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THE PHYLOGENY OF THE FISSICULATE BLASTOIDS

ALBERT BREIMER and DONALD B. MACURDA Jr.

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ABSTRACT

The fissiculate blastoids, a group of stemmed echinoderms, arose in the Silurian in the North Atlantic Basin. The most primitive family, the phaenoschismatids (12 genera), diversified in this area but never expanded beyond it during their existence (Silurian-Mississippian). The phaenoschismatids were conservative throughout their history. They were the stem group from which the four other main fissiculate families arose during the Devonian and Mississippian. The orophocrinids (7 genera) began in the Devonian, were widespread in the Atlantic region in the Mississippian; only one Permian survivor is known from southeast Asia. Their main evolutionary trend was to conceal the hydrospires and to increase the food gathering capacity by an expansion of the number of brachioles. The nymphaeoblastids (4 genera) also arose in the Devonian and had one Permian survivor but their environmental distribution is usually different from that of other fissiculates. They also showed an evolutionary trend to lengthen the ambulacra. The neoschismatids (7 genera) began in the Mississippian in the Atlantic Basin but their maximum development is found in the southwest Pacific during the Permian. They undertook wide experimentation in ambulacral development and life modes. The fifth major fissiculate family, the codasterids (5 genera), also began in the Mississippian and their main development is Permian. One genus, *Angioblastus*, provides the only record of a Pennsylvanian fissiculate and is found on four continents. This group is characterized by an emphasis on neoteny during their evolution. The other two fissiculate families with a single genus apiece (the astrocrinids and ceratoblastids), represent special evolutionary experiments. One genus *(Indoblastus)* remains unassigned to a family. The apparent absence of Pennsylvanian blastoids represents an artifact of the geologic record, not an evolutionary crisis in blastoid evolution. In addition to the four main fissiculate families, the phaenoschismatids also gave rise polyphyletically to the spiraculates. Some examples of convergent evolution are found in the fissiculates. The use of a computerized quantitative phyletics program demonstrates the utility of this type of program in reconstructing the phylogeny of fossil organisms.

Detailed internal study of the fissiculates has revealed for the first time the presence of a gonopore in the blastoids. This is a pore in the anal interarea, either internal or external, which is internally connected with a canal or duct, which leads to a tube- or collar-shaped extension formed by the anal deltoids. Internal studies have also shown the configuration of the fissiculate nervous system. It is lodged orally in canals in the skeletal mass; there is an oral ring with cross connectives in the deltoids and radial extensions in the lancets. The nervous system may

extend into the brachioles via branches from the radial elements. The water-vascular system was well developed; there was an oral ring canal with five radial extensions down the center of the ambulacral tract and side branches to the brachioles. All of these had lateral extensions in the form of podia which were lodged in the minor grooves, below the ambulacral cover plates. The hydrospires performed a respiratory function. Folds of early forms were thick-walled and not differentiated into hydrospire lamellae and inflated hydrospire ducts as in later forms. In late Paleozoic fissiculate hydrospires slits have evolved to become very short elliptical openings.

In the early fissiculates, thecal shape results almost entirely from the lateral secretion of calcite, and secondary deposition is absent. The basals are a prominent part of the theca and have one of the highest growth rates. With time, the basals are deemphasized, and different types of stem attachment areas evolved. The ambulacra reach a larger relative size due to increased growth in the upper part of the radials and the deltoids. In late Paleozoic, there was a much greater frequency of secondary calcite secretion on the radials and deltoids; this produced much greater variation in thecal form. Regression analysis of numerous data matrices was used to demonstrate the shifts in ontogenetic patterns.

The fissiculate blastoids normally inhabited shallow to moderately deep environments, corresponding to modern-day shelves. They are most always found preserved in carbonate or marly sediments; they were not well adapted to environments with moderate or high rates of clastic sedimentation. Most fissiculates had a long slender stem and the brachioles extended two to three times the height of the theca. These animals were elevated above the sea floor and the brachioles formed a filtration fan in the shape of a funnel, the tip of which was directed into prevailing currents in a manner analogous to that of some modern rheophile crinoids (Type I). Other life modes were affected by the fissiculates. Some forms had long cylindrical stem plates which were relatively inflexible and supported the theca like a column a short distance above the sea floor; the brachioles formed a funnel for catching a particulate rainment; the open end of the funnel was directed upward (rheophobe, Type II). The Type I blastoids were similar to the high-crowned trees of a forest, the Type II analogous to the underbrush in their vertical zonation on the sea floor.

In some fissiculate groups, there is a tendency to elongate the ambulacra. Some of these occur in areas of greater clastic sedimentation. The stem was similar to that of Type I, but the longer ambulacra permitted the formation of a much more complex filtration apparatus, which would have greater efficiency (Type III).

Some Permian fissiculates were adapted to living directly on the sea floor (Type IV). The stem was still functional, apparently acting as an anchor. The massive bases provided stability; the ambulacra were restricted to the upper surface.

Restudy of all known fissiculate species in the laboratory and field on five continents has produced a revised phylogenetic classification. The fissiculate families are redefined and the genera assigned to them revised. The following new genera are proposed: *Dolichoblastus* (type species: *Codaster shimanski* Arendt, Breimer, and Macurda, 1968); *Leptoschisma* (type species: *Codaster lorae* Dunbar, 1920); *Pachyblastus* (type species: *Pachyblastus dicki* n. sp.); *Tympanoblastus* (type species: *Codonaster pousirewskii* Stuckenberg, 1875); *Xenoblastus* (type species: *Pentremites decussatus* Shumard, 1858). The following genera are placed in synonymy: *Agmoblastus* Fay, 1961 (=*Angioblastus* Wanner, 1931); *Deltoschisma* Fay, 1961 (= *Pentremitidea* d'Orbigny, 1850); *Microblastus* Van Eykeren, 1942 (= *Timoroblastus* Wanner, 1924); *Paracodaster* Yakovlev, 1940 (= *Angioblastus* Wanner, 1931); *Sagittoblastus* Yakovlev, 1937 (= *Angioblastus* Wanner, 1931); *Sundablastus* Wanner, 1924 (= *Indoblastus* Wanner, 1924); *Trionoblastus* Fay, 1961 (= *Heteroschisma* Wachsmuth, 1883). The following new species are described: *Angioblastus boliviensis*, *Angioblastus ellesmerensis*, *Brachyschisma* ? *oostheizeni*, *Neoschisma australe*, *Notoblastus stellaris*, *Pachyblastus dicki*, *Phaenoschisma* ? *saharae*. Twenty-seven specific names are newly referred, and twenty-six specific names are newly rejected (synonyms or *nomen dubium*).

INTRODUCTION

The blastoids are a class of stemmed echinoderms which flourished worldwide during much of the Paleozoic, from Silurian to Permian. The first species was described in 1819. Most of those discovered during the 1800's were mid Paleozoic in age (Silurian to Mississippian) and Etheridge and Carpenter (1886) wrote a monograph summarizing all of the material known to that time. Scientists and amateur collectors subsequently continued to add to our knowledge of mid Paleozoic faunas but the most important discovery of the 20th century was the Permian faunas of Timor, Indonesia, which were monographed by J. Wanner over three decades.

In preparation for the Treatise on Invertebrate Paleontology, Part S, R. O. Fay published a series of papers during the 1960's which redescribed many of the older species and in 1967 Fay and Wanner published the most comprehensive systematic treatment of the blastoids since Etheridge and Carpenter's work of 1886.

In 1964, during a visit of Macurda with Breimer in Amsterdam, we discovered that we both had mutual interests in problems of blastoid evolution and different approaches than utilized by previous workers: Breimer with his internal anatomical studies and Macurda with his quantitative ontogenetic treatment. We felt these types of studies could provide a clearer insight into the morphology and evolution of the blastoids than previous efforts which were based on limited data and inadequate illustrations and study. Therefore, in 1967, we commenced a study of half of the blastoids, the fissiculates (those which lack hydrospire pores, and have completely or partially exposed hydrospire systems or hydrospire clefts). These forms, which range from Silurian through Permian, are ancestral to the spiraculates which we intend to monograph in a later project. During this study we have had two advantages over earlier workers: direct primary access to all known material in both laboratory and field, throughout the world, and new strategies by which to understand these organisms. Readers conversant with the Treatise will find many changes and additions. We do not belabor these but feel they are a natural outgrowth of the vast amount of new information accumulated during this study. We wish the following to be considered as a progress report in understanding the blastoids; it summarizes and tries to interpret as clearly as possible everything we now know, but the continued discovery of new forms and new methods of study will require its revision.

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CHAPTER I

SYSTEMATICS

INTRODUCTION

The means of arranging organisms into a taxonomic hierarchy is divided between different schools. The systematics which we propose in the following chapter is an evolutionary taxonomy. For the first two years of this study, we avoided any discussion of higher taxonomic units than species and confined our attention to the accumulation of all the information we could gather on each species. (Our definition of a species is based upon the zoological concept of interbreeding populations; in paleontology this can only be simulated by studying the distribution of many characteristics within local populations from a single stratigraphic horizon. For further discussion see MACURDA, 1965^{b}, p. 1054–5). With all basic information in hand in 1969, we looked at the geographic and stratigraphic distribution of approximately 20 characters. These appear to have natural groupings which led to the genera and families as defined below. Our classification is completely different from that of FAY and WANNER, 1967; different criteria are used in the generic and familial definitions. The largest change is in the families. Previously these were defined on the basis of 1 invariant character per family. By employing large numbers of characters and viewing them within the framework of an evolutionary model, we feel our classification much more closely approaches an evolutionary taxonomy and facilitates the interpretation of blastoid evolution.

SYSTEMATIC PALEONTOLOGY

CLASS BLASTOIDEA

ORDER FISSICULATA

I. Family PHAENOSCHISMATIDAE Etheridge & Carpenter 1886

Diagnosis: theca conical or biconical with distinct ambulacral sinuses and interambulacral pyramids; – deltoids with pronounced DR sectors, developed only in ambulacral sinuses, and with incipient DD sectors, allowing ambulacra to almost reach peristome; deltoid crest generally sloping upward; – ambulacra linear to lanceolate (rarely petaloid); lancet generally concealed; many side plates and brachioles; – hydrospire groups generally developed across full width of RD suture; hydrospire slits parallel to longer axis of ambulacrum, may be partly or entirely concealed by side plates; – composition of anal area generally complex: one superdeltoid present, either one subdeltoid or two cryptodeltoids and a hypodeltoid; exceptionally only epi- and hypodeltoid present, if so epideltoid unusually shaped as a two-winged plate; hypodeltoid may be atrophied; subdeltoid or cryptodeltoids forming anal hydrospires, if present; exceptionally also formed on epideltoid. *Sil.* – *Miss.;* N. Am., Eur.

Genera assigned: *Phaenoschisma* Etheridge and Carpenter, 1882, type genus (1.9), *Caryoblastus* Breimer, Macurda, and Prokop 1968 (1.4), *Cryptoschisma* Etheridge and Carpenter 1886 (1.5), *Decaschisma* Fay 1961^b (1.1), *Dolichoblastus* n. gen. (1.11), *Heteroschisma* Wachsmuth 1883 (1.8), *Kazachstanoblastus* Arendt, Breimer, and Macurda 1968 (1.12), *Leptoschisma* n. gen. (1.3), *Pentremitidea* d'Orbigny 1850 (1.6), *Phaenoblastus* Fay 1961^b (1.10), *Pleuroschisma* Reimann 1945 (1.7), *Polydeltoideus* Reimann and Fay 1961 (1.2).

1.1 Genus *Decaschisma* Fay 1961^b

Type species: *Codaster pulchellus* Miller & Dyer 1878, by designation herein (synonym: *Codaster pentalobus* Hall 1879). (Pl. I, figs. 1–3).

Diagnosis: theca biconical in lateral profile, pentagonal to pentalobate in plan view; vault low; angle of ambulacral sinus 50°–70°; interambulacral pyramids moderately developed; deltoid crest sloping moderately upward from origin; – ambulacra linear; lancet concealed; – 10 hydrospire groups, number of hydrospire slits strongly reduced in anal interarea; hydrospire slits partly concealed by ambulacrum; – 3 anal deltoids: super-, sub-, and hypodeltoid; gonopore present in suture between super- and subdeltoid; subdeltoid forms anal hydrospires; hypodeltoid contributes to external wall of theca. *Sil.*; Ind., Tenn., USA.

– Other Species assigned: none.

1.2 Genus *Polydeltoideus* Reimann & Fay 1961

Type species: *P. enodatus* Reimann & Fay 1961, by original designation. *Sil.*; Okla., USA. (Pl. I, figs. 8, 12).

Diagnosis: theca biconical in lateral profile, slightly pentalobate in plan view; vault low; angle of ambulacral sinus 90°; interambulacral pyramids low; deltoid crest sloping slightly upward from origin; – ambulacra linear, lancet concealed; – 10 hydrospire groups, number of hydrospire slits strongly reduced in anal interarea; hydrospire slits partly concealed by ambulacrum; – 5 anal deltoids: super-, sub-, 2 para-, and a hypodeltoid; gonopore present in suture between super- and subdeltoid; subdeltoid forms anal hydrospires; hypodeltoid contributes to external wall of theca. *Sil.*; Okla., USA; Bohemia, Czechoslovakia (?).

– Other Species assigned:
  (?) *Polydeltoideus plasovae* Prokop 1962; *L. Dev.*; Bohemia, Czechoslovakia.

1.3 *Leptoschisma* Breimer & Macurda new genus

Type species: Codaster lorae Dunbar 1920, by original designation herein. (Pl. I, figs. 4–7).

Diagnosis: theca obconical in lateral profile, pentagonal in plan view, vault moderate; angle of ambulacral sinus 50°; interambulacral pyramids not very prominent; deltoid crest sloping moderately upward from origin; – ambulacra linear, lancet concealed; – 10 hydrospire groups, number of hydrospire slits generally reduced in anal interarea; hydrospire slits mostly concealed by ambulacrum; – 3 anal deltoids: super-, sub-, and hypodeltoid; gonopore present between super- and subdeltoid; subdeltoid forms anal hydrospires; hypodeltoid inferred to be present in horizontal position aboral from anus. *L. Dev.*, Tenn., USA.

– Other Species assigned: none

Comparison: Leptoschisma is distinguished from other genera in its family by its number of anal deltoids and by the configuration and relative prominence of the vault.

1.4 Genus *Caryoblastus* Breimer, Macurda & Prokop 1968

Type species: C. bohemicus Breimer, Macurda & Prokop 1968, by original designation. *L. Dev.;* Bohemia. (Pl. I, figs. 10, 11).

Diagnosis: theca with low conical, concave pelvis and high parabolic vault in lateral profile, pentagonal in plan view; angle of ambulacral sinus 35°; interambulacral pyramids strongly developed; deltoid crest sloping steeply upward from origin; – ambulacra linear, lancet concealed; – 10 hydrospire groups, number of hydrospire slits most always reduced by one in anal interarea; hydrospire slits concealed by ambulacrum, not occupying full width of RD suture; hydrospires conjoined internally; – 4 anal deltoids: super-, two crypto-, and a hypodeltoid; gonopore present in suture between superdeltoid and one of the cryptodeltoids; both cryptodeltoids form anal hydrospires; hypodeltoid inferred to be present in subhorizontal position aboral from anus. *L. Dev.*; Bohemia, Czechoslovakia; Spain.

– Other Species assigned:
Caryoblastus sp., *L. Dev.*, Spain. (Pl. I, figs. 15, 16).

1.5 Genus *Cryptoschisma* Etheridge & Carpenter 1886

Type species: Pentremites schultzii De Verneuil & d'Archiac, 1845, by monotypy. (Pl. I, figs. 9, 13, 17).

Diagnosis: theca conical in lateral profile, pentagonal in plan view; vault very low, slightly convex; angle of ambulacral sinus 120°; interambulacral pyramids faint; deltoid crest sloping slightly upward from origin; – ambulacra petaloid, in contact with deltoid crest at greatest width; lancet completely exposed; – 8 hydrospire groups; hydrospire slits concealed by ambulacrum; – 4 anal deltoids: super-, two crypto-, and a hypodeltoid; hypodeltoid does not contribute to external wall of theca; – strong secretion of secondary calcite on basals. *L. Dev.*, Spain.

– Other Species assigned: none.

1.6 Genus *Pentremitidea* d'Orbigny 1850, (Synonym: *Deltoschisma* Fay 1961[b])

Type species: Pentremites pailletti De Verneuil 1844, by subsequent designation of ETHERIDGE & CARPENTER 1886, p. 173. *L. Dev.*, Spain (Pl. I, figs. 22–24).

Diagnosis: theca conical in lateral profile, slightly pentalobate in plan view; vault low; angle of ambulacral sinus 70°–85°; interambulacral pyramids not very prominent; deltoid crest sloping moderately upward from origin; – ambulacra linear to lanceolate, lancet concealed; – 8 hydrospire groups, hydrospire slits almost or completely concealed by ambulacrum; – 4 anal deltoids: super-, two crypto-, and a hypodeltoid. *L. Dev.*, Spain.

– Other Species assigned:
  Pentremitidea archiaci (Etheridge & Carpenter 1882); *L. Dev.*, Spain. (Pl. I, figs. 14, 18–21).
  Pentremitidea lusitanica Etheridge & Carpenter 1882; *L. Dev.*, Spain. (Pl. II, figs. 2, 3).

1.7 Genus *Pleuroschisma* Reimann 1945

Type species: Pentremites lycorias Hall 1862, by original designation. (Synonyms: *Pleuroschisma ontario* Reimann 1945, *Pleuroschisma hibbardi* Reimann 1945). *M. Dev.*, N.Y., USA; Ont., Canada. (Pl. II, figs. 4, 7, 8, 10).

Diagnosis: theca biconical in lateral profile, pentagonal in plan view; vault high; angle of ambulacral sinus 60°–80°; interambulacral pyramids strongly developed; deltoid crest sloping moderately upward from origin; – ambulacra linear, lancet concealed; – 10 hydrospire groups, number of hydrospire slits in anal interarea equal or almost equal to strongly reduced; hydrospire slits widely exposed; – 4 anal deltoids: super-, two crypto-, and a hypodeltoid; gonopore present in suture between superdeltoid and cryptodeltoids; cryptodeltoids form anal hydrospires, hypodeltoid contributing to external wall of theca. *L. Dev.*, Spain; *M. Dev.*, N.Y., USA; Ont., Canada.

– Other Species assigned:
  Pleuroschisma verneuili (Etheridge & Carpenter 1882), (Synonym: *Phaenoschisma nobile* Etheridge & Carpenter 1883. *L. Dev.*, Spain. (Pl. II, figs. 5, 9, 11).

1.8 Genus *Heteroschisma* Wachsmuth 1883, (Synonym: *Trionoblastus* Fay 1961[b]).

Type species: Heteroschisma gracile Wachsmuth 1883, by original designation. *M. Dev.*, Mich., USA. (Pl. III, figs. 10, 11).

Diagnosis: theca biconical in lateral profile, pentagonal in plan view; vault low to moderate; angle of ambulacral sinus 80°–155°; interambulacral pyramids faint to moderate; slope of deltoid crest variable from slightly downward to moderately upward; – ambulacra linear to lanceolate, lancet concealed; – 8 hydrospire groups, hydrospire slits exposed; – 2 anal deltoids, super- and subdeltoid, hypodeltoid atrophied; gonopore present in suture between super- and subdeltoid. *M. Dev.*; N. York, Ohio, Ind., Ky., Mich., Ill., Iowa, Mo., USA; Ont., Canada.

– Other Species assigned:

Heteroschisma alatum (Reimann 1935); *M. Dev.*, Mich., USA. (Pl. III, figs. 7–9).

Heteroschisma alternatum (Lyon 1857); *M. Dev.*, N.Y., Ind., Ohio, Ky., USA. (Pl. III, figs. 1, 2, 5, 6).

(Synonyms: *Codaster americanus* Shumard 1858,
Codaster pyramidatus Shumard 1858,
Codaster robustus Cline & Heuer 1950).

Heteroschisma canadense (Billings 1869); *M. Dev.*, Ont., Canada. (Pl. III, figs. 3, 4).

(Synonym: *Codaster hindei* Etheridge & Carpenter 1882)

Heteroschisma subtruncatum (Hall 1858); *M. Dev.*, Iowa, USA. (Pl. III, figs. 15, 20).

1.9 Genus *Phaenoschisma* Etheridge & Carpenter 1882.

Type species: Pentatrematites acutum G. B. Sowerby 1834, by subsequent designation of ETHERIDGE & CARPENTER 1886, p. 273. *L. Carb.*, Eng., Ire. (Pl. IV, figs. 3, 5, 10, 14).

Diagnosis: theca biconical in lateral profile, pentagonal in plan view; vault moderate; angle of ambulacral sinus about 90°; interambulacral pyramids low to moderate; slope of deltoid crest variable from slightly downward to moderately upward; – ambulacra lanceolate, half of width of lancet exposed; – 10 hydrospire groups, number of hydrospire slits in anal interarea slightly reduced; hydrospire slits partially exposed; – 2 anal deltoids: epi- and hypodeltoid; gonopore formed by epideltoid; anal hydrospires formed by epideltoid; hypodeltoid rudimentary, not contributing to external wall of theca. *L. Carb.*; Eng., Ire.; *Miss.*; Ind., Ill., Mo., Okla., N. M., USA.

– Other Species assigned:

Phaenoschisma chouteaui Macurda 1964; *Miss.*; Mo., USA. (Pl. III, figs. 16, 21, 23).

Phaenoschisma conicum (Fay 1962); *Miss.*; N.M., USA. (Pl. III, figs. 18, 24, 25).

Phaenoschisma gracillimum (Rowley & Hare 1891); *Miss.*; Ill., Mo., USA. (Pl. III, figs. 14, 19).

Phaenoschisma laeviculum (Rowley 1900); *Miss.*; Mo., Okla., USA. (Pl. III, figs. 26, 27; Pl. IV, figs. 19, 21).

(?) *Phaenoschisma benniei* Etheridge & Carpenter 1886; *L. Carb.*; Scotland. (Pl. V, figs. 8, 11, 13).

(?) *Pentremoblastus conicus* Fay & Koenig 1963; *Miss.*; Ill., USA. (Pl. IV, figs. 4, 9).

(?) *Phaenoschisma rossica* Arendt, Breimer & Macurda 1968; *L. Carb.*, USSR. (Pl. V, figs. 12, 15).

(?) *Phaenoschisma saharae* n. sp.

Phaenoschisma? *saharae* n. sp.

Pl. V, figs. 4, 5, 10

Pentremites sp., Pareyn, 1961, t. 2, p. 223, 224.

Type: Holotype – Coll. Pareyn, no. 437a, Université de Caen, France. *L. Carb.*, Visean-Namurian, Algeria.

Diagnosis: A *Phaenoschisma* ? with a conical pelvis, short vault, with a narrow lancet, exposed throughout the ambulacral length, and prominent hypodeltoid which contributes to the external thecal wall. BA axis lacking.

Description: Three specimens known. Theca of moderate size, conical in lateral view, with short, broadly convex, slightly angular vault and conical pelvis with a straight or very slightly convex profile. Outline in plan view pentagonal, with slightly concave interambulacral areas; greatest width at ambulacral tips which are angular. Length about twice the width. Approximate dimensions smaller specimen (Pl. V, fig. 10): L.: 15.2 mm; W.: 8.7 mm; vault: 3.5 mm; pelvis: 11.7 mm.

Basalia three, in normal position, pentagonal in plan view, becoming rounded proximally, conical in lateral view, forming approximately one-half of the pelvis. Stem attachment area broad (2.5 mm), formed by secondary calcite secretion; proximal surface almost flat with crenellae almost at edge.

Radials quadrate in plan view, projecting slightly above peristome, with two straight or a convex lower edge(s); lateral edges slightly convex, widening up to plane of ambulacral tip, then contracting adorally; upper edges slightly concave, confined to ambulacral sinus, inclined inward toward one another. Parabolic sinus indents upper one-third of radial with small lip with keel at aboral end. RD sector confined to moderate ambulacral sinus. Hydrospire slits developed in adoral part of sector, apparently infilled in aboral part; slits do not occupy outermost part of RDF.

Deltoids four, together with epideltoid forming border to peristome; aboral parts confined to ambulacral sinus. Deltoid hexagonal in plan view, slightly concave in lateral view due to deltoid crest which rises above peristome. Adoral part of deltoid small. Crest originates at narrowest exposed point of deltoid, curves slightly upward from its origin to interambulacral pyramid; sides curve downward into ambulacral sinus; only aboral part of DR sector ornamented with hydrospire slits, adoral part apparently being infilled.

Anal deltoids apparently two, an epi- and hypodeltoid. Configuration of epideltoid as for adoral and lateral parts of regular deltoid, except position corresponding to crest now occupied by anus and hypodeltoid. Epideltoid prongs extend to radial, forming part of ambulacral sinus. Anus ovoid, opens directly upward, level slightly below that of peristome. Hypodeltoid of moderate size, pentagonal in outline, projecting upward to form counterpart of regular interambulacral pyramid. Aboral surface almost vertical, slopes steeply downward on outer surface of theca to external part of very slightly convex hyporadial suture. Surface is ornamented with growth lines as is external portion of anal RD sectors. Lateral surfaces of hypodeltoid slope downward into adjacent ambulacral sinuses, smooth; lower edge against radial in aboral part and epideltoid in adoral part; V-shaped. Epi-hypodeltoid suture straight; slopes upward to level of anus. Adoral face of hypodeltoid concave, dropping steeply down into anus.

Ambulacra five, positioned in ambulacral sinus which they moderately fill; almost reaching peristome. In plan view ambulacrum sublanceolate in smaller specimen, becoming almost linear in larger; slightly convex in lateral view. Strongly convex in cross section except for indentation of ambulacral tract. Lancet exposed along midline of ambulacrum (0.4 mm), almost to aboral tip. Side plates quadrate, with straight ad- and aboral edges which incline aborally from ambulacral midline; outer aboral edge of side plate embayed by large triangular side plate which forms part of lateral edge of ambulacrum. Detail of brachiolar facet not preserved, on outer sloping edge of convex ambulacrum. 3 side plates per mm.

Ten hydrospire groups, developed in middle portion of ambulacral sinus; ad- and aboral parts of sinus are smooth, apparently a result of secondary infilling of slits by calcite. Hydrospire slits extend from ambulacrum out to near end of radiodeltoid suture but not occupying its full width. Functional area of each hydrospire group thus has a somewhat ovoid outline. Hydrospire slits completely exposed except for those near or beneath ambulacral overhang. Number of hydrospire slits in anal interarea reduced. Dimensions for larger specimen (437b): No. Reg. Hydro. Sl.: 9; W. Fld.: 1.4 mm; No. Anal Hydro. Sl.: 4(a); W. Fld.: 0.5 mm.

Remarks: The above description is based upon two specimens from the collections of Professor Claude Pareyn, Université de Caen, nos. 437a and b; the former is designated as the holotype. The smaller specimen is somewhat crushed and the oral region faulted; the larger is missing most of its basals and weathered. Intrastratal solution has affected the detail of the oral area in these specimens and some of the calcite has been altered to a brown microcrystalline calcite, thus obliterating some sutures. Cleavage reflections on the C side of the anus of 437a appear to indicate that the prong beside the anus can be traced into what would correspond with the adoral part of the epideltoid but this is not certain. The critical area where a suture would be is weathered in the larger specimen. A third specimen (Pareyn Coll. no. 518) from a different locality does not permit a resolution of this question.

This blastoid belongs to the family Phaenoschismatidae because of ambulacral sinuses, interambulacral pyramids, thecal and ambulacral shape. If it has only two anal deltoids, then this characteristic is shared in common with other representatives of the same age. The partial closure of the hydrospire slits is a feature seen in some other Mississippian blastoids. Uncertainties concerning the anal deltoids do not permit a positive generic assignment but if there is an epi- and hypodeltoid, this most closely resembles a new Lower Mississippian genus from Montana being described by James Sprinkle and Raymond Gutschick. They will re-assign it to their genus. It differs from their form in the partial closure of the hydrospire slits. The specific name is derived from its occurrence in the western Sahara.

Occurrence: (1) Couverture stratifiée du Djebel Ioucha (massifs récifaux du Grand Erg occidental, rive gauche de la Zousfana), Horizon: Ioucha 10 (= Dalle à *Syringothyris*), Formation d'Akacha-Mazzer, Zone P^2 (Viséen supérieur) (no. 437a and b), (2) Col du Teniet el Aouidja au Nord du Chabet el Oubeur (rive gauche de la Zousfana), Horizon: "Mouizeb el Atchane" (Sommet de la formation d'El Guelmouna), zone E^1, Namurien inférieur (no. 518). Sahara occidental. (Pareyn, personal communication). Both of these localities are just southeast of Bechar in northwest Algeria, Département de la Saoura, near the Moroccan border. The first is at 31° 5′ N, 1° 32′ W, the second and stratigraphically higher is at 31° 1′ N, 2° 4′ W. For further detail, see the geologic maps which accompany Pareyn, 1961. The discovery of this form by Professor Pareyn is very significant as it fills a void in our knowledge of Upper Mississippian or Upper Visean-Lower Namurian fissiculate blastoids.

1.10 Genus *Phaenoblastus* Fay 1961^b

Type species: *Pentremites caryophyllatus* De Koninck & Le Hon 1854, by original designation. *L. Carb.*, Belg. (Pl. IV, figs. 8, 12).

Diagnosis: theca obconical in lateral profile, rounded pentagonal in plan view, vault prominent; angle of ambulacral sinus 95°; interambulacral pyramids moderately developed, deltoid crest curving downward from origin; – ambulacra petaloid, lancet broadly exposed; – 10 hydrospire groups, number of hydrospire slits reduced in anal interarea; hydrospire slits partially exposed; – 4 anal deltoids: super-, two crypto-, and a hypodeltoid; cryptodeltoids form anal hydrospires; hypodeltoid inferred to be present, not contributing to external wall of theca. *L. Carb.*, Belg.; *Miss.*, Mo., USA.

– Other Species assigned:
Phaenoblastus pecki (Macurda 1964), *Miss.*, Mo., USA. (Pl. IV, figs. 11, 15, 18).

(?) 1.11 *Dolichoblastus* Breimer & Macurda new genus

Type species: *Codaster shimanskii* Arendt, Breimer & Macurda 1968, by original designation herein. (Pl. VI, figs. 1, 4).

