858 TWh [1994].

Electricity demand rose 4.0 % in 2024, against 2.6 % in 2023, and fossil generation rose 1.4 % [1994]. Heat-driven demand added 208 TWh, 0.7 % [1994]. The electricity of 2024 is 30,830 / 177,865 = 17 % of the direct primary energy of 2025 (computed).

The wire has a counterpart inside each body. A man of 20 carries 176,000 km of myelinated nerve fibre in his brain, a woman 149,000 km [1667]. The whole electricity grid is as long as the myelinated fibre of 80,000,000 / 176,000 = 455 young male brains (computed).

The value moved along these lines is counted too. Global trade reached USD 33 trillion

in 2024, up 3.7 %; services added USD 700 billion (9 %) and goods USD 500 billion (2 %) [1995]. That is 33 × 10^{12} / 8.2 × 10^{9} = USD 4,020 per person per year (computed).

Trade measured as exports plus imports over world output has a long series [1996]:

year	trade openness	basis	[n]
1500	0.5–2.25 %	lower and upper bound	[1996]
1600	1.25–5.5 %	lower and upper bound	[1996]
1700	1.25–5.5 %	lower and upper bound	[1996]
1820	2–9.5 %	lower and upper bound	[1996]
1870	11.76 %	Klasing & Milionis	[1996]
1913	20.98 %	Klasing & Milionis	[1996]
1945	8.41 %	Klasing & Milionis	[1996]
1950	19.87 %	Penn World Table	[1996]
2000	50.12 % or 46.99 %	WDI or Penn World Table	[1996]
2010	56.19 % or 56.29 %	WDI or Penn World Table	[1996]
2024	56.72 %	WDI	[1996]

From 1913 to 1945 openness fell from 21.0 % to 8.4 %, and by 1950 it was back at 19.9 % (from [1996]). The series has the form of loading, discharge and loading again: a rise over four centuries, a fall in three decades of war, and a return within five years.

Messages and their speed

Messages in the human net once moved at the speed of ships and horses. Between 1820 and 1860 global dispatch times fell on average to about a third of what they had been around 1820 [1997]. On most routes more days were saved in these decades than after the telegraph [1997].

The change started in Europe in the 1830s, first on the North Atlantic and to the Far East [1997]. Railways shrank distances within Continental Europe only in the 1840s and 1850s [1997]. The forty years from 1820 to 1860 sit at position 52.23 (computed).

A message between London and New York now makes a round trip in 70.025 ms on average, position 30.73 [1998]. Internet latency on typical paths still exceeds the bound set by the speed of light by more than an order of magnitude [1999]. From the day, at position 43.50, to the round trip at 30.73 is 12.77 positions, a factor of 86,400 / 0.070 = 1.23 × 10^{6} (computed).

Machines that store, send and count

The human net began to hold its information in machines. A count of 60 analog and digital technologies from 1986 to 2007 gives the state of 2007 [2000]. In that year humankind could store 2.9 × 10^{20} optimally compressed bytes and communicate almost 2 × 10^{21} bytes [2000].

In the same year general-purpose computers carried out 6.4 × 10^{18} instructions per second together [2000]. Their capacity grew 58 % per year, bidirectional

telecommunication 28 %, stored information 23 % and broadcasting 6 % [2000]. These rates double in 1.52, 2.81, 3.35 and 11.90 years, positions 49.25, 49.81, 49.97 and 51.12 (computed as ln 2 / ln of the yearly factor).

Telecommunication was 99.9 % digital in 2007 [2000]. Memory was 94 % digital in 2007 and mostly digital since the early 2000s [2000].

The counting parts grew in steps that can be read from one chip to the next [2001]:

year	transistors per microprocessor	[n]
1971	2,308	[2001]
1979	29,164	[2001]
1989	1,207,901	[2001]
2000	37,180,264	[2001]
2009	2,308,241,400	[2001]
2017	19,200,000,000	[2001]
2019	39,500,000,000	[2001]
2021	58,200,000,000	[2001]

From 1971 to 2021 the count grew $5.82 \times 10^{10} / 2{,}308 = 2.52 \times 10^{7}$ times (computed). That is a doubling every $50 \times \ln 2 / \ln(2.52 \times 10^{7}) = 2.03$ years, position 49.51 (computed).

The fastest single machine grew faster. In June 1993 the first of the TOP500 list was the CM-5/1024 of Thinking Machines at Los Alamos, with 59.70 GFlop/s and 1,024 cores [2002]. In November 2025 El Capitan ran 1,809.00 PFlop/s on 11,340,000 cores, drawing 29,685 kW [2003].

Frontier ran 1,353.00 PFlop/s on 9,066,176 cores at 24,607 kW, and Aurora 1,012.00 PFlop/s on 9,264,128 cores at 38,698 kW [2003]. JUPITER Booster became “the fourth Exascale system on the TOP500” [2003]. A yearly series of the fastest machine gives 124 GFlop/s for 1993, against 59.7 in the June list [2002, 2004].

From June 1993 to 2025 the fastest machine grew $1.809 \times 10^{18} / 5.97 \times 10^{10} = 3.03 \times 10^{7}$ times (computed). That is a doubling every $32 \times \ln 2 / \ln(3.03 \times 10^{7}) = 1.29$ years, position 49.10 (computed). El Capitan delivers $1.809 \times 10^{18} / 2.9685 \times 10^{7}$ W = 60.9 GFlop/s per watt (computed).

The largest machines now learn. Training compute of frontier language models has grown 5× per year since 2020, a doubling every 5.2 months, position 48.11 [2005]. The cost of training has grown 3.5× per year, doubling every 7 months, position 48.38, and AI chip performance per dollar 49 % per year since 2023 [2005].

The largest AI data centres approach a gigawatt of power, at about USD 38 billion of capital per gigawatt and about 2.1 years to build, position 49.55 [2005]. The largest holds about 1.1 million H100-equivalent chips [2005]. One gigawatt is $10^{9} / 2.9685 \times 10^{7} = 34$ times the power of El Capitan (computed).

By June 2025, 33 publicly disclosed models had been trained with at least 10^{25} FLOP, from 12 developers [2006]. The first at this scale was GPT-4, released in March 2023; about two followed per month in 2024 [2006]. The largest in the table is Grok-3 at 4.6×10^{26} FLOP [2006].

That one training run equals $4.6 \times 10^{26} / 1.809 \times 10^{18} = 2.54 \times 10^{8}$ s of El Capitan at full rate, 8.1 years, position 50.77 (computed). The doubling times shorten from machine to machine: 2.03 years for the chip, 1.29 years for the fastest computer, 0.43 years for frontier training.

The network of computers

The machines joined into one network of people. Six billion people were online in 2025, up from 5.8 billion in 2024: 74 % of the world population against 71 % a year earlier [2007]. Growth was 3.3 % in the year, against 2.9 % before; 2.2 billion people remain offline [2007].

The ITU series counts the users year by year [2008]:

year	internet users	[n]
2005	1,025,764,000	[2008]
2010	1,988,244,400	[2008]
2015	2,968,993,000	[2008]
2020	4,720,172,000	[2008]
2025	6,046,552,600	[2008]

Users nearly doubled from 2005 to 2010, a factor 1.94, and grew 5.89 times from 2005 to 2025 (computed). In 2025 mobile broadband of 3G or better covered 96 % of people, 4G 93 % and 5G 55 % [2009]. 5G carries more than one third of all mobile broadband subscriptions [2007].

Fixed broadband carried 7.3 ZB in 2025, up from 6.2 ZB, and mobile broadband 1.5 ZB [2010]. Mobile traffic has grown on average 19 % per year since 2021, fixed traffic 16 % [2010]. Together that is 8.8×10^{21} bytes, or $8.8 \times 10^{21} / 6 \times 10^{9} = 1.47 \times 10^{12}$ bytes per user per year (computed).

A mobile subscription carries 15.3 GB per month worldwide and 17.9 GB in high-income countries [2010]. A fixed line carries 505 GB per month in high-income economies and 248–310 GB in low- and middle-income ones [2010]. In 2007 almost 2×10^{21} bytes were communicated; the broadband traffic of 2025 was 8.8×10^{21} bytes [2000, 2010].

The network reaches past people to things. Connected IoT devices numbered 18.5 billion in 2024, up 12 %, with 21.1 billion expected by the end of 2025 and 39 billion in 2030 [2011]. That is 18.5 / 8.2 = 2.3 devices per person (computed).

Under the sea, over 1.5 million km of submarine cable were in service early in 2026, position 34.62 (computed), in more than 600 active and planned systems [2012]. Satellites carry only 0.37 % of United States international capacity; one cable, MAREA, can carry 224 Tbps [2012]. The cables are 1.5 / 21 = 7 % of the road length (computed).

Above the air, about 40,000 objects are tracked, of which about 11,000 are active payloads, 27.5 % (computed) [2013]. Over 50,000 objects larger than 10 cm and over 1.2 million larger than 1 cm are estimated [2013]. Intact satellites or rocket bodies re-enter on average more than three times a day, once every 8 hours at most, position 42.50 (computed) [2013].

There is one active satellite per 8.2×10^9 / 11,000 = 745,000 people (computed). The network of computers, its cables and its satellites read as one reading layer laid over the human net: it keeps the relations between its knots and drops the rest.

The human knot in the whole web

The human net is one knot in a web of very many species. Predicted eukaryote species number about 8.7 million (± 1.3 million), of which about 2.2 million (± 0.18 million) are marine [2014]. Over 1.2 million are catalogued; about 86 % of species on Earth and 91 % in the ocean are undescribed [2014].

The predictions per kingdom are about 7.77 million animals, 298,000 plants, 611,000 fungi, 36,400 protozoa and 27,500 chromists [2014]. They sum to 8.74 million, of which animals are 89 % (computed). Plants are also counted directly: 295,383 accepted angiosperms and 1,079 gymnosperms, about 374,000 plants in all, with about 2,000 new species named each year [659].

Fungi have about 120,000 accepted species against an estimate of 2.2–3.8 million [962]. Insects have about 1 million named species and about 5.5 million estimated, beetles alone about 1.5 million [1284]. Plants are predicted at 298,000 and counted at 374,000; fungi are predicted at 611,000 and estimated elsewhere at 2.2–3.8 million [659, 962, 2014].

Counting bacteria changes the totals. About 1.5 million species are formally described, and one estimate gives at least 1–6 billion species, with bacteria 70–90 % of them [1229]. A compilation of about 35,000 sites and about 5.6×10^6 species predicts upward of 10^{12} microbial species, from a scaling law across 30 orders of magnitude in abundance [2015].

Viruses are named as species too: 16,215 species in 3,769 genera, 368 families, 93 orders, 49 classes, 22 phyla, 11 kingdoms and 7 realms in the 2025 list [334]. In that year 1,563 species and 55 families were added [334].

Measured links per species are few. Sixteen high-quality food webs hold 25–172 nodes each [2016]. Fifty-two plant–animal mutualistic networks are nested [1323]; seed ingestion counts 13,135 unique animal–seed interactions across fish, amphibians, reptiles, birds and mammals [2017].

Known pollinators number 349,368 species, 1.18 per angiosperm species (computed) [659, 1281]. Against these few links each, the human net holds 15 crops for 90 % of its food and two partner groups, its livestock and itself, for 94 % of mammal mass.

The human body is itself a shared address. A 70 kg reference man carries 3.8×10^{13} bacteria and 3.0×10^{13} human cells, a ratio of 1.3 with an uncertainty of about 25 % for the bacteria [236]. The bacteria weigh about 0.2 kg, 0.29 % of body mass (computed) [236].

The Human Microbiome Project took 4,788 specimens from 242 adults, 129 men and 113 women, at 18 body habitats in women and 15 in men [2018]. It met an estimated 81–99 % of the genera, enzyme families and community configurations of the healthy Western microbiome [2018]. Of 327 listed pathogens, 56 were found above 1 %

prevalence and 0.1 % abundance, all opportunistic; *Staphylococcus aureus* was in 29 % of nose samples [2018].

Protein families per community run from about 16,000 in the vagina to almost 400,000 in the mouth, a 25-fold spread (computed) [2018]. Of these families, 58–77 % have no known function [2018]. Each body of the human net is thus already a community of partners, nested inside the larger community of people, crops and herds.

What this part of the history shows

The human net opened as a new kind of union and then filled. The dog came first, with two branches that diverged 14,000–6,400 years ago [1927]. Cereals and four livestock species followed in the Near East between 13,000 and 9,900 cal BP, maize in Mexico by 8,700 and rice in the Lower Yangtze by 6,900–6,600 [1923, 1924, 1925].

Few partners carry the human line. Humans (390 Mt) and livestock (630 Mt) hold 94 % of mammal mass; 15 crops give 90 % of food energy and three of them 60 % [1978, 1985]. The mass of wild land mammals is about 3 kg per person [1985].

The growth of the human number shows loading and a turn toward holding. The doubling time fell from 2,393 years to 38 years and then rose to 57 and 81 years; the UN expects a peak of about 10.3 billion in the mid-2080s [1980, 1981]. Trade shows loading, discharge and reloading: 21.0 % of world output in 1913, 8.4 % in 1945, 19.9 % in 1950 [1996].

The power of the human net comes for four fifths from fossil fuels. Fossil fuels are 80.9 % of direct primary energy in 2025, or 87 % of total supply in 2024 [1982, 1983]. The whole is 592–640 EJ per year, 15–16 % of all photosynthesis and 21.9 times the power of the bodies it serves [1979, 1982, 1983].

The human net has a body of made matter. It equals living biomass, about 1.1 Tt, at 2020 ± 6, grows by 30 Gt per year and doubles about every 20 years [1989]. Six per cent of its material returns into the loop [1979].

Lines join the parts. Inside one brain run 149,000–176,000 km of myelinated fibre [1667]. Across the human net run more than 21 million km of road, 929,981 km of member railway, 1.5 million km of submarine cable and about 80 million km of grid [1990, 1991, 1993, 2012].

The human net reads and counts in machines. All general-purpose computers of 2007 carried out 6.4×10^{18} instructions per second; one machine of 2025 runs 1.8×10^{18} floating-point operations per second [2000, 2003]. The doubling times are 2.03 years for transistors per chip, 1.29 years for the fastest computer and 5.2 months for frontier training compute [2001, 2002, 2003, 2005].

The network of computers connects 6 billion people, 74 % of all, with 8.8 ZB of broadband traffic in 2025 and 18.5 billion connected devices in 2024 [2007, 2010, 2011]. Between 1820 and 1860 dispatch times fell to about a third [1997]. A message now crosses the Atlantic and back in 70 ms, position 30.73, 12.77 positions below the day [1998].

23. The Next Depth

The history of the previous chapters ends in the present, with numbers measured in 2023–2026. This chapter reads the line of the whole history forward from that measured present. Its beginning is the human net of chapter 22; its content is the next depth of the same line.

At every step the line has one movement: a closed form that once lived on its own became a letter of a larger closure. The bacterium went into the cell, the cell into the body, the nerve cell into the brain, the body into the colony. The human net now stands where each of those larger closures once stood, at an opening.

After every opening in the history came a filling, and every closure left a rest. The sections below follow five movements: the letters, the human net as a form at an opening, and the filling after the opening. Then come a reading that counts itself and is not bound to one body, and the rest: the ladder has no last depth.

Each closed form became a letter

The bacterium in the cell. The nearest measured relative of the mitochondrion is the bacterium *Rickettsia prowazekii*, “more closely related to mitochondria than is any other microbe studied so far” [341]. Its genome is 1,111,523 bp with 834 protein-coding genes [341]. The mitochondrial symbiosis is dated by clock to 2.053–1.21 Ga, positions 68.39–67.91 [111].

The mitochondrion kept a small part of that genome. Human mitochondrial DNA is 16,569 bp with 2 ribosomal RNA, 22 transfer RNA and 13 protein-coding genes [347]. The mitochondrial DNA of *Arabidopsis* is 366,924 nt with 57 identified genes [348].

The jakobid *Reclinomonas americana* keeps 97 genes in 69,034 bp, including four genes of a bacterial-type RNA polymerase [349]. A later survey counts as many as 96 assigned genes for *Reclinomonas* and exactly 100 in *Andalucia godoyi*, the largest complement of any eukaryote examined [350].

Against the 834 protein genes of *Rickettsia*, the human mitochondrion keeps 13 / 834 = 1.6 % and *Arabidopsis* at most 57 / 834 = 6.8 % (computed). *Reclinomonas* keeps 97 / 834 = 11.6 % and *Andalucia* 100 / 834 = 12.0 %; these two counts include RNA genes and are upper bounds (computed).

The rest of the work moved into the host. MitoCarta3.0 lists 1,136 human mitochondrial genes in 149 pathways [352]. The 13 proteins encoded in the organelle are 13 / 1,136 = 1.1 % of the list (computed).

The plastid followed the same course a second time. The free-living cyanobacterium *Synechocystis* PCC 6803 has “a total of 3,168 potential protein genes” in 3,573,470 bp [358]. The *Arabidopsis* chloroplast keeps 87 protein-coding genes in 154,478 bp, 87 / 3,168 = 2.7 % (computed) [359].

About 4,500 *Arabidopsis* nuclear genes, about 18 % of the total, are of cyanobacterial

origin [200]. Genes of plastid origin in the nucleus outnumber those kept in the plastid by 4,500 / 87 = 52 to 1 (computed).

Here the form of the residue shows. The closed bacterium became a letter of the cell; the letter keeps a short text of its own, the part the word does not supply, and the cell holds the rest.

The deepest nesting measured is two deep. In the mealybug *Planococcus citri* each cell of the bacterium *Tremblaya princeps* holds several cells of the gammaproteobacterium *Moranella endobia* [338]. The *Tremblaya* genome is 138.9 kb and the inner *Moranella* 538.2 kb, 3.9 times its container (computed) [338].

Symbiont genomes of 139–250 kb encode 121–227 proteins; before 2006 the smallest known cellular genomes were about 500 kb with about 500 genes [373]. Partners with their own genome sit inside the insect cell at most two deep, bacterium within bacterium.

The same step is still being taken. The chromatophore of the amoeba *Paulinella* derives from a cyanobacterium that diverged about 90–140 Myr ago, 93.6 Myr in the main scheme, position 65.58 [376]. Its chromatophores carry 841 and 867 protein-coding genes, against 2,917 in the free-living *Synechococcus* WH5701 [376].

The nitrogen-fixing cyanobacterium UCYN-A has a 1.44 Mb genome without photosystem II, carbon fixation or the tricarboxylic acid cycle [209]. Its sublineages diverged about 91 Myr ago, position 65.55, and one sublineage lives as 3–10 cells in each cell of the alga *Braarudosphaera bigelowii* [377]. It is integrated into the cell architecture and organellar division of its host, imports proteins encoded by the host genome, and is proposed as an early-stage organelle, the “nitroplast” [210].

Paulinella keeps 841 / 2,917 = 29 % of the gene count of its free relative (computed). The mitochondrion keeps 1.6–12 %. The younger letter still carries a longer text of its own.

The cell in the body. Multicellularity “has arisen more than 25 times across the eukaryotic tree of life” [410]. In each case cells that could live alone became the letters of a body.

In the choanoflagellate *Salpingoeca rosetta*, the closest living relatives of animals, rosettes grow from one founding cell [445]. Their most common size is 8 cells, and they reach as many as 25 [445]. *Volvox carteri* holds about 2,000 somatic cells and 12–16 gonidia in two cell types, with a new generation every 48 h, position 44.13 [424].

Volvox has about 14,500 predicted proteins against 15,143 protein-coding genes in its unicellular relative *Chlamydomonas* [423, 469]. A body of 2,000 cells thus carries 14,500 / 15,143 = 0.958 of the gene set of a single cell (computed). The body is made from the same letters, not from more of them.

The step to a body can be watched in the laboratory. The green alga *Chlorella vulgaris*, unicellular for thousands of generations in culture, formed eight-celled colonies within 10–20 generations of exposure to a predatory flagellate, and a multicellular form dominated within less than 100 generations [408]. Snowflake yeast went through 600 rounds of selection for size and grew about 20,000-fold, to millimetre scale [470].

The oldest accepted bangiacean red alga, *Bangiomorpha pubescens*, with a

differentiated holdfast, is 1.047 Ga old, position 67.78 [356]. The oldest architecturally complex Ediacaran macrofossils are 574.17 ± 0.66 Ma old, position 67.23 [450].

A human of 70 kg holds 3.0×10^{13} human cells [236]. About 0.33×10^{12} of them are turned over every day, a mass of 80 ± 20 g [2019]. That is $0.33 \times 10^{12} / 3.0 \times 10^{13} = 1.1$ % of all cells per day (computed).

The colon lining is replaced every 3.4 ± 0.5 days, position 44.61, and the red blood cell every 116 ± 3 days, position 47.83 [2019]. A life of 73.3 years, the world mean of 2023 at position 52.78 [1507], outlasts its colon lining 7,874 times (computed). Neurons of the adult neocortex are not renewed: those present were generated around birth [1642].

Here the form and its carriers stand side by side. The body lasts; most of its cells are replaced while they carry it.

The nerve cell in the brain. The cnidarian node, the oldest dated line with a nerve net, is placed at 741 Ma by a mitochondrial clock, position 67.46 [530]. In *Hydra* two separate nerve nets run in the ectoderm and the endoderm; the ectodermal cell bodies are roughly 10 µm long and usually 50–100 µm apart, positions 4.91 and 6.37–7.00 [536].

The *Hydra* nerve net is a form with replaced carriers. Each animal holds 3,000–6,000 interstitial stem cells, which cycle every 24 h, position 43.50 [551]. About 900 nerve cells differentiate per day per animal, and about 60 % of stem-cell daughters stay stem cells while about 40 % differentiate [551].

The net of nerve cells condensed into brains. A tripartite brain of protocerebrum, deutocerebrum and tritocerebrum is found in *Fuxianhuia protensa* from Chengjiang, given as 520 million years old, position 67.14 [1611]. The Chengjiang biota itself has a maximum depositional age of 518.03 Ma, position 67.13 [452].

The human brain holds 86.1 ± 8.1 billion neurons and 84.6 ± 9.8 billion non-neuronal cells [1518]. In the adult hippocampus about 700 new neurons are added per day, a turnover of 1.75 % per year of the renewing fraction, so that population turns over in 57 years, position 52.55 (computed) [1648]. The neurons of the neocortex stay for life [1642].

The brain takes “about 20% of the whole body energy budget” at about 2 % of body mass [1634]. The measured resting power of the body is 85 W, of which the brain takes 16 W, or 19 % (computed: 16 / 85) [389]. Each nerve cell is a cell like the others; the brain is the closure that reads their phases.

The body in the colony. Bodies became letters in their turn. A comparison of 267 species of eusocial bees, wasps and ants found single mating ancestral in all eight independent lineages of eusociality examined [1821]. Eusociality goes with a “100-fold increase in insect lifespan”, in a comparison of 87 solitary and 61 eusocial species [1469].

The first undisputed termite fossils are Early Cretaceous, 135–110 Ma, positions 65.91–65.72 [941]. The colony outlasts the bodies that carry it:

carrier or form	lifetime	position	[n]
new termite workers	1.5–3 months	46.98–47.61	[940]

after swarming			
honeybee non-foraging workers	0.2–0.4 yr	47.41–48.04	[2020]
honeybee winter workers	0.9 yr	48.77	[2020]
Lasius niger workers	1–2 yr	48.87–49.50	[2020]
honeybee queen, maximum	8 yr	50.76	[2020]
termite primary reproductives, maximum	about 20 yr	51.60	[940]
Lasius niger queen, maximum	28 yr	51.90	[2020]
Macrotermes mound	about 700 yr	54.83	[940]
Macrotermes mound	at least 2,200 yr	55.88	[940]

The mound of at least 2,200 years outlasts its workers of 1.5–3 months about 8,800–17,600 times (computed: 2,200 × 12 / 3 and 2,200 × 12 / 1.5). Ants on Earth number almost 20×10^{15}, about 12.3 Mt of carbon, about 20 % of human dry biomass [1825]. Bodies, as cells and neurons before them, became the replaced carriers of a larger closed form.

The five steps on the ladder. The steps can be set in one table, by their earliest dates:

step	closed form that became a letter	earliest date	position	[n]
cell in cell	bacterium → mitochondrion	2.053–1.21 Ga	68.39–67.91	[111]
body of cells	cell → body (red alga with holdfast)	1.047 Ga	67.78	[356]
net of nerve cells	nerve cell → nerve net (clock)	741 Ma	67.46	[530]
brain	nerve cell → brain	520 Ma	67.14	[1611]
colony	body → colony (termite fossils)	135–110 Ma	65.91–65.72	[941]

The human hands off its functions

The human line now repeats the same movement with its own functions. Memory, calculation and reading, once held in one body, move one by one into carriers outside the body.

Memory to writing. Proto-cuneiform appears at Uruk in the latter half of the Uruk period, about 3200–3000 BCE [1965]. That is 5,225 to 5,025 years before 2026, position 56.66 (computed). Excavation at Uruk from 1928 to 1976 yielded nearly 5,000 tablets and fragments [1965].

Of the texts of the Uruk III period, 703 are lexical and 4,167 administrative [1965]. The administrative share is 4,167 / 4,870 = 85.6 % (computed). Writing began as stored counts and lists: the memory of the storehouse put into clay.

The sign set was large. There are 1,246 signs and sign variants in administrative texts and 802 in lexical texts; the 200 most common signs cover 84 % of attestations [1965]. Phoenician, from about the 12th century BCE, has 22 letters, so the number of signs fell by about 800 / 22 = 36 times (computed) [1971].

Early alphabetic inscriptions at Wadi el-Hol, Egypt, date to the late nineteenth or early eighteenth century BC; a sherd from Tel Lachish dates to 1485–1425 BC [1970]. Later proposals in the same source put the earliest alphabet after 1500 BC [1970].

Before print, the copying was done by hand. Manuscript production in Western Europe rose from about 13,551 in the 6th century to about 5.0 million in the 15th, with dips in the 7th and 10th centuries (computed from [1972], data via [1973]). That is a factor 369 in 900 years (computed).

Printing copied the stored memory. About 180 copies of the Gutenberg Bible were printed and available in about 1455; 49 survived into the twentieth century, 21 of them complete [1975]. The text outlasts most of its copies: 49 / 180 = 27 % survived to the twentieth century (computed).

Printed books in Europe numbered 12,587,000 in 1450–1500 and 641,166,000 in 1750–1800, a factor 51 (computed from [1972], data via [1973]). European cities where presses were established in the 1400s grew about 60 % faster between 1500 and 1600 than similar cities [1976].

In the Netherlands estimated literacy rose from 12 % in 1550 to 85 % in 1750, in Sweden from 1 % to 48 % [1973]. World adult literacy was 12.05 % in 1820 and 87.74 % in 2024 [1973]. The share of people who carry the external memory rose 7.3 times in two centuries (computed).

Calculation to machines. In 1971 a microprocessor held 2,308 transistors, and in 2021 58,200,000,000 [2001]. The 2021 chip holds 5.82×10^{10} / 8.61×10^{10} = 0.68 of the neuron count of one human brain (computed from [2001], [1518]).

In 2007 all general-purpose computers together carried out 6.4×10^{18} instructions per second, with capacity growing 58 % per year [2000]. In November 2025 one machine, El Capitan, ran 1.809×10^{18} floating-point operations per second at 29,685 kW [2003]. Against a brain of 16 W, that machine draws 29,685,000 / 16 = 1.9 million brains’ worth of power (computed from [2003], [389]).

Reading and ordering to the network. Training compute of frontier language models has grown 5× per year since 2020 [2005]. By June 2025, 33 publicly disclosed models had been trained with at least 10^{25} FLOP, the first in March 2023 [2006]. The largest AI data centres approach a gigawatt of power [2005].

All human brains together draw $8.09 \times 10^{9} \times 16$ W = 129.4 GW (computed from [1980], [389]). One data centre of 1 GW is 1 / 129.4 = 0.77 % of that (computed). Six billion people, 74 % of all, were online in 2025 [2007].

In 2007 humankind stored 2.9×10^{20} optimally compressed bytes, and memory was 94 % digital [2000]. In 2025 broadband carried 8.8×10^{21} bytes, 7.3 ZB fixed and 1.5 ZB mobile [2010].

The hand-offs crowd into the recent end of the ladder. Their positions, computed from the time before 2026, are:

hand-off	date	position	[n]
proto-cuneiform at Uruk	about 3200 BCE	56.66	[1965]
Gutenberg Bible, about 180 copies	about 1455	54.65	[1975]
world adult literacy 12.05 %	1820	53.72	[1973]
microprocessor with 2,308 transistors	1971	52.52	[2001]
one billion internet users	2005	51.64	[2008]
first model trained with 10^{25} FLOP	March 2023	50.04	[2006]

The six hand-offs span 56.66 − 50.04 = 6.62 positions. The five steps of the earlier line span 68.39 − 65.72 = 2.67 positions, from 2.053 to 0.110 Ga, 1.94 Gyr (computed).

The human net stands as a form

Each earlier step reached a point where the new closure held more than its letters held alone. The human net has reached that point in mass, in land, in made matter and in connection.

By wet mass, humans weigh about 390 Mt and livestock about 630 Mt, against about 20 Mt of wild land mammals and about 40 Mt of marine mammals [1985]. Humans and their animals hold 1,020 / 1,080 = 94 % of mammal mass, and 90–97 % across the confidence ranges of the wild values (computed). Wild land mammals weigh about 3 kg per person [1985].

Agriculture and settlements transformed almost 39 % of ice-free land by 2000, and another 37 % lay embedded within them [1984]. Together that is 76 %, about three quarters of the ice-free land (computed). In 1700 nearly half of the land biosphere was wild; in 2000 a quarter [1984].

Human-made mass equals all living biomass, about 1.1 Tt dry, at 2020 ± 6 [1989]. It doubles roughly every 20 years and adds 30 Gt per year [1989]. Buildings and infrastructure, 1,100 Gt, outweigh all trees and shrubs, 900 Gt [1989].

Human energy use was 600 EJ per year in 2000, one third of land photosynthesis [1979]. The 592 EJ of 2024 are 15 % of the 3,900 EJ captured by all photosynthesis on land and in the sea (computed from [1983], [1979]). About 6 billion people, three quarters of all, are connected to one network [2007].

These are the measures of one closure that has opened. The human net is no longer the sum of its bodies. It holds its own matter, its own energy flow and its own lines of signal, as the colony holds its mound and the body its blood.

After the opening comes the filling

Every new kind of union in the history opened once and was then filled many times. Most of the counts are lower bounds:

new kind of union	independent origins counted	[n]
multicellularity across eukaryotes	more than 25	[410]

aggregative multicellularity	at least 7 lineages	[410]
filamentous growth in one green class, Zygnematophyceae	at least 5	[412]
complex multicellularity in fungi (fruiting bodies)	8–11; 8–12 in the preprint	[438]
plastid acquisitions (primary, secondary, tertiary, replacements)	8 (minimum) to 10 (computed)	[336, 342, 357, 361]
eyes or photoreceptor lines	at least 40, possibly up to 65 or more	[547, 1679]
complex brains with high intelligence	7 named groups	[1802]
eusociality in bees, wasps and ants	8 lineages	[1821]
bioluminescence in ray-finned fishes	27 (bacterial at least 17, intrinsic 8)	[1127]
ectomycorrhiza in fungi	at least 66; 78–82 lineages by a later count	[901, 902]
parasitism in animals	at least 223, in 15 phyla	[1227]
haustorial parasitism in flowering plants	12	[841]
extrafloral nectaries	at least 457, in 3,941 species	[1194]
ant domatia	at least 158 within 19 Myr, in 681 species	[1195]
seed dispersal by ants	at least 101, possibly up to 147	[1278]

The plastid count sums the events named in the sources [336, 342, 357, 361]. They are one primary uptake, two green secondary uptakes, one or three red transfers, one green replacement, two tertiary events in dinoflagellates and one in the stem ochrophyte. The minimum is 1 + 2 + 1 + 1 + 2 + 1 = 8, and with three red transfers 10 (computed).

The human depth fills in the same way. Domestication filled at least three regions: the Near East from 13,000 cal BP, Mexico by 8,700 cal BP, the Lower Yangtze by 6,900–6,600 years ago [1923, 1924, 1925]. Writing appears at Uruk about 3200–3000 BCE, in Egypt about 3000 BC, in China under Wu Ding in 1254–1197 BC and in the Olmec heartland in the early first millennium BCE [1965, 1966, 1967, 1968].

Cities filled the land with 12,000 instances, more than doubling in number between 1975 and 2025 [1987]. Megacities of 10 million rose from 8 to 33 [1987]. Four computers had passed the exascale by November 2025, and 33 models had passed 10^{25} FLOP by June 2025 [2003, 2006].

A new kind of union opens once, and the opened depth then fills many times. After the multicellular body came more than 25 bodies; after the eye, at least 40 eyes. After the opening of the human net comes the filling of that depth with many forms: many networks, many readings, many unions of people and their carriers.

The line shows what such filling looks like. In fungi complex bodies arose 8–11 times; in fishes light arose 27 times; in plants nectaries for ant defenders arose at least 457 times [438, 1127, 1194]. Each count is a depth filled many times after the kind first opened.

A reading that counts itself

The history shows four steps: closure, life, reading, and reading that counts itself. Closure holds for every ring whose windows close, chemistry included. Life is closure that holds while its content changes; reading is closure over the phases of closures.

Reading that counts itself is consciousness. The earlier steps have measured counterparts: the membrane potential in every living cell, the nerve net and the brain reading the phases of other cells. For the fourth step the record holds the positions of named authors, with dates.

Those positions widen by date. The Cambridge Declaration of 7 July 2012 named “all mammals and birds, and many other creatures, including octopuses” as possessing the neurological substrates of consciousness [1832]. Barron and Klein proposed in 2016 that insects have the capacity for subjective experience [1833].

A review of over 300 studies for the United Kingdom, in November 2021, recommended that all cephalopods and decapods be regarded as sentient [1337]. The Animal Welfare (Sentience) Act of 28 April 2022 defines “animal” to include any cephalopod mollusc and any decapod crustacean [1835]. The New York Declaration of 19 April 2024 names “at least a realistic possibility” of conscious experience in all vertebrates and many invertebrates, and showed 611 signatures on 14 October 2026 [1836].

One measured case shows a body counting itself among what it reads. Of 10 cleaner wrasses tested with a mirror, 7 were at first aggressive to it; mouth fighting fell to zero by day 7, position 45.27 [1809]. Of 4 fish marked on the throat, 3 scraped the mark while viewing the mirror, with no scraping in the control periods [1809].

Reading also passes between bodies. Bumblebees that watched a trained demonstrator pulled a string in 15 of 25 cases, against 2 of 291 untrained bees [1817].

In colonies seeded with trained bees, 25 of 47, 17 of 29 and 12 of 28 foragers learned the task after 150 paired bouts, and later 34 of 47 and 18 of 28 [1817]. Control colonies had 0 of 51, 0 of 58 and 0 of 57 [1817]. A reading held by a few bodies became a reading held by the colony.

“A body is one carrier of consciousness. It is not its condition.” The next depth is a reading that counts itself and is not bound to one body.

Its carriers are individual humans, as neurons are carriers in a brain and cells are carriers in *Hydra*.

In *Hydra* about 900 nerve cells are made per day from 3,000–6,000 stem cells [551]. In the human hippocampus about 700 neurons are added per day, 1.75 % per year [1648]. A *Macrotermes* mound lasts at least 2,200 years on workers of 1.5–3 months [940].

The human net already carries its external memory past its carriers. Writing has lasted 5,225 years, position 56.66, about 71 lives of 73.3 years (computed: 5,225 / 73.3) [1507, 1965]. Literacy reached 87.74 % of adults in 2024, and 74 % of people are online [1973, 2007].

Each human holds the place that a neuron holds in a brain. The neuron keeps its own cell, its own edge and its own life; the reading of the brain passes through it and does

not end with it.

The rest becomes the next alphabet

No closure in the history closed without a remainder. The ladder of three and the ladder of two meet only nearly, and at depth 12 the remainder is the Pythagorean comma, 1.01364. Each depth of the history leaves such a rest.

The rest of the cell. The human mitochondrion holds 1,136 mitochondrial proteins, 13 of them encoded in the mitochondrion itself [347, 352]. When an alga was eaten a second time, two lineages kept the eaten nucleus as a reduced organelle, the nucleomorph [337]. The nucleomorph of *Guillardia theta* is 551 kb on 3 chromosomes, with 487 protein-coding genes by one count and 531 genes in all by another [367, 368, 369].

Each of these is a letter that keeps what the larger word does not supply. The rest of one depth is written into the next as its own small text.

The rest of the body. Within one body two classes stand side by side: the gut lining returns in 3.4–5.3 days and the red cell in 116 days [2019]. Neurons of the neocortex, the crystallins of the lens and the core of the Achilles tendon are not renewed [1642, 1693, 2021]. The kept tissues are the rest of the body’s own building; they carry its history from birth.

