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TREMADOCIAN STYLOPHORAN ECHINODERMS FROM THE TAEBAEKSAN BASIN, KOREA

SEUNG-BAE LEE,[1] BERTRAND LEFEBVRE,[2] AND DUCK K. CHOI[1]

[1] School of Earth and Environmental Sciences, Seoul National University, Seoul 151-747, Korea, <sblee77@snu.ac.kr>, <dkchoi@snu.ac.kr> and
[2] UMR Biogéosciences, Université de Bourgogne, 6 boulevard Gabriel, 21000 Dijon, France, <bertrand.lefebvre@u-bourgogne.fr>

ABSTRACT—Abundant isolated elements of cornute and mitrate stylophorans were recovered from the upper Tremadocian Tumugol Formation in the Taebaeksan Basin, Korea. Cornute skeletal elements comprise a diverse assemblage of marginals and brachials of cothurnocystid affinities, suggesting the presence of no fewer than four different species. Mitrate remains include numerous isolated adorals, marginals, and aulacophoral plates with typical peltocystidan morphologies. Two adorals are identified as *Anatifopsis* sp., while all the others are attributable to *A. cocaban*. However, the two previously documented peltocystidans of Korea, *A. cocaban* and *A. truncata*, are sufficiently distinct from other *Anatifopsis* species to warrant assignment to a new genus, *Taebaekocystis*. Cladistic analyses suggest that Lagynocystida is the sister group of the clade uniting peltocystidans and mitrocystitidans and that the adorals of *Taebaekocystis* n. gen. and associated isolated peltocystidan elements possibly account for several different types of peltocystidans, intermediate in morphology between Peltocystidae and Kirkocystidae.

INTRODUCTION

STYLOPHORANS ARE nonradiate echinoderms known from Middle Cambrian to Upper Carboniferous strata. The class Stylophora Gill and Caster, 1960 embraces the two orders Cornuta Jaekel, 1901 and Mitrata Jaekel, 1918, which share the same basic organization with a flexible appendage (aulacophore) articulated with a flattened, asymmetrical body (theca). Both theca and appendage are composed of numerous skeletal elements, each consisting of a single crystal of calcite with typical stereomic microstructure of echinoderm plates (Ubaghs, 1968; Smith, 1990). The phylogenetic position of stylophorans has been controversial for many years. These calcite-plated, asymmetrical fossils were originally interpreted as primitive, nonradiate echinoderms (Bather, 1929; Chauvel, 1941; Gill and Caster, 1960; Ubaghs, 1975; Kolata and Jollie, 1982; Parsley, 1988; Sprinkle, 1992), whereas other researchers regarded them as primitive chordates retaining an echinoderm-like stereomic skeleton, the ''calcichordates'' (Jefferies, 1968; Cripps, 1991; Daley, 1992; Gil Cid et al., 1996; Ruta, 1997). In this study, stylophorans are considered to be derived echinoderms (Sumrall, 1997; Dzik, 1999), closely related to arm-bearing groups (e.g., asterozoans, crinoids; Nichols, 1972; David et al., 2000). The orientation and anatomical terminology used herein are those proposed by Ubaghs (1963, 1968) and the identification of homologous skeletal elements (plates) follows the scheme proposed by Lefebvre and Vizcaïno (1999) and Lefebvre (2000a, 2001).

Numerous isolated skeletal elements of stylophorans were collected from the lower part of the Tumugol Formation (upper Tremadocian) of the Taebaeksan Basin, Korea (Fig. 1). The Tumugol Formation has yielded diverse and abundant fossils, including bivalves, brachiopods, cephalopods, conodonts, echinoderms, gastropods, and trilobites (Kobayashi, 1934; Choi and Lee, 1988; Seo et al., 1994). However, except in the case of conodonts and trilobites, little attention has been paid so far to other fossil groups. Stylophorans from the Tumugol Formation comprise cothurnocystid cornutes and peltocystidan mitrates. Cothurnocystid cornutes are asymmetrical stylophorans, with a long, relatively rigid aulacophore and a delicate theca consisting of large polyplated integumentary areas bordered by a narrow marginal frame (Fig. 2.1). Peltocystidans are nearly symmetrical forms with a long and highly flexible appendage and a massive theca characterized by two very large plates, the adorals. In some peltocystidans (kirkocystids), adorals not only cover the whole upper thecal surface, but they also extend on the lateral edges of the lower side (Fig. 2.2–2.4). The isolated adorals of Korean peltocystidan mitrates were originally described as *Anatifopsis cocaban* Kobayashi, 1960 and *A. truncata* Kobayashi, 1960 from the Mungok Formation, Yongwol Group, but they were interpreted as isolated valves of cirriped crustaceans (Kobayashi, 1960) or problematica (Choi and Lee, 1988; Choi and Kim, 1989; Choi, 1990). Probable affinities of *A. cocaban* and *A. truncata* with peltocystidan mitrates were recently suggested by Domínguez and Gutiérrez (1990) and Lefebvre (1999). Based on detailed morphometric analyses of isolated peltocystidan adorals from the Tremadocian of Korea, Lee et al. (2004) demonstrated that Korean peltocystidan adorals are highly variable in shape and distinct from comparable elements from Europe and North Africa. Subsequent examination of the morphology of Korean adorals enabled us to suggest the presence of a new genus *Taebaekocystis*, to which *A. cocaban* and *A. truncata* are assigned.

The aims of this paper are 1) to describe the first record of Tremadocian cornutes from Korea; 2) to describe isolated thecal and aulacophoral skeletal elements of peltocystidan mitrates from the Tumugol Formation; and 3) to perform the first character-based cladistic analysis of peltocystidan mitrates, so as to determine the phylogenetic position of *Taebaekocystis*.

GEOLOGIC SETTING, FOSSIL LOCALITIES, AND AGE

The Cambrian–Ordovician sedimentary rocks of the Choson Supergroup are distributed in the Taebaeksan Basin, central-eastern part of the Korean Peninsula (Fig. 1). The Choson Supergroup is an upper Lower Cambrian to lower Upper Ordovician siliciclastic-carbonate sequence resting unconformably on the Precambrian granitic gneiss and metasedimentary rocks. It is in turn overlain unconformably by post-Ordovician sedimentary rocks. Based on lithologic successions and geographic distributions, the Choson Supergroup can be divided into five groups: the Taebaek, Yongwol, Yongtan, Pyongchang, and Mungyong groups (Choi, 1998). All stylophoran specimens investigated herein were collected from the Tumugol Formation of the Taebaek Group. The Taebaek Group comprises, in ascending order, the Changsan/Myonsan, Myobong, Taegi, Sesong, Hwajol, Tongjom, Tumugol, Makkol, Chigunsan, and Tuwibong Formations (Kobayashi, 1966; Choi, 1998). The Cambrian–Ordovician boundary was drawn at the base of the Tongjom Formation by Kobayashi (1966), but recently Choi et al. (2003) suggested that the newly defined Cambrian–Ordovician boundary (Cooper et al., 2001) should be placed within the lower part of the Tongjom Formation.

All specimens described in this study are from two separate localities exposed in the southeastern corner of the Taebaeksan

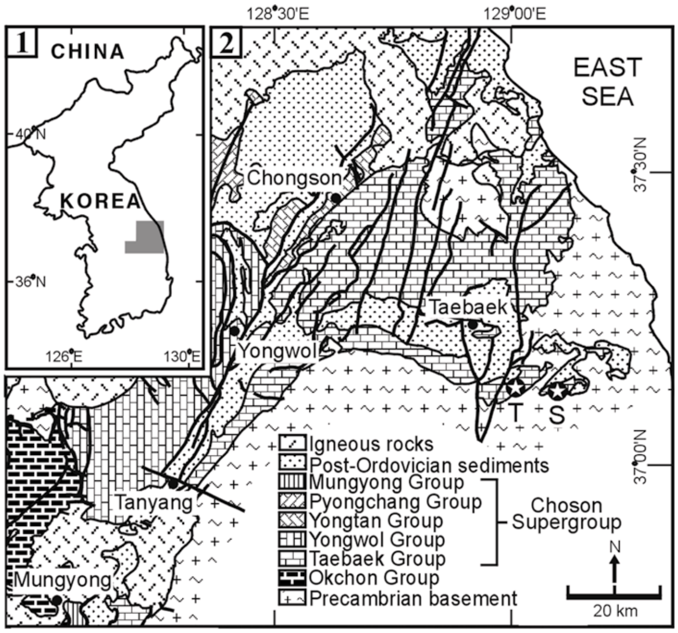

FIGURE *1*—Locality maps. *1*, Map of Korean peninsula showing the position of *2*; *2*, simplified geologic map showing the distribution of the Choson Supergroup in the Taebaeksan Basin, Korea. Two circled stars in the lower right position represent fossil localities, Tongjom (T) and Sokkaejae (S) sections.

Basin: the Tongjom section situated about 15 km southeast of Taebaek and the Sokkaejae section exposed about 9 km east from the Tongjom section (Fig. 1). About 150 isolated skeletal elements were collected from the calcareous shale slabs.

The Tongjom section measures about 120 m thick and represents approximately the lower two-thirds of the Tumugol Formation (Fig. 3). The Tumugol Formation at the section comprises shale, calcareous shale, nodular limestone, lime mudstone, packstone to grainstone, and limestone conglomerate. Kim et al. (1991) recognized three trilobite biozones within the formation: *Asaphellus*, *Protopliomerops*, and *Kayseraspis* zones in ascending order. The *Asaphellus* and *Protopliomerops* zones are attributed to the late Tremadocian, and the *Kayseraspis* Zone to the early Arenigian. Stylophoran specimens were collected from eight fossil horizons of the *Asaphellus* Zone of the section (Fig. 3).

The Sokkaejae section occurs along a mountain trail at an altitude of approximately 1,000 m, where a nearly complete succession of the Taebaek Group (about 1,100 m thick) is exposed (Choi et al., 2004). Good exposure along the trail reveals that the Tumugol Formation measures about 200 m thick. The lower part (ca. 75 m thick) is characterized by a monotonous lithology composed largely of calcareous shale. The upper part (ca. 125 m thick) is an alternating succession of ribbon rock, bioturbated limestone, limestone conglomerate, and bioclastic grainstone to packstone. The calcareous shale facies yields abundant invertebrate fossils including brachiopods, echinoderms, gastropods, ostracods, plumulitids, and trilobites, while other parts of the formation are poorly fossiliferous. The stylophorans were recovered from nine fossiliferous intervals of the lower calcareous shale facies (upper Tremadocian) of the Tumugol Formation (Fig. 3).

SYSTEMATIC PALEONTOLOGY

All specimens are deposited in the paleontological collections of Seoul National University with registered SNUP numbers. Several specimens with PA numbers were originally studied by Kobayashi (1960) and are currently stored at the University Museum, University of Tokyo, Japan.

