

# Cambrian Chordates and Vetulicolians

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Note: Taxonomies are provisional because this is a preprint.

**Abstract** Deuterostomes make a sudden appearance in the fossil record during the Early Cambrian. Two deuterostome groups, the chordates and the vetulicolians, are of particular interest for understanding the evolutionary dynamics of the Cambrian evolutionary event. Lagerstätten in China and elsewhere have dramatically improved our understanding of the range of variation in these ancient animals. Cephalochordate and vertebrate body plans are well established at least by Cambrian Series 2. Taken together, roughly a dozen chordate genera and fifteen vetulicolian genera document an explosive radiation of deuterostomes at the base of the Cambrian. A new vetulicolian (••• nov. gen. nov. sp.) with a polygonal anterior section and a narrow, unsegmented posterior region ('tail') bearing possible myotomes provides new insight into the affinities of the various body plans that emerged during the Early Cambrian. It seems clear that the advent of deuterostomes near the Cambrian boundary involved *both* a reversal of gut polarity and a two-sided retinoic acid gradient, with a gradient discontinuity at the midpoint of the organism that is reflected in the sharp division of vetulicolians into anterior and posterior sections.

**Keywords** chordates, vetulicolians, cephalochordates, vertebrates, tunicates, Cambrian, Chenjiang Biota, Burgess Shale, *Banffia*, *Vetulicolia*, *Myllokunmingia*, *Metaspriggina*, agnathans, deuterostomes, all-trans-retinoic acid (ATRA), morphogen gradients

## 1. Introduction

In his 1888 book *The Geological Evidences of Evolution*, Angelo Heilprin, Curator of Invertebrate Paleontology and the Philadelphia Academy of Natural Sciences, made the following prediction [1]:

Looking at the animal kingdom broadly. We find that of the two great divisions into which that kingdom is divided, the backboneed or vertebrate animals, like the fish, reptile, amphibian, and quadruped, and those

without backbone, the Invertebrata, like the coral, starfish, crab, etc., only the latter is represented in the earliest period, the Cambrian, in which indisputable animals remains have been found. Not a vestige of any of the higher forms has here been met with. But let me warn you against this non-appearance. It is by no means impossible, or indeed unlikely, that backboneed animals already lived during this period of time, and that their remains will still someday be discovered.

Heilprin's prediction [1] concerning the discovery of Cambrian vertebrates was vindicated 111 years later with the description of *Myllokunmingia* in 1999.

In a debate over the number of phyla in the Cambrian, S. J. Gould [2] said of the enigmatic Burgess Shale form *Banffia* (classified here as a vetulicolian):

Consider *Banffia*, namesake of the more famous national park adjoining Yoho and the Burgess Shale. Walcott's 'worm'—with an annulated front portion separated from a saclike posterior—is almost surely a weird wonder.

In spite of reconstructing the animal backwards, Gould was correct to consider *Banffia* a weird wonder, in other words, a member of a previously unknown phylum. This revelation was troubling for Burgess Shale researchers such as Derek Briggs and Richard Fortey, who work to limit the recorded number of new Cambrian phyla and thereby de-emphasize the significance of the Cambrian Explosion [3]. Their efforts were thwarted by recognition of the new Early Cambrian phylum Vetulicolia [4], an advance that added credence to the concept of a sudden, rather than muted and long drawn-out, Cambrian Explosion [5, 6].

## 2. Chinese Breakthrough

Two developments in paleontology were to have great impact on both the study of Proterozoic-Cambrian paleobiology and Cambrian chordates. Continuing early Western interest in Chinese Proterozoic and Cambrian strata

and fossils [7], modern paleontological analysis of the boundary interval began in the late 1970s and early 1980s [8-10]. A critical subsequent event was discovery in the mid-1980s of the Chengjiang Lagerstätte of the Yunnan Province, China, dated to Cambrian Series 2 [11].

Apart from *Pikaia*, which had long been known from the Burgess Shale (but not recognized as a chordate until 1979), the soft-bodied preservation of the Chengjiang fossils, colorfully preserved in iron oxides, has provided an astonishing glimpse at the soft-bodied Early Cambrian fauna, such as the giant sclerite-lacking lobopodian *Paucipodia inermis*. Other examples of exceptional fossil preservation include five genera of scleroctenophores (skeletonized comb jellies) recently described from Chengjiang [12].

Discoveries from the Wulongqing Formation (Guanshan Biota; Cambrian Series 2, Stage 4) of Yunnan, China have amplified this signal [13], as have even more recent discoveries from the Qingjiang biota [14]. Included in this suite of fossils are the oldest known chordates.

### 3. Cambrian Chordates

A major impediment to the study of Cambrian chordates (including the phyla/subphyla Cephalochordata, Urochordata [tunicates] and Vertebrata) is that, for many forms, the most taxonomically diagnostic features (with the exceptions, fortunately, of myomeres and the notochord) tend to be the ones most prone to rapid decay, thus leading to the potential absence of key apomorphies. This results in ‘stemward slippage,’ in other words, a fossil specimen appearing more primitive than it actually is because the key derived characters are not preserved [15]. Described genera of Cambrian chordates are as follows.

#### *Cathaymyrus*

Assigned to the Cephalochordata [16], *Cathaymyrus* includes two, possibly synonymous, species, *C. diadexus* and *C. haikoensis*. Some researchers consider the genus to be ‘a chordate of uncertain affinity’ [11], with D. Shu calling it “an amphioxus-like creature” [4]. The animal is remarkable for its elongate, narrowly tapered body divided by S-shaped myomeres. A notochord and a discontinuous gut trace may be present [17]. The animal may possess a notochord but lacks a well-defined cranial region. *Cathaymyrus* is possibly synonymous with *Zhongxiniscus* [11].

