J. Paleont., 82(4), 2008, pp. 851–855
Copyright © 2008, The Paleontological Society
0022-3360/08/0082-851$03.00

ONTOGENY OF THE MIDDLE CAMBRIAN TRILOBITE *SHANTUNGIA SPINIFERA* WALCOTT, 1905 FROM NORTH CHINA AND ITS TAXONOMIC SIGNIFICANCE

TAE-YOON PARK,[1] SANG JUNE MOON,[1] ZUOZHEN HAN,[2] AND DUCK K. CHOI[1]
[1]School of Earth and Environmental Sciences, Seoul National University, Seoul 151-747, Korea, <id7@snu.ac.kr>, <sangjune@snu.ac.kr>, <dkchoi@snu.ac.kr>; and [2]College of Geo-information Science and Technology, Shandong University of Science and Technology, Shandong 266510, China, <zuozhenhan@yahoo.com>

THE CAMBRIAN trilobite *Shantungia* Walcott, 1905 is a monotypic genus, with *S. spinifera* Walcott, 1905 as the genotype and is characterized by its long frontal spine extending medially from the anterior cranidial border. The genus has hitherto been known restricted in occurrence to the traditional *Drepanura* Zone of North China (Walcott, 1913; Endo and Resser, 1937; Qiu et al., 1983; Zhang and Jell, 1987). As *Drepanura* Bergeron, 1899 is preoccupied by a collembolan insect and *Neodrepanura* Özdikmen, 2006 was proposed as a replacement, this zone is referred to as the *Neodrepanura* Biozone herein.

Recently collected trilobites from the Kushan Formation in Shandong Province of North China contain forty specimens of *Shantungia spinifera*, including protaspid and meraspid forms. Interestingly, the juvenile specimens of *S. spinifera* are morphologically closely comparable to the specimens recently assigned to *Oculishumardia hunania* Peng et al., 2003 from the uppermost middle Cambrian *Liostracina bella* Zone of South China (Peng et al., 2004). Peng et al. (2003) claimed that *Oculishumardia* is the oldest shumardiid and phylogenetically represents an intermediate stage between ptychoparioids and shumardiids.

This note describes the ontogenetic development of *Shantungia spinifera* from North China and, based on this information, raises the possibility that *Oculishumardia* may represent meraspid stages of a damesellid trilobite and will explore its taxonomic and phylogenetic significance.

FOSSIL LOCALITY

All of the specimens examined in this study were collected from the Kushan Formation of the Tangwangzhai section, Shandong Province, China (Fig. 1). The Tangwangzhai section (116°51′42″E and 36°30′33″N) has served as the type section of middle Cambrian to Furongian (upper Cambrian) strata of North China and comprises the Changhia, Kushan, and Chaumitien formations in ascending order (Bureau of Geology and Mineral Resources of Shandong Province, 1996). The Kushan Formation in the section measures ca. 62 m in thickness and is generally poorly exposed due to weathering and vegetation cover. The lower part of the Kushan Formation is dominated by purple to greenish-gray shale with an alternating sequence of shale and lime mudstone facies forming the lowermost 3 m. The middle to upper part of the formation consists largely of limestone/shale couplets and limestone conglomerates with sporadic intercalations of grainstone and shale beds.

The biostratigraphy of the Kushan Formation at the Tangwangzhai section has yet to be fully resolved, but it was recently suggested that it comprises the *Blackwelderia-Damesella*, *Neodrepanura*, and *Chuangia* zones in ascending order (Bureau of Geology and Mineral Resources of Shandong Province, 1996). The *Blackwelderia-Damesella* Zone has been known to yield *Damesella* Walcott, 1905, *Blackwelderia* Walcott, 1906, *Teinistion* Monke, 1903, and *Monkaspis* Kobayashi, 1935. The *Neodrepanura* Zone comprises *Neodrepanura*, *Shantungia*, *Blackwelderia*, and *Liostracina* Monke, 1903. The *Chuangia* Zone is recognized by the dominant occurrence of *Chuangia* Walcott, 1911.

