PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2005) **272**, 2003–2007
doi:10.1098/rspb.2005.3159
Published online 18 August 2005

An Early Cambrian problematic fossil: *Vetustovermis* and its possible affinities

Jun-yuan Chen[1,*], Di-ying Huang[1] and David J. Bottjer[2]

[1]*Nanjing Institute of Geology & Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China*
[2]*Department of Earth Sciences, University of Southern California, Los Angeles, CA 90089, USA*

The Early Cambrian problematic fossil *Vetustovermis* (Glaessner 1979 *Alcheringa* **3**, 21–31) was described as an annelid or arthropod. Anatomical analysis of 17 new specimens from the Lower Cambrian Maotianshan Shale at Anning, Kunming (South China) does not support its affinities with annelids or arthropods. Anatomical features instead resemble other animal groups including modern flatworms, nemertines and molluscs. The presence of a pelagic slug-like form and ventral foot, as well as a head with eyes and tentacles indicates a possible affinity with molluscs, but these characters are not present only in molluscs; some of them are shared with other animal groups, including flatworms and nemertines. For example, a ventral foot-like structure is found in nemertines, 'turbellarians', and some polychaete groups. The well differentiated head is seen in separate bilaterian groups, but among molluscs it did not occur before the evolutionary level of the Conchifera. Unlike the ctenia-gills in molluscs, the gills in *Vetustovermis* are bar-like. All the characters displayed in this 525 million-year old soft-bodied animal fail to demonstrate clear affinity with molluscs or any other known extant or extinct animal groups, but argue for representing an independently evolved animal group, which flourished in Early Cambrian and possibly in Middle Cambrian time.

Keywords: mollusc; Early Cambrian problematic; evolution

1. INTRODUCTION

Ancestral molluscs are widely accepted to have been shell-less resembling modern aplacophorans, or to be lacking continuously biomineralized exoskeletons like extant chitons (Brusca & Brusca 2002). Radular grazing trace fossils (*Radulichnus*) (Erwin & Davidson 2002; Seilacher 1999, 2003), together with large imprints of possible soft-bodied molluscs (*Kimberella*) (Erwin & Davidson 2002; Fedonkin & Waggoner 1997; Seilacher 1999, 2003) from the latest Neoproterozoic Ediacarian indicate that macroscopic soft-bodied molluscs may have a deep Precambrian evolutionary history. Perhaps early molluscs that were shell-less are not easily recognized and have been extremely rarely recorded in the literature (Sutton *et al.* 2001). Radular grazing traces preserved together with circular impressions (about 10 cm) found in Lower Cambrian strata suggest the presence of soft-bodied macroscopic molluscs in Cambrian time (Dornbos *et al.* 2004). No soft-bodied molluscs are recorded from the Early Cambrian, perhaps due to difficulties in preservation or recognition. However, a potential example is *Vetustovermis planus*, first described as an annelid by Glaessner in 1979 (Glaessner 1979) and as an arthropod by Luo and Hu in 1999 (Luo *et al.* 1999). In this study we provide new evidence arguing that the Early Cambrian *Vetustovermis planus* is the representative of the independently evolved mollusc-like soft-bodied animal group that possibly occurred also in the Middle Cambrian Burgess Shale fauna.

* Author for correspondence (chenjunyuan@163.net).

2. ANATOMICAL ANALYSIS

All 17 specimens in the present study were collected from the Lower Cambrian Maotianshan Shale near Kunming, South China, at Shankou village of Anning, in a 2-cm-thick microturbidite mud layer. The animal *Vetustovermis planus* ranges in adult size, mostly 5–6 cm, with a few up to 10 cm in length. Because the body was flattened dorsoventrally in life, all the animals were buried in an original life position with the flattened ventral margin parallel to the bedding plane. The head is small and has a rounded front margin (figures 1*a*, 2*a*,*b*,*f*,*h* and 3*g*). A pair of large cephalic tentacles (figures 1*a*, 2*b*,*f*,*l* and 3*b*,*d*,*e*) project from the middle part of the head on its dorsal surface. The eyes are large and attached to an area near the base of the tentacles with a short stalk (figures 2*a*,*b*,*f*,*l* and 3*a*,*b*).