#### *Cheungkongella*

*Cheungkongella* is an attached, spindle-shaped sessile suspension feeding animal that is thought to be either an early tunicate [18] or a cambroernid (an extinct non-chordate deuterostome clade that includes forms such as the eldoniids, *Phlogites* and *Herpetogaster* [19]). D. Shu [4] considers *Cheungkongella* to be the oldest known urochordate.

#### *Haikouichthys*

This agnathan fish (Fig. 1) was described from the Eoredlichia Zone, Qiongzhusi Formation near Ercaicun, Yunnan, China [20]. Sense organs and associated structures identified in this chordate include eyes, nasal sacs, and otic capsules [4]. Possibly synonymous with *Myllokunmingia* [11].

#### *Haikouella*

This early chordate and possible agnathan [20] is represented by two species, *Haikouella lanceolata* and *H. jianshanensis* [21]. Filamentous gills are present that are similar to those of *Yunnanozoon*. In some specimens the gill filaments coming from the gill structure appear to be paired. Fin rays are present in *Haikouella*, as are W-shaped (zigzag) myomeres. Tiny (100 micron) structures that are likely pharyngeal teeth are among the first such structures recorded in the deuterostome fossil record. The presence of these teeth serve to distinguish as an agnathan chordate as opposed to the otherwise similar Cambrian hemichordate *Yunnanozoon* [23-26]. Interestingly, *Haikouella* is interpreted to have had both a ventral and a dorsal nerve chord [4].

#### *Metaspriggina*

The first appearance of gill bar structures (pharyngeal gills) occurs in the Middle Cambrian fossil from the Burgess Shale *Metaspriggina walcotti* (Fig. 2). Initially thought to be related to the Ediacaran ecdysozoan genus *Spriggina*, *Metaspriggina* is now known to be a notochord-bearing chordate with features such as eyes and pharyngeal bars that are comparable to those of fish [27, 28]. In addition, the myomers of *Metaspriggina* have a distinct dorsal curve and W-shaped pattern formed by an added chevron in the ventral region. Although possibly due to homoplasy, this myomeral configuration strongly resembles the fish configuration, suggesting that *Metaspriggina* might very well be ancestral to the gnathostomatan.

#### *Myllokunmingia*

The most ancient putative vertebrate is *Myllokunmingia fengjiao* from the Lower Cambrian Eoredlichia Zone, Qiongzhusi Formation near Ercaicun, Yunnan, China [11, 16 but see 29]. Its assignment to the vertebrates is supported by its filamentous gills, dorsal fin, W-shaped myomeres and especially, by paired sense organs in the head region. Fin rays are present in *Myllokunmingia*, as are W-shaped (zigzag) myomeres. *Myllokunmingia* is possibly synonymous with *Haikouichthys* [11].

#### *Pikaia*

*Pikaia gracilens* (Fig. 3) was initially described as a polychaete worm [30, 31] in early descriptions of soft-bodied forms from the Burgess Shale (Middle Cambrian, *Bathyriscus-Elrathina* Zone). *Pikaia* eventually became famously known as the earliest described Cambrian chordate

[2]. In a definitive breakthrough that initiated the study of Cambrian chordates, Simon Conway Morris in 1979 noted the similarity of *Pikaia* to the living cephalochordates *Amphioxus* and *Branchiostoma*, and thus extended the geological range of Chordata back to the Middle Cambrian [32].

The previous most ancient chordate fossils were latest Cambrian to Cambro-Ordovician dermal plates of ‘ostracoderm’ fishes such as *Anatolepis*, *Sacabambaspis*, *Arandaspis* and *Astraspis*, the latter well known from the Middle Ordovician Harding Sandstone, Cannon City, Colorado, USA [33-35]. Recent analyses of *Pikaia* have placed it as a basal chordate [36, 37], and indeed a basal chordate affinity seems plausible but other possibilities such as assignment to a new higher taxon cannot be dismissed considering that *Pikaia* may have formed a cuticle as occurs in some nonvertebrate cephalochordates [38].

Large specimens of *Pikaia* reach 4 cm in length. Originally thought [32] to bear a notochord, the structure running along the animal’s back is now called the ‘dorsal organ,’ and a notochord and/or notochord plus nerve cord may occur in a position ventral to the dorsal organ [39]. True notochords of course do occur in modern *Amphioxus* and *Branchiostoma*. Unique features of *Pikaia* include short appendage-like structures possibly attached to the gill slits, and hagfish-like tentacles at the anterior end of the animal.

An analysis of swim mechanics in *Pikaia* concluded that it must have been a slow swimmer because it lacked the fast-twitch fibers that allow rapid motion in modern fish and other living chordates [39].

### *Shankouclava*

Known only from the Lower Cambrian Maotianshan Shale at Anning, Kunming, South China, *Shankouclava anningense* (Fig. 4) is widely regarded as the oldest known tunicate, thanks to its striking similarity to an individual zooid of the living, colonial aplousobranch tunicate *Clavelina* [40]. A stolon-bearing, club-shaped animal, *Shankouclava* reaches 4 cm in length. In addition to its branchial basket, a possible endostyle occurs on the fossil.

### Undescribed *Shankouclava*-like form

A new fossil tunicate strongly resembling *Shankouclava*, but bearing tentacles, awaits description [11].

