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LONG STALKED EOCRINOIDS IN THE BASAL MIDDLE CAMBRIAN KAILI BIOTA, TAIJIANG COUNTY, GUIZHOU PROVINCE, CHINA

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ABSTRACT—Long-stemmed eocrinoids are limited to two species in the basal Middle Cambrian Kaili Biota, which occupies the middle portion of the Kaili Formation, Taijiang County, Guizhou Province, China. The Kaili Biota contains preserved soft-bodied organisms shared with either the Chengjiang Fauna (Southwest China) or the Burgess Shale Fauna (British Columbia) or with both. Echinoderms are preserved as limonitic external molds that produce excellent latex casts. *Sinoeocrinus lui* Zhao et al., 1994 has a complex ontogenetic development, which is described in terms of morphology of holdfast, number of thecal plate circlets, addition and morphology of thecal pores, ambulacral arrangement, and number of brachioles relative to thecal height. Because of the complex ontogeny the following species are now seen to be synonymous with *S. lui*: S. *curtobrachiolus* Zhao et al.,1994; *S. lepidus* Zhao et al., 1994; *S. longus* Zhao et al., 1994; *S. minus* Zhao et al., 1994; *Paragogia globosa* Zhao et al., 1994; and *Curtoeocrinus guizhouensis* Zhao et al., 1994. A second and rare eocrinoid of undetermined familial and ordinal placement, *Balangicystis rotundus* n. gen. and sp., has an unusually long holdfast and poreless thecal plates with prominent radial ridges. *Sinoeocrinus lui* and *Balangicystis rotundus* inhabited the outer shelf in disaerobic fine-grained shales and mudstones. Megascopic infauna in their community is not present.

INTRODUCTION

EOCRINOIDS ARE perhaps the most primitive echinoderm group. Gogiids (Lower and Middle Cambrian) possess many plesiomorphic characters that may have evolved within the group and still persist throughout the phylum. For example, ontogeny in the gogiid species discussed herein clearly demonstrates the transition from a 2-2 to a 2-1-2 symmetry pattern, the forerunner of typical echinoderm pentamery.

In the basal Middle Cambrian Kaili Formation that crops out on the mountain ridges above Balang in Taijiang County, Guizhou Province, (southwest) China, gogiids are numerous. Of two species, the long stalked, *Sinoeocrinus lui* Zhao et al., 1994 is discussed herein; the short stalked ''*Sinoeocrinus globus*'' Zhao et al., 1999 (nomen nudum, the species has been named and illustrated but never described) will be discussed elsewhere. *Sinoeocrinus lui* is of special interest because it is a primitive form and displays a complex ontogeny from the earliest juvenile stage to the most advanced mature forms. Growth stages include modifications in the stalk or holdfast, appearance and extensive development in the sutural pores or epispires, modifications in the symmetry of the ambulacra, and additions in number of brachiole bases adjacent to the mouth and at the ends of the ambulacral splits. Discussion of morphologic changes is scaled against the height of the theca (thecal height = TH). Thecal height is determined by measuring the distance between the top of the ambulacrum to the bottom of the basal ''series'' of thecal plates (thecal plates with the most distally placed sutural pores). Using total height of the animal or combined thecal and holdfast height is ruled out by limitations in preservation, and at all stages there is considerable variation in holdfast length relative to thecal height. Thecal height, used in millimeter increments, has proven to be a reliable metric. Over 1,200 specimens, ranging from small juveniles to advanced mature individuals, were available for study. Because of the continuous size range the ontogenetic changes could be recorded and a single long stalked species was determined to be present. In comparison, Zhao et al. (1994), then having only 90 specimens, quite understandably on the basis of morphological gaps determined that seven species assignable to three long stalked genera were present. It is now possible to roughly scale most gogiids against the ontogenetic changes displayed by *S. lui* to determine specimen maturity and intraspecies variability.

The morphology and attachment mode of the attachment disk directly to siliciclastic sediments and the morphology and deployment of the long cover plates on the brachioles bring new interpretive insights on how these animals lived in their communities.

PALEOECOLOGY

Gogiid eocrinoids are found in Lower and Middle Cambrian sediments on the margins of at least four then-existing continents (North America, Gondwana, Siberia, and South China [Robison, 1965; Ubaghs, 1968; Zhao et al., 1994, 1999]). They are known to have inhabited a rather wide range of bottom conditions and a rather wide range of water depths. Evidence for living in energetic shallow-water, carbonate-rich environments is manifest mostly through disarticulated remains or from attachment disks. The vast majority of entire or nearly entire specimens are found in deeper water siliciclastic sediments that indicate turbid water obrution deposition patterns. Specimens in this paleoenvironment may be current aligned, indicating that they had broken loose from their attachment disks and were subsequently transported by currents, but specimens are also found living in place, attached to the bottom or to other organisms. The distance that specimens were transported is speculative, but because they commonly are not abraded or fragmented, we assume that both distance and travel time were short. Even with somewhat limited and ambiguous data for shallow-water habitation, it is clear that gogiids ranged from shallow-water carbonate banks to outer shelf/slope deposits (below storm wave base), which were composed of silt to clay-grain-sized siliciclastics (Robison, 1991). Some of the best data for shallow-water habitation comes from upper Middle Cambrian carbonate shelf deposits in eastern Siberia (118°E, 71°N) (Siberian plate). Attachment disks, individual plates, and partially disarticulated gogiids have been collected in the Moyer Formation along the banks of the Tyung River. Possibly two undescribed gogiid genera are present (S. Rozhnov and C. Sumrall, personal commun., 2005). They are associated with small microbial bioherms that reflect shallow-water conditions: estimated depths range between 5 and 40 m. In some localities, shallow-water interference ripples are found with the gogiids. The bioherms are part of a distal shelf setting; shorewards there are ca. 100 km of dolomites interpreted as being deposited in hypersaline conditions; in adjacent deeper water slope sediments gogiids have not been found.

The greatest diversity of gogiids is from the western margin of North America (Laurentia) in various Lower to Middle Cambrian Formations (see Robison, 1965, 1991; Sprinkle, 1973, 1976). As in Siberia, disarticulated plates are found in shallow-water clastic carbonates, but articulated specimens are found most commonly in a wide range of essentially quiet water conditions ranging from shallow-water limey shales to deeper water, disaerobic, outer-shelf, siliciclastic shales and claystones. This is especially true of the outer-shelf depositional setting of the Spence Shale, where gogiids are particularly abundant (Sprinkle, 1976; Robison, 1991). Specimens from this formation, as well as from shallower water deposits, are commonly broken loose from their attachment disk and subsequently aligned by currents, so that the brachioles are splayed across the bottom, downcurrent from the theca (C. Sumrall, personal commun., 2005). In general, gogiids on the western margin of North America are thought to have occupied gradual slopes in a quiet turbid current regime (especially Spence Shale), but spasmodic, more intense turbid currents, producing obrution deposits, were also capable of breaking gogiids loose from their attachment disks.

In the Czech Republic (marginal Gondwana) the Middle Cambrian Jince Formation of the Přibram-Jince Basin (Litavka Valley, approximately 55 km southwest of Prague) contains an indigenous suite of gogiids or gogiidlike genera (*Acanthocystites* Barrande, 1887 and *Akadocrinus* Prokop, 1962). They were living in a quiet-water disaerobic silt/mudstone facies with more vigorous turbid flow and the presence of rare probable tempestites composed of laminated, fine-grained carbonate sands (depth of deposition 150–200? m) (R. Mikuláš, personal commun., 2002). The sides of the basin are regarded as steeper than a normal marginal shelf because of its probable graben or rift origin, and the increased slope is in part responsible for the energetic turbulent flow (Havlíček, 1998). Gogiids in the Jince Formation are not commonly found in fine-grained/fine-bedded mudstones/shales but in several units of slightly sandy shales. There is clearly a predilection for a more active current environment. It is from this more energetic depositional environment that Parsley and Prokop (2004) developed the hypothesis that most, if not all, Lower and Middle Cambrian echinoderms with polyplated attachment disks attached to the bottom or to other organisms by use of a biological adhesive, most likely mutable collagen fibers.

Recently, extremely abundant gogiids from the Lower and Middle Cambrian Kaili Formation (and including the Kaili Biota which, is basal Middle Cambrian in age), Guizhou Province, China (South China plate), were described for the first time by Huang and Zhao (1985), and subsequently in more detail by Zhao et al. (1994, 1999). The Kaili gogiids are all outer-shelf inhabitants: most are in place and only a few appear to be broken loose and current-oriented. Kaili gogiids lived in deeper and quieter water than those from western North American or Bohemian localities. They are in disaerobic environments where sedimentation consists of finely bedded, turbid-flow, siliciclastic mudstones.

Sprinkle (1973, p. 80) noted that in North American localities each commonly has only one species. While this occupation of a community by a single species is common in North America, in the Kaili Biota two gogiids, *Sinoeocrinus lui* Zhao et al., 1994 and "*Sinoeocrinus globus*," lived in the same community; the latter species is about three times more abundant than the former (Parsley and Zhao, 2002). Possibly the locality where the two species occur (Miaobanpo quarry) is a happenstance occurrence of community overlap, but additional localities, especially the upslope, are necessary to test this hypothesis. A third rare eocrinoid species, *Balangicystis rotundus* n. gen. and sp., is possibly a gogiid.

With over 1,200 specimens of long-stemmed gogiids in the Kaili Biota, especially from the Miaobanpo quarry, it is possible for the first time to observe gogiid ontogeny in considerable detail.

