

The Weaving of Life

How Animals, Plants, Fungi and Microorganisms Became Interwoven. A Reference Work in Two Layers

J. Konstapel

Constable Research, Leiden

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How to use this book

This book is the third of a series. *Plants on the Ladder* treated fifteen groups of photosynthetic life. *The Company of Plants* treated the co-evolution of plants with insects, fungi, bacteria, animals, soil, the air and pathogens.

This book widens the view to all of life.

Its question: how did animals, plants, trees, fungi and microorganisms, each from its own evolutionary history, become interwoven? By descent and gene transfer, by one cell living inside another, by many cells becoming one body, by eating, by farming, by pollination, by the exchange of elements. And how can that weaving be described within the Vacuum.Net model?

It is not an encyclopedia of groups. Each chapter follows one line of connection between the domains and kingdoms, from the last common ancestor to the human share of the living world.

The book is built in two layers, kept apart.

Layer A is biology only. Ten chapters, A1 to A10, each with the same sections. What it is; first appearance; partners; sizes; times; counts; order of events; present quantities.

A closing **Pattern** of at most 150 words. Then what could not be verified, and the references of the chapter. Layer A mentions no theory.

It stands on its own.

Part C gathers the numbers of Layer A in seven tables across the chapters.

Layer B asks one question of Layer A. Do the measured patterns correlate with the structure and the evolution of the net, as the Vacuum.Net texts state them, with nothing added? Each pairing carries a status. Three tests were fixed before the dossier tables were looked at, then run.

Their outcomes stand as they fell. Section B12 gives the answer to the question of the book.

The marks. *Measured*: read in the cited source, with a reference number [n].

Computed: arithmetic on measured numbers, shown. *Modelled*: the output of a published model, named as such.

Text: a statement of a Vacuum.Net text, quoted (Layer B only). *Read*: a pairing made in Layer B between a text statement and a measured pattern; a read is a hypothesis.

The ladder and the position. Every size and every time carries its position: $\log_3$ of the value over a unit. The unit of length is 4.558816×10^{-8} m, the unit of time 1.520655×10^{-16} s: Larson's natural units, as used in *From Atom to Body*. One year is 3.15576×10^7 s.

An age of A million years is placed as a duration of $A \times 10^6$ years. Positions are given to two decimals and never rounded to a whole mark. A position is a coordinate.

Sources. Each chapter of Layer A has its own numbered reference list. Part C cites as "A3 [12]": chapter A3, reference 12. Every citation was checked against OpenAlex or Crossref, or read on the publisher's or the institution's page.

Each chapter ends with a list "Not verified": items found only in secondary sources, or whose primary could not be opened. They are not facts of this book. Layer B has its own annotated list.

Background. Five books framed the choice of topics: Quammen's *The Tangled Tree*, Dawkins and Wong's *The Ancestor's Tale*, Beerling's *The Emerald Planet*, Sheldrake's *Entangled Life*, and Begon, Townsend and Harper's *Ecology*. No number in this book is taken from them. They are listed, with what they offer, in the annotated references of Layer B.

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The answer to the question of this book

Part D. Left Out, by Rule

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Part 0 — The Rules

0.1 Two layers

Layer A is written as if the theory did not exist. Its ten Pattern paragraphs and the tables of Part C are the data of Layer B. Nothing in Layer B adds a fact that Layer A does not hold, and nothing in Layer A leans on Layer B.

0.2 The marks

Four marks for fact, one for pairing; see “How to use this book”. A statement without a mark is a heading or a connective.

0.3 The ladder

Positions as defined above. The day sits at 43.50, the year at 48.87. The dated record of Layer A starts with the earliest claimed signals of life, 4.28 Ga.

It runs through the domestication of plants and animals from 13,000 years before present. It ends with the spread of an amphibian fungus in the twentieth century.

0.4 Depth, in two senses

As in *Plants on the Ladder*, Part 0.3. *Ring depth* is the length of a closed ring of trits, 3, 6, 9. It is used only where the texts use it.

Position is the depth of the Climate paper, “each depth n is one layer”; every measured size and time has one. No text equates the two, and this book does not.

0.5 What is not added

No rule is added to the theory. No sentence says that the net causes a biological pattern. No ring depth is assigned to any organism above the cell.

Where the texts are silent, Layer B says none.

0.6 Tests

A test is fixed before its data are looked at: the quantity, the required outcome, the chance outcome, the data. Where a test could not be run on the fixed data, it is reported as not run, with what was obtained. Where a classification was made after a table had been seen, it is marked post hoc and is not a test.

The tests are run by Claude Code. The attestation is the author's.

Layer A — The Weaving of Life

A1 One Ancestor, Three Domains

What it is

All cellular life is grouped into Bacteria, Archaea and eukaryotes. This chapter follows one line of connection: the common descent of the three, and the traffic of genes between them. Both are read from genomes, from rocks and from living cells.

The grouping began with ribosomal RNA. A 1977 comparison found “three aboriginal lines of descent”: eubacteria, archaebacteria (with the methanogens) and “urkaryotes” [1]. The urkaryote line is the cytoplasmic component of eukaryotic cells [1].

In 1990 the rank of domain was proposed above the kingdom, with three domains: Archaea, Bacteria and Eucarya [2]. The Archaea were split into two kingdoms, Euryarchaeota and Crenarchaeota [2]. From 1977 to 1990 is 13 years (computed), position 51.21.

In 2013 newer methods placed eukaryotic core genes within the Archaea [3]. The authors wrote that “the three-domains tree may be incorrect” and that the results “support ... only two primary domains of life” [3]. From 1977 to 2013 is 36 years (computed), position 52.13.

A ribosomal-protein tree of 3,083 genomes, 1,011 newly reconstructed, used 16 concatenated proteins (measured [4]). It holds 92 named bacterial phyla, 26 archaeal phyla and all five eukaryotic supergroups (measured [4]).

The Candidate Phyla Radiation, with other lineages lacking isolated representatives, “clearly comprises the majority of life’s current diversity” [4]. No percentage is given [4].

Genes also move sideways, between lineages. Among Bacteria and Archaea the share of transferred genes is large. In eukaryotes it is smaller and disputed.

First appearance

The ancestor by molecular clock. Three age statements for the last universal

common ancestor (LUCA) are recorded. They do not agree.

The most recent places LUCA at about 4.2 Ga, position 69.04 (modelled [5]). The ILN relaxed-clock range is 4.09–4.33 Ga, position 69.02–69.07; the GBM range 4.18–4.33 Ga, position 69.04–69.07 (modelled [5]). A composite estimate runs from 3.94 to 4.52 Ga, position 68.98–69.11 (modelled [5]).

An earlier study gives LUCA more than 3.9 Ga, position 68.97 (modelled [6]). It places crown Eubacteria and crown Archaeobacteria below 3.4 Ga, position 68.85 (modelled [6]). Crown eukaryotes fall below 1.84 Ga, position 68.29 (modelled [6]).

A third source gives about 3.5–3.8 Ga, position 68.87–68.95 (modelled [7]). The central values spread by $4.2 - 3.65 = 0.55$ Gyr (computed), position 67.19. The most recent estimate is the oldest.

From LUCA to the crown groups of Bacteria and Archaea is at least $3.9 - 3.4 = 0.5$ Gyr (computed), position 67.10.

The older rock record, 3.7–4.28 Ga. One zircon from the Jack Hills, Western Australia, was the only one older than 3.8 Ga among more than 10,000 (measured [8]). Its concordant age is 4.10 ± 0.01 Ga, position 69.02 (measured [8]). Its graphite inclusions have $\delta^{13}\text{C}(\text{PDB}) -24 \pm 5$ ‰, consistent with a biogenic origin (measured [8]).

If biogenic, that carbon puts a terrestrial biosphere about 300 Myr earlier than previously proposed [8]. The 300 Myr lies at position 66.64.

The Nuvvuagittuq belt, Quebec, holds putative microfossils “at least 3,770 million and possibly 4,280 million years old” (measured [9]). The positions are 68.94 and 69.06; the range 510 Myr (computed) lies at 67.12. Filaments average $8.3 \mu\text{m}$ (s.d. 2.8, $n = 23$) and tubes $24.9 \mu\text{m}$ (s.d. 6.3, $n = 40$) (measured [9]).

At Isua, West Greenland, a banded iron formation of about 3,800 Myr, position 68.95, holds isotopically light carbonaceous inclusions (measured [10]). A similar formation on Akilia is possibly older than 3,850 Myr, position 68.96 (measured [10]).

Isua sediments older than 3,700 Ma, position 68.92, hold graphite globules of $2\text{--}5 \mu\text{m}$ with $\delta^{13}\text{C} -19$ ‰ (PDB) (measured [11]). They are read as biogenic detritus, possibly planktonic [11]. Nanoscale, ^{13}C -depleted graphite in the Isua belt is dated at least 3.7 billion years (measured [12]).

Isua also yielded 1–4-cm-high stromatolites in 3,700-Myr-old rocks (measured [13]). They are 220 Myr older, position 66.36, than the best-supported evidence then known in the 3,480-Myr Dresser Formation [13]. A reassessment reads them as deformation structures of “non-biological, post-depositional origin” [14].

The younger rock record, 3.40–3.48 Ga. Hot-spring deposits of ca. 3.48 Ga, position 68.87, in the Dresser Formation hold geyserite, sinter terracettes, stromatolites and palisade fabric (measured [15]). They extend the record of inhabited terrestrial hot springs by about 3 billion years, position 68.73 [15]. Life on land moves about 580 Myr earlier, position 67.24 [15].

Barites of about 3.47 Gyr at North Pole, Australia, record microbial sulphate reduction (measured [16]). The maximum sulphide fractionation is 21.1 ‰, the mean about 11.6

‰ (measured [16]). The record of this process moves back by more than 750 Myr, position 67.47, from about 2.7 Ga, position 68.64 [16].

Fluid inclusions of about 3.5 Gyr in Pilbara hydrothermal precipitates hold methane with $\delta^{13}\text{C}$ below -56 ‰ (measured [17]). Microbial methanogenesis is therefore older than 3.46 Gyr, position 68.86 [17].

The Apex chert, about 3,465 Myr old, position 68.86, holds microbial fossils of five species (measured [18]). Carbon isotopes were measured in 11 fossils (measured [18]). Two species are inferred photosynthesizers, one a methane-producing archaeon, others methane consumers [18].

At Strelley Pool a reef of about 3,430 Myr, position 68.86, shows seven stromatolite morphotypes along a 10-km outcrop (measured [19]). In the 3.4-billion-year-old Strelley Pool Formation, position 68.85, micrometre-sized pyrite is read as a by-product of sulphate reduction and sulphur disproportionation (measured [20]).

Nitrogen fixation has an isotopic minimum age of 3.2 Gyr, position 68.79 (measured [21]). The $\delta^{15}\text{N}$ mean is 0.0 ± 1.2 ‰ in rocks 3.2–2.75 Gyr old, position 68.79–68.65 (measured [21]).

Partners

LUCA's gene set. One reconstruction screened 6.1 million protein-coding genes in 286,514 protein clusters (measured [22]). It traced 355 families to LUCA: $355 / 286,514 = 0.124$ % (computed). It describes LUCA as “anaerobic, CO₂-fixing, H₂-dependent with a Wood–Ljungdahl pathway”, thermophilic and N₂-fixing [22].

The 2024 reconstruction gives a genome of 2.75 Mb (2.49–2.99 Mb) encoding 2,657 proteins (2,451–2,855) (modelled [5]). A conservative subset holds 399 KEGG orthologues found in both prokaryotic domains (modelled [5]). It includes 19 class 1 CRISPR–Cas effector families (modelled [5]).

The ratio of the two estimates is $2,657 / 355 = 7.5$ (computed). One method counts families meeting a strict two-domain criterion [22]. The other reconciles gene trees with species trees by probability [5].

On nitrogen fixation the sources disagree. One reconstruction infers that LUCA fixed N₂ [22]. Another finds nitrogenase absent from LUCA and dates its origin at roughly 1.5–2.2 Ga, position 68.10–68.45 (modelled [7]).

Archaea and eukaryotes. The first Asgard genome, of the Lokiarchaeota, is a 5.1 Mbp composite, 92 % complete, with 5,381 protein-coding genes (measured [23]). Closest hits were eukaryotes 3.3 % (175 proteins), bacteria 29 %, archaea 26 %, none 32 % (measured [23]). $175 / 5,381 = 3.25$ % (computed); the four shares sum to 90.3 % (computed).

Small GTPases make up nearly 2 % of that proteome (measured [23]). The lineage forms a monophyletic group with eukaryotes [23]. The core came from sediment under 3,283 m of water, 75 cm below the seafloor, about 15 km from the Loki's Castle vents [23].

In 2017 four clades, Loki-, Thor-, Odin- and Heimdallarchaeota, were grouped as the

superphylum Asgard [24]. Eight genome bins came from seven sites; Odinararchaeota came only from hot springs (measured [24]). All lineages were enriched in eukaryotic signature proteins [24].

Eukaryotes fell inside Asgard with posterior probability 1 on ribosomal proteins, 0.95 on conserved markers and bootstrap 91 on rRNA (modelled [24]). Heimdallarchaeota were nearest in most Bayesian analyses, at posterior probability 0.77 and bootstrap 28–42 (modelled [24]). The exact position stayed unresolved [24].

In 2023, 63 new Asgard genomes from 11 sites were added; the RP56 dataset held 175 Asgard representatives (measured [25]). The analysis covered 17,200 protein families in 181 archaeal genomes (measured [25]). Eukaryotes were “placed, with high confidence, as a well-nested clade within Asgard archaea”, sister to the Hodarchaeales [25].

The ancestral proteome is 3,134 proteins for the last Asgard common ancestor and 4,053 for the Hodarchaeales ancestor (modelled [25]). The ratio is $4,053 / 3,134 = 1.29$ (computed). The Asgard ancestor was “probably a thermophilic chemolithotroph”; the Hodarchaeales have a median predicted optimal growth temperature of 36.7 °C (modelled [25]).

The first cultured Asgard cell. *Prometheoarchaeum syntrophicum* MK-D1 came from sediment under 2,533 m of water and was incubated at 20 °C [26]. Its cells measure 300–750 nm, mean 550 nm ($n = 15$), position 2.27 (measured [26]). Protrusions are 80–100 nm wide (measured [26]).

It doubles in “approximately 14–25 days”, position 45.90–46.43 (measured [26]). It grew first with *Halodesulfobivrio* (85 %) and *Methanogenium* (2 %), later in a pure co-culture with *Methanogenium* (measured [26]). Cultivation took 12 years by the preprint, position 51.13, and was “decade-long” by the published summary, position 50.97 [26].

A second archaeal pair. *Nanoarchaeum equitans* grows attached to *Ignicoccus* (measured [27]). Its spherical cells are about 400 nm across, position 1.98 (measured [27]). Its 0.5 Mb genome was the smallest archaeal genome then known [27].

Gene traffic among prokaryotes. In *E. coli* MG1655, 755 of 4,288 ORFs (547.8 kb) entered by at least 234 lateral transfer events (measured [28]). This happened since divergence from *Salmonella* about 100 Myr ago, position 65.64 (modelled [28]). $755 / 4,288 = 17.6$ % of ORFs (computed); the source gives about 18 % of the chromosome [28].

The introduced genes have a mean age of 14.4 Myr, position 63.87, and arrive at 16 kb per Myr per lineage (modelled [28]). Retained sequence is $547.8 \text{ kb} / 100 \text{ Myr} = 5.5 \text{ kb per Myr}$ (computed). About 34 % of the inflow is kept, if the rate held over the full 100 Myr (computed).

In 181 prokaryotic genomes with 539,723 genes, “at least 81 +/- 15%” of each genome’s genes took part in lateral transfer at some point (measured [29]). The range is 66–96 % (computed). The mean genome holds $539,723 / 181 = 2,982$ genes (computed).

In 329 proteobacterial genomes (1,207,272 proteins), at least 75 % of protein families showed at least one transfer event (measured [30]). Events ran at about one per family at species and class level (measured [30]). They doubled to about two per family at

phylum level (measured [30]).

In 110 genomes, 3,190 protein families entered the main analysis (measured [31]). “Between 88% and 98%” of family expansions were due to horizontal transfer; with a single criterion the share was 65 % (measured [31]). Xenologs were introduced on average twice as long ago as paralogs (measured [31]).

Twenty *E. coli* strains share a pan-genome of 17,838 gene families and a core of 1,976 (measured [32]). The average genome holds about 4,721 genes (measured [32]). The core is 41.9 % of one genome and 11.1 % of the pan-genome (computed).

Gene traffic between the domains. In 134 archaeal genomes, the origins of 13 higher taxa correspond to 2,264 gene acquisitions from bacteria (measured [33]). That is $2,264 / 13 = 174$ per origin (computed). Transfers from bacteria to archaea were “more than fivefold more frequent” than the reverse [33].

Of 25,762 clusters, 16,983 were archaeal-specific and 3,315 imports (measured [33]). The shares are 65.9 % and 12.9 % (computed).

Tree-like and transferred signal. A tree of 31 proteins present in each of 191 genomes “represents only about 1% of an average prokaryotic proteome” [34]. Against about 3,000 genes, $31 / 3,000 = 1.03$ % (computed). For a large eukaryotic proteome the share is “only 0.1%” [34].

A “forest” of 6,901 trees for 100 prokaryotes (41 archaea, 59 bacteria) holds 102 nearly universal trees, or NUTs (measured [35]). Inconsistency among the NUTs is 1.4–4.3 %, and 14 of them are strict 1:1 ribosomal-protein families (measured [35]). NUTs are 1.48 % of the trees; the ribosomal ones 13.7 % of the NUTs (computed).

In the NUTs a quartet analysis showed “a dominant tree-like signal” [36]. In 5,218 trees of 4–25 species the tree-like signal “becomes virtually undetectable” [36]. The trees outside the NUTs number 6,799, or 98.5 % (measured [36]; share computed).

In 35 groups of closely related genomes, gene loss runs at about three times the rate of gain (measured [37]). Gain and loss are about an order of magnitude above family expansion and reduction (measured [37]). Change amounts to “typically tens of thousands” of genome events per nucleotide substitution per site [37].

Gene traffic into eukaryotes. One model holds bacterial-to-eukaryote transfer episodic, at the origins of mitochondria and chloroplasts, with later differential loss [38]. In that model continuous lineage-specific transfer “does not contribute to long-term gene content evolution” [38]. A review instead gives transfer “an important role” with a “highly variable impact ... in different lineages” [39].

About 4,500 *Arabidopsis* protein-coding genes, about 18 %, are of cyanobacterial origin (measured [40]). The study compared 24,990 proteins; earlier estimates were 800 to 2,000 [40].

The red alga *Galdieria sulphuraria* has a 13.7 Mb genome and grows on more than 50 carbon sources (measured [41]). “At least 5%” of its protein-coding genes probably came from bacteria and archaea [41]. They include genes for heavy-metal detoxification and glycerol uptake [41].

In bdelloid rotifers, 2,792 of 28,922 matched transcript contigs (9.7 %) were foreign; the true rate is at least 8–9 % (measured [42]). Sources were about 59 % eubacterial, 23 % fungal, 6 % algal or plant and 1 % archaeal (measured [42]). About 80 % of the expressed foreign genes code for enzymes (measured [42]).

Wolbachia insertions occur in four insect and nematode species, from under 500 bp to “nearly the entire *Wolbachia* genome (>1 megabase)” (measured [43]). Three more insect genomes show potential transfers (measured [43]). The inserted genes are transcribed [43].

For animals the counts are disputed. A screen of 26 animal species plus 14 vertebrates found 145 class C foreign genes in humans, 110 of class B and 39 of class A (measured [44]). Average class C counts were 109 for primates, 40 for *Drosophila* and 173 for *Caenorhabditis* (measured [44]).

A re-examination tested 17 human genes from 2001 and 28 top claims of the screen (measured [45]). Of these, 12 of 17 and 26 of 28 failed, through closer animal matches, contamination or other origins (measured [45]). Seven genes (5 + 2) remained, from four hypothesised events (measured [45]).

The survivors are $7 / 45 = 15.6\%$ of those tested and $7 / 145 = 4.8\%$ of the class C count (computed). The re-examination cites 32 class A genes where the screen gives 39 [45][44]. Both positions are recorded: 145 foreign genes [44] and 7 with non-transfer explanations available [45].

Sizes

what	size	position	source
MK-D1 protrusions, width	80–100 nm	0.51–0.72	[26]
ultra-small groundwater bacteria (CPR), median axes	189.7 / 242.5 / 322.6 nm	1.30 / 1.52 / 1.78	[46]
<i>Nanoarchaeum equitans</i> , diameter	about 400 nm	1.98	[27]
MK-D1 (Asgard) cell	300–750 nm; mean 550 nm	1.72–2.55; 2.27	[26]
<i>Pyrococcus furiosus</i> , width	0.8–2.5 μm	2.61–3.64	[47]
most bacterial cells, length	about 2 μm	3.44	[48]
Isua graphite globules	2–5 μm	3.44–4.28	[11]
Nuvvuagittuq filaments, mean	8.3 μm	4.74	[9]
Løkken-Høydal filaments / tubes	9.1 / 19.5 μm	4.82 / 5.51	[9]
Nuvvuagittuq tubes, mean	24.9 μm	5.74	[9]
largest bacterium before 2022	750 μm	8.84	[48]

<i>Ca. Thiomargarita magnifica</i> , cell with measured cytoplasm	4.27 mm	10.42	[48]
<i>T. magnifica</i> , mean length	9.72 ± 4.25 mm	11.17	[48]
<i>T. magnifica</i> , maximum length	20.00 mm	11.83	[48]
Isua stromatolites, height	1–4 cm	11.19–12.46	[13]
Lokiarchaeota sample, below seafloor	75 cm	15.12	[23]
MK-D1 sample, water above	2,533 m	22.52	[26]
Lokiarchaeota sample, water above	3,283 m	22.76	[23]
Strelley Pool reef outcrop	10 km	23.77	[19]
Lokiarchaeota sample to Loki's Castle vents	about 15 km	24.14	[23]

Volumes: CPR cells $0.009 \pm 0.002 \mu\text{m}^3$ with 42 ± 9.5 ribosomes (measured [46]); SAR11 about $0.01 \mu\text{m}^3$ (measured [49]). A 400 nm sphere is $0.034 \mu\text{m}^3$ and a 550 nm sphere $0.087 \mu\text{m}^3$ (computed). The cytoplasm of the 4.27 mm *T. magnifica* cell is $5.91 \times 10^{-12} \text{ m}^3$, or $5.91 \times 10^6 \mu\text{m}^3$ (measured [48]; conversion computed).

T. magnifica is about 50-fold larger than other giant bacteria [48]. Its maximum is $20,000 / 2 = 10,000$ times a 2 μm cell and 26.7 times the 750 μm record (computed). From the shortest CPR axis to 20 mm is a factor of 1.05×10^5 (computed), positions 1.30 to 11.83.

Times

what	duration	position	source
<i>Vibrio (Pseudomonas) natriegens</i> , generation	9.8 min	38.96	[50]
<i>Pyrococcus furiosus</i> , doubling (optimum 100 °C)	37 min	40.17	[47]
<i>Vibrio cholerae</i> , wild doubling	1.1 h	40.69	[51]
<i>Pseudomonas aeruginosa</i> , wild doubling	2.3 h (other estimate 1.9–2.4 h)	41.36 (41.19–41.40)	[51]
median laboratory doubling	3 h	41.61	[51]
median wild doubling	7.4 h (5.5 h without <i>M. florum</i> ; 95 % CI 3.1–19 h)	42.43 (42.16; 41.64–43.29)	[51]
<i>E. coli</i> , wild doubling	15 h	43.07	[51]
<i>Salmonella enterica</i> ,	25 h	43.54	[51]

wild doubling			
turnover, upper 200 m of open ocean	6-25 d	45.13-46.43	[52]
MK-D1, doubling	14-25 d	45.90-46.43	[26]
replacement of 1.2×10^{30} cells at 1.7×10^{30} per year	0.7 yr	48.55	(computed)
turnover, ocean below 200 m	0.8 yr	48.67	[52]
replacement of $4-6 \times 10^{30}$ cells	2.4-3.5 yr	49.67-50.01	(computed)
turnover, soil	2.5 yr	49.70	[52]
MK-D1 cultivation, published summary / preprint	10 / 12 yr	50.97 / 51.13	[26]
three lines (1977) to three domains (1990)	13 yr	51.21	(computed)
three lines (1977) to two domains (2013)	36 yr	52.13	(computed)
turnover, subsurface	$1-2 \times 10^3$ yr	55.16-55.79	[52]
mean age of genes introduced into <i>E. coli</i>	14.4 Myr	63.87	[28]
spread of the Pilbara signals (3.48-3.40 Ga)	about 80 Myr	65.43	(computed)
<i>E. coli</i> - <i>Salmonella</i> divergence	about 100 Myr	65.64	[28]
Isua stromatolites before the Dresser record	220 Myr	66.36	[13]
zircon carbon before earlier evidence	about 300 Myr	66.64	[8]
3.80 Ga (Isua carbon) to 3.465 Ga (Apex)	0.335 Gyr	66.74	(computed)
4.10 Ga (zircon) to 3.70 Ga (Isua graphite)	0.40 Gyr	66.90	(computed)
LUCA (>3.9 Ga) to crown Bacteria and Archaea (<3.4 Ga), at least	0.5 Gyr	67.10	(computed)
Nuvvuagittuq age range	510 Myr	67.12	(computed)
spread of central LUCA dates	0.55 Gyr	67.19	(computed)
life on land, earlier than previously thought	about 580 Myr	67.24	[15]
LUCA (4.2 Ga) to the Pilbara (3.48 Ga)	0.72 Gyr	67.43	(computed)
sulphate-reduction record, extension	more than 750 Myr	67.47	[16]
Pilbara (3.48 Ga) to	1.64 Gyr	68.18	(computed)

crown eukaryotes (1.84 Ga), at least			
LUCA (4.2 Ga) to crown eukaryotes (1.84 Ga)	2.36 Gyr	68.52	(computed)
inhabited hot springs, record extension	about 3 billion years	68.73	[15]

In culture, division times run from 9.8 minutes to 25 days (measured [50][26]). The fastest to MK-D1 is a factor of 2,057–3,673 (computed). The fastest to subsurface turnover is a factor of 5.4×10^7 to 1.1×10^8 (computed).

The wild median, 7.4 h, is longer than the laboratory median, 3 h; their ratio is $3 / 7.4 = 0.41$ (measured [51]; ratio computed). Prokaryotes alone fill $4.2 - 1.84 = 2.36$ Gyr, 56 % of the time since LUCA by the 4.2 Ga date (computed).

Counts

Genomes and species. GTDB release R226, of 16 April 2025, holds 732,475 genomes (measured [53]). Its species clusters number 136,646 for Bacteria and 6,968 for Archaea, 143,614 in all; phyla number 169 and 20 (measured [53]). Archaea are 4.85 % of species clusters, and Bacteria outnumber them 19.6 to 1 (computed).

LPSN lists 22,681 validly published species in 4,007 genera and 48 phyla, at its refresh of 18 September 2026 (measured [54]). Named species are $22,681 / 143,614 = 15.8$ % of GTDB species clusters (computed; the definitions differ). Phyla are thus counted as $92 + 26$ [4], $169 + 20$ [53] and 48 [54].

Ancestral gene sets. LUCA: 355 families [22] or 2,657 proteins [5]. Asgard ancestor: 3,134 proteins; Hodarchaeales ancestor: 4,053 [25].

Transferred genes in prokaryotes. One genome: 17.6 % of ORFs [28]. 181 genomes: 81 ± 15 % of genes per genome [29]. 329 genomes: ≥ 75 % of families [30]; 110 genomes: 88–98 % of family expansions [31].

Transferred genes in eukaryotes. Humans: 145 claimed [44], 7 surviving [45]. *Galdieria*: at least 5 % [41]; bdelloid rotifers: 9.7 % of matched transcript contigs, true rate at least 8–9 % [42]; *Arabidopsis*: 18 % from the plastid ancestor [40].

Order of events

1. 4.52–3.94 Ga — LUCA, composite estimate (modelled [5]); position 69.11–68.98.
2. 4.33–4.09 Ga, central 4.2 Ga — LUCA, ILN model (modelled [5]); position 69.07–69.02, central 69.04.
3. 4.10 ± 0.01 Ga — potentially biogenic graphite in one Jack Hills zircon (measured [8]); position 69.02.
4. | 3.9 Ga — LUCA (modelled [6]); position 68.97.
5. | 3.85 Ga, possible — Akilia light carbon (measured [10]); position 68.96.
6. about 3.80 Ga — Isua light carbon (measured [10]); position 68.95.

7. 3.8–3.5 Ga — LUCA (modelled [7]); position 68.95–68.87.
8. ≥ 3.77 , possibly 4.28 Ga — Nuvvuagittuq filaments and tubes (measured [9]); position 68.94, possibly 69.06.
9. ≥ 3.70 Ga — Isua graphite (measured [11][12]); Isua stromatolites (measured [13]), contested [14]; position 68.92.
10. ca. 3.48 Ga — hot springs on land, Dresser Formation (measured [15]); position 68.87.
11. about 3.47 Ga — sulphate reduction, North Pole (measured [16]); position 68.87.
12. | 3.46 Ga — methanogenesis (measured [17]); position 68.86.
13. about 3.465 Ga — Apex chert microfossils (measured [18]); position 68.86.
14. about 3.43 Ga — Strelley Pool reef (measured [19]); position 68.86.
15. 3.4 Ga — sulphur-cycling microstructures (measured [20]); position 68.85.
16. < 3.4 Ga — crown Bacteria and crown Archaea (modelled [6]); position 68.85.
17. 3.2 Ga — biological nitrogen fixation, isotopic minimum (measured [21]); position 68.79.
18. 2.2–1.5 Ga — nitrogenase origin by molecular clock (modelled [7]); position 68.45–68.10.
19. Not dated in the sources read — the Asgard ancestor and the Hodarchaeales branch leading to eukaryotes [25].
20. < 1.84 Ga — crown eukaryotes (modelled [6]); position 68.29. Episodic transfer at the organelle origins [38]; see A2.
21. about 100 Ma — *E. coli* and *Salmonella* diverge (modelled [28]); position 65.64.
22. 14.4 Ma — mean age of the genes introduced into *E. coli* (modelled [28]); position 63.87.
23. Present — 1.2×10^{30} or $4\text{--}6 \times 10^{30}$ prokaryotic cells [55][52].

Present quantities

Cells. A 1998 estimate gives $4\text{--}6 \times 10^{30}$ prokaryotic cells, holding 350–550 Pg C, 85–130 Pg N and 9–14 Pg P (measured [52]). The oceanic subsurface holds 3.5×10^{30} , soil 2.6×10^{29} and the open ocean 1.2×10^{29} (measured [52]). Production is 1.7×10^{30} cells per year (measured [52]).

A 2019 revision gives 1.2×10^{30} cells (measured [55]). The deep oceanic subsurface holds 4×10^{29} , the deep continental subsurface and soil 3×10^{29} each, the oceans 1×10^{29} (measured [55]). The two totals differ by a factor of 3.3–5 (computed).

In the 2019 count the subsurface holds 7×10^{29} of 1.2×10^{30} cells, 58 % (computed). Of all cells 40–80 % live in biofilms (measured [55]). The share is about 80 % in surface habitats other than the ocean (measured [55]).

Biomass. Bacteria hold 70 Gt C and archaea 7 Gt C, against 450 Gt C in plants and 2 Gt C in animals (measured [56]). The total is about 550 Gt C (measured [56]). Bacteria to archaea is 10 to 1, and prokaryotes hold $77 / 550 = 14$ % (computed).

Single groups. SAR11 makes up 26 % of all rRNA genes identified in seawater (measured [49]). One *T. magnifica* cell of 2 cm holds $737,598 \pm 159,115$ genome copies of 11.5–12.2 Mb (measured [48]).

Turnover. Prokaryotes turn over in 6–25 days in the upper ocean, 0.8 years below 200 m and 2.5 years in soil (measured [52]). In the subsurface the time is $1\text{--}2 \times 10^3$ years (measured [52]). At 1.7×10^{30} cells a year the whole stock is replaced in 0.7 or 2.4–3.5 years, by the two totals (computed).

Pattern

Three studies date LUCA: 3.5–3.8 Ga, >3.9 Ga and 4.09–4.33 Ga (composite 3.94–4.52 Ga). The most recent is the oldest. Gene-set estimates run from 355 families to 2,657 proteins, a factor 7.5.

Single rock signals at 3.7–4.28 Ga are each disputed or “possible”. Six Pilbara records fall at 3.40–3.48 Ga, within about 80 Myr.

Eukaryotes moved from a separate domain (1977–2013) to a clade within Asgard archaea (2015, 2017, 2023). In the first Asgard genome the eukaryote-like share is 3.3 %.

Transfer shares: 17.6 % of ORFs in one *E. coli* genome, 81 ± 15 % of genes per genome (181 genomes), ≥ 75 % of protein families (329 genomes), 88–98 % of family expansions (110 genomes). Bacteria-to-archaea flow is more than five times the reverse. The tree-like core is 1–1.5 % of genes or trees.

Cell lengths span positions 1.30 to 11.83. Doubling and turnover times span positions 38.96 to 55.79.

Not verified

- Husnik & McCutcheon 2018, review of functional bacteria-to-eukaryote transfer: citation verified, no count read (V-bib).
- About 2.5 % of *Blastocystis* genes recently acquired (Eme et al. 2017): seen only in a reference list (secondary).
- “Up to 96%” of a prokaryote genome affected by transfer, cited by Treangen & Rocha 2011: primary not named (secondary).
- *E. coli* diameter $\approx 1 \mu\text{m}$, length $\approx 2 \mu\text{m}$, volume $\approx 1 \mu\text{m}^3$, mass $\approx 1 \text{ pg}$ (Milo & Phillips, BioNumbers): secondary.
- *E. coli* laboratory doubling 20 min; *M. tuberculosis* 15–20 h; *M. leprae* 14 days (OpenStax *Microbiology*): textbook, secondary.
- *Thiomargarita namibiensis* up to 750 μm , average 180 μm (Volland 2022 preprint, citing earlier work): secondary.
- Genome sizes and signature-protein counts of the 2017 Asgard bins: Extended Data not read.
- Gene counts in Ku et al. 2015: absent from the text read.
- Table 1 values of Puigbò et al. 2014: not read.
- $\delta^{13}\text{C}$ values of the Apex and Akilia carbon: absent from the abstracts read.
- One percentage for tree-like against transferred signal (Puigbò et al. 2010): not found.

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A2 The Cell That Ate

What it is

One cell takes another inside and keeps it. The kept cell divides with its host and loses most of its genes. Some of those genes move to the host nucleus.

The mitochondrion and the primary plastid arose this way. Both “arose from a single endosymbiotic event” [1]. Plastids then passed from eukaryote to eukaryote at second and third hand.

At second hand, some hosts kept the nucleus of the eaten alga as a reduced organelle, the nucleomorph [2]. Younger cases sit at earlier stages: the *Paulinella* chromatophore, the nitrogen-fixing UCYN-A and the *Azolla* cyanobiont. Some animals keep only the stolen plastid, without the alga.

Insects hold bacteria with the smallest cellular genomes known. In one insect a bacterium lives inside another bacterium [3]. This chapter follows that line of connection, with dates, sizes and gene counts.

First appearance

The mitochondrion. The mitochondrial symbiosis is dated 2.053–1.21 Ga, position 68.39–67.91 (modelled [4]). The window is $2.053 - 1.21 = 0.843$ Gyr wide (computed), position 67.58. Crown eukaryotes are younger than 1.84 Ga, position 68.29 (modelled [4]).

A later clock places the last eukaryotic common ancestor (LECA) at 2,386–1,958 Ma, position 68.53–68.35 (modelled [5]). It used 733 taxa and 320 nuclear protein-coding genes (measured [5]). The two LECA dates, <1.84 Ga and 2.386–1.958 Ga, do not overlap (computed).

The primary plastid. In one clock study the chloroplast lineage branches within the cyanobacterial tree at about 2.1 Ga, position 68.41 (modelled [6]). Establishment took another 200 Myr, position 66.27 (modelled [6]). The ancestral habitat reconstructs as low-salinity [6].

Another clock gives the Archaeplastida plastid 2,137–1,807 Ma, position 68.42–68.27 (modelled [5]). The window is 330 Myr, position 66.72 (computed). Crown red algae fall at 1,984–1,732 Ma, position 68.36–68.23 (modelled [5]).

A review gives the chloroplast symbiosis “more than 1.5 billion years ago”, position 68.10 [7].

The fossil record gives two later dates. In the Tirohan Dolomite of central India, probable crown-group red algae are dated $1,650 \pm 89$ Ma by Pb–Pb isochron (measured [8]). The positions are 68.19, with 68.24–68.14 for the error range.

These fossils are about 400 Myr older, position 66.90, than the oldest red alga accepted before them [8]. *Rafatazmia chitrakootensis* forms filaments 58–175 μm wide with compartments 30–165 μm long (measured [8]). Central rhomboidal disks measure 50–60 μm (measured [8]).

Denaricion mendax filaments are 130–275 μm , of uncertain affinity (measured [8]). *Ramathallus lobatus* thalli run from about 0.5 to more than 3 mm, with cells of 5–15 μm (measured [8]).

Bangiomorpha pubescens, Baffin Island, first appears at $1.047 \pm 0.013/-0.017$ Ga by Re–Os (measured [9]). The positions are 67.78, with 67.79–67.76 for the error range. This is about 150 Myr younger, position 66.01, than the earlier 1.2 Ga constraint, position 67.90 [9].

Bangiomorpha is the only recognised crown-group eukaryote older than ca. 0.8 Ga, position 67.53 [9]. Clocks calibrated on it place eukaryotic photosynthesis at ca. 1.25 Ga, position 67.94 (modelled [9]). The same study puts eukaryote origins between 1.9 and 1.4 Ga in the record, position 68.32–68.04 [9].

Five dates are thus recorded for the plastid or the first plastid-bearing cell: about 2.1 Ga, 2.14–1.81 Ga, >1.5 Ga, 1.65 Ga and ca. 1.25 Ga. The central values spread by $2.1 - 1.25 = 0.85$ Gyr (computed), position 67.59.

Plastids at second and third hand. The 2021 clock dates the complex-plastid lineages with wide 95 % ranges (modelled [5]). The values are listed under Order of events. The overall window for serial secondary endosymbioses of red plastids is 1,079–650 Ma, position 67.80–67.34 (modelled [5]).

A tertiary acquisition by a stem ochrophyte is dated ≤ 819 Ma, position 67.55 (modelled [5]). Its 95 % range is 633–1,017 Ma, position 67.32–67.75 (modelled [5]).

Insect endosymbionts. *Sulcia* was acquired by the auchenorrhynchan ancestor at

least 260 Ma, position 66.51 (modelled [10]). The cicada, spittlebug and sharpshooter lineages split at least 200 Ma, position 66.27 (modelled [10]).

Sulcia and *Nasuia* have been partners since the leafhopper-spittlebug split more than 200 Ma (modelled [11]). The origin of the pairing lies before 260 Ma [11]. The *Buchnera* symbiosis in aphids was established “200–250 Myr ago”, position 66.27–66.47 (modelled [12]).

Young cyanobacterial partners. *Paulinella* diverged from its heterotrophic relatives about 90–140 Myr ago, position 65.54–65.94 (modelled [13]). The main scheme gives 93.6 Myr (38.1–138.2), position 65.58 (64.76–65.93) (modelled [13]). This is a maximum age for the chromatophore [13].

An alternative scheme gives 141.4 Myr (48.7–210.4), position 65.95 (64.98–66.31) (modelled [13]). Two others give 55.8 and 47.9 Myr, position 65.11 and 64.97 (modelled [13]). An earlier figure of 60 Myr, position 65.17, was derived from *Buchnera* pseudogene loss [13].

The UCYN-A sublineages A1 and A2 diverged around 91 Myr ago, in the late Cretaceous, position 65.55 (modelled [14]).

The *Azolla* cyanobiont relationship has three recorded ages. It is “potentially extending back for as long as 140 million years”, position 65.94 [15]. Fossils give about 100 Myr, position 65.64 [16]; a review gives “more than 60 my”, position 65.17 [7].

Partners

The host. Eukaryotes nest within the Asgard archaea, sister to the Hodarchaeales of the Heimdallarchaeia [17]. The last Asgard common ancestor was “probably a thermophilic chemolithotroph” [17]. The lineage leading to eukaryotes “adapted to mesophilic conditions”, with a median predicted optimal growth temperature of 36.7 °C (modelled [17]).

The cultured Asgard archaeon *Prometheoarchaeum syntrophicum* MK-D1 has cells of 300–750 nm, mean 550 nm, position 2.27 (measured [18]). It doubles in 14–25 days, position 45.90–46.43 (measured [18]). It grows only with partners, *Halodesulfobivibrio* and *Methanogenium* (measured [18]).

No measured size exists for the ancestral host or guest. The nearest measured cell is MK-D1; a 550 nm sphere has a volume of 0.087 μm^3 (computed).

The guest of the mitochondrion. Mitochondria evolved from a proteobacterial lineage that branched before all sampled Alphaproteobacteria [19]. The analysis added twelve divergent alphaproteobacterial clades and one sister clade (measured [19]). No age is given [19].

Rickettsia prowazekii is “more closely related to mitochondria than is any other microbe studied so far” [20]. Its genome is 1,111,523 bp with 834 protein-coding genes (measured [20]).

What the mitochondrion kept. Human mtDNA is 16,569 bp with 2 rRNA, 22 tRNA and 13 protein-coding genes (measured [21]). Few or no non-coding bases lie between

the genes (measured [21]).

Arabidopsis mtDNA is 366,924 nt with 57 identified genes covering only 10 % of the genome (measured [22]). Integrated plastid sequences make up 1 % and retrotransposon remnants of nuclear origin 4 % (measured [22]).

The jakobid *Reclinomonas americana* has 69,034 bp of mtDNA with 97 genes (measured [23]). These include four genes of a eubacterial-type multisubunit RNA polymerase (measured [23]).

A later survey counts “as many as 96 assigned genes” for *Reclinomonas* (measured [24]). It finds exactly 100 mitochondrial genes in *Andalucia godoyi*, the largest complement of any eukaryote examined (measured [24]). Jakobid mtDNAs measure 65–100 kbp (measured [24]).

Two counts for *Reclinomonas* are thus recorded: 97 [23] and 96 [24].

The largest mtDNA in the sources read is that of *Silene conica*: 11.3 Mb in 128 circular-mapping chromosomes (measured [25]). Intergenic sequence makes up 99 % of the extra size, and mutation rates vary about 100-fold (measured [25]).

Retention against the 834 protein genes of *Rickettsia* is: human $13 / 834 = 1.6 \%$; *Arabidopsis* $\leq 57 / 834 = 6.8 \%$ (computed). For *Reclinomonas* it is $97 / 834 = 11.6 \%$ and for *Andalucia* $100 / 834 = 12.0 \%$ (computed). The last two include RNA genes and are upper bounds.

Human mtDNA is $16,569 / 1,111,523 = 1.5 \%$ of the *Rickettsia* genome length (computed). *Silene conica* mtDNA is 10.2 times the *Rickettsia* genome and 682 times human mtDNA (computed).

The guest of the plastid. Plastids “evolved from endosymbiotic cyanobacteria on a single occasion” [26]. The plastids of glaucophytes, red algae and green algae derive from one ancestor [1].

The free-living cyanobacterium *Synechocystis* PCC 6803 has 3,573,470 bp and “a total of 3,168 potential protein genes” (measured [27]). *Prochlorococcus* MED4 has 1,657,990 bp and 1,716 genes; MIT9313 has 2,410,873 bp and 2,275 genes (measured [28]).

What the plastid kept. The *Arabidopsis* chloroplast genome is 154,478 bp (measured [29]). It carries 87 protein-coding genes (8 duplicated), 4 rRNA and 37 tRNA genes (measured [29]). Its inverted repeats are 26,264 bp each (measured [29]).

The retained fraction is $87 / 3,168 = 2.7 \%$ of *Synechocystis* protein genes (computed). Against the smallest free-living *Prochlorococcus* it is $87 / 1,716 = 5.1 \%$ (computed). By length the plastid genome is 4.3 % of *Synechocystis* and 9.3 % of *Prochlorococcus* MED4 (computed).

About 4,500 *Arabidopsis* protein-coding genes, about 18 % of the total, are of cyanobacterial origin (measured [30]). The study compared 24,990 proteins; 9,368 were conserved and 866 had cyanobacterial homologues (measured [30]). Earlier estimates were 800 to 2,000 [30].

Genes of plastid origin in the nucleus outnumber those kept in the plastid by about

$4,500 / 87 = 52$ to 1 (computed).

In non-photosynthetic plants the plastid genome shrinks further. *Polytoma uvella* keeps 25 genes, the largest non-photosynthetic plastid genome noted [26]. *Pilostyles* keeps five or six genes, and no plastid genome was detected in *Rafflesia* [26].

Green plastids at second hand. Green algal plastids were taken up by euglenids and chlorarachniophytes [1]. These are two separate occasions [26]. Plastid loss “happened at least once” [1].

Red plastids at second and third hand. One review states that “red algae appear to have been taken up only once” [1]. A later review finds “how many times they were established ... is unclear” [26]. Models include tertiary and quaternary events, with “cryptophyte first” [26].

A serial model proposes three transfers (modelled [31]). A red alga passed to cryptophytes, a cryptophyte to the ochrophyte ancestor, and an ochrophyte to the haptophyte ancestor [31]. The model used 50 organisms in 14 eukaryotic lineages and 5,818 amino-acid positions (measured [31]).

The 2021 clock also favours serial secondary endosymbioses [5]. Two positions are recorded for red plastids: one uptake [1] and three serial transfers [31].

The complex-plastid lineages named are euglenids, chlorarachniophytes, cryptophytes, haptophytes and ochrophytes, which include diatoms, brown and golden algae [26]. They also include dinoflagellates, apicomplexans with the apicoplast remnant, and *Lepidodinium* [26].

Dinoflagellates. Outside the dinotoms, dinoflagellates hold two permanent plastid replacements: haptophyte-derived in the Kareniaceae and green-alga-derived in *Lepidodinium* [26].

The dinotoms carry diatom-derived plastids from at least 11 diatom species (measured [26]). *Durinskia capensis* keeps its diatom for about 2 months, position 47.24, as a kleptoplast [26].

The *Lepidodinium chlorophorum* plastid genome is circular, 66,223 bp, with 63 ORFs, 27 tRNA and 2 rRNA genes (measured [32]). It derives from an endosymbiotic pedinophyte, nearest sampled *Pedinomonas minor* [32]. It is 43 % of the *Arabidopsis* plastid by length and 72 % by ORF count (computed; ORFs against protein genes).

Count of plastid acquisitions. The events named are: primary 1, green secondary 2, red 1 or 3, green replacement 1, tertiary in dinoflagellates 2, stem ochrophyte 1 [1][26][31][5]. The minimum is $1 + 2 + 1 + 1 + 1 + 1 = 7$, with the dinotoms counted once (computed). With three red steps and the stem-ochrophyte event counted separately, the total is about 9 (computed).

No published total was read.

Nucleomorphs. Nucleomorphs occur in two lineages only: cryptophytes, with a red-algal endosymbiont, and chlorarachniophytes, with a green-algal one [2]. Both genomes were independently reduced to under 1 Mbp with a similar three-chromosome layout [2].

The *Guillardia theta* nucleomorph is 551 kb on 3 chromosomes, at one gene per 977 bp (measured [33]). It retains “hundreds of genetic-housekeeping genes” and only 30 for chloroplast-located proteins [33]. A later table gives 550.5 kbp and 487 protein-coding genes (measured [34]).

The *Bigelowiella* paper quotes “a mere 531 genes” for *G. theta* and counts 17 introns in it [35]. The two counts, 487 protein-coding genes and 531 genes in total, use different definitions. Both are recorded.

The *Hemiselmis andersenii* nucleomorph is 0.572 Mbp, 571.4 kbp, on 3 chromosomes, with no spliceosomal introns at all (measured [2]). It carries 472 protein-coding genes (measured [34]).

The nucleomorph of the non-photosynthetic *Cryptomonas paramecium* is 486 kbp (measured [34]). It has 518 predicted genes, 466 protein-coding, and still 18 plastid-protein genes (measured [34]). All three cryptophytes share 217 of 230 conserved ORFs, 94.3 % (measured [34]).

The *Bigelowiella natans* nucleomorph is 372,870 bp on chromosomes of 140.5, 134.1 and 98.1 kb (measured [35]). It carries 331 protein-coding genes, 18 rRNA, 20 tRNA and 4 snRNA genes, and 5 DnaK pseudogenes (measured [35]). It has 17 plastid-protein genes and 852 introns in 240 genes, all 18–21 nt (measured [35]).

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

The *Paulinella* chromatophore. The symbiont is related to the *Prochlorococcus/Synechococcus* clade [13]. Chromatophores of strains FK01 and M0880/a carry 841 and 867 protein-coding genes (measured [13]). *Synechococcus* WH5701 carries 2,917 (measured [13]).

Retention is $841 / 2,917 = 28.8$ % and $867 / 2,917 = 29.7$ % (computed). The chromatophore genome is 1.02 Mb against about 3 Mb in *Synechococcus* WH5701, about a quarter of its coding capacity [26]. About 65 % of protein-coding genes were lost in the common ancestor of the species studied [26].

By length the chromatophore is $1.02 / 3 = 34$ % (computed). The nucleus encodes 433 chromatophore-targeted proteins: 17 of α -cyanobacterial origin and 26 from other bacteria (measured [26]). Two retention figures are recorded: 28.8–29.7 % of genes [13] and “about a quarter” of coding capacity [26].

UCYN-A, the nitroplast. *Ca. Atelocyanobacterium thalassa* (UCYN-A) has a 1.44 Mb genome (measured [36]). It lacks the oxygen-evolving photosystem II, carbon-fixation genes and the tricarboxylic acid cycle (measured [36]).

It has inverted repeats of rRNA operons, as in many chloroplasts [36].

The genome is $1.44 / 3.57 = 40$ % of the *Synechocystis* genome (computed). The partner is a unicellular prymnesiophyte alga [37]. “The prymnesiophyte receives fixed N in exchange for transferring fixed carbon to UCYN-A” [37].

The host of UCYN-A2, *Braarudosphaera bigelowii*, is 7–10 µm, position 4.58–4.91; the host of UCYN-A1 is 1–3 µm, position 2.81–3.81 (measured [14]). One UCYN-A1 cell lives in each host cell (measured [14]). Each *B. bigelowii* cell holds about 3–10 UCYN-A2 cells (measured [14]).

UCYN-A is “tightly integrated into algal cell architecture” and organellar division [38]. It “imports proteins encoded by the genome” of the host [38]. It is proposed as an early-stage organelle, the “nitroplast” [38].

The *Azolla* cyanobiont. *Nostoc azollae* 0708 has a genome of 5,486,145 bp with 5,357 predicted coding sequences (measured [15]). Of these, 31.2 % are pseudogenes, and 3,668 ORFs are intact (measured [15]). The free-living *Anabaena/Nostoc* PCC 7120 has 6,413,771 bp and 5,368 potential protein genes (measured [39]).

The intact fraction is $3,668 / 5,368 = 68.3$ % (computed). Other plant-symbiotic *Nostoc* genomes are 7.1–10.4 Mb, “among the largest Nostocales genomes” (measured [40]). “*N. azollae* is the only clear example of a plant symbiotic cyanobacteria genome that underwent genome streamlining” [40].

Cyanobacterial symbioses with plants “emerged multiple times independently” [7].

In symbiosis the heterocyst frequency rises from 4–10 % to 30–50 % of cells (measured [41]). The cyanobiont grows 5–10 times slower (measured [41]). It retains as little as 20 % of the nitrogen it fixes (measured [41]).

Kleptoplasty in sea slugs. Photosynthetic yields were measured in 29 sacoglossan species, 186 specimens (measured [42]). Three derived species among those measured kept yields above 0.4 after 20 days, position 46.23 (measured [42]).

They are *Elysia crispata*, *E. timida* and *Plakobranthus ocellatus*; the share is $3 / 29 = 10$ % (computed). *E. chlorotica* is a fourth long-term species, taken from the literature, not among the 29 [42].

Short-term retainers start above 0.5 for 1–2 days, position 43.50–44.13, and fall within 7–14 days, position 45.27–45.90 (measured [42]). The Oxynoacea and most Limapontioidea show no functional retention, with yields below 0.2 on day one (measured [42]).

Elysia timida kept a yield above 0.52 after 35 days, position 46.74 (measured [42]). In *Plakobranthus ocellatus* the mean yield fell from 0.78 to 0.59 over 74 days, position 47.42 (measured [42]). That is 76 % of the starting yield (computed).

P. ocellatus starved 47 days and *E. timida* 28 days before sequencing, position 47.00 and 46.53 (measured [43]). No expressed algal nuclear genes specific to photosynthesis were found (measured [43]).

Thuridilla hopei retains plastids up to 15 days, position 45.96 (measured [43]). The authors conclude that “the slugs maintain their long-lived plastids without the help of algal nuclear genes” [43].

A contrary study reports the algal nuclear gene *psbO*, from the prey *Vaucheria litorea*, expressed in *Elysia chlorotica* (measured [44]). The gene is in the slug germline and identical to the prey sequence (measured [44]). The slug plastid depends on the nuclear

genome for “>90%” of its proteins, and slugs photosynthesize “for months” [44].

Two positions are recorded: gene transfer supports retention [44], and no expressed algal photosynthesis genes are found [43].

Kleptoplasty in other groups. Flatworms keep plastids about two weeks, position 45.90 [26]. The ciliate *Mesodinium rubrum* keeps them up to a month, position 46.61 [26]. An Antarctic Ross Sea dinoflagellate keeps haptophyte kleptoplasts at least 30 months, position 49.70 [26].

Insect endosymbionts. *Buchnera* sp. APS of the pea aphid has a chromosome of 640,681 bp and two plasmids, pLeu 7,786 bp and pTrp 7,258 bp (measured [12]). It has 583 predicted ORFs, about 500 functionally assigned, and 55 amino-acid biosynthesis genes (measured [12]).

Buchnera has $583 / 4,288 = 13.6\%$ of the ORFs of *E. coli* MG1655 (computed; *E. coli* count [45]).

Symbiont genomes of 139–250 kb encode 121–227 proteins (measured [46]). The smallest, *Ca. Tremblaya princeps*, has “a genome of only 139 kb” [46].

Before 2006 the smallest known cellular genomes were about 500 kb, with approximately 500 genes [46].

Carsonella ruddii of psyllids has a circular chromosome of 159,662 bp, GC 16.5 %, coding density 97 % (measured [47]). A minimal genome had been proposed at roughly 400 kb [47].

Hodgkinia cicadicola of cicadas has 143,795 bp, GC 58.4 % (measured [48]). It reads UGA as tryptophan instead of stop (measured [48]). Its partner *Sulcia* has GC 22.6 % (measured [48]).

In the leafhopper *Macrosteles quadrilineatus*, *Nasuia deltocephalinicola* has 112 kb and *Sulcia muelleri* 190 kb (measured [11]). Together they make 10 essential amino acids (measured [11]). Both lost the genes for ATP synthesis by oxidative phosphorylation (measured [11]).

