

RAPID COMMUNICATION

A NEW METAZOAN FROM THE MIDDLE CAMBRIAN OF UTAH AND THE NATURE OF THE VETULICOLIA

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Abstract: A new metazoan, *Skeemella clavula* gen. et sp. nov., is described from the Middle Cambrian Pierson Cove Formation of the Drum Mountains, Utah, USA. *Skeemella* is similar to vetulicolians, but differs from other examples of this group in the relative proportions of the anterior and posterior sections, the large number of divisions, and the elongate bifid termination. The posterior section is

arthropodan in character. The similarity of this fossil to vetulicolians throws hypotheses of their deuterostome affinity into question and highlights their problematic status.

Key words: vetulicolian, Cambrian, deuterostome, arthropod.

THE very name vetulicolian conjures up creatures from another planet. These extraordinary fossils, with a head shield-like anterior and narrow segmented trunk-like posterior, are the latest Cambrian group to be accorded phylum status (Shu *et al.* 2001). As Bengtson (1986, p. 3) pointed out, such status formalizes the definition of a fossil taxon as problematic: one 'that cannot be recognized as belonging to a known phylum'. Although phyla are characterized by morphological distance from other phyla, the real issue is establishing the place of the taxon within a scheme of relationships (Budd and Jensen 2000; Briggs and Fortey 2005). Problematic status is often a reflection of incomplete preservation (Conway Morris 1991), and data from newly discovered fossil species may augment the range of character states known to be present in a higher taxon. Taxa may fall within a stem because the characters that define the crown group are not preserved (Hennig 1981). In this context, the discovery of a new genus and species strikingly similar to vetulicolians, an extinct phylum that was established on the basis of just five genera (Shu *et al.* 2001), is significant.

In 1987 *Vetulicola cuneata*, from the Lower Cambrian Qiongzhusi Formation, Chengjiang, China, was described (as *V. cuneatus*) as a large bivalved arthropod (Hou 1987) on the basis of four head shields, just one of which showed two trunk segments. Chen and Zhou (1997) studied some 300 specimens of *V. cuneata*, including examples with the trunk, and used it, together with their new

species *Banffia confusa*, to erect a new class of stem-group arthropods, the Vetulicolida. They argued that *Banffia constricta* from the Burgess Shale belongs to the same class, extending its range to North America. Shu *et al.* (2001) included these taxa in their new phylum Vetulicolia along with *Didazon*, *Xidazon* and *Pomatrum* (Luo *et al.* 1999). (The Vetulicolia do not qualify as a phylum in the scheme of Budd and Jensen 2000 because they do not include members of a crown group; but see Briggs and Fortey 2005.) Based on their analysis of these taxa Shu *et al.* (2001, 2003) regarded vetulicolians as primitive deuterostomes, a view reiterated in their phylogeny of deuterostomes (Shu *et al.* 2004). This conclusion partly rested on their interpretation of the perforations in the anterior body region as gill slits. The similarity of the vetulicolian body plan to a tunicate tadpole larva suggested to Gee (2001), however, that these animals could be the sister group of chordates. Lacalli (2002) and R.P.S. Jefferies (pers. comm. 2003) considered the possibility that vetulicolians are stem tunicates. In contrast, the presence of a cuticle and possible mid-gut diverticulae (Butterfield 2003), as well as telescoping posterior segments (Mallatt *et al.* 2003), prompted others to argue that the original assignment of vetulicolians to the arthropods may be correct. Caron (2001, in press) redescribed *Banffia constricta* from the Middle Cambrian Burgess Shale, and assigned it to a new class of vetulicolians, expressing doubt about the deuterostome affinities of the group.

As Hou *et al.* (2004, p. 188) remarked 'there is currently no agreement about the systematic position of the group'.

The new metazoan, tentatively referred to *Vetulicolia*, was discovered in the Middle Cambrian Pierson Cove Formation of the Drum Mountains, Utah, USA. The Drum Mountain Lagerstätte is one of a number of Burgess Shale-type biotas from Utah that have yielded important data on Cambrian diversity (Gunther and Gunther 1981; Briggs and Robison 1984; Conway Morris and Robison 1986, 1988; Robison 1991). Few other taxa, however, are unique to this Lagerstätte, apart from the supposed uniramous arthropod *Cambropodus gracilis* (Robison 1990). The fossil occurs in a platy calcareous shale within a sequence that is interpreted as representing a protected, low-energy, subtidal environment (Rees 1986; Robison 1991).

SYSTEMATIC PALAEOLOGY

Phylum? VETULICOLIA Shu *et al.*, 2001
Class? VETULICOLIDA Chen and Zhou, 1997

Genus SKEEMELLA gen. nov.

