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Simple Sponges or Complex Jellies? Why Ctenophores Remain as Metazoa's Most Likely Ancestor

Biology * Evolution * Genetics

Introduction: The Phylogenomic Pendulum from Ctenophores to Porifera

In the grand library of life on Earth, the opening chapter of the animal kingdom has remained stubbornly contested. For over a century, evolutionary biologists have debated which lineage represents the sister group to all other metazoans -- the earliest branch to diverge from the common animal ancestor. Resolving this root is fundamental to understanding the origins of biological complexity: did the earliest animals already possess muscles, nerves, and a through-gut, or were they simple, sedentary filter-feeders devoid of differentiated tissues and organs?

This debate has traditionally pitted morphologically simple sponges (Phylum Porifera, such as the bath sponge) against complex, gelatinous comb jellies (Phylum Ctenophora, such as the lobed comb jelly). For decades, the "Sponge-Sister" hypothesis prevailed, aligning with a gradualist model of evolution in which anatomical complexity accrued incrementally. However, 21st-century high-throughput DNA sequencing upended this consensus, repeatedly recovering the "Ctenophore-Sister" topology -- a scenario implying that complex neuromuscular systems either evolved twice via convergent evolution or were secondarily lost in sponges.

In November 2025, a high-profile study in Science by Jacob L. Steenwyk and Nicole King titled "Integrative phylogenomics positions sponges at the root of the animal tree" appeared to resolve the conflict in favor of sponges.[1][2] Yet within three months, the paper was formally retracted.[4] Independent researchers auditing the open-source code and matrices identified critical analytical flaws in the study's bioinformatic pipeline; when corrected, the dataset completely reversed its signal, strongly supporting ctenophores.[5] This report examines the biological stakes of the metazoan root, the methodological promise and failure of the 2025 study, and the forensic statistics that triggered its rapid retraction.

The Biological Stakes of the Deepest Metazoan Branch

Sponges and comb jellies represent fundamentally divergent architectures of multicellular life. Sponges are sessile aquatic animals lacking true tissues, organs, a mouth, or a digestive tract. Their bodies operate as flagellated water-canal systems wherein specialized collar cells (choanocytes) -- closely resembling colonial protist choanoflagellates -- filter bacteria and organic particulates from seawater.[6][7] Under the classical Sponge-Sister hypothesis, the last common ancestor of animals (the Urmetazoan) was a simple, nerve-free choanoflagellate-like colony, and tissues, muscles, and nervous systems evolved once in the lineage leading to Cnidaria and Bilateria.[10]

Ctenophores, by contrast, are active pelagic predators propelled by eight rows of iridescent fused cilia (ctenes). They possess a unidirectional through-gut with

mouth and anal pores, smooth muscle cells, an apical gravity-sensing organ, and a decentralized nerve net that coordinates locomotion and bioluminescence.[8][9] Placing ctenophores as the sister group to all other animals introduces a major evolutionary paradox:

* Secondary Loss Hypothesis: The Urmetazoan already possessed a nervous system and muscles, which were subsequently lost in the lineage leading to Porifera (and Placozoa) as an adaptation to a sedentary filter-feeding lifestyle.[2]

* Independent Origin (Convergence) Hypothesis: The Urmetazoan was simple, and ctenophores evolved their neurons, synapses, and musculature independently from Cnidaria and Bilateria.[9]

Since Casey Dunn and colleagues published the first phylogenomic analysis placing ctenophores at the metazoan root in 2008, skeptics argued that the Ctenophore-Sister signal was a statistical artifact of Long Branch Attraction (LBA), wherein rapidly evolving ctenophore sequences are artificially pulled toward distant outgroups.[5][6] Although a landmark 2023 Nature study by Schultz et al. used conserved chromosomal genetic linkage (macrosynteny) on chromosomes to bypass sequence-level LBA and strongly validate Ctenophore-Sister, sequence-based phylogenomic methods remained divided.[12]

