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Bockeliecrinites, a new name for *Protocrinites rugatus* Bockelie, 1984 (Diploporita, Blastozoa), and its taxonomic significance

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As part of a broader study of the family Protocrinitidae, all specimens of *'Protocrinites' rugatus* Bockelie, 1984, have been examined. The species differs significantly from *Protocrinites oviformis* Eichwald, 1840, type species of *Protocrinites s.s.* and is proposed as type species of a new genus *Bockeliecrinites. Bockeliecrinites* has an aboral cup composed of a single, conical, centrodorsal plate above which is a closed circlet of five, inter-radial, lateral plates. All species of *Protocrinites* have an aboral cup with two closed circlets of at least four plates. Food grooves extend beyond the last brachiole-bearing adambulacral plate. As a result, lateral branches to brachioles did not always develop in the same order as the adambulacral plates themselves. *Bockeliecrinites* lived in a distal environment with frequent turbidite deposits and its preservation shows that some specimens were buried alive. Delicate structures such as brachioles and stem remain attached to thecae. Cover plates of food grooves, mouth, anus and respiratory diplopores are all preserved in some specimens. The last have never been reported before in any diploporite. *Bockeliecrinites* was probably derived from the 'eocrinoid' *Rhopalocystis* Ubaghs, 1963, with which it shares a centrodorsal plate and cover plates to its respiratory epispires. The lineage may extend back to the Cambrian genera *Peridionites* Whitehouse, 1941 and *Cymbionites* Whitehouse, 1941. If so, both ambulacralian and anambulacralian diploporites had a common origin and the class Diploporita may be monophyletic.

Introduction

Diploporites fall into two broad categories (Paul, 1988), those with a definite ambulacral structure, the Ambulacralia of Paul & Toom (2021) and those which lack any regular ambulacra, the Anambulacralia Paul & Toom (2021; Fig. 1A herein). In the Ambulacralia, the main ambulacral axis is formed by an alternating series of thecal plates, each of which bears a single facet for an erect feeding structure (Fig. 2). In the Anambulacralia, facets for the feeding structures are either confined to the oral plates very close to the mouth or the narrow food grooves extend over the thecal surface without both flooring and cover plates. Periodically the food grooves give rise to lateral branches that terminate in ambulacral facets. In diploporites the feeding structures that arose from ambulacral facets are only very rarely preserved.

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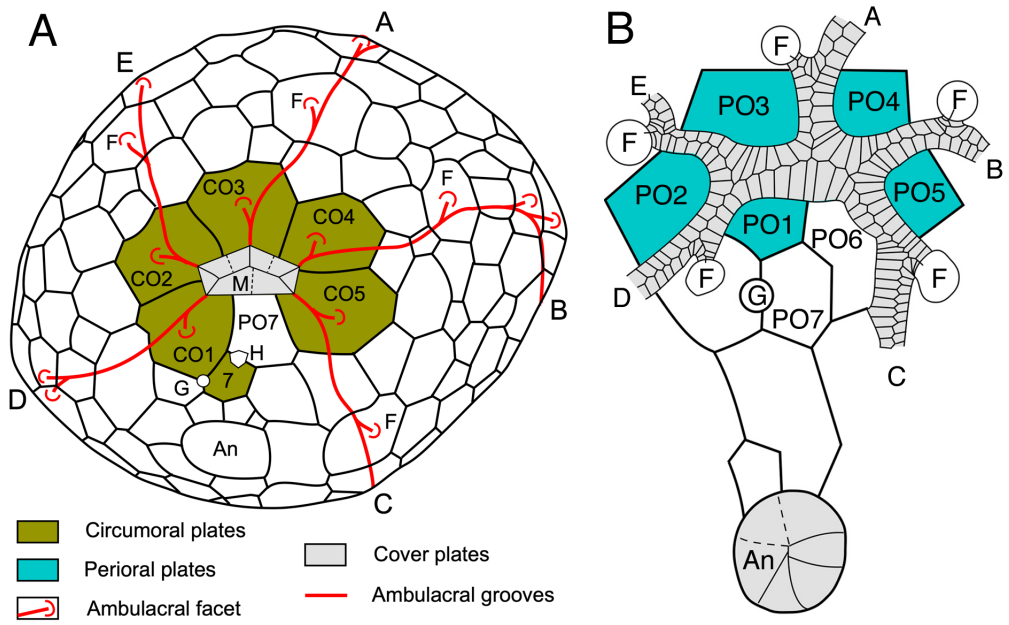

Figure 1. Drawings of oral areas and ambulacra of (A) Glyptosphaerites leuchtenbergi *(Volborth, 1846); (B)* Bockeliecrinites rugatus *(Bockelie, 1984). In Glyptosphaerites (A), the mouth (M) is covered by a small number of large cover plates called palatals, and surrounded by six plates. Five radial circumorals (CO1–CO5) bear the first ambulacral facet (F), which always branches to the left of the extensive food grooves. The sixth plate (PO7) shares the hydropore (H) with plate CO7. The gonopore (G) is associated with circumoral CO1. The anus (An) is widely separated from the mouth. In* Bockeliecrinites *(B), the mouth is covered by small biserial cover plates and surrounded by six interradial plates called periorals (PO1–PO6). Broad food grooves give rise to brachiole facets (F) on the first 'adambulacral' plates. The first facets always branch left. The gonopore (G) is shared by perioral PO7 and the first adambulacral plate of ambulacrum D. The anus is widely separated from the mouth and covered by a simple anal pyramid (An). In* Glyptosphaerites*, food grooves lack floor and cover plates, and ambulacral facets occur randomly on underlying thecal plates. In* Bockeliecrinites*, biserial cover plates extend along the food grooves, which give rise regularly to brachioles alternately left and right. Each brachiole arises from a single adambulacral plate. A–E ambulacra labelled according to Carpenter's (1884, 1891) system. A, redrawn from Regnéll (1945, p. 155, fig. 18a); B, redrawn from Bockelie (1984, p. 15, fig. 11A).*

Originally, the genus *Glyptosphaerites* Müller (1854) was taken as type genus of a major taxon within the Ambulacralia, the Glyptosphaeritida Bernard, 1895 (e.g., Kesling, 1968, p. S234), but has been shown to lack the most diagnostic character of the Ambulacralia (Paul, 1984, p. 65; Paul & Toom 2021, p. 224). *Glyptosphaerites* (Fig. 1A) lacks the organised ambulacral structure shown by the other three families within the Glyptosphaeritida: the Protocrinitidae, Bather, 1899, Dactylocystidae Jaekel, 1899, and Gomphocystitidae Miller, 1889. Paul (1984, p. 65) recommended replacing the formal taxon Glyptosphaeritida by Protocrinitida and this was repeated by Paul & Fone (1997, p. 156) and Paul & Toom (2021, p. 226), who redescribed *Glyptosphaerites,* but presented only a brief diagnosis of the Ambulacralia. Here, I redescribe and rename the Norwegian species '*Protocrinites' rugatus* Bockelie, 1984 (Figs. 1B & 2), as it differs in its thecal structure from *Protocrinites* Eichwald, 1840, the type genus of the family Protocrinitidae Bather, 1899. This is part of a broader study to establish the characters of the family Protocrinitidae, now that it typifies a larger taxon, the Protocrinitoida.