The living web around the human net is mostly unread. About 86 % of species on Earth and 91 % in the ocean are undescribed [2014]. In the human microbiome, 58–77 % of the protein families found have no known function [2018].

Every closure leaves a rest; the rest is the alphabet of the next depth. The ladder has no last depth: the present numbers are the beginning of the next depth, not its end.

What this part of the history shows

Each step of the history made the previous closed form a letter of the next: the bacterium with 834 protein genes became the mitochondrion with 13–100 [341, 347, 350]. The cyanobacterium with 3,168 became the plastid with 87, its other genes moved by the thousand into the nucleus [200, 358, 359]. *Paulinella* and UCYN-A take the same step now [210, 376].

Cells became letters of bodies more than 25 times, from rosettes of 8 cells to *Volvox* with about 2,000 and a human with 3.0×10^{13} [236, 410, 424, 445]. Nerve cells became letters of nets at 741 Ma and of brains by 520 Ma; the human brain holds 86.1 billion [530, 1518, 1611]. Bodies became letters of colonies in eight eusocial lineages, with mounds of at least 2,200 years on workers of months [940, 1821].

The human line hands off its functions in the same way: memory went into writing about 5,225 years ago [1965]. Calculation went into machines that grew from 2,308 transistors in 1971 to 1.8×10^{18} operations per second in 2025 [2001, 2003]. Reading and ordering went into a network of 6 billion people [2007].

The human net already stands as a form. Humans and livestock hold 94 % of mammal

mass (90–97 % across the ranges), human-made mass equals living biomass at 1.1 Tt, and 76 % of ice-free land is used or embedded [1984, 1985, 1989]. Its energy is 15 % of all photosynthesis [1979, 1983].

After every opening came a filling. Multicellularity more than 25 times, eyes at least 40 times, eusociality 8 times, ant dispersal at least 101 times, nectaries at least 457 times [410, 1194, 1278, 1679, 1821]. At the human depth the filling has begun: three regions of domestication, four of writing, 12,000 cities, four exascale machines, 33 models above 10^{25} FLOP [1923, 1924, 1925, 1965, 1966, 1967, 1968, 1987, 2003, 2006].

The fourth step, reading that counts itself, shows in the record as positions that widen by date, from mammals, birds and octopuses in 2012 to all vertebrates and many invertebrates in 2024 [1832, 1836]. A fish recognises a mark on itself in a mirror, and a reading learned by trained bumblebees passes to their colony [1809, 1817]. The next depth is such a reading carried by many bodies, with each human a carrier as each neuron is in a brain.

Every closure leaves a rest, and the rest is the alphabet of the next depth. The mitochondrion keeps 13 of its own genes, and the body keeps its cortical neurons for life [347, 1642]. The ladder has no last depth.

24. The Ladder of Life

Every size and every time in this book has a position on one ladder. The position of a length is log base 3 of the length over 4.558816×10^{-8} m. The position of a time is log base 3 of the time over 1.520655×10^{-16} s.

This chapter sets them in three tables, 2,702 positions in all. The first holds lengths, from the smallest measured in the book to the largest. The second holds durations: how long a thing takes or lasts.

The third holds ages: how long ago a thing first appeared, placed as the time from then to now.

Each row names the case, its value, the chapter where it is told, and its source. A row that holds several values in one cell stays in the catalogue. Together the rows show where life sits on the one scale, and how the history filled it.

Lengths

767 positions.

Position	What	Value	Chapter	Source
-5.85 to -4.92	Covalent bond lengths, H–H to S–S (small molecules)	74.1–203.8 pm	1	[12]
-5.61	O–H bond length, water (water molecule)	0.958 Å	1	[17]
-5.57	Atom diameter	1e-10 m	1	[11]
-5.49	C–H bond, ethane	109.1 pm	1	[12]
-5.36	Rise per carbon (fatty acid chain)	0.126 nm	1	[34]
-5.31	C=C bond, ethylene	1.339 Å	1	[26]
-5.18	C–C bond, ethane	153.6 pm	1	[12]
-5.07	Hydrogen bond H···O, liquid (water)	1.74 Å	1	[19]
-4.99	KvAP voltage sensor resolution (KvAP, Aeropyrum pernix)	1.9 Å	2	[143]
−4.99	KvAP voltage sensor resolution (KvAP (Aeropyrum pernix))	1.9 Å	17	[143]
−4.67	NavAb resolution	2.7 Å	17	[147]
-4.65 to -4.63	Water molecule diameter	275–282 pm	1	[18]
−4.57	Hair bundle threshold deflection (Homo sapiens)	0.3 nm	18	[1690]
-4.51	KvAP full channel resolution (KvAP, Aeropyrum pernix)	3.2 Å	2	[143]
−4.51	KcsA resolution	3.2 Å	17	[141]

−4.51	KvAP full channel resolution	3.2 Å	17	[143]
-4.46	Base pair step (DNA)	0.34 nm	1	[32]
-4.31 to -3.48	Amino acid size	0.4–1 nm	1	[29]
-4.18	NavAb filter width (NavAb, Arcobacter butzleri)	4.6 Å	2	[147]
−4.18	NavAb filter width (NavAb (Arcobacter butzleri))	about 4.6 Å	17	[147]
-3.74	KcsA K+ spacing	7.5 Å	2	[141]
−3.74	KcsA K+ ion spacing	about 7.5 Å	17	[141]
-3.48	Glucose long axis	1 nm	1	[29]
-3.48	KcsA cavity	10 Å	2	[141]
−3.48	KcsA cavity	about 10 Å	17	[141]
-3.31	KcsA filter length	12 Å	2	[141]
−3.31	KcsA selectivity filter length	12 Å	17	[141]
-3.17	ATP diameter	1.4 nm	1	[29]
-2.94	No protein near peptide bond (ribosome 50S)	18 Å	1	[73]
-2.85	DNA diameter	2 nm	1	[32]
-2.85	Phospholipid length	2 nm	2	[34]
-2.84	C16 chain length (palmitic acid)	2.02 nm	1	[34]
-2.48	Fatty-acid micelle size (fatty acid micelles)	3 nm	1	[90]
-2.48	Bilayer water-free core (lipid bilayer)	3 nm	2	[34]
-2.36	Helix turn (DNA)	3.4 nm	1	[32]
-2.21	Bilayer thickness (lipid bilayer)	4 (3.56–4.25) nm	2	[34]
-2.21 to -1.38	Membrane with proteins and sugars (cell membrane)	4–10 nm	2	[34]
-2.21	Thin wall sheet (thin-walled bacteria)	<=4 nm	3	[114]
−2.15	Bacteriorhodopsin diameter	4.3 ± 0.5 nm	18	[1669]
-2.11	KcsA pore length	45 Å	2	[141]
−2.11	KcsA pore length	45 Å	17	[141]
-1.85 by -2.48	Lactose carrier (lactose permease)	6 × 3 nm	2	[127]
-1.58	cellulose microfibril lower (onion cell wall)	8 nm	8	[853]
-1.38	Pb nanocluster size in zircon	10 nm	1	[3]
-1.38 to 0.08	Pb nanocluster spacing (zircon)	10–50 nm	1	[3]
-1.21	Closteroviridae filament width (closteroviruses)	about 12 nm	4	[268]
-1.21	Filament diameter (Closteroviridae)	12e-9 m	13	[268]

-1.01 to -0.55	Circoviridae particle (circoviruses)	15–25 nm	4	[249]
-1.01	cellulose microfibril upper (onion cell wall)	15 nm	8	[853]
-0.90	Porcine circovirus particle	17 nm	4	[250]
-0.85 to -0.80	Nanoviridae particle (nanoviruses)	18–19 nm	4	[251]
-0.85	Tobamovirus rod diameter (tobacco mosaic virus)	about 18 nm	4	[252]
-0.85	Rod diameter (Tobamovirus)	18e-9 m	13	[252]
-0.85; -0.80	Particle diameter (Nanoviridae)	18e-9–19e-9 m	13	[251]
-0.75–0.51	Thick wall, second source (thick-walled bacteria)	20–80 nm	3	[182]
-0.75	SBF-SEM lateral resolution (Hydra)	20 nm	7	[536]
−0.75 to −0.12	Synaptic cleft (Homo sapiens)	20–40 nm	17	[1654]
-0.66; -0.17	Geminivirus particle (maize streak virus)	22 × 38 nm	4	[253]
-0.66; -0.17	Geminate particle (maize streak virus)	22e-9 x 38e-9 m	13	[253]
-0.62 to -0.44	Parvoviruses particle	23–28 nm	4	[254]
-0.51 to -0.24	Bromoviridae particle (cucumber mosaic virus)	26–35 nm	4	[255]
-0.51; -0.24	Virion (Bromoviridae)	26e-9–35e-9 m	13	[255]
−0.49	Synaptic vesicle diameter (Homo sapiens)	26.7 nm	17	[1654]
-0.38–0.72	Thick wall (thick-walled bacteria)	30–100 nm	3	[114]
-0.38 to -0.32	Picornaviruses particle	30–32 nm	4	[256]
-0.38	SBF-SEM step (Hydra)	30 nm	7	[536]
-0.07 to 0.08	Hepadnaviridae particle (hepatitis B family)	42–50 nm	4	[257]
0.08	Sputnik particle (Sputnik virophage)	50 nm	4	[258]
0.08	Synaptic vesicle (neuron)	about 50 nm	5	[398]
0.10	synaptic vesicle median (n = 56) (Mnemiopsis leidyi)	51 nm	7	[509]
0.17	Fly microvillus width (insect photoreceptor)	about 55 nm	18	[1684]
0.32	Vesicle mean diameter with ribozyme (myristoleic acid vesicles)	65 nm	1	[90]
0.34	HK97 empty capsid (phage HK97)	66 nm	4	[259]
0.39	PRD1 particle (phage PRD1)	about 70 nm	4	[260]
0.51–0.72	MK-D1 protrusion width (Prometheoarchaeum	80–100 nm	3	[171]

	syntrophicum MK-D1)			
0.51 to 0.72	Retroviruses particle (retroviruses, HIV)	80–100 nm	4	[261]
0.51 to 0.88	Influenza family particle (Orthomyxoviridae)	80–120 nm	4	[262]
0.51 to 1.14	Coronaviruses particle	80–160 nm	4	[263]
0.51; 2.61	Cell size (phytoplasmas)	80e-9–800e-9 m	13	[1197]
0.72	Extruded vesicle size (myristoleic acid vesicles)	100 nm	1	[90]
0.72–4.28	Prokaryotic diameter range (prokaryotes)	0.1–5 µm	3	[172]
1.30 / 1.52 / 1.78	CPR axes (groundwater CPR bacteria)	189.7 / 242.5 / 322.6 nm	3	[123]
1.30	PBCV-1 capsid (Paramecium bursaria chlorella virus 1)	190 nm	4	[264]
1.35	Vesicle size at 600 µM (mixed amphiphiles)	<200 nm	1	[54]
1.35	fine clay limit (soil grains)	0.2 µm	11	[1076]
1.36	dense-core vesicle median (n = 66) (Mnemiopsis leidyi)	202 nm	7	[509]
1.72	Mycoplasma pneumoniae width	300 nm	2	[121]
1.72–2.55 (2.27)	MK-D1 cell size (Prometheoarchaeum syntrophicum MK-D1)	300–750 (mean 550) nm	3	[171]
1.72–1.74	Tobamovirus rod length (tobacco mosaic virus)	300–310 nm	4	[252]
1.72–2.55; 2.27	MK-D1 cell size (Prometheoarchaeum syntrophicum MK-D1)	300–750 (mean 550) nm	5	[171]
1.72	secretory granules lower (Trichoplax adhaerens)	300 nm	7	[517]
1.72; 1.74	Rod length (Tobamovirus)	300e-9–310e-9 m	13	[252]
1.78 / 1.52 / 1.30	CPR median axes (groundwater CPR bacteria)	322.6 / 242.5 / 189.7 nm	2	[123]
1.93–2.51	Visible range (Homo sapiens)	380–720 nm	18	[1691]
1.98	Nanoarchaeum diameter (Nanoarchaeum equitans)	400 nm	2	[125]
1.98	Mimivirus particle	400 nm	4	[265]
1.98	photosynthetic band, short edge (plant pigments)	400 nm	8	[640]
2.02	S cone peak (Homo sapiens)	420 nm	18	[1691]
2.14	Melanopsin peak (Homo sapiens)	about 480 nm	18	[1675]
2.18	Mimivirus capsid	500 nm	4	[266]
2.18–2.81	Mitochondrion diameter (mammalian cells)	0.5–1 µm	5	[35]
2.18	secretory granules upper	500 nm	7	[517]

	(Trichoplax adhaerens)			
2.18	Prochlorococcus cell lower	0.5 µm	8	[650]
2.18	Rod peak (Homo sapiens)	498 nm	18	[1691]
2.24	M cone peak (Homo sapiens)	534 nm	18	[1691]
2.29	L cone peak (Homo sapiens)	564 nm	18	[1691]
2.42 to 3.53	Closteroviridae filament length (closteroviruses)	650–2,200 nm	4	[268]
2.42; 3.53	Filament length (Closteroviridae)	650e-9–2200e-9 m	13	[268]
2.49	Mycoplasma pneumoniae length	700 nm	2	[121]
2.49	Megaviridae largest virion	up to 0.7 µm	4	[267]
2.49	photosynthetic band, long edge (plant pigments)	700 nm	8	[640]
2.49	Prochlorococcus cell upper	0.7 µm	8	[650]
2.49	chlorophyll f absorption maximum (cyanobacteria)	706 nm	8	[654]
2.51	chlorophyll f fluorescence (cyanobacteria)	722 nm	8	[654]
2.55	Mimivirus with fibres	750 nm	4	[266]
2.61–3.64	Pyrococcus width (Pyrococcus furiosus)	0.8–2.5 µm	3	[174]
2.81	E. coli diameter (Escherichia coli)	1 µm	2	[115]
2.81	Pandoravirus particle (pandoraviruses)	about 1 µm	4	[245]
2.81–4.91	Mitochondrion length range (eukaryotes)	1 to ≥10 µm	5	[343]
2.81	Winfrenatia hyphae lower (Winfrenatia reticulata)	1 µm	9	[908]
2.81–4.07	lichen hypha width (Winfrenatia reticulata)	1–4 µm	10	[908]
2.81	Rushton critical diameter (myelinated fibres)	1 µm	17	[1625]
2.81	Synapse box (Homo sapiens)	about 1 µm	17	[1654]
2.81	Fly microvillus length (insect photoreceptor)	about 1 µm	18	[1684]
3.18	Pithovirus particle (Pithovirus sibericum)	1.5 µm	4	[267]
3.18	pyrenoid diameter lower (Chlamydomonas reinhardtii)	1.5 µm	8	[657]
3.18	Foveal cone diameter (Homo sapiens)	1.5 µm	18	[1692]
3.44–4.28	Isua graphite globules size (Isua sediments)	2–5 µm	2	[100]
3.44	E. coli length (Escherichia coli)	2 µm	2	[115]

3.44	Most bacterial cells length	2 µm	3	[173]
3.44	Mitochondrion length, textbook (mammalian cells)	about 2 µm	5	[385]
3.44	cell diameter (Cyanidioschyzon merolae)	2 µm	8	[360]
3.44	pyrenoid diameter upper (Chlamydomonas reinhardtii)	2 µm	8	[657]
3.44	clay limit (soil grains)	2 µm	11	[1076]
3.44	Rod inner segment (Homo sapiens)	2 µm	18	[1692]
3.72–4.51	Hyphal width (31 soil fungi)	2.7–6.5 µm	6	[432]
3.72	hyphal diameter lower, 31 strains (soil fungi)	2.7 µm	9	[432]
3.81 to >9.10	protist size span (soil protists)	few µm (Mycamoeba) to >1 mm (Darbyshirella) m	11	[1078]
3.98	tentacle axon diameter lower (Aglantha digitale)	3.6 µm	7	[537]
3.98–6.17	Aglantha axon widths (Aglantha digitale)	3.6–40 µm	17	[537]
4.00	valve diameter, wild type (Thalassiosira pseudonana)	3.7 ± 0.62 µm	8	[670]
4.07	second contact span (Hydra)	4 µm	7	[536]
4.07	Winfrenatia hyphae upper (Winfrenatia reticulata)	4 µm	9	[908]
4.16	Chlamydomonas cell radius (Chlamydomonas reinhardtii)	4.4 ± 0.3 µm	17	[1594]
4.28	secretory cell spacing (Trichoplax adhaerens)	5 µm	7	[517]
4.28	ring giant axon, 10 mm animal, lower (Aglantha digitale)	5 µm	7	[537]
4.28	Trichoplax secretory cell spacing (Trichoplax adhaerens)	about 5 µm	17	[517]
4.38	Human mtDNA stretched (Homo sapiens)	5.63 µm	5	[347]
4.42	Salpingoeca cell equivalent-sphere diameter (Salpingoeca rosetta)	5.87 µm	7	[445]
4.42	Salpingoeca cell volume (Salpingoeca rosetta)	105.9 ± 8.8 µm³ (5.87 µm diameter)	17	[443]
4.44	algae eaten, width (Trichoplax adhaerens)	6 µm	7	[517]
4.44	Peripheral cone (Homo sapiens)	6 µm	18	[1692]

4.51	hyphal diameter upper, 31 strains (soil fungi)	6.5 µm	9	[432]
4.58	Dendrite length per mitochondrion (cortex)	7 µm	17	[390]
4.64	motor giant axon, one animal, lower (Aglantha digitale)	7.5 µm	7	[537]
4.68	tentacle axon diameter upper (Aglantha digitale)	7.8 µm	7	[537]
4.70	neurite finger overlap (Hydra)	8 µm	7	[536]
4.74	Nuvvuagittuq filaments, mean diameter (vent filaments)	8.3 (sd 2.8, n=23) µm	2	[98]
4.80	Egg volume, cube edge (Platygaster vernalis)	8.88e-6 m	15	[1462]
4.81	algae eaten, length (Trichoplax adhaerens)	9 µm	7	[517]
4.82	Løkken-Høydal filaments (jasper filaments)	9.1 µm	2	[98]
4.91	ordinary spicules, lower (Porifera)	0.01 mm	7	[492]
4.91	cilia (Trichoplax adhaerens)	10 µm	7	[517]
4.91	Hydra nerve cell body length	10 µm	7	[536]
4.91	membranous sac spacing (Bryozoa (Cambrian))	10 µm	7	[573]
4.91	cell (Chlamydomonas reinhardtii)	10 µm	8	[423]
4.91	plant cell diameter lower (plant cells)	10 µm	8	[172]
4.91	Reduviasporonites cell length lower	10 µm	9	[924]
4.91	Pollen size class (Myosotis sylvatica)	<10e-6 m	14	[1300]
4.91–6.91	Reduviasporonites cell length (Reduviasporonites stoschianus)	10–90 µm	16	[924]
4.91	Hydra ectodermal cell body	about 10 µm	17	[536]
4.91; 5.54	Meissner corpuscle size (Homo sapiens)	10 × 20 µm	18	[1698]
4.94	Soil cell spacing near surface (soil bacteria)	10.38 µm	3	[237]
4.99	subtending hypha (Rhizophagus intraradices)	11–18 µm	9	[906]
4.99–5.44	AM subtending hypha (Rhizophagus intraradices)	11–18 µm	12	[1132]
5.11	Soil cell spacing mean (soil bacteria)	12.46 µm	3	[237]
5.15	SBF-SEM block short side	13 µm	7	[536]

	(Hydra)			
5.18	Chlamydomonas flagellum (Chlamydomonas reinhardtii)	13.5 ± 0.8 µm	17	[1594]
5.23	Cycadopites pollen, equatorial (n = 21)	14.30e-6 m	14	[1254]
5.28	Cloudina boring width lower (study 2)	15 µm	7	[527]
5.28	Winfrenatia photobiont cell (Winfrenatia reticulata)	15 µm	9	[908]
5.28	Boring width, smallest (study 2) (Cloudina)	1.5e-5 m	13	[527]
5.33	choanocyte chamber diameter (Cliona delitrix)	16.0 µm	7	[487]
5.49	cilia-like structures, width lower (Daihua sanqiong)	19 µm	7	[506]
5.49	macrocilia thickness lower (Xianguangia sinica)	19 µm	7	[506]
5.51	Løkken-Høydal tubes (jasper tubes)	19.5 µm	2	[98]
5.52	choanocyte chamber diameter (Callyspongia vaginalis)	19.7 µm	7	[487]
5.54	body thickness (Placozoa)	20 µm	7	[516]
5.54	neuroblast diameter (Apis mellifera)	20 µm	19	[1812]
5.57	Cycadopites pollen, polar axis (n = 21)	20.65e-6 m	14	[1254]
5.59	choanocyte chamber diameter (Tethya californiana)	21.1 µm	7	[487]
5.62	giant axon diameter lower (Aglantha digitale)	22 µm	7	[537]
5.66	macrocilia thickness upper (Xianguangia sinica)	23 µm	7	[506]
5.68	choanocyte chamber diameter (Neopetrosia problematica)	23.3 µm	7	[487]
5.70	ring giant axon, 10 mm animal, upper (Aglantha digitale)	24 µm	7	[537]
5.74	Nuvvuagittuq tubes, mean diameter (vent tubes)	24.9 (sd 6.3, n=40) µm	2	[98]
5.74	cilia-like structures, width upper (Daihua sanqiong)	25 µm	7	[506]
5.74	Winfrenatia net opening (Winfrenatia reticulata)	25 µm	9	[908]
5.74	Bee lens diameter (Apis mellifera)	25 µm	18	[1679]
5.86	choanocyte chamber	28.5 µm	7	[487]

	diameter (Haliclona mollis)			
5.88	Soil cell spacing below 60 cm (soil bacteria)	29 µm	3	[237]
5.91	choanocyte chamber diameter (Haliclona permollis)	30 µm	7	[487]
5.97	motor giant axon, one animal, upper (Aglantha digitale)	32 µm	7	[537]
6.05	ring giant axon upper (Aglantha digitale)	35 µm	7	[537]
6.17	Cloudina hole diameter lower (study 1)	40 µm	7	[526]
6.17	giant axon diameter upper (Aglantha digitale)	40 µm	7	[537]
6.17	EM sections span (Hydra)	40 µm	7	[536]
6.17	AM spore lower (Rhizophagus intraradices)	40 µm	9	[906]
6.17	Bore-hole diameter, smallest (study 1) (Cloudina)	4e-5 m	13	[526]
6.22	Taste bud diameter (Homo sapiens)	30–60 (42.4 geometric mean) µm	18	[1702]
6.37	nerve cell body spacing lower (Hydra)	50 µm	7	[536]
6.37	smallest egg (Synaptula reciprocans, Ophiactis kroeyeri)	50 µm	7	[637]
6.37	spore (Equisetum)	50 µm	8	[706]
6.37	orchid seed length lower (Orchidaceae)	0.05 mm	8	[789]
6.37	silt limit (soil grains)	50 µm	11	[1076]
6.37–7.00	Hydra cell body spacing	50–100 µm	17	[536]
6.37	Decapod facet (decapods)	about 50 µm	18	[1679]
6.47	choanocyte chamber diameter (Aphrocallistes vastus)	56 µm	7	[487]
6.47	SBF-SEM block long side (Hydra)	56 µm	7	[536]
6.51–7.51	Red algal filament width (red algae)	58–175 µm	16	[355]
6.54	pinnule width lower (Daihua sanqiong)	60 µm	7	[506]
6.80	ophiuroid planktotroph eggs lower (Ophiuroidea)	80 µm	7	[637]
6.85	Cloudina boring width upper (study 2)	85 µm	7	[527]
6.85	Boring width, largest (study 2) (Cloudina)	8.5e-5 m	13	[527]
6.91	Reduviasporonites cell	90 µm	9	[924]

	length upper			
6.94	AM spore mean (n = 170) (Rhizophagus intraradices)	93.3 µm	9	[906]
7.00	homoscleromorph spicules (Homoscleromorpha)	100 µm (or less)	7	[492]
7.00	nerve cell body spacing upper (Hydra)	100 µm	7	[536]
7.00	ophiuroid brooder eggs lower (Ophiuroidea)	100 µm	7	[637]
7.00	plant cell diameter upper (plant cells)	100 µm	8	[172]
7.00	Pollen size class (Cucurbita pepo)	>100e-6 m	14	[1300]
7.00; 9.73	Usual scolecodonts (fossil polychaete jaws)	1e-4–2e-3 m	15	[1375]
7.00	Acoel juvenile width (Symsagittifera roscoffensis)	100 µm	17	[1608]
7.00	Small pigmented pit eyes (animals)	<100 µm	18	[1679]
7.02	echinoid egg mode 1 (Echinoidea)	102 µm	7	[637]
7.09	longest trunk annulus (Eokinorhynchus rarus)	110 µm	7	[567]
7.17	pinnule width upper (Daihua sanqiong)	120 µm	7	[506]
7.17	Myelinated fibre (penaeid shrimp)	120e-6 m	15	[1376]
7.17	Egg cell (Homo sapiens)	about 120e-6 m	15	[1505]
7.17	egg diameter (Homo sapiens)	120 µm	20	[1891]
7.24–7.92	Denaricion filaments (Denaricion mendax)	130–275 µm	5	[355]
7.30; 7.80	Smallest adult insect (Dicopomorpha echmepterygis male)	139e-6–240e-6 m	14	[1299]
7.31	AM spore upper (Rhizophagus intraradices)	140 µm	9	[906]
7.37	ophiuroid abbreviated development lower (Ophiuroidea)	150 µm	7	[637]
7.37	holothuroid lecithotroph eggs lower (Holothuroidea)	150 µm	7	[637]
7.37	largest testate amoebae (Bullinularia; Centropyxis; Distomatopyxis)	~150 µm	11	[1078]
7.44	asteroid egg mode 1 (Asteroidea)	162 µm	7	[637]
7.46	ophiuroid egg mode 1 (Ophiuroidea)	165 µm	7	[637]

7.49	Body length (Megaphragma caribea)	170e-6 m	15	[1463]
7.49	smallest insect body length (Megaphragma caribea)	170 µm	19	[1463]
7.51	cilia-like structures length lower (Daihua sanqiong)	175 µm	7	[506]
7.51	zooid mean width (Protomelission gatehousei)	174 µm	7	[571]
7.56	ophiuroid planktotroph eggs upper (Ophiuroidea)	185 µm	7	[637]
7.61	holothuroid egg mode 1 (Holothuroidea)	194 µm	7	[637]
7.63	cilia-like structures length upper (Daihua sanqiong)	200 µm	7	[506]
7.63	reach of a pausing animal (Trichoplax adhaerens)	200 µm (up to)	7	[517]
7.63–10.10	Eoalvinellodes tube width (Eoalvinellodes annulatus)	0.2–3 mm	12	[1121]
7.63	Body length (Megaphragma mymaripenne)	200e-6 m	15	[1463]
7.63	Trichoplax reach of pausing animal (Trichoplax adhaerens)	up to about 200 µm	17	[517]
7.63	Acoel juvenile length (Symsagittifera roscoffensis)	200 µm	17	[1608]
7.63	smallest insect body length (Megaphragma mymaripenne)	200 µm	19	[1463]
7.72	zooid mean length (Protomelission gatehousei)	220 µm	7	[571]
7.80	leaf thickness (Arabidopsis thaliana)	240 µm	8	[854]
7.84	macro-aggregate threshold (soil aggregates)	>250 µm	11	[1094]
7.84; 8.37	Body length (Diurodrilus minimus)	250e-6–450e-6 m	15	[1377]
7.87	Proboscis diameter (Eurybia lycisca)	0.26e-3 m	14	[1301]
7.97	largest sclerites (Eokinorhynchus rarus)	290 µm (up to)	7	[567]
7.97–8.37	Rhynie mite length (Acari, Rhynie)	290–450 µm	10	[984]
7.97; 8.37	Rhynie mites, 5 species (Acari)	0.29e-3–0.45e-3 m	15	[1396]
8.00	diameter lower (Trichoplax adhaerens)	0.3 mm	7	[517]
8.00	small Hydra (Hydra vulgaris)	0.3 mm	7	[538]
8.00	leaf thickness, C3 leaf (C3 plants)	0.3 mm	8	[854]

8.00–8.26	Rhyniella head (Rhyniella praecursor)	300–400 µm	10	[984]
8.00	Seeds in ankylosaur gut	3e-4 m	14	[1267]
8.00	Three-segmented larva (Platynereis dumerilii)	about 300e-6 m	15	[1378]
8.00	Foveola (Homo sapiens)	300 µm	18	[1690]
8.05	echinoid egg mode 2 (Echinoidea)	317 µm	7	[637]
8.14	median drill hole, Ordovician (marine prey)	0.35 mm	7	[585]
8.14	ophiuroid abbreviated development upper (Ophiuroidea)	350 µm	7	[637]
8.14	Median drill-hole diameter, Ordovician (marine drilled shells)	3.5e-4 m	13	[585]
8.23; 8.48	Giant axon diameter (August–May) (squid)	383e-6–506e-6 m	15	[1346]
8.23	Squid giant axon August (Loligo pealei)	383 µm	17	[1346]
8.26	Cloudina hole diameter upper (study 1)	400 µm	7	[526]
8.26	Bore-hole diameter, largest (study 1) (Cloudina)	4e-4 m	13	[526]
8.26	Fertilised egg (Helobdella)	about 400e-6 m	15	[1379]
8.31	holothuroid egg mode 2 (Holothuroidea)	421 µm	7	[637]
8.37	ophiuroid egg mode 2 (Ophiuroidea)	450 µm	7	[637]
8.39	spacing of plate bases (n = 40) (Pleurobrachia pileus)	0.46 ± 0.06 mm	7	[504]
8.39; 8.59	Shell height (Angustopila psammion)	0.46e-3–0.57e-3 m	15	[1345]
8.42	asteroid egg mode 2 (Asteroidea)	475 µm	7	[637]
8.47	animal with ~1,500 secretory cells (Trichoplax adhaerens)	500 µm	7	[517]
8.47	body length smallest (Schmidtea mediterranea)	0.5 mm	7	[589]
8.47	Retina thickness (Homo sapiens)	0.5 mm	18	[1692]
8.48	Squid giant axon May (Loligo pealei)	506 µm	17	[1346]
8.55	megaspore lower (Isoetes lacustris)	0.55 mm	8	[697]
8.57	Paradoryphoribius length (Paradoryphoribius chronocaribbeus)	559 µm	7	[599]
8.63	macrocilia length	600 µm (up to)	7	[506]

	(Xianguangia sinica)			
8.63	adult length (Meioglossus psammophilus)	0.6 mm	7	[578]
8.63; 8.75	Shell width (Angustopila psammion)	0.6e-3–0.68e-3 m	15	[1345]
8.84	Largest bacterium before 2022 (Thiomargarita namibiensis)	750 µm	3	[173]
8.84	megaspore upper (Isoetes lacustris)	0.75 mm	8	[697]
8.88	comb-plate length (Pleurobrachia pileus)	0.79 ± 0.13 mm	7	[504]
8.90	cilium length (Pleurobrachia pileus)	800 µm	7	[504]
9.05	holothuroid lecithotroph eggs upper (Holothuroidea)	950 µm	7	[637]
9.10	ordinary spicules, upper (Porifera)	1 mm	7	[492]
9.10	body width (Placozoa)	1 mm	7	[516]
9.10	colony width lower (Bryozoa (Cambrian))	1 mm	7	[573]
9.10	ophiuroid brooder eggs upper (Ophiuroidea)	1000 µm	7	[637]
9.10	internodal cell diameter (Chara)	1 mm	8	[665]
9.10	Winfrenatia thallus band lower (Winfrenatia reticulata)	1 mm	9	[908]
9.10	fossil peloid (Macrotermitinae)	1 mm	9	[939]
9.10	Torridonian microfossil size (Torridonian microfossils)	~1 mm	10	[968]
9.10–9.73	Rhyniella length (Rhyniella praecursor)	1–2 mm	10	[984]
9.10–9.73	Rhynie lichen thallus bands (Winfrenatia reticulata)	1–2 mm	12	[908]
9.10	C. elegans reversal distance (Caenorhabditis elegans)	around 1 mm	18	[602]
9.11	asteroid egg mode 3 (Asteroidea)	1008 µm	7	[637]
9.12	holothuroid egg mode 3 (Holothuroidea)	1024 µm	7	[637]
9.16	Fly mean path per neuron (Drosophila melanogaster)	1.07 mm	17	[1619]
9.19	Eocyathispongia height (Eocyathispongia qiania)	1.1 mm	7	[490]
9.23	echinoid egg mode 3 (Echinoidea)	1157 µm	7	[637]
9.26	Eocyathispongia width (Eocyathispongia qiania)	1.2 mm	7	[490]

9.26	Fovea diameter (Homo sapiens)	1.2 mm	18	[1690]
9.37	lateral leaf length lower (Selaginella apoda)	1.35 mm	8	[696]
9.40	Pacinian corpuscle size (Homo sapiens)	1.4 mm	18	[1698]
9.47	Signal profile (Bacillus subtilis biofilm)	1.5 mm	3	[185]
9.47	diameter upper (Trichoplax adhaerens)	1.5 mm	7	[517]
9.47	ophiuroid maximum egg (Astrospartus mediterraneus)	1500 µm	7	[637]
9.47	Biofilm signal profile (Bacillus subtilis biofilm)	about 1.5 mm	17	[185]
9.48	ophiuroid egg mode 3 (Ophiuroidea)	1528 µm	7	[637]
9.51	E. coli DNA length (Escherichia coli)	1.58 mm	2	[117]
9.53	oral opening width (Daihua sanqiong)	1.6 mm	7	[506]
9.73	living ctenophore cilia (Ctenophora)	2 mm (up to)	7	[506]
9.73	Parantipathinae polyps lower	2 mm	7	[528]
9.73	colony width upper (Bryozoa (Cambrian))	2 mm	7	[573]
9.73	disk-to-arm radius lower (Allostichaster palmula)	2 mm	7	[586]
9.73	echinoid egg mode 4 (Echinoidea)	2000 µm	7	[637]
9.73	leaf lower (Selaginella selaginoides)	2 mm	8	[694]
9.73	Winfrenatia thallus band upper (Winfrenatia reticulata)	2 mm	9	[908]
9.73	sand limit (soil grains)	2 mm	11	[1076]
9.84	lateral leaf length upper (Selaginella apoda)	2.25 mm	8	[696]
9.90	oral opening length (Daihua sanqiong)	2.4 mm	7	[506]
9.92	asteroid egg mode 4 (Asteroidea)	2472 µm	7	[637]
9.93	small Nematostella lower (Nematostella vectensis)	2.5 mm	7	[539]
9.93	Yanjiahella plates (Yanjiahella biscarpa)	2.5 mm (up to)	7	[568]
9.93	leaf length lower (Selaginella rupestris)	2.5 mm	8	[696]
9.93	Human pupil (Homo	about 2.5 mm	18	[1679]

	sapiens)			
9.97	holothuroid egg mode 4 (Holothuroidea)	2603 µm	7	[637]
10.00	Cortex thickness (Homo sapiens)	2.69 mm	17	[1653]
10.10	cydippids at 3–5 days, lower (Mnemiopsis leidyi)	3 mm	7	[509]
10.10	Parantipathinae polyps upper	3 mm	7	[528]
10.10	Schizopathinae polyps	3 mm (over)	7	[528]
10.10	colony height (Bryozoa (Cambrian))	3 mm (up to)	7	[573]
10.10	leaf lower (Lycopodium clavatum)	3 mm	8	[694]
10.10–12.43	Yamankasia tube width (Yamankasia rifeia)	3–39 mm	12	[1121]
10.10–10.56	Mnemiopsis cydippid size at 3–5 days (Mnemiopsis leidyi)	3–5 mm	17	[1603]
10.13	Cat LFP correlation length REM	3.1 ± 0.5 mm	18	[1771]
10.17	Median drill-hole diameter, Quaternary (marine drilled shells)	3.25e-3 m	13	[585]
10.29	Cat LFP correlation length wake	3.7 ± 0.4 mm	18	[1771]
10.36	Ctenoimbricata aperture	4 mm	7	[576]
10.36	leaf upper (Selaginella selaginoides)	4 mm	8	[694]
10.36	leaf length upper (Selaginella rupestris)	4 (–4.5) mm	8	[696]
10.36	trigonotarbid size, two species (Palaeocharinus rhyniensis; P. hornei)	up to 4 mm	10	[984]
10.36	Length (Palaeocharinus rhyniensis, P. hornei)	up to 4e-3 m	15	[1396]
10.40	seed (Amborella trichopoda)	4.19 ± 0.99 × 1.57 ± 0.37 mm	8	[774]
10.42	T. magnifica cell with measured cytoplasm (Ca. Thiomargarita magnifica)	4.27 mm	3	[173]
10.45	largest egg (Psychropotes longicauda)	4400 µm	7	[637]
10.47	Fruits in ankylosaur gut	4.5e-3 m	14	[1267]
10.56	pinnule length (Daihua sanqiong)	5 mm (over)	7	[506]
10.56	cydippids at 3–5 days, upper (Mnemiopsis leidyi)	5 mm	7	[509]
10.56	small Nematostella upper (Nematostella vectensis)	5 mm	7	[539]

