Ontogeny of a New Species of the Cambrian Series 3 (Middle Cambrian) Trilobite Genus *Liostracina* Monke, 1903 from North China and the Taxonomic Position of the Superfamily Trinucleoidea

Author(s): Tae-Yoon S. Park , Ji-Hoon Kihm , Imseong Kang , and Duck K. Choi
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ONTOGENY OF A NEW SPECIES OF THE CAMBRIAN SERIES 3 (MIDDLE CAMBRIAN) TRILOBITE GENUS *LIOSTRACINA* MONKE, 1903 FROM NORTH CHINA AND THE TAXONOMIC POSITION OF THE SUPERFAMILY TRINUCLEOIDEA

TAE-YOON S. PARK,[1] JI-HOON KIHM,[1] IMSEONG KANG,[2] AND DUCK K. CHOI[2]

[1]Division of Polar-Earth System Sciences, Korea Polar Research Institute, Incheon 406–840, Korea, <taeyoon.park@hotmail.com>; <jhkihm@kopri.re.kr>; and [2]School of Earth and Environmental Sciences, Seoul National University, Seoul 151–747, Korea, <imseongkang@gmail.com>; <dkchoi@snu.ac.kr>

ABSTRACT —The Order Asaphida was grouped by the presence of a ventral median suture and a globular protaspis. The Superfamily Trinucleoidea has been assigned to the Order Asaphida, based on the recognition of a globular protaspis in the Ordovician representatives of the group, and the presence of a ventral median suture in the middle Cambrian genus *Liostracina* which has been regarded as a primitive sister-group to the post-Cambrian trinucleoideans. Recent studies demonstrate that the ventral median suture and the globular protaspis could have evolved multiple times in the trilobite evolutionary history, casting doubt on the traditional concept of the Order Asaphida. Inclusion of the Trinucleoidea into the Order Asaphida, therefore, has to be tested. It has recently been revealed that *Liostracina simesi* Jago and Cooper, 2005 did not possess a ventral median suture, implying that there could have been variable types of ventral suture within the genus *Liostracina*. Here we report the ontogeny of *Liostracina tangwangzhaiensis* n. sp. from the Cambrian Series 3 (middle Cambrian) strata of Shandong Province of North China. The material for this study includes protaspides, which are of flat, benthic morphology, contrasting to the globular protaspid morphology of the Ordovician trinucleoideans. The benthic protaspid morphology of *L. tangwangzhaiensis* indicates an independent evolution of the globular protaspis within the Superfamily Trinucleoidea. Together with the variable types of ventral suture within the genus *Liostracina*, the benthic protaspid morphology of *Liostracina* leads us to propose that the Superfamily Trinucleoidea be excluded from the Order Asaphida.

INTRODUCTION

THE TRILOBITE Superfamily Trinucleoidea is a monophyletic group characterized by the convex and pyriform glabella, the long and narrow adaxial part of thoracic pleurae, the triangular pygidium with very narrow doublure, and the basket-and-lid style of enrollment (Fortey and Chatterton, 1988). The traditional Order Asaphida, as defined by Fortey and Chatterton (1988) and Fortey (1990), was supposedly diagnosed by the presence of a ventral median suture and the globular protaspis, termed as the "asaphoid" protaspis. The Superfamily Trinucleoidea was included in the Asaphida by Fortey and Chatterton (1988) and Chatterton et al. (1994), and this assignment has been followed by subsequent studies (Fortey, 1997; Peng et al., 2004; Adrain, 2011). Fortey and Chatterton (1988) and Chatterton et al. (1994) based the argument on: 1) the presence of a planktonic "asaphoid" protaspis in the Ordovician representatives; 2) the presence of a pre-occipital tubercle in many trinucleoids; 3) the existence of the primitive trinucleoid forms which resemble the general "ptychoparioid" morphology near the Cambrian–Ordovician boundary; and 4) the identification of a Cambrian sister group, the Liostracinidae, which has a ventral median suture. Recent studies, however, cast doubt on the traditional concept of the Order Asaphida. Adrain et al. (2009) raised a question on the inclusion of the Remopleuridioidea into the Order Asaphida. Park and Choi (2009, 2010, 2011a) and Zhu et al. (2010) proved the polyphyletic origins of a ventral median suture in trilobite phylogeny, and Park and Choi (2011a) demonstrated that the globular protaspis, termed "asaphoid" protaspis, also could have evolved multiple times. Park and Choi (2011a) accordingly noted that "as the possession of both a ventral median suture and a highly globular protaspis does not guarantee the Asaphida-affinity, the inclusion of the Superfamily Trinucleoidea within the Order Asaphida would require further examination."

The genus *Liostracina* Monke, 1903 occurs exclusively in the Guzhangian stage of the Cambrian Series 3 of East Gondwana including North China, South China, Korea, Australia, and Antarctica. *Liostracina* is the type genus of the family Liostracinidae, which has been treated as a primitive member of the Trinucleoidea by Fortey and Chatterton (1988) and Chatterton et al. (1994). Of the *Liostracina* species, *Liostracina volens* Öpik, 1967 apparently possessed a ventral median suture (Öpik, 1967, pl. 35, figs. 3, 4), which was considered as crucial evidence for the inclusion of the Trinucleoidea into the Order Asaphida (Fortey and Chatterton, 1988; Chatterton et al., 1994). However, Park and Choi (2011c) recently documented silicified specimens of *Liostracina simesi* Jago and Cooper, 2005 from Korea, which has a subtriangular rostellum or rostral plate-like structure throughout the ontogeny, not a ventral median suture. Furthermore, *Liostracina* sp. 1 from Korea documented by Park and Choi (2011c) has a peculiar ventral structure which was presumed to be a fused rostral plate or ventral extension of the anterior cranidial border (Park and Choi, 2011c, fig. S7, 10–12). This variable ventral structure among the *Liostracina* species raises the possibility that the possession of a ventral median suture was not a plesiomorphic condition of the Liostracinidae, hence questioning the assignment of the Trinucleoidea to the Order Asaphida.