By identifying his 'growth zone', Bockelie (1984, p. 28–29, fig. 16) effectively divided the theca of *Protocrinites rugatus* into three parts: an aboral cup, an intermediate 'growth zone' where new thecal plates were added, and an ambulacral zone or vault (Fig. 2). In *P. rugatus* the basal cup consists of a single, basal, 'centrodorsal' plate surmounted by a closed circlet of five, subequal plates which are inter-radial in position (Fig. 3). The vault consists of the usual six, inter-radial, 'perioral' plates that form

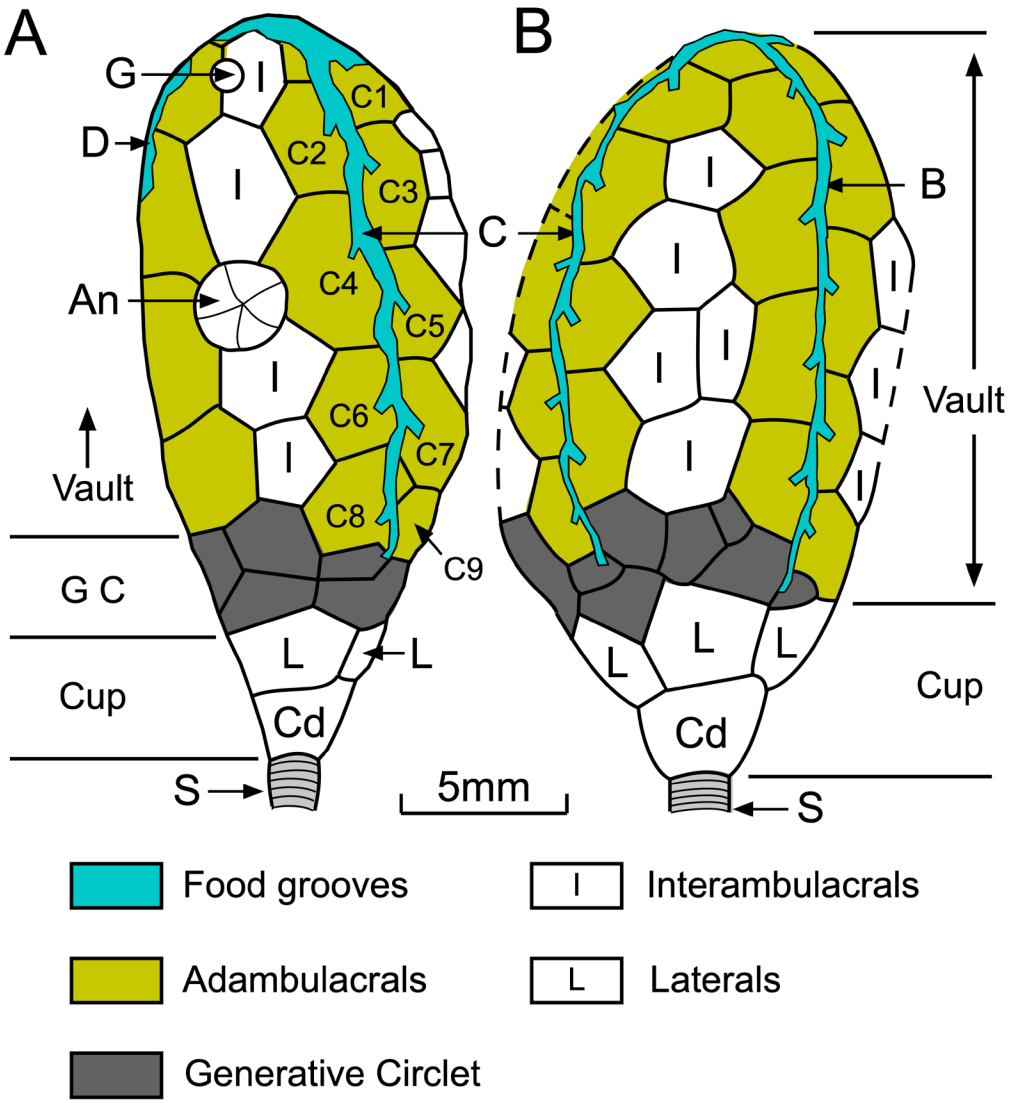

Figure 2. Adult Bockeliecrinites rugatus *(Bockelie, 1984), PMO 101.132. Lateral views of the CD (A) and BC (B) interambulacra showing the basic morphology, including the stem (S), cup, generative circlet (G C), and vault. The cup consists of a single centrodorsal plate (Cd) below and a closed circlet of five interradial lateral plates (L) above. The vault consists of the oral plates plus five, biserial ambulacra and five, usually uniserial interambulacra. Food grooves of the B, C and D ambulacra are shown. Food grooves give rise to lateral branches ending in a brachiole facet, one on each adambulacral plate. Food grooves extend beyond the last brachiole-bearing facet. Adambulacral plates of the C ambulacrum are numbered (C1, C2, etc.) in (A). Interambulacral plates (I) are usually arranged uniserially, but occasional pairs occur in the widest parts of the interambulacra. Between the cup and the vault is the generative circlet where new, undifferentiated thecal plates are added during growth. The anus (An) is covered by a simple anal pyramid and occurs laterally in the CD interambulacrum slightly above mid thecal height. A circular gonopore (G) occurs at the top of the CD interambulacrum. Redrawn from Bockelie (1984, fig. 16A, B).*

the mouth frame (Fig. 1B) and from which five, biserial, mural ambulacra radiate. Ambulacral food grooves extend beyond the last brachiole-bearing adambulacral plate (Fig. 2). Between the ambulacra are five interambulacra, each consisting of a single series of plates except in the widest parts of the theca where two plates may occur side by side (Fig. 2B). This tripartite structure is characteristic of all protocrinitid genera examined so far. Details differ and apparently provide a reliable basis on which to define individual genera. In *Protocrinites s.s.*, the aboral cup consists of two closed circlets of primary plates, a basal circlet of four to six plates and a second circlet above with at least six plates. Occasional small secondary plates may also occur.