In dorsal view, the anterior 15% of the trunk is broadly triangular (figures 1*a* and 2*a*,*b*,*e*,*f*,*l*) and the remainder is an elongated oval (figures 1*a* and 2*b*,*e*,*k*). The preserved dorsal integument is presumably thick and, therefore, the split surface of the rock usually passes near it, leaving both the spine-like structures on the dorsal integument and the gills below it exposed on the surface (figures 1*a* and 2*a*,*b*,*f*,*j*,*l*). The spine-like structures are about 1 mm in diameter and three-dimensional, and depending upon angle of compaction are preserved with a round to short conic shape (figure 2*a*,*g*,*l*). Three-dimensional preservation, however, suggests that these spine-like structures were hard. The same structures in the holotype of *Vetustovermis planus* Glaessner 1979 were interpreted as remains of annelid parapodia (Glaessner 1979). Arguing against this interpretation, however, is the fact that these spine-like structures are distributed randomly. A flat, thin

Received 19 April 2005
Accepted 11 May 2005

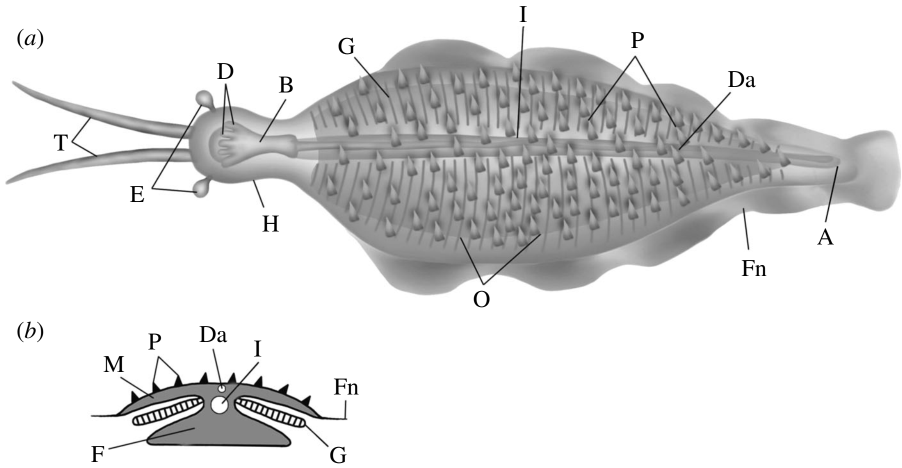

Figure 1. Anatomical features of the Early Cambrian mollusc-like organism *Vetustovermis planus* Glaessner 1979. (*a*) dorsal view; (*b*) reconstructed cross section. Abbreviations (also used in figures 2 and 3): A, anus; B, buccal mass and stomach; D, diverticula; Da, dorsal aorta; E, eye; F, foot; Fn, fin; G, gills; H, head; I, intestine; M, mantle; O, outer margin of foot; P, spine-like structure; T, cephalic tentacles.

'shelf' projects from the trunk in the horizontal plane, and is interpreted as a fin. This fin is relatively wide (3 mm in width, ranging from 15 to 40% of the width of the trunk) and uniform in width (figure 2*a*,*b*,*i*,*j*). It extends continuously along most of the trunk, both laterally and posteriorly, but the trunk's triangular anterior part is finless. Parts of the fins are occasionally preserved in a vertically folded manner, suggesting that they were flexible (figure 2*f*,*i*).

About 50 pairs of transversely extending bars dominate the trunk. They are here interpreted as gills, but they were previously described as body segments of annelids or arthropods. These bars are usually black in colour, suggesting that they are rich in organic matter. Unlike the intersegmental septa of annelids and the joints of sclerites in arthropods, these bars consist of two separate lateral sets divided from one another in the dorsal midline and the lateral margin of the bar series is slightly separated from the trunk margin, as would be expected for gills. In addition, the successive gills are slightly separated from one another (figure 2*a*–*c*,*e*,*f*,*j*), as opposed to being fused together, as would be expected for body segments. These bars are more or less straight and evenly spaced over the whole trunk (figure 2*a*–*c*,*f*,*j*). Figure 2*j* shows that the gill bars are tilted anteriorly and overlap one another as a result of dorsal compaction. The common occurrence of deformation indicates that they were soft and flexible (figure 2*j*). The soft and flexible transverse bars could be gut branches (termed gut diverticula) known from flatworms. Unlike gut diverticula, however, these bars are widely separate from the gut (figure 2*c*,*e*).