This study describes the ontogenetic development of a new species of *Liostracina* collected from the *Neodrepanura* Zone of

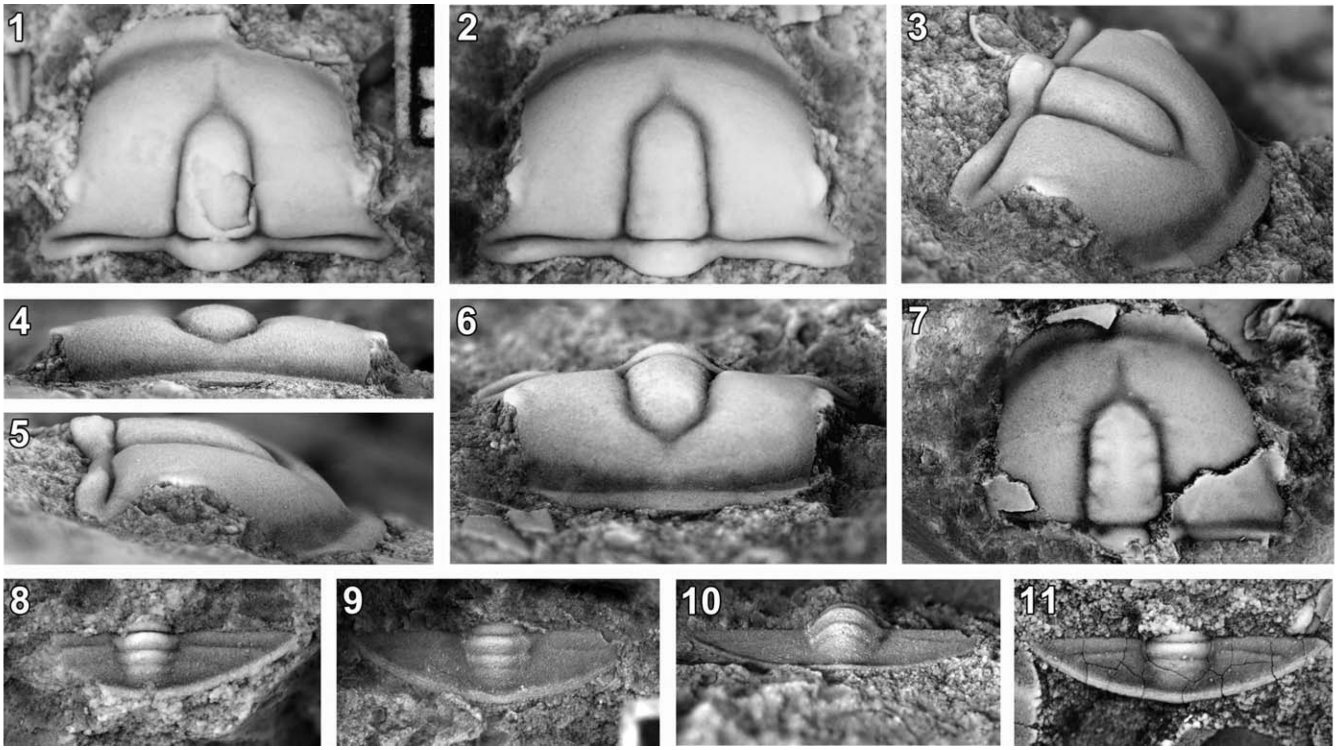

FIGURE 1—*Liostracina tangwangzhaiensis* new species from the Gushan Formation, Tangwangzhai section, Shandong Province, China. *1–7*, cranidia: *1*, GNSM-3962-001, dorsal view, ×10; *2–6*, holotype, GNSM-3962-002: *2*, dorsal view, ×10; *3*, oblique anterolateral view, ×8; *4*, anterior view, ×10; *5*, lateral view, ×10; *6*, oblique anterior view, ×10; *7*, partly exfoliated cranidium, GNSM-3963, dorsal view, ×6.5; *8–11*, pygidia: *8*, GNSM-3964, dorsal view, ×14; *9*, *10*, GNSM-3965: *9*, dorsal view, ×10; *10*, oblique posterior view, ×10; *11*, GNSM-3966, dorsal view, ×10.

the Gushan (Kushan) Formation in Shandong Province of North China. The material for this study includes thirteen protaspides, the morphology of which is expected to provide crucial information on the taxonomic position of the Superfamily Trinucleoidea.

FOSSIL LOCALITY AND MATERIAL

All of the specimens for this study were collected from the Gushan Formation of the Tangwangzhai section, Shandong Province, North China (E 116°51′42″ and N 36°30′33″). The Gushan Formation in this section is about 62 m in thickness and poorly exposed. The specimens were collected from the interval between 43 m and 48 m above the base of the formation. The immature and mature specimens of *Shantungia spirifera* were recovered from the same interval (Park et al., 2008). The location map of the Tangwangzhai section and a detailed lithologic and biostratigraphic description of the Gushan Formation in this section was given by Park et al. (2008) and is not repeated herein. Other trilobites occurring in this interval include *Pseudagnostus* sp., *Kormagnostus* sp., *Clavagnostus* sp., *Neodrepanura presminili* (Bergeron, 1899), *Bergeronites ketteleri* (Monke, 1903), and *Shantungia spirifera* Walcott, 1905.

A total of 81 specimens representing a range of ontogenetic stages were recovered including 13 protaspides, 64 cranidia, and four pygidia.

SYSTEMATIC PALEONTOLOGY

The morphological terms basically follow those of Whittington and Kelly (1997), but the term glabella excludes the occipital ring. All of the specimens are housed in the paleontological collections of Gwacheon National Science Museum, and are registered with numbers prefixed by GNSM. Terms in description always are always referred to standard plane: Length refers to sagittal distance, while width means maximum transverse distance.