Specimens of *Shantungia spinifera* were collected from discontinuous limestone lenses embedded within heavily weathered shale facies, which occupy the interval between 43 m and 48 m above the base of the Kushan Formation. The association of *Neodrepanura* indicates that the interval belongs to the *Neodrepanura* Zone of latest middle Cambrian age. Specimens are not particularly abundant but represent a range of ontogenetic stages of *Shantungia spinifera*. The material comprises six protaspides, 24 morphologically immature and six mature cranidia. In addition, three pygidia and one librigena were also recovered. All of the specimens are deposited in the paleontological collections of Seoul National University, Korea, with registered numbers under the acronym SNUP.

ONTOGENY

Length and width measurements were taken for a total of 30 morphologically immature cranidia (Fig. 2). The protaspid exoskeletons form two distinct groups, and the first two clusters of post-protaspid immature cranidia may correspond to the earliest two meraspid instars. Nevertheless we do not attempt to distinguish any clustering for the post-protaspid immature cranidia, as the small number of specimens decreases the confidence of instar-corresponding clustering. Instead, we broadly divide the ontogenetic development of the post-protaspid morphologically immature cranidia into the early and late phases for the purpose of description. The morphological maturity has been assumed to be achieved by the appearance of the

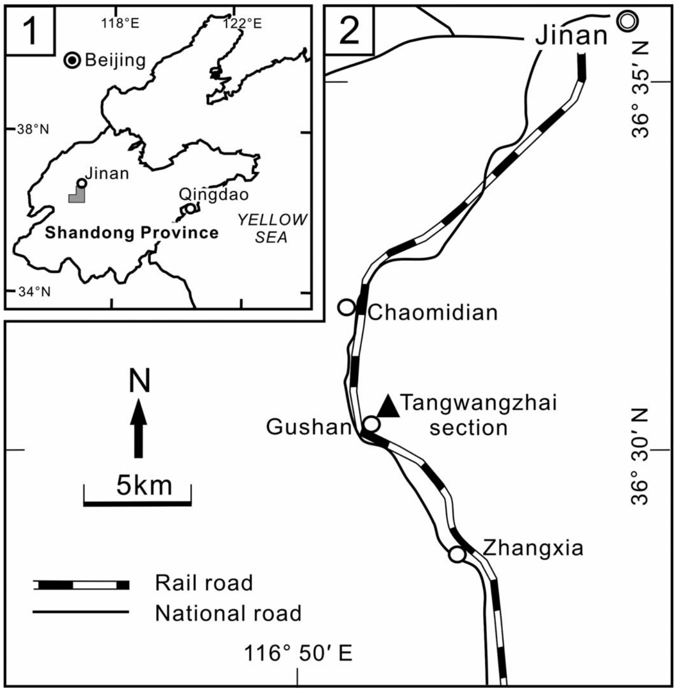


FIGURE 1—Location maps. *1,* Index map showing the approximate location of the study area in Shandong Province, China (shaded); *2,* The Tangwangzhai section (solid triangle), from which the study material was collected, is situated close to Gushan, which is located about 25 km southwest of Jinan, capital of the Shandong Province.

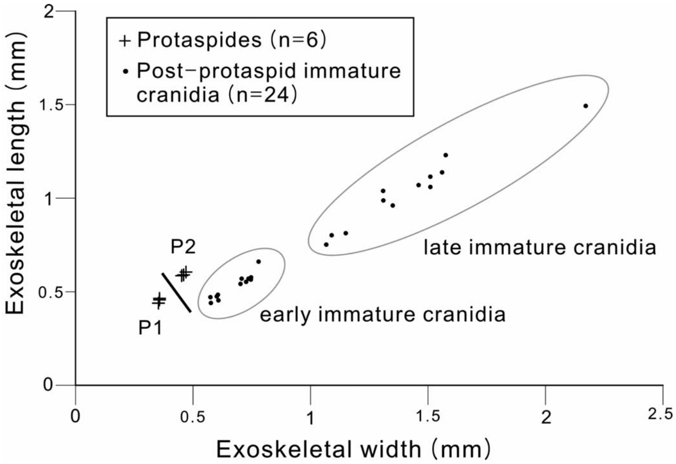


FIGURE 2—Length and width dimensions of protaspides and post-protaspid immature cranidia of *Shantungia spinifera* Walcott, 1905 from the Kushan Formation, Tangwangzhai section, Shandong Province, China. P1 and P2 denote the protaspid groups 1 and 2, respectively.

frontal spine and the differentiation of the frontal area into a preglabellar field and an anterior cranidial border by a clearly-incised cranidial border furrow.

