MORPHOLOGY AND FUNCTION OF EXOTHECAL PORE-STRUCTURES IN CYSTOIDS

by C. R. C. PAUL

ABSTRACT. Humatirhombs, humatipores, and diplopores have external respiratory exchange surfaces. Their thecal canals open internally and body fluids flowed through them in life. Four types of humatirhomb are distinguished on morphology and arrangement of canals. Raised and buried humatipores occur and diplopores may have had extensile podia in life.

All cystoid pore-structures were respiratory. Exothecal pore-structures were individually less efficient in exchange than endothecal (dichoporite) pore-structures. Their relative inefficiency is due to requirements of protection and is counteracted by their large number per theca. Cystoids with exothecal pore-structures attain great size. Less efficient pore-structures (humatirhombs, humatipores) have shorter stratigraphic ranges and become extinct before more efficient types (pectinirhombs, cryptorhombs, diplopores).

Recent echinoderms as a group lack a specialized circulatory system and utilize varied exchange surfaces as did cystoids. Efficient exchange surfaces must be thinner than 1–3 mm: cystoid exchange surfaces are 0·01–0·1 mm thick. Diplopores and humatipores may have been connected to an internal water vascular system but humatirhombs were not. Rhombifera probably had external radial water vessels but Diploporita lacked them. Some Rhombifera may have had both internal and external branches of the water vascular system. Classes Rhombifera and Diploporita are defined and cystoid classification is reviewed.

THE cystoids constitute a heterogeneous grouping of primitive echinoderms which range from the basal Ordovician just into the Upper Devonian. The vital organs of cystoids (and other primitive echinoderms) were completely enclosed within a rigid cup or theca which provided them with protection. At the same time the theca restricted communication with the ambient sea water from which both food and oxygen necessary for life were obtained. The purpose of this paper is to show that three major types of pore-structure which occur in cystoids evolved in response to the respiratory 'problems' created by the rigid theca. These pore-structures in cystoids, and by implication similar pore-structures in other primitive echinoderms, were effectively gills.

Traditionally cystoid pore-structures have been grouped into 'diplopores' and 'pore-rhombs' on morphological grounds. Functionally however division of all echinoderm pore-structures into endothecal and exothecal groups, where primary exchange from sea water to body fluids took place within and outside the theca respectively, is more appropriate (text-fig. 1). The morphology and function of endothecal (dichoporite) pore-structures in cystoids have been described (Paul 1968). The present paper considers exothecal pore-structures for which Hudson (1915, p. 166) originally proposed the term 'exospires'.

Three basic types of exothecal pore-structures occur in cystoids: one type of rhomb and two types of dipore. Brief descriptions of their morphology were given in Paul (1968). In the next two sections the morphology of exothecal pore-structures in cystoids is described and they are analysed functionally as exchange structures. Since the most likely form of exchange is oxygen and carbon dioxide transfer a section on respiration

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in recent echinoderms follows. The last two sections deal with the water vascular system in cystoids and with the taxonomic and evolutionary implications of this study.

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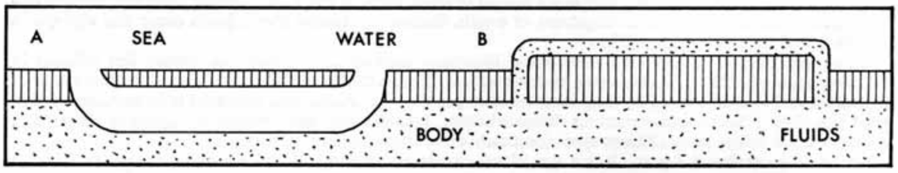
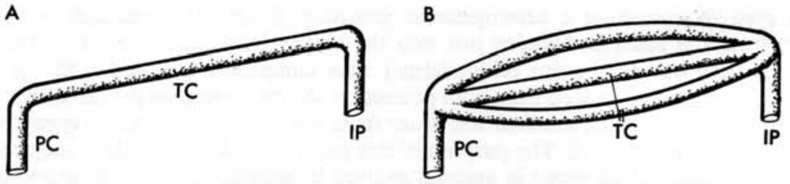


TEXT-FIG. 1. Diagrammatic representations of endothecal (A) and exothecal (B) canals. In A sea-water flows through the canal and exchange takes place within the theca; in B body fluids flow in the canal and exchange takes place outside the theca. Thecal wall shown with vertical lines. In this and following diagrams the external medium is towards the top of the figure.



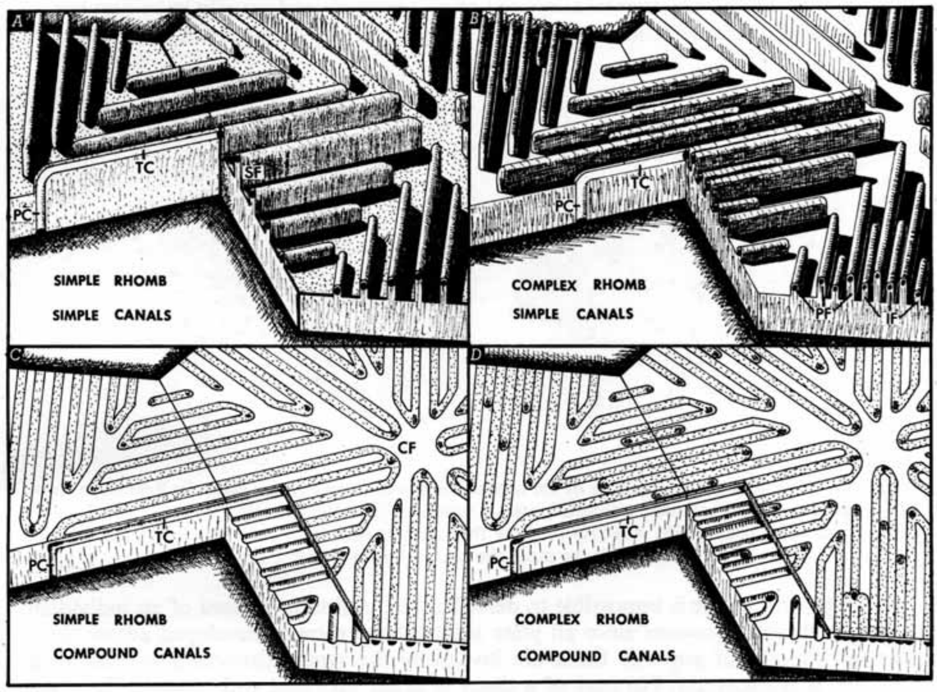
TEXT-FIG. 2. Simple (A) and compound (B) thecal canals. In A a single tangential canal (TC) connects a pair of perpendicular canals (PC); in B three tangential canals connect the perpendicular canals. Thecal canals open in internal pores (IP) in all exothecal pore-structures.

MORPHOLOGY OF EXOTHECAL PORE-STRUCTURES IN CYSTOIDS

All cystoid pore-structures are composed of U-shaped thecal canals (text-fig. 2) with one or more connections (tangential canals) between the limbs of the U (perpendicular canals). The openings (thecal pores) of exothecal canals are internal. The three types of exothecal pore-structures in cystoids are humatirhombs, humatipores, and diplopores s.s. (Paul 1968, p. 700).

1. *Humatirhombs* (text-figs. 3*a–d*, Pls. 1–4)

Humatirhombs (humare: Lat. to bury) are composed of a set of thecal canals (*fistulipores*, fistula, Lat. a canal), all of which arise from pores on the inner surface of one plate, pass through the plate, and cross a plate suture to pores on the internal surface of an adjacent plate (text-fig. 3). The pores are always simple and circular (Pl. 4, fig. 2). The tangential canals may be single (simple fistulipores, text-fig. 3*a–b*) or multiple (compound fistulipores, text-fig. 3*c–d*) and they lie either just below the external surface (Pls. 3–4) or in the crests of ridges on the external surface of the theca (Pl. 1). Usually only simple fistulipores are associated with ridges (text-fig. 3*a–b*).

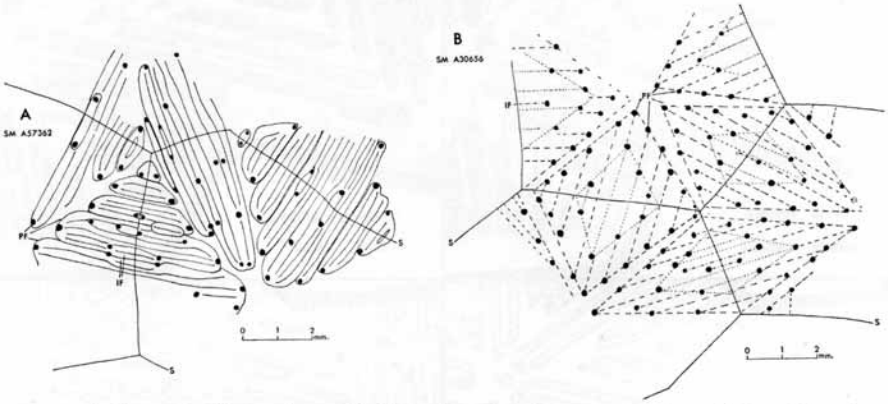


TEXT-FIG. 3. Four types of humatirhomb. A, simple humatirhombs with simple fistulipores (SF), B, complex humatirhombs with simple fistulipores, C, simple humatirhombs with compound fistulipores (CF), D, complex humatirhombs with compound fistulipores. In humatirhombs with simple fistulipores (A, B) the tangential canals (TC) are raised in ridges; humatirhombs with compound fistulipores (C, D) have tangential canals buried beneath plate surfaces. Complex humatirhombs (B, D) have both principal fistulipores (PF) and shorter intermediate fistulipores (IF). PC = perpendicular canal.

Four types of humatirhomb may be distinguished on the structure and arrangement of fistulipores. In *simple humatirhombs* all the fistulipores run the entire length of the rhomb from margin to margin (text-fig. 3*a*, *c*). *Complex humatirhombs* (text-fig. 3*b*, *d*) have additional shorter fistulipores within the intra-rhomb area. Both types of humatirhomb may be composed of either simple or compound fistulipores. Thus four types of humatirhomb may be recognized:

Simple humatirhombs with simple fistulipores (text-fig. 3*a*)
Complex humatirhombs with simple fistulipores (text-fig. 3*b*)
Simple humatirhombs with compound fistulipores (text-fig. 3*c*)
Complex humatirhombs with compound fistulipores (text-fig. 3*d*)

Humatirhombs are characteristic of, and confined to, the superfamily Caryocystitida, members of which have thecae composed of an indefinite and usually large number of thecal plates which are randomly arranged. The number of thecal plates often increases during growth and it is impossible to describe the position in a theca of an individual plate or rhomb. However since all plate sutures have rhombs developed across them and all rhombs of any one theca are invariably the same, distinction of individual rhombs is unnecessary. No part of a theca is better provided with rhombs than any other part.



TEXT-FIG. 4. Camera lucida drawings of the humatirhombs of *Caryocystites lagenalis* Regnéll to show principal (PF) and intermediate (IF) fistulipores. A, traces of tangential canals (SM A57362). B, traces of perpendicular canals (SM A30656) to show that intermediate fistulipores define smaller rhombs within the main rhomb. S = plate suture.

EXPLANATION OF PLATE 1

Stereophotos of simple humatirhombs with simple fistulipores.

Figs. 1, 2, 7. *Lophotocystis granatum* (Wahl.). 1, 2, Two small weathered examples to show fine granules on external surface. 1, RM Ec4353; 2, RM Ec4352; 7, SM A57330, Part of a large example with well-developed humatirhombs. All ×3.

Figs. 3–6. *Ulrichocystis eximia* Bassler. 3, 4, Unweathered isolated plate; 3, oblique sutural view to show tangential canals beneath external ridges, ×6; 4, external surface, ×4. 5, 6, Another isolated plate; 5, weathered external surface to show exposed tangential canals and positions of perpendicular canals; 6, internal surface to show canals partially covered near plate centre, both ×4 (cf. text-fig. 13*b*). Specimens in author's colln.

