



# Three-dimensionally phosphatized meiofaunal bivalved arthropods from the Upper Cambrian of Western Hunan, South China

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With 7 figures

**Abstract:** Meiofaunas are important ecological players in modern marine ecosystems, but their Cambrian fossil record is rather poor, even in some of the best-known Lagerstätten, such as the Burgess Shale biota, which are typically dominated by macroscopic animals. In this regard, the Upper Cambrian Wangcun Lagerstätte in South China is unusual in its richness in meiofaunal animals. Here, we described new material of three-dimensionally phosphatized meiofaunal bivalved arthropods from a single horizon in the Paibian Stage, Furongian Series of Wangcun section, Western Hunan, South China. New bivalved arthropods include *Albrunnicola bengtsoni* (bradoriid), *Mengdongella elliptica* gen. et sp. nov., and an indeterminate phosphatocopine Gen. et sp. indet. The new discovery extends the stratigraphic and geographic ranges of *A. bengtsoni*, which was previously only known from Lower Cambrian strata of Australia and Antarctic. The shield of *A. bengtsoni* bears pits that might have facilitated respiration or sensing. *Mengdongella elliptica* is a new bivalved arthropod of uncertain affinity, with antero-dorsal spines functioning as sensory organs. These new findings highlight the importance of the Orsten-type taphonomic window in revealing the diversity of meiofaunal ecdysozoans in Cambrian oceans.

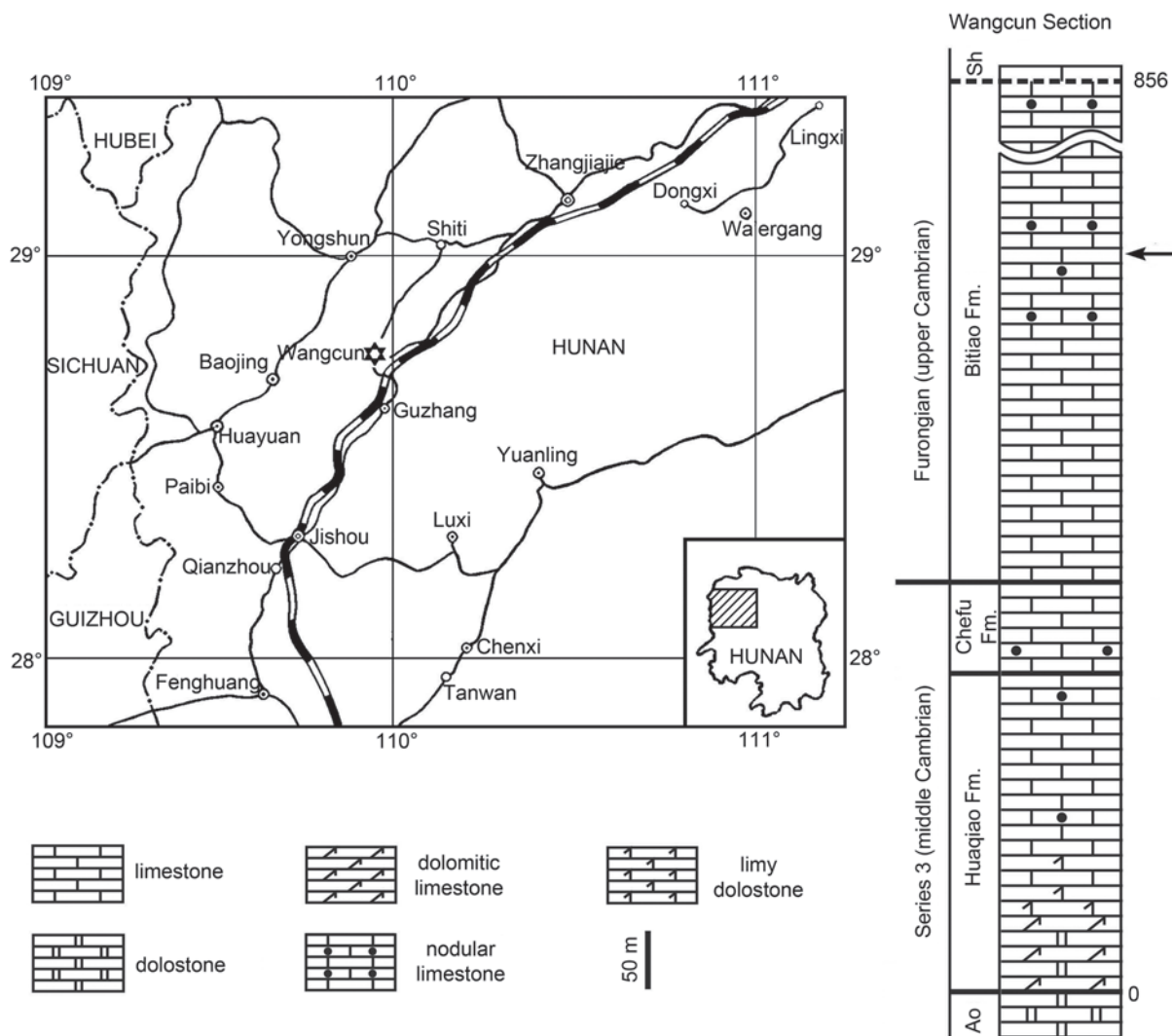
**Key words:** Orsten-type preservation, bivalved arthropods, meiofauna, Paibian Stage, Furongian Series, Wangcun Lagerstätte, South China.

## 1. Introduction

Ecdysozoan animals (AGUINALDO et al. 1997) have a reasonably good fossil record because of their recalcitrant cuticles that are resistant to taphonomic decay. In Cambrian Konservat-Lagerstätten with exceptionally preserved fossils, for example Burgess Shale-type Lagerstätten, ecdysozoan animals are with no doubt the most abundant and diverse (CONWAY MORRIS 1986; ZHAO et al. 2010, 2014). In typical Burgess Shale-type Lagerstätten, such as the Early Cambrian Chengjiang biota (HOU et al. 2004; CHEN 2004) and the Middle Cambrian Burgess Shale biota (GOULD 1989; BRIGGS et al. 1994), macroscopic animals are dominant and they are typically preserved in flattened two-dimensional

manners (GAINES et al. 2008). In contrast, Orsten-type Lagerstätten tend to preserve microscopic (generally between 100 µm and 2 mm) and cuticle-bearing ecdysozoans in three dimensions through the impregnation or encrustation of cuticles by calcium-phosphate (MÜLLER & WALOSSEK 1985, 1991; MAAS et al. 2006). Hence, Orsten-type fossils, along with small carbonaceous fossils (SCFs; HARVEY & BUTTERFIELD 2008, 2016; BUTTERFIELD & HARVEY 2011; HARVEY & PEDDER 2013; HARVEY et al. 2012a, b), complement typical Burgess Shale-type Lagerstätten and provide a rare window onto meiofaunal ecdysozoans in Cambrian oceans.

