number and arrangement of plates, as well as aulacophore, unknown. [This nominal genus, based on scanty and poorly preserved material, was placed among Anomalocystidae by JAEKEL (1918) and CHAUVEL (1941). Possibly it belongs in the Lagynocystida.] *M.Ord.*, Boh.——FIG. 362, *1*. **S. ensifer* (BARRANDE); *1a,b*, different specimens, orientation unknown, ×1.5 (2).

[References for the chapter on Stylophora are included with those for Homostelea and Homoiostelea (*see* p. *S*624).]

HOMOSTELEA

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INTRODUCTION

The subclass Homostelea, here elevated to class rank, was proposed by GILL & CASTER (1960,*43*) to embrace the two orders Cincta JAEKEL *(55)*[2] and Digitata GEKKER (1938,*39*), which GILL & CASTER included in the class Carpoidea JAEKEL *(54)*. Subsequently, the Digitata were assigned to the class Eocrinoidea by UBAGHS (1950,*86*). Therefore, as here understood, the Homostelea contain only the single order Cincta.

Within the Cincta are placed *Trochocystites* BARRANDE (1887) and a few related genera, all of which belong to the Middle Cambrian of the Old World. That it is appropriate to classify *Trochocystites* in a family group of its own was first recognized by JAEKEL when he defined the Trochocystitidae. At the same time he united this assemblage with the Mitrocystidae *(54)* in a suborder named Marginata of the order Heterostelea (class Carpoidea). The Mitrocystitidae now are recognized as a family of the order Mitrata in the class Stylophora. BATHER *(13)* maintained the Trochocystitidae—incorrectly spelled Trochocystidae, as given by him (BATHER, 1902, in Zoological Record) earlier and generally

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[1] I am much indebted to KENNETH E. CASTER and RAYMOND C. MOORE for translating my manuscript, and to the following persons for loan of specimens or permission to study collections: Prof. JACQUES AVIAS, Université de Montpellier, France; Dr. ALBERT BREIMER, Vrije Universteit, Amsterdam, Netherlands; Abbé ROBERT COURTESSOLE et M. GÉRARD GRIFFE, Carcassonne, France; Dr. HERMANN JAEGER, Humboldt-Universität, Berlin, Germany; Dr. R. P. S. JEFFERIES, British Museum (Natural History), London, Great Britain; Dr. FERDINAND PRANTL, Národní Museum, Prague, Czechoslovakia; Dr. GERTA WEHRLI-OLBERTZ, Ernst-Moritz-Arndt-Universität, Greifswald, Germany. Photographs, drawings and assemblage of figures have been prepared by Mrs. MARIE MASSON. To all these people I express deep thanks.

[2] Numbers enclosed by parentheses, other than years, indicate serially numbered publications in the list of references at end of this chapter.

accepted by other authors—but rejected the Marginata, assigning the family instead to the suborder Heterostelea of the order Amphoridea (class Cystoidea).

In 1918 Jaekel *(55)* described two new genera of echinoderms more or less similar to *Trochocystites* and grouped all of them together in a new order named Cincta. The genus designated as *Trochocystoides* was placed in the Trochocystitidae and one named *Gyrocystis* in the new family Gyrocystidae.

Other authors generally have treated the genera mentioned as members of a single family of the class Carpoidea *(32,41)* or grouped them with most other "carpoids" as mere so-called cystoids referred to the family Anomalocystidae of Meek (1872) (Zittel, 1895, 1910, 1913; Bather, 1900; Delage & Hérouard, 1903) or its equivalent, correctly designated, Anomalocystitidae Bassler (1938) (Bassler & Moodey, 1943). The Anomalocystitidae now are classified as a family of the Mitrata in the class Stylophora.

The Homostelea have nothing in common with other "carpoids" except the depressed form of their asymmetrical body girdled by a marginal framework and their complete lack of radial symmetry. They differ from all of them in the localization of their two main thecal orifices near one pole of the body and in having one or two epithecal grooves on the marginal frame leading to one of the orifices. In addition, they differ from the Stylophora in possessing a pedunculate appendage or stele and in lacking a brachial appendage comparable to the stylophoran aulacophore. They are separated from the Homoiostelea by the nature of the stele, primarily composed throughout its length of a double series of similar plates, and likewise by the absence of an arm.

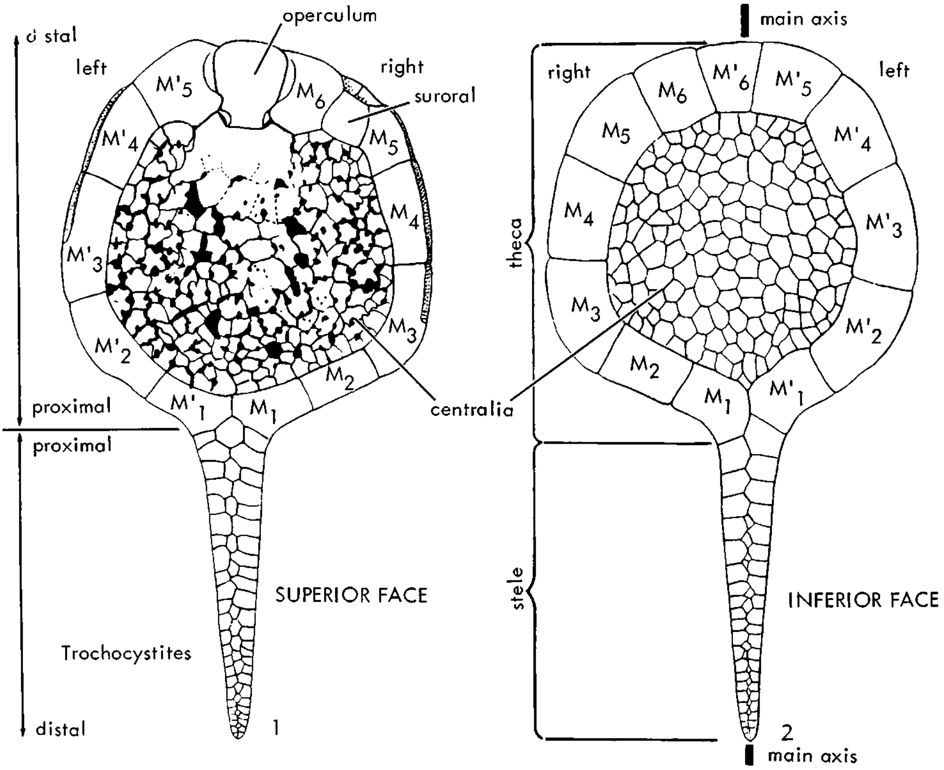

Fig. 363. Morphological features of Homostelea, based on **Trochocystites bohemicus* Barrande, M.Cam., Boh.; *1,2,* upper and lower faces, ×3 (Ubaghs, n).

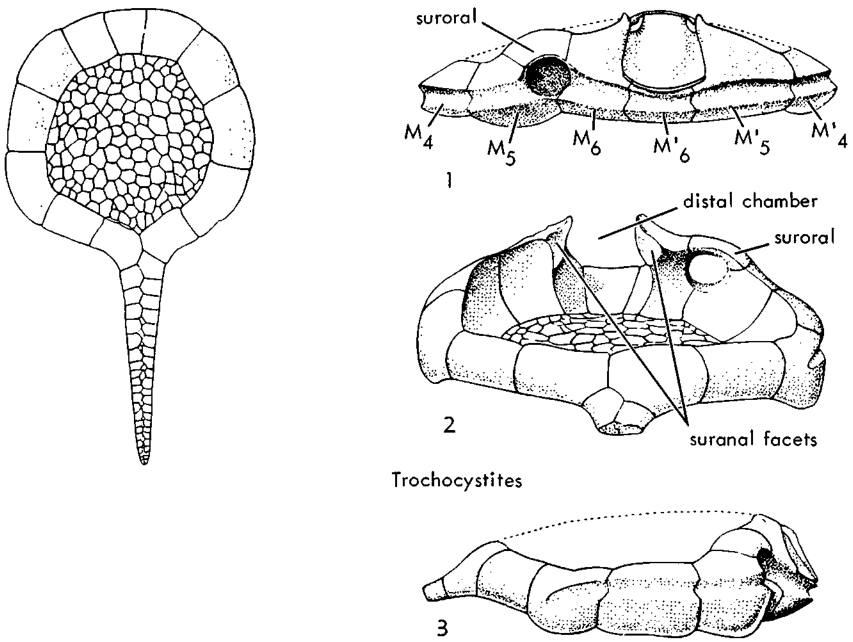

FIG. 364. Morphological features of Homostelea, based on **Trochocystites bohemicus* BARRANDE, M.Cam., Boh.; *1-3,* distal, proximal, and right lat. views, ×3 (Ubaghs, n).

MORPHOLOGY

GENERAL FEATURES

The skeletal parts of the Homostelea consist of a **theca** and a **stele,** the latter being essentially only a much-narrowed and tapering extension of the former. The theca is asymmetrical, although it may display some tendency toward bilateral symmetry (Fig. 363).

In outline the theca may be almost circular, oval, pyriform, or subtriangular. When pyriform, the stele emerges from the constricted part of the theca, and when subtriangular, from the apex of the triangle. Invariably, the theca grows thinner toward the stele.

The theca is flattened and shows two very dissimilar faces—a flat or concave one, on which the living animal presumably reposed, and an opposite convex one. The integuments covering a large median part of the two faces contain many small plates named **centralia** or **centrals.** Peripherally these meet the inner edges of thick plates that form the stout marginal framework of the theca and accordingly are named **marginalia** or **marginals.** On the convex upper face of the theca the marginal frame is pierced by two orifices which are located near to one another at the extremity opposite to the stele (Fig. 364,*1,2*). The smaller of the orifices is bounded laterally by a pair of marginals and above by a supplementary fixed plate named **suroral** (=eporal, JAEKEL, 1918[1]) resting on edges of the marginals (Fig. 364,*1,2*; 365,*3,4*). One or two epithecal grooves hollowed into the outer face of some of the marginals lead to this orifice. The neighboring relatively large orifice is bounded by three marginals, two laterally and one below, and is protected above by an apparently movable plate designated as **operculum** (Fig. 363,*1*; 364,*1*; 365,*3*).

The stele is flattened like the theca. It tapers distally away from the theca and shows the same organization throughout its length. It is composed of two series of opposed or alternating plates which meet along the mid-line of each face except

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[1] Such terms as eporal, epanal, epicentral, and hypocentral, of combined Greek-Latin origin, here are replaced by terms with components derived from a single one of these languages.

where a varying number of tiny ossicles is intercalated between them. A narrow axial canal enclosed by the stele opens between two of the marginals into the thecal cavity.

ORIENTATION AND NOMENCLATURE

The plane in which the theca is flattened is termed the **extension plane** (BATHER, 1913) or extensiplane (GILL & CASTER, 1960). The two faces of the theca are differentiated with respect to this plane and the probable attitude of the living animal as **superior or upper face** (=obverse face, BATHER, 1913) and **inferior or lower face** (=reverse face, BATHER, 1913). The **main axis** of the theca and stele runs longitudinally midway between their lateral margins and marks the position of the **symmetry plane** (BATHER, 1913) oriented at right angles to the extension plane. The body tends toward bilateral symmetry as defined by this plane.

Length is measured along the main axis and **width** normal to this axis in the extension plane. **Height or thickness** is defined as the distance between the two thecal faces normal to the extension plane.

For purposes of description, the junction of theca and stele is defined as marking the most **proximal or adsteleal** pole of the theca and the opposite extremity along the main axis of the **distal or absteleal** pole of the theca (Fig. 363). Similarly, the proximal part of the stele lies closest to the theca and the distal part nearest to its tip.

Right side and **left side** are purely conventional designations of halves of the

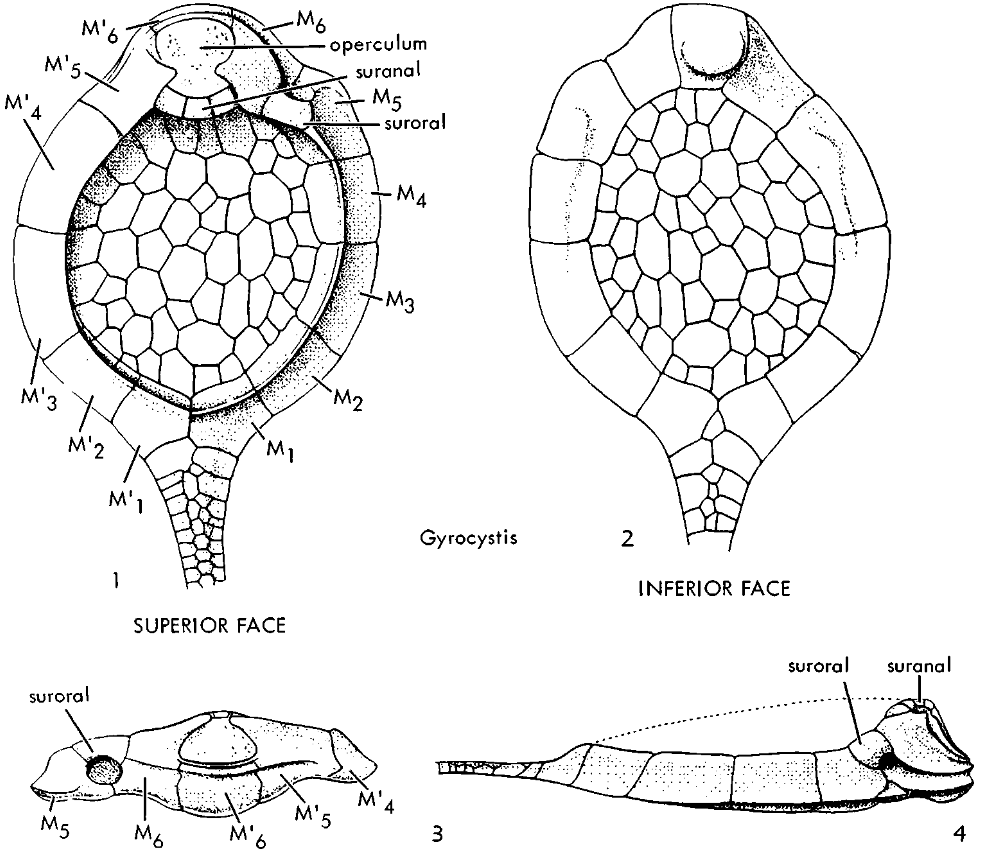

FIG. 365. Morphological features of Homostelea, based on *_Gyrocystis barrandei_ (MUNIER-CHALMAS & BERGERON), M.Cam., Fr.; _1_, upper face, supracentrals lacking, ×3; _2-4_, lower, distal, and right lat. views, ×3 (Ubaghs, n).

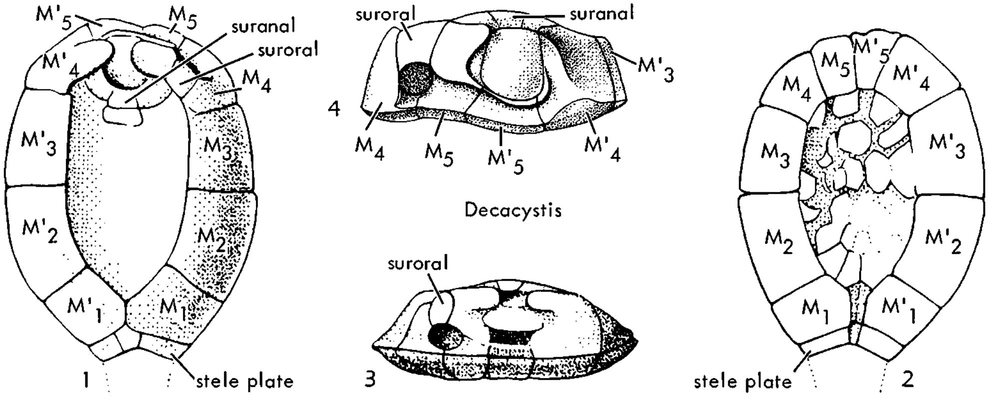

FIG. 366. Morphological features of Homostelea, based on *Decacystis*.——*1-3*. **D. hispanica* GISLÉN, M. Cam., Spain; upper, lower, and distal views, ×3 (10).——*4*. *D.* sp. cf. **D. hispanica* GISLÉN, M.Cam., Spain; distal view, ×5 (Ubaghs, n).

theca and stele on opposite sides of the symmetry plane when the fossil is oriented with the inferior thecal face directed downward and the stele toward the observer (downward in figures). According to convention, the marginal plates are designated by the symbols M_1, M_2, M_3 . . . on the right side of the theca beginning at the stele and by the symbols M'_1, M'_2, M'_3 . . . on the left side similarly (Fig. 363). It should be observed that identity in form of these symbols does not indicate homologies of the marginals in Homostelea and Stylophora.

MARGINALIA

The framework formed by the marginal plates comprises the strong peripheral part of the theca. The mode of designating individual marginal plates has just been explained. All are thick and they are joined firmly to one another. Both their positions and numbers (10 to 12 in different genera) are constant. The upper face of each plate may be distinctly convex (e.g., *Trochocystites,* Fig. 364,*2,3*), slightly convex to slightly concave (e.g., *Trochocystoides*), flat (e.g., *Decacystis,* Fig. 366,*3,4*), or almost flat to strongly concave (e.g., *Gyrocystis,* Fig. 365,*1*), whereas the lower face of each plate invariably is flat or convex and the inner (interior) face concave (Fig. 364,*2*). The external intersection of the upper and lower faces may be sharp-angled or regularly rounded and consequently its cross section varies from triangular (e.g., *Decacystis, Gyrocystis*) or inverted T-shaped (e.g., *Gyrocystis*) to more or less U-shaped (e.g., *Trochocystites*).

Prominent localized swellings or tumescences generally characterize the lower face of the marginals, but never in the proximal part of the theca. The swellings have lateral positions in *Trochocystites* and extend over several plates on both sides (Fig. 364,*2,3*). Opposite to the stele in *Gyrocystis* a large boss is seen beneath the main thecal orifice, generally flanked on both sides by less prominent elongate swellings (Fig. 365,*2*). The variations in shape and size of the prominences may reflect the microenvironments of individuals, though the precise nature of their function is unknown. Probably they helped to anchor the animals.

CENTRALIA

The superior and inferior plated integuments of the median part of the theca are affixed to the upper and lower inner edges of the marginal framework. Along the lines of attachment many small depressions observed in some specimens probably mark the sites of supple ligamentary bundles (see Fig. 370,*3*). Collectively, the plates of the central regions of the theca are designated as **centralia or centrals.**

The centrals of the superior thecal face are distinguished as **supracentralia or supracentrals** [=epicentralia, JAEKEL, 1918]. For the most part these small plates are discrete and in the living animal were probably united flexibly, thus accounting for their rare preservation. They are almost unknown in *Gyrocystis* and *Decacystis* except for isolated platelets, but in *Trochocystites bohemicus* they consist of small irregular and maladjusted ossicles with uneven integumentary spaces between them (Fig. 367,*1*). The spaces may have the aspect of generally distributed sutural pores with elliptical outlines. In places they are bordered internally by calcareous crests, and collectively they may form a transverse crescent (Fig. 367,*2-4*). As in eocrinoids and some other primitive echinoderms, these sutural

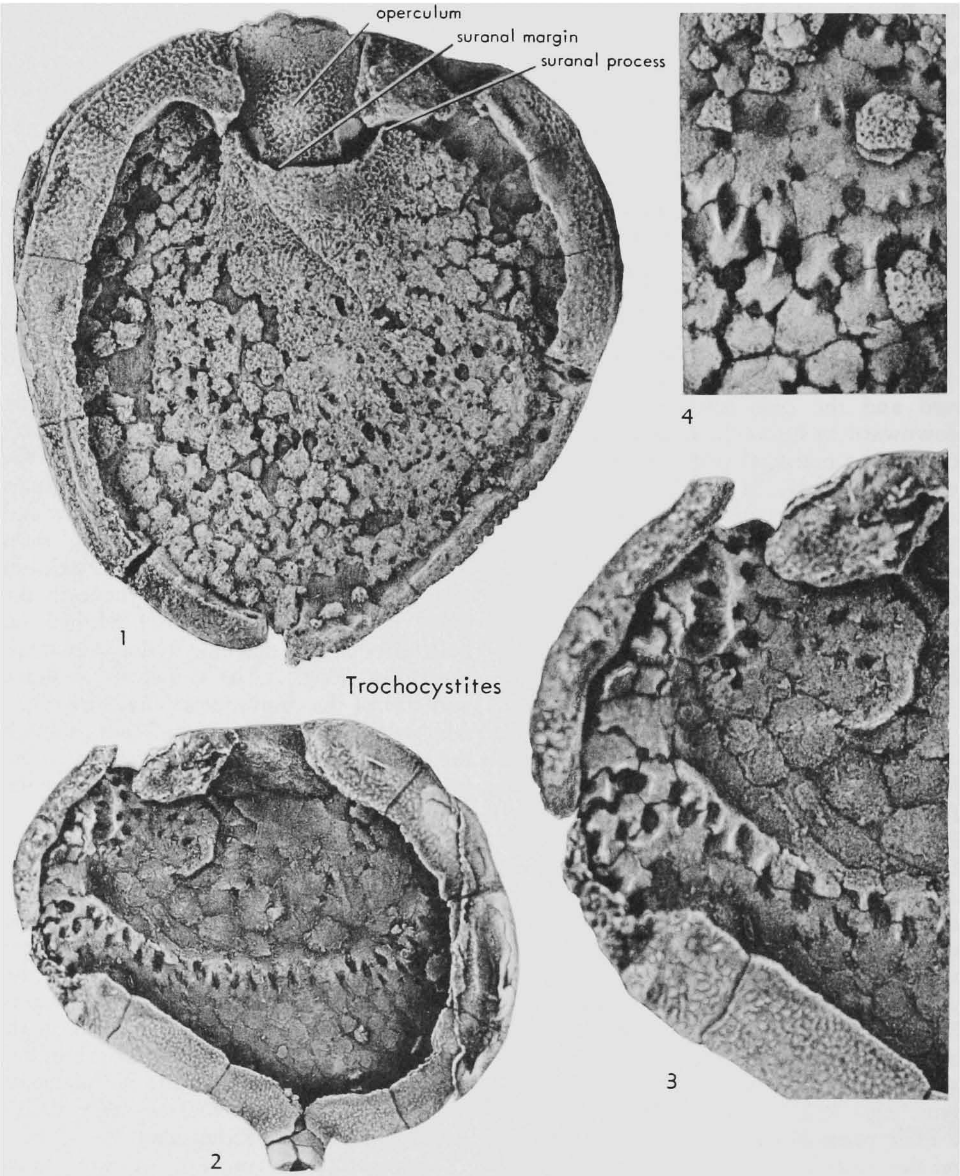

FIG. 367. Centrals of superior thecal face in *_Trochocystites bohemicus_ BARRANDE, M.Cam., Boh.; *1,* upper face, external side, ×4; *2,3,* internal side of supracentral pavement, ×4; *4,* internal side of some supracentrals showing sutural pores, ×7.5 (Ubaghs, n).

"pores" probably were not actual openings in the theca but merely small uncalcified parts of the integument or spaces occupied by papulae-like organs that served for gaseous exchange between coelomic fluids and sea water.

The integument of the lower thecal surface inside of the marginal frame was occupied completely by more or less numerous polygonal plates which formed a tessellated pavement (Fig. 363,*2*; 365,*2*). These plates are called **infracentralia or infracentrals** [=hypocentralia, JAEKEL, 1918].

A few special features of the superior face of the theca call for notice. In *Trochocystites* from near the middle, plates of the centralia become more tightly united in a distal direction toward the large thecal orifice so as to form a thick firm border around it, which is distinguished as the **suranal margin** (Fig. 367,*1*). Laterally and distally this margin is produced into two **suranal processes,** each of which rests against the **suranal facet** of a large apophysis borne by one of the pair of marginals that frame the orifice laterally (Fig. 364,*2*; 367,*1*). No

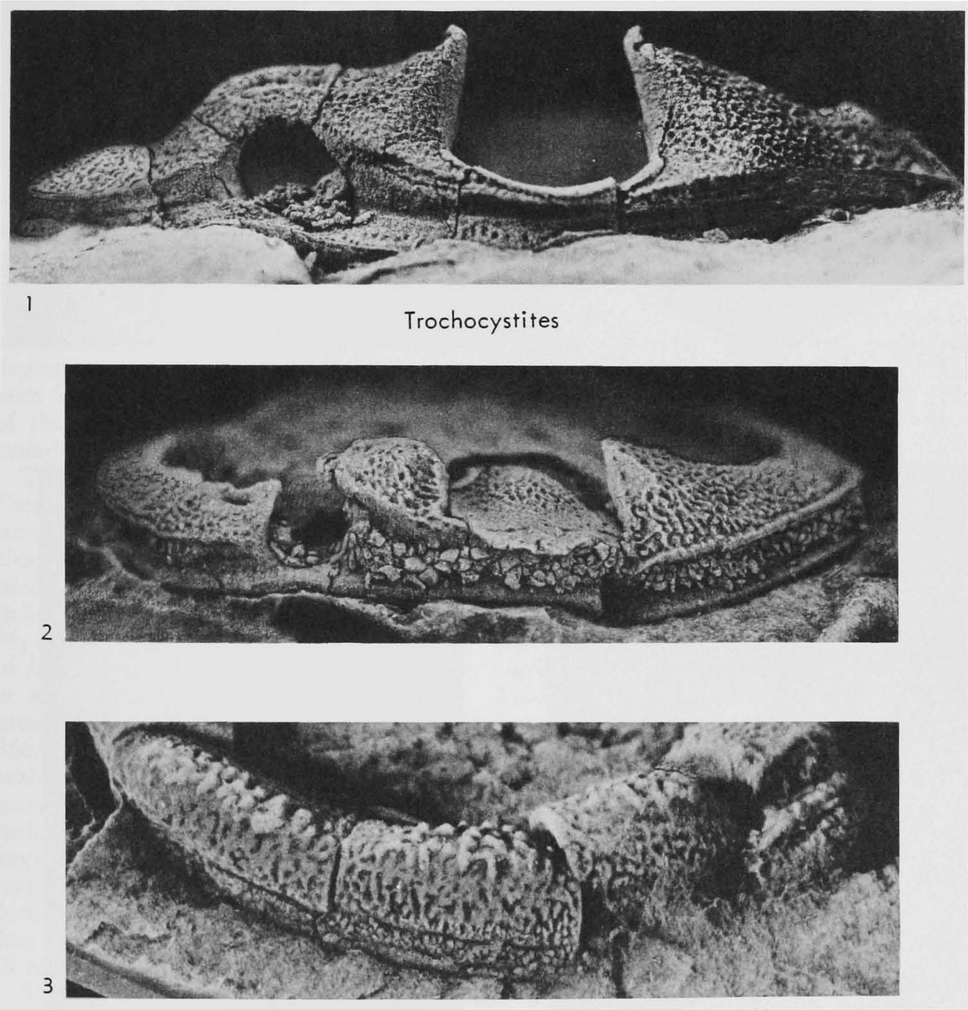

FIG. 368. Marginal grooves of **Trochocystites bohemicus* BARRANDE, M.Cam., Boh.; *1,* distal view showing empty grooves with tiny serial depressions which presumably served for attachment of cover plates along their margins, ×7.5; *2,* distal view of specimen showing grooves partially filled with cover plates, ×7.5; *3,* right lat. view showing grooves protected by cover plates, ×7.5 (Ubaghs, n).

continuous suranal margin is seen in *Decacystis* and *Gyrocystis,* but instead the larger orifice is bordered proximally by three or four thick **suranal plates** (=epanals, JAEKEL, 1918) (Fig. 365,*1*; 366,*1*).

ORIFICES AND MARGINAL GROOVES

The marginal framework on the upper face of the theca is pierced by two openings—not three, as reported erroneously by BARRANDE (1887), HAECKEL (1897), and BATHER (1900). The orifices are unequal in size and shape and they differ constantly in location. The larger one is found near the absteleal pole of the theca and the smaller at a short distance from it to the right.

The small orifice is located between two marginal plates and is circular. Above it is an arched plate known as the **suroral** which laterally rests on edges of the marginals (Fig. 364,*1*; 365,*4*; 366,*3,4*). A groove leading to right from the orifice and another

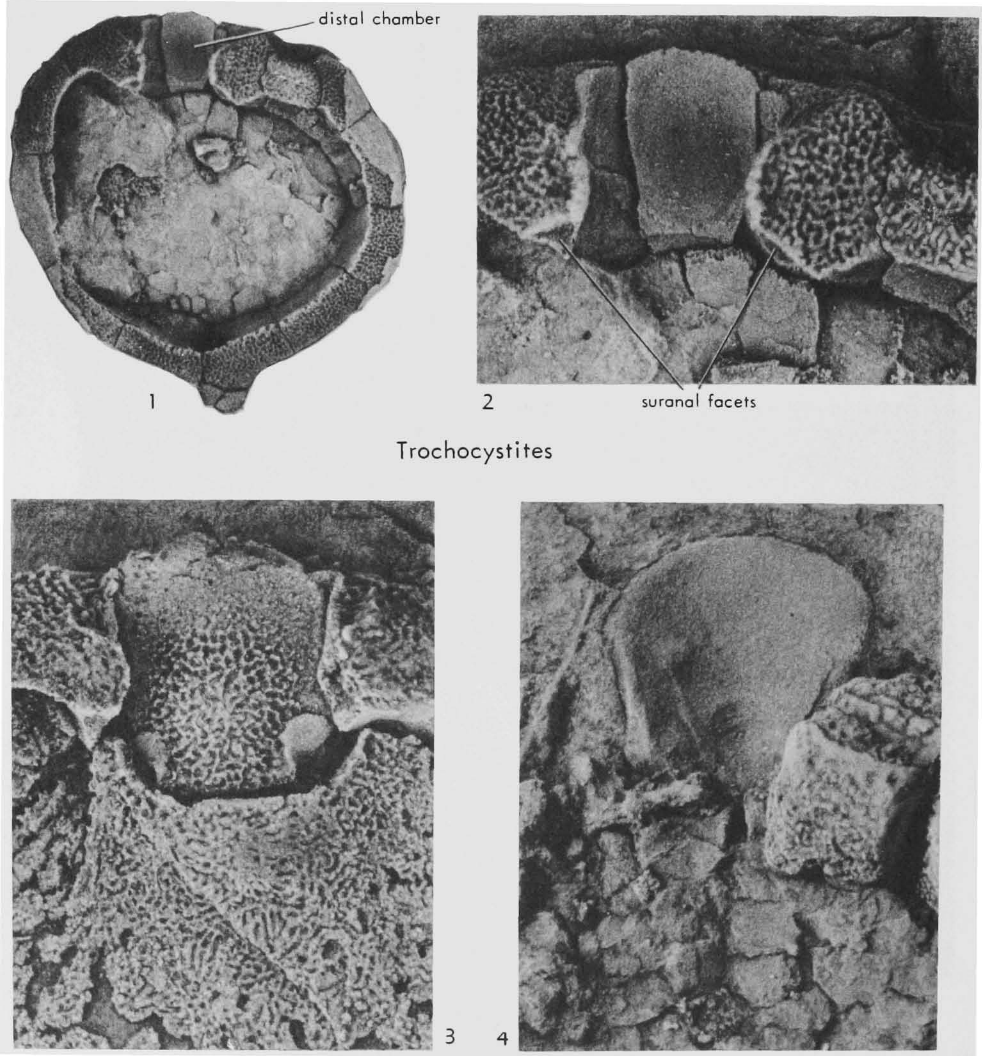

FIG. 369. Distal chamber and operculum of **Trochocystites bohemicus* BARRANDE, M.Cam., Boh.; *1,* upper face of theca with centrals not preserved, distal chamber open (without operculum), ×3; *2,* distal chamber, ×7.5; *3,4,* external and internal sides of operculum, ×7.5 (Ubaghs, n).

to the left are excavated in the outer face of adjacent marginals along the periphery of the theca just above the boundary between its superior and inferior faces. The grooves are long in *Trochocystites* and *Trochocystoides*, shorter in *Gyrocystis*, and still shorter in *Decacystis*. The right groove traverses marginals M_5 and M_4 in *Trochocystites* to a termination on M_3 (Fig. 363,*1*; 364,*1-3*), whereas in *Trochocystoides* it is confined to M_4 and M_3. The right-hand groove remains undeveloped in *Decacystis* or can barely be detected in a few specimens (Fig. 366,*4*). The left groove passes under the salient lower lip of the large orifice and is terminated on M'_3 in *Trochocystites* (Fig. 363,*1*; 364,*1*), and *Trochocystoides*. In *Gyrocystis* the left groove ends on M'_5 (Fig. 365,*1,3*) and in *Decacystis* on M'_4 (Fig. 366,*4*).

The marginal grooves of Homostelea range from shallow to deep. Those of *Trochocystites* and *Trochocystoides* are deep and in some specimens of the former marked by distinct borders (Fig. 368,*2*). The floor of the grooves is angular and smooth but each side bears a series of tiny depressions which seem to be attachment seats for cover plates (Fig. 368,*1*). The ends of the grooves away from the orifice are rounded and generally quite distinct.

The floor of the grooves in *Gyrocystis* rises rather abruptly near their distal extremity and their termination is not always clear. The right groove, in particular, leaves hardly any trace—at best only a very faint indication on the superior faces of M_5 and M_4 (Fig. 365,*1*). The corresponding groove of *Decacystis* is generally not differentiated at all, whereas the left one, deeply impressed proximally, vanishes on M_4 (Fig. 366,*4*). The grooves and the opening to which they lead are observed in many specimens to be filled with very tiny irregular ossicles, which may be so associated as to suggest that they are remnants of a pavement (Fig. 368,*2,3*). Morphologically and functionally the ossicles seem to be equivalent to the cover plates of the food grooves of many pelmatozoans.

