

MIDDLE FURONGIAN (LATE CAMBRIAN) SHUMARDIIDES FROM THE SESONG FORMATION, TAEBAEK GROUP, KOREA

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ABSTRACT—The trilobite family Shumardiidae is characterized by small size, lack of eyes, yoked librigenae, and a small number of thoracic segments. Here we report the successive occurrence of three middle Furongian shumardiid species from the Sesong Formation of Korea: *Elaphraella? taebaeksanensis* n. sp., *Elaphraella microforma*, and *Elaphraella nodus*. They appear to represent the oldest shumardiid morphology known so far. This genus lacks the anterolateral swellings on the glabella and has a conical glabella. Its yoked librigenae also encompass a comparatively wide genal field. *Elaphraella? taebaeksanensis* has a highly inflexed facial suture which may reflect the presence of small palpebral lobes. Taken together, the plesiomorphic morphology of the Shumardiidae can be summarized as having a conical glabella, small palpebral lobes, highly arched anterior cephalic margin, a wide librigenal field, and no anterolateral swellings on the glabella.

INTRODUCTION

THE FAMILY Shumardiidae was established by Lake (1907) and the familial concept was later discussed by Kobayashi (1935), Shergold (1991), and Waisfeld et al. (2001). The shumardiids are characterized by small size and blindness. The presence of palpebral lobes has been a matter of contention as it may be significant in elucidating the ancestry of the Shumardiidae. *Akoldinioidia dydimacantha* Peng, 1992 was described as possessing moderately large palpebral lobes, but the specimens are poorly preserved, so that the palpebral lobe-like structure may not have been a primary structure of the trilobite. For instance, one large specimen (Peng, 1992, figs. 20J, 20K, 21B) shows the palpebral lobe-like structure only on the right side of cranidium while the left side of the cranidium does not display any indication of facial suture, and thus the presence of palpebral lobes in *A. dydimacantha* is doubtful. More recently, Peng et al. (2003) reported a new genus *Oculishumardia* from the upper middle Cambrian of South China which had large palpebral lobes, and considered it as an evolutionary intermediate between the primitive ptychoparioids and derived shumardiids. However, Park et al. (2008) demonstrated that *Oculishumardia* actually represents immature stages of some dameselliid trilobites, and proposed two hypotheses for the ancestry of the Shumardiidae: 1) shumardiids originated from a stock of dameselliids, or 2) shumardiids have no phylogenetically close relationship with *Oculishumardia*. Park et al. (2008) noted that the morphology of the currently known unequivocal oldest shumardiids (i.e., *Elaphraella* Lu and Qian, 1983 and some of *Liriannica* Shergold, 1980) is not comparable to that of *Oculishumardia*-like forms, supporting the second hypothesis. Accordingly, it can be concluded that there has been no convincing evidence of palpebral lobes in any shumardiid trilobites.

This study reports the successive occurrence of three middle Furongian shumardiid species: *Elaphraella? taebaeksanensis* new species, *Elaphraella microforma* Lu and Qian, 1983 and *Elaphraella nodus* (Qian, 1994) from the upper part of the Sesong Formation, Taebaek Group, Korea. *Elaphraella* has hitherto been known as the oldest shumardiid trilobite, and has a conical glabella. However, because the original report of *Elaphraella* was based on a few crack-out cranidia in poor preservation, the morphology of this early shumardiid is incompletely understood. The upper part of the Sesong Formation produces silicified trilobite sclerites including a

number of cranidia, thoracic segments, and pygidia belonging to *Elaphraella*. The new shumardiid species *Elaphraella? taebaeksanensis* occurs stratigraphically lower than *E. microforma* and *E. nodus*, thus representing the oldest shumardiid so far known. The morphological information of these three shumardiid species should provide a useful insight on the evolution of the shumardiid trilobites.

GEOLOGICAL SETTING, FOSSIL LOCALITY, AND MATERIAL

The geological setting of the Taebaeksan Basin was described in detail in Choi et al. (2004) and Park and Choi (2010a). The Sesong Formation is late middle Cambrian to middle Furongian in age, and is composed mainly of nodular shale, siltstone, fine-grained sandstone, and limestone conglomerate. The upper part of the formation comprises siltstone and fine-grained sandstone with intercalations of limestone conglomerate (Fig. 1). The sandstone within the formation is laminated and/or crudely stratified. The formation was interpreted to have formed in an outer shelf environment (Kwon et al., 2006).

The biostratigraphic scheme of the Sesong Formation and the overlying Hwajeol Formation was originally proposed by Kobayashi (1935). This was emended by Sohn and Choi (2005) who recognized five biozones within the Sesong Formation: the *Stephanocare*, *Neodrepanura*, *Prochuangia*, *Chuangia*, and *Kaolishania* zones in ascending order. The *Stephanocare* and *Neodrepanura* zones are Cambrian Series 3 in age, while the *Prochuangia*, *Chuangia*, and *Kaolishania* zones belong to the Furongian.

All the specimens employed in this study were recovered from the upper part of the Sesong Formation at the Sagundari section (N 129°01'03.4", E 37°04'57.0") (see Park and Choi, 2010a for locality map). The section exposes the interval across the boundary between the Sesong and Hwajeol formations and is approximately 32 m thick. The Sesong Formation occupies the lower 19-m-thick interval and consists mainly of siltstone and fine-grained sandstone with sporadic intercalations of limestone conglomerate beds which laterally pinch out (Fig. 1). The upper 13-m-thick interval belongs to the Hwajeol Formation and comprises largely limestone-shale couplets and limestone conglomerates. The lower part of the Hwajeol Formation at the Sagundari section is known to produce well-preserved silicified trilobite sclerites, which have been used for recent ontogenetic studies of three trilobite

