

# Post-embryonic development of the Early Ordovician (ca. 480 Ma) trilobite *Apatokephalus latilimbatus* Peng, 1990 and the evolution of metamorphosis

Tae-Yoon S. Park,\* and Ji-Hoon Kihm

Division of Polar Earth-System Sciences, Korea Polar Research Institute, Incheon 406-840, Korea

\*Author for correspondence (e-mail: tspark@kopri.re.kr)

**SUMMARY** In many marine invertebrates metamorphosis entails a shift from a free-swimming larva to a benthic juvenile or adult. However, how the metamorphosis-entailing “indirect development” in arthropods arose from direct-developing ancestor is poorly understood. Trilobites left a rich fossil record, and some trilobite lineages had a metamorphosis-undergoing early developmental stage, termed the “asaphoid protaspis”-stage, providing a good opportunity to elucidate the rise of indirect development. Among others, the Ordovician representatives of Remopleuridioidea are known to possess a highly bulbous “asaphoid protaspis,” while the Furongian (Late Cambrian) remopleuridioidean genus *Haniwa* did not possess it. Here we show the post-embryonic development of the remopleuridioidean trilobite, *Apatokephalus latilimbatus*, from the Tremadocian (485.4 Ma–477.7 Ma) Dongjeom Formation, Korea. The post-embryonic development of *A. latilimbatus* contains a free-swimming

“commutavi protaspis” (a term replacing “asaphoid protaspis”). Interestingly, the earlier protaspis stage shows more similar morphology and size to the meraspis than the commutavi protaspis stage does. This indicates that the commutavi protaspis stage was intercalated into the ancestral direct development as a specialized stage for a better dispersal, and thus the “commutavi protaspis” of *A. latilimbatus* represents the initial phase of the evolution of indirect development. The duration of the free-swimming phase became longer in more derived remopleuridioidean trilobites, implying that the intercalated free-swimming strategy became emphasized during subsequent evolution. The morphological gap between the commutavi protaspis and the subsequent earliest meraspis provides a convincing case for the “selective independence” of developmental stages, explaining the various morphologies of commutavi protaspides in many trilobite lineages.

## INTRODUCTION

Indirect development with metamorphosis is widely observed in many animal groups, and in many marine invertebrates it usually entails a shift from a free-swimming larva to a benthic juvenile or adult (Nielsen 2000; Hadfield et al. 2001). How such indirect development evolved in the first place has been an interesting issue of debate. Nielsen (2000, 2008) suggested that the benthic adult stage was added to the holopelagic ancestral development, while others preferred that the larval stages were intercalated into the ancestral direct development (Wolpert 1999; Degnan and Degnan 2006; Raff 2008). Nevertheless, there seems to be little doubt in that the indirect developments in arthropods evolved from the direct-developing ancestral condition (e.g., Walossek 1993; Hadfield et al. 2001). There have been some fossil ontogenies which imply the rise of indirect development from direct development in arthropods (see Haug and Haug 2013; Haug et al. 2013). However, direct fossil evidence for the initial rise of metamorphosis-entailing development has been unsatisfactory.

Due to the biomineralized exoskeleton, trilobites left the best fossil record among the Paleozoic arthropod group. The ontogeny of trilobites has been well-studied, providing research subject of various aspects (e.g., Chatterton and Speyer 1997; Hughes et al. 2006; Hughes 2007; Park and Choi 2009; Gerber and Hopkins 2011; Fusco et al. 2014; Webster 2015). One of the interesting features of trilobite ontogeny is that some lineages have been considered to have a metamorphosis-entailing development (Chatterton and Speyer 1997). With the exceptionally ample fossil record and the indirect development in some lineages, trilobite fossil records may provide a good opportunity to detect the rise of indirect development from the ancestral direct development.

The “asaphoid protaspis” is a term coined for the protaspides (trilobites of the earliest developmental phase during which trunk is still conjoined to cephalon) which had a spherical to ovoid exoskeleton with an enrolled rather than inturned doublure (relatively narrow continuation of dorsal exoskeleton onto ventral surface) (Fortey and Chatterton 1988). The bulbous, nonadult-like morphology of “asaphoid protaspides” was noted as evidence

for free-swimming planktonic life mode; the one or more prominent pairs of submarginal spines enhance hydrodynamic efficiency of the organisms, corroborating the free-swimming life mode (Speyer and Chatterton 1989). The “asaphoid protaspis” is interpreted to have undergone a metamorphosis to attain an adult-like (benthic) meraspid morphology. On the other hand, other protaspides are relatively flat in lateral view, and have been regarded to be of benthic lifestyle, being termed “adult-like” protaspides implying a direct development (Speyer and Chatterton 1989). The possession of “asaphoid protaspis” was regarded as an autapomorphy characterizing *Asaphida sensu* Fortey and Chatterton (1988), assuming that the “asaphoid protaspis” arose a single time in trilobite evolutionary history. However, not only did Chatterton et al. (1999) and Lerosey-Aubril and Feist (2005a, b) show that the bulbous planktonic protaspis evolved in other orders than *Asaphida*, but also Park and Choi (2011a) and Park et al. (2014) revealed that the “asaphoid protaspides” of some superfamilies within the Order *Asaphida sensu* Fortey and Chatterton (1988) had evolved independently.

The representatives of Remopleuridioidea are known to possess an “asaphoid protaspis” (Fortey and Chatterton 1988); Ross (1951b) described protaspides of *Menoparia genalunata* Ross, 1951a from the late Tremadocian of the Garden City Formation, Utah, and Whittington (1959) described those of *Remopleurides eximius* Whittington, 1959 from the Middle Ordovician Edinburg Formation, Virginia. Protaspides of the both species are spherical with three large pairs of sharp, conical spines, and have a very narrow ventral opening due to the highly enrolled morphology for free-swimming life mode. In contrast, a Furongian (Late Cambrian) remopleuridioidean did not entail “asaphoid protaspis” in its development (Park and Choi 2011a). Therefore, there must have been a *de novo* evolution of the “asaphoid protaspis,” and the rise of indirect development, within the remopleuridioidean lineage between the Furongian and the late Tremadocian.

This study documents the entire post-embryonic development of the Tremadocian remopleuridioidean trilobite *Apatokephalus latilimbatus* Peng, 1990 from the upper part of the Dongjeom Formation, Korea. The developmental mode and the protaspid morphology of this Tremadocian remopleuridioidean may provide vital information for the evolution of metamorphosis in trilobite development.

## FOSSIL LOCALITY, MATERIALS, AND METHODS

Material for this study was recovered from the Dongjeom Formation at the Seokgaejae Section (129° 08' 45.05" E, 37° 04' 27.9" N), which is located ca. 25 km southeast of Taebaek City, where a nearly complete succession of the Taebaek Group is exposed (Choi et al. 2004). The Dongjeom Formation in the Seokgaejae section is mainly composed of sandstone, with about 10-m-thick carbonate facies in the upper part (Choi et al.

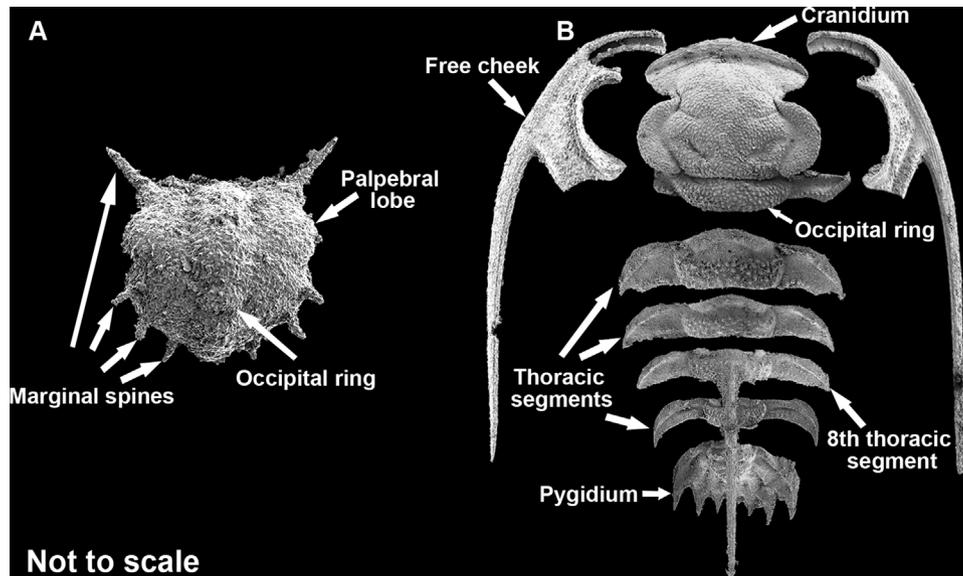
2004). To date, only lower part of the Dongjeom Formation has been known to be fossiliferous. Kobayashi (1953) established the *Pseudokainella* Zone in the lower part of the formation, but later, three biozones have been recognized from the lower part: the *Eosaukia* Fauna, *Pseudokoldinioidia* Zone and the *Richardsonella* Fauna, in ascending order (Lee and Choi 2007). The lowermost *Eosaukia* Fauna extends down to the underlying Hwajeol Formation. Apart from trilobites, stylophoran echinoderms were documented from the lowermost part of the formation (Lee et al. 2005). However, fossils have not been recognized from the middle and upper parts of the Dongjeom Formation. Preliminary research has revealed that the carbonates from the upper part of the formation contain numerous silicified sclerites of several species of trilobites and brachiopod valves. The specimens for this study were collected from a single horizon of limestone nodule-bearing shale at the ca. 10 m below the boundary between the Dongjeom Formation and the overlying Dumugol Formation.