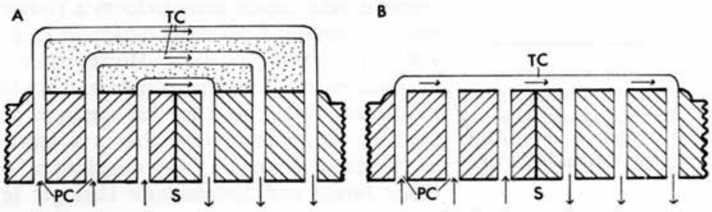
Fig. 8. *Lophotocystis* sp. nov. (Shole'shook, S. Wales). SM A53070c. Latex impression of fragmentary example. ×2.

Fig. 9. *Lophotocystis malaisei* (Regnéll). SM A 50361. Latex impression of part of theca. ×2.

All figures whitened with ammonium chloride sublimate.

The distribution of the four types of humatirhomb within the superfamily Caryocystitida does not correspond to taxonomic subdivisions. The first two types of humatirhomb (text-fig. 3*a–b*) are confined to the genera *Ulrichocystis* Bassler and *Lophotocystis* nov. (= *Heliocrinites* of the 'planata' group of Regnéll 1951, p. 22; Bather 1906, p. 18; see Appendix 2, p. 26). *Lophotocystis* has tangential canals developed in prominent ridges on the external surface of the theca (Pl. 1). The humatirhombs of *Ulrichocystis* are simple and their tangential canals are less distinctly raised (Pl. 1, figs. 3–4).

The third and most common type of humatirhomb (text-fig. 3*c*) occurs in all species of *Heliocrinites* s.s. (i.e. Regnéll's 'plicata' group, 1951, p. 22), all Echinosphaeritidae and *Caryocystites dubia* (Angelin) = *C. angelini* Auctt. The fourth type (text-fig. 3*d*) occurs only in *C. lagenalis* Regnéll as far as is known.



TEXT-FIG. 5. Two possible interpretations of the structure of the canals in *Stichocystis* Jaekel as seen in longitudinal section. In A each pair of perpendicular canals (PC) is connected by a separate tangential canal (TC). In B a single tangential canal connects all perpendicular canals. The tangential canals were made entirely of soft tissue and are not preserved. Both the pairing of the perpendicular canals and the efficiency of currents (indicated by arrows) favour interpretation A. S = plate suture.

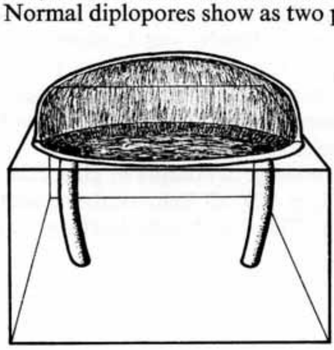
The genus *Stichocystis* Jaekel which on other morphological grounds belongs in the Caryocystitida bears unusual rhombs with sets of perpendicular canals developed in ridges on the external surface of the plates. Not all details of the structure of these rhombs are known but they seem to be functionally and morphologically related to humatirhombs. I interpret them as having a rhomb-in-rhomb structure (text-fig. 5*a*) but this is not certain. These rhombs may bear the same relationship to simple humatirhombs that multi-disjunct pectinirhombs bear to disjunct pectinirhombs.

The next two types of exothecal pore-structures (diplopores and humatipores) are *dipores* which consist of a single thecal canal, not a set of canals (Paul 1968, p. 700).

2. *Diplopores* (text-figs. 6–8, Pls. 5–6)

Diplopores are dipores composed of a simple thecal canal, the tangential portion of which was not normally calcified and probably formed a papula or podium in life. As a result only the pair of perpendicular canals is preserved in fossils, which led Müller (1854) to propose the term 'Doppelporen' or diplopore (see Huxley 1854).

If a diplopore is considered as a functional rather than a morphological unit, the pores are internal and the supposed podium represents the tangential portion of the thecal canal (text-fig. 6). No podium has yet been found preserved but diplopore tangential canals are sometimes calcified in the Aristocystitidae and Sphaeronitidae. Normal diplopores show as two pores which are usually paired within a shallow depression (*peripore*) on the external surface of the theca. Peripores may have rims, or peripheral or central tubercles (text-fig. 7*a–d*). In general morphology, diplopores strongly resemble the pore-pairs of echinoids.



TEXT-FIG. 6. Diagrammatic representation of the structure of a diplopore. The two perpendicular canals open into a depression, the peripore, over which a podium or papula extended in life.

Only the two perpendicular canals of a diplopore are preserved in most fossils. They may pass straight through the plates, follow sinuous courses, or unite with one or more other perpendicular canals (text-fig. 8). Previously it has been assumed that when two perpendicular canals unite to form a Y-shaped canal both branches fed the same diplopore (e.g. Chauvel 1941, figs. 39*c–e*, p. 100). However, in the only example where I have been able to trace the course of the two branches they fed separate diplopores (text-fig. 8*b*). Functionally this is a more efficient arrangement since it allows circulation. In *Codiacystis* Jaekel and *Sphaeronites* Hisinger large pits, off which a number of perpendicular canals branch, occur on the internal surfaces of the plates. These pits could be centres of radiation for afferent and efferent canals but this is not certain. They show up as prominent tubercles on internal moulds (e.g. Barrande 1887, pl. 19, figs. 30, 32–33, 35–36).

Diplopores show wide variations in morphology but no clearly defined types exist. Diplopores of certain genera and families may have characteristic morphology however (e.g. *Haplosphaeronis*, Pl. 6, figs. 1–3; *Sphaeronites* s.s. Pl. 5, figs. 1–2). Diplopores occur in all superfamilies of the Diploporita. They are usually randomly distributed over a theca but may be more prolific on certain parts of the theca (or of individual thecal plates) than on other parts. In the Aristocystitidae certain areas of the theca may have sealed canals. Usually these areas were permanently in contact with something solid

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EXPLANATION OF PLATE 2

Complex humatirhombs with simple fistulipores.

Fig. 2. *Lophotocystis araneus* (Schlotheim), RM Ec5370. Note intermediate fistulipores in rhombs.
Fig. 7. *Lophotocystis* sp. RM Ec25233a.

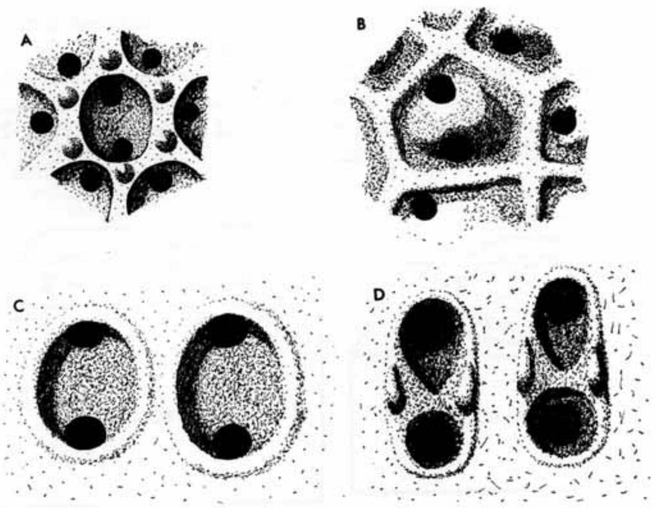
Simple humatirhombs with compound fistulipores.

Fig. 1. *Heliocrinites stellatus* Regnéll, RM Ec25985. Note compound fistulipores with pairs of tangential canals.

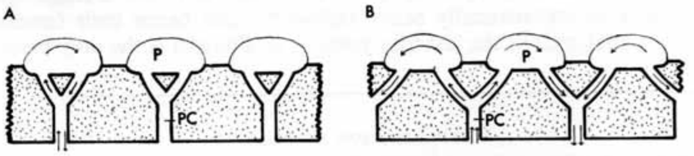
Fig. 3. *Echinosphaerites aurantium aurantium* (Gyll.), SM A57365. Note fistulipores reach plate centres.
Fig. 5. *Echinosphaerites aurantium suecicus* Jaekel, SM A57343. Note large area without fistulipores in centres of large plates.

Figs. 4, 6. *Heliocrinites ovalis* Angelin. Two examples with weathered surfaces revealing tangential canals in groups of two and three, 4, RM Ec3324; 6, RM Ec3327.

Figs. 1, 2, 4, 6, 7, ×3, whitened with ammonium chloride sublimate; Figs. 3, 5, ×5, photographed under water.



TEXT-FIG. 7. Four diplopores with different arrangements of tubercles and ridges associated with their peripores. A, *Sphaeronites pomum* (Gyll.). Oval peripores deeply impressed into the plate surface and with spine-like tubercles on the ridges between them (Pl. 5, fig. 2). B, *Sphaeronites globulus* (Ang.). Polygonal peripores with a large flat-topped central tubercle which produces moat-like channels within the peripore (Pl. 5, fig. 3). C, *Archegocystis* sp. nov. (Shole'shook, S. Wales). Oval peripores with simple raised rims (cf. Pl. 6, fig. 4). D, *Haplosphaeronis* sp. nov. (Shole'shook, S. Wales). Peripore divided into pyriform and circular depressions by a subcentral ridge, peripheral ridge with two tubercles between pores (Pl. 6, fig. 2).



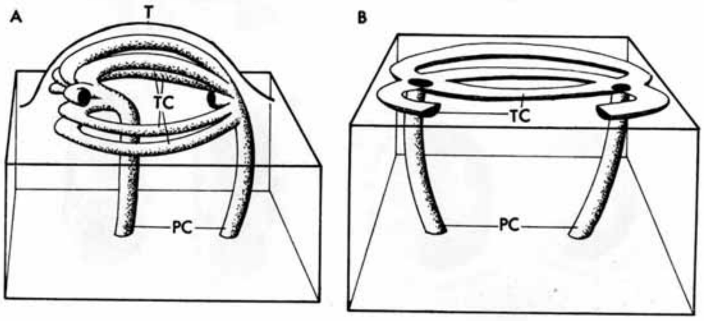
TEXT-FIG. 8. Two possible arrangements of Y-shaped perpendicular canals in diplopores. Current systems (indicated by arrows) are more efficient in B than in A. P = podia, PC = perpendicular canal.

during life (e.g. ambulacral facets, attachment areas, etc.). In the Dactylocystidae diplopores are confined to five ambulacral tracts.

3. *Humatipores* (text-fig. 9, Pl. 7)

A *humatipore* is a dipore which consists of a wholly calcified compound thecal canal (text-fig. 9). In undamaged humatipores no pores show on the external surface. Two internal circular pores lead to two or more tangential canals which may lie either beneath the flat external surface of the plates (buried humatipores, text-fig. 9*b*, Pl. 7, figs. 1, 5–10), or in a prominent external tubercle (text-fig. 9*a*, Pl. 7, figs. 2–4).

Humatipores are characteristic of, and confined to, the family Holocystitidae Miller. Buried humatipores occur in all five genera of Holocystitidae but tubercular humatipores are confined to the genera *Holocystites* s.s. and *Pustulocystis* Paul. Humatipores are always evenly developed over a theca.



TEXT-FIG. 9. Diagrammatic representations of the morphology of A, raised, and B, buried humatipores. In both, part of one tangential canal (TC) is cut away for clarity. PC = perpendicular canal, T = tubercle.

4. *Haplopores*

A number of species of the Aristocystitidae have been claimed (Bather 1900; Chauvel 1941) to bear haplopores: a type of pore-structure which consists of a single perpendicular canal. Since I have not examined all the relevant species I cannot state that haplopores do not occur in cystoids. However I have not seen a single specimen of a cystoid which characteristically bears haplopores and hence their functional morphology is not analysed. In the last fifty years or so Chauvel is the only person to have

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EXPLANATION OF PLATE 3

Simple humatirhombs with compound fistulipores.