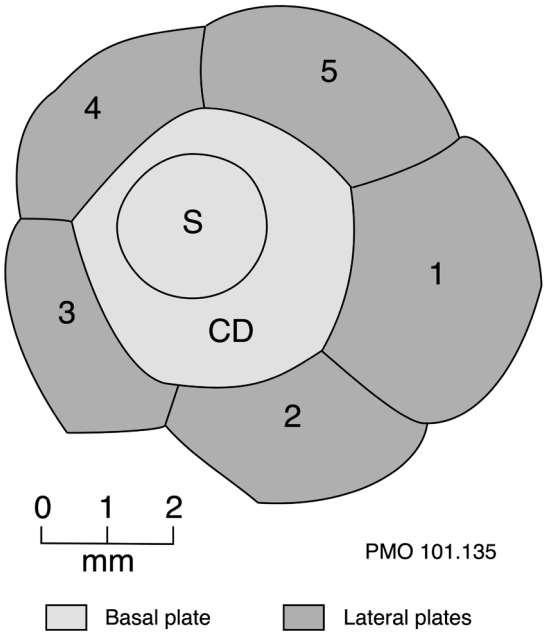

Figure 3. Basal view of the cup in Bockeliecrinites rugatus *(Bockelie, 1984) specimen PMO 101.135, showing the circular stem facet (S), single centrodorsal plate (CD) and the five lateral plates (1–5) forming a closed circlet. Compare with Fig. 4F.*

The presence of a single, 'centrodorsal' plate in the aboral cup of *'P.' rugatus* suggests affinities with the 'eocrinoid' *Rhopalocystis* Ubaghs, 1963, and a possible origin for protocrinitoid diploporites. The stratigraphically youngest protocrinitids are recorded from the Devonian of North America (Sumrall et al., 2009), but so far, no Silurian examples have been identified. Paul (1968a, p. 413) tentatively reassigned *'Strobilocystites ?? kearsagensis'* Stauffer, 1930, to the dactylocystid genus *Revalocystis* Jaekel, 1918, and accepted Waite's (1953) Silurian age for the Kennett Formation, from which it came. Subsequently, it has been determined that *'S. kearsagensis'* has diplopores in both its ambulacral and interambulacral plates and is, therefore, a protocrinitid. Furthermore, Savage (1976) reported Eifelian conodonts from the Kennett Formation, so the age is undoubtedly Middle Devonian as originally suggested by Stauffer (1930).

According to Bockelie (1984, p. 29) all but one of the specimens of *'P.' rugatus* came from the same boulder. They appear to have been buried alive by a sudden influx of sediment and are exceptionally well preserved. Several examples preserve the stem and brachioles still attached to the theca as well as oral, ambulacral and brachiolar cover plates in situ. Furthermore, specimens preserve cover plates over the diplopores, a feature known in rare examples of *Protocrinites* too. Bockelie (1984, p. 29) also identified at least one juvenile example with only two brachioles per ambulacrum. All these features suggest that *Bockeliecrinites* gen. nov. is an excellent example on which to establish the characters and phylogenetic relationships of protocrinitid diploporites.

Material and methods

All the specimens are preserved as natural external moulds. Latex casts have been made from these and kindly loaned by the palaeontology section, Natural History Museum, University of Oslo (PMO). Stereophotos were made using a seesaw which rotates specimens through approximately 12 degrees. Measurements were made using a Kyowa binocular microscope with a graticule eyepiece.

Ambulacral terminology follows Carpenter (1884, 1891); thecal plate terminology follows Paul (1971, 1973, 2017), except where new terms are added herein specifically for the Protocrinitoida.

Systematic Palaeontology

Class DIPLOPORITA Müller, 1854
Subclass AMBULACRALIA Paul & Toom, 2021
Family Protocrinitidae Bather 1899

Diagnosis. – Ambulacralians with a dorsal cup composed of two circlets of primary plates; five biserial, mural ambulacra composed of adambulacral plates with one or more brachiole facets each, separated by interambulacra with one or more columns of plates; food grooves that extend beyond the most distal facet-bearing adambulacral plate; periproct separated from the peristome by several plates in the CD interambulacrum; diplopores in both ambulacral and interambulacral plates.

Remarks. – The Protocrinitidae appears to be a well-defined family, but with more generic diversity than previously thought. Kesling (1968, p. S238) included four genera; *Eumorphocystis* Branson & Peck, 1940, *Fungocystites* Barrande, 1887, *Protocrinites* Eichwald, 1840 and *Regnellicystis* Bassler, 1950. Of these, the first and last are usually considered synonyms and currently referred to the family Eumorphocystidae (Parsley, 1982; Sheffield & Sumrall, 2019*a, b*). *Fungocystites* has peri-oral plates, two of which (PO1 and PO6) contribute to the borders of both the periproct and the peristome, food grooves that enter the mouth along sutures between orals, and it appears to have been directly attached. No protocrinitid has these characters, but they are all shared with gomphocystitids. Furthermore, *Fungocystites* has one completely preserved ambulacrum (B) that spirals clockwise and has five ambulacral facets on the outside of the spiral, a character of all other gomphocystitids. This leaves only *Protocrinites*; however, Kesling (1968, p. S237) wrongly attributed *Estonocystis* Jaekel, 1918, to the family Dactylocystidae Jaekel, 1899, because Jaekel's original figure (Jaekel, 1918, p. 102, fig. 94) showed no diplopores in the interambulacra. Protocrinitids are distinguished from dactylocystids by the presence of diplopores on both adambulacral and interambulacral plates, whereas in dactylocystids diplopores are confined to the adambulacral plates. All species currently attributed to both protocrinitid genera have aboral cups composed of two closed circlets of primary plates. The exact number of plates in both circlets varies. *Protocrinites rugatus* is unique in having an aboral cup composed of a single, centrodorsal plate above which is a closed circlet of five interradial plates. These differences justify the recognition of a distinct genus, for which I propose the name *Bockeliecrinites* in recognition of Bockelie's contributions to echinoderm research. All protocrinitid genera have mural ambulacra that form part of the thecal wall because they are formed of thecal plates.

