MORPHOLOGY AND FUNCTION OF DICHOPORITE PORE-STRUCTURES IN CYSTOIDS

by C. R. C. PAUL

ABSTRACT. The cystoids, a diverse and artificial group of extinct Palaeozoic echinoderms, are characterized by the possession of pore-structures developed in the thecal wall and composed of thecal canals which open in thecal pores. Thecal canals may occur singly to form dipores, or in sets perpendicular to plate sutures to form rhombs. Five basic types of pore-structure are recognised: *pectinirhombs*, *cryptorhombs*, *humatirhombs*, *humatipores*, and *diplopores*. The first two are composed of dichopores, thecal canals which connect external pores and through which sea-water flowed in life. The dichopores of pectinirhombs open in slits; those of cryptorhombs open in pores, one of which is sieve-like. Pectinirhombs and cryptorhombs are characteristic of, and confined to, the super-families Glyptocystitida and Hemicosmitida respectively; humatirhombs characterize the superfamily Caryocystitida. Five types of pectinirhombs and one type of cryptorhomb are recognized.

Pectinirhombs and cryptorhombs agree closely with the paradigm of an exchange system and were respiratory structures. Evolution of pectinirhombs proceeded from less to more efficient types independently in all families of Glyptocystitida. The three rhombiferan superfamilies probably acquired their rhombs independently. Rhombifera and Diploporita are regarded as separate classes. The former contains two Orders: Dichoporita and Fistuliporita.

THE cystoids, an extinct group of Palaeozoic echinoderms, are characterized, inter alia, by the possession of pore-structures in the calcareous wall of the theca. Although various authors from Müller (1854) to Regnéll (1945) and Kesling (1963) have emphasized the importance of these pore-structures in cystoid morphology and taxonomy, they have not been the subject of complete morphological or functional analyses. Stainbrook (1941) and Sinclair (1948) considered the function of pectinirhombs in one genus each and Delpey (1942) the function of pectinirhombs and cryptorhombs. The last-named author suggested that pectinirhombs and cryptorhombs were balancing organs but most authors have accepted a respiratory function for all pore-structures. Functionally all cystoid pore-structures fall into two groups: dichoporite and non-dichoporite. This paper deals with the dichoporite pore-structures (pectinirhombs and cryptorhombs) after a brief review of the morphology of the five basic types of pore-structure recognized. Function in non-dichoporite pore-structures will be the subject of a future paper.

The cystoids of this account correspond to the class Cystoidea of Kesling (1963) but only to the subclass Hydrophoridea of Regnéll (1945). The hydrospires of blastoids and epispires of certain eocrinoids and crinoids are not considered nor are the peculiar pore-structures of paracrinoids like *Comarocystites* Billings. Knowledge of the morphology of cystoid pore-structures has grown piecemeal, virtually every researcher adding some contribution. One result of this is a rather imprecise terminology often related to ill-defined concepts. In reviewing the morphology of pore-structures an attempt has been made to introduce a systematic terminology and to define the concepts upon which this terminology is based. Previous usage has been followed as far as possible. Throughout this account the classification is that of Kesling (1963) unless otherwise stated.

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MORPHOLOGY OF CYSTOID PORE-STRUCTURES

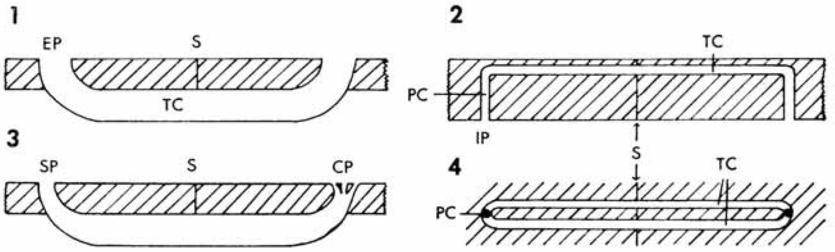
A. GENERAL

The term *pore-structure* embraces all the structures dealt with. All pore-structures are composed of thecal canals and thecal pores. These have not always been distinguished from each other in the past but Kesling (1963) noted that two separate concepts are involved in the terms pore and canal.

Thecal pores are perforations in the surfaces of the thecal wall. They cannot have a separate existence without the thecal canals to which they give rise, i.e. thecal pores bear the same relationship to thecal canals that the two ends of a stick do to the stick. Pores in the external surface of the thecal wall are *external pores* (text-fig. 1) and correspondingly, *internal pores* (text-fig. 2) are developed in the internal surface of the thecal wall. External pores may be slit-like, and are then referred to as *slits* (text-fig. 12), or they may be either *simple* or sieve-like (text-figs. 3, 20). When simple a single thecal canal terminates in a single pore, when sieve-like the canal divides near the external surface of the thecal wall and opens in a cluster of small pores. Apparently internal pores are always simple and circular in cross-section.

Thecal canals are tubular structures which connect, or terminate in, thecal pores. Thecal canals are analogous to the entire stick plus its ends. The portions of thecal canals which are approximately perpendicular to the surface of the thecal wall are termed *perpendicular canals* (text-fig. 2) and those tangential to the surface, *tangential canals* (text-fig. 2). All thecal canals are composed of one or more tangential canals which connect a pair of perpendicular canals and they all commence and terminate in two thecal pores, both of which lie in the same surface of the thecal wall (with the possible exception of haplopores). Tangential canals may be incompletely calcified or uncalcified, i.e. made of soft tissue only as in diplopores, in which case only the pair of perpendicular canals is preserved in fossils. Thecal canals may be *compound* (text-fig. 4) when several tangential canals connect a pair of perpendicular canals, or *simple* (text-figs. 1, 2) when one tangential canal connects the perpendicular canals. Here thecal canals are considered as functional units rather than morphological units. Portions of canals composed entirely of soft tissue, as is the case with external papulae, are considered integral parts of the canal even though their former existence can only be inferred in fossils.

Previously two types of pore-structures have been recognized: 'pore rhombs' (or more simply and accurately, *rhombs*) and 'diplopores'. The latter term has been used in both a specialized and a generalized sense. The new term *dipore* is proposed to cover all types of pore-structures within the Diploporita and *diplopore* is restricted to one type of dipore following current usage.



TEXT-FIGS. 1–4. Thecal pores and thecal canals.

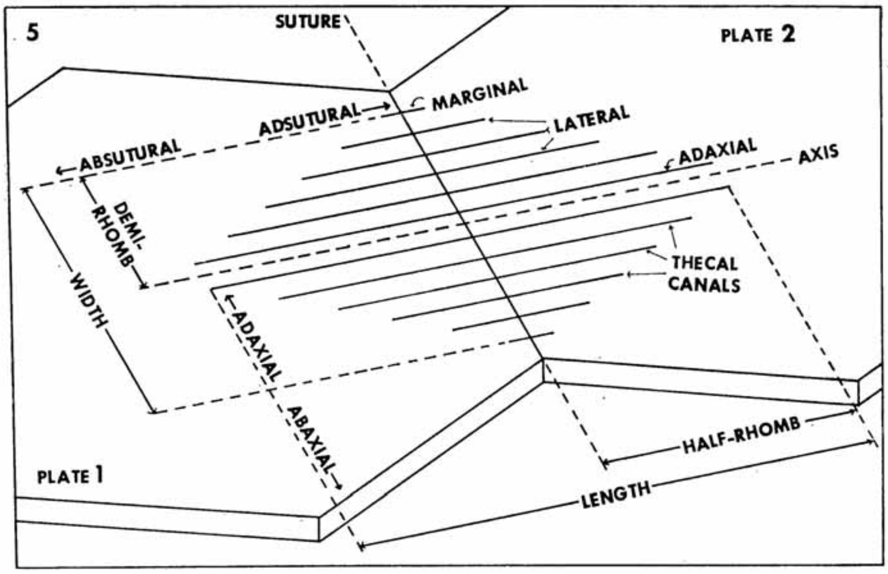
1. Diagrammatic longitudinal section through a pectinirhomb dichopore to show external pores.
2. Diagrammatic longitudinal section through a simple fistulipore to show internal pores.
3. Diagrammatic longitudinal section through a cryptorhomb dichopore to show simple and sieve-like external pores.
4. Diagrammatic plan view of a compound fistulipore with surface layer removed to show two perpendicular canals connected by a pair of tangential canals.

CP, sieve pore; EP, external pore; IP, internal pore; SP, simple pore; PC, perpendicular canal; TC, tangential canal; S, plate suture. In text-figs. 1–3 and all other figures unless otherwise stated, the external surface of the thecal wall is towards the top of the figure.

Rhombs (fig. 5) *may be defined as pore-structures composed of a set of thecal canals each of which arises in one thecal plate, crosses a plate suture and terminates in an adjacent plate, the whole set having a rhombic outline in plan view*. Rhombs have their thecal canals developed more or less perpendicular to the plate suture and were randomly orientated with respect to other features in the theca since plate sutures occur in almost all possible orientations. Rhombs are therefore orientated and described with respect to their sutures (text-fig. 5).

The outline of a rhomb may be described as indicated in text-figs. 6–11. Rhombs may be composed of two types of thecal canal. Jaekel (1899) proposed the term *dichopore* for the canals (and their terminal pores) of the Rhombifera, Jaekel's Dichoporita. Subsequently dichopore has been restricted to the canals of pectinirhombs. A fundamental difference exists between canals which terminate in internal pores and those with external pores. No complete canal can have both. Here the term dichopore is restricted to rhomb canals with external pores (text-figs. 1, 3) and the new term *fistulipore* (fistula = canal) is proposed for rhomb canals with internal pores (text-figs. 2, 4). There are two types of rhombs composed of dichopores and a third composed of fistulipores. *Pectinirhombs* (text-figs. 15–19) are composed of dichopores which open in slits, whereas *cryptorhombs* (text-fig. 20) are composed of dichopores which open in pores. *Humatirhombs* are rhombs composed of fistulipores.

Dipores may be defined as pore-structures composed of a single thecal canal randomly orientated with respect to the thecal plates. Dipores are composed of one type of thecal canal, which resembles a fistulipore in connecting internal pores but differs in rarely crossing plate sutures. There were two types of dipore. A *diplopore* is a dipore composed of a simple thecal canal in which the tangential portion was uncalcified, i.e. the tangential portion formed a papula in life and only the two perpendicular portions of the canal are found fossil. *Humatipores* are dipores composed of compound thecal canals in which all the tangential canals were fully calcified.

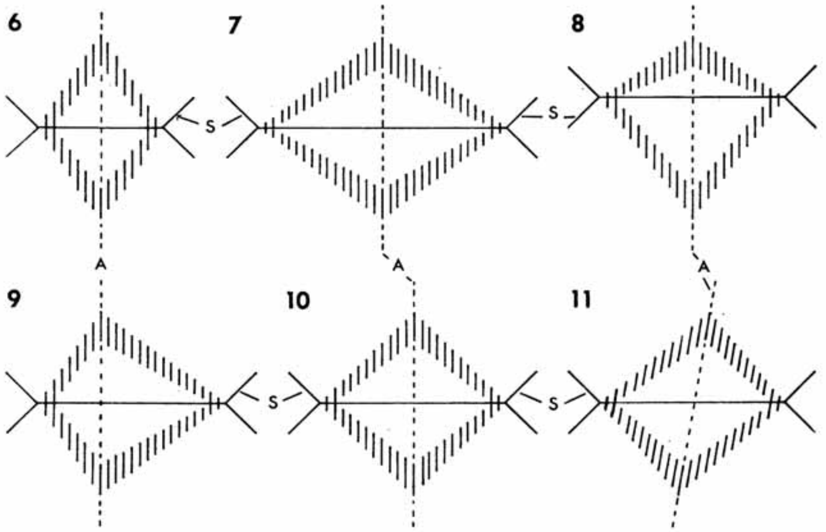


TEXT-FIG. 5. Diagram of the principal features of a rhomb. Every rhomb is developed in two thecal plates (1 and 2). A plate *suture* divides the rhomb into two *half-rhombs* and the *width* is measured along it. Perpendicular to the suture lies the rhomb *axis* which divides the rhomb into two *demi-rhombs* and along which the *length* is measured. Thecal canals adjacent to the axis are *adaxial*, those away from the axis *lateral* and the outermost one or two are *marginal*. Positions and directions (*adsutural*, *adaxial*, etc.) are defined with respect to the plate suture and the rhomb axis.

These five major types of pore-structure are recognized: pectinirhombs, cryptorhombs, humatirhombs, diplopores, and humatipores. The first two differ fundamentally from the other three in that they are composed of thecal canals (dichopores) which connect external pores. Hudson (1911, 1915) recognized this distinction and described dichoporite pore-structures as endothecal and non-dichoporite as exothecal. These general terms may be applied to all types of pore-structures in primitive echinoderms.

A sixth type of pore-structure, haplopores, has been attributed to cystoids. Haplopores, as here understood, consist of a single, blind (in life), perpendicular canal which opens in a single internal pore. No true haplopores have been observed in any cystoids examined by the writer but this does not imply that none ever existed.

The first information on the structure of the thecal wall, which is intimately related to the morphology of pore-structures, was given by Barrande (1887). Barrande maintained that there were three layers to the thecal wall and that the outer and inner layers sealed the thecal canals which were confined to the middle layer. Several subsequent authors have described an epithecal layer sealing canals externally but the present writer has found no evidence to support Barrande's statement. Barrande described the surfaces of his layers (as preserved in moulds in most cases) and not cross-sections. All subsequent authors also described surfaces not sections. When the external surface was without pores Barrande claimed an epithecal layer was present; when pores were visible on the external surface he claimed the epitheca was eroded before preservation. However, external surfaces with and without pores may result from the type of canal developed. A rhombiferan with dichopores will have pores in the external surface but one with fistulipores will not *unless* the outer walls of the tangential canals are eroded.