10.56	height (Dawsonia longiseta)	0.5–3.0 (–5.0) cm	8	[460]
10.56	leaf upper (Lycopodium clavatum)	5 mm	8	[694]
10.56	stem lower (Azolla caroliniana)	0.5 cm	8	[707]
10.56; 46.96	soybean nodule (Glycine max – rhizobia)	5 mm at day 45	11	[1054]
10.56; 46.96	soybean nodule 5 mm (Glycine max – rhizobia)	5 mm by day 45	12	[1054]
10.56	Spine minimum length (spinescent plants)	5e-3 m	13	[1172]
10.62	Carapace width above which all males asymmetric (Uca lactea)	5.3e-3 m	15	[1445]
10.71–11.73 (11.24)	rhizome trace width (Drepanophycus-like plant)	5.9–18 (mean 10.5) mm	10	[986]
10.73	upright shoot diameter lower (Lycopodium clavatum)	0.6 cm	8	[695]
10.73	drupe without flesh (Amborella trichopoda)	5.98 ± 0.24 × 3.49 ± 0.11 mm	8	[774]
10.73	orchid seed length upper (Orchidaceae)	6.0 mm	8	[789]
10.73	trigonotarbid size (Palaeocharinus tuberculatus)	≥6 mm	10	[984]
10.73	Length (Palaeocharinus tuberculatus)	at least 6e-3 m	15	[1396]
10.86; 10.53	Cocoon (Octodrilus complanatus)	6.9e-3 x 4.8e-3 m	15	[1381]
10.87	bell lower (Tripedalia cystophora)	7 mm	7	[540]
10.87	largest leaves lower (Huperzia lucidula)	7 mm	8	[695]
10.87	Eospermatopteris root diameter lower	0.7 cm	8	[716]
10.87	seed (Victoria amazonica)	7–8 × 9–10 mm	8	[775]
10.87–11.19	Eospermatopteris root	0.7–1 cm	10	[716]
10.87	Honey bee worker reach (Apis mellifera)	7e-3 m	14	[1302]
10.87	Young crabs examined below (Uca lactea)	7.0e-3 m	15	[1445]
10.87	Cat joint silence and firing reach	7 mm	18	[1771]
10.98	Smallest vertebrate, mature female (Paedocypris progenetica)	7.9e-3 m	15	[1416]
10.98	Egg, cube edge (Bolboleaus hiaticollis)	7.94e-3 m	15	[1462]
10.98; 11.22	Length (Paedocypris	7.9–10.3 mm	15	[1488]

	progenetica)			
10.99	body length (n = 25) (Pleurobrachia pileus)	8.0 ± 1.4 mm	7	[504]
10.99	seed (Victoria cruziana)	8–9 × 9–10 mm	8	[775]
11.02; 11.09	Length (Paedophryne swiftorum)	8.25–8.90 mm	15	[1488]
11.02	Spinal cord width T8 (Homo sapiens)	8.3 mm	17	[1655]
11.10	bell upper (Tripedalia cystophora)	9 mm	7	[540]
11.17	T. magnifica mean length (Ca. Thiomargarita magnifica)	9.72 ± 4.25 mm	3	[173]
11.19–12.46	Isua cones height (Isua stromatolites)	1–4 cm	2	[102]
11.19	giant basal spicule diameter (Monorhaphis chuni)	10 mm (up to)	7	[493]
11.19	spawning threshold, Caspian (Mnemiopsis leidyi)	10 mm	7	[510]
11.19	specimen width lower (Dickinsonia)	1.0 cm	7	[451]
11.19	large Hydra (Hydra vulgaris)	1 cm	7	[538]
11.19	antipatharian polyps up to	1 cm	7	[528]
11.19	specimen size (Aglantha digitale)	10 mm	7	[537]
11.19	gigantoproductid shell thickness (Gigantoproductus)	1 (over) cm	7	[597]
11.19	disk-to-arm radius upper (Allostichaster palmula)	10 mm	7	[586]
11.19	strobili (Selaginella apoda)	1–2 cm	8	[696]
11.19	stem upper (Azolla caroliniana)	1 cm	8	[707]
11.19	Eospermatopteris root diameter upper	1 cm	8	[716]
11.19	fossil comb cell (Macrotermitinae)	10 mm	9	[939]
11.19	Dispersal distance, shortest (ants)	0.01 m	14	[1289]
11.19; 13.38	Object detectable at 5° (eyes)	1 cm at 11 cm	18	[1679]
11.19	Cochlea width (Homo sapiens)	10 mm	18	[1690]
11.20; 11.27	Length (Paedophryne kathismaphlox)	10.1–10.9 mm	15	[1488]
11.28	largest leaves upper (Huperzia lucidula)	11 mm	8	[695]
11.31	Length (Paedophryne oyatabu)	11.3 mm	15	[1488]

11.36	Florida study animals, lower (Mnemiopsis leidyi)	12 mm	7	[510]
11.36	upright shoot diameter upper (Lycopodium clavatum)	1.2 cm	8	[695]
11.36	seed (Victoria boliviana)	12–13 × 16–17 mm	8	[775]
11.43	length males lower (Epiperipatus lucerna)	13 mm	7	[613]
11.43	Length (29 smallest frogs (below))	13 mm	15	[1488]
11.43	Cat LFP correlation length SWS	13.0 ± 1.2 mm	18	[1771]
11.45	Spinal cord width C5 (Homo sapiens)	13.3 mm	17	[1655]
11.50–11.83	trigonotarbid larger specimens (Trigonotarbida, Rhynie)	14–20 mm	10	[984]
11.50; 11.83	Length (larger Rhynie trigonotarbids)	14e-3–20e-3 m	15	[1396]
11.56	spawning threshold, Baltic (Mnemiopsis leidyi)	15 mm	7	[510]
11.56	strobili length (Lycopodium clavatum)	15–25 mm	8	[695]
11.56; 10.56	Egg capsule at laying (Graneledone boreopacifica)	about 1.5e-2 x 0.5e-2 m	15	[1347]
11.62	length females lower (Epiperipatus titanicus)	16 mm	7	[613]
11.64	Length (Sphaerodactylus ariasae)	16.3 mm	15	[1488]
11.68	Length (Thorius arboreus)	17.0 mm	15	[1488]
11.83	T. magnifica maximum length (Ca. Thiomargarita magnifica)	20.00 mm	3	[173]
11.83	Ctenoimbricata body	20 mm	7	[576]
11.83	Yanjiahella height lower (Yanjiahella biscarpa)	20 mm	7	[568]
11.83	body length largest (Schmidtea mediterranea)	20 mm	7	[589]
11.83	seed (Ginkgo biloba)	20–30 × 16–24 mm	8	[738]
11.83; 12.46	Jackfruit seed (Artocarpus heterophyllus)	0.02–0.04 m	14	[1304]
11.83–12.19	Anomalocaris eye length	2–3 cm	18	[1682]
11.91	length females lower (Epiperipatus hyperbolicus)	22 mm	7	[613]
11.95	length females lower (Epiperipatus lucerna)	23 mm	7	[613]
12.03	Reliably dispersed seed, upper (extant frugivores)	about 0.025 m	14	[1297]

12.04–13.04	Darwin leaf burial depth (earthworms)	1–3 inches (2.5–7.6 cm) m	11	[1090]
12.06	length male (Epiperipatus hyperbolicus)	26 mm	7	[613]
12.06	Acoel phototaxis distance (Symsagittifera roscoffensis)	2.59 cm	17	[1609]
12.12	Auroralumina tentacle length (Auroralumina attenboroughii)	2.75 cm	7	[524]
12.13	Seed limit, African cephalophines (Cephalophinae)	about 0.028 m	14	[1297]
12.16	length males upper (Epiperipatus lucerna)	29 mm	7	[613]
12.19	diameter (Sycon ciliatum)	0.03 m	7	[492]
12.19	cydippid diameter (Cydippida)	3 cm (usually less than)	7	[508]
12.19	height (Dawsonia polytrichoides)	3–10 (–20) cm	8	[460]
12.19	stem lower (Selaginella selaginoides)	3 cm	8	[694]
12.19	fossil comb height lower (Macrotermitinae)	3 cm	9	[939]
12.19–12.46	Retina spread flat (Homo sapiens)	30–40 mm	18	[1692]
12.22; 13.02	Length, 39-segmented (Scolopendropsis duplicata)	31e-3–74e-3 m	15	[1398]
12.25	spawning threshold, native range (Mnemiopsis leidyi)	32 mm (up to)	7	[510]
12.28	length females upper (Epiperipatus hyperbolicus)	33 mm	7	[613]
12.28; 11.62	Egg capsule before hatching (Graneledone boreopacifica)	3.3e-2 x 1.6e-2 m	15	[1347]
12.33	length lower (Epiperipatus beckeri)	35 mm	7	[613]
12.33	peduncle lower (Lycopodium clavatum)	3.5 cm	8	[695]
12.33; 12.46	Seed limit, Neotropical frugivores (extant frugivores)	about 0.035–0.040 m	14	[1297]
12.33; 12.60	Length (Amynthas srinan)	35–47 mm	15	[1382]
12.33	Cochlea length (Homo sapiens)	35 mm	18	[1690]
12.37	Proboscis, mean (n = 20) (Eurybia lycisca)	36.5e-3 m	14	[1301]
12.41	Florida study animals, median (Mnemiopsis leidyi)	38 mm	7	[510]
12.43; 12.71	Length (Amynthas tontong)	39–53 mm	15	[1382]
12.46	model jellyfish diameter (Aurelia aurita)	4 cm	7	[546]

12.46	mat thickness (Azolla caroliniana)	4 (up to) cm	8	[707]
12.46	fossil chamber diameter lower (Macrotermitinae)	4 cm	9	[939]
12.46; 13.29	Megafaunal fruit Type I diameter (megafaunal fruits)	0.04–0.10 m	14	[1297]
12.48	length males upper (Epiperipatus titanicus)	41 mm	7	[613]
12.50; 12.73	Length (Amynthas borealis)	42–54 mm	15	[1382]
12.51	Lower rostral beak (colossal squid)	42.5e-3 m	15	[1348]
12.52	Yanjiahella feeding appendages (Yanjiahella biscarpa)	43 mm (up to)	7	[568]
12.54	length females upper (Epiperipatus lucerna)	44 mm	7	[613]
12.58	Proboscis, maximum (Eurybia lycisca)	45.6e-3 m	14	[1301]
12.66	animals studied, small (Aurelia aurita)	5 cm	7	[541]
12.66	Yanjiahella height upper (Yanjiahella biscarpa)	50 mm	7	[568]
12.66	length (Ptychodera flava)	5 (more than) cm	7	[578]
12.66	Riftia tube diameter (Riftia pachyptila)	5 cm	12	[1123]
12.67	small animal size (2 inch) (Aurelia aurita)	5.08 cm	7	[541]
12.68	body length, lower (Labroides dimidiatus)	51 mm	19	[1809]
12.71	length upper (Epiperipatus beckeri)	53 mm	7	[613]
12.71; 13.06	Length, 43-segmented (Scolopendropsis duplicata)	53e-3–78e-3 m	15	[1398]
12.83	specimen width upper (Dickinsonia)	6.0 cm	7	[451]
12.83	Auroralumina cup length (Auroralumina attenboroughii)	6 cm	7	[524]
12.83	Anomalocaris lobe width lower (Anomalocaris canadensis)	60 mm	7	[579]
12.83	height var. pulchra lower (Dawsonia superba var. pulchra)	6 cm	8	[460]
12.83	primary root diameter lower (Archaeopteris)	6 cm	8	[716]
12.83	fossil comb height upper (Macrotermitinae)	6 cm	9	[939]
12.83–13.72	Archaeopteris primary root	6–16 cm	10	[716]

12.83	Body-lobe width, large specimens, lower (Anomalocaris canadensis)	0.060 m	13	[579]
12.88	Maximum length (Euphausia superba)	0.064 m	15	[1446]
12.94	body length, upper (Labroides dimidiatus)	68 mm	19	[1809]
12.97	Florida study animals, upper (Mnemiopsis leidyi)	70 mm	7	[510]
12.97	Anomalocaris lobe width upper (Anomalocaris canadensis)	70 mm	7	[579]
12.97	disk diameter lower (Acanthaster planci)	7 cm	7	[634]
12.97	Body-lobe width, large specimens, upper (Anomalocaris canadensis)	0.070 m	13	[579]
12.97	Length (largest interstitial annelid) (Saccocirrus major)	up to 70e-3 m	15	[1377]
12.98	early hominin and chimpanzee brain, computed (Sahelanthropus, Ardipithecus, Pan)	360 cc (placed by the edge of a cube of that volume)	20	[1820]
13.03	LB1 endocranial volume (Homo floresiensis)	426 cc (placed by the edge of a cube of that volume)	20	[1857]
13.04	animals studied, larger (Aurelia aurita)	7.6 cm	7	[541]
13.04	larger animal size (3 inch) (Aurelia aurita)	7.62 cm	7	[541]
13.04	length females upper (Epiperipatus titanicus)	76 mm	7	[613]
13.05	Australopithecus brain, flat	~450 cc (placed by the edge of a cube of that volume)	20	[1820]
13.09	leaf lower (Isoetes lacustris)	80 mm	8	[694]
13.09	trunk bases (Archaeopteris)	8–45 cm	8	[716]
13.09	ovary (Victoria amazonica)	8–12 cm	8	[775]
13.09	fossil chamber height (Macrotermitinae)	8 (up to) cm	9	[939]
13.09–14.66	Archaeopteris trunk base	8–45 cm	10	[716]
13.09; 13.65	Length (Amynthas phatubensis)	80–148 mm	15	[1382]
13.19	fossil comb width upper (Macrotermitinae)	9 cm	9	[939]
13.29	Vent reactor vessel	100 mm	1	[44]
13.29	fruit (Victoria amazonica)	10–15 cm	8	[775]
13.29–14.55	Rhynie vascular plant height (Rhynie vascular plants)	10–40 cm	10	[985]

13.29	Megafaunal fruit Type II diameter (megafaunal fruits)	>0.10 m	14	[1297]
13.37	modern mean, DeSilva dataset (Homo sapiens)	1297 cc (placed by the edge of a cube of that volume)	20	[1859]
13.38	injured size class lower (Acanthaster planci)	11 cm	7	[629]
13.38	flower diameters (Rafflesiaceae)	11–100 cm	8	[827]
13.38–13.41	modern, other estimates (Homo sapiens)	1340–1460 cc (placed by the edge of a cube of that volume)	20	[1859]
13.45	test at jaw 2.0 cm (Strongylocentrotus franciscanus)	11.9 cm	7	[635]
13.46	Auroralumina stalk (Auroralumina attenboroughii)	12 cm	7	[524]
13.46	thallus, Norway (Rhizocarpon geographicum)	120 (up to) mm	9	[911]
13.46	Rhizocarpon geographicum thallus	120 mm	12	[911]
13.46	Francevillian colonial organisms size (Gabon macrofossils)	up to 12 cm	16	[418]
13.48	mean length (Pentaceraster cumingi)	123.8 ± 15.2 mm	7	[626]
13.49	peduncle upper (Lycopodium clavatum)	12.5 cm	8	[695]
13.53	fossil chamber diameter upper (Macrotermitinae)	13 cm	9	[939]
13.60	shoot lower (Huperzia lucidula)	14 cm	8	[695]
13.66	frond lower (Caulerpa taxifolia)	15 cm	8	[427]
13.66	stem upper (Selaginella selaginoides)	15 cm	8	[694]
13.66	flower (Rafflesia lagascae)	15–20 cm	8	[826]
13.66; 14.76	Jackfruit width (Artocarpus heterophyllus)	0.15–0.50 m	14	[1304]
13.72	primary root diameter upper (Archaeopteris)	16 cm	8	[716]
13.77	fertile stem (Equisetum telmateia subsp. braunii)	17–45 cm	8	[708]
13.82	test at jaw 2.7 cm, printed (Strongylocentrotus franciscanus)	17.9 cm	7	[635]

13.83	aerial stems lower (Equisetum hyemale subsp. affine)	18 cm	8	[708]
13.84	disk diameter mean (n = 389) (Acanthaster planci)	18.23 ± 0.21 cm	7	[634]
13.87	largest reported test (Strongylocentrotus franciscanus)	19 (more than) cm	7	[635]
13.92	Auroralumina total length (Auroralumina attenboroughii)	20 cm	7	[524]
13.92	Burgessomedusa umbrella height (Burgessomedusa phasmiformis)	20 cm (up to)	7	[532]
13.92	injured size class upper (Acanthaster planci)	20 cm	7	[629]
13.92	shoot upper (Huperzia lucidula)	20 (–100) cm	8	[695]
13.92	Eospermatopteris base lower	20 cm	8	[716]
13.92	half of root mass, global (plants)	20 cm	8	[884]
13.92–14.76	Eospermatopteris base	20–50 cm	10	[716]
13.92; 15.29	Jackfruit length (Artocarpus heterophyllus)	0.20–0.90 m	14	[1304]
13.92	Burgessomedusa umbrella (Burgessomedusa phasmiformis)	up to 20 cm	17	[532]
13.97	Mantle length (Graneledone boreopacifica)	0.212 m	15	[1347]
14.12	height var. pulchra upper (Dawsonia superba var. pulchra)	25 cm	8	[460]
14.23	flower (Victoria amazonica)	28 (up to) cm	8	[775]
14.29	gigantoproductid shell width (Gigantoproductus)	30 (over) cm	7	[597]
14.29	frond upper (Caulerpa taxifolia)	30 cm	8	[427]
14.29	axial internode (Chara)	30 cm	8	[665]
14.29	creeping stem lower (Lycopodium clavatum)	30 cm	8	[694]
14.29	vegetative stem lower (Equisetum telmateia subsp. braunii)	30 cm	8	[708]
14.29	leaf lower (Pteridium aquilinum)	30 cm	8	[709]
14.29	Eospermatopteris root depth	30 cm	8	[716]
14.29	half of root mass, trees	30 cm	8	[884]
14.29	mineral binding depth (soil)	below ~30 cm	11	[1046]

14.29	mirror short side (mark test)	30 cm	19	[1809]
14.38	Nectar spur (Angraecum sesquipedale)	0.33 m	14	[1266]
14.45	Longest insect, body (Phobaeticus chani female)	0.357 m	14	[1303]
14.46	disk diameter upper (Acanthaster planci)	36 cm	7	[634]
14.55	Helicolocellus height (Helicolocellus cantori)	0.4 m (more than)	7	[491]
14.55	stem diameter (Encephalartos transvenosus)	0.4–0.45 m	8	[736]
14.62–14.66	Spinal cord length (Homo sapiens)	43–45 cm	17	[1656]
14.66	mirror long side (mark test)	45 cm	19	[1809]
14.71	tested stems (Equisetum hyemale)	476–767 mm	8	[710]
14.72	largest thallus (Rhizocarpon alpicola)	480 mm	9	[912]
14.74	newborn median length, girls (Homo sapiens)	49.1 cm	20	[1904]
14.75	newborn median length, boys (Homo sapiens)	49.9 cm	20	[1904]
14.76	length, largest calcareous sponge (Sycon ciliatum)	0.5 m (over)	7	[492]
14.76	internodal cell length (Chara)	0.5 m	8	[665]
14.76	Eospermatopteris base upper	50 cm	8	[716]
14.76	stem diameter (Lepidozamia hopei)	50 cm	8	[735]
14.76	stem diameter (Macrozamia moorei)	50–80 cm	8	[735]
14.76	fruit length (Lodoicea maldivica)	50 (up to) cm	8	[791]
14.84	Arthropleura width	~55 cm	10	[1009]
14.87	Longest insect, overall (Phobaeticus chani female)	0.567 m	14	[1303]
14.92	mature trunk (Liriodendron tulipifera)	0.6–1.5 m	8	[776]
14.92	Early Cretaceous bird with plant remains	0.6 m	14	[1267]
14.99	Dawsonia (Dawsonia superba)	65 cm	6	[460]
15.06	insect wingspan maximum (insects)	70 cm	8	[728]
15.06	maximum insect wingspan (Carboniferous–Permian insects)	~70 cm	10	[728]
15.06	Largest fossil wingspan	about 0.70 m	15	[728]

	(Carboniferous–Permian insects)			
15.12	Loki sample below seafloor (Loki’s Castle sediment)	75 cm	3	[168]
15.14; 14.46	Arthropleura partial remains	76 × 36 cm	10	[1009]
15.19; 16.85	Measured females (28) (Somniosus microcephalus)	0.81–5.02 m	15	[1417]
15.29	arm tip to arm tip (Evasterias echinosoma, Pisaster brevispinus)	90 (nearly) cm	7	[586]
15.29	trunk base (Encephalartos woodii)	900 (up to) mm	8	[737]
15.34	Herrin coal stand basal diameter (Lepidodendron)	95 (34–144) cm	8	[693]
15.34 (14.40–15.72)	Herrin basal diameter (Lepidodendron)	95 (34–144) cm	10	[693]
15.37	diameter, largest in 12 transects (Xestospongia muta)	0.98 m	7	[495]
15.39	stolon (Caulerpa taxifolia)	1 (upwards of) m	8	[427]
15.39	creeping stem upper (Lycopodium clavatum)	100 cm	8	[694]
15.39	vegetative stem upper (Equisetum telmateia subsp. braunii)	100 (–200) cm	8	[708]
15.39	Eospermatopteris root reach	1–2 m	8	[716]
15.39	stem diameter, cultivated (Ginkgo biloba)	1–4 m	8	[738]
15.39	flower (Rafflesia arnoldii)	1 (nearly) m	8	[827]
15.39–16.02	Eospermatopteris root reach	1–2 m	10	[716]
15.39	Dispersal distance, typical (ants)	about 1 m	14	[1289]
15.39	Compound eye reduced periphery (model eye)	about 1 m	18	[1679]
15.55	root depth (Archaeopteris)	1.2–1.6 m	8	[716]
15.55–15.81	Archaeopteris root depth	1.2–1.6 m	10	[716]
15.55 (14.29)	Mahoning stump diameter (lycopsids)	1.2 (taper ≥0.3) m	10	[725]
15.57	height, largest in 12 transects (Xestospongia muta)	1.23 m	7	[495]
15.69	dickinsoniid maximum size (Dickinsoniidae)	1.4 m	7	[451]
15.69	Ankylosaur body length (ankylosaur, Early Cretaceous)	1.4 m	14	[1267]

15.76	height (Equisetum hyemale)	150 cm	8	[710]
15.83	height at 19, girls (Homo sapiens)	163.2 cm	20	[1906]
15.87	Human height (human reference man)	1.70 m	6	[236]
15.89	Shell diameter, Seppenrade specimen 1895 (Parapuzosia seppenradensis)	1.74 m	15	[1344]
15.90	height at 19, boys (Homo sapiens)	176.5 cm	20	[1906]
15.92	leaf upper (Pteridium aquilinum)	180 (–500) cm	8	[709]
15.97	lycopsid root mound (lycopsid (possible))	1.9 m	8	[716]
15.97	lycopsid root mound, Cairo (possible lycopsid)	1.9 m	10	[716]
16.02	2 m specimen, size (Scolymastra joubini)	2 m	7	[500]
16.02	Aegirocassis length (Aegirocassis benmoulae)	2 (more than) m	7	[583]
16.02	scale tree trunk diameter (Lepidodendron and allies)	2 m	8	[461]
16.02	leaf (Lepidozamia hopei)	200–300 cm	8	[735]
16.02	stem (Macrozamia moorei)	2–7 m	8	[735]
16.02	lycopsid trunk diameter (arborescent lycopsids)	2 m	10	[461]
16.02	Body length (Aegirocassis benmoulae)	>2 m	13	[583]
16.10	aerial stems upper (Equisetum hyemale subsp. affine)	220 cm	8	[708]
16.10	Bomb-pulse sharks (Somniosus microcephalus)	up to 2.20 m	15	[1417]
16.14	leaf breadth (Victoria amazonica)	2.3 (up to) m	8	[775]
16.18	old-growth d.b.h. (Liriodendron tulipifera)	2.4–3.7 m	8	[776]
16.22	length (Balanoglossus gigas)	2.5 (up to) m	7	[578]
16.26	Road per person (roads)	2.6 m	22	[1980; 1990]
16.27	Arthropleura length	2.63 m	10	[1009]
16.39	giant basal spicule length (Monorhaphis chuni)	3 m (up to)	7	[492; 493]
16.39	stem (Cycas media)	3 (–6) m	8	[735]
16.39	inflorescence (Amorphophallus titanum)	3 (up to about) m	8	[794]
16.39	Riftia tube length (Riftia pachyptila)	3 m	12	[1123]
16.45	Rhynie chert section	c. 3.2 m	10	[983]
16.47	Ocean sunfish, record	3.3 m	15	[1418]

	length			
16.53	permafrost sample depth (Adineta (bdelloid rotifer))	3.5 m	7	[595]
16.78	maximum rooting depth, global mean (plants)	4.6 ± 0.5 m	8	[885]
16.85	stem height (Equisetum giganteum)	5 (over) m	8	[711]
16.85	stem (Cycas angulata)	5 (–12) m	8	[735]
16.90	growth depth (Victoria)	5.25 (up to) m	8	[775]
17.02	measured tree ferns (Dicksonia antarctica, Cyathea australis)	6 (up to) m	8	[712]
17.02	trunk (Encephalartos woodii)	6 (up to) m	8	[737]
17.08	Greenland shark, survey maximum	6.4 m	15	[1418]
17.16	maximum rooting depth, trees	7.0 ± 1.2 m	8	[885]
17.16	Giant manta, disc width	at least 7 m	15	[1418]
17.17	Great white shark, dataset maximum	7.13 m	15	[1418]
17.25	Oarfish, dataset maximum	7.72 m	15	[1418]
17.28	Prototaxites	8 m	6	[436]
17.28	Gilboa tree height (Wattieza/Eospermatopteris)	8 (at least) m	8	[715]
17.28; 17.48	First estimates of total length (colossal squid)	8–10 m	15	[1348]
17.28	Oarfish, maximum	just under 8 m	15	[1418]
17.41	Burrow length per core after 6 weeks (Lumbricus terrestris)	9.2 m	15	[1088]
17.48	mound height (Macrotermitinae)	10 m	9	[940]
17.48–18.95	lycopsid maximum heights by taxon (arborescent lycopsids)	10–50 m	10	[692]
17.52	asymptotic height (Phyllostachys edulis)	10.46–15.66 m	8	[798]
17.57	root system radius (Archaeopteris)	11 m	8	[716]
17.57	largest sampled culm (Phyllostachys edulis)	11.04 m	8	[797]
17.57	Archaeopteris root system	11 across m	10	[716]
17.57–18.54	Archaeopteris height (base diameter)	11–32 m	10	[716]
17.65	stem (Encephalartos transvenosus)	12–13 m	8	[736]
17.65	Compound eye for human resolution (model eye)	about 12 m	18	[1679]

17.67	Basking shark, record	12.27 m	15	[1418]
17.79	reported girth (Ginkgo biloba)	14 m	8	[738]
17.85	modern peat thickness	15 (up to) m	9	[922]
17.85	mound width (Macrotermitinae)	15 (more than) m	9	[940]
17.85	modern peat thickness	15 m	10	[1002]
17.85; 19.11	Collected depth below ground (Eumillipes persephone)	15–60 m	15	[1397]
17.88 (17.97–18.09)	Yunnan palaeosol exposed (Xujiachong palaeosol)	15.5 (originally 17.0–19.4) m	10	[986]
17.89	burrows A. icterica (Aporrectodea icterica)	15.7 m	11	[1088]
17.97	Schagen palaeosol section (Mpumalanga palaeosols)	17 m	10	[228]
17.97	Schagen section (palaeosol)	17 m	11	[228]
18.02–18.39	Archaeopteris height (regression)	18–27 m	10	[716]
18.06	baobab Platland height (Adansonia digitata)	18.9 m	8	[830]
18.06	Whale shark, largest accepted	18.8 m	15	[1418]
18.11	stem height (Lepidozamia hopei)	20 (up to) m	8	[735]
18.11	typical tree height (Ginkgo biloba)	20–40 m	8	[738]
18.11	culm height (Phyllostachys edulis)	20 (more than) m	8	[797]
18.11	height (Fagus sylvatica)	20–30 (up to 50) m	8	[831; 832]
18.11	Whale shark, discounted claim	about 20 m	15	[1418]
18.17	Burrow length per core after 6 weeks (Aporrectodea nocturna)	21.2 m	15	[1088]
18.24	average height (Pinus sylvestris)	23–27 m	8	[752]
18.34	Length (blue whale (comparison))	25.8 m	15	[1488]
18.34	Mean adult length (Balaenoptera musculus)	25.8 m	15	[1488]
18.45	tallest in New York plantation at 74–77 years (Pinus sylvestris)	29.0 m	8	[753]
18.48–19.11	Lost City chimney height	30–60 m	1	[53]
18.48	height at maturity (Picea abies)	30–60 m	8	[755]
18.48	height (Quercus robur)	30–40 (34 at	8	[828; 829]

		maturity) m		
18.50	mature height (Liriodendron tulipifera)	30.5–45.7 m	8	[776]
18.54	height estimate upper (Archaeopteris)	32 m	8	[716]
18.60	baobab Platland girth (Adansonia digitata)	34.11 m	8	[830]
18.70	Burrow depth (Silene stenophylla, Siberia)	38 m	14	[1314]
18.74	maximum height (Pinus sylvestris)	40 (over) m	8	[752]
18.83	Male nerve cord cable (Drosophila melanogaster)	44 m	17	[1618]
18.85	scale tree height (Lepidodendron and allies)	45 m	8	[461]
18.85	lycopsid stature (arborescent lycopsids)	c. 45 m	10	[461]
18.95	scale tree height, second source (arborescent lycopsids)	10–50 m	8	[692]
18.95	height (Picea abies)	50–60 m	8	[754]
18.97	Half the seeds within (small passerines; Prunus mahaleb)	51 m	14	[1311]
19.11	Macrocystis length (Macrocystis pyrifera)	60 (more than) m	8	[365]
19.11	common height (Sequoia sempervirens)	60–84 m	8	[756]
19.13	old-growth height (Liriodendron tulipifera)	61 m	8	[776]
19.13	thickest coal beds	61 (up to) m	9	[922]
19.13	coal bed thickness	61 (rare maximum) m	10	[1002]
19.17	reported maximum height (Ginkgo biloba)	64 m	8	[738]
19.23	deepest roots (Boscia albitrunca)	68 m	8	[885]
19.25	rare tree height (trees)	70 (exceeding) m	8	[823]
19.34	Dispersal distance, longest (ants)	77 m	14	[1289]
19.58	height (Eucalyptus regnans)	100 (up to) m	8	[824]
19.59	champion (Sequoia sempervirens)	101 m	8	[756]
19.66	Half the seeds beyond (medium-sized birds)	110 m	14	[1311]
19.68	tallest in Silvics (1964) (Sequoia sempervirens)	112.1 m	8	[757]
19.69	tallest measured (Sequoia sempervirens)	112.7 m	8	[462]

19.76	height limit estimate lower (Sequoia sempervirens)	122 m	8	[462]
19.82	height limit estimate upper (Sequoia sempervirens)	130 m	8	[462]
19.94	Fly brain path length (Drosophila melanogaster)	about 149 m	17	[1619]
19.95	in-place measurement depth (Aphrocallistes vastus)	150 m	7	[496]
20.21	Golfo Dulce depth	200 m	3	[220]
20.21	Golfo Dulce depth (coastal bay)	200 m	11	[220]
20.58	deep-sea corals depth lower (black corals, zoanthids)	300 m	7	[542]
20.81	Michigan genet side 1992 (Armillaria gallica)	387.3 m	9	[960]
21.03	Half the seeds beyond (carnivorous mammals)	495 m	14	[1311]
21.03	mean foraging distance, spring (Apis mellifera)	493 m	21	[1929]
21.04; 21.67	Cline width between pure populations (Partula suturalis)	about 0.5–1 km	15	[1357]
21.30	Pando side of equal square (Populus tremuloides (Pando))	660 m	8	[846]
21.54	Michigan genet side 2018 (Armillaria gallica)	866.0 m	9	[961]
21.67; 23.77; 17.48	Megafauna vs extant dispersal distances (megafauna; extant frugivores)	1e3–1e4 vs 1e1–1e3 m	14	[1297]
21.84	Lomatia population extent (Lomatia tasmanica)	1.2 km	8	[839]
21.90	mean foraging distance, autumn (Apis mellifera)	1275 m	21	[1929]
21.98	Brooding depth (Graneledone boreopacifica)	1,397 m	15	[1347]
22.04	Highland networks lower connectance above (pollination networks)	1,500 m	14	[1325]
22.37	mean foraging distance, summer (Apis mellifera)	2156 m	21	[1929]
22.39	respiration chambers depth lower (abyssal ophiuroids, holothuroids)	2200 m	7	[639]
22.52	MK-D1 sample water depth (Prometheoarchaeum syntrophicum MK-D1)	2533 m	3	[171]
22.54	Mahoning transects (drowned lycopsid forest)	2585 m	10	[725]

22.67	deep-sea corals depth upper (black corals, zoanthids)	3000 m	7	[542]
22.71	Oregon genet side (Armillaria ostoyae)	3106.4 m	9	[439]
22.76	Loki sample water depth (Loki's Castle sediment)	3283 m	3	[168]
22.84	respiration chambers depth upper (abyssal ophiuroids, holothuroids)	3600 m	7	[639]
22.89	Oregon isolates apart (Armillaria ostoyae)	3810 m	9	[439]
23.19	Median dispersal (forest elephants)	5,300 m	14	[1310]
23.30	lower depth limit (Asteroidea)	6000 m	7	[586]
23.38	Mean dispersal (forest elephants)	6,500 m	14	[1310]
23.62	scale height (atmosphere)	8.5 km	11	[1049]
23.66	deepest sponge (carnivorous), below surface (Cladorhizidae)	8840 m	7	[492]
23.77	Strelley Pool reef outcrop	10 km	2	[108]
23.77–25.23	ozone layer	90 % at 10–50 km	11	[1070]
24.08	10 % of seeds beyond (forest elephants)	14,100 m	14	[1310]
24.12	Joggins sea cliffs	14.7 km	10	[993]
24.14	Loki sample to vents (Loki's Castle)	15 km	3	[168]
24.14	genet extent (Posidonia oceanica)	15 (up to) km	8	[800]
24.22	95 % quantile (forest elephants)	16,400 m	14	[1310]
25.03	Average maximum over 96 elephants (forest elephants)	40,100 m	14	[1310]
26.23	Hadza–Sandawe distance (Hadza; Sandawe)	150 km	21	[1959]
28.80	distance from East African Rift (Sahelanthropus site)	2500 km	20	[1841]
29.59	main supercolony extent (Linepithema humile)	>6000 km	19	[1824]
31.97	Myelinated fibre at 80, women (Homo sapiens)	82,000 km	17	[1667]
32.13	Myelinated fibre at 80, men (Homo sapiens)	97,200 km	17	[1667]
32.52	Myelinated fibre at 20, women (Homo sapiens)	149,000 km	17	[1667]
32.67	Myelinated fibre at 20, men (Homo sapiens)	176,000 km	17	[1667]
34.18	UIC railway lines worked	929,981 km	22	[1991]

35.25–35.66	Additional roads by 2050	3.0–4.7 million km	22	[1990]
38.24	Existing electricity grid	about 80 million km	22	[1993]

Durations

1071 positions.