Superfamily TRINUCLEOIDEA Hawle and Corda, 1847
Family LIOSTRACINIDAE Raymond, 1937

Remarks.—The familial concept was intensively discussed by Öpik (1967). As for the supra-familial assignment of this family to the Trinucleoidea, Fortey and Chatterton (1988) noted an overall similarity between the undoubted primitive Tremadocian trinucleoidean *Orometopus* Brögger, 1898 and *Liostracina*. The assignment of the Liostracinidae into the Trinucleoidea is acceptable given the morphological features of *Liostracina* noted by Fortey and Chatterton (1988). Subsequent studies also treated the Liostracinidae as a member of the Trinucleoidea (Peng et al., 2004; Adrain, 2011).

Genus LIOSTRACINA Monke, 1903

Type species.—*Liostracina krausei* Monke, 1903 from the *Neodrepanura* Zone of the Gushan Formation, Shandong Province, North China.

Other species.—*L. volens* Öpik, 1967 from the O'Hara Shale and the Georgina Limestone, Queensland, Australia; *L. nolens* Öpik, 1967 from the Georgina Limestone, Queensland, Australia; *L. bella* Lin and Zhou *in* Lin et al., 1983 from the Tuanshan Formation, Jiangsu, China; *L. bilimbata* Zhang *in* Qiu et al., 1983 (=*L. suixiensis* Bi *in* Qiu et al., 1983) from the Gushan Formation, Anhui, China; *L. qingyangensis* Qian and Qiu *in* Qiu et al., 1983 from the Tuanshan Formation, Anhui, China; and *L. simesi* Jago and Cooper, 2005 from the Spurs Formation, northern Victoria Land, Antarctica.; *L. kaulbacki* Shergold, Laurie and Shergold, 2007 from the Skewthorpe Formation, Bonaparte Basin, Australia.