The Promise and Pitfalls of Integrative Phylogenomics

Steenwyk and King sought to reconcile sequence-based phylogenetics by unifying its two dominant paradigms: concatenation (stitching hundreds of aligned genes into a single supermatrix to maximize statistical power, which can be misled by Incomplete Lineage Sorting, or ILS) and coalescence (inferring individual gene trees and summarizing them to account for ILS, which is vulnerable to low phylogenetic signal in short single-gene alignments).[1][13]

Their proposed "integrative phylogenomics" pipeline assembled 869 genes across 100 species (sponges, ctenophores, cnidarians, bilaterians, and non-animal outgroups) and scored every gene under both paradigms -- calculating a concatenation log-likelihood difference (ln L) and a coalescence quartet-support score.[3][5] Genes that disagreed between the two methods were discarded as "inconsistent noise," retaining only genes that consistently favored either Sponge-Sister or Ctenophore-Sister. Across 785 topology tests on their filtered matrices and 10 historical datasets, the authors reported 490 tests significantly supporting Sponge-Sister and 0 supporting Ctenophore-Sister, concluding that filtering out inconsistent loci resolved the animal tree of life in favor of Porifera.[1]

| Analytical Dimension | | Concatenation (Supermatrix) | | Coalescence (Gene Tree Summary) | | 2025 "Integrative" Pipeline (Flawed) | | Corrected Re-Analysis (Dunn et al., 2026) |

| Primary Unit of Analysis | | Combined alignment of all loci | | Individual single-gene trees | | Loci scored as consistent across both methods | | Properly optimized and informative loci |

| Concatenation Metric (ln L) | | Site-wise log-likelihood across supermatrix | | Not applicable | | Calculated on unresolved polytomous constraint trees (ln L in thousands) | | Calculated on fully resolved ML trees (ln L [-10, +10]) |

| Coalescence Quartet Scoring | | Not applicable | | ASTRAL quartet topology frequencies | | Collapsed clade nodes created massive sampling bias for sponges (29 spp. vs. 13 ctenophores) | | Uncollapsed informative quartets spanning all 4 focal clades |

| Uninformative "Ghost" Loci | | Diluted across supermatrix | | Excluded if missing focal taxa | | 45 of 56 genes lacking ctenophores or outgroups scored as "Sponge-Sister" | | 56 taxally incomplete genes removed prior to topology testing |

| Consistent Gene Count (92.5 Matrix) | | Varies by evolutionary model | | Often favors Ctenophore-Sister | | 82 Sponge-Sister vs. 6 Ctenophore-Sister | | 174 Sponge-Sister vs. 370 Ctenophore-Sister |

Forensic Bioinformatics: Dissecting the Analytical Errors

Shortly after publication, Casey Dunn (Yale University), Xiaofan Zhou, Jingxuan Chen, and colleagues audited the publicly deposited data and scripts, uncovering three severe methodological flaws that had fabricated the pro-sponge signal.[5][14]

* The Unresolved Constraint Tree Artifact (Concatenation Flaw): For single genes, log-likelihood differences (ln L) between competing hypotheses typically fall in the single or low double digits. Steenwyk and King reported single-gene ln L values in the thousands.[14] The critics discovered that the authors had passed multifurcating constraint trees (containing unresolved polytomies for internal clade relationships) directly to IQ-TREE using the -z evaluation flag without first optimizing internal branch topologies.[5] Consequently, IQ-TREE scored arbitrary, unoptimized star-like topologies, generating massive artificial likelihood penalties. When Dunn's team properly inferred the maximum-likelihood constrained trees before comparing likelihoods, ln L values returned to normal ranges (-10 to +10) and the majority of genes flipped to favor Ctenophore-Sister.[5]

* Collapsed-Node Quartet Bias (Coalescence Flaw): The dataset contained more than twice as many sponges (29 species) as ctenophores (13 species).[14] When scoring gene-tree quartets against reference topologies, the authors collapsed non-focal clades into single nodes. Because of this collapsing error, any quartet containing two sponges and two non-sponges was automatically tallied as supporting the Sponge-Sister hypothesis regardless of where ctenophores branched. Given the heavy oversampling of sponges, millions of uninformative quartets swamped the coalescence metric.[5]