Figs. 1, 7. *Heliocrinites* sp. nov. (Rhiwlas, N. Wales). 1, GSM 102326, Part of an unweathered theca with tangential canals filled with dark sediment, ×5, photographed under water. 7, GSM 102325, Stereophotos of weathered theca to show tangential canals in groups of two to four, ×3.

Fig. 3. *Echinosphaerites aurantium americanum* Bassler. Example with tangential canals reaching plate centres (cf. Pl. 4, fig. 1), ×4 (author's colln.).

Figs. 4, 6. *Caryocystites dubia* (Angelin). 4, SM A57333, A large weathered theca. 6, SM A57335, Stereophotos of a small example to show tangential canals in groups of two to four, both ×2.

Fig. 5. *Heliocrinites guttaeformis* Regnéll. RM Ec4780. An example with prominent tangential canals, ×3.

Complex humatirhombs with compound fistulipores.

Fig. 2. *Caryocystites lagenalis* Regnéll. SM A57362. Stereophotos to show details of rhombs (cf. Pl. 4 fig. 6), ×6.

All figs. except fig. 1 whitened with ammonium chloride sublimate.

examined cystoid species which may bear haplopores. He wrote (1941, p. 60): 'If one reserves the name haplopores (canaux haploporiques) for these sinuous ramifying canals, the canals of *Aristocystis* [sic], *even though united in pairs*, are incontestably haplopores' (my italics). But if the perpendicular canals were paired circulation was possible and whatever modifications occurred within the plates, *functionally* the structure is the same as a typical diplopore (text-fig. 6). Hence I regard the pore-structures of *Aristocystites* as diplopores. Only one true haplopore has come to my notice in an isolated plate of *Eucystis* sp. from Knock, Westmorland which also bears several typical diplopores. I interpret this as a damaged or incompletely developed diplopore.

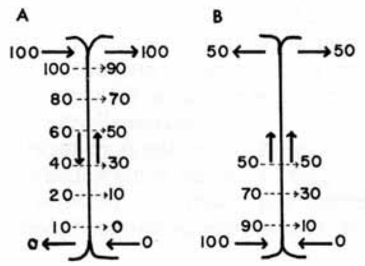
FUNCTION OF EXOTHECAL PORE-STRUCTURES IN CYSTOIDS

Untestable functional interpretations are inherently weak, since they can be neither substantiated nor disproved, and undesirable since they cast doubt on the validity of all functional interpretations. Many functional hypotheses are open to test however, by Rudwick's paradigm method (Rudwick 1964). To test a functional hypothesis the detailed morphology of a fossil structure is compared with that of an ideal structure (paradigm) which would serve the supposed function with maximum efficiency. Close comparison indicates that the fossil structure could have served the supposed function efficiently but does not prove that in fact it did so.

The paradigm method can be used to test the mechanics, but not the physiology of the structures investigated. It depends on acceptance of 'mechanical uniformity' (i.e. that the 'laws' of mechanics applied in the past as they do now) but may be totally independent of knowledge of living organisms. All morphological structures have more or less well-defined mechanical effects. Their function is taken to be that effect which is most beneficial to the vital needs of the organism or which confers most selective advantage on the organism. By considering effects rather than function, analysis may be made more rigorous and conclusions stated more positively. For example rigidity is an undeniable mechanical property of triangles. The triangulation 'ornament' of ridges connecting plate centres which is so commonly found in echinoderms undoubtedly increased the strength and rigidity of the test. This is not an interpretation: it is a fact. If we try to explain this effect in terms of function or selective advantage, then we make interpretations. In doing so we may draw sound conclusions if we can demonstrate that a vital function necessary for the survival of the organism (e.g. nutrition, protection, respiration, excretion, etc.) was performed more efficiently with, than without, the structure involved. Echinoderm tests with triangulation 'ornament' provided better protection for the enclosed vital organs than those without this 'ornament', by virtue of their increased strength and rigidity. Thus we may conclude that *most probably* the *function* of triangulation 'ornament' was protection but *undoubtedly* its *effect* was to increase the strength and rigidity of the test.

The following analysis is an attempt to estimate the mechanical efficiency of cystoid pore-structures as exchange systems and they are compared with the appropriate paradigm. Any exchange system must have an exchange surface to prevent mixing of fluids. The amount of exchange is controlled by the following factors:

1. The area of the exchange surface: the larger the area the greater the amount of exchange.
2. The resistance to exchange of the exchange surface: the thinner the surface the less its resistance will be.
3. The concentration gradient across the exchange surface: the higher the gradient (i.e. the greater the difference in concentration of the exchange substance on either side of the exchange surface) the greater the potential exchange. A counter-current system (text-fig. 10*a*) is the most efficient method of maintaining a high concentration gradient.



TEXT-FIG. 10. Idealized exchange systems. A, counter current; B, concurrent. Maximum potential exchange in B is half that of A. Figures represent percent concentration of the exchange substance. Heavy arrows indicate current directions, light arrows indicate exchange.

Thus the paradigm of an exchange system will have a large area of exchange surface which is as thin as is compatible with its strength and a counter-current system. A more detailed account of the above is presented in Paul 1968, pp. 708–709.

Detailed functional analysis

In exothecal pore-structures the fluids within the canals were body fluids. A healthy animal presumably had control over both their composition and circulation. Hence devices to prevent recirculation and choking of the canals by foreign particles were unnecessary and cannot in fact be recognized. The exchange surfaces were outside the theca and therefore liable to mechanical damage. This brings into opposition two requirements of the paradigm: the thinner the exchange surface the greater the amount of exchange but the greater the chances of rupture and mixing. With the above ideas in mind the detailed morphology of exothecal pore-structures in cystoids will be compared with the paradigm of an exchange system and estimates of the efficiencies of the various types made.

1. *The area of the exchange surface*. Four of the five basic types of cystoid pore-structures have calcified exchange surfaces which are frequently preserved in fossils and the areas of which can be measured or at least estimated fairly accurately. Echinoderm skeletal material is a meshwork of fine calcite rods and soft tissue fibres; exchange would have taken place through the latter. Only about half the exchange surface area (the soft tissue half) functioned actively in exchange during life.

In cystoids individual calcified exothecal pore-structures are much less efficient than endothecal (dichoporite) pore-structures in terms of the area of exchange surface. The

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EXPLANATION OF PLATE 4

Stereophotos of simple humatirhombs with compound fistulipores.

Fig. 1. *Echinosphaerites aurantium americanum* Bassler. Weathered example with fistulipores which do not reach plate centres in largest plates, ×4 (author's colln.).

Figs. 2, 3. *Echinosphaerites aurantium* s.l. 2, BMNH E7803, Internal surface of part of theca to show openings of perpendicular canals (cf. Pl. 1, fig. 6), ×2. 3, BMNH (unreg.), Weathered portion of theca, ×3.

Fig. 4. *Heliocrinites guttaeformis* Regnéll. RM Ec4763. Portion of weathered theca with large rhombs, ×3.

Fig. 5. *Caryocystites dubia* (Angelin). SM A57332. Example with unweathered external surface showing outlines of rhombs, ×2.

Stereophotos of complex humatirhombs with compound fistulipores.

Fig. 6. *Caryocystites lagenalis* Regnéll. SM A57362. Note intermediate fistulipores, ×2.

ratio A_e/A_t where A_e is the area of the exchange surface and A_t is the area of the thecal surface occupied by the pore-structure is a measure of the efficiency of an individual pore-structure. In endothecal pore-structures this ratio is always greater than one and in one measured pectinirhomb was 7·84. Table 1 shows that this ratio varies from 0·28–0·86 in humatirhombs. All three types of exothecal pore-structure in cystoids exhibit modifications of their basic design which increase the ratio A_e/A_t but no evolutionary trends towards increased efficiency are apparent in contrast to pectinirhombs (Paul 1968).

TABLE 1. Estimates of the ratio A_e/A_t in humatirhombs

Species	*Ratio*	*Humatirhomb type*
Lophotocystis angustiporus (Regnéll)	0·37	Simple rhombs with simple fistulipores
L. granatum (Wahl.)	0·30–0·42	,, ,, ,,
L. sp. (Shole'shook)	0·28	,, ,, ,,
L. malaisei (Regnéll)	0·28–0·41	,, ,, ,,
Ulrichocystis eximia Bassler	0·59–0·67	,, ,, ,,
L. sp. nov. (Skålberget)	0·42	Complex rhombs with simple fistulipores
Heliocrinites ovalis Ang.	0·58–0·68	Simple rhombs with compound fistulipores
H. guttaeformis Regnéll	0·38–0·80	,, ,, ,,
H. sp. nov. (Rhiwlas)	0·43	,, ,, ,,
Echinosphaerites aurantium (Gyll)	0·29	,, ,, ,,
E. a. suecicus Jaekel	0·75	,, ,, ,,
E. a. americanum Bassler	0·57–0·77	,, ,, ,,
Caryocystites dubia (Ang.)	0·71	,, ,, ,,
C. lagenalis Regnéll	0·86	Complex rhombs with compound fistulipores

For simple fistulipores raised in ridges: $A_e \simeq (1{\cdot}5 \times FW)$, and $A_t = (RS+RW)$ where RS = ridge separation, RW = ridge width, and FW = fistulipore width.

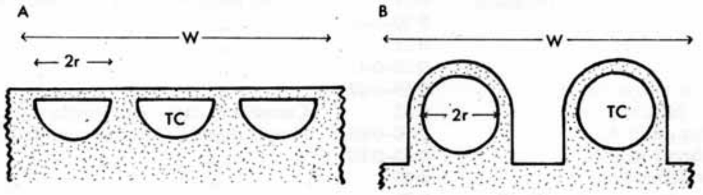
For compound fistulipores buried in plates: $A_e \simeq FW$ and $A_t \simeq FW+IFW$. (IFW = separation of fistulipores.)

For complex rhombs the area covered by intermediate fistulipores is calculated and the ratio A_e/A_t doubled for that area, i.e. $\{A_e(\text{total})+A_e(\text{complex})\}/A_t$. Thus if the complex rhomb area is half the total rhomb area the total exchange area $= 1{\cdot}5A_e/A_t$.

In an ideal simple humatirhomb without raised ridges the ratio of the width of the tangential canals to the width of the gap between them is a close approximation to A_e/A_t. When the two widths are equal A_e/A_t is approximately 0·5. Humatirhombs with compound fistulipores generally have more closely spaced tangential canals than those with simple fistulipores. However, the latter are usually raised in ridges and have a larger area of exchange surface than buried tangential canals (text-fig. 11). The increase in area due to the ridges is as much as 50%. Both arrangements (i.e. raised simple fistulipores and buried compound fistulipores) seem to be alternative methods of increasing the ratio A_e/A_t.

In terms of exchange surface area humatirhombs are individually much less efficient than dichoporite pore-structures. However, every plate suture bears a humatirhomb in all Caryocystitida and there are thus several hundred rhombs per theca. The total exchange area *per theca* was probably as high as in dichoporite cystoids with only 1–25 rhombs per theca. Since almost all the thecal surface is covered with humatirhombs the ratio A_e/A_t is only slightly greater than the ratio of the total exchange area to the total thecal surface area. Thus anything from about 25% to 75% of the thecal surface area was exchange surface in humatirhomb-bearing cystoids but only about half actively functioned in exchange.

Humatipores are very similar to humatirhombs in terms of exchange area but it is much more difficult to measure or estimate A_e/A_t. An increase in the number of tangential canals increases the exchange area per humatipore (text-fig. 9*b*). Equally, raising the humatipore into a prominent tubercle increases exchange area (text-fig. 9*a*). With regard to exchange area *per humatipore* buried humatipores are less efficient than tubercular humatipores. However, the former are frequently more densely packed than the latter. Again this seems to reflect two alternatives: fewer, more efficient structures or a larger number of less efficient structures. In humatipore-bearing cystoids total exchange area *per theca* probably lies within the same limits as for humatirhomb-bearing cystoids.