The trilobite and conodont biostratigraphic data of the overlying Dumugol Formation indicates that the Dumugol Formation spans the late Tremadocian to Arenig (Kim et al. 1991; Seo et al. 1994; Choi et al. 2003). The new fossiliferous interval of the upper part of the Dongjeom Formation, therefore, may belong to the late middle Tremadocian or, at least, early late Tremadocian. Further research on the biostratigraphy of this interval is needed for more detailed age data.

The remopleuridioidean genus *Apatokephalus* has been documented rarely from the overlying Dumugol Formation which contains the *Asaphellus*, *Protopliomerops*, and *Kayserspis* zones, in ascending order. Kobayashi (1934) reported two *Apatokephalus* species, *A. octopoides* Kobayashi, 1934 and *Apatokephalus* sp., and Kim et al. (1991) documented *Apatokephalus?* sp. from the *Protopliomerops* Zone. However, the morphology of the *Apatokephalus* species recovered from the upper part of the Dongjeom Formation for this study is most similar to the *Apatokephalus latilimbatus* Peng, 1990 which was originally documented from the Jiangnan slope belt of South China.

The rock samples were digested by hydrochloric acid, and numerous silicified trilobite sclerites were collected from the residues. Interestingly, ca. 97% consists of *Apatokephalus latilimbatus* (528 out of 546) (Fig. 1); the remaining 18 sclerites are possibly assignable to immature specimens of *Asaphellus* species. In addition, there are sixty hypostomes and ten protaspides which are currently unidentified. For the ontogenetic research of *Apatokephalus latilimbatus*, 110 protaspis shields, 107 cranidia, 83 free cheeks, 108 thoracic segments, and 120 post-protaspis pygidia, including fragmentary specimens were collected. All of the specimens illustrated in this study are deposited in the paleontological collections of Korea Polar Research Institute, prefixed with KOPRIF.

To visualize the allometric growth of cranidial development, 17 landmarks were selected for calculation of the Partial



**Fig. 1.** Basic anatomy of *Apatokephalus latilimbatus* Peng, 1990. (A) Dorsal shield of protaspis. KOPRIF1207. Note that free cheek is lacking. (B) Disarticulated dorsal sclerites of morphologically mature developmental phase. KOPRIF1230, 1241, 1242, 1242, 1245, 1247, 1247, 1249, 1251, 1251, and 1266. The tectonic distortion of the cranium (KOPRIF1230) has been graphically restored.

Procrustes distances of well-preserved 85 post-protaspid cranidia by the reference of the consensus of three smallest cranidia, and they were plotted against the centroid size. Centroid size is the square root of the sum of squared distances of all landmarks from the centroid of the landmarks (Bookstein 1991). Landmarks of each specimen were marked using the program Image J, developed by Wayne Rasband (<http://imagej.nih.gov/ij>), while CoordGen 6.0 and Regress7a, developed by David Sheets (<http://www.canisius.edu/~sheets/morphsoft.html>) was used to obtain the centroid size and the Procrustes coordinates.

## ONTOGENY OF APATOKEPHALUS LATILIMBATUS

### Trilobite ontogeny

The embryonic stages of trilobites are not known. Post-embryonic development of trilobites was comprehensively summarized by Chatterton and Speyer (1997), and Hughes et al. (2006) refined several concepts in a modern sense. Traditionally, post-embryonic development of trilobites has been divided into three periods or phases in terms of trunk articulation (Chatterton and Speyer 1997): protaspid, meraspid, and holaspid phases. The earliest protaspid phase is characterized by having the dorsal sclerites of trunk segment conjoined to the cephalon. The meraspid phase began when the first articulation appeared between the cephalon and the trunk, and thoracic segments were released from the anteriormost end of meraspid pygidium while new segments are proliferated at the terminal growth zone of the meraspid pygidium during this

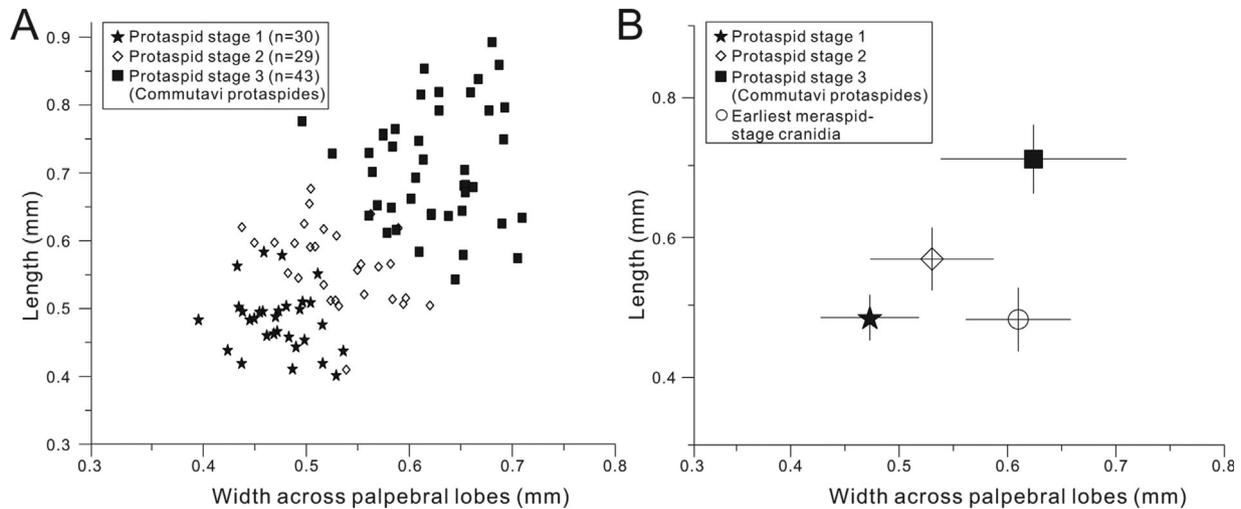
phase. The number of thoracic segments defines the degree of meraspid phase. The holaspid phase began when the last thoracic segment was released. Later, Hughes et al. (2006) suggested a new division of trilobite ontogeny into two phases with respect to trunk segment generation; the anamorphic phase represents the period during which new trunk segments appeared, while the subsequent epimorphic phase is the period during which the number of segments in the trunk did not increase any more.

### Protaspid phase

The protaspides of *A. latilimbatus* can be differentiated into the three stages by size and morphology. They roughly form three different size-clusters in the bivariate plots of exoskeletal length versus the width across the palpebral lobes (palpebral width afterward) (Fig. 2).

The first stage protaspides (Fig. 3, A–F) are subcircular in outline, 0.41–0.58 mm long and 0.39–0.54 mm wide (palpebral width), with the trunk downsloping in lateral view. Four pairs of marginal spines are present; the first pair projecting anteriorly from the cranium; the second pair projecting laterally just behind the palpebral lobes; the third pair projecting dorso-laterally from the middle of trunk lateral margin, and; the last pair projecting ventrally at the rear of the trunk. Small palpebral lobes are not recognizable in dorsal view, but recognized in the lateral view (Fig. 3B). The axial furrows are wide and shallow. The axis of the trunk is weakly inflated.

The second stage protaspides (Fig. 3, G–L) are sub-circular or sub-oval in outline; 0.41–0.67 mm long and 0.43–0.62 mm



**Fig. 2.** (A) scatter plots of length versus the width across palpebral lobes for protaspis exoskeletons of *Apatokephalus latilimbatus* Peng, 1990. (B) The mean scores of the protaspides and the earliest stage meraspid cranidia of *A. latilimbatus*. One-standard deviation bars are extended to horizontal and vertical sides of the mean. The width between the palpebral lobes could be regarded as homologous measure for the protaspides and meraspides. Note that the palpebral width of the earliest stage meraspid cranidia is slightly smaller than that of the commutavi protaspides, indicating that the size decreased, or, at least, did not increase during the metamorphosis between the two stages.

wide (palpebral width). The glabella is sub-parallel to slightly expanded in the middle, well-defined by axial furrows; a short preglabellar field is present (Fig. 3, H and L). The occipital ring is distinguished by a moderately incised occipital furrow. The palpebral lobes are well-defined in dorsal view. The trunk has more than three segments, which are defined by shallow interring furrows in the axis. Four pairs of marginal spines are present; the posterior two pairs are in the trunk.

The third stage protaspides (Fig. 3, M–U) are sub-oval in outline; 0.54–0.89 mm long and 0.49–0.84 mm wide (palpebral width). The trunk region is more enrolled and bulbous than the previous stage; the surface of the trunk is almost effaced. The glabella is slightly expanded in the middle. The palpebral lobes are not consistently recognizable in the dorsal view (e.g., Fig. 3O); small palpebral lobes are recognized in lateral views (Fig. 3, P and T). Three pairs of marginal spines are present; only the posterior-most pair projects from the trunk.

