Cambrian Chordates and Early Fin Evolution

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Abstract

An enigmatic bilaterian from the Chengjiang biota, *Shenzianyuloma yunnanense*, is assigned to an enigmatic Cambrian group, the vetulicolians. In *Shenzianyuloma*, a clear notochord can be observed, as can cone-in-cone myomeres. Unlike other vetulicolians and *Yunnanozoon*, *Shenzianyuloma* lacks arthropod-like segmentation in the posterior part of its body. Removal of matrix from the *Shenzianyuloma* holotype has revealed a broader, more laterally flattened tail. Also present in the freshly prepared area is evidence that *Shenzianyuloma* possessed a possible ventral fin ray box, comparable to that of *Amphioxus* and *Branchiostoma*, implying that *Shenzianyuloma* had an even greater top-to-bottom tail width than hitherto known. A new tail reconstruction for *Shenzianyuloma* shows greater lateral area than in previous reconstructions, indicating a more efficient posterior organ of propulsion. A possible dorsal fin spine can also now be recognized in *Shenzianyuloma*. The revised reconstruction of *Shenzianyuloma* provides insight into early chordate fin evolution, and is sufficiently unique to require the erection of ••• n. fam. within Class Vetulicolida. Early bilaterians such as yunnanozoans and *Shenzianyuloma* are crucial for assessing the morphological innovations, and combination of traits, associated with the appearance of vertebrates.

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Introduction

It has been recently remarked that vertebrate evolution is “a puzzle that researchers will continue to explore, being driven by a curiosity to understand our own origins” (Hockman, 2022). The puzzle has a long history, dating at least as far back as Angelo Heilprin's prescient inference (Heilprin, 1888) that vertebrates would one day be discovered in Cambrian strata (McMenamin, 2019).

Deuterostomes are one of three major eumetazoan groups that appear during the Cambrian Explosion. In subsequent geologic time, members of the Phylum Chordata became the most successful deuterostome representatives. The deuterostome body plan is in stark contrast to that of the protostomes, with its gut that runs backwards (with respect to the protostomous condition), and a body plan that is essentially upside down (with a dorsal as opposed to ventral nerve chord). Deuterostomes are presumably descended from the protostomes. The gut direction reversal that distinguishes the group evidently required a fast evolutionary transition from the protostomous to the deuterostomous state, as a 'two anus' or 'two mouth' condition would seem to be nonviable, in other words, generally speaking (and ignoring the blind guts of some lophophorates) the alimentary system must flow one direction or the other. Interestingly, no confirmed deuterostome fossils are known from before the Cambrian boundary—*not a single one*. This curious absence suggests a deuterostome origin at or near the beginning of the Cambrian, and adds considerably to the percieved magnitude of the Cambrian Explosion.

Well-represented in the Chengjiang Lagerstätte and other Cambrian deposits, deuterostomes undergo an explosive radiation near the base of the Cambrian, as shown by the appearance of: the cambroernids (an extinct clade consisting of *Eldonia*, *Phlogites* and *Herpetogaster*); hemichordates (acorn worms and graptolites); vetulicolians (an enigmatic group with a tadpole-shaped *baüplan*), echinderms, and chordates. Early jawless fishes from the first half of the Cambrian are represented by *Myllokunmingia* and *Haikouichthys*. *Metaspriggina* and the famous *Pikaia* occur in Middle Cambrian strata. *Metaspriggina* was initially mistaken as an Ediacaran survivor, hence its genus name derived from *Spriggina*. *Metaspriggina* has eyes and nostrils, a notochord, a cranium, pharyngeal bars or gill bars of cartilage, and W-shape myomeres with an additional chevron that allows direct comparisons with modern fish. The gill bars in *Metaspriggina* are a crucial feature that may in fact serve to help define the crown craniate-cephalochordate clade. The list of vertebrate features in *Myllokunmingia* is extensive: craniate condition, notochord, distinct head region, pericardial cavity with pharynx, cartilage internal skeleton, myomeres with chevrons, dorsal fin, and a *paired* ventral fin.

Yunnanozoans, represented by soft-bodied fossils from the Early Cambrian, have recently been reinterpreted as early vertebrates by Baoyu Jiang and coauthors (Tian et al., 2022) at Nanjing University. These exquisite bilaterian fossils, abundant in the Chengjiang biota (Cambrian, *ca*. 518 Ma) of China, show characters such as early evidence for a pharyngeal arch skeleton consisting of cellular cartilage. But in spite of these features that may be precursors to the skull and jaw, yunnanozoans appear to lack a notochord. Myomeres are also absent from the yunnanozoan *baüplan*, placing these creatures in a crucial stem position with regard to the crown craniate-cephalochordate clade.

