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ONTOGENY AND VENTRAL MEDIAN SUTURE OF THE PTYCHASPIDID TRILOBITE *ASIOPTYCHASPIS SUBGLOBOSA* (SUN, 1924) FROM THE FURONGIAN (UPPER CAMBRIAN) HWAJEOL FORMATION, KOREA

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ABSTRACT—The order Asaphida has been characterized by the possession of a globular protaspis and a ventral median suture. The superfamily Dikelocephaloidea was included in the Asaphida, although there has been no reliable ontogenetic information for this superfamily, and thus whether dikelocephaloids had a protaspis of globular shape has remained unclear. The ontogenetic study of the dikelocephaloid trilobite, *Asioptychaspis subglobosa*, from Korea reveals that the protaspis of *A. subglobosa* is not of globular morphology but of general benthic adult-like morphology, heralding that the Dikelocephaloidea may not be closely related to other trilobite groups within the Order Asaphida. This protaspid morphology is clearly distinguished from the highly globular protaspis of the Remopleuridioidea, which has been considered the sister group to the Dikelocephaloidea. In addition, the ontogenetic development of the free cheeks shows that *A. subglobosa* possessed anteriorly yoked free cheeks during the early phase of development but formed a ventral median suture by splitting the yoked cheeks in the later phase of ontogeny. This contrasts with the previously suggested mode of ventral median suture formation of the Order Asaphida. This alternative mode of ventral median suture formation of *A. subglobosa*, along with non-asaphoid protaspid morphology, warrants removal of the Dikelocephaloidea from the current Order Asaphida. This study further demonstrates that the ventral median suture did not evolve only once in the evolutionary history of trilobites. With the addition of the mode here documented for *Asioptychaspis*, the ventral median suture is now known to have developed independently and in a different fashion at least three times in the history of Cambrian trilobites.

INTRODUCTION

THE ORDER Asaphida Salter, 1864 was emended by Fortey and Chatterton (1988) to include trilobite families that possess a ventral median suture and an inflated and effaced protaspis, which they termed the "asaphoid protaspis." Fortey and Chatterton (1988) placed superfamilies Anomocaroidea, Trinucleoidea, Dikelocephaloidea, Remopleuridioidea, Cyclopygoidea, and Asaphoidea within the Asaphida. The Dikelocephaloidea had been shown to possess a ventral median suture (Fortey and Chatterton, 1988), but the ontogeny of this group was not well known. Hu (1971) referred some protaspides to the ptychaspidid trilobite *Ptychaspis bullasus* Lochman and Hu, 1959. However, this assignment was questioned and disregarded by Fortey and Chatterton (1988). As a result, whether the protaspid morphology of the Dikelocephaloidea is globular or not remained uncertain. Nevertheless, Fortey and Chatterton (1988, text-figs. 1, 2, and 3) predicted from their cladistic analysis that the Dikelocephaloidea possessed an asaphoid protaspis, owing to its position as the sister-group to the Remopleuridioidea, which was known to have a highly globular asaphoid protaspis. Other features interpreted as synapomorphies uniting these two superfamilies include a posterior glabellar bulge, inflated palpebral lobes, and the absence of eye ridges (Fortey and Chatterton, 1988, text-figs. 1, 2, and 3, and table 2).

Chatterton et al. (1994, fig. 14) provided a hypothesis on the evolutionary origin of the ventral median suture through reduction of a rostral plate to form a small, inverted triangular plate (rostellum), and eventual loss of that structure. Chatterton and Ludvigsen (1998) documented that in *Pterocephalia norfordi* Chatterton and Ludvigsen, 1998 a rostellum disappears during ontogeny to form a ventral median suture and argued that this ontogenetic process parallels the phylogenetic loss of the rostellum within the basal Asaphida. Fortey and Chatterton (1988) also noted that the ventral median suture can be lost secondarily to form fused free cheeks within different lineages, citing the fused free cheeks of the Nileidae and the Superfamily Trinucleiodea as examples of this derived condition.

The concept of the Order Asaphida (Fortey and Chatterton, 1988; Fortey, 1990) and the mode of evolution of ventral median suture (Chatterton et al., 1994) have been accepted and employed widely in subsequent studies. However, doubts on the monophyletic origin of the ventral median suture have been expressed in recent studies (Whittington, 2003, 2007). Park and Choi (2009) reported that the tsinaniid trilobite, *Tsinania canens* (Walcott, 1905), developed a ventral median suture by the reduction of a triangular rostral plate behind the connective suture during ontogeny, demonstrating that a ventral median suture might independently have evolved within the Order Corynexochida. The monophyly of the Order Asaphida was also challenged by Adrain et al. (2009) who questioned the inclusion of the superfamily Remopleuridioidea into the Order Asaphida.

This study explores the ontogeny of a dikelocephaloid trilobite, *Asioptychaspis subglobosa* (Sun, 1924), from the middle Furongian Hwajeol Formation, Taebaeksan Basin, Korea. The protaspid morphology and the development of the cephalic ventral structure of *A. subglobosa* raise considerable doubt regarding placement of the superfamily Dikelocephaloidea within the Order Asaphida.

FOSSIL LOCALITY AND MATERIAL

The Cambro-Ordovician sedimentary rocks in Korea, Joseon Supergroup, are exposed in the Taebaeksan Basin, central-eastern part of the Korean peninsula (Fig. 1). The Joseon Supergroup was divided into the Taebaek, Yeongwol, Yongtan, Pyeongchang, and Mungyeong groups (Choi, 1998). Of these, the Taebaek Group consists mainly of carbonates with subordinate siliciclastic rocks, representing a shallow marine continental shelf environment (Choi et al., 2004). The

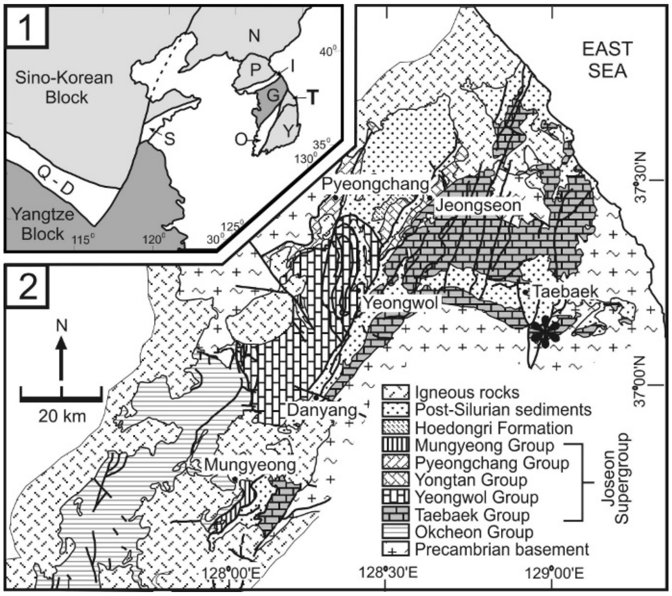

FIGURE *1*—Location maps. *1*, tectonic map of Korean peninsula and surrounding area which shows the location of the Taebaeksan Basin. Q–D = Qinling–Dabie belt, S = Sulu Belt, N = Nangnim Massif, P = Pyeongnam Basin, I = Imjingang Belt, G = Gyeonggi Massif, O = Okcheon Belt, T = Taebaeksan Basin, Y = Yeongnam Massif; *2*, Geological map of the Taebaeksan Basin which shows the distribution of the lower Palaeozoic Joseon Supergroup in the Taebaeksan Basin. The asterisk indicates the location of the Sagundari section from which the material for this study was collected.