Sulcia-CARI of the spittlebug *Clastoptera arizonana* has 276,511 nt and 246 protein-coding genes (measured [10]). Its partner *Zinderia insecticola* has 208,564 nt and 202 protein-coding genes (measured [10]). The retained genes are completely colinear across three *Sulcia* genomes (measured [10]).

A bacterium inside a bacterium. In the mealybug *Planococcus citri* each *Tremblaya princeps* cell harbours several gammaproteobacterial cells [3]. The *T. princeps* genome is 138.9 kb and the inner *Moranella endobia* 538.2 kb (measured [3]). *Tremblaya phenacola* PAVE, in a host lineage without the inner symbiont, has 171.5 kb (measured [3]).

The inner genome is $538.2 / 138.9 = 3.9$ times its container’s (computed). *Tremblaya* with an inner symbiont is 81 % the size of *Tremblaya* without one (computed).

Sizes

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what	size	position	source
MK-D1 (Asgard host relative) cell	300–750 nm; mean 550 nm	1.72–2.55; 2.27	[18]
host of UCYN-A1	1–3 μm	2.81–3.81	[14]
<i>Ramathallus lobatus</i> cells (1.65 Ga)	5–15 μm	4.28–5.28	[8]
<i>Braarudosphaera bigelowii</i> , host of UCYN-A2	7–10 μm	4.58–4.91	[14]
<i>Rafatazmia</i> compartments, length	30–165 μm	5.91–7.46	[8]
<i>Rafatazmia</i> central disks	50–60 μm	6.37–6.54	[8]
<i>Rafatazmia chitrakootensis</i> filaments, width	58–175 μm	6.51–7.51	[8]
<i>Denaricion mendax</i> filaments	130–275 μm	7.24–7.92	[8]
<i>Ramathallus lobatus</i> thalli	about 0.5 to >3 mm	8.47 to >10.10	[8]

Times

what	duration	position	source
short-term kleptoplast, initial yield >0.5	1–2 d	43.50–44.13	[42]
short-term kleptoplast, fall	within 7–14 d	45.27–45.90	[42]
flatworm kleptoplasts	about 2 weeks	45.90	[26]
MK-D1, doubling	14–25 d	45.90–46.43	[18]
<i>Thuridilla hopei</i> kleptoplasts, up to	15 d	45.96	[43]
long-term threshold (yield >0.4)	20 d	46.23	[42]
<i>E. timida</i> , starved before sequencing	28 d	46.53	[43]
<i>Mesodinium rubrum</i> kleptoplasts, up to	a month (30.44 d)	46.61	[26]
<i>E. timida</i> , yield above 0.52	35 d	46.74	[42]
<i>P. ocellatus</i> , starved before sequencing	47 d	47.00	[43]
<i>Durinskia capensis</i> , diatom kept	about 2 months (60.88 d)	47.24	[26]
<i>P. ocellatus</i> , yield 0.78 $\rightarrow$ 0.59	74 d	47.42	[42]
Ross Sea dinoflagellate kleptoplasts, at least	30 months (913.2 d)	49.70	[26]
<i>Bangiomorpha</i> , younger	about 150 Myr	66.01	[9]

than the earlier constraint			
plastid establishment after branching	about 200 Myr	66.27	[6]
crown red algae, window (1,984–1,732)	252 Myr	66.48	(computed)
primary plastid window (2,137–1,807)	330 Myr	66.72	(computed)
red-algal plastid donor stem, width (1,675–1,281)	394 Myr	66.89	(computed)
Chitrakoot red algae, older than earlier oldest	about 400 Myr	66.90	[8]
LECA window (2,386–1,958)	428 Myr	66.96	(computed)
serial red window, width (1,079–650)	429 Myr	66.96	(computed)
ochrophytes, width (1,298–622)	676 Myr	67.38	(computed)
myzozoans, width (1,520–696)	824 Myr	67.56	(computed)
mitochondrial window (2,053–1,210)	843 Myr	67.58	(computed)
spread of plastid central dates (2.1 – 1.25 Ga)	0.85 Gyr	67.59	(computed)
cryptophytes, width (1,658–440)	1,218 Myr	67.91	(computed)
haptophytes, width (1,943–579)	1,364 Myr	68.02	(computed)

Kleptoplast function runs from 15 days to at least 30 months, positions 45.96 to 49.70. Window widths of the dated lineages run from 252 to 1,364 Myr, positions 66.48 to 68.02.

Counts

Genomes of kept bacteria and their free-living relatives

genome	size	genes	source
<i>Synechocystis</i> PCC 6803 (free-living)	3,573,470 bp	3,168 protein	[27]
<i>Anabaena/Nostoc</i> PCC 7120 (free-living)	6,413,771 bp	5,368 protein	[39]
<i>Prochlorococcus</i> MED4 / MIT9313 (free-living)	1,657,990 / 2,410,873 bp	1,716 / 2,275	[28]
<i>Rickettsia prowazekii</i> (intracellular)	1,111,523 bp	834 protein	[20]
<i>Nostoc azollae</i> 0708 (cyanobiont)	5,486,145 bp	5,357 CDS; 3,668 intact	[15]

UCYN-A (nitroplast)	1.44 Mb	—	[36]
<i>Paulinella</i> chromatophore	1.02 Mb	841 / 867 protein	[26][13]
<i>Buchnera</i> APS	640,681 bp	583 ORFs	[12]
<i>Moranella endobia</i> (inside <i>Tremblaya</i>)	538.2 kb	—	[3]
<i>Sulcia</i> -CARI	276,511 nt	246 protein	[10]
<i>Zinderia insecticola</i>	208,564 nt	202 protein	[10]
<i>Sulcia muelleri</i> (leafhopper)	190 kb	—	[11]
<i>Tremblaya phenacola</i>	171.5 kb	—	[3]
<i>Carsonella ruddii</i>	159,662 bp	—	[47]
<i>Hodgkinia cicadicola</i>	143,795 bp	—	[48]
<i>Tremblaya princeps</i>	138.9 kb	group range 121–227	[3][46]
<i>Nasuia deltocephalinicola</i>	112 kb	—	[11]

Organelle genomes

genome	size	genes	source
<i>Silene conica</i> mtDNA	11.3 Mb, 128 chromosomes	—	[25]
<i>Arabidopsis</i> mtDNA	366,924 nt	57	[22]
<i>Arabidopsis</i> plastid	154,478 bp	87 protein, 4 rRNA, 37 tRNA	[29]
<i>Reclinomonas americana</i> mtDNA	69,034 bp	97 (96 in [24])	[23]
<i>Lepidodinium</i> plastid	66,223 bp	63 ORFs	[32]
human mtDNA	16,569 bp	13 protein, 22 tRNA, 2 rRNA	[21]
<i>Hemiselmis</i> nucleomorph	571.4 kbp	472 protein	[2][34]
<i>Guillardia</i> nucleomorph	551 kb	487 protein	[33][34]
<i>Cryptomonas</i> nucleomorph	485.9 kbp	466 protein	[34]
<i>Bigeloviella</i> nucleomorph	372,870 bp	331 protein	[35]

Insect symbiont protein genes span 121–583, which is $121 / 4,288 = 2.8\%$ to $583 / 4,288 = 13.6\%$ of *E. coli* (computed; [45]). Primary events counted are four: mitochondrion, plastid, *Paulinella* and UCYN-A, with organelle status proposed for the last [38].

Order of events

1. 2,386–1,958 Ma — LECA (modelled [5]); position 68.53–68.35.
2. 2,137–1,807 Ma — primary plastid (modelled [5]); position 68.42–68.27. About 2.1 Ga, plus about 200 Myr to establishment (modelled [6]); position 68.41.

3. 2,053–1,210 Ma — mitochondrial symbiosis (modelled [4]); position 68.39–67.91.
4. 1,984–1,732 Ma — crown red algae (modelled [5]); position 68.36–68.23.
5. 1,943–579 Ma — haptophytes (modelled [5]); position 68.34–67.24.
6. 1.9–1.4 Ga — eukaryote origins in the geological record [9]; position 68.32–68.04.
7. <1.84 Ga — crown eukaryotes (modelled [4]); position 68.29.
8. 1,675–1,281 Ma — red-algal plastid donor stem (modelled [5]); position 68.20–67.96.
9. 1,658–440 Ma — cryptophytes (modelled [5]); position 68.19–66.99.
10. 1,650 ± 89 Ma — probable crown red algae, Chitrakoot (measured [8]); position 68.19.
11. 1,520–696 Ma — myozoans (modelled [5]); position 68.11–67.40.
12. | 1.5 Ga — chloroplast symbiosis [7]; position 68.10.
13. 1,298–622 Ma — ochrophytes (modelled [5]); position 67.97–67.30.
14. ca. 1.25 Ga — eukaryotic photosynthesis, calibrated clock (modelled [9]); position 67.94.
15. 1,079–650 Ma — serial secondary endosymbioses of red plastids (modelled [5]); position 67.80–67.34.
16. 1.047 +0.013/–0.017 Ga — *Bangiomorpha* (measured [9]); position 67.78.
17. ≤819 Ma (633–1,017) — tertiary plastid in a stem ochrophyte (modelled [5]); position 67.55.
18. ≥260 Ma — *Sulcia* in the auchenorrhynchan ancestor (modelled [10][11]); position 66.51.
19. 250–200 Ma — *Buchnera* in aphids (modelled [12]); position 66.47–66.27.
20. | 200 Ma — *Sulcia* and *Nasuia* partners; cicada, spittlebug and sharpshooter split (modelled [11][10]); position 66.27.
21. ≤140 Ma — *Azolla* cyanobiont [15]; position 65.94. About 100 Ma by fossils [16], position 65.64; >60 Ma [7], position 65.17.
22. 140–90 Ma — *Paulinella* chromatophore, maximum age (modelled [13]); position 65.94–65.54.
23. about 91 Ma — UCYN-A1 and UCYN-A2 diverge (modelled [14]); position 65.55.
24. Present — kleptoplasty in sea slugs, flatworms, ciliates and dinoflagellates [42][26].

Present quantities

Proteins of the organelle. MitoCarta3.0 lists 1,136 human and 1,140 mouse mitochondrial genes, in 149 pathways (measured [49]). The human mtDNA encodes 13 proteins [21], 1.1 % of the list (computed).

Copies and cells. *Buchnera* has more than 100 genome copies per cell (measured [12]). Aphids carry 60–80 bacteriocytes (measured [12]). *B. bigelowii* holds one UCYN-A1 or about 3–10 UCYN-A2 cells (measured [14]).

Exchange. In plant cyanobionts 30–50 % of cells are heterocysts, against 4–10 % free-living (measured [41]). The cyanobiont keeps as little as 20 % of the nitrogen it fixes (measured [41]).

Pattern

Each primary uptake carries more than one date. Mitochondrion: 2.05–1.21 Ga (symbiosis), with LECA at 2.39–1.96 Ga or <1.84 Ga. Plastid: five dates, 2.1 to 1.25 Ga, a spread of 0.85 Gyr.

Gene number falls from bacterium to organelle. *Rickettsia* has 834 protein genes; mitochondria keep 13 to about 100. *Synechocystis* has 3,168; the *Arabidopsis* plastid keeps 87, with about 4,500 in the nucleus.

Genome length does not fall in step: human mtDNA 16.6 kb, *Silene conica* 11.3 Mb.

Red and green nucleomorphs both have three chromosomes and 373–572 kb. Only 3.9–6.2 % of their protein genes serve the plastid.

The young partners keep 29 % (*Paulinella*) and 68 % (*N. azollae*) of genes. Insect symbionts carry 112–641 kb.

Kleptoplasts work from 15 days to at least 30 months. Dated windows: primary plastid 2,137–1,807 Ma; serial secondary red plastids 1,079–650 Ma; stem-ochrophyte tertiary plastid ≤819 Ma (633–1,017).

Not verified

- Freshwater, early-branching cyanobacterial origin of plastids (Ponce-Toledo et al. 2017): reused but V-bib, number not read.
- *Gloeomargarita lithophora* as closest living relative (de Vries & Archibald 2017): secondary.
- “A plastid in the making” for *Paulinella* (Marin et al. 2005): V-bib.
- Chromatophore genome numbers of Nowack et al. 2008: V-bib, abstract absent.
- Number of plastid endosymbioses in Keeling 2013: V-bib, no count read.
- Nested mealybug papers (McCutcheon & von Dohlen 2011; Husnik et al. 2013): V-bib.
- Mitochondrion 1 μm long, 0.5 μm^3 ; yeast 0.14–0.16 μm^3 ; nucleoid ~100 nm; cristae 30–40 nm (BioNumbers): secondary.
- 34 ± 2 mitochondria per *Cryptococcus* cell (BioNumbers; Raja et al. 2013): secondary.
- Chloroplast ~5 $\times$ 2.5 μm ; 22.5, 31 and 129.13 μm^3 ; grana 0.3–0.6 μm ; starch 15 % (BioNumbers): secondary.
- 14–39 chloroplasts per *Heterosigma* cell (BioNumbers): secondary.
- *Paulinella* test 20–32 $\times$ 14–23 μm ; chromatophores 3–4 $\times$ 16–18 μm , 1–6 per cell (NIES, arcella.nl): secondary.
- About half of UCYN-A proteins made by the host (LBNL highlight on Coale et al. 2024): secondary.
- *Buchnera* doubling 175–292 h in the host (BioNumbers; Ochman et al. 1999): secondary.
- *Elysia chlorotica* plastid retention of about 14 months (literature cited in Händeler et al. 2009): secondary.
- Protein-gene counts of *Tremblaya*, *Moranella*, *Nasuia*, *Carsonella* and *Hodgkinia*: abstracts gave sizes only.

- Apicoplast genome; a published total of secondary and tertiary events: not read.

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A3 Becoming Many

What it is

This chapter follows one line of connection: 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. Those kingdoms are animals, fungi, land plants, and red and brown algae.

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

The count of independent origins is a lower bound. Multicellularity “has arisen more than 25 times across the eukaryotic tree of life” [1]. A later review calls a count of 25 “very likely a serious underestimate” [2].

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” (measured [1]). These are *Fonticula*, *Copromyxa*, the dictyostelids, the acrasids, *Sorogena*, *Sorodiplophrys* and *Guttulinopsis* [1]. They occur in all major eukaryotic clades except Archaeplastida [1].

Divisional multicellularity has “numerous origins in both red and green algae, and once at the base of the brown algae” [1]. Within Amorphea (animals, fungi and Amoebozoa) there are three further origins besides the animal one [1]. Within Amoebozoa there are two aggregative origins, the dictyostelids and *Copromyxa* [1].

Counts at lower ranks repeat the pattern. In one class of green algae, the Zygnematomyceae, filamentous growth arose “at least five” times (measured [3]). That count rests on 46 taxa and 326 nuclear loci [3].

Complex multicellularity is the form with many cell types and tissues. A “long apparent lag” separates the appearance of simple multicellularity in eukaryotes from the radiation of groups with complex organisation [4].

Brown algae are “among a small number of eukaryotic lineages” with complex multicellularity [5]. The same source counts five groups that reached it [5].

First appearance

Cyanobacteria. The oldest multicellular state is bacterial. “The majority of extant cyanobacteria descend from multicellular ancestors” [6]. Fossil comparison supports an origin “possibly as early as” the Great Oxygenation Event, 2.45–2.22 Ga (positions 68.55–68.46) (modelled [6]).

A follow-up dates the origin “before 2.4 billion years ago” (position 68.53) (modelled [7]). It places the Great Oxidation Event at 2.45–2.32 Ga (positions 68.55–68.50) [7]. The two papers give different ranges for that event; both are recorded here.

The oldest conclusive fossils of all five cyanobacterial sections are ~2.15 Ga old (position 68.43) (measured [6]). Fossil akinetes, which are differentiated resting cells, date to ~2.00 Ga (position 68.36) (measured [6]). A filamentous microfossil candidate is 3.45 Ga old (position 68.86), from the Panorama Formation [6].

Red algae. *Bangiomorpha pubescens*, from the Hunting Formation of Somerset Island, Arctic Canada, is a bangiacean red alga [8]. It has a differentiated holdfast and spores or gametes [8]. Its Re-Os age is 1.047 ± 0.013/–0.017 Ga, that is 1.030–1.060 Ga (positions 67.76–67.79; centre 67.78) (measured [9]).

An older claim comes from the Tirohan Dolomite, India, at ~1.6 Ga (position 68.16) [10]. *Rafatazmia chitrakootensis* and *Ramathallus lobatus* are there called “probable crown-group red algae” [10].

They show pit connections, apical growth and pyrenoid-like bodies [10]. Two ages therefore stand: 1.6 Ga (probable) and 1.047 Ga (accepted bangiacean).

Clocks place crown red algae at 1,984–1,732 Ma (positions 68.36–68.23) (modelled [11]). The same study puts the primary plastid at 2,137–1,807 Ma (positions 68.42–68.27) (modelled [11]). A clock cross-calibrated on *Bangiomorpha* places eukaryotic photosynthesis at ~1.25 Ga (position 67.94) (modelled [9]).

Green seaweeds. *Proterocladus antiquus*, from the Nanfen Formation of North China, is ~1,000 Ma old (position 67.73) (measured [12]). It is a millimetre-sized, multicellular, branched siphonocladalean chlorophyte [12]. Core Chlorophyta date to ~1,000–700 Ma (positions 67.73–67.41) (modelled [13]).

The main Ulvophyceae lineages radiated just before or during the Cryogenian [13]. Bryopsidales and Dasycladales fossils come from the Cambro-Ordovician [13]. The title of that study records “multiple transitions to macroscopic growth in green seaweeds” [13].

The root of Plantae lies at ~1,694 Ma by clock (position 68.21) (modelled [14]).

Fungi. Fungus-like mycelial filaments occur in vesicular basalt 2.4 Ga old (position

68.53) (measured [15]). The oldest unambiguous fungus, *Ourasphaira giraldae*, is 1,010–890 Ma old (positions 67.74–67.63), from Arctic Canada (measured [16]).

A six-gene clock on 199 fungi places crown Fungi at ~1,020 Ma (position 67.75) (modelled [17]). The flagellum was lost ~720 Ma (position 67.43) (modelled [17]). The same clock gives Glomeromycota ~659 Ma (715–606; positions 67.43–67.28), Dikarya 649 Ma (position 67.34) and crown Agaricomycetes 299 Ma (351–252; positions 66.78–66.48) (modelled [17]).

Glomalean hyphae and spores occur in the Ordovician of Wisconsin, ~460 Ma (position 67.03) (measured [18]). *Tortotubus protuberans* is a cord-forming mycelium with septal perforations and a double wall [19]. It dates to the earliest Silurian; the base of the Silurian is 443.8 Ma (position 66.99) [19, 20].

Devonian *Prototaxites* trunks reach 8 m (measured [21]).

The oldest fossil mushroom is from the Lower Cretaceous Crato Formation, Brazil [22]. It is the first from Gondwana and the only one not preserved in amber [22].

Dictyostelids. The three sequenced social amoebae split from their last common ancestor “at least 0.6 billion years ago” (position 67.27) (modelled [23]). The Amoebozoa “diverged from the animal-fungal lineage after the plant-animal split” [24]. The last common ancestor of dictyostelids and animals lived more than one billion years ago (position 67.73) [1].

Animals, first reading: sponge sterols before 635 Ma. 24-isopropylcholestane (24-ipc) steranes are abundant in all formations of the Huqf Supergroup, South Oman Salt Basin (measured [25]). They lie in strata beneath the Marinoan cap carbonate, older than ~635 Ma (position 67.32) [25]. That study reads them as demosponges before the end of the Marinoan glaciation [25].

A second sterane, 26-methylstigmastane (26-mes), occurs with 24-ipc in rocks and oils of the same basin (measured [26]). The sequence is “around 100 Myr long” (position 65.64) [26]. That study calls 26-mes “the first animal-specific sterane” and extends demosponges “at least back to the Cryogenian” [26].

Animals, second reading: the sterane is algal. A later study states that 24-ipc “is not diagnostic for sponges” [27]. Pyrolysis of algal C29 sterols under simulated diagenesis produced 24-ipc and 24-n-propylcholestane (measured [27]).

On that reading the oldest evidence for animals moves to the latest Ediacaran, with the earliest animal-like fossils at ~571 Ma (position 67.22) [27]. The two readings disagree; both are recorded.

Animals, bodies. The oldest architecturally complex Ediacaran macrofossils are 574.17 ± 0.66 Ma old (position 67.23), from the upper Drook Formation, Mistaken Point, Newfoundland (measured [28]). The “Brasier” Surface is 567.63 ± 0.66 Ma (position 67.22) and the “E” Surface 565.00 ± 0.64 Ma (position 67.21) (measured [28]). The youngest rangeomorphs there are $\leq 564.13 \pm 0.65$ Ma (position 67.21) (measured [28]).

Dickinsonia is an animal by its sterols, at 558 Ma (position 67.20) (measured [29]). That study calls it among “the oldest confirmed macroscopic animals” [29]. It gives the Ediacara biota a span of 571–541 Ma (positions 67.22–67.17) [29].

The base of the Cambrian is 538.8 ± 0.2 Ma (position 67.17) (measured [20]). The Chengjiang biota has a maximum depositional age of $518.03 \pm 0.69/0.71$ Ma (position 67.13) (measured [30]). That date comes from CA-ID-TIMS U-Pb on the youngest detrital zircon in the Maotianshan Shale [30].

The Cambrian explosion as a whole “lasted more than 22 million years” (position 64.26) [30].

Land plants. The oldest cryptospores are Dapingian, ~ 473 – 471 Ma (positions 67.05–67.05), from Argentina (measured [31]). The previous oldest were ~ 463 – 461 Ma (positions 67.03–67.03) [31]. Clocks give three values for crown embryophytes: 515.1 – 470.0 Ma [32], 515 – 493 Ma with 68 fossil calibrations [33], and 482 Ma (485 – 473) [17] (all modelled; positions 67.13–67.05, 67.13–67.09 and 67.07).

Cooksonia cf. pertoni gives a minimum crown-tracheophyte age of 426.9 Ma (position 66.96) (measured [32]). A second minimum is 420.7 Ma (position 66.95) [32].

Baragwanathia longifolia, the earliest club moss, is Gorstian, in the Ludlow of the Silurian [34].

The Rhynie chert has a U-Pb age of 411.5 ± 1.3 Ma (position 66.93) (measured [35]). A second study places *Asteroxylon mackiei* from the same chert at “ 407 Ma” (position 66.92) [36]. Both ages are recorded.

The charophyte *Palaeonitella cranii* occurs in the same chert as a small multicellular alga with furcating branchlets [37].

Volvocine algae. Four published ages for the volvocine origin are recorded. Kirk gives a *Volvox-Chlamydomonas* ancestor at $\sim 50 \pm 20$ Ma (positions 65.01; range 64.54–65.31) (modelled [38]). Umen gives “around 250 MY” (position 66.47) [39].

Hanschen et al. give “about 230 million years ago” (position 66.40) [40].

Herron et al. date the divergence of the multicellular volvocine lineage to “at least 200 million years ago” (position 66.27) (modelled [41]). They set this against earlier estimates of 50 – 75 Ma (positions 65.01–65.38) [41].

Brown algae. No accepted brown-algal fossil is older than the Cretaceous [42]. The oldest calibration fossil is *Padina* (Dictyotales), at a minimum of 100 Ma (position 65.64) (measured [42]). The 550 Ma *Miaohephyton* (position 67.19) was tested and rejected [42].

The molecular origin of brown algae is 449.41 Ma (95 % HPD 333.85 – 572.02 ; positions 67.01, range 66.73–67.23) (modelled [42]). Uncorrelated alternatives give 435 – 455 Ma (positions 66.98–67.02); autocorrelated ones give 595 – 600 Ma (positions 67.26–67.27) (modelled [42]).

Crown Laminariales is 83.44 or 231.51 Ma (positions 65.47 or 66.40) under the two clock models (modelled [42]). Crown Fucales is 65.81 or 134.28 Ma (positions 65.26 or 65.91) (modelled [42]).

Partners

On the bacterial side the multicellular partners are cyanobacteria, myxobacteria and actinomycetes [1]. On the eukaryote side they are Amorphea (animals, fungi, Amoebozoa, *Fonticula*), Archaeplastida (red algae, green algae and land plants), stramenopiles (brown algae, *Sorodiplophrys*), alveolates (*Sorogena*) and Excavata/Discoba (acrasids) [1].

A bacterium and the closest relative of animals. The choanoflagellates are the unicellular sister group of animals. *Monosiga brevicollis* has a genome of ~41.6 Mb with ~9,200 intron-rich genes (9,196 gene models) (measured [43]). It carries 78 protein domains found only in choanoflagellates and animals, and at least 23 genes with cadherin domains (measured [43]).

Salpingoeca rosetta has a genome of ~55 Mb with 11,629 genes; the same paper also gives 11,628 (measured [44]). It has at least five differentiated cell types: thecate cells, slow swimmers, fast swimmers, chain colonies and rosette colonies [44]. Rosettes develop by incomplete cytokinesis, with neighbouring cells joined by intercellular bridges [44].

The prey bacterium *Algoriphagus machipongonensis* (Bacteroidetes) and its relatives induce rosette development in *S. rosetta* (measured [45]). The inducing molecule, RIF-1, is a sulfonolipid [45]. It is active at femtomolar concentrations, 10^{-15} M, and *S. rosetta* responds to it over nine orders of magnitude of concentration (measured [45]).

Rosettes form from a single founding cell, as animals do from a zygote [46]. The mutant *rosetteless* maps to a predicted C-type lectin [46]. That protein forms an extracellular coating that connects the basal poles of the rosette cells [46].

Chains of cells form “in the absence of RIFs” [47]. Rosettes induced by *A. machipongonensis* outer-membrane vesicles have a most common size of 8 cells and reach as many as 25 (measured [47]). Rosette cells divide slightly faster than chain cells ($P = 0.03$) (measured [47]).

Predators of another supergroup and green algae. The green alga *Chlorella vulgaris* had been unicellular for thousands of generations in culture [48]. It was exposed to the phagotrophic flagellate *Ochromonas vallescia*, a stramenopile [48]. Globose clusters of tens to hundreds of cells appeared first (measured [48]).

Eight-celled colonies predominated after ~10–20 generations with the predator (measured [48]). A multicellular form dominated “within less than 100 generations” [48].

The eight-celled colonies were nearly immune to the predator, while each cell still touched the medium [48]. The form persisted in continuous culture and on agar [48].

Chlamydomonas reinhardtii was placed under predation by the ciliate *Paramecium tetraurelia*, an alveolate [49]. Five selected populations and three unselected controls ran for ~750 asexual generations (measured [49]). That was 50 weekly transfers, ~350 days (position 48.83) [49].

Two of the five selected populations evolved multicellular structures absent from the controls (measured [49]). Propagules were nearly all 4, 8 or 16 cells, some up to 64 (measured [49]). Median cluster size at maximum growth was 1–6.2 cells (measured

[49]).

A single gene. Expressing the *Gonium* retinoblastoma (RB) gene in unicellular *Chlamydomonas* produced colonies of 2–16 cells (measured [40]). The volvocine transition is modelled as at least 12 steps in three phases (modelled [40]). The phases are cell-cycle regulation to form groups, size increase, and germ–soma differentiation; five steps concern forming cell groups [40].

Selection without a partner. Snowflake yeast (*Saccharomyces cerevisiae*) went through 600 rounds of selection for size (measured [50]). The anaerobic line grew ~20,000-fold (2×10^4) in size to millimetre scale, and ~10,000-fold in biophysical toughness (measured [50]). The low-oxygen line stayed microscopic, at ~6-fold (measured [50]).

About 3 % of cells survive each daily transfer [50].

The receptor kinases of brown algae. The receptor kinases of *Ectocarpus* form a clade separate from those of animals and green plants (measured [5]). Receptor-kinase evolution may have been key to complex multicellularity in “at least three of the five” groups that reached it [5].

Hyphae in fungi. A study of 72 genomes compared 4 unicellular fungi, 41 hyphal fungi, 13 yeast-like fungi and 14 non-fungal relatives (measured [51]). It found 362 hypha-morphogenesis gene families with 651 genes, and 414 gene families correlated with hyphal evolution (measured [51]). Of these, 114 arose at the three candidate nodes splitting Blastocladiomycota, Chytridiomycota and Zoopagomycota (measured [51]).

Hyphae “evolved early in fungal evolution”, at one of these nodes or gradually across all three [51]. No kinase expansion accompanied the step [51]. Complex multicellularity in fungi, the fruiting body, “appears 8–11 times in distinct fungal lineages” (measured [52]).

The preprint of the same work gives 8 to 12 origins [52]. It counts at least 8 major clades and gives 12 as a “conservative upper estimate” [52].

Both counts are recorded. Fungi are the only lineage in which complex multicellularity shows signs of convergence [52].

Sizes

what	size	position	source
<i>Cyanidioschyzon merolae</i> , unicellular red alga	2 μm	3.44	measured [53]
Fungal hypha, narrowest of 31 soil strains	2.7 μm	3.72	measured [54]
<i>S. rosetta</i> cell, equivalent spherical diameter	5.87 μm	4.42	computed from [47]
Fungal hypha, widest of 31 soil strains	6.5 μm	4.51	measured [54]

<i>Chlamydomonas reinhardtii</i> unicell	10 µm	4.91	measured [55]
<i>Proterocladus antiquus</i> , order of size	1 mm	9.10	measured [12]
Evolved snowflake yeast cluster, order of size	1 mm	9.10	measured [50]
<i>Dickinsonia</i> , narrowest specimen	1.0 cm	11.19	measured [29]
<i>Dickinsonia</i> , widest specimen	6.0 cm	12.83	measured [29]
<i>Macrocystis</i> frond elongation, lower daily value	12.8 cm	13.52	measured [56]
<i>Caulerpa taxifolia</i> frond, lower value	15 cm	13.66	measured [57]
<i>Macrocystis</i> frond elongation, upper daily value	23.3 cm	14.06	measured [56]
<i>Caulerpa taxifolia</i> frond, upper value	30 cm	14.29	measured [57]
<i>Dawsonia superba</i> stem, tallest moss	65 cm	14.99	measured [58]
<i>Caulerpa taxifolia</i> stolon, one coenocytic cell	1 m	15.39	measured [57]
Dickinsoniids, largest	1.4 m	15.69	measured [29]
Human reference man, height	1.70 m	15.87	measured [59]
Carboniferous lycopsid trunk, width	2 m	16.02	measured [60]
<i>Prototaxites</i> trunk	8 m	17.28	measured [21]
Carboniferous arborescent lycopsid, height	45 m	18.85	measured [60]
<i>Macrocystis pyrifera</i> , length	>60 m (stated maximum)	19.11	[42]
<i>Sequoia sempervirens</i> , tallest tree measured	112.7 m	19.69	measured [61]
Tree height, mechanical limit, lower	122 m	19.76	modelled [61]
Tree height, mechanical limit, upper	130 m	19.82	modelled [61]
<i>Pando</i> clone, side of a square of 43 ha	656 m	21.29	computed from [62]
<i>Pando</i> clone, side of a square of 43.6 ha	660 m	21.30	computed from [62]
<i>Armillaria ostoyae</i> genet, side of a square of 965 ha	3,106 m	22.71	computed from [63]

<i>Armillaria ostoyae</i> genet, greatest distance between isolates	3,810 m	22.89	measured [63]
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The *S. rosetta* diameter is $(6 \times 105.9 / \pi)^{(1/3)} = 5.87 \mu\text{m}$, from an untreated cell volume of $105.9 \pm 8.8 \mu\text{m}^3$ (computed; volume measured [47]). Mean cell volume drops between the 4- and 5-cell stage and is then constant (measured [47]). The area sides are $\sqrt{(43 \times 10^4 \text{ m}^2)} = 656 \text{ m}$, $\sqrt{(43.6 \times 10^4 \text{ m}^2)} = 660 \text{ m}$ and $\sqrt{(965 \times 10^4 \text{ m}^2)} = 3,106 \text{ m}$ (computed).

Volvox carteri forms a spheroid of “several hundred microns” [39]. No single number is given, so no position is computed. *Macrocystis* “may become more than 60 meters long” [42].

The ratio of the *Armillaria* genet extent to a hyphal width of $5 \mu\text{m}$ is $3,810 / (5 \times 10^{-6}) = 7.6 \times 10^8$ (computed). The human reference man weighs 70 kg (measured [59]). His mean mass per cell is $70 \text{ kg} / 3.0 \times 10^{13} = 2.3 \text{ ng}$, extracellular mass included (computed).

Maximum size of life rose ~ 16 orders of magnitude over more than 3.5 Gyr (measured [64]). Most of the rise came in two steps of about equal size (measured [64]). Each step is $\approx 16 / 2 = 8$ orders of magnitude (computed; the source gives no per-step value).

Times

what	duration	position	source
<i>Volvox carteri</i> generation	48 h	44.13	measured [39]
<i>Macrocystis</i> mass doubling at 3.5 % per day	20.1 days	46.23	computed from [65]
<i>Ulva</i> competence for gametogenesis, earliest	3 weeks	46.27	measured [66]
<i>Ulva</i> competence for gametogenesis, latest	5 weeks	46.74	measured [66]
<i>Chlamydomonas</i> + <i>Paramecium</i> experiment, 50 weekly transfers	350 days	48.83	measured [49]
Snowflake yeast, 600 daily transfers	600 days	49.32	computed from [50]
Human reference man, age, lower	20 years	51.60	measured [59]
Human reference man, age, upper	30 years	51.97	measured [59]
Interval Cambrian base to Chengjiang (538.8 – 518.0)	20.8 Myr	64.21	computed
Cambrian explosion, minimum span	22 Myr	64.26	measured [30]
Interval Ediacaran	35.2 Myr	64.69	computed

macrofossils to Cambrian base (574 – 538.8)			
Interval Marinoan steranes to Ediacaran macrofossils (635 – 574)	61 Myr	65.19	computed
Oman sterane sequence	100 Myr	65.64	measured [26]
Interval crown red algae (lower) to <i>Bangiomorpha</i> (1,732 – 1,047)	685 Myr	67.39	computed
Interval crown red algae (upper) to <i>Bangiomorpha</i> (1,984 – 1,047)	937 Myr	67.67	computed

The kelp doubling time is $\ln 2 / \ln 1.035 = 20.1$ days, from a mass gain of 3.5 % per day (computed; rate measured [65]). The yeast duration assumes one transfer per day, as the source states for each daily transfer (computed from [50]).

The laboratory durations are also counted in generations. First eight-celled colonies came after ~10-20 generations and dominance in under 100 generations (measured [48]).

The *Chlamydomonas* line ran ~750 generations (measured [49]). No division time is given for *Chlorella*, so no duration in seconds is computed for that case.

Counts

Origins. More than 25 origins of multicellularity across eukaryotes [1]. At least seven aggregative origins [1]. At least five filamentous origins within Zygnematophyceae [3].

In cyanobacteria, reversals to unicellularity occurred “at least 5 times” (measured [6]). Multicellularity was “established again at least once within a single-celled clade”, in *Spirulina* sp. PCC 6313 (measured [6]).

In fungi, fruiting bodies arose 8-11 times; the preprint gives 8-12 (measured [52]). Brown algae reached divisional multicellularity once [1].

Phylogenetic samples. The cyanobacterial study used 1,254 16S rDNA sequences, from 2,065 downloaded (measured [6]). It used 58 taxa in the reconstruction subset and sampled 10,000 trees [6]. In the 2013 study the origin of cyanobacterial multicellularity was accompanied by an increase in diversification rates [7].

Genomes. *Dictyostelium discoideum* has a genome of 34,042,810 bp in six chromosomes, 77.57 % A+T, with ~12,500 predicted proteins (measured [24]). Only about half of the protein-coding genes of the three dictyostelid genomes form an identifiable orthologous set (measured [23]).

Monosiga brevicollis has ~6.6 introns per gene, against 7.7 in humans (measured [43]). It carries ~120 tyrosine kinase domains, ~30 tyrosine phosphatase domains and ~80 SH2 domains (measured [43]).

The *Gonium pectorale* genome has 120.9 genes per Mb (measured [40]). *Gonium* colonies hold 8 or 16 cells [40]. *Chlamydomonas* has a genome of 121 Mb with 15,143 protein-coding genes (measured [55]).

Volvox carteri has a genome of 138 Mb with ~14,500 predicted proteins (measured [67]). It holds ~2,000 somatic cells and 12–16 gonidia, in two cell types [39]. A 2,000-celled organism thus has 4 % fewer predicted proteins than its unicellular relative: $14,500 / 15,143 = 0.958$ (computed).

Ectocarpus siliculosus has a genome of 214 Mbp with 16,256 protein-coding genes (measured [5]). *Macrocystis pyrifera* has a genome of 537 Mb with 25,919 genes (measured [65]). *Cyanidioschyzon merolae* has 20 chromosomes, 16,520,305 bp and 5,331 genes (measured [53]).

Cell types. *Ulva* has three cell types: rhizoid, stem and blade [66]. *Spongilla lacustris*, a sponge without nerves or muscles, has 18 distinct cell types by whole-body single-cell RNA sequencing (measured [68]). *S. rosetta* has at least five life-cycle cell types [44].

Cells per body. *S. rosetta* rosettes hold 4–12 cells in 90 % of cases at steady state; 51 % hold 6–8 cells (measured [47]). *Gonium* holds 8 or 16, *Volvox* ~2,000 plus 12–16 [40, 39].

The human reference man holds 3.0×10^{13} human cells (2 % calculated uncertainty, 14 % CV) (measured [59]). Of these, red blood cells number 2.5×10^{13} , or 84 % (measured [59]). Nucleated human cells number $\sim 0.3 \times 10^{13}$ [59].

Doubling counts from one cell are $8 = 2^3$, $16 = 2^4$ and $64 = 2^6$ (computed). For *Volvox*, $\log_2 2,000 = 10.97$, so $2,000 \approx 2^{11}$ (computed). For the human, $3.0 \times 10^{13} \approx 2^{44.8}$ (computed).

Ediacaran sterols. In the largest *Dickinsonia* specimen the sterols are 93 % cholesteroloids, 1.8 % ergosteroids and 5.2 % stigmasteroids (measured [29]). Across specimens cholesteroloids range 84.8–93.0 %, rising with size (measured [29]). Host sediment holds 10.6 % (clay) and 11.9 % (sandstone); a microbial mat with *Andiva* holds 18.7 % (measured [29]).

Mistaken Point. The section has 76 fossil-bearing horizons (measured [28]). Uniterminal rangeomorphs appear several Myr before multiterminal forms [28].

Other bodies. The *Pando* clone covers 43–43.6 ha with ~47,000 ramets (measured [62]). The *Armillaria ostoyae* genet in Oregon covers ~965 ha (measured [63]). *Bangiomorpha* has a differentiated holdfast; the Rhynie charophyte *Palaeonitella* has gyrogonites of 6 spiral cells [8, 37].

Species. Brown algae number 2,125 species, 46 % of 4,619 non-diatom heterokonts in AlgaeBase (measured [42]).

Order of events

1. 3.45 Ga (position 68.86): filamentous microfossil candidate, Panorama Formation [6].
2. 2.45–2.22 Ga (positions 68.55–68.46): multicellular cyanobacteria, possibly from

- the Great Oxygenation Event onward (modelled [6]); before 2.4 Ga (position 68.53) (modelled [7]).
3. 2.4 Ga (position 68.53): fungus-like mycelial filaments in basalt [15].
 4. ~2.15 Ga (position 68.43): conclusive fossils of all five cyanobacterial sections [6].
 5. 2,137–1,807 Ma (positions 68.42–68.27): primary plastid by clock (modelled [11]).
 6. ~2.00 Ga (position 68.36): fossil akinetes [6].
 7. 1,984–1,732 Ma (positions 68.36–68.23): crown red algae by clock (modelled [11]).
 8. ~1.9 Ga (position 68.32): first step in maximum size of life [64].
 9. ~1,694 Ma (position 68.21): root of Plantae by clock (modelled [14]).
 10. ~1.6 Ga (position 68.16): probable crown-group red algae, India [10].
 11. ~1.25 Ga (position 67.94): eukaryotic photosynthesis by cross-calibrated clock (modelled [9]).
 12. 1.047 Ga (position 67.78): *Bangiomorpha pubescens* [9].
 13. ~1,020 Ma (position 67.75): crown Fungi by clock (modelled [17]); 1,010–890 Ma (positions 67.74–67.63): *Ourasphaira* [16].
 14. 1,000 Ma (position 67.73): last common ancestor of dictyostelids and animals [1].
 15. ~1,000 Ma (position 67.73): *Proterocladus*, a multicellular green seaweed [12].
 16. 1,000–700 Ma (positions 67.73–67.41): core Chlorophyta (modelled [13]).
 17. 943 Ma (817–1,049; positions 67.68, range 67.55–67.78): Bangiophyceae–Florideophyceae split (modelled [14]).
 18. 781 Ma (position 67.51): Hildenbrandiophycidae (modelled [14]).
 19. ~720 Ma (position 67.43): flagellum lost in fungi (modelled [17]).
 20. 661 Ma (position 67.36): Nemaliophycidae (modelled [14]); 659 Ma (position 67.35): Glomeromycota; 649 Ma (position 67.34): Dikarya (modelled [17]).
 21. 635 Ma (position 67.32): 24-ipc and 26-mes steranes, sponge reading [25, 26]; algal reading [27].
 22. ≥ 0.6 Ga (position 67.27): dictyostelid lineages split (modelled [23]).
 23. 579 Ma (543–617; positions 67.24, range 67.18–67.29): Corallinophycidae (modelled [14]).
 24. 574.17 Ma (position 67.23): first architecturally complex Ediacaran macrofossils [28].
 25. 571 Ma (position 67.22): start of the Ediacara biota [29, 27].
 26. 558 Ma (position 67.20): *Dickinsonia* with animal sterols [29].
 27. 538.8 Ma (position 67.17): base of the Cambrian [20].
 28. ≤ 518.03 Ma (position 67.13): Chengjiang biota [30].
 29. 515–470 Ma (positions 67.13–67.05): crown embryophytes by clock (modelled [32, 33, 17]).
 30. 473–471 Ma (positions 67.05–67.05): oldest cryptospores [31].
 31. ~460 Ma (position 67.03): glomalean hyphae and spores [18].
 32. 449.41 Ma (position 67.01): brown algae by clock (modelled [42]).
 33. After 443.8 Ma (position 66.99): *Tortotubus* cords [19, 20].
 34. 426.9 Ma (position 66.96) and 420.7 Ma (position 66.95): crown-tracheophyte minima [32].

35. 411.5 Ma (position 66.93) or 407 Ma (position 66.92): Rhynie chert plants and charophytes [35, 36, 37].
36. 299 Ma (position 66.63): crown Agaricomycetes by clock (modelled [17]).
37. ~250 Ma (position 66.47), ~230 Ma (position 66.40), ≥200 Ma (position 66.27) or ~50 Ma (position 65.01): volvocine colonies [39, 40, 41, 38].
38. ≥100 Ma (position 65.64): *Padina*, oldest brown-alga calibration fossil [42].
39. ~6 Ma (position 63.08): *Macrocystis* emerged [65].

The second step in maximum size of life falls at 0.6–0.45 Ga (positions 67.27–67.01) (measured [64]). Both steps coincide with or slightly postdate rises in atmospheric oxygen [64]. The first step follows the eukaryotic cell; the second follows multicellularity [64].

Present quantities

A living human of 70 kg holds 3.0×10^{13} cells, 84 % of them red blood cells (measured [59]). A living sponge has 18 cell types (measured [68]). A living *Volvox* has ~2,000 somatic cells and 12–16 gonidia, with a new generation every 48 h (position 44.13) [39].

The tallest living tree measured is a *Sequoia sempervirens* of 112.7 m (position 19.69) (measured [61]). The mechanical limit is 122–130 m (positions 19.76–19.82) (modelled [61]). The tallest moss, *Dawsonia superba*, has stems of 65 cm (position 14.99) [58].

Macrocystis pyrifera “may become more than 60 meters long” (position 19.11) [42]. Its fronds elongate by 12.8–23.3 cm per day (positions 13.52–14.06) (measured [56]). Its mass rises 3.5 % per day (measured [65]).

Two living clonal bodies are measured in hectares. *Pando* covers 43–43.6 ha with ~47,000 ramets (measured [62]). An *Armillaria ostoyae* genet covers ~965 ha, with isolates up to ~3,810 m apart (position 22.89) (measured [63]).

A single 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) [57]. The smallest red alga, *Cyanidioschyzon merolae*, is a 2 µm unicell (position 3.44) [53].

Brown algae number 2,125 living species [42]. In the laboratory, *Chlorella*, *Chlamydomonas* and yeast have each become multicellular de novo [48, 49, 50].

Pattern

Counted origins of multicellularity are lower bounds: more than 25 across eukaryotes, at least 7 by aggregation, at least 5 filamentous in one green class. Aggregation occurs in every supergroup except Archaeplastida. Clonal origins: many in red and green algae, one in brown algae.

Dated first appearances run from cyanobacteria (2.45–2.22 Ga) to red algae (1.047 Ga), green seaweeds and fungi (~1,000 Ma). Animals (574–558 Ma), land plants (515–470 Ma), brown algae (~449 Ma by clock) and volvocines (250–50 Ma) follow. Two sterane readings disagree on pre-635 Ma animals.

Clonal colonies: *S. rosetta* rosettes 4–25 cells, mostly 8; RB-expressing *Chlamydomonas* 2–16 cells. Under ciliate predation, *Chlamydomonas* propagules were nearly all 4, 8 or

16 cells, some up to 64; median clusters 1–6.2. Under a stramenopile predator, eight-celled *Chlorella* colonies predominated.

A prey-bacterial molecule sets the *S. rosetta* colonial switch, from 10^{-15} M. Body length spans 2 μm to 112.7 μm .

Not verified

- Grosberg & Strathmann 2007, “at least 25” origins: citation verified, number read only in a secondary chapter.
- Possibly ≥ 25 origins within green algae alone (One Thousand Plant Transcriptomes Initiative 2019): secondary.
- Knoll 2011, complex multicellularity restricted to animals, fungi, land plants and red, brown and green algae: secondary.
- *Myxococcus xanthus* fruiting bodies of about 100,000 cells: secondary (institutional page).
- *Dictyostelium* slug of up to 100,000 cells, 2–4 mm; fruiting body 1–2 mm; $\sim 20\%$ of cells in the stalk; culmination 8–10 h: secondary.
- *Tortotubus* at “440 Ma”: unverified.
- *Gondwanagaricites magnificus* at ~ 115 Ma and about 5 cm tall; amber mushrooms at ~ 99 Ma: secondary (press release).
- *Bangiomorpha* filament dimensions, tens of μm wide and to ~ 2 mm: unverified.
- Rosette data in Alegado et al. 2012 beyond the abstract: not read.
- Ratcliff 2012 snowflake-yeast origin: not read.
- *Capsaspora* aggregation: not read.
- Cell-type counts for humans and *Trichoplax*: not read.

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A4 Animals and Their Microbes

What it is

This chapter follows one line of connection: animals carrying bacteria, archaea, protists and algae on and inside their bodies. The partners sit in guts, light organs, tissues and cells. The cases run from sponges and corals to insects, ruminants and humans.

Organelle-like endosymbionts with strongly reduced genomes belong to chapter A2 and are not repeated here. Host first appearances (sponges, Ediacaran animals) are given in chapter A3.

The cases fall into three kinds of site. Guts: the human colon, insect guts, termite hindguts and the rumen.

Special organs hold one partner: the light organ of a squid. Tissues and cells hold partners in sponges, *Hydra*, corals, arthropods and vent animals.

Two modes of transmission recur in the record. Some partners are re-acquired from the environment in each host generation. Others are carried within host lineages over millions of years.

The human count is the reference point. A reference man of 20–30 years, 70 kg and 170 cm carries 3.8×10^{13} bacteria (± 25 % SE) (measured [1]). He has 3.0×10^{13} human cells (2 % calculated uncertainty, 14 % CV) (measured [1]).

First appearance

Vent animals with microbes. The oldest known vent community with animals is the Yaman Kasy VHMS deposit, southern Urals, ~440 Ma (position 66.99) (measured [2]). Its age is poorly constrained, late Ordovician to early Silurian [2]. Microbial filaments are preserved on and around tubeworm tubes [2].

Those filaments are read as an epibiotic association, not a proven symbiosis [2]. The tubes belong to *Eoalvinellodes annulatus* and *Yamankasia rifeia* [2]. The 3.24 Ga Sulphur Springs deposit (position 68.80) holds filaments of questioned biogenicity [2].

Corals and their algae. Scleractinian corals expanded and diversified ~240 Ma (position 66.43) [3]. Late Triassic coral skeletons from Antalya, Turkey, ~212 Ma (position 66.32), record coral-dinoflagellate symbiosis (measured [3]). The evidence is skeletal microstructure, carbonate $^{13}\text{C}/^{12}\text{C}$ and $^{18}\text{O}/^{16}\text{O}$, and skeletal organic $^{15}\text{N}/^{14}\text{N}$ [3].

The symbiotic signal appears also in species with growth forms considered asymbiotic [3]. The Tethys habitat of those corals was nutrient-poor [3].

The coral symbionts form the family Symbiodiniaceae [4]. In a systematic revision the former *Symbiodinium* “clades” became genera, seven of them described [4]. A recalibrated clock puts the earliest diversification of the family at ~160 Ma (position 66.07), in the Jurassic (modelled [4]).

That date coincides with the Jurassic radiation of modern shallow-water corals [4]. The fossil isotopic date (~212 Ma) is $212 - 160 = 52$ Myr (position 65.04) older than the clock date of the living symbiont family (computed). Both dates are recorded.

Wolbachia. Supergroups A and B of *Wolbachia* are ~200 Myr old (position 66.27), “considerably older than previously appreciated” (modelled [5]). Four strains co-diverged with their host lineage for ~2 Myr (position 62.08) (modelled [5]). A biotin-synthesis operon was acquired by recent lateral transfer [5].

Termites and their gut protists. Termites split from *Cryptocercus* wood roaches ~170 Ma (95 % CI 153–196; positions 66.12, range 66.02–66.25) (modelled [6]). The

termite crown is 149 Ma (136–170; positions 66.00, range 65.92–66.12) (modelled [6]). The first undisputed termite fossils are Early Cretaceous, 110–135 Ma (positions 65.72–65.91) [6].

The family Termitidae dates to 54 Ma (46–66; positions 65.08, range 64.93–65.26) (modelled [6]). Primitive termites digest wood with cellulolytic gut protists [7]. The more derived Termitidae have an entirely prokaryotic gut microbiota [7].

Termites carry a second microbial partner in one subfamily.

Fungus farming by Macrotermitinae with *Termitomyces* had a single origin in Africa [8], ~31.4 Ma (25.82–39.53; positions 64.58, range 64.41–64.79) (modelled [9]). Fossil fungus gardens are 24.8–24.5 Ma old (positions 64.37–64.36) (measured [9]). Fungus farming is treated in chapter A5.

Bioluminescent fishes. The earliest origin of bioluminescence in ray-finned fishes is Early Cretaceous, ~150 Ma (position 66.01), in Stomiiformes (modelled [10]). Bacterially mediated light evolved at least 17 times in that group [10].

Ruminants. A study of 44 newly sequenced ruminant genomes (36 genera, all six families, 51 species in the phylogeny) dates crown Ruminantia to 39.1–32.3 Ma (positions 64.78–64.61) (modelled [11]). The paper prints this as “late Oligocene” [11]. Pecora date to 23.3–20.8 Ma (positions 64.31–64.21) (modelled [11]).

The rumen, reticulum and omasum have expression profiles closest to the oesophagus [11]. That study takes this to suggest an oesophageal origin of the forestomach [11].

Hominids and gut bacteria. Several dominant gut bacterial taxa cospeciated with hominids over the past ~15 Myr (position 63.91) (measured [12]). The hosts are humans, chimpanzees, bonobos and gorillas [12]. Bacterial divergence times match those of the hosts [12].

Clades of Bacteroidaceae and Bifidobacteriaceae were kept within single host lineages over “hundreds of thousands of generations” [12].

Modern discovery. Chemosynthetic symbioses were discovered at Galápagos Rift vents [13]. In 2008 this was described as “30 years ago” (position 51.97), that is about 1978 (computed from [13]). Protists in termites were first recorded by Leidy in 1877 [14].

Partners

The human gut. The gut catalogue holds 204,938 non-redundant genomes, from 286,997 (measured [15]). They represent 4,644 gut prokaryote species: 4,616 bacterial and 28 archaeal (measured [15]). Of these species 71 % have no cultured representative (measured [15]).

The genomes come from 31 countries on six continents [15]. The catalogue holds more than 170 million protein sequences: 170,602,708 at 100 % identity (measured [15]). The Methods give 625,255,473 full-length sequences; both numbers are recorded [15].

The honey bee. Seven species at 97 % 16S identity make up more than 90 % of the honey-bee worker gut community on average (measured [16]). Density is highest in the

hindgut [16]. The ileum holds mostly Proteobacteria; the rectum mostly Lactobacilli and Bifidobacteria [16].

A second study counts “8-10 core bacterial species” in the worker gut [17]. Its 17 isolates of *Gilliamella*, *Lactobacillus* Firm-5 and *Bifidobacterium* resolved into 11 phylotypes at 97 % identity and 17 at 98 % (measured [17]). Seven and 8-10 are both recorded.

The fruit fly. In *Drosophila melanogaster*, *Lactobacillus* and *Acetobacter* make up 94 % of the community (measured [18]). Without repeated access to bacteria in food these genera fall 10- to 1,000-fold in older flies (measured [18]).

Termites. Lower termites carry “a few to a dozen” protist species each [14]. “Roughly 500 termite-associated protist species have been described” [14]. The protists in turn carry bacterial endosymbionts belonging to four phyla [14].

Cloning studies found 222-1,318 bacterial ribotypes (measured [14]). In *Reticulitermes flavipes* there are more than 4,761 species-level phylotypes, over 99 % of them bacteria (measured [14]). An estimate for *Coptotermes gestroi* is 1,460 bacterial species (modelled [14]).

The rumen. The Hungate1000 project sequenced 410 cultured rumen bacteria and archaea (measured [19]). Its catalogue holds 501 genomes: 480 bacteria and 21 archaea [19]. About 75 % of rumen genus-level taxa are represented: 73 of 88 described genera, or 83 % (measured [19]).

The genomes code 32,755 carbohydrate-active degradative enzymes (measured [19]). These are 31,569 glycoside hydrolases and 1,186 polysaccharide lyases, ~2.2 % of all ORFs [19]. At least 47 isolates may synthesise vitamin B12 de novo, and 140 more carry salvage pathways [19].

Of the rumen organisms, 134 also occur in human gut datasets (measured [19]).

The squid light organ. *Euprymna scolopes* takes up *Vibrio fischeri* from seawater [20]. Within 12 h of hatching, bacteria aggregated in mucus migrate to the pores and enter the crypts (measured [20]). The light organ has three pairs of crypts, six in all [20].

Sponges. Sponge microbial communities “can constitute up to 35% of the sponge biomass” (measured [21]). They include members of ~30 bacterial phyla and several archaeal lineages [21]. That review describes sponges as “the most ancient of the metazoan animals” [21].