The relatively large orifice of the theca opens into a sort of chamber—here called **distal chamber**—which is hollowed entirely into the thick framework of marginals at the absteleal pole of the theca. The chamber is truncate cone-shaped, expanding toward the interior of the theca, with which it is confluent (Fig. 364,*2*; 369,*1,2*). Its lower distal margin extends laterally outward as a lip which projects over the left marginal groove (Fig. 368,*1*). The walls of the chamber are smooth. Its concave floor, sloping toward the thecal interior, is formed by the upper surface of M'_6 in *Trochocystites* and *Gyrocystis* or of M'_5 in *Decacystis*. The side walls are cut into the two adjacent marginals and its ceiling is formed by a special plate termed the **operculum** (=*Analklappe*, JAEKEL, 1918; anal valve, GISLÉN, 1927; *clapet buccal*, CUÉNOT, 1953). The marginals which flank the orifice and partially overhang the operculum bear strong apophyses which extend more or less convergently inward and upward at the sides of the orifice (Fig. 364,*2*;368,*1*). A little below the summit of each apophysis is an articulatory fossette named the **suranal facet,** which receives a suranal process (e.g., *Trochocystites,* Fig. 364,*2*) or plate (e.g., *Decacystis, Gyrocystis,* Fig. 365,*1*; 366,*1*).

The operculum is a convex oval plate, wrinkled externally and smoothly concave internally (Fig. 369,*3,4*). It expands slightly in a distal direction with its lateral and distal edges adjusted to the walls of the chamber covered by it, but neither fused to these walls nor articulated with them. The proximal edge of the operculum is joined to the suranals (e.g., *Gyrocystis, Decacystis*) or suranal margin (e.g., *Trochocystites*) probably by a loose suture or ligamentary articulation and both extremities of this edge are more or less deeply notched. The notches are bordered in some specimens of *Trochocystites* by a smooth upbent lip which probably provided the attachment for muscles that served to open the operculum (Fig. 369,*3*). In closed position, the operculum sloped steeply downward distally, and when opened, probably an elliptical orifice was left between it and the lower margin of the distal chamber.

The structures just described have been subjects of diverse and often conflicting interpretations.

In view of SPENCER *(80)*, CUÉNOT *(32)*, NICHOLS *(68)*, and GEKKER *(41)*, the chamber of the large orifice (distal chamber) represents a stomodeal pouch or vestibule that was protected by the operculum and provided with protrusible tentacles for the capture of nutrients. It functioned then as a mouth and the small orifice was inferred to be the anus. CUÉNOT and GEKKER supposed that the marginal grooves on either side of the "anus" served for transport of excreta away from the oral field, whereas SPENCER and NICHOLS offered no guess concerning their function. If the grooves really carried excreta, in the case of *Decacystis* they would bring this waste into contact with the mouth.

JAEKEL *(54, 55)*, BATHER *(13)*, and GISLÉN *(45)* adopted an opposite interpretation, concluding that the large orifice corresponds morphologically to the anus and the small one to the mouth. These suppositions are based mainly on the presence of the marginal grooves connected to the small orifice and the resemblance of these grooves to the food grooves of pelmatozoans—certainly a fact. Since the grooves are much shorter in *Gyrocystis* and especially *Decacystis* than in *Trochocystites*, JAEKEL (1918) and GISLÉN (1930, 1934) judged that by evolution they tended to disappear, their reduction being correlated with change from buccal to anal feeding. They imagined that anal respiration analogous to that in crinoids and holothuroids existed in the Homostelea. If so, introduction of water into the digestive tube through the anus would have brought in small food particles and would have led eventually to reversal of the alimentary current, rendering the presence of nutritive grooves superfluous.

The interpretation just stated is opposed by the following observations: 1) though anal respiration does occur in crinoids and holothuroids, anal nutrition is entirely unknown in any echinoderm; 2) it is by no means established that the approximately contemporaneous genera *Trochocystites, Gyrocystis,* and *Decacystis* are progressive stages of a single lineage and consequently an inferred trend toward disappearance of their marginal prooves is quite unproved, for the contrary is possible or the three genera may belong to different lineages; 3) the alleged reduction of the grooves affects neither the dimensions of the small orifice nor the width of the left groove near it, and even in *Decacystis* the well-developed nature of the orifice and associated groove indicates that they must have been functional.

Differences between characters of the grooves in various genera and even in individuals belonging to the same genus (mainly *Gyrocystis* and *Decacystis*) suggest another explanation. In *Trochocystites,* which has long, deep, sharply terminated grooves, the food-capturing organs housed by them must have been totally affixed to the theca (epithecal) or nearly so. In *Gyrocystis* and above all in *Decacystis,* which have shorter and shallower grooves, difficult to perceive in some individuals and generally without clear terminations, the food-gathering organs must have projected more or less freely into the water (exothecal) away from their proximal attachments. This does not signify that the Homostelea possessed a pair of brachioles inserted on either side of the oral aperture, as imagined by HAECKEL *(49)* and MELÉNDEZ *(62)*. Instead, the organization suggests the presence of a sort of two-branched lophophore which was epithecal in some genera and partly exothecal in others.

What then are the morphological implications of the large orifice, distal chamber, and operculum, and how did they probably function? The infundibular shape of the distal chamber and its protruding lower lip suggest the existence of a protrusive organ, which perhaps was a kind of tube designed for jet expulsion of excreta, or possibly a cloaca *(45)* into which not only the digestive tube but organs such as gonads could have emptied. The operculum doubtless would have protected these organs. BATHER (1925) considered this cover to be "a movable shield to guide the excreta [away] from the inflowing food-stream." Certainly, the fact that the operculum is attached by its proximal border, with apophyses of the adjacent marginals overhanging it, proves that this plate could not turn its distal edge so as to extend in front of the theca to support food-catching organs of some sort, as supposed by JAEKEL *(55)*, CUÉNOT *(32)*, NICHOLS *(68)*, and MÜLLER (1963).

STELE

The stele tapers throughout its length and shows the same organization from one end to the other (Fig. 363, 370). Consequently, it is impossible to differentiate dissimilar parts, as in the Homoiostelea. The stele is depressed and like the theca shows a flattened inferior surface, which is slightly and regularly rounded, and a gabled superior surface with a median ridge above planate or slightly concave flanks. The two surfaces meet laterally in keels (Fig. 370,*1,2*).

Passage from the stele to the marginal framework of the theca is entirely gradational, for outlines of the stele comprise prolongation of the thecal contours. Also, the upper surface of the stele rises evenly to the superior face of the proximal marginals M_1 and M'_1 meeting it confluently. Its lower surface is at the level of the inferior face of these marginals and continuous with it. Above all, the form, size, and ornament of the first stele ossicles (most proximal ones) are transitional to plates of the thecal frame (Fig. 370,*1,2*). The passage is so gradual in *Decacystis* that GISLÉN *(44)* classed as marginals two plates that by analogy with other genera belong to the stele (Fig. 366,*1,2*).

The stele is composed basically of two series of opposed or alternating ossicles (called sphenoids by JAEKEL, 1918), with both conditions commonly present in the same stele. Along the mid-line of both faces a variable number of small supplementary plates (called intersphenoids by JAEKEL, 1918) generally are intercalated. They are polygonal or lozenge-shaped platelets inserted like wedges between the main plates and those on opposite surfaces of the stele do not correspond to each other.

An axial canal of very small diameter extends throughout the stele but becomes enlarged toward its proximal end where it opens into the thecal cavity through a short

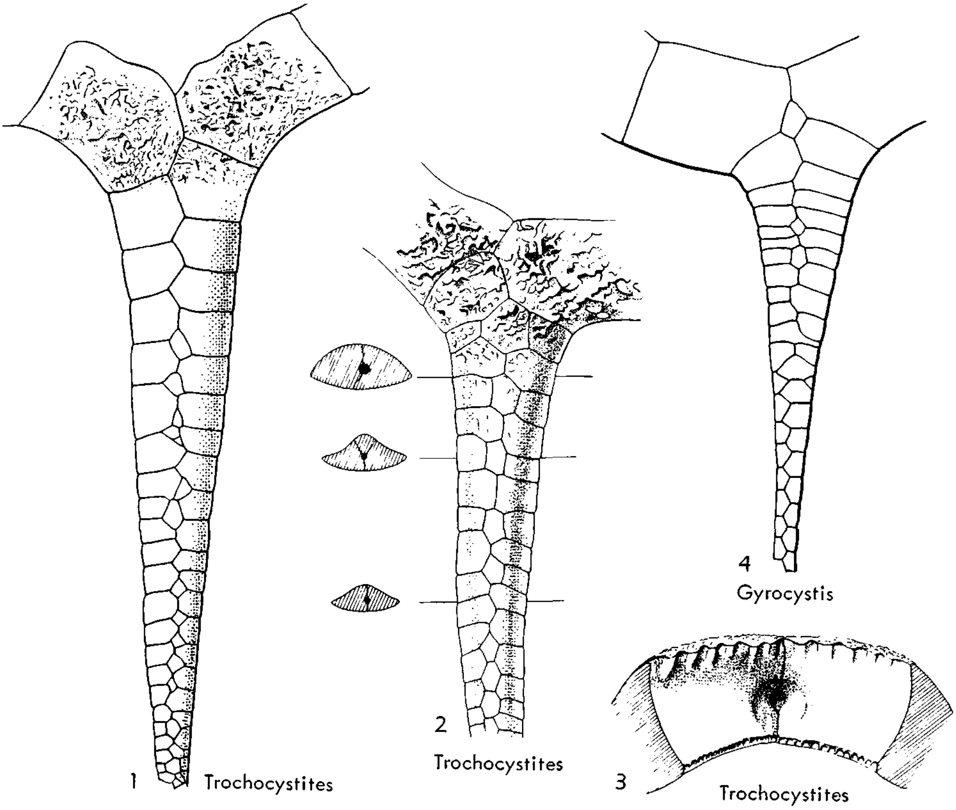

FIG. 370. Stele of Homostelea.——*1-3*. **Trochocystites bohemicus* BARRANDE, M.Cam., Boh.; *1*, lower face; *2*, upper face and transverse sections; *3*, thecal opening of axial canal of stele, all ×3.75 (Ubaghs, n).——*4*. **Gyrocystis barrandei* (MUNIER-CHALMAS & BERGERON), M.Cam., Fr.; lower face, × 3.75 (Ubaghs, n).

funnel excavated in the junction faces of marginals M_1 and M'_1. The floor of the funnel is at the level of the internal faces of the infracentrals, but its ceiling is well below the internal faces of the supracentrals (Fig. 370,*3*).

The stele of the Homostelea thus can be considered as a tubular extension of the theca having the morphologic nature of a peduncle. Nothing indicates that it is homologous to the stem of a Crinozoa, however, and in fact it may have been developed from quite a different body region. Further, nothing indicates that the stele served the same function as the crinozoan stem. Its depressed form, lack of flexible union with the theca, as well as union of its component ossicles, its rigid aspect, the lack of evidence that it served as means of fixation, seems to indicate that the stele never fulfilled the role of support, although it may have helped to stabilize the animal. Many fossils show the stele pointed obliquely downward from the plane of the lower thecal surface, suggesting that it was thrust into sea-bottom sediment during life.

THEORETICAL CONSIDERATIONS

According to WALTHER (1886) and HAECKEL (1896), the symmetry plane of the Homostelea should correspond to the plane of bilateral symmetry of the dipleurula and the theca interpreted as depressed dorsoventrally. This homology was challenged by NEUMAYR (1889) and rejected by BATHER *(11,13,21)*, of whom the latter judged that the extension plane of the homostelean theca should be considered as equivalent to the sagittal plane of the dipleurula, and its two surfaces then would be right and left. It may be noted that in 1900 BATHER identified the concave (inferior) thecal face as right and the opposite convex (superior) face as left, but in 1913 transposed these identifications. Subsequently (BATHER, *20,21*) became convinced that the "carpoids" comprise a group of their own, distinct from all other echinoderms, and postulated that they were derived from a dipleurula fixed by its ventral surface and not by its preoral lobe. Thus attached, the ancestral organism would have reversed positions of its head and tail, acquiring a Y-shaped form with the tail pointed downward and the body upward with mouth and anus located at extremities of the divergent upper branches of the Y. No torsion of internal organs is postulated by this hypothesis. The Homostelea would have been derived from this archetype by shortening of the stem and branches and close approach of the two apertures to one another.

CHAUVEL *(30)* adopted another initial premise and consequences deduced from it, namely, a dipleurula attached by its preoral lobe rather than its ventral surface, thus having at the outset the imagined ancestral pelmatozoan condition with mouth at the body pole opposite to its point of fixation, with anus in lateral position, and with internal organs, particularly the digestive tube, subjected to a characteristic torsion. Then appearance of the two lobes bearing the mouth and anus would have led, as in the preceding hypothesis, to a Y-shaped ancestor which by convergence of the two apertures and development of ambulacral grooves could have yielded *Trochocystites* and genera allied to it. In sum, the Homostelea and other "carpoids" would have the same origin as the pelmatozoan echinoderms but because of their very early separation from the primitive stock would retain in common with others only the stem (stele), constructed on a very special plan, however.

Based on the postulate that the digestive tube of most primitive echinoderms had an arcuate shape with concavity on the ventral side, GISLÉN *(45)* concluded that the space between the mouth and anus represents an extremely shortened ventral surface. The approach of mouth and anus toward one another and their displacement to the superior face of the theca must constitute secondary phenomena, however, corresponding to the stage of asymmetry distinguished by HEIDER (1912) in the ontogenetic development of echinoderms generally. If the Homostelea belong to an equivalent phylogenetic stage, their left somatocoel should be found beneath the superior thecal face and the right one next to the inferior face. Also, the right axocoel should have been already much reduced and the left one well developed, located possibly beneath the anal operculum. The left hydrocoel should have extended beneath the ambulacral groove, thus being confined to the right anterior border of the body, whereas the right hydrocoel probably was much reduced.

Even if the concept of GISLÉN seems to accord with indications drawn from the study of early ontogenetic stages of living echinoderms, like other hypotheses it remains purely speculative. The interior of the homostelean theca has preserved such little trace of the organs and cavities enclosed by it that effort to reconstruct their true organization seems futile. No basis allows assertion that their stele is homologous to the pelmatozoan stem or that their digestive tube displayed the helicoidal torsion characteristically present in crinoids.

GLOSSARY OF MORPHOLOGICAL TERMS USED FOR HOMOSTELEA

[Terms considered as synonyms or terms of lesser importance are printed in italics].

absteleal. Directed away from stele.

adsteleal. Directed toward stele.

Analklappe. See operculum.

anal valve. See operculum.

axial canal. Longitudinal passageway through stele.

central(s) (pl., **centralia**). Plate(s) located inside marginal framework either on lower or upper face of theca (*see* infracentral and supracentral). theca (*see* infracentral and supracentral).

clapet buccal. See operculum.

dimere. Any ossicle of two main series which compose stele.

distal. Referring to direction away from junction of theca and stele.

distal chamber. Enclosed space hollowed into marginal framework between large orifice and thecal cavity.

epanal. See suranal plate.

epicentral(s) (epicentralia). See supracentral(s) (pl., supracentralia).

eporal. See suroral.

extension plane. Plane in which theca is depressed (syn., extensiplane).

extensiplane. See extension plane.

frame (framework). Series of plates which constitute margin of theca, i.e., marginals and suroral.

hypocentral(s) (hypocentralia). See infracentral(s) (pl., infracentralia).

inferior. Directed toward inferior face.

inferior face. Flattened or concave side of theca or stele, presumably toward sea bottom in life position (*syn.,* lower face, reverse face).

infracentral(s) (pl., **infracentralia**). Plate(s) located inside framework on inferior face of theca.

intersphenoid. Any supplementary small plate along mid-line of stele.

left side. Referring to side corresponding with left of observer, when theca is placed on its inferior face with aulacophore toward observer; opposite of right side.

lower. See inferior.

main axis. Imaginary longitudinal straight line through stele and prolonged across theca.

marginal(s) (pl., **marginalia**). Ossicle(s) of series framing theca.

marginal groove. Furrow running on outer side of marginals and leading to small orifice (mouth) (considered as ambulacral furrow).

obverse. See superior.

operculum. Seemingly movable plate covering distal chamber.

proximal. Referring to direction toward junction of theca and stele.

reverse. See inferior.

right side. Referring to side corresponding with right of observer, when theca is placed on its inferior face with aulacophore toward observer; opposite of left side.

sphenoid. See dimere.

stele. Relatively slender and tapering peduncular prolongation of body.

superior. Directed toward superior face.

superior face. Convex side of theca or stele presumably directed upward in life position; opposite of inferior face (*syn.,* upper face, obverse face).

supracentral(s) (pl., **supracentralia**). Plate(s) located inside marginal framework on superior face of theca.

suranal facet. Small slightly concave surface on framework serving for articulation of suranal process or suranal plate.

suranal margin. Thick firm proximal upper border of distal chamber; apparently composed of fused supracentrals.

suranal plate. Ossicle of series forming proximal upper margin of distal chamber.

suranal process. Lateral outgrowth uniting suranal margin with marginal framework.

suroral. Fixed thecal place above small orifice (mouth); included in marginal framework.

symmetry plane. Plane passing through main axis and perpendicular to extension plane.

theca. Body skeleton exclusive of stele.

upper. See superior.

MODE OF LIFE

That the Homostelea reposed on one of their thecal faces is proved beyond doubt by the depressed form of their body, by differentiation of the two surfaces of their theca and stele, and by the distal termination of the stele in a point, indicating that it was manifestly incapable of serving for vertical support. The surface of the theca that rested on the substrate can only be the one designated as inferior, as denoted by its flat or concave form, conformation of the marginal frame, and absence on this side of the body of orifices and associated structures having presumed respiratory function, which are concentrated on the opposite face.

Nonetheless, BATHER *(13)* considered it difficult to imagine such organisms as resting directly on a sea bottom occupied by the kind of sediments—muddy sands or marly limes—which is represented by the rocks commonly associated with the remains of these "carpoids," for in his view the sand grains and clay particles would have fouled the food grooves and filled the mouth much too easily. Accordingly, he supposed that the animals attached themselves like a cupping glass to the thallus of algae, no traces of which are preserved, of course. The protuberances and other inequalities of the underside of the marginal frame make a sucking action of the inferior thecal face quite impossible, however. It appears, then, that the Homostelea could not have lived in the manner imagined by BATHER.

We may recall that the nutritive grooves of the homostelean theca are protected by a cover of platelets. Possibly, as suggested by NICHOLS *(68)*, these animals led a semi-sessile existence on the sea bottom, exploring with their tentacles the area around them while fixed at a given place by their stele dug into the sediment—indicated, as previously mentioned, by the oblique downward attitude of the stele in many fossils. Perhaps they lived in still more fixed location, for the stele appears to have had almost no capacity for movement—indeed, they may have led a partial burrowing existence, limited to gathering food particles suspended in the sea water by their tentacular or mucociliary action and to producing vibratile respiratory currents on the surface of their body. Previously stated are reasons for support of the hypothesis that a sort of lophophore functioned in relation to the marginal grooves.

PHYLOGENY

The origin of the Homostelea and their descent—if such there may be—are equally mysterious. Confined within limits of the Middle Cambrian, these "carpoids" are tied to other echinoderms by no known intermediate links. They have long been regarded, it is true, as Pelmatozoa (Crinozoa), the modified ancestral characters of which must have been produced correlatively with acquisition of a recumbent and partially free mode of life. In support of this interpretation their possession of epithecal furrows analogous to the food grooves of pelmatozoans and close association of their mouth and anus near the thecal pole opposite to the stem have been cited. Accordingly, *Trochocystites* was said to be derived from a form resembling *Aristocystites* by lateral compression of the body *(11)*, or from a vermiform eocrinoid similar to *Cigara (55)*, or from a form *(Eikocystis)* supposedly related to *Stromatocystites (24)*.

These are only conjectures, at best. Detailed comparisons reveal no real resemblance of Homostelea to the pelmatozoan echinoderms and bring to light no certain homology with them. Quite unlike these echinoderms which display a fundamental radial symmetry from the moment of their appearance, the Homostelea exhibit not a trace of such symmetry. Their stele has a twofold structure that is unmatched by the stem of crinozoans. Their principal orifices of the theca possess entirely individual traits, and if the depressed form of their body, girdled by a massive frame, is not an exclusive attribute, at least these are constant characters which canont be explained—by lateral compression or play of secondary transformations—as derivatives of diagnostic pelmatozoan features.

When compared with other "carpoids," some of the Cornuta are not to be overlooked, for their theca, like that of the Homostelea, is framed by thick marginal plates and the integument of their superior and inferior faces is reinforced by small plates. KIRK *(56)* saw in *Trochocystites* the possible source of other "carpoids," Bather *(20)* viewed *Mitrocystites* and its allies as derivatives of a form close to *Trochocystites,* and Gislén *(45)* in agreement with Jaekel *(55)* delineated a morphological series beginning with *Trochocystites* and ending in the Mitrata which was thought to illustrate the progressive reduction and ultimate disappearance of ambulacral grooves in the course of evolution.

Nothing is less certain, however, than descent of the Mitrata from the Homostelea, or more broadly, any kinship whatever between the Homostelea and Stylophora. The former are distinguished from the latter by: 1) the presence of a stele, comprising a peduncular prolongation of the theca; 2) the absence of a brachial process possibly correlatable with the stylophoran aulacophore; 3) adjacent location of the two main thecal orifices near one pole of the body in contrast to their positions at opposite extremities of the theca in the Stylophora; 4) the peculiar nature of the homostelean orifices and their close association with the marginal frame; 5) the presence of one or two epithecal grooves excavated in the marginals and connected to one of the orifices; 6) the existence of a special plate termed operculum protecting the large orifice, quite without equivalent in the Stylophora; and 7) entire absence of such structures as the infundibulum, scutulae, septum, and internal marginal grooves which are found inside the theca of stylophorans.

Among the Homostelea and Stylophora, then, not a single morphological character can be considered to be homologous. The presence of a marginal framework in each group is not a significant phylogenetic link, since the same structure is seen in other classes (e.g., Eocrinoidea, Edrioasteroidea) with a high degree of resemblance.

A comparison of homosteleans with the Homoiostelea yields no more certain indication of affinities. To be sure, a peduncular prolongation of the theca is found in both groups, but in the Homostelea this displays the same organization throughout its length, whereas in the Homoiostelea it is clearly divided in characteristic manner into two quite distinct regions. Moreover, the relations of stele to theca and of the axial cavity of the stele, narrow in the one group and wide in the other, to the cavity of the theca show no similitude. Other features show still greater differences. For example, the Homostelea lack a brachial process such as occurs in the Homoiostelea. The mouth and anus lie close together in the former group but far apart in the latter. The two thecal faces generally are much less differentiated in the Homostelea than in the Homoiostelea, and the marginal frame, which is a constant attribute of the first, ordinarily is lacking in the second. Therefore, no justification seems to exist for placing the two groups in the same class, as hitherto done.

Concerning interrelationships of *Trochocystites, Gyrocystis,* and *Decacystis,* no significant facts allow elucidation. These genera are contemporaneous, or nearly so. Intermediate forms are lacking and the trends of their evolution are unknown.

SYSTEMATIC DESCRIPTIONS

Class HOMOSTELEA
Gill & Caster, 1960

[*nom. transl.* Ubaghs, herein (*ex* subclass Homostelea Gill & Caster, 1950)]

Homalozoa with skeleton composed of theca and stele; theca depressed in plane (extension plane) passing through main orifices and stele attachment, with convex surface (superior face) and opposite flat or slightly concave surface (inferior face) united in girdling frame of thick marginal plates; superior face formed within marginals by numerous loosely joined plates termed supracentrals except near pole opposed to stele where they fuse or are replaced by row of stout suranal plates; at absteleal pole and excavated in marginal frame is large thecal orifice inferred to mark location of anus; it is protected by apparently movable plate designated as operculum; adjacent is smaller circular orifice that probably represents mouth; periphery of theca adjacent to presumed mouth bearing one or generally two epithecal grooves hollowed in outer face of marginals, grooves connected to mouth and protected by multitude of minute cover plates; inferior thecal face formed within marginals of close-fitting polygonal infracentrals, without orifices. Stele tapered, depressed in same plane as theca, with convex superior

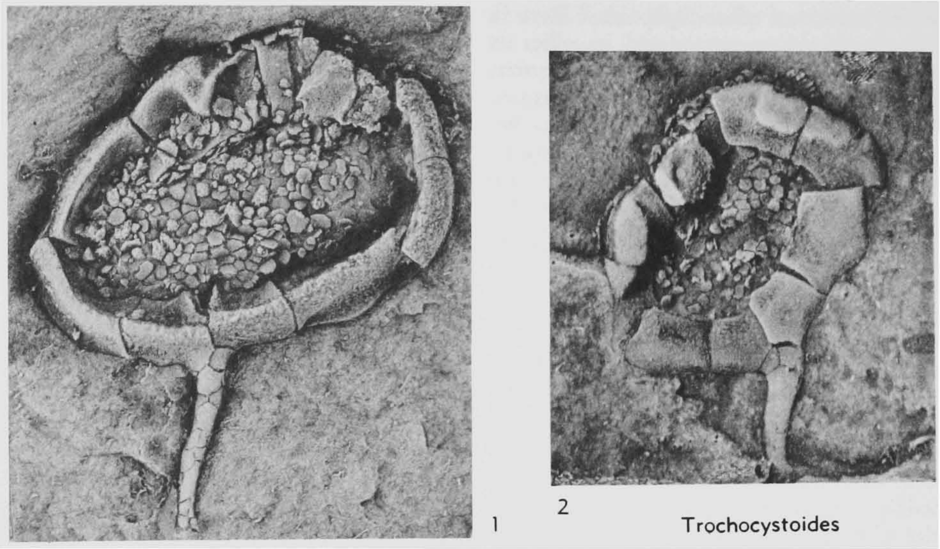

Fig. 371. *Trochocystitidae.*——*1. Trochocystoides* sp. cf. **T. parvus* Jaekel, M.Cam., Boh.; upper face, ×5 (Ubaghs, n).——*2.* **T. parvus* Jaekel, M.Cam., Boh.; lower face (?holotype), ×5 (Ubaghs, n).

face in form of ridge and flat or slightly convex inferior face which meet laterally as angled keels, constructed of two rows of opposed or alternating ossicles (dimeres) between which variable number of small irregular platelets commonly are intercalated on superior and inferior faces; narrow axial cavity of stele confluent with thecal cavity. *M.Cam.*

Order CINCTA Jaekel, 1918

[=suborder Marginata Jaekel, 1901 *(partim)*]

Characters of class. *M.Cam.*

Family TROCHOCYSTITIDAE Jaekel, 1901

[=Trochocystidae Bather, 1902 *(nom. van.)*]

Well-developed marginal groove on each side of small circular orifice (mouth), both of them long and deep; centrals of inferior thecal face small and numerous. *M.Cam.*

Trochocystites Barrande, 1887 [**T. bohemicus*; M] [=*Trochocystites* Barrande, 1859 *(nom. nud.)*; *Trochocystis* Haeckel, 1896 *(nom. van.)* (obj.); *Trigonocystis* Haeckel, 1896 (type, *T. trigona*)]. Marginals typically 12, with rounded upper external slope, knobs on lower face of M_2, M_3, M_4 and M'_2, M'_3, M'_4; marginal grooves generally ending on M_3 and M'_3; suranals indistinctly separable from adjoining centrals. *M.Cam.*, Boh.-?Ger.(Bavaria)-?Fr.——Fig. 364,*1-3*. **T. bohemicus,* Boh.; *1-3,* distal, proximal, lat. views of theca, ×3 (Ubaghs, n). [See also Fig. 363, 367-370.]

Trochocystoides Jaekel, 1918 [**T. parvus;* M]. Marginals typically 10, with slightly convex to concave upper external slope, knobs on lower face of M_3, M_4 and M'_3, M'_4; marginal grooves ending on M_3 and M'_3; stele relatively narrow, distinctly convex on upper face, slightly so on lower face. [A single specimen identified by Jaekel as **T. parvus* which I have been able to study shows only the lower side (Fig. 371,*2*). It seems to belong to the same species as a small form that was confounded by Barrande with **Trochocystites bohemicus.* None of the specimens examined by me, however, exactly show features reported by Jaekel to be diagnostic of this genus.] *M.Cam.,* Boh.——Fig. 371,*1,2.* **T. parvus*; *1,* upper side of specimen (cf. **T. parvus*) figured by Barrande (1887, pl. 3, fig. 6, 7), ×5 (Ubaghs, n); *2,* lower side of another specimen (?holotype), ×5 (Ubaghs, n).

Family GYROCYSTIDAE Jaekel, 1918

Marginal grooves relatively short, right one very much reduced or even wanting; centrals of inferior thecal face comparatively larger and fewer than in Trochocystitidae; suranals distinct, three or four. *M.Cam.*

Gyrocystis Jaekel, 1918 [**G. platessa*; M (=**Trochocystites barrandei* Munier-Chalmas & Bergeron, 1889; ?*T. occidentalis* Jaekel, 1901)] [=*Sucocystis* Termier & Termier, 1958 (type, *S. theronensis*)]. Marginals typically 12, with flat or concave upper external face, generally with prominent knob on marginal beneath large thecal orifice and less prominent swellings on either side; marginal grooves ending on M_5 and M'_5. *M.Cam.*, Fr.-Morocco.——FIG. 365,*1-4*. **G. barrandei* (MUNIER-CHALMAS & BERGERON), Fr.; *1-4*, upper, lower, distal, and right lat. views of theca, ×3 (Ubaghs, n).

Decacystis GISLÉN, 1927 [**D. hispanica*; M]. Marginals 10, with flat upper external face; right marginal groove wanting, left one ending on M'_4. *M.Cam.*, Spain-France.——FIG. 366,*1-3*. **D. hispanica*, Spain; *1-3*, upper, lower, and distal views of theca, ×3 (10).——FIG. 366,*4*. *D.* sp. cf. **D. hispanica*, Spain; distal view of theca, ×5 (Ubaghs, n).

[References for the chapter on Homostelea are included with those for Stylophora and Homoiostelea (*see* p. S624).]

HOMOIOSTELEA

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[In the preparation of this section it has been necessary to re-examine much original type materials of BARRANDE, BATHER, JAEKEL, THORAL, and UBAGHS, and to study extensive supplementary material. To the officers and staff of the Narodni Museum, Prague; British Museum (Natural History), London; Museum of Humboldt University, East Berlin; Department of Geology, University of Lyon; Montpellier University, Lyon; University of Greifswald; Hunter Museum, Glasgow; United States National Museum, Washington; Geological Survey of Canada; Victoria National Museum, Melbourne; and to private collectors, R. COURTESSOLE and G. and G. GRIFFE, Carcassonne, FR. KRANTZ, Bonn, and many others, deepest thanks. Very special thanks go to GEORGES UBAGHS, RONALD PARSLEY, and EDMUND D. GILL.]

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INTRODUCTION

The Homoiostelea (U.Cam.-L.Dev.) form a part of the former class Carpoidea JAEKEL (1902) and are coextensive taxonomically, as herein revised, with JAEKEL's order Soluta. They share with other "carpoids" the possession of fundamental asymmetry of skeletal organization and show varying degrees of superimposed bilateralization; moreover, a tendency toward flatness (depression) is common to all. They possess an exothecal arm, plated theca and tail-like stele (heterostele).

THECAL APPENDAGES

The name Homoiostelea (similar stele) comes from GILL & CASTER (1960), who attempted to point up axial differentiation of the "tails" in the Soluta, and also in the Cornuta and Mitrata (Stylophora), into three zones, as against the condition in the Homostelea (=JAEKEL's Cincta) where zonation does not exist. It was the assumption of previous authors that all carpoid steles are homologous, both in origin and function. It now appears, as a result of work by UBAGHS (1961) on Cornuta and (elsewhere in this volume) on Mitrata (these two orders of JAEKEL comprising the new class Stylophora), that the functions of the solutan "tail" and arm were both performed by the single serial appendage of stylophorans, the aulacophore. Herein lies the basis for a difference of opinion as to the homologies and orientation of the whole organism as between the Soluta and Cincta on one hand and the Stylophora on the other.

UBAGHS (*Treatise,* p. S496) correlates the stylophoran aulacophore with the solutan arm because of their common subvective function. Consequently, he prefers to designate the base of the aulacophore, like the base of the arm, as anterior (see Fig. 325-326, 343-350, this volume), since both presumably lead to the mouth of the organisms. But, whereas mouths are always anterior in position in primordial bilaterians, "carpoids" appear to have undergone two stages of metamorphism beyond that condition: some degree of radial superimposition, perhaps associated with fixation; and secondary freedom and very advanced secondary superimposition of bilateralization, which is never complete. In most eleutherozoic echinoderms "anterior" is conventionally the direction of forward movement, and this seldom coincides with the position of the oral-anal axis or mouth.

It is my opinion that in this complex of convergently adapted eleutherozoans, which might be termed the "cladus Carpoidea," all exothecal tetramerous organs are modified biserial arms, and hence are all radial homologues. According to this view, all "carpoid" heterosteles are radially homologous. The stylophoran aulacophore has primitively retained the radiate subvective function, the while also serving the free-moving "tail" function of the heterostele in other "carpoid" classes. All seem best designated as heterosteles in accord with JAEKEL's original proposal (1901). The aulacophore is, then, a special kind of heterostele.

The convergent form of "carpoids" seems to have been selectively determined in accord with hydrodynamic principles and correlated with bottom-moving in a flatfish-like manner. A swollen anterior body (theca), usually rounded anteriorly, and depressed, more or less parallel-sided, and bearing a posterior caudal appendage (heterostele) for steering and locomotion, is the recurrent plan. The recurrent analogy of the heterostele to a fish tail in all three classes of "carpoids" seems to have orientational validity.

The steles ("tails") of Homostelea and Homoiostelea are apparently completely homologous both in origin (probably from a biserial arm) and in caudal, wholly locomotor, function. In the former, however, the mosaic plating and lack of axial zonation of the component meres bespeak much less motility of the stele than in the homoiosteles, where zonation and either marked imbrication or flexible integumentary suturing of the proximal stele meres is usual. In both classes the proximal steles (proxisteles) are tetramerous and the distal steles (dististeles) dimerous; this is achieved in both instances by the distal diminution of alternate series of tetrameres (see Fig. 378). In the Stylophora, the dististele (distal aulacophore) appears to be uniserial. In the homosteles the close proximity of mouth and anus on the anterior thecal margin localizes the oral-anal axis to a short line on the distal margin, whereas in the homoiosteles the axis is lateral (never in the axial plane) or diagonal, due to the wide separation of the two apertures. If mouth and anus determine anterior and posterior orientation of the organisms, in neither case is the caudal stele posterior. In no instance has the solutan mouth been observed to fall on the morphologic axial plane of the organism. In some stylophorans, where derived bilateral symmetry is most advanced among "carpoids," the oral-anal axis and axial or bisymmetry-plane do seem to coincide. However, in this last class, the anus lies on the leading, distal (anterior) margin of the theca and the mouth at the base of the aulacophore (subvective tail).