Position	What	Value	Chapter	Source
8.00	Hydrogen bond lifetime near 0 °C (water)	1 ps	1	[19]
8.49	Proton hop O to O (water)	1.7 ps	1	[21]
9.06–9.22	Hydrogen bond exchange in liquid water	3.2–3.8 ps	1	[16]
18.48	Lipid neighbour exchange (lipid bilayer)	1e-7 s	2	[128]
22.67	Hair cell receptor potential (Homo sapiens)	about 10 µs	18	[1690]
26.01; 26.20	Strike force peak interval (Odontodactylus scyllarus)	390e-6–480e-6 s	15	[1448]
26.03–26.60	Synaptic delay frog	0.4–0.75 ms	17	[1664]
26.29	NaChBac Cole–Moore shift	533 µs	2	[150]
26.40	chronaxie lower (Virgularia)	0.6 ms	7	[558]
26.40–26.87	Virgularia chronaxie	0.6–1 ms	17	[558]
26.66	chronaxie (Pennatula phosphorea)	0.8 ms	7	[558]
26.66	Pennatula chronaxie (Pennatula phosphorea)	about 0.8 ms	17	[558]
26.87	chronaxie upper (Virgularia)	1 ms	7	[558]
26.87	Utricularia door	1 (less than) ms	8	[835]
27.03	motor giant spike at half amplitude lower (Aglantha digitale)	1.2 ms	7	[537]
27.17	motor giant spike at half amplitude upper (Aglantha digitale)	1.4 ms	7	[537]
27.23	Minimum escape reaction (Undinula vulgaris	1.5e-3 s	15	[1444]

	(myelinated))			
27.23	Undinula reaction time (Undinula vulgaris)	1.5 ms	17	[1624]
27.29	ring giant spike (Aglantha digitale)	1.6 ms	7	[537]
27.29	Minimum escape reaction (Neocalanus gracilis (myelinated))	1.6e-3 s	15	[1444]
27.29	Aglantha synaptic delay to muscle (Aglantha digitale)	about 1.6 ms	17	[537]
27.29	Neocalanus reaction time (Neocalanus gracilis)	1.6 ms	17	[1624]
27.40	synaptic delay ring giant to motor giant upper (Aglantha digitale)	1.8 ms	7	[537]
27.50	escape-burst impulse lower (Aglantha digitale)	2 ms	7	[537]
27.50–28.13	Paramecium off latency (Paramecium caudatum)	2–4 ms	17	[1585]
27.50–27.87	Aglantha escape burst (Aglantha digitale)	2–6 impulses of 2–3 ms	17	[537]
27.50	Impulse duration (Homo sapiens neuron)	about 2 ms	17	[1663]
27.87	escape-burst impulse upper (Aglantha digitale)	3 ms	7	[537]
27.87	Human cone inactivation fast (Homo sapiens cone)	about 3 ms	18	[1688]
27.90	Minimum escape reaction (Labidocera madurae (non-myelinated))	3.1e-3 s	15	[1444]
27.90	Labidocera reaction time (Labidocera madurae)	3.1 ms	17	[1624]
28.01	minimum repeat interval, ring giant (Aglantha digitale)	3.5 ms	7	[537]
28.33	Copepod kick interval (Calanoida)	5 ms	17	[1624]
28.33–28.65	Ripples (Mammalia hippocampus)	140–200 Hz (5–7.14 ms) ms	18	[1741]
28.35	Odontella recovery from inactivation	5.1 ± 0.4 ms	17	[1595]

	(Odontella sinensis)			
28.58	Minimum escape reaction (Pleuromamma xiphias (non-myelinated))	6.6e-3 s	15	[1444]
28.58	Pleuromamma reaction time (Pleuromamma xiphias)	6.6 ms	17	[1624]
28.59	Fastest fibre per metre (Homo sapiens)	6.7 ms	17	[1623]
28.76–28.96	Sound to brain (Homo sapiens)	8–10 ms	18	[1710]
28.96	Human cone inactivation slow (Homo sapiens cone)	about 10 ms	18	[1688]
28.96–29.80	Mouse hippocampal gamma	40–100 Hz (10–25 ms) ms	18	[1744]
28.96–29.96	Membrane time constant (neurons)	10–30 ms	18	[1741]
29.33	myoepithelial impulse lower (Aglantha digitale)	15 ms	7	[537]
29.33	Proteorhodopsin photocycle	15 ms	18	[1668]
29.50	Chlamydomonas response time (Chlamydomonas reinhardtii)	0.018 ± 0.009 s	17	[1594]
29.55	Macaque green cone integration (Macaca fascicularis)	19 ± 9.8 ms	18	[1689]
29.59	Human cone time to peak (Homo sapiens cone)	about 20 ms	18	[1688]
29.59–30.22	Light to brain (Homo sapiens)	20–40 ms	18	[1710]
29.59	Spike-timing window (rat hippocampal culture)	20 ms	18	[1788]
29.59–52.43	Memory duration span	20 ms to 50 yr (10.90 decades) s	18	[1788; 1801]
29.73	Chlamydomonas flagellar beat (Chlamydomonas reinhardtii)	43.2 ± 8.0 Hz (23 ms) ms	17	[1594]
29.80	LTP train (rat)	400 Hz, 25 ms	18	[1790]
29.90	Macaque red cone integration (Macaca fascicularis)	28 ± 14 ms	18	[1689]

29.96–28.13	Paramecium reversal latency (Paramecium caudatum)	30 to ≤4 ms	17	[1585]
30.15–30.82	Paramecium ciliary beat (Paramecium caudatum)	13–27 Hz (37–77 ms) ms	17	[1586]
30.22	absolute refractory period lower (Pennatula phosphorea)	40 ms	7	[558]
30.22–30.43	Paramecium electrotonic time constant (Paramecium caudatum)	40–50 ms	17	[1587]
30.22–30.43	Pennatula absolute refractory (Pennatula phosphorea)	40–50 ms	17	[558]
30.22–30.33	Mouse activated rhodopsin lifetime (mouse rod)	40–45 ms	18	[1678]
30.23	time to peak of escape contraction (Aglantha digitale)	40.5 ms	7	[537]
30.37	Macaque foveal cone time to peak (Macaca fascicularis)	47 ± 14 ms	18	[1689]
30.43	absolute refractory period upper (Pennatula phosphorea)	50 ms	7	[558]
30.43–33.95	Paramecium ciliary reversal (Paramecium caudatum)	50 ms to 2.4 s	17	[1585]
30.43–31.06	Odontella action potential (Odontella sinensis)	50–100 ms	17	[1595]
30.44	Macaque green cone time to peak (Macaca fascicularis)	51 ± 13 ms	18	[1689]
30.51	Macaque red cone time to peak (Macaca fascicularis)	55 ± 18 ms	18	[1689]
30.52–30.89	Spindles (Mammalia)	12–18 Hz (55.6–83.3 ms) ms	18	[1741]
30.73	myoepithelial impulse upper (Aglantha digitale)	70 ms	7	[537]
30.73	London–New York ping (internet)	70.025 ms	22	[1998]
30.85–31.43	Sharp-wave ripple event (Mammalia hippocampus)	80–150 ms	18	[1741]

30.89–31.26	Alpha (Mammalia)	8–12 Hz (83.3–125 ms) ms	18	[1740]
30.89–31.52	Rodent theta (rodents)	6–12 Hz (83.3–167 ms) ms	18	[1741]
30.92	Rat NREM OFF period	85.8 ± 5.9 ms	18	[1772]
31.00	half relaxation of escape contraction (Aglantha digitale)	94 ms	7	[537]
31.03	Chlamydomonas time to peak (Chlamydomonas reinhardtii)	97 ± 18 ms	17	[1594]
31.06	escape contraction complete (Aglantha digitale)	100 ms	7	[537]
31.06	flytrap closure (Dionaea muscipula)	100 ms	8	[834]
31.06	Aglantha escape contraction (Aglantha digitale)	about 100 ms	17	[537]
31.06	Heart AV delay (Homo sapiens heart)	100 ms	17	[1627]
31.15–31.52	Mouse hippocampal theta	6–9 Hz (111–167 ms) ms	18	[1744]
31.24	Mouse GNAT2C rod decay (mouse rod)	122 ms	18	[1678]
31.30	Flytrap half-depolarization 30 °C (Dionaea muscipula)	0.13 ± 0.02 s	17	[1599]
31.30	Detection time (Homo sapiens)	131 ms	17	[1665]
31.36–31.48	Reaction to sound (Homo sapiens)	140–160 ms	18	[1710]
31.39	NCL visual latency (Corvus corone corone)	144 ms	19	[1829]
31.43	Mimosa Ca rise before leaflet movement (Mimosa pudica)	up to 0.15 s	17	[1600]
31.46	Reaction to touch (Homo sapiens)	155 ms	18	[1710]
31.52–31.89	Carnivore theta (carnivores)	4–6 Hz (167–250 ms) ms	18	[1741]
31.59–31.69	Reaction to light (Homo sapiens)	180–200 ms	18	[1710]
31.69	Paramecium refractoriness (Paramecium caudatum)	up to 200 ms	17	[1587]

31.69	Cone recovery after flash (Homo sapiens)	about 200 ms	18	[1690]
31.75	Simple reaction time (Homo sapiens)	213 ms	17	[1665]
31.80	Heart sinus to last ventricle (Homo sapiens heart)	225 ms	17	[1627]
31.89	facilitation peak (Pennatula phosphorea)	250 ms	7	[558]
31.89	shortest beat interval, small animals (Aurelia aurita)	0.25 s	7	[541]
31.89	Aurelia beat interval small (Aurelia aurita)	about 0.25 s	17	[541]
31.89–32.06	Ventricular action potential (Homo sapiens heart)	250–300 ms	17	[1627]
31.89–33.15	Human theta (Homo sapiens)	1–4 Hz (0.25–1 s) s	18	[1741]
31.92	Mouse wild-type rod decay (mouse rod)	258 ms	18	[1678]
32.03	Flytrap half-depolarization 10 °C (Dionaea muscipula)	0.29 ± 0.08 s	17	[1599]
32.06	SS1 absolute refractory period (Calliactis parasitica)	300 ms	7	[557]
32.06	Calliactis SS1 absolute refractory (Calliactis parasitica)	about 300 ms	17	[557]
32.06	Sensory rhodopsin photocycle (sensory rhodopsins)	≥300 ms	18	[1668]
32.32	shortest common beat interval (Dactylometra quinquecirrha)	0.4 s	7	[541]
32.36	pacemaker period at 2.4 Hz (light-off overshoot) (Tripedalia cystophora)	0.42 s	7	[540]
32.52	task sample and baseline (Corvus corone corone)	500 ms	19	[1829]
32.69	second facilitation peak (Pennatula phosphorea)	600 ms	7	[558]
32.69	Chlamydomonas body rotation (Chlamydomonas	1.67 ± 0.35 Hz (0.60 s) s	17	[1594]

	reinhardtii)			
32.73	pacemaker period at 1.6 Hz (Tripedalia cystophora)	0.625 s	7	[540]
32.78–33.78	Neocortical slow oscillation (Mammalia)	0.5–1.5 Hz (0.667–2 s) s	18	[1741]
32.83	absolute refractory period (Aurelia aurita)	0.7 s	7	[541]
32.83–33.78	Slow 1 class (Mammalia cortex)	0.7–2 s	18	[1741]
32.89	beat interval, larger animals (Aurelia aurita)	0.75 s	7	[541]
32.91	Chlamydomonas adaptation time (Chlamydomonas reinhardtii)	0.764 ± 0.190 s	17	[1594]
32.95 (32.69–33.15)	Heartbeat (Homo sapiens)	0.8 (0.6–1.0) s	18	[1725]
32.97	Rat NREM ON period	815.5 ± 119.9 ms	18	[1772]
33.12	Chlamydomonas reorientation (Chlamydomonas reinhardtii)	0.96 ± 0.36 s	17	[1594]
33.15	Lipid crosses bacterium (lipid bilayer)	1 s	2	[128]
33.15	pacemaker period in dark (~1 Hz) (Tripedalia cystophora)	1 s	7	[540]
33.15	Chara streaming stop	<1 s	17	[1596]
33.15	Chara corallina action potential 40 °C	about 1 s	17	[1597]
33.15	Vertebrate cascade (vertebrate rod)	about 1 s	18	[1675]
33.15	Octopus quiet-sleep events	12–18 Hz, up to 1 s	18	[1350]
33.15	task delay (Corvus corone corone)	1000 ms	19	[1829]
33.32; 33.52	Heartbeat at rest (Octopus vulgaris)	1.2–1.5 s	15	[1349]
33.46	SS1 relative refractory period (Calliactis parasitica)	1400 ms	7	[557]
33.46	Calliactis SS1 relative refractory	about 1,400 ms	17	[557]

	(Calliactis parasitica)			
33.78	pacemaker period at 0.5 Hz (Tripedalia cystophora)	2 s	7	[540]
33.78–34.15	Chara half-amplitude duration	about 2–3 s	17	[1596]
33.78–35.25	Chara absolute refractory period	2–10 s	17	[1596]
33.78	Flytrap action potential (Dionaea muscipula)	2 s	17	[1599]
33.78	Slowest fibre per metre (Homo sapiens)	2 s	17	[1623]
33.78–34.62	Slow 2 class (Mammalia cortex)	2–5 s	18	[1741]
34.15	SS1 fails above one shock per (Calliactis parasitica)	3 s	7	[557]
34.43	Breath (Homo sapiens)	3.3–5 s	18	[1726]
34.62	regenerating rhopalium pacemaker period, day 8 (Tripedalia cystophora)	5 s	7	[559]
34.62	Regenerating rhopalium pacemaker day 8 (Tripedalia cystophora)	about 0.2 Hz (5 s) s	17	[559]
34.62–35.62	Slow 3 class (Mammalia cortex)	5–15 s	18	[1741]
35.11	Acoel geotaxis (Symsagittifera roscoffensis)	8.6 s	17	[1609]
35.25	Vesicle transport 10 µm (cell)	10 s	5	[406]
35.25	Mayer waves (Homo sapiens)	about 10 s	18	[1727]
35.25	Ultra-slow rhythm (Mammalia)	0.1 Hz (10 s) s	18	[1741]
35.25	C. elegans tap habituation plateau (Caenorhabditis elegans)	about 7 taps at 10 s	18	[602]
35.25	chant breathing cycle (Homo sapiens)	10 s	21	[1733]
35.33	Bird SWS episode flight (birds in flight)	10.89 ± 0.81 s	18	[1767]
35.62–36.51	Slow 4 class (Mammalia cortex)	15–40 s	18	[1741]

36.19	Bird SWS episode land (birds in flight)	28.25 ± 1.75 s	18	[1767]
36.22	absolute refractory period (Rhabdocalyptus dawsoni)	29 s	7	[499]
36.25	pause onset after peptide pulse (Trichoplax adhaerens)	30 s	7	[517]
36.25	Chara corallina action potential 3.5 °C	about 30 s	17	[1597]
36.25	Trichoplax pause onset (Trichoplax adhaerens)	about 30 s	17	[517]
36.34	regenerating rhopalium pacemaker period, day 6 (Tripedalia cystophora)	33.3 s	7	[559]
36.34	Regenerating rhopalium pacemaker day 6 (Tripedalia cystophora)	about 0.03 Hz (33 s) s	17	[559]
36.66	Infraslow rat NREM	47 s	18	[1490]
36.70	Infraslow NREM rhythm (pigeon)	49 s	15	[1490]
36.71	Infraslow mouse blood volume	50 s	18	[1490]
36.71	self-control delay, lower (cuttlefish)	50 s	19	[1805]
36.73	Infraslow human N2 (Homo sapiens)	51 s	18	[1490]
36.79	Flower handling time (Eurybia lycisca)	54.5 ± 28.5 s	14	[1301]
36.88	Stentor habituation stimuli (Stentor coeruleus)	30 at 1-min intervals min	18	[1775]
36.88	C. elegans long-term memory protocol (Caenorhabditis elegans)	4 blocks of 20 taps at 60 s, 1 h apart s	18	[602]
37.08	Octopus active-sleep bout	75 ± 28 s	18	[1350]
37.14	Lizard SW–REM cycle (Pogona vitticeps)	80 s	18	[1491]
37.19–37.61	Infraslow lizards range (7 lizard species)	84–134.5 s	18	[1490]

37.25	Chara relative refractory period	up to 90 s	17	[1596]
37.30	relative refractory period, lower (Rhabdocalyptus dawsoni)	95 s	7	[499]
37.30–37.34	Glass sponge relative refractory period (Rhabdocalyptus dawsoni)	95–100 s	17	[499]
37.34	relative refractory period, upper (Rhabdocalyptus dawsoni)	100 s	7	[499]
37.34	Infraslow bearded dragon blood volume (Pogona vitticeps)	100 s	18	[1490]
37.46	Infraslow lizards mean (7 lizard species)	113.2 ± 6.8 s	18	[1490]
37.51–37.88	Darwin burial loose mould (earthworms)	2–3 min	11	[1090]
37.51	Jasmonic acid rise after wounding, early (Arabidopsis)	120 s	13	[1191]
37.51–37.88	Bee colour memory minimum (Apis mellifera)	2–3 min	18	[1787]
37.58	self-control delay, upper (cuttlefish)	130 s	19	[1805]
37.71	Stentor 2.5-min interval (Stentor coeruleus)	2.5 min	18	[1775]
37.86	Infraslow chameleon skin (panther chameleon)	175.7 ± 18.3 s	18	[1490]
37.87	single feeding pause (n = 64) (Trichoplax adhaerens)	2.97 ± 0.96 min	7	[517]
37.88	Optogenetic recall (mouse)	3 min light	18	[1796]
38.14–38.51	first compound tool time (Corvus moneduloides)	4–6 min	19	[1828]
38.17	group pause (Trichoplax adhaerens)	4.13 min	7	[517]
38.18	Chara streaming recovery	about 250 s	17	[1596]
38.34	Jasmonic acid rise after wounding, late (Arabidopsis)	300 s	13	[1191]
38.34; 39.98	Gut passage, mostly	5–30 min	14	[1293]

	(Mediterranean passerines)			
38.34	naïve attempt length (Bombus terrestris)	5 min	19	[1817]
38.65	pacemaker counting block (Tripedalia cystophora)	7 min	7	[540]
38.65–39.98	humpback song length (Megaptera novaeangliae)	7–30 min	21	[1936]
38.77	Short-tailed shrew sleep cycle	about 8 min	18	[1768]
38.89	repeat of pause under peptide (n = 33) (Trichoplax adhaerens)	9.11 ± 4.22 min	7	[517]
38.96	Vibrio natriegens generation	9.8 min	3	[177]
38.98	PWN effect (Trichoplax adhaerens)	10 min	7	[519]
38.98	Biofilm imaging interval (Bacillus subtilis biofilm)	10 min	17	[186]
38.98	Trichoplax PWN effect (Trichoplax adhaerens)	about 10 min	17	[519]
38.98 / 40.61	First / last REM period (Homo sapiens)	about 10 min / up to 1 h	18	[1728]
38.98	C. elegans salt reversal (Caenorhabditis elegans)	within 10 min	18	[602]
38.98–39.61	Bee colour memory rise (Apis mellifera)	10–20 min	18	[1787]
39.21	group pause cycle (n = 38) (Trichoplax adhaerens)	12.9 ± 2.0 min	7	[517]
39.34	progamic phase lower (angiosperms)	15 min	8	[740]
39.34	Stentor recovery (Stentor coeruleus)	90 % within 15 min	18	[1775]
39.61	E. coli shortest division (Escherichia coli)	20 min	2	[157]
39.61	Phage T4 cycle (phage T4 in E. coli)	20 min	4	[278]
39.69	P. aeruginosa lag (Pseudomonas aeruginosa)	22 ± 13 (30 pulses) min	3	[187]
39.69	P. aeruginosa lag	22 ± 13 min	17	[187]

	(Pseudomonas aeruginosa)			
39.73; 40.74	Gut passage species means (Mediterranean passerines)	22.9–69.4 min	14	[1293]
39.85	B. subtilis motile lag (Bacillus subtilis)	26 ± 9 (44 pulses) min	3	[187]
39.85	Motile B. subtilis lag (Bacillus subtilis)	26 ± 9 min	17	[187]
40.17	Pyrococcus doubling (Pyrococcus furiosus)	37 min	3	[174]
40.27	E. coli genome copy time (Escherichia coli)	>=2500 s	2	[156]
40.27	Bird daily sleep in flight (birds in flight)	0.69 h	18	[1767]
40.44	Phage lambda cycle (phage λ in E. coli)	50 min	4	[278]
40.44	traversal of 30 cm internode (Characeae)	3000 s	8	[665]
40.45	Octopus quiet-sleep bout	50.5 ± 16.43 min	18	[1350]
40.54–41.14	Vibrio doubling (Vibrio fischeri)	0.93–1.8 h	12	[1151]
40.61	Thalidomide racemization half-life, serum	1 h	1	[61]
40.61	Cross-replicating ligase doubling time (cross-replicating RNA enzymes)	1 h	1	[84]
40.61	Eukaryotic M (human cell)	1 h	2	[158]
40.61	Gnetales pollen germination	1–72 h	8	[740]
40.61	Octopus interval between active bouts	about 60 min	18	[1350]
40.61	Guinea pig REM	1 h	18	[1768]
40.69	V. cholerae wild doubling (Vibrio cholerae)	1.1 h	3	[178]
40.69	Cortisol half-life (Homo sapiens)	66 min	18	[1737]
40.98	cell death peak lower (Nematostella vectensis)	1.5 h	7	[539]
40.98–41.16	Sleep cycle (Homo sapiens)	90–110 min	18	[1728]
40.98; 42.07	Aplysia rapid protocol (Aplysia	4 sessions, 40 stimuli, 1.5 h apart	18	[1783]

	californica)	over 5 h		
41.11	Migrating motor complex (Homo sapiens)	90–120 min	18	[1729]
41.14	Asiatic elephant sleep cycle	1.8 h	18	[1768]
41.24	S phase to mitosis lower (Nematostella vectensis)	2 h	7	[560]
41.24	Induced volatiles onset (Zea mays)	2 h	13	[1193]
41.28	P. aeruginosa peak interval (Pseudomonas aeruginosa)	2.1 h	3	[187]
41.36	P. aeruginosa wild doubling (Pseudomonas aeruginosa)	2.3 (1.9–2.4) h	3	[178]
41.36; 41.14	Wild elephant matriarchs (African elephant)	2.3 and 1.8 (2.0 combined) h	18	[1769]
41.48	Drosophila longest immobility (Drosophila melanogaster)	up to 157 min	18	[1765]
41.61	Median laboratory doubling (bacteria)	3 h	3	[178]
41.61	protist division (soil protists)	a few hours (3 h) h	11	[1078]
41.61–41.87	Elephant and giraffe daily sleep (elephant; giraffe)	3–4 h	18	[1768]
41.61	Physarum transfer by fusion (Physarum polycephalum)	3 h	18	[1777]
41.61	Early LTP and synaptic tag (rat)	<3 h	18	[1789]
41.61	ball rolling per day (Bombus terrestris)	3 h	19	[1818]
41.64–42.36	Captive elephant reports (African elephant)	3.10–6.90 h	18	[1769]
41.85 / 41.14	Captive African elephant sleep / REM	3.9 / 1.8 h	18	[1768]
41.87	Eukaryotic G2 (human cell)	4 h	2	[158]
41.87	light period 4 h (Mnemiopsis leidyi)	4 h	7	[510]
41.87	sleep-like ultradian rhythm (Hydra)	4 h	7	[556]

41.87	S phase to mitosis upper (Nematostella vectensis)	4 h	7	[560]
41.87–42.24	regrowth (Vibrio fischeri)	4–6 h	12	[1151]
41.87	Sesquiterpenoid onset (Zea mays)	4 h	13	[1193]
41.87	DmHKT1 maximum (Dionaea muscipula)	4 h	17	[1598]
41.87	Hydra ultradian rhythm (Hydra vulgaris)	4 h	18	[556]
42.07	Influenza A release period (influenza A in humans)	about 5 h	4	[279]
42.07	Utricularia spontaneous firing lower	5 h	8	[835]
42.10	string-pulling training time per bee (Bombus terrestris)	309 ± 18 min	19	[1817]
42.15–42.22	Mammal sleep regression (mammals)	TST = 17.946 × Mb^−0.076 (5.46–5.87 h for elephants)	18	[1769]
42.24	Influenza A to first release (influenza A in humans)	about 6 h	4	[279]
42.24	median G2 of neoblasts (planarians)	6 h	7	[591]
42.24	Planarian neoblast G2 (planarians)	about 6 h	17	[591]
42.24–42.70	Lizard oscillation per night (Pogona vitticeps)	6–10 h	18	[1491]
42.32	Bushtail possum REM	6.6 h	18	[1768]
42.38	light period 7 h (Mnemiopsis leidyi)	7 h	7	[510]
42.43	Median wild doubling (bacteria)	7.4 (3.1–19) h	3	[178]
42.44–42.62	rhizosphere generation time (rhizosphere bacteria)	7.5–9.1 h	11	[179]
42.50	Eukaryotic S (human cell)	8 h	2	[158]
42.50	light period 8 h (Mnemiopsis leidyi)	8 h	7	[510]
42.50	Platypus REM	8 h	18	[1768]
42.71	Octopus quiet sleep	about 10.1 h	18	[1350]

	per day			
42.79	Water molecule dissociation	11 h	1	[20]
42.79	Eukaryotic G1 (human cell)	11 h	2	[158]
42.79	light period 11 h (Mnemiopsis leidyi)	11 h	7	[510]
42.82 (42.59–43.05)	Influenza A infected cell life (influenza A in humans)	11.4 (8.8–14.7) h	4	[279]
42.87	Thalidomide racemization half-life, buffer	12 h	1	[61]
42.87–43.29	Rhizosphere bacterial turnover	12–19 h	3	[179]
42.87	labelling to nematoblast (Hydra)	12 h	7	[551]
42.87	cell death peak upper (Nematostella vectensis)	12 h	7	[539]
42.87	squid colonisation (Euprymna scolopes – Vibrio fischeri)	within 12 h of hatching	12	[1151]
42.87	Peripheral phase shift by feeding (mouse)	up to 12 h	18	[1722]
43.07	E. coli wild doubling (Escherichia coli)	15 h	3	[178]
43.07–43.33	M. tuberculosis division (Mycobacterium tuberculosis)	15–20 h	3	[157]
43.17	LTP decay 5 trains (rat)	0.7 (0 of 6 stable) d	18	[1790]
43.19–44.80	Membrane protein half-life (rat liver cells)	17–100 h	2	[130]
43.19	planning delay (Corvus corax)	17 h	19	[1827]
43.24	labelling to visible nerve cell (Hydra)	18 h	7	[551]
43.24	progamic phase (Austrobaileya scandens)	18 h	8	[740]
43.24	Hydra labelling to nerve cell	about 18 h	17	[551]
43.24–43.33	Bats and opossums daily sleep (bats; opossums)	18–20 h	18	[1768]
43.29	No RNA leakage (vesicles)	19 h	1	[90]

43.33	Utricularia spontaneous firing upper	20 h	8	[835]
43.42	hatching after spawning, lower (Mnemiopsis leidyi)	22 h	7	[509]
43.42–43.57	Mnemiopsis hatching (Mnemiopsis leidyi)	22–26 h	17	[1603]
43.50	Eukaryotic cycle (human cell)	24 h	2	[158]
43.50	development to juveniles (Mnemiopsis leidyi)	24 h	7	[510]
43.50	nerve-net cydippid age (Mnemiopsis leidyi)	1 day	7	[513]
43.50	division interval lower (Trichoplax adhaerens)	1 day	7	[522]
43.50	interstitial stem cell cycle (Hydra)	24 h	7	[551]
43.50	nerve differentiation from stem cells (Hydra)	1 day	7	[551]
43.50	Prochlorococcus generation	1 day	8	[650; 652]
43.50	MED4 transcriptome cycle (Prochlorococcus MED4)	24 h	8	[653]
43.50	division cycle under 12:12 LD (Cyanidioschyzon merolae)	24 h	8	[660]
43.50	CAM acid rhythm under water (Isoetes)	24 h	8	[691]
43.50; 44.80	doubling young vs old roots (rhizosphere bacteria)	24 vs >100 h	11	[179]
43.50; 44.13	Adult pollinating fig wasp life (Agaonidae)	24–48 h	14	[1261]
43.50	KaiC phosphorylation cycle (Synechococcus elongatus)	24 h	18	[1718]
43.50	C. elegans massed training (Caenorhabditis elegans)	80 taps, no 24 h retention	18	[602]
43.50	Aplysia ganglion decrement (Aplysia californica)	24 h later	18	[1783]

43.50–44.13	Bee eLTM (Apis mellifera)	1–2 d	18	[1465]
43.50	LTP decay 20 trains (rat)	1.0 (1 of 6) d	18	[1790]
43.51	Human intrinsic circadian period (Homo sapiens)	24.18 h	18	[1723]
43.54	S. enterica wild doubling (Salmonella enterica)	25 h	3	[178]
43.56	Darwin burial compact sand (earthworms)	25 h 40 min	11	[1090]
43.56	S. elongatus luminescence period (Synechococcus elongatus)	25.6 ± 0.1 h	18	[1718]
43.57	hatching after spawning, upper (Mnemiopsis leidyi)	26 h	7	[509]
43.61	circadian period, single cell (Acetabularia)	27 h	8	[662]
43.68	doubling time (Wolffia microscopica)	29.3 h	8	[796]
43.70	interstitial stem cell cycle, later account upper (Hydra)	30 h	7	[552]
44.05; 43.63	Mitochondrial half-life (mouse liver)	1.83 (1.16 on restricted diet) days	5	[387]
44.09	Median protein half-life (mouse cells)	46 h	5	[405]
44.09	Wild elephants without sleep (African elephant)	up to 46 h	18	[1769]
44.13	Glycine detectable (Miller apparatus)	2 days	1	[40]
44.13	neurons appear after muscle (Ctenophora)	2 days	7	[479]
44.13	division interval upper (Trichoplax adhaerens)	2 days	7	[522]
44.13	neurite extension in grafts lower (Hydra)	2 days	7	[536]
44.13	generation (Volvox carteri)	48 h	8	[424]
44.13	Azolla doubling time	2 days	8	[705]
44.13	turnover of plant matter, ocean lower (ocean plants)	2 days	8	[850]

44.13	Ctenophore neurons after muscle (Ctenophora)	about 2 d	17	[479]
44.13–44.50	Hydra neurite extension in grafts	days 2–3 d	17	[536]
44.13	Physarum stimulus withheld (Physarum polycephalum)	2 d	18	[1776]
44.13–47.60	infant scan ages (Homo sapiens)	2–90 d	20	[1900]
44.17	pollen tube time to cover 1 mm (gymnosperms)	50 h	8	[741]
44.26–46.68	Soil bacterial turnover 20 °C	2.3–33 (mean 9.3) days	3	[179]
44.44	minimum generation time, MY6 (Caenorhabditis elegans)	67.3 h	7	[604]
44.50	stem population doubling lower (Hydra)	3 days	7	[552]
44.50	labelling to nematocyte lower (Hydra)	72 h	7	[551]
44.50	age at maturity (Caenorhabditis elegans)	3 days	7	[605]
44.50	pluteus age (Strongylocentrotus purpuratus)	3 days	7	[632]
44.50	pollen germination (cycads)	several days (3)	8	[740]
44.50–44.76	Hydra stem population doubling	3–4 d	17	[552]
44.50	Bee lLTM (Apis mellifera)	≥3 d	18	[1465]
44.51	minimum generation time, N2 (Caenorhabditis elegans)	73.0 h	7	[604]
44.59	LTP decay 4 × 5 trains (rat)	3.3 (3 of 6) d	18	[1790]
44.61	Colon lining turnover (Homo sapiens)	3.4 ± 0.5 days	23	[2019]
44.64	mean generation time, MY6 (Caenorhabditis elegans)	84 h	7	[604]
44.70	mean generation time, N2 (Caenorhabditis elegans)	90 h	7	[604]

44.70; 44.51	C. elegans generation (Caenorhabditis elegans N2)	90 (min 73.0) h	11	[604]
44.76	stem population doubling upper (Hydra)	4 days	7	[552]
44.76	labelling to nematocyte upper (Hydra)	96 h	7	[551]
44.76	Pupariation after larval hatching (Drosophila melanogaster)	about 96 h	15	[1466]
44.76–44.96	Hydra tentacle renewal	4–5 d	17	[536]
44.96	tentacle tissue renewal upper (Hydra)	5 days	7	[536]
44.96	resting length window (Nematostella vectensis)	5 days	7	[539]
44.96	Physarum habituation phase (Physarum polycephalum)	5 d	18	[1776]
44.96	Octopus observational learning (Octopus vulgaris)	5 d	18	[1785]
44.96	adult lifespan at 25 °C (Megaphragma mymaripenne)	5 days	19	[1463]
45.09	sinking time 1000 m, fastest (particles)	5.7 d	11	[1041]
45.13–46.43	Open-ocean prokaryote turnover (marine prokaryotes)	6–25 days	3	[160]
45.13	regeneration day 6 (Tripedalia cystophora)	6 days	7	[559]
45.13	turnover of plant matter, ocean upper (ocean plants)	6 days	8	[850]
45.13	Return of nicotine response (Nicotiana (wild tobacco))	6 d	13	[1178]
45.27	Sparking duration (Miller apparatus)	1 week	1	[39]
45.27	symbiont doubling time (Symbiodiniaceae)	7 (3–74) days	7	[535]

45.27	clone scoring lower (Hydra)	1 week	7	[553]
45.27	nematocyte differentiation upper (Hydra)	7 days	7	[551]
45.27	doubling time of FMRFamide giant neurons (Tripedalia cystophora)	1 week	7	[559]
45.27	oral regeneration time (Nematostella vectensis)	7 days	7	[539]
45.27	freezing test duration (Adineta (bdelloid rotifer))	7 days	7	[595]
45.27	apical cell specified lower (Marchantia)	7 days	8	[682]
45.27	Egg to adult 28 C; maturity (Drosophila melanogaster)	7 d	15	[1466; 1467]
45.27	All tissues shifted after (mouse)	1 week wk	18	[1722]
45.27	Zebrafish larvae age	7 days post-fertilisation d	18	[1766]
45.27	Aplysia rapid habituation retention (Aplysia californica)	>1 week wk	18	[1783]
45.27–45.90	CA1 spine lifetime (mouse)	about 1–2 weeks wk	18	[1793]
45.27	mouth fighting at zero by (Labroides dimidiatus)	7 days	19	[1809]
45.39	regeneration day 8 (Tripedalia cystophora)	8 days	7	[559]
45.39 (45.41)	water residence atmosphere	8 (8.2) d	11	[24; 1068]
45.39	soybean root-hair curling (Glycine max – rhizobia)	peak day 8 d	12	[1054]
45.48	adult lifespan at 15 °C (Megaphragma mymaripenne)	8.8 days	19	[1463]
45.50–46.81	Ice reaction duration (t5+1 polymerase)	9–38 days	1	[81]
45.50	survival without food, 20 °C (Mnemiopsis leidyi)	9 days	7	[511]
45.50	Physarum whole experiment (Physarum polycephalum)	9 d	18	[1776]

45.57	atmosphere residence check	9.7 d	11	[1065; 1066]
45.60	Mitochondrial lifetime (liver cell)	about 10 days	5	[388]
45.60	apical cell specified upper (Marchantia)	10 days	8	[682]
45.60	Longest flight (birds in flight)	10.02 d	18	[1767]
45.60	mirror behaviour nearly ended (Labroides dimidiatus)	10 days	19	[1809]
45.76–46.23	water residence rivers	12–20 d	11	[24]
45.83	egg to reproductive adult (Mnemiopsis leidyi)	13 days (as few as)	7	[510]
45.85	mushroom fruiting shift, 83 species (Fungi)	13.3 ± 1.2 days	9	[966]
45.90–46.43	MK-D1 doubling (Prometheoarchaeum syntrophicum MK-D1)	14–25 days	3	[171]
45.90	M. leprae division (Mycobacterium leprae)	14 days	3	[157]
45.90	Anammox division (anammox planctomycete)	2 weeks	3	[180]
45.90	Flatworm kleptoplasts (flatworms)	about 2 weeks d	5	[357]
45.90	clone scoring upper (Hydra)	2 weeks	7	[553]
45.90	regrowth of rhopalial neural elements (Tripedalia cystophora)	2 weeks (within)	7	[559]
45.90	memory retention (planarians)	14 (at least) days	7	[592]
45.90	three sporophyte tissues (Marchantia)	2 weeks	8	[682]
45.90	anammox division time (anammox planctomycete)	~2 weeks (1.21e6 s) s	11	[180]
45.90	reactive N in atmosphere	~2 weeks d	11	[224]
45.90–47.37	soft tissue decay (wildebeest carcasses)	2–10 weeks d	11	[1103]
45.90; 46.90	Honey bee worker	2–6 weeks	14	[1307]

	normal lifespan (Apis mellifera)			
45.90–46.27	Hydra whole-tissue renewal	2–3 wk	17	[536]
45.90	Planarian memory (planarians)	≥14 d	18	[592]
45.90–46.90	CA1 full turnover (mouse)	2–3 times lifetime (2–6 weeks) wk	18	[1793]
45.95	lifespan, MY6 (Caenorhabditis elegans)	14.7 days	7	[604]
45.96	Thuridilla hopei	up to 15 d	5	[383]
45.96	soybean nodule swelling (Glycine max – rhizobia)	day 15 d	12	[1054]
45.96; 47.69	Fig cycle inside syconium (Ficus)	15–100 d	14	[1261]
45.98	conifer pollen germination (conifers)	0.5–9 months	8	[740]
46.06	lifespan, N2 (Caenorhabditis elegans)	16.7 days	7	[604]
46.08	radicle after stratification (Amborella trichopoda)	17 days	8	[774]
46.13	ball rolling experiment (Bombus terrestris)	18 days	19	[1818]
46.23	Long-term threshold (sea slugs)	yield >0.4 after 20 d	5	[339]
46.23	mass doubling time (Macrocystis pyrifera)	20.1 days	8	[464]
46.23	maximum growth rate reached (Phyllostachys edulis)	20 days	8	[798]
46.23; 46.86	Honey bee drone maximum (Apis mellifera)	20–40 d	14	[1307]
46.27	TMV HR protection (tobacco)	up to 3 weeks	4	[313]
46.27	renewal of all tissues upper (Hydra)	3 weeks	7	[536]
46.27	growth period (Nematostella vectensis)	3 weeks	7	[539]
46.27	growth to gametogenesis lower (Ulva mutabilis)	3 weeks	8	[425]