Class STYLOPHORA Gill and Caster, 1960
Order CORNUTA Jaekel, 1901
Figure 4

Description.—Three isolated marginals M′1 (0.6–0.8 mm long), all in internal (upper) view (Fig. 4.11–4.13). Skeletal elements characterized by T-shape outlines, presence of left apophysis (on right anterior branch), and possession of zygal crest on

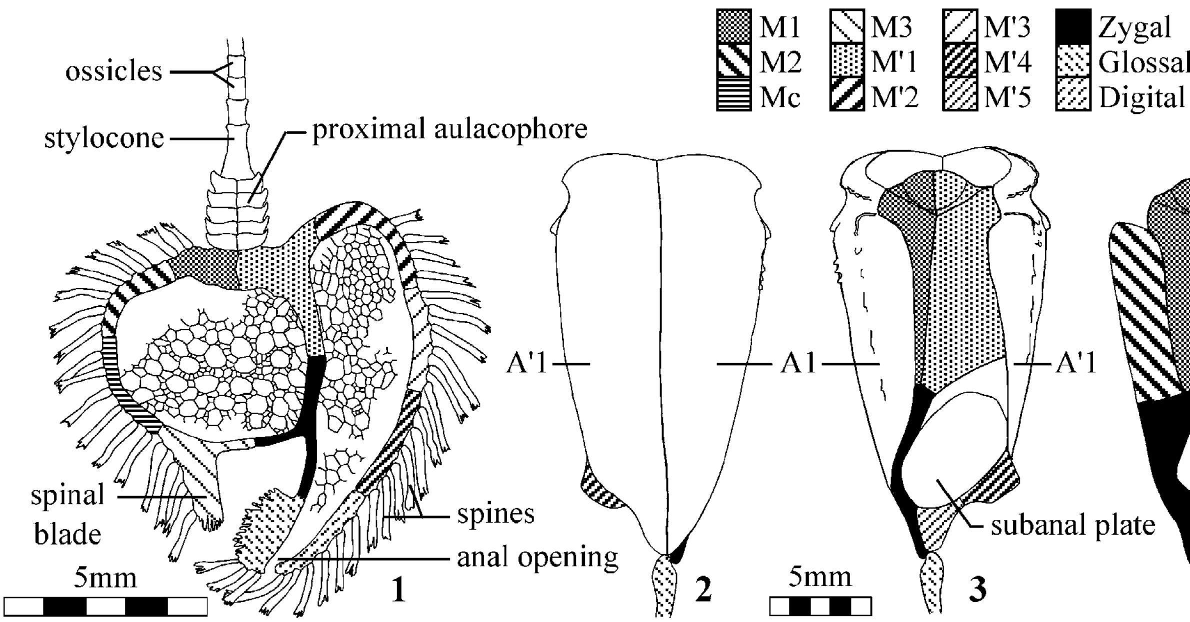

FIGURE 2—Morphology of a cothurnocystid cornute and of a peltocystidan mitrate. Identification of marginals based on Lefebvre (2001). *1*, *Chauvelicystis vizcainoi* Daley, 1992 (Cornuta), Lower Ordovician, Montagne Noire (southern France); redrawn and modified after Ubaghs (1983); *2*–*4*, *Balanocystites primus* (Barrande, 1887) (Mitrata), Middle Ordovician, Bohemia (Czech Republic); redrawn after Lefebvre (1999, 2001); *2*, upper thecal surface; *3*, lower thecal surface; *4*, lower thecal surface, adorals (A′1, A1) and integument omitted.

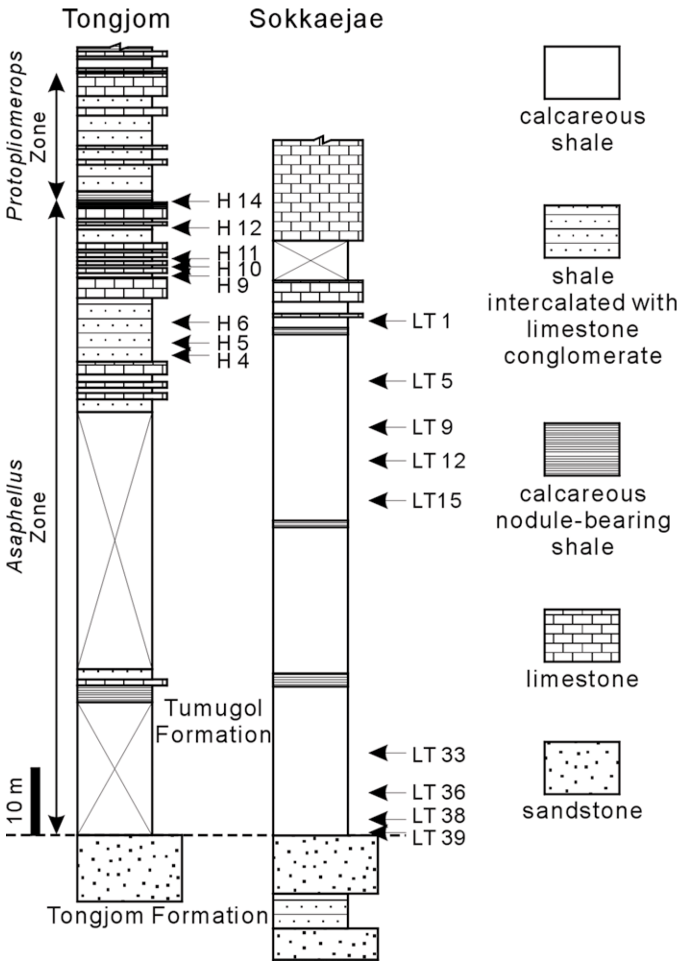

FIGURE 3—Generalized columnar sections of the two fossil localities of the Tumugol Formation, showing lithology and fossil horizons.

internal surface of posterior (or zygal) branch. Three distinct morphologies exhibited by isolated marginal M′1: 1) convex anterior margin and short, stout zygal branch (Fig. 4.11); 2) convex anterior margin and long, narrow posterior branch (Fig. 4.12); and 3) concave anterior margin and left branch with thickened abaxial extremity (Fig. 4.13).

Several Y-shaped skeletal elements with spinal blade (strong flattened spike directed downwards and rearwards, located at right posterior angle of theca in boot-shaped cornutes). Spinal-bearing marginals corresponding either to marginals M3 or Mc. Spinal-bearing plates about 0.9–2.4 mm long, consisting of two marginal branches (belonging to thecal frame) with massive stereom, and one spike (spinal blade) consisting usually of fibrillar stereom. Typically, anterior marginal branch of spinal-bearing plates stouter and larger than posterior marginal branch. At least four distinct morphologies within isolated spinal-bearing plates: 1) short anterior branch, elongate posterior branch, and long spinal blade with a sharp posterior extremity (Fig. 4.1, 4.2); 2) short anterior and posterior marginal branches, and long, fibrillar, posteriorly spatulate spinal blade (Fig. 4.9, 4.10); 3) anterior marginal branch much longer than posterior one, delimiting an angle of about 60° with it, and short spinal blade (Fig. 4.5–4.7); and 4) posterior marginal branch slightly longer than anterior one, delimiting an angle of about 80° with it, and short spinal blade (Fig. 4.4).

Two different morphologies of posterior marginals flanking anal opening (glossal, digital): 1) fan-shaped marginals (about 1.5 mm long), characterized by narrow and elongate anterior portion, and large, spatulate posterior region showing typical radiating fibrillar ornamentation; such plates usually corresponding either to digital or glossal elements (Fig. 4.8); 2) elbow-shaped glossals (about 1.2 mm long), characterized by large, rounded spatulate area exhibiting strong fibrillar ornamentation radiating from L-shaped, narrow marginal fringe (Fig. 4.20).

Identification of other marginals more problematic. Some curved plates without ornamentation possibly correspond to several different lateral marginals, such as M2, Mc, M3, or M′2 (Fig. 4.3).

Small isolated spiny elements (Fig. 4.14, 4.15; about 0.5 mm long), identical to those articulated to thecal frame in several cothurnocystid cornutes (Chauvelicystinae Daley, 1992; Fig. 2.1), and consisting of a thickened, massive, proximal articular base, and a long narrow spine, with typical fibrillar ornamentation (see Chauvel, 1966; Ubaghs, 1969, 1983; Lefebvre and Vizcaïno, 1999).

Numerous isolated stylocones in upper view, corresponding to elongate and narrow quadrangular elements (0.5–0.7 mm long), with distinct longitudinal median groove on upper (internal) surface (Fig. 4.17–4.19). Median groove bordered by two raised longitudinal lips diverging proximally on each side of proximal cavity, with no sign of transverse channels. Median groove disappearing through a proximal notch into short proximal cavity of stylocone. At least two articular facets for cover plates visible on each side of median groove on stylocone. More posterior brachials relatively long, quadrangular, clearly showing longitudinal median groove, but apparently with no transverse channels (Fig. 4.16). Isolated cover plates flat, subcircular to elliptical, with thick articulatory facet on lower edge, and typical radiating ornamentation.

Material examined.—More than 40 isolated cornute fragments from the Tumugol Formation, Sokkaejae and Tongjeom sections, Korea, including marginal elements, spines originally articulating to the marginal frame, several brachials (stylocones, ossicles), and cover plates.

Occurrence.—*Asaphellus* Zone (late Tremadocian), Tumugol Formation, Korea.

Discussion.—In cornutes, intraspecific variation is usually reduced (Cripps, 1988; Lee et al., 2005). Consequently, the wide array of morphologies exhibited by various skeletal elements (e.g., M′1, spinal-bearing marginals, and posterior marginals) suggests the presence of several (at least four) species of cornutes in the Tumugol Formation. Their precise taxonomic assignment is, however, impossible due to the absence of complete and well-preserved specimens. Nevertheless, the occurrence of cothurnocystid cornutes is strongly supported by: 1) the fan-shaped posterior marginals (Fig. 4.8, 4.20; these plates are narrow and elongate in amygdalothecids and hanusiids); 2) the presence of spines articulated to the marginal frame (Fig. 4.14, 4.15; apomorphy of the Chauvelicystinae; Daley, 1992; Lefebvre and Vizcaïno, 1999; Lee et al., 2005); and 3) the brachials with no transverse channels (Fig. 4.16; observed only in most Chauvelicystinae and in some Scotiaecystinae Caster and Ubaghs *in* Ubaghs, 1968; see Ubaghs, 1969, 1983; Lefebvre and Vizcaïno, 1999). Strong spinal blades occur mostly within the Cothurnocystidae Bather, 1913 as M3 or rarely as Mc (Scotiaecystinae; Lefebvre and Vizcaïno, 1999; Lefebvre, 2001), but they can be also present in some primitive hanusiids as M3 or M′3 (e.g., *Drepanocarpos* Smith and Jell, 1999, *Galliaecystis* Ubaghs, 1969, and *Hanusia* Cripps, 1989).