Derivation of name. In recognition of Holly and Ken Skeem, Oasis, Utah, USA, who collected the anterior part of the fossil. The posterior counterpart was collected subsequently by SLH and RDJ.

Type and only known species. *Skeemella clavula*.

Diagnosis. Bipartite, cuticularized body. Short wide head shield-like anterior region divided longitudinally, with straight dorsal margin, curving ventral margin, and made up of nine segments separated by thinner membranes. Narrow vermiform posterior region of 43 segments, tergites separated by flexible membranes, terminating in an elongate unsegmented flattened structure that projected posteriorly into two spines.

Skeemella clavula sp. nov.
Text-figure 1

Derivation of name. Latin *clavula*, small club, referring to the outline of the specimen, which resembles a club with handle.

Holotype and only specimen. KUMIP 310501 and UU 04083.01 partial part and partial counterpart of a complete specimen.

Type locality and horizon. Drum Mountains, about 30 km north-east of Wheeler Amphitheater, Utah, 39°30'2"N, 112°59'39"W; lowermost Pierson Cove Formation, mid *Ptychagnostus atavus* Zone *sensu* Peng and Robison (2000), Middle Cam-

brian (for geological descriptions of this unit in the Drum Mountains, see Robison 1964, 1991; Hintze and Robison 1975; Gunther and Gunther 1981; Rees 1986; Schneider 2000; Langenburg 2003). The specimen is in close stratigraphic association with the trilobites *Asaphiscus wheeleri* Meek, *Brachyaspidion sulcatum* Robison and *Olenoides nevadensis* (Meek), the bivalved arthropod *Canadaspis* cf. *perfecta* (Walcott), the priapulids *Selkirkia willoughbyi* Conway Morris and Robison, 1986 and *Selkirkia* sp. of Conway Morris and Robison, 1986, an unidentified lingulid brachiopod, and the alga *Margaretia doris* Walcott (R. Robison, pers. comm. 2004).

Diagnosis. As for genus.

