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이학석사 학위논문

Ontogeny of the ptychaspidid trilobite
Quadraticephalus elongatus from the Furongian
(late Cambrian) Hwajeol Formation, Korea

화절층에서 발견된 후기 캄브리아기 삼엽충
*Quadraticephalus elongatus*의 개체발생과정
연구

2012 년 8 월

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Ontogeny of the ptychaspidid trilobite
Quadraticephalus elongatus from the
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Abstract

The development of trilobite pygidium involves both articulation process at the frontal part and the formation of new segments at the rear end, and hence the development of meraspid pygidium accompanies complicated morphological changes. This study deals with the ontogeny of the Furongian (late Cambrian) ptychaspid trilobite, *Quadraticephalus elongatus* (Kobayashi, 1935), from the Hwajeol Formation of the Taebaek Group, Taebaeksan Basin, Korea, with a special focus on the segmentation process during the meraspid pygidial development. Compared to the ontogeny of a ptychaspid trilobite, *Asioptychaspis subglobosa* (Sun, 1924), which is assumed to be an ancestral species of *Q. elongatus*, the convexity of the cranidium of *Q. elongatus* increased in a slower rate; the yoked free cheek of *Q. elongatus* split to form a ventral median suture in a later developmental stage; and, a rim-like ridge, which disappeared in the early holaspid pygidium of *A. subglobosa*, maintained in the holaspid period of *Q. elongatus*. These morphological changes with growth imply that a pedomorphism was involved in the evolution of *Q. elongatus*. Eleven stages are recognized for the meraspid pygidial development, which began with an accumulation phase during

which the number of segments within the pygidium increased from 3 to 7, followed by an equilibrium phase with 7 segments, and ended up with a depletion phase during which the number of segments within the pygidium decreased down to 4. During the depletion phase, the pygidial length did not increase or even slightly decreased. The onset of epimorphic phase, in which the total number of trunk segments does not increase anymore, precedes the onset of holaspid period during ontogeny, demonstrating that the developmental mode of *Q. elongatus* is protomeric.

Keywords : Cambrian, trilobite, ontogeny, *Quadraticephalus elongatus*, Taebaeksan Basin, Hwajeol Formation

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I. Introduction

Trilobite ontogeny has been traditionally divided into the protaspid, meraspid, and holaspid periods, based on the development of articulated joints in trunk region (Chatterton and Speyer, 1997). During the meraspid period of trilobites, the anterior-most segment in the pygidium was released into the thoracic region at each molting, while new segments were formed at the rear end of pygidium (Chatterton and Speyer, 1997). When trilobites attained the final number of thoracic segments, the segment release from the pygidium ceased, but the cessation of the new segment formation at the rear end did not always concurrently occur. Hughes et al. (2006) proposed a novel ontogenetic scheme which focuses on the generation of trunk segments: an anamorphic phase during which the number of segments increased, and an epimorphic phase during which the number of segments did not increase anymore. Because meraspid pygidium is where both segment release and segment formation took place during development, the growth pattern of meraspid pygidium is not simple. One of the important research subjects in the study of trilobite ontogeny is to observe the developmental process of meraspid pygidium in the light of the segmentation process. Simpson et al. (2005) reported a complex

segmentation process of meraspid pygidium of the Ordovician plimerid trilobite *Hintezia plicamarginis* Simpson et al., 2005. Park and Choi (2010a, 2011a) recognized a depletion phase in the pygidial development of *Cyclolorenzella convexa* (Resser and Endo in Endo and Resser, 1937) and *Haniwa quadrata* Kobayashi, 1933, in which the total number of segments in pygidium decreased mainly because the generation of new segments in the posterior part of the pygidium could not compensate the release from the anterior part of the pygidium.

The middle to late Furongian Hwajeol Formation of the Taebaek Group, Taebaeksan Basin, Korea contains three trilobite biozones: the *Asioptychaspis* Zone, *Quadraticephalus* Zone, and the sauikiid-dominated fauna in ascending order (Sohn and Choi, 2007). Recently, the ontogeny of well-preserved silicified trilobites from the *Asioptychaspis* Zone have been described in detail: they include *Tsinania canens* (Walcott, 1905), *Asioptychaspis subglobosa* (Sun, 1924), and *Haniwa quadrata* Kobayashi, 1933 (Park and Choi, 2009, 2010b, 2011a). However, those from the overlying *Quadraticephalus* Zone remain to be studied.

The family Ptychaspidae was considered to belong to the Order Asaphida Salter, 1864 (Fortey and Chatterton, 1988; Fortey, 1997). However, several recent studies disputed the monophyly of the Order Asaphida (Whittington, 2003, 2007; Park and Choi, 2009; 2010b; 2011a;

Adrain et al., 2009). While reporting the ontogeny of the ptychaspidid trilobite, *Asioptychaspis subglobosa* (Sun, 1924) from the *Asioptychaspis* Zone of the Hwajeol Formation, Park and Choi (2010b) demonstrated that the ventral median suture of this trilobite has been attained by a mode different from the previously suggested mode of the Order Asaphida by Fortey and Chatterton (1988), and suggested that the Ptychaspididae should be excluded from the Order Asaphida. Lately, Adrain (2011) placed the Ptychaspididae under the Order Uncertain.

This study deals with the ontogeny of a ptychaspidid trilobite, *Quadraticephalus elongatus* (Kobayashi, 1935), from the *Quadraticephalus* Zone of the Hwajeol Formation, Korea. Given the stratigraphic occurrences, comparable mature morphology, and similar ontogenetic changes, *Q. elongatus* is assumed to be a descendant species of *A. subglobosa*, although a cladistic analysis is required to confirm the probable ancestor–descendant relationship. A special attention is given to the segmentation process during the pygidial development of *Q. elongatus*.

II. Fossil locality and material

The Joseon Supergroup is a Cambro–Ordovician siliciclastic–carbonate succession of the Taebaeksan Basin, which is located in the central–eastern part of the Korean peninsula (Fig. 1). The Joseon Supergroup has been divided into five groups according to distinct lithologic succession, faunal contents, and geographic distribution: i.e., the Taebaek, Yeongwol, Yongtan, Pyeongchang, and Mungyeong groups (Choi, 1998). The Taebaek Group is distributed in the eastern part of the Taebaeksan Basin and represents a shallow marine continental shelf environment (Choi et al., 2004; Kwon et al., 2006). The Cambro–Ordovician Taebaek Group comprises in ascending order the Jangsan/Myeonsan, Myobong, Daegi, Sesong, Hwajeol, Dongjeom, Dumugol, Makgol, Jigunsan, and Duwibong formations. The Cambrian–Ordovician boundary lies within the lowermost part of the Dongjeom Formation (Choi et al., 2003). The Hwajeol Formation consists dominantly of alternating limestone and shale beds, with frequent intercalation of limestone conglomerate beds (Choi et al., 2004). The formation is considered to have formed in inner to outer ramp environments (Kwon et al., 2006)

All the material employed in this study were collected from the *Quadraticephalus* Zone of the lowermost part of the Hwajeol Formation at the Seokgaejae section (Fig. 1). The Seokgaejae section is exposed along a forest road cut, ca. 12 km southeast of Taebaek City. The Hwajeol Formation in this section measures ca. 60 m in thickness with the lowermost part of the formation covered and hence the lowermost *Asioptychaspis* Zone of the formation is not recognized in the section (Choi et al. 2004; Sohn and Choi, 2007).

Limestone samples containing silicified trilobites were collected from the interval 3–8 m above the base of the exposed part of the formation. The rock samples were digested with 9% hydrochloric acid and silicified sclerites were secured from the residue. Collected trilobite sclerites belong to *Quadraticephalus elongatus* Kobayashi, 1935, *Lophosaukia orientalis* (Kobayashi, 1933), *Haniwa sosanensis* (Kobayashi, 1933), *Haniwa* sp., *Hamashania pulchra* (Kobayashi, 1942), *Akoldinioidia* sp., and *Micragnostus* sp. The sclerites of *Q. elongatus* employed in this study include 38 protaspides, 476 cranidia, 97 free cheeks, 259 pygidia, and 36 thoracic segments. All of the specimens illustrated in this study are deposited in the paleontological collections of Seoul National University with registered SNUP numbers.

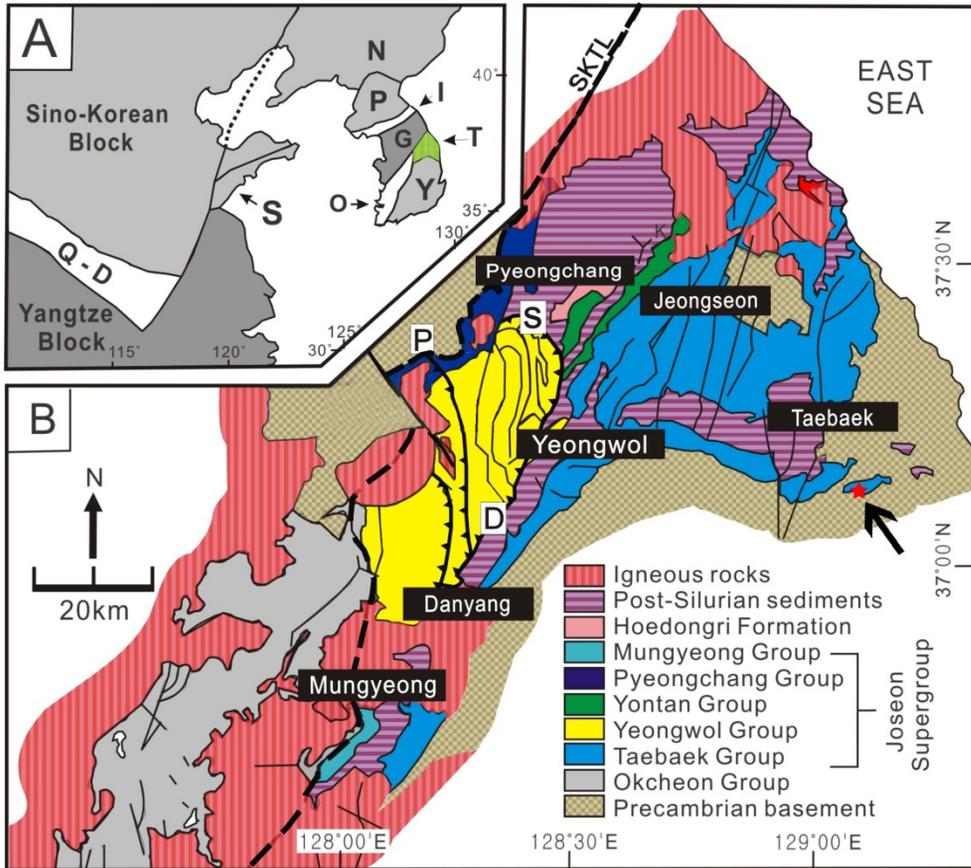


Fig. 1 Location maps. (A) Tectonic maps of Korean peninsula and surrounding area that shows the location of the Taebaeksan Basin. Q-D - Qinling-Dabie belt, S - Sulu Belt, N - Nangnim Massif, P - Pyeongnam Basin, I - Imjingang Belt, G - Gyeonggi Massif, O - Okcheon Belt, T - Taebaeksan Basin, Y - Yeongnam Massif. (B) Geological map of the Taebaeksan Basin showing the distribution of the lower palaeozoic Joseon Supergroup in the Taebaeksan Basin. The Asterisk and arrow indicates the location of the Seokgaejae section from which the material for this study was collected.