46.27	gemma to new gemma cups (Marchantia)	3 weeks	8	[683]
46.27	Long-term habituation retained, minimum (Aplysia)	3 weeks	15	[1351]
46.27	Aplysia long-term habituation (Aplysia californica)	≥3 weeks after 5 daily sessions wk	18	[1351]
46.35	internode 18 rapid growth (Phyllostachys edulis)	23 days	8	[797]
46.35; 46.90	Honey bee worker caged (Apis mellifera)	23–42 d	14	[1307]
46.39	cotyledons after radicle (Amborella trichopoda)	24 days	8	[774]
46.53	infection to first eggs lower (root-knot nematodes)	28 days	7	[617]
46.53	sporangia after fertilisation (Marchantia)	4 weeks	8	[683]
46.53	sinking time 1000 m, compact (aggregates)	28 d	11	[1041]
46.53; 46.90	Root-knot nematode first eggs after infection (Meloidogyne)	28–42 d	13	[617]
46.53	Maturity (Nothobranchius furzeri)	28 d	15	[1419]
46.57	Menstrual cycle median (Homo sapiens)	29.3 (16.9 + 12.4) d	18	[1730]
46.60	arm regrowth time (Coscinasterias acutispina)	30 days (within)	7	[624]
46.60–48.87	Olfactory neuron lifespan (Homo sapiens)	30 days to 1 year d	18	[1699]
46.60	Mimosa retention (Mimosa pudica)	a month d	18	[1778]
46.60	Barrel cortex stable spines (mouse)	about 50 % for ≥1 month d	18	[1791]
46.61	Mesodinium kleptoplasts (Mesodinium rubrum)	up to a month d	5	[357]

46.61	second fission after first lower (Coscinasterias acutispina)	1 month	7	[624]
46.61	fertilisation to ovule fall (Ginkgo biloba)	1 month	8	[738]
46.65	LTP decay 50 trains short baseline (rat)	32 (1 of 9) d	18	[1790]
46.71	Cocoon production after mating (Octodrilus complanatus)	34 ± 3 d	15	[1381]
46.74	Elysia timida	>0.52 after 35 d	5	[339]
46.74	growth to gametogenesis upper (Ulva mutabilis)	5 weeks	8	[425]
46.86	full height reached (Phyllostachys edulis)	40 days	8	[798]
46.90	infection to first eggs upper (root-knot nematodes)	42 days	7	[617]
46.90	burrow experiment (earthworms)	6 weeks (42 d) d	11	[1088]
46.90	LTP decay lateral perforant path (rat)	42 (3 of 4) d	18	[1790]
46.90–47.85 (47.34)	Stable-LTP recording span (rat)	42–119 (mean 68) d	18	[1790]
46.90	juvenile age studied (Octopus bimaculoides)	6 weeks	19	[1355]
46.96	culm height time lower (Phyllostachys edulis)	45 days	8	[797]
46.98	new workers after swarming lower (Macrotermitinae)	1.5 months	9	[940]
46.98; 47.61	New workers after swarming (termites)	1.5–3 months	15	[940]
46.98–47.61	new workers after swarming (fungus-growing termites)	1.5–3 months	19	[940]
46.98–47.61	Termite new workers (Macrotermitinae)	1.5–3 months	23	[940]
47.04	shrinkage period (Nematostella vectensis)	7 weeks	7	[539]
47.06	Acoel brain neuropil regenerated (Symsagittifera roscoffensis)	about 70 % by 50 days d	17	[1609]
47.20	maximum longevity	58 (0.16 yr) days	7	[605]

	in captivity (Caenorhabditis elegans)			
47.23	culm height time upper (Phyllostachys edulis)	60 days	8	[797]
47.23	Egg incubation (Dermochelys coriacea)	60 d	15	[1489]
47.24	Durinskia diatom (Durinskia capensis)	about 2 months d	5	[357]
47.24	life cycle on soil (Arabidopsis thaliana)	2 months	8	[836]
47.24	Infant rhythms pronounced (Homo sapiens)	about 2 months mo	18	[1724]
47.28; 48.02	Interval between penis switches (Nala)	64–143 d	15	[1468]
47.31; 47.06; 47.37	Cocoon incubation (Octodrilus complanatus)	66 ± 2 (50–70) d	15	[1381]
47.41–48.04	non-foraging worker lifespan (Apis mellifera)	0.2–0.4 y	19	[1822]
47.42	Plakobranchus (Plakobranchus ocellatus)	0.78 → 0.59 over 74 d (76 %)	5	[339]
47.44	Leaf lifespan, shortest (280 species)	2.5 months	13	[1189]
47.45	starvation period (Nematostella vectensis)	11 weeks	7	[539]
47.49	survival without food, 3 °C (Mnemiopsis leidyi)	80 days	7	[511]
47.53	Degree Heating Week window (corals)	12 weeks	12	[565]
47.60	stratification (Amborella trichopoda)	90 (at least) days	8	[774]
47.61	second fission after first upper (Coscinasterias acutispina)	3 months	7	[624]
47.61	new workers after swarming upper (Macrotermitinae)	3 months	9	[940]
47.61	Synapse peak hearing cortex (Homo sapiens)	3 months mo	17	[1666]

47.61	auditory synapse density peak (Homo sapiens)	3 months	20	[1666]
47.77	Maximum longevity (Drosophila melanogaster)	0.3 yr	15	[1467]
47.82	Time per successful infection (marine virus particle)	10^7 s (116 days)	4	[286]
47.83	Red blood cell lifetime (Homo sapiens)	116 ± 3 days	23	[2019]
47.87	delay of third founder’s fission (Coscinasterias acutispina)	4 months	7	[624]
47.87	full life cycle in a dish (Physcomitrella)	4 months	8	[684]
47.87	pollination to fertilisation lower (Ginkgo biloba)	4 months	8	[738]
47.91	LTP decay one-year animal (rat)	127 d	18	[1790]
47.94	stratification to cotyledons (Amborella trichopoda)	131 days	8	[774]
47.94; 49.50	Hatching after deposition (Lumbricus terrestris)	132–731 d	15	[1089]
48.07	pollination to fertilisation upper (Ginkgo biloba)	5 months	8	[738]
48.24	adult age studied, at least (Octopus bimaculoides)	6 months	19	[1355]
48.27	synaptogenesis begins, before (Homo sapiens)	27 weeks	20	[1666]
48.29	litter half-life rain forest	0.53 yr	11	[927]
48.45	gestation (Pan troglodytes)	229 d	20	[1894]
48.56	wood half-life, fastest (Heliocarpus appendiculatus)	0.71 years	9	[926]
48.59	gestation from ovulation, median (Homo sapiens)	268 (range 37) d	20	[1905]
48.63	water residence soil	280 d	11	[24]
48.63	gestation (Homo	280 d	20	[1893]

	sapiens)			
48.67	Deep-ocean prokaryote turnover (marine prokaryotes)	0.8 years	3	[160]
48.70	fruit enlargement (Lodoicea maldivica)	10 months	8	[791]
48.77	winter worker lifespan (Apis mellifera)	0.9 y	19	[1822]
48.87	annual life (Physcomitrella)	1 year	8	[677]
48.87	pollination to fertilisation (Pinus)	1 (up to) year	8	[743]
48.87	seasonal cycle (vegetation)	1 year	8	[865]
48.87	Termitomyces fruiting cycle	1 year	9	[940]
48.87–49.50	Oromurcia adult life (Oromurcia sudetica)	1–2 yr	11	[1081]
48.87	Hatching peaks apart (Lumbricus terrestris)	about 12 months	15	[1089]
48.87–49.50	worker lifespan (Lasius niger)	1–2 y	19	[1823]
48.88	LTP longest record (rat)	369 d	18	[1790]
48.94	progamic phase upper (angiosperms)	13 months	8	[740]
48.94	Adult spine half-life (mouse)	>13 months d	18	[1792]
49.01	Frozen; earlier brooding record (colossal squid; Bathypolypus arcticus)	14 months	15	[1347; 1348]
49.07	frontal synapse density peak, after (Homo sapiens)	15 months	20	[1666]
49.10	Supercomputer doubling time (computers)	1.29 years	22	[2002; 2003]
49.18	fine litter turnover, global lower	1.4 years	9	[925]
49.24	age at maturity (Strongylocentrotus franciscanus)	550 days	7	[638]
49.35	cortical thickness peak (Homo sapiens)	1.7 (1.3–2.1) y	20	[1901]
49.38	interval between births (Homo sapiens)	639 d	20	[1893]

49.41	fine-root lifetime (roots)	1.8 yr	11	[1092]
49.50	age at maturity (Strongylocentrotus purpuratus)	730 days	7	[638]
49.50	needle life, low-elevation pines (Pinus)	2–4 years	8	[759]
49.50	seed crops every (Quercus robur)	2–4 years	8	[829]
49.50–50.13	Oromurcia egg to adult (Oromurcia sudetica)	2–4 yr	11	[1081]
49.50	Negative autocorrelation lag, two-year acorn oaks (Quercus)	2 yr	14	[1316]
49.50	Maximum lifespan (Tivela, Argopecten)	2 yr	15	[1352]
49.51	Transistor doubling time (chips)	2.03 years	22	[2001]
49.63	litter half-life median	2.3 yr	11	[927]
49.63	interval between births (Pan troglodytes)	840 d	20	[1894]
49.70	Soil prokaryote turnover (soil prokaryotes)	2.5 years	3	[160]
49.70	Ross Sea dinoflagellate (Antarctic dinoflagellate)	≥30 months d	5	[357]
49.79	sinking time 1000 m, slow (aggregates)	1000 d	11	[1041]
49.81	archaeological weaning age, 39 populations (Homo sapiens)	2.80 ± 1.32 y	20	[1895]
49.87	95 % wood mass loss lower	3 years	9	[926]
49.87	Maximum lifespan (Mytilus californianus)	3 yr	15	[1352]
49.87–50.50	Spanish exponential loss (Homo sapiens)	first 3–6 yr	18	[1801]
49.88	weaning (Pan troglodytes)	1111 d	20	[1894]
49.93	Maximum lifespan (Thyasira)	3.2 yr	15	[1352]
49.98	fine litter turnover, global upper	3.4 years	9	[925]

50.11	litter half-life tundra	3.9 yr	11	[927]
50.11	Oscillation period (Perissodus microlepis)	3.9 yr	15	[1420]
50.13	Fisheries reference period (world fisheries)	4 (1988–1991) yr	13	[1237]
50.13	Maximum lifespan (Corbicula, Yoldia)	4 yr	15	[1352]
50.15	Oscillation period (Perissodus straeleni)	4.1 yr	15	[1420]
50.22	Egg brooding (record) (Graneledone boreopacifica)	53 months	15	[1347]
50.24	growth study duration (Xestospongia muta)	4.5 years	7	[495]
50.34	sexual maturity, grafted (Ginkgo biloba)	5 years	8	[738]
50.34	first seed (Sequoia sempervirens)	5–15 years	8	[756; 757]
50.34	first flowers, Michigan (Pinus sylvestris)	5–8 (average 10–15) years	8	[753]
50.34	fruit ripening (Lodoicea maldivica)	5 (7) years	8	[791]
50.34	fine litter turnover, forests	5 years	9	[925]
50.42	Leaf lifespan, longest (280 species)	66.2 months	13	[1189]
50.49–50.63	air–land CO2 exchange time (atmosphere – land)	5.9–6.9 yr	11	[807; 851; 1112]
50.49	grey matter peak (Homo sapiens)	5.9 (5.8–6.1) y	20	[1901]
50.50	severe bleaching return interval (median) (coral reefs)	6 years	7	[566]
50.50	earlier frozen survival lower (bdelloid rotifers)	6 years	7	[595]
50.50; 52.13	bleaching return time (corals (100 reefs))	median 6 yr (1980–2016)	12	[566]
50.50–51.80	Spanish permastore (Homo sapiens)	6–25 yr	18	[1801]
50.64	bone decay (wildebeest bone)	~7 yr	11	[1103]

50.64; 51.39	Masting wavelet band (Fagus sylvatica)	7–16 yr	14	[1318]
50.76	base flowering interval (Chusquea)	8 years	8	[799]
50.76	Honey bee queen maximum (Apis mellifera)	8 yr	14	[1307]
50.76	male sexual maturity (Pan troglodytes)	2920 d	20	[1894]
50.76	mortality doubling time after 30 (Homo sapiens)	8 y	20	[1893]
50.89	female sexual maturity (Pan troglodytes)	3376 d	20	[1894]
50.97	earlier frozen survival upper (bdelloid rotifers)	10 years	7	[595]
50.97	scale tree life, earlier estimate lower (arborescent lycopsids)	10 years	8	[461]
50.97–51.34	lycopsid lifespan, earlier estimate (arborescent lycopsids)	10–15 yr	10	[692]
51.05	clonal culture duration (Trichoplax adhaerens)	11 years	7	[522]
51.05	eastward song spread, South Pacific (Megaptera novaeangliae)	11 years	21	[1938]
51.13 / 50.97	MK-D1 cultivation (Prometheoarchaeum syntrophicum MK-D1)	12 / 10 years	3	[171]
51.13	wood half-life, base	12.0 years	9	[926]
51.13	Net synapse removal ends (Homo sapiens)	12 yr	17	[1666]
51.17	total cerebrum peak (Homo sapiens)	12.5 (12.14–12.89) y	20	[1901]
51.20	female sexual maturity (Homo sapiens)	4745 d	20	[1893]
51.21	1977 to 1990 (—)	13 years	3	[162]
51.21	coarse woody detritus turnover (forests)	13 years	9	[925]
51.27	Extra maturity at 10 C (Proteus anguinus)	14 yr	15	[1489]

51.27	male sexual maturity (Homo sapiens)	5110 d	20	[1893]
51.30	subcortical grey matter peak (Homo sapiens)	14.4 (14.0–14.7) y	20	[1901]
51.33–51.38	soil carbon stock/flux 1 m	14.9–15.8 yr	11	[1045; 1047]
51.34	scale tree life, earlier estimate upper (arborescent lycopsids)	15 years	8	[461]
51.34	first flowers (Liriodendron tulipifera)	15–20 years	8	[776]
51.34	base flowering interval (Phyllostachys)	15 years	8	[799]
51.34	gap turnover lower (BCI secondary forest)	15 years	8	[877]
51.34	8 to 9 billion expected (Homo sapiens)	about 15 (until 2037) years	22	[1981]
51.45	Mean spacing of extreme mast years (computed) (Fagus sylvatica)	17.0 yr	14	[1318]
51.55	turnover of plant matter, land (land plants)	19 years	8	[850]
51.60	lifespan (Gigantoproductus okensis)	20 years	7	[597]
51.60	sexual maturity lower (Ginkgo biloba)	20 years	8	[738]
51.60	first flowers (Picea abies)	20–30 (–40) years	8	[754]
51.60	minimum seed-bearing age (Quercus robur)	20 years	8	[829]
51.60	termite reproductive lifespan (Macrotermitinae)	20 (up to about) years	9	[940]
51.60	termite royal pair life (termites)	≤~20 yr	12	[940]
51.60	TR4 spore survival in soil (Fusarium TR4)	>20 yr	13	[1225]
51.60	Primary reproductives maximum (termites)	about 20 yr	15	[940]
51.60	Vertebral fusion	20 yr	15	[1508]

	begins after (Homo sapiens)			
51.60	Anthropogenic mass doubling (technosphere)	about 20 years	22	[1989]
51.60	Termite primary reproductives maximum (Macrotermitinae)	about 20 yr	23	[940]
51.64	One billion internet users	2005 (1,025,764,000) year	23	[2008]
51.67	mean observation per study, computed (Pan troglodytes)	21.6 years	21	[1939]
51.72	white-nose count span (Pseudogymnoascus destructans)	23 years	9	[949]
51.72	soil carbon stock/flux 2 m	23 yr	11	[1046; 1047]
51.76	Maximum lifespan (Mesodesma, Geukensia, Mytilus edulis)	24 yr	15	[1352]
51.80	reproductive age (Lodoicea maldivica)	25 years	8	[791]
51.90	chytridiomycosis discovered (Batrachochytrium)	1998 year	9	[946]
51.90	Sr31 deployment to breakdown (wheat; Puccinia graminis)	28 yr	13	[1204; 1215]
51.90	queen maximum longevity (Lasius niger)	28 y	19	[1823]
51.93	white matter peak (Homo sapiens)	28.7 (28.1–29.2) y	20	[1901]
51.96	father’s mean age (Iceland)	29.7 years	20	[1889]
51.97	sexual maturity upper (Ginkgo biloba)	30 years	8	[738]
51.97	reactive N in land ecosystems	~30 yr	11	[224]
51.97	Spanish stable retention (Homo sapiens)	up to 30 yr	18	[1801]
51.97	hunter-gatherer life expectancy (Homo sapiens)	~30 y	20	[1893]
51.98	frozen in moss and revived (Acutuncus	30.5 years	7	[611]

	antarcticus)			
52.02	flowering interval (Bambusa bambos)	32 years	8	[799]
52.11	Maximum lifespan (Architeuthis dux)	35 yr	15	[1352]
52.13	1977 to 2013 (—)	36 years	3	[163]
52.13	Amazon stem residence lower (Amazonia)	36 years	8	[878]
52.23	minimum seed-bearing age (Picea abies)	40–60 years	8	[755]
52.23	first seed in open (Fagus sylvatica)	40–50 years	8	[831; 832]
52.25	oldest cohort ages (Hydra)	41 years	7	[555]
52.29	Oldest recorded spider (Gaius villosus)	43 yr	15	[1401]
52.34	needle life (Pinus longaeva)	45 (up to about) years	8	[759]
52.34–52.52	menopause age (Homo sapiens)	45–55 y	20	[1899]
52.39	chemosynthetic symbiosis discovery (Galápagos Rift vents)	~1978 year	12	[1122]
52.43	Chickenpox antibody half-life (humans)	50 years	4	[332]
52.43	maximum longevity (Strongylocentrotus purpuratus)	50 years	7	[638]
52.43	Lr34 durable resistance (wheat)	>50 yr	13	[1216]
52.55	Hippocampal turnover time (Homo sapiens)	57 yr	17	[1648]
52.55	Wu Ding reign length, computed (Shang China)	57 years	21	[1967]
52.60	Akinete dormancy (cyanobacteria)	60 years	3	[181]
52.60	flowering interval (Phyllostachys nigra f. henonis)	60 years	8	[799]
52.60	first seed in stands (Fagus sylvatica)	60–80 years	8	[832]
52.60	Bd emergence to decline peak lower (Batrachochytrium dendrobatidis)	60 years	9	[946; 947]

52.60	akinete dormancy (Nostoc)	up to 60 yr	12	[181]
52.64	healthy life expectancy, 2023 (Homo sapiens)	62.8 y	20	[1507]
52.68	regrowth to 90 % biomass (Neotropical forest)	66 years	8	[879]
52.71–52.84	adaptive lifespan, hunter-gatherers (Homo sapiens)	68–78 y	20	[1897]
52.78	Life expectancy at birth (Homo sapiens)	73.3 yr	15	[1507]
52.82	Amazon stem residence upper (Amazonia)	77 years	8	[878]
52.86	Bd emergence to decline peak upper (Batrachochytrium dendrobatidis)	80 years	9	[946; 947]
52.91	ideal average lifespan (Fries) (Homo sapiens)	85 y	20	[1917]
52.95	highest life expectancy 2021, Hong Kong (Homo sapiens)	88 y	20	[1915]
53.06	large red urchins age (Strongylocentrotus franciscanus)	100 (or more) years	7	[635]
53.06	scale tree life, centuries (arborescent lycopsids)	100 (centuries) years	8	[692]
53.06	full size (Lodoicea maldivica)	100 years	8	[791]
53.06	oak reference tree age (Quercus robur)	100 years	8	[837]
53.06–55.16	reactive N in peatlands	100–1000 yr	11	[224]
53.06–55.16	soil formation 1 cm compilation	100–1000 yr	11	[1097]
53.06	Maximum longevity, wild (Homarus americanus)	100 yr	15	[1451]
53.11	Maximum lifespan (Cyrtodaria siliqua)	105 yr	15	[1352]
53.23	flowering interval (Phyllostachys bambusoides)	120 years	8	[799]
53.24	chestnut blight first noticed	1904 (122 years ago) year	9	[955]

	(Cryphonectria parasitica)			
53.25	maximum longevity (Homo sapiens)	122.5 y	20	[1893]
53.25	longest verified life (Jeanne Calment)	122 y 164 d	20	[1916]
53.28	age of largest transect sponge (Xestospongia muta)	127 years	7	[495]
53.29 (128 years to 2026)	First virus described (tobacco mosaic virus)	1898 year	4	[323]
53.29	Human recognition of a virus, 1898 to 2026 (viruses)	128 yr	13	[333]
53.39	FAM-1 lineage sampled (Phytophthora infestans)	144 (1845–1987) yr	13	[1220]
53.43	lifespan (Fagus sylvatica)	150–300 years	8	[831]
53.43	protists first recorded (termite protists)	1877 (Leidy) year	12	[1126]
53.53	Maximum lifespan (Panopea generosa)	168 yr	15	[1352]
53.56	wood half-life, slowest (Eucalyptus camaldulensis)	173 years	9	[926]
53.61	time for 6 m trunk at 3.3 cm per year (Dicksonia antarctica)	182 years	8	[712]
53.69	largest British Columbia red urchins age (Strongylocentrotus franciscanus)	200 years	7	[635; 638]
53.69	viable seed to age (Pinus sylvestris)	200 (at least) years	8	[753]
53.69	lifespan (Picea abies)	200–300 years	8	[754]
53.69	natural death (Liriodendron tulipifera)	200–250 (300) years	8	[776]
53.79	gap turnover upper (BCI secondary forest)	222 years	8	[877]
53.87	Time to 75 % loss, amphibians	241.7 yr	16	[1543]
53.90	seed viability (Sequoia sempervirens)	250 (more than) years	8	[757]

53.90	Longevity (Lamellibrachia luymesi)	250 yr	15	[1384]
53.92–53.94	A-horizon loss time (soil)	256–263 yr	11	[1095]
54.06–62.73	Hawaiian chronosequence (Hawaii soils)	300 yr to 4.1 Myr	11	[1059]
54.06	water residence groundwater	~300 yr	11	[24]
54.06	Longevity (Escarpia laminata, Seepiophila jonesi)	300 yr	15	[1384]
54.16	Time to 75 % loss, mammals	334.4 yr	16	[1543]
54.20	lifespan (Lodoicea maldivica)	350 (up to) years	8	[791]
54.29	time to form 1 cm (soil)	385 yr	11	[1095]
54.31–55.41	time to bedrock (soil)	394–1325 yr	11	[1095]
54.32	scale tree life, 40 m tree (arborescent lycopsids)	400 (200–800) years	8	[692]
54.32 (53.69–54.95)	lycopsid lifespan, revised (arborescent lycopsids)	~400 (200–800) yr	10	[692]
54.54	Maximum lifespan, Ming (Arctica islandica)	507 yr	15	[1352]
54.59	Time to 75 % loss, birds	536.6 yr	16	[1543]
54.65	Gutenberg Bible date (Mainz)	~1455 year	21	[1974; 1975]
54.77	heartwood years, oldest climbed (Eucalyptus regnans)	651 years	8	[825]
54.79	oldest tree in cambial study (Ginkgo biloba)	667 years	8	[739]
54.83	mound age (Macrotermitinae)	700 years	9	[940]
54.83–55.88	termite mounds (termites)	~700 to 2200 yr	12	[940]
54.83	mound age (Macrotermes)	700 y	19	[940]
54.90	95 % wood mass loss upper	750 years	9	[926]
54.95–57.25	Background time for last-century losses (vertebrates)	800–10,000 yr	16	[1572]
55.10	naming time at 2,500 per year (Fungi)	938 years	9	[910]

55.16	Peptide bond lifetime in water	1000 years	1	[15]
55.16–55.79	Subsurface turnover (subsurface prokaryotes)	1000–2000 years	3	[160]
55.16	oldest Chinese ginkgo, estimate lower (Ginkgo biloba)	1000 years	8	[734]
55.16	lifespan in some cases (Quercus robur)	1000 (over) years	8	[828]
55.16	management before morphology, at least (plants and animals)	1000 years	20	[1921]
55.16	Management before morphology (crops and herds)	at least 1,000 years	22	[1921]
55.24	baobab Platland age (Adansonia digitata)	1100 years	8	[830]
55.24	margin over Spanish stencil (Homo sapiens)	1.1 kyr	21	[1955]
55.40	proto-cuneiform to first alphabet, computed (writing)	~1300 years	21	[1965; 1970]
55.40–56.49	Livestock spread to new regions	1,300–4,300 years	22	[1923]
55.46	baobab Chapman age (Adansonia digitata)	1400 years	8	[830]
55.53	baobab Grootboom age (Adansonia digitata)	1500–1600 years	8	[830]
55.53	Michigan genet stability (Armillaria gallica)	1500 (more than) years	9	[960]
55.67	doubling time 10,000 BCE to year 0, computed (Homo sapiens)	1758 years	20	[1980]
55.69	baobab Holboom age (Adansonia digitata)	1800 years	8	[830]
55.74	Oregon genet age lower (Armillaria ostoyae)	1900 years	9	[439]
55.79	giant barrel sponges, age (Xestospongia)	2000 years (or more)	7	[492]
55.79	baobab Glencoe age (Adansonia digitata)	2000 years	8	[830]
55.79	Germinated ancient seed (Phoenix	about 2,000 yr	14	[1313]

	dactylifera, Masada)			
55.79	proto-cuneiform to Phoenician, computed (writing)	~2000 years	21	[1965; 1971]
55.83	baobab Dorslandboom age (Adansonia digitata)	2100 years	8	[830]
55.88	oldest Sequoia by ring count (Sequoia sempervirens)	2200 years	8	[757]
55.88	mound age, older (Macrotermitinae)	2200 (at least) years	9	[940]
55.88	mound age, at least (Macrotermes)	2200 y	19	[940]
55.92	upper age estimate (Xestospongia muta)	2300 years	7	[495]
55.99	Michigan genet minimum age 2018 (Armillaria gallica)	2500 years	9	[961]
55.99–56.10	Wild cultivation to domestic grain (cereals)	2,500–2,800 years	22	[1923]
56.02	age of deep soil carbon mineralised	2567 ± 226 years	9	[929]
56.03–56.69	Neanderthal–modern overlap (Homo)	2,600–5,400 years	20	[1876]
56.08	age (Gerardia)	2742 years	7	[542]
56.16	oldest Chinese ginkgo, estimate upper (Ginkgo biloba)	3000 years	8	[734]
56.16–56.93	CaCO3 neutralisation (carbon cycle)	3–7 kyr	11	[1113]
56.19	Ocean residence time	3100 years	1	[24]
56.23	ocean residence check	3240 yr	11	[1065; 1066]
56.27–56.90	obliquity lag (climate)	3.4 to 6.8 kyr	11	[1027]
56.35; 13.69	15.5 cm thallus age (Rhizocarpon alpicola)	~3700 yr	12	[912]
56.48	age (Leiopathes)	4265 years	7	[542]
56.49	chimpanzee stone sites (Pan troglodytes)	~4300 years	21	[1940]
56.53	lichen thallus age (Rhizocarpon)	4500 (at least) years	9	[912]
56.53	lichen age West Greenland (Rhizocarpon)	≥4500 yr	12	[912]

56.59	radiocarbon age soil carbon	4830 ± 1730 (789 profiles) yr	11	[1048]
56.60	oldest Pinus longaeva, Wheeler Peak	4900 years	8	[760]
56.60	Methuselah, crossdated (Pinus longaeva)	4850 years	8	[852]
56.62	Carbon-cycle disruption (carbon cycle)	<5 kyr	16	[1559]
56.88	Potyvirus radiation (potyviruses)	about 6,600 years	4	[310]
56.88	Potyvirus radiation (Potyviridae)	about 6,600 yr	13	[310]
57.12	Oregon genet age upper (Armillaria ostoyae)	8650 years	9	[439]
57.16	lichen thallus age, older (Rhizocarpon)	9000 years	9	[912]
57.16	480 mm thallus age (Rhizocarpon alpicola)	~9000 yr	12	[912]
57.25	PETM warming duration (Earth)	about 10,000 yr	13	[1173]
57.25	Basenji, Dingo, Singing Dog introduced after domestication (Canis familiaris)	>10,000 years	22	[1926]
57.34	lifespan (Monorhaphis chuni)	11000 ± 3000 years	7	[494]
57.34	Holocene record (EPICA Dome C)	11000 yr	11	[1034]
57.34	Holocene carbon cycle not in equilibrium	11000 yr	11	[1035]
57.34; 57.25	Onset of domestication (humans)	11,000–10,000 yr	14	[1322]
57.38	domestication span (plants and animals)	11,500 years	20	[1920]
57.42	present interglacial so far (climate)	~12000 yr	11	[1030]
57.46	clone age minimum (Posidonia oceanica)	12500 years	8	[800]
57.49	Jurupa Oak clone (Quercus palmeri)	13000 (more than) years	8	[838]
57.56	Pando upper age (Populus tremuloides (Pando))	14000 years	8	[463]

57.62	AnAge maximum longevity (Scolymastra joubini)	15000 years	7	[500]
57.62–57.42	deglaciation interval (climate)	15000–12000 yr	11	[858]
57.62	Hadza–Sandawe common ancestry (Hadza; Sandawe)	>15,000 years	21	[1959]
57.68	water residence glaciers	16000 yr	11	[24]
57.68	Post-glacial nut-tree range shifts (nut trees)	last 16,000 yr	14	[1276]
57.72	margin over Maros-Pangkep minimum (Homo sapiens)	16.6 kyr	21	[1955]
57.88–59.35	phosphate residence in ocean	20000–100000 yr	11	[1052]
57.97	End of interval after base of Triassic (stratigraphy)	0.022 Myr	16	[435; 1021]
58.01	2 m specimen, age estimate (Scolymastra joubini)	23000 years	7	[500]
58.05	age of revived rotifer lower (Adineta (bdelloid rotifer))	23960 years	7	[595]
58.07	age of revived rotifer upper (Adineta (bdelloid rotifer))	24485 years	7	[595]
58.12	High-resolution interval (marine invertebrates)	about 26 kyr	16	[1570]
58.19	interglacial after Termination V (climate)	~28000 yr	11	[1030]
58.25	Pithovirus age in permafrost (Pithovirus sibericum)	>30,000 years	4	[267]
58.25	midden record (packrat middens)	30000 yr	11	[858]
58.25	High-productivity ecosystem at crater (Chicxulub crater biota)	within 30 kyr	16	[1561]
58.25	Neanderthal presence until (2010)	~30,000 years	20	[1872]
58.25	drawing margin over later drawings, at least (Homo sapiens)	30,000 years	21	[1952]
58.34	Impact within extinction (Chicxulub	within 33 kyr	16	[1559]

	impact)			
58.39	engravings before Upper Palaeolithic, at least (Homo sapiens)	35,000 years	21	[1951]
58.39	click-speaker split, older (Hadza; Sandawe)	>35,000 years	21	[1959]
58.40	babirusa painting, minimum (Homo sapiens)	35.4 kyr	21	[1953]
58.48	time to form 1 m (soil)	38500 yr	11	[1095]
58.51	oldest Maros hand stencil, minimum (Homo sapiens)	39.9 kyr	21	[1953]
58.54	obliquity period (climate)	41 kyr	11	[1027]
58.59	Lomatia tasmanica clone	43600 (at least) years	8	[839]
58.62	modern humans in Europe, more than (Homo sapiens)	45,000 years	20	[1883]
58.62–58.70	shared Neanderthal admixture (Homo sapiens)	45,000–49,000 years	20	[1883]
58.64	revived from permafrost (Panagrolaimus kolymaensis)	46000 years	7	[612]
58.72	Altai layer age, at least (Neanderthal)	50,000 years	20	[1871]
58.74	Leang Karampuang narrative art, at least (Homo sapiens)	51,200 years	21	[1954]
58.88	end-Permian extinction duration (biosphere)	60 ± 48 kyr	11	[1021]
58.88	Kebara human hyoid (Homo (Kebara 2))	~60,000 years	21	[1945]
58.90	End-Permian extinction duration (marine biota)	60 ± 48 (61 computed) kyr	16	[1021]
58.96	Madjedbebe occupation (Homo sapiens)	~65,000 years	20	[1882]
59.03	Blombos overlying dune, OSL (Homo sapiens)	70,000 years	21	[1951]
59.06	Blombos abstract drawing (Homo sapiens)	~73,000 years	21	[1952]

59.11	Blombos engraved ochre, TL (Homo sapiens)	77,000 years	21	[1951]
59.15	shared genet age lower (Posidonia oceanica)	80000 years	8	[800]
59.17	Taforalt beads (Nassarius gibbosulus; Homo sapiens)	~82,000 years	21	[1950]
59.35	CO2 swings (late Paleozoic climate)	~1e5 yr	10	[1004]
59.35; 63.97	LPIA CO2 swings (atmosphere)	~1e5 in 16 Myr record yr	11	[1004]
59.35	Corral Bluffs first step (mammals; plants)	~100 kyr	16	[1562]
59.35–59.62	Skhul bead layer (Nassarius gibbosulus; Homo)	100,000–135,000 years	21	[1948]
59.35	Blombos ochre workshop (Homo sapiens)	~100,000 years	21	[1949]
59.49	bottleneck duration (human ancestors)	117,000 years	20	[1870]
59.59	Krapina talons age (Neanderthal)	~130 kyr	21	[1947]
59.72	organic P maximum (Hawaii soils)	~150000 yr	11	[1059]
59.72	End-Triassic crisis within onset of flood basalts (marine biota)	<150 kyr	16	[1556]
59.78–62.38	End-Permian duration (table) (all species)	160 kyr–2.8 Myr	16	[1543]
59.78	Xiahe Denisovan mandible	≥160,000 years	20	[1875]
59.83	PETM duration (climate)	~170 kyr	11	[1025]
59.87	Misliya maxilla (Homo sapiens)	≥177,000 years	20	[1880]
59.97	Omo I earlier estimate (Homo sapiens)	~197 kyr	20	[1879]
59.98	shared genet age upper (Posidonia oceanica)	200000 years	8	[800]
59.98; 59.35	Life-cycle divergence (Magicicada)	200,000–100,000 yr	14	[1309]
59.98	End of Nama to Cambrian base	0.2 Myr	16	[435; 1539]

	(Ediacara biota)			
59.98	Crater record span (Chicxulub crater biota)	about 200 kyr	16	[1561]
60.12	Omo I minimum age (Homo sapiens)	233 ± 22 kyr	20	[1879]
60.13–60.45	H. naledi age (Homo naledi)	236,000–335,000 (226,000 in significance statement) years	20	[1858]
60.32	End-Triassic carbon spike within boundary (carbon cycle)	<290 kyr	16	[1556]
60.35	Export production recovery elsewhere (marine plankton)	300 kyr	16	[1561]
60.35	Corral Bluffs second step (mammals; plants)	~300 kyr	16	[1562]
60.35	Local mammal diversity recovered (mammals)	within 300 kyr	16	[1563]
60.57	Neanderthal–Denisovan split, PSMC (Neanderthals–Denisovans)	381,000 years	20	[1871]
60.66	Vostok record (Vostok ice core)	4 cycles over 420000 yr	11	[1029]
60.71–60.76	Neanderthal–Denisovan split, allele sharing (Neanderthals–Denisovans)	445,000–473,000 years	20	[1871]
60.72	Southern Ocean record (sediments)	450000 yr	11	[1026]
60.81	carbon-cycle volatility after extinction (carbon cycle)	~500 kyr	11	[1021]
60.81	First three splits within (Pteropodidae)	about 0.5 Myr	14	[1275]
60.81	End-Permian carbon-cycle volatility (carbon cycle)	about 500 kyr	16	[1021]
60.81	Eye evolution time (model eye)	a few hundred thousand years ($<5 \times 10^5$ generations) yr	18	[1679; 1681]
60.90–61.20	modern–archaic split, allele sharing (Homo)	550,000–765,000 years	20	[1871]