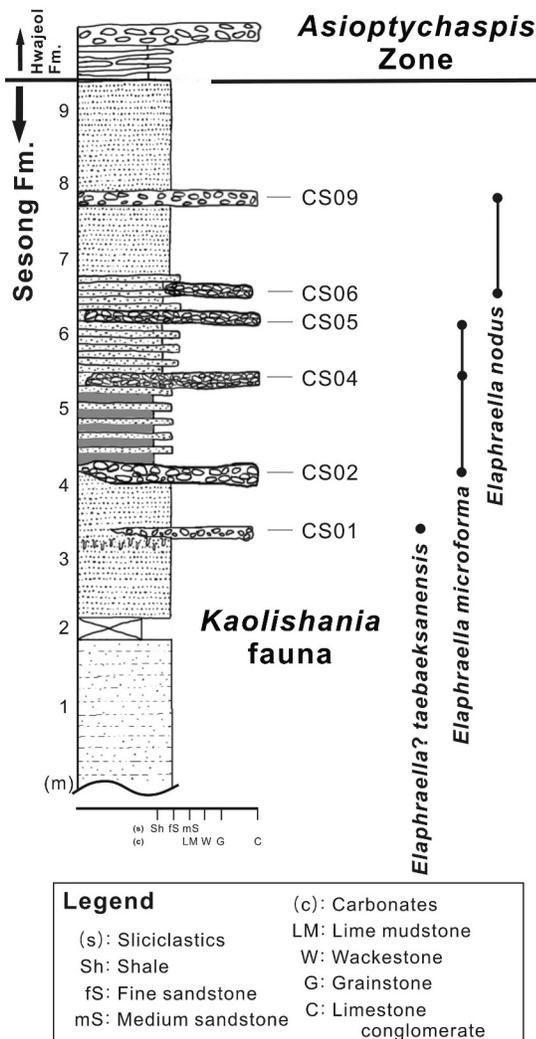


FIGURE 1—Lithological columns of the Sesong Formation exposed in the Sagundari section, with stratigraphic occurrences of *Elaphraella? taebaeksanensis* new species, *Elaphraella microforma* Lu and Qian, 1983, and *Elaphraella nodus* (Qian, 1994).

species such as *Tsinania canens* (Walcott, 1905), *Asioptychaspis subglobosa* (Sun, 1924), and *Haniwa quadrata* Kobayashi, 1933 (Park and Choi, 2009, 2010a, 2011).

The Sesong Formation in the Sagundari section comprises six limestone conglomerate beds which are marked as CS01, CS02, CS04, CS05, CS06, and CS09, in ascending order (Fig. 1). Rock samples of limestone conglomerate beds were dissolved out using hydrochloric acid, and more than 200 silicified trilobite sclerites of the three shumardiid trilobites were collected for this study. The associated trilobites include *Shirakiella* sp., *Taishania?* sp., *Acanthometopus* sp., *Pagodia?* sp., *Kaolishania granulosa* Kobayashi, 1933, kaolishaniid genus and species indeterminate, and *Lingyuanspis* sp. Kobayashi (1960) reported the occurrence of five trilobite genera from the *Kaolishania* Zone, based on fragmentary specimens: *Pseudagnostus*, *Kaolishania*, *Shirakiella*, *Tingocephalus*, and *Taipaikia*. However, Kobayashi (1960) did not provide any detailed biostratigraphic data, and no subsequent research has been done for the *Kaolishania* Zone. The studied interval may be regarded as part of the *Kaolishania* Zone, as proposed by Kobayashi (1935), which is presumably equivalent to the *Kaolishania* Zone of North China (Sun, 1935;

Zhang and Jell, 1987; Qian, 1994; Duan et al., 2005). However, as *Kaolishania* occurs only from the lowermost horizon (CS01) of the studied interval and the full stratigraphic range of *Kaolishania* is currently unavailable, the fossil content of the studied interval is provisionally called the *Kaolishania* fauna herein (Fig. 1). The *Kaolishania* fauna underlies the *Asioptychaspis* Zone which occupies the lowermost part of the Hwajeol Formation (Fig. 1).

SYSTEMATIC PALEONTOLOGY

The morphological terms generally follow Whittington and Kelly (1997), but the term glabella used herein excludes the occipital ring. All of the specimens described in this paper are housed in the paleontological collections of Seoul National University, Korea with registered SNUP numbers.

Family SHUMARDIIDAE Lake, 1907 Genus ELAPHRAELLA Lu and Qian, 1983

Trianguraspis QIAN, 1994, p. 52–53.

Type species.—*Elaphraella microforma* Lu and Qian, 1983, p. 240.

Other species.—*Elaphraella paiensis* (Endo in Endo and Resser, 1937), *E. nodus* (Qian, 1994), and *E.? taebaeksanensis* new species.

Emended diagnosis.—A genus of the Shumardiidae having a conical broad-based glabella and a row of marginal spines on the posterior margin of occipital ring and posterior border, but lacking palpebral lobes, anterolateral glabellar lobes and glabellar furrows.

Discussion.—Lu and Qian (1983) gave a diagnosis on the basis of two poorly preserved cranidia (Lu and Qian, 1983, pl. 2, figs. 9, 10) and mistakenly described this genus as having small palpebral lobes and distinct palpebral ridges. These features cannot be recognized from the holotype which is an internal mold (Lu and Qian, 1983, pl. 2, fig. 10), hence the emended diagnosis is given herein. This genus displays wide morphological variation especially in marginal spines and tubercles. The strongly tuberculated holotype of *Trianguraspis nodus* Qian, 1994, the type species of the genus, is considered to fall within the range of morphological variation of *Elaphraella*. *Koldinioidia paiensis* Endo in Endo and Resser, 1937 differs from the typical *Koldinioidia* in having a conical broad-based, rather than parallel-sided to slightly tapering forward glabella, and can be assigned to *Elaphraella*. However, the poor illustrations of *Elaphraella paiensis* (Endo in Endo and Resser, 1937), do not allow a proper taxonomic examination, and we suggest that the species concept of *E. paiensis* should be restricted to the holotype (Endo in Endo and Resser, 1937, pl. 71, fig. 5).