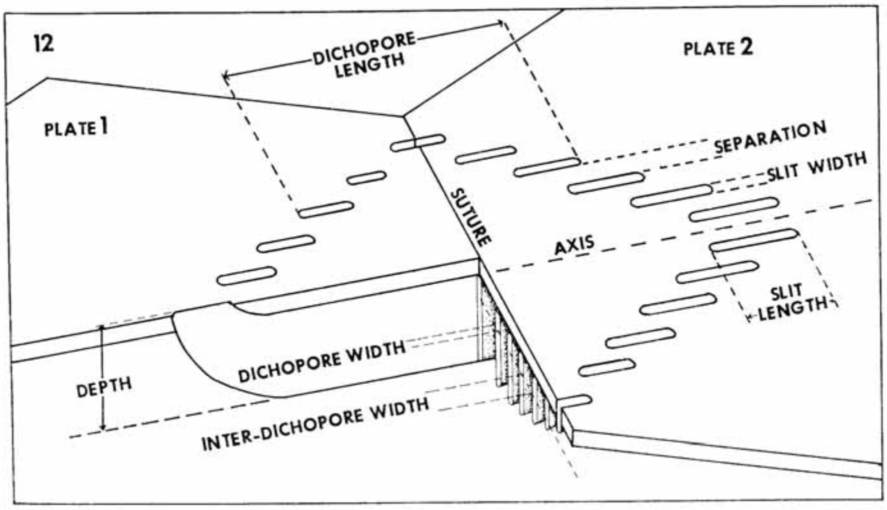


TEXT-FIGS. 6–11. Outlines of rhombs.

Rhombs in which the length exceeds the width are *compressed* (6); the converse, *depressed* (7). Rhombs with unequal half-rhombs are *unequal* (8); the converse, *equal* (6, 7). Rhombs with unequal demi-rhombs are *asymmetrical* (9); the converse, *symmetrical* (6, 7, 8). These features occur in combination. A symmetrical, equal rhomb which is neither depressed nor compressed is *ideal* (10). Rhombs with thecal canals oblique to the suture are *oblique* (11).

A, rhomb axis (an imaginary line); S, plate suture. Text-figs. 6–11 represent disjunct pectinirhombs in plan view but the terms may be applied to all types of rhombs. Rhombs which are 'depressed' into the theca may be termed *sunken* to avoid confusion with those with depressed outlines.

A similar distinction may be made between diplopores, with tangential canals which were of soft tissue and never preserved, and humatipores with fully calcified tangential canals. The description of sealed dichopores in cryptorhombs may possibly result from post-mortem calcification. However, it is more probably due to a misinterpretation of sieve pores as a progressive sealing of the canals. Finally sealed canals do not necessarily indicate the presence of a separate layer sealing them. All thin sections prepared by the author lack any indication of separate layers sealing the canals but the thecal wall is definitely not uniform in structure.



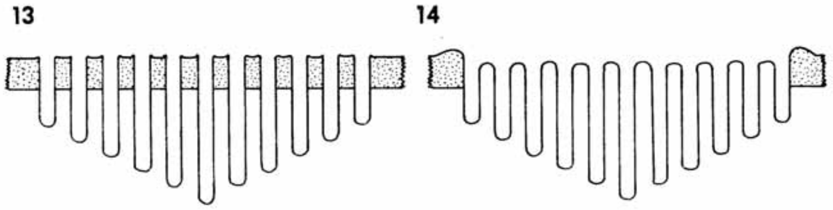
TEXT-FIG. 12. Diagram to illustrate the principal features and measurements of pectinirhomb dichopores and slits. Dichopore and slit lengths and widths are measured in the same direction as rhomb lengths and widths. In this figure and text-figs. 15–20 the external surface of the thecal wall faces the top of the figures and part of the rhomb is removed to show internal features.

B. THE MORPHOLOGY OF PECTINIRHOMBS

Pectinirhombs are rhombs composed of dichopores which open externally in slits (text-fig. 12). The term pectinirhomb was first used by E. Forbes (1848, as 'pectinated rhomb') for the rhombs of the superfamily Glyptocystitida. The various features of pectinirhomb morphology will now be described.

The pores (text-figs. 1, 12) of pectinirhombs are slits. The principal measurements of slits and dichopores are shown in text-fig. 12. There may be a single *conjunct* slit along the entire length of a dichopore (text-figs. 15, 17). Alternatively the dichopore may open in a pair of *disjunct* slits, one at each end (text-figs. 16, 18). One disjunct slit is generally longer than the other and all the longer slits occur in one half-rhomb, a fact first noted by Stainbrook (1941, p. 93) for the pectinirhombs of *Strobilocystites* White. The slit lengths are also approximately proportional to the length of the dichopores to which they give rise and thus marginal slit lengths are less than adaxial slit lengths (text-fig. 32).

The canals (text-figs. 1, 12) of pectinirhombs are dichopores. Pectinirhomb dichopores are *discrete* (text-fig. 13) when each dichopore is a separate entity and the inter-dichopore space is covered by a thin strip of unmodified thecal plate. The inter-dichopore spaces may vary in width in a pectinirhomb with discrete dichopores, and the dichopores open externally in slits each provided with an individual *slit rim*. *Confluent dichopores* (text-fig. 14) are dichopores in which the walls of adjacent dichopores are confluent and the inter-dichopore spaces are covered with dichopore walls. In such cases the inter-dichopore widths are constant and equal to the dichopore widths. Confluent dichopores open in slits grouped into *vestibules* (text-figs. 17, 18) and collectively surrounded by a *vestibule rim*. In disjunct pectinirhombs with confluent dichopores one half-rhomb has a complete *closed rim* which surrounds the slits on both the ab- and ad-sutural sides. The other half-rhomb has an *open rim* on the ab-sutural side only (text-fig. 18). A number of types of pectinirhomb may therefore be recognized on the character of the slits and dichopores. Five types are in fact recognized:

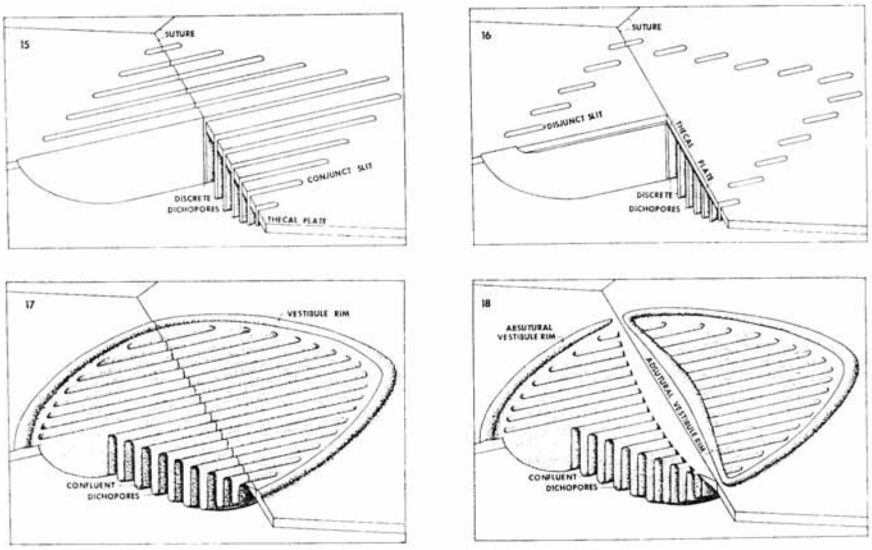


TEXT-FIGS. 13–14. Discrete and confluent dichopores.
13. Discrete. Each dichopore is separated from adjacent dichopores by a strip of unmodified thecal plate.
14. Confluent. The walls of adjacent dichopores are continuous and the pectinirhomb is made of isoclinal folds. Both figures represent sutural views of conjunct pectinirhombs.

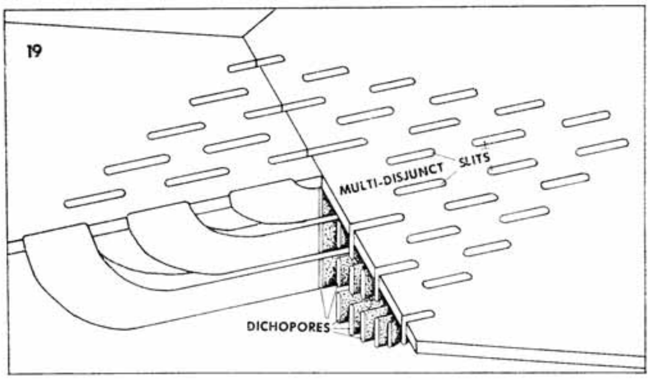
1. Conjunct pectinirhombs with discrete dichopores (text-fig. 15)
2. Disjunct ,, ,, ,, ,, (text-fig. 16)
3. Conjunct ,, ,, confluent ,, (text-fig. 17)
4. Disjunct ,, ,, ,, ,, (text-fig. 18)
5. Multi-disjunct pectinirhombs (text-fig. 19)

The structure of multi-disjunct pectinirhombs is not yet fully known.

Conjunct pectinirhombs are much less common than disjunct pectinirhombs and discrete dichopores are only found in Ordovician genera. Conjunct pectinirhombs with discrete dichopores are only found in the genus *Cheirocrinus s.l.*: seven species have this type of pectinirhomb. Conjunct pectinirhombs with confluent dichopores occur in the genera *Homocystites* Barrande, *Pleurocystites* Billings, and *Regulaecystis* Dehm. Disjunct pectinirhombs with discrete dichopores occur in the Cheirocrinidae, Rhombiferidae, Cystoblastidae, and Echinoencrinitinae. The Scoliocystinae, Callocystitidae, and *Praepleurocystis* Paul have disjunct pectinirhombs with confluent dichopores. Multi-disjunct pectinirhombs occur in two Upper Ordovician species of *Cheirocrinus s.l.*, *C. jamesi* (McCoy), and *C. interruptus* (Jaekel). The transition from discrete to confluent dichopores seems to have been gradual and to have taken place independently in several



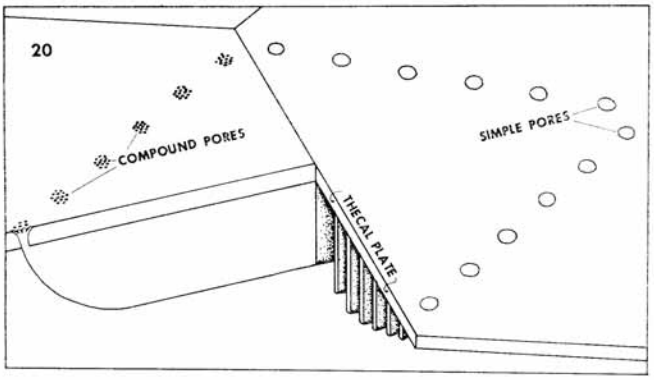
TEXT-FIGS. 15–18. Diagram to illustrate the morphology of pectinirhombs.
15. Conjunct with discrete dichopores.
16. Disjunct with discrete dichopores.
17. Conjunct with confluent dichopores.
18. Disjunct with confluent dichopores.



TEXT-FIG. 19. Diagram to illustrate the interpretation of the morphology of a multidisjunct pectinirhomb.

families. In particular the pectinirhombs of *Glyptocystites spp.* are intermediate in character. Isolated demi-rhombs only occur in species which have pectinirhombs with discrete dichopores.

All five types of pectinirhomb are confined to and characteristic of the superfamily Glyptocystitida. Members of this superfamily have thecae composed of a definite number of plates arranged in five circlets. There are 4 basals (BB), 5 infra-laterals (ILL), 5 laterals (LL), 4, 5, or 6 radials (RR), and 7 orals (OO). The plates are numbered clockwise around the theca from the left of the periproct. The positions of pectinirhombs on the theca may be denoted by citing the two plates in which the half-rhombs are developed. Thus pectinirhomb L4:R3 has one half-rhomb in L4 and the other in R3. Pectinirhombs are only developed across certain sutures and some positions are occupied more frequently than others. No orals ever bear pectinirhombs and there is no marked preference for pectinirhombs to develop across sutures between different circlets (inter-circlet sutures) as opposed to sutures between plates of the same circlet (intra-circlet sutures).



TEXT-FIG. 20. Diagram of the morphology of a cryptorhomb.

C. THE MORPHOLOGY OF CRYPTORHOMBS

Cryptorhombs are rhombs composed of dichopores which open externally in pores (text-fig. 20). The term cryptorhomb is proposed because the entire length of the tangential part of all the dichopores is hidden from external view so that in many species the rhombs are inconspicuous.

The pores of cryptorhombs (text-figs. 3, 20) may be simple or sieve-like (compound pores of text-fig. 20). In almost all cases examined each dichopore opened in a sieve-pore at one end and a simple pore at the other. In all complete cryptorhombs one half-rhomb has sieve-pores only and the other has simple pores only. A few dichopores may be reversed with respect to the others in some incomplete cryptorhombs. The dichotomous branching of the perpendicular canal which opens in a sieve-pore may proceed evenly in all branches to produce clusters of 2, 4, 8, 16, or 32 individual pores, or unevenly, producing intermediate numbers of individual pores. The individual pores may be circular, oval, or dumb-bell shaped: this depends on the stage of branching. Individual pores are usually surrounded by *pore rims* and may be set in shallow depressions or raised in rounded tubercles. Within a sieve-pore, individual pores may be arranged randomly or in rows. Simple pores may be developed on tubercles, or in or beside ridges on the plates. Nearly all simple pores have strongly developed rims.

Cryptorhomb dichopores (text-figs. 3, 20) resemble discrete dichopores of pectinirhombs in the sense that the inter-dichopore spaces are covered by unmodified thecal plate. Dichopores may be evenly developed throughout a cryptorhomb, which then has a regular rhombic outline and is *complete*. *Incomplete cryptorhombs* have few, irregularly spaced, dichopores and irregular outlines. Cryptorhomb dichopores may be weakly calcified within the theca.

Only one type of cryptorhomb (text-fig. 20), which corresponds in structure to a disjunct pectinirhomb with discrete dichopores, has been recognized. However, cryptorhombs may be complete or incomplete and the unusual rhombs of *Polycosmites* Jaekel may represent a second type of cryptorhomb, corresponding to multi-disjunct pectinirhombs in structure. Unfortunately no specimens are available.

Cryptorhombs are confined to and characteristic of the superfamily Hemicosmitida, members of which have thecae composed of a definite number of plates arranged in 3 or 4 circlets. These are designated by the same symbols as in the Glyptocystitida but the arrangement of plates is less constant. There may be 3 or 4 basals, 6 or 10 infra-laterals, 8 or 9 laterals, and, in the Hemicosmitidae, 9 radials. In the Caryocrinitidae the oral area is covered by a special 'tegmen' which apparently replaces the radial circlet. Cryptorhombs are not developed in tegminals but may be present in all other plates. In many species complete cryptorhombs are predominantly developed across inter-circlet sutures while incomplete cryptorhombs are confined to intra-circlet sutures of the lateral and infra-lateral circlets. There are thus rings of complete cryptorhombs which correspond to the inter-circlet sutures. Furthermore the arrangement of the pores of complete cryptorhombs is constant (text-fig. 21). In the BB:ILL ring sieve-pores occur in the basals; in the ILL:LL ring they are in the laterals; in the LL:RR ring (Hemicosmitidae only) they are in the radials. Incomplete cryptorhombs complicate this arrangement but functionally they are of minor importance.

