

Ancestral echinoderms from the Chengjiang deposits of China

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Deuterostomes are a remarkably diverse super-phylum, including not only the chordates (to which we belong) but groups as disparate as the echinoderms and the hemichordates. The phylogeny of deuterostomes is now achieving some degree of stability, especially on account of new molecular data, but this leaves as conjectural the appearance of extinct intermediate forms that would throw light on the sequence of evolutionary events leading to the extant groups. Such data can be supplied from the fossil record, notably those deposits with exceptional soft-part preservation. Excavations near Kunming in southwestern China have revealed a variety of remarkable early deuterostomes, including the vetulicolians and yunnanozoans. Here we describe a new group, the vetulocystids. They appear to have similarities not only to the vetulicolians but also to the homalozoans, a bizarre group of primitive echinoderms whose phylogenetic position has been highly controversial.

One of the principal unsolved questions in metazoan phylogeny concerns the origin and earliest evolution of the echinoderms. Molecular data indicate echinoderms to be the sister group of hemichordates^{1,2}, but the two phyla are so disparate that attempts to envisage a common ancestor are highly conjectural. In large part this is because the echinoderm body plan has undergone radical reorganization. This includes a pervasive pentamery³, a unique water vascular system and calcitic stereom (mesodermal skeleton), loss of pharyngeal gill slits⁴, and major redeployment of developmental genes⁵. Whereas the Cambrian record of echinoderms is otherwise fairly extensive, many of the early forms have a bizarre appearance^{6–8}, and are the subject of continuing phylogenetic controversy. In part this is because of unresolved differences of opinion^{4,6,9} concerning possible similarities (for example, gill slits¹⁰) to other deuterostomes.

The Chengjiang fossil Lagerstätte^{11,12} has yielded important information on several key steps in early deuterostome evolution. These include stem-group forms, notably vetulicolians^{13–15} and yunnanozoans^{16,17}, as well as more familiar groups such as tunicates^{18,19} and vertebrates^{20,21}. The record of echinoderms is, however, much less satisfactory. A possible crinoid²² is more likely to be a lophophorate¹², whereas a supposed eocrinoid¹¹ has little similarity to other members of this group and may be arthropodan. The exclusion of stenohaline organisms, including echinoderms²³, in the Chengjiang biota is consistent with evidence for decreased seawater salinity. Here, however, we describe a new group, the vetulocystids, which we interpret as members of the Ambulacraria^{24,25}, specifically belonging to the stem group which also includes primitive echinoderms known as the homalozoans⁷. Two new taxa (*Vetulocystis catenata* gen. et sp. nov. and *Dianchicystis jianshanensis* gen. et sp. nov.) are recognized. Other material (all from the Haikou locality) is assigned to forms A and B (Fig. 3) on account of apparent differences in anatomy, but the relatively poor preservation makes it premature to use a formal taxonomy.

Total group Ambulacraria
Stem group Vetulocystida
Family Vetulocystidae fam. nov.
Vetulocystis catenata gen. et sp. nov.

Etymology. *vetus* (Latin) meaning old; the generic name is also based on its bag-like shape; *catena* (Latin) meaning chain; the specific name is a pun on missing link.

Holotype. Early Life Institute, Northwest University, Xi'an (ELI-Ech-04-001).

Referred material. ELI-Ech-04-002.

Locality. Shankou section, near Anning, about 30 km west of Kunming.

Horizon. Qiongzhusi (Chiungchussu) Formation, Yu'an-shan Member (*Eoredlichia* zone), Lower Cambrian.

Diagnosis. Bipartite body, globose theca and tail. Latter apparently with two segments, expanding posteriorly, with central strand, possibly intestine with terminal anus. Theca with three principal openings. Mouth, right, antero-dorsal, pyramidal with approximately 55 articulating platelets. Postero-dorsal opening, left, pyramidal with numerous ribs. Respiratory organ, right postero-dorsal, with folds.

Dianchicystis jianshanensis gen. et sp. nov.

Etymology. The generic name refers to Dianchi lake, near to the locality. The specific name is after Jianshan, the locality where the specimens are collected.

Holotype. Early Life Institute, Northwest University, Xi'an (ELI-Ech-04-003).

Referred material. ELI-Ech-04-004–006.

Locality. Specimens were collected from Jianshan, near Haikou, about 40 km south of Kunming.

Horizon. As for *V. catenata*.

