

Diversity of cnidarians and cycloneuralians in the Fortunian (early Cambrian) Kuanchuanpu Formation at Zhangjiagou, South China

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Abstract.—The latest discovery of microfossils from the lower Cambrian (Fortunian Stage) Zhangjiagou Lagerstätte in South China are presented. This lagerstätte is rich in exceptionally preserved microfossils, including embryos of *Olivoooides multisulcatus*, *Olivoooides mirabilis*, and *Pseudoooides prima*; hatched stages of *O. multisulcatus*, *O. mirabilis*, *Hexaconularia sichuanensis*, and *Quadrapyrgites quadratacris*; and cycloneuralians represented by *Eopriapulites sphinx*. The largest known fragment of *O. mirabilis* implies that its adult length can be more than 9.0 mm with at least 50 annuli, and the longest known specimen of *Q. quadratacris* has at least 18 annuli. These unusually large specimens refute the non-feeding larvae hypothesis for *Olivoooides* and *Quadrapyrgites*.

Based on the current material, it is inferred that (1) early cnidarians have a high diversity in the Fortunian Stage; (2) *P. prima* might represent the embryonic stages of *H. sichuanensis*; (3) adults of *Olivoooides* and *Quadrapyrgites* may have reached centimeter-scale dimensions with more than 50 annuli; (4) *Olivoooides* and *Quadrapyrgites* may be better interpreted as coronate scyphozoans; (5) cycloneuralians also had a high diversity in the Zhangjiagou Lagerstätte; and (6) cycloneuralians might have originally been part of the early Cambrian meiofauna rather than belonging to the macrobenthos. Such ancestral cycloneuralians might have been *Eopriapulites*-like, possessing pentaradially symmetric, backward pointing, and internally hollow introvert scalids used as locomotory devices.

Introduction

Molecular studies have suggested the first appearance of eumetazoans in the Ediacaran Period or earlier (Peterson et al., 2008; Erwin et al., 2011). However, this is not supported by fossil evidence because undisputed animal fossils in Precambrian rocks are extremely rare. The nature of fossil embryos from the Ediacaran Doushantuo Formation of South China (Xiao et al., 1998) is vague and has remained hotly debated (Xue et al., 1999; Bailey et al., 2007; Hultgren et al., 2011; Chen et al., 2014). The material assigned to the earliest bilaterian animal *Vernanimalcula guizhouena* Chen et al., 2004 represents, most likely, artifacts of diagenesis (Bengtson et al., 2012). On the other hand, the fossil evidence demonstrates that all major groups of animals are already present early in the Cambrian Period (Budd, 2003a, 2013; Chen et al., 2007; Erwin et al., 2011; Erwin and Valentine, 2013; Budd and Jackson, 2015). This indicates that the early evolution of animals took place well within the end of the Precambrian (Zhu et al., 2017).

Cambrian strata preserve the earliest unambiguous animals and are thus crucial for uncovering not only the origin but also

the major early steps and significant developments in metazoan evolution. The Fortunian Stage, the oldest stage of the Cambrian Period (Peng et al., 2012), is well known for the occurrence of skeletal remains known as small shelly fossils (SSFs). SSFs have a worldwide distribution, such as in Siberia (Voronova and Missarzhevsky, 1969; Val'kov, 1983), Australia (Bengtson et al., 1990), and South China (Qian and Bengtson, 1989; Steiner et al., 2004a), and they form the foundation of a global biostratigraphic correlation (Steiner et al., 2004a, 2007). Another important group of exceptionally preserved microfossils include taxa such as *Olivoooides* Qian, 1977 (Bengtson and Yue, 1997; Donoghue et al., 2006a; Dong et al., 2016), *Quadrapyrgites* Li et al., 2007 (Liu et al., 2014a; Steiner et al., 2014), *Pseudoooides* Qian, 1977 (Steiner et al., 2004b), a sea anemone (Han et al., 2010), the oldest known scalidophoran animals (Liu et al., 2014b; Zhang et al., 2015; Shao et al., 2016), the oldest known eumetazoan larvae (Zhang and Dong, 2015), and a plausible deuterostomian animal (Han et al., 2017). These exceptionally preserved microfossils have stimulated divergent interpretations and exciting debate on the origin and early evolution of animals.

In the early Cambrian, the present-day southern Shaanxi and northern Sichuan Provinces were located at the northern edge of the Yangtze Platform (Steiner et al., 2004a). On the

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Yangtze Platform, sediments deposited during the Fortunian Stage contain abundant SSFs and non-mineralized microfossils, which were exceptionally preserved by three-dimensional phosphatization. Representatives of such localities are the Meishucun section in Yunnan Province (Qian and Bengtson, 1989; Yang et al., 2014) and the Shizhonggou section in Shaanxi Province (Steiner et al., 2004a).

This paper presents the latest discoveries from another fossil locality, the Zhangjiagou section in southern Shaanxi Province, China. The Zhangjiagou section has yielded, besides abundant SSFs, representatives of the taxa *Olivoooides*, *Pseudoooides*, and *Quadrapyrgites*, and a diverse suite of cycloneuralians. The current study focuses on the early diversification of the cnidarians (*Olivoooides*, *Pseudoooides*,

Quadrapyrgites, and *Hexaconularia*) and cycloneuralians from this Fortunian Konservat-Lagerstätte.

Geological background and age constraint

The Zhangjiagou Lagerstätte (Fig. 1.1) is located in Dahe Village, Xixiang County, Hanzhong City, Shaanxi Province, China (Fig. 2). The fossil locality was first measured and described as Zhangjiagou section by Li (1984), and later as Hexi section by Steiner et al. (2014) and as Xixiang section by Liu et al. (2014a, b). The suite of limestone-dominated deposits was identified as Kuanchuanpu Formation (Li, 1984). The Kuanchuanpu Formation at Zhangjiagou section is ~21 m thick and consists of four members in ascending order (Fig. 2): the 1st member is a



Figure 1. The Zhangjiagou section in southern Shaanxi Province, South China. (1) Overall view; the boundary between the Ediacaran Dengying Formation and the Cambrian Kuanchuanpu Formation, and the subdivisions (the 1st, 2nd, and part of 3rd members) within the lower part of the Kuanchuanpu Formation, are marked; (2) close-up of the boundary between the 1st and 2nd members of Kuanchuanpu Formation; (3) hand specimens of phosphatic limestone from the lower part of the 2nd member.

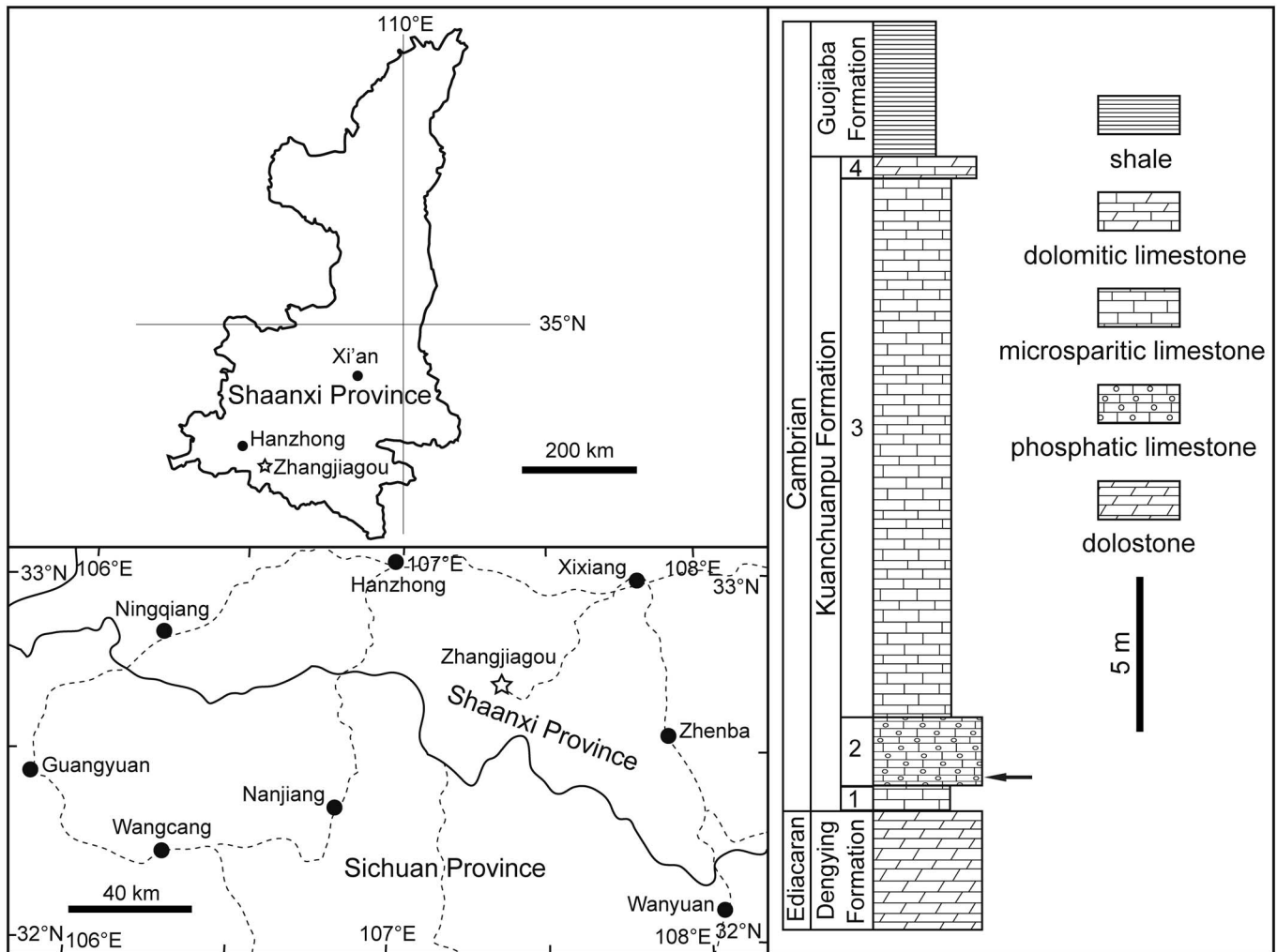


Figure 2. Location map and stratigraphic column of the Zhangjiagou section in southern Shaanxi Province, South China. Arrow indicates the key horizon yielding the present materials. Revised from Liu et al. (2014b).

light-gray microsparitic limestone (0.8 m); the 2nd member a phosphatic limestone (2.2 m); the 3rd member consists of thick-bedded, dark microsparitic limestone (17.4 m); and the 4th member is a thin-bedded dolomitic limestone (0.6 m). The Kuanchuanpu Formation is underlain conformably by siliceous dolostone of the Ediacaran Dengying Formation, and overlain disconformably by black shale of the Guojiaba Formation. The fossil collection reported here is exclusively from the lower part of the 2nd member (Figs. 1.2, 2). The phosphatic limestone from the 2nd member contains abundant apatite (Fig. 1.3), implying that the Fortunian Yangtze Sea contained a high amount of phosphate, which increased preservation potential of the microfossils.