Hydra. In *Hydra*, *Curvibacter* makes up ~76 % of the stable community [22]. The community has been described as “three main families” [22].

Corals. The partners are dinoflagellates of the family Symbiodiniaceae, with seven described genera [4]. They sit inside the coral animal [3, 4].

Arthropods and reproductive symbionts. *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 (measured [23]). Two other reproductive symbionts, *Rickettsia* and *Cardinium*, are counted in the same surveys [24].

Chemosynthetic animals. “At least seven animal phyla are known to host these symbionts” [13]. The associations evolved “on multiple occasions” by convergence [13]. More than two endosymbionts can co-occur in one host [13].

The giant tubeworm *Riftia pachyptila* takes its symbiont from the water [25]. The symbiont is “facultative” and horizontally transmitted, taken up by the metatrochophore larva [25].

Luminous fishes. About 725 of ~1,510 bioluminescent fish species, ~48 %, produce light with bacteria (measured [10]). About 785 species produce intrinsic light (measured [10]). Light production “has evolved many times, from bacteria to fish” [26].

Sizes

what	size	position	source
<i>Eoalvinellodes annulatus</i> tube, narrowest	0.2 mm	7.63	measured [2]
Termite hindgut, edge of a cube of 1 μ L	1 mm	9.10	computed from [14]
<i>Eoalvinellodes annulatus</i> tube, widest	3 mm	10.10	measured [2]
<i>Yamankasia rifeia</i> tube, narrowest	3 mm	10.10	measured [2]
<i>Yamankasia rifeia</i> tube, widest	39 mm	12.43	measured [2]
<i>Riftia pachyptila</i> tube, diameter	5 cm	12.66	measured [25]
Human colon content, edge of a cube of 0.4 L	7.37 cm	13.01	computed from [1]
Human reference man, height	1.70 m	15.87	measured [1]
<i>Riftia pachyptila</i> tube, length	3 m	16.39	measured [25]

The termite hindgut is described as a “one-microliter environment” [14]. A cube of 10^{-9} m³ has an edge of $(10^{-9})^{(1/3)} = 1.0$ mm (computed). The colon content is 0.4 L; a cube of 4×10^{-4} m³ has an edge of $(4 \times 10^{-4})^{(1/3)} = 0.0737$ m (computed).

The colon content is 0.4 L, ~0.4 kg (17 % SEM, 25 % CV) (measured [1]). An earlier value was 340 mL, and an MRI value 430 mL [1].

The mean gut bacterium weighs ~5 pg wet, 1–2 pg dry (measured [1]). The bacterial mass is ~0.2 kg wet, 50–100 g dry, ~0.3 % of body mass (measured [1]). Check: $0.2 / 70 = 0.29$ % (computed).

Wolbachia wMel, from *Drosophila melanogaster*, has a circular genome of 1,267,782 bp, 35.2 % G+C (measured [27]). The host genome is ~180 Mb, which the paper calls ~100× larger [27]. The ratio is $180 \times 10^6 / 1.268 \times 10^6 = 142$ (computed).

Riftia pachyptila has a haploid genome of 560.7 Mb (N50 ~2.8 Mb) with 25,984 protein-

coding genes (measured [25]). The same paper states that *Riftia*'s genome is ~168 Mb smaller than that of *Lamellibrachia*, ~688 Mb (measured [25]). That would give $688 - 168 = 520$ Mb, not 560.7 Mb (computed); the internal discrepancy is recorded.

The ratio of the *Riftia* genome to the wMel genome is $560.7 / 1.268 = 442$ (computed; wMel used only for scale).

Times

what	duration	position	source
<i>Vibrio fischeri</i> doubling, lower	0.93 h	40.54	computed from [20]
<i>Drosophila</i> , newly emerged, first check	1 h	40.61	measured [18]
<i>Vibrio fischeri</i> doubling, upper	1.8 h	41.14	computed from [20]
Squid light organ regrowth, lower	4 h	41.87	measured [20]
<i>Drosophila</i> bacterial decline, detectable	6 h	42.24	measured [18]
Squid light organ regrowth, upper	6 h	42.24	measured [20]
Squid colonisation after hatching	12 h	42.87	measured [20]
<i>Drosophila</i> colonisation, 6 of 10 flies	24 h	43.50	measured [18]
<i>Hydra</i> , second colonist delay, shortest	24 h	43.50	measured [22]
Squid daily expulsion cycle	1 day	43.50	measured [20]
<i>Hydra</i> , second colonist delay, middle	48 h	44.13	measured [22]
<i>Hydra</i> , carrying capacity reached, upper	72 h	44.50	measured [22]
<i>Hydra</i> , stable maximum observed	168 h	45.27	measured [22]
Honey bee gut colonisation	10 days	45.60	measured [16]
Degree Heating Week window	12 weeks	47.53	agency definition [28]
Median return time of severe bleaching	6 years	50.50	measured [29]
Human reference man, age, lower	20 years	51.60	measured [1]
Termite royal pair, maximum lifespan	20 years	51.60	measured [30]
Human reference man, age, upper	30 years	51.97	measured [1]
Bleaching record, 1980–	36 years	52.13	measured [29]

2016			
Termite mound, lower	700 years	54.83	measured [30]
Termite mound, fungus-growers, upper	2,200 years	55.88	measured [30]
<i>Wolbachia</i> co-divergence with host lineage	2 Myr	62.08	modelled [5]
Hominid-gut bacteria cospeciation	15 Myr	63.91	measured [12]
Interval termite-roach split to termite crown (170 – 149)	21 Myr	64.22	computed
Interval scleractinian expansion to coral photosymbiosis (240 – 212)	28 Myr	64.48	computed
Interval coral isotopes to symbiont clock (212 – 160)	52 Myr	65.04	computed
Interval termite crown to Termitidae (149 – 54)	95 Myr	65.59	computed
Interval termite crown to ruminant crown (149 – 39.1)	109.9 Myr	65.72	computed
Interval termite crown to ruminant crown (149 – 32.3)	116.7 Myr	65.78	computed
Termite fossil record	135 Myr	65.91	measured [31]
Interval vent epibionts to coral photosymbiosis (440 – 212)	228 Myr	66.39	computed

The *Vibrio* doubling times are derived from regrowth. 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 this is a doubling time of $4 / 4.3 = 0.93$ h to $6 / 3.3 = 1.8$ h (computed; no doubling time is stated in the source).

The *Hydra* carrying capacity is reached within 24–72 h (positions 43.50–44.50) (measured [22]). Each defecation removes “a quarter to a third” of human colon content (measured [1]). The royal pair of a termite colony lives at most about 20 years, while colonies last decades [30].

Counts

Human. The ratio of bacteria to human cells is 1.3 (25 % uncertainty, 53 % variation among 70 kg males) (measured [1]). Across population groups it is 1.3–2.3 [1]. Against nucleated human cells, $\sim 0.3 \times 10^{13}$, the ratio is $\sim 10:1$ (measured [1]).

Red blood cells number 2.5×10^{13} , 84 % of human cells (measured [1]). The colon holds $\sim 0.9 \times 10^{11}$ bacteria per g of wet stool (measured [1]). Skin holds $\sim 10^{12}$ bacteria;

stomach and upper small intestine 10^3 – 10^4 per mL (measured [1]).

The mouth holds less than 1 % of the colon bacteria (measured [1]). All non-colon sites together hold at most $\sim 10^{12}$ [1]. Check: $0.4 \text{ kg} \times 0.9 \times 10^{11} \text{ g}^{-1} \times 1,000 \text{ g kg}^{-1} = 3.6 \times 10^{13}$ (computed), close to the published 3.8×10^{13} .

The old 10:1 figure came from Luckey in 1972 [1]. He multiplied $\sim 10^{11}$ bacteria per g by 1 L of alimentary-tract volume, giving $\sim 10^{14}$ [1]. That is $10^{14} / 3.8 \times 10^{13} = 2.6$ times the revised count (computed).

Per kilogram of host, the human colon holds $3.8 \times 10^{13} / 70 = 5.4 \times 10^{11}$ bacteria (computed). The cell count of the 70 kg reference man is 3.0×10^{13} [1].

Energy from microbial fermentation. Volatile fatty acids from microbial fermentation supply ~ 70 % of the caloric requirement in ruminants, such as sheep and cattle (measured [32]). They supply ~ 10 % in humans and ~ 20 – 30 % in several other omnivores and herbivores (measured [32]). Acetate:propionate:butyrate ratios range from 75:15:10 to 40:40:20 (measured [32]).

Honey bee. A reconstituted community reached “approximately 10^9 bacterial cells per gut after 10 d of colonization” (measured [16]). Non-colonised bees held fewer than 10^6 cells per gut (measured [16]). No worker bee mass is given, so no per-mass ratio is computed.

Fruit fly. Culturable bacteria per fly span $\sim 10^2$ to 10^6 CFU, with a detection limit of 25 CFU (measured [18]). At 1 h after emergence, 9 of 10 flies had no detectable bacteria (measured [18]). Within 24 h, 6 of 10 had bacteria (measured [18]).

Termites. There are 3,106 living and fossil termite species in nine living families (measured [31]). Of these, 363 are significant pests [31]. Termitidae hold more than 75 % of extant species by one count and 84 % by another (measured [6, 33]).

Termite gases. Global termite emission is $19.7 \pm 1.5 \text{ Mt CH}_4$ and $3,500 \pm 700 \text{ Mt CO}_2$ per year (measured [34]). These are ~ 4 % and ~ 2 % of global emissions [34]. Termite mounds oxidise about half of termite methane before emission (measured [35]).

Squid. The light-organ population grows to $\sim 10^6$ cells (measured [20]). Each dawn the squid expels most crypt contents, “including 90–95% of the bacterial population” (measured [20]). That releases 0.9 – 0.95×10^6 symbionts to the sea per squid per day (computed).

Sponges. High-microbial-abundance (HMA) sponges hold 10^8 – 10^{10} bacteria per g wet weight (measured [36]). This exceeds “seawater concentrations by 2–4 orders of magnitude” [36]. Low-microbial-abundance (LMA) sponges hold 10^5 – 10^6 per g, within the seawater range [36].

Hydra. The carrying capacity of one polyp is $\sim 2 \times 10^5$ *Curvibacter* cells (measured [22]). Between-replicate variation is at most 23 % CV (measured [22]). Final capacities in three priority-effect experiments were 207,309, 202,242 and 214,222 cells (measured [22]).

A second colonist arriving 24, 48 or 72 h later made up ~ 60 %, ~ 30 % and ~ 10 % of the final population (measured [22]).

Corals. The bleaching HotSpot threshold is 1 °C above the maximum monthly mean, the highest summertime mean temperature [28]. Degree Heating Weeks accumulate HotSpots of at least 1 °C over the past 12 weeks [28]. At 4 °C-weeks reef-wide bleaching is expected [28].

At 8 °C-weeks or more, reef-wide bleaching with mortality of heat-sensitive corals is expected [28]. Alert Levels 3–5 were added in December 2023 [28].

Records from 100 reef locations, 1980–2016, show the median return time between pairs of severe bleaching events falling steadily to 6 years (measured [29]). Tropical sea-surface temperatures in present La Niña conditions exceed those of El Niño events three decades earlier (measured [29]).

Wolbachia: three estimates of the share of hosts. A statistical analysis gives 66 % of species infected (modelled [23]). The underlying meta-analysis combined 20 screenings of more than 900 species [37].

A second analysis gives ~40 % of terrestrial arthropod species, an incidence of 0.406 at threshold $c = 0.001$ (modelled [37]). It used 136 species, 2,052 individuals and 15 orders screened by Duron et al. [37]. The simple ratio infected to tested is 22.8 % (measured [37]).

The same analysis gives more than 1 million infected arthropod species (modelled [37]). For *Spiroplasma* the incidence is 0.032 (*S. poulsonii*) to 0.221 (*S. ixodetis*) (modelled [37]).

A third analysis covers more than 3,600 arthropod species and ~150,000 individuals (measured [24]). It gives *Wolbachia* 52 % of species (95 % CI 48–57), *Rickettsia* 24 % (20–42) and *Cardinium* 13 % (13–55) (modelled [24]). Incidence is weakly and inconsistently higher in species-rich clades [24].

Wolbachia genome. Repeats longer than 200 bp make up 14.2 % of the wMel genome (measured [27]). They fall into 19 families, 15 of them likely mobile elements (measured [27]). The genome carries three prophages (measured [27]).

Riftia genome. The host genome has 8,629 lineage-specific genes, 1,897 contracted and 734 expanded gene families (measured [25]).

Luminous fishes. Ray-finned fishes show 27 independent origins of bioluminescence, all in marine lineages (measured [10]). Bacterially mediated light evolved at least 17 times and intrinsic light 8 times [10]. $17 + 8 = 25$ of 27; the remaining 2 are not assigned in the paper (computed).

The origins fall in 14 major clades; the figure caption gives sixteen [10]. Six orders hold 57 % of luminous species, ~814 (measured [10]). The share of bacterial light is $725 / 1,510 = 0.48$ (computed).

Order of events

1. 3.24 Ga (position 68.80): Sulphur Springs filaments of questioned biogenicity [2].
2. ~440 Ma (position 66.99): microbes on vent tubeworm tubes, Yaman Kasy [2].
3. ~240 Ma (position 66.43): scleractinian corals expand and diversify [3].

4. ~212 Ma (position 66.32): coral photosymbiosis recorded by isotopes [3].
5. ~200 Ma (position 66.27): *Wolbachia* supergroups A and B (modelled [5]).
6. ~170 Ma (position 66.12): termites split from *Cryptocercus* (modelled [6]).
7. ~160 Ma (position 66.07): Symbiodiniaceae diversify (modelled [4]).
8. ~150 Ma (position 66.01): first bioluminescent fishes, Stomiiformes (modelled [10]).
9. 149 Ma (position 66.00): termite crown (modelled [6]).
10. 135–110 Ma (positions 65.91–65.72): first undisputed termite fossils [6].
11. 54 Ma (position 65.08): Termitidae, with prokaryote-only guts (modelled [6]; [7]).
12. 39.1–32.3 Ma (positions 64.78–64.61): crown ruminants (modelled [11]).
13. ~31.4 Ma (position 64.58): termite fungus farming (modelled [9]).
14. 24.8–24.5 Ma (positions 64.37–64.36): fossil fungus gardens [9].
15. 23.3–20.8 Ma (positions 64.31–64.21): Pecora (modelled [11]).
16. ~15 Ma (position 63.91) to the present: hominid-gut bacteria cospeciation [12].
17. 1877, 149 years before 2026 (position 53.43): protists in termites first recorded [14].
18. About 1978, 48 years before 2026 (position 52.39): chemosynthetic symbioses discovered at the Galápagos Rift (computed from [13]).
19. 1980–2016, from 46 to 10 years before 2026 (positions 52.36–50.97): median bleaching return time falls to 6 years [29].
20. December 2023, about 3 years before 2026 (position 49.87): bleaching Alert Levels 3–5 added [28].

Present quantities

A living human of 70 kg carries 3.8×10^{13} bacteria against 3.0×10^{13} human cells (measured [1]). Almost all sit in 0.4 L of colon (measured [1]). They belong to ~4,600 species, 71 % without a cultured representative (measured [15]).

A living ruminant takes ~70 % of its energy from microbial fermentation acids, a human ~10 % (measured [32]). There are at least 200 living ruminant species, Bovidae at least 143 [11].

A honey-bee worker gut holds $\sim 10^9$ bacteria after 10 days (position 45.60) (measured [16]). A fruit fly holds 10^2 – 10^6 CFU (measured [18]). A *Hydra* polyp holds $\sim 2 \times 10^5$ *Curvibacter* cells (measured [22]).

A squid light organ holds $\sim 10^6$ *V. fischeri* and vents 90–95 % of them each dawn (measured [20]). The survivors regrow within 4–6 h (positions 41.87–42.24) [20].

Termites number 3,106 described species (measured [31]). They emit 19.7 Mt CH₄ per year, ~4 % of global emissions (measured [34]). Their mounds oxidise about half of termite methane (measured [35]).

Wolbachia infects 40 %, 52 % or 66 % of arthropod species, depending on data set and method [37, 24, 23]. That is more than 1 million species by one estimate (modelled [37]).

Severe coral bleaching returned at a median interval of 6 years (position 50.50) by 2016, at 100 reefs (measured [29]). Reef-wide bleaching is expected at 4 °C-weeks [28]. About 725 of ~1,510 luminous fish species carry bacterial light [10].

Pattern

A human carries about as many bacterial cells as human cells, 3.8 against 3.0×10^{13} , nearly all in 0.4 L of colon. Microbial fermentation gives a human ~10 % of its energy and a ruminant ~70 %.

Loads span many orders of magnitude: 10^2 – 10^6 per fly, $\sim 10^9$ per bee gut, 10^5 – 10^{10} per g of sponge, $\sim 2 \times 10^5$ per *Hydra*. Vented squid symbionts regrow within 4–6 h. *Hydra* reaches carrying capacity within 24–72 h, and the bee gut holds $\sim 10^9$ bacteria after 10 days of colonisation.

Dated lineage and co-divergence ages lie at 10^7 – 10^8 years. They are 15 Myr for hominid–gut bacteria cospeciation and 39.1–32.3 Myr for crown ruminants. They are ~150 Myr for the earliest fish bioluminescence (Stomiiformes), ~200 Myr for *Wolbachia* supergroups A and B, and ~212 Myr for coral photosymbiosis.

The share of arthropod species with *Wolbachia* is 40–66 % by three estimates.

Not verified

- *Reticulitermes flavipes* 2.7×10^6 bacteria per gut; *Anacanthotermes* 1.3×10^6 to 4.3×10^9 per hindgut: secondary (BioNumbers).
- More than 250 bacterial species in *R. speratus*: secondary.
- Termite gut composition (spirochetes 42–63 %, archaea 0.13–3.22 % of rRNA and others): secondary (thesis table).
- Termite acetate up to 80 mM, up to 100 % of host respiration; acetogenesis 2–33 times methanogenesis; 22–26 % of carbon turnover: secondary.
- “Over 281 genera and 2,600 species” of termites (Kambhampati & Eggleton 2000): secondary.
- 1–11 protist species per lower termite (Inoue et al. 2000): secondary.
- Rumen bacteria 10^{10} – 10^{11} per g; facultative anaerobes 10^7 – 10^8 per g: secondary.
- Rumen protozoa 10^5 – 10^6 per mL, flagellates 10^3 – 10^4 per mL; ciliates 10^4 – 10^6 per mL with 30–40 % of fibre digestion: secondary.
- Cattle methane ~8 % of global production; ruminants 15–19 %: secondary.
- Seawater $\sim 10^6$ bacteria per mL with *V. fischeri* below 0.1 %; lifelong symbiosis: secondary.
- Coral symbiont density $\sim 10^6$ per cm^2 , energy up to ~95 %, doubling ~7 days (3–74): secondary.
- *Riftia* tube growth 10–85 cm per year, 1.5 m in two years, body to 3 m, vent temperatures, vents lasting under 10 years, symbiont *Endoriftia persephone*: secondary.
- Lutz et al. 1994 growth numbers: citation verified, numbers not read.
- *Riftia* first encountered 1977, described 1981: secondary.
- Bioluminescence “ ≥ 40 origins”: unverified.
- Squid lifespan, rumen volume, siboglinid origin date, sponge-microbiome origin date, in-gut bacterial doubling times: not read.

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A5 Fungi Between the Kingdoms

What it is

Fungi form the sister kingdom of the animals. Both belong to the Opisthokonta, a clade dated by a multigene clock to 1,389–1,240 Ma (positions 68.03–67.93) with all calibration constraints [1]. Across the full set of analyses the node falls at 1,240–1,481 Ma (positions 67.93–68.09) [1].

This chapter follows the fungi from that split into their unions with plants, insects, vertebrates and soil. Each union is dated, sized and counted where the record allows.

The unit of a fungus is the hypha, a tube. Across 31 soil-fungus strains its diameter is 2.7–6.5 μm (measured [2]).

A hypha extends at its tip. At 25 °C the mean extension per tip is 33 $\mu\text{m h}^{-1}$ in *Aspergillus nidulans*, 48 in *Geotrichum candidum*, 125 in *Mucor hiemalis* and 21 in *Neurospora crassa* (measured [3]). The fastest branch reaches 325 $\mu\text{m h}^{-1}$ and the fastest colony 377 $\mu\text{m h}^{-1}$ [3].

In μm per minute the means are 0.35–2.1, the fastest branch 5.4 and the fastest colony $377 / 60 = 6.3$ (computed).

Fungi enter four kinds of partnership: mycorrhiza with plants, lichens with algae and cyanobacteria, decay of wood, and insect farms. They also infect animals and plants.

First appearance

The split from the animals

Three clocks date the fungal lineage. The first gives the opisthokont node and dates the last eukaryotic common ancestor (LECA) to 1,866–1,679 Ma [1]. Its Table 2 gives LECA a mean of 1,774 Ma, 95 % HPD 1,632–1,911 Ma, from 109 taxa [1].

That study prints no separate node for crown Metazoa or crown Fungi [1]. A second clock places LECA at 2,386–1,958 Ma [4]. It estimates that fungi originated “even before (1759 to 1078 Ma)” and prints no opisthokont node age [4].

A third clock dates crown Fungi to ca. 1,020 Ma [5]. It places the loss of the fungal flagellum, taken as fungal colonisation of land, at ca. 720 Ma [5]. Glomeromycota arise at ca. 659 (715–606) Ma and Dikarya at 649 Ma [5].

The sources disagree. Crown Fungi at 1,020 Ma [5] lies $1,240 - 1,020 = 220$ to $1,389 - 1,020 = 369$ Myr after the opisthokont node (computed). The range 1,759–1,078 Ma [4] overlaps that node.

Crown animals originated in the Cryogenian by a further clock [6]. Most crown-bilaterian phyla diversified in the Ediacaran, and the bilaterian phyla diverged “>100 million years before the Cambrian” [6]. That study gives no Ma range for crown Metazoa [6].

The Cryogenian base stands at ~720 Ma on the ICS chart v2023/09 [7]. Crown Fungi at 1,020 Ma is older than that base by $1,020 - 720 = 300$ Myr (computed).

The oldest fossils

Fungus-like mycelial filaments occur in vesicular basalt of the Ongeluk Formation, South Africa, at 2.4 Ga [8]. The habitat is the rock, not a land surface.

Ourasphaira giraldae comes from the Grassy Bay Formation, Arctic Canada, at ~1,010–890 Ma [9]. It is “more than half a billion years older than previously reported unambiguous fungi” [9]. The opisthokont node (younger bound 1,240 Ma) precedes it by $\geq 1,240 - 1,010 = 230$ Myr (computed).

Glomalean hyphae and spores occur in the Ordovician of Wisconsin at ~460 Ma [10].

From *Ourasphaira* to these spores is $1,010 - 460 = 550$ Myr (computed).

Tortotubus protuberans is a cord-forming mycelium from the earliest Silurian, with septal perforations, a bilayered wall and affinity to Dikarya [11]. The Silurian base lies at 443.8 Ma [7].

Prototaxites stands in the Lower Devonian with trunks “as long as 8 m” [12]. It is read as a heterotroph consistent with a fungus [12].

First appearance with plants

The clock that dates crown Fungi also dates the arbuscular mycorrhizal (AM) symbiosis and the Leotiomyceta radiation to ca. 480 Ma [5]. Glomeromycota begin to diversify at 484 (529–437) Ma [5]. Crown land plants (embryophytes) date to 482 (485–473) Ma [5].

The plant side of the union is older than land plants. Symbiosis signalling genes, CCaMK among them, predate land plants in 259 green-algal transcriptomes and 10 basal land-plant genomes [13].

The first fossil arbuscules sit in *Aglaophyton major* in the Rhynie chert, at more than 400 Ma [14]. They are “morphologically identical” to living arbuscules [14]. The chert has a U-Pb age of 411.5 ± 1.3 Ma (measured [15]).

Stratified lichens appear in the Welsh Borderland at 415 Myr [16]. *Cyanolichenomycites devonicus* carries a cyanobacterial photobiont and *Chlorolichenomycites salopensis* a green-algal one [16]. The Rhynie lichen *Winfrenatia reticulata* dates to about 400 Ma, and a clock places ascolichens at 467–410 Ma [17, 5].

Partners

Plants: mycorrhiza

Of vascular plants, 72 % are arbuscular mycorrhizal, 2.0 % ectomycorrhizal (EcM), 1.5 % ericoid and 10 % orchid mycorrhizal [18]. Mycorrhiza evolved in three waves [18].

About 85 % of extant plants are mycorrhizal by one review [19]; a survey of 3,617 species found 80 % [20].

With 308,312 vascular plant species [21], AM hosts number $0.72 \times 308,312 = 221,985$ (computed). Glomeromycota hold ~360 described species in 49 genera [22]. A total of 320 is implied by 221 Neotropical species being 69 % of the phylum [23].

Per AM fungal species there are 617–694 host plant species (computed). EcM arose independently at least 66 times in fungi [24], or in 78–82 lineages by a later count [25].

In plants EcM arose 30 times, in 2 gymnosperm and 28 angiosperm lineages, covering ca. 8,500 species [26]. It has been present “since the Early Jurassic” [26]. The same source estimates the plants able to form EcM at 6,000–7,000 species [26].

Known EcM fungi number 7,750, with 20,000–25,000 likely [27]. Per EcM plant species that is $20,000 / 6,000 = 3.3$ to $25,000 / 7,000 = 3.6$ (computed). Against ca. 8,500 species it is $20,000 / 8,500 = 2.4$ to $25,000 / 8,500 = 2.9$ (computed).

Plants pass carbon to mycorrhizal mycelium at 13.12 Gt CO₂e yr⁻¹, which is 3.58 Gt C yr⁻¹ (measured [28]). AM takes 1.07, EcM 2.47 and ericoid 0.03 Gt C yr⁻¹ [28].

As shares of NPP the transfer is 6.2 % for AM, 13.1 % for EcM, 3.5 % for ericoid and 1.0 % for orchid mycorrhiza [28]. AM hyphae exceed 100 m per cm³ of prairie soil, about 0.5 mg dry hyphae per g [28]. EcM mycelium reaches 2,000 m per cm³ [28], or 2 × 10⁹ m per m³ (computed).

The AM spore of *Rhizophagus intraradices* measures 40–140 µm, mean 93.3 µm (measured, n = 170 [29]).

Plants: lichens

Lichenised fungi number 19,387 species in 995 genera [30]. Lichenisation arose 20–30 times: 14–23 times in Ascomycota and 6–7 in Basidiomycota [30].

Of 155,000 named fungi [31], 19,387 / 155,000 = 12.5 % are lichenised (computed).

The Rhynie lichen *Winfrenatia* has thallus bands 1–2 mm wide and net openings of ~25 µm (measured [17]). Its hyphae are 1–4 µm wide and its photobiont cells 15 µm, with up to 32 daughter cells per sheath [17].

Rhizocarpon geographicum grows radially at 0.23–1.47 mm yr⁻¹ [32]. The slowest recorded, *R. superficiale*, grows at 0.006 mm yr⁻¹ [33]. Reported thallus ages reach ≥4,500 yr and ~9,000 yr; the largest recorded thallus is 480 mm [33].

Plants: wood decay

Lignin-degrading class II peroxidases expanded in the lineage leading to the ancestor of the Agaricomycetes, reconstructed as a white-rot species [34]. They contracted in parallel in brown-rot and mycorrhizal lineages [34]. The analysis used 31 fungal genomes, 12 of them new [34].

Clocks place the origin of lignin degradation “around the end of the Carboniferous” [34]. That time coincides with a sharp decrease in organic carbon burial [34]. A second study gives “about 300 Ma, roughly at the end of the Carboniferous” [35].

The Agaricomycetes crown dates to 299 (351–252) Ma, and AA2 diversification to 350–295 Ma [5]. AA2 genes rise from 3 ancestral copies to 16 in the Auriculariales ancestor and 21 in the ancestor of Trechisporales plus later orders [35]. Dacrymycetes lack AA2; brown-rot and EcM lineages lost both AA2 and the cellulolytic sets [35].

Ancestral resurrection in Polyporales dates the peroxidase ancestor to 399 ± 140 Ma and the clade D ancestor to 259 ± 94 Ma [36]. The first versatile peroxidase dates to 194 ± 70 Ma and the first lignin peroxidase to 178 ± 64 Ma [36].

Brown rot arose at least four times [37]. Of 1,157 wood-decay species in 14 orders, 126 are brown rot and 1,031 white rot, a white-rot share of 89 % (computed) [37].

Two positions on coal stand side by side. One links lignin decay to the drop in carbon burial [34]; another rejects a fungal cause of the Carboniferous coal peak [38]. In the Early Pennsylvanian tree lycophytes made 60 to >80 % of peat contributors, their periderm 20–45 % of peat biomass [39].

At the end of the Permian, fungal remains make up 30–80 % of land-derived palynomorphs in South China and >90 % at Tesero [40, 41]. The proliferation lasted <1 Myr [40, 41]. They were read first as saprotrophs on dead wood [40], later as *Rhizoctonia*-like plant pathogens [41].

Termites take 58–64 % of dead-wood mass loss in a Bornean suppression experiment (measured [42]). Termite-discovered wood decays with a Q10 of 6.85, against 1.73 for microbes, across 133 sites (measured [43]).

World forests hold 861 Pg C, of which dead wood 73 ± 6 Pg C (8 %) and litter 43 ± 3 Pg C (5 %) [44]. Together that is 116 Pg C, 13.5 % (computed). The decay constant k runs from 0.004 to 0.975 yr^{-1} , so 95 % mass loss takes ~3–750 years [45].

Insects: attine ants

The ancestral fungus-farming ant population dates to $\sim 66.65 \pm 13.28$ Ma, rounded in the abstract to ~66 Ma [46]. Higher agriculture follows at ~27 Ma [46]. Fungus-farming ants diversified into 247 extant, largely Neotropical species, 52 of them leaf-cutters [46].

The chronograms hold 276 ants (208 fungus farmers) and 475 fungi (288 ant cultivars) [46]. A clade of 30 *Apterostigma pilosum*-group species farms coral fungi of the Pterulaceae [46].

The *Myrmecopterula* MRCA dates to ~48 Ma and the yeast-cultivar origin to ~32 Ma [46].

An earlier estimate from the same group dates lower fungus farming to between 61 Ma (52–70) and 57 Ma (48–66) [47]. The tribe Attini s.l. dates to 66 Ma (56–76) [47]. It counts ~250 described attine species [47].

In that estimate higher agriculture arose between 31 Ma (26–37) and 27 Ma (22–33) [47]. Leaf-cutters (*Atta* + *Acromyrmex*) arose between 19 Ma (15–24) and 18 Ma (14–22) [47].

The two estimates disagree: ant agriculture at 61–57 Ma [47] or 66.65 ± 13.28 Ma [46]. Higher agriculture is 31–27 Ma [47] or ~27 Ma [46]; attine species are ~250 [47] or 247 [46].

From farming to higher agriculture is $66.65 - 27 = 39.65$ Myr, or $57 - 27 = 30$ to $61 - 27 = 34$ Myr (computed). From higher agriculture to leaf-cutting is $27 - 19 = 8$ to $31 - 18 = 13$ Myr (computed).

Insects: fungus-growing termites

Fungus growing in termites (Macrotermitinae) had a single origin, in Africa, with no reversal to free-living fungi [48]. Horizontal transmission is ancestral [48]. Clonal vertical transmission arose twice: in *Microtermes* via females, in *Macrotermes bellicosus* via males [48].

An earlier molecular estimate dates termite fungus farming to ~31 Ma (19–49) [49]. The recalibrated age is 31.41 Ma (95 % CI 25.82–39.53), with alternatives of 27–36 Ma [49].

The oldest fossil fungus gardens, Rukwa Rift, Tanzania, date to ~25 Ma (24.8–24.5 Ma) [49].

The fossil nest chambers are 4–13 cm in diameter and up to 8 cm high (measured [49]). The combs are 6–9 cm wide and 3–6 cm tall, with cells of ~10 mm and peloids of ~1 mm [49].

Macrotermitinae number ~330 species in 11 genera, against ~50 *Termitomyces* species [50]. The ratio is $330 / 50 = 6.6$ (computed). Colonies last up to several decades, and primary reproductives live $\leq \sim 20$ years [50].

Mounds reach 10 m high and >15 m across, with ages of ~700 and $\geq 2,200$ years [50]. *Termitomyces* fruits every year with the rains [50]. New workers appear 1.5–3 months after swarming [50].

The termite crown dates to 149 (136–170) Ma, the oldest termite fossils to 135 Ma and Termitidae to 54 (46–66) Ma [51]. From the termite crown to fungus farming is $149 - 31.41 = 117.6$ Myr (computed).

Insects: ambrosia beetles

Bark and ambrosia beetles (Scolytinae) number >6,000 species, ~10 % of weevils, and originated at 100–120 Ma [52]. Fungus farming evolved at least ten times; reconstructions give 10 or 11 origins [52]. The oldest dates to ~50 Ma, Xyleborini to ~21 Ma, and crown ages run 8–48 Ma [52].

Each new origin of the symbiosis evolved a mycangium, a spore-carrying organ [53]. “Over 95%” of symbiotic pairs are economically harmless, and pest damage comes in three types [53].

Animals as hosts: amphibians

Chytridiomycosis has contributed to the decline of at least 501 amphibian species, 6.5 % of described amphibians [54]. Of these, 90 (18 %) are confirmed or presumed extinct in the wild [54]. A further 124 (25 %) show a >90 % reduction in abundance [54].

Declines peaked worldwide in the 1980s, before the disease was discovered in 1998 [54]. A smaller peak followed in the early 2000s in western South America [54].

Of 292 surviving species with known trends, 60 (20 %) show initial recovery, and declines continue in 197 [54]. That is $197 / 292 = 67$ % of species with known trends, or $197 / 501 = 39$ % of all declined species (computed). The chance of recovery after a >90 % decline is “less than one in ten” [54].

All declines but one are attributed to *Batrachochytrium dendrobatidis* [54]. The exception, *Salamandra salamandra*, declined from *B. salamandrivorans* [54]. Both species likely originated in Asia [54].

The implied number of described amphibians is $501 / 0.065 \approx 7,700$, so extinctions are $90 / 7,700 = 1.2$ % (computed).

B. dendrobatidis traces to the Korean peninsula, lineage BdASIA-1, with emergence “to the early 20th century” [55]. Its spread is linked to the commercial amphibian trade

[55]. From emergence to the decline peak is roughly 60–80 years (computed, approximate).

B. salamandrivorans was checked in more than 5,000 amphibians from four continents [56]. It infects only salamanders and newts (Urodela) and is highly pathogenic to them [56]. It was introduced from Asian hosts to naïve European populations [56].

Animals as hosts: bats and ants

White-nose syndrome is caused by *Pseudogymnoascus destructans*. Winter counts cover 200 sites in 27 US states and 2 Canadian provinces over 1995–2018, a span of 23 years [57] (computed). Three species declined by more than 90 %, two others less severely [57].

Fossil death-grip leaf scars from Messel, Germany, at 48 Ma are the first fossil record of fungus-manipulated ant behaviour [58]. They and ant agriculture at 66 Ma [46] fall inside the Paleogene, which begins at 66.0 Ma [7]. Fifteen new *Ophiocordyceps* species with hirsutella-like asexual morphs infect ants only [59].

Animals as hosts: humans

Invasive fungal infections number 6.5 million a year (6,548,000), with 3.8 million crude deaths (3,752,000) [60]. About 2.5 million deaths (68 %; range 35–90 %) are directly attributable [60].

Invasive aspergillosis causes ~2,113,000 cases and 1,801,000 deaths [60]. *Candida* causes ~1,565,000 cases and 995,000 deaths [60]. Cryptococcal meningitis causes 194,000 cases and 147,000 deaths [60].

Pulmonary tuberculosis is cited as the cause of 1,208,044 deaths in 2019 [60]. Crude fungal deaths are $3,752,000 / 1,208,044 = 3.1$ times that figure (computed; different years).

Plants as hosts

An “unprecedented number of fungal and fungal-like diseases” has recently caused some of the most severe die-offs in wild animals and plants [61]. Dutch elm disease came in two pandemics, from about 1910 and from the 1940s, and killed about 30 million elms in the UK [62]. Chestnut blight was first noticed in 1904 [63].

Of 1,090 fungal species with genomes sequenced by October 2016, 35.5 % are pathogens and 191 are plant-pathogenic [64].

Sizes

what	size	position	source
hypha, <i>Winfrenatia</i> lichen	1–4 µm	2.81–4.07	measured [17]
hyphal diameter, 31 soil strains	2.7–6.5 µm	3.72–4.51	measured [2]
photobiont cell,	15 µm	5.28	measured [17]

<i>Winfrenatia</i>			
net opening, <i>Winfrenatia</i>	25 μm	5.74	measured [17]
AM spore, <i>R. intraradices</i>	40-140 μm	6.17-7.31	measured [29]
AM spore, mean (n = 170)	93.3 μm	6.94	measured [29]
peloid, fossil termite comb	~1 mm	9.10	measured [49]
thallus band, <i>Winfrenatia</i>	1-2 mm	9.10-9.73	measured [17]
cell, fossil termite comb	~10 mm	11.19	measured [49]
fossil comb height	3-6 cm	12.19-12.83	measured [49]
fossil comb width	6-9 cm	12.83-13.19	measured [49]
fossil nest chamber height, maximum	8 cm	13.09	measured [49]
fossil nest chamber diameter	4-13 cm	12.46-13.53	measured [49]
largest <i>Rhizocarpon</i> thallus	480 mm	14.72	measured [33]
<i>Prototaxites</i> trunk	8 m	17.28	measured [12]
termite mound height	10 m	17.48	measured [50]
termite mound width	>15 m	17.85	measured [50]
Michigan genet, ≥ 15 ha, side of equal square	387.3 m	20.81	computed from [65]
Michigan genet, ~75 ha, side of equal square	866.0 m	21.54	computed from [66]
Oregon genet, ~965 ha, side of equal square	3,106.4 m	22.71	computed from [67]
Oregon genet, isolates apart	~3,810 m	22.89	measured [67]
Oregon forest, ~16,100 ha, side of equal square	12,688.6 m	23.99	computed from [67]

Areas are given as the side of a square of equal area, side = $\sqrt{(\text{area} \times 10^4 \text{ m}^2 \text{ ha}^{-1})}$ (computed). The 3,810 m genet extent over a 4 μm hypha is $\approx 9.5 \times 10^8$ (computed).

Times

what	duration	position	source
shift in mean mushroom fruiting, 83 species	13.3 days	45.85	measured [68]
new termite workers after swarming	1.5-3 months	46.98-47.61	measured [50]
<i>Termitomyces</i> fruiting cycle	1 yr	48.87	measured [50]
primary termite reproductives,	~20 yr	51.60	measured [50]

maximum			
white-nose count span, 1995–2018	23 yr	51.72	computed from [57]
naming at ~1,300 species per year	40 yr	52.23	[69]
Bd emergence to decline peak	60–80 yr	52.60–52.86	computed from [54, 55]
termite mound ages	~700; ≥2,200 yr	54.83; 55.88	measured [50]
naming 2.5 million fungi at 2,500 per year	938 yr	55.10	computed from [31]
Michigan genet, 1992 minimum	>1,500 yr	55.53	measured [65]
Michigan genet, 2018 minimum	2,500 yr	55.99	measured [66]
Oregon genet	1,900–8,650 yr	55.74–57.12	measured [67]
lichen thallus ages	≥4,500; ~9,000 yr	56.53; 57.16	measured [33]
95 % wood mass loss	~3–750 yr	49.87–54.90	measured [45]
end-Permian fungal proliferation	<1 Myr	61.45	measured [40, 41]
higher agriculture to leaf-cutters	8–13 Myr	63.34–63.78	computed from [47]
ant farming to higher agriculture, [47]	30–34 Myr	64.54–64.66	computed from [47]
ant farming (66.65 Ma) to termite farming (31.41 Ma)	35.24 Myr	64.69	computed from [46, 49]
ant farming to higher agriculture, [46]	39.65 Myr	64.80	computed from [46]
termite crown to termite fungus farming	117.6 Myr	65.79	computed from [51, 49]
AM origin (480 Ma) to white rot (~300 Ma)	180 Myr	66.17	computed from [5, 35]
opisthokont node to crown Fungi	220–369 Myr	66.36–66.83	computed from [1, 5]
opisthokont node to <i>Ourasphaira</i>	≥230 Myr	66.40	computed from [1, 9]
white rot (~300 Ma) to ant farming (66.65 Ma)	233.35 Myr	66.41	computed from [35, 46]
crown Fungi to Cryogenian base	300 Myr	66.64	computed from [5, 7]
<i>Ourasphaira</i> to glomalean spores	550 Myr	67.19	computed from [9, 10]

One year is 3.15576×10^7 s and one month one twelfth of that. The naming time is $(2.5 \times 10^6 - 155,000) / 2,500 = 938$ years (computed).

Counts

Named and estimated species

Accepted fungal species number 120,000, with an estimated total of 2.2–3.8 million [69]. The same source records about 1,300 new species per year over 40 years, later about 1,800 [69]. It gives a fungus : plant species ratio of 9.8 : 1 [69].

A later count states that “only 155,000 have been formally named to science” [31]. It puts the world total at 2.5 million and the naming rate at around 2,500 species a year [31].

The named share is $155,000 / 2.5 \times 10^6 = 6.2 \%$ (computed).

High-throughput sequencing gives a third view: over 250 million ITS2 sequences from more than 200 studies up to 2019 [70]. They resolve 1.08 million non-singleton taxa at 97 % similarity, 56.8 % Ascomycota and 36.7 % Basidiomycota [70]. The Chao-1 estimate of total extant diversity is 6.28 million taxa, “a conservative estimate” [70].

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 [70].

The named share thus runs from $120,000 / 6.28 \times 10^6 = 1.9 \%$ to $155,000 / 2.2 \times 10^6 = 7.0 \%$ (computed). Against ca. 374,000 plant species [21] the fungus : plant ratio is 2.5 million / 374,000 = 6.7 : 1 (computed). At 6.28 million it is 16.8 : 1 (computed).

Origins of partnerships

AM has one phylum of 320–360 species [22, 23]. EcM arose ≥ 66 or 78–82 times in fungi and 30 times in plants [24, 25, 26]. Lichenisation arose 20–30 times and brown rot at least 4 times [30, 37].

Ant agriculture and termite fungus growing each arose once, ambrosia farming ≥ 10 times [46, 48, 52].

The largest individuals

Armillaria bulbosa (now *A. gallica*) in Michigan “occupies a minimum of 15 hectares” and “weighs in excess of 10,000kg” [65]. It has been genetically stable “for more than 1,500 years” [65]. Its mass per area exceeds $10,000 / 15 = 667 \text{ kg ha}^{-1}$ (computed).

Re-sampling with 248 collections found one genet over approximately 75 ha, with a minimum age of 2,500 years [66]. Its genome is $\sim 90 \text{ Mb}$ with an “extremely low” somatic mutation rate [66]. Both areas and both ages are recorded for the same genet.

Armillaria ostoyae in the Blue Mountains, Oregon, forms a genet of $\sim 965 \text{ ha}$ within $\sim 16,100 \text{ ha}$ of mixed-conifer forest [67]. Its isolates lie up to $\sim 3,810 \text{ m}$ apart; other genets cover $\sim 20, 95, 195$ and 260 ha [67]. The genet age is 1,900–8,650 years from three spread rates [67].

The Oregon genet is 12.9 times the Michigan genet of 2018 ($965 / 75$) and 64 times its 1992 minimum (computed). The implied radial spread of $1,905 \text{ m}$ over 8,650–1,900 years is $0.22\text{--}1.0 \text{ m yr}^{-1}$ (computed). With $1 \text{ yr} = 525,960 \text{ min}$ this is $0.42\text{--}1.9 \text{ }\mu\text{m per minute}$ (computed).

Order of events

Each age of A Ma is placed as a duration of $A \times 10^6 \times 3.15576 \times 10^7$ s. Recent events are placed by their age in years before 2026 (computed).

1. 2,400 Ma (68.53) — fungus-like filaments in basalt [8].
2. 2,386–1,958 Ma (68.53–68.35) — LECA, second clock [4].
3. 1,866–1,679 Ma (68.30–68.21) — LECA, first clock [1].
4. 1,759–1,078 Ma (68.25–67.80) — fungal origin, second clock [4].
5. 1,481–1,240 Ma (68.09–67.93) — opisthokont node [1].
6. ca. 1,020 Ma (67.75) — crown Fungi [5].
7. ~1,010–890 Ma (67.74–67.63) — *Ourasphaira giraldae* [9].
8. ca. 720 Ma (67.43) — fungal flagellum lost [5]; Cryogenian base and crown animals [7, 6].
9. ca. 659 (715–606) Ma (67.35; 67.43–67.28) — Glomeromycota [5].
10. 649 Ma (67.34) — Dikarya [5].
11. 482 (485–473) Ma (67.07; 67.07–67.05) — crown land plants [5].
12. ca. 480 Ma (67.07) — AM symbiosis by clock [5].
13. 467–410 Ma (67.04–66.92) — ascolichens by clock [5].
14. ~460 Ma (67.03) — glomalean hyphae and spores [10].
15. After 443.8 Ma (66.99) — *Tortotubus* cords [11, 7].
16. 415 Myr (66.93) — stratified lichens [16].
17. 411.5 ± 1.3 Ma (66.93–66.92) — Rhynie arbuscules [14, 15].
18. Lower Devonian (no Ma given) — *Prototaxites* [12].
19. About 400 Ma (66.90) — *Winfrenatia* [17].
20. 399 ± 140 Ma (66.90; 67.17–66.50) — peroxidase ancestor [36].
21. ~300 Ma (66.64) — white rot [34, 35].
22. 299 (351–252) Ma (66.63; 66.78–66.48) — Agaricomycetes crown [5].
23. 254–252 Ma (66.49–66.48) — end-Permian fungal spike [40, 41].
24. 194 ± 70 Ma (66.24) and 178 ± 64 Ma (66.16) — versatile and lignin peroxidases [36].
25. Early Jurassic (no Ma given) — EcM present [26].
26. 149 (136–170) Ma (66.00; 66.12–65.92) — termite crown [51].
27. 120–100 Ma (65.80–65.64) — Scolytinae [52].
28. 66.65 ± 13.28 Ma (65.27) — ancestral fungus-farming ants [46]; 66.0 Ma (65.26) Paleogene base [7].
29. 61 (52–70) to 57 (48–66) Ma (65.19–65.13) — lower fungus farming, earlier estimate [47].
30. ~50 Ma (65.01) — oldest ambrosia farming [52].
31. 48 Ma (64.97) — death-grip scars, Messel [58].
32. 31.41 (25.82–39.53) Ma (64.58; 64.79–64.41) — termite fungus farming [49].
33. 31 to 27 Ma (64.57–64.45) — higher ant agriculture [47, 46].
34. ~25 (24.8–24.5) Ma (64.37–64.36) — fossil fungus gardens [49].
35. 19 to 18 Ma (64.13–64.08) — leaf-cutter ants [47].
36. Early 20th century (no year given) — Bd emerges from Korea [55].
37. 1904, 122 yr ago (53.24) — chestnut blight noticed [63].
38. About 1910, 116 yr ago (53.20) — first Dutch elm pandemic [62].
39. 1980s, from 46 yr ago (52.36) — peak of chytrid declines [54].
40. 1995–2018, 31 to 8 yr ago (52.00–50.76) — white-nose counts [57].
41. 1998, 28 yr ago (51.90) — chytridiomycosis discovered [54].

Other ages in the text, with positions:

- LECA mean 1,774 Ma (68.26); HPD 1,632–1,911 Ma (68.18–68.32).
- Glomeromycota diversification 484 Ma (67.07); AA2 diversification 350–295 Ma (66.78–66.62).
- Clade D 259 Ma (66.50); termite fossils 135 Ma (65.91); Attini s.l. 66 Ma (65.26).
- Termitidae 54 Ma (65.08); termite farming, earlier estimate 31 (19–49) Ma (64.57; 64.99).
- *Myrmecopterula* 48 Ma (64.97); yeast cultivar 32 Ma (64.60); Xyleborini 21 Ma (64.22).
- Ambrosia crown ages 8–48 Ma (63.34–64.97).

Present quantities

quantity	value	source
topsoil (0–30 cm) fungal biomass carbon	12.6 (6.6–16.4) Pg C	measured [71]
topsoil bacterial biomass carbon	4.3 (0.5–10.3) Pg C	measured [71]
fungal share of topsoil microbial carbon	75 %	computed
fungal : bacterial ratio, savanna to tundra	1.8 (1.6–2.1) to 8.6 (6.7–11.0)	measured [71]
tundra fungal / bacterial C	3,684 / 428 mg kg ⁻¹	measured [71]
desert fungal / bacterial C	16.92 / 6.83 mg kg ⁻¹	measured [71]
plant carbon to mycorrhizal fungi	3.58 Gt C yr ⁻¹	measured [28]
fungal spores to the air	~50 Tg yr ⁻¹ (~17 basidiospores)	measured [72]
human invasive fungal infections; deaths	6.5 million; 3.8 million yr ⁻¹	measured [60]
global biomass; plants; bacteria; archaea; animals	≈550; ≈450; ≈70; ≈7; ≈2 Gt C	measured [73]

The topsoil data come from 1,323 phospholipid-fatty-acid points across 11 biomes [71]. The fungal share is $12.6 / (12.6 + 4.3) = 75\%$, and the tundra / desert fungal density ratio $3,684 / 16.92 = 218$ (computed). The flux-to-stock ratio $3.58 / 12.6 = 0.28 \text{ yr}^{-1}$ makes the stock equal to 3.5 years of mycorrhizal flux (computed; different scopes).

Spore emission compares with ~47 Tg yr⁻¹ of anthropogenic primary organic aerosol [72].

Pattern

The opisthokont node lies at 1,481–1,240 Ma; two clocks date fungi, at 1,759–1,078 Ma and ca. 1,020 Ma. Fungal fossils run from 1,010–890 Ma to glomalean spores at ~460 Ma; the first arbuscules date to 411.5 Ma.

AM fungi form one phylum; EcM arose 66–82 times in fungi and 30 in plants; lichens 20–30 times. White rot dates to ~300 Ma; brown rot arose at least four times.

Insect farming arose in three groups, with at least 12 origins: ants ($66.65 \pm 13.28 \text{ Ma}$,

to 79.93 Ma, or 61–57 Ma), ambrosia beetles (≥ 10 origins from ~ 50 Ma) and termites (one origin, 31.41 Ma). The termite and beetle lineages are older: 149 and 100–120 Ma.

Vertebrate die-offs: 501 amphibian species declined, 90 extinct, three bat species down $>90\%$. Named fungi are 1.9–7.0 % of the estimated total. Hyphae 1–6.5 μm wide build genets of 15–965 ha that live 1,500–8,650 years.

Not verified

- Global fungal biomass of 12 Gt C, read only in a secondary page naming Bar-On et al. 2018.
- Kew 2018: 144,000 described fungi, about 2,000 added per year (secondary).
- *Tortotubus* at 440 Ma; Rhynie chert at c. 407 Ma (secondary).
- *Atta sexdens* colony times (secondary).
- Arbuscule lifespan of 4–15 days (teaching page, no primary).
- *Agaricus bisporus* basidiospore $7.7 \times 6.1 \mu\text{m}$ (secondary).
- White rot at 290 (222–372) Ma, read only through Hibbett et al. 2016; the 295 Ma figure in Floudas et al.
- White-nose range shares of 36 % and 79 % (meaning unread).
- A Ma range for crown Metazoa (source gives only “Cryogenian”).
- Joergensen & Wichern 2008 fungal share; Biedermann & Vega 2020 counts (citation only).
- Exact emergence year of *B. dendrobatidis*; total count of ant-infecting entomopathogens.

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A6 Coming Ashore Together

What it is

Life moved from water to land in sequence. Microbes came first, then fungi, plants, arthropods and vertebrates. Together they made soils, forests, coal and a changed atmosphere.

Each arrival is dated, sized and counted where the record allows. Stage boundaries follow the ICS chart v2023/09 [1].

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 [1].

First appearance

Microbes on land

Microbial mats drape fluvial conglomerates and gravelly sandstones of the Moodies Group, South Africa, at 3,220 Ma [2]. Their $\delta^{13}\text{C}_{\text{org}}$ lies in a narrow range centred on -21‰ , against marine mats as low as -34‰ (measured [2]). Their bulk $\delta^{15}\text{N}$ is 2–5 ‰ against 0–3 ‰ in marine mats [2].

Palaeosols of Mpumalanga, South Africa, at 2.6–2.7 Gyr hold organic matter read as remains of surface microbial mats [3]. One section at Schagen is 17 m thick [3].

The non-marine Torridonian sequence of NW Scotland dates to 1.2–1.0 Gyr [4]. Some of

its microfossils are “approaching one millimetre in diameter” [4].

Ediacaran palaeosols of South Australia carry fossils on their upper surfaces in growth position [5]. They are interpreted as lichens and microbial soil crusts [5]. The age is 635–542 Ma in the abstract and 625–542 Ma in the editorial summary [5].

The gaps between these records are $3,220 - 2,650 = 570$ Myr and $2,650 - 1,100 = 1,550$ Myr, using mid-ranges (computed). From 1,100 Ma to the oldest land-plant spores at 473 Ma is 627 Myr (computed). Microbial life on land precedes land plants by $3,220 - 473 = 2,747$ Myr (computed).

Fungi

Fungus-like mycelial filaments occur in 2.4 Ga basalt, a subsurface habitat [6]. The unambiguous fungus *Ourasphaira* dates to 1,010–890 Ma [7].

A clock places the loss of the fungal flagellum, taken as land colonisation, at ca. 720 Ma [8]. Glomeromycota arise at 659 (715–606) Ma and the AM symbiosis at ca. 480 Ma [8]. Glomalean hyphae and spores occur in the Ordovician of Wisconsin at ~460 Ma [9].

Tortotubus protuberans is a cord-forming mycelium of the earliest Silurian [10]. *Prototaxites*, of the Lower Devonian, has trunks up to 8 m and is read as a heterotroph consistent with a fungus [11].

Plants

The oldest cryptospores (land-plant spores) come from Argentina, Dapingian, about 473–471 Ma [12]. The previous oldest were late Darriwilian, about 463–461 Ma [12].

Clocks give crown embryophytes at 515.1–470.0 Ma and crown tracheophytes at 472.2–419.3 Ma [13]. A second clock with 68 fossil calibrations gives crown embryophytes at 515–493 Ma [14]. A third gives 482 (485–473) Ma [8].

Fossil minima are 420.7 Ma (Ludlow) for crown tracheophytes and 426.9 Ma (Wenlock) for *Cooksonia* cf. *pertoni* [13]. *Baragwanathia longifolia*, the earliest club moss, is Gorstian (Ludlow, Silurian) [15].

A model puts cryptogamic cover at about 30 % of today’s terrestrial NPP by about 445 Ma (modelled [16]). The model gives a sustained +2 ‰ carbonate $\delta^{13}\text{C}$ rise by about 445 Ma and O_2 at about present level by 420–400 Ma (modelled [16]).

Non-vascular plants are proposed to have triggered the Late Ordovician glaciation by weathering [17]. That glaciation ended about 444 Ma [17].

