



Echinoderm model systems, homology, and phylogenetic inference: Comment and reply to Paul (2021)

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Understanding the phylogenetic relationship among derived blastozoans has been a goal of researchers since phylogenetic methodologies were first applied to Paleozoic echinoderms. Paul (2021) proposed a new “pan-dichoporites” group to circumscribe early Paleozoic blastozoans. Unfortunately, this work includes many inaccuracies, non-reproducible analyses, and nonstandard method choices that confuse rather than advance the understanding of echinoderm paleobiology. Herein, we focus on key aspects of philosophy, methodology, and data reproducibility the publication of Paul (2021) raises that need to be addressed and considered by echinoderm researchers as they assess the concept of pan-dichoporite echinoderms.

The phylogenetic concept of Echinodermata was defined (Sumrall 2020a) as the crown clade originating with the most recent common ancestor of *Asterias rubens* Linnaeus, 1758 (Asterozoa); *Ophiura ophiura* Linnaeus, 1758 (Ophiurozoa); *Strongylocentrotus purpuratus* (Stimpson, 1857) (Echinozoa); *Cucumaria frondosa* (Gunnerus, 1767) (Holothurozoa), *Metacrinus rotundus* Carpenter, 1885 (Crinozoa); and *Xyloplax medusiformis* Baker, Rowe, and Clark 1986 (Concentricyclozoa). As defined, this clade circumscribes five extant groups nested in two clades. Eleutherozoa includes Asterozoa (including *Xyloplax* see Janies et al. 2011), Ophiurozoa, Holothurozoa, and Echinozoa. Crinozoa forms a separate clade. In contrast, there are more than 20 distinct echinoderm clades that are extinct. Among extant groups, Echinozoa is often used as a model system to describe all Echinodermata despite having extremely high rates of missing data because of its highly apomorphic morphologies in echinoderm-wide morphological datasets (see Deline 2021). Echinoids diverged from their closest relatives (Holothurozoa) more than 450 million years ago with crown echinoids originating in the Permian (Thompson et al. 2017).

To better understand body-wall homologies, common ontogenetic patterns, major events in body plan evolution, and the identification of synapomorphies among morphologically disparate echinoderm clades, Mooi et al. (1994) proposed the Extraxial-Axial Theory (EAT) largely based on a novel understanding of larval development in extant echinoids. A discussion of the validity of EAT is outside the scope of this commentary, but its use by Paul (2021) does raise important philosophical questions. Are eleutherozoans, including echinoids, an appropriate model to understand morphologically diverse extinct

echinoderm clades such as the blastozoans and other pelmatozoans?

Assumptions that Paleozoic echinoderms would have had similar developmental pathways to extant echinoids are problematic. At present, very little information exists on the larval histories of Paleozoic pelmatozoans (Sumrall and Sprinkle 1998; Sevastopulo 2005). This lack of developmental data should be mentioned as a caveat in all studies invoking EAT as a model for homology among non-eleutherozoan taxa. For example, ocular plate rule (OPR) and radial water vessels (RWV) are concepts based on extant eleutherozoans, but ocular plates are documented only in echinoids and asteroids and do not occur in other groups.

Universal Elemental Homology (UEH) is a homology hypothesis that takes into account comparative anatomy, ontogeny, function, and position to identify homologous plates across taxa (Sumrall 2010; Sumrall and Waters 2012). EAT and UEH are two different schemes for understanding homology that should not be considered mutually exclusive. Sumrall and Waters (2012: 956) attempted to underscore this point with the following: “The EAT theory has been useful for understanding homology at the highest taxonomic levels where deep structure is illuminated by these regional homologies. Universal elemental homology (described here for stemmed echinoderms) takes the understanding of homology to the next level by allowing the identification, in many cases, of individual plates across clades. Thus, evolutionary changes in shape or plate contact relationships can be used to generate characters that are useful for reconstructing phylogeny at the lowest taxonomic levels.”

The plate nomenclature update from Sumrall and Waters (2012) was useful in showcasing the critical issue with plate naming systems in echinoderm paleobiology. The work by Paul (2021) seemingly reproduces a version of this update but following the EAT schema. Paul (2021) largely ignores the efforts to understand the homologous oral plates in blastozoans in the UEH schema outside of stating they are incongruent with EAT (Sumrall and Waters 2012). We completely understand that authors may not fully agree with UEH; however, when disagreement arises between homology schemes a case should be presented to showcase the efficacy of one approach as better than the other rather than to completely disregard the body of published work.

Similar to the issues that arise with applying EAT to blastozoans, UEH does not work when applied to echinoids. The

homologous skeletal elements outlined in UEH do not exist in echinoids, which would all be rendered as non-applicable data in morphological and phylogenetic downstream analyses. Therefore, the homology scheme employed to assess and generate character state data for the echinoderm group is important in understanding small (e.g., Blastoidea) and large group (e.g., Blastozoa) evolutionary patterns. Our hypotheses of homology must be critically evaluated, as phylogenetic inferences are sensitive to these data and can lead us to erroneous understandings of evolutionary relationships.