Order MITRATA Jaekel, 1918

Suborder PELTOCYSTIDA Jefferies, 1973

Emended diagnosis.—Suborder of mitrates with asymmetrical to nearly bilaterally symmetrical theca; lower thecal surface composed of reduced number of marginal plates (M′2 lost); apophyses

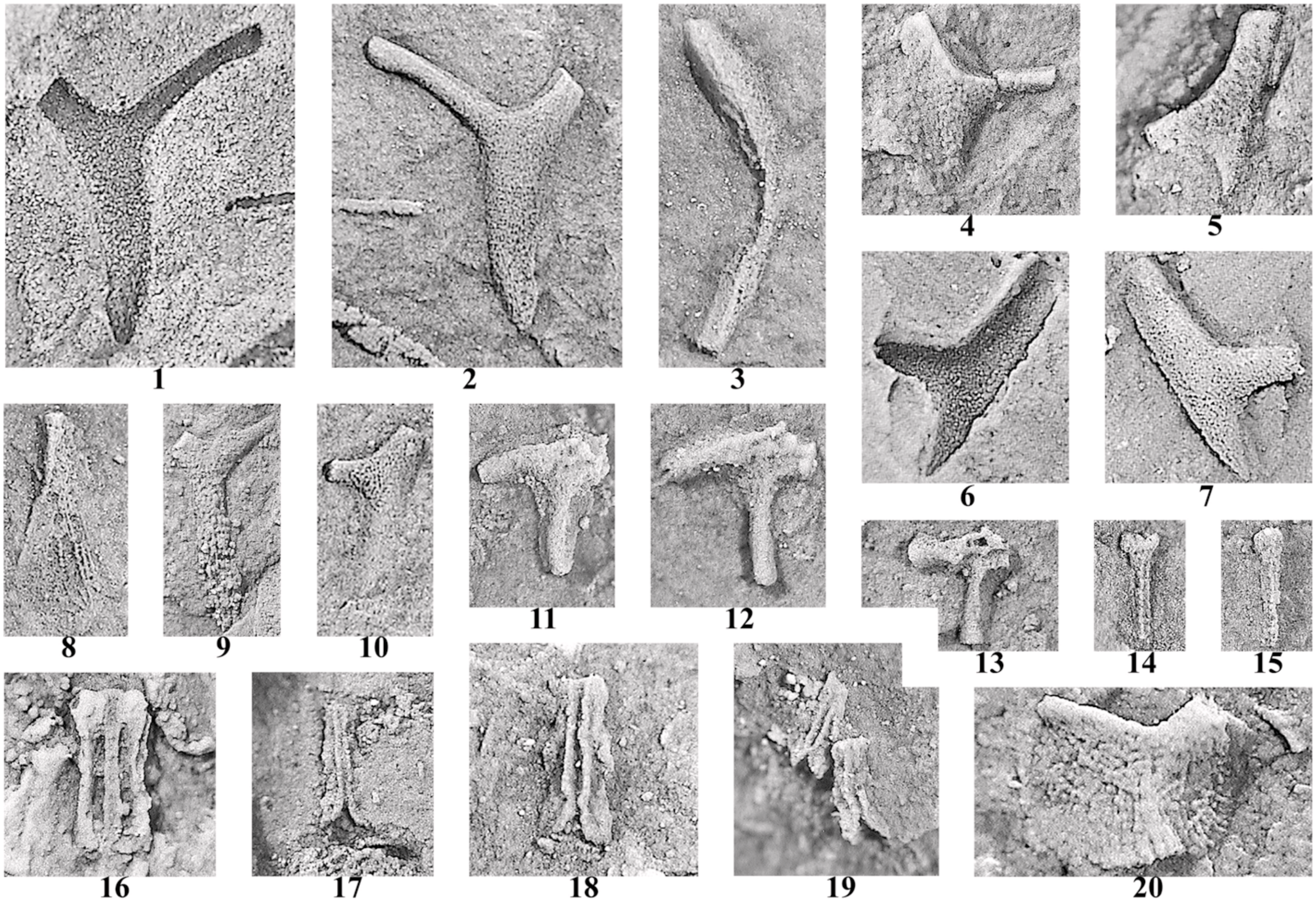

FIGURE 4—Isolated skeletal elements of cornutes from the *Asaphellus* Zone, Tumugol Formation of Tongjom and Sokkaejae sections, Taebaeksan Basin, Korea. Stratigraphic intervals in brackets. *1–13, 20,* Marginal elements; *1, 2,* upper surface of spinal blade, SNUP2504 (H14), natural mold and latex cast, ×16.8; *3*, upper surface of curved lateral marginal, SNUP2512 (H5), latex cast, ×16.8; *4*, lower surface of spinal blade, SNUP2509 (H14), latex cast, ×26.9; *5*, upper surface of spinal blade, SNUP2523 (LT33), latex cast, ×21.3; *6, 7*, lower surface of spinal blade, SNUP2502 (H14), natural mold and latex cast, respectively, ×21.3; *8*, posterior marginal, SNUP2501 (H14), latex cast, ×21.3; *9*, lower surface of spinal blade, SNUP2506 (H14), latex cast, ×20.2; *10*, upper surface of spinal blade, SNUP2503 (H14), latex cast, ×21.3; *11*, upper surface of M′1, SNUP2510 (H14), latex cast, ×28.3; *12*, upper surface of M′1, SNUP2508 (H14), latex cast, ×28.3; *13*, upper surface of M′1, SNUP2507 (H14), latex cast, ×28.3; *20*, posterior marginal, SNUP2514 (LT39), latex cast, ×25.5. *14, 15,* Latex cast of spiny element; *14*, SNUP2540 (LT9), ×36.1; *15*, SNUP2544 (LT9), ×30.7. *16–19,* Arm elements; *16,* brachial, SNUP2511 (H14), latex cast, ×28.3; *17,* stylocone, SNUP2541 (LT9), latex cast, ×31.1; *18,* stylocone, SNUP2517 (LT39), latex cast, ×28.3; *19*, two stylocones, SNUP2518 (LT39), latex cast, ×28.3.

with no hornlike processes; plate Z in marginal position; one or two infracentral areas; glossal as exothecal process, articulated to posterior extremity of theca; digital absent; periproct floored by anal plate; two very large adorals covering most or all of upper thecal surface; variously developed knobs on adorals, when adorals extend on lower thecal surface; no right adoral orifice and no pairs of pores on lower surface; long and flexible aulacophore; proximal aulacophore consisting of tetrameric rings with inferolaterals and tectals of subequal size; small integumentary platelets often present between proximal rings; stylocone and proximal ossicles spinose; no transverse channels along median longitudinal groove.

Discussion.—Peltocystida includes three families, Peltocystidae Ubaghs, 1968, Kirkocystidae Caster, 1952, and Jaekelocarpidae Kolata et al., 1991. Members of the Peltocystida have been often grouped with *Lagynocystis* (Barrande, 1887) in the family Lagynocystidae Jaekel, 1918, and/or in the suborder Lagynocystida Caster, 1952, on the basis of the possession of a single posterior exothecal process both in *Lagynocystis* and in peltocystidans (Jaekel, 1918; Chauvel, 1941; Caster, 1952, 1983; Ubaghs, 1968, 1979; Derstler, 1979; Domínguez and Gutiérrez, 1990). The suborder Peltocystida was proposed by Jefferies (1973), based on the observation that posterior exothecal processes are not homologous in *Lagynocystis* (digital) and in other peltocystidans (glossal). Plate homologies and cladistic analyses (see below) both strongly support the separation of Peltocystida from Lagynocystida, and the monophyly of the suborder Peltocystida (Jefferies, 1986; Parsley, 1991, 1997, 1998; Kolata et al., 1991; Vizcaïno and Lefebvre, 1999; Lefebvre, 2000b, 2001). Morphology of post-Ordovician peltocystidans (e.g., "*Mitrocystites*" *styloideus* Dehm, 1934; *Jaekelocarpus oklahomaensis* Kolata et al., 1991) is still poorly known and their origin is unclear. However, a recent reinvestigation of the anatomy of *Jaekelocarpus oklahomaensis* based on better-preserved specimens (Domínguez et al., 2002, fig. 1) confirms the presence of three marginal elements overlooked in previous descriptions.

ISOLATED PELTOCYSTIDAN ELEMENTS

Figures 5–7

Description.—Isolated marginals M′1 3–8 mm long, polygonal, with well-defined transverse anterior groove (on posterior wall of

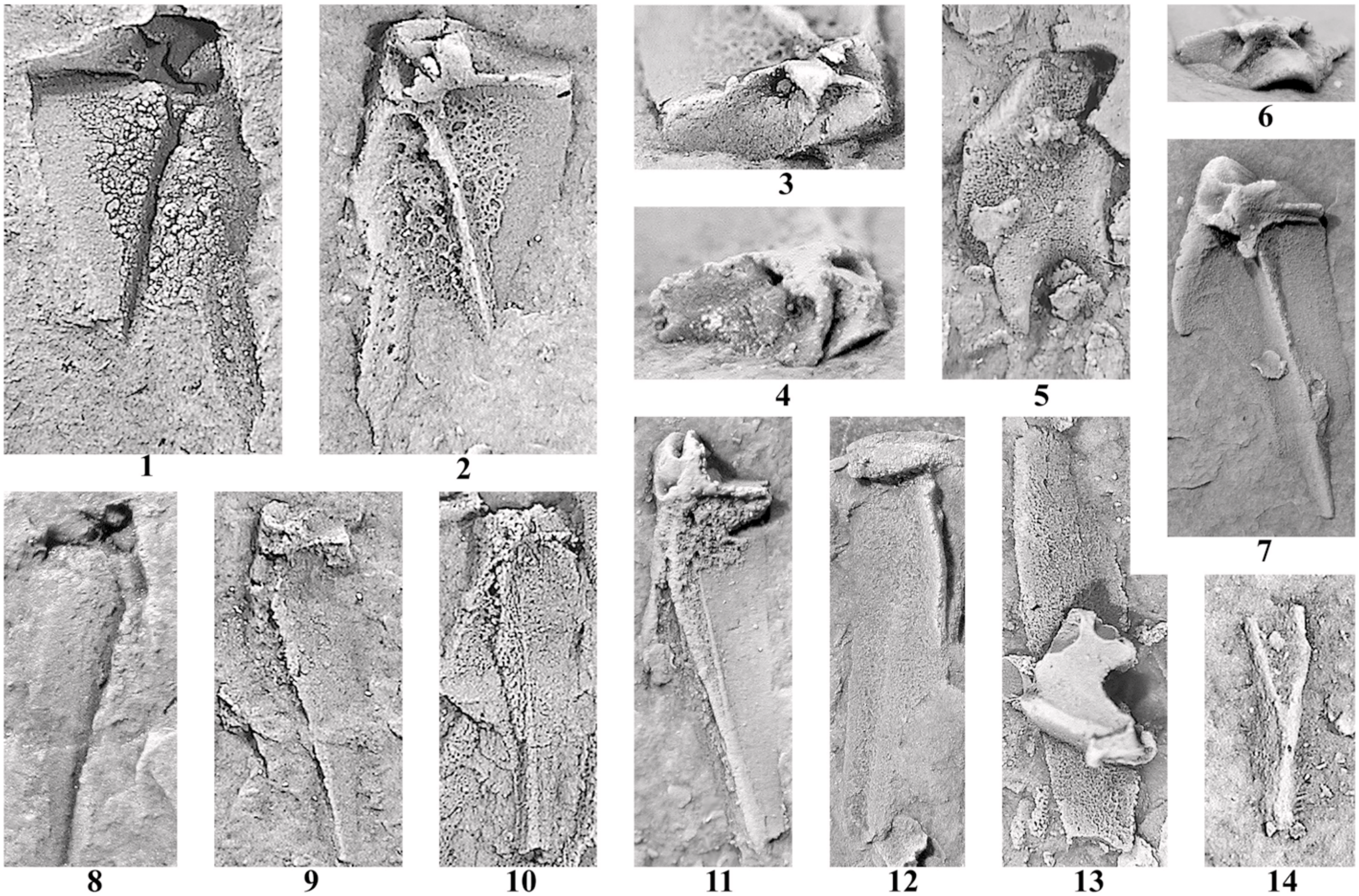

FIGURE 5—Isolated peltocystidan marginal elements from the *Asaphellus* Zone, Tumugol Formation of Sokkaejae section, Taebaeksan Basin, Korea. Stratigraphic intervals in brackets. *1–3,* Type C marginal M′1, SNUP2543 (LT9); *1, 2*, plan view of internal mold and latex cast, respectively, ×10.7; *3*, front view of latex cast, ×13.0. *4, 11,* Latex cast of type A marginal M′1, SNUP2527 (LT9); *4*, front view, 17.1; *11*, plan view, 8.9. *5,* Latex cast of lower surface of polygonal marginal Z, SNUP2548 (LT9), ×16.7. *6, 7,* Latex cast of type B marginal M′1, SNUP2549; *6*, front view, ×7.6; *7*, plan view, ×6.6. *8, 9,* Marginal M′1, SNUP2513 (LT39); *8*, plan view of internal mold, ×12.7; *9*, plan view of latex cast, ×12.7. *10,* Latex cast of SNUP2533 (LT9); plan view of marginal M′1, ×13.4. *12,* Latex cast of SNUP2547 (LT36), lower surface of marginal M′1, ×7.4. *13,* Latex cast of SNUP2542 (LT9), plan view of marginal (M2 or M′3), ×13.6. *14,* Latex cast of Y-shaped marginal Z, SNUP2519 (LT38), ×14.3.