* The "Ghost Gene" Smoking Gun: Resolving whether sponges or ctenophores are the sister group to other animals mathematically requires a gene alignment to include sequences from four groups: Porifera, Ctenophora, other metazoans, and non-animal outgroups. Dunn et al. discovered that 56 of the 869 genes completely lacked either ctenophores, outgroups, or both -- yet the authors' pipeline scored 45 of these taxally incomplete "ghost genes" as providing "consistent support for Sponge-Sister."[5]

When the Dunn team removed the 56 uninformative loci and corrected the IQ-TREE constraint optimization and quartet-scoring scripts on the primary 92.5 matrix, the results inverted completely: instead of 82 consistent genes for Sponge-Sister versus 6 for Ctenophore-Sister, the corrected integrative pipeline yielded 370 consistent

genes supporting Ctenophore-Sister versus 174 supporting Sponge-Sister.[5] Demonstrating exemplary scientific integrity, Steenwyk and King verified the critique and requested the retraction of their paper on January 9, 2026, which Science finalized in February 2026.[4][14]

Consilience with Macrosynteny and Neural Evolution

The reversal of the corrected 2025 sequence matrices brings sequence-based phylogenomics into direct consilience with chromosomal macrosynteny.[11][12] Unlike individual nucleotide substitutions -- which are prone to saturation and back-mutation over half a billion years -- macrosynteny tracks ancient, irreversible chromosomal fusions and gene linkages across the genome. As Schultz et al. (2023) demonstrated, sponges, cnidarians, and bilaterians share derived chromosomal rearrangements and mixing events that are absent in ctenophores and unicellular outgroups, providing an independent, rare-genomic-change confirmation of the Ctenophore-Sister root.[12]

| Evolutionary Trait | | Sponge-Sister Hypothesis | | Ctenophore-Sister Hypothesis | | Empirical Genomic & Physiological Evidence |

| Origin of Nervous Systems | | Single origin in ParaHoxozoa (after sponge divergence). | | Independent convergent evolution in Ctenophora OR secondary loss in Porifera. | | Ctenophore neurons lack canonical bilaterian neurotransmitter pathways (e.g., serotonin/dopamine) and use distinct synaptic proteins.[9] |

| Origin of Musculature & Gut | | Single gradualist accumulation of complex tissues. | | Dual evolution of striated/smooth muscle and through-gut, or porous simplification. | | Ctenophore mesoderm and pre-synaptic scaffolding utilize distinct developmental gene regulatory networks.[9][15] |

| Chromosomal Macrosynteny | | Requires convergent chromosomal fusions in Cnidaria/Bilateria and Porifera. | | Supported by shared derived chromosomal linkages uniting Sponges + Cnidaria + Bilateria. | | Schultz et al. (2023) demonstrated statistically robust syntenic synapomorphies excluding Ctenophora.[11][12] |

With Ctenophore-Sister reinforced by both corrected integrative phylogenomics and macrosynteny, neurobiologists are increasingly favoring the independent, convergent origin of the ctenophore nervous system.[9] Ctenophore neural nets lack many canonical bilaterian synaptic scaffolding proteins and classic neurotransmitter systems, utilizing unique peptide signaling molecules and gap-junction-like innexins to build functional neural circuits from a distinct genetic toolkit.[9]

Open Science and the Self-Correcting Record

The rapid publication, audit, and retraction of the 2025 Science paper stands as both a cautionary tale against "black-box" bioinformatic pipelines and a triumph of open-science transparency. Because the original authors made their data matrices publicly accessible and the reviewing community audited the command-line parameters in real time, a major distortion of the evolutionary record was corrected in under 90 days.[4][5] Far from rehabilitating the century-old gradualist narrative of the simple ancestral sponge, the episode has solidified the position of Ctenophora as

the earliest-branching animal lineage -- revealing that the dawn of animal life was marked by parallel evolutionary experiments in biological complexity.