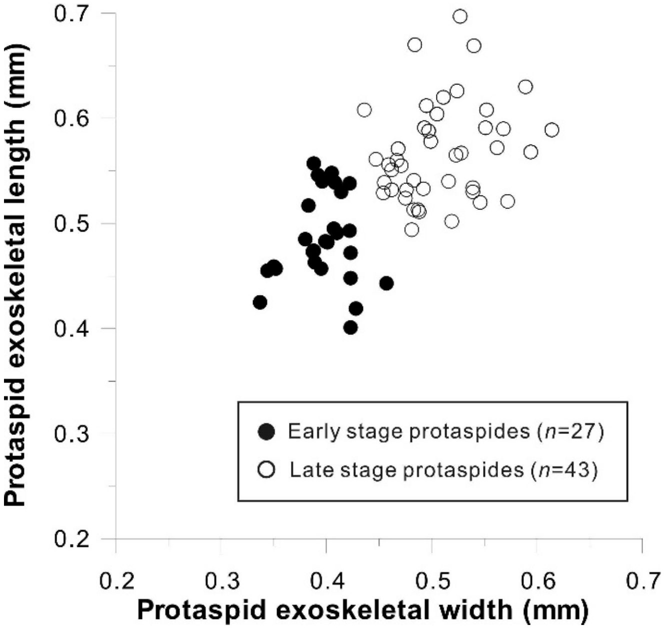

FIGURE *2*—Scatter plots of length versus width for protaspid exoskeletons of *Asioptychaspis subglobosa* (Sun, 1924).

Taebaek Group comprises in ascending order the Jangsan/Myeonsan, Myobong, Daegi, Sesong, Hwajeol, Dongjeom, Dumugol, Makgol, Jigunsan, and Duwibong formations (Choi et al., 2004). The Cambrian-Ordovician boundary lies within the lowermost part of the Dongjeom Formation.

All the material for this research was recovered from the lowermost part of the Hwajeol Formation at the Sagundari section (129°01′03.4″E, 37°04′57.0″N) in the Taebaeksan Basin (Fig. 1). The Hwajeol Formation is an alternating succession of limestone and shale beds, with numerous intercalated limestone conglomerate layers (Choi et al., 2004). It is interpreted to represent inner to outer ramp environments (Kwon et al., 2006). The formation contains three trilobite faunas: an *Asioptychaspis* Zone fauna, a *Quadraticephalus* Zone fauna, and a saukiid-dominated fauna, in ascending order (Sohn and Choi, 2005). The fauna that characterizes the *Asioptychaspis* Zone occurs within the lowermost 3 m interval of limestone-shale couplet facies. Sohn and Choi (2007) recently reported the occurrence of *Pseudagnostus planulatus* (Raymond, 1924), *Asioptychaspis subglobosa* (Sun, 1924), *Haniwa sosanensis* Kobayashi, 1933, and *Tsinania canens* (Walcott, 1905) from the *Asioptychaspis* Zone at the Sagundari section and correlated this biozone to the *Ptychaspis-Tsinania* Zone of North China, which is middle Furongian in age (see Sohn and Choi, 2007).

Samples of the silicified fossil-containing limestone-shale couplet were collected from the horizon 2.5 m above the base of the formation, and were etched out with hydrochloric acid. Invariably, disarticulated silicified sclerites of several trilobite species were recovered from the residues, including *Pseudagnostus planulatus*, *Asioptychaspis subglobosa*, *Tsinania canens*, *Haniwa* sp., *Koldinioidia* sp., and a dikelocephaloid gen. et sp. indeterminate. The specimens of *Tsinania canens* were described in detail by Park and Choi (2009). Seventy protaspides, 447 cranidia, 129 free cheeks, 51 thoracic segments, and more than two hundred post-protaspid pygidia were obtained for the ontogenetic study of *Asioptychaspis subglobosa*. All the specimens illustrated in this study are deposited in the paleontological collections of Seoul National University with registered SNUP numbers.

ONTOGENY

Morphological terms employed in this study generally 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). Length and width measurements were taken for all protaspides and post-protaspid cranidia. Since a significant number of the specimens have experienced tectonic distortion, it is hard to recognize any biologically significant clustering of the data within bivariate plots. The protaspides were divided into two stages (Fig. 2) according to size and morphology, although it is not clear whether the two stages represent biologically meaningful instar-corresponding clusters within the protaspid period. Likewise, we do not attempt to divide the post-protaspid cranidial development, as the morphological development might have been continuous or biologically significant instar clustering was obscured due to tectonic distortion. As for the post-protaspid pygidia, division of meraspid and holaspid periods has been made with reference to the relative position of a raised rim-like ridge (see below) during development.

Protaspid period.—The early stage protaspides (Fig. 3.1–3.12) are oval in outline and measure 0.40–0.56 mm long and 0.34–0.46 mm wide. The exoskeleton is moderately convex, probably due to the downsloping trunk. The axis tapers slightly forward and is indicated by faint axial furrows. The occipital furrow is weakly incised. A pair of short genal spines projects rearward. The trunk can be distinguished from the cranidium by the posterior cranidial margin marked by change in slope behind the occipital spine. The trunk takes up about one-fourth of the exoskeletal length in dorsal view. The trunk slopes down strongly posteriorly, with a prominently elevated