apophyses), and scutulae facing both laterally and upwards. At least three different morphologies evidenced within isolated M′1, and designated below as morphotypes A (eight specimens), B (one specimen), and C (one specimen). Type A marginals M′1 (Figs. 5.8–5.12, 6.1, 6.2) corresponding to long and narrow skeletal elements, with a strongly concave anterior margin, a straight to slightly concave adaxial edge (suture along M1), a short and sharp posterior extremity, and an abaxial border consisting of two subequal parts: a low, concave posterior region and an upfolded, straight anterior portion, subparallel to adaxial edge. In frontal view, left half of apophysis cup slightly wider than high, separated from narrow abaxial field by strong apophysis crest. Left scutula small and shallow. Antero-abaxial corner of lower surface forming low protuberance. Zygal crest merging anteriorly with abaxial margin, at sharp angle. Low longitudinal ridge running from posterior wall of left apophysis, right of left scutula, and converging posteriorly towards zygal crest. Type A M′1 mostly flat or slightly depressed in external (lower) aspect, except for downwards recurved edges along anterior margin and anterior half of abaxial side. Course of zygal crest visible on lower (external) surface of M′1 as a low, oblique, depressed area. Type B M′1 (Figs. 5.6, 5.7, 6.3, 6.4) a long and broad marginal, with concave anterior margin, straight adaxial edge, and abaxial border consisting of two unequal parts: a long, strongly concave low posterior portion and a shorter, oblique, gently convex, and upfolded anterior region. Posterior extremity of plate incompletely preserved, possibly narrow and elongate. In frontal view, left half of apophysis cup slightly wider than high, separated from relatively large abaxial field by strong apophysis crest. Left scutula deep and large. Antero-abaxial corner of lower surface presumably forming a strong and large protuberance directed downwards. Course of zygal crest straight to slightly bent, nearly perpendicular to posterior wall of left apophysis and subparallel to adaxial edge of M′1. Large, raised bump (platform) at junction between transverse anterior groove and zygal crest. Type C marginals M′1 (Figs. 5.1–5.3, 6.5, 6.6) corresponding to relatively large and broad, posteriorly poorly preserved skeletal element, with slightly concave anterior margin, straight adaxial edge, and abaxial border consisting of two unequal parts: a long, slightly concave low posterior region and a shorter, upfolded, straight anterior portion, subparallel to adaxial edge. In frontal view, left half of apophysis cup about two times wider than tall, separated from large abaxial field by low apophysis crest. Left scutula large and deep. Antero-abaxial corner of lower surface presumably forming a strong protuberance. Zygal crest oblique to posterior wall of left apophysis

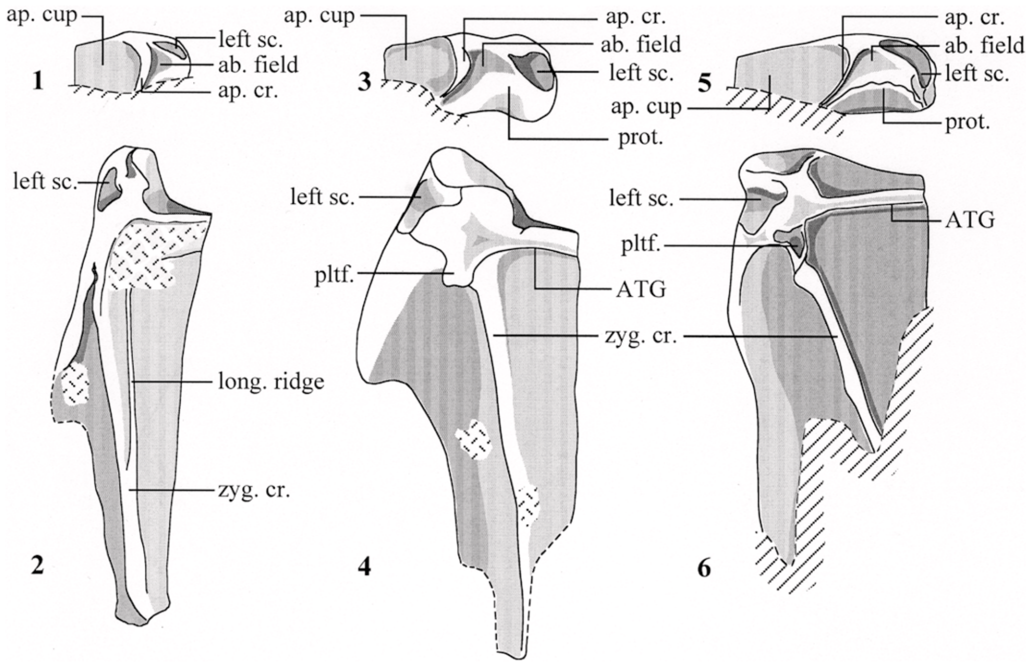

FIGURE 6—Line drawings of three types of marginal M′1 presenting locations and nomenclatures of anatomical features, based on SNUP2548, SNUP2549, and SNUP2543, respectively. ab. field = abaxial field; ap. cr. = apophysis crest; ap. cup = apophysis cup; ATG = anterior transverse groove; left sc. = left scutula; long. ridge = longitudinal ridge; pltf. = platform; prot. = protuberance; zyg. cr. = zygal crest.

and anteriorly connected to abaxial margin of M′1 by an accessory septum. Large and deep platform at junction between transverse anterior groove and zygal crest.

Two isolated marginals M1, both in internal aspect: one from Sokkaejae (stratigraphic level LT-36), small (1.6 mm long) and well preserved, and other from Tongjom (stratigraphic level H12), incomplete and poorly preserved. M1 from Sokkaejae comparable to associated type C marginals M′1, with broad outline and slightly concave anterior margin. Internal (upper) surface depressed and particularly deep posteriorly to posterior wall of right apophysis and along anterior portion of right (abaxial) margin. Right half of apophysis cup relatively deep, as wide as tall, and separated from narrow abaxial field by strong apophysis crest.

At least two morphotypes of zygal plates Z in Sokkaejae section: 1) elongate, small, subtriangular elements, with (in internal aspect) typical Y-shaped ridge resulting from the joining at sharp angle of the posterior portion of zygal crest with the abaxial edge of Z; 2) large polygonal elements (only documented in external aspect), with posterior protuberance for articulation of glossal.

A long and narrow quadrangular isolated element (Fig. 5.13; about 4 mm long) from Sokkaejae (stratigraphic level LT9) possibly corresponding to lateral marginal M2 in upper (internal) aspect. Adaxial edge thickened and nearly straight (suture along M1), whereas abaxial border much thinner and slightly convex. Posterior edge of M2 thickened and slightly concave; anterior margin much thinner and convex.

Stylocones represented by six small (1–1.3 mm long), bobbin- to saddle-shaped elements, all in lower view, with broad anterior and posterior regions connected by narrow neck. Anterior region V-shaped, with articulating surface. Posterior region large, decreasing rapidly in height proximally. Sculpture weak on lower surface, consisting of low median longitudinal crest posteriorly and, sometimes, weak, laterally compressed, downwards and rearwards recurved median spine, anteriorly. Upper (inner) surface of isolated ossicles rather broad, with a well-marked longitudinal median groove and no transverse channels. Isolated cover plates high (up to 1.3 mm) spearheadlike, curved, with thickened articular process protruding on lower edge. Three incomplete articulated arms with left and right series of cover plates articulated to ossicles; upper edges of cover plates alternating with left plates consistently slightly preceding right ones (Fig. 7.1).

Material examined.—Peltocystidan elements comprise about 20 marginals: a dozen of M′1 (with left apophysis, left scutula, and anterior portion of zygal crest; Figs. 5.1–5.4, 5.6–5.12, 6), marginals M1 (with right apophysis and right scutula), zygal plates Z (with posterior portion of zygal crest and/or protuberance for the articulation of glossal; Fig. 5.5, 5.14), and one lateral marginal (Fig. 5.13). Also included are stylocones (Fig. 7.2–7.4, 7.7, 7.8), portions of arms with ossicles and articulated cover plates (Fig. 7.1, 7.6), and several scattered ossicles and cover plates (Fig. 7.5, 7.9, 7.10).

Occurrence.—*Asaphellus* Zone (upper Tremadocian), Tumugol Formation of Korea.

Discussion.—Isolated mitrate elements in the present collection cannot be attributed to either mitrocystitidans or lagynocystidans, due to the absence of hornlike process on the apophyses on M1 and M′1, high and spearheadlike cover plates, presence of a well-developed zygal crest (M′1, Z), low apophyses (M1, M′1), and bobbin-shaped stylocone. These morphological features suggest peltocystidan affinities. This conclusion is indirectly supported by the occurrence of numerous isolated peltocystidan adorals in the same stratigraphic levels and localities. Recognition of several morphotypes within isolated marginals (e.g., M′1, Z) suggests the occurrence of more than one species (?genera), but precise taxonomic assignment is difficult by the absence of complete, articulated specimens.

Although they show obvious peltocystidan affinities, none of the M′1 marginals in this collection can be assigned confidently to any of the three families of Peltocystida. Comparison with other peltocystidan mitrates reveals that the three types of M′1 are intermediate in morphology between Peltocystidae and Kirkocystidae (see cladistic analyses below). The robust aspect, short accessory septum, and wide apophysis cup of type C marginals

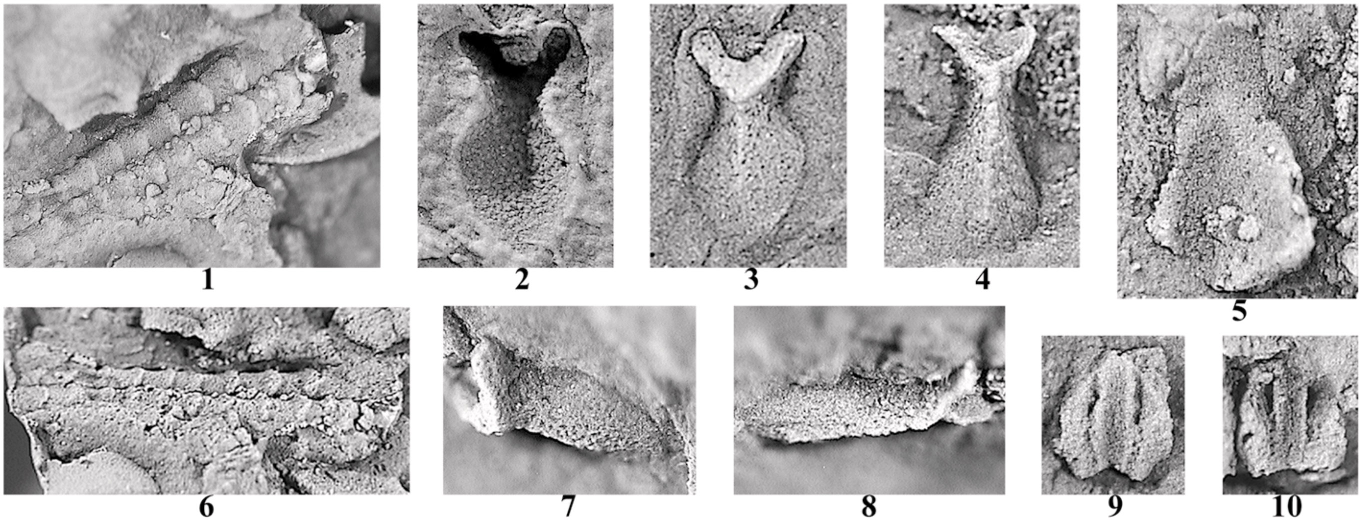

FIGURE 7—Fragments of peltocystidan aulacophores, arms, and isolated brachials from the *Asaphellus* Zone, Tumugol Formation of Sokkaejae section, Taebaeksan Basin, Korea. Stratigraphic intervals in brackets. *1, 6,* Portion of the arm showing the two series of alternating cover plates in connection with, and articulated to, the underlying ossicles SNUP2534 (LT9), plan view and lateral view, respectively, ×14.2. *2, 3, 7,* Saddle-shaped stylocone, SNUP2516 (LT39), plan view of latex cast from the external mold and lateral view of latex cast, respectively, ×25.5. *4, 8,* A stylocone SNUP2536 (LT9), plan view and lateral view of latex cast, respectively, 33.1. *5,* Isolated single cover plate showing stout and protruded articulatory facet on rhombic plate, SNUP2539 (LT9), latex cast, ×36.8. *9, 10,* Plan view of upper surface of a single ossicle (brachial) showing no transverse groove, SNUP2537 (LT9) and SNUP2538 (LT9), latex casts, ×35.3.

