ONTOGENY OF THE FURONGIAN (LATE CAMBRIAN) TRILOBITE *PROCERATOPYGE* CF. *P. LATA* WHITEHOUSE FROM NORTHERN VICTORIA LAND, ANTARCTICA, AND THE EVOLUTION OF METAMORPHOSIS IN TRILOBITES

by TAE-YOON S. PARK, JI-HOON KIHM, JUSUN WOO, YOUNG-HWAN G. KIM *and* JONG-IK LEE

Division of Polar-Earth System Sciences, Korea Polar Research Institute, Incheon, 406-840, Korea; typark@kopri.re.kr, jhkihm@kopri.re.kr, jusunwoo@kopri.re.kr, dave8379@kopri.re.kr, jilee@kopri.re.kr

Abstract: There were multiple origins of metamorphosis-undergoing protaspides in trilobite evolution: within the superfamilies Remopleuridioidea, Trinucleoidea, and within the Order Asaphida. Recent studies have revealed that the protaspides of the Cambrian representatives of the Remopleuridioidea and the Trinucleoidea did not undergo metamorphosis. However, ontogeny of the Cambrian members of the Order Asaphida has remained unknown. This study documents the ontogeny of the Furongian asaphoidean ceratopygid trilobite, *Proceratopyge* cf. *P. lata* Whitehouse, from northern Victoria Land, Antarctica. Two stages for the protaspid phase, five developmental stages for the post-protaspid cranidia, and ten stages for the post-protaspid pygidia have been identified. Interestingly, the protaspis directly developed into a meraspis without metamorphosis. A new cladistic analysis resulted in a single most parsimonious tree, according to which the presence of the bulbous commutavi protaspis turns out to be a synapomorphy for Asaphidae + Cyclopygoidea, not a synapomorphy for the Order Asaphida as previously suggested. In addition, it is inferred that there was convergent evolution of indirectly-developing commutavi protaspides during the Furongian and Early Ordovician. Metamorphosis-entailing planktonic larvae evolved in many different metazoan lineages near the Cambrian–Ordovician transition, due to the escalating ecological pressure of the Great Ordovician Biodiversification Event. Since the bulbous commutavi protaspid morphology is thought to be an adaptation for a planktonic life mode, the convergent evolution of the indirect development in the three trilobite lineages at this period might have been a result of adaptation to the early phase of the Great Ordovician Biodiversification Event.

Key words: metamorphosis, Cambrian, Ordovician, trilobite, protaspis.

Tᴙɪʟᴏʙɪᴛᴇ metamorphosis is known to have occurred at various developmental stages. The Ordovician illaenoid trilobite, *Failleana calva* Chatterton & Ludvigsen, 1976, had a bulbous early stage protaspis which metamorphosed into a flat late stage protaspis (Chatterton & Speyer 1997, fig. 159). A similar metamorphosis within the protaspid phase is also known in the Cambrian illaenoid *Tsinania canens* (Walcott, 1905; see Park & Choi 2009). A sudden morphological change in developmental stages later than the protaspid phase has also been reported. Chatterton *et al.* (1999) documented a metamorphosis occurring in the middle of meraspid phase in the development of telephinid trilobites. A pair of large pygidial spines of *Tsinania canens*, which existed for most of the meraspid phase and the early holaspid phase, suddenly degenerated (Park & Choi 2009). A similar phenomenon is known from a closely-related tsinaniid trilobite *Shergoldia laevigata* Zhu *et al.*, 2007. Among others, however, the most prominent and best-known case is the transition from a commutavi protaspis (protaspis which underwent metamorphosis into a subsequent meraspid phase; *sensu* Park & Kihm 2015) having a bulbous morphology to the earliest stage meraspis having a flat morphology. Fortey & Chatterton (1988) termed the bulbous protaspis 'asaphoid protaspis', and regarded it as a synapomorphy to group the Order 'Asaphida (*sensu* Fortey & Chatterton 1988; Fortey 1990)'. Subsequently however, following the emendation of the concept of the

Order Asaphida, it has been revealed that the bulbous commutavi protaspides independently evolved in Remopleuridioidea, Trinucleoidea, and Asaphida (Park & Choi 2011; Park *et al.* 2014; Park & Kihm 2015).

Interestingly, while the Ordovician representatives of Trinucleoidea and Remopleuridioidea had bulbous protaspides which metamorphosed into flat meraspides, the Furongian (late Cambrian) representatives of the two lineages did not undergo metamorphosis at the transition between protaspid/meraspid phases (Park & Choi 2011; Park *et al.* 2014). For the Asaphida, several Ordovician asaphid trilobites are known to have had commutavi protaspides (see Fortey & Chatterton 1988; Chatterton & Speyer 1997), but ontogeny of the Cambrian representatives of the Asaphida has not been documented, and thus whether there was metamorphosis at the protaspid/meraspid transition in Cambrian asaphide trilobites has remained unknown.

The families Ceratopygidae and Asaphidae form the Superfamily Asaphoidea (see Adrain 2011). In turn, superfamilies Asaphoidea and Cyclopygoidea (Taihungshaniidae + Nileidae + Cyclopygidae) form the current Order Asaphida (see Park & Choi 2009, 2010a, 2011; Park *et al.* 2014). Ceratopygidae spans the Cambrian Series 3 to the Furongian, whereas the oldest members of the Asaphidae occur no earlier than the middle Furongian (see the generic list in Jell & Adrain 2003). All the members of the Cyclopygoidea are known from the Ordovician. Therefore, it is likely that the Cambrian ceratopygids retained more plesiomorphic features than the other members of the Asaphida.

This study documents the post-protaspid ontogeny of the ceratopygid trilobite, *Proceratopyge* cf. *P. lata* Whitehouse, 1939, recovered from the Furongian deposits of northern Victoria Land, Antarctica. The genus *Proceratopyge* Wallerius, 1895, which is characterized by a pair of pygidial spines, belongs to the Ceratopygidae and occurred from the upper Cambrian Series 3 to the Furongian. Three protaspides have been recovered for this study, which are the first report of Cambrian protaspides of the Order Asaphida. Whether this Cambrian asaphide species had direct development or indirect development with metamorphosis has significant implications for the origin of the bulbous commutavi protaspis in the Order Asaphida.

FOSSIL LOCALITY AND MATERIAL

Early Palaeozoic successions of northern Victoria Land, Antarctica were formed during the Ross Orogeny, and represented by an accretionary complex of sedimentary rocks in three tectonic terranes: the Wilson, Bowers and Robertson Bay terranes, from inboard to outboard

(Bradshaw *et al.* 1985; Kleinschmidt & Tessensohn 1987; Fig. 1A). The Bowers Supergroup of the Bowers Terrane contains Cambrian fossils which can be used for international correlation (Shergold *et al.* 1976; Shergold & Cooper 1985; Cooper *et al.* 1996). The Bowers Supergroup is divided into the Sledgers, Mariner and Leap Year groups in ascending order, which spans the Cambrian Series 3 to the Lower Ordovician. Of them, the Mariner Group is subdivided into the Edlin, Spurs and Eureka formations in ascending order. All of the specimens for this study were collected from the Spurs Formation at Eureka Spurs, which is located at the head of Mariner Glacier (72°41′46″ S, 165°59′40″ E; Fig. 1B–C). This section has served as the type section of the Mariner Group. Despite the reports of trilobites from several horizons of the Spurs Formation (Andrew & Laird 1976; Cooper *et al.* 1976; Shergold & Cooper 1985), trilobites from only one horizon were documented by Shergold *et al.* (1976).