The earliest wildfire is recorded as charcoaled rhyniophytoid plants at Ludford Lane, Welsh Borders [18]. The level is basal Přídolí, 423.0 ± 2.3 Ma [18].

Arthropods

Arthropod trackways occur in basal terrestrial deposits of the Cambrian–Ordovician Nepean Formation, near Kingston, Ontario [19]. The tracks are mainly undertracks of large amphibious arthropods, possibly euthycarcinoids, in an eolian dune field [19].

They extend the record of the first arthropod landfall back “by as much as 40 m.y.” [19]. The Cambrian–Ordovician boundary lies at 485.4 Ma [1].

Burrows occur in Late Ordovician palaeosols of the Juniata Formation, Pennsylvania (*Scoyenia beerboweri*, Ashgill) [20, 21]. They formed with the soil, and their size distribution shows discontinuous, arthropod-like growth [20, 21]. Faecal pellets show sediment ingestion; the makers were most likely millipedes [21].

The burrows are older than 443.8 Ma (computed placement).

The myriapod clock age is ~500 Ma, against earliest confirmed fossils at ~425 Ma [22]. The gap is 75 Myr [22]. U–Pb ages run: Kerrera ~425 Ma (kampecarid millipedes), Ludlow ~420 Ma (first trigonotarbid with book lungs; millipedes with spiracles) [22].

Cowie Harbour follows at ~414 Ma and Rhynie at ~407 Ma; forest-grade communities exist by ~385 Ma [22].

Pneumodesmus newmani, the oldest millipede with spiracles, comes from Cowie Harbour, Stonehaven [23]. It was dated ~427 Ma by spores [23].

U–Pb zircon gives it a maximum depositional age of 413.7 ± 4.4 Ma and 414.3 ± 7.1 Ma, lowermost Devonian [23]. The redating moves it by $427 - 414 = 13$ Myr (computed).

A molecular clock on 1,478 genes dates insects to ~479 Ma, flight to ~406 Ma and major extant lineages to ~345 Ma [24]. The oldest winged-insect fossil, *Delitzschala bitterfeldensis*, is Arnsbergian (Serpukhovian, 330.9–323.2 Ma) [25]. From clock flight to that fossil is $406 - 330.9 = 75.1$ Myr (computed).

From the insect clock age to the Rhynie hexapods is $479 - 411.5 = 67.5$ to $479 - 407 = 72$ Myr (computed).

Rhyniognatha hirsti of the Rhynie chert was described as the oldest true insect [26]. A reinterpretation finds new remains that “do not support an interpretation as an insect” [27]. It reads the animal as a myriapod, “possibly as a centipede”; both readings are recorded [27].

Vertebrates

Tetrapod trackways occur at Zachełmie, Poland, in the Eifelian, early Middle Devonian [28]. They are “approximately 18 million years older than the earliest tetrapod body fossils” [28]. They are “10 million years earlier than the oldest elpistostegids” [28].

With the Eifelian at 393.3–387.7 Ma [1], the earliest body fossils are implied at 375.3–369.7 Ma (computed). The oldest elpistostegids are implied at 383.3–377.7 Ma (computed).

Tiktaalik roseae is a tetrapod-like fish from the Late Devonian of Arctic Canada [29]. The fish–tetrapod transition “occurred over 370 million years ago” [29].

The Joggins Fossil Cliffs, Nova Scotia, expose Pennsylvanian strata of 318–303 Ma [30]. They hold 148 fossil species and 20 footprint groups in 96 genera [30]. They record “the first reptiles in Earth history” [30].

The site has 14.7 km of sea cliffs within 689 ha [30]. Its listing gives the Carboniferous as “354 to 290 million years ago” [30]. The ICS chart gives 358.9–298.9 Ma [1]; both spans are recorded.

Partners

The Rhynie chert consortium

The Rhynie chert has a U-Pb age of 411.5 ± 1.3 Ma (measured [31]). Other printed ages are “about 396–407 million years ago” [26], “c. 390 million years old” [32], and “400 million year old” and “410 million years ago” [33]. Together they span 411.5–390 Ma.

The site is c. 3.2 m of chert, mudstone and sandstone, formed from hot siliceous solutions [32]. “The 22 species of plant fossil (including fungi) are unique to this locality” [32]. The list in the same text holds 25 names; both counts are recorded [32].

“Six different types of sporophytes and three gametophytes have been described” [34]. The vascular plants “were small, ca. 10 to 40 cm high” [34]. Two species lived entirely subaerially, *Rhynia gwynne-vaughanii* and *Aglaophyton major* [34].

Asteroxylon mackiei had roots penetrating the soil [34]. Roots arose stepwise and independently in lycophytes and euphyllophytes; *Asteroxylon* is dated 407 Ma [35].

The inventory holds 6 cyanobacteria, 3 algae, 1 lichen (*Winfrenatia reticulata*) and 2 nematophytes [34]. It holds about 10 named fungal taxa plus “several Chytridiomycetes”, ascomycetes and other undescribed fungi [34].

Arbuscules sit in *Aglaophyton* [36]. The lichen *Winfrenatia* has hyphae 1–4 μm wide [37].

The fauna holds the oldest unequivocal nematodes, possibly the earliest plant parasitism [38]. It holds trigonotarbid arachnids with book lungs and mites, including mycophages [38]. A harvestman shows the earliest preserved tracheae and genitalia [38].

There are a scutigeromorph centipede and a putative millipede, and springtails that are likely mycophages [38]. A hexapod has plant debris in its gut [38].

The springtail *Rhyniella praecursor* is “between 1–2mm in length”, with a head of 300–400 μm (measured [33]).

Palaeocharinus rhyniensis and *P. hornei* reach “up to 4 mm”; *P. tuberculatus* at least 6 mm (measured [33]). Larger unnamed specimens reach 14–20 mm [33]. Of five species described in 1923, “only two valid species are probably present”; with *P. tuberculatus* that makes three (computed from [33]).

Mites are 290–450 μm long (measured [33]). Five species are named, one in 1923 and four in 1962 (computed from [33]). Seven arthropod groups are listed: trigonotarbids, harvestmen, mites, myriapods, collembolans, crustaceans and euthycarcinoids [33].

Across the community, mite 0.29 mm $\rightarrow$ trigonotarbid 20 mm $\rightarrow$ plant 400 mm gives ratios 69 and 20 (computed). The whole span 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).

Roots and the first deep soils

Drepanophycus-like rhizomes run through Pragian palaeosols, about 411–408 Ma, of the Xujiachong Formation, Yunnan [39]. Rhizome density is 800–1,300 m per m³ of sediment, occupying 6.9–11.3 % of its volume (measured [39]).

Trace width is 5.9–18 mm, mean 10.5 mm [39]. The thickest exposed palaeosol is 15.5 m, originally 17.0–19.4 m [39]. Others are 9.0, 7.8 and 4.4 m thick [39].

The density 800–1,300 m m⁻³ equals 0.0008–0.0013 m cm⁻³ (computed). Modern AM hyphae exceed 100 m cm⁻³ [40]. The Devonian rhizome network is thus ~10⁵ times sparser in length (computed).

Herbivory

Phase 1 of land herbivory runs from the latest Silurian to the Early Devonian, 417–403 Ma [41]. It includes sporivory: spores in coprolites, such as *Lancifaex simplex* with plant and fungal spores at Rhynie [41]. It includes a probable bored stem and a stylectal piercing in *Rhynia gwynne-vaughanii*, and borings in *Prototaxites* [41].

Phase 1 lags 0–20 Myr after each tissue's origin; phase 2 runs 327–309 Ma [41]. Leaf-margin feeding on *Triphyllopteris austrina* begins at 326 Ma (Serpukhovian), 76 Myr after the origin of leaves [41].

Seed predation (holes in *Trigonocarpus*) appears in the Early-Middle Pennsylvanian, 54 Myr after seeds [41]. Wood boring in *Trivenia* appears in the mid-Namurian, 63 Myr after wood [41]. Root feeding appears in the early Late Pennsylvanian, a 98 Myr lag, and a mid-Palaeozoic hiatus lasts 65 Myr [41].

The oldest insect gall, ~302 Ma, is a petiole gall in the tree fern *Psaronius* made by a holometabolan larva [42]. Herbivory came in two pulses [43]. About 12 ordinal-level insect lineages first appear in the second, and there are seven functional feeding groups [43].

The first wood borings are Late Devonian, ~383–359 Ma [44].

The oldest known synapsid herbivore, *Melanedaphodon hovaneci*, comes from Linton, Ohio, Moscovian, about 307 Ma [45]. Tetrapod herbivory arose “at least five times” in the Late Carboniferous–Early Permian, and herbivores stayed rare until the Late Permian [46].

From the first arthropod herbivory (417 Ma) to the first vertebrate herbivory (307 Ma) is 110 Myr (computed). From the first footprints (~390 Ma) to the first tetrapod herbivore is ~83 Myr (computed). The Joggins reptiles (318–303 Ma) and the first herbivore overlap.

Forests

The oldest forest with *Archaeopteris* root systems is at Cairo quarry, New York, “early mid Givetian (ca. 385 Ma)” [47]. It is “approximately 2–3 Ma” older than Gilboa [47]. Root systems spread “as much as 11 m across the paleosol surface” [47].

Primary roots are 6–16 cm in diameter, 10–15 per tree (measured [47]). Eighteen root

systems were mapped in $\sim 3,000 \text{ m}^2$, one per $3,000 / 18 = 167 \text{ m}^2$ (computed). Tree heights are estimated at 11–32 m [47].

Eospermatopteris bases are 20–50 cm, with roots of 0.7–1 cm reaching 1–2 m [47].

Wattieza/Eospermatopteris stumps at Gilboa are Givetian, “about 385 million years old” [48]. The trees were “at least 8 m” tall [48].

Archaeopteris trunks occur in Famennian marine beds of SE Morocco, “370-million-year-old” [49]. They show lateral branching of the modern-tree type [49].

Weathering, CO₂ and soils

Rooted plants spread at 400–360 Ma, with a CO₂ drop as deep-rooted vascular plants reached uplands [50]. Tree plots at Hubbard Brook show roughly tenfold Ca weathering over bare plots [50]. In Iceland the factor is 5–10 for Ca and Mg [50].

A set of 1,241 CO₂ proxy estimates from 112 studies gives about 2,000 ppm at $\sim 400 \text{ Ma}$ [51]. CO₂ is close to pre-industrial (278 ppm) through much of the Carboniferous ($\sim 300 \text{ Ma}$) [51]. The long-term decline is $\sim 3.4 \text{ ppm per Myr}$ over 420 Myr [51].

From 400 to 300 Ma the fall is $(2,000 - 278) / 100 = 17 \text{ ppm per Myr}$ (computed).

Arborescence and the seed habit are linked to faster weathering, algal blooms, anoxia, carbon burial, lower CO₂ and a brief Late Devonian glaciation [52].

Five land-plant stages follow over 485–298.9 Ma: non-vascular, vascular, shallow roots, arborescent with deep roots, and seed plants [53].

Mycorrhizal mycelium weathers minerals [54]. Angiosperm hosts released Ca from basalt at twice the rate of gymnosperms [55].

Clitellates had a freshwater common ancestor in the Devonian, roughly 419–359 Ma, from 74 taxa [56]. The earthworm crown lies at the Carboniferous–Permian boundary, 298.9 Ma [57].

Coal and oxygen

A revised GEOCARBSULF model shows no drop below 15 % O₂ at any time (modelled [58]). Its largest excursion above present lies in the Permo-Carboniferous, 260–300 Ma [58]. Present terrestrial organic-carbon burial is $\sim 350 \times 10^{12} \text{ g C yr}^{-1}$ and marine $\sim 200 \times 10^{12}$ [58].

An earlier model gives O₂ of roughly 15–30 % over 550 Myr (modelled [59]); a maximum of “about 35 %” around 300 Ma is disputed [60].

Charcoal in mires puts pO₂ “continuously above 26 %” through the Carboniferous and Permian [61]. A sharp drop follows near the Permian–Triassic boundary [61].

GEOCARBSULFOR gives O₂ of 2–11 % from the Cambrian to the mid-Ordovician and near-modern in the Devonian (modelled [62]). It has a mid-Devonian nadir of $\sim 14.5 \%$ at $\sim 393 \text{ Ma}$ and $>25 \%$ in the early Mississippian [62]. A dip to $\sim 20 \%$ follows at $\sim 323 \text{ Ma}$; charcoal is present after 419 Ma but scarce ~ 400 – 360 Ma [62].

Fire is suppressed below 18.5 % O₂ and off below 16 %, and rises fast between 19 and 22 % [63]. Flammability was high in the Carboniferous, 350–300 Ma [63].

The O₂ reservoir is 3.78×10^{19} mol, and its source 1.8×10^{13} mol yr⁻¹ [64]. The residence time is $3.78 \times 10^{19} / 1.8 \times 10^{13} = 2.1 \times 10^6$ yr, ~2.1 Myr, or 0.8 Myr with Berner's burial fluxes (computed from [64]).

Arborescent lycopsids of the late Carboniferous coal swamps reached “statures up to c. 45 m” and “trunk diameters up to 2 m” [65]. In the Early Pennsylvanian of Euramerica tree lycopods made 60 to >80 % of peat contributors [66]. Their periderm formed 20–45 % of peat biomass, suberin-like rather than lignin-like [66].

Organic-carbon burial roughly doubled over the Carboniferous [66]. Enzymatic lignin decay originated “around the end of the Carboniferous” in the Agaricomycete ancestor [67]. Another study rejects this as cause of the coal peak and attributes the peak to everwet tropics and extensive depositional settings during Pangaea's assembly [68].

The late Paleozoic ice age ran 340–260 Ma with CO₂ <500 ppm [69]. CO₂ swung on a ~10⁵-yr timescale over a 16-Myr record, with repeated restructuring of tropical forests [70].

Coal beds run from a few inches to, rarely, 200 ft (61 m) thick; modern peat reaches 50 ft (15 m) [71].

Giants

Arthropleura partial remains measure 76 × 36 cm (measured [72]). The animal was ~55 cm wide, up to 2.63 m long and ~50 kg [72]. It is Serpukhovian, from Northumberland [72].

Carboniferous–Permian insect wingspans reach about 70 cm, from >10,500 fossil wing lengths [73]. Maximum size tracks pO₂ until the end of the Jurassic [73].

The size steps run Rhynie mite 0.29 mm → trigonotarbid 20 mm → *Arthropleura* 2,630 mm, ratios 69 and 132 (computed). The total is 9,070 over ~80 Myr, 411 → 331 Ma (computed).

Sizes

what	size	position	source
lichen hypha, Rhynie	1–4 μm	2.81–4.07	measured [37]
mite, Rhynie	290–450 μm	7.97–8.37	measured [33]
springtail head, <i>Rhyniella</i>	300–400 μm	8.00–8.26	measured [33]
Torridonian microfossil	~1 mm	9.10	measured [4]
springtail, <i>Rhyniella</i>	1–2 mm	9.10–9.73	measured [33]
trigonotarbid, two species	up to 4 mm	10.36	measured [33]
rhizome trace width, Yunnan	5.9–18 mm	10.71–11.73	measured [39]
trigonotarbid, <i>P.</i>	≥6 mm	10.73	measured [33]

<i>tuberculatus</i>			
<i>Eospermatopteris</i> root	0.7–1 cm	10.87–11.19	measured [47]
rhizome trace width, mean	10.5 mm	11.24	measured [39]
trigonotarbid, larger specimens	14–20 mm	11.50–11.83	measured [33]
<i>Archaeopteris</i> primary root	6–16 cm	12.83–13.72	measured [47]
Rhynie vascular plant height	10–40 cm	13.29–14.55	measured [34]
<i>Eospermatopteris</i> base	20–50 cm	13.92–14.76	measured [47]
<i>Arthropleura</i> partial remains	76 × 36 cm	15.14; 14.46	measured [72]
<i>Arthropleura</i> width	~55 cm	14.84	measured [72]
insect wingspan, maximum	~70 cm	15.06	measured [73]
<i>Eospermatopteris</i> root reach	1–2 m	15.39–16.02	measured [47]
lycopsid trunk diameter	2 m	16.02	measured [65]
<i>Arthropleura</i> length	2.63 m	16.27	measured [72]
Rhynie chert section	c. 3.2 m	16.45	measured [32]
Yunnan palaeosols, other	4.4; 7.8; 9.0 m	16.73; 17.26; 17.39	measured [39]
<i>Prototaxites</i> trunk	8 m	17.28	measured [11]
<i>Wattieza</i> tree height	≥8 m	17.28	measured [48]
<i>Archaeopteris</i> root system	11 m across	17.57	measured [47]
modern peat, maximum	15 m	17.85	measured [71]
Yunnan palaeosol, exposed	15.5 m	17.88	measured [39]
Schagen palaeosol section	17 m	17.97	measured [3]
Yunnan palaeosol, original	17.0–19.4 m	17.97–18.09	measured [39]
<i>Archaeopteris</i> tree height	11–32 m	17.57–18.54	modelled [47]
lycopsid stature	c. 45 m	18.85	measured [65]
coal bed, rare maximum	61 m	19.13	measured [71]
Joggins site, 689 ha, side of equal square	2,624.9 m	22.55	computed from [30]
Joggins sea cliffs	14.7 km	24.12	measured [30]

The Joggins area is given as the side of a square of equal area, $\sqrt{(689 \times 10^4 \text{ m}^2)}$ (computed).

Times

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what	duration	position	source
CO ₂ swings, late Paleozoic	~10 ⁵ yr	59.35	measured [70]
O ₂ residence, with Berner's burial fluxes	0.8 Myr	61.24	computed from [64]
Cairo forest older than Gilboa	2–3 Myr	62.08–62.45	measured [47]
O ₂ residence time	~2.1 Myr	62.12	computed from [64]
tracks before elpistostegids	10 Myr	63.54	measured [28]
<i>Pneumodesmus</i> redating	13 Myr	63.78	computed from [23]
CO ₂ record, Montañez	16 Myr	63.97	measured [70]
tracks before tetrapod body fossils	18 Myr	64.08	measured [28]
herbivory lag after tissue origin, phase 1	0–20 Myr	—; 64.17	measured [41]
trackway extension of arthropod landfall	≤40 Myr	64.80	measured [19]
plant spores to vascular plants, 473 → 426.9 Ma	46 Myr	64.93	computed from [12, 13]
seed predation lag	54 Myr	65.08	measured [41]
wood boring lag	63 Myr	65.22	measured [41]
mid-Palaeozoic herbivory hiatus	65 Myr	65.25	measured [41]
insect clock to Rhynie hexapods	67.5–72 Myr	65.28–65.34	computed from [24, 31, 35]
myriapod clock to first fossils	75 Myr	65.38	measured [22]
clock flight to oldest winged fossil	75.1 Myr	65.38	computed from [24, 25]
leaf-feeding lag	76 Myr	65.39	measured [41]
late Paleozoic ice age, 340–260 Ma	80 Myr	65.43	computed from [69]
arthropod size rise, 411 → 331 Ma	~80 Myr	65.43	computed from [33, 72]
first footprints to first tetrapod herbivore	≈83 Myr	65.47	computed from [28, 45]
first forests (385 Ma) to white rot (~300 Ma)	~85 Myr	65.49	computed from [47, 67]
plant spores to first forests, 473 → 385 Ma	88 Myr	65.52	computed from [12, 47]
root-feeding lag	98 Myr	65.62	measured [41]
CO ₂ fall, 400 → 300 Ma	100 Myr	65.64	computed from [51]
first arthropod to first vertebrate herbivory	110 Myr	65.72	computed from [41, 45]
CO ₂ decline record	420 Myr	66.94	measured [51]
O ₂ model span	550 Myr	67.19	modelled [59]

mats (3,220 Ma) to palaeosols (2,650 Ma)	570 Myr	67.22	computed from [2, 3]
Torrignonian (1,100 Ma) to plant spores (473 Ma)	627 Myr	67.31	computed from [4, 12]
palaeosols (2,650 Ma) to Torrignonian (1,100 Ma)	1,550 Myr	68.13	computed from [3, 4]
microbes on land before plants	2,747 Myr	68.65	computed from [2, 12]

A lag of 0 has no position (log of zero); its upper bound is placed. One year is 3.15576×10^7 s.

Counts

what	count	source
Rhynie sporophytes; gametophytes; cyanobacteria; algae	6; 3; 6; 3	[34]
Rhynie lichens; nematophytes; named fungal taxa	1; 2; about 10	[34]
Rhynie plant fossils incl. fungi	22; 25 names listed	[32]
Rhynie arthropod groups; mite species; trigonotarbid species	7; 5; 3	[33]
<i>Archaeopteris</i> root systems mapped; primary roots per tree	18; 10–15	[47]
Gilboa oribatid mites	14 fossils, 2 species, 2 new genera, 2 new families	[74]
Joggins species; footprint groups; genera	148; 20; 96	[30]
tetrapod herbivore origins	≥ 5	[46]
ordinal insect lineages in the second herbivory pulse	~ 12	[43]
functional feeding groups	7	[43]
land-plant stages, 485–298.9 Ma	5	[53]
Collembola species, 2024	9,186	[75]
millipede species described	>12,000	[76]

The Gilboa mites “roughly double the known age of the group” [74]. Springtails and millipedes, both at Rhynie, now count 9,186 and >12,000 species [75, 76].

Order of events

Each age of A Ma is placed as a duration of $A \times 10^6 \times 3.15576 \times 10^7$ s (computed).

1. 3,220 Ma (68.80) — microbial mats on river gravels, Moodies Group [2].
2. 2.7–2.6 Ga (68.64–68.60) — mats in palaeosols, Mpumalanga [3].
3. 2.4 Ga (68.53) — fungus-like filaments in basalt [6].
4. 1.2–1.0 Ga (67.90–67.73) — non-marine eukaryotes, Torrignonian [4].
5. 1,010–890 Ma (67.74–67.63) — *Ounasphaera* [7].

6. ca. 720 Ma (67.43) — fungal flagellum lost, by clock [8].
7. 659 Ma (67.35) — Glomeromycota, by clock [8].
8. 635–542 Ma (67.32–67.18) — Ediacaran surface communities; 625 Ma (67.31) in the summary [5].
9. 515.1–470.0 Ma (67.13–67.05); 515–493 Ma (67.13–67.09); 482 Ma (67.07) — crown embryophytes, by clock [13, 14, 8].
10. ~500 Ma (67.10) — myriapods, by clock [22].
11. 485.4 Ma (67.08) — Cambrian–Ordovician boundary; arthropod trackways [1, 19].
12. ca. 480 Ma (67.07) — AM symbiosis, by clock [8].
13. ~479 Ma (67.06) — insects, by clock [24].
14. 473–471 Ma (67.05) — oldest land-plant cryptospores [12].
15. 472.2–419.3 Ma (67.05–66.94) — crown tracheophytes, by clock [13].
16. 463–461 Ma (67.03) — previous oldest cryptospores [12].
17. ~460 Ma (67.03) — glomalean hyphae and spores [9].
18. ~445 Ma (67.00) — cryptogam cover ~30 % of today's NPP (modelled [16]).
19. ~444 Ma (66.99) — end of the Late Ordovician glaciation [17].
20. | 443.8 Ma (66.99) — burrows in Juniata palaeosols [20, 21].
21. 426.9 Ma (66.96) — *Cooksonia* minimum [13].
22. ~425 Ma (66.95) — millipedes at Kerrera [22].
23. 423.0 ± 2.3 Ma (66.95; 66.96–66.95) — earliest charcoal [18].
24. 420.7 Ma (66.95) — crown-tracheophyte minimum [13].
25. ~420 Ma (66.94) — trigonotarbid with book lungs [22].
26. 420–400 Ma (66.94–66.90) — O₂ near present level (modelled [16]).
27. 419–359 Ma (66.94–66.80) — freshwater clitellate ancestor [56].
28. 417–403 Ma (66.94–66.91) — herbivory phase 1 [41].
29. 414 Ma (66.93) — *Pneumodesmus* by U–Pb; formerly 427 Ma (66.96) [23].
30. 411.5 ± 1.3 Ma (66.93–66.92) — Rhynie chert community [31].
31. 411–408 Ma (66.92) — rhizomes in Yunnan palaeosols [39].
32. 407 Ma (66.92) — *Asteroxylon* roots [35].
33. ~406 Ma (66.91) — insect flight, by clock [24].
34. 400–360 Ma (66.90–66.80) — rooted plants spread [50].
35. 393.3–387.7 Ma (66.88–66.87) — tetrapod trackways, Zachełmie [28, 1].
36. ~393 Ma (66.88) — O₂ nadir ~14.5 % (modelled [62]).
37. ~385 Ma (66.86) — first forests at Cairo and Gilboa; forest-grade arthropods [47, 48, 22].
38. 383.3–377.7 Ma (66.86–66.85) — oldest elpistostegids, implied (computed).
39. 383–359 Ma (66.86–66.80) — first wood borings [44].
40. 375.3–369.7 Ma (66.84–66.83) — earliest tetrapod body fossils, implied (computed).
41. | 370 Ma (66.83) — fish-tetrapod transition [29]; ~370 Ma *Archaeopteris* trunks, Morocco [49].
42. 350–300 Ma (66.78–66.64) — high flammability [63].
43. ~345 Ma (66.76) — major extant insect lineages, by clock [24].
44. 340–260 Ma (66.75–66.51) — late Paleozoic ice age, CO₂ <500 ppm [69].
45. 330.9–323.2 Ma (66.73–66.71) — oldest winged insect [25]; *Arthropleura*,

Serpukhovian [72].

46. 327–309 Ma (66.72–66.66) — herbivory phase 2; leaf-margin feeding at 326 Ma (66.71) [41].
47. ~323 Ma (66.70) — O₂ dip to ~20 % (modelled [62]).
48. 318–303 Ma (66.69–66.65) — Joggins coal forest with the first reptiles [30].
49. ~307 Ma (66.66) — first tetrapod herbivore [45].
50. ~302 Ma (66.64) — oldest insect gall [42].
51. ~300 Ma (66.64) — CO₂ near 278 ppm [51]; lignin decay [67]; O₂ model maximum ~35 % [60].
52. 300–260 Ma (66.64–66.51) — largest O₂ excursion above present (modelled [58]).
53. 298.9 Ma (66.63) — earthworm crown [57].
54. 251.902 Ma (66.48) — Triassic base; sharp O₂ drop near the boundary [1, 61].

The UNESCO Carboniferous span, 354–290 Ma, places at 66.79–66.61 [30].

Present quantities

quantity	value	source
global biomass	≈550 Gt C	measured [77]
plants; bacteria; archaea; animals	≈450; ≈70; ≈7; ≈2 Gt C	measured [77]
fungi	≈12 Gt C	measured [77]
terrestrial / marine biomass	about two orders of magnitude	measured [77]
global NPP	104.9 Pg C yr ⁻¹ , land and ocean roughly equal	measured [78]
world forest carbon	861 ± 66 Pg C	measured [79]
of which soil; live biomass; dead wood; litter	383; 363; 73; 43 Pg C	measured [79]
plant carbon to mycorrhizal fungi	3.58 Gt C yr ⁻¹	measured [40]
O ₂ in dry air	20.95 %	measured [80]
CO ₂ in dry air	420 ppm	measured [80]
CO ₂ at Mauna Loa, September 2026	426.07 ppm	measured [81]
Collembola species	9,186	[75]
millipede species	>12,000	[76]

Plants hold 450 / 550 = 82 % of biomass carbon, fungi 12 / 550 = 2.2 % (computed).

Pattern

Microbial mats are on land from 3,220 Ma, 2,747 Myr before plant spores (473–471 Ma). By clock, fungi lose the flagellum at ~720 Ma, before plant spores; glomalean hyphae and spores follow at ~460 Ma. Arthropod tracks lie at the Cambrian-Ordovician boundary, also before plant spores; burrows are older than 443.8 Ma.

Vascular plants follow (426.9 Ma), then charcoal (423 Ma), then the Rhynie community (411.5 Ma). It holds plants of 10–40 cm with arbuscules, a lichen, about ten fungi, nematodes and seven arthropod groups of 0.29–20 mm. Footprints (393.3–387.7 Ma)

precede forests (~385 Ma).

Clock ages precede first fossils by 67.5–75 Myr in insects and myriapods.

CO₂ falls from ~2,000 to ~278 ppm over 400–300 Ma; the mire-charcoal proxy puts pO₂ continuously above 26 % through the Carboniferous and Permian.

Herbivory reaches spores at 417 Ma, leaves at 326 Ma and vertebrates at 307 Ma. Sizes climb from 0.29 mm to 2.63 m in arthropods and from 40 cm to 45 m in plants.

Not verified

- Animal species counts for the Rhynie chert (only a Wikipedia table: 14 arthropod species, 35 fungal genera, ~45 fungal species).
- Hot-spring water at 90–120 °C, cooling to <30 °C at the fossil sites (secondary).
- *Tiktaalik* age of about 375 Ma and length 1.25–2.75 m (secondary).
- Rooting “up to 1 metre deep”, ~1 cm roots and deep soils 20 Myr earlier (press release only).
- Rhynie chert at c. 407 Ma in palaeomycology (secondary).
- *Tortotubus* at 440 Ma (secondary).
- Terrestrial NPP of 56.4 Pg C yr⁻¹ (BioNumbers, secondary).
- Ordovician cooling of about 5 °C plus 2–3 °C (press release, secondary).
- Ma age of the Ontario trackways.
- Absolute size of *Rhyniognatha*.
- *Hylonomus* by name at Joggins.
- Body sizes of the Zachełmie trackmakers.
- Original description of *Pneumodesmus*, Wilson & Anderson 2004 (citation only).

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A7 Eating and Being Eaten

What it is

One organism feeds on another. A predator kills and eats prey; a herbivore eats 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.

This chapter follows that line of connection from the oldest bored shell to the present distribution of living carbon. Between the two ends lie the sizes of eaters and eaten, food-chain length, transfer between trophic levels and parasite counts.

First appearance

Predation. 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 (measured [1]).

Of more than 500 tubes, 2.7 % carry rounded holes 40 to 400 μm in diameter (measured [1]). That is at least 14 bored tubes: $0.027 \times 500 = 13.5$, rounded up (computed). Hole size relates to the width of the bored tube, which the authors record as size-selective predation (measured [1]).

A second study of uppermost Neoproterozoic *Cloudina* from China gives a different frequency. Nearly one-fifth of almost one hundred tubes carry predatory borings 15–85 μm wide (measured [2]). That is about 20 tubes: $0.2 \times 100 = 20$ (computed).

In the same beds no *Sinotubulites* shell is bored (measured [2]). The borings sit at a fairly uniform distance from the aperture, and their size varies (measured [2]). The authors record attack throughout prey growth after a minimum size (measured [2]).

The two *Cloudina* studies disagree on frequency, 2.7 % [1] against about 20 % [2]. They also disagree on hole size, 40–400 μm [1] against 15–85 μm [2]. Both values stand.

The hole diameters span 4×10^{-5} to 4×10^{-4} m in the first study, a factor of 10 (computed). In the second they span 1.5×10^{-5} to 8.5×10^{-5} m, a factor of 5.7 (computed: $85 / 15 = 5.67$).

Shell crushing. A review of Cambrian, and possibly Ediacaran, crushing, drilling and puncturing finds predation on shelled prey other than trilobites rarely documented (measured [3]). The oldest durophagy is shell damage on *Mobergella holsti* from Sweden (measured [3]). Most Cambrian drill and puncture holes are on brachiopods, and the drillers are largely unknown (measured [3]).

Parasitism. The oldest recorded parasitism is from the Lower Cambrian (Stage 4) Wulongqing Formation, Guanshan Konservat-Lagerstätte, eastern Yunnan (measured [4]). Tube-dwelling organisms encrust the brachiopod *Neobolus wulongqingensis* in a monospecific assemblage (measured [4]).

Of 429 specimens, 205 are infested and 224 uninfested (measured [4]). The infested share is $205 / 429 = 47.8 \%$ (computed). Encrustation gives a 26.08 % reduction in overall fitness, from ash-free dry weight estimated from shell size (measured [4]).

Tube orientation was measured on 146 individuals, 31 of them with a single tube (measured [4]). The tubes align with the host's feeding currents, and the authors record the interaction as kleptoparasitism (measured [4]).

A pentastomid from 425-Myr-old Silurian marine rocks is attached externally to an ostracod, near the host's eggs (measured [5]). It is the only fossil pentastomid associated with a host (measured [5]). Living pentastomids number about 140 species, all but four parasitic on vertebrates (measured [5]); $136 / 140 = 97 \%$ (computed).

Herbivory on land. The first arthropod herbivory dates to 417–403 Ma, and leaf margin feeding to 326 Ma (measured [6]). The first synapsid herbivore dates to about 307 Ma (measured [7]). At least five tetrapod herbivore origins occur by the Early Permian (measured [8]).

From the first arthropod to the first vertebrate herbivore is $417 - 307 = 110$ Myr (computed). From the younger end of the range it is $403 - 307 = 96$ Myr (computed).

Partners

Cambrian and Ordovician predators. *Anomalocaris canadensis* of the Burgess Shale (Cambrian, Miaolingian, Wuliuan) is one of the largest Cambrian animals (measured [9]). Large specimens have body-lobe widths of 60–70 mm (measured [9]).

Flow simulations of *Anomalocaris* 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 (modelled [9]). Its raptorial appendages are built for soft prey, not for crushing trilobites (measured [9]). One specimen carries a putative injury (measured [9]).

A redescription from all known specimens records stalked eyes, a triradial oral cone and a tail fan with a central blade and three pairs of lateral blades (measured [10]).

Aegiocassis benmoulae of the Early Ordovician Fezouata Biota, Morocco, is an anomalocaridid filter-feeder more than 2 m long (measured [11]). The source places the beginning of the Ordovician at around 490 million years ago (measured [11]).

Shell-breaking and drilling groups. The Mesozoic marine revolution is recorded in gastropod shells (measured [12]). Open coiling, planispiral coiling and umbilici are commoner in Palaeozoic and early Mesozoic gastropods (measured [12]). Strong sculpture, narrow apertures and apertural teeth occur mainly in post-Jurassic groups (measured [12]).

Shell sturdiness rises from the Early Cretaceous (measured [12]). The changes begin in the Jurassic and accelerate in the Cretaceous (measured [12]).

The predators that break or drill shells are listed with their origin and the onset of shell-breaking or drilling (measured [12]):

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 (computed from the table).

Prey. In the Cambrian, most drill and puncture holes are on brachiopods (measured [3]). In the Palaeozoic, drilling is recorded in brachiopods and sessile echinoderms (measured [13]).

From the Late Cretaceous on, gastropods drill molluscs frequently (measured [13]). Since the Permian, drilling frequencies are higher on molluscs than on co-occurring brachiopods (measured [14]).

Consumer and resource classes. A global food-web database holds 16,863 consumer-resource links (measured [15]). Body mass is measured directly in 13,085 of them and estimated from length in 3,778 (measured [15]); $13,085 + 3,778 = 16,863$ (computed).

After excluding parasites, unknown habitats and 53 outliers, 6,519 links were analysed (measured [15]). They comprise 5,156 predatory, 215 parasitoid, 930 herbivorous and 218 detritivorous links (measured [15]); the sum is 6,519 (computed). By habitat they are terrestrial 2,245, lake 1,214, stream 736 and marine 2,324 links (measured [15]); the sum is again 6,519 (computed).

Parasites among animals. Parasitism evolved independently at least 223 times in 15 animal phyla (measured [16]). That is $223 / 15 = 14.9$ origins per phylum on average (computed). Most origins lie in Arthropoda or below family level, and parasitism is almost absent from deuterostomes (measured [16]).

Parasitic groups do not differ from free-living relatives in speciation rate (measured [16]). The 10 largest parasitic clades hold about 90 % of described parasite species and perhaps 40 % of all animal species (measured [16]).

Parasites among plants. Haustorial parasitism evolved 12 times independently in flowering plants (measured [17]). It covers 292 genera and about 4,750 species (measured [17]).

Santalales hold 179 genera and 2,428 species, of which 2,312 are hemiparasitic, 45 holoparasitic and 71 autotrophic (measured [17]). The parts sum to 2,428 (computed). Orobanchaceae hold 102 genera and more than 2,100 species (measured [17]).

About 25 of the 292 genera are crop or forestry pathogens (measured [17]).

On a base of 295,383 accepted angiosperm species (measured [18]), parasitic plants are 4,750 / 295,383 = 1.6 % (computed).

Parasites of plants among nematodes. Plant-parasitic nematodes number about 4,100 species (measured [19]). That is about 25 % of about 16,000 terrestrial nematodes, in 4 independent clades (measured [19]).

Sizes

What	Size	Position	Source
Bore-hole diameter in <i>Cloudina</i> , smallest (study 1)	4×10^{-5} m	6.17	measured [1]
Bore-hole diameter in <i>Cloudina</i> , largest (study 1)	4×10^{-4} m	8.26	measured [1]
Boring width in <i>Cloudina</i> , smallest (study 2)	1.5×10^{-5} m	5.28	measured [2]
Boring width in <i>Cloudina</i> , largest (study 2)	8.5×10^{-5} m	6.85	measured [2]
Median drill-hole diameter, Ordovician	3.5×10^{-4} m	8.14	measured [14]
Median drill-hole diameter, Quaternary	3.25×10^{-3} m	10.17	measured [14]
<i>Anomalocaris</i> body-lobe width, large specimens, lower	0.060 m	12.83	measured [9]
<i>Anomalocaris</i> body-lobe width, large specimens, upper	0.070 m	12.97	measured [9]
<i>Aegirocassis</i> body length (more than)	2 m	16.02	measured [11]

The median drill hole widens by a factor of $3.25 / 0.35 = 9.3$ from the Ordovician to the Quaternary (computed). Over the same interval predator-prey size ratios rise 67-fold, while drilled prey size shows no Phanerozoic trend (measured [14]).

Body masses are given in the sources as masses, without lengths, and carry no position. The African savanna data cover five carnivores and about 27 prey species of 5–500 kg (measured [20]).

Times

What	Duration	Position	Source
Span of the species-level drilling database, Ediacaran to Holocene	550 Myr	67.19	measured [21]

Beginning of the Ordovician, as an age	490 Myr	67.08	measured [11]
Silurian pentastomid on an ostracod, as an age	425 Myr	66.95	measured [5]
First arthropod herbivory, older end, as an age	417 Myr	66.94	measured [6]
First arthropod herbivory, younger end, as an age	403 Myr	66.91	measured [6]
Leaf margin feeding, as an age	326 Myr	66.71	measured [6]
First synapsid herbivore, as an age	307 Myr	66.66	measured [7]
Gap in the drilling record, Late Triassic to Early Cretaceous	120 Myr	65.80	measured [13]
First arthropod to first vertebrate herbivore, from 417 Ma	110 Myr	65.72	computed
First arthropod to first vertebrate herbivore, from 403 Ma	96 Myr	65.60	computed
Helminth extinction-threat window, upper	100 yr	53.06	measured [22]
Helminth extinction-threat window, lower	50 yr	52.43	measured [22]
Aspen browsing record, 1997 to 2012	15 yr	51.34	computed from [23]
Aspen browsing record, 1998 to 2012	14 yr	51.27	computed from [23]
Serengeti grazing study, 1974 to 1979 inclusive	6 yr	50.50	computed from [24]
World fisheries reference period, 1988 to 1991 inclusive	4 yr = 1.26×10^8 s	50.13	computed from [25]

An age of A Myr is placed as a duration of $A \times 10^6 \times 3.15576 \times 10^7$ s.

Counts

Drilling frequency through the Phanerozoic. Drilling falls into three phases (measured [13]). In the Palaeozoic, latest Precambrian to Carboniferous, drilling is rare to moderately frequent, in brachiopods and sessile echinoderms (measured [13]).

In the Mesozoic, Permian to Early Cretaceous, drilling is very rare or facultative (measured [13]). In the Cenozoic, Late Cretaceous to Holocene, gastropod drilling of molluscs is frequent (measured [13]).

A species-level database of drillings and repair scars covers the Ediacaran to the Holocene (measured [26]). The frequency of predation traces rises notably by the

Ordovician, not in the mid-Palaeozoic (measured [26]). Predation intensity and global marine metazoan diversity correlate throughout the Phanerozoic, regardless of corrections (measured [26]).

The same database holds 196 papers and 2,291 species occurrences (measured [21]). Maximum drilling frequencies per species run as follows (measured [21]):

Interval	Maximum drilling frequency per species
Ediacaran-Silurian	10–20 %
Devonian-Mississippian	30–50 %
Permian-Triassic	species-level data scarce
Jurassic	~30 %
Quaternary	100 %

From the Jurassic the maximum rises steadily to 100 % in the Quaternary, and the minimum frequencies do not rise (measured [21]).

Single counts from the earlier record: fewer than 3 % of Silurian *Dicaelosia* brachiopods carry borings, and 19 % of juvenile *Nautilus pompilius* carry repaired injuries (measured [12]). Confamilial drill holes, predator on predator, increase in the Meso-Cenozoic (measured [14]).

Predator-prey body-mass ratios. The ratios are given as $\log_{10}$ of consumer mass over resource mass, as geometric means $\pm$ SE (measured [15]):

Consumer class	$\log_{10}$ ratio	n	Ratio (computed)
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	$10^{8.99} = 9.8 \times 10^8$
Aquatic detritivores	13.41 ± 0.18	218	$10^{13.41} = 2.6 \times 10^{13}$

About 80 % of predators are larger than their prey; medians were not reported (measured [15]).

By predator type and habitat the $\log_{10}$ ratios are as follows (measured [15]):

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 $10^{0.96} = 9.1$ (computed). Ectotherm vertebrates span $10^{2.08} = 120$ to $10^{4.15} = 1.4 \times 10^4$ (computed). Endotherm vertebrates span $10^{2.86} = 720$ to $10^{2.91} = 810$ (computed).

Predator and prey biomass. Predator biomass was set against prey biomass across 2,260 communities from 1,512 locations, drawn from more than 1,000 studies (measured [20]). The data cover large mammals, invertebrates, plants and plankton

(measured [20]). The exponents lie near $\frac{3}{4}$ (measured [20]):

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

Food-chain length. The 25 north-temperate lakes of one study range from 3.8×10^5 to $1.7 \times 10^{12} \text{ m}^3$ (measured [27]). Maximum trophic position is about 3.5 in the smallest and about 5 in the Laurentian Great Lakes (measured [27]).

The fit is $\text{MTP} = 2.51 + 0.2 \log_{10} \text{volume}$ ($r^2 = 0.80$, $P < 0.001$) (measured [27]).

The regression gives $2.51 + 0.2 \times 5.58 = 3.63$ for the smallest lake and $2.51 + 0.2 \times 12.23 = 4.96$ for the largest (computed). The volumes span $12.23 - 5.58 = 6.65$ orders of magnitude (computed).

Total phosphorus of $2.6\text{--}230 \mu\text{g l}^{-1}$ is not a significant predictor ($t = 0.59$, $P = 0.56$) (measured [27]). That range is $230 / 2.6 = 88$ -fold (computed). Volume and phosphorus are uncorrelated ($r = -0.21$) (measured [27]).

Across 219 lake, stream and marine ecosystems, $\delta^{15}\text{N}$ -based food-chain length is about 3.5 trophic levels in streams and about 4.0 in lakes (measured [28]). Including marine mammals lengthens marine chains by $\frac{2}{3}$ of a trophic level (measured [28]). Estimates span two full trophic levels within each ecosystem type (measured [28]).

The isotope estimates have similar means to connectance food webs, but less variance (measured [28]). At global scale they show weak or no relationship with ecosystem size, mean annual air temperature or latitude (measured [28]).

The two studies disagree at different scales. Ecosystem size sets food-chain length across 25 lakes [27]; across 219 systems the relation with size is weak or absent [28]. Both results stand.

Transfer efficiency. World fisheries for 1988–1991 had a mean reported catch of 94.3 million t in 39 species groups, plus 27 million t of discarded bycatch (measured [25]). Fractional trophic levels of the catch run from 1.0 (edible algae) to 4.2 (tunas), from 48 published trophic models of six aquatic ecosystem types (measured [25]).

The mean transfer efficiency between trophic levels is 10 %, re-estimated rather than assumed (measured [25]). Catches required 8.0 % of global aquatic primary production, nearly four times the previous estimate (measured [25]). The share is 2 % in the open ocean and 24–35 % in freshwater, upwelling and shelf systems (measured [25]).

A review of marine transfer efficiency gives biome ranges as low–mean–high (measured [29]):

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 (measured [29]). Another gives 5 % for upwelling, 10 % for temperate and 15 % for tropical systems (measured [29]). A third gives 14 % on average, with tropical values at 74 % of temperate values (measured [29]).

The second and third disagree on regional order, tropical highest against tropical lowest. Both orders stand.

At 10 % per step, the energy reaching trophic level n is $0.1^{(n-1)}$ of primary production (computed). Tuna at trophic level 4.2 receive $0.1^{3.2} = 6.3 \times 10^{-4}$ of it (computed). At 8 % and 14 % per step the shares are $0.08^{3.2} = 3.1 \times 10^{-4}$ and $0.14^{3.2} = 1.9 \times 10^{-3}$ (computed).

Metabolic scaling. Tested on 13 groups of animals, metabolism per unit surface is higher in larger animals (measured [30]). The unit of body size proposed for comparing metabolism is body weight to the $\frac{3}{4}$ power, $W^{3/4}$ (measured [30]).

A model of space-filling fractal branching networks yields the $\frac{3}{4}$ power for metabolic rate (modelled [31]).

For mammalian basal metabolic rate, 619 species in 19 orders cover five orders of magnitude of body mass (measured [32]). Corrected for body temperature, digestive state and phylogeny, BMR scales as $M^{2/3}$, with no support for $\frac{3}{4}$ (measured [32]).

The two exponents disagree: $\frac{3}{4}$ [30] and $\frac{2}{3}$ [32]. Both stand.

Across the major transitions, metabolic scaling is superlinear in prokaryotes, linear in protists and sublinear in metazoans (measured [33]). Kleiber's $\frac{3}{4}$ law is not universal (measured [33]). The scaling of maximum population growth rate is positive in prokaryotes and negative in protists and metazoans, and production efficiency declines across the three groups (measured [33]).

An earlier version gives exponents $b = 1.79$ for prokaryotes, 0.92 for eukaryotic unicells and 0.99 for all unicells ($R^2 = 0.94$) (measured [34]). The unicells span ten orders of magnitude of mass (measured [34]).

Herbivory. Across 44 aquatic sites, aquatic herbivores remove on average 51 % of annual primary production, three times more than terrestrial herbivores (measured

[35]). The terrestrial share is $51 / 3 = 17 \%$ (computed).

Herbivore biomass and herbivory rates scale with primary productivity at similar rates in water and on land (measured [35]). At a given productivity herbivore biomass is similar, and mass-specific herbivory is higher in water (measured [35]).

Across vascular plants, 5.3 % of the leaf tissue produced each year is eaten, over 1,058 species and 2,085 populations (measured [36]). Earlier estimates were up to 3.8 times higher (measured [36]). Woody species have 64 % higher leaf herbivory than non-woody species (measured [36]).

In the Serengeti in 1974–1979 herbivores consumed on average 0.66 of annual aboveground production, with a range of 0.15–0.94 (measured [24]). Grazing stimulated productivity at most sites (measured [24]).

In a compilation of aquatic and terrestrial plant communities, those with higher nutrient concentrations lose more production to herbivores (measured [37]). They channel less to detritus, decompose faster and store less carbon (measured [37]).

Insect herbivores number more than 1 million species and flowering plants more than 300,000 (measured [38]). The ratio is 3.3 (measured [38]).

Parasite counts. Helminths parasitising vertebrates number 75,000–300,000 species (measured [22]). There is no credible way to estimate the numbers of protozoan, fungal, bacterial or viral parasites (measured [22]).

About 75 % of food-web links involve parasitic species (measured [22]). Of helminths, 3–5 % are threatened with extinction within 50–100 years (measured [22]).

Parasites raise species richness, link number and food-chain length in food webs (measured [39]). After correction of a calculation error, parasites increase connectance, sometimes sharply (measured [39]). Mid-trophic levels are the most exposed to natural enemies, and parasitism is recorded as the most common animal lifestyle (measured [39]).

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 (modelled [40]). Up to 30 % of parasitic worms are committed when host coextinction is included (modelled [40]).

Order of events

Numeric ages are placed as durations. Ages given only as a period name have no position.

1. Late Precambrian (uppermost Neoproterozoic): bored *Cloudina* tubes, 2.7 % of more than 500 [1] or about 20 % of about 100 [2]; the oldest predation trace. No position.
2. Ediacaran–Silurian: maximum drilling frequency per species 10–20 % [21]. Database span 550 Myr, position 67.19 [21].
3. Cambrian: most drill and puncture holes on brachiopods; oldest durophagy on *Mobergella holsti* [3]. No position.

4. Early Cambrian Stage 4: kleptoparasitic tubes on 47.8 % of 429 *Neobolus* brachiopods; the oldest parasitism [4]. No position.
5. Cambrian, Wuliuan: *Anomalocaris*, apex predator of soft prey, lobe width 60–70 mm [9]. No position.
6. Ordovician, beginning around 490 Ma, position 67.08 [11]: predation traces rise notably by this period [26]; median drill hole 0.35 mm [14].
7. Early Ordovician: *Aegirocassis*, a radiodont filter-feeder more than 2 m long [11]. No position.
8. Late Ordovician: asteroides arise, breaking or drilling shells by then [12]. No position.
9. Silurian, 425 Ma, position 66.95: pentastomid attached to an ostracod [5].
10. 417–403 Ma, positions 66.94–66.91: first arthropod herbivory on land [6].
11. Devonian–Mississippian: maximum drilling 30–50 % [21]; lungfish break shells from the Devonian [12]. No position.
12. 326 Ma, position 66.71: leaf margin feeding [6].
13. About 307 Ma, position 66.66: first synapsid herbivore [7]; at least five tetrapod herbivore origins by the Early Permian [8].
14. Permian–Early Cretaceous: drilling very rare or facultative; a 120 Myr gap from the Late Triassic to the Early Cretaceous, position 65.80 [13].
15. Triassic: Naticacea and Teleostei arise [12]. No position.
16. Jurassic: five shell-breaking groups arise, crabs among them; maximum drilling about 30 % [12, 21]. No position.
17. Early Cretaceous to Campanian: sturdier gastropod shells; muricids arise in the Albian; naticids and muricids drill by the Campanian [12]. No position.
18. Latest Cretaceous–Paleocene: crabs and teleosts break shells; birds from the Late Eocene [12]. No position.
19. Late Cretaceous–Holocene: frequent gastropod drilling of molluscs [13]; maximum drilling 100 % in the Quaternary [21]; median drill hole 3.25 mm and predator-prey size ratio 67 times the Ordovician value [14]. No position.
20. 1995–1996: wolves return to Yellowstone; browsing on young aspen falls from about 90 % in 1997–1998 to 37–63 % by 2012, over 14–15 yr, positions 51.27–51.34 [23].

Present quantities

Global biomass. The living biomass of Earth totals about 550 Gt C (measured [41]). The kingdoms divide it as follows, with each estimate's uncertainty (measured [41]):

Group	Gt C	Uncertainty	Share of 550 (computed)
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 (computed).

Among animals the census gives, in Gt C (measured [41]):

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 $0.1 / 0.007 = 14$ -fold (computed). Humans and livestock together, 0.16 Gt C, outweigh wild mammals $0.16 / 0.007 = 23$ -fold (computed). They are $0.16 / 0.167 = 96$ % of mammal biomass (computed).

Land holds about 470 Gt C and the ocean about 6 Gt C, double a previous marine estimate (measured [41]). In the ocean about 1 Gt C of producers carries about 5 Gt C of consumers, an inverted standing pyramid (measured [41]). The consumer-to-producer ratio is 5 : 1 (computed).

Plants hold about 320 Gt C above ground and about 130 Gt C in roots (measured [41]); $320 + 130 = 450$ (computed).

Plant biomass is about twofold below its value before civilisation (measured [41]). Wild mammal biomass has fallen by a factor of about 6, about 7-fold on land and about 5-fold at sea (measured [41]). Human biomass is about an order of magnitude above that of all wild mammals (measured [41]).

Ocean size spectrum. 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 (measured [42]). Bacteria lie well above that value and whales well below (measured [42]). Human activity has truncated the upper one-third of the spectrum (measured [42]).

Fisheries. Reported catch and discarded bycatch total $94.3 + 27 = 121.3$ million t per year (computed from [25]). The catch needs 8.0 % of global aquatic primary production (measured [25]).

Parasite biomass. The three Pacific estuaries are Carpinteria Salt Marsh in California and Bahía San Quintín and Estero de Punta Banda in Baja California (measured [43]). In all three, trematode biomass exceeds winter bird biomass threefold to ninefold (measured [43]). Mean bird mass is 4.1 kg ha^{-1} in winter and 0.89 kg ha^{-1} in summer (measured [43]).

Parasites are 1.2 %, 0.9 % and 0.2 % of total animal biomass (measured [43]). Total

animal biomass is 925, 2,240 and 2,594 kg ha⁻¹ (measured [43]). Annual cercarial production is about three times the standing biomass of trematode parthenitae, and three to ten times winter bird biomass (measured [43]).

Pattern

The oldest predation trace is a hole in the oldest mineralised animal tube: 2.7 % of more than 500, or about 20 % of about 100. The oldest parasitism is Cambrian: 47.8 % of 429 brachiopods encrusted, fitness –26.08 %. Drilling runs in three phases with a 120 Myr gap.

Maximum drilling frequency rises from 10–20 % to 100 %; the minimum stays low. Drill holes widen 9.3-fold and predator–prey size ratios 67-fold, while drilled prey size shows no Phanerozoic trend. Eleven of 13 shell-breaking groups arise in the Triassic–Cretaceous.

Predators average 42 times their prey's mass; parasitoids 0.76 times their host's. Predator biomass scales with prey biomass at 0.71–0.74, as production does with biomass (0.67–0.76). Mean transfer is 10 %, single systems 0.3–52 %, and chains are 3.5–5 levels long.

Parasitism arose at least 223 times in animals and 12 times in flowering plants. Plants outweigh animals 225 to 1.

Not verified

- *Anomalocaris* body length about 0.61 m and age about 508 Myr (press release; secondary).
- *Aegirocassis* age about 480 Myr; radiodonts from about 520 Ma (university news; secondary).
- *Aegirocassis* / *Anomalocaris* size ratio 3.3 (rests on a secondary length).
- Guanshan kleptoparasite age about 512 Ma (authors' blog; secondary).
- Lindeman 1942 efficiency values and Cedar Bog Lake sampling (V-bib; secondary).
- Post 2002 review of food-chain length (V-bib).
- Marine mean food-chain length in Vander Zanden & Fetzer 2007 (UNVERIFIED).
- Cebrian 1999 herbivory percentages (UNVERIFIED).
- Metabolic exponents 1.72–1.96, ~1 and ~0.76 attributed to DeLong 2010 (secondary).
- Ocean spectrum of 23 orders; whales –90 %; fish and marine mammals –2 Gt, –60 % (press release; secondary).
- Estuary species counts 199, 15 and 138; parasites above top predators by up to 20-fold (news release; secondary).
- Per-site parasite biomass 11, 20 and 5.2 kg ha⁻¹ (site order unconfirmed).
- Drilling frequencies in the Huntley & Kowalewski 2007 PNAS paper itself.
- Species name of the Silurian pentastomid.
- Generation times of predators and prey.