One of the most interesting features of *Elaphraella* is the row of marginal spines on the posterior margin of the occipital ring, posterior cranial border, and axial rings of the thoracic segments and pygidium. Similar structures were observed in the Ordovician shumardiid trilobites, *Kweichowilla salasae* Waisfeld et al., 2001, *K. sterrenae* Waisfeld et al., 2001, and *Changchowilla riojana* (Benedetto and Cañas in Benedetto et al., 1986) (see Waisfeld et al., 2001). However, the marginal spines of *Elaphraella* are more sharply pointed than those of *K. salasae*, *K. sterrenae*, and *C. riojana*. There seems to be a variation in the length of the marginal spines in *Elaphraella*: some specimens have notably long marginal spines (Fig. 2.8, 2.11), while others possess a rather smooth posterior margin (Fig. 2.4).

Elaphraella is morphologically comparable to some specimens of *Liriamica* Shergold, 1980. *Liriamica* was reported from the *Peichianshania* *tertia*–*quarta* and *Hapsidocare*

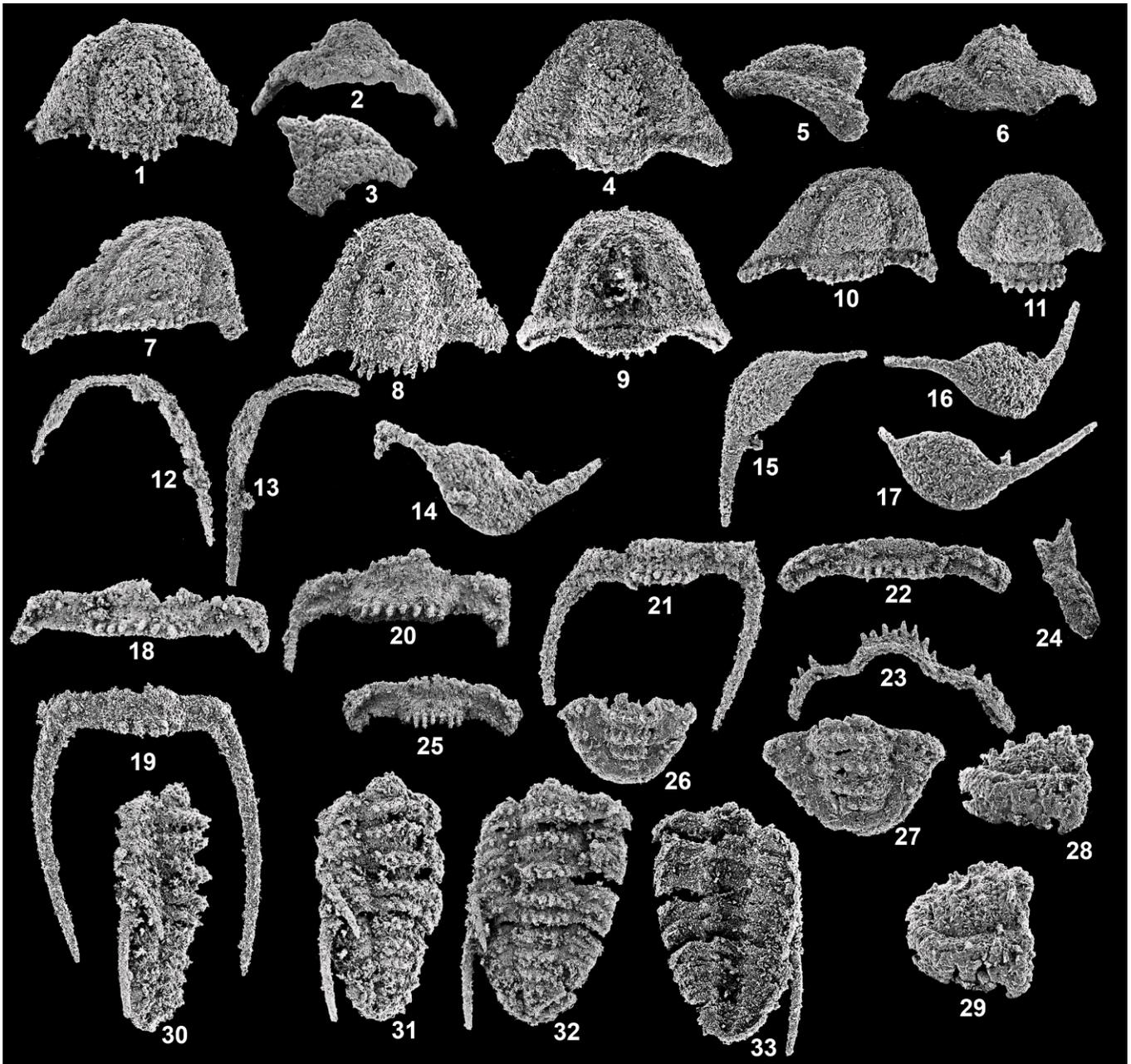


FIGURE 2—*Elaphraella microforma* Lu and Qian, 1983. 1–11, cranidia: 1–3, SNUP6076, dorsal, anterior, and lateral views; 4–6, SNUP6077, dorsal, lateral, and anterior views; 7, SNUP6078; 8, SNUP6079; 9, SNUP6080, ventral view; 10, SNUP6081; 11, SNUP6082; 12–17, librigenae: 12, SNUP6083, dorsal view; 13–14, SNUP6084, dorsal and oblique anterolateral views; 15–17, SNUP6085, dorsolateral, anterolateral, and lateral views; 18–25, thoracic segments: 18, SNUP6086; 19, SNUP6087; 20, SNUP6088; 21, SNUP6089; 22–24, SNUP6090, dorsal, anterior, and lateral views; 25, SNUP6091; 26–29, pygidia: 26, SNUP6092; 27–29, SNUP6093, dorsal, lateral, and oblique lateral views; 30–33, a thoracopygon, SNUP6094, lateral, oblique lateral, dorsal, and ventral views. All figures, $\times 17$.

lilyensis Assemblage Zone of western Queensland, Australia, which is correlated with the *Kaolishania* Zone of North China and Korea. Although *Liriannica* includes only one species, *Liriannica antyx* (Shergold, 1980), three different forms are readily recognized at different stratigraphic intervals. The holotype of *Liriannica antyx* (Shergold, 1980, pl. 18, figs. 6, 8) has a slightly forward-tapering glabella, relatively wide fixigenal areas, and a trapezoidal cranidial outline. On the other hand, two of the illustrated specimens (Shergold, 1980, pl. 18, figs. 9–12) collected from 40 m below the holotype-bearing horizon are distinguishable from the holotype in having a triangular cranidial outline,

narrower fixigenal areas, and a conical glabella, and may be better assigned to *Elaphraella*. The specimen (Shergold, 1980, pl. 18, fig. 7) from 60 m above the holotype-bearing horizon shows the morphological features comparable to *Akoldinioidia* Zhou in Zhou and Zhang, 1984, which has weakly bulging anterolateral glabellar lobes, parallel-sided glabella, and a semicircular cranidial outline.