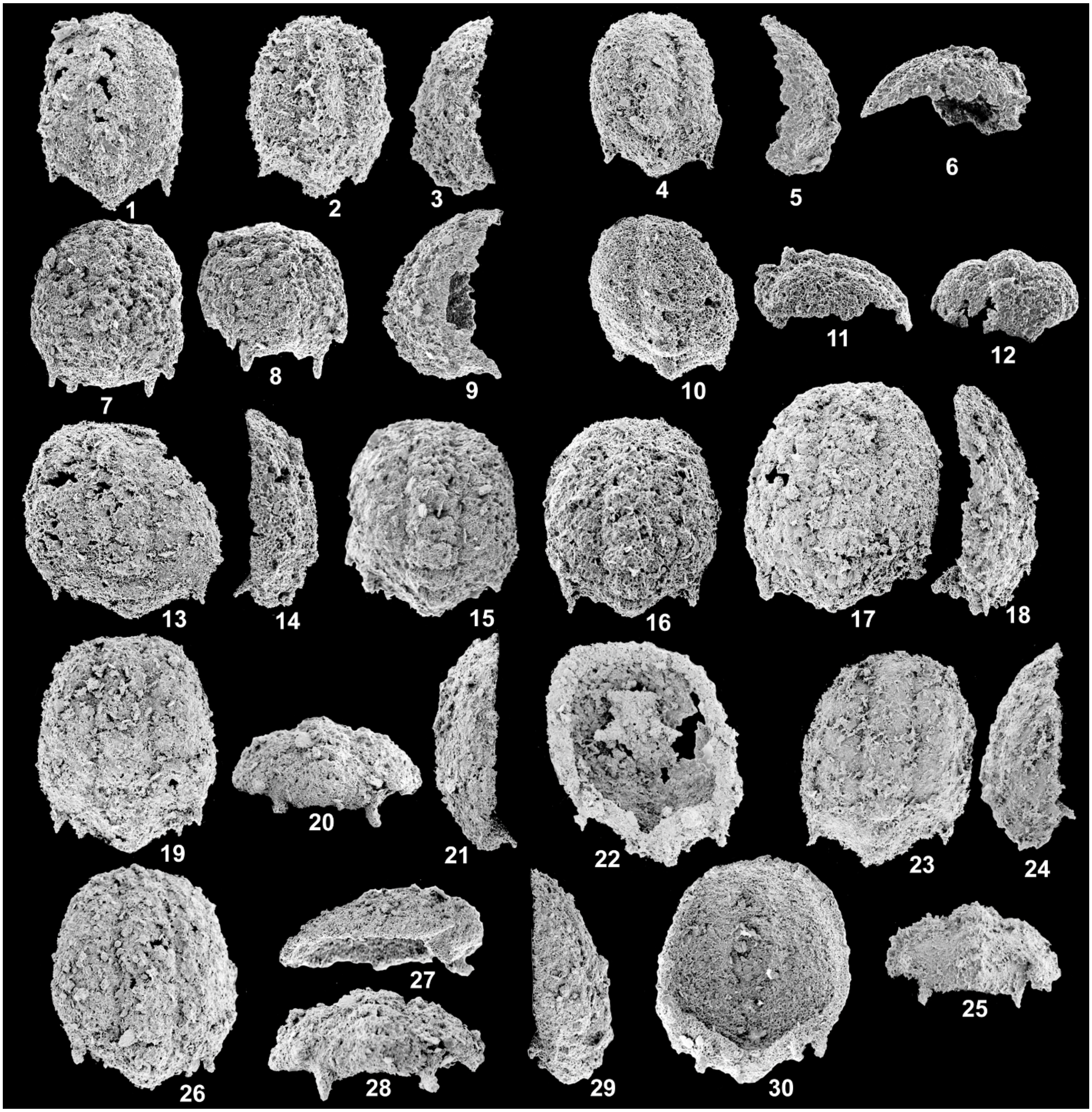

FIGURE 3—Protaspides of *Asioptychaspis subglobosa* (Sun, 1924). *1–12*, early stage protaspides. *1*, SNUP4849, dorsal view; *2–3*, SNUP4850, dorsal and lateral views; *4–6*, SNUP4851, dorsal, lateral, and anterolateral views; *7–9*, SNUP4852, dorsal, oblique posterior, and lateral views; *10–12*, SNUP4853, dorsal, lateral, and posterior views; *13–30*, late stage protaspides; *13–14*, SNUP4854, dorsal and lateral view; *15*, SNUP4855, dorsal view; *16*, SNUP4856, dorsal view; *17–18*, SNUP4857, dorsal and lateral views. *19–21*, SNUP4858, dorsal, posterior, and lateral views. *22*, SNUP4859, ventral view; *23–25*, SNUP4860, dorsal, lateral, and posterior views; *26–30*, SNUP4861, dorsal, lateral, ventro-lateral, posterior, and ventral views. All figures, ×60.

central part of the axis, which makes the lateral view of the protaspides slightly incurved downward. The postero-median trunk margin is moderately arched upwards in posterior view. Most specimens lack pygidial spines, but some (Fig. 3.7–9) have a pair of short pygidial spines directed obliquely downward.

The late stage protaspides (Fig. 3.13–3.30) are less convex than those of the early stages. The occipital furrow is clearly incised and the posterior cranidial margin is marked by a change in slope. The posterior cranidial margin is directed backward abaxially. The trunk occupies about 0.3 of the exoskeletal length in dorsal view. The trunk has at least three axial rings, although poor preservation hampers a precise count. The postero-median trunk margin is slightly arched upwards in posterior view. A pair of short pygidial spines project obliquely downward, but they are hardly recognizable in dorsal view. One specimen (Fig. 3.22) retains the free cheek and the hypostome: the free cheek is fused, and the slightly

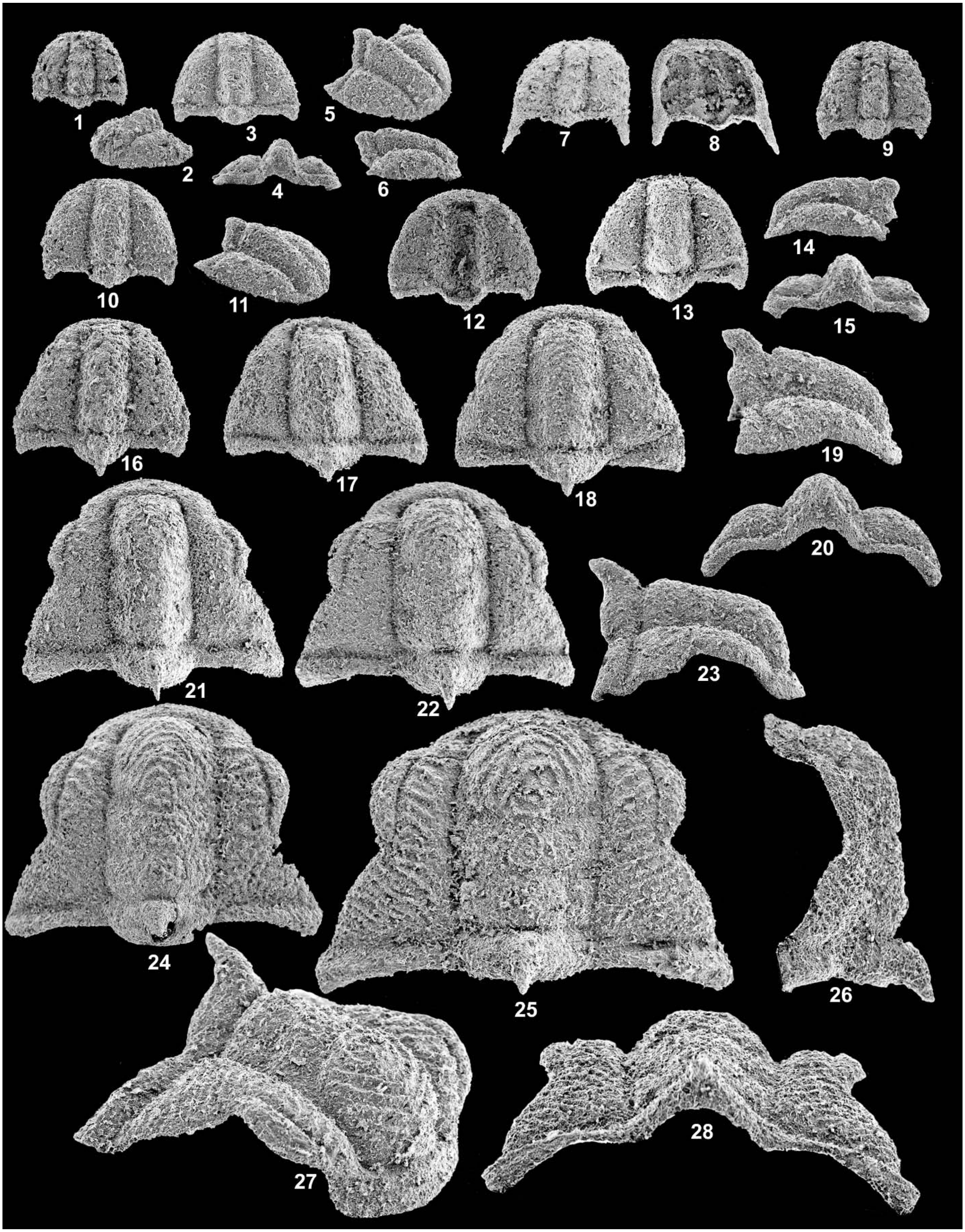

FIGURE 4—Post-protaspid cranidia of *Asioptychaspis subglobosa* (Sun, 1924). *1–2*, SNUP4862, dorsal and oblique anterolateral views; *3–6*, SNUP4863, dorsal, posterior, oblique anterolateral, and lateral views; *7–8*, yoked free cheek-retaining cranidium, SNUP4864, dorsal and ventral views;

displaced hypostome possesses a pair of prominent lateral projections.