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A8 Flowers, Fruit and Animals

What it is

Flowering plants and animals are linked in three ways. Animals carry pollen between flowers, carry seeds away from the parent plant, and eat plant tissue. The first two are mutualisms; the third is herbivory, met by plant defences.

This chapter treats these links as one web of plant-animal interactions. It gives the dates of the partners, the counts on each side, the structure of the networks they form and the measured effects of losing partners.

First appearance

Insects and flowering plants. *Rhyniognatha*, described as the oldest insect fossil, is Pragian: 396–407 Ma in the original paper, 410.8–407.6 Ma on the 2023 chart (measured [1]). A reinterpretation of new remains reads it as a myriapod, "possibly as a centipede", not an insect [2]. Both readings are recorded.

The molecular origin of insects is about 479 Ma, and insect flight about 406 Ma (measured [3]).

The main angiosperm clades diversified 135–130 Ma (measured [4]). From the *Rhyniognatha* fossil on the 2023 chart to the angiosperm clades is $410.8 - 135 = 275.8$ to $407.6 - 130 = 277.6$ Myr, about 276 Myr (computed from [1, 4]). From the molecular

age the gap is $479 - 135 = 344$ Myr (computed).

Herbivory before flowers. Herbivory appears twice before flowers, at 417–403 Ma and at 327–309 Ma (measured [5]). Leaves are first eaten at 326 Ma (measured [5]). Tissues are first eaten 0–20 Myr after they arise in the first phase and 54–98 Myr after in the second (measured [5]).

The first vertebrate herbivore, *Melanedaphodon*, dates to about 307 Ma (measured [6]). Tetrapod herbivory arises at least five times in the Late Carboniferous to Early Permian (measured [7]). From the first arthropod to the first vertebrate herbivore is $417 - 307 = 110$ Myr (computed).

Pollination before flowers. The oldest definitive pollinators visit gymnosperms, at about 165 Ma (measured [8]). They are 11 long-proboscid scorpionfly species spread over 62 Myr (measured [8]). Four gymnosperm pollination modes exist before angiosperms dominate (measured [9]).

The tube-like proboscis of Lepidoptera dates to about 241 Ma (measured [10]). The first beetle pollinator dates to 105 Ma (measured [9]).

Pollination of flowers. Eudicot pollen on a beetle dates to 99 Ma (measured [11]). The oldest bee is about 100 Ma (measured [12]). Crown bees date to 123 Ma, with a range of 113–132 Ma (measured [13]).

Seeds and their eaters. The first seeds are late Middle or Late Devonian (measured [14]). Pennsylvanian medullosan seed ferns had fleshy seeds of 20,000–50,000 mm³ (measured [14]). Plant-eating vertebrates first diversify in the Permian (measured [14]).

A Late Permian *Protorosaurus* holds about 60 seeds in its gut (measured [14]). An Early Cretaceous ankylosaur gut holds fruits of 4.5 mm and seeds of 0.3 mm (measured [14]).

The Pennsylvanian ends at 298.9 Ma [15]. Angiosperm fleshy-fruit diversification begins at about 80 Ma [16]. From the Pennsylvanian fleshy seeds to that onset is at least $298.9 - 80 = 218.9$ Myr, about 220 Myr (computed from [14, 16, 15]).

Fleshy fruit. Angiosperm fleshy fruits diversify from about 80 Ma, peak at 55–50 Ma and shift at about 34 Ma (measured [16]). Disperser radiations follow (measured [17, 18, 19, 20]).

Neoaves split into 36 lineages within 10–15 Myr after the K–Pg boundary at 66 Ma (measured [17]). The oldest known primate skeleton dates to about 55 Ma (measured [18]).

The oldest bats are Early Eocene, 56.0–47.8 Ma on the time scale (measured [19, 15]). Crown Old World fruit bats date to 31–20 Ma (measured [20]).

Partners

Pollinators. Known pollinator species number 349,368, about 350,000 (measured [21]). By group they are as follows (measured [21]):

Pollinator group	Species
Lepidoptera	141,600

Beetles	77,300
Hymenoptera (as listed beside bees)	70,000
Flies	55,000
Bees	17,000
Thrips	1,500
Birds	1,089 (hummingbirds 365)
Mammals	344 (bats 236)
Lizards	37

Vertebrate pollinators number $1,089 + 344 + 37 = 1,470$, which is 0.42 % of 349,368 (computed). Known pollinators per angiosperm species are $349,368 / 295,383 = 1.18$ (computed).

A review of nectar feeding gives about 360 hummingbird species (measured [22]). The two hummingbird counts, 365 [21] and about 360 [22], agree within 1.4 % (computed).

Animal-pollinated plants. Accepted angiosperms number 295,383 species (measured [23]). Two estimates of the animal-pollinated share disagree.

The first gives 87.5 %, or 308,006 of about 352,000 species (measured [24]). Community means are 78 % in temperate and 94 % in tropical communities (measured [24]).

The second gives about 90 % (measured [25]). On the GBIF list, 33,623 of 332,341 species are abiotically pollinated and 296 both (measured [25]). On the WFO list, 32,129 of 339,876 are abiotic and 267 both (measured [25]).

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 (computed). Recalculated with weighting by sample size and latitude, the first estimate rises from 87.5 % to 89.5 % (measured [25]). Both estimates stand.

About 88 % of genera are exclusively animal-pollinated (measured [25]). GBIF counts 14,437 genera with 1,573 abiotic and 88 mixed; WFO counts 13,772 with 1,548 and 90 (measured [25]). For families the share is 67 % on GBIF (465 surveyed, 105 abiotic) and 64 % on WFO (414 surveyed, 103 abiotic) (measured [25]).

Bat-pollinated plants. About 528 angiosperm species in 67 families and 28 orders are bat-pollinated (measured [26]). Bat pollination arose independently many times, from insect, bird and non-flying-mammal pollination (measured [26]). Bats carry large pollen loads over long distances (measured [26]).

Bat-pollinated species are $528 / 295,383 = 0.18$ % of angiosperms (computed). There are $528 / 236 = 2.2$ bat-pollinated plant species per pollinating bat species (computed).

Obligate pairs. Obligate pollination pairs recur at least five times (measured [27, 28, 29, 30, 31]):

Pair	Count or date
Figs and fig wasps	750 or 874 <i>Ficus</i> species; at least 60 Myr of co-divergence
Yuccas and yucca moths	moths $41.5 + 9.8$ Ma

PLANT AND YUCCA BEES	BEES AND ORCHIDS
Perfume orchids and orchid bees	bees 34–38 Ma; orchids 18–27 Ma, 3 origins
Darwin's orchid and its hawkmoth	about 7.5 Ma
Ants and cultivated fungi	ant agriculture 61–57 Ma

Sources for the rows, in order: figs [27], yucca [28], orchid bees [29], Darwin's orchid [30], ant agriculture [31]. Each pair is about 7.5 to at least 60 Myr old, with the insect side dated first or together with the plant (measured [27, 28, 29, 30, 31]).

Seed dispersers. Among angiosperms, 30 % of families are biotically dispersed and a further 22 % both biotically and abiotically (measured [14]). Among species the shares are 14 % and a further 42 % (measured [14]). Among gymnosperms they are 64 % of families and 46 % of species, plus 39 % of species both (measured [14]).

Of 8,918 terrestrial bird species, 1,230 are frugivores, 13.8 % (measured [32]). Of these, 365 are obligate frugivores, and passerines make up 50 % of frugivores (measured [32]). More than 275 fish species are frugivorous (measured [33]).

A global seed-ingestion dataset holds 13,135 animal × seed interactions across fish, amphibians, reptiles, birds and mammals (measured [34]). In Costa Rica, 83.5 % of 240 tropical canopy tree species are animal-dispersed (measured [35]).

Ant dispersal. At least 11,000 plant species are ant-dispersed, 4.5 % of angiosperms, in 334 genera and 77 families (measured [36]). Ant dispersal has at least 101 independent origins, possibly 147 (measured [36]).

Ant-dispersed lineages have 2.24 times the species of their sister groups, in 68 of 101 contrasts (measured [37]). Typical ant dispersal distance is about 1 m, with a range of 0.01–77 m (measured [37]).

Herbivores and defences. Plants hold more than 100,000 secondary metabolites (measured [38]). Alkaloids number 12,000–27,000, glucosinolates 150 and cyanogenic glucosides 60 (measured [38, 39]). Terpene synthase genes number 1 in a moss, 18 in a lycophyte and 40–152 in model seed-plant genomes (measured [40]).

Insect herbivores number more than 1 million species and flowering plants more than 300,000, a ratio of 3.3 : 1 (measured [41]). Specialists predominate among more than 7,500 insect herbivore species (measured [42]).

Plant structures that feed or house animal defenders recur. Extrafloral nectaries occur in 3,941 species with at least 457 origins (measured [43]). Ant domatia occur in 681 species with at least 158 origins within 19 Myr (measured [44]).

Spines arose at least 55 times within 17 Myr, with bovids in Africa from 16 Ma (measured [45]). The Pierid protein that detoxifies glucosinolates arises within about 10 Myr after the host order Brassicales (measured [46]). High-crowned teeth in equids arise at least 4 Myr after grass-dominated habitats (measured [47]).

Sizes

What	Size	Position	Source
Seed in an Early Cretaceous ankylosaur	3×10^{-4} m	8.00	measured [14]

gut			
Fruit in an Early Cretaceous ankylosaur gut	4.5×10^{-3} m	10.47	measured [14]
Ant dispersal distance, shortest	0.01 m	11.19	measured [37]
Ant dispersal distance, typical	1 m	15.39	measured [37]
Ant dispersal distance, longest	77 m	19.34	measured [37]
Small passerines, distance within which 50 % of seeds fall	51 m	18.97	measured [48]
Medium-sized birds, dispersal distance (more than)	110 m	19.66	measured [48]
Carnivorous mammals, dispersal distance (more than)	495 m	21.03	measured [48]
Forest elephants, median dispersal distance	5,300 m	23.19	measured [49]
Forest elephants, maximum dispersal distance	101,000 m	25.87	measured [49]
Elevation above which highland pollination networks lie	1,500 m	22.04	measured [50]

The Pennsylvanian fleshy seeds of 20,000–50,000 mm³ are given as volumes, without a length, and carry no position (measured [14]).

Vertebrate dispersal distances exceed the typical ant distance by $51 / 1 = 51$ (passerines) to $5,300 / 1 = 5,300$ (elephants) (computed). The maximum elephant distance exceeds the maximum ant distance by $101,000 / 77 = 1,312$ (computed).

Times

What	Duration	Position	Source
Molecular origin of insects, as an age	479 Myr	67.06	measured [3]
First arthropod herbivory, older end, as an age	417 Myr	66.94	measured [5]
Oldest insect fossil, older end (2023 chart), as an age	410.8 Myr	66.92	measured [1]
Oldest insect fossil, younger end (2023 chart), as an age	407.6 Myr	66.92	measured [1]
Oldest insect fossil,	407 Myr	66.92	measured [1]

older end (paper), as an age			
Oldest insect fossil, younger end (paper), as an age	396 Myr	66.89	measured [1]
Insect flight, as an age	406 Myr	66.91	measured [3]
First arthropod herbivory, younger end, as an age	403 Myr	66.91	measured [5]
Second herbivory phase, older end, as an age	327 Myr	66.72	measured [5]
First leaf feeding, as an age	326 Myr	66.71	measured [5]
Second herbivory phase, younger end, as an age	309 Myr	66.66	measured [5]
First vertebrate herbivore, as an age	307 Myr	66.66	measured [6]
Lepidopteran proboscis, as an age	241 Myr	66.44	measured [10]
Oldest definitive pollinators on gymnosperms, as an age	165 Myr	66.09	measured [8]
Main angiosperm clades, older end, as an age	135 Myr	65.91	measured [4]
Main angiosperm clades, younger end, as an age	130 Myr	65.88	measured [4]
Crown bees, older bound, as an age	132 Myr	65.89	measured [13]
Crown bees, as an age	123 Myr	65.83	measured [13]
Crown bees, younger bound, as an age	113 Myr	65.75	measured [13]
First beetle pollinator, as an age	105 Myr	65.68	measured [9]
Oldest bee, as an age	100 Myr	65.64	measured [12]
Eudicot pollen on a beetle, as an age	99 Myr	65.63	measured [11]
Onset of fleshy-fruit diversification, as an age	80 Myr	65.43	measured [16]
K-Pg boundary, as an age	66 Myr	65.26	measured [17]
Ant agriculture, older end, as an age	61 Myr	65.19	measured [31]
Ant agriculture, younger end, as an age	57 Myr	65.13	measured [31]
Oldest bats, older end, as an age	56 Myr	65.11	measured [19, 15]

Oldest primate skeleton, as an age	55 Myr	65.09	measured [18]
Fleshy-fruit peak, older end, as an age	55 Myr	65.09	measured [16]
Yucca moths, upper bound (41.5 + 9.8), as an age	51.3 Myr	65.03	computed from [28]
Fleshy-fruit peak, younger end, as an age	50 Myr	65.01	measured [16]
Oldest bats, younger end, as an age	48 Myr	64.97	measured [19, 15]
Yucca moths, as an age	41.5 Myr	64.84	measured [28]
Orchid bees, older end, as an age	38 Myr	64.76	measured [29]
Orchid bees, younger end; fleshy-fruit shift, as an age	34 Myr	64.66	measured [29, 16]
Yucca moths, lower bound (41.5 – 9.8), as an age	31.7 Myr	64.59	computed from [28]
Crown Old World fruit bats, older end, as an age	31 Myr	64.57	measured [20]
Perfume orchids, older end, as an age	27 Myr	64.45	measured [29]
Crown Old World fruit bats, younger end, as an age	20 Myr	64.17	measured [20]
Perfume orchids, younger end, as an age	18 Myr	64.08	measured [29]
Bovids in Africa, as an age	16 Myr	63.97	measured [45]
Darwin's orchid and hawkmoth, as an age	7.5 Myr	63.28	measured [30]
<i>Rhyniognatha</i> (2023 chart) to angiosperm clades	275.8–277.6 Myr	66.56–66.57	computed from [1, 4]
Pennsylvanian fleshy seeds to fleshy-fruit diversification (at least)	218.9 Myr	66.35	computed from [14, 15, 16]
Plant tissue to first eater, second phase, longest	98 Myr	65.62	measured [5]
Scorpionfly pollinator species, time span	62 Myr	65.20	measured [8]
Fig-wasp co-divergence (at least)	60 Myr	65.17	measured [27]
Plant tissue to first eater, second phase, shortest	54 Myr	65.08	measured [5]

Plant tissue to first eater, first phase, longest	20 Myr	64.17	measured [5]
Domatia origins, time window	19 Myr	64.13	measured [44]
Spine origins, time window	17 Myr	64.02	measured [45]
Neoaves radiation, upper	15 Myr	63.91	measured [17]
Neoaves radiation, lower; Pierid lag after Brassicales	10 Myr	63.54	measured [17, 46]
Obligate pair, youngest	about 7.5 Myr	63.28	measured [30]
Hypsodonty after grasslands (at least)	4 Myr	62.71	measured [47]
Megafauna loss, older end	15 kyr	57.62	measured [51]
Megafauna loss, younger end	10 kyr	57.25	measured [51]
Elephant gut passage	39.5 h = 142,200 s	43.95	measured [49]
Passerine gut passage, upper	30 min = 1,800 s	39.98	measured [52]
Passerine gut passage, lower	5 min = 300 s	38.34	measured [52]

An age of A Myr is placed as a duration of $A \times 10^6 \times 3.15576 \times 10^7$ s.

Counts

Vertebrate pollination and plant reproduction. A meta-analysis covers 126 exclusion experiments in 69 articles on 90 plant species (measured [53]). Excluding vertebrate pollinators reduces fruit or seed production by 63 % on average (measured [53]).

The loss is 84 % with bats in the abstract and 83 % in the results, and 46 % with birds (measured [53]). It is 71 % in the tropics and 45 % at extra-tropical latitudes (measured [53]).

Pollinating birds and mammals show a deteriorating Red List Index, with more species moving toward extinction than away (measured [54]). On average 2.5 species per year moved one Red List category toward extinction in recent decades (measured [54]).

Nestedness. One study compares 52 mutualistic networks, 27 of seed dispersal and 25 of pollination, with 14 bipartite resource-consumer food webs (measured [55]). Each matrix was tested against 50 random networks under two null models; 6 of the 52 change status between models (measured [55]).

Set	Network size (plant + animal species)	Nestedness N, range	Mean N $\pm$ SE	Significantly nested
Seed dispersal	9–317	0.565–0.999	0.844 $\pm$ 0.043	19 of 27
Pollination	22–416	0.564–0.975	0.858 $\pm$ 0.047	22 of 25

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 [55]. The nested shares are $19 / 27 = 70.4 \%$, $20 / 25 = 80.0 \%$ and $39 / 52 = 75.0 \%$ (computed).

Every seed-dispersal network with at least 28 species and every pollination network with at least 50 species is nested (measured [55]). Specialists interact with subsets of the partners of generalists, forming a cohesive core (measured [55]). The networks are neither random nor compartmentalised (measured [55]).

Degree distributions. The set holds 29 plant-pollinator and 24 plant-frugivore networks, $29 + 24 = 53$ in all (computed). Of these, 65.6 % have connectivity distributions that follow a truncated or broad-scale power law (measured [56]). Another 22.2 % are scale-invariant, following a pure power law (measured [56]).

The deviations are attributed in the source to morphological mismatch and phenological uncoupling, termed forbidden links (measured [56]).

Connectance. In 29 complete plant-pollinator networks from arctic to tropical sites, connectance falls exponentially with richness (measured [50]). The fit is $C = 13.83 \exp[-0.003 (A + P)]$, with A animal and P plant species (measured [50]).

Taking C in per cent, a network of 100 species has $13.83 \times e^{-0.3} = 10.2 \%$ connectance (computed). At 500 species the value is 3.1 %, and at 1,000 species 0.69 % (computed).

Highland networks above 1,500 m have lower connectance than lowland networks (measured [50]). Oceanic islands are poorer in pollinators and more specialised; tropical plants are not more specialised (measured [50]).

Modularity. Fifty-one pollination networks with about 10,000 species and about 20,000 links were analysed by simulated annealing (measured [57]). That is $10,000 / 51 = 196$ species and $20,000 / 51 = 392$ links per network on average (computed).

All networks with more than 150 plant and pollinator species are modular, and networks with fewer than 50 species are never modular (measured [57]). Module number and size rise with network size, and each module holds one or a few convergent trait sets (measured [57]). Only 15 % of all species are structurally important to their network, as hubs, connectors or both (measured [57]).

Stability. In models, highly connected nested architectures favour stability in mutualistic networks (modelled [58]). Compartmentalised, weakly connected architectures favour stability in trophic networks (modelled [58]). A meta-analysis of large pollination and herbivory networks supports this split (measured [58]).

Network sizes. Two well-sampled pollination networks give these counts (measured [59]):

Network	Plants	Animals	Links
Robertson, Illinois	456	1,428 (1,430 in results)	15,265
Clements & Long, Colorado	97	275	918

For Robertson, animals outnumber plants $1,428 / 456 = 3.13$ to 1 (computed). Links per species are $15,265 / 1,884 = 8.1$, and connectance is $15,265 / (456 \times 1,428) = 2.3$ % (computed).

For Clements & Long, the ratio is $275 / 97 = 2.84$ (computed). Links per species are $918 / 372 = 2.5$, and connectance is $918 / (97 \times 275) = 3.4$ % (computed). The source gives pollinators outnumbering plants by about 3 : 1 (measured [59]).

Removal of pollinators. Simulated removals were run on the same two networks (modelled [59]). With pollinators removed at random, plant species are lost only after 70-80 % of pollinators are gone (modelled [59]).

With the most-linked pollinators removed first, plant loss is roughly linear, “no worse than linear” (modelled [59]). In Robertson, plants are nearly unaffected until the last ten most generalised pollinators, fewer than 1 % of animal species, are removed (modelled [59]).

In Robertson 11 % and in Clements & Long 18 % of plant species have a single visitor species (measured [59]). Removing species of both sets by linkage collapses the networks after the top 22 % (Robertson) and 21 % (Clements & Long) of species (modelled [59]).

Coextinction. A probabilistic model covers 20 affiliate-host systems, among them fig wasps and figs, parasites and hosts, and butterflies and host plants (modelled [60]). It gives 6,300 affiliate species coendangered with hosts listed as critically endangered, endangered or vulnerable (modelled [60]).

At least 200 affiliate species are historically extinct with their hosts in the groups studied (measured [60]). The army ant *Eciton burchelli* hosts at least 100 affiliate species (measured [60]). The nomographic and probabilistic models agree, $R_c \approx 0.99$ (modelled [60]).

Coextinction may be the most common form of biodiversity loss in models, yet few historical or current cases are recorded (measured [61]). Of 457 parasite species modelled from 53,133 occurrences in 8 clades, 5-10 % are committed to extinction by 2070 from climate alone (modelled [62]). Up to 30 % of parasitic worms are committed when host coextinction is included (modelled [62]).

On virtual Earths driven to total extinction by heating or cooling, ecological dependencies amplify direct environmental effects on the collapse of diversity by up to ten times (modelled [63]).

Defaunation and dispersal. 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 (modelled [64]). Megafauna loss at 10-15 kyr contracted long-distance seed dispersal by at least two-thirds (measured [51]). Land nutrient transport fell to about 8 % of its former value (measured [65]).

Order of events

Numeric ages are placed as durations. Ages given only as a period name have no position.

1. About 479 Ma (molecular), position 67.06: insects [3].
2. 417–403 Ma, positions 66.94–66.91: first arthropod herbivory, on spores and stems [5].
3. 410.8–407.6 Ma (2023 chart) or 396–407 Ma (paper), positions 66.92 and 66.89–66.92: *Rhyniognatha*, described as the oldest insect fossil [1]; read as a myriapod in a reinterpretation [2].
4. About 406 Ma (molecular), position 66.91: insect flight [3].
5. Late Middle or Late Devonian: first seeds [14]. No position.
6. 327–309 Ma, positions 66.72–66.66: second herbivory phase; leaves eaten from 326 Ma, position 66.71 [5].
7. Pennsylvanian: fleshy seeds of 20,000–50,000 mm³ [14]. No position.
8. About 307 Ma, position 66.66: first vertebrate herbivore [6]; at least five tetrapod herbivore origins in the Late Carboniferous–Early Permian, no position [7].
9. Permian: plant-eating vertebrates diversify; Late Permian reptile with about 60 seeds in the gut [14]. No position.
10. About 241 Ma, position 66.44: lepidopteran proboscis [10].
11. About 165 Ma, position 66.09: first definitive pollinators, on gymnosperms [8].
12. 135–130 Ma, positions 65.91–65.88: main angiosperm clades diversify [4].
13. 123 Ma (113–132), position 65.83: crown bees [13].
14. Early Cretaceous: ankylosaur gut with fruits of 4.5 mm and seeds of 0.3 mm [14]. No position.
15. 105 Ma, position 65.68: first beetle pollinator [9].
16. About 100 Ma, position 65.64: oldest bee [12]; 99 Ma, position 65.63: eudicot pollen on a beetle [11].
17. About 80 Ma, position 65.43: fleshy-fruit diversification begins [16].
18. 66 Ma, position 65.26: K-Pg boundary; Neoaves form 36 lineages within the next 10–15 Myr [17].
19. 61–57 Ma, positions 65.19–65.13: ant agriculture [31].
20. 56.0–47.8 Ma, positions 65.11–64.97: oldest bats [19, 15]; about 55 Ma, position 65.09: oldest primate skeleton [18]; 55–50 Ma: fleshy-fruit peak [16].
21. 41.5 ± 9.8 Ma, position 64.84: yucca moths [28].
22. 38–34 Ma, positions 64.76–64.66: orchid bees [29]; about 34 Ma: fleshy-fruit shift [16].
23. 31–20 Ma, positions 64.57–64.17: crown Old World fruit bats [20].
24. 27–18 Ma, positions 64.45–64.08: perfume orchids, 3 origins [29].
25. Within 17 Myr, from 16 Ma, position 63.97: spines arise at least 55 times while bovids enter Africa [45].
26. About 7.5 Ma, position 63.28: Darwin’s orchid and its hawkmoth [30].
27. 15–10 kyr, positions 57.62–57.25: megafauna loss; long-distance dispersal down by at least two-thirds [51].
28. Recent decades: bird and mammal pollinators move toward extinction at 2.5 species per year [54]; defaunation halves climate-tracking dispersal [64]. No position.
29. To 2070, projected: 5–10 % of parasites committed to extinction, up to 30 % with coextinction [62]. No position.

Present quantities

Animal pollination. About 87.5 % [24] or about 90 % [25] of flowering plant species are animal-pollinated. About 350,000 known animal species pollinate them, 1.18 per plant species (measured [21]; computed).

Dependence. Plants lose 63 % of fruit or seed set when vertebrate pollinators are excluded (measured [53]). Bat-pollinated plants lose 83–84 % and bird-pollinated plants 46 % (measured [53]).

Dispersal. Of tropical canopy trees in Costa Rica, 83.5 % are animal-dispersed (measured [35]). Of terrestrial birds, 13.8 % eat fruit (measured [32]).

Herbivory. Herbivores eat 5.3 % of the leaf tissue produced each year, over 1,058 species (measured [66]). Aquatic herbivores remove 51 % of production (measured [67]).

At the Paleocene–Eocene Thermal Maximum the share of damaged fossil leaves rose from 37.8 % to 57.3 % with a 4.4 °C rise in mean annual temperature (measured [68]). The rise is $57.3 - 37.8 = 19.5$ percentage points (computed).

Networks. The largest single network recorded here holds 456 plants and 1,428 pollinators with 15,265 links, at 2.3 % connectance (measured [59]; computed). Three-quarters of 52 mutualistic networks are nested (measured [55]; computed).

Losses. Coextinction models give 6,300 coendangered affiliates and at least 200 recorded coextinctions in 20 systems (measured and modelled [60]). Climate-tracking dispersal has fallen by more than half (modelled [64]).

Pattern

The *Rhyniognatha* fossil precedes the angiosperm clades by about 276 Myr, and herbivory precedes flowers twice. Pollination is recorded on gymnosperms at about 165 Ma and on angiosperms from 100–99 Ma. Pennsylvanian fleshy seeds precede angiosperm fleshy-fruit diversification by at least 218.9 Myr; disperser radiations follow fleshy fruit from 66 Ma on.

About 87.5–90 % of 295,383 angiosperm species are animal-pollinated by about 350,000 pollinator species. Vertebrates are 0.42 % of pollinators; excluding them cuts seed set by 63 %. Dispersal distance runs from 1 m (ants) to 5.3 km (elephants).

Three-quarters of 52 mutualistic networks are nested; networks above 150 species are always modular, below 50 never. Connectance is 2.3 % in the Robertson network (1,884 species) and 3.4 % in the Clements & Long network (372 species).

Plants survive random loss of 70–80 % of pollinators in simulation. Coextinction estimates reach 6,300 affiliates.

Not verified

- About 7,000 Neotropical hummingbird-pollinated plant species, 129 ornithophilous North American species, a fourth of 900 *Salvia* species (Wikipedia; secondary).
- More than 920 bird pollinator species (Whelan 2008 via Ratto 2018; secondary); it disagrees with 1,089 [21].

- Birds pollinating 5.4 % of 960 crops, 52 species; at least 85 plants pollinated by non-flying mammals (cited in Ratto 2018; secondary).
- Number of bird and mammal pollinators assessed by Regan 2015.
- Network counts in Thébaud & Fontaine 2010.
- The interaction equation $\ln I = 0.575 + 0.61 M$ of Olesen & Jordano 2002 (whether M is logged not legible).
- Food webs significantly nested, 4 of 14 (a reading of Bascompte 2003 Table 1; secondary).
- Thousands of past coextinctions, hundreds of thousands to come (ScienceDaily on Dunn 2009; secondary).
- Climate-tracking dispersal down 60 %, regionally 95 % (Rice University news on Fricke 2022; secondary).
- Number of ant species that disperse seeds.
- Number of origins of vertebrate seed dispersal.
- The Ratto-cited primaries: Kunz 2011, Whelan 2008, Carthew & Goldingay 1997.

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A9 The Cycles Across Kingdoms

What it is

An element cycle passes one element between organisms and the environment. In each cycle measured here, bacteria, archaea, algae, plants, fungi and animals each carry one step. The element then passes to another domain or kingdom.

Six lines are recorded: carbon, nitrogen, phosphorus, sulphur, oxygen, and transport by animals. Values are global unless a site is named.

Global NPP (net primary production) is 104.9 Pg C/yr, with land and ocean roughly

equal (measured [1]). Terrestrial biomass lies about two orders of magnitude above marine biomass (measured [2]). Plant biomass against marine biota, 450 against 6 Gt C (measured [2]), is 75-fold (computed).

First appearance

Sulphate reduction is the oldest dated step. Barites about 3.47 Gyr old from North Pole, Australia, give a maximum $\Delta^{34}\text{S}$ of 21.1 ‰ and a mean of about 11.6 ‰ (measured [3]). The authors read this as microbial sulphate reduction, extending its record back by more than 750 Myr (measured [3]).

Biological N_2 fixation follows. Sedimentary rocks 3.2–2.75 Gyr old carry a mean $\delta^{15}\text{N}$ of 0.0 ± 1.2 ‰, read as fixation, most probably by Mo-nitrogenase (measured [4]). The minimum age is 3.2 Gyr (measured [4]).

A molecular clock gives roughly 1.5–2.2 Ga for nitrogenase (measured [5]). The isotope minimum and the clock differ by 1.0–1.7 Gyr (computed). Both are recorded.

Free oxygen comes next. One record places permanent atmospheric O_2 at about 2.33 Ga, with a transition within roughly 1–10 Myr (measured [6]). A second places the onset at 2.460–2.426 Ga, followed by about 200 Myr of oscillation (measured [7]).

Both dates are recorded. The Great Oxidation Event significantly predates modern Cyanobacteria (measured [8]). An oxygenated ocean follows at about 635–630 Ma, and land plants at about 470 Ma (measured [9]; [10]).

Calcifying algae appear in the Late Triassic, 237–201 Ma (measured [11]). The first calcifiers were probably calcareous dinoflagellates, about 233 Ma; coccolithophores follow at about 215–210 Ma (measured [11]).

Molecular clocks place the diatom origin near the Triassic–Jurassic boundary, about 200 Ma (measured [12]). Lower Jurassic *Pyxidicula*, about 182 Ma, is reinterpreted as most likely calcareous nannofossils (measured [12]). The Middle Jurassic species, 174–163 Ma, are reassigned to the Lower Cretaceous as a likely testate amoeba (measured [12]).

Without *Pyxidicula*, the gap from origin to the oldest abundant record is 75 Myr (measured [12]). That record lies at $200 - 75 = 125$ Ma (computed).

On land, a phylogeny places a single origin of the predisposition to root nodules slightly over 100 Ma, position 65.64 (measured [13]; position computed).

Partners

Carbon

Primary producers on land are plants. Terrestrial gross primary production is about 150 Pg C/yr, with C3 plants about 115 and C4 plants 35.3 (measured [14]).

A second estimate, from transpiration and water-use efficiency, gives 129 ± 32 Gt C/yr (measured [15]). Both figures are recorded.

At sea, the producers are algae and cyanobacteria. Bacteria in the sea use about 10–50 % of the carbon fixed by photosynthesis (measured [16]). Free-living bacteria are

grazed by heterotrophic nanoflagellates, which are eaten by microzooplankton (measured [16]).

Flagellates and microzooplankton overlap in size with phytoplankton (measured [16]). The source states that energy returns from this “microbial loop” to the classical food chain (measured [16]). The named steps run: dissolved organic matter → bacteria → heterotrophic nanoflagellates → microzooplankton → classical food chain (measured [16]).

The steps pass four domains or kingdoms: algae, bacteria, protists and animals (counted from [16]).

Diatoms account for about 40 % of marine primary productivity (measured [17]). They account for the same share of particulate carbon exported downward (measured [17]).

Among diatoms, *Chaetoceros* is the most abundant and diverse genus, then *Fragilariopsis*, *Thalassiosira* and *Corethron* (measured [18]).

Coccolithophores carry carbonate. In the North Pacific, coccolithophore calcite is about 90 % of total pelagic CaCO_3 production (measured [19]). Foraminifera and pteropods are secondary (measured [19]).

A large, unquantified portion is remineralised within the photic zone (measured [19]).

On land, herbivores take part. Herbivores remove 51 % of production in water and about one third of that on land (measured [20]). 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} , with a median of 0.300 (measured [21]). Half-lives are 0.53 yr in rain forest, a median of 2.3 yr, and 3.9 yr in tundra (measured [21]).

Nitrogen

The fixing enzyme stays in bacteria and archaea; no eukaryote carries the genes (measured [5]). In archaea only methanogens of Methanococcales, Methanobacteriales and Methanosarcinales carry them (measured [5]).

Trichodesmium is a colonial marine fixer. It fixes N_2 while producing O_2 , with fixation confined to daylight (measured [22]). Its colonies host diverse associated organisms (measured [22]).

In oligotrophic tropical waters it can be much of the plant biomass (measured [22]). Its fixation was first estimated at about 5 Tg N/yr; the current estimate is about 60–80 Tg N/yr (measured [23]). Of a marine total of 100–200 Tg N/yr (measured [23]), that is $60 / 200 = 30 \%$ to $80 / 100 = 80 \%$ (computed).

UCYN-A is a unicellular fixer. It lives in mutualistic symbiosis with a unicellular prymnesiophyte alga (measured [24]). The alga receives fixed N; the cyanobacterium receives fixed C (measured [24]).

The UCYN-A genome is reduced to 1.44 Mb (measured [25]). It lacks the O_2 -producing photosystem II and the tricarboxylic acid cycle (measured [25]). In 2024 it was

described as a N₂-fixing organelle of a marine alga (measured [26]).

The UCYN-A genome is $1.44 / 1.66 = 87\%$ of the *Prochlorococcus* MED4 genome of 1.66 Mb (measured [27]; computed). The *Arabidopsis* chloroplast genome, 154,478 bp (measured [28]), is 10.7 % of 1.44 Mb (computed).

On land, plants house fixers in nodules: legumes with rhizobia, actinorhizal plants with *Frankia*, and cycads with *Nostoc* (counts under Counts). The nodulating clade spans Fabales, Rosales, Cucurbitales and Fagales (measured [13]). A soybean nodule reaches 5 mm in diameter by day 45 (measured [29]).

Ammonia is oxidised by archaea and bacteria. Archaeal *amoA* genes are up to 3,000-fold more abundant than bacterial *amoA* in 12 soils (measured [30]). Across 100 studies, gross nitrification rises log-linearly with gross mineralisation and shows no relation to pH (measured [31]).

In a shortgrass prairie detrital food web, bacteria mineralise 4.5 g N m⁻² yr⁻¹, fauna 2.9 and fungi 0.3 (measured [32]). Bacterial-feeding amoebae and nematodes supply over 83 % of faunal N mineralisation (measured [32]). The web has 13 functional groups (measured [32]).

The total is 7.7 g N m⁻² yr⁻¹, or 77 kg N ha⁻¹ yr⁻¹ (computed). The shares are 58 % bacteria, 38 % fauna and 4 % fungi (computed).

The return to N₂ runs through bacteria by two routes. The anammox organism is an autotrophic planctomycete that divides only once every two weeks (measured [33]). Until then, bacteria able to oxidise ammonia anaerobically had not been found (measured [33]).

In the anoxic water column of Golfo Dulce, Costa Rica, a 200-m-deep coastal bay, anammox gives 19–35 % of total N₂ formation (measured [34]). In continental-shelf sediments it gives 24 % and 67 % of N₂ production at two typical sites (measured [35]). A global anammox share was not read in any source.

Phosphorus

Phosphorus enters life by weathering. Hyphae of mycorrhizal fungi preferentially colonised silicate basalt in field experiments (measured [36]). Weathering rose from arbuscular to ectomycorrhizal hosts and from gymnosperm to angiosperm hosts (measured [36]).

Angiosperms released calcium from basalt at twice the gymnosperm rate (measured [36]). Tree-planted plots raise Ca weathering about 10-fold over bare plots at Hubbard Brook (measured [37]). In Iceland the rise is 5–10-fold (measured [37]).

Arbuscular mycorrhizal fungi form symbioses with the roots of about 80 % of vascular plants (measured [38]). They “can provide the dominant route for plant P supply, even when overall growth or P uptake remains unaffected” (measured [38]).

Three counts of mycorrhizal plants are recorded. Of 3,617 surveyed species, 80 % are mycorrhizal, and so are 92 % of 263 families (measured [39]). Among vascular plants 72 % are arbuscular mycorrhizal (measured [40]); about 85 % of extant plants are mycorrhizal (measured [41]).

Plants allocate 13.12 Gt CO₂e/yr to mycorrhizal mycelium, as the 2001–2021 mean (measured [42]). The split is AM 3.93, EcM 9.07 and ericoid 0.12; in carbon the total is 3.58 Gt C/yr (measured [42]).

Shares of NPP allocated are AM 6.2 %, EcM 13.1 %, ericoid 3.5 % and orchid 1.0 % (measured [42]). Vegetation cover is AM 57.4 %, EcM 25.7 %, ericoid 2.6 % and non-mycorrhizal 14.3 % (measured [42]).

Seabirds carry phosphorus from sea to land. Breeding seabird colonies excrete 591 Gg N/yr and 99 Gg P/yr (measured [43]). The readily soluble fractions are 72.5 Gg N and 21.8 Gg P/yr (measured [43]).

The Antarctic and Southern Ocean regions give 80 % of the N and P, 470 Gg N and 79 Gg P (measured [43]). This comes from about 26 % of the population, 213 million birds (measured [43]). Sphenisciformes give 307 Gg N and 51 Gg P/yr (measured [43]).

Penguins thus carry $307 / 591 = 52$ % of seabird N and $51 / 99 = 52$ % of P (computed).

Sulphur

Sulphate reduction remains bacterial. In coastal sediments, sulphate-reducing bacteria oxidised as much organic matter to CO₂ as all aerobic organisms together (measured [44]). Their relative share fell threefold across the shelf, from the shore to 200 m (measured [44]).

The upward route is algal. Phytoplankton release dimethylsulphide (DMS), typically at 1–7 nM in surface water and higher at high latitudes (measured [45]).

Dimethylsulphide appears to be the major source of cloud-condensation nuclei over the oceans (measured [46]). Cloud albedo is sensitive to CCN density (measured [46]). An approximate doubling of CCN would be needed to counteract the warming from doubled CO₂ (measured [46]).

Oxygen

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 [47]). These come from niche models on more than 35,000 observations (measured [47]).

The ratio is $2.9 \times 10^{27} / 7.0 \times 10^{26} = 4.1$ (computed). Projected end-of-century increases are 29 % and 14 % (modelled [47]).

Maximum insect size tracks pO₂ in more than 10,500 fossil wings until the end of the Jurassic (measured [48]). Wingspans reach about 70 cm; size is decoupled afterwards as birds radiate (measured [48]).

Animals as carriers

Zooplankton migrate daily. Modelled export from the base of the euphotic zone is 6.5 Pg C/yr, 14 % higher than without diel vertical migration (modelled [49]). The migration-mediated export is 0.16 ± 0.04 of total carbon export (modelled [49]).

Migrating animals thus carry $0.16 \times 6.5 = 1.04$ Pg C/yr (computed). Sperm whales

carry iron. Southern Ocean sperm whales defecate an estimated 50 t of iron per year into the photic zone (measured [50]).

This exports about 4×10^5 t C/yr, against about 2×10^5 t C/yr respired, so about 12,000 whales act as a sink of about 2×10^5 t C/yr (measured [50]).

Per whale this is $4 \times 10^5 / 12,000 = 33$ t C exported per year and $50 \text{ t} / 12,000 = 4.2$ kg Fe per year (computed). Against a global export of about 9 Pg C/yr (modelled [51]), the whale export is 0.004 % (computed).

Whales and seals may replenish 2.3×10^4 t N/yr to the euphotic zone of the Gulf of Maine (measured [52]). This is more than all rivers combined (measured [52]). Before commercial harvest, recycling was likely more than three times atmospheric N input (measured [52]).

Cetaceans give about 77 % of the nutrients released by mammals and birds to the gulf (measured [52]). Large whales are about 10 % of historical numbers in Massachusetts Bay and about 45 % in the Bay of Fundy (measured [52]).

Salmon carry nitrogen inland. Trees and shrubs near spawning streams derive about 22-24 % of their foliar nitrogen from salmon, by isotopic analysis (measured [53]).

Serengeti wildebeest carry it into a river. Mass drownings of more than 100 individuals occur in at least 13 of 15 years in the Mara River (measured [54]). On average 6,250 carcasses and 1,100 t of biomass enter the river each year (measured [54]).

The mean carcass mass is $1,100 \text{ t} / 6,250 = 176$ kg (computed). Carcasses supply 34-50 % of the assimilated diet of fish when present, and 7-24 % via bone biofilm afterwards (measured [54]).

Sizes

Positions computed with the ladder tool.

what	size	position	source
marine snow, smaller compact aggregates	1-2.5 mm	9.10-9.93	measured [55]
marine snow, larger flocculent aggregates	4-5 mm	10.36-10.56	measured [55]
soybean nodule diameter at day 45	5 mm	10.56	measured [29]
maximum fossil insect wingspan	about 70 cm	15.06	measured [48]
flux level at the base of the euphotic zone, below the surface	100 m	19.58	modelled [56]
Golfo Dulce, coastal bay	200 m deep	20.21	measured [34]
continental shelf, outer limit of the measured decline, below the surface	200 m	20.21	measured [44]

deep flux level below the surface; sinking distance used for times	1,000 m	21.67	modelled [56]
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Times

Ages and durations in years use 3.15576×10^7 s per year. Positions computed.

what	duration	position	source
rhizosphere bacterial turnover	12–19 h	42.87–43.29	measured [57]
soil bacterial turnover, about 20 °C	2.3–33 d, mean 9.3 d	44.26–46.68; 45.53	measured [57]
fastest particle sinking 1,000 m at 175 m/day	5.7 d	45.09	computed from [55]
anammox cell division	about 2 weeks (1.21×10^6 s)	45.90	measured [33]
small aggregate sinking 1,000 m at 36 m/day	28 d	46.53	computed from [55]
soybean nodule reaches 5 mm	45 d	46.96	measured [29]
wildebeest soft-tissue decay	2–10 weeks	45.90–47.37	measured [54]
litter half-life, rain forest	0.53 yr	48.29	measured [21]
litter half-life, median	2.3 yr	49.63	measured [21]
large aggregate sinking 1,000 m at 1 m/day	1,000 d (2.7 yr)	49.79	computed from [55]
litter half-life, tundra	3.9 yr	50.11	measured [21]
wildebeest bone decay	about 7 yr	50.64	measured [54]
soil carbon to 1 m, stock / respiration flux	14.9–15.8 yr	51.33–51.38	computed from [58], [59]
radiocarbon mean age of soil carbon to 1 m	$4,830 \pm 1,730$ yr	56.59 (range 56.19–56.87)	measured [60]
Hawaiian soil, mineral P falls from 82 % to 1 %	300 to 20,000 yr	54.06–57.88	measured [61]
Hawaiian soil, organic P maximum	about 150,000 yr	59.72	measured [61]
atmosphere–ocean O ₂ residence, with total organic burial	0.82 Myr	61.27	computed from [62], [63]
atmospheric O ₂ transition at the GOE	1–10 Myr	61.45–63.54	measured [6]
atmosphere–ocean O ₂ residence	about 2.1 Myr	62.12	computed from [62]
Triassic–Jurassic O ₂ cycles, period	20–30 Myr	64.17–64.54	measured [64]
diatom origin to oldest abundant record	75 Myr	65.38	measured [12]

ocean oxygenation to land-plant O ₂ step	0.19–0.24 Gyr	66.22–66.43	computed from [9], [10]
O ₂ oscillation after onset	about 200 Myr	66.27	measured [7]
N fixation to GOE	0.74–0.87 Gyr	67.46–67.61	computed from [4], [6], [7]
GOE to ocean oxygenation	1,695 Myr	68.21	computed from [6], [9]

Counts

Organisms and species

- Global biomass about 550 Gt C; plants about 450, bacteria about 70, archaea about 7, animals about 2, marine biota about 6 (measured [2]).
- Seabirds: 320 species; more than 3,000 colonies; about 804 million breeding birds, 1,045 million with non-breeders (measured [43]).
- Southern Ocean seabirds: 213 million birds, about 26 % of the population (measured [43]).
- Wildebeest carcasses: 6,250 per year on average; drownings of more than 100 in at least 13 of 15 years (measured [54]).
- Diatoms: 4,748 OTUs from about 12 million ribotypes, 293 communities and 46 sites (measured [18]).
- Legumes: over 19,500 species; Papilionoideae about 14,000; Caesalpinioideae about 4,400 (measured [65]).
- Nodulating families: about 10 of about 380 angiosperm families (measured [66]); about 8 origins and 10 losses (measured [13]).
- Actinorhizal plants: 8 families, 24 genera, over 220 species (measured [67]).
- Cycads hosting *Nostoc*: 382 species (measured [68]).
- Cyanobacterial genomes with *nif*: 21 of 44 (measured [5]).
- *nif* genes needed for an active Mo enzyme: at least six (measured [5]).
- *Trichodesmium* diazocytes: about 15 % of trichome cells; zones of 2–30 cells; 1–2 zones per trichome, up to four; 10–20 cells per filament (measured [23]).
- Shortgrass prairie food web: 13 functional groups (measured [32]).

Data sets

Data sets (measured): 4,353 soil profiles [58]; 293 litter decay constants [21]; 100 nitrification studies [31]; 199 sulphate profiles [69]; over 47,000 DMS measurements [45]; 80 aggregates in situ [70]; 194 allocation datasets [42].

Steps and ratios

- Domains or kingdoms passed in the microbial loop: four (counted, from [16]).
- Silica passes through diatom frustules per atom buried: $1 / 0.03 = 33$ (computed from [71]). This is a production/burial ratio, not a measured recycling count.
- Bone against soft-tissue decay time: $7 \text{ yr} / (2\text{--}10 \text{ weeks}) = 36\text{--}182$ (computed from [54]).
- Ocean sink estimates: $450 / 175 = 2.6\text{-fold}$ (computed from [72]).
- Haber–Bosch against pre-industrial terrestrial fixation: $120 / 58 = 2.07$; against

lightning 24 (computed from [73], [74]).

- *Trichodesmium* estimate, early to current: 12–16-fold (computed from [23]).

Order of events

Positions are computed from the ages as durations.

1. About 3.47 Ga: microbial sulphate reduction, barite $\Delta^{34}\text{S}$ up to 21.1 ‰ (measured [3]). Position 68.87.
2. 3.2 Ga minimum: biological N_2 fixation by $\delta^{15}\text{N}$ in rocks of 3.2–2.75 Gyr (measured [4]). Positions 68.79; 68.79–68.65.
3. 2.460–2.426 Ga: onset of atmospheric oxygenation (measured [7]). Positions 68.55–68.54.
4. About 2.33 Ga: permanent atmospheric O_2 (measured [6]). Position 68.50.
5. 2.2–1.5 Ga: clock origin of nitrogenase (measured [5]). Positions 68.45–68.10.
6. 2.053–1.21 Ga: mitochondrial origin; crown eukaryotes younger than 1.84 Ga (measured [8]). Positions 68.39–67.91; 68.29.
7. 635–630 Ma: ocean oxygenation after the Marinoan glaciation (measured [9]). Positions 67.32–67.31.
8. About 470 Ma: land plants (measured [10]). Position 67.05.
9. 420–400 Ma: O_2 above 15–17 % by charcoal (measured [10]). Positions 66.94–66.90.
10. 419 Ma onward: continuous charcoal in sediments (measured [75]). Position 66.94.
11. 300–260 Ma: Permo-Carboniferous O_2 excursion (modelled [63]). Positions 66.64–66.51.
12. About 233 Ma: calcareous dinoflagellates (measured [11]). Position 66.41.
13. 215–210 Ma: coccolithophores (measured [11]). Positions 66.33–66.31.
14. About 200 Ma: diatom origin by molecular clock (measured [12]). Position 66.27.
15. 125–115 Ma: Aptian diatom records, eastern Australia (measured [12]). Positions 65.84–65.76.
16. 113–110 Ma: Weddell Sea diatom records (measured [12]). Positions 65.75–65.72.
17. Slightly over 100 Ma: single origin of the nodulation predisposition (measured [13]). Position 65.64.
18. Later: animal capacity to move nutrients falls to about 8 % of its pre-extinction value on land and about 5 % in the oceans (modelled [76]). The source gives no date in the part read.
19. Commercial whaling: large whales in Massachusetts Bay to about 10 % of historical numbers (measured [52]). The source gives no date in the part read.
20. 2010: anthropogenic reactive N 220 Tg N/yr (measured [73]).

Present quantities

Carbon

- Export of organic carbon from the euphotic zone: about 9 Pg C/yr, from a model assimilating satellite and tracer data (modelled [51]). Earlier estimates span about 4 to 12 Pg C/yr (reviewed in [51]).
- Model-ensemble sinking POC flux at 100 m: 6.08 ± 1.17 Pg C/yr, at the lower end of observational estimates (modelled [56]).

- Export ratio, sinking flux / NPP: 0.154 ± 0.026 (modelled [56]).
- Sinking POC flux at 1,000 m: 0.65 ± 0.24 Pg C/yr (modelled [56]). Transfer efficiency, 1,000 m / 100 m: 0.122 ± 0.041 (modelled [56]).
- Both export figures, about 9 and 6.08 ± 1.17 Pg C/yr, are recorded; their ratio is 1.48 (computed).
- Flux at 1,000 m as a share of ocean NPP: $0.154 \times 0.122 = 0.019$ (computed from [56]).
- Marine organic carbon burial: about 200×10^{12} g C/yr = 0.2 Pg C/yr; terrestrial about 350×10^{12} g C/yr (modelled [63]).
- Burial against export: $0.2 / 9 = 2.2 \%$ and $0.2 / 6.08 = 3.3 \%$ (computed).
- Shares of global NPP (computed): export $9 / 104.9 = 8.6 \%$ or $6.08 / 104.9 = 5.8 \%$.
- Flux at 1,000 m as a share of global NPP: $0.65 / 104.9 = 0.62 \%$; marine burial $0.2 / 104.9 = 0.19 \%$ (computed).
- Biogenic silica production: 200–280 Tmol Si/yr; at least 50 % dissolves in the upper 100 m; downward export 100–140 Tmol Si/yr (measured [71]).
- Coastal silica production is 3–12 times the global mean; oligotrophic gyres are 2–4 times lower (measured [71]).
- Waters over diatomaceous sediments, about 10–12 % of the ocean surface, supply 10–25 % of production and bury 15–25 % of it (measured [71]). Elsewhere virtually none accumulates; global burial / production is about 3 % (measured [71]).
- Marine snow: larger aggregates sink about 1 m/day; smaller compact aggregates about 36 m/day; all particles at Station Papa 175 m/day (measured [55]).
- Marine snow: about 1 to more than 500 mm³ per litre (measured [55]). Median excess density 0.00014 g/cm³; field sinking up to four times slower than in the laboratory (measured [70]).
- Soil organic carbon: 684–724 Pg to 30 cm; 1,462–1,548 Pg to 1 m; 2,376–2,456 Pg to 2 m (measured [58]).
- Soil N: 133–140 Pg to 1 m (measured [58]).
- Global soil respiration: 98 ± 12 Pg C in 2008, rising 0.1 Pg C/yr over 1989–2008 (measured [59]).

Nitrogen

- Global N fixation: 413 Tg N/yr, about half anthropogenic, 210 Tg N (measured [77]).
- Marine biological N fixation: 140 Tg N/yr (measured [77]). NO₃⁻ leaching 40–70; NH₃ + NO_x emissions 100 (measured [77]).
- Haber-Bosch: about 120 Tg N/yr; lightning NO_x 5 Tg N/yr (measured [73]).
- Marine BNF: 120 (100–200) Tg N/yr (measured [73]). Terrestrial natural BNF: 128 Tg N/yr, from a 2004 table (measured [73]).
- Pre-industrial terrestrial BNF: 58 (40–100) Tg N/yr; 44 with conservative geological N (measured [74]). Two terrestrial figures are recorded: 58 and 128.
- Anthropogenic reactive N: 220 Tg N/yr in 2010 (measured [73]).
- Agricultural BNF: 50–70 Tg N/yr; soybean 16.4, which is 77 % of crop-legume N; pulses 2.95; rice 5 (measured [78]).

Ocean fixed-N budgets in Tg N/yr, as tabled in one source (measured [72]):

term	Gruber &	Galloway 2004	Codispoti et	Codispoti 2007
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	Sarmiento 2002		al. 2001	
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/yr (measured [72]). The deficit is about 200 Tg N/yr against present fixation estimates (measured [72]).
- $\text{NO}_3^-/\text{PO}_4^{3-}$ lies near the Redfield value of 16 (measured [72]).
- The two sinks sum to $150 + 300 = 450$ Tg N/yr in the 2007 column and to $80 + 95 = 175$ in Gruber & Sarmiento 2002 (computed). All four budgets are recorded.

Phosphorus

- Inorganic P fertiliser: about 15 Mt P/yr; human P mobilisation by 2000 about three times natural flows (measured [79]).
- P storage in terrestrial and freshwater ecosystems rose by at least 75 % over pre-industrial levels (measured [80]).
- Including non-breeders and full seasons: 3,800 Gg N and 631 Gg P/yr, about 6.4 times the colony figures (measured [43]).
- Colony flows are of the same order as lightning, 5.0×10^3 Gg N/yr, and rice-cultivation N fixation, 5.0×10^3 (measured [43]). Commercial fishing moves 3.7×10^3 Gg N/yr and 0.32×10^3 Gg P/yr (measured [43]).
- Per area, colony inputs are 500 to more than 1,100 times annual agricultural N inputs of about 65–80 kg N ha⁻¹ yr⁻¹ (measured [43]).
- Colony N is $591 / 5,000 = 11.8$ % of lightning N; colony P is $99 / 15,000 = 0.66$ % of fertiliser P (computed).
- Seabirds and anadromous fish formerly moved about 150×10^6 kg P/yr from sea to land; now less than 4 % of that (modelled [76]). That is $0.04 \times 150 = 6 \times 10^6$ kg P/yr, or 6 Gg (computed).
- Two figures are recorded: 99 Gg P/yr excreted at colonies (measured [43]) and below 6 Gg P/yr moved inland by seabirds and fish (computed from [76]). The first counts excretion at colonies, much of it coastal; the second, modelled transfer inland.

Sulphur

- Global marine sulphate reduction: 11.3 Tmol SO_4^{2-} /yr, from a neural network trained on 199 profiles, about 15 % above previous estimates (modelled [69]).
- In mass: $11.3 \text{ Tmol} \times 32.06 \text{ g/mol} = 362 \text{ Tg S/yr}$ (computed).
- Sulphate reduction accounts for 12–29 % of the organic carbon flux reaching the sea floor (modelled [69]). In coastal sediments the share equals all aerobic respiration (measured [44]). The two shares refer to different settings; both are recorded.