Protaspid period.—Although there are only six protaspid specimens, two size clusters are clearly formed (Fig. 2). The smaller cluster is referred to the protaspid group 1, whereas the larger one is protaspid group 2.

Protaspid group 1 dorsal sclerites (Fig. 3.1–3.2) are oval in outline and measure 0.44–0.46 mm long and 0.35–0.36 mm wide. The axis is indicated by faintly-incised axial furrows and tapers slightly posteriorly. Segmentation of the axis is not discernible except for the occipital ring, which is recognized by a shallow occipital furrow and posterior cranidial marginal furrow. Sclerites assigned to the protaspid group 2 (Fig. 3.3–3.7) differ from those of protaspid group 1 by their larger size (0.59–0.60 mm long and 0.45–0.47 mm wide). The axis is convex and clearly defined by axial furrows. The occipital ring is defined by a shallow occipital furrow and deep posterior cranidial marginal furrow. No other segmentation is observed in the exoskeletons.

The family Damesellidae has been assigned to the Order Lichida (Fortey, 1990, 1997), but the protaspid morphology observed here shows little affinity with the reported protaspid morphology of lichid trilobites (cf. Chatterton and Speyer, 1997), suggesting that the damesellid trilobites had nothing to do with the lichids. Alternatively, if this trilobite group was closely related to lichid trilobites, the protaspid morphology described in this study may represent the plesiomorphic condition of this rather ‘‘primitive’’ sister taxon of lichid trilobites. A better-resolved conclusion is expected to be drawn from ontogenetic studies of other damesellid trilobites.

Post-protaspid morphologically immature cranidia.—Disarticulated post-protaspid immature cranidia are differentiated into two groups (Fig. 2), which are referred to as early and late phases of development based on the size and appearance of palpebral lobes.

The early morphologically immature cranidia (Fig. 3.8–3.11) are small, 0.44–0.66 mm long and 0.58–0.78 mm wide, and are characterized by a semi-circular outline with subparallel axial furrows and no indication of a preglabellar furrow and palpebral lobes. The occipital ring is faintly indicated by a shallow, transverse occipital furrow. The posterior border furrows are transverse, and the posterolateral projections of the fixigenae are deflected posteriorly.

The late morphologically immature cranidia (Fig. 3.12–3.15) are larger than the early immature cranidia, ranging from 0.75–1.49 mm long and 1.07–2.17 mm wide. The notable morphological changes in the late immature cranidia are the appearance of palpebral lobes, a forward-tapering glabella with a faint indication of a preglabellar furrow in larger specimens (Fig. 3.14–3.15), and the differentiation of the frontal area into a preglabellar field and anterior cranidial border. With growth, the palpebral lobes become comparatively shorter, and the anterior cranidial margin gets more acuminate. In specimens 0.96–1.23 mm long (Fig. 3.13–3.14), the anterior cranidial border is subtriangular in plan view, sculptured with sub-horizontally aligned ridges and grooves. The largest morphologically immature cranidium (Fig. 3.15) is poorly preserved but displays intermediate morphological features between the smaller immature cranidia and morphologically mature cranidia. Its anterior cranidial border is slightly upturned, and the palpebral lobes are dorsally more elevated than those of smaller immature cranidia with a kidney-shaped outline.

Morphologically mature cranidia.—The small mature cranidia (Fig. 3.16) are fragmentary, ranging from 2.13–2.37 mm long and 3.42–3.78 mm wide. The glabella is subconical in outline with anteriorly-tapering axial furrows. The frontal area is clearly differentiated into a short preglabellar field with median depression and a transversely triangular upturned anterior cranidial border. The most conspicuous morphological feature of this group is the prolongation of the frontal spine on the anterior cranidial border.