Diagnosis. Similar to *V. catenata*, but tail tapering, with oblique striations. Anterior cone with ribs, but not arranged in platelets. Tail traversed by weakly developed furrows, possibly segmental.

All material was collected from the Lower Cambrian Qiongzhusi Formation, exposed in a wide area around Kunming, Yunnan. The best preserved material is assigned to *Vetulocystis* gen. nov. and *Dianchicystis* gen. nov., that differ most obviously with respect to the tail-like structure. The two specimens of *V. catenata* (Fig. 1) were collected from the Shankou section, near to Anning, whereas *Dianchicystis* (Fig. 2) is represented by four specimens from the Jianshan locality, near Haikou. All the specimens (including forms A and B) show typical Chengjiang preservation, and may owe their preservation to burial during storm events²³. Typically, specimens are isolated, but one enigmatic association (not illustrated) may represent the aggregation of two or more decayed individuals.

The anatomy of vetulocystids

Vetulocystids possess a common body plan that consists of an inflated theca and a shorter tail-like structure, the latter assumed to be posterior (Figs 1–3). Apart from the antero-posterior axis the remaining body orientations are more speculative because of the lack of unequivocal axial markers and the risk of circular reasoning in drawing comparisons to other groups. Tentatively, the surface carrying the two cones and respiratory organ is regarded as dorsal. Typically the theca is longer than it is wide, and whereas there is some taxonomic consistency in thecal shape the more globose examples may also reflect original flexibility and an ability to change shape. With the exception of form A (Fig. 3a, c) the integument is always strongly wrinkled (Figs 1a, d, f, g, 2a–h and 3d, g), but the absence of brittle failure argues against mineralization. In addition, despite the large-scale reticulation, the outlines of the wrinkles are irregular, of variable strength and overall have very variable and

inconsistent angular relationships. None of these features appears to be consistent with the theca being composed of calcareous plates separated by sutures. Apart from the two cones and the respiratory organ, the outer surface of the theca is smooth and shows no other evidence for mineralization. Mouldic impressions of the inner side in *Vetulocystis*, however, reveal a more irregular texture (Fig. 1f, g). In a number of specimens amorphous black/grey material can be seen within the thecal cavity, and probably represents otherwise indeterminate soft-parts.

The theca bears two prominent truncated cones, each with well developed radial ribs that converge on a central opening (Figs 1a, c, d, f, g, 2a–i, l and 3a, c–g). In *D. jianshanensis* the more anterior cone (Fig. 2a–d) consists of a series of plate-like structures (evidently unmineralized), each bearing a central rib and on either side one or two other ribs, so that in total the cone bore about 55 ribs. The plate-like structures appear to be attached to a common basal membrane