recall those of the primitive peltocystid *Peltocystis cornuta* Thoral, 1935 from the Saint-Chinian Formation (Arenigian) of Montagne Noire (see Ubaghs, 1969), whereas the narrow and elongate type A marginals can be attributed to undescribed *Anatifopsis*-like, primitive kirkocystids from the Fillmore Formation (Ibexian) of western Utah (Sumrall, personal commun., 2003). However, the type C marginals differ from M′1 of *Peltocystis* Thoral, 1935 in: 1) the presence of a large platform at the junction between transverse anterior groove and zygal crest; 2) the location and orientation of the scutula; and 3) the absence of a deep transverse groove in the front wall of the apophysis (= "sillon" in Ubaghs, 1969, p. 87). The type A M′1 also differs from similar plates of previously described Kirkocystidae in: 1) the presence of a low longitudinal ridge to the right of the zygal crest; 2) the location and orientation of the scutula; and 3) the various shapes of the apophysis cup. The type B marginal M′1 is morphologically intermediate between the type A (e.g., apophysis cup as wide as high, absence of accessory septum) and the type C (e.g., strong antero-abaxial protuberance, platform at junction between zygal crest and transverse anterior groove).

The two morphotypes of zygal plates are also morphologically intermediate between Peltocystidae and Kirkocystidae, and thus cannot be assigned confidently to either family. The external aspect of large polygonal Z plates is very similar to that of *Peltocystis* (see Ubaghs, 1969, fig. 32), whereas the internal morphology of small triangular plates recalls features of kirkocystids (see Fig. 2.4; Lefebvre, 1999, fig. 79.3). Narrow marginals M1 and M2 are more kirkocystid-like (see Fig. 2.4; Jefferies, 1986, fig. 8.39; Lefebvre, 2001, fig. 9.3).

Isolated Korean brachials are mostly comparable to those of other Peltocystida in having a bobbin-shaped stylocone and no median longitudinal groove. The drastically reduced sculpture on their lower surface, however, precludes their assignment to any of the peltocystidan families, as brachials are strongly sculptured in Peltocystidae, Kirkocystidae, and Jaekelocarpidae. The low median longitudinal crest on the lower surface of stylocones is comparable to that of *Peltocystis* (see Ubaghs, 1969) and of some specimens of *Anatifopsis* Barrande, 1872 (see Lefebvre, 1999). The cover plates are unique and morphologically intermediate between those of *Peltocystis* and Kirkocystidae.

In conclusion, all isolated mitrate skeletal elements from the Tumugol Formation show undisputable peltocystidan affinities and are very likely to belong to primitive peltocystidans, which are morphologically intermediate between Peltocystidae and Kirkocystidae (see cladistic analyses below).

Genus TAEBAEKOCYSTIS new genus

Type species.—*Anatifopsis cocaban* Kobayashi, 1960 from the Mungok Formation, Yongwol, Korea.

Diagnosis.—Peltocystidan mitrate with asymmetrical, planoconvex theca composed of at least two adorals, a glossal, a zygal plate Z, and a reduced number of marginals; adorals short, convex, broad, subequal in size; postero-adaxial margin of adorals gently curved to quadrangular; area of anterior region of adorals (anteriorly to s2) comparable in size to that of posterior region (posteriorly to s2); strong ornamentation on antero-abaxial edges of lower thecal surface.

Etymology.—Named after the city of Taebaek, close to the fossil localities, where all the specimens considered in this study were collected.

Discussion.—In the absence of complete, articulated specimens, *Taebaekocystis* is here mostly defined by adoral plate characters. The morphological nomenclature used for adoral description is shown in Figure 8. The assignment of these adorals to a new genus is justified by their unique morphology among peltocystidans, which appears intermediate between those of Peltocystidae and Kirkocystidae. Thus, the position of co-opercula and the general morphology of adorals suggest that these plates are larger in *Taebaekocystis* than in Peltocystidae, but smaller than in Kirkocystidae. As far as the internal aspect of adorals is concerned, *Taebaekocystis* is more similar to Kirkocystidae than to Peltocystidae (e.g., internal molds divided into three regions by two deep transverse grooves s1 and s2, reduced growth of the internal calcitic layer, and course of growth lines). This observation led Lee et al. (2004) to assign these skeletal elements to kirkocystid mitrates. However, in their morphometric analysis of isolated adorals

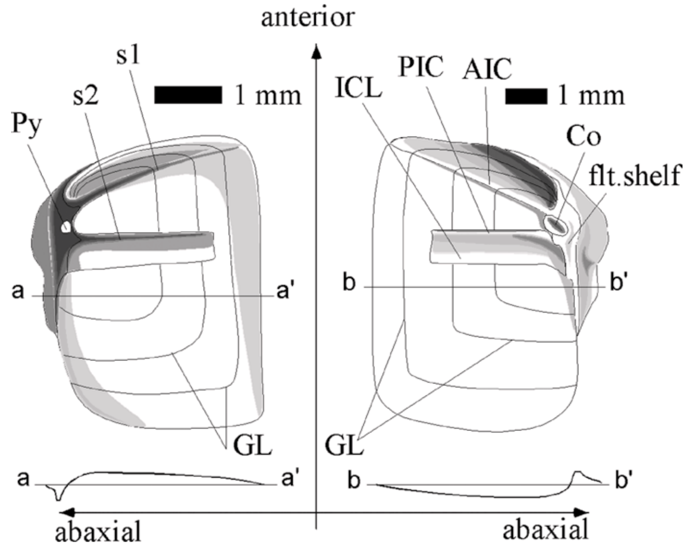

FIGURE 8—Reconstruction of representative adorals of *Taebaekocystis* n. gen. based on internal mold of SNUP2526 (*left*) and latex cast of SNUP2546 (*right*), presenting characteristic morphological features and transections. AIC = anterior internal crest; Co = co-operculum; flt. shelf = flattened shelf; GL = growth line; ICL = internal calcitic layer; PIC = posterior internal crest; Py = pyriform body; s1 and s2 = deep transverse groove on adoral, "sillon."

from the Tumugol Formation, Lee et al. (2004) demonstrated that all of them, except two specimens (described below as *Anatifopsis* sp.), are distinct in morphology from all kirkocystid adorals recorded from Europe and North Africa, and that they are comparable to similar elements described as *Anatifopsis cocaban* and *A. truncata* by Kobayashi (1960) from the Mungok Formation (late Tremadocian) of Yongwol, Korea (see location in Fig. 1).

The morphometric analyses performed by Lee et al. (2004, fig. 10) indicate that morphological disparity of adorals is greater within *Taebaekocystis* than in the whole family Kirkocystidae. Lee et al. (2004) further suggested that this morphological variability was possibly related to the paedomorphosis of *Taebaekocystis*, comparable to those of similar plates in juvenile kirkocystids (see Neige et al., 1997; Zelditch et al., 2003). The recognition of several morphotypes within co-occurring isolated peltocystidan marginals and the great morphological disparity of *Taebaekocystis* may reflect the existence of several species. However, correlation between *Taebaekocystis* adorals and the various morphotypes of isolated marginals is impossible due to the absence of complete specimens and the association of undisputable kirkocystid adorals (*Anatifopsis* sp.) and *Taebaekocystis* in the highest stratigraphic levels of the Sokkaejae and Tongjom sections. For these reasons, isolated peltocystidan marginals and aulacophoral plates from the Tumugol Formation have not been assigned to *Taebaekocystis* (although they might belong to this genus), while most adorals have been attributed to its type species, *T. cocaban*.

TAEBAEKOCYSTIS COCABAN (Kobayashi, 1960)
Figures 8, 9

Anatifopsis cocaban KOBAYASHI, 1960 (in part), p. 265, pl. 13, figs. 2–5 (not pl. 13, fig. 6 = *T. truncata* [KOBAYASHI, 1960]); CHOI AND KIM, 1989, p. 409, pl. 2, figs. 1–11; DOMÍNGUEZ AND GUTIÉRREZ, 1990, p. 125, fig. 1; DOMÍNGUEZ ALONSO, JEFFERIES, AND GIL CID, 2002, p. 54; LEE, LEFEBVRE, AND CHOI, 2004, p. 732, fig. 4.1–4.9.
Balanocystites cocaban (KOBAYASHI, 1960). LEFEBVRE, 1999, p. 366.

Diagnosis.—A species of *Taebaekocystis* n. gen. characterized by adorals with straight to strongly convex upper (adaxial) margin.

Description.—Adorals, small quadrangular elements (2–10 mm long), with great morphological variability. Adorals thicker and stouter anteriorly than posteriorly, usually as long as wide, or slightly longer than wide. Anterior and upper (adaxial) margins of adorals straight to strongly curved. Posterior adaxial corner of adorals sharp and quadrangular, or regularly curved towards abaxial end of plate. Posterior and lower (abaxial) margins of adorals slightly concave, straight, or convex. External surface smooth, strongly convex anteriorly, and nearly flat posteriorly. On external surface, adoral crest corresponding to low or strong transverse ridge along anterior border of adorals.

Internal surface of adorals almost entirely flat, except along lateral edge of antero-abaxial corner, recurved and forming a flattened shelf (Fig. 8). Numerous concentric growth lines on internal surface of adorals, indicating that region around co-operculum represents the growth center of the plate. Growth lines oblique to abaxial border, and parallel to anterior, adaxial, and posterior margins of adorals. Anterior edge of adorals often thick, sometimes forming low ridge, increasing in height abaxially. Internal surface of adorals divided into three regions by two strong transverse ridges, corresponding to deep grooves (s1 and s2) on internal molds. Posterior region (posteriorly to s2) comparable in extension to anterior region (anteriorly to s2), or slightly greater. Anterior groove of internal molds (s1) corresponding to a strong transverse ridge (anterior internal crest; Fig. 8) on inner surface of adoral. Course of s1 straight to curved, nearly perpendicular to strongly oblique to abaxial (lower) margin of adorals, and equivalent to that of adoral crest on external surface. Area between anterior edge of adorals and s1 (i.e., aulacophore insertion cavity) narrow and elongate, crescent-shaped, or pear-shaped. Posterior groove of internal molds (s2) corresponding to sharp anterior edge (posterior internal crest; Fig. 8) of relatively narrow, transverse strip of calcite extending from posterior to co-operculum (adaxially) towards abaxial margin. Posterior groove not always entirely visible on internal molds when internal calcitic strip broken away (Fig. 9.13). Upper (internal) surface of calcitic strip typically concave and bearing transverse groove. Depth of groove greater in right adorals (A1) than in left ones (A′1), and diminishing abaxially in both right and left elements. Transverse grooves s1 and s2 strongly oblique or subparallel, always converging abaxially towards co-operculum. Co-operculum corresponding to small cavity at antero-abaxial corner of adorals, and forming crescentic structure ("pyriform body") in internal molds.