TEXT-FIG. 11. Diagram to illustrate the exchange areas of (A) buried, and (B) raised tangential canals (TC) in fistulipores. Width of exchange area in one canal in A is $2r$, in B it is πr. In rhomb width W and length l areas are $6rl$ in A and $2\pi rl$ in B. Since $\pi \simeq 3$ two canals in B have the same exchange area as three canals in A.

Some diplopores resemble echinoid pore-pairs very strongly and probably gave rise to podia analogous, if not homologous, to echinoid tube-feet. The podia are never

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EXPLANATION OF PLATE 5

Stereophotos of diplopores.

Fig. 1. *Sphaeronites* sp. nov. (Råbäck, Västergötland, Sweden). SM A35317. A small theca with densely packed diplopores over entire surface.

Fig. 2. *Sphaeronites pomum* (Gyll.) SM (unreg.). Note spinose tubercles between deeply sunken peripores (cf. text-fig. 6A).

Fig. 3. *Sphaeronites globulus* (Angelin). SM A57321. Note polygonal peripores with large flat-topped central tubercle (cf. text-fig. 6B).

Fig. 4. *Sphaeronites* sp. nov. (Skålberget, Dalarna, Sweden). SM A57407. Note irregular diplopores like those of *S. globulus*.

Fig. 5. *Sphaeronites pyriformis* (Forbes). BMNH E16340.

Fig. 6. *Sphaeronites litchi* (Forbes). GSM 7431. Note very prominent central tubercles (cf. fig. 8 this plate).

Stereophotos of echinoid pore-pairs.

Fig. 7. *Arbacia punctulata* (Lam.). Note tubercles around pore-pairs (author's colln.).

Fig. 8. *Echinocorys scutatus* (Leske). SM (unreg.). Pore-pairs of buccal tube-feet. Note large central tubercle (cf. fig. 6, this plate).

Figs. 1–6 × 3, 7, 8 × 4. All whitened with ammonium chloride sublimate.

preserved, so measurement of their surface area is impossible. Nevertheless the area of podium wall could not have been less than the area of the peripore and since it was entirely made of soft tissue all the area could have functioned in exchange. Thus in diplopores A_e/A_t must have been greater than or equal to 1. Most diplopores have rims and tubercles associated with their peripores as do most echinoid pore-pairs. In the latter the rims and tubercles are attachment structures for the longitudinal muscles of the tube-feet (Nichols 1959, p. 70). As a broad generalization, the more strongly developed the rims, etc. are, the stronger the muscles and the greater the flexibility of the tube-feet. For example, many regular sea urchins have much more prominent rims and tubercles associated with pore-pairs on the oral surface up to the ambitus, and the tube-feet on this surface are the main ones used in locomotion. In some cases the comparison between diplopores and pore-pairs is so strong (e.g. *Sphaeronites* and *Echinocorys* oral tube-feet, Pl. 5, cf. figs. 3–6 with fig. 8) that the conclusion that they represent almost identical structures seems inescapable. Although impossible to prove, available evidence strongly suggests that some diplopores had extensile podia. This would increase their efficiency as exchange surfaces in two ways: it increases the area and it decreases the thickness of the exchange surface.

The density of packing of diplopores varies from genus to genus or even species to species. In *Archegocystis* the number of diplopores could apparently increase or decrease during life (Paul 1971). This forms a very delicate exchange mechanism that could respond to changes of the environment. Such was definitely not the case in *Sphaeronites*, all species of which have diplopores evenly developed all over the theca. The latter genus shows an interesting evolutionary trend towards larger diplopores throughout the Middle and Upper Ordovician.

Many representatives of the Aristocystitidae have sealed diplopores in some part of the theca. Chauvel (1966, p. 109) has interpreted this as a 'maladie calcaire' reminiscent of W. D. Lang's fatalistic trends in various calcium carbonate secreting organisms (Lang 1923*a*, *b*). Calcification of diplopores decreases their efficiency by at least halving their exchange surface area but it does not necessarily render them useless. Indeed calcification is much more likely to represent protection against predators eating soft tissue podia than ill health. Cystoids lacked spines, at least as far as is known; so podia were not mechanically protected as sea urchin tube-feet are.

The following conclusions can be drawn as regards area of exchange surface:

(i) Individual exothecal pore-structures are very much less efficient than individual endothecal pore-structures but far more of them are developed on any one cystoid. The total area for exchange *per theca* was probably the same for both endothecal and exothecal pore-structures. In humatirhombs available measurements indicate that the total exchange area was between 25% and 75% of the total thecal surface area.

(ii) In humatirhombs the raising of tangential canals in ridges, and the development of compound and additional fistulipores increase exchange area. In humatipores production of many tangential canals and development of tubercular humatipores both increase exchange area. Some diplopores may have had extensile podia which also increased exchange area. Within the limits of their geometry all three types of exothecal pore-structure tend to maximize their exchange area. Diplopores were probably the most efficient of the three but were liable to predation since their exchange surfaces were made entirely of soft tissue.

(iii) Although individually inefficient all exothecal pore-structures probably provided adequate exchange area per theca by sheer weight of numbers.

2. *The resistance to exchange of the exchange surface*. For maximum efficiency the exchange surface should be as thin as possible; however, rupture and mixing of fluids must be prevented. Exothecal pore-structures are much more susceptible to mechanical damage than endothecal pore-structures since their exchange surfaces are external. It is not surprising therefore that measurable exothecal exchange surfaces are thicker (0·05–0·10 mm) than endothecal exchange surfaces (always less than 0·03 mm and reaching as little as 0·007 mm). Nevertheless the thecal wall in most cystoids with exothecal pore-structures is 1–3 mm thick and often much thicker in aristocystitids. Chauvel (1966, p. 27) records a maximum thickness of 26 mm in *Maghrebocystis*. Although exchange surfaces of humatipores and humatirhombs are thicker than those of endothecal pore-structures they are still very much thinner than the thecal wall. Since no measurements of thickness are possible in diplopores their efficiency in terms of resistance to exchange cannot be estimated. However, extensible podia would have had very thin walls in all probability.

Exothecal pore-structures do not seriously weaken the theca and no strengthening structures have been recognized. Again this contrasts with pectinirhombs (Paul 1968).

3. *Maintenance of a concentration gradient*. The most efficient method of maintaining a concentration gradient is a counter-current system (text-fig. 10*a*). The best evidence for current directions is given by protective devices and devices to prevent recirculation. Unfortunately neither type of device is necessary with exothecal pore-structures since the fluids flowing in the thecal canals were body fluids. Neither type of device has been recognized. Some indirect evidence of currents and their directions of flow is available, however.

Nearly all recent echinoderms have ciliated external epithelia and cystoids probably had too. From purely hydrodynamic considerations fluids within the canals would not have moved without cilia due to the viscous effect of the boundary layer (Paul 1968, pp. 719, 721). Almost certainly both internal and external ciliary currents were present in cystoids. The humatirhombs of *Lophotocystis granatum* (Wahlenberg) have fine granules developed on the ridges. In the best preserved example the granules are elongate parallel to the rhomb axes (Pl. 1, figs. 1–2). If a ciliated epithelium was present

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EXPLANATION OF PLATE 6

Stereophotos of diplopores.

Figs. 1, 3. *Haplosphaeronis oblonga* (Angelin). 1, SM A57381, An example with oval peripores without rims. 3, SM A57356, An example with peripores with strongly raised rims.

Fig. 2. *Haplosphaeronis* sp. nov. (Shole'shook, S. Wales). SM A57520. Latex impression of theca showing asymmetrical diplopores (cf. text-fig. 6D).

Fig. 4. *Archegocystis stellulifera* (Salter). BMNH E16200. Latex impression showing elongate and oval diplopores with simple rims (cf. text-fig. 6C).

Fig. 5. *Aristocystites bohemicus* Barrande. SM A49868c. Latex impression showing irregular peripores between gonopore (left) and hydropore (right). Even though the peripores are very irregular it is still possible to see that the perpendicular canals are arranged in pairs as in typical diplopores.

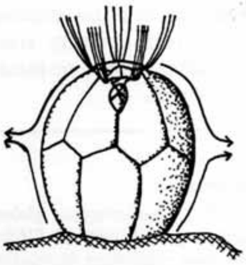
Fig. 6. *Triamara* sp. USNM 166580. Example with small oval peripores. ×4.

Figs. 1–5 ×3. All whitened with ammonium chloride sublimate.

these granules would have increased the area of ciliated surface and enhanced the currents parallel to the rhomb axis. Such granules are similar to those on the periplastronal areas of recent spatangoid sea urchins and are present on other species of *Lophotocystis*. Granular ornament is also characteristic of most species of humatipore-bearing cystoids although the granules are not elongate. Since all the thecal surface is covered with humatirhombs in caryocystitid cystoids, external currents of different rhombs would interfere with each other. Nevertheless, water in contact with the external surface of the theca would be continually changed.

Evidence for the presence and direction of currents in Diploporita is virtually non-existent. However the genera *Holocystites* and *Haplosphaeronis* regularly have asymmetrical dipores and this asymmetry may be associated with current flow. Clearly, internal fluids came up one perpendicular canal and descended down the other. Which canal was efferent and which afferent is not certain in either genus. In *Holocystites*, which bears humatipores, one perpendicular canal is subcentral and one peripheral (text-fig. 9*a*, Pl. 7, figs. 2, 3). I suggest that body fluids ascended the subcentral perpendicular canal but the alternative direction seems equally plausible. From the point of view of exchange either direction would seem to be equally efficient.

Some species of *Haplosphaeronis* have asymmetrical diplopores. The peripore rim is thickened and raised and the peripore floor raised between the perpendicular canals, but closer to one than the other. Thus one canal opens in a roughly circular depression and the other in a pyriform depression (text-fig. 7*d*, Pl. 6, fig. 2). The diplopores of *Haplosphaeronis* are elongate and most are aligned in an oral–aboral direction. In the oral half of the theca the pyriform depression is adoral in the diplopore but the converse is true in the aboral half of the theca. If the theca was orientated with the mouth upwards, surface ciliary cleaning currents may have moved in an aboral direction on the upper half of the theca as they do in many recent sea urchins. A current in the reverse direction in the aboral half of the theca would also help to keep the theca clean (text-fig. 12). If such external currents were present, alignment of the diplopores parallel to them would allow internal counter-currents to operate. Recent sea urchins with specialized respiratory tube-feet have opposed external and internal currents. Again the opposite current directions would seem equally plausible and equally efficient in exchange.



TEXT-FIG. 12. Possible surface current directions in *Haplosphaeronis* Jaekel. Such currents would help to clean the thecal surface.

The pattern of external currents proposed for *Haplosphaeronis* involves flow from the oral and aboral extremities towards the ambitus. Precisely similar current patterns were proposed for the external currents of dichoporite rhombiferans (Paul 1968). Since the two groups are not closely related, similar external cleaning currents may have preceded the evolution of internal respiratory currents. The latter probably developed in a fixed relationship to the former, namely counter to them.

In summary, there is little direct evidence for the presence or direction of currents in exothecal pore-structures. However, in at least one example of each major type there is some indirect evidence for currents. Indeed the basic morphology of thecal canals is ideal for current flow since one perpendicular canal could act as the afferent canal and the other as the efferent. In all but two genera the two perpendicular canals are identical and it is generally impossible to say which canal was which.

Conclusions

All three exothecal pore-structures (humatirhombs, humatipores, and diplopores) differ from the paradigm of an exchange system to some degree and they were individually less efficient than endothecal pore-structures in terms of the area and thickness of the exchange surface and possibly of current systems too. This relative inefficiency can be explained in terms of the need to prevent rupture of the exchange surface. Although individually less efficient than endothecal pore-structures, exothecal pore-structures still allowed exchange to take place. Indeed if currents were present this would inevitably have been their effect.