Genus Bockeliecrinites nov.

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Type species. – *Protocrinites rugatus* Bockelie, 1984

Included species. – the genus is monotypic.

Diagnosis. – Protocrinitids with an aboral cup consisting of a single centrodorsal plate above which is a closed circlet of five interradial lateral plates.

Description. – *Bockeliecrinites* had a rooted stem composed of circular columnals; an elongate theca higher than wide in which the vault or ambulacral zone constituted about ¾ of the thecal height; five long, biserial, mural ambulacra that extended down to the aboral cup and were composed of alternating adambulacral plates each of which bore a single brachiole facet; brachioles exceeded thecal height. The peristome was composed of six, inter-radial peri-oral plates, two in the CD inter-ambulacrum and one each in the other four interambulacra. The periproct was a large, circular opening

in the CD interambulacrum, covered by a simple pyramid of anal cover plates and separated from the peristome by up to four plates. It occupied the full width of the CD interambulacrum and plates from both ambulacra contribute to the periproct border (Fig. 2A). A circular gonopore lies across the PO7:Ad1 suture of the D ambulacrum. Plates are covered by a rough sculpture and bear oval diplopores with cover plates. In common with other protocrinitids, each adambulacral plate bears two rows of aligned diplopores, more or less perpendicular to the margins of the food groove; one above and the other below the brachiole facet.

Bockeliecrinites rugatus (Bockelie, 1984)

1984 *Protocrinites rugatus* Bockelie, p. 29, Figs. 11a, 13a-h, 16a-c, 17a-c, pl. 1, Figs. 1–8.
2017 *Protocrinites rugatus* Bockelie; Cole, p. 818.
2021 *Protocrinites rugatus* Bockelie; Paul & Toom, p. 225, fig. 1b.

Holotype. – PMO 101.138. Paratypes PMO 101.130–137, 101.139–142, 101.458–462.

Diagnosis. – A species of *Bockeliecrinites* with strongly rugose plate surface.

Material. – Holotype, 17 paratypes, PMO 101.130–142, 101.458–462, plus PMO 207.593 and PMO 251.228; 21 specimens (PMO 101.462 includes two crushed partial thecae), all preserved as external moulds.

Type locality and horizon. – Upper Ordovician (Sandbian), Coelosphaeridium Beds of the Furuberget Formation (Owen et al., 1990), northern part of the Oslo Region. The type specimens derive from a loose boulder, but equivalent sediments and equivalent fauna are restricted to the Toten–Brummundalen areas in the northernmost part of the Oslo Region according to Bockelie (1984, p. 29).

Description

Stem. – The stem is composed of circular columnals of at least three generations and not differentiated into proximal and distal parts. About 10 mm remain in PMO 101.140 (Fig. 4A) composed of over 30 columnals. Latera are convex with a rough surface.

Theca. – The theca is oval to inverted pyriform and reaches 23–24 mm high by 15–16 mm wide. It is composed of an aboral cup with a single basal and an upper circlet of five more or less equal lateral plates (Figs. 3 & 4F), plus an adoral vault composed of the ambulacra and interambulacra, separated by the generative circlet of small undifferentiated plates (Figs. 2 & 4C). Ambulacra are biserial and composed of large adambulacral plates each of which bears a single brachiole (Fig. 4B, E). Large specimens have nine brachioles per ambulacrum, which alternate left and right regularly (Figs. 2 & 4B, J). As is common with all diploporites with multiple brachioles per ambulacrum, the first is always to the left looking in the direction of growth (Fig. 4K). The food grooves extend from the mouth along the common sutures between the adambulacral plates, decline in width and extend beyond the last brachiole-bearing adambulacral (Fig. 5). Food grooves on thecal plates and brachioles are covered by biserially-arranged cover plates (Fig. 4C, H) which are continuous with those covering the mouth (Fig. 4G, K). Brachioles are biserial, extend from the facets and may reach at least as long as the theca is high. None is complete, but preserved examples reach 15 mm (Fig. 4H). Cover plates extend along the side branches of the food grooves and up the brachioles.

Interambulacra are typically uniserial, but in some cases additional plates are incorporated at the widest part of the theca (Figs. 2 & 4C)

