## KAILIDISCUS, A NEW PLESIOMORPHIC EDRIOASTEROID FROM THE BASAL MIDDLE CAMBRIAN KAILI BIOTA OF GUIZHOU PROVINCE, CHINA

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ABSTRACT—A new genus and species of edrioasteroid grade echinoderm, *Kailidiscus chinensis*, is described from the Kaili Biota of the basal lower Middle Cambrian Kaili Formation from Guizhou Province, China. This echinoderm has a strong resemblance to isorophid edrioasteroids, bearing a well-developed peripheral rim, long curved ambulacra, and slightly imbricate interambulacral plating at maturity. However, the presence of pore-bearing, double biserial floor plates, tiered cover plates, lack of radially positioned oral frame plates, and unincorporated hydropore/gonopore are unknown in isorophids. Many of these features bear strong resemblance to eocrinoids and helicoplacoids, attesting to the plesiomorphic nature of this taxon. Despite the obvious anatomical differences, specimens of this species preserve a complete ontogeny that resembles that of isorophids. Juveniles show a discoidal theca with straight ambulacra that transitions to an inflated theca with strongly curved ambulacra with maturity.

#### INTRODUCTION

AMBRIAN ECHINODERMS often show plesiomorphic morphologies that are difficult to interpret and reconcile with features found in more crownward taxa. These morphologies are a manifestation of the early radiation of echinoderms prior to the stereotypy found once descendant lineages are established. Plesiomorphic morphologies can be identified in the irregular plating of the theca, complexities of the ambulacral system, and in unusual combinations of features that are both confusing and open to differing interpretations. Kailidiscus chinensis n. gen and sp. is no exception, combining morphologies that are similar to two clades of edrioasteroids (isorophids and edrioasterids), eocrinoids, and asteroids. Notable among its unusual features is the presence of quadruserial floor plates arranged into adradial and abradial series with four rows of podial pores, separate hydropore and gonopore pyramids, and an oral frame composed of floor plates that wrap around the integrated interambulacral plates. This species provides insights into morphologies that are consistent with the plesiomorphic pentaradiate echinoderm condition and shed new light on the origin of edrioasteroids (Sumrall and Wray, 2007).

Crownward edrioasteroids comprise two well-defined clades, isorophids and edrioasterids (Bell, 1976a; Guensburg and Sprinkle, 1994). Isorophids (Fig 1.4) are characterized by a plesiomorphically discoidal theca that is attached to the substrate by a peripheral rim encircling the oral surface, thin ambulacra with a single series of uniserial floor plates, and simple biserial to complex cyclic cover plates (Bell, 1976a). Early, well-known taxa typically have imbricate interambulacral plates and an integrated or semi-integrated combined hydropore/gonopore located in the proximal right of the CD interambulacrum. The ventral surface is unplated, but presumably in life was covered by soft tissue (Bell, 1976a).

In contrast, edrioasterids (Fig. 1.1) have a globular theca attached to the substrate by an attachment disk that grades into a short, imbricately plated stalk connecting the attachment disk to the base of the theca (Bell, 1979; Guensburg and Sprinkle, 1994; Sumrall and Deline, 2009). Edrioasterids bear extremely wide ambulacra that are straight or curved depending on taxon.

The ambulacral floor plates are biserial, bear sutural pores, and are broadly exposed on the thecal exterior (Bell, 1976a). The cover plates are arranged into a simple biseries and lack intrathecal and intrambulacral extensions. The thick interambulacral plates are tessellate, and the hydropore/gonopore is integrated into a pair of proximally integrated interradial plates that form a portion of the mouth frame.

Historically, Edrioasteroidea has been applied to any sessile echinoderm lacking erect feeding appendages such as brachioles and arms that is not obviously a member of some other clade, such as Helicoplacoidea (Bell, 1980; Smith, 1985; Smith and Jell, 1990; Guensburg and Sprinkle, 1994). This nebulous definition has led to the classification of a group based on plesiomorphy rather than on shared derived characters. Within this array of taxa, isorophids and edrioasterids appear to form a monophyletic group. These taxa are united by the presence of uniserial, radially positioned oral frame plates that attach the food grooves into the peristomial opening, biserial ambulacral cover plates, and an unplated aboral surface. These taxa also generally lack exothecal respiratory structures in the thecal plating except for the unusual Isorophid? Thresherodiscus Foerste, where diplopores are present adradially (Sumrall and Gahn, 2006).

Several other early edrioasteroid grade echinoderms have been described from the Cambrian and Ordovician. These taxa lie outside isorophids and edrioasterids and probably represent a stem lineage to more crownward edrioasteroid taxa and perhaps Eleutherozoa (Smith, 1985). These taxa have been reviewed by several authors and fall into poorly differentiated groups pending fuller phylogenetic treatment. Here we introduce these groups to allow comparison with *Kailidiscus chinensis* n. gen and sp. *Camptostroma* Rudemann is not discussed for want of diagnostic material. A more thorough phylogenetic treatment of these taxa is in preparation to be published elsewhere.

# DISCUSSION OF GROUPS OF EDRIOASTEROID GRADE ECHINODERMS

Stromatocystitidae.—Stromatocystitidae Bassler, 1936 includes Stromatocystites Pompechj and related taxa. It is