SYMMETRY AND ORIENTATION

Inasmuch as the homoiosteles are depressed (that is, flattened[1]) asymmetric

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[1] Like all echinoderms, the homoiosteles were presumably bilaterians showing a fundamental asymmetry in their embryological development. However, the identification of their original bilaterian coordinates is highly speculative, as is also the degree to which their observed skeletal asymmetry correlates, if in any wise, with that of the dipleurulan

creatures which exhibit bilateral tendencies, they pose special problems in geometric nomenclature. It is quite impossible to employ the terms dorsum (dorsal), venter (ventral), and right and left sides in their true bilaterian morphologic sense. However, it now develops that the last two can be used pretty consistently in the Soluta in a purely descriptive conventional sense, thus rendering unnecessary the substitute and less clear terms which BATHER (1913) proposed. Synonymous names for morphology and symmetry components are indicated (Fig. 372).

Two planes of reference can be distinguished in the Homoiostelea: 1) the plane of flattening, which BATHER (1913) called the **extension plane,** and GILL & CASTER (1960) the **extensiplane;** and 2) the plane normal to this and passing through the axis, which BATHER termed the **symmetry plane,** with respect to which all forms show some degree of bilateralism, hence sometimes called the "bilateral plane" or bisymmetry plane. The main course of the organic axis is judged from the symmetry plane of the stele, which is then projected through the theca. Shortening normal to the extensiplane is **depression** (flattening), and in the extensiplane, normal to the symmetry plane, **compression** (shortening of the width).

Whereas in unmodified bilaterians the **oral-anal axis** coincides with the axial and bisymmetry planes, and hence determines the historic anterior and posterior orientation, in homoiosteles, like most other "carpoids," there is no such coincidence. In fact, the two axes usually meet at a high angle, or, exceptionally, cross one another. Hence the "anterior" and "posterior" labels on solutans are conventional and ecologic rather than historical and physiologic. Being, like all "carpoids," vagile benthos, the solutans (=homoiosteles) possessed a caudal organ that served a propulsive or steering function, or both. This organ was the tail, *"tige,"* or stele (heterostele), or, in the Stylophora, the aulacophore, a subvective stele. The caudal appendage was **functionally posterior.** Neither the position of the mouth or anus nor the trend of the oral-anal axis serves among homoiosteles (or in other "carpoids") to establish conventional, functional anterior and posterior.

The depression of the theca usually results in the existence of two thecal surfaces or **faces.** In the past, these, where recognized, have been variously denominated with respect to the correlation with arm-mouth or anus. Thus BATHER (1913) distinguished the "adbrachial" (="brachial" of authors) and "antibrachial," or "anal," and "antanal" faces. (In "carpoid" descriptions **ant-, anti-, counter** and **opposite** have been used synonymously.) BATHER (1913) also employed **obverse** and **reverse** for the thecal faces which he judged to have been respectively upper and lower in life. However, he was unable consistently to employ these terms, and did not attempt to use them in describing homoiosteles. With exception of the seemingly almost fusiform (data for this conclusion doubtful) *Heckericystis,* the seemingly truly globular *Dehmicystis,* and the nummuloid *Rutroclypeus,* the two faces can be identified consistently and homologized. Therefore, the denominations obverse (upper, carapace) and reverse (lower, plastron) are quite acceptable. Since the position of the anus is highly variable, both as to the side and face on which it occurs—and to some degree the same is true of the solutan arm—face denominations with respect to these organs are misleading. BATHER (1913) also identified the **sides** (flanks) in terms of the anus and arm position. Since top and bottom faces are now pretty generally recognizable in homoiosteles, there seems to be no good reason for not using the simple terms right and left for the sides.

The distance between the two faces of the theca is the **height** or **thickness;** it is usually measured in the symmetry plane. The distance between the sides is **width; length** is an axial dimension. The plane of contact of the stele and theca is conventionally known as the **proximal plane.** However, it is notable that this is apparently not the same plane of reference commonly employed among Crinozoa. Directions toward the proximal plane are **proximal** and away from it **distal.**

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larva. It now seems quite probable that more than one mode of flattening of the bilaterian body has occurred among "carpoids" and that to characterize them all as pleuronect creatures (lying on one side, like flounders) is too comprehensive a generalization, and possibly quite a wrong one. This is a certainty: every "carpoid" is a multiple palimpsest of superimposed symmetries.

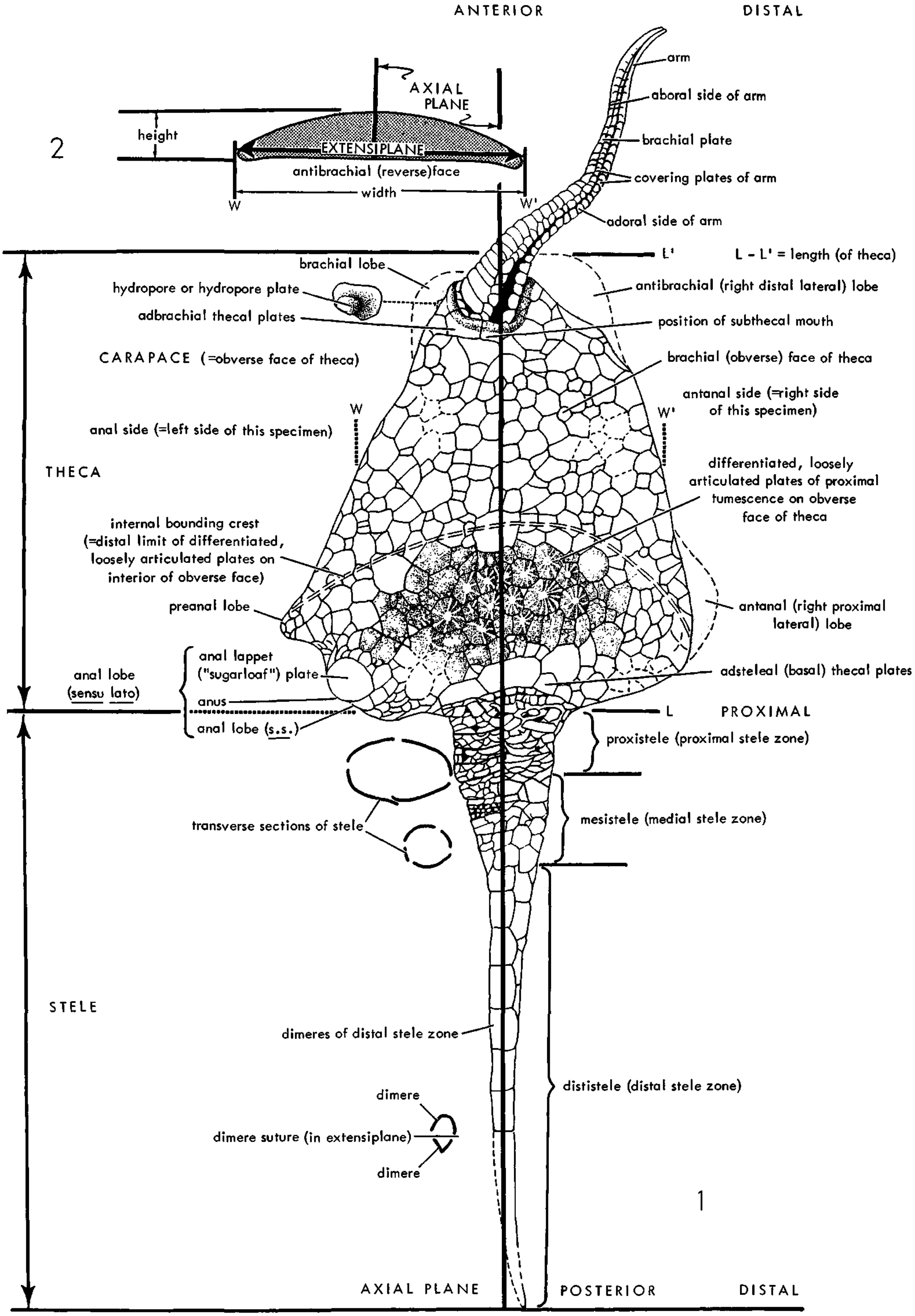

FIG. 372. Homoiostele morphology and orientation (based on **Dendrocystites sedgwicki* (BARRANDE), a generalized solutan "carpoid"). *1,* extensiplane view obverse side, ×1.7; *2,* generalized cross section of theca, ×1.7 (Caster, n; drawn by Elizabeth A. Dalvé from photos and sketches of Barrande specimens from Praha).

MORPHOLOGY

GENERALITIES

The morphologic nomenclature of the Homoiostelea is given in Figure 372. However, this figure hardly conveys the aspect of more advanced members of the class which are commonly strongly homeomorphic with the stylophorans. The body is composed of three regions: 1) the anterior (really anterolateral) biserial **arm,** which commonly has been called a "brachiole" *(13, 43)*; 2) the main body, which was invested with a **theca** of calcareous plates; and 3) the **stele** or **heterostele,** as JAEKEL *(54)* preferred in order to counter the common mistake of referring to the posterior appendage as a "column" or "stem" under the misapprehension that it is homologous with the pelmatozoan column. It is also commonly called a tail or *"tige,"* which best describes its apparent function in life. Undoubtedly, there was in life the usual echinodermal mesodermal fleshy investiture of all calcareous parts. The labyrinthine canals in the skeleton (stereom), occupied in life by fleshy strands (stroma), are commonly preserved (e.g., CASTER & EATON, 1956, described similar histology in Mitrata). Most of the fleshy anatomy of the organism was housed in the theca, but significant extensions undoubtedly reached into the large lumens of the arm and proxistele. The plates of both arm and stele are **bilaterally** arranged; those of the theca quite imperfectly so (*Syringocrinus,* see Fig. 393; *Iowacystis,* see Fig. 394) or not at all (*Dendrocystites,* Fig. 372; *Dehmicystis,* see Fig. 388; *Rutroclypeus,* see Fig. 391, 392; *Girvanicystis,* Fig. 373, 374, see Fig. 389, 390). Plates adjacent to arm, anus, and stele are to some degree regularized, and consistently identifiable in certain genera and to some degree homologous. In some forms, the plate size, number, arrangement, and ornament differ on the two faces, sometimes markedly so; this is termed **facial differentiation.** There may also be **regional differentiation** of plates within a face or organ.

ARM AND RELATED STRUCTURES

Although the exothecal subvective organ

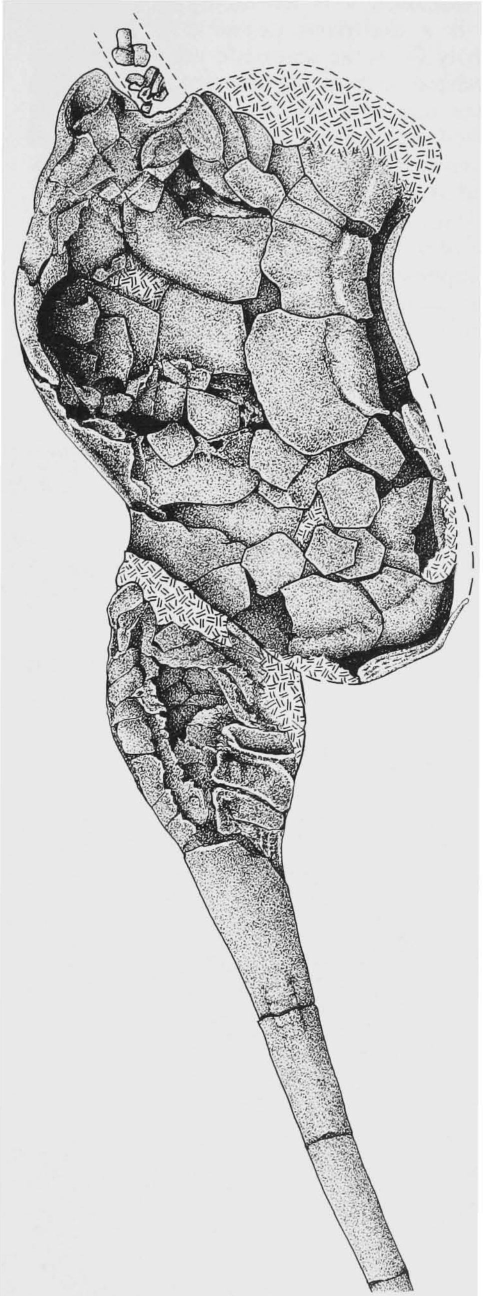

FIG. 373. Morphological features of **Girvanicystis batheri* CASTER, n. gen., n. sp., U.Ord., Scot. (Girvan), showing obverse face of somewhat deformed paratype having well-defined marginal groove for reception of thickened margin of reverse face, ×2.4 (Caster, n; drawn by E. A. Dalvé from photo of BMNH, Begg Coll. no. E5830).

in homoiosteles has been commonly called a brachiole, it is technically an **arm** since it is a skeletized extension of the body cavity (as is the stele) and not a solid serial skeleton such as are true brachioles. It has been termed a "proboscis," under the mistaken impression that it bore a terminal mouth; it also has been erroneously identified as an anal structure. The arm is usually a long, tapering, broadly based organ (e.g., *Dendrocystites*), subterete or somewhat compressed, and covered by two matching but unequal biseries of plates (i.e., it is essentially tetramerously invested) arranged bilaterally. The larger biseries, termed **brachial plates,** usually cover about two-thirds of the arm flanks and meet tightly or flexibly on the **aboral** side; the aboral suture is usually zigzag, reflecting the alternation of the brachial biseries; no aboral suture has been found in *Minervaecystis* (See Fig. 381). There may be slight distal imbrication of the brachial plates. Each plate is about twice as wide as long, and bowed. The adoral gape between the bowed brachials is covered by the matching lesser biseries of plates, the **cover plates,** which articulated with the brachials and met ad-

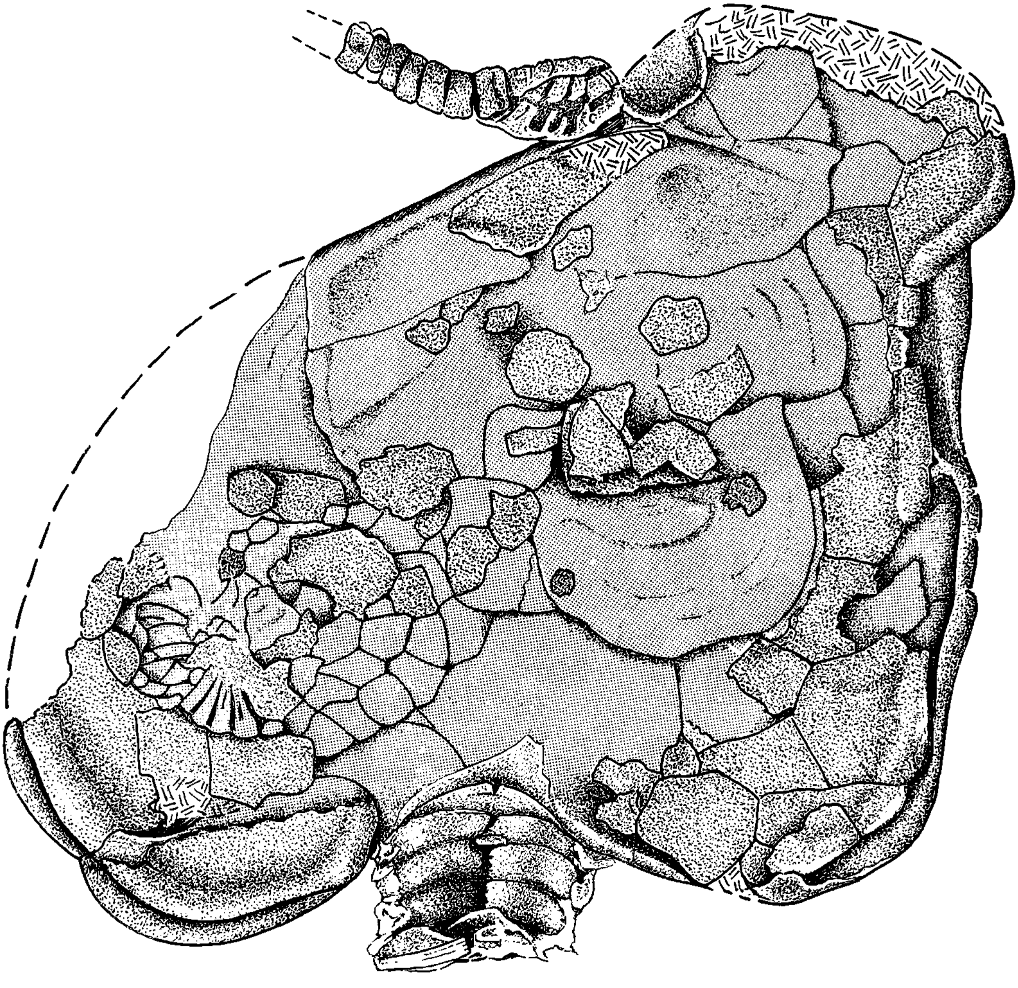

FIG. 374. Morphological features of **Girvanicystis batheri* CASTER, n. gen., n. sp., U.Ord., Scot. (Girvan); obverse face of paratype with pillbox articulation of two faces along extensiplane, ×3.7 (tone pattern on exterior of obverse plates, interior surface of reverse plates stippled) (Caster, n; drawing by E. A. Dalvé from photo of BMNH, Begg Coll. no.E5824).

orally along a zigzag line. The relative width of brachials and cover plates is variable within taxa; they may form a confluent arm surface, or the cover plates may rise in a gable on the adoral side and their articulation with the brachials be a depressed line. Internally both brachials and cover plates bear articulatory muscle scars. The adoral gape of the brachial plates presumably defines the ciliated food groove (ambulacrum) of the living animal. This leads to the concealed mouth, which presumably was situated near the end of the groove, within the theca. As in all other echinoderms, the normal feeding position of the arm was undoubtedly with the adoral side of the arm and the associated ambulacral groove upwardly exposed when the cover plates were open. Thus, the life position of the arm determines the orientation of the whole organism. This is the ultimate recourse in the sometimes perplexing problem of thecal orientation and face determination of the fossil. The adoral features of the arm correspond in position to the obverse side of the theca.

The mouth and gut being unknown, the intestinal course is speculative between the base of the arm and the anus. Of a certainty, it does not follow the oral-anal axis, and the asymmetrical form of the homoiostele theca suggests that it has an arcuate, or perhaps even looped course, and that it probably does not lie wholly in the extensiplane.

The transition from arm to theca is abrupt; nothing has been observed which would support Bather's (1913) contention that the solutan arm skeleton passes gradationally into thecal skeleton (Fig. 375). The arms, so far as known, are consistently tetrameral (except possibly in *Minervaecystis,* see Fig. 381, where quite probably the lack of an aboral suture reflects ankylosis of a biseries). Adbrachial thecal plating is rarely four-part, and the junction between the theca and arm is consistently integumentary, in keeping with the manifest motility of the arm as a whole. In *Dendrocystites sedgwicki* (Fig. 372, see Fig. 383) adults many small polygonal plates occupy the contact zone. These may be sclerites of the integument, or more likely represent the breakup of larger adbrachial plates in the same man-

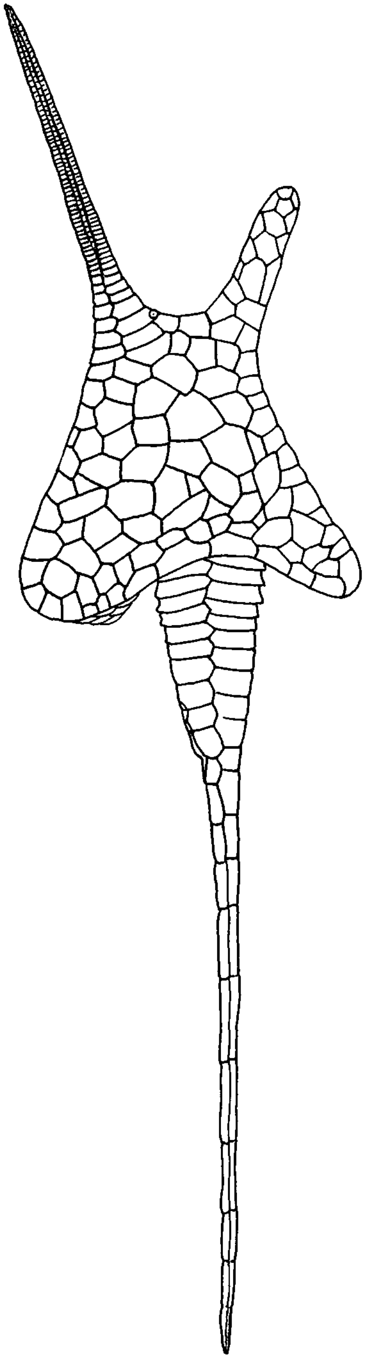

Fig. 375. Complete skeleton of **Dendrocystoides scoticus* (Bather) viewed from obverse side (reconstr.), U.Ord., Scot. (Girvan), ×1.3 (Bather, 1913).

ner as observed in the proxistele of this species. These small plates may have been the basis for much of BATHER's speculation about the relation of arm plating to thecal.

The large adbrachial plates of the theca are always distinctive. They are generically consistent in number and form. They may be a more or less rigid circlet of strongly fused plates, as in *D. sedgwicki* adults; a thickened rim may be developed on them around the arm orifice, as in *Girvanicystis;* this becomes a prominent bordering flange in *Iowacystis* (see Fig. 394). In *D. barrandei* (see Fig. 384, 385), and the Scottish *Dendrocystoides* (Fig. 375, 387), and the French *Minervaecystis* (see Fig. 381), adbrachials strongly geniculate to encircle the arm base and laterally imbricate to form a scalelike sheath. The number of adbrachials in the circlet varies from perhaps six in *Dendrocystites* to four (or fewer) in *Iowacystis.* In In *Girvanicystis* (see Fig. 389, 390) there are apparently four adbrachials, two obverse and two reverse, which are deeply excavated to form the brachial foramen. The size and shape of this foramen depends on the configuration of the proximal arm. Certainly within genera, and possibly more widely, the various adbrachial plates can be homologized.

One adbrachial, lying on the left side of the arm base and usually extending well onto the adoral surface, consistently bears an organ which probably represents a hydropore. In *Dendrocystites* and *Dendrocystoides* this takes the form of a single (see Fig. 386) or multiple (Fig. 376) warty tumescence on the plate. In *Minervaecystis* (see Fig. 381) two distinct prominences, one of which may be gonadal, appear on this plate. In *Girvanicystis* (see Fig. 390) a rimmed pore is developed in the same position, and two produced phialine pores in *Iowacystis* (see Fig. 394); here again, the lesser pore tube may be gonadal. Some of the illustrations of *Rutroclypeus* (see Fig. 391, 392) suggest the presence of a similarly located warty prominence, although it was not originally observed. Since the hydropore structures in most solutans are usually in a slightly inferior position on the adoral side of the arm aperture, they are best seen on specimens revealing the reverse face of the theca.

The arm generally emerges from the left distal area of the theca and from the marginal zone of the obverse face. In *Girvanicystis* (Fig. 373, 374) the arm position is normal, but the foramen is excavated on the peculiar bounding suture between the two faces; also, more of its excavation lies in the two reverse adbrachials than in the obverse ones. Correlating with a recurrent tendency among homoiosteles for the distal theca to become narrow, the arm becomes nearly axial in position (e.g., *Heckericystis,* see Fig. 384,*1*; *Dendrocystites barrandei,* see Fig. 384,*2*; *Dendrocystoides*), or crosses the axis to lie consistently on the right distal side of the theca, as in the deltoidal *Iowacystis* (see Fig. 394). Probably the arm commonly lies in the plane of balance of these usually highly irregular organisms; this seems very much the case in the anomalous girvanicystids.

In *Dendrocystites* and *Dendrocystoides* (and no doubt elsewhere) occur what might be termed mirror anomalies in the position of the arm. Thus, right-armed individuals may occur in a dominantly left-armed assemblage. Only the locus of the arm shifts, however, without any reversal of orientation of correlated structures (i.e., in right-armed forms, the adbrachial hydropore plate is still consistently on the left side of the brachial foramen).

The arm and anus commonly occur on the left side of the theca, as seen in *Dendrocystites, Dendrocystoides,* and *Girvanicystis.* When the arm shifts to an axial or near-axial position this may be hard to prove, and in *Iowacystis* (see Fig. 394) the oral-anal axis crosses the symmetry plane. In forms exhibiting the mirror anomaly, the arm and anus are on opposite sides. But in quite another category is *Minervaecystis* (see Fig. 381), the oldest well-documented homoiostele, where the anus lies on the left proximal lobe and the arm in the exceptional right distal position. This is the best example of the "opposite" condition of mouth and anus. In this inadequately known genus we may be observing a mirror anomaly with respect to the anus. No transitional stages in either the brachial "mirrors" or in attaining the reversed anal position are known.

THECA

The homoiostele theca is depressed, asymmetrical, and multiplated, and recurrently it exhibits a tendency toward bilateralism. The differential flattening in the extensiplane results in a wide variety of depressed thecae. The degree of flattening has usually been exaggerated during fossilization and thecal topography commonly is masked thereby. Moreover, what were tight sutures between thecal plates have been opened in the process and an illusion of thecal flexibility created, whereas in life the form was fixed and relatively rigid. However, since the inferior thecal face, usually the reverse face (*Girvanicystis* is resupinated in this respect), is commonly planate or nearly so, it is less deformed and usually gives a fair clue to the living thecal outline.

But since all homoiosteles are essentially asymmetrical, the form of the thecal perimeter in the extensiplane is difficult to describe. *Dendrocystites* is subcordiform; *D. barrandei* and *Heckericystis* subvasiform?; *Dendrocystoides* irregularly shrubby or tunicate; *Girvanicystis* obliquely subcordiform; *Minervaecystis* and *Syringocrinus* ovoid; *Iowacystis* triangular; *Rutroclypeus* circular; *Dehmicystis* probably globular. In addition, hourglass-shaped, subquadrate, and subtrapezoidal forms are known.

Lateral lobation is especially characteristic of the dendrocystitid solutans, but is seldom seen elsewhere in the class. There are two broad unequal **proximal lobes,** the left being usually the larger. In most specimens the left lobe would correlate with BATHER's (1913) "anal" lobe and the right with his "antanal" lobe. In *Minervaecystis* the larger proximal lobe and "anal" lobe is on the right. Both lobes are usually broadly, but asymmetrically, curved and the left one especially may have considerable posterior development *(Dendrocystites)*. In some *Dendrocystoides* either proximal lobe may be produced posterolaterally as an attenuate process. In *Dendrocystoides,* and in *Girvanicystis* especially, a broad, rounded, right **distal lateral lobe** (BATHER's "antibrachial" lobe) is developed. In right-armed variants a corresponding lobation may occur on the left side, but never to the same degree as on the right. The distal lateral lobe may grade into or be distinct from a **distal lobe,** which is rarely developed on the thecal asymmetry axis; the distal lobe, when developed, extends forward from the base of the arm. In *Dendrocystites sedgwicki* the distal lobe is commonly well developed, but distal lateral lobation is inconspicuous. Both a distal and a distal lateral lobe occur in *Girvanicystis* (see Fig. 390) and are broadly confluent. In addition to these broad and usually depressed extensions of the thecal faces, long, hollow, hornlike plated processes occur in *Dendrocystoides* (Fig. 376, see 386, 387). The most frequently encountered of these lies in an "antibrachial" position, usually right distolateral. However, these processes can develop almost anywhere on the theca, reverse or obverse face. The "antibrachial" horn may arise from either face, or on the flank, or may arise in common with the arm from a distal thecal tumescence. Several such horns have been observed on a single specimen. In a few specimens what appears to be a terminal perforation of a horn has been seen.

The left proximal lobe (usually the "anal" lobe) shows secondary lobation in several genera, especially where the anus is marginal or nearly so. The anus itself is in these specimens associated with the larger, rounded, posterior lobe, the true anal lobe, usually bearing BATHER's "sugarloaf" plate, the anal plate, or anal lappet; this is the **anal lobe,** *s.s. (Dendrocystites, Dendrocystoides)* (see discussion of anus, below). Distally from the true anal lobe and usually marking the widest part of the theca, is a subangular **preanal lobe,** best seen in the above two genera. In *Dendrocystites* this lobe is swollen and possibly bears a marginal aperture. Internally the inside surface of the obverse thecal plates bears an undulatory imprint of a soft-part structure which leads to the apex of this lobe; this may be an organ or conduit.

Heckericystis, as restored by GEKKER [HECKER] (1940), was inflated and not facially differentiated; however, it does show a proximal lateral bulge on the anal side. At the present time it is impossible to assess the accuracy of the restoration of this form.

Although the thecal plates of homoiosteles are commonly imbricated when encountered, this seems to be due to deformation. The plating appears to have been mosaic, with either firm sutures or integumentary junctures. Even among the supposedly wholly flexible dendrocystitids, there is good evidence that the thecal configuration was quite constant in life and that many of the plates were firmly joined (e.g., Fig. 382,*1*).

Restudy of the types of the Bohemian *Dendrocystites sedgwicki* and of considerable new material indicates that young specimens bore fewer and relatively larger

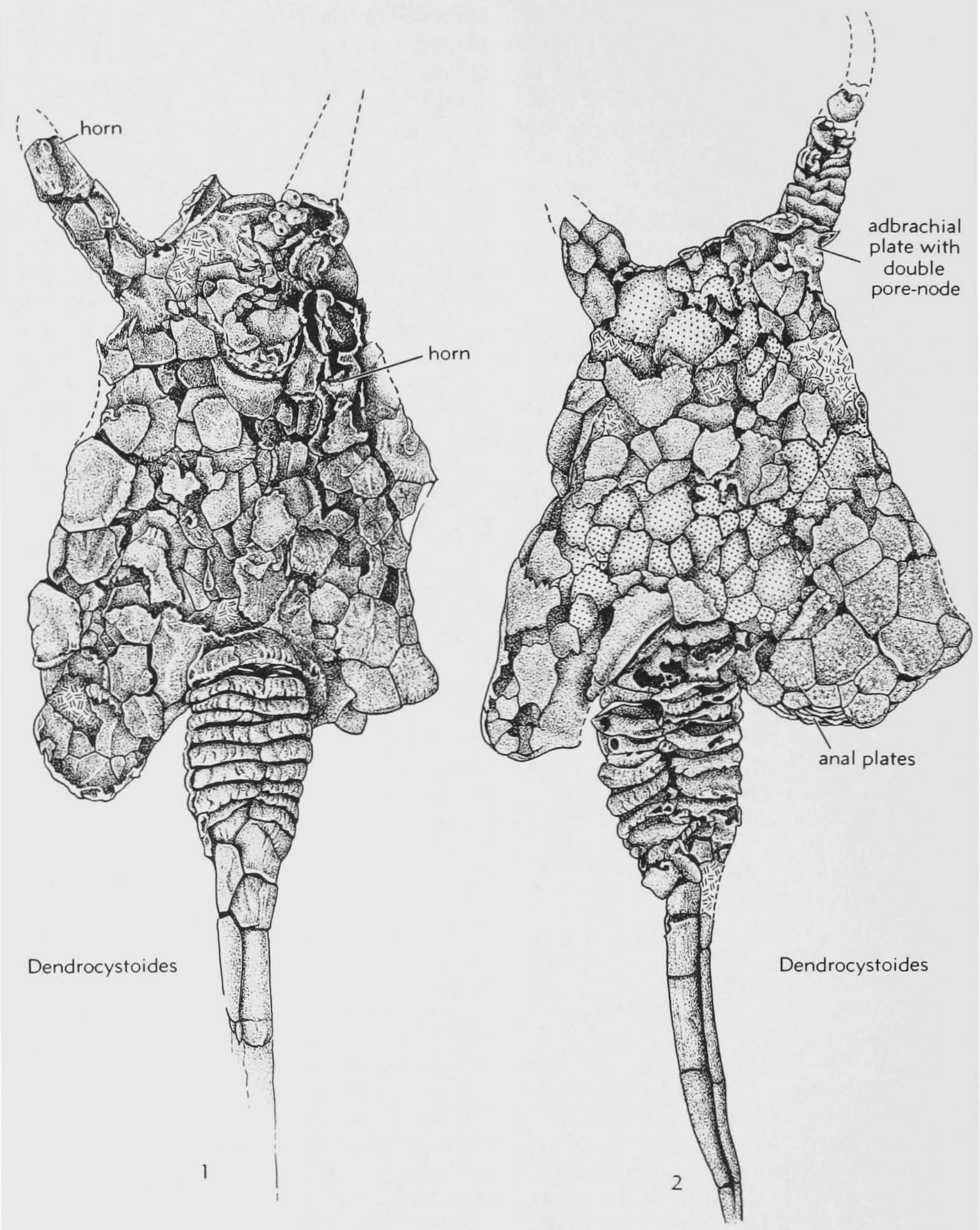

FIG. 376. Morphological features of **Dendrocystoides scoticus* (BATHER), U.Ord., Scot. (Girvan); *1,* reverse face of theca with thecal spine arising from deep in face, stele well preserved, ×2.3; *2,* reverse face of another specimen with double pore node on adbrachial plate, coarse dot pattern indicating interior of obverse plates, ×2.2 (Caster, n; drawings by E. A. Dalvé from photos from BMNH specimens H5A and H103A).

plates than adults (see Fig. 383). New plates seem to have been added in rosettes around previously introduced plates. A very similar mode of plate increment was noted by GILL & CASTER (1961) in the Australian rutroclypeids.

Around the arm, anus, and stele foramina considerable regularization of plate number and form is seen; there is also considerable plate differentiation on the two faces of convexi-planate forms, such as *Dendrocystites, Dendrocystoides, Iowacystis, Syringocrinus,* and *Girvanicystis.* The only known exceptions to the rule of facial differentiation among homoiosteles are the apparently vasiform *Heckericystis,* globular *Dehmicystis,* and biplanate, nummuloidal *Rutroclypeus* (see Fig. 391, 392). The planate face bears fewer and larger plates than the convex one, as a rule, although the reverse is true in *Minervaecystis* and *Iowacystis.* Moreover, the plates of the planate face (usually the reverse) commonly are tightly sutured, whereas those of the convex face (usually obverse) are generally wholly or in part joined integumentally. In *Girvanicystis* (Fig. 373, 374) the convexities are reversed, and both faces are covered by tightly joined plates.

