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Journal of Paleontology; Jan 2005; 79, 1; ProQuest
pg. 139

J. Paleont., 79(1), 2005, pp. 139–151
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0022-3360/05/0079-139$03.00

LATEST CAMBRIAN CORNUTES (ECHINODERMATA: STYLOPHORA) FROM THE TAEBAEKSAN BASIN, KOREA

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ABSTRACT—The oldest echinoderms and first cornute stylophorans ever reported from Korea are described, based on more than 40 specimens collected from the Late Cambrian of the Taebaeksan Basin. New material doubles the number of stylophorans described from Asia and the number of specimens of Late Cambrian stylophorans recorded throughout the world. Three different cornutes are identified: *Sokkaejaecystis serrata* n. gen. and sp. and two genus and species indeterminate forms A and B. *Sokkaejaecystis serrata* and indeterminate form B are assigned to the Chauvelicystinae, while the systematic position of indeterminate form A within cornutes is difficult to assess. This new material suggests paleobiogeographic connections between echinoderm faunas from Korea, western North America (Wyoming), and western Europe (Montagne Noire, Shropshire). A cladistic analysis of selected cothurnocystids shows that *Sokkaejaecystis* n. gen. is closely related to *Prochauvelicystis* and the sister group of a clade uniting *Ampelocarpus* with *Lyricocarpus*. The analysis also confirms the placement of *Milonicystis* within the Chauvelicystinae and questions the monophyly of the genus *Chauvelicystis*.

INTRODUCTION

ECHINODERMS ARE extremely rare fossils in the Late Cambrian rocks throughout the world. In this study, we report the oldest echinoderm remains (latest Cambrian) ever discovered in Korea, based on new materials from the Tongjom Formation of the Taebaeksan Basin. This material comprises more than 40 specimens of cornute stylophorans, with numerous isolated plates and columnals of a *Macrocystella*-like rhombiferan blastozoan. This study focuses on the description of three cornute stylophorans, *Sokkaejaecystis serrata* n. gen. and sp., and genus and species indeterminate forms A and B. The new specimens have doubled the number of stylophorans reported from Asia, formerly including only the two mitrates *Anatifopsis cocaban* Kobayashi, 1960 and *A. truncata* Kobayashi, 1960 from the Early Ordovician of Korea (Kobayashi, 1960; Choi and Kim, 1989; Domínguez and Gutiérrez, 1990) and the cornute *Mongolocarpos minzhini* Rozhnov, 1990 from the Late Silurian of Mongolia. The new echinoderm fauna from the Taebaeksan Basin is comparable to other Late Cambrian assemblages reported from the western and eastern United States (Ulrich, 1929; Ubaghs, 1963; Sprinkle, 1973; Bell and Sprinkle, 1980; Sumrall et al., 1997), Australia (Jell et al., 1985; Smith and Jell, 1990, 1999), and southern France (Ubaghs, 1998). In these regions, Late Cambrian echinoderm faunas are low in diversity and comprise stylophorans, eocrinoids, and/or *Macrocystella*-like blastozoans, with rare edrioasteroids and solutes (Sumrall et al., 1997). The Late Cambrian stylophorans are generally poorly known and have been described based on limited, fragmentary material. They have been reported from the western United States (15 specimens; Ubaghs, 1963; Sumrall et al., 1997), Montagne Noire, southern France (five specimens; Ubaghs, 1998), and Australia (12 specimens; Smith and Jell, 1999). The new Korean material (more than 40 specimens) greatly expands our knowledge of the Late Cambrian stylophorans and suggests paleobiogeographic connections with Laurentia and the northern margin of Gondwana. One Korean cornute (genus and species indeterminate form A) could be closely related to *Acuticarpus? republicensis* (Sumrall et al., 1997) from the Franconian of Wyoming and possibly to *Amygdalotheca griffei* (Ubaghs, 1969) from the Arenigian of Montagne Noire (France). The two other cornutes (*Sokkaejaecystis serrata* n. gen. and sp. and genus and species indeterminate form B) share a number of morphological features with slightly younger forms from the Tremadocian of Shropshire, England (*Flabellicarpus* Martí Mus, 2003 and *Prochauvelicystis* Daley, 1992), and the early Arenigian of Montagne Noire and Morocco (*Chauvelicystis* Ubaghs, 1969). Biogeographical affinities of Late Cambrian and Early Ordovician Korean (Australo–Sinian) faunas with those from North America and western Europe (e.g., Montagne Noire) have been already suggested, based on trilobites (Shergold et al., 2000; Choi et al., 2001; Alvaro et al., 2003).

GEOLOGIC SETTING, FOSSIL LOCALITY, AND GEOLOGIC AGE

The Taebaeksan Basin occupies the central eastern part of the Korean peninsula (Fig. 1) and comprises mainly the Cambrian–Ordovician Choson Supergroup and the Carboniferous–Permian Pyongan Supergroup. The Choson Supergroup rests unconformably on Precambrian granitic gneiss and metasedimentary rocks and is overlain unconformably by post-Ordovician sedimentary rocks. The lower Paleozoic sedimentary rocks are shallow marine in origin and consist of limestone, sandstone, and shale. In the early Paleozoic, the Taebaeksan Basin was a shallow-marine, mixed-siliciclastic-carbonate system with progressively deeper water to the west (Chough et al., 2000). This siliciclastic-carbonate system persisted throughout the Cambrian, until rapid accumulation of carbonate sediments in the Yongwol area resulted in the formation of a widespread carbonate platform across the Taebaeksan Basin in the Ordovician. Sedimentological features reveal that the carbonate platform was characterized by low relief spotted with shoals, lagoons, and tidal flats (Choi et al., 2001). The marine sedimentation paused over the whole Taebaeksan Basin in the Late Ordovician, and most of the Taebaeksan Basin was emergent during the mid–Paleozoic until marine transgression resumed in the Late Carboniferous.

The Choson Supergroup is a siliciclastic-carbonate succession ranging from late Early Cambrian to early Late Ordovician. Kobayashi et al. (1942) first recognized that the lithologic successions of the Choson Supergroup are different from place to place and consequently designated five types of sequences in the Choson Supergroup. However, Choi (1998) noted the inappropriateness of the stratigraphic nomenclature of the Choson Supergroup and proposed the Taebaek, Yongwol, Yongtan, Pyongchang, and Mungyong groups, which replace the previous lithostratigraphic scheme.

The Taebaek Group is distributed in the eastern half of the Taebaeksan Basin (Fig. 1.1) and comprises the Changsan/Myonsan, Myobong, Taegi, Sesong, Hwajol, Tongjom, Tumugol, Makkol, Chigunsan, and Tuwibong Formations in ascending order (Kobayashi, 1966; Choi, 1998). The Tongjom Formation, from

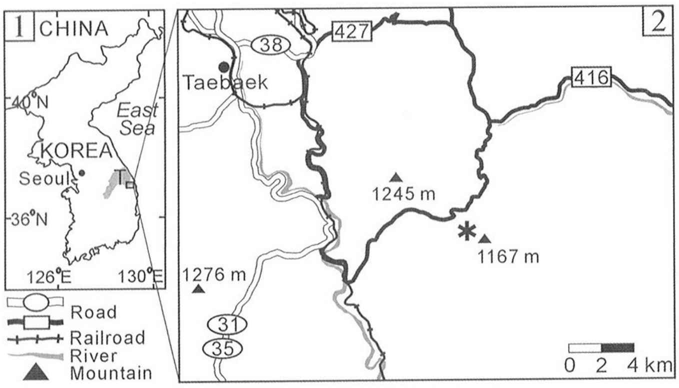

FIGURE *1*—Locality maps. *1,* Map of Korean peninsula showing the location of the Taebaeksan Basin (T); *2,* index map of Taebaek area showing fossil locality (*).

which the stylophorans were recovered, consists largely of light- to dark-gray sandstone with occasional shale and limestone layers and had been considered to be poorly fossiliferous. *Pseudokainella iwayai* Kobayashi, 1953 was the only known trilobite from the formation.

All of the stylophoran fossils considered in this study were collected from the lowermost part of the Tongjom Formation, exposed along a mountain trail in the southeastern corner of the Taebaeksan Basin (Fig. 1). The mountain trail exposes a nearly complete succession of the Taebaek Group (c. 1,400 m thick) and is called the Sokkaejae section. The Tongjom Formation in the section yields abundant invertebrate fossils, including trilobites, brachiopods, and echinoderms. Good exposure along the trail reveals that the Tongjom Formation measures about 88 m in thickness and is divisible into the lower, middle, and upper parts (Fig. 2). The lower part (20 m thick) is composed predominantly of laminated calcareous mudstone/sandstone with occasional intercalations of thin sandstone and limestone conglomerate beds. The middle part comprises a 45-m-thick coarsening upward sequence of massive to bedded sandstone. The upper part (23 m thick) is an alternating unit of flaser-type sandstone with intercalations of wavy and lenticular mud layers and massive sandstone, but also contains a few packstone beds in its uppermost portion.

