

Primitive deuterostomes from the Chengjiang Lagerstätte (Lower Cambrian, China)

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Cambrian fossil-Lagerstätten (sites of exceptional fossil preservation), such as those from Chengjiang (Lower Cambrian) and the Burgess Shale (Middle Cambrian), provide our best window into the Cambrian 'explosion'. Such faunas are known from about 40 localities, and have yielded a widely disparate series of taxa ranging from ctenophores to agnathan fish. Recent excavations of the Chengjiang fossil-Lagerstätte, known from a series of sites near Kunming in Yunnan, south China, have resulted in the discovery of several new forms. In conjunction with material described earlier, these provide evidence for a new group of metazoans, the vetulicolians. Several features, notably a series of gill slits, suggest that this group can throw light on an early stage of deuterostome diversification.

The origin and evolution of metazoan bodyplans, an important aspect of the Cambrian 'explosion', represents a productive area for interdisciplinary research, between molecular biology and palaeontology^{1,2}. The extant representatives of the various phyla are, however, typically disparate in anatomy, and may be markedly different from their Cambrian ancestors. As a result, molecular phylogenies do not reveal how different bodyplans emerged, what the animals actually looked like, or how they functioned and what ecological milieux they inhabited. This historical dimension may be revealed by the fossil record, where potentially the assembly of character states can be traced within a given stem group³.

Deuterostome form is remarkably protean. Few characters are widely shared, and apart from embryological features, such as the fate of the blastopore, which does not form the mouth and can be the presumptive anus (to which exceptions are known⁴), and radial cleavage, the most notable macroscopic features in common are the gill slits^{5,6} and endostyle⁷ (albeit in terms of the dorsal epibranchial ridge in the primitive enteropneust hemichordates⁸). Gill slits, however, have been lost in all extant echinoderms, and neither is there an unequivocal trace of the endostyle in this phylum. In other cases, such as the purported homology between the hemichordate stomochord and chordate/urochordate notochord, doubt remains as to the validity of such a comparison^{8,9}. Apart from recognition of certain striking larval similarities, notably between the tornaria larvae of enteropneusts and certain echinoderm larvae, overall classical methods of comparison, such as those largely based on embryology¹⁰, led to relatively little progress until rejuvenation with molecular methods. An emerging consensus^{11–16} points to a series of significant similarities between the chordates (vertebrates and the more primitive cephalochordates) and urochordates. Evidence is also growing for a closer relationship between the echinoderms and hemichordates^{14–16}.

Even so, the evolution and ecology of the first deuterostomes remains highly conjectural. Here we report a suite of fossils, representing at least four taxa, from the Chengjiang fossil-Lagerstätte (south China). They are characterized by a bipartite body, the anterior section of which has a series of perforations, evidently precursors of gill slits. This clade is referred to as the vetulicolians, which as the class Vetulicolida was erected by Chen and Zhou¹⁷ to encompass the genera *Vetulicola* and *Banffia*. Here we expand the concept to include *Xidazoon*¹⁸, *Didazoon* nov. gen., and

*Pomatrum*¹⁹, and define a distinctive bodyplan (equivalent to a phylum) designated the Vetulicolia. These animals appear to be primitive deuterostomes.

Phylum Vetulicolia nov.

Class Vetulicolida Chen & Zhou 1997¹⁷

Family Didazoonidae Shu & Han fam. nov.

Genus *Didazoon* Shu & Han gen. nov.

Didazoon haoae Shu & Han sp. nov.

Etymology. The generic name abbreviates in Chinese the China University of Geosciences. The species name is to honour Y. Hao, for her encouragement of this work.

Holotype. Early Life Institute, Northwest University, Xi'an, ELI-0000196.

Referred material. ELI 0000197–0000217.

Stratigraphy and locality. Qiongzhusi (Chiungchussu) Formation, Yu'an-shan Member (*Eoredlichia* zone), Lower Cambrian. Specimens collected in Dabanqiao area (Kunming), about 60 km north-west of Chengjiang, and 50 km northeast of Haikou, from where *Xidazoon* was collected.

Diagnosis. Bipartite, cuticularized body, anterior segmented region and voluminous mouth, ventral margin flattened, widens posteriorly. On either side the anterior bears five circular structures, in the form of a cowl with posteriorly directed opening and basin-like interior, apparently connected to interior. A prominent constriction separates dorsal region of anterior from posterior section. The latter, composed of seven segments, tapers in both directions, with rounded posterior termination. Internal anatomy includes alimentary canal, possibly voluminous in anterior, and in posterior narrow intestine, straight or occasionally coiled. Dark strand located along ventral side of anterior section, possibly representing endostyle.

The body of *Didazoon haoae* is composed of two sections (Fig. 1a, c, d, f). On the assumption that *Didazoon* is related to *Vetulicola* (see below), where the segmented 'tail' (that is, the posterior section) evidently arises from the dorsal side, this would indicate a comparable orientation in *Didazoon*. The anterior unit is semi-quadrate in lateral view, and was laterally compressed. The leading boundary of the anterior section shows a weak pleating and is arcuate (Fig. 1a, b, d, e), suggesting a voluminous opening. The anterior section is now filled with sediment, an arrangement indicating that in life the anterior cavity was spacious. The anterior rim and dorsoventral

margins, however, are flatter. In particular the ventral margin has a bladed appearance (Fig. 1a, b, d, e), with a progressive widening posteriorly. The exterior shows a prominent series of segments, totalling six. The membranes separating the segments are fairly broad, and this may have conferred a degree of flexibility.