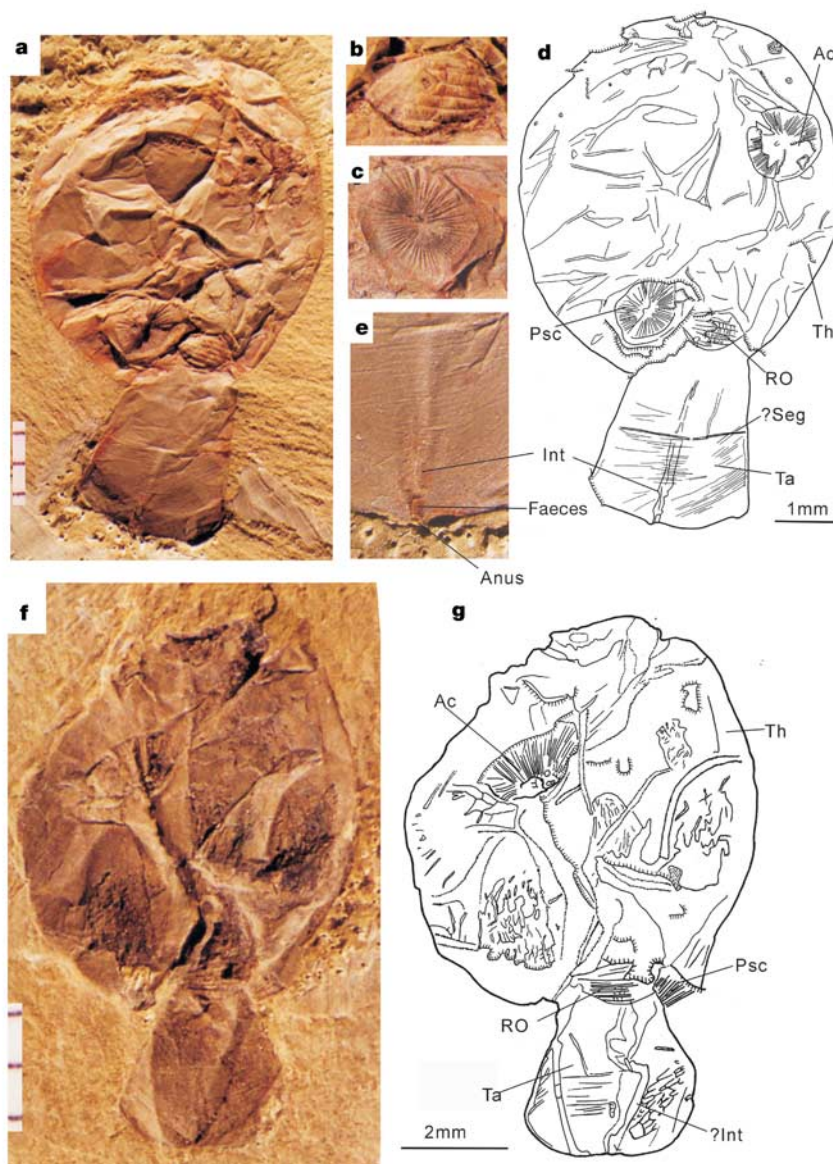


Figure 1 Two specimens of *Vetulocystis catenata* from Anning, Kunming, Yunnan. **a–e**, ELI-Ech-04-001A; **a**, entire specimen, note anterior cone is partially obscured by thecal surface; **b**, detail of respiratory organ, note cuticle missing from left-hand side; **c**, detail of the posterior cone; **d**, interpretative drawing; **e**, detail of posterior strand and sediment infill (?faeces) adjacent to ?anus. **f, g**, ELI-Ech-04-002; **f**, entire specimen,

apparently interior view of theca; **g**, interpretative drawing. Scale bars where shown on photographs are millimetric. Abbreviations: Ac, anterior cone; RO, respiratory organ; Psc, posterior cone; ?Seg, ?segment boundary; Int, possible intestine (strand); Ta, tail; Th, theca. Question marks indicate that identification of body part is tentative.

and presumably also articulated by means of connecting membranes. Towards the distal opening of the cone, finer ribs are interpolated and they presumably conferred a flexibility to assist with closure. In *V. catenata* the ribs of the anterior cone (Fig. 1a, f) appear to be individually linked to the common membrane rather than attached to plates. The anterior cone in the two named vetulocystid genera shows one apparently important difference. In *D. jianshanensis* the anterior cone is separated from the thecal surface by a basal constriction (Fig. 2a–d), whereas in *V. catenata* the equivalent structure was evidently recessed and partially obscured by the thecal surface (Fig. 1a, d). This difference may be original, but it is possible that the anterior cone was surrounded by a zone of more flexible cuticle that allowed it to be retracted into the theca. In form B (Fig. 3d, g) the anterior cone is relatively indistinct, but otherwise apparently similar to *Vetulocystis*. Adjacent to it, however, there is a striated structure. Although this may represent part of the mouth, it may alternatively be a separate organ. The equivalent cone of form B (Fig. 3a, c, e, f) differs from the other vetulocystids in being located more posteriorly.

The posterior cone in *Vetulocystis* and *Dianchicystis* is located close to the theca–tail junction (Figs 1a, c, d and 2a–h, j). It is uniformly ribbed, and presumably was moderately flexible in life. In the holotype of *D. jianshanensis* (Fig. 2a, b) this cone has a lenticular outline, but so far as can be judged in other specimens of this species and *V. catenata* it was more circular in outline. In forms A and B (Fig. 3a, c, d–g) the posterior cone is located towards the centre of the theca, and in the latter taxon is apparently composed of more massive plates (Fig. 3d, g).

