



A NEW HELMETIID ARTHROPOD FROM THE EARLY CAMBRIAN CHENGJIANG LAGERSTÄTTE, SOUTHWEST CHINA

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ABSTRACT—A new arthropod, *Haifengella corona* new genus new species is described from the early Cambrian Chengjiang Lagerstätte (Series 2, Stage 3), Yunnan Province, southwest China. It is readily assignable to helmetiida based on gross morphology of the tergum. The new helmetiid is unique in having the marginal spines extending over one-third of the total body width. The weakly sclerotized tergum consists of six thoracic tergites with edge-to-edge tergite articulations. The sub-trapezoidal cephalic shield has a pair of long spines projecting from each posterolateral corner. A prehypostomal sclerite (anterior sclerite) recesses in the anterior margin of the cephalic shield, and a pair of bulges that are close to the prehypostomal sclerite in the cephalic shield are presumed to be the position of ventral eyes. Each of the thoracic tergites exhibits a pair of long spines projecting from the posterolateral corners. The semicircular pygidium carries one terminal spine and two pairs of lateral spines.

INTRODUCTION

THE HELMETIIDA Novozhilov, 1960 is a group of weakly sclerotized Cambrian arthropods that have aroused interest on account of their trilobite affinities. Because of edge-to-edge tergite articulations and the supposed shared derived character of dorsoventral mismatch, they are considered closely related with trilobites as their possible sister taxon (Edgecombe and Ramsköld, 1999; Cotton and Braddy, 2004; Ortega-Hernández et al., 2013; Stein et al., 2013). Characteristic features of helmetiids include: 1) tergum broadly to narrowly oval in outline, with a smooth surface absence of cuticular ornament and axial region; 2) cephalic shield with prehypostomal sclerite in recess in anterior margin of cephalic shield; 3) a single pair of ventral compound eyes, normally preserved as bulges of the cephalic shield located on the sides of prehypostomal sclerite; 4) moderate number of thoracic tergites and a large pygidium; 5) tergites with narrow overlap in the axial region and meeting edge to edge along the margins, though they may also be fused into a single shield (Hou and Bergström, 1997). The first species to be described was *Helmetia expansa* Walcott, 1918 from the middle Cambrian Burgess Shale, but details of the ventral morphology of this species are still poorly known (Størmer, 1959; Simonetta and Delle Cave, 1975; Conway Morris et al., 1982; Briggs et al., 1994). Among exceptionally well-preserved arthropods from the Chengjiang Lagerstätte, Helmetiida is represented with five species: *Kuamaia lata* Hou, 1987; *Kuamaia muricata* Hou and Bergström, 1997; *Rhombicalvaria acanthi* Hou, 1987; *Saperion glumaceum* Hou, Ramsköld, and Bergström, 1991, and *Skioldia aldna* Hou and Bergström, 1997. Together these six species comprise a substantial proportion of the taxon Helmetiida (Hou and Bergström, 1997). Together with *Tegopelte gigas* Simonetta and Delle Cave, 1975 from the Burgess Shale, these species were resolved in a clade from analysis of Cambrian arthropods (Edgecombe and Ramsköld, 1999; Cotton and Braddy, 2004; Hendricks and Lieberman, 2008; Paterson et al., 2010, 2012; Stein et al., 2013). One other Chengjiang species, *Kwanyinaspis maotianshanensis* Zhang and Shu, 2005, and *Australimicola spriggi* Paterson, García-Bellido, and Edgecombe, 2012 from

the Emu Bay Shale, share certain characters with Helmetiida, with *Kwanyinaspis* interpreted as a basal helmetiid (Paterson et al., 2010, 2012). Helmetiids are closely related to trilobites, nektaspids and xandarellids according to a number of phylogenetic analyses of Cambrian arthropods (Edgecombe and Ramsköld, 1999; Cotton and Braddy, 2004; Hendricks and Lieberman, 2008; Paterson et al., 2010, 2012; Stein et al., 2013), though they may be closer to trilobites than to nektaspids (Edgecombe and Ramsköld, 1999; Cotton and Braddy, 2004; Ortega-Hernández et al., 2013). In the present paper a new helmetiid arthropod, *Haifengella corona* n. gen. n. sp., from the Chengjiang Lagerstätte is described based on the morphology of its tergum.