Myomeres have been described from another bilaterian deuterostome from the Chengjiang biota, *Shenzianyuloma yunnanense* McMenamin, 2019 (Fig. 1). *Shenzianyuloma* is assigned to the Vetulicolia, a likewise enigmatic group of chordates. New information gained by fresh preparation of the holotype provides new information about the morphology of this key taxon.

Materials & Methods

The holotype specimen of *Shenzianyuloma yunnanense* was subjected to renewed preparation for this study. Preparation consisted of gently scraping away the soft yellow Chengjiang matrix with a mechanical preparation tools. Matrix was removed from the ventral side of the tail region, exposing a much larger tail region, along with features that had not been observed previously.

Results

As a result of renewed examination of the holotype of*Shenzianyuloma yunnanense*, several new features were observed. First, a dorsal fin spine is now recognized as being present on the fossil (Figure 1). Dorsal fin spines in teleosts are associated with deeper bodied fish (Price et al., 2015), and this would accord with the deeper body (angel fish shape) of *Shenzianyuloma yunnanense*. Wider-bodied fishes tend, in contrast, to develop pectoral fin spines (Price et al., 2015). A possible possible ventral fin ray box occurs on the ventral part of the *Shenzianyuloma* tail (Figure 2). Although this putative fin ray box does not show the boxwork partitions of the ventral fin ray boxes of of *Amphioxus* and *Branchiostoma*, this may be a vagary of taphonomy. The structure interpreted here as the ventral fin ray box in *Shenzianyuloma* does not appear to be merely a fold exposing part of the left side of the animal.