III. Ontogeny

Morphological terms employed in this study follow those of Whittington and Kelly (1997) and Chatterton and Speyer (1997), but the term ‘meraspid pygidium’ is used instead of transitory pygidium (see Hughes et al., 2006). The term ‘equilibrium phase’ and ‘depletion phase’ are also used instead of stasis phase and shedding state, respectively (see Simpson et al., 2005). Sagittal length and transverse width were measured for all protaspides, post-protaspid cranidia, and post-protaspid pygidia. A number of specimens suffered from tectonic distortion, to some extent, and thus it was difficult to recognize any biologically meaningful clustering from the length-width bivariate plots. However, meraspid pygidia were divided into 11 stages according to segment number and overall morphology.

i. Protaspid period

The protaspides are oval in outline and measure 0.35–0.55 mm long and 0.34–0.48 mm wide (Fig. 2). Exoskeleton is convex with steeply downsloping protopygidial region, and the axis becomes indistinct anteriorly. A pair of genal spines project rearward. The trunk is distinguished from the head by the posterior cranial margin. In some,

but not all, specimens, a pair of pygidial spines project ventrally (Fig. 2.8, 2.9).

ii. Post-protaspid cranidial development

Cranidia shorter than 0.50 mm (Fig. 3.1–3.4) are semi-oval in outline, with parallel-sided glabella and deep axial furrows. Preglabellar field is not recognized in dorsal view, but is seen in oblique anterior view (Fig. 3.3), marked off by a faintly incised preglabellar furrow. The frontal part of the glabella downslopes steeply. Occipital ring is convex, long medially, and well defined by a deep occipital furrow. Posterior cranidial border widens abaxially.

Cranidia of 0.50–0.64 mm in length (Fig. 3.5–7) are sub-trapezoidal in outline. Preglabellar field is recognized in the dorsal view. Glabella tapers forward slightly, and axial furrows are deeply incised. A short and tumid occipital spine projects posteriorly. The ventral margin is nearly straight in lateral view (Fig. 3.7).

Cranidia longer than 0.64 mm (Fig. 3.8–3.11) display a weakly recognizable preglabellar field in dorsal view. The convexity of cranidia becomes stronger due to steeply down-sloping frontal lobe (Fig. 3.10).

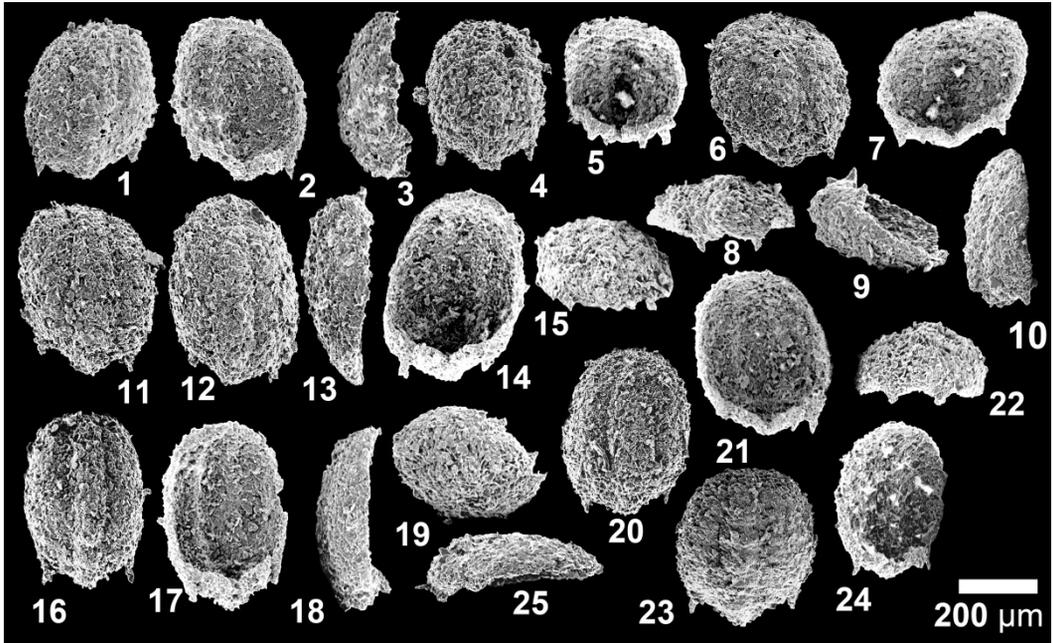


Fig. 2 Protaspides of *Quadraticephalus elongatus* (Kobayashi, 1935). 1-3, SNUP6256, dorsal, ventral, and lateral views; 4-5, SNUP6257, dorsal and ventral views; 6-10, SNUP6258, dorsal, ventral, posterior, oblique ventrolateral, and lateral views; 11, SNUP6259, dorsal view; 12-15, SNUP6260, dorsal, lateral, ventral, and posterior views; 16-19, SNUP6261, dorsal, ventral, lateral, and oblique posterolateral views; 20-22, SNUP6262, dorsal, ventral, and posterior views; 23-25, SNUP6263, dorsal, ventral, and lateral views.

Preglabellar field downslopes more gently. The lateral cranial margin is sinuous, probably due to the formation of the palpebral lobes.

In the cranidia of 0.79–1.2 mm long (Fig. 3.12–3.16), the posterior part of the cranidia progressively widens transversely at a faster rate than the anterior part. The cranial outline becomes almost trapezoidal, with more-or-less straight anterior cranial margin. Preglabellar field is well-recognized in dorsal view (Fig. 3.13) and steeply downsloping anteriorly (Fig. 3.15). Palpebral lobes are 0.26–0.29 of the cranial length. Fingerprint-like prosopon is faintly developed on the glabellar surface (Fig. 3.12). S1 and S2 glabellar furrows are faintly indicated. Posterior border furrow is nearly straight and posterior cranial border does not widen as much abaxially as that of smaller cranidia.

In the cranidia longer than 1.22 mm (Fig. 3.17–3.21), the anterior margin of the preglabellar field becomes angulate. Palpebral lobes are relatively larger, 0.33–0.36 of the cranial length. Palpebral furrows are clearly impressed. Fingerprint-like prosopon is distinct on glabella front but is weakly impressed on the posterior part of the genal field and occipital ring (Fig. 3.17, 3.18). S1 and S2 furrows are clearly incised.

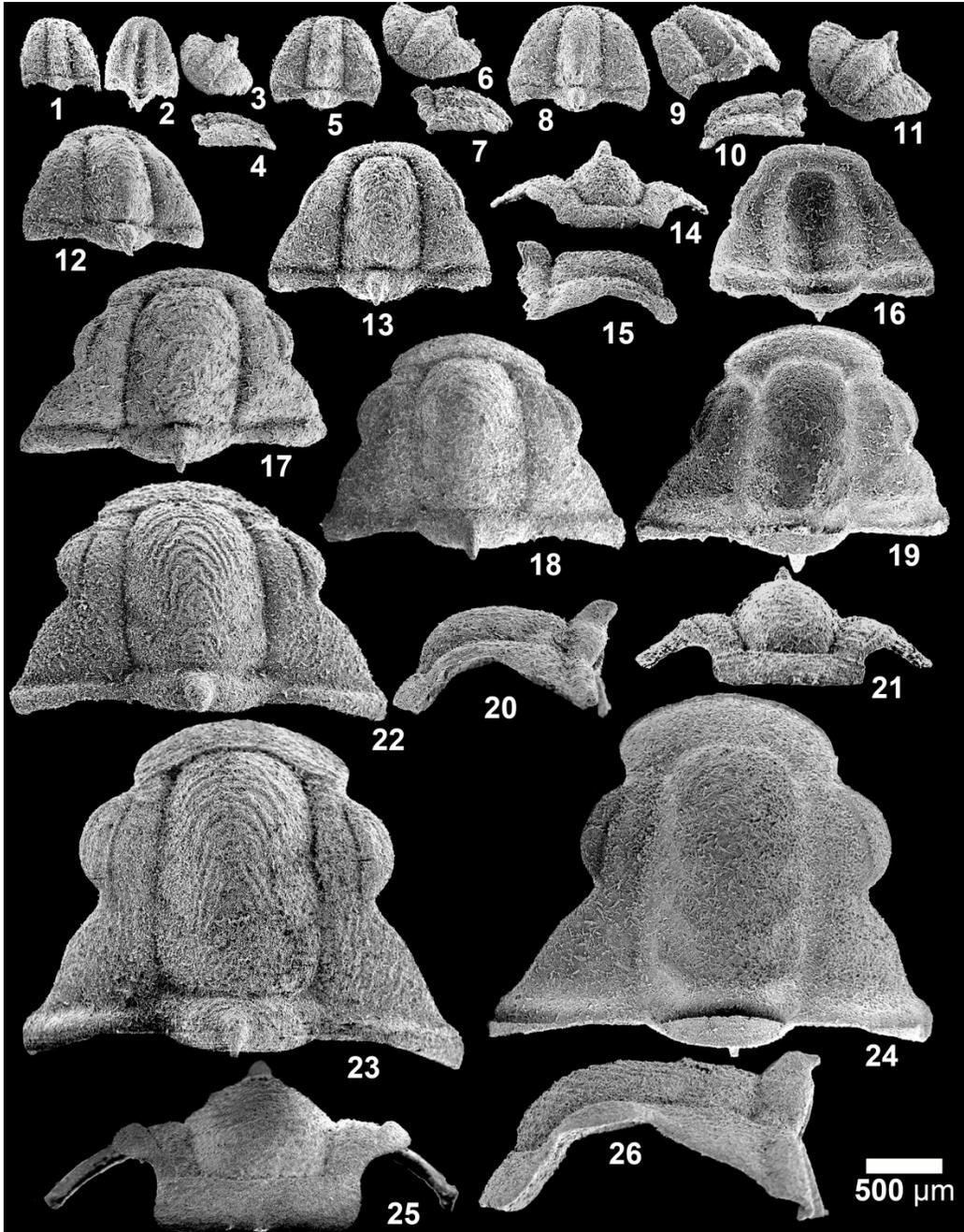


Fig. 3 Post-protaspid cranidia of *Quadraticephalus elongatus* (Kobayashi, 1935).