### Post-protaspis cranidia

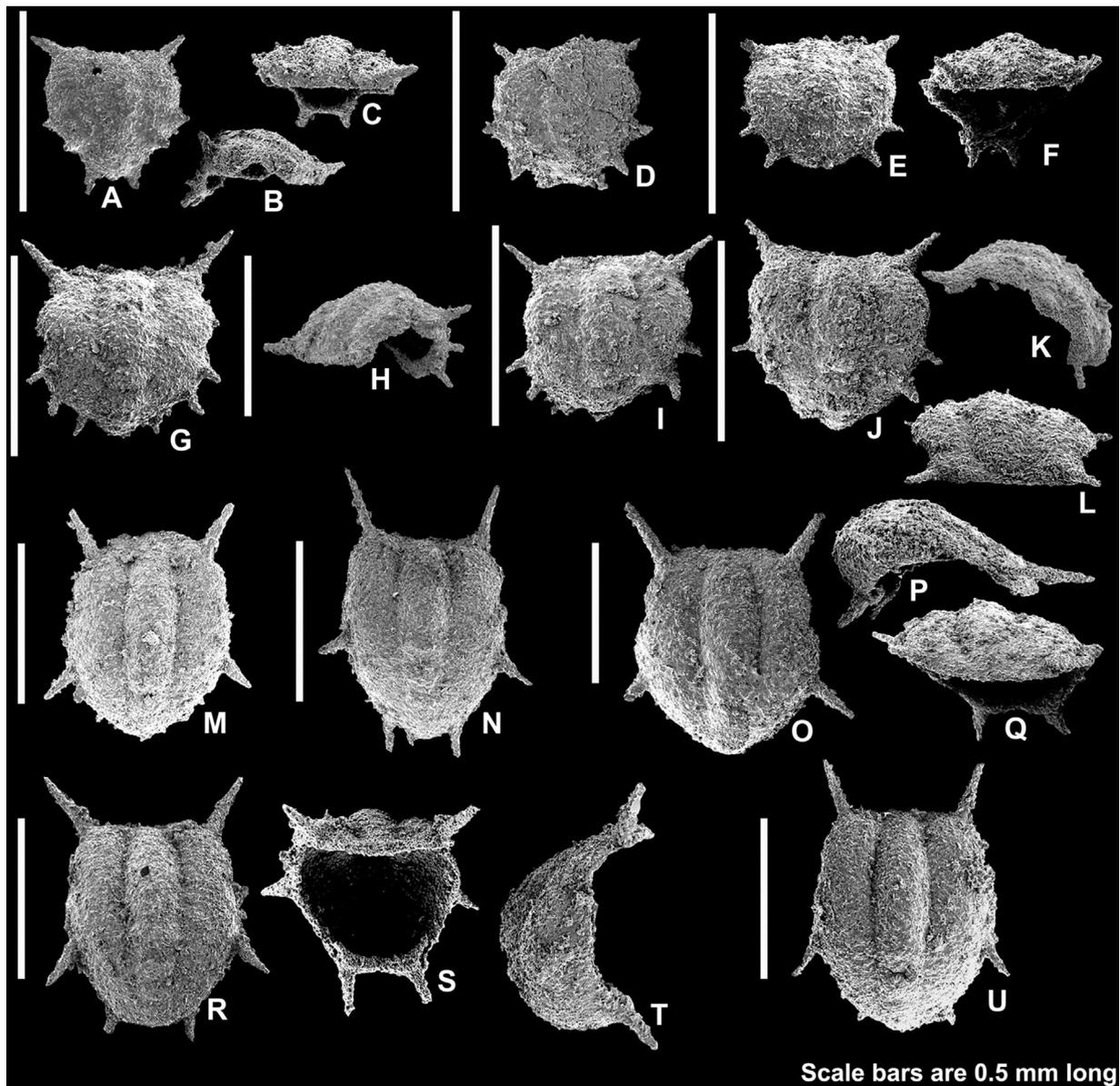
The posterior-lateral projections of *A. latilimbatus* are usually not well-preserved. Therefore, the width across the palpebral lobes (palpebral cranial width hereafter) is measured and plotted against the cranial length (Fig. 4A). Four developmental stages have been recognized for the post-protaspis cranidia of *A. latilimbatus* according to morphological changes with growth (Fig. 5). The first developmental stage likely represents the earliest meraspid instar, given the unique morphology with a pair of anterior spines.

The developmental stage 1 cranidia (Fig. 5, A–E) are 0.39–0.58 mm long with the palpebral cranial width of

0.54–0.66 mm. They are sub-trapezoidal in outline with parallel-sided, well-defined axial furrows. The glabellar front is rounded. The occipital furrow is shallow, and the posterior occipital margin is rounded rearward. The anterior border is short, about 0.05–0.07 of the cranial length with a pair of diagonally projecting anterior spines at each flank. The anterior cranial margin is straight or weakly curved rearward. The palpebral lobes are weakly defined by shallow palpebral furrows, ca. 0.4 of the cranial length. The anterior branch of facial suture is very short, due to the presence of the diagonally projecting anterior spines. The posterior fixigenal projections are abaxially short and tumid, and the posterior border furrows are shallow.

The developmental stage 2 cranidia (Fig. 5, F–J) are 0.49–1.10 mm long with the palpebral cranial width of 0.60–1.23 mm. The anterior cranial spines became disappeared. The glabellar frontal margin is more rounded than that of developmental stage 1, and wide S1 and S2 glabellar furrows are impressed shallowly. The occipital furrow is moderately incised. The anterior border becomes well-defined by a border furrow; the length is 0.09–0.13 of the cranial length. The anterior cranial margin is straight in the middle and abaxially curved rearward. The palpebral lobes are well-distinguished by weakly impressed palpebral furrows, and anteriorly continue to thick palpebral ridges. The posterior fixigenal projections are longer abaxially than those of the previous stage. The posterior cranial margin is straight and abaxially curved forward. The allometric growth during this stage is most severe (Fig. 4B).

The developmental stage 3 cranidia (Fig. 5, K–Q) are 0.88–1.35 mm long with the palpebral cranial width of 1.00–1.76 mm. Compared to the previous stage, the cranidia have more rounded anterior cranial margin. The S1 and S2

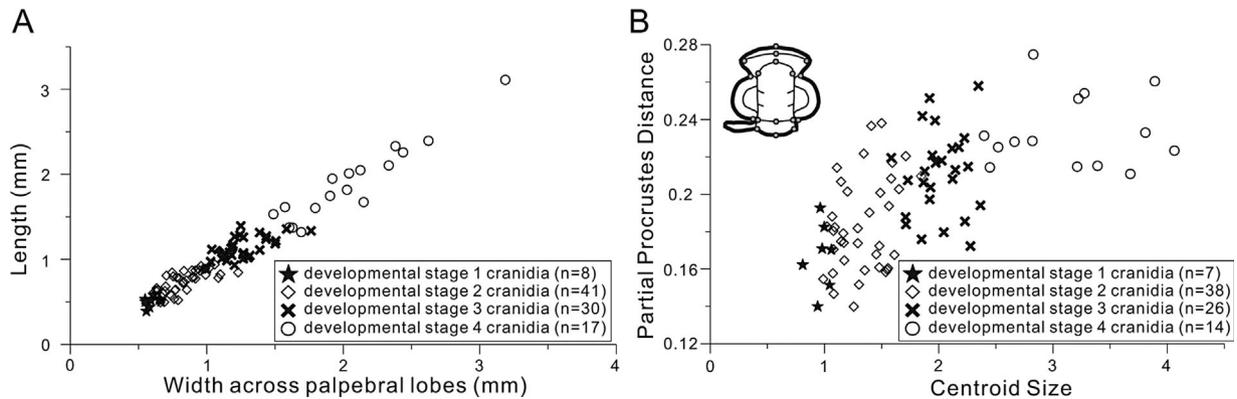


**Fig. 3.** Protaspides of *Apatokephalus latilimbatus* Peng, 1990. (A–F) stage 1 protaspides. (A–C) KOPRIF1204; (A) dorsal, (B) lateral, and (C) anterior views. (D) KOPRIF1205, dorsal view. (E, F) KOPRIF1206; (E) dorsal and (F) anterior views. (G–L) stage 2 protaspides. (G) KOPRIF1207, dorsal view. (H) KOPRIF1208, antero-lateral view. (I) KOPRIF1209, dorsal view. (J–L) KOPRIF1210; (J) dorsal, (K) lateral, and (L) anterior views. (M–U) stage 3 protaspides (commutavi protaspides). (M) KOPRIF1211, dorsal view. (N) KOPRIF1212, dorsal view. (O–Q) KOPRIF1213; (O) dorsal, (P) lateral, and (Q) anterior views. (R–T) KOPRIF1214, (R) dorsal, (S) antero-ventral, and (T) lateral views. (U) KOPRIF1215, dorsal view.

furrows become wider and deeper, and S3 furrows are still not recognizable. The occipital furrow is moderately incised. Notably, a short preglabellar field appears between the anterior cranial border and the glabellar frontal margin, and thus the length of the whole preglabellar area is ca. 0.13–0.18 of the cranial length. The anterior border furrow is curved forward. The palpebral furrows are deeper, and the palpebral lobes are thicker than those of the previous stage. The palpebral ridges are disappeared and the anterior and posterior tips of the palpebral

lobes almost reach the glabella. The anterior branches of facial suture are forwardly divergent. The slope of the Partial Procrustes distance against the centroid size becomes gentler during this stage (Fig. 4B).