Post-protaspid cranidial development.—The cranidia shorter than 0.6 mm (Fig. 4.1–4.12) are semi-circular in outline, with sub-parallel to slightly tapering-forward glabella, marked by moderately to deeply incised axial furrows. The frontal area slopes down strongly anteriorly. The occipital ring is strongly convex, long medially, and tapered abaxially. The posterior cranidial border furrows are transverse and clearly incised, and the posterior cranidial border abruptly widens abaxially forming a posterolateral projection which makes up the inner part of the base of genal spine in a specimen which retains the free cheeks (Fig. 4.7–4.8). The anterior part of the lateral margin is weakly sinuous in lateral view, probably reflecting the position of the eye. The preglabellar furrow is weakly impressed, and a short preglabellar field is recognized even at this early phase of cranidial development.

As the cranidia develop, the outline becomes sub-trapezoidal: the preglabellar furrow is more clearly impressed, defining a very short preglabellar field (Fig. 4.13). The lateral margin is sinuous in lateral view (Fig. 4.14). The frontal lobe of the glabella slopes down more strongly forwards as a result of inflation of the frontal lobe, while the downslope of the preglabellar field is slightly less (Fig. 4.14). In larger specimens (Fig. 4.16, 4.17), the palpebral lobes are visible in dorsal view, and the length of the palpebral lobes is 0.27–0.29 of the cranidial length. The posterior cranidial border gently widens abaxially. The occipital spine becomes larger and pointed. With growth, the preglabellar field becomes longer; S1 and S2 glabellar furrows are weakly impressed at the flanks of the glabella; fossulae-like impressions become more prominent at the antero-lateral corners of the glabella; the frontal lobe becomes more convex; and palpebral furrows become clearly incised (Fig. 4.18–4.23). The palpebral lobes are elevated (Fig. 4.23). A fingerprint-like prosopon faintly emerges on the surface of the frontal part of glabella (Fig. 4.18). The frontal lobe becomes more swollen so that the anterior part is almost vertical in lateral view (Fig. 4.23). The posterior cranidial furrows run transversely. The occipital spine, which projects obliquely upward, becomes longer and pointed. Weak eye ridges are recognizable in some specimens (Fig. 4.22).

In the cranidia longer than 1.2 mm (Fig. 4.24–4.28, Fig. 5.1–5.5), the palpebral furrows are more clearly impressed; eye ridges are prominent; the fingerprint-like prosopon becomes distinct on the surface of the frontal lobe of the glabella, extending to the posterior part of the glabella; S1 and S2 glabellar furrows are trans-glabellar; and ridge-like prosopon has appeared on the genal surface. The convexity of the frontal part increases, and the preglabellar field becomes more steepening forward, resulting in a shorter preglabellar field in dorsal view (Fig. 4.24, 4.25, Fig. 5.1–5.3) and more anteriorly situated palpebral lobes. The palpebral lobes are 0.35–0.37 of the cranidial length. The occipital ring is rectangular in outline, with comparatively shortened occipital spine (Fig. 4.25, Fig. 5.1–5.3).

In the subsequent development (Fig. 5.6–5.16), the convexity of the frontal part of the cranidium continues to increase, producing a preglabellar field that is nearly vertical in lateral view (Fig. 5.7), and hence it is not seen in dorsal view (Fig. 5.6, 5.12, 5.13). The fingerprint-like prosopon on the frontal lobe of the glabella does not extend onto the vertical part (Fig. 5.8, 5.10). The palpebral lobes become more elevated (Fig. 5.7) and occupy 0.36–0.38 of the cranidial length. The occipital spine becomes relatively shorter and is not recognizable in dorsal view (Fig. 5.6, 5.11, 5.13). The posterior cranidial margin runs horizontally abaxially, and then it abruptly diverges backwards; the tips of the posterolateral projections are situated posterior to the posterior margin of the occipital ring in dorsal view (Fig. 5.6, 5.11, 5.13).

In the cranidia longer than 5 mm (Fig. 5.17–5.22), the palpebral lobes become relatively shorter, becoming ca. 0.30 of the cranidial length. The occipital spine is reduced. The prosopon on the frontal lobe of the glabella becomes clearer and small pits appear on the surface of the frontal lobe of glabella, but the prosopon on the L2 and L1 disappears. The ridge-like prosopon on the posterior part of the fixed cheek becomes less prominent than the prosopon on the frontal glabellar lobe, but that on the palpebral area remains relatively prominent (Fig. 5.17, 5.21).

The proportion of the cranidial length to the cranidial width becomes smaller with growth, apparently due to the increased convexity of the frontal part of the cranidium, which results in the steep slanting of the frontal area. In the cranidia shorter than 0.6 mm, the sagittal length is ca. 0.8 of the maximum width, while in the cranidia longer than 3 mm, the sagittal length measures ca. 0.6 of the maximum width.

Free cheek development.—The free cheeks remain anteriorly yoked during earlier phases of development (Fig. 6.1–6.8). The smallest free cheek available (Fig. 6.1, 6.2) is of simple morphology with a stout, broad-based genal spine. The genal field is very narrow so that, in dorsal view, the doublure is seen from the anterior tip all the way down to the base of the genal spine. The doublure projects slightly adaxially near the base of the genal spine, which is somewhat high in lateral profile (Fig. 6.3) and constitutes about one-third of the free cheek length.

With growth, the anterior-medial part of the doublure thickens slightly (Fig. 6.4–6.8). The librigenal field widens so that only the anterior part of the doublure can be seen in dorsal view. The oblique lateral view displays a slightly sinuous inner margin, probably indicating the position of the eye. The length of the genal spine is 0.40–0.45 of the whole free cheek length. The largest yoked free cheeks (Fig. 6.8) have a weakly curved backward anterior margin.

Subsequently, the yoked free cheeks split in the center, and thus the cheeks abut along a median suture (Fig. 6.9–6.25). Notable developmental changes include: broadening of the librigenal field; the appearance of ridge-like prosopon on the adaxial portion of librigenal field and on the genal spine, which runs parallel to the lateral margin of the free cheek; the position of the eye becoming recognizable at the inner margin; the tube-shaped doublure; appearance of the elevated eyesocle; and the genal spine becoming as long as about 0.5 of the whole librigenal length. A short abaxial extension of the posterior cranidial furrow is impressed obliquely near the base

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9, SNUP4865, dorsal view; *10–11*, SNUP4866, dorsal and oblique anterolateral views; *12*, SNUP4867, ventral view; *13–15*, SNUP4868, dorsal, lateral, and posterior views; *16*, SNUP4869, dorsal view; *17*, SNUP4870, dorsal view; *18–20*, SNUP4871, dorsal, lateral, and posterior views; *21*, SNUP4872, dorsal view; *22–23*, SNUP4873, dorsal and lateral views; *24*, SNUP4874, dorsal view; *25–28*, SNUP4875, dorsal, lateral, oblique anterolateral, and posterior views. All figures, ×40.