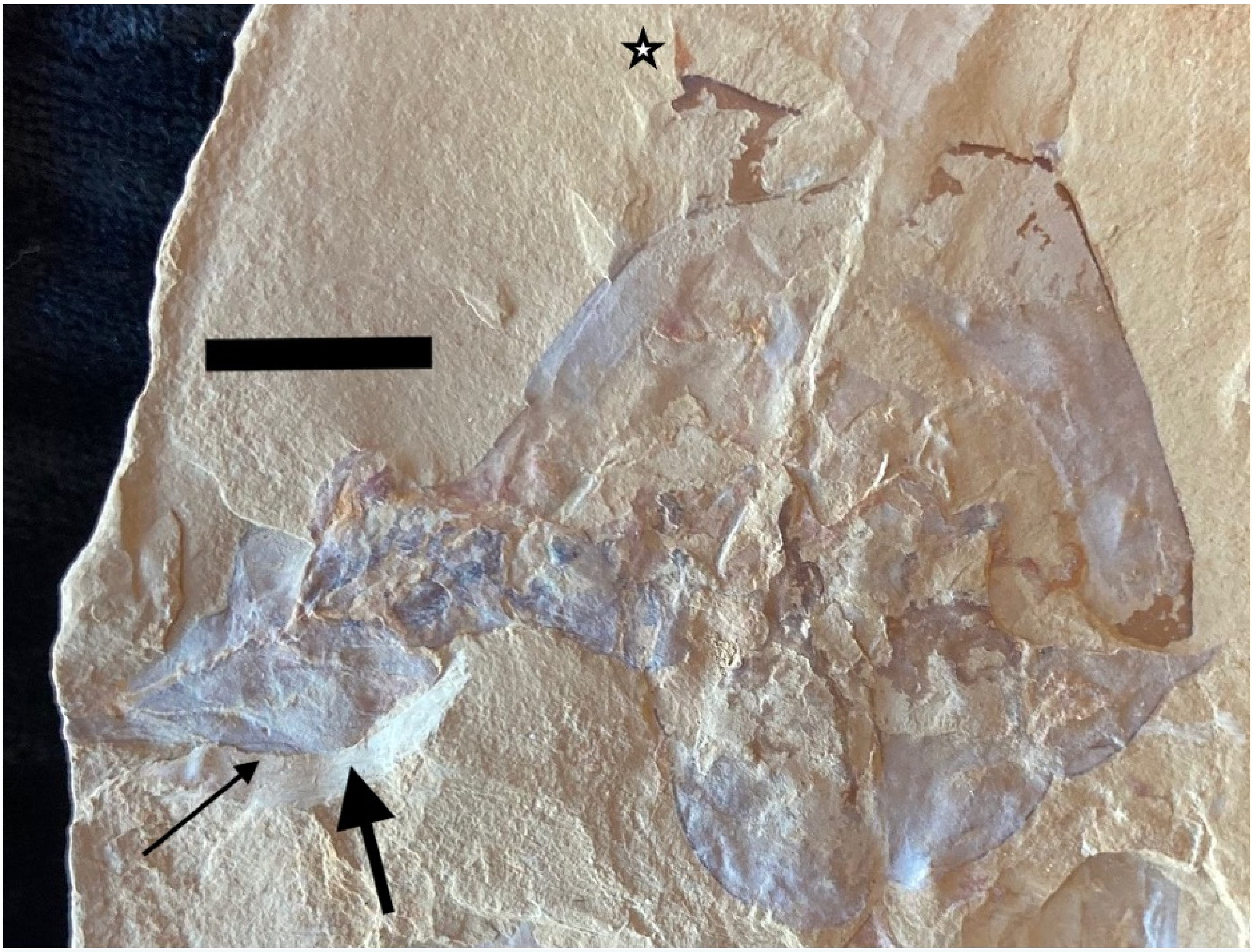

Figure 1. *Shenzianyuloma yunnanense* McMenamin, 2019. View of the holotype, showing freshly prepared area in the ventral region of the tail (thick arrow); possible possible ventral fin ray box (thin arrow); and possible dorsal fin spine (star). Scale bar = 1 cm.

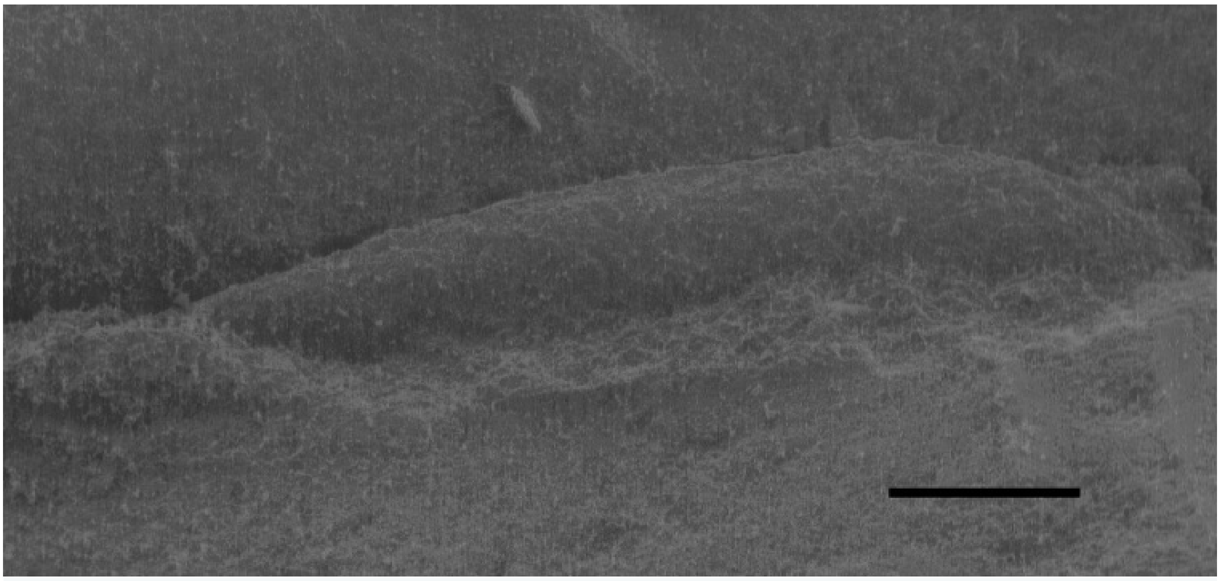

Figure 2. *Shenzianyuloma yunnanense* McMenamin, 2019. Scanning electron microscope view of the possible ventral fin ray box

region. Scale bar = 500 microns.

Discussion

Paleoartist Apokryltaros (Figure 3) reconstructed *Shenzianyuloma* with a pointed dorsal fin, which differed from the rounded dorsalmost tip of the dorsal fin in the original reconstruction (McMenamin, 2019), but which proved to be a close approach to a more accurate reconstruction. A revised *Shenzianyuloma yunnanense* reconstruction, based on the new data from holotype preparation, is shown in Figure 3. In this reconstruction, the tail is rendered deeper in accord with the new data from the holotype, and the dorsal fin spine has been added.