In the dendrocystitids the obverse topography is complex. Both a proximal and a distal plated swelling is present. A **distal tumescence** lies just proximal to the arm insertion and most probably correlates with the forward part of the gut. This prominence was firmly plated. *Dendrocystites barrandei* shows a localized distention adjacent to the arm; this, when flattened in preservation, is probably what BATHER had before him when he described an "antibrachial hump." This may correlate with the common antibrachial process or horn in *Dendrocystoides,* although other plated protuberances, horns, spines, etc., occur on other regions of the theca in this genus.

The **proximal tumescence** (Fig. 372) is a far larger and presumably more important elevation of the theca. This is a transversely oval zone, occupying the widest part of the obverse theca. The plates covering this area have usually collapsed and become imbricated during fossilization, reflecting their integumentary union in life. The proximal border of the zone is the firmly sutured adsteleal circlet of plates; the distal border is a bounding arc of thecal plates, firmly sutured and usually medially upbent proximally, to which the plates of the tumescence were flexibly united. Internally, along the transplate line of geniculation of the bounding arc, there is a sulcar ridge. This extends from the apex of the "antanal" right proximal lobe to the apex of the preanal lobe of the left proximal lobe. Both the bending of the plates of the bounding arc and the internal sulcus serve as indices of the obverse face of the theca, a matter that is often not easy to determine in fragmental material. In *Dendrocystites sedgwicki* the loosely joined plates of the proximal tumescence are somewhat larger than those over the rest of the theca, also thicker and umbonate, with marginal bosses at the plate angles (and in some specimens between them) or with prominent radial ridges (not plicae as usually described), which are not visible on the interior surface. In *D. barrandei* the plates of this tumescence are unornamented. In *Syringocrinus* (see Fig. 393) and *Iowacystis* (see Fig. 394) much of the obverse face seems to be occupied by the homologue of this tumescence, likewise covered by flexibly united plates. In some specimens of *D. sedgwicki* there is a secondary out-pouching of the theca on the adanal side of the proximal tumescence, which may have accommodated a large cloaca, perhaps bearing respiratory trees.

In the convexi-planate forms, where, to employ turtle nomenclature, the obverse face was carapace-like and the reverse, plastron-like, the latter was possibly flexibly conformable to the substrate surface, although seemingly generally more or less rigid and somewhat concave. In the resupinate *Girvanicystis* (Fig. 373, 374) the reverse face is very convex, and bears striking prominences which involve the flexuring of plates; the obverse face was apparently concave and essentially "opercular" in relation to the reverse. The juncture of the two faces, except possibly at the distal margin, was like that of a pillbox (Fig. 374) and conspicuously integumental on the extensiplane; both faces seem to have been composed of rigidly united plates.

Clearly in most, if not all homoiosteles, there is provision in the thecal organization for expansion and contraction of the soft anatomy, or pumping action of the cloaca.

This seems clearly to be the meaning of the proximal tumescence in dendrocystitids, of the many and loosely united plates of the obverse faces in *Iowacystis* and *Syringocrinus,* and of the extensiplane peripheral suture in *Girvanicystis.*

In *Syringocrinus* and *Iowacystis,* and to some degree in *Minervaecystis,* the thecae are homeomorphic with the Stylophora. This entails the development of a turtle-like (testudinate) investiture wherein the obverse face is very like a carapace and the reverse like a plastron. Some thecal plates become definitely lateral in position. In *Minervaecystis* and *Syringocrinus* a loaf-like thecal form is invested with thin plates which form a curved mosaic on the flanks. In *Iowacystis* the lateral plates are constant in number and position, very thick, and geniculate onto both faces to form a **marginal frame** within which are the **somatic plates;** obverse somatics are **supracentrals;** reverse, **infracentrals.** *Rutroclypeus* has the aspect of having been pressed in a die, the polyplating being but little, if to any degree, correlated with the nummuloidal thecal form that results.

The thecal plates adjacent to orifices have been to some extent regularized so that some of them can be consistently identified and homologized. This is especially true of adbrachials and adsteleals, but less so of adanals. Adsteleal plates are commonly larger, thicker, and more firmly united than most thecal plates; thus they form an **adsteleal girdle** about the steleal foramen. In *Dendrocystites* the girdle is well developed, but the number of plates in it is variable. However, a single axial one on the obverse and two adaxial ones on the reverse face are constant. *Girvanicystis* and *Iowacystis* have single axial adsteleal plates on each face. Four symmetrically disposed adsteleals encircle the steleal aperture in *Syringocrinus.* In *Girvanicystis* the extensiplane peripheral suture passes through both the arm and stele apertures. In *Dendrocystites sedgwicki,* and probably elsewhere, the median adsteleal plates bear internal, elevated muscle ridges or platforms, some with apophyses, for attachment of the strong proxistele muscles. Around the inner margin of the adsteleal girdle there is commonly a shallow, narrow groove, presumably for the attachment of integument.

ORNAMENT

The thecal plates are commonly granular *(Dendrocystites, Girvanicystis),* but *Minervaecystis* seems to be smooth. *Iowacystis* is extremely granular and papillose with a prominent labyrinthine ornament on the marginal plates. Central plate bosses *(Heckericystis),* umbones *(D. sedgwicki),* and long spines *(Rutroclypeus),* marginal bosses and radial ribs are external ornament. In *Girvanicystis* certain thecal plates are warped into spines and comblike excrescences which affect the entire plate, as do radial plicae of certain large plates in this genus. The supracentrals of *Iowacystis* are radially plicated. The plated spines and excrescences of *Dendrocystoides* are unique.

ANUS

The homoiostele anus is usually very large, although it has not been discovered in *Rutroclypeus* despite an abundance of fossil materials. It commonly lies in the left proximal lobe; however, in *Minervaecystis* it is right proximal. The aperture is usually near or at the thecal margin, but may invade either the obverse or reverse face. *Girvanicystis* is unusual in that it deeply invades the reverse face of the left proximal lobe. When the anus is at or near the margin its presence is usually indicated by the development of the anal lobe *(s.s.)* on the proximal lobe.

Usually special anal plates effect the anal closure; **adanal plates** surround the anal orifice; between them there may be many flexibly united platelets constituting a periproctal zone. In *Minervaecystis* the anus is closed by a low pyramid of long trigonal plates which radially imbricate over the aperture. In *Dendrocystoides* many small platelets are puckered around the anus, and the closure seems to have been sphincteral, as BATHER (1913) supposed. Here the anus is in a posterior inframarginal position. The adanal plates of the obverse face form a trigonal lappet over the anal area and extend posteriorly to form a projecting anal lobe. The lappet plates are coarsely grained and ridged externally. In *Dendrocystites sedgwicki* the anal lappet bears a swollen median plate of subtrigonal outline. This is BATHER's "sugarloaf" or epianal **(suranal)**

plate. Laterally and subjacent to the lappet there were on either side of the anus itself groups of long platelets which may represent relics of an anal pyramid or specialized periproct.

In *Dendrocystites barrandei* (see Fig. 384,*2*) the anal orifice lies on the posterior left flank or slightly on the reverse face of the rounded flank. Although an ovate anal lobe exists on the flattened specimens, indicating an anal bulge of the theca, no lappet has been observed, despite BATHER's (1913) drawing of both lappet and "epianal" plate. A large, truncated oval adanal plate is present and usually stands at a high angle in the fossils. This may be the antecedent homologue of the suranal in *D. sedgwicki*. But in *D. barrandei,* the older species, its position is *beneath* the anus (subanal), rather than above it (suranal). The broad base of this plate seems to bear articulatory apophyses and is notched as though a sutural pore of some kind were present.

Iowacystis bears the most specialized of homoiostele anal apparatuses. The marginal anus, located at the left posterior angle of the triangular theca, is closed by a pair of calcareous quarter-spheres which serve as opposable valves, opening on the extensiplane and making, when closed, a large hemispherical boss. The valves are probably modified subanal and suranal plates. Surrounding the anal boss is a rosette of quadrangular adanal plates.

The anuses of *Minervaecystis* and *Girvanicystis* (see Fig. 389) lie well within the proximal lateral thecal face. It is left and obverse in the former, and left, reverse in the latter. In *Girvanicystis* the suranal plate is seen to be large and near the center of a large proctal area which is otherwise occupied by tessellated, or perhaps slightly imbricating, periproct plates. Although previous studies of the Rhenish Devonian solute *Dehmicystis globulus* (DEHM) had not revealed the anal apparatus, it is now quite clear (see Fig. 388,*2*). The theca is here reevaluated as having been essentially globular in life, rather than flattened in the rutroclypeid manner, as GILL & CASTER (1960) supposed. The anal zone is large and circular and, although postlateral and marginal on the flattened specimen, does not appear to be associated with thecal lobation. Narrow trigonal plates form a low pyramid over the anal aperture; additional periproctal or adanal plates surround the pyramid, and a large suranal plate seems to be poorly preserved. The anus of *Syringocrinus* remains problematic despite rather full knowledge of the thecal anatomy (PARSLEY & CASTER, 1965). The many small, flexibly united, supracentral plates are probably the homologue of the proximal tumescence of *Dendrocystites,* developed as the pumping apparatus; still the appearance is very much like a periproct zone in other echinoderms. However, there is no aperture within this supracentral area.

STELE

The very name of the class signifies that the stele is a primary taxobasis thereof. It is also an organ of fundamental import in the economy of homoiosteles. Like the arm, the demarcation between stele and theca is sharp, rather than gradational; the juncture is always muscular and integumental, the skeletal plating on the two sides of this juncture, of distinct organization (Fig. 377, 378). Like the arm, the stele (heterostele) or tail is bilaterally tetramerous, i.e., is composed of four series of plates, and possesses, at least proximally, a large central lumen. Among homoiosteles, in contrast to the Stylophora, where the stele (aulacophore) is quite similar in plane and caudal function, the homoiostele organ had no subvective function, although it may well have evolved from an arm.

Three axial zones of the heterostele are differentiable: the proximal zone or **proxistele,** mesial or **mesistele,** and distal or **dististele** (Fig. 372, 375; see Fig. 381, 384). The proxistele is fundamentally tetraserial, i.e., tetramerous, four plates completing a circle; and the dististele biserial, i.e., dimerous. The transition from four-part to two-part symmetry occurs in the mesistele (see Fig. 384). This is achieved through distal suppression of alternate series of tetrameres and concomitant rotation of the resulting biseries, so that the dimere suture lies for most of its length in the projected extensiplane of the theca, and the dimeres thus take on a corresponding obverse and reverse orientation.

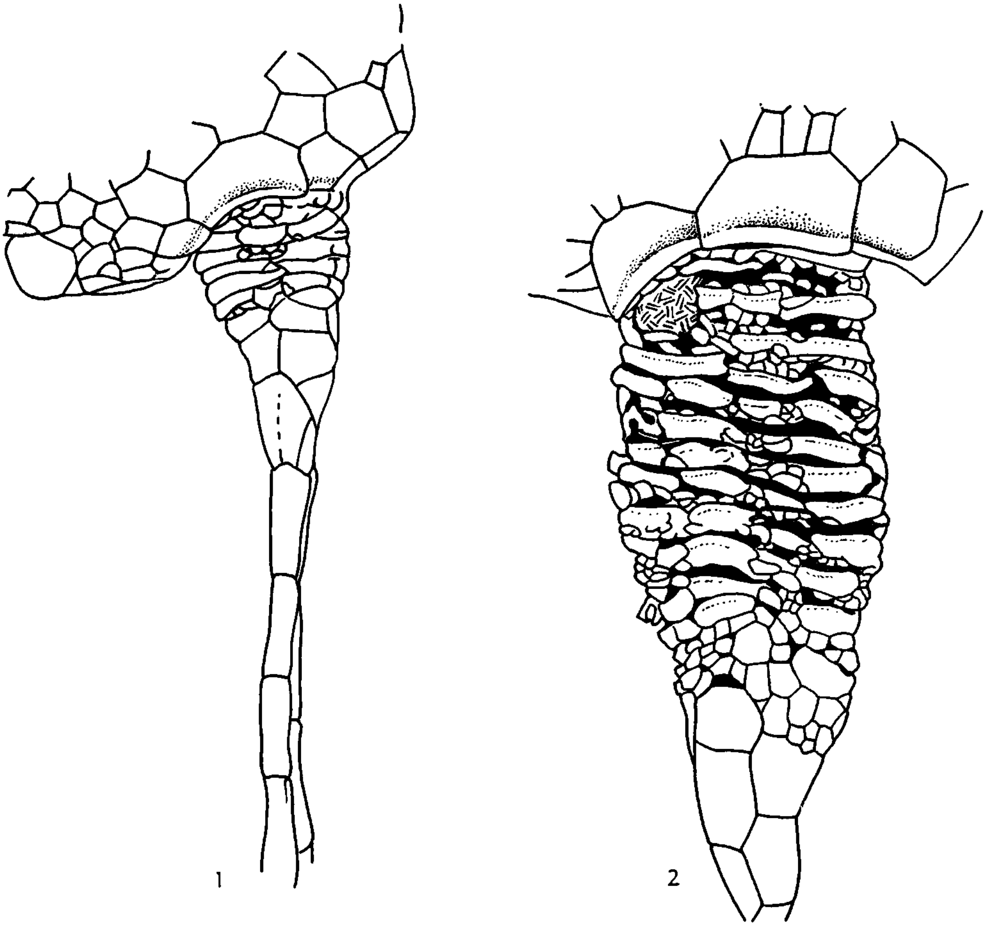

FIG. 377. Morphological features of homoiostelean steles illustrated by obverse views of immature specimens showing two stages in stele development, both identified as **Dendrocystites sedgwicki* (BARRANDE), M.Ord., Eu.(Boh.); *1*, tetramerous proxistele with few platelets both between annuli and between tetrameres of same ring but distal transition from proxistele to mesistele unobscured by platelets, ×3.8; *2*, specimen showing later stage of stele ontogeny in which each annulus is composed of at least 8 meres with many platelets between them in ring, as well as between adjacent rings, transition from proxistele to mesistele obscured by rosetting around major plates, ×3.3 (Caster, n; drawings by E. A. Dalvé based on specimens from Narodni Museum, Praha, Frič and Barrande Colls.).

PROXISTELE

The proximal stele, or proxistele, was the main zone of mobility in the homoiostele. It is strongly plated, usually in the form of telescopically imbricating tetramere rings. Internally the large lumen presumably contained a complex of muscle fibers which served as attachment of the heterostele to the theca and performed as the main locomotor organ of the creature. Movements of extension and contraction of the ring-covered area, right and left, up and down and, by differential contraction of the muscles, somewhat rotatory, are implied. Prominent ridges or platforms inside the stele aperture of the theca were the concentrated zone of proximal muscle fixation; the inside surface of the bourrelets of the rings were distal fixation sites; the conical lumen of the mesistele probably served as the main seat of distal attachment of lengthening and shortening muscles. Probably the main locomotor function of the dististele was controlled in the proxistele.

The archetypical proxistele plan would seem to be that of the single unnamed Upper Cambrian homoiostele described (1963) by UBAGHS from Nevada, and the Lower Ordovician *Minervaecystis* from France. In both, well-developed, axially imbricating, tetramere rings are present. This organization, which is the dominant one in the Homoiostelea, is shared with the mitrate Stylophora (anomalocystitids), where the aulacophore shows an identical organization, which is here assumed to be homologous. This proxistele condition is termed **anomalocystitoid** (Fig. 379, see Fig. 381,*6*). The archetypic proxistele was essentially terete (possibly slightly compressed), the tetrameres of each ring flexibly meeting end-to-end on the obverse symmetry-plane, on the extensiplane laterally, and slightly imbricating on the reverse symmetry plane. The combined telescoping of rings and sagittal imbrication of the tetrameres on the reverse face creates a characteristic zigzag shingling on the reverse mid-line; all of which is "anomalocystitoid," although in most homoiosteles and Stylophora the proxistele (proximal aulacophore) tends to be somewhat depressed.

In *Minervaecystis* (see Fig. 381) the proxistele is exceptionally long, distally tapering, and comprising some 25 to 30 long, thin, imbricating rings. Since both in this genus and in the Nevada form the proxisteles are preserved in an inflated condition, it seems that the constituent tetrameres of the telescoping rings were relatively firmly joined obversely and laterally; reversely they show a slight zigzag imbrication.

Each tetramere is thickened proximally into a **bourrelet** which curves outward as a thickened rim; distally the rings thin to a feather edge. Because of axial imbrication, the bourrelet is normally deeply concealed beneath the thin margin of the proximally adjacent ring.

Several solutans show a marked tendency for the distal stele to twist to the right, thus bringing what are proximally and serially (and probably historically) obverse skeletal elements to a lateral position, and concomitantly lateral ones to the reverse position (see Fig. 384). Correlated with this torsion, the tetramerous condition of the proxistele passes within the mesistele zone into the dimerous condition of the dististele. In this process the distal dimere suture, which is continuous with the sagittal sutures of the proxistele, comes to lie in the extensiplane. In *Minervaecystis* this dextral torsion (Fig. 378,*2d*) of the mid-stele zone is uniquely recorded by a crest which passes across the mesistele diagonally onto the distal proxistele plates: the left reverse tetrameres (to the right of the observer when the reverse surface is viewed) each bear subangular longitudinal median folds which continue as a low keel onto the mesistele where the fold axis crosses the symmetry plane. It appears that in life the organism lay with the left half proxistele distally twisted toward the right, so that the keel came to lie in a position normal to the sea floor. It was functionally a proximal continuation of the pectinate keel or rudder on the proximal reverse dimeres.

In *Syringocrinus* (see Fig. 393) of the Middle Ordovician of Canada the slightly compressed proxistele comprises 11 or 12 smooth, imbricating rings, of which the tetrameres imbricate both obversely and reversely on the symmetry plane. In *Iowacystis*, of the Upper Ordovician, the proxistele is very short, comprising 5 or 6 rings, each of which bears an encircling railroad rail-like flange at its mid-length. The ring margins are smooth and apparently without a bourrelet; they imbricate telescopically. The lateral tetramere sutures are tight, but those on the symmetry plane imbricate slightly on both faces. The whole proxistele is slightly depressed. *Rutroclypeus* of the Australian Lower Devonian has a remarkably depressed theca and a correspondingly much-depressed proxistele of unusual trigonal outline, which first led to its identification as the buckler of a xiphosuran. All of the tetrameres were loosely joined and the two faces in close proximity. The tetrameres strongly imbricate on the symmetry plane of both faces. In keeping with the spinose theca, most specimens show a prominent spine on each tetramere. This is perhaps the most anomalocystitoid of solutan proxisteles.

Heckericystis, of the Baltic Middle Ordovician, is shown by GEKKER [HECKER] as possessing a terete proxistele, recalling the swollen proximal columnals of the cystoid *Pleurocystites,* of 12 or 13 narrow rings. Although it is supposed that the rings are tetramerous, no sutures have been reported. Both GEKKER (1940) and GILL & CASTER (1961) assumed that the rings were nonimbricating and united by integument only. This may be a misconception.

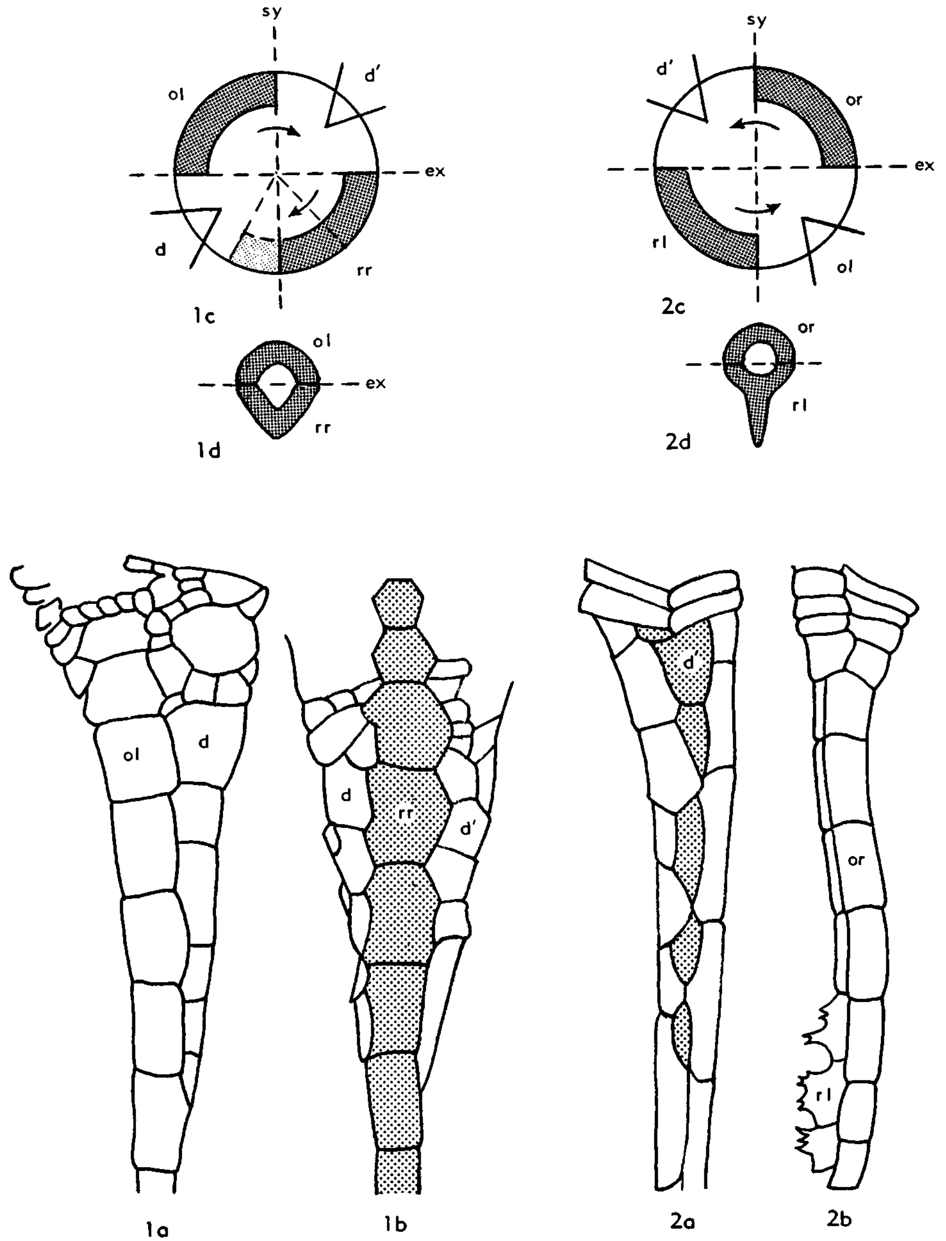

FIG 378. Mesistele transition from tetrameral condition of proxistele to dimeral condition of dististele in Homoiostelea.

1. **Dendrocystites sedgwicki* (BARRANDE), M.Ord., *1a,b,* obverse and reverse faces of stele (reverse tetramere series stippled); *1c,* schematic cross section of proxistele in which those tetramere series which persist through mesistele and into dististele are stippled, and those which become evanescent in this passage are indicated by chevrons; *1d,* dimere disposition in dististele (Caster, n; based on materials in Narodni Museum, Praha).

2. *Minervaecystis* UBAGHS & CASTER, n. gen., L.Ord.; *2a,* left view of mesistele (left obverse tetramere series dotted; *2b,* obverse face of same stele (keeled reverse dimeres turned sideward during fossilization); *2c,d,* same analysis of this genus as shown in *1c,d* (Caster, n; based on holotype of **M. vidali,* courtesy G. Ubaghs).

[Explanation: Arrows indicate direction of rotation of persisting tetramere series when traced through

The Bohemian Middle Ordovician *Dendrocystites sedgwicki* and the Scottish Upper Ordovician *Dendrocystoides* and *Girvanicystis* show many small platelets in association with the proxistele tetrameres, or, in the first instance, seemingly in lieu of them (Fig. 372, see Fig. 382). Every stage from complete tetrameres to rudimentary remnants submerged in a melange of platelets can be seen. *Dendrocystites barrandei* (BATHER), of the Lower Middle Ordovician of Bohemia, and related undescribed forms, commonly preserve distinct tetrameres, or identifiable remnants thereof, the while adding platelets in the annulus series with them so as to create penta-, hexa- or polymere annuli. Between the flanged rings of the tetramere plates many very small platelets occupy the zone of integumentary junction. In what appear to be young individuals of *D. sedgwicki,* the *D. barrandei* plan is closely approximated and the tetramere elements readily identified. In adult and typical *D. sedgwicki* most evidence of the tetramerous proxistele is eradicated by the multiplicity of platelet development and the reduction in size of the tetramere elements. This proliferation occurs both within the annuli and between them, all sclerites being flexibly joined. This is the most inflated of homoiostele proxisteles and certainly the most flexible one. However, close scrutiny does reveal among the platelets a few which exhibit the characteristic flange and bourrelet of the tetrameres. These are found in the circles of larger platelets. The wider zones of small plates seem to have been folded into rugae between the more prominent rings. The whole proxistele lumen of the fossils is commonly choked with discrete platelets.

In some specimens of *Dendrocystites sedgwicki* the disposition of the platelets in the prominent rings suggests that they may derive from the splitting of tetrameres. It is also clear that in *Dendrocystites* the process of rosetting, by which small plates develop in the sutures around large plates, operates both in the theca and the proxistele-mesistele.

Dendrocystoides (Fig. 376; see Fig. 386) of the Upper Ordovician consistently shows many small polygonal plates in the proxistele lumen, but little or no evidence of them externally; they probably were embedded in the integument which connected the telescoping rings. Here, too, there is a remarkable range in surface nature of the tetrameres, and apparently all at the same growth stages of the type species. Thin, smooth, squamose tetrameres are found along with thick, rugose, pitted or radiately ribbed ones, with frayed or spinose distal margins (Fig. 379). *Girvanicystis,* from the same beds, has a depressed anomalocystitoid proxistele with rugosely flanged and carinate tetrameres (Fig. 374, see Fig. 390). Adjacent to the flange both distally and proximally there are many external adherent subpolygonal platelets which seem to pertain to tissues originally covering the stele. Here no platelets have been observed inside the lumen.

BATHER (1913 and elsewhere) apparently largely employed the proxistele morphology of *Dendrocystites sedgwicki* in formulating his idea that the solutan stele derived from thecal plates by regularization. He imagined the regularized stele to grade into the essentially chaotic theca. In the process, perhaps by fusion of platelets or by differential growth and reduction, tetrameres would emerge. However, in this species no gradation from stele to theca occurs, and instead of being a primitive solutan, it now appears to be one of the most advanced, at any rate in stele development. The multiplating is derived from the anomalocystitoid condition, from tetrameres (plus supplements), rather than being antecedent to them. What are judged to be young forms of the species, in association with adults, show tetrameres along with a few platelets. The antecedent *D. barrandei* BATHER of Bohemia, which was still recognizably anomalocystitoid in adulthood, closely parallels the young forms

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[*Continued from facing page*]

mesistele; plate sutures or margins which were on symmetry-plane in proxistele come to lie on extensiplane of dististele; *d,d′,* tetrameres of series which distally disappear; *d,* reverse; *d′,* obverse; *ex,* extensiplane of theca projected through stele; *ol,* obverse left tetramere; *or,* obverse right tetramere; *rl,* reverse left tetramere; *rr,* reverse right tetramere; *sy,* bisymmetry-plane.]

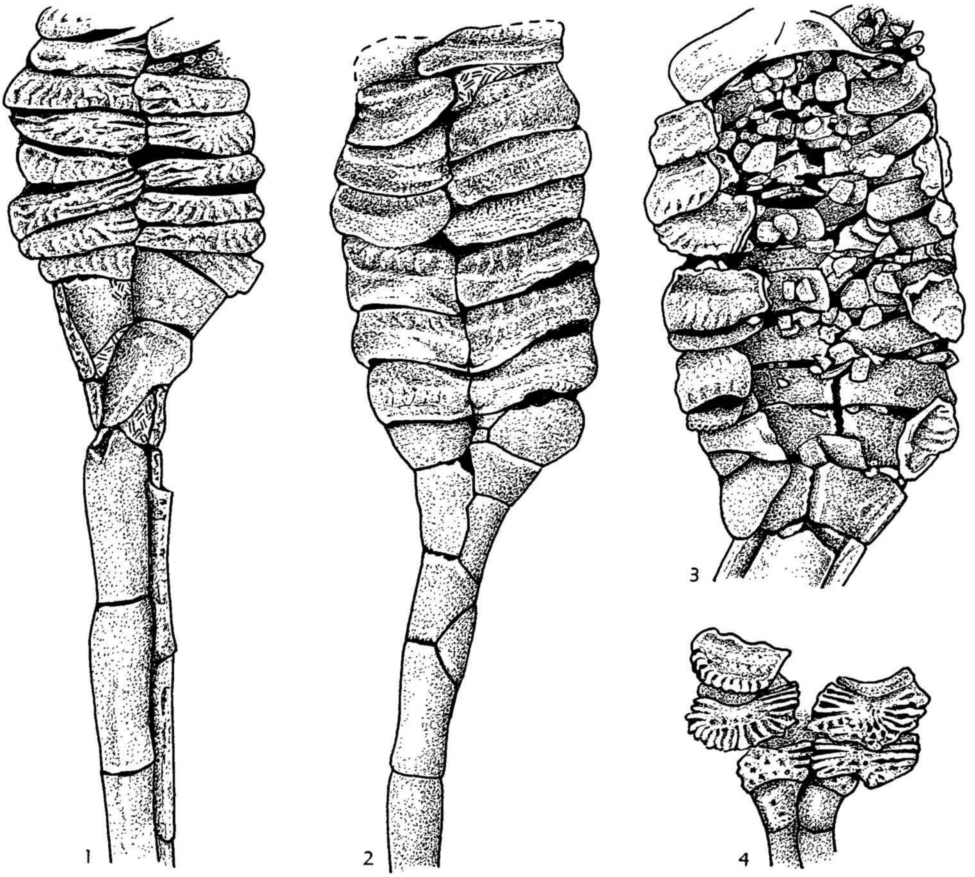

FIG. 379. Reverse views of four anomalocystitoid steles of **Dendrocystoides scoticus* (BATHER), U.Ord., Scot. (Girvan), showing variations within the species, in specimens of essentially same stage of growth, in nature of ornament and presence of internal integumental platelets. *1,2,4,* exterior reverse faces, torsion of mesistele well shown in *1* and aspects of radial ribbing in *2,4*; *3,* internal view of obverse face showing many small platelets concentrated mainly in integumental zone between annuli. (Caster, n; drawings by E. A. Dalvé based on specimens in Hunterian Museum, University of Glasgow: *1,* no. E5803, ×4; *2,* no. E5718, ×3.5; *3,* no. E5827, ×3.8; *4,* no. E5719, ×4.3).

of *D. sedgwicki,* and was at about the same stage of platelet development as the Scottish *Dendrocystoides* and *Girvanicystis.*

PROXISTELE INSERTION

The proxistele is inserted well within the stele foramen, which is usually recessed into the proximal thecal margin. The aperture conforms in shape to the proxistele, from circular to very depressedly ovate. The adsteleal plates of both thecal faces are to some degree regularized and can be homologized within limits. They were commonly rigidly fused to form an adsteleal girdle, a marginal flange of which extended over the proximal proxistele. Just inside the flange there is usually a shallow groove, probably for integument attachment; deeper within the aperture, and mainly developed on or adjacent to the symmetry plane, each genus shows characteristic scars, calluses, or paired apophyses which were places of attachment of the powerful proxistele muscles. In *Dendrocystites sedgwicki* strong bilateral apophyses are present both reversely and obversely, so tilted as to suggest that obverse tetrameres were connected by muscles to the reverse apophyses, and reverse to the obverse.

MESISTELE

The mesistele is a relatively rigidly plated conical coupling between the proxistele and the dististele. It served mainly as the distal termination of proximal muscle strands responsible for the main movements of the dististele "tail." Within the mesistele the transition from the proximal tetramerous condition to distal dimerous was made. It is usually possible, especially in anomalocystitoid forms, to trace across the mesistele (Fig. 378) the serial homologies between tetrameres and dimeres, or biseries. (Biseries, biserial, is employed for **alternate** positioning of plates, with a resultant zigzag suture; dimeres, dimerous, for **opposite**, semicylindrical plates having a rectilinear suture.) In these the distal tracing of tetramere series reveals that alternate ones persist and diminish in the passage of the mesistele zone. Alternate series commonly become evanescent in the distal mesistele. However, in *Iowacystis* (see Fig. 394) and *Syringocrinus* remnants of the diminishing series persist as discontinuous intercalates on the zigzag sutures of the distal biseries. The correlation between tetramere quadrants and dimeres or biseries have taxonomic import (Fig. 376).

In *Minervaecystis* (Fig. 378), the oldest well-known solutan, the mesistele is relatively simple. The obverse right series of tetrameres passes directly into the tightly sutured right series of the mesistele, which in turn is serially continuous with the right dimere series of the proximal dististele; the left obverse tetrameres align with two or three plates which appear as intercalates on the mesistele equivalent of the proximally zigzag and distally dimerous suture of the dististele. Tracing the left obverse tetramere series distally, it is seen to diminish serially in size and finally to disappear in transit of the mesistele. On the reverse face the left tetramere series continues the length of the mesistele and aligns with the left series of the proximal dististele; the right reverse tetramere series, similarly traced, peters out in two or three distally diminishing plates.

This general plan, alternate tetrameres aligned serially with dimeres and their alternates disappearing distally within the mesistele, seems usual among homoiosteles. In *Dendrocystites* (Fig. 378,*1*) wherein the general structural scheme is common to all other anomalocystitoid solutes, quadrants antipodal to those in *Minervaecystis* persist and diminish distally; however, the basic relationships are the same, and the dimere series is thus to be identified and serially homologized with proxistele tetrameres.

In *Dendrocystites sedgwicki* (Fig. 372, 377), where auxiliary platelets and rosetting obscure serial relationships, the juveniles suggest that the prevailing homologies pertain.