### *Yunnanozoon*

The debate regarding the chordate [24, 25], hemichordate [26] or even vetulicolian affinities of *Yunnanozoon lividum* (Fig. 5) has underscored the challenges in interpreting this early chordate-like animal. One of the most strikingly beautiful members of the Chengjiang biota (occurring at both Chengjiang area and in Haikou), *Yunnanozoon* has been variously assigned to the cephalochordates, stem-bilaterians, stem-deuterostomes, stem-ambulacrarians, stem-chordates, stem-hemichordates, crown hemichordates, cristozoans,

vetulicolians and craniates, with one group of researchers concluding that it is best considered at present “as a bilaterian of uncertain affinity” [11].

Known from hundreds of specimens ranging from 2-6 cm in length, *Yunnanozoon* differs from the otherwise comparable *Haikouella* by having pharyngeal teeth that are an order of magnitude larger (1 mm) and yet, ironically, *Yunnanozoon* has a stomach that is not as large. Seriation occurs in *Yunnanozoon* as indicated by multiple (13!) paired gonads. As in *Haikouella lanceolata*, in some specimens the gill filaments coming from the gill arch appear to be paired. Although there exists no clear evidence for a notochord nor myomeres in *Yunnanozoon*, filamentous structures attached to body axis-parallel rods occur on both sides of the anterior end of the animal. It seems evident that the filamentous arches functioned as gills.

### *Zhongjianichthys*

This slender eel-like creature, 1.1 cm in length, has a thick integument [22]. No myomeres are visible in the fossil but these may be masked by its thick skin in the unique holotype. Thought by some [11] to be a preservational variant of *Myllokunmingia*, *Zhongjianichthys* is considered here to be a valid, distinct genus, although possibly synonymous with *Cathaymyrus* [11]. If myomeres are indeed absent, there may be a parallel between *Zhongjianichthys* and a genetically altered zebrafish (*Danio*) that shows normal development of fast muscle striations but never develops myotomes due to gene knockouts (*tbx6*<sup>-</sup>, *her1*<sup>-</sup>, *her7*<sup>-</sup>) that stop the segmentation clock [41]. These knockouts also lead to deformed vertebrae (scoliosis, etc.) but the mutant fish is nevertheless able to swim, the biomechanical demands being less in an aquatic environment than for tetrapods on land. *Zhongjianichthys* may represent an early chordate with an altered segmentation clock and no myotomes, but nevertheless with an ability to swim. Anterior sensory structures include eyes, nasal sacs and a curious ‘anterior-dorsal lobe’ [4] that may be comparable to the rostral organ of the coelacanth [42].

### *Zhongxiniscus*

*Zhongxiniscus* (Fig. 6) is a slender cephalochordate-like animal known from Haikou, Kunming, China [17]. Although *Zhongxiniscus* has along its dorsal margin triangular fins, the genus appears to lack both fin rays and W-shaped myomeres, developing instead S-shaped, narrow (140-145 microns width) myomeres as in *Cathaymyrus*.

## 4. Vetulicolians

These awkward creatures, typified by the eponymous genus *Vetulicolia*, have the general appearance of a segmented tadpole. They are best known from *Lagerstätten* such as Chengjiang [11], and have been recently been reported from the newly-discovered Qingjiang biota [14].

The overall shape of vetulicolians is somewhat reminiscent of bivalve early crustacean *Canadaspis* from the Burgess Shale, a probable ancestor of the ostracods, known for their hinged carapaces that serve as bivalve shells. But the resemblance to the anterior tagmosis of crustaceans forming their carapace is superficial. The lateral line in vetulicolians represents a potential plane of flexure and this may be a characteristic of their unusual body plan.

Diego García-Bellido and his coauthors [43] concluded that “the common ancestor of the Vetulicolia + Tunicata include distinct anterior and posterior body regions—the former being non-fusiform and used for filter feeding and the latter originally segmented—plus a terminal mouth, absence of pharyngeal bars, the notochord restricted to the posterior body region, and the gut extending to the end of the tail.” I concur with this diagnosis, and this makes the vetulicolians a key higher taxon for evolutionary studies of the Cambrian radiation of deuterostomes.

### **Banffia**

*Banffia constricta* (Fig. 7), the earliest described putative vetulicolian, is a common constituent of the Middle Cambrian Burgess Shale biota. *Banffia* can attain 10 cm length. Originally assigned to the annelids, a lack of appendages has proved to be an insurmountable obstacle for assigning *Banffia* to Arthropoda.

As characteristic for vetulicolians, *Banffia* is divided into an anterior part and a posterior part. The posterior has a characteristic twist and numerous (40-50) narrow segments. There is a “crossing pattern” twisted section at the constriction between the anterior and posterior sections. The anus is at the end of the posterior section, and occurs in the center of a forked structure called the caudal notch [44]. The anterior section or ‘carapace’ is elongate pill-shaped and largely smooth. The anterior tip of the animal bears a corona-like structure of concentric rings or ‘circlets’. The structure is presumed to be the mouth of the animal.

Fine anastomosing ridges on *Banffia*, identified as “micro-ichnofossils” [44], are in fact part of the structure of the animal and may represent vascular canals of some type. No ‘gill slits’ are present, and this has impeded comparisons with other vetulicolians. J.-B. Caron [44] sees the “presence of mid-gut diverticulae in *Banffia*” to represent a possible link to protostomes.

*Banffia episoma* of Utah has a considerably diminished anterior section [45]. *Banffia confusa* from Chengjiang has gill slits on its anterior section and is thus securely placed in the Vetulicolia [44].

### **Beidazoon**

*Beidazoon venustum* is considered a ‘dwarf vetulicolian’ reaching only 8-14 mm in length [46]. Tubercles occur on the anterior section. Thus the possibility that the fossil may represent a juvenile cannot be excluded. *Beidazoon* is one of the ‘hard shell’ vetulicolians [46].