1-4, SNUP6264, dorsal, ventral, oblique anterolateral, and lateral views; *5-7*, SNUP6265, dorsal, oblique anterolateral and lateral views; *8-11*, SNUP6266, dorsal, oblique posterolateral, lateral, and oblique anterolateral views; *12*, SNUP6267, dorsal view; *13-16*, SNUP6268, dorsal, anterior, lateral, and ventral views; *17*, SNUP6269, dorsal view; *18-21*, SNUP6270, dorsal, ventral, lateral, and anterior views; *22*, SNUP6271, dorsal view; *23-26*, SNUP6272, dorsal, ventral, anterior, and lateral views.

In the cranidia of 1.54–2.60 mm long (Fig. 3.22–3.26), the fingerprint-like prosopon is more clearly developed on the whole surface of glabella, genal field, and occipital ring. Linear ornamentations are dimly developed on the surface of the palpebral lobe and the preglabellar field. The S1 and S2 glabellar furrows are moderately impressed. Palpebral lobes are 0.37–0.39 of the cranidial length. The abaxially widening posterior border is slightly bent posteriorly. The occipital ring is somewhat oval in outline, with the occipital spine obliquely directed posteriorly. The relative size of the occipital spine at this stage is the largest among the whole developmental stages.

Cranidia of 2.60–3.3 mm long (Fig. 4.1–4.4) have laterally convex anterior branches of facial suture. Palpebral lobes and occipital spine become relatively short; palpebral lobes are 0.31–0.34 of the total length of the cranidia. Occipital spine projects upward. While the convexity of the whole cranidia does not change much, the preglabellar field continues to become longer. The surface ornamentation including the fingerprint-like prosopon is less distinct and not recognized on the surface of palpebral lobes. S1 and S2 glabellar furrows are faintly indicated. An extremely faint impression is recognizable in the place for the S3 glabellar furrow (Fig. 4.1). The posterior cranidial margin runs abaxially

straight from the flank of the occipital ring, and then abruptly directs obliquely rearward.

In the cranidia longer than 3.3 mm (Fig. 4.5–4.8), the preglabellar field is relatively long. The overall convexity is slightly less than that of the smaller cranidia (Fig. 4.5). The ornamentation on the surface including the fingerprint-like prosopon becomes less distinct; it is reduced in relief and recognized only on the surface of the frontal lobe of glabella, preglabellar field, and the posterior part of the genal field. Palpebral lobes become relatively shorter; less than 0.3 of the length of the cranidia. Glabellar furrows are more clearly incised. The occipital spine is subdued.

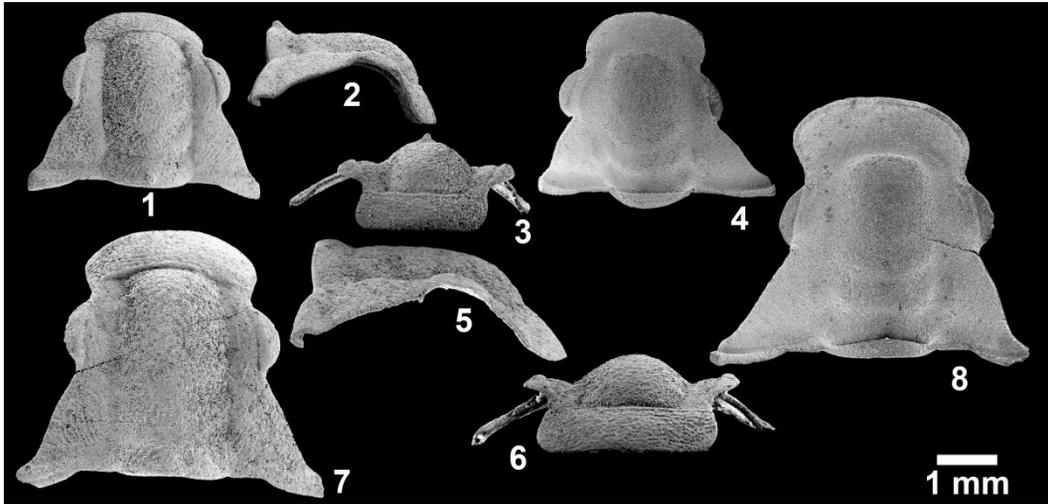


Fig. 4 Post-protaspid cranidia of *Quadraticephalus elongatus* (Kobayashi, 1935). 1-4, SNUP6273, dorsal, lateral, anterior, and ventral views; 5-8, SNUP6274, dorsal, lateral, anterior, and ventral views.

iii. Free cheek development

Free cheeks are yoked during the earlier phases of development (Fig. 5.1–5.6). The smallest free cheek available (Fig. 5.1–5.3) has a simple morphology with moderately long and broad librigenal spines. The genal spines are relatively short, 0.32–0.35 of the whole free cheek length. The librigenal field is narrow.

With growth, the librigenal fields become broader and the genal spines become relatively longer, 0.40–0.44 of the whole free cheek length (Fig. 5.5–5.6). The genal spines are weakly curved abaxially toward the posterior tip. Ridge-like prosopon running subparallel to the outer margin is faintly recognized on the surface of the librigenal field.

Free cheeks longer than 2.5 mm (Fig. 5.7–5.8) represent the splitting of the previously yoked free cheek. This mode of ventral median suture formation is the same as that of the ptychaspideid trilobite, *A. subglobosa* (Park and Choi, 2010a). The anterior part of doublure is inturned, forming a tube-like appearance. The outward curvature of the genal spine is prominent (Fig. 5.7)

As the free cheeks grow (Fig. 5.9–5.21), palpebral lobes are prominently elevated. The librigenal field becomes broad. The ridge-like

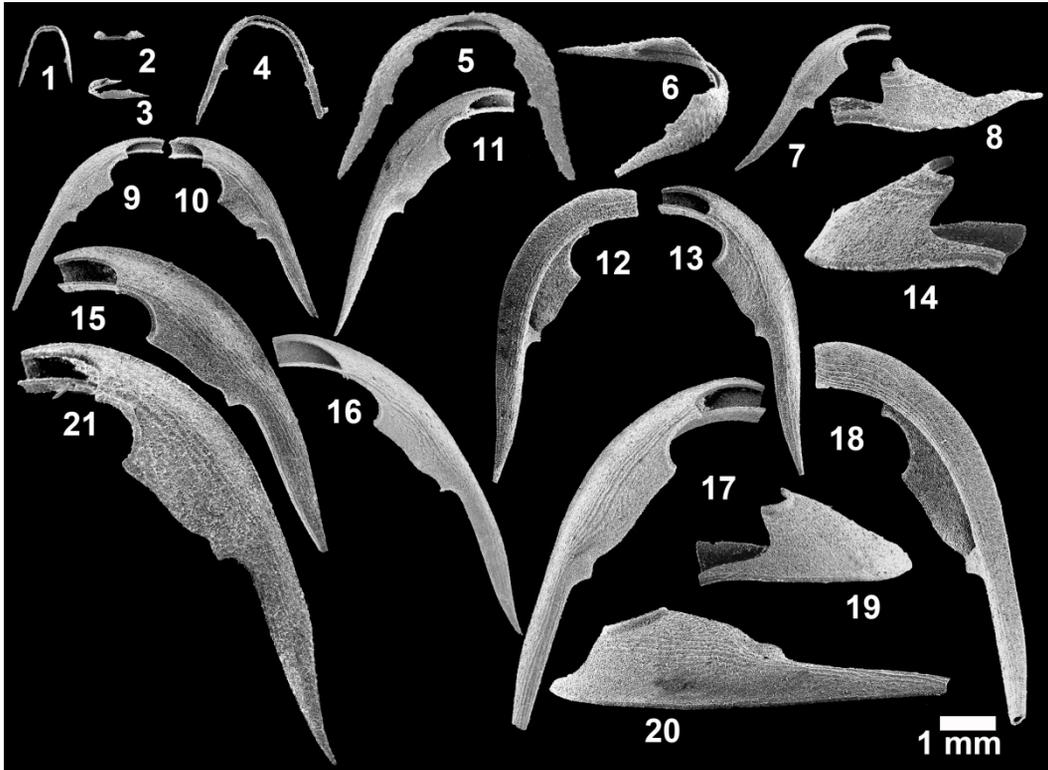


Fig. 5 Free cheeks of *Quadraticephalus elongatus* (Kobayashi, 1935). 1-6, yoked-form free cheeks of early developmental phase: 1-3, SNUP6275, dorsal, anterior, and oblique lateral views; 4, SNUP6276, dorsal view; 5-6, SNUP6277, dorsal and oblique lateral views; 7-21, split-form free cheeks of late developmental phase: 7-8, SNUP6278, dorsal and lateral views; 9, SNUP6279, dorsal view; 10, SNUP6280, dorsal view; 11, SNUP6281, dorsal view; 12-14, SNUP6282, ventral, dorsal, and anterior views; 15, SNUP6283, dorsal view; 16, SNUP6284, dorsal view; 17-20, SNUP6285, dorsal, ventral, anterior, and lateral views; 21, SNUP6286, dorsal view.

prosoxon is well-developed on the abaxial part of the librigenal field and extends onto the whole part of the genal spine. Of the ridges, two or three ridges are prominent along the paradoublural line.

iv. Thoracic segment development

Two thoracic segment-articulated morphologically immature specimens (Fig. 6) help us to understand the anterior-posterior aspect of the thoracic segments within an individual as well as the immature thoracic segment morphology. The anterior-most thoracic segment has a broader articulating facet than those posterior to it (Fig. 6.1, 6.2). In morphologically immature specimens, as situated more posteriorly, the thoracic segments become more arched in dorsal view (Fig. 6), whereas only extremely weak curvature in dorsal view is recognizable from a probably posteriorly-situated thoracic segment (Fig. 7.15). This aspect is also noted in a morphologically mature complete specimen of *Quadraticephalus wallcotti* Sun 1924 (see Zhang and Jell, 1987, pl. 114, fig. 1); even the posterior-most thoracic segment hardly shows any curvature.