The lower part of the 2nd member of the Kuanchuanpu Formation at Zhangjiagou section has yielded abundant SSFs, including the taxa *Anabarites* Missarzhevsky in Voronova and Missarzhevsky, 1969 (Fig. 3.1–3.6), *Protohertzina* Missarzhevsky, 1973 (Fig. 3.7–3.9), long and internally hollow tubes (Fig. 3.10, 3.11), *Acanthocassis* He and Xie, 1989 (Fig. 3.12), multi-branched fossils (Fig. 3.13), maikhanellid shells (Fig. 3.14), and siphononuchitid spicule bundles (Fig. 3.15, 3.16). The occurrence of *Anabarites trisulcatus*

Missarzhevsky in Voronova and Missarzhevsky, 1969 (Fig. 3.1), *Protohertzina anabarica* Missarzhevsky, 1973 (Fig. 3.7, 3.8), and *Protohertzina unguiformis* Missarzhevsky, 1973 (Fig. 3.9) indicates that the key horizon yielding the present materials is part of the SSFs *Anabarites trisulcatus*-*Protohertzina anabarica* Assemblage Zone, which has been estimated to be ca. 535 Ma (Steiner et al., 2007, 2014) within the Fortunian Stage (Peng et al., 2012).

Materials and methods

All specimens were extracted from the phosphatic limestone (Fig. 1.3) from the lower part of the 2nd member of the Kuanchuanpu Formation at Zhangjiagou section in southern Shaanxi, South China (Figs. 1.1, 2). The rock samples were dissolved in acetic acid following procedures described in Müller (1985). Rock fragments were immersed in diluted acetic acid (~8%), and residues were retrieved regularly after seven days of reaction. The undissolvable residues were air dried, and microfossils were handpicked using a binocular microscope. Selected microfossils were mounted on aluminum stubs of pin type for

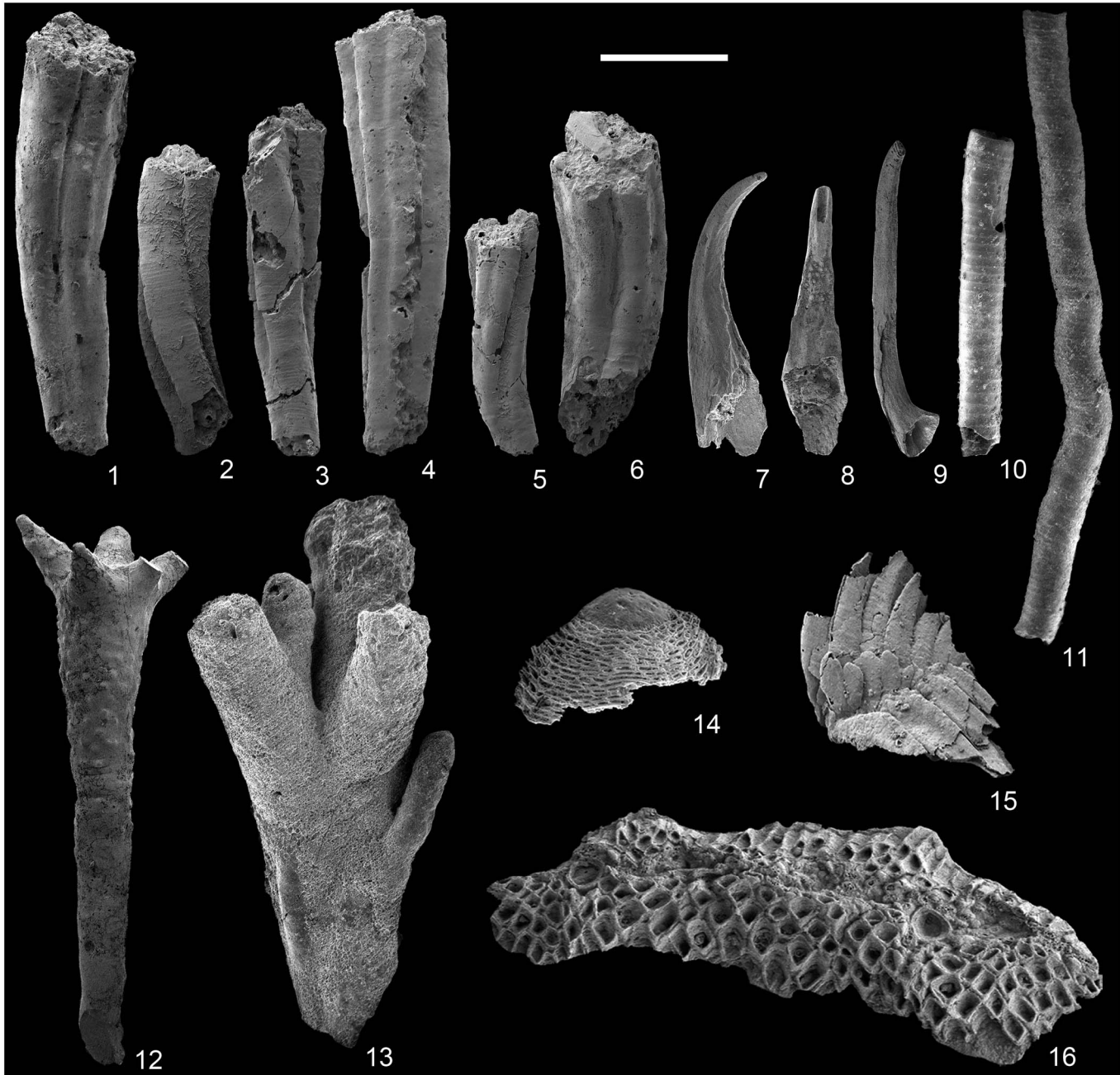


Figure 3. Small shelly fossils from the Zhangjiagou Lagerstätte. (1) *Anabarites trisulcatus* Missarzhevsky in Voronova and Missarzhevsky, 1969, UMCU.XXAN14068; (2, 3) *Anabarites* ex gr. *A. trisulcatus* Missarzhevsky in Voronova and Missarzhevsky, 1969, form 2; (2) UMCU.XXAN14069; (3) UMCU.XXAN14070; (4–6) *Anabarites hexasulcatus* (Missarzhevsky, 1974); (4) UMCU.2014WB526; (5) UMCU.2014WB528; (6) UMCU.2014WB238; (7, 8) *Protohertzina anabarica* Missarzhevsky, 1973; (7) UMCU.2014HZ001; (8) UMCU.2014HZ002; (9) *Protohertzina unguiformis* Missarzhevsky, 1973, UMCU.2014HZ003; (10, 11) long tubes with annular rings, internally hollow; (10) UMCU.2013XXG002; (11) UMCU.2013XXG001; (12) *Acanthocassis orthacanthus* (Yang and He, 1984) He and Xie, 1989, with a long stalk and five major branches, UMCU.XJ5-3A; (13) a multi-branched specimen, possible internal mold, UMCU.2014XXG001; (14) a maikhanellid shell, UMCU.XXMH1416; (15, 16) siphononuchitid spicule bundles; (15) UMCU.XXLG1406; (16) UMCU.XXLG1410. Scale bar represents 1 mm (1–13), and 410 μ m (14–16).

observation under scanning electron microscopy (SEM). SEM images were further processed using Adobe Photoshop CS5, with the background cleared away and the brightness and contrast of the whole images adjusted. Photographs of the Zhangjiagou section (Fig. 1.1, 1.2) and the hand specimens of the phosphatic limestone (Fig. 1.3) were taken using a Canon 5DsR digital camera (with a Canon EF 11–24 mm F/4 lens), and were also processed using Adobe Photoshop CS5, with

brightness and contrast of the whole images adjusted. The location map and stratigraphic column of the Zhangjiagou section were produced using Adobe Illustrator CS5.

The data matrices of the phylogenetic analyses are provided in the Supplementary Data (Data matrices 1–4), and were analyzed using software TNT (Goloboff et al., 2008). For each calculation, the TNT settings remained almost the same. For example, all characters were equally weighted, the gap mode was treated as

missing, and the TNT memory was enlarged to 10,000 trees. In the phylogenetic analysis of cnidarians, collapsing rule 3 (max. length = 0) is adopted, consistent with the default collapsing rule of PAUP (Swofford, 2002), because PAUP was adopted in the original phylogenetic analysis of Dong et al. (2016) with default settings. In the phylogenetic analysis of cycloneurians, collapsing rule 1 (min. length = 0) is adopted, and this is the default collapsing rule of TNT. Traditional search (heuristic search with 1,000 random stepwise addition replicates saving up to 10 trees per replicate, followed by TBR branch swapping) was adopted. The cladograms were redrawn with Adobe Illustrator CS5.

Repositories and institutional abbreviations.—The current specimens are now deposited in the collection of the University Museum of Chang'an University (UMCU), Xi'an, China.

Results

Olivoooides multisulcatus.—Materials assigned to *Olivoooides multisulcatus* Qian, 1977 are less common in our collection, and only three specimens are presented here (Fig. 4.1–4.3). They represent a progressive developmental sequence from a late embryonic stage (Fig. 4.1) to a large individual (Fig. 4.3). *Olivoooides multisulcatus* differs from *O. mirabilis* (Yue in Xing et al., 1984) mainly by their different sizes, with the embryos and hatched stages being much smaller than those of *O. mirabilis* (Steiner et al., 2014). In addition, the hatched stages of *O. multisulcatus* have five rows of triangular thickenings on their post-embryonic tissues (Fig. 4.3).

Olivoooides mirabilis.—*Olivoooides mirabilis* is represented by two specimens here, including a pre-hatching embryo (Fig. 4.4) and a fragment of a large individual (Fig. 4.5). The fragment (Fig. 4.5) is part of the abapical end, with three distal annuli and one cirlet of 10 terminal lobes preserved. It should be noted that the diameter of this fragment is ~3.16 mm. If the maximum diameter of the hatched stages is positively related with the total length, the completely preserved length is estimated to be ~8.6 mm, with at least 50 annuli. This is a very large individual, and it implies that the adults of *O. mirabilis*, and perhaps those of *Olivoooides multisulcatus* and *Quadrropygites quadratacris*, could have reached centimeter-scale dimension with more than 50 annuli on their post-embryonic tissue.

Pseudoooides prima.—Only three embryos assignable to *Pseudoooides prima* Qian, 1977 were recovered (Fig. 5.1–5.3). The embryos have a so-called “germ-band” area made of 12 compartments separated into six pairs by a median furrow and five lateral furrows. These compartments are arranged in biradial symmetry, defining the fundamental symmetry pattern of *P. prima*. The remaining part of the embryos is undifferentiated. The fossils are usually internally hollow or filled with secondary mineral matter. Generally, they are slightly collapsed and, therefore, the outer surface is much wrinkled.

Quadrropygites quadratacris.—The general morphology of *Quadrropygites quadratacris* has been described by Steiner et al. (2014) and Liu et al. (2014a), and will not be repeated here. Liu et al. (2014a) reconstructed the post-embryonic development of *Q. quadratacris* and demonstrated the growth mode of the terminal lobes and annuli. The current material also exhibits a

difference in the number of annuli of the post-embryonic tissue, ranging from two (Fig. 6.1, 6.2), three (Fig. 6.3), four (Fig. 6.4), five (Fig. 6.5), six (Fig. 6.6), seven (Fig. 6.7), 10 (Fig. 6.8), 11 (Fig. 6.9), 14 (Fig. 6.10), to at least 18 (Fig. 6.11). Combined with the previously reported data (Liu et al., 2014a; Steiner et al., 2014), the number of annuli on the post-embryonic tissues of *Q. quadratacris* extended continuously from one to at least 18, and this is interpreted to be a consecutive post-embryonic developmental sequence. It should be noted that the specimen with 18 annuli (Fig. 6.11) is exceptionally large, ~3.28 mm long and 1.2 mm maximum width. Its abapical end is broken, thus the total length and number of annuli are uncertain.