Large numbers of exothecal pore-structures are developed in any one theca which compensates for their individual inefficiency. For example, the ratio A_e/A_t is an estimate of individual efficiency in terms of exchange surface area. An average value for humatirhombs is probably about 0·5, for pectinirhombs about 10. In equal-sized thecae with equal-sized rhombs there should be 20 times as many humatirhombs as pectinirhombs to achieve the same amount of exchange. This ratio of humatirhombs to pectinirhombs is easily exceeded in practice since humatirhombs are developed in all available space on a theca. The exchange surfaces are thicker in humatirhombs than in pectinirhombs and hence the ratio should be higher than 20 to 1.

There can be little doubt that the mechanical effect of exothecal pore-structures in cystoids was to allow exchange between sea water and body fluids. Since oxygen and carbon dioxide transfer constitute the most likely form of this exchange, exothecal pore-structures were respiratory structures. It is now pertinent to consider respiration in more detail.

EXPLANATION OF PLATE 7

Humatipores.

Figs. 1, 5, 7. *Trematocystis globosus* (Miller). 1, USNM S3058b. Note tangential canals exposed by weathering. 5, 7, FMNH 8766a; 5, General view of plate, ×6 approx. 7, Detail of humatipores to show plate meshwork in weathered tangential canals, ×25 approx.

Figs. 2–3. Stereophotos of *Holocystites alternatus* (Hall). BMNH E7629. 2, Detail of single humatipore, ×25 approx. 3, General view of plate showing tubercular humatipores with radiating tangential canals, ×6 approx.

Fig. 4. *Holocystites scutellatus* Hall. Detail of some weathered tubercular humatipores, ×10 (author's colln.).

Fig. 6. *Brightonicystis gregarius* Paul. SM A32814a. Detail of humatipores with 6–8 tangential canals, ×5.

Fig. 8. Stereophotos of *Pentacystis sphaeroidalis* (Miller and Gurley). FMNH 6000. Detail of weathered humatipores, ×13.

Fig. 9. Stereophotos of *Pentacystis simplex* Paul. AMNH 20271a. Detail of pit bored into cystoid by parasite which shows tangential canals of three humatipores parallel to the sides of the pit. These canals were formed *after* the pit was bored, ×10.

Fig. 10. Stereophotos of *Trematocystis rotundus* (Miller).

All figures whitened with ammonium chloride sublimate.

RESPIRATION IN RECENT AND FOSSIL ECHINODERMS

A specialized respiratory system consists of three distinct parts. The respiratory system in vertebrates, for example, includes: (i) an external exchange surface (lungs or gills) whereby oxygen is gained from (and carbon dioxide lost to) the surrounding medium, (ii) a circulation system (blood stream) to distribute oxygen internally, and (iii) internal exchange surfaces (the capillaries) whereby oxygen is transferred from the circulation system for use in cellular metabolism. Unless sites of metabolism are very close to the external exchange surfaces some system of oxygen transport is vital for efficient respiration. Most triploblastic metazoa have a specialized circulation system but recent echinoderms do not.

The preceding analysis of exothecal pore-structures in cystoids considered only the first part, i.e. the external exchange surfaces, and depended on paradigmatic methods. This section considers the internal portions of the respiratory system, and depends more on biological uniformitarianism. It is pertinent to consider what is known of respiration in recent echinoderms.

Recent echinoderms

Relatively little systematic information is available on respiration in recent echinoderms. Farmanfarmaian (1966, p. 245) in his summary uses Harvey's (1928) equation for the diffusion of oxygen into a spherical organism to prove conclusively that no echinoderm could rely on diffusion alone to gain oxygen from sea-water. Harvey's equation is as follows:

$$C_o = Ar^2/6D$$

where C_o is the concentration in atmospheres of oxygen in sea water; A is the rate of oxygen consumption by the organism in ml O_2/grm/minute; r is the radius of the sphere in cm; and D is the diffusion coefficient in atmospheres/cm/cm^2. Using the following values, the equation can be solved for r (which is the depth to which oxygen will penetrate into an echinoderm by diffusion alone).

$C_o = 0{\cdot}21$ (Farmanfarmaian 1966)

$D = 0{\cdot}000011$ (Krogh 1941)

$A = 0{\cdot}001233$ maximum and $0{\cdot}000166$ minimum (Farmanfarmaian 1966)

$$\begin{aligned} r^2 &= \frac{6D.C_o}{A} \\ &= \frac{6\times 0{\cdot}000011\times 0{\cdot}21}{0{\cdot}001233} \quad \text{or} \quad \frac{6\times 0{\cdot}000011\times 0{\cdot}21}{0{\cdot}000166} \\ &= 0{\cdot}0112408 \quad \text{or } 0{\cdot}0834939 \\ \therefore\ r &= 1{\cdot}06\text{ mm} \quad \text{or } 2{\cdot}89\text{ mm} \end{aligned}$$

Farmanfarmaian argues that the success of the echinoderms is to a large extent dependent upon the development of specialized respiratory surfaces (i.e. external exchange surfaces) since they are clearly essential to survival. For efficient respiration these surfaces must be significantly less than 1–3 mm thick. Recent echinoderm respiratory surfaces include respiratory trees and tentacles (holothurians), podia (all classes), papulae (asteroids), peristomial gills (regular echinoids), genital bursae (ophiuroids), and the general external surface (all classes). All but the last fall well within the thickness limits established above.

An efficient external exchange surface requires currents to replenish depleted fluids. Such currents are either oscillatory, involving current reversals, or circulatory. Oscillatory currents occur in blind structures, for instance in the respiratory trees of holothurians and the peristomial gills of regular echinoids. Circulatory currents occur in closed ring-shaped structures such as the tube-foot/ampulla system of echinoids. Recent echinoderms possess no specialized circulation system to distribute oxygen internally. Oxygen must be transferred into the fluids of the major coelomic pouches via the external exchange surfaces and all organs involved in metabolism are either bathed in these fluids or directly in sea water.

The role of the water vascular system in respiration needs some clarification. Farmanfarmaian (1966, p. 250) has conclusively shown that in sea urchins the tube-foot/ampulla systems transfer oxygen from sea water to coelomic fluids. But the radial water vessels are much less involved in respiration than the tube-foot/ampulla system because they are not directly in contact with sea water and are blind structures without circulatory currents. The water vascular system can only transfer oxygen into coelomic fluids efficiently where there is a tube-foot/ampulla system in which the tube-foot is external and the ampulla is internal (text-fig. 13). Hence the respiratory contribution of the water vascular system in crinoids, which have an almost totally external water vascular system, is negligible. This would be equally true of external branches of the water vascular system in cystoids if these were present.

In crinoids with large calyces and no calycal pore-structures, migration of coelomocytes would seem the only plausible way to oxygenate organs within the calyx. However, the role of coelomocytes in respiration (summarized in Endean, 1966) among recent echinoderms is not understood. Systematic movement of coelomocytes could explain the absence of a distinct circulation system in echinoderms. However, it is almost impossible to observe whether such movements of coelomocytes actually occur. One type of coelomocyte found in recent holothurians contains haemoglobin (i.e. the haemocytes). Wandering haemocytes would inevitably carry oxygen and carbon dioxide with them but again the actual course of wandering is impossible to observe. Haemocytes are unknown in recent crinoids and were presumably absent in fossil groups such as cystoids.

It may be noted that Farmanfarmaian (1966, p. 246) rejects the suggestion that the digestive tract can be involved in respiration.

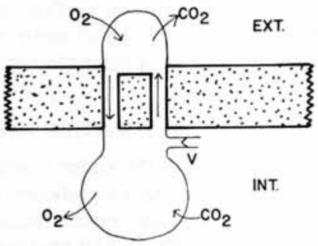
In summary: recent echinoderms respire through a variety of specialized external exchange surfaces but lack any internal circulation system to distribute the oxygen so gained. No recent echinoderm relies exclusively on one type of external exchange surface and all types are made entirely of soft tissue. Efficient external exchange surfaces in recent echinoderms must be significantly less than 1–3 mm thick.

Comparison of recent and fossil echinoderms

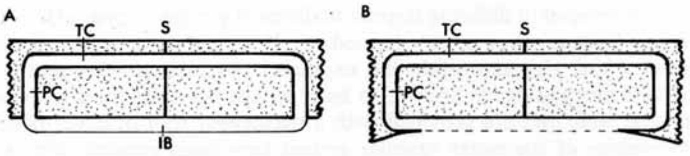
Comparison of primary exchange surfaces in recent echinoderms and cystoids demonstrates both similarities and differences. Perhaps the most obvious difference is total lack of calcified exchange surfaces in recent echinoderms whereas these are commonly present in four of the five basic types of cystoid pore-structures and occur rarely in the fifth. A second important difference is the apparent lack of oscillatory currents in cystoids. These two features may be correlated. It is difficult to develop an oscillatory current in a rigid calcified structure whereas soft tissue is ideally suited to produce the expansions and contractions necessary for oscillation. Perhaps the most important similarity is the wide variety of respiratory exchange surfaces which may be internal (e.g. holothurians) or external (e.g. asteroids and echinoids) among recent echinoderms just as in cystoids.

The over-all efficiency of a respiratory system depends not only on the external exchange surfaces but also on the internal distribution of oxygen. It is relevant therefore to speculate on the nature of the internal connections of cystoid pore-structures. If a cystoid relied on diffusion alone to distribute oxygen internally it would be advantageous to have pore-structures developed evenly over the entire surface. All internal organs would then be approximately equidistant from an oxygen source. The dichopores of pectinirhombs and cryptorhombs extended into internal coelomic spaces. In the Hemicosmitida, cryptorhombs are more or less evenly developed over the theca and probably no internal circulation was developed. The supposed internal ciliary countercurrents in the cryptorhombs and movement of organs may have provided adequate circulation of coelomic fluids within any one coelomic pouch. In the Glyptocystitida, however, there is a progressive reduction in the number of pectinirhombs per theca and all Silurian and Devonian species have four or fewer pectinirhombs. This is believed to be correlated with the development of a specialized internal circulation system. Grooves on internal moulds of Callocystitidae from the Middle Silurian of North America provide some evidence as to the path of this circulation system (Paul 1967*a*). Since the grooves are apparently connected to the hydropore the supposed circulation system is believed to have been associated with the water vascular system.

The thecal canals of exothecal pore-structures could represent simple evaginations of internal coelomic pouches in which case all the canals could have been connected to one coelomic pouch. Alternatively each coelomic pouch could have had a number of such evaginations. Both humatirhombs and humatipores are always developed over the entire thecal surface and hence the latter alternative would seem more likely. However, Nichols (1962, p. 135, figs. 18*d–f*) has proposed that the fistulipores of humatirhombs form discrete closed systems in themselves (text-fig. 14*a*). The tangential canals of fistulipores correspond to Nichols's 'external bulb'. Distinct evidence of the corresponding 'internal bulb' is found in the humatipores of *Ulrichocystis*. Traces of canals are found on the internal surfaces of the plates (Pl. 1, fig. 6) and the central portions of the plates show partially calcified canals internally. A section through a fistulipore of *Ulrichocystis* resembles text-fig. 14*b*. Such a system is less efficient than simple evaginations of the coelom since there are two exchange surfaces not one. If such internal-canals were generally present in humatirhombs this might explain why humatirhombs are confined to the Ordovician whereas other rhombs survived well into the Devonian. However, the evidence for such internal canals is preserved only in *Ulrichocystis* which is unique among the Caryocystitida in having recumbent arms. Clearly, *Ulrichocystis* is not a typical caryocystitid cystoid and it is unwise to regard it as such.



