MACROCYSTELLA CALLAWAY, THE EARLIEST GLYPTOCYSTITID CYSTOID

by C. R. C. PAUL

ABSTRACT. *Macrocystella mariae* Callaway 1877, type species of *Macrocystella*, has a stem which is divisible into proximal and distal portions; a theca composed of 4 basal, 5 infra-lateral, 5 lateral, 6 radial, and some oral plates; a large periproct surrounded by 5 thecal plates; biserial unbranched brachioles grouped into 5 ambulacra and arising from the margins of the flattened oral surface. In all these respects it agrees with *Mimocystites bohemicus* Barrande 1887, type species of *Mimocystites* which becomes a subjective junior synonym of *Macrocystella*. *Macrocystella azaisi* (Thoral) has 7 orals and thus *Macrocystella* differs from the rhombiferan *Cheirocrinus* Eichwald only in the absence of pectinirhombs. The Macrocystellidae are therefore transferred to the rhombiferan superfamily Glyptocystitida.

Macrocystella evolved into *Cheirocrinus* by the acquisition of pectinirhombs. In *Macrocystella* respiration probably took place through all the thecal plates which are very thin. In *Cheirocrinus* respiration was restricted to the pectinirhombs thus allowing much thicker and stronger thecal plates to develop.

Macrocystella led a freely vagrant existence and may have had internal buoyancy devices. The stem did not provide permanent fixture and may have been used as a organ of locomotion in conjunction with the brachioles.

THE cystoidea, as currently defined (Kesling 1963) is probably an artificial group. The main character which is used to unite the cystoids as a class is the possession of pore-structures (rhombs and dipores) developed in the thecal plates. However similar pore-structures are found in at least some representatives of other Palaeozoic echinoderm classes (blastoids, crinoids, paracrinoids, eocrinoids, for example) and one genus of rhombiferan cystoids entirely lacks pore-structures. This paper deals with another genus, *Macrocystella* Callaway 1877, which lacks true pore-structures but which is thought to be the oldest known representative of the Glyptocystitida, one of the three major rhombiferan superfamilies. *Macrocystella* has a complex taxonomic history (see below) and has been variously regarded as an eocrinoid, a rhombiferan cystoid or as a link between these classes. Close comparison indicates that *Macrocystella* is identical to the rhombiferan genus *Cheirocrinus* Eichwald in all details except the possession of pectinirhombs. Hence *Macrocystella* is regarded as a rhombiferan. It is believed that the absence of pectinirhombs in *Macrocystella* is a primitive character. Many Ordovician pelmatozoans independently developed thecal or calycinal pore structures, apparently in response to respiratory needs. To group all such echinoderms together obscures their true relationships. It is essential to consider other characters in addition to the possession of pore-structures, especially when the latter are so variable.

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PREVIOUS RESEARCH

Macrocystella (type species *M. mariae* Callaway 1877) was first described from the Lower Ordovician (Tremadoc) Shineton Shales of Shropshire. Barrande (1887, p. 163) described a closely similar genus, *Mimocystites*, for a single species, *M. bohemicus* Barrande. Jaekel (1899, p. 171) suggested that these two genera were synonymous but used the name *Mimocystites*. Jaekel regarded *Mimocystites* as the progenitor of the cystoids and most closely related to the rhombiferan *Cheirocrinus* Eichwald. Bather (1899, p. 920) proposed the family Macrocystellidae which he assigned to the Rhombifera. He did not elucidate the composition of the Macrocystellidae but later (1900, p. 56) included *Macrocystella*, *Mimocystites* and *Lichenoides* Barrande 1887. Although Bather thought *Macrocystella* and *Mimocystites* hardly differed he used both names. Bather's reconstruction of *Macrocystella mariae* (1900, p. 95, fig. 18) was inaccurate in depicting branched arms and considerably influenced subsequent opinions on the affinities of *Macrocystella*.

Jaekel (1918, p. 27) retained both *Macrocystella* and *Mimocystites* (possibly because of Bather's reconstruction of the former) and placed them, with his new genus *Polyptychella*, in the Macrocystellidae. A separate family was proposed for *Lichenoides*. The Macrocystellidae and Lichenoidae were assigned respectively to the orders Plicata and Reducta of the Eocrinoidea. Thoral (1935, p. 113) considered *Macrocystella* and *Mimocystites* to be distinct but based his opinion of the former on the original description. Bassler and Moodey (1943) reverted to Bather's classification, included *Lichenoides* in the Macrocystellidae and that family in the Rhombifera. Cuénot (1948) also assigned *Macrocystella* to the Rhombifera and later (1953) regarded *Mimocystites* as a junior synonym. Moore (1954, p. 127, fig. 2*a*) published an inaccurate plate diagram of *Macrocystella* which depicts 5 basals, 5 radials, 5 orals, and a minute periproct. Moore regarded *Macrocystella* as an eocrinoid. Sdzuy (1955) accepted *Macrocystella* and *Mimocystites* as separate genera only if published reconstructions were accurate. He based his opinion of *Macrocystella* on Bather's (1900) and Moore's (1954) work, the accuracy of which he doubted. More recently Prokop (1966) and Ubaghs (1968) have suggested that *Macrocystella* and *Mimocystites* are synonymous. Ubaghs regards *Macrocystella* as most closely related to *Cheirocrinus*.

Quite apart from the synonymy of *Macrocystella* and *Mimocystites* another problem arises as to the status of *Cystidea* Barrande 1868. Barrande (1867, p. 179) published two nomina nuda, *Cystidea sedgwicki* and *C. bohemicus*. Later he introduced *C. bavarica* (Barrande 1868, p. 106) this time accompanied by a description and figures. Barrande made it quite clear in both publications that he intended *Cystidea* as a collective group name not a formal generic name and he so used it again (1887), erecting several more species. *Cystidea bavarica* Barrande is a valid binomen and could be construed to be type species of the genus *Cystidea* Barrande by monotypy. Pompeckj (1896, p. 90) and Sdzuy (1955, p. 170) have attributed *Cystidea bavarica* to *Macrocystella*. There is no doubt they are correct in this action and therefore *Cystidea* Barrande 1868, if accepted as an available generic name, should take precedence over both *Macrocystella* and *Mimocystites*. Such action is not in the interests of nomenclatorial stability. No author has accepted *Cystidea* as a valid generic name whereas *Macrocystella* has been widely used and is figured and described in standard text-books in English, French, and German. Application has therefore been made to the International Commission on Zoological Nomenclature for the suppression of *Cystidea* Barrande 1868 under the Plenary Powers (Paul 1967*b*). In anticipation of a favourable decision, *Macrocystella* is used throughout this work.

The systematics and composition of the Macrocystellidae and the suggested synonymy between *Macrocystella* and *Mimocystites* can only be settled after a revised account of the morphology of *Macrocystella mariae* has been given. Latex impressions of the original specimens of *M. mariae* have been re-examined and additional material studied. This has been compared with Barrande's (1887) and Jaekel's (1899) descriptions and figures of *Mimocystites bohemicus*, with latex impressions of some of Barrande's original material and additional material of *M. bohemicus* in the Schary Collection, Museum of Comparative Zoology, Harvard. Latex impressions of *M. azaisi* (Thoral) have added further information.

Macrocystella and *Mimocystites* are identical and quite distinct from *Lichenoides* to judge from Ubagh's (1953) account of *L. priscus* Barrande. *Polyptychella* Jaekel was founded on isolated plates and its systematic position cannot be settled without further information. The Macrocystellidae thus contains the single genus *Macrocystella*. As previously stated the Macrocystellidae is assigned to the Rhombifera (Glyptocystitida).

SYSTEMATIC PALAEONTOLOGY

Superfamily GLYPTOCYSTITIDA Bather 1899

Diagnosis. A superfamily of Rhombifera with well-developed stem divided into proximal and distal portions; theca composed of 4 basals, 5 infra-laterals, 5 laterals, 4–6 radials, and 7 orals; with pectinirhombs (when pore structures are developed).

All Glyptocystitida are characterized by a theca composed of 25–7 thecal plates arranged in five circlets termed basal, infra-lateral, lateral, radial, and oral. All but two genera—*Macrocystella* and *Amecystis* Ulrich and Kirk—have pectinirhombs. These characters distinguish glyptocystitids from members of the other two major rhombiferan superfamilies, the Hemicosmitida and Caryocystitida. The former have thecal plates arranged in three or four circlets and slightly different rhombs. The latter have a large variable number of plates, some of which may be added during growth, and a completely different type of rhomb (Paul 1968).