Abbreviations.—EAT, Extraxial-Axial Theory; UEH, Universal Elemental Homology.

Data inputs and phylogenetic inference

Phylogenetic tools are powerful, but the output is highly dependent on the data input. For reproducibility, all published studies should include supplemental files of all files used to perform the analysis. Paul (2021) stated that he only used early Paleozoic blastozoans, though the eublastoid used in this analysis is a Carboniferous genus when there are Silurian taxa that would have been better suited (e.g., *Polydeltoideus* or *Troosticrinus*). There is also an inaccuracy listed in Table 1 with the placement of *Macurdablastus* in Stephanocrinidae. This taxonomic placement is not supported by previous work (e.g., Broadhead 1984; Bodenbender and Fisher 2001; Bauer et al. 2019).

Phylogenetic characters are assumed to be both heritable and independent of one another. These assumptions require the removal of character sets that break these assumptions such as ecology and stratigraphy (Sumrall 1997). Swofford and Olsen (1990) present the challenges that would arise in computing phylogenetic trees if dependent characters were used. In Paul (2021), no character explanations were provided to clarify the thought behind character constructions, making it difficult to ascertain the morphologies encompassed by each character state. However, many characters used in the analysis appear to be constructed outside of these assumptions or use arbitrary ranges that do not describe alternate expressions of homology (Weins 2001; Wiley and Lieberman 2011). Many characters are also coded incorrectly. For example, character 11 is “radials being present or absent”. Those with missing radials (e.g., *Thomacystis*) should then be coded as non-applicable in other characters involving radial plates, though they are in Paul (2021) as a “?”. Three of the fourteen taxa are missing more than 10 of the 24 characters (42%). Missing data has a large effect on tree topology, especially in such a small dataset. This is critical because character selection (and taxon selection) can have large influences on tree outputs (Wiley and Lieberman 2011).

For any phylogenetic analysis, it is commonplace for character descriptions and codings to be publicly available, allowing readers to follow and understand the author’s justifications for character description and character state transformation selections. Missing character data can artificially alter tree topologies as it relates to accuracy and support (Scotland et al. 2003). Two taxa in the work of Paul (2021) are missing 11 and 12 charac-

ters. This, in concert with the three parsimony-uninformative characters, problematically leaves fewer than 50% of the characters scored for these taxa, possibly resulting in a decrease in accuracy of reconstructed trees (Huelsenbeck 1991; Hartmann and Vision 2008). With too much information missing, maximum parsimony will recover many alternate topologies and the consensus summary trees may be misleading (Wilkinson 1995). Best practices suggest that results are more resolved when there are at least two to three times the characters than there are taxa (Scotland et al. 2003).

Phylogeny.—General methodological and interpretive errors exist in the recent Paul (2021) work. For example, there is a rather lengthy discussion regarding the placement of the unusual glyptocystitoid *Rhombifera* in the blastozoan evolutionary history. The author suggests that inclusive blastoids (i.e., eublastoids, coronoids, *Lysocystites*, *Macurdablastus*) are most closely related to *Rhombifera* (Paul 2021: 48). However, the results of the phylogenetic analysis (Paul 2021: 59) do not align with this assessment as *Rhombifera* is not recovered as the sister group to the inclusive Blastoidea. There is no discussion on why *Rhombifera* is not sister taxa to the inclusive Blastoidea as one would expect given the earlier sections. The author concludes that the ambulacrals of *Lysocystites* are *Rhombifera* radials and eublastoid lancets. Paul (2021) does not discuss that if this is the case, we would expect to see ambulacrals on *Thomacystis* and *Caryocrinites* as well, given the results of his phylogeny. The phylogenetic analysis performed here used a heuristic search method for 14 taxa. However, best practices in phylogenetics suggest that a heuristic search for this particular analysis is inappropriate, as the size of the dataset allows for the use of exact methods (i.e., exhaustive searches or branch and bound searches; Swofford and Olsen 1990).

Support indices are useful measures that allow researchers to gain information on the dataset and resulting tree topology, but they provide little information about support for monophyletic groups within the tree (Wiley and Lieberman 2011). Other measures of nodal support (i.e., bootstrap) that resample the character matrix would be more valuable here. The author describes 100% support in reference to the 50% majority rule consensus tree but this information indicates that of the six resulting trees the relationships were recovered 100% of the time. It is not indicating that the nodes are 100% supported. Upon request, the PAUP nexus and log files were sent for re-analysis. Our intention was not to correct the character coding dataset, rather to illustrate pathways for improvement. We were able to replicate the exact results from PAUP for the parsimony analysis. With this tree topology, we ran a bootstrap analysis, resampling all 24 characters for 100 replicates to determine nodal support. Only six of the 11 nodes had $\geq 50\%$ support. Unsurprisingly, inclusive Blastoidea is found at 79%; *Caryocrinites* + *Thomacystis* found at 76%; the large grouping of all taxa except *Akado-crinus* and *Cambrocrinus* is at 72%. Support for *Macurdablastus* and *Codaster* is at 68%. *Lysocystites* and *Stephanocrinus* is at 65%. Finally, the large grouping of *Macrocystella* upward is supported at 50% (Fig. 1A). Since parsimony analysis excludes