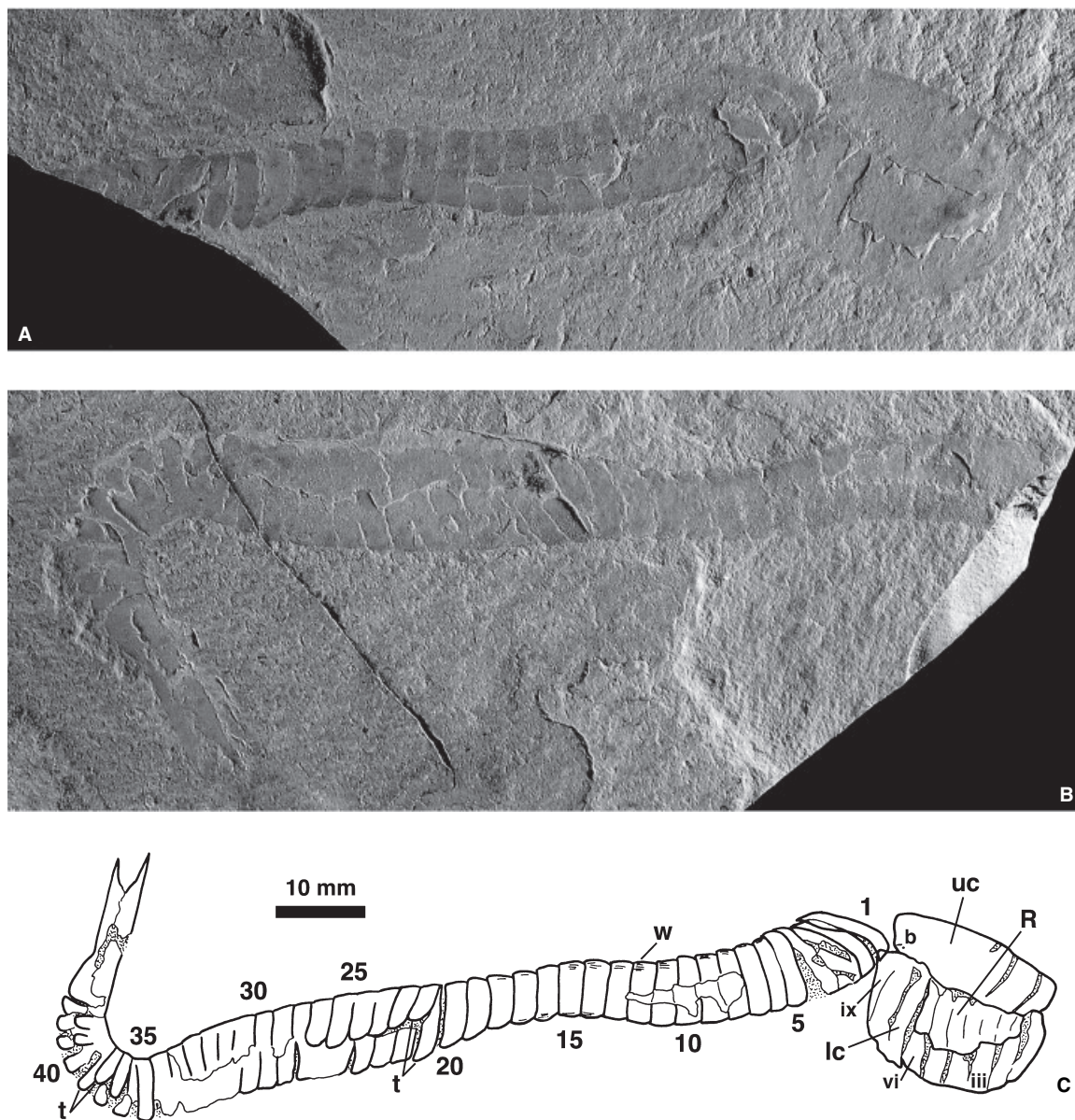
Description

It is clearly impossible to determine orientation to bedding based on a single specimen. However, the lack of preserved bilateral symmetry, together with a comparison with specimens of *Vetulicola cuneata*, suggests that the specimen is preserved in lateral (rather than dorsoventral) aspect. The skeleton does not appear to have been mineralized in life and probably consisted of a toughened organic cuticle, of which only an impression is preserved. The surface is stained red to purple, presumably by iron oxides. A few fragments of linguliform brachiopod shells on the anterior part of the body were superimposed fortuitously; they also occur scattered elsewhere on the bedding plane surface. The skeleton was infilled with sediment prior to flattening. The more labile soft tissues are not preserved.

The body is divided into two distinct regions, a short expanded anterior section, and a long posterior section with a bifid termination. The anterior section of the body (Text-fig. 1A) is subrectangular in outline, 20 per cent longer than wide, 2.2 cm long (maximum) with a gently convex dorsal margin and a more strongly convex ventral margin. The remainder of the body (Text-fig. 1A–C), which is segmented and essentially vermiform, is 12 cm long, giving a total length of the animal of more than 14 cm.

Anterior section. The anterior section of the body (Text-fig. 1A, C) is assumed to be a flattened tube-like structure. The evidence does not reveal whether the divisions of the skeleton are open ventrally and/or dorsally (like a head shield), or whether they form a series of rings. The specimen is divided longitudinally into an upper and lower component by a break in the cuticle that lies just dorsal of the midline. The detailed configuration of this break cannot be determined in the absence of this portion of the counterpart. The break appears to extend to the posterior margin where the cuticle immediately ventral to it forms a small triangular projection.

Most of the left side of the anterior section of the body is preserved on the part, whereas most of the right side remains on the missing piece of the counterpart. The ventral portion preserves evidence of nine divisions. They are separated by lines of sediment that extend to varying degrees to the ventral margin. This variation is probably taphonomic; the lines may represent areas of more flexible membrane that have decayed. The divi-



TEXT-FIG. 1. A–C, *Skeemella clavula* gen. et sp. nov. A, KUMIP 310501, part, lateral view of anterior section and portion of posterior section; $\times 1.5$. B, UU 04083.01, counterpart, lateral view of posterior section; $\times 1.5$. C, camera lucida drawing of part and counterpart combined. Roman numerals refer to divisions evident in the lower component of the anterior section, arabic numbers to segments in the posterior section. Abbreviations: uc, lc, upper and lower component of anterior section; R, cuticle of the right side of the anterior section; b, fragments of brachiopod shells; w, wrinkles reflecting compaction of the cuticle; t, terminations of the tergites in individual segments of the posterior section.

sions in the dorsal portion are more difficult to discern. The area of the right side preserved on the part also shows faint divisions, but these are not emphasized by sediment. There appear to be seven, which are shorter in length than those on the left side, perhaps because the flexible membrane that separated the divisions was not extended.