TEXT-FIG. 13. O$_2$ and CO$_2$ exchange in a tube-foot/ampulla system. V = valve. Arrows indicate current and exchange directions.



TEXT-FIG. 14. Interpretation of the structure of fistulipores. A, Nichols's (1962) interpretation with a soft tissue internal bulb (IB). B, diagrammatic section through fistulipore of *Ulrichocystis* which tends to confirm Nichols's interpretation. PC = perpendicular canal, TC = tangential canal, S = suture.

The situation with diplopores is equally complex and ambiguous. Many diplopores have raised rims and tubercles associated with them (text-fig. 7) which strongly resemble similar features associated with echinoid pore-pairs. In echinoids these ridges are the points of insertion for longitudinal muscles of the tube-feet. If the rims and tubercles of diplopores represent similar muscle attachments then diplopore 'podia' were extensible. Mechanical and hydrostatic considerations require compensating reservoirs for extensile podia. Nichols (1962, p. 135, figs. 18*a–c*) again proposed internal and external 'bulbs' for diplopores but he did not envisage extensile structures. Extensible podia imply a hydraulic system which is bound to leak just as tube-feet leak. If lost fluid is to be replenished some connection to a large reservoir is needed. The most obvious suggestion is that diplopores were connected to an internal development of the water vascular system. It may be significant that diplopores are not always evenly developed over the entire thecal surface: in the Dactylocystidae diplopores are confined to five ambulacral tracts which quite strongly resemble the ambulacra of echinoids. Now it is necessary to consider the nature of the water vascular system in cystoids.

WATER VASCULAR SYSTEM OF CYSTOIDS

The nature of the water vascular system in cystoids is pertinent to the function of the pore-structures and significant to echinoderm evolution in general. In recent crinoids the water vascular system consists of a circumoesophageal ring canal off which five radial canals branch and pass up the arms beneath the floors of the ciliated food grooves. Since cystoids are probably most closely related to crinoids, among living echinoderms, it has generally been assumed that their water vascular system was essentially similar to that of extant crinoids.

Examination of the food-gathering system of cystoids should provide evidence about the nature of the water vascular system. Food grooves have been described as hypothecal (within the theca), epithecal (on the external surface of the theca), and exothecal (free of the thecal surface in arms and brachioles). It is more accurate to say that food-gathering systems contain some hypothecal, epithecal, and exothecal portions. The first usually provides no evidence about the water vascular system; the latter two may do so but are developed to differing degrees in different groups of cystoids. The epithecal portion of the food grooves is very limited in all Rhombifera but fortunately in the Glyptocystitida and Hemicosmitida the exothecal portions are frequently preserved and hence their morphology is known. In both groups the main food grooves are relatively deep and wide and are provided with a permanent roof of cover plates. Should external extensions of the water vascular system have been present, they would have been adequately protected from damage. The spacious main food groove could have housed extensions of the water vascular, haemal, perihaemal, and oral nervous systems in the same manner as these are housed in the arms of recent crinoids.

Exothecal ambulacral appendages of the Caryocystitida are almost never preserved. Barrande (1887, pls. 23, 25) figures some examples of *Arachnocystis infaustus* with three long brachioles preserved and *Ulrichocystis eximia* has three recumbent arms. Specimens of the latter species collected by the writer show a wide main food groove with recessed ledges on either side for the insertion of cover plates. Again if external branches of the tubular coelomic systems were present they would have been adequately housed and protected.

In diploporites virtually nothing is known about the exothecal ambulacral appendages since there are only two reports of preserved structures in the literature. Fortunately epithecal portions of the food grooves are frequently extensive. At least two distinct types of epithecal food grooves occur among Diploporita. The first type consists of very narrow and shallow grooves with no evidence of any covering structures. Possibly the grooves were provided with soft tissue lappets but this is of course unknown. If these shallow grooves housed extensions of the water vascular system, etc. these extensions would have been very delicate and yet apparently they were inadequately protected from damage. It seems quite plausible that diploporites with shallow grooves lacked external extensions of the water vascular system in which case one would imagine that internal extensions were present.

The second type of diploporite food groove is found in the Aristocystitidae. Here the food groove runs along the base of a massive ambulacral tract, 5–10 mm wide which is lined with ambulacral pores in *Aristocystites* and *Triamara* (Paul 1971) and probably in other genera too. In all genera the ambulacral tracts are covered with immovable cover plates arranged in four series. In the absence of diplopores the ambulacral pores of *Triamara* and *Aristocystites* would be taken as clear evidence of internal ampullae. These ambulacral pores are however only specialized diplopores which happen to open within the ambulacral tracts. The ambulacral podia could have been connected to external radial water vessels lying in the floors of the ambulacral tracts but no such external connection is available for the supposed podia of the diplopores on the general thecal surface. If the ambulacral podia were connected to the water vascular system so were all diplopores and these connections must have been internal.

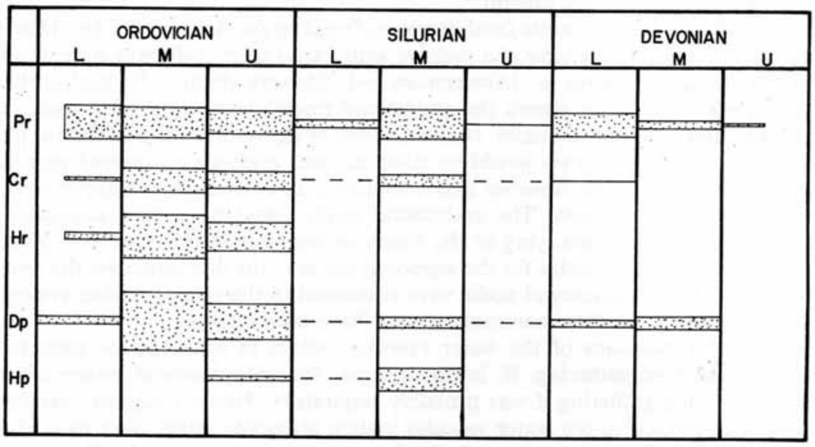
The principal functions of the water vascular system in echinoderms seem to be respiration and food gathering. If, in diploporites, the water vascular system did not contribute to food gathering it was probably respiratory. Hence I suggest that diplopores were connected to the water vascular system internally rather than to a wholly unique internal organ system although this latter idea is quite plausible. Humatipore-bearing cystoids evolved from diplopore-bearing cystoids so these too probably had an internal water vascular system. Oral pores, which correspond to the ambulacral pores of the Aristocystitidae, occur in all genera of Holocystitidae.

In summary, study of the food gathering organs and pore-structures in cystoids suggests that (i) Diploporita probably had an internal water vascular system connected to the dipores, (ii) most rhombiferans probably had external radial water vessels in the ambulacra, and (iii) the Callocystitidae (rhombiferans) may well have had both internal and external extensions of the water vascular system.

EVOLUTIONARY AND TAXONOMIC IMPLICATIONS

Evolutionary

The evolutionary significance of the above suggestions about the water vascular system is considerable. Recent echinoderms have either internal or external branches (radial canals) of the water vascular system. This has generally been assumed to have been the case with all fossil echinoderms too, and, until the recent discovery of helicoplacoids (Durham and Caster 1963) external branches were considered to be the primitive ancestral condition. However, internal branches may have developed as early as Lower Cambrian in the helicoplacoid *Waucobella* (Durham 1967). In the more advanced Glyptocystitida, among cystoids, there is evidence of both internal and external branches. Bather imagined that external branches evolved first and internal branches developed later by the radial vessels 'sinking' through the thecal plates. Both types of branch could have evolved quite independently by growing out radially from the ring canal either beneath or above the thecal plates. If such were the case both internal and external branches could have developed within the same animal, an idea which needs further investigation. The most important implication of the idea is that internal and external branches of the water vascular system need not necessarily be homologous.



TEXT-FIG. 15. Distribution in time of the five major types of cystoid pore-structures. *Pr*, pectinirhombs; *Cr*, cryptorhombs; *Hr*, humatirhombs; *Dp*, diplopores; *Hp*, humatipores. Width of stippled area proportional to number of species with each type of pore-structure.

Exothecal pore-structures were individually less efficient than endothecal pore-structures as exchange systems. Among exothecal pore-structures diplopores were probably the most efficient in terms of area and thickness of the exchange surface but less so in terms of preventing rupture and mixing. The distribution in time of all five types of cystoid pore-structures is summarized in text-fig. 15. All five types first appear in the Ordovician: humatipores in the Ashgill (Upper Ordovician), the others in the Tremadoc or Arenig (Lower Ordovician). Humatirhombs are confined to the Ordovician while humatipores appear late in the Ordovician and survived to the Middle Silurian when they flourished briefly in North America. Diplopores are common in the Ordovician, rather rare in the Silurian and have a second peak in the Lower and Middle Devonian. The endothecal pore-structures, pectinirhombs and cryptorhombs, are common in the Ordovician and dominate cystoid faunas in the Silurian and Devonian. Thus it seems that within the Rhombifera the least efficient type survived for the briefest period and became extinct first. In the Diploporita the situation is more complex. To a large extent humatipores and diplopores are mutually exclusive in time. Diplopores are replaced by humatipores as the dominant type in the middle Silurian but reassert themselves again in the Devonian. The less efficient type again survived for the shorter period and became extinct first. A possible explanation for these reversals in relative abundance may lie in the susceptibility to rupture of diplopores. Although humatipores are less efficient than diplopores they are much less likely to be ruptured and certainly would not be subject to predation. Later Devonian diplopores may have evolved the ability to secrete noxious substances to inhibit predation. It is also possible that the reversals of dominance are artifacts of preservation or collection failure. Two points may be made: (i) If it were not for the *Holocystites* fauna of North America, which contains almost all known Silurian diploporites, there would be no dominance of humatipores in the Silurian. (ii) The Sphaeronitidae is a large and varied family in the Ordovician and to a lesser extent in the Devonian too, but to date not one single undoubted specimen of Sphaeronitidae has been collected from Silurian strata. (*Allocystites* Miller is not a diploporite cystoid let alone a sphaeronitid and *Austrocystites* Brown is not sufficiently well known to be certain of its affinities.)

From an evolutionary and functional point of view exothecal pore-structures were relatively unsuccessful. However, they can hardly be regarded as failures. All three types were able to support very much larger thecae than either endothecal type. Thecae 100–150 mm in major diameter are not at all unusual in the Caryocystitidae, Aristocystitidae, or Holocystitidae. Even *Echinosphaerites* exceeds 100 mm in diameter and *Calyx* may reach a length of 450 mm (Chauvel 1941, pl. 1, fig. 1). Thecae of dichoporite cystoids rarely exceed 35 mm in diameter and 60 mm is about the limit with the exception of the spindle-shaped genus *Rhombifera*. In the Ordovician the Caryocystitidae and Diploporita were very successful both in terms of individuals and species. This is also true of the Holocystitidae in the Middle Silurian. Diplopore-bearing cystoids survived into the Middle Devonian. Thus although less successful than cystoids with endothecal pore-structures, those with exothecal pore-structures formed an important experiment in echinoderm evolution.

Taxonomic

The principal characters which are claimed to unite the cystoids as a group are: (i) a theca which is not readily divisible into a ventral tegmen and a dorsal calyx, (ii) biserial, unbranched ambulacral appendages called brachioles, (iii) pore-structures developed in the thecal wall. The first character is generally present but *Caryocrinites* is an exception with a distinct tegmen. Evidence for the second character is incomplete. In the Diplorita only three genera have exothecal ambulacral appendages preserved: two are undoubtedly *uniserial* and the third may be biserial (Chauvel 1966). Apparently all three superfamilies of Rhombifera have biserial structures, however branched and pinnate recumbent arms are present in the Glyptocystitida, pinnate free arms in the Hemicosmitida and pinnate recumbent arms in the Caryocystitida. Cystoid pore-structures belong to five distinct types some of which are so distinct from others as to preclude close relationship. Furthermore, similar pore-structures are developed in some crinoids, paracrinoids, and eocrinoids and in all blastoids and parablastoids. Clearly, the presence of pore-structures is not unique to cystoids nor are cystoid pore-structures of a unique type. Evidence for external branches of the water vascular system is tenuous to say the least in the Diploporita but quite strong in the Rhombifera. To summarize:

the characters which are supposed to unify the cystoids are not found throughout the group nor are they confined to the group. The Diplorita and Rhombifera share no common characteristic that they do not also share with at least one other class of primitive echinoderms.

