Evolution: Assembling the Deuterostome body plan

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Starfish, graptolites and humans look as different as can be, yet are more closely related to each other than to any other phylum. Disc-shaped Cambrian fossils join the dots between these disparate body plans to plot out their evolutionary origins.

In the aftermath of the Cambrian explosion, c. 530 million years ago, the antecedents to the extant animal phyla shared the seas with a ragtag collection of rogues whose relationships to living taxa are obscure. These evolutionary dead-ends nevertheless inform the cartography of the roadmap connecting the simple cone, blob and quilt-like organisms of the latest Precambrian[1] to modern body plans. Among these problematica are cambroernids[2]: sessile, centimeter-scale organisms characterized by paired inflorescences of branching tentacles and a chunky, C-shaped gut. Cambroernids' favored position on the tree of life is in our own neck of the woods, among the deuterostomes – the group comprising chordates (vertebrates and sea squirts), echinoderms (starfish and sea lilies), and hemichordates (colonial organisms including the extinct graptolites)[6]. However, aspects of their anatomy occur across a miscellany of phyla – paired tentacles (cnidarians; certain annelids[3]; lophophorates[4]); epidermal segmentation (annelids; arthropods); curvature of the gut (early lophotrochozoans[5]). A new study by Li and coauthors[7] takes on the challenge of distinguishing the genuine homologies that reliably relate cambroernids to specific extant phyla from superficial or chance resemblances.

Li et al. target *Rotadiscus*, a cambroernid that dwelt upon a toughened concave disk[4], marked with concentric and radial ridges like a supernumerary dartboard. Near the base of the tentacles, the authors report an intriguing new organ: a pair of spirals recalling the volute atop an Ionic column. In certain derived deuterostomes (particularly tunicate chordates), similar volutes mark the opening of the coelomopore – the hole that connects the innards of the tentacular system to the surrounding seawater. The preservation of such an aperture in three dimensions and in varying orientations is not necessarily beyond the remit of the often counterintuitive taphonomic pathways involved in the preservation of non-mineralized anatomy.

Given that similar coelomopore coverings have arisen multiple times within tunicates[8], often differing in important details (such as whether spirals diverge or converge) – and noting the wide distribution of volute structures across the tree of life[9] – it is conceivable that cambroernid volutes evolved convergently, as the authors' phylogenetic analysis concludes. But if the structure does nonetheless denote a coelomopore associated with a tentacular apparatus, this feature could be key to establishing deep homologies between the disparate body forms of the deuterostome groups.

To fully unlock the significance of the fossil, it is necessary to establish that Cambroernids are indeed plausible deuterostomes, and where they might sit within this group. Li et al. approach this question through Bayesian analysis of a chimeric morphological dataset – a quantitative, if not necessarily definitive, approach. A cynic might question whether the 330 characters, not all of which are independent, necessarily capture a representative subset of all morphological and genetic variation across the animal kingdom; or whether the emphasis towards characters that can only be coded in extant taxa (only 73 characters are coded in *Rotadiscus*) is sufficient to resolve fossil affinities. The characters' configuration also imposes *a*

priori judgement on potential homology. For instance, the decision to treat the lophophore separately from deuterostome tentacles forces an implicit designation of *Rotadiscus* as a deuterostome, and also precludes the analysis from identifying deep homologies across the animal kingdom – an issue exacerbated by the fact that features the authors associate with deuterostomes (a coelomopore, mesocoel-derived tentacles) are not coded as present where they occur outside that group.

Of course, building a morphological dataset to span an entire kingdom is no small undertaking. Caveats notwithstanding, the analysis does consistently recover cambroernids within a monophyletic Deuterostomia, though their specific position within this clade is highly uncertain – even despite Bayesian analyses' propensity for overconfidence in a preferred result[10]. The highest posterior probability (~58%) is associated with a position sister to Ambulacraria; non-trivial probabilities also accompany positions alongside Chordata (18%), Deuterostomia (11%), Hemichordata (8%) and Echinodermata (5%) (Fig. 1). Parsimony analysis paints a slightly different picture, preferring a sister-group relationship between cambroernids and chordates (reflecting a shared presence of segmentation), though a position alongside hemichordates or ambulacrarians can also be supported after correcting[11] for inapplicable data (Fig. 1).