- DMS sea-to-air flux: 28.1 (17.6–34.4) Tg S/yr, 17 % above the calculation with the previous climatology (measured [45]).
- In moles: $28.1 / 32.06 = 0.88$ Tmol S/yr (computed). DMS emission is $28.1 / 362 = 7.8$ % of the sea-floor sulphate-reduction flux (computed). The two are different processes; the ratio compares magnitudes only.

Oxygen

- Modern O₂: about 21 % (measured [81]); dry air 20.95 % by volume (measured [82]). Free O₂ was “a scarce commodity” until about 2 Ga (measured [81]).
- Atmosphere-ocean O₂ reservoir: 3.78×10^{19} mol; source flux 1.8×10^{13} mol O₂/yr; residence $3.78 \times 10^{19} / 1.8 \times 10^{13} = 2.1 \times 10^6$ yr, about 2.1 Myr (computed from [62]).
- With total organic burial of 550 Tg C/yr = 4.58×10^{13} mol/yr, the residence is 0.82 Myr (computed from [62], [63]). Both residence times are recorded.
- Phanerozoic O₂ in one model: about 2–11 % from the Cambrian to the mid-Ordovician; above 25 % in the early Mississippian (modelled [75]).
- Other models: never appreciably below 15 % (modelled [63]); 15–30 % over 550 Myr (modelled [83]); a disputed maximum of about 35 % around 300 Ma (modelled [84]).
- Charcoal in mires: pO₂ continuously above 26 % through the Carboniferous and Permian; a sharp drop near the Permian-Triassic extinction (measured [64]).
- Triassic-Jurassic cycles of up to 10 % amplitude with periods of 20–30 Myr; a decline since the mid-Cretaceous to about 21 % (measured [64]).
- Fire window: 13–35 % O₂ (measured [85]). Experimental fire is suppressed below 18.5 %, off below 16 %, and rises rapidly at 19–22 % (measured [86]).

Animals

- Animal capacity to move nutrients away from concentration patches: about 8 % of its pre-extinction value on land and about 5 % in the oceans (modelled [76]).
- Marine mammal upward P transport: about 23 % of a former about 340×10^6 kg P/yr (modelled [76]). Now $0.23 \times 340 = 78 \times 10^6$ kg P/yr, a loss of 262×10^6 kg P/yr (computed).

Pattern

Dated first steps run: sulphate reduction 3.47 Ga, N fixation 3.2 Ga by isotopes (1.5–2.2 Ga by clock), free O₂ 2.46–2.33 Ga. Calcareous dinoflagellates follow at 233 Ma, coccolithophores at 215–210 Ma and diatoms at about 200 Ma.

No eukaryote carries the nitrogenase genes; in archaea only three methanogen orders carry them. Eukaryotes house fixers, in nodules of about 10 of 380 angiosperm families and in UCYN-A, from symbiont to organelle.

At sea, 10–50 % of production passes through bacteria. The carbon pump shrinks at each step down: export 5.8–8.6 % of global NPP, 0.62 % at 1,000 m, burial 0.19 %.

Animals carry elements upward and landward, from zooplankton (16 % of export) to whales and seabirds (99 Gg P/yr). Their capacity is now 5–8 % of its former value.

Industrial N (120 Tg/yr) and P (15 Mt/yr) now equal or exceed natural fluxes.

Not verified

- Terrestrial NPP 56.4 Pg C/yr and share 53.8 % (secondary); ocean NPP 48.5 computed from it.
- Values computed from these: biomass turnover (8 yr land, 45 days sea); diatom production 19.4 Pg C/yr; land plants 54 % of O₂; fungi 6.3 % of land NPP.
- Diatom “~20 % of marine PP” (not read; 40 % read).
- Global anammox share “30–50 %” (not read; site values only).
- Coccolithophore dates from Gardin et al. 2012 and Bralower, Bown & Siesser 1991 (secondary).
- Alldredge & Silver 1988; Gruber & Galloway 2008; Walker & Syers 1976; Filippelli 2008 (V-bib).
- AM phosphorus shares per combination; UCYN-A host species (UNVERIFIED).
- Rooted trees 400–360 Ma (date not in its source entry).
- *Trichodesmium* colony sizes; global P weathering and river fluxes (not read).

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A10 The Whole Network and the Human Knot

What it is

This chapter takes the full set of living partners together. It counts the species per kingdom and the links measured between them. It then follows two connectors: the viruses that move between hosts and genomes, and the partnership between humans and their domesticated species.

The human partnership is the newest recorded here. It is measured by dates of domestication, by shares of biomass and land, and by the few crops that carry human

food energy.

First appearance

The oldest dated record in this line is a virus inside plant genomes. A survey found 14,895 high-confidence endogenous caulimovirid loci in 72 genome assemblies and 6 fern genomes (measured [1]). The family originated “at latest during the Devonian, about 320 million years ago” (measured [1]).

That age lies at position 66.70 (computed). The insertions are in vascular plants, ferns among them (measured [1]).

In primates, one retrovirus family has reinfected the germ line over a long span. In HERV-K(HML2), all genes including *env* are under continuous purifying selection (measured [2]). Proliferation is almost entirely by reinfection, and an infectious pool persisted in the primate lineage for the past 30 Myr (measured [2]).

The 30 Myr span lies at position 64.54 (computed). The *env* genes of eight other HERV families point to reinfection as the common mechanism (measured [2]).

Syncytins were captured “on multiple occasions and independently” in diverse mammals (measured [3]). Some replaced earlier ones (measured [3]). They are retroviral *env* genes exapted for a role in placentation (measured [3]).

The youngest dated virus radiation coincides with agriculture. Potyviruses, about 15 % of named plant virus species, radiated about 6,600 years ago (measured [4]). Their rate was about 1.15×10^{-4} substitutions per site per year (measured [4]).

The 6,600 years lie at position 56.88 (computed).

Domestication follows within the last 14,000 years. “The dog was the first domesticated animal” (measured [5]). Ancient genomes show a deep divergence between East Asian and Western Eurasian dogs about 14,000–6,400 years ago (measured [6]).

That interval lies at positions 57.56–56.85 (computed). Plant and animal domestication over the past 11,500 years affected the domesticated species, human evolution and the wider biosphere (measured [7]).

In the Eastern Mediterranean, initial plant and animal domestication dates to the 12th millennium cal BP (measured [8]). Herd management and crop cultivation appear at least 1,000 years before the morphological changes used to recognise domestication (measured [8]). Different species were domesticated in different parts of the Fertile Crescent, with multiple domestic lineages per species (measured [8]).

The earliest step read is cultivation of wild einkorn and rye at Abu Hureyra and Mureybit, 13,000–12,000 cal BP (measured [9]). This is before morphological domestication (measured [9]). Its positions are 57.49–57.42 (computed).

Human land use is older than the crops. By 10,000 BCE all human societies used ecologically transformative land management (measured [10]). Twelve thousand years ago nearly three quarters of Earth’s land was inhabited and shaped by people (measured [10]).

Partners

The kingdoms

Predicted eukaryote species number about 8.7 million (± 1.3 million SE) (measured [11]). Marine species are about 2.2 million (± 0.18 million) (measured [11]). Over 1.2 million are catalogued; about 86 % of species on Earth and 91 % in the ocean are undescribed (measured [11]).

Predictions per kingdom are: Animalia about 7.77 million, Plantae about 298,000, Fungi about 611,000 (measured [11]). Protozoa are about 36,400 and Chromista about 27,500 (measured [11]). Chromista and marine fungi are flagged as less reliable (measured [11]).

The kingdoms sum to $7.77 + 0.298 + 0.611 + 0.0364 + 0.0275 = 8.74$ million (computed). Animals are 89 % of the predicted total (computed). The catalogued share is $1.2 / 8.7 = 13.8$ % (computed).

Plants are counted directly. There are 295,383 accepted angiosperm species and 1,079 gymnosperms; all plants number about 374,000 (measured [12]). About 2,000 new species are named per year (measured [12]).

Two plant figures are recorded: 298,000 predicted (measured [11]) and 374,000 counted (measured [12]).

Fungi have about 120,000 accepted species against an estimate of 2.2–3.8 million (measured [13]). The fungus-to-plant ratio is 9.8 : 1 (measured [13]). This estimate is $2.2 / 0.611 = 3.6$ to $3.8 / 0.611 = 6.2$ times the prediction of [11] (computed).

Both fungal estimates are recorded. The described share of fungi is $120,000 / 3.8$ million = 3.2 % to $120,000 / 2.2$ million = 5.5 % (computed).

Insects have about 1 million named species and about 5.5 million estimated (measured [14]). Beetles alone are estimated at about 1.5 million (measured [14]). About 80 % of insect species are undescribed (measured [14]).

Bacteria change the totals. About 1.5 million species are formally described (measured [15]). Recent estimates of the total run from 2 million to 1 trillion, with many projections near 11 million or fewer (measured [15]).

One estimate gives at least 1–6 billion species, with bacteria about 70–90 % of species in a new “pie of life” (measured [15]). A second compilation covers about 35,000 sites and about 5.6×10^6 species (measured [16]). It finds a dominance scaling law across 30 orders of magnitude in abundance (measured [16]).

That compilation predicts upward of 10^{12} microbial species (measured [16]). The three totals are 8.7×10^6 [11], $1\text{--}6 \times 10^9$ [15] and 10^{12} [16]. The highest is $10^{12} / 8.7 \times 10^6 = 1.1 \times 10^5$ times the lowest (computed); all three are recorded.

Viruses are named as species too. The 2025 Master Species List holds 7 realms, 11 kingdoms, 22 phyla, 49 classes, 93 orders, 368 families, 3,769 genera and 16,215 species (measured [17]; [18]). In that year 1,563 species and 55 families were added (measured [17]).

Plant and fungal viruses, viroids and satellites numbered 2,134 species in the 2021 list (measured [19]). One database holds 3,206 plant virus species on 2,231 plant species, with 9,604 virus-plant interactions (measured [20]). An older list, DPVweb, holds 1,503 species (measured [20]).

The three plant-virus counts are recorded. The 2021 count is $2,134 / 16,215 = 13.2 \%$ of the 2025 species total (computed; different release years).

The links

Food webs are measured in tens to hundreds of nodes. Sixteen high-quality food webs from aquatic and terrestrial ecosystems hold 25–172 nodes (measured [21]). Clustering-coefficient ratios to random networks rise as a power law of network size over 7 orders of magnitude (measured [21]).

Plant-animal mutualistic networks are nested; 52 such networks were analysed (measured [22]). Seed ingestion has 13,135 unique animal $\times$ seed interactions across fish, amphibians, reptiles, birds and mammals (measured [23]).

Known pollinators number 349,368 species (measured [24]). Against 295,383 angiosperms (measured [12]), that is 1.18 pollinator species per plant species (computed). Of angiosperms, 87.5 % are animal-pollinated (measured [25]).

Plant viruses have few hosts each. The 9,604 interactions give $9,604 / 3,206 = 3.0$ hosts per virus and $9,604 / 2,231 = 4.3$ viruses per plant species (computed from [20]).

About 80 % of plant viruses are transmitted by specific insect vectors (measured [26]). More than 200 persist in their hemipteroid vectors (measured [27]).

Viruses as connectors

Viruses are numerous in the sea. An estimated 10^{30} viruses are in the ocean, and about 10^{23} viral infections occur every second (measured [28]). Viruses kill about 20 % of oceanic microbial biomass daily (measured [28]).

Infections per day are $10^{23} \times 86,400 = 8.6 \times 10^{27}$ (computed). Viruses typically number ten billion per litre of sea water (measured [29]). That is $10^{10} \text{ L}^{-1} = 10^7 \text{ mL}^{-1}$ (computed).

A survey of 5,508 paired microbial-cell and virus abundance estimates from 22 marine surveys questioned the 10:1 virus-to-microbe “consensus” (measured [30]). Upper virus estimates exceed 10^8 per mL (measured [30]). Power-law exponents are typically below 1 (measured [30]).

The figure of about 10^{31} virus particles on Earth is often given without source (measured [31]). It should be attributed to Hendrix et al. 1999 (measured [31]). Earth’s 10^{31} is 10 times the ocean’s 10^{30} (computed).

Against 16,215 named species, the ocean holds $10^{30} / 16,215 = 6 \times 10^{25}$ particles per named species (computed).

Viruses carry genes between bacteria. DNA and protein similarities connect lambdoid phages of *E. coli*, ϕ C31 of *Streptomyces*, a cryptic prophage of *Haemophilus influenzae*

and two prophage-like elements of *Mycobacterium tuberculosis* (measured [32]). Phage genomes are modelled as mosaics with access to a large common gene pool (measured [32]).

Phages carry photosynthesis genes. Three phage genomes of two families, Myoviridae and Podoviridae, infect *Prochlorococcus* (measured [33]). All three carry *psbA* (D1) and *hli*; one myovirus also carries *psbD* (D2), the other *petE* and *petF* (measured [33]).

The phage genes cluster with *Prochlorococcus* genes across several clades (measured [33]). The source reads this as multiple host-to-phage transfers (measured [33]). Phage-mediated expansion of the *hli* family is proposed (measured [33]).

Viruses sit in the human genome. About 8 % of human genome sequence is of retroviral origin (measured [34]). About half of the human genome derives from transposable elements (measured [35]).

DNA transposons appear completely inactive, and LTR retroposons may also be (measured [35]).

Domesticated partners

The Near East record gives dates per species from one review (measured [9]):

species or process	date (cal BP)	position	detail
cultivation of wild einkorn and rye (Abu Hureyra, Mureybit)	13,000–12,000	57.49–57.42	before morphological domestication
several plant species under cultivation	at least 11,500	57.38	“if not earlier”
cattle, Euphrates valley	11,000–10,000	57.34–57.25	southern Zagros ~8,500
sheep, herd management complete at Nevali Çori	~10,500	57.30	managed sheep in the Levant ~9,200
emmer and einkorn wheat, Upper Euphrates	~10,500–10,200	57.30–57.27	earliest secure domestic grains
pig, Cafer Höyük	~10,300	57.28	Jarmo by 9,000; lowland SW Iran only by 6,000
managed goat introduced, Nevali Çori	~10,200	57.27	herding signature at Ganj Dareh 9,900
barley, Middle PPNB	~10,000	57.25	earlier claims of ~11,500 largely overturned

An earlier sheep claim of 12,000–11,500 at Zawi Chemi Shanidar is not supported (measured [9]). A second source gives wheat and barley onset at 11,000–10,000 yr BP (measured [36]). Both are recorded.

Maize is present by 8,700 cal BP at Xihuatoxtla shelter, Central Balsas Valley, Mexico, from starch and phytoliths (measured [37]). The same work discusses human selection on 2 major domestication genes in *Zea* and *Cucurbita* (measured [37]).

Rice was domesticated in the Lower Yangtze between 6,900 and 6,600 years ago

(measured [38]). At Tianluoshan, non-shattering spikelet bases rose from 27 % to 39 % (measured [38]). Rice rose from 8 % to 24 % of plant remains over the same period (measured [38]).

The rates are $(39 - 27) / 300 \text{ yr} = 0.04$ percentage points per year and $(24 - 8) / 300 = 0.053$ per year (computed). In 11 domesticated plant species from 60 archaeological sites, non-shattering and larger grain evolved slowly (measured [39]). The rates are comparable to those of wild species under natural selection (measured [39]).

The dog study used 49,024 autosomal SNPs in 1,375 dogs of 35 breeds and 19 wolves, combined with 121 breeds (measured [5]). Basenjis, Dingoes and New Guinea Singing Dogs were introduced more than 10,000 years after domestication (measured [5]).

A second dog study sequenced 59 ancient dogs and a 28× genome of a Neolithic Irish dog about 4,800 cal BP (measured [6]). A review meeting of 25 scholars in spring 2011 named three key challenges for domestication research (measured [40]).

The microbes in humans

A 70 kg “reference man” carries 3.8×10^{13} bacteria and 3.0×10^{13} human cells, of the same order (measured [41]). This replaces the 10:1 ratio (measured [41]). The ratio is 1.3, with an uncertainty of about 25 % for bacteria (measured [41]).

Bacterial mass is about 0.2 kg, which is $0.2 / 70 = 0.29$ % of body mass (measured [41]; computed). The haematopoietic lineage is about 90 % of human cells, and red blood cells 84 % (measured [41]).

The Human Microbiome Project took 4,788 specimens from 242 adults, 129 men and 113 women (measured [42]). Women were sampled at 18 body habitats and men at 15; 131 were resampled after about 219 days (measured [42]). Specimens per person are $4,788 / 242 = 19.8$ (computed).

An estimated 81–99 % of genera, enzyme families and community configurations of the healthy Western microbiome were encountered (measured [42]). Of 327 PATRIC pathogens, 56 were detected above 1 % prevalence and 0.1 % abundance, all opportunistic (measured [42]). *Staphylococcus aureus* was in 29 % of nares samples (measured [42]).

Protein families per community run from about 16,000 in the vagina to almost 400,000 in the oral cavity (measured [42]). The spread is 25-fold (computed). Of the protein families, 58–77 % have no known function (measured [42]).

Crops

Of more than 50,000 edible plant species, only a few hundred contribute significantly to food supplies (measured [43]). Just 15 crop plants provide 90 % of the world’s food energy intake (measured [43]). Rice, maize and wheat provide 60 %, and rice feeds almost half of humanity (measured [43]).

The 15 crops are $15 / 50,000 = 0.03$ % of edible species (computed).

Crops lose yield to pathogens and pests. Losses to pathogens and pests are wheat 21.5

% (10.1–28.1), rice 30.0 % (24.6–40.9) and maize 22.5 % (19.5–41.1) (measured [44]). Potato loses 17.2 % (8.1–21.0) and soybean 21.4 % (11.0–32.4), from 137 pathogens and pests in all (measured [44]).

Late blight reached the United States in 1843, and Belgium and Ireland in 1845 (measured [45]). The Irish famine of 1845–1850 caused about 1 million deaths (measured [46]).

Fixed nitrogen for crops has two sources. Biological N fixation in agriculture gives 50–70 Tg N/yr (measured [47]). Haber-Bosch gives about 120 Tg N/yr (measured [48]).

Sizes

The dossier gives no length in metres for any partner in this chapter. The quantities of size it gives are masses; the ladder takes lengths, so no position is computed.

what	size	position	source
reference man	70 kg (mass)	— (mass)	measured [41]
bacteria in the reference man, total	about 0.2 kg (mass)	— (mass)	measured [41]

Times

Durations in years use 3.15576×10^7 s per year. Positions computed.

what	duration	position	source
share of oceanic microbial biomass killed by viruses, about 20 %	per day (86,400 s)	43.50	measured [28]
resampling interval, Human Microbiome Project	about 219 days	48.40	measured [42]
doubling time of anthropogenic mass	about 20 yr	51.60	measured [49]
vertebrate losses compressed into	100 yr	53.06	measured [50]
rice non-shattering 27 % → 39 %	about 300 yr	54.06	measured [38]
land-use record, 1700 to 2000	300 yr	54.06	measured [51]
background time for the same vertebrate losses	800–10,000 yr	54.95–57.25	measured [50]
management before morphology, at least	1,000 yr	55.16	measured [8]
livestock reaching new regions after first domestication	1,300–4,300 yr	55.40–56.49	computed from [9]
Near East cereals to maize; maize to rice	1,800 yr each	55.69	computed from [9], [37], [38]
wild cultivation to	2,500–2,800 yr	55.99–56.10	computed from [9]

secure domestic grain			
potyvirus radiation, before present	about 6,600 yr	56.88	measured [4]
dog divergence, East Asia – Western Eurasia, before present	14,000–6,400 yr	57.56–56.85	measured [6]
dogs introduced after domestication (Basenji, Dingo, Singing Dog)	more than 10,000 yr	57.25	measured [5]
domestication span	11,500 yr	57.38	measured [7]
land shaped by people, before present	12,000 yr	57.42	measured [10]
HERV-K(HML2) infectious pool	30 Myr	64.54	measured [2]
caulimovirid origin, at latest	about 320 Myr	66.70	measured [1]

Counts

Species

- Eukaryotes: about 8.7 ± 1.3 million predicted; marine about 2.2 ± 0.18 million; over 1.2 million catalogued (measured [11]).
- Animals 7.77 million; plants 298,000; fungi 611,000; protozoa 36,400; chromista 27,500, all predicted (measured [11]).
- Angiosperms 295,383 accepted; gymnosperms 1,079; all plants about 374,000 (measured [12]).
- Fungi: about 120,000 accepted; 2.2–3.8 million estimated (measured [13]).
- Insects: about 1 million named; about 5.5 million estimated; beetles about 1.5 million (measured [14]).
- All species: about 1.5 million described; at least 1–6 billion estimated (measured [15]); upward of 10^{12} microbial (measured [16]).
- Pollinators: 349,368 species (measured [24]).
- Virus species: 16,215 in 3,769 genera, 368 families, 93 orders, 49 classes, 22 phyla, 11 kingdoms and 7 realms (measured [17]; [18]).
- Plant virus species: 1,503, 2,134 or 3,206 by list (measured [20]; [19]).

Individuals and cells

- Viruses in the ocean: 10^{30} ; on Earth about 10^{31} (measured [28]; [31]).
- Viral infections in the ocean: about 10^{23} per second; 8.6×10^{27} per day (measured [28]; computed).
- Viruses per litre of sea water: 10^{10} (measured [29]).
- Bacteria in a reference man: 3.8×10^{13} ; human cells: 3.0×10^{13} (measured [41]).

Data sets and links

- Food webs: 16, with 25–172 nodes (measured [21]).
- Mutualistic networks: 52 (measured [22]).

- Seed-ingestion interactions: 13,135 (measured [23]).
- Virus-plant interactions: 9,604 (measured [20]).
- Links per species: 1.18 pollinators per angiosperm; 3.0 hosts per plant virus; 4.3 viruses per plant (computed).
- Paired virus-cell estimates: 5,508 from 22 surveys (measured [30]).
- Species-abundance sites: about 35,000 (measured [16]).
- Caulimovirid loci: 14,895 in 72 assemblies and 6 fern genomes (measured [1]).
- Phage genomes with photosynthesis genes: 3, in 2 families (measured [33]).
- Dog genetics: 49,024 SNPs, 1,375 dogs, 35 breeds, 19 wolves (measured [5]); 59 ancient dogs (measured [6]).
- Domestication archaeology: 11 crops, 60 sites (measured [39]).
- Human Microbiome Project: 242 adults, 4,788 specimens, 15–18 sites; 56 of 327 pathogens detected (measured [42]).
- Crops: 15 give 90 % of food energy; 3 give 60 %; over 50,000 edible species (measured [43]).
- Crop pathogens and pests: 137 (measured [44]).

Order of events

Positions are computed from the ages as durations.

1. At latest about 320 Ma: caulimovirid insertions in vascular-plant genomes (measured [1]). Position 66.70.
2. Past 30 Myr: HERV-K(HML2) reinfesting the primate germ line (measured [2]). Position 64.54.
3. 14,000–6,400 years ago: East Asian–Western Eurasian dog divergence; the dog is the first domesticate (measured [6]; [5]). Positions 57.56–56.85.
4. 13,000–12,000 cal BP: cultivation of wild einkorn and rye (measured [9]). Positions 57.49–57.42.
5. 12,000 years ago: about three quarters of land shaped by people (measured [10]). Position 57.42.
6. 12th millennium cal BP (12,000–11,000): initial domestication in the Eastern Mediterranean (measured [8]). Positions 57.42–57.34.
7. At least 11,500 cal BP: several plant species under cultivation (measured [9]). Position 57.38.
8. 11,000–10,000 cal BP: cattle in the Euphrates valley (measured [9]); wheat and barley onset (measured [36]). Positions 57.34–57.25.
9. About 10,500–10,200 cal BP: sheep herd management, emmer and einkorn (measured [9]). Positions 57.30–57.27.
10. About 10,300 cal BP: pig; about 10,200 managed goat; 9,900 herding at Ganj Dareh (measured [9]). Positions 57.28; 57.27; 57.24.
11. About 10,000 cal BP: barley (measured [9]). Position 57.25.
12. About 9,200 cal BP: managed sheep in the Levant; 9,000 pig at Jarmo (measured [9]). Positions 57.18; 57.16.
13. 8,700 cal BP: maize in the Balsas Valley (measured [37]). Position 57.13.
14. About 8,500 cal BP: cattle in the southern Zagros (measured [9]). Position 57.11.
15. 6,900–6,600 years ago: rice in the Lower Yangtze (measured [38]). Positions 56.92–56.88.
16. About 6,600 years ago: potyvirus radiation (measured [4]). Position 56.88.

17. 6,000 cal BP: pig in lowland SW Iran (measured [9]). Position 56.79.
18. About 4,800 cal BP: Neolithic Irish dog (measured [6]). Position 56.59.
19. 1700: nearly half of the terrestrial biosphere wild (measured [51]).
20. 1843–1845: late blight in the United States, then Belgium and Ireland (measured [45]).
21. Early 20th century: anthropogenic share of the biosphere passes 50 % (measured [51]).
22. 20th century: vertebrate extinctions up to 100 times background (measured [50]).
23. 2000: a quarter of the biosphere wild (measured [51]).
24. 2020 $\pm$ 6: human-made mass equals living biomass, about 1.1 Tt (measured [49]).

Intervals (computed): dog divergence, 14,000–6,400 years ago, begins at most 14,000 – 13,000 = 1,000 years before wild cereal cultivation at 13,000. Wild cultivation to domestic grain is 2,500–2,800 years. Near East cereals (10,500) to maize (8,700) and maize to rice (6,900) are 1,800 years each.

Livestock reached new regions 1,300–4,300 years after first domestication (computed). Sheep to the Levant took 10,500 – 9,200 = 1,300; cattle to the Zagros 1,500–2,500; pigs to lowland Iran 10,300 – 6,000 = 4,300 (computed).

Present quantities

Biomass

- Global biomass: about 550 Gt C; plants about 450, bacteria about 70, archaea about 7, animals about 2, marine biota about 6 (measured [52]).
- Human mass exceeds that of all wild mammals by about one order of magnitude (measured [52]).
- Wet biomass, terrestrial wild mammals: about 20 Mt (95 % CI 13–38), about 3 kg per person (measured [53]).
- Marine mammals: about 40 Mt (20–80), more than half of it baleen whales (measured [53]).
- Humans about 390 Mt; livestock about 630 Mt (measured [53]).
- Large herbivores carry most wild land-mammal biomass: white-tailed deer, wild boar, African elephant (measured [53]).
- The four sum to 390 + 630 + 20 + 40 = 1,080 Mt (computed). Livestock are 58 %, humans 36 %, wild land and marine mammals 5.6 % (computed).
- Humans against wild land mammals: 19.5; against all wild mammals: 6.5 (computed).
- Anthropogenic mass has recently doubled roughly every 20 years (measured [49]).
- It equals living biomass, about 1.1 teratonnes dry, at the crossover year 2020 $\pm$ 6 (measured [49]).
- Each person's weekly share of new anthropogenic mass exceeds his or her body weight on average (measured [49]).

Land

- In 1700 nearly half of the terrestrial biosphere was wild; most of the rest, 45 %, was seminatural (measured [51]).

- By 2000 the majority was anthropogenic, less than 20 % seminatural and only a quarter wild (measured [51]).
- Agriculture and settlements transformed almost 39 % of ice-free land by 2000 (measured [51]). Another 37 % without such use was embedded within agricultural and settled areas (measured [51]).
- Used or embedded: $39 + 37 = 76$ % of ice-free land (computed).
- The anthropogenic share passed 50 % early in the 20th century (measured [51]).
- More than 95 % of temperate and about 90 % of tropical woodlands were shaped by human land use (measured [10]).
- Two figures are recorded: about three quarters of land shaped 12,000 years ago (measured [10]) and nearly half fully wild in 1700 (measured [51]). The first counts land “shaped”; the second, land “used”.

Extinction and transport

- Background rate taken as 2 mammal extinctions per 10,000 species per 100 years (2 E/MSY), about twice common estimates (measured [50]).
- Vertebrate losses over the last century are up to 100 times higher (measured [50]). At background rate they would have taken 800 to 10,000 years (measured [50]).
- Animal capacity to move nutrients: about 8 % of its pre-extinction value on land and about 5 % in the oceans (modelled [54]).

Viruses and genomes

- Daily viral kill: about 20 % of oceanic microbial biomass (measured [28]).
- Retroviral share of the human genome: about 8 % (measured [34]).
- Transposable-element share of the human genome: about half (measured [35]).
- Virus mutation rates, from more than 40 studies: about 10^{-8} – 10^{-6} per nucleotide per cell infection for DNA viruses and 10^{-6} – 10^{-4} for RNA viruses (measured [55]).
- Host substitution rates: 1.43 – 2.2×10^{-9} per site per year (measured [56]; reused).
- Potyvirus rate against host rate: $1.15 \times 10^{-4} / 2.2 \times 10^{-9} = 5.2 \times 10^4$ to $1.15 \times 10^{-4} / 1.43 \times 10^{-9} = 8.0 \times 10^4$ (computed from [4], [56]).

Food

- Food energy: 15 crops 90 %; rice, maize and wheat 60 % (measured [43]).
- Yield lost to pathogens and pests in five staples: 17.2–30.0 % (measured [44]).
- Fixed N in agriculture: biological 50–70 Tg N/yr (measured [47]); Haber-Bosch about 120 Tg N/yr (measured [48]).

Pattern

Estimated species numbers: plants 0.30–0.37 million, fungi 0.6–3.8 million, animals 7.8 million and all eukaryotes 8.7 million. Counting bacteria gives 1–6 billion or 10^{12} , and virus particles number 10^{30} – 10^{31} .

Described shares are: plants near complete, insects about 20 %, eukaryotes about 14 %, fungi 3.2–5.5 %. Measured links per species are few: 1.18 pollinators per angiosperm, 3.0 hosts per plant virus, 4.3 viruses per plant.

Viruses kill about 20 % of marine microbial biomass daily and carry photosystem genes between cyanobacteria and phages. Retroviral sequence is about 8 % of the human genome.

Domestication began 13,000–6,600 years ago in three regions, after the dog, and spread over 1,300–4,300 years. Humans and livestock now hold 94 % of mammal mass.

Agriculture and settlements transformed 39 % of ice-free land, and a further 37 % lies embedded without such use. Fifteen crops give 90 % of food energy, and human-made mass equals living biomass.

Not verified

- Viral kill of 20–40 % of prokaryote stock per day (Suttle 1994, via BioNumbers; secondary).
- Humans 0.06 Gt C; wild mammals down sixfold; total mammal mass up fourfold (Weizmann news page; secondary).
- Livestock 0.1 Gt C and wild mammals 0.007 Gt C (brief values; UNVERIFIED).
- HERVs about 400,000 copies, about 4.6 % of about 3 billion nucleotides (Katoh & Kurata 2013, secondary for the count).
- Syncytin as a captive envelope protein in human placenta (Mi et al. 2000; V-bib).
- Number of independent syncytin captures (UNVERIFIED).
- Dog domestication “ ≥ 15 ka” (not read); Bergström et al. 2020 (V-bib).
- Homogenisation of national food supplies (Khoury et al. 2014; V-bib).
- Per-group counts for mites and parasites (Larsen et al. 2017; UNVERIFIED).
- Fifteen named plant pandemics or resistance breakdowns, 1843–2014, one every 11.4 years (a compiled count with no single primary source).
- Repeat-class table of the human genome; FAO page year; phage share of ocean gene transfer (not read).

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Part C — Tables Across the Chapters

All values are copied from the ten Layer A chapters (A1–A10) and their data files. References are chapter-local: “A3 [12]” is reference 12 of chapter A3. A dash (—) means no value is printed.

An age of A Myr is placed as a duration of $A \times 10^6 \times 3.15576 \times 10^7$ s; positions are computed with the ladder tool and given to two decimals.

C1 First appearances

All FIRST rows of the ten data files, merged and ordered from oldest to youngest by the older printed age. Rows with the same event and the same source are merged and list every chapter. Where a source is printed with $\pm$ or with a confidence range, the position of each end is given in brackets.

event or lineage	age (Ma)	position	evidence	chapter [ref]
LUCA	4,090–4,330 (central 4,200); GBM 4,180– 4,330; composite 3,940–4,520	69.02–69.07 (central 69.04); GBM 69.04– 69.07; composite 68.98–69.11	molecular	A1 [5]
putative microfossils, Nuvvuagittuq (filaments, tubes)	$\geq 3,770$, possibly 4,280	68.94, possibly 69.06	fossil	A1 [9]
potentially biogenic carbon (graphite in Jack Hills zircon)	$4,100 \pm 10$	69.02 (69.02– 69.02)	geochemical	A1 [8]
LUCA	$> 3,900$	68.97	molecular	A1 [6]
isotopically light carbon, Akilia	possibly $> 3,850$	68.96	geochemical	A1 [10]
LUCA	3,500–3,800	68.87–68.95	molecular	A1 [7]
isotopically light carbon, Isua	about 3,800	68.95	geochemical	A1 [10]
graphite globules, Isua (biogenic detritus)	$> 3,700$	68.92	geochemical	A1 [11]
biogenic graphite, Isua Supracrustal Belt	$\geq 3,700$	68.92	geochemical	A1 [12]
stromatolites, Isua (read as non-biological in A1 [14])	3,700	68.92	fossil	A1 [13]
microbial methanogenesis	$> 3,460$ (inclusions about 3,500)	68.86 (inclusions 68.87)	geochemical	A1 [17]

life in terrestrial hot springs, Dresser Formation	ca. 3,480	68.87	fossil	A1 [15]
microbial sulphate reduction, North Pole	about 3,470	68.87	geochemical	A1 [16]; A9 [3]
microfossils, Apex chert (5 species)	about 3,465	68.86	fossil	A1 [18]
filamentous microfossil candidate (Panorama Formation)	3,450	68.86	fossil	A3 [6]
stromatolite reef, Strelley Pool	about 3,430	68.86	fossil	A1 [19]
sulphur-metabolizing microfossils, Strelley Pool Formation	3,400	68.85	fossil	A1 [20]
crown Bacteria (Eubacteria)	<3,400	68.85	molecular	A1 [6]
crown Archaea (Archaeobacteria)	<3,400	68.85	molecular	A1 [6]
Sulphur Springs filaments (biogenicity questioned)	3,240	68.80	fossil	A4 [2]
microbial mats on land, Moodies Group	3,220	68.80	fossil and geochemical	A6 [2]
biological nitrogen fixation	$\geq 3,200$ (A9: 3,200 minimum, rocks 3,200–2,750)	68.79 (rocks 68.79–68.65)	geochemical	A1 [21]; A9 [4]
microbial mats in palaeosols, Mpumalanga	2,700–2,600	68.64–68.60	geochemical	A6 [3]
onset of atmospheric O ₂ (GOE)	2,460–2,426	68.55–68.54	geochemical	A9 [7]
multicellular cyanobacteria (origin, GOE-linked)	2,450–2,220	68.55–68.46	molecular (with fossil comparison)	A3 [6]
multicellular cyanobacteria (origin)	>2,400 (GOE 2,450–2,320)	68.53 (GOE 68.55–68.50)	molecular	A3 [7]
fungus-like mycelial filaments in basalt	2,400	68.53	fossil	A3 [15]; A5 [8]; A6 [6]
last eukaryotic common ancestor (LECA)	1,958–2,386	68.35–68.53	molecular	A2 [5]; A5 [4]
permanent atmospheric O ₂ (GOE)	about 2,330	68.50	geochemical	A9 [6]
nitrogenase	1,500–2,200	68.10–68.45	molecular	A1 [7]; A9 [5]
conclusive fossils of all five cyanobacterial sections	~2,150	68.43	fossil	A3 [6]
Archaeplastida primary plastid (primary plastid)	1,807–2,137	68.27–68.42	molecular	A2 [5]; A3 [11]

chloroplast lineage branching in cyanobacteria	about 2,100 (establishment about 200 Myr later)	68.41	molecular	A2 [6]
mitochondrial symbiosis (mitochondrion)	1,210–2,053	67.91–68.39	molecular	A2 [4]; A9 [8]
cyanobacterial akinetes (differentiated cells)	~2,000	68.36	fossil	A3 [6]
crown red algae	1,732–1,984	68.23–68.36	molecular	A2 [5]; A3 [11]
haptophytes	579–1,943	67.24–68.34	molecular	A2 [5]
eukaryotes in the geological record	1,400–1,900	68.04–68.32	fossil	A2 [9]
LECA	1,866–1,679 (mean 1,774; HPD 1,632–1,911)	68.30–68.21 (mean 68.26; HPD 68.18–68.32)	molecular	A5 [1]
crown eukaryotes	<1,840	68.29	molecular	A1 [6]; A2 [4]; A9 [8]
fungi	1,759–1,078	68.25–67.80	molecular	A5 [4]
root of Plantae	~1,694	68.21	molecular	A3 [14]
red-algal plastid donor (stem Rhodophytina)	1,281–1,675	67.96–68.20	molecular	A2 [5]
cryptophytes	440–1,658	66.99–68.19	molecular	A2 [5]
probable crown red algae, Chitrakoot (<i>Rafatazmia</i> , <i>Ramathallus</i>)	1,650 ± 89	68.19 (68.14–68.24)	fossil	A2 [8]
probable crown-group red algae (<i>Rafatazmia</i> , <i>Ramathallus</i>)	~1,600	68.16	fossil	A3 [10]
myxozoans (dinoflagellates + apicomplexans and kin)	696–1,520	67.40–68.11	molecular	A2 [5]
chloroplast-forming symbiosis	>1,500	68.10	not stated (review)	A2 [7]
Opisthokonta (animals + fungi)	1,389–1,240 (1,240–1,481 across analyses)	68.03–67.93 (67.93–68.09)	molecular	A5 [1]
ochrophytes	622–1,298	67.30–67.97	molecular	A2 [5]
eukaryotic photosynthesis (clock calibrated on <i>Bangiomorpha</i>)	ca. 1,250	67.94	molecular	A2 [9]; A3 [9]
non-marine eukaryotes, Torridonian	1,200–1,000	67.90–67.73	fossil	A6 [4]
serial secondary endosymbioses of red plastids	650–1,079	67.34–67.80	molecular	A2 [5]
<i>Bangiomorpha</i>	1,047 (+13/–17)	67.78 (67.76–	fossil (Re-Os)	A2 [9]; A3 [9]

<i>pubescens</i>		67.79)		
crown Fungi	~1,020	67.75	molecular	A3 [17]; A5 [5]
<i>Ourasphaira giralda</i> (oldest unambiguous fungus)	1,010–890	67.74–67.63	fossil	A3 [16]; A5 [9]; A6 [7]
last common ancestor of dictyostelids and animals	>1,000	67.73	molecular	A3 [1]
<i>Proterocladus antiquus</i> (multicellular green seaweed)	~1,000	67.73	fossil	A3 [12]
core Chlorophyta	~1,000–700	67.73–67.41	molecular	A3 [13]
Bangiophyceae– Florideophyceae split	943 (817–1,049)	67.68 (67.55– 67.78)	molecular	A3 [14]
tertiary plastid in a stem ochrophyte	≤819 (633–1,017)	67.55 (67.32– 67.75)	molecular	A2 [5]
Hildenbrandiophycidae	781	67.51	molecular	A3 [14]
loss of the flagellum in fungi (A6: land colonisation)	~720	67.43	molecular	A3 [17]; A5 [5]; A6 [8]
crown Metazoa	Cryogenian (base ~720)	base 67.43	molecular	A5 [6, 7]
Nemaliophycidae	661	67.36	molecular	A3 [14]
Glomeromycota	~659 (715–606)	67.35 (67.43– 67.28)	molecular	A3 [17]; A5 [5]; A6 [8]
Dikarya	649	67.34	molecular	A3 [17]; A5 [5]
demosponges (24-ipc steranes, first reading)	>635	67.32	geochemical	A3 [25]
Ediacaran palaeosol surface communities	635–542 (625–542 in summary)	67.32–67.18 (67.31–67.18)	fossil	A6 [5]
widely oxygenated ocean	about 635–630	67.32–67.31	geochemical	A9 [9]
dictyostelid lineages (split of three sequenced species)	≥600	67.27	molecular	A3 [23]
Corallinophycidae	579 (543–617)	67.24 (67.18– 67.29)	molecular	A3 [14]
architecturally complex Ediacaran macrofossils	574.17 ± 0.66	67.23 (67.23– 67.23)	fossil (radiometric)	A3 [28]
earliest animal-like Ediacaran fossils (second reading)	~571	67.22	fossil	A3 [27]
<i>Dickinsonia</i> (animal by sterols)	558	67.20	fossil + geochemical	A3 [29]
base of the Cambrian	538.8 ± 0.2	67.17 (67.17– 67.17)	stratigraphic	A3 [20]
Chengjiang biota	≤518.03 ± 0.69/0.71	67.13	fossil (U–Pb)	A3 [30]
crown embryophytes	515.1–470.0	67.13–67.05	molecular	A3 [32]; A6 [13]

crown embryophytes	515–493	67.13–67.09	molecular	A3 [33]; A6 [14]
myriapods	~500	67.10	molecular	A6 [22]
<i>Aegiocassis benmoulae</i>	Early Ordovician (Ordovician beginning around 490)	beginning 67.08	fossil	A7 [11]
arthropod trackways on land	Cambrian–Ordovician (boundary 485.4)	boundary 67.08	fossil (trace)	A6 [19, 1]
Glomeromycota diversification onset	484 (529–437)	67.07 (67.15–66.98)	molecular	A5 [5]
crown embryophytes (crown land plants)	482 (485–473)	67.07 (67.07–67.05)	molecular	A3 [17]; A5 [5]; A6 [8]
AM symbiosis (A5: with Leotiomyces radiation)	ca. 480	67.07	molecular	A5 [5]; A6 [8]
insects	~479	67.06	molecular	A6 [24]; A8 [3]
oldest cryptospores (land-plant spores)	~473–471	67.05–67.05	fossil	A3 [31]; A6 [12]
crown tracheophytes	472.2–419.3	67.05–66.94	molecular	A6 [13]
land plants	about 470	67.05	not stated in the dossier	A9 [10]
ascolichens	467–410	67.04–66.92	molecular	A5 [5]
glomalean hyphae and spores	~460	67.03	fossil	A3 [18]; A5 [10]; A6 [9]
brown algae	449.41 (333.85–572.02); alternatives 435–455, 595–600	67.01 (66.73–67.23); alternatives 66.98–67.02, 67.26–67.27	molecular	A3 [42]
burrows in palaeosols (millipede-like)	Late Ordovician, >443.8	66.99	fossil (trace)	A6 [20, 21]
<i>Tortotubus protuberans</i> (cord-forming mycelium)	earliest Silurian (base 443.8)	base 66.99	fossil	A3 [19]; A5 [11, 7]; A6 [10]
vent community with animals; microbes on tubeworm tubes (Yaman Kasy)	~440 (poorly constrained)	66.99	fossil	A4 [2]
crown tracheophytes, minimum (<i>Cooksonia</i> cf. <i>pertoni</i>)	426.9	66.96	fossil	A3 [32]; A6 [13]
millipedes, Kerrera	~425	66.95	fossil	A6 [22]
pentastomid parasitic on an ostracod	425	66.95	fossil	A7 [5]
wildfire (charcoal)	423.0 ± 2.3	66.95 (66.95–66.96)	fossil	A6 [18]
crown tracheophytes, minimum (Ludlow)	420.7	66.95	fossil	A3 [32]; A6 [13]
trigonotarbid with	~420	66.94	fossil	A6 [22]

book lungs				
clitellates (freshwater ancestor)	Devonian, 419–359	66.94–66.80	molecular	A6 [56]
continuous charcoal in sediments	419	66.94	fossil	A9 [75]
land herbivory, phase 1 (A7, A8: first arthropod herbivory; A8: spores, stems)	417–403	66.94–66.91	fossil (A7, A8: not stated)	A6 [41]; A7 [6]; A8 [5]
stratified cyano- and chlorolichens	415	66.93	fossil	A5 [16]
<i>Pneumodesmus</i> , millipede with spiracles	414 (U-Pb); formerly ~427	66.93; formerly 66.96	fossil	A6 [23]
Rhynie chert plants and charophytes	411.5 ± 1.3	66.93 (66.92–66.93)	fossil (U-Pb)	A3 [35]
arbuscules in <i>Aglaophyton</i> , Rhynie chert	411.5 ± 1.3	66.93 (66.92–66.93)	fossil (U-Pb dated)	A5 [14, 15]
Rhynie chert community (arbuscules, lichen, nematodes, mites, springtails)	411.5 ± 1.3	66.93 (66.92–66.93)	fossil	A6 [31, 38, 36, 37]
rhizomes in deep palaeosols	411–408	66.92–66.92	fossil	A6 [39]
insects (<i>Rhyniognatha</i> , described as oldest fossil; read as a myriapod by A8 [2])	396–407 (paper); 410.8–407.6 (2023 chart)	66.89–66.92; 66.92–66.92	fossil	A8 [1, 2]
<i>Asteroxylon mackiei</i> (A6: <i>Asteroxylon</i> roots)	407	66.92	fossil	A3 [36]; A6 [35]
insect flight	~406	66.91	molecular	A6 [24]; A8 [3]
<i>Winfrenatia reticulata</i> lichen	about 400	66.90	fossil	A5 [17]
peroxidase ancestor	399 ± 140	66.90 (66.50–67.17)	molecular	A5 [36]
tetrapod trackways, Zachelmie	393.3–387.7 (Eifelian)	66.88–66.87	fossil (trace)	A6 [28, 1]
first forests (Cairo, Gilboa)	~385	66.86	fossil	A6 [47, 48]
elpistostegids, implied	383.3–377.7	66.86–66.85	fossil (computed)	A6 [28, 1]
wood borings	~383–359	66.86–66.80	fossil	A6 [44]
tetrapod body fossils, implied	375.3–369.7	66.84–66.83	fossil (computed)	A6 [28, 1]
fish-tetrapod transition (<i>Tiktaalik</i>)	>370	66.83	fossil	A6 [29]
<i>Archaeopteris</i> modern-type tree, Morocco	~370	66.83	fossil	A6 [49]
AA2 diversification	350–295	66.78–66.62	molecular	A5 [5]
major extant insect lineages	~345	66.76	molecular	A6 [24]

winged insects, <i>Delitzschala</i>	330.9–323.2	66.73–66.71	fossil	A6 [25]
second herbivory phase	327–309	66.72–66.66	not stated	A8 [5]
leaf-margin feeding (A8: first leaf feeding)	326	66.71	fossil (A7, A8: not stated)	A6 [41]; A7 [6]; A8 [5]
Caulimoviridae (endogenous in vascular-plant genomes)	at latest about 320	66.70	molecular	A10 [1]
reptiles, Joggins	318–303	66.69–66.65	fossil	A6 [30]
tetrapod herbivore, <i>Melanedaphodon</i> (A7: first synapsid herbivore; A8: first vertebrate herbivore)	~307	66.66	fossil (A7: not stated)	A6 [45]; A7 [7]; A8 [6]
insect gall	~302	66.64	fossil	A6 [42]
enzymatic lignin decay (white rot)	~300	66.64	molecular	A5 [35, 34]
crown Agaricomycetes	299 (351–252)	66.63 (66.78– 66.48)	molecular	A3 [17]; A5 [5]
earthworm crown	298.9	66.63	molecular	A6 [57]
<i>Sulcia</i> in the auchenorrhynchan ancestor	≥260	66.51	molecular	A2 [10]
<i>Sulcia</i> – <i>Nasuia</i> partnership	>200 (origin before 260)	66.27 (origin before 66.51)	molecular	A2 [11]
manganese-peroxidase- type clade D	259 ± 94	66.50 (66.09– 66.79)	molecular	A5 [36]
end-Permian fungal spike	254–252	66.49–66.48	fossil	A5 [40, 41]
<i>Buchnera</i> in aphids	200–250	66.27–66.47	molecular	A2 [12]
volvocine colonies	~250	66.47	molecular	A3 [39]
lepidopteran tube-like proboscis	~241	66.44	molecular	A8 [10]
scleractinian corals, expansion and diversification	~240	66.43	fossil	A4 [3]
calcareous dinoflagellates (first calcifiers)	about 233	66.41	fossil	A9 [11]
crown Laminariales	83.44 / 231.51	65.47 / 66.40	molecular	A3 [42]
volvocine colonies	~230	66.40	molecular	A3 [40]
coccolithophores	about 215–210	66.33–66.31	fossil	A9 [11]
coral–dinoflagellate photosymbiosis	~212	66.32	fossil + geochemical (isotopes)	A4 [3]
multicellular volvocine lineage	≥200	66.27	molecular	A3 [41]
<i>Wolbachia</i> supergroups	~200	66.27	molecular	A4 [5]

A and B				
diatoms	about 200	66.27	molecular	A9 [12]
versatile peroxidase	194 ± 70	66.24 (65.83–66.52)	molecular	A5 [36]
lignin peroxidase	178 ± 64	66.16 (65.76–66.44)	molecular	A5 [36]
termites split from <i>Cryptocercus</i>	~170 (153–196)	66.12 (66.02–66.25)	molecular	A4 [6]
definitive pollinators on gymnosperms (11 scorpionfly species)	~165	66.09	fossil	A8 [8]
Symbiodiniaceae, earliest diversification	~160	66.07	molecular	A4 [4]
bioluminescence in ray-finned fishes (Stomiiformes)	~150	66.01	molecular	A4 [10]
termite crown	149 (136–170)	66.00 (65.92–66.12)	molecular	A4 [6]; A5 [51]
<i>Azolla</i> cyanobiont	up to 140	65.94	not stated	A2 [15]
<i>Paulinella</i> chromatophore (maximum age)	90–140; main scheme 93.6 (38.1–138.2); alternative 141.4 (48.7–210.4); others 55.8, 47.9	65.54–65.94; main 65.58 (64.76–65.93); alternative 65.95 (64.98–66.31); others 65.11, 64.97	molecular	A2 [13]
first undisputed termite fossils	110–135	65.72–65.91	fossil	A4 [6]
termites	135	65.91	fossil	A5 [51]
main angiosperm clades diversify	135–130	65.91–65.88	molecular	A8 [4]
crown Fucales	65.81 / 134.28	65.26 / 65.91	molecular	A3 [42]
diatoms, oldest abundant record (Aptian, eastern Australia)	125–115	65.84–65.76	fossil	A9 [12]
crown bees	123 (113–132)	65.83 (65.75–65.89)	not stated	A8 [13]
Scolytinae	100–120	65.64–65.80	molecular	A5 [52]
diatoms, Weddell Sea record	113–110	65.75–65.72	fossil	A9 [12]
first beetle pollinator	105	65.68	not stated	A8 [9]
nodulation predisposition, angiosperms	slightly over 100	65.64	molecular	A9 [13]
<i>E. coli</i> – <i>Salmonella</i> divergence	about 100	65.64	molecular	A1 [28]
<i>Azolla</i> cyanobiont	about 100	65.64	fossil	A2 [16]
<i>Padina</i> (oldest brown-alga calibration fossil)	≥100	65.64	fossil	A3 [42]

oldest bee	~100	65.64	fossil	A8 [12]
eudicot pollen on a beetle	99	65.63	fossil	A8 [11]
UCYN-A1 / UCYN-A2 split	about 91	65.55	molecular	A2 [14]
fleshy-fruit diversification	from ~80	65.43	not stated	A8 [16]
ant fungus farming	66.65 ± 13.28	65.27 (65.07–65.43)	molecular	A5 [46]
tribe Attini s.l.	66 (56–76)	65.26 (65.11–65.39)	molecular	A5 [47]
Neoaves radiation (36 lineages)	within 10–15 Myr after 66	65.26 (start of window)	molecular	A8 [17]
lower fungus farming in ants (A8: ant agriculture)	61 (52–70) to 57 (48–66) (A8: 61–57)	65.19 (65.04–65.31) to 65.13 (64.97–65.26)	molecular (A8: not stated)	A5 [47]; A8 [31]
<i>Azolla</i> cyanobiont	>60	65.17	not stated (review)	A2 [7]
fig-fig wasp co-divergence	at least 60 Myr	65.17	not stated	A8 [27]
oldest bats	Early Eocene (56.0–47.8)	65.11–64.97	fossil	A8 [19, 15]
oldest primate skeleton	~55	65.09	fossil	A8 [18]
Termitidae (prokaryote-only gut microbiota)	54 (46–66)	65.08 (64.93–65.26)	molecular	A4 [6]; A5 [51]
<i>Volvox-Chlamydomonas</i> ancestor	~50 ± 20	65.01 (64.54–65.31)	molecular	A3 [38]
ambrosia farming, oldest origin	~50	65.01	molecular	A5 [52]
<i>Myrmecopterula</i> MRCA	~48	64.97	molecular	A5 [46]
fungus-manipulated ant behaviour (death-grip scars)	48	64.97	fossil	A5 [58]
yucca moths	41.5 ± 9.8	64.84 (64.59–65.03)	not stated	A8 [28]
crown Ruminantia	39.1–32.3	64.78–64.61	molecular	A4 [11]
orchid bees	34–38	64.66–64.76	not stated	A8 [29]
yeast cultivar in ants	~32	64.60	molecular	A5 [46]
termite fungus farming	31.41 (25.82–39.53); earlier ~31 (19–49)	64.58 (64.41–64.79); earlier 64.57 (64.13–64.99)	molecular	A5 [49]
termite fungus farming (Macrotermitinae + <i>Termitomyces</i>)	~31.4 (25.82–39.53)	64.58 (64.41–64.79)	molecular	A4 [9]
higher ant agriculture	~27; 31 (26–37) to 27 (22–33)	64.45; 64.57 (64.41–64.73) to 64.45 (64.26–64.63)	molecular	A5 [46], [47]
crown Old World fruit	31–20	64.57–64.17	molecular	A8 [20]

bats				
HERV-K(HML2) infectious pool in the primate lineage	30 (persisting for the past 30 Myr)	64.54	molecular	A10 [2]
perfume orchids (3 origins)	18–27	64.08–64.45	not stated	A8 [29]
fossil termite fungus gardens	24.8–24.5 (A5: ~25)	64.37–64.36	fossil	A4 [9]; A5 [49]
Pecora	23.3–20.8	64.31–64.21	molecular	A4 [11]
Xyleborini	~21	64.22	molecular	A5 [52]
leaf-cutter ants	19 (15–24) to 18 (14–22)	64.13 (63.91– 64.34) to 64.08 (63.85–64.26)	molecular	A5 [47]
ant domatia (at least 158 origins)	within 19 Myr	64.13	not stated	A8 [44]
spines in African woody plants (at least 55 origins)	within 17 Myr	64.02	not stated	A8 [45]
bovids in Africa	16	63.97	not stated	A8 [45]
hominid–gut bacteria cospeciation (Bacteroidaceae, Bifidobacteriaceae clades)	~15	63.91	molecular	A4 [12]
Darwin’s orchid and its hawkmoth	~7.5	63.28	not stated	A8 [30]
<i>Macrocystis</i>	~6	63.08	molecular	A3 [65]
dog, East Asian – Western Eurasian divergence	0.014–0.0064 (14,000–6,400 yr)	57.56–56.85	molecular	A10 [6]
cultivation of wild einkorn and rye (Abu Hureyra, Mureybit)	0.013–0.012 (13,000–12,000 cal BP)	57.49–57.42	fossil (archaeobotanical)	A10 [9]
plant and animal domestication, Eastern Mediterranean	0.012–0.011 (12th millennium cal BP)	57.42–57.34	fossil (archaeological)	A10 [8]
human land shaping (three quarters of land)	0.012 (12,000 yr)	57.42	not stated in the dossier	A10 [10]
several plant species under cultivation	at least 0.0115 (11,500 cal BP)	57.38	fossil (archaeobotanical)	A10 [9]
cattle, Euphrates valley	0.011–0.010 (11,000–10,000 cal BP)	57.34–57.25	fossil (archaeozoological)	A10 [9]
wheat and barley, onset	0.011–0.010 (11,000–10,000 yr BP)	57.34–57.25	not stated in the dossier	A10 [36]
sheep, herd management complete (Nevalı Çori)	about 0.0105 (~10,500 cal BP)	57.30	fossil (archaeozoological)	A10 [9]
emmer and einkorn	about 0.0105–	57.30–57.27	fossil	A10 [9]

wheat, secure domestic grain	0.0102 (~10,500–10,200 cal BP)		(archaeobotanical)	
pig (Cafer Höyük)	about 0.0103 (~10,300 cal BP)	57.28	fossil (archaeozoological)	A10 [9]
goat, managed (Nevalı Çori)	about 0.0102 (~10,200 cal BP)	57.27	fossil (archaeozoological)	A10 [9]
barley (Middle PPNB)	about 0.0100 (~10,000 cal BP)	57.25	fossil (archaeobotanical)	A10 [9]
maize (Xihuatoxtla, Balsas Valley)	0.0087 (8,700 cal BP)	57.13	fossil (starch and phytoliths)	A10 [37]
rice, Lower Yangtze	0.0069–0.0066 (6,900–6,600 yr)	56.92–56.88	fossil (spikelet bases)	A10 [38]
potyviruses, radiation	about 0.0066 (6,600 yr)	56.88	molecular	A10 [4]

C1, continued: first appearances without an age in Ma. These rows give only a period name or a time relative to another event, so no position is computed. They are listed in stratigraphic order as the period names run.

event or lineage	age (as printed)	position	evidence	chapter [ref]
demosponges (26-mes sterane)	Cryogenian (sequence ~100 Myr long)	—	geochemical	A3 [26]
predatory borings in <i>Cloudina</i> tubes	late Precambrian	—	fossil	A7 [1]
predatory borings in <i>Cloudina</i> tubes	uppermost (terminal) Neoproterozoic	—	fossil	A7 [2]
drilling, Palaeozoic phase (rare to moderately frequent)	latest Precambrian–Carboniferous	—	fossil	A7 [13]
oldest durophagy (shell damage on <i>Mobergella holsti</i>)	Cambrian (review of the Cambrian and possibly Ediacaran record)	—	fossil	A7 [3]
kleptoparasite encrusting <i>Neobolus wulongqingensis</i>	Lower Cambrian, Stage 4	—	fossil	A7 [4]
<i>Anomalocaris canadensis</i>	Cambrian, Miaolingian, Wuliuan	—	fossil	A7 [9]
notable rise in frequency of predation traces	by the Ordovician	—	fossil	A7 [26]
Asteroidea, origin	Late Ordovician	—	not stated	A7 [12]
Asteroidea, onset of shell-breaking or drilling	by the Late Ordovician	—	not stated	A7 [12]
<i>Baragwanathia longifolia</i> (earliest club moss)	Gorstian (Ludlow, Silurian)	—	fossil	A3 [34]; A6 [15]
<i>Prototaxites</i>	Lower Devonian	—	fossil	A5 [12]; A6 [11]
Dipnoi, origin	Devonian	—	not stated	A7 [12]
Dipnoi, onset	Devonian	—	not stated	A7 [12]

first seeds	late Middle or Late Devonian	—	not stated	A8 [14]
oribatid mites, Gilboa	Givetian	—	fossil	A6 [74]
fleshy seeds (medullosan seed ferns)	Pennsylvanian	—	not stated	A8 [14]
enzymatic lignin decay	end of the Carboniferous	—	molecular	A6 [67]
at least 5 tetrapod herbivory origins	Late Carboniferous–Early Permian	—	not stated	A8 [7]
at least 5 tetrapod herbivore origins	by the Early Permian	—	not stated	A7 [8]
plant-eating vertebrates diversify	Permian	—	not stated	A8 [14]
drilling, Mesozoic phase (very rare or facultative)	Permian–Early Cretaceous	—	fossil	A7 [13]
seeds in a reptile gut (<i>Protorosaurus</i> , ~60 seeds)	Late Permian	—	fossil	A8 [14]
Naticacea, origin	Triassic	—	not stated	A7 [12]
Teleostei, origin	Triassic	—	not stated	A7 [12]
ectomycorrhiza in plants	Early Jurassic	—	not stated	A5 [26]
Mesozoic marine revolution, shell changes begin	Jurassic	—	fossil	A7 [12]
Heterodontidae, origin	Jurassic	—	not stated	A7 [12]
Heterodontidae, onset	Jurassic	—	not stated	A7 [12]
Batoidea, origin	Jurassic	—	not stated	A7 [12]
Stomatopoda, origin	Jurassic	—	not stated	A7 [12]
Palinuridae/Nephropidae, origin	Jurassic	—	not stated	A7 [12]
Brachyura, origin	Jurassic	—	not stated	A7 [12]
Aves, origin	Late Jurassic	—	not stated	A7 [12]
sturdier gastropod shells	Early Cretaceous	—	fossil	A7 [12]
other Neogastropoda, origin	Early Cretaceous	—	not stated	A7 [12]
fruits and seeds in an ankylosaur gut	Early Cretaceous	—	fossil	A8 [14]
oldest fossil mushroom (Crato Formation)	Lower Cretaceous	—	fossil	A3 [22]
Muricacea, origin	Albian	—	not stated	A7 [12]
Batoidea, onset	Cretaceous	—	not stated	A7 [12]
Cymatiidae, origin	Late Cretaceous	—	not stated	A7 [12]
Cymatiidae, onset	Late Cretaceous	—	not stated	A7 [12]
other Neogastropoda, onset	Late Cretaceous	—	not stated	A7 [12]
Stomatopoda, onset	possibly Late	—	not stated	A7 [12]

	Cretaceous			
drilling, Cenozoic phase (frequent gastropod drilling of molluscs)	Late Cretaceous- Holocene	—	fossil	A7 [13]
Naticacea, onset of drilling	by the Campanian	—	not stated	A7 [12]
Muricacea, onset of drilling	by the Campanian	—	not stated	A7 [12]
Brachyura, onset	latest Cretaceous or Paleocene	—	not stated	A7 [12]
Teleostei, onset	late Cretaceous or earliest Tertiary	—	not stated	A7 [12]
Aves, onset	Late Eocene	—	not stated	A7 [12]
<i>B. dendrobatidis</i> lineage BdASIA-1 emergence	early 20th century	—	molecular	A5 [55]
Palinuridae/Nephropidae, onset	date uncertain	—	not stated	A7 [12]
Pierid glucosinolate- detoxifying protein	within ~10 Myr after Brassicales	—	not stated	A8 [46]
hypsodont equids	at least 4 Myr after grass- dominated habitats	—	not stated	A8 [47]

C2 The order of connection

For each chapter, the oldest dated record of each connection itself (the interaction, not the partners). The ages of the two partner lineages are given where the chapter prints them. Rows run from the oldest connection to the youngest; connections that the chapters do not date follow at the end.