Laterally, five oval-shaped structures are located on either side of the anterior section (Fig. 1a–f). They are interpreted as gills. The anteriormost is smallest, the next two are the largest and may imbricate, and the two posteriormost show a progressive size decrease. Each consists of a convex cowl, sometimes with concentric lineations, with a posterior opening. An internal cavity has a basin-like floor. An opening into the interior is inferred to exist towards the anterior of each cavity. Faint imprints of apparently tubular units may represent internal connections between these structures. Towards the ventral margin there is a darker strand of material (Fig. 1a, b, d, e), possibly representing the endostyle, as it is a consistent feature, which extends posteriorly and further back rises dorsally towards the narrow alimentary canal that extends into the posterior section.

The constriction shows creasing and was probably quite flexible (Fig. 1a, d), suggesting a degree of independence between anterior and posterior regions. The elongate posterior section tapers in either direction. It consists of seven segments, of which the last has a rounded termination. A narrow gut trace is well preserved, and sometimes filled with fine-grained material. In one specimen the infill has a spiral arrangement, which is also seen in *Vetulichola* (Fig. 5a, b and Supplementary Information Fig. III). Towards either margin narrow strands, sometimes branched, may represent vascular tissue.

New information on *Xidazoon* and *Vetulichola*

Continued collecting has led to new data on *Xidazoon*¹⁸ and *Vetulichola*^{17,20,21}. Since the original description¹⁸ of *Xidazoon* more

specimens (Fig. 2a–f and Supplementary Information Fig. I) have been found from Mafang and Dazicun, in the Haikou area²². These show some important but hitherto unrecognized features. In particular, the anterior section bears a series of up to five cowl-like structures (Figs 2a, b, d, e and 3c, d), similar to those of *Didazoon* in shape, size and location. In one specimen, associated dark, circular areas are possibly indicative of the actual openings into the interior (Fig. 2d). A step-like arrangement along the right-hand margin of the holotype¹⁸ is probably the hitherto unrecognized lateral expression of these openings. The prominent circular feeding apparatus is well preserved in several specimens (Fig. 2c, f and Supplementary Information Fig. I). Despite distortion it shows approximately 30 plates, thus exceeding the number estimated to occur in the holotype¹⁸. A persistent feature is a rather dark region running close to the ventral and posterior margins (Fig. 2a, d), which is quite similar to that in *Didazoon*, and is tentatively interpreted as an endostyle. Folding in the anterior section (Fig. 2c and Supplementary Information Fig. I) suggests that in life it was thin-walled, although one specimen shows that the presumed venter had a keel-like arrangement (Supplementary Information Fig. I).

Didazoon and *Xidazoon*, which are found in localities separated by about 50 km and may belong to different faunal assemblages, share many similarities, but the differences justify generic separation. *Didazoon* has a more cuticularized anterior section with a series of clear segmental boundaries, whereas in *Xidazoon* only the first segment is moderately well defined. The greater flexibility of the anterior section of *Xidazoon* is reflected in both its folding and a propensity for the more posterior region to decay. The anterior margin of *Didazoon*, similar to that of *Vetulichola rectangulata* (Fig. 4f and Supplementary Information Fig. I), appears to have been more rigid and may have had a less flexible feeding apparatus. The constriction in this taxon appears to be better defined and shorter