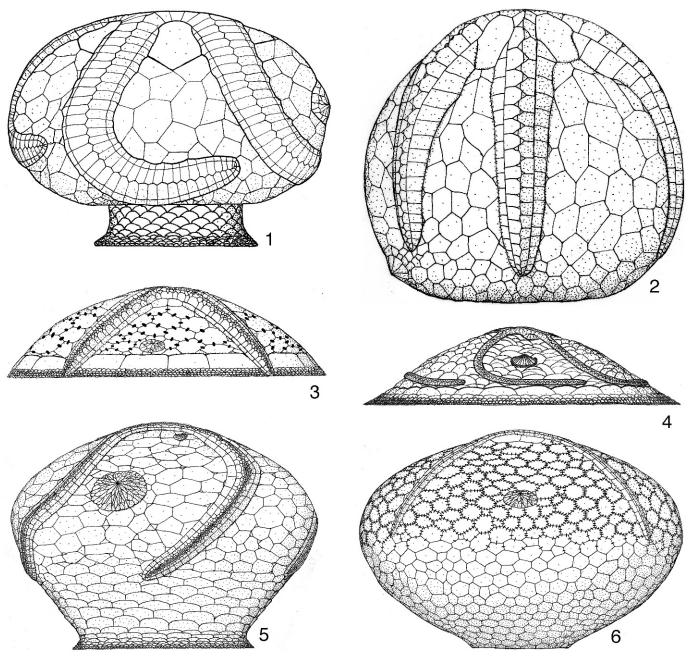


FIGURE 1—Comparison of thecal morphology between the major clades of edrioasteroids. 1, the edrioasterid Edrioaster bigsbyi (Billings) showing a globular theca and a short pedunculate zone; 2, The totiglobid Totiglobus nimius Bell and Sprinkle showing a globular theca lacking a pedunculate zone and cover plates arranged into a double biseries (modified from Bell and Sprinkle, 1978); 3, the cambrasterid Cambraster cannati Cabibel, Termier, and Termier, showing a peripheral rim and straight ambulacra with epispires on the oral surface, cover plates conjectural; 4, the Isorophid Ulrichidiscus kaskaskiensis showing a discoidal theca with narrow ambulacra lacking epispires on the oral surface (Modified from Sumrall, 1993); 5, Kailidiscus chinensis n. gen. and sp. showing a small peripheral rim, expanding pedunculate zone, and wide ambulacra; 6, the stromatocystid Stromatocystites pentangularis Pompeckj showing a globular theca lacking pedunculate zone and bearing epispires on the oral surface, cover plates conjectural.

characterized by a semi-flexible theca with a fully plated aboral surface and raised ambulacra bearing multitiered cover plates (Parsley and Prokop, 2004) (Fig. 1.6). The peristome and ambulacra are poorly understood both internally and externally, largely because the mouth frame and floor plates cannot be seen through the fully plated aboral surface. The floor plates are broadly exposed on the thecal exterior and are likely homologues to the abradial floor plates of *Kailidiscus* n. gen. It is unknown whether adradial floor plates are present. The cover plates seem to be configured into a multi-tiered arrangement as noted for other early echinoderm groups such

as helicoplacoids, cinctans, and *Kailidiscus*. The interambulacral plating bears epispires and the distal-most aboral surface bears a circular adhesion disk. Unlike isorophids, the discoidal to somewhat inflated theca lacks a peripheral rim, bearing instead a circular adhesion disk.

Cambraster and associated taxa.—Cambraster Cabibel, Termier, and Termier, 1958 resembles isorophids in gross morphology, but many of the details suggest affinities to Stromatocystites. From oral aspect Cambraster appears to have a well-defined peripheral rim that is strongly differentiated from the interambulacral plating. This rim, however, is

plated quite unlike a peripheral rim because: 1, none of the plates are in contact with the substrate, 2, the plates do not follow the progression of large proximal plates that grade into smaller, more distal circlets, and 3, the entire structure, at least in some taxa, is bisected by the extension of the ambulacra (Jell et al, 1985; Smith and Jell, 1990) (Fig. 1.3). The mouth frame is plated by proximally integrated interradial plates that form the peristomial opening and the proximal contact of the floor plate system. The plating of the ambulacral system bears biserial floor plates that are broadly exposed externally (probable homologues to the abradial floor plates of Kailidiscus) and bear podial pores; the adradial plates seem to be absent. The cover plates are arranged into a multitiered system, but the details are unknown. The interambulacral plates bear epispires and are fully adjacent. Unlike in isorophids, the bottom surface is fully plated forming an adhesion disk that is very similar to those seen in Stromatocystites (Jell et al, 1985; Smith and Jell, 1990). This surface also separates the marginal ring on the oral surface from the substrate. The plating on this surface is irregular though concentrically organized in some taxa and obscures viewing the internal anatomy of the ambulacra and oral frame except for the most gross details where taphonomically disrupted.

Totiglobus.—Totiglobus Bell and Sprinkle is an unusual edrioasteroid grade echinoderm known from two described species from the middle Cambrian of North America. This taxon shows similarities to edrioasterids but differs substantially in many of the details (Fig 1.2). The mouth frame is formed from proximally integrated interradial plates that articulate to the proximal-most floor plates. The ambulacra are essentially similar to edrioasterids', bearing biserial floor plates with sutural pores and a roof of cover plates that leave the abradial edges of the floor plates broadly exposed (Bell and Sprinkle, 1978). The cover plates, however, are formed into a double biseries, which is unknown in edrioasterids. The hydropore/gonopore and periproct are identical to edrioasterids' as is the globular thecal shape (Bell and Sprinkle, 1978; Sprinkle, 1985). The attachment surface differs greatly from other edrioasteroid grade echinoderms, bearing two plate layers over a fully plated ventral surface (Bell and Sprinkle, 1978). An interior set of plates shows radial spur and groove structures covering a basal thecal cavity. This depression is in turn covered by an irregular array of polygonal plates that decrease in size towards the center of the disk (Bell and Sprinkle, 1978). Externally, however, this adhesion disk resembles structures seen on the aboral surface of Stromatocystites and Cambraster. Edrioasterids instead have a small attachment holdfast connected to the theca by a short imbricated plate that is rarely preserved (Bell, 1976a; Guensburg and Sprinkle, 1994; Sumrall and Deline, 2009).

Edrioblastoids.—Edrioblastoids are a group of bud-shaped edrioasteroids that bear strong resemblance to edrioasterids and likely are a subclade within that group (Smith and Jell, 1990; Guensburg and Sprinkle, 1994). In edrioblastoids, the short stalk has been elaborated and organized into an elongate stem extending from the base of the theca. The ambulacral construction appears to be formed from the interradial fusion of floor plates and the integrated interradial plates, forming large compound elements termed deltoids. These plates retain the edrioasterid-like podial pores and the wide expression of the floor plates on the thecal exterior. Despite sporadic study for nearly a century (Bather, 1914; Fay, 1962; Mintz, 1970; Smith and Jell, 1990; Guensburg and Sprinkle, 1994) this group remains poorly documented and awaits comprehensive study.

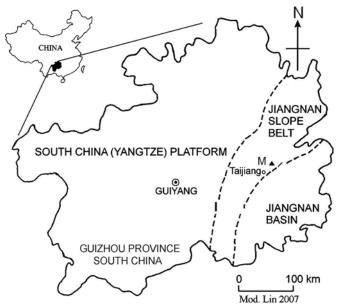


FIGURE 2—Map of the south China (Yangtze) Platform showing the location of the Kaili Formation from which specimens of *Kailidiscus chinensis* n. gen. and sp. were collected. M indicates the location of the Miaobanpo (fossil) Quarry from which the specimens were collected.