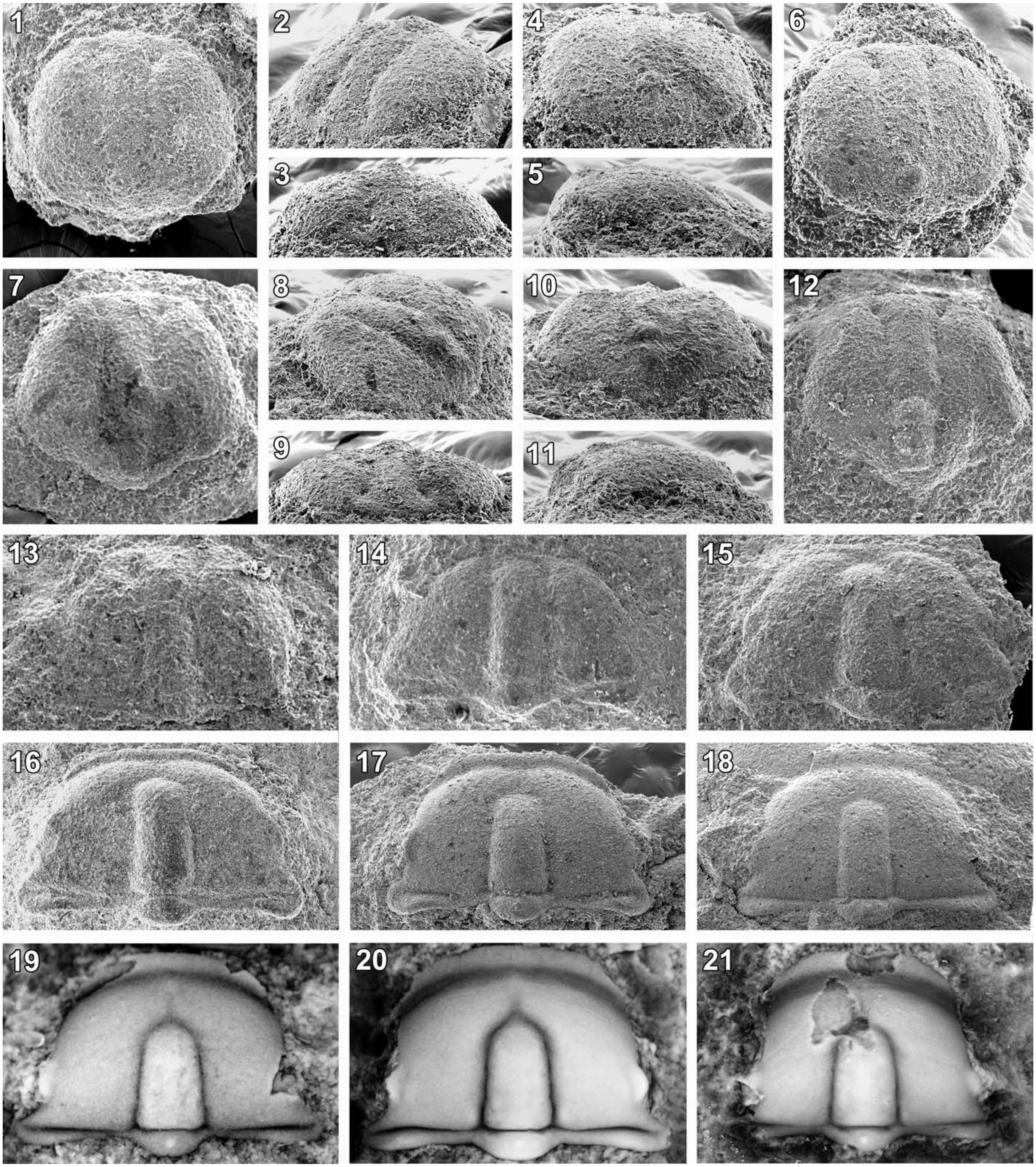

FIGURE 2—*Liostracina tangwangzhaiensis* new species from the Gushan Formation, Tangwangzhai section, Shandong Province, China. *1–6*, early stage protaspides: *1–5*, GNSM-3967-001: *1*, dorsal view, ×100; *2*, oblique anterolateral view, ×100; *3*, anterior view, ×100; *4*, oblique posterior view, ×100; *5*, lateral view, ×100; *6*, GNSM-3967-002, dorsal view, ×100; *7–12*, late stage protaspides: *7–11*, GNSM-3967-003: *7*, dorsal view, ×80; *8*, oblique posterolateral view, ×75; *9*, anterior view, ×80; *10*, oblique posterior view, ×80; *11*, lateral view, ×80; *12*, GNSM-3967-004, dorsal view, ×90; *13–16*, early phase morphologically immature cranidia: *13*, cranidium representing the first instar, GNSM-3968-001, dorsal view, ×100; *14*, cranidium representing the second instar, GNSM-3969-001, dorsal view, ×100; *15*, cranidium representing the third instar, GNSM-3968-002, dorsal view, ×55; *16*, cranidium representing the fourth instar, GNSM-3969-002, dorsal view, ×40; *17–19*, late phase morphologically immature cranidia: *17*, GNSM-3970, dorsal view, ×30; *18*, GNSM-3968-003, dorsal view, ×25; *19*, GNSM-3971, dorsal view, ×20; *20*, *21*, morphologically mature cranidia: *20*, GNSM-3962-002, dorsal view, ×10; *21*, GNSM-3972, dorsal view, ×8.

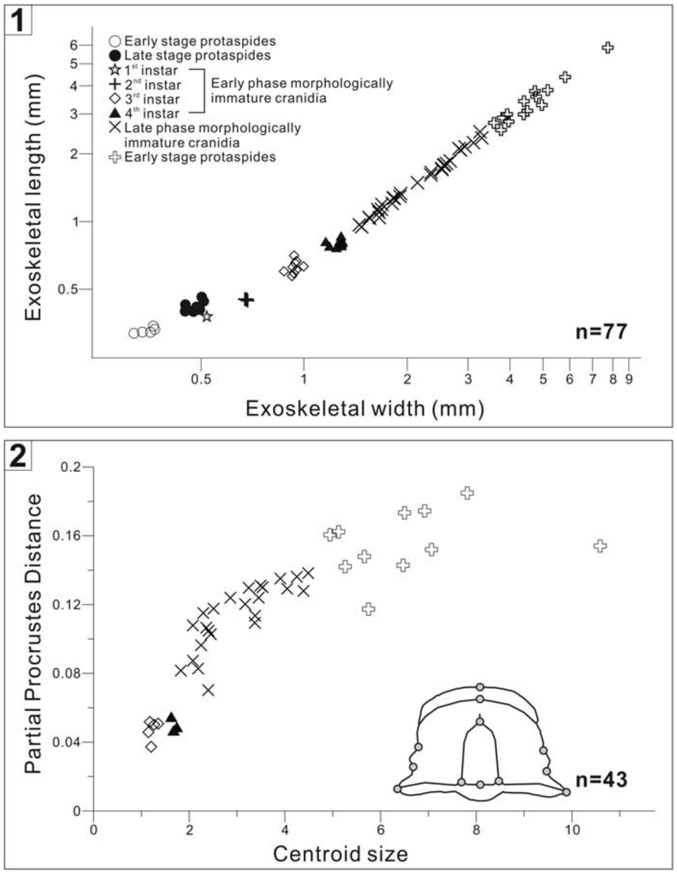

FIGURE 3—*1*, length and width dimensions of protaspides and post-protaspid cranidia of *Liostracina tangwangzhaiensis* new species from the Gushan Formation, Tangwangzhai section, Shandong Province, China; the axes are on a natural logarithmic scale; *2*, partial Procrustes distance of cranidia from a reference form of the consensus of the three smallest cranidia of the third instar; the schematic drawing shows the selected landmarks on cranidium. The slope of the Procrustes distance becomes significantly less steep within the late phase morphologically immature cranidia, indicating that the 'geometrically' mature morphology has been nearly attained.

Liostracina (?) *pauper*, Resser and Endo *in* Endo and Resser, 1937 from the Taitzu Formation, Liaoning Province, China; *L.*(?) *paupiforme*, Endo, 1944 from the Taitzu Formation, Liaoning, China and; *L. bifurcata* Zhang *in* Qiu et al., 1983 from the Gushan Formation, Jiangsu, China may belong to *Liostracina*, but each of these species was based on a single specimen, too poorly preserved for stable taxonomic position.

Remarks.—A detailed discussion on the generic concept was given by Öpik (1967) who summarizes the cranidial characters of the genus as follows: 1) general ptychoparioid design in dorsal aspect; 2) small steeply adaxially sloping palpebral lobes placed in the rear and far apart; 3) long, slightly tapering, narrow, and prominent glabella; 4) presence of the median preglabellar furrow; 5) presence of prominent bacculae flanking the glabellar rear; and 6) relatively short posterior border. The presence of bacculae seems to be variable among these features. For example, *Liostracina* sp. 1 from the Taebaeksan Basin, Korea, displays no trace of bacculae (Park and Choi, 2011c, fig. S7). *Liostracina simesi* from Antarctica possess prominent bacculae (Jago and Cooper, 2005, fig. 4A–4E), while *L. simesi* documented from the Taebaeksan Basin, Korea shows less prominent bacculae (Park and Choi, 2011c, fig. S6). The new species described in this study also bears no bacculae.