The presumed respiratory organ is situated immediately adjacent to the theca–tail junction (except in form A (Fig. 3a, b, e) where it is considerably more anterior), and is transversely lenticulate (except in form B (Fig. 3d, g) where it appears to be more triangular in outline). Generally, details are difficult to discern, but in the holotype of *V. catenata* the structure is exceptionally clear (Fig. 1a, b, d). The surface appears to be cuticular and consists of a series of prominent ridges, separated by narrow grooves. In addition, each ridge has a series of transverse wrinkles. The internal structure of the respiratory organ is rather speculative. In the other specimen (Fig. 1f, g), however, the equivalent area shows a series of

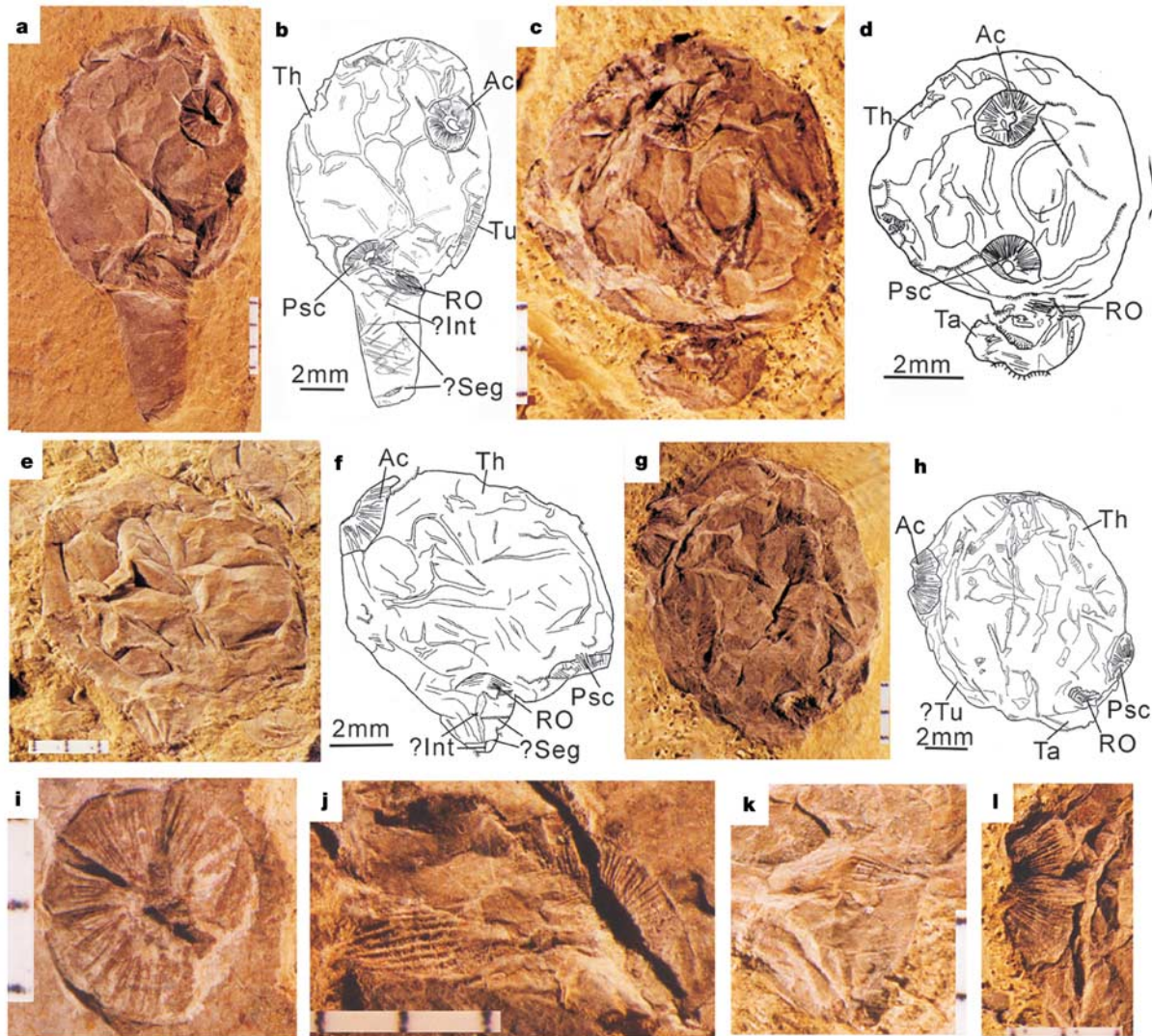


Figure 2 Four specimens of *D. jianshanensis* from Haikou, Kunming, Yunnan. **a, b, i, j**, ELI-Ech-04-003A; **a**, entire specimen; **b**, interpretative drawing; **i**, detail of anterior cone; **j**, detail of respiratory organ and posterior cone in counterpart. **c, d**, ELI-Ech-04-004A; **c**, entire specimen; **d**, interpretative drawing. **e, f, k, l**, ELI-Ech-04-