Fossils occur exclusively in the lower part of the Tongjom Formation, which occupies the middle portion of the Sokkaejae section with geographic coordinates of 129°08′39″E and 37°04′19″N (Fig. 1). Stylophorans were recovered from three stratigraphic levels (010514b, 010521, and 021025): *Sokkaejaecystis serrata* n. gen. and sp. from the level 010514b, genus and species indeterminate form A from the level 021025, and genus and species indeterminate form B from the level 010521, respectively. Fossils are invariably preserved as flattened molds and, where available, latex casts have been prepared for observation and photographs. Aside from stylophorans, the lower part of the Tongjom Formation yields three trilobite faunal assemblages: in ascending order, the *Mictosaukia*, *Missisquoia–Onychopyge*, and *Richardsonella* faunas (Fig. 2). Although these trilobite faunas have yet to be studied in more detail, they generally indicate a close affinity with latest Cambrian faunas known elsewhere. The *Mictosaukia* fauna shares a number of taxa with the *Mictosaukia–Fatocephalus* fauna of North China (Zhou and Zhang, 1985; Duan et al., 1986; Chen et al., 1988), South China (Peng, 1984, 1990), and Assemblage I of the Pacoota Sandstone, Australia (Shergold, 1991). The *Missisquoia–Onychopyge* fauna can be equated with the *Missisquoia* Zone of North China (Zhou and Zhang, 1985; Duan et al., 1986) and North America (Ross et al., 1997) and partly with the *Leiostegium constrictum–Shenjiawania brevica* and *Onychopyge–Hysterolenus* zones of South China (Peng, 1984, 1990). The *Richardsonella* fauna is most likely contemporaneous with the *Richardsonella–Platypeltoides* Zone (uppermost Cambrian) of North China (Chen et al., 1988), while closely comparable trilobite assemblages are not known in other parts of the world. Even though the occurrence of *Yosimuraspis* Kobayashi, 1960 in the *Richardsonella* fauna cannot rule out the possibility that part of the *Richardsonella* fauna may belong to the Ordovician (cf. Kim and Choi, 2000), the geologic age for the lower stratigraphic intervals yielding the stylophorans (Fig. 2) can most likely be bracketed within the latest Cambrian.

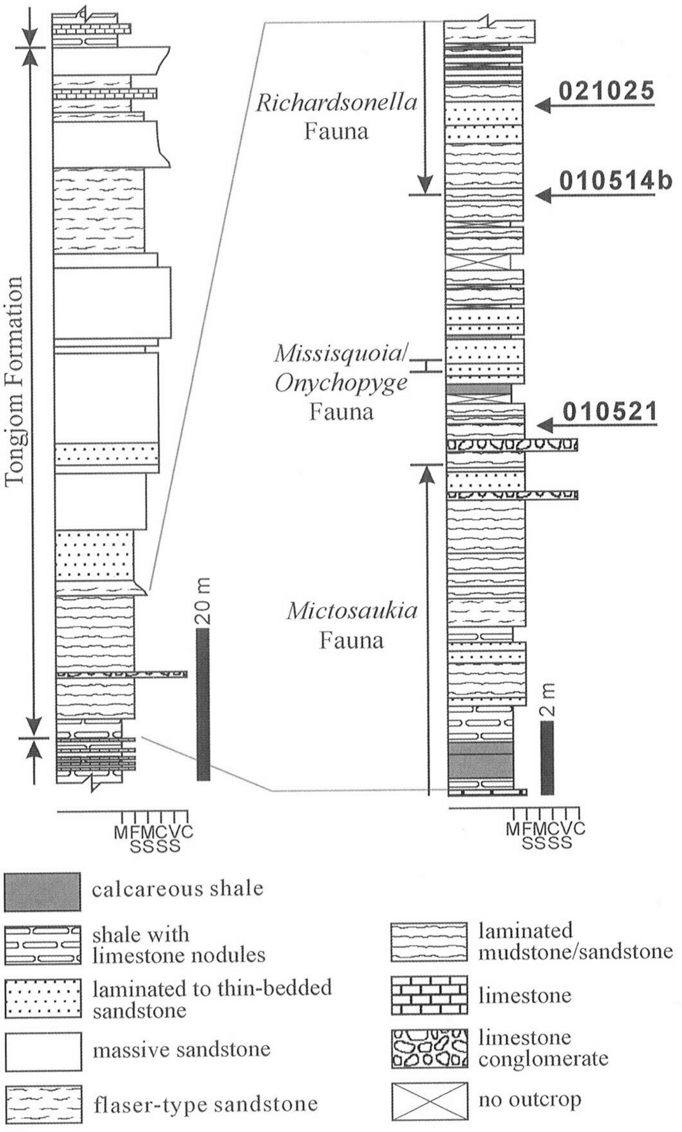

FIGURE 2—Lithologic columnar section of the Tongjom Formation in the Sokkaejae Section. Arrows with locality numbers indicate the stratigraphic horizons yielding the stylophorans described in this study.

SYSTEMATIC PALEONTOLOGY

All specimens described in this paper are reposited in the paleontological collections of Seoul National University, Korea, under the registered SNUP numbers.

Class STYLOPHORA Gill and Caster, 1960

Discussion.—Stylophorans (cornutes and mitrates) are an extinct class of nonpentameral Paleozoic echinoderms known from

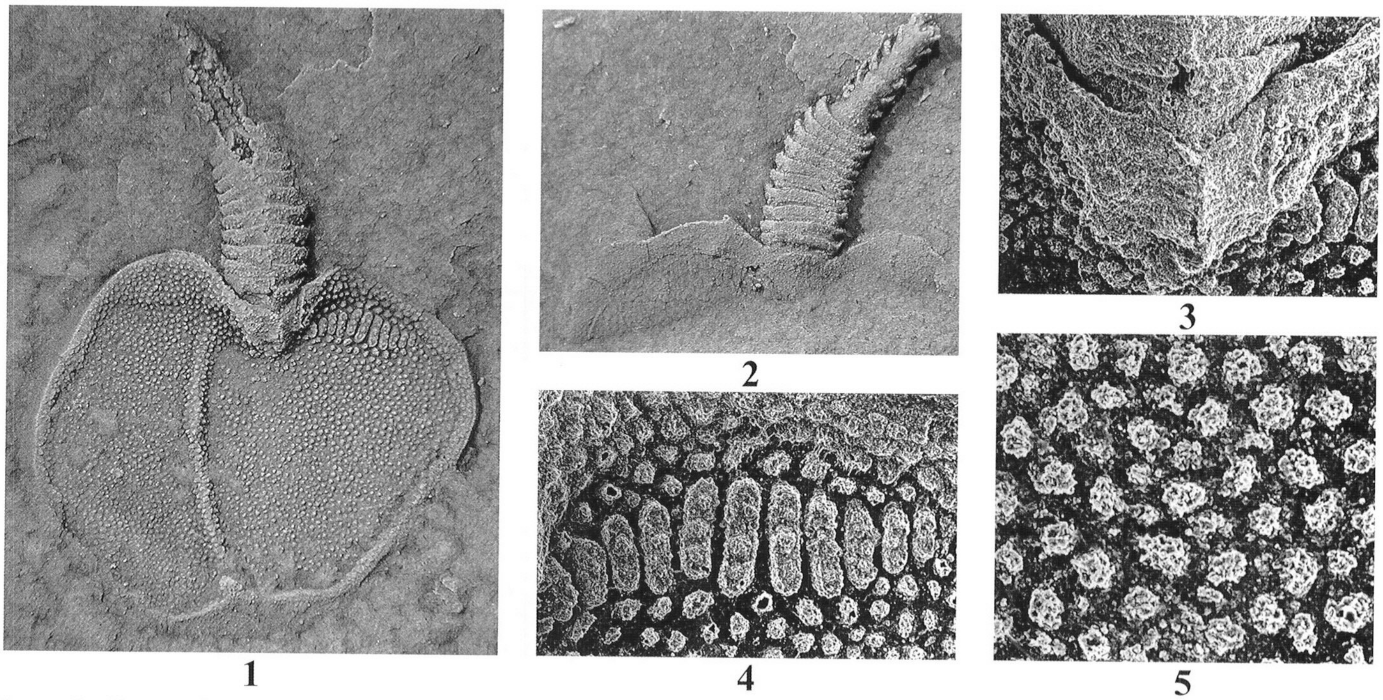

FIGURE 3—Genus and species indeterminate form A, latex casts of SNUP2563 from horizon 021025, Late Cambrian, Tongjom Formation, Taebaeksan Basin, Korea. *1,* Upper aspect of thecal surface and articulated aulacophore, ×6.6; *2,* partly preserved anterior thecal surface and articulated aulacophore in lower aspect, ×6.4; *3,* detailed SEM image around adorals, ×23; *4,* close-up (SEM) of cothurnopores, ×25; *5,* SEM image of supracentral platelets, ×60.

early Middle Cambrian to Late Carboniferous. All stylophorans share the same basic organization with a delicate, articulated, flexible appendage inserted into a flattened asymmetrical body (theca). Because of the unusual morphology and asymmetry, the systematic position of these fossils (primitive echinoderms or early chordates) and the interpretation of their appendage (as a pelmatozoan stem, feeding arm, or chordate tail) has been controversial over the years (Jefferies, 1967; Philip, 1979; Ubaghs, 1981; Chauvel, 1981; Parsley, 1988; Kolata et al., 1991). Stylophorans are here considered as derived echinoderms, with a bipartite body consisting of a theca and a feeding arm (Ubaghs, 1961, 1968; Chauvel, 1981; Parsley, 1988; Sumrall, 1997; Lefebvre and Vizcaïno, 1999; David et al., 2000). Orientation and anatomy follow the terminology of Ubaghs (1968, 1969), and plate homologies are mostly based on Lefebvre and Vizcaïno (1999) and Lefebvre (2001).