Orsten-type Lagerstätten are important because they capture microscopic ecdysozoans that are rare in classical Burgess Shale-type Lagerstätten. For ex-



**Fig. 1.** Location map and stratocolumn of the Wangcun section in Western Hunan, South China. The key fossil horizon yielding the present material is denoted by an arrow, about 650 m above the base of the Huaqiao Formation. Ao, Aoxi Formation; Sh, Shenjiawan Formation. Revised from DONG et al. (2005a).

ample, there are no convincing crustaceans in classical Burgess Shale-type Lagerstätten, although meiofaunal crustaceans are abundant and diverse in the Orsten-type Lagerstätten (MAAS et al. 2006) and small carbonaceous fossil assemblages (HARVEY & BUTTERFIELD 2008; BUTTERFIELD & HARVEY 2011; HARVEY & PEDDER 2013; HARVEY et al. 2012a, b). As another example, some of the oldest known cycloneuralian fossils are found in Orsten-type preservation (LIU et al. 2014; ZHANG et al. 2015; SHAO et al. 2016), and these fossils provide key insights into the origin and early divergence of cycloneuralians and ecdysozoans. Thus, Orsten-type

Lagerstätten (or, in general, three-dimensionally phosphatized biotas) need to be scrutinized very closely to uncover the Cambrian diversification of ecdysozoans, particularly if many early ecdysozoans may have been meiofaunal (HARVEY & BUTTERFIELD 2016).

Here, we describe new three-dimensionally phosphatized bivalved arthropods from Paibian Stage (Upper Cambrian) of Wangcun section in Western Hunan Province of South China. The new material represents part of a Cambrian meiofauna dominated by ecdysozoans and inarticulate brachiopods.



**Fig. 2. A-F** – *Albrunnicola bengtsoni* HINZ-SCHALLREUTER, 1993 from the Upper Cambrian of Wangcun section. A, NIGP160499, left lateral view; B, NIGP165204, left lateral view; C, NIGP165191, left lateral view, area in rectangle is enlarged in Fig. 3A; D, NIGP165192, left lateral view, area in rectangle is enlarged in Fig. 3B; E, NIGP165189, left lateral view, areas in rectangles 1 to 5 are enlarged in Fig. 3C-G; F, NIGP165190, right lateral view. Scale bar applies to all images.



## 2. Materials and methods

The specimens illustrated in this paper are housed at Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences. They were recovered from the Bitiao Formation at Wangcun section, Western Hunan, South China (Fig. 1). The key horizon yielding the present specimens is a thin-bedded and dark gray limestone that occurs 650 m above the base of the Huaqiao Formation (Fig. 1). Based on conodont biostratigraphy (DONG & ZHANG 2017), this horizon is part of the conodont *Westergaardodina* cf. *calix-Prooneotodus rotundatus* Zone, belonging to the Paibian Stage of the Furongian Series (PENG et al. 2012). This horizon has previously yielded abundant fossil embryos of *Markuelia hunanensis* (DONG et al. 2004, 2005b, 2010; DONG 2007, 2009), trunk fragments of palaeoscoleids (DUAN et al. 2012; DUAN & DONG 2013), and a single Type-A larva in Orsten-type preservation (ZHANG et al. 2016).

Rock samples from the key horizon at Wangcun section (Fig. 1) were collected and processed in NIGP. The rock samples were first crushed into walnut-sized pieces (2–3 cm in diameter), and then dissolved in acetic acid following procedures described by MÜLLER (1985). Rock fragments were immersed in diluted acetic acid (~10%), and residues were retrieved regularly after three days of reaction in summer (environment temperature around 40 °C). The residues were dried naturally, and microfossils were handpicked under an Olympus SZ binocular microscope. We obtained abundant three-dimensionally phosphatized ecdysozoans, including fossil embryos assignable to *Markuelia*, cuticular fragments of palaeoscoleids, and bivalved arthropods, together with other microfossils such as sponge spicules and abundant inarticulate brachiopods. The current paper focuses on the bivalved arthropods only.

Selected microfossils were mounted on aluminum stubs for observation under an LEO1530VP field-emission environmental scanning electron microscope (SEM) at NIGP, and the figures were processed using Adobe Photoshop CS5.

## 3. Systematic palaeontology

Arthropoda sensu lato sensu MAAS et al., 2004

Phylum Arthropoda v. SIEBOLD, 1848

Class uncertain

Order Bradoriida RAYMOND, 1935

Family Hipponicharionidae SYLVESTER-BRADLEY in  
BENSON, 1961

Genus *Albrunnicola* MARTINSSON, 1979,

Type species: *Longispina oelandica* ANDRES 1969.

*Albrunnicola bengtsoni* HINZ-SCHALLREUTER 1993

Figs. 2, 3

- 1986 *Hipponicharion* sp. – GAZDZICKI & WRONA, fig. 7e.
- 1990 *Hipponicharion* sp. – BENGTON in BENGTON et al., p. 325, fig. 207A.
- 1993 *Albrunnicola bengtsoni* n. sp. – HINZ-SCHALLREUTER, p. 424.
- 2001 *Albrunnicola bengtsoni*. – MELNIKOVA in GRAVESTOCK et al., p. 210, fig. 26a, b.
- 2006 *Albrunnicola bengtsoni*. – SKOVSTED et al., p. 26, fig. 10A–H.
- 2007 *Albrunnicola bengtsoni*. – TOPPER et al., p. 85, fig. 10A–K.
- 2009 *Albrunnicola bengtsoni*. – WRONA, p. 357, figs. 5A, B, 6A–D, 7A–D, 8A, B, 9A, B.
- 2016 *Albrunnicola bengtsoni*. – BETTS et al., p. 198, fig. 20G, H.

**Material:** Six specimens, NIGP160499, 165189–165192, and 165204.

**Description:** Bivalved bradoriids. Shields are inverted triangular in lateral profile. The dorsal line is straight (Fig. 2A, C, F), with a single dorsal furrow demarcating the right and left valves. The shield has slight anterior and posterior swings, thus it is longest slightly ventral to the dorsal line. The valves are highest at or slightly anterior to the anterior-posterior midline (am-plete or slightly pre-plete). The anterior lobe is strong (Fig. 3C), with the inflation extending first postero-ventrally and then postero-dorsally. The marginal rim is weak (Fig. 3A, B), and the duplicature is relatively narrow and extends along the whole inner margin of the valves (Fig. 3A, B). The valve surface is ornamented with imbricated pits with lateral wings (Fig. 3). The pits are more concentrated at the anterior, posterior, middle, and dorsal parts of the valves (Fig. 3C, D, E, G), and relatively sparse at the ventral part (Fig. 3F). The angular bisectors of the angles of the two lateral wings point mainly to the mid-dorsal part of the shield (Fig. 3A, B, E, F, G). Internal soft-part anatomy was not preserved.

**Measurements:** The current specimens are more or less of equal size, possibly representing the same instar. The shield is about 1.7 mm long and 1.4 mm high. Anterior lobe is 450 µm in size. The pits are about 2.8 µm in diameter, and each lateral wing is about 6.7 µm long. The lateral wings form an angle of about 150°.

**Fig. 3. A–G** – Close-up views of *Albrunnicola bengtsoni* HINZ-SCHALLREUTER, 1993 from the Upper Cambrian of Wangcun section. A, NIGP165191 (Fig. 2C); B, NIGP165192 (Fig. 2D); C–G, NIGP165189 (Fig. 2E). Scale bar between A and B applies to A and B, scale bar below C applies to C, D, and F, and scale bar to the right of G applies to E and G.