Small thoracic segments are generally transverse in dorsal view (Fig. 7.1-7.10) with convex axial ring. The axis is 0.35-0.40 of the entire

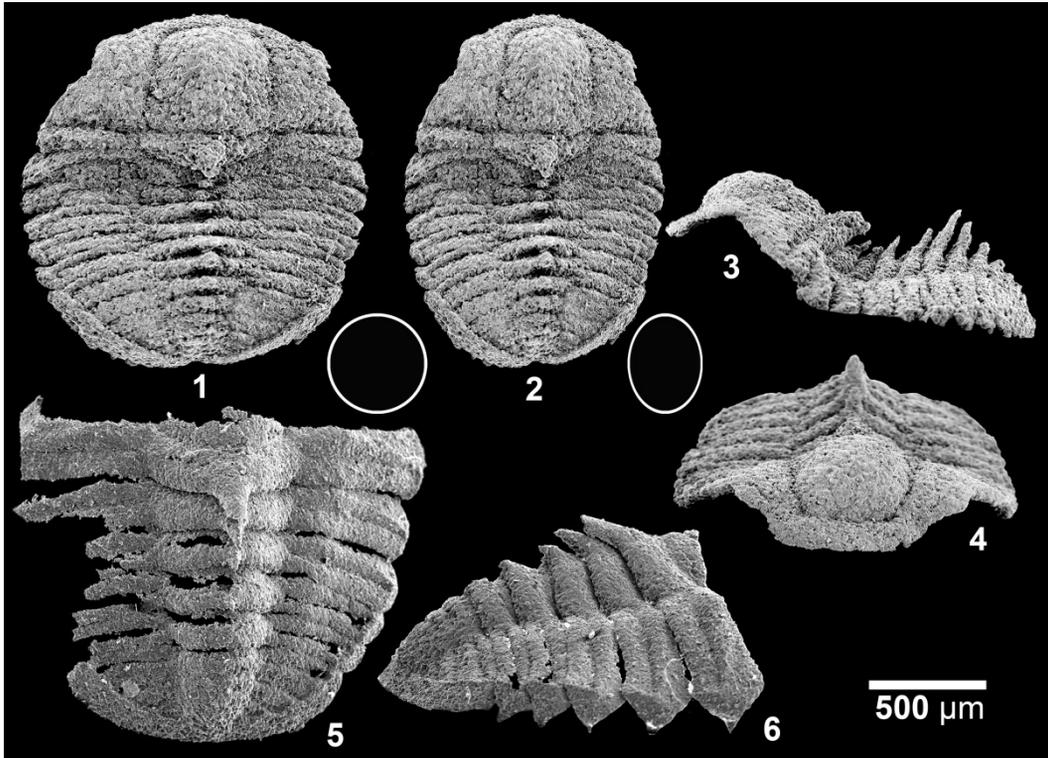


Fig. 6 Meraspid degree 6 exoskeleton of *Quadraticephalus elongatus* (Kobayashi, 1935) retaining the trunk, with free cheeks missing. 1,3-4, original meraspid specimen that is considered to have been deformed only laterally in a single planar direction: 1, SNUP6287, dorsal view; 2, with Adobe Photoshop, the specimen image in fig. 6.1 is compressed along the sagittal axis, the laterally compressed white circle represents the amount of compression; 3, lateral view; 4, anterior view; 5-6, fragmentary holaspid specimen of *Q. elongatus* which consists of the pygidium and the five posterior-most thoracic segments, SNUP6288, dorsal and lateral views.

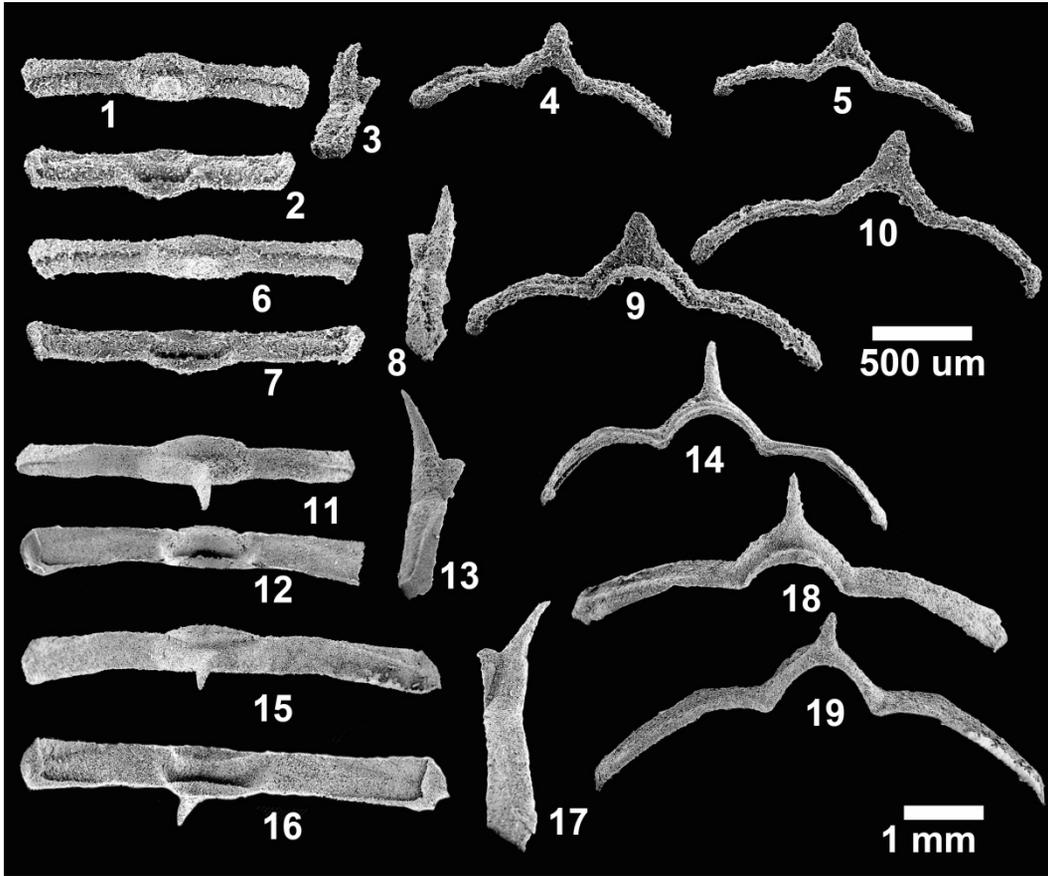


Fig. 7 Thoracic segments of *Quadraticephalus elongatus* (Kobayashi, 1935). 1–10, thoracic segments at early developmental phase with 500 μm scale: 1–5, SNUP6289, dorsal, ventral, lateral, posterior, and anterior views; 6–10, SNUP6290, dorsal, ventral, lateral, anterior, and posterior views; 11–19, thoracic segments at late developmental phase with 1mm scale: 11–14, SNUP6291, dorsal, ventral, lateral, and anterior views; 15–19, SNUP6292, dorsal, ventral, lateral, anterior, and posterior views.

width of the thoracic segment. The axial spine is broad-based, long, and weakly curved forward or upward. The lateral tip of some thoracic pleurae has an obliquely truncated end (Fig. 7.8). In large specimens (Fig. 7.11–7.19), the axial spine is longer, 0.28–0.33 of the height of the thoracic segment (Fig. 7.13), which directs upward and rearward, showing the opposite orientation to that of smaller thoracic segments (compare Fig. 7.3 with 7.13). Panderian processes are recognized in anterior view (Fig. 7.14, 7.18). The lateral tip of pleurae is weakly pointed (Fig. 7.13, 7.17). Given the morphology of a complete specimen of degree 6 meraspis (Fig. 6.1–6.4), there is a tendency that the axial spine reaches its maximum length in the fifth thoracic segment, and is progressively shorter in the anterior and posterior to the fifth segment. Thus the posterior-most thoracic segment in the morphologically immature holaspis specimen (Fig. 6.5–6.6) has no trace of axial spine at all.

v. Post-protaspis pygidial development

The mature pygidia of *Quadraticephalus elongatus* observed in this study have a different morphology from those described by Sohn and Choi (2007, figs. 5, N, P, T and U). The pygidia illustrated by Sohn and Choi (2007) belong to *Haniwa* as pointed out by Park and Choi (2011a). Based on the morphology including the number of axial rings within a

meraspid pygidium, the meraspid pygidia are divided into 11 stages. This is also concordant to the eleven thoracic segments retaining morphologically mature complete holaspid specimen of *Quadraticephalus* (see Zhang and Jell, 1987, pl. 114, fig. 1). Counting the number of pygidial segments may be difficult due to the ambiguity caused by the rear end of axis where new segments are proliferated. In this study, only obviously recognizable segments were counted, and the ambiguous last segment is referred as the terminal piece.

Pygidia of stage A (Fig. 8.1–8.3) are inverted sub-trapezoidal in outline with medially indented posterior margin and are approximately twice wide as long. The smallest trunk in this stage is 0.22 mm long and 0.40 mm wide. Although the specimens are not so well-preserved to reveal morphologic details, it appears to have three axial rings with a short axial spine that projects anteriorly. A pair of spines at the posterior margin of trunk is weakly curved adaxially. $n=3$.