Order CORNUTA Jaekel, 1901
Genus and species INDETERMINATE FORM A
Figures 3, 4

Description.—Known from part and counterpart of a single, relatively large specimen (SNUP 2563) showing almost complete upper thecal surface, anteriormost portion of lower thecal side, and part of aulacophore (proximal region and base of arm). Theca heart-shaped (cordiform), with rounded, gently curved outlines, approximately 9.5 mm wide and 7.6 mm long. Anterior edge of thecal frame slightly concave at aulacophore insertion on lower surface and more deeply excavated on upper side. Left posterior extremity of theca too poorly preserved to allow observation of periproctal area and putative opening/closure of thecal frame. No ornamentation on lower surface of anterior marginals and lateral edges of theca (e.g., protuberances, knobs, spinal blade). Lateral and posterior sides of theca surrounded by a thin, downward-recurved, peripheral flange, developed by outer edges of marginals. Peripheral flange narrow and relatively steep along lateral sides, becoming wider and nearly flat posteriorly. Supracentral area delimited by narrow, raised, continuous ridge emitted by upper surface of marginals. Supracentrals extremely numerous (several hundred polygonal platelets) and small (diameter approximately 0.15 mm), all bearing a small, blunt or club-shaped central protuberance. Infracentrals poorly preserved, apparently polygonal and much larger than supracentrals. Precise number of major thecal plates difficult to assess, because of incomplete preservation of lower surface and presence of numerous fractures sometimes difficult to distinguish from sutures. Thecal frame apparently made of two adorals, a zygal plate in central position, and more than nine marginals (at least four on the left and five on the right).

M_1 small, quadrangular element, with concave anterior and posterior edges. M'_1 T-shaped, with anterior region comparable in morphology to M_1, and long, relatively narrow, gently curved posterior, zygal branch. On internal (upper) surface of M'_1, zygal crest anteriorly low, increasing in height in a posterior direction, and with triangular cross section. Posterior portion of zygal crest borne by a plate in central position: the zygal plate Z. Zygal plate relatively narrow and straight, in contact with M'_1 anteriorly, and with two marginals posteriorly (identified here as M_4 on the right and the glossal, G on the left, by comparison with other cornutes). Zygal plate slightly wider posteriorly than anteriorly. Precise number and limits of marginals on right thecal side difficult to assess, due to fractures. M_2 gently curved, apparently fractured into two subequal portions, and forming right anterior corner of theca. Right portion of thecal frame between M_2 and Z possibly formed by two long, subequal, curved marginals (M_3 and M_4), or by three smaller elements (Mc, M_3, and M_4). Glossal pentagonal, sutured to Z and M_4 (on the right), and to a small, narrow marginal on the left. M'_2 well preserved, curved element, comparable in morphology to M_2, forming left anterior corner of theca. M'_3 gently curved marginal, slightly shorter than M'_2. Sutures between more posterior left marginals hardly discernable. M'_4

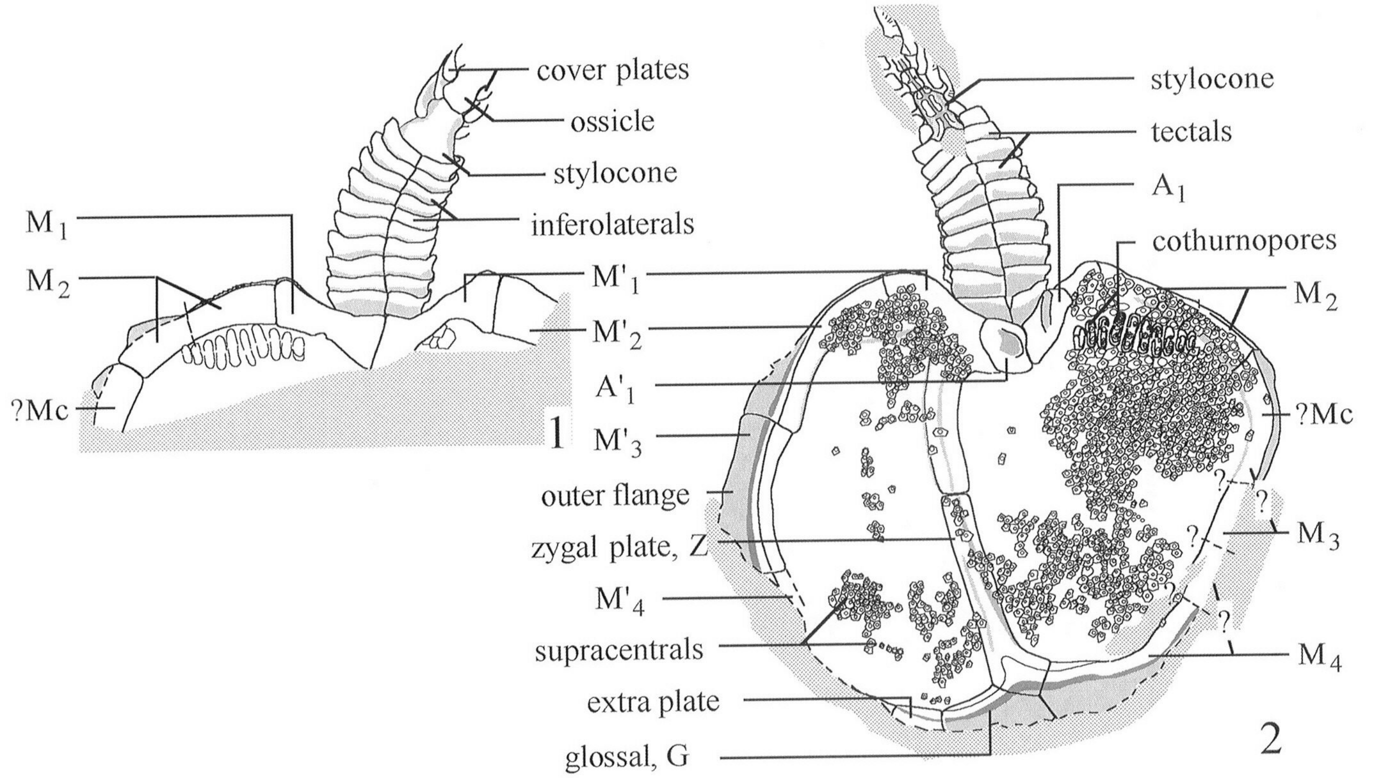

FIGURE 4—Genus and species indeterminate form A, camera lucida drawings based on SNUP2563, Late Cambrian, Tongjom Formation, Taebaeksan Basin, Korea, ×8. *1*, Lower aspect; *2*, upper aspect.

apparently relatively short element. Two adorals on anterior edge of upper surface, at aulacophore insertion. Left adoral A'_1 more or less rounded, slightly depressed element. Right adoral A_1 quadrangular plate, larger than A'_1, with longitudinal groove surrounded by raised lips leading to anterior opening, at A_1-M_1 suture (right adoral orifice). Presence of 11 small cothurnopores (0.3–0.65 mm long), forming elongate rhombic structure in right anterior corner of supracentral area, right of A_1. Cothurnopores narrow, each consisting of two U-shaped plates enclosing several tiny cones with an apical pore (generally, at least three to six cones by cothurnopore).

Preserved portion of aulacophore about 5.2 mm long, consisting of proximal region and base of arm. Proximal aulacophore well preserved, slightly flexed leftwards, and made of 10 telescopic rings. Each ring consisting of two inferolaterals (below) and two tectals (above), with inferolaterals and tectals nearly subequal in size and joining at about lateral midline. Lower surface of proximal aulacophore flat and upper surface strongly convex, domed. Anterior edge of each ring slightly raised and overlapping depressed posterior portion of next, more anterior (distal) ring. Stylocone funnel-shaped, with enlarged posterior region, and straight, narrower distal portion. Lower surface of stylocone nearly smooth and rounded. Upper (internal) surface of stylocone showing deep proximal notch, longitudinal median groove, with two pairs of transverse channels leading to lateral depressions. Two pairs of opened cover plates articulated to stylocone. Four ossicles preserved anteriorly to stylocone, showing similar smooth lower surface, longitudinal median groove and one pair of transverse channels on internal side. Two cover plates preserved in open position articulated to lateral edges of each ossicle.

Material examined.—Part and counterpart of a single specimen SNUP 2563.

Occurrence.—Lower part of the Tongjom Formation, uppermost Cambrian, stratigraphic level 021025, Sokkaejae section (Fig. 2), Taebaeksan Basin, Korea.

Discussion.—SNUP 2563 is clearly a cornute, as evidenced by the possession of cothurnopores, a delicate marginal frame enclosing large integumentary areas, and brachials with a smooth lower surface. The phyletic position of SNUP 2563 within cornutes is, however, difficult to assess, because of the possession of a zygal plate in central position and the poor preservation of its marginal frame (precise number of elements unknown). The occurrence of the zygal plate in central position represents the primitive condition in stylophorans (Lefebvre and Vizcaïno, 1999; Lefebvre, 2001). In cornutes, this plesiomorphic condition occurs in amygdalothecids (e.g., *Amygdalotheca* Ubaghs, 1969), hanusiids (e.g., *Galliaecystis* Ubaghs, 1969), stem-group cothurnocystids (e.g., *Archaeocothurnus* Sumrall, 1997, and *Ponticulocarpus* Sumrall and Sprinkle, 1999), and is retained in some cothurnocystids (e.g., *Milonicystis* Chauvel, 1986). The precise number of marginal elements on the right thecal side, and thus the putative occurrence of the cothurnocystid marginal Mc, is unknown because of poor preservation. Presence of three marginals (Mc, M_3, and M_4) between M_2 and Z would suggest affinities of SNUP 2563 with cothurnocystids, such as *Milonicystis kerfornei* Chauvel, 1986 from the Middle Ordovician of Brittany, France (Chauvel, 1986; Cripps and Daley, 1994). If only two marginals occur (M_3 and M_4), the morphology of SNUP 2563 would be more comparable to that of amygdalothecids and/or stem-group cothurnocystids. The presence of respiratory structures (cothurnopores) is also a plesiomorphic feature for stylophorans. They are present in *Ceratocystis* Jaekel, 1901, primitive hanusiids (*Drepanocarpos* Smith and Jell, 1999), cothurnocystids (e.g., *Chauvelicystis*, *Cothurnocystis* Bather, 1913, *Phyllocystis* Thoral, 1935;

Ubaghs, 1969), and possibly primitive mitrates (*Lobocarpus* Ubaghs, 1998).