THE FUNCTION OF DICHOPORITE PORE-STRUCTURES

A. THE BASIS OF FUNCTIONAL INTERPRETATIONS

The principles on which this functional analysis of cystoid pore-structures has been based were outlined by Rudwick (1964*b*) but a brief résumé will now be given. It is necessary first to assume that any organ under investigation was functional and to suggest a function for it. This assumption may be tested in fossils only if it is possible to predict a structure which would serve the function efficiently and which is directly comparable with the preserved hard parts of the fossil. This prediction has been termed a *paradigm* by Rudwick (1960) and is assumed to have maximum efficiency within the limits imposed by the materials of which the fossil structure is made. A close morphological similarity between the fossil structure and the paradigm would be expected if the former functioned efficiently. Where such similarity is found it is probable that the postulated function was served in life but this cannot be said to have been proved absolutely.

Three points arise in this connection. 1. The preserved hard parts of the fossil did not constitute the entire structure in life, i.e. at the time of functioning. It is necessary to reconstruct the unpreserved soft parts and in doing so it is assumed that the soft (unpreserved) parts of the fossil bore the same relationship to the preserved hard parts that the soft parts of related living organisms do to their hard parts. For example, Sinclair's (1948, p. 306) suggestion that the dichopores of the pectinirhombs of *Glyptocystites* were lined with ciliated epithelium may be accepted since dichopores are invaginations of the external surface of the thecal wall and nearly all modern echinoderms have an external ciliated epithelium.

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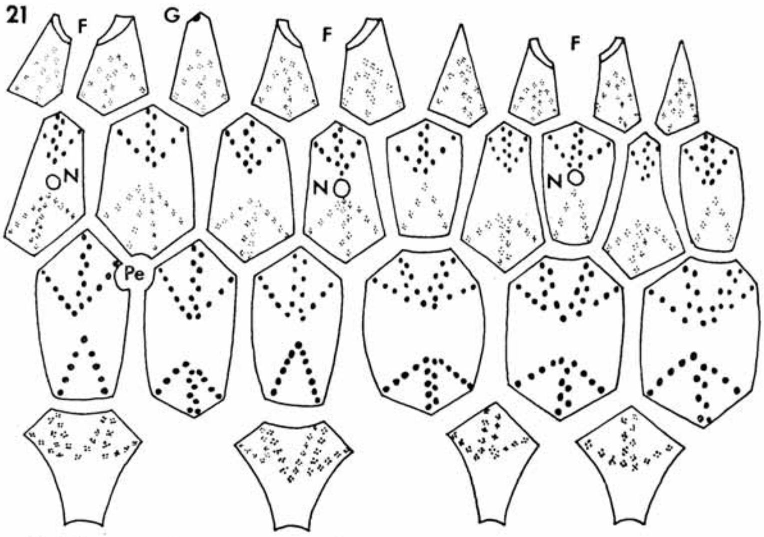


TEXT-FIG. 21. Diagrammatic representation of the distribution of simple and sieve-pores in the theca of *Hemicosmites extraneus* Eichwald. Only complete cryptorhombs are shown. F, arm facet; G, gonopore; N, node in lateral plates; Pe, periproct. Based on RM. Ec5381.

2. The second assumption that the fossil structure functioned efficiently is only a working assumption and may be modified to fit any case. To test any postulated function a close morphological similarity between the fossil structure and the paradigm is sought. If it is found, the fossil structure could have served the function efficiently. If not, it cannot be concluded that the structure did not serve the postulated function but only that it was inefficient if it did.

The early functional morphologists evolved as an empirical law the idea that any given organ is only developed to the minimum efficiency conducive with survival (*minimum survival efficiency*) and not the maximum potential efficiency. A low relative efficiency in an organ may result from a low minimum survival efficiency, perhaps due to a lack of competition or low selective pressures. At present this is an hypothetical consideration since evaluation of minimum survival efficiencies in fossils is impossible and there is little information from living animals.

Any structure may form part of two (or more) functional systems, or may have two (or more) concomitant functions, each with different structural requirements. Such structures may become a compromise between the ideal cases. If it is possible to suggest the two (or more) functions, it may become possible to test whether departure from one paradigm is due to approximation to another.

A low relative efficiency in one structure may be compensated for by a high efficiency elsewhere in the system. Equally minimum survival efficiency may be achieved by a few efficient organs or a large number of less efficient organs. Thus the second assumption that the fossil structure functioned efficiently is only a working assumption and considerable information on the functioning of a fossil structure may be gained even when there is not a close comparison with the paradigm.

3. There is always a danger of using teleological language in functional analyses since 'function' and 'purpose' are sometimes used synonymously. Yet no fossil ever evolved a structure to serve a purpose. To investigate the 'effect' of a structure need neither imply function nor purpose. Thus if a chance rock fall produces a narrow crack between two boulders through which the tide washes, the crack will prevent particles of a diameter greater than its width from passing between the boulders. The crack may be analysed in the same way as zigzag slits in brachiopods (Rudwick 1964*a*) or pectinirhomb slits (p. 715) and will be found to have the same effect. Since it was a chance rock fall which produced the crack there can be no purpose behind it nor does it serve any function. Rudwick (1964*a*) concluded that if zigzag slits in brachiopods were protective they could have served this function efficiently. That is: the effect of zigzag slits in brachiopods was to reduce the maximum size of particles that could enter (or leave) the mantle cavity for any given gape. If fossil brachiopods behaved in a similar manner to living brachiopods, those with zigzag slits were better 'protected' from large particles than those without (for any given gape). This may have been beneficial to these brachiopods. The 'function' of a structure may be considered as a 'beneficial effect' or better still as the most beneficial of its several effects. Although the purpose of functional analyses is to determine the 'function' of structures, it is the mode of functioning, i.e. the sum of the 'effects' of the detailed morphology of the structures, which is investigated. In the next sections attempts are made to interpret the effects of the detailed morphology of pectinirhombs and cryptorhombs, having assumed that they were functional in life.

B. THE GENERAL FEATURES OF EXCHANGE SYSTEMS

Most authors have accepted a respiratory function for all cystoid pore-structures. It is true that Delpey (1942) has suggested that pectinirhombs and cryptorhombs were balancing organs and Hyman (1955) among others, has suggested that some canals may have been nutritive. However, Sinclair (1948, pp. 307–8) has shown how unlikely it is that pectinirhombs or cryptorhombs were balancing organs. If thecal canals were nutritive, they would be evenly distributed or at least present in all thecal plates. This is not always the case with pectinirhombs, cryptorhombs, and diplopores but apparently it is the case with humatipores and humatirhombs. The most plausible function for pore-structures is respiration. If pore-structures were respiratory this was achieved by diffusion of oxygen and carbon dioxide and the pore-structures formed part of an exchange system. To test this hypothesis the paradigm of an exchange system must be examined.

The most essential feature of an exchange system is that only the 'exchange substance' or 'substances' should be exchanged; direct mixing must be prevented. There must be an *exchange surface* which allows the passage of the exchange substances while keeping the *donor* and *acceptor fluids* separate. In respiration the donor current for oxygen is also the acceptor current for carbon dioxide. Throughout donor current is used with reference to oxygen exchange. The rate of exchange will depend on the following factors:

1. *The area of the exchange surface*. The larger the area of the exchange surface, the greater the amount of exchange. The exchange surface should be as large as its strength will allow. Echinoderm skeletal calcite is a meshwork of calcite rods and soft tissue. Oxygen and carbon dioxide diffused not through the skeletal calcite but rather through the soft tissues. In echinoderms no more than half the area of an exchange surface was available for exchange because of this meshwork structure.

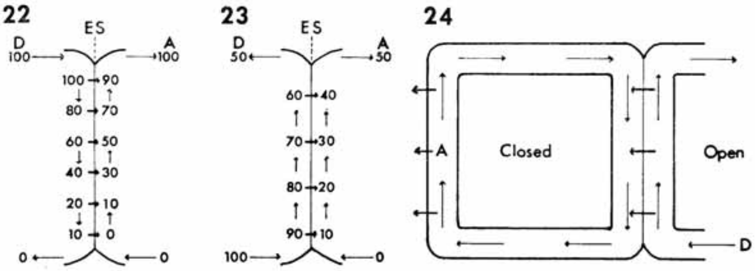
2. *The resistance to exchange of the exchange surface*. The resistance of an exchange surface will be proportional to its thickness and will depend on its nature. Although the walls of the thecal canals are heterogeneous only the soft tissue functioned as exchange surface. The thinner the walls are, the lower their resistance to exchange, and their strength, will be. The paramount function is to maintain separation between two fluids; rupture of the exchange surface could be fatal. The exchange surface may be as thin as is compatible with this stipulation.

3. *The concentration gradient across the exchange surface*. No exchange will take place unless there is a gradient across the exchange surface, i.e. unless the concentrations of the exchange substances in the donor and acceptor fluids are different. In a static system the exchange substances would flow from higher concentrations to lower until the concentrations were equal when flow would cease. It is therefore necessary to have a current system to maintain the gradient. The most efficient system is a counter-current system (text-fig. 22). In a closed (internal) current system (text-fig. 24) an animal has control over the composition of the fluids circulating. In an open current system (text-fig. 24) however, devices to prevent recirculation of exhausted fluids and choking by extraneous particles are desirable.

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 (with provisions to prevent recirculation and choking where necessary). This paradigm will fit any exchange system such as a radiator (heat exchange), a kidney (urea excretion) or a gill (oxygen and carbon dioxide diffusion). It has not been developed purely for the present analysis.

C. DETAILED FUNCTIONAL INTERPRETATIONS

From a purely functional point of view there are two types of cystoid pore-structures: dichoporite and non-dichoporite. In dichoporite pore-structures the current which flowed through the thecal canals was the donor current (for oxygen) and formed part of an open current system. The exchange surfaces were within the thecal cavity (endothecal) and protected from mechanical damage. In this section the detailed morphology of dichoporite pore-structures (pectinirhombs and cryptorhombs) will be compared with the paradigm of an exchange system and estimates of the relative efficiencies of the various types of rhomb made.



TEXT-FIGS. 22–4. Current and exchange systems.

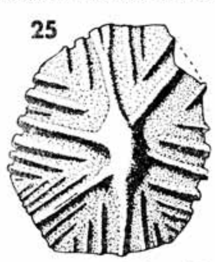
22. A counter-current system. In the ideal case all the exchange substance is transferred from the donor to the acceptor current.

23. A system with both currents flowing in the same direction. The maximum potential exchange is 50%.

24. Diagram to illustrate closed and open current systems. In the donor current there is a potential danger of the entrance becoming choked with particles and of re-circulation from the exit.

A, acceptor current; D, donor current; ES, exchange surface. Figures represent concentrations of exchange substance; heavy arrows represent exchange; light arrows represent current directions.

1. *The area of the exchange surface*. An increase in the area of the exchange surface means an increase in the amount of exchange. In the simplest hypothetical case exchange would take place through the thecal wall. Oxygen requirements would be proportional to the volume, and rate of exchange to the surface area, of the theca. Throughout growth oxygen requirements would increase faster than the amount of exchange, thus limiting maximum size. Evaginations or invaginations of the thecal wall can counteract this effect without involving a change of gross thecal shape. Both are found in the Glyptocystitida. *Macrocystella* Callaway, the earliest known form, has externally ridged thecal plates (text-fig. 25). The ridges are formed by folds in the plates and are evaginations of the thecal wall. They increased the area, and also the strength, of the plates which are uniformly very thin (0·1 mm. in *M. mariae* Callaway). Exchange probably took place through the entire area of the thecal wall in *Macrocystella*.



TEXT-FIG. 25. An isolated thecal plate of *Macrocystella mariae* Callaway to show external ridges which are effectively evaginations of the thecal wall.

Pectinirhombs first appear in *Cheirocrinus* Eichwald, a direct descendent of *Macrocystella* (see Paul 1968). Dichopores are invaginations of the thecal wall which allow a differentiation of function between the thicker thecal plates (rarely if ever less than 0·5 mm.) and the thin dichopore walls (usually 0·01 mm.). Exchange was probably restricted to the dichopore walls. These allow a large area for exchange within a small area of thecal surface. In *Cheirocrinus granulatus* (Jaekel) RM. Ec5384 (Pl. 135, figs. 3–5) one half-rhomb has a ratio of exchange area to thecal surface area of 7·84 : 1.

This ratio indicates the relative exchange efficiencies of different types of rhomb. In dichoporite rhombs the closer the spacing of the dichopores and the greater their length and depth, the higher the ratio will be. Available measurements of spacing are summarized in Table 1. Dichopore width (W) would probably be given by $W = 2 (h+l)$, where h = height of lining epithelial cells and l = length of cilia attached to the epithelial cells. At the limit of closeness of spacing the dichopores would be evenly spaced and the dichopore and inter-dichopore widths would be equal. This is the case in pectinirhombs with confluent dichopores and in complete cryptorhombs but not always in pectinirhombs with discrete dichopores nor in incomplete cryptorhombs. These latter were less efficient and tend to have higher values for spacing (Table 1).

Large pectinirhombs tend to have depressed outlines, a large number of dichopores, and to occur in large thecae. In any exchange system there is a distance within which all the exchange substance will be removed from the donor current as it flows along the exchange surface. This limits the length of a dichopore and the longest dichopores of both compressed and depressed pectinirhombs are about the same length (7–9 mm.). The exchange area of a pectinirhomb or cryptorhomb may be more efficiently increased by the addition of new dichopores than by the lengthening of existing dichopores. This may partly account for the tendency of large pectinirhombs to have depressed outlines (i.e. width greater than length). Maximum dichopore lengths in cryptorhombs are greater than those of pectinirhombs and oxygen exchange may have been less rapid in the former.

To summarize, the structure of dichoporite rhombs compares closely with the paradigm of an exchange system as regards the area of the exchange surface. Pectinirhombs with confluent dichopores were relatively more efficient than those with discrete dichopores in terms of exchange area.