The developmental stage 4 cranidia (Fig. 5, S–V) are longer than 1.3 mm with the palpebral cranial width more than 1.5 mm. Cranidia become morphologically mature during this stage. The surface becomes granulated. Most significant morphological feature of this stage is bulging of L2 and L1, eventually occupying



**Fig. 4.** (A) scatter plots of length versus the width across palpebral lobes for post-protaspid cranidia of *Apatokephalus latilimbatus*. (B) Partial Procrustes distances of cranidia of *A. latilimbatus* from a reference form of the consensus of the three smallest cranidia; the schematic drawing shows the selected landmarks on cranidium. The slope of the Partial Procrustes distance becomes almost horizontal within the developmental stage 4, representing the attainment of morphological maturity.

the space between the palpebral lobes; this is one of the important morphological features to diagnose the genus *Apatokephalus* (see Ebbestad 1999). S1 glabellar furrows are distinct, directed obliquely backward, and detached from the axial furrows due to the bulging of L1 and L2; S2 glabellar furrows are moderately incised and directed obliquely backward; S3 glabellar furrows are shallowly incised and directed obliquely forward. The occipital furrow is deeply incised. The relative length of the preglabellar field becomes slightly shorter, and thus the length of the whole preglabellar area is ca. 0.13–0.15 of the cranidial length. A series of pits appear along the anterior border furrow. The anterior cranidial margin is weakly angulated. The palpebral lobes are ca. 0.42–0.48 of the cranidial length. The anterior branches of facial suture diverge forward and the posterior branches of facial suture become horizontally straight. The posterior cranidial margin is straight initially, but then it is bent at an angle of about 40°.

### Free cheeks

The smallest free cheeks (Fig. 6, A and B) have the size and morphology which match the developmental stage 1 cranidia; the length of the genal spine is ca. 1.2 of the maximal length of the genal field; the lateral furrow is wide and shallow. With development, the relative length of the genal spine gets longer, ca. 2.4 of the maximal length of the genal field; the eye socle gets relatively longer; the posterior border runs obliquely anteriorly; the genal field becomes granulated, and; the terrace lines appear on the genal spine. A prominent visual surface is attached on a narrow eye socle (Fig. 6, H, J, and O).

### Thoracic segments

It has been known that *A. latilimbatus* has twelve thoracic segments in holaspis phase, with a long axial spine in the eighth thoracic segment (Peng 1990). Although all the thoracic

segments for this study are disarticulated, the relative width of the axis could be helpful to determine whether they were located in the frontal part or in the rear part of the thorax. As shown in the articulated specimens of *A. latilimbatus* from South China (Peng 1990, pl. 11, Figs. 4 and 5), the relative width of the axis is smaller in the rear part of the thorax, especially behind the long spine-bearing eighth segment.

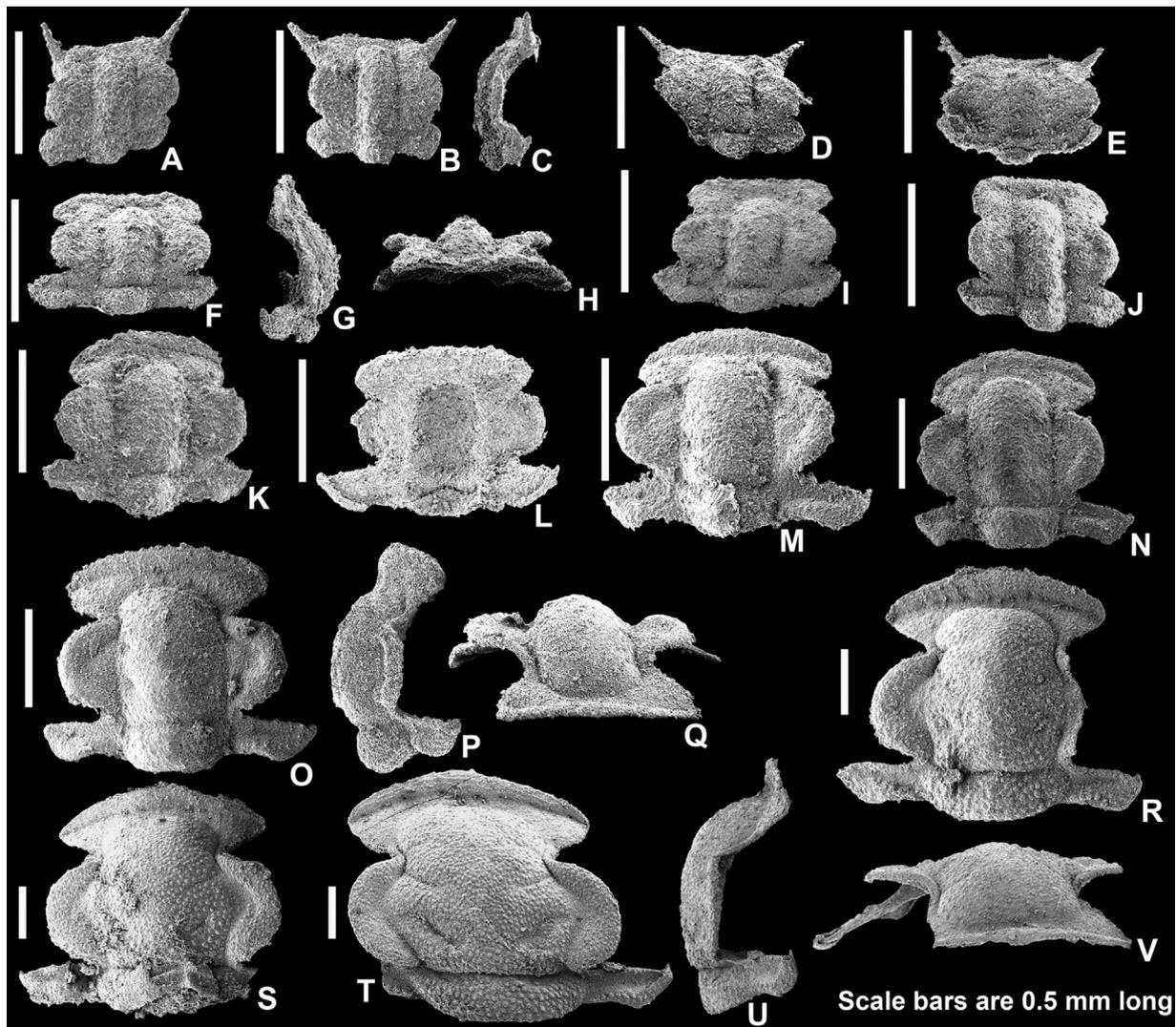
The thoracic segments from the frontal part of the thorax (Fig. 7, A–F) have a wide axis; the ratio of the axial width to the width of the thoracic segment is 0.43–0.48. The morphologically immature thoracic segments (Fig. 7, A–C) have less-pointy lateral tips, whereas those of the morphologically mature thoracic segments are weakly spinose and directed backward. The axial ring is more strongly granulated in morphologically mature specimens (Fig. 7, D and E).

The eighth thoracic segments (Fig. 7, G–I) have a ratio of the axial width to the width of the thoracic segment around 0.43, but in smaller specimens it is around 0.3. The long axial spine is ca. 1.1 of the width of the thoracic segment. It should be noted that the large articulated specimen of *A. latilimbatus* from South China has an exceptionally long axial spine (Peng 1990, pl. 11, Fig. 4), which may be ascribed to the large size of the specimen.

The thoracic segments behind the eighth segments (Fig. 7, J–L) usually have the ratio of the axial width to the width of the thoracic segment below ca. 0.4. More located backward, the lateral tips of the thoracic segments are more directed backward.