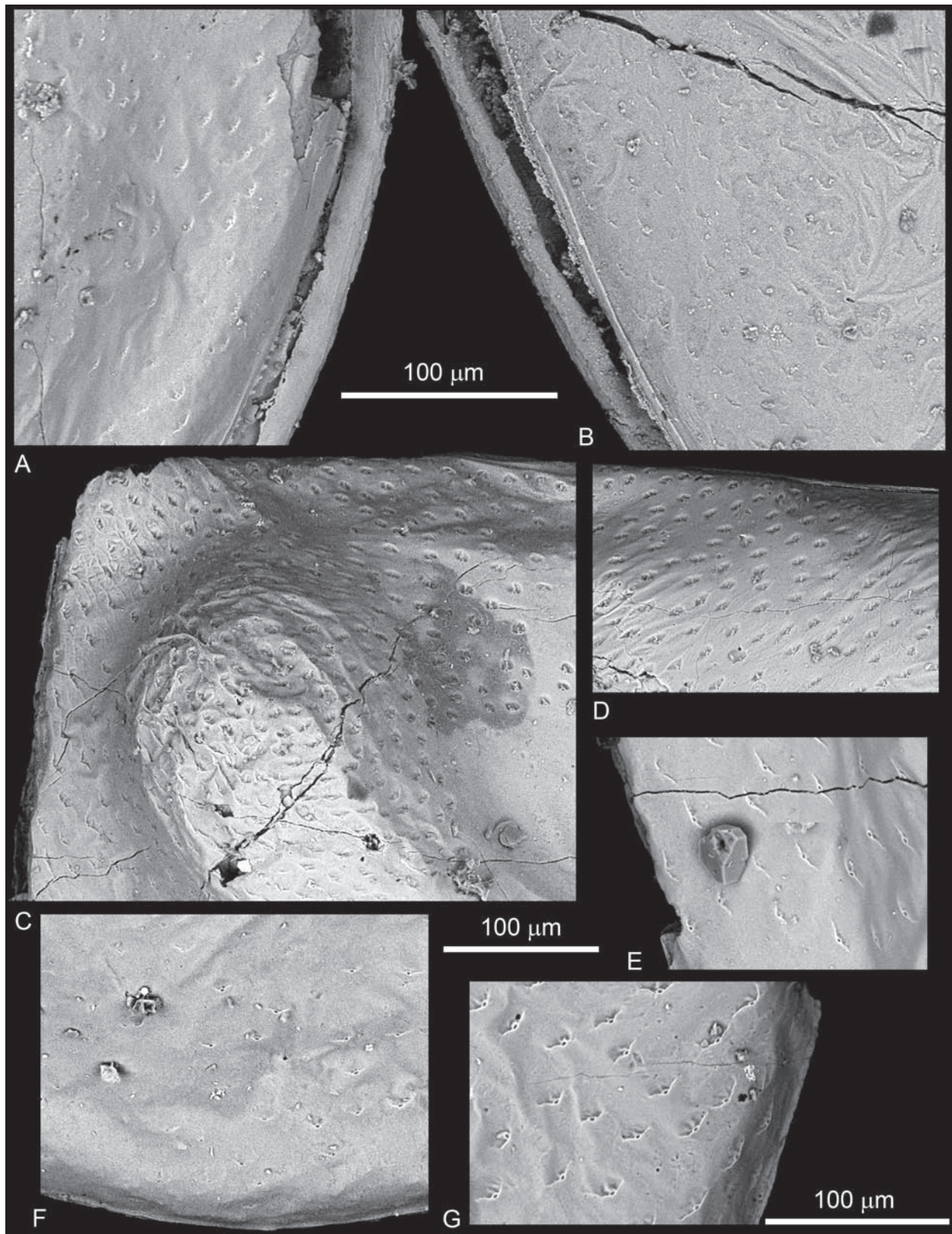
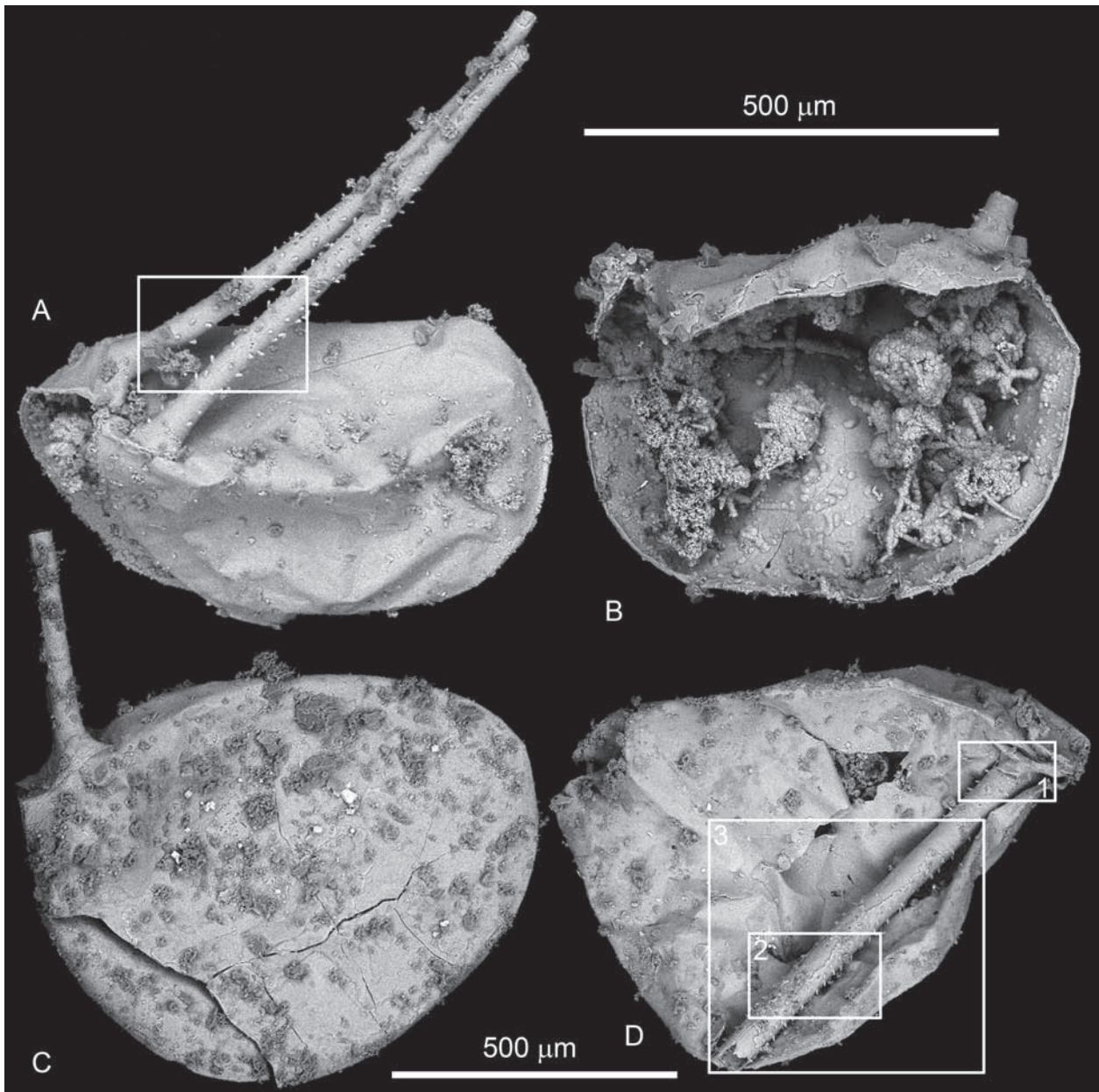


Fig. 3.





**Fig. 4. A-D** – *Mengdongella elliptica* gen. et sp. nov. from the Upper Cambrian of Wangcun section. A, holotype, NIGP165196, left lateral view, area in rectangle is enlarged in Fig. 5A; B, NIGP165205, right lateral view, right valve partly missing; C, NIGP165194, left lateral view; D, NIGP165206, areas in rectangles 1, 2, and 3 are enlarged in Fig. 5B, C, and D, respectively. Scale bar above B applies to A and B, and scale bar between C and D applies to C and D.