The trunk contains an elongated oval structure ventrally, which is interpreted as a muscular foot like that in extant molluscs. The foot is large, occupying most of the trunk. Only the most lateral parts of the gill-bars are exposed in specimens split along the ventral surface (figure 2*d*,*i*,*k*), because the foot obscures them. The lateral margin of the foot is also visible in most specimens split along the dorsal surface (figure 2*b*,*e*,*i*,*k*), as projections beyond the outer margin of the trunk proper. These relationships suggest that the foot is relatively thick. The ventral foot also shows a striking resemblance with the ventral sole in some modern flatworms.

In dorsal view, the gills are separated by an axial band-like structure (*ca* 3 mm in width) into the right and left gill parts. This axial structure is seen in most specimens (figures 2*c*,*e*,*f*,*i*,*j*,*l* and 3*c*–*e*), representing a dorsal projection of the trunk proper, and in the holotype it was incorrectly described as a large gut.

Vetustovermis planus possesses a complete gut. Although a mouth or radula are not seen, the head contains a bulb-like structure interpreted as a buccal/stomach mass (figure 2*a*,*b*,*d*–*f*,*h*,*l*). This is commonly preserved in three-dimensions, with an expanded, anterior, ramified part. The ramified structures are interpreted as gut diverticula (figure 2*a*,*b*,*h*). The intestine is represented by a wide, partially mud-filled, three-dimensional tube-like structure (*ca* 0.5–1 mm in diameter) that extends axially within the trunk proper (figures 1, 2*c*–*e*,*i*,*l* and 3*c*,*e*), with an anal opening just in front of the end of the trunk (figure 2*b*,*e*,*k*).

A slender, dorsally situated tube-like structure (*ca* 0.2 mm in diameter) seen in several specimens (figures 1*b* and 2*a*,*b*,*e*,*j*) is interpreted as a median dorsal aorta as seen in extant polyplacophorans.

3. LIFE STYLE AND PHYLOGENETIC IMPLICATIONS

The flattened body and horizontal fins of *Vetustovermis planus* could have been an adaptation to support the animal as it moved on the soft seafloor, as well as for gliding or swimming near the seafloor. The large surface area of the gills may have provided effective gas exchange for an active life style. The well developed sense organs including a pair of large, stalked eyes and large cephalic tentacles suggest that *Vetustovermis planus* was attuned to the presence of food resources as well as possible predators.

Vetustovermis planus resembles molluscs by having a flat foot, a polyplacophoran-like flexible elongated body, and serial pairs of gills on each side of the trunk (Brusca & Brusca 2002). The dorsal conic spine-like structures could be a homology of cuticular