### **Bullivetula**

*Bullivetula variola* is considered here to possibly be synonymous with (a juvenile of) *Beidazoon venustum*. Pronounced tubercles and pits occur on the anterior section [47].

### **Didazoon**

Somewhat resembling *Pomatrum*, *Didazoon haoae* (Fig. 8) has an anterior section divided into six segments, a posterior section divided into seven segments, and a creased junction between the two [48]. *Didazoon* is one of the ‘soft shell’ vetulicolians [46]. Five gill ports have been identified on either side of the anterior section. The tail section is advanced dorsally.

### **Heteromorphus**

*Heteromorphus confusus* was originally assigned to *Banffia*, and the possibility exists that more genera and species will need to be described with ongoing study of these morphologically-variable fossils [47]. *Heteromorphus* is one of the ‘soft shell’ vetulicolians [46].

### **Heteromorphus subtype new species Form A**

This undescribed form is a ‘soft shell’ vetulicolian with an apparently unsegmented posterior region (‘tail’) that is “covered with numerous wrinkles” [46]. The rather thick tail is thought to be either an extension of both the dorsal and ventral partitions of the anterior section, or, more probably, only an extension of the dorsal part of the anterior section [46].

### **Nesonektris**

*Nesonektris aldridgei* (Fig. 9) is a vetulicolian described in 2014 from the Cambrian Emu Bay Shale Konservat-Lagerstätte of Kangaroo Island, Australia. It has a rather rectangular anterior portion and a flattened, paddle-like posterior section. Narrow, diamond-shaped intersegmental membranes occur between posterior section segments. Gill structures are not evident on the anterior section, but a lateral groove appears on both right and left sides of the anterior section along the line where one would expect to find gill structures [43].

The animal attained 1.7 cm length. An “axial, rod-like structure in the posterior body region,” filling much of the “tail cavity,” has been interpreted as a notochord [43], thus lending support to the deuterostome interpretation of vetulicolians. An alternate interpretation is that the thick rod structure represents a wide posterior gut region.

### **Ooedigera**

*Ooedigera*’s relatively large size (up to 42 mm) and

tubercled ornamentation on its anterior section sets it apart from other vetulicolians. *Ooedigera* (Fig. 10) is known from the Lower Cambrian Sirius Passet Lagerstätte of Greenland [49]. If the tubercled ornamentation is considered a juvenile trait, as in the possible juveniles *Beidazoon* and *Bullivetula*, then *Ooedigera* might be considered to be a neotenus form.

### *Pomatrum*

*Pomatrum ventralis* has a typical overall vetulicolian body form, with an egg-shaped anterior portion and a flattened, beaver-tail like posterior section or ‘tail’. *Pomatrum* (Fig. 11) is one of the ‘soft shell’ vetulicolians [46]. *Pomatrum* is remarkable for its circlet mouth consisting of concentric zones of 30 or more plates. Five gill structures (G<sub>1</sub>-G<sub>5</sub>) are present on either side of the anterior portion [46]. The anterior section is smooth apart from some transverse grooves. The posterior region has ten or more segments, with the anterior most partitions becoming fainter and more closely spaced [46].

### *Skeemella*

Perhaps the strangest animal assigned to the vetulicolians, *Skeemella* occurs in Middle Cambrian strata of Utah, USA [50]. *Skeemella* has a relatively small anterior section and a highly elongated posterior section that is curiously divided into dorsal and ventral plates or half-rings. A telson-like, double-pointed or forked posterior tip occurs at the end of the vermiform posterior section. This structure is presumed here to be homologous to the caudal notch of *Banffia*.

*Skeemella*'s placement in the Vetulicolia is controversial, and as summarized by an anonymous author on Wikipedia: “Either *Skeemella* is not a vetulicolian, researchers do not yet have enough data to correctly interpret *Skeemella*, or vetulicolians are not deuterostomes.” *Skeemella* is considered here to be both deuterostome and vetulicolian, with the dorsal-ventral partition in the posterior region, with ‘lateral line’ partition between them on both sides of the animal, represents an extension of the ‘gill’-bearing lateral line structure seen on the anterior end of vetulicolians. Some type of Hox-related genetic modification has evidently led to caudal extension of the vetulicolian lateral line in *Skeemella*.

### *Vetulicola*

The type species of the genus is *Vetulicola cuneata* [47], and it remains the best known species in the genus. *Vetulicola* (Fig. 12) is one of the ‘hard shell’ vetulicolians [46]. The overall shape of the animal resembles a swimming mango with a ventral keel, a shark or orca-like dorsal fin, and a segmented, dorsally-advanced arthropod-like posterior section. Spindle-shaped gill structures are present, showing what are interpreted as gill pouches, gill filaments, and gill slits [4, 13, 46]. Up to three orders of faint annulations occur on the anterior body section. Tubercles do not ornament the anterior section. Seven segments are seen on the posterior section. *Vetulicola rectangulata* has a relatively slender

posterior region (Fig. 12) but it is otherwise similar to *V. cuneata*. *Vetulicola longbaoshanensis* from the Gushan Biota has more elaborate gill structures [13], somewhat resembling that of an undescribed new taxon of vetulicolian from the Qingjiang Biota [14, *Supplementary Materials*].

### Vetulicolian gen. et sp. indet. A

This vetulicolian, 28 mm in length, has a posterior section that is similar to *Ooedigera peeli* but “with a broader flattened area ventrally than dorsally” [49]. The single known specimen has a relatively smooth surface.

### *Xidazoon*

*Xidazoon* is a possible junior synonym of *Pomatrum*.