Diagnosis: theca conical in lateral profile, pentagonal in plan view, vault low; angle of ambulacral sinus 110°; interambulacral pyramids faint; upper surface of deltoid elevated above peristome; deltoids develop moderate DD growth sector; – ambulacra lanceolate, lancet narrowly exposed along adoral half of ambulacrum; – 8 hydrospire groups, hydrospire slits exposed; – 2 anal deltoids, epi- and hypodeltoid; hypodeltoid present in horizontal position aboral from anus; – radial wings present along interradial sutures. *L. Carb.*, Kazachstan, USSR.

– Other Species assigned: none.

Comparison: *Dolichoblastus* is distinguished from other genera in its family by the number of anal deltoids, reduction of the ambulacral sinuses, and presence of radial wings.

(?) 1.12 Genus *Kazachstanoblastus* Arendt, Breimer & Macurda 1968.

Type species: *K. carinatus* Arendt, Breimer & Macurda 1968, by original designation. (Pl. V, figs. 14, 16, 17).

Diagnosis: theca rounded biconical in lateral profile, pentagonal in plan view; vault high, angle of ambulacral sinus 85°; interambulacral pyramids strongly developed; deltoid crest sloping moderately upward from origin; – ambulacra sublanceolate; lancet exposed over entire length of ambulacrum; – regular hydrospire structures absent; – 2 anal deltoids; epi- and hypodeltoid; hypodeltoid not contributing to external wall of theca. *L. Carb.*, Kazachstan, USSR.

– Other Species assigned: none.

2. Family OROPHOCRINIDAE Jaekel 1918

Diagnosis: theca typically with broadly conical pelvis and convex vault; ambulacral sinuses absent; – deltoids with incipient DD sectors and external DR sectors, allowing ambulacra to reach peristome; – ambulacra long, linear to lanceolate, convex lengthwise; many side plates and brachioles; lancet concealed or exposed; – primitively hydrospire slits exposed in concave areas next to ambulacra, but gradually concealed by ambulacra, becoming closed off by lateral contact of side plates and radials, may be atrophied in later members; in forms with closure, infilling and overgrowth of hydrospires by secondary radial calcite; – composition of anal area complicated in early members, becoming simplified in later members; subdeltoid, cryptodeltoids, and usually epideltoid forming anal hydrospires; usually large hypodeltoid present contributing to external wall of theca; – secondary calcite may be deposited on external surfaces of radials and deltoids, producing radial prongs and elevated deltoids. *M. Dev.-Perm.*; N. Am., Eur., S. Afr., S. Am. (?), S.E. Asia.

Genera assigned: *Orophocrinus* Von Seebach 1865, type genus (2.3), *Brachyschisma* Reimann 1945 (2.1), *Katoblastus* Macurda 1967^a (2.2), *Acentrotremites* Etheridge and Carpenter 1883 (2.4), *Mastoblastus* Arendt, Breimer, and Macurda 1968 (2.5), *Pentablastus* Sieverts-Doreck 1951 (2.6), *Anthoblastus* Wanner 1924^b (2.7).

2.1. Genus *Brachyschisma* Reimann 1945

Type species: *Codaster corrugatus* Reimann 1935, by original designation. (Synonyms: *Codaster curtus* Reimann 1935 , *Brachyschisma subumbrosum* Reimann 1945, *Brachyschisma subcrassum* Reimann 1945). *M. Dev.*, USA. (Pl. VI, figs. 2, 5, 6, 15).

Diagnosis: theca with conical pelvis and restricted basal circlet and low hemispherical vault; decagonal in plan view; – ambulacra lanceolate, conspicuous; lancet concealed; – 9 hydrospire groups, that on *D* anal side absent; hydrospire slits exposed, situated in shallow, restricted concavities on both sides the ambulacra; number of hydrospire slits in *C* anal group reduced; – 3 anal deltoids, super-, sub-, and hypodeltoid; subdeltoid forms *C* anal hydrospires; hypodeltoid contributing to external wall of theca. *M. Dev.*; N.Y., USA. *Dev.*, S. Afr., S. Am. ?

– Other Species assigned:
Brachyschisma oostheizeni Breimer & Macurda n. sp. *Dev.*, S. Afr.

Brachyschisma? *oostheizeni* n. sp.
Pl. VI, figs. 3, 10

Type: Holotype: specimen in Oostheizen collec., Zwartskraal, Prince Albert, South Africa in Pl. VI, fig. 3. To be deposited in South Africa Museum, Cape Town. *Dev.*, S. Afr.

Diagnosis: A *Brachyschisma* species with conical theca, broadly convex angular vault, convex deltoids, and fine to moderate growth lines.

Description: Six specimens known. Theca broadly conical, with wide, broad convex vault, and conical pelvis; profile of latter slightly concave near tip of radials. Pelvis approximately two-three times length of vault. Greatest width at aboral tips of ambulacra; cross section here angular decagonal with indented interambulacral areas. Thecas of intermediate size, length and width, about subequal, largest specimen approaches 20 mm. Pelvic angle large.

Basals form conical base of theca, tapering to a proximal stem attachment area. Detail of latter unknown, diameter approximately 1.5 mm. Azygous basal unknown.

Radials five, forming upper half of pelvis and part of vault profile. In lateral view radial is triangular, with straight base along interradial suture, slightly convex oral facing edge and slightly concave basal facing edge. Height of radial large relative to width. In plan view radial is hexagonal, with straight lateral edges, slightly convex lower edges, and straight upper edges; moderate radial sinus. Aboral tip of radial a rounded point. RD sector at pronounced angle to RR sector, former being part of upper convex surface, latter part of vertical side of calyx. RD sector forms slightly sloping shoulder to ambulacrum which is strongly elevated above it. Aborally, RD sector becomes less distinct and merges into round tip of radial.

Deltoids four, bordering peristome, adoral end small, aboral part relatively much larger, both rhombic-shaped. Deltoid is slightly convex in lateral view; adoral part apparently relatively flat, aboral part has very pronounced hump in center (up to 0.8 mm above edges) which extends to edge of calyx outline; slopes downward laterally to lowest edge of ambulacra and into slightly concave RD sector.

Number of anal deltoids unknown. Hypodeltoid present, with slightly convex aboral suture, lies in same plane as anal sector of RD sector of *D* radial, merging evenly with it. Anus opens on upper surface of calyx; outline indeterminate.

Ambulacra five, lanceolate rounded tip (tip of radial projecting slightly beyond), convex in lateral view, strongly elevated above surrounding plates at RD suture (up to 0.8 mm), decreasing ad- and aborally therefrom. Form high points of vault profile. Lancet concealed. Pentagonal side plates form two rows of plates centered along ambulacral groove. Form half of ambulacral width, slope inward toward food groove. Outer side plates form outward sloping and vertical edges of ambulacrum, completely separating side plates from radial or deltoid. 3 side plates per mm.

Eight hydrospire groups preserved, outline triangular, with slits in slight concavity in RD sector on aboralmost part of deltoid occupying full width of RDF. Lacking on *D* side of anus. *C* side not observed. Five to eight hydrospires observed in different specimens; most of length is developed on radial, very short on deltoids.

Remarks: The above description is based on six fragmentary specimens preserved as external casts in a greenish shale. They are too fragile to permit casting. The only other Devonian blastoid which resembles them in form is *Brachyschisma* but the lack of knowledge on the number of anal deltoids prevents a generic assignment of this form.

These specimens were collected by Mr. Roy Oostheizen, Zwartskraal, Prince Albert, South Africa, and will be deposited by him in the South African Museum, Cape Town.

2.2 Genus *Katoblastus* Macurda 1967^{a}

Type species: *Pentremites pūzos* Münster 1843, by original designation. *L. Carb.*, Belg. (Pl. VI, figs. 9, 11, 14).

Diagnosis: theca obconical with prominent vault; pentagonal in plan view; – ambulacra linear to lanceolate, not conspicuous, lancet exposed for $\frac{2}{3}$ of ambulacral length; – 10 hydrospire groups, number of hydrospire slits generally slightly reduced in anal interarea, hydrospire slits almost completely concealed; hydrospire cleft extending full length of ambulacrum; – 4 anal deltoids: super-, 2 crypto-, and a hypodeltoid; cryptodeltoids form anal hydrospires; hypodeltoid contributing to external wall of theca. *L. Carb.*, Belg.

– Other Species assigned:
  Katoblastus konincki Macurda 1967^{a}, *L. Carb.*, Belg. (Pl. VI, figs. 7, 8, 12).

2.3 Genus *Orophocrinus* Von Seebach 1865

Type species: *Pentremites stelliformis* Owen & Shumard 1850, by original designation. *Miss.*, Ill., Iowa, Mo., USA. (Pl. VII, figs. 9–11).

Diagnosis: theca with conical or concave-conical pelvis and convex vault of variable height, pentagonal to decagonal in plan view; – ambulacra linear to lanceolate, conspicuous; lancet exposed throughout length of ambulacrum; – 10 hydrospire groups, hydrospire folds conjoined internally, hydrospire slits completely concealed, not reduced in number in anal interarea; opening to hydrospire group a restricted hydrospire cleft, ranging from $\frac{1}{3}$ to $\frac{2}{3}$ ambulacral length; – 2 anal deltoids: epi- and hypodeltoid; epideltoid forms anal hydrospires, hypodeltoid subhorizontal, contributing to external wall of theca; – radial growth under aboral part of lancet progressively closing off hydrospire cleft. *L. Carb., (Tourn.* and *Viséan)*, Eng., Ire., Belg.; *Miss. (Kinderhookian* and *Osagean)*, Ill., Iowa, Mo., Ark., Okla., N. M., Ariz., Mont., USA.

– Other Species assigned:
  Orophocrinus catactus Macurda, 1965^{b}; *Miss.*, Mo., Ark., Okla., N. M., USA. (Pl. VIII, figs. 2, 5).
  Orophocrinus celticus Macurda 1965^{b}; *L. Carb.*, Ire. (Pl. IX, figs. 1, 2).
  Orophocrinus conicus Wachsmuth & Springer 1888; *Miss.*, Iowa, USA. (Pl. VII, figs. 1, 2, 4; Pl. IX, fig. 7).
  Orophocrinus gracilus (Meek & Worthen 1870); *Miss.*, Iowa, Mo., USA. (Pl. VII, figs. 5–7).
  Orophocrinus orbignyanus (De Koninck 1844); *L. Carb.*, Belg. (Pl. VII, figs. 3, 8).

Orophocrinus pentangularis (Sowerby 1834); *L. Carb.*, Eng., Ire. (Pl. IX, figs. 3, 6).

Orophocrinus praelongus Bailey 1886; *L. Carb.*, Ire. (Pl. VIII, figs. 1, 3; Pl. IX, figs. 4, 5).

Orophocrinus saltensis Macurda 1965b; *Miss.*, Ariz. (Pl. IX, figs. 8, 9; Pl. X, fig. 4).

Orophocrinus verus (Cumberland 1826); *L. Carb.*, Eng., Ire. (Pl. VIII, figs. 4, 6; Pl. X, fig. 7).

2.4 Genus *Acentrotremites* Etheridge & Carpenter 1883

Type species: *Mitra elliptica* Cumberland 1826, by monotypy. (Pl. X, figs. 3, 5).

Diagnosis: theca with flattened base, and prominent parabolic vault; pentagonal in plan view; – ambulacra sublanceolate, not conspicuous; lancet concealed; – 10 hydrospire groups, hydrospire folds conjoined internally, hydrospire slits completely concealed, hydrospire cleft present along ambulacra, extending half of length of ambulacra; radial margin bordering ambulacra serrate, breaking up hydrospire cleft into openings resembling hydrospire pores; – anal deltoids 2 or 4; hypodeltoid subvertical, contributing to external wall of theca; – radial growth progressively closing off hydrospire cleft. *L. Carb.*, Eng., Wales.

– Other Species assigned: none.

2.5 Genus *Mastoblastus* Arendt, Breimer, & Macurda 1968

Type species: *M. ornatus* Arendt, Breimer, & Macurda 1968, by original designation (Pl. X, figs. 1, 2, 6).

Diagnosis: theca obconical with prominent vault; pentagonal in plan view; – ambulacra sublanceolate, conspicuous; lancet exposed throughout length of ambulacrum; – hydrospires rudimentary or vestigial; hydrospire cleft almost completely eliminated; – 2 anal deltoids: epi- and hypodeltoid; hypodeltoid subhorizontal, contributing to external wall of theca; – radials involved in formation of saclike structures in interambulacral position. *L. Carb.*, Kazachstan, USSR.

– Other Species assigned: none.

2.6 Genus *Pentablastus* Sieverts-Doreck 1951

Type species: *P. supracarbonicus* Sieverts Doreck 1951, by original designation. (Pl. IX, figs. 10–12).

Diagnosis: theca ellipsoidal with depressed base; vault very prominent; pentagonal in plan view; – ambulacra sublanceolate, not conspicuous; lancet concealed; – 10 hydrospire groups, hydrospire folds conjoined internally, hydrospire slits completely concealed, not reduced in number in anal interarea; opening to hydrospires a restricted hydrospire cleft, extending $\frac{1}{3}$ of length of ambulacrum; – 2 anal deltoids, epi- and hypodeltoid; epideltoid forms anal hydrospires; hypodeltoid subvertical, contributing to external wall of theca; – radial growth under aboral part of lancet progressively closing off hydrospire cleft, also incorporating aboral parts of hydrospires; – radials divided into infra- and supraradials. *M. Carb.*, Spain.

– Other Species assigned: none.

2.7 Genus *Anthoblastus* Wanner 1924^b.

Type species: *A. brouweri* Wanner 1924^b, by original designation. *Perm.*, Timor, Indonesia. (Pl. XI, figs. 1–3).

Diagnosis: theca with wide outward flaring pelvis and broadly arcuate vault; stellate in plan view; deltoids conspicuous, pentagonal to hexagonal; – ambulacra depressed, elongate, lanceolate; lancet in form of elongate scoop, exposed; – 10 hydrospire groups, one folded hydrospire sac in each group mostly formed by deltoids, opening to hydrospire sac via short cleft mostly between lancet and deltoid; – 2 anal deltoids, epi- and hypodeltoid; epideltoid forming anal hydrospire sacs, hypodeltoid pronged, contributing to external wall of vault; – deposition of calcite on outer surface of radial and deltoids. *Perm.*, Timor, Indonesia.

– Other Species assigned:
Anthoblastus stelliformis Wanner 1924^b; *Perm.*, Timor, Indonesia. (Pl. XI, figs. 5, 6, 8, 9).

3. Family NYMPHAEOBLASTIDAE Wanner 1940

Diagnosis: theca ovoid or globose; ambulacral sinuses absent; – deltoids with incipient DD sectors and external DR sectors, allowing ambulacra to reach peristome; subdued deltoid crest in early members; – ambulacra linear to sublanceolate, convex lengthwise and extending almost to base of theca; lancet concealed or exposed, with many side plates and brachioles; – hydrospire slits numerous, developed across full width of RD suture, except in ultimate members, parallel longer axis of ambulacrum, completely exposed, except in ultimate member; secondary infilling of hydrospire slits may occur; – composition of anal area apparently simple: epi- and hypodeltoid, either one or the other forming anal hydrospires. *Dev.-Perm.*, N. Am., Eur., S. Afr., Asia, Austr.

Genera assigned: *Nymphaeoblastus* Von Peetz 1907, type genus (3.3), *Pachyblastus* n. gen. (3.1), *Xenoblastus* n. gen. (3.2), *Sphaeroschisma* Wanner 1924^b (3.4).

3.1 *Pachyblastus* Breimer & Macurda new genus

Type species: *P. dicki* Breimer & Macurda new species, by original designation herein.

Diagnosis: theca with low conical pelvis and high parabolic vault; rounded pentagonal in plan view; – ambulacra linear, conspicuous, lancet exposed (?); – 10 hydrospire groups, hydrospire slits completely exposed, occupying full width of RD suture, reduced in number in anal interarea; hydrospire slits functional over entire areas of RD and DR sectors; – number of anal deltoids unknown; hypodeltoid present, contributing to external wall of theca; – subdued crest present on deltoid. *Dev.*, S. Afr.

– Other Species assigned: none.

Comparison: *Pachyblastus* is distinguished from other members of its family by its conical basals and ambulacra which extend two-thirds to three-quarters of the thecal length.

Pachyblastus dicki n. sp.
Pl. XII, figs. 1, 2; Pl. XIII, fig. 1

Type: Holotype: specimen in R. I. Dick Collec., Cape Town Univ., figured in Pl. XII, fig. 2. To be deposited in South African Museum, Cape Town, RSA. *Dev.*, Bokkeveld Beds, Road from Hex River Pass to Montague Koo, 8.7 miles south of turnoff from N9, east of de Doorns, Cape Province, S. Afr.

Diagnosis: A *Pachyblastus* species with oblate spheroidal theca, ambulacra extending two-thirds to three-quarters of thecal length, and widely exposed, well-developed hydrospire fields.

Description: Approximately 12 incomplete thecae known, preserved as molds and casts. Theca oblate spheroidal, with short, broad pelvis forming one-quarter to one-third length of theca, and tall, strongly paraboloid vault. Pelvic profile conical, slightly concave; pelvic angle about 80°. Ambulacra extend well below equator of theca, forming outline of paraboloid vault, curving inward proximally. Cross section is rounded pentagonal, with very slightly indented or inflated interambulacral areas. Greatest width subequatorial. Thecas large, being over 40 mm in length, with corresponding widths between 15 and 20 mm.

Basalia form one-half of broad conical slightly concave pelvis. Stem diameter about 2 mm. Azygous basal unknown. Zygous basal pentagonal, with concave median upper edge, slightly concave upper lateral edges, and straight lateral edges.

Radials five, forming upper half of pelvis and lower three-fourths of vault. Radials quadrate in plan view, with slightly convex lower and lateral edges; radial sinus very deep narrow V. Radial a low triangle in lateral view, with a slightly concave face on the lower edge and short proximal facing edge, and a long, convex, adorally facing edge. Entire width of RD sector occupied by hydrospire slits which extend from aboral tip of ambulacrum onto deltoid.

Deltoids are rhombic-shaped plates, being narrow near the peristome, expanding aborally and forming upper two-sevenths of parabolic vault. Deltoid is convex in lateral view and slightly convex in cross section. Adoral part of plate small, aboral part large, ornamented with a low rounded crest from which hydrospire slits extend across radiodeltoid suture, giving appearance of many inverted chevrons. Ambulacrum slightly elevated above deltoid.

Number of anal deltoids unknown. Hypodeltoid present, with pentagonal shape and corresponding to aboral part of deltoid in curvature and position on calyx. Ornament of hypodeltoid unknown; plate apparently separated from ambulacra by exposed hydrospires on prongs of epi- or other anterior deltoid.

Ambulacra five, linear in plan view, width tapering gradually aborally. Convex in lateral view, extending from near peristome to sub-equatorial position, recurving slightly proximally. Slightly elevated above surrounding plates throughout length. In cross section ambulacrum has broad, shallow, V-shaped interior with short downward-sloping lateral edges where brachioles are attached. Suggestion that lancet is exposed (up to 1 mm) given by dislocated side plates. Details of side and outer side plates unknown. Ambulacral side grooves long, 4 per mm; minor grooves only on adoral side of groove; admedial ones long. Brachiolar facets small, heart-shaped, with small ridge dividing center where two brachiolar plates attached; facet faces laterally outward on edge of ambulacrum. Brachioles preserved, more than 25 mm long.

Ten hydrospire groups, completely exposed, occupying full width of RD sector and most of aboral part of deltoid, each field being slightly convex lengthwise and triangular in outline; up to nine hydrospires per regular group, reduced to 3 in anal interarea when there are seven in a regular group (here width of fields 1.0 and 2.8 mm respectively).

3.2 *Xenoblastus* Breimer & Macurda new genus

Type species: Pentremites decussatus Shumard 1858, by original designation herein. *Miss.*, Ky., USA. (Pl. XIII, figs. 2–6, 8).

Diagnosis: theca ellipsoidal, with flat base and very prominent vault; pentagonal in plan view; – ambulacra linear, conspicuous; lancet concealed in aboral part, unknown in adoral part; – 10 hydrospire groups; hydrospire slits completely exposed, not occupying full width of RD suture; degree of reduction in number of anal hydrospire slits unknown; hydrospire slits progressively infilled in RD sector; – number of anal deltoids unknown; probably epi- and hypodeltoid; – faint crest on deltoid. *Miss.*, Ky., USA; *L. Carb.*, Belg.

– Other Species assigned:
Xenoblastus sp., *L. Carb.*, Belg. (Pl. XIII, fig. 7).

3.3 Genus *Nymphaeoblastus* Von Peetz 1907

Type species: N. miljukovi Von Peetz 1907, by original designation (?).

(Synonym: *N. anossofi* Yakovlev 1926a). *L. Carb.*, USSR., Japan. (Pl. XIV, figs. 1–5).

Diagnosis: theca ellipsoidal in lateral profile, with depressed base, and very prominent vault, rounded pentagonal in plan view; – ambulacra linear to sublanceolate; lancet probably concealed; – 10 hydrospire groups, hydrospire slits completely exposed, occupying full width of RD suture, not reduced in number in anal interarea; functional length of hydrospire slits short, especially on deltoid; – 2 anal deltoids: small epi- and large hypodeltoid; hypodeltoid forming anal hydrospires, contributing to external wall of theca. *L. Carb.; Tournaisian* and *Visean*, Kazachstan; *L. Visean.*, Turkestan; *Visean*, Japan, Austr.

– Other Species assigned:

Nymphaeoblastus kazachstanensis Yakovlev 1941; *L. Carb.*, USSR. (Pl. XIV, fig. 6).

Nymphaeoblastus bancrofti McKellar 1964; *Miss.*, Austr. (Pl. XV, figs. 2, 8).

3.4 Genus *Sphaeroschisma* Wanner 1924^b

Type species: *Sphaeroschisma somoholense* Wanner, 1924^b, by original designation. (Pl. XV, figs. 4, 5, 7).

Diagnosis: theca spheroidal, with very prominent vault, circular in plan view; – ambulacra linear, lancet exposed; – 10 hydrospire groups; hydrospire slits partially concealed by ambulacra, not occupying full width of RD suture; number of hydrospire slits per group variable; – number of anal deltoids unknown; probably epi- and hypodeltoid. *Perm.*, Timor, Indonesia.

– Other Species assigned: none.

4. Family ASTROCRINIDAE Austin & Austin 1843

Diagnosis: provisionally similar to generic diagnosis since family is mono-generic. *L. Carb.*, Eng., Scot., Ire.

Genera assigned: *Astrocrinus* Morris 1843.

4.1 Genus *Astrocrinus* Morris 1843, (Synonym: *Zygocrinus* Bronn 1848).

Type species: *A. tetragonus* (Austin & Austin 1843) by original designation. (Synonym: *A. benniei* Etheridge 1876). (Pl. XI, figs. 4, 7; Pl. XV, figs. 1, 3, 6).

Diagnosis: stalkless tetralobate theca with external bilateral symmetry according to axis through *D*-radius and *AB*-interradius; *A*, *B*, *C*, and *E* ambulacra well developed, linear, curving around theca; *D* ambulacrum short, petaloid, horizontal; – probably 3 basals, one elongate supporting small modified *D* radial; *C* and *E* radials with modified posterior limbs; – 4 anal deltoids: super-, two crypto-, and a hypodeltoid (inferred to be present); cryptodeltoids form anal hydrospires; – 10 hydrospire groups, hydrospire slits concealed by ambulacra; number of hydrospires reduced on either side of antero-posterior axis and on either side of axis of bilateral symmetry; hydrospire folds conjoined internally; entrance to hydrospires via hydrospire cleft. *L. Carb.*, Eng., Scot., Ire.

– Other Species assigned: none.

5. Family NEOSCHISMATIDAE Wanner 1940

Diagnosis: theca cylindrical to cup-shaped; wide and shallow ambulacral sinuses may be present; – deltoids with well-developed DR sectors, larger than DD sectors, which are variably developed; deltoid crest usually developed, sloping downward; – ambulacra linear to lanceolate, almost reaching peristome in early members, becoming somewhat removed in later members; may also be reduced; lancet exposed; – hydrospire slits typically numerous, developed across full width of wide RD growth front, parallel to longer axis of ambulacrum, completely exposed; secondary infilling of hydrospire slits of general occurrence, especially in later members; – composition of anal area simple: epi- and hypodeltoid; epideltoid forming anal hydrospires, which occasionally are also formed on hypodeltoid; – secondary calcite may be deposited on external surfaces of radials and deltoids, producing radial prongs and elevated deltoids. *Miss.-Perm.;* N. Am., Eur., S.E. Asia, Austr.

Genera assigned: Neoschisma Wanner 1924[a], type genus (5.2), *Hadroblastus* Fay 1962 (5.1), *Notoblastus* Brown 1942 (5.3), *Austroblastus* McKellar 1969 (5.4), *Thaumatoblastus* Wanner 1924[b] (5.5), *Dipteroblastus* Wanner 1940 (5.6), *Timoroblastus* Wanner 1924[a] (5.7).

5.1 Genus *Hadroblastus* Fay 1962

Type species: H. convexus Fay 1962, by original designation. *Miss.*, N.M., USA. (Pl. XVI, figs. 8, 10–13).

Diagnosis: theca biconvex in lateral profile, vault and pelvis of about equal height; pentagonal in plan view; broad, shallow ambulacral sinus may be present; deltoid with variably developed crest and hardly developed DD sector; – ambulacra linear to lanceolate, near peristome, conspicuous; lancet exposed throughout length of ambulacrum; – 10 hydrospire groups; hydrospire slits completely exposed; number of hydrospire slits in anal interarea generally reduced, degree of reduction variable, rarely equal; – 2 anal deltoids: epi- and hypodeltoid; epideltoid (and rarely also hypodeltoid) form anal hydrospires; hypodeltoid contributing to external wall of vault. *Miss.*, Ind., Ky., Iowa, Mo., Ark., Okla., N.M., Mont., USA; *L. Carb.*, Ire.?

– Other Species assigned:

Hadroblastus blairi (Miller & Gurley 1895); *L. Miss.*, Mo., USA. (Pl. XVI, figs. 1–6).

(Synonym: *Codaster jessiae* Miller & Gurley 1896).

Hadroblastus whitei (Hall 1861); *L. Miss.:* Iowa, Mo., Ark., Okla., USA. (Pl. XVI, figs. 9, 14, 15; Pl. XVII, figs. 1–15). (Synonym: *Codaster grandis* Rowley & Hare 1891).

Hadroblastus kentuckyensis (Shumard 1858); *L. Miss.*, Ky., USA. (Pl. XVIII, figs. 3, 5, 6).

Hadroblastus sp. ?; *L. Carb.*, Ire. (Pl. XVIII, figs. 2, 4).

Remark: The species *Pentephyllum adarense* Haughton 1859 from the L. Carb. of Ireland is very similar in thecal shape to *Hadroblastus*, especially to the specimens of *Hadroblastus whitei* from the Miss., St. Joe Fm., Okla., USA, (Pl. XVI, figs. 9, 14, 15). A synonymy of the generic names *Hadroblastus* Fay 1962 and *Pentephyllum* Haughton 1859 cannot be established. The type specimen of *P. adarense* Haughton 1859 is lost, and no other specimens are known, despite recent search at the type locality. This prevents the formulation of a generic diagnosis for *Pentephyllum*. The generic name *Pentephyllum* Haughton 1859 is recommended to be treated as a *nomen dubium*.

5.2 Genus *Neoschisma* Wanner 1924^{a}

Type species: *N. verrucosum* Wanner 1924^{a}, by original designation. *Perm.*, Timor, Indonesia. (Pl. XIX, fig. 5; Pl. XX, fig. 7).

Diagnosis: theca high, cup-shaped; vault $\frac{1}{3}$ of height of pelvis, upper surface of vault flattened; pentagonal in plan view, angles of pentagon in interambulacral areas; ambulacral sinus present on radial; – deltoid without crest, with moderately developed DD sector; – ambulacra small, lanceolate to petaloid, moderately removed from peristome; lancet exposed; – 10 hydrospire groups; hydrospire slits completely exposed; number of hydrospire slits strongly reduced in anal interarea; strong secondary infilling of hydrospire slits during growth; – 2 anal deltoids: epi- and hypodeltoid; epideltoid (and sometimes also hypodeltoid) forming anal hydrospires; hypodeltoid contributing to external wall of vault. *Perm.*, Timor, Indonesia; W. Austr.

– Other Species assigned:

Neoschisma timorense Wanner 1940; *Perm.*, Timor, Indonesia. (Pl. XX, figs. 4, 8).

Neoschisma australe Breimer & Macurda n. sp.; *Perm.*, W. Austr.

Neoschisma australe n. sp.
Pl. XIX, figs. 1–4, 6–8

Type: Holotype: UMMP 58682. L. Perm., Callytharra Fm., outcrops on south bank of Wooramel River, $\frac{1}{2}$ mile west of Callytharra Springs, 60 mi. NW of Byro Station, 25° 52′ S, 115° 30′ E, West Australia.

Diagnosis: A species of *Neoschisma* with a conical theca, flat vault rather than scalloped, numerous closely spaced hydrospire slits, and hydrospire slits developed on both the epi- and hypodeltoid.

Description: One partial theca, plus numerous isolated plates, form the basis for the description of this species. Theca broadly conical in lateral view with flat vault; ambulacra restricted. Pelvic profile smooth. Outline in plan view decagonal, with slightly depressed ambulacral areas; greatest extension in interambulacral areas. Greatest width just below top, at upper junction of radials with aboral tip of deltoids. Length probably greater than width and exceeded 35 mm in largest specimens.

Basalia three, in normal position, pentagonal in plan view, becoming rounded proximally; conical in lateral profile, slightly concave near base due to proximal extension of broad stem attachment area. Latter deposited by secondary calcite secretion, forming broad proximal cylinder whose diameter increases ontogenetically, from 2.0 to 5.0 mm. Crenellar facets at edge of attachment area.

Radials quadrate to V-shaped in plan view, depending on stage of development of radial limbs. Limbs extend slightly or well above ambulacra. Radials form upper part of broadly conical pelvis and extend upward to near highest point of theca at aboral tip of deltoid. Lower edge of radial has two straight or a single convex edge(s). Radial width widens adorally along straight lateral edges; upper edges slope inward toward ambulacrum with extremely broad V-shaped profile which becomes steeper with growth. Small notch at center for ambulacrum; radial sinus very short. Radial straight to very slightly concave (medially) in lateral profile. Surfaces of RR and RB sectors ornamented with growth lines as in basals; full width of RD sectors occupied by hydrospire slits; strong secondary infilling, so remnants of infilled slits visible. Ambulacrum does not extend to origin of radial, forming a small radial sinus. Aboral end apparently displaced adorally (relatively) during growth; area between ambulacrum and origin filled with nodose ornament. Where inner part of hypodeltoid abuts against radial, hydrospire slits missing and broad convex humped area formed. Later, hydrospires usually added on hypodeltoid and radial anal interareas most always have well developed anal hydrospire slits.