### Post-protaspid pygidia

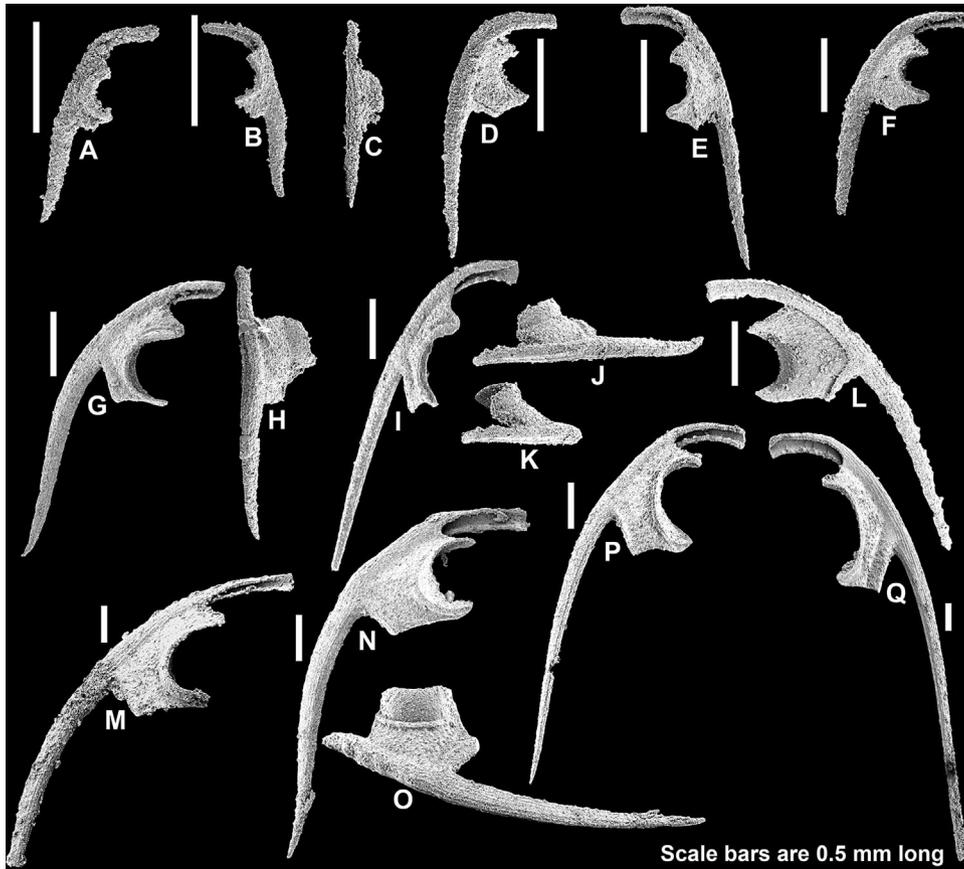
The post-protaspid pygidial development of *A. latilimbatus* is divided into meraspis degrees 2–11, and the holaspis phase (Fig. 8). The position of a long axial spine-bearing segment, which is going to be the eighth thoracic segment, plays a key role in distinguishing the meraspis developmental stages. The



**Fig. 5.** Post-protaspis cranidia of *Apatokephalus latilimbatus*. (A–E) developmental stage 1 cranidia. (A) KOPRIF1216, dorsal view. (B, C) KOPRIF1217, dorsal view and lateral view. (D) KOPRIF1218, dorsal view. (E) KOPRIF1219, ventral view. (F–J) developmental stage 2 cranidia. (F–H) KOPRIF1220; (F) dorsal, (G) lateral, and (H) anterior views. (I) KOPRIF1221, dorsal view. (J) KOPRIF1222, dorsal view. (K–Q) developmental stage 3 cranidia. (K) KOPRIF1223, dorsal view. (L) KOPRIF1224, ventral view. (M) KOPRIF1225, dorsal view. (N) KOPRIF1226, dorsal view. (O–Q) KOPRIF1227; (O) dorsal, (P) lateral, and (Q) anterior views. (R–U) developmental stage 4 cranidia. (R) KOPRIF1228, dorsal view. (S) KOPRIF1229, dorsal view. (T–V) KOPRIF1230; (T) dorsal, (U) lateral, and (V) anterior views.

pygidial development is likely to be protomeric, in which onset of epimorphic phase occurs before the onset of the holaspis phase. A detailed description of each developmental stage and interpretation in terms of segmentation will be discussed elsewhere. The pygidia of the earliest meraspis stage discovered for this study apparently belong to the meraspis degree 2. The meraspis degree 2 pygidia (Fig. 8, A and B) have five segments in front of the axial spine-bearing segment, and are semicircular in outline and 0.35–0.43 mm long and 0.44–0.58 mm wide. The axial spine on the sixth segment at this stage is short and tumid with a rounded tip. It is notable that the width of these pygidia is smaller than that of the commutavi protaspides. Because the

degree 0 pygidia could be hardly larger than degree 2 protaspides, it can be inferred that there was a decrease in width at the metamorphosis from the commutavi protaspis. The pygidia of the meraspis degrees 3–7 could be recognized by the decrease in the number of segments in front of the axial spine-bearing segment (Fig. 8, C–M). There is a wide size variation in the meraspis degree 4 pygidia (Fig. 8, E–I). In the meraspis degree 7 pygidia, the axial spine-bearing segment became the anteriormost segment (Fig. 8M). However, due to the release of the axial spine-bearing segment into the thorax as the eighth thoracic segment, distinguishing subsequent meraspis degrees is not confident (Fig. 8, N–Q). The holaspis pygidia (Fig. 8,



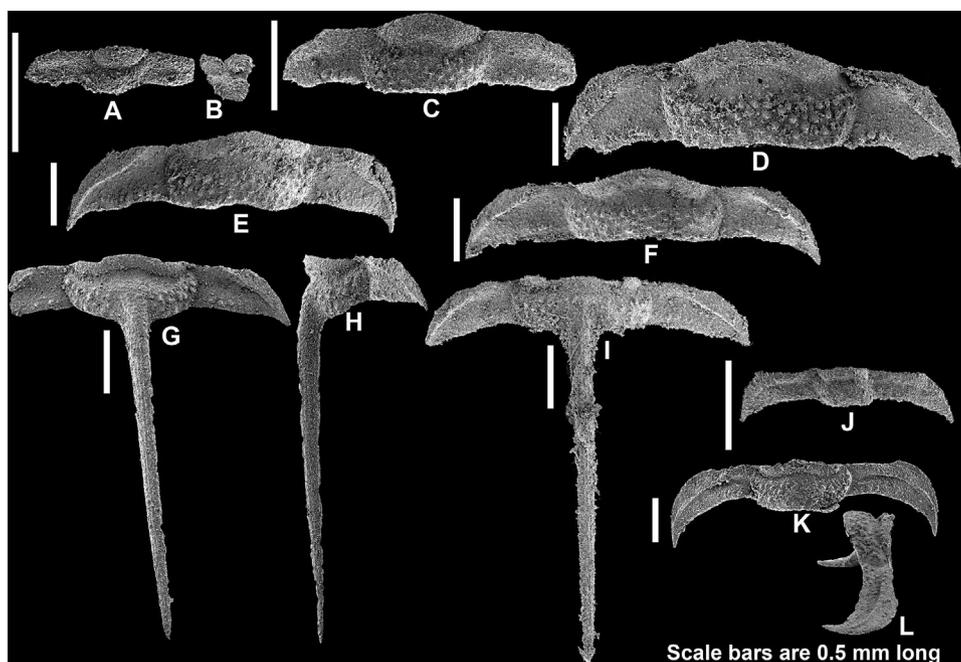
**Fig. 6.** Free cheeks of *Apatokephalus latilimbatus*. (A) KOPRIF1231, dorsal view. (B, C) KOPRIF1232; (B) dorsal view and (C) lateral view. (D) KOPRIF1233, ventral view. (E) KOPRIF1234, dorsal view. (F) KOPRIF1235, dorsal view. (G, H) KOPRIF1236; (G) dorsal and (H) lateral views. (I–K) KOPRIF1237; (I) dorsal, (J) antero-lateral, and (K) anterior views. (L) KOPRIF1238, ventral view. (M) KOPRIF1239, dorsal view. (N, O) KOPRIF1240; (N) dorsal and (O) lateral views. (P) KOPRIF1241, dorsal view. (Q) KOPRIF1242, dorsal view.

R–V) are longer than 0.51 mm and wider than 0.87 mm. They are distinguished from the meraspide degree 8–11 pygidia by the flat pleural field and the wider axis. The smallest holaspide specimen lack the tiny pygidial spines in dorsal view, but larger specimens show a pair of tiny marginal spines behind the three pairs of prominent marginal spines.

### COMMUTAVI PROTASPIS, A NEW TERMINOLOGY TO REPLACE “ASAPHOID PROTASPIS”

Many Cambrian ptychoparioids, which retained plesiomorphic conditions of subsequent trilobites, are known to have possessed a slightly inflated early stage protaspis which became typical adult-like protaspis in subsequent development (Fortey and Chatterton 1988). Park and Choi (2011b) argued that such morphological change could be considered as a metamorphosis, and the highly bulbous protaspis (“asaphoid protaspis”) may have been a result of delayed timing of the metamorphosis. The presence of the more adult-like earlier stage protaspis in the

development of *A. latilimbatus*, however, clearly demonstrates that the bulbous protaspis is a result of a de novo evolution, not a delay of timing of metamorphosis as suggested by Park and Choi (2011b). Therefore, a specific terminology for the de novo protaspide stage is required. Fortey and Chatterton (1988) termed it “asaphoid protaspis.” However, because the highly bulbous planktonic protaspis which metamorphosed into the meraspide phase evolved several times in different trilobite lineages, “asaphoid protaspis” should be replaced; the term itself implies a close phylogenetic relationship with the Order Asaphida. Simple descriptive terms such as “bulbous protaspis,” and “nonadult-like protaspis” are unsatisfactory, since they could also be applied to the inflated early stage protaspides of middle Cambrian ptychoparioids. Here we suggest a new term, “commutavi protaspis” (Latin “commutavi,” meaning “alter wholly”), referring to the severe morphological change between the protaspide and meraspide phases. The commutavi protaspis is applied only to the bulbous protaspis of the last protaspide stage with planktonic life mode (life-history strategy I). For example, the adult-like stage 2 protaspis of *Apatokephalus latilimbatus* in



**Fig. 7.** Thoracic segments of *Apatokephalus latilimbatus*. (A–F) thoracic segments before the eighth segments. (A, B) KOPRIF1243; (A) dorsal view and (B) lateral view. (C) KOPRIF1244, dorsal view. (D) KOPRIF1245, dorsal view. (E) KOPRIF1246, dorsal view. (F) KOPRIF1247, dorsal view. (G–I) eighth segments with a long axial spine. (G, H) KOPRIF1248; (G) dorsal view and (H) lateral view. (I) KOPRIF1249, dorsal view. (J–L) segments behind the eighth segment. (J) KOPRIF1250, dorsal view. (K, L) KOPRIF1251; (K) dorsal and (L) lateral views.

this study is followed by the commutavi protaspis stage which undergoes a metamorphosis into the meraspis of benthic life mode. The commutavi protaspis is a descriptive term without any implication for phylogeny. Commutavi protaspis independently arose within the superfamilies Asaphoidea (Chatterton 1980), Remopleuridioidea (Ross 1951b; Whittington 1959; Park and Choi 2011a; this study), Trinucleoidea (Chatterton et al. 1994; Park et al. 2014), and the Order Proetida (Chatterton et al. 1999; Lerosey-Aubril and Feist 2005a, b). It is interesting to note that all of the known commutavi protaspides occurred after the Cambrian. This may be related to the increasing predation pressure due to the Ordovician radiation (Nützel et al. 2006; Nützel 2014).