ELAPHRAELLA MICROFORMA Lu and Qian, 1983
Figure 2

Elaphraella microforma LU AND QIAN, 1983, p. 250, pl. 2, figs. 9, 10; QIAN, 1994, p. 51, pl. 4, figs. 6–8, 10.

Koldinoidea triangularis ZHANG AND JELL, 1987, p. 243, pl. 119, fig. 10; pl. 120, fig. 4.

Diagnosis.—A species of *Elaphraella* with relatively slender marginal spines and a highly sinuous facial suture in lateral view.

Description.—Cranidium subtriangular in outline. Glabella convex, conical, approximately two-thirds of cranial length, and more than one-third of cranial width; axial furrows well incised, and preglabellar furrows moderately to well incised; glabellar furrows absent. Occipital ring one-fourth of glabellar length, convex; posterior margin weakly convex backwards, sculptured with closely spaced short spines directed posteriorly upwards; occipital furrow simple and weakly incised. Preglabellar field short and strongly downsloping. Anterior border absent. Palpebral lobes absent; palpebral ridges absent. Fixigenae convex, narrow, and peripherally downsloping; posterolateral margin of fixigenae projecting backwards. Facial suture sinuous in lateral view. Posterior border transverse, downsloping abaxially, becoming longer abaxially, sculptured with short spines directed posteriorly upwards; posterior border furrow narrow, clearly incised, transverse and curved backwards at lateral margin.

Librigenae anteriorly yoked with narrow doublure. Genal field wide, strongly downsloping peripherally. Frontal part of doublure highly arched upward in anterior view. Genal spines usually as long as cranial length.

Thorax of six segments. Axis convex, weakly tapering backwards, approximately 40% of thoracic width; axial ring short, convex, and sculptured with short spines directed posteriorly. Pleurae curved backwards, flat, and lateral margin abaxially downsloping; anterior pleural band sculptured with three short spines directed posteriorly upwards; pleural furrow transverse, moderately deep, and narrow; posterior pleural band smooth; pleural spines short and curved backwards; long macropleural spines on the third and fourth segments, directed backwards, slightly curved inwards; third macropleural spines directed upwards.

Pygidium inverted subtriangular in outline. Axis tapering backwards with four axial rings, approximately one-third of pygidial width; axial furrows clearly incised; axial rings convex, sculptured with small spines. Pleural region flat and downsloping peripherally with three pleurae; pleural furrow narrow and shallow, interpleural furrow narrow; anterior pleural band sculptured with small spines. Postaxial ridge absent. Postaxial area smooth, downsloping. Pygidial border undifferentiated.

Material examined.—Forty-five cranidia, six librigenae, 22 thoracic segments, three pygidia, and one thoracopygon.

Occurrence.—The *Kaolishania* fauna of the Sesong Formation, Taebaeksan Basin, Korea; CS02, CS04, and CS05 of the Sagundari section. Associated trilobites include *Taishania?* sp., *Shirakiella* sp., a kaolishaniid genus and species indeterminate, and *Lingyuanaspis* sp. This species was also known from the *Kaolishania* Zone of Northeast China (Lu and Qian, 1983; Qian, 1994).

Discussion.—Zhang and Jell (1987) suggested that the specimens of *Koldinoidea paiensis* Endo in Endo and Resser, 1937 reported by Endo (1939) were different from the holotype of the species, and established a new species *Koldinoidea triangularis* for those specimens. The specimens of *Koldinoidea triangularis* are indistinguishable from *Elaphraella microforma*, and thus are placed in synonymy.

Shumardiids generally have macropleurae only on the fourth thoracic segment. A thoracopygon of *E. microforma* (Fig. 2.30–2.33) comprises six thoracic segments with the

macropleurae on the third and fourth thoracic segments. The presence of macropleurae on the third and fourth segments is also known in *Koldinoidea dydimacantha* (Peng, 1992) which is the oldest species of *Koldinoidea*. This feature may be a character of primitive shumardiids. It is noteworthy that the juvenile specimens of *Akoldinoidea shanjiangensis* Peng et al., 2003 have somewhat long spines on the third thoracic segment, which reduce in size with subsequent growth (see Peng et al., 2003). The Tremadocian shumardiid *Acanthopleurella grindrodi* Groom, 1902 was also described as possessing macropleurae on the third and fourth segments (Fortey and Rushton, 1980).

Functional morphology.—Fortey and Rushton (1980, p. 83) suggested that the macropleural spines of shumardiids have functioned as supporting the trilobite on the sediment surface during enrollment. Waisfeld et al. (2001, p. 836) argued that these spines had functioned as snowshoe-like devices to prevent the animals sinking deep into soft sediments, along with advantage of enlarging the dimension of the animals so as to restrict the size and number of predators. The suggested function of snowshoe devices was based on the observation that the macropleural spines run parallel with the ventral margin of the exoskeleton when the animal was resting on the sediments. However, unlike the macropleural spines of other shumardiid trilobites, the macropleural spines on the third thoracic segment of *Elaphraella microforma* are directed obliquely upwards and rearwards (Fig. 2.30–2.32), having a different direction from the macropleural spines of the fourth thoracic segment. This may indicate that at least macropleural spines on the third segments of *Elaphraella microforma* did not play a function of support on the sediment surface. The diagonally upwardly-directed macropleural spines on the third segment may have 1) been a stopping device to prevent the extra dorsal flexibility of body, or 2) had a defensive function with advantage of enlarging the animal against predators when enrolled.