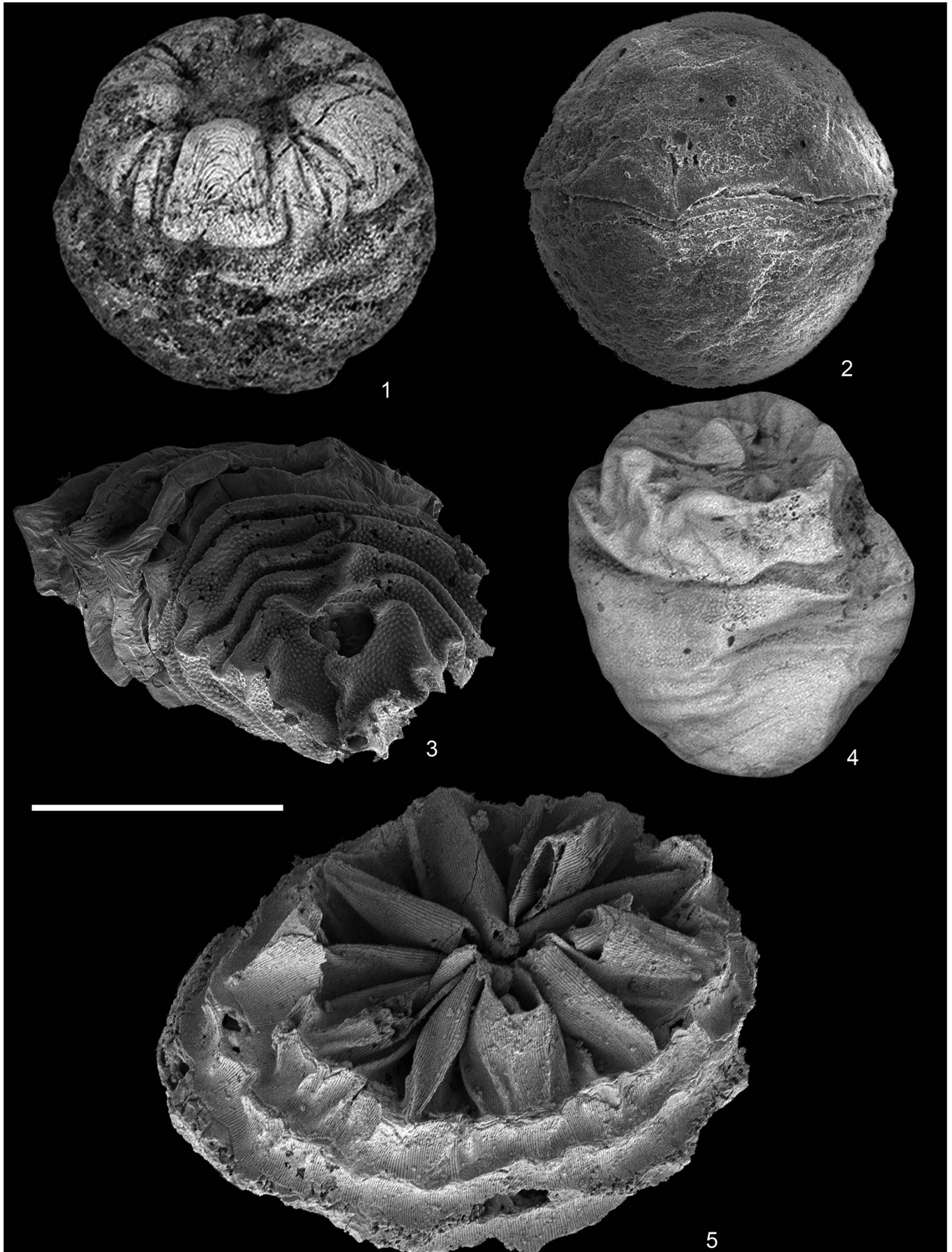
Eopriapulites sphinx.—*Eopriapulites sphinx* Liu and Xiao in Liu et al., 2014b is a millimeter-sized animal. The adult body length/width ratio is about more than 10, thus the animal looks a little slender (Shao et al., 2016). A detailed description of *E. sphinx* was given in Liu et al. (2014b) and Shao et al. (2016), and so is not repeated here. The ontogeny and developmental mode of *E. sphinx* is currently unknown because its embryonic and younger juvenile stages are lacking.

The current specimens (Fig. 7.1, 7.4) are proposed to be trunk parts of very large juveniles or adults. They are regarded as conspecific with *Eopriapulites sphinx* due to co-occurrence and identical morphology of the trunk annuli (Fig. 7.2, 7.3, 7.5, 7.6). UMCU.2014XXSY018 (Fig. 7.1) is ~2.55 mm long and 550 μm wide, whereas UMCU.2014XSY016 (Fig. 7.4) has a width of 750 μm. These specimens are preserved in the Orsten-type preservation, and this type of preservation usually includes individuals no larger than 2 mm in size, and larger specimens would be fragmented during taphonomy (Maas et al., 2006). Evidently, the original animals that yielded these fragments should have a body length far more than 2 mm in size, possibly even centimeter scale.

Phylogenetic perspectives

Pseudoooides prima.—*Pseudoooides prima* is reported with only embryonic stages exclusively from the Fortunian Stage of South China (Steiner et al., 2004b; Donoghue et al., 2006b). The information on *P. prima* comes exclusively from the outer surface because no internal structures have been discovered yet. The affinity of *Pseudoooides* has been debated for a long time (Donoghue et al., 2015). Steiner et al. (2004b) interpreted the paired compartments as a possible “germ band”, and compared them with the “germ band” of modern arthropod embryos. Based on this assumption, Steiner et al. (2004b) connected the embryos of *P. prima* and some co-occurring arthropod or arthropod-like fragments in a consecutive ontogenetic sequence. The occurrence of arthropod fossils in the Fortunian Stage is dubious, although a number of SSFs can be interpreted as arthropod fragments (Yuan et al., 2002). However, an arthropod affinity of *P. prima* is unlikely and was challenged by Donoghue et al. (2006b, 2015) because the anatomy of *P. prima* is unusual for any modern arthropods.

Here, we propose a new hypothesis, namely that the material of *Pseudoooides prima* is actually synonymous with embryos of the taxon of co-occurring hexangulaconulariids. Hexangulaconulariids exhibit biradial symmetry, and contain two genera: *Arthrochites* and *Hexaconularia* (Conway Morris and Chen, 1992). In the Kuanchuanpu Formation of Zhangjiagou section, *P. prima* co-



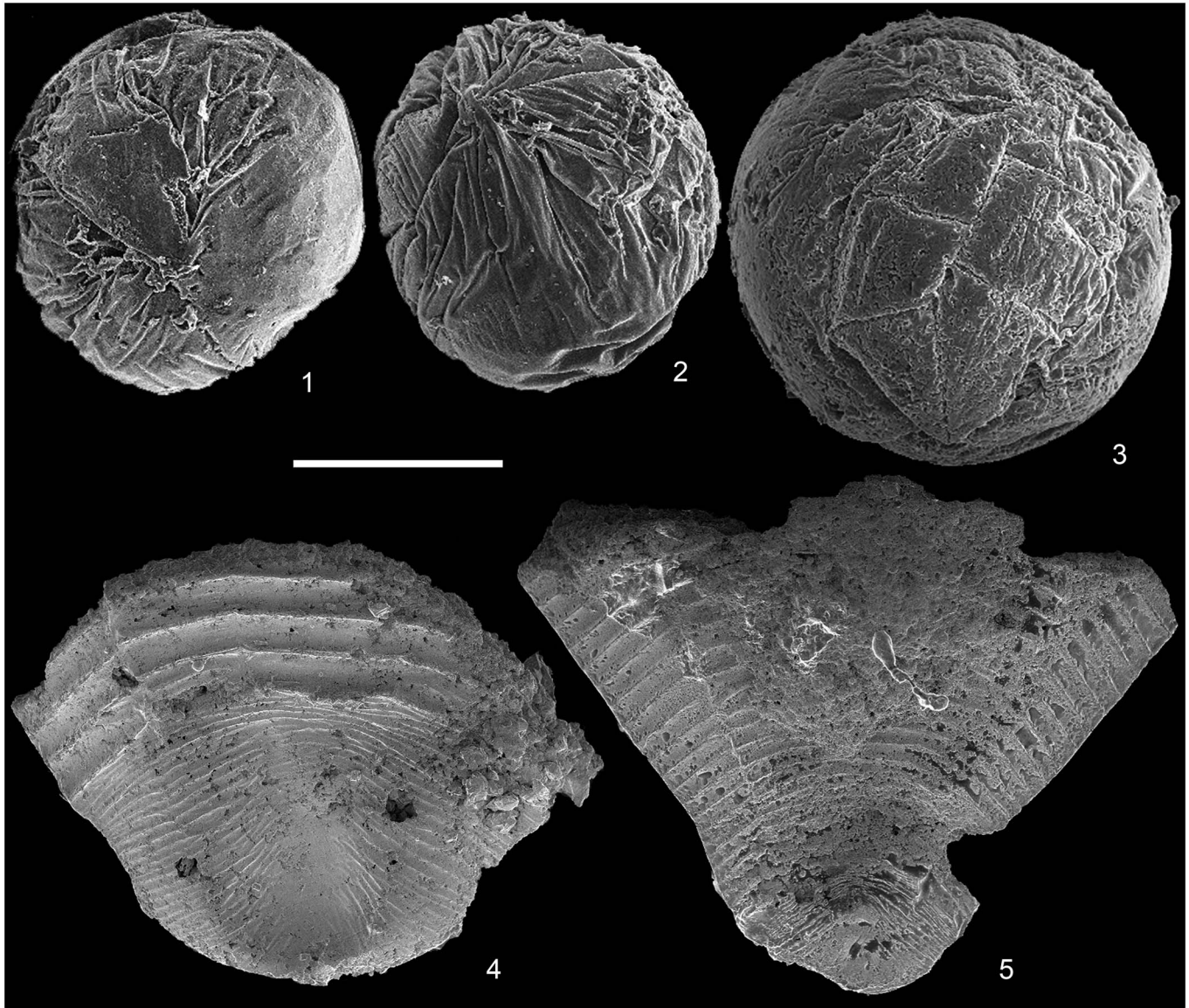


Figure 5. Embryos of *Pseudoooides prima* Qian, 1977 (1–3) and hatched stages of *Hexaconularia sichuanensis* He and Yang, 1986 (4, 5) from the Zhangjiagou Lagerstätte. (1) UMCU.XXPT230; (2) UMCU.XXPT220; (3) UMCU.XXPT200; (4) UMCU.2013ZS001; (5) UMCU.2013ZS002. Scale bar represents 200 μm (1–3), 270 μm (4), and 593 μm (5).

occurred with *Hexaconularia sichuanensis* (Fig. 5.4, 5.5). Material of *H. sichuanensis* is biradially symmetric (Van Iten et al., 2010), while the pinched “germ band” area of *P. prima* is also biradially symmetric. Animals with biradial symmetry are less common in the Kuanchuanpu Formation, thus *P. prima* and *H. sichuanensis*, both with biradial symmetry, are possibly conspecific, at least being close relatives. In *Olivoooides* and *Quadrapyrgites*, the embryonic tissues were retained in the hatched stages as the apical parts. Likewise, the pinched “germ-band” area of *P. prima* embryos might be compared with the apical area of *H. sichuanensis*, both of which are biradially symmetric. But evidently, there is a large morphological gap between them, and a detailed investigation of that matter, including recovery of more embryos of later

embryonic stages of *P. prima*, is urgently demanded. Since hexangulaconulariids were regarded as an intermediate form between conulariids and *Olivoooides* (Bengtson and Yue, 1997), a similar phylogenetic position is assumed for *Pseudoooides*, and *Pseudoooides* might also be a coronate scyphozoan.