**Fig. 5. A-E** – Close-up views of *Mengdongella elliptica* gen. et sp. nov. from the Upper Cambrian of Wangcun section. A, NIGP165196 (Fig. 4A); B, C, E, NIGP165206 (Fig. 4D); D, NIGP165193 (Fig. 6A).

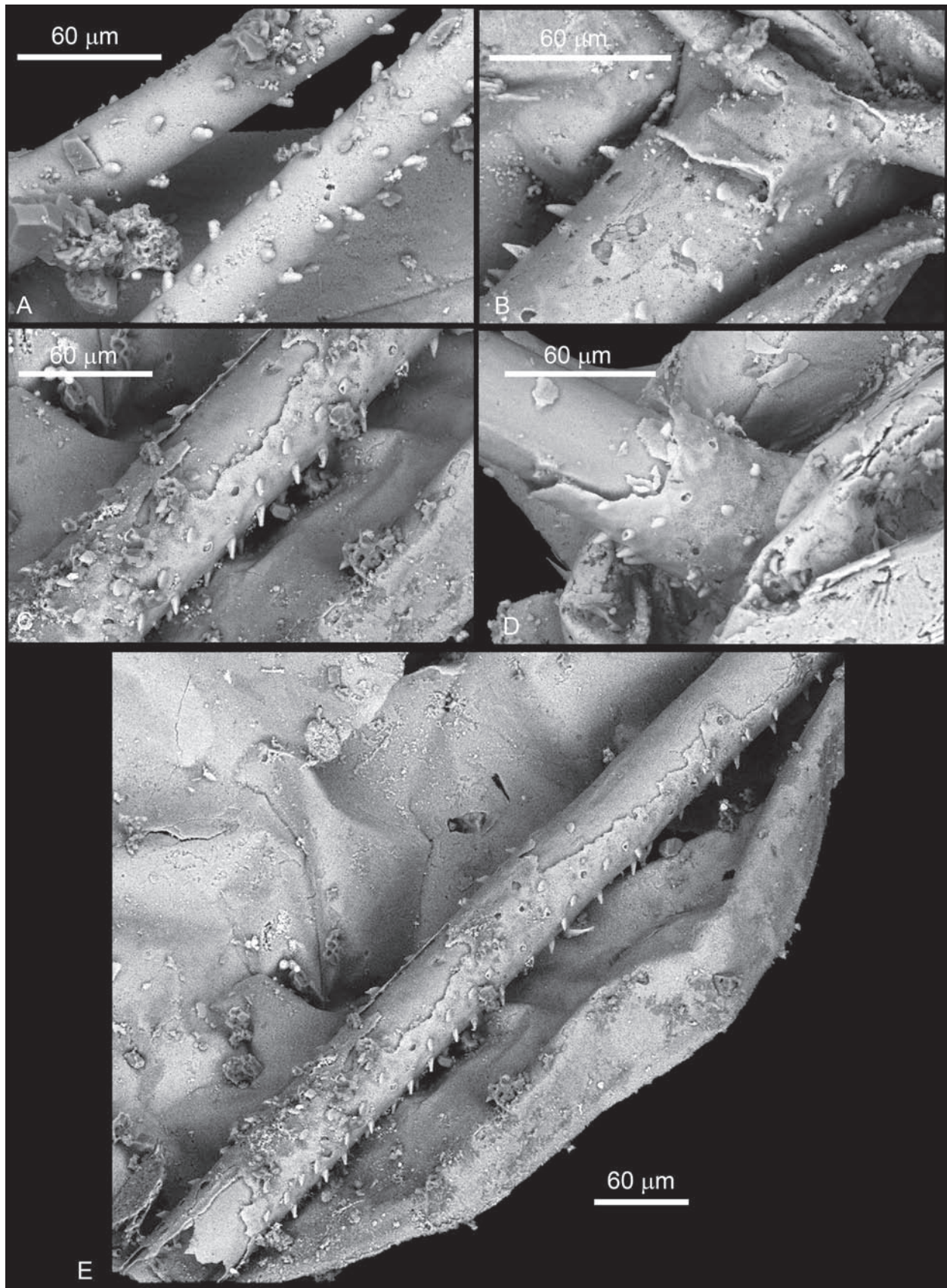


Fig. 5.



Class, Order, and Family uncertain

Genus *Mengdongella* nov.

**Etymology:** With reference to Mengdong River, along which the Wangcun section is exposed.

**Type species:** *Mengdongella elliptica* gen. et sp. nov.

**Diagnosis:** As for the type species.

**Occurrence:** Conodont *Westergaardodina* cf. *calix-Prooneotodus rotundatus* Zone, Bitiao Formation, Furongian (Upper Cambrian); Wangcun section, Yongshun County, Western Hunan, South China.

*Mengdongella elliptica* gen. et sp. nov.

Figs. 4, 5, 6A-D, 7

**Etymology:** With reference to the elliptic profile of the shield.

**Holotype:** NIGP165196 (Fig. 4A).

**Material:** Eight specimens, NIGP165193-165196, 165205-165208.

**Diagnosis:** Bivalved arthropods with a shield of elliptic profile; shield slightly pre-plete; duplicature narrow; dorsal line arched; a pair of spines at antero-dorsal position of the valves; spines long, internally hollow, with regularly arranged conical or scale-like structures on the surface.

**Description:** *Mengdongella elliptica* is a bivalved arthropod. The two valves are demarcated from each other by a single dorsal furrow (Figs. 4A, 6D). The dorsal line is arched (Figs. 4C, 6A, D), and the valves are thus elliptic in lateral profile. The shield is longest slightly ventral to the dorsal line, and highest slightly anterior to the anterior-posterior midline (pre-plete). The valves are smooth without any structures or ornaments (Fig. 6A, B, D). The duplicature is narrow, extending along the whole inner margins of the valves (Figs. 4B, 6A). A pair of spines are situated at the antero-dorsal position of the valves. The spines are long, exceeding the length of the shield (Figs. 4A, 6D). The surface of the spines is ornamented with small conical (Figs. 5A-E, 7A, B) or scale-shaped (Fig. 7C, D) structures. The conical or scale-shaped structures have slender tips directed apically 45 degrees to the spines. They are distributed uniformly on the surface of the spines (Figs. 5E, 7A). These structures appear internally hollow (Figs. 5, 7D), but this might be due to secondary coating. The soft-body anatomy within the bivalved shield is not preserved (Fig. 4B).

**Measurements:** The material of *Mengdongella elliptica* includes specimens of different sizes and at different ontogenetic stages. Their shields range in length from 640  $\mu\text{m}$  (Fig. 4A) to 970  $\mu\text{m}$  (Fig. 6D). The spines of the smallest specimen (Fig. 4A) are at least 680  $\mu\text{m}$  long, a little longer than the shield length, and those of the largest specimen (Fig.

6D) are at least 1.1 mm, also a little longer than the shield length. The scale-shaped structures of the largest specimen (Fig. 7C) are about 3.5  $\mu\text{m}$  wide at base and 6.5  $\mu\text{m}$  long, and the conical structures on the smallest specimen (Fig. 5A) are about 6.7  $\mu\text{m}$  wide at base and 8.8  $\mu\text{m}$  long.