Deltoids four, together with epideltoid forming borders of oral opening. Deltoid rhombic in plan view, with short facet at adoral tip where plate borders oral opening. Adoral edges straight, relatively long, bordering adjacent deltoid and ambulacrum. Aboral edges straight, converging to a point, bearing short hydrospire slits along full length. Deltoid usually flat in lateral profile but may be slightly concave with aboral part curving upward (rarely convex to S-shaped). Plate is convex in cross section, particularly the aboral portion. DDF bears minor grooves and furrows as part of broad (0.6 mm) shallow ambulacral tract. Ambulacral tract bordered by broad, smooth ridges. Adoral end and sides of lancet cause a small indentation along DAF; ornament paralleling DAF more bumpy and irregular. Origin of plate located near adoral end and former outlines of plate visible from rhombic shaped growth ornament on upper surface of plate; some irregular lumpy ornament may also be present. Aboral growth ridges are broad and smooth; at same time that calcite was added to lateral edges, there was also a downward component to produce the convex cross section and gradual elevation of the origin relative to the surrounding plates. Aboral tip of deltoid may be produced into a short blade or hook and sharp, irregular keel may occupy upper aboral surface.

Anal deltoids two, an epi- and hypodeltoid. Epideltoid corresponds to adoral part of regular deltoid. Surface ornamented with slightly nodose ornament which is highest around anus. Epi-hypodeltoid suture straight; epi-radial suture straight and at a right angle to length of ambulacrum. Hypodeltoid corresponds to aboral part of regular deltoid. Adoral part of hypodeltoid forms a very high collar to anus; buildup apparently produced by secondary deposition. Elevated area slopes downward to outer part of hypodeltoid which looks like aboralmost part of regular deltoid, including formation of hydrospire slits. Anus ovoid, longer than wide, surrounded by high collar with aboral groove which is directed outward and upward. On interior surface of hypodeltoid, a low, thin ridge originates near aboral edge of anus, then curves downward into *D* portion of plate, somewhat dividing plate internally.

Ambulacra five, lanceolate, removed from oral opening, of moderate length, not reaching to radial origin. Lancet lanceolate, adoral part relatively long, exposed, bordering deltoids and bearing ambulacral tract. Aboral part of ambulacrum which borders radials relatively short, lancet concealed, and space occupied by relatively tall side plates which fill excavated space in radial sinus between end of lancet (indicated by that part opening into thecal interior) and end of excavated area. Side plates, thin, wide, with brachioles probably attached at edge of ambulacrum in parabolic arc but details of facets not preserved.

Ten hydrospire groups, developed across full width of RDF in regular interareas and across epi- and part of hypodeltoid suture in anal interarea (rarely absent). Hydrospire slits short, closely spaced except for occasional irregularities in outer part of hydrospire field. When deltoid aborally produced, hydrospire slits are not developed to aboral tip of plate.

Oral opening pentagonal.

Occasional irregularities in plate development encountered such as apparent presence of part of an extra radial or deltoid. Stereomic lineations well preserved.

5.3 Genus *Notoblastus* Brown 1942

Type species: N. brevispinus Brown 1942, by original designation. *Perm.*, N.S.W., Austr. (Pl. XXII, fig. 1).

Diagnosis: theca low cylindrical to cup-shaped, vault relatively low; decagonal in plan view; – deltoid with variably developed crest and moderately developed DD sector; – ambulacra lanceolate, moderately removed from peristome, conspicuous; lancet widely exposed; – 10 hydrospire groups; hydrospire slits completely exposed; number of hydrospire slits in anal interarea reduced; strong secondary infilling of hydrospire slits during growth; – 2 anal deltoids: epi- and hypodeltoid; epideltoid forming anal hydrospires; hypodeltoid contributing to external wall of vault; – short prong at origin of radial. *Perm., (Artinsk);* W. Austr., N.S.W., Queensl.; *Perm.*, Timor, Indonesia.

– Other Species assigned:

Notoblastus oyensi (Wanner 1940); *Perm.*, Timor, Indonesia. (Pl. XX, figs. 3, 5, 6).

Notoblastus cornutus (McKellar 1969); *Perm.*, Queensl., Austr. (Pl. XXII, figs. 4, 5).

Notoblastus stellaris Breimer & Macurda n. sp.; *Perm.*, W. Austr.

Notoblastus stellaris n. sp.

Pl. XX, fig. 1; Pl. XXI, figs. 1, 2, 7, 8

Type: Holotype: UMMP 58683. L. Perm., Callytharra Fm., outcrops on south bank of Wooramel River, ½ mi. west of Callytharra Springs, 60 mi. NW of Byro Station, 25° 52′ S, 115° 30′ E, West Australia.

Diagnosis: A species of *Notoblastus* with a cup-shaped theca, slightly convex vault, with well developed radial prongs, the lower part of the radial is convex, and an extremely pronounced ridge divides the ad- and aboral parts of the deltoid.

Description: One partial theca, plus isolated plates, form the basis for this description. Theca cup-shaped in lateral view, with broadly convex vault; radials have upward flaring blade-shaped prong with serrate tip. Outline in plan view pentagonal; profile interrupted by radial prongs. Greatest width just below top, at junction of vault and pelvis. Length less than width, latter approaching 20 mm in larger specimens.

Basalia three, in normal position, pentagonal in plan view, convex in lateral view, forming lower convex portion of cup-shaped pelvis. Stem attachment area a circular area at proximal tip of basals with crenellar facets at edge of attachment area; low raised rim borders area. Thirty-nine crenellae in ring when diameter 1.6 mm.

Surface of basals has broad low growth lines ornamented with granulose ornament parallel to BR fronts; BB sectors slightly evident.

Radials hexagonal in plan view, with two straight or a convex lower edge(s), with relatively straight sides (width usually increases slightly orally), and two straight adoral edges which converge upward. Adoral center embayed by a short radial sinus. Radial convex in lateral view with blade-shaped radial prong extending outward and upward; wider in lower part than upper. Radial prongs are relatively large, cover origin of radial, are relatively thin, and have a serrated tip. RB and RR sectors ornamented with smooth growth lines; inner portion of plate has granulose ornament. Small beaded ridge separates RD and RR sectors. RD sector ornamented with parallel ridges indicating infilled hydrospire slits; latter occupy full width of RDF. Radial sinus bordered by broad low ridge.

Deltoids four, together with epideltoid (?) forming border to oral opening. Deltoid hexagonal in plan view, with DAF being shortest edge; convex in lateral view, with aboral portion curving downward. Plate slightly convex in cross section. Short edge bordering oral opening slightly concave. DDF long, straight, well developed, bearing ambulacral tract with minor lobes and grooves; bordered by ridge with fluted ornament. DAF short, slightly concave, caused by indentation of lancet. Ornament bordering DAF leads into dividing ridge. Aboral edges straight, bearing short hydrospire slits along full width of DRF. A pronounced V-shaped ridge, adorally pointed, divides the adoral (DD and DA sectors) from the aboral (DR) sectors. Ridge produced by secondary upbuilding and may be strongly serrate. Adoral part of plate ornamented with irregular granulose ornament or granulose ornament which parallels DDF. Aboral part of plate divided medially by crest which may have teeth or knobs along top; development not as pronounced as dividing ridge. Each DR sector ornamented with ridges indicating infilled hydrospire slits (may be smooth adorally).

Anal deltoids unknown from isolated plates; may be fragments preserved in crushed oral area of holotype. Growth lines on radials in anal interarea suggest large hypodeltoid.

Ambulacra five, broadly lanceolate, removed from oral opening, almost straight in lateral view, convex in cross section. Strongly elevated above surrounding plates. Lancet broadly lanceolate, exposed to aboral tip of ambulacrum, with side plates arrayed along sides. Upper surface bears main and arcuate inner portion of side ambulacral tracts. Brachiolar facet small, heart-shaped, on lateral downward sloping edge of ambulacrum. Facet equally developed on side and outer side plates. Outer side plate wedge-shaped, becomes wider below facet; both side and outer side plate form a series of bulbous knobs at their lower abmedial extremities below the facet. Main groove bordered by minor lobes and grooves as are both sides of side grooves. 2.5 Side plates per mm.

Ten hydrospire fields, those in anal interarea reduced in number. Functional length of slit very short; occupying full width of RDF, closely spaced.

Oral opening ovoid-pentagonal.

5.4 Genus *Austroblastus* McKellar 1969

Type species: *A. whitehousei* McKellar 1969, by original designation. (Pl. XXIII, figs. 1, 6, 8; Pl. XXIV, fig. 1).

Diagnosis: theca beaker-shaped, vault relatively prominent, pentagonal in plan view; broad, shallow ambulacral sinus present; – deltoid with prominent crest and moderately developed DD sector; – ambulacra lanceolate, moderately removed from peristome; lancet exposed; – 10 hydrospire groups; hydrospire slits completely exposed; very strong secondary infilling of hydrospire slits during growth; – 2 anal deltoids: epi- and hypodeltoid, both forming anal hydrospires; hypodeltoid contributing to external wall of vault; – growth of radial underneath lancet. *Perm. Artinsk;* Queensl., Austr.

– Other Species assigned: none.

5.5 Genus *Thaumatoblastus* Wanner 1924^{b}

Type species: *T. longiramus* Wanner 1924^{b}, by original designation. (Pl. XXIV, fig. 2; Pl. XXV, fig. 1–8; Pl. XXVIII, fig. 5). (Synonym: *T. longispinus* Wanner 1924^{b}).

Diagnosis: pelvis cup-shaped, vault probably flattened, but only radials known; theca strongly stellate in plan view due to pronounced development of radial prongs; – ambulacra linear, conspicuous, extending to tip of radial prong; lancet exposed; – 10 hydrospire groups, hydrospire slits completely exposed; number of hydrospire slits reduced in anal interarea; strong secondary infilling of hydrospire slits on radials during growth; – number of anal deltoids unknown. *Perm.;* Timor, Indonesia; W. Austr., Tasm., Austr.

– Other Species assigned: none.

5.6 Genus *Dipteroblastus* Wanner 1940

Type species: *D. permicus* Wanner 1940, by original designation. (Pl. XXI, fig. 6; Pl. XXII, figs. 2, 3, 6; Pl. XXIII, fig. 4).

Diagnosis: theca tending to develop bilateral symmetry by pronounced development of *B* and *D* ambulacra, conical or cup-shaped in lateral profile; flattened vault; elongate in plan view; – deltoid with faint crest, slightly developed DD sectors; – regular ambulacra small; *B* and *D* ambulacra elongate, hypertrophied, with exposed lancets; – 10 hydrospire groups, hydrospire slits completely exposed; number of hydrospire slits reduced in anal interarea; secondary infilling of hydrospire slits on radials during growth; – 2 anal deltoids: epi- and hypodeltoid; epideltoid forming anal hydrospires; hypodeltoid contributing to external wall of vault. *Perm.*, Timor, Indonesia.

– Other Species assigned: none.

5.7 Genus *Timoroblastus* Wanner 1924[a], (Synonym: *Microblastus* Van Eykeren 1942)

Type species: *T. coronatus* Wanner 1924[a], by original designation. *Perm.*, Timor, Indonesia. (Pl. XXIII, figs. 2, 3, 5, 7; Pl. XXVI, figs. 1, 4, 5, 8–11); Pl. XXVII, figs. 1, 3–5, 9). (Synonym: *Microblastus pocilliformis* Van Eykeren 1942).

Diagnosis: theca boxlike, with straight or sloping sides; convex to concave base and flattened vault; pentagonal to stellate in plan view; angles of pentagon in interambulacral areas; – deltoids conspicuous, with subequal DR and DD sectors; – ambulacra small, petaloid; – 10 hydrospire groups; hydrospire slits short; only rarely occupying full width of RD suture; admedial hydrospire slit mostly concealed; – 2 anal deltoids: epi- and hypodeltoid; latter contributing to external wall of vault. *Perm.*, Timor, Indonesia.

– Other Species assigned:
Timoroblastus weiensis Wanner 1940; *Perm.*, Timor, Indonesia. (Pl. XXIV, figs. 3–5).

6. Family CODASTERIDAE Etheridge & Carpenter 1886

Diagnosis: theca cup-shaped; ambulacral sinuses absent; deltoids forming flat roof of theca; with well-developed DD sectors which in ultimate members are equal to or larger than DR sectors; deltoid crest subdued; – ambulacra lanceolate in early members; short, petaloid or rhombiform with few side plates and brachioles in ultimate members; well removed from peristome; lancet exposed; – hydrospire slits few, short, developed across full width of restricted RD growth front, generally not parallel to longer axis of ambulacrum, completely exposed; – composition of anal area simple: epi- and hypodeltoid; hypodeltoid small, may be atrophied; epideltoid rarely forming anal hydrospires; – secondary calcite may be deposited on external surfaces of radials and deltoids, producing a radial prong and (?) elevated deltoids. *Miss.-Perm.;* Eur., N. Am., S. Am., S.E. Asia.

Genera assigned: *Codaster* M'Coy 1849, type genus (6.1), *Angioblastus* Wanner 1931 (6.2), *Tympanoblastus* n. gen. (6.3), *Pterotoblastus* Wanner 1924 (6.4), ? *Nannoblastus* Wanner 1924[b] (6.5).

6.1 Genus *Codaster* M'Coy 1849

Type species: *C. acutus* M'Coy 1849, by subsequent designation of JOYSEY, 1953. (Pl. XXVI, figs. 2, 3, 6, 7; Pl. XXVII, figs. 2, 6–8; Pl. XXVIII, figs. 1, 2, 4, 8, 9). (Synonym: *C. trilobatus* M'Coy 1849).

Diagnosis: theca cup-shaped, vault low to flat; pentagonal in plan view; deltoid with faint crest and moderatrly developed DD sectors; – ambulacra lanceolate, slightly removed from peristome; lancet exposed throughout length of ambulacrum; – 10 hydrospire groups; admedial hydrospire slit of each group concealed by ambulacrum; number of hydrospire slits in anal interarea strongly reduced; slight secondary infilling of hydropsire slits during growth. *L. Carb.;* Eng., Ire.

– Other Species assigned: none.

Remarks: *Codonaster conicus* Whidborne 1889, *Codaster gratiosus* S. A. Miller 1880, (Pl. V, figs. 7, 9) and *Codaster superbus* Rowley 1905 are all to be considered *nomina dubia,* because they are based on unrecognizable fragments.

6.2 Genus *Angioblastus* Wanner 1931, (Synonyms: *Sagittoblastus* Yakovlev 1937, *Paracodaster* Yakovlev 1940, and *Agmoblastus* Fay 1961).

Type species: *A. variabilis* Wanner 1931, by original designation. *U. Perm.,* Timor, Indonesia. (Pl. XXVIII, figs. 3, 6; Pl. XXIX, fig. 14; Pl. XXX, figs. 1–4, 6–9, 12). (Synonym: *A. depressus* Wanner 1940).

Diagnosis: theca cup-shaped to globose, vault low, constricted; rounded pentagonal to pentagonal in plan view; – deltoid with subequal DR and DD sectors; small deltoid crest variably developed; ambulacra small, generally rhombiform; – typically 8 hydrospire groups, hydrospire slits short, completely exposed; number of hydrospire slits variable per species; – usually 2 anal deltoids: epi- and hypodeltoid, latter contributing to external wall of theca; gonopore present on epideltoid; – RA growth front present. *Penn.;* Okla., USA, Canadian Arctic; *L. Perm.,* Bolivia; Ural Mts., USSR; *Perm.,* Timor, Indonesia.

– Other Species assigned:

Angioblastus boliviensis n. sp.; *L. Perm.,* Bolivia. (Pl. XXIX, figs. 19–21).

Angioblastus dotti (Moore & Strimple 1942); *Penn.,* Okla., USA. (Pl. XXIX, figs. 1–5).

Angioblastus ellesmerensis n. sp.; *Penn.,* Canadian Arctic. (Pl. XXIX, figs. 6, 8–10).

Angioblastus miloradovitchi (Yakovlev 1940); *L. Perm.,* USSR. (Pl. XXX, figs. 10, 11).

Angioblastus wanneri (Yakovlev 1926); *L. Perm*, Ural Mts, USSR. (Pl. XXIX, figs. 7, 11–13, 15–18).

Angioblastus boliviensis n. sp.

Pl. XXIX, figs. 19–21

Type: Holotype: USNM 160591. L. Perm., Zudanez syncline about one mile south of village of Zudanez, Bolivia.

Diagnosis: A species of *Angioblastus* which is cylindrical in outline, has a convex lower base, a medial ridge dividing the radial, a vault which almost reaches the edge of the profile in plan view, and a deltoid keel which is more well developed than the ridge separating the ad- and aboral parts of the deltoid.

Description: One theca forms the basis for this description. Theca cylindrical in lateral profile, with long pelvis and convex base and convex vault. Outline in plan view pentagonal with slight lip at points of pentagon due to ridge on radials. Deltoids and ambulacra extend almost to edge of profile in plan view. Greatest width is subequatorial near junction of radials with basals. Length slightly greater than width; pelvic angle 38°.

Basalia three, in normal position, pentagonal in plan view, extending almost to edge of thecal profile, convex in lateral profile, forming bowl-shaped base to theca. Stem attachment area weathered; apparently a small circular area at proximal end of basals.

Azygous basal quadrate in plan view, with straight lateral and distal edges. Convex in lateral view, BR sector convex parallel and normal to BR axis, merging smoothly over relatively flat surface. Zygous basals pentagonal in plan view, with concave distal medial edge and straight distal lateral and lateral edges. Convex in lateral profile. BR sectors convex parallel to BR axis, medial sector convex, lateral sectors flat normal to BR axes, merging smoothly. Surface of basals ornamented with granulose ornament.

Radials hexagonal in plan view, with a convex or two straight lower edges, with two straight lateral edges which parallel one another in *C* and *E* radials or slowly converge adorally in other radials, and two straight upper edges which converge adorally. Upper edge of radial embayed by a short arcuate sinus in which ambulacrum is sited. Radial quarter moon shaped profile in lateral view, with convex upper surface and slightly concave lower surface. RB sector slightly convex parallel to RB axis and straight normal to it. Each radial is divided medially by a strong ridge which extends from origin to radial-basal suture where it fades out. Apparently produced by secondary deposition. RB sectors separated by this ridge, RR sectors very slightly convex parallel to RR axis, slightly convex normal to it. RD sector small, inclining upward from RR sector, straight parallel and normal to RD axis. Hydrospire slits occupy full width of RDF. Origin of radial dominated by collar built up from surface of plate to form a border to ambulacrum. Growth lines visible in outer parts of RR and RB sectors with granulose ornament in the inner part.

Deltoids four, together with epideltoid forming border to oral opening. Deltoid hexagonal in plan view, with width expanding to maximum along straight DDF, then contracting along straight DAF and finally to aboral point along DRF. Deltoid extremely convex in lateral view due to medial buildup. Deltoid is dominated by a medial ridge which divides aboral part of plate and projects into adoral part of plate. Ridge is very convex in lateral profile. Two lower ridges project outward laterally from this, separating aboral (DR sector) from adoral (DA and DD sectors) part of plate. Adoral part of plate slopes downward adorally from ridges; aborally plate surface drops steeply downward into hydrospire field.

Anal deltoids one, an epideltoid with hypodeltoid apparently atrophied. Epideltoid corresponds to adoral part of regular deltoid, with lateral ridges forming a high adoral collar. Anus is egg-shaped, wider aborally, bordered by epideltoid and two radial limbs, and opening upward at outer edge of theca.

Ambulacra five, relatively small, broadly lanceolate, removed from oral opening, slightly convex in lateral profile and cross section, center elevated very slightly above level of surrounding radial but below surface of deltoids. Lancet only exposed adorally as a rhombic-shaped area; side plates meet along center line; their outer edges embayed by small triangular-shaped outer side plate. Details of brachiolar facets not preserved. Three side plates per mm; Amb. L. 2.0 mm; W. 1.2 mm.

Eight hydrospire groups, developed across full width of RDF which is narrow. Three slits per group, functional length short (0.3 mm). Ridges visible in RD and DR sectors indicating infilling of earlier portions of slits.

Oral opening pentagonal, 0.8 mm wide.

Angioblastus ellesmerensis, n. sp.
Pl. XXIX, figs. 6, 8–10

Type: Holotype: GSC 67261. Penn., Atokan, unnamed formation, with argillaceous limestone and siltstone, east side of Van Hauen Pass, Ellesmere Island, Canadian Arctic Archipelago.

Diagnosis: A species of *Angioblastus* with a cup-shaped theca, with tapering sides, a pentagonal cross section and well developed vault, a deltoid with a very strong ridge separating the ad- and aboral sections and a crest which originates lower than the ridge's upper surface, and the occasional development of anal hydrospires.

Description: Three thecae, the holotype and two specimens from another locality, form the basis for the description of this species. Theca cup-shaped in lateral profile, with convex tapering sides and a moderately convex vault; ambulacra restricted. Outline in plan view pentagonal, with greatest width just below aboral tip of ambulacra. Deltoids and ambulacra extend to edge in plan view. Length slightly greater than width, vault less than pelvis. Pelvic angle 60°.

Basalia three, in normal position, pentagonal in plan view, becoming rounded proximally, convex in lateral profile, forming lower half of convex pelvis. Stem attachment area a mound-shaped area at proximal tip of basals produced by secondary deposition.

Azygous basal quadrate in plan view, with very slightly sinusoidal distal edges and very slightly convex lateral edges. Plate is convex in lateral view. BR sectors are convex parallel to BR axis and slightly convex normal to it; adjacent sectors merge smoothly through slightly concave trough. Zygous basals are pentagonal in plan view, with a slightly concave distal medial edge, very slightly sinusoidal distal lateral edges, and very slightly convex lateral edges. Convex in lateral profile. Medial and lateral BR sectors as for azygous basals, again merging smoothly through a slightly concave trough. Surface of basals are ornamented with broad smooth growth lines parallel to BRF; also visible in BB sector but much narrower.

Radials five, forming upper part of pelvis. Hexagonal in plan view, with two straight or a convex lower edge, two straight lateral edges which slowly diverge upward, and two straight upper edges which converge adorally. Upper edge of radial embayed by short sinus for ambulacrum. Radial has low lateral profile, triangular, with slightly convex aboral facing edge, short straight adoral facing edge, and very slightly concave lower edge. RB sector is very slightly convex parallel to RB axis and slightly convex normal to it; adjacent RB sectors merge smoothly with one another over broad convex area and with RR sectors over flat surface. RR sectors straight parallel to RR axis and slightly convex normal to it. Small ridge separates RD from RR sectors; former meets latter at an angle. RD sector small, straight parallel and normal to RD axis. Area around origin of radial apparently produced into slight knob. RR and RB sectors ornamented by smooth, broad growth lines parallel to fronts; small tubercles found in earlier formed parts of sectors. Width of RD sector occupied by hydrospire slits, being infilled aborally.

Deltoids four, together with epideltoid, forming border to oral opening. Deltoid hexagonal in plan view. Short straight edge bordering peristome. DDF well developed, straight; DAF relatively large, concave; DRF straight, converging aborally. Deltoid slightly convex in lateral profile, with profile interrupted by pronounced buildup on deltoid. Adoral part of plate separated from aboral part by very strong, arcuate ridge which slopes downward adorally unto smooth adoralmost part of plate and drops down steeply aborally to aboral part of plate. Crest present aborally, divides plate, originates below level of arcuate ridge and is not equal to it. Adoral parts of DR sectors slope downward toward hydrospire fields which occupy full width of DRF.

One anal deltoid, an epideltoid, while hypodeltoid is apparently atrophied. Epideltoid corresponding to adoral part of regular deltoid, with arcuate ridge forming adoral collar to anus. Latter ovoid, egg-shaped, wider aborally, opening upward on outer part of upper surface.

Ambulacra five, relatively small, removed from oral opening, lanceolate in plan view, slightly elevated above surrounding plates. Lancet apparently only exposed adorally but underlies length of ambulacrum. Side plates present, embayed by small triangular outer side plates abmedially. Minor lobes and grooves border main groove but detail of side grooves and facets not preserved. Three side plates per mm.

Normally eight hydrospire groups, developed across full width of RDF; functional length very short (0.3–0.4 mm). One specimen, the largest, has anal hydrospires developed across the epi-radial suture with 1 on the *C* side and 3 on the *D* (8 in regular groups). Apparently lacking in other specimens.

Oral opening pentagonal.

Remarks. The holotype (Pl. XXIX, figs. 6, 9, 10) was collected from the locality given under type. The other specimens (e.g., Pl. XXIX, fig. 8) forming part of this description (used primarily for the pelvis) were collected about 16 miles away from the flanks of a small bioherm on the north side of Hare Fiord, Ellesmere Island, at 81° 07.5′ N, 80° 17′ W. They are part of a crackout fauna so the specimen cleaves through rather than around the upper part of the vault. However, plate outlines and hydrospires are clearly outlined by cleavage reflection.

6.3 *Tympanoblastus* Breimer & Macurda new genus

Type species: Codonaster pousirewskii Stuckenberg 1875, by original designation herein. *L. Perm.*, USSR. (Pl. XXX, figs. 5, 14; Pl. XXXI, figs. 3, 6). (Synonym: *Codaster barkhatovae* Yakovlev, 1941).

Diagnosis: theca conical to cup-shaped; vault low; pentagonal in plan view; – deltoid with prominent DD growth sector and subdued DR growth sector; prominent angle between outer surfaces of sectors; small deltoid crest; – ambulacra rhombiform; – 8 hydrospire groups, hydrospire slits short, completely exposed, occupying full width of RD suture; – 2 anal deltoids: epi- and hypodeltoid; hypodeltoid contributing to external wall of theca. *L. Perm.;* Ural Mts., Petshoraland, USSR.

– Other Species assigned:

Tympanoblastus elongatus (Yakovlev 1937); *L. Perm.*, Ural Mts., USSR. (Pl. XXX, fig. 13; Pl. XXXI, fig. 1).

Comparison: Tympanoblastus is distinguished from other genera in its family by its flat vault, highly developed DD sectors, the downward bending DR sectors, and its relatively large ambulacra.

6.4 Genus *Pterotoblastus* Wanner 1924^a

Type species: P. gracilis Wanner 1924^a, by original designation. *Perm.*, Timor, Indonesia; Thailand. (Pl. XXXI, figs. 11, 12; Pl. XXXII, figs. 3, 4, 6, 9, 10).

Diagnosis: theca cup-shaped, vault low; pentagonal or stellate in plan view; – deltoids with unequal growth sectors, DD sector larger; small deltoid crest may be present; – ambulacra lanceolate, extending aborally beyond lancet; lancet rhombiform, exposed; – 8 hydrospire groups, hydrospire slits short, completely exposed, occupying full width of RD suture; – 1 or 2 anal deltoids: epi- and hypodeltoid; gonopore present in epideltoid; hypodeltoid most always atrophied; – secondary deposition of calcite on radial producing radial prong or vertical built up underneath ambulacra. *Perm.*; Timor, Indonesia; Thailand.

– Other Species assigned:
  Pterotoblastus brevialatus Wanner 1931; *Perm.*, Timor, Indonesia. (Pl. XXXI, figs. 2, 5, 7, 9, 13–15).
  Pterotoblastus decemcostis Wanner 1931; *Perm.*, Timor, Indonesia; holotype, only known specimen, now missing.
  Pterotoblastus ferrugineus Wanner 1940; *Perm.*, Timor, Indonesia. (Pl. XXXI, figs, 4, 8).

(?) 6.5 Genus *Nannoblastus* Wanner 1924^b

Type species: *Nannoblastus pyramidatus* Wanner 1924^b, by original designation. *Perm.*, Timor, Indonesia. (Pl. XXXIII, figs. 1, 2, 5–7).

Diagnosis: theca with rhombic lateral profile, pentalobate in plan view; – deltoids very conspicuous, pentagonal, forming the entire vault with ambulacral troughs; – ambulacra small, petaloid; lancet exposed; – as far as known only 6 hydrospires present; missing at both sides of *C* and *D* ambulacra; hydrospire slits concealed; – 2 anal deltoids: epi- and hypodeltoid, latter contributing to external wall of vault; – RA growth front present; – deposition of calcite on outer surface of deltoid. *Perm.*, Timor, Indonesia.

– Other Species assigned:
  N. cuspidatus Wanner 1924^b; *Perm.*, Timor, Indonesia. (Pl. XXXII, figs. 7, 8).

7. Family CERATOBLASTIDAE Breimer & Macurda n. fam.

Diagnosis: provisionally similar to generic diagnosis since family is mono-generic. *Perm.*, Timor, Indonesia.

Comparison: The Ceratoblastidae differ from other fissiculate families in the extremely elongate theca, structure of the ambulacra, and presence of pores through some deltoids.

Genera assigned: *Ceratoblastus* Wanner, 1940, type genus (7.1).

7.1 Genus *Ceratoblastus* Wanner 1940

Type species: *C. nanus* Wanner 1940, by original designation. (Pl. XXXII, figs. 5, 11).

Diagnosis: theca horn-shaped, with flat, restricted vault; pentagonal in plan view; – deltoids small, mostly confined to peristomial area; – ambulacra wide, petaloid, occupying most of vault area; formed by a circle of 10 exposed plates (2 per amb.), alternating with deltoids, and probably also by side plates; – regular hydrospire structures absent; 2 large pores in *BC* and *DE* interrays lead to saclike structures pending from *BC* and *DE* deltoids; – one anal deltoid an epideltoid, situated between mouth and anus. *Perm.*, Timor, Indonesia.

– Other Species assigned: none.

INCERTAE SEDIS

Genus *Indoblastus* Wanner 1924[a], (Synonym: *Sundablastus* Wanner 1924).

Type species: *I. granulatus* Wanner 1924[a], by original designation. *Perm.*, Timor, Indonesia. (Pl. XXXII, fig. 2; Pl. XXXIII, fig. 4). (Synonym: *Indoblastus nuciformis* Wanner 1940).

Diagnosis: theca oblate to cup-shaped with low vault, rounded pentagonal in plan view; – deltoids rhombic, with DR sectors larger than DD sectors; deltoid crest absent; – ambulacra lanceolate, conspicuous, removed from peristome; lancet concealed; – 8 hydrospire slits, absent on anal interarea; mostly concealed by ambulacra; – 2 anal deltoids, epi- and hypodeltoid; latter contributing to external wall of vault. *Perm.*, Timor, Indonesia.

– Other Species assigned:
Indoblastus weberi (Wanner 1924[a]); *Perm.*, Timor, Indonesia. (Pl. XXXIII, fig. 3).