Perhaps this uncertainty simply reflects the limitations of the underlying dataset. A more interesting possibility is that cambroernids resemble the last common ancestor of the deuterostome phyla. Logically, this common ancestor must be essentially identical to the latest stem-deuterostomes and the earliest stem-group chordates and ambulacrarians – meaning that these positions are necessarily indiscriminable under a perfect phylogenetic analysis.

Taking cambroernids as a proxy for the ancestral deuterostome would provide a long-awaited opportunity to draw homologies between the disparate body plans of the individual phyla[6]. Start with the coelomopore: its identification in *Rotadiscus* gives a palaeontological basis for the developmentally informed equivalence between coelomic openings in hemichordates, chordates and echinoderms. From this, it follows that the associated mesosomal vascular systems – the tentacles of hemichordates and cephalochordates, and the tube feet of echinoderms – are likely derived from the tentacles of a cambroernid-like ancestor.

At the other end of the organism, basal members of each deuterostome lineage, including cambroernids[2], exhibit a distinct post-anal structure, meaning that such a stalk or tail was another likely feature of the ancestral deuterostome. (Li et al.[7] likely reach the opposite conclusion because a post-anal stalk is coded as absent, without explanation, in the stalked basal cambroernid *Herpetogaster*, and their analysis omits basal echinoderm taxa that bear muscular stalks[12].)

Finally, the ancestral deuterostome is held to have gill slits in the trunk[6], as do basal members of each phylum (Fig. 1) – but not cambroernids, possibly excluding them from the deuterostome crown. (Openings at the base of the *Herpetogaster* collar have been putatively interpreted as gill slits[2], but in light of *Rotadiscus*, their anterior location suggests an interpretation as coelomopores.) Pharyngeal slits would thus represent a deuterostome synapomorphy, rather than a potential inheritance from the ancestral bilaterian[13]. If the hemichordate prosome, echinoderm ambulacrum[14], and cephalochordate rostrum also have a common root (Fig. 1), then the absence of an equivalent preoral structure in cambroernids would further support a position outside the deuterostome crown.

The establishment of plausible deuterostome homologies provides morphological support for the monophyly of Deuterostomia, which molecular data have struggled to confirm or refute[13]. And in providing a coherent model for the deuterostome common ancestor, cambroernids link disparate body organizations, thus clarifying their origins. Indeed, the tripartite cambroernid blueprint – a differentiated 'head' bearing the mouth and tentacles; an elongate trunk; and a muscular aboral structure – shapes our expectations for the deeper reaches of the bilaterian tree, particularly as a similar configuration can be found – with a little imagination – in early protostomes (which alongside deuterostomes make up the Bilateria) and in the bilaterian outgroup, Cnidaria. That the earliest bilaterian shared certain features with extant deuterostomes is hardly in doubt: indeed, chaetognaths (possibly sister to all other protostomes[15]) and phoronids were previously assigned to Deuterostomia, before their distinctive developmental pathways were reinterpreted as a shared inheritance from the common bilaterian ancestor. Might the urbilaterian resemble deuterostomes in other ways? Extant phoronids – with a mesosome-derived tentaculate lophophore, a trunk, and a post-anal ampulla[16] – and the Cambrian stem-chaetognath *Amiskwia*[17] – with a tentacle-bearing "head", a finned trunk, and a muscular post-anal tail – can each be squared with a cambroernid body organization (Fig. 1), whilst deeper in the tree, polypoid cnidarians comprise circumoral tentacles, a trunk, and a basal plate that might at a push – notwithstanding the absence of an anus – be equated with deuterostomes' postanal attachment stalk. Taken together, this provides a speculative but plausible pathway from a cnidarian-like antecedent, via a tripartite basal bilaterian and progressively more cambroernid-like intermediaries, to crown-group deuterostomes. This reconstruction envisages early bilaterians as macroscopic, soft-bodied, sessile suspension feeders – in other words, organisms that are likely to require exceptional circumstances in order to enter the sedimentary or fossil record. In contrast

111 to protostomes, whose origins might be read fairly literally from the trace, shelly and organic
112 microfossil records[18], a complete account of deuterostome origins is therefore likely to hinge on
113 the recognition of further representatives in sites of exceptional preservation.