**Comparisons:** *Mengdongella elliptica* gen. et sp. nov. bears arched dorsal line, and thus differs from bradoriids, phosphatocopines, and *Cambrolongispina* ZHANG et al. 2014 that have straight dorsal lines. As bivalved shields convergently evolved among arthropods of distant affinities, the phylogenetic affinity of *M. elliptica* is currently unknown. The antero-dorsal spines can be oriented antero-dorsally (Fig. 6A, B), anteriorly (Fig. 6D), or postero-dorsally (Fig. 4A), probably due to taphonomic distortion of the valves. We infer, on the basis of NIGP165194 (Fig. 4C), that these spines were directed antero-dorsally when alive. *Cambrolongispina reticulata* ZHANG et al. 2014 also has antero-dorsal spines that are ornamented, but these ornaments are paddle-shaped structures aligned in a single row along the posterior edge of the spines. In contrast, the conical or scale-shaped structures on the spines of *M. elliptica* are distributed uniformly on the entire surface of the spines.

Class and Order uncertain

Suborder Phosphatocopina MÜLLER, 1964

Gen. et sp. indet.

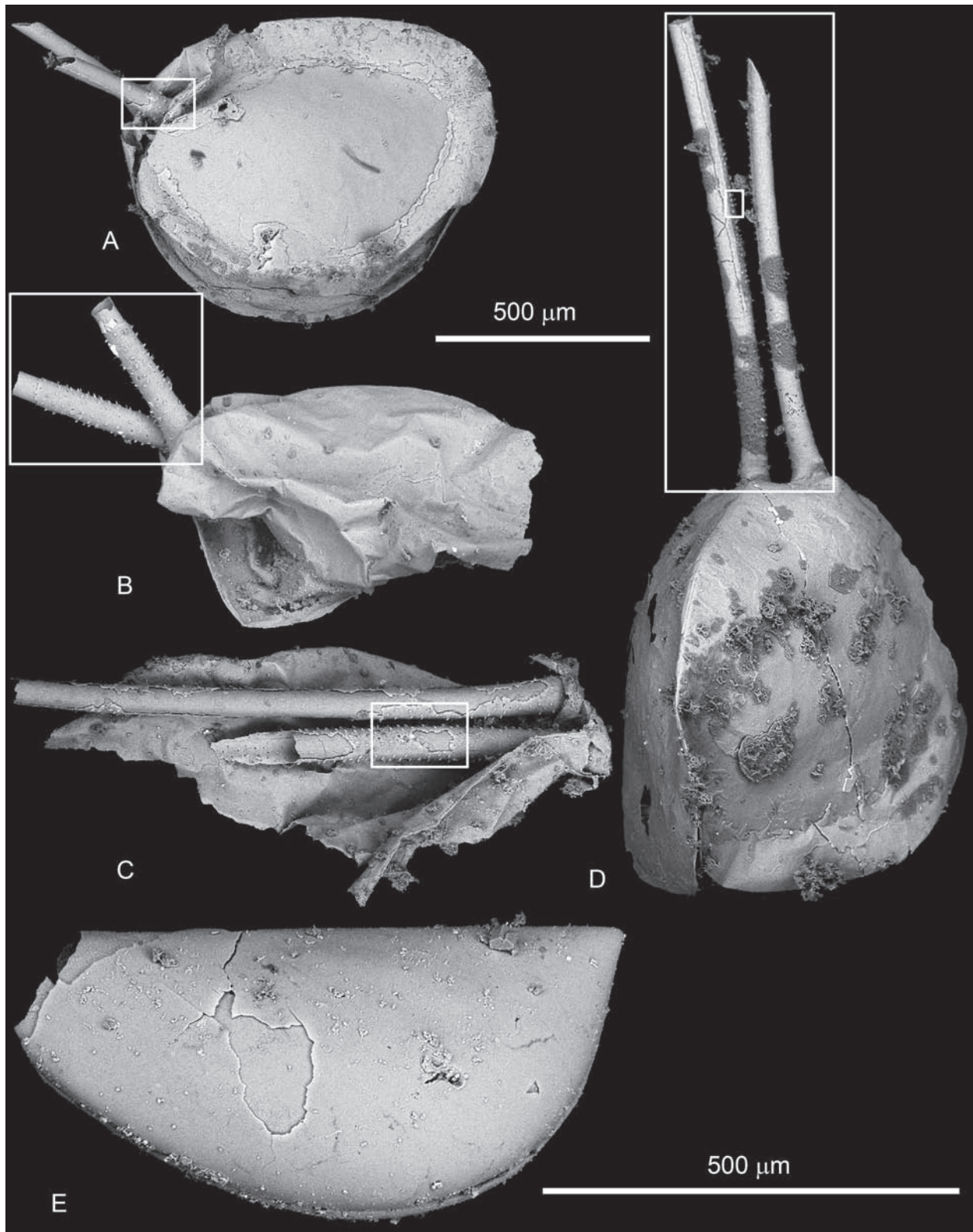
Fig. 6E

**Material:** One specimen, NIGP165197.

**Description:** The bivalved shield, with one end missing, is estimated to be about 800  $\mu\text{m}$  long and 350  $\mu\text{m}$  high. The completely preserved end is assumed to be anterior. The shield is longest at its dorsal line, and highest slightly anterior to the anterior-posterior midline (pre-plete). The valve surface is smooth without any lobes, spines, or other ornaments.

**Remarks:** Gen. et sp. indet. lacks key bradoriid characters such as valve lobes. Its shield with smooth valve surface and straight dorsal line is reminiscent of phosphatocopines. Phosphatocopines are abundant in the Upper Cambrian of Sweden (MAAS et al. 2003). At Wangcun, phosphatocopines were also reported from a single horizon about 100 m below the current horizon (DONG et al. 2005a; ZHANG et al. 2010). In the current horizon, phosphatocopines are relatively rare. The orientation of Gen. et sp. indet. is somewhat ambiguous. The completely preserved end is interpreted to be anterior, consistent with the general orientation of most phosphatocopines, because phosphatocopines generally have am-plete (highest position at anterior-posterior midline) or pre-plete (highest position anterior to anterior-posterior midline) shields (MAAS et al. 2003), while bradoriids generally have post-plete (highest position posterior to anterior-posterior midline) shields (ZHANG 2007).





**Fig. 6. A-D** – *Mengdongella elliptica* gen. et sp. nov. from the Upper Cambrian of Wangcun section. A, NIGP165193, left lateral view, area in rectangle is enlarged in Fig. 5D; B, NIGP165207, left lateral view, area in rectangle is enlarged in Fig. 7A; C, NIGP165208, a fragment, dorsal view, area in rectangle is enlarged in Fig. 7B; D, NIGP165195, dorsal view, area in small rectangle is enlarged in Fig. 7C, and area in large rectangle is enlarged in Fig. 7D. **E** – Gen. et sp. indet., same provenance, NIGP165197, right lateral view. Scale bar between A and B applies to A-D, and scale bar to the right of E applies to E only.

#### 4. Discussion

Bradoriids are relatively rare in the Late Cambrian (WILLIAMS et al. 2007), but in our collection we have obtained numerous specimens of *Albrunnicola bengtsoni*. *A. bengtsoni* was previously reported only from the Early Cambrian of South Australia and Antarctic (WRONA 2009), and the type horizon and locality of *A. bengtsoni* is the Lower Cambrian Parara Limestone, Kulpara Road section, Yorke Peninsula, South Australia (BENGTON et al. 1990). The current material shows that this species has a long stratigraphic range and wide palaeogeographic distribution. During the Cambrian Period, South China, Australia, and Antarctic were peri-Gondwana continents located around the palaeo-equator. The common occurrence of *A. bengtsoni* on these three continents indicates a free exchange of arthropod animals among them.