MATERIAL AND METHODS

The specimens described here were collected from the Mafang section (Fig. 1) where they occur in the mudstone-dominated Maotianshan Shale Member of the Yu'an-shan Formation, Cambrian Series 2, Stage 3, *Eoredlichia*–*Wudingaspis* Zone, in Yunnan Province, southwest China (Chen et al., 1996; Zhu et al., 2001). Detailed locality information and fossil taphofacies were presented by Zhao et al. (2009). This species is extremely rare in the Chengjiang biota and is represented by two specimens, which have been deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China (NIGPAS prefix). The specimens are complete and preserved as a flattened impression on slabs of mudstone. Light photographs were taken using a Nikon D300s digital camera with a Nikon AF-S VR105mm macro lens, under low angle fiber optic directional illumination from the top (cephalic shield) to enhance the relief of the compressed fossil. Terminology follows standard trilobite terminology (Whittington, 1997), which is complemented with descriptive terminology applied to exceptionally preserved arthropods from the Burgess Shale Lagerstätten (Stein et al., 2013). The term prehypostomal sclerite replacing rostral plate or anterior sclerite follows that of Patterson et al. (2010) for the sclerite found in a number of fossil taxa between the hypostome and the head shield.

Placement of *Haifengella* in the family Helmetiidae is based on the following features: prehypostomal sclerite recesses in

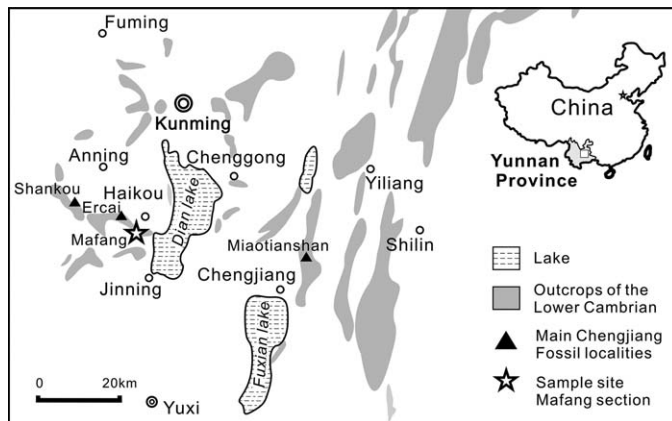


FIGURE 1—Distribution of lower Cambrian outcrops near Kunming, Yunnan Province, showing the most important localities of the Chengjiang Lagerstätte.

anterior margin of cephalic shield and a pair of stalked eyes accommodate in dorsal bulges in cephalic shield (Edgecombe and Ramsköld, 1999); moderate number of thoracic tergites and a large pygidium with a broad-based terminal spine and lateral marginal spines; tergites do not overlap laterally but meet edge-to-edge (Hou and Bergström, 1997).

SYSTEMATIC PALEONTOLOGY

Phylum ARTHROPODA von Siebold and Stannius, 1845
 Class ARTIPODA Hou and Bergström, 1997
 Order HELMETIIDA Novozhilov, 1960
 Family HELMETIIDAE Simonetta and Delle Cave, 1975
 HAIFENGELLA new genus

Type species.—*Haifengella corona* new species.

Diagnosis.—As for the type species.

Etymology.—Derived from Haifeng (also called “Mafang” by local residents), the name of a village north of the Mafang section.

Remarks.—Helmetiidae includes three other genera, namely *Helmetia* Walcott, 1918, *Kuamaia* Hou, 1987, and *Rhombicalvaria* Hou, 1987. *Helmetia* from the Burgess Shale differs from the Chengjiang genera in having a transverse frontal margin with a prominent pair of lateral spines and a much larger body (the body size of *Helmetia* is >20 cm versus Chengjiang genera <8 cm) (Briggs et al., 1994). *Haifengella* differs from *Kuamaia* in having six thoracic tergites and much longer pleural spines and marginal spines of pygidial shield. Both *Haifengella* and *Rhombicalvaria* have elongate spines, but *Haifengella* has six thoracic tergites and two pairs of tail spines, versus nine and one (respectively) in *Rhombicalvaria*.