The geology team of Korea Polar Research Institute visited Eureka Spurs, which is *c.* 225 km north to the Jang Bogo station (Fig. 1B) during the 2012–2013, 2013–2014, and 2014–2015 seasons, and measured a *c.* 1100 m interval which includes most of the Spurs Formation and the Eureka Formation. The Spurs Formation at this section measures *c.* 700 m in thickness, and consists mainly of fissile mudstone, intercalated by thin beds of fine sandstone and limestone (Laird & Bradshaw 1983; Stump 1995), which was considered to have deposited on an open marine, probably low-gradient shelf or platform (Andrew & Laird 1976). It should be noted that this area underwent some structural deformation, and thus structural repetitions, such as the deformed sandstone (Fig. 1D), are present at the section. However, the morphology of the fossils from the limestone for this study has not been significantly influenced by the structural deformation in the area. Structural deformation has been also recognized in northern part of the Bowers Terrane (Capponi *et al.* 1999; Federico *et al.* 2006). A total of 15 trilobite-occurring horizons were identified, and the material for this study was collected from the horizon which is 246 m above the base of the exposure (Fig. 1D).

Shergold *et al.* (1976) documented trilobites from a horizon at Eureka Spurs and regarded the specimens of *Proceratopyge* from this section as *Proceratopyge* cf. *P. lata* Whitehouse, 1939. Based on the cranidial morphology, the specimens herein are identified as *Proceratopyge* cf. *P. lata* Whitehouse, 1939, following Shergold *et al.* (1976). Other trilobites co-occurring from the horizon are *Olentella?* sp. and aphelaspidid gen. et sp. indet. *Proceratopyge lata* is known to occur in the Idamean of Qeensland, Australia (Shergold, 1982). The occurrence of *Proceratopyge* cf. *P. lata*, therefore, suggests that the horizon in the Eureka Spurs represents the Paibian Stage. A total of 310 specimens representing a range of ontogenetic
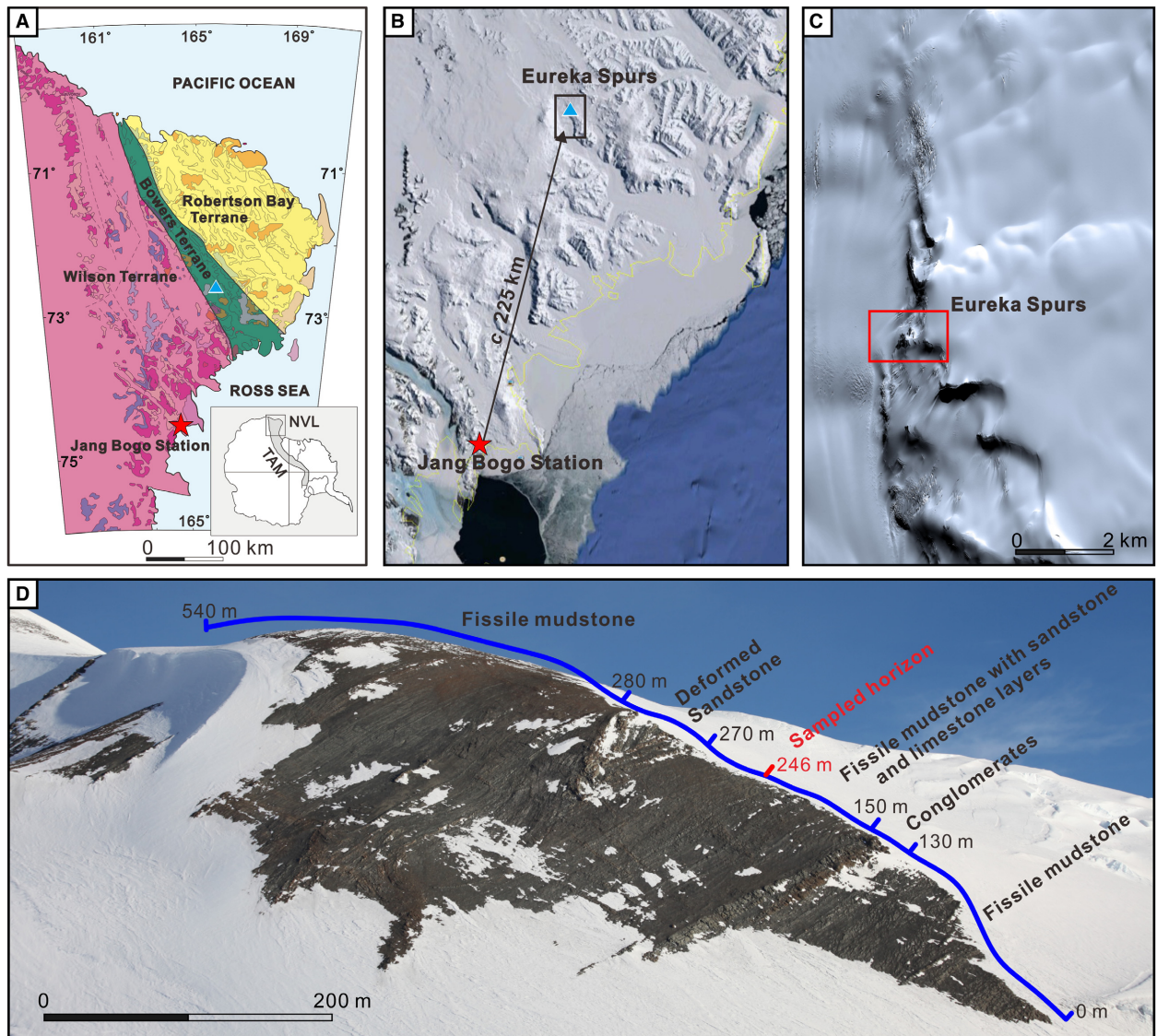
FIG. 1. A, tectonic map of northern Victoria Land, Antarctica, superimposed on a geological map modified from Crispini *et al.* (2011); the location of Jang Bogo Station is represented by a red star. B, satellite map showing the location of Eureka Spurs, which is *c.* 225 km north of Jang Bogo Station; the rectangle area is magnified in C. C, satellite map of Eureka Spurs; the rectangle indicates the cliff studied for this research, which corresponds to 'Eureka Spur number 3' of Andrew & Laird (1976). D, outcrop photograph of the studied cliff at Eureka Spurs; the sampled horizon is 246 m above the base of the exposure. *Abbreviations*: NVL, northern Victoria Land; TAM, Transantarctic Mountains.

stages were recovered, which includes three protaspides, 124 post-protaspid cranidia, and 183 post-protaspid pygidia.