To date, the paleogeographical occurrence of *Liostracina* is restricted to East Gondwana: i.e., North China (Monke, 1903; Walcott, 1913; Endo and Resser, 1937; Endo, 1944; Qiu et al., 1983; Zhang and Jell, 1987; Zhang et al., 1995), South China (Egorova et al., 1963; Zhou et al., 1977; Lin et al., 1983; Peng et al., 2004), Korea (Park and Choi, 2011c), Australia (Öpik, 1967), and Antarctica (Jago and Cooper, 2005). Species of *Liostracina* generally show a high level of endemism; the occurrence of each species is restricted to its own province. Although Egorova et al. (1963) and Zhou et al. (1977) reported *L. krausei*, which is a representative species of North China, from South China, these specimens have been synonymized with *L. bella* (see Peng et al., 2004). In this regard, the common occurrence of *L. simesi* from northern Victoria Land of Antarctica and the Taebaeksan Basin of Korea is noteworthy (Park and Choi, 2011c). *Liostracina simesi* from the Sesong Formation, Korea occurs in a very short interval, and constitutes a fauna of low diversity which appeared after a significant mass extinction of the damesellids-dominated fauna of the *Neodrepanura* Zone (Park and Choi, 2011c). It is therefore inferred that *L. simesi* may have briefly inhabited the Taebaeksan Basin as an opportunistic species.

LIOSTRACINA TANGWANGZHAIENSIS new species
Figures 1, 2

Diagnosis.—This species is easily distinguished from other species of *Liostracina* in having a forward converging anterior branch of the facial suture, and in lacking bacculae and eye-ridges. In addition, this species has a cranidium of markedly lower convexity. Especially the convexity of the glabella is the lowest among the species of *Liostracina*.

Description.—Cranidium semicircular in outline, low in convexity; cranidial width about 1.5 times cranidial length; surface smooth. Glabella subcylindrical in outline, slightly to moderately tapering forward, with weakly pointed glabellar frontal margin; glabellar length 0.51 of cranidial length; glabellar width 0.22 of cranidial width. Lateral glabellar furrows absent in testaceous cranidium (Figs. 1.1, 1.2, 2.21), but three pairs of lateral glabellar furrows faintly observable in internal molds (Fig. 1.7). Axial furrows moderately deep; shallow median preglabellar furrow extending forward from glabellar front, but not reaching anterior border furrow; a weak swelling located between median preglabellar furrow and anterior cranidial border furrow. Preglabellar field length 0.18 of cranidial length; anterior cranidial border furrow wide and shallow; anterior border flat, moderately wide, length 0.11 of cranidial length. Occipital ring semicircular in outline, abaxially connected to posterior cranidial border; small occipital node located at center of occipital ring. Short palpebral lobes situated slightly posterior to glabellar midlength; length 0.16 of cranidial length. Eye ridges absent or extremely faintly visible, they are more clearly defined on the internal mold. Anterior branch of facial suture initially running parallel, but then smoothly converging forward; posterior branch of facial suture diverging backward at angle of about 45° relative to an exsagittal line. Bacculae absent. Posterior cranidial border defined by a deeply incised posterior cranidial border furrow, border narrow, but becoming gently wider abaxially.

Pygidium weakly triangular in outline, short and wide; width about 4 times length including the articulating half ring. Axial width 0.23 of pygidial width; axis convex, tapering slightly backwards, composed of three axial rings and a terminal piece with rounded posterior margin. Pleural field flat; pleural furrows subtransvers, reaching border furrow; border extremely narrow and convex.

Etymology.—Referring to the Tangwangzhai section, from which the specimens were collected.

Types.—Holotype cranidium: GSNM-3962-002 (Fig. 1.2–1.6)