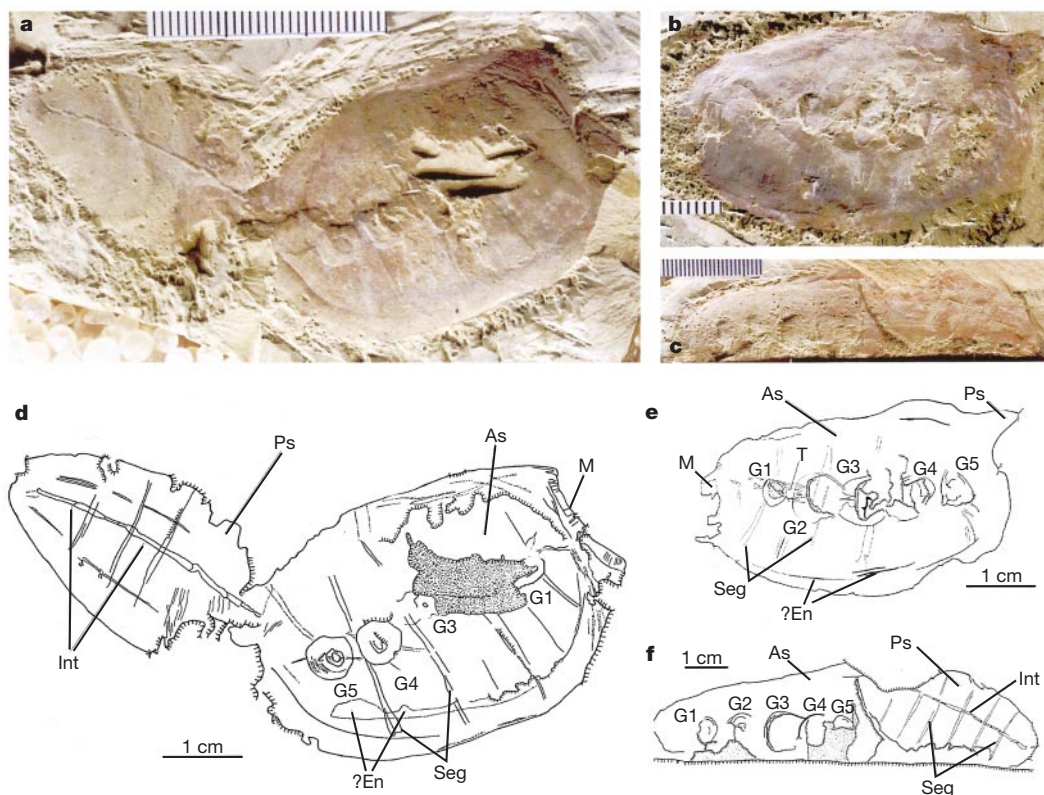


Figure 1 The Lower Cambrian vetulicolian *Didazoon haoae* Shu & Han gen. et sp. nov. from Dabanqiao, Yunnan. **a**, Specimen ELI-0000196, entire specimen, compare **d**. **b**, ELI-0000198, anterior section and remnant of posterior, compare **e**. **c**, ELI-0000200A,

anterior incomplete but with prominent gills, segmented posterior with intestine, compare **f**. In **a–c**, millimetric scale bars are shown. As, anterior section; ?En, presumed endostyle; G1–5, gill1–gill5; Int, intestine; M, mouth; Ps, posterior section; Seg, segments.

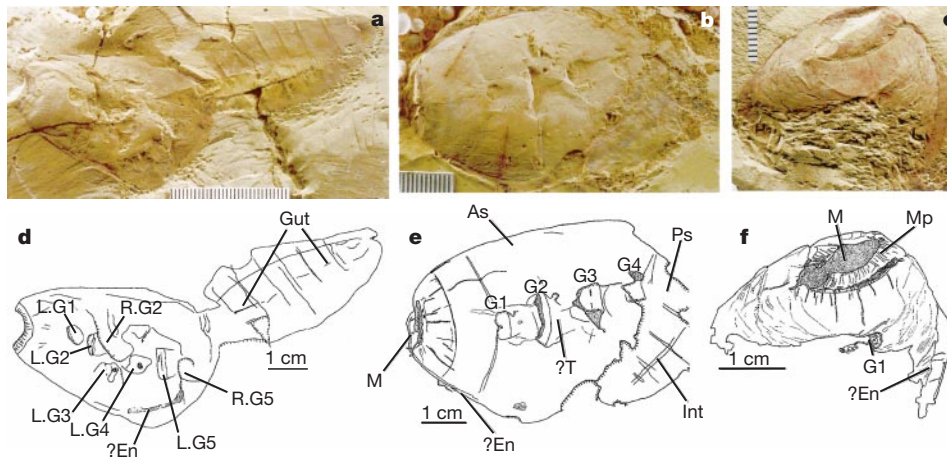


Figure 2 The Lower Cambrian vetulicolian *Xidazoon stephanus* from Haikou, Kunming. **a**, ELI-0000203A, entire specimen, although the anterior is crushed it appears to show five left gills and two right gills, including possible openings, compare **d**. **b**, ELI-0000202, entire specimen with gills, compare **e**. **c**, ELI-0000204A, anterior section, incomplete but

with well preserved mouth, compare **f**. In **a–c**, millimetric scale bars are shown. As, anterior section; ?En, presumed endostyle; L. G1–5, left gill1–gill5; R. G2, 5, right gills 2, 5; Int, intestine; M, mouth; Mp, mouth plates; Ps, posterior section; ?T, possible tube connecting gills.

than in *Xidazoon*. Moreover, they differ in the gill structures (compare Fig. 1a, d with Fig. 2a, b, d, e).

Vetulicola is represented by two species, *V. cuneata*^{17,20,21} (Fig. 4a–e and Supplementary Information Fig. I) and *V. rectangulata*¹⁹ (Fig. 4f, g and Supplementary Information Fig. I). Their principal difference is in the anterior: the former species shows prominent lobate extensions, whereas in *V. rectangulata* the anterior margin is almost straight in lateral view, similar to that in *Didazoon*. *Vetulicola* has a strongly bipartite bodyplan (Fig. 4a), reminiscent of phyllocarid arthropods. The laterally compressed anterior section forms a sort of ‘carapace’, consisting of four prominent and rather rigid plates. A sediment infill indicates the interior was voluminous. The venter forms a keel-like structure (Fig. 4g), and the lateral midlines consist of a narrow groove associated with five openings (Fig. 4a–f and Supplementary Information Fig. II). At its posterior end there is a median and arcuate dorsal process (Fig. 5f). Little is known about the anatomy of the interior. Excavation has failed to reveal evidence for limbs or other appendages within the carapace-like structure, nor are there signs of eyes. Their inclusion in reconstructions (in Fig. 137 of ref. 17; p. 38 of ref. 21) seems to be questionable. A series of small, blunt pegs lining the interior, which give the anterior section a characteristically ‘beaded’ appearance, may have been used to attach tissue, possibly involved with food collection.