The large morphologically mature cranidia (Fig. 3.17–3.20) range from 4.44–7.94 mm long and 7.44–9.87 mm wide. The cranidium excluding the frontal spine is subpentagonal in outline. The glabella is subconical with a weak constriction at the anterior portion in larger specimens. A pair of small anterolateral swellings are recognized in the largest specimen (Fig. 3.20), but they are not well defined in smaller specimens. Lateral glabellar furrows are weakly impressed. The subrectangular occipital ring is defined by a moderately incised occipital furrow. The preglabellar field is short and ornamented medially with an anastomosing ridge-and-groove pattern similar to a caecal network. With growth, the anterior cranidial border and frontal spine become longer, while the palpebral lobes become comparatively smaller and more posteriorly situated. Bacculae are more prominent on larger cranidia than on smaller ones. Posterolateral projections of fixigenae are short, deflected posteriorly. Posterior border furrows are clearly incised.

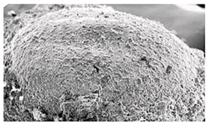
DISCUSSION

Oculishumardia Peng et al., 2003 was established based on small (less than 1.5 mm in cranidial length) trilobites from the

→

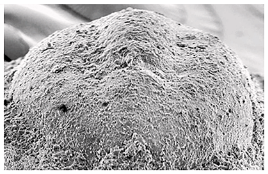
FIGURE 3—*Shantungia spinifera* Walcott, 1905 from the Kushan Formation, Tangwangzhai section, Shandong Province, China. *1–2,* Protaspid group 1 exoskeleton, SNUP5080, *1,* dorsal view, ×70, *2,* oblique lateral view, ×55; *3–6,* protaspid group 2 exoskeleton, SNUP5081, *3,* dorsal view, ×70 , *4,* lateral view, ×70, *5,* posterior view, ×70, *6,* oblique lateral view, ×55; *7,* protaspid group 2 exoskeleton, dorsal view, SNUP5082, ×70; *8,* morphologically immature cranidium, early phase of development, dorsal view, SNUP5083, ×60; *9–10,* dorsal and lateral views of morphologically immature cranidium, early phase of development, SNUP5084, ×60; *11,* morphologically immature cranidium, early phase of development, dorsal view, SNUP5085, ×55; *12,* morphologically immature cranidium, late phase of development, dorsal view, SNUP5086, ×45; *13,* morphologically immature cranidium, late phase of development, dorsal view, SNUP5087, ×35; *14,* morphologically immature cranidium, late phase of development, dorsal view, SNUP5088, ×30; *15,* morphologically immature cranidium, late phase of development, dorsal view, SNUP5089, ×20; *16,* morphologically mature cranidium, dorsal view, SNUP5090, ×15; *17–18,* dorsal and oblique lateral views of morphologically mature cranidium, SNUP5091, ×6; *19,* morphologically mature cranidium, dorsal view, SNUP5092, ×6.5; *20,* morphologically mature cranidium, dorsal view, SNUP5093, ×4.5.