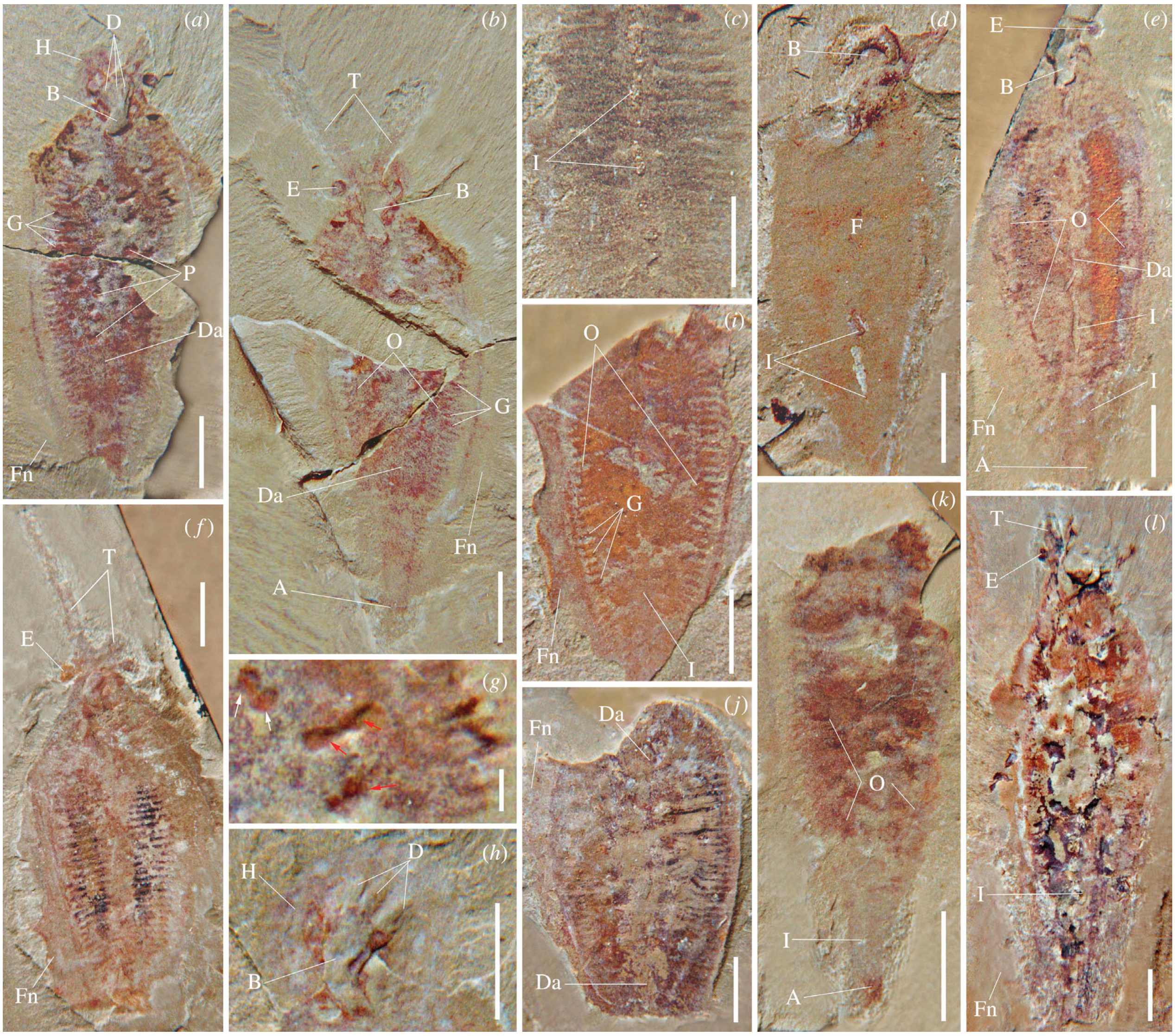

Figure 2. *Vetustovermis planus* Glaessner 1979 from the Lower Cambrian Maotianshan Shale, at Shankou village, Anning, Kunming. (*a*) and (*b*) a nearly complete specimen (coll. no. SK70001) with rock split along a plane near to the dorsal surface to separate it into a part (*a*) and a counterpart (*b*), showing: a round small head (*a*) that carries a pair of cephalic tentacles (*b*) and stalked eyes (*a* and *b*); a buccal mass and stomach with anterior diverticula (*a*); lateral margins of a large ventral foot that lie near the outer margins of the trunk (*b*); the imprints of dorsal spine-like structures; dorsal artery intestine; and an anus. (*c*) a trunk, showing gills and a mud-filled intestine (coll. no. SK70010). (*d*) ventral view of an animal showing a large foot with its outer margins near margins of the trunk proper (coll. no. SK70011). (*e*) a sagittal plane near to dorsal surface (coll.no. SK7002a) showing gills, lateral fins, dorsal aorta and an intestine with an anus. (*f*) a sagittal plane near to dorsal surface (coll. no: SK70007) showing cephalic tentacle, eye, lateral fins, and a dorsal artery. (*g*) enlargement of figure 2*a*, showing conic (red arrow) and rounded (white arrow) imprints of spine-like structures. (*h*) head of an animal (coll. no. SK70012) showing a round head, a three dimensionally preserved buccal mass and stomach with anterior diverticula. (*i*) a sagittal plane near ventral surface of a trunk (coll. no. SK70009b) showing ventral foot with its outer margins and the gills in lateral area of the trunk proper; intestine; and folded lateral fins. (*j*) a sagittal plane near dorsal surface of a trunk (coll. no. SK70013) showing gills extended axially near to the centre and some of the gills bent; the imprints of spine-like structures; and a median dorsal aorta. (*k*) ventral view of a trunk (coll. no. SK70003) showing ventral foot and its outer margins, and an anus near terminal end of the trunk. (*l*) a sagittal plane near dorsal surface of a trunk (coll. no. SK70008a) showing imprints of spine-like structures, lateral fins and an intestine. Scale bars, all are 5mm except for (*g*) which is 1 mm.