Pygidia of stage B (Fig. 8.4–8.6) possess four axial rings and are sub-rectangular in outline and longer than wide (Fig. 8.4). The lateral margins are convex. The articulating half ring is clearly visible. The pleural and interpleural furrows are weakly incised. A pair of posterior

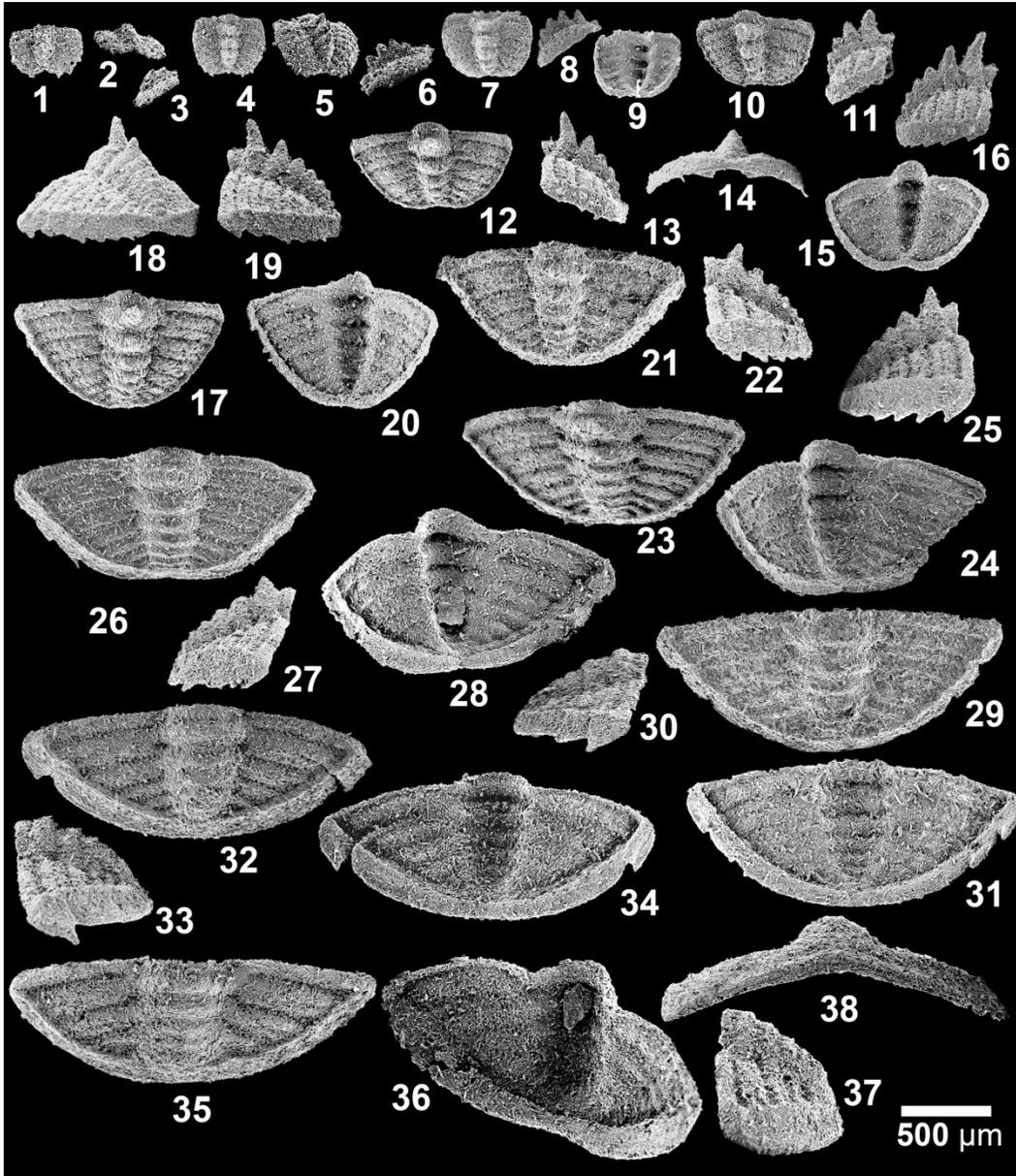


Fig. 8 Post-protaspis pygidia of *Quadraticephalus elongatus* (Kobayashi, 1935). 1-20, meraspis pygidia in accumulation phase: 1-3, SNUP6293, Stage A, dorsal, oblique posterior, and lateral views; 4-6, SNUP6294, Stage B, dorsal, oblique

posterolateral, and lateral views; 7–9, SNUP6295, Stage C, dorsal, lateral, and ventral views; 10–11, SNUP6296, Stage D, dorsal and lateral views; 12–15, SNUP6297, Stage E, dorsal, lateral, posterior, and ventral views; 16, SNUP6298, Stage E, lateral view; 17–20, SNUP6299, Stage F, dorsal, posterolateral, lateral, and ventral views; 21–25, meraspid pygidia in equilibrium phase: 21–22, Stage G, SNUP6300, dorsal and lateral views; 23–25, SNUP6301, Stage H, dorsal, ventral, and lateral views; 26–34, meraspid pygidia in depletion phase: 26–28, SNUP6302, Stage I, dorsal, lateral, and ventral views; 29–31, SNUP6303, Stage J, dorsal, lateral, and ventral views; 32–34, SNUP6304, Stage K, dorsal, lateral, and ventral views; 35–38, holaspid pygidium, SNUP6305, dorsal, ventrolateral, lateral, and posterior views.

marginal spines is present. In lateral view (Fig. 8.6), the axial spines are prominent. $n=14$.

Pygidia of stage C (Fig. 8.7–8.9) have five axial rings. They are similar to those of stage B, but develop narrow marginal border (Fig. 8.8). The border is of low convexity, not clearly recognizable in dorsal view (Fig. 8.7). A pair of posterior marginal spines is absent. The axial spines become longer. In ventral view, the doublure become wider along the posterior margin than that at the lateral margin (Fig. 8.9). $n=30$.

Pygidia of stage D (Fig. 8.10–11) are semi-circular in outline . The pleural and interpleural furrows are distinctly impressed. The pygidial border is developed. With the increase of the convexity, the anteromost axial spine is directed upward and forward. The posterior margin displays an anterior median indentation. $n=48$.

In the stage E (Fig. 8. 12–8.16), the pygidia bear six axial rings and are wider than long. The pleural and the interpleural furrows are more clearly impressed. The pygidial border becomes wider and steeper, with a rim along the edge of pleural field (Fig. 8.12). In lateral view, the posterior part of pygidial border is slightly thicker than the anterior part of the pygidial border (Fig. 8.13, 8.16). The anteromost axial spine is longest; in the earlier stages, the spine is shorter than or is similar in

length to other spines (Fig. 8.13). Some specimens display serrated ventral margin (Fig. 8.16), which corresponds to spinose lateral end of thoracic pleurae. $n=47$.

Pygidia of stage F (Fig. 8.17–8.20) have seven axial rings and a terminal piece and are semi-circular in outline. The equilibrium phase begins with this stage. The axial spines become shorter and the postermost axial spine is hard to recognize. On the lateral view, the serrated ventral margin displays six marginal spines, indicating that the trunk at this stage has six prothoracic segments (Fig. 8.19, 8.20). After the stage F, the number of prothoracic segments decreases due to the successive release of prothoracic segments into thoracic region at each molting. $n=23$.

In stage G (Fig. 8.21, 8.22), the pygidial border becomes prominent and the rim is strongly raised; the serrated lateral margin is also visible in dorsal view; and anterior spines are longer and more distinct. The antermost spine is curved posteriorly, unlike that in stage F. Five prothoracic segments are recognized. The pygidial morphology is nearly identical to that of meraspid degree 6 specimen (Fig. 6.1–6.4), indicating that the stage G corresponds to the meraspid degree 6. $n=11$.

The stage H is the last stage of the equilibrium phase (Fig. 8.23–8.25). The pygidial morphology of this stage is similar to that of stage G except for possession of four protothoracic segments. $n=8$.

From the stage I, the number of the axial rings is reduced and it corresponds to the onset of the depletion phase (sensu Simpson et al. 2005). The pygidium of stage I (Fig. 8.26–8.28) has six axial rings and a terminal piece. The axial spines become notably shorter and so only the antermost one is distinguishable. The high pygidial border becomes inclined adaxially and forwardly, so that the highest contour of the border shows a rim-like ridge. Pygidia of stage I have three protothoracic segments (Fig. 8.27). $n=11$.

In sequential growth, the pygidia of stage J (Fig. 8.29–8.31) release one protothoracic segment while retaining six axial rings and a terminal piece, leaving only two protothoracic segments. $n=7$.

Pygidia of stage K have five axial rings and a terminal piece (Fig. 8.32–8.34). The rim along the pleural field is strongly raised. The axial spines are not recognized (Fig. 8.33). Only one protothoracic segment is present. $n=12$.

Pygidia with four axial rings and a terminal piece (Fig. 8.35–8.38) show no trace of protothoracic segments in lateral view (Fig. 8.37), hence

entering into the holaspid period. The inter-ring furrows, pleural furrows and interpleural furrows become weakly impressed and then disappear (Fig. 9). The rim-like ridge along the pleural field becomes weaker and terrace lines parallel to pygidial margin appear in the border and double (Fig. 9.6, 9.8). The anterior margin is nearly transverse (Fig. 9.6), hence corresponding to extremely low curvature in the posterior-most thoracic segment, as mentioned above.

