Nine That Almost Closes

The centriole, the sperm tail and the closure rule of the Vacuum.Net, read through the work of Miguel Ricardo Leung

J. Konstapel
Constable Research, Leiden
16 November 2026

Abstract

Miguel Ricardo Leung studies the structure of sperm, eggs and motile cilia with cryo-electron microscopy. His work shows lattices, rings, seams and a clear left–right bias. This essay reads those findings in the language of the Vacuum.Net theory. The aim is description, not proof.

Four results converge. First, one cilium runs through the three elementary closures of the theory in order: triplet, doublet, singlet. Second, the ninefold ring of the centriole is a helix forced to close. Third, that ring does not quite close. The measured angle between SAS-6 dimers is 38–39°, not 40°. Fourth, the residue reappears as a twist of 9–17° along the centriole. A helical scaffold locks that twist. In mammalian sperm Leung and colleagues show that this scaffold splits into two rods. The lock is released and the tail beats to the left.

One pattern holds across these layers: near-closure, carry, storage, direction. The essay separates structural correspondences from numerical coincidences. It ends with open questions and an annotated reference list.

1. Introduction

Leung works at the Hubrecht Institute and University Medical Center Utrecht. Earlier he worked in the group of Tzviya Zeev-Ben-Mordehai at Utrecht University and at Oxford. His fifteen papers since 2018 cover the sperm tail, the sperm head, the egg and the tools to see them.

He calls his method “structure first”. One looks at the native structure before one names its parts. Proteins are identified from the map itself. This fits the approach of this essay. The Vacuum.Net theory also starts from form and treats names as secondary.

The question is simple. Can Leung’s findings be written in the language of the theory? The theory is not tested here. It is used as a reading frame. Where the frame fits, we say so. Where it only matches a number, we say that too.

2. Method

The work followed four steps. Collect first. Pursue each question that comes up in depth. Draw short conclusions. Then collect again and look for convergence.

- All seventeen PubMed records under “Leung MR” were retrieved. Fifteen belong to Miguel Ricardo Leung. Two belong to other authors and were excluded.
- Twelve full texts were read from PubMed Central. All measurements, symmetries and periods were extracted.
- Background literature on the cartwheel, the transition zone and the centriole scaffold was added where a question required it.
- The theory was taken from *The Vacuum.Net Theory, Ninth Edition* (27 October 2026). Theorems are cited as T1, T2, and so on.

Each correspondence received one of three labels. *Structural*: the biology and the theory describe the same form. *Magnitude*: two numbers agree, but the link is not shown. *Numerical*: only a count matches. The last kind is reported but not used to argue.

3. The theory in brief

The Vacuum.Net theory rests on one strand and the trinity: the values −1, 0 and +1. These are the digits of balanced ternary. Five axioms follow. N1: every distinction is a loop of the one strand. N2: a loop persists only if it closes; what does not close passes on as tension. N3: the first passage fixes direction; the net carries its history as its shape. N4: the response of the medium depends on its state. N5: what does not close at one scale is the material of the next.

Several theorems matter here.

- T7 (elementary closures). Every closed word breaks down into three pieces. A standing (0), length 1. A meeting (x, −x), length 2. A ring (x, x, x), length 3. A meeting is the shortest closure with winding number 0. A ring is the shortest with winding number ±1.
- T7.1 (carry). A standing and a meeting close with carry 0. Nothing passes on. A ring closes with carry ±1. It becomes one passage of the next scale.
- T11 (seam rule). Joining two different closed windows always leaves tension.
- T14 (algebraic home). The trit lives in the Eisenstein integers. That is the hexagonal lattice, with turns of 60° and 120°.
- T15–T18 (two ladders). Merging meetings doubles; merging rings triples. The ladders ×2 and ×3 never meet exactly. Their best near-meeting at depth 12 leaves the Pythagorean comma.
- T19–T20 (first knot). The trefoil is the first knot. It is chiral.