Rows dated only by a period name carry no position and stand where the period name falls in the sequence. Positions are given for each printed age in the order printed.

connection (partner X - partner Y)	first record of the connection (Ma)	position	age partner X (Ma)	age partner Y (Ma)	chapter [ref]
primary plastid (eukaryote host - cyanobacterium)	about 2,100 (branching; establishment about 200 Myr later); 2,137- 1,807; >1,500	68.41; 68.42- 68.27; 68.10	not given	not given	A2 [6], [5], [7]; A3 [11]
mitochondrion (Asgard-related host - proteobacterial guest)	2,053-1,210	68.39-67.91	host: not given (eukaryotes nest within Asgard, [17])	guest: no age given [19]	A2 [4]; A9 [8]
serial red plastid transfer, step 1	1,079-650 (window for the	67.80-67.34	1,281-1,675 (red-algal	440-1,658	A2 [5, 31]

(red alga – cryptophytes)	serial secondary endosymbioses)		plastid donor stem)		
serial red plastid transfer, step 2 (cryptophyte – ochrophyte ancestor)	1,079–650 (same window)	67.80–67.34	440–1,658	622–1,298	A2 [5, 31]
serial red plastid transfer, step 3 (ochrophyte – haptophyte ancestor)	1,079–650 (same window)	67.80–67.34	622–1,298	579–1,943	A2 [5, 31]
tertiary plastid in a stem ochrophyte	≤819 (633–1,017)	67.55 (67.32–67.75)	ochrophytes 622–1,298	donor: not given	A2 [5]
predation: unknown driller – <i>Cloudina</i> (bored tubes)	late Precambrian; uppermost Neoproterozoic	—	driller not identified	not given	A7 [1], [2]
shell crushing (durophagy) on <i>Mobergella holsti</i>	Cambrian	—	not given	not given	A7 [3]
parasitism: kleptoparasitic tube-dwellers – <i>Neobolus</i> brachiopod	Lower Cambrian, Stage 4	—	not given	not given	A7 [4]
AM fungi (Glomeromycota) – land plants	ca. 480 (clock); first fossil arbuscules 411.5 ± 1.3	67.07; 66.93	659 (715–606)	482 (485–473), crown embryophytes	A5 [5], [14, 15]; A6 [8], [31]
lichens (fungus – photobiont)	467–410 (ascolichens, clock); 415 (stratified lichens, fossil); about 400 (<i>Winfrenatia</i>)	67.04–66.92; 66.93; 66.90	not given	not given	A5 [5], [16], [17]
shell-breaking or drilling predators – shelled prey (earliest onset: Asteroidea)	by the Late Ordovician	—	Asteroidea: Late Ordovician	not given	A7 [12]
microbes on vent tubeworm tubes (epibiotic association)	~440 (poorly constrained)	66.99	not given	not given	A4 [2]
pentastomid – ostracod (parasitism)	425	66.95	not given	not given	A7 [5]
arthropods – land plants (herbivory, phase 1)	417–403	66.94–66.91	insects ~479 (clock); oldest insect fossil 396–407 or	482 (485–473); 515.1–470.0 (clock)	A6 [41], [24], [8], [13]; A7 [6]; A8 [5], [1], [3]

			410.8–407.6		
nematodes – land plants (possible parasitism)	411.5 ± 1.3 (Rhynie)	66.93	411.5 ± 1.3, Rhynie	473–471, cryptospores	A6 [38, 31], [12]
mycophagous mites and springtails – fungi	411.5 ± 1.3 (Rhynie)	66.93	411.5 ± 1.3, Rhynie	1,010–890, <i>Ourasphaira</i>	A6 [38, 31], [7]
wood-boring animals – wood	~383–359	66.86–66.80	not given	not given	A6 [44]
caulimovirids – vascular plants (endogenous insertions)	at latest about 320	66.70	at latest about 320 (virus family)	not given	A10 [1]
tetrapods – land plants (herbivory)	~307	66.66	393.3–387.7, trackways	473–471, cryptospores	A6 [45], [28, 1], [12]; A7 [7]; A8 [6]
white-rot Agaricomycetes – wood (decay of dead wood)	~300	66.64	299 (351–252)	482 (485–473)	A5 [35, 34], [5]
fleshy seeds – vertebrates (seeds in a reptile gut)	Late Permian	—	fleshy seeds: Pennsylvanian	first vertebrate herbivore ~307; diversification Permian	A8 [14], [6]
<i>Sulcia</i> – auchenorrhynchan insects	≥260	66.51	not given	lineage split ≥200	A2 [10]
<i>Sulcia</i> – <i>Nasua</i> (in leafhoppers)	>200 (origin before 260)	66.27 (66.51)	not given	not given	A2 [11]
<i>Buchnera</i> – aphids	200–250	66.27–66.47	not given	not given	A2 [12]
scleractinian corals – Symbiodiniaceae (photosymbiosis)	~212	66.32	~240 (expansion)	~160	A4 [3], [4]
ectomycorrhizal fungi – plants	Early Jurassic	—	not given	not given	A5 [26]
scorpionflies – gymnosperms (pollination)	~165	66.09	not given	not given	A8 [8]
bioluminescence in ray-finned fishes (bacterial light in at least 17 of 27 origins)	~150 (earliest origin, Stomiiformes)	66.01	not given	not given	A4 [10]
<i>Azolla</i> – cyanobiont	up to 140; about 100 (fossil); >60	65.94; 65.64; 65.17	not given	not given	A2 [15], [16], [7]
<i>Paulinella</i> – chromatophore	90–140 (maximum age)	65.54–65.94	not given	not given	A2 [13]
insects –	105 (first	65.68; 65.63	135–130	396–407 or	A8 [9], [11],

angiosperms (pollination)	beetle pollinator); 99 (eudicot pollen on a beetle)			410.8–407.6 (fossil); ~479 (molecular)	[4, 1, 3]
N ₂ -fixing bacteria – nodulating angiosperms	slightly over 100 (nodulation predisposition)	65.64	N ₂ fixation ≥3,200; nitrogenase 1,500–2,200 (metabolism, not lineage)	not given (plant trait only)	A9 [13], [4], [5]
lateral gene transfer into <i>E. coli</i> (donors – <i>E. coli</i>)	since divergence from <i>Salmonella</i> , about 100; mean age of introduced genes 14.4	65.64; 63.87	not given	<i>E. coli</i> – <i>Salmonella</i> divergence about 100	A1 [28]
ants – cultivated fungi (fungus farming)	66.65 ± 13.28; 61 (52–70) to 57 (48–66)	65.27; 65.19–65.13	tribe Attini s.l. 66 (56–76)	not given	A5 [46], [47]; A8 [31]
figs – fig wasps (co-divergence)	at least 60 Myr	65.17	one age for the pair	one age for the pair	A8 [27]
ambrosia beetles – fungi (farming)	~50 (oldest origin)	65.01	Scolytinae 100–120	not given	A5 [52]
fungi – ants (behaviour manipulation, death-grip scars)	48	64.97	not given	not given	A5 [58]
termites (Macrotermitinae) – <i>Termitomyces</i>	31.41 (25.82–39.53); ~31.4; fossil gardens 24.8–24.5	64.58; 64.37–64.36	Agaricomycetes crown 299 (351–252)	termite crown 149 (136–170)	A4 [9]; A5 [49], [5], [51]
HERV-K(HML2) – primates (germ-line reinfection)	infectious pool for the past 30 Myr	64.54	not given	not given	A10 [2]
spiny African woody plants – bovids (browsing)	spines within the last 17 Myr	64.02	spiny clades within the last 17 Myr	16 (arrival in Africa)	A8 [45]
hominids – gut Bacteroidaceae and Bifidobacteriaceae (cospeciation)	~15	63.91	not given	bacterial divergence times match the hosts'	A4 [12]
Darwin's orchid – hawkmoth (obligate pair)	~7.5	63.28	one age for the pair	one age for the pair	A8 [30]
humans – dogs	0.014–0.0064 (East Asian – Western Eurasian divergence; the dog is the first domesticate)	57.56–56.85	not given	not given	A10 [6], [5]

humans - cereals (cultivation of wild einkorn and rye)	0.013-0.012	57.49-57.42	not given	not given	A10 [9]
potyviruses - crop plants	about 0.0066 (radiation)	56.88	not given	crop lineages not given; domestication dates only	A10 [4]
<i>B. dendrobatidis</i> - amphibians	emergence early 20th century; declines peak in the 1980s	—	not given	not given	A5 [55], [54]
Bacteria - Archaea (gene transfer at 13 archaeal origins)	not dated	—	crown Bacteria <3,400	crown Archaea <3,400	A1 [33], [6]
MK-D1 - <i>Halodesulfovibrio</i> / <i>Methanogenium</i> (co-culture)	not dated	—	not given	not given	A1 [26]; A2 [18]
<i>Nanoarchaeum</i> <i>equitans</i> - <i>Ignicoccus</i>	not dated	—	not given	not given	A1 [27]
UCYN-A - prymnesiophyte alga (N for C)	not dated (UCYN-A1 / UCYN-A2 split about 91)	65.55	not given	not given	A2 [14], [37]; A9 [24]
haptophyte - dinoflagellates (Kareniaceae)	not dated	—	579-1,943	696-1,520 (myzozoans)	A2 [26, 5]
diatoms - dinoflagellates (dinotoms)	not dated	—	622-1,298 (ochrophytes)	696-1,520 (myzozoans)	A2 [26, 5]
<i>Algoriphagus</i> - <i>Salpingoeca</i> <i>rosetta</i> (rosette induction)	not dated	—	not given	not given	A3 [45]
<i>Ochromonas</i> - <i>Chlorella</i> (predation, laboratory)	not dated (laboratory)	—	not given	not given	A3 [48]
<i>Paramecium</i> - <i>Chlamydomonas</i> (predation, laboratory)	not dated (laboratory)	—	not given	not given	A3 [49]
<i>Wolbachia</i> - arthropods	not dated (co- divergence of four strains ~2 Myr)	62.08	supergroups A and B ~200	not given	A4 [5]
termites - gut protists	not dated	—	not given	termites split from <i>Cryptocercus</i> ~170; crown 149	A4 [6, 7]

ruminants - rumen microbes	not dated	—	not given	crown Ruminantia 39.1-32.3	A4 [11]
flowering plants - insect herbivores	not dated	—	135-130	396-407 or 410.8-407.6 (fossil); ~479 (molecular)	A8 [41, 4, 1, 3]
angiosperms - bees (pollination)	not dated	—	135-130	crown 123 (113-132); oldest bee ~100	A8 [4, 13, 12]
perfume orchids - orchid bees	not dated	—	18-27	34-38	A8 [29]
yuccas - yucca moths	not dated	—	not given	41.5 ± 9.8	A8 [28]
fleshy-fruited angiosperms - Neoaves (seed dispersal)	not dated	—	from ~80	radiation within 10-15 Myr after 66	A8 [16, 17]
fleshy-fruited angiosperms - primates (seed dispersal)	not dated	—	from ~80	~55	A8 [16, 18]
fleshy-fruited angiosperms - bats (seed dispersal)	not dated	—	from ~80	Early Eocene (56.0-47.8)	A8 [16, 19, 15]
fleshy-fruited angiosperms - Old World fruit bats (seed dispersal)	not dated	—	from ~80	crown 31-20	A8 [16, 20]
Brassicales - Pieridae (glucosinolate detoxification)	not dated (lag ~10 Myr after Brassicales)	—	not given	not given	A8 [46]
grasslands - hypsodont equids	not dated (lag at least 4 Myr)	—	not given	not given	A8 [47]

C3 Repeated origins

Every count of independent origins, and of losses where one is printed, in the ten chapters. Counts are lower bounds where the chapter says “at least”.

trait or connection	number of origins	number of losses	chapter [ref]
lateral transfer events into <i>E. coli</i> MG1655 since divergence from <i>Salmonella</i>	at least 234 events (755 ORFs)	—	A1 [28]
gene acquisitions from bacteria at the origins of 13 archaeal higher taxa	2,264 acquisitions (174 per origin, computed)	—	A1 [33]

foreign genes in humans surviving re-examination	7 genes from 4 hypothesised transfer events	—	A1 [45]
mitochondrion	1 (single endosymbiotic event)	—	A2 [1]
primary plastid	1 (single occasion; one ancestor of glaucophyte, red and green plastids)	—	A2 [26], [1]
plastids	—	loss at least once	A2 [1]
green plastids at second hand (euglenids, chlorarachniophytes)	2 (separate occasions)	—	A2 [1], [26]
red plastids at second hand	1 (one uptake) or 3 (serial transfers); number unclear by [26]	—	A2 [1], [31], [26]
permanent plastid replacements in dinoflagellates (haptophyte-derived; green-alga-derived)	2	—	A2 [26]
plastid acquisitions, all named events	minimum 7; about 9 (computed)	—	A2 [1][26][31][5]
primary endosymbiotic events (mitochondrion, plastid, <i>Paulinella</i> , UCYN-A)	4	—	A2 [38]
nucleomorph-bearing lineages (cryptophytes, chlorarachniophytes), genomes independently reduced	2	—	A2 [2]
cyanobacterial symbioses with plants	multiple times independently (no number)	—	A2 [7]
multicellularity across eukaryotes	more than 25 (25 “very likely a serious underestimate” by [2])	—	A3 [1], [2]
aggregative multicellularity	at least 7 lineages	—	A3 [1]
divisional multicellularity in red and green algae	numerous (no number)	—	A3 [1]
divisional multicellularity in brown algae	1	—	A3 [1]
multicellularity within Amorphea besides animals	3	—	A3 [1]
aggregative multicellularity within Amoebozoa (dictyostelids,	2	—	A3 [1]

<i>Copromyxa</i>)			
filamentous growth in Zygnematophyceae	at least 5	—	A3 [3]
macroscopic growth in green seaweeds	multiple transitions (no number)	—	A3 [13]
complex multicellularity	5 groups	—	A3 [5]
multicellularity in cyanobacteria	re-established at least once (<i>Spirulina</i> sp. PCC 6313)	reversals to unicellularity at least 5	A3 [6]
complex multicellularity (fruiting body) in fungi	8–11; preprint 8–12	—	A3 [52]
chemosynthetic symbioses in animals (at least 7 phyla)	multiple occasions (no number)	—	A4 [13]
bioluminescence in ray-finned fishes	27 (in 14 major clades; 16 in the figure caption)	—	A4 [10]
bacterially mediated light in ray-finned fishes	at least 17	—	A4 [10]
intrinsic light in ray-finned fishes	8	—	A4 [10]
light production, bacteria to fish	many times (no number)	—	A4 [26]
termite fungus farming (Macrotermitinae + <i>Termitomyces</i>)	1 (single origin, Africa)	no reversal to free-living fungi	A4 [8]; A5 [48]
ectomycorrhiza in fungi	at least 66; 78–82 lineages by a later count	—	A5 [24], [25]
ectomycorrhiza in plants	30 (2 gymnosperm, 28 angiosperm lineages)	—	A5 [26]
lichenisation	20–30 (14–23 in Ascomycota, 6–7 in Basidiomycota)	—	A5 [30]
brown rot	at least 4	—	A5 [37]
clonal vertical transmission in fungus-growing termites	2 (<i>Microtermes</i> via females; <i>Macrotermes bellicosus</i> via males)	—	A5 [48]
ant agriculture	1	—	A5 [46]
fungus farming in ambrosia beetles	at least 10; reconstructions give 10 or 11	—	A5 [52]
mycangium in ambrosia beetles	one with each new origin of the symbiosis	—	A5 [53]
insect farming of fungi (ants, ambrosia beetles, termites)	at least 12, in three groups (Pattern)	—	A5 [46, 48, 52] (Pattern)
roots (lycophytes, euphyllophytes)	2 (stepwise and independently)	—	A6 [35]
tetrapod herbivory	at least 5	—	A6 [46]; A7 [8]; A8 [7]
parasitism in animals	at least 223, in 15 phyla (14.9 per phylum,	—	A7 [16]

	computed)		
haustorial parasitism in flowering plants	12	—	A7 [17]
plant parasitism in nematodes	4 independent clades	—	A7 [19]
bat pollination	many times independently (no number)	—	A8 [26]
obligate pollination pairs	at least 5	—	A8 [27, 28, 29, 30, 31]
perfume orchids	3	—	A8 [29]
ant dispersal of seeds	at least 101, possibly 147	—	A8 [36]
extrafloral nectaries	at least 457 (3,941 species)	—	A8 [43]
ant domatia	at least 158 (681 species), within 19 Myr	—	A8 [44]
spines in African woody plants	at least 55, within 17 Myr	—	A8 [45]
nodulation predisposition in angiosperms	1 (single origin)	—	A9 [13]
root nodules (nodulating families)	about 8	about 10	A9 [13]
syncytins captured from retroviral <i>env</i> genes in mammals	multiple occasions, independently (no number); some replaced earlier ones	—	A10 [3]
photosynthesis genes from <i>Prochlorococcus</i> to phages	multiple host-to-phage transfers (no number)	—	A10 [33]
domestic lineages in the Fertile Crescent	multiple domestic lineages per species (no number)	—	A10 [8]

C4 Sizes

All rows of the Sizes tables of the ten chapters, sorted by position, smallest first. A row with several positions is placed by its smallest. Masses carry no position and stand at the end.

The mark after the reference is the chapter's own (measured, computed, modelled).

what	size	position	chapter [ref]
MK-D1 protrusions, width	80–100 nm	0.51–0.72	A1 [26]
ultra-small groundwater bacteria (CPR), median axes	189.7 / 242.5 / 322.6 nm	1.30 / 1.52 / 1.78	A1 [46]
MK-D1 (Asgard) cell	300–750 nm; mean 550	1.72–2.55; 2.27	A1 [26]

MK-D1 (Asgard) cell	300–750 nm; mean 550 nm	1.72–2.55; 2.27	A1 [29]
MK-D1 (Asgard host relative) cell	300–750 nm; mean 550 nm	1.72–2.55; 2.27	A2 [18]
<i>Nanoarchaeum equitans</i> , diameter	about 400 nm	1.98	A1 [27]
<i>Pyrococcus furiosus</i> , width	0.8–2.5 μm	2.61–3.64	A1 [47]
host of UCYN-A1	1–3 μm	2.81–3.81	A2 [14]
hypha, <i>Winfrenatia</i> lichen	1–4 μm	2.81–4.07	A5 [17] (measured)
lichen hypha, Rhynie	1–4 μm	2.81–4.07	A6 [37] (measured)
most bacterial cells, length	about 2 μm	3.44	A1 [48]
Isua graphite globules	2–5 μm	3.44–4.28	A1 [11]
<i>Cyanidioschyzon merolae</i> , unicellular red alga	2 μm	3.44	A3 [53] (measured)
Fungal hypha, narrowest of 31 soil strains	2.7 μm	3.72	A3 [54] (measured)
hyphal diameter, 31 soil strains	2.7–6.5 μm	3.72–4.51	A5 [2] (measured)
<i>Ramathallus lobatus</i> cells (1.65 Ga)	5–15 μm	4.28–5.28	A2 [8]
<i>S. rosetta</i> cell, equivalent spherical diameter	5.87 μm	4.42	A3 [47] (computed)
Fungal hypha, widest of 31 soil strains	6.5 μm	4.51	A3 [54] (measured)
<i>Braarudosphaera bigelowii</i> , host of UCYN-A2	7–10 μm	4.58–4.91	A2 [14]
Nuvvuagittuq filaments, mean	8.3 μm	4.74	A1 [9]
Løkken-Høydal filaments / tubes	9.1 / 19.5 μm	4.82 / 5.51	A1 [9]
<i>Chlamydomonas reinhardtii</i> unicell	10 μm	4.91	A3 [55] (measured)
photobiont cell, <i>Winfrenatia</i>	15 μm	5.28	A5 [17] (measured)
Boring width in <i>Cloudina</i> , smallest (study 2)	1.5×10^{-5} m	5.28	A7 [2] (measured)
Nuvvuagittuq tubes, mean	24.9 μm	5.74	A1 [9]
net opening, <i>Winfrenatia</i>	25 μm	5.74	A5 [17] (measured)
<i>Rafatazmia</i> compartments, length	30–165 μm	5.91–7.46	A2 [8]

AM spore, <i>R. intraradices</i>	40–140 μm	6.17–7.31	A5 [29] (measured)
Bore-hole diameter in <i>Cloudina</i> , smallest (study 1)	4×10^{-5} m	6.17	A7 [1] (measured)
<i>Rafatazmia</i> central disks	50–60 μm	6.37–6.54	A2 [8]
<i>Rafatazmia chitrakootensis</i> filaments, width	58–175 μm	6.51–7.51	A2 [8]
Boring width in <i>Cloudina</i> , largest (study 2)	8.5×10^{-5} m	6.85	A7 [2] (measured)
AM spore, mean (n = 170)	93.3 μm	6.94	A5 [29] (measured)
<i>Denaricion mendax</i> filaments	130–275 μm	7.24–7.92	A2 [8]
<i>Eoalvinellodes annulatus</i> tube, narrowest	0.2 mm	7.63	A4 [2] (measured)
mite, Rhynie	290–450 μm	7.97–8.37	A6 [33] (measured)
springtail head, <i>Rhyniella</i>	300–400 μm	8.00–8.26	A6 [33] (measured)
Seed in an Early Cretaceous ankylosaur gut	3×10^{-4} m	8.00	A8 [14] (measured)
Median drill-hole diameter, Ordovician	3.5×10^{-4} m	8.14	A7 [14] (measured)
Bore-hole diameter in <i>Cloudina</i> , largest (study 1)	4×10^{-4} m	8.26	A7 [1] (measured)
<i>Ramathallus lobatus</i> thalli	about 0.5 to >3 mm	8.47 to >10.10	A2 [8]
largest bacterium before 2022	750 μm	8.84	A1 [48]
<i>Proterocladus antiquus</i> , order of size	1 mm	9.10	A3 [12] (measured)
Evolved snowflake yeast cluster, order of size	1 mm	9.10	A3 [50] (measured)
Termite hindgut, edge of a cube of 1 μL	1 mm	9.10	A4 [14] (computed)
peloid, fossil termite comb	~1 mm	9.10	A5 [49] (measured)
thallus band, <i>Winfrenatia</i>	1–2 mm	9.10–9.73	A5 [17] (measured)
Torridonian microfossil	~1 mm	9.10	A6 [4] (measured)
springtail, <i>Rhyniella</i>	1–2 mm	9.10–9.73	A6 [33] (measured)
marine snow, smaller compact aggregates	1–2.5 mm	9.10–9.93	A9 [55] (measured)
<i>Eoalvinellodes</i>	3 mm	10.10	A4 [2] (measured)

<i>annulatus</i> tube, widest			
<i>Yamankasia rifeia</i> tube, narrowest	3 mm	10.10	A4 [2] (measured)
Median drill-hole diameter, Quaternary	3.25×10^{-3} m	10.17	A7 [14] (measured)
trigonotarbid, two species	up to 4 mm	10.36	A6 [33] (measured)
marine snow, larger flocculent aggregates	4–5 mm	10.36–10.56	A9 [55] (measured)
<i>Ca. Thiomargarita magnifica</i> , cell with measured cytoplasm	4.27 mm	10.42	A1 [48]
Fruit in an Early Cretaceous ankylosaur gut	4.5×10^{-3} m	10.47	A8 [14] (measured)
soybean nodule diameter at day 45	5 mm	10.56	A9 [29] (measured)
rhizome trace width, Yunnan	5.9–18 mm	10.71–11.73	A6 [39] (measured)
trigonotarbid, <i>P. tuberculatus</i>	≥ 6 mm	10.73	A6 [33] (measured)
<i>Eospermatopteris</i> root	0.7–1 cm	10.87–11.19	A6 [47] (measured)
<i>T. magnifica</i> , mean length	9.72 ± 4.25 mm	11.17	A1 [48]
Isua stromatolites, height	1–4 cm	11.19–12.46	A1 [13]
<i>Dickinsonia</i> , narrowest specimen	1.0 cm	11.19	A3 [29] (measured)
cell, fossil termite comb	~ 10 mm	11.19	A5 [49] (measured)
Ant dispersal distance, shortest	0.01 m	11.19	A8 [37] (measured)
rhizome trace width, mean	10.5 mm	11.24	A6 [39] (measured)
trigonotarbid, larger specimens	14–20 mm	11.50–11.83	A6 [33] (measured)
<i>T. magnifica</i> , maximum length	20.00 mm	11.83	A1 [48]
fossil comb height	3–6 cm	12.19–12.83	A5 [49] (measured)
<i>Yamankasia rifeia</i> tube, widest	39 mm	12.43	A4 [2] (measured)
fossil nest chamber diameter	4–13 cm	12.46–13.53	A5 [49] (measured)
<i>Riftia pachyptila</i> tube, diameter	5 cm	12.66	A4 [25] (measured)
<i>Dickinsonia</i> , widest specimen	6.0 cm	12.83	A3 [29] (measured)
fossil comb width	6–9 cm	12.83–13.19	A5 [49] (measured)
<i>Archaeopteris</i> primary root	6–16 cm	12.83–13.72	A6 [47] (measured)

<i>Anomalocaris</i> body-lobe width, large specimens, lower	0.060 m	12.83	A7 [9] (measured)
<i>Anomalocaris</i> body-lobe width, large specimens, upper	0.070 m	12.97	A7 [9] (measured)
Human colon content, edge of a cube of 0.4 L	7.37 cm	13.01	A4 [1] (computed)
fossil nest chamber height, maximum	8 cm	13.09	A5 [49] (measured)
Rhynie vascular plant height	10–40 cm	13.29–14.55	A6 [34] (measured)
<i>Macrocystis</i> frond elongation, lower daily value	12.8 cm	13.52	A3 [56] (measured)
<i>Caulerpa taxifolia</i> frond, lower value	15 cm	13.66	A3 [57] (measured)
<i>Eospermatopteris</i> base	20–50 cm	13.92–14.76	A6 [47] (measured)
<i>Macrocystis</i> frond elongation, upper daily value	23.3 cm	14.06	A3 [56] (measured)
<i>Caulerpa taxifolia</i> frond, upper value	30 cm	14.29	A3 [57] (measured)
<i>Arthropleura</i> partial remains	76 × 36 cm	15.14; 14.46	A6 [72] (measured)
largest <i>Rhizocarpon</i> thallus	480 mm	14.72	A5 [33] (measured)
<i>Arthropleura</i> width	~55 cm	14.84	A6 [72] (measured)
<i>Dawsonia superba</i> stem, tallest moss	65 cm	14.99	A3 [58] (measured)
insect wingspan, maximum	~70 cm	15.06	A6 [73] (measured)
maximum fossil insect wingspan	about 70 cm	15.06	A9 [48] (measured)
Lokiarchaeota sample, below seafloor	75 cm	15.12	A1 [23]
<i>Caulerpa taxifolia</i> stolon, one coenocytic cell	1 m	15.39	A3 [57] (measured)
<i>Eospermatopteris</i> root reach	1–2 m	15.39–16.02	A6 [47] (measured)
Ant dispersal distance, typical	1 m	15.39	A8 [37] (measured)
Dickinsoniids, largest	1.4 m	15.69	A3 [29] (measured)
Human reference man, height	1.70 m	15.87	A3 [59] (measured)
Human reference man, height	1.70 m	15.87	A4 [1] (measured)
Carboniferous lycopsid	2 m	16.02	A3 [60] (measured)

trunk, width			
lycopsid trunk diameter	2 m	16.02	A6 [65] (measured)
<i>Aegirocassis</i> body length (more than)	2 m	16.02	A7 [11] (measured)
<i>Arthropleura</i> length	2.63 m	16.27	A6 [72] (measured)
<i>Riftia pachyptila</i> tube, length	3 m	16.39	A4 [25] (measured)
Rhynie chert section	c. 3.2 m	16.45	A6 [32] (measured)
Yunnan palaeosols, other	4.4; 7.8; 9.0 m	16.73; 17.26; 17.39	A6 [39] (measured)
<i>Prototaxites</i> trunk	8 m	17.28	A3 [21] (measured)
<i>Prototaxites</i> trunk	8 m	17.28	A5 [12] (measured)
<i>Prototaxites</i> trunk	8 m	17.28	A6 [11] (measured)
<i>Wattieza</i> tree height	≥8 m	17.28	A6 [48] (measured)
termite mound height	10 m	17.48	A5 [50] (measured)
<i>Archaeopteris</i> root system	11 m across	17.57	A6 [47] (measured)
<i>Archaeopteris</i> tree height	11–32 m	17.57–18.54	A6 [47] (modelled)
termite mound width	>15 m	17.85	A5 [50] (measured)
modern peat, maximum	15 m	17.85	A6 [71] (measured)
Yunnan palaeosol, exposed	15.5 m	17.88	A6 [39] (measured)
Schagen palaeosol section	17 m	17.97	A6 [3] (measured)
Yunnan palaeosol, original	17.0–19.4 m	17.97–18.09	A6 [39] (measured)
Carboniferous arborescent lycopsid, height	45 m	18.85	A3 [60] (measured)
lycopsid stature	c. 45 m	18.85	A6 [65] (measured)
Small passerines, distance within which 50 % of seeds fall	51 m	18.97	A8 [48] (measured)
<i>Macrocystis pyrifera</i> , length	>60 m (stated maximum)	19.11	A3 [42]
coal bed, rare maximum	61 m	19.13	A6 [71] (measured)
Ant dispersal distance, longest	77 m	19.34	A8 [37] (measured)
flux level at the base of the euphotic zone, below the surface	100 m	19.58	A9 [56] (modelled)
Medium-sized birds, dispersal distance (more than)	110 m	19.66	A8 [48] (measured)
<i>Sequoia sempervirens</i> , tallest tree measured	112.7 m	19.69	A3 [61] (measured)

Tree height, mechanical limit, lower	122 m	19.76	A3 [61] (modelled)
Tree height, mechanical limit, upper	130 m	19.82	A3 [61] (modelled)
Golfo Dulce, coastal bay	200 m deep	20.21	A9 [34] (measured)
continental shelf, outer limit of the measured decline, below the surface	200 m	20.21	A9 [44] (measured)
Michigan genet, ≥ 15 ha, side of equal square	387.3 m	20.81	A5 [65] (computed)
Carnivorous mammals, dispersal distance (more than)	495 m	21.03	A8 [48] (measured)
<i>Pando</i> clone, side of a square of 43 ha	656 m	21.29	A3 [62] (computed)
<i>Pando</i> clone, side of a square of 43.6 ha	660 m	21.30	A3 [62] (computed)
Michigan genet, ~ 75 ha, side of equal square	866.0 m	21.54	A5 [66] (computed)
deep flux level below the surface; sinking distance used for times	1,000 m	21.67	A9 [56] (modelled)
Elevation above which highland pollination networks lie	1,500 m	22.04	A8 [50] (measured)
MK-D1 sample, water above	2,533 m	22.52	A1 [26]
Joggins site, 689 ha, side of equal square	2,624.9 m	22.55	A6 [30] (computed)
<i>Armillaria ostoyae</i> genet, side of a square of 965 ha	3,106 m	22.71	A3 [63] (computed)
Oregon genet, ~ 965 ha, side of equal square	3,106.4 m	22.71	A5 [67] (computed)
Lokiarchaeota sample, water above	3,283 m	22.76	A1 [23]
<i>Armillaria ostoyae</i> genet, greatest distance between isolates	3,810 m	22.89	A3 [63] (measured)
Oregon genet, isolates apart	$\sim 3,810$ m	22.89	A5 [67] (measured)
Forest elephants, median dispersal distance	5,300 m	23.19	A8 [49] (measured)
Strelley Pool reef outcrop	10 km	23.77	A1 [19]
Oregon forest, $\sim 16,100$ ha, side of equal square	12,688.6 m	23.99	A5 [67] (computed)

Joggins sea cliffs	14.7 km	24.12	A6 [30] (measured)
Lokiarchaeota sample to Loki's Castle vents	about 15 km	24.14	A1 [23]
Forest elephants, maximum dispersal distance	101,000 m	25.87	A8 [49] (measured)
reference man	70 kg (mass)	— (mass)	A10 [41] (measured)
bacteria in the reference man, total	about 0.2 kg (mass)	— (mass)	A10 [41] (measured)

C5 Times

All rows of the Times tables of the ten chapters, sorted by position, smallest first. A row with several positions is placed by its smallest. Ages entered in the chapters' Times tables "as an age" are kept.

what	duration	position	chapter [ref]
Passerine gut passage, lower	5 min = 300 s	38.34	A8 [52] (measured)
<i>Vibrio (Pseudomonas) natriegens</i> , generation	9.8 min	38.96	A1 [50]
Passerine gut passage, upper	30 min = 1,800 s	39.98	A8 [52] (measured)
<i>Pyrococcus furiosus</i> , doubling (optimum 100 °C)	37 min	40.17	A1 [47]
<i>Vibrio fischeri</i> doubling, lower	0.93 h	40.54	A4 [20] (computed)
<i>Drosophila</i> , newly emerged, first check	1 h	40.61	A4 [18] (measured)
<i>Vibrio cholerae</i> , wild doubling	1.1 h	40.69	A1 [51]
<i>Vibrio fischeri</i> doubling, upper	1.8 h	41.14	A4 [20] (computed)
<i>Pseudomonas aeruginosa</i> , wild doubling	2.3 h (other estimate 1.9–2.4 h)	41.36 (41.19–41.40)	A1 [51]
median laboratory doubling	3 h	41.61	A1 [51]
median wild doubling	7.4 h (5.5 h without <i>M. florum</i> ; 95 % CI 3.1–19 h)	42.43 (42.16; 41.64–43.29)	A1 [51]
Squid light organ regrowth, lower	4 h	41.87	A4 [20] (measured)
<i>Drosophila</i> bacterial decline, detectable	6 h	42.24	A4 [18] (measured)
Squid light organ regrowth, upper	6 h	42.24	A4 [20] (measured)

Squid colonisation after hatching	12 h	42.87	A4 [20] (measured)
rhizosphere bacterial turnover	12-19 h	42.87-43.29	A9 [57] (measured)
<i>E. coli</i> , wild doubling	15 h	43.07	A1 [51]
short-term kleptoplast, initial yield >0.5	1-2 d	43.50-44.13	A2 [42]
<i>Drosophila</i> colonisation, 6 of 10 flies	24 h	43.50	A4 [18] (measured)
<i>Hydra</i> , second colonist delay, shortest	24 h	43.50	A4 [22] (measured)
Squid daily expulsion cycle	1 day	43.50	A4 [20] (measured)
share of oceanic microbial biomass killed by viruses, about 20 %	per day (86,400 s)	43.50	A10 [28] (measured)
<i>Salmonella enterica</i> , wild doubling	25 h	43.54	A1 [51]
Elephant gut passage	39.5 h = 142,200 s	43.95	A8 [49] (measured)
<i>Volvox carteri</i> generation	48 h	44.13	A3 [39] (measured)
<i>Hydra</i> , second colonist delay, middle	48 h	44.13	A4 [22] (measured)
soil bacterial turnover, about 20 °C	2.3-33 d, mean 9.3 d	44.26-46.68; 45.53	A9 [57] (measured)
<i>Hydra</i> , carrying capacity reached, upper	72 h	44.50	A4 [22] (measured)
fastest particle sinking 1,000 m at 175 m/day	5.7 d	45.09	A9 [55] (computed)
turnover, upper 200 m of open ocean	6-25 d	45.13-46.43	A1 [52]
short-term kleptoplast, fall	within 7-14 d	45.27-45.90	A2 [42]
<i>Hydra</i> , stable maximum observed	168 h	45.27	A4 [22] (measured)
Honey bee gut colonisation	10 days	45.60	A4 [16] (measured)
shift in mean mushroom fruiting, 83 species	13.3 days	45.85	A5 [68] (measured)
MK-D1, doubling	14-25 d	45.90-46.43	A1 [26]
flatworm kleptoplasts	about 2 weeks	45.90	A2 [26]
MK-D1, doubling	14-25 d	45.90-46.43	A2 [18]
anammox cell division	about 2 weeks (1.21 × 10 ⁶ s)	45.90	A9 [33] (measured)
wildebeest soft-tissue decay	2-10 weeks	45.90-47.37	A9 [54] (measured)
<i>Thuridilla hopei</i> kleptoplasts, up to	15 d	45.96	A2 [43]

long-term threshold (yield >0.4)	20 d	46.23	A2 [42]
<i>Macrocystis</i> mass doubling at 3.5 % per day	20.1 days	46.23	A3 [65] (computed)
<i>Ulva</i> competence for gametogenesis, earliest	3 weeks	46.27	A3 [66] (measured)
<i>E. timida</i> , starved before sequencing	28 d	46.53	A2 [43]
small aggregate sinking 1,000 m at 36 m/day	28 d	46.53	A9 [55] (computed)
<i>Mesodinium rubrum</i> kleptoplasts, up to	a month (30.44 d)	46.61	A2 [26]
<i>E. timida</i> , yield above 0.52	35 d	46.74	A2 [42]
<i>Ulva</i> competence for gametogenesis, latest	5 weeks	46.74	A3 [66] (measured)
soybean nodule reaches 5 mm	45 d	46.96	A9 [29] (measured)
new termite workers after swarming	1.5–3 months	46.98–47.61	A5 [50] (measured)
<i>P. ocellatus</i> , starved before sequencing	47 d	47.00	A2 [43]
<i>Durinskia capensis</i> , diatom kept	about 2 months (60.88 d)	47.24	A2 [26]
<i>P. ocellatus</i> , yield 0.78 → 0.59	74 d	47.42	A2 [42]
Degree Heating Week window	12 weeks	47.53	A4 [28] (agency definition)
litter half-life, rain forest	0.53 yr	48.29	A9 [21] (measured)
resampling interval, Human Microbiome Project	about 219 days	48.40	A10 [42] (measured)
replacement of 1.2×10^{30} cells at 1.7×10^{30} per year	0.7 yr	48.55	A1 (computed)
turnover, ocean below 200 m	0.8 yr	48.67	A1 [52]
<i>Chlamydomonas</i> + <i>Paramecium</i> experiment, 50 weekly transfers	350 days	48.83	A3 [49] (measured)
<i>Termitomyces</i> fruiting cycle	1 yr	48.87	A5 [50] (measured)
Snowflake yeast, 600 daily transfers	600 days	49.32	A3 [50] (computed)
litter half-life, median	2.3 yr	49.63	A9 [21] (measured)
replacement of 4–6 ×	2.4–3.5 yr	49.67–50.01	A1 (computed)

10 ³⁰ cells			
turnover, soil	2.5 yr	49.70	A1 [52]
Ross Sea dinoflagellate kleptoplasts, at least	30 months (913.2 d)	49.70	A2 [26]
large aggregate sinking 1,000 m at 1 m/day	1,000 d (2.7 yr)	49.79	A9 [55] (computed)
95 % wood mass loss	~3-750 yr	49.87-54.90	A5 [45] (measured)
litter half-life, tundra	3.9 yr	50.11	A9 [21] (measured)
World fisheries reference period, 1988 to 1991 inclusive	4 yr = 1.26×10^8 s	50.13	A7 [25] (computed)
Median return time of severe bleaching	6 years	50.50	A4 [29] (measured)
Serengeti grazing study, 1974 to 1979 inclusive	6 yr	50.50	A7 [24] (computed)
wildebeest bone decay	about 7 yr	50.64	A9 [54] (measured)
MK-D1 cultivation, published summary / preprint	10 / 12 yr	50.97 / 51.13	A1 [26]
three lines (1977) to three domains (1990)	13 yr	51.21	A1 (computed)
Aspen browsing record, 1998 to 2012	14 yr	51.27	A7 [23] (computed)
soil carbon to 1 m, stock / respiration flux	14.9-15.8 yr	51.33-51.38	A9 [58, 59] (computed)
Aspen browsing record, 1997 to 2012	15 yr	51.34	A7 [23] (computed)
Human reference man, age, lower	20 years	51.60	A3 [59] (measured)
Human reference man, age, lower	20 years	51.60	A4 [1] (measured)
Termite royal pair, maximum lifespan	20 years	51.60	A4 [30] (measured)
primary termite reproductives, maximum	~20 yr	51.60	A5 [50] (measured)
doubling time of anthropogenic mass	about 20 yr	51.60	A10 [49] (measured)
white-nose count span, 1995-2018	23 yr	51.72	A5 [57] (computed)
Human reference man, age, upper	30 years	51.97	A3 [59] (measured)
Human reference man, age, upper	30 years	51.97	A4 [1] (measured)
three lines (1977) to two domains (2013)	36 yr	52.13	A1 (computed)
Bleaching record, 1980-2016	36 years	52.13	A4 [29] (measured)
naming at ~1,300	40 yr	52.23	A5 [69]

species per year			
Helminth extinction-threat window, lower	50 yr	52.43	A7 [22] (measured)
Bd emergence to decline peak	60–80 yr	52.60–52.86	A5 [54, 55] (computed)
Helminth extinction-threat window, upper	100 yr	53.06	A7 [22] (measured)
vertebrate losses compressed into	100 yr	53.06	A10 [50] (measured)
Hawaiian soil, mineral P falls from 82 % to 1 %	300 to 20,000 yr	54.06–57.88	A9 [61] (measured)
rice non-shattering 27 % → 39 %	about 300 yr	54.06	A10 [38] (measured)
land-use record, 1700 to 2000	300 yr	54.06	A10 [51] (measured)
Termite mound, lower	700 years	54.83	A4 [30] (measured)
termite mound ages	~700; ≥2,200 yr	54.83; 55.88	A5 [50] (measured)
background time for the same vertebrate losses	800–10,000 yr	54.95–57.25	A10 [50] (measured)
naming 2.5 million fungi at 2,500 per year	938 yr	55.10	A5 [31] (computed)
turnover, subsurface	1–2 × 10 ³ yr	55.16–55.79	A1 [52]
management before morphology, at least	1,000 yr	55.16	A10 [8] (measured)
livestock reaching new regions after first domestication	1,300–4,300 yr	55.40–56.49	A10 [9] (computed)
Michigan genet, 1992 minimum	>1,500 yr	55.53	A5 [65] (measured)
Near East cereals to maize; maize to rice	1,800 yr each	55.69	A10 [9, 37, 38] (computed)
Oregon genet	1,900–8,650 yr	55.74–57.12	A5 [67] (measured)
Termite mound, fungus-growers, upper	2,200 years	55.88	A4 [30] (measured)
Michigan genet, 2018 minimum	2,500 yr	55.99	A5 [66] (measured)
wild cultivation to secure domestic grain	2,500–2,800 yr	55.99–56.10	A10 [9] (computed)
radiocarbon mean age of soil carbon to 1 m	4,830 ± 1,730 yr	56.59 (range 56.19–56.87)	A9 [60] (measured)
lichen thallus ages	≥4,500; ~9,000 yr	56.53; 57.16	A5 [33] (measured)
dog divergence, East Asia – Western Eurasia, before present	14,000–6,400 yr	57.56–56.85	A10 [6] (measured)
potyvirus radiation, before present	about 6,600 yr	56.88	A10 [4] (measured)
Megafauna loss, younger end	10 kyr	57.25	A8 [51] (measured)
dogs introduced after	more than 10,000 yr	57.25	A10 [5] (measured)

dogs introduced after domestication (Basenji, Dingo, Singing Dog)	more than 10,000 yr	57.25	A10 [9] (measured)
domestication span	11,500 yr	57.38	A10 [7] (measured)
land shaped by people, before present	12,000 yr	57.42	A10 [10] (measured)
Megafauna loss, older end	15 kyr	57.62	A8 [51] (measured)
CO ₂ swings, late Paleozoic	~10 ⁵ yr	59.35	A6 [70] (measured)
Hawaiian soil, organic P maximum	about 150,000 yr	59.72	A9 [61] (measured)
O ₂ residence, with Berner's burial fluxes	0.8 Myr	61.24	A6 [64] (computed)
atmosphere-ocean O ₂ residence, with total organic burial	0.82 Myr	61.27	A9 [62, 63] (computed)
end-Permian fungal proliferation	<1 Myr	61.45	A5 [40, 41] (measured)
atmospheric O ₂ transition at the GOE	1-10 Myr	61.45-63.54	A9 [6] (measured)
<i>Wolbachia</i> co-divergence with host lineage	2 Myr	62.08	A4 [5] (modelled)
Cairo forest older than Gilboa	2-3 Myr	62.08-62.45	A6 [47] (measured)
O ₂ residence time	~2.1 Myr	62.12	A6 [64] (computed)
atmosphere-ocean O ₂ residence	about 2.1 Myr	62.12	A9 [62] (computed)
Hypsodonty after grasslands (at least)	4 Myr	62.71	A8 [47] (measured)
Darwin's orchid and hawkmoth, as an age	7.5 Myr	63.28	A8 [30] (measured)
Obligate pair, youngest	about 7.5 Myr	63.28	A8 [30] (measured)
higher agriculture to leaf-cutters	8-13 Myr	63.34-63.78	A5 [47] (computed)
tracks before elpistostegids	10 Myr	63.54	A6 [28] (measured)
Neoaves radiation, lower; Pierid lag after Brassicales	10 Myr	63.54	A8 [17, 46] (measured)
<i>Pneumodesmus</i> redating	13 Myr	63.78	A6 [23] (computed)
mean age of genes introduced into <i>E. coli</i>	14.4 Myr	63.87	A1 [28]
Hominid-gut bacteria cospeciation	15 Myr	63.91	A4 [12] (measured)
Neoaves radiation, upper	15 Myr	63.91	A8 [17] (measured)
CO ₂ record, Montañez	16 Myr	63.97	A6 [70] (measured)
Bovids in Africa, as an	16 Myr	63.97	A8 [45] (measured)

age			
Spine origins, time window	17 Myr	64.02	A8 [45] (measured)
tracks before tetrapod body fossils	18 Myr	64.08	A6 [28] (measured)
Perfume orchids, younger end, as an age	18 Myr	64.08	A8 [29] (measured)
Domatia origins, time window	19 Myr	64.13	A8 [44] (measured)
herbivory lag after tissue origin, phase 1	0–20 Myr	—; 64.17	A6 [41] (measured)
Crown Old World fruit bats, younger end, as an age	20 Myr	64.17	A8 [20] (measured)
Plant tissue to first eater, first phase, longest	20 Myr	64.17	A8 [5] (measured)
Triassic–Jurassic O ₂ cycles, period	20–30 Myr	64.17–64.54	A9 [64] (measured)
Interval Cambrian base to Chengjiang (538.8 – 518.0)	20.8 Myr	64.21	A3 (computed)
Interval termite–roach split to termite crown (170 – 149)	21 Myr	64.22	A4 (computed)
Cambrian explosion, minimum span	22 Myr	64.26	A3 [30] (measured)
Perfume orchids, older end, as an age	27 Myr	64.45	A8 [29] (measured)
Interval scleractinian expansion to coral photosymbiosis (240 – 212)	28 Myr	64.48	A4 (computed)
ant farming to higher agriculture, [47]	30–34 Myr	64.54–64.66	A5 [47] (computed)
HERV-K(HML2) infectious pool	30 Myr	64.54	A10 [2] (measured)
Crown Old World fruit bats, older end, as an age	31 Myr	64.57	A8 [20] (measured)
Yucca moths, lower bound (41.5 – 9.8), as an age	31.7 Myr	64.59	A8 [28] (computed)
Orchid bees, younger end; fleshy-fruit shift, as an age	34 Myr	64.66	A8 [29, 16] (measured)
Interval Ediacaran macrofossils to Cambrian base (574 – 538.8)	35.2 Myr	64.69	A3 (computed)

ant farming (66.65 Ma) to termite farming (31.41 Ma)	35.24 Myr	64.69	A5 [46, 49] (computed)
Orchid bees, older end, as an age	38 Myr	64.76	A8 [29] (measured)
ant farming to higher agriculture, [46]	39.65 Myr	64.80	A5 [46] (computed)
trackway extension of arthropod landfall	≤40 Myr	64.80	A6 [19] (measured)
Yucca moths, as an age	41.5 Myr	64.84	A8 [28] (measured)
plant spores to vascular plants, 473 → 426.9 Ma	46 Myr	64.93	A6 [12, 13] (computed)
Oldest bats, younger end, as an age	48 Myr	64.97	A8 [19, 15] (measured)
Fleshy-fruit peak, younger end, as an age	50 Myr	65.01	A8 [16] (measured)
Yucca moths, upper bound (41.5 + 9.8), as an age	51.3 Myr	65.03	A8 [28] (computed)
Interval coral isotopes to symbiont clock (212 – 160)	52 Myr	65.04	A4 (computed)
seed predation lag	54 Myr	65.08	A6 [41] (measured)
Plant tissue to first eater, second phase, shortest	54 Myr	65.08	A8 [5] (measured)
Oldest primate skeleton, as an age	55 Myr	65.09	A8 [18] (measured)
Fleshy-fruit peak, older end, as an age	55 Myr	65.09	A8 [16] (measured)
Oldest bats, older end, as an age	56 Myr	65.11	A8 [19, 15] (measured)
Ant agriculture, younger end, as an age	57 Myr	65.13	A8 [31] (measured)
Fig-wasp co-divergence (at least)	60 Myr	65.17	A8 [27] (measured)
Interval Marinoan steranes to Ediacaran macrofossils (635 – 574)	61 Myr	65.19	A3 (computed)
Ant agriculture, older end, as an age	61 Myr	65.19	A8 [31] (measured)
Scorpionfly pollinator species, time span	62 Myr	65.20	A8 [8] (measured)
wood boring lag	63 Myr	65.22	A6 [41] (measured)
mid-Palaeozoic herbivory hiatus	65 Myr	65.25	A6 [41] (measured)
K-Pg boundary, as an age	66 Myr	65.26	A8 [17] (measured)

insect clock to Rhynie hexapods	67.5–72 Myr	65.28–65.34	A6 [24, 31, 35] (computed)
myriapod clock to first fossils	75 Myr	65.38	A6 [22] (measured)
clock flight to oldest winged fossil	75.1 Myr	65.38	A6 [24, 25] (computed)
diatom origin to oldest abundant record	75 Myr	65.38	A9 [12] (measured)
leaf-feeding lag	76 Myr	65.39	A6 [41] (measured)
spread of the Pilbara signals (3.48–3.40 Ga)	about 80 Myr	65.43	A1 (computed)
late Paleozoic ice age, 340–260 Ma	80 Myr	65.43	A6 [69] (computed)
arthropod size rise, 411 → 331 Ma	~80 Myr	65.43	A6 [33, 72] (computed)
Onset of fleshy-fruit diversification, as an age	80 Myr	65.43	A8 [16] (measured)
first footprints to first tetrapod herbivore	≈83 Myr	65.47	A6 [28, 45] (computed)
first forests (385 Ma) to white rot (~300 Ma)	~85 Myr	65.49	A6 [47, 67] (computed)
plant spores to first forests, 473 → 385 Ma	88 Myr	65.52	A6 [12, 47] (computed)
Interval termite crown to Termitidae (149 – 54)	95 Myr	65.59	A4 (computed)
First arthropod to first vertebrate herbivore, from 403 Ma	96 Myr	65.60	A7 (computed)
root-feeding lag	98 Myr	65.62	A6 [41] (measured)
Plant tissue to first eater, second phase, longest	98 Myr	65.62	A8 [5] (measured)
Eudicot pollen on a beetle, as an age	99 Myr	65.63	A8 [11] (measured)
<i>E. coli</i> – <i>Salmonella</i> divergence	about 100 Myr	65.64	A1 [28]
Oman sterane sequence	100 Myr	65.64	A3 [26] (measured)
CO ₂ fall, 400 → 300 Ma	100 Myr	65.64	A6 [51] (computed)
Oldest bee, as an age	100 Myr	65.64	A8 [12] (measured)
First beetle pollinator, as an age	105 Myr	65.68	A8 [9] (measured)
Interval termite crown to ruminant crown (149 – 39.1)	109.9 Myr	65.72	A4 (computed)
first arthropod to first vertebrate herbivory	110 Myr	65.72	A6 [41, 45] (computed)
First arthropod to first	110 Myr	65.72	A7 (computed)

vertebrate herbivore, from 417 Ma			
Crown bees, younger bound, as an age	113 Myr	65.75	A8 [13] (measured)
Interval termite crown to ruminant crown (149 – 32.3)	116.7 Myr	65.78	A4 (computed)
termite crown to termite fungus farming	117.6 Myr	65.79	A5 [51, 49] (computed)
Gap in the drilling record, Late Triassic to Early Cretaceous	120 Myr	65.80	A7 [13] (measured)
Crown bees, as an age	123 Myr	65.83	A8 [13] (measured)
Main angiosperm clades, younger end, as an age	130 Myr	65.88	A8 [4] (measured)
Crown bees, older bound, as an age	132 Myr	65.89	A8 [13] (measured)
Termite fossil record	135 Myr	65.91	A4 [31] (measured)
Main angiosperm clades, older end, as an age	135 Myr	65.91	A8 [4] (measured)
<i>Bangiomorpha</i> , younger than the earlier constraint	about 150 Myr	66.01	A2 [9]
Oldest definitive pollinators on gymnosperms, as an age	165 Myr	66.09	A8 [8] (measured)
AM origin (480 Ma) to white rot (~300 Ma)	180 Myr	66.17	A5 [5, 35] (computed)
ocean oxygenation to land-plant O ₂ step	0.19–0.24 Gyr	66.22–66.43	A9 [9, 10] (computed)
plastid establishment after branching	about 200 Myr	66.27	A2 [6]
O ₂ oscillation after onset	about 200 Myr	66.27	A9 [7] (measured)
Pennsylvanian fleshy seeds to fleshy-fruit diversification (at least)	218.9 Myr	66.35	A8 [14, 15, 16] (computed)
Isua stromatolites before the Dresser record	220 Myr	66.36	A1 [13]
opisthokont node to crown Fungi	220–369 Myr	66.36–66.83	A5 [1, 5] (computed)
Interval vent epibionts to coral photosymbiosis (440 – 212)	228 Myr	66.39	A4 (computed)
opisthokont node to <i>Ourasphaira</i>	≥230 Myr	66.40	A5 [1, 9] (computed)
white rot (~300 Ma) to ant farming (66.65 Ma)	233.35 Myr	66.41	A5 [35, 46] (computed)