ONTOGENY OF *PROCERATOPYGE* CF. *P. LATA*

The general aspects of trilobite ontogeny were discussed by Chatterton & Speyer (1997) and Hughes *et al.* (2006), and are not repeated here. Length and width were measured for the protaspides and pygidia. Because there are not many post-protaspid cranidia with well-preserved posterolateral projections and the pre-glabellar area, the glabellar length and the palpebral cranidial width were measured for size-plotting for the post-protaspid cranidia. Three specimens of protaspides probably represent two instars of the early stage and late stage. The protaspides have a slightly effaced surface and a relatively narrow glabellar width, which continued into the smallest post-protaspid cranidia and the smallest meraspid pygidia. There are two different types of protaspides recovered
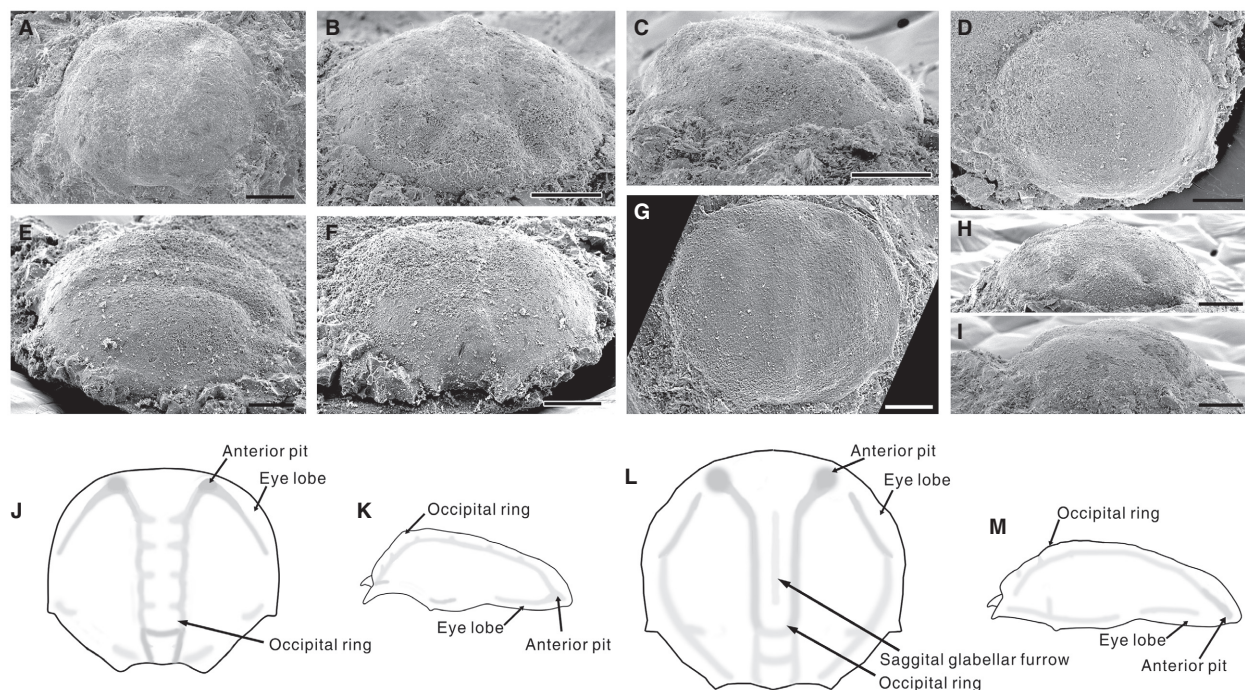
FIG. 2. Protaspides of *Proceratopyge* cf. *P. lata* Whitehouse, 1939 from the Spurs Formation at Eureka Spurs, northern Victoria Land, Antarctica, and their reconstructions. A–C, early stage protaspis, KOPRIF30001: A, dorsal view; B, oblique anterior view; C, lateral view. D–I, late stage protaspides; D–F, KOPRIF30002: D, dorsal view; E, oblique lateral view; F, oblique posterior view; G–I, KOPRIF30003: G, dorsal view; H, anterior view; I, lateral view. J–K, reconstructions of early stage protaspis: J, dorsal view; K, lateral view. L–M, reconstructions of late stage protaspis: L, dorsal view; M, lateral view. All scale bars represent 0.1 mm.

from the studied horizon. The other protaspides than those of *Proceratopyge* cf. *P. lata* are generally similar to those of the basal Furongian aphelaspidid trilobites (see Lee & Chatterton, 2005), which developed into morphologically similar meraspid cranidia, hence being easily discerned from the protaspides of *Proceratopyge* cf. *P. lata*.

Early protaspid stage. The early protaspid stage is represented by a single protaspis (Fig. 2A–C). The protaspid exoskeleton is circular in outline and measure 0.37 mm long and 0.46 mm wide, with the surface weakly effaced. The cranidium is semicircular in outline. The glabella is indicated by shallowly incised axial furrows. The frontal lobe is enlarged. The glabellar width at the basal part is 0.22 of the cranidial width. A pair of anterior pits is relatively large and well-impressed. The eye lobes are located at the antero-lateral sides of exoskeleton. The boundary between the cranium and the trunk is recognizable only by the slightly protruded the occipital ring. The trunk downsloping backward is small and inverted-trapezoidal in outline, taking up about 0.16 of the exoskeletal length. A pair of small and tumid posterior spines is present.

Late protaspid stage. The two late stage protaspides (Fig. 2D–I) are also circular in outline, 0.41–0.45 mm long and 0.51–0.54 mm wide. The exoskeletons are slightly less convex in lateral view than the early stage protaspis. The cranidium is semi-circular in outline. The glabella is weakly recognized by shallow and wide axial furrow. The frontal lobe is still enlarged. The glabellar width at the basal part is 0.17–0.19 of the cranidial width. There seems to be a shallow and faint sagittal glabellar furrow in the middle part of glabellar. The occipital ring is less prominent than the previous stage, so that it is hard to recognize the boundary between the cranidium and the pygidium. The trunk developed narrow lateral borders which are defined by shallow furrows.

Development of post-protaspid cranidium. The traditional division of post-protaspid trilobite ontogeny into meraspid and holaspid phases is impossible for disarticulated cranidia, and thus the post-protaspid cranidial ontogeny of *Proceratopyge* cf. *P. lata* is divided into five developmental phases according to size and morphology (Fig. 3). It is not clear whether the developmental stage 1 cranidia at hand include the earliest meraspid degree cranidia.

The developmental stage 1 cranidia (Fig. 4A–D) are 0.44–0.65 mm long with the maximal cranidial width across the palpebral lobes (palpebral cranidial width hereafter) of 0.59–0.79 mm (n = 4). They are trapezoidal in outline with a moderately-effaced surface. The almost parallel-sided and narrow axial furrows are generally
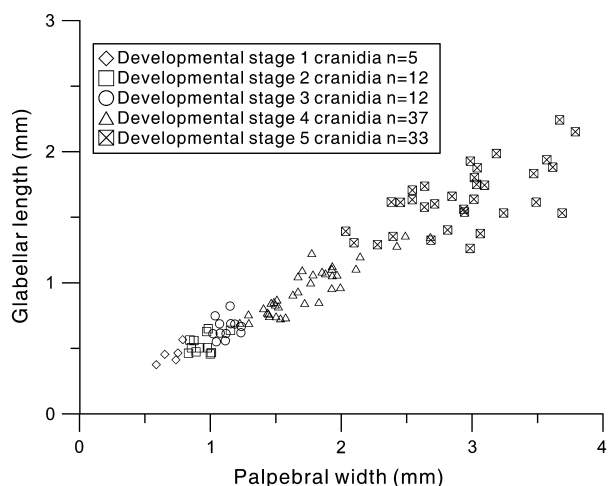
FIG. 3. Scatter plot of glabellar length versus palpebral cranidial width dimensions of cranidia of *Proceratopyge* cf. *P. lata* Whitehouse, 1939 from the Spurs Formation at Eureka Spurs, northern Victoria Land, Antarctica. The 14 largest cranidia and 11 fragmentary post-protaspid cranidia are excluded.

faintly incised, but clearly incised near the occipital ring due to the dorsally inflated posterior part of glabella. The glabellar width is *c.* 0.23–0.25 of the cranidial width. The shallow and narrow occipital furrow is rounded backward. The occipital ring is narrow with the rounded posterior margin. The eye lobes are hardly distinguishable in the lateral margin.

