

Keynote lecture

Phylogenomic analysis of Brachiopoda: revealing the evolutionary history of biomineralization with an integrated palaeontological and molecular approach

Aodhán D. Butler

Department of Geological Sciences, Stanford University, USA.

Michael Eitel

Dept. of Earth & Environmental Sciences, Palaeontology & Geobiology, Ludwig-Maximilians-Universität, Munich, Germany.

Gert Wörheide

Dept. of Earth & Environmental Sciences, Palaeontology & Geobiology, Ludwig-Maximilians-Universität, Munich, Germany

Sandra J. Carlson

University of California, Davis, Department of Earth and Planetary Sciences, USA.

Erik A. Sperling

Department of Geological Sciences, Stanford University, USA.

Within Lophotrochozoa, brachiopods and allied clades are among the first biomineralized Cambrian metazoans to appear and represent a major component of the oldest known fossil record of animals. While the brachiopod fossil record is ultimately the key to determining character homology and polarity during the evolution of the brachiopod body plan, reading this record has been clouded by disagreement about relationships among the crown clades. Specifically, the monophyly of brachiopods with respect to phoronids, and the relationships of the calcitic to phosphatic-shelled brachiopods. Much of this phylogenetic uncertainty stems from difficulties in rooting the brachiopods and their sister groups within Lophotrochozoa. Phylogenomics—the analysis of hundreds to thousands of orthologous genes in concatenated supermatrices—has been instrumental in resolving difficult phylogenetic relationships in diverse metazoan clades. We have conducted the first such extensive phylogenomic investigation of Brachiopoda/Phoronida with analyses that combine novel sequence data with all publicly available brachiopod and phoronid transcriptomes and a broad range of protostome outgroups. Analyses were run under best fitting evolutionary models utilizing a published 106-gene lophotrochozoan ortholog set. Preliminary results strongly (99% bootstrap) support a monophyletic Brachiopoda with Phoronida as sister group within Lophotrochozoa. Weak bootstrap support (~50%) is found for Inarticulata.

Continued original morphological and systematic investigations remain critical in the molecular era. In tandem with the new molecular efforts we are also developing a comprehensive collaborative morphological database through the MorphoBank platform for living and fossil brachiopods. In addition, we are also generating a set of best-practice molecular clock calibration points. This encompasses *a priori* evaluation of relevant paleontological, phylogenetic, stratigraphic, and geochronological data, all of which are critical to establishing effective and well supported time calibration points.

This combined dataset will allow us to test, under a Bayesian

analytical framework, the hypothesis that the Cambrian explosion was a synchronous period of rapid molecular evolution, in addition to the rapid appearance of high-level morphological disparity (Erwin et al., 2011). Testing the relationship between molecular and morphological evolution in the Cambrian has important implications for arbitrating between potential driving mechanisms including ecological opportunism, body size evolution, and changes to gene regulation (Lee et al., 2013) and for understanding how evolutionary rates vary across geologic and clade history (e.g. (Hopkins and Smith, 2015)). Combining fossil and molecular data in this integrated framework provides novel insights into brachiopod biomineralization and evolutionary patterns during the Cambrian radiation.

Hypotheses for brachiopod and phoronid phylogeny

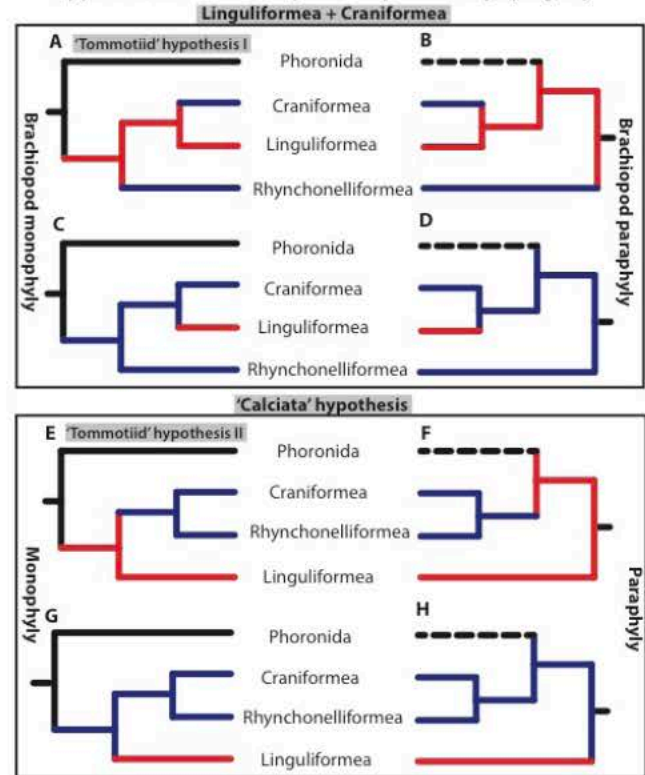


Fig. 1: Implications for the evolution of brachiopods. Brachiopods may be monophyletic (A,C,E,G) or paraphyletic (B,D,F,H) with respect to phoronids. Shifting the root position implies different evolutionary gain/loss events (e.g. secondary loss of shell in phoronids). Within brachiopods, the Craniiformea may be more closely related to Linguliformea or Rhynchonelliformea. Colors depict evolution of biomineralization assuming a single origin of mineral secretion. Blue = calcitic, Red = phosphatic, Dashed line = secondary loss. The 'tommotiid ancestry' hypothesis would correspond to A and E, with a phosphatic ancestral state for brachiopods.

References

- Erwin, D.H., Laflamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D., and Peterson, K.J., 2011. The Cambrian conundrum: Early divergence and later ecological success in the early history of animals. *Science*, 334, p. 1091–1097.
- Hopkins, M.J., and Smith, A.B., 2015. Dynamic evolutionary change in post-Paleozoic echinoids and the importance of scale when interpreting changes in rates of evolution. *Proceedings of the National Academy of Sciences*, 112, p. 3758–3763, doi: 10.1073/pnas.1418153112.
- Lee, M.S.Y., Soubrier, J., and Edgecombe, G.D., 2013. Rates of phenotypic and genomic evolution during the Cambrian explosion. *Current Biology*, 23, p. 1889–1895.