Family MACROCYSTELLIDAE Bather 1899 emend. Jaekel 1918

Diagnosis. A family of Glyptocystitida without pectinirhombs; with cylindrical theca having 6 radials; large periproct surrounded by 5 thecal plates and covered with a flexible plated integument; brachioles confined to oral surface, grouped into 5 ambulacra.

Genus MACROCYSTELLA Callaway 1877

1868 *Cystidea* Barrande, p. 106.
1877 *Macrocystella* Callaway, p. 669, pl. 24, fig. 13.

1880 *Macrocystella* Callaway; Zittel, p. 420.
1887 *Mimocystites* Barrande, p. 163, pl. 28 (1), figs. 1–20.
1891 *Macrocystella* Callaway; Carpenter, p. 13.
1891 *Mimocystis* [*sic*] Barrande; Carpenter, p. 13.
1896 *Mimocystis* [*sic*] Barrande; Haeckel, p. 149.
1899 *Macrocystella* Callaway; Jaekel, p. 171.
1899 *Mimocystites* Barrande; Jaekel, p. 172, fig. 33.
1900 *Macrocystella* Callaway; Bather, p. 56, fig. 18.
1900 *Mimocystis* [*sic*] Barrande; Bather, p. 56.
1913 *Macrocystella* Callaway; Springer, p. 157.
1918 *Macrocystella* Callaway; Jaekel, p. 27.
1918 *Mimocystites* Barrande; Jaekel, p. 27.
1935 *Mimocystites* Barrande; Thoral, p. 110, 113.
1943 *Macrocystella* Callaway; Bassler and Moodey, p. 6.
1943 *Mimocystites* Barrande; Bassler and Moodey, p. 6.
1948 *Macrocystella* Callaway; Regnéll, p. 11.
1948 *Macrocystella* Callaway; Cuénot, p. 18, fig. 17.
1953 *Macrocystella* Callaway; Cuénot, p. 619.
1953 *Mimocystites* Barrande; Choubert, Termier, and Termier, p. 137.
1954 *Macrocystella* Callaway; Moore, p. 127, fig. 2*a*.
1954 *Mimocystites* Barrande; Termier and Termier, p. 92, figs. *a–e*.
1955 *Macrocystella* Callaway; Sdzuy, p. 269.
1966 *Macrocystella* Callaway; Prokop, p. 820.

non *Cystidea* Barrande 1867 (nomen nudum) nec Barrande 1887 nec Haeckel 1896 (indeterminate echinoderm fragments).

Diagnosis. As for family.

Regional distribution and stratigraphic range. Macrocystella is recorded from the Tremadoc of England and Wales (*M. mariae* Callaway), Bavaria (*M. bavarica* (Barrande) 1868), Bohemia (*M. bohemicus* Barrande 1887), and France (*M. azaisi* (Thoral) 1935). *Macrocystella* is also recorded from Greenland, the South American Cordillera and Korea (for detailed references see Regnéll, 1948, pp. 11–12). Choubert, Termier, and Termier record *Macrocystella* from the Llandeilo of Morocco. Available specimens confirm the genus from the Llandeilo of Pu-piao, Northern Shan States, Burma, (SM), from the Tremadoc of Mexico (USNM) and possibly from the Caradoc of Corwen, Wales, and Girvan, Scotland (BMNH). *M. pachecoi* Meléndez (1944) from the Ashgill of Aragon, Spain is probably a *Heliocrinites*. *Macrocystella* thus ranges from the Tremadoc to the Llandeilo and possibly Caradoc (Lower–Middle Ordovician).

Macrocystella mariae Callaway 1877

Plate 111, figs. 1, 3–6; Plate 112, figs. 1–3, 5–10; Plate 113, fig. 2

1877 *Macrocystella mariae* Callaway, p. 670, pl. 24, fig. 13.
1896 *Macrocystella mariae* Callaway; Haeckel, p. 149, pl. 4, fig. 30.
1900 *Macrocystella mariae* Callaway; Bather, p. 56, fig. 18.
1905 *Macrocystella mariae* Callaway; Fearnsides, p. 617.
1911 *Macrocystella mariae* Callaway; Kirk p. 16, pl. 2, fig. 17.
1913 *Macrocystella mariae* Callaway; Springer, p. 157, fig. 249.
1927 *Macrocystella mariae* Callaway; Stubblefield and Bulman, pp. 111, 118.
1943 *Macrocystella mariae* Callaway; Bassler and Moodey, pp. 27, 175.
1952 *Macrocystella mariae* Callaway; Termier and Termier, p. 363, fig. 9.
1953 *Macrocystella mariae* Callaway; Cuénot, p. 618, fig. 15.
1955 *Macrocystella mariae* Callaway; Sdzuy, p. 270, pl. 1, fig. 14.
1964 *Macrocystella mariae* Callaway; Castell, p. 58, pl. 3, fig. 6.

Diagnosis. A species of *Macrocystella* of small size; with 10–15 brachioles, triangular in section; circular outer proximal columnals with thin, blade-like external flanges.

Type. BU 409 (Pl. 113, fig. 2) is selected as lectotype. It is possibly the original of Callaway 1877, pl. 24, fig. 13 and is from the Shineton Shales of Shineton, Shropshire. Parts of other specimens on this slab are accepted as paralectotypes.

Horizon and locality. Stubblefield and Bulman (1927) record *M. mariae* from the *Clonograptus tenellus* and *Shumardia pusilla* zones (Middle and Upper Tremadoc respectively) of the Wrekin. *M. mariae* is also recorded from the *Shumardia pusilla* zone of Arenig (Fearnsides, 1905, p. 617) and *Macrocystella* sp. from the same zone near Portmadoc, Caernarvonshire (Fearnsides 1910, pp. 161–2).

Material. Crushed remains of four more or less complete thecae, one complete stem and many isolated thecal plates and fragments.

Description. A. Stem

The stem has a proximal and a distal portion. One complete proximal portion (Pl. 112, fig. 8) has 20 outer proximals each with a blade-like unornamented external flange. This crushed portion tapers from 5 mm. adorally to 2 mm. in approximately 15 mm. At the junction with the distal stem small distal columnals appear between the flanged columnals. Throughout the preserved portion of the distal stem, flanged and unflanged columnals alternate but this alternation becomes less obvious distally.

The distal portion of the stem (Pl. 111, fig. 1) tapers gradually from 1 mm. proximally to 0·5 mm. at the tip. It is about 35 mm. long. The topmost distal columnal is a thin annulus; the terminal distals are cylindrical and about three times as high as wide. There is no alternation of flanged and unflanged distals in this stem. Preserved proximal stems are straight or quite strongly curved. Curved distal stems are also preserved but there is no evidence to support Bather's (1900) interpretation of the distal stem with a distinct distal coil.

Counterparts of isolated columnals indicate the mode of construction and articulation of the stem. Both proximal and distal portions are composed of two types of columnals. Outer proximals (text-figs. 1*a*–*b*) are annular. Each has a smooth, sharp-edged outer flange and a narrow inner flange (text-fig. 2, Pl. 112, fig. 7). Outer proximals alternate with inner proximals and the latter abut against the inner flanges of the former (text-fig. 2). The inner wall of each outer proximal has two sockets set opposite each other on both the upper and lower surfaces. The inner flanges are thickened adjacent to these sockets to form fulcra (text-fig. 2). If the sockets on one surface are orientated N.–S., those on the opposite surface of the same columnal lie NW.–SE. (text-figs. 1*a*–*b*). Both upper and lower surfaces of the inner proximals are flattened to form facets,

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EXPLANATION OF PLATE 111

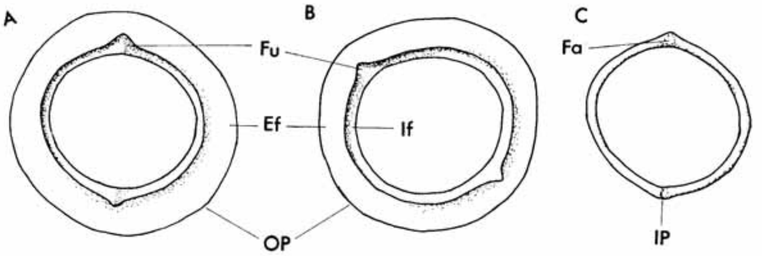
Stereophotos of *Macrocystella mariae* Callaway and *M. azaisi* (Thoral)

Figs. 1, 3–6. *M. mariae* Callaway. 1. Complete stem showing proximal and distal portions. BMNH E29113. 3. Left lateral view of crushed theca. BMNH E29110a. 4. Right lateral view of same theca. BMNH E29109a. 5. Anterior lateral view of another crushed theca. BMNH E29109b. 6. Posterior view of crushed theca to show outline of periproct and small periproctal plates. BMNH E29113.