### *Yuyuanozoon*

Known only from the holotype, *Yuyuanozoon magnificissimi* (Fig. 13) is another vetulicolian from Chengjiang [40]. Its anterior section is ovoid and comparatively smooth, with five pairs of gill structures arranged in a chain-like array on either side of the anterior section of the animal. *Yuyuanozoon* reaches over 20 cm in length. As typical for vetulicolians, its posterior section is divided into seven segments. The posterior section is cylindrical, rather than being flattened as in some other vetulicolians. The anterior section has six segments.

The large mouth region [51, 52] suggests that *Yuyuanozoon* may have been well suited to filter feeding similar to a modern salp or doliolid. Indeed, an unidentified modern doliolid (possibly genus *Doliolum*) bears resemblance to the anterior section of *Yuyuanozoon magnificissimi* [Fig. 13], which might imply a filter feeding lifestyle for the latter.

## 5. Angelfish Vetulicolian

A new species of vetulicolian (••• nov. gen. nov. sp.; informal name *angelfish vetulicolian*) from the Early Cambrian Chengjiang Biota (Burgess Shale-Type (BST) deposit; Maotianshan Shale, 518 Ma), represents the earliest example of ‘angelfish’ body form in a nectobenthic deuterostome (Figs. 14-16). A specimen of the brachiopod *Diadonga pista* occurs on the same slab (Fig. 14).

The preserved length of the animal is 5 cm, with an anterior body region 4 cm deep (Fig. 14-15). It has a dorsal fin (Fig. 14-15) with a saw tooth margin. The anterior of the animal is blunt, with a ventral beak.

Although its posterior is not segmented, ••• nov. gen. nov. sp. has four clearly defined segments in the ventral part of its anterior portion, whereas the dorsal part of the anterior section where the dorsal fin attaches is smooth, almost domal.

Segment 1 of the ventral anterior forms the ‘mandible’ of the beak. Segments 2-4 increase in depth in a posterior direction, with segment 4 extending downward to form the

edge of a ventral keel. The posterior section seems to occur as an extension of this segmented ventral part of the anterior section. This would be inverse to the pattern proposed for *Heteromorphus* subtype new species Form A [46], where the posterior section is thought to be likely an extension of the dorsal half of the anterior section.

The dorsal part of the anterior section appears to be unsegmented, rather developing a triangular fin that mirrors the profile of ventral segments 1-4 to give the angelfish body shape. As second, much smaller dorsal fin is posterior to the first dorsal fin (Fig. 15).

Three (of a presumed original five) gill structures are preserved at the interface between the segmented ventral and smooth dorsal parts of the anterior section (Fig. 15). The posterior-most preserved gill structure preserves paired gill filaments that trail downward from the gill structure.

The posterior section of *••• nov. gen. nov. sp.* has a distinct posterior gut trace surrounded above and below by anteriorly slanting myotome-like structures.

Sagittal plane expansion of the angelfish vetulicolian provides a striking morphological contrast to the dorsal-ventral flattening of the anterior section of the Burgess Shale vetulicolid *Banffia constricta* (Fig. 7), thereby expanding our knowledge of the range of form in this important group of early deuterostomes.

*•• nov. gen. nov. sp.* resembles “*Heteromorphus* subtype new species Form A” [46] in being a ‘soft shell’ form that: lacks segmentation in its posterior section or tail; lacks a prominent constriction between the anterior and posterior portions of the body; and has a very blunt, rectangular anterior end. Angelfish vetulicolian differs from “*Heteromorphus* subtype new species Form A” by having: a narrower tail that lacks wrinkles, but has anteriorly slanting myotome-like structures; a wedge beak; and several flap- or scoop-like fins along the dorsal edge of its posterior section. A gut trace extends to the preserved end of the tail in angelfish vetulicolian. As in *Haikouella* and *Myllokunmingia*, gill filaments that proceed from the gill structure in angelfish vetulicolian appear to be paired.

A unique ‘dorsal fin’ in *••• nov. gen. nov. sp.* mirrors the profile of the ventral cuticular plate. The anterior end of the latter forms a ‘wedge beak’ similar to that described from *Vetulicola cuneata*. The wedge beak-bearing cuticular plate consists of three articulating sections, implying a dentary-like mobility in what appears to be the earliest beak-like ‘jaw’ structure reported from a deuterostome. Whether or not the angelfish vetulicolian also has a vertical mouth (‘M’ in [46]) as inferred for “*Heteromorphus* subtype new species Form A” is unknown. If so, angelfish vetulicolian may have had a dual oral apparatus, a biting beak at the lower part of the mouth (i.e., jaw with horizontal opening) and a blunt, elongate ‘M’ mouth opening that forms a vertical gape for the purposes of filter feeding like a modern doliolid.

If the anteriorly slanting myotome-like structures of *•• nov. gen. nov. sp.* are indeed myotomes, this strongly supports the hypothesis that vetulicolians are deuterostomes rather than arthropod-like protostomes.

## Swim dynamics

The seemingly awkward body shape of virtually all vetulicolians begs the question of how these creatures were able to swim and to maintain their position in the water column. The roughly triangular, angelfish-like body form of angelfish vetulicolian, complete with a protruding lower ‘jaw,’ is well known from the freshwater angelfish *Pterophyllum*, the marine angelfish *Pomacanthus*, and a variety of fossil fishes including *Eoplatex papilio* and the pycnodont *Proscinetes*. Lacking pectoral fins or their functional equivalents, *••• nov. gen. nov. sp.* would presumably have been incapable of labriform swimming, and would have relied instead on less-efficient tail propulsion. Jets of water from the gill structures may have also helped to propel angelfish vetulicolian forward. The dorsal fins on both the anterior and posterior sections imply at least a certain degree of hydrodynamic stability in the water column.