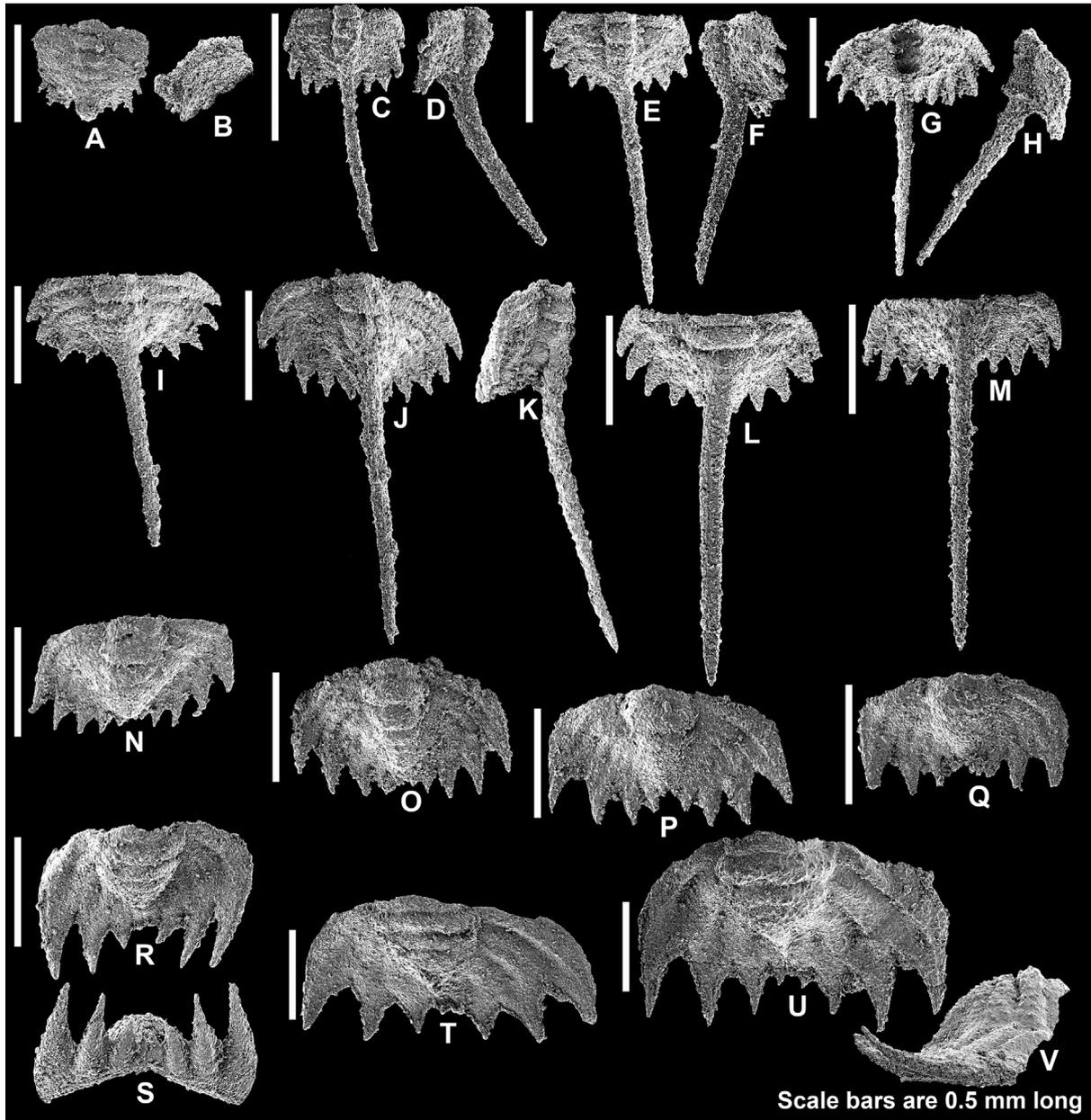
## DISCUSSION

### Evolution of indirect development

In the indirect development of *Apatokephalus latilimbatus*, the different cranial morphology between the commutavi protaspides and the earliest meraspides, and the enrolled and bulbous trunk with effaced surface of the commutavi protaspides evince the presence of a metamorphosis. The moderately convex cranidium of the stage 3 protaspis became the relatively flat earliest meraspis cranidium (see Fig. 9, I and K). Interestingly, the stage 2 protaspides of *A. latilimbatus* show more similarities to

the earliest meraspis morphology in having well-defined palpebral lobes (see Fig. 9, F, H, and J); the lateral view of this protaspis stage is even similar to that of the latest protaspis stage of *Haniwa quadrata* (see Fig. 9, G and M). Moreover, it should be emphasized that the size of the commutavi protaspides is slightly larger than the meraspides of the earliest stage; not only they are wider than the earliest meraspis cranidia (Figs. 2B and 9), but also they must have been wider than the meraspis degree 0 pygidia, given the smaller width of the meraspis degree 2 pygidia. These results clearly demonstrate that the free-swimming commutavi protaspis stage was additionally intercalated to the otherwise direct development, and that this stage was not for the development of the subsequent morphology (Fig. 10B). Instead, it can be inferred that the commutavi protaspis stage appeared for a specialized purpose of this stage; for the exploitation of the free-swimming planktonic life mode, which is a better dispersal. Compared to the ancestral direct development as shown in the Furongian remopleuridioean *Haniwa quadrata*, the Tremadocian remopleuridioean *Apatokephalus latilimbatus* intercalated a free-swimming stage in the middle of the direct development, and, therefore, this case could be a firm fossil evidence for how indirect development evolved from the ancestral direct development in trilobites and arthropods.

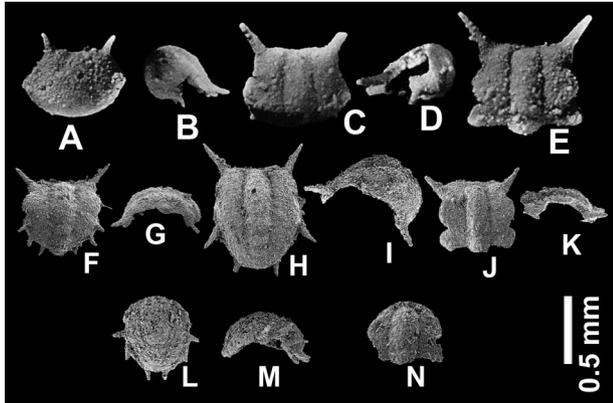
In the more derived remopleuridioean trilobites, the free-swimming stage seems to have become longer and more dominant in the earlier phase of development. The late Tremadocian



**Fig. 8.** Meraspid and holaspid pygidia of *Apatokephalus latilimbatus*. (A–Q) meraspid pygidia. (A, B) meraspid degree 2 pygidium, KOPRIF1252; (A) dorsal and (B) lateral views. (C, D) meraspid degree 3 pygidium, KOPRIF1253; (C) dorsal and (D) lateral views. (E–I) meraspid degree 4 pygidia. (E, F) KOPRIF1254; (E) dorsal and (F) lateral views. (G, H) KOPRIF1255; (G) ventral and (H) lateral views. (I) KOPRIF1256, dorsal view. (J, K) meraspid degree 5 pygidium, KOPRIF1257; (J) dorsal and (K) lateral views. (L) meraspid degree 6 pygidium, KOPRIF1258, dorsal view. (M) meraspid degree 7 pygidium, KOPRIF1259, dorsal view. (N–Q) meraspid pygidia of degrees 8–11, KOPRIF1260–KOPRIF1263, respectively, dorsal views. (R–V) holaspid pygidia. (R, S) KOPRIF1264; (R) dorsal and (S) posterior views. (T) KOPRIF1265, dorsal view. (U, V) KOPRIF1266; (U) dorsal and (V) lateral views.