Remark: FAY (1961[b]) described the genus *Hyperoblastus* as being a fissiculate. We are transferring it to the spiraculates, and will discuss its systematic placement in this subclass in a later monograph.

Epilogue: The new phylogenetic classification of the fissiculate blastoids, as given above, is the result of a complete revision of all of the genera and species known up to now. The revision of the fissiculates is based upon three important types of evidence: (1) a complete systematic redescription of the known species, (2) a thorough study of their anatomy, and (3) a firm knowledge of their biometrical ontogeny.

The systematic redescription of the species of the fissiculate blastoids will be presented separately by Macurda in a forthcoming publication of the Museum of Paleontology, University of Michigan, USA. In the present monograph we have confined ourselves to presenting the new family and genus diagnoses, along with description of the new species. The available space prevented the inclusion of the descriptions of badly or inadequately known species. The full impact of our revised phylogenetic classification is reflected in several lists following below. The lists are given for the sake of completeness and easy reference.

LIST OF FAMILIES AND GENERA OF THE BLASTOIDEA FISSICULATA

1. Fam. Phaenoschismatidae Etheridge & Carpenter 1886
    - 1.1 *Decaschisma* Fay 1961^{b}; *Sil.*, Ind., Tenn., USA.
    - 1.2 *Polydeltoideus* Reimann & Fay 1961; *Sil.*, Okla., USA; Czech.?
    - 1.3 *Leptoschisma* n. gen.; *L. Dev.*, Tenn., USA.
    - 1.4 *Caryoblastus* Breimer, Macurda, & Prokop 1968; *L. Dev.*, Czech.; Spain
    - 1.5 *Cryptoschisma* Etheridge & Carpenter 1886; *L. Dev.*, Spain
    - 1.6 *Pentremitidea* d'Orbigny 1850; *L. Dev.*, Spain
    - 1.7 *Pleuroschisma* Reimann 1945; *L. Dev.*, Spain; *M. Dev.*, N.Y., USA; Can.
    - 1.8 *Heteroschisma* Wachsmuth 1883; *M. Dev.*, USA.
    - 1.9 *Phaenoschisma* Etheridge & Carpenter 1882; *L. Carb.*, Eur.; *Miss.*, USA.
    - 1.10 *Phaenoblastus* Fay 1961^{b}; *L. Carb.*, Belg.; *Miss.*, Mo., USA.
    - ? 1.11 *Dolichoblastus* n. gen.; *L. Carb.*, USSR.
    - ? 1.12 *Kazachstanoblastus* Arendt, Breimer, & Macurda 1968; *L. Carb.*, Kazachst., USSR.

2. Fam. Orophocrinidae Jaekel 1918
    - 2.1 *Brachyschisma* Reimann 1945; *M. Dev.*, N.Y.; *Dev.*, S. Afr., S. Am. ?
    - 2.2 *Katoblastus* Macurda 1967^{a}; *L. Carb.*, Belg.
    - 2.3 *Orophocrinus* Von Seebach 1865; *L. Carb.*, Eur.; *Miss.*, USA.
    - 2.4 *Acentrotremites* Etheridge & Carpenter 1883; *L. Carb.*, Eng., Wales.
    - 2.5 *Mastoblastus* Arendt, Breimer, & Macurda 1968; *L. Carb.*, USSR.
    - 2.6 *Pentablastus* Sieverts–Doreck 1951; *M. Carb.*, Spain.
    - 2.7 *Anthoblastus* Wanner 1924^{b}; *Perm.*, Timor, Indonesia.

3. Fam. Nymphaeoblastidae Wanner 1940
    - 3.1 *Pachyblastus* n. gen.; *Dev.*, S. Afr.
    - 3.2 *Xenoblastus* n. gen.; *Miss.*, Ky., USA; *L. Carb.*, Belg.
    - 3.3 *Nymphaeoblastus* Von Peetz 1907; *L. Carb.*, E. Eur., Asia, Austr.
    - 3.4 *Sphaeroschisma* Wanner 1924^{b}; *Perm.*, Timor, Indonesia.

4. Fam. Astrocrinidae Austin & Austin 1843
    - 4.1 *Astrocrinus* Morris 1843; *L. Carb.*, Eng., Scot., Ire.

5. Fam. Neoschismatidae Wanner 1940
    - 5.1 *Hadroblastus* Fay 1962; *Miss.*, USA; *L. Carb.*, Eur. ?
    - 5.2 *Neoschisma* Wanner 1924^{a}; *Perm.*, Timor, Indonesia; W. Austr.
    - 5.3 *Notoblastus* Brown 1942; *L. Perm.*, Austr.; *Perm.*, Timor, Indonesia.
    - 5.4 *Austroblastus* McKellar 1969; *L. Perm.*, Austr.
    - 5.5 *Thaumatoblastus* Wanner 1924^{b}; *Perm.*, Timor, Indonesia; W. Austr., Tasm., Austr.
    - 5.6 *Dipteroblastus* Wanner 1940; *Perm.*, Timor, Indonesia.
    - 5.7 *Timoroblastus* Wanner 1924^{a}; *Perm.*, Timor, Indonesia.

6. Fam. Codasteridae Etheridge & Carpenter 1886
    - 6.1 *Codaster* M'Coy 1849; *L. Carb.*, Eng., Ire.
    - 6.2 *Angioblastus* Wanner 1931; *Penn.*, Okla., USA; Canadian Arctic; *L. Perm.*, Ural Mts., USSR; Bolivia; *Perm.*, Timor, Indonesia.
    - 6.3 *Tympanoblastus* n. gen.; *L. Perm.*, Ural Mts., Petshoraland, USSR.
    - 6.4 *Pterotoblastus* Wanner 1924^{a}; *Perm.*, Timor, Indonesia; Thailand.
    - ? 6.5 *Nannoblastus* Wanner 1924^{b}; *Perm.*, Timor, Indonesia.

7. Fam. Ceratoblastidae Breimer & Macurda new fam.
    - 7.1 *Ceratoblastus* Wanner 1940; *Perm.*, Timor, Indonesia.

8. Incertae Sedis

    Indoblastus Wanner 1924^{a}; *Perm.*, Timor, Indonesia.

LIST OF NEWLY ERECTED GENERIC NAMES IN THE BLASTOIDEA FISSICULATA SINCE PUBLICATION OF THE TREATISE, PART S, 1967

Austroblastus McKellar 1969 *(*A. whitehousei)*, Neoschismatidae; *Perm.*, Austr., Queensl.

Caryoblastus Breimer, Macurda, & Prokop 1968 *(*C. bohemicus)*, Phaenoschismatidae; *L. Dev.*, Boh., Czech.

Dolichoblastus Breimer & Macurda n. gen. *(*Codaster shimanskii)*, ? Phaenoschismatidae; *Carb.*, *L. Nam.*, Kazachstan, USSR.

Katoblastus Macurda 1967^{a} *(*Pentremites püzos)*, Orophocrinidae; *L. Carb.*, Belg.

Kazachstanoblastus Arendt, Breimer, & Macurda 1968 *(*K. carinatus)*, ? Phaenoschismatidae; *Carb.*, *L. Nam.*, Kazachstan, USSR.

Leptoschisma Breimer & Macurda n. gen. *(*Codaster lorae)*, Phaenoschismatidae; *L. Dev.*, Tenn., USA.

Mastoblastus Arendt, Breimer, & Macurda 1968 *(*M. ornatus)*, Orophocrinidae; *Carb.*, *L. Nam.*, Kazachstan, USSR.

Pachyblastus Breimer & Macurda n. gen. *(*P. dicki)*, Nymphaeoblastidae, *Dev.*, S. Afr.

Tympanoblastus Breimer & Macurda n. gen. *(*Codonaster pousirewskii)*, Codasteridae, *L. Perm.*, USSR.

Xenoblastus Breimer & Macurda n. gen. *(*Pentremites decussatus)*, Nymphaeoblastidae; *Miss.*, Kentucky, USA.

* Type species.

LIST OF NEWLY ERECTED SPECIFIC NAMES IN THE BLASTOIDEA FISSICULATA SINCE PUBLICATION OF THE TREATISE, PART S, 1967

Angioblastus *boliviensis* Breimer & Macurda n. sp.; *Perm.*, Bolivia.

Angioblastus *ellesmerensis* Breimer & Macurda, n. sp.; *Penn.*, Canad. Arctic.

Austroblastus *whitehousei* McKellar 1969; *L. Perm.*, Queensl., Australia.

Brachyschisma ? *oostheizeni* Breimer & Macurda n. sp.; *Dev.*, S. Afr.

Caryoblastus *bohemicus* Breimer, Macurda, & Prokop 1968; *L. Dev.*, Boh., Czech.

Dolichoblastus *shimanskii* (Arendt, Breimer, & Macurda, 1968); *Carb.*, *L. Nam.*, Kazachstan, USSR.

Katoblastus *konincki* Macurda 1967ª; *L. Carb.*, Belg.

Kazachstanoblastus *carinatus* Arendt, Breimer, & Macurda 1968; *Carb.*, *L. Nam.*, Kazachstan, USSR.

Mastoblastus *ornatus* Arendt, Breimer, & Macurda 1968; *Carb.*, *L. Nam.*, Kazachstan, USSR.

Neoschisma *australe* Breimer & Macurda n. sp.; *Perm.*, W. Austr.

Notoblastus *cornutus* (McKellar 1969); *Perm.*, Queensland, Austr.

Notoblastus *stellaris* Breimer & Macurda n. sp.; *Perm.*, W. Austr.

Pachyblastus *dicki* Breimer & Macurda n. sp.; *Dev.*, S. Afr.

? Phaenoschisma *rossica* Arendt, Breimer, & Macurda 1968; *Carb.*, *L. Nam.*, Kazachstan, USSR.

? Phaenoschisma *saharae* Breimer & Macurda n. sp.; *L. Carb.*, Algeria.

LIST OF NEWLY REJECTED GENERIC NAMES IN THE BLASTOIDEA FISSICULATA

Agmoblastus Fay 1961ª *(*Paracodaster dotti)* = Angioblastus Wanner 1931.

Deltoschisma Fay 1961ᵇ *(*Phaenoschisma archiaci)* = Pentremitidea d'Orbigny 1850.

Microblastus Van Eykeren 1942 *(*M. pocilliformis)* = Timoroblastus Wanner 1924ª.

Paracodaster Yakovlev 1940 *(*P. miloradovitchi)* = Angioblastus Wanner 1931.

Sagittoblastus Yakovlev 1937 *(*Timoroblastus wanneri)* = Angioblastus Wanner 1931.

Sundablastus Wanner 1924^a *(*S. weberi)* = Indoblastus Wanner 1924^a.

Trionoblastus Fay 1961^a *(*Pentremites subtruncatus)* = Heteroschisma Wachsmuth 1883.

* Type species.

LIST OF NEWLY REJECTED SPECIFIC NAMES IN THE BLASTOIDEA FISSICULATA

Angioblastus *depressus* Wanner 1940 = A. *variabilis* Wanner 1931.

Astrocrinus *benniei* Etheridge 1876 = A. *tetragonus* (Austin & Austin 1843).

Brachyschisma *subcrassum* (Reimann 1945) = B. *corrugatum* (Reimann 1935).

Brachyschisma *subumbrosum* (Reimann 1945) = B. *corrugatum* (Reimann 1935).

Codaster *americanus* Shumard 1858 = Heteroschisma *alternatum* (Lyon 1857).

Codaster *barkhatovae* Yakovlev 1941 = Tympanoblastus *pousirewskii* (Stuckenberg 1875).

Codaster *curtus* Reimann 1935 = Brachyschisma *corrugatum* (Reimann 1935).

Codaster *grandis* Rowley & Hare 1891 = Hadroblastus *whitei* (Hall 1861).

Codaster *gratiosus* S. A. Miller 1880 = *nomen dubium.*

Codaster *hindei* Etheridge & Carpenter 1882 = Heteroschisma *canadense* (Billings 1869).

Codaster *jessiae* Miller & Gurley 1896 = Hadroblastus *blairii* (Miller & Gurley 1895).

Codaster *pentalobus* Hall 1879 = Decaschisma *pulchellum* (Miller & Dyer 1878).

Codaster *pyramidatus* Shumard 1858 = Heteroschisma *alternatum* (Lyon 1857).

Codaster *robustus* Cline & Heuer 1950 = Heteroschisma *alternatum* (Lyon 1857).

Codaster *superbus* Rowley 1905 = *nomen dubium.*

Codonaster *conicus* Whidborne 1898 = *nomen dubium*

Decaschisma *pentalobum* (Hall 1879) = *D. pulchellum* (Miller & Dyer 1878).

Indoblastus *nuciformis* Wanner 1940 = I. *granulatus* Wanner 1924^a.

Microblastus *pocilliformis* Van Eykeren 1942 = Timoroblastus *coronatus* Wanner 1924^a.

Nymphaeoblastus *anossofi* Yakovlev 1926 = N. *miljukovi* Von Peetz 1907.

Phaenoschisma *nobile* Etheridge & Carpenter 1883 = Pleuroschisma *verneuili* (Etheridge & Carpenter 1882).

Pleuroschisma *hibbardi* Reimann 1945 = Pleuroschisma *lycorias* (Hall 1862).

Pleuroschisma *ontario* Reimann 1945 = Pleuroschisma *lycorias* (Hall 1862).

Pterotoblastus *brevialatus* var. *depressa* Wanner 1931 = Angioblastus *variabilis* Wanner 1931.

Thaumatoblastus *longispinus* Wanner 1924^b = T. *longiramus* Wanner 1924^b.

Trionoblastus *pyramidatus* (Shumard 1858) = Heteroschisma *alternatum* (Lyon 1857).

LIST OF NEWLY REFERRED SPECIFIC NAMES IN THE BLASTOIDEA FISSICULATA

Agmoblastus *dotti* = Angioblastus dotti.
Codaster *alatus* = Heteroschisma alatum.
Codaster *canadensis* = Heteroschisma canadense.
Codaster *corrugatus* = Brachyschisma corrugatum.
Codaster *lorae* = Leptoschisma lorae.
Codaster *shimanskii* = Dolichoblastus shimanskii.
Codonaster *pousirewskii* = Tympanoblastus pousirewskii.
Deltoschisma *archiaci* = Pentremitidea archiaci.
Neoschisma *cornutum* = Notoblastus cornutus.
Paracodaster *miloradovitchi* = Angioblastus miloradovitchi.
Pentremites *decussatus* = Xenoblastus decussatus.
Phaenoschisma *archiaci* = Pentremitidea archiaci.
Phaenoschisma *benniei* = ?
Phaenoschisma ? *kentuckyensis* = Hadroblastus kentuckyensis.
Phaenoschisma *pecki* = Phaenoblastus pecki.
Phaenoschisma *rossica* = ?
Phaenoschisma *verneuili* = Pleuroschisma verneuili.
Pterotoblastus *oyensi* = Notoblastus oyensi.
Sagittoblastus *elongatus* = Tympanoblastus elongatus.
Sagittoblastus *wanneri* = Angioblastus wanneri.
Sundablastus *weberi* = Indoblastus weberi.
Timoroblastus *wanneri* = Angioblastus wanneri.
Trionoblastus *alatus* = Heteroschisma alatum.
Trionoblastus *canadensis* = Heteroschisma canadense.
Trionoblastus *gracilis* = Heteroschisma gracile.
Trionoblastus *pyramidatus* = Heteroschisma alternatum.
Trionoblastus *subtruncatus* = Heteroschisma subtruncatum.

GLOSSARY OF TERMS FOR BLASTOID DESCRIPTIONS

During this study, we have found certain terms commonly used for blastoids to be inadequately defined or we have lacked a term to convey our ideas. We therefore compiled the following glossary. Other terms are as defined in the Treatise, Part S (BEAVER, FAY and MOORE, 1967):

Ambulacral area. Part of blastoid body wall formed by ambulacral plates, but excluding brachioles. Synonym of ambulacral field.

Ambulacral field. See ambulacral area.

Ambulacral groove system. New term, replacing food groove and median groove. Groove system present (1) along median line of ambulacrum and on interdeltoid suture *(main ambulacral groove)*, (2) inbetween side plates *(ambulacral side groove)*, and (3) on brachioles *(brachiolar groove)*. Main and side grooves provided with *minor grooves* and *lobes* at both sides all along their course. If overgrown by lancet (*Astrocrinus*, orbitremitids) ambulacral groove system converts into *ambulacral duct system* within the lancet. Ambulacral groove system now interpreted to have lodged the blastoid water-vascular system. The terms minor grooves and lobes substitute for "ambulacral furrows" and for "cover plate lobes and furrows".

Ambulacral furrows. Term to be suppressed in favor of "minor groove" (See: ambulacral groove system).

Ambulacral plates. The plates forming the ambulacral area (lancet, side plates and outer side plates), and bearing the ambulacral tract and ambulacral groove systems.

Ambulacral tract system. New term, replacing food groove. Concave tract on brachioles, ambulacral areas, and interdeltoid sutures with ambulacral grooves in its bottom, and covered by ambulacral cover plates. Present along median part of ambulacral area and interdeltoid sutures *(main tract)*, on lancet and/or side plates *(side tract)*, and on brachioles *(brachiolar tract)*.

Ambulacral sinus. In phaenoschismatids the depressed areas of the vault inbetween interambulacral pyramids, formed by RD and DR sectors.

Ambulacrum. Synonym of ambulacral area, or ambulacral field.

Calyx. Term suppressed in favor of theca.

Conjunct deltoid process. Term suppressed in favor of interambulacral pyramid.

Cover plate, -furrow, -socket. Terms suppressed in favor of minor grooves (See ambulacral groove system).

Deltoid crest. Redefined as sharp ridge between two DR sectors of the same deltoid, which are not lying in the same plane. Most prominent in phaenoschismatids, but subdued or absent in codasterids and neoschismatids.

Deltoid body. Large aboral part of deltoid inbetween deltoid lip and radial limb. Term mostly applicable to phaenoschismatids and spiraculates with incipient DD growth. Deltoid body is formed by welldeveloped DR growth sectors. Term is not applicable to codasterids and neoschismatids with considerable DD growth in the deltoids.

DD sectors. Adoral sectors of deltoid comprising those parts that have grown toward the opposing deltoids, and toward the oral opening. Initiated early in ontogenetic development, forming peristomial ring around oral opening, before DR sectors are introduced. Peristomial ring of DD sectors preserved as such in phaenoschismatid and spiraculate ontogeny, but obscured by later ontogenetic growth in DD sectors in codasterids and neoschismatids.

DR sectors. Aboral sectors of deltoid comprising those parts that have grown aborally toward an opposing radial plate. Initiated later in ontogenetic development than DD sectors. DR sectors normally form part of hydrospires.

Deltoid lip. Small adoral part of deltoid inbetween oral opening and deltoid crest. Deltoid lips form peristomial ring. Term mostly applicable to phaenoschismatids and spiraculates with incipient DD growth. Deltoid lip is formed by incipient DD growth sectors. Term is not applicable to codasterids and neoschismatids with considerable DD growth in the deltoids.

Dorsal. To be suppressed in favor of aboral.

Food groove. Term suppressed in favor of ambulacral groove and ambulacral tract.

Fused hydrospire plate. Term suppressed in favor of subradial and sublancetal calcite deposits.

Hydrospiralium. To be suppressed in favor of hydrospire group.

Hydrospire cleft. Term redefined as the cleft separating ambulacral plates from adjoining radial and deltoid plates.

Hydrospire duct. Terminal inflated portion of hydrospire fold.

Hydrospire group. Group of hydrospire folds present in one of the ten usual blastoid positions. Term is informally used. Replaces formal term hydrospiralium.

Hydrospire lamellae. Parts of hydrospires in-between hydrospire slits and hydrospire ducts, formed by thin, parallel lamellae.

Hydrospire slit. Elongate opening of individual hydrospire.

Hydrospire tube. Synonym of hydrospire duct.

Interambulacral pyramids. New term, mostly for structures in phaenoschismatid blastoids. Defined as interradially disposed pyramidal areas, formed by RD and DR growth sectors, and alternating with ambulacral sinuses.

Pentagonal canal. Part of oral nervous system in peristomial ring; running from tips of lancets through DD sectors.

Peristomial cavity. Open space within peristomial ring just below oral opening.

Peristomial ring. Ring formed very early in ontogeny by DD growth sectors around the oral opening (mouth). Ring preserved in mature blastoids if DD growth is incipient (phaenoschismatids, spiraculates), but lost if DD growth is continued ontogenetically. Ring encloses central part of oral nervous system.

Spiracular slit. Term suppressed in favor of hydrospire cleft.

Stereomic microstructure. Term referring to the typical meshwork in echinoderm skeletal plates.

Stereomic lineations. Term indicating major linear elements in stereomic microstructure; visible both externally and internally, as in anatomic sections.

Subbasal plate. Term suppressed, indicates either topmost columnal or secondary calcite on basals.

Sublancet. Term suppressed, indicates secretion of secondary calcite under the lancet.

Subradial. Term suppressed, indicates secretion of secondary calcite.

Transverse commissure. Part of oral nervous system in peristomial ring; connects sides of pentagonal canal over interdeltoid suture.

Ventral. To be suppressed in favor of adoral.

CHAPTER II

ANATOMY

A deltailed anatomical study has been made of as many species of the fissiculate blastoids as could possibly be made available for sectioning. The acetate peel technique described by BREIMER & VAN EGMOND, 1968, was used. Sections have been made both serially and normal to the longer or polar axis of the theca (from mouth to center of basal circlet). In the majority of cases sectioning has been confined to the vault, because information was needed on composition of the anal interarea, the ambulacral and hydrospire systems, and the internal organ systems, such as the nervous and reproductive systems, that could have expressions in the skeleton. Each of these systems in the fissiculate blastoids is located in the vault.

The collection of peel sections thus formed is lodged in the Institute of Earth Sciences, Free Reformed University, Amsterdam, in the collection of Dr. A. Breimer, and will be kept complete and intact for better consultation by specialists interested in this matter.

The chapter on Anatomy begins with a section providing information on the descriptive anatomy in each of the species studied, arranged in order of their families and accompanied by general remarks on anatomy of families if such is required. A later section deals with the comparative anatomy of different organ systems in the fissiculate blastoids. This latter section is considered to be of more general interest and application.

DESCRIPTIVE ANATOMY

1. Family PHAENOSCHISMATIDAE

As members of the same family the phaenoschismatids share many common characters in their general plan of construction and mode of organisation of their main thecal elements. This similarity of characters is reflected in their anatomy. Therefore a general description of anatomical features common to all phaenoschismatids, and corresponding closely to their essential diagnostic characters, is given. The purpose of this description is to avoid monotonous repetition of all of these general statements later when anatomy of species is briefly dealt with.

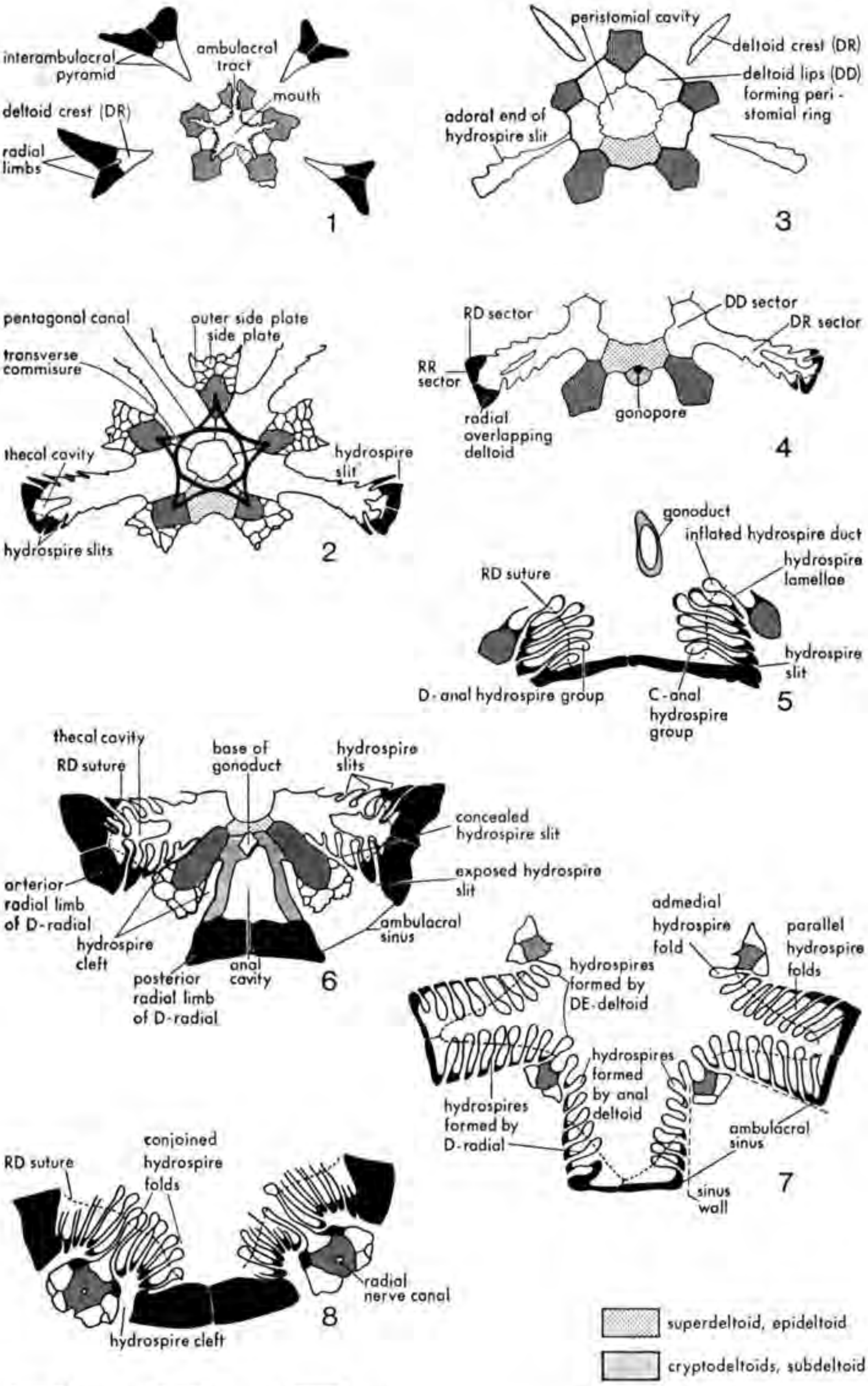
Phaenoschismatids have their vault differentiated into ambulacral sinuses and trigonal interambulacral pyramids (Pl. I, fig. 8; textfig. 1). The walls of ambulacral sinuses are built by DR and RD growth sectors. The trigonal interambulacral pyramids are built by the walls of two different ambulacral sinuses; the third surface is formed by two adjoining radial limbs. The deltoids are visible only in the sinus wall and have no exposure outside the sinus. The adoral portions of the deltoids are formed by incipient DD sectors, which form a ring around the peristome. The main bodies of the deltoids are formed by DR growth sectors, which have an external exposure only in the sinus wall. The RD suture is only visible in the ambulacral sinus. The deltoid bodies are overlapped by the radial limbs.

The radials are prominent plates, forming large parts of the external body wall. RD sectors are only exposed in the sinus wall. RR sectors are entirely external, contributing to interambulacral pyramids and overlapping the deltoid bodies.

Ambulacra are situated in the ambulacral sinuses. Lancets are elongate, and extend over the entire length of the ambulacrum. The oral end of the lancet abuts against the peristomial ring of deltoid lips; the aboral end is supported (partly enclosed and underlain) by the central part of the radial body. Lateral sufaces of lancet and side plates are not (with exception of *Kazachstanoblastus*) in lateral contact with R and D in the sinus wall, thus separating the ambulacrum from the sinus wall by a hydrospire cleft. Hydrospires are built across the full width of DR and RD growth fronts. The RD suture runs across the hydrospire fields; it is respresented in textfigures by a broken line.

The stable characters described above are present in each of the phaenoschismatid species which are described separately below. They are not repeated under each of these specific descriptions, but they should be kept in mind when reading the detailed anatomical description of each species. The anatomical description for each species details the variable characters in the phaenoschismatids which can be summarized as follows.

Textfig. 1. Explanation of terms used for anatomical descriptions of fissiculate blastoids. (1) Section through the mouth and the four interambulacral pyramids of *Pentremitidea paillетti* (L. Dev., Spain). (2) Section below the mouth through lower part of peristomial ring of *Heteroschisma canadense* (M. Dev., Ontario), showing central part of oral nervous system (transverse commissures partly restored). (3) Section just below the mouth through upper part of peristomial ring and the four deltoid crests of *Decaschisma pulchellum* (M. Sil., Indiana). (4) Posterior half of section below the mouth through lower part of peristomial ring of *Decaschisma pulchellum* (M. Sil., Indiana), showing opening of gonopore. (5) Posterior part of section below peristomial ring of *Pleuroschisma verneuili* (L. Dev., Spain), showing gonoduct formed by anal deltoids. (6) Posterior half of section below the mouth through lower part of peristomial ring of *Polydeltoideus enodatus* (M. Sil., Okla.). (7) Posterior half of section below peristomial ring through ambulacral sinuses and hydrospire structures of *Pleuroschisma lycorias* (M. Dev., Ontario). (8) Posterior part of section through hydrospire cleft of *Orophocrinus verus* (L. Carb., Engl.), showing characters of hydrospire structures. All figures oriented with posterior side of sections at bottom. Standard legends for thecal plates are uniformly used in all textfigures.


interambulacral pyramid
ambulacral tract
mouth
deltoid crest (DR)
radial limbs
1
peristomial cavity
deltoid crest (DR)
deltoid lips (DD) forming peri-stomial ring
adoral end of hydrospire slit
3
pentagonal canal
outer side plate
side plate
transverse commisure
thecal cavity
hydrospire slit
hydrospire slits
2
RD sector
DD sector
DR sector
RR sector
radial overlapping deltoid
gonopore
4
gonoduct
inflated hydrospire duct
hydrospire lamellae
RD suture
hydrospire slit
D-anal hydrospire group
C-anal hydrospire group
5
thecal cavity
RD suture
base of gonoduct
hydrospire slits
concealed hydrospire slit
exposed hydrospire slit
anterior radial limb of D-radial
hydrospire cleft
ambulacral sinus
anal cavity
posterior radial limb of D-radial
6
admedial hydrospire fold
parallel hydrospire folds
hydrospires formed by DE-deltoid
hydrospires formed by anal deltoid
hydrospires formed by D-radial
ambulacral sinus
sinus wall
7
RD suture
conjoined hydrospire folds
radial nerve canal
hydrospire cleft
8
superdeltoid, epideltoid
cryptodeltoids, subdeltoid
hypodeltoid
Deltoid
Radial
Lancet

The vault is of variable height. There may be either 4 or 5 interambulacral pyramids; the one in the *CD* interray may be absent (e.g. *Heteroschisma*). The interambulacral pyramids are of variable height, either rising above the peristome (e.g. *Pleuroschisma verneuili*), being even (e.g. some *Heteroschisma canadense*), or remaining below the peristome (e.g. *Phaenoblastus*). The deltoid crest may either slope upward or downward from its origin. The ambulacral sinuses may be deep, steep-walled with a V-shaped cross section (e.g. *Pleuroschisma verneuili*), shallow (e.g. *Pentremitidea*), or wide (e.g. *Cryptoschisma*, *Heteroschisma alternatum*).