STRATIGRAPHY

The Kaili Formation was originally described by Lu (1963) for a Cambrian sequence near Nangao in Danzhai County, Guizhou Province. The formation is named for nearby Kaili County. The most intensely studied sections of the formation are on two parallel mountain ridges to the north-northwest and overlook the village of Balang in Taijiang County (Fig. 1). They are the Wuliu section (214 m thick: described in detail, Zhao et al., 2001a); the second is the Miaobanpo section (157 m thick, described in detail, Yuan et al., 2002), about 1 km to the north of the Wuliu section) (Fig. 2). Most of the lower Wuliu section (about 53 m), comprising the *Bathynotus–Nangaops* Assemblage Zone, is not exposed in the Miaobanpo section.

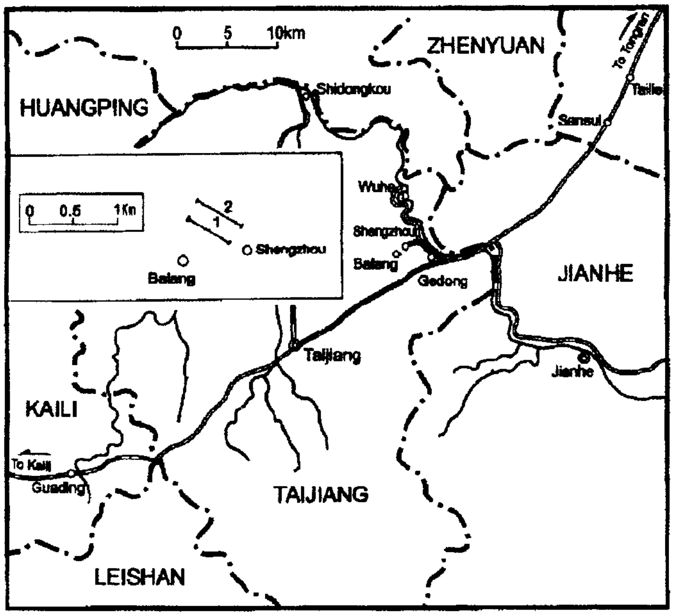


FIGURE *1*—Locality map of the Wuliu and Miaobanpo sections above the village of Balang, Taijiang County, Guizhou Province, in Southwest China. Inset is a more detailed locality sketch map of the Wuliu (1) and Miobanpo (2) sections on the mountain ridges to the north-northwest of Balang. Modified from Zhao et al., 2001b.

The Kaili Biota (Zhao et al., 1999) and the essentially equivalent Kaili Lagerstätten (Zhu et al., 1999) is present in the mid-portion of the Kaili Formation, ranging from the 53 to 164 m horizons in the Wuliu section and apparently occupying about the same stratigraphic interval as in the extensively collected Miobanpo section (Fig. 2). The entire biota is defined biostratigrapically by the *Xingrenaspis–Oryctocephalus* Assemblage Zone and contains representatives of 12 phyla, over 110 animal genera, about 20 genera of algae, and 20 ichnogenera (compilation based on Zhao et al., 1999, 2002). Almost all of the eocrinoids discussed in this paper come from an active fossil quarry in the Miaobanpo section and are found approximately 3–5 m above the base of the Kaili Biota. Like the Chengjiang Biota (Upper Lower Cambrian of Yunnan Province) and the Burgess Shale (Middle Cambrian of British Columbia), the straigraphically interposed Kaili Biota has preserved soft-bodied organisms, including preserved soft parts of hard-part–bearing organisms. *Ottoia*, Walcott, 1911; *Marrella* Walcott, 1912; *Naraoia*, Walcott, 1912; and *Wiwaxia* Matthew, 1899 are present in both the Burgess Shale and the Kaili Formation, and *Ottoia* and *Naraoia* are also found in the Chengjiang Fauna.

The Kaili Formation rests conformably on the upper Lower Cambrian Tsinghsutung Formation, which in the Wuliu section is interpreted as 2–4 m of shelf limestones and dolomites. The onset of the Kaili deposition is marked by a sharp change from the basal limestones grading into fine-grained siliciclastic sediments.

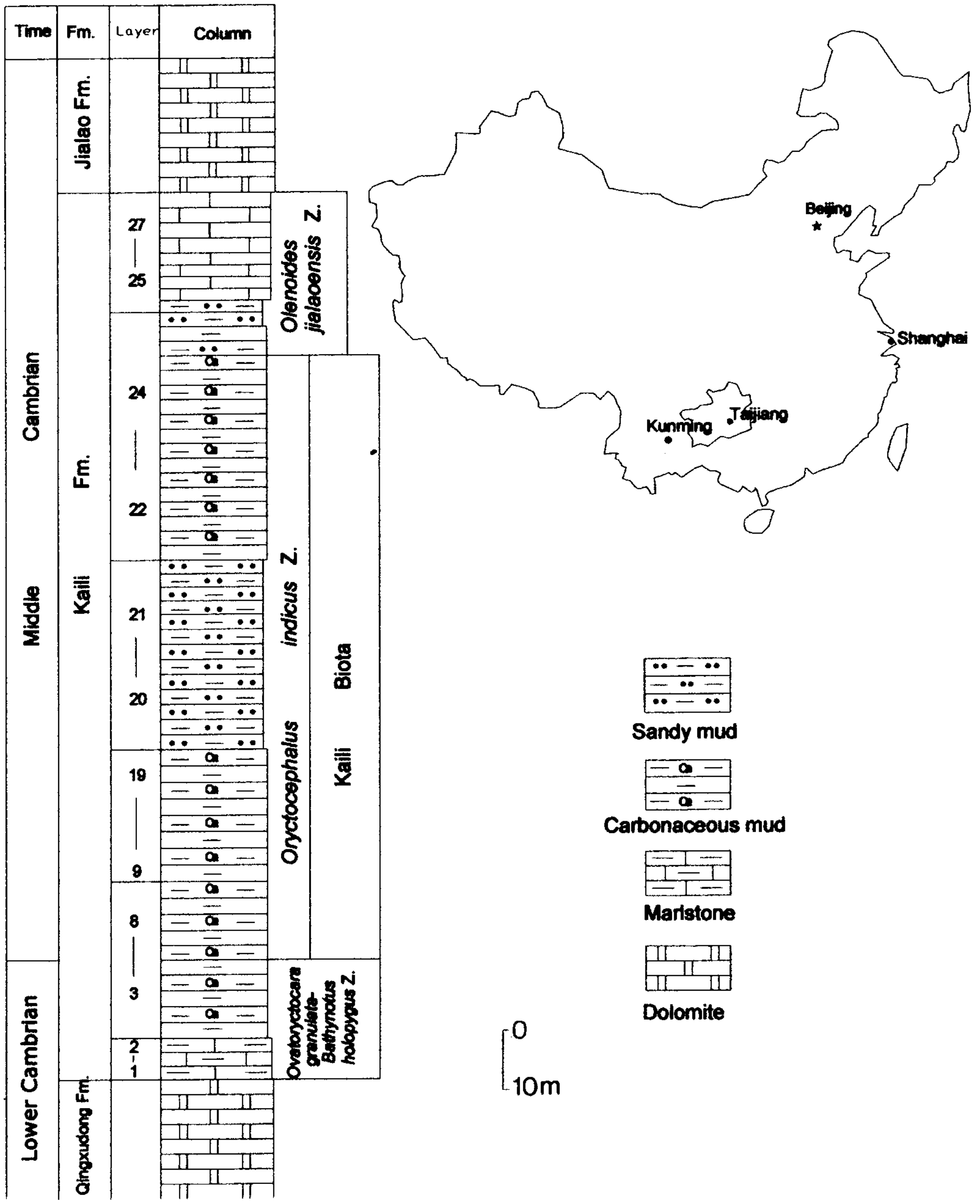


FIGURE 2—Stratigraphic column of the Miabanpo section, Lower and Middle Cambrian Kaili Formation, Kaili Biota, basal Middle Cambrian, on a mountain ridge to the north-northwest of the village of Balang in Taijiang County, Guizhou Province, China. Inset map of China shows section locality.

Depth of deposition increased dramatically, and most of the Kaili Biota (middle part of the formation) appears to be an outer-shelf setting. Sedimentation suggests a slow turbid deposition pattern of fine siltstones and (mostly) mudstones in 1–5 mm thick beds. There is no evidence of infauna or bioturbation. Zhao et al. (1999) argued that deposition depth of the Kaili Biota was between 150 and 200 m. This is based on the assumption that 150 m places the finely bedded mudstones below storm wave base (there is no evidence for wave modification of bedding) and 200 m places the sediments in the lower range of the photic zone (algae are present but could have been introduced by turbid flow). These figures seem reasonable, but there seems to be little evidence to reject an even deeper setting.

Overlying the Kaili Biota section is the upper part (164–214 m) of the Kaili Formation (*Olenoides jailaoensis* Range Zone). The upper part of the Kaili Formation *Olenoides jailaoensis* Range Zone is characterized by interbedded shales and limestones that indicate shallowing conditions. At the top of the formation are massive thick-bedded limestones. Bioturbation in this part of the section is readily observed. Overlying the formation are dolomitic siltstones of the Jailao Formation (Zhao et al., 1999, 2001a, 2001b).