The pits with lateral wings on the valve surface of *Albrunnicola bengtsoni* were previously described as small pits (SKOVSTED et al. 2006), “small pits of U- to V-shaped indentations” (TOPPER et al. 2007), or crescentic pits (WRONA 2009). Sometimes, the lateral wings of these pits were developed into scales (WRONA 2009). The pits might have housed sensory setae (TOPPER et al. 2007), or might have functioned to enlarge the surface area of the valves in order to facilitate respiration. This type of pits might be convergently evolved in bradoriids of distant affinities, for example, *Quadricona madonnae* TOPPER et al., 2011 (TOPPER et al. 2011, fig. 6J) and *Parahoulongdongella bashanensis* SHU, 1990 (TOPPER et al. 2011, fig. 7D). Thus, they are not phylogenetically informative.

We speculate that the spines of both *Mengdongella elliptica* gen. et sp. nov. and *Cambrolongispina reticulata* may have functioned as sensory organs. The antero-dorsal spines of *M. elliptica* resemble more or less the disassociated sclerites assigned to the form genus *Mongolitubulus* MISSARZHEVSKY, 1977, and similar spines have also been reported from the Middle Cambrian Huaqiao Formation at the Wangcun and Paibi sections in Western Hunan (ZHU & DONG 2004). Recent studies suggested that *Mongolitubulus*-like sclerites are convergent rather than homologous structures (LI et al. 2012). For example, some *Mongolitubulus*-like sclerites may be the spines of eodiscoid trilobites (LI et al. 2012),

while others may be the spines of bradoriids (SKOVSTED et al. 2006; TOPPER et al. 2013), or of hallucigeniid lolo-podians (CARON et al. 2013). It should be noted that the conical or scale-shaped structures of *M. elliptica* differ from the scaly sculptures of *Mongolitubulus* in that the latter are more densely spaced and more regularly distributed. Therefore, the spines of *M. elliptica* are better not assigned to the form genus *Mongolitubulus*.

#### 5. Conclusions

Three-dimensionally phosphatized bivalved arthropods were recovered from the Paibian Stage, Furongian Series of the Upper Cambrian at the Wangcun section, Western Hunan, South China. These new arthropod fossils include *Albrunnicola bengtsoni*, *Mengdongella elliptica* gen. et sp. nov., and an indeterminate phosphatocope Gen. et sp. indet. Bivalved arthropods from Wangcun are preserved with their shields only, and the lack of anatomic information about their soft-bodied structures hinders their phylogenetic assignment. The new discovery extends the occurrence of *A. bengtsoni* from the Lower Cambrian of Australia and Antarctic to the Upper Cambrian of South China. The pits on the shield of *A. bengtsoni* may have housed sensory setae, or functioned as respiratory organs to facilitate respiration and gas exchange through the shield. The antero-dorsal spines of *M. elliptica* may have functioned as sensory organs to detect water currents and preys/predators nearby, and the conical or scale-shaped structures on the spines may also be related to the sensory function.

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**Fig. 7. A-D** – Close-up views of *Mengdongella elliptica* gen. et sp. nov. from the Upper Cambrian of Wangcun section. A, NIGP165207 (Fig. 6B); B, NIGP165208 (Fig. 6C); C, D, NIGP165195 (Fig. 6D).



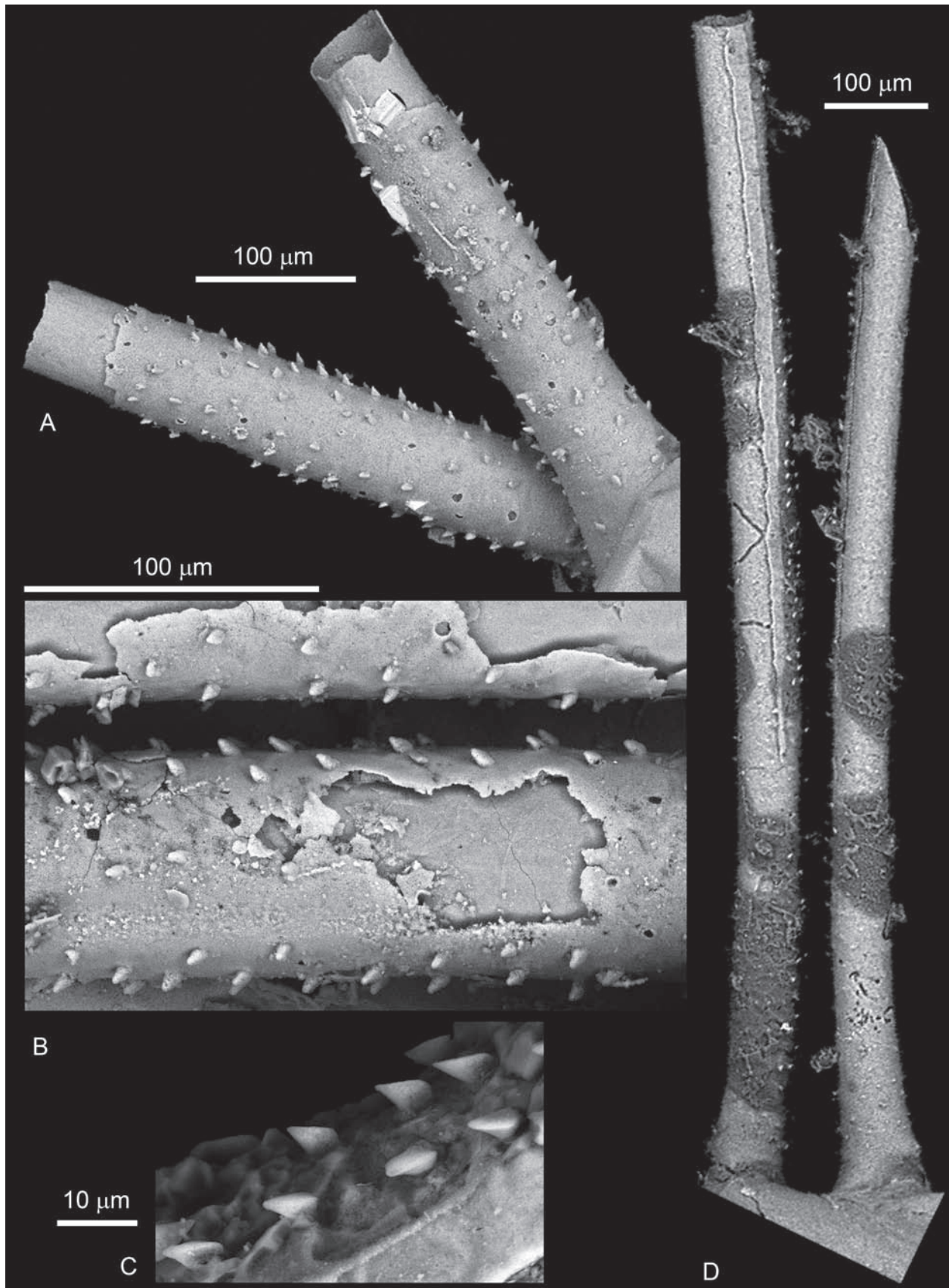


Fig. 7.