*Menoparia* is considered as a descendant of *Apatokephalus*, based on the highly similar morphology and the successive stratigraphic occurrences (Ross 1953); the presence of a pair of anterior spines in the earliest meraspid stage in both species (Fig. 9) corroborates the close relationship between *Apatokephalus* and *Menoparia*. Although the large commutavi protaspis of *M. genalunata* has a

similar anterior cranial outline to that of *A. latilimbatus*, it is markedly different in having a highly enrolled posture which forms a spherical shape in lateral view (Fig. 9D). This implies that that the specialized morphology for dispersal became even more adapted for dispersal in the descendant. In contrast to the more adult-like earlier stage protaspis of *A. latilimbatus*, the earlier stage protaspis



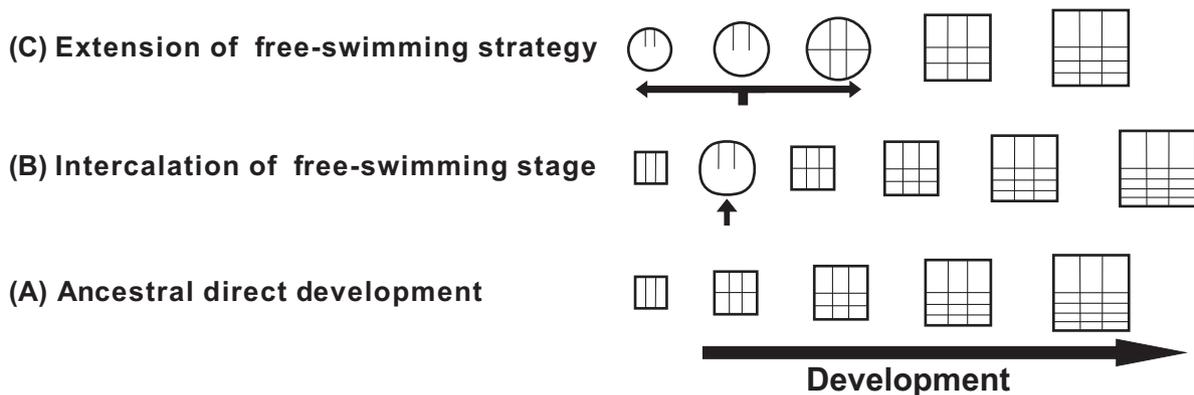
**Fig. 9.** (A–E) protaspides and earliest meraspis stage cranium of *Menoparia genalunata* Ross, 1951a (late Tremadocian); (A, B) early stage protaspis, YPM 18384, dorsal and lateral views, respectively; (C, D) late stage protaspis, YPM 18384, dorsal and lateral views, respectively; (E) earliest meraspis cranium, YPM 18387, dorsal view. (F–J) protaspides and earliest meraspis stage cranium of *Apatokephalus latilimbatus* Peng, 1990 (early late Tremadocian?); (F, G) stage 2 protaspides; (F) KOPRIF1207, dorsal view, (G) KOPRIF1210, lateral view; (H, I) stage 3 protaspis, KOPRIF1214, dorsal and lateral views, respectively; (J) earliest meraspis cranium, KOPRIF1217, dorsal view. (K–M) Protaspis and earliest meraspis stage cranium of *Haniwa quadrata* Kobayashi, 1933 (Furongian); (K, L) late stage protaspis, KOPRIF16006, dorsal and lateral views, respectively; (M) smallest meraspis cranium, KOPRIF16008, dorsal view. Note that the stage 2 protaspis of *A. latilimbatus* has a similar lateral outline (G) to that of *H. quadrata* (L); the trunk of commutavi protaspis of *M. genalunata* (D) is a more enrolled than that of *A. latilimbatus* (I); in *M. genalunata*, the earlier protaspis stage becomes highly enrolled (B). Specimens prefixed with YPM are housed in Yale Peabody Museum. Images of (A–E) are re-illustrated from Ross (1951b).

of *M. genalunata* has a highly globular morphology (Fig. 9, A and B), which means the free-swimming strategy was extended to the earlier developmental stage in the descendant species. In *M. genalunata*, the cranidial width of the earliest meraspis is almost similar to the width of the commutavi protaspis (Fig. 9E), not becoming smaller as in the case of *A. latilimbatus* (Figs. 2B and 9J), indicating that the descendant trilobite likely evolved a more effective way of growth without size-decreasing after metamorphosis. In the (likely more derived) Middle Ordovician remopleuridioidean, *Remopleurides eximius*, the free-swimming strategy was extended even into the later developmental stage; the spherical protaspis developed into a meraspis similar to the preceding protaspis morphology (see Chatterton and Speyer 1997, fig. 158), so that metamorphosis took place in the early meraspis phase (Fig. 10C).

To sum up, given the developmental strategies shown in the remopleuridioidean trilobite lineage, it can be concluded that the indirect development first evolved as an intercalation of a de novo free-swimming stage into the ancestral direct development, and the de novo free-swimming strategy became more intensified and extended in the early developmental phase in the descendants (Fig. 10).

**Selective independence in indirect development**

In closely related animals, morphology from early developmental stage is expected to be more similar to each other than that from the later developmental stage; this is known as von Baer’s law. It can be intuitively accepted, but there are several examples against von Baer’s law (e.g., Dahms 2000; Scholtz 2005; Poe 2006). It



**Fig. 10.** Simplified diagram for the evolution of metamorphosis in the remopleuridioidean lineage. The increase in the number of horizontal lines represents the increase of articulations in thorax with development. (A) ancestral direct development as shown in *Haniwa quadrata* (Late Cambrian). (B) intercalation of the de novo free-swimming stage shown in the Tremadocian *Apatokephalus latilimbatus* (arrow); the less-circular shape of the intercalated stage represents that the less-spherical morphology of the commutavi protaspis of *A. latilimbatus*, compared to that of *Menoparia genalunata*. (C) extension of the de novo free-swimming strategy both into the earlier developmental stage as shown in *Menoparia genalunata* (a probable descendant of *Apatokephalus*), and into the later developmental stage as shown in *Remopleurides eximius* (a likely more derived remopleuridioidean). The intensification of the free-swimming spherical morphology is represented by more circular shape. The extension of the free-swimming strategy into the earlier and later developmental phases is represented by an arrow pointing to both sides.

has been suggested that developmental stages have a selective independence (Scholtz 2005; Haug and Haug 2013): that is, ontogenetically earlier stages can be evolutionarily altered even though the ontogenetically later stages are conserved (Scholtz 2005). The evolution of the commutavi protaspis along the lineage of the remopleuridioidean trilobites shown in this study could provide convincing fossil evidence for such “selective independence” of developmental stages. Because the morphology of the commutavi protaspis is not related to that of the subsequent meraspis, the commutavi protaspis could be morphologically labile: that is, regardless the similarities in the mature morphology, the commutavi protaspis could evolve into a markedly different shape. In this regard, it is not surprising that commutavi protaspides of various lineages have different morphology in the first place, although they once were collectively termed “asaphoid protaspides” (see Fortey and Chatterton 1988; Chatterton and Speyer 1997; Chatterton et al. 1994, 1999; Lerosey-Aubril and Feist 2005a, b); not only because they independently evolved in different lineages, but also because of the selective independence at this stage. This is evident in that the commutavi protaspides of a close phylogenetic relationship, show different morphologies. The commutavi protaspides of the Middle Ordovician asaphid *Isotelus* sp. described by Evitt (1961) have a pair of anteriorly projecting marginal spines, while those of *I. parvirugosus* Chatterton and Ludvigsen, 1976 lack the anteriorly projecting marginal spines (Chatterton 1980, Fig. 3). Two trinucleoidean commutavi protaspides also have somewhat different morphology (see Chatterton et al. 1994, Fig. 1).

The selective independence is not restricted to morphology; the developmental strategy during early phase could be easily altered in indirect development. The above-mentioned intensification of free-swimming strategy in the derived remopleuridioideans may have been a result of a longer exposure to the selective pressure on the early developmental stage specialized for dispersal.

## CONCLUSIONS

The post-embryonic development of the Tremadocian remopleuridioidean *Apatokephalus latilimbatus* shows the earliest evolution of the free-swimming commutavi protaspis (a term replacing “asaphoid protaspis”), thus it represents the initial phase of the evolution of indirect development. Interestingly, the earlier stage protaspis had a more similar appearance to the meraspis than the commutavi protaspis did, and the size of the commutavi protaspis is larger than that of the subsequent meraspis. This indicates that the commutavi protaspis stage was an additional intercalation to the ancestral direct development, and that this stage evolved for a better dispersal. Because its morphology is less related to the morphology of the subsequent meraspis stage, the morphological evolution of commutavi protaspis could be

rather labile. In addition, the extension of free-swimming strategy in the derived remopleuridioideans shows how the intercalated free-swimming stage became intensified with subsequent evolution. It also provides a convincing case for the “selective independence” of developmental stages, explaining the various morphologies of commutavi protaspides in many trilobite lineages.

## Acknowledgments

We are grateful to Nigel Hughes and an anonymous reviewer for constructive comments which significantly improved the manuscript. This study was supported by the Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (PN14090, KOPRI).