The developmental stage 2 cranidia (Fig. 4E–H) are 0.50–0.74 mm long with the palpebral cranidial width of 0.74–1.15 mm (n = 15). The semi-circular outline and the relatively wider glabellar distinguish this stage cranidia from the developmental stage 1 cranidia. The steeply downsloping frontal part makes this stage cranidia more convex than the cranidia of other developmental stages. The glabellar width is *c.* 0.22–0.25 of the cranidial width. The occipital furrow is moderately incised. The posteriorly-rounded occipital furrow is shallow, but wider than that of the previous developmental stage. The occipital ring became relatively longer (sag.). The pre-glabellar area appeared as a narrow strip. The eye lobes are recognized by a slightly sinuous lateral margin. The anterior branches of the facial suture are rounded and convergent forward. The posterior branches of the facial suture are straight and divergent backward at an angle of *c.* 45–60° relative to the posterior margin. The posterior border is weakly recognized by an extremely faint posterior border furrow.

The developmental stage 3 cranidia (Fig. 4I–L) are 0.75–0.89 mm long with a palpebral cranidial width of 1.02–1.24 mm (n = 13). The clear presence of an anterior cranidial border and the eye lobes distinguish this developmental stage from the cranidia of the previous stage. The glabella is parallel-sided or weakly tapering forward.

The basal glabellar width is *c.* 0.26–0.27 of the cranidial width. The width of the short (sag.) anterior cranidial border is *c.* 0.40–0.49 of the cranidial width. The length of the eye lobes is *c.* 0.40 of the cranidial length. The posterior branches of the facial suture are rounded and divergent backward. The posterior cranidial border widens abaxially, defined by a shallow and moderately wide posterior border furrow.

The developmental stage 4 cranidia (Fig. 4M–P) are 0.93–1.97 mm long with a palpebral cranidial width of 1.23–2.43 mm (n = 40). Compared to the cranidia of the previous stage, the glabella is relatively wider; the glabellar front is more rounded; the occipital furrows are shallower; the anterior border is wider (trans.) and deflected; a narrow pre-glabellar field appears; the pre-glabellar area is 0.15–0.18 of the cranidial length; the rounded eye protruded laterally; the length of the eye lobes is *c.* 0.42 of the cranidial length; the rounded anterior branches of the facial suture are weakly tapering forward to slightly divergent forward; the posterior branches of the facial suture are rounded and strongly divergent backward; the posterior border furrow is moderately incised.

The developmental stage 5 cranidia (Fig. 4Q–W) are longer than 2.08 mm with a palpebral cranidial width of more than 2.12 mm (n = 47). The glabellar slightly tapers forward with moderately rounded glabellar front. The S1, S2, and S3 glabellar furrows are short and shallow, being detached from the axial furrow; in the largest cranidium, S1 furrows are more clearly impressed than the other glabellar furrows (Fig. 4W). The occipital furrow is shallowly incised. The occipital ring is rounded backward. The pre-glabellar area is 0.20–0.24 of the cranidial length. The length of the palpebral lobes is *c.* 0.30–0.34 of the cranidial length. The palpebral ridge is weakly visible. The anterior branches of the facial suture are divergent forward. The posterior branches of the facial suture run almost horizontal. The posterior border slightly widens abaxially, defined by a wide and moderately deep posterior border furrow.

Development of post-protaspid pygidium. Shergold (1982, pl. 16, fig. 1) documented a complete holaspid specimen of *Proceratopyge lata* which has nine thoracic segments. Accordingly, nine meraspid degrees, M0–M8, are expected for *P. lata*. This study deals with disarticulated material of *Proceratopyge* cf. *P. lata*, and thus the number of thoracic segments during meraspid phase is not known. Nevertheless, since the holaspid pygidium of *Proceratopyge* has a macropleural segment as the anteriormost segment, the number of segments in front of the macropleural segment of the disarticulated meraspid pygidia could help define the meraspid degree. The present material enables the pygidial developmental stages to be tracked from the holaspid phase down to the meraspid degree 4. The
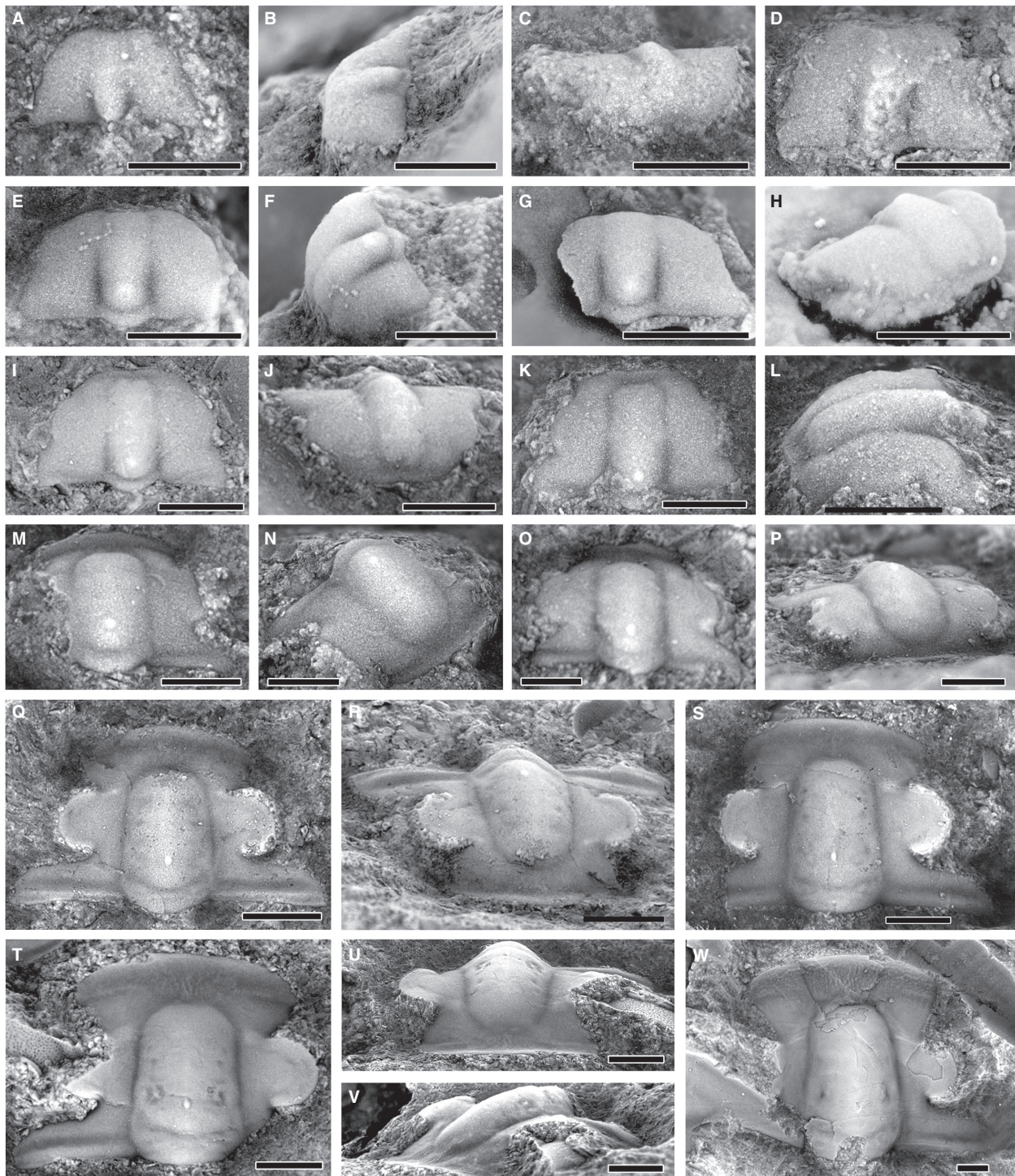
FIG. 4. Post-protaspid cranidia of *Proceratopyge* cf. *P. lata* Whitehouse, 1939 from the Spurs Formation at Eureka Spurs, northern Victoria Land, Antarctica. A–D, developmental stage 1 cranidia; A–C, KOPRIF30004: A, dorsal view; B, oblique lateral view; C, oblique anterolateral view; D, KOPRIF30005. E–H, developmental stage 2 cranidia; E–F, KOPRIF30006: E, dorsal view; F, oblique lateral view; G–H, KOPRIF30007: G, dorsal view; H, oblique anterolateral view. I–L, developmental stage 3 cranidia; I–J, KOPRIF30008: I, dorsal view; J, oblique anterior view; K–L, KOPRIF30009: K, dorsal view; L, oblique lateral view. M–P, developmental stage 4 cranidia; M–N, KOPRIF30010: M, dorsal view; N, oblique anterolateral view; O–P, KOPRIF30011: O, dorsal view; P, slightly oblique anterior view. Q–W, developmental stage 5 cranidia; Q–R, KOPRIF30012: Q, dorsal view; R, oblique anterior view; S, KOPRIF30013; T–V, KOPRIF30014: T, dorsal view; U, anterior view; V, anterolateral view; W, KOPRIF30015. Scale bars represent 0.5 mm (A–P); 1 mm (Q–W).
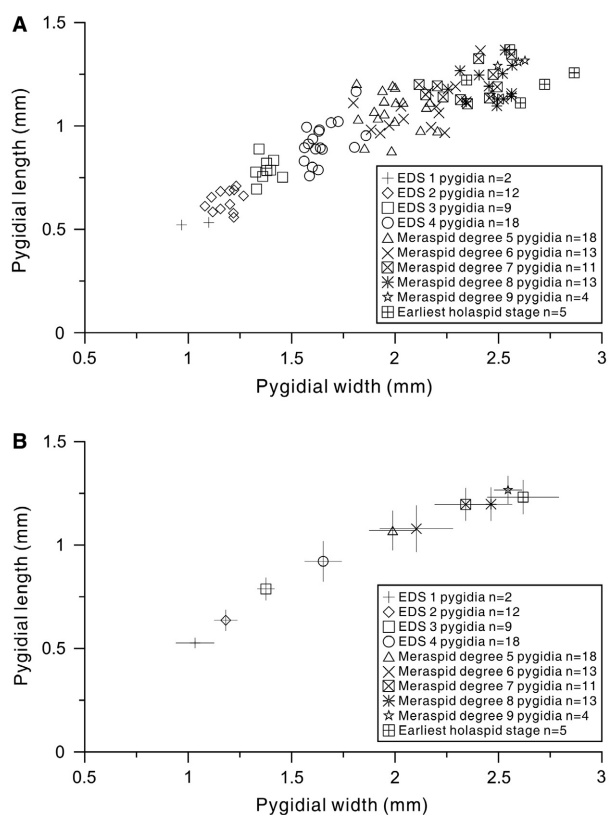
FIG. 5. The relationship between the developmental stages and the size of the post-protaspid pygidia of *Proceratopyge* cf. *P. lata* Whitehouse, 1939 from the Spurs Formation at Eureka Spurs, northern Victoria Land, Antarctica. Large holaspid pygidia are excluded. A, scatter plot of pygidial length versus width. B, the mean for each stage, and the standard deviation bars extending to horizontal and vertical sides of the mean. EDS represents the early developmental stage.