Walcottidiscus.—Walcottidiscus from the Burgess Shale is an extremely large early edrioasteroid grade echinoderm that is poorly documented because of poor preservation. The two described species, Walcottidiscus typicalis Bassler, 1935 and Walcottidiscus magister Bassler, 1936, appear to be conspecific and bear two sets of ambulacral floor plates with four rows of podial pores, and multitiered ambulacral cover plates. The aboral surface is unplated and the attachment surface seems to be formed by a peripheral rim (Smith, 1985). The hydropore, gonopore, and anal pyramid are unknown in the type material. In most respects Walcottidiscus is very similar to Kailidiscus chinensis n. gen and sp. Restudy of the type material of Walcottidiscus shows it to have extremely poor preservation and consequently at present this taxon cannot be diagnosed.

## LOCALITY AND STRATIGRAPHY

All specimens of *Kailidiscus chinensis* n. gen. and sp. were collected from the mid-third of the Lower to basal Middle Cambrian Kaili Formation, of the Jiangnan Slope belt on the eastern margin of the South China (Yangtze) Platform (Lin et al., 2008) (Fig. 2). Because of its Burgess Shale-like preservation, including soft-part preservation and the grouping of numerous deeper water organisms, the fauna from this part of the section has been termed the Kaili Biota (Zhao et al., 1996). The Kaili Formation encompasses a complete tectonic sequence, as evidenced by shallow water carbonates near its base grading into ever fining organic rich and increasingly disaerobic siliciclastics to essentially mid section (Fig. 3). The upper portion reverses this sequence where it is capped with shallow water carbonates at the upper formational boundary (Zhu et al., 1999). The material described in this paper comes from the Miaobanpo (fossil) Quarry which is excavated near the top of an east-west trending mountain ridge about two kilometers north of the village of Balang, Jianhe County, Guizhou Province. Most of the material comes from the interval 30 to 40 m above the base of the formation (Fig. 3) (Zhao et al., 2005). These deeper water sediments are primarily black to greenish black, shale to silt-sized siliciclastics.

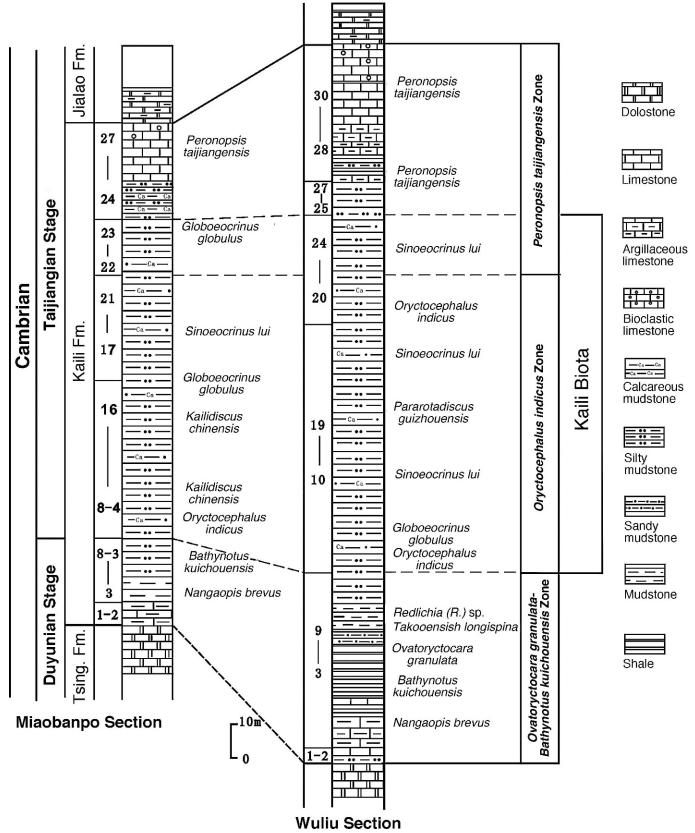


FIGURE 3—Stratigraphic columns showing the stratigraphic position of *Kailidiscus chinensis* n. gen. and sp. and other associated fauna within the Miaobanpo and Wuliu Sections. Zonation follows Zhao et al. (2007).

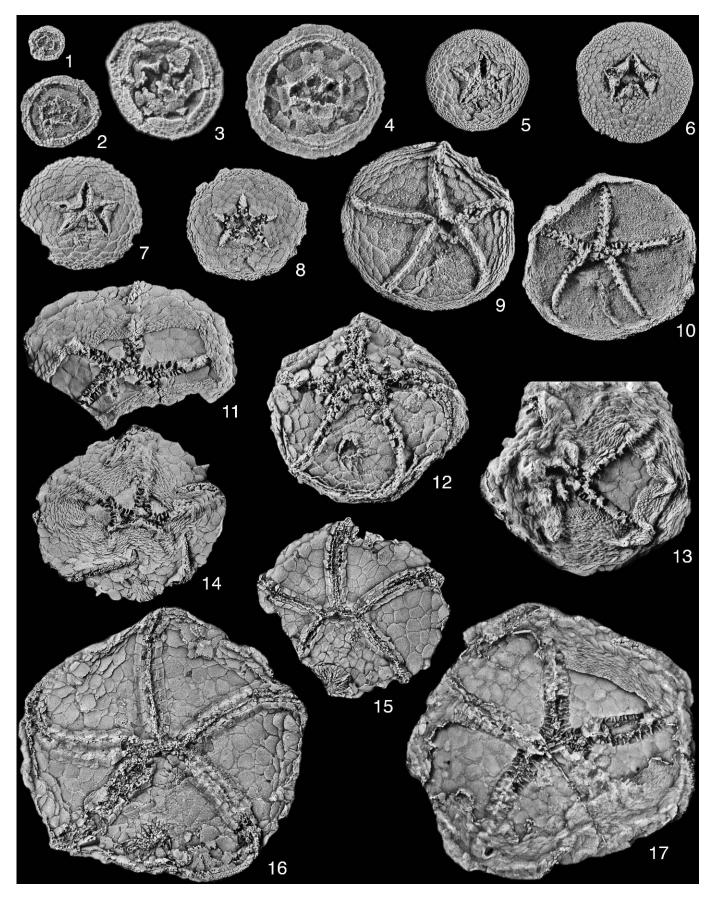


FIGURE 4—Ontogeny of *Kailidiscus chinensis* n. gen. and sp. All photographs are of latex casts of natural molds. 1, interior view of extremely small juvenile paratype GM 3295a showing proportionately large pentagonal peristome bounded by integrated interradial plates,  $\times 20$ ; 2, interior view of small

Bedding in the form of fine laminae is mostly from suspension obrution sedimentation. Deposition is interpreted to be between 150 to 200 m water depth along the outer shelf to upper slope of the Jiangnan Slope belt on the eastern margin of the South China (Yangtze) Platform (Lin et al., 2008). Disruption of sedimentation on any scale is rare with an almost total lack of bioturbation. There is little evidence for unidirectional flow, but some levels show alignment of equal sized specimens resting on current-swept surfaces.