## REFERENCES

- Bookstein, F. L. 1991. *Morphometric tools for landmark data*. Cambridge University Press, New York, p. 435.
- Chatterton, B. D. E. 1980. Ontogenetic studies of Middle Ordovician trilobites from the esbataottine formation, Mackenzie mountains, Canada. *Palaeontogra. Abt. A* 171: 1–74.
- Chatterton, B. D. E., and Ludvigsen, R. 1976. Silicified Middle Ordovician trilobites from the South Nahanni River area. District of Mackenzie, Canada. *Palaeontographica (A)* 154: 1–106.
- Chatterton, B. D. E., and Speyer, S. E. 1997. Ontogeny. In R. L. Kaesler (ed.), *Treatise on invertebrate paleontology, Part O, Arthropoda 1. Trilobita, revised*. Geological Society of America and University of Kansas, Boulder and Lawrence, pp. 173–247.
- Chatterton, B. D. E., Speyer, S. E., Hunt, A. S., and Fortey, R. A. 1994. Ontogeny and relationships of Trinucleoidea (Trilobita). *J. Paleontol.* 68: 523–540.
- Chatterton, B. D. E., Edgecombe, G. D., Vaccari, N. E., and Waisfeld, B. G. 1999. Ontogenies of some Ordovician Telephinoidea from Argentina, and larval patterns in the Proetida (Trilobita). *J. Paleontol.* 73: 219–239.
- Choi, D. K., Kim, D. H., Sohn, J. W., and Lee, S.-B. 2003. Trilobite faunal successions across the Cambrian–Ordovician boundary intervals in Korea and their correlation with China and Australia. *J. Asian. Earth Sci.* 21: 781–793.
- Choi, D. K., et al. 2004. Taebaek Group (Cambrian–Ordovician) in the Seokgaegjae section, Taebaeksan Basin: a refined lower Paleozoic stratigraphy in Korea. *Geosci. J.* 8: 125–151.
- Dahms, H. U. 2000. Phylogenetic implication of the Crustacean nauplius. *Hydrobiologia* 417: 91–99.
- Degnan, S. M., and Degnan, B. M. 2006. The origin of the pelagobenthic metazoan life cycle: what’s sex to do with it? *Integr. Comp. Biol.* 46: 683–690.
- Ebbestad, J. O. R. 1999. Trilobites of the Tremadoc Bjørkåsholmen formation in the Oslo Region, Norway. *Fossils Strata* 47: 1–118.
- Evitt, W. R. 1961. Early ontogeny in the trilobite family Asaphidae. *J. Paleontol.* 35: 986–995.
- Fortey, R. A., and Chatterton, B. D. E. 1988. Classification of the trilobite suborder Asaphina. *Palaeontology* 31: 165–222.
- Fusco, G., Hong, P. S., and Hughes, N. C. 2014. Positional specification in the segmental growth pattern of an early arthropod. *P. R. Soc. Lond. B. Bio.* 281: 20133037.
- Gerber, S., and Hopkins, M. J. 2011. Mosaic heterochrony and evolutionary modularity: the trilobite genus *Zacanthopsis* as a case study. *Evolution* 65: 3241–3252.
- Hadfield, M. G., Carpizo-Ituarte, E. J., del Carmen, K., and Nedved, B. T. 2001. Metamorphic competence, a major adaptive convergence in marine invertebrate larvae. *Am. Zool.* 41: 1123–1131.
- Haug, J. T., and Haug, C. 2013. An unusual fossil larva, the ontogeny of achelatan lobsters, and the evolution of metamorphosis. *Bull. Geosci.* 88: 195–206.

- Haug, J. T., Audo, D., Charbonnier, S., and Haug, C. 2013. Diversity of developmental patterns in achelate lobsters today and in the Mesozoic. *Dev. Genes Evol.* 22: 363–373.
- Hughes, N. C. 2007. The evolution of trilobite body patterning. *Annu. Rev. Earth Planet. Sci.* 35: 401–434.
- Hughes, N. C., Minelli, A., and Fusco, G. 2006. The ontogeny of trilobite segmentation: a comparative approach. *Paleobiology* 32: 602–627.
- Kim, K. H., Choi, D. K., and Lee, C. Z. 1991. Trilobite biostratigraphy of the Dumugol Formation (Lower Ordovician) of Dongjeom area, Korea. *J. Paleont. Soc. Korea* 7: 106–115.
- Kobayashi, T. 1933. Upper Cambrian of the Wuhutsui basin, Liaotung, with special reference to the limit of Chaumitien (or Upper Cambrian) of eastern Asia and its subdivision. *Jpn. J. Geol. Geogr.* 11: 55–155.
- Kobayashi, T. 1934. The Cambro-Ordovician formations and faunas of South Chosen. Paleontology, Part II, Lower Ordovician faunas. *J. Fac. Sci. Imperial Univ. Tokyo, Sect. II* 3: 521–585.
- Kobayashi, T. 1953. On the Kainellidae. *Jpn. J. Geol. Geogr.* 23: 37–61.
- Lee, S.-B., and Choi, D. K. 2007. Trilobites of the *Pseudokoldinoidea* Fauna (uppermost Cambrian) from the Taebaek Group, Taebaeksan Basin, Korea. *J. Paleont.* 81: 1454–1465.
- Lee, S.-B., Lefebvre, B., and Choi, D. K. 2005. Latest Cambrian cornutes (Echinodermata: Stylophora) from the Taebaeksan Basin, Korea. *J. Paleont.* 79: 139–151.
- Lerosey-Aubril, R., and Feist, R. 2005a. First Carboniferous protaspid larvae (Trilobita). *J. Paleont.* 79: 702–718.
- Lerosey-Aubril, R., and Feist, R. 2005b. First Ontogeny of a new cyrtosymboline trilobite from the Famennian of Morocco. *Acta Palaeontol. Pol.* 50: 449–464.
- Nielsen, C. 2000. The origin of metamorphosis. *Evol. Dev.* 2: 127–129.
- Nielsen, C. 2008. How did indirect development with planktotrophic larvae evolve? *Biol. Bull.* 216: 203–215.
- Nützel, A. 2014. Larval ecology and morphology in fossil gastropods. *Palaeontology* 57: 479–503.
- Nützel, A., Lehnert, O., and Frýda, J. 2006. Origin of planktotrophy-evidence from early mollusks. *Evol. Dev.* 8: 325–330.
- Park, T.-Y., and Choi, D. K. 2009. Post-embryonic development of the Furongian (Late Cambrian) trilobite *Tsinania canens*: implications for life mode and phylogeny.
- Park, T.-Y., and Choi, D. K. 2011a. Ontogeny of the Furongian (Late Cambrian) remopleuridioid trilobite *Haniwa quadrata* Kobayashi, 1933 from Korea: implications for trilobite taxonomy. *Geol. Mag.* 148: 288–303.
- Park, T.-Y., and Choi, D. K. 2011b. Constraints on using ontogenetic data for trilobite phylogeny. *Lethaia* 44: 250–254.
- Park, T.-Y. S., Kihm, J.-H., Kang, I., and Choi, D. K. 2014. 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. *J. Paleontol.* 82: 395–402.
- Peng, S. 1990. Tremadocian stratigraphy and trilobite fauna of northwestern Hunan. 2. Trilobites from the Penjiazui Formation and the Madaoyu Formation in the Jiangnan Slope belt. *Beringeria* 2: 55–171.
- Poe, S. 2006. Test of Von Baer's law of the conservation of early development. *Evolution* 60: 2239–2245.
- Raff, R. A. 2008. Origins of the other metazoan body plans: the evolution of larval forms. *Philos. Trans. R. Soc. Lond. B.* 363: 1473–1479.
- Ross, R. J., Jr. 1951a. Stratigraphy of the garden city formation in northeastern Utah, and its trilobite faunas. *Pea. Mus. Bull.* 6: 1–161.
- Ross, R. J., Jr. 1951b. Ontogenies of three garden city (Early Ordovician) trilobites. *J. Paleont.* 25: 578–586.
- Ross, R. J., Jr. 1953. Additional garden city (Early Ordovician) trilobites. *J. Paleont.* 27: 633–646.
- Scholtz, G. 2000. Evolution of the nauplius stage in malacostracan crustaceans. *J. Zool. Syst. Evol. Research* 38: 175–187.
- Scholtz, G. 2005. Homology and ontogeny: pattern and process in comparative developmental biology. *Theor. Biosci.* 124: 121–143.
- Seo, K.-S., Lee, H.-Y., Ethington, R. L. 1994. Early Ordovician conodonts from the Dumugol Formation in the Baegunsan Syncline, Eastern Yeongweol and Samcheog areas, Kangweon-Do, Korea. *J. Paleontol.* 68: 599–616.
- Speyer, S. E., and Chatterton, B. D. E. 1989. Trilobite larvae and larval ecology. *Hist. Biol.* 3: 27–60.
- Walossek, D. 1993. The Upper Cambrian *Rehbachella* and the phylogeny of Branchiopoda and Crustacea. *Fossils Strata* 32: 1–202.
- Webster, M. 2015. Ontogeny and intraspecific variation of the early Cambrian trilobite *Olenellus gilberti*, with implications for olenelline phylogeny and macroevolutionary trends in phenotypic canalization. *J. Syst. Palaeontol.* 13: 1–74.
- Whittington, H. B. 1959. Silicified Middle Ordovician trilobites: Remopleurididae, Trinucleidae, Raphiophoridae, Endymionidae. *Bull. Mus. Comparat. Zool. Harv.* 121: 371–496.
- Wolpert, L. 1999. From egg to adult to larva. *Evol. Dev.* 1: 3–4.