005; **e**, entire specimen; **f**, interpretative drawing; **k**, detail of respiratory organ and tail with possible strand. **g, h, i, l**, ELI-Ech-04-006; **g**, entire specimen; **h**, interpretative drawing; **l**, detail of anterior cone. Scale bars where shown on photographs are millimetric. Abbreviations: as in Fig. 1 with the addition of ?Tu, possible tube.

folded structures within a cavity. This suggests that internally the respiratory organ may have had a lamellate organization. Analysis of the functional morphology of the gill depends on various inferences and so is open to conflicting interpretations as to the possible direction of water flow. The holotype of *D. jianshanensis* (Fig. 2a, b) has a tube-like extension that extends towards, and possibly connects with, the posterior opening. In other specimens of this species (Fig. 2c–h), however, the respiratory organ and posterior opening are separated (as is even more evident in forms A and B (Fig. 3)). In *V. catenata* the respiratory organ and posterior opening are juxtaposed (Fig. 1a, d, f, g), and in this species a direct connection is conceivable.

In *V. catenata* the tail-like structure has a modest posterior expansion (Fig. 1a, d, f, g), and in the holotype has a transverse lineation. This could represent a segmental demarcation. Finer transverse striations are interpreted as cuticular folding. In the other specimen (Fig. 1f, g) a tripartite-like structure may reflect post-mortem folding, although a subdued lenticular ornamentation may be original. In the holotype a median strand extends to the posterior margin (Fig. 1a, d). It has a complex structure, but is three-dimensional and in one section appears to contain sediment (Fig. 1e). It could, therefore, represent the intestine, with gut contents, leading to a terminal anus. In the other specimen (Fig. 1f, g) the possible course of the intestine is more tentative. Identifying the strand as an intestine makes more problematic the function of the posterior cone. The tail-like structure in *D. jianshanensis* shows some important differences. This is most evident in the holotype which shows a slight taper with a blunt termination, and also two sets of oblique striations (Fig. 2a, b). In another specimen of *D. jianshanensis* the tail shows a transverse division (Fig. 2e, f), which may be segmental. The prominent

longitudinal structure is more likely to represent post-mortem folding than an intestine (Fig. 2e, f, k).

Functional biology of vetulocystids

Functional interpretations are critical in assessing both the palaeoecology and phylogenetic position of the vetulocystids. The two cones are similar (Fig. 1a, c, d, f, g and 2c, d, i, l), and identification of their respective functions is not straightforward. The anterior cone, however, is interpreted as the mouth. The closest similarity of this structure appears to lie with a number of extinct echinoderms. Thus, the putative mouth of some stylophorans^{26–28} is also pyramidal, whereas in some pentremitid blastoids the mouth is covered by a series of summit plates²⁹. An alternative location for the mouth is at the anterior end of the theca. Whereas some specimens (Fig. 2g, h) show recesses in this area, they are irregular and inconsistently preserved. The primary function of the posterior opening was presumably as the anus, possibly combined with other functions (for example, as a gonopore). It is similar to the pyramidal plated anus of many echinoderms, including the solutans^{30,31}, ctenocystoids³², cystoids³³ and some eocrinoids³⁴. The case for the lenticular structure being a respiratory organ seems to be strong. The direction of water flow and the exact site of respiratory exchange, however, are more conjectural. Here it is hypothesized that water initially entered the animal through the mouth and exited through either the respiratory organ itself or the posterior opening. Gas exchange may have been through sheets of tissue suspended in an internal cavity. Because of these uncertainties comparisons with other respiratory structures are not straightforward. There are, however, some similarities to various echinoderm respiratory structures, although these comparisons need not have specific phylogenetic implications. Moreover, the exactness of comparison depends on