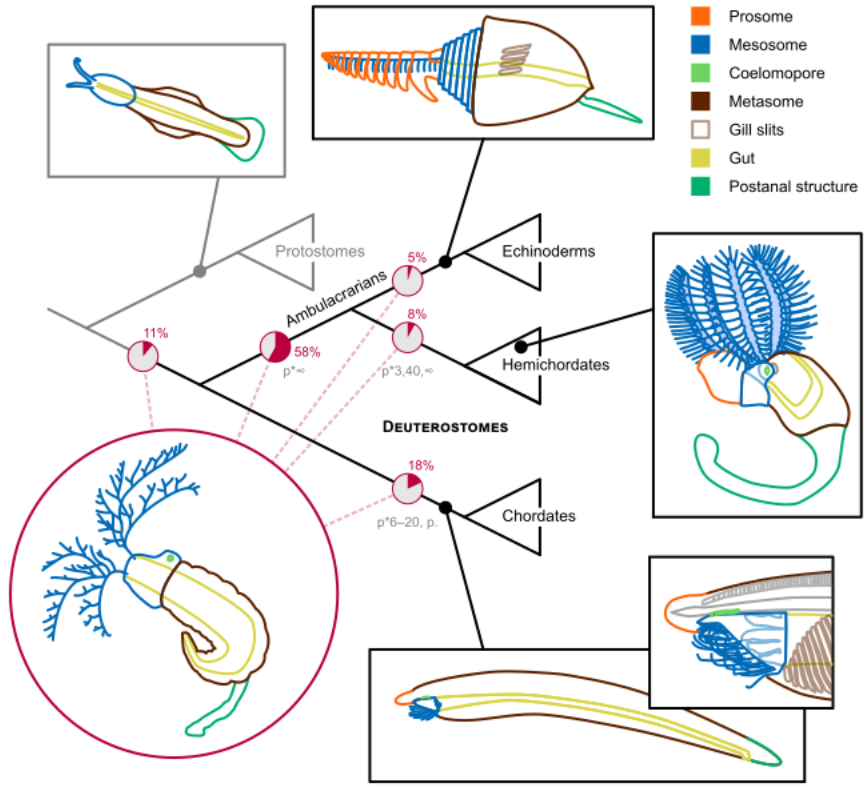

Figure 1. Phylogenetic position of Cambroernids, and implied homology framework.

Pies denote Bayesian posterior probability (%) that cambroernids (circled) occupy specified edge. *p* denotes most parsimonious positions with (*p**) and without (*p.*) correction[11] for inapplicable tokens at specified concavity constants (*k* = 3, 6, 10, 20, 40, ∞). Bayesian probabilities computed following Li et al.[7]; parsimony results calculated using TNT[19] (courtesy of the Willi Hennig Society) and the R package 'TreeSearch'[20]. Colors indicate potential homology of body regions and structures among early-diverging deuterostomes, clockwise from top: *Amiskwia* (Chaetognatha), *Jaekelocarpus* (Stylophora), *Cephalodiscus* (Pterobranchia), *Branchiostoma* (Cephalochordata) and *Herpetogaster* (Cambroernida).

References

1. Budd, G.E., and Jensen, S. (2000). A critical reappraisal of the fossil record of the bilaterian phyla. Biological Reviews *75*, 253–295. 10.1111/j.1469-185X.1999.tb00046.x.

2. Caron, J.-B., Conway Morris, S., and Shu, D.-G. (2010). Tentaculate fossils from the Cambrian of Canada (British Columbia) and China (Yunnan) interpreted as primitive deuterostomes. PLoS ONE *5*, e9586.

3. Temereva, E., Rimskaya-Korsakova, N., and Dyachuk, V. (2021). Detailed morphology of tentacular apparatus and central nervous system in *Owenia borealis* (Annelida, Oweniidae). Zoological Lett *7*, 15. 10.1186/s40851-021-00182-y.

4. Dzik, J., Zhao, Y.-L., and Zhu, M.-Y. (1997). Mode of life of the Middle Cambrian eldonioid lophophorate *Rotadiscus*. Palaeontology *40*, 385–396.