HAIFENGELLA CORONA new species

Figure 2.1–2.2, 2.4–2.6

Diagnosis.—Cephalic shield with a pair of elongate spines projecting from posterolateral corners; the prehypostomal sclerite large; six thoracic tergites with long pleural spines; large pygidium with two pairs of long marginal spines and terminal spine, tail spines stronger and broader than pleural spines.

Description.—General: specimen oval in dorsal aspect, length about 23–28 mm, maximum width 13–17 mm at second and third thoracic tergites (excluding marginal spines) (Fig. 2.1, 2.2). Dorsum divided into a cephalic shield, six thoracic tergites of similar shape, and a pygidial shield. The ratio of three parts is 1:1.8:1.4. No clear overlap between neighboring tergites. Weakly sclerotized exoskeleton flattened, midline raised into very low

rounded ridge, indicating dorsal profile originally like that of low roof with flat sloping sides (Fig. 2.3).

Head: cephalic shield sub-trapezoidal, with smoothly rounded lateral margins. Single pair of elongate spines projects up to about 4 mm from posterolateral corners. Ratio of cephalic shield width to length about 2.25 (Fig. 2.1, 2.2). Large oval prehypostomal sclerite projects beyond anterior margin of cephalic shield. Situated behind prehypostomal sclerite is oval-shaped hypostome, the upper part of the hypostome delimited anteriorly by prehypostomal sclerite and laterally and posteriorly by faint ridge (Fig. 2.1, 2.4). Single pair of low bulges on posterior part of sides of prehypostomal sclerite marks presumed position of eyes (Fig. 2.2). Cephalic shield lacks defined axial region.

Thorax: six thoracic tergites, with anterior three tergites virtually equal length and longer than posterior tergites. Second and third tergites broadest, with body smoothly tapering in both directions from there. Thoracic tergites overlap slightly in axial portion; no overlap in pleural regions (Fig. 2). First tergite arches posteriorward in axially region, posterior tergites apparently straight (Fig. 2.1). The arching of tergite is considered a compaction artifact, which have been discussed by Stein et al. (2013). Lateral marginal spines increase in length from cephalic shield to third thoracic tergite, being nearly equal length posterior to this site. Longest lateral spines in third tergite about 5 mm, or almost two-fifths of maximum width of body (excluding spine) (Fig. 2.1, 2.5).

Tail: pygidium broad and large, longer than cephalic shield, semicircular and bearing one terminal spine and two pairs of lateral spines (Fig. 2.6). All spines elongate pointed, with broad base compared to lateral spines. Anterior spines shorter than posterior paired spines. Posterior paired spines longer and broader than terminal spine. Length of longest spine same as length of pygidium (excluding end spine). Anus presumably located behind base of terminal spine based on dark trace (Fig. 2.2, 2.6).

Etymology.—Latin *corona*, crown; referring to the outline of the pygidium in dorsal view.

Type.—Holotype: NIGPAS158639; paratype: NIGPAS158640.

Occurrence.—Mafang section (N 24°46', E 102°35'), Miaotianshan Shale Member, Yu'an Shan Formation, lower Cambrian Series 2, Stage 3, Yunnan Province, China.

Remarks.—The specimen of *Haifengella corona* is dorsoventrally compressed, oval in dorsal outline, and has a non-wrinkled surface. Preservation of helmetiids from the Burgess Shale and Chengjiang is similar, indicating that their carapace has the same degree of convexity and stiffness. The slightly arched posterior margins of the cephalic shield and anterior thoracic tergites indicate that these elements were tilted slightly backward before compression. This arching thus reveals something of the original convexity, which apparently decreased progressively from the cephalic shield to the pygidium. There was no axial lobe and no furrows in the trunk. The morphology of the antennae and limbs is unknown.