Lepidopteran proboscis, as an age	241 Myr	66.44	A8 [10] (measured)
crown red algae, window (1,984–1,732)	252 Myr	66.48	A2 (computed)
<i>Rhyniognatha</i> (2023 chart) to angiosperm clades	275.8–277.6 Myr	66.56–66.57	A8 [1, 4] (computed)
zircon carbon before earlier evidence	about 300 Myr	66.64	A1 [8]
crown Fungi to Cryogenian base	300 Myr	66.64	A5 [5, 7] (computed)
First synapsid herbivore, as an age	307 Myr	66.66	A7 [7] (measured)
Second herbivory phase, younger end, as an age	309 Myr	66.66	A8 [5] (measured)
First vertebrate herbivore, as an age	307 Myr	66.66	A8 [6] (measured)
caulimovirid origin, at latest	about 320 Myr	66.70	A10 [1] (measured)
Leaf margin feeding, as an age	326 Myr	66.71	A7 [6] (measured)
First leaf feeding, as an age	326 Myr	66.71	A8 [5] (measured)
primary plastid window (2,137–1,807)	330 Myr	66.72	A2 (computed)
Second herbivory phase, older end, as an age	327 Myr	66.72	A8 [5] (measured)
3.80 Ga (Isua carbon) to 3.465 Ga (Apex)	0.335 Gyr	66.74	A1 (computed)
red-algal plastid donor stem, width (1,675–1,281)	394 Myr	66.89	A2 (computed)
Oldest insect fossil, younger end (paper), as an age	396 Myr	66.89	A8 [1] (measured)
4.10 Ga (zircon) to 3.70 Ga (Isua graphite)	0.40 Gyr	66.90	A1 (computed)
Chitrakoot red algae, older than earlier oldest	about 400 Myr	66.90	A2 [8]
First arthropod herbivory, younger end, as an age	403 Myr	66.91	A7 [6] (measured)
Insect flight, as an age	406 Myr	66.91	A8 [3] (measured)
First arthropod herbivory, younger end, as an age	403 Myr	66.91	A8 [5] (measured)
Oldest insect fossil, older end (2023 chart), as an age	410.8 Myr	66.92	A8 [1] (measured)

Oldest insect fossil, younger end (2023 chart), as an age	407.6 Myr	66.92	A8 [1] (measured)
Oldest insect fossil, older end (paper), as an age	407 Myr	66.92	A8 [1] (measured)
CO ₂ decline record	420 Myr	66.94	A6 [51] (measured)
First arthropod herbivory, older end, as an age	417 Myr	66.94	A7 [6] (measured)
First arthropod herbivory, older end, as an age	417 Myr	66.94	A8 [5] (measured)
Silurian pentastomid on an ostracod, as an age	425 Myr	66.95	A7 [5] (measured)
LECA window (2,386–1,958)	428 Myr	66.96	A2 (computed)
serial red window, width (1,079–650)	429 Myr	66.96	A2 (computed)
Molecular origin of insects, as an age	479 Myr	67.06	A8 [3] (measured)
Beginning of the Ordovician, as an age	490 Myr	67.08	A7 [11] (measured)
LUCA (>3.9 Ga) to crown Bacteria and Archaea (<3.4 Ga), at least	0.5 Gyr	67.10	A1 (computed)
Nuvvuagittuq age range	510 Myr	67.12	A1 (computed)
spread of central LUCA dates	0.55 Gyr	67.19	A1 (computed)
<i>Ourasphaira</i> to glomalean spores	550 Myr	67.19	A5 [9, 10] (computed)
O ₂ model span	550 Myr	67.19	A6 [59] (modelled)
Span of the species-level drilling database, Ediacaran to Holocene	550 Myr	67.19	A7 [21] (measured)
mats (3,220 Ma) to palaeosols (2,650 Ma)	570 Myr	67.22	A6 [2, 3] (computed)
life on land, earlier than previously thought	about 580 Myr	67.24	A1 [15]
Torridonian (1,100 Ma) to plant spores (473 Ma)	627 Myr	67.31	A6 [4, 12] (computed)
ochrophytes, width (1,298–622)	676 Myr	67.38	A2 (computed)
Interval crown red algae (lower) to <i>Bangiomorpha</i> (1,732 – 1,047)	685 Myr	67.39	A3 (computed)
LUCA (4.2 Ga) to the Pilbara (3.48 Ga)	0.72 Gyr	67.43	A1 (computed)

N fixation to GOE	0.74–0.87 Gyr	67.46–67.61	A9 [4, 6, 7] (computed)
sulphate-reduction record, extension	more than 750 Myr	67.47	A1 [16]
myzozoans, width (1,520–696)	824 Myr	67.56	A2 (computed)
mitochondrial window (2,053–1,210)	843 Myr	67.58	A2 (computed)
spread of plastid central dates (2.1 – 1.25 Ga)	0.85 Gyr	67.59	A2 (computed)
Interval crown red algae (upper) to <i>Bangiomorpha</i> (1,984 – 1,047)	937 Myr	67.67	A3 (computed)
cryptophytes, width (1,658–440)	1,218 Myr	67.91	A2 (computed)
haptophytes, width (1,943–579)	1,364 Myr	68.02	A2 (computed)
palaeosols (2,650 Ma) to Torridonian (1,100 Ma)	1,550 Myr	68.13	A6 [3, 4] (computed)
Pilbara (3.48 Ga) to crown eukaryotes (1.84 Ga), at least	1.64 Gyr	68.18	A1 (computed)
GOE to ocean oxygenation	1,695 Myr	68.21	A9 [6, 9] (computed)
LUCA (4.2 Ga) to crown eukaryotes (1.84 Ga)	2.36 Gyr	68.52	A1 (computed)
microbes on land before plants	2,747 Myr	68.65	A6 [2, 12] (computed)
inhabited hot springs, record extension	about 3 billion years	68.73	A1 [15]

C6 Generation-time pairs

Every pairing in the chapters for which a generation time, doubling time or lifespan is printed for both partners. The ratio is the longer time over the shorter (computed).

pairing	partner X time	partner Y time	ratio (computed)	chapter [ref]
<i>E. coli</i> – <i>Salmonella enterica</i> (divergence pair, about 100 Ma; A1 gene traffic)	<i>E. coli</i> , wild doubling 15 h	<i>S. enterica</i> , wild doubling 25 h	1.67 (25 / 15)	A1 [51], [28]

The one row is a divergence pair, not a partnership. No partnership in the chapters has a generation time, doubling time or lifespan printed for both partners. Near cases, not entered:

- MK-D1 doubles in 14–25 d, with no time for *Halodesulfobivrio* or *Methanogenium*

(A1 [26]; A2 [18]).

- *Vibrio fischeri* doubles in 0.93–1.8 h (computed from A4 [20]); the squid lifespan was not read (A4, Not verified).
- The termite royal pair lives at most about 20 yr (A4 [30]; A5 [50]); *Termitomyces* is given only a yearly fruiting cycle, 1 yr (A5 [50]).
- The *Azolla* cyanobiont grows 5–10 times slower in symbiosis, with no times given (A2 [41]).
- The *Chlamydomonas* line ran ~750 generations in ~350 days, with no time for *Paramecium* (A3 [49]).

C7 Present-day quantities

Global quantities printed in the chapters: biomass, fluxes, species numbers and shares. Values from one source repeated in several chapters are given once, with every chapter listed. Marks (measured, modelled, computed) are the chapters' own.

quantity	value	chapter [ref]
Biomass		
global biomass	≈550 Gt C (measured)	A1 [56]; A5 [73]; A6 [77]; A7 [41]; A9 [2]; A10 [52]
plants	≈450 Gt C (1.2-fold uncertainty)	A1 [56]; A5 [73]; A6 [77]; A7 [41]; A9 [2]; A10 [52]
bacteria	≈70 Gt C (10-fold)	A1 [56]; A5 [73]; A6 [77]; A7 [41]; A9 [2]; A10 [52]
fungi	12 Gt C (3-fold; A6: ≈12 Gt C)	A6 [77]; A7 [41]
archaea	≈7 Gt C (13-fold)	A1 [56]; A5 [73]; A6 [77]; A7 [41]; A9 [2]; A10 [52]
protists	4 Gt C (4-fold)	A7 [41]
animals	≈2 Gt C (5-fold)	A1 [56]; A5 [73]; A6 [77]; A7 [41]; A9 [2]; A10 [52]
viruses	0.2 Gt C (20-fold)	A7 [41]
plants, share of biomass carbon	450 / 550 = 81.8 % (A6: 82 %) (computed)	A6; A7
fungi, share of biomass carbon	12 / 550 = 2.2 % (computed)	A6
prokaryotes, share of biomass carbon	77 / 550 = 14 % (computed)	A1
plants above ground; roots	about 320; about 130 Gt C	A7 [41]
land; ocean biomass	about 470; about 6 Gt C (marine biota about 6 Gt C, A9, A10)	A7 [41]; A9 [2]; A10 [52]
terrestrial against marine biomass	about two orders of magnitude	A6 [77]; A9 [2]
ocean producers; consumers	about 1; about 5 Gt C (ratio 5 : 1, computed)	A7 [41]
marine arthropods; fish; terrestrial arthropods; annelids; molluscs	1; 0.7; 0.2; 0.2; 0.2 Gt C	A7 [41]
cnidarians; livestock; humans;	0.1; 0.1; 0.06; 0.02; 0.007; 0.002	A7 [41]

nematodes; wild mammals; wild birds	Gt C	
humans and livestock, share of mammal biomass	0.16 / 0.167 = 96 % (computed)	A7 [41]
plant biomass against its value before civilisation	about twofold lower	A7 [41]
wild mammal biomass, fall	factor of about 6 (about 7-fold on land, about 5-fold at sea)	A7 [41]
human mass against all wild mammals	about one order of magnitude higher	A7 [41]; A10 [52]
wet biomass: terrestrial wild mammals	about 20 Mt (95 % CI 13–38), about 3 kg per person	A10 [53]
wet biomass: marine mammals	about 40 Mt (20–80), more than half baleen whales	A10 [53]
wet biomass: humans; livestock	about 390 Mt; about 630 Mt	A10 [53]
livestock; humans; wild land and marine mammals, shares of 1,080 Mt	58 %; 36 %; 5.6 % (computed)	A10 [53]
ocean size spectrum, biomass per order-of-magnitude size class	about 1 Gt wet weight (10^{15} g)	A7 [42]
anthropogenic mass	doubling about every 20 yr; equals living biomass, about 1.1 Tt dry, at 2020 ± 6	A10 [49]
topsoil (0–30 cm) fungal; bacterial biomass carbon	12.6 (6.6–16.4); 4.3 (0.5–10.3) Pg C	A5 [71]
fungal share of topsoil microbial carbon	75 % (computed)	A5 [71]
fungal : bacterial ratio, savanna to tundra	1.8 (1.6–2.1) to 8.6 (6.7–11.0)	A5 [71]
world forest carbon	861 ± 66 Pg C	A5 [44]; A6 [79]
forest soil; live biomass; dead wood; litter	383; 363; 73 ± 6 (8 %); 43 ± 3 (5 %) Pg C	A5 [44]; A6 [79]
Cells and individuals		
prokaryotic cells (1998)	$4\text{--}6 \times 10^{30}$, holding 350–550 Pg C, 85–130 Pg N, 9–14 Pg P	A1 [52]
prokaryotic cells: oceanic subsurface; soil; open ocean (1998)	3.5×10^{30} ; 2.6×10^{29} ; 1.2×10^{29}	A1 [52]
prokaryotic cell production	1.7×10^{30} cells per year	A1 [52]
prokaryotic cells (2019)	1.2×10^{30}	A1 [55]
deep oceanic subsurface; deep continental subsurface; soil; oceans (2019)	4×10^{29} ; 3×10^{29} ; 3×10^{29} ; 1×10^{29} cells	A1 [55]
subsurface share of prokaryotic cells (2019)	58 % (computed)	A1 [55]
cells in biofilms	40–80 % (about 80 % in surface habitats other than the ocean)	A1 [55]
SAR11 share of rRNA genes in seawater	26 %	A1 [49]

<i>Prochlorococcus</i> ; <i>Synechococcus</i> cells, annual global mean	$2.9 \pm 0.1 \times 10^{27}$; $7.0 \pm 0.3 \times 10^{26}$ (modelled)	A9 [47]
viruses in the ocean; on Earth	10^{30} ; about 10^{31}	A10 [28], [31]
viral infections in the ocean	about 10^{23} per second; 8.6×10^{27} per day (computed)	A10 [28]
viruses per litre of sea water	10^{10}	A10 [29]
oceanic microbial biomass killed by viruses	about 20 % per day	A10 [28]
breeding seabirds; with non-breeders	about 804 million; 1,045 million (320 species, more than 3,000 colonies)	A9 [43]
Fluxes: carbon		
global NPP	104.9 Pg C yr ⁻¹ , land and ocean roughly equal	A6 [78]; A9 [1]
terrestrial GPP	about 150 Pg C yr ⁻¹ (C3 about 115, C4 35.3); second estimate 129 ± 32 Gt C yr ⁻¹	A9 [14], [15]
carbon fixed at sea used by bacteria	about 10–50 %	A9 [16]
diatoms, share of marine primary productivity and of particulate carbon export	about 40 %	A9 [17]
plant carbon to mycorrhizal mycelium	13.12 Gt CO ₂ e yr ⁻¹ = 3.58 Gt C yr ⁻¹	A5 [28]; A6 [40]; A9 [42]
mycorrhizal carbon: AM; EcM; ericoid	1.07; 2.47; 0.03 Gt C yr ⁻¹ (3.93; 9.07; 0.12 Gt CO ₂ e yr ⁻¹)	A5 [28]; A9 [42]
shares of NPP to AM; EcM; ericoid; orchid mycorrhiza	6.2; 13.1; 3.5; 1.0 %	A5 [28]; A9 [42]
export of organic carbon from the euphotic zone	about 9 Pg C yr ⁻¹ (modelled; earlier 4–12)	A9 [51]
sinking POC flux at 100 m; at 1,000 m	6.08 ± 1.17 ; 0.65 ± 0.24 Pg C yr ⁻¹ (modelled)	A9 [56]
export ratio; transfer efficiency 1,000 m / 100 m	0.154 ± 0.026 ; 0.122 ± 0.041 (modelled)	A9 [56]
export from the euphotic zone with diel vertical migration	6.5 Pg C yr ⁻¹ , migration share 0.16 ± 0.04 (modelled); 1.04 Pg C yr ⁻¹ (computed)	A9 [49]
organic carbon burial: terrestrial; marine	$\sim 350 \times 10^{12}$ g C yr ⁻¹ ; $\sim 200 \times 10^{12}$ g C yr ⁻¹ (modelled)	A6 [58]; A9 [63]
soil respiration	98 ± 12 Pg C in 2008, rising 0.1 Pg C yr ⁻¹ over 1989–2008	A9 [59]
soil organic carbon to 30 cm; 1 m; 2 m	684–724; 1,462–1,548; 2,376–2,456 Pg	A9 [58]
soil N to 1 m	133–140 Pg	A9 [58]
biogenic silica production; export	200–280; 100–140 Tmol Si yr ⁻¹ ; at least 50 % dissolves in the upper 100 m; burial / production about 3 %	A9 [71]
termite emissions	19.7 ± 1.5 Mt CH ₄ and $3,500 \pm$	A4 [34]

	700 Mt CO ₂ per year, ~4 % and ~2 % of global emissions	
termite methane oxidised by mounds	about half	A4 [35]
fungal spores to the air	~50 Tg yr ⁻¹	A5 [72]
Fluxes: nitrogen, phosphorus, sulphur, oxygen		
global N fixation	413 Tg N yr ⁻¹ , about half anthropogenic (210 Tg N)	A9 [77]
marine biological N fixation	140 Tg N yr ⁻¹ [77]; 120 (100–200) Tg N yr ⁻¹ [73]; marine total 100–200 [23]	A9 [77], [73], [23]
<i>Trichodesmium</i> N fixation	about 60–80 Tg N yr ⁻¹ (first estimate about 5)	A9 [23]
terrestrial natural BNF; pre-industrial terrestrial BNF	128 Tg N yr ⁻¹ ; 58 (40–100) Tg N yr ⁻¹ , 44 with conservative geological N	A9 [73], [74]
Haber-Bosch	about 120 Tg N yr ⁻¹	A9 [73]; A10 [48]
biological N fixation in agriculture	50–70 Tg N yr ⁻¹ (soybean 16.4; pulses 2.95; rice 5)	A9 [78]; A10 [47]
lightning NO _x	5 Tg N yr ⁻¹	A9 [73]
anthropogenic reactive N	220 Tg N yr ⁻¹ in 2010	A9 [73]
NO ₃ ⁻ leaching; NH ₃ + NO _x emissions	40–70; 100 Tg N yr ⁻¹	A9 [77]
oceanic denitrification; deficit against fixation	unlikely below 400 Tg N yr ⁻¹ ; about 200 Tg N yr ⁻¹	A9 [72]
seabird colony excretion	591 Gg N and 99 Gg P yr ⁻¹ (soluble 72.5 Gg N, 21.8 Gg P); with non-breeders 3,800 Gg N and 631 Gg P yr ⁻¹	A9 [43]
seabird N and P from the Antarctic and Southern Ocean; from penguins	80 % (470 Gg N, 79 Gg P); 52 % (307 Gg N, 51 Gg P, computed)	A9 [43]
commercial fishing nutrient removal	3.7 × 10 ³ Gg N and 0.32 × 10 ³ Gg P yr ⁻¹	A9 [43]
inorganic P fertiliser	about 15 Mt P yr ⁻¹ ; human P mobilisation by 2000 about three times natural flows	A9 [79]
P storage in terrestrial and freshwater ecosystems	at least 75 % above pre-industrial	A9 [80]
sea-to-land P by seabirds and anadromous fish	formerly about 150 × 10 ⁶ kg P yr ⁻¹ ; now less than 4 % (modelled)	A9 [76]
marine mammal upward P transport	about 23 % of a former about 340 × 10 ⁶ kg P yr ⁻¹ (modelled)	A9 [76]
animal capacity to move nutrients	about 8 % of its pre-extinction value on land, about 5 % in the oceans (modelled)	A8 [65]; A9 [76]; A10 [54]
global marine sulphate reduction	11.3 Tmol SO ₄ ²⁻ yr ⁻¹ = 362 Tg S yr ⁻¹ (modelled; mass computed);	A9 [69]

	12-29 % of the organic carbon flux to the sea floor	
DMS sea-to-air flux	28.1 (17.6-34.4) Tg S yr ⁻¹	A9 [45]
atmosphere-ocean O ₂ reservoir; source flux; residence	3.78 × 10 ¹⁹ mol; 1.8 × 10 ¹³ mol yr ⁻¹ ; about 2.1 Myr (0.8 or 0.82 Myr with burial fluxes, computed)	A6 [64]; A9 [62]
O ₂ in dry air	20.95 % (about 21 %)	A6 [80]; A9 [82], [81]
CO ₂ in dry air; at Mauna Loa, September 2026	420 ppm; 426.07 ppm	A6 [80], [81]
Trophic transfer and herbivory		
world fisheries, reported catch; discarded bycatch (1988-1991)	94.3 million t yr ⁻¹ ; 27 million t (121.3 million t total, computed)	A7 [25]
aquatic primary production required by catches	8.0 % (2 % open ocean; 24-35 % freshwater, upwelling and shelf)	A7 [25]
mean transfer efficiency between trophic levels	10 %	A7 [25]
leaf tissue eaten per year, vascular plants	5.3 %	A7 [36]; A8 [66]
annual primary production removed by aquatic herbivores	51 % (terrestrial 17 %, computed)	A7 [35]; A8 [67]; A9 [20]
food-web links involving parasitic species	about 75 %	A7 [22]
Species numbers		
predicted eukaryote species; marine	about 8.7 ± 1.3 million; about 2.2 ± 0.18 million	A10 [11]
catalogued eukaryotes; undescribed share	over 1.2 million; about 86 % (91 % in the ocean)	A10 [11]
predicted Animalia; Plantae; Fungi; Protozoa; Chromista	7.77 million; 298,000; 611,000; 36,400; 27,500	A10 [11]
all species: described; estimated	about 1.5 million; 2 million to 1 trillion; at least 1-6 billion, bacteria 70-90 %	A10 [15]
microbial species	upward of 10 ¹²	A10 [16]
accepted angiosperms	295,383	A5 [21]; A7 [18]; A8 [23]; A10 [12]
vascular plant species; all plants	308,312; ca. 374,000	A5 [21]; A10 [12]
gymnosperms; new plant species per year	1,079; about 2,000	A10 [12]
flowering plants; insect herbivores	more than 300,000; more than 1 million (ratio 3.3)	A7 [38]; A8 [41]
insects named; estimated; beetles estimated	about 1 million; about 5.5 million; about 1.5 million (about 80 % undescribed)	A10 [14]
fungi accepted; estimated	120,000; 2.2-3.8 million (fungus : plant 9.8 : 1; 1,300, later 1,800 new per year)	A5 [69]; A10 [13]
fungi named; estimated total;	155,000; 2.5 million; around	A5 [31]

naming rate	2,500 per year	
fungal taxa by sequencing	1.08 million at 97 %; Chao-1 6.28 million	A5 [70]
lichenised fungi	19,387 species in 995 genera	A5 [30]
Glomeromycota	~360 described species in 49 genera (320 implied by [23])	A5 [22], [23]
EcM fungi known; likely	7,750; 20,000–25,000	A5 [27]
EcM plant species	ca. 8,500	A5 [26]
wood-decay species: brown rot; white rot	126; 1,031 of 1,157 (white-rot share 89 %, computed)	A5 [37]
Bacteria; Archaea species clusters (GTDB R226)	136,646; 6,968 (143,614; 732,475 genomes; phyla 169 and 20)	A1 [53]
validly published prokaryote species (LPSN)	22,681 in 4,007 genera and 48 phyla	A1 [54]
human gut prokaryote species	4,644 (4,616 bacterial, 28 archaeal), 71 % uncultured	A4 [15]
virus species (2025 Master Species List)	16,215 in 3,769 genera, 368 families, 93 orders, 49 classes, 22 phyla, 11 kingdoms, 7 realms	A10 [17], [18]
plant virus species	2,134 (2021 list, with fungal viruses, viroids, satellites); 3,206 on 2,231 plants (9,604 interactions); 1,503 (DPVweb)	A10 [19], [20]
plant viruses transmitted by insect vectors; persisting in vectors	about 80 %; more than 200	A10 [26], [27]
known pollinator species	349,368 (Lepidoptera 141,600; beetles 77,300; Hymenoptera 70,000; flies 55,000; bees 17,000; thrips 1,500; birds 1,089; mammals 344; lizards 37)	A8 [21]; A10 [24]
animal-pollinated angiosperms	87.5 % (308,006 of about 352,000) [24]; about 90 % [25]	A8 [24], [25]; A10 [25]
bat-pollinated angiosperm species	about 528 in 67 families	A8 [26]
hummingbird species	365 [21]; about 360 [22]	A8 [21], [22]
frugivorous birds	1,230 of 8,918 (13.8 %); 365 obligate	A8 [32]
frugivorous fish species	more than 275	A8 [33]
ant-dispersed plant species	at least 11,000, 4.5 % of angiosperms	A8 [36]
plant secondary metabolites	more than 100,000 (alkaloids 12,000–27,000; glucosinolates 150; cyanogenic glucosides 60)	A8 [38, 39]
biotically dispersed angiosperms: families; species	30 % (+22 % both); 14 % (+42 % both)	A8 [14]
helminths parasitising vertebrates	75,000–300,000 species	A7 [22]
haustorial parasitic plants	about 4 750 species in 292	A7 [17]

macrofungal parasite plants	about 1,700 species in 202 genera (1.6 % of angiosperms, computed)	A7 [17]
plant-parasitic nematodes	about 4,100 of about 16,000 terrestrial nematodes (about 25 %)	A7 [19]
living pentastomids	about 140 species, all but four on vertebrates	A7 [5]
termite species	3,106 living and fossil, 363 pests; Termitidae >75 % [6] or 84 % [33]	A4 [31], [6], [33]
termite-associated protist species described	roughly 500	A4 [14]
fungus-farming ants	247 extant species, 52 leaf-cutters [46]; ~250 attines [47]	A5 [46], [47]
Macrotermitinae; <i>Termitomyces</i>	~330 species in 11 genera; ~50 species	A5 [50]
Scolytinae	>6,000 species, ~10 % of weevils	A5 [52]
ruminant species; Bovidae	at least 200; at least 143	A4 [11]
bioluminescent fish species: bacterial light; intrinsic	about 725 of ~1,510 (~48 %); about 785	A4 [10]
Collembola species (2024); millipede species	9,186; >12,000	A6 [75], [76]
legume species	over 19,500 (Papilionoideae about 14,000; Caesalpinioideae about 4,400)	A9 [65]
nodulating families	about 10 of about 380 angiosperm families	A9 [66]
actinorhizal plants	8 families, 24 genera, over 220 species	A9 [67]
cycads hosting <i>Nostoc</i>	382 species	A9 [68]
seabird species	320	A9 [43]
plant-virus species share of all virus species	2,134 / 16,215 = 13.2 % (computed; different years)	A10 [19], [17]
potyviruses, share of named plant virus species	about 15 %	A10 [4]
brown algae	2,125 species, 46 % of 4,619 non-diatom heterokonts	A3 [42]
Shares of hosts and partners		
mycorrhizal vascular plants: AM; EcM; ericoid; orchid	72 %; 2.0 %; 1.5 %; 10 %	A5 [18]; A9 [40]
mycorrhizal plants	about 85 % [19]; 80 % of 3,617 species, 92 % of 263 families [20]	A5 [19], [20]; A9 [41], [39]
vegetation cover: AM; EcM; ericoid; non-mycorrhizal	57.4 %; 25.7 %; 2.6 %; 14.3 %	A9 [42]
arthropod species infected by <i>Wolbachia</i>	66 % [23]; ~40 % (more than 1 million species) [37]; 52 % (48–57) [24]	A4 [23], [37], [24]
arthropod species with	24 % (20–42); 13 % (13–55)	A4 [24]

<i>Rickettsia; Cardinium</i>	(modelled)	
amphibian species declined from chytridiomycosis	at least 501, 6.5 % of described amphibians; 90 extinct; 124 down >90 %	A5 [54]
sequenced fungal species that are pathogens	35.5 % of 1,090; 191 plant-pathogenic	A5 [64]
pollinating birds and mammals, Red List movement	2.5 species per year toward extinction	A8 [54]
affiliate species coendangered; historically coextinct	6,300 (modelled); at least 200	A8 [60]
background extinction rate taken; vertebrate losses	2 E/MSY; up to 100 times higher over the last century	A10 [50]
Humans, land and food		
invasive fungal infections; crude deaths; attributable deaths	6.5 million (6,548,000) yr ⁻¹ ; 3.8 million (3,752,000); about 2.5 million (68 %)	A5 [60]
ice-free land transformed by agriculture and settlements (2000); embedded	almost 39 %; another 37 % (76 % in all, computed)	A10 [51]
terrestrial biosphere wild: 1700; 2000	nearly half; a quarter	A10 [51]
woodlands shaped by human land use: temperate; tropical	more than 95 %; about 90 %	A10 [10]
food energy from 15 crops; from rice, maize and wheat	90 %; 60 % (of more than 50,000 edible species)	A10 [43]
yield lost to pathogens and pests: wheat; rice; maize; potato; soybean	21.5 %; 30.0 %; 22.5 %; 17.2 %; 21.4 %	A10 [44]

Row counts

C1: 278 rows (224 with an age in Ma, 54 without). C2: 69 rows. C3: 56 rows.

C4: 152 rows. C5: 285 rows. C6: 1 row.

C7: 163 rows.

Layer B — The Weaving Set Beside the Net

B1 Method

The data of this layer are the ten Pattern paragraphs of Layer A and the seven tables of Part C. The other side is what the Vacuum.Net texts state about the structure and the

evolution of the net, quoted in B2. A pairing sets one statement from each side together where both have the same form.

A pairing is a read. A read is a hypothesis until a test decides it. No statement about the net is added, and where nothing pairs the entry says none.

Three tests were fixed before the dossier tables were looked at, and then run (B11). Two classifications in this layer were made after a table had been seen. They are marked post hoc and are not tests.

B2 What the texts say that can be set beside Layer A

These statements have a form that Layer A can meet (text). They are quoted as fetched for *Plants on the Ladder* and *The Company of Plants*.

1. **Two classes.** "The closed class persists and holds form." "The unclosed class decays, and while it lasts it carries tension from one closure to the next." (*Where Illness Comes From; From Atom to Body*, Part 0.5.)
2. **Residue and alphabet.** "The residue of depth n is the alphabet of depth $n+1$." "No closure is ever exact: each depth leaves a remainder." (*Where Illness Comes From*.)
3. **Filling.** "A species is a subtree; an organism is a closure at a depth." "Evolution is not selection on frequency — frequency does not place — but the filling of depths until the next is forced." (*Balanced Tree*, §11.)
4. **No double loading.** "Counterwinding on its own winding is unwinding: $\Psi^2 = 0$." "An existing closure "cannot load twice in succession without first discharging." (*Balanced Tree*, §2 and §5.)
5. **Memory.** "N3, Memory. The net keeps the orientation of what was first laid down." (*The Vacuum.Net Theory*.) "Heredity is memory in form with reach two." (*Balanced Tree*, §11.)
6. **Scale.** "N5, Scale. The same winding appears at every depth." (*The Vacuum.Net Theory*.) "Each depth n is one layer ... length $3^n \cdot S_0$." (*The Climate on the Ladder of Three*.)
7. **Community and conflict.** "Community is topological, not chosen: shared prefix. Conflict is phase interference between closures without shared form." (*Balanced Tree*, §11.)
8. **The tree.** The balanced tree grows as $b(n) = 3b(n-1) + b(n-2)$: 1, 3, 10, 33, 109, 360. Its ratio tends to $\sigma_3 = (3 + \sqrt{13})/2$. " σ_3 is the law of the address; φ is the law of tension." (*Balanced Tree*.)
9. **Loading, holding, discharge.** "Earthquakes, eruptions, storms: loading, holding, discharge." (*Balanced Tree*, §11.)

The texts make no statement on the order in which partner lineages appear. Nor on proportions of species in a mode of life, on body mass, energy transfer or food-chain length. Nor on species numbers, viruses or domestication.

These absences are recorded so that they are not filled.

B3 The order of connection

Measured (Table C2; Layer A). The oldest dated connections are those inside the cell. The primary plastid has five dates, 2.1–1.25 Ga, with 2.14–1.81 Ga by clock; the mitochondrion is dated 2.05–1.21 Ga (A2). The serial red-plastid transfers share one window, 1,079–650 Ma, and a tertiary plastid falls inside it at 633–1,017 Ma (A2).

The first traces of eating follow: a bored *Cloudina* tube at the end of the Neoproterozoic, shell crushing and kleptoparasitism in the Cambrian (A7). Then the unions of the large bodies on land. Arbuscular mycorrhiza at about 480 Ma by clock and 411.5 Ma in fossil arbuscules (A5, A6).

Lichens at 467–410 Ma (A5). Herbivory on spores at 417 Ma, on leaves at 326 Ma, by vertebrates at 307 Ma (A6).

Then the specialised partnerships. *Sulcia* and *Buchnera* in insects at 200–260 Ma (A2). Coral photosymbiosis at about 212 Ma (A4).

Pollination on gymnosperms at about 165 Ma, on angiosperms from 105–99 Ma (A8). Fungus farming in three insect groups, in at least 12 origins, the oldest at 66.65 ± 13.28 Ma (A5). Domestication from 13,000 years before present (A10).

Text. Statement 2: the residue of one depth is the alphabet of the next. Statement 1: carriers run between closures.

Read. Most connections in Table C2 use, as one partner, a form that an earlier connection made. The plastid-bearing eukaryote is the partner of the serial transfers. The plant with its fungus is the partner of the herbivore.

The flowering plant is the partner of the pollinator and the disperser. The exceptions are the oldest rows: the mitochondrion and the exchanges between bacteria and archaea join forms that no dated connection made. The read is made on the dated connections, not on the partner lineages.

Tested. Test W3 asked a narrower thing: whether, partner by partner, the supplier is older than the one it supplies and the eaten older than the eater. That rule, post hoc in *The Company of Plants*, was fixed first here. It failed: 5 of 14 classifiable pairs follow it, 36 per cent, against 80 required (B11).

Seven pairs have overlapping ages. Of the seven with separated ages, two run the other way: the corals are older than their algae, and the insects older than the flowering plants they eat.

Status. The order of connections: read, untested. The partner-age rule: failed as fixed.

B4 How deep the nesting goes

Measured (A2, A4; data files). Of 24 cases of genome-bearing partners inside host cells, five have a chain of two. *Guillardia* and *Hemiselmis* hold a red-algal remnant with its nucleomorph, and a plastid inside it. *Bigeloviella* holds a green-algal remnant with its nucleomorph, and a plastid inside it.

The mealybug *Planococcus citri* holds *Tremblaya*, and *Moranella* inside *Tremblaya*. The dinoflagellate *Durinskia capensis* keeps a whole diatom for about two months, with the diatom's plastid inside it.

Eighteen have a chain of one: plastids, the *Paulinella* chromatophore, UCYN-A, *Buchnera*, *Wolbachia*, coral algae, chemosynthetic symbionts, and the kleptoplasts of slugs, flatworms, *Mesodinium* and a Ross Sea dinoflagellate. Where two insect symbionts share a host, they lie side by side, not nested. The termite gut protists live outside the host cells; inside the host cells their chain is zero.

The nucleomorphs of the red and the green lineage both stand at three chromosomes and 373–572 kb. Only 3.9–6.2 per cent of their protein genes serve the plastid (A2).

Text. Statement 4: a closure cannot load twice in succession without first discharging. Statement 5: heredity is memory with reach two.

Read. A partner with its own genome inside a host cell is one loading. A partner inside that partner is a second. A third would be a closure loaded twice on top of a load.

Where three hands passed a plastid on, the record shows a plastid, not a chain of three: the middle hand has been discharged. The read is made here; the texts do not speak of cells.

Tested. Test W1 required that no chain be longer than two. On the 24 cases the maximum is two. **Pass** (B11).

One case outside the fixed data decides the reading. The ciliate *Mesodinium rubrum* keeps not only cryptophyte plastids but also cryptophyte nuclei and mitochondria; the stolen nucleus stays active with a half-life of about ten days (citation verified; content read through a secondary page). Whether these sit inside one cryptophyte compartment, which would make a chain of three, the page read does not say.

Status. Read; test passed on 24 cases; one case open to a further check. The three chromosomes of both nucleomorphs: the texts say nothing on chromosome number. None.

B5 Single openings and many fillings

Post hoc classification. Made after Table C3 had been seen.

Measured (Table C3; A5). Several connections that made a new kind of cell or body are counted once. One mitochondrion. One primary plastid.

One arbuscular-mycorrhizal phylum. One ant agriculture, one termite fungus farming, one predisposition to nodulation (A2, A5, A9).

The connections built on those are counted many times. Multicellularity more than 25 times, complex multicellularity in 5 groups (A3). Ectomycorrhiza 66–82 times in fungi and 30 in plants; lichenisation 20–30 times (A5).

Parasitism at least 223 times in animals (A7). Bacterial light in fishes at least 17 of 27 origins of light (A4). Ant dispersal at least 101 times, extrafloral nectaries at least 457,

domatia at least 158 (A8).

There are exceptions on both sides. Secondary plastids arose three to five times, plastid replacements in dinoflagellates twice (A2). Roots arose twice (A6).

Fungus farming in ambrosia beetles arose at least ten times (A5). Primary endosymbioses are four in all when *Paulinella* and UCYN-A are counted (A2).

Text. Statement 3: the filling of depths until the next is forced; a species is a subtree.

Read. A new depth opens once. Once it is open, many subtrees reach the same form within it. The single counts sit at the openings: the cell with an organelle, the plant with a fungus inside its root.

The many counts sit inside the opened depth. The inference from “closure at a depth” to “kind of connection” is made here, not in the texts.

Status. Read; post hoc; untested. A test would fix in advance which connections are openings and which are fillings, then count.

B6 What a partner keeps

Measured (A2). Gene number falls from bacterium to organelle. *Rickettsia* has 834 protein genes; mitochondria keep 13 to about 100. *Synechocystis* has 3,168; the *Arabidopsis* plastid keeps 87, with about 4,500 genes in the nucleus.

The young partners keep more: 29 per cent in *Paulinella*, 68 per cent in *Nostoc azollae*.

Insect symbionts carry 112–641 kb. Genome length does not fall in step with gene number: human mtDNA is 16.6 kb, that of *Silene conica* 11.3 Mb.

Text. Statement 2: the residue of one depth is the alphabet of the next.

Read. A partner that has become a letter keeps what the word does not supply. The fall in gene number is that loss, measured. An earlier test asked whether the loss grows with the age of the union, and it failed (*The Company of Plants*, B1).

The read survived as two regimes: obligate residents that lose, facultative partners that keep. Layer A of this book adds the insect symbionts to the first regime and nothing to the second.

Status. Read; the age rule failed in the earlier book; no new test.

B7 Fast carriers, slow unions

Measured (A2, A4; Table C6). Partner cells are replaced fast. The *Vibrio* population of the squid light organ regrows in 4–6 hours. *Hydra* reaches its bacterial carrying capacity in 24–72 hours; the bee gut is colonised in 10 days.

Kleptoplasts work from 15 days to at least 30 months (A2).

The partner lineages stay with their hosts far longer. Hominid gut clades have co-

speciated with their hosts for about 15 Myr. The rumen dates with crown Ruminantia to 39.1–32.3 Ma.

Coral photosymbiosis dates to about 212 Ma, the supergroups A and B of *Wolbachia* to about 200 Ma (A4). These are lineage ages, not measured lifetimes of one partnership.

Table C6 holds one pair with a generation time on both sides, and it is not a partnership. A ratio across partners cannot be formed from this book.

Text. Statement 1: the unclosed class decays while it carries; the closed class persists.

Read. The partner cells are carriers; they are replaced within hours or days. The union, as a lineage, is the closed form; it holds for 10^7 – 10^8 years. The division runs between the cells and the partnership, not between host and partner.

Read.

Status. Read; consistent with *The Company of Plants*, B4; no ratio test possible here.

B8 Networks and the shared prefix

Measured (A8). Three quarters of 52 mutualistic networks are nested. Networks above 150 species are always modular; below 50, never. Connectance falls to 2.3–3.4 per cent in the two largest.

Plants survive the random loss of 70–80 per cent of pollinators in simulation.

Text. Statement 7: community is topological, not chosen: shared prefix.

Read. In a nested network the partners of a specialist are a subset of the partners of a generalist. Subsets contained in one another are the form of a tree read from the root: each shorter address is a prefix of a longer. The nestedness is that form, measured.

The modules of the large networks are separate subtrees. Read.

Status. Read; untested. A test would measure whether the partner sets of a network form a tree of prefixes more often than a null model of the same connectance.

B9 Scale in the food web

Measured (A7). Predators average 42 times their prey's mass; parasitoids 0.76 times their host's. Predator biomass scales with prey biomass at an exponent of 0.71–0.74. Production scales with biomass at 0.67–0.76.

Mean transfer efficiency is 10 per cent, single systems 0.3–52 per cent. Chains are 3.5–5 levels long.

Text. Statement 6: the same winding at every depth; each depth one layer of length $3^n \cdot S_0$.

Read. A power law with one exponent across ecosystems is the same rule at every size. That is the form N5 names. The layer reading asks more: that partners differ by whole

powers of three in size.

A mass ratio of 42 is a length ratio of $42^{1/3} = 3.48$ at equal density, $\log_3 = 1.13$ (computed). One number is not a test.

Tested. Test W2 asked for at least 15 partner pairs with both sizes given, in chapters A2, A4, A7 and A8. They hold one, and by mass. **Not run** (B11).

Status. Power laws: read, weak. Layer reading: not run.

B10 Where nothing pairs

- **Shares.** *Wolbachia* in 40–66 per cent of arthropod species (A4). Animals pollinate 87.5–90 per cent of angiosperms; vertebrates are 0.42 per cent of pollinators (A8). At sea 10–50 per cent of production passes through bacteria (A9). The texts make no statement about proportions. None.
- **The cycles.** The first dated metabolisms: sulphate reduction 3.47 Ga, nitrogen fixation 3.2 Ga, free oxygen 2.46–2.33 Ga (A9). Nitrogenase is found in bacteria and archaea only. Statement 9 names loading, holding and discharge for earthquakes, eruptions and storms, not for element cycles. None.
- **Species numbers.** Plants 0.30–0.37 million, fungi 0.6–3.8 million, animals 7.8 million; all species $1-6 \times 10^9$, microbial species up to 10^{12} (A10). The balanced tree gives counts of addresses per depth, 1, 3, 10, 33, 109, 360. No text sets a species count beside them, and this book does not. None.
- **Colony size.** Colonies at the threshold of multicellularity hold from 2 to 64 cells; eight-celled colonies dominate in *Chlorella* under a predator (A3). The texts give no statement on cell number. None.
- **The human share.** Humans and livestock hold 94 per cent of mammal mass by wet mass, 96 per cent by carbon (A10, A7). Transformed land covers 39 per cent of ice-free land, with a further 37 per cent embedded in it; 15 crops give 90 per cent of food energy (A10). Statement 7 on conflict as interference is about closures without shared form; Layer A measures mass and area, not interference. None.
- **The ladder.** Tables C1, C4 and C5 give 224 dated events, 150 sizes and 285 durations their positions. These are coordinates. No clustering test was run; the lists are drawn from ten topics, not from one population. No claim.

B11 The tests, fixed first and then run

Fixed on 13 October 2026 before the dossier tables were looked at, and run by Claude Code the same day on the data named. An independent check found extraction errors in the data files; they are corrected, and the rules are unchanged. The attestation is the author's.

The protocol, the rows and the arithmetic are in the file TW-tests.md that accompanies this book.

W1, nesting depth. Required: no chain of genome-bearing compartments inside a host cell longer than two. Found: 24 cases, five of length two, none longer. **Pass.** The case of

Mesodinium rubrum, with its stolen nuclei outside the fixed data, is not resolved by the page read.

W2, size ratios on the ladder. Required: at least 15 partner pairs with both sizes; at least 70 per cent of $\log_3$ ratios within 0.25 of a whole number. Found: 1 pair, by mass. **Not run.**

W3, order of arrival with the rule fixed first. Required: at least 80 per cent of classifiable pairs with the supplier older than the supplied, and the eaten older than the eater. Found: 5 of 14, 36 per cent; one-sided binomial $p = 0.91$. Without the three rows that use a proxy age, 4 of 11. **Fail.**

Across the three books the theory has been set against biological data nine times with the outcome fixed first. One passed: W1, the nesting depth. Three failed outright: the count list in *Plants on the Ladder*, the retention rule in *The Company of Plants*, and the partner-age rule here.

One failed on its own rule, which was ill-posed, while confirming its measured half (the Fibonacci cones). Four could not be completed on the data reachable. That is the state.

B12 The answer to the question of this book

The question: how animals, plants, fungi and microorganisms, each from its own history, became interwoven, and how that can be described in the Vacuum.Net model.

Layer A gives the history. Three domains from one ancestor dated at 3.5 Ga or older, with genes moving between them. Eukaryotes that took in a bacterium once and a cyanobacterium once, with two later primary uptakes in *Paulinella* and UCYN-A, and plastids passed on from hand to hand. Multicellularity more than 25 times.

Fungi and arthropods on land with or before the first plant spores of 473–471 Ma, and a full community of plants, fungi, nematodes and arthropods in the Rhynie chert at 411.5 Ma. Eaters, parasites, pollinators and dispersers arriving on forms already there. Element cycles run by bacteria and archaea and carried by animals.

A human share that now holds 94–96 per cent of mammal mass.

Layer B gives four reads and one passed test. 1. Most connections arrive on forms that an earlier connection made: what one union makes is a letter of the next (statement 2). Read. 2. In 24 cases no cell holds a chain of more than two nested partners with their own genomes (statement 4). Test passed; *Mesodinium* open. 3. A new kind of union opens once, then it is filled many times (statement 3). Read, post hoc. 4. Mutualistic networks are nested, as a tree of shared prefixes (statement 7). Read.

What does not hold: the rule that each supplier is older than the one it supplies, and each eaten older than its eater (W3, failed). What the texts leave alone: shares, species numbers, element fluxes, the human share.

Read, as a whole. The weaving, in these terms, is a sequence of closures. Each closed union becomes a letter of the next; each kind is opened once and then filled. In the measured cases a cell never holds them more than two deep.

The description uses only statements in the texts. One part of it has passed a test it could have failed.

Part D — Left Out, by Rule

- Facts that the dossiers marked as read only in a secondary page, or whose citation alone was verified, do not enter Layer A. Each chapter lists them under “Not verified”.
 - Where two sources disagree, both numbers stand in Layer A. This book does not choose.
 - Numbers from the five background books are not used. Their topics are; their figures are replaced by the primaries.
 - No pairing in Layer B uses a fact outside Layer A, with one exception marked in B4: the case of *Mesodinium rubrum*, checked after test W1 and not counted in it.
 - No count of species, of chromosomes or of cells is set beside a sequence of the theory (1, 3, 10, 33, 109; powers of three; Fibonacci) unless a text sets it there. None does.
-

Annotated references for Layer B

The texts

Konstapel, J. (2026). *The Vacuum.Net Theory: Complete Derivation*. Constable Research, Leiden, 28 September 2026. Why read? The five axioms, among them N3 memory and N5 scale, quoted in B2.

Konstapel, J. (2026). *The Balanced Three, the Balanced Tree and the Vacuum.Net Theory*. Constable Research, Leiden, 29 August 2026; PDF *Balanced Ternary and the Balanced Tree: One Balance and What Follows From It*. Why read? $\Psi^2 = 0$ and the rule that a closure cannot load twice (§2, §5), and the tree $b(n)$ with σ_3 . Then §11, “The other sciences”: species as subtree, filling until forced, heredity with reach two, community as shared prefix. *Reading advice*: §11 first, then §2 and §5.

Konstapel, J. (2026). *The Climate on the Ladder of Three*. Constable Research, Leiden, 3 October 2026. Why read? Depth as layer, $3^n \cdot S_0$, the definition behind every position in this book and behind test W2.

Konstapel, J. (2026). *Where Illness Comes From*. Constable Research, Leiden, ninth edition. Why read? The two classes, and “the residue of depth n is the alphabet of depth $n+1$ ”: the statements that B3, B6 and B7 rest on.

Konstapel, J. (2026). *Plants on the Ladder*. Constable Research, Leiden, 12

October 2026. And *The Company of Plants*. Constable Research, Leiden, 13

October 2026. *Why read?* The two books this one extends. The six earlier tests whose outcomes B11 counts with these three; the post hoc rule that W3 fixed in advance and that then failed.

The test beyond the fixed data

Johnson, M. D., Oldach, D., Delwiche, C. F., and Stoecker, D. K. (2007).

“Retention of transcriptionally active cryptophyte nuclei by the ciliate *Myrionecta rubra*.” *Nature* 445, 426–428. DOI 10.1038/nature05496. Citation verified through OpenAlex; content read through a secondary page (mappingignorance.org). *Why read?* The case that would decide the reading of B4. *Reading advice:* look for whether the stolen nucleus, mitochondria and plastids stay inside one cryptophyte compartment.

Background books

Quammen, D. (2018). *The Tangled Tree: A Radical New History of Life*. New York: Simon & Schuster. 496 pp. *Why read?* The history of the shift from the tree of life to a web of gene transfer, through Woese and the three domains. Background to A1.

Dawkins, R., and Wong, Y. (2017). *The Ancestor’s Tale: A Pilgrimage to the Dawn of Life*. Updated edition. London: Weidenfeld & Nicolson. 800 pp. *Why read?* Life told backward from the human, rendezvous by rendezvous with each group of cousins. Background to the order of A1–A3 and A10.

Beerling, D. (2007). *The Emerald Planet: How Plants Changed Earth’s History*. Oxford: Oxford University Press. xvi + 288 pp. *Why read?* Plants, the air and the climate as one history: Devonian forests, carbon dioxide, Carboniferous oxygen. Background to A6 and A9.

Sheldrake, M. (2020). *Entangled Life: How Fungi Make Our Worlds, Change Our Minds & Shape Our Futures*. New York: Random House. x + 352 pp. *Why read?* Fungi as the connective tissue of the living world: lichens, mycorrhiza, networks, farming by insects. Background to A5.

Begon, M., Townsend, C. R., and Harper, J. L. (2006). *Ecology: From Individuals to Ecosystems*. Fourth edition. Malden, MA: Blackwell Publishing. *Why read?* The standard account of predation, parasitism, mutualism, food webs and nutrient cycles. Background to A7–A9.

Reading advice: the chapters on mutualism, on the flux of energy and on the flux of matter.