The general morphology of gen. and sp. indeterminate form A superficially resembles that of *Phyllocystis*, more specifically *P. blayaci* Thoral, 1935 (early Arenigian, Montagne Noire, France), which is also characterized by a heart-shaped theca and the presence of numerous cothurnopores (Thoral, 1935; Ubaghs, 1969). However, a more careful scrutiny suggests that the morphology of *P. blayaci* is clearly different from that of SNUP 2563 in possessing the following morphological features: 1) presence of protuberances on lower surface of anterior marginals; 2) absence of a thin, downward-recurved outer flange; 3) much larger and less numerous supracentrals, all with a smooth upper surface (no protuberances); 4) larger, wider and less numerous cothurnopores; 5) presence of A_0; 6) less numerous proximal rings; and, most importantly, 7) zygal plate Z not in central position.

SNUP 2563 also recalls *Acuticarpus*? *republicensis*, a poorly known cornute from the Late Cambrian of Wyoming (Sumrall et al., 1997). *Acuticarpus*? *republicensis* is based on a single, incomplete specimen with most of the aulacophore and a portion of upper thecal surface. Precise number of marginals and putative closure/opening of thecal frame are not documented in *A.*? *republicensis*, because of incomplete preservation. However, SNUP 2563 is comparable with *A.*? *republicensis* by the possession of rounded, heart-shaped thecal outlines, without any lateral protuberance (e.g., spinal), and of marginals with a smooth lower surface, an outer flange, and a narrow ridge on upper surface. The Korean specimen differs from *A.*? *republicensis* in the number of proximal rings (10 instead of five), the number and morphology of anterior cothurnopore U-plates (more massive, defining a much smaller posterior opening in the American form), the number of adorals (three in *A.*? *republicensis*), and the smaller size and protuberated morphology of supracentrals.

Although incompletely preserved, SNUP 2563 also shares many morphological features with *Amygdalotheca griffei* (early Arenigian, Montagne Noire, southern France; Ubaghs, 1969) in having: 1) smooth lower surface; 2) outer flange; 3) numerous tiny supracentrals with mushroom-like protuberances; 4) zygal plate Z in central position; 5) loss of the median adoral (A_0); and 6) possible presence of small, extra marginal plates in the periproctal area, between M'_4 and G. However, the Korean specimen is older and differs from *Amygdalotheca* in the presence of cothurnopores. These comparisons suggest that SNUP 2563 possibly represents a close relative of *Acuticarpus*? *republicensis* and/or of *Amygdalotheca griffei*. Nonetheless, the poor preservation and incompletely known morphologies of SNUP 2563 and both of *A.*? *republicensis* and *A. griffei* preclude more detailed comparisons and a more precise taxonomic assignment of the Korean material.

Family COTHURNOCYSTIDAE Bather, 1913

Subfamily CHAUVELICYSTINAE Daley, 1992

Discussion.—The subfamily Chauvelicystinae was originally defined as a clade of cornutes characterized by the possession of spines articulated to, at least, the left side of the thecal frame (Daley, 1992). The two genera, *Chauvelicystis* (early Arenigian, Anti-Atlas, Morocco, and Montagne Noire, France) and *Prochauvelicystis* (Tremadocian, Shropshire, England), were assigned to this subfamily by Daley (1992). The monophyletic nature of the clade uniting *Prochauvelicystis* with *Chauvelicystis* has been supported by several cladistic analyses (Cripps, 1991; Cripps and Daley, 1994; Parsley, 1997, 1998). Diagnosis of the subfamily was later modified by Lefebvre and Vizcaïno (1999) to include all cothurnocystid cornutes characterized by a posteriorly open marginal frame frequently surrounded by articulated spines. Following this expanded definition, three more genera were included in the Chauvelicystinae by Lefebvre and Vizcaïno (1999) and Lefebvre (2001): *Ampelocarpus* Lefebvre and Vizcaïno, 1999, *Lyricocarpus* Ubaghs, 1994 (early Arenigian, Montagne Noire, France), and *Milonicystis* (Llandeilian, Brittany, France). Two more genera of cothurnocystid cornutes are here assigned to the subfamily Chauvelicystinae: *Flabellicarpus* (Tremadocian, Shropshire, England) and *Sokkaejaecystis* n. gen. (Late Cambrian, Korea). The assignment of *Flabellicarpus* to the Chauvelicystinae is motivated by its morphology comparable to that of a spineless *Chauvelicystis* and by the results of cladistic analyses supporting a clade uniting *Flabellicarpus* with *Chauvelicystis* (Martí Mus, 2002; see below). Martí Mus (2002) suggested that the primitive cornute *Ponticulocarpus* (Middle Cambrian, Utah) was the sister group of the clade (*Chauvelicystis* + *Flabellicarpus*). Reexamination of casts of the type material of *Ponticulocarpus* confirms that this cornute possesses a posteriorly closed marginal frame (presence of both M_5 and M'_5; see Sumrall and Sprinkle, 1999) and shows that no marginal Mc is present between M_2 and M_3. These observations suggest that *Ponticulocarpus* cannot be considered as a member of the Chauvelicystinae (closed marginal frame), nor even as a cothurnocystid cornute (absence of Mc).

Genus SOKKAEJAECYSTIS new genus

Type species.—*Sokkaejaecystis serrata* n. sp.

Diagnosis.—A small boot-shaped spiny cornute, with smooth lower surface; posteriorly open thecal frame consisting of 10 marginals, two adorals, and large integumentary areas; right thecal margin made of three marginals, M_2, Mc, and M_3, with strong lateral blades; left thecal side comprising three marginals, $M'_{2/3}$, M'_4, and digital, with spiny outer flange; expanded, fanlike glossal with fibrillar ornamentation and serrated outer margin; right adoral orifice present; no cothurnopores; supracentrals numerous, with central processs; large anal pyramid; proximal aulacophore made of eight to 11 rings, with spines articulated to some inferolaterals; brachials with keeled lower surface.

Etymology.—The genus is named for the Sokkaejae section, Taebaeksan Basin, Korea, from which all specimens were collected.

Occurrence.—Lower part of the Tongjom Formation, latest Cambrian, stratigraphic level 010514b, Sokkaejae section (Fig. 2), Taebaeksan Basin, Korea.

Discussion.—*Sokkaejaecystis* is a cothurnocystid cornute (Mc marginal on right thecal side) and the oldest indisputable known member of the Chauvelicystinae (open marginal frame, marginal spines). Within this subfamily, *Sokkaejaecystis* shares some morphological features with *Flabellicarpus* and *Chauvelicystis*, such as the presence of large infracentral areas enclosed by a delicate, narrow marginal frame. However, *Sokkaejaecystis* differs from the latter genera in the possession of blades on right marginals, a spiny flange restricted to the left thecal side, and in the absence of one adoral (A_0), two marginals (M_4, and M'_2 or M'_3), and cothurnopores. *Sokkaejaecystis* also shows an affinity with *Prochauvelicystis* (general outline, spiny flange restricted to left thecal side, ornamented right marginals, large periproctal area; see cladistic analysis below), but differs in the absence of one adoral (A_0), one marginal (M_4), and cothurnopores, and in the possession of larger infracentral areas and a longer, spiny proximal aulacophore. Within the Chauvelicystinae, *Sokkaejaecystis* is also comparable to *Ampelocarpus* and *Lyricocarpus* in lacking two marginals and the median adoral, but is clearly distinct in possessing spiny proximal rings, large infracentral areas, and a greater number of marginals between M_1 and Z. Comparisons with other Chauvelicystinae show that *Sokkaejaecystis* differs significantly from all described forms and consequently supports the assignment of the Korean material to a new genus.