The most obvious feature of the anterior section is a series of openings¹⁷, located along the lateral midlines. They total five on each side, and have a complex structure. Each consists of a prominent and spacious pouch. This may be filled with sediment, but when empty each shows a low ridge with filament-like structures on the floor (Fig. 3e–l and Supplementary Information Fig. II). Anterior to this is a steep wall that near its base has an elongate area. Typically this is filled with sediment, and is interpreted as the inhalant aperture. A peculiar feature of the internal cavity is that it extends posteriorly to define a prominent tapering tube sloping upwards towards the outer surface. It is not clear whether this tube opened into the next-posterior pouch, in a position above its inhalant aperture, or was blind. The exhalant aperture is located in the lateral groove, and consists of an elliptical opening surrounded by a series of very fine filaments (Figs 3e–j and 4c; see also Supplementary Information Fig. II). Adjacent to the exhalant openings, the cuticle on the dorsal and ventral plates forms semi-elliptical structures (Fig. 3i, j and Fig. 4a, f). These seem previously¹⁷ to have been mistaken for the actual openings, but as they lie above the apertures they evidently represent protective

cuticular thickenings. Each complex is interpreted as a gill, with internal respiratory filaments.

The posterior region forms a tail (Fig. 4a, e and Supplementary Information Fig. I) consisting of seven somites, not eight as reported¹⁷, each strongly cuticularized, and separated by broad membranes. The last segment has a rounded termination. The tail region is dorsoventrally asymmetric, and probably provided propulsive strokes by lateral movements. The posterior region often demonstrates a gut trace, sometimes coiled and with prominent fine-grained contents (Fig. 5b and Supplementary Information III).

The *Xidazoon–Didazoon* connection is further extended by reference to the already published, but poorly known, Chengjiang taxon *Pomatrum ventralis*¹⁹. The anterior section and feeding circlet is similar to those in *Didazoon*. On the anterior of an incomplete specimen there are two quadrate cowls, the forward conspicuously smaller in size, evidently equivalent to the gills of *Didazoon*. The major difference between *Pomatrum* and *Didazoon* (as well as *Xidazoon*) concerns the posterior section, which extends from the dorsal side as a narrow tail-like structure, as in *Vetulicola*.

The vetulicolian clade (*Didazoon*, *Pomatrum*, *Vetulicola* and *Xidazoon*) is well defined by the following diagnostic features: a bipartite body, consisting of a voluminous anterior with five sets of gill openings; and a posterior section with seven segments. These taxa appear to occupy various ecologies. *Didazoon* and *Xidazoon* were probably benthic and epifaunal, whereas the box-like anterior and elongate tail of *Vetulicola* indicate greater mobility, perhaps as an active swimmer. *Vetulicola* is rather arthropod-like, but we interpret this as an example of evolutionary convergence. A carapace construction consisting of four large plates is unknown in arthropods. Most importantly, there is no evidence for any sort of associated appendage. In addition, there is no evidence that *Vetulicola* moulted its skeleton. Growth was presumably by accommodation, and the presence of surface membranes around all the margins and along the lateral mid-lines of the animal (Fig. 5c–f and Supplementary Information Fig. IV) suggests that the skeleton was internal.

The most striking difference between the vetulicolians and arthropods, however, concerns the series of five gills. In *Xidazoon*, *Didazoon* and *Pomatrum*, they consist of hood-like structures that in life concealed the openings. In *Vetulicola* these gills are more complex, but their homology is in little doubt both because of the overall similarities of the bodyplan and *Didazoon* and *Pomatrum* acting as a morphological intermediate between *Xidazoon* and