## PRESERVATION AND TAPHONOMY

Specimens of Kailidiscus chinensis n. gen. and sp. are preserved as internal and external molds in silicilastic shales. This affords the opportunity to study the specimens in both part and counterpart to fully document the structure of these edrioasteroids. It has been shown that internal structures in part/counterpart derived from moldic edrioasteroid specimens can greatly aid in the understanding of overall anatomy (Sumrall and Zamora, in press). Molds are commonly stained and partly filled with iron oxides, suggesting oxidation of early diagenetic pyrite precipitated during the decay of the organisms under disaerobic conditions. The fact that the mouth frame is clear and undisturbed in all specimens showing the lower surface shows conclusively that the bottom surface of the theca was not plated. Natural molds of the specimens were cast with latex, darkened with India ink and whitened with a sublimate of ammonium chloride (NH<sub>4</sub>Cl) for study and photography.

Specimens of *K. chinensis* were apparently attached directly to a stabilized substrate. This type of attachment required an indurated substrate and this may be a common condition for echinoderm attachment for much of the Early through Middle Cambrian (Parsley and Prokop, 2004; Parsley and Zhao, 2006; Dornbos, 2006; Zhao, et al., 2007, 2008).

Specimens of *K. chinensis* are all preserved after undergoing severe thecal collapse pressing the inner surface of the upper thecal plates into the substrate or in some cases other portions of the theca that lie directly below the upper surface. This thecal collapse typically manifests itself in the slight elevation of the ambulacra, oral surface, and peripheral rim above the more generally depressed interambulacral areas (Bell, 1976a; Sumrall, 2001). However, this taphonomic effect is much more subdued in *K. chinensis* than is generally seen in peripheral rim bearing taxa. This may result from the fundamental difference in construction of the ambulacra, which are much broader and proportionately thinner than are generally seen in isorophids.

In most cases, the thecae are fully articulated, showing little evidence of post mortem disarticulation. Most deviations result from differential compaction and irregularities in outline stemming from the detachment of specimens from the substrate prior to burial. Evidence for this detachment

comes largely from the curled edges of the peripheral rim generally seen when viewed from below. This edge curling is quite unlike the crisp clean circular outline of peripheral rims observed when specimens are still attached to the substrate. Such curling is apparent only on the largest specimens.

A few of the specimens show post mortem disarticulation of the thecal wall. Here, plates from a small portion of the theca are scattered about while the vast majority of the theca remains fully articulated. The lack of broken plates and other evidence of predation suggests disarticulation by decompositional gases bursting from the thecae after burial (Sprinkle, 1973). Also radial fracturing of the theca results from polar-oriented compaction of a formerly inflated theca.

#### ONTOGENY

Specimens of *Kailidiscus chinensis* n. gen. and sp. used in this study include a complete growth series with specimens smaller than 1.0 mm through mature individuals in excess of 30 mm in diameter (Fig. 4). Many of these specimens are preserved as part/counterpart, allowing for the identifications of ontogenetic transformations from both the internal and external aspect.

The earliest ontogentic stages of *Kailidiscus chinensis* n. gen. and sp. are documented only from internal views of the theca (Fig. 4.1–4.4). The smallest of these specimens has a thecal diameter (TD =) of 0.5 mm and is interpreted to be just post larval. These specimens show that the first elements of the ambulacra to form are the integrated interradial plates (IIP) that form the bifurcation points of the five ambulacra. Also evident are the first elements of the proximal-most circlet of peripheral rim plates. By TD = 1.0 mm the IIE have enlarged, but there is no hint of floor plates of either the adradial or abradial series (Fig. 4.2). The IIPs are in broad contact along their lateral margins, forming the edge of the mouth frame. The peristomial opening is distinctly pentagonal, with a wide posterior margin reflecting the incipient 2-1-2 (Sprinkle, 1973; Sumrall and Wray, 2007).

By TD = 2.5 mm the first adradial floor plates begin to develop along the distal most portion of the sutures between the IIPs (Fig. 4.4). At this point the peristome is still formed by the border of the IIPs and the adradial floor plates form only the distal-most portion of the ambulacra. Cover plates are poorly known at this stage of development, but were already present as shown by traces of cover plates seen through the peristomial opening (Fig. 4.4). The first interambulacral plates perhaps one per interambulacrum, are also present by this ontogenetic stage. The ambulacra are straight and the peripheral rim has at least two circlets of plates and is proportionately less prominent, as has been shown for other edrioasteroid taxa (Bell, 1976b).

By TD = 5.5 mm the IIPs are separated on both the interior and exterior of the organism (Fig. 4.5–4.8). This change is

juvenile paratype GM 3295b showing enlargement of the integrated interradial plates, and the lack of ambulacral floor plates, ×20; 3, interior view of juvenile paratype GM 3295c showing the expansion of interambulacra, ×20; 4, interior view of juvenile paratype GM1670 showing the first emplacement of adradial floor plates distal to the integrated interradial plates, compare to Figure 7.3, ×15; 5, exterior view juvenile paratype GM 1331 showing short straight ambulacra and a well defined bounding peripheral rim, ×5; 6, exterior view of juvenile paratype GM 3035 ×5; 7, 8, exterior and interior views of juvenile paratype GM 1898 showing adradial floor plates along the proximal margin of the integrated interradial plates, and the interior of the ambulacral floor plates, ×5; 9, 10, exterior and interior views of advanced juvenile paratype GM 8052 showing the beginning of ambulacral curvature, imbricate interambulacral plates, and the oral surface bounded by the peripheral rim, ×4; 11, aboral view of small mature paratype GM 746. Note small width of the peripheral rim and plating of the pedunculate zone above, and the interior view of the proximal ambulacra and oral frame seen through the unplated aboral surface, ×4; 12, oral surface of small mature paratype GM 9292, ×3; 13, aboral view of small mature paratype GM 3600 showing irregularly folded peripheral rim, ×4; 14, 15, aboral and oral views of small mature holotype GM 3428 showing nature and extent of the ambulacra, and thecal morphology. Note that the tips of the ambulacra extend well onto the aboral surface, ×3; 16, 17, oral and aboral views of extremely large mature paratype GM 2146, counterpart GM 3665 showing ambulacral curvature and intercalation of plates in the interambulacral areas, ×2.