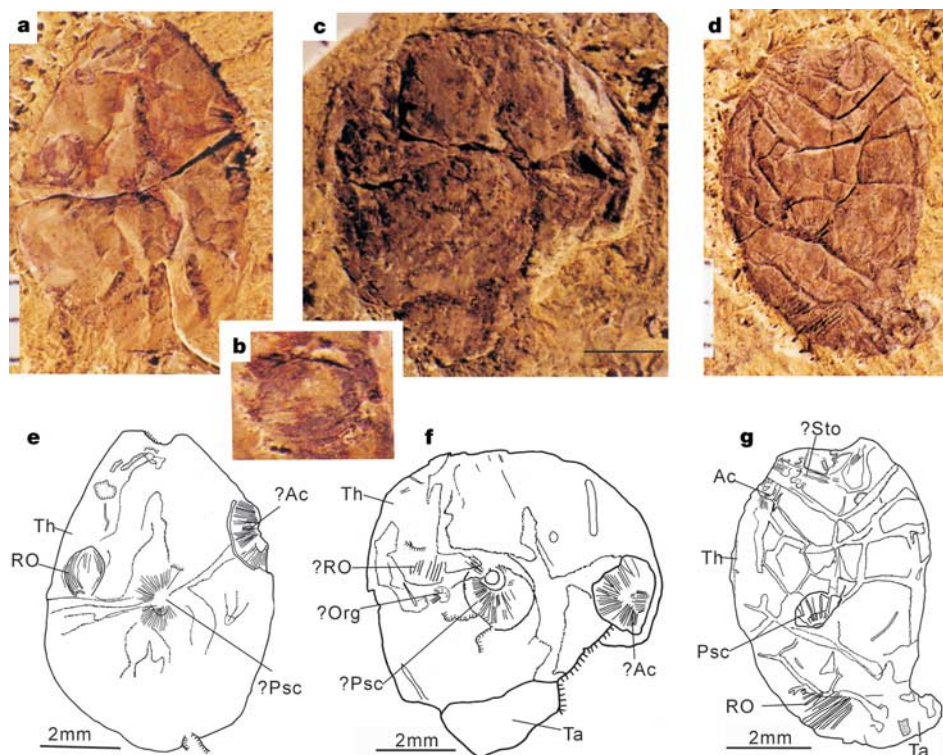


Figure 3 Form A (a–c, e, f) and form B (d, g), both from Haikou, Kunming, Yunnan. a, b, e, ELI-Ech-04-007; a, entire specimen, composite photograph of part (anterior section) and counterpart; b, detail of respiratory organ; e, interpretative drawing, composite of both part and counterpart. c, f, ELI-Ech-04-008; c, entire specimen; f, interpretative drawing. d, g, ELI-Ech-04-009A; d, entire specimen; g, interpretative drawing. Scale bars where shown on photographs are millimetric. Abbreviations: as in Fig. 1 with the additions, ?Org, unknown organ; ?Sto, striated organ.

f, interpretative drawing. d, g, ELI-Ech-04-009A; d, entire specimen; g, interpretative drawing. Scale bars where shown on photographs are millimetric. Abbreviations: as in Fig. 1 with the additions, ?Org, unknown organ; ?Sto, striated organ.

the functional arrangement of the vetulocystid respiratory organ. Thus if water exited through the organ itself, there is a similarity to the lamellar gills (lamellipores) of some cornute stylophorans^{26,27}, although in this context it is important also to note that the gill slits of the stylophorans show a wide variability of form^{26,27}. Alternatively, if gas exchange was across the outer surface of the gill with no direct access to the interior body cavity, there is an analogy to the pore rhombs of cystoids^{33,35}.

Vetulocystids were presumably semi-sessile, but a slow locomotion, possibly by sideways movement of the tail, is conceivable. Much of the time, however, they may have been stationary, possibly with the tail embedded in the sediment to provide anchorage and the theca either upright or more probably semi-prostrate with the thecal openings located on the upper surface. On the basis of the identification of the three thecal openings, it is hypothesized that suspended food particles (and possibly sea water) entered the mouth, perhaps by muscular pumping. The oral chamber may have been large and if so could have ended adjacent to the posteriorly located respiratory organ. In some specimens of *D. jianshanensis* a darker area, sometimes with faint segmentation, runs along the margin of the theca (Fig. 2a, b, g, h). It may represent a specialized organ, possibly within the anterior gut. The intestine may have looped anteriorly before exiting through the posterior cone.

The evolutionary link to echinoderms

A number of groups have adopted a body plan similar to the vetulocystids. Comparison, for example, could be made to the tunicates. Whereas this group is generally placed close to the cephalochordates and craniates, some molecular data² indicate an instability in phylogenetic placement such that a more primitive position in the deuterostomes remains conceivable. In this model, the two cones would be equivalent to the atrial and branchial siphons of tunicates. The similarity between the vetulocystid

cones and tunicate siphons is, however, only approximate, although in the extant *Chelyosoma* the siphons consist of two plated cones³⁶. A comparison could also be made with respect to the vetulocystid respiratory organ and tunicate branchial basket. The latter, however, occupies a much larger proportion of the body space, and as far as can be discerned the vetulocystid respiratory organ does not have similar microstructure. Precise comparisons between vetulocystids and tunicates, therefore, are not straightforward. In addition, tunicates from Chengjiang^{18,19} have no notable similarity to the vetulocystids.