FUNCTIONAL MORPHOLOGY

Gogiids and many cystoids in various ordinal groups superficially resemble crinoids (stem, theca, and exothecal feeding appendages). However, morphological analysis strongly suggests that eocrinoids and cystoids with similar gross morphology fed and anchored quite differently than crinoids. To compare them closely is likely to be misleading. Because of the large number of *Sinoeocrinus lui* specimens examined and the quality of preservation, functional morphological inferences can be made with confidence. These inferences can be broadly applied to other Cambrian gogiids as well. Discussion will focus first on the functioning of the attachment disk, holdfast, sutural pores, thecal openings, and brachioles, and, second, on the functional (feeding) posture of the entire animal.

Attachment disk.—Parsley and Prokop (2001, 2004) proposed that the polyplated attachment disk, both thecal or on the end of a holdfast, used to anchor many Lower and Middle Cambrian echinoderms such as helicoplacoids, gogiids, lichenoidids, and stromatocystitids, extruded an adhesive to attach the organism to either the seafloor or to another organism. Trilobite exuviae and inarticulate brachiopods are commonly utilized. Cementation by calcium carbonate to shells or hardgrounds has not been observed in these organisms of this age. A ''bioglue'' readily available and universal in echinoderm plating is extensible collagen that could be extruded from the sutures between the platelets. These fibers would do little to disrupt the sediment under the disk but could encompass a sediment body of sufficient mass and cohesion to firmly anchor the animal.

An alternative anchoring mechanism proposed by Guensburg and Sprinkle (2004) and Wilbur (2004) proposes that the attachment disk is suctorial. In spite of the cupped profile of the attachment disk's ventral surface we question whether this mechanism can function in unlithified sediments. Attachment of *S. lui* to unconsolidated sediment is common in the Kaili Formation and the zone of attachment in our opinion is too small to anchor the animal in this manner.

Holdfast and transitional plates.—The lower thecal and upper holdfast plating undergoes a distinct ontogenetic progression even though its organization is not uniform or well organized. Under the ambulacral plates, five rows of thecal plates are present in the earliest juveniles. The top three series are nearly equidimensional and the other two are elongate and transitionally taper towards the holdfast plates. These ''transitional'' plates develop sutural pores in early ontogeny and are therefore considered to be thecal. One or two more series of elongated transitional plates may be added and is not uncommon in specimens with thecal heights greater than 10 mm. In adult specimens, each plate in the lowermost thecal plate series has a sutural pore on its uppermost suture and the lowermost suture has a simple, uninterrupted suture. In juvenile specimens lacking or with few sutural pores, the gradation between theca and holdfast can be somewhat arbitrary, but the holdfast ornament is distinct.

Holdfast plates are bulbous with a tumid spine extending from the central part of the plate. Distally, near the attachment disk, small intercalated plates are common and this condition is consistent throughout ontogeny (Fig. 7.1). Small intercalates are interposed between the spinose holdfast plates as the animal grows. Proximally, as the larger holdfast plates grow, they add bulbous pustules and even with small intercalates interspersed between them, it is clear that this part of the holdfast loses flexibility. The distal end of the holdfast retains a more juvenile aspect (single-bossed plates and small intercalates) and is the zone of flexibility that allows the animal to heel over in the current. It is this area that is commonly preserved bent and it is the part of the holdfast that is commonly found at the end of holdfasts broken from the attachment disk.

Sutural pores/epispires.—Very small specimens with a thecal height less than 3 mm ($TH < 3$ mm) lack sutural pores, and all respiratory exchange must take place over the integument and possibly to a limited degree through the walls of the gut. Thecal pores first appear between the uppermost thecal plates and ambulacral plates at a TH of about 3 mm, and at about a TH of 6 mm pores open in the ''transitional'' plates of the lower theca. At TH ca. 8 mm, the sutural pores develop on all thecal plates (but not uniformly on all suture faces), and at a TH of 9–10 mm early formed pores show signs of maturity in becoming oval, with a distinct raised rim around the periphery. Respiratory pores are present in almost all thecal plates in large ($TH > 10$ mm) specimens and open at the surface between thecal plates in a fairly predictable order. Later-formed pores are more circular and the rims are less distinct. From this TH the pores (usually one on each plate facet) enlarge by deepening and widening so that the plates take on a sprocket shape. Commonly the pore opening enlarges so that it incorporates three plates. The resultant pore is triangular, especially at a TH greater than 12 mm. Resorption plays a role in the enlargement process and is especially obvious in larger specimens.

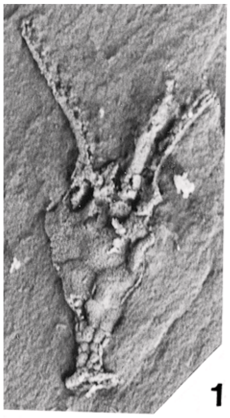
These simple to increasingly complex pore structures have been called epispires (Hudson, 1911; Ubaghs, 1968; Sprinkle, 1973; Broadhead, 1982) and the term carries with it the concept that these structures from their earliest stages are respiratory in function. It seems reasonable that protruding from the pores were papulae or papulae-like structures. Respiratory exchange occurred between seawater and circulating internal body fluids across the ''papulae'' (Ubaghs, 1968; Sprinkle, 1973). Broadhead (1982) suggested that the ''papulae'' might have been protected by spiculose mesoderm. There is no evidence for any sort of spiculose covering over the pore areas based on the current fossil material.

As the theca grows and adds volume, the rate of pore introduction, pore size, and complexity increases. This is especially true at TH of >12 mm, where almost all of the thecal plates have attained a sprocket shape, and at a TH of >18 mm where the pores are almost all triangular. At this size, the third series of brachioles is added, increasing the number from 10 to 15. There is a high probability that with increased food-gathering potential by the addition of brachioles, the respiratory requirements were increased, hence the somewhat sharp increase in respiratory surface area.

Anal pyramid and thecal pores.—Hydropore, gonopore, or probable combined hydropore and gonopore openings have not been observed in the over 1,200 specimens examined. The most logical position for them is in one or more of the sutural pores that were co-opted for the hydropore's intake of water for the water-vascular system and the gonopore's extrusion of sex products.

The anal pyramid has not been observed on small specimens, but on specimens of TH greater than 17 mm it is occasionally preserved. It is made up of a numerous elongate series of subrectangular platelets, and, like pyramids of other early Paleozoic blastozoans, it appears to be a pressure valve (Figs. 5.3, 5.5, 7.2).

Brachioles.—The structural makeup of blastozoan brachioles is well known (Ubaghs, 1968; Sprinkle, 1973) but their function and deployment is still somewhat speculative (Rozhnov, 2002). Examination of brachioles in many specimens of *S. lui*, plus brachioles in many other blastozoan genera, has failed to produce evidence (imprints) of a longitudinal water vessel in the food groove or the presence of ampullae for podia (Sprinkle, 1973). Articulatory surfaces in brachioles lack the fossae for interarticular ligaments and flexor muscles that are present in the arms of crinozoans (Hyman, 1955). Rather, interossicle articulatory surfaces in blastozoan brachioles are essentially featureless (Parsley and Zhao, 2004). Some blastozoan genera have a small central lumen that is probably for a nerve cord, but all lack the large interossicle canal present in crinozoans. The smooth simple interossicle (muscular?) articulation of biserial brachioles is probably incapable of producing the turgid reflexed feeding cones of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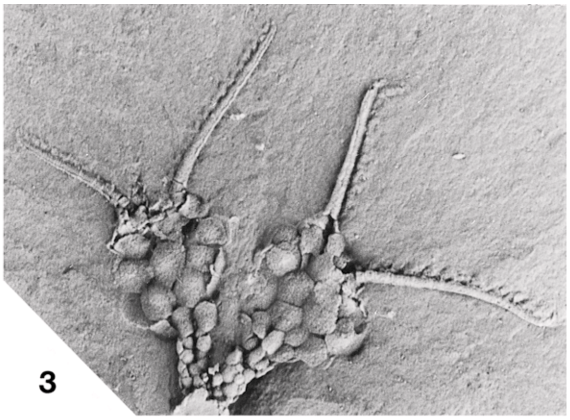
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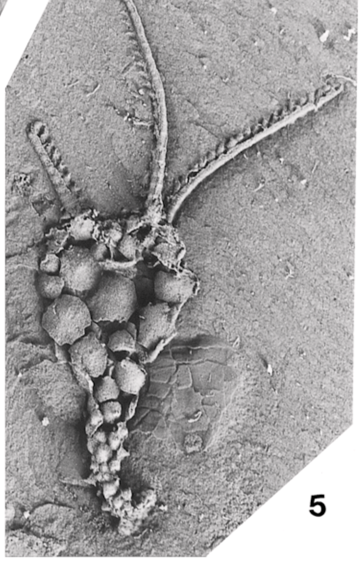
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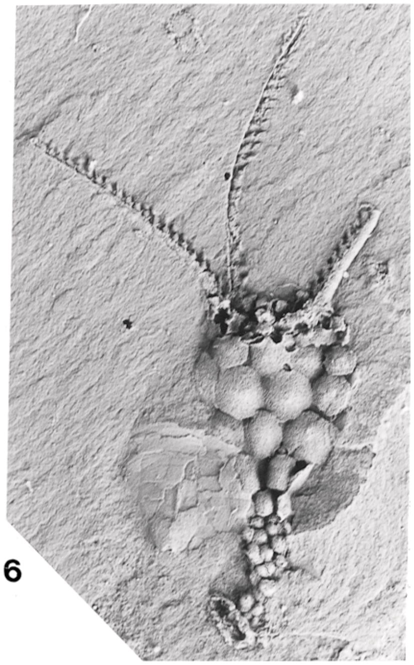
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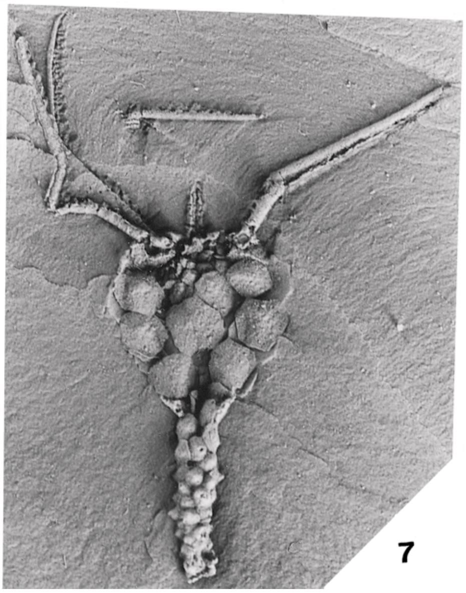
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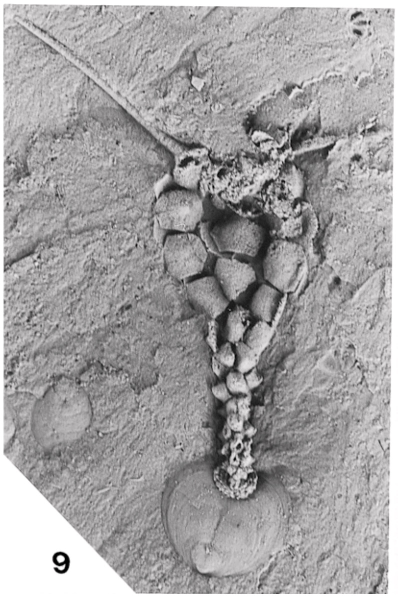
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crinoids (Meyer, 1971). Nonblastoid blastozoans commonly have few unbranched brachioles (two to five or several multiples of five). Sievelike structures, constructed with pinnulated arms in crinozoans, were not structurally possible in blastozoans. Nor was it likely that the brachioles were erect structures and simply opened their food grooves to food floating by in the current or raining down by gravity. Such a deployment feeding process would be rather inefficient (Rozhnov, 2002).