ELAPHRAELLA NODUS (Qian, 1994)

Figure 3

Trianguraspis nodus QIAN, 1994, p. 52, pl. 4, figs. 9, 11, 12.

Trianguraspis pergranulosa QIAN, 1994, p. 53, pl. 4, fig. 13.

Diagnosis.—A species of *Elaphraella* with slightly curved facial suture in lateral view, and a rim-like ridge on pygidium, which bounds posterior end of axis, and is often ornamented with tumid marginal spines.

Material examined.—Thirty-nine cranidia, 25 librigenae, 26 thoracic segments, seven pygidia, and one complete meraspis.

Occurrences.—The uppermost two horizons of *Kaolishania* fauna of the Taebaeksan Basin, Korea; CS06 and CS09 of the Sagundari section. Associated trilobites include *Shirakiella* sp., *Pagodia* sp., *Lingyuanaspis* sp. and *Acanthometopus* sp. This species is also known from the *Acanthometopus* Zone of Northeast China (Qian, 1994).

Discussion.—Qian (1994) established *Trianguraspis* based on poorly-preserved flattened cranidia of *T. nodus*, noting that this trilobite is ornamented with stout nodes, and has a slightly depressed anterior cranial border. The presence of node-like ornamentations is subject to the high intraspecific morphological variation within the present collection which ranges from completely smooth surfaces (Fig. 3.10–3.13, 3.17, 3.35) to highly granulated surfaces (Fig. 3.18, 3.19, 3.37, 3.38). The anterior cranial border is not identifiable on the holotype specimen of *T. nodus* (Qian, 1994, pl. 4, fig. 9), and presumably a row of granules at the anterior cranial margin (Fig. 3.19) was mistakenly recognized as an anterior cranial