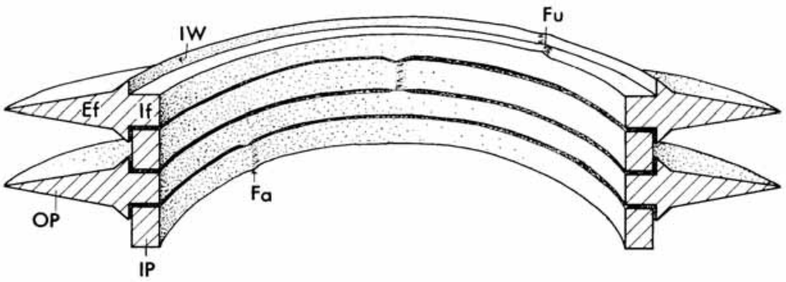
Fig. 2. *M. azaisi* (Thoral). Proximal and part of distal stem to show ornament of flanges on outer proximals. BMNH E23697.

All figures of latex impressions whitened with ammonium chloride sublimate. All × 2.

at the same two opposite points (text-figs. 1*c*, 2). The outer margin of an inner proximal protrudes at these points and the protrusions key into the sockets in the inner wall of the outer proximals above and below (text-fig. 2). The fulcra on the outer proximals and the facets on the inner proximals articulate and the axis of articulation changes by approximately 45° with each outer proximal. This results in a right-handed spiral arrangement of articulation facets in *M. azaisi* and presumably in other *Macrocystella*.



TEXT-FIG. 1. Proximal stem columnals of *Macrocystella mariae* Callaway. *a*, *b*. Opposite sides of one outer proximal columnal (OP) in the same orientation to show different orientations of fulcra (Fu). *c*. Inner proximal columnal (IP). Ef, external flange; Fa, facet; If, internal flange.



TEXT-FIG. 2. Diagrammatic reconstruction of part of proximal stem of *Macrocystella mariae* Callaway to show arrangement of outer (OP) and inner (IP) columnals and spiral arrangement of facets (Fa) and fulcra (Fu). Ef, external flange; If, internal flange; IW, inner wall of outer proximal columnal. This has been drawn as a left-handed spiral although *M. azaisi* is known to show a right-handed spiral.

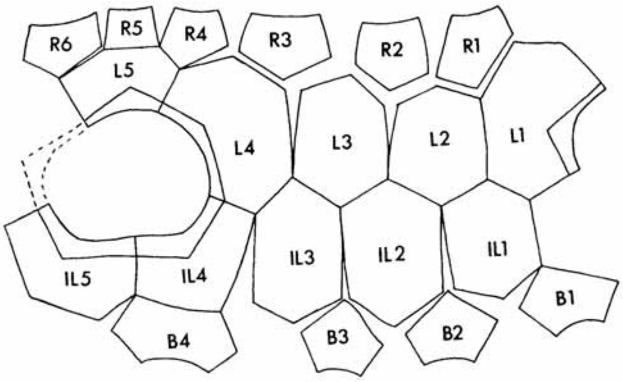
Each inner proximal is keyed into the sockets of the outer proximals above and below. Thus although highly flexible, the stem was quite resistant to rotation about its axis. Both inner and outer proximals are annular and the proximal stem has a wide lumen. Flexing of the proximal stem was probably achieved by muscles housed in this lumen. The mechanical keying of the columnals prevented rotation which would have sheared such muscles.

Larger (sometimes flanged) and smaller (unflanged) distals alternate in the distal stem but this becomes less apparent distally. The most proximal distals, which appear to be newly formed, are annular but most distals are cylindrical. All distals have narrow lumina and the articulating surfaces are smooth (Pl. 112, fig. 3).

The nature of the outer proximals may prove to be a useful specific character. In *M. mariae* the outer proximals are approximately circular with thin, blade-like outer flanges (Pl. 111, fig. 1, Pl. 112, fig. 7). In *M. bavarica* the outer flanges are also thin and sharp-edged but are produced into ten angles or incipient spines (Sdzuy, 1955, pl. 1, figs. 8–10, text-fig. 1*h*). In *M. azaisi* the outline is circular but the flanges are thicker and have fine irregular granules or spines encircling them (Pl. 111, fig. 2, Pl. 113, figs. 1, 8). The outer flanges of *M.* sp. nov. from Mexico have four rounded lobes arranged in two pairs.

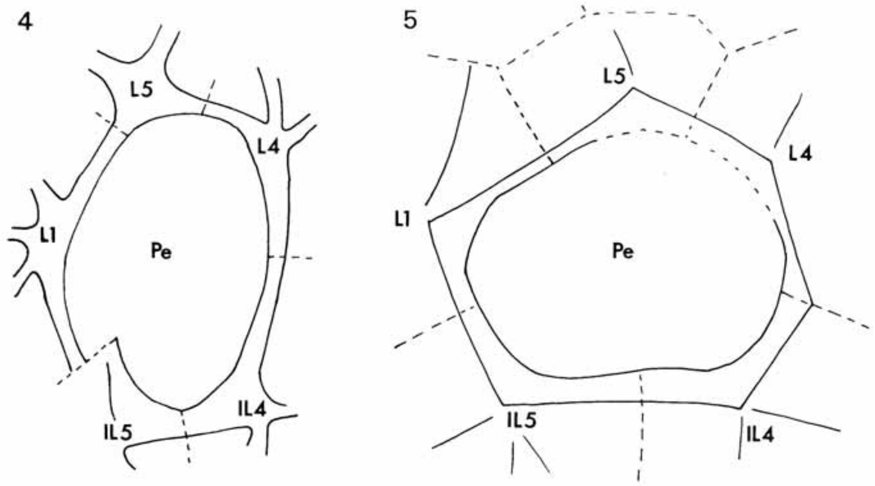
B. Theca

All known thecae are crushed and it is impossible to describe all thecal plates from one specimen. BMNH E29109–10 are counterparts which show two crushed thecae in different orientations. There is another theca which shows details of the periproct. A composite plate arrangement and a reconstruction based on these specimens are depicted in text-figs. 3 and 15. The theca was composed of five circlets of plates, four of which can be seen in *M. mariae*. The subvective system was confined to the oral surface from the margins of which the brachioles arose in five groups.



TEXT-FIG. 3. Diagrammatic reconstruction of plate arrangement of *Macrocystella mariae* Callaway. Based on BMNH E29109a–b, E29110a–b, and E29113. B1–B4 basals, IL1–IL5 infra-laterals, L1–L5 laterals, R1–R6 radials.

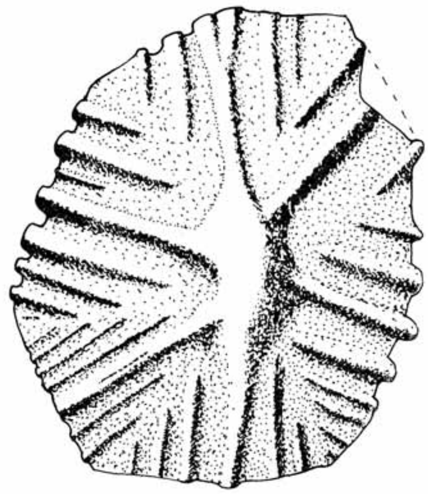
Some details of text-fig. 3 are restored but all plates shown existed. The four basals (BB) unite aborally to form an invagination around the stem. One basal (presumably B4) was hexagonal (Pl. 112, fig. 2). The infra-laterals (ILL) form a closed circlet; IL4 and IL5 contribute to the periproct border. IL1, IL2, and IL3 are roughly hexagonal. The five laterals (LL) apparently form a closed circlet; L1, L4, and L5 contribute to the periproct border. L5 is distinctly smaller than the other laterals and has a radial (R5) directly adoral to it. One pair of counterparts (Pl. 111, figs. 3, 4) seem to have three hexagonal laterals which means either there were six laterals in this specimen or only L1 and L5 contributed to the periproct border. Unfortunately the relevant portion of this theca is crushed and this appearance may be misleading. The six radials (RR) form a closed circlet; one is directly adoral to L5. There are seven orals (OO) in *M. azaisi*.