## 6. Developmental Biology of Chordate/Vetulicolian Origins

Several aspects should be mentioned with regard to developmental biology when considering the origin of Chordata and related Cambrian animals. For example, the distinction between the tiny pharyngeal teeth of *Haikouella* and the larger pharyngeal teeth of *Yunnanozoon*, homologous features [6] between the two genera, represents the range of variation seen in the early chordate anterior sleritome.

The dorsal myomere chevrons in *Metaspriggina*, an apparent addition to the *Metaspriggina* body plan, may represent an example of concentric morphological addition similar to that seen in the ichthyosaur-like reptile *Hupesuchus* with its curious rows of bone above the neural spines [42].

The body division into two halves in vetulicolians has been invoked as an illustration of Romer’s somato-visceral theory [48, 53]. A discontinuity in all-*trans*-retinoic acid (ATRA)-FGF morphogen signaling molecules also seems to have occurred at the animal’s midline; thus in vetulicolians the anterior part of the animal and the posterior part of the animal may have been dominated by different molecular signaling regimes. For example, a dual retinoic acid gradient is involved in down-regulating FGF8 to permit somitogenesis. Interestingly, the gradient is at a minimum value at the head/tail junction, and reaches a maximum in the anterior section [54].

The (ATRA)-FGF double-sided retinoic acid gradient signal isolation seems to be particularly pronounced in *Skeemella* [50]. Somite/segmentation formation is dramatically favored in the posterior section and more subdued (although still present) in the anterior section, suggesting that the same posterior-generated signaling factor is influencing segmentation in both the posterior

(influence strong) and anterior (influence weak) sections, with the presumed ATRA gradient dropping off sharply across the anterior-posterior sections division [48]. Here we see a potential unification of the morphogenetic field and gradient signaling approaches, with a morphogenetic field discontinuity demarcating fields of morphogen signaling factor influence.

The serial gene duplications known to have occurred in vertebrates, gnathostomes and teleost fish evidently cannot be linked to the “evolution of complexity in vertebrates” [29].

## 7. Conclusions

Among living chordates, molecular phylogeny shows that tunicates are more closely related to vertebrates (they jointly form the Olfactores) than vertebrates are to lancelets (Cephalochordata [55, 56]). Curiously, in the latter analysis “the monophyly of deuterostomes remained poorly supported” [56]. The reliability of molecular clocks based on these data (“most major lineages of deuterostomes arose prior to the Cambrian Explosion” [55]) is open to question, considering that few if any deuterostome fossils are known from strata deposited before the Cambrian boundary. In any case, the general consensus is that vertebrates first appeared in the Cambrian [57]. Figure 16 shows inferred phylogenetic relationships between vetulicolians, urochordates, cephalochordates, and vertebrates. Note that, due to uncertainties about its affinities, *Yunnanozoan* is not included in the analysis in Fig. 16.

A possible exception to this general rule of Cambrian chordate appearance is the tentative identification of *Burykhia hunti* from Ediacaran strata of the White Sea region, Russia and *Ausia fenestrata* from the Nama Group in Namibia, as potentially the oldest known ascidians [58]. It is far from certain, however, whether or not these members of the Ausiidae are indeed urochordates, considering that their morphology consists of tubes or bags with serial perforations. The presence of a zig-zag medial suture in *Burykhia* suggests rather that the fossils are more properly allied with frondose ‘vendobiont’ Ediacarans such as *Charnia*, *Rangia*, *Phyllozoon* and *Pteridinium*.

In any case, it now seems quite plausible that the advent of deuterostomes near the Cambrian boundary involved *both* a reversal of gut polarity and a two-sided retinoic acid gradient, with a gradient discontinuity at the midpoint of the organism that is reflected in the characteristic division of vetulicolians into morphologically distinct anterior and posterior sections.

## 8. Systematic Paleontology

**Kingdom Animalia**

### Superphylum Deuterostomia

#### Phylum Vetulicolia

#### Genus **••• nov. gen.**

**Description:** A vetulicolian with an unsegmented posterior section (‘tail’) and anterior section that is segmented only in its ventral part, where four segments occur. Gill structures occur between the dorsal and ventral parts of the anterior section. At the anterior of the animal, a wedge beak forms from segment 1 at the juncture between the dorsal and ventral anterior section parts. The sagittal crest bears two dorsal fins, a tall one with a denticulate margin, and lower one to the posterior. A thin keel forms the ventral margin, and the anterior-ventral profile roughly matches that of the main dorsal fin. The dorsal part of the narrow, dorsally-advanced posterior section bears three fins, two larger and flap-shaped and a posterior one that is much smaller.

The posterior section has a distinct gut trace, and is flanked by forward slanting imbricate structures that are interpreted here as myotomes.

**Discussion:** The posterior tip of **••• nov. gen. nov. sp.** is unknown due to breakage in the holotype. The presence of myotomes strongly suggest that **••• nov. gen. nov. sp.** is both a deuterostome and a chordate.

**••• nov. gen. nov. sp.** resembles “*Heteromorphus* subtype new species Form A” [46] in being a ‘soft shell’ vetulicolian form that: lacks segmentation in its posterior section or tail; lacks a prominent constriction between the anterior and posterior portions of the body; and has a very blunt, rectangular anterior. **••• nov. gen. nov. sp.** differs from “*Heteromorphus* subtype new species Form A” by having: a narrower tail that lacks wrinkles; anteriorly slanting myotome-like structures; a wedge beak; and several flap- or scoop-like fins along the dorsal edge of its posterior section. A gut trace extends to the preserved end of the tail in angelfish vetulicolian. As in *Haikouella* and *Myllokunmingia*, gill filaments that proceed from the gill structure in angelfish vetulicolian appear to be paired.