earlier pygidial degrees cannot be confirmed due to the unclear segmental boundaries within the immature pygidia. The earlier stages are divided into the early developmental stages 1–4, according to the size and morphology (Fig. 5). It is noteworthy that there are three times of stagnancy in length increase during development (Fig. 5B). The pygidial length did not increase between meraspid degrees 4 and 5, or between the meraspid degrees 6 and 7. At the meraspid/holaspid transition, there is even a decrease in pygidial length. Such stagnancy in pygidial size during development has been documented several times for trilobites (Simpson *et al.* 2005; Park & Choi 2010b, 2011; Kihm *et al.* 2013), and has been interpreted as being related to the presence of a depletion phase during which the formation of new segments at the rear end of the pygidium ceased and the release of thoracic segments at the anterior of the pygidium continued (see Simpson *et al.* 2005; Hughes *et al.* 2006). However, since the segmental number in the rear end of immature

pygidia of *Proceratopyge* cf. *P. lata* is hard to count, it cannot be determined whether the stagnancy is due to the presence of a depletion phase. One teratological pygidium was discovered, which incompletely released the last thoracic segment (Fig. 6AA). This pygidium failed to release the anteriormost segment into the thorax during the meraspid/holaspid phase transition because the right part of the posterior margin of the 'last thoracic segment' is fused to the anterior margin of the 'holaspid pygidium'. This specimen is also significantly larger than the meraspid degree 8 pygidia, and is not plotted in Figure 5.

The early developmental stage 1 pygidia (Fig. 6A–C) are 0.52–0.53 mm long and 0.97–1.01 mm wide (n = 2), and characterized by their small size and having a rather effaced surface. They are inverted trapezoidal in outline, with the posterior margin indented medially. The axial width is *c.* 0.20 of the pygidial width. The axial furrows are weakly incised and become fainter rearward. The anteriormost inter-ring furrow is weakly incised. The wide pleural furrow of the anteriormost segment is faintly impressed.

The early developmental stage 2 pygidia (Fig. 6D–F) are 0.56–0.71 mm long and 1.08–1.23 mm wide (n = 12). They are similar to the early developmental stage 1 pygidia, but the axis is more raised. The two anteriormost inter-ring furrows are recognizable.

The early developmental stage 3 pygidia (Fig. 6H–I) are 0.69–0.88 mm long and 1.33–1.41 mm wide (n = 9). They are semi-circular in outline, with the posterior margin indented medially. The axial width is 0.21–0.25 of the pygidial width.

The early developmental stage 4 pygidia (Fig. 6J–L) are 0.75–1.17 mm long and 1.56–1.86 mm wide (n = 18), and characterized by having a small pair of pygidial spines at the posterior margin. The axial width is 0.21–0.22 of the pygidial width. The axial furrows are more incised than those of previous stages. The pleural furrows and inter-pleural furrows are weakly impressed in the anterior part, and become fainter rearward. The lateral margin is slightly serrated, due to the tiny pleural spines of the segments destined to be released during subsequent development. There seem to be six segments in front of the macropleural spine-bearing segment. If this is the case, this developmental stage may correspond to meraspid degree 3.