4. What Leung has found

Leung's papers fall into five groups. Table 1 gives the measurements used in this essay.

Structure	Key findings (source)
Axoneme	Repeat of 96 nm, built on the 8-nm tubulin dimer; up to three radial spokes per repeat; 181 proteins in the sperm doublet, 34 new (Nature 2025).
TRiC chaperonin	Two stacked rings of eight subunits; tethered to the radial spokes only in mammalian sperm; held in the open state (Nature 2025; Cytoskeleton 2025).
Sperm neck	Proximal centriole with triplets; distal centriole with splayed doublets; inner scaffold split into left and right rods; left rods ~50% longer; right side slides ~300 nm; head tilts left (EMBO J 2021; Nat Commun 2021).
Head–tail junction	SUN5–Nesprin3 trimers in a hexagonal lattice; 7.2 nm between trimers; uniform membrane spacing of 13.19 ± 1.25 nm; loss causes head–tail detachment (PNAS 2026).
Egg storage	Cytoplasmic lattices of at least 13 proteins; tubulin stored as unpolymerised dimers, two per 38-nm repeat; PADI6 rings of five dimers in a spiral staircase (Nature 2026).
Midpiece	Arrays on mitochondria at ~120° and ~60° to the axis; pores ~5 nm apart; each particle spans eight pores (PNAS 2021).

Table 1. Measurements from Leung's papers used in this essay.

5. Four layers of convergence

5.1 One organelle, three closures in order

A motile cilium starts at a basal body. That basal body is a ring of nine triplet microtubules. At the transition zone the C-tubules end. The A- and B-tubules continue as doublets in the axoneme. Near the tip the B-tubule ends. The A-tubule runs on as a singlet. In human sperm a doublet can also split into two singlets.

From base to tip the cilium thus runs 3 → 2 → 1. These are the three elementary closures of T7, in the same order. The match goes beyond counting. A ring goes round. The triplet barrel turns: its A–C linkers twist the triplets like an iris diaphragm. A meeting goes back and forth. The axoneme does exactly that. Its beat is an oscillation with no net turn. Label: structural.

The C-tubule is what closes the ring. Each A–C linker joins the A-tubule of one triplet to the C-tubule of the next. When C is lost, the round closure is lost. The doublets can then slide. Leung sees this in the distal centriole of mammalian sperm. It has splayed doublets instead of triplets and it is compliant.

The transition is also a weak point. Many ciliopathy mutations map to the transition zone. In sperm, the dynamic basal complex sits at the same place. T11 predicts this. A seam between two kinds of closure always carries tension. Label: structural.

5.2 Why nine

Ninefold symmetry starts in the cartwheel. Nine SAS-6 dimers join into one ring. The ring of nine is built from pairs: meetings that together go round.

SAS-6 does not want a ring. Free in solution, a computed assembly of nine dimers forms a shallow helix. A surface turns that helix into a ring. This is N2 at work: what closes persists. Rings of seven to ten dimers occur. Nine is the majority. An open ring of nine closes after about 4 s. An open ring of eight takes about 10 s. The cell chooses the form that closes fastest, not the form that lasts longest. Label: structural.

Nine is odd and divisible by three. By T7 a meeting needs even length and a ring a length divisible by three. A ring of nine cannot be split into pairs. Banterle and colleagues state the same in protein terms. An odd number of spokes cannot divide evenly between bound and unbound. This breaks planar and radial symmetry. They propose that this gives the cartwheel its handedness. The theory reads it as N3: the residue becomes direction. Label: structural.

Two further readings are weaker. The theory has nine closing windows of twenty-seven (T3). Two trits give exactly nine addresses, −4 to +4 (T12). The Lo Shu square holds these nine and closes on every trit level. These are numerical correspondences only. Known exceptions point the same way, though. Axonemes with 10, 12, 14, 16 or 18 doublets exist. These counts are even and fit a ladder of pairs. The centriole stays at eight or nine.