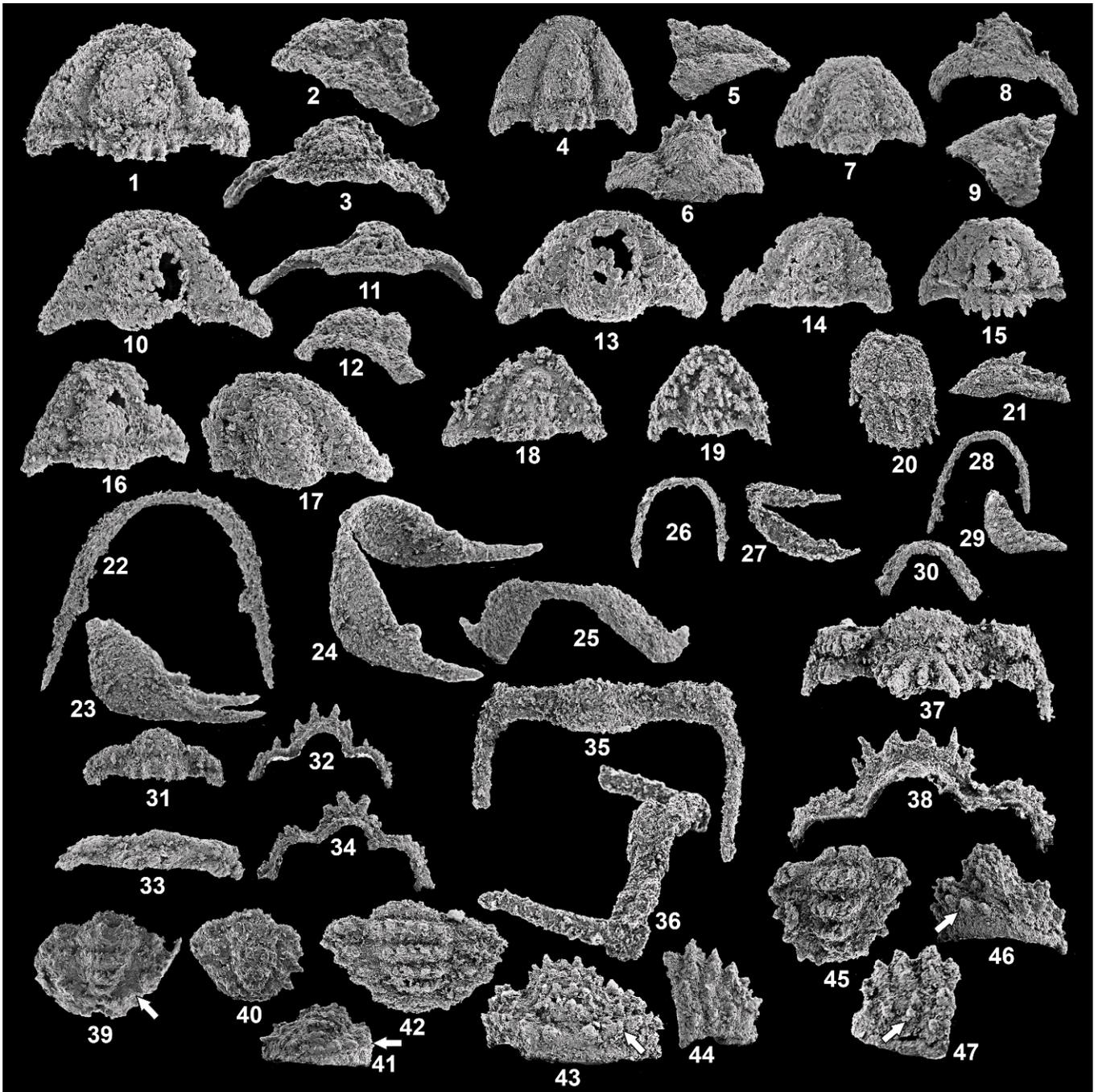


FIGURE 3—*Elaphraella nodus* (Qian, 1994). 1–19, cranidia: 1–3, SNUP6095, dorsal, lateral, and anterior views; 4–6, SNUP6096, dorsal, lateral, and anterior views; 7–9, SNUP6097, dorsal, anterior, and lateral views; 10–12, SNUP6098, dorsal, anterior, and lateral views; 13, SNUP6099; 14, SNUP6100; 15, SNUP6101; 16, SNUP6102; 17, SNUP6103; 18, SNUP6104; 19, SNUP6105; 20–21, a poorly preserved complete meraspis, SNUP6106, dorsal and lateral views; 22–30, librigenae: 22–25, SNUP6107, dorsal, lateral, oblique lateral, and anterior views; 26–27, SNUP6108, dorsal and oblique lateral views; 28–30, SNUP6109, dorsal, lateral, and anterior views; 31–38, thoracic segments: 31–32, SNUP6110, dorsal and anterior views; 33–34, SNUP6111, dorsal and anterior views; 35–36, SNUP6112, dorsal and oblique anterolateral views; 37, SNUP6113, dorsal view; 38, SNUP6114, anterior view; 39–47, pygidia: 39, SNUP6115; 40–41, SNUP6116, dorsal and posterior views; 42–44, SNUP6117, dorsal, posterior, and lateral views; 45–47, SNUP6118, dorsal, posterior, and lateral views. The arrows indicate the position of the rim-like ridge, which is often enhanced by a row of tumid tubercles. All figures, $\times 17$.

border. This species is closely similar to *E. microforma* in cranidia morphology (e.g., Fig. 3.1), and hence is assigned to *Elaphraella*. Qian (1994) also reported *T. pergranulosa* based on a single cranidium in poor preservation, mentioning that it also has an anterior cranial border. However, the anterior part of the holotype cranidium is not preserved (Qian, 1994, pl. 4, fig. 13), and the presence of the anterior cranial border

in this species is also doubtful. Overall, the holotype of *T. pergranulosa* displays the morphological features of *Elaphraella*, and thus is treated as a morphological variety of *Elaphraella nodus*. Qian (1994) reported this species from the *Acanthometopus* Zone of Northeast China, which overlies the *Kaolishania* Zone. The specimens in this study were recovered from the uppermost two horizons of the *Kaolishania* fauna in

association with *Acanthometopus* sp., and this stratigraphic occurrence also supports the synonymization of the *Trianguraspis* with *Elaphraella*.

Elaphraella nodus is distinguished from *E. microforma* in having relatively broad and short marginal spines on the cranidium, coarse and rod-like tubercles on the thoracic segments and pygidium, and a rim-like ridge on the pygidium. Although there are some variations, the facial suture is less sinuous than that of *E. microforma*, which can be clearly seen in the lateral views of librigenae (Fig. 3.23, 3.24, 3.27, 3.29). The rim-like ridge on the pygidium (Fig. 3.39, indicated by an arrow) is usually enhanced by a row of coarse tubercles (Fig. 3.40–3.47, indicated by arrows). Other trilobites with a rim-like ridge on the pygidium include ptychaspid trilobites, *Euptychaspis* Hupé, 1953 (see Adrain and Westrop, 2004, 2005) and *Asioptychaspis* Kobayashi, 1933 (see Park and Choi, 2010a), and diceratocephalid trilobites, *Cyclolorenzella convexa* and *Diceratocephalus cornutus* (see Park and Choi, 2010b). Considering the distant phylogenetic relationships among these trilobite families, the rim-like ridge in pygidium must have evolved several times over different lineages. This structure may be related to a certain function, such as a device for coaptation when enrolled.

ELAPHRAELLA? TAEBAEKSANENSIS new species

Figure 4

Diagnosis.—A shumardiid trilobite having a highly sinuous facial suture with conical glabella, but lacking anterolateral glabellar lobes and glabellar furrows.

Etymology.—From the name of Mt. Taebaeksan which is located close to the Sagundari section.

Types.—Holotype cranidium: SNUP 6119 (Fig. 4.1–4.3) from the *Kaolishania* fauna of the Sesong Formation, Taebaeksan Basin, Korea; the lowermost horizon of the upper part of the Sesong Formation at the Sagundari section, CS01. Paratypes: SNUP6121, 6122, and 6123.

Description.—Cranidium subtrapezoidal in outline, as long as wide. Surface smooth. Glabella convex, conical, about one-third of cranial width; axial furrows moderately incised and preglabellar furrows unclear; lateral glabellar furrows absent. Occipital ring sub-oval in outline, half as long as wide; posterior margin convex backwards; straight occipital furrow moderately incised. Preglabellar field gently downsloping. Anterior border absent. Facial suture sinuous in dorsal view. Fixigenal field moderately convex, downsloping peripherally. Posterior border transverse, downsloping abaxially, becoming longer abaxially; posterior border furrow wide, clearly incised.

Librigenae yoked with narrow doublure. Wide genal field strongly downsloping peripherally. Frontal part of doublure highly arched upward in anterior view. Genal spines about 40% of cranial length.

Axis of thoracic segments convex, one-third of thoracic width; axial ring short, convex anteriorly. Surface smooth. Pleural furrow transverse, moderately incised. Long macropleural spines, if present, directed backwards, slightly curved inwards. The macropleural spines of the largest thoracic segment (Fig. 4.29, 4.30) are directed backward and obliquely downward.

Pygidium not available.

Discussion.—Although this oldest shumardiid species displays a unique morphology with highly sinuous facial suture, it is assigned to *Elaphraella* with reservation due to the poor preservation of the present collection and the absence of pygidium at hand. The facial suture of this trilobite is highly sinuous in dorsal view, whereas the facial suture of other shumardiids is more-or-less straight in dorsal

view. The poorly preserved surface structure of the specimens hampers to make it clear whether the highly sinuous facial suture reflects the presence of small palpebral lobes. It can, at least, be argued that shumardiids may have evolved from a trilobite with small palpebral lobes and highly sinuous facial suture. This contrasts with the presence of large palpebral lobes of the *Oculishumardia*-like forms, and supports the second hypothesis of Park et al. (2008) in which the *Oculishumardia*-like forms of immature damesellids had nothing to do with the Shumardiidae. The preglabellar furrow is hardly seen in large cranidia, but is clearly-impressed in smaller cranidia (Fig. 4.6–4.9). The Furongian shumardiids with a clearly-impressed preglabellar furrow (e.g., *Elaphraella* Lu and Qian, 1983 and *Akoldinioidia* Zhou in Zhou and Zhang, 1984) may have been a result of a pedomorphic evolution.