## References

- AGUINALDO, A.M.A., TURBEVILLE, J.M., LINFORD, L.S., RIVERA, M.C., GAREY, J.R., RAFF, R.A. & LAKE, J.A. (1997): Evidence for a clade of nematodes, arthropods and other moulting animals. – *Nature*, **387**: 489–493.
- ANDRES, D. (1969): Ostracoden aus dem mittleren Kambrium von Öland. – *Lethaia*, **2**: 165–180.
- BENGTSON, S., CONWAY MORRIS, S., COOPER, B.J., JELL, P.A. & RUNNEGAR, B.N. (1990): Early Cambrian Fossils from South Australia. – *Memoirs of the Association of Australian Palaeontologists*, **9**: 364 pp.; Brisbane (Association of Australian Palaeontologists).
- BENSON, R.H. (1961): Systematic description. – In: MOORE R.C. & PITRAT C.W. (Eds.): *Treatise on Invertebrate Paleontology*: 99–421; Lawrence (University of Kansas Press & Geological Society of America).
- BETTS, M.J., PATERSON, J.R., JAGO, J.B., JACQUET, S.M., SKOVSTED, C.B., TOPPER, T.P. & BROCK, G.A. (2016): A new Lower Cambrian shelly fossil biostratigraphy for South Australia. – *Gondwana Research*, **36**: 176–208.
- BRIGGS, D.E.G., ERWIN, D.H. & COLLIER, F.J. (1994): *The Fossils of the Burgess Shale*. – 238 pp.; Washington (Smithsonian Institution Press).
- BUTTERFIELD, N.J. & HARVEY, T.H.P. (2011): Small carbonaceous fossils (SCFs): A new measure of early Paleozoic paleobiology. – *Geology*, **40**: 71–74.
- CARON, J.-B., SMITH, M.R. & HARVEY, T.H.P. (2013): Beyond the Burgess Shale: Cambrian microfossils track the rise and fall of hallucigeniid lobopodians. – *Proceedings of the Royal Society, (B)*, **280**: 20131613.
- CHEN, J. (2004): *The Dawn of Animal World*. – 366 pp.; Nanjing (Jiangsu Science & Technology Press).
- CONWAY MORRIS, S. (1986): The community structure of the Middle Cambrian Phyllopod bed (Burgess Shale). – *Palaeontology*, **29**: 423–467.
- DONG, X.-P. (2007): Developmental sequence of Cambrian embryo *Markuelia*. – *Chinese Science Bulletin (English Edition)*, **52**: 929–935.
- DONG, X.-P. (2009): Cambrian fossil embryos from Western Hunan, South China. – *Acta Geologica Sinica (English Edition)*, **83**: 429–439.
- DONG, X.-P., BENGTSON, S., GOSTLING, N.J., CUNNINGHAM, J.A., HARVEY, T.H.P., KOUCHINSKY, A., VAL'KOV, A.K., REPETSKI, J.E., STAMPANONI, M., MARONE, E. & DONOGHUE, P.C.J. (2010): The anatomy, taphonomy, taxonomy and systematic affinity of *Markuelia*: Early Cambrian to Early Ordovician scalidophorans. – *Palaeontology*, **53**: 1291–1314.
- DONG, X.-P., DONOGHUE, P.C.J., CHENG, H. & LIU, J.-B. (2004): Fossil embryos from the Middle and Late Cambrian period of Hunan, south China. – *Nature*, **427**: 237–240.
- DONG, X.-P., DONOGHUE, P.C.J., LIU, Z., LIU, J. & PENG, F. (2005a): The fossils of Orsten-type preservation from Middle and Upper Cambrian in Hunan, China – Three-dimensionally preserved soft-bodied fossils (Arthropods). – *Chinese Science Bulletin (English Edition)*, **50**: 1352–1357.
- DONG, X.-P., DONOGHUE, P.C.J., CUNNINGHAM, J.A., LIU, J. & CHENG, H. (2005b): The anatomy, affinity, and phylogenetic significance of *Markuelia*. – *Evolution & Development*, **7**: 468–482.
- DONG, X.-P. & ZHANG, H.Q. (2017): Middle Cambrian through lowermost Ordovician conodonts from Hunan, South China. – *Journal of Paleontology*, **91**: 1–89.
- DUAN, B.C. & DONG, X.-P. (2013): Furongian (Late Cambrian) palaeoscolecid cuticles from Hunan Province, South China: the growth impact on the worm cuticle. – *Acta Scientiarum Naturalium Universitatis Pekinensis*, **49**: 591–602.
- DUAN, B., DONG, X.-P. & DONOGHUE, P.C.J. (2012): New palaeoscolecid worms from the Furongian (Upper Cambrian) of Hunan, South China: Is *Markuelia* an embryonic palaeoscolecid? – *Palaeontology*, **55**: 613–622.
- GAINES, R.R., BRIGGS, E.G. & ZHAO, Y. (2008): Cambrian Burgess Shale-type deposits share a common mode of fossilization. – *Geology*, **36**: 755–758.
- GAZDZICKI, A. & WRONA, R. (1986): Polskie badania paleontologiczne w Antarktyce Zachodniej (1986). – *Przegląd Geologiczny*, **34**: 609–617.
- GOULD, S.J. (1989): *Wonderful Life: The Burgess Shale and the Nature of History*. – 347 pp.; New York (Norton).
- GRAVESTOCK, D.I., ALEXANDER, E.M., DEMIDENKO, Y.E., ESAKOVA, N.V., HOLMER, L.E., JAGO, J.B., LIN, T.R., MELNIKOVA, L.M., PARKHAEV, P.Y., ROZANOV, A.Y., USHATINSKAYA, G.T., ZANG, W.L., ZHEGALLO, E.A. & ZHURAVLEV, A.Y. (2001): The Cambrian biostratigraphy of the Stansbury Basin, South Australia. – *Transactions of the Palaeontological Institute*, **282**: 1–343.
- HARVEY, T.H.P. & BUTTERFIELD, N.J. (2008): Sophisticated particle-feeding in a large Early Cambrian crustacean. – *Nature*, **452**: 868–871.
- HARVEY, T.H.P. & BUTTERFIELD, N.J. (2016): Exceptionally preserved Cambrian loriciferans and the early animal invasion of the meiobenthos. – *Nature Ecology & Evolution*, **1**: 0022.
- HARVEY, T.H.P., ORTEGA-HERNÁNDEZ, J., LIN, J.P., ZHAO, Y.L. & BUTTERFIELD, N.J. (2012a): Burgess Shale-type microfossils from the Middle Cambrian Kaili Formation, Guizhou Province, China. – *Acta Palaeontologica Polonica*, **57**: 423–436.
- HARVEY, T.H.P. & PEDDER, B.E. (2013): Copepod mandible palynomorphs from the Nolichucky Shale (Cambrian, Tennessee): Implications for the taphonomy and recovery of small carbonaceous fossils. – *Palaios*, **28**: 278–284.
- HARVEY, T.H.P., VÉLEZ, M.I. & BUTTERFIELD, N.J. (2012b): Exceptionally preserved crustaceans from Western Canada reveal a cryptic Cambrian radiation. – *Proceedings of the National Academy of Sciences of the United States of America*, **109**: 1589–1594.
- HINZ-SCHALLREUTER, I. (1993): Cambrian ostracodes mainly from Baltoscandia and Morocco. – *Archiv für Geschichte der Naturwissenschaften*, **1**: 369, 370, 385–448.
- HOU, X., ALDRIDGE, R.J., BERGSTRÖM, J., SIVETER, D.J., SIVETER, D.J. & WANG, H. (2004): *The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life*. – 233 pp.; Oxford (Blackwell).
- LI, G.X., STEINER, M., ZHU, M.Y. & ZHAO, X. (2012): Early Cambrian eodiscoid trilobite *Hupeiiscus orientalis* from South China: ontogeny and implications for affinities of *Mongolitubulus*-like sclerites. – *Bulletin of Geosciences*, **87**: 159–169.
- LIU, Y.H., XIAO, S., SHAO, T.Q., BROCE, J. & ZHANG, H.Q.