5.3 The ring does not quite close

If nine dimers close a ring exactly, each step is 40°. The measured angles are 39° ± 4° (N = 144) and 38° ± 3° (N = 215). Assume the ± values are standard deviations. Then the standard errors are 0.33° and 0.20°. The gap to 40° is three and ten standard errors. The natural turn holds 9.2 to 9.5 dimers. After nine steps 9° to 18° are missing. The ring is a near-closure, as in T16–T18.

Nature handles this residue in two ways. In the nematode *C. elegans* SAS-6 forms a spiral, not a ring. The spiral still fits ninefold symmetry. It returns after nine steps, one level higher. This is T7.1: close at your own scale and pass the carry up. In other species the rings close and stack. They stack in two alternating ways: in register, or with a slight rotational offset. In the model that fits the map, the offset is about 6.5°.

The Pythagorean comma of T18, written as an angle, is 7.04° of a full turn. That is close to 6.5°. But 6.5° is a value imposed in a model, not a measurement. Label: magnitude, weak.

Both ladders also appear along the axis. In *Trichonympha* the spokes of two rings merge into a 17-nm unit (×2). In *Paramecium* and *Chlamydomonas* the unit is 25 nm and holds three ring pairs (×3). The same organelle uses either ladder, by species. Label: structural.

5.4 The twist accumulates and is released in sperm

If the ring leaves a residue, where does it go? Two studies answer this. Li and colleagues show that the A–C linker twists along the procentriole. The angle falls from 93° to 83° over 90 nm. The result is a left-handed iris motion. They note that the triplet angle must end where the axoneme doublets begin.

Le Guennec and colleagues measured the triplet angle along whole centrioles. In *Paramecium* it falls from ~115° to ~106°. In *Chlamydomonas* it falls from ~120° to ~109°. Further on it stays fixed at ~100° and ~103°. The total twist is 15–17°. A helical inner scaffold then locks it. That scaffold is a two-start helix in *Paramecium* (pitch 17 nm). It is a three-start helix in *Chlamydomonas* (pitch 49.5 nm). Both ladders appear once more.

The ring left 9–18° open. The triplets turn 9–17°. The centriole seems to unwind along its length what the cartwheel could not close. The data come from different species and methods. Label: magnitude.

The reading fits the theory well. The twist runs toward the seam. It is the carry that the ring (×3) hands to the meeting (×2), as T7.1 describes. The scaffold stores it as fixed form, as N3 describes: the history becomes the shape.

Here the line returns to Leung. The inner scaffold is made of POC1B, CETN1, POC5 and related proteins. In the distal centriole of mammalian sperm, Leung and colleagues show that exactly these proteins split into a left and a right rod. The left rods are longer. The right side slides about 300 nm forward. The head tilts left. Four doublets on the left work against three on the right, with two at rest. What other cells lock, sperm release. The stored twist becomes a left-handed beat. Label: structural.

Layer	Biology	Theory
Ring	Nine SAS-6 dimers; 38–39° per step	Near-closure (T16–T18)
Residue	9–18° open per ring	Tension that does not close (N2)
Carry	Spiral in C. elegans; offset stacking elsewhere	Ring passes carry to next scale (T7.1)
Accumulation	Triplets twist 15–17° along the centriole	Carry handed toward the seam (T11)
Storage	Helical scaffold, two or three starts	History stored as shape (N3)
Release	Scaffold splits into rods in sperm; beat to the left	Stored direction becomes motion (N3, T19)

Table 2. The chain from cartwheel to sperm beat, read in the terms of the theory.

6. Further correspondences

Leung's other work fits the same reading. These points were collected but not pursued in depth.

- *Hexagonal lattice of rings.* SUN5 forms trimers in a hexagonal lattice. These are rings of three in the Eisenstein lattice of T14. The lattice holds the head to the tail. When it fails, the head detaches. The seam needs reinforcement. Label: structural.
- *Storage as closure without carry.* The egg stores tubulin as single dimers, not as polymer. A meeting closes with carry 0 (T7.1). Nothing passes on. It waits. Label: structural.