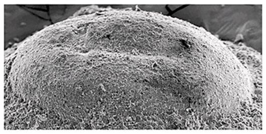

1


2

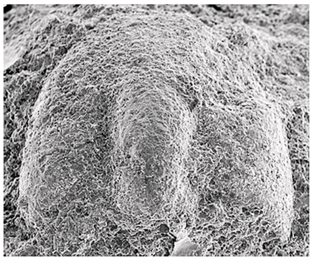

3

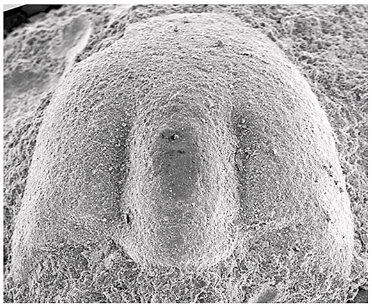

4


5

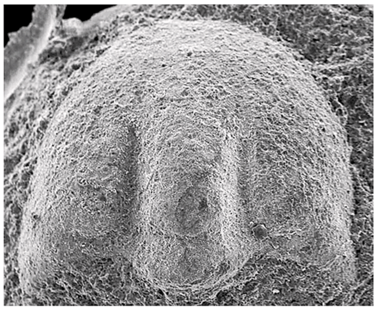

6


7

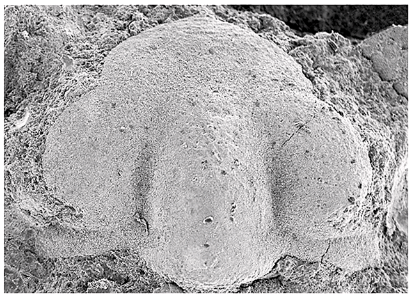

8

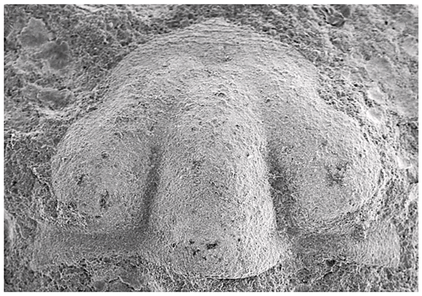

9


10

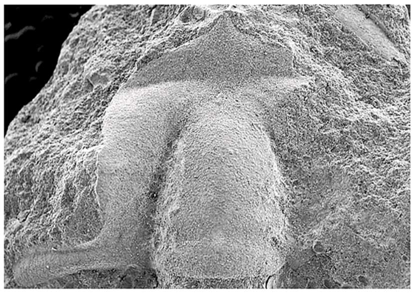

11

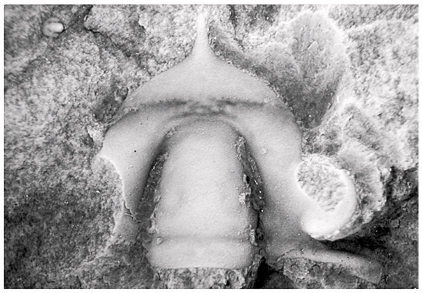

12


13

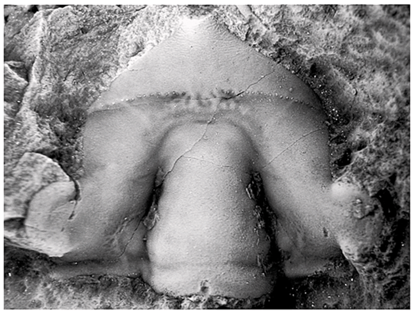

14


15


16


17


19


20


18

Liostracina bella Zone of the Huaqiao Formation in South China (cf. Peng et al., 2004) and was suggested to be one of the oldest shumardiids. The diagnostic features of this genus have been summarized as having palpebral lobes, glabella with weakly-defined anterolateral swellings, a pair of bacculae, weak lateral glabellar furrows, a long, anteriorly-sloping preglabellar field, and a faint preglabellar furrow (Peng et al., 2003). In these respects, the immature specimens of *Shantungia spinifera* are morphologically similar to *Oculishumardia*. Nonetheless there are apparent differences between *O. hunania* and the immature specimens of *S. spinifera*: morphological features shown only in *O. hunania* include anterolateral swellings on the glabella, indication of glabellar furrows, a pair of bacculae, and well-defined occipital and posterior border furrows. However, such morphological features are expressed in the morphologically mature cranidia of *S. spinifera*. In addition, the illustrated specimens of *O. hunania* demonstrate that the palpebral lobes are more prominent on larger cranidia (Peng et al., 2004, volume 2, pl. 65, figs. 13–14; pl. 66, figs. 3–6) than on smaller ones (Peng et al., 2004, volume 2, pl. 65, figs. 10–12; pl. 66, figs. 7–8) and that the preglabellar furrow and anterior border are not recognizable in the smaller specimens. Similar ontogenetic changes are also apparent in *S. spinifera* (Fig. 3).

The morphological similarity between *Oculishumardia* and the immature cranidia of *S. spinifera* indicates that *O. hunania* may represent morphologically immature stages of some damesellid trilobites occurring in the same stratigraphic interval in South China. The collection data of the polymerid trilobites from the Wangcun and Paibi sections in South China (Peng et al., 2004, volume 2, text-figs. 2 and 3) show that *Teinistion posterocostum* (Yang *in* Zhou et al., 1977) is the most likely candidate for mature forms of *O. hunania*, as *Teinistion* is morphologically comparable to *Shantungia* but differs in lacking a prominent frontal spine and in having well-defined eye ridges.