Type.—Lectotype PA2419 (Kobayashi, 1960, pl. 13, fig. 3); the lectotype was designated by Choi and Kim (1989).

Material examined.—More than 60 internal molds and several external molds of isolated left and right adorals from the Sokkaejae and Tongjom sections, Taebaeksan Basin, Korea.

Occurrence.—*Asaphellus* Zone (Tremadocian), Mungok and Tumugol Formations of Korea.

TAEBAEKOCYSTIS TRUNCATA (Kobayashi, 1960)
Figure 10.1, 10.2

Anatifopsis truncatum KOBAYASHI, 1960, p. 266, pl. 13, fig. 1; LEFEBVRE, 1999, p. 366.
Anatifopsis cocaban KOBAYASHI, 1960 (in part), p. 265, pl. 13, fig. 6 (only).
Anatifopsis truncata KOBAYASHI, 1960. DOMÍNGUEZ AND GUTIÉRREZ, 1990, p. 125; DOMÍNGUEZ ALONSO, JEFFERIES, AND GIL CID, 2002, p. 54; LEE, LEFEBVRE, AND CHOI, 2004, p. 733, fig. 4.13.

Diagnosis.—A species of *Taebaekocystis* n. gen. characterized by adorals with deep notch on upper (adaxial) margin.

Description.—Adorals small, quadrangular, nearly as tall as long (4.5 mm high and 6 mm long, respectively), with sinuous

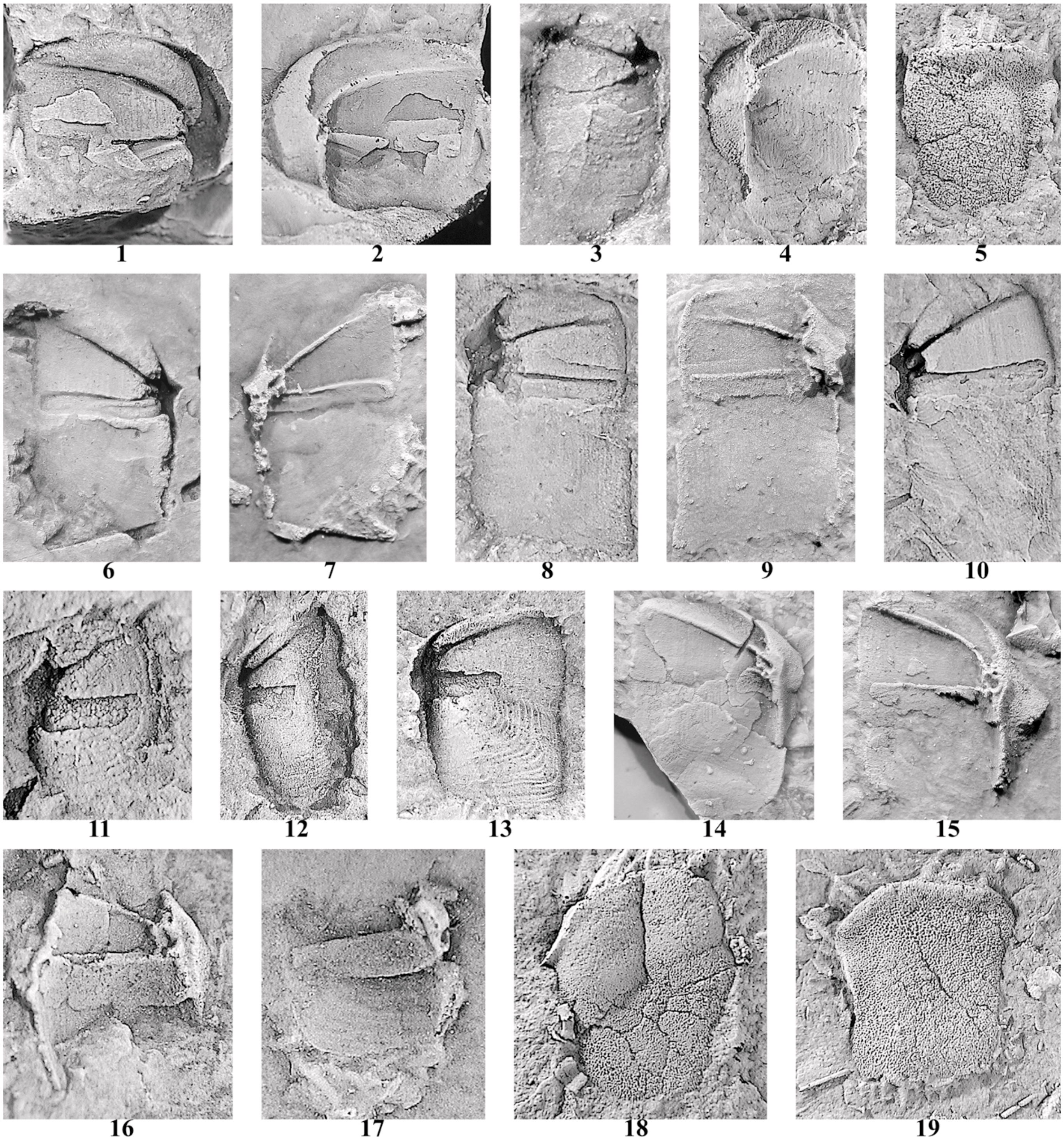

FIGURE 9—Isolated adorals of *Taebaekocystis cocaban* (Kobayashi, 1960) from the *Asaphellus* Zone, Tumugol Formation of Tongjom and Sokkaejae sections, Taebaeksan Basin, Korea. Stratigraphic intervals in brackets. *1–7,* Right adorals; *1, 2*, SNUP25 (H12), internal mold and latex cast, respectively, ×5.7; *3*, SNUP2520 (LT36), internal mold, ×14.3; *4*, SNUP2530 (LT9), latex cast of internal mold, ×7.1; *5*, SNUP2532 (LT9), latex cast of external mold, ×7.2; *6, 7*, SNUP54 (H6), internal mold and latex cast, respectively, ×6.4. *8–19,* Left adorals; *8, 9*, SNUP2525 (LT33), internal mold and latex cast, respectively, ×5.3; *10*, SNUP2515 (LT39), internal mold, ×6.4; *11*, SNUP2521 (LT36), internal mold, ×17.7; *12*, SNUP136 (H14), internal mold, ×7.2; *13*, SNUP2526 (LT15), internal mold, ×7.2; *14*, SNUP2546 (LT9), latex cast of internal mold, ×4.8; *15*, SNUP20 (H11), latex cast of internal mold, ×6.8; *16*, SNUP104 (H6), latex cast of partly preserved internal mold, ×10.7; *17*, SNUP55 (H9), latex cast of a partly preserved internal mold showing very short posterior portion, ×10.7; *18*, SNUP2524 (LT33), latex cast of external mold, ×7.2; *19*, SNUP2531 (LT9), latex cast of external mold, ×7.2.

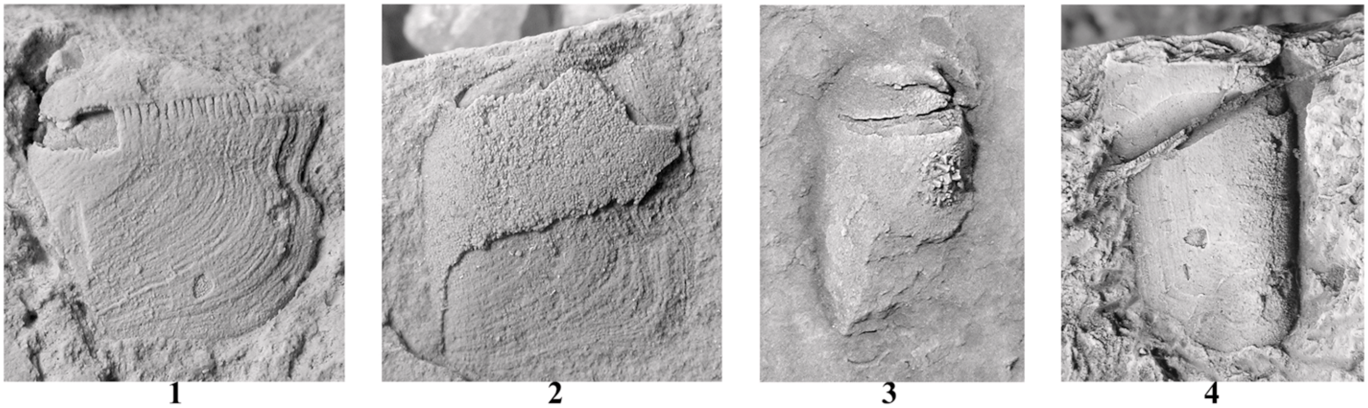

FIGURE *10*—Adorals of *Taebaekocystis truncata* (Kobayashi, 1960) and *Anatifopsis* sp. from Korea. *1,* Natural internal mold of a left adoral of *T. truncata* (PA2422); holotype, figured in Kobayashi (1960, pl. 13, fig. 1); Mungok Formation (Tremadocian), Yongwol, Korea; ×8.7. *2*, *T. truncata* (PA2421); syntype of *A. cocaban* Kobayashi, 1960, figured in Kobayashi (1960, pl. 13, fig. 6); Mungok Formtaion (Tremadocian), Yongwol, Korea; ×7.0. *3*, SNUP2545; natural internal mold of a right adoral of *A.* sp.; Tumugol Formation (*Asaphellus* Zone) of Sokkaejae (LT1); ×9.8. *4*, SNUP131; natural internal mold of a right adoral of *A.* sp.; Tumugol Formation (*Asaphellus* Zone, Tremadocian) of Tongjom (H12), ×4.3.

adaxial margin, produced by deep concave notch, posteriorly to s2. Adaxial notch also visible on concentric growth lines. Anterior region of adoral poorly preserved (s1 and s2 poorly visible in holotype). Posterior margin much wider than anterior margin in holotype, but as wide as anterior margin in second specimen. Postero-adaxial corner of the adoral rounded in holotype and quadrangular in other specimen.

Type.—Holotype, internal mold of a left adoral illustrated by Kobayashi (1960, pl. 13, fig. 1); refigured herein (Fig. 7.1).

Material examined.—Holotype (PA2422) and internal mold of one left adoral (PA2421) assigned to *Anatifopsis cocaban* by Kobayashi (1960, pl. 13, fig. 6). Both specimens were collected from the Mungok Formation (Tremadocian), Yongwol area, Korea (see Figs. 1, 3).

Occurrence.—Mungok Formation (Tremadocian), Yongwol, Korea.

Discussion.—The type specimen of *T. truncata* was originally inadequately prepared, and the anterior portion was covered by sediment. Accordingly, the illustrated type specimen of *T. truncata* (Kobayashi, 1960, pl. 13, fig. 1) looks different from the other *Anatifopsis* specimens (see discussion in Lefebvre, 1999, p. 366). Reexamination of the original material confirms that this specimen belongs to peltocystidans, but is morphologically distinct from other adorals referred to *T. cocaban*, and that one of the specimens of *T. cocaban* illustrated in the lower left corner of plate 13, figure 6 is also assignable to *T. truncata*.