60.91–60.96	modern–archaic split, PSMC (Homo)	553,000–589,000 years	20	[1871]
60.98	CAMP magma pulses (Central Atlantic Magmatic Province)	4 pulses over about 600 kyr	16	[1555]
61.05	K–Pg to oldest legume (Fabaceae)	0.65 Myr	16	[1129]
61.07–61.20	Asteriornis to K–Pg (Asteriornis maastrichtensis)	0.66–0.76 Myr	16	[1526]
61.12	Corral Bluffs third step (mammals; plants)	~700 kyr	16	[1562]
61.12	Lomekwi margin over Oldowan (hominins)	700,000 years	20	[1847]
61.17	EPICA record (EPICA Dome C)	8 cycles over ~740000 yr	11	[1030]
61.23	fire, Gesher Benot Ya’aqov (hominins)	~790,000 years	20	[1866]
61.24	Azolla event duration	800000 years	8	[381; 703]
61.24	O2 residence with Berner burial (atmosphere)	0.8 Myr	10	[1008]
61.24	Azolla phase duration	~800 kyr	11	[703]
61.27	O2 residence with total burial (atmosphere–ocean)	0.82 Myr	11	[860; 863]
61.45–63.54	Oxygenation duration (atmosphere)	1–10 Myr	3	[225]
61.45	end-Permian proliferation duration (fungi)	1 (less than) Myr	9	[923; 924]
61.45	phosphorus pulses (ocean)	≤1 Myr	11	[721]
61.45	End-Permian fungal proliferation (fungi)	<1 Myr	16	[924]
61.45–62.45	Ammonoid diversification after end-Permian (ammonoids)	1–3 Myr	16	[1551]
61.45	Mammal richness doubled (mammals)	within 1 Myr	16	[1562]
61.75	End-Ordovician to base of Silurian (stratigraphy)	1.4 Myr	16	[435]
61.81	Lost City crust age	1.5 Myr	1	[52]
61.81	Metazoan reefs after end-Permian	1.5 Myr	16	[1554]

	(sponges; serpulids; microbialites)			
61.87	Carnian humid pulses (climate)	about 1.6/1.7 Myr	16	[1558]
62.08–62.45	Cairo older than Gilboa (forests)	2–3 Myr	10	[716]
62.08	Wolbachia co-divergence (Wolbachia – host)	~2 Myr	12	[1124]
62.12	oxygen residence time (atmosphere–ocean)	2.1 Myr	8	[860]
62.12	O2 residence time (atmosphere)	~2.1 Myr	10	[1008]
62.28	Cairo older than Gilboa by (Archaeopteris)	2–3 Myr	8	[716]
62.28 to <48.87	K–Pg duration (table) (all species)	2.5 Myr to under 1 yr	16	[1543]
62.38	Difference article age to chart (stratigraphy)	2.8 Myr	16	[435; 1545]
62.45–62.71	Track shift duration (Dinosauria)	3–4 Myr	16	[1558]
62.50; 62.83	Clausiliid coiling reversals, one per (Clausiliidae)	3.2–4.6 Myr	15	[1353]
62.53–62.03	End-Ordovician duration (marine animals)	3.3–1.9 Myr	16	[1543]
62.68	Cooksonia to first fire (land plants and fire)	3.9 Myr	10	[455; 970]
62.71	Hypsodont Equinae after grasslands	at least 4 Myr	13	[1170]
62.85	Early Triassic duration (stratigraphy)	4.7 Myr	16	[435]
62.91–63.08	End-Permian shocks repeated (environment)	5–6 Myr	16	[1551]
62.91	Early Triassic assumed recovery span (marine biota)	5 Myr	16	[1554]
62.96	benthic d18O stack (57 records)	5.3 Myr	11	[1027]
63.34	higher agriculture to leaf-cutting lower (Attini)	8 Myr	9	[937]
63.34–63.45	Stable complex ecosystem after end-	8–9 Myr	16	[1551]

	Permian (marine ecosystems)			
63.37–60.98	End-Triassic duration (table) (all species)	8.3 Myr–600 kyr Myr	16	[1543]
63.51	Insect herbivory recovery after K–Pg (plant–insect associations)	9.7 (65.5 to 55.8 Ma) Myr	16	[990]
63.54	duration of oxygenation change (Earth atmosphere)	10 Myr	8	[225]
63.54	tracks before elpistostegids (tetrapods)	10 Myr	10	[991]
63.54–63.91	coccolithophores to diatom clock (nannoplankton)	10–15 Myr	11	[668; 1024]
63.54	Herbivory recovery after K–Pg (plant–insect record)	about 10 (65.5 to 55.8 Ma) Myr	13	[990]
63.54	Nitrile-specifier protein origin after Brassicales (Pieridae)	within about 10 Myr	13	[1181]
63.54	White Sea duration (Ediacara biota)	10 Myr	16	[1539]
63.54	Lizards and snakes to Cretaceous levels (Squamata)	10 Myr	16	[1564]
63.54–63.91	Neoaves lineages after K–Pg	36 within 10–15 Myr	16	[1526]
63.54	Extinction–origination lag (marine genera)	roughly 10 Myr	16	[1574]
63.63	Nama duration (Ediacara biota)	11 Myr	16	[1539]
63.63	PBDB time bins (marine invertebrates)	48 bins of about 11 Myr	16	[1552]
63.70	Scleractinians after end-Permian	11.9 Myr	16	[528]
63.78	higher agriculture to leaf-cutting upper (Attini)	13 Myr	9	[937]
63.78	Pneumodesmus redating (Pneumodesmus newmani)	13 Myr	10	[978]
63.78	Age difference (computed) (Pneumodesmus newmani)	about 13 Myr	15	[978]

63.80	Kellwasser to Hangenberg interval (marine animals)	13.3 Myr	16	[435]
63.86	first macrofossils to Haootia (Ediacaran)	14.17 Myr	7	[450; 523]
63.86	Haootia after first complex fossils (Haootia quadriformis)	14.17 Myr	17	[450; 523]
63.87	Introduced genes mean age (Escherichia coli)	14.4 Myr	3	[188]
63.91	hominid gut cospeciation (Bacteroidaceae; Bifidobacteriaceae – hominids)	~15 Myr	12	[1131]
63.91	Dinosaur radiation possibly earlier by (Dinosauria)	15 Myr	15	[1524]
63.91	Avalon duration (Ediacara biota)	15 Myr	16	[1539]
63.91	gut bacteria cospeciation with hominids (Homo, Pan, Gorilla gut bacteria)	15 Myr	20	[1131]
63.93	K–Pg to passerine crown (Passeriformes)	15.3 Myr	16	[1526]
63.97	CO2 record length (late Paleozoic climate)	16 Myr	10	[1004]
63.98	first macrofossils to Dickinsonia (Metazoa)	16.17 Myr	7	[450; 451]
64.02	Spinescence window (southern African woody plants)	17 Myr	13	[1172]
64.07–64.17	End-Permian to Carnian Pluvial Episode (Dinosauria)	17.9–19.9 Myr	16	[1558]
64.08	tracks before body fossils (tetrapods)	18 Myr	10	[991]
64.13	Domatia window (ant-plants)	19 Myr	13	[1195]
64.14	Dickinsonia to Cambrian base (Metazoa)	19.2 Myr	7	[435; 451]
64.17	Tissue-to-eater lag, first phase, maximum (arthropods)	20 Myr	13	[987]

64.21	Cambrian base to Chengjiang (Metazoa)	20.77 Myr	7	[435; 452]
64.22	split to crown (termites)	21 Myr	12	[941]
64.26	Cambrian explosion span (animals)	>22 Myr	6	[452]
64.26	explosion duration (Metazoa)	22 (more than) Myr	7	[452]
64.30	Ecdysozoa clock lead over traces	23 (at least) Myr	7	[525]
64.33	coal forest duration lower (coal forests)	23.9 Myr	8	[435; 724]
64.34	Herbivory recovery after P–Tr (plant–insect record)	24 (to 228 Ma) Myr	13	[990]
64.34	Insect herbivory collapse to recovery (Permian–Triassic) (plant–insect associations)	24 (252 to 228 Ma) Myr	16	[990]
64.35	Pennsylvanian duration	24.3 Myr	10	[435]
64.38	crown cnidarian record extended	25 Myr	7	[524]
64.38	C4 origin before dominance (Poaceae)	at least 25 Myr	13	[1169]
64.38	Cambrian radiation duration (animals)	as little as 25 Myr	18	[1679]
64.41	Mammal maximum body size rise (land mammals)	26 Myr	16	[1565]
64.45	coal forest duration upper (coal forests)	27.2 Myr	8	[435; 724]
64.48	skeleton to photosymbiosis (Scleractinia)	28 Myr	7	[528; 533]
64.48	coral expansion to photosymbiosis (corals)	28 Myr	12	[533]
64.51–62.08	Devonian duration (all species)	29–2 Myr	16	[1543]
64.54	HERV-K(HML2) pool (primates)	30 Myr	4	[306]
64.54	shortening by Mongolian or Namibian spicules (Silicea)	30 Myr	7	[486]
64.54	Ediacara biota span	30 Myr	7	[451]
64.54	farming to higher agriculture, earlier lower (Attini)	30 Myr	9	[937]

64.54	Dinosaur radiation duration (Dinosauria)	30 Myr	16	[1557]
64.56–64.62	Carnian Pluvial Episode to end-Triassic (Dinosauria)	30.6–32.6 Myr	16	[1558]
64.57	step 551 to 520 Ma (Porifera)	31 Myr	7	[486; 491]
64.66	farming to higher agriculture, earlier upper (Attini)	34 Myr	9	[937]
64.68	Protomelission first-occurrence shift (Bryozoa)	35 Myr	7	[571]
64.68	Late Triassic length (stratigraphy)	over 35 Myr	16	[1558]
64.69	first macrofossils to Cambrian base (Metazoa)	35.2 Myr	7	[435; 450]
64.69	ant farming to termite farming (Fungi)	35.24 Myr	9	[936; 939]
64.69	Oldest complex fossils to Cambrian base (Ediacara biota)	35.4 Myr	16	[435; 450]
64.80	interval for 1 % of genes to move chromosome (Metazoa)	40 Myr	7	[472]
64.80	sand-dollar gap lower (Scutelloida)	40 Myr	7	[623]
64.80	farming to higher agriculture, later estimate (Attini)	39.65 Myr	9	[936]
64.80	trackway extension of landfall (arthropods)	≤40 Myr	10	[971]
64.80–65.01; 65.25	Sand dollar origin before first fossils (Scutelloida)	40–50, possibly 65 Myr	16	[623]
64.85	predisposition vs nodulation age gap (Leguminosae)	42 Myr	12	[213; 1128]
64.85	First farming to leaf-cutting (computed) (Attini)	42 Myr	14	[937]
64.85	Split minus Chengjiang limit (computed) (Vertebrata)	41.97 Myr	15	[1409; 1411]
64.89	gap between clock intervals (Cnidaria)	44.2 Myr	7	[485; 530]
64.89	gap Tremadocian	44 Myr	7	[571]

	record to clock origins (Bryozoa)			
64.93	spores to Cooksonia (land plants)	46 Myr	10	[454; 455]
64.99	step 600 to 551 Ma (Porifera)	49 Myr	7	[490; 491]
65.01	sand-dollar gap upper (Scutelloida)	50 Myr	7	[623]
65.01	Doushantuo earlier than previous (ocean)	>50 Myr	11	[449]
65.01	Record extension (insect pollination of angiosperms)	at least 50 Myr	14	[1259]
65.02	Interval end-Permian to end-Triassic (Big Five)	50.5 Myr	16	[435]
65.04	photosymbiosis to symbiont clock (Scleractinia)	52 Myr	7	[533; 534]
65.04	isotope vs clock symbiont date (corals – Symbiodiniaceae)	52 Myr	12	[533; 534]
65.08	seed predation lag (Trigonocarpus)	54 Myr	10	[987]
65.08	Lag after origin of seeds (seed predation, Trigonocarpus) (seed predators)	54 Myr	13	[987]
65.09	Horse tooth-wear survey span (Equidae, North America)	55 Myr	13	[1171]
65.17	Azolla review age (Azolla–Nostoc)	>60 Myr	5	[354]
65.17–65.80	clitellate ancestor to earthworm crown (Clitellata)	60–120 Myr	11	[1000; 1001]
65.17	Fig–wasp co-divergence (10 fig and wasp lineage pairs)	at least 60 Myr	14	[1262]
65.19	Marinoan steranes to first macrofossils (Metazoa)	61 Myr	7	[446; 450]
65.20	Scorpionfly pollination interval (Mecoptera)	62 Myr	14	[1252]
65.20	Diversity cycle 62 Myr (marine genera)	62 ± 3 Myr	16	[1569]
65.22	wood boring lag (Trivenia)	63 Myr	10	[987]

65.22	Lag after origin of wood (Trivenia) (wood borers)	63 Myr	13	[987]
65.25	sand-dollar gap possible (Scutelloida)	65 Myr	7	[623]
65.25	mid-Palaeozoic herbivory hiatus (land herbivory)	65 Myr	10	[987]
65.25	Mid-Palaeozoic herbivory hiatus (arthropods)	65 Myr	13	[987]
65.25	Period with at least 14 reversals (Clausiliidae)	more than 65 Myr	15	[1353]
65.28–65.34	insect clock to Rhynie hexapods (Hexapoda)	67.5–72 Myr	10	[458; 979]
65.29	AM clock to Rhynie (AM symbiosis)	68.5 Myr	12	[299]
65.31	Minimum age of Glossata extended by	about 70 Myr	14	[1251]
65.35	AM origin to Rhynie (arbuscular mycorrhiza)	73 Myr	9	[299; 894]
65.35	Interval end-Ordovician to Late Devonian (Big Five)	73.0 Myr	16	[435]
65.38	crown Deuterostomia width	75.1 Myr	7	[485]
65.38	crown Protostomia width	75.0 Myr	7	[485]
65.38	myriapod clock-fossil gap (Myriapoda)	75 Myr	10	[975]
65.38	clock flight to oldest winged fossil (Pterygota)	75.1 Myr	10	[979; 980]
65.38	diatom origin to abundant record (Bacillariophyta)	75 Myr	11	[668]
65.39	leaf-feeding lag (land herbivory)	76 Myr	10	[987]
65.39	Lag after origin of leaves (leaf feeders)	76 Myr	13	[987]
65.43	Marsupial env conserved (marsupials, tammar wallaby)	>80 Myr	4	[301]
65.43	ice age duration (climate)	80 Myr	10	[1003]
65.47	footprints to first tetrapod herbivore	~83 Myr	10	[991; 994]

	(tetrapods)			
65.49	first forests to white rot (forests and fungi)	~85 Myr	10	[716; 913]
65.49–65.54	coccolithophores to abundant diatoms (nannoplankton)	85–90 Myr	11	[668; 1024]
65.49	Gap before soft complex eyes reappear (fossil eyes)	about 85 Myr	18	[1683]
65.52	spores to first forests (land plants)	88 Myr	10	[454; 716]
65.54	crown to lobate–cydippid split, lower (Ctenophora)	90 Myr	7	[472; 480]
65.55	UCYN-A sublineage divergence	about 91 Myr	23	[377]
65.57	crown Bilateria width	92.6 Myr	7	[485]
65.58	Paulinella chromatophore age	90–140 (93.6 main) Myr	23	[376]
65.59	crown to Termitidae (termites)	95 Myr	12	[941]
65.60	Arthropod to vertebrate herbivory gap, from 403 Ma (land herbivores)	96 Myr	13	[987; 994]
65.62	root feeding lag (land herbivory)	98 Myr	10	[987]
65.62	Lag after origin of roots (root feeders)	98 Myr	13	[987]
65.64	E. coli–Salmonella divergence (E. coli, Salmonella)	100 Myr	3	[188]
65.64	Azolla fossils (Azolla–Nostoc)	about 100 Myr	5	[381]
65.64	26-mes sterane (Oman basin)	sequence about 100 Myr	6	[447]
65.64	26-mes sterane sequence span (Demospongiae (sterane reading))	100 Myr	7	[447]
65.64	Azolla–Nostoc partnership (Azolla, Nostoc azollae)	100 Myr	8	[381]
65.64	Gradual CNL expansion (angiosperms)	first about 100 Myr	13	[1211]
65.64	Congeneric splits (Ciona, Molgula)	more than 100 Myr	15	[1414]
65.67	gap fossil floor to	104–133 Myr	8	[766; 769]

	clock (Angiospermae)			
65.72	arthropod to vertebrate herbivory (land herbivory)	110 Myr	10	[987; 994]
65.72–65.78	termite crown to ruminant crown (termites; ruminants)	109.9–116.7 Myr	12	[941; 1130]
65.73	crown Cnidaria width	110.3 Myr	7	[485]
65.79	termite crown to fungus farming (Isoptera)	117.6 Myr	9	[939; 941]
65.80	Gap in drilling record, Late Triassic to Early Cretaceous (marine shelled prey)	120 Myr	13	[581]
65.81	crown Eumetazoa width	120.3 Myr	7	[485]
65.81	Interval Late Devonian to end-Permian (Big Five)	120.3 Myr	16	[435]
65.88	step 890 to 760 Ma (Porifera)	130 Myr	7	[488; 489]
65.88	Difference of two oxidation onsets (atmosphere)	0.13 Gyr	16	[225; 226]
65.91	termite fossil record (Isoptera)	135 Myr	12	[1149]
65.91	Interval end-Triassic to end-Cretaceous (Big Five)	135.4 Myr	16	[435]
65.92	Dinosaur dominance after end-Triassic (Dinosauria)	136 Myr	16	[1555]
65.94	Azolla relationship age (Azolla–Nostoc)	≤140 Myr	5	[378]
65.94	spicule gap without glass sponges (Silicea)	140 Myr	7	[486]
65.94	Diversity cycle 140 Myr (marine genera)	140 ± 15 Myr	16	[1569]
66.01	metazoan stem duration, lower	150 Myr	7	[473]
66.01	clitellate lineage radiation (Clitellata)	~150 Myr	11	[1000]
66.01–66.27	Metazoan stem duration (animals)	about 150–200 Myr	17	[473]
66.07	step 760 to 600 Ma (Porifera)	160 Myr	7	[489; 490]
66.10	clock origin to first	166.83 Myr	7	[450; 530]

	macrofossils (Cnidaria)			
66.11	Chengjiang to ctenophore crown (Ctenophora)	168 Myr	7	[452; 480]
66.15	Gall earlier than estimates by (insect galls)	about 175 Myr	13	[989]
66.16	Glomeromycota before crown land plants (Glomeromycota – embryophytes)	177 Myr	10	[299]
66.17	AM origin to white rot (Fungi)	180 Myr	9	[299; 914]
66.18	clock origin to Auroralumina (Cnidaria)	181 Myr	7	[524; 530]
66.19	crown Metazoa interval width	183.7 Myr	7	[485]
66.22	crown to lobate–cydippid split, upper (Ctenophora)	190 Myr	7	[472; 480]
66.27–66.47	Buchnera symbiosis (aphids)	200–250 Myr	5	[372]
66.27	metazoan stem duration, upper	200 Myr	7	[473]
66.27	spicule gap, title (Silicea)	200 Myr	7	[486]
66.27	oscillation after onset (Earth atmosphere)	200 Myr	8	[226]
66.27	coccolithophores influence on climate (Haptophyta)	200 (over) Myr	8	[364]
66.27	Ginkgo unchanged form (Ginkgo biloba)	200 (more than) Myr	8	[733; 734]
66.27; 68.47	GOE oscillation (atmosphere)	~200 (to 2250–2240 Ma) Myr	11	[226]
66.27	Wolbachia supergroups A and B	~200 Myr	12	[1124]
66.35	Pennsylvanian fleshy seeds to fleshy-fruit onset (computed) (seed plants)	at least 218.9 Myr	14	[435; 1267; 1270]
66.36	Isua cones older than Dresser (Isua stromatolites)	220 Myr	2	[102]
66.36	opisthokont node to crown Fungi lower	220 Myr	9	[299; 890]
66.40	opisthokont node to	230 (at least) Myr	9	[430; 890]

	Ourasphaira (Fungi)			
66.41	white rot to ant farming (Fungi)	233.35 Myr	9	[914; 936]
66.43	spicule gap, text (Silicea)	240 Myr	7	[486]
66.43	Silicea node to first uncontested spicules	239 Myr	7	[486]
66.54	sulphate reduction to N fixation (cycles)	0.27 Gyr	11	[105; 110]
66.56; 66.57	Insect fossil to angiosperm clades (computed) (insects; angiosperms)	275.8–277.6 Myr	14	[783; 981]
66.64	Biosphere earlier than proposed (Earth)	300 Myr	2	[96]
66.64	conifer fossil record (Pinophyta)	300 (more than) Myr	8	[749]
66.64	crown Fungi older than Cryogenian base	300 Myr	9	[299; 435]
66.64	Convergence span (insects)	300 Myr	13	[1183]
66.64	Amniote scaling shifts (amniotes)	4 over 300 Myr	17	[1498]
66.74	Isua carbon to Apex fossils (—)	0.335 Gyr	2	[107]
66.78	gap to next undisputed sponge body fossils (Porifera)	350 Myr	7	[488]
66.83	opisthokont node to crown Fungi upper	369 Myr	9	[299; 890]
66.85	Span first to last Big Five event	379.2 Myr	16	[435]
66.90	Zircon graphite to Isua graphite (—)	0.40 Gyr	2	[101]
66.90	stomata age (land plants)	400 (more than) Myr	8	[688]
66.94	centipede fossil record (Chilopoda)	420 Myr	10	[977]
67.01	COI1 receptor conservation (Marchantia polymorpha; Arabidopsis)	about 450 Myr	13	[1190]
67.10	LUCA to crown groups (—)	>=0.5 Gyr	2	[111]
67.10	Cav genes conserved (Cnidaria)	500 (at least) Myr	7	[148]
67.10	Eucrustaceans	past 500 Myr	15	[1440]

	common in record			
67.10	Cnidarian Cav conserved	at least 500 Myr	17	[148]
67.12	Nuvvuagittuq age range (Nuvvuagittuq belt)	510 Myr	2	[98]
67.17	crown Fungi to AM origin	540 Myr	9	[299]
67.17	crown Fungi to AM origin (Fungi – plants)	540 Myr	12	[299]
67.19	NK cluster kept (Porifera and Bilateria)	550 Myr (more than)	7	[497]
67.19	Ourasphaira to glomalean spores (Fungi)	550 Myr	9	[430; 433]
67.19	Species-level drilling database span (marine fossil record)	550 Myr	13	[582]
67.22	gap mats to palaeosols (land microbes)	570 Myr	10	[228; 967]
67.24	Life on land earlier than thought (Dresser Formation)	580 Myr	2	[104]
67.31	gap Torridonian to plant spores (land microbes)	627 Myr	10	[454; 968]
67.39–67.67	Crown red algae to Bangiomorpha	685–937 Myr	6	[356]
67.43	LUCA to Pilbara (—)	0.72 Gyr	2	[97]
67.46–67.61	N fixation to free O2 (cycles)	0.74–0.87 Gyr	11	[110; 225; 226]
67.47	Sulfate reduction record extension (North Pole barites)	>750 Myr	2	[105]
67.47	Caspr/neurexin IV conservation (animals)	over 750 Myr	17	[1376]
67.73–68.22	isotope vs clock gap (nitrogenase)	1.0–1.7 Gyr	11	[110; 112]
67.74–67.85	sulphate reduction to free O2 (cycles)	1.01–1.14 Gyr	11	[105; 225; 226]
68.13	gap palaeosols to Torridonian (land microbes)	1550 Myr	10	[228; 968]
68.21	gap 2.33 Ga to 635 Ma (ocean)	1695 Myr	8	[225; 449]
68.21	GOE to ocean oxygenation	1695 Myr	11	[225; 449]

	(atmosphere-ocean)			
68.52	LUCA to crown eukaryotes (—)	2.36 Gyr	2	[111]
68.65	microbes on land before plants (land microbes)	2747 Myr	10	[454; 967]
68.73	Inhabited hot springs record extension (Dresser Formation)	3 Gyr	2	[104]

Ages

864 positions, oldest last.

Position	What	Value	Chapter	Source
55.93–55.71	San Bartolo Maya writing	300 BC–AD 200	21	[1969]
56.16	third change point (hominins)	0.003 ± 0.001 Ma	20	[1820]
56.16	third change point, small-brained Homo included (hominins)	0.003 ± 0.001 (rate −16.74 ± 7.55) Ma	20	[1820]
56.16	brain decrease from (DeSilva) (Homo sapiens)	~3 ka	20	[1820]
56.18	end of Shang (Shang China)	~1041 BC	21	[1967]
56.22	Phoenician from	~12th century BCE	21	[1971]
56.24–56.22	Wu Ding reign (Shang China)	1254–1197 BC	21	[1967]
56.40–56.38	Wadi el-Hol inscriptions (early alphabet)	late 19th/early 18th century BC	21	[1970]
56.40–56.38	Proto-Sinaitic, earliest evidence (early alphabet)	19th century BC	21	[1970]
56.59	Neolithic Irish dog genome (Canis familiaris)	4,800 cal BP	22	[1927]
56.63	Abydos U-j labels (Egypt)	ca. 3000 BC	21	[1966]
56.66–56.63	Uruk III, proto-cuneiform (Mesopotamia)	3200–3000 BCE	21	[1965]
56.69–56.66	Uruk IV (Mesopotamia)	3350–3200 BCE	21	[1965]
56.71–56.69	Uruk V (Mesopotamia)	3500–3350 BCE	21	[1965]
56.79	Pig, lowland south-west Iran (Sus scrofa)	6,000 cal BP	22	[1923]
56.88	Potyvirus radiation (Potyviridae)	6,600 years ago	22	[310]
56.92–56.88	rice, Lower Yangtze (Oryza sativa)	6,900–6,600 years ago	20	[1925]
57.11	Cattle, southern Zagros (Bos taurus)	8,500 cal BP	22	[1923]
57.13	maize, Xihuatoxtla (Zea mays)	8,700 cal BP	20	[1924]
57.16	Pig, Jarmo (Sus scrofa)	9,000 cal BP	22	[1923]
57.18	Managed sheep, Levant (Ovis aries)	9,200 cal BP	22	[1923]

57.24	Goat herding, Ganj Dareh (Capra hircus)	9,900 cal BP	22	[1923]
57.25–58.88	non-African bottleneck (Homo sapiens)	10–60 kyr ago	20	[1881]
57.25	barley, Middle PPNB (Hordeum vulgare)	~10,000 cal BP	20	[1923]
57.27	Managed goat, Nevali Çori (Capra hircus)	10,200 cal BP	22	[1923]
57.28	pig, Cafer Höyük (Sus scrofa)	~10,300 cal BP	20	[1923]
57.30	sheep herd management, Nevali Çori (Ovis aries)	~10,500 cal BP	20	[1923]
57.30–57.27	emmer and einkorn domestic grain (Triticum)	~10,500–10,200 cal BP	20	[1923]
57.34–57.25	cattle, Euphrates valley (Bos taurus)	11,000–10,000 cal BP	20	[1923]
57.38	several plant species under cultivation (plants)	≥11,500 cal BP	20	[1923]
57.38	Several plant species under cultivation (crops)	at least 11,500 cal BP	22	[1923]
57.42–57.34	Initial domestication Eastern Mediterranean (plants and animals)	12th millennium cal BP	22	[1921]
57.49–57.42	cultivation of wild einkorn and rye (Triticum monococcum; Secale)	13,000–12,000 cal BP	20	[1923]
57.56–56.85	East Asian–Western Eurasian dog divergence (Canis familiaris)	14,000–6,400 years ago	20	[1927]
57.84–57.88	ice at LGM positions (ice sheets)	19–20 ka	11	[1032]
58.34–58.14	LGM ice maximum (ice sheets)	33.0–26.5 ka	11	[1032]
58.54–58.50	end of Mousterian (Neanderthal)	41,030–39,260 cal BP	20	[1876]
58.58	El Sidrón hyoid SDR-034 (Neanderthal)	~43 ka	21	[1946]
58.60	Leang Bulu’ Sipong 4 previous date (Homo sapiens)	43.9 ka	21	[1954]
58.66–58.68	Zlatý kůň individual (Homo sapiens)	47–48 ka	20	[1883]
58.72	Leang Bulu’ Sipong 4 re-dated, at least (Homo sapiens)	50.2 ± 2.2 ka	21	[1954]
58.78	Leang Karampuang scene minimum (Homo sapiens)	53.5 ± 2.3 ka	21	[1954]
58.88–60.18	elevated effective size (Homo sapiens)	60–250 kyr ago	20	[1881]
58.98	Spanish hand stencil minimum (attribution disputed) (Neanderthal?)	66.7 ka	21	[1955]
59.00	Liang Metanduno stencil minimum (Homo sapiens)	67.8 ka	21	[1955]
59.05	Liang Metanduno calcite U-series (Homo sapiens)	71.6 ± 3.8 ka	21	[1955]
59.35–58.88	H. floresiensis small-bodied (Homo floresiensis)	100–60 ka	20	[1867]

59.35–59.52	population differentiation start (Homo sapiens)	100–120 kyr ago	20	[1881]
59.96	previous oldest H. sapiens (Homo sapiens)	~195 ka	20	[1878]
60.31	Jebel Irhoud tooth U-series/ESR (Homo sapiens)	286 ± 32 ka	20	[1878]
60.39	Jebel Irhoud TL age (Homo sapiens)	315 ± 34 ka	20	[1877]
60.81–60.61	higher body mass from (Homo)	0.5–0.4 Ma	20	[1867]
61.23	Controlled fire, Gesher Benot Ya’aqov (Homo)	790,000 years ago	22	[1866]
61.35	Antarctic ice increase	~900 ka	11	[1028]
61.38–61.26	bottleneck span (human ancestors)	930,000–813,000 years ago	20	[1870]
61.45	SRGAP2D duplication (Homo)	1 Ma	20	[1860]
61.45	fire, Wonderwerk Cave (hominins)	~1.0 Ma	20	[1865]
61.65–61.12	mid-Pleistocene transition (climate)	1250–700 ka	11	[1028]
61.66	Cheaters (yucca moths)	1.26 ± 0.96 Ma	14	[1263]
61.66	Shangchen youngest layer (hominins)	1.26 Ma	20	[1854]
61.76	previous earliest Acheulean, computed (hominins)	1.41 Ma	20	[1850]
61.81	second change point (hominins)	1.49 ± 0.14 Ma	20	[1820]
61.87	precession phase jump (climate)	~1.6 Ma	11	[1027]
61.87	modern stature from (Homo)	1.6 Ma	20	[1867]
61.96	Acheulean, Kokiselei 4 (hominins)	1.76 Ma	20	[1850]
61.98	OH 7 age (Homo habilis)	1.8 Ma	20	[1852]
62.01–61.97	Dmanisi occupations (Homo)	1.85–1.78 Ma	20	[1855]
62.06	second change point, small-brained Homo included (hominins)	1.97 ± 0.12 (rate 0.20 ± 0.01) Ma	20	[1820]
62.08–62.45	proposed SRGAP2C function onset (Homo)	2–3 Ma	20	[1860]
62.09–62.05	Drimolen H. erectus and Paranthropus (Homo erectus; Paranthropus robustus)	2.04–1.95 Ma	20	[1853]
62.12	first change point (hominins)	2.10 ± 0.07 Ma	20	[1820]
62.12	first change point, small-brained Homo included (hominins)	2.10 ± 0.05 (rate 0.72 ± 0.51) Ma	20	[1820]
62.13	Shangchen oldest layer (hominins)	2.12 Ma	20	[1854]
62.20	H. habilis lineage origin, before (Homo habilis)	2.3 Ma	20	[1852]
62.24	SRGAP2C duplication (Homo)	2.4 Ma	20	[1860]
62.32–62.31	Oldowan, Bokol Dora 1 (hominins)	2.61–2.58 Ma	20	[1848]
62.32–62.28	Oldowan, Gona (hominins)	2.6–2.5 Ma	20	[1849]
62.38–	earliest Homo, LD 350-1	2.80–2.75 Ma	20	[1851]

62.37				
62.45	C4 grasslands	8–3 Ma	8	[809]
62.50	Diversification burst (yucca moths)	3.2 ± 1.8 Ma	14	[1263]
62.53	Lomekwi 3 tools (hominins)	3.3 Ma	20	[1847]
62.56	SRGAP2B duplication (Homo)	3.4 Ma	20	[1860]
62.59–62.08	Australopithecus flat period	3.5–2.0 Ma	20	[1820]
62.61	A. bahrelghazali age (Australopithecus bahrelghazali)	3.58 ± 0.27 Ma	20	[1842]
62.63	Laetoli hominin footprints (Australopithecus afarensis)	3.66 Ma	20	[1846]
62.68; 62.28	Species-group splits (Magicicada)	3.9–2.5 Ma	14	[1309]
62.68–62.75	A. anamensis age (Australopithecus anamensis)	3.9–4.2 Ma	20	[1844]
62.79	Ar. ramidus sediments (Ardipithecus ramidus)	4.4 Ma	20	[1843]
62.91	C4 dominance in Africa after (Poaceae)	5 Ma	13	[1169]
62.91; 62.71	Southern African fire-prone grasslands (Poaceae)	5–4 Ma	13	[1169]
62.95–63.05	Ardipithecus kadabba age	5.2–5.8 Ma	20	[1837]
63.08	Macrocystis emergence	6 Ma	8	[464]
63.08–63.22	Sahelanthropus fauna age (Sahelanthropus tchadensis)	6–7 Ma	20	[1841]
63.08	Orrorin age (Orrorin tugenensis)	~6 Ma	20	[1837]
63.15–63.00	human–chimpanzee split, molecular studies cited 2001 (Homo–Pan)	6.5–5.5 Ma	20	[1837]
63.16	Horse enamel mainly C4 (Equidae)	6.6 Ma	13	[1169]
63.19–63.24	Toumaï level, 10Be/9Be (Sahelanthropus tchadensis)	6.8–7.2 Ma	20	[1842]
63.22; 63.08	C4 grasslands, North America (Poaceae)	7–6 Ma	13	[1169]
63.22–63.34	human–chimpanzee split, generation-time clock (Homo–Pan)	≥7–8 Ma	20	[1838]
63.27	Moth split from African morgani (Xanthopan)	7.4 ± 2.8 Ma	14	[1266]
63.28	Orchid split from A. sororium (Angraecum sesquipedale)	7.5 ± 5.2 Ma	14	[1266]
63.34	C4 plants abundant	8–6 Ma	8	[808]
63.34	ambrosia crown ages (Scolytinae)	8–48 Ma	9	[944]
63.34–63.08	C4 expansion (C4 plants)	8–6 Ma	11	[808]
63.34–62.45	C4 grasslands (C4 grasses)	8–3 Ma	11	[809]
63.36	Niger Delta grass pollen above 50 % after (Poaceae, Africa)	8.2 Ma	13	[1169]
63.39;	South Asian grass pollen >90 %	8.5–6.5 Ma	13	[1169]

63.15	(Poaceae)			
63.54	Physcomitrella within Funariaceae	10 Ma	8	[677]
63.63	cycad genus radiations lower (Cycadales)	11 Ma	8	[731]
63.71	living cycad species age (Cycadales)	12 (not much older than) Ma	8	[730]
63.72	human–chimpanzee split, CpG clock (Homo–Pan)	12.1 Ma	20	[1839]
63.78	minimum calibration (Julescraneia, Paleocystophora)	13 Ma	8	[365]
63.91	oldest orchid fossil (Meliorchis caribea)	15–20 Ma	8	[787]
63.92	human–gorilla split, CpG clock (Homo–Gorilla)	15.1 Ma	20	[1839]
63.97	Paradoryphoribius chronocaribbeus age	16 Ma	7	[599]
63.97	Sphagnum reference species	16 Ma	8	[676]
63.97	Horned bovids in Africa (Bovidae)	16 Ma	13	[1172]
64.02	Orthologous EPRVs (Picea)	≥16.9 Ma	4	[300]
64.02	Orthologous insertions (Picea)	at least 16.9 Ma	13	[300]
64.07	Latest date of hypsodont Equinae (computed)	17.9 Ma	13	[1170]
64.08; 64.45	Perfume orchid lineage (Catasetinae)	18–27 Ma	14	[1265]
64.13	leaf-cutters origin (Atta + Acromyrmex)	19 (15–24) to 18 (14–22) Ma	9	[937]
64.13; 64.08	Leaf-cutter ants (Atta + Acromyrmex)	19 (15–24) to 18 (14–22) Ma	14	[937]
64.17	Sphagnum Miocene diversification	7–20 Ma	8	[676]
64.17	cycad genus radiations upper (Cycadales)	20 Ma	8	[731]
64.17	Grasslands in drier habitats, North America (Poaceae)	about 20 Ma	13	[1169]
64.17; 64.38	Perfume orchid lineage (Zygopetalinae)	20–25 Ma	14	[1265]
64.22	Xyleborini	21 Ma	9	[944]
64.22; 64.41	Perfume orchid lineage (Stanhopeinae)	21–26 Ma	14	[1265]
64.26	C3 grasslands, Central Great Plains (Poaceae)	by 21.9 Ma	13	[1170]
64.28; 64.20; 64.35	Crown age (molecular) (Passerides subclade)	22.4 (20.6–24.2) Ma	15	[1527]
64.31–64.21	Pecora	23.3–20.8 Ma	12	[1130]
64.37	oldest fossil fungus gardens (Macrotermitinae)	24.8–24.5 Ma	9	[939]
64.37–64.36	fossil fungus gardens (Macrotermitinae)	24.8–24.5 Ma	12	[939]