Vetulocystids, however, have some intriguing similarities to two groups with a bipartite body plan. The first are the vetulicolians, interpreted as stem-group deuterostomes^{13,14} (see also ref. 15) possessing segmentation and gill slits. The second is an assemblage of early Palaeozoic echinoderms known as the homalozoans, which comprise the cinctans, ctenocystoids, solutes and stylophorans⁷. Similarities of the vetulocystids to the vetulicolians^{13,14} are generalized, but include a body defined by a large anterior section with a presumed pharyngeal opening and a posterior tail (Fig. 1a, d). More specific comparisons with the vetulicolians may include segmentation of the tail (Fig. 1a, d), and tentatively the identification of the strand as the intestine (Fig. 1e). The body plan of vetulocystids also has anatomical parallels to the homalozoans. Interpretations of these bizarre echinoderms are very contentious, both in terms of possible polyphyly and particularly in identification of key features that critically depend on whether the model adopted looks to echinoderm^{6,37} or chordate^{4,9,27} characteristics. Although morphologically disparate, the homalozoans arguably represent a series of key stages in early echinoderm evolution⁸, notably the retention of a bipartite body and, in cinctans and solutes,³⁸ the acquisition of a feeding arm or ambulacrum (and water vascular system linked to the possibly more primitive hydropore). In addition, there is a corresponding reduction and ultimate loss of the pharyngeal gill

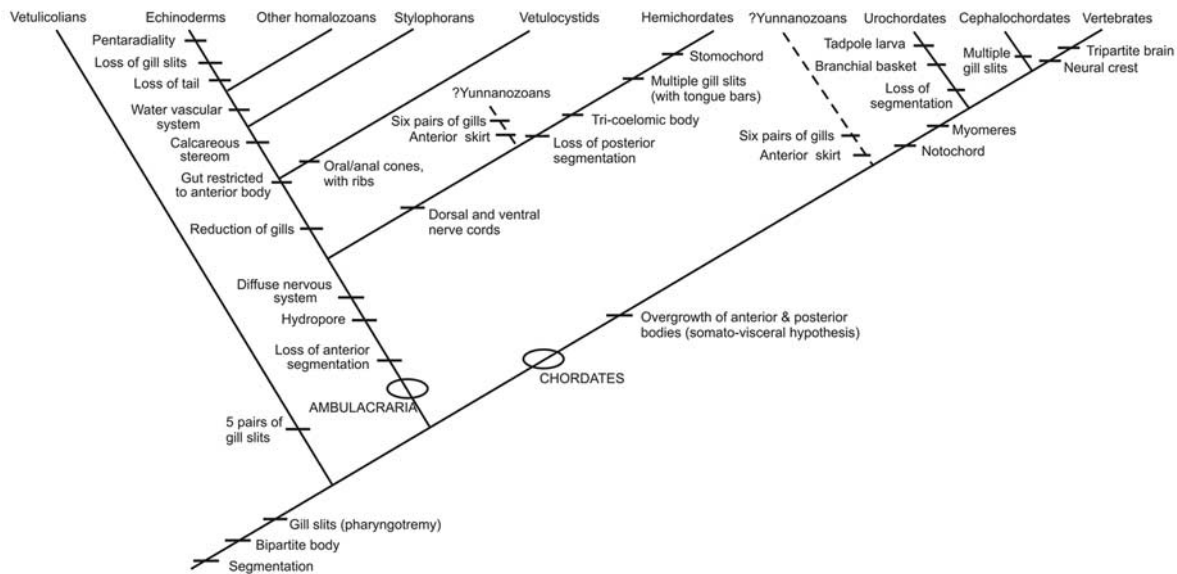


Figure 4 Phylogeny of early deuterostomes. Plesiomorphic to all deuterostomes are segmentation^{25,43} and a bipartite body, the anterior of which possesses gill slits^{24,25,44}. The posterior is a tail-like structure, segmented with an intestine and terminal anus^{13,14}. Vetulicolians^{13,14} may be the most primitive known deuterostomes, showing segmentation of the entire body, and an anterior with five pairs of gill slits. Extant members of the Ambulacraria^{24,25} are the echinoderms and hemichordates. Vetulocystids are regarded as more derived than the hemichordates, but retain the bipartite body and a respiratory organ that also characterize the most primitive echinoderms (homalozoans⁹). In more primitive Ambulacraria the gut extended along the posterior tail, but either just before or after the