characterized by the extension of the adradial ambulacral floor plates around the proximal edge of each IIP (Fig 4.7). At this point the oral frame transitions from being bordered by the IIPs to being bordered by the proximal most adradial floor plates in each ambulacrum. Podial pores are evident along the edges of the ambulacral floor plates and between the IIPs and the proximal-most adradial floor plates (Fig. 4.7). Externally the proximal most adradial floor plates are seen separating the IIPs from the cover plate series. At this developmental stage the ambulacra begin to elongate and both the adradial and abradial floor plates are expressed. Both of these plate series extend to the tips of the ambulacra. The abradial floor plates are difficult to see internally but are broadly expressed externally. The cover plate series articulates with the abradial floor plates in an articulation notch about at the midpoint of each plate, leaving them broadly exposed from the exterior. Also at this stage the periproct, hydropore, and gonopore first become evident, but they may have formed earlier in ontogeny. The ambulacra are still straight and short but have distinctly pointed termini. Interambulacra plates are numerous, squamose, and imbricate, but they are not well differentiated from the plates of the peripheral rim (Fig. 4.5–4.7). The peripheral rim is relatively narrow and is poorly differentiated proximally to distally, as is typical for later isorophid taxa (Bell, 1976a).

By TD = 12 mm, specimens assume a stereotypical isorophid appearance (Fig. 4.9, 4.10). The 2-1-2 ambulacral symmetry has fully developed, and the periproct, hydropore, and gonopore are prominent. The ambulacra have become much more prominent by increasing in both width and length. The greater width results from both an increase in diameter of the ambulacral tunnel and the relative width of the external expression of the abradial floor plates (Fig. 4.9). The ambulacra are generally straight but with a prominent clockwise curvature of the ambulacra tips as they reach the peripheral rim and the limits of the oral surface (Fig. 4.9). The ambulacral floor plates are clearly differentiated between adradial and abradial series, with four rows of pores piercing the ambulacral floor plates (Fig. 4.10). The interambulacra are unchanged except for a proportional increase in area as the peripheral rim and oral area become proportionately less prominent with age (Bell, 1976b). The interambulacra retain their squamose, imbricate plate pattern with relatively few new plates being added. At this point the peripheral rim is better defined but proportionately very narrow and confining to the areal extent of the oral surface. The first rows of highly imbricate peduncular plates are beginning to form in a zone from the edge of the interambulacral plating and the peripheral rim (Fig. 4.9).

By TD = 18 mm two important ontogenetic changes have occurred. Most noticeable is the extension of the pedunculate zone with a concomitant slowing in the growth of the peripheral rim. This results in the theca greatly enlarging in height and transitioning from a low blister in form to a more highly inflated theca (Figs. 1.5, 4.11, 4.13-4.14). The ambulacra are not confined to the oral surface but continue to curve clockwise around the theca, extending into the peduncular plating beyond the thecal ambitus (Figs. 1.5, 4.14). This is readily seen on the aboral surfaces of some specimens where there is a relatively small peripheral rim bounded by highly imbricate peduncular plates, with the distal tips of the ambulacra extending over onto this surface from the upper face (Fig. 4.14). Secondly, the interambulacral plating is transitioning between squamose, imbricate plates to tessellate, adjacent plates (Fig. 4.12, 4.15). These plate fields do not appear to be entirely rigid but rather to have some flexibility as has been shown for other edrioasteroids that are similarly plated, e.g., discocystinids (Sumrall, 1993, 1996). Unlike the latter, the plating of *Kailidiscus* is very thin and the sutures slightly depressed, suggesting somewhat greater flexibility. At this stage the number of interambulacral and periproctal plates also increases through plate intercalation. This trend continues throughout ontogeny.

By TD = 35 mm little has changed. The ambulacra are extremely wide and prominent and the cover plate patterns are fully expressed. The tips of the ambulacra continue to extend across the pedunculate zone and increase in width (Fig. 4.16–4.17). The periproct has grown to extreme size and has shifted to the distal left interambulacral area (Fig 4.16). Numerous interambulacral plates have been added, forming complex patterns of small and large interambulacral plates that show no repeating patterns of insertion. The peripheral rim is roughly 60 percent the diameter of the theca and relegated to an aboral holdfast structure (Fig. 4.17).

Discussion.—Unlike isorophid edrioasteroids, Kailidiscus chinensis n. gen. and sp. inserts interambulacral plating irregularly throughout the interambulacral areas. As specimen diameter increases in isorophid taxa, new interambulacral plates are added only along the margins of the ambulacra (Bell, 1976b). These are manifested as small plate intercalates dispersed randomly along the contact between the interambulacral areas and the ambulacral cover plates. In Kailidiscus, new plates are added at three plate junctions between plates (Fig 4.16). These new plates can add anywhere in the interambulacral fields and often occur in clusters near the middle of the interambulacral areas. This pattern of insertion is similar to that seen in edrioasterids and may be plesiomorphic for edrioasteroid grade echinoderms.

The transition of a peripheral-rim-bearing edrioasteroid from a discoidal form in juveniles to an inflated theca at maturity is a common theme among edrioasteroids (Smith, 1983; Sumrall, 2001; Sumrall et al., 2006). This often occurs in large taxa that are space-limited by the small size of their attachment surfaces or in some cases by intense crowding. In the case of *Kailidiscus*, space does not seem to be a contributing factor.

## SYSTEMATIC PALEONTOLOGY

Class Edrioasteroidea Billings, 1858 Order uncertain Family uncertain Genus Kailidiscus new genus

Type species.—Kailidiscus chinensis n. gen. and sp. Diagnosis.—Same as for species by monotypy.

Etymology.—Kailidiscus n. gen is derived from the name of the formation from which the specimens were collected.