Haifengella corona, the type species from the Chengjiang Lagerstätte, is the only species currently assigned to the genus. The elongate spines arising from the pygidium together with the greatly extended lateral spines serve to distinguish *Haifengella corona* from other described Cambrian helmetiids except *Rhombicalvaria acantha* Hou, 1987 (Walcott, 1918; Hou, 1987; Hou and Bergström, 1997) (Fig. 3). Though the specimen of *Haifengella corona* is smaller than the published specimens of *Rhombicalvaria acantha* Hou, 1987 (Hou, 1987, pl. 3, figs. 3, 4), we do not consider it to be a young individual of the latter, as there are obvious differences between *Rhombicalvaria* and *Haifengella*, the former has one pair of spines in the sides of subtriangular pygidium and nine thoracic tergites, instead of the

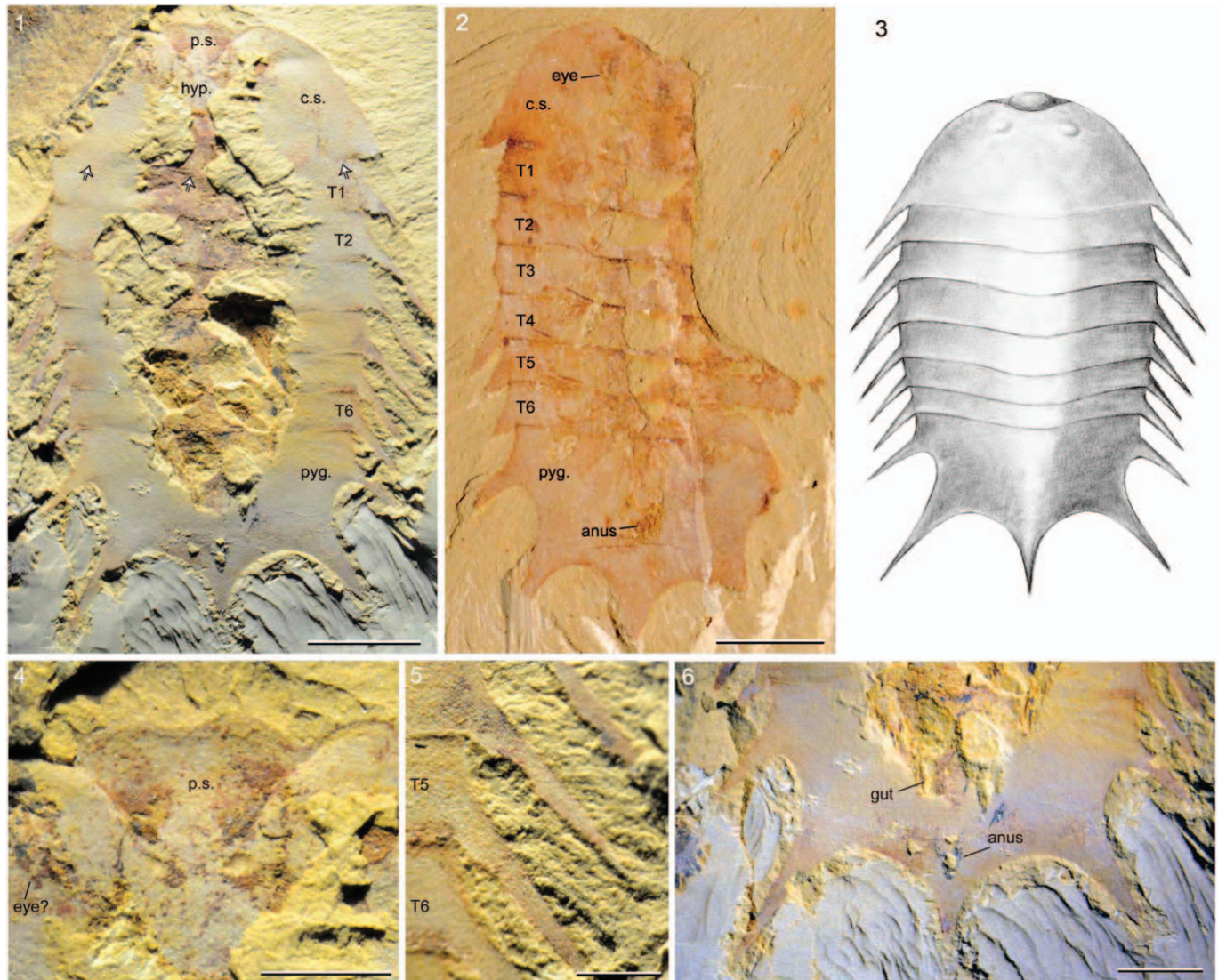


FIGURE 2—*Haifengella corona* n. gen. n. sp. from the lower Cambrian (Series 2, Stage 3) Maotianshan Shale Member, middle part of the Yu'an-shan Formation (*Eoredlichia*–*Wudingaspis* Zone) in the Mafang section, Haikou near Kunming, Yunnan Province; 1, 4–6, NIGPAS158639; 2, NIGPAS158640: 1, 2, dorsal view of a complete specimen preserved parallel to bedding (arrows point to the boundary between the cephalic shield and the first thoracic tergite); 3, reconstruction of *Haifengella corona* n. gen. n. sp. in dorsal view; 4–6, enlarged from the image 1: 4, detail of the anterior part of the cephalic shield; 5, lateral spines; 6, detail of the pygidium. Scale bars: 1, 2=5 mm; 4–6=2 mm. Abbreviations: p.s.=prehypostomal sclerite; hyp.=hypostome; c.s.=cephalic shield; pyg.=pygidium; T=thoracic tergite.