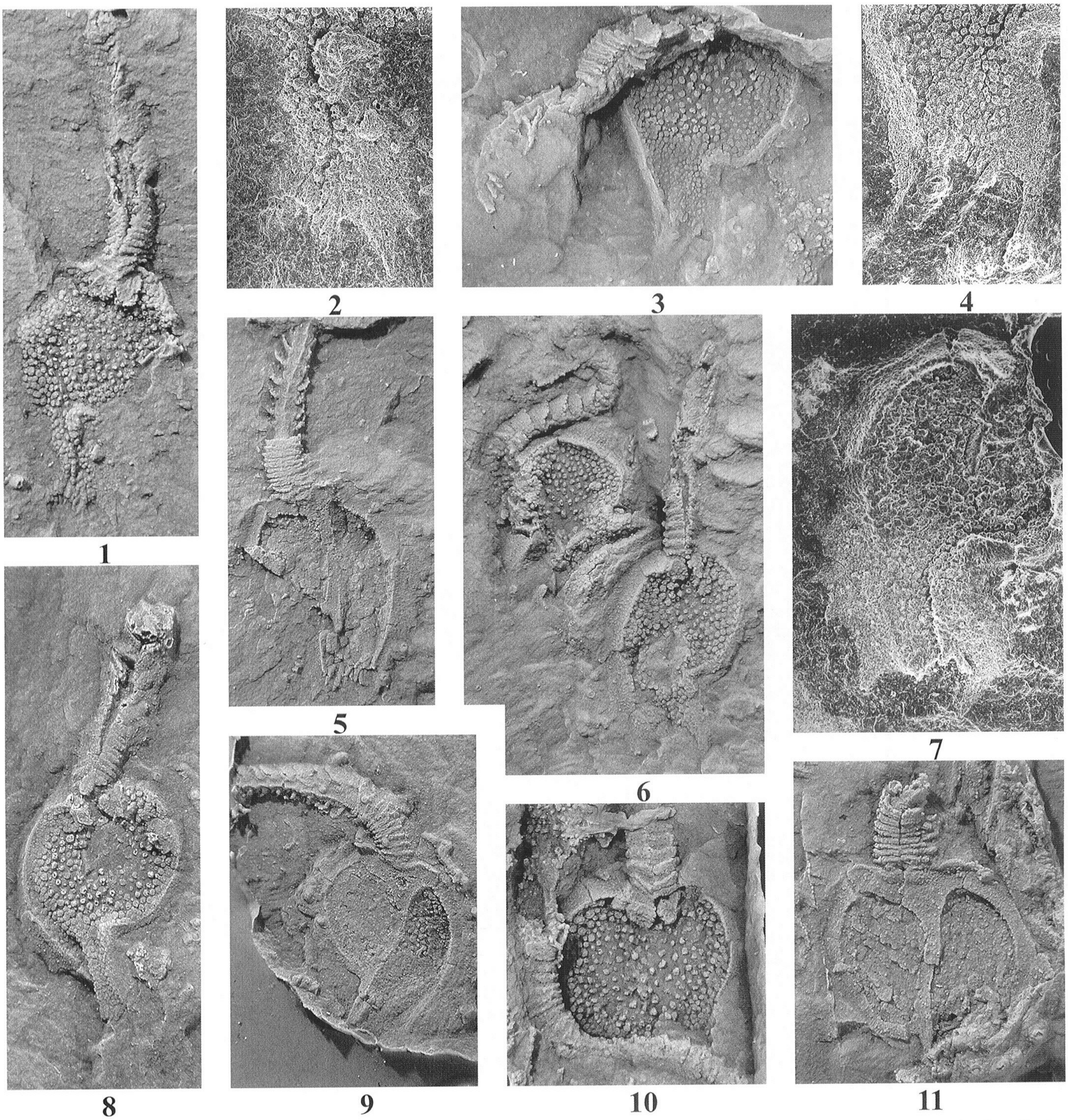

FIGURE 5—Latex casts of *Sokkaejaecystis serrata* n. gen. and sp., all from horizon 010514b, Late Cambrian, Tongjom Formation, Taebaeksan Basin, Korea. *1, 2, 5,* SNUP2560, holotype; *1,* theca and aulacophore in upper aspect, ×9.5; *2,* detailed scanning electron microscopic (SEM) image of periproctal area, with anal pyramid and glossal, ×18.5; *5,* theca and aulacophore in lower aspect, ×7.5; *3, 4,* SNUP2550; *3,* theca and proximal aulacophore in upper aspect, ×9.5; *4,* SEM image of periproctal area, with anal pyramid, digital, and glossal, in upper aspect, ×20.5; *6,* SNUP2552 (left) and SNUP2553 (right), both with theca and complete aulacophore in upper aspect, ×8.5; *7,* SNUP2551, SEM image of upper thecal surface, ×13.5; *8,* SNUP2549: aulacophore and theca in upper aspect, ×8.5; *9,* SNUP2554: theca and aulacophore in lower aspect, ×7.5; *10, 11,* SNUP2555; *10,* thecal surface and proximal aulacophore in upper aspect, ×9; *11,* theca, proximal aulacophore, and stylocone in lower aspect, ×9.

SOKKAEJAECYSTIS SERRATA new species
Figures 5–7

Diagnosis.—Same as the generic diagnosis.

Description.—Small, boot-shaped theca, slightly longer than wide, with posteriorly open marginal frame, spiny flange articulated to left thecal side, and strong blades borne by right marginals. Thecal length and width both comprise between 4 and 5 mm. Longest preserved aulacophores slightly longer than theca (5–6 mm), with spiny proximal portion, and brachials with keeled lower surface. Narrow and delicate thecal frame consisting of 10 marginals (including digital, glossal, and zygal plate) and two adorals. Thecal height maximal along steep anterior edge, regularly decreasing in a posterior direction. Anterior thecal margin rounded, with slight invagination at M_1-M'_1 suture for aulacophore insertion on lower surface, and deeper, V-shaped excavation on upper surface. Anterior extremity of lower surface of M_1 and M'_1 slightly recurved downwards, especially below apophyses cups. Lateral thecal margins with serrated outer flanges, strongly recurved downwards and rearwards anteriorly, and subhorizontal posteriorly. Right outer flange made of six strong blades emitted by marginals M_2, Mc, and M_3, anteriorly, and of large, denticulate lateral expansion of glossal, posteriorly. Blades on right thecal side increasing in size and strength in a posterior direction. Left outer flange consisting of $M'_{2/3}$ lateral blade anteriorly, and of 15–16 large, flattened, blunt spines sutured to $M'_{2/3}$, M'_4, and digital, posteriorly. Thecal spines partly overlapping, forming an irregular longitudinal row. Size of spines slowly decreases in a posterior direction. Spines tightly sutured to, rather than articulated to, one and sometimes two left marginals. Radiating, fibrillar ornamentation on marginal blades, glossal, and thecal spines.

M_1 small, trapezoidal plate, with convex anterior margin. M'_1 T-shaped, with sinuous anterior edge, massive anterior region comprising very reduced right and left branches (sutured along M_1 and $M'_{2/3}$, respectively), and relatively narrow and long zygal, posterior portion. Zygal plate Y-shaped, with long and straight anterior, zygal branch (sutured to M'_1), and very reduced right and posterior branches, perpendicular to each other and of comparable extension. No M_4 observed on upper surface of Z. Right thecal side consisting of three marginals of comparable size, between M_1 and Z: M_2, Mc, and M_3. M_2 and M_3 slightly arched plates forming right anterior and posterior corners of theca, respectively. M_2 pentagonal, massive marginal with small, blunt lateral blade. Mc straight, relatively massive element, with three well-developed lateral blades. M_3 more delicate plate, with two strong blades. Glossal consisting of a narrow, elongate marginal portion, anteriorly sutured to Z, and of a large, lateral expansion with serrated margins and fibrillar ornamentation. Glossal forms right flank of periproctal area. $M'_{2/3}$ massive, curved marginal, forming left anterior corner of thecal frame. Strong, blunt lateral blade with fibrillar ornamentation on anterior half of outer margin of $M'_{2/3}$. M'_4 and digital straight, relatively narrow, elongate plates of comparable extension. Posterior extremity of digital sharp, with fibrillar ornamentation, along left flank of periproctal area. Two adorals on anterior edge of upper thecal surface, along aulacophore insertion. Left adoral A'_1 small, rounded element articulated to M'_1. Right adoral A_1 transversely elongate plate, with deep longitudinal groove bordered by raised lips, leading to an anterior notch, at A_1-M_1 suture (right adoral orifice). Supracentral area made of several dozen small, polygonal platelets (0.1–0.2 mm in diameter), all with central, blunt to mushroomlike protuberance. Infracentral areas consisting of numerous, smooth, polygonal platelets, larger than supracentral elements. Left infracentral area narrow, anteroposteriorly elongated, with left side gently curved along $M'_{2/3}$, M'_4, and digital, anterior extremity rounded, and right margin straight along M'_1, Z, and glossal. Right infracentral area smaller than left one, with rounded outlines, slightly longer than wide, and framed by six marginals (M'_1, M_1, M_2, Mc, M_3, and Z). Periproctal area pyramid-shaped, formed by numerous elongate platelets with sharp posterior extremity. Right anterior corner of supracentral area well preserved in many specimens, without any sign of respiratory structures (e.g., cothurnopores).

Complete, well-preserved aulacophores slightly longer than theca. Proximal portion made of eight to 11 telescopic, highly flexible rings, each consisting of four plates: two inferolaterals (below) and two tectals (above). Proximal rings approximately pentagonal in cross section. Inferolaterals slightly larger than tectals, forming flat lower surface and subvertical lateral walls of proximal rings. Upper surface of each proximal ring roofed by inclined tectals. Anterior margin of each ring forming a thickened, slightly raised lip, overlapping the depressed posterior portion of next, more anterior (distal) ring. Well-developed facets present in lower, abaxial (lateral) corner of each inferolateral. A small, elongate spine (about 0.25–0.4 mm long) articulated to facets of inferolaterals belonging to proximal rings 2, 4, 6, 8, and 10. Longest observed arm consisting of 11 brachials (stylocone and 10 ossicles) and associated cover plates. Lower surface of all brachials ornamented with strong longitudinal median crest. Stylocone relatively large (about 0.75 mm long), funnel-shaped, with expanded proximal portion, and narrower distal region. Upper surface of stylocone showing proximal notch and longitudinal median groove. Lateral sides of median groove delimited by raised lips, interrupted by two pairs of transverse channels leading to lateral depressions. Longitudinal median groove and one pair of transverse channels also present on upper surface of each ossicle. Two pairs of cover plates articulated to stylocone, and one pair to each more distal brachial. Cover plates preserved in open position, sometimes collapsed above upper surface of brachials. Cover plates relatively large, slightly curved elements, with radiating fibrillar ornamentation and rounded upper edge. Cover plates of a same series clearly overlapping each other.