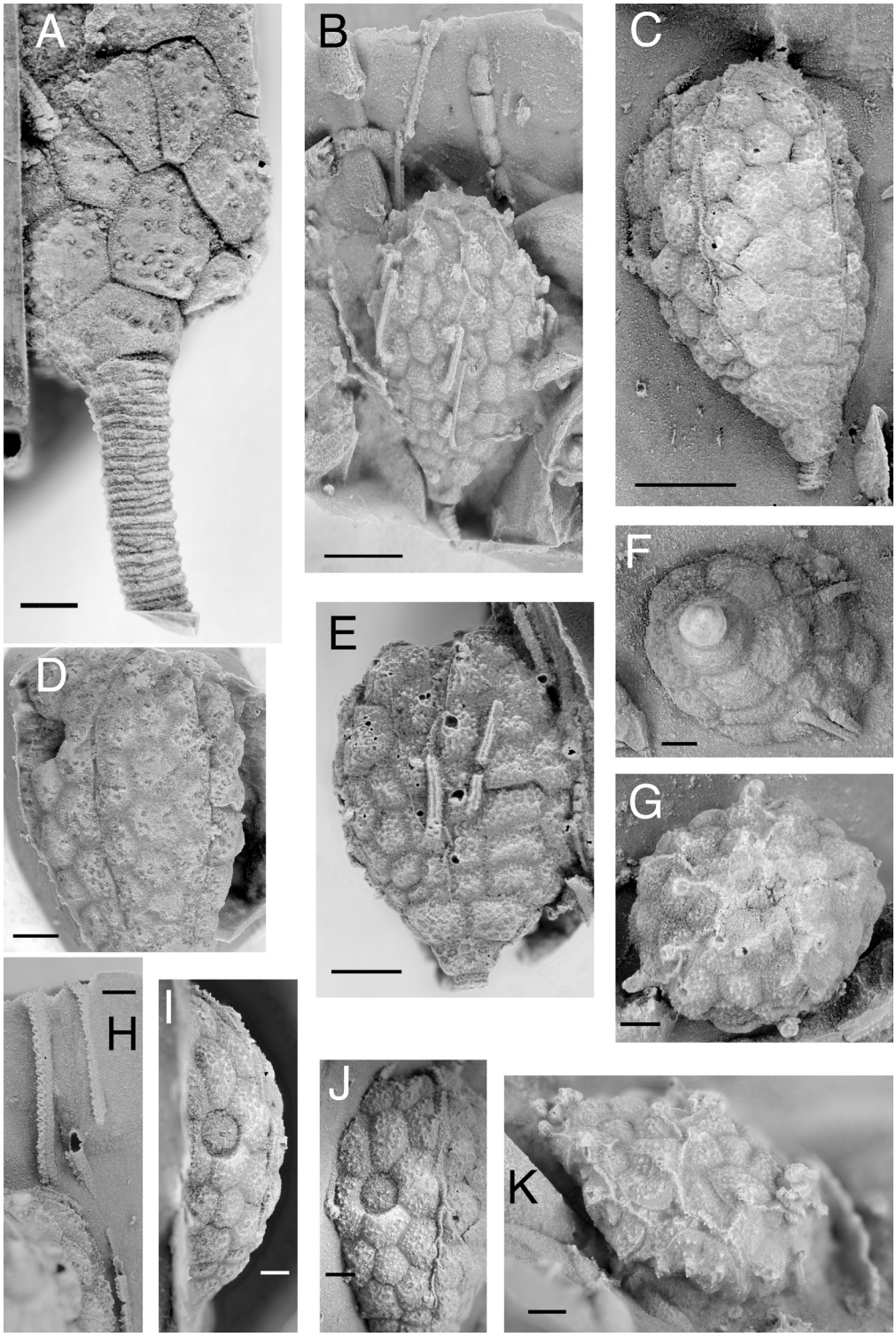

Figure 4. Photographs of latexes of Bockeliecrinites rugatus *(Bockelie, 1984). (A) PMO 101.140 showing the heteromorphic stem and centrodorsal plate with diplopores. (B, K) PMO 101.136 (B) showing brachioles arising alternately along the ambulacra. (K) showing the oral area with cover plates over food grooves and the 2–1–2 arrangement of ambulacra. Tubercles in the CD interambulacrum may represent possible hydropore and gonopore. (C, I, J) PMO 101.132 (C) showing a well-preserved theca with top of the stem and a brachiole attached. The dorsal cup (below) consists of the centrodorsal and circlet of 'lateral' plates; the adoral vault of ambulacra with food grooves which retain cover plates and interambulacra; the two separated by the generative circlet of small undifferentiated plates. (I, J) two views showing the periproct with cover plates in place with adambulacral plates of both adjacent ambulacra contributing to the periproct border (J). Note the rugose ornament. (D) PMO 101.142 a worn partial theca showing food grooves and diplopores without cover plates. Note the curved row of diplopores adjacent to the food groove (centre right). (E) PMO 101.138 showing biserial ambulacra with brachioles alternating and uniserial interambulacra. (F) PMO 101.135 showing an aboral view of the basal cup with the centrodorsal and five 'lateral' plates. (G) PMO 101.130 showing the oral area with multiple cover plates centrally and five ambulacra in a 2–1–2 arrangement and a gonopore in the CD interambalcrum. (H) PMO 101.133 showing a brachiole with cover plates. Scale bars = 2 mm, except Figs. B, C = 5 mm.*

Figure 5. Stereophotographs of Bockeliecrinites rugatus *(Bockelie, 1984) specimen PMO 251.228, showing the main food groove in ambulacrum E covered by small cover plates and extending beyond the terminal brachiole. Scale bar = 2 mm.*

Thecal orifices. – The mouth is at the top of the theca, directly opposite the stem attachment. The oral frame is composed of six peri-oral plates, two in the posterior CD interambulacrum and one each in the other four (Figs. 1B & 4G, K). The A ambulacrum extends anteriorly, with two lateral ambulacra on each side. The lateral ambulacra divide close to the mouth to give a total of five in the characteristic 2–1–2 arrangement (Figs. 1B & 4G, K). Peri-oral plates entirely lack brachiole facets (Figs. 1B & 4K), but bear abundant diplopores.

The anus is a circular orifice a little above mid height in the CD interambulacrum (Fig. 4I, J). It is covered by a simple anal pyramid and adambulacral plates of both the C and D ambulacra contribute to the border (Figs. 2A & 4J), usually adambulacrals C4 and D5.

A possible hydropore occurs across the PO6:PO1 suture and more obvious gonopore across the PO7: Ad1 suture of the D ambulacrum (Figs. 1B & 4G).

Pore structures. – Diplopores occur in all thecal plates that are large enough to include them. This includes the centrodorsal (Fig. 4A, E), other cup plates (the laterals) and all peri-oral, adambulacral and interambulacral plates. Only the smallest undifferentiated plates in the generative circlet lack them. The arrangement on adambulacrals is significant. In the main body of the plates, they are scattered randomly, but two rows of parallel diplopores line the edges of the food grooves, above and below the brachiole facet (Fig. 4D centre right). Diplopores are not always conspicuous in *B. rugatus* because when covered by small cover plates they blend into the surrounding thecal surface (Fig. 6).

Remarks. – The key characters of *Bockeliecrinites* are the aboral cup composed of a single, conical centrodorsal plate above which is a closed circlet of five inter-radial lateral plates. The adambulacral plates bear single brachiole facets, which were not always developed in the same order as the adambulacrals. *Bockeliecrinites* was adapted to life in a distal environment with frequent turbidity current events. The preservation of the specimens shows they were buried alive. Delicate structures such as the brachioles and cover plates of food grooves, mouth, anus and diplopores are all preserved in the available specimens.

Figure 6. Stereophotos of part of Bockeliecrinites rugatus (*Bockelie, 1984) specimen PMO 101.139 unknown ambulacrum, showing covered diplopores between brachioles 3 and 4. Scale bar = 0.5 mm.*