The assignment of these specimens to *Taebaekocystis* is based upon the comparable size of the anterior and posterior regions and the extremely short, flat to slightly convex morphology of the adorals. Their outlines differ from those of *T. cocaban* by the presence of a deep notch on their adaxial margin. Therefore, the possibility that the two adorals of *T. truncata* represent teratological specimens or morphological variants of *T. cocaban* cannot be excluded (see Fig. 9.13). The presence of a deep notch on their adaxial margin suggests that the adorals of *T. truncata* were probably not tightly sutured adaxially to each other.

Family KIRKOCYSTIDAE Caster, 1952

Emended diagnosis.—Peltocystidan mitrates with asymmetrical, plano-convex theca composed of two adorals, a glossal, a zygal plate Z, and six marginal plates; adorals large, convex, elongate, subequal in size, covering entire upper surface and large abaxial portions of lower surface; posterior extremity of adorals truncated or sharp; two internal, fingerlike, transverse strips of calcite extending from antero-abaxial corner of each adoral posteriorly to co-operculum; area of anterior region of adorals (anteriorly to s2) much smaller than that of posterior region (posteriorly to s2); prominent ornamentation on lower thecal surface, consisting of an anterior transverse crest and isolated knobs on A1 and A′1, and of a U-shaped ‘‘collerette’’ on M1, M′1, and adorals; apophyses higher than wide, with strong apophysis crests; scutulae in lateral position on M1 and M′1; no accessory septum; two marginals, M2 and M′3, entirely overlapped by adorals; M′5 reduced and inserted in a cavity along the glossal, or located posteriorly to Z and M′4; wide tesselated left infracentral area comprising large subanal plate; glossal articulated to posterior extremity of Z; right infracentral area absent; strong ornamentation on lower surface of proximalmost brachials.

Discussion.—Caster (1952) erected the subfamily Kirkocystinae to include three genera, *Kirkocystis* Bassler, 1950, *Balanocystites* Barrande, 1887, and *Anatiferocystis* Chauvel, 1941. Ubaghs (1968) elevated the subfamily Kirkocystinae to family rank, and proposed the synonymy of *Kirkocystis* with *Anatiferocystis*. *Anatiferocystis*, *Kirkocystis*, and *Guichenocarpos* Chauvel, 1981 are here considered as junior synonyms of *Anatifopsis*, and *Sagittacystis* Parsley et al., 2000 as a junior synonym of *Balanocystites* (Jefferies, 1986; Domínguez and Gutiérrez 1990; Lefebvre, 1999, 2001, 2003). *Anatifopsis* and *Balanocystites* are well-defined genera, with unique adoral morphologies, differences in the plate pattern of their lower surface skeleton, and distinct sculptures on the lower surface of brachials (Jefferies, 1986; Lefebvre, 1999, 2001, 2003; Lee et al., 2004). Specific identification within these two genera is, however, difficult, as some of them have been established exclusively on isolated adorals (e.g., *Anatifopsis bohemica* Barrande, 1872 and *A. ancora* Domínguez and Gutiérrez, 1990), whereas others are known from complete, articulated thecae [e.g., *Anatifopsis papillata* (Bassler, 1943)]. In some cases, internal molds of adorals and complete thecae can be assigned to the same kirkocystid species. For example, reexamination of the type specimens of *Anatifopsis prima* Barrande, 1872 (isolated adorals) and *Balanocystites lagenula* Barrande, 1887 (complete thecae), both from the Sárka Formation (Abereiddian) of Bohemia, reveals that they belong to a single species, *Balanocystites primus* (Barrande, 1887) (see also Jefferies, 1986; Lefebvre, 1999, 2001, 2003; but see Parsley et al., 2000). However, it is difficult to establish if *Anatifopsis spinosa* (Ubaghs, 1979), described from complete specimens from the Letná Formation

(Caradocian) of Bohemia, should be synonymized with the associated *A. acuta* Barrande, 1872, which is based upon a single, posteriorly incomplete adoral.

Genus ANATIFOPSIS Barrande, 1872

Type species.—*Anatifopsis bohemica* Barrande, 1872.

Emended diagnosis.—Kirkocystids with short, broad, posteriorly truncated adoral plates overlapping most of lower surface skeleton; adorals with straight to sigmoidal ''carène''; s1 and s2 subparallel, converging abaxially towards co-opercula forming an angle of about 10°; subanal plate more or less oblique relative to lower thecal surface; M′5 inserted into a small cavity on right anterior extremity of glossal; proximal aulacophore consisting of reduced number of tetrameric rings; lower surface of stylocone with single spine; deep transverse furrows on lateral sides of brachial spines.

ANATIFOPSIS sp.
Figure 10.3, 10.4

Anatifopsis sp. LEE, LEFEBVRE, AND CHOI, 2004, p. 745, fig. 4.10.

Description.—Adoral from Sokkaejae (about 4 mm long) much smaller than that from Tongjom (about 9 mm long). Adorals quadrangular, much longer than wide, characterized by posterior region (posteriorly to s2) much larger than anterior region (anteriorly to s2), with straight anterior margin, and straight to slightly curved adaxial and abaxial margins. Posterior border short but poorly preserved. Internal surface of adorals strongly concave, both anteriorly and posteriorly. Narrow aulacophore insertion cavity (anteriorly to s1), small co-operculum preserved against posterior wall of s1 (Fig. 10.3), and subparallel, slightly diverging s1 and s2.

Material examined.—Two internal molds of isolated right adorals from the highest levels of the Sokkaejae and Tongjom sections (LT1 and H12, respectively), Taebaeksan Basin, Korea.

Occurrence.—*Asaphellus* Zone (late Tremadocian), Tumugol Formation, Korea.

Discussion.—The assignment of these isolated elements to *Anatifopsis* is based on the morphometric analysis of Korean adorals (Lee et al., 2004). The analysis shows that these two plates are clearly separated from those of *Taebaekocystis* n. gen. and cluster with adorals of *Anatifopsis*. They are different from *Taebaekocystis* in having a large posterior region (posteriorly to s2), narrow aulacophore insertion cavity (anteriorly to s1), and strong convexity. The strongly convex adorals of *Anatifopsis* sp. suggest that these plates probably extended onto the lower thecal surface. The poor preservation of Korean *Anatifopsis*, however, makes it difficult to compare this material with other species of *Anatifopsis*.

PHYLOGENETIC ANALYSIS

Aims of the analysis.—Several cladistic analyses have attempted to explore stylophoran phylogeny, but most focus either on cornutes (Cripps, 1988, 1991; Daley, 1992; Lefebvre and Vizcaïno, 1999; Martí Mus, 2002) or on mitrocystitidan mitrates (Beisswenger, 1994; Ruta, 1997, 1999; Ruta and Theron, 1997; Lefebvre, 2000b). Peltocystida have seldom been included in phylogenetic analyses, presumably due to their poorly known morphology (but see Derstler, 1979; Jefferies, 1986; Parsley, 1997, 1998; Lefebvre, 2001). The phylogenetic position of peltocystidans within mitrates has been long debated and is still unclear. Most authors followed Jaekel (1918) in grouping peltocystidan mitrates with *Lagynocystis pyramidalis* (Barrande, 1887), mainly based on the reduced number of plates and the presence of a single exothecal spine articulated to the posterior edge of the theca. Peltocystids were originally assigned to the family Lagynocystidae (Jaekel, 1918; Chauvel, 1941), but later to the suborder Lagynocystida (Caster, 1952; Ubaghs, 1968). However, Jefferies (1973) observed that exothecal spines were not homologous within all lagynocystidan mitrates. Consequently, he proposed a new suborder Peltocystida to distinguish digital-bearing mitrates (lagynocystidans) from glossal-bearing forms (peltocystidans). The resulting division of mitrates into three suborders (Mitrocystitida, Lagynocystida, and Peltocystida) has been widely accepted by most authors (Jefferies, 1986; Parsley, 1991; Kolata et al., 1991; Vizcaïno and Lefebvre, 1999; Lefebvre, 1999, 2001; but see Derstler, 1979; Ubaghs, 1979; Caster, 1983; Domínguez and Gutiérrez, 1990). However, phylogenetic relationships among the suborders of mitrates have been controversial; suggestions have included: 1) Mitrocystitida as sister group of a clade uniting Lagynocystida with Peltocystida (Derstler, 1979); 2) Peltocystida as sister group of a clade comprising Lagynocystida and Mitrocystitida (Parsley, 1997, 1998); and 3) Lagynocystida as sister group of a clade including Peltocystida and Mitrocystitida (Jefferies, 1973, 1986; Lefebvre and Vizcaïno, 1999; Lefebvre, 2000b, 2001). The present analysis attempts to investigate the phylogenetic position of peltocystidans within mitrates and of *Taebaekocystis* n. gen. within peltocystidans. To explore phylogenetic relationships within mitrates, two nonmitrate outgroups (a primitive stylophoran and a cornute), a primitive mitrate (*Lobocarpus* Ubaghs, 1998), and representatives of the three mitrate suborders Lagynocystida, Mitrocystitida, and Peltocystida are included.

Ingroup and outgroup taxa.—*Ceratocystis perneri* Jaekel, 1901 (Skryje Shales, Middle Cambrian, Bohemia) and *Arauricystis primaeva* (Thoral, 1935) (Saint-Chinian Formation, lower Arenigian, Montagne Noire) have been chosen as outgroups. *Ceratocystis* is the most primitive stylophoran known and has been often chosen as outgroup in cladistic analyses of stylophorans (Derstler, 1979; Cripps, 1988; Parsley, 1997, 1998; Lefebvre and Vizcaïno, 1999; Lefebvre, 1999, 2000b, 2001). *Arauricystis primaeva* is a primitive, boot-shaped cothurnocystid cornute (Jefferies, 1973, 1986; Derstler, 1979; Cripps, 1988, 1991; Daley, 1992; Parsley, 1997, 1998; Lefebvre, 1999, 2001).

Ingroup taxa include *Taebaekocystis cocaban* (Kobayashi, 1960) and seven other mitrates: *Lobocarpus vizcainoi* Ubaghs, 1998, *Lagynocystis pyramidalis*, *Mitrocystites mitra* Barrande, 1887, *Peltocystis cornuta*, *Jaekelocarpus oklahomaensis*, *Anatifopsis trapeziiformis* Thoral, 1935, and *Balanocystites primus* (Barrande, 1872). *Lobocarpus vizcainoi* (Val d'Homs Formation, Upper Cambrian, Montagne Noire) was described as a phyllocystid cornute (Ubaghs, 1998; Smith and Jell, 1999), but the reinterpretation of its anatomy demonstrates that it represents the most primitive and oldest known mitrate (Vizcaïno and Lefebvre, 1999; Lefebvre, 1999, 2000b, 2001). *Lagynocystis pyramidalis* and *Mitrocystites mitra* (both from the Sárka Formation, Abereiddian of Bohemia) are the type species of lagynocystidan and mitrocystitidan mitrates, respectively. *Peltocystis cornuta* (Saint-Chinian Formation, Arenigian, Montagne Noire, France) and *Jaekelocarpus oklahomaensis* (Golf Course Formation, Pennsylvanian, Oklahoma) are the type species and only known representatives of Peltocystidae and Jaekelocarpidae, respectively. *Anatifopsis trapeziiformis* (Saint-Chinian Formation, Arenigian, Montagne Noire, France) is the oldest known member of this genus (Lefebvre, 1999; Lee et al., 2004); the choice of *A. trapeziiformis* in the analysis rather than the type species *A. bohemica* is justified by the absence of data on the lower surface skeleton and aulacophore in the latter (the type species was described from internal molds of isolated adorals; Barrande, 1872; Domínguez and Gutiérrez, 1990; Lefebvre, 1999). *Balanocystites primus* (Sárka Formation, Abereiddian, Bohemia; Fig. 2) and *Taebaekocystis cocaban* (Mungok Formation, Tremadocian, Korea) are the type species of their respective genera.