Since *Oculishumardia* was considered to represent the evolutionary intermediate stage between ptychoparioids and shumardiids (Peng et al., 2003), the ancestry of the family Shumardiidae should be explored. For the purpose of taxonomic and terminological clarity, the term ''stem-group shumardiids'' is used for the middle Cambrian taxa possibly related to the Shumardiidae, while the ''crown-group shumardiids'' refers to the post-middle Cambrian shumardiid trilobites characterized mainly by the lack of eyes, yoked librigena, small size, long macropleural spines, and a small number (usually no more than six) of thoracic segments. Accordingly, it can be said that the possibility of *Oculishumardia* being a juvenile form of some damesellid trilobites leads to two hypotheses on the ancestry of post-middle Cambrian crown-group shumardiid trilobites. First, if *Oculishumardia*-like forms truly represent the middle Cambrian stem-group shumardiids, it can be inferred that a stock of middle Cambrian damesellids gave rise to shumardiid trilobites through paedomorphic evolution. If this is the case, the current classification in which the family Shumardiidae is placed within the Order Ptychopariida (Fortey, 1997) turns out to be inappropriate, and the Shumardiidae should be included in the Order Lichida, to which the superfamily Dameselloidea is assigned. Second, if the post-middle Cambrian crown-group shumardiids arose from some ptychoparioids, and the middle Cambrian *Oculishumardia*-like forms of immature damesellid trilobites had no close phylogenetic relationship with shumardiids, the synapomorphies of *Oculishumardia* and other crown-group shumardiids proposed by Peng et al. (2003, p. 200) are results of convergent evolution. The assessment of these hypotheses would be largely dependent on the morphology of the oldest member of the crown-group shumardiids. The oldest crown-group shumardiids reported so far are *Elaphraella* Lu and Qian, 1983 from the late Changshanian stage of North China, and some specimens of *Liriamnica* Shergold, 1980 (pl. 18, figs. 9, 11; two specimens from the lowermost horizon) from the middle Iverian stage of Australia. These oldest crown-group shumardiids clearly differ from *Oculishumardia*-like forms in having a distinctly incised preglabellar furrow and no anterolateral swellings on the glabella. Accordingly, at present, the second hypothesis, in which damesellids have nothing to do with the crown-group shumardiids, is more probable.

CONCLUSIONS

The immature cranidia of *Shantungia spinifera* from North China reveal that the specimens assigned to *Oculishumarida hunania* may represent the immature forms of some damesellid trilobites. As *Oculishumardia* was claimed to be the oldest shumardiid representing a phylogentically intermediate form between ptychoparioids and shumardiids by Peng et al., 2003, this result leads to two hypotheses on the ancestry of shumardiid trilobites: 1) the shumardiids may possibly have arisen from a stock of some damesellids or 2) the *Oculishumardia*-like forms of immature damesellids had no close phylogenetic relationship with shumardiids. The morphology of the oldest crown group shumardiid trilobites known so far suggests that the second hypothesis, in which damesellid trilobites were not closely related to shumardiid trilobites, is more likely.

ACKNOWLEDGMENTS

We are grateful to Mark Webster, Nigel Hughes, and Brian Pratt for their insightful comments and constructive suggestions on the manuscript. Thanks are extended to Jitao Chen for his help in collecting specimens in the field. Financial support for this study has come from the Korea Research Foundation (Grant No. KRF-2006-312-C00437). This paper is a contribution of the BK 21 Project of the School of Earth and Environmental Sciences, Seoul National University.

REFERENCES

BERGERON, J. N. 1899. Étude de quelques trilobites de Chine. Bulletin de la Societé Géologique de France, 3rd Series, 27:499–519.

BUREAU OF GEOLOGY AND MINERAL RESOURCES OF SHANDONG PROVINCE. 1996. Stratigraphy (Lithostratic) of Shandong Province, P. One, Preface to Cambrian and Ordovician. China University of Geosciences Press, Wuhan. 168 p. (In Chinese)

CHATTERTON, B. D. E. AND S. E. SPEYER. 1997. Ontogeny, p. 173–247. *In* R. L. Kaesler (ed.), Treatise on Invertebrate Paleontology, Pt. O, Arthropoda 1, Trilobita 1 (Revised). Geological Society of America and University of Kansas Press, Lawrence.