Updates... (Nov 24, 2026): Upgraded exact publication dates across References 5, 8, 9, and 13 via GitHub, OpenAlex, and PubMed metadata, and standardized the References section heading, list ID, and item IDs across all 15 references.

References

* Steenwyk, J. L., & King, N. (Nov 13, 2025). Integrative phylogenomics positions sponges at the root of the animal tree (Retracted). Science. -- https://doi.org/10.1126/science.adw9456

* University of California, Berkeley News (Nov 19, 2025). Did the first animal look like a sponge or a comb jelly? The debate continues. -- https://news.berkeley.edu/2025/11/19/did-the-first-animal-look-like-a-sponge-or-a-comb-jelly-the-debate-continues/

* Steenwyk, J. L., & King, N. (Nov 13, 2025). Integrative phylogenomics positions sponges at the root of the animal tree (Author manuscript PDF). -- https://jlsteenwyk.com/publication_pdfs/2025_Steenwyk_and_King_Science.pdf

* Thorp, H. H. (Feb 5, 2026). Retraction of Research Article "Integrative phylogenomics positions sponges at the root of the animal tree". Science. -- https://doi.org/10.1126/science.aef5589

* Dunn, C. W., Zhou, X., Chen, J., et al. (Dec 22, 2025). sk25: Audit and corrected re-analysis of Steenwyk & King (2025). GitHub repository. -- https://github.com/caseywdunn/sk25

* Dunn, C. W., Hejnol, A., Matus, D. Q., et al. (Mar 5, 2008). Broad phylogenomic sampling improves resolution of the animal tree of life. Nature, 452, 745-749. -- https://doi.org/10.1038/nature06614

* zbek, S., Balasubramanian, P. G., Chiquet-Ehrismann, R., Tucker, R. P., & Adams, J. C. (Dec 15, 2010). The evolution of extracellular matrix. Molecular Biology of the Cell, 21(24), 4300-4305. -- https://doi.org/10.1091/mbc.E10-03-0251

* Podar, M., Haddock, S. H. D., Sogin, M. L., & Harbison, G. R. (Nov 1, 2001). A molecular phylogenetic framework for the phylum Ctenophora using 18S rRNA genes. Molecular Phylogenetics and Evolution, 21(2), 218-230. -- https://doi.org/10.1006/mpev.2001.1036

* J kely, G., Paps, J., & Nielsen, C. (Jan 13, 2015). The phylogenetic position of ctenophores and the origin(s) of nervous systems. EvoDevo, 6, 1. -- https://doi.org/10.1186/2041-9139-6-1

* Mulhair, P. O., & Redmond, A. K. (Nov 13, 2025). Sponging away phylogenomic incongruence. Science. -- https://doi.org/10.1126/science.aec6305

* Copley, R. R. (Nov 28, 2025). Sponges, ctenophores, and the statistical significance of syntenies. Molecular Biology and Evolution, 42(12), msaf321. -- https://doi.org/10.1093/molbev/msaf321

* Schultz, D. T., Haddock, S. H. D., Bredeson, J. V., Green, R. E., Simakov, O., & Rokhsar, D. S. (May 17, 2023). Ancient gene linkages support ctenophores as sister

to other animals. Nature, 618, 110-117. -- https://doi.org/10.1038/s41586-023-05936-6

* Warnow, T. (May 22, 2015). Concatenation Analyses in the Presence of Incomplete Lineage Sorting. PLoS Currents. -- https://doi.org/10.1371/currents.tol.8d41ac0f13d1abedf4c4a59f5d17b1f7

* Dunn, C. W., Zhou, X., Chen, J., & Shen, X.-X. (2025). Technical eLetter on Steenwyk & King (2025). Shen Lab PDF. -- https://shenxlab.com/pdfs/2025_Dunn_etal_Science_eletter.pdf

* Koutsouveli, V., et al. (Jan 21, 2025). The chromosome-level genome of the ctenophore Mnemiopsis leidyi A. Agassiz, 1865 reveals a unique immune gene repertoire. Genome Biology and Evolution, 17(2), evaf006. -- https://doi.org/10.1093/gbe/evaf006