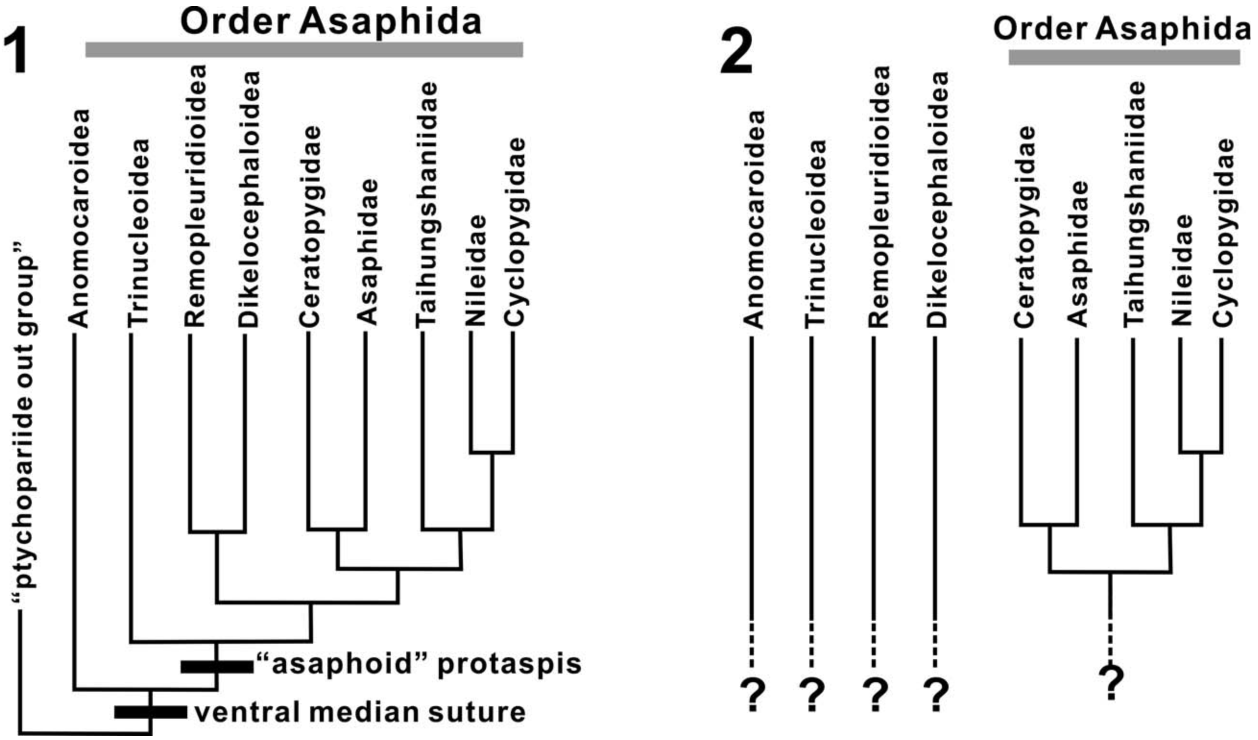

FIGURE 4—*1*, a tree describing the phylogenetic relationships within the traditional Order Asaphida, based on Fortey and Chatterton (1988, text-fig. 1) and Chatterton et al. (1994, fig. 13); the presence of ventral median suture and the "asaphoid" protaspis plays a pivotal role in defining the traditional Order Asaphida in this phylogenetic tree; *2*, a schematic tree describing the current status of the Order Asaphida, based on Park and Choi (2009, 2010, 2011a), and this study. As the presence of ventral median suture and the globular ("asaphoid") protaspis evolved multiple times in the trilobite evolutionary history, the superfamilies included in the Order Asaphida due to the presence of these characters should be excluded from the order. The current concept of the Order Asaphida is defined by the presence of the petaloid facet and the pre-occipital tubercle, and contains only five families. The origins of the Order Asaphida, as well as those of the Anomocaroidea, Trinucleoidea, Remopleuridioidea, and Dikelocephaloidea, become unclear. See Adrain (2011) for a different view on the assignment of the family Remopleurididae.

from the *Neodrepanura* Zone of the Gushan Formation, Tangwangzhai section, Shandong Province, China. Paratypes: ten cranidia of various developmental stages (GSNM-3962-001, GSNM-3963, GSNM-3968-001, GSNM-3968-002, GSNM-3968-003, GSNM-3969-001, GSNM-3969-002, GSNM-3970, GSNM-3971, GSNM-3972) and three pygidia (GSNM-3964, GSNM-3965, GSNM-3966).

Material.—Thirteen protaspides, 64 cranidia, and four pygidia, including immature specimens.

Occurrence.—*Neodrepanura* Zone of the Gushan Formation, Tangwangzhai section, Shandong Province, North China.

Remarks.—*Liostracina tangwangzhaiensis* occurs in association with damesellid trilobites, such as *Neodrepanura premesnili*, *Bergeronites ketteleri*, and *Shantungia spirifera*. In the Jiulongshan section of Shandong Province, *Liostracina krausei* has been documented in association with such damesellids (Zhang and Jell, 1987). It is interesting to note that *L. krausei* has not been discovered from the Tangwangzhai section, although it has been widely documented throughout the whole of North China (see Zhang and Jell, 1987).

ONTOGENY OF *LIOSTRACINA TANGWANGZHAIENSIS*

Length and width were measured for all the protaspides and morphologically immature and mature cranidia (Fig. 3.1). The allometric growth of cranidia is visualized by plotting partial Procrustes distance against centroid size (see Zelditch et al., 2004) of the 12 landmarks from each specimen (Fig. 3.2). The reference configuration was the consensus of the three smallest cranidia of the third instar. The reference configuration represents the shape of the species at its early ontogenetic stages (Webster, 2011). Selected were 43 well-preserved cranidia in which the twelve landmarks were available (Fig. 3.2). The first and second post-protaspid instars were not included because the palpebral lobes are not well-defined in those immature specimens. The software ImageJ was used to digitize landmarks coordinates (freely available at http://rsb.info.nih.gov/ij). The Procrustes coordinates and the centroid size were obtained by CoordGen7a, while plotting of the partial Procrustes distance against the centroid size were graphically represented by Regress7a (both softwares are freely available at http://www.canisius.edu/~sheeets/morphsoft.html).

Two groupings were recognized for the protaspid exoskeletons, which probably represent two instars; the early stage protaspides and the late stage protaspides. The conventional division of the post-protaspid trilobite ontogeny into meraspid/holaspid periods is impossible for *L. tangwangzhaiensis* because all the specimens are disarticulated. Instead, the post-protaspid cranidial ontogeny of *L. tangwangzhaiensis* is divided into the early phase morphologically immature cranidia, the late phase morphologically immature cranidia, and the morphologically mature cranidia (Fig. 3.1). The early phase morphologically immature cranidia are defined as the cranidia in the earlier developmental phase during which the instar-corresponding groupings are recognized. The cranidia larger than the early phase morphologically immature cranidia, but smaller than the morphologically mature cranidia are referred to the late phase morphologically immature cranidia. The general slope of the plots for the partial Procrustes distance against centroid size becomes almost horizontal in the middle of the late phase morphologically immature cranidia (Fig. 3.2), which means the allometric development slackens, nearly attaining the 'geometrically' mature morphology. The morphologically mature cranidia are the largest cranidia the length of which is over 2.5 mm. The mature morphology has been described above, and thus the description of the morphologically mature cranidia is not repeated here.

Protaspid period.—Two size clusters are observed from the bivariate plots (Fig. 3). The smaller cluster is referred to the early stage protaspides, while the larger one to the late stage protaspides. The overall morphology of both protaspid stages is rather flat, compared to the globular "asaphoid" protaspides of the Ordovician trinucleoideans, indicating a benthic mode of life (Chatterton and Speyer, 1997).

The early stage protaspides (Fig. 2.1–2.6), represented by five specimens, are circular in outline and measure 0.31–0.34 mm long and 0.32–0.38 mm wide. The cranidium is semicircular in outline. The glabella is indicated by moderately-incised parallel-sided axial furrows. The glabellar maximum width is 0.22–0.24 of the cranidial width. A pair of anterior pits is relatively large and well-impressed. The boundary between the cranidium and the trunk is recognizable only by the presence of the occipital ring which weakly protrudes dorsally. The trunk downsloping steeply backward is small, making up about 0.18 of the exoskeletal length, on which no feature is observed.