Throughout the class the same modifications of the meres take place in the transition from a tetraseries to a biseries. Those tetramere quadrants which are serially vacated by the distally diminishing alternate series are serially invaded by the persisting series as their configuration changes from quarter circles to semicircles. On both faces the proportional serial enlargement is across the symmetry plane; the original extensiplane (lateral) sutures remain constant in position. The effect of this opposing proportional enlargement of the serially persisting plates is that of distal rotation of the stele. When the dimere condition is fully attained, the two half cylinders meet on the extensiplane and in obverse and reverse position, each astride the symmetry plane, rather than being half-right and half-left, as in the proxistele. Customary representations of the dimeres meeting on the symmetry plane seem to be in all cases 90 degrees out of life orientation. The diagonal carina of the reverse face of the *Minervaecystis* proximal stele, mentioned above, which crosses the symmetry plane, conforms to this principle of distal stele rotation. Apparently the rotation is one of the oldest of homoiostele traits, and seems to correlate with the development of an obverse keel or "caudal" fin in free-moving animals. In *Iowacystis,* where no such modification is known, the rotation seems to be suppressed, and for that matter, mesistele plate organization persists through much, if not all, of the distal stele.

The nature of serial transitions of *Minervaecystis* suggests that historically the whole stele was covered by a tetraseries of alternating plates. In this respect *Iowacystis* is the most generalized solute yet encountered; however, the rest of the highly specialized anatomy of this genus suggests that this is a derived simplicity. Unfortunately, there are as yet no ontogenetic data available on stele development, and neither the mode of, nor focus of, stele plate origination is known.

The mesistele of *Syringocrinus,* M.Ord., Canada, is both anomalous and instructive. It has been called a dendrostyloid by PARSLEY & CASTER (1965) because of its homeomorphic resemblance to the styloid of the Stylophora. It is unusually long, petiolate, and covered by rigidly sutured asymmetrical plates (see Fig. 393). It is lachrymal in cross section, i.e., rounded on the obverse face (in life) and keeled on the reverse (see Fig. 393,*1a*). Prominent nodes occur on the left side of the keel; none on the right. The plating is triserial, the right side being invested by a biseries, while the left has a continuous axial row of long plates separating the plates of the biseries. These axials are serial homologies of discontinuous left intercalates which extend through most of the dististele. In the mesistele the axial plates cover most of the rounded surface. The suture between the biseries on the right side of the mesistele is rectilinear and continues as a straight suture to the end of the dististele.

The main mesistele plating in this genus is a disparate biseries, three long plates on the obverse face occupying exactly the same distance as five nodose ones on the keel side. The five plates bear the nodes or bosses at mid-length and marginally on the left side of the keel; these continue onto the first two dististele keeled plates. The distal keel margins are subspinously produced as imbricating caps which give the keel a characteristic serrate appearance; this continues essentially for the length of the tail. These serrations and nodes on the rigid mesistele are the basis for comparing this organ with the mitrate stylocone.

The presence of a narrow, apparently unsutured, annulus between the proxistele and mesistele makes direct correlation between the serial plating of the two zones difficult. The annulus may bespeak unusual rotational activity in this zone in the living organism. It is also no doubt correlated with the usual sinistral rotation of plate series in the mesistele. It is assumed that the keeled edge of the distal mesistele and dististele was, in the main, downwardly directed in life, and that the lanceolate expansion of the dististele served mainly as a laterally moving caudal fin. However, the nodes on the left side of the keel-forming plates of the middle stele zone, and the markedly different plating on the two sides of the post-proxistele tail, pose problems of symmetry, balance, and serial homology. It is no doubt significant that the asymmetrical ornament and the direction of the distal serial rotation are both sinistral. The nodes may have served as a counterbalance to inherent muscular forces tending to return the tail to a primordial orientation, such that the dimere suture would lie in the sagittal plane. The extra plating on the left side of the tail may have a similar correlation. As for the serial homologies between the proxistele and the rest of the tail, this is most speculative. Probably, as in other sinistrally rotating homoiosteles, the axial plates of the mesistele, and their discontinuous correlates along the zigzag suture of the left dististele, are serial homologues of the right obverse quadrants of the proxistele. If this is so, then what is the meaning of a single small plate (see Fig. 393,*1a*) on the suture between the first axial and an adjacent nodose plate? It may be adventitious; in other solutes one would tend to correlate it with a tetramere series, it being the only tetramerous element in the mesistele. If this is elected, then *Syringocrinus* is unique in having distally diminished both obverse tetramere series, and in having the resultant biseries wholly of reverse derivation. On the other hand, the compelling evidence of sinistral rotation argues for disregarding this platelet, and correlating the nodose keel plates of the biseries as left obverse in origin, as in *Dendrocystites.* In this genus the left reverse tetrameres diminish distally in the mesistele, but in *Syringocrinus,* if the right plates of the biseries are to be correlated, as is conventional, with the right reverse series, they do not appear in the mesistele. The left reverse series would seem to have no postannulus correlates. This reasoning is supported by the rectilinear suture on the right side of the tail. Intercalated plates, representing a distally diminishing tetramere series, are generally associated with the biserial zigzag relationship of plates; straight sutures derive from zigzag, just as opposite plates derive from alternate. In these terms the right side of the *Syringocrinus* tail is considerably more specialized than the left. The annulus of this genus might be likened to a temporal hiatus, in the crossing of which much that transpired has been eliminated from the record.

In *Dendrocystites sedgwicki* (Fig. 372, 377) the mesistele is a tessellated, multiplated, conical connection between the very flexible and profusely plated proxistele and the dimerous dististele. The adult mesisteles usually show an advanced condition of rosetting by which earlier-formed plates become isolated among many platelets which form in circles around them. However, on both larger steles and especially so on immature ones, it is possible to trace through five or six large plates the continuous serial course of dimeres into the tetramere series (Fig. 377). On the obverse mesistele the left half of the face is occupied by a continuation of the distal dimere series; the right side, by a distally diminishing series of six or seven plates which alternate with the left series. Laterally and at the junction with the dimere series, small plates may be intercalated; proximally the initial large plate of the diminishing series is commonly rosetted. This series disappears at a shoulder on the first obverse dimere. On the reverse face of the mesistele the inferiorly oriented dististele dimeres pass without interruption through a series of six or seven median plates. This median series of mesistele plates seems to correspond to a right proxistele series. A low axial keel is present on these median plates, and continues onto the corresponding dististele plates. On the right side of the median series the distally diminishing series of the obverse face covers about one-third of the reverse face; on the left there is another distally diminishing series of plates bounding the reverse medians; this series disappears on a left shoulder of the first dististele dimere on this side. Obviously, the mesistele bears tetramerous elements, just as in the much older *Minervaecystis,* but with this basic difference: the apparent rotation in the mesistele zone is in an opposite direction in the two genera (Fig. 378,*1c,2c*), and antipodal quadrants distally continue and diminish.

Dendrocystoides show the basic mesistele gradation from four-part to two-part symmetry, accompanied by lateral rotation of keeled dimeres to a reverse position, the dististele being largely biserial. In *Iowacystis* the mesistele is undifferentiated from the dististele. In the mesistele zone there are no axial intercalates on the obverse face; on the reverse, one series of axial inserts is preserved. Both mesistele and dististele are somewhat depressed, and no rotation is in evidence.

DISTISTELE

Ordinarily the dististele is a long, rather firmly plated "tail," subequal in length to the remainder of the stele and in some specimens as long as the rest of the organism (some specimens of *Dendrocystoides*). Its plating is dominantly biserial or dimerous, usually passing from the first condition to the second distally. The basic orientation of the biseries, as described in morphology of the mesistele, is bilateral, one element deriving from the right or left obverse face, and the other from the left or right reverse, and consistently in a antipodal manner. Distal rotation either to right or left usually brings the biseries-dimeres to a fully obverse-reverse orientation with the sutures between the semicylinders lying in the projection of the thecal extensiplane. In *Dendrocystites sedgwicki* the dististele is attenuated and nearly terete, only a low keel occurring on the reverse dimere. In *Dendrocystites* and *Rutroclypeus* some specimens suggest a slight degree of prehensileness in the distal "tail." In *Heckericystis* a terete and highly attenuate dististele has been illustrated by GEKKER [HECKER] (1940). Usually the dististele is markedly flattened, and commonly asymmetrically. Whereas this flattening is always morphologic *depression,* the accompanying distal rotation creates the appearance of compression. The obverse members of the biseries are usually somewhat horseshoe-shaped in section; the reverse ones angular or keeled, some extending downward in a blade or comb. This asymmetry creates a caudal fin. This is lanceolate in profile in *Syringocrinus,* with serrations along the reverse edge created by distal imbrications of reverse dimeres; in *Minervaecystis* the pectinate comb of the keel might be likened to a "heterocercal" fish tail. In *Iowacystis* the biserial elements are essentially symmetrical and bilaterally disposed. They are depressed, being somewhat flattened in the extensiplane. Either no rotation occurs here, or in terms of the conditions illustrated in Figure 378 the two distally persisting homologues of the proxistele tetrameres rotate in opposite directions to occupy the vacated quadrants.

Because of the asymmetry and flattening of the dististele in most homoiosteles, the organ is usually preserved with the plane of depression parallel to the bedding; hence the usual restorations show the zigzag or rectilinear suture in the sagittal plane rather than the extensiplane. *Iowacystis* is the only form known so far in which the fossil dististele is actually preserved wholly in life position, and in this unique genus the suture was sagittal. *Girvanicystis* (Fig. 373) appears to have a very long dististele, composed of unequal but very long dimeres, but the suture lies in the extensiplane.

OCCURRENCE

DISTRIBUTION

Homoiostelea range in time from the Cambrian of Nevada and Upper Tremadocian (Lower Ordovician) of France well into the Lower Devonian of Victoria, Australia, and Germany. The maximum expansion came in the Middle and Upper Ordovician of Europe and North America. No Silurian representatives are yet known, and none from Asia, Africa, South America, or Antarctica.

PRESERVATION

Although homoiosteles, like other "carpoids," are among the rarest fossils, under exceptional circumstances they are abundant (see Fig. 385). In the Girvan Upper Ordovician of Scotland, the Middle Ordovician of Drabov and Zahorăny, Bohemia, and the Kingland district of Victoria, Australia, extraordinary concentrations have been encountered. Such deposits are clastic polymict sediments, and the fossil concentrations are commonly on single bedding planes. This probably represents the death setting under conditions of roily flow. The carcasses seem to be hydrodynamically oriented (see Fig. 385). Presumably roiliness was especially injurious to microphages such as these. The occurrences usually preserve the fossils as collapsed thecae, quite probably attesting to their rapid burial. Moreover, they are now encountered as ochre-stained molds comprising the residue from solution of the stereom lime and reduction of a pyrite filling of the stroma canals of the skeleton. Rapid burial of the living animal would probably create a reducing environment inside the labyrinth of canals of the skeleton; this setting is commonly one propitious for pyrite deposition. The resultant sediment, being relatively porous, permits ready circulation of water during weathering, and resultant solution of lime and oxidation of the pyrite. The sulphuric acid released in the transition from pyrite to limonite abetted solution of the calcium carbonate. In less porous clastics, like the fine-grained micaceous shales such as cover some specimens (see Fig. 383), the stereom is still intact. Lime ooze was especially fine for the preservation of dead skeletal parts in essentially living articulation. No concentrations of remains have yet been found in such deposits. Probably homoiosteles, like other "carpoids," were far more abundant in Paleozoic seas than fossils indicate; their delicate and commonly inflated thecae, whether tightly or loosely plated, were prone to destruction. Dissociated plates have never been reported. However, this is more artifactual than real. Commonly, beds which contain homoiosteles also contain many other echinoderms, starfishes, other "carpoids," cystoids, machaerids, and eocrinoids. Other organisms are usually rare in this echinoderm facies.

PHYLOGENY AND EVOLUTION

"Carpoids" as a whole have proved enigmatic as to broader phylogenetic relationship.

Homoiostelea share with other "carpoids" indubitable echinoderm relationships. They appear, however, to lie completely outside

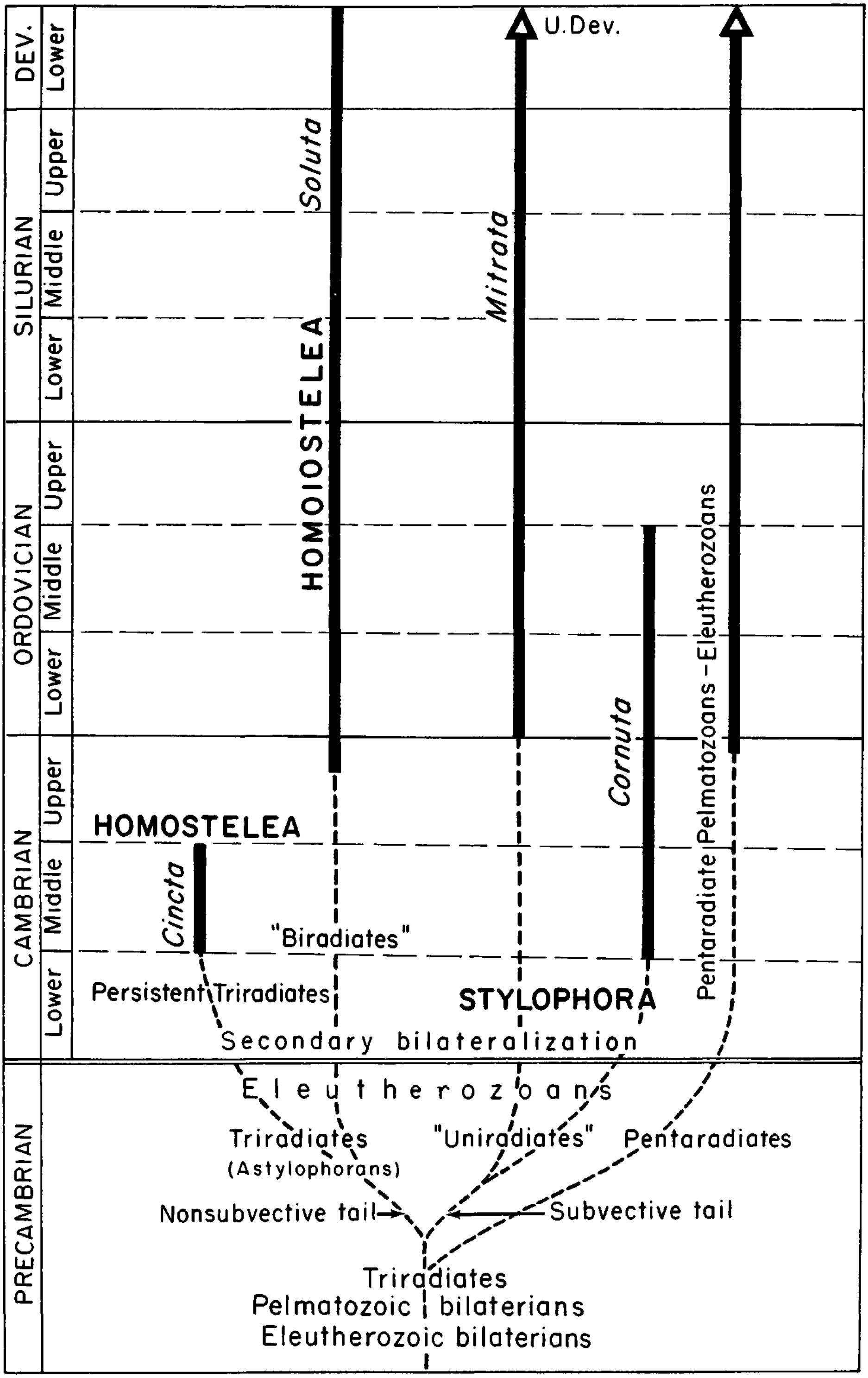

FIG. 380. Speculative phylogeny of "carpoid" classes (Caster, n).

any other echinoderm evolution. This is so fundamental that it presumably denotes a separate course, or courses, since pre-Phanerozoic times. It is my opinion that comparative "carpoid" morphology bespeaks a common ancestry of the three classes (Fig. 380). The still quite unknown triradial archetype would lie not only in the "carpoid" ancestry, but presumably also in that of all pentaradial pelmatozoans or pelmatozoan-derived classes.

This hypothesis entails the radial homologizing of arm and stele in the homoiosteles; according to this theory both were originally biserial subvective organs. Hence, the homoiosteles are termed "biradiates" (Fig. 380), the third radius having been suppressed prior to our encounter with the class. The aulacophore "tail-arm" of the Stylophora was the sole radial survivor there, and this group is labeled "uniradiates."

Within the class Homoiostelea there are too many hiatuses in the record and too much morphologic differentiation between the forms so far encountered to make phylogenetic speculation very meaningful. However, a few generalities are in order. Much has been discovered since the speculations of Bather (1900, 1913, 1930) and Jaekel (1899, 1901, 1921), which have largely colored all subsequent thinking about "carpoid" relations. In that phase of echinodermology the "Amphoridea" concept played a prominent role; since the "carpoids" were thought of as Pelmatozoa, and all fixed forms were supposed to derive from a loosely plated saclike form fixed at one extremity, regularization of plates was postulated as focusing on the point of fixation and at the arm base; both arms and peduncle were thought of as regularized extensions of the theca. Thus, when Barrande's *Dendrocystites sedgwicki* of the Bohemian Middle Ordovician was supposed to be one of the oldest "carpoids" (although the Cincta: Homostelea were then and still are oldest of all), its theca composed of many, apparently loosely articulated and little-if-at-all-regularized plates, its polyplated proxistele, and many small plates in the zone between first plates of the arm biseries and large thecal plates, all seemed —especially to Bather—to support the "Amphoridea" hypothesis. Now, with better knowledge of the organization of Bather's *D. barrandei*, from somewhat lower in the Bohemian Ordovician, of the juvenile stages of *D. sedgwicki* itself, and especially with the discovery of the Tremadocian *Minervaecystis* and a comparable stele from the Nevada Cambrian, the *Dendrocystites* support of the "Amphoridea" hypothesis fails. Instead of polyplating of the stele and gradational plating from theca to arm being archetypical, both are now seen to be specializations. In both the oldest forms and in juveniles of the specialized ones, tetramerous proxisteles and adbrachial regularized plates are the rule. *D. sedgwicki*, in the new light, is a highly specialized form, in which interstitial platelets and fractionation of antecedent large plates both occur.

Minervaecystis is far from a primitive homoiostele, and in many respects (e.g., its pectinate dististele keel) is very specialized. In its stele anatomy, however, it probably is the most primitive form yet known. Thus, far, no data are available which might indicate what organization of the proxistele may have antedated the tetramerous one. If the appendage is a modified arm, as here urged, its biserial nature and cover-plate series may be very ancient indeed (e.g., eocrinoids). Certainly this genus possesses the largest number of tetramere annuli known. Even so, its mesistele and dististele represent advanced locomotor specialization.

Until it is known how stele plates proliferated, any biogenetic interpretation of the axial differentiation of the stele is risky. When the stele was thought of as "another kind of stele," (i.e., column, hence "heterostele"), small attention was paid it. Its growth would be presumed to be mainly by intercalation of new skeletal elements at the proximal plane as in "other Pelmatozoa." Thus, if any biogenetic significance were to be attached to axial differentiation, the more distal elements would reflect an older phylogenetic state. If, on the other hand, the stele is a modified arm, it presumably grew like arms, with distal increments of parts. Thus it might be, and here is urged, that the distal succession from tetrameres to biseries to dimeres is quite possibly palingenetic[1] and Jacksonian,[2] hence of considerable phylogenetic importance. The very long series of tetrameres in *Minervaecystis* would seem to support this concept; likewise the well-documented transition from four-part to two-part symmetry of the oldest mesisteles, and distal transition from biseries to dimeres in manyististeles. (However, in *Minervaecystis* and *Dendrocysittes sedgwicki* the distal sequence is from dimeres to biseries. Thus the latter may well correlate with the prehensile flexibility of the tip of the tail.) In general, the older solutes have more armlike steles, solutan arms being basically tetramerous.

Within the Homoiostelea too many geologic and morphologic gaps separate the known genera to make lineage speculation worthwhile. Except at the species level, relationships are obscure. Although GILL & CASTER (1960) indulged in a bit of speculation in this field, further information does not especially enhance their surmises. As the classification brings out, the generic differentia are, for the most part, comparable to family taxobases used elsewhere in the phylum.

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[1] Palingenesis, a succession of ontogenetic events which appear in the same order as the phylogenetic events which they supposedly recapitulate; this would be documentation of biogenesis.

[2] ROBERT TRACY JACKSON attempted to apply the "biogenetic law" (biogenesis) to serially developing organs such as an ambulacral series of plates. It was his contention that the ontogeny of such a series tends to rehearse the evolutionary history of the organ.

SYSTEMATIC DESCRIPTIONS

Class HOMOIOSTELEA Gill & Caster, 1960

[*nom. transl.* CASTER, herein (*ex* subclass Homoiostelea GILL & CASTER, 1960) (of the class Carpoidea JAEKEL)] [=order Amphoridea HAECKEL, 1896 (of class Cystidea) *(partim)*; Dendrocystidae BATHER, 1899 (of order Amphoridea); order Soluta JAEKEL, 1901 (of class Carpoidea, subclass Heterostelea); suborder Heterostelea BATHER, 1913 (of order Amphoridea); class Carpoidea BATHER, 1929 *(partim)*; superorder Astylophora GILL & CASTER, 1960 (of subclass Homoiostelea)]

Ancient, eleutherozoic, asymmetrical echinoderms without obvious radial symmetry elements; usually depressed, and tending toward bisymmetry; theca of fixed form, multiplated; plates usually both facially and regionally differentiated (adsteleal, abbrachial, adanal); some regional provision for visceral expansion and contraction usual in thecal plating; single biserial, usually distal-lateral, arm bearing biserial cover plates; mouth subthecal; anus posterolateral in most forms; heterostele ("tail") posterior, long and composed of axially differentiated plates: proxistele flexible and fundamentally tetramerous; mesistele transitional from four-part to two-part plate symmetry: dististele usually biserial proximally and dimerous distally; adbrachial plate bearing hydropore and gonopore, where known. *U.Cam.-L.Dev.*

Order SOLUTA Jaekel, 1901

[=suborder Soluta JAEKEL, 1901 (of class Carpoidea, order Heterostelea, *partim*); suborder Soluta JAEKEL, 1918; order Soluta, GILL & CASTER, 1960]

Characters of class. *U.Cam.-L.Dev.*

Seven families and ten genera of Soluta are recognized as follows:

1) Minervaecystidae UBAGHS & CASTER, n.fam., *?U. Cam.,L.Ord.*, Eu.(France)-N.Am.(USA).
    - *Minervaecystis* UBAGHS & CASTER, n.gen., *U. Cam.*, N.Am.(Nev.) ("unnamed solutan," UBAGHS, 1963); *L.Ord.*, Eu.(France). (**Dendrocystis vidali* THORAL).
2) Dendrocystitidae BASSLER, *M.Ord.-L.Dev.*, Eu.-N.Am.
    - *Dendrocystites* BARRANDE, *M.Ord.*, Eu.(Boh.). (**Cystidea sedgwicki* BARRANDE); *D. barrandei* BATHER.
    - *Dendrocystoides* JAEKEL, *U.Ord.*, Eu.(Scot.). (**Dendrocystis scotica* BATHER).
    - *Heckericystis* GILL & CASTER, *M.Ord.*, Eu. (Est.). (**Dendrocystites kuckersianus* HECKER).
    - *Dehmicystis* CASTER, n.gen., *L.Dev.*, Eu.(Ger.). (**Dendrocystites (Dendrocystoides?) globulus* DEHM).
3) Girvanicystidae CASTER, n.fam., *U.Ord.*, Eu. (Scot.).
    - *Girvanicystis* CASTER, n.gen., *U.Ord.*, Eu. (Scot.). (**G. batheri* CASTER, n.sp.).
4) Rutroclypeidae GILL & CASTER, *L.Dev.*, Australia.
    - *Rutroclypeus* WITHERS, *L.Dev.*, Australia (Victoria). (**R. junori* WITHERS); *R. withersi* GILL & CASTER.
5) Syringocrinidae PARSLEY & CASTER, *M.Ord.*, N. Am.(Can.).
    - *Syringocrinus* BILLINGS, *M.Ord.*, Can.(Ont.). (**S. paradoxicus* BILLINGS); *S. sinclairi* PARSLEY & CASTER.
6) Iowacystidae GILL & CASTER, *U.Ord.*, N.Am. (USA).

Iowacystis Thomas & Ladd, *U.Ord.*, USA (Iowa). (**I. sagittaria* Thomas & Ladd).

7) Belemnocystitidae Parsley, n.fam.[1] *M.Ord.*, USA.

Belemnocystites Miller & Gurley, *M.Ord.*, USA(Ky.). (**B. wetherbyi* Miller & Gurley).

Family MINERVAECYSTIDAE

Ubaghs and Caster, new family

Characters of *Minervaecystis*. *?U.Cam., L. Ord.*

Minervaecystis Ubaghs & Caster, **new genus** [**Dendrocystites vidali* Thoral, 1935; M] [=*Dendrocystis* sp., Bather, 1913]. Large solutans with inflated, somewhat depressed theca, unequally biconvex, or possibly convexisubplanate; ovoid in profile, without lobation; thecal plates large, thin, nonimbricate, unornamented except near anus where they are granular; obverse plates somewhat smaller than reverse ones; flanks covered by regularly curving tessellation; facial differentiation gradual over the flanks. Arm and anus opposite; arm emerging abruptly, without plate gradation, from distal right margin of obverse face or slightly on flank; anus on proximal left in obverse face near posterior margin; arm long, narrow and very flexible in life, compressed, slightly angular aborally, presumably biserial and composed of opposite brachial plates, however, no aboral suture in evidence; confluent brachiole pairs imbricate distally; cover plates large, subequal in width to brachial flank, meeting in low arch over ambulacral groove, apparently not quite in series with brachials. Adbrachial circlet of plates forms imbricating collar or sheath about arm base; left, obverse, lateral sheath plate bearing 2 hemispherical prominences which presumably represent hydropore and gonopore. Anus covered by low circular "pyramid" of elongate subtrigonal plates. Stele very long and complexly zoned; proxistele inflated, slightly compressed, nearly terete, tetramerous and anomalocystitoid, comprising some 25 to 30 annular, telescopically imbricating rings, last 6 or 7 progressively diminishing in diameter toward mesistele and last tetrameres about twice as long as others, each tetramere bearing proximal external bourrelet or thickened lip which deeply imbricates beneath proximal adjacent tetramere, distal margins of tetrameres scalelike and feather-edged, also with low angular fold crossing each left reverse tetramere at mid-width in alignment with carina which diagonally crosses mesistele and becomes prominent keel on proximal dististele; mesistele short, mainly covered by 2 series of plates, one of which aligns with right obverse tetrameres and other, with left reverse, distally continuing as dististele dimeres-biseries (Fig. 378); alternate tetrameres aligned with 2 series of 2 or 3 distally diminishing plates which lie between dominant series of mesistele; mesistele zone short, and making distal transition from 4-part to 2-part symmetry; almost no mesistele in some specimens; dististele very long, narrow tail showing compression of double series of plates, and rotation (Fig. 378); proximal dististele composed of 2 or 3 long dimeres, suturing on extensiplane, reverse dimeres being carinate; mesial zone of long plates which show distal transition from dimerous to biserial, each of 3 proximal plates in this zone reversely bearing very high, comblike blade at about mid-length of postproxistele tail; distal dististele forms narrowly lanceolate, caudal fin composed of biserial plates, flattened in extensiplane (plane of zigzag suture); obverse fin plates asymmetrically rounded, reverse ones angular; stele elements all flexibly joined *?U.Cam.*, N.Am.(Nev.); *L.Ord.(Tremadoc.)*, Eu.(France).——Fig. 381. **M. vidali* (Thoral), Tremadoc., France; *1*, reverse face of holotype, ×2; *2*, oral detail of holotype arm and adbrachial pore plate, ×6; *3*, aboral view of holotype arm (note lack of aboral suture), ×6; *4*, anal pyramid of holotype, ×6; *5*, lateral view of mesistele and proximal dististele, ×4; *6*, obverse aspect of complete stele with cross sections at indicated places, ×3.5; *7*, detail of distal 2 pectinate dimeres of dististele, ×12 (Ubaghs, n). [See Fig. 378,*2*.]

Family DENDROCYSTITIDAE

Bassler, 1938

[=Dendrocystidae Bather, 1899]

Theca widely variable, but always asymmetrical; usually depressedly inflated; faces poorly or well differentiated; most plates tessellated and firmly joined; always some provision for expansion and contraction of viscera by flexible union of some thecal plates; arm and anus commonly on left side, but variable in position; proxistele fundamentally tetramerous and anomalocystitoid, but commonly modified by the addition of secondary platelets and possibly modified by tetramere fusing into narrow annuli; mesistele showing distal transition from four-part to two-part symmetry of plate series; obverse left and reverse right tetramere series distally continuous with biseries-dimeres of dististele. *M.Ord.-L.Dev.*

Dendrocystites Barrande, 1887, p. 142[2] [**Cystidea*

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[1] While this section of the *Treatise* was in preparation, *Belemnocystites* was discovered by Ronald L. Parsley of the University of Cincinnati to be a solutan and in Parsley's opinion a new family is essential for its inclusion. His more detailed analysis will appear elsewhere.

[2] Several authors have attributed new taxa published in *Système Silurien . . . de la Bohême: Classe de Echinodermes, Ordre des Cystidées* (v. 7, pt. 1) to Waagen, who served as Barrande's posthumous editor. In the introduction to the volume, Waagen took pains to deny any share in authorship; thus the new taxa presented therein belong to Barrande.

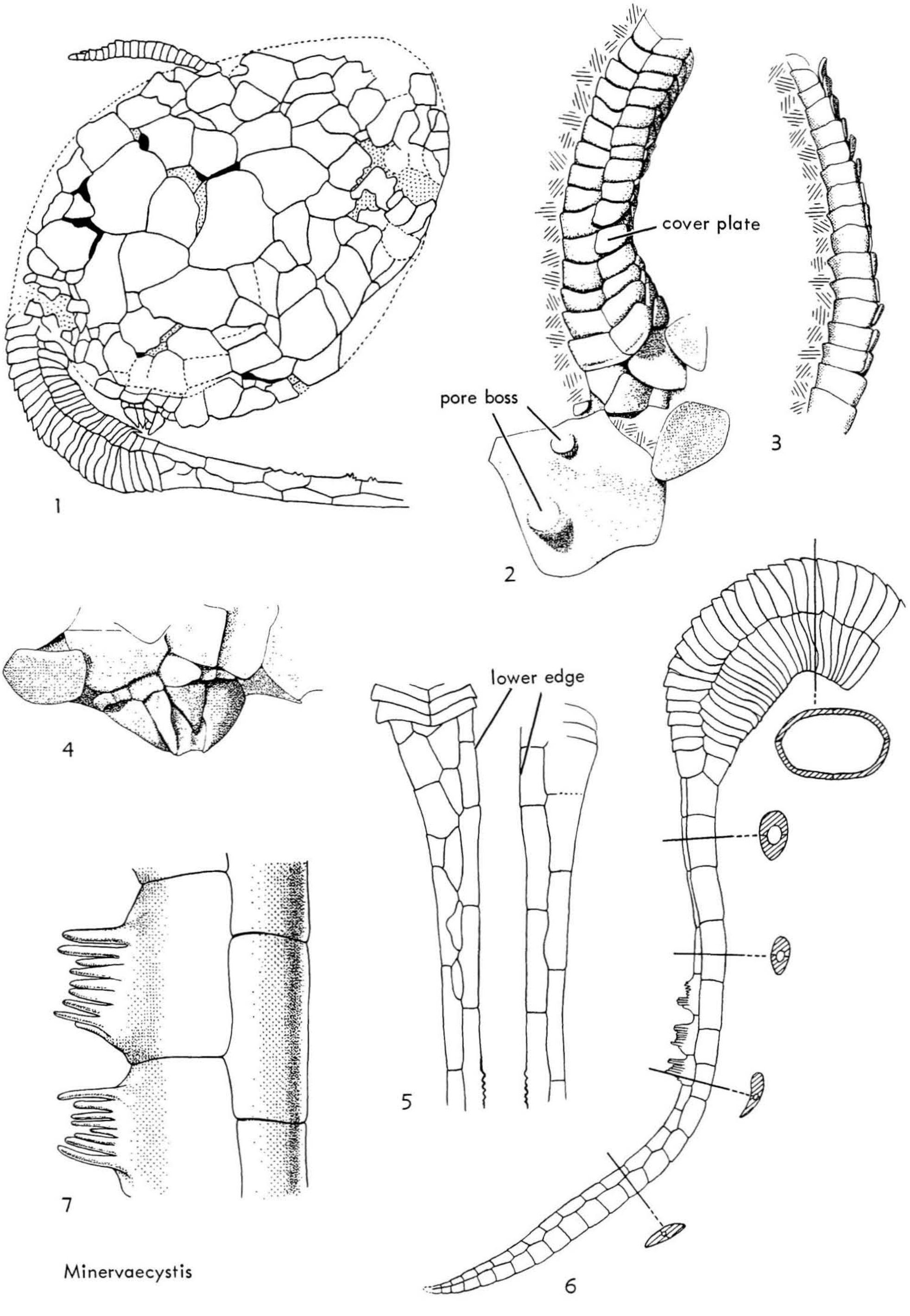

Fig. 381. Minervaecystidae (p. S606).