TEXT-FIGS. 4–5. Camera lucida drawings of the periproct (Pe) of *Macrocystella mariae* Callaway. 4. BMNH E29110b cf. Pl. 2, fig. 9. 5. BMNH E29113 cf. Plate 1, fig. 6. IL4–IL5 infra-laterals, L1, L4, L5 laterals.

The mouth, gonopore, and hydropore have not been detected in *M. mariae* but were all on the oral surface in *M. azaisi* (text-figs. 11*a*, *b*). Critical details of the periproct show in BMNH E29110b, and more clearly, in BMNH E29113 (text-figs. 4, 5). There are five plates around the periproct which is large. The periproct was covered by a thin, flexible, plated integument in life. Some small periproctal plates are preserved (Pl. 111, fig. 6) but the position of the anal pyramid in unknown.

The outlines of the individual thecal plates vary with their positions in the theca. Periproct border plates can be recognized easily, as can basals and radials. The remaining five laterals and infra-laterals are difficult to distinguish from each other. All plates have raised umbones from which ridges radiate to the middles of the sides, connecting centres of adjacent plates (text-fig. 6). Auxiliary ridges are developed parallel to the primary ridges to form 'rhombs'. These 'rhombs' are not true rhombs as they are composed of folds in the thecal plates. There is no development of thin-walled thecal canals. The external ridges of *Macrocystella* are formed by the folds in the plates and are not solid strengthening struts such as occur in *Cheirocrinus*. The thecal plates of *M. mariae* are approximately 0·1 mm. thick.



TEXT-FIG. 6. Isolated thecal plate of *Macrocystella mariae* Callaway to show folds. BMNH E29119.

C. Subvective system

The exothecal portion of the subvective system consists entirely of brachioles. These are long, slender, biserial, unbranched structures. The most complete brachioles (Pl. 112, fig. 10) have approximately 120 brachiolar plates and are slightly longer than the thecal height (up to 16 mm.). The brachioles have a triangular cross-section with sides twice the width of the adoral surface (text-fig. 7). The food groove ran down the centre of the adoral surface and was covered by lappets in life. The lappets are between one and a half times and twice as numerous as the brachiolars and apparently were flexible. Some have been preserved covering the food groove; others in an 'open' position (Pl. 112, fig. 10). The lappets alternate and each one imbricates over its more distal neighbour (text-fig. 8).

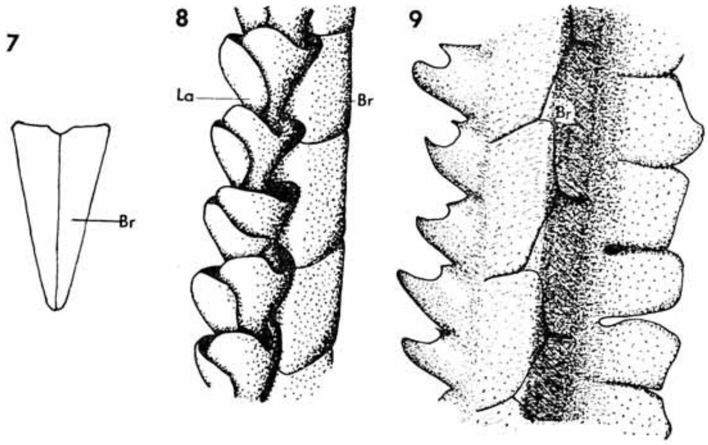
EXPLANATION OF PLATE 112

Figs. 1–3, 5–10. *M. mariae* Callaway. 1. Internal and external views of two isolated thecal plates. The internal view (above) shows the folds in the plates. The other plate was one of five bordering the periproct (probably L1). BMNH E29112, × 5. 2. External view of B4 and an isolated distal columnal. BMNH E29112, × 5. 3. Three isolated thecal plates. All originally bordered the periproct. BMNH E29112, × 5. 5. Internal mould of isolated thecal plate BMNH E29119, × 3. 6. Inner proximal columnal within outer proximal columnal. BMNH E29112, × 2. 7. Outer proximal columnal showing inner flange and fulcra. BMNH E7574, × 1·5. 8. Crushed stem and theca. Note the larger distals are flanged. BMNH E7574, × 1·5. 9. Stereophotos of posterior lateral view of crushed theca showing periproct. Counterpart to Plate 1, fig. 5. BMNH E29110b, × 2. 10. Detail of brachioles to show lateral, ab- and adoral views. BMNH E29109, × 3.

Fig. 4. *M. azaisi* (Thoral). Lateral view of theca and stem. BMNH E23697, × 2.

All except Fig. 5 latex impressions, all whitened with ammonium chloride sublimate.

They coalesce towards the margins of the brachiole to form a continuous narrow band (text-fig. 9). The free portions were able to curl in on themselves. This curling in is not preservational and the lappets may have been only partially calcified in life.



TEXT-FIGS. 7–9. Brachioles of *Macrocystella mariae* Callaway. 7. Diagrammatic section through brachiole without lappets. 8. Camera lucida drawing of portion of brachiole with lappets (La) closed over food groove. Note that the lappets alternate and imbricate. 9. Camera lucida drawing of aboral view of brachiole with lappets in 'open' position. Br brachiolar plate. Text-figs. 8–9 based on BMNH E29113.

No more than three brachioles arise in any one ambulacrum and there were presumably 10–15 brachioles in all. There is no evidence to support Bather's (1900, fig. 18) reconstruction of branched brachioles. BMNH E29110a shows three brachioles in one radius (Pl. 111, fig. 3): all three are separate entities from their origin at the margin of the theca.

Macrocystella mariae Callaway is characterized by the following: 1. A stem which is divisible into two portions: a short, rapidly tapering, highly flexible, proximal portion composed of two types of annular columnals with a wide lumen; and a long distal portion composed of cylindrical columnals with a narrow lumen.

2. A theca with plate formula 4BB, 5ILL, 5LL, 6RR, ?OO.

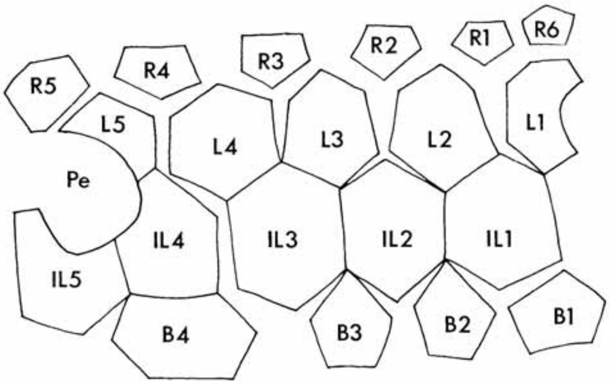
3. A large periproct surrounded by five thecal plates and covered with a flexible plated integument.

4. Biserial, unbranched brachioles which arise from the margins of the flat oral surface and are grouped into five ambulacra.

COMPARISON WITH *MIMOCYSTITES* BARRANDE

Mimocystites bohemicus Barrande has a subvective system which is confined to the flat oral surface and consists of about twenty brachioles grouped into five ambulacra.

Three brachioles were present in one radius of an available specimen (UC latex impression of original of Barrande 1887, pl. 28 (I), fig. 14). The theca is composed of 4BB, 5ILL, 5LL, 6RR, and some OO. Jaekel's analysis of the arrangement of thecal plates (1899, p. 201, fig. 36) is reproduced here in a slightly modified form (text-fig. 10). This interpretation differs slightly from that of *Macrocystella mariae*. Only two laterals (L1 and L5) contribute to the periproct border and L1 has a straight upper border with R6 directly adoral to it. This is an unexpected arrangement. Two specimens in the Schary collection (MCZ) apparently show the arrangement figured for *Macrocystella mariae*. However one specimen of *M. mariae* (Counterparts BMNH E29109a and 29110a) has apparently three hexagonal laterals as shown in Jaekel's figure of *Mimocystites bohemicus*. It seems possible that the plate arrangement varied slightly in different specimens. *Mimocystites azaisi* Thoral has a plate arrangement identical to that in *Macrocystella mariae*. Both the present and Jaekel's interpretations agree in most respects, particularly in the five plates around the periproct.