64.40; 64.33; 64.47	Crown age (molecular) (Corvides)	25.7 (23.8–27.7) Ma	15	[1527]
64.40 (64.33–64.47)	crow line crown (Corvides)	25.7 (23.8–27.7) Ma	19	[1527]
64.43–64.66	Oligocene hepadnavirus EVEs (Neoaves)	26.6–34.2 Ma	4	[275]
64.45	higher agriculture (Attini)	27 Ma	9	[936]
64.51	sunflower WGD-2 (Helianthus)	29 Ma	8	[822]
64.54	Filovirus and parvovirus EVEs (animals)	≥30 Ma	4	[305]
64.54	C4 grass emergence (late Oligocene) (Poaceae)	about 30 Ma	13	[1172]
64.57	higher agriculture, earlier estimate (Attini)	31 (26–37) to 27 (22–33) Ma	9	[937]
64.57	termite fungus farming, earlier estimate (Macrotermitinae)	31 (19–49) Ma	9	[939]
64.57; 64.45	Higher agriculture (Attini)	31 (26–37) to 27 (22–33) Ma	14	[937]
64.57; 64.17	Crown Old World fruit bats (Pteropodidae)	31–20 Ma	14	[1275]
64.58	termite fungus farming, recalibrated (Macrotermitinae)	31.41 (25.82–39.53) Ma	9	[939]
64.58 (64.41–64.79)	fungus farming origin (Macrotermitinae – Termitomyces)	~31.4 (25.82–39.53) Ma	12	[938; 939]
64.59; 64.84; 65.03	Moths colonise yuccas (Tegeticula; Yucca)	41.5 ± 9.8 Ma	14	[1263]
64.60	yeast-cultivar origin (Attini)	32 Ma	9	[936]
64.66; 64.76	Orchid bee MRCA (Euglossini)	34–38 Ma	14	[1265]
64.66	Eocene–Oligocene climate shift (Earth)	around 34 Ma	14	[1270]
64.66	Seed and fruit size decline, Eocene–Oligocene (angiosperms)	about 34 Ma	16	[1271]
64.78	Passeriformes basal split	about 39 Ma	14	[1272]
64.80	Mammal maximum body size levels off (land mammals)	40 Ma	16	[1565]
64.85	Malvoideae-feeding clade (Bruchinae)	about 42 Ma	13	[1164]
64.85; 64.76	Pooid and PACMAD phytoliths, North America (Poaceae)	42–38 Ma	13	[1169]
64.96; 64.91; 65.00	Crown age (molecular) (Tyranni–Passeri)	47.3 (45.1–49.8) Ma	15	[1527]
64.97	Myrmecopterula MRCA	48 Ma	9	[936]
64.97	death-grip leaf scars, Messel (Ophiocordyceps)	48 Ma	9	[950]
64.98	Azolla bloom date	~48.5 Ma	11	[704]

65.01	Volvocine age, Kirk (volvocines)	50 ± 20 Ma	6	[466]
65.01	volvocine ancestor, value 1 (Volvox–Chlamydomonas)	50 ± 20 Ma	8	[466]
65.01	Arctic Azolla event	50 Ma	8	[381; 703]
65.01	oldest ambrosia farming (Scolytinae)	50 Ma	9	[944]
65.01	Ordinal divergences complete (Aves)	by 50 Ma	14	[1272]
65.01	Bird ordinal divergences complete by (Neoaves)	50 Ma	16	[1526]
65.02; 64.98; 65.06	Crown age (molecular) (Passeriformes crown)	50.7 (48.3–53.0) Ma	15	[1527]
65.02	Passerine crown (Passeriformes)	50.7 Ma	16	[1526]
65.02 (64.98–65.06)	passerine crown (Passeriformes)	50.7 (48.3–53.0) Ma	19	[1527]
65.06	Gymnophallidae, London Clay	52.93 Ma	7	[588]
65.06; 65.02	Early Eocene Climatic Optimum herbivory (plant–insect record)	53–51 Ma	13	[990]
65.08	crown Ectocarpales, uncorrelated	54.08 Ma	8	[365]
65.08	Termitidae	54 (46–66) Ma	9	[941]
65.08 (64.93–65.26)	Termitidae origin	54 (46–66) Ma	12	[941]
65.09; 65.01	Peak of seed and fruit size diversity (angiosperms)	55–50 Ma	14	[1270]
65.09	Oldest primate skeleton (basal tarsiiform, China)	about 55 Ma	14	[1273]
65.11	PETM age (climate)	~56 Ma	11	[1025]
65.11; 64.97	Oldest bat (Onychonycteris finneyi)	Early Eocene (56.0–47.8) Ma	14	[435; 1274]
65.11	Base of the Eocene (stratigraphy)	56.0 Ma	16	[435]
65.13	Convolvulaceae-feeding clade (Spermophagus)	about 57 Ma	13	[1164]
65.17	Azolla cyanobiont, review (Azolla – Nostoc azollae)	>60 Ma	12	[354]
65.17	Scatter-hoarding may begin (rodents; corvids)	about 60 Ma	14	[1276]
65.19	lower fungus farming, earlier estimate (Attini)	61 (52–70) to 57 (48–66) Ma	9	[937]
65.19; 65.13	Lower fungus farming (Attini)	61 (52–70) to 57 (48–66) Ma	14	[937]
65.20	Base of the Selandian (stratigraphy)	61.6 Ma	16	[435]
65.22	Oryzeae with / without fossils	63 / 28 Ma	8	[785]
65.25	earlier crown hypothesis (Ctenophora)	65 Ma	7	[480]
65.25	oldest legume fossil (Leguminosae)	65.35 Ma	12	[1129]
65.25	Dinosaur dominance end age (Dinosauria)	65.4 Ma	16	[1555]

65.25	K–Pg age (Schulte) (Chicxulub impact)	approximately 65.5 Ma	16	[1560]
65.25	Oldest legume fossil (Fabaceae)	65.35 Ma	16	[1129]
65.26; 65.91	Fucales	65.81 or 134.28 Ma	6	[365]
65.26	crown Fucales, uncorrelated	65.81 Ma	8	[365]
65.26	Attini s.l.	66 (56–76) Ma	9	[937]
65.26	Intensified NLR expansion from K–Pg (angiosperms)	66 Ma	13	[1211]
65.26	K–Pg boundary (Earth)	66 Ma	14	[1272]
65.26	K–Pg boundary (Earth)	66.043 ± 0.011 Ma	15	[1527]
65.26	Base of the Paleogene (end-Cretaceous boundary) (marine and land biota)	66.0 Ma	16	[435]
65.26	K–Pg extinction age (all species)	around 66 Ma	16	[1559]
65.26	K–Pg age (Stiller) (stratigraphy)	66.043 ± 0.011 Ma	16	[1526]
65.27	Lameta coprolite phytoliths (Poaceae)	67–65 Ma	8	[785]
65.27	ancestral fungus-farming ants (Attini)	66.65 ± 13.28 Ma	9	[936]
65.27; 65.30	Basal Neoaves divergences	67–69 Ma	14	[1272]
65.27; 65.61	Hormogastridae calibration	67–97 Ma	15	[1017]
65.27; 65.25; 65.29	Crown age (molecular) (Columbaves)	66.5 (65.2–67.9) Ma	15	[1527]
65.27	Asteriornis age (Asteriornis maastrichtensis)	66.8–66.7 Ma	16	[1526]
65.28; 65.26; 65.30	Crown age (molecular) (Mirandornithes)	67.4 (66.2–68.9) Ma	15	[1527]
65.29	Circovirus EVEs (animals)	≥68 Ma	4	[305]
65.34	Ehrhartoideae with fossils	72 Ma	8	[785]
65.34; 65.26	Maastrichtian (Earth)	72.1–66.0 Ma	13	[435]
65.38	Orthologous EPRVs (Pinus)	≥75 Ma	4	[300]
65.38	Gymnophallidae trace	75.22 Ma	7	[588]
65.38	Orthologous insertions (Pinus)	at least 75 Ma	13	[300]
65.39	orchid MRCA (Orchidaceae)	76–84 Ma	8	[787]
65.41; 65.45	Seed beetle subfamily origin (Bruchinae)	78–81 Ma	13	[1164]
65.43	Onset of fleshy-fruit diversification (angiosperms)	about 80 Ma	14	[1270]
65.46 to 63.72	Hepadnavirus endogenization span (birds)	>82 to <12.1 Ma	4	[275]
65.46	oldest raphid diatoms	82 Ma	8	[669]
65.47; 66.40	Laminariales	83.44 or 231.51 Ma	6	[365]
65.47	crown Laminariales, uncorrelated	83.44 Ma	8	[365]

65.47	Asteraceae crown	83 Ma	8	[821]
65.47	Campanian base (Earth)	83.6 Ma	13	[435]
65.47; 65.34	Campanian (Earth)	83.6–72.1 Ma	14	[435]
65.48	Palaeognathae split (Aves)	about 84 Ma	14	[1272]
65.50	Welwitschia WGD (Welwitschia mirabilis)	86 (78–96) Ma	8	[751]
65.50	Bambusoideae–PACMAD split (Poaceae)	86 / 72 Ma	8	[785]
65.52	Galloanseres–Neoaves split	about 88 Ma	14	[1272]
65.54	Thalassiosira–Phaeodactylum divergence (diatoms)	90 Ma	8	[362]
65.55	UCYN-A1/A2 split	about 91 Ma	5	[377]
65.55	UCYN-A A1/A2 divergence	~91 Ma	12	[377]
65.57	Bornavirus EVEs (16 mammal genomes)	≥93 Ma	4	[305]
65.62	Day-flying butterflies (Papilionoidea)	about 98 Ma	14	[1250]
65.63	cestode tentacle in amber (Cestoda)	98.79 ± 0.62 Ma	7	[588]
65.63	Cycad-pollinating beetle (Cretoparacucujus cycadophilus)	about 99 Ma	14	[1254]
65.63	Oldest eudicot pollination (Angimordella burmitina)	99 Ma	14	[1259]
65.64	Nodulation predisposition origin (Fabidae)	>100 Ma	3	[213]
65.64	oldest calibration fossil (Padina)	100 (minimum) Ma	8	[365]
65.64	palm crown (Arecaceae)	100 (108–92) Ma	8	[782]
65.64	Scolytinae origin	100–120 Ma	9	[944]
65.64	nodulation predisposition origin (angiosperms)	slightly over 100 Ma	11	[213]
65.64	nodulation predisposition (Fabidae)	slightly over 100 (32223 species phylogeny) Ma	12	[213]
65.64	Azolla cyanobiont, fossils (Azolla – Nostoc azollae)	~100 Ma	12	[381]
65.64	Long-proboscid mode documented until (long-proboscid insects)	about 100 Ma	14	[990]
65.64	Oldest bee (Melittosphex burmensis)	approximately 100 Ma	14	[1258]
65.64	Palaeognathae–Neognathae split (Aves)	about 100 Ma	14	[1272]
65.64	oldest bee fossil (Anthophila)	100 Ma	19	[1257]
65.66	Sphagnum WGD 2	102–122 Ma	8	[676]
65.68	First beetle pollinator (Darwinylus marcosi)	about 105 Ma	14	[1253]
65.68; 65.64	Long-proboscid flies with gymnosperm pollen (Zhangsolvidae)	about 105 and 100 Ma	14	[1255]
65.71–66.10	EPRV burst 3 (Pinus taeda)	108–166.1 Ma	4	[300]
65.71; 66.41	Insertion bursts, Pinus taeda	108–232.9 Ma	13	[300; 316]

65.72	Welwitschia–Gnetum divergence (Gnetales)	110 (over) Ma	8	[751]
65.72	Mayoa pollen floras (Araceae)	110–120 Ma	8	[781]
65.72–65.91	first termite fossils (termites)	110–135 Ma	12	[941]
65.74	orchid crown, second clock (Orchidaceae)	112 Ma	8	[788]
65.74	Arabidopsis paleopolyploidy	112 Ma	8	[820]
65.75	Magnoliaceae–Lauraceae split (Magnoliidae)	113–128 Ma	8	[771]
65.75	earliest grass fossils (Poaceae)	113–101 Ma	8	[784]
65.75–65.72	Weddell Sea diatoms (Bacillariophyta)	113–110 Ma	11	[668]
65.77	Liriodendron WGD	116 Ma	8	[771]
65.78	γ triplication (core eudicots)	117 Ma	8	[819]
65.80–66.19	EPRV burst 1 (Pinus taeda)	119.3–183.6 Ma	4	[300]
65.80; 65.64	Gymnosperm modes replaced (angiosperms)	120–100 Ma	14	[990]
65.80; 65.72	Asteridae (angiosperms)	119–110 Ma	14	[783]
65.81	first trematode egg (Trematoda)	120.2 Ma	7	[588]
65.81	Yixian Ginkgo with modern ovules	121 (over) Ma	8	[732]
65.82–66.21	EPRV burst 2 (Pinus taeda)	122–187.8 Ma	4	[300]
65.83; 65.76	Rosidae (angiosperms)	123–115 Ma	14	[783]
65.83; 65.75; 65.89	Crown bees (Anthophila)	about 123 (113–132) Ma	14	[1257]
65.83; 62.08	Floras in seed-size study (25 angiosperm floras)	about 124 to about 2 Ma	14	[1271]
65.83 (65.75–65.89)	crown bees (Anthophila)	123 (113–132) Ma	19	[1257]
65.84	Gnetales crown calibration	125 (at least) Ma	8	[719]
65.84	Archaefructus	124.6 (at least) Ma	8	[767]
65.84–65.76	Aptian diatoms, eastern Australia (Bacillariophyta)	125–115 Ma	11	[668]
65.85	Leefructus mirus	122.6–125.8 Ma	8	[818]
65.85; 65.81	Pentapetalae (angiosperms)	126–121 Ma	14	[783]
65.86	root of Poaceae	128 (107–129) Ma	8	[785]
65.86	oldest tricolpate pollen (eudicots)	127–125 Ma	8	[818]
65.88	oldest confirmed flowers (Angiospermae)	130 (no older than about) Ma	8	[766]
65.91	crown Fucales, autocorrelated	134.28 Ma	8	[365]
65.91	crown Ectocarpales, autocorrelated	135.60 Ma	8	[365]

65.91	monocot, magnoliid, eudicot diversification (Angiospermae)	135–130 Ma	8	[783]
65.91	oldest termite fossils (Isoptera)	135 Ma	9	[941]
65.91; 65.88	Magnoliids, monocots, eudicots diversify (angiosperms)	135–130 Ma	14	[783]
65.91–65.72	First undisputed termite fossils (Isoptera)	135–110 Ma	23	[941]
65.92	crown-angiosperm calibration (Angiospermae)	136–139.35 Ma	8	[766]
65.94	angiosperm MRCA range (Angiospermae)	140–250 Ma	8	[766]
65.94	Azolla cyanobiont, genome age (Azolla – Nostoc azollae)	≤140 Ma	12	[378]
65.94; 66.17	Angiosperm radiation (angiosperms)	140–180 Ma	13	[1196]
65.98–65.25	high flammability Cretaceous (fire)	145–65 Ma	11	[1007]
65.98	Cretaceous base (Earth)	145.0 Ma	13	[435]
65.99	Nymphaeaceae–Cabombaceae (Nymphaeales)	147–185 Ma	8	[769]
66.00	termite crown (Isoptera)	149 (136–170) Ma	9	[941]
66.00 (65.92–66.12)	termite crown (termites)	149 (136–170) Ma	12	[941]
66.00 (65.92–66.12)	termite crown age (Isoptera)	149 (136–170) Ma	19	[941]
66.01	first fish bioluminescence (Stomiiformes)	~150 Ma	12	[1127]
66.01	Angiosperm crown (angiosperms)	151 Ma	13	[299]
66.01; 65.94	Age (Parviraptor estesi)	about 150–140 Ma	15	[1486]
66.02–66.41	EPRV burst 4 (Pinus taeda)	151.4–232.9 Ma	4	[300]
66.03	Agaricomycetidae	154 Ma	9	[299]
66.04	Kimmeridgian snakes (Portugalophis lignites, Diablophis gilmorei)	about 155 Ma	15	[1486]
66.05	cycad crown, nuclear clock (Cycadales)	158.1 Ma	8	[719]
66.07	lobate–cydippid divergence, lower (Lobata/Cydippida)	160 Ma	7	[472]
66.07	Symbiodiniaceae diversification	160 Ma	7	[534]
66.07–66.20	earthworm north–south split (earthworm families)	161–186 Ma	11	[1017]
66.07	Oldest eutherian (Juramaia sinensis)	about 160 Ma	15	[1502]
66.09	Oldest definitive pollinating insects (long-proboscid insects)	about 165 Ma	14	[990]
66.09	Oldest boganiid (Palaeoboganium jurassicum)	about 165 Ma	14	[1254]

66.10	Oldest snake (Eophis underwoodi)	about 167 Ma	15	[1486]
66.12	Ginkgo Early Jurassic	170 Ma	8	[732]
66.12 (66.02–66.25)	termite–Cryptocercus split (termites)	~170 (153–196) Ma	12	[941]
66.13	monocot–eudicot split (Angiospermae)	171–203 Ma	8	[769]
66.14–66.08	Middle Jurassic ‘diatoms’ reassigned (testate amoeba)	174–163 Ma	11	[668]
66.16	first lignin peroxidase (Polyporales)	178 ± 64 Ma	9	[915]
66.17	Magnoliidae crown	178.78–126.82 Ma	8	[770]
66.18	Pyxidicula reinterpreted (nannofossils)	~182 Ma	11	[668]
66.19	Pinaceae crown	183 (233–150) Ma	9	[299]
66.22	Marsupial–eutherian split (mammals)	about 190 Ma	4	[301]
66.22	diatom crown / stem (Bacillariophyta)	190 / 199 (250–183) Ma	8	[669]
66.22	Sphagnum WGD 1	189–247 Ma	8	[676]
66.24	first versatile peroxidase (Polyporales)	194 ± 70 Ma	9	[915]
66.26	Pinaceae MRCA	198.4 Ma	8	[719]
66.27	Cicada, spittlebug, sharpshooter split (Auchenorrhyncha)	≥200 Ma	5	[370]
66.27	Sulcia–Nasuia partnership (leafhoppers)	>200 (origin before 260) Ma	5	[371]
66.27	Volvocine age, Herron (volvocines)	≥200 (earlier 50–75) Ma	6	[468]
66.27	diatom clock origin (Bacillariophyta)	200 Ma	8	[668]
66.27–66.20	Pangaea break-up (continents)	200–185 Ma	11	[1017]
66.27	leech cocoon calibration (Hirudinea)	201 Ma	11	[1017]
66.27; 66.51	Sulcia–Nasuia partnership (Sulcia; Nasuia)	>200 (origin >260) Ma	12	[371]
66.27–66.47	Buchnera symbiosis origin (Buchnera – aphids)	200–250 Ma	12	[372]
66.27	Jurassic base (Earth)	201.4 Ma	13	[435]
66.27	Glossata wing scales at Triassic–Jurassic boundary	201.4 Ma	14	[435; 1251]
66.27; 66.56	Crown cycad molecular ages (Cycadales)	about 200–274.5 Ma	14	[1254]
66.27	Base of the Jurassic (end-Triassic boundary) (marine and land biota)	201.4 ± 0.2 Ma	16	[435]
66.32	photosymbiosis isotopes (Scleractinia)	212 Ma	7	[533]
66.32	coral photosymbiosis isotopes (corals – dinoflagellates)	~212 Ma	12	[533]
66.32	Late Triassic photosymbiotic corals (Scleractinia)	about 212 Ma	16	[528]
66.33–66.31	coccolithophores (Haptophyta)	~215–210 Ma	11	[1024]
66.36	Age (Odontochelys semitestacea)	about 220 Ma	15	[1485]
66.38	Base of the Norian (stratigraphy)	about 227 Ma	16	[435]

66.40	Volvocine age, Hanschen (volvocines)	about 230 Ma	6	[467]
66.40	crown Laminariales, autocorrelated	231.51 Ma	8	[365]
66.40–66.27	Dinosaur radiation span (Dinosauria)	230–200 Ma	16	[1557]
66.41	crown angiosperms, clock (Angiospermae)	234–263 Ma	8	[769]
66.41	calcareous dinoflagellates (Dinophyceae)	~233 Ma	11	[1024]
66.41–66.40	Carnian Pluvial Episode (climate)	234–232 Ma	16	[1558]
66.42–66.27	calcifying algae (nannoplankton)	237–201 Ma	11	[1024]
66.42	Base of the Carnian (stratigraphy)	about 237 Ma	16	[435]
66.43	oldest scleractinians	240 Ma	7	[528]
66.43	Oldest scleractinian corals	about 240 Ma	16	[528]
66.44	Tube-like proboscis (Lepidoptera)	about 241 Ma	14	[1250]
66.44	Vampire squid–dumbo octopus split (Coleoidea)	242 ± 38 Ma	15	[1343]
66.44 (66.29–66.57)	vampire squid and dumbo octopus lineages (Vampyromorpha, Cirrata)	242 ± 38 Ma	19	[1343]
66.46	Base of the Anisian (Middle Triassic) (stratigraphy)	247.2 Ma	16	[435]
66.47	Volvocine age, Umen (volvocines)	around 250 Ma	6	[424]
66.47	volvocine ancestor, value 2 (Volvox–Chlamydomonas)	250 Ma	8	[424]
66.47–66.43	low flammability Early–Middle Triassic (fire)	250–240 Ma	11	[1007]
66.47–66.43	Flammability low to absent (land ecosystems)	250–240 Ma	16	[1007]
66.48	end-Permian spike age younger (fungi)	252 Ma	9	[924]
66.48	O2 drop at Permian–Triassic (atmosphere)	251.902 Ma	10	[435; 727]
66.48	end-Permian extinction onset (biosphere)	251.941 ± 0.037 Ma	11	[1021]
66.48	end-Permian extinction end (biosphere)	251.880 ± 0.031 Ma	11	[1021]
66.48	Herbivory collapse, Permian–Triassic (plant–insect record)	about 252 Ma	13	[990]
66.48	Base of the Triassic (end-Permian boundary) (marine and land biota)	251.902 ± 0.024 Ma	16	[435]
66.48	Base of the Olenekian (stratigraphy)	251.2 Ma	16	[435]
66.48	End-Permian extinction start (Meishan) (marine biota)	251.941 ± 0.037 Ma	16	[1021]
66.48	End-Permian extinction end (Meishan) (marine biota)	251.880 ± 0.031 Ma	16	[1021]
66.48	Diversity nadir (marine genera)	251 Ma	16	[1569]
66.49	end-Permian spike age older (fungi)	254 Ma	9	[923]
66.50	Eucestoda eggs in proglottids	259.1 Ma	7	[588]

66.50	clade D ancestor (Polyporales)	259 ± 94 Ma	9	[915]
66.51	Sulcia acquisition (Auchenorrhyncha)	≥260 Ma	5	[370]
66.51	lobate–cydippid divergence, upper (Lobata/Cydippida)	260 Ma	7	[472]
66.51	Sulcia acquisition (Sulcia – Auchenorrhyncha)	≥260 Ma	12	[370]
66.51	Base of the Wuchiapingian (stratigraphy)	259.51 ± 0.21 Ma	16	[435]
66.51	Guadalupian event (marine biota)	about 260 Ma	16	[1548]
66.52	Crossozamia younger	265.1 Ma	8	[729]
66.52	Base of the Capitanian (stratigraphy)	264.28 ± 0.16 Ma	16	[435]
66.54	Guadalupian event (marine biota)	about 270 Ma	16	[1548]
66.55	Crossozamia older	272.3 Ma	8	[729]
66.55; 66.74; 66.27	Chitonida (clock)	272 (336–201) Ma	15	[1341]
66.56	freshwater triclad trails (Tricladida)	274.4 Ma	7	[588]
66.59	Kungurian base (Earth)	283.5 Ma	13	[435]
66.63	Crown Agaricomycetes	299 (351–252) Ma	6	[299]
66.63	Permian base (—)	298.9 Ma	8	[435]
66.63	earthworm crown (earthworms)	298.9 Ma	10	[1001]
66.63	earthworm crown (Crassiclitellata)	298.9 Ma	11	[435; 1001]
66.63	Permian base (Earth)	298.9 Ma	13	[435]
66.63; 66.48	Permian vertebrate diversification (plant-eating vertebrates)	298.9–251.902 Ma	14	[435; 1267]
66.64	Isoetes divergence from other CAM lineages	300 (more than) Ma	8	[691]
66.64	seed plants minimum origin (Spermatophyta)	300 (before) Ma	8	[719]
66.64	lignin degradation origin (Agaricomycetes)	300 Ma	9	[913; 914]
66.64	oldest insect gall (Psaronius petiole gall, holometabolan larva)	~302 Ma	10	[989]
66.64	enzymatic lignin decay (Agaricomycete ancestor)	end of Carboniferous (~300) Ma	10	[913]
66.64–66.51	O2 maximum excursion (atmosphere)	300–260 Ma	10	[863]
66.64	Lepidoptera crown	about 300 Ma	14	[1250]
66.64	Oldest gall (holometabolan larva) (Psaronius petioles)	about 302 Ma	15	[989]
66.65	first cestode egg (Cestoda)	304.8 Ma	7	[588]
66.65	rainforest collapse (Euramerican coal forests and tetrapods)	~305 Ma	10	[726]
66.66	Kasimovian base (—)	307.0 Ma	8	[435]
66.66	first synapsid herbivore (Melanedaphodon hovaneci)	~307 Ma	10	[994]

66.66	Second herbivory phase, younger end (arthropods)	309 Ma	13	[987]
66.66	Oldest synapsid herbivore (Melanedaphodon hovaneci, Linton, Ohio)	about 307 Ma	13	[994]
66.68; 66.66	Moscovian stage (Earth)	315.2–307.0 Ma	13	[435]
66.69–66.65	Joggins strata (Joggins coal forest)	318–303 Ma	10	[993]
66.70	Caulimoviridae origin	about 320 Ma	4	[298]
66.71	leaf-margin feeding (Triphyllopteris austrina)	326 Ma	10	[987]
66.71–66.68	coal forest expansion (Carboniferous coal forests)	late Bashkirian 323.2–315.2 Ma	10	[724]
66.71; 66.63	Pennsylvanian (Earth)	323.2–298.9 Ma	14	[435]
66.72–66.66	herbivory phase 2 (insects)	327–309 Ma	10	[987]
66.72	Second herbivory phase, older end (arthropods)	327 Ma	13	[987]
66.73	Serpukhovian base (—)	330.9 Ma	8	[435]
66.73–66.71	oldest winged insect (Delitzschala bitterfeldensis)	330.9–323.2 Ma	10	[980]
66.73	coal forests spread (Carboniferous coal forests)	330.9 Ma	10	[724]
66.73; 66.71	Oldest winged insect fossil (Serpukhovian) (Delitzschala bitterfeldensis)	330.9–323.2 Ma	14	[435; 980]
66.75–66.51	late Paleozoic ice age (climate)	340–260 (CO2 <500 ppm) Ma	10	[1003]
66.75–66.51	late Paleozoic ice age (climate)	340–260 (CO2 <500) Ma	11	[1003]
66.76	major extant insect lineages (Insecta)	~345 Ma	10	[979]
66.76	Main living insect lineages (Insecta)	about 345 Ma	14	[979]
66.78	crown ctenophore diversity, clock (Ctenophora)	350 ± 88 (262–438) Ma	7	[480]
66.78	AA2 diversification (Agaricomycetes)	350–295 Ma	9	[299]
66.78	forested ecosystems diversified (mycorrhizal forests)	>350 Ma	10	[998]
66.78–66.64	high flammability (fire)	350–300 Ma	10	[1007]
66.78 (66.51–66.98)	Crown living ctenophores (Ctenophora)	350 ± 88 Ma	17	[480]
66.79–66.61	UNESCO Carboniferous span	354–290 Ma	10	[993]
66.80	Carboniferous base (—)	358.9 ± 0.4 Ma	8	[435]
66.80	rooted plants and CO_2 drop (land plants)	400–360 Ma	8	[722]

66.80	Archaeopteris extinction	Devonian/Carboniferous boundary 358.9 Ma	10	[435; 717]
66.80; 66.92; 66.63	Crown Polyplacophora (clock)	357 (408–298) Ma	15	[1341]
66.80	Base of the Carboniferous (Hangenberg) (marine biota)	358.9 ± 0.4 Ma	16	[435]
66.82	earliest seeds (Spermatophyta)	365 Ma	8	[718]
66.83	Moroccan Archaeopteris trunks	370 Ma	8	[717]
66.83	Famennian base (—)	372.2 ± 1.6 Ma	8	[435]
66.83	fish–tetrapod transition (Tiktaalik roseae)	>370 Ma	10	[992]
66.83	Fish–tetrapod transition (Tiktaalik roseae)	over 370 Ma	15	[992]
66.83	Base of the Famennian (Kellwasser) (marine biota)	372.2 ± 1.6 Ma	16	[435]
66.84–66.83	implied earliest tetrapod body fossils (tetrapods)	375.3–369.7 Ma	10	[435; 991]
66.84	Frasnian–Famennian crisis age (article) (marine animals)	about 375 Ma	16	[1545]
66.85	monopisthocotylean hooks, table	377.7 Ma	7	[588]
66.85	monopisthocotylean hooks, text	378.9 ± 1.2 Ma	7	[588]
66.86	Gilboa stumps age (Wattieza/Eospermatopteris)	385 Ma	8	[715]
66.86	Cairo Archaeopteris forest	385 Ma	8	[716]
66.86	Runcaria heinzelinii	385 Ma	8	[718]
66.86	forest-grade arthropod communities (arthropods)	~385 Ma	10	[975]
66.86–66.80	first wood borings (Late Devonian borers)	~383–359 Ma	10	[988]
66.86–66.85	implied oldest elpistostegids (Elpistostegalia)	383.3–377.7 Ma	10	[435; 991]
66.86	Cairo forest age (Archaeopteris forest, Cairo)	ca. 385 Ma	10	[716]
66.86	Base of the Frasnian (stratigraphy)	382.7 ± 1.6 Ma	16	[435]
66.87	Hangman forest, Eifelian younger (Calamophyton)	387.7 Ma	8	[435; 714]
66.87; 67.00; 66.73	Stolidobranch split (clock) (Tunicata)	389 ± 32 (449–333) Ma	15	[1414]
66.88	oxygen nadir, model (atmosphere)	14.5 % at 393 Ma	8	[673]
66.88	Hangman forest, Eifelian older (Calamophyton)	393.3 Ma	8	[435; 714]
66.88	Rhynie printed age (GCR) (Rhynie chert)	c. 390 Ma	10	[983]
66.88–66.87	tetrapod trackways (tetrapods, Zachełmie)	393.3–387.7 Ma	10	[435; 991]
66.88–66.87	oldest standing forest (Calamophyton, Hangman Sandstone)	Eifelian 393.3–387.7 Ma	10	[714]

66.88; 66.87	Tetrapod trackways, Eifelian (Zachełmie, Poland)	393.3–387.7 Ma	15	[991]
66.89–66.92	Rhynie printed age (Engel & Grimaldi) (Rhynie chert)	396–407 Ma	10	[981]
66.89; 66.92	Oldest insect fossil, age in paper (Rhyniognatha hirsti, Rhynie chert)	396–407 Ma	14	[981]
66.90	hornwort divergence (Anthocerotophyta)	400 (more than) Ma	8	[678]
66.90	Physcomitrella–flowering plants	400 (more than) Ma	8	[680]
66.90	fern–seed plant divergence (Monilophyta)	400 Ma	8	[700]
66.90	Rhynie arbuscules (Aglaophyton major)	400 (more than) Ma	9	[893]
66.90	Winfrenatia reticulata	400 Ma	9	[908]
66.90	Polyporales peroxidase ancestor	399 ± 140 Ma	9	[915]
66.90	arbuscules in Aglaophyton (Aglaophyton major – AM fungus)	~400 Myr old Ma	10	[893]
66.90–66.80	rooted plants spread (vascular plants)	400–360 Ma	10	[722]
66.90–66.80	charcoal scarce (fire record)	400–360 Ma	10	[673]
66.90–66.80	charcoal scarce (fire)	~400–360 Ma	11	[673]
66.90	arbuscules in Aglaophyton (Aglaophyton major – AM fungus)	>400 Ma	12	[893]
66.90	Age (Websteroprion armstrongi)	about 400 Ma	15	[1375]
66.91	insect flight clock age (Pterygota)	~406 Ma	10	[979]
66.91	First herbivory phase, younger end (arthropods on land plants)	403 Ma	13	[987]
66.91	Molecular origin of insect flight (Pterygota)	about 406 Ma	14	[979]
66.92	Asteroxylon (Asteroxylon mackiei)	407 Ma	6	[459]
66.92	Rhynie chert nematodes older (Nematoda)	410.8 Ma	7	[598]
66.92	Rhynie chert nematodes younger (Nematoda)	407.6 Ma	7	[598]
66.92	Rhynie chert, alternative age	407 Ma	9	[894]
66.92	Rhynie fauna (U-Pb, Brookfield) (Rhynie arthropods)	~407 Ma	10	[975]
66.92	rhizomes in palaeosols (Drepanophycus-like plant, Yunnan)	411–408 Ma	10	[986]
66.92	Rhynie–Windyfield soil fauna (nematodes, mites, arthropods)	410.8–407.6 Ma	11	[435; 598]
66.92; 66.92	Pragian stage on 2023 chart (Earth)	410.8–407.6 Ma	14	[435]
66.92; 66.92	Rhynie chert mites; harvestman (Acariformes; Opiliones)	410.8–407.6 Ma	15	[598]
66.93	Rhynie chert	411.5 ± 1.3 Ma	6	[458]
66.93	Palaeonitella cranii, Rhynie chert	411.5 ± 1.3 Ma	8	[428;

				458]
66.93	crown monilophytes (Monilophyta)	411.5–384.9 Ma	8	[455]
66.93	stratified lichens (Cyanolichenomycites, Chlorolichenomycites)	415 Ma	9	[907]
66.93	Cowie Harbour fauna (millipedes)	~414 Ma	10	[975]
66.93	Shropshire land animals (two centipedes and one trigonotarbid)	~414 Ma	10	[976]
66.93	Rhynie chert U-Pb age (Rhynie chert community)	411.5 ± 1.3 Ma	10	[458]
66.93	oldest unequivocal nematodes (Nematoda, Rhynie)	411.5 Ma	10	[458; 598]
66.93	harvestman tracheae and genitalia (Opiliones, Rhynie)	411.5 Ma	10	[458; 598]
66.93	Earliest land animals with direct evidence (2 centipedes, 1 trigonotarbid, Shropshire)	about 414 Ma	15	[976]
66.94	clock Hexactinellida (soft bound)	418 (291–515) Ma	7	[486]
66.94	oxygen above 15–17 % (atmosphere)	420–400 Ma	8	[672]
66.94	charcoal continuous from (atmosphere)	419 Ma	8	[673]
66.94	crown mosses, study 2 (Bryophyta (mosses))	420–364 Ma	8	[456]
66.94	vascular plants evolved (Tracheophyta)	420 Ma	8	[690]
66.94–66.90	O2 near present level (atmosphere)	420–400 Ma	10	[672]
66.94	first trigonotarbids with book lungs (Trigonotarbida)	~420 Ma	10	[975]
66.94–66.91	herbivory phase 1 (arthropods on spores and stems)	417–403 Ma	10	[987]
66.94–66.80	freshwater clitellate ancestor (Clitellata)	419–359 (74 taxa) Ma	10	[1000]
66.94	continuous charcoal (fire record)	from 419 Ma	11	[673]
66.94–66.80	clitellate freshwater ancestor (Clitellata)	419–359 (74 transcriptomes) Ma	11	[1000]
66.94	First herbivory phase, older end (arthropods on land plants)	417 Ma	13	[987]
66.94; 66.80	Clitellate MRCA in fresh water (Clitellata)	419–359 Ma	15	[1000]
66.94	First book-lung arachnids (trigonotarbids)	about 420 Ma	15	[975]
66.95	crown tracheophytes minimum (Tracheophyta)	420.7 Ma	8	[455]
66.95	earliest wildfire (rhyniophytoid charcoal, Ludford Lane)	423.0 ± 2.3 Ma	10	[970]
66.95	earliest myriapod fossils, Kerrera (kampecarid millipedes)	~425 Ma	10	[975]
66.95–66.94	Pneumodesmus faunal age (Pneumodesmus newmani)	423–419 Ma	10	[978]
66.95	Silurian pentastomid on ostracod, age	425 Ma	13	[1160]