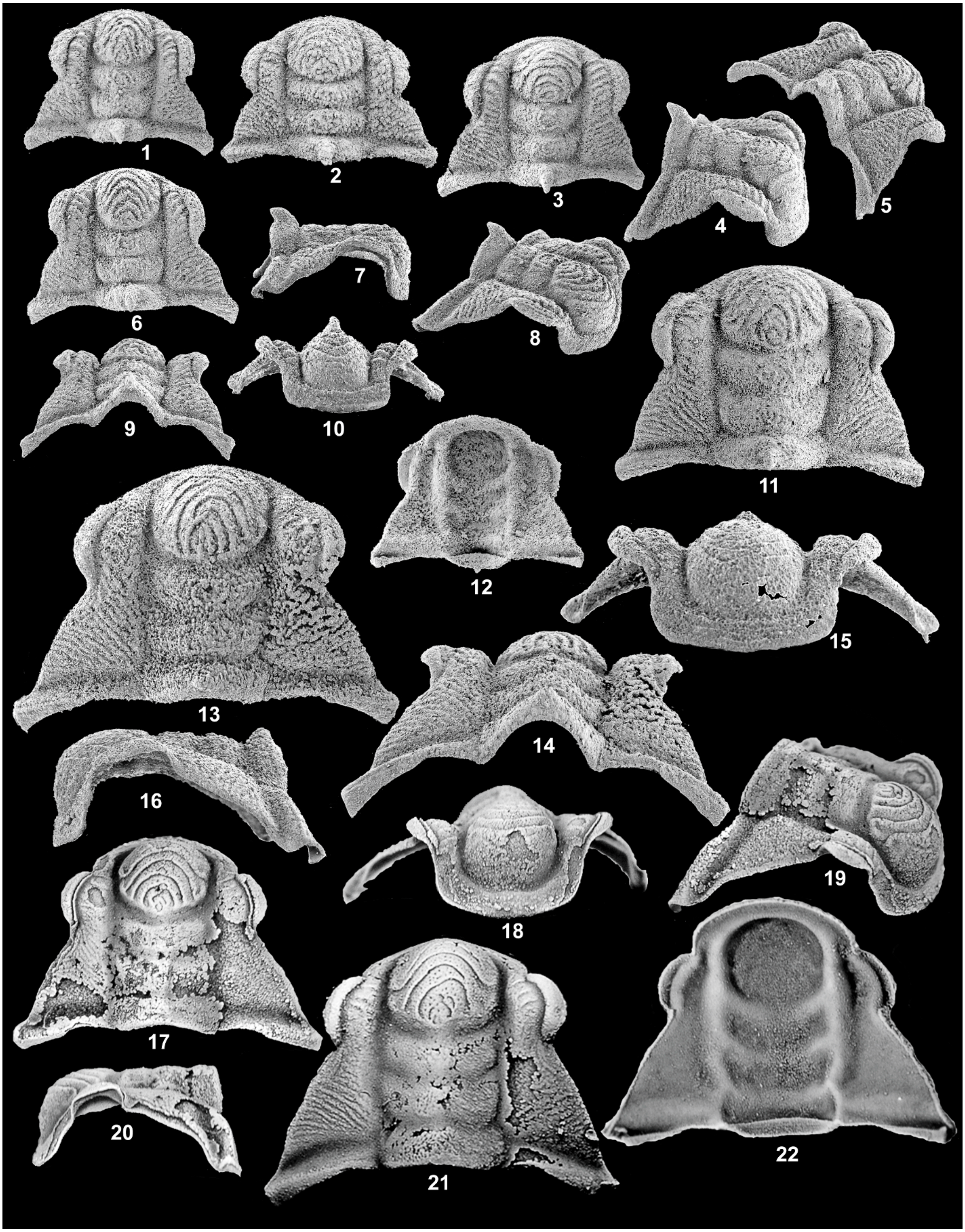

FIGURE 5—Post-protaspid cranidia of *Asioptychaspis subglobosa* (Sun, 1924). *1*, SNUP4876, dorsal view; *2*, SNUP4877, dorsal view; *3–5*, SNUP4878, dorsal, oblique lateral, and oblique posterolateral views; *6–10*, SNUP4879, dorsal, lateral, oblique anterolateral, posterior, and anterior views; *11*,

of the genal spine. With growth, the anterior tip of the doublure thickens dorso-ventrally, becoming pointed downward (Fig. 6.15, 6.16, 6.19, and 6.25), and the eye-socle becomes more highly-incurved. The genal spines are straight and project slightly outward in smaller specimens (Fig. 6.1–6.12), while in larger specimens they are weakly incurved and directed slightly inward (Fig. 6.13–6.25).

Thoracic segment development.—Although there is no specimen with the trunk articulated, the relative position of the thoracic segments within the thorax can be roughly divided into three parts according to morphology: thoracic segments of the anterior part of the thorax (Fig. 7.1–7.9), those from the middle part of the thorax (Fig. 7.10–7.24), and those from the posterior part of the thorax (Fig. 7.25–7.33). Considering the thoracic morphology of a nearly complete specimen of another ptychaspidid trilobite from North China, *Quadraticephalus walcotti* Sun, 1924, illustrated in Zhang and Jell, 1987 (pl. 114, fig. 1), the thoracic segments of the anterior part of the thorax can be distinguished from those from the middle part of the thorax in having a wider axis. Those from the posterior part of the thorax are characterized by a ridge-like prosopon near the lateral tip, which must be related to the ridge-like prosopon in the border of pygidium (Fig. 8.30).

Thoracic segments from the anterior part of the thorax (Fig. 7.1–7.9) can be distinguished by their relatively wide axis; they are slightly arched forward; the maximum width of the axis is about one-third of the entire width of the thoracic segment; the axial ring is strongly convex, with a small axial spine (Fig. 7.2) or node (Fig. 7.7); there is a prominent articulating facet on the anterolateral margin; the pleural furrows are weakly incised; the articulating half ring is demarcated by a moderately incised articulating furrow; and the lateral tip of each pleuron has an obliquely truncated lateral margin.

Thoracic segments from the middle part of the thorax (Fig. 7.10–7.24) are transverse or slightly arched forward. The width of the axis is 0.20–0.30 of the width of the thoracic segment. A narrow doublure is placed at the posterolateral corner of the ventral surface, which becomes broader at the lateral tip of the pleurae (Fig. 7.23). Short terrace lines and a panderian notch are on the doublure at the lateral tip. The panderian process is clearly recognizable in posterior view (Fig. 7.24). Small specimens (Fig. 7.10–7.12) bear a very small articulating facet on the anterolateral margin, which becomes broader with growth. The pleural furrows are moderately impressed and transverse in the smallest specimen, while in larger specimens they become shallower and slightly curved backward. A tumid and short axial spine projects upward and slightly forward in smaller specimens (Fig. 7.10–7.15). In larger specimens, the axial spine becomes shorter and directed backward (Fig. 7.16–7.22), or obliterated (Fig. 7.24). There is a short pleural spine directed obliquely backward in the largest specimen (Fig. 7.23).

Thoracic segments from the posterior part of thorax (Fig. 7.25–7.33) are slightly or moderately arched forward. The width of the axis is about one-fourth the width of the thoracic segment. Pleural furrows and articulating furrow are shallow and relatively wide. A ridge-like prosopon along the lateral margin is present near the lateral tip. Small specimens (Fig. 7.25–7.27) bear a short ridge running along the lateral margin which must correspond to the anteriorly diverging rim-like ridge in the meraspid pygidia (see below). There is no axial projection in any small specimen (Fig. 7.25–7.27), whereas a short axial node is observed in larger specimens. Short pleural spines are directed backward and slightly inward in large specimens.

Post-protaspid pygidial development.—The pygidia of *A. subglobosa* in this study are quite different from those described by Sohn and Choi (2007, fig. 4, S and T), who mistakenly assigned the pygidia with sub-rhomboidal outline and distinct pleural furrows to *A. subglobosa*. The pygidia illustrated by Sohn and Choi (2007) should belong to other species associated with *A. subglobosa*. There is no fully articulated specimen at hand, and thus it is hard to recognize meraspid degrees and the stage at which the holaspid period began in the pygidial development. Nevertheless, once the forwardly-divergent rim-like ridges appear in the meraspid pygidium, the relative position of the structure can be used to understand the dynamics of development, and hence it is possible to distinguish meraspid pygidia from holaspid pygidia.

The smallest meraspid pygidium (Fig. 8.1, 8.2) is 0.28 mm long and 0.48 mm wide, and has three or four axial rings, each bearing a short tumid axial spine. There is no furrow on the pleural field, and the articulating half ring, defined by shallow articulating furrow, does not protrude forward. A pair of very short pygidial spines is present at the posterior margin. In a slightly larger meraspid pygidium (Fig. 8.3, 8.4), there are four or five axial rings with longer tumid axial spines. The articulating half ring slightly protrudes forward. Pleural and interpleural furrows are weakly incised. The posterior margin slightly displays a posterior indentation.