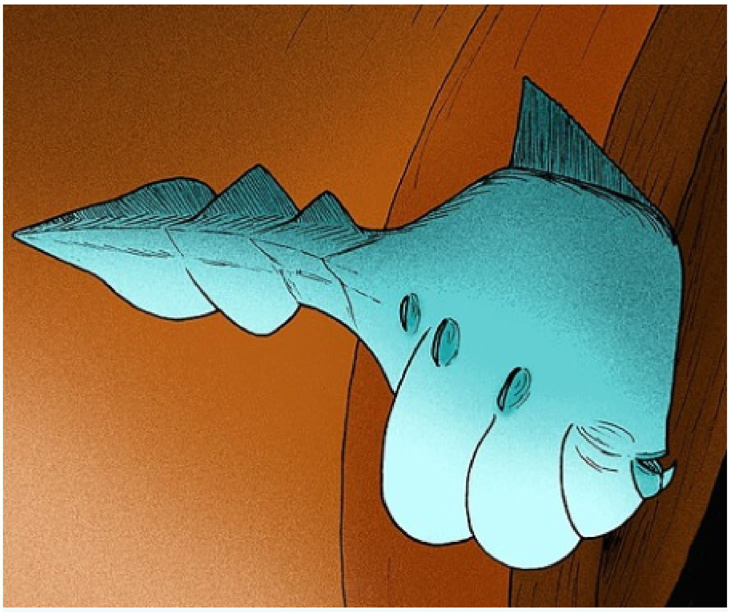

Figure 3. *Shenzianyuloma yunnanense* McMenamin, 2019. Reconstruction of *Shenzianyuloma yunnanense* with a pointed dorsal fin. Image Credit: Apokryltaros, used here with background modification per CC BY-SA 4.0.

Shenzianyuloma is placed here in Class Vetulicolida along with *Nesonektris*, an Australian vetulicolian (Garcia-Bellido and Paterson, 2014). The revised reconstruction of *Shenzianyuloma* is sufficiently unique to require the erection of ••• n. fam. within Vetulicolida.

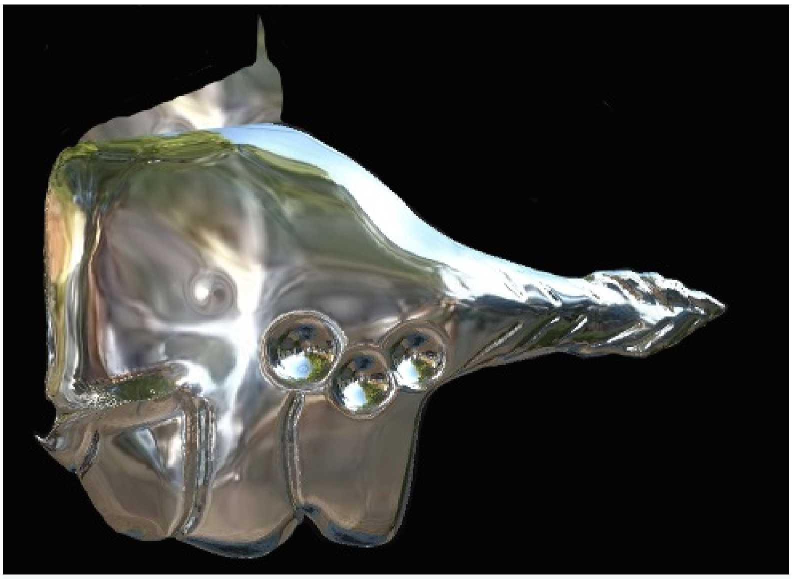

Figure 4. *Shenzianyuloma yunnanense* McMenamin, 2019. Revised reconstruction showing deeper tail and dorsal fin spine.

Conclusions

In the Chengjiang vetulicolian *Shenzianyuloma*, a clear notochord can be observed, as can cone-in-cone myomeres. Unlike other vetulicolians and *Yunnanozoon*, *Shenzianyuloma* lacks arthropod-like segmentation in the posterior part of its body. Removal of matrix from the *Shenzianyuloma* holotype has revealed a broader, more laterally flattened tail than originally thought. Also present in the freshly prepared area is evidence that *Shenzianyuloma* possessed a possible ventral fin ray box, comparable to that of *Amphioxus* and *Branchiostoma*, implying that *Shenzianyuloma* had an even greater top-to-bottom tail width than hitherto known. A new tail reconstruction for *Shenzianyuloma* shows greater lateral area than in previous reconstructions, indicating a more efficient posterior organ of propulsion. A possible dorsal fin spine can also now be recognized in *Shenzianyuloma*. Early bilaterians such as yunnanozoans and *Shenzianyuloma* are crucial for assessing the morphological innovations, and combination of traits, associated with the appearance of vertebrates. The revised reconstruction of *Shenzianyuloma* is sufficiently unique to require the erection of the new family ••• within Class Vetulicolida.

Future directions of research dealing with early chordates should focus on mechanisms discerned from developmental biology, as for instance investigation into the evolutionary development of dorsal and ventral fins in *Shenzianyuloma*. Dermal fin rays are thought to be of mesodermal rather than neural crest origin (Lee et al., 2013). We might speculate here that the *Shenzianyuloma* ventral fin ray box is under the control of genes known to regulate posterior and proximal fin growth in vertebrates, such as *Shh*, *Gli3*, and 3’ Hox (Nakamura et al., 2015). Teleost fin rays show unambiguous proximal-distal polarity (Christou et al., 2018); this may be an ancient and conserved feature associated with the proximodistal transition from fin ray box to fin. Steps should now be taken to determine the regulatory gene control of development of the ventral fin ray box in *Amphioxus* and *Branchiostoma*. Results here will provide modern analogs for understanding the developmental biology of early chordate fin evolution.

ZooBank entry

[for new family; pending]

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