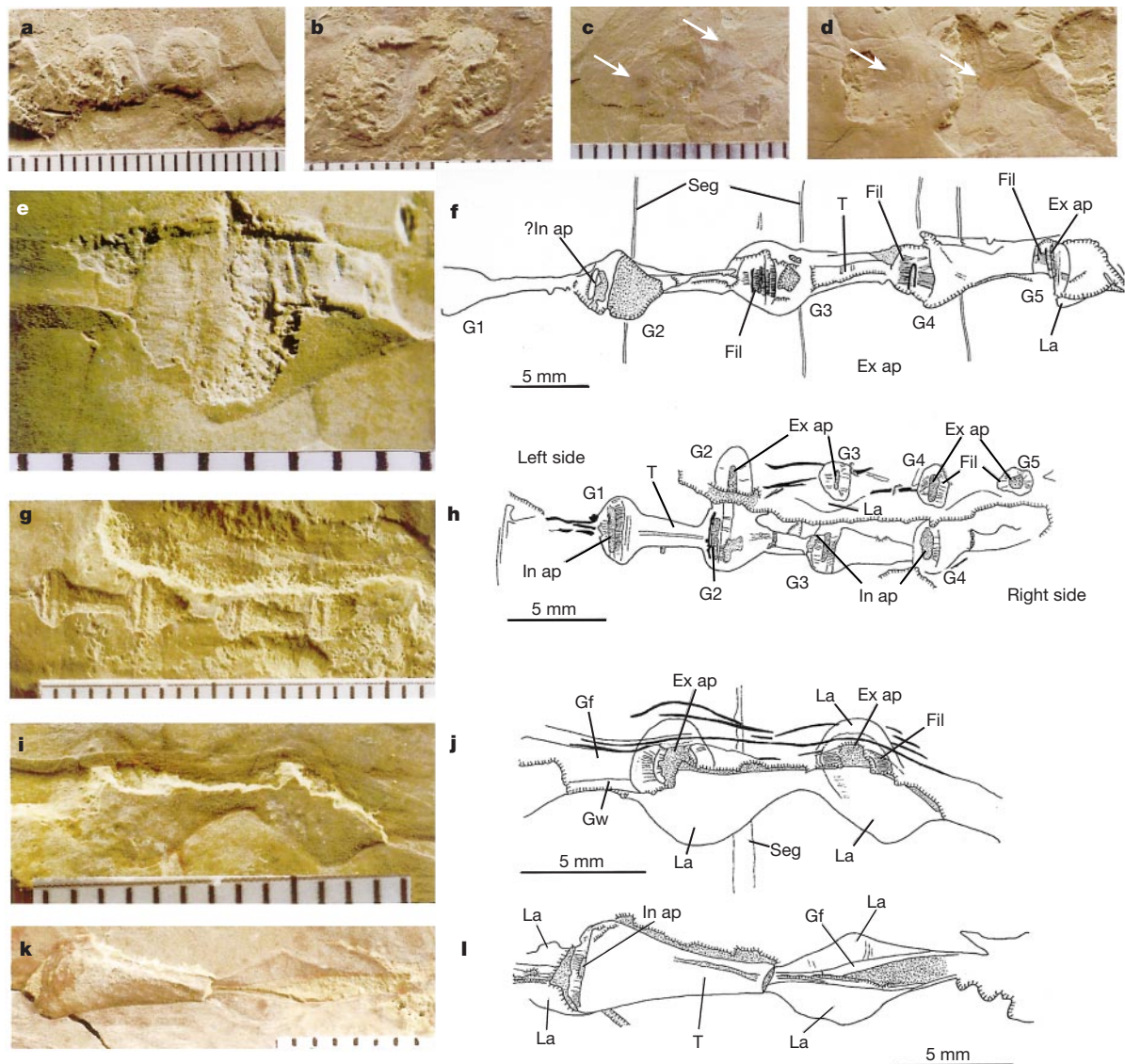


Figure 3 Gill structures of vetulicolians. **a–d**, Details of gills of specimens ELI-0000196 (*Didazon*), 201 (*Didazon*), 203A (*Xidazon*) and 202 (*Xidazon*), respectively, compare Figs 1a and 2a. **e, f**, Details of the left gill 4 and all left gills of ELI-0000216 (*Vetulicola cuneata*), respectively; compare Fig. 4a. **g, h**, Details of gills on two levels representing respectively lower (left side, gills G2–5) and upper (right side, gills G1–4) of

ELI-0000215 (*Vetulicola cuneata*), compare Fig. 4e. **i, j**, Details of left gills 4 and 5 of ELI-0000210 (*Vetulicola rectangulata*). **k, l**, Details of gills viewed from interior of specimen ELI-0000212 (*Vetulicola rectangulata*). In **a–e, g, i, k**, millimetric scale bars are shown. Ex ap, exhalant aperture; Fil, filaments; Gf, groove floor; Gw, groove wall; G1–5, gill1–gill5; In ap, inhalant aperture; La, lappet; Seg, segments; T, tube.



Figure 4 The Lower Cambrian vetulicolian *Vetulicola cuneata* (**a–e**) from Chengjiang and *Vetulicola rectangulata* (**f, g**) from Haikou, Kunming. **a**, ELI-0000216, compare Fig. 3e. **f**, Specimen ELI-0000207, two animals, upper with interior excavated to reveal right-hand gill pouches (**c**), lower with well-preserved gills, detail shown in **d**.

e, ELI-0000215, entire specimen and detail of gills on left- and right-hand sides of the anterior section, compare Fig. 3g. **f**, ELI-0000209, anterior section with lappets on gills. **g**, ELI-0000211A, ventral view of anterior section showing mouth cone. Millimetric scale bars are shown.

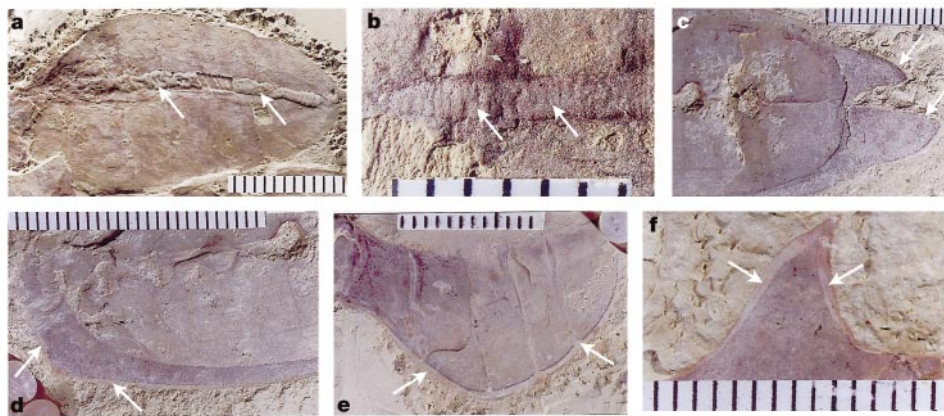


Figure 5 Coiled guts (arrows in **a** and **b**) and surface membranes (arrows in **c–f**) of vetulicolians. **a**, ELI-0000197 (*Didazon*). **b**, ELI-0000309A (*Vetulicola*). **c–f**, *Vetulicola*. **c**, Anterior of ELI-0000218. **d**, Postero-ventral of the anterior section in ELI-0000218.

e, Posterior section of ELI-0000302B. **f**, Dorsal ‘fin’ of ELI-0000338A. Millimetric scale bars are shown.