Discussion.—Kailidiscus includes only the type species K. chinensis. Two other described edrioasteroids are closely related to Kailidiscus but are not diagnosable with present material. Walcottidiscus typicalis Bassler, 1935, is known from two specimens in the USNM that are preserved as flattened specimens broken through on shale slabs (Fig. 5.4, 5.5). The poor preservation allows only a few of the diagnostic characteristics to be ascertained with certainty. The cover plates are arranged into multitiers, though the details are lacking, the floor plates are arranged into adradial and abradial series with four rows of podial pores, and the ambulacra curve clockwise. These features are consistent with Kailidiscus n. gen., but the hydropore, gonopore, and oral frame are not preserved in the type material of Walcottidiscus and therefore cannot be determined. Other non-type material in the Royal Ontario Museum belonging to this taxon has not

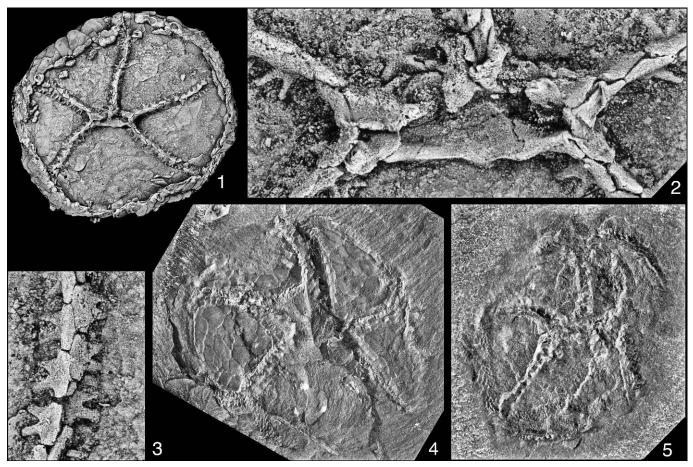


FIGURE 5—Undiagnosible taxa closely related to Kailidiscus chinensis n. gen. and sp. 1–3. "Stromatocystites walcotti" Schuchert, USNM 376690, all images are of latex cast of internal mold; I, interior of the oral surface showing clockwise curved ambulacra and large periproct in the distal left CD interambulacrum (note that this is an internal view and, therefore, a mirror image of the external surface) ×1.5; 2, internal view of mouth frame showing the extension of the adradial floor plate series forming the peristomial opening, ×10; 3, adradial floor pates of the A ambulacrum. Note the adradial podial pores between plates on each side, and the edges of the abradial podial pores along the lateral margins of the plates, ×10; 4, the holotype of Walcottidiscus magister Bassler, USNM 90755, uncoated. This specimen is an internal mold of the oral surface with a matrix plug covering the A ambulacrum, oral area, and the CD interambulacrum, ×1; 5, holotype of Walcottidiscus typicalis Bassler, USNM 90754, uncoated. This specimen is a partial internal mold showing the interior of the A–C ambulacra with the peripheral rim folded over the D and E ambulacra. A partial distal tip of the D ambulacrum is visible on the extended pedunculate zone, ×4.

been studied in detail and may shed more light on the details of anatomy of *W. typicalis*. Regardless, the large coarser plating of the interambulacra (Fig. 5.4) serves to separate *W. typicalis* from *K. chinensis* (Fig. 6.2).

One specimen assigned to "Stromatocystites walcotti" by Smith (1985, text fig. 7, also see, Guensburg and Sprinkle, 1994, Fig 3b) conforms well to *Kailidiscus* and may in fact be Walcottidiscus typicalis. The specimen, USNM 376690, (Fig 5.1–5.3) is associated with the type material of Stromatocystites walcotti Schuchert, but it is clear from the labeling that the specimen has been disassociated with the collecting data. On this specimen one can see the adradial floor plates, hints of the abradial floor plates, and four rows of podial pores (Fig. 5.3). Also clearly present is the clockwise curvature of the ambulacra, and the complex oral frame of Kailidiscus formed from the proximal most adradial floor plates and the integrated interradial plates (Fig. 5.2). The periproct is also offset to the posterior left side of the CD interambulacrum. Unfortunately, because this specimen is preserved as an internal mold of the oral surface, no information is available concerning the cover plates, hydropore, gonopore, interambulacral plating, or the nature of the aboral surface (Fig. 5.1).

This taxon is closely related to *Kailidiscus* and *Walcottidiscus* but unassignable at present.

## KAILIDISCUS CHINENSIS new species Figures 1.5, 4, 6–8

Diagnosis.—Plesiomorphic edrioasteroid grade echinoderm bearing five wide, clockwise curving ambulacra with exposed quadruserial floor plates bearing four rows of podial pores; abradial floor plates broadly exposed; multitiered ambulacral cover plates, inflated theca with imbricate pedunculate zone; unplated dorsal surface; separate hydropore and gonopore pyramids excluded from oral frame; and large irregularly plated periproct offset to the posterior left CD interambulacrum.

Description.—Edrioasteroid grade echinoderm with large inflated theca, wide clockwise curving ambulacra, and proportionately small peripheral rim at maturity (Figs. 4, 6); oral area wide with ambulacra arranged in 2-1-2 pattern, formed from complex arrangement of integrated interradial plates (IIP), adradial floor plates, and multitiered cover plates (Figs. 6.4, 6.8, 7.1, 7.2); IIPP positioned at most proximal point of interambulacra except CD, where two IIPP present;

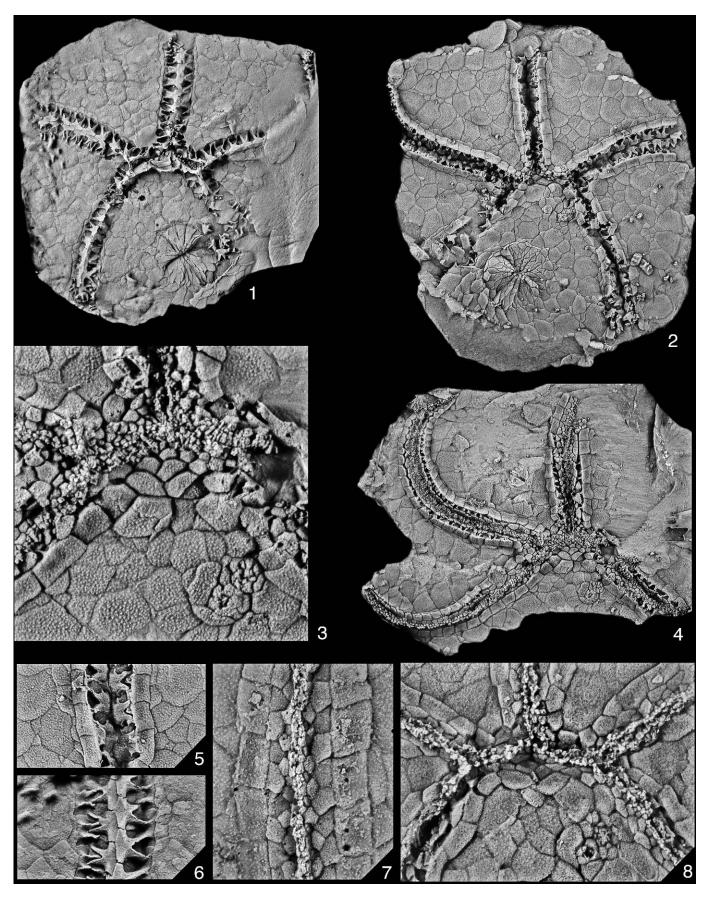


FIGURE 6—All specimens *Kailidiscus chinensis* n. gen. and sp. photographs of latex casts of natural molds. 1, 2, 5, 6, large paratype GM 2103; 1, interior view of oral surface showing large periproct, hydropore and gonopore orifices, and double-biserial ambulacral floor plates, ×2.5; 2, exterior view