Etymology.—*Serrata*, Latin, sawtoothlike, refers to the serrated aspect of lateral thecal sides.

Type.—SNUP2560 is designated as the holotype (Fig. 5.1, 5.2, 5.5). It is one of the best-preserved specimens showing nearly complete lower thecal frame, most of the upper thecal surface with both adorals, well-exposed periproctal area with glossal and digital, complete proximal aulacophore with articulated spines, and proximal half of the arm.

Other material examined.—Forty specimens include 12 thecae preserved in both upper and lower aspects, 10 upper and eight lower thecal surfaces. Among them, 27 specimens are preserved with articulated aulacophores. In addition, three isolated pieces of distal aulacophores (arms) and seven poorly preserved specimens are included in the collection.

Occurrence.—Same as the genus.

Genus and species INDETERMINATE FORM B
Figures 8, 9

Description.—Known from part and counterpart of a single small specimen (SNUP2562) showing right portion of theca and apparently complete aulacophore. Preserved portion of thecal frame about 2.6 mm long and 2.8 mm wide, consisting of six marginals and a zygal plate. Regularly curved and almost smooth thecal outlines, with slight anterior concavity at the aulacophore insertion. Extremely reduced ornamentation on lower thecal surface, comprising a low, downward-directed ridge along the anterior edge of the theca (M'_1, M_1, and anterior portion of M_2), and a small, triangular, blunt, spinal blade borne by M_3. Numerous, small protuberances forming two, possibly three, more-or-less regular longitudinal rows on lateral, external flanks of right


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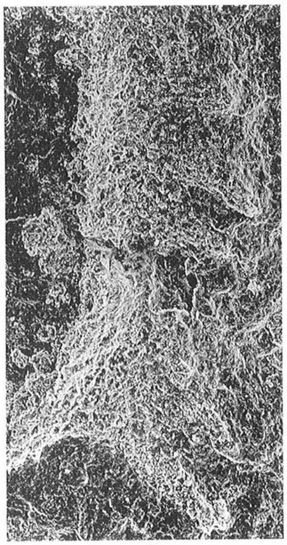
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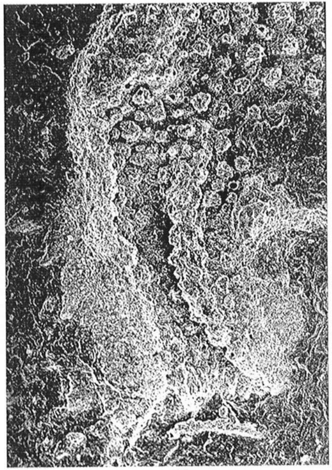
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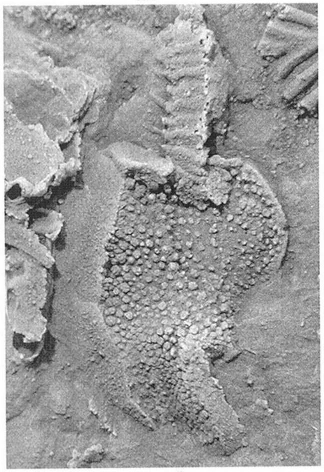
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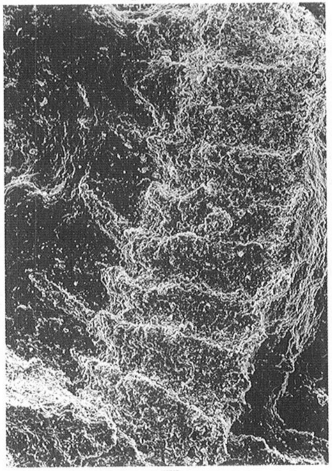
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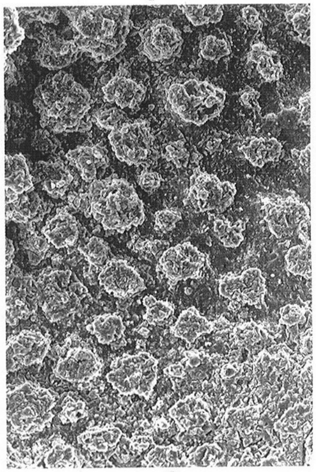
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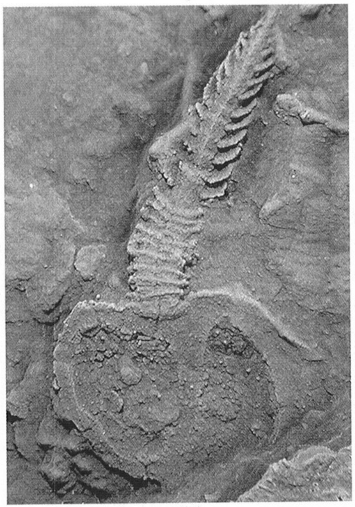
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marginals M_2 (posterior portion), Mc, and M_3 (anteriorly to spinal blade).

M_1 subrectangular, large element, with sinuous anterior and posterior edges. M'_1 L-shaped, with massive anterior region comparable in morphology and extension to M_1, and thinner, apparently relatively short posterior, zygal portion. Adorals not preserved, but articulation facets for A'_1 and A_1 present on upper surface of M'_1 and M_1, respectively. Left and posterior sides of theca not preserved, with the exception of anteriormost portion of M'_2. Right side of theca consisting of three marginals between M_1 and zygal plate, Z: M_2, Mc, and M_3. M_2 regularly arched plate forming right anterior corner of thecal frame. Mc straight to slightly curved marginal forming most of right side of theca. Length of Mc comparable to that of M_2. M_3 small, curved element forming right posterior corner of theca and bearing reduced spinal blade. Morphology of zygal plate Z poorly known, probably Y-shaped; only right branch of zygal plate preserved, in contact with M_3. Apparently, no marginal M_4 above Z. Upper thecal surface covered by several dozens of small, polygonal supracentral platelets, approximately 0.15 mm in diameter. Low, blunt protuberance on upper (external) surface of each supracentral. Infracentrals poorly preserved, apparently consisting of polygonal elements with smooth lower surface. Size of infracentrals similar to that of supracentrals. Periproct not observed (left posterior region of theca missing). Presence of about four relatively large cothurnopores in right anterior corner of upper thecal surface. Each cothurnopore made of two U-shaped plates, with anterior element longer than posterior one. Cothurnopores in central position larger than lateral ones. No structures (pores, cones) clearly visible within U-shaped elements.

Apparently complete aulacophore, about 4.4 mm long, preserved in extended position. Proximal portion of aulacophore consisting of eight imbricated rings. Each ring overlapped by its more posterior (proximal) neighbor. Upper surface of rings made of two series of small tectals, missing or possibly collapsed into proximal aulacophore cavity. Lower surface and lateral walls of each proximal ring made of two subequal, symmetrical inferolaterals. Lower surface of inferolaterals flat to slightly convex, with raised anterior edge and more depressed posterior region. Sharp, protruding facet developed on lower abaxial (lateral) corner of each inferolateral, for articulation with a small, spiny element. At least two such spines preserved along right side of proximal aulacophore, articulated to rings 3 and 4. Arm consisting at least of 12 brachials (stylocone and 11 more distal ossicles) and two series of open, partly collapsed cover plates. Brachials rapidly decreasing in size distally. Low longitudinal median crest on lower surface of brachials. Upper surface of brachials poorly preserved, showing longitudinal median furrow. Proximal notch visible on internal surface of stylocone. Stylocone funnel-shaped, long, and narrow (length approximately 0.8 mm). Two pairs of cover plates articulated to stylocone, and one pair to each ossicle. Fan-shaped cover plates, with massive, narrow lower extremity, and thinner, wider, curved upper edge. Ornamentation consisting of radiating lines on external surface of cover plates.

Material examined.—Part and counterpart of a single specimen SNUP2562.

Occurrence.—Lower part of the Tongjom Formation, uppermost Cambrian, stratigraphic level 010521, Sokkaejae section (Fig. 2), Taebaeksan Basin, Korea.