Sedgwicki BARRANDE, 1867, p. 179; OD] [=*Dendrocystis* BATHER, 1889, p. 268 (obj.) *(nom. van.)*]. (Diagnosis based on type species.) Large dendrocystitids with lobately triangular thecal outline, especially in usual flattened state; theca depressedly inflated, obverse and reverse faces differentiated both in configuration and in plate details, obverse face usually convex and topographically complex, reverse flat to concave and simple; thecal margins usually rounded, may be subangular or sutural; position of arm, anus and thecal lobation asymmetrical; prominent, angular left proximal lobe, but only very faint lobate rounding on right side; left lobe composite, with large angular preanal lobe and rounded anal lobe *(s.s.)*; distal margin moderately lobate. Arm commonly distal and sinistral, emerging from obverse thecal face; may be nearly axial and in some individuals dextral. Anus marginal and usually on posterior lateral face of left proximal lobe, rarely on right side, when large proximal lobe is also dextral. Thecal plates many, tessellated, firmly united in life (not imbricated as in usual crushed specimen), except for localized flexible junction, these plates about equal in size and number on both faces, relatively large and few in juveniles but abundant and smaller in adults; plate increment mainly by sutural intercalates (rosetting). Obverse face somewhat swollen in distal third, with broad oval tumescence of flexibly joined, large, ornamented, polygonal plates in widest proximal part of theca (apparently to accommodate expansion and contraction of viscera); larger movable plates bearing central boss and radiating costae; ribs increase in width and elevation toward plate margins, smaller (younger) plates bearing low central umbo and peripheral nodes, latter increasing in prominence and extending toward center of plate with increase in plate size. Mobile tumescence proximally bordered by tightly fused girdle of adsteleal plates and distally by bounding arc of unornamented, firmly united thecal plates, each of which upwardly geniculates at low angle toward tumescent area, and on inner surface bears low bounding ridge on line of geniculation. This ridge can be traced across plates of internal obverse face from preanal lobe to widest part of right proximal lobation. [The bounding ridge and geniculated plates serve in complexly preserved and incomplete specimens as an excellent key to the obverse face.] Brachial orifice nearly circular and surrounded by constant number of adbrachial plates, one on left side bearing wartlike node which is apparently madrepore-hydropore. Adbrachials, like entire distal thecal plates, firmly joined in life, with low flange developed adjacent to orifice; between adbrachials and tetramerous arm, several circlets of small platelets intervene in largest specimens and are inconspicuous in juveniles. Marginal anus covered above by rounded lappet which makes outline of anal lobe *(s.s.)*; center of lappet occupied by ovate-subtrigonal, convex suranal plate (BATHER's "sugarloaf plate"); this is distally margined by arc of small, polygonal plates, and laterally-reversely by radiating narrow plates (probably periproctal); preanal lobe very prominent and angular. Arm slightly compressed and longer than theca; aboral suture between brachial biseries apparently open; brachials about twice as wide as cover plates, with which they are essentially in annular series; cover plates meeting in zigzag adorally. Stele long and axially differentiated into 3 zones: proxistele basically anomalocystitoid, but in adulthood many small platelets are developed so as to conceal juvenile 4-part symmetry. [This is especially true of *Dendrocystites* where young forms show tetrameres (or octameres) between which platelets form on all sides.] The ephebic proxistele is an alternating series of 6 to 8 larger and smaller rings of platelets, the first being composed of larger firmly united elements, and the second of many plates loosely joined. Despite rosetting, the mesistele bears evidence of tetramere series, 2 of which persist distally into the dimerous series; 2 alternates diminish in size and disappear in length of the mesistele. Here, as in *Minervaecystis,* the dististele is proximally dimerous and distally biserial; plates of distal extremity loosely joined, and faceted so as to permit some prehension; dististele may be somewhat compressed, and reversely keeled. *M.Ord.,* En.(Boh.), questionable elsewhere.——FIG. 382, 383. **D. sedgwicki* (BARRANDE), M.Ord., Boh.; 382, rubber molds of type and topotype specimens in National Museum, Praha (all photos Caster, n); 382,*1,* oblique view into undeformed proximal interior of obverse thecal face (proxistele insertion as in life, anal lappet at right) showing tessellation of plates and rigidity of test (BARRANDE type), ×2; 382,*2,* obverse view of immature form in which proxistele tetrameres are in process of fractionation (note rosetting of proximal mesistele), ×2; 382, *3,* reverse view of interior surface of obverse plates showing usual imbrication of plates due to compression during fossilization (note hydropore pustule on adbrachial plate, multiple platelets of proxistele, and carination of axial series of mesistele) (BARRANDE type), ×1.5; 382,*4,* obverse view of topotype with complete stele which lacks evident keeling and shows distal dimere sutures beveled as for some degree of prehension (Barrandium, Praha), ×1; 382,*5,* obverse view of young individual with short tetramerous proxistele and tessellated thecal plates which are relatively few and very large (topotype, Barrandium, Praha), ×2; 383,*1-3,* obverse views of new material (Narodni Museum, Praha) showing calcareous plates intact, ×1 (Caster, n.).——FIG. 384,*2;* 385. *D. barrandei* BATHER, Low.M.Ord., Boh.; 384,*2,* specimen figured by BATHER (1913), ×1.7; 385, rubber mold of part of slab covered by oriented specimens in usual state of preservation of homoio-

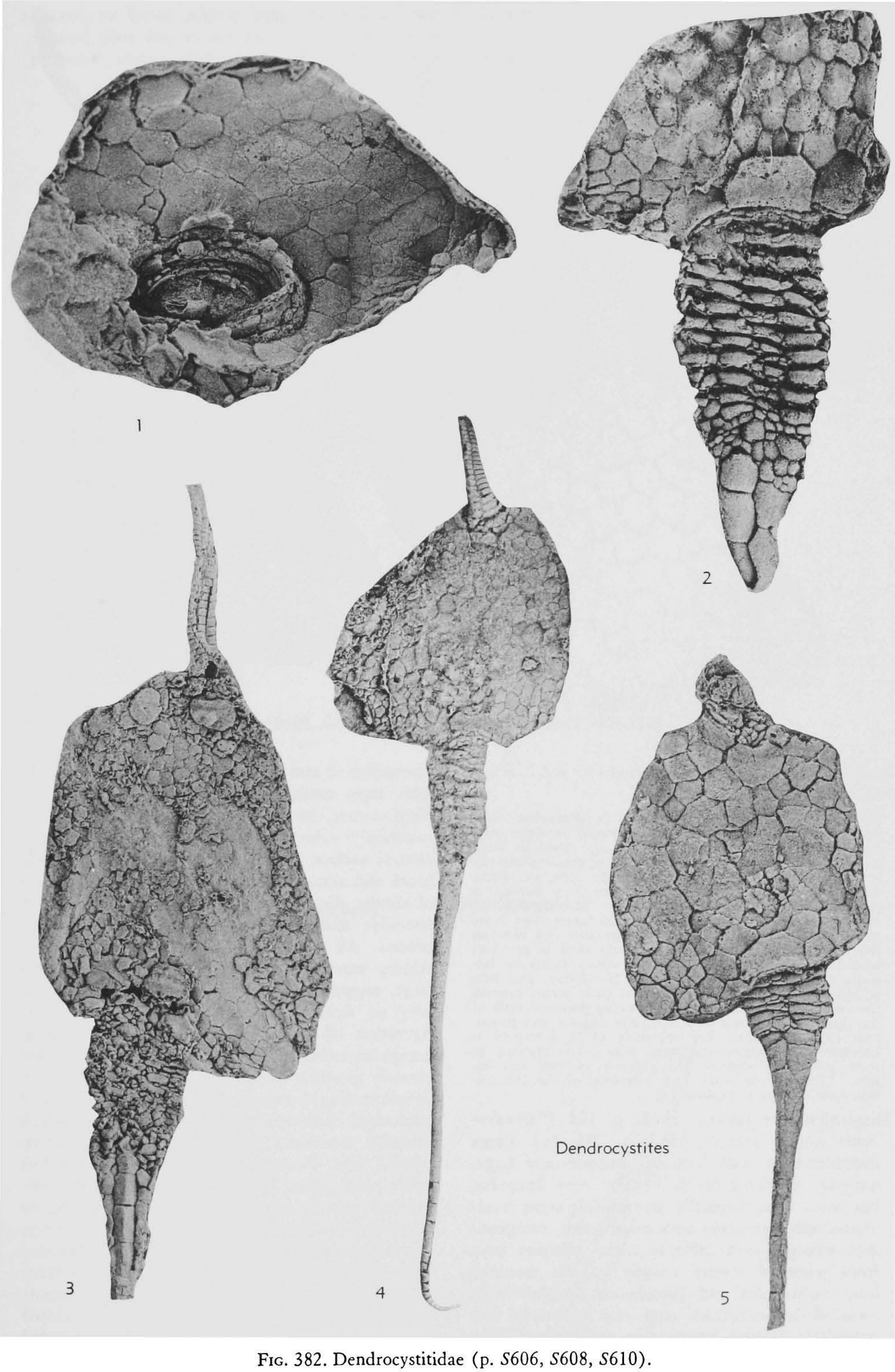

FIG. 382. Dendrocystitidae (p. *S*606, *S*608, *S*610).

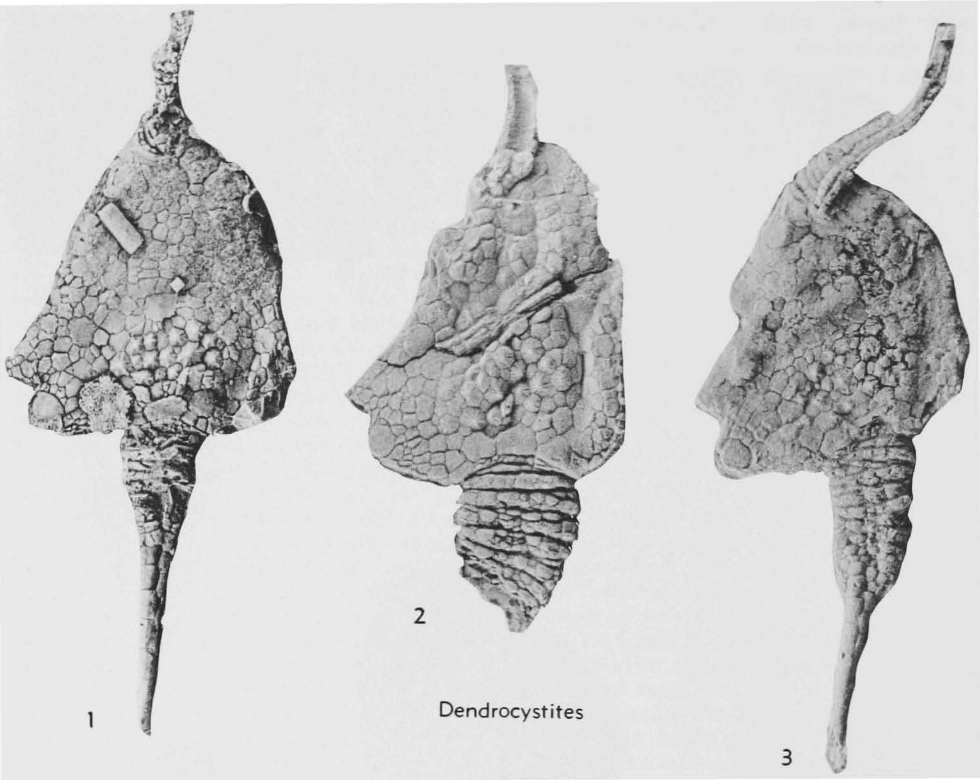

FIG. 383. Dendrocystitidae (p. S606, S608, S610).

steles (note tetramerous proxisteles), ×2.7 (Caster, n). [See Fig. 387.]

[Although it shares several traits with *Dendrocystites sedgwicki*, the form designated as *D. barrandei* is more pyriform, less lobate, and more symmetrical. Also, its faces are less well differentiated and more of its thecal plates are loosely articulated, a maximal tumescent zone not being distinguished. Probably the species named by BATHER is generically distinct from *Dendrocystites*. The thecal plates of *D. barrandei* are relatively fewer and larger than those of *D. sedgwicki*, with rosetting unimportant and platelets few. The arm of *D. barrandei* is nearly axial in position, with large geniculating adbrachials which imbricate laterally to form an adbrachial sheath. No obvious anal lobe or lappet is seen and a single subanal plate occurs beneath the anus on the reverse side or rounded posterior wall of the theca. The preanal lobe is equally angular and prominent in both species. The proxistele of *D. barrandei* is tetramerous and anomalocystitoid, with a few platelets in some individuals between the tetramere sutures and annuli. The mesistele bears clear indication of distal transition from tetrameres to dimeres.]

Dendrocystoides JAEKEL, 1918, p. 123 [**Dendrocystis scotica* BATHER, 1913, p. 391; M]. Large dendrocystitids with hornlike processes and large, unequal, proximal lobes. Outline very irregular, but main theca generally trapezoidal; some hourglass-shaped; arm and anus on left side, marginal; arm emerges from obverse distal margin; anus from posterior reverse margin of left proximal lobe; subangular and protuberant preanal lobe; rounded inconspicuous anal one. Obverse face irregularly convex; reverse face nearly flat. Theca commonly much constricted just proximal of emergence of arm and antibrachial process. Usually with large antibrachial horn arising from right distal corner, its dimensions highly variable, but commonly subequal to arm; it may arise from obverse surface or distally; commonly very broad-based and almost lobelike; supplementary processes of similar dimensions may occur on distal left or laterally; antianal lobe may be extended in a process. All processes plated like theca, and containing extension of thecal cavity. Thecal plates large, angularly polygonal and nonimbricating in life; no striking differentiation in size or configuration of two faces; surface finely granular except on reverse face near anus, where plates are coarsely granular or pitted. Adbrachial plates rise as imbricating sheath about base of arm; left lateral adbrachial bearing complex tumescence which probably represents hydropore. Arm long, compressed and flexible; aboral suture ligamental; cover plates about half as wide as brachials; ambulacral groove narrow, cover plates standing at high angle over it and meeting adorally in zigzag, but in series with brachials to which they articulate; cover plate-brachial suture line sharply depressed; internally each cover plate grooved for its whole width. Anus may have been sphincterally closed and slitlike; its region on posterior surface crowded with very long and narrow periproct plates; anus floored by broad reverse lappet in which ovate subanal plate lies to one side of concentration of periproct plates. Stele long and differentiated. Proxistele tetramerous and anomalocystitoid, with many small polygonal integumentary plates in zone of flexible tissue between tetramere rings; best

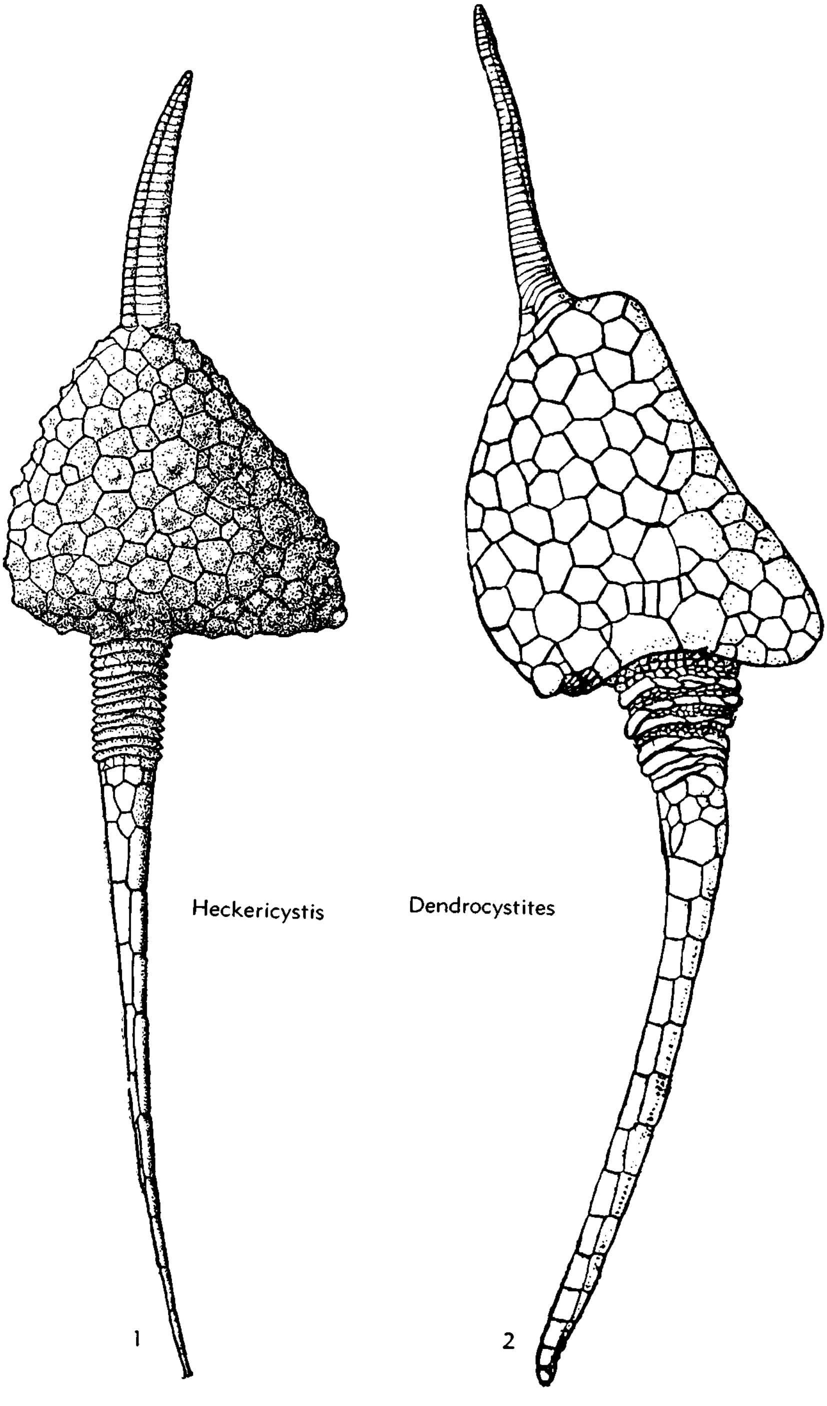

Fig. 384. Dendrocystitidae (p. S606, S608, S610, S613).

seen in specimens preserving inside view of tetrameres. Externally proxistele meres may be smooth, thin and almost scalelike, or very much thickened and complexly, radially rugose in completely unique manner. Mesistele reminiscent of *Minervaecystis,* with biseries of dististele correlating across mesistele with tetrameres in same manner as in that genus. Dististele very long and narrow, terete and composed of long dimeres proximally; these shift to alternating position distally; actual end of stele not seen. Dimere orientation obverse and reverse; suture in extensiplane. *U.Ord.,* Eu.(Scot.).

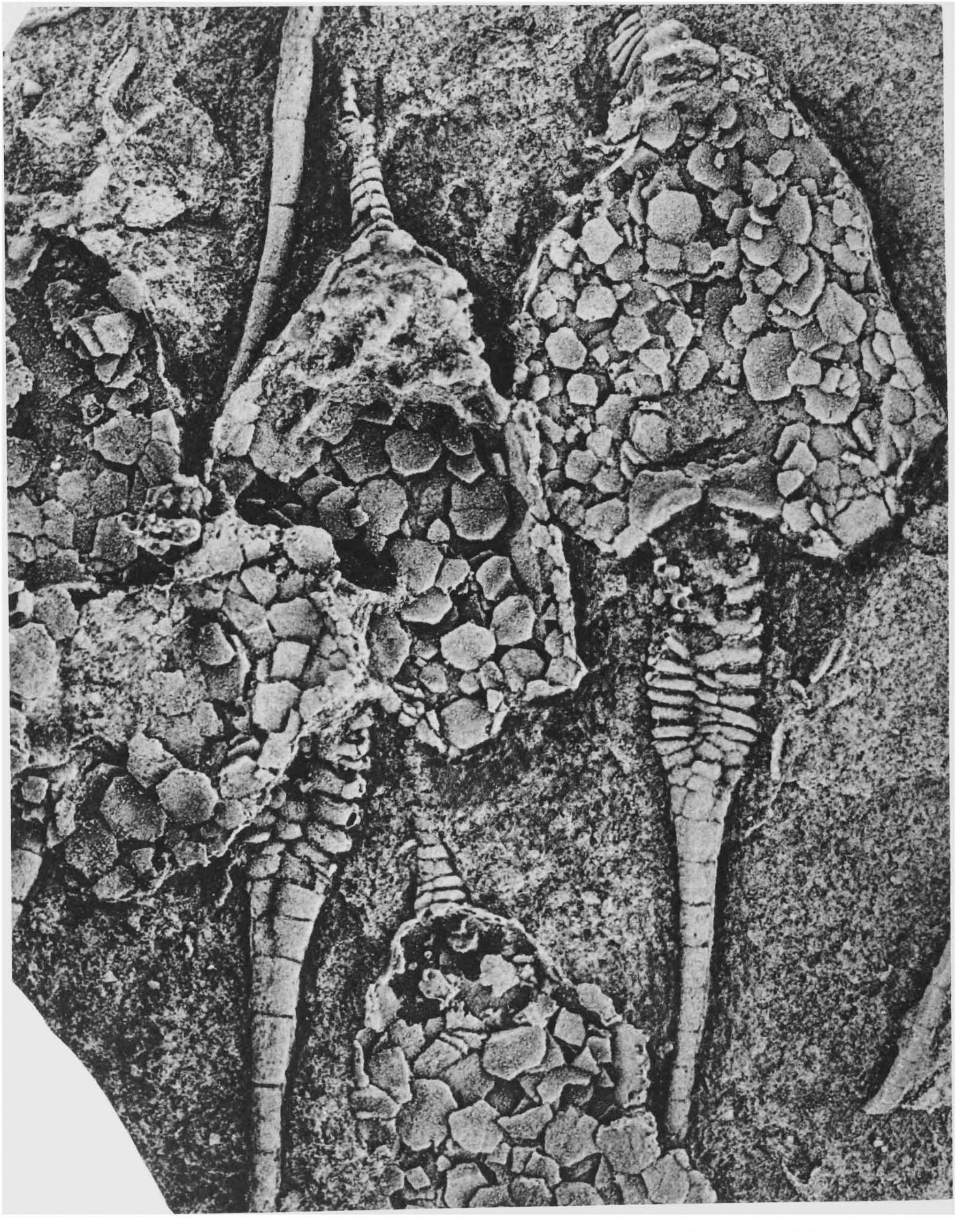

FIG. 385. *Dendrocystites barrandei* BATHER (Dendrocystitidae) (p. S606, S608, S610).

——FIG. 386, 387. **D. scoticus* (BATHER); 386, reverse face of BMNH E23700, fairly complete but with somewhat disarranged thecal plates, ×2.1 (Caster, n; drawing by E. A. Dalvé); 387, *1-6,* rubber molds of topotypes, all from BMNH; 387,*1,* reverse face showing usual imbrication of plates induced by compression during fossilization, with complete "antibrachial" horn, large hydropore pustule on right side of figure; arm slightly twisted so as to conceal aboral suture of brachial biseries (E23700), ×2.2; 387,*2,* reverse view showing proximal plates in tessellated life position (note granular ornament on these plates) imbricate periproct plates on posterior margin of anal lobe at right, hydropore pustule apparently with 2 pores, proximal stele unornamented (E5732), ×2.2; 387,*3,* arm detail, obverse view with adbrachials in place, hydropore pustule prominent (E5823), ×2; 387,*4,* reverse view of highly ornamented proxistele (note also many platelets inside lumen) (E5827), ×2.5; 387,*5,* reverse view of ornamented proxistele and interior surface of obverse tetrameres showing bourrelets (note axial rotation of keel in mesistele) (E5719), ×2.2; 387,*6,* reverse view of distal theca and arm (note biserial meeting of cover plates) (E5822), ×2 (all Caster, n). [See Fig. 376, 379.]

Heckericystis GILL & CASTER, 1960, p. 16 [**Dendrocystites kuckersiana* GEKKER [HECKER], 1940, p. 23; M]. Theca inflated, asymmetrically trigonal in profile; probably somewhat depressed, proximal subangular anal lobe; arm distal; anus at apex of anal lobe and apparently closed by or beneath prominent mammelon (or "sugarloaf plate"); thecal plates small and polygonal, each with central prominence; nothing known of facial or regional thecal differentiation. Arm biserial and moderately long; stele long and terete throughout, differentiated into 3 zones. Proxistele sheathed in many narrow elevated rings, probably tetramerous, but no sutures reported; intervening zones apparently integumentary; mesistele shown as composed of 3 circlets of polygonal platelets decreasing in number in each ring distally and suggesting transition from tetramerous to dimerous; dististele attenuate, sheathed in dimeres which are laterally opposed proximally, and obversely-reversely in distal region. *M.Ord. (Kuckers),* Est.——FIG. 384, *1.* **H. kuckersiana* (GEKKER) [HECKER], ×1.7 *(43).*

Dehmicystis CASTER, **new genus** [**Dendrocystites (Dendrocystoides?) globulus* DEHM, 1934, p. 20; M]. Spherically inflated (or moderately depressed), appearing circular when crushed; thinly plated, unornamented; anus large, circular and proximal, covered by large pyramid of elongate trigonal imbricating plates; some periproctal plates between anal pyramid and adanal thecal plates. Proxistele anomalocystitoid, very flexible; dististele long and dimerous. [GILL & CASTER (1960) tentatively assigned this species to *Rutroclypeus,* but further examination of the holotype reveals a large circular anal area, and strongly supports DEHM's original idea that the theca was inflated in life; hence the new assignment.] Only incomplete holotype known. *L.Dev. (Bundenbach),* Eu. (Ger.).——FIG. 388,*1,2.* **D. globulus* (DEHM); *1,* original figure, ×1.1 *(34)*; *2,* drawing from

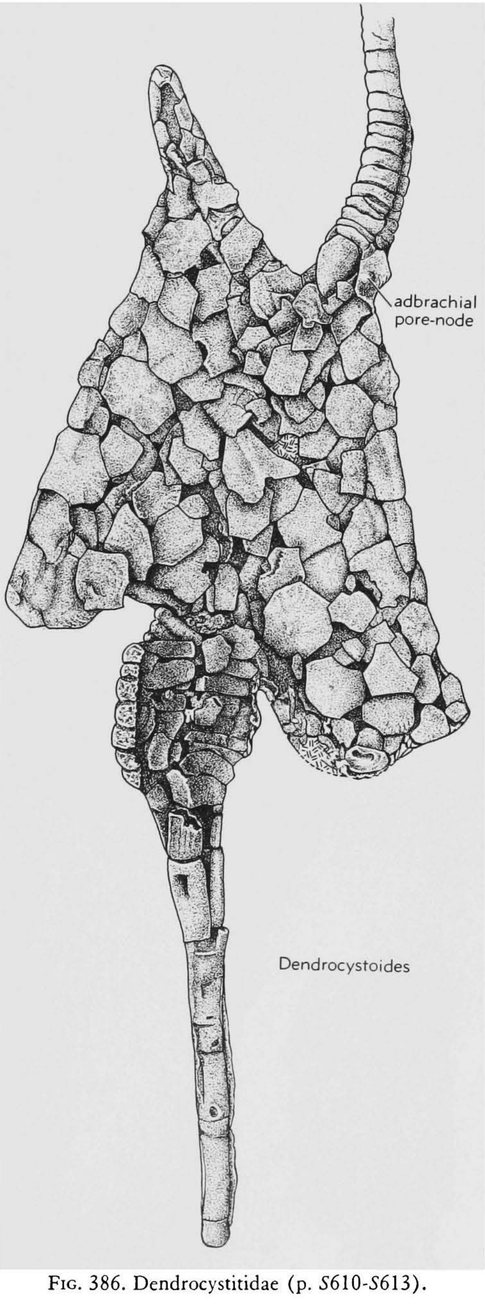

FIG. 386. Dendrocystitidae (p. S610-S613).

photograph of holotype and only known specimen (note anal pyramid), ×1.4 (Caster, n).

Family GIRVANICYSTIDAE Caster, new family

Solutans covered by relatively few large plates rigidly fused into two opposable faces united by flexible peripheral suture on extensiplane; prominent crest and spines on reverse face; proxistele anomalocystitoid, with many small platelets on proximal exterior of tetrameres. *U.Ord.*

Girvanicystis Caster, **new genus** [**G. batheri* Caster, **new species**; M]. Large, obliquely cordiform

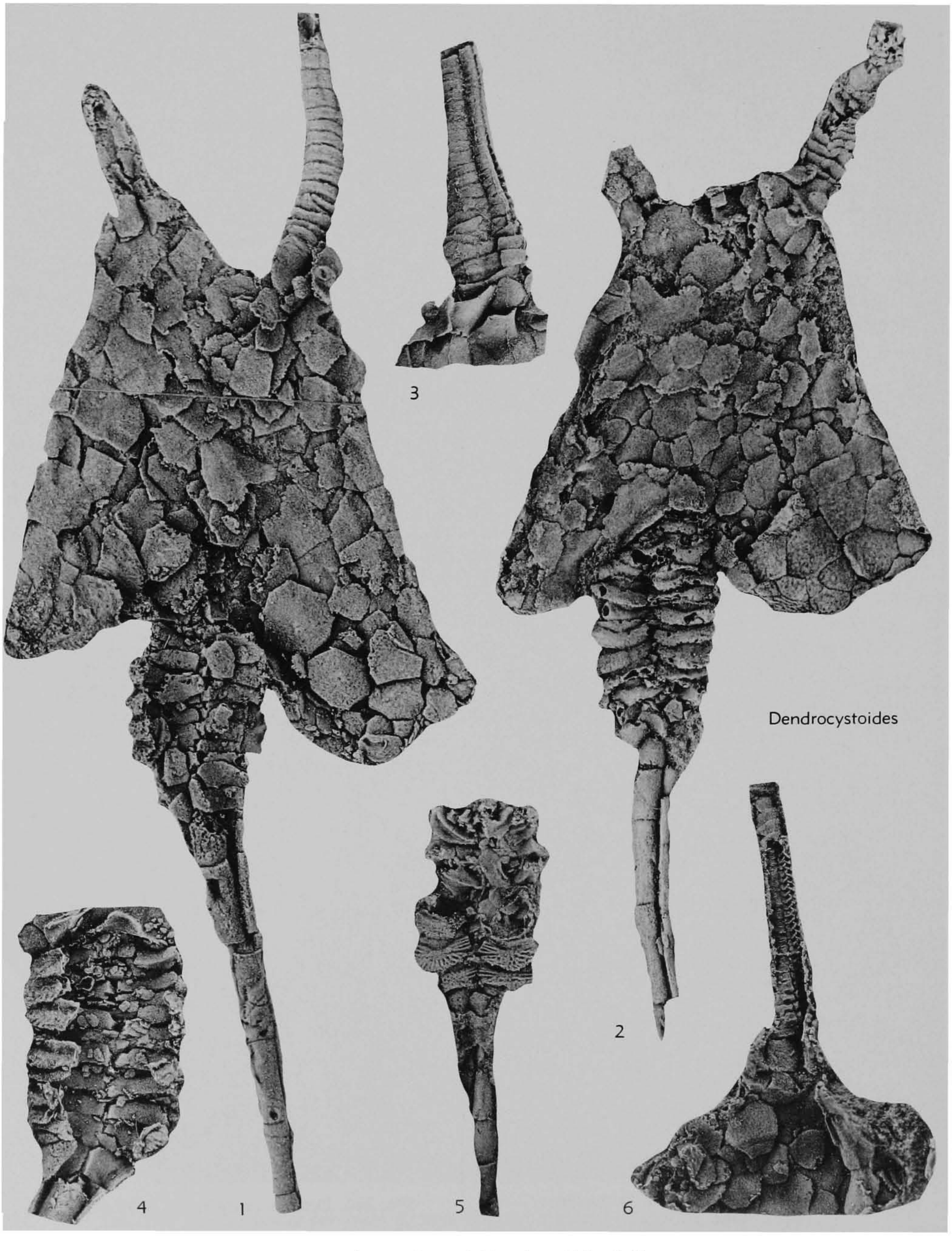

Fig. 387. Dendrocystitidae (p. S610-S613).

dendrocystitid, prominently and asymmetrically trilobate, with very large, unequal, rounded proximal lobes, anal one being larger; right anterolateral rounded lobe which extends well on distal side of level of arm insertion. Arm and anus on left side; anus well within reverse face of anal lobe; arm inserted on perimeteral suture between 2 thecal faces and essentially on thecal axis of balance. Deep rounded proximal re-entrant for insertion of stele. Thecal profile complex, but in general subplano-convex, obverse face being far less inflated than reverse one; marginally, except in immediate vicinity of arm base, both faces subplanate (perhaps slightly concavo-convex), in broad zone and apparently nearly in contact in life; obverse face apparently rose in broad axial arch, whereas reverse one shows distinct zones of tumescence: central area of anal lobe distended and bearing periproct with very high, asymmetric tumescence on distal side of this on left of thecal axis and extended to distal margin where it formed vertical distal wall of theca; beneath arm

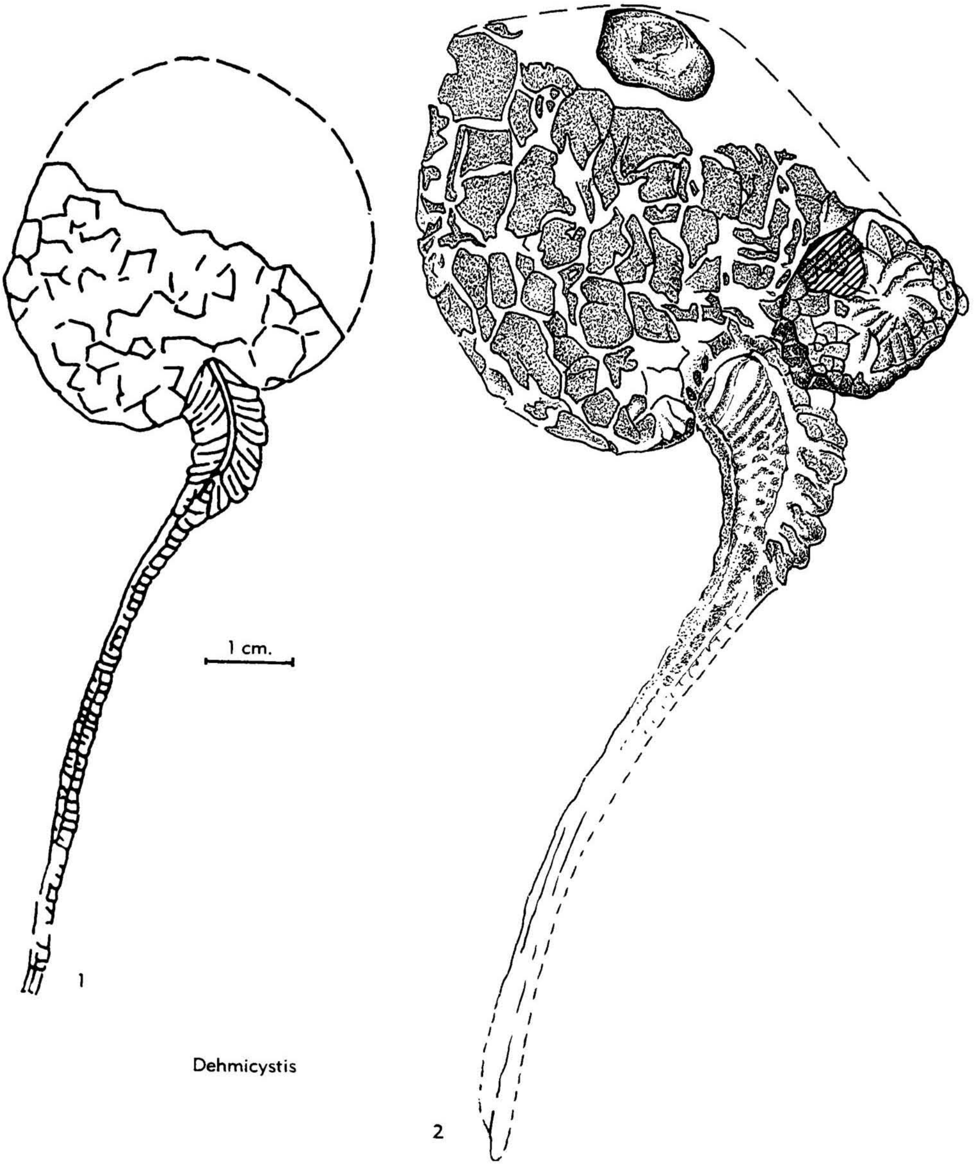

Fig. 388. Dendrocystitidae (p. S613).

insertion reverse theca was bowed angularly and sharply. [Thecal surfaces appear to have been largely rigid in life, their contact sutural and integumentary; with obverse face narrower and shorter than reverse one, and with something of an opercular nature; both perimeters are thickened considerably and in such way that they articulated in pillbox manner with obverse margin lying within the reverse one and fitting into a smooth deep groove just inside the thickened margin of the reverse face.] Thecal plates extraordinarily large, those of reverse side being larger and (discounting periproct area) fewer than obverse. Tight fusion of plates of both faces manifest and breakage does not always seem to follow old suture lines. On right distal lateral side of reverse theca, just proximal of anterior lobe, several large plates fuse to form radially broadly pleated stellate plate of very large size; single large axial adsteleal plate present in both faces. Aside from the marginal thickenings of the 2 faces and surface granulation, scattered hollow excrescences are the only other "ornament"; several plates in the distal and right distal area of the obverse face each bear a high sharp or blunt broad-based spine; on the obverse proximal region the adsteleal and several other plates bear groups of small warts or tubercles. Anus in central area of reverse face of anal lobe, covered by broad, low circlet ("pyramid") of elongate, lunate, imbricating plates; this in turn is surrounded by circle of many relatively small polygonal plates, probably loosely articulated also in life, a periproct zone; the whole is set within a subcircular foramen through the large plates which firmly invest this part of the theca. Arm emerging on extensiplane and from facial suture, but with brachial orifice more excavated in vertical wall of obverse plates in distal region than in obverse "opercular" surface; apparently 4 large plates complete adbrachial series, those of obverse side sutured (not imbricated) and showing transverse marginal excavation to accommodate oral surface of arm; adbrachial margin flanged; near flange on left obverse adbrachial, tiny perforation with collared neck may represent hydropore. Proxistele tetramerous, anomalocystitoid, with imbrication of ring pairs on both obverse and reverse axial sutures; imbricate telescoping of rings sharply defined, each ring bearing circular median crest or flange and showing on distal postflange margin many small polygonal platelets, apparently originally embedded in investing integument (but no platelets have been observed inside proxistele). Mesistele showing usual dendrocystitoid transition from tetramerous to dimerous condition, exhibits slight median reverse keel and passes into dististele within short distance; dimeres are opposite there for most of length and are sutured in extensiplane; disistele relatively stout and long. *U.Ord.*, Scot. ——Fig. 389, 390. **G. batheri*; 389, reverse face of holotype, presumably upwardly oriented in life (note adbrachial spinous hydropore) (BMNH, Gray Coll., 28473), ×3.4; 390, obverse face of paratype (obverse plates coarsely stippled, interior of reverse plates finely so) (note flanged hydropore with radii on interior of adbrachial plate which bears spine in surface) (BMNH, Begg. Coll., E5791), ×3.1 (all Caster, n). [See Fig. 373, 374.]

