Early Cambrian sipunculan worms from southwest China

Di-Ying Huang¹, Jun-Yuan Chen^{1*}, Jean Vannier² and J. I. Saiz Salinas³

¹Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

²Université Claude Bernard Lyon 1, UFR Sciences de la Terre, UMR 5125 du CNRS, Bâtiment Géode, 2, rue Raphaël Dubois, 69622 Villeurbanne, France

³Departamento de Zoología y DCA, Facultad de Ciencias, Universidad del País Vasco, Apartado 644, 48080 Bilbao, Spain

We report the discovery of sipunculan worms from the Lower Cambrian Maotianshan Shale, near Kunming (southwest China). Their sipunculan identity is evidenced by the general morphology of the animals (sausage-shaped body with a slender retractable introvert and a wider trunk) and by other features, both external (e.g. perioral crown of tentacles, and hooks, papillae and wrinkle rings on the body surface) and internal (U-shaped gut, and the anus opening near the introvert–trunk junction). The three fossil forms (*Archaeogolfingia caudata* gen. et sp. nov., *Cambrosipunculus tentaculatus* gen. et sp. nov. and *Cambrosipunculus* sp.) have striking similarities to modern sipunculans, especially the Golfingiidae to which their evolutionary relationships are discussed. This study suggests that most typical features of extant sipunculans have undergone only limited changes since the Early Cambrian, thus indicating a possible evolutionary stasis over the past 520 Myr.

Keywords: sipunculans; early evolution; Early Cambrian; China

1. INTRODUCTION

Sipunculans (peanut worms) form a small phylum of non-segmented coelomate worms with approximately 150 described species living in a variety of marine habitats throughout the world (Cutler 1994). Their origin and evolutionary history have not been satisfactorily resolved because of the lack of reliable fossil evidence. *Otoia prolifica* from the Middle Cambrian Burgess Shale was interpreted as a sipunculan first by Walcott (1911) and then by Howell (1962). Banta & Rice (1976) suggested that it was an early aschelminth rather than a sipunculan, but it is, in fact, a priapulid (Conway Morris 1977). The sipunculan affinities of the poorly preserved *Lecthaylus* from the Silurian (Weller 1925) and Carboniferous (Muir & Botting 2002), *Epitrachys rugosus* from the Jurassic (Ehlers 1869) and known trace fossils such as *Trypanites* (Pemberton *et al.* 1980) remain highly questionable. The ribbon-shaped *Valvasoria* from the Triassic (Kolar-Jurkovsek & Jurkovsek 1997) was suggested to have a nematode or sipunculan affinity but it is most probably seaweed remains. Some authors have envisaged sipunculan affinities for hyolithids (Runnegar *et al.* 1975; Runnegar 1982). Like sipunculans, the extinct mollusc-like hyolithids had a convoluted U-shaped gut with an anteriorly placed anus. Hyolithids, however, had a very unusual mineralized exoskeleton consisting of a pointed shell and an operculum-like lid anteriorly, and some species were provided with a pair of helens. These exoskeletal characters make a sipunculan affinity very unlikely. The assumption that sipunculans may have colonized endobenthic habitats as early as the Cambrian and even the Precambrian has been proposed by some authors (Cutler & Gibbs 1985; Cutler 1994).

2. NEW FOSSIL EVIDENCE

We report the occurrence of sipunculan worms from the Lower Cambrian Maotianshan Shale at Shankou village, near Anning, Kunming (southwest China). The specimens were discovered in a *ca.* 2 cm thick shale layer deposited by a microturbiditic mudflow from an adjacent shallower area (Chen & Zhou 1997). The six specimens used in the present study belong to two separate genera, namely *Archaeogolfingia* gen. nov. and *Cambrosipunculus* gen. nov., and comprise three forms: *A. caudata* (figures 1a, 2a,d,e and 3a), *C. tentaculatus* (figures 1b, 2b,f,g and 3b) and *Cambrosipunculus* sp. (figures 2c,h and 3c).

(a) *Archaeogolfingia caudata*

The worm is mid-sized, *ca.* 4 cm long (including the caudal appendage) and 0.5 cm wide. It has a relatively elongate introvert, which tapers forwards. The anterior part of the introvert is unknown owing to the tip being withdrawn (figures 2a and 3a). It has a distinctly thicker trunk with a rather constant diameter, which is approximately the same length as the introvert (figures 2a and 3a). The trunk (*ca.* 15 mm long) bears fine ring-like wrinkles along its mid-section (the wrinkles are absent in the anterior 2 mm and the posterior 6 mm sections; figures 2a and 3a) and terminates posteriorly in a cone-shaped end (figures 2a,e and 3a). The wrinkle pattern of *Archaeogolfingia* is similar to those of some living sipunculans in a contracted attitude. The trunk is covered with minute spot-like papillae, which are more densely distributed at the posterior end, also typical of many modern sipunculans (figures 2e and 3a). It ends in a slender projection with a tapering shape (figures 2a,e and 3a), which resembles the caudal appendage of some modern golfingiid sipunculans such as *Golfingia anderssoni*, *G. muricaudata*, *Nephasoma flagriferum* and *N. bulbosum* (Saiz Salinas 1993; Cutler 1994). The digestive tract has a U-shape, recurving near the posterior end of the trunk