Vetulicola. In *Xidazon* and *Didazon* the gills are relatively simple, and filamentous structures comparable to those in *Vetulicola* have not been observed. The pouch-like gills of *Vetulicola* are probably a reflection of both a more active mode of life and more rigid construction of the body, possibly decreasing overall gas permeability.

Vetulicolians as deuterostomes

Gill slits are, of course, one of the defining features of the deuterostomes. In the relative simple form, as seen in *Xidazon* and *Didazon*, their primary function may have been discharge of excess sea water. As such, they would have achieved what is believed to have been the original function of the deuterostome gill slits²³, although functionally they are usually also used for respiration and/or suspension feeding. We acknowledge that given the obvious dissimilarity of these apertures to the gill slits of even the most primitive of extant deuterostomes, widely regarded as the hemichordate acorn worms, it might be more sensible to interpret the lateral openings of vetulicolians as an example of evolutionary convergence. The gill slits of the acorn-worms are, however, evidently specialized, to judge from their striking similarity to the equivalent structures in amphioxus, although within the deuterostomes the hemichordates and cephalochordates are phylogenetically relatively remote^{14–16}. If the original function of the apertures was indeed the disposal of sea water^{23,24}, the familiar close packing of gill slits seen in most deuterostomes would have resulted principally from the demands of respiration. Moreover, the gill slits (although their interpretation is controversial) of cornute calcichordates²⁵, such as *Cothurnocystis*, are also large and widely spaced, and it is only in derived forms, such as *Scotiaecystis*, that these gill slits again become more closely packed.

Two other features in the vetulicolians may be consistent with a position within the deuterostomes. One is the dark ventral strand in

the anterior section, possibly equivalent to an endostyle. Second, the evidence that the skeleton was internal suggests that it was of mesodermal derivation. Further evidence for a deuterostome affinity may, however, lie with a proposed link between the vetulicolians and the Chengjiang clade represented by *Haikouella*²⁶ and *Yunnanozoon*^{27–29}. These animals were interpreted as craniates, but while few dispute features such as the gill slits, many of the interpretations of a specifically craniate anatomy³⁰ are open to question. It seems likely that these taxa are more basal within the deuterostomes, with a position closer to the hemichordates^{28,31}. Despite obvious differences, vetulicolians and yunnanozoans may be related. The former has a bipartite bodyplan, while yunnanozoans are divided into an anterior section (with proboscis and collar)²⁸, bearing a series of gill slits, and a segmented and cuticular posterior. The yunnanozoan body is elongate and vaguely fish-like, but evidence for partial separation between the two regions (Fig. 6 and Figs 2e and 3d in ref. 28) suggests that the yunnanozoan bodyplan arose from of an overlap of two discrete sections.

Discussion

Vetulicola was widely accepted as “a very strange arthropod”^{17,19,32,33} (but see ref. 34). Structures that perforate the anterior body wall are, however, interpreted as the precursors of the gill slits³⁴, a defining character of the deuterostomes. Similarities between the vetulicolians and yunnanozoans may give an important clue as to a subsequent stage in deuterostome evolution, given that the gill slits of the latter are closer in organization to other primitive deuterostomes. The bipartite body of vetulicolians is also reminiscent of the hypothetical animal invoked by Romer’s somato-visceral theory³⁵. This posited an effectively bipartite organization in which the ‘somatic’ component (with musculature and a segmented nervous system) became increasingly integrated with a visceral unit that was largely composed of a pharyngeal branchial basket.

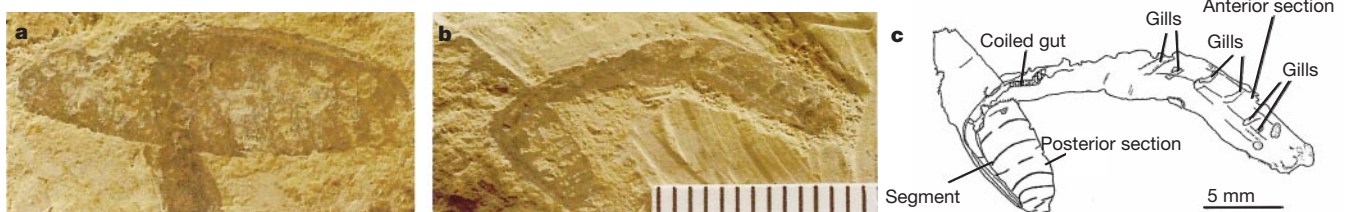


Figure 6 The Lower Cambrian *Yunnanozoon lividum* from Chengjiang, Yunnan. **a**, Part, complete specimen, Specimen NWU93-1406A. **b**, Counterpart, detail of posterior section

and its attachment to anterior section, NWU93-1406B. **c**, Camera-lucida drawing with details of part and counter-part combined. In **b**, a millimetric scale bar is shown.