The late stage protaspides (Fig. 2.7–2.12) are distinguished from the early stage protaspides by having a sub-pentagonal outline, and larger size (0.39–0.46 mm long and 0.45–0.52 mm wide). Eight specimens were collected for this stage. The exoskeletons are slightly less convex in lateral view than those of the early stage protaspides. The cranidium is narrowing anteriorly. The weakly convex glabella is parallel-sided or slightly expanding forward, defined by well-incised axial furrows. The glabellar width is 0.22–0.23 of the cranidial width. A pair of anterior pits is still impressed. The occipital ring is defined by a shallow and wide occipital furrow and a moderately impressed posterior cranidial marginal furrow. The trunk is inverted triangular in outline. The trunk is larger than that of the early stage protaspis, probably due to the generation of new segments at the rear end of the trunk, taking up about 0.30 of the exoskeletal length. The anterior-most axial lobe is weakly protruding behind the occipital ring.

Early phase morphologically immature cranidia.—Four instars were recognized for the early phase morphologically immature cranidia.

The first instar is represented by a single, smallest meraspid cranidium (Fig. 2.13) which is poorly preserved, 0.38 mm long and 0.53 mm wide (estimated). The overall morphology of the cranidium is similar to the cranidial morphology of the late stage protaspides. The relative width of the glabella is not measurable due to poor preservation. The posterior border furrows seem to be present, but are damaged in the specimen.

The second instar is represented by the grouping of three cranidia, 0.44–0.45 mm long and 0.68–0.69 mm wide (Fig. 3). The cranidia of this grouping are characterized by the first appearance of the narrow preglabellar area (Fig. 2.14). The glabellar front is weakly rounded. The glabellar width is about 0.22 of the cranidial width. The occipital ring is oval in outline. The posterior cranidial border is marked off by well-incised posterior cranidial border furrow. The posterior cranidial border widens abaxially.

Nine cranidia comprise the third instar (Fig. 3). They are 0.57–0.71 mm long and 0.88–1.01 mm wide. The cranidia of this instar are characterized by the first appearance of the anterior cranidial border (Fig. 2.15). The anterior cranidial border furrow extends backward to meet the glabellar front, apparently forming a plectrum-like appearance. The length of the whole preglabellar area is 0.12 of the cranidial length. The glabella is weakly tapering forward. The glabellar width is about 0.21 of the cranidial width. The palpebral lobes are recognized for the first time slightly anterior to the glabellar midlength, the length of which is 0.28 of the cranidial length. The occipital ring is semi-oval in outline. A tumid occipital node is present.

The fourth instar is represented by a grouping of eight cranidia, 0.76–0.85 mm long and 1.17–1.30 mm wide (Fig. 3). This instar is characterized by the first appearance of the preglabellar field (Fig. 2.16). The length of the preglabellar area has increased to become 0.15 of the cranidial length. The length of the preglabellar field is 0.08 of the cranidial length. A shallow preglabellar median furrow connects the anterior cranidial border furrow and the preglabellar furrow. The length of the palpebral lobes is 0.23 of the cranidial length.

Late phase morphologically immature cranidia.—The rest of the allometric development occurs in this phase (Fig. 2.17–2.19) to attain the mature morphology. The size of the cranidia in this phase ranges from 0.95–2.50 mm long and 1.45–3.30 mm wide. The developmental changes in this phase include an increase in the relative length of the preglabellar field; the anterior cranidial border furrow widening; an increase in the relative length of the anterior cranidial border; the palpebral lobes become comparatively shorter, moving rearward to slightly posterior to the glabellar midlength; the glabellar front becomes pointed; the preglabellar median furrow disconnects from the anterior cranidial border; the occipital node diminishes; and the posterior cranidial border slightly deflects rearward.

DISCUSSION

Ordovician trinucleoidean protaspides have been documented several times (Whittington, 1959; Shaw, 1968; Fortey and Chatterton, 1988; Speyer and Chatterton, 1989; Chatterton et al., 1994; Waisfeld et al., 2011). All of these protaspides are highly convex, so that they were regarded as "asaphoid" protaspides (Chatterton et al., 1994) which must have undergone a radical metamorphosis between the protaspid and meraspid periods (Fortey and Chatterton, 1988; Chatterton and Speyer, 1997). Intuitively, the metamorphosis during ontogeny seems to provide a good dividing point of ontogenetic stage, so that homologizing the so-called "asaphoid" protaspides from different superfamilies could be justified. However, as pointed out by Park and Choi (2011b), there is no logical reason to regard the pre-metamorphic protaspides of different species as necessarily in a homologous developmental stage. This is particularly significant given the independent origination of highly globular protaspis within the Superfamily Remopleuridioidea (Park and Choi, 2011a). In this respect, homologizing the highly convex trinucleoidean protaspides with the genuine "asaphoid" protaspides of the family Asaphidae could be inappropriate in the first place. Besides, all the globular trinucleoidean protaspides are Ordovician in age, hence possibly far from the plesiomorphic condition of the group. The Cambrian trinucleoidean *Liostracina tangwangzhaiensis* obviously shows a non-globular protaspid morphology. This fact implies that the globular protaspid morphology of the Ordovician trinucleoideans is likely to be a result of an independent evolution within the Superfamily Trinucleoidea. Accordingly, the globular protaspides of the Ordovician trinucleoideans cannot be regarded as a synapomorphy for grouping the Trinucleoidea with the asaphid trilobites. The three independent originations of the highly globular protaspid morphology (in Trinucleoidea, Remopleuridioidea, and Asaphidae) may sound striking, but Park and Choi (2011b) already provided a logical perspective for such polyphyletic originations. However, it cannot be completely ruled out that the non-globular protaspis morphology of *L. tangwangzhaiensis* was a secondary reversal from a globular condition. Further studies on the protaspid morphology of other liostracinid-related trilobites would be required to test this possibility.