TEXT-FIG. 10. Jaekel's (1899) interpretation of the plate arrangement of *Mimocystites bohemicus* Barrande with modern notation of plates. B1–B4 basals, IL1–IL5 infra-laterals, L1–L5 laterals, R1–R6 radials. Cf. text-fig. 3.

EXPLANATION OF PLATE 113

Stereophotos of *M. mariae* Callaway, *M. azaisi* (Thoral) and *M. azaisi multicristata* (Thoral).

Fig. 2. *M. mariae* Callaway. Lateral view of lectotype. BU 409.

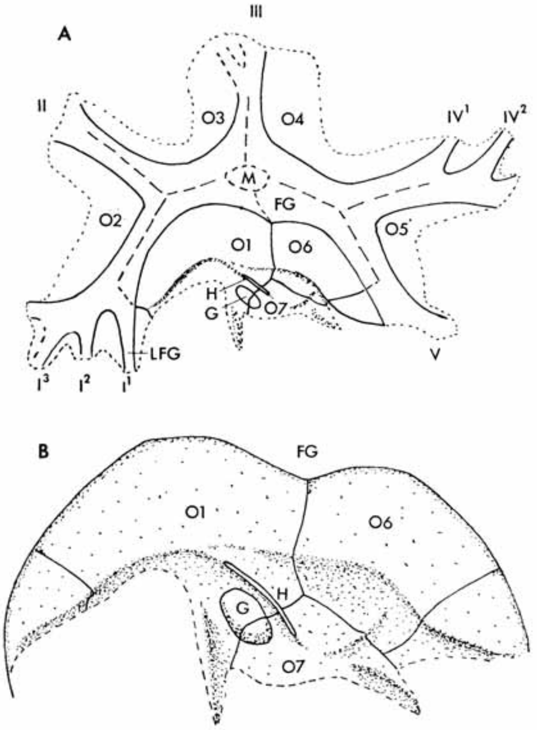
Figs. 1, 3, 5, 8. *M. azaisi* (Thoral). 1. Anterior lateral view of theca to show well-developed folds in B2 and ornament of stem flanges. CU. 3. Lateral view of another theca. CU. 5. Oral view of same. 8. Lateral view of another theca to show well-developed folds in B2 and ornament of stem flanges. CU.

Figs. 4, 6, 7. *M. azaisi multicristata* (Thoral). 4. Oblique oro-lateral view to show ornament of orals and lateral food grooves alternating in ambulacrum IV (left). CU. 6. Interior view of oral surface of same theca. 7. Lateral view of same theca to show more strongly developed folds in radial plates.

All figures of latex impressions whitened with ammonium chloride sublimate. All × 2.

The thecal plates of *Mimocystites bohemicus* and *M. azaisi* are identical to those of *Macrocystella mariae* except in the number of folds, which is variable in each species.

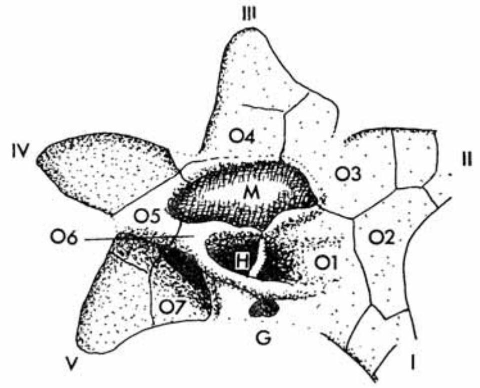
The proximal stem of *Mimocystites bohemicus* is identical to that of *Macrocystella mariae* except that the outer proximals have thicker flanges which are less blade-like. *Mimocystites azaisi* has still thicker flanges, the peripheries of which are granulose or spinose (Pl. 111, fig. 2, Pl. 113, figs. 1, 8).



TEXT-FIG. 11. Camera lucida drawing of oral surface of *Macrocystella azaisi* (Thoral). *a*, entire surface to show oral plates and arrangement of food grooves. Cf. Plate 113, fig. 5. CU. *b*, detail of gonopore and hydropore area of same. FG, food groove; G, gonopore; H, hydropore; LFG, lateral food groove; M, position of mouth which was probably much larger than shown; O1–O7, orals. I–V, ambulacra; I^1, I^2, I^3, facets of ambulacrum I; IV^1, IV^2, facets of ambulacrum IV.

The type species and one other species of *Mimocystites* therefore exhibit all the features which characterize *Macrocystella mariae*. All three are congeneric.

Specimens from the Montagne Noire, France (UC latex impressions) have yielded additional information on the morphology of *Macrocystella*. One example of *M. azaisi* (Thoral) has an almost complete oral surface (text-fig. 11*a*, Pl. 113, fig. 5). Another example of *M. azaisi multicristata* (Thoral) shows both the internal and external surfaces of the oral area (text-fig. 12, Pl. 113, figs. 4, 6). There were seven orals, arranged as shown in text-fig. 11*a*. A slit-like hydropore and an oval gonopore are developed across the common suture of O1 and O7 (text-fig. 11*b*). There are five main ambulacral grooves each of which has lateral branches leading to brachiole facets. Apparently the branches are consistently to the left of ambulacra I and IV in the example of *M. azaisi* (Pl. 113, fig. 5) but regularly alternate in ambulacrum IV in the example of *M. azaisi multicristata* (Pl. 113, fig. 4). Details of the other ambulacra are not well preserved in either specimen.



TEXT-FIG. 12. Camera lucida drawing of internal oral surface of *Macrocystella azaisei multicristata* (Thoral). cf. Plate 113, fig. 6. CU. G, supposed internal opening of gonopore; H, supposed internal opening of hydropore; M, mouth; O1–O7, orals; I–V ambulacra.

In internal view the mouth is large (4·6 mm. × 1·7 mm.) and is covered by ambulacral cover plates. The orals and ambulacral flooring plates are visible (Pl. 113, fig. 6). The latter are between, not on, the orals and form part of the thecal wall. Only primary ambulacral flooring plates can be detected. Close to the mouth is a deep pit which apparently connected to the hydropore. This pit is separated from the mouth and the supposed gonopore by two internal ridges, one on each side. The gonopore is apparently represented by a small circular pit some distance from the mouth (text-fig. 12). Unfortunately the critical area of the external oral surface is not preserved and it is not possible to match up external and internal openings. Ambulacra IV and V are more deeply impressed than I, II, and III. Another pit is developed obliquely under the aboral of the two internal ridges near the hydropore (Pl. 113, fig. 6). The significance of this is unknown.

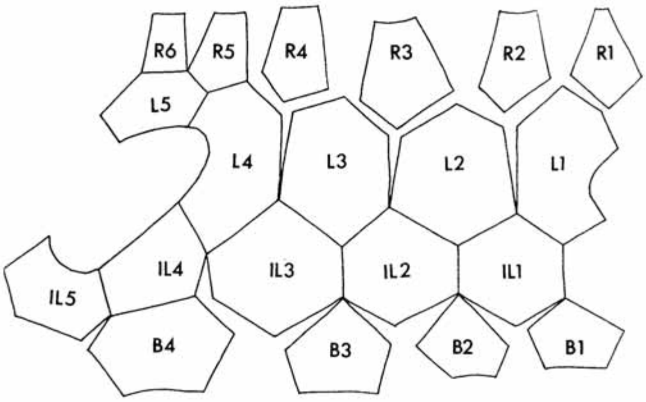
COMPARISON WITH OTHER PELMATOZOA

Several authors have grouped *Macrocystella* with *Lichenoides* while others have placed them in separate families. In addition *Macrocystella* has been variously assigned within the Pelmatozoa.

The most recent and most complete account of the morphology of *Lichenoides* is that of Ubaghs (1953) who showed that it completely lacks a stem. The thecal plates are arranged in four circlets but the total number is variable, 5–12 basals, 5 infra-laterals, 5–7 laterals, and 5–7 radials. (The homologies with the Glyptocystitida implied by the use of the same terms for the plate circlets are unjustified.) All the infra-laterals, laterals, and radials bear epispires. These are a type of pore-structure with a single sutural pore which leads to a narrow channel in the external surface of both adjacent plates (see

Ubaghs 1953, figs. 3, 11). There is no lateral periproct in *Lichenoides*. The brachioles arise from both lateral and radial plates and apparently they are not grouped into five radii.