Although originally applied to the first chordates, this concept might be more relevant to the appearance of basal deuterostomes. In addition, the coiled gut commonly seen in both vetulicolians (Fig. 5a, b and Supplementary Information Fig. III) and *Yunnanozoon* (Fig. 6 and Figs 2e and 3d in ref. 28), as well as in various less-advanced fish³⁶, is also consistent with deuterostome affinities of vetulicolians. An alternative although less likely possibility is that this coiled structure incorporates the equivalent of the notochord, perhaps as a series of stacked discs. The sporadic occurrence of the coiling and irregular convolutions, however, make a gut interpretation more probable (see Supplementary Information Figs I and III).

Antecedents of vetulicolians are problematic. Possibly the most primitive representative of this clade is *Banffia*, known from the Burgess Shale³⁷ and Chengjiang^{17,21}. A detailed description is not yet available, but the correspondences include the bipartite body connected by a narrow constriction, and a segmented posterior, albeit with finer divisions than other vetulicolians. The anterior bore a mouth with a cirlet of cuticular folds (J. Caron, personal communication), but equivalents to the vetulicolian gills have not been recognized.

If vetulicolians represent primitive deuterostomes, their body-plan could point to a deeper origination, somewhere within the protostomes. To date, however, neither the Neoproterozoic nor Cambrian fossil record seems to contain taxa that might serve as such an evolutionary link. The role of vetulicolians in the early deuterostome evolution is, however, more intriguing. The extant phyla are both highly disparate and derived. Various differences in gene expression patterns, especially between the hemichordates and more advanced chordates, indicate redeployments³⁸, such as the use of *Brachyury*^{9,39}, or significant re-organization as in the nervous system^{40–42}. In contrast, the gill slits^{5,6} and probably the endostyle⁸ are primitive features. It is worth mentioning that *Vetulicola* itself has a certain resemblance to a giant ‘tadpole’ (Fig. 4a). This concept has played a central role in speculations on the origins of the chordates⁴³. The development of a propulsive tail and a large anterior feeding chamber with pharyngeal openings may in itself give further insights into the subsequent evolution of the chordate bodyplan, including the calcichordates. Finally, we note that the co-occurrence of stem-group deuterostomes and agnathan fish⁴⁴ are consistent with an ‘explosion’ of metazoan bodyplans in the latest Neoproterozoic and early Cambrian. □

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1. Conway Morris, S. Evolution: Bringing molecules into the fold. *Cell* **100**, 1–11 (2000).
2. Valentine, J. W., Jablonski, D. & Erwin, D. H. Fossils, molecules and embryos: new perspectives on the Cambrian explosion. *Development* **126**, 851–859 (1999).
3. Budd, G. E. & Jensen, S. A critical reappraisal of the fossil record of the bilaterian phyla. *Biol. Rev.* **75**, 253–295 (2000).
4. Fioroni, P. Zur Signifikanz des Blastoporus-Verhaltens in evolutiver Hinsicht. *Rev. Suisse Zool.* **87**, 261–272 (1980).
5. Ogasawara, M. *et al.* Developmental expression of *Pax 1/9* genes in urochordate and hemichordate gills: insight into function and evolution of the pharyngeal epithelium. *Development* **125**, 2539–2550 (1999).
6. Okai, N. *et al.* Characterization of gill-specific genes of the acorn worm *Ptychodera flava*. *Dev. Dyn.* **217**, 309–319 (2000).
7. Ogasawara, M. *et al.* Ascidian homologs of mammalian thyroid transcription factor-1 gene are expressed in the endostyle. *Zool. Sci.* **16**, 559–565 (1999).
8. Ruppert, E. E., Cameron, C. B. & Frick, J. F. Endostyle-like features of the dorsal epibranchial ridge of an enteropneust and the hypothesis of dorsal-ventral axis inversion in chordates. *Invert. Biol.* **118**, 202–212 (1999).
9. Peterson, K. J. *et al.* A comparative molecular approach to mesodermal patterning in basal deuterostomes: the expression pattern of *Brachyury* in the enteropneust hemichordate *Ptychodera flava*. *Development* **126**, 85–95 (1999).
10. Schaeffer, B. Deuterostome monophyly and phylogeny. *Evol. Biol.* **21**, 179–235 (1987).