2. *The resistance to exchange of the exchange surface.* For maximum efficiency an exchange surface should be as thin as its strength will allow. Dichopore walls vary in thickness from less than 0·01 mm. up to 0·03 mm. in rare cases, whereas the thecal wall is 0·1 mm. thick in *Macrocystella mariae* Callaway, rarely, if ever, less than 0·5 mm. in *Cheirocrinus* and many Glyptocystitida have thecal walls 2–3 mm. thick. Dichopore walls are very much thinner than other skeletal elements and pectinirhombs were potentially weak areas of the theca. The morphology of dichopores, as thin tubes or isoclinal folds, allows great strength and rigidity for a thin surface. It also allows a large surface area without increasing the volume of the theca and thus satisfies both this and the previous requirements.

Pectinirhombs with conjunct slits were particularly susceptible to fracture or distortion by forces acting on the surface of the theca. It was essential to maintain rigidity for normal functioning and this could be achieved by solid ridges in the positions shown in text-fig. 26. Such ridges impart both strength and rigidity. Ridges are found in the positions suggested in some cystoids with conjunct pectinirhombs. In species of *Cheirocrinus* with discrete dichopores the ridges are often incorporated in the plate 'ornament' of radiating ridges. These ridges strengthened the plates in general and may only

TABLE 1. Spacing of Dichopores in Pectinirhombs. The values for spacing are determined by measuring 10 dichopores and 10 inter-dichopore spaces and expressing the average as 1 slit per 0.xxx mm. In pectinirhombs with fewer than 10 dichopores the average was based on the maximum number of dichopores measurable. The averages for each type of pectinirhomb are based on the total number of measurements (No.)

Species	*Spacing*		*No. of measurements*
	Average	*Range*	
A. Conjunct pectinirhombs with discrete dichopores			
Cheirocrinus sp.	0·316	0·217–0·415	2
C. giganteus Leuchtenberg	0·273	..	1
C. granulatus (Jaekel)	0·253	..	1
C. cf. *atavus* (Jaekel)	0·106	..	1
C. languedocianus Thoral	0·370	0·350–0·390	4
B. Conjunct pectinirhombs with confluent dichopores			
Homocystites alter Barrande	0·215	0·205–0·225	2
H. constrictus (Bather)	0·2025	0·201–0·204	2
Pleurocystites elegans Billings.	0·196	..	1
P. filitextus Billings	0·241	..	1
P. cf. *rugeri* Salter	0·20 approx.	..	1
P. squamosus Billings	0·171	..	1
C. Disjunct pectinirhombs with discrete dichopores			
Cheirocrinus sp.	0·174	..	1
C. anatiformis (Hall)	0·257	0·25–0·27	4
C. forbesi Billings	0·273	0·25–0·29	6
Echinoencrinites angulosus Pander	0·27	0·21–0·31	3
E. senckenbergii von Meyer	0·33	0·32–0·34	3
E. reticulatus Jaekel	0·427	0·41–0·44	3
Erinocystis sp.	0·38	..	1
D. *Glyptocystites* type			
Glyptocystites ehlersi Kesling	0·197	0·19–0·20	3
G. multiporus Billings	0·193	0·18–0·20	10
G. regnelli Sinclair	0·206	0·20–0·22	5
G. batheri Sinclair	0·225	0·205–0·245	7
E. Disjunct pectinirhombs with confluent dichopores			
Sphaerocystites multifasciatus Hall	0·223	0·212–0·225	4
Jaekelocystis hartleyi Schuchert	0·168	0·150–0·180	4
Lepadocystis moorei (Meek)	0·169	0·165–0·175	6
Apiocystites pentrematoides Forbes	0·208	0·200–0·214	3
Strobilocystites calvini White	0·276	0·265–0·285	6
Lovenicystis angelini (Haeckel)	0·218	0·201–0·236	2
Lipsanocystis traversensis Ehlers and Leighley	0·152	0·151–0·154	14
Tetracystis oblongus (Forbes)	0·156	0·153–0·159	3
Lepocrinites gebhardii Conrad	0·250	..	2
Pseudocrinites gordoni Schuchert	0·167	0·160–0·174	6
P. bifasciatus Pearce	0·177	0·168–0·187	3
P. pyriformis Paul	0·257	0·233–0·272	3
Staurocystis quadrifasciatus (Pearce)	0·193	0·190–0·201	6
Glansicystis baccata (Forbes)	0·205	0·190–0·220	6
	Over-all averages	*Range*	*No.*
Type A	0·306	0·106–0·415	9
B	0·205	0·171–0·241	8
C	0·300	0·174–0·440	21
D	0·205	0·193–0·245	25
E	0·192	0·151–0·285	68

incidentally have strengthened the pectinirhombs. In *Homocystites constrictus* (Bather) (Pl. 134, fig. 5) and *Pleurocystites* spp. (Pl. 134, figs. 7, 8) rims occur which are independent of the plate ridges and whose strengthening effect was confined to the area immediately adjacent to the pectinirhombs.

In fully developed disjunct pectinirhombs the intra-rhomb areas between the slits would resist forces acting on the thecal surface. In disjunct pectinirhombs with discrete dichopores the intra-rhomb areas tend to be large (Pl. 135, figs. 1, 9) and this partly restores the strength of the rhomb-bearing plates. In cryptorhombs (Pl. 138, fig. 4; Pl. 139, fig. 1), with only rows of pores, this restoration is virtually complete. In disjunct pectinirhombs with confluent dichopores the intra-rhomb areas tend to be smaller but the adsutural portions of the vestibule rims develop within them (Pl. 136, fig. 3; Pl. 137, fig. 1). During growth of a disjunct pectinirhomb some marginal slits were conjunct and subject to the same weakness as conjunct pectinirhombs. In disjunct pectinirhombs with confluent dichopores the absutural portions of vestibule rims arise early in development in exactly the position postulated to strengthen conjunct pectinirhombs (Pl. 137, fig. 1). No such rims are present in disjunct pectinirhombs with discrete dichopores.

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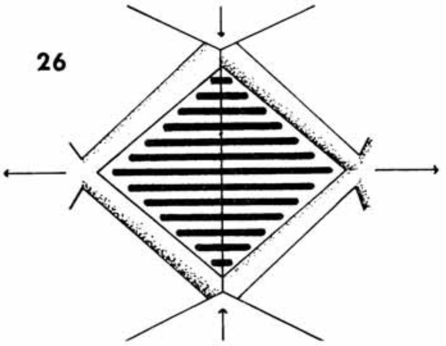

TEXT-FIG. 26. A conjunct pectinirhomb with ridges which deflect forces acting within the plate and impart rigidity to the pectinirhomb.

Uncalcified dichopores would allow a greater exchange area than calcified dichopores since only the soft tissues function as exchange surface. In pectinirhombs distortion or disarticulation would probably occur if the dichopores were uncalcified but in cryptorhombs strength is provided by the covering of thecal plate. It is still essential to have rigid dichopore walls to prevent the dichopores themselves from distorting (under pressure differences or due to gravity) since this would interrupt the functioning of the cryptorhomb. A maximum movement of only 0·05 mm. by two adjacent dichopore walls would completely close a dichopore or inter-dichopore space. Calcification of dichopores imparts rigidity at the expense of the available area of exchange.

Most pectinirhombs and cryptorhombs have strengthening structures closely associated with them indicating they were areas of weakness. The conclusion that this weakness was mainly due to the dichopore walls seems inescapable. Dichopore walls were not only thin absolutely but relatively so thin that the limits of their strength were reached and strengthening devices became necessary to counteract this weakness. In this respect dichoporite pore-structures agree closely with the paradigm of an exchange system. Further conclusions are that conjunct pectinirhombs were intrinsically weaker than disjunct pectinirhombs and all pectinirhombs were weaker than cryptorhombs. Strengthening devices in pectinirhombs with confluent dichopores apparently allowed a weaker structure with a better exchange area to thecal surface area ratio. Disjunct pectinirhombs with confluent dichopores were strengthened throughout a longer period of their growth than those with discrete dichopores.

3. *Protective devices and devices to prevent recirculation.* The currents which flowed within dichopores formed part of an open current system. Therefore devices to prevent choking by extraneous particles and recirculation of deoxygenated sea-water would have been beneficial to exchange. Such devices are also very useful in determining current directions since they indicate which pores were entrances and which exits. Clearly it is more efficient to modify the entrance (rather than the exit) with a protective device since this will prevent entry of harmful particles. Equally, exhausted sea-water in the vicinity of the entrance will be sucked in by the in-current. Recirculation can only be prevented by modifying the exit to direct the out-current away from the entrance and into the ambient sea-water for remixing. Protective devices, which will be considered first, indicate entrances and devices to prevent recirculation indicate exits.

A protective device is a structure which reduces the maximum size of particles that may pass through an aperture without interfering with the functioning of the aperture. There are only three classes of structure which fulfil these requirements: meshes, grilles, and narrow slits. Paradigms for all three have been defined by Rudwick (1961, meshes and grilles; 1964*a*, slits). The maximum particle which can pass through the device is termed the critical particle and is of critical diameter. In an ideal protective device the critical diameter is the same at all points within the aperture.

Two types of harmful particle may be recognized. *Passive particles* are any particles in suspension (animal or plant debris, sediment, etc.) which may choke the dichopores but not attack the cystoid. *Active particles* are organisms which may attack the cystoid

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EXPLANATION OF PLATE 134

Stereophotos of conjunct pectinirhombs

A. with discrete dichopores.

Fig. 1. *Cheirocrinus giganteus* Leuchtenberg. BMNH E16130, basal rhombs.

Figs. 2, 4 *Cheirocrinus* sp. SM A3138 (fig. 4), SM A3139 (fig. 2). External moulds of isolated plates.

Fig. 3. *Cheirocrinus granulatus* (Jaekel). RM Ec5384.

Fig. 9. *Cheirocrinus languedocianus* Thoral. Ubaghs coll. latex impression showing incomplete pectinirhombs and demirhombs in radial and lateral plates.

B. with confluent dichopores.

Fig. 5. *Homocystites constrictus* (Bather). HM 3541a, latex impression showing rhombs B2:IL2, L1:L2, and R1:R2. Note the rim on L2 (middle rhomb).

Fig. 6. *Pleurocystites rugeri* Salter. LU 3175, latex impression of L3:L4.

Fig. 7. *Pleurocystites elegans* Billings. SM A53059. L3:L4.

Fig. 8. *Pleurocystites filitextus* Billings. BMNH E16047. L4:L3.

Figs. 1, 8, 9 ×2, figs. 2–7 ×3. All whitened with ammonium chloride sublimate.

by boring into it, attaching to it or browsing off cilia, etc. Dichopores may be regarded as long thin tubes whose critical diameter at any given point is the minimum width. Complete protection against passive particles may be achieved if the critical diameter of the entrance is less than that of any other point along the tube. Any spherical particle capable of entering the tube will pass right through without becoming lodged. Complete protection against active particles, which may be able to swim against currents, can only be achieved if the critical diameters of both the entrance and the exit are less than the diameter of the smallest active particle. As nothing is known about active particles it is impossible to investigate protection against them. Only passive particles are considered below.

TABLE 2. Ratios of slit lengths and areas in disjunct pectinirhombs

		Ratios	
Species	*Rhomb*	*Lengths* $\frac{\textit{longer slit}}{\textit{shorter slit}}$	*Areas* $\frac{\textit{longer slit}}{\textit{shorter slit}}$
A. Discrete dichopores			
Echinoencrinites angulosus BMNH E29102	B2:IL1	1·27 (7)	0·82 (5)
	B2:IL2	1·21 (11)	0·84 (11)
E. reticulatus RM Ec5515	B2:IL1	1·25 (6)	0·94 (6)
	B2:IL2	1·27 (8)	1·31 (8)
	L4:R3	1·11 (9)	0·94 (9)
E. senckenbergii BMNH E29095	B2:IL1	1·54 (8)	0·97 (8)
	B2:IL2	1·43 (6)	1·06 (6)
	L4:R3	1·16 (10)	0·87 (10)
Cheirocrinus anatiformis	R2:R3	1·14 (15)	1·08 (15)
B. Confluent dichopores			
Glyptocystites multiporus	L1:L2	1·46 (9)	1·46 (9)
Staurocystis quadrifasciatus	L1:R5	1·37 (18)	0·97 (18)
Lovenicystis angelini RM Ec5053	L1:R5	1·77 (13)	1·38 (13)
RM Ec5066	L1:R5	1·30 (17)	0·98 (17)
Glansicystis baccata Bu Ho55	L1:R5	1·15 (9)	1·09 (9)
	L4:R3	1·43 (9)	1·19 (9)
GSM 7380	L1:R5	2·63 (8)	1·91 (8)

Figures in brackets represent the number of measurements upon which each ratio was based.

The dichopores of pectinirhombs open as slits and if protected the entrances should form protective slits. In conjunct pectinirhombs each slit runs the entire length of the dichopore and acts as both entrance and exit. In *Cheirocrinus ?atavus* (Jaekel) BMNH E23515 and *Pleurocystites filitextus* Billings BMNH E7600b (Pl. 140, fig. 2) slit widths are slightly less than dichopore widths within the theca. In these cases the slits were protective.

In disjunct pectinirhombs the slits of the two half-rhombs were of different lengths. In many cases the longer slits are also narrower. To satisfy the requirements of a protective device the critical diameter of the incurrent slit must be reduced without reducing current flow. If protection is achieved by reducing the width, constant current velocity may be maintained by a corresponding increase in slit length since the velocity is inversely proportional to the cross-sectional area of the slit. In the ideal case the ratio of entrance to exit slit length will be greater than unity but the ratio of the areas will equal unity. Available measurements are shown in Table 2. In cases where the longer slits were also narrower they could have been protective. In cases where the slit widths are equal they could still have been protective if both were narrower than the dichopore width within the theca.

The pectinirhombs of *Lipsanocystis magnus* Stumm (Pl. 140, fig. 4) show microscopic bars across the slits of both half-rhombs. These bars reduce the critical diameter of both apertures. Preservation is not quite adequate to determine which slits are better protected or if any difference exists. The formation of these microscopic grilles may be unique to *L. magnus*; perhaps a response to its muddy environment or to active particles since both apertures are modified. Alternatively it may be that the preservation of most glyptocystitids is not adequate for these delicate structures to be detectable. In the latter case the arguments for protective devices in pectinirhombs may need some modification.