Olivoooides and *Quadrapyrgites*.—*Olivoooides* and *Quadrapyrgites* have exclusively been reported from the Cambrian Fortunian Stage of South China (Donoghue et al., 2015). Due to comparable morphology and ontogenetic sequence, Steiner et al. (2014) proposed that *Olivoooides* and *Quadrapyrgites* should be sister groups, constituting the taxon Olivoooidae Steiner et al., 2014, and might be early cycloneuralians.

Figure 4. *Olivoooides multisulcatus* Qian, 1977 (1–3) and *Olivoooides mirabilis* (Yue in Xing et al., 1984) (4, 5) from the Zhangjiagou Lagerstätte. (1) An embryo with five principal lobes and five subordinate lobes in pentaradial symmetry, UMCU.XXPT004; (2) an embryo with initially developed triangular thickenings, UMCU.2014XXPT006; (3) a hatched individual, latero-apical view, UMCU.2014XXPT008; (4) an embryo, UMCU.XXPT005, lateral view; (5) a fragment of the oral part, UMCU.2014XXPT009. Scale bar represents 500 μm (1–3), 856 μm (4), and 1.32 mm (5).

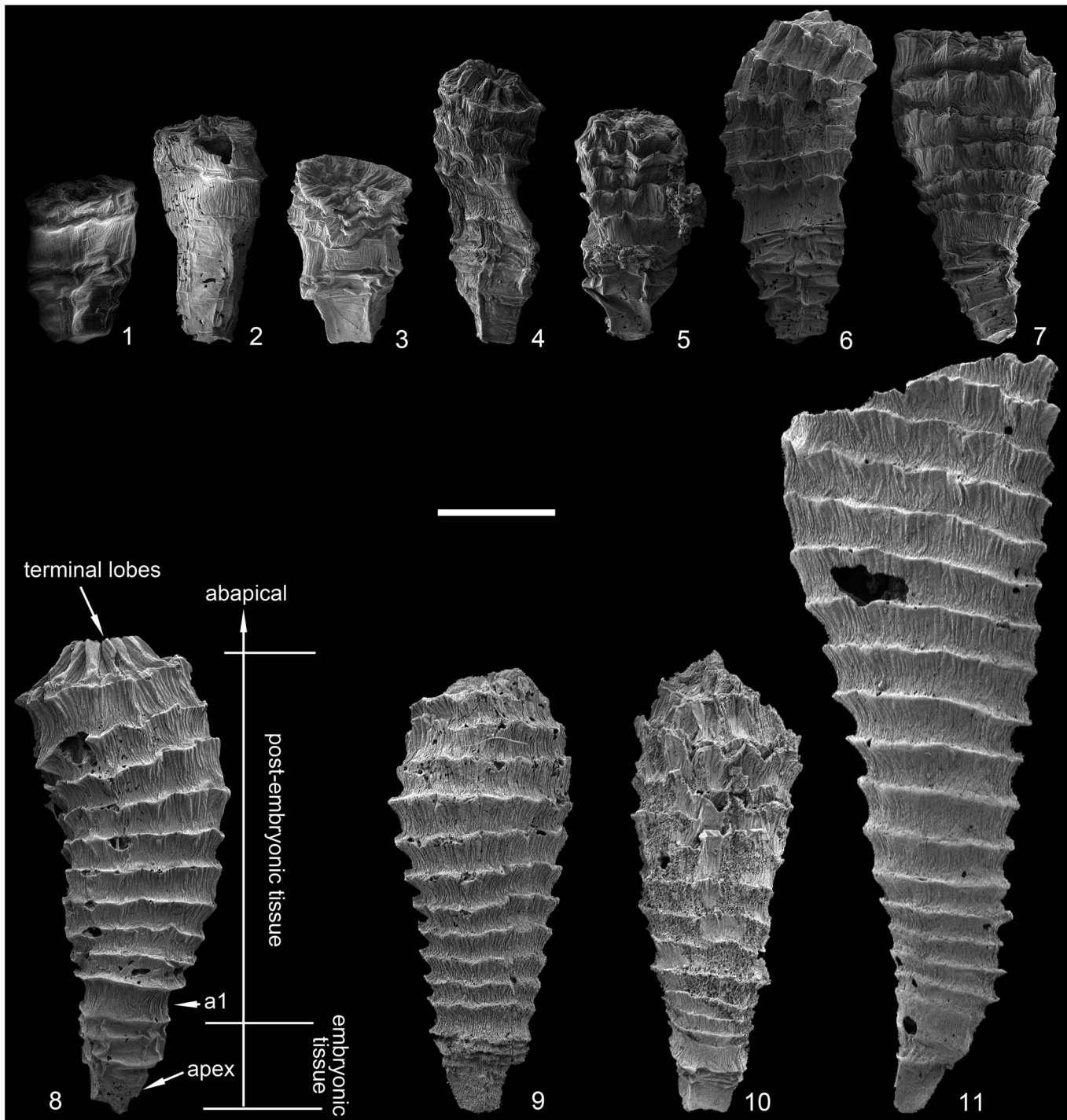


Figure 6. Hatched stages of *Quadrapyrgites quadratacris* (Li, 1984) Steiner et al., 2014 from the Zhangjiagou Lagerstätte. (1, 2) With two annuli; (1) UMCU.2014XQ001; (2) UMCU.XQ002; (3) with three annuli, UMCU.XQ005; (4) with four annuli, UMCU.XQ006; (5) with five annuli, UMCU.XQ007; (6) with six annuli, UMCU.XQ008; (7) with seven annuli, UMCU.XQ009; (8) with 10 annuli, UMCU.2014XQ015; (9) with 11 annuli, UMCU.2014XQ016; (10) with 14 annuli, UMCU.2014XQ017; (11) with at least 18 annuli, UMCU.2014XQ018. Abbreviation a1 represents 1st annulus. Scale bar represents 500 μm .

As radiate animals, the affinity of olivoids falls better within Cnidaria (but see Steiner et al., 2014; see discussion below). Under the cnidarian hypothesis, the preserved tubes of olivoids are interpreted as periderm (exoskeleton) that completely embraces the internal soft part anatomy. Among modern cnidarians, only coronate scyphozoans have this type of periderm, thus *Olivoides* was regarded as a coronate scyphozoan when it was interpreted as a fossil

embryo for the first time (Bengtson and Yue, 1997; Yue and Bengtson, 1999). As the sister group of *Olivoides*, the taxon *Quadrapyrgites* should have the same affinity. The coronate scyphozoan hypothesis has been cited by other researchers and now takes a central place for the affinity of *Olivoides* and *Quadrapyrgites* (Bengtson and Yue, 1997; Dong et al., 2013, 2016; Liu et al., 2014a).

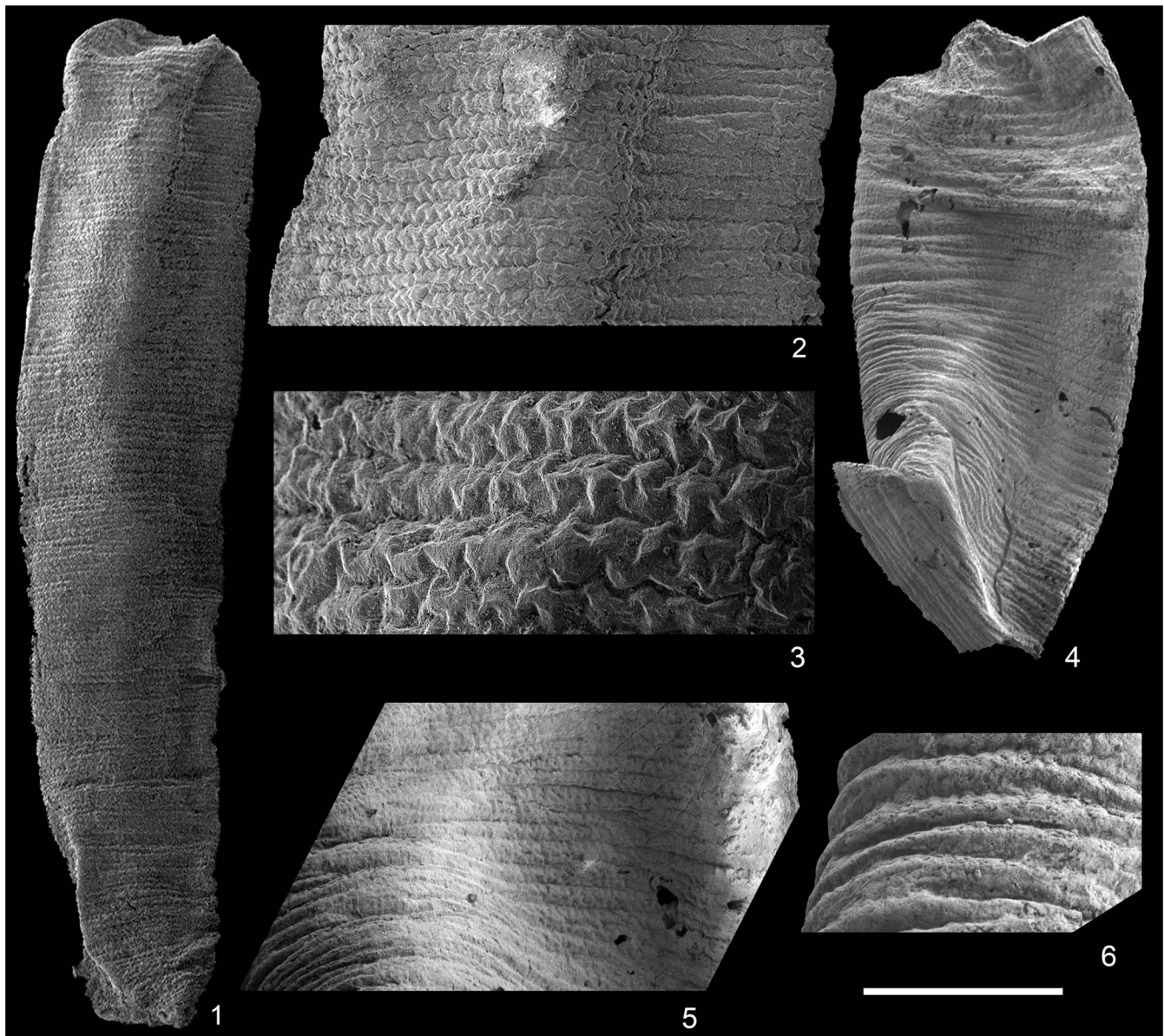


Figure 7. *Eopriapulites sphinx* Liu and Xiao in Liu et al., 2014b from the Zhangjiagou Lagerstätte. (1) A trunk part representing part of a large individual, UMCU.2014XXSY018; (2) close-up of (1), showing the dense annuli; (3) close-up of (1), showing the zig-zag-shaped structures on the annuli; (4) a trunk part of a very large individual, UMCU.2014XSY016; (5, 6) close-up views of (4), showing the dense annuli. Scale bar represents 500 μm (1, 4), 194 μm (2), 63 μm (3), 232 μm (5), and 91 μm (6).