two pairs in semicircular pygidium and six thoracic tergites of *Haifengella*; the cephalic shield is very different in shape and size; the cephalic shield of *Rhombicalvaria* is relatively short and much rounded posterior margins; the marginal spines are also very different in shape, length and position. The spines of *Rhombicalvaria acantha* Hou, 1987 are curved, much longer in the pygidium than in the thoracic tergites and cephalic shield. More importantly, the small specimens of *Rhombicalvaria acantha* Hou, 1987 collected by the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPS158585), show *Rhombicalvaria acantha* Hou, 1987 has developed nine thoracic tergites and its morphological features are consistent with its adult when it is similar with the body size of *Haifengella carona*. Based on this fact, we can rule out the possibility of ontogenetic variation. The other Chengjiang species *Kuamaia lata* Hou, 1987 is most similar in general body form to *Haifengella carona*, although it lacks long

marginal spines (Hou and Bergström, 1997, figs. 57A, 57E, 57G). *Kuamaia lata* has seven thoracic tergites, with much shorter spines. *Haifengella carona* has the same number of thoracic tergites with *Helmetia expansa* Walcott, 1918, but the anterior margin of the *Helmetia expansa* cephalic shield extended into a spine at each corner and a much larger body (over 200 mm in length; Briggs et al., 1994, fig. 141), which differs with all other helmetiid arthropod species from the Chengjiang fauna.

Overall, *Haifengella corona* n. gen. n. sp. resembles helmetiids based on gross morphology of the tergum. The prehypostomal sclerite in a recess of the cephalic shield, tergites meeting edge-to-edge and pygidium with a broad based terminal spine and lateral marginal spines, demonstrate that *Haifengella* n. gen. is readily assignable to Helmetiida. Furthermore, the absence of information on the ventral morphology of