We propose, based on many exothecal brachiole-bearing genera, that brachioles were streaming structures that formed down-current loose cones or loose bunches and whose deployment disrupted essentially the smooth flow to produce a slowed, turbulent, roily flow around and through the brachioles (Parsley, 1998; Parsley and Zhao, 2004). Such erratic flow increased the opportunity for a food particle to come in contact with an open cover plate or the food groove itself. In the case of *S. lui* and other gogiid genera, small specimens have cover plates quite out of proportion to the size of the supporting ossicles, suggesting that they were important not only in food capture but in creating turbulent flow as well. Even in the largest specimens the cover plates are disportionally large and apparently were feeding-current modifying structures (Parsley and Zhao, 2004).

Fixation and feeding posture.—Specimens of *S. lui* are fixed by the attachment disk to a piece of shell, exuviae, or directly to the siliciclastic bottom. The attachment disk is rather small relative to the adult animal, so a strong anchoring medium, a probable bio-adhesive, is clearly necessary (Parsley and Prokop, 2001, 2004).

The attachment disk is sharply differentiated from the holdfast. The thinnest part of the holdfast is just above the disk and has a simple (small polyplated) juvenile morphology. It is the most flexible part of the holdfast and the part most prone to breakage. In our interpretation, it is from this ‘‘juvenile’’ region that the animal heels over in the current so that the brachioles (especially the distal ends) stream near-parallel to the seafloor. The more rigid proximal part of the holdfast and the theca add a sufficient vertical component to keep the brachioles above the seafloor (Parsley and Zhao, 2004).

Many gogiid specimens from the Jince Formation in Bohemia and from a number of Cambrian formations in western North America (especially the Spence Shale, Robison, 1991) commonly break free from the attachment disk at the distal, narrow, ‘‘juvenile’’ portion of the holdfast. Dislodgement of individuals by uprooting of the attachment disk appears to be rare. Specimens broken free from the attachment disk are commonly current-oriented (C. Sumrall, personal commun., 2005). Specimens of *S. lui* in the Kaili Biota commonly appear to be simply bent over and splayed out on the bottom. In contrast with gogiid specimens in the Jince Formation and Spence Shale, which are in shallower water and higher energy conditions, there is little evidence for current-aligned Kaili Biota specimens.

SYSTEMATIC PALEONTOLOGY

Subphylum BLASTOZOA Sprinkle, 1973

Discussion.—Sprinkle (1973) established this subphylum for echinoderms with a globular multiplated calyx and biserial appendages (brachioles), which ostensibly lack central lumens. Brachioles are devoid of impressions that evidence radiating water vascular canals and podia associated with the food grooves (alternative viewpoints on this issue have been discussed by Paul and Smith, 1984; Smith, 1990; Brower, 1999). One or two series of cover plates extend over the food groove of each brachiole. Respiratory structures developed between thecal plates are common. The simplest are circular to oval respiratory pores but in ‘‘cystoid’’ groups they include pore rhombs, diplopores, fistulipores, and humatopores. Blastozoans have a variety of holdfast structures, and attachment is common to most but not all of them. Many eocrinoids have relatively unorganized holdfasts made up of small platelets. More advanced forms have simple holomerous columnals but none display the pentameral pattern seen in crinoids. Parsley (1999) included the Homostelea in the Blastozoa even though this class does not possess brachioles. The morphology of the homostele theca, including the U-shaped gut, morphology of the anal pyramid, and simple transverse 1-1 ambulacral area, fits into the broad concept of Blastozoa.

Class EOCRINOIDEA Jaekel, 1918

Discussion.—The Eocrinoidea have been variously diagnosed (for example Ubaghs, 1968; Sprinkle, 1973; Broadhead, 1982), but the diagnoses are so broad that they essentially define those blastozoans that are not clearly assignable, by default, to a cystoid or blastoid group. Cystoid and blastoid groups are generally defined by the morphology of their respiratory pore structures (e.g., diplopores, fistulipores, and pore rhombs). Most authors view the class as paraphyletic but a detailed cladistic analysis of the class is beyond the scope of this work (Paul and Smith, 1984; Smith, 1984; Paul, 1988).

Order GOGIIDA Broadhead, 1982

Emended and renamed Unnamed Order #1 of Sprinkle, 1973, p. 76.

Diagnosis.—Emended from Sprinkle, 1973. Eocrinoids with attachment disk and stalklike structure ranging from poorly organized holdfast to column with essentially holomeric elements, transverse ambulacral system on the upper face of theca (probably with 2-1-2 branching in mature specimens), and loosely organized theca (regular series of plates are present in adult *Sinoeocrinus* with almost all plates having well-developed sutural pores. Brachioles of typical construction; straight or variously twisted or coiled, and commonly have tall covering plates over food grooves.

Discussion.—Broadhead named and slightly emended Sprinkle's Unnamed order #1 in part by introducing the concept that the circular to elongate epispires (sutural pores) are ‘‘overlain by

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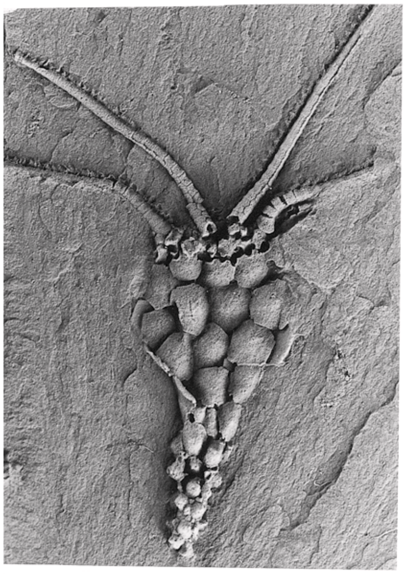
FIGURE 3—*Sineocrinus lui* Zhao et al., 1994. All specimens are latex casts whitened with NH_4Cl. All specimens are from the Kaili Formation (Kaili Biota), Miobanpo Section = GTBM or the Wuliu Section = GTB, to the north-northwest of Balang, Taijiang County, Guizhou Province, China. TH = Thecal height. *1,* Smallest known juvenile, TH = 1.4 mm, ambulacral pattern is 2-2, GTBM 15335, ×11.4; *2,* juvenile, sutural pores under the ambulacral plates, TH = 2.2 mm, typical juvenile holdfast, GTBM 931420, ×10.2; *3,* paired juveniles sharing the same attachment disk, TH = 1.5 mm, note tall cover plates on brachioles, GTBM 94001, ×12.3; *4,* theca with well-developed sutural pores under ambulacrals, 2-2 ambulacral pattern, TH = 3.2 mm, note unusually long holdfast, GTBM 9-40002, ×6.9; *5,* juvenile with 2-2 ambulacral pattern, TH = 3.2 mm, GTBM 9487, ×8.3; *6,* juvenile with well-developed sutural pores under ambulacrals, 2-2 ambulacral pattern, note circular attachment disk, TH = 3.5 mm, GTBM 953689, ×7.6; *7,* juvenile with early formed 2-1-2 ambulacral pattern, TH = 3.8 mm, GTBM 95001, ×7.4; *8,* juvenile with unusual brachiole arrangement, 2-1-2 but posterior right brachiole has anomalously added an adjacent second brachiole, TH = 5.1 mm, GTB 1531896, ×5.7; *9,* juvenile specimen with well-developed attachment disk and attached to an inarticulate brachiopod, TH = 4 mm, GTBM 955808, ×6.8.