Thus while *Lichenoides* resembles *Macrocystella* in having definite plate circlets and biserial, unbranched brachioles it differs in the absence of a stem and lateral periproct, in the presence of epispires and brachioles on lateral and radial plates, and in the total number and position of the thecal plates. These differences are considered to be important taxonomically. The Lichenoidae and Macrocystellidae are maintained as separate families as suggested by Jaekel (1918) and Ubaghs (1953).



TEXT-FIG. 13. Plate arrangement in *Cheirocrinus radiatus* Jaekel. Based on Jaekel, 1899, p. 213, fig. 36. B1–B4, basals; IL1–IL5, infra-laterals; L1–L5, laterals; R1–R6, radials.

Among cystoids *Macrocystella* most closely resembles *Cheirocrinus* Eichwald. This latter genus is characterized by a stem with proximal and distal portions. The construction and articulation of the stem are identical to that of *Macrocystella* and the helical arrangement of the articulations of the proximal stem was described by Billings (1858) in *Cheirocrinus anatiformis* (Hall) (= *Glyptocystites logani* Billings).

The theca of *Cheirocrinus* is composed of 27 plates arranged in 5 circlets: 4BB, 5ILL, 5LL, 6RR, and 7OO. The periproct is large, surrounded by 5 thecal plates (IL4, IL5, L1, L4, and L5) and was covered by a flexible plated integument in life. L5 is directly adoral to the periproct and has R5 directly adoral to it (text-fig. 13). The subvective system is restricted to the flat oral surface and there are 20–5 brachioles grouped into 5 ambulacra whose flooring plates lie between the orals, not on them. *Cheirocrinus* differs from *Macrocystella* in the possession of pectinirhombs.

Macrocystella and *Cheirocrinus* have in common many distinctive features of which perhaps the most important is the detailed structure of the stem. This type of stem is characteristic of and confined to the superfamily Glyptocystitida. It is most unlikely that such a complex organ developed independently in two groups which share other common characteristics. *Macrocystella* probably gave rise to *Cheirocrinus* and through it to the other Glyptocystitida as originally suggested by Jaekel (1899).

Thoral (1935) thought it possible to recognize in the Montagne Noire a lower horizon with *Macrocystella azaisi* (upper Tremadoc) and a higher horizon with *Cheirocrinus languedocianus* (basal Arenig). In Britain *M. mariae* occurs below the oldest *Cheirocrinus*. *Macrocystella* seems to be a characteristic fossil of the Tremadoc whereas the oldest known *Cheirocrinus* are all Arenig. Stratigraphic evidence agrees with the idea that *Macrocystella* evolved into *Cheirocrinus*.

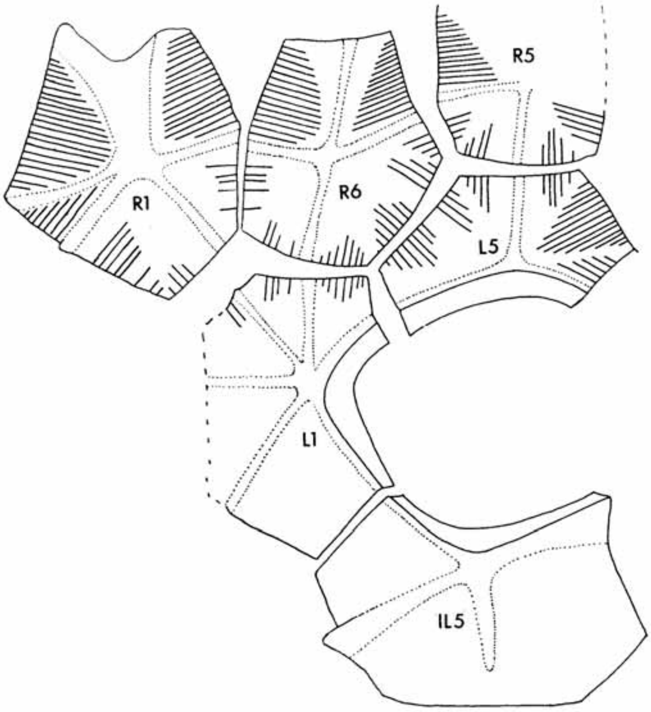
In the past the main objections to the inclusion of *Macrocystella* in the Rhombifera were its branched arms and lack of rhombs. The former was an error but the latter is more important. Regnéll (1945) has stressed that the main character which unites the cystoids as a class is the presence of pore-structures. Detailed study of cystoid pore-structures (Paul, 1968) suggests the Rhombifera should be regarded as a distinct class. The rhomb-less *Macrocystella* is included in the Rhombifera on the same grounds that led Kesling (1963) to include *Amecystis* in the Rhombifera. *Amecystis* is effectively a *Pleurocystites* without pectinirhombs, just as *Macrocystella* is a *Cheirocrinus* without pectinirhombs. The many similarities outweigh this single distinction.

THE EVOLUTION OF PECTINIRHOMBS

The rhombs of *Cheirocrinus* are fully developed pectinirhombs (which Bather regarded as a highly specialized type of rhomb) even in the earliest species known. There is no evidence of a gradual evolution of pectinirhombs. If *Macrocystella* evolved into *Cheirocrinus*, pectinirhombs either appeared 'suddenly' or pre-existing structures broke through the thecal plates to appear as pectinirhombs. The internal surfaces of isolated plates in both *Macrocystella* and *Cheirocrinus* show no features which could be incipient pectinirhombs. Pectinirhombs were functional throughout their growth; they are present as external features from the earliest stages. They did not develop internally and become external features later in growth. Rather sudden appearance therefore seems more likely.

All rhombs have generally been accepted as respiratory organs. In the simplest case respiration would have taken place through the thecal wall. The amount of oxygen required would have been proportional to the volume, and the amount of respiratory exchange to the surface area, of the theca. The oxygen requirements would thus increase with growth faster than the amount of exchange. This difficulty can be overcome, without materially altering the over-all thecal shape, by the production of evaginations or invaginations of the thecal wall. *Macrocystella* has the former in the folds of the thecal plates. The dichopores of pectinirhombs are invaginations and produce a slightly better volume to surface area ratio.

Exchange is facilitated by a large surface area and a thin exchange surface. Either invaginations or evaginations are almost equally effective in increasing the surface area but the latter are exposed and liable to mechanical damage. The ridges in the thecal plates of *Macrocystella* probably facilitated exchange by increasing the surface area. The thecal plates were extremely thin (0·1 mm.) and although strengthened by the ridges they were still very fragile. The dichopores of pectinirhombs are within the theca and therefore protected. Dichopore walls are much thinner than thecal plates (usually 0·01 mm.). In *Macrocystella* the entire thecal wall probably took part in exchange. In *Cheirocrinus* a differentiation of function is seen. Without decreasing the amount of exchange it became possible to have much thicker and stronger thecal plates. Exchange was restricted to specialized areas, namely the pectinirhombs. The thecal plates of *Cheirocrinus*, especially in early species like *C. languedocianus*, are still thin compared with later glyptocystitids but they are thicker (usually more than 0·5 mm.) than those of *Macrocystella*.



TEXT-FIG. 14. Pectinirhombs of a specimen of *Cheirocrinus languedocianus* Thoral. Note the incomplete pectinirhombs. Based on camera lucida drawings of the individual plates. CU. Symbols as in text-fig. 3.

In *Macrocystella* all thecal plates are ridged and all probably contributed to respiration. However the distribution of ridges in *M. azaisi* is uneven. More and better-developed ridges occur on radial plates (Pl. 113, fig. 7) and associated with B2 (Pl. 113, figs. 1, 8). This is quite independent of the variation between *M. azaisi* and *M. azaisi multicristata*. Sdzuy (1955, figs. 1*d–g*) figured a similar concentration of ridges on B2 in *M. bavarica*. In *Cheirocrinus languedocianus*, probably the earliest known species of *Cheirocrinus*, dichopores are developed across more sutures than in later species (text-fig. 14). Many sutures bear one or two demi-rhombs and some have only a few randomly spaced dichopores. These latter form incomplete pectinirhombs which have not been recorded in later glyptocystitids. Clearly the arrangement is more random than in later species which have a reduced number of pectinirhombs. All species of *Cheirocrinus* have pectinirhombs on radials and on B2 however. The similarity between the distribution of ridges in *Macrocystella* and of pectinirhombs in *Cheirocrinus* indicates a concentration of respiratory activity in the same areas of their thecae, probably reflecting a similar internal organization, and confirming the idea that *Macrocystella* and *Cheirocrinus* are related.