Discussion.—The assignment of specimen SNUP2562 to cothurnocystid cornutes is supported by the possession of a Mc marginal on the right side of the theca (between M_2 and M_3). Affinities of SNUP2562 with Chauvelicystinae are mainly suggested by the possession of small spines articulated to the proximal aulacophore and the presence of a low longitudinal median keel on the lower surface of all brachials. Within cothurnocystid cornutes, these two characters have been described only in Chauvelicystinae. Spines articulated to proximal rings have been reported in *Chauvelicystis ubaghsi* (Chauvel, 1966, p. 101), *Sokkaejaecystis serrata* n. gen. and sp. (see above), and occur possibly also in *C. spinosa* Ubaghs, 1969 and *C. vizcainoi* (Ubaghs, 1983; personal observation). A longitudinal median crest on the lower surface of brachials is present in *Chauvelicystis vizcainoi* (Ubaghs, 1983, p. 45), *C. spinosa* (personal observation), and *Sokkaejaecystis serrata* (see above). Spines articulated to the theca have not been observed in SNUP2562, but the presence of longitudinal rows of protuberances along the right side of the theca recalls the situation in spine-bearing Chauvelicystinae. In *Chauvelicystis*, similar bumps are present. They correspond to facets for the articulation of two rows of spines along lateral edges of marginals. The smooth, rounded thecal outlines of SNUP2562 are clearly different from those of *Sokkaejaecystis* n. gen. and *Prochauvelicystis*, but bear some resemblence with those of *Flabellicarpus rushtoni* (Martí Mus, 2002) and *Chauvelicystis spinosa*. The Korean cornute is similar to *F. rushtoni* in the possible absence of spines, comparable outlines for the right thecal side, and the possession of a short spinal blade, but differs from *F. rushtoni* in the absence of a large outer flange along marginals, and in the possession of a smaller number of cothurnopores and of fewer, low-protuberated supracentrals. Morphology of marginals, cothurnopores, and supracentrals in SNUP2562 are more reminiscent of the situation in *Chauvelicystis spinosa*, but the Korean specimen differs from *C. spinosa* in the possession of a spinal blade, of a shorter right thecal side, and possibly in the absence of spines.

CLADISTIC ANALYSIS

Phylogenetic analysis.—Relatively few cladistic analyses have been devoted to cornutes and none of them has included more than four different species of Chauvelicystinae (Cripps, 1988, 1991; Cripps and Daley, 1994; Parsley, 1997, 1998; Lefebvre, 2001; Martí Mus, 2002). Assignment of nearly symmetrical forms (e.g., *Lyricocarpus*, *Milonicystis*) to the Chauvelicystinae and, thus, monophyly of the subfamily have been questioned in previous analyses (Cripps, 1991; Cripps and Daley, 1994; Parsley, 1997, 1998; Lefebvre, 2001). A cladistic analysis was performed to determine the phylogenetic position of *Sokkaejaecystis serrata* n. gen. and sp. within the Chauvelicystinae and to investigate phyletic relationships within this subfamily. Ingroup taxa include

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FIGURE 6—Latex casts of *Sokkaejaecystis serrata* n. gen. and sp., all from horizon 010514b, Late Cambrian, Tongjom Formation, Taebaeksan Basin, Korea. *1–3*, SNUP2556; *1*, theca and aulacophore in upper aspect, ×8.5; *2*, SEM image of spinal blades, on right thecal side, ×33; *3*, theca and aulacophore in lower aspect, ×8.5; *4*, SNUP2559, lower aspect of thecal surface and proximal aulacophore with articulated spines, ×9.5; *5*, SNUP2558, SEM image showing upper aspect of anal pyramid and spines on left posterior thecal side, ×17. *6–8*, SNUP2557; *6*, upper aspect of thecal surface and proximal aulacophore, ×8.5; *7*, SEM image of proximal aulacophore showing spines articulated to proximal rings in upper aspect, ×30; *8*, SEM picture of supracentral platelets with mushroomlike protuberances, ×58. *9*, *10*, SNUP2561; *9*, thecal surface and nearly complete aulacophore in upper aspect, ×8.5; *10*, lower aspect of thecal surface and nearly complete aulacophore, ×8.5; *11*, *12*, SNUP2548; *11*, thecal surface and aulacophore in lower aspect, ×7.5; *12*, SEM image of spines on left thecal side, in upper aspect, ×20.5.

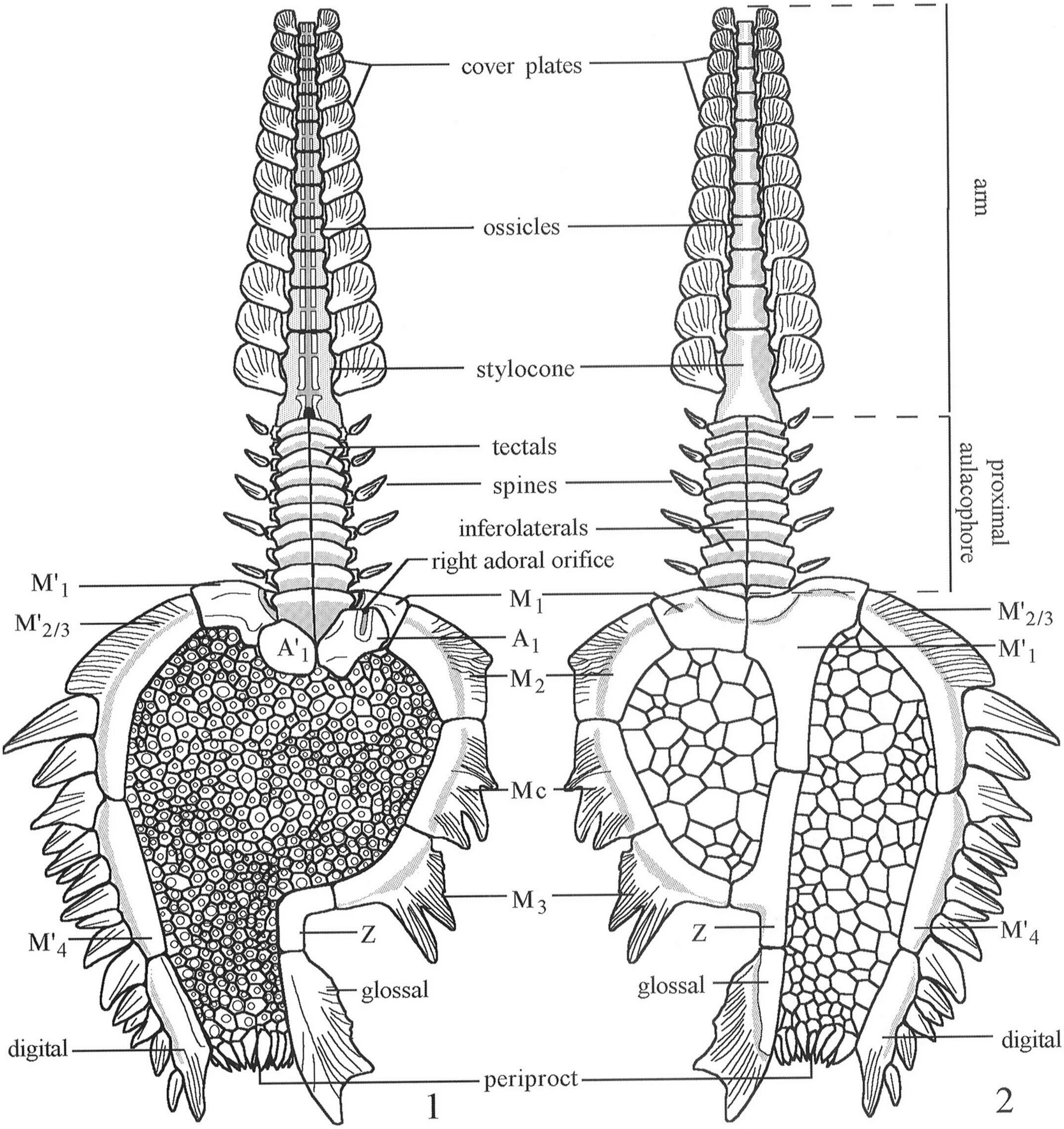

FIGURE 7—Reconstruction of *Sokkaejaecystis serrata* n. gen. and sp., Late Cambrian, Tongjom Formation, Taebaeksan Basin, Korea, ×20. *1,* Upper aspect; *2,* lower aspect.

all described Chauvelicystinae (seven genera, nine species; see Appendix 1). Outgroup taxa comprise one member of each of the three other cothurnocystid subfamilies: Cothurnocystinae, Phyllocystinae, and Scotiaecystinae (Appendix 1). These 12 taxa were scored for 15 unordered and unweighted characters (see Appendices 2, 3). Morphological data were based on direct observation of specimens when possible, and complemented by information from relevant papers by Chauvel (1966, 1986), Ubaghs (1969, 1983, 1994), Daley (1992), Cripps and Daley (1994), Lefebvre and Vizcaïno (1999), and Martí Mus (2002). The phylogenetic analysis was perfomed using PAUP 3.1.1 (Swofford, 1993), under the ACCTRAN optimization. A heuristic search found 185

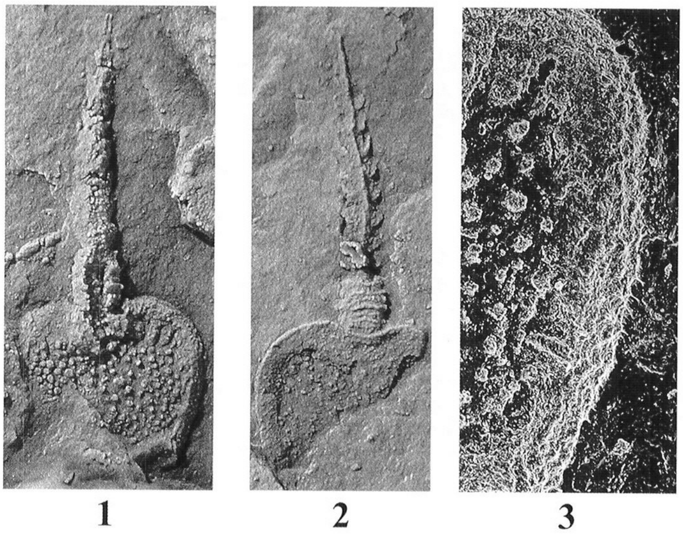

FIGURE 8—Genus and species indeterminate form B, latex casts of SNUP2562 from the horizon 010521, Late Cambrian, Tongjom Formation, Taebaeksan Basin, Korea. *1,* Upper aspect of theca and aulacophore, ×9; *2,* lower aspect of theca and aulacophore, ×9; *3,* SEM image showing longitudinal rows of small protuberances on outer flank of right marginals, ×33.

shortest trees (35 steps) with a consistency index of 0.657. The 50 percent majority-rule consensus tree of these 185 trees is presented and discussed below (Fig. 10).