11. Turbeville, J. M., Schulz, J. R. & Raff, R. A. Deuterostome phylogeny and the sister group to the chordates: evidence from molecules and morphology. *Mol. Biol. Evol.* **11**, 648–655 (1994).
12. Wada, H. & Satoh, N. Details of the evolutionary history from invertebrates to vertebrates, as deduced from the sequences of 18S rDNA. *Proc. Natl Acad. Sci. USA* **91**, 1801–1804 (1994).
13. Lacalli, T. C. The nature and origin of deuterostomes: some unresolved issues. *Invert. Biol.* **116**, 363–370 (1997).
14. Bromham, L. D. & Degnan, B. M. Hemichordate and deuterostome evolution: robust molecular phylogenetic support for a hemichordate + echinoderm clade. *Evol. Dev.* **1**, 166–171 (1999).
15. Cameron, C. B., Garey, J. R. & Swalla, B. J. Evolution of the chordate body plan: New insights from phylogenetic analyses of deuterostome phyla. *Proc. Natl Acad. Sci. USA* **97**, 4469–4474 (2000).
16. Gee, H. in *Major Events in Early Vertebrate Evolution* (ed. Ahlberg, P. E.) *Syst. Anal. Spec.* **61**, 1–14 (2001).
17. Chen, J.-Y. & Zhou, G.-Q. Biology of the Chengjiang fauna. *Bull. Natl Mus. Nat. Sci. Taiwan* **10**, 11–105 (1997).
18. Shu, D.-G. *et al.* A pipiscid-like fossil from the Lower Cambrian of south China. *Nature* **400**, 746–749 (1999).
19. Luo, H.-L. *et al.* Early Cambrian Chengjiang Fauna from Kunming Region, China (Yunnan Sci. Technol. Press, Kunming, 1999).
20. Hou, X.-G. Early Cambrian large bivalved arthropods from Chengjiang, eastern Yunnan. *Acta Palaeont. Sinica* **26**, 286–297 (1987).
21. Chen, J.-Y. *et al.* The Chengjiang Biota: A Unique Window of the Cambrian Explosion (National Museum of Natural Science, Taiwan, 1996).
22. Zhang, X.-L. *et al.* New sites of Chengjiang fossils: crucial windows on the Cambrian explosion. *J. Geol. Soc. Lond.* **158**, 211–218 (2001).
23. Gilmour, T. H. J. Feeding in pterobranch hemichordates and the evolution of gill slits. *Can. J. Zool.* **57**, 1136–1142 (1979).
24. Gilmour, T. H. J. Feeding in tornaria larvae and the development of gill slits in enteropneust hemichordates. *Can. J. Zool.* **60**, 3010–3020 (1982).
25. Jefferies, R. P. S. *The Ancestry of the Vertebrates* (British Museum (Natural History), London, 1986).
26. Chen, J.-Y., Huang, D. Y. & Li, C. W. An early Cambrian craniate-like chordate. *Nature* **402**, 518–522 (1999).
27. Chen, J.-Y. *et al.* A possible early Cambrian chordate. *Nature* **377**, 720–722 (1995).
28. Shu, D.-G., Zhang, X. & Chen, L. Reinterpretation of *Yunnanozoon* as the earliest known hemichordate. *Nature* **380**, 428–430 (1996).
29. Dzik, J. *Yunnanozoon* and the ancestry of chordates. *Acta Palaeont. Polonica* **40**, 341–360 (1995).
30. Holland, N. D. & Chen, J.-Y. Origin and early evolution of the vertebrates: new insights from advances in molecular biology, anatomy, and paleontology. *BioEssays* **23**, 142–151 (2001).
31. Shu, D.-G., Chen, L., Zhang, X.-L., Han, J. & Li, Y. Chengjiang Lagerstätte and earliest-known chordates. *Zool. Sci.* **18**, 447–448 (2001).
32. Hou, X.-G. *et al.* The Chengjiang Fauna: Exceptionally Well-preserved Animals From 530 Million Years Ago (Yunnan Sci. Technol. Press, Kunming, 1999).
33. Hou, X.-G. & Bergström, J. Arthropods of the Lower Cambrian Chengjiang fauna, southwest China. *Fossils Strata* **45**, 1–116 (1997).
34. Shu, D.-G., Zhang, X.-L. & Chen, L. in *Progress in Geology of China (1993–1996)* (Papers to 30th International Geological Congress) 42–45 (Chinese Geological Society, Beijing, 1996).
35. Romer, A. S. The vertebrate as a dual animal–somatic and visceral. *Evol. Biol.* **6**, 121–156 (1972).
36. Romer, A. S. *The Vertebrate Body* (Saunders, Philadelphia, 1964).
37. Walcott, C. D. Middle Cambrian annelids. *Smithson. Misc. Coll.* **57**, 109–144 (1911).
38. Taguchi, S. *et al.* Characterization of a hemichordate fork head/*HNF-3* gene expression. *Dev. Genes Evol.* **210**, 11–17 (2000).
39. Tagawa, K., Humphreys, T. & Satoh, N. Novel pattern of *Brachyury* gene expression in hemichordate embryos. *Mech. Dev.* **75**, 139–143 (1998).
40. Lacalli, T. C. Apical organs, epithelial domains, and the origin of the chordate central nervous system. *Am. Zool.* **34**, 533–541 (1994).
41. Tagawa, K., Humphreys, T. & Satoh, N. *T-Brain* expression in the apical organ of hemichordate tornaria larvae suggests its evolutionary link to the vertebrate forebrain. *J. Exp. Zool. (Mol. Dev. Evol)* **288**, 23–31 (2000).
42. Nielsen, C. Origin of the chordate central nervous system and the origin of chordates. *Dev. Genes Evol.* **209**, 198–205 (1999).
43. Gee, H. *Before the Backbone: Views on the Origin of the Vertebrates* (Chapman & Hall, London, 1996).
44. Shu, D.-G. *et al.* Lower Cambrian vertebrates from South China. *Nature* **402**, 42–46 (1999).

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