MODE OF LIFE

The stem of *Macrocystella* lacks a root structure or anchoring device and there is little evidence for Bather's reconstruction of a distal coil to the stem. Whatever benefits were conferred on *Macrocystella* by the possession of a well-developed stem, they were not associated with permanent attachment. *M. mariae* and other species of *Macrocystella* are found in fine-grained sediments in which there is little evidence for suitable attachment surfaces. Nevertheless the general morphology of the theca and subvective system suggests *Macrocystella* habitually held its theca upright. Only free-floating or free-swimming modes of life can satisfy both lines of reasoning.

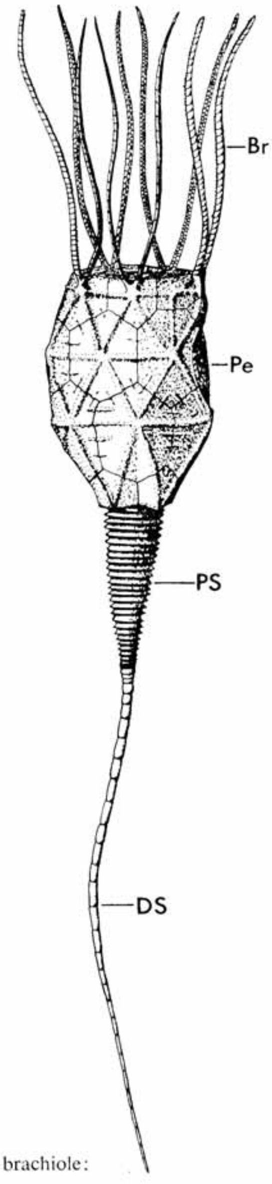
The distal stem in *Macrocystella* and in other early glyptocystitids tapers gradually to a small diameter and ends abruptly. The terminal portion of the stem is not modified as in *Brockocystis* Foerste or *Lepocrinites* Conrad and there is no way to be certain that the last distal columnal preserved was the terminal columnal in life. It is possible that *Macrocystella* broke free prior to death and was buried some distance from its point of attachment. However *M. mariae* and other apparently free glyptocystitids are frequently preserved in clay-grade sediments with little associated fauna which could have acted as substrata for attachment. No *Macrocystella*, *Cheirocrinus* nor *Pleurocystites* has ever been found with a root structure or anchoring device, yet many specimens are excellently preserved with brachioles, periproctal membranes, and other delicate structures intact. Some specimens from the Trenton Limestone of Ottawa and the Starfish Bed of Girvan, Scotland (for example) suggest that death was due to burial alive and therefore that the specimens are complete. The terminal diameter of the distal stem (0·5 mm.) compared with the total length (50 mm.), in *M. mariae* indicates that if attached the stem was extremely weak at this point. *Macrocystella* may have been attached early in its development but the evidence strongly suggests that it was free for the major portion of its life.

Pentameral symmetry is well developed in *Macrocystella*: there are circlets of five plates and five ambulacra. The theca is cylindrical not flattened on one side. Bather argued that pentameral or radial symmetry was developed in fixed animals and he associated departures from pentamery in echinoderms, particularly flattening of the theca, with departures from an upright fixed position. *Pleurocystites*, another free glyptocystitid, has a markedly flattened theca which apparently lay on the sea floor. If *Macrocystella* and *Cheirocrinus* also lay on the sea floor one would expect a similar flattening of their thecae. The persistance of *Macrocystella* and *Cheirocrinus* after the appearance of *Pleurocystites* suggests the former were adapted to a different mode of life. The subvective system in *Macrocystella* and *Cheirocrinus* is confined to the oral surface and forms a cone of collection. Paul (1967*a*) suggested that such an arrangement is better adapted to collect falling food particles in a relatively still sea and requires an upright theca. Both *Macrocystella* and *Cheirocrinus* have respiratory surfaces developed all round the theca and some of these would have been fouled if the theca rested on the sea floor. *Pleurocystites* however has all its pectinirhombs on one side of the theca, presumably the upper side in life. All these lines of evidence indicate that *Macrocystella* and *Cheirocrinus* habitually held their thecae upright. However, when upright, *Macrocystella* is very top heavy (text-fig. 15) and the theca would have rested on the sea floor if the stem were free.

Without a root structure or anchoring device the stem could exert no leverage against the substrate and would have been useless to maintain the theca upright. The distal stem may have been partially buried in the substrate but its whiplike form would provide little resistance in soft mud. There is no evidence for partial burial of the stem during life in specimens which apparently died by entombment. Other pelmatozoans which were fixed in soft sediments have well-developed branching root structures (e.g. *Eucalyptocrinites* and *Caryocrinites*). Even recent brachiopods which live in soft sediments have branching root-like pedicles. If *Macrocystella* and *Cheirocrinus* were free and habitually held their thecae upright they could only achieve this if they floated or swam actively. Both modes of life are known in other pelmatozoans.

Recent free-swimming crinoids have negative buoyancy (i.e. they are denser than sea water) and this has generally been assumed to obtain in all echinoderms. If the coelomic fluids and organic tissues are of neutral buoyancy, the only element which contributes to negative buoyancy is the skeleton, the effective density of which is 0·8 gm. per cc. when fully immersed in sea water. An echinoderm with negative buoyancy will sink when at rest. Recent free crinoids maintain their position by swimming. They are characterized by a well-developed subvective system with multiple branched arms and, in most cases, by the complete absence of a stem and marked reduction of the calyx: certainly none has a calyx comparable in size to a cystoid theca. Swimming is wholly achieved by the arms, buoyancy devices are absent (there is nowhere to house them) and dead weight in the form of stem and thecal plates is minimal.

In *Macrocystella* there is a relatively undeveloped subvective system, a large theca, and a well-developed stem. Dead weight was considerable and the brachioles may have been relatively inefficient organs of locomotion. The flattening of the brachioles in *M. mariae* is in the opposite direction to that one would expect if they were used actively in swimming.



TEXT-FIG. 15. A reconstruction of *Macrocystella mariae* Callaway. Br, brachiole: DS, distal stem; Pe, periproct; PS, proximal stem.

However if the lappets were folded in during an upstroke and extended during a downstroke the brachioles could have been fairly efficient swimming organs. The relatively large theca has very thin plates and could well have housed buoyancy devices. Quite small gas bubbles would have significantly altered the total buoyancy: in *M. mariae* a bubble 3 mm. in diameter would completely compensate for the weight of a theca 10 mm. in diameter and 15 mm. high. *Brockocystis* Foerste, another apparently free glyptocystitid, has hollow, bulbous thecal plates each of which could have housed a gas bubble. The stem bulb in *Brockocystis* is also hollow. It is not impossible that *Macrocystella* had buoyancy chambers but there is no direct evidence for this.

Function of the stem. Most authors, with the notable exception of E. Kirk (1911), have taken stems in pelmatozoans to imply permanent fixture. It is therefore surprising to find among early stemmed pelmatozoans an almost total lack of definite root structures or anchoring devices. What benefit did the possession of a stem confer if it was not attachment?

If an ancestral stem-less form were permanently attached, the development of a stem could have raised the theca off the substrate. This would reduce the chances of accidental burial, of fouling by mud-laden currents, and it could have placed the echinoderm above other benthonic organisms competing for food particles as suggested by Kesling and Mintz (1961). What may have been attempts to raise the theca, or at least the oral surface, are seen in edrioasteroids and some diploporites but none of these produces a true stem, only aboral stem-like projections of the theca. Alternatively if an ancestral stem-less form were free, a stem would weight the theca aborally. This would maintain the animal upright if the theca were buoyant or if the subvective system were used in swimming. However, a simple weight placed aborally would satisfy this requirement.

The form of the stem in *Macrocystella* could have allowed considerable variation in buoyancy when the stem was in contact with the substrate. If the theca was buoyant but the weight of the stem gave the whole animal negative buoyancy, equilibrium could have been reached if part of the stem rested on the sea floor. The flexible proximal stem would still allow the theca to be held upright; buoyancy would hold the theca upright without any effort on the part of the animal. *Macrocystella* probably rested with its theca near but not on the substrate and moved about by means of its brachioles and stem. This interpretation seems preferable to one without a buoyant theca even though there is no direct evidence for buoyancy devices. If *Macrocystella* used its brachioles to maintain an upright posture it could not have rested in an upright position. As recent free crinoids feed when at rest it is difficult to imagine how *Macrocystella* fed under these circumstances.