There are two alternative solutions: either to resurrect the old class Cystoidea for cystoids, paracrinoids, eocrinoids, blastoids, and parablastoids or to recognize the Rhombifera and Diploporita as separate classes. I prefer the second to emphasize the distinctiveness of the latter two groups but in either case the Rhombifera and Diploporita have the same taxonomic rank as the Eocrinoidea, Paracrinoidea, etc. Paul (1967*b*, 1968) suggested that the Diploporita and Rhombifera be recognized as distinct classes but without presenting all the evidence or defining the classes. Now that detailed evidence, at least as regards the pore-structures, has been presented, formal definitions of the major taxa of cystoids may be given as follows:

CLASS DIPLOPORITA Müller 1854, nom. transl.

Definition. Crinozoa with exothecal pore-structures (dipores) which consist of a single thecal canal, globular or pyriform theca generally composed of a large number of randomly arranged plates, which are usually all pierced by pore-structures. With or without a true stem, ambulacral appendages uniserial but very rarely preserved, water vascular system probably internal.

The lower divisions within the class are as in Kesling (1963, 1968) except that the Holocystitidae is separated from the Aristocystitidae and the latter is elevated to Superfamily rank (Paul 1971).

CLASS RHOMBIFERA Zittel 1880 nom. transl.

Definition. Crinozoa with exothecal or endothecal pore-structures (rhombs) which consist of rhombic sets of thecal canals, globular pyriform or oval theca, with true stem at least early in development, ambulacral appendages biserial (arms or brachioles), water vascular system probably with external radial branches.

ORDER DICHOPORITA Jaekel 1899 emend. Paul 1968

Definition. Rhombifera with endothecal pore-structures (pectinirhombs and cryptorhombs) composed of dichopores, with theca composed of a small number of plates arranged in three to five circlets, pore-structures only developed across certain sutures, true stem throughout life.

This order contains two superfamilies, the Glyptocystitida and the Hemicosmitida. The family Polycosmitidae is assigned to the Hemicosmitida, otherwise the classification is as given in Kesling 1963, 1968.

ORDER FISTULIPORITA Paul 1968

Definition. Rhombifera with exothecal pore-structures (humatirhombs) composed of fistulipores, with theca composed of a large number of plates which may be added during growth and are randomly arranged, pore-structures developed across all possible sutures, true stem lost in adult or possibly totally absent in rare examples.

This order contains one superfamily, the Caryocystitida. Detailed classification as in Kesling 1963, 1968 except that the family Stichocystidae is added. Kesling's superfamily Polycosmitida thus becomes defunct.

Even this classification, which is more complex than previous classifications, may oversimplify cystoid evolution. In particular the relationship between the two rhombiferan orders is more assumed than real. The only character unique to the two orders is the presence of rhombs. However fistulipores could not have evolved from dichopores nor vice versa. Rhombic structures or ornament may develop in any animal or plant group with a tesselated pavement of polygonal units. Rhombs can be recognized in most classes of echinoderms, in fish with heavily armoured bodies, in tortoiseshell scutes, even in some calcareous algae. The rhombic outline is a geometrical result of the mode of growth of closely fitting polygons and has no other significance. The presence of respiratory rhombs in the Dichoporita and Fistuliporita is due to parallel or convergent evolution and, in the absence of other shared characteristics, implies no particularly close relationship.

APPENDIX 1

List of species with exothecal pore-structures examined in this study.

Class RHOMBIFERA Müller	*Type of pore-structure*	
Order FISTULIPORITA Paul	Humatirhombs	
Superfamily CARYOCYSTITIDA	Fistulipores	Rhombs
Family CARYOCYSTITIDAE		
Lophotocystis granatum (Wahl.)	simple	simple
L. malaisei (Regnéll)	„	„
L. angustiporus (Regnéll)	„	„
L. sp. nov. (Haverfordwest, Wales)	„	„
L. araneus (Schlotheim)	„	complex
L. sp. (Skålberget, Sweden)	„	„
Heliocrinites ovalis (Angelin)	compound	simple
H. guttaeformis Regnéll	„	„
H. stellatus Regnéll	„	„
H. balticus Eichwald	„	„
H. sp. nov. (Rhiwlas, Wales)	„	„
Caryocystites dubia Angelin (= *C. angelini* Auctt.)	„	„
C. lagenalis Regnéll	„	complex
Family Echinosphaeritidae		
Echinosphaerites aurantium (Gyll.)	compound	simple
E. aurantium suecicus Jaekel	„	„
E. aurantium americanum Bassler	„	„
E. arachnoides Forbes	„	„
Family Ulrichocystidae		
Ulrichocystis eximia Bassler	simple	„
Class Diploporita Müller		
Superfamily Sphaeronitida		
Family Sphaeronitidae	Pore-structures	
Sphaeronites pomum (Gyll.)	Diplopores s.s.	
S. sp. nov. (Råbäck, Sweden)	„	
S. globulus (Angelin)	„	
S. sp. nov. (Skålberget, Sweden)	„	
S. litchi (Forbes)	„	
S. pyriformis (Forbes)	„	
S. sp. (Glyn Ceiriog, Wales)	„	
Haplosphaeronis oblonga (Angelin)	„	
H. kiaeri Jaekel	„	
H. sp. nov. (Haverfordwest, Wales)	„	
Eucystis barrendena Haeckel	„	
E. flavus (Barrande)	„	

E. munitus (Forbes)	Diplopores s.s.
E. quadrangularis Regnéll	„
E. angelini Regnéll	„
E. raripunctata Angelin	„
Archegocystis stellulifera (Salter)	„
'*Sphaeronis*' *dalecarlicus* Angelin	„
'*Sphaeronis*' *punctatus* Forbes	„
Family Holocystitidae	
Holocystites cylindricus (Hall)	Humatipores
H. alternatus (Hall)	„
H. abnormis Hall	„
H. scutellatus Hall	„
Pentacystis simplex Paul	„
P. wykoffi (Miller)	„
P. sphaeroidalis (Miller & Gurley)	„
Trematocystis globosus (Miller)	„
T. rotundus (Miller)	„
Pustulocystis pentax Paul	„
P. ornatissimus (Miller)	„
Brightonicystis gregarius Paul	„
Superfamily Aristocystitida	
Family Aristocystitidae	
Aristocystites bohemicus Barrande	Diplopores
A. subcylindricus Barrande	„
A. sp. (Knock, England)	„
Triamara tumida (Miller)	„
T. ventricosa (Miller)	„
T. multiporata Paul	„
T. laevis Paul	„
T. sp. (Big Creek, Indiana, U.S.A.)	„
Sinocystis loczyi Reed	„
'*Sphaeronis*' *shihtienensis* Reed	„
Superfamily Glyptosphaeritida	
Family Glyptosphaeritidae	
Glyptosphaerites leuchtenbergi (Volborth)	„
Family Dactylocystidae	
?*Revalocystis kearsargensis* (Stauffer)	„
Family Gomphocystitidae	
Gomphocystites indianensis Miller	„
Family Protocrinitidae	
?*Regnellicystis* sp. (Rye Cove, Virginia, U.S.A.)	„

APPENDIX 2

Formal definitions of *Lophotocystis* nov. and *Heliocrinites* s.s.:

Genus *Lophotocystis* nov. (Lophotos, Gr. crested).

Type species. Echinosphaerites granatum Wahlenberg.

Definition. A genus of Caryocystitidae with globular theca, fifty to several hundred thecal plates not folded about rhomb axes; humatirhombs with simple fistulipores raised in distinct ridges on external surface of plates.

Genus *Heliocrinites* Eichwald 1840.

Type species. Echinosphaerites balticum Eichwald.

Definition. A genus of Caryocystitidae with oval to globular theca, fifty to several hundred plates usually folded about rhomb axes to produce a surface ornament of triangular depressions; humatirhombs with compound fistulipores almost completely or totally buried within plates.

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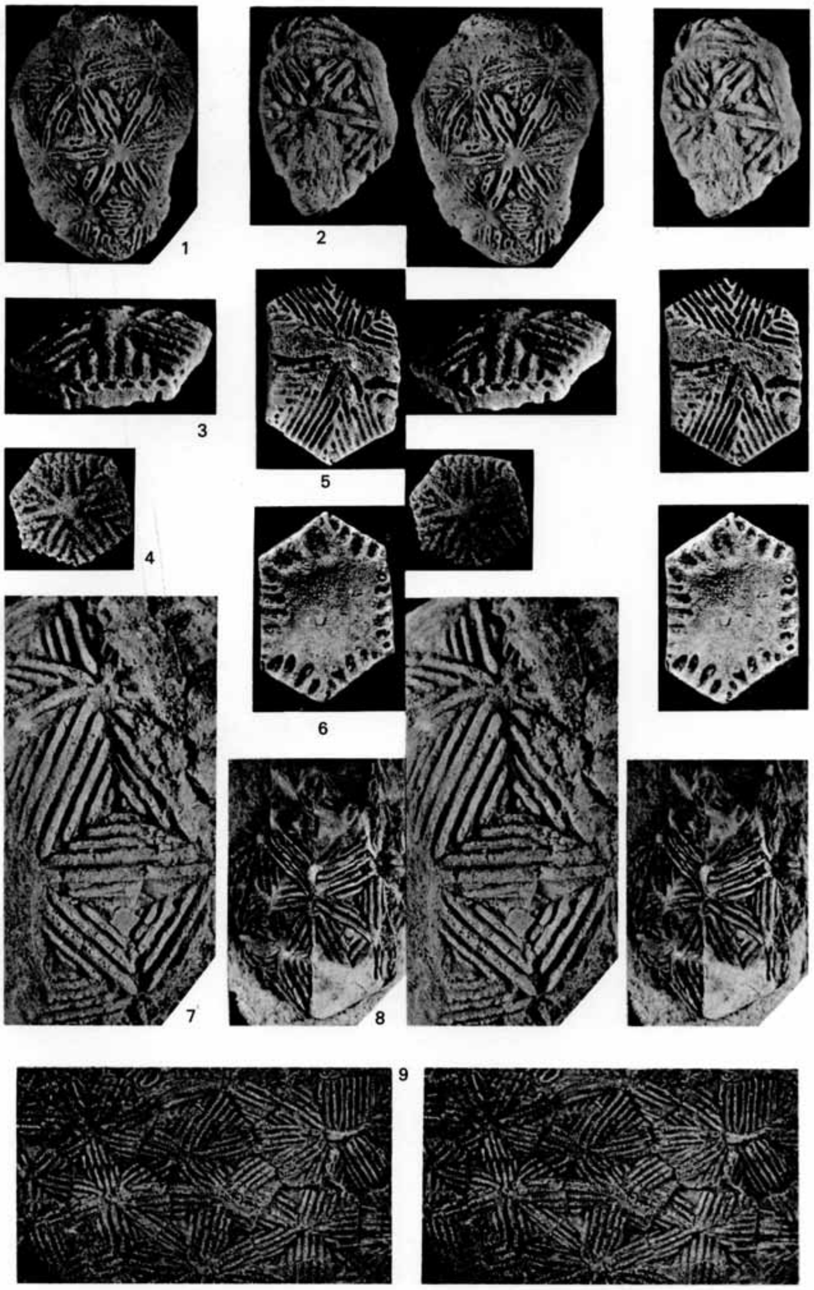