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

Figure 1. Reconstructions of the Early Cambrian sipunculan worms from southwest China. (a) *Archaeogolfingia caudata* gen. et sp. nov., and (b) *Cambrosipunculus tentaculatus* gen. et sp. nov. Abbreviations: Ap, ascending portion of digestive tract; An, anus; Ca, caudal appendage; Dp, descending portion of digestive tract; Pd, protruding part of digestive tract (see figures 2f and 3b); Ho, hook; Iv, introvert; Te, tentacle; Tr, trunk.

(figures 2a and 3a). The descending portion of the gut is rather straight and is filled with mud in its posterior section (figures 2a and 3a), and the ascending portion has a wavy trajectory and is characterized by a dark colour (figures 2d and 3a). The digestive tract ends in a conspicuously rounded structure near the trunk–introvert junction, which represents the anus (figures 2d and 3a).

(b) *Cambrosipunculus tentaculatus*

The worm is mid-sized, ca. 4 cm long and 0.4 cm wide (at the posterior trunk level). It has a tapering body shape with no clear boundary between introvert and trunk (figures 2b and 3b). The introvert is relatively elongate and has a slightly tapering shape (figures 2b and 3b). Similar to most extant forms, the anterior part of the introvert is armed with hooks. These hooks are of two types: a distal ring of larger hooks, and moderate scattered hooks (ca. 90–130 µm in length) located farther back along the anterior part of the introvert (figures 2g and 3b). The tip of the introvert is crowned with more than 10 short and simple peripheral tentacles. These tentacles bear a blunt tip and are slightly contracted at the base (figures 2b,f and 3b). Such a tentacular crown is not visible in all specimens, presumably owing to the inversion of the introvert tip. The trunk is longer than the introvert (trunk ca. 60%

of the entire worm length) and has a rounded posterior end (figures 2b and 3b). Fine papillae are present over the trunk but no wrinkled pattern is clearly expressed. The digestive tract has a U-shape, recurving near the posterior end of the trunk (figures 2b and 3b). Both the descending and ascending portions of the gut are rather straight and close to each other. The gut is dark coloured in its anterior descending portion and is filled with mud in its posterior descending portion and most ascending portion (figures 2b and 3b). The digestive tract terminates in a circle-like structure representing the anus (figure 3b).

(c) *Cambrosipunculus* sp.

The twisted body shape of this worm recalls the attitude of a moribund worm. It is ca. 3 cm long and 0.45 cm wide. It has a rather thin introvert and a thicker trunk with a tapering shape (figures 2c and 3c). The introvert is incomplete anteriorly owing to the tip being withdrawn. The relatively smooth trunk has a rounded termination and is distinctly longer than the introvert (figures 2c and 3c). The dark-coloured digestive tract recurves in the posterior trunk (figures 2c and 3c). The anus is emphasized by a small volcano-like structure located near the introvert–trunk junction (figures 2c,h and 3c; a laterally compressed specimen).

3. SIPUNCULAN AFFINITIES

The affinity of these 520-Myr-old worms with modern sipunculans is supported by their possession of

- (i) an anteriorly tapering body with a slender retractible introvert and a wider trunk;
- (ii) a mouth surrounded with tentacles;
- (iii) a caudal appendage, as seen in a few modern golfingiid sipunculans;
- (iv) a U-shaped digestive tract with the anus opening near the introvert–trunk junction; and
- (v) hooks, wrinkle rings and papillae on the body surface.

The vast majority of Cambrian worms described so far are priapulids. *Archaeogolfingia* gen. nov. and *Cambrosipunculus* gen. nov. clearly differ from all Cambrian priapulids from the Burgess Shale (e.g. *Ottoia*, *Louisella*; Conway Morris 1977) and also from *Corynetis* and *Anningvermis* from the Maotianshan Shale (Huang *et al.* 2004) in their recurving gut, the absence of an eversible spiculated pharynx, their tapering body shape and the absence of annulations (especially along their elongate introvert). Unique superficial resemblances to Middle Cambrian Burgess Shale *Ancalagon* in their tapering body shape and anterior hooks (see Conway Morris 1977, especially in the young specimen in pl. 24, fig. 8; Conway Morris 1977; Conway Morris & Crompton 1982; Briggs *et al.* 1994) are worth mentioning here. However, the gut morphology of *Ancalagon* (straight and wide through the entire trunk) is clearly different from that of a sipunculan.