The meraspid degree 4 pygidia (Fig. 6M–O) are 0.98–1.21 mm long and 1.81–2.21 mm wide (n = 18), and can be easily distinguished from the previous stage by having five pairs of moderately incised pleural furrows, which indicate five segments, in front of the macropleural spine-bearing segment. The axial furrows are well incised, but the rear end of the axis is not clearly discernible. The inter-ring furrows are weakly impressed in front of the macropleural spine-bearing segment. The pleural furrows
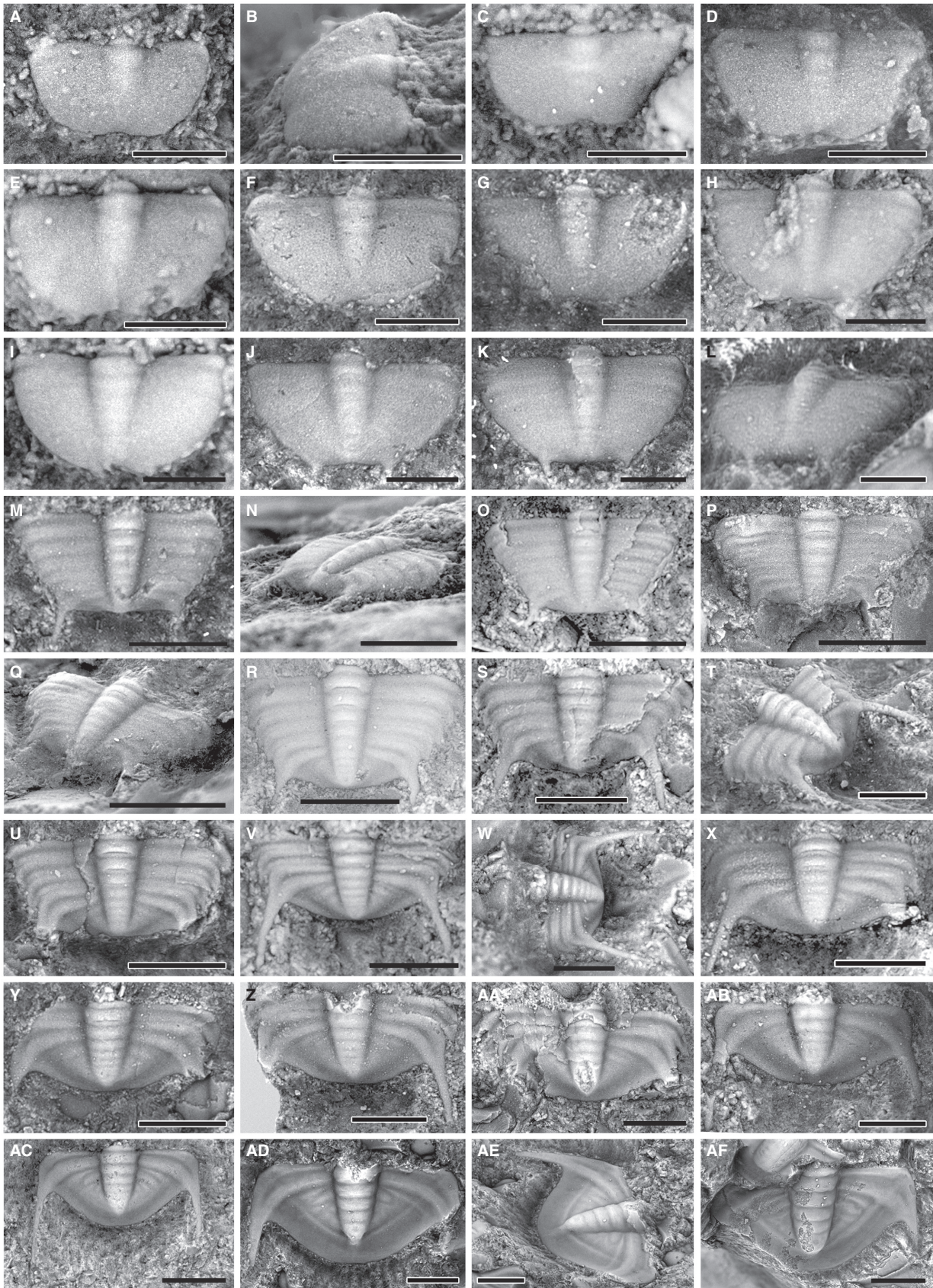
reach the lateral margin. The macropleural spines are thin and longer than 0.41 of the pygidial length.

The meraspid degree 5 pygidia (Fig. 6P–R) are 0.97–1.36 mm long and 1.80–2.41 mm wide (n = 13), and have four segments in front of the macropleural spine-bearing segment. The rear end of the axis is rounded and slightly touches the posterior margin in dorsal view. The inter-ring furrows are moderately impressed at the anterior part, but become fainter rearward. The pleural furrows in front of the macropleural spine-bearing segment do not reach the lateral margin, due to the enhancement of the pleural spines. The posterior band of the macropleural spine-bearing segment is longer (sag.) than those of the other segments. The posterior margin is smooth, and the posterior border is moderately wide near the macropleural spine, but gets narrow rearward. The posterior border furrow is shallow and wide.

The meraspid degree 6 pygidia (Fig. 6S–U) are 1.14–1.35 mm long and 2.12–2.47 mm wide (n = 11), and have three segments in front of the macropleural spine-bearing segment. The axial width is *c*. 0.21–0.22 of the pygidial width. The rear end of the axis does not reach the posterior margin in dorsal view, due to widening of the posterior border. The pleural furrows are faintly impressed in the pleural field behind the macropleural spine-bearing segment. The macropleural spines are thin and longer than 0.63 of the pygidial length. The macropleural spines slightly diverge rearward.

The meraspid degree 7 pygidia (Fig. 6V–X) are 1.11–1.37 mm long and 2.26–2.57 mm wide (n = 13), and have two segments in front of the macropleural spine-bearing segment. The inter-ring furrows are more incised than those of the previous stages. The posterior band is longer (sag.) than the anterior band in the macropleural spine-bearing segment. The pleural and interpleural furrows behind the macropleural spine-bearing segment are more impressed than in the previous stages. The macropleural spines are longer than 0.74 of the pygidial length.

Meraspid degree 8 (Fig. 6Y–Z) is represented by five fragmentary specimens, 1.15–1.47 mm long and 2.46–3.01 mm wide (n = 5). The meraspid degree 8 pygidia are similar to the meraspid degree 7 pygidia, but differ in having one segment in front of the macropleural spine-bearing segment.

The holaspid pygidia (Fig. 6AB–AF) are longer than 1.12 mm and wider than 2.35 mm (n = 82). The outline is semi-circular to sub-triangular, *c*. 1.90 wider than long. Four or five axial-rings can be defined by inter-ring furrows. The axial furrows are deeply incised, but become shallower rearward. The macropleural spines are almost parallel-sided, longer than 1.16 of the pygidial length. The posterior border is 0.10 times the pygidial length in smaller holaspides, but becomes 0.21 of the pygidial length with development. In larger specimens, a paradoublural line appears near the boundary between the pleural field and the posterior border.

REMARKS ON PRE-OCCIPITAL TUBERCLE

Emending the concept of the Order Asaphida, Park *et al.* (2014) concluded that the Order Asaphida contains five families (Ceratopygidae, Asaphidae, Taihungshaniidae, Nileidae and Cyclopygidae) which can be grouped by the presence of petaloid facet and pre-occipital tubercle. Although the pre-occipital tubercle is seen in trilobite groups other than Asaphida, such as the Trinucleaoidea (see Chatterton *et al.* 1994), the presence of a pre-occipital tubercle is still a synapomorphy that unites the Asaphida. The position of the pre-occipital tubercle in ceratopygids and asaphids is relatively close to the occipital ring (see Fortey & Chatterton 1988, text-fig. 12b, c), whereas that of the more derived group, the Cyclopygoidea, is almost in the centre of glabella. For instance, documenting the ontogeny of the taihungshaniid trilobite *Taihungshania miqueli* (Bergeron, 1893), Berard *et al.*