Posterior section. The posterior section (Text-fig. 1A–C) consists of 43 divisions. The first division just overlaps the dorsal half of

the anterior section, and may have been attached there. The first four divisions have been displaced relative to those behind and the nature of their original contact with the anterior section of the body is not preserved. The more anterior divisions are just over 10 mm wide (i.e. normal to the longitudinal axis of the posterior section), narrowing to about 7 mm at division 17 and then widening again as far as about division 25 before tapering beyond. They also become shorter toward the posterior end. The preserved width of the divisions varies from 2.7 to 3.5 times that

of the length. Where both surfaces are preserved they are separated by an infilling of sediment. The divisions immediately following division 20 and further posteriorly, where curvature of the body is at a maximum, preserve the cuticle on both sides, each of which shows a separate rounded termination. Thus it is clear that the cuticle does not form rings but was open ventrally; this is presumed to have been the case throughout the posterior section. Where the terminations are offset, depending on attitude to bedding, the preserved width of the posterior section is increased (like folding a strip of paper off the mid-length); where they are more nearly superimposed it is narrower. The difference in attitude to bedding may reflect twisting of the trunk, either in life or post-mortem; the variation in width reflects folding of a single tergite rather than two separate plates. The wrinkles that are evident along the lateral margins of the divisions reflect the compaction of a vertical component of the cuticle in that position. The posterior section of the body was capable of flexure; it bends through nearly 120 degrees toward its posterior extremity. The greater separation between the tergites on the convex rather than the concave side of the body reflects stretching of the flexible membrane that connected them. No trace of a gut is preserved.

The posterior section of the body terminates in two elongate structures (Text-fig. 1B, C) almost 2 cm long that overlap proximally and extend posteriorly into narrow spines. These spines may have been arranged side by side in life.

DISCUSSION

The nature of *Skeemella* echoes the debate over a deuterostome versus arthropod affinity of vetulicolians. *Skeemella* shares the following characters with vetulicolians: (1) a bipartite body that is prominently cuticularized and consists of distinct anterior and posterior parts; (2) a head shield-like anterior section that is segmented and divided longitudinally; (3) a narrower segmented posterior part; (4) attachment of the posterior part to the posterodorsal margin of the anterior part; (5) segments of the posterior part separated by thinner membranes allowing flexure; (6) no evidence of eyes or segmented appendages. At least characters 1–5, however, are also found in Arthropoda, and *Skeemella* lacks evidence of the five pairs of gill slits diagnostic of vetulicolians.

Six genera are currently assigned to the Vetulicolia: *Banffia*, *Didazon*, *Pomatrum*, *Vetulicola*, *Xidazon* and *Yuyuanozoon* (Chen *et al.* 2003). Only *Banffia*, from the Middle Cambrian Burgess Shale (Walcott 1911), and *Vetulicola*, from the Lower Cambrian Mural Formation of Alberta (Butterfield 2000), have been reported from outside China. *Banffia confusa* (Chen and Zhou 1997; see also Chen *et al.* 1996) from Chengjiang, however, may not be referable to *Banffia* Walcott (Caron in press). The number and nature of the divisions in *Skeemella* serve to distinguish it from all vetulicolian genera. For example, there are nine divisions in the anterior section of *Skeemel-*

la, as opposed to the six separated by five gill openings that are characteristic of all described vetulicolians (Shu *et al.* 2001; Chen *et al.* 2003) except *Banffia constricta*, which lacks evidence of divisions and gills (Caron in press). The posterior section of the specimen of *Skeemella* includes 43 discrete divisions, a similar number to that in *Banffia* (Caron 2001), but the posterior section is about 5.5 times longer than the anterior whereas these sections are approximately equal in other vetulicolians. The twisting in the posterior section of *Skeemella* also resembles that in specimens of *Banffia* (Caron in press), but with only one specimen known, the possibility that it is a taphonomic effect cannot be eliminated. The segments in *Skeemella*, however, are much longer and more strongly sclerotized than those in *Banffia* and appear to represent tergite-like structures rather than the rings that have been described from vetulicolians. The bifid posterior termination in *Skeemella* mirrors the caudal notch in *Banffia constricta* (Caron in press) but it is relatively longer. *Skeemella* is unlike any known arthropod. Thus the new Pierson Cove Formation specimen represents a new genus and species.

Skeemella does not preserve evidence of the structures interpreted as gills in described vetulicolians (Shu *et al.* 2001), but it is possible that these were either not preserved, or they were concealed by the cuticle, as is often the case in *Vetulicola*. Alternatively, the position of the gills may be represented by the V-shaped indentations along the longitudinal break in the head shield. There is no evidence of an oral structure, but the mouth was presumably positioned in the anterior opening.