4. EVOLUTIONARY IMPLICATIONS

Cutler (1994) proposed a plausible historical representation of the major cladogenetic events experienced by the

Sipuncula. According to his view, the most crucial split, leading to the two extant classes (Phascolosomatidea and Sipunculidea) within the phylum, was placed early in the Palaeozoic, tentatively in the transition from the Ediacaran to the Cambrian period. In spite of the limited preservation of the Lower Cambrian sipunculans, we determine that all these new fossils should be classified as a sister-group of the modern class Sipunculidea (figure 4), based on (i) the presence of simple hooks not well arranged in rings as shown by *Cambrosipunculus* and (ii) the short tail at the posterior end of the trunk of *Archaeogolfingia*, which is still present in a few representatives of the class Sipunculidea. *Archaeogolfingia* and *Cambrosipunculus* are also strikingly similar to the modern golfingiids in numerous other detailed aspects of their morphology such as the general body design, the perioral crown of digitiform tentacles and the fine ring-like wrinkles of the median trunk (*Archaeogolfingia*; Saiz Salinas 1993; Cutler 1994). The non-helicoidal structure of their guts recalls that of *Phascolion*, which was tentatively assigned to Golfingiidae on the basis of molecular evidence (Maxmen *et al.* 2003). However, it is uncertain whether the relatively simple gut structure of *Phascolion* is an ancestral character or a derived character related to its peculiar habitat (it usually lives in gastropod or scaphopod shells; Saiz Salinas 1993; Cutler 1994). Some important familial traits of Golfingiidae, such as the presence of retractor muscles and a pair of nephridia, could not be seen in our fossil material. Thus, these new fossil sipunculans display what may be understood as a close evolutionary relationship to modern Golfingiidae. To us, the uncoiled shape of the intestine that characterizes *Archaeogolfingia* and *Cambrosipunculus* does not justify the creation of a new family. Therefore, their golfingiid systematic position is not proposed in the present study owing to the absence of some internal features in the fossil preservation.

In contrast to the helicoidal digestive tract of modern sipunculans (Saiz Salinas 1993; Cutler 1994) that of Cambrian forms appears remarkably simple (U-shaped tube). The partly mud-filled intestine and the presence of tiny hooks in the anterior part of the introvert suggest that these animals scraped or gathered material from the sediment surface like many modern animals (Cutler 1994). The shorter and simpler intestine of the Early Cambrian sipunculans may reflect faster processing of a large quantity of sediment with a low food content. Detailed comparisons between *Cambrosipunculus*, *Archaeogolfingia* and the Recent forms suggest that the intestine of sipunculans has evolved from a straight form (*Cambrosipunculus*) and intermediate wavy form (*Archaeogolfingia*) towards the more complex helicoidal structure known in modern sipunculans. This interpretation may be supported by the presence of a straight intestine in the pelagospheran larvae of modern sipunculans (Cutler 1994; Jaeckle & Rice 2002). Simple folded (i.e. lacking a regular coil and consisting of a few loose loops) intestines are extremely rare among Recent adult sipunculans (*Phascolion*; Cutler 1994). Cutler (1994) proposed that sipunculans were living in soft-bottomed burrows at least by the mid-Palaeozoic (Devonian) and probably earlier (Cambrian). The U-shaped recurved gut with an

anteriorly placed anus suggests that the Cambrian sipunculans were sedentary organisms that lived in burrows, as are modern forms.

The remote ancestry of sipunculan worms and more precisely the golfingiids had long been assumed (Early Palaeozoic; Murina 1975). Our interpretation indicates that the golfingiid-like sipunculans may provide a possible example of morphological stasis over 520 Myr. According to Cutler (1994), the stock that changed least from the revised hypothetical ancestral sipunculan became the present-day genus *Apionsoma*, and he thinks that some golfingiid ancestors were present in the Early Palaeozoic. Recent golfingiid forms live in softer sediments and are thus more easily fossilized than the phascolosomatid forms that lived in burrows or tunnels within hard rocks or coral. The extent of diversity in Cambrian time remains unclear. The new fossil evidence indicates that some golfingiid-like types were present in the Early Cambrian. The presence of the simple gut strongly suggests that the full crown-group body plan of modern sipunculans had not yet been achieved at this time and that the attributes of modern families had not yet evolved at this early stage.

The discovery of Lower Cambrian sipunculans adds to the increasing list of present-day animal phyla (more than one-third) (Chen & Huang 2002) that are now firmly recognized in the Early Cambrian. Sipunculans belong to the large clade of protostome animals called Lophotrochozoa, which also includes molluscs, annelids and lophophorates. Recent evidence from mitochondrial gene sequences favours an annelid affinity (Boore & Staton 2002; Staton 2003). This could mean that the non-segmented sipunculans were derived secondarily from a segmented ancestor. If sipunculans did evolve from segmented worms, then their body plan must have changed extensively at or before the start of the Cambrian, followed by a remarkable period of stasis for the past half billion years.