The coronate scyphozoan hypothesis is largely dependent on similarity between olivoids and the periderm of modern coronate scyphozoans, because no convincing internal soft-part anatomy of olivoids has been reported. In addition to the possible periderm shared between olivoids and modern coronate scyphozoans, Dong et al. (2016) proposed a second feature, the periderm teeth, as a possible uniting character. Dong et al. (2016) regarded the “inner walls” within the embryos as possible ectoderm, and most importantly, the “paired pentaradial projections” as periderm teeth. In their phylogenetic analysis, *Olivoides* and *Quadrorygites* are resolved as sister groups of coronate scyphozoans, and the monophyly of conulariids, Coronatae, *Olivoides* and *Quadrorygites* is well supported by two synapomorphies (the presence of an all-embracing periderm and the presence of periderm teeth). However, the periderm teeth interpretation

might be dubious. According to Jarms (1991), the periderm teeth of coronate scyphozoans should be located on the inner side of the periderm. If this is applied to the specimens of *Olivoides*, the periderm teeth should be located on the inner side of the stellate tissues or on the inner side of the striated tissues. But in Dong et al.’s (2016) interpretations, the periderm teeth are located on the inner side of the “inner walls” (possible ectoderm according to their interpretation), while the periderm, on which the periderm teeth should be located, is not preserved at all. Furthermore, as part of the periderm, the periderm teeth should have the same fossilization potential, but in most cases, the inner side of the tubes is smooth without any signs of the development of periderm teeth. Therefore, the periderm teeth interpretation for the “internal pentaradial projections” is dubious.

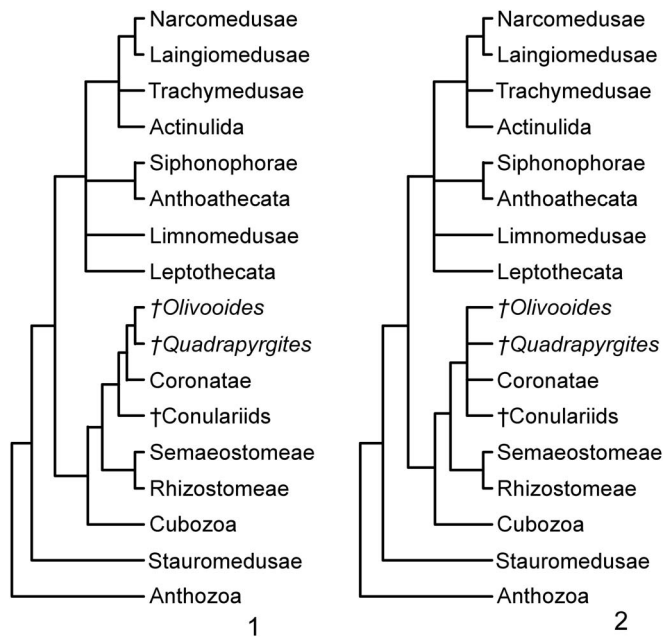


Figure 8. Suggested phylogenetic positions of *Olivoooides* and *Quadrapyrgites*. (1) Strict consensus tree derived from analysis of the original dataset of Dong et al. (2016); (2) strict consensus tree derived from analysis excluding character 88 (presence or absence of periderm teeth). Symbol † in this figure and in Figure 9 denotes extinct taxa.

In order to test the phylogenetic positions of *Olivoooides* and *Quadrapyrgites*, we carried out a phylogenetic analysis. The selected taxa and characters follow Dong et al. (2016). First, we re-analyzed Dong et al.'s dataset (Datamatrix 1), and got 10 most parsimonious trees (MPTs), Tree Length (TL) = 127, Consistency Index (CI) = 0.740, Retention Index (RI) = 0.738. The strict consensus tree presented (Fig. 8.1) is consistent with Dong et al.'s result (2016, their fig. 10A). In order to test the bearing of the presence of periderm teeth (the 88th character) upon the topology of the phylogenetic tree, we deleted the coding of the 88th character, and re-analyzed the revised datamatrix (Datamatrix 2). We got 40 MPTs, TL = 126, CI = 0.738, RI = 0.734. The strict consensus tree is presented (Fig. 8.2). The monophyly of *Olivoooides*, *Quadrapyrgites*, Conulariids, and Coronatae is still supported, but the internal relationships are collapsed.

Without the inclusion of the presence of periderm teeth, the internal relationships of *Olivoooides*, *Quadrapyrgites*, conulariids, and Coronatae are not resolved in the current study (Fig. 8.2). However, the monophyly of *Olivoooides*, *Quadrapyrgites*, conulariids, and Coronatae is still supported by one character—the presence of an all-embracing periderm. The interpretation of the periderm teeth is highly doubted, and should not be coded in the phylogenetic analysis currently.

Eopriapulites sphinx.—The cuticular scalids of modern scalidophorans are internally hollow up to the tip and contain sensory cells that lead to a hole distally, whereas the hooks of nematoids are solid (Schmidt-Rhaesa, 1998). Modern scalidophorans have, plesiomorphically, both longitudinal and circular muscles in their

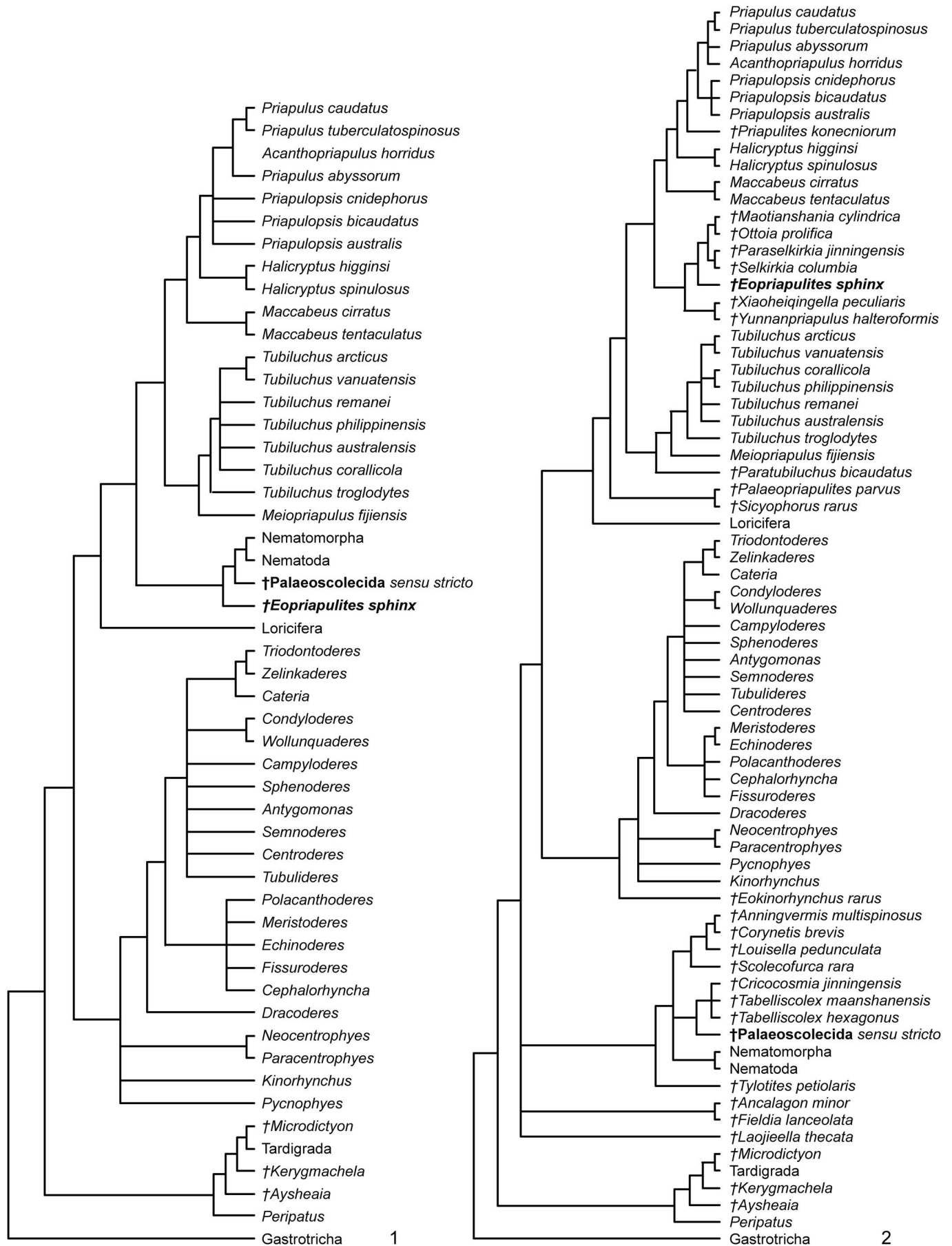
subepidermal muscle tube. Contraction of the circular muscles during locomotion causes annular wrinkling of their cuticle, thus scalidophorans could be annulated. In contrast, nematoids lack circular muscles, retaining only longitudinal muscles, and they evolved internal cuticular longitudinal thickenings. These two features together result in a different mode of locomotion, a kind of wriggling in zig-zag shape. The trunk of nematoids is usually long and thin. However, annulation may occur in certain nematodes like in *Desmoscolex frontalis* (Decraemer, 1986, his fig. 5B). *Eopriapulites sphinx* has a body consisting of internally hollow introvert scalids, collar scalids, and an annulated trunk, suggesting a systematic position within the Scalidophora. However, *E. sphinx* lacks characters that allow it to be assigned to any in-group Scalidophora, and this taxon is interpreted as a stem-lineage derivative of Scalidophora, an assignment that is also supported by phylogenetic analyses (Liu et al., 2014b; Shao et al., 2016).

The exact phylogenetic assignment of *Eopriapulites* is founded on the assumption that the ground pattern of each node in the phylogenetic tree of Cycloneuralia is well resolved. But unfortunately, there are many conflicts and uncertainties about the ground pattern characters of Cycloneuralia and its in-groups, Nematoida, and Scalidophora. For example, it is uncertain whether the stem species (= last common ancestor) of Cycloneuralia has internally hollow or solid introvert scalids/hooks. The occurrence of both longitudinal and circular muscles in the body wall of Scalidophora is a plesiomorphic feature retained from the last common ancestor of Cycloneuralia/Nemathelminthes and Bilateria (Ax, 2003; Nielsen, 2012). Absence of circular muscles in modern nematoids is a secondary loss, hence an autapomorphy of Nematoida. Therefore, assignment of *Eopriapulites* to the Scalidophora based on internally hollow scalids and an annulated trunk might be incorrect because these two characters may be simply plesiomorphic states, referring to the stem species of Cycloneuralia. *Eopriapulites* would still belong to Cycloneuralia, but assignment to an in-group requires knowledge about more morphologically significant details.