Growth

Specimen PMO 101.458 (Fig. 7) is a juvenile example, with a spherical theca about 5 mm in diameter and was described by Bockelie (1984, p. 30, fig. 17C). The aboral cup is hidden, but remains of ambulacra B, C and D, each of which bears two brachioles or brachiole facets, are visible. The periproct, covered by a simple anal pyramid is present in the CD interambulacrum below two interambulacral plates (I Fig. 7). Adambulacral plates C4 and D3 contribute to the periproct border. Remains of the incomplete second brachiole in ambulacrum D extend to the edge of the latex, at least 8.5 mm. The food groove in ambulacrum C extends beyond the second brachiole facet. During growth the adambulacral plates are added alternately on either side of the main food groove. As the tip of the food groove extends, adjacent undifferentiated plates must have been modified as adambulacral plates by the insertion of a lateral food groove and development of a brachiole, as soon as the plate was large enough. Thus, although the adambulacral plates were developed in sequence along each ambulacrum, it is clear from PMO 101.458, that the brachioles were not formed in the same sequence. The first plate in each ambulacrum is the oral plate to the right of the food groove as viewed in the direction of growth. The next plate to develop was the first adambulacral plate, which is always to the left, so adambulacral plates can be numbered along the ambulacrum from 1. This results in a pattern in which odd numbers are always to the left and the even numbers always on the right (C1–C9 in Fig. 2; 1–4 in Fig. 7 also in the C ambulacrum). If the brachioles were formed in the same order, adambulacral plate 2 should have a lateral food groove and brachiole facet, before adambulacral plate 3. This is clearly not the case in PMO 101.458. In ordinary circumstances one might dismiss this as possibly an aberrant individual. However, *Protocrinites fragum* Eichwald, 1855, is characterised by lacking a brachiole facet on adambulacral plate 2 in any ambulacrum, even in large examples with several facets per ambulacrum (Hecker 1964, pl. 5, fig. 2). *Protocrinites fragum* is also the species that lacks a stem and was free living as an adult (see Eichwald, 1855), and has a theca larger in diameter than height. I think it is a genus distinct from either *Protocrinites* or *Bockeliecrinites.*

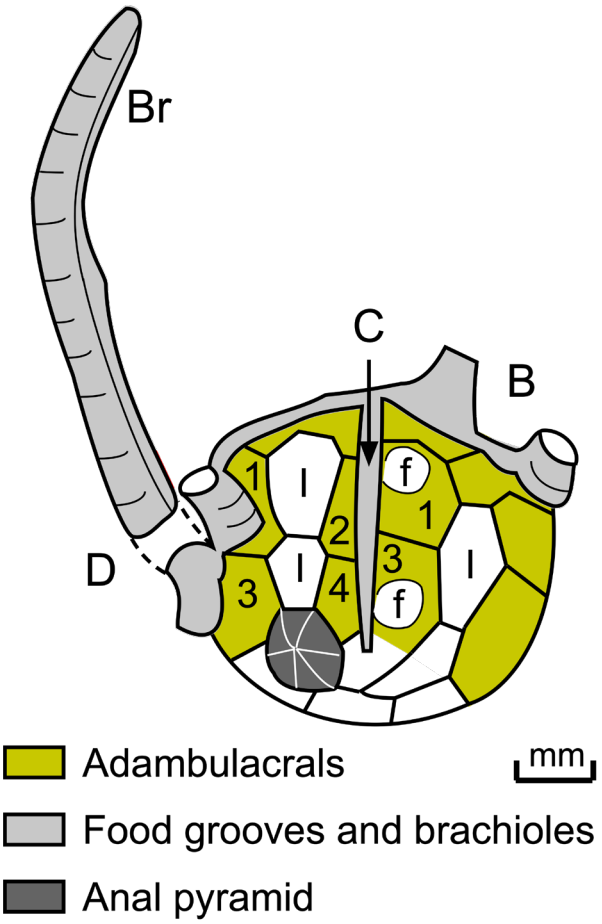

Figure 7. Diagram of thecal plating and ambulacra of PMO 101.458, a juvenile specimen of Bockeliecrinites rugatus *(Bockelie, 1984) 5 mm in diameter showing parts of the B, C and D ambulacra, each with two brachioles (Br) or brachiole facets (f). As viewed in growth direction (down the diagram), both brachioles are on the left of each ambulacrum. Thus, they are developed on adambulacral plates 1 and 3. Adambulacral plate 2 lacks a brachiole facet. This is most clearly seen in ambulacrum C. Note the food groove in ambulacrum C extends beyond the second facet. The ambulacra are separated by interambulacral plates (I); two and the anal pyramid in the CD interambulacrum, probably two in the BC interambulacrum. The lower part of the cup is not seen, so precise interpretation of the aboral plates is uncertain. Redrawn and slightly modified from Bockelie (1984, fig. 17c).*

The extension of the food groove beyond the last adambulacral plate not only means that lateral branches to brachioles were added subterminally, but also enables this modification of the order of development of brachioles as well. Finally, PMO 101.136 (Fig. 4B) has one of largest thecae of all the specimens (about 25 mm high). Ambulacrum A has nine brachioles and no trace of the food groove beyond the last brachiole A9. If this pattern is consistent, it would appear that *B. rugatus* reached a maximum size and added the last brachiole terminally.

Palaeoecology

Many examples of *B. rugatus* preserve parts of the stem, brachioles, ambulacral and diplopore cover plates still in place on or attached to the theca. They all indicate rapid burial (Bockelie, 1984, p. 29). Indeed, it is likely these examples were killed by being entombed in turbidite sediments. One or two examples of small, disc-shaped bryozoan colonies are buried edge-on in the sediment (Fig. 4C bottom right), which is consistent with them being picked up by approaching currents and

becoming embedded in soft sediment when they fell back onto the surface. All examples of *B. rugatus* with brachioles attached to the theca have the brachioles orientated upwards towards the oral surface and extending beyond the theca straight and parallel (Fig. 4B, E, H). The stem extends straight below the theca (Fig. 4A). This not only suggests that the stem, theca and brachioles were orientated by the currents, but also that the stem was attached and held the theca in place in the currents that buried it. Had the stem been free, or had it broken, the rest of the diploporite would have moved with the currents. The first part of the body to impact on the sediment would have been the extended brachioles, which would have been bent, crumpled or broken. It is possible that specimen PMO 101.135 (Fig. 4F) represents such an example.

The disc-shaped bryozoans do not exceed 10 mm in diameter and preserve growth rings on the under surface. This may have been because the soft sediment had very little load-bearing capacity. Equally, it is consistent with the idea that currents strong enough to move the colonies occurred frequently and hence the colonies did not have time to grow larger. This, in turn, would imply that the diploporites with their theca elevated well above the sediment surface survived such currents and were only killed when a significant amount of sediment accompanied a major turbidite event.