The Laurentian genus *Clelandia* Cossmann 1902 is comparable to *Elaphraella? taebaeksanensis* in having a highly sinuous facial suture and a conical glabella, albeit *Clelandia* is upper Sunwaptan to lower Ibexian (see Westrop et al., 1993) in age, hence younger than *Elaphraella? taebaeksanensis*. Westrop et al. (1993) suggested that *Clelandia* differs from shumardiids in having a marked inflexion of facial suture and a conspicuous anterior cranial arch. These features are now shown by the primitive shumardiid *Elaphraella? taebaeksanensis*, and thus suggest a possible close phylogenetic relationship between shumardiids and *Clelandia*.

Material examined.—Thirteen cranidia, six librigenae, and 12 thoracic segments.

Occurrence.—*Kaolishania* fauna of the Taebaeksan Basin, Korea; CS01 of the Sagundari section. Associated trilobites include *Kaolishania granulosa* Kobayashi, 1933, *Taishania?* sp., and *Shirakiella* sp.

DISCUSSION

The morphology of the two primitive shumardiid trilobites, *Elaphraella? taebaeksanensis* and *Elaphraella microforma* allows us to infer the probable plesiomorphic condition of the Shumardiidae. They have a conical glabella, sinuous facial suture, a highly arched upward anterior cephalic margin, and wide librigenal field. This implies that the Shumardiidae originated from an ancestral stock with such morphological features, possibly with anteriorly located small palpebral lobes (Fig. 5). The morphology of *Elaphraella nodus*, the youngest of the three shumardiid species in this study, is also significant in that it has a facial suture which is less sinuous (slightly curved) than those of the older two species, and a rim-like ridge in the pygidium. Less sinuous facial sutures are seen in many younger shumardiids like *Akoldinioidia shanjiangensis* Peng et al. 2003, *Koldinioidia orientalis* (Mansuy, 1916) (see Zhu and Peng, 2006), and the Ordovician shumardiids (see Waisfeld et al., 2001). It is also noteworthy that some younger shumardiids have a rather inclined posterior pygidial margin which looks like a rim-like ridge (see Choi et al., 1994; Peng et al., 2003). Therefore, such features in *Elaphraella nodus* may be synapomorphies of this shumardiid and other younger shumardiids (Fig. 5).

It is noticeable that the species of *Elaphraella* form a paraphyletic group in the hypothetical phylogenetic tree (Fig. 5), and this paraphyly may necessitate a discussion. Since the rise of the cladistics-based classification, the monophyletic group is regarded as a desirable taxonomic group, and the paraphyletic group is treated as something to be avoided. Recently, however, many studies have argued that a concept of strict monophyly may lead to unsatisfactory classifications (e.g., Nordal and Stedje, 2005; Brummitt, 2006;