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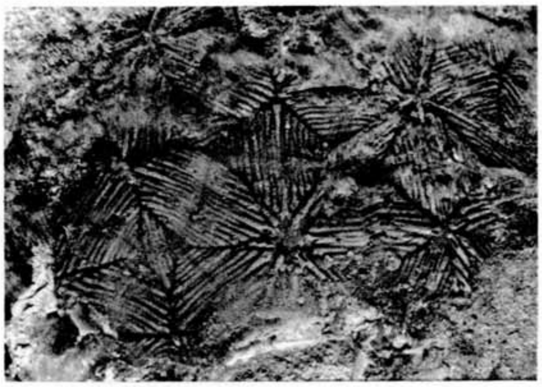
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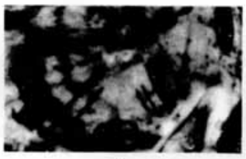

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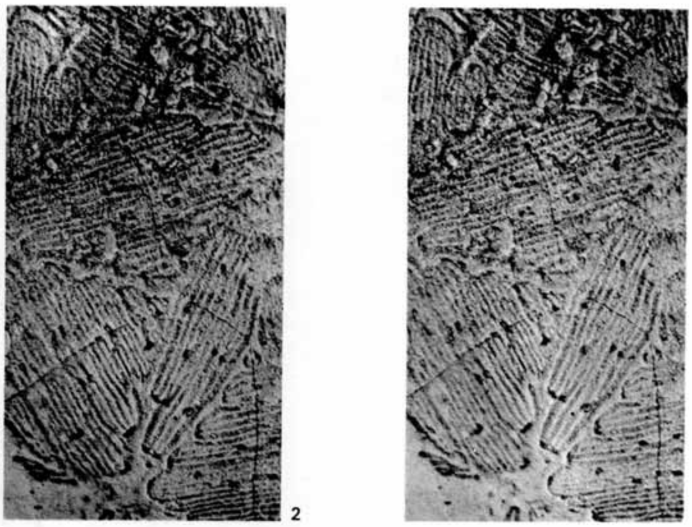

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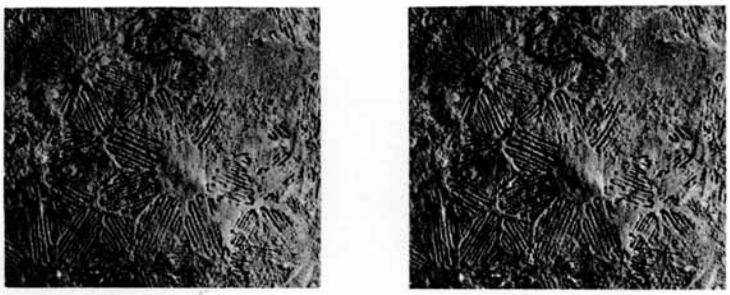

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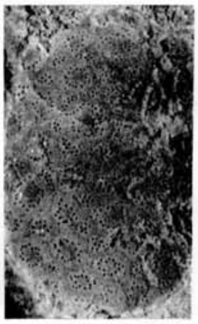

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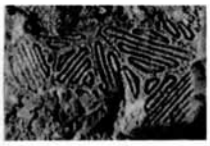

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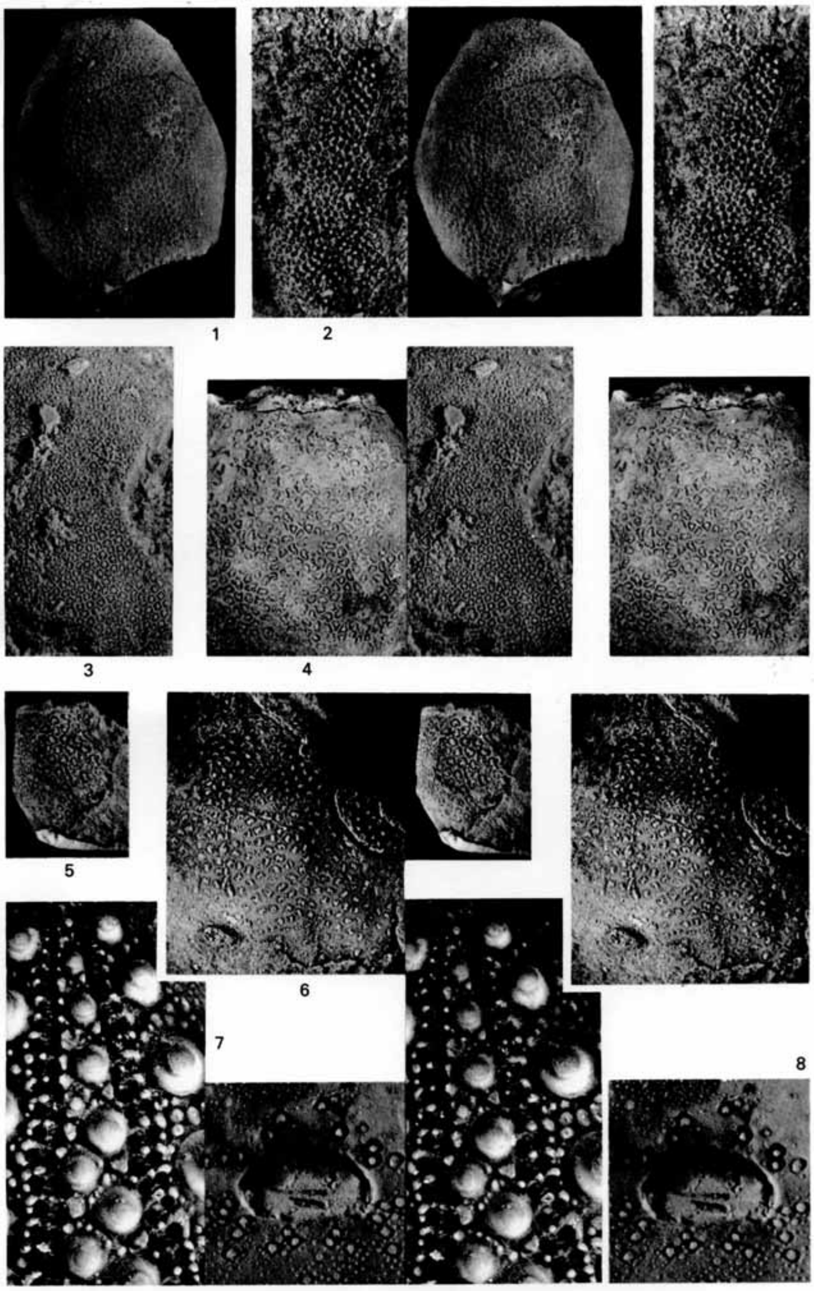

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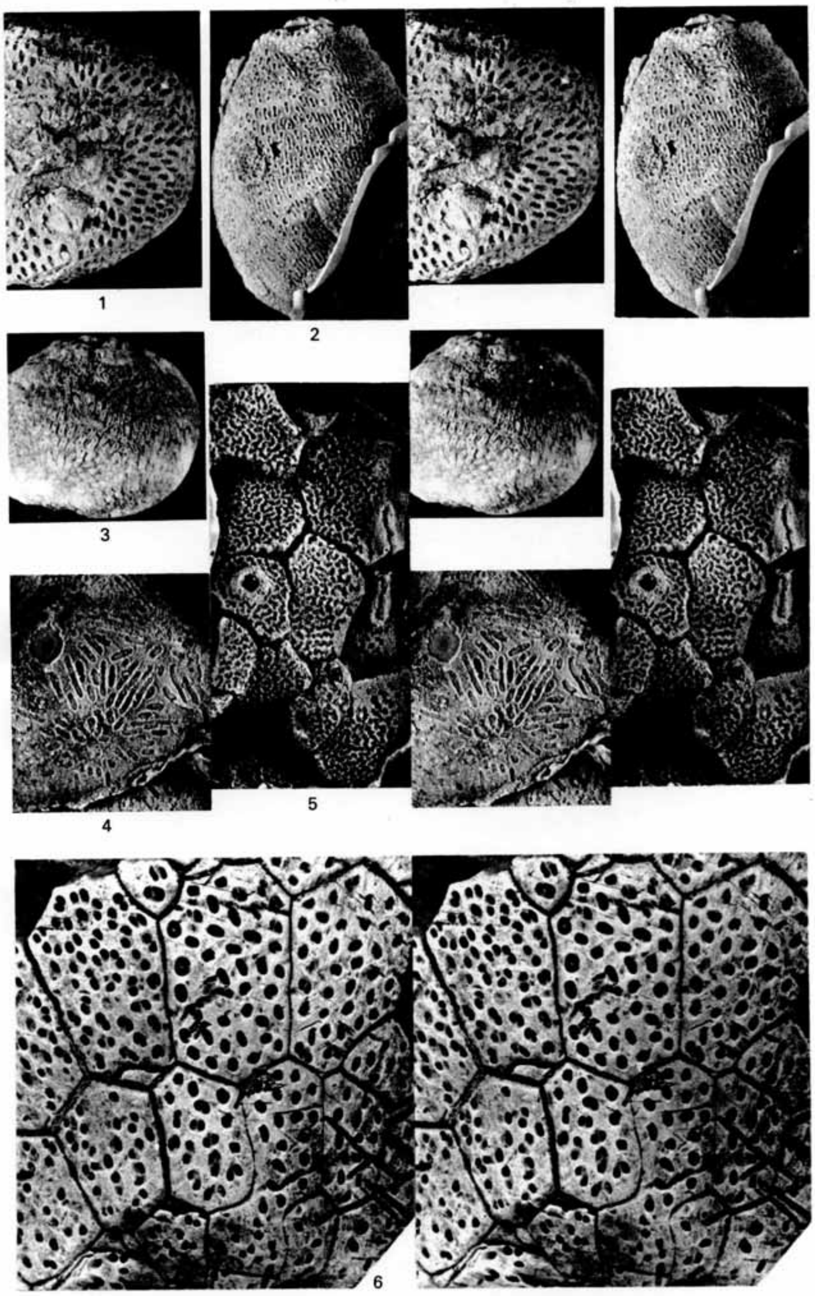

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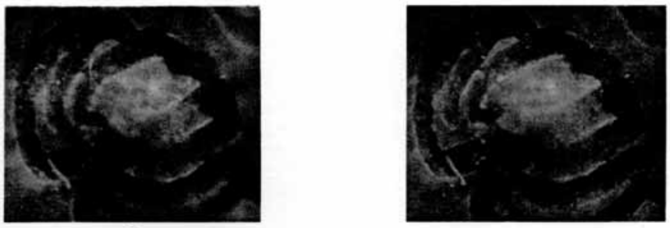

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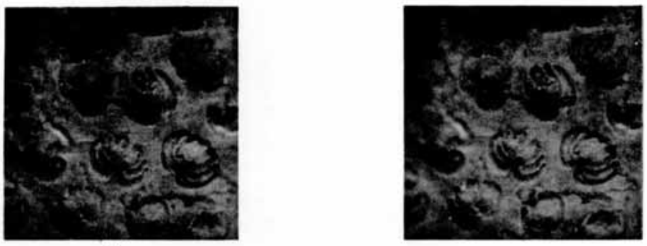

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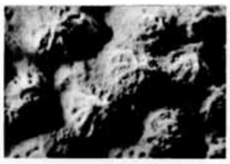

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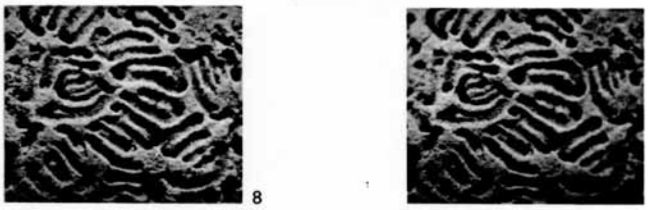

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