Macrocystella is imagined to have had a slightly buoyant theca but to have been weighed down by the stem. Under these circumstances it could have rested with the stem on the sea floor, the theca upright and the brachioles extended to feed. In times of short food supply *Macrocystella* swam away actively by means of its brachioles and stem, moving just above the sea floor. *Macrocystella* may have drifted under the influence of gentle currents but current action was not strong in the environment of deposition of *M. mariae*. Occasionally *M. mariae* was overwhelmed by a sudden influx of mud possibly brought about by turbidity currents. *Macrocystella* seems to have lived in much deeper water than most later glyptocystitids (see Paul 1967*a*).

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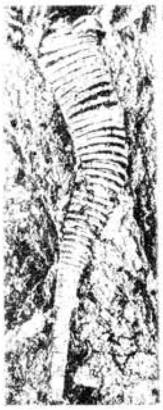


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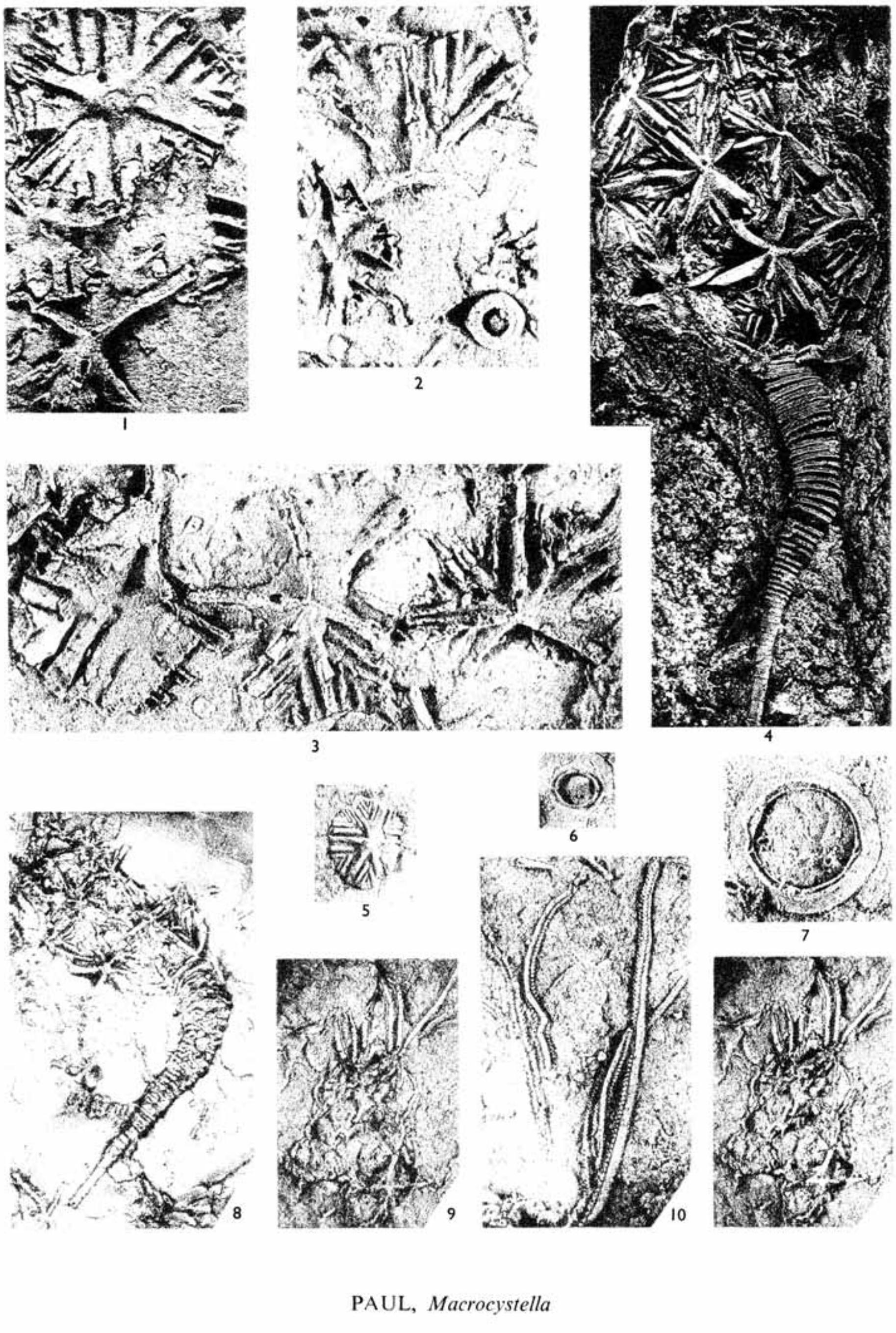

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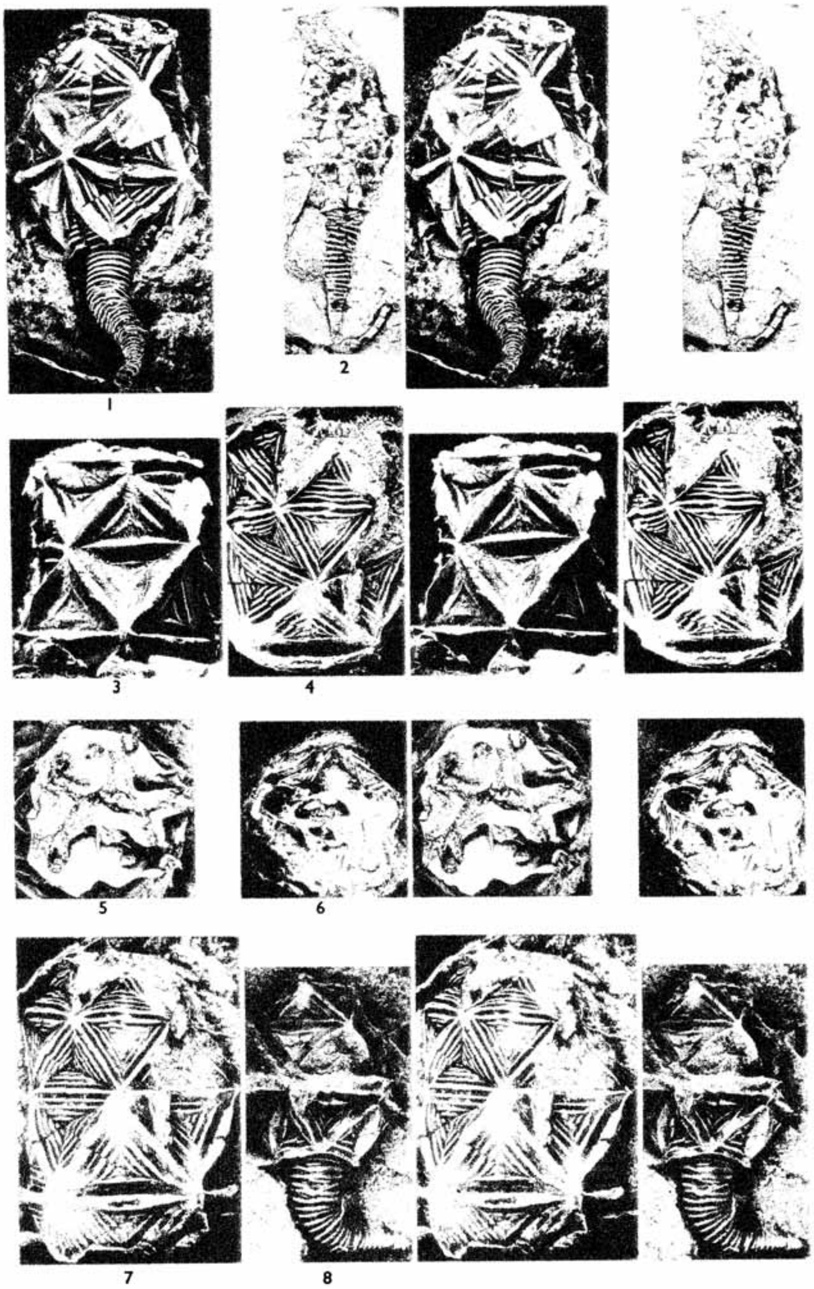

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