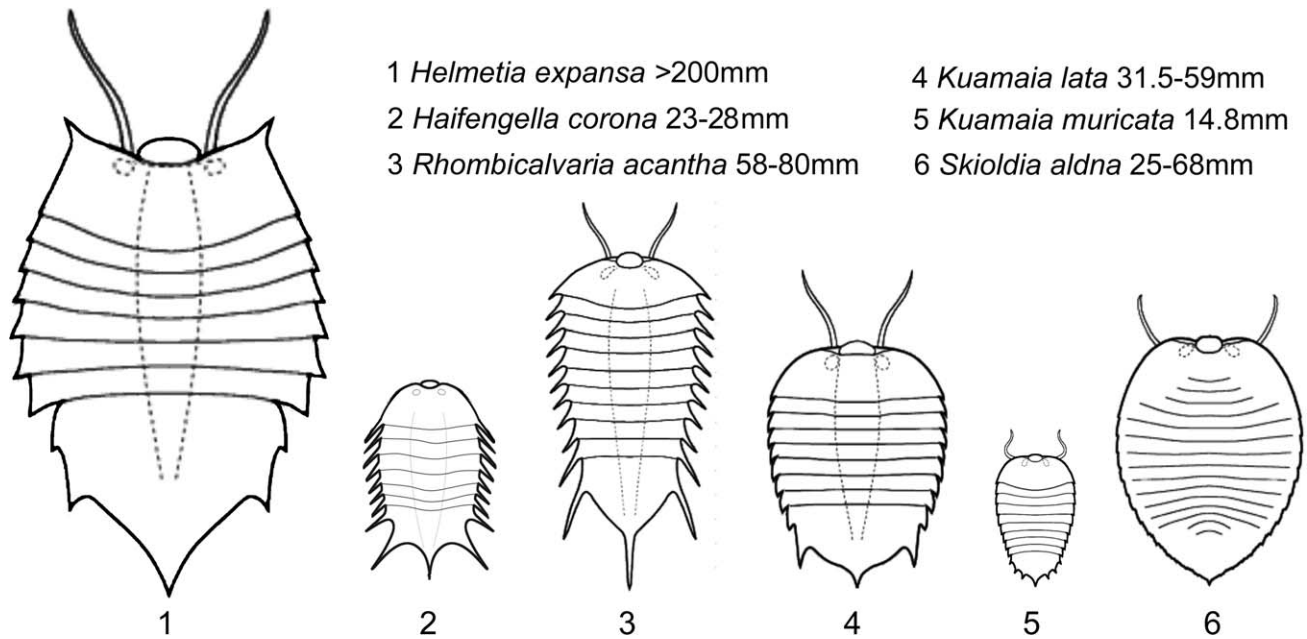


FIGURE 3—General structure of *Haifengella corona* n. gen. n. sp. (2) compared with that of other helmetiids. Data on body size (length) taken from Hou (1987); Briggs et al. (1994), and Hou et al. (1997). In order to facilitate comparisons of body structure body size has been adjusted (*Helmetia expansa* is reduced because it is much larger than the other species, while *Kuamaia muricata* is magnified because it is much smaller).

Haifengella n. gen. makes detailed phylogenetic discussions impossible.