TABLE 3. Critical diameters in pectinirhombs and cryptorhombs

	Entrance			*Exit*		
Rhomb type	*Average*	*Range*	*No.*	*Average*	*Range*	*No.*
Pectinirhombs						
conjunct discrete	0·115	0·02–0·19	6	..	..	..
conjunct confluent	0·066	0·05–0·08	8	..	..	..
disjunct discrete	0·113	0·05–0·18	10	0·162	0·12–0·20	8
confluent disjunct	0·075	0·07–0·095	5	0·104	0·09–0·012	5
Cryptorhombs	0·058	0·04–0·07	13	0·20	0·10–0·35	13

No. = Number of rhombs of each type measured. In pectinirhombs with variable slit widths the average width of all slits was calculated.

In cryptorhombs the dichopores open as pores, at least one of which is sieve-like, being composed of a cluster of fine pores. If sieve-pores were protective they formed protective meshes. Measurements given in Table 3 show that the critical diameters of sieve-pores are much less than those of simple pores. The areas (Table 4) of simple and sieve-pores are often approximately equal however. Again protection could be provided while interfering to the least extent possible with current flow.

Particles prevented from entering dichopores by protective devices would choke the slits and pores themselves unless removed. Clearance could be achieved by surface ciliary currents, the particles being carried in the same direction as the currents within the

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EXPLANATION OF PLATE 135

Stereophotos of disjunct pectinirhombs

A. with discrete dichopores.

Fig. 1. *Cheirocrinus* sp. nov. SM A15966. Latex impression of isolated plate.

Figs. 2–5. *Cheirocrinus granulatus* (Jaekel). RM Ec5384. Fig. 2, internal surface of basal plate; figs. 3–5, views of isolated half-rhomb to show relationship between dichopores and slits.

Fig. 6. *Cheirocrinus* sp. BMNH E15983.

Fig. 7. *Echinoencrinites senckenbergii* von Meyer. BMNH E29102, rhombs B2:IL1 and B2:IL2.

Fig. 8. *Echinoencrinites reticulatus* Jaekel. BMNH E29095. B2:IL1 and B2:IL2.

Figs. 9, 12. *Cheirocrinus anatiformis* (Hall). GSC. B2:IL2 (fig. 9) and radials (fig. 12).

Fig. 10. *Echinoencrinites reticulatus* Jaekel. RM Ec5515. B2:IL1.

B. with confluent dichopores.

Fig. 11. *Glyptocystites multiporus* Billings. GSC 1387g (Lectotype). B2:IL1, B2:IL2, and R1:R2. Note the adsutural rim on R2 (large upper rhomb).

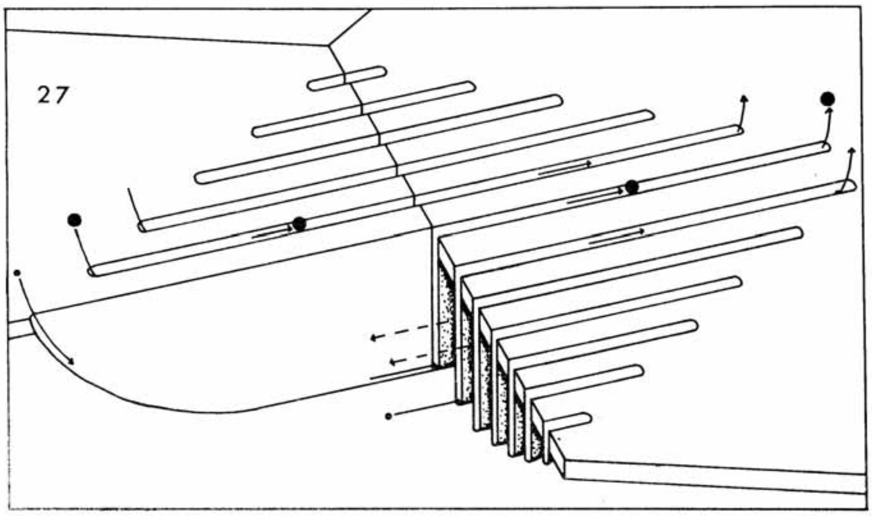
Figs. 1, 6–9, 11, 12 ×2, figs. 2–5, ×3, fig. 10, ×5. All whitened with ammonium chloride sublimate.

TABLE 4. Areas of simple and sieve-pores in cryptorhombs

Specimen	*Area of sieve-pore (entrance)*	*Area of simple pore (exit)*
Hemicosmites sp. RM Ec5364	0·0707 sq. mm.	0·0471 sq. mm.
H. extraneus RM Ec5283	0·0226	0·0201
H. sp. nov. RM Ec2280	0·0154 (radials) 0·0502 (laterals)	0·0314–0·0572
H. cf. *verrusosus* BMNH E15994	0·0491	0·0433 0·0201–
H. malum RM Ec5517	0·0201 (basals) 0·0402 (laterals)	0·0254
H. cf. *pyriformis* BMNH E7592	0·0314	0·0227
Caryocrinites ornatus SM A50958*	0·0308	0·0154
C. roemeri BMNH E29105*	0·0628	0·0628
C. septentrionalis RM Ec25493	0·0226	0·0314
Thomacystis tuberculata BMNH E16300	0·0176	0·0176

Unless otherwise stated the area of sieve-pores was taken from lateral plates: all areas of simple pores are from infra-lateral plates.

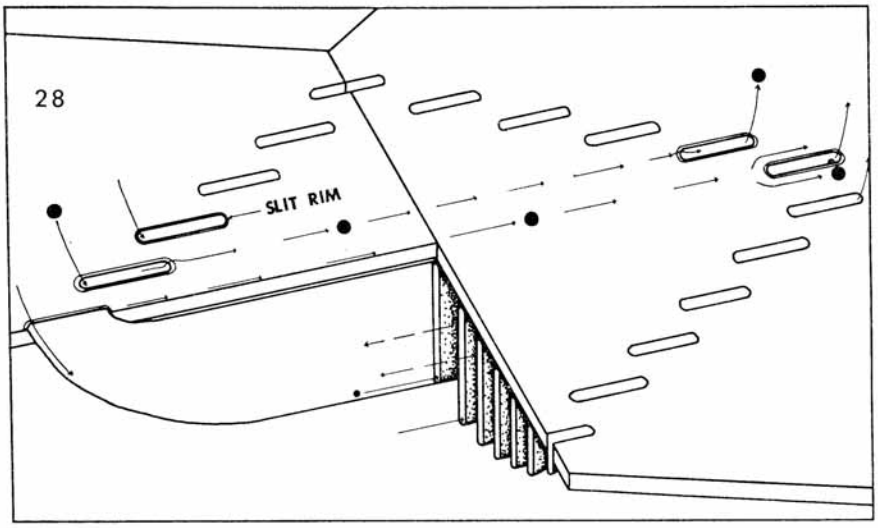
* These specimens have sieve-pores at both ends of dichopores in complete cryptorhombs. However, there are fewer larger pores per cluster where one would normally expect simple pores.

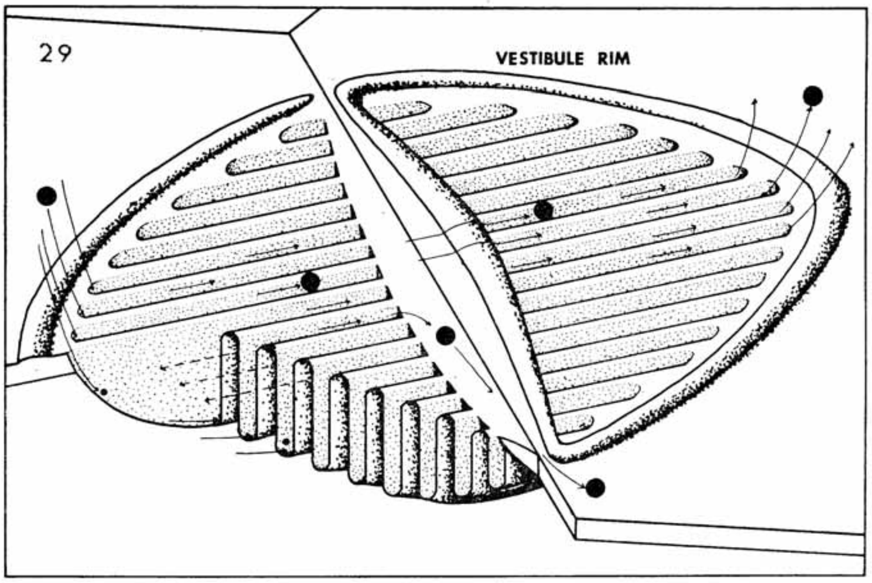


TEXT-FIG. 27. Supposed paths of extraneous particles in conjunct pectinirhombs. Solid arrows indicate external currents; dashed arrows internal currents.

dichopores. In conjunct pectinirhombs particles strained from the in-current would be passed along the slit until they reached the out-current and would then be carried away from the theca (text-fig. 27). Similar currents could have been present in disjunct pectinirhombs and cryptorhombs but the slit, vestibule, and pore rims would render them less effective (text-figs. 28, 29).

We may conclude that the narrower slits of disjunct pectinirhombs and the sieve-pores of cryptorhombs reduced the critical diameters of these apertures, which were





TEXT-FIGS. 28, 29. Possible paths of extraneous particles in disjunct pectinirhombs. Note that the slit and vestibule rims make it more difficult for the excurrent to remove the particles.

therefore entrances. Absolute critical diameters shown in Table 3 indicate that cryptorhombs were better protected than pectinirhombs. However the latter, particularly conjunct pectinirhombs, were better able to prevent the protective devices themselves from becoming choked. This may account for the occurrence of conjunct pectinirhombs in all but one rhomb-bearing member of the Pleurocystitidae. Members of this family were probably vagrant with the theca resting on the substrate (Paul 1967*c*) and may have encountered many more particles than more typically pelmatozoan cystoids.

For maximum efficiency devices to prevent recirculation of exhausted sea-water must do so while interfering with current flow to the least possible extent. The most fundamental requirement is to have two apertures and to keep them apart. How far apart will depend on the volume, velocity, and direction of the out-current. Even if the entrances were capable of detecting oxygen-depleted water they could not prevent it from entering without arresting or reversing the currents. Recirculation can only be prevented effectively by modifying the exit to direct the out-current away from the entrance.

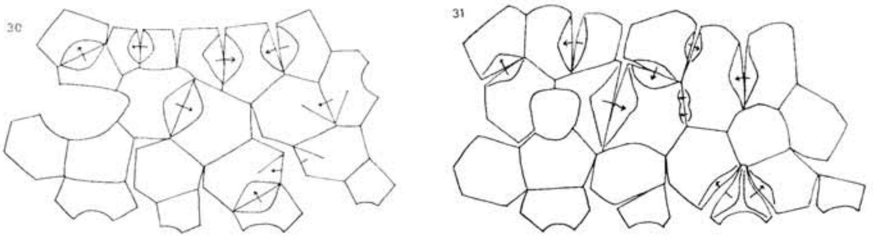
Recirculation may occur within a single rhomb or from one rhomb into another. In a theca with many rhombs recirculation of the second type may be prevented by grouping exits together. In general where two or more apertures are found within a single plate they are either exits or entrances (text-figs. 30, 31). Recirculation within a single rhomb may be prevented by mechanical barriers or by devices to project the out-current through the boundary layer into the ambient sea-water for remixing. The *boundary layer* is the layer of fluid immediately adjacent to the surface of an immersed solid, within which viscosity is the most important single force controlling flow. Cilia beat within the boundary layer and without them water in contact with the external surface of an echinoderm would remain unchanged in all but the most turbulent seas. Water emerging from the dichopores would be recirculated by surface cilia unless forced through this layer. Mechanical barriers between the entrance and exit were therefore probably less efficient than were devices to project the out-current through the boundary layer.

The best method to determine the effects of such structures is to construct models and test them under simulated conditions as close as possible to those under which they operated in life (cf. Rudwick 1961, Jefferies and Minton 1965). Time has not been available to do this and the conclusions outlined below are tentative.

The conjunct pectinirhombs of *Homocystites constrictus* (Bather) (Pl. 134, fig. 5) have distinct rims on one half-rhomb only. Water passing along the dichopores towards these rims would be deflected away from the theca. Where two half-rhombs are developed in a single plate they are either rimmed or unrimmed. Current directions shown in text-fig. 30 are derived from the presence of these rims.

Sinclair (1948) suggested that the adsutural ridges on one half-rhomb of each pectinirhomb in *Glyptocystites* spp. were mechanical barriers to recirculation. This suggestion seems likely although as yet without practical confirmation. Again where two or more half-rhombs occur in one plate they are either with or without ridges. In text-fig. 31 the arrows point to the plates with ridges.

Disjunct pectinirhombs with confluent dichopores have a closed vestibule rim on one half-rhomb and an open rim on the other. The absutural portion of the closed rim would have directed the out-current away from the theca. The adsutural portion would have acted as a mechanical barrier to recirculation as Sinclair suggested for the pectinirhombs of *Glyptocystites*. In addition the closed vestibule rims united all the currents of the constituent dichopores and probably reinforced them. If out-currents they would have passed through the boundary layer more readily. The pectinirhombs of *Jaekelocystis hartleyi* Schuchert (Pl. 137, figs. 7, 9, 10) have closed vestibule rims which form a pore 0·5 mm. in diameter. This pore would considerably increase the velocity of currents passing through it. In disjunct pectinirhombs with a constant slit width in both half-rhombs, the shorter slits would have had faster currents. Fast in-currents would be more likely to suck in extraneous particles but fast out-currents would be more likely to pass through the boundary layer and disperse. Shorter slits and closed vestibule rims therefore probably indicate exits.



TEXT-FIGS. 30, 31. Current patterns in *Cheirocrinus* and *Glyptocystites*.

30. Diagram to show the arrangement of thecal plates and pectinirhombs in *Cheirocrinus anatiformis* (Hall).

31. Diagram to show the arrangement of thecal plates and pectinirhombs in *Glyptocystites ehlersi* Kesling.

Arrows indicate supposed current directions in the pectinirhombs. Note where more than one half-rhomb is developed within a single plate they are usually of the same type (i.e. either entrance or exit). Plate outlines based on Kesling 1962 (text-fig. 30) and 1961 (text-fig. 31).