In order to further test the phylogenetic position of *Eopriapulites*, we carried out a number of phylogenetic analyses. The coded characters followed those used by Zhang et al. (2015), and the data matrices are provided in the Supplementary Data (Datamatrices 3 and 4). The palaeoscolecoid species, *Palaeoscolex piscatorum* Whittard, 1953, *Chalazoscolex pharkus* Conway Morris and Peel, 2010, *Xystoscolex boreogyrus* Conway Morris and Peel, 2010, and *Guanduscolex minor* Hu et al., 2008, are replaced with Palaeoscolecida sensu stricto (Harvey et al., 2010). *Markuelia humanensis* is not included in the analysis. Dong et al. (2004) proposed that *M. humanensis* should be a direct developer without larval stages, and under such condition *M. humanensis* can be included in the phylogenetic analysis because the adults and the pre-hatching embryos have similar morphology. However, further development of *M. humanensis* is unknown because we lack information on its post-embryonic, free-living stages (Haug et al., 2009).

Parsimony analysis (Datamatrix 3) including extant cycloneuralians plus *E. sphinx* and Palaeoscolecida sensu stricto yielded 429 MPTs (TL = 249, CI = 0.683, RI = 0.898). The 50% majority rule consensus tree (Fig. 9.1) resolves *E. sphinx* and Palaeoscolecida

Figure 9. Suggested phylogenetic positions of *Eopriapulites* and Palaeoscolecida sensu stricto. (1) 50% majority rule consensus tree derived from analysis including extant cycloneuralians plus *Eopriapulites sphinx* and Palaeoscolecida sensu stricto; (2) 50% majority rule consensus tree derived from analysis including extant and extinct cycloneuralians.



sensu stricto as close relatives of extant Nematoida. Parsimony analysis (Datamatrix 4) with large sampling including extant and extinct cycloneurians yielded 1080 MPTs (TL = 338, CI = 0.55, RI = 0.854). The 50% majority rule consensus tree (Fig. 9.2) resolves Palaeoscolecida sensu stricto, together with some cycloneurians from Burgess Shale-type lagerstätten, as close relatives of extant Nematoida, while *E. sphinx* and some other early cycloneurians are resolved within crown-group Priapulida.

From previous and the current analyses, it is evident that the phylogenetic position of *Eopriapulites* is heavily influenced by the taxa included in the analyses. *Eopriapulites* can be resolved as stem-lineage derivative of Scalidophora (Liu et al., 2014b; Shao et al., 2016), stem-lineage derivative of Nematoida, or even crown-group Priapulida, thus its position is heavily unstable. Based on current knowledge of the ground pattern of Scalidophora, Nematoida, and Cycloneuralia, *Eopriapulites* has an uncertain position and should be assigned to total-group Cycloneuralia.

Discussion

Debate about the affinity of olivoids.—Though traditionally accepted as possible coronate scyphozoans, many other hypotheses have been proposed for *Olivoides* and/or *Quadrapyrgites*, including the echinoderm hypothesis (Chen, 2004), cubozoan cnidarian hypothesis (Han et al., 2016a, b), stem-lineage cycloneurialian hypothesis (Steiner et al., 2014), and stem lineage of Diploblastica hypothesis (Yasui et al., 2013). The echinoderm hypothesis has been criticized by many authors (e.g., Dong et al., 2013, 2016; Liu et al., 2014a) and can be effectively rejected. The discussion here focuses on the stem-lineage cycloneurialian hypothesis in light of the oldest known cycloneurians recovered from the Fortunian Stage in recent years, and on the cubozoan hypothesis that competes with the scyphozoan hypothesis within a broader cnidarian interpretation.

Bengtson and Yue (1997) originally noted the similarity between *Punctatus* tubes and the loricate larvae of Priapulida. Steiner et al. (2014) compared the olivoid tubes with the preloricate larvae of modern priapulids. Modern pre-loricate larvae of priapulids do not feed and lack an anus, but an anus is developed immediately after the second loricate larval stage (Wennberg et al., 2009). The known material assigned to olivoids lacks an anus throughout the whole ontogeny (Yasui et al., 2013; Steiner et al., 2014). Annuli are added one by one during elongation of the tubes (Liu et al., 2014a). Based on the Zhangjiagou material (Figs. 4.5, 6.11), the adults of olivoids are estimated to have reached centimeter scale with more than 50 annuli. Accordingly, if olivoids actually represented cycloneurians, the absence of an anus would imply growth to 50 annuli requiring at least 49 separate molts without any food intake. The physiological energetics of molting requires corresponding nutrition that does not support a non-feeding larvae hypothesis. Olivoids are interpreted here as being radially symmetric, contrasting completely with the bilateral symmetry of cycloneurians. The oldest known cycloneurians, exemplified by *Eopriapulites* and *Eokinorhynchus* (Zhang et al., 2015; Shao et al., 2016), along with the younger *Shergoldana* (Maas et al., 2007) had already developed an introvert armored with scalids. Olivoids lack not only an anus, but also the specific characteristics of cycloneurians, such as an introvert with scalids. Therefore, the stem-lineage cycloneurialian hypothesis is not supported here.

Han et al. (2013, 2016a, b) regarded some fossil embryos from the Kuanchuanpu Formation at the Shizhonggou section as cubozoans. This hypothesis was based on plausible internal biological structures, such as possible tentacles, frenula, oral marginal lappets, and gastric saccule-like humps, which might be more compatible with those of modern cubomedusozoans. Among these fossil embryos belonging to species of *Olivoides* and *Quadrapyrgites*, Han et al. (2016b) recognized a series of the same internal structures of embryos of *Olivoides multisulcatus* and described them following the terminology of modern cubomedusozoans. This methodology implies that the embryos are direct developers, and they would hatch directly into juvenile cubomedusozoans without passing a planular phase and a polypoid phase. Following this hypothesis, the hatched stages of *Olivoides* and *Quadrapyrgites* have to be regarded as stalked medusoid stages, with the periderm embracing the internal cubomedusozoans completely. The current material from the Zhangjiagou section implies that the stalked stages are continuously developed, extending from small hatchlings with only one annulus to large individuals with ~50 annuli. Medusoid stages in a stalked lifestyle occur only in modern staurozoans, which are interpreted as the sister group of all other Medusozoa (Miranda et al., 2016). Accordingly, the cubozoan hypothesis demands that the stalked medusoid forms occurred independently twice—once in early cubozoans, such as olivoids, and once in modern staurozoans. It also demands that the all-embracing periderm occurred independently twice—once in early cubozoans, such as olivoids, and once in modern coronate scyphozoans. This is a rather un-parsimonious evolutionary scenario for early cnidarian evolution, thus is not favored here.

Eopriapulites as an ancestral cycloneurialian.—It has previously been proposed that the ancestral cycloneurians were macroscopic, “priapulid-like,” introvert-bearing animals. Accordingly, macroscopic palaeoscolecids from the Burgess Shale-type lagerstätten were proposed to represent ancestral cycloneurians or even ancestral ecdysozoans (Budd, 2001, 2003b; Harvey et al., 2010). The palaeoscolecids range from the early Cambrian to late Silurian, ca. 520–420 Ma (Harvey et al., 2010). A potential ancestor should have occurred at least no later than other members of its lineage. But based on the current data, at least three fossil cycloneurians have occurred earlier than the earliest palaeoscolecids: *Markuelia secunda* Val’kov in Val’kov and Karlova, 1984 from the Pestrotsvet Formation of Siberia (ca. 521–525 Ma); *Eopriapulites sphinx* and *Eokinorhynchus rarus* from the lower Fortunian Stage of South China (ca. 535 Ma). The occurrence of these cycloneurians implies that the cycloneurians should have been rooted in the Fortunian Stage, or possibly even earlier, and that the ancestral cycloneurialian/ecdysozoan hypothesis of palaeoscolecids is challenged.

Eopriapulites and *Markuelia* occurred in the Terreneuvian Series, not long after eumetazoan origin and diversification, and earlier than the first occurrence of palaeoscolecids (Cambrian Series 2). Again, *Eopriapulites* and *Markuelia*, with their similar and seemingly plesiomorphic morphology, have been proposed to be early scalidophorans (Shao et al., 2016) or in-group scalidophorans (Dong et al., 2010). However, the current analysis indicates that at least *Eopriapulites* might also be a close relative of Nematoida (Fig. 9.1). The uncertain phylogenetic assignments with

Scalidophora or Nematoida imply that *Eopriapulites* has characters that are shared with both Scalidophora and Nematoida (i.e., with the stem of Cycloneuralia). This is very similar to the younger *Shergoldana australiensis*, which also has been assigned to total group Cycloneuralia. The specific character combination of the only known but exceptionally 3D-preserved specimen of this species, has both nematoid and scalidophoran characters, implying an assignment outside any in-group. An assignment to Nematoida or Scalidophora can even be ruled out based on its well-known morphology (Maas et al., 2007).

A new hypothesis proposed here is that Cycloneuralia might have originated in the Fortunian small shelly faunas rather than in the early Cambrian macrobenthos, implying that the ancestral cycloneurians should have been microscopic, vermiform, introvert-bearing, and have characters more like *Eopriapulites sphinx*. Previous studies have shown that *Markuelia* might be more basal than *Eopriapulites* (Shao et al., 2016), implying that pentaradially symmetric arrangements of introvert scalids occurred earlier than hexaradially symmetric forms. Therefore, the last common ancestor of Cycloneuralia might have possessed an introvert with internally hollow and pentaradially arranged introvert scalids. Internally hollow and pentaradially arranged introvert scalids may have been inherited by the last common ancestor of Scalidophora and possibly also by the lineage leading to modern Nematoida, therefore might have been lost autapomorphically early in this lineage.

Conclusions

The Fortunian Zhangjiagou Lagerstätte has yielded three-dimensionally phosphatized microfossils of radiate animals and cycloneurians. Radiate animals include embryos of *Olivoooides multisulcatus*, *Olivoooides mirabilis*, and *Pseudoooides prima*, as well as putative hatched stages of *O. multisulcatus*, *O. mirabilis*, *Hexaconularia sichuanensis*, and *Quadrapyrgites quadratacris*. These radiate animals represent the diversification of cnidarians in the Fortunian Stage. Cycloneurians are represented by *Eopriapulites sphinx* and trunk fragments possibly related with *Eokinorhynchus rarus* (Zhang et al., 2015, their unnamed forms I and II).

These exceptionally preserved microfossils provide important information on the early diversification of cnidarians and cycloneurians. Based on these fossils, we propose (1) cnidarians have a high diversity in the Fortunian Stage of South China, and symmetry patterns include biradial (*Pseudoooides* and *Hexaconularia*), triradial (*Anabarites*), tetradial (*Quadrapyrgites*), and pentaradial (*Olivoooides* and *Qiniscyphus* Liu, Shao, and Zhang in Liu et al., 2017) symmetry; (2) *P. prima* might be the embryonic stage of the co-occurring *H. sichuanensis*, with the biradial symmetry as a possible uniting feature; (3) the adults of *Olivoooides* and *Quadrapyrgites* might have had a length exceeding 1 cm with more than 50 annuli on the post-embryonic surface, and the unusually large specimens of *Olivoooides* and *Quadrapyrgites* can refute the non-feeding larvae hypothesis for *Olivoooides* and *Quadrapyrgites*; (4) because of the lack of convincing internal soft-part anatomy, *Olivoooides* and *Quadrapyrgites* might better be assigned to coronate scyphozoans, with the all-embracing periderm as a key uniting feature; and (5) the cycloneurians, and possibly the ecdysozoans or nemathelminths, might have originated in the

Fortunian small shelly faunas as part of the meiofauna rather than in the macrobenthos, with their ancestors being similar in morphology with *Eopriapulites sphinx*. As a consequence, ancestral cycloneurians might have possessed pentaradially arranged and internally hollow introvert scalids. Such scalids may have been inherited by the last common ancestors of Scalidophora and Nematoida, used originally exclusively or mainly for locomotion, but were lost early in the crown-group of the Nematoida.