- *State, not constant*. TRiC and adenylate kinases switch between open and closed states depending on where they sit. This matches N4. Label: structural.
- *Hexagonal angles in the midpiece*. Mitochondrial arrays run at ~120° and ~60° to the axis. These are the turns of T14. Label: magnitude.
- *Counts*. The axonemal repeat is 96 nm, twelve dimers; twelve is a closure depth (T17). Thirteen appears as protofilament count, protein count and membrane spacing; thirteen is the capacity of three trits (T12.3). The centriole holds 27 tubules, the full trit cube. Label: numerical only.

7. Limits and open questions

Several points need care.

- The angle data come from one study. Whether ± denotes standard deviation must be checked in the paper.
- The 6.5° stacking offset is a model value. A direct measurement is needed.
- The residue of the ring and the twist of the triplets were measured in different species. The match is one of magnitude, not of mechanism.
- No count closes the transition. The basal body has 27 tubules; the axoneme has 20. The central pair starts where the C-tubules end, but the books do not balance.

Four questions follow.

- How large is the triplet twist in the mammalian centriole, and in the distal centriole of sperm?
- Is the released twist exactly the left torque of the beat, four doublets against three?
- The step of about 8.5 nm appears in the ring spacing, the A–C linker and the scaffold helix. Is it the unit of this depth?
- Why does *Trichonympha* choose ×2 and *Chlamydomonas* ×3?

8. Conclusion

Leung's work shows a cell that builds with rings, pairs and seams. Read through the Vacuum.Net, one pattern runs from protein to motion. A ring of nine almost closes. The residue passes on as twist. A helix stores it. In sperm the store is opened and the tail beats to one side.

This is not a proof of the theory. It shows that a large body of structural biology can be written in its terms with little strain. The strongest links are structural, not numerical. They concern how things close, where they fail and why they turn.

Leung's own stance helps here. Look at the structure first. Name it later. The cilium, seen that way, already speaks the language of closure.

Annotated references

Work of M. R. Leung

Leung, M.R., Roelofs, M.C., Ravi, R.T., et al. (2021). The multi-scale architecture of mammalian sperm flagella and implications for ciliary motility. EMBO Journal 40, e107410. doi:10.15252/embj.2020107410

Annotation. In-cell cryo-ET of sperm from three species. Shows triplets in the proximal centriole and remodelled triplets in the mouse. The base text for sections 5.1 and 5.4.

Khanal, S., Leung, M.R., Royfman, A., et al. (2021). A dynamic basal complex modulates mammalian sperm movement. Nature Communications 12. doi:10.1038/s41467-021-24011-0

Annotation. Shows the distal centriole as splayed doublets with asymmetric left and right rods. Gives the ~300 nm sliding and the left bias. Central to section 5.4.

Leung, M.R., Zeng, J., Wang, X., et al. (2023). Structural specializations of the sperm tail. Cell 186. doi:10.1016/j.cell.2023.05.026

Annotation. High-resolution doublet structures from sea urchin and bovine sperm. Over 60 decorating proteins. Useful for anyone following the axoneme further.

Leung, M.R., Sun, C., Zeng, J., et al. (2025). Structural diversity of axonemes across mammalian motile cilia. Nature. doi:10.1038/s41586-024-08337-5

Annotation. The 96-nm repeat across four cell types. Source of the radial spoke and TRiC findings in Table 1.

Brown, A., Leung, M.R., Zeev-Ben-Mordehai, T., Zhang, R. (2025). TRiC is a structural component of mammalian sperm axonemes. Cytoskeleton. doi:10.1002/cm.22005

Annotation. Short perspective. Discusses why a folding machine sits fixed in the open state. Relevant to the question of state versus constant (N4).