5. Budd, G.E., and Jackson, I.S.C. (2016). Ecological innovations in the Cambrian and the origins of the crown group phyla. Philosophical Transactions of the Royal Society B: Biological Sciences *371*, 20150287. 10.1098/rstb.2015.0287.

6. Nanglu, K., Cole, S.R., Wright, D.F., and Souto, C. (2023). Worms and gills, plates and spines: the evolutionary origins and incredible disparity of deuterostomes revealed by fossils, genes, and development. Biological Reviews *98*, 316–351. 10.1111/brv.12908.

7. Li, Y.-J., Dunn, F.S., Murdock, D.J.E., Guo, J., Rahman, I.A., and Cong, P.-Y. (2023). Cambrian stem-group ambulacrarians and the nature of the ancestral deuterostome. Current Biology, this issue.

8. Braun, K., Leubner, F., and Stach, T. (2020). Phylogenetic analysis of phenotypic characters of Tunicata supports basal Appendicularia and monophyletic Ascidiacea. Cladistics *36*, 259–300. 10.1111/cla.12405.

9. Slater, B.J., Harvey, T.H.P., Bekker, A., and Butterfield, N.J. (2020). *Cochleatina*: an enigmatic Ediacaran–Cambrian survivor among small carbonaceous fossils (SCFs). Palaeontology *63*, 733–752. 10.1111/pala.12484.

10. Suzuki, Y., Glazko, G.V., and Nei, M. (2002). Overcredibility of molecular phylogenies obtained by Bayesian phylogenetics. Proceedings of the National Academy of Sciences *99*, 16138–16143. 10.1073/pnas.212646199.

11. Brazeau, M.D., Guillerme, T., and Smith, M.R. (2019). An algorithm for morphological phylogenetic analysis with inapplicable data. Systematic Biology *68*, 619–631. 10.1093/sysbio/syy083.

12. Smith, A.B. (2008). Deuterostomes in a twist: the origins of a radical new body plan. Evolution & Development *10*, 493–503. 10.1111/j.1525-142X.2008.00260.x.

13. Kapli, P., Natsidis, P., Leite, D.J., Fursman, M., Jeffrie, N., Rahman, I.A., Philippe, H., Copley, R.R., and Telford, M.J. (2021). Lack of support for Deuterostomia prompts reinterpretation of the first Bilateria. Science Advances *7*, eabe2741. 10.1126/sciadv.abe2741.

14. Lefebvre, B., Guensburg, T.E., Martin, E.L.O., Mooi, R., Nardin, E., Nohejlová, M., Saleh, F., Kouraïss, K., El Hariri, K., and David, B. (2019). Exceptionally preserved soft parts in fossils from the Lower Ordovician of Morocco clarify stylophoran affinities within basal deuterostomes. Geobios *52*, 27–36. 10.1016/j.geobios.2018.11.001.

15. Marlétaz, F., Martin, E., Perez, Y., Papillon, D., Caubit, X., Lowe, C.J., Freeman, B., Fasano, L., Dossat, C., Wincker, P., et al. (2006). Chaetognath phylogenomics: a protostome with deuterostome-like development. Current Biology *16*, R577-8. 10.1016/j.cub.2006.07.016.

16. Temereva, E.N., and Malakhov, V.V. (2015). Metamorphic remodeling of morphology and the body cavity in *Phoronopsis harmeri* (Lophotrochozoa, Phoronida): the evolution of the phoronid body plan and life cycle. BMC Evolutionary Biology *15*, 229. 10.1186/s12862-015-0504-0.

17. Vinther, J., and Parry, L.A. (2019). Bilateral jaw elements in *Amiskwia sagittiformis* bridge the morphological gap between gnathiferans and chaetognaths. Current Biology *29*, 881-888.e1. 10.1016/j.cub.2019.01.052.

18. Slater, B.J., and Bohlin, M.S. (2022). Animal origins: The record from organic microfossils. Earth-Science Reviews *232*, 104107. 10.1016/j.earscirev.2022.104107.

19. Goloboff, P.A., and Morales, M.E. (2023). TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. Cladistics *39*, 144–153. 10.1111/cla.12524.

20. Smith, M.R. (2023). TreeSearch: morphological phylogenetic analysis in R. The R Journal *14*, 305–315. 10.32614/RJ-2023-019.