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APPENDIX: SYSTEMATIC PALAEONTOLOGY

Phylum: Sipuncula Sedgwick, 1898
Class: Sipunculidea Cutler & Gibbs, 1985
Order and family uncertain

Archaeogolfingia gen. nov.

Derivation of name

Alluding to the possible Cambrian ancestry of Golfingiidae.

Type species

Archaeogolfingia caudata gen. et sp. nov.

Diagnosis

Elongate body. Tapering introvert approximately as

Figure 2. Lower Cambrian sipunculans from Shankou village, near Kunming. (a,d,e) *Archaeogolfingia caudata* gen. et sp. nov., holotype (SK 69001a); (b,f,g) *Cambrosipunculus tentaculatus* gen. et sp. nov., holotype (SK 69002a); (c,h) *Cambrosipunculus* sp. (SK 69003a). (a) Complete specimen showing Al, Ca, Dl, Iv and Tr. (b) Complete specimen showing ascending and descending portions parallel to each other, An, Iv, Te and Tr. (c) Twisted specimen (SK 69003a), showing An, Dl, Iv and Tr. (d) SK 69001b showing wavy ascending portion of gut Al, An and straight Dl. (e) Enlargement of posterior part of (a), showing Ca and trunk papillae. (f) Enlargement of anterior part of (b), showing Pd and Te. (g) Enlargement of (b), showing Ho. (h) Enlargement of (c), showing protruding An. Scale bars, 5 mm (a–e) and 2 mm (f–h). Abbreviations as in figure 1.

long as trunk. Trunk with rather constant diameter, covered with tiny papillae and finely wrinkled into rings; trunk bears a cone-shaped end and a terminal tapering caudal appendage. U-shaped intestine recurving near the posterior end of the trunk; descending portion straight; ascending portion with wavy trajectory and anus opening on the anterior part of the trunk.

Archaeogolfingia caudata gen. et sp. nov.

(figures 1a, 2a,d,e and 3a)

Derivation of name

Alluding to the caudal appendage exhibited in this species.

Material

Two specimens (holotype and an incomplete

Figure 3. Camera lucida drawings of figure 2: (a) figure 2a; (b) figure 2b; (c) figure 2c. Abbreviations as in figure 1.

Figure 4. The phylogenetic relationships within the phylum Sipuncula showing the incorporation of the Lower Cambrian sipunculans as a sister-group of the class Sipunculidea. (Modified from Cutler 1994.)

specimen), both deposited in the collections of the Early Life Research Centre, Chengjiang, Yunnan Province, China.

Holotype

Complete specimen (SK 69001 a,b), 31 mm long (excluding caudal appendage) and 4.8 mm wide; introvert strongly curved with invaginated tip. Trunk preserved in assumed contracted attitude.

Type locality

Shankou village, Anning City near Kunming, Yunnan Province, southwest China; Lower Cambrian Maotianshan Shale Member in the middle part of the Yu'an-shan Formation (*Eoredlichia*–*Wutingaspis* Zone).

Cambrosipunculus gen. nov.

Derivation of name

Alluding to its Cambrian age.

Type species

Cambrosipunculus tentaculatus gen. et sp. nov.

Diagnosis

Elongate body tapering gradually towards anterior end. Introvert crowned by a circle of more than 10 short simple perioral tentacles, armed with a ring of distal large hooks and moderate scattered hooks farther back; trunk approximately as long as introvert, with a rather rounded posterior end, wrinkles faintly indicated, papillae covered in the trunk. U-shaped intestine recurving near the posterior end

of the trunk, with descending and ascending portions both straight and running parallel to each other. Anus opening in mid-section of body.

Remarks

Cambrosipunculus differs from *Archaeogolfingia* in the absence of a caudal appendage and in having an intestine consisting of two parallel straight portions, whereas the descending loop of the intestine in *Archaeogolfingia* is wavy.

Cambrosipunculus tentaculatus gen. et sp. nov.

(figures 1b, 2b,f,g and 3b)

Derivation of the name

Alluding to the oral tentacles.

Material

Two specimens (one complete and one nearly complete), both deposited in the collections of the Early Life Research Centre, Chengjiang, Yunnan Province, China.

Holotype

Complete specimen (SK 69002 a,b), 37 mm long and 4.0 mm wide; curved introvert crowned with tentacles and intestine protruding slightly outside.

Type locality

Shankou village, Anning City near Kunming, Yunnan Province, southwest China; Lower Cambrian Maotianshan Shale Member in the middle part of the Yu'an-shan Formation (*Eoredlichia*–*Wutingaspis* Zone).

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