spicules of polyplacophorans and aplacophorans. This variety of characters is not specific to any crown group of molluscs (Brusca & Brusca 2002). The head has paired tentacles and stalked, basal eyes. Despite a number of conchiferans also having such a well differentiated head, this character probably was absent among more primitive molluscs. Thus, the character of a sluggish head yields no strong implication of a molluscan affinity. The gills in *Vetustovermis* are also simply bar-shaped and different from molluscan gills, thereby giving only weak support for a molluscan affinity.

Although arthropods and annelids can also have stalked eyes and tentacles, they lack the ventral foot, instead using leg-like appendages for locomotion. Thus, the foot is the best evidence for lack of an arthropod or annelid affinity. One might argue that the axial band-like visceral cavity of *Vetustovermis planus* is a notochord and that the transverse bars are not gills but myomeres, thereby indicating this

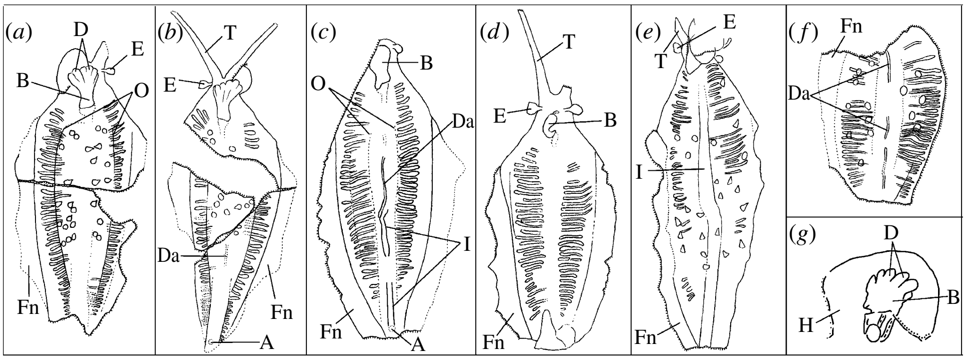

Figure 3. Interpretive drawing of *Vetustovermis planus* Glaessner 1979. Diagrams are the following figure parts: (*a*) figure 2*a*; (*b*) figure 2*b*; (*c*) figure 2*e*; (*d*) figure 2*f*; (*e*) figure 2*l*; (*f*) figure 2*j*; (*g*) figure 2.

animal was a chordate. However, no known chordate has stalked eyes or a ventral foot.

Vetustovermis planus resembles some planktonic nemertines, especially *Nectonemertes* and *Balaenanemertes*, in several respects (Gibson 1972; Hyman 1951). These include an anterior tentacle, lateral fins, ventral foot and a series of internal gut caecae comparable to the 'gill' of *Vetustovermis planus*. Nemertines however, lack a protective cuticle or exoskeleton as well as stalked eyes, but have a characteristic eversible proboscis. Presence of spine-like protective structures and stalked eyes and absence of a proboscis do not support a nemertine affinity for this animal.

The ventral flat foot also represents a trait that is shared with many turbellarians (free living flatworms) (Hyman 1951; Ruppert *et al.* 2004). The combined existence of a head, and elaborated paired tentacles and stalked eyes gives no support for an affinity of this animal to flatworms. Some polychaetes such as the sea mouse (*Aphrodite aculeate*) also bear a ventral muscular, creeping sole; myzostomids have a circular body with fused parapodia, which also forms a ventral foot like structure. However, the sea mouse is covered with a thick felt-like or hair layer, and myzostomids have numerous extended cirri (Rouse & Fleijel 2001; Ruppert *et al.* 2004).