The final important point is that Cambrian cycloneurians cannot all be treated simply as “priapulids” as pointed out by Maas et al. (2007) and Maas (2013) because such an assignment is not justified by any characters. Again, following Maas (2013), we emphasize that the morphology of Cambrian cycloneurians, including *Eopriapulites sphinx*, does not give any hint that Cycloneuralia is the sister taxon of Panarthropoda, as indicated by the Ecdysozoa hypothesis.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (41572007, 41572009), the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (173121), the Youth Innovation Promotion Association, Chinese Academy of Sciences (2016283), Quality Project of Chang’an University (0012-310600161000, 0012-310627171808), College Students’ Innovative Entrepreneurial Training Program of Chang’an University (201710710062, 201710710063, 201710710240, 0012-310600161000, 0012-310627171808) and The Tenth “Challenge Cup” Competition of Chang’an University (C-P-B-2, C-P-B-6, C-P-B-8). Two anonymous referees provided careful revisions and constructive suggestions to this paper. Jisuo Jin and Brock Glenn provided careful technical edits and language polishing. Correspondence should be addressed to HZ (hqzhang@nigpas.ac.cn) or YL (stotto@163.com).

Accessibility of Supplementary Data

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1cn6b>

References

- Ax, P., 2003, *Multicellular Animals: Order in Nature-System Made by Man*, v. III: Berlin Heidelberg, New York, Springer-Verlag, 317 p.
- Bailey, J.V., Joye, S.B., Kalanetra, K.M., Flood, B.E., and Corsetti, F.A., 2007, Evidence of giant sulphur bacteria in Neoproterozoic phosphorites: *Nature*, v. 445, p. 198–201.
- Bengtson, S., and Yue, Z., 1997, Fossilized metazoan embryos from the earliest Cambrian: *Science*, v. 277, p. 1645–1648.
- Bengtson, S., Conway Morris, S., Cooper, B.J., Jell, P.A., and Runnegar, B.N., 1990, Early Cambrian Fossils from South Australia. *Memoir 9 of the Association of Australian Palaeontologists*: Brisbane, Association of Australian Palaeontologists, 364 p.
- Bengtson, S., Cunningham, J.A., Yin, C., and Donoghue, P.C.J., 2012, A merciful death for the “earliest bilaterian”: *Vernanimalcula*: *Evolution & Development*, v. 14, p. 421–427.
- Budd, G.E., 2001, Tardigrades as “stem-group arthropods”: the evidence from the Cambrian fauna: *Zoologischer Anzeiger*, v. 240, p. 265–279.
- Budd, G.E., 2003a, The Cambrian fossil record and the origin of the phyla: *Integrative and Comparative Biology*, v. 43, p. 157–165.
- Budd, G.E., 2003b, Arthropods as ecdysozoans: the fossil evidence, *in* Legakis, A., Sfenthourakis, S., Polymeni, R., and Thessalou-Legaki, M.,

- eds., *The New Panorama of Animal Evolution: Proceedings of the 18th International Congress on Zoology*, p. 479–487.
- Budd, G.E., 2013, At the origin of animals: the revolutionary Cambrian fossil record: *Current Genomics*, v. 14, p. 344–354.
- Budd, G.E. and Jackson, I.S.C., 2015, Ecological innovations in the Cambrian and the origins of the crown group phyla: *Philosophical Transactions B*, v. 371, p. 20150287.
- Chen, J.-Y., 2004, *The Dawn of Animal World*: Nanjing, Jiangsu Science and Technology Press, 366 p.
- Chen, J.-Y., Bottjer, D.J., Oliveri, P., Dornbos, S.Q., Gao, F., Ruffins, S., Chi, H., Li, C.-W., and Davidson, E.H., 2004, Small bilaterian fossils from 40 to 55 million years before the Cambrian: *Science*, v. 305, p. 218–222.
- Chen, J.-Y., Waloszek, D., Maas, A., Braun, A., Huang, D.-Y., Wang, X.-Q., and Stein, M., 2007, Early Cambrian Yangtze Plate Maotianshan Shale macrofauna biodiversity and the evolution of predation: *Palaeogeography Palaeoclimatology Palaeoecology*, v. 254, p. 250–272.
- Chen, L., Xiao, S., Pang, K., Zhou, C., and Yuan, X., 2014, Cell differentiation and germ-soma separation in Ediacaran animal embryo-like fossils: *Nature*, v. 516, p. 238–241.
- Conway Morris, S., and Chen, M., 1992, Carinacitiids, hexangulaconulariids, and *Punctatus*: problematic metazoans from the early Cambrian of South China: *Journal of Paleontology*, v. 66, p. 384–406.
- Conway Morris, S., and Peel, J.S., 2010, New palaeoscolecidan worms from the Lower Cambrian: Sirius Passet, Latham Shale and Kinzers Shale: *Acta Palaeontologica Polonica*, v. 55, p. 141–156.
- Decraemer, W., 1986, Marine nematodes from Guadeloupe and other Caribbean Islands. VI. Taxonomy of the *Desmoscolex frontalis* complex (Desmoscolecini): *Bulletin du Muséum national d' Histoire naturelle de Paris, Series 4*, v. 8A, 2, p. 295–311.
- Dong, X.-P., Donoghue, P.C.J., Cheng, H., and Liu, J.-B., 2004, Fossil embryos from the Middle and Late Cambrian period of Hunan, south China: *Nature*, v. 427, p. 237–240.
- Dong, X.-P., Bengtson, S., Gostling, N.J., Cunningham, J.A., Harvey, T.H.P., Kouchinsky, A., Val'kov, A.K., Repetski, J.E., Stamparoni, M., Marone, E., and Donoghue, P.C.J., 2010, The anatomy, taphonomy, taxonomy and systematic affinity of *Markuelia*: early Cambrian to Early Ordovician scalidophorans: *Palaeontology*, v. 53, p. 1291–1314.
- Dong, X.-P., Cunningham, J.A., Bengtson, S., Thomas, C.-W., Liu, J., Stamparoni, M., and Donoghue, P.C.J., 2013, Embryos, polyps and medusae of the early Cambrian scyphozoa *Olivooides*: *Proceedings of the Royal Society B (Biological Sciences)*, v. 280, p. 20130071.
- Dong, X.-P., Vargas, K., Cunningham, J.A., Zhang, H.Q., Liu, T., Chen, F., Liu, J.-B., Bengtson, S., and Donoghue, P.C.J., 2016, Developmental biology of the early Cambrian cnidarian *Olivooides*: *Palaeontology*, v. 59, p. 387–407.
- Donoghue, P.C.J., Kouchinsky, A., Bengtson, S., Cunningham, J., Dong, X.-P., Repetski, J.E., Val'kov, A.K., and Waloszek, D., 2006a, Fossilized embryos are widespread but the record is temporally and taxonomically biased: *Evolution & Development*, v. 8, p. 232–238.
- Donoghue, P.C.J., Bengtson, S., Dong, X.-P., Gostling, N.J., Hultgren, T., Cunningham, J.A., Yin, C., Yue, Z., Peng, F., and Stamparoni, M., 2006b, Synchrotron X-ray tomographic microscopy of fossil embryos: *Nature*, v. 442, p. 680–683.
- Donoghue, P.C.J., Cunningham, J.A., Dong, X.-P., and Bengtson, S., 2015, Embryology in deep time, in Wanninger, A., ed., *Evolutionary Developmental Biology of Invertebrates 1: Introduction, Non-Bilateria, Acoelomorpha, Xenoturbellida, Chaetognatha*: Wien, Springer-Verlag, p. 45–63.
- Erwin, D.H., and Valentine, J.W., 2013, *The Cambrian Explosion: The Construction of Animal Biodiversity*: Greenwood Village, Colorado, Roberts and Company, 406 p.
- Erwin, D.H., Laffamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D., and Peterson, K.J., 2011, The Cambrian conundrum: early divergence and later ecological success in the early history of animals: *Science*, v. 334, p. 1091–1097.
- Goloboff, P., Farris, J.S., and Nixon, K., 2008, TNT, a free program for phylogenetic analysis: *Cladistics*, v. 24, p. 774–786.
- Han, J., Kubota, S., Uchida, H.-O., Stanley, G.D. Jr., Yao, X., Shu, D., Li, Y., and Yasui, K., 2010, Tiny sea anemone from the lower Cambrian of China: *PLoS One*, v. 5, p. e13276.
- Han, J., Kubota, S., Li, G., Yao, X., Yang, X., Shu, D., Li, Y., Kinoshita, S., Sasaki, O., Komiya, T., and Yan, G., 2013, Early Cambrian pentamerous cubozoan embryos from South China: *PLoS One*, v. 8, p. e70741.
- Han, J., Kubota, S., Li, G., Ou, Q., Wang, X., Yao, X., Shu, D., Li, Y., Uesugi, K., Hoshino, M., Sasaki, O., Kano, H., Sato, T., and Komiya, T., 2016a, Divergent evolution of medusozoan symmetric patterns: evidence from the microanatomy of Cambrian tetramerous cubozoans from South China: *Gondwana Research*, v. 31, p. 150–163.
- Han, J., Li, G.X., Kubota, S., Ou, Q., Toshino, S., Wang, X., Yang, X.G., Uesugi, K., Masato, H., Sasaki, O., Kano, H., Sato, T., and Komiya, T., 2016b, Internal microanatomy and zoological affinity of the early Cambrian *Olivooides*: *Acta Geologica Sinica (English Edition)*, v. 90, p. 38–65.
- Han, J., Conway Morris, S., Ou, Q., Shu, D.G., and Huang, H., 2017, Meiofaunal deuterostomes from the basal Cambrian of Shaanxi (China): *Nature*, v. 542, p. 228–231.
- Harvey, T.H.P., Dong, X.-P., and Donoghue, P.C.J., 2010, Are palaeoscolecid ancestral ecdysozoans?: *Evolution & Development*, v. 12, p. 177–200.
- Haug, J.T., Maas, A., Waloszek, D., Donoghue, P.C.J., and Bengtson, S., 2009, A new species of *Markuelia* from the Middle Cambrian of Australia: *Memoirs of the Association of Australasian Palaeontologists*, v. 37, p. 303–313.
- He, T.G., and Xie, Y.S., 1989, Some problematic small shelly fossils from the Meishucunian of the lower Cambrian in the western Yangtze Region: *Acta Micropalaeontologica Sinica*, v. 6, p. 111–127.
- He, Y.X., and Yang, X.H., 1986, Early Cambrian coelenterates from Nanjiang, Sichuan: *Bulletin of the Chengdu Institute of Geology and Mineral Resources*, v. 7, p. 31–43.
- Hu, S.X., Li, Y., Luo, H., Fu, X.P., You, T., Pang, J.Y., Liu, Q., and Steiner, M., 2008, New records of palaeoscolecid worms from the early Cambrian of Yunnan, China: *Acta Geologica Sinica (English Edition)*, v. 82, p. 244–248.
- Hultgren, T., Cunningham, J.A., Yin, C., Stamparoni, M., Marone, F., Donoghue, P.C.J., and Bengtson, S., 2011, Fossilized nuclei and germination structures identify Ediacaran “animal embryos” as encysting protists: *Science*, v. 334, p. 1696–1699.
- Jarms, G., 1991, Taxonomic characters from the polyp tubes of coronate medusae (Scyphozoa, Coronatae): *Hydrobiologia*, v. 216/217, p. 463–470.
- Li, P., Hua, H., Zhang, L., Zhang, D., Jin, X., and Liu, Z., 2007, Lower Cambrian phosphatized *Punctatus* from southern Shaanxi and their ontogeny sequence: *Chinese Science Bulletin*, v. 52, p. 2820–2828.
- Li, Z., 1984, The discovery and its significance of small shelly fossils in Hexi area: Xixiang, Shaanxi, *Geology of Shaanxi*, v. 2, p. 73–77.
- Liu, Y., Li, Y., Shao, T., Zhang, H.Q., Wang, Q., and Qiao, J., 2014a, *Quadrapyrgites* from the lower Cambrian of South China: growth pattern, post-embryonic development, and affinity: *Chinese Science Bulletin*, v. 59, p. 4086–4095.
- Liu, Y., Xiao, S., Shao, T., Broce, J., and Zhang, H.Q., 2014b, The oldest known priapulid-like scalidophoran animal and its implications for the early evolution of cycloneuralians and ecdysozoans: *Evolution & Development*, v. 16, p. 155–165.
- Liu, Y., Shao, T.Q., Zhang, H.Q., Wang, Q., Zhang, Y.N., Chen, C., Liang, Y.C., and Xue, J.Q., 2017, A new scyphozoa from the Cambrian Fortunian Stage of South China: *Palaeontology*, v. 60, p. 511–518.
- Maas, A., 2013, Gastrotricha, Cycloneuralia and Gnathifera: the fossil record, in Schmidt-Rhaesa, A., ed., *Handbook of Zoology: Gastrotricha, Cycloneuralia and Gnathifera*: Berlin, De Gruyter, p. 11–28.
- Maas, A., Braun, A., Dong, X.-P., Donoghue, P.C.J., Müller, K.J., Olempska, E., Repetski, J.E., Siveter, D.J., Stein, M., and Waloszek, D., 2006, The ‘Orsten’—more than a Cambrian Konservat-Lagerstätte yielding exceptional preservation: *Palaeoworld*, v. 15, p. 266–282.
- Maas, A., Waloszek, D., Haug, J.T., and Müller, K.J., 2007, A possible larval roundworm from the Cambrian ‘Orsten’ and its bearing on the phylogeny of Cycloneuralia: *Memoirs of the Association of Australasian Palaeontologists*, v. 34, p. 499–519.
- Miranda, L.S., Hirano, Y.M., Mills, C.E., Falconer, A., Fenwick, D., Marques, A.C., and Collins, A.G., 2016, Systematics of stalked jellyfishes (Cnidaria: Staurozoa): *PeerJ*, v. 4, p. e1951.
- Missarzhevsky, V.V., 1973, Konodontobraznye organizmy iz pogranichnykh sloev kembriya i dokembriya Sibirskoi platformy i Kazakhstana. [Conodont-shaped organisms from Precambrian–Cambrian boundary strata of the Siberian Platform and Kazakhstan]: *Trudy Instituta Geologii i Geofiziki SO AN SSSR*, v. 49, p. 53–57.
- Missarzhevsky, V.V., 1974, Novye dannye o drevneishikh okamenelostyakh rannego kembriya Sibirskoi platformy. [New data on the oldest fossils of the early Cambrian of the Siberian Platform], in Zhuravleva, I.T., and Rozanov, A.Y., eds., *Biostratigrafiya i paleontologiya nizhnego kembriya Evropy i severnoi Azii*. [Biostratigraphy and paleontology of the Lower Cambrian of Europe and northern Asia]: Moscow, Nauka, p. 179–189.
- Müller, K.J., 1985, Exceptional preservation in calcareous nodules: *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, v. 311, p. 67–73.
- Nielsen, C., 2012, *Animal Evolution: Interrelationships of the Living Phyla*: Oxford, Oxford University Press, 402 p.
- Peng, S., Babcock, L.E., and Cooper, R.A., 2012, The Cambrian Period, in Gradstein, F.M., Ogg, J.G., Schmitz, M., and Ogg, G., eds., *Geological Time Scale 2012*: Oxford, Elsevier, p. 437–488.
- Peterson, K.J., Cotton, J.A., Gehling, J.G., and Pisani, D., 2008, The Ediacaran emergence of bilaterians: congruence between the genetic and geological fossil records: *Philosophical Transactions of the Royal Society of London B Biological Sciences*, v. 363, p. 1435–1443.