bifurcation leading to the vetulocystids the gut became restricted to the anterior body. Here we depict the former possibility. All echinoderms, including homalozoans, possess a stereom, but the most primitive representatives retain gill slits. The acquisition of a water-vascular system and ambulacra was a subsequent development. The position of the extinct yunnanozoans remains controversial. Here we indicate two alternatives, either closer to the chordates¹⁷ or the hemichordates^{16,21,41,45}. In support of the latter hypothesis is the lack of evidence for key craniate features, including eyes, a complex brain, a notochord and myomeres, but the possible presence of both dorsal and ventral nerve cords.

slits. Whereas the shared possession of a bipartite body plan might be the result of evolutionary convergence, the vetulocystids possess a series of thecal openings that appear to correspond to those seen in the homalozoans. Detailed comparisons are certainly not straightforward because their relative positioning in the homalozoan groups^{8,26,38,39} is variable (as may also be the case in the vetulocystids, especially in forms A and B) presumably reflecting the widely varying thecal morphologies and inferred rearrangements of the pharyngeal cavity and coeloms. Analysis is further complicated because in only some homalozoans is there evidence for an ambulacrum. The morphology of the homalozoan tail is also variable, and presumably is connected to functional requirements that evidently shifted from being primarily locomotory^{27,31} to one of sessile attachment⁴⁰. Nevertheless, the arrangement in the vetulocystids in dorsal aspect and a clockwise direction—of mouth, respiratory organ (possibly serving as a pharyngeal opening) and anus—is similar to the arrangement in homalozoans.

A provisional phylogeny is given in Fig. 4. It is necessarily tentative because (a) the functional interpretation of vetulocystids is based on various assumptions, discussed above, (b) the position of the yunnanozoans is controversial with proposals encompassing relationships closer to the hemichordates⁴¹, pre-chordates¹⁶ and craniates¹⁷, (c) the position of the homalozoans within the echinoderms³⁷, and their inter-relationships, remain very contentious^{7,8}, and (d) the various groups ('phyla') of deuterostome are anatomically very disparate and many of the key intermediate stages are still conjectural. The scheme illustrated here, however, is rooted in the two major suppositions; the concept of the Ambulacraria^{24,25} (that is, echinoderms and hemichordates as a sister group¹) and the vetulicolians as stem-group deuterostomes^{13,14}.

In this phylogeny the vetulocystids mark a key stage in the early evolution of the Ambulacraria, specifically marking the transformation from an active vetulicolian-like organism to a semi-sessile bipartite animal which pre-figures the homalozoan echinoderms. With respect to the vetulicolians, important changes include the reduction of the respiratory organ (assumed to be equivalent to the pharyngeal opening of other deuterostomes) to a single structure adjacent to the tail, and restriction of the gut to the theca with concomitant development of oral and anal cones. On the assumption that the vetulocystids provide a key link between the vetulicolians and the homalozoans, two questions depend on presently equivocal evidence. The first revolves around the interpretation of the posterior strand as a possible intestine (Fig. 1e). If correct, this suggests that the restriction of the alimentary canal to the anterior theca took place either in vetulocystids more advanced than *V. catenata* or in the earliest homalozoans (Fig. 4). The second question concerns the evidence for posterior segmentation in some vetulocystids, and the obvious differences to the complex and variable tail structures seen in cinctans⁸, solutes^{31,39} and stylophorans^{26,27}.

In the Ambulacraria the hydropore of echinoderms is assumed to be homologous with the protocoele pore of hemichordates⁴. An equivalent structure would be difficult to recognize in the vetulocystids unless the enigmatic structures (the unknown organ and the striated organ), only seen in forms A (Fig. 3c, f) and B (Fig. 3d, g), are identified. There is, however, no evidence for a water vascular system in the vetulocystids. We suggest that it was this innovation (and the associated ambulacra), together with the evolution of a calcitic stereom skeleton, that marks the appearance of true echinoderms. It will be apparent that the discovery of the vetulocystids is further support for the 'calcichordates'²⁷ being interpreted as echinoderms^{6,42}, and not being material to the origins of the tunicates, cephalochordates and vertebrates. In contrast, however, to hypotheses that regard these curious animals as highly derived echinoderms^{6,37} it seems that they occupy a basal position⁸. □

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