abradial floor plate series terminate at junction with IIPP; five to six adradial floor plates positioned proximally and adambulaerally to IIPP on thecal exterior (Figs. 6.8, 7.1); interior of IIPP sculpted with flutes that form distal edges of most proximal set of adradial podial pores where in contact with similar flutes in distal edges of most proximal set of adradial floor plates (Figs. 6.1, 7.2); peristomial opening bordered by proximal edges most proximal set of adradial floor plates; exact number of plates and arrangement not fully documented in present material and with slight variation between specimens (Fig. 7.2); in general, biserial adradial floor plates forming food grooves of B and C ambulacra and D and E ambulacra join at bifurcation point of shared ambulacra, whereas adradial floor plates of A ambulacrum join mouth frame separately; between ambulacrum A and bifurcation points, adradial floor plates split and connect such that right set of B connects to left set of A and right set of A joins to left set of E with one or two plates spanning connection (Fig. 7.2); similarly left set of C connects to right set of D with approximately three connecting plates; radially positioned oral frame plates as in other edrioasteroids are diagnostically absent from oral frame; ambulacra extremely wide (Fig. 6), all curved clockwise, formed from two sets of biserial floor plates forming food groove and podial pores and multitiered cover plates covering food groove (Fig. 8); ambulacra wide, nearly straight proximally, then strongly curved clockwise and down theca onto pedunculate zone, extend beyond thecal ambitus in mature specimens, ending in blunt termination (Fig. 4.14-4.17); proximal ambulacra where in contact with IIPP lacking abradial floor plates and bear modified and more narrowly exposed adradial floor plates resulting in pinched look proximally; floor plates arranged in both adradial and abradial series; adradial series forms biseries along perradial suture at base of food groove, wrapping proximally around IIPP, adradial floor plates very long along perradial suture, articulations between adjacent plates across perradial suture forming extremely shallow zig-zag (Figs. 6.5-6.6, 8.1-8.2); articulation between adjacent plates on same side of perradial suture very narrow, forming broad U-shaped adradial end on adradial pore set (Fig. 8.1); abradial end of adradial floor plate with two projections forming shallow V of adradial end of abradial pore set; articulations between adradial and abradial floor plates oblique, forming long narrow separation between adjacent adradial and abradial podial pores (Figs. 6.5-6.6, 8.1-8.2); abradial floor plates extend from distal edges of IIPP to distal tip of ambulacra, broadly exposed on oral surface, typically forming parallelogram in outline with abradial plate margin, extending slightly further distally than adradial margins (Figs. 6.5, 8.2), exposure much longer than wide except along inner right side where curved where exposure is more equant (Fig. 6.4); slight notch formed along adradial edge of exposed portion for cover plate articulation; internal portion of abradial floor plate narrowly articulated to adjacent abradial plate forming broad U-shaped abradial end of abradial podial pores; adradial end of abradial

plates with two projections forming deep V-shaped projection of adradial end of abradial pores (Figs. 6.5-6.6, 8.1-8.2); four rows of podial pores tear-drop shaped; adradial pores broad adradially funneling into ambulacral tunnel; abradial sets broad abradially, funnel into thecal interior (Fig. 6.5, 6.6); cover plates arranged into multitiered pattern, most fully developed in straight portions of proximal ambulacra, distal to IIPP; one cover plate package present per abradial floor plate mirrored across ambulacrum (Figs. 6.7, 8.3); basal tier of two plates, proximal plate 1 radially elongate, distal plate 2 equant; secondary tier of five plates, plates 1 and 4 largest, plate 2 transversely elongate (Fig. 8.3); third tier plates more irregularly with small equant plates and lesser numbers of transversely elongate plates (Fig. 8.3); fourth tier of elongate, digitate, and feather like ctenoid plates, generally larger than third tier and generally transversely elongate (Fig. 8.3); interambulacral plates numerous, relatively small, imbricate and squamose early in ontogeny, becoming polygonal and adjacent at maturity (Fig. 4); most of interambulacral fields plated with larger, early-formed plates; less mature plates added haphazardly at corners of larger plates forming small triangular ossicles (Fig. 6.2); less mature plates also added along edges of ambulacral floor plates; hydropore and gonopore placed in proximal right CD interambulacrum (Figs. 6.3, 7.1), non-integrated into oral area, pierce interambulacral area with separate, circular openings (Figs. 6.1, 7.2); larger opening, here termed hydropore, plated with small low cone, of polygonal plates that decrease in size toward center, larger plates on periphery somewhat transversely elongate whereas central plates more equant (Figs. 6.3, 7.1); smaller opening, here termed gonopore, about 60 percent diameter of hydropore, outline indents hydropore in proximal right quadrant and abradial floor plate of C ambulacrum, formed into small low cone of uniformly small equant plates that slightly decrease in size towards periphery (Figs. 6.3, 7.1); periproct circular, extremely large 8 mm across in 34 mm diameter specimen (Fig. 6.2), positioned in the distal left CD interambulacrum (Fig. 6.2); periproct covered with a complex series of lathe-shaped periproctal plates arranged into approximately 10 to 15 irregular composite triangular wedges forming the cover; each wedge formed from four to five circlets of irregular plates (Fig. 6.2); interior surface of periproctal pyramid not demarked from interambulacral plates by well-defined hinge (Fig. 6.1); pedunculate zone positioned between edge of oral surface and peripheral rim, well developed at maturity with eight to ten irregular circlets of highly proximally imbricate, squamose plates (Fig. 4.11, 4.13–4.14); pedunculate zone positioned sub-ambitally and expands in diameter proximally from proportionately small peripheral rim to expanded oral surface; peripheral rim, smaller than thecal diameter at maturity, approximately 9 mm in 18 mm diameter specimen, plated with approximately seven irregular circlets of extremely small irregular plates that decrease in diameter distally (Fig. 3.13); all plates equant and slightly bulbous; attachment surface of peripheral rim on

of oral surface showing curved ambulacra with cover plates stripped and intercalating immature interambulacral plates being inserted in center of interambulacra, ×2.5; 5, detail of the food groove of ambulacrum B in food groove aspect showing adradial floor plates along the perradial suture and abradial floor plates largely forming broadly exposed floor plate shelves beyond the cover plate articular surface, ×5; 6, internal view of the same floor plates showing adradial pores broadest near the perradial suture and abradial pores broadest perradially; ×5; 3, 4, paratype GM 70; 3, detail of exterior peristome and proximal CD interambulacrum showing the complex multitiered cover plates, and hydropore and gonopore pyramids, ×7.5; 4, exterior view of oral surface showing curved ambulacra with cover plates fallen into the food grooves, ×2.5; 7, detail of ambulacrum A of paratype GM 2146 showing multitiered cover plates articulated to abradial floor plates that are broadly exposed, ×9; 8, detail of the peristome and hydropore/gonopore of holotype GM 3428, ×7.5.