66.95	Earlier complete jawed fishes (Gnathostomata)	about 425 Ma	15	[1412]
66.96	Cooksonia cf. pertoni minimum	426.9 Ma	8	[455]
66.96	Cooksonia minimum (Cooksonia cf. pertoni)	426.9 Ma	10	[455]
66.96	Pneumodesmus spore age (Pneumodesmus newmani)	~427 Ma	10	[978]
66.97	crown lycophytes, study 1 (Lycopodiophyta)	432.5–392.8 Ma	8	[455]
66.97	crown lycophytes, study 2 (Lycopodiophyta)	431–411 Ma	8	[456]
66.97	crown euphyllophytes, study 2 (Euphyllophyta)	432–414 Ma	8	[456]
66.97	Next soft complex eyes (fossil eyes)	about 430 Ma	18	[1683]
66.98	crown euphyllophytes, study 1 (Euphyllophyta)	437.6–402.2 Ma	8	[455]
66.98	oldest scorpion (scorpion, Waukesha Biota, Wisconsin)	437.5–436.5 Ma	10	[974]
66.98–66.88	deep-ocean oxygenation	435–392 Ma	11	[672]
66.98; 66.98	Oldest scorpion (Waukesha Biota scorpion)	437.5–436.5 Ma	15	[974]
66.98	Oldest complete jawed vertebrates (Xiushanosteus mirabilis, Shenacanthus vermiformis)	around 436 Ma	15	[1412]
66.99	Silurian base (ICS chart)	443.8 Ma	6	[435]
66.99	clock Hexactinellida (hard bound)	440 (326–543) Ma	7	[486]
66.99	marine trails, Katian, table (Platyhelminthes)	444.0 Ma	7	[588]
66.99	Ordovician glaciation before (Earth)	444 Ma	8	[674]
66.99	crown liverworts, study 1 (Marchantiophyta)	443.6–405.3 Ma	8	[455]
66.99	crown liverworts, study 2 (Marchantiophyta)	440–412 Ma	8	[456]
66.99	Silurian base (Tortotubus after) (Tortotubus protuberans)	443.8 Ma	9	[434; 435]
66.99	end of Late Ordovician glaciation (climate)	~444 Ma	10	[674]
66.99	soil burrows (Scoyenia beerboweri (likely millipedes), Juniata Formation)	>443.8 Ma	10	[972; 973]
66.99	oldest non-marine trace fossils (Juniata burrows)	>443.8 Ma	11	[435; 972]
66.99	Tortotubus mycelium (Tortotubus protuberans)	earliest Silurian, after 443.8 Ma	12	[434]
66.99	Yaman Kasy vent community (tubeworms with microbial filaments)	~440 Ma	12	[1121]
66.99	Late Ordovician burrows (Scoyenia beerboweri)	older than 443.8 Ma	15	[973]
66.99	Base of the Silurian (Rhuddanian)	443.8 ± 1.5 Ma	16	[435]

	(stratigraphy)			
67.00	marine trails, Katian, text (Platyhelminthes)	445.2 ± 0.9 Ma	7	[588]
67.00	carbonate δ13C rise of 2 ‰ (ocean)	445 Ma	8	[672]
67.00	crown mosses, study 1 (Bryophyta (mosses))	448.6–344.3 Ma	8	[455]
67.00	Leotiomyceta radiation	446 (467–425) Ma	9	[299]
67.00	Oldest horseshoe crab (Lunataspis aurora)	about 445 Ma	15	[1394]
67.00; 67.07; 66.92	Appendicularian split (clock) (Tunicata)	447 ± 20 (484–411) Ma	15	[1414]
67.00	Base of the Hirnantian (end-Ordovician boundary) (marine biota)	445.2 ± 1.4 Ma	16	[435]
67.01	Retrovirus origin (retroviruses, jawed vertebrates)	>450 Ma	4	[297]
67.01	Tracheophytes (vascular plants)	452 Ma	4	[299]
67.01	cladorhizid–spongillid divergence (Demospongiae)	450 Ma	7	[472]
67.01	brown algae clock origin (Phaeophyceae)	449.41 (333.85–572.02) Ma	8	[365]
67.01	crown tracheophytes, study 2 (Tracheophyta)	452–447 Ma	8	[456]
67.01	Jawed vertebrate origin (molecular) (Gnathostomata)	around 450 Ma	15	[1412]
67.01	Ordovician agnathans (jawless fishes)	450 Ma	18	[1679]
67.01	Vertebrate sleep signatures age (zebrafish)	over 450 Ma	18	[1766]
67.03	Glomalean hyphae (Ordovician Wisconsin)	about 460 Ma	6	[433]
67.03	previous oldest cryptospores (Embryophyta)	463–461 Ma	8	[454]
67.03	glomalean hyphae and spores (Glomeromycota)	460 Ma	9	[433]
67.03	previous oldest cryptospores (land plants)	463–461 Ma	10	[454]
67.03	glomalean hyphae and spores (Glomales-like fungi, Wisconsin)	~460 Ma	12	[433]
67.04	ascolichens, clock (Lecanoromycetes)	467–410 Ma	9	[299]
67.04–66.92	ascolichens (clock) (Lecanoromycetes)	467–410 Ma	12	[299]
67.05	Cryptospores (Argentina)	473–471 (previous 463–461) Ma	6	[454]
67.05	oldest cryptospores (Embryophyta)	473–471 Ma	8	[454]
67.05	land colonisation (Embryophyta)	470 Ma	8	[672]
67.05	crown embryophytes, study 1, younger (Embryophyta)	470.0 Ma	8	[455]
67.05	crown tracheophytes, study 1	472.2–419.3 Ma	8	[455]

	(Tracheophyta)			
67.05	oldest cryptospores (land plants, Argentina)	473–471 Ma	10	[454]
67.05–66.94	crown tracheophytes (clock) (Tracheophyta)	472.2–419.3 Ma	10	[455]
67.05	land plants colonise land	~470 Ma	11	[672]
67.06	clock Calcarea (hard bound)	475 (382–564) Ma	7	[486]
67.06	Setaphyta vs hornworts (Bryophyta)	479–450 Ma	8	[456]
67.06	second bryophyte divergence (Bryophyta)	478.7–438.0 Ma	8	[455]
67.06	insect clock age (Insecta (1,478 genes))	~479 Ma	10	[979]
67.06	Molecular origin of insects (Insecta)	about 479 Ma	14	[979]
67.07	Crown embryophytes (land plants)	482 (485–473) Ma	6	[299]
67.07	AM symbiosis origin (arbuscular mycorrhiza)	480 Ma	9	[299]
67.07	Glomeromycota diversification	484 (529–437) Ma	9	[299]
67.07	crown land plants (Embryophyta)	482 (485–473) Ma	9	[299]
67.07	AM symbiosis origin (clock) (arbuscular mycorrhiza)	ca. 480 Ma	10	[299]
67.07 (67.15–66.98)	Glomeromycota diversification	~484 (529–437) Ma	12	[299]
67.07	AM symbiosis origin (AM fungi – plants)	~480 Ma	12	[299]
67.08	beginning of the Ordovician (—)	490 Ma	7	[583]
67.08	arthropod trackways on land (euthycarcinoid-like arthropods, Nepean Formation, Ontario)	Cambrian–Ordovician, boundary 485.4 Ma	10	[435; 971]
67.08	Beginning of the Ordovician (Earth)	490 Ma	13	[583]
67.08; 67.13; 67.01	Crown Aculifera (clock)	488 (517–453) Ma	15	[1341]
67.09	crown Eleutherozoa youngest median	492.1 Ma	7	[623]
67.10	crown bryophytes, study 2 (Bryophyta)	500–473 Ma	8	[456]
67.10	first bryophyte divergence (Bryophyta)	496.5–456.2 Ma	8	[455]
67.10	bryophyte–tracheophyte ancestor (Embryophyta)	500 Ma	8	[679]
67.10	myriapod clock age (Myriapoda)	~500 Ma	10	[975]
67.10	Cyclostome–gnathostome split (Vertebrata)	more than 500 Ma	15	[1410]
67.10	Cyclostome–gnathostome split (vertebrates)	>500 Ma	17	[1614]
67.11	crown bryophytes, study 1 (Bryophyta)	506.4–460.3 Ma	8	[455]
67.12	ecdysozoan body fossils younger bound	508 Ma	7	[525]
67.12	bilateral plated stem echinoderms (Ctenoimbricata, Courtessolea)	510 Ma	7	[576]
67.12	Ahnfeltiophycidae/Rhodymeniophycidae	508 Ma	8	[420]
67.12	Mandibulate (Tokummia katalepsis)	508 Ma	15	[1441]

67.13	Chengjiang (Maotianshan Shale)	≤518.03 ± 0.69/0.71 Ma	6	[452]
67.13–67.05	Crown embryophytes (land plants)	515.1–470.0 Ma	6	[455]
67.13–67.09	Crown embryophytes (land plants)	515–493 (68 calibrations) Ma	6	[456]
67.13	Chengjiang biota, maximum age	518.03 ± 0.69/0.71 Ma	7	[452]
67.13	crown embryophytes, study 1, older (Embryophyta)	515.1 Ma	8	[455]
67.13	crown embryophytes, study 2 (Embryophyta)	515–493 Ma	8	[456]
67.13–67.05	crown embryophytes (clock 1) (Embryophyta)	515.1–470.0 Ma	10	[455]
67.13–67.09	crown embryophytes (clock 2, 68 calibrations) (Embryophyta)	515–493 Ma	10	[456]
67.13	Oldest vertebrates; Chengjiang zircon limit (Myllokunmingia, Haikouichthys)	518.03 or younger Ma	15	[1409]
67.13	Emu Bay compound eyes (Cambrian arthropods)	about 515 Ma	18	[1683]
67.13	Chengjiang maximum age (Chengjiang biota)	≤518.03 Ma	23	[452]
67.14	first uncontested sponge spicules (Porifera)	520 Ma	7	[486]
67.14	first echinoderms with stereom (Echinodermata)	520 Ma	7	[568]
67.14	ecdysozoan body fossils older bound	520 Ma	7	[525]
67.14	Possible earliest cephalopod (Bonavista Formation, Newfoundland)	about 522 (4 specimens) Ma	15	[1342]
67.14	Crown Annelida calibration minimum	520 Ma	15	[1017]
67.14	Cambrian Stage 3 base (stratigraphy)	about 521 Ma	17	[435]
67.14	Chengjiang brain age (printed) (Fuxianhuia; Alalcomenaeus)	520 Ma	17	[1393; 1611]
67.14	possible earliest cephalopod (Bonavista Formation specimens, Newfoundland)	522 Ma	19	[1342]
67.14	vertebrate origin, before (Vertebrata)	520 Ma	19	[1806]
67.14	position: sensory consciousness at vertebrate origin (Feinberg & Mallatt 2013) (Vertebrata)	before 520 Ma	19	[1806]
67.14	Tripartite fossil brain (Fuxianhuia protensa)	520 Ma	23	[1611]
67.16	crown Cnidaria, younger bound	531.5 Ma	7	[485]
67.16	Eokinorhynchus rarus	535 Ma	7	[567]
67.17	Cambrian base (ICS chart)	538.8 ± 0.2 Ma	6	[435]
67.17	Helicolocellus cantori, younger bound	539 Ma	7	[491]
67.17	Ediacara biota end	541 Ma	7	[451]
67.17	Cambrian base (—)	538.8 ± 0.2 Ma	7	[435]
67.17	Na^+-selective channel divergence (Cnidaria)	540 (more than) Ma	7	[148]

67.17	Base of the Cambrian (stratigraphy)	538.8 ± 0.2 Ma	16	[435]
67.17	Cnidarian Na-selective channels diverge	more than 540 Ma	17	[531]
67.18	diversification of major cnidarian taxa	543 Ma	7	[530]
67.18	Sepkoski record span (marine genera)	0–542 Ma	16	[1569]
67.19	Helicolocellus cantori, older bound	551 Ma	7	[491]
67.19	Crown Mollusca calibration maximum (Nama Group)	549 Ma	15	[1341]
67.19–67.17	Nama assemblage (Ediacara biota)	550–539 Ma	16	[1539]
67.20	Dickinsonia age	558 Ma	6	[451]
67.20	Auroralumina younger bound (Auroralumina attenboroughii)	557 Ma	7	[524]
67.20	earliest potential ecdysozoan traces	556 (younger than) Ma	7	[525]
67.20; 67.20	White Sea beds age (Kimberella)	558 ± 1 to 555.3 ± 0.3 Ma	15	[1339]
67.20	Suggested chordate origin (Chordata)	about 555 Ma	15	[1409]
67.21	E Surface (Mistaken Point)	565.00 ± 0.64 Ma	6	[450]
67.21	Youngest rangeomorphs (Mistaken Point)	≤564.13 ± 0.65 Ma	6	[450]
67.21	E Surface (Ediacaran macrobiota)	565.00 ± 0.64 Ma	7	[450]
67.21	youngest rangeomorphs, Mistaken Point (Rangeomorpha)	564.13 ± 0.65 Ma	7	[450]
67.21	Haootia quadriformis	560 Ma	7	[523]
67.21	Auroralumina older bound (Auroralumina attenboroughii)	562 Ma	7	[524]
67.21	Cyclostome–gnathostome split (Vertebrata)	around 560 Ma	15	[1411]
67.21–67.19	White Sea assemblage (Ediacara biota)	560–550 Ma	16	[1539]
67.21	Haootia muscle impression (Haootia quadriformis)	about 560 Ma	17	[523]
67.21	Cyclostome–gnathostome ancestor (vertebrates)	around 560 Ma	17	[1411]
67.22	Algal sterane reading (Ediacaran)	earliest animal-like fossils about 571 Ma	6	[448]
67.22	Brasier Surface (Mistaken Point)	567.63 ± 0.66 Ma	6	[450]
67.22–67.17	Ediacara biota span	571–541 Ma	6	[451]
67.22	earliest animal-like Ediacaran fossils (algal reading) (Metazoa)	571 Ma	7	[448]
67.22	Brasier Surface (Ediacaran macrobiota)	567.63 ± 0.66 Ma	7	[450]
67.22	Ediacara biota start	571 Ma	7	[451]
67.22–67.17; 64.60	Ediacara biota span	571–539 (32 Myr) Ma	17	[1607]
67.23	Mistaken Point macrofossils (Drook Formation)	574.17 ± 0.66 Ma	6	[450]

67.23	crown Protostomia, younger bound	578.1 Ma	7	[485]
67.23	first complex Ediacaran macrofossils, Mistaken Point (Ediacaran macrobiota)	574.17 ± 0.66 Ma	7	[450]
67.23–67.21	Avalon assemblage (Ediacara biota)	575–560 Ma	16	[1539]
67.23	Oldest complex Ediacaran macrofossils, Mistaken Point (Ediacara biota)	574.17 ± 0.66 Ma	16	[450]
67.24	Corallinophycidae (red algae)	579 (543–617) Ma	6	[420]
67.24	Ecdysozoa clock origin	579 (or earlier) Ma	7	[525]
67.24	Corallinophycidae	579 (543–617) Ma	8	[420]
67.24–67.19	earlier oxygenation estimate (ocean)	580–550 Ma	11	[449]
67.25	crown Deuterostomia, younger bound	587.2 Ma	7	[485]
67.26	crown Bilateria, younger bound	595.7 Ma	7	[485]
67.27	Dictyostelid split (social amoebae)	≥0.6 Ga	6	[440]
67.27	Eocyathispongia qiania	600 Ma	7	[490]
67.27	sponges diverged from other animals (Porifera)	600 Ma (more than)	7	[473]
67.27	Root prior (Mollusca clock)	600 + 100 Ma	15	[1341]
67.27	Sponge divergence (Porifera)	more than 600 Ma	17	[473]
67.31	crown Eumetazoa, younger bound	625.9 Ma	7	[485]
67.32	24-ipc steranes (Huqf Supergroup, Oman)	>635 Ma	6	[446]
67.32–67.31	Doushantuo oxygenation (South China)	635–630 Ma	6	[449]
67.32	24-ipc steranes below Marinoan cap carbonate (Demospongiae (sterane reading))	635 Ma (older than)	7	[446]
67.32	ocean oxygenation after Marinoan	635–630 Ma	8	[449]
67.32–67.18	Ediacaran surface communities (Ediacara Member palaeosols, South Australia)	635–542 (625–542 in summary) Ma	10	[969]
67.32–67.31	ocean oxygenation, Doushantuo	635–630 Ma	11	[449]
67.32–67.18	Ediacaran palaeosols (Charniodiscus; Dickinsonia; Tribrachidium)	635–542 Ma	11	[969]
67.32	Ediacaran base (chart)	~635 Ma	11	[435]
67.32	Base of the Ediacaran (stratigraphy)	about 635 Ma	16	[435]
67.32	Sponge steranes older than (Porifera)	about 635 Ma	17	[446; 447]
67.33	crown Cnidaria, older bound	641.8 Ma	7	[485]
67.33	bilaterian phyla diverged before (Cambrian base + 100 Myr)	638.8 Ma	7	[435; 485]
67.33–67.16	Crown Cnidaria	641.8–531.5 Ma	17	[485]
67.34	Dikarya	649 Ma	6	[299]
67.34	crown Metazoa, younger bound	649.8 Ma	7	[485]

67.35	Glomeromycota	about 659 (715–606) Ma	6	[299]
67.35	crown Protostomia, older bound	653.1 Ma	7	[485]
67.35	Glomeromycota origin	659 (715–606) Ma	9	[299]
67.35–67.23	Crown Protostomia	653.1–578.1 Ma	17	[485]
67.36	Nemaliophycidae (red algae)	661 Ma	6	[420]
67.36	crown Deuterostomia, older bound	662.3 Ma	7	[485]
67.36	Nemaliophycidae	661 Ma	8	[420]
67.36–67.25	Crown Deuterostomia	662.3–587.2 Ma	17	[485]
67.39	crown Bilateria, older bound	688.3 Ma	7	[485]
67.39–67.26	Crown Bilateria	688.3–595.7 Ma	17	[485]
67.40	clock Demospongiae (hard bound)	692 (650–711) Ma	7	[486]
67.41	clock Demospongiae (soft bound)	699 (660–749) Ma	7	[486]
67.41	core Chlorophyta, clock younger	700 Ma	8	[422]
67.43	Flagellum lost (Fungi)	about 720 Ma	6	[299]
67.43	hard maximum used (Metazoa)	713 Ma	7	[486]
67.43	Cryogenian base (—)	720 Ma	9	[435]
67.43	loss of fungal flagellum (Fungi)	720 Ma	9	[299]
67.43	fungal flagellum lost (clock) (Fungi)	ca. 720 Ma	10	[299]
67.46	clock Silicea (hard bound)	740 (683–789) Ma	7	[486]
67.46	cnidarian origin, mitochondrial clock	741 (686–819) Ma	7	[530]
67.46 (67.39–67.55)	Cnidarian node (mitochondrial clock)	741 (686–819) Ma	17	[530]
67.47	crown Eumetazoa, older bound	746.2 Ma	7	[485]
67.47–67.31	Crown Eumetazoa	746.2–625.9 Ma	17	[485]
67.48	Otavia sponge-like fossils	760 Ma	7	[489]
67.48	clock Silicea (soft bound)	759 (698–832) Ma	7	[486]
67.48	clock Calcarea + Epitheliozoa	754 (695–820) Ma	7	[486]
67.51	Hildenbrandiophycidae (red algae)	781 Ma	6	[420]
67.51	clock Metazoa (soft bound)	781 (718–838) Ma	7	[486]
67.51	Hildenbrandiophycidae	781 Ma	8	[420]
67.53	animal–unicellular split, clock (Metazoa and unicellular relatives)	800 Ma	7	[472]
67.53	Animal–unicellular divergence (animals)	more than 800 Ma	17	[472]
67.55 (67.32–67.75)	Tertiary plastid, stem ochrophyte (ochrophytes)	≤819 (633–1,017) Ma	5	[342]
67.57	crown Metazoa, older bound	833.5 Ma	7	[485]
67.57–67.34	Crown Metazoa	833.5–649.8 Ma	17	[485]

67.63	possible poriferan body fossils, Stone Knife Formation (Porifera (disputed))	890 Ma	7	[488]
67.63	Ourasphaira giraldae younger	890 Ma	9	[430]
67.64	fossil thylakoids, Grassy Bay Fm, younger (cyanobacteria)	900 Ma	8	[648]
67.68	Bangiophyceae–Florideophyceae (red algae)	943 (817–1,049) Ma	6	[420]
67.68	Bangiophyceae–Florideophyceae split (Rhodophyta)	943 (817–1,049) Ma	8	[420]
67.73	Heterokont secondary endosymbiosis (heterokonts)	about 1,000 Ma	5	[362]
67.73–67.41	Core Chlorophyta	1,000–700 Ma	6	[422]
67.73	Dictyostelid–animal ancestor (dictyostelids and animals)	>1,000 Ma	6	[410]
67.73	Proterocladus antiquus	1000 Ma	8	[421]
67.73	core Chlorophyta, clock older	1000 Ma	8	[422]
67.73	secondary endosymbiosis of a red alga (heterokonts)	1 Ga	8	[362]
67.73	Nav-like channels emerge (eukaryotes)	more than 1 Ga	17	[148]
67.74–67.63	Ourasphaira (Ourasphaira giraldae)	1,010–890 Ma	6	[430]
67.74	fossil thylakoids, Grassy Bay Fm, older (cyanobacteria)	1010 Ma	8	[648]
67.74	Ourasphaira giraldae older	1010 Ma	9	[430]
67.74–67.63	oldest unambiguous fungus (Ourasphaira)	1010–890 Ma	10	[430]
67.75	crown Fungi	1020 Ma	9	[299]
67.78	Bangiomorpha (Bangiomorpha pubescens)	1.047 +0.013/−0.017 Ga	5	[356]
67.78 (67.76–67.79)	Bangiomorpha age (Bangiomorpha pubescens)	1.047 +0.013/−0.017 Ga	6	[356]
67.78	Bangiomorpha pubescens age	1047 (+13/−17) Ma	8	[356]
67.78	Bangiomorpha age (Bangiomorpha pubescens)	1.047 Ga	23	[356]
67.80–67.34	Serial secondary red uptakes (red plastids)	1,079–650 Ma	5	[342]
67.90–67.73	non-marine eukaryotes (Torridonian microfossils, NW Scotland)	1200–1000 Ma	10	[968]
67.93	opisthokont node, all constraints younger (Opisthokonta)	1240 Ma	9	[890]
67.94	Eukaryotic photosynthesis, calibrated clock (eukaryotes)	about 1.25 Ga	5	[356]
67.94	eukaryotic photosynthesis, clock (Archaeplastida)	1.25 Ga	8	[356]
67.97–67.30	Ochrophytes	1,298–622 Ma	5	[342]
68.03	opisthokont node, all constraints older	1389 Ma	9	[890]

	(Opisthokonta)			
68.09	opisthokont node, full analyses older (Opisthokonta)	1481 Ma	9	[890]
68.10–68.45	Nitrogenase origin by clock	1.5–2.2 Ga	2	[112]
68.10	Chloroplast symbiosis, review (plastid)	>1.5 Ga	5	[354]
68.10–68.45	nitrogenase clock origin	1500–2200 Ma	11	[112]
68.11–67.40	Myzozoans (dinoflagellates, apicomplexans)	1,520–696 Ma	5	[342]
68.16	Indian red algae (Rafatazmia; Ramathallus)	about 1.6 Ga	6	[355]
68.16	Tirohan Dolomite red algae (Rafatazmia, Ramathallus)	1.6 Ga	8	[355]
68.19 (68.24–68.14)	Chitrakoot red algae (Tirohan Dolomite, India)	1,650 ± 89 Ma	5	[355]
68.19–66.99	Cryptophytes	1,658–440 Ma	5	[342]
68.19	Crown red algae, Tirohan Dolomite	1,650 ± 89 Ma	16	[355]
68.20–67.96	Red-algal plastid donor stem (Rhodophytina)	1,675–1,281 Ma	5	[342]
68.21	Root of Plantae	about 1,694 Ma	6	[420]
68.21	root of Plantae	1694 (1,484–1,925) Ma	8	[420]
68.23	fossil thylakoids, McDermott Fm, younger (Navifusa majensis)	1730 Ma	8	[648]
68.23	crown red algae younger (Rhodophyta)	1732 Ma	8	[342]
68.25	fungal origin, second clock (Fungi)	1759–1078 Ma	9	[342]
68.26	fossil thylakoids, McDermott Fm, older (Navifusa majensis)	1780 Ma	8	[648]
68.27	primary plastid origin younger (Archaeplastida)	1807 Ma	8	[342]
68.29	Crown eukaryotes	<1.84 Ga	2	[111]
68.29	crown eukaryotes younger than (Eukaryota)	1840 Ma	11	[1015]
68.30	Eoentophysalis belcherensis younger bound	1854 Ma	8	[648]
68.32–68.04	Eukaryote origins in rock record (eukaryotes)	1.9–1.4 Ga	5	[356]
68.34–67.24	Haptophytes	1,943–579 Ma	5	[342]
68.36	Fossil eukaryote cells (eukaryotes)	about 2 Ga	5	[343]
68.36–68.23	Crown red algae	1,984–1,732 Ma	5	[342]
68.36	Fossil akinetes (cyanobacteria)	about 2.00 Ga	6	[415]
68.36	crown red algae older (Rhodophyta)	1984 Ma	8	[342]
68.36	free O2 scarce until (atmosphere)	~2000 Ma	11	[1014]

68.36	Free oxygen scarce until (atmosphere)	about 2 Ga	16	[1014]
68.37	Eoentophysalis belcherensis older bound	2018 Ma	8	[648]
68.39–67.91; 67.58	Mitochondrial symbiosis (mitochondrion)	2.053–1.21 (window 0.843 Gyr) Ga	5	[111]
68.39	end of Lomagundi excursion (carbon cycle)	~2060 Ma	11	[226]
68.39–67.91	mitochondrial origin (mitochondrion)	2053–1210 Ma	11	[1015]
68.39	End of Lomagundi excursion (carbon cycle)	about 2.060 Ga	16	[226]
68.39–67.91	Mitochondrial symbiosis (eukaryotes)	2.053–1.21 Ga	16	[111]
68.39–67.91	Mitochondrial symbiosis date (mitochondrion)	2.053–1.21 Ga	23	[111]
68.41	Francevillian colonial organisms age (Gabon macrofossils)	2.1 Ga	16	[418]
68.42–68.27; 66.72	Archaeplastida plastid	2,137–1,807 (window 330 Myr) Ma	5	[342]
68.42–68.27	Primary plastid clock (Archaeplastida)	2,137–1,807 Ma	6	[342]
68.42	primary plastid origin older (Archaeplastida)	2137 Ma	8	[342]
68.43	Five sections fossils (cyanobacteria)	about 2.15 Ga	6	[415]
68.47	Oxygen oscillation until (atmosphere)	2.250–2.240 Ga	16	[226]
68.50	Lasting oxygen (atmosphere)	2.33 Ga	3	[225]
68.50	Permanent oxygen (atmosphere)	about 2.33 Ga	6	[225]
68.50	permanent atmospheric oxygen (Earth atmosphere)	2.33 Ga	8	[225]
68.50	permanent atmospheric O2 (atmosphere)	~2330 Ma	11	[225]
68.53	Cyanobacterial multicellularity, follow-up	before 2.4 (GOE 2.45–2.32) Ga	6	[416]
68.53	Fungus-like filaments (vesicular basalt)	2.4 Ga	6	[429]
68.53	LECA, second clock (Eukaryota)	2386–1958 Ma	9	[342]
68.53	fungus-like filaments in basalt (Ongeluk Formation)	2.4 Ga	9	[429]
68.53	fungus-like filaments in basalt (subsurface fungi)	2400 Ma	10	[429]
68.53–68.45	palaeosol O2 rise (atmosphere)	2400–2200 (about 2300) Ma	11	[860]
68.53	Multicellularity in cyanobacteria before	2.4 Ga	16	[416]
68.53–68.35	LECA (733 taxa, 320 genes) (eukaryotes)	2,386–1,958 Ma	16	[342]
68.54	Ongeluk magmatism age (Kaapvaal Craton)	2426 ± 3 Ma	11	[226]
68.54	Ongeluk Formation magmatism age	2.426 ± 0.003 Ga	16	[226]

	(Kaapvaal Craton)			
68.55–68.54	GOE onset (atmosphere)	2460–2426 Ma	3	[226]
68.55–68.46	Cyanobacterial multicellularity origin	2.45–2.22 Ga	6	[415]
68.55	onset of Great Oxidation, older bound (Earth atmosphere)	2.46 Ga	8	[226]
68.57	Oxygen build-up from biology (atmosphere)	2.5 Ga	3	[227]
68.57	oxygen rising, summary (Earth atmosphere)	2.5 Ga	8	[227]
68.60–68.64	Palaeosol microbial mats (South African palaeosol)	2.6–2.7 Ga	3	[228]
68.60–68.64	mats in palaeosols (Mpumalanga palaeosols)	2600–2700 Ma	10	[228]
68.60–68.64	Mpumalanga palaeosols (microbial mats)	2600–2700 Ma	11	[228]
68.79	Nitrogen fixation minimum age (biological N2 fixation)	3.2 Ga	2	[110]
68.79–68.65	biological N2 fixation, isotopes (Mo-nitrogenase fixers)	3200–2750 (minimum 3200) Ma	11	[110]
68.80	microbial mats on land (Moodies Group mats, South Africa)	3220 Ma	10	[967]
68.80	Sulphur Springs filaments (questioned microbes)	3240 Ma	12	[1121]
68.85	Sulfur-metabolising microfossils (Strelley Pool Formation)	3.4 Ga	2	[109]
68.85	Crown Bacteria and Archaea (Bacteria, Archaea)	<3.4 Ga	2	[111]
68.86	Methanogenesis older than (Pilbara)	3.46 Ga	2	[106]
68.86	Apex chert age	3465 Ma	2	[107]
68.86	Strelley Pool reef age	3430 Ma	2	[108]
68.86	Strelley Pool stromatolites age	3.43 Ga	3	[108]
68.86	Panorama filament (Panorama Formation)	3.45 Ga	6	[415]
68.86	Strelley Pool stromatolites	3430 Ma	8	[108]
68.87	Dresser hot springs on land (Dresser Formation)	3.48 Ga	2	[104]
68.87	Sulfate reduction age (North Pole barites)	3.47 Ga	2	[105]
68.87–68.95	LUCA third study	3.5–3.8 Ga	2	[112]
68.87–68.95	LUCA age, older study (last universal common ancestor)	3.5–3.8 Ga	4	[112]
68.87	microbial sulphate reduction (barites, North Pole, Australia)	~3470 Ma	11	[105]
68.87–68.95	LUCA without nitrogenase	3500–3800 Ma	11	[112]
68.92	Isua graphite globules age (Isua	>3700 Ma	2	[100]

	sediments)			
68.92	Isua biogenic nanoscale graphite (Isua Supracrustal Belt)	>=3.7 Ga	2	[101]
68.92	Isua cones age (Isua stromatolites)	3700 Ma	2	[102]
68.94	Nuvvuagittuq microfossil minimum age (Nuvvuagittuq belt)	3770 Ma	2	[98]
68.95–69.00	Oldest exposed crust (granitoid gneiss)	3800–4000 Ma	1	[4]
68.95	Isua light carbon (Isua banded iron formation)	3800 Ma	2	[99]
68.96	Spike date from CAI age (inner solar system)	3867 Ma	1	[7]
68.96	Akilia light carbon (Akilia banded iron formation)	>3850 Ma	2	[99]
68.97–69.06	Ages of analysed Jack Hills zircons	3910–4280 Ma	1	[4]
68.97	Late heavy bombardment spike (inner solar system)	3.9 Ga	1	[6]
68.97	3.9 Ga peak as argon artefact (Apollo samples)	3.9 Ga	1	[5]
68.97	LUCA earlier study	>3.9 Ga	2	[111]
68.97	LUCA age, older study (last universal common ancestor)	>3.9 Ga	4	[111]
68.98–69.11	LUCA composite range	3.94–4.52 Ga	2	[97]
68.98–69.11	LUCA composite range (last universal common ancestor)	3.94–4.52 Ga	17	[97]
69.00	Oldest components of Acasta Gneiss	4030 Ma	1	[2]
69.02–68.95	Bombardment window (inner solar system)	4.1–3.8 Ga	1	[6]
69.02	Graphite in Jack Hills zircon	4.10 ± 0.01 Ga	1	[96]
69.02–69.07	LUCA age	4.09–4.33 (3.94–4.52) Ga	1	[97]
69.02–69.07	LUCA ILN interval	4.09–4.33 Ga	2	[97]
69.04	LUCA central age	4.2 Ga	2	[97]
69.04–69.07	LUCA GBM interval	4.18–4.33 Ga	2	[97]
69.04 (69.02–69.07)	LUCA age (last universal common ancestor)	about 4.2 (4.09–4.33) Ga	17	[97]
69.06	Earlier oldest Yilgarn detrital zircons	4276 Ma	1	[2]
69.06	Hydrosphere interacting with crust (Earth)	4300 Ma	1	[4]
69.06	Nuvvuagittuq microfossil possible age (Nuvvuagittuq belt)	4280 Ma	2	[98]
69.08	Oldest detrital zircon, Jack Hills (zircon, Yilgarn Craton)	4404 ± 8 Ma	1	[2]
69.08	Silicate Earth mixing ended before	4.4 Ga	1	[3]

69.10	Magma ocean, Moon-forming impact (Earth)	4.5 Ga	1	[3]
69.10	Meteorite age (carbonaceous meteorites)	4.5 Ga	1	[62]
69.11	Formation of the Earth	4550 Ma	1	[2]
69.12	Age of CAIs, first solids (solar system)	4567.30 ± 0.16 Ma	1	[1]
69.12	Chondrule formation, oldest (solar system)	4567.32 ± 0.42 Ma	1	[1]
69.12	Chondrule formation, youngest (solar system)	4564.71 ± 0.30 Ma	1	[1]

What the ladder shows

The ladder holds the whole book on one scale. In length it runs from the bond between two hydrogen atoms, 74.1 pm at −5.85, to the electricity grid of the human net, about 80 million km at 38.24. That is 44 positions: a factor of three, 44 times over.

Living bodies fill a band inside it. The smallest adult insect, a male *Dicopomorpha* of 139 µm, stands at 7.30. The blue whale, 25.8 m, stands at 18.34.

Clones and fungal genets reach further than bodies. Two isolates of one *Armillaria* genet in Oregon lie 3,810 m apart, at 22.89. A *Posidonia* meadow clone reaches 15 km, at 24.14.

Above them stand the fibre of the brain and the works of the human net. The myelinated fibre in one human brain, 176,000 km in a man of twenty, stands at 32.67. The railways stand at 34.18 and the electricity grid at 38.24.

In time the ladder starts with the life of a hydrogen bond in water, about 1 ps at 8.00. The giant spike of the jellyfish *Aglantha* lasts 1.2–1.6 ms, at 27.03–27.29. The interstitial stem cells of *Hydra* complete a cycle in 24 h, at 43.50.

All its tissues are renewed in two to three weeks, at 45.90–46.27.

The year stands at 48.87. A black coral of *Leiopathes* lived 4,265 years, at 56.48, and the sponge *Monorhaphis* about 11,000 years, at 57.34. The clone of *Lomatia tasmanica* is at least 43,600 years old, at 58.59.

The longest bound for a living thing is a clone again. Shared genets of *Posidonia* 15 km apart give a minimum age of 80,000–200,000 years, at 59.15–59.98. The form lasts while its carriers are replaced: the stem cells turn over in days, the clone holds for tens of thousands of years.

The ages run from the first solids of the solar system, 4,567.30 Ma at 69.12, and the oldest zircon, 4,404 Ma at 69.08. The oldest traces of life, 3.43–3.48 Ga, stand at 68.86–68.87. Every later appearance in the book stands below them on the ladder of ages.

The youngest ages in the table are those of writing. The Uruk phases of 3500–3000 BCE stand at 56.71–56.63, the Maya writing of San Bartolo at 55.93–55.71. The events of the last two centuries are told as durations to 2026.

The residue of one depth becomes the alphabet of the next, and the ladder shows it

rung by rung. The bacterium becomes the mitochondrion of a larger cell, the cell becomes the body, the body the colony. The humans of the last chapters are the letters of the human net.

The ladder does not end at the top row of these tables. “A ladder driven by a rest cannot end.” The next depth stands above the last position written here.

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