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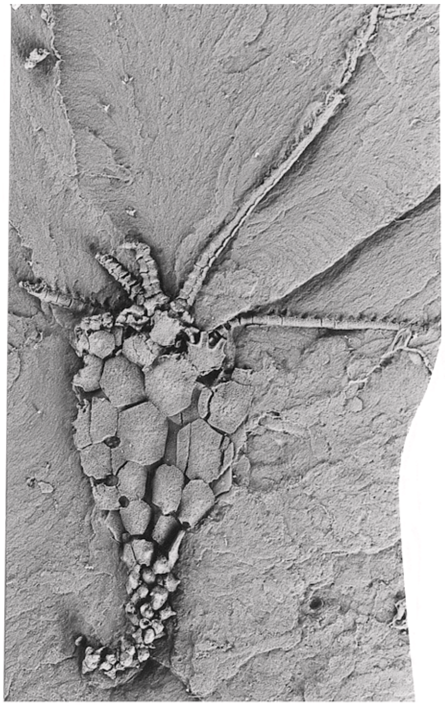

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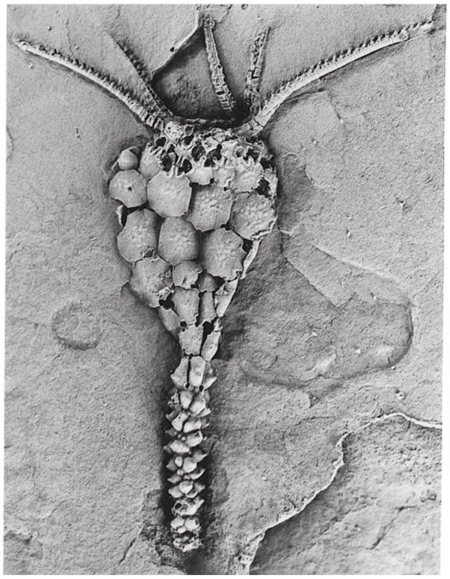

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covering plates or by thin epistereom'' (Broadhead, 1982, p. 125). Our observations do not support the presence of hard tissue over the sutural pores. We find that Sprinkle's taxonomic concept is more complete and comprises a probable paraphyletic grouping especially if the genera *Lichenoides* Barrande, 1846 and *Rhopalocystis* Ubaghs, 1963 are excluded. Lower to Middle Cambrian.

Family EOCRINIDAE Jaekel, 1918 emend.
=Sinoeocrinidae Zhao et al., 1994 (pars)
=Lichenoididae Jaekel, 1918, Zhao et al., 1994 (pars)

Diagnosis.—Calyx plates numerous, commonly irregularly arranged, but in very small juveniles at least three or more well-defined series are developed under ambulacrum; thecal plates have epispires that morphologically vary considerably in ontogeny. Ambulacral system confined to upper (or oral) thecal surface, consisting of three to five simple ambulacral grooves leading to exothecal brachioles. Brachioles may be straight, twisted, or coiled. Holdfast, variable in length, irregularly multiplated with distal flattened, multiplated attachment disk. Lower to Middle Cambrian (modified from Sprinkle, 1973).

Discussion.—Genera comprising the family include *Gogia* Walcott, 1917, *Sinoeocrinus*, *Acanthocystites*, and *Akadocrinus*. Zhao et al. (1994) introduced the family Sinoeocrinidae and the genus *Sinoeocrinus* with five species. In addition they proposed the monotypic genus *Paragogia* (Zhao et al., 1994) that was placed in the Eocrinidae. The sinoeocrinoids were described as forms with fewer and regularized thecal plates, smaller sutural pores, fewer brachioles, and more regularized stem plates. The study was based on 90 specimens. More than 1,200 specimens have been examined for this paper and it is clear that the species of *Sinoeocrinus*, *Paragogia*, and *Curtoeocrinus* Zhao et al., 1994 (originally placed in the Lichenoididae by Zhao et al., 1994, and now seen as a preservational variant) in the Kaili Biota are part of a single growth series and only a single species, *Sinoeocrinus lui*, is present (Parsley and Zhao, 2002).

Genus SINOEOCRINUS Zhao et al., 1994

Paragogia ZHAO ET AL., 1994, p. 322, 314, text fig. 7, pl. II, fig. 2.
Curteocrinus ZHAO ET AL., 1994, p. 323; 315, fig. 8; pl. IV; fig. 1, pl. V; figs. 1–5.

Type species.—*Sinoeocrinus lui* Zhao et al., 1994.

Other species.—Zhao et al., 1994 named six other species belonging to *Sinoeocrinus*, *Paragogia*, and *Curteocrinus*. The species are *Sinoeocrinus curtobrachiolus* Zhao et al., 1994; *Sinoeocrinus lepidus* Zhao et al., 1994; *Sinoeocrinus longus* Zhao et al., 1994; *Sinoeocrinus minus* Zhao et al., 1994; *Paragogia globosa* Zhao et al., 1994; and *Curtoeocrinus guizhouensis* Zhao et al., 1994. All are now seen as various growth stages of *S. lui*.

Diagnosis.—Gogiid with at least three series of near equidimensional, essentially hexagonal plates developed directly under apical ambulacrum and two series of elongated transitional plates between them and first holdfast plates in small juveniles (TH $<$ 3 mm). Larger juveniles and mature specimens irregularly plated because of subsequent plate intercalation. Thecal plates comprising basal part of theca irregular and similar to plates of holdfast except that they have sutural pores. Ambulacral area restricted to upper thecal surface and arranged in 2-1-2 pattern except in early juveniles where pattern is 2-2. Depending on ontogenetic stage, straight brachioles number 4, 5, 10, or 15. Cover plates unusually tall. Holdfast variable in length and composed of numerous bossed platelets. Attachment disk slightly expanded and composed of several layers of small platelets.

Description.—Same as for the type species.

Etymology.—*Sino*, pertaining to China.

Occurrence.—Kaili Formation, basal Middle Cambrian, Wuliu-Zengjiyan section and especially the Miobanpo section, north-northwest of the village of Balang, Taijaing County, Guizhou Province.

Discussion.—*Sinoeocrinus* is similar to various growth stages of some *Gogia* species, e.g., *G. prolifica* Walcott, 1917 and *G. hobbsi* Sprinkle, 1973. A comprehensive comparison between *Sinoeocrinus* and *Gogia* is difficult because *Gogia* is such a varied genus that future cladistic analysis, taking into account growth stages, will probably result in the establishment of at least three or more new genera. However, there are characters particular to *Sinoeocrinus* that set the genus apart from *Gogia* as we now understand it. Sutural pores in adult/very mature specimens are distinct from those in *Gogia*. They are unusually wide and are less numerous.

The holdfast is *Sinoeocrinus* is less organized than in *Gogia*. In *Gogia* the column is commonly thinner, more tetherlike, and in some species has well defined rows of platelets resembling a column.

The anal pyramid in *Sinoeocrinus* is different than other gogiids. The valvular platelets are not triangular (pie-slice–shaped) as they are in *Gogia* but they are a series of elongated, slightly tapering, rectangular platelets that form the domelike anal pyramid.

Cover plates over the food grooves of the brachioles in *Sinoeocrinus* are long, tall, and while seemingly tightly articulated do not form vaults over the grooves of the free-standing brachioles. They appear to stand vertically open to splayed obliquely outwards. Some species of *Gogia* also appear to share this character (*G. longidactlyus* Walcott, 1886), but in this species and in all other species of *Gogia* the cover plates are slightly to considerably shorter.

SINOEOCRINUS LUI Zhao et al., 1994 emend.
Figures 3–7

Sinoeocrinus lui ZHAO ET AL., 1994, p. 320, pl. 1, fig. 1; pl. 2, fig. 1, p. 309, text-fig. 2.
Sineocrinus curtobrachiolus ZHAO ET AL.,1994, p. 320, pl. 2, figs. 3, 4, p. 310, text-fig. 3.
Sinoeocrinus lepidus ZHAO ET AL., 1994, p. 320–321, pl. 4, figs. 3, 6, 8; p. 310, text-fig 4.
Sinoeocrinus longus ZHAO ET AL., 1994, p. 321, pl. 4, figs. 2, 4; p. 311, text-fig. 5.