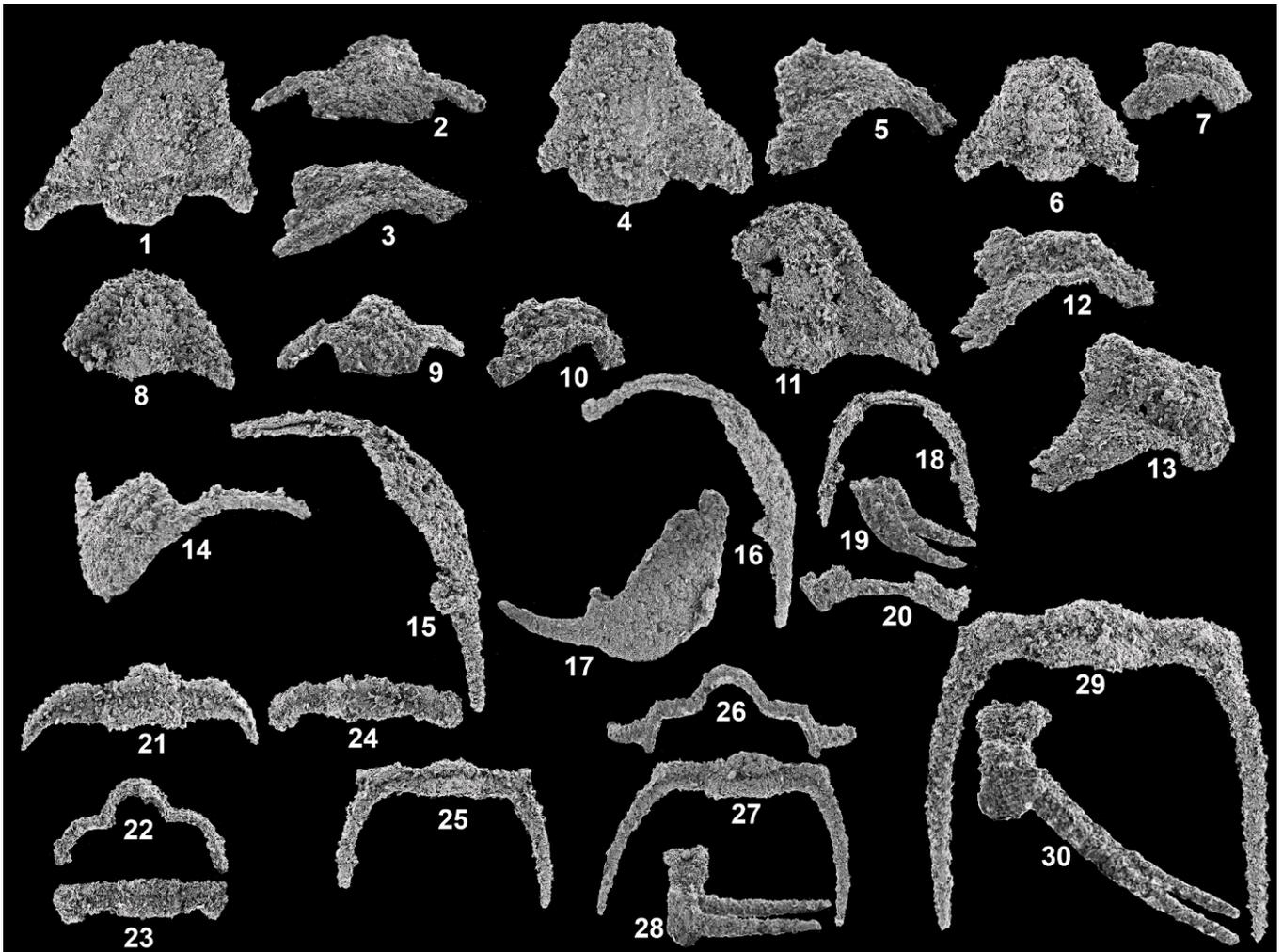


FIGURE 4—*Elaphraella? taebaeksanensis* new species. 1–3, cranidia: 1–3, holotype, SNUP6119, dorsal, anterior, and lateral views; 4–5, SNUP6120, dorsal and lateral views; 6–7, SNUP6121, dorsal and slightly anterolateral views; 8–10, SNUP6122, dorsal, anterior, and lateral views; 11–13, SNUP6123, dorsal, lateral, and oblique anterolateral views; 14–20, librigenae: 14–15, SNUP6124, anterior and dorsal views; 16–17, SNUP6125, dorsal and lateral views; 18–20, SNUP6126, dorsal, lateral, and anterior views; 21–30, thoracic segments: 21, SNUP6127; 22–23, SNUP6128, anterior and dorsal views; 24, SNUP6129; 25, SNUP6130; 26–28, SNUP6131, anterior, dorsal and lateral views; 29–30, SNUP6132, dorsal and lateral views. All figures, $\times 17$.

Hörandl, 2006). Indeed, the traditional taxonomy is often considered incompatible with a concept of strict monophyly (see Brummitt, 2002), because the traditional Linnean classification is based mainly on characters, without a priori knowledge of phylogenetic relationship. This contradiction has led to many well-known paraphyletic groups such as Reptilia, Dinosauria, and Pongidae. This issue becomes more complicated for paleontologists as paleontological data deals with evolution over time. At any given time, evolution occurs at species level while in Hennigian principles of cladistic classification certain dichotomies should represent a division at higher taxonomic rank. For example, two congeneric fossil species of similar morphology from a certain stratigraphic horizon should be differentiated at generic level if the two different lineages from the two species evolved into two different genera in younger strata. This is referred as the “boundary paradox” by Podani (2009, 2010).

In this study, we assume that *E. microforma* is a direct ancestral taxon of *E. nodus*, considering the close morphological similarity and the successive stratigraphic occurrences. If only these two species of *Elaphraella* are concerned, there would be no doubt in assigning the two morphologically

similar trilobites into the same genus. However, if we consider the synapomorphies shared by *E. nodus* and other derived shumardiids, the genus *Elaphraella* would be rendered paraphyletic as in Figure 5. Should *E. microforma* and *E. nodus* be separated at generic level due to the synapomorphies of *E. nodus* and other derived shumardiids? Such problems can be solved if paraphyletic grouping is allowed in classification, as suggested by many researchers (see Brummitt, 2002; Podani, 2009, 2010). In fact, in the recent debates over the usage of paraphyletic taxa the advantages of paraphyletic taxa are well explicated (e.g., Brummitt, 2002, 2003, 2006, 2008; Nordal and Stedje, 2005; Van Wyk, 2007; Hörandl, 2007, 2010; Podani, 2009, 2010). The advantage of the recognition of paraphyly is also appreciated in this study, and hence *Elaphraella* is suggested to be paraphyletic.

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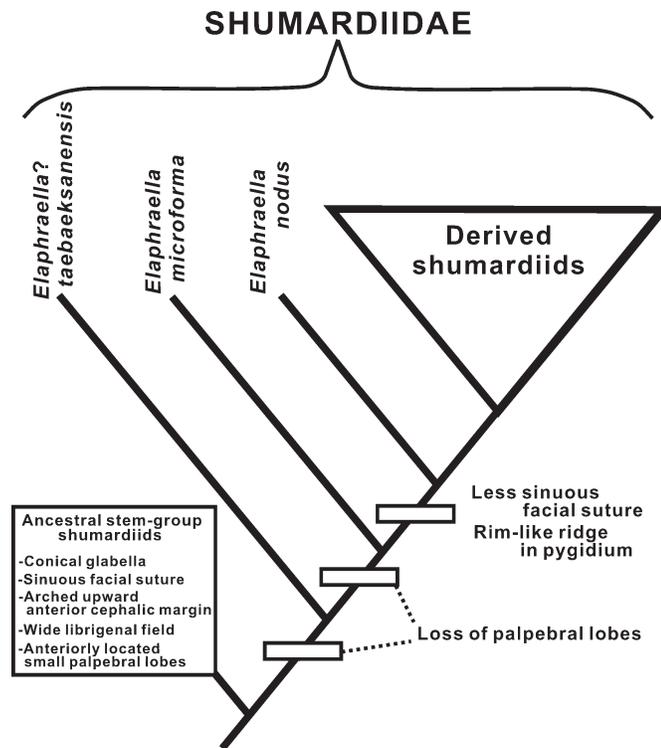


FIGURE 5—A simplified phylogenetic tree representing the evolutionary scenario of the Shumardiidae discussed in the text. Given the morphology of *Elaphraella? taebaeksanensis* and *Elaphraella microforma*, the hypothetical ancestral stem-group of shumardiids must have had a conical glabella, a highly sinuous facial suture, a wide librigenal field, and small palpebral lobes. Due to the poor preservation of *E.? taebaeksanensis*, it is not clear whether the palpebral lobes were lost before the evolution of *E.? taebaeksanensis* or before the evolution of *E. microforma*. The slightly curved facial suture and the rim-like ridge in pygidium of *Elaphraella nodus* might have been synapomorphies with the derived shumardiids. The genus *Elaphraella* is treated as a paraphyletic group in this tree (see text).

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