Many cryptorhombs have simple pores developed beside or within ridges on the plate surface. These ridges could have directed currents away from the theca. In *Caryocrinites septentrionalis* Regnéll (Pl. 139, fig. 5) the ridges beside simple pores are more strongly developed than those associated with sieve-pores. In *Hemicosmites* spp. (Pl. 138, figs. 1, 5) simple pores are developed into chimney-like tubercles and may be interpreted as chimneys. The further away from the thecal surface the out-current emerges the less likely it is to be recirculated by surface ciliary currents. These were therefore probably exits.

EXPLANATION OF PLATE 136

Stereophotos of disjunct pectinirhombs with confluent dichopores

Figs. 1, 7. *Pseudocrinites gordoni* Schuchert. BMNH E23122. L1:R5 (fig. 1) and B2:IL2 (fig. 7). Note the vestibule rims typical of this type of pectinirhomb.

Fig. 2. *Callocystites jewetti* Hall. GSC 14686. L4:R3.

Fig. 3. *Pseudocrinites pyriformis* Paul. BU Ho10. L1:R5.

Figs. 4, 5. *Lovenicystis angelini* (Jaekel). RM Ec5066. L4:R3 (fig. 4) and L1:R5 (fig. 5).

Fig. 6. *Strobilocystites calvini* White. UI. L4:R3.

Fig. 8. *Sphaerocystites multifasciata* Hall. BMNH 22960. B2:IL2.

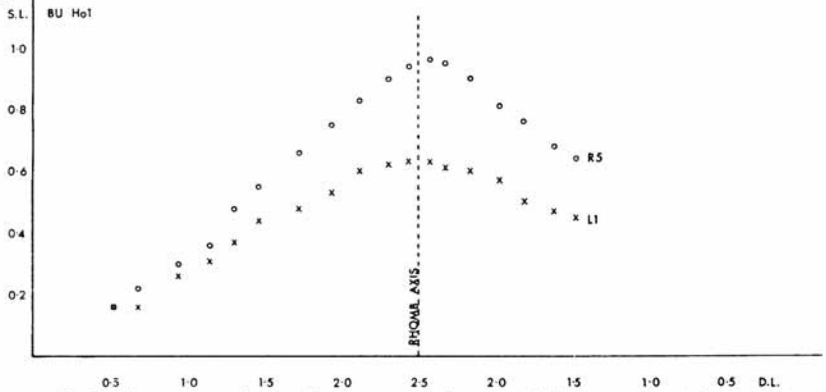
Fig. 9. *Pseudocrinites perdewi* Schuchert. USNM 35072. L4:R3.

Figs. 1, 3–5, 7, 8 × 3, figs. 2, 6, 9 × 2. All whitened with ammonium chloride sublimate.

To conclude, devices which prevented recirculation are apparently present in most cryptorhombs and disjunct pectinirhombs but are generally absent from conjunct pectinirhombs. Suggested entrances were described under protective devices and exits under devices to prevent recirculation. In all cases these interpretations should be, and in fact are, complementary. Thus in disjunct pectinirhombs longer slits were interpreted as entrances and shorter slits as exits. In cryptorhombs sieve-pores were interpreted as entrances and simple pores as exits. Closed vestibule rims in pectinirhombs were interpreted as being associated with exits and they always occur on the half-rhombs with shorter slits. All these interpretations confirm each other and also confirm the presence and direction of donor currents within dichoporite pore-structures.

4. *The maintenance of a concentration gradient.* A counter-current system is the most efficient method of maintaining a concentration gradient. Ciliary currents within the dichopores would be expected on *a priori* grounds as suggested by Sinclair (1948). The viscous effect of the boundary layer would be even more marked in a restricted space such as a dichopore. No matter how turbulent the seas, water within the dichopores would not be disturbed without cilia.

32



TEXT-FIG. 32. Graph to show relationship between slit length and dichopore length in pectinirhomb L1:R5 of *Staurocystis quadrifasciatus* (Pearce), BU Ho 1. Lower scale reversed about the rhomb axis for clarity. Note that the slit lengths are proportional to the dichopore lengths and the slit lengths in L1 are constantly less than those of R5.

If currents were present, sea-water flowed within the dichopores forming the donor current which was part of an open current system. The best evidence for the presence and direction of the donor current has been outlined in the preceding section. Additional evidence is found in the relationship between slit and dichopore lengths in pectinirhombs and between pore counts and dichopore length in cryptorhombs. Adaxial dichopores are longer and deeper than marginal dichopores. If the current velocity were constant in all dichopores more water would pass through the larger dichopores per unit time. The capacity of the dichopore would be proportional to its cross-sectional area and, since the width is constant, capacity would be proportional to dichopore depth. For constant velocities of in-current and out-current across a rhomb, slit length must be proportional to dichopore capacity. Dichopore depth is not readily measurable but in some instances e.g. *Staurocystis quadrifasciatus* (Pearce) (Pl. 137, fig. 1, text-fig. 32) slit length is almost exactly proportional to dichopore length. In the cryptorhombs of *Caryocrinites ornatus* Say (Pl. 138, fig. 3) the number of pores per sieve-pore cluster increases adaxially as does the total area of the entrance. The morphology of these rhombs would allow constant current velocities across the rhombs and within all dichopores, if currents were present. Ciliary currents are likely to have been of similar velocities in all dichopores.

It is more difficult to confirm the presence and direction of internal acceptor currents as they formed a closed current system, but there is some indirect evidence. In rhombs with closely spaced dichopores the inter-dichopore spaces were entirely within the boundary layer. Ciliary currents between dichopores would be expected on the same *a priori* grounds used to postulate their presence within dichopores. The width of dichopores was probably controlled by the combined thicknesses of ciliated epithelium, and lengths of cilia, lining them. If the dichopore width were much greater, dead water would accumulate within the dichopore. Alternatively cilia on opposite sides of the dichopore would interfere with each other if the dichopores were thinner. Where inter-dichopore widths equal dichopore widths both were probably controlled by the presence of cilia. This suggests that internal ciliated currents were present. The most efficient internal current is a counter-current.

Internal currents within a rhomb could only act efficiently if the external currents in all the dichopores were counter to them. With very rare exceptions in some incomplete cryptorhombs, current directions in all dichopores of one rhomb were apparently the same. Currents in all dichopores could have been counter to an internal current.

EXPLANATION OF PLATE 137

Stereophotos of disjunct pectinirhombs with confluent dichopores

Fig. 1. *Staurocystis quadrifasciatus* (Pearce). BU Ho1. L1:R5.

Figs. 2, 4. *Glansicystis baccata* (Forbes), typical form. GSM 7380. B2:IL2 (fig. 2) and L1:R5 (fig. 4).

Fig. 3. *Lipsanocystis traversensis* Ehlers and Leighley. UMMP 56222. L4:R3.

Fig. 5. *Schizocystis armata* (Forbes). GSM 7381. B2:IL2.

Figs. 6, 8. *Glansicystis baccata* (Forbes), common form. BU Ho55. L4:R3 (fig. 6) and L1:R5 (fig. 8).

Figs. 7, 9, 10. *Jaekelocystis hartleyi* Schuchert. BMNH E23121. L4:R3 (fig. 7), L1:R5 (fig. 9), and B2:IL2 (fig. 10). Note that the vestibules in IL2, L1, and L4 are small pores.

Figs. 1, 2, 4–10 × 3, fig. 3 × 2. All whitened with ammonium chloride sublimate.

EXPLANATION OF PLATE 138

Stereophotos of cryptorhombs

Fig. 1. *Hemicosmites* sp. RM Ec5364. Infra-lateral with simple pores.

Fig. 2. *Hemicosmites extraneus* Eichwald. RM Ec5283. Laterals with simple pores and radials with sieve-pores.

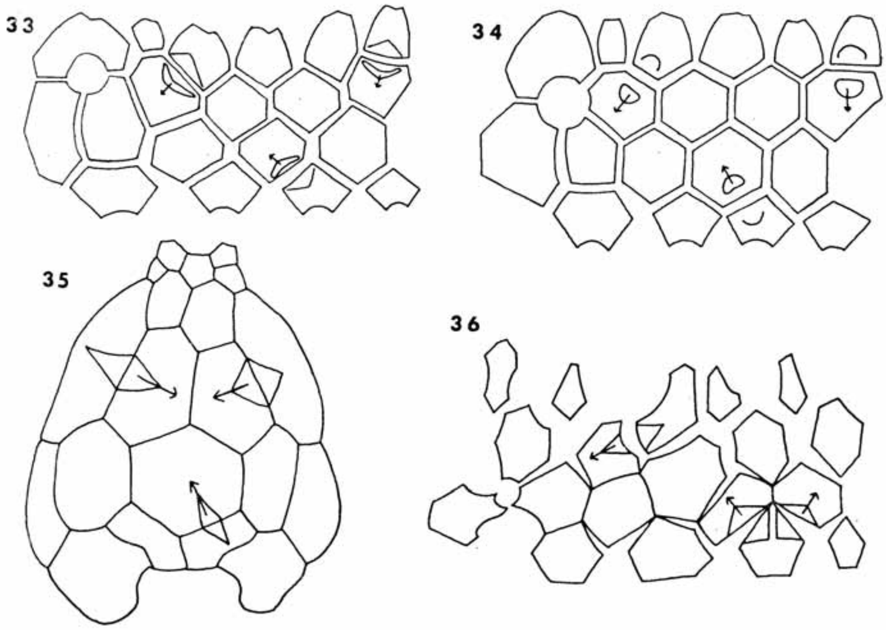
Figs. 3, 6. *Caryocrinites ornatus* Say. BMNH E29091. Internal (fig. 6) and external (fig. 3) views of isolated lateral plate. Note that the number of individual pores in a cluster increases towards centre of plate (fig. 3).

Fig. 5. *Hemicosmites* cf. *verrucosus* Eichwald. BMNH E15994. Infra-laterals and laterals. Note chimney-like simple pores.

Figs. 4, 7. *Caryocrinites ornatus* Say. BMNH E29084. Internal (fig. 7) and external (fig. 4) views of isolated infra-lateral plate. Note that only simple pores occur in the infra-lateral.

Figs. 1, 2 × 3, figs. 3–7 × 2. All whitened with ammonium chloride sublimate.

In any cystoid relying on diffusion alone to distribute oxygenated fluids internally it would be advantageous to have rhombs over the entire external surface as all internal organs would be equidistant from an oxygen source. An approximation to this distribution of rhombs is found in *Cheirocrinus* and *Glyptocystites* (pectinirhombs) and in most cryptorhomb bearing genera. As the latter grew, relatively large areas without cryptorhombs were developed adjacent to the intra-circlet sutures of the infra-lateral and lateral circlets. It is within just these areas that incomplete cryptorhombs develop relatively late in ontogeny. The distribution and development of cryptorhombs, and of pectinirhombs in *Cheirocrinus* and *Glyptocystites*, suggests that internal circulations were inefficient or lacking. Cystoids with only a few rhombs probably required some sort of internal circulation. Independent evidence for this is found in the Callocystitinae (Paul 1967*b*). In all cystoids with few rhombs the same external current pattern is found (text-figs. 33–6). This could reflect a fixed internal circulation but only if there were a constant relationship between donor and acceptor current directions. The most efficient relationship is a counter-current system.



TEXT-FIGS. 33–6. Current directions in cystoids with three pectinirhombs.

33. *Staurocystis quadrifasciatus* (Pearce).
34. *Glansicystis baccatus* (Forbes).
35. *Pleurocystites* sp.
36. *Erinocystis* sp.

Note the current directions in all four have the same basic pattern. Plate outlines after Paul 1967*a* (text-figs. 33–4), Breimer 1963 (text-fig. 35), and Jaekel 1899 (text-fig. 36).

As regards maintenance of a concentration gradient, there is considerable direct evidence for the presence of external currents within dichopores and some indirect evidence for internal counter-currents between dichopores. Again dichoporite pore-structures agree closely with the paradigm of an exchange system in this respect.

In general most details of dichoporite pore-structures agree remarkably well with the paradigm of an exchange system and would have been beneficial to exchange. Oxygen, and corresponding carbon dioxide, diffusion is the most likely form of this exchange and hence it seems that pectinirhombs and cryptorhombs were most probably respiratory organs.

D. EVOLUTIONARY AND TAXONOMIC IMPLICATIONS

The distribution of different types of pectinirhomb within the Glyptocystitida is summarized in text-fig. 37. Throughout the detailed functional analysis it was suggested that conjunct pectinirhombs were inherently less efficient than disjunct pectinirhombs (except in clearing the slits of extraneous particles) and that discrete dichopores were less efficient than confluent dichopores.

With the possible exception of *Scoliocystis* Jaekel, conjunct pectinirhombs are confined to the Cheirocrinidae and Pleurocystitidae. Their presence in the early (Arenig, L. Ordovician) cheirocrinids is probably primary. The appearance of conjunct pectinirhombs with confluent dichopores in later cheirocrinids like *Homocystites constrictus*

EXPLANATION OF PLATE 139

Stereophotos of cryptorhombs

Fig. 1. *Hemicosmites malum* Pander. RM Ec5517. Note the 'hidden rhombs'.

Fig. 2. *Hemicosmites* sp. RM Ec5702. Internal surface of isolated infra-lateral.

Figs. 3, 6. *Thomacystis tuberculata* Paul. BMNH E16300. Complete theca (fig. 3) and external mould of isolated basal plate (fig. 6). Latter shows cast of two dichopores which bifurcate near external surface of plate to form sieve-pore (cf. Pl. 140, fig. 5).

Fig. 4. *Caryocrinites roemeri* Jaekel. BMNH E29105. Infra-lateral and lateral plates; both show sieve-pores.

Fig. 5. *Caryocrinites septentrionalis* Regnéll. RM Ec25493. Note rims beside simple pores are more strongly developed than those by sieve-pores.

Fig. 7. *Caryocrinites ornatus* Say. SM A50958.

Fig. 8. *Hemicosmites* cf. *pyriformis* von Buch. BMNH E7592.

Figs. 1, 4, 8 × 2, figs. 2, 3, 5–7 × 3. All whitened with ammonium chloride sublimate.

EXPLANATION OF PLATE 140

Fig. 1. *Echinoencrinites angulosus* Pander. RM Ec5490, section 9. Vertical section through one dichopore in B2:IL2. Note structure of thecal plate. × 35.