ENDO, R. AND C. E. RESSER. 1937. The Sinian and Cambrian formations and fossils of southern Manchoukuo. Manchurian Science Museum Bulletin, 1: 1–474.

FORTEY, R. A. 1990. Ontogeny, hypostome attachment and trilobite classification. Palaeontology, 33:529–576.

FORTEY, R. A. 1997. Classification, p. 289–302. *In* R. L. Kaesler (ed.), Treatise on Invertebrate Paleontology, Pt. O, Arthropoda 1, Trilobita 1 (Revised). Geological Society of America and University of Kansas Press, Lawrence.

KOBAYASHI, T. 1935. The Cambro–Ordovician formations and faunas of South Chosen, Palaeontology, P. III, Cambrian faunas of South Chosen with a special study on the Cambrian genera and families. Journal of the Faculty of Science, Imperial University of Tokyo, Section 2, 4:49–344.

LU, Y. H. AND Y.-Y. QIAN. 1983. New zonation and correlation of the Upper Cambrian Changshanian Stage in North China. Acta Palaeontologica Sinica, 22:234–254. (In Chinese)

MONKE, H. 1903. Beiträge zur Geologie von Schantung. P. 1, Obercambrische Trilobiten von Yen-tsy-yai. Jahrbuch der Königliche Preussische Geologische Landesanstalt, Berlin, 23:103–151.

ÖZDIKMEN, H. 2006. Nomenclatural changes for fourteen trilobites genera. Munis Entomology and Zoology, 1:179–190.

PENG, S.-C., L. E. BABCOCK, N. C. HUGHES, AND H.-L. LIN. 2003. Upper Cambrian shumardiids from north-western Hunan, China, p. 229–240. *In* P. D. Lane, D. J. Siveter, and R. A. Fortey (eds.), Trilobites and their relatives. Special Papers in Palaeontology 70.

PENG, S.-C., L. E. BABCOCK, AND H.-L. LIN. 2004. Polymerid Trilobites from the Cambrian of Northwestern Hunan, China. Science Press, Beijing, Volume 1, 333 p. and Volume 2, 355 p.

QIU, H.-A., Y.-H. LU, Z.-L. ZHU, D.-C. BI, T.-R. LIN, Q.-Z. ZHANG, Y.-Y. QIAN, T.-Y. JU, N.-R. HAN, AND X.-Z. WEI. 1983. Trilobita, p. 28–254. *In* Palaeontological Atlas of East China, 1: Volume of Early Palaeozoic, Geological Publishing House, Beijing. (In Chinese)

SHERGOLD, J. H. 1980. Late Cambrian trilobites from the Chatsworth Limestone, western Queensland. Bureau of Mineral Resources, Geology, and Geophysics Bulletin, 186:1–111.

WALCOTT, C. D. 1905. Cambrian faunas of China. Proceedings of the U.S. National Museum, 29:1–106.

WALCOTT, C. D. 1906. Cambrian faunas of China. Proceedings of the U.S. National Museum, 30:563–595.

WALCOTT, C. D. 1911. Cambrian faunas of China. Smithsonian Miscellaneous Collections, 57:69–109.

WALCOTT, C. D. 1913. The Cambrian faunas of China. *In* Research in China. Volume 3. Carnegie Institution of Washington, Publication 54:3–276.

ZHANG, W.-T. AND P. A. JELL. 1987. Cambrian Trilobites of North China, Chinese Cambrian Trilobites Housed in the Smithsonian Institution. Science Press, Beijing, 459 p.

ZHOU, T.-M., Y.-J. LIU, X.-S. MENG, AND Z.-H. SUN. 1977. Trilobita, p. 104–266. *In* X.-F. Wang (ed.), Palaeontological Atlas of South-central China, Volume 1, Early Palaeozoic. Geological Publishing House, Beijing. (In Chinese)

ACCEPTED 7 JANUARY 2008