The variable height of the vault is linked with the variable degree of inclination of the ambulacra. This degree of inclination may be expressed as the angle between the longer axis of an ambulacrum and the polar axis of the theca. Low inclination exists when this angle approaches 90° (e.g. *Phaenoschisma gracillimum*), high inclination when this angle approaches 30° (e.g. *Phaenoblastus caryophyllatus*). The ambulacra may be very much depressed in the sinuses (e.g. *Pleuroschisma verneuili*) or almost completely fill the sinus (e.g. *Cryptoschisma*, *Pentremitidea*).

The form of the ambulacra and the degree of exposure of the lancets is variable between phaenoschismatid genera as is the composition of the anal area. The elements composing the latter are fully discussed in the anatomic descriptions of the species. Hydrospire formation in phaenoschismatids has certain stable features, but many variable ones also exist; for example, the number of hydrospire groups present per genus is variable, the number of hydrospires per group is variable in ontogeny and possibly also per species, and the degree of exposure of hydrospire slits in the walls of the ambulacral sinuses is variable at the species level.

To facilitate an understanding of the peel sections, an illustration (textfig. 1) has been drawn which shows the major anatomical details to be seen in the sections along with their terminology. Sections have been made normal to the longer or polar axis of the theca, in order to establish the overall proportions and mutual interrelations of thecal elements constituting the vault. This mode of sectioning has the disadvantage that the plane of section makes an acute angle with the longer axes of the ambulacra and ambulacral sinuses. As a consequence, all angles in the sections are smaller than the true angles. For example: the true angle of the ambulacral sinus, by definition, is to be measured in a plane perpendicular to the longer axis of the ambulacrum. However, the plane of sectioning is oblique to the longer axis of ambulacra. Hence, the plane of sectioning makes a smaller angle with the walls of the ambulacral sinus than a perpendicular plane does. So, the true angle of the ambulacral sinus is larger than the corresponding angle between sinus walls in the sections. The same is true, *mutatis mutandis*, for the angle between the sinus wall and the direction of the hydrospire lamellae, and for the angle between sinus wall and the sides of ambulacra.

Decaschisma pulchellum (Miller & Dyer, 1878)
Textfigure 2; Pl. I, figs. 1–3

Total height of sectioned specimen 9.20 mm. Upper 2.90 mm, forming hydrospire-bearing vault, sectioned into 51 subsequent peel sections at mean intervals of 0.06 mm. In textfigure 2 thirteen selected transverse sections are shown.

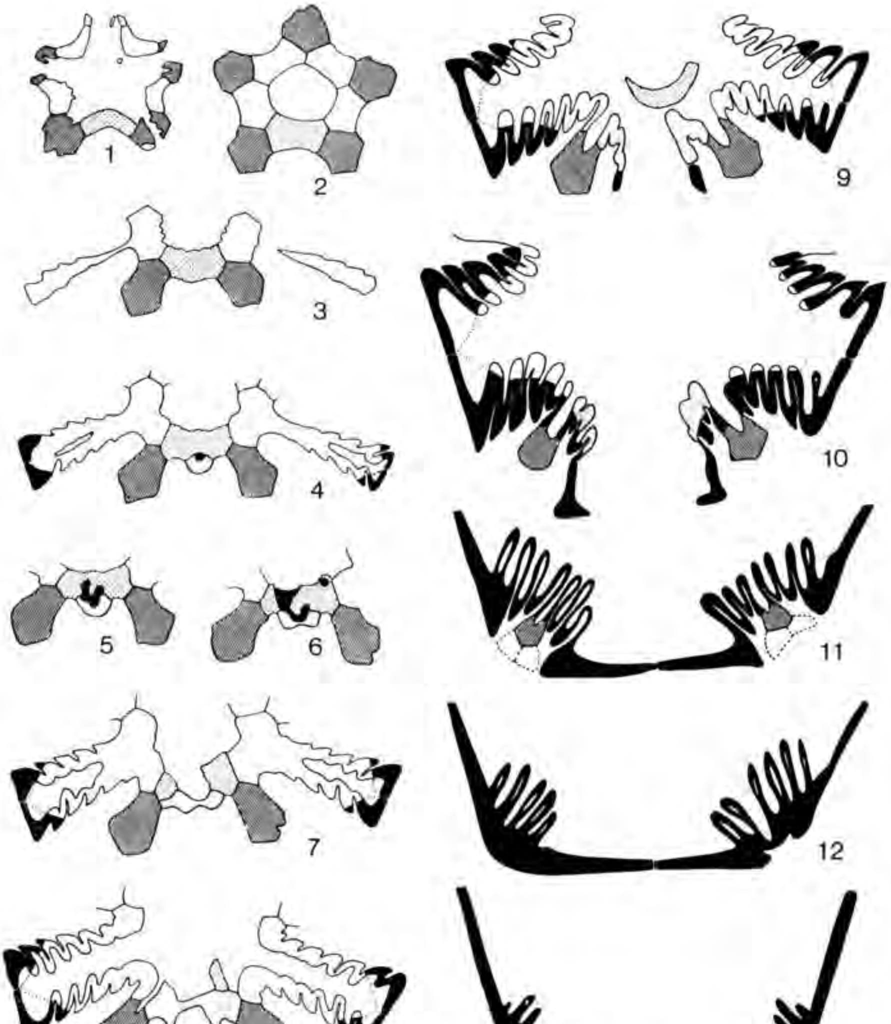
Vault moderately developed; theca has pentagonal cross section. Interambulacral pyramids present in all 5 interrays, rising to about the level of the peristome (figs. 2.1, 2). Deltoid crest subhorizontal. Ambulacral sinuses well defined, steep-walled with V-shaped cross section; walls of sinus form angle of about 60°.

Deltoids small. Peristomial ring composed of deltoid lips shown fig. 2.2. No traces of ring canals found in peristomial ring. Main bodies of deltoids extend internally to 1.70 mm below top of theca (fig. 2.10). Radial limbs moderately developed, bend strongly inward. Only radial limbs sectioned.

At posterior side super- and subdeltoid preserved; both plates clearly in optical discontinuity. No hypodeltoid preserved in sectioned specimen (fig. 2.10) but known from other specimens. Hypodeltoid contributing to external wall of theca. Superdeltoid small, isomorphic, corresponding with deltoid lips of regular deltoids, forming part of peristomial ring (figs. 2.2, 3). Subdeltoid relatively large, two-winged structure, composed of two descending limbs, connected by fragile jugum (fig. 2.8); subdeltoid limbs correspond to deltoid bodies of regular deltoids, exposed in *C* and *D* ambulacral sinuses, forming hydrospires (figs. 2.9, 10). Small gonopore present in suture between super- and subdeltoid (fig. 2.4); pore supported by small notch on subdeltoid. Internally, superdeltoid projected into spoonlike structure, inferred to be part of the gonoduct.

Ambulacra linear, slightly inclined, moderately depressed in ambulacral sinuses. Lancets almost parallel-sided; contact with peristomial ring shown fig. 2.2; contact with radial bodies not shown in textfigures. External surface of lancet strongly beveled for reception of side plates. Internal surface of lancet concave where bordering thecal cavity, in discrete contact with admedial hydrospire lamellae. Lateral surface of lancet not in contact with R and D in sinus wall. No side plates and outer side plates preserved in sectioned specimen. Side plates known to completely conceal the lancet (except adoralmost end) from other specimens.

Hydrospires formed across full width of DR and RD growth sectors. In sections RD suture runs across hydrospire folds, represented in textfigures by broken line. Ten hydrospire groups present. At posterior side hydrospires formed by subdeltoid and corresponding RD sectors. In regular fields number of hydrospire folds is 6 in sectioned specimen, in *C* and *D* anal fields number is 3 (figs. 2.10, 11). Hydrospires placed parallel to one another and at acute angle with the sinus wall. Hydrospires thick-walled, not differentiated into hydrospire lamellae and inflated hydrospire



Textfig. 2. *Decaschisma pulchellum* (Miller & Dyer, 1878). Sil., Waldron Shale; Hartsville, Ind., USA; spec. Field Museum, Univ. Chicago collec. 18874. Series of 13 transverse sections from peel numbers 5, 10, 15, 20, 21, 23, 25, 30, 35, 40, 45, 47, and 49, cut resp. 0.14, 0.29, 0.44, 0.59, 0.63, 0.70, 0.76, 0.95, 1.20, 1.70, 2.20, 2.40, and 2.60 mm below top of theca. All figures × 13, showing posterior half of section, unless otherwise stated. (1, 2) Peristome. (3–10) Composition of anal area and structures allied to reproductive system; note presence of super- and subdeltoid; 4, note gonopore; 5, 6 anal area only. (9–13) Composition of ambulacral and hydrospire structures; note presence of hydrospires at *C* and *D* anal sides; 11, 12, 13, *C* and *D* radials only. See textfig. 1 for further explanation.

ducts, not pending deeply into thecal cavity. This is probably the primitive hydrospire construction. Hydrospire slits all situated in sinus wall, partly concealed when ambulacrum intact. Entrance to hydrospires by way of cleft between side of ambulacrum and sinus wall. Cleft extends over entire length of ambulacrum. Hydrospires functional over entire length. No secondary infilling of secondary calcite in hydrospire slits.

Polydeltoideus enodatus Reimann & Fay, 1961
Textfigure 3; Pl. I, figs. 8, 12

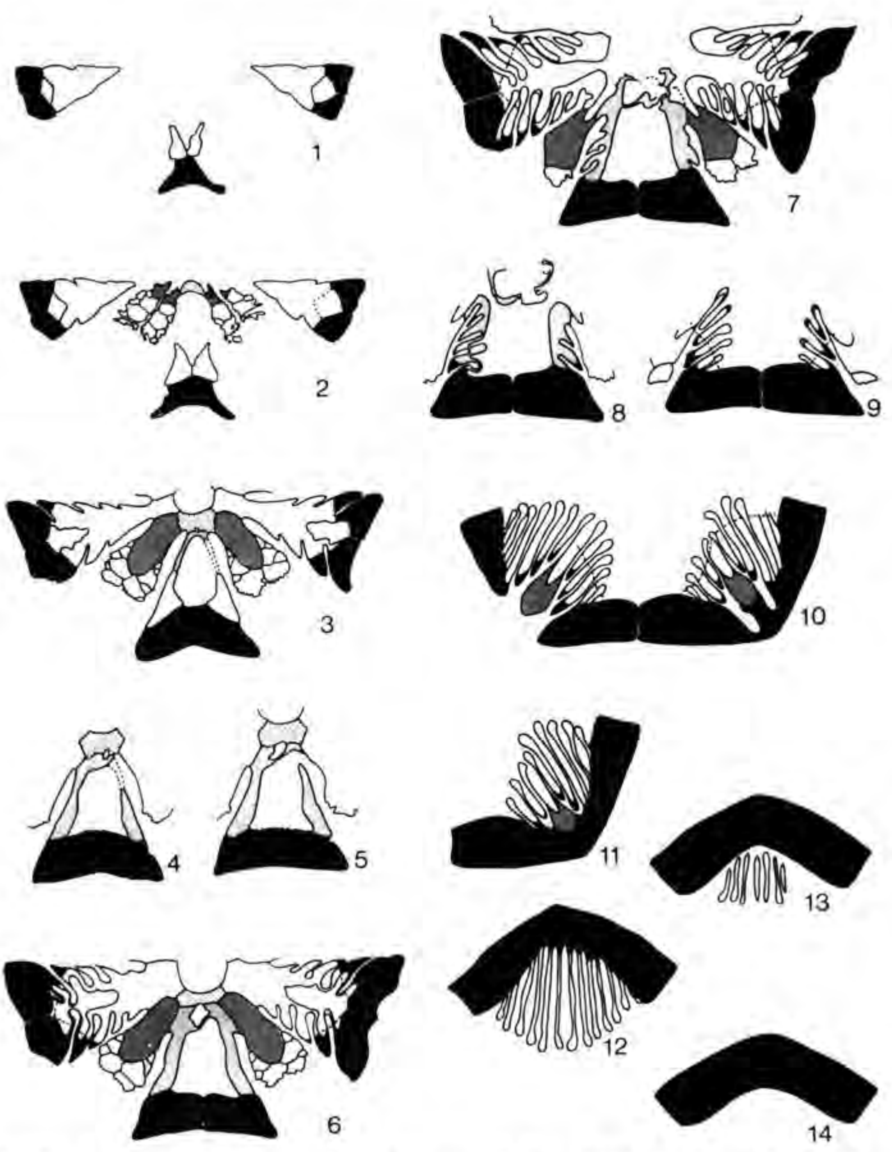
Total height of sectioned specimen 16 mm. Upper 3.06 mm forming hydrospire-bearing vault, sectioned into 41 subsequent transverse peel sections at mean intervals of 0.075 mm. In textfigure 3 fourteen selected sections are shown.

Vault moderately developed; theca has slightly pentalobate cross section. Interambulacral pyramids present in all 5 interrays, rising 0.75 mm above peristome (figs. 3.1–3). Deltoid crest sloping slightly upward. Ambulacral sinuses well defined, steep-walled with V-shaped cross section; walls of sinus form angle of 90°.

Deltoids small. Peristomial ring composed of deltoid lips shown fig. 3.3. No traces of ring canals found in peristomial ring. Main bodies of deltoids extend internally to 1.71 mm below top of theca (fig. 3.10). Radial limbs moderately developed, bend inward. Only radial limbs sectioned.

At posterior side 5 anal deltoids: superdeltoid, subdeltoid, two paradeltoids, and a hypodeltoid. Superdeltoid small, isomorphic, corresponding with deltoid lips of regular deltoids, forming part of peristomial ring (fig. 3.3). Subdeltoid relatively large, two-winged structure, composed of two descending limbs connected by fragile jugum (figs. 3.5–7); subdeltoid limbs correspond to deltoid bodies of regular deltoids, exposed in *C* and *D* ambulacral sinuses, forming hydrospires (figs. 3.7–9). Small gonopore present in suture between super- and subdeltoid (fig. 3.3). Internally pore leads into wider canal formed mainly by subdeltoid. This canal (figs. 3.5–8) is inferred to be part of the gonoduct. Two paradeltoids (figs. 3.2, 3, shown in white) form top of posterior interambulacral pyramid, which rises about as high as other interambulacral pyramids. Anus (fig. 3.3) passes externally between subdeltoid and two paradeltoids. Hypodeltoid relatively large, overlapped by posterior radial limbs (fig. 3.6), supporting two paradeltoids, contributing to external wall of theca.

Ambulacra inclined, linear, moderately depressed in ambulacral sinus. Lancets almost parallel-sided; contact with peristomial ring shown fig. 3.3, contact with radial body shown fig. 3.11. Internal surface of lancet concave where bordering thecal cavity, internally in discrete contact with admedial hydrospire lamellae (figs. 3.7, 10). Lateral surface of lancet nowhere in contact with R and D in sinus wall. External surface of lancet strongly beveled, completely covered by side plates over entire length, except at



Textfig. 3. *Polydeltoideus enodatus* Reimann & Fay, 1961. Sil., Henryhouse Fm., Pontotoc Co., Okla., USA; spec. USNM loc. 6219. Series of 14 transverse sections, resp. from peels numbered 10, 12, 17, 19, 20, 21, 23, 24, 26, 28, 29, 33, 39, and 41, cut resp. 0.34, 0.43, 0.71, 0.82, 0.87, 0.96, 1.19, 1.29, 1.50, 1.71, 1.81, 2.21, 2.80, and 3.06 mm below top of theca. All figures × 8, showing posterior half of section, unless otherwise stated. (1) Above peristome, through interambulacral pyramids. (2) Peristome. (3–8) Composition of anal area and structures allied to reproductive system; note presence of super-, sub- and hypodeltoid and two paradeltoids; 3, note gonopore; 4, 5, 8, 9, anal area only. (9–13) Composition of ambulacral and hydrospire structures; note presence of hydrospires at *C* and *D* anal sides; 11, *C* radial; 12–14, *A* radial. See textfig. 1 for further explanation.

oral extremity. Lancet concealed. Side plates and outer side plates present. Side plates have lateral contact along median line of ambulacrum. Small outer side plates alternate with larger side plates. Outer side plates placed at lateral periphery of ambulacrum. No lateral contacts of side plates and outer side plates with R and D in sinus wall. Ambulacra stand freely in ambulacral sinus.

Hydrospires formed across full width of RD and DR sectors. In sections RD suture runs across hydrospire folds, represented in textfigures by broken line. Ten hydrospire groups present. At posterior side hydrospires formed by subdeltoid and corresponding RD sectors. In regular fields number of hydrospire folds in sectioned specimen is 6 or 7; in *C* and *D* anal fields number is reduced to 4 or 5 (figs. 3.8–11). Hydrospires placed parallel to one another at acute angle with sinus wall. Hydrospires thin-walled, extending fairly deep into thecal cavity. Admedial folds differentiated into hydrospire lamellae and inflated hydrospire ducts. Hydrospire folds lying closest to ambulacra have inflated tips converging; the others diverge (fig. 3.12). Hydrospire slits all situated in sinus wall. Abmedial one or two hydrospire slits are exposed (figs. 3.6, 7), others concealed by ambulacrum when intact. Entrance to exposed hydrospires direct, otherwise by way of cleft between side of ambulacrum and sinus wall. Clefts extend over entire length of ambulacrum, leaving these structures without lateral contact with sinus wall. Configuration of hydrospire folds shown figs. 3.11–13 is produced by inclination of ambulacra in combination with thick body wall. It may not necessarily imply that infilling of hydrospire slits occurred.

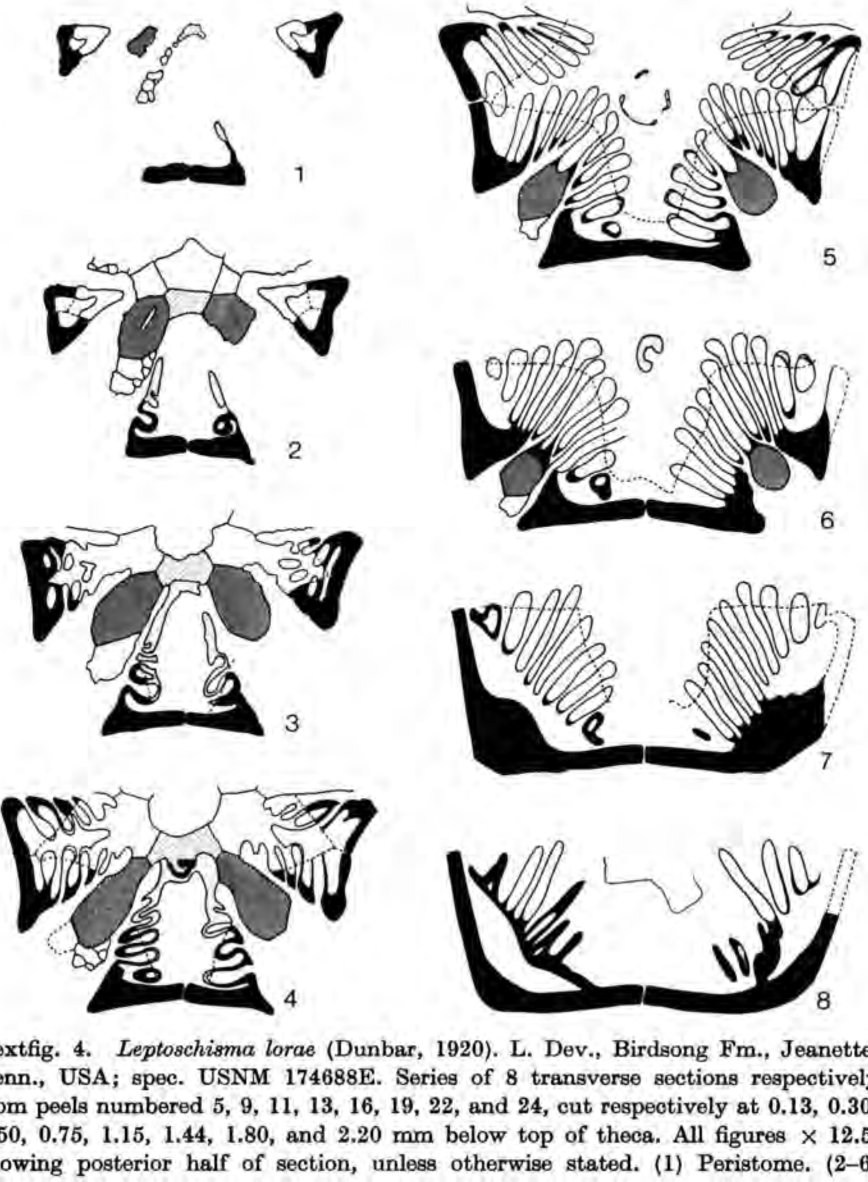
Leptoschisma lorae (Dunbar, 1920)
Textfigure 4; Pl. I, figs. 4–7

Total height of sectioned specimen 5.9 mm (basals missing). Upper 2.70 mm, forming hydrospire-bearing vault, sectioned into 26 subsequent transverse peel sections at mean intervals of 0.10 mm. In textfigure 4 eight selected sections are shown.

Theca thick-plated with pentagonal cross section. Vault well developed. Interambulacral pyramids present in all 5 interrays, rising 0.50 mm above peristome (figs. 4.1–3). Deltoid crest sloping moderately upward from origin. Ambulacral sinuses well defined, steep-walled with V-shaped cross section; walls of sinus form angle of 50°.

Deltoids relatively well developed. Peristomial ring composed of distinct deltoid lips shown fig. 4.3. No traces of ring canals found in peristomial ring. Main bodies of deltoids extend internally to 1.80 mm below top of theca (fig. 4.7). Radial limbs well developed, bend inward. Only radial limbs sectioned.

At posterior side two anal deltoids preserved: a super- and a subdeltoid. Superdeltoid small, isomorphic, corresponding with deltoid lips of regular deltoids, forming part of peristomial ring (figs. 4,2, 3). Subdeltoid relatively large, two-limbed structure, composed of two descending limbs, connected by a jugum (fig. 4.4; subdeltoid limbs correspond to deltoid bodies of regular deltoids, form *C* and *D* sinus walls, form hydrospires (figs. 4.3–5). Small gonopore present in suture between super- and subdeltoid, (fig. 4.4). Internally pore leads into wider canal, mainly formed by subdeltoid



Textfig. 4. *Leptoschisma lorae* (Dunbar, 1920). L. Dev., Birdsong Fm., Jeanette, Tenn., USA; spec. USNM 174688E. Series of 8 transverse sections respectively from peels numbered 5, 9, 11, 13, 16, 19, 22, and 24, cut respectively at 0.13, 0.30, 0.50, 0.75, 1.15, 1.44, 1.80, and 2.20 mm below top of theca. All figures × 12.5, showing posterior half of section, unless otherwise stated. (1) Peristome. (2–6) Composition of anal area and structures allied to reproductive system; note presence of super- and subdeltoid; 4, note gonopore; 5, 6, note gonoduct. (3–8) Composition of ambulacral and hydrospire structures; note presence of hydrospires at *C* and *D* anal sides; 6, 7, 8, *C* and *D* radials only. See textfig. 1 for further explanation.

(figs. 4.5, 6). This canal is inferred to be part of the gonoduct. No hypodeltoid preserved, nor is there much space for one (figs. 4.1, 2). From other specimens hypodeltoid inferred to be present as a small trigonal plate in subhorizontal position aboral from anus.

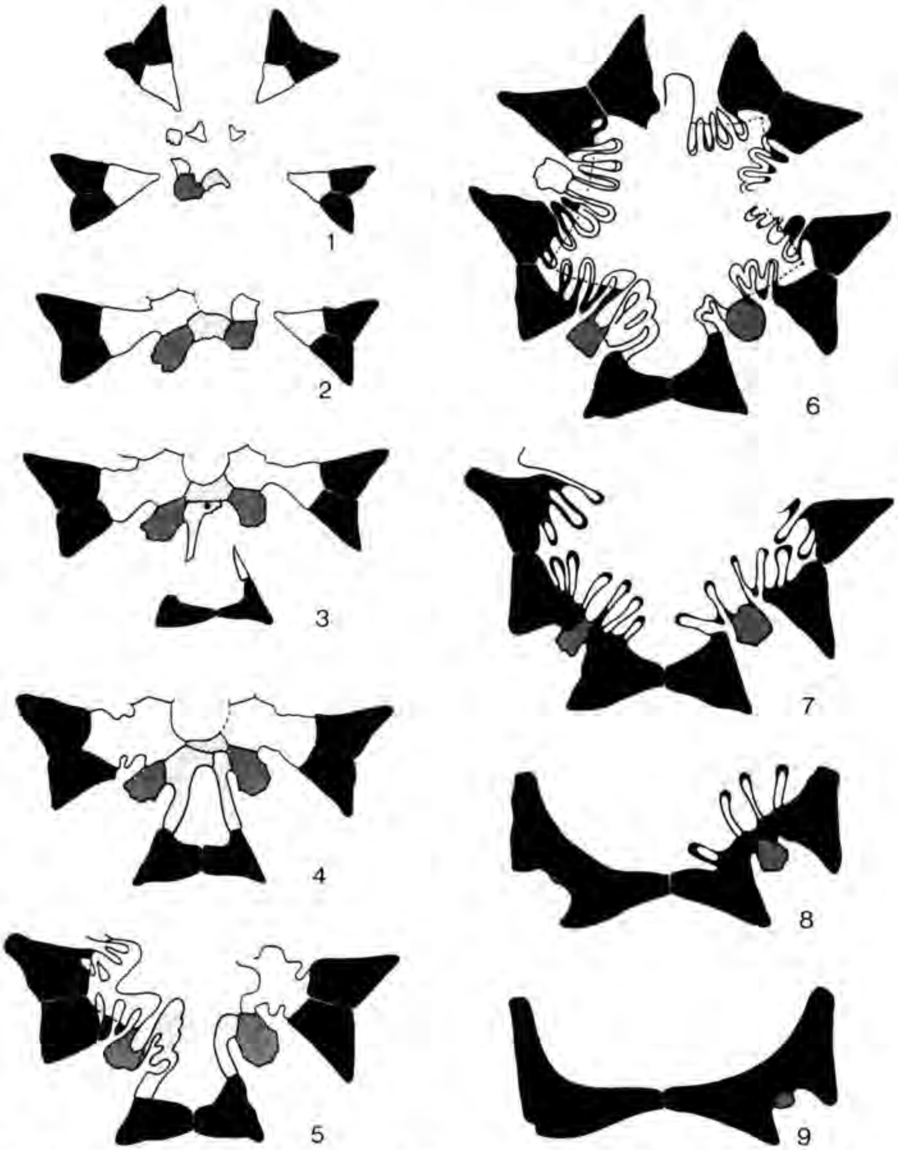
Ambulacra well inclined, linear, slightly depressed in ambulacral sinuses. Lancets almost parallel-sided, contact with peristomial ring shown fig. 4.3, contact with radial body not shown. Internal surface of lancet concave where bordering thecal cavity (fig. 4.5), in contact with admedial hydrospire lamellae (figs. 4.5, 6). Lateral surface of lancet nowhere in contact with R and D in sinus wall. External surface of lancet strongly beveled, completely covered by side plates, except at oral extremity. Side plates and outer side plates present in part of *D* ambulacrum (figs. 4.1–6). Small outer side plates alternate with larger side plates. Outer side plates placed at lateral periphery of ambulacrum. No lateral contacts of side plates and outer side plates with R and D in sinus wall. Ambulacra stand freely in ambulacral sinus.

Hydrospires formed across full width of RD and DR growth sectors. In sections RD suture runs across hydrospire folds, represented in textfigures by broken line. Ten hydrospire groups present. At posterior side hydrospires formed by subdeltoid and corresponding RD sectors. In regular fields number of hydrospire folds is 6 in sectioned specimen, but may be reduced by one in anal interarea. In fig. 4.5 there are 6 folds at *D* anal side, and 5 at *C* anal side. Hydrospires placed subparallel at acute angle with sinus wall. Hydrospires thin-walled, extending deeply into thecal cavity. Admedial folds differentiated into hydrospire lamellae and inflated hydrospires ducts (fig. 4.6). Innermost folds have inflated tips converging (fig. 4.5). Hydrospire slits all situated in sinus wall, mostly concealed by ambulacrum when latter intact. Entrance to hydrospires by way of cleft between side of ambulacrum and sinus wall. Clefts extend over almost entire length of ambulacrum, leaving this structure without contact with the sinus wall. Configuration of hydrospire folds shown figs. 4.7, 8 produced by deep protrusion of hydrospires into thecal cavity. It proves that hydrospire folds, even at their aboral extremities, penetrate rapidly and directly in thecal cavity and are not gradually deepening in adoral direction.

Caryoblastus bohemicus Breimer, Macurda, & Prokop, 1968
Textfigure 5; Pl. I, figs. 10, 11

Total height of sectioned specimen 5.6 mm. Upper 2.5 mm, forming hydrospire-bearing vault, sectioned into 56 subsequent tranverse peel sections at mean intervals of 0.04 mm. In textfigure 5 nine selected sections are shown.

Theca thick-walled, with pentagonal cross section. Vault well developed. Interambulacral pyramids present in all 5 interrays, rising 0.75 mm above



Textfig. 5. *Caryoblastus bohemicus* Breimer, Macurda & Prokop, 1968. L. Dev., Slivenec Ls.; Konvarka, Bohemia; spec. Geol. Surv., Czechoslovakia, Prague. Series of 9 transverse sections resp. from peels numbered 15, 20, 25, 30, 35, 40, 45, 50, and 55, cut resp. 0.44, 0.60, 0.75, 0.91, 1.09, 1.28, 1.52, 1.90, and 2.40 mm below top of theca. All figures × 12.5, showing posterior half of section, unless otherwise stated. (1) Peristome, complete section. (2–5) Composition of anal area, note presence of superdeltoid and two cryptodeltoids. (5–9) Composition of ambulacral and hydrospire structures; note presence of hydrospires at *C* and *D* anal sides; 8, 9 *C* and *D* radials only. See textfig. 1 for further explanation.

peristome (figs. 5.1–3). Deltoid crest sloping upward from origin. Ambulacral sinuses prominently developed, deep, steep-walled, with almost U-shaped cross section; walls of ambulacral sinus form angle of 35°.