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REFERENCES

- BRIGGS, D. E. G., D. H. ERWIN, AND F. J. COLLIER. 1994. The fossils of the Burgess Shale. Smithsonian Institution Press, Washington, D.C.
- CHEN, J., G. ZHOU, M. ZHU, AND K. YEH. 1996. The Chengjiang Biota—A Unique Window of the Cambrian Explosion. The National Museum of Natural Science, Taichung. (In Chinese)
- CONWAY MORRIS, S., H. B. WHITTINGTON, D. E. G. BRIGGS, C. P. HUGHES, AND D. L. BRUTON. 1982. Atlas of the Burgess Shale. Palaeontological Association, London.
- COTTON, T. J. AND S. J. BRADY. 2004. The phylogeny of arachnomorph arthropods and the origin of the Chelicerata. *Transactions of the Royal Society of Edinburgh—Earth Sciences*, 94:169–193.
- EDGEcombe, G. D. AND L. RAMSKÖLD. 1999. Relationships of Cambrian Arachnata and the systematic position of Trilobita. *Journal of Paleontology*, 73:263–287.
- HENDRICKS, J. R. AND B. S. LIEBERMAN. 2008. New phylogenetic insights into the Cambrian radiation of arachnomorph arthropods. *Journal of Paleontology*, 82:585–594.
- HOU, X. 1987. Three new large arthropods from lower Cambrian, Chengjiang, eastern Yunnan. *Acta Palaeontologica Sinica*, 26:272–285. (In Chinese)
- HOU, X. AND J. BERGSTRÖM. 1997. Arthropods of the lower Cambrian Chengjiang fauna Southwest China. *Fossils and Strata*, 45:1–116.
- HOU, X., L. RAMSKÖLD, AND J. BERGSTRÖM. 1991. Composition and preservation of the Chengjiang fauna—a lower Cambrian soft-bodied biota. *Zoologica Scripta*, 20:395–411.
- NOVOZHILOV, N. I. 1960. Klass Merostomoidea Störmer, 1944, Chlenistonogie, Trilobitoobraznye i Rakoobraznye [Arthropoda, Trilobitomorpha and Crustacea]. *Osnovy Paleontologii*, p. 195–197.
- ORTEGA-HERNÁNDEZ, J., D. A. LEGG, AND S. J. BRADY. 2013. The phylogeny of aglaspidid arthropods and the internal relationships within Artiopoda. *Cladistics*, 29:15–45.
- PATERSON, J. R., G. D. EDGEcombe, D. C. GARCÍA-BELLIDO, J. B. JAGO, AND J. G. GEHLING. 2010. Nektaspid arthropods from the lower Cambrian Emu Bay Shale Lagerstätte South Australia, with a reassessment of lamellicephalid relationships. *Palaeontology*, 53:377–402.
- PATERSON, J. R., D. C. GARCÍA-BELLIDO, AND G. D. EDGEcombe. 2012. New Artiopodan arthropods from the early Cambrian Emu Bay Shale Konservat-Lagerstätte of South Australia. *Journal of Paleontology*, 86:340–357.
- SIMONETTA, A. M. AND L. DELLE CAVE. 1975. The Cambrian non trilobite arthropods from the Burgess Shale of British Columbia: A study of their comparative morphology taxonomy and evolutionary significance. *Palaeontographica Italica*, 69:1–37.
- STEIN, M., E. G. BUDD, J. S. PEEL, AND D. A. HARPER. 2013. *Arthroaspis* n. gen., a common element of the Sirius Passet Lagerstätte (Cambrian, North Greenland), sheds light on trilobite ancestry. *BMC Evolutionary Biology*, 13:99.
- STÖRMER, L. 1959. Trilobitomorpha, Trilobitoidea, p. 22–37. In R. C. Moore (ed.), *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1*. Geological Society of America, Boulder and University of Kansas Press, Lawrence, Kansas.
- VON SIEBOLD, C. T. E. AND F. H. STANNIUS. 1845. *Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere*. Veit, Berlin.
- WALCOTT, C. D. 1918. Geological explorations in the Canadian Rockies. Explorations and fieldwork of the Smithsonian Institution in 1917. Smithsonian Miscellaneous Collections, 68:4–20.
- WHITTINGTON, H. B. 1997. Morphology of the exoskeleton, p. 1–85. In R. L. Kaesler (ed.), *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Trilobita, revised volume 1: Introduction, Order Agnostida, Order Redlichiida*. Geological Society of America, Boulder, Colorado, and University of Kansas Press, Lawrence, Kansas.
- ZHANG, X. AND D. SHU. 2005. A new arthropod from the Chengjiang Lagerstätte, early Cambrian, southern China. *Alcheringa*, 29:185–194.
- ZHAO, F., J.-B. CARON, S. HU, AND M. ZHU. 2009. Quantitative analysis of taphofacies and paleocommunities in the early Cambrian Chengjiang Lagerstätte. *Palaios*, 24:826–839.
- ZHU, M., G. LI, J. ZHANG, M. STEINER, Y. QIAN, AND Z. JIANG. 2001. Early Cambrian Stratigraphy of East Yunnan, Southwestern China: A Synthesis. In M. Zhu, H. Van Iten, S. Peng, and G. Li (eds.), *The Cambrian of South China*. *Acta Palaeontologica Sinica*, 40:4–39.

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