- Qian, Y., 1977, Hyolitha and some problematica from the Lower Cambrian Meishucun Stage in central and southwestern China: *Acta Palaeontologica Sinica*, v. 16, p. 255–275.
- Qian, Y., and Bengtson, S., 1989, Palaeontology and biostratigraphy of the Early Cambrian Meishucunian Stage in Yunnan Province: *South China, Fossils and Strata*, v. 24, p. 1–156.
- Schmidt-Rhaesa, A., 1998, Phylogenetic relationships of the nematomorpha—a discussion of current hypotheses: *Zoologischer Anzeiger*, v. 236, p. 203–216.
- Shao, T.Q., Liu, Y.H., Wang, Q., Zhang, H.Q., Tang, H., and Li, Y., 2016, New material of the oldest known scalidophoran animal *Eopriapulites sphinx*: *Palaeoworld*, v. 25, p. 1–11.
- Steiner, M., Li, G., Qian, Y., and Zhu, M., 2004a, Lower Cambrian Small Shelly Fossils of northern Sichuan and southern Shaanxi (China), and their biostratigraphic importance: *Geobios*, v. 37, p. 259–275.
- Steiner, M., Zhu, M., Li, G., Qian, Y., and Erdtmann, B.-D., 2004b, New Early Cambrian bilaterian embryos and larvae from China: *Geology*, v. 32, p. 833–836.
- Steiner, M., Li, G., Qian, Y., Zhu, M., and Erdtmann, B.-D., 2007, Neoproterozoic to early Cambrian small shelly fossil assemblages and a revised biostratigraphic correlation of the Yangtze Platform (China): *Palaeogeography Palaeoclimatology Palaeoecology*, v. 254, p. 67–99.
- Steiner, M., Qian, Y., Li, G., Hagadorn, J.W., and Zhu, M., 2014, The developmental cycles of early Cambrian *Olivooidea* fam. nov. (?Cycloneuralia) from the Yangtze Platform (China): *Palaeogeography Palaeoclimatology Palaeoecology*, v. 398, p. 97–124.
- Swofford, D.L., 2002, PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods). Version 4: Sunderland, MA, Sinauer Associates.
- Val'kov, A.K., 1983, Rasprostranenie drevneishikh skeletnykh organizmov i korrelyatsiya nizhnei granitsy kembriya v yugo-vostochnoi chasti Sibirskoi platformy [Distribution of the oldest skeletal organisms and correlation of the lower boundary of the Cambrian in the southeastern part of the Siberian Platform], in Khomentovsky, V.V., Yakshin, M.S., and Karlova, G.A., eds., *Pozdnii dokembrii i rannii paleozoi Sibiri, Vendskie otlozheniya*: SO AN SSSR, Novosibirsk, Institut Geologii i Geofiziki, p. 37–48.
- Val'kov, A.K., and Karlova, G.A., 1984, Fauna iz perekhodnykh vendko-kembriiskikh sloev nizhnego techeniya r. Gonam. [The fauna of the transitional Vendian-Cambrian beds in the lower reaches of the River Gonam], in Khomentovsky, V.V., Shenfil, Y.Y., and Yashin, M.S., eds., *Stratigrafiya pozdnego dokembriya i rannego paleozoya, Srednyaya Sibir*: Novosibirsk, Institut Geologii i Geofiziki, p. 12–41.
- Van Iten, H., Zhu, M., and Li, G., 2010, Redescription of *Hexaconularia* He and Yang, 1986 (lower Cambrian, South China): implications for the affinities of conulariid-like small shelly fossils: *Palaeontology*, v. 53, p. 191–199.
- Voronova, L.G., and Missarzhevsky, V.V., 1969, Nakhodki vodoroskei i trubok chervei v pogranichnnykh sloyakh kembriya i dokembriya nal severe Sibirskoi platformy. [Discovery of algae and worm tubes in the Precambrian-Cambrian boundary beds of the northern part of the Siberian Platform]: *Doklady AN SSSR*, v. 184, p. 207–210.
- Wennberg, S.A., Janssen, R., and Budd, G., 2009, Hatching and earliest larval stages of the priapulid worm *Priapulius caudatus*: *Invertebrate Biology*, v. 128, p. 157–171.
- Whittard, W.F., 1953, *Palaeoscolex piscatorum* gen. sp. nov., a worm from the Tremadocian of Shropshire: *The Quarterly Journal of the Geological Society of London*, v. 109, p. 125–136.
- Xiao, S., Zhang, Y., and Knoll, A.H., 1998, Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite: *Nature*, v. 391, p. 553–558.
- Xing, Y., Ding, Q., Luo, H., He, T., and Wang, Y., 1984, The Sinian-Cambrian Boundary of China: *Bulletin of the Institute of Geology, Chinese Academy of Geological Sciences*, v. 10, p. 1–262.
- Xue, Y., Zhou, C., and Tang, T., 1999, “Animal embryos”, a misinterpretation of Neoproterozoic microfossils: *Acta Micropalaeontologica Sinica*, v. 16, p. 1–4.
- Yang, B., Steiner, M., Li, G., and Keupp, H., 2014, Terreneuvian small shelly faunas of East Yunnan (South China) and their biostratigraphic implications: *Palaeogeography Palaeoclimatology Palaeoecology*, v. 398, p. 28–58.
- Yang, X.H., and He, T.G., 1984, New small shelly fossils from lower Cambrian Meishucun Stage of Nanjiang Area, northern Sichuan: *Professional Papers in Stratigraphy and Palaeontology*, v. 13, p. 35–47.
- Yasui, K., Reimer, J.D., Liu, Y., Yao, X., Kubo, D., Shu, D., and Li, Y., 2013, A diploblastic radiate animal at the dawn of Cambrian diversification with a simple body plan: distinct from Cnidaria?: *PLoS One*, v. 8, p. e65890.
- Yuan, X., Xiao, S., Parsley, R.L., Zhou, C., Chen, Z., and Hu, J., 2002, Towering sponges in an Early Cambrian Lagerstätte: disparity between nonbilaterian and bilaterian epifaunal tierers at the Neoproterozoic-Cambrian transition: *Geology*, v. 30, p. 363–366.
- Yue, Z., and Bengtson, S., 1999, Embryonic and post-embryonic development of the Early Cambrian cnidarian *Olivooidea*: *Lethaia*, v. 32, p. 181–195.
- Zhang, H.Q., and Dong, X.-P., 2015, The oldest known larva and its implications for the plesiomorphy of metazoan development: *Science Bulletin*, v. 60, p. 1947–1953.
- Zhang, H.Q., Xiao, S., Liu, Y.H., Yuan, X.L., Wan, B., Muscente, A.D., Shao, T.Q., Gong, H., and Cao, G., 2015, Armored kinorhynch-like scalidophoran animals from the early Cambrian: *Scientific Reports*, v. 5, p. 16521.
- Zhu, M.Y., Zhuravlev, A.Y., Wood, R.A., and Sukhov, S.S., 2017, A deep root for the Cambrian explosion: implications of new bio- and chemostratigraphy from the Siberian Platform: *Geology*, v. 45, p. 459–462.

Accepted 23 August 2017