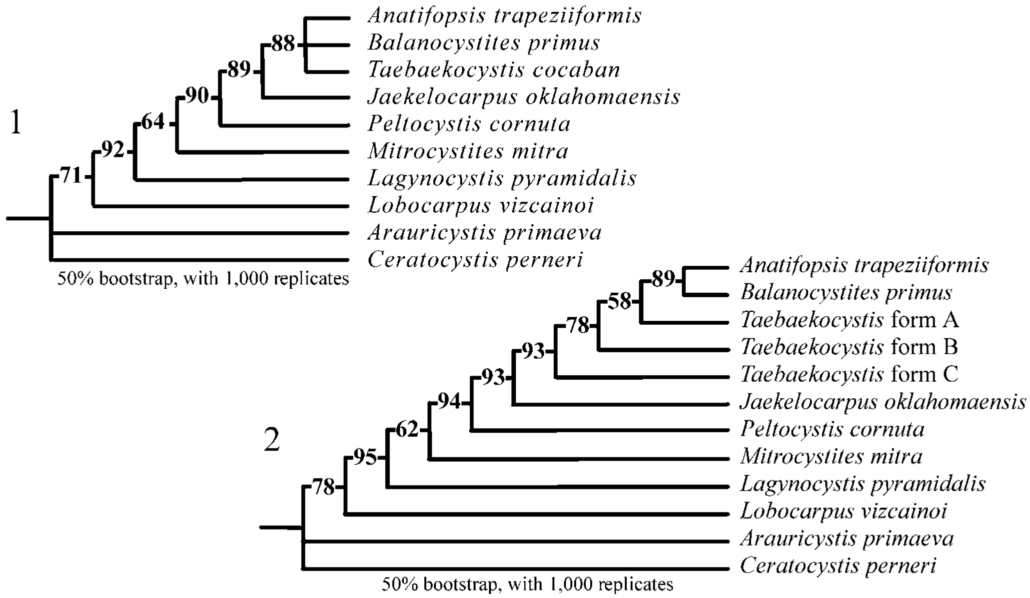

FIGURE *11*—Results of cladistic analyses of peltocystidan mitrates and other selected stylophorans. *1,* Cladogram with characters of *Taebaekocystis* adorals only. *2,* Cladogram obtained from combined information on *Taebaekocystis* adorals and associated marginals.

Selection of characters.—A total of 29 characters has been selected. Almost all characters are discrete and rely on well-established plate homologies (Lefebvre and Vizcaïno, 1999; Lefebvre, 1999, 2000b, 2001). Contrary to some other cladistic analyses (e.g., Cripps, 1991; Daley, 1992; Parsley, 1997), characters describing the degree of (a)symmetry of thecal outlines have not been considered, since these are prone to convergence (Lefebvre, 2001).

Material and methods.—Morphological data are based upon direct observation of specimens and latex casts and/or complemented by relevant data from the literature (Ubaghs, 1967, 1968, 1969; Jefferies, 1973, 1986; Kolata et al., 1991; Domínguez et al., 2002). *Taebaekocystis* has been defined from isolated adorals (see above). However, the great morphological disparity observed in *Taebaekocystis* adorals and associated marginals suggests the probable co-occurence of several morphotypes (?species) of peltocystid mitrates in the Tumugol Formation (Lee et al., 2004). To accommodate this problem, two cladistic analyses were performed using PAUP 3.1.1 (Swofford, 1993) under the ACCTRAN optimization, with all characters unordered and unweighted. In the first analysis, only characters related to isolated adorals were considered for *Taebaekocystis* (see Appendix). A heuristic search found three shortest trees (67 steps; CI = 0.791; RI = 0.754; RC = 0.597), a 50% majority consensus tree of which is presented in Figure 11.1. In the second analysis, three associations of various isolated peltocystidan elements (adorals, brachials, cover plates, and marginals) from the Tumugol Formation were considered: *Taebaekocystis* form A (*T. cocaban* adorals and type A marginals M′1), *Taebaekocystis* form B (*T. cocaban* adorals and type B marginals M′1), and *Taebaekocystis* form C (*T. cocaban* adorals and type C marginals M′1; see Appendix). A heuristic search found one shortest tree (70 steps; CI = 0.786; RI = 0.779; RC = 0.612; Fig. 11.2).

Results and discussion.—Both cladistic analyses (Fig. 11.1, 11.2) support Lagynocystida as a sister group of the clade uniting Peltocystida and Mitrocystitida, as proposed by previous authors (Jefferies, 1973, 1986; Lefebvre and Vizcaïno, 1999; Lefebvre, 2000b, 2001). These analyses further demonstrate that *Lobocarpus* is the sister group of all other mitrates, which is comparable to the findings of Lefebvre (1999), but differs from those of Lefebvre (2000b). Lefebvre (2000b) suggested a more derived position for *Lobocarpus*, either as sister group of the Mitrocystitida or as sister group of the clade uniting Peltocystida and Mitrocystitida.

The first cladistic analysis, based upon the morphology of isolated adorals, shows that *Taebaekocystis* forms a clade with the two kirkocystid genera *Anatifopsis* and *Balanocystites* (Fig. 11.1). The second analysis indicates that *Taebaekocystis* may form a paraphyletic group (Fig. 11.2). In this context, Korean peltocystidans with type C M′1 marginal would represent the most primitive (*Peltocystis*-like) forms, whereas those with type A marginal would be more derived (kirkocystid-like). Both analyses, however, indicate that peltocystidans from the Tumugol Formation are intermediate in morphology between primitive Peltocystidae (*Peltocystis*) and Kirkocystidae. This result is consistent with the conclusions of Lee et al. (2004), who identified a peramorphocline characterized by the progressive acquisition of more elongate adorals extending to the lower thecal surface in their morphometric analysis of Ordovician peltocystidans. These analyses also suggest that the relatively basal position of *Jaekelocarpus* Kolata, Frest, and Mapes, 1991 (the youngest peltocystidan) within the peltocystidan clade (as sister group of the clade uniting *Taebaekocystis* and Kirkocystidae) may result from its strongly paedomorphic morphology, evidenced by globular theca and reduced extension of adorals. The present analysis confirms that *Peltocystis* is the most primitive known peltocystidan mitrate and the sister group of the clade comprising Jaekelocarpidae and Kirkocystidae (Fig. 11.1, 11.2; see also Parsley, 1997, 1998; Lefebvre, 2001).

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APPENDIX

		1	11111	11112	22222	2222
Character number	12345	67890	12345	67890	12345	6789
Data matrix 1						
Anatifopsis trapeziiformis	30312	21212	11011	11012	14122	2113
Balanocystites primus	30312	21012	11011	21012	14122	2113
Taebaekocystis cocaban	???1?	?????	?????	?????	13122	2?1?
Peltocystis cornuta	11111	01112	11101	21012	12111	1012
Jaekelocarpus oklahomaensis	?111?	21113	11011	1101?	12132	0112
Mitrocystites mitra	11112	01000	01101	21111	01131	0011
Lagynocystis pyramidalis	30111	11101	21020	31111	011??	?011
Lobocarpus vizcainoi	00??0	01300	0110?	00???	?????	?00?
Ceratocystis perneri	00?00	00000	00000	00000	01000	0000
Arauricystis primaeva	20002	00012	20112	00100	00000	0001
Data matrix 2						
Anatifopsis trapeziiformis	30312	21212	11011	11012	14122	2113
Balanocystites primus	30312	21012	11011	21012	14122	2113
Taebaekocystis form A	20212	???12	?????	11012	13122	2?1?
Taebaekocystis form B	20213	???12	?????	11012	13122	2?1?
Taebaekocystis form C	11213	???12	?????	11012	13122	2?1?
Peltocystis cornuta	11111	01112	11101	21012	12111	1012
Jaekelocarpus oklahomaensis	?111?	21113	11011	1101?	12132	0112
Mitrocystites mitra	11112	01000	01101	21111	01131	0011
Lagynocystis pyramidalis	30111	11101	21020	31111	011??	?011
Lobocarpus vizcainoi	00??0	01300	0110?	00???	?????	?00?
Ceratocystis perneri	00?00	00000	00000	00000	01000	0000
Arauricystis primaeva	20002	00012	20112	00100	00000	0001

List of characters used in the phylogenetic analysis. The character states are indicated by numerals in brackets (? = missing information).

1. Apophyses: (0) absent, or present with left half of apophysis cup, (1) larger than high, (2) as large as high, (3) higher than large.
2. Accessory septum: (0) absent, or (1) present.
3. Scutulae: (0) asymmetrical, or symmetrical and (1) in upper, (2) intermediate, or (3) lateral position.
4. Co-opercula: (0) absent, or (1) present.
5. Transverse anterior groove on posterior wall of apophyses: (0) absent, (1) faint, or well marked and with platform at junction with zygal crest (2) absent, or (3) present.
6. Marginals M3 and M4: (0) both present, or (1) one or (2) both absent.
7. Marginal M5: (0) present, or (1) absent.
8. Marginal M'5: (0) in marginal position, (1) modified as anal plate, (2) reduced and adjacent to the glossal, (3) in central position.
9. Zygal plate: (0) in central, or (1) in marginal position.
10. Glossal: (0) included in marginal frame, (1) absent, or as exothecal appendage posteriorly articulated to (2) zygal, or (3) modified infracentral platelet.
11. Digital: (0) included in marginal frame, (1) absent, or (2) as exothecal appendage posteriorly articulated to M'4.
12. Spinal blade: (0) present, or (1) absent.
13. Right infracentral area: (0) absent, or (1) present.
14. Left infracentral area: (0) consisting of a small and constant number of large elements, (1) tesselated, or (2) absent.
15. Proximal aulacophore: (0) unorganized, or organized and (1) mitratelike (tectals same size as inferolaterals), or (2) cornutelike (tectals smaller than inferolaterals).
16. Spine(s) on lower surface of stylocone: (0) absent, (1) one, (2) two, or (3) more.
17. Median crest on lower surface of stylocone: (0) absent, or (1) present.
18. Transverse channels on each side on median longitudinal groove: (0) absent, or (1) present.
19. Interbrachial articulations: (0) none, or (1) well developed.
20. Cover plates: (0) fan-shaped, (1) massive and flat, or (2) tall and bent.
21. Adorals: (0) three, or (1) two.
22. Adorals: (0) reduced, (1) large, or very large and (2) limited to upper surface, (3) expanding into lower surface, or (4) overlapping lower surface skeleton.
23. Anterior transverse crest on adorals: (0) absent, or (1) present.
24. Fingerlike internal structures in adorals: (0) absent, or present and (1) faint, (2) as one or two narrow calcitic strips, or (3) forming a ramified ''palmar'' complex.
25. Anterior internal crest (s1): (0) absent, or present and (1) short, or (2) long (crossing the plate transversely).
26. Posterior internal crest (s2): (0) absent, or present and (1) short, or (2) long (crossing the plate transversely).
27. Supracentrals: (0) present, or (1) absent.
28. Respiratory structures on upper surface: (0) present, or (1) absent.
29. Periproct: (0) posterior slit, (1) anal pyramid, or slit along anal plate equivalent to highly modified (2) marginal M'5, or (3) infracentral platelet.