Ancestral molluscs are widely accepted to have lacked a mineralized shell. Trace fossils that suggest grazing with a radula (*Radulichnus*) (Erwin & Davidson 2002; Seilacher 1999, 2003), together with large imprints of possible molluscs lacking a mineralized shell (*Kimberella*) from the latest Neoproterozoic (Erwin & Davidson 2002; Fedonkin & Waggoner 1997; Seilacher 1999, 2003), imply that macroscopic molluscs have a deeper evolutionary history. *Vetustovermis* bears a number of morphological features that are found in *Kimberella*, which has been interpreted to have a non-mineralized but stiff univalve shell. Like *Vetustovermis*, *Kimberella* has many structures (crenellations) that may have been gills, has a broad flat foot, showing metamerism, and its shell bears many impressions, which may be the remains of sclerites or spicules.

Vetustovermis shows a similarity with shell-less sea slugs, which are gastropods that evolved from the shelled ancestors (Yonge 1960). The similarity is thus superficial, as a result of convergent evolution.

In summary, some characters as mentioned may indicate a possible molluscan affinity of *Vetustovermis*. These characters, however, are found separately within different molluscan groups. For instance, an elaborated head and eyes did not occur in primitive molluscs before the level of Conchifera; serial pairs of gills are seen only in the Polyplacophora and Tryblidia; and an oval foot is known in Tryblidia, polyplacophorans and archaeogastropods only (Brusca & Brusca 2002; Ruppert *et al.* 2004). A molluscan affinity for this animal, therefore, is poorly grounded. These soft-bodied animals with the characters described here could represent an independently evolved animal lying outside of molluscs. Similar animals have also been recorded from Middle Cambrian Burgess Shale. Several Burgess Shale problematic creatures, including *Nectocaris* (Conway Morris 1976), *Amiskwia* (Walcott 1911), and *Odontogriphus* (Conway Morris 1976), are likely candidates for interpretation as *Vetustovermis*-like soft-bodied animals. Although the single specimen of *Nectocaris* has been viewed as laterally compacted, we suspect that it is a subdorsally compacted specimen. If this alternative interpretation is correct, the resemblance with *Vetustovermis* is thus striking by sharing a number of features including a slug-like head that carries a pair of cephalic tentacles and stalked eyes, a trunk that was laterally finned with a triangular anterior portion, and a large number of transverse gills spread over most of the trunk. *Amiskwia* also shares a number of features with *Vetustovermis planus*. They include a flat body with a slug-like head and lateral and posterior fins on the trunk. Although the gross morphology of *Odontogriphus* appears significantly different from *Vetustovermis planus*, its potential affinity with *Vetustovermis* is suggested by its dorso-ventrally flattened body and series of transverse lines on the trunk (comparable to the gills of *Vetustovermis*).

Vetustovermis planus resembles the Carboniferous problematic *Tullimonstrum gregarium* in several important respects (Foester 1979). These include a dorso-ventrally flat trunk, lateral fins, a distinct visceral mass, stalked eyes, and a series of transverse segments. Foester has tentatively interpreted *Tullimonstrum gregarium* as a prosobranch gastropod (Conway Morris 1976).

We thank Ellis L. Yochelson for critical examination of an earlier version of this manuscript, J. Mallet and Stephen Dornbos for constructive comments, and Z. L. Yang and S. R. Song for technical assistance. The constructive comments and valuable input from two anonymous referees are gratefully acknowledged. This work is supported by the National Science Foundation of China (Grants no. 40132010, 40302004), the National Department of Science and Technology of China (G 2000077700) and the Chinese Academy of Sciences (Grant no. KZCX3-SW-141).

APPENDIX A: SYSTEMATIC PALAEONTOLOGY

Genus *Vetustovermis* Glaessner 1979

(= *Petalium* Luo and Hu 1999).

Type species: *Vetustovermis planus* Glaessner 1979 (=*Petalium latus* Luo and Hu 1999).