The two major alternative interpretations of vetulicolians are that they represent stem deuterostomes or stem arthropods. The case for these placements relies, to some extent, on different interpretations of the same features (Table 1). The striking distinction between the anterior and posterior sections of *Skeemella* is more reminiscent of Romer's (1972) 'dual-animal' model for the vertebrate ancestor (Gee 2001) than is the morphology of previously described vetulicolians. The interpretation of the five serial structures in the anterior section of vetulicolians as gills is critical to a deuterostome affinity (Shu *et al.* 2001, 2004). The evidence for an endostyle (Shu *et al.* 2001), also a deuterostome character, is more equivocal (Caron in press). Butterfield (2003) argued that the three-dimensional nature of the putative gills favours their interpretation as early mineralized structures typical of the mid-gut glands that occur in the Burgess Shale arthropod *Leancoilia* (Butterfield 2002). The arrangement of the disputed structures in vetulicolians, however, is more ordered than that of the mid-gut glands preserved in the arthropods. Mid-gut glands (gut diverticulae) do occur in *Banffia constricta*, but only in the posterior section, and

TABLE 1. Characters preserved in *Skeemella* and vetulicolians and their distribution in relevant living taxa. ‘Total vetulicolian’ summarizes the occurrence of character states within the diversity of the group. 1, strengthened organic cuticle. 2, perforations in body anterior. 3, gills. 4, mid-gut glands (in *Vetulicola* and ‘total vetulicolian’ mid-gut glands and gills are alternative interpretations of the same structures). 5, discretely cuticularized posterior segments. 6, mouth terminal with cirlet of plates. 7, total of 13 divisions in the body. 8, moulting (not observed in vetulicolians). 9, appendages and eyes present. 10, endostyle present (interpretation not definitive: Shu *et al.* 2001). 11, gut coiled. 12, bifid trunk termination.

	1	2	3	4	5	6	7	8	9	10	11	12
<i>Skeemella</i>	+	+	?	?	+	?	–	–	–	?	?	+
<i>Vetulicola</i>	+	+	+	+	+	+	+	–	–	+	+	–
<i>Banffia constricta</i>	+	–	–	+	+	+	–	–	–	–	–	+
‘Total vetulicolian’	+	+	+	+	+	+	+	–	–	+	+	+
Arthropoda	+	–	–	+	+	±	–	+	+	–	–	+
Deuterostomes	–	+	+	–	–	–	–	–	–	+	+	–
Kinorhynchs	+	–	–	–	+	+	+	+	–	–	–	+

there is no evidence of gills in this animal (Caron in press). Although many specimens of Chengjiang arthropods preserve no appendages, it is unlikely that limbs could project beyond the skeleton of the vetulicolians, or even lie within the head shield, without leaving a trace. Examination of many tens of specimens of Chinese vetulicolians has not revealed evidence of appendages (D. J. Siveter, pers. comm. 2004).

Shu *et al.* (2001) cited the apparent surface membranes that surround the cuticle of *Vetulicola* as evidence that the skeleton is internal, thus precluding an arthropod affinity. Caron (in press), on the other hand, suggested that this feature might simply represent an outer cuticle layer, or newly moulted cuticle. It is difficult to reconcile an internal skeleton in *Vetulicola* with the flexible articulation between segments and the spines that project from the rear of the head shield and the ventral margin of the trunk segments. However, evidence for a surface membrane, which appears to be confined to *Vetulicola*, has not been recorded in Chengjiang arthropods. Shu *et al.* (2001) also noted that a head shield of four large plates is unknown in the arthropods. Arthropods, however, are a remarkably diverse group; the two valves of lepadomorph barnacles, for example, are strengthened by two plates each, although there is a fifth along the junction between them.

Skeemella differs from described vetulicolians in that the posterior section is made up of tergites rather than cuticle rings; it also terminates in a telson-like structure. Both are arthropod rather than deuterostome characters. The ventral spines in the anterior trunk segments of *Vetulicola*, however, also suggest a possible differentiation between dorsal and ventral cuticle.

CONCLUSION

The vetulicolians present an interesting taphonomic and phylogenetic problem and they highlight the difficulty of

separating homology from convergence. The status of Phylum Vetulicolia requires further testing through explicit hypotheses of character coding and a cladistic analysis of relationships among both deuterostomes and all relevant protostomes, a task beyond the scope of the present contribution. Such a comparison might even include the Phylum Kinorhyncha (Table 1), which shares a circular mouth, cuticular plates, 13 body divisions and terminal spines on the trunk (Neuhauser 1994). Like former celebrated Cambrian problematica, including *Anomalocaris*, *Hallucigenia* and *Microdictyon* (Briggs and Fortey 2005), a definitive resolution of the nature of vetulicolians will only follow the discovery of new evidence in addition to that provided by *Skeemella clavula*.

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