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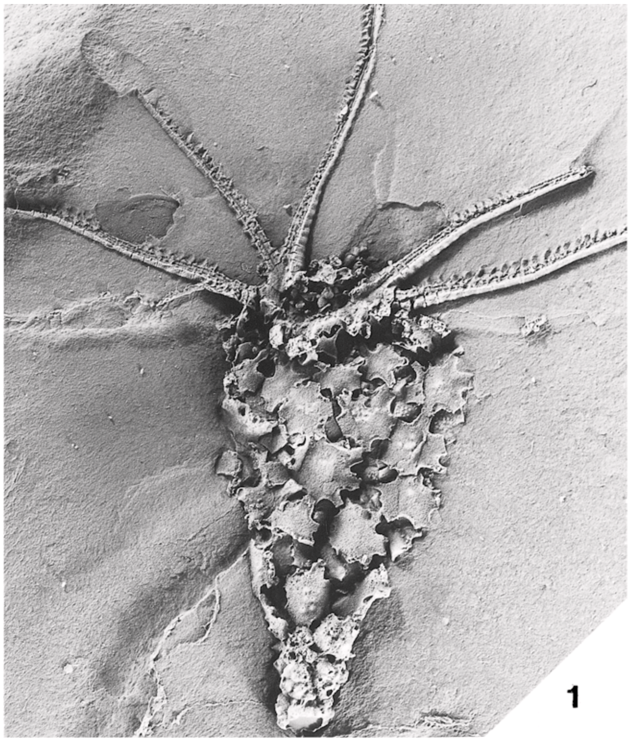
FIGURE 4—*Sineocrinus lui*. All specimens are latex casts whitened with NH_4Cl. All specimens are from the Kaili Formation (Kaili Biota), Miobanpo Section = GTBM or the Wuliu Section = GTB, to the north-northwest of Balang, Taijiang County, Guizhou Province, China. TH = Thecal height. *1,* Late juvenile stage, apparently a 2-2 ambulacral stage with well-developed sutural pores under the ambulacrals and incipient pores forming on lowermost thecal plates, TH = 5.4 mm, GTBM95265, ×5.8; *2,* late juvenile specimen, sutural pores under the ambulacrals and basal thecal plates, five brachioles, 2-1-2 ambulacral pattern, TH = 6.7 mm, GTBM 941154, ×5.1; *3,* late juvenile specimen, incipient sutural pores developing on all thecal plates, ?five brachioles, TH = 9 mm, GTBM 943486, ×3.1; *4,* late juvenile specimen, incipient sutural pores developed on all thecal plates, TH = 8.8 mm, GTB 161, ×4.4; *5,* early adult specimen, in addition to incipient sutural pores on all plates, pores under ambulacrals are quite mature having well-developed rims and oval openings, probably 10 brachioles (broken brachiole bases are present), TH = 11 mm, GTBM 931382, ×3.6; *6,* unusually small adult specimen, 10 brachioles, note immature sutural pores and the attachment disk, GTBM 932206, ×4.6; *7,* adult specimen, note maturing sutural pores and developing pustulose ornament on thecal plates, TH = 11 mm, GTBM 953277, ×3.6.



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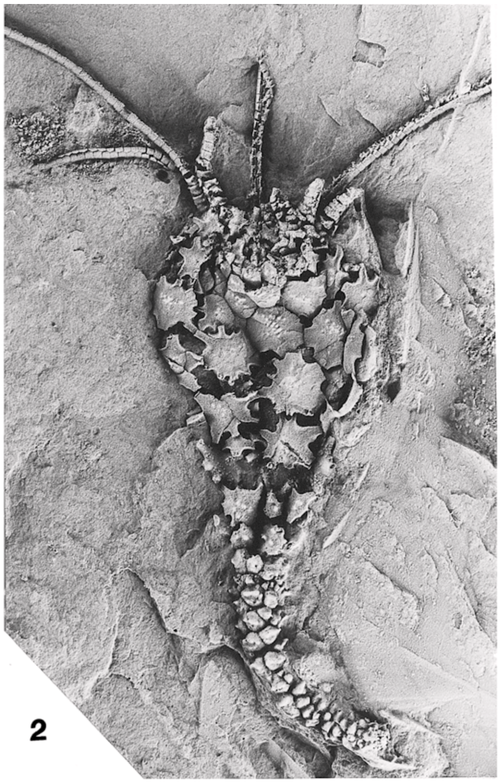

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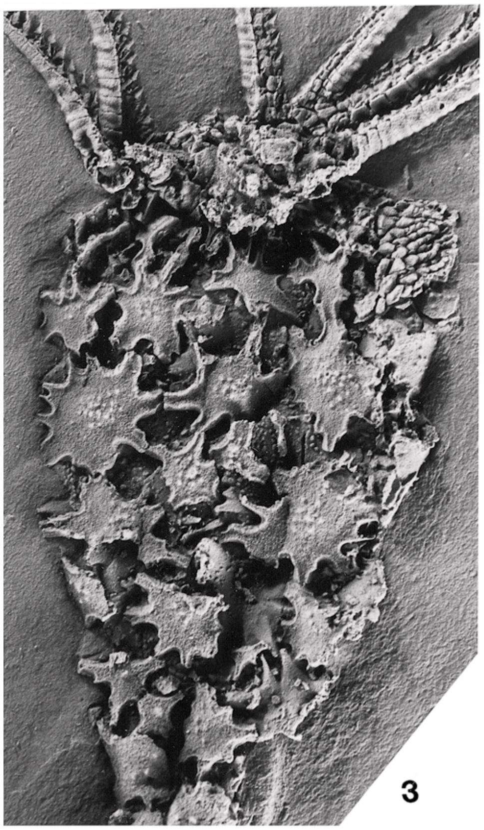

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FIGURE 6—*Sinoeocrinus lui*. Latex cast whitened by NH$_4$Cl. From the Kaili Formation (Kaili Biota) Miobanpo Section, north-northwest of Balang, Taijiang County, Guizhou Province, China. Advanced mature/gerontic specimen, TH = 21+ mm, 15 brachiole stage, note triple brachiole bases, mature sutural pores, and surface ornament on thecal plates, GTMB 101233, ×3.9.

Sinoeocrinus minus ZHAO ET AL., 1994, p. 321, pl. 3, figs. 1–8; p. 312, text-fig. 6.

Paragogia globosa ZHAO ET AL., 1994, p. 322, pl. 2, fig. 2; p. 313, text-fig. 7.

Curtoeocrinus guizhouensis ZHAO ET AL., 1994, p. 323, pl. 4, fig. 1; pl. 5, figs. 1–4; p. 315, text-fig. 8.

(Page numbers of species descriptions are from the English translation, which is in the second part of the paper; the first part is in Chinese.)

Diagnosis.—Same as for the genus.

Description.—Because the species has a complex ontogeny, description based on typically mature, but not gerontic, morphology. Mature morphology occurs at thecal heights of about 10–17 mm.

Theca composed of five or more irregular series of plates under ambulacrum to form, together with holdfast, clavate-shaped organism. Each thecal plate facet has sutural pore. In larger adults, sutural pores have enlarged by resorption, especially in top three series and have well-developed sutural rims (Fig. 5.3–5.5). Sutural pores between first thecal series and lower sutures of ambulacral plates especially well developed. First thecal plate series has about 14 plates; second series and the others down to the proximal transitional plate series with holdfast apparently have about eight plates each (Fig. 4.5). Elongate transitional series especially reduced and theca markedly necks down towards the holdfast (Figs. 3–5). In distal transitional series, upper suture of each plate has sutural pore, the lower one does not, and width of series smoothly matches that of holdfast (Fig. 4.5).

Anal pyramid located below right posterior ambulacral branch. An estimated 20 or so longitudinal series of subrectangular-shaped platelets, six to eight platelets per series, form dome-shaped pyramid (Figs. 5.3, 5.5, 7.2). Hydropore and gonopore have not been identified.

Across theca's arcuate upper surface is biserial ambulacral series. Food grooves in adult specimens arranged in 2-1-2 pattern and in main transversely situated food groove is large oval mouth opening. Near its lateral ends transverse food groove splits and each branch terminates in pair of brachiole facets. Facet pair also developed on anterior midpoint of mouth's outer margin. In typical adult specimen 10 brachioles present and typically in length are about one and a half to twice height of theca. Brachioles straight, taper gradually, appear quite flexible (Fig. 4.6). There are two series of cover plates: first is small, triangular, and overridden by taller second series. When viewed laterally second series tall, inclined distally, with slot that bisects upper face. Viewed down length of brachiole, cover plates are slightly fan-shaped with expanded base and arcuate upper surface. Expanded base fits into longitudinal groove that runs length of brachiole; one on each side of food groove. Axial portion of cover plate's distal face appears to line up with sides of food groove, so that when cover plates are open, broad V-shaped surface is formed by paired tall cover plates and food groove (Fig. 5.4). When cover plates are closed, slots on upper surface of tall series intermesh.

Material examined.—Over 1,200 specimens were examined. Specimens of major importance are illustrated in Figures 3–7. All specimens are housed in the Paleontology Museum of Guizhou University (GTM and GTBM), Guiyang, China.

DISCUSSION

The ontogenetic development of this species is complex, and because of the number of specimens examined it is possible to describe it in detail from the earliest juvenile to gerontic stages. Ontogenetic stages in other gogiids are probably similar and the stages described herein for *S. lui* should be useful in understanding the ontogeny and degree of maturity in specimens of other related species. The stages are described in terms of thecal height (TH). Ontogenetic stage and thecal height are rather consistent but total height is not. The length of the holdfast is quite variable throughout the life of the animal. Morphology of the sutural pores and numbers of brachiole bases at the ends of the ambulacral branches are fairly consistent in terms of thecal height. Subjectively, the morphological stages based on thecal height can be divided into juvenile, advanced juvenile, mature, and advanced mature or gerontic stages. The greatest changes are seen in juveniles; adults are relatively stable in morphology except for growth, intercalation of platelets in the holdfast and theca, and formation and modification of sutural pores; advanced adult/gerontic specimens add the final brachiole set and greatly modify the sutural pores and surface ornament.