Deltoids relatively small. Peristomial ring composed of deltoid lips partly shown in figs. 5.2–4. No traces of ring canals found in peristomial ring. Main bodies of deltoids extend internally to 1.28 mm below top of theca (fig. 5.6). Radial limbs well developed, bend inward. Only radial limbs sectioned.

At posterior side four anal deltoids: superdeltoid, two cryptodeltoids, and hypodeltoid. Superdeltoid (figs. 5.2–4) small, isomorphic, corresponding with deltoid lips of regular deltoids, forming part of peristomial ring. Two cryptodeltoids (figs. 5.3–6) relatively large, corresponding to deltoid bodies of regular deltoids, forming *C* and *D* sinus walls and meeting one another at aboral side of superdeltoid; cryptodeltoids hydrospire-forming. Suture between cryptodeltoids well established, in sectioned specimen displaced to right side of anteroposterior axis (fig. 5.4). Two cryptodeltoids in optical continuity as if they were one plate or derived from one plate; cryptodeltoids in optical discontinuity with superdeltoid. Cryptodeltoids not observed to contribute to gonoduct. No hypodeltoid preserved in sectioned specimen. Only relatively small area available for hypodeltoid (fig. 5.3); when present during life, small, trigonal, and in subhorizontal position aboral from anus.

Ambulacra inclined, linear, well depressed in ambulacral sinuses. Lancets almost parallel-sided; contact with peristomial ring shown figs. 5.3, 4, contact with radial body at level of fig. 5.7. Internal surface of lancet concave where bordering thecal cavity (figs. 5.5, 6), in contact with admedial hydrospire lamellae. Lateral surface of lancet nowhere in contact with R and D in sinus wall. External surface of lancet sculptured for reception of side plates, which themselves are not preserved in sectioned specimen. From other specimens preserving side plates it is observed that side plates are not in lateral contact with R and D in sinus wall. Ambulacra appear to stand freely in the sinus.

Hydrospires formed across DR and RD growth sectors, but not occupying full width of RD suture. Note absence of hydrospire folds in top of ambulacral sinus (figs. 5.1–4). In sections RD suture runs across hydrospire fields, represented in textfigure by broken line. Ten hydrospire groups present. At posterior side hydrospires formed by two cryptodeltoids and corresponding RD sectors. Number of hydrospires per group variable, more numerous at anterior side than at posterior side; in regular groups 3 or 4 folds in sectioned specimen, in posterior interray number reduced to 2 or 3 folds. Note that larger *D* cryptodeltoid forms 3 folds, and smaller *C* cryptodeltoid only 2. Hydrospires not placed parallel to one another, but conjoined, hence number of hydrospire slits in sinus wall not reflecting exact number of hydrospire folds. Hydrospires thin-walled in portion formed by radials, but thick-walled in portion formed by deltoids (compare fig. 5.6 to fig. 5.7); in former portion hydrospires weakly differentiated into hydrospire lamellae and inflated hydrospire ducts. Hydrospire slits situated in sinus wall, completely concealed by ambulacrum when intact. Entrance to hydrospires by way of cleft between side of ambulacrum and sinus wall. Clefts extend over almost entire length of ambulacra. Probably slight infilling by secondary calcite present at aboral ends of hydrospire slits, restricting their functional length.

Cryptoschisma schultzii (De Verneuil & d'Archiac, 1845)
Textfigure 6; Pl. I. figs. 9, 13, 17

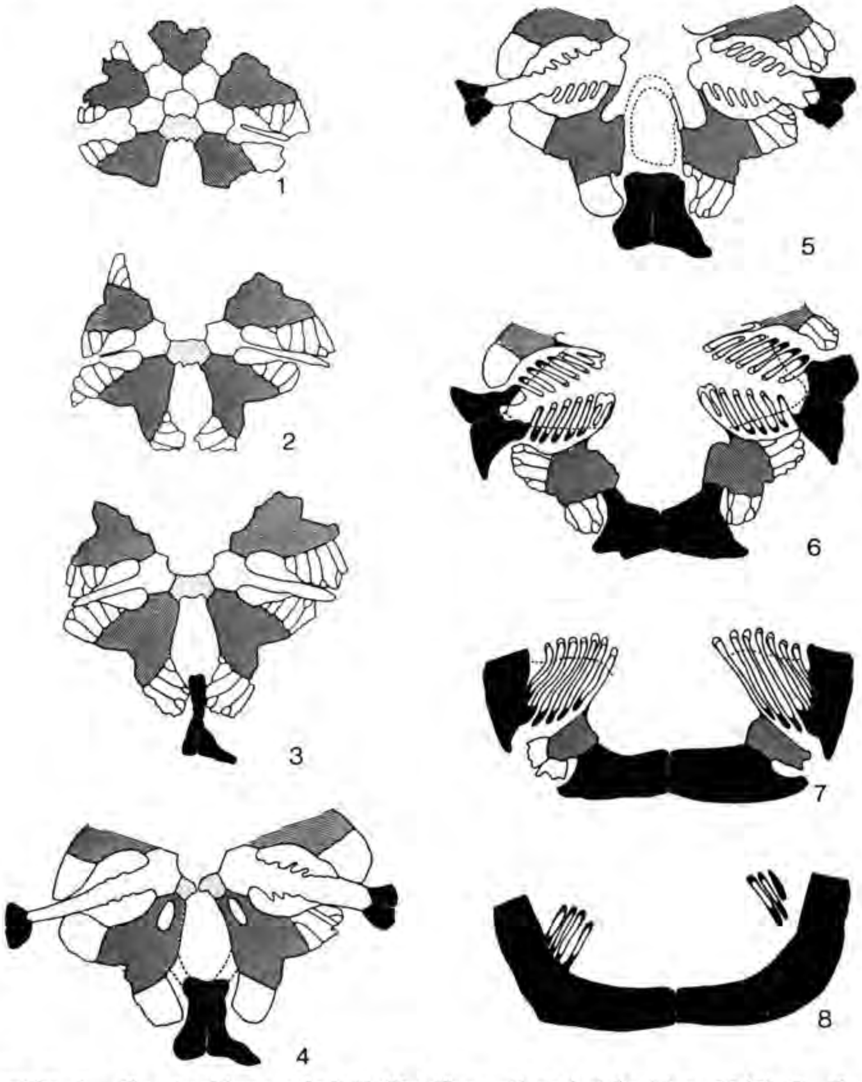
Total height of sectioned specimen 9.50 mm. Uper 2.05 mm, forming almost flat roof of theca with pendant hydrospire structures, sectioned into 32 subsequent transverse peel sections at mean intervals of 0.065 mm. In textfigure 6 eight selected sections are shown.

Theca thick-walled, with rounded pentagonal cross section. Vault very low. Interambulacral pyramids low, present in all five interrays, remaining at level of peristome (fig. 6.1). Deltoid crest subhorizontal. Ambulacral sinuses very wide, shallow, with broadly V-shaped cross section; walls of sinus form angle of 120°.

Deltoids relatively small plates. Peristomial ring composed of deltoid lips shown fig. 6.1. No traces of ring canals found in peristomial ring. Main bodies of deltoids extend internally to 1.05 mm below top of theca (fig. 6.7). Radial limbs slightly developed, not bent inward.

At posterior side two anal deltoids preserved: super- and hypodeltoid; two cryptodeltoids known to exist in other specimens, but stripped off from sectioned specimen. Superdeltoid small, isomorphic, corresponding with deltoid lips of regular deltoids, forming part of peristomial ring (figs. 6.1–4). Hypodeltoid (figs. 6.3–5) small, overlapped by posterior radial limbs, externally forming a crest separating *C* and *D* ambulacra (fig. 6.3). Cryptodeltoids occupied lateral sides of trigonal anal area in fig. 6.4 (indicated by dashed lines), but did not meet laterally at adoral side of anus, nor were they in contact with superdeltoid. Anus passes inbetween super-, crypto-, and hypodeltoid. No evidence found for structures belonging to reproductive system.

Ambulacra petaloid, not depressed in sinuses, not inclined. Lancets elongate rhombiform. Upper or external surface widely exposed (figs. 6.2–6), carrying side plates and outer side plates along lateral sides. Lower or internal surface partly in contact with deltoids in peristomial ring (figs. 6.1–3), partly bordering thecal cavity (figs. 6.5, 6), and partly abutting against radial (fig. 6.7). Lancet also supported by admedial hydrospire lamellae of each group (figs. 6.6, 7). Otherwise lateral surfaces of lancet not in contact with deltoids or radials in ambulacral sinus. At lateral extremities of ambulacrum some side plates may come in contact with deltoid crest (figs. 6.3–5), but at a lower level they prove not to be in contact with the underlying radial (figs. 6.6, 7); hence lateral contact of side plates with deltoid crest is superficial, leaving an open cleft below. Ambulacra stand freely in basin-shaped sinuses, but their lateralmost tips just touch the deltoid crests. Adoral parts of ambulacral sinuses cut off



Textfig. 6. *Cryptoschisma schultzii* (De Verneuil and d'Archiac, 1845). L. Dev., Ferroñes, Asturias, Spain; spec. Inst. Earth Sci., Free Ref. Univ., Amsterdam. Series of 8 transverse sections resp. from peel numbers 3, 5, 10, 14, 15, 20, 25, and 30, but resp. at 0.04, 0.09, 0.19, 0.35, 0.40, 0.65, 1.05 and 1.65, mm below top of theca. All figures × 8, showing posterior half of section, unless otherwise stated. (1) Peristome. (2–6) Composition of anal area, note presence of super- and hypodeltoid, and loss of two cryptodeltoids, position of which is given in 4 by dashed lines; 3, 4 note spiraclelike structures. (3–8) Composition of ambulacral and hydrospire structures; note absence of hydrospires at *C* and *D* anal sides; 7, 8, *C* and *D* radials only. See textfig. 1 for further explanation.

externally from rest of sinus; in external view may easily be taken for spiraclelike structures.

Hydrospires formed across full width of DR and RD growth sectors. In sections RD suture runs across hydrospire folds, represented in textfigures by broken line. Eight hydrospire groups present, those on *C* and *D* anal side absent. Number of hydrospire folds is 7 in regular fields of sectioned specimen. Hydrospires placed parallel to one another, thin-walled, clearly differentiated into hydrospire lamellae and inflated hydrospire ducts (figs. 6.6, 7). Hydrospires descending into thecal cavity till 1.75 mm below top of theca. Hydrospire slits all situated in sinus wall, completely concealed by ambulacrum when intact. Entrance to hydrospires by way of cleft between ambulacrum and sinus wall. Cleft partly bridged over by lateral contact of some side plates with deltoid crest at greatest width of petaloid ambulacra. Passage of water is freely possible over full length of hydrospire slits.

Pentremitidea pailletti (De Verneuil, 1844)
Textfigure 7; Pl. I, figs. 22–24

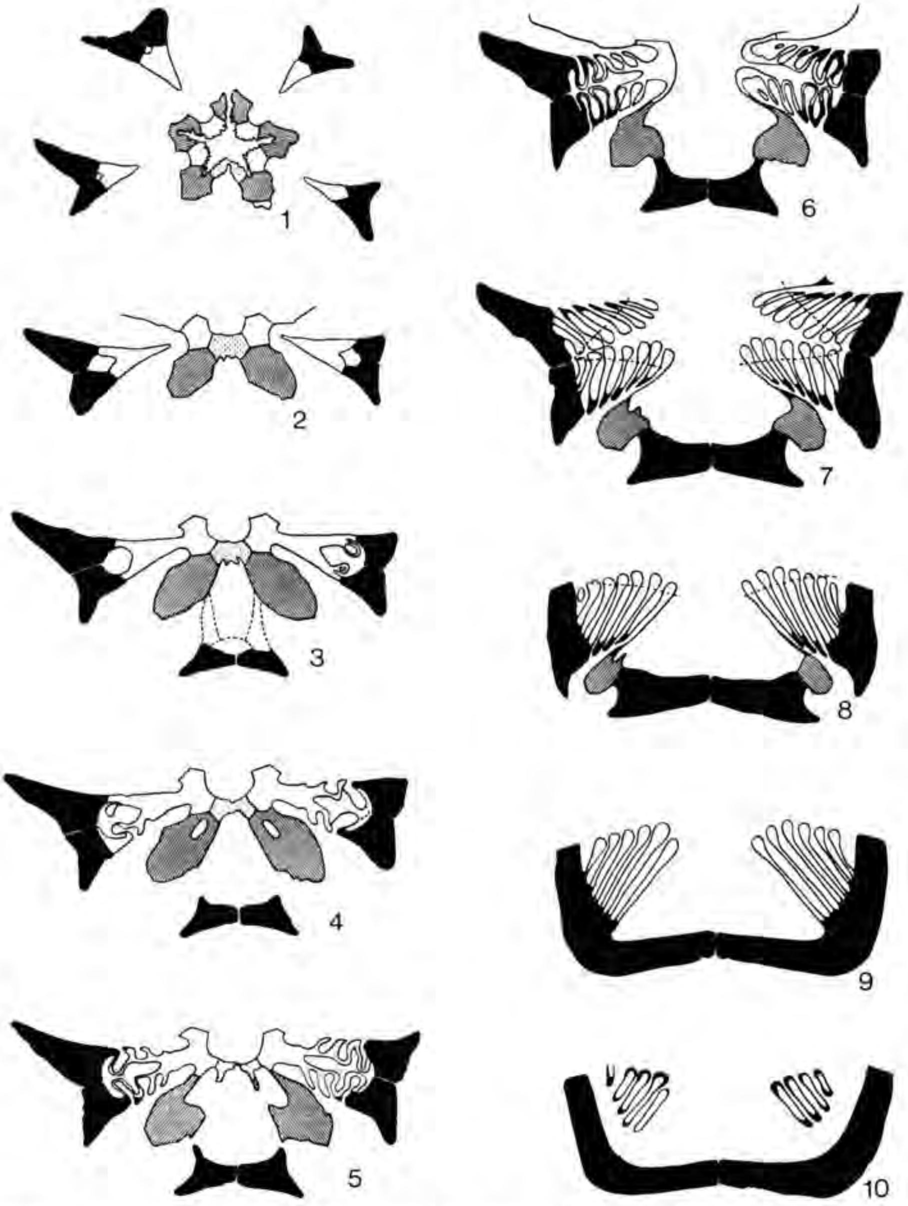
Total height of sectioned specimen 11.45 mm. Upper 4.45 mm, forming hydrospire-bearing vault, sectioned into 37 subsequent transverse peel sections at mean intervals of 0.12 mm. In textfigure 7 ten selected sections are shown.

Theca thick-walled, with pentalobate cross section. Vault low. Ambulacral sinuses narrow and shallow, almost completely occupied by lanceolate ambulacra. Angle of ambulacral sinus 70°. Interambulacral pyramids not well expressed, due to strongly bent-in radial limbs, and short upward sloping deltoid crest.

Deltoids small. Peristomial ring composed of deltoid lips shown figs. 7.2–4. No traces of ring canals found in peristomial ring. Main bodies of deltoids extend internally to 1.70 mm below top of theca. Radial limbs relatively well developed, bend strongly inward. Only radial limbs sectioned.

At posterior side only small, isomorphic superdeltoid preserved. Two cryptodeltoids and a hypodeltoid known to exist in well preserved specimens; their position indicated in fig. 7.3 by dashed lines. Cryptodeltoids small, one at each side of anal opening, not in contact with superdeltoid. Hypodeltoid small, overlapped by posterior radial limbs, not contributing very much to external wall of theca. No evidence found for structures belonging to reproductive system.

Ambulacra lanceolate, slightly inclined, not depressed in ambulacral sinus. Lancets almost parallel-sided; contact with peristomial ring shown figs. 7.1, 2, contact with radial body shown fig. 7.8. Internal surface of lancet concave where bordering thecal cavity (figs. 7.5–8), in contact with admedial hydrospire lamellae. Lateral surface of lancets nowhere



Textfig. 7. *Pentremitidea pailletti* (De Verneuil, 1844). L. Dev., Ferroñes, Asturias, Spain; spec. Inst. Earth Sci., Free Ref. Univ., Amsterdam. Series of 10 transverse sections resp. from peel numbers 35, 37, 39, 40, 41, 42, 45, 48, 51, and 60, cut resp. at 0.40, 0.60, 0.80, 0.90, 1.00, 1.10, 1.40, 1.70, 2.00, and 2.90 mm below top of theca. All figures × 8, showing posterior half of section, unless otherwise stated. (1) Peristome, complete section. (2–5) Composition of anal area, note presence of superdeltoid, note loss of two cryptodeltoids and hypodeltoid, position of which is given in 3 by dashed lines. (4–10) Composition of ambulacral and hydrospire structures; note absence of hydrospires at *C* and *D* anal sides; 8, 9, 10, *C* and *D* radials only. See textfig. 1 for further explanation.

in contact with R and D in sinus wall. Ambulacra stand freely in ambulacral sinus. *C* and *D* lancets modified, having extra lateral rim for making contact with posterior radial limbs (fig. 7.6), due to lack of anal hydrospires. No side plates or outer side plates preserved in sectioned specimen.

Hydrospires formed across full width of DR and RD growth sectors. In sections RD suture runs across hydrospire folds, represented in textfigures by broken line. Eight hydrospire groups present, those on *C* and *D* anal sides absent. Number of hydrospire folds in regular fields is seven in sectioned specimen (fig. 7.7). Hydrospires placed subparallel to one another, at acute angle to sinus wall. Hydrospires very thin-walled over all of their length, differentiated into thin hydrospire lamellae and inflated hydrospire ducts (fig. 7.7), penetrating deeply into thecal cavity. Hydrospire slits situated in sinus wall, completely concealed by ambulacrum when intact. Entrance to hydrospires by way of cleft between side of ambulacrum and sinus wall. Clefts extend over almost entire length of ambulacrum, leaving these structures without any lateral contact with the sinus wall. Hydrospires functional over entire length. Configuration of hydrospires as in figs. 7.9, 10 produced by thick thecal wall in combination with low inclination of ambulacra.

Pentremitidea archiaci (Etheridge & Carpenter, 1882)
Textfigure 8; Pl. I, figs. 14, 18–21

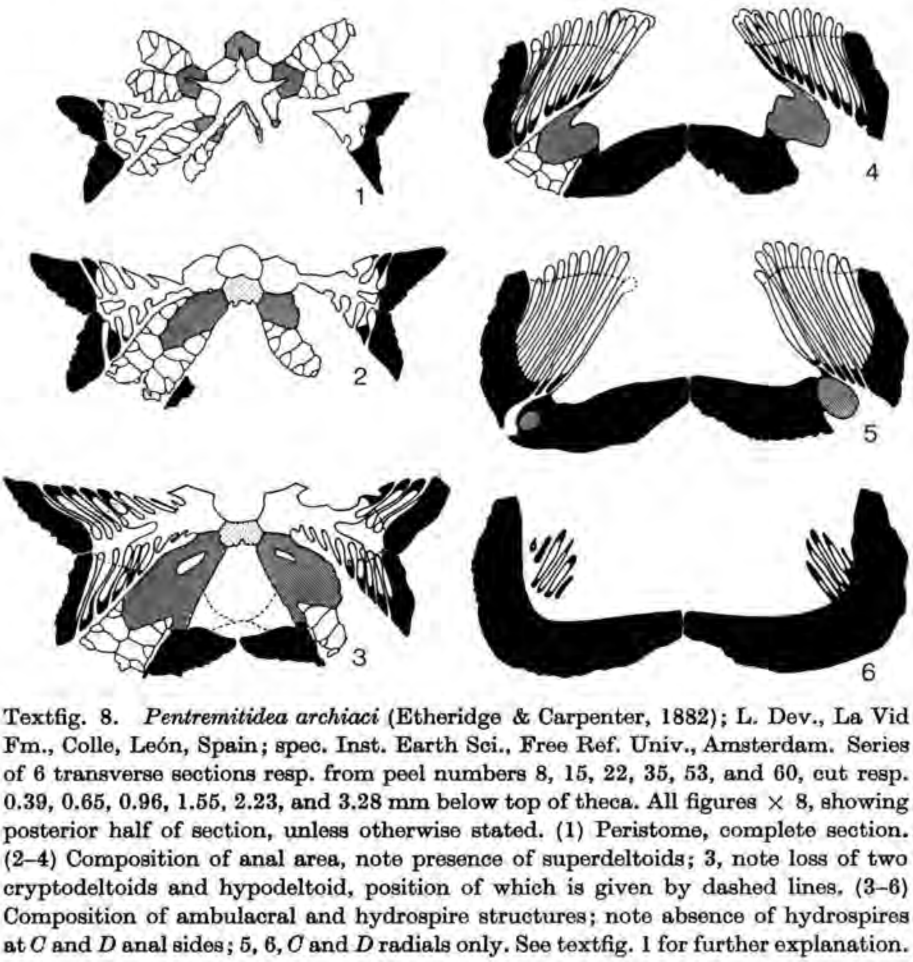
Total height of sectioned specimen 7.2 mm. Upper 3.82 mm, forming hydrospire-bearing vault, sectioned into 66 subsequent transverse peel sections at mean intervals of 0.06 mm. In textfigure 8 six selected sections are shown.

Theca thick-walled, with rounded pentalobate cross section. Vault low. Interambulacral pyramids not well expressed in external view. Ambulacral sinuses narrow and shallow, almost completely occupied by ambulacra. Angle of ambulacral sinus 85°. Interambulacral pyramids not well expressed, due to strongly bent-in radial limbs, and short upward-sloping deltoid crest.

Deltoids small. Peristomial ring composed of deltoid lips shown figs. 8.2, 3. No traces of ring canals found in peristomial ring. Main bodies of deltoids extend internally to 2.50 mm below top of theca (fig. 8.5). Radial limbs relatively well developed, bend strongly inward.

At posterior side only small, isomorphic superdeltoid preserved (figs. 8.1–3). Two cryptodeltoids and a hypodeltoid known to exist in well preserved specimens, occupying most of triangular area in center of section 22 (fig. 8.3, indicated by dashed lines). Cryptodeltoids small, one at each side of anal opening, not in contact with superdeltoid. Hypodeltoid small, overlapped by posterior radial limbs, not contributing very much to external body wall. No definite structures relating to reproductive system found in posterior interray. Possibly a small notch in aboral surface of superdeltoid may be interpreted as forming part of the gonopore (figs. 8.2, 3).

Ambulacra lanceolate, slightly inclined, not depressed in ambulacral sinuses. Lancets almost parallel-sided; contact with peristomial ring shown figs. 8.1–3, contact with radial body shown fig. 8.5. Internal surface of lancet concave where bordering thecal cavity (fig. 8.4), in contact with admedial hydrospire lamellae (fig. 8.4). Lateral surface of lancet nowhere in contact with R and D in sinus wall. *C* and *D* lancets modified, having extra lateral rim for contact with posterior radial limbs (fig. 8.3), due to lack of anal hydrospires. Side plates and outer side plates present.



Textfig. 8. *Pentremitidea archiaci* (Etheridge & Carpenter, 1882); L. Dev., La Vid Fm., Colle, León, Spain; spec. Inst. Earth Sci., Free Ref. Univ., Amsterdam. Series of 6 transverse sections resp. from peel numbers 8, 15, 22, 35, 53, and 60, cut resp. 0.39, 0.65, 0.96, 1.55, 2.23, and 3.28 mm below top of theca. All figures × 8, showing posterior half of section, unless otherwise stated. (1) Peristome, complete section. (2–4) Composition of anal area, note presence of superdeltoids; 3, note loss of two cryptodeltoids and hypodeltoid, position of which is given by dashed lines. (3–6) Composition of ambulacral and hydrospire structures; note absence of hydrospires at *C* and *D* anal sides; 5, 6, *C* and *D* radials only. See textfig. 1 for further explanation.

Side plates have lateral contact along medial line of ambulacrum. Lancet completely concealed, except at oralmost extremity. Side plates not in lateral contact with R and D in sinus wall. Side plates alternate with outer side plates (figs. 8.2, 3), former placed at lateral periphery of ambulacrum, without contacts with sinus wall. Ambulacra stand freely in sinus.

Hydrospires formed across full width of RD and DR growth sectors. In sections RD suture runs across hydrospire fields, represented in textfigures by broken line. Eight hydrospire groups present, those on *C* and *D* anal side absent. Number of hydrospire folds in regular fields is 10 in sectioned specimen (fig. 8.4). Hydrospires placed parallel to one another, at acute angle to sinus wall. Hydrospires extremely thin-walled, differentiated into thin hydrospire lamellae and inflated hydrospire ducts, extending deeply into thecal cavity. Hydrospire slits situated in sinus wall, mostly concealed by ambulacra when intact. Entrance to hydrospires by way of cleft between side of ambulacrum and sinus wall. Hydrospires functional over entire length.

Pentremitidea lusitanica Etheridge & Carpenter, 1882
Textfigure 9; Pl. II, figs. 2, 3

Total height of sectioned specimen 21 mm. Upper 7.86 mm, forming hydrospire-bearing vault, sectioned into 75 subsequent transverse peel sections at mean intervals of 0.1 mm. In textfigure 9 a selected section is shown, the only purpose being to show the close comparison of the essential anatomic characters to other species of *Pentremitidea*.

At posterior side only small, isomorphic superdeltoid preserved (fig. 9). Two cryptodeltoids and a hypodeltoid known to exist in well preserved specimens, occupying most of triangular anal area. Cryptodeltoids small,

Textfig. 9. *Pentremitidea lusitanica* Etheridge & Carpenter, 1882. L. Dev., La Vid Fm., Colle León, Spain; spec. Inst. Earth Sci., Free Ref. Univ., Amsterdam. Transverse section through upper vault region, from peel number 32, cut 1.51 mm below top of theca; × 7.5. Note presence of superdeltoid, and loss of two cryptodeltoids and hypodeltoid. Note absence of hydrospires at *C* and *D* anal sides. See textfig. 1 for further explanation.

one at each side of anal opening, not in contact with superdeltoids. Hypodeltoid small, overlapped by posterior radial limbs, not contributing very much to external body wall. No definite structures relating to reproductive system found in posterior interray.

Eight hydrospire groups exist, those on *C* and *D* anal side absent. Hydrospire slits situated in sinus wall, completely covered by ambulacrum when intact. Entrance to hydrospire slits by way of cleft between ambulacra and sinus wall. It is very difficult to judge whether or not during life the side plates and outer side plates came in contact with R and D in sinus wall, partially bridging the gap of the ambulacral cleft. Textfigure 9 suggests so, even to an extent that one may think of the formation of a spiraclelike structure (see *AB* interray in textfigure 9). However, caution should be used in the interpretation of this since it seems possible that lateral contacts of side plates and outer side plates with R and D in sinus wall is due to partial mechanical distortion of the sectioned specimen after fossilization. The seeming obliqueness of textfigure 9 is also due to slight mechanical distortion of the specimen.

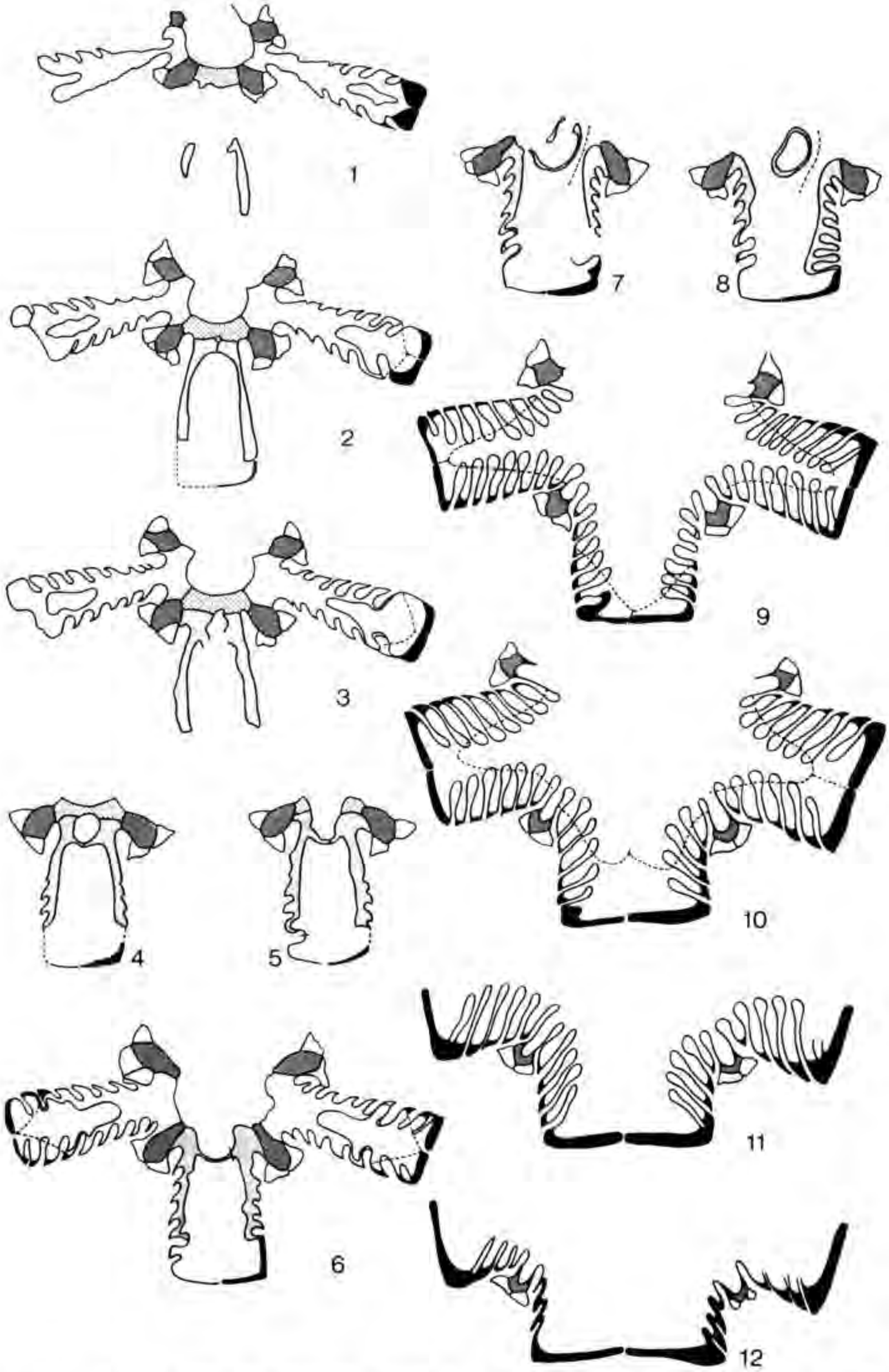
Pleuroschisma lycorias (Hall, 1862)
Textfigure 10; Pl. II, figs. 4, 7, 8, 10

Total height of sectioned specimen 7.5 mm. Upper 3.62 mm, forming hydrospire-bearing vault, sectioned into 59 subsequent transverse peel sections at mean intervals of 0.065 mm. In textfigure 10 twelve selected sections are shown.