The subsequent meraspid pygidia possess five or six axial rings and a narrow pygidial border, defined by change in slope (Fig. 8.5, 8.6). The narrow border is high and steep, forming a raised rim (Fig. 8.6). The tumid anteriormost axial spine is directed upward and forward, as is the second anteriormost axial spine. The larger meraspid pygidia (Fig. 8.8–8.15) have five to seven axial rings. The pleural furrows are clearly incised, and the interpleural furrows are shallow. The doublure is smooth and moderately wide with a weakly serrated lateral margin that reflects the posterolateral tip of each segment conjoined in the meraspid pygidium (compare Fig. 8.7 and 8.16). The posterior indentation gradually disappears.

With subsequent development, the high and steep border becomes inclined adaxially and forwardly (Fig. 8.17–8.20), so that the highest contour of the border is indicated by a rim-like ridge bounding the posterior end of the axis in dorsal view (Fig. 8.17, 8.19). Then, the border begins to incline, and no more segments are generated at the posterior end. The number of axial rings only decrease during subsequent development, reaching to the holaspid phase; from seven axial rings in the meraspid pygidia (Fig. 8.17–8.20) to four axial rings in the holaspid pygidia (Fig. 8.25, 8.26). As the onset of the epimorphic phase, during which the number of segments in the trunk remained constant, precedes the onset of the holaspid phase, the developmental mode of *A. subglobosa* is protomeric (sensu Hughes et al., 2006). The area outside and posterior to the rim-like ridge becomes wider with growth

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SNUP4880, dorsal view; *12*, SNUP4881, ventral view; *13–16*, SNUP4882, dorsal, oblique posterior, anterior, and lateral views; *17–20*, SNUP4883, dorsal, anterior, oblique anterolateral, and lateral views; *21–22*, SNUP4884, dorsal and ventral views. *1–16*, ×15. *17–22*, ×6.

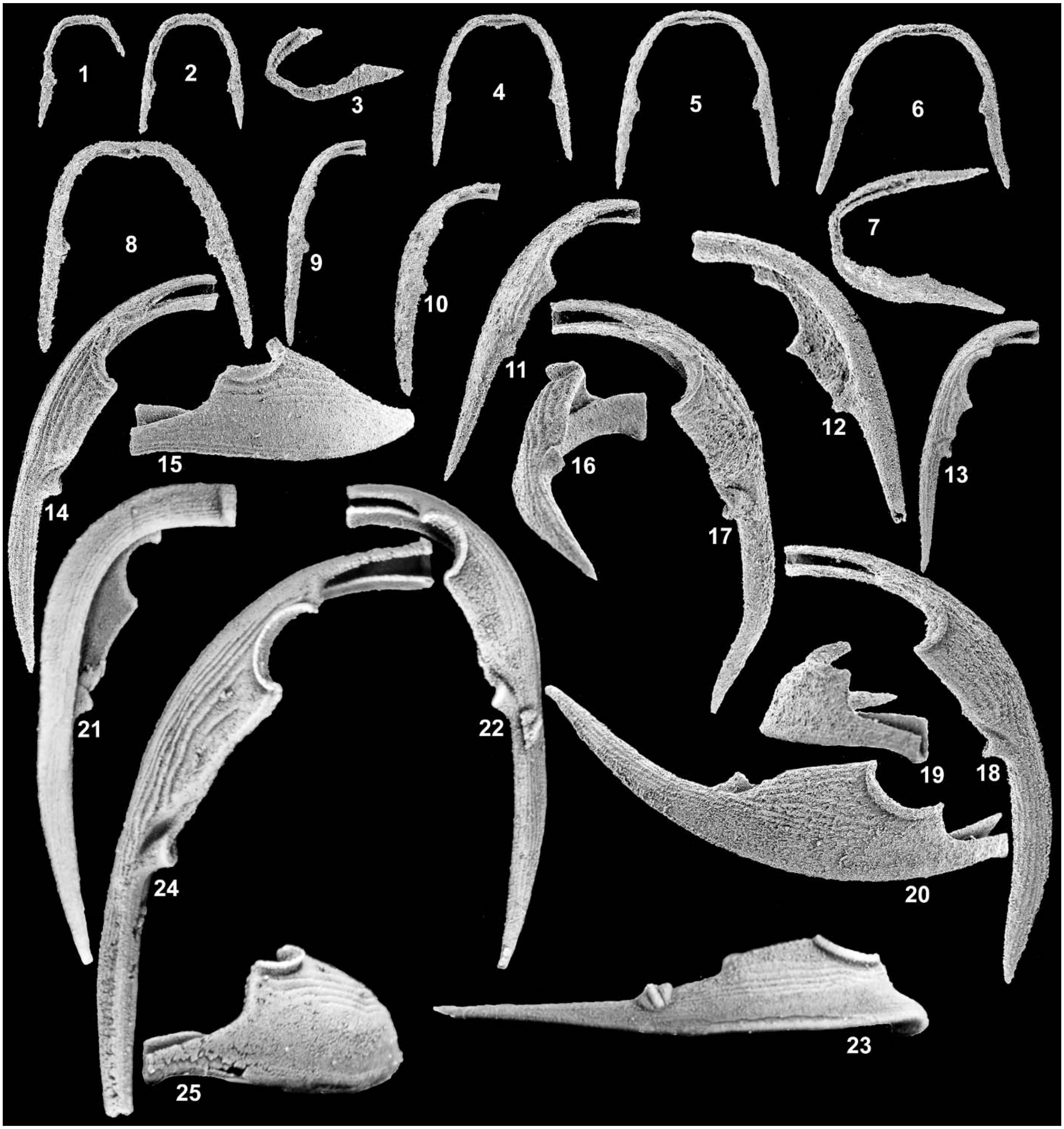

FIGURE 6—Free cheeks of *Asioptychaspis subglobosa* (Sun, 1924). *1–8*, anteriorly yoked free cheeks at early developmental phase: *1*, SNUP4885, dorsal view; *2–3*, SNUP4886, dorsal and oblique anterolateral views; *4*, SNUP4887, dorsal view; *5*, SNUP4888, dorsal view; *6–7*, SNUP4889, dorsal and oblique lateral views; *8*, SNUP4890, dorsal view; *9–23*, not-yoked free cheeks at late developmental phase. *9*, SNUP4891, dorsal view. *10*, SNUP4892, dorsal view; *11*, SNUP4893, dorsal view; *12*, SNUP4894, ventral view; *13*, SNUP4895, dorsal view; *14–16*, SNUP4896, dorsal, anterolateral, and oblique posterior views; *17*, free cheek with abnormal genal spine, SNUP4897, dorsal view; *18–20*, SNUP4898, dorsal, anterior, and oblique anterolateral views; *21–23*, SNUP4899, ventral, dorsal, and lateral views; *24–25*, SNUP4900, dorsal and anterior views. *1–12*, ×26. *13–20*, ×13. *21–25*, ×8.

(Fig. 8.21–8.28). The large holaspid pygidia have obsolete pleural and interpleural furrows and lack the rim-like ridge. The border is often ornamented with anastomosing ridges and grooves (Fig. 8.30), and the doublure is considerably wide (Fig. 8.32), compared to those of other ptychaspidids (see Adrain and Westrop, 2005).