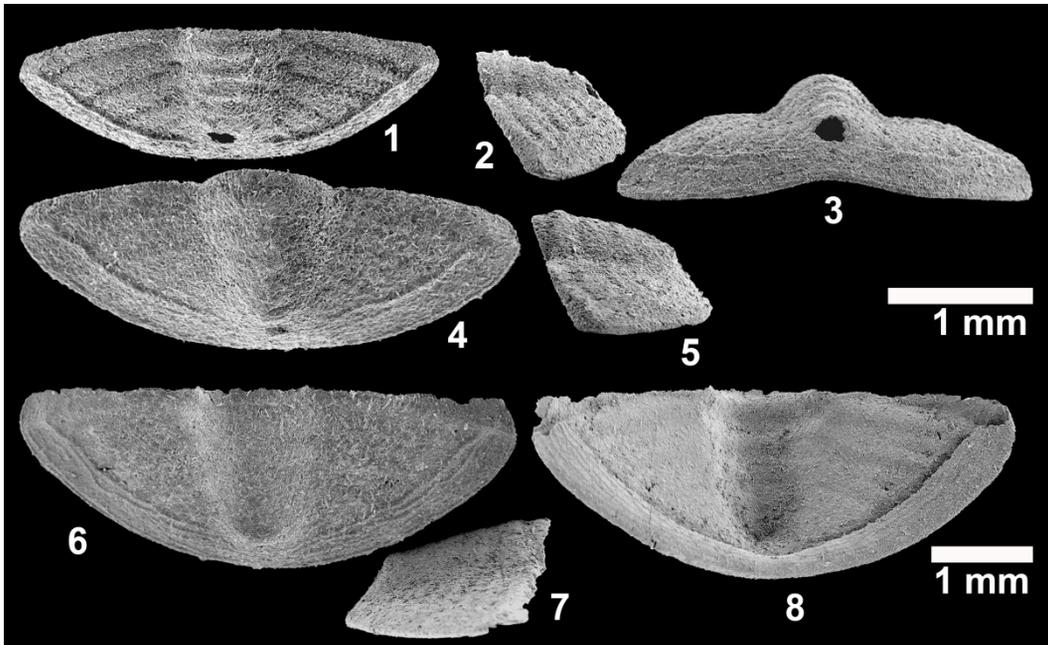


Fig. 9 Holaspid pygidia of *Quadraticephalus elongatus* (Kobayashi, 1935). 1-3, SNUP6306, dorsal, lateral, and posterior views; 4-5, SNUP6307, dorsal and lateral views; 6-8, SNUP6308, dorsal, lateral, and ventral views.

IV. Ontogenetic comparison with *Asioptychaspis subglobosa*

Since the ontogeny of *Asioptychaspis subglobosa* (Sun, 1924), a probable ancestral species of *Q. elongatus*, was already reported (Park and Choi, 2010b), a detailed comparison of the ontogeny of the two species is available. It is thus possible to examine if some morphologically novel features of *Q. elongatus* were induced by heterochronic changes during development. This study assumes that specimens of the two species with similar size represent a similar developmental stage.

i. Protaspides

The protaspides of *Asioptychaspis subglobosa* were divided into two stages; the early stage protaspides and the late stage protaspides (Park and Choi, 2010b). In contrast, the protaspides of *Quadraticephalus elongatus* cannot be divided into distinct stages. Interestingly, the size and overall morphology of the protaspides of *Q. elongatus* are closely similar to the early stage protaspides of *A. subglobosa* (Fig. 10). Although the presence of both genal and pygidial spines in some of the

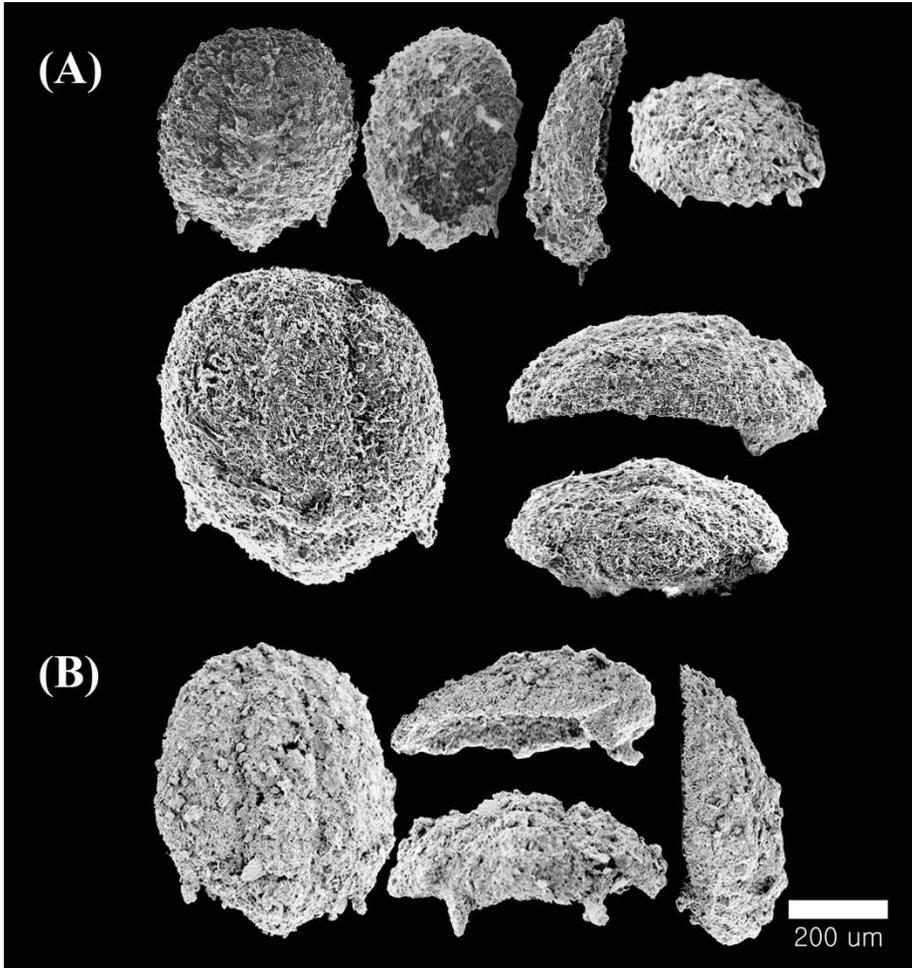


Fig. 10 Comparison of protaspides between *Quadraticephalus elongatus* (Kobayashi, 1935) (A) and *Asioptychaspis subglobosa* (Sun, 1924) (B).

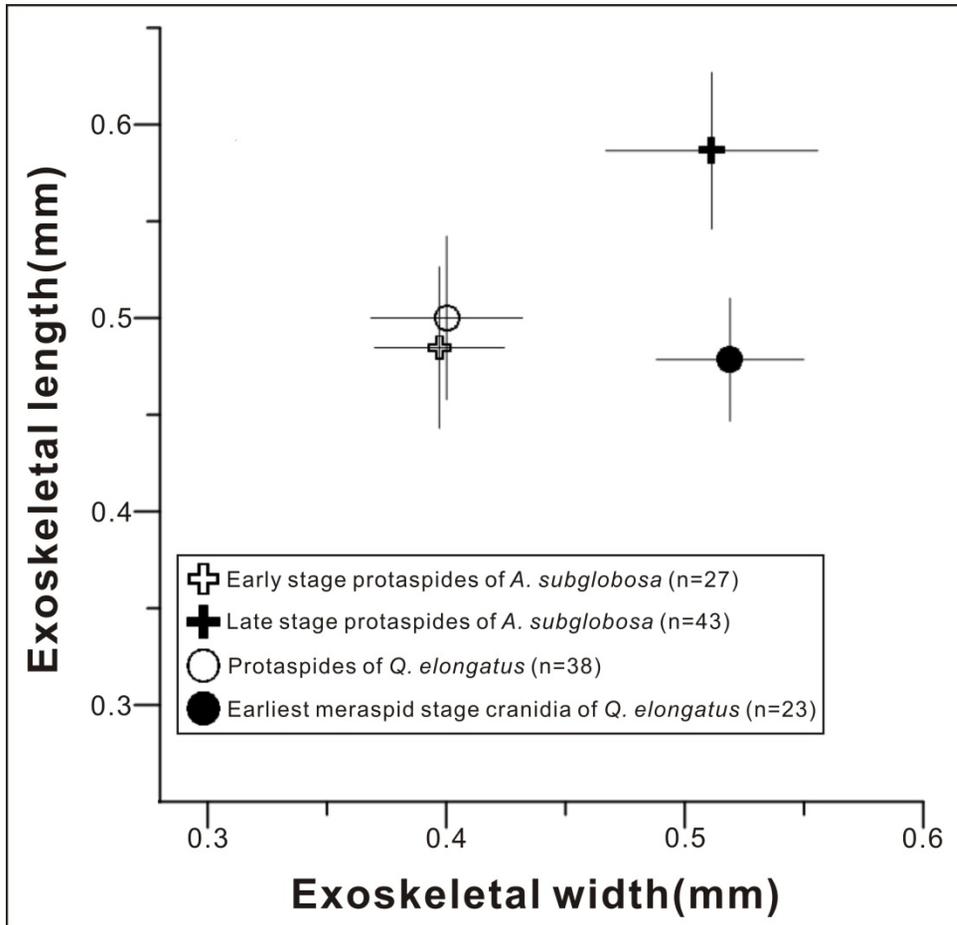


Fig. 11 The mean scores of the protaspid size of *Quadraticcephalus elongatus* (Kobayashi, 1935) and *Asioptychaspis subglobosa* (Sun, 1924), and the earliest meraspid stage size of *Q. elongatus*. One standard deviation bars are extended to horizontal and vertical side of the mean. It is noticeable that the size of the early stage protaspides of *A. subglobosa* is similar to that of the single staged-protaspides of *Q. elongatus*, and the earliest meraspid stage cranidia of *Q. elongatus* show similar width to the late stage protaspides of *A. subglobosa*. This implies that the first articulation appeared earlier in development for *Q. elongatus*.

protaspides of *Q. elongatus* is rather comparable to the late stage protaspides of *A. subglobosa*, the overall shape and morphology such as relatively indistinct axial furrows are comparable to those of the early stage protaspides of *A. subglobosa* (see Park and Choi, 2010b, fig. 3). Moreover, some early stage protaspides of *A. subglobosa* also display both genal and pygidial spines (Park and Choi, 2010b, fig. 3.7–3.9). With subsequent molting, an articulation appeared in *Q. elongatus*, indicating that this species has entered into the meraspid period, while the morphologically comparable early stage protaspides of *A. subglobosa* developed into the late stage protaspides with the articulation not yet appeared. This is well represented in the bivariate plots of the protaspides of both species and the earliest meraspid cranidia of *Q. elongatus* (Fig. 11). This means that the first articulation appeared earlier in *Q. elongatus* than in *A. subglobosa*.