Theca thin-walled, with pentagonal cross section. Vault high. Interambulacral pyramids present in all five interrays, rising only very slightly above peristome. Deltoid crest sloping moderately upward from origin. Ambulacral sinuses well defined, steep-walled with V-shaped cross section; walls of sinus form angle of 70°.

Deltoids relatively well developed. Peristomial ring composed of deltoid lips shown figs. 10.1–3. No traces of ring canals found in peristomial ring. Main bodies of deltoids extend internally to 2.12 mm below top of theca (fig. 10.10). Radial limbs well developed, only very slightly bent inward. Only radial limbs sectioned.

At posterior side 4 anal deltoids: superdeltoid, two cryptodeltoids, and hypodeltoid. Superdeltoid small, isomorphic, corresponding with deltoid lips in regular deltoids, forming part of peristomial ring (figs. 10.1–5). Cryptodeltoids large, corresponding to deltoid bodies in regular deltoids, overlapped by posterior radial limbs, exposed in *C* and *D* ambulacral sinuses, forming hydrospires (figs. 10.1–9). Gonopore present in suture between superdeltoid and cryptodeltoids at position of intercryptodeltoid suture (figs. 10.2, 4); gonopore leading internally into wider canal, formed by *C* cryptodeltoid in sectioned specimen (figs. 10.7, 8). This canal inferred to be part of the gonoduct. Hypodeltoid missing in sectioned specimen,



Textfig. 10. *Pleuroschisma lycorias* (Hall, 1862). M. Dev., Hungry Hollow Fm., Hungry Hollow, Arkona, Ontario, Canada; spec. UMMP 35033. Series of 12 transverse sections resp. form peels numbered 7, 10, 11, 12, 13, 16, 18, 20, 26, 36, 46, and 56, cut resp. 0.45, 0.62, 0.67, 0.73, 0.78, 0.93, 1.07, 1.19, 1.56, 2.12, 2.67 and 3.27 mm below top of theca. All figures × 12, showing posterior half of section, unless otherwise stated. (1) Peristome. (2–8) Composition of anal area and structures allied to reproductive system; note presence of superdeltoid and two cryptodeltoids; 2, note gonopore; 8, note gonoduct; 4, 5, 7, 8, anal area only. (3–12) Composition of ambulacral and hydrospire structures; note presence of hydrospires at *C* and *D* anal sides; 11, 12, *C* and *D* radials only. See textfig. 1 for further explanation.

but sections (figs. 10.1–4) reveal that there is place for one. Known from other specimens.

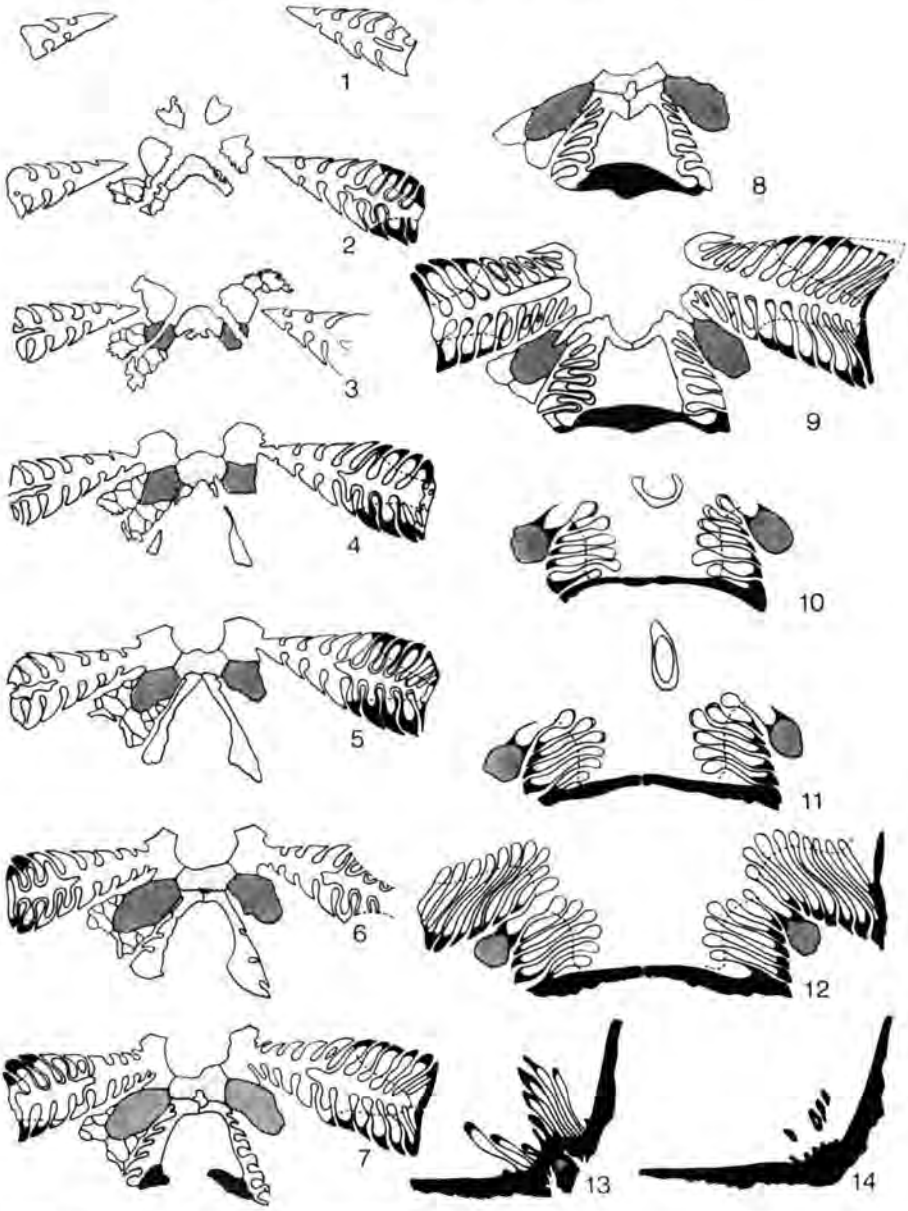
Ambulacra linear, much inclined, depressed in ambulacral sinuses. Lancets thin, parallel-sided; contact with peristomial ring shown figs. 10.2,3, contact with radial body not shown. Internal surface of lancet concave where bordering thecal cavity (figs. 10.9–12), in discrete contact with admedial hydrospire lamellae (fig. 10.9–12). Lateral surface of lancet nowhere in contact with R and D in sinus wall. External surface of lancet strongly beveled, completely covered by side plates over entire length; lancet not exposed except at adoralmost end. Side plates and outer side plates present. Side plates in lateral contact along median line of ambulacrum. No lateral contacts of side plates and outer side plates with R and D in sinus wall (except the one case shown fig. 10.6 in *B* ambulacrum which is possibly due to slight mechanical distortion of the specimen). Ambulacra stand freely in ambulacral sinus.

Hydrospires formed across full width of DR and RD growth sectors. In sections RD suture runs across hydrospire folds, represented in textfigures by broken line. Ten hydrospire groups exist. At posterior side hydrospires formed by two cryptodeltoids and corresponding radial limbs. In regular fields number of hydrospire folds is 8 or 9 in sectioned specimen (section 26, fig. 10.9). In *C* and *D* anal fields number of folds is reduced to 7, thus a slight reduction of hydrospires in anal interarea. Hydrospires placed parallel to one another and at acute angle to the sinus wall. Hydrospires thin-walled, not extending deeply into thecal cavity, differentiated into thin hydrospire lamellae and inflated hydrospire ducts over almost all of their length. Hydrospire slits situated in wall of ambulacral sinus, widely exposed when ambulacrum intact; one or two admedial folds have slits concealed by ambulacrum. Entrance to hydrospire folds mostly direct (for exposed slits) or by way of cleft between side of ambulacrum and sinus wall. Cleft extending over entire length of ambulacrum. Hydrospires functional over entire length of slits. No secondary infilling of calcite at ends of hydrospires observed.

Pleuroschisma verneuili (Etheridge & Carpenter, 1882)
Textfigure 11; Pl. II, figs. 5, 9, 11

Total height of sectioned specimen 17 mm. Upper 5.23 mm, forming hydrospire-bearing vault, sectioned into 80 subsequent transverse peel sections at mean intervals of 0.065 mm. In textfigure 11 fourteen selected sections are shown.

Theca thin-walled, with pentagonal cross section. Vault well developed. Interambulacral pyramids highly developed, present in 4 regular interrays, absent in posterior interray, rising to about 1 mm above peristome. Deltoid crest sloping upward from origin. Ambulacral sinuses prominent, steep-walled, with V-shaped cross section; walls of sinus form angle of about 80°.



Textfig. 11. *Pleuroschisma verneuili* (Etheridge & Carpenter, 1882). L. Dev., La Vid Fm., Colle, León, Spain; spec. Inst. Earth Sci., Free Ref. Univ., Amsterdam. Series of 14 transverse sections resp. from peel numbers 5, 10, 12, 14, 16, 19, 20, 21, 23, 29, 38, 47, 71, and 80, cut resp. 0.12, 0.32, 0.43, 0.54, 0.65, 0.82, 1.00, 1.20, 1.50, 2.12, 2.95, 3.33, 4.74, and 5.23 mm below top of theca. All figures × 8, showing posterior half of section, unless otherwise stated. (1) Section above peristome. (2) Peristome. (3–10) Composition of anal area and structures allied to reproductive system; note presence of superdeltoid, two cryptodeltoids and a hypodeltoid; 6, note gonopore; 10, 11, note gonoduct; 8, 10, 11, anal area only. (4–14) Composition of ambulacral and hydrospire structures; note presence of hydrospires at *C* and *D* anal sides; 13, 14, *C* radial only. See textfig. 1 for further explanation.

Deltoids well developed. Peristomial ring composed of deltoid lips shown figs. 11.3–6. No traces of ring canals found in peristomial ring. Main bodies of deltoids with major external exposure in sinus wall (figs. 9.2–7), extending internally to 3.33 mm below top of theca (fig. 11.12). (Sections show an "exposure" of deltoids on external side of body wall: figs. 11.2, 4, 5 in *BC* deltoid; figs. 11.6, 7 in *DE* deltoid, but this may be due to partial weathering of interambulacral pyramids). Radial limbs well developed, posterior limbs of *C* and *D* radials bent inward, others not bent inward. Only radial limbs sectioned.

At posterior side 4 anal deltoids: superdeltoid, two cryptodeltoids, and hypodeltoid. Superdeltoid small, isomorphic, corresponding to deltoid lips in regular deltoids, forming part of peristomial ring (figs. 11.3–8). Cryptodeltoids large, corresponding to deltoid bodies in regular deltoids, overlapped by posterior radial limbs, slightly exposed in *C* and *D* ambulacral sinus, forming hydrospires (figs. 11.6–11). Gonopore present in suture between superdeltoid and cryptodeltoids at position of intercryptodeltoid suture (figs. 11.6–8). Internally gonopore leads into wider canal formed by the *C* – cryptodeltoid (figs. 11.10, 11). This canal inferred to be part of gonoduct. Hypodeltoid relatively large, with main exposure on external wall of theca, slightly overlapped by posterior radial limbs (figs. 9.7–10).

Ambulacra linear, inclined, strongly depressed in ambulacral sinuses. Lancets parallel-sided; contact with peristomial ring shown figs. 11.4–7, contact with radial body shown fig. 11.13. Internal surface of lancet concave where bordering thecal cavity (fig. 11.9), in contact with admedial hydrospire lamellae (figs. 11.9–12). Lateral surface of lancet nowhere in contact with R and D in sinus wall. External surface of lancet strongly beveled, completely covered by side plates over entire length; lancet not exposed except at adoralmost end. Side plates and outer side plates present. Side plates in lateral contact along median line of ambulacrum. Small outer side plates alternate with larger side plates. Outer side plates placed at lateral periphery of ambulacrum. No lateral contacts of side plates and outer side plates with R and D in sinus wall. Ambulacra stand freely in ambulacral sinuses.

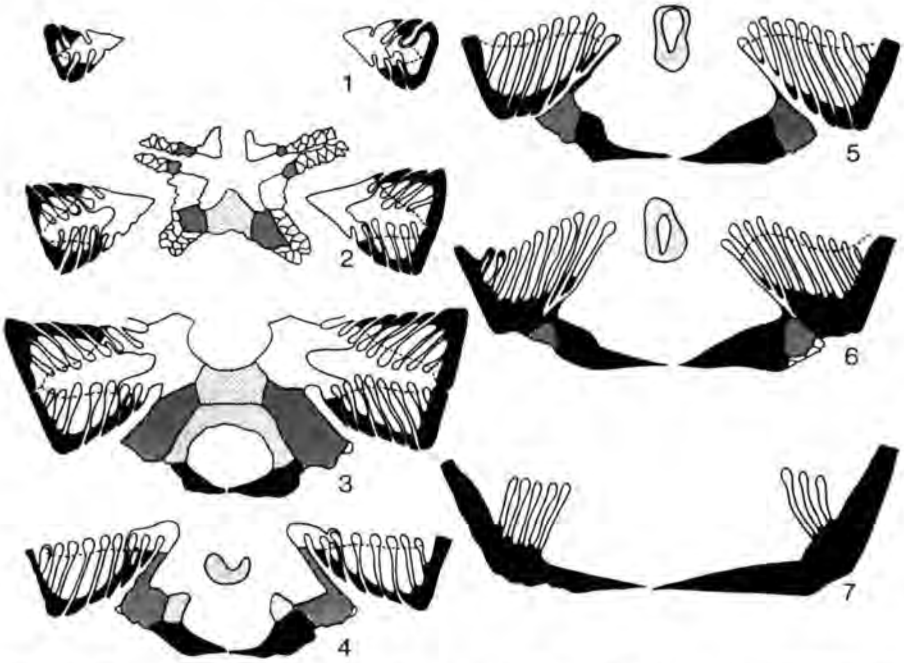
Hydrospires built across full width of DR and RD growth sectors. In sections RD suture runs across hydrospire folds, represented in text-figures by broken line. Ten hydrospire groups present. At posterior side hydrospires formed by cryptodeltoids and corresponding RD sectors. In regular fields total number of hydrospire folds is 13 in sectioned specimen (fig. 11.9). In *C* and *D* anal fields number of hydrospire folds reduced to 6. Strong reduction of hydrospire fields at posterior side. Hydrospires placed parallel to one another, at acute angle to sinus wall. Hydrospires thin-walled, differentiated into thin hydrospire lamellae and inflated hydrospire ducts, hanging deeply in thecal cavity. Hydrospire slits situated in wall of ambulacral sinus, widely exposed when ambulacrum intact, some admedial hydrospire folds have slits concealed by ambulacrum. Entrance to hydrospires mostly direct (for exposed slits), otherwise by way of cleft between side of ambulacrum and sinus wall. Clefts extend over entire length of ambulacrum. Hydrospires functional over full length of slits. No secondary infilling of calcite observed in hydrospires.

Heteroschisma gracile Wachsmuth, 1883

Textfigure 12; Pl. III, figs. 10, 11

Total height of sectioned specimen 14.5 mm. Upper 3.95 mm, forming hydrospire-bearing vault, sectioned into 53 subsequent transverse peel sections at mean intervals of 0.074 mm. In textfigure 12 seven selected sections are shown.

Theca thick-walled, with pentagonal cross section. Vault moderately developed. Interambulacral pyramids present in 4 regular interrays, rising 1.42 mm above peristome, absent at posterior interray (fig. 12.1).



Textfig. 12. *Heteroschisma gracile* Wachsmuth, 1883. M. Dev., Thunderbay Ls., Partridge Point, Alpena, Mich., USA; spec. UMMP 30745. Series of 7 transverse sections resp. from peels numbered 15, 25, 35, 37, 40, 43, and 49, cut resp. 0.47, 0.92, 1.42, 1.57, 1.87, 2.17, and 2.99 mm below top of theca. All figures × 8, showing posterior half of specimen, unless otherwise stated. (1) Above peristome, through top of interambulacral pyramids. (2) Peristome. (3–6) Composition of anal area and structures allied to reproductive system; note presence of super- and subdeltoid; 5, 6, note gonoduct. (2–7) Composition of hydrospire structures; note absence of hydrospire at *C* and *D* anal sides; 4, 5, 6, 7, *C* and *D* radials only. See textfig. 1 for further explanation.

Deltoid crest sloping moderately upward. Ambulacral sinuses relatively well expressed, steep-walled, with V-shaped cross section; walls of ambulacral sinus form angle of 80°.

Deltoids relatively weakly developed. Peristomial ring of deltoid lips shown fig. 12.2. No traces of ring canals found in peristomial ring. Main bodies of deltoids extend internally to 1.87 mm below top of theca. Radial limbs moderately developed, bend moderately inward. Only radial limbs sectioned.

At posterior side 2 anal deltoids: superdeltoid and subdeltoid. Superdeltoid small, isomorphic, corresponding with deltoid lips in regular deltoids, forming part of peristomial ring (figs. 12.2, 3). Subdeltoid relatively small, horseshoe-shaped, its wings overlapped by posterior radial limbs, corresponding to deltoid bodies in regular deltoids, not forming hydrospires (figs. 12.2–7). Gonopore in suture between two anal deltoids not observed. Subdeltoid produced into a tubelike extension internally, interpreted as the gonoduct (figs. 12.5, 6).

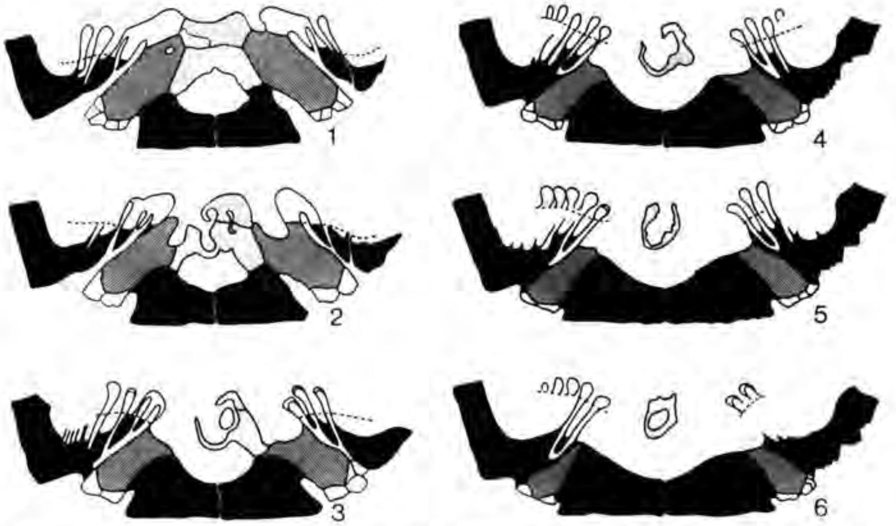
Ambulacra linear, moderately inclined, depressed in ambulacral sinus. Lancets parallel-sided; contact with peristomial ring shown fig. 12.3, contact with radial body fig. 12.6. Internal surface of lancet flat where bordering thecal cavity, in contact with admedial hydrospire lamellae. Lateral surface of lancet nowhere in contact with R and D in sinus wall. *C* and *D* lancets in direct lateral contact with subdeltoid and posterior radial limbs owing to lack of anal hydrospires. External surface of lancet poorly preserved in sectioned specimen, but known from other specimens not to be exposed except at adoralmost end. Side plates and outer side plates present (figs. 12.2, 6). Side plates have lateral contacts along median line of ambulacrum. No lateral contacts of side plates and outer side plates with R and D in sinus wall. Ambulacra stand freely in ambulacral sinus.

Hydrospires formed across full width of DR and RD growth sectors. In section RD suture runs across hydrospire folds, represented in textfigure by broken line. Eight hydrospire groups exist, those on *C* and *D* anal sides absent (figs. 12.2–7), due to none hydrospire-forming subdeltoid. In regular fields number of hydrospire folds is 10 or 11 in sectioned specimen (fig. 12.6). Hydrospires thin-walled, extending deeply into thecal cavity, placed parallel to one another, differentiated into thin hydrospire lamellae and inflated hydrospire ducts. Hydrospire slits situated in wall of ambulacral sinus, mostly exposed when ambulacra intact. Number of exposed hydrospire slits not reflecting exact number of hydrospire folds, because one or two admedial folds have slits concealed by ambulacrum. Entrance to hydrospires either direct (for exposed slits) or by way of cleft between side of ambulacrum and sinus wall. Clefts extend over entire length of ambulacrum, leaving these structures without lateral contact with sinus wall. Hydrospires functional over full length. No secondary infilling of calcite at ends of hydrospires observed.

Heteroschisma alatum (Reimann, 1935)
Textfigure 13; Pl. III, figs. 7–9

Total height of sectioned specimen 11.80 mm. Upper 3.88 mm, forming hydrospire-bearing vault, sectioned into 34 subsequent peel sections at mean intervals of 0.11 mm. In textfigure 13 six selected sections are shown.

Theca thick-walled, with pentalobate cross section. Vault moderately developed. Interambulacral pyramids present in 4 regular interrays, absent in posterior interray, rising slightly above peristome. Deltoid crest sloping slightly upward. Ambulacral sinuses relatively well defined, steep-walled with V-shaped cross section; walls of sinus form angle of 90°. Due to poor state of preservation of sectioned specimen only composition of anal area, gross ambulacral structure, and hydrospire system shown.



Textfig. 13. *Heteroschisma alatum* (Reimann, 1935); M. Dev., Potter Farm Fm., Alpena, Mich., USA; spec. USNM, unregistered. Series of 6 transverse sections resp. from peels numbered 21, 22, 23, 24, 25, and 26, cut resp. 1.68, 1.78, 1.88, 1.98, 2.07, and 2.16 mm below top of theca. All figures × 8, showing sections through anal area and *C* and *D* radials. (1–6) Composition of anal area and structures allied to reproductive system; note super- and subdeltoid; 1, 2, note gonopore; 4, 5, 6, note gonoduct; note absence of hydrospires at *C* and *D* anal sides. See textfig. 1 for further explanation.

At posterior side 2 anal deltoids: superdeltoid and subdeltoid. Superdeltoid small, isomorphic, corresponding to deltoid lips in regular deltoids. Subdeltoid relatively large, with two wings being overlapped by posterior radial limbs, corresponding to deltoid bodies of regular deltoids, not forming hydrospires (figs. 13.1, 2). Gonopore probably present at level of section 22 (fig. 13.2) in suture between super- and subdeltoid. Subdeltoid produced into a tubelike structure internally, inferred to be the gonoduct.

Ambulacra sublanceolate, moderately inclined, moderately depressed in ambulacral sinuses. Lancets have flat or slightly convex internal surfaces where bordering thecal cavity, otherwise internally in contact with admedial hydrospire lamellae. Lateral surface of lancet not in contact with R and D in sinus wall (figs. 13.1, 2). *C* and *D* lancets in direct lateral contact with subdeltoid and posterior radial limbs, owing to lack of anal hydrospires. External surface of lancet beveled, lancet not exposed (figs. 13.1–3) except at adoralmost end. Side plates and outer side plates present (fig. 13.1). Side plates in lateral contact along median line of ambulacrum. No lateral contacts of side plates and outer side plates with R and D in sinus wall. Ambulacra stand freely in ambulacral sinus.

Hydrospires formed across full width of DR and RD growth sectors. In sections RD suture runs across hydrospire fields, represented in textfigure by broken line. Eight groups of hydrospires present, those on *C* and *D* anal side absent (figs. 13.1–6). Number of hydrospire folds in regular fields is about 7 in sectioned specimen. Hydrospires thin-walled, extending well into thecal cavity, slightly conjoined, differentiated into hydrospire lamellae and inflated hydrospire ducts (figs. 13.4–6). Hydrospire slits situated in wall of ambulacral sinus, nearly completely exposed when ambulacra intact. A cleft separates sides of ambulacra from sinus wall.

Heteroschisma alternatum (Lyon, 1857)

Textfigure 14; Pl. III, figs. 1, 2, 5, 6

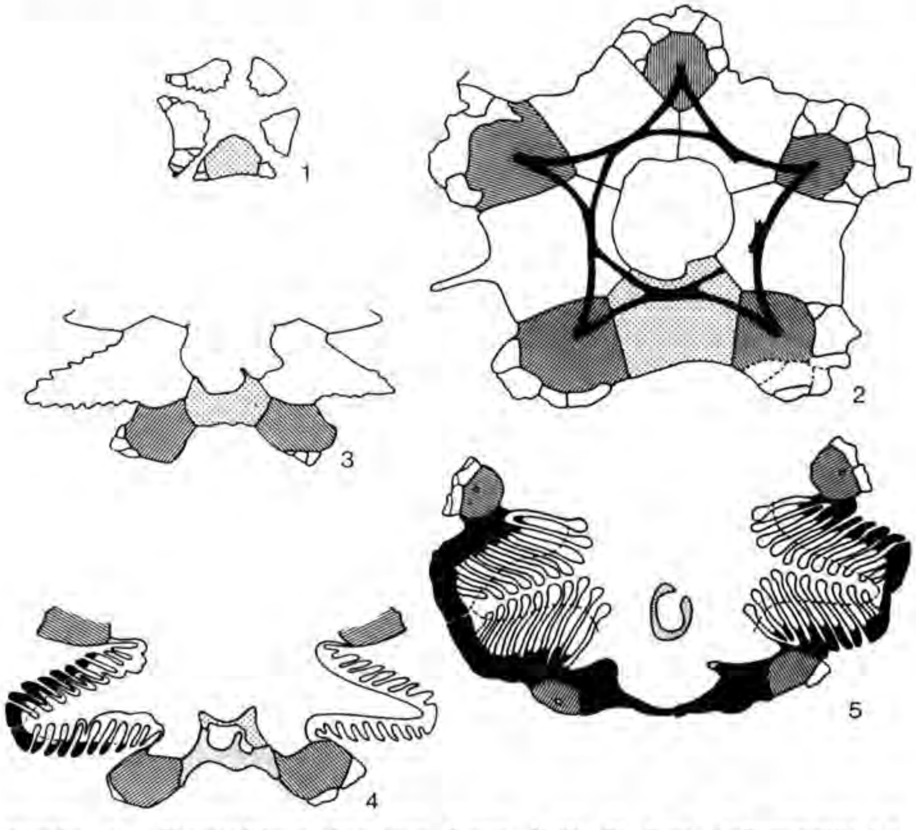
Total height of sectioned specimen 12.50 mm. Upper 3.38 mm, forming hydrospire-bearing vault, sectioned into 34 subsequent transverse peel sections at mean intervals of 0.096 mm. In textfigure 14 five selected sections are shown.

Theca relatively thin-plated, with pentagonal cross section. Vault low. Interambulacral pyramids faint, present in 4 regular interrays, absent in posterior interray, remaining below top of theca, which is at peristome (fig. 14.1). Deltoid crest sloping downward. Ambulacral sinuses not well expressed, wide and shallow, walls of ambulacral sinus form angle of 155°.

Deltoids relatively strong development. Peristomial ring of deltoid lips shown fig. 14.2. Ring canals of oral nervous system preserved in peristomial ring of plates (fig. 14.2), traversing deltoid lips, consisting of a pentagonal ring canal with angles at contacts with radial nerve canals in lancets, and chiasmas forming over interdeltoid sutures. Main bodies of deltoids extend internally to 1.53 mm below top of theca (fig. 14.5). Radial limbs slightly developed, not bent inward. Only radial limbs sectioned.

At posterior side 2 anal deltoids: superdeltoid and subdeltoid. Superdeltoid relatively large, isomorphic, corresponding with deltoid lips in regular deltoids, forming part of peristomial ring (fig. 14.2). Subdeltoid small, corresponding to deltoid bodies in regular deltoids, not forming hydrospires (figs. 14.4, 5). Gonopore observed (fig. 14.4) in suture between super- and subdeltoid. Subdeltoid produced into tubelike structure internally, inferred to be gonoduct (fig. 14.5).

Ambulacra lanceolate, slightly inclined, not depressed in sinus. Lancets almost parallel-sided; contact with peristomial ring shown figs. 14.2, 3, contact with radial body shown fig. 14.5. Lancet traversed by radial nerve trunk (fig. 14.5). Internal surface of lancet convex, in contact with admedial hydrospire lamellae (fig. 14.4). Lateral surface of lancet nowhere in contact with R and D in sinus wall. *C* and *D* lancets in direct lateral contact with subdeltoid (fig. 14.4) and posterior radial limbs owing to lack of anal hydrospires. External surface of lancet beveled, completely covered by side plates, lancet not exposed except at adoralmost end.



Textfig. 14. *Heteroschisma alternatum* (Lyon, 1857). M. Dev., Jeffersonville Ls., Falls of the Ohio, Kentucky, Indiana, USA; spec. Field Museum 19053. Series of 5 transverse sections resp. from peels numbered 4, 6–10, 15, 19, and 24, cut resp. 0.11, 0.23–0.38, 0.69, 0.99, and 1.53 mm below top of theca. Figures × 10 (except fig. 2), showing posterior half of sections, unless otherwise stated. (1) Peristome, complete section. (2) Ring canals of oral nervous system, complete section, × 20. (3–4) Composition of anal area and structures allied to reproductive system; 4, note presence of super- and subdeltoid. (4–5) Composition of hydrospire structures; note absence of hydrospires at *C* and *D* anal sides; 5, note gonoduct. See textfig. 1 for further explanation.

Side plates and outer side plates present (fig. 14.2). Side plates in lateral contact along median line of ambulacrum. No lateral contacts of side plates and outer side plates with R and D in sinus wall. Ambulacra stand freely in ambulacral sinus.