Origin of the Protocrinitidae

Bockeliecrinites nov. gen. shares with the epispire-bearing 'eocrinoid' *Rhopalocystis* Ubaghs, 1963 (Fig. 8A), a single 'centrodorsal' plate at the base of the theca (CD in Fig. 8A). Since such plates are rarely present in blastozoans, it is worth comparing the two genera to see if this reflects evolutionary affinity or is merely a case of convergence. *Rhopalocystis* is now known from several species, all from the Tremadocian or Floian of Morocco (Allaire et al., 2017, p. 690, fig. 3). The type species, *R. destombesi* Ubaghs, 1963, is recorded throughout the known stratigraphic range. It is characterised by a stem composed of small, circular, bead-like columnals, which are heteromorphic (alternating thicker and thinner) proximally, but become more uniform distally. Although distal stems are less commonly preserved, it has become accepted that in life the distal stem was not attached, but tapered to a point (Ubaghs, 1963, p. 27, fig. 1). Paul (1968*b*) came to the same conclusion about the distal stem of *Macrocystella* Callaway, 1877, and Kirk (1911) cited numerous similar examples among pelmatozoans generally, so this is not exceptional. The interpretation of the thecal plating has changed several times (Allaire et al., 2017, p. 697) and this process continues. Allaire et al. (2017, p. 697) described the theca as being composed of seven primary circlets of plates; three aboral circlets, including the 'centrodorsal' plate, four infralaterals (IL, Fig. 8A) and six laterals (L, Fig. 8A) surmounted by ten columns of plates, five single radial columns each with four plates (R, Fig. 8A) intercalated between which were multiplated inter-radial areas. Thus, the seven circlets consist of the three lower circlets plus the four superposed radials and supraradials. In practice, the four upper circlets cannot really be recognised as plate circlets even ignoring the difficulties caused by larger examples having small intercalated plates to add to the thecal complexity. If one considers the growth of the theca, and Allaire et al. (2017) provided abundant and excellent evidence for growth changes, then the theca can better be divided into three zones: the lower cup, consisting of the three well-defined plate circlets, the upper cup, which consists of plates added adorally in columns that can easily be divided into five single columns each of four radially-positioned plates (R, Fig. 8A) and five interradial columns each usually of two or three columns, and finally the oral surface or vault consisting of the six interradial oral frame plates (PO1–PO6, Fig. 8B), from which five, mural, biserial ambulacra (A–E, Fig. 8B) radiate giving rise to lateral branches alternately that terminate in brachiole facets (F, Fig. 8B), the first of which branches left as viewed in the direction of growth in all ambulacra.

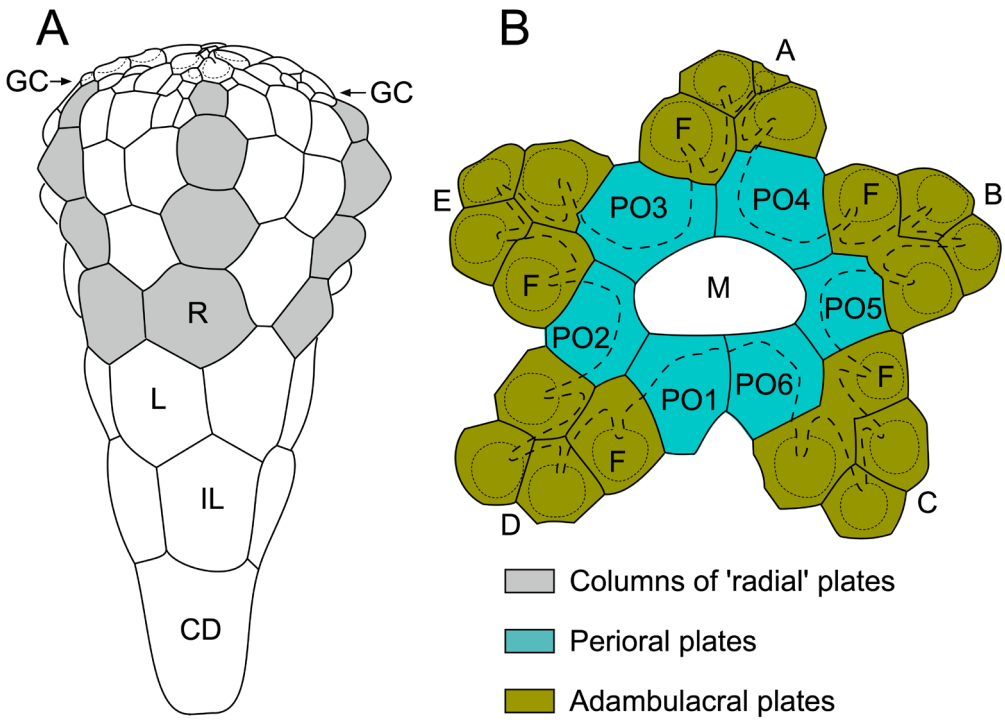

Figure 8. Lateral (A) and oral (B) views of Rhopalocystis destombesi *Ubaghs, 1963. The aboral cup lies below the generative circlet (GC in A) and consists of an aboral centrodorsal plate (CD), above which is a closed circlet of four 'infralateral' plates (IL) alternating with a closed circlet of six 'lateral' plates (L). Above this are five, radial, uniserial columns of 'radial' plates (R) alternating with multiserial columns of inter-radial plates. The columns of radial plates align with the tips of the ambulacra in the vault (above GC in A) and the columns of inter-radial plates fill in the spaces between them. (B) shows the oral surface and ambulacra in the vault. The mouth (M) is surrounded by a closed circlet of six Inter-radial 'perioral' plates (PO1–PO6). The ambulacra (A–E) form part of the body wall (i.e., are mural ambulacra) and are biserial. The food grooves lie along the sutures between the periorals, with lateral branches alternating along the ambulacra and giving rise to brachiole facets, the first of which (F) always lie on the left side of the ambulacra as viewed in growth direction. New adambulacral plates are added at the tips of the ambulacra (see ambulacrum A) in the generative circlet, as are small interambulacral plates. (A) Redrawn and simplified from Ubaghs (1963, p. 28, fig. 2.1), (B) from Ubaghs (1963, p. 33, fig. 7.2).*

Bockeliecrinites gen. nov. has a similar heteromorphic stem with circular columnals. The theca can be divided into three portions: a basal cup consisting of the single centrodorsal (CD, Fig. 3) and a circlet of five plates above (1–5, Fig. 3), then there is the generative circlet (GC, Fig. 2A) where small, new, undifferentiated plates were added, and above this the vault, consisting of the five biserial ambulacra (Fig. 2), alternating with the interambulacral plates. As in all other echinoderms, the ambulacra grew at their tips by the addition of new adambulacral plates (David & Mooi, 1998). Except for the newest one or two, each adambulacral plate bore a lateral branch of the food groove leading to an erect, biserial brachiole. At the top of the theca the pentagonal peristome was formed of six, interradial 'oral' plates (PO1–PO6, Fig. 1B), two in the CD interambulacrum and one each in the other four interambulacra, from which the biserial ambulacra radiated, each with the first brachiole facet to the left (F, Fig. 1B).