**Etymology:** **•••**

**••• nov. gen. nov. sp.**  
Figures 14-15

**Holotype:** Field sample 1 of 6/25/2019; IGM [TBA].

**Description:** As for genus.

**Etymology:** **•••**

**Informal name:** Angelfish Vetulicolian.

**Age and Locality Information:** Early Cambrian

Chengjiang Biota (Burgess Shale-Type (BST) deposit; Maotianshan Shale, 518 Ma).

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## Figures

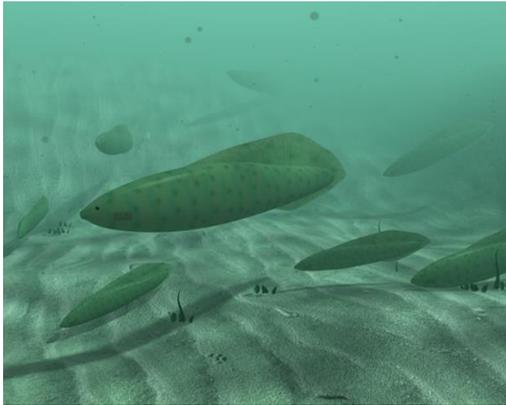


Figure 1. *Haikouichthys ercaicunensis*. Animals are approximately 2.5 cm in length. Image credit: Talifero. Used here per CC BY-SA 3.0.

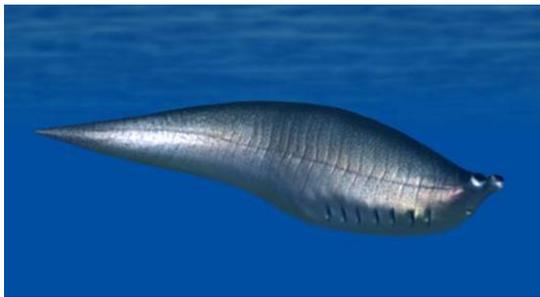


Figure 2. *Metaspriggina walcotti*. Length of animal 10 cm. PaleoArt credit: Nobu Tamura. Used here per CC BY-SA 4.0.



Figure 3. *Pikaia gracilens*. Length of animal 4 cm. Jellyfish in the background is a scyphozoan. PaleoArt credit: Nobu Tamura. Used here per CC BY-SA 4.0.



Figure 4. Cambrian tunicate *Shankouclava anningense*. The animal is 4 cm in height. Image credit: Apokryltaros. Used here per CC BY-SA 3.0.

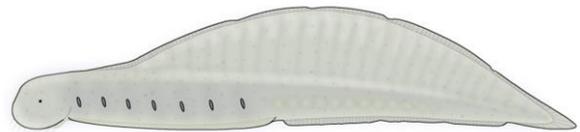


Figure 5. *Yunnanozoon lividum*. Animal is 6 cm in length. PaleoArt credit: Cyrus Theedishman. Used here per CC BY-SA 3.0.

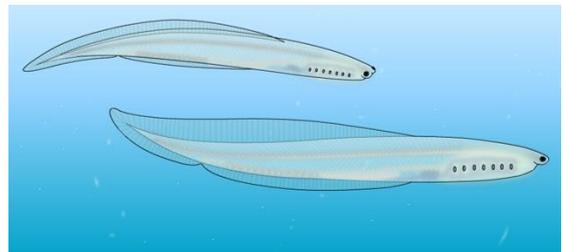


Figure 6. *Zhongxiniscus*. Length of animal 1 cm. PaleoArt credit: Cyrus Theedishman. Used here per CC BY-SA 3.0.

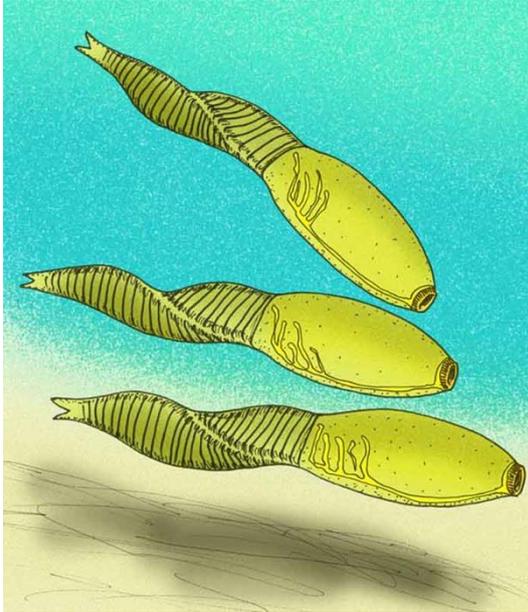


Figure 7. *Banffia constricta*. Length of animal 10 cm. PaleoArt credit: Apokryltaros. Used here per CC BY-SA 3.0.

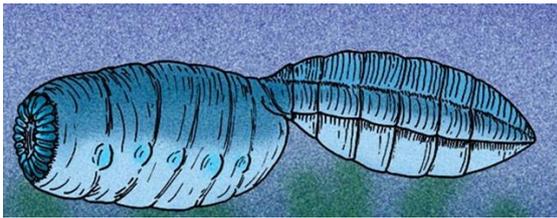


Figure 8. *Didazoon haoae*. PaleoArt credit: Stanton F. Fink. Used here per CC BY-SA 2.5.

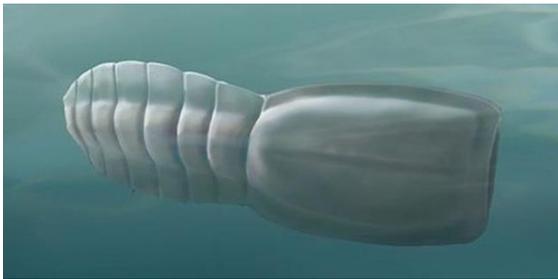


Figure 9. *Nesonektris aldridgei*. Image credit: Modified from D. García-Bellido. Used here per CC BY-SA 4.0.