FIG. 6. Post-protaspid pygidia of *Proceratopyge* cf. *P. lata* Whitehouse, 1939 from the Spurs Formation at Eureka Spurs, northern Victoria Land, Antarctica. A–C, early developmental stage 1 pygidia; A–B, KOPRIF30016: A, dorsal view; B, oblique lateral view; C, KOPRIF30017. D–F, early developmental stage 2 pygidia; D, KOPRIF30018; E, KOPRIF30019; F, KOPRIF30020. G–I, early developmental stage 3 pygidia; G, KOPRIF30021; H, KOPRIF30022; I, KOPRIF30023. J–L, early developmental stage 4 pygidia; J, KOPRIF30024; K–L, KOPRIF30025: K, dorsal view; L, oblique posterolateral view. M–O, meraspid degree 4 pygidia; M–N, KOPRIF30026: M, dorsal view; N, oblique posterolateral view; O, KOPRIF30027. P–R, meraspid degree 5 pygidia; P–Q, KOPRIF30028: P, dorsal view; Q, oblique posterolateral view; R, KOPRIF30029. S–U, meraspid degree 6 pygidia; S–T, KOPRIF30030: S, dorsal view; T, oblique anterolateral view; U, KOPRIF30031. V–X, meraspid degree 7 pygidium; V–W, KOPRF30032: V, dorsal view and W, oblique lateral view; X, KOPRIF30033. Y–Z, meraspid degree 8 pygidia; X, KOPRIF30034; Y, KORPIF30035. AA, teratological pygidium which failed to release the anteriormost segment into thorax during the meraspid/holaspid phase transition, due to the fusion of the right part of the posterior margin of the 'last thoracic segment' to the anterior margin of the 'holaspid pygidium', KOPRIF30036. AB–AF, holaspid pygidia; AB, earliest holaspid stage pygidium, KOPRIF30037; AC, KOPRIF30038; AD–AE, KOPRIF30039: AD, dorsal view; AE, oblique lateral view; AF, KOPRIF30040. Scale bars represent 0.5 mm (A–L); 1 mm (M–AB); 2 mm (AC–AF).

(1999) described the transitionally-appearing tubercular structure in the centre of the glabella as the 'median tubercle' and 'median ridge'. A similar positional variation of the dorsal organ has been observed amongst extant crustaceans. Lerosey-Aubril & Meyer (2013) noted that the sensory dorsal organ (SDO) of various crustaceans is innervated from the tritocerebrum, indicating that SDO belongs to the third cephalic segment. However, there are more posteriorly situated sensory dorsal organs as well, called 'posterior SDO' in many crustacean groups (Lerosey-Aubril & Meyer 2013). It is interesting to note that there is an ontogenetic variation in the position of the pre-occipital tubercle of *Proceratopyge* cf. *P. lata* in this study. The earliest immature post-protaspid cranidium had a highly-elevated area close to the occipital furrow, as if it was part of the L1 glabellar lobe (Fig. 4A–C). This elevated area moved forward, shrinking into a tubercle during subsequent development (Fig. 4M, O). The final position of the pre-occipital tubercle is between the S1 glabellar furrows, although the furrows are not clearly recognizable (Fig. 4Q–W).

DISCUSSION

Relationships within the Order Asaphida

Protaspides of the Cambrian asaphide trilobite *Proceratopyge* cf. *P. lata*, had a rather flat morphology, indicating that having a globular 'asaphoid protaspis' (*sensu* Fortey & Chatterton 1988) is probably not a synapomorphy for the Order Asaphida. It is important that the phylogenetic relationships within the Asaphida should be elucidated first. Two different topologies for the relationship between the Asaphoidea (Ceratopygidae and Asaphidae) and Cyclopygoidea (Taihungshaniidae, Nileidae and Cyclopygidae) were suggested by Fortey & Chatterton (1988): (1) Asaphoidea appears as a sister group to Cyclopygoidea in the tree in which particularly important characters are weighted (Fortey & Chatterton 1988, text-fig. 1); and (2) Ceratopygidae forms a sister group to Asaphidae + Cyclopygoidea in the two parsimonious trees (Fortey & Chatterton 1988, text-figs 2 and 3). Since the Asaphidae and the Cyclopygoidea are already known to have possessed commutavi protaspis (Evitt 1961; Chatterton 1980; Tripp & Evitt 1986; Fortey & Chatterton 1988; Speyer & Chatterton 1989; Berard *et al.* 1999), the lack of commutavi protaspis in the Ceratopygidae leads to three different hypotheses on the evolution of commutavi protaspis, depending on the phylogenetic relationships within the Order Asaphida. If Asaphoidea forms the sister group to Cyclopygoidea as suggested in text-figure 1 of Fortey & Chatterton (1988), the commutavi protaspides could have evolved twice independently; once in the asaphid lineage,

and again in the cyclopygoidean lineage (Fig. 7A). Alternatively, the commutavi protaspis could be a synapomorphy for the whole group Asaphida, with the loss of the character within the Ceratopygidae (Fig. 7B). However, given the invariable Ordovician occurrences of cyclopygoideans and the fact that no asaphids occurred earlier than the middle Furongian, the non-commutavi protaspis of the early Furongian *Proceratopyge* does not support this possibility. If Ceratopygidae forms the sister group to Asaphidae + Cyclopygoidea as in the parsimonious cladograms of Fortey & Chatterton (1988, text-figs 2–3), the evolution of a commutavi protaspis would be a single event forming a syanpomorphy for Asaphidae + Cyclopygoidea (Fig. 7C). In this case, the Superfamily Asaphoidea is rendered paraphyletic, as it then gives rise to the Cyclopygoidea.

In order to test these hypotheses, a cladistic analysis for the Order Asaphida (*sensu* Park *et al.* 2014) was performed based on the new information on the protaspid morphology. The phylogenetic relationships were analysed using TNT version 1.1 (Goloboff *et al.* 2008). A total of 42 characters and and the outgroup 'Ptychopariina' were employed from Fortey & Chatterton (1988). Character coding for Cyclopygidae, Nileidae, Taihungshaniidae, Ceratopygidae and Asaphida was taken from Fortey & Chatterton (1988), except for their character 12 (protaspis type: 0, ptychoparioid type; 1, asaphoid type); this character was originally coded as '?' for both Taihungshaniidae and Ceratopygidae. According to Berard *et al.* (1999) and this study, character 12 can be coded for Taihungshaniidae and Ceratopygidae as '1' and '0', respectively. Random addition sequences followed by tree bisection-reconnection (TBR) branch swapping were employed. The analysis yielded a single most parsimonious tree of 50-steps tree length, with a consistency index of 0.900, and a retention index of 0.839. The relationship within the Asaphida (*sensu* Park *et al.* 2014) in the one single most parsimonious tree we obtained complies with the two parsimonious trees of Fortey & Chatterton (1988, text-figs 1–2), in which Ceratopygidae forms a sister group to Asaphidae + Cyclopygoidea (Fig. 7C). Therefore, based on the new phylogenetic analysis, it can be concluded that having a globular 'asaphoid protaspis (*sensu* Fortey & Chatterton 1988)' is not a synapomorphy for the Order Asaphida, but a synapomorphy for Asaphidae + Cyclopygoidea (Fig. 7C).