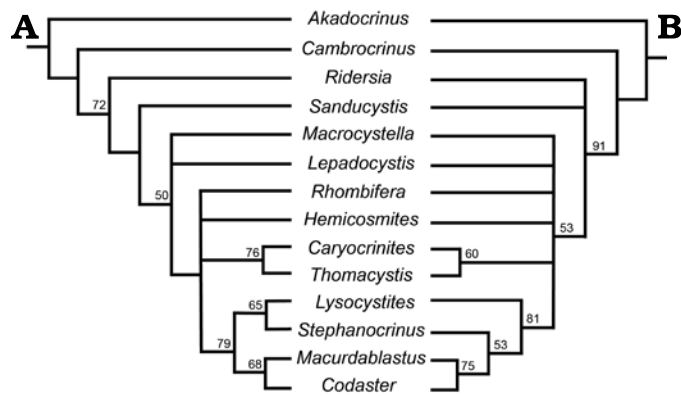


Fig. 1. Tree comparison between two phylogenetic inference methods with bootstrap support at the nodes. **A.** Phylogenetic hypothesis from Paul (2021) inferred via maximum parsimony. **B.** Phylogenetic hypothesis inferred via maximum likelihood.

any characters that are considered “parsimony uninformative”, this includes three characters of the 24, we also re-analyzed the dataset with maximum likelihood to see if utilizing all 24 characters with the mKv model (Lewis 2001) provided differing results. Three trees were retained with a LnL score of 150.4167 with six nodes which had $\geq 50\%$ support (Fig. 1B). The major difference between the recovered trees is the placement of *Ridersia*, which is not surprising given the number of missing characters (8/24) for that taxon (Fig. 1). In this tree the support for *Ridersia* upward is much higher at 91% than in the parsimony results. The relationships between the inclusive Blastoidea match those proposed by Bauer et al. (2019) and the support is slightly higher than that of the parsimony tree at 81%. In this analysis, *Rhombifera* is always sister taxon to *Lepadocystis*, which was an unresolved grouping in Paul’s (2021) parsimony tree. Most notably, the taxon that is unstable across the three most likely trees (*Ridersia*) is not the taxon (*Lepadocystis*) that was unstable in the parsimony analysis (Fig. 1).

The pan-naming convention in Paul (2021) is used incorrectly for the proposed pan-dichoporites. As laid out in the PhyloCode (Cantino and De Queiroz 2020), pan groups are designated as total groups that include the related name-bearing crown groups. For example, Echinodermata is a crown clade including all descendants of the last common ancestor of Echinoidea, Asteroidea, Ophiuroidea, Holothuroidea and Crinoidea (Sumrall 2020a). This circumscribes a clade that includes all modern taxa and such fossil taxa that are descended from the most inclusive node. Sumrall (2020b) defined Pan-Echinodermata as the total group echinodermata; that is, the stem lineage that includes all taxa closer to Echinodermata than to any other crown. This effectively aligns with the traditional non-phylogenetic diagnosed Echinodermata including stylophorans and other basal taxa. The pan-naming convention simply cannot be used for extinct lineages. There is no crown group within blastozoans as the last known members were extinct by the end of the Permian. Likewise, there is no total group in the blastozoans because there is no set of taxa closer to a non-extant crown lineage than another crown lineage. Pan-dichoporites is effectively a synonym of Blastozoa and while they were not formally defined

either by PhyloCode rules or by ZooBank, names for several derived echinoderm clade names were previously suggested by Sumrall (1997).

Stratigraphy.—Stratigraphy has played an interesting role in understanding echinoderm evolutionary relationships. The concept of stratocladistics (Bodenbender and Fisher 2001) was established using blastoids. However, stratigraphic information should not be incorporated into a phylogenetic character matrix (Sumrall 1997); it is information that is unrelated to the heritable traits of the animals. However, it can be incorporated into other aspects of phylogenetic analysis as a parameter to better understand and analyze clades of interest. On several occasions the author makes targeted remarks regarding the stratigraphic occurrences of fossils and the evolution of these groups. These statements are problematic in different ways. The first reads, “Both the suggestions that *Hemicosmites* preceded the glyptocystitoids and that *Lysocystites* preceded the remaining blastoids sensu lato are counter to known stratigraphy of occurrences” (p. 59). This frame of thinking excludes considerations of evolutionary processes and is not in terms of the most recent common ancestor but instead only of the terminal taxa. These thoughts are exclusive and can be confusing to readers. In another section the author writes, “It has become fashionable to ignore stratigraphy and the grounds of the incompleteness of the fossil record” (p. 59). This is ignoring the recent and large body of work utilizing stratigraphy in concert with phylogeny in fossil invertebrates (e.g., Congreve et al. 2019; Lam et al. 2018, 2021; Bauer 2021). Stratigraphy is not being ignored, rather it is more fully and appropriately being utilized. Just because a taxon is stratigraphically older does not mean it is ancestral.

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