Moecking, J., Doroshev, S., Leung, M.R., Zeev-Ben-Mordehai, T. (2026). SUN5 forms a regular protein lattice reinforcing the sperm head–tail junction. PNAS. doi:10.1073/pnas.2520626123

Annotation. Trimers in a hexagonal lattice with 7.2 nm spacing. The clearest case of rings in the Eisenstein lattice in this essay.

Kılıç, Z.I., van Loenhout, J., Chaillet, M., et al., Leung, M.R. (2026). Cytoplasmic lattices are megadalton storage complexes in mammalian oocytes. Nature. doi:10.1038/s41586-026-10513-8

Annotation. Leung as last author. Tubulin stored as single dimers. The basis for reading storage as closure without carry.

Leung, M.R. (2026). Structure first: exploration and discovery with cryo-electron microscopy. Journal of Cell Science. doi:10.1242/jcs.264215

Annotation. Leung's statement of method. Read this first to understand his approach.

Leung, M.R., Zenezini Chiozzi, R., Roelofs, M.C., et al. (2021). In-cell structures of conserved supramolecular protein arrays at the mitochondria–cytoskeleton interface in mammalian sperm. PNAS 118, e2110996118. doi:10.1073/pnas.2110996118

Annotation. Arrays at 120° and 60° on the mitochondrial surface. A lead not yet followed.

Leung, M.R., Ravi, R.T., Gadella, B.M., Zeev-Ben-Mordehai, T. (2021). Membrane remodeling and matrix dispersal intermediates during mammalian acrosomal exocytosis. Frontiers in Cell and Developmental Biology 9, 765673. doi:10.3389/fcell.2021.765673

Annotation. Paracrystalline acrosome matrix disassembles step by step. A possible case of stored order released gradually.

Ravi, R.T., Leung, M.R., Zeev-Ben-Mordehai, T. (2020). Looking back and looking forward: contributions of electron microscopy to the structural cell biology of gametes and fertilization. Open Biology 10, 200186. doi:10.1098/rsob.200186

Annotation. Accessible review. Good entry point to gamete structure for non-specialists.

Cartwheel, centriole and transition zone

Kitagawa, D., Vakonakis, I., Olieric, N., et al. (2011). Structural basis of the 9-fold symmetry of centrioles. Cell 144, 364–375. doi:10.1016/j.cell.2011.01.008

Annotation. SAS-6 forms rod-shaped dimers that join into rings of nine. The starting point for section 5.2.

van Breugel, M., Hirono, M., Andreeva, A., et al. (2011). Structures of SAS-6 suggest its organization in centrioles. Science 331, 1196–1199. doi:10.1126/science.1199325

Annotation. Parallel crystal work. Confirms the two interfaces that build the ring.

Hirono, M. (2014). Cartwheel assembly. Philosophical Transactions of the Royal Society B 369, 20130458. doi:10.1098/rstb.2013.0458

Annotation. Short review. Explains how the ninefold symmetry starts from nine SAS-6 dimers.

Hilbert, M., et al. (2013). Caenorhabditis elegans centriolar protein SAS-6 forms a spiral that is consistent with imparting a ninefold symmetry. PNAS 110, 11373–11378. doi:10.1073/pnas.1302721110

Annotation. The open alternative: a spiral instead of a ring, with the same symmetry. Key evidence for the carry reading in section 5.3.

Hilbert, M., et al. (2016). SAS-6 engineering reveals interdependence between cartwheel and microtubules in determining centriole architecture. Nature Cell Biology 18, 393–403. doi:10.1038/ncb3329

Annotation. Engineered rings from five- to tenfold. In cells the symmetry returns to eight or nine.

Guichard, P., et al. (2017). Cell-free reconstitution reveals centriole cartwheel assembly mechanisms. Nature Communications 8, 14813. doi:10.1038/ncomms14813

Annotation. Rings stack preferentially in pairs. Useful for the vertical ladders.

Banterle, N., Nievergelt, A.P., de Buhr, S., et al. (2021). Kinetic and structural roles for the surface in guiding SAS-6 self-assembly to direct centriole architecture. Nature Communications 12, 6180. doi:10.1038/s41467-021-26329-1

Annotation. The most important single source. Gives the 38–39° angle, ring lifetimes and the odd-number argument for chirality.