Revised diagnosis: A soft-bodied animal with unknown affinity, 1.5–6 cm long, few up to 10 cm; flat body is elongate and consists of a small but distinct head and elongate oval trunk. Head is broadly rounded anteriorly, having a pair of cephalic tentacles and elongate stalked eyes. Trunk bears a wide fin, which extends continuously along trunk both laterally and posteriorly. Dorsal integument bears rounded spine-like structures. Foot is flat and broad, occupying major part of ventral surface of body. An axial trunk proper, which lies dorsally to foot, divides the branchial cavity into two lateral parts. The gills are numerous and transversely extended, with *ca* 50 pairs. The alimentary canal is differentiated into a diverticulated stomach mass and a straight intestine, with an anus opening near terminal end of the trunk. A median aorta is narrow and dorsally situated.

Remarks: In 1999 two specimens identical to *Vetustovermis* Glaessner were recorded by Luo and Hu from the Lower Cambrian Maotianshan Shale at Haikou, near Kunming, but they assigned them as a new species within a new genus, *Petalium* (Luo *et al*. 1999).

Vetustovermis planus Glaessner 1979

(= *Petalium latus* Luo and Hu 1999).

Revised diagnosis: Same as in the generic revised diagnosis.

Locality and stratigraphy. Holotype is from the lower part of the Emu Bay Shale, South Australia, of late Early Cambrian age. All the Chinese specimens came primarily from the Lower Cambrian Maotianshan Shale near Kunming, South China, at Shankou village of Anning, except for the two specimens described by Luo and Hu (Glaessner 1979), collected from Ercai village, Haikou, in the same strata. The Maotianshan Shale is interpreted as of early Atdabanian age, *ca* 525 million years old.

REFERENCES

Brusca, R. C. & Brusca, G. J. 2002 *Invertebrates*, 2nd edn. Massachusetts: Sinauer Association.

Conway Morris, S. 1976*a* Neues Jabrbuch fur Geologie und Palaeotologie. *Monotshefte* **12**, 705–713.

Conway Morris, S. 1976*b* A new Cambrian lophophorate from the Burgess Shale of British Colombia. *Palaeontology* **19**, 199–222.

Dornbos, S. Q., Bottjer, D. J. & Chen, J.-Y. 2004 Evidence for seafloor microbial mats and associated metazoan lifestyles in Lower Cambrian phosphorites of Southwest China. *Lethaia* **37**, 127–137.

Erwin, D. H. & Davidson, E. H. 2002 The last common bilaterian ancestor. *Development* **129**, 3021–3032.

Fedonkin, M. A. & Waggoner, B. M. 1997 The Late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. *Nature* **388**, 868–871. (doi:10.1038/42242.)

Foester, M. W. 1979 A reappraisal of Tullimonstrum. In *Mazon creek fossils* (ed. M. H. Nitecki), pp. 269–302. New York: Academia Press.

Gibson, R. 1972 *Nemerteans*. London: Hutchinson University Library.

Glaessner, M. F. 1979 Lower Cambrian Crustacea and annelid worms from Kangaroo Island, South Australia. *Alcheringa* **3**, 21–31.

Hyman, L. H. 1951 *The invertebrates*, vol. 2. New York: McGraw-Hill.

Luo, H.-L., Hu, S.-X. & Chen, L.-Z. 1999 *Early Cambrian Chengjiang fauna from Kunming region, China*. Kunming, China: Yunnan Science & Technology Press.

Rouse, G. W. & Fleijel, F. 2001 *Polychaetes*. Oxford University Press.

Ruppert, E. E., Fox, R. S. & Barnes, R. D. 2004 *Invertebrate zoology*, 7th edn. Thomson & Brooks/Cole.

Seilacher, A. 1999 Biomat-related lifestyles in the Precambrian. *Palaios* **14**, 86–93.

Seilacher, A. 2003 *Paleontological Res.* **7**, 43–54.

Sutton, M. D., Briggs, D. E. G., Siveter, D. J. & Siveter, D. J. 2001 An exceptionally preserved vermiform mollusc from the Silurian of England. *Nature* **410**, 461–463. (doi:10.1038/35068549.)

Walcott, C. D. 1911 Middle Cambrian annelids. *Smithsonian Miscellaneous Collections* **57**, 109–144.

Yonge, C. M. 1960 General characters of mollusca. In *Treatise on Invertebrate Paleontology: Part I., Mollus* (ed. R. C. Moore), pp. 13–136. Geologic Society of America and Kansas City Press, Lawrence, Kansas press.