- (2014): The oldest known priapulid-like scalidophoran animal and its implications for the early evolution of cycloneuralians and ecdysozoans. – *Evolution & Development*, **16**: 155-165.
- MÜLLER, K.J. (1964): Ostracoda (Bradiorina) mit phosphatischen Gehäusen aus dem Oberkambrium von Schweden. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **121**: 1-46.
- MÜLLER, K.J. (1985): Exceptional preservation in calcareous nodules. – *Philosophical Transactions of the Royal Society of London, (B)*, **311**: 67-73.
- MÜLLER, K.J. & WALOSSEK, D. (1985): A remarkable arthropod fauna from the Upper Cambrian "Orsten" of Sweden. – In: BOWES, D.R. & WATERSTON, C.D. (Eds.): *Fossil arthropods as living animals*: 161-172; Edinburgh (Royal Society of Edinburgh).
- MÜLLER, K.J. & WALOSSEK, D. (1991): 'Orsten' arthropods – small in size but of great impact on biological and phylogenetic interpretations. – *GFF*, **113**: 88-90.
- MAAS, A., BRAUN, A., DONG, X.-P., DONOGHUE, P.C.J., MÜLLER, K.J., OLEMPKA, E., REPETSKI, J.E., SIVETER, D.J., STEIN, M. & WALOSZEK, D. (2006): The 'Orsten' – More than a Cambrian Konservat-Lagerstätte yielding exceptional preservation. – *Palaeoworld*, **15**: 266-282.
- MAAS, A., WALOSZEK, D., CHEN, J.Y., BRAUN, A., WANG, X.Q. & HUANG, D.Y. (2004): Phylogeny and life habits of early arthropods – predation in the Early Cambrian sea. – *Progress in Natural Science*, **14**: 158-166.
- MAAS, A., WALOSZEK, D. & MÜLLER, K.J. (2003): Morphology, ontogeny and phylogeny of the Phosphatocopina (Crustacea) from the Upper Cambrian 'Orsten' of Sweden. – *Fossils and Strata*, **49**: 1-238.
- MARTINSSON, A. (1979): *Albrunnicola*, a new name for the Cambrian ostracode genus *Longispina* ANDRES 1969. – *Lethaia*, **12**: 27.
- MISSARZHEVSKY, V.V. (1977): Konodonty (?) i fosfantnye problematiki kembriya Mongolii i Sibiri [Conodonts (?) and phosphatic problematica from the Cambrian of Mongolia and Siberia]. – In: TATARINOV, L.P. (Ed.): *Bespozvonochnye Paleozoya Mongolii*: 10-19; Nauka, Moscow (Trudy Sovmestnaya Sovetsko-Mongolskaya Paleontologicheskaya Ekspeditsiya).
- PENG, S., BABCOCK, L.E. & COOPER, R.A. (2012): The Cambrian Period. – In: GRADSTEIN, F.M., OGG, J.G., SCHMITZ, M. & OGG, G. (Eds.): *Geological Time Scale 2012*: 437-488; Oxford (Elsevier).
- RAYMOND, P.E. (1935): *Leancoilia* and other Mid-Cambrian Arthropoda. – *Bulletin of the Museum of Comparative Zoology*, **76**: 205-230.
- SHAO, T.Q., LIU, Y.H., WANG, Q., ZHANG, H.Q., TANG, H.H. & LI, Y. (2016): New material of the oldest known scalidophoran animal *Eopriapulites sphinx*. – *Palaeoworld*, **25**: 1-11.
- SIEBOLD, C.T. v. (1848): *Lehrbuch der vergleichenden Anatomie der Wirbellosen Thiere. Erster Theil*. – 679 pp.; Berlin (Veit & Co.).
- SKOVSTED, C.B., BROCK, G.A. & PATERSON, J.R. (2006): Bivalved arthropods from the Lower Cambrian Mernmerna Formation, Arrowie Basin, South Australia and their implications for identification of Cambrian 'small shelly fossils'. – *Memoirs of the Association of Australasian Palaeontologists*, **32**: 7-41.
- TOPPER, T.P., SKOVSTED, C.B., BROCK, G.A. & PATERSON, J.R. (2007): New bradoriids from the lower Cambrian Mernmerna Formation, South Australia: systematics, biostratigraphy and biogeography. – *Memoirs of the Association of Australasian Palaeontologists*, **33**: 67-100.
- TOPPER, T.P., SKOVSTED, C.B., BROCK, G.A. & PATERSON, J.R. (2011): The oldest bivalved arthropods from the early Cambrian of East Gondwana: Systematics, biostratigraphy and biogeography. – *Gondwana Research*, **19**: 310-326.
- TOPPER, T.P., SKOVSTED, C.B., HARPER, D.A.T. & AHLBERG, P. (2013): A bradoriid and brachiopod dominated shelly fauna from the Furongian (Cambrian) of Västergötland, Sweden. – *Journal of Paleontology*, **87**: 69-83.
- WILLIAMS, M., SIVETER, D.J., POPOV, L. & VANNIER, J.M.C. (2007): Biogeography and affinities of the bradoriid arthropods: Cosmopolitan microbenthos of the Cambrian seas. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **248**: 202-232.
- WRONA, R. (2009): Early Cambrian bradoriidae and phosphatocopide arthropods from King George Island, West Antarctica. – *Polish Polar Research*, **30**: 347-377.
- ZHANG, H.Q., DONG, X.-P. & MAAS, A. (2010): *Hesslandona angustata* (Phosphatocopida, Crustacea) from the Upper Cambrian of western Hunan, South China, with comments on phosphatocopid phylogeny. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **259**: 157-175.
- ZHANG, H.Q., DONG, X.-P., WALOSZEK, D. & MAAS, A. (2016): An orthonauplius of 'Orsten'-type preservation from the Upper Cambrian (Furongian) of South China. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **279**: 175-183.
- ZHANG, H.Q., DONG, X.-P. & XIAO, S. (2014): New bivalved arthropods from the Cambrian (Series 3, Drumian Stage) of western Hunan, South China. – *Acta Geologica Sinica*, **88**: 1388-1396.
- ZHANG, H.Q., XIAO, S., LIU, Y.H., YUAN, X.L., WAN, B., MUSCENTE, A.D., SHAO, T.Q., GONG, H. & CAO, G. (2015): Armored kinorhynch-like scalidophoran animals from the early Cambrian. – *Scientific Reports*, **5**: 16521.
- ZHANG, X.G. (2007): Phosphatized bradoriids (Arthropoda) from the Cambrian of China. – *Palaeontographica, (A)*, **281**: 93-173.
- ZHAO, F., CARON, J.-B., BOTTJER, D.J., HU, S., YIN, Z. & ZHU, M. (2014): Diversity and species abundance patterns of the early Cambrian (Series 2, Stage 3) Chengjiang Biota from China. – *Paleobiology*, **40**: 50-69.
- ZHAO, F., ZHU, M. & HU, S. (2010): Community structure and composition of the Cambrian Chengjiang Biota. – *Science in China (Earth Sciences)*, **53**: 1784-1799.
- ZHU, C.F. & DONG, X.-P. (2004): Affinities and functional morphology of the Middle Cambrian ornamented tubules from Western Hunan, China. – *Progress in Natural Science*, **14**: 907-911.

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