Thus, in comparing *Rhopalocystis* and *Bockeliecrinites* gen. nov., the following similarities emerge:

1. Both have a similar, heteromorphic stem composed of bead-like circular columnals.

2. Both have a basal cup to the theca that from bottom up consists of a single 'basal' plate, a second circlet of four (*Rhopalocystis*; Fig. 8B) or five (*Bockeliecrinites*; Fig. 2) 'infralateral' plates, above which is a circlet of six 'lateral' plates in *Rhopalocystis*, which apparently has no equivalent in *Bockeliecrinites* gen. nov.

3. Above this level *Rhopalocystis* has its single columns of 'radial' plates alternating with more complex interradial columns (Fig. 8B), whereas *Bockeliecrinites* gen. nov. has its 'generative circlet' of newly added plates (Fig. 2).

4. Both have an upper vault consisting a relatively large peristome whose frame is composed of six, interradial peri-oral plates two in the CD interambulacrum, one each in the other interambulacra and none of which bears a brachiole facet (Figs. 1B & 8B).

5. In both genera the oral frame plates give rise to five mural, biserial ambulacra, each with the first brachiole to the left, but thereafter alternating regularly, and with each brachiole arising from a single adambulacral plate (Figs. 2 & 8B). In between are less regular interambulacral plates.

6. Both have the periproct in the CD interambulacrum close to the mouth and separated from it by a small number of thecal plates.

7. Small cover plates are present over the epispires of *Rhopalocystis* and the diplopores of *Bockeliecrinites*. Again, blastozoans with cover plates over their epispires or diplopores are rare. One such genus is *Protocrinites*.

The only other blastozoan genera sharing as many common features with *Bockeliecrinites* as *Rhopalocystis* are also protocrinitids.

The prime differences are:

1. *Rhopalocystis* has sutural epispires, whereas *Bockeliecrinites* has fully-developed diplopores.

2. Allaire et al. (2017) record neither gonopore nor hydropore in *Rhopalocystis*, whereas a slit-like hydropore occurs across the O6:O7 suture and a circular gonopore in a tubercle across the O7:Ad1 suture in *Bockeliecrinites.*

3. The aboral cup occupies the majority of the theca in *Rhopalocystis*. The ambulacra have four or fewer brachioles and are confined to a gently curved oral surface. In *Bockeliecrinites* the ambulacral surface occupies the majority of the cup and each ambulacrum may have up to eleven adambulacral plates.

These differences are partly related to mode of life and partly to evolution. Paul & Toom (2021) have shown how the diplopores of *Glyptosphaerites* probably evolved from sutural pores identical to epispires. Both epispires and diplopores would have facilitated respiratory gas exchange; the latter are more efficient because they maintain a one-way circulation which kept the oxygenated body fluids separate from those rich in CO2 (Paul 1968c, p. 710; Paul & Toom 2021, p. 230). Equally, expanding the relative size of the ambulacral surface would have increased the feeding capacity of *Bockeliecrinites* relative to that of *Rhopalocystis.*

Paul (1988) traced the sphaeronitoid diploporites back to the Middle Cambrian 'eocrinoid' *Lichenoides,* Barrande, 1846, because it had a mouth frame composed of at least five, radial orals (circumorals of Paul, 1971) and 'naked' epithecal food grooves that spread over the theca onto the orals and thecal plates below the orals, but entirely lacked any trace of both flooring and cover plates. In sphaeronitoids, where the oral cover plates are preserved, they consist of six 'palatal' plates (Paul, 1971, p. 6, fig. 1), except for *Glyptosphaerites*, where there appear to have been eleven (Paul & Toom, 2021, p. 227, fig. 5). Otherwise, sphaeronitoid food grooves are also 'naked' and lack floor or cover plates. *Oretanocalix* Gutiérrez-Marco, 2000, the only aristocystitid genus with all five ambulacra developed, has six primary oral cover plates (Paul & Gutiérrez-Marco 2022, p. 166, fig. 8), which are most

likely homologous with sphaeronitoid palatals. Like all aristocystitids where the details of the oral frame are known, *Oretanocalix* has a mouth frame composed of eight plates, including five, radial orals (circumorals). Thus, there are reasons for believing that the diploporite families Aristocystitidae, Holocystitidae and Sphaeronitidae are related and form a monophyletic taxon, which Paul & Toom (2021) called the Anambulacralia.

Jell & Sprinkle (2021) have reconstructed the ambulacra of *Periodionites* Whitehouse, 1941, *Cymbionites* Whitehouse, 1941, and *Thorntonites* Jell & Sprinkle, 2021, showing a sequence of ambulacral structures by which the regular ambulacralian ambulacra could have been derived from the original anambulacralian structure of *Lichenoides*. The isolated plates of the Australian genera also have 'naked' food grooves that lack any trace of floor and cover plates. They merely introduce a progressively more organised ambulacral structure that could easily result in the regular, biserial ambulacra of *Rhopalocystis*, and ultimately the Protocrinitidae and other ambulacralian diploporites.

Conclusions

All the available specimens of *'Protocrinites' rugatus* Bockelie, 1984, have been examined. This has resulted in the conclusion that it differs significantly from *Protocrinites oviformis* Eichwald, 1840, type species of *Protocrinites s.s*. and it has been made the type species of a new genus *Bockeliecrinites*. The key characters of *Bockeliecrinites* are:

1. an aboral cup composed of a single, conical centrodorsal plate above which is a closed circlet of five, inter-radial, lateral plates, and

2. adambulacral plates bearing single brachiole facets, which were not always developed in the same order as the adambulacrals themselves.

In contrast, all species of *Protocrinites* have an aboral cup composed of two circlets of at least four plates each. *Bockeliecrinites* was adapted to life in a distal environment with frequent turbidity current events. The preservation of the specimens shows they were buried alive. Delicate structures such as the brachioles and cover plates of food grooves, mouth, anus and diplopores are all preserved in some of the available specimens. *Bockeliecrinites* was probably derived from the 'eocrinoid' *Rhopalocystis* Ubaghs, 1963, and the lineage can probably be traced back to the Cambrian genera *Peridionites* Whitehouse, 1941 and *Cymbionites* Whitehouse, 1941.

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