Family RUTROCLYPEIDAE
Gill & Caster, 1960

[Rutroclypeidae Gill & Caster, 1960, p. 22]

Solutans with nummuloidally depressed thecae, with or without prominent lobation, covered by many small polygonal plates which may be smooth, centrally umbonate, or prominently spinose; arm nearly axial, emerging from obverse face, no other facial differentiation; proxistele anomalocystitoid, dististele dimerous, with suture in symmetry plane. *L.Dev.*

Rutroclypeus Wither, 1933, p. 18[1] [*emend.* Gill & Caster, 1960, p. 30] [**R. junori*; M]. Thecal outline circular, nummuloidally depressed, giving impressions of polyplated (commonly hexagonally) sphere which has been pressed into nummuloidal mold; lobation may develop *(R. withersi)*; thecal margins vertical, coinlike, with plates and sutures falling as they may without any evident adjustment to form, plates small and usually bearing umbo, boss, or elongate solid spine in type species (although holotype is sparsely spinose). Juveniles show relatively fewer, larger, and less spiny plates than adults and they are more fusiform in outline, as well as possibly less depressed. Plate increment in *R. withersi* (possibly mainly on its lobations) is by exaggerated rosetting (see *Dendrocystites sedgwicki*) and hundreds of tiny platelets appear around larger primary plates, each with miniscule spine, thus creating appearance recalling miliary spines about bosses of echinoids. [These zones of small plates seem to have been flexibly joined and may be a form of facial differentiation. The spines may extend onto the proxistele, one to a plate, and apparently only on the obverse face; a single median proximal one on the mesistele has been noted.] Adult arm short and inserted distally to left of axis and within obverse disc; no adbrachial thecal plate differentiation noted, but some evidence indicates that at least one adoral plate bears swollen hydropore tumescence like that of Dendrocystitidae. Juvenile arm proportionately shorter and broader than in adults and axially inserted or nearly so. Anus unknown but must be marginal (slight marginal swelling adjacent to stele may mark spot). Stele long and differentiated; proxistele tetramerous, triangular

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[1] Originally described as a xiphosuran arthropod.

in outline, and flatly anomalocystitoid (more inflated in juveniles); mesistele very short and conical, its plating recording transition from proximal tetramerous to distal dimerous arrangement (see *Minervaecystis*); dististele long and narrow, becoming spatulate distally in some specimens, with dimeres opposite apparently throughout its length and somewhat depressed, suture is in symmetry plane. *L.Dev.*, Australia(Victoria).——FIG. 391,*1*. **R. junori;* diagrammatic sketch of holotype,

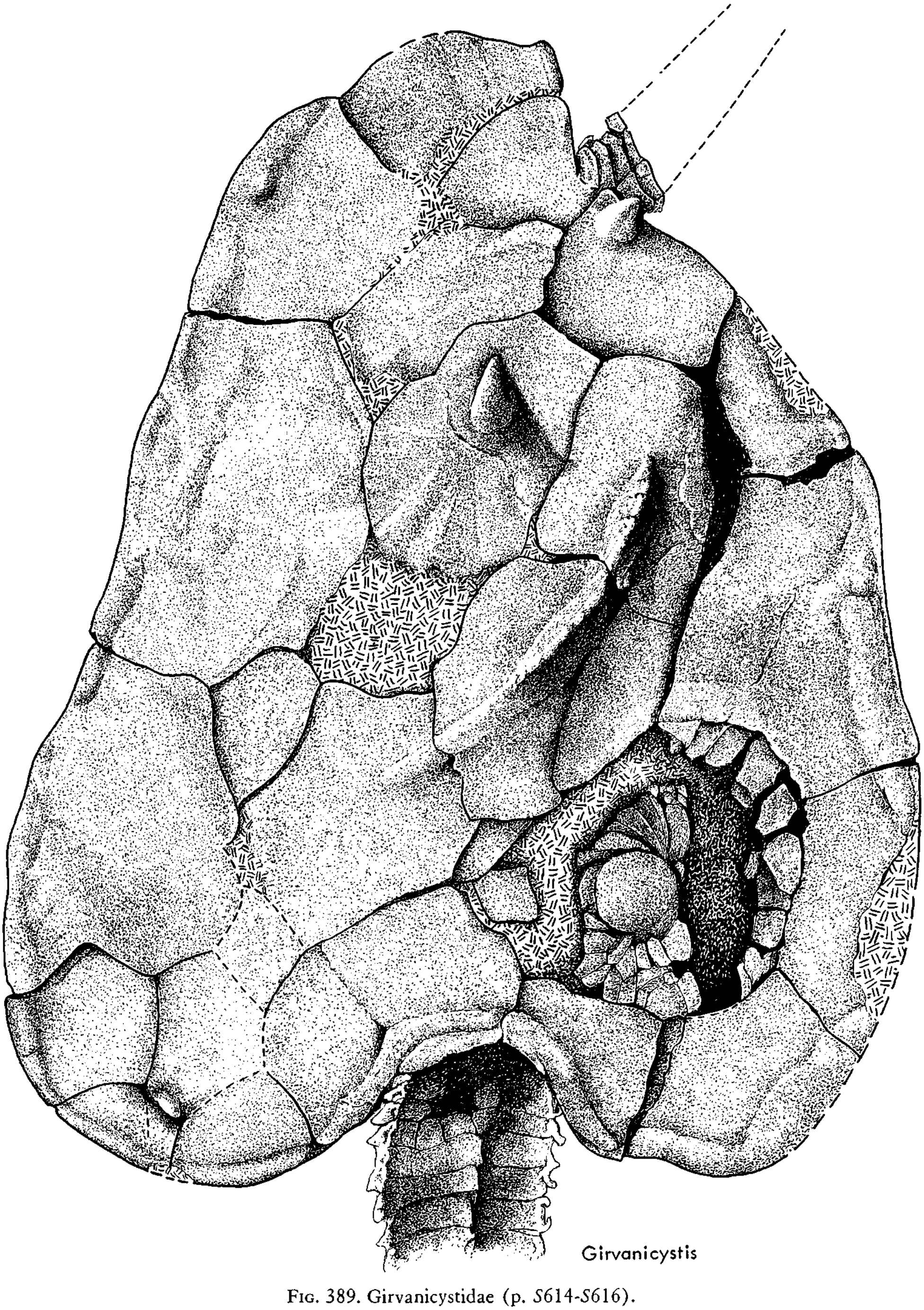


FIG. 389. Girvanicystidae (p. S614-S616).

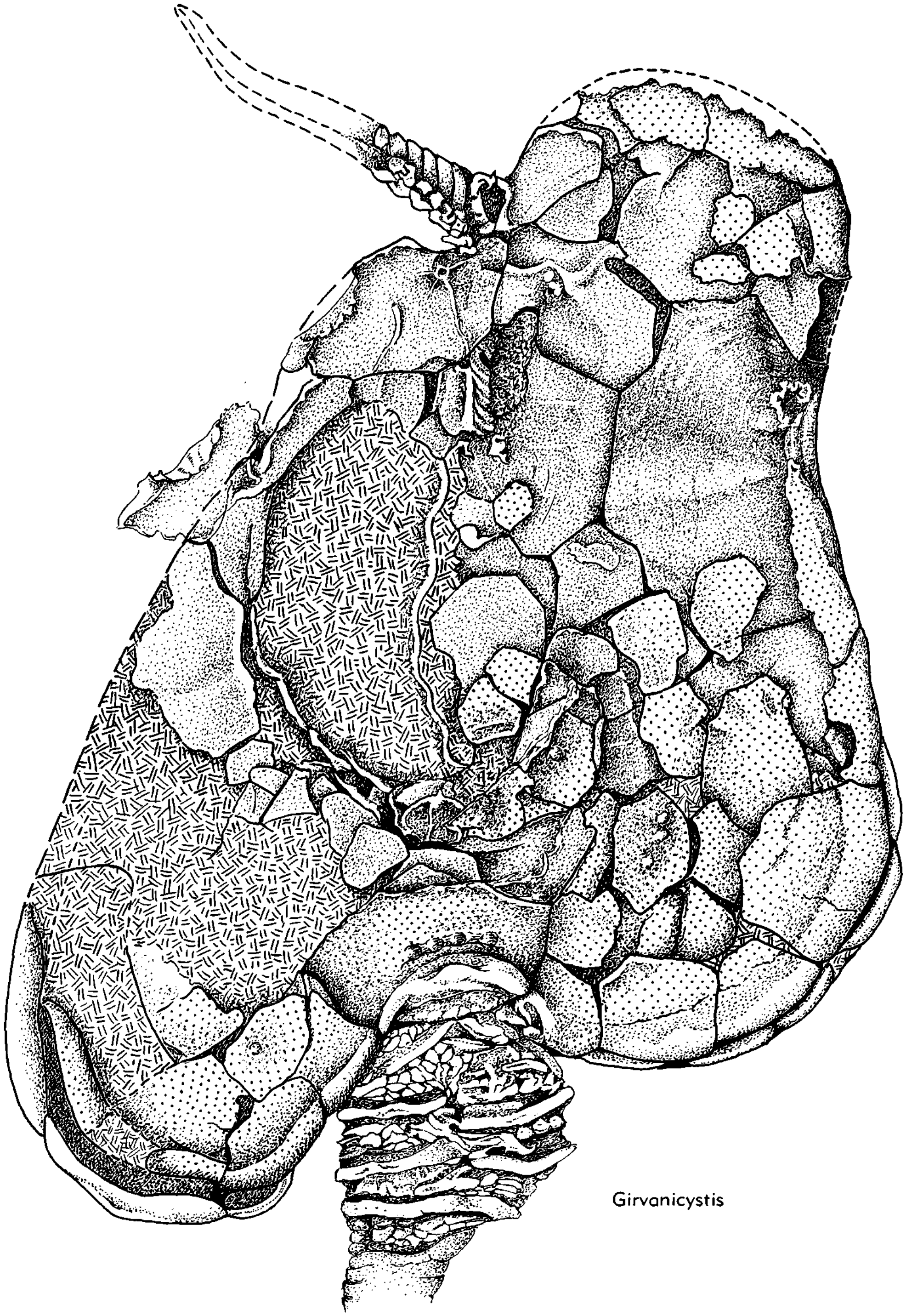


FIG. 390. Girvanicystidae (p. S614-S616).

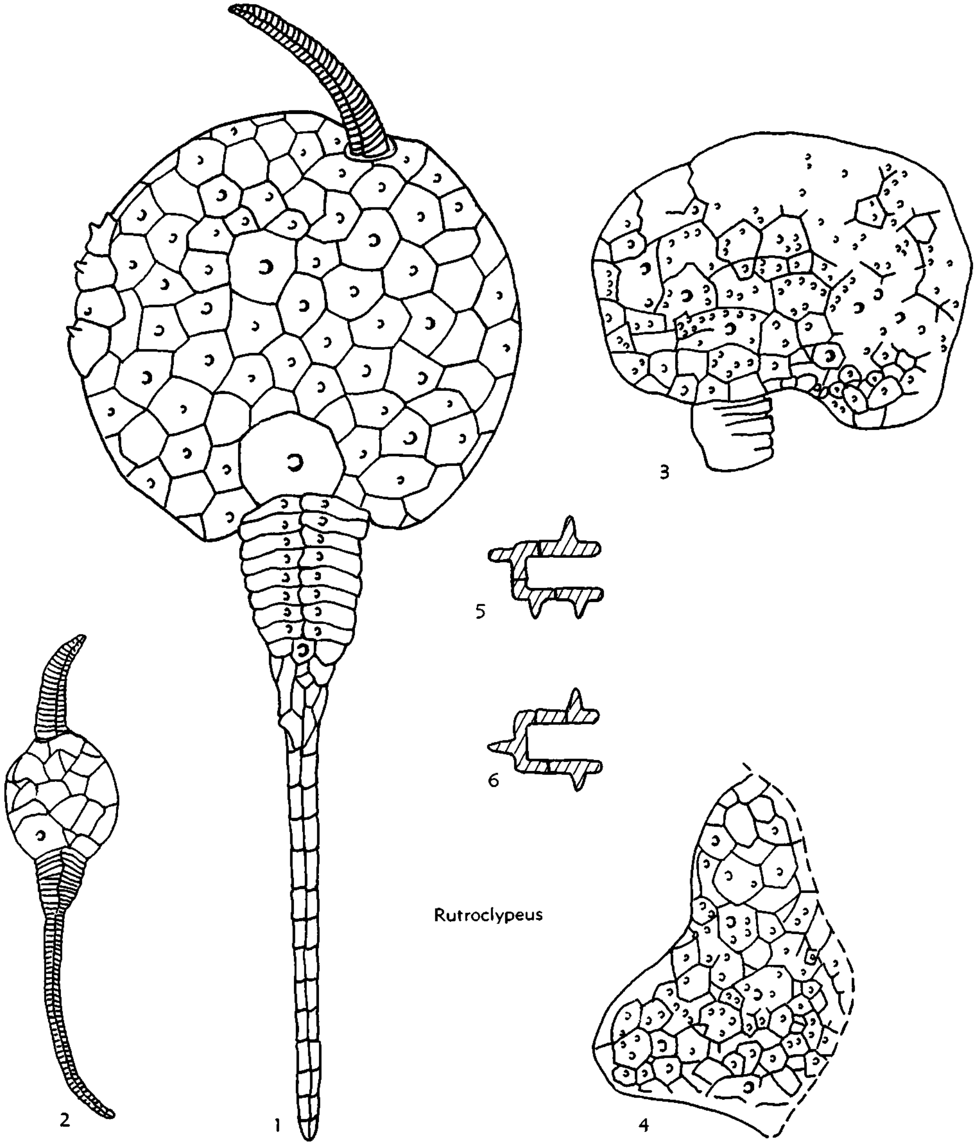


FIG. 391. Rutroclypeidae (p. *S*616-*S*617, *S*619).

×1.7 (Caster, n).——FIG. 391,*2*. *R. victoriae* GILL & CASTER, somewhat crushed juvenile specimen showing its relatively few larger plates and large arm, ×1.7 (Caster, n).——FIG. 391,*3-6*. *R. withersi* GILL & CASTER; *3*, specimen showing thecal lobation (?anal) and miliary granules, ×1.7; *4*, partial theca (holotype) with pronounced (?anal) lobe, ×1.7; *5,6*, diagrammatic cross sections of thecal periphery showing nummuloidal geniculation of plates, enl. (all Caster, n).——FIG. 392. *R. wilkinsi* GILL & CASTER; stereoscopic views of antanal side of theca showing spines on all of its plates but none on proxistele, ×1.8 *(43)*.

Family SYRINGOCRINIDAE
Parsley & Caster, 1965

[Syringocrinidae PARSLEY & CASTER, 1965, p. 115]

Elongate, ovoid, rigid and inflated theca; facially differentiated, convexi-planate (or inferiorly concave), covered mainly by few

FIG. 392. **Rutroclypeus wilkinsi* GILL & CASTER (Rutroclypeidae) (p. S616-S617, S619).

large plates, few large infracentrals, many small, flexibly joined supracentrals in ovoid area, and possibly partially surrounded by larger supracentrals; anus unknown. Arm long, terete, emerging from distal left margin of theca. Stele axially differentiated; proxistele anomalocystitoid, inflated; mesistele long, petiolate to lanceolate dististele; proximal mesistele unit an annulus; remaining surface with three series of plates, two of which are in series with dististele biseries and third in median position, composed of distally diminishing series of long plates; dististele biserial, becoming nearly dimerous at end with suture in extensiplane, along which considerable compression forms finlike structure, reverse dististele plates keeled and spinose. *M.Ord.*

Syringocrinus BILLINGS, 1859, p. 65 [**S. paradoxicus*; M]. Characters of family. [The pseudostylocone of the mesistele and proximal dististele is an especially typical feature. Restorations (Fig. 393) depict all available information on this genus.] *M.Ord.*, Can.(Ont.).——FIG. 393,*1*. *S. sinclairi* PARSLEY & CASTER; restorations based on type specimens; *1a*, obverse face with cross sections of stele indicated in life orientation, ×3.8; *1b*, reverse face, ×3.8 *(69)*.——FIG. 393,*2*. **S. paradoxicus*; views of holotype; *2a*, BATHER's (1913) drawing of stele as known to him, ×1.9; *2b*, present condition after bit of preparation, ×1.9 *(43)*.

Family IOWACYSTIDAE Gill & Caster, 1960

[Iowacystidae GILL & CASTER, 1960, p. 20]

Trigonal, much-depressed solutes with advanced differentiation of thecal plates, including rigid frame of marginal plates and characteristic supracentral and infracentral plates; arm on distal right side of obverse face; anus marginal at proximal left corner, closed by bivalved boss. Stele somewhat depressed, with short tetramerous proxistele which is narrowly annular, inconspicuous mesistele, and dominantly biserial (not dimerous) disistele with suture in symmetry plane. *U.Ord.*

Iowacystis THOMAS & LADD, 1926, p. 6 [**I. sagittaria*; M]. (Diagnosis based on restudy of type materials by PARSLEY & CASTER, 1965.) Thecal outline in form of isosceles triangle, with rigid marginal framework and high facial differentiation; facial surfaces parallel, one with few rigidly united large infracentrals, highly ornamented, and other with many large supracentrals which are flexibly joined together and also highly ornamented; single large median adsteleal plate on

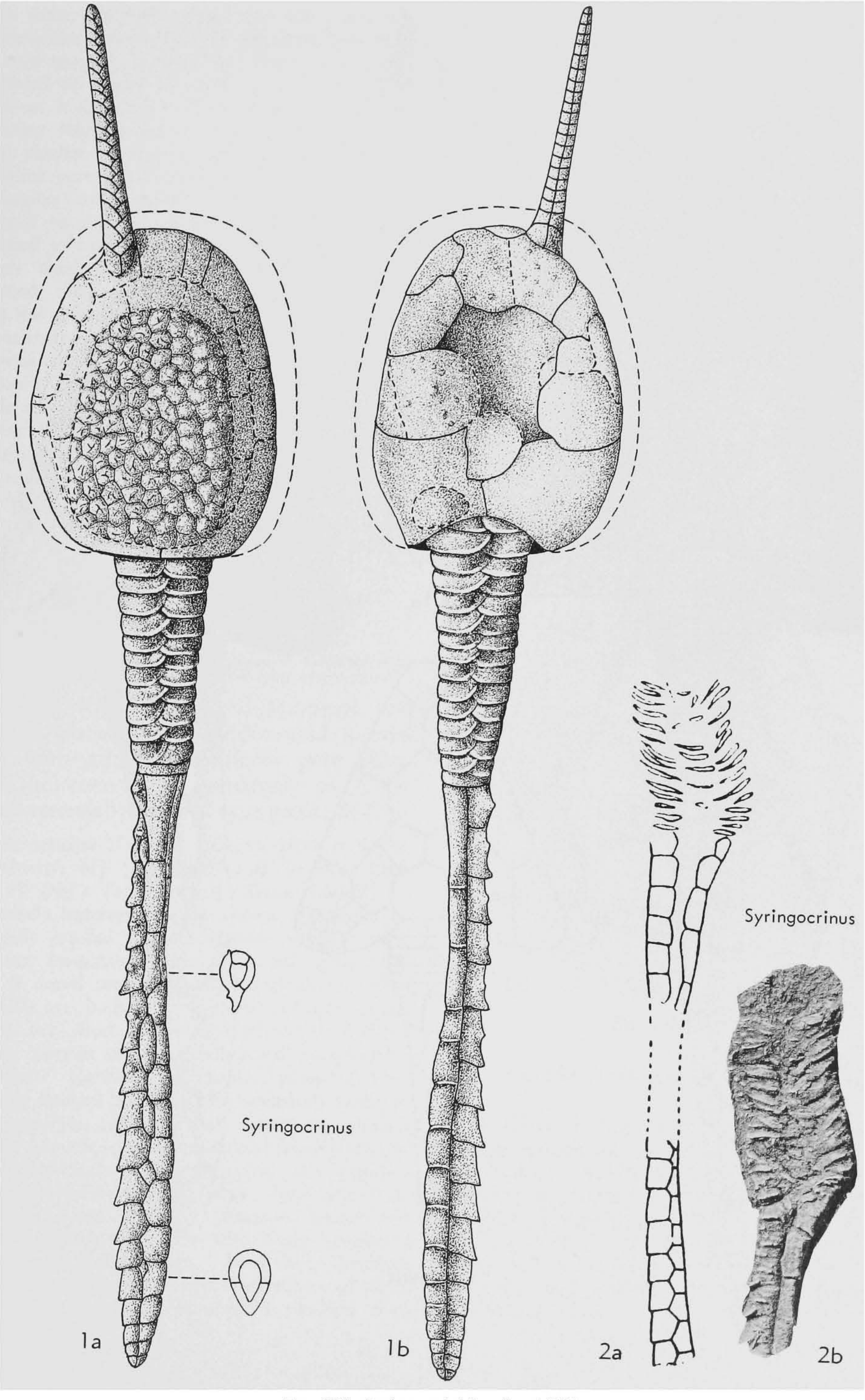


FIG. 393. Syringocrinidae (p. *S*620).

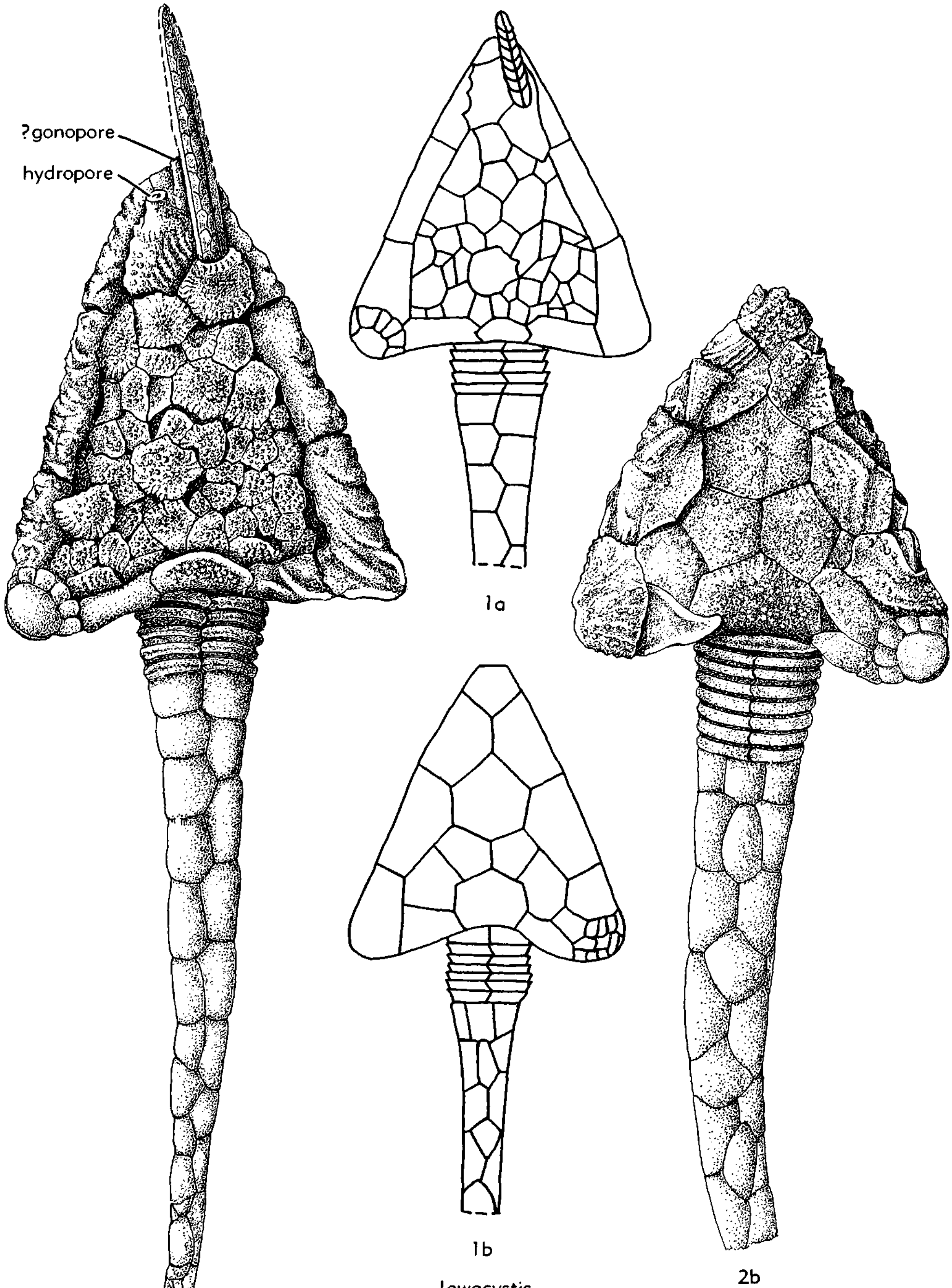


FIG. 394. Iowacystidae (p. *S*620, *S*623).

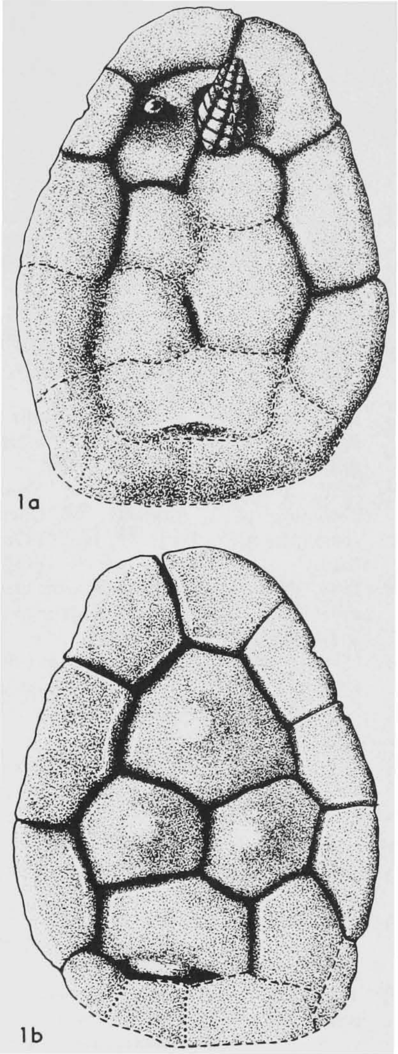
each face, also with adanal and adbrachial differentiation; anus closed by bivalved boss of 2 quarter-spheres parting in extensiplane, surrounded by circlet of small quadrilateral plates and on reverse side with 3 large adanal plates, creating lobelike aspect; left adoral plate bearing phialine hydropore aperture, with smaller phialine pore distally from it (?gonopore). Arm emerging from right distal supracentrals and located on sutural complex between 4 plates excavated to form brachial orifice; arm terete, relatively short and narrow. Stele somewhat depressed, thick and stubby, axially differentiated but less so than in most homoiosteles, with 5 or 6 carinate tetrameres; mesistele visible only on reverse side, where 1st 2 pairs of biseries of distal plates are separated by large median plates; dististele with several more such inserts discontinuous along reverse surface; mesistele and dististele merging on obverse side, dististele biserial (not dimeral) with suture in symmetry plane. *U.Ord.*, USA(Iowa).——FIG. 394. **I. sagittaria*; *1a,b,* obverse and reverse faces, ×1.7 *(84)*; *2a,b,* same, based on restudy of types, ×2.5, ×2.25 *(69)*.

Family BELEMNOCYSTITIDAE Parsley, new family

[Family diagnosis and revised diagnosis of *Belemnocystites* furnished by RONALD L. PARSLEY, University of Cincinnati]

Solutes with regularized marginal and somatic plates; single nonterminal biserial arm with adjacent coniform pore plate. Stele holomerous or apparently so. Characters essentially those of type genus. *M.Ord.*

Belemnocystites MILLER & GURLEY, 1894, p. 6 [**B. wetherbyi*; M] [=*Belemnocystis* BATHER, 1900, p. 51 (obj.) *(nom. van.)*]. Theca suboval, depressedly biconvex in cross section; depression especially marked in somatic areas, with 11 regularized marginals, 5 ventral somatic plates, and *ca.* 6 dorsal somatic plates, marginals extending equally over both faces. Single biserial arm appears to be very short, extending anteriorly from dorsal distal somatic area; left adbrachial plate bearing coniform aperture, presumably hydropore. Stele deeply inserted into theca, not extensively anchored to proximal adsteleals, but mainly to adjacent large somatic plates; proxistele undifferentiated and apparently holomerous (*ca.* 15 ?annular) segments with very large lumen; distal stele structure unknown. Granular prosopon, poorly preserved, plates apparently with fairly prominent concentric growth rings. Anus not identified, probably lateral, in proximal left corner of theca. [This genus bears a number of common traits with *Iowacystis* (e.g., configuration, location and interrelationship of the arm and pore plate, unusual somatic biconvexity of the theca, and similar nature and symmetry of the ventral somatic plates, including what appears to be an azygous adanal plate).] *M.Ord.*, USA(Ky.).——FIG. 395,*1*. **B. wetherbyi*; *1a,b,* obverse and reverse faces, based on holotype, ×3 (Parsley, n). [?=*Myeinocystites* STRIMPLE, 1953.]



Belemnocystites

FIG. 395. Belemnocystitidae (p. S623).