Fig. 2. *Pleurocystites filitextus* Billings. BMNH E7600b. Vertical section through B2:IL2 × 35.

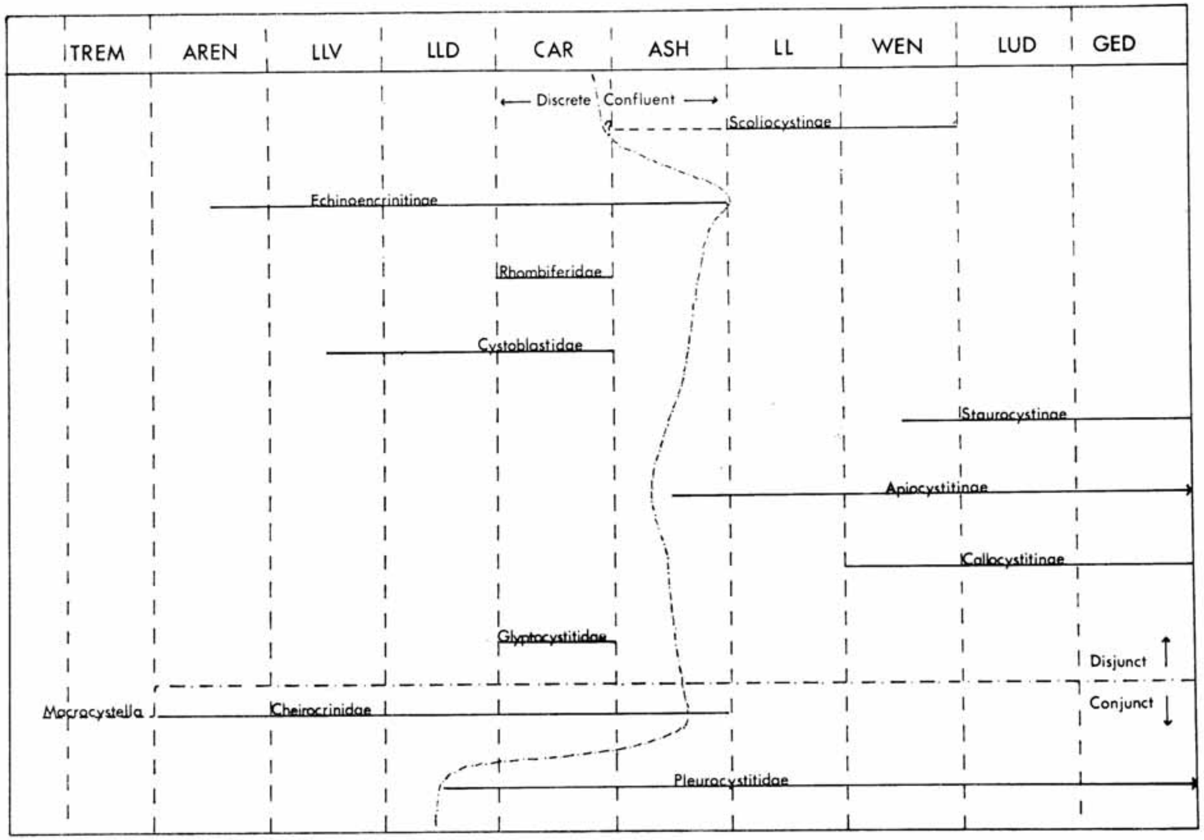
Fig. 3. *Cheirocrinus jamesii* (M'Coy). RSM 1870.12.879. External mould of isolated plate showing multi-disjunct pectinirhomb. × 6.

Fig. 4. *Lipsanocystis magnus* Stumm. UI 32001. Detail of slits in L4:R3 to show microscopic bars across slits. × 25.

Figs. 5, 6. *Hemicosmites* sp. nov. Sections through thecal plates to show sieve-pore (fig. 5) and simple pore (fig. 6). × 30 approx.

Fig. 7. *Strobilocystites calvini* White. UI. Sutural view of isolated plate to show dichopores. Photographed under xylol. × 25.

Fig. 8. *Echinoencrinites angulosus* Pander. RM Ec5490, section 3. Tangential section through B2:IL1 × 3.



TEXT-FIG. 37. Diagram to illustrate the stratigraphic range of the families of the Glyptocystitida, the distribution of conjunct and disjunct pectinirhombs and of confluent and discrete dichopores.

(Bather) (Ashgill, U. Ordovician), may be due to the mode of life. These pectinirhombs are more highly developed than those of earlier species. The retention of conjunct pectinirhombs in the Pleurocystitidae is probably due to the mode of life as suggested by Paul (1967*c*).

Confluent dichopores are unknown before the Llandeilo (M. Ordovician) while discrete dichopores are unknown after the Ashgill or possibly even the Caradoc (Late Middle Ordovician). Between these time limits there was a change from discrete to confluent dichopores independently in all evolutionary lines. The change may have been gradual in some cases: the pectinirhombs of *Glyptocystites* Billings are somewhat intermediate in character. All Silurian and Devonian glyptocystitids (with the exception of two species of Pleurocystitidae) have disjunct pectinirhombs with confluent dichopores, the most efficient type. Apparently throughout the evolution of the Glyptocystitida there was a progression from less to more efficient types of pectinirhomb. There is no evidence for a gradual change from conjunct to disjunct pectinirhombs but this is not surprising since it is difficult to see, on geometrical grounds, how a transition could exist.

At present no estimate of the functional efficiency of multi-disjunct pectinirhombs can be made. It is also much more difficult to compare the relative exchange efficiencies of pectinirhombs and cryptorhombs. The latter show much less variation and as yet no evolutionary trends have been recognized.

Within the Glyptocystitida (but not within the Rhombifera as a whole) there is evidence of a progressive decrease in the number of pectinirhombs in one theca. Bather (1913) explained this reduction in the Pleurocystitidae as a result of the anus partly taking over respiration. However, this explanation cannot be applied to the Callocystitidae, for example, which lack the extensive periproctal membrane supposedly used in respiration per anum. The reduction in the number of pectinirhombs could be due to the development of an internal circulation to distribute more efficiently oxygen gained from the pectinirhombs. Some independent evidence for such a circulation system has been described by Paul (1967*b*). The Glyptocystitida alone show this trend.

Rudwick (1961, 1964*a*) has emphasized that there may be a limited number of different structures which can perform a given function efficiently. In these cases it is inherently likely that the same or similar structures may have evolved independently several times. This was undoubtedly the case with confluent dichopores. It is also undoubtedly the case with rhombs as a whole. Fistulipores and dichopores represent basically different structures and there is no feasible way to evolve one from the other. The fistuliporite and dichoporite rhombs of the Rhombifera were independently acquired and the possession of rhombs is a polyphyletic character within the class. The Glyptocystitida and Hemicosmitida (dichoporite) can be separated from the Caryocystitida (fistuliporite) on several characters, e.g. plating arrangement, mode of growth, presence of true stem, besides the type of thecal canal present. The dichoporite superfamilies form natural units but it is still possible that they acquired their rhombs independently. It is easy to envisage that cryptorhombs evolved from disjunct pectinirhombs but there is no evidence at all for such a transition and both types of rhomb appear simultaneously in the Arenig. Furthermore, a rhomb-less ancestor for the Glyptocystitida is known (*Macrocystella*) which has an identical plate arrangement to later Glyptocystitida but which is quite distinct from all Hemicosmitida.

The cystoidea as currently understood (Kesling 1963, 1968) form a polyphyletic group despite the recognition of the Eocrinoidea, Paracrinoidea, etc. as distinct classes. It is suggested that the Diploporita and Rhombifera should also be regarded as separate classes. Within the Rhombifera two orders, the Dichoporita (Jaekel 1899 emend.) and Fistuliporita nov., may be recognized. The former corresponds to the Pectinirhombifera (Delpey 1942, p. 207) but as the distinctive character is the possession of dichopores not pectinirhombs, an emended use of Jaekel's Dichoporita is preferred.

Since its first inception as a class to include all non-crinoid, non-blastoid Pelmatozoa, the Cystoidea has been subject to the removal of constituent groups as their distinctiveness was realized. This process is here carried to the limit and as neither Diploporita nor Rhombifera can be considered the more typical cystoids, the formal name Cystoidea must fall into disuse. The concept of a 'cystoid' is still useful in a general sense similar to that now reserved for 'Dinosaur'. Cystoid may be used to embrace the Eocrinoidea, Paracrinoidea, Rhombifera, Diploporita, Parablastoidea, Edrioblastoidea, and possibly the Blastoidea *s.s.* These classes share many common characteristics which separate them from 'carpoids' and 'edrioasteroids', two other groups once included within the Cystoidea *s.l.*

APPENDIX

List of species with dichoporite pore-structures examined.

Class Rhombifera Müller		
Order Dichoporita Jaekel emend.	Rhomb type	
Superfamily Glyptocystitida Bather	Pectinirhombs	
Family Macrocystellidae Bather emend. Jaekel	slits	dichopores
Macrocystella mariae Callaway	—	—
M. bohemicus (Barrande)	—	—
M. azaisei (Thoral)	—	—
Family Cheirocrinidae Jaekel		
Cheirocrinus sp. (Ngwetung, Burma)	conjunct	discrete
C. atavus (Jaekel)	,,	,,
C. giganteus (Leuchtenberg)	,,	,,
C. languedocianus Thoral	,,	,,
C. granulatus (Jaekel)	conjunct and disjunct	,,
C. anatiformis (Hall)	disjunct	,,
C. sp. nov. (Tramore, Eire)	,,	,,
C. sp. (Katlino, U.S.S.R.)	,,	,,
C. interruptus (Jaekel)	multi-disjunct	unknown
C. jamesi (M'Coy)	,,	,,
Homocystites alter Barrande	conjunct	confluent
H. constrictus (Bather)	,,	,,
Family Echinoencrinitidae Bather		
Subfamily Echinoencrinitinae Paul		
Echinoencrinites angulosus Pander	disjunct	discrete
E. senckenbergii von Meyer	,,	,,
E. reticulatus Jaekel	,,	,,
Erinocystis sp.	,,	,,
Subfamily Scoliocystinae Jaekel emend. Paul		
Schizocystis armata (Forbes)	,,	confluent
Glansicystis baccata (Forbes)	,,	,,
Osculocystis monobrachiolata Paul	,,	,,

Family Rhombiferidae Kesling	slits	dichopores
Rhombifera bohemica	disjunct	discrete
Family Pleurocystitidae		
Amecystis laevis (Raymond)	—	—
A. sp. nov. (Neebish Channel, Michigan)	—	—
Praepleurocystis watkinsi (Strimple)	disjunct	confluent
Pleurocystites elegans Billings	conjunct	"
P. filitextus Billings	"	"
P. squamosus Billings	"	"
P. rugeri Salter	"	"
P. quadratus (Bather)	"	"
P. gibbus (Bather)	"	"
Regulaecystis pleurocystoides Dehm	"	"
Family Glyptocystitidae Bather		
Glyptocystites ehlersi Kesling	disjunct	?confluent
G. multiporus Billings	"	"
G. regnelli Sinclair	"	"
G. batheri Sinclair	"	"
Family Callocystitidae Bernard		
Callocystites jewetti Hall	"	"
C. canadensis Billings	"	"
C. subglobosus (Hall)	"	"
Sphaerocystites multifasciatus Hall	"	"
S. bloomfieldensis Schuchert	"	"
Hallicystis imago (Hall)	"	"
H. elongata Jaekel	"	"
H. attenuata Paul	"	"
Lepadocystis moorei (Meek)	"	"
Brockocystis tecumseth (Billings)	disjunct	confluent
Jaekelocystis hartleyi Schuchert	"	"
Lovenicystis angelini (Haeckel)	"	"
Apiocystites pentrematoides Forbes	"	"
Lepocrinites gebhardii Conrad	"	"
Prunocystites fletcheri Forbes	"	"
Lipsanocystis traversensis Ehlers & Leighley	"	"
L. magnus Stumm	"	"
Tetracystis fenestratus Troost	"	"
T. chrysalis Schuchert	"	"
T. oblongus (Forbes)	"	"
T. elegans (Hall)	"	"
Strobilocystites calvini White	"	"
Staurocystis quadrifasciatus (Pearce)	"	"
Pseudocrinites bifasciatus Pearce	"	"
P. pyriformis Paul	"	"
P. gordoni Schuchert	"	"
P. perdewi Schuchert	"	"
P. stellatus Schuchert	"	"
P. clarki Schuchert	"	"
Superfamily Hemicosmitida Jaekel	cryptorhombs throughout	
Family Hemicosmitidae		
Hemicosmites pyriformis von Buch		
H. extraneus Eichwald		

H. sp. nov. (Kullsberg, Sweden) cryptorhombs throughout
H. malum Pander
H. cf. *verrucosus* Eichwald
H. sp. (Karrast, Estonia)
H. sp. (Uxnörm, Estonia)

Family Caryocrinitidae Bernard

Caryocrinites ornatus Say
C. roemeri Jaekel
C. septentrionalis Regnéll
C. elongatus (Rowley)