The discrepancy in the first articulation timing in these two closely related trilobite species is significant in respect of the issue raised by Park and Choi (2011b). Because protaspid morphology of related taxa tends to be more similar to each other than to those of less related taxa, protaspid morphology has long been employed to determine the phylogenetic relationship and higher-level classification without any logical justification. Park and Choi (2011b), however, pointed out that

there is a logical pitfall in just comparing the protaspid morphology of different taxa, because the timing of first articulation which differentiates the meraspid period from the protaspid period is not necessarily the same among different trilobite taxa: closely related species may display different timing of first articulation. The fact that the single-staged protaspides of *Q. elongatus* correspond to the early stage protaspides of *A. subglobosa* corroborates Park and Choi (2011b)' s argument. Although *A. subglobosa* and *Q. elongatus* have a close phylogenetic relationship, there is a clear discrepancy in the timing of first articulation between the two species. The late stage protaspides of *A. subglobosa* are more homologous to the first meraspid stage, not the protaspid stage, of *Q. elongatus*. Therefore, as noted by Park and Choi (2011b), care must be taken when using protaspid morphology for phylogenetic relationship of trilobites.

ii. Eyes

When comparing of the ratio of the palpebral lobe length to the cranial length (Fig. 12), palpebral lobes become recognizable earlier in *A. subglobosa*. However, after the specimen gets the ratio 0.36–0.39, the stage of eye diminishing get into faster at *Q. elongatus*.

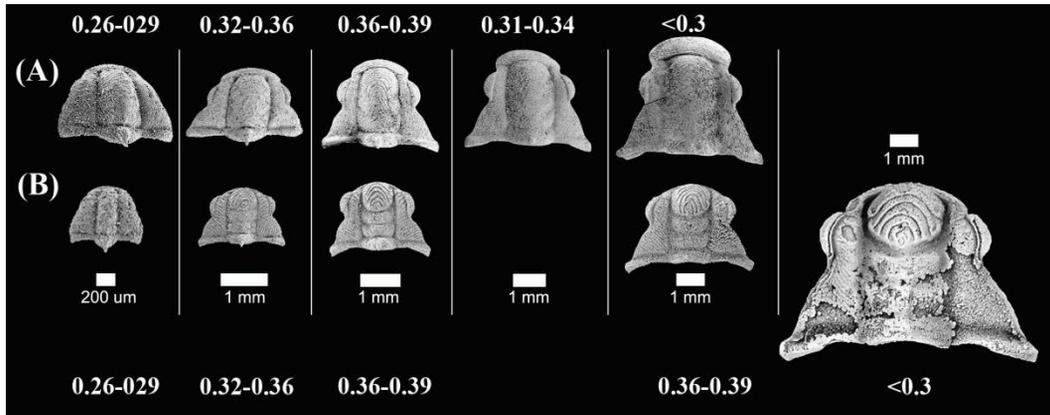


Fig. 11 Comparison of ratio of palpebral length to cranial length between *Quadraticephalus elongatus* (Kobayashi, 1935) (A) and *Asioptychaspis subglobosa* (Sun, 1924) (B).

iii. Cranidium

One of the most notable differences between *Q. elongatus* and *A. subglobosa* is the convexity of the cranidium (Fig. 13). When the two species are young, morphology of cranidia is similar to each other. During with growth, however, the convexity of cranidia of two species becomes gradually different. The convexity of *A. subglobosa* becomes more prominent dramatically than that of *Q. elongatus*. Difference in convexity may induce divaricating *Q. elongatus* from *A. subglobosa*.



Fig. 12 Comparison of convexity between *Quadraticephalus elongatus* (Kobayashi, 1935) (A) and *Asioptychaspis subglobosa* (Sun, 1924) (B).

iv. Free cheeks

Free cheeks of the two species display a similar developmental pattern. Park and Choi (2010b) presented three different modes of the ventral median suture (VMS) formation: *A. subglobosa* shows the third mode of VMS formation in which an initially yoked free cheek splits along the sagittal line during development to form a VMS. *Quadraticephalus elongatus* also displays the same mode of VMS formation with *A. subglobosa*, but differs in the timing of the splitting. The largest yoked free cheek of *A. subglobosa* is 1.2 mm long, whereas that of *Q. elongatus* is 2.5 mm long, suggesting that the former attains the VMS in an earlier developmental stage (Fig. 14).

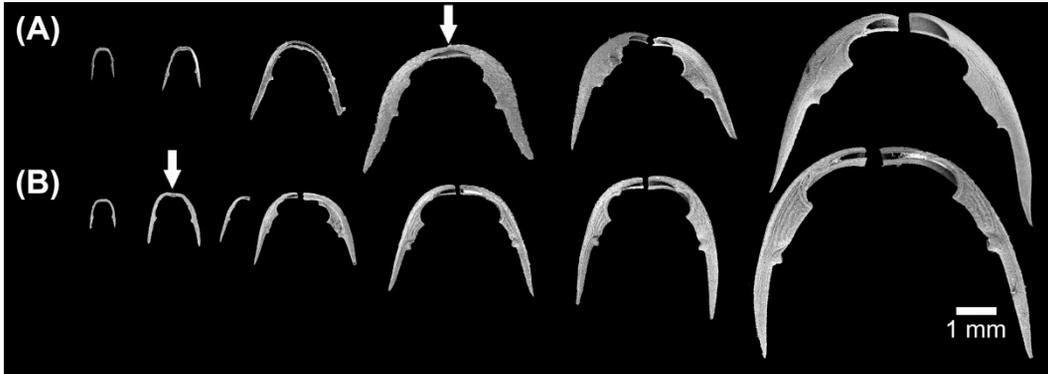


Fig. 13 Comparison of the development of free cheek between (A) *Quadraticephalus elongatus* (Kobayashi, 1935) and (B) *Asioptychaspis subglobosa* (Sun, 1924). The splitting timing of the initially yoked free cheek of *Q. elongatus* is later in development, compared that of *A. subglobosa*. The white arrows represent the latest developmental stage of each species, in which the free cheeks remained yoked.

v. Meraspid pygidia

Meraspid pygidia of both species show a similar segmentation pattern and morphology. The smallest specimens available for both species have three or four axial rings. In the subsequent development, the number of segments increases (accumulation phase) until there are seven segments within the pygidium (equilibrium phase). Subsequently, the number of segments within the pygidium decreases (depletion phase) until only four segments remain to enter the holaspid period. The meraspid pygidial morphology of the two species is also almost identical, but in the holaspid period the rim-like ridge of *Q. elongatus* is prominent and did not disappear, whereas that of *A. subglobosa* only remained in the earliest holaspid period and subsequently disappeared.

vi. Summary

The cranidial convexity change and the timing of free cheek-splitting during development indicate that the rate of morphological change is apparently slower in *Q. elongatus* than its ancestral species, *A. subglobosa*. Moreover, the mature pygidia of *Q. elongatus* retain morphological features which disappeared during the development in *A. subglobosa*. It can, therefore, be postulated that a pedomorphism must have been involved in the evolution of *Q. elongatus*.

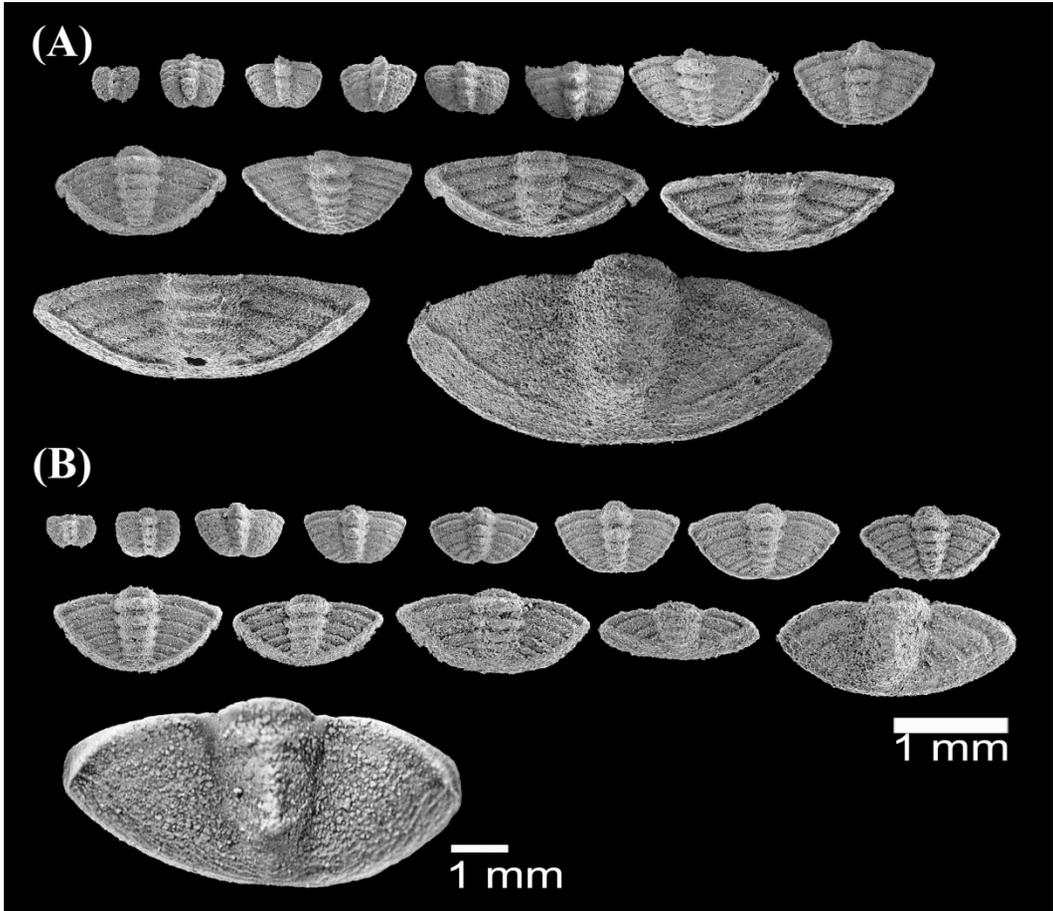


Fig. 14 Comparison of meraspid and holaspid pygidia between *Quadraticephalus elongatus* (Kobayahsi, 1935) (A) and *Asioptychaspis subglobosa* (Sun, 1924) (B).