Thecal height 1.4–4 mm.—(Juveniles) The smallest known specimen has a TH of 1.4 mm (Fig. 3.1). It has a 2-2 ambulacral pattern and this condition persists to approximately TH 4 mm

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FIGURE 5—*Sinoeocrinus lui*. All specimens are latex casts whitened with NH$_4$Cl. All specimens are from the Kaili formation (Kaili Biota), Miobampo Section = GTBM or the Wuilu Section = GTB, to the north-northwest of Balang, Taijiang County, Guizhou Province, China. TH = Thecal height. *1,* Adult displays a large oval oral opening, 10 brachiole stage, TH = 11 mm, GTBM 952688, ×4.3; *2,* adult, 10 brachiole stage, TH = 16 mm, note immature/juvenile plating at distal end of holdfast, GTBM 95001, ×3.2; *3, 5,* mature adult with well-developed anal pyramid, sutural pores mature with prominent rims, TH = 18.5 mm, 10 brachiole stage, proximal holdfast with mature plating, GTBM 10220, ×4.7 and 3.2, respectively; *4,* mature adult specimen, TH = 17.4 mm, 10 brachiole stage, note mature aspects of sutural pores and proximal holdfast, GTBM 101233b, ×2.9.

when the median brachiole is added to produce the typical 2-1-2 pattern (Fig. 3.7, 3.8). Brachiole cover plates are very large relative to the biserial brachiolar plates (Fig. 3.1–3.8). Directly under the ambulacral plates are three series of fairly well-defined and essentially equidimensional thecal plates, which persist throughout ontogeny (Fig. 3). At this stage, incipient circular sutural pores first appear in specimens with TH 1.5 mm, and by TH 3.5 mm they are well developed with a distinct elevated rim (Fig. 3.2–3.6). No other sutural pores are present, and it would appear that the bulk of respiratory exchange occurred across the integument. Sutural pores occur rarely and sporadically across the upper series of thecal plates, starting at TH of ca. 3.2–3.5 mm, but normally in the TH 1.4–4 mm stage sutural pores are limited to being just below the ambulacrum. In these early stages the holdfast grows rapidly. At TH 1.4 mm the holdfast is about 0.6 mm in height and is composed of three or four series of primary elements (Fig. 3.1). The rate of growth and intercalation of smaller secondary platelets increases above TH 1.5 mm. Between TH 1.4 and 4 mm the ratio of thecal height to holdfast length can vary from 0.5 to over 2.0 and the numbers of primary (large) to smaller intercalated (secondary) platelets are also quite variable (Fig. 3.4, 3.8). From the smallest to the largest specimens, a well-developed polyplated disklike holdfast is present. The central part of the undersurface is slightly concave, and toward the outer margin displays a polyplated ring structure (Fig. 3.1, 3.2, 3.5, 3.6, 3.9).

Thecal height 5.0–9 mm.—(Advanced juveniles) At about TH 5 mm, the median brachiole facets with incipient exothecal brachiole is extant; 2-1-2 symmetry is achieved (Fig. 3.7). Irregular opening of incipient sutural pores is common at TH 6-9 mm on both primary plates and especially close to the holdfast on transitional plates (Fig. 3.2, 3.4, 3.6). Directly under the ambulacrum the pores are ovoid and have well-developed rims (Fig. 3.1–3.3). At about TH 6 mm the holdfast primary plates develop a low tumid spine (Fig. 3.2, 3.6). Wide ratios of thecal height to holdfast length remain about the same. Attachment disks appear to add several layers of small platelets and probably extended farther into the substrate than in smaller specimens. At about TH 8–9 mm the brachiole bases and brachioles double in number and result in an animal with 10 long, straight exothecal brachioles (Fig. 3.6). At this thecal height pustulose ornament begins to form on (especially) the larger upper thecal plates (Fig. 3.6).

Thecal height 10–17 mm.—(Mature) Above TH of 10 mm there are far fewer specimens, and many larger specimens appear to have broken holdfasts. Attainment of larger size, those above TH 10–12 mm may be dependent on the ability of the individual to resist periodic strong uprooting or holdfast fracturing currents. From TH 10–12 mm thecal pores are present over the entire theca, and are in various stages of development (Fig. 4.5, 4.7). Over TH of 12 mm sutural pores on the upper part of the theca are commonly complex and pores closer to the holdfast are commonly less complex but are deeply embayed into the plate and the marginal rims are well developed (Fig. 5.2). In between these upper and lower series of plates, thecal plates develop complex sutural pores more slowly, and commonly the entire theca does not display complex sutural pores until ca. TH 17–18 mm (Fig. 5.2). In the TH 14–16 mm range the holdfast is divisible into two distinct sections. The proximal section is composed of large primary plates which at this stage have two to seven irregularly positioned pustules. Some primaries are in direct contact, others are partly to completely surrounded by small intercalates. Distally the more immature pattern of primary plates (with a single, rounded, and tumid pustule) and irregularly intermixed secondary plates prevails. The distal section is more flexible than the proximal section, and it is in the transition between the two sections where breakage commonly occurs (Fig. 5.2). Larger specimens do not commonly have the attachment disk preserved but when present it is subcylindrical in profile and made up of five or six circlets of small platelets (Fig. 7.1).

Thecal height 17–23 mm.—(Advanced mature or gerontic) Specimens in this size range are rare and morphologically distinctive. All plates of the theca are covered with well-developed complex sutural pores, and differentiation between thecal and holdfast plates (without pores) is easily determined (Fig. 5.4, 5.5). The sutural pores are enlarged and this process clearly requires resorption of plate material. Specimens from TH 17 and up are more likely to have the anal pyramid preserved along the right lateral just below the right-hand posterior ambulacral branch (Figs. 5.3, 5.5, 7.2). At approximately TH 19 mm the final series of brachiole bases and exothecal brachioles appears, bringing the total to 15. At TH 20+ mm, maximum development of the sutural pores is evident (Fig. 6).

ORDER AND FAMILY Uncertain

Discussion.—*Balangicystis* n. gen. is not assignable to any existing higher taxonomic units of the Eocrinoidea. Specimens of the genus are adequately preserved to determine that it is indeed a new genus but the overall morphological generalities are not sufficiently evident to create new familial or ordinal taxa.

Genus BALANGICYSTIS new genus

Type species.—*Balangicystis rotundus* n. gen. and sp.

Diagnosis.—Eocrinoid with ?five wedge-shaped basals above which in adult specimens at least six irregular circlets of polygonal plates with commonly five raised, flat-topped rays extend from plate center to plate angles. Sutural pores between thecal plates absent. Ten or 15 brachioles in an essentially transversely elongated 2-1-2 pattern across upper face of the theca. Brachioles longer than height of theca and robust relative to thecal size. Tall cover plates present. Holdfast composed of short circlets of five or six platelets, some with prominent circular boss. At least 40 holdfast circlets present in juvenile and adult specimens.

Description.—Theca broadly expands from base to tops of basals. Above basals at least six circlets of plates, consisting of about 10 plates each. Circlets straight-sided and circular. No sutural pores at any stage of ontogeny. Thecal plates embossed with raised flat-topped (commonly) pentagonal rays. Theca's upper surface gently arched; 10 or 15 brachioles extend from ambulacral area. Brachioles robust relative to size of theca and about 1.5×–2× height of theca in length. Food grooves covered by tall cover plates. Holdfast long, thin composed of over 40 circlets of small platelets. Commonly five or six platelets per circlet and some of platelets with prominent raised globular or hooked-spine boss. Holdfast length 2×–3× height of theca.

Etymology.—From the village of Balang, Taijiang County, Guizhou Province, China.

Occurrence.—Fossil quarry in the Miaobanpo section, Kaili Formation, approximately 2–3 m above the base of the Kaili Biota part of the section.

Discussion.—About five specimens are known of the rare genus. The two specimens available for study, one juvenile and one mature, are preserved with the lateral side of the theca resting on the bedding plane. The ambulacral surface has not been observed. The geometry of the ambulacra is not known, but because of the transversely located brachiolar bases it is assumed that the animal has a typical 2-1-2 arrangement. Because of the limited number of specimens, the ontogeny of the animal is not clear but from a thecal height of 3.5–7.5 mm at least four circlets of thecal plates are added. What appears to be a 10 brachiole stage of development is acquired in early ontogeny (thecal height less than 3.5 mm). An individual specimen in a private collection clearly indicates that this genus can attain the 15 brachiole stage. The long but rather robust holdfast appears to hold the theca and brachioles