Discussion.—Results of the analysis indicate that *Sokkaejaecystis* n. gen. is the sister group of a clade uniting *Ampelocarpus* with *Lyricocarpus.* A sister-group relationship between *Ampelocarpus* and *Lyricocarpus* was already suggested by Lefebvre and Vizcaïno (1999) and Lefebvre (2001, p. 614–615). *Ampelocarpus, Lyricocarpus,* and *Sokkaejaecystis* form a clade defined by three synapomorphies (absence of A_0, M_4, and cothurnopores). *Prochauvelicystis* is the sister group of the clade uniting *Sokkaejaecystis* with *Ampelocarpus* and *Lyricocarpus.* These four genera form a monophyletic group defined by one synapomorphy (loss of one anterior left marginal). This result suggests close affinities between Gondwanan stylophorans from low (Korea) and much higher (Shropshire, Montagne Noire) paleolatitudes in the Late Cambrian–Early Ordovician time interval. The placement of *Prochauvelicystis* differs from the results obtained by previous phylogenetic analyses, all suggesting that it was more closely related to *Chauvelicystis* than to *Lyricocarpus* (Parsley, 1997, 1998; Lefebvre, 2001).

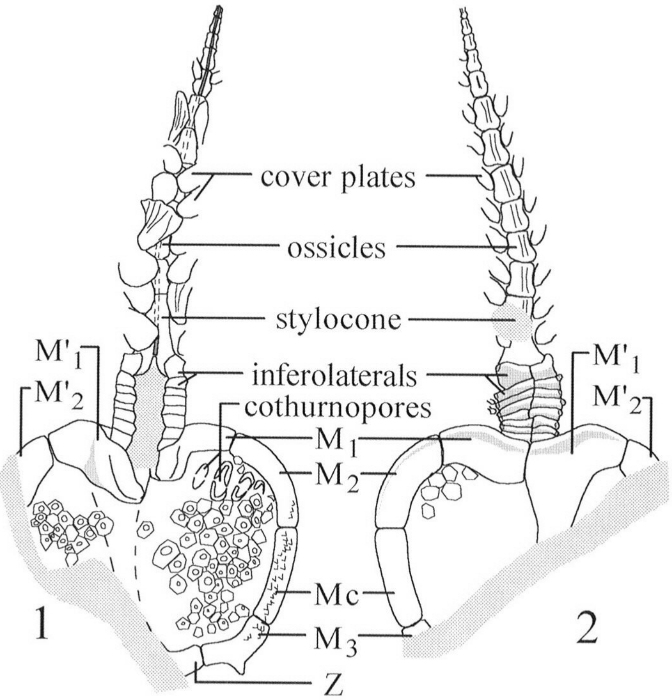

FIGURE 9—Genus and species indeterminate form B, camera lucida drawings based on SNUP2562, Late Cambrian, Tongjom Formation, Taebaeksan Basin, Korea, ×13. *1,* Upper aspect; *2,* lower aspect.

The analysis also supports the identification of *Milonicystis* as a derived member of the Chauvelicystinae (Lefebvre and Vizcaïno, 1999; Lefebvre, 2000, 2001), and differs from other interpretations of this fossil (Chauvel, 1986; Cripps and Daley, 1994; Parsley, 1997, 1998). Other important results concern the possible paraphyly of the genus *Chauvelicystis,* the monophyly of the Chauvelicystinae, and the basal placement of *Flabellicarpus* within this subfamily (Martí Mus, 2002).

ACKNOWLEDGMENTS

This paper is a contribution of the BK 21 Project (Earth and Environmental Sciences) of Seoul National University and of team C "Macroévolution et dynamique de la biodiversité" of the UMR CNRS 5561 Biogéosciences (Université de Bourgogne, Dijon). Financial support for this study has come from the Korea Research Foundation (Grant no. 2002-070-C00087). The authors

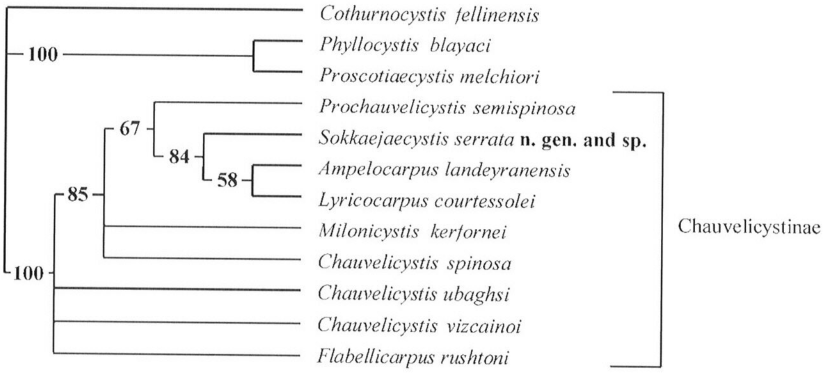

FIGURE 10—Cladistic analysis of the Chauvelicystinae and selected other cothurnocystids. Fifty percent majority-rule consensus tree of the 185 most parsimonious trees (35 steps) obtained in the analysis. Numbers on the branches indicate bootstrap values.

are particularly grateful to J. Sprinkle and D. R. Kolata for reviewing the manuscript and making many helpful remarks, to C. Sumrall for sending latex casts of the type material of *Ponticulocarpus robisoni*, and to J. P. Kundura, E. Monceret, A. Prieur, and D. Vizcaïno for access to comparative material of Montagne Noire Chauvelicystinae housed in public and private collections.

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Accepted 31 March 2004

APPENDIX 1

List of taxa included in phylogenetic analysis

Ingroup taxa (Chauvelicystinae): *Ampelocarpus landeyranensis* Lefebvre and Vizcaïno, 1999 and *Lyricocarpus courtessolei* Ubaghs, 1994 (Landeyran Formation, early Arenigian, Montagne Noire, southern France); *Chauvelicystis spinosa* Ubaghs, 1969 and *C. vizcainoi* Daley, 1992 (Saint–Chinian Formation, early Arenigian, Montagne Noire, southern France); *C. ubaghsi* (Chauvel, 1966) (Upper Fezouata Formation, early Arenigian, western Anti–Atlas, Morocco); *Flabellicarpus rushtoni* (Martí Mus, 2002) and *Prochauvelicystis semispinosa* Daley, 1992 (Arenaceous Beds, Tremadocian, Shropshire, western England); *Milonicystis kerfornei* Chauvel, 1986 (Traveusot Formation, Llandeilian, Brittany, western France); and *Sokkaejaecystis serrata* n. gen. and sp. (Tongjom Formation, Late Cambrian, Taebaeksan Basin, Korea).

Outgroup taxa (other cothurnocystids, early Arenigian, Montagne Noire): *Cothurnocystis fellinensis* Ubaghs, 1969 and *Phyllocystis blayaci* Thoral, 1935 (Saint–Chinian Formation) and *Proscotiaecystis melchiori* (Ubaghs, 1983) (Landeyran Formation).

APPENDIX 3

List of characters used in phylogenetic analysis

Character states are indicated by numerals in parentheses (?, missing information).

1. Marginals M'_2 and M'_3 (0) both present, (1) one absent.
2. Marginal M_4 (0) present on lower surface, (1) present on upper surface, (2) absent.
3. Marginal M_5 (0) present, (1) absent.
4. Marginal M'_5 (0) present, (1) absent.
5. Glossal (0) large and "fan-like," (1) straight and narrow, (2) absent.
6. Digital (0) large and "fan-like," (1) straight and narrow, (2) absent.
7. Lower surface of marginals (0) with protuberances, (1) smooth.
8. Ornamentation (0) absent, (1) flange, or spines (2) on left thecal side, or (3) both thecal sides.
9. Spinal blades (0) on M_3, (1) on Mc, (2) on both M_3 and Mc, (3) absent.
10. Right infracentral area (0) large, (1) reduced or absent.
11. Adoral A_0 (0) present, (1) absent.
12. Cothurnopores (0) numerous (10 or more) and closely packed, (1) few (nine or less) and clearly separated from each other, (2) absent.
13. Supracentrals (0) smooth, (1) with protuberance.
14. Spines on proximal aulacophore (0) absent, (1) present.
15. Lower surface of brachials (0) smooth, (1) with longitudinal median keel.

Appendix 2—Data matrix

Character number	1–5	6–10	11–15
Taxa			
Ampelocarpus landeyranensis	12111	11331	12101
Cothurnocystis fellinensis	01000	00000	01100
Chauvelicystis spinosa	01111	11330	01101
Chauvelicystis ubahgsi	01110	11300	?1?1?
Chauvelicystis vizcainoi	01110	11300	011?1
Flabellicarpus rushtoni	01110	11100	0010?
Lyricocarpus courtessolei	12111	11?31	12101
Milonicystis kerfornei	00111	11130	02101
Phyllocystis blayaci	02002	20030	01000
Prochauvelicystis semispinosa	11111	11221	01?00
Proscotiaecystis melchiori	02010	00010	?0000
Sokkaejaecystis serrata n. gen. and sp.	12110	11220	12111