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ADDENDUM

CAMPTOSTROMATOIDS

By J. Wyatt Durham

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Class CAMPTOSTROMATOIDEA Durham, 1966

[*nom. correct.* Durham, herein (*pro* Camptostromoidea Durham, 1966, p. 1219)]

Free-living, apparently medusaeform radially symmetrical echinoderms; body wall heavily plated and containing several different types of ossicles; mouth and anus at opposite poles, with no elongation along this axis; sutural pores abundant on oral and external lateral surfaces but absent from region of aboral pole; detailed organization uncertain but presumably radial; arms radail, plated, attached to periphery of test; seemingly no calcareous ring. *L.Cam.(Olenellus Zone).*

The genus *Camptostroma,* for which this class has been established, was originally (ref. *1*) described by Ruedemann *(4)* as a probable floating "tubularian hydrozoan." Subsequently Kieslinger *(3)* included it in the Scyphozoa, an assignment that was followed by Harrington & Moore *(2)* in part F of the *Treatise on Invertebrate Paleontology.* Careful examination of the type and other original material (all external molds) suggested that *C. roddyi* was an echinoderm (a possibility recognized by Ruedemann). Fortunately, a recently discovered specimen retains the original calcite plates, the cleavage and reticulate microstructure of which confirm assignment to

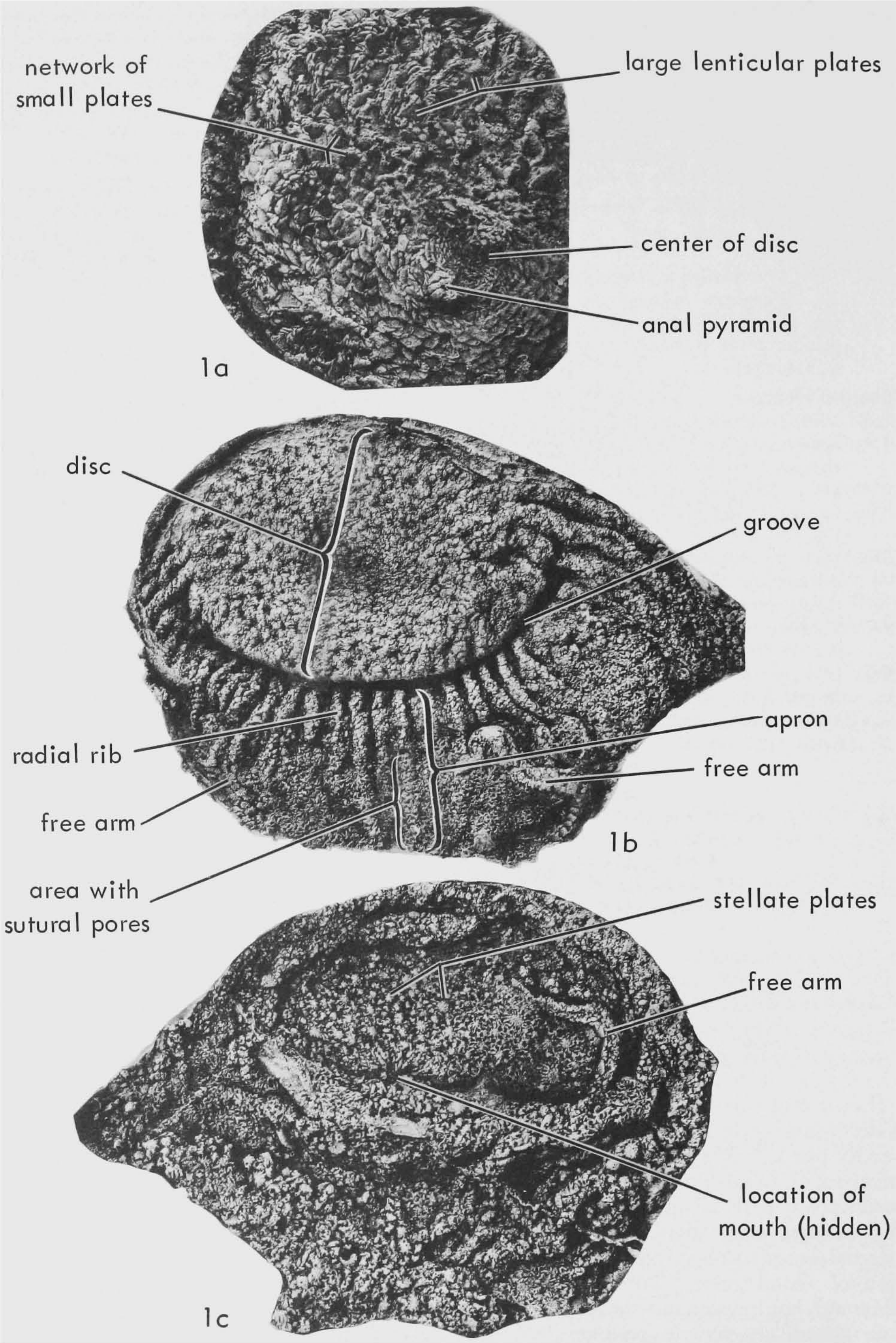

FIG. 396. Camptostromatidae (p. S630).

the echinoderms. *C. roddyi,* the type species (other species referred to *Camptostroma* do not appear to be congeneric), occurs in shales of the Lower Cambrian Kinzers Formation of Pennsylvania, in the same strata that contain lepidocystoids. About 15 specimens of *C. roddyi* have been found, but none are as complete as the type and some are very poor. Disassociated plates apparently referable to *Camptostroma* are abundant in some limestones associated with the shales.

Some details of the organization and structure of the test of *Camptostroma roddyi* have not been resolved, but it appears to have been medusaeform in shape, with a centrally domed aboral surface and a peripheral radially ridged apron with a few marginal free arms, and with the oral surface concave. Except immediately around the peristome, sutural pores are abundant on the oral surface and extend onto the upper margin of the peripheral apron. On the oral surface (but not on the peripheral apron) the small plates with sutural pores are arranged around larger stellately ridged plates. On the upper surface of the distal margin of the peripheral apron is an area of uniformly small plates, deeply incised for sutural pores. Proximally the poriferous area merges into a nonporiferous, strongly ribbed area built of small plates. Centrally the aboral domed disc is built of large flat lenticular plates imbedded in a network of numerous small plates. When the surface is contracted the flat plates are more or less overlapped by the meshwork of small plates, but when expanded these plates are the most conspicuous elements of this surface. A conspicuous raised structure considered to be an anal pyramid is present, slightly off center, on the aboral surface of some specimens. It appears to be composed of about seven elongate plates. The peripheral free arms are incompletely preserved on the available specimens but were relatively slender and had large plates on the aboral surface. Their length appears to have been sufficient to reach to the mouth. The number of arms is uncertain but seems to have been between four and eight. The central domed area is set off from the peripheral apron by a well-marked groove on the type and some other individuals, but there is a possibility that this groove may be an artifact of burial. The peristomial area, although surrounded by plates of several types, in contrast to other areas of the test, seems to be composed largely of flattened lenticular plates without sutural pores.

None of the plates of the test are firmly sutured to one another, and away from the peristomial region the plates seem to have been distributed through a thick body wall much as in many holothurians. Presumably the tissues would have decayed rapidly after death, the plates becoming disassociated and scattered easily. No evidence of a pentaradiate symmetry is recognizable, but the numerous radial ridges surrounding the aboral disc indicate a well-defined radial symmetry. On a nonleached specimen more than 40 of these ridges were observed, but on the holotype (although marginally incomplete) there appear to have been about 60. Another specimen seems to have had at least 50 ridges.

It is suggested that the sutural pores contained tube feet more or less similar to those of modern echinoderms and that they were connected by an internal radial plexus of the water-vascular system. Presumably the tube feet served primarily for respiration, but they probably also were utilized in food gathering or transport of food toward the mouth. The few slender arms do not suggest that they were used for locomotion—probably they were primarily food-gathering organs. The mouth seems to have been relatively small, so that food was probably of small particle size. No madreporite or genital aperture has been recognized, but the plates are so numerous and often so disarranged in detail that it would be easy to overlook these features.

The mode of life of *Camptostroma* is somewhat uncertain, but in view of the apparent medusaeform body it is suggested that it was probably pelagic or bathypelagic. It may have been comparable to the pelagic holothurian *Pelagothuria* or bathypelagic types such as *Benthodytes* and *Galatheathuria.* A comparison might also be made with the free-living comatulid crinoids, but the body structure is not at all comparable to that of the crinoids. The camptostromoid test, built of several different types of ossicles in intimate relationship, is suggestive of that of some holothurians, especially

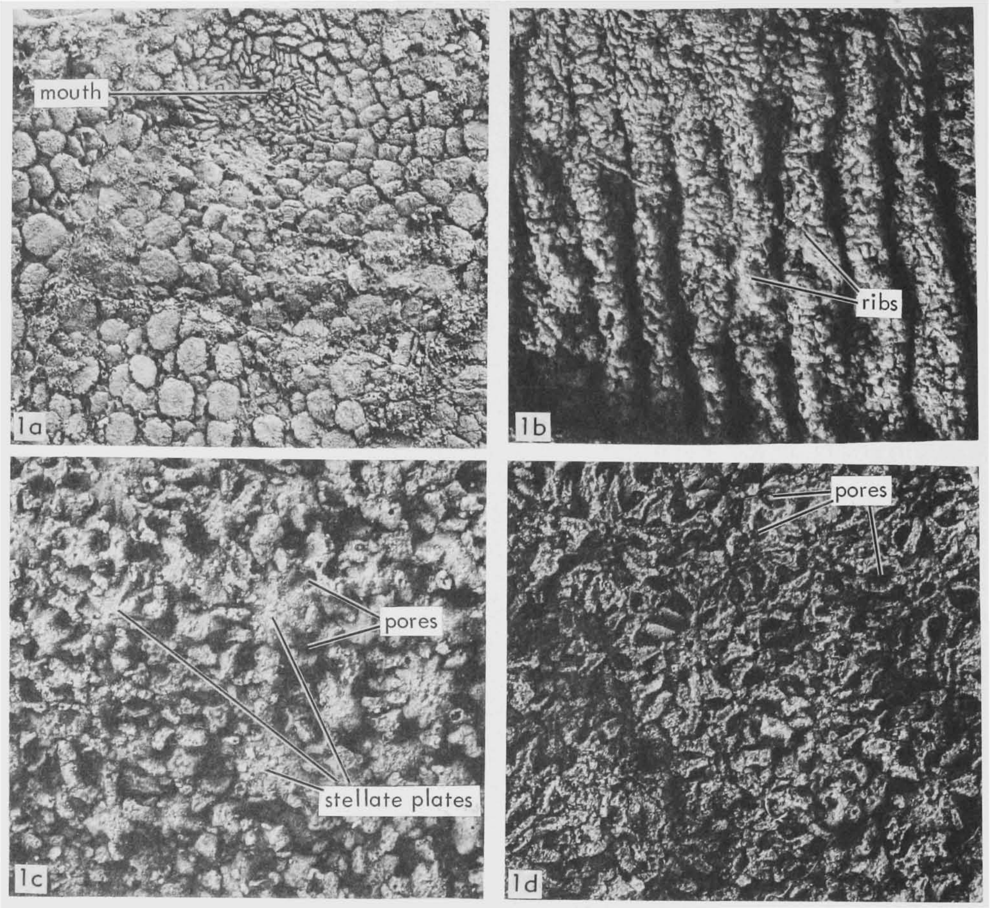

FIG. 397. Camptostromatidae (p. S630).

members of the Dactylochirotida and Dendrochirotida. However, the presence of peripheral arms that are heavily plated (adoral plated arms known in the Devonian holothurian *Palaeocucumaria,* 5) instead of adoral nonplated arms, the apparent lack of pentaradiate or bilateral symmetry, and the absence of elongation along the oral-aboral axis distinguish camptostromatoids from holothurians. Further, although the densely plated test of *Camptostroma* makes recognition of a calcareous ring difficult, no evidence of one was observed and it is assumed that it was absent. Grossly, the camptostromatoids might be compared with the ophiocistioids, but the lack of firmly sutured plates and the multiple types of ossicles in the wall of the test readily differentiate the camptostromatoids.

Family CAMPTOSTROMATIDAE Durham, new family

Characters of class. *L.Cam.(Olenellus Zone).*

Camptostroma RUEDEMANN, 1933, p. 5 [**C. roddyi*; OD]. Test medusaeform, with few heavily plated peripheral arms; anus on aboral surface near center, with well-developed pyramid; most areas of wall composed of several types of ossicles; sutural pores on oral surface and upper distal margin of peripheral apron. *L.Cam.(Olenellus Zone),* USA (Pa.).——FIG. 396-397. **C. roddyi*; 396,*1a,* part of aboral disc, ×2.5; 396,*1b-c,* aboral, oral views of same individual, ×1.4; *397,1a,* adoral region, ×5; 397,*1b,* ribbed area of apron, ×5; 397,*1c,* detail of mid-oral surface, ×10; 397,*1d,* detail of aboral surface of distal portion of apron, ×10 (P. M. Kier, n).

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LEPIDOCYSTOIDS

By J. Wyatt Durham

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Class LEPIDOCYSTOIDEA Durham, new class

Free-living, placoid echinoderms with differentiated oral and aboral surfaces; oral surface with numerous small plates with sutural pores, free biserial arms, and anal aperture; character of oral aperture unknown; aboral surface with numerous imbricating plates originating at apex of surface; anus marginal on oral surface, with well-developed anal pyramid; arms grooved, with cover plates, arranged in concentric circlets on oral surface, oldest outermost, resting on flat basal plates; arms presumably for feeding; organs in sutural pores presumably respiratory. *L.Cam.(Olenellus Zone).*

This group of echinoderms is known from a few more or less crushed specimens from the Kinzers Formation of Pennsylvania, where they occur in the same strata as medusaeform camptostromatoids. Most individuals seem referable to the single described species, *Lepidocystis wanneri* Foerste (1). Two specimens have three circlets of arms, probably with five arms to a circlet (no specimen has a complete circlet of arms; it is possible that there might be only four). Arms of each circlet are aligned along radii from the presumed central location of the mouth. One smaller specimen (Fig. 398,*1b*), preserved partly in the round (either immature or else representing another species), seems to have only a single circlet of free arms (but draped along the side of the test during burial). The basal plates of the outermost arms are adjacent to the margin of the aboral imbricating plates, but the bases of the inner arms are set in the midst of the small, marginally incised plates of the oral surface. There is one cover plate to each segment of the arm, with the distal margin of the cover plate serrate and slightly overlapping the proximal margin of the next. The oral surface is covered with small, relatively thick plates, with three or four deep marginal grooves for sutural pores (one to each face). These pores are very numerous and the oral surface must have been densely covered with the organs that extended through them. It is assumed that these organs were respiratory in function and connected by an internal plexus of the water-vascular system.

No feature recognizable as a mouth has been observed, but it seems probable that this was centrally located on the oral surface. It is uncertain how food was transported from the arms: food particles may have been transferred to the mouth by the arms themselves; they may have been moved from the base of the arms to a central mouth by ciliary action; or there may have been subvective channels from the arms. A well-developed anal pyramid built of numerous plates is situated marginally on the oral surface midway between two of the outermost arms. Two specimens indicate that the elongated portion of the test covered with imbricating plates was more or less conical and that the oral surface was arched. The presence of presumed respiratory organs in the sutural pores on the oral surface suggests that *Lepidocystis* lived up-

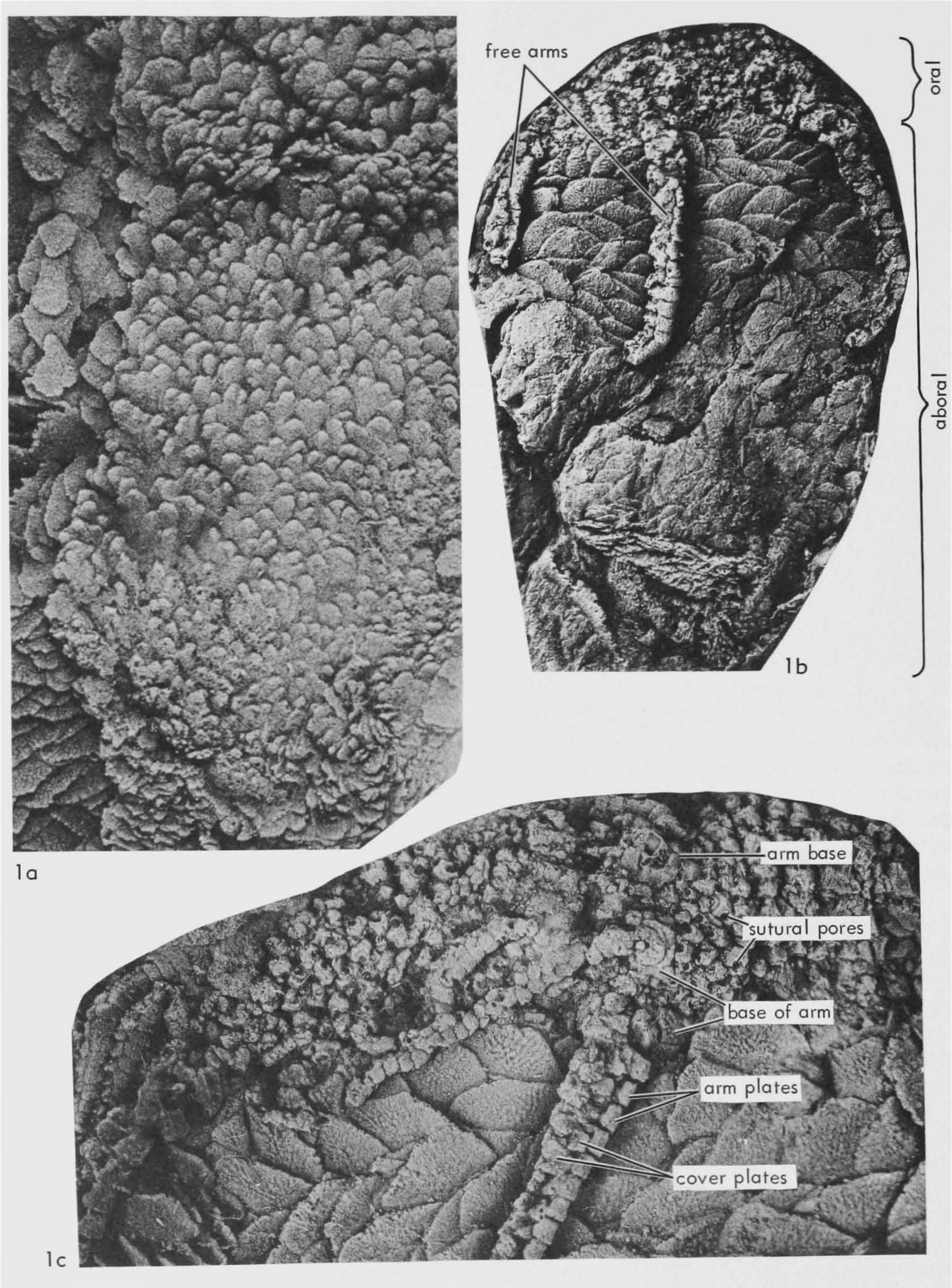

FIG. 398. Lepidocystidae (p. S634).

right on the sea floor with the apical portion of the aboral surface imbedded in sediment (Fig. 399).

The lepidocystoids differ from eocrinoids by restriction of the sutural pore-bearing area to the interbrachial oral surface, the presence of imbricating plates on the aboral surface, the circlets of arms on the oral surface, and the mode of attachment of the arms. They differ from most edrioasteroids, cystoids, and helicoplacoids by the presence of sutural pores, and from camptostromatoids by the possession of only a single type of plate in any area, as well as the position of the anus on the oral surface. They differ from the edrioasteroid *Stromatocystites,* which has sutural pores on the oral surface, by the presence of free arms.

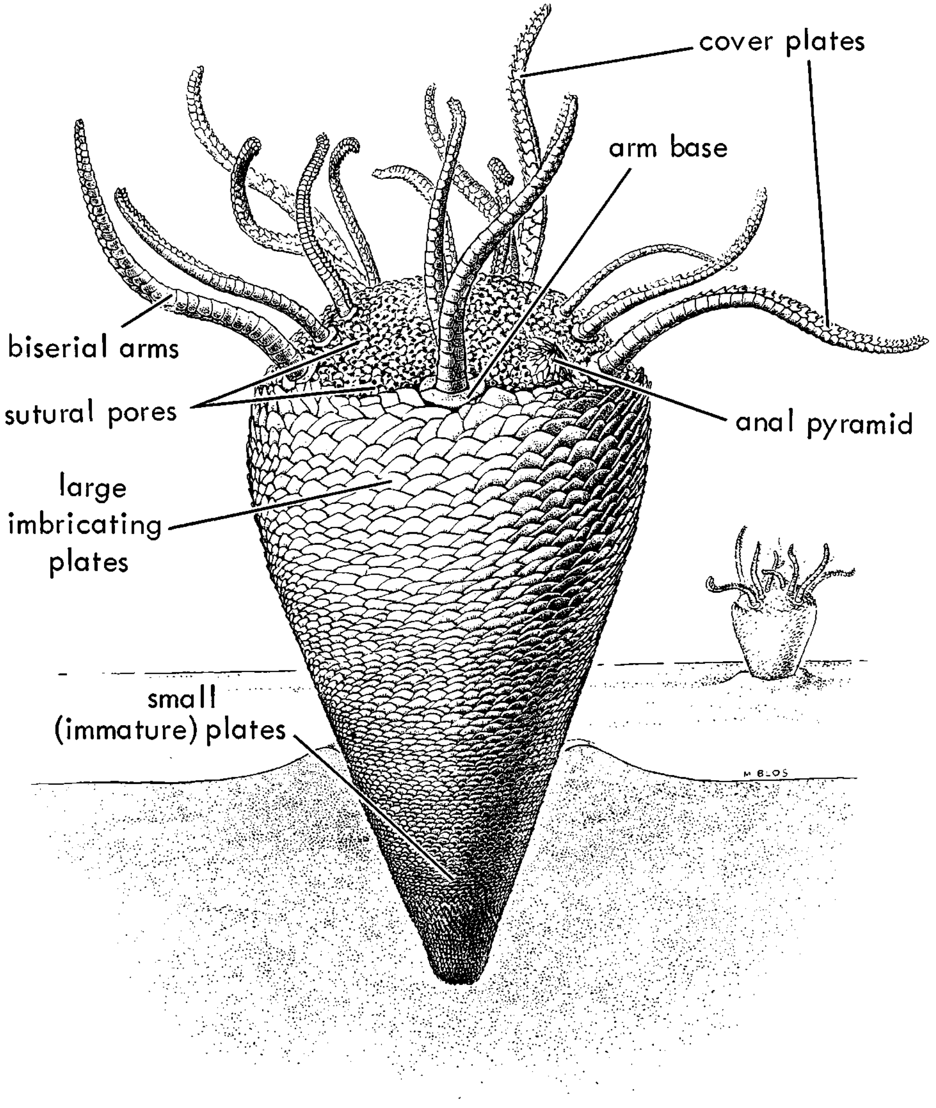

Fig. 399. Lepidocystidae (p. *S*634).

Family LEPIDOCYSTIDAE Durham, new family

Characters of class. *L.Cam.(Olenellus Zone).*

Lepidocystis FOERSTE, 1938, p. 212 [**L. wanneri*; M]. Aboral surface of test conical, built of numerous scalelike imbricating plates, those of oral surface small, heavy, deeply incised by single large sutural pore on each side; anus at margin of oral surface, with well-developed anal pyramid. *L.Cam.(Olenellus Zone),* USA(Pa.).——FIG. 398-399. **L. wanneri*; 398,*1a,* detail of small adapical plates, ×8.5; 398,*1b,* small individual with free arms draped along side of test, ×3.1; 398,*1c,* part of oral surface of specimen with 3 circlets of arms, ×4; 399, restoration showing probable mode of life, approx. ×1.5 (Durham, n).

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CYMBIONITES AND PERIDIONITES—UNCLASSIFIED MIDDLE CAMBRIAN ECHINODERMS

By GEORGES UBAGHS

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INTRODUCTION

Cymbionites and *Peridionites* are nominal genera proposed in 1941 by WHITEHOUSE (ref. *11*) on the basis of fossils found in lowermost Middle Cambrian strata (Zone of *Xystridura*) of Queensland, Australia. Specimens of the first-mentioned form were obtained in abundance from the basal 40 feet of the zone and less numerous representatives of the second in a bed of limestone approximately 24 feet higher in the section.

For the purpose of classifying these two genera, both of which are monotypic, WHITEHOUSE introduced new families named Cymbionitidae and Peridionitidae, which respectively were assigned to the new classes Cycloidea and Cyamoidea, and both were placed in a new subphylum of the Echinodermata named Haplozoa.

DESCRIPTION

Each of the two fossil forms displays a thick calcareous skeleton comprised of a few plates disposed around a median crateriform depression. The animals are judged to have been free-living on the sea bottom, for no trace of fixed attachment has been observed.

The remains of *Cymbionites* consist of a hemispherical or thimble-shaped body with average diameter of 12 mm. (Fig. 400,*1a*). Less commonly the fossils are barrel- or saucer-like. Typically they are composed of five tightly joined massive plates of wedge-shaped form, with sutures discernible only on weathered specimens. The median depression, variable in depth, possesses fluted sides. A transverse section through the bottom of the depression commonly shows the presence of a tiny central plate additional to the five main ones and surrounded by them in manner that entirely conceals the small central plate in view of the exterior. The festooned edge of the calyx bears a minute peripheral groove.

The skeleton of *Peridionites* resembles a biconvex half-lens having almost perfect semicircular outline in side view and an elliptical shape in apical view (Fig. 400, *2a-e*). The fossils are diminutive in size, with maximum diameter mostly less than 10 mm. Biradial in form, they are composed of five massive calcareous plates—a median apical one adjoined by two large terminal plates and two smaller mediolateral plates located on opposite sides of a moderately deep central cavity which is

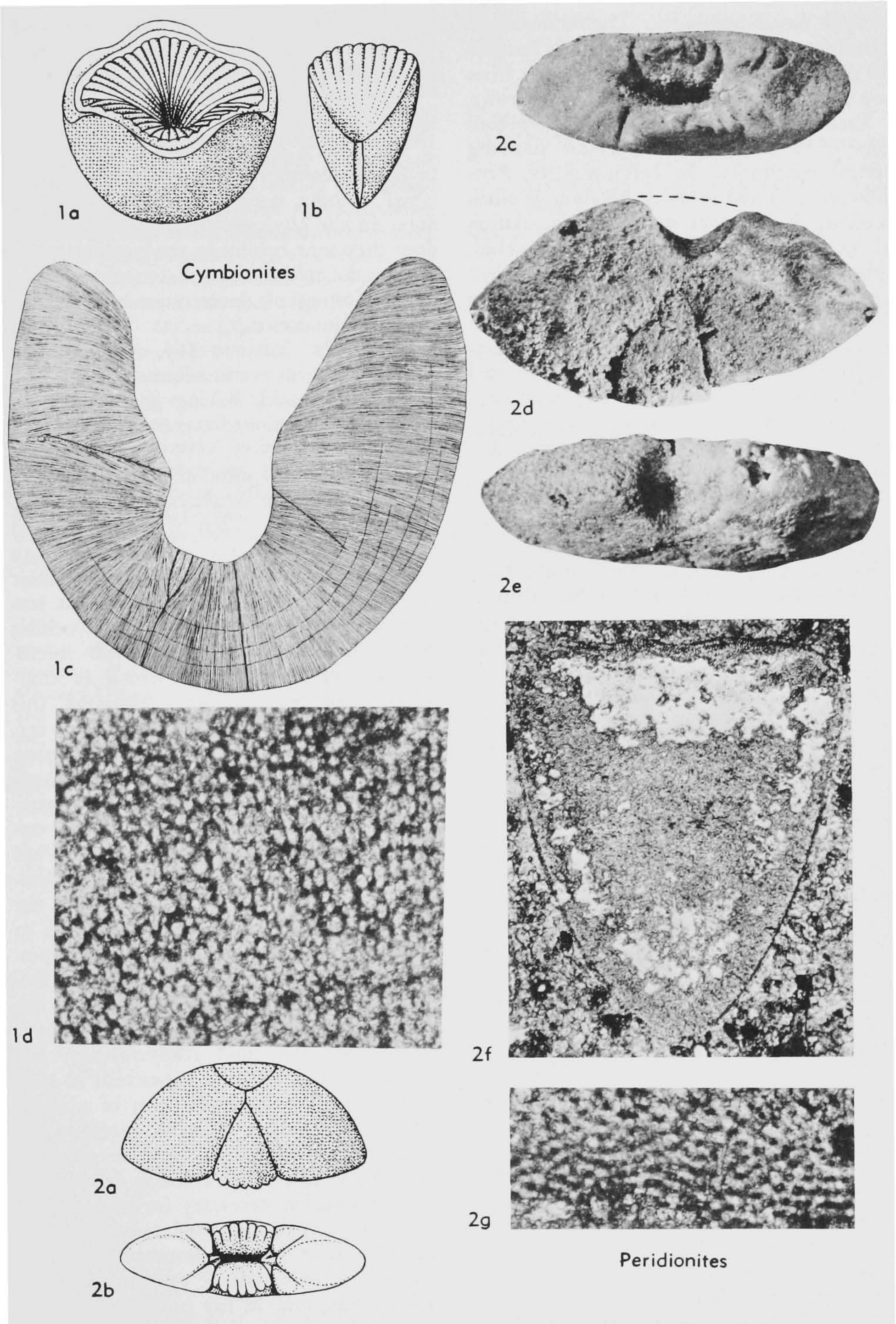

FIG. 400. **Cymbionites craticula* WHITEHOUSE *(1)*; **Peridionites navicula* WHITEHOUSE *(2)* (unclassified M.Cam. echinoderms) (p. *S*637).

radially fluted internally. The truncate abapical face of each terminal plate is marked by three shallow depressions set off from one another by diverging narrow furrows.

Each plate in both of these genera consists of a single calcite crystal showing optical continuity. In specimens of *Peridionites* subjected to dolomitization or silicification, the original stereomic reticulation of the plates generally cannot be observed, although it may be visible locally in small patches of the surface (Fig. 605,*2f,g*). On the other hand, the reticular microstructure of plates belonging to *Cymbionites* commonly is very evident. They are composed of close-packed "but intermittently impinging" prismatic fibers with a calcite network optically continuous with the fibers between them (Fig. 400,*1c,d*).

INTERPRETATIONS

These two genera of fossils have been interpreted in extraordinarily different ways.

1) In the view of WHITEHOUSE *(11)* both forms are echinoderms. *Peridionites* is considered to be the dorsal skeleton of a bilaterally symmetrical five-segmented organism which corresponds morphologically to the dipleurula stage in larval development of echinoderms. *Cymbionites* is judged to be the aboral skeleton of an essentially radiate organism equivalent to the pentactula stage in ontogeny of eleutherozoic echinoderms. Asteroids, ophiuroids, and echinoids are thought to be derivatives of the Cycloidea (class represented solely by the genus *Cymbionites* as now known), and those in their turn are supposed to come from the Cyamoidea (class represented only by *Peridionites* among yet discovered fossils). The Cyamoidea are interpreted as ancestral also to the Homalozoa ("Carpoidea" and Machaeridia) in one line and to the Pelmatozoa [Crinozoa] (Cystoidea, Blastoidea, Edrioasteroidea, Crinoidea) in another line. These concepts have been accepted by some *(7)* but rejected by most workers *(1-3, 5, 6, 8, 9)*.

2) According to GISLÉN *(2)* (as well as TERMIER & TERMIER, 9), *Cymbionites* is an echinoderm provisionally interpretable as a cystoid with only the basal part of the theca calcified. *Peridionites,* however, is not an echinoderm but possibly a ctenophore modified for benthonic existence like the modern *Platyctenida* and distinguished by having a calcareous skeleton.

3) Neither of the two discussed fossils is an echinoderm, in the opinion of CUÉNOT & TÉTRY *(1)*. Instead, both are considered to be representatives of phyla which vanished without producing known descendants. In the phylogeny of the animal kingdom they may belong in the great gap separating the cnidarians and ctenophores from the beginning of deuterostomians marked by the echinoderms.

4) Finally, SCHMIDT *(6),* who accepted both genera as echinoderms, interpreted them as eocrinoids having greatly reduced thecae that functioned merely as stabilizing structures.

The temerity of some of these hypotheses contrasts with the weakness of evidence in support of them. That *Cymbionites* and *Peridionites* are truly echinoderms can hardly be doubted, for not only are their plates composed of single crystals but reasonably well-preserved specimens exhibit unequivocal traces of honeycomb microstructure of the stereom which is characteristic of the phylum. Although this much is established, nothing more is certain. Do the fossils constitute complete skeletons, as their morphology and manner of preservation (including lack of associated fragments) seem to indicate, or, oppositely, are they incomplete remains? What was the nature of soft parts originally associated with the skeletons? How may the remains be oriented correctly in relation to morphology of the organisms? Such questions presently are unanswerable. *Cymbionites*—but not *Peridionites*—suggests the basal part of the theca of such crinozoans as *Parorthocrinus* and *Rhopalocystis,* but the resemblance is quite superficial in that it relates only to external form of a small part of the body *(10),* thus meriting no serious consideration of possible relationships. Inasmuch as these fossils fail to provide information necessary for understanding of the organization of animals represented by them, it seems improper to assign them either to extant or extinct classes of echinoderms, and in my opinion not even to recognize them as distinct families. Beyond statement of what can be observed, all is speculation.

SYSTEMATIC DESCRIPTIONS

Cymbionites Whitehouse, 1941, p. 9 [**C. craticula*; M]. Echinodermal remains consisting of calcareous dome-shaped bodies composed typically of 5 equal curved plates of thick wedge-shaped form, firmly joined together laterally and apically as cuplike structure with fluted wall surrounding more or less deep central depression; stereom composed of closely packed prismatic fibers with calcite meshwork in optical continuity with fibers occurring between them; each plate consisting of single crystal. *M.Cam.(Xystridura Zone)*, Australia(Queensl.).——Fig. 400,*1*. **C. craticulata*; *1a,b,* oblique lat. view of complete specimen and single isolated plate, ×3 *(11)*; *1c,* long. (vertical) sec. showing sutures and growth lines, ×7 *(11)*; *1d,* tang. sec. showing honeycomb structure of stereom, ×120 (Ubaghs, n).

Peridionites Whitehouse, 1941, p. 5 [**P. navicula*; M]. Echinodermal remains comprising calcareous dome-shaped bodies which are laterally compressed and biradial in form, composed of 5 plates including single apical plate, 2 large end plates, and 2 somewhat smaller mediolateral plates bordering narrow deep central fossa; each plate comprising single crystal with originally reticulate stereom. *M.Cam.(Xystridura Zone)*, Australia (Queensl.).——Fig. 400,*2*. **P. navicula; 2a,b,* lat. and truncate faces, ×5 *(11)*; *2c-e,* truncate, lat., and apical faces (*2d,e,* holotype, with apical plate lacking), ×5.6 (Queensland Univ. photographs, n); *2f,* long. (vertical) sec. of end plate showing preserved remnant of honeycomb stereom structure on upper edge, ×15 (Ubaghs, n); *2g,* tang. thin sec. showing stereom reticulation, ×120 (Ubaghs, n).

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