Nazarov, S., Bezler, A., Hatzopoulos, G.N., et al. (2020). Novel features of centriole polarity and cartwheel stacking revealed by cryo-tomography. EMBO Journal 39, e106249. doi:10.15252/embj.2020106249

Annotation. Rings stack in register or with a rotational offset. Source of the 6.5° model value.

Klena, N., Le Guennec, M., Tassin, A.M., et al. (2020). Architecture of the centriole cartwheel-containing region revealed by cryo-electron tomography. EMBO Journal 39, e106246. doi:10.15252/embj.2020106246

Annotation. Compares four species. Gives the 25-nm unit of three ring pairs.

Guichard, P., Gönczy, P. (2016). Basal body structure in Trichonympha. Cilia 5, 9. doi:10.1186/s13630-016-0031-7

Annotation. Review of the long Trichonympha cartwheel. Source of the 8.25-nm and 16.5-nm periods.

Li, S., Fernandez, J.J., Marshall, W.F., Agard, D.A. (2019). Electron cryo-tomography provides insight into procentriole architecture and assembly mechanism. eLife 8, e43434. doi:10.7554/eLife.43434

Annotation. Measures the A–C linker twist and names the left-handed iris motion.

Le Guennec, M., Klena, N., Gambarotto, D., et al. (2020). A helical inner scaffold provides a structural basis for centriole cohesion. Science Advances 6, eaaz4137. doi:10.1126/sciadv.aaz4137

Annotation. Measures triplet angle along the centriole and describes the helical scaffold. The key link to Leung's rods.

Meehl, J.B., et al. (2016). Tetrahymena Poc1 ensures proper intertriplet microtubule linkages to maintain basal body integrity. Molecular Biology of the Cell 27, 2394–2403. doi:10.1091/mbc.E16-03-0165

Annotation. Loss of Poc1 reduces triplet twist. Supports the role of the scaffold in storing twist.

Greenan, G.A., et al. (2018). Insights into centriole geometry revealed by cryotomography of doublet and triplet centrioles. eLife 7, e36851. doi:10.7554/eLife.36851

Annotation. Mammalian centrioles have a proximal core with A–C linkers and a distal part with incomplete C-tubules.

Greenan, G.A., et al. (2020). Electron cryotomography of intact motile cilia defines the basal body to axoneme transition. Journal of Cell Biology 219, e201907060. doi:10.1083/jcb.201907060

Annotation. Describes the triplet-to-doublet conversion and notes the concentration of ciliopathy mutations at the transition zone.

Zabeo, D., Croft, J.T., Höög, J.L. (2019). Axonemal doublet microtubules can split into two complete singlets in human sperm flagellum tips. FEBS Letters 593, 892–902. doi:10.1002/1873-3468.13379

Annotation. Describes the tip of the tail: doublets end or split into singlets. Completes the 3 → 2 → 1 sequence.

Bezler, A., et al. (2022). Atypical and distinct microtubule radial symmetries in the centriole and the axoneme of Lecudina tuzetae. Molecular Biology of the Cell 33, ar75. doi:10.1091/mbc.E22-04-0123

Annotation. A six- or fivefold axoneme on an eightfold centriole. Lists known exceptions with 10 to 18 doublets.

The Vacuum.Net theory

Konstapel, J. (2026). The Vacuum.Net Theory, Ninth Edition (Foundations 9.2, Physics 9.0). Constable Research, Leiden. constable.blog, 29 October 2026.

Annotation. The primary reference for all axioms and theorems used here.

Konstapel, J. (2026). One Rule at Every Scale: Knots, Ternary Closure and the Lo Shu. constable.blog, 8 November 2026.

Annotation. Shows the closure rule on every trit level of the Lo Shu square. Background to the reading of nine in section 5.2.