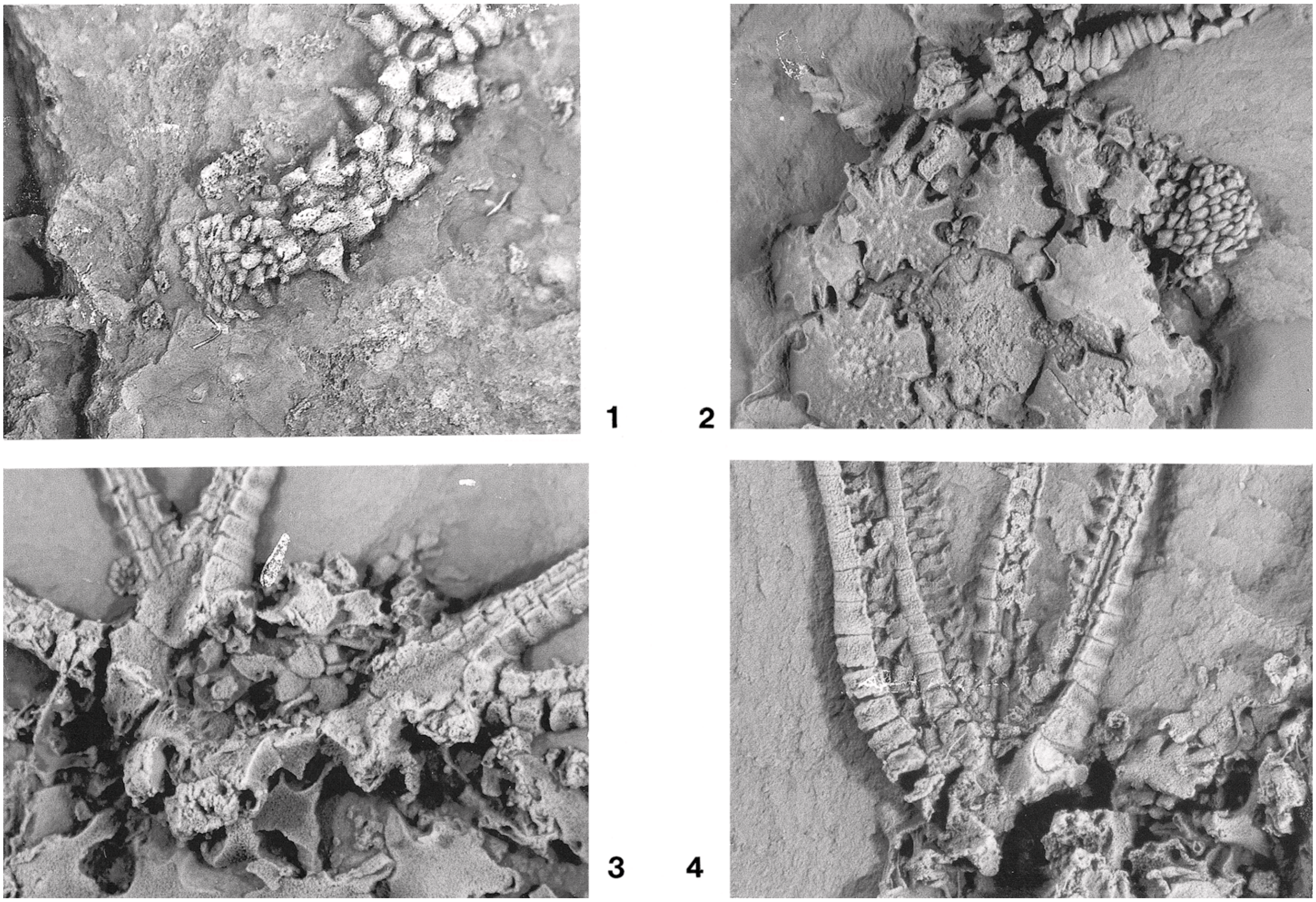

FIGURE 7—Details of *Sinoeocrinus lui*. Latex casts whitened by NH_4Cl. *1,* Distal end of holdfast and eroded attachment disk, note the thornlike ornament on holdfast plates, enlargement from Figure 4.6, ×13; *2,* details of mature thecal plates and multiplated anal pyramid, GTBM 92, ×7; *3,* details of the oval oral opening and adjacent brachioles, enlargement from Figure 5.1, ×10; *4,* details of brachiole structure, note tall cover plates and exposed food groove, GTBM 931098, ×10.

sufficiently off the bottom so that the brachioles do not drag on the bottom.

The attachment disk is not known but it is probably a well-developed, polyplated disklike structure. The rarity of this genus may be because it is an exotic to the community at Miaobanpo and may have drifted in after breaking loose from a shallower-water, upslope community or its larvae occasionally may have drifted downslope into the area from a shallower-water community and colonized there successfully.

BALANGICYSTIS ROTUNDUS new species
Figure 8

Crinozoa n. gen and sp. ZHAO ET AL., 1994, p.14, pl. 4, fig. 2.

Diagnosis.—Species is monotypic and its diagnosis is the same as for genus.

Description.—Species is monotypic and description is the same as for genus.

Etymology.—*Rotundus*, Latin for circular, round; as characterized by its thecal cross section.

Types.—Holotype; GTBM 9-4: paratype; GTBM 91526a. Types are housed in the Palaeontology Museum of the Guizhou University, Guiyang, Guizhou Province, China.

Occurrence.—Both holotype and paratype are from the quarry in the Miobanpo Section, Kaili Formation, Kaili Biota, 1 km north-northwest of Balang, Taijiang County, Guizhou Province, China.

Discussion.—The greatly elongated holdfast is proportionally unusual for a Cambrian echinoderm. Its length clearly indicates that this species fed optimally on detritus and microorganisms far enough above the bottom to avoid at least some of the sediment transported along the bottom and to place the theca and brachioles into a less disaerobic environment. Juvenile and mature specimens apparently do not have thecal sutural pore respiratory structures, but the surface of the water-sediment interface, where this species is found clearly suggests strongly disaerobic to anoxic conditions.

ONTOGENY AND PHYLOGENY

Ambulacral symmetry.—The common element in almost all nonstylophoran and homoiostelean primitive echinoderm ambulacra is the transverse part of the ambulacra radiating from the mouth: the 1-1 pattern. The 1-1 pattern is present in the Middle Cambrian Cincta and Ctenocystoidea. [In these classes, the food grooves are impressed on the lateral sides of the thecal framing plates. Friedrich (1993) interprets the food grooves in cinctans as part of recumbent brachioles. Our examination of this class does not support his hypothesis. Sprinkle and Robison (1978) limit the subvective structures in Ctenocystoidea to the anterior ctenoid plates.] Parsley (1999) argued that the transverse 1-1 pattern in

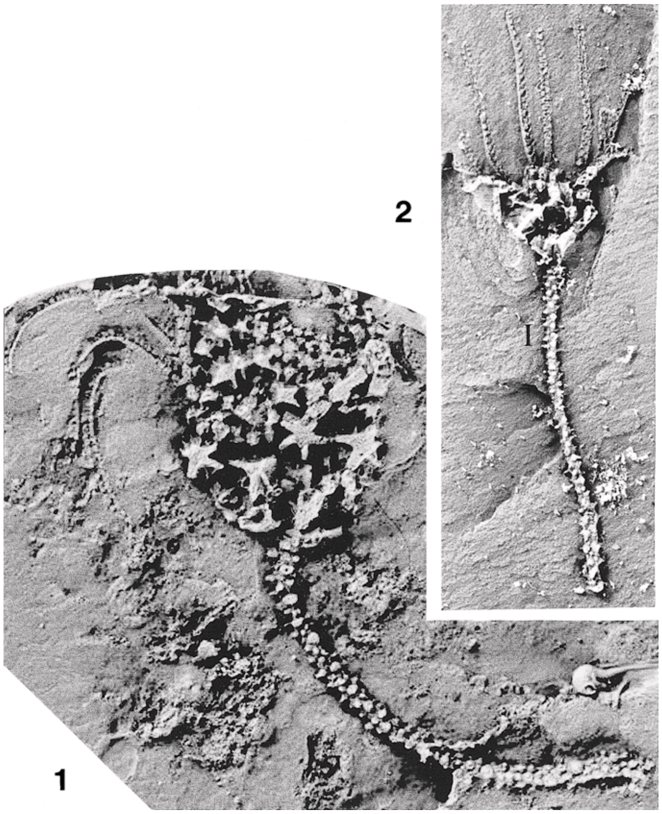

FIGURE 8—*Balangicystis rotundus* n. gen. and sp. Latex casts whitened by NH_4Cl, Kaili Formation (Kaili Biota), Miobampo Section, north-northwest of Balang, Taijiang County, Guizhou Province, China. *1,* Holotype specimen, GTBM 9-4, ×3; *2,* paratype specimen, theca with at least two fewer series of thecal plates than the adult holotype, GTBM 91526a, ×10.

the Middle Cambrian Cincta is a plesiomorphic character that, along with the U-shaped gut, placed them in the Blastozoa. The diploporid *Aristocystites* Barrande, 1887 (Middle Ordovician, Bohemia and Spain) has a well-developed 1-1 ambulacral system but it may also be simplified from a more complex pattern (Paul and Smith, 1984; Parsley, 1990). Because the 1-1 pattern adjacent to the mouth is common to virtually all early echinoderms (except the stylophorans and homoiostelians) and is all that is present in Cambrian Cincta and Ctenocystida, it can be considered the plesiomorphic condition for almost all early echinoderms.

The earliest ontogenetic development of the ambulacral system in *S. lui* (TH 1.4 mm) is a 2-2 pattern, where the ends of the proximal transverse ambulacra (1-1) split and extend exothecally as free-standing brachioles. In this species the central anterior brachiole emerges on the midanterior edge of the transversely oval mouth, where the thecal height reaches about 5 mm, producing the typical 2-1-2 early blastozoan ambulacral pattern. If ontogeny does indeed predict phylogeny, then this Middle Cambrian gogiid would appear to be an intermediate predictor of the earlier 1-1 and 2-2 plesiomorphic stages that develop into the 2-1-2 stage. And, the 2-1-2 pattern appears ancestral to normal pentradial symmetry. The best place to view this transition is in the stromatocystids (Hotchkiss, 1998). These Lower and Middle Cambrian edrioasteroid-like forms have a 2-1-2 pattern, but in some species it is hard to detect because they are essentially pentaradial (Parsley and Prokop, 2004).

Holdfast.—In adult specimens of *Sinoeocrinus lui*, a clearly differentiated holdfast is present. The plates adjacent to the theca show several cycles of plate intercalation based on plate size and contrast sharply with the area adjacent to the attachment disk which has a simple, unorganized plate pattern of essentially small, equally sized platelets. The distal plate pattern is present proximally in juvenile specimens. This overall holdfast pattern differs from the Lower Cambrian *Gogia ojenai* Durham, 1979, or the co-occurring Middle Cambrian Kaili species *Sinoeocrinus globus* Zhao, Huang, and Gong, 1999, which have thicker holdfasts that are composed of small, equally sized platelets. This simpler holdfast appears to be a retention and elaboration of early juvenile morphology.

The more elaborate proximal holdfast in *S. lui* appears to be an adaptation to stiffen the structure in order to keep the theca and brachioles well above the bottom in the presence of currents.

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