Evolution of the metamorphosis-undergoing protaspis

We have shown that commutavi protaspides evolved three times independently, within the lineages of the Remopleuridioidea, the Trinucleoidea and the Asaphida. Interestingly, so far, it appears that the Cambrian representatives of these lineages underwent an ontogeny without any significant metamorphosis (Park & Choi 2011;
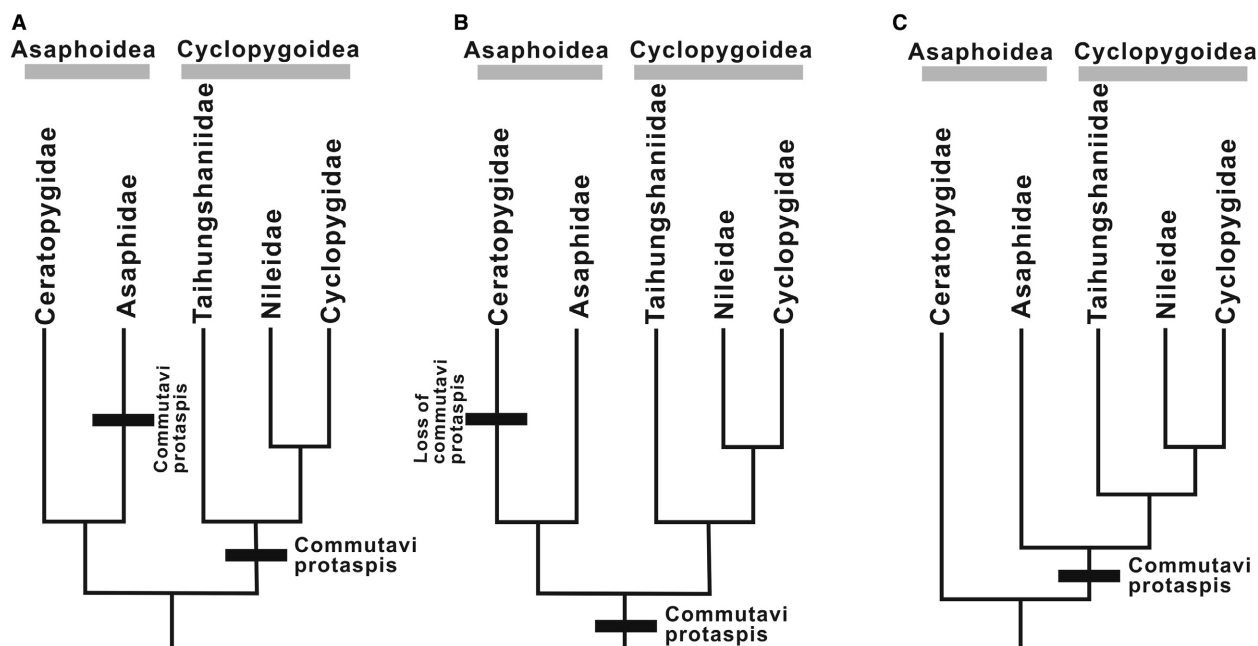
FIG. 7. Cladograms showing the phylogenetic relationships within the Order Asaphida. A–B, relationships according to text-figure 1 of Fortey & Chatterton (1988) in which particularly important characters were weighted: A, the case in which commutavi protaspides evolved twice independently; B, the case in which the presence of commutavi protaspis was a synapomorphy to form the Asaphida, with the loss of the character in the Ceratopygidae. C, relationships according to text-figures 2–3 of Fortey & Chatterton (1988), which is in accordance with the new cladistic analysis executed in this study; the evolution of commutavi protaspis is a synapomorphy for Asaphidae + Cyclopygoidea.

Park *et al.* 2014; this study), whereas by the time of the Early Ordovician, commutavi protaspis which metamorphosed into a meraspid phase with a flat morphology already existed in each lineage; Demeter (1973) documented asaphid commutavi protaspides from the Lower Ordovician, and Fortey & Chatterton (1988) illustrated those of the Lower Ordovician trinucleoidean *Ampyxoides inermis* Fortey, 1975, while those of the Early Ordovician remopleuridioideans were described by Ross (1951) and Park & Kihm (2015). Although commutavi protaspis has not been documented in the Cambrian (Fortey 2001), the possibility cannot be ruled out that commutavi protaspides of these lineages originated sometime during the Furongian; that is to say that asaphid trilobites were already present by the middle Furongian. It is remarkable to note that there were independent evolutions of commutavi protaspides during the Furongian and Early Ordovician. This may be ascribed to the increasing ecological pressure near the dawn of the Great Ordovician Biodiversification Event (GOBE; see Harper 2006; Servais *et al.* 2010; Harper *et al.* 2015). Traditionally, bulbous commutavi protaspides (non-adult like) have been regarded as having a planktonic mode of life, whereas flat (adult like) protaspides had a benthic mode of life (Fortey & Chatterton 1988; Speyer & Chatterton 1989; Chatterton & Speyer 1997). This dichotomous division of protaspid life mode should be scrutinized in a modern

light, because the small flat protaspides could also have had a facultative planktonic life mode. Nevertheless, as Speyer & Chatterton (1989) noticed, having a non-adult like, bulbous morphology of commutavi protaspides would have been more suitable for planktonic life mode than having an adult-like, flat morphology. Having a bulbous protaspid morphology, therefore, may have been advantageous in dispersal and/or escaping from benthic predators. At the time around the Cambrian–Ordovician transition, an increase of predation may have triggered the evolution of planktotrophic larvae as an escape strategy from the benthic predators (Peterson 2005; Nutzel *et al.* 2006; Nützel 2014). As a result, metamorphosis-entailing planktonic larvae evolved in different metazoan lineages, with multiple convergent evolution of indirect development in lineages at the Cambrian–Ordovician transition (Peterson 2005; Nutzel *et al.* 2006; Nützel 2014). In this regard, the convergent evolution of the metamorphosis-entailing indirect development in the three trilobite lineages during the Furongian and Early Ordovician may also have been a result of adaptation to the early phase of the GOBE. However, according to the trends of species richness of trilobite clades in the Ordovician by Adrain (2013), the clades with bulbous commutavi protaspides did not necessarily diversify throughout the Ordovician. Instead, other clades such as the Lichida and the Phacopida, which had non-adult like

flat protaspides, tended to diversify during the Middle and Upper Ordovician (Adrain 2013). This indicates that having a commutavi protaspis may have been the solution of only a few trilobite lineages in the early phase of the GOBE.

CONCLUSIONS

The ontogeny of the Cambrian ceratopygid, *Proceratopyge* cf. *P. lata* Whitehouse, 1939 from northern Victoria Land, Antarctica reveals that the protaspid morphology of this Cambrian asaphide trilobite is rather flat, and developed directly into a similar-looking meraspid morphology. The phylogenetic relationships within the Order Asaphida revealed by a cladistic analysis, demonstrate that the presence of a bulbous commutavi protaspis is not a synapomorphy for the Order Asaphida, but a synapomorphy for Asaphidae + Cyclopygoidea. To date, there are three independent appearances of commutavi protaspides: within the lineages of the Remopleuridioidea, the Trinucleoidea and the Asaphida (*sensu* Park *et al*. 2014). It is interesting to note that the Cambrian representatives of the three lineages had a directly developing protaspis of a flat morphology, while those of the Early Ordovician representatives had a bulbous, metamorphosis-undergoing commutavi protaspis. It has been suggested that the bulbous morphology of commutavi protaspides is an adaptation to planktonic life mode, thus the convergent evolution of commutavi protaspides during the Furongian and Early Ordovician in three different trilobite lineages might have arisen as an escape strategy from benthic predators and/or for a better dispersal. Many metazoan lineages evolved metamorphosis-entailing planktonic larvae at this period, due to the escalating ecological pressure of the Great Ordovician Biodiversification Event, and the originations of commutavi protaspides in three different trilobite lineages might have been a result of adaptation to the early phase of the GOBE.

DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.mm4cc

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