V. Segmentation process

The meraspid pygidia of *Quadraticephalus elongatus* undergo dynamic changes in the number of segments during development. Because the complete holaspid specimen of *Q. elongatus* has not been recovered, the final number of thoracic segments is unclear. However, a nearly complete specimen of *Quadraticephalus*, illustrated by Zhang and Jell (1987, pl. 114, fig. 1; described under the name of *Changia walcotti* Sun, 1924), has 11 thoracic segments. Considering that the meraspid degree 6 specimen of *Q. elongatus* with a complete trunk (Fig. 6.1–6.4) has a pygidial morphology similar to the pygidial developmental stage G, and four more pygidial developmental stages are differentiated after the stage G before entering into the holaspid period, *Q. elongatus* must have had 11 thoracic segments in the holaspid period (Fig. 16).

The meraspid pygidia of *Q. elongatus* increase the length and width from the stage A to F, and this period corresponds to an accumulation phase during which the number of segments within the pygidium increases from 3 to 7 (Fig. 16). During the stage F–H, the meraspid pygidial development enters into an equilibrium phase during which the number of segments within the pygidium does not change (Fig. 16).

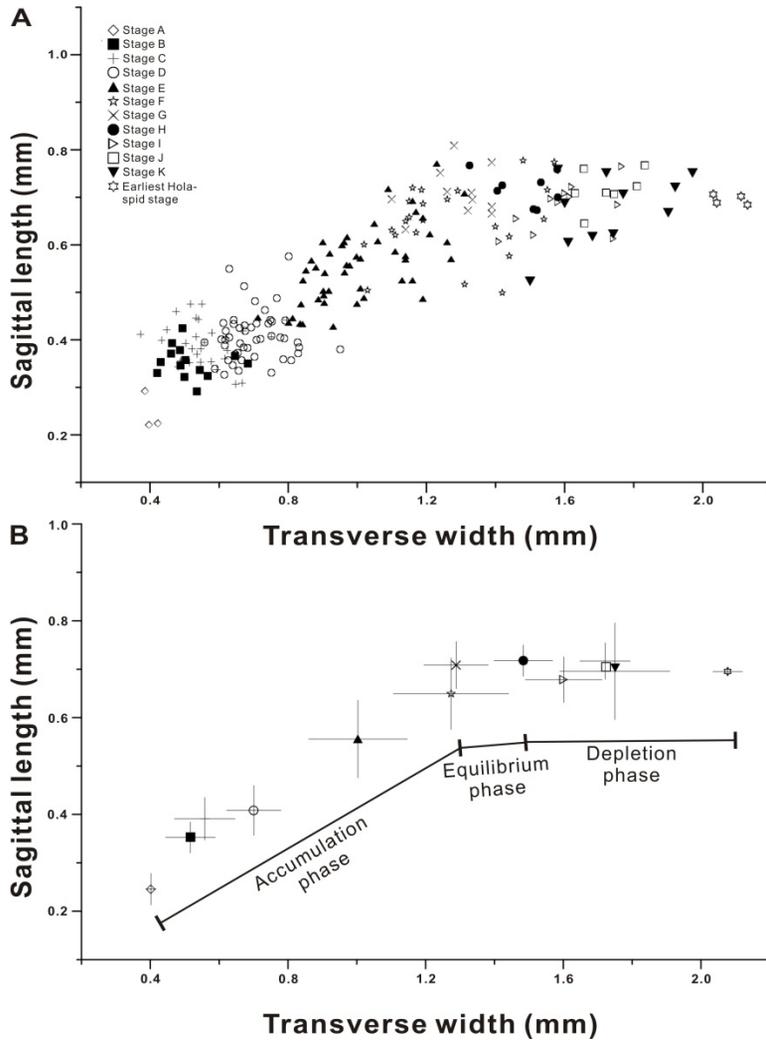


Fig. 16 The relationship between the developmental stages and the size of the meraspid and earliest hoalspid pygidium of *Quadraticephalus elongatus* (Kobayashi, 1935). (A) Scatter plots of pygidial length versus width. (B) The mean for each stage, and the standard deviation bars extending to horizontal and vertical sides of the mean.

The rate of sagittal length increase of pygidium slows down during these stages (Fig. 17). Subsequently, the formation of new segments in the rear end of the pygidium ceased, but the release of thoracic segments at the anterior of the pygidium maintained. Accordingly, the number of segments decreases down to 4 in the pygidium, representing a depletion phase (Fig. 16). During this phase, the sagittal length of pygidium does not increase or slightly decreases, while transverse width increases (Fig. 17). It can be inferred that increase of the length due to the size increase of pygidial segments could not compensate the decrease of length caused by release of the anterior-most segment into the thorax. Such stagnancy in size during pygidial development has been reported in several trilobite species including *Hintzeia plicamarginis* Simpson et al., 2005 (Simpson et al., 2005), *Cyclolorenzella convexa* (Resser and Endo in Endo and Resser, 1937) (Park and Choi, 2010a), and *Haniwa quadrata* Kobayashi, 1933 (Park and Choi, 2011a). All of these cases have been considered to be related to the presence of a depletion phase during pygidial development. It is noteworthy that the depletion phase has been recorded among phylogenetically remotely related trilobite lineages. The total number of segments does not increase anymore since the stage J, and the holaspid period begins after stage K. Hence, the developmental mode of *Q. elongatus* is protomeric (sensu Hughes et al., 2006) in which the epimorphic phase precedes the onset of the holaspid period.

VI. Conclusion

The ontogenetic study of *Quadraticephalus elongatus* makes it possible to compare its ontogenetic development with the probable ancestral species, *Asioptychaspis subglobosa* (Sun, 1924). The single-staged protaspides of *Q. elongatus* are considered homologous to the early stage protaspides of *A. subglobosa*. Subsequently, *Q. elongatus* entered into the earliest meraspid stage with the appearance of the first articulation, while the early stage protaspides of *A. subglobosa* developed into the late stage protaspides. This indicates that phylogenetically closely related trilobites could have a different timing of first articulation, corroborating Park and Choi (2011b)'s argument that protaspides of different trilobite species cannot always be regarded to be in a homologous stage. Although the earliest cranidial morphology of *A. subglobosa* and *Q. elongatus* is similar to each other, the overall convexity increases more slowly in *Q. elongatus*. The free cheek of *Q. elongatus* was initially yoked, but subsequently splitted to form a ventral median suture as in *A. subglobosa*. However, the splitting occurred later in development in *Q. elongatus* than in *A. subglobosa*. The two species display similar meraspid pygidial development, but the rim-like ridge did not disappear in the holaspid pygidia of *Q. elongatus*. In short, the comparison of the ontogeny of the two ptychaspidid species reveals that

paedomorphosis played a role in the development to attain the mature morphology of *Q. elongatus*.

The meraspid pygidia of *Q. elongatus* are divided into 11 stages according to size and morphology. The number of segments within the meraspid pygidium begins with 3 and increases to 7 (the accumulation phase). Subsequently, it does not change for a while (the equilibrium phase), and eventually decreases to 4 (the depletion phase). The total number of trunk segments reached its maximum during the beginning of the depletion phase (epimorphic phase) and the holaspid period begins at the end of the depletion phase. Therefore, the developmental mode of *Q. elongatus* is protomeric.

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요약(국문초록)

삼엽충 꼬리의 발달과정은 앞부분의 관절화 과정과 뒷부분의 새로운 체절 형성으로 이루어져 있으며 이로 인해 성장기에서의 꼬리 발달과정은 매우 복잡한 양상을 보인다. 이번 연구는 우리나라 태백산분지 태백층군의 화절층에서 산출되는 후기 캄브리아기 삼엽충 *Quadraticephalus elongatus* (Kobayashi, 1935)의 꼬리 발달과정 중 일어나는 마디 분절과정에 초점을 맞춰 진행하였다. 조상종으로 추정되는 *Asioptychaspis subglobosa* (Sun, 1924)와 비교해 볼 때, *Q. elongatus* 쪽의 머리가 더 느린 속도로 블록해 지는 것을 볼 수 있다. 또한 유리볼의 경우에도 *Q. elongatus*가 더 늦은 시기에 둘로 나뉘며, 꼬리에서도 rim-like ridge가 더 늦게까지 관찰된다. 성장과정에서의 이러한 형태학적 차이는 *Q. elongatus*의 진화과정 중 미진화 (paedomorphism)가 발생했음을 보여준다. 성장기 꼬리는 총 11단계로 구성되어 있으며, 이 단계들은 마디 숫자가 3개에서 7개로 늘어나는 축적상 (accumulation phase), 7개의 마디 숫자를 유지하는 평형상 (equilibrium phase), 마디 숫자가 다시 4개까지 줄어드는 감소상 (depletion phase)로 묶을 수 있다. 특히, 감소상에서는 꼬리의 길이가 정체되거나 약간 줄어드는 경향을 보인다. Trunk의 마디 숫자가 더 이상 증

가하지 않는 epimorphic phase가 가슴 마디 숫자가 더 이상 증가하지 않는 holaspid phase보다 먼저 나타나기 때문에 *Q. elongatus*의 발달 방식은 protomeric이라고 할 수 있다.

주요어 : 캄브리아기, 삼엽충, 개체발생과정, *Quadricephalus elongatus*, 마디 분절과정, 화절층

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고마움을 전합니다.

저에게 대학원 생활을 익숙하게 해주고 선배로써 많은 조언을 해준 윤환이와 힘들 때 힘이 되어준 원규, 영준이, 재현이 에게도 감사합니다. 그리고 짧지 않은 시간 동안 언제나 옆에서 의지가 되고 힘이 되어준 예지에게도 감사의 말을 전합니다.

마지막으로 공부하는 동안 언제나 옆에서 묵묵히 응원해주신 아버지, 어머니 그리고 우리 지용이. 제가 하고 싶다고 하는 것은 언제나 찬성하시고 하게 해 주셔서 감사합니다. 제 뒤에 든든한 가족이 있었기에 제가 공부에 매진 할 수 있었습니다. 앞으로는 더욱 믿음직한 장남이 되도록 노력하겠습니다.