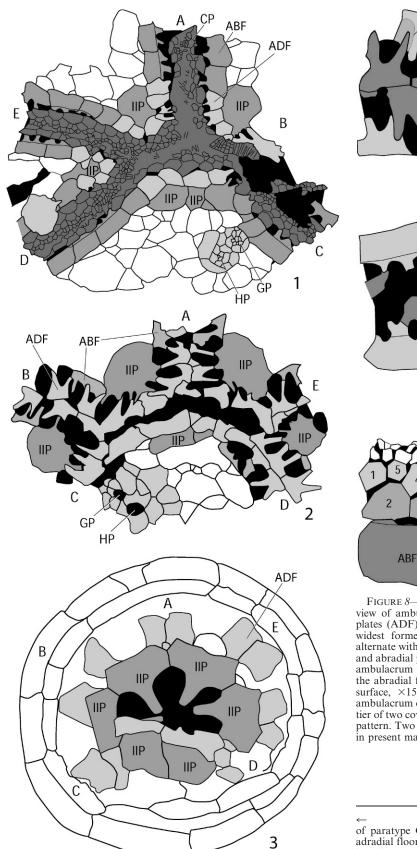
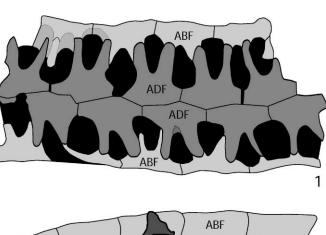
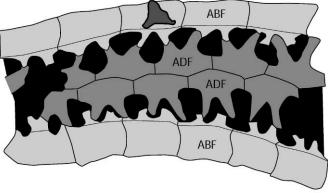


FIGURE 7—Plating of the peristome of *Kailidiscus chinensis* n. gen. and sp. 1, External view of mature paratype GM70 showing ambulacral cover plates fallen into the food grooves,  $\times 50$ ; 2, interior view of the oral frame





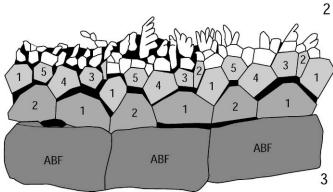


FIGURE 8—Ambulacra of Kailidiscus chinensis n. gen. and sp. 1, interior view of ambulacral floor plates of paratype GM 2103. Adradial floor plates (ADF) meet along the perradial suture. Adradial pore pairs are widest formed along their sutures. Abradial floor plates (ABF) are alternate with IFP. Note that the adradial pore pairs are widest adradially and abradial pore pairs are widest abradially, ×15; 2, food groove view of ambulacrum with cover plates stripped of paratype GM 2103. Note that the abradial floor plates extend well beyond the cover plate articulation surface, ×15; 3, view of the left side of a mature somewhat distal ambulacrum of paratype GM 70. Abradial floor plates articulate to lowest tier of two cover plates. The second tier consists of five plates in a repeated pattern. Two additional tiers appear to be present, though details unclear in present material. Uppermost tier includes ctenoid plates, ×30.

of paratype GM 2103 showing integrated interradial plates contacting adradial floor plates that form the mouth frame, ×55; 3, interior view of juvenile paratype GM 1670 showing that early in ontogeny the integrated interradial plates contact along their adjacent sutures and the proximal most adradial floor plates do not reach the mouth frame, ×30. A–E are ambulacral designations; ABF = abradial floor plate; ADF = adradial floor plate; CP = cover plate; GP = probable gonopore; HP = probable hydropore; IIP = integrated interradial plate.

extremely small specimens suggestive of radial spur and groove structures, but cannot be confirmed in larger material; lower surface of theca nonplated (Fig 4.11, 4.13–4.14).

Types.—The type series for Kailidiscus chinensis includes holotype GM 3428 and paratypes GM-70, 746, 1331, 1670, 1898, 2103, 2146, 3295a, b, c, 3035, 3600, 3665, 8052, 9292. All specimens are reposited in the collections of the Museum of Paleontology, Guizhou University, Guiyang, China.

Occurrence.—Kailidiscus chinensis n. gen. and sp. is known from the mid-third of the Kaili Formation, basal Middle Cambrian, of the Jiangnan Slope belt on the eastern margin of the South China (Yangtze) Platform. The material was collected in the Miaobanpo (fossil) Quarry located near the top of an east-west trending mountain ridge about two kilometers north of the village of Balang, Jianhe County, Guizhou Province.

*Etymology*.—The trivial name refers to the Peoples Republic of China where the specimens were collected.

Discussion.—The interpretation of the mouth frame being plated by modified adradial floor plates is based on the continuation of this plate series from the ambulacra. Only the outer plates of this series are present as they wrap around the peristomial opening (Fig. 4.2). The integrated interradial plates act as analogs if not homologues to the abradial floor plates with which they are contiguous. They also bear the abradial portion of podial pores that are shared with the adradial floor plates that form the mouth frame (Fig 7.2). These plates may also be homologues to oral plates (sensu Sumrall, 2010) found in other clades of stemmed echinoderms suggesting a deep origin of these elements.

The four rows of podial pores are also highly unusual because they appear to be different on each side of the floor plate series. The adradial set funnel into the ambulacral tunnel, whereas the abradial set funnels into the thecal interior from the ambulacral tunnel. At present we have no explanation for this observation.

The interpretation of the two pores in the proximal right CD interambulacrum as the hydropore and gonopore is somewhat conjectural. The hydropore is thought to be the larger and the gonopore the smaller, but admittedly this is scanty evidence. Regardless both pores are present and pierce the thecal wall separately unlike the integrated condition seen in later edrioasteroids (Kesling, 1960; Bell, 1976a; Sumrall, 1993) (Figs. 6.3, 7.1–7.2).

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