Chatterton et al. (1994) provided two hypotheses for the phylogenetic position of the Trinucleoidea within the Order Asaphida. The first hypothesis is based upon the ventral cephalic suture types of the adult stage, in which the Trinucleoidea was treated as having a fused ventral suture, hence regarded as the most derived group within the Order Asaphida (Chatterton et al., 1994, fig. 13). The second hypothesis is based on the protaspid morphology with a subtriangular rostral plate. The Trinucleoidea was treated as having a rostral plate-bearing condition being located at more basal position than in the first hypothesis, between the "basal Asaphida" and, the group of "Anomocaroidea" and other Asaphida (Chatterton et al., 1994, fig. 15). Because the Ordovician trinucleoideans possessed a globular protaspis, the presence of the "asaphoid" protaspis was regarded as a synapomorphy which is more inclusive than the presence of a ventral median suture in this phylogenetic hypothesis. Importantly, in both hypotheses, the Trinucleoidea was not treated as having a ventral median suture. This is contradictory to the assumption of Fortey and Chatterton (1988) and Chatterton et al. (1994) that the Cambrian trinucleoidean *Liostracina* possessed a ventral median suture. As the presence of a ventral median suture in *Liostracina* was one of the two significant grounds for the inclusion of the Trinucleoidea within the Order Asaphida (Fortey and Chatterton, 1988; Chatterton et al., 1994), the two hypotheses on the phylogenetic position of the Trinucleoidea within the Order Asaphida provided by Chatterton et al. (1994) should be questioned in the first place. In addition, as mentioned above, there are different types of ventral suture in other species of *Liostracina*: i.e., a rostellum or rostral plate-bearing type in *L. simesi*, and a peculiar, fused rostral plate-like or ventral extension of the anterior cranidial border-like structure in *Liostracina* sp. 1 (Park and Choi, 2011c, fig. S7, 10–12). It is not likely that the apparent ventral median suture of *L. volens* was the plesiomorphic condition of *Liostracina* among the various ventral structures shown by *Liostracina* species. Because the presence of a rostral plate is the most plesiomorphic condition in trilobite evolutionary history, it is more plausible that a rostellum or the rostral plate-bearing state of *L. simesi* was the plesiomorphic condition for *Liostracina*, and the apparent ventral median suture of *L. voles* could have been a result of an independent evolution of the species. Another liostracinid trilobite, *Doremataspis ornata* Öpik, 1967 was described as having a wide rostral plate (Öpik, 1967, fig. 139), corroborating that the ventral median suture was not the plesiomorphic condition for *Liostracina*.

Taken together, a species of the Cambrian trinucleoidean *Liostracina* did not possess a globular protaspis, and the plesiomorphic condition of the ventral structure was not a ventral median suture. Therefore, the inclusion of the Superfamily Trinucleoidea within the Order Asaphida is untenable.

The original concept of the Order Asaphida comprised six superfamilies: i.e., the Anomocaroidea, Dikelocephaloidea, Remopleuridioidea, Asaphoidea, Cyclopygoidea, and Trinucleoidea (Fortey and Chatterton, 1988; Fortey, 1990). In their phylogenetic analysis, the Anomocaroidea, Dikelocephaloidea, and Remopleuridioidea were positioned at the basal part of the cladogram, while the Asaphoidea (Ceratopygidae and Asaphidae) and the Cyclopygoidea (Taihungshanidae, Nileidae, and Cyclopygidae) formed the most derived taxa (Fortey and Chatterton, 1988, text-fig. 1). However, by demonstrating that a ventral median suture and a globular protaspis were independently derived multiple times in trilobite evolutionary history, Park and Choi (2010, 2011a) concluded that the Dikelocephaloidea and the Remopleuridioidea should be excluded from the Order Asaphida. Since the presence of ventral median suture alone cannot guarantee membership in the Order Asaphida, the inclusion of the Anomocaroidea within the Order Asaphida is also questioned. In addition, this study demonstrates that there is no logical ground to include the Trinucleoidea in the Order Asaphida. In short, only the monophyly of the two superfamilies, the Asaphoidea and Cyclopygoidea, can be maintained within the Order Asaphida on the basis of the presence of the petaloid facet and the pre-occipital tubercle (see Fortey and Chatterton, 1988), while the other four superfamilies should be excluded from the Order Asaphida (Fig. 4). The Anomocaroidea, Dikelocephaloidea, and Remopleuridioidea were all excluded from the Order Asaphida in the recent classification of trilobites by Adrain (2011).

CONCLUSIONS

The ontogeny of the Cambrian trinucleoidean trilobite, *Liostracina tangwangzhaiensis* new species shows that this primitive trinucleoidean possessed a non-globular, presumably benthic protaspid morphology which is contrasting to the globular, "asaphoid" protaspid morphology of the Ordovician trinucleoideans. This observation implies that the presence of a benthic protaspis is the plesiomorphic condition for the Trinucleoidea, and the globular protaspid morphology evolved independently within the Trinucleoidea. Therefore, the globular protaspis of the Ordovician trinucleoideans cannot be homologized with the "asaphoid" protaspis of the Asaphidae. Furthermore, the various ventral structures present in *Liostracina* indicate that the apparent ventral median suture of *L. volens* is likely to be a derived condition, not the plesiomorphic condition of the genus. Because the presence of a ventral median suture in the Cambrian trinucleoidean trilobite, *Liostracina*, and the globular protaspides of the Ordovician trinucleoideans were regarded as the two main criteria for the inclusion of the Trinucleoidea within the Order Asaphida, the lack of an invariable ventral median suture and a globular protaspis in *Liostracina* suggests that the Trinucleoidea should be excluded from the Order Asaphida. Taken together with other recent studies, only the two superfamilies, the Asaphoidea and Cyclopygoidea should remain in the Order Asaphida.

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