It is noteworthy that the high and steep pygidial border of meraspid pygidium of *A. subglobosa* resembles the raised rim-like border in mature pygidia of many ptychaspidid trilobites in Laurentia, such as *Ptychaspis* Hall, 1863, *Keithiella* Rasetti, 1944, and *Idiomesus* Raymond, 1924 (see Westrop, 1986). The rim-like ridge of late meraspid and early holaspid pygidia of *A.*

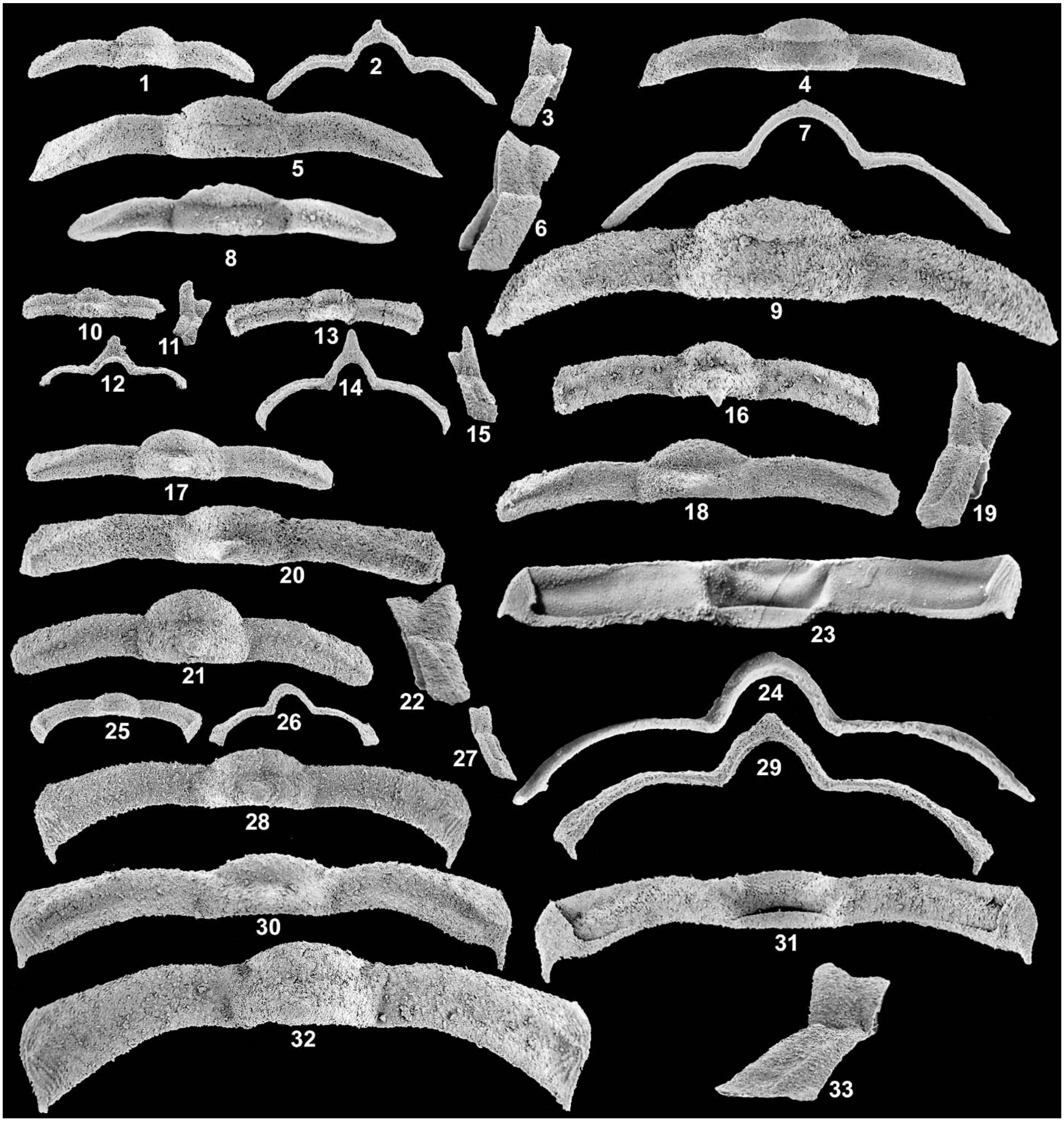

FIGURE 7—Thoracic segments of *Asioptychaspis subglobosa* (Sun, 1924). *1–9*, thoracic segments of anterior part of thorax: *1–3*, SNUP4901, dorsal, posterior, and lateral views; *4*, SNUP4902, dorsal view; *5–7*, SNUP4903, dorsal lateral, and posterior views; *8*, SNUP4904, dorsal view; *9*, SNUP4095, dorsal view; *10–24*, thoracic segments of middle part of thorax: *10–12*, SNUP4906, dorsal, lateral, and posterior views; *13–15*, SNUP4907, dorsal, posterior, and lateral views; *16*, SNUP4908, dorsal and lateral views; *17*, SNUP4909, dorsal view; *18–19*, SNUP4910, dorsal view; *20*, SNUP4911, dorsal view; *21–22*, SNUP4912, dorsal and lateral views; *23–24*, SNUP4913, ventral and posterior views. *25–33*, thoracic segments of posterior part of thorax: *25–27*, SNUP4914, dorsal, posterior, and lateral views; *28–29*, SNUP4915, dorsal and posterior views; *30–31*, SNUP4916, dorsal and ventral views; *32–33*, SNUP4917, dorsal and lateral views. *1–22*, ×16. *23–24*, ×13. *25–29*, ×16. *30–33*, ×13.

subglobosa is also comparable to that of the Laurentian ptychaspidid trilobite, *Euptychaspis* Hupé, 1953 (see Adrain and Westrop, 2004, 2005). These morphological similarities suggest a close phylogenetic relationship between *Asioptychaspis* and the Laurentian ptychaspidids. In addition, the rim-like ridge may be related to the sculptural ridges running obliquely forward on the pleural field in the pygidia of two late middle Cambrian diceratocephalid trilobites, *Cyclolorenzella convexa* and *Diceratocephalus cornutus*, from Korea (Park and Choi, in press). The ridges of the diceratocephalids are derived from the raised rim-like border of meraspid pygidium during ontogeny. However, the rim-like ridge of ptychaspidids is