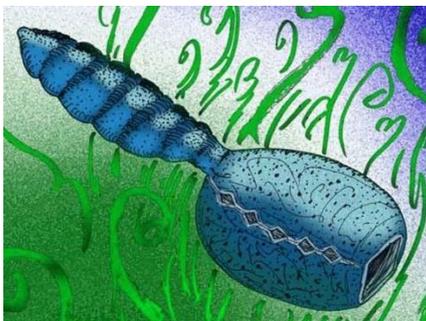


Figure 10. *Ooedigera*. Length of animal 4.2 cm. PaleoArt credit: Apokryltaros. Used here per CC BY-SA 3.0.



Figure 11. *Pomatrum*. Stanton F. Fink. Used here per CC BY-SA 2.5.

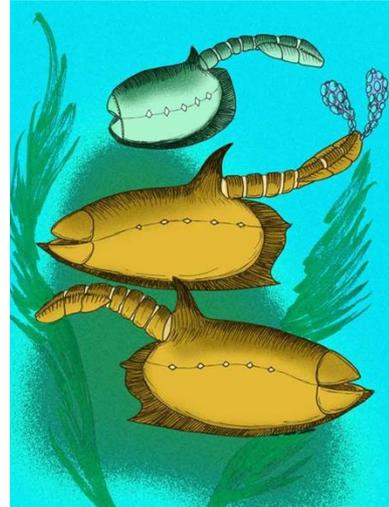


Figure 12. *Vetulicola rectangularata* (top specimen) and *Vetulicola cuneata* (center and bottom specimens). Note wedge beak in *Vetulicola cuneata*. PaleoArt credit: Apokryltaros. Used here per CC BY-SA 3.0.

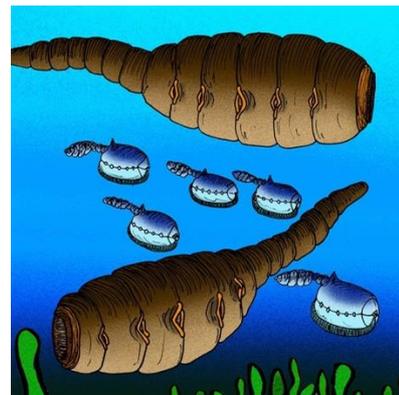


Figure 13. *Yuyuanozoon magnificissimi* with smaller *Vetulicola rectangularata* swimming behind. PaleoArt credit: Apokryltaros. Used here per CC BY-SA 3.0.

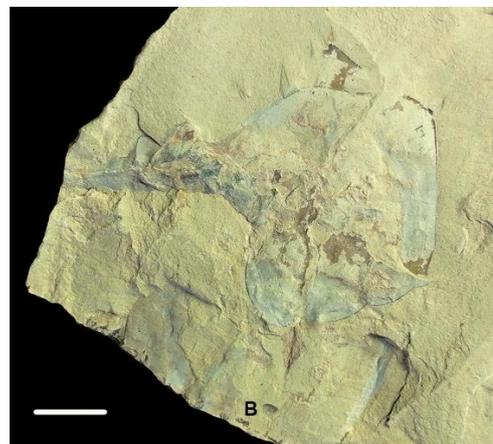


Figure 14. ••• nov. gen. nov. sp. Holotype. **B**, Epifaunal brachiopod *Diadonga pista*. Scale bar in cm.

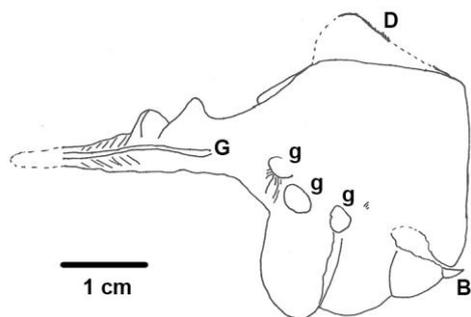


Figure 15. ••• nov. gen. nov. sp. Line art sketch showing morphology of the specimen. **B**, wedge beak; **D**, dorsal fin; **g**, gill structure; **G**, presumed gut trace. Scale bar 1 cm.

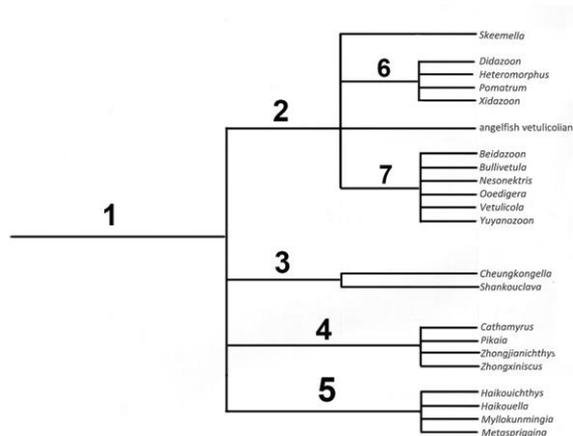


Figure 16. Inferred phylogenetic relationships of Cambrian chordates and vetulicolians. **1**, Deuterostomia (blastopore becomes anus); **2**, Vetulicolia (five pairs of gill structures); **3**, Urochordata (branchial basket); **4**, Cephalochordates (full notochord); **5**, Vertebrata (neural crest); **6**, 'soft-shell' vetulicolians; **7**, "hard shell" vetulicolians. *Yunnanozoan* is not included in this analysis due to uncertainty regarding its phylogenetic position.

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