Family Thomacystidae Paul

Thomacystis tuberculata Paul

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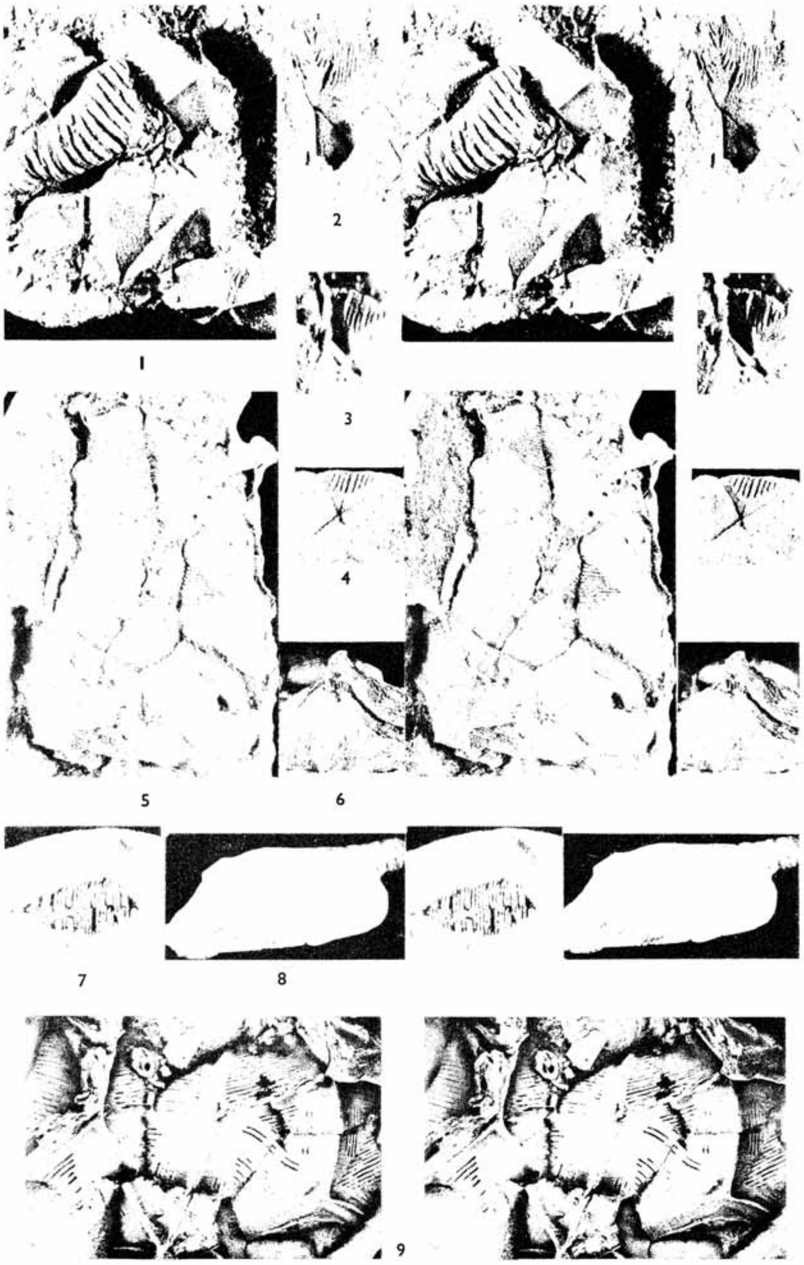

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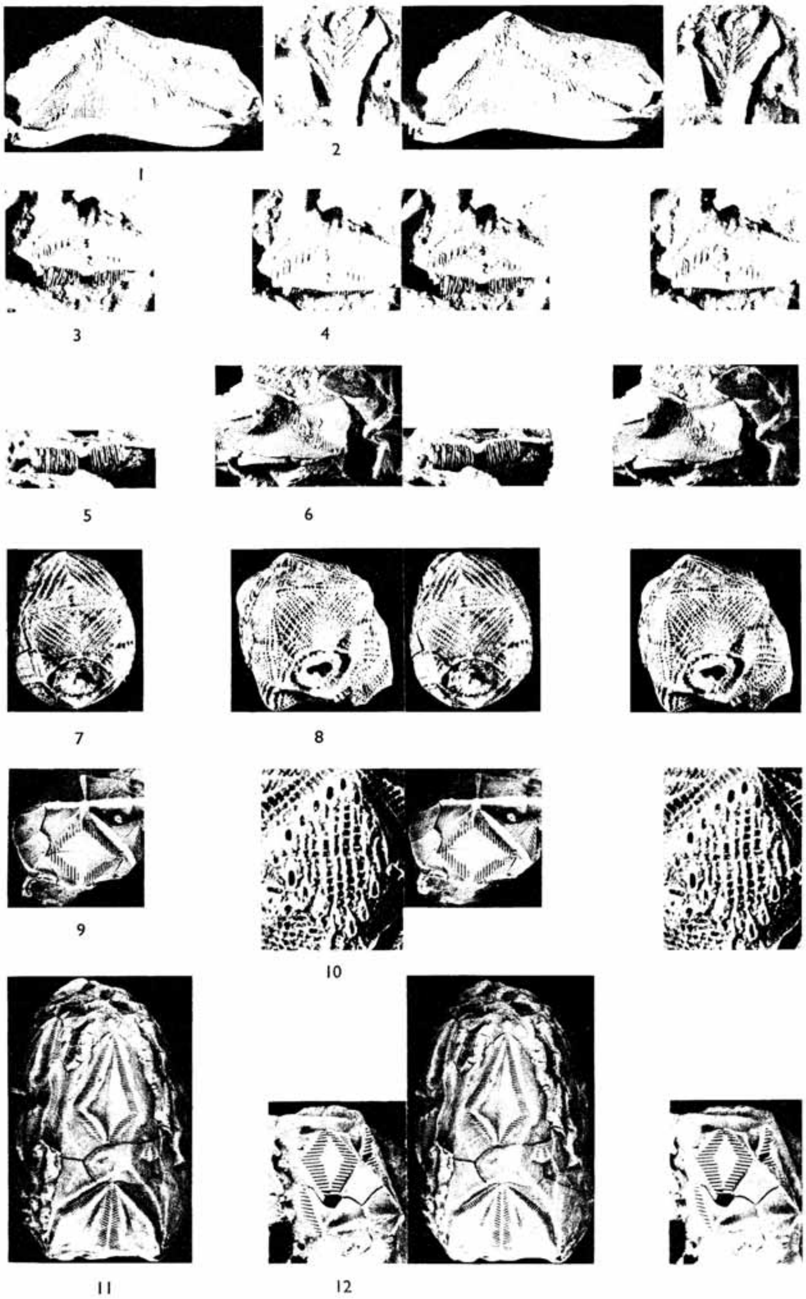

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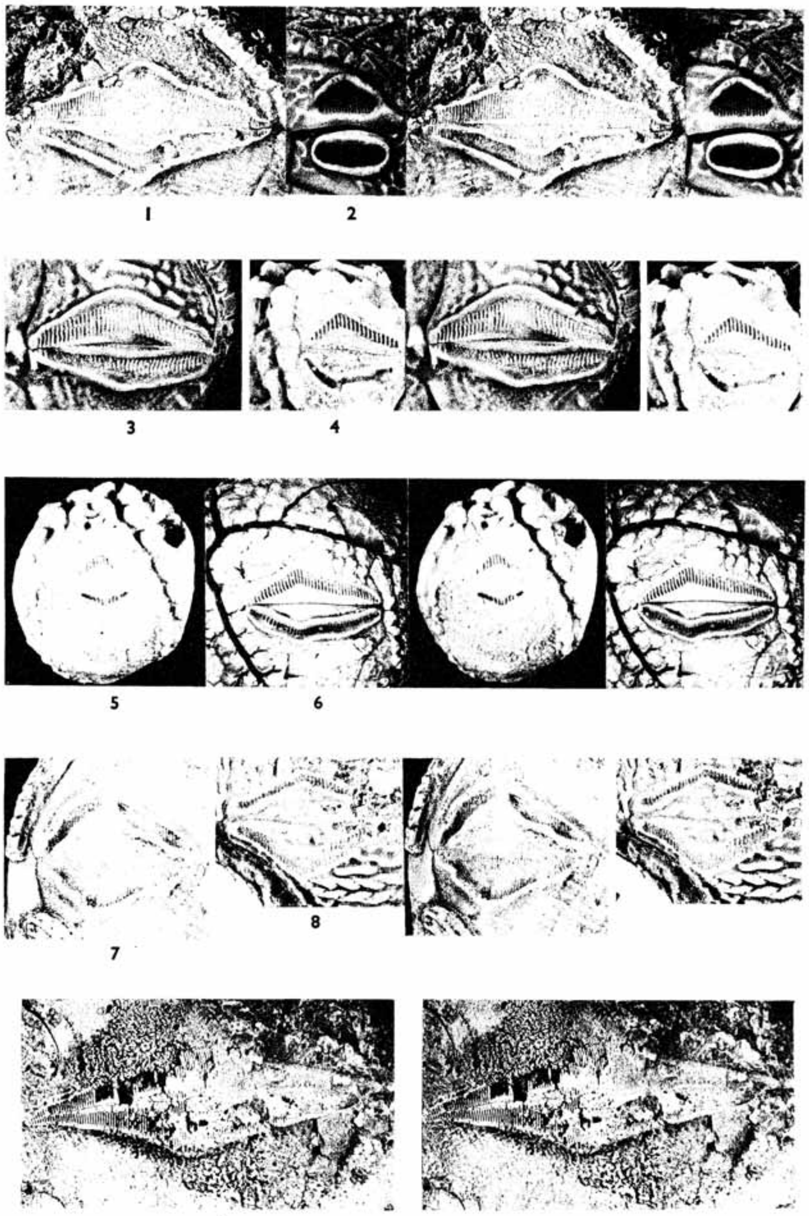

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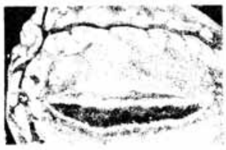


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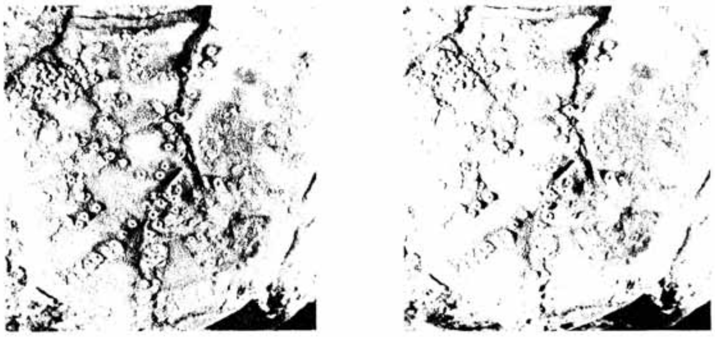
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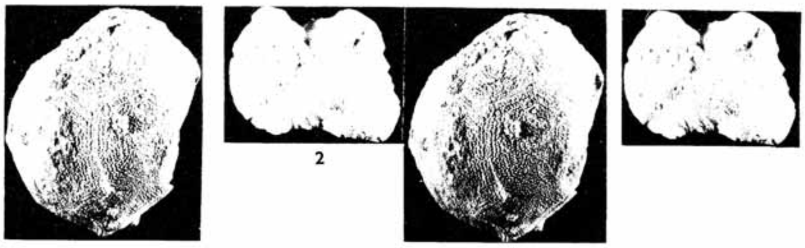
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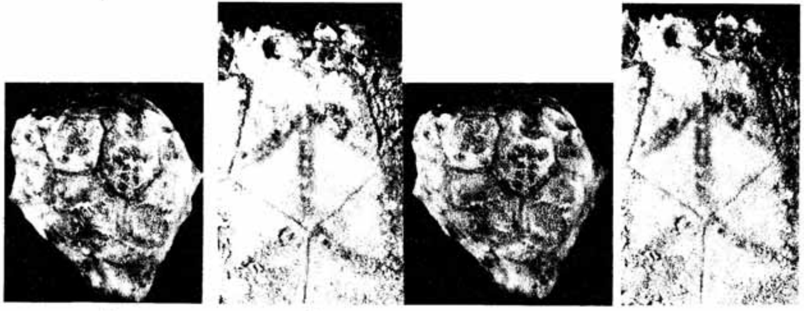
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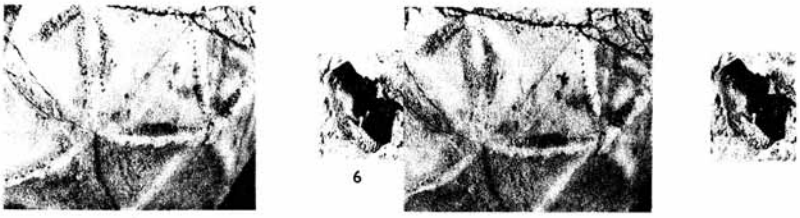
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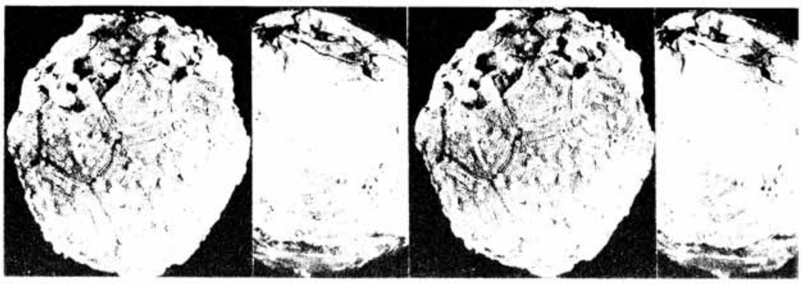
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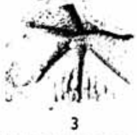
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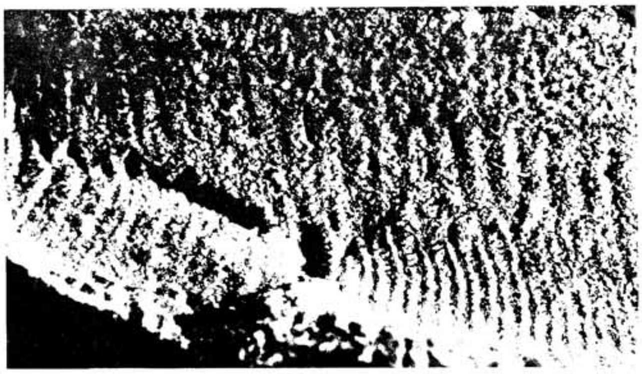
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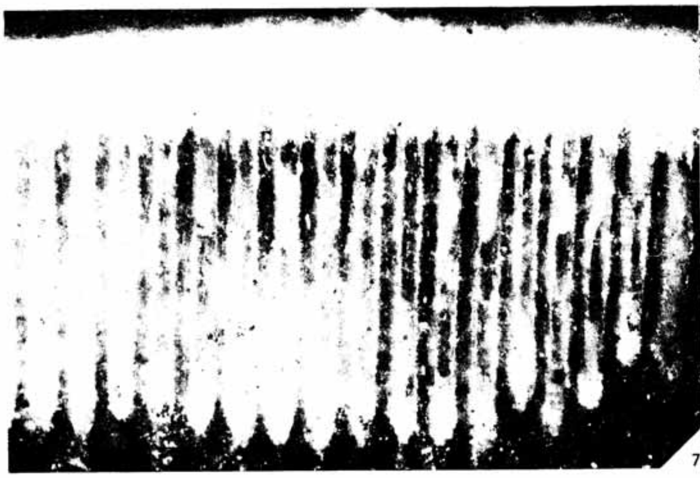
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