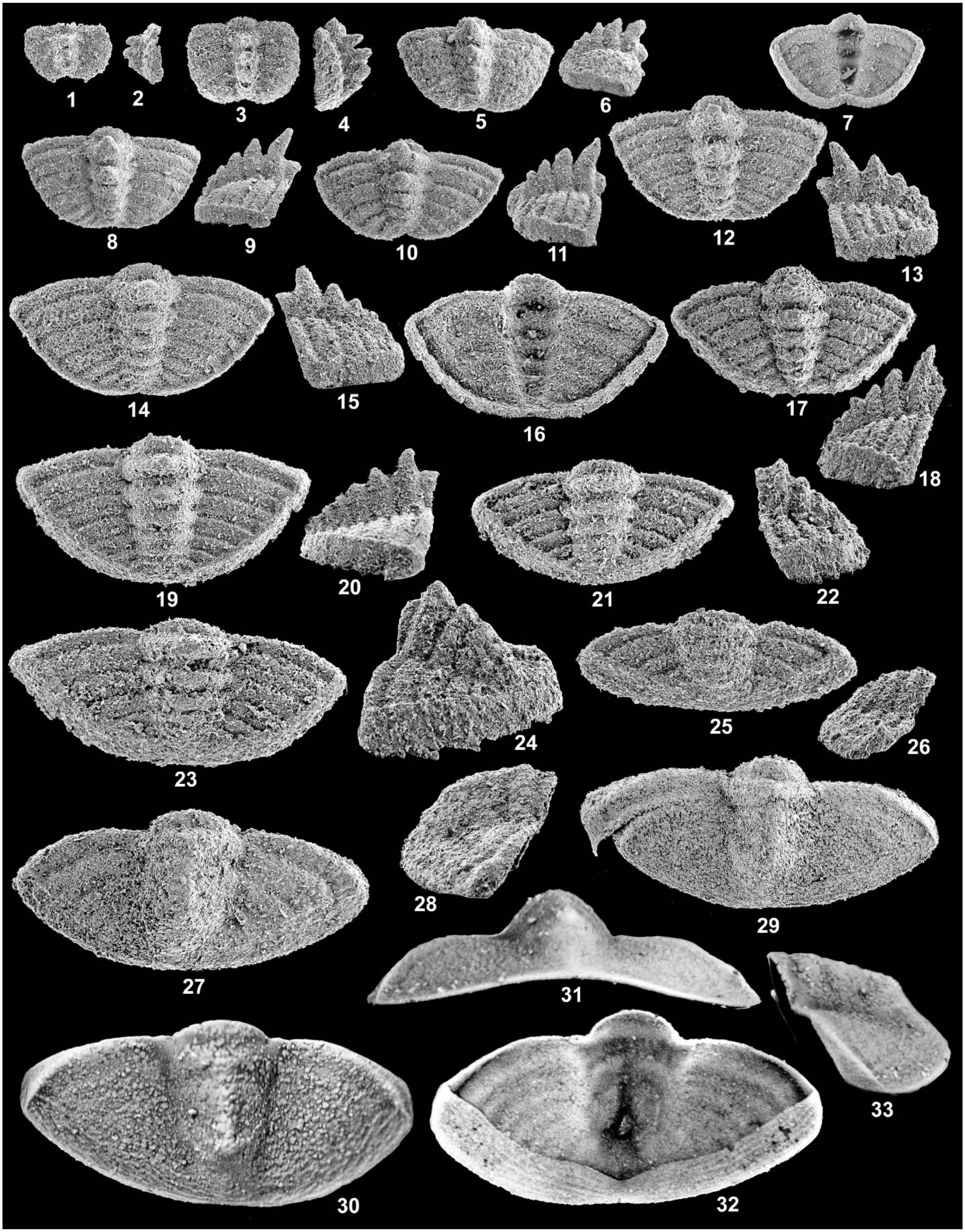

FIGURE 8—Post-protaspid pygidia of *Asioptychaspis subglobosa* (Sun, 1924). *1–24*, meraspid pygidia: *1–2*, SNUP4918, dorsal and lateral views; *3–4*, SNUP4919, dorsal and lateral views; *5–6*, SNUP4920, dorsal and lateral views; *7*, SNUP4921, ventral view; *8–9*, SNUP4922, dorsal and lateral views;

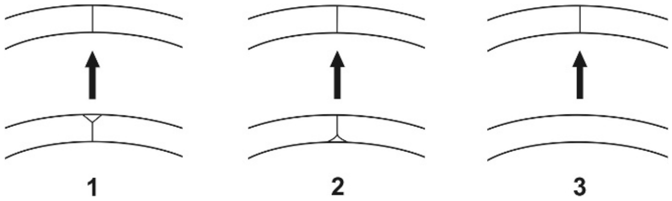

FIGURE 9—Three different modes of ventral median suture (VMS) formation during ontogeny. *1*, VMS formed by disappearance of an inverted-triangular rostellum as in *Pterocephalia* (Chatterton and Ludvigsen, 1988). This mode is consistent with the model proposed by Chatterton et al. (1994). *2*, VMS formed by disappearance of a triangular rostral plate as in *Tsinania canens* (Park and Choi, 2009). *3*, VMS formed by splitting of yoked free cheeks as in *Asioptychaspis subglobosa* (this study).

distinguished from that of the diceratocephalids in that it bounds the posterior end of the axis, while in diceratocephalids the segment from which the sculptural ridges diverge (RDS; sensu Park and Choi, in press) moves forward during development, so that several segments appear behind RDS.

DISCUSSION

Contrary to Fortey and Chatterton's (1988) contention that the superfamily Dikelocephaloidea may have had an asaphoid protaspis, the dikelocephaloid trilobite, *Asioptychaspis subglobosa*, did not possess an asaphoid protaspis in its ontogeny. The asaphoid protaspis as defined by Fortey and Chatterton (1988) is characterized by a spherical to ovoid shape with an enrolled rather than inturned doublure, which subsequently metamorphosed into a benthic meraspis. The protaspid morphology of *A. subglobosa* is, however, benthic and adult-like, and no significant metamorphosis has been involved during the protaspid/meraspid transition. Therefore, the position of the Dikelocephaloidea in the cladogram of Fortey and Chatterton (1988) turns out to be problematic: the protaspis of *A. subglobosa* is easily differentiated from the highly globular asaphoid protaspis of the Remopleuridioidea, which was regarded as the sister group of the Dikelocephaloidea.

The ontogenetic development of *A. subglobosa* clearly demonstrates that the free cheeks remain yoked anteriorly during the early phase of ontogeny but are split by a ventral median suture in later development. This ontogenetic change likely reflects a phylogenetic evolution of ventral median suture of *A. subglobosa* from a yoked free cheek-retaining ancestor. This mode of ventral median suture formation is different from the mode proposed by Chatterton et al. (1994) in which a ventral median suture was formed by loss of a small rostellum during ontogeny. Such morphological transformation of the ventral structure was documented in the ontogeny of *Pterocephalia*, and it was regarded as the ontogenetic change that parallels the phylogenetic evolutionary change (Chatterton and Ludvigsen, 1998). Chatterton et al. (1994) went further to suggest that yoked free cheeks may have been derived from the fusion of a ventral median suture. However, as the ventral median suture of *A. subglobosa* formed by splitting of yoked free cheeks, the ventral median suture of *A. subglobosa* is not homologous to those of the typical asaphide trilobites. In this regard, it is tempting to consider that the Laurentian ptychaspidid, *Macronoda* Lochman, 1964, which was described as having yoked free cheeks by Adrain and Westrop (2005), retains the plesiomorphic condition.

Taken together with the mode of ventral median suture formation in *Tsinania canens* documented by Park and Choi (2009), it can be concluded that there are, for now, three different modes of ventral median suture (VMS) formation (Fig. 9): i.e., 1) VMS formed by the loss of an inverted-triangular rostellum in front of a connective suture (Chatterton et al., 1994) as in the ontogeny of *Pterocephalia*; 2) VMS formed by the reduction of a triangular rostral plate behind a connective suture as in the ontogeny of *Tsinania canens* (Park and Choi, 2009); and 3) VMS formed by splitting of yoked free cheeks as in the ontogeny of *Asioptychaspis subglobosa* (this study).

In short, the ventral median suture of *Asioptychaspis subglobosa* had a different origin from those of the typical asaphide trilobites included in the cladistic analysis of Fortey and Chatterton (1988). Therefore, the inclusion of the superfamily Dikelocephaloidea in the cladistic analysis is found to be inappropriate, and the Dikelocephaloidea should be excluded from the Order Asaphida. The membership of other trilobites within the Order Asaphida also needs to be critically re-examined.

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10–11, SNUP4923, dorsal and lateral views; *12–13*, SNUP4924, dorsal and lateral views; *14–15*, SNUP4925, dorsal and lateral views; *16*, SNUP4926, ventral view; *17–18*, SNUP4927, dorsal and lateral views; *19–20*, SNUP4928, dorsal and lateral views; *21–22*, SNUP4929, dorsal and lateral views; *23–24*, SNUP4930, dorsal and posterolateral views. *25–32*, holaspid pygidia: *25–26*, SNUP4931, dorsal and lateral views; *27–28*, SNUP4932, dorsal and lateral views; *29*, pygidium with incompletely released segment at left anterior margin, SNUP4933, dorsal view; *30–33*, SNUP4934, dorsal, posterior, ventral, and lateral views. *1–26*, ×35. *27–28*, ×30. *29*, ×13. *30–33*, ×10.

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