Hydrospires formed across full width of RD and DR growth sectors. In sections RD suture runs across hydrospire fields, represented in textfigures by broken line. Eight hydrospire groups present, those on *C* and *D* anal hydrospire fields absent (figs. 14.4, 5). Maximum number of hydrospire folds in a regular field is 11 in sectioned specimen (fig. 14.5). Hydrospire folds thin-walled, not extending very deeply into thecal cavity, placed parallel to one another, differentiated into hydrospire lamellae and inflated hydrospire ducts (fig. 14.5). Hydrospire slits situated in wall of ambulacral sinus, completely exposed when ambulacra intact. Entrance to hydrospires is direct. Hydrospire cleft hardly developed. Hydrospire slits functional over entire length. No secondary infilling of calcite at ends of hydrospires observed.

Heteroschisma canadense (Billings, 1869)
Textfigure 15; Pl. III, figs. 3, 4

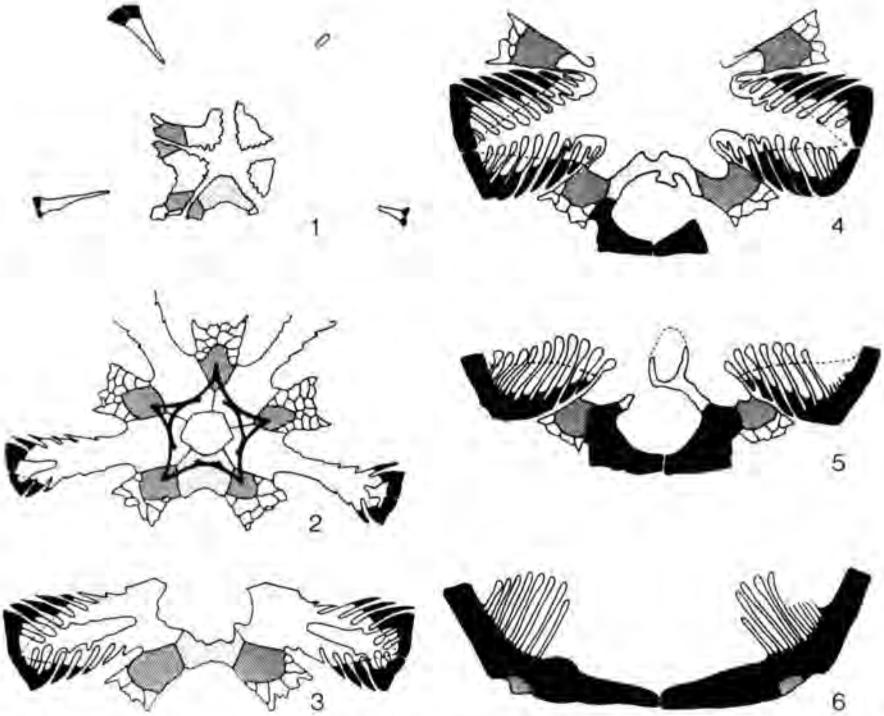
Total height of sectioned specimen 10.6 mm. Upper 2.9 mm forming hydrospire-bearing vault, sectioned into 34 subsequent transverse peel sections at mean intervals of 0.085 mm. In textfigure 15 six selected sections are shown.

Theca relatively thick-plated, with pentagonal cross section. Vault low. Interambulacral pyramids low, present in 4 regular interrays, absent in posterior interray, rising about to level of peristome (fig. 15.1). Deltoid crest subhorizontal. Ambulacral sinuses wide, well expressed, with V-shaped cross section. Walls of ambulacral sinus form angle of 120°.

Deltoids not strongly developed. Peristomial ring of deltoid lips shown fig. 15.2. Ring canals of oral nervous system preserved in peristomial ring of plates (fig. 15.2), traversing deltoid lips, consisting of a pentagonal ring canal with angles of pentagon at contacts with radial nerve canals in lancets, and chiasmas forming over interdeltoid sutures. Main bodies of deltoids extend internally to 1.22 mm below top of theca (fig. 15.5). Radial limbs weakly developed, not bent inward. Only radial limbs sectioned.

At posterior side 2 anal deltoids: superdeltoid and subdeltoid. Superdeltoid small, isomorphic, corresponding to deltoid lips in regular deltoids, forming part of peristomial ring (fig. 15.2). Subdeltoid relatively small, horseshoe-shaped, its wings overlapped by posterior radial limbs, corresponding to deltoid bodies in regular deltoids, not forming hydrospires (figs. 15.4, 5). No gonopore observed in suture between two anal deltoids. Spoonlike projections of subdeltoid (fig. 15.5) interpreted as part of gonoduct.

Ambulacra sublanceolate, slightly inclined, moderately depressed in ambulacral sinus. Lancets parallel-sided; contact with peristomial ring shown fig. 15.2, contact with radial body shown fig. 15.6. Internal surface of lancet flat where bordering thecal cavity, in contact with admedial hydrospire lamellae. Lateral surface of lancets nowhere in contact with R and D in sinus wall. *C* and *D* lancets in direct lateral contact with subdeltoid and posterior radial limbs owing to lack of anal hydrospires. External surface of lancets strongly beveled, completely covered by side plates, lancet not exposed except at adoralmost end. Side plates and outer side plates present (figs. 15.3, 4). Side plates in lateral contact along median line of ambulacrum. No lateral contacts of side plates and outer side plates with R and D in sinus wall. Ambulacra stand freely in ambulacral sinus.



Textfig. 15. *Heteroschisma canadense* (Billings, 1869). M. Dev., Hungry Hollow Fm., Hungry Hollow, Arkona, Ontario, Canada; E. P. Wright collec. USNM. Series of 6 transverse sections, resp. from peels numbered 1, 10, 16, 21, 25, and 30, cut resp. 0.05, 0.31, 0.56, 0.93, 1.22, and 2.15 mm below top of theca. All figures × 8.5, showing posterior half of specimen, unless otherwise stated. (1) Peristome. (2) Composition of oral nervous system; note circumoral nerve canals leading into lancets; almost complete section. (2–5) Composition of anal area and structures allied to reproductive system; note presence of super- and subdeltoid; 5, note gonoduct (3–6) Composition of ambulacral and hydrospire structures; note absence of hydrospires at *C* and *D* anal sides; 5, 6, *C* and *D* radials only. See textfig. 1 for further explanation.

Hydrospires formed across full width of DR and RD growth sectors. In sections RD suture runs across hydrospire folds, represented in textfigures by broken line. Eight hydrospire groups present, those on *C* and *D* anal sides absent (figs. 15.4–6). Maximum number of hydrospire folds in a regular group is 10 (figs. 15.4, 5). Hydrospire folds thin-walled, extending fairly deep into thecal cavity, placed parallel to one another, differentiated into hydrospire lamellae and inflated hydrospire ducts (fig. 15.5). Hydrospire slits situated in sinus wall, mostly exposed when ambulacra intact. One or two admedial folds have slits concealed by ambulacrum. Entrance to hydrospire folds either direct (for exposed slits) or by way of cleft between ambulacrum and sinus wall. Clefts extend over almost entire length of ambulacrum. Hydrospires functional over entire length. No secondary infilling of calcite at ends of hydrospires observed.

Heteroschisma subtruncatum (Hall, 1858)
Textfigure 16; Pl. III, figs. 15, 20

Total height of sectioned specimen 9.5 mm. Upper 2.67 mm, forming hydrospire-bearing vault, sectioned into 27 subsequent transverse peel sections at mean intervals of 0.098 mm. In textfigure 16 six selected sections are shown.

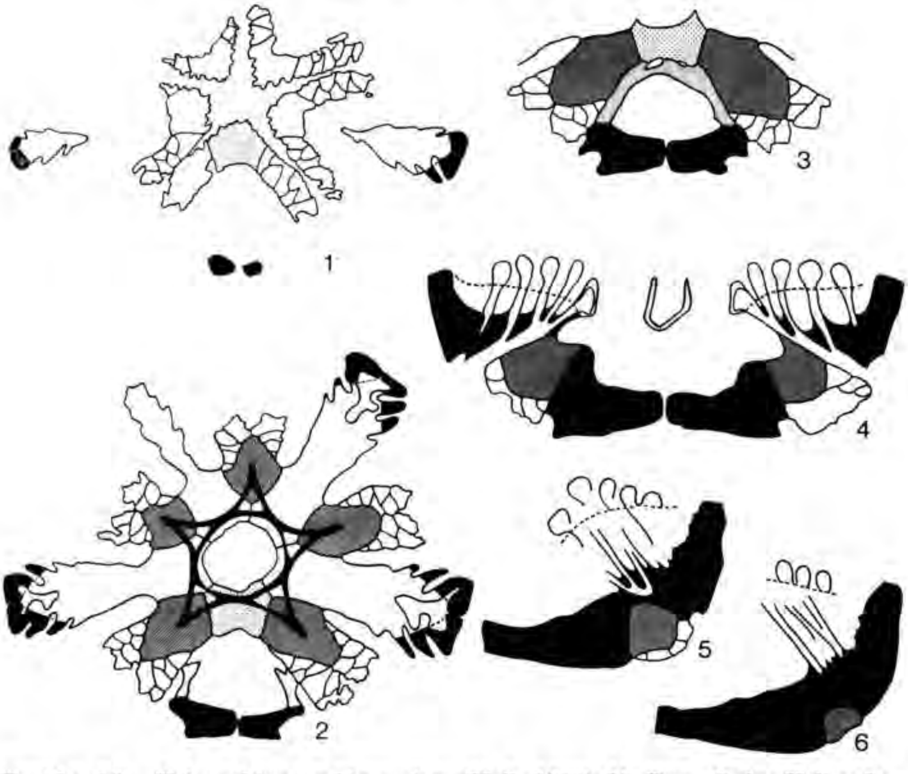
Theca thick-walled, with rounded pentagonal cross section. Vault low. Interambulacral pyramids low, present in 4 regular interrays, absent in posterior interray, rising slightly above peristome (fig. 16.1). Deltoid crest subhorizontal. Ambulacral sinuses well expressed, steep-walled with V-shaped cross section. Walls of ambulacral sinus form angle of 100°.

Deltoids relatively well developed. Peristomial ring composed of deltoid lips shown fig. 16.2 Ring canals of oral nervous system preserved in peristomial ring of plates (fig. 16.2), consisting of a pentagonal ring canal traversing deltoid lips, with angles of pentagon at contacts with radial nerve canals in lancets, and chiasmas formed over interdeltoid sutures. Main bodies of deltoids extend internally to 1.37 mm below top of theca. Radial limbs moderately developed, bend slightly inward. Only radial limbs sectioned.

At posterior side two anal deltoids: superdeltoid and subdeltoid. Superdeltoid isomorphic, corresponding with deltoid lips in regular deltoids, forming part of peristomial ring (figs. 16.2, 3). Subdeltoid horseshoe-shaped, its extremities overlapped by posterior radial limbs (figs. 16.1–3), corresponding to deltoid bodies in regular deltoids, not forming hydrospires (figs. 16.2–4). Gonopore observed (fig. 16.3) in suture between two anal deltoids. Spoonlike projection of subdeltoid (fig. 16.4) interpreted as part of gonoduct.

Ambulacra linear, slightly inclined, slightly depressed in ambulacral sinuses. Lancets about parallel-sided; contact with peristomial ring shown fig. 16.2, contact with radial body shown figs. 16.5, 6. Internal surface of lancet flat to concave where bordering thecal cavity, internally in contact with admedial hydrospire lamellae. Lateral surface of lancet nowhere in contact with R and D in sinus wall. *C* and *D* lancets in direct lateral contact with subdeltoid (fig. 16.3) and posterior radial limbs (fig. 16.4), owing to lack of anal hydrospires. External surface of lancet strongly beveled, completely covered with side plates, lancet not exposed (fig. 16.2) except at adoralmost end. Side plates and outer side plates present. Side plates in lateral contact along median line of ambulacrum. No lateral contacts of side plates and outer side plates with R and D in sinus wall. Ambulacra stand freely in ambulacral sinus.

Hydrospires formed across full width of DR and RD growth sectors. RD suture runs across hydrospire fields, represented in textfigure by broken line. Eight hydrospire groups present, those on *C* and *D* anal



Textfig. 16. *Heteroschisma subtruncatum* (Hall, 1858). M. Dev., Cedar Valley Ls., Linwood, Iowa, USA; spec. Univ. Iowa 11507. Series of 6 transverse sections resp. from peels numbered 3, 8, 10, 14, 16, and 18, cut resp. 0.06, 0.24, 0.38, 0.87, 1.17, and 1.37 mm below top of theca. All figures × 11.5. (1) Peristome. (2) Composition of oral nervous system; note circumoral nerve canals leading into lancets; complete section. (2–4) Composition of anal area and structures allied to reproductive system; note presence of super- and subdeltoid; 3, note gonopore, anal area only; 4, note gonoduct. (2–5) Composition of ambulacral and hydrospire structures; note absence of hydrospires at *C* and *D* anal sides; 5, 6, *C* radial only. See textfig. 1 for further explanation.

sides absent. Maximum number of hydrospire folds in a regular field is 5 in sectioned specimen (fig. 16.4). Hydrospire folds thin-walled, relatively short, not extending deeply into thecal cavity, not placed strictly parallel to one another bud admedial folds more or less conjoined (fig. 16.4), differentiated into hydrospire lamellae and inflated hydrospire ducts. Hydrospire slits situated in sinus wall, mostly exposed when ambulacra intact. Innermost one or two admedial folds have slits concealed by ambulacrum. Entrance to hydrospires either direct (for exposed slits) or by way of cleft between side of ambulacrum and sinus wall. Clefts extend over almost entire length of ambulacra. Hydrospires functional over entire length. No secondary infilling of calcite at ends of hydrospire slits observed.

Phaenoschisma acutum (Sowerby, 1834)
Textfigure 17; Pl. IV, figs. 3, 5, 10, 14

Total height of sectioned specimen 9.92 mm. Specimen sectioned into 67 subsequent transverse peel sections. Upper 5.13 mm, forming hydrospire-bearing vault, sectioned into 39 subsequent sections at mean intervals of 0.13 mm. In textfigure 17 seven selected sections are shown.

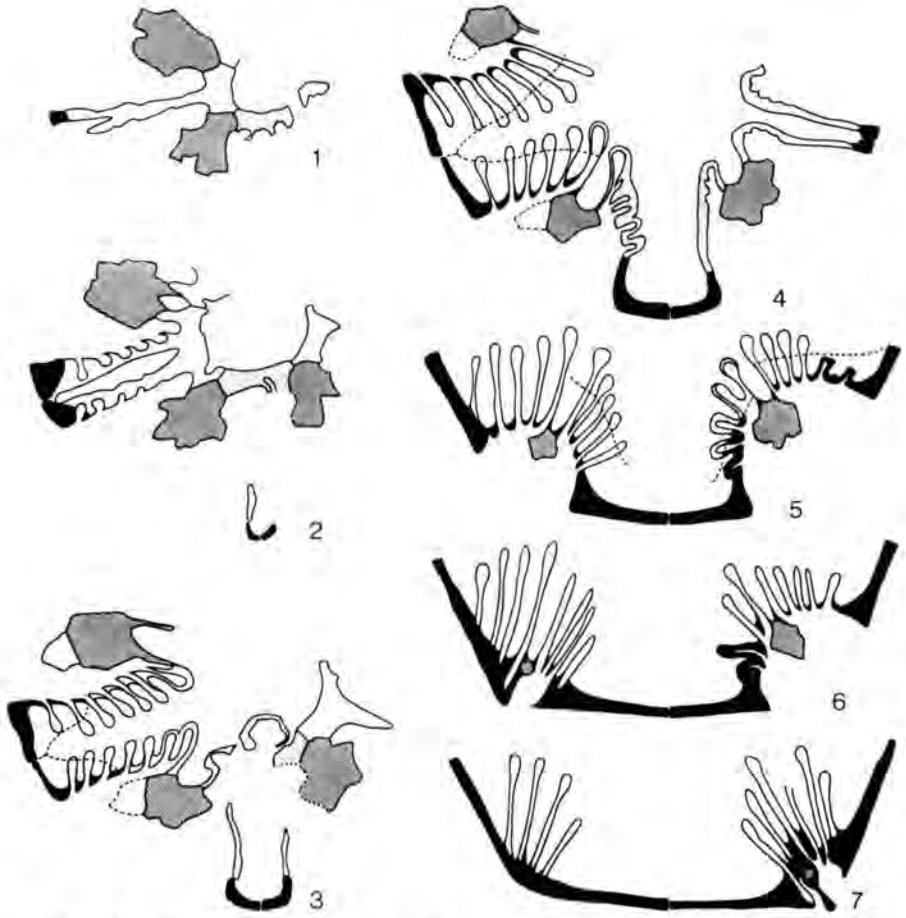
Theca thin-walled, with pentagonal cross section. Vault well developed. Interambulacral pyramids present in all 5 interrays, rising up to about level of peristome (fig. 17.1). Deltoid crest subhorizontal. Ambulacral sinuses well expressed, with U-shaped cross section. Walls of ambulacral sinus form angle of 90°.

Deltoids relatively well developed. Peristomial ring composed of deltoid lips shown figs. 17.1, 2. No canal system observed in peristomial ring. Main bodies of deltoids extend internally to 3.73 mm below top of theca (fig. 17.6). Radial limbs well developed, bend slightly inward.

At posterior side one anal deltoid present: an epideltoid, unusually formed as a two-winged plate, corresponding closely to a regular deltoid; no hypodeltoid observed, nor is there much space for one (fig. 17.2). (See, however, *P. laeviculum*). Epideltoid is hydrospire-forming. Gonopore not definitely observed. Epideltoid forming ring- or tubelike structure (fig. 17.3), inferred to be part of gonoduct. Latter would open in notch at aboral side of central portion of epideltoid (fig. 17.2).

Ambulacra lanceolate, much inclined, slightly depressed in ambulacral sinuses. Lancets not parallel-sided; contact with peristomial ring shown figs. 17.1, 2, contact with radial body shown figs. 17.6, 7, where aboral tip of lancet is enclosed in radial body. Cross section of lancet six-sided, with greatest width at mid-height, aboral portion tapering. Internal surface of lancet flat to concave where bordering thecal cavity, internally in contact with admedial hydrospire lamellae. Lateral surface of lancet nowhere in contact with R and D in sinus wall, sides of lancets beveled for reception of side plates. No side plates or outer side plates preserved in sectioned specimen. Position of side plates and outer side plates indicated in figs. 17.3, 4 by broken line, inferred to have left central part of lancet exposed to exterior. Ambulacra appear to stand freely in sinuses.

Hydrospires are built across full width of DR and RD growth sectors. In sections RD sutures run across hydrospire fields, represented in textfigure by broken line. Ten groups of hydrospires present. *C* and *D* anal hydrospires formed by wings of epideltoid and corresponding posterior radial limbs. Number of hydrospires in a regular field is 7 in sectioned



Textfig. 17. *Phaenoschisma acutum* (Sowerby, 1834). L. Carb., Clitheroe Ls., Calamine Mine, near Whitewell, Yorkshire, England; spec. Inst. Earth Sci., Free Ref. Univ., Amsterdam. Series of 7 transverse sections resp. from peels numbered 66, 61, 56, 52, 45, 38, and 28, cut resp. 0.18, 0.68, 1.18, 1.78, 2.98, 3.73, and 5.13 mm below top of theca. All figures × 8, showing posterior half of sections, unless otherwise stated. (1) Peristome. (2–4) Composition of anal area and structures allied to reproductive system; note presence of single epideltoid; 3, note gonoduct. (3–7) Composition of ambulacral and hydrospire structures; note presence of hydrospires at *C* and *D* anal sides; 6, 7, aboral end of ambulacrum; C and D radials only. See textfig. 1 for further explanation.

specimen; at *C* and *D* anal sides number of hydrospires reduced to 5 (figs. 17.3–7). Hydrospire folds thin-walled, well developed, extending fairly deep into thecal cavity, placed subparallel to one another at acute angle with sinus wall. Folds differentiated in hydrospire lamellae and inflated hydrospire ducts (fig. 17.5). Hydrospire slits situated in wall of ambulacral sinus, partly exposed when ambulacra intact. Innermost 3 or 4 admedial folds have slits concealed by ambulacrum. Entrance to hydrospires either direct or by way of wide cleft between side of ambulacrum and sinus wall. Clefts extend over full length of ambulacra. Hydrospires functional over entire length. No secondary infilling of calcite observed at ends of hydrospire slits.

Phaenoschisma conicum (Fay, 1962)

Textfigure 18; Pl. III, figs. 18, 24, 25

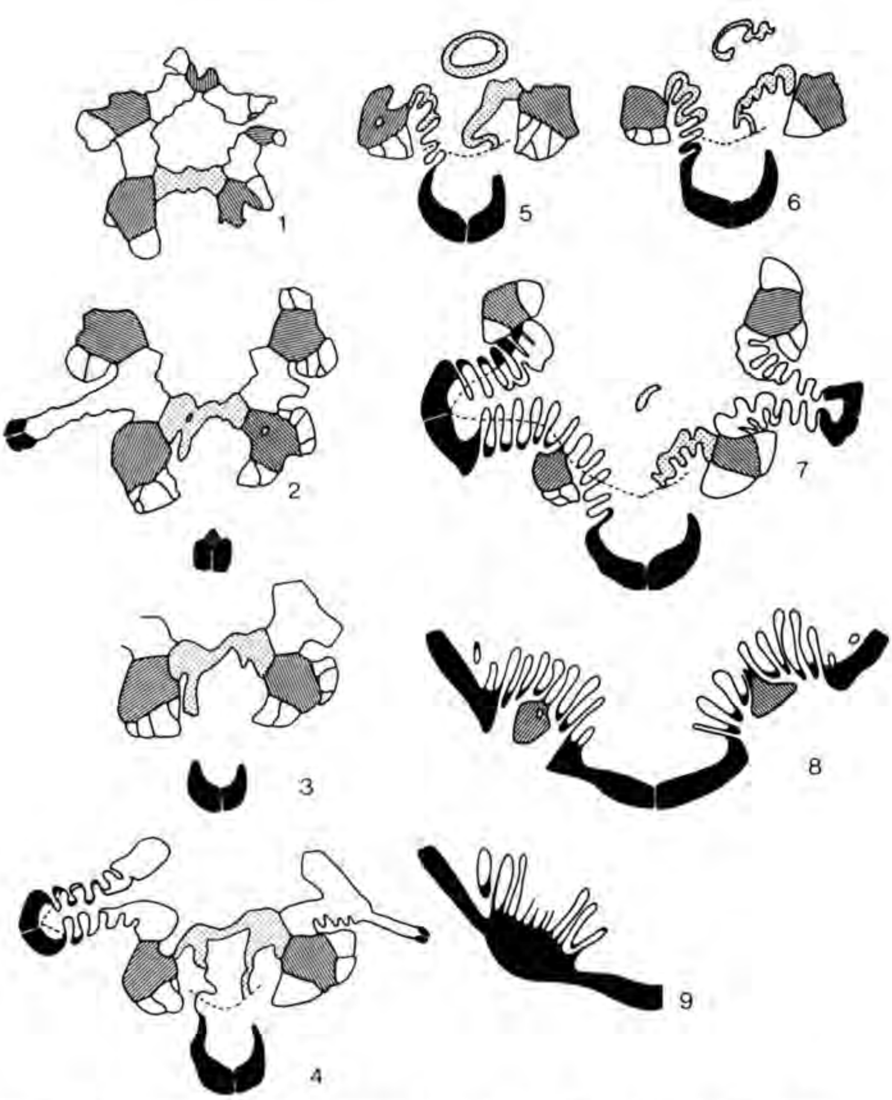
Total height of sectioned specimen 9 mm. Upper 2.75 mm, forming hydrospire-bearing vault, sectioned into 28 subsequent transverse peel sections at mean intervals of 0.098 mm. In textfigure 18 nine selected sections are shown.

Theca thin-plated, with pentagonal cross section. Vault moderate. Interambulacral pyramids present in all 5 interrays, rising till slightly below peristome (figs. 18.1, 2). Deltoid crest subhorizontal. Ambulacral sinus well expressed, steep-walled with U-shaped cross section. Walls of ambulacral sinus form angle of about 100°.

Deltoids relatively small. Peristomial ring composed of deltoid lips shown fig. 18.1. No canal systems observed in peristomial ring. Main bodies of deltoids extend internally to 1.09 mm below top of theca (fig. 18.7). Radial limbs moderately developed, bend moderately inward. Only radial limbs sectioned.

At posterior side two anal deltoids: epideltoid and hypodeltoid. Epideltoid large, formed as two-winged plate, corresponding closely to regular deltoids. Hypodeltoid very small, rudimentary (fig. 18.2), overlapped by posterior radial limbs, without exposure on external wall of theca. Epideltoid is hydrospire-forming. Gonopore not observed. Central portion of epideltoid produced into tubelike structure internally (figs. 18.5, 6), interpreted to be gonoduct. Uncertain how and where gonoduct opened to exterior, probably in notch at center part of epideltoid.

Ambulacra lanceolate, moderately inclined, depressed in ambulacral sinuses. Lancets not parallel-sided. Contact with peristomial ring shown figs. 18.1, 2, contact with radial body not shown. Lancet with convex outer and concave internal surface, internally in contact with admedial hydrospire lamellae. Lateral surface of lancet nowhere in contact with R and D in sinus wall. Side plates and outer side plates present (figs. 18.1–7), situated at outer lateral sides of lancet, not in lateral contact along median line of ambulacrum; lancet exposed, at least over upper $\frac{2}{3}$ of its



Textfig. 18. *Phaenoschisma conicum* (Fay, 1962). Miss., Lake Valley Fm., Lake Valley, New Mexico, USA; spec. USNM unregistered. Series of 9 transverse sections from peels numbered 11, 14, 16, 17, 18, 19, 20, 23, and 24, cut resp. 0.21, 0.49, 0.69, 0.79, 0.89, 0.99, 1.09, 1.59, and 1.79 mm below top of theca. All figures × 15. (1) Peristome, complete section. (2–7) Composition of anal area and structures allied to reproductive system; note presence of epideltoid and hypodeltoid; 2, note hypodeltoid; 5, 6, note base of gonoduct. (2–9) Composition of ambulacral and hydrospire structures in *C* and *D* ambulacra; note presence of hydrospires at *C* and *D* anal sides; 8, aboral end of ambulacrum, *C* and *D* radials only; 9, aboral end of hydrospires, *D* radial only. See textfig. 1 for further explanation.

length. Side plates and outer side plates not in lateral contact with R and D in sinus wall, but separated from it by hydrospire cleft. Ambulacra appear to stand freely in ambulacral sinus.

Hydrospires formed across full width of DR and RD growth sectors. In sections RD sutures run across hydrospire fields, represented in textfigures by broken line. Ten groups of hydrospires present. *C* and *D* anal hydrospires formed by wings of epideltoid and corresponding posterior radial limbs. Number of hydrospire folds in a regular field is 6 in sectioned specimen, at *C* and *D* anal sides number of folds is reduced to 5 (figs. 18.6, 7). Hydrospire slits situated in wall of ambulacral sinus, partly exposed when ambulacra intact. Innermost three folds per group have slits concealed by ambulacrum. Entrance to hydrospires either direct or by way of wide hydrospire cleft between ambulacrum and sinus wall. Clefts extend over full length of ambulacra. Hydrospires functional over entire length. No secondary infilling of hydrospires observed.

Phaenoschisma gracillimum (Rowley & Hare, 1891)

Textfigure 19; Pl. III, figs. 14, 19

Total height of sectioned specimen 9.09 mm. Upper 1.25 mm, forming hydrospire-bearing vault, sectioned into 33 subsequent transverse peel sections at mean intervals of 0.04 mm. In textfigure 19 six selected sections are shown.

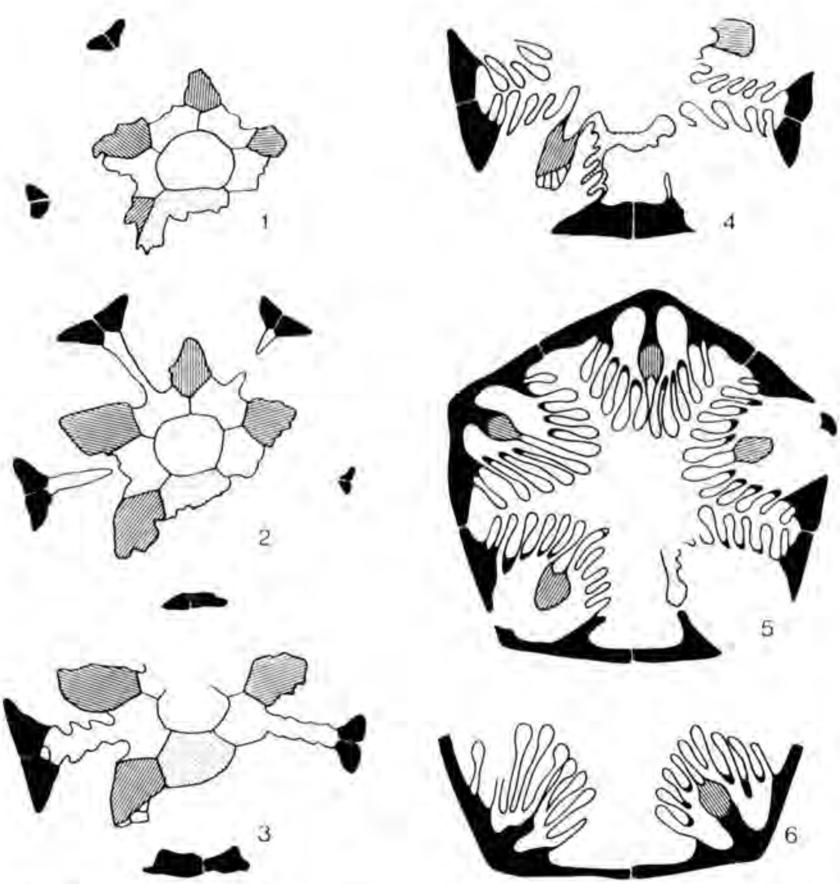
Theca thin-walled, with pentagonal cross section. Vault very low. Interambulacral pyramids present in all five interrays, rising to about level of peristome (figs. 19.1, 2). Deltoid crest sloping slightly downward. Ambulacral sinuses well expressed, shallow, with U-shaped cross section; walls of sinus form angle of about 110°.

Deltoids relatively small. Peristomial ring composed of deltoid lips shown figs. 19.1, 2. No canal systems observed in peristomial ring. Main bodies of deltoids extend downward to 0.70 mm below top of theca. Radial limbs weakly developed, bend moderately inward. Only radial limbs sectioned.

At posterior side two anal deltoids: epideltoid and hypodeltoid. Epideltoid large, formed as two-winged plate (fig. 19.4), corresponding closely to regular deltoids. Hypodeltoid very small, rudimentary (fig. 19.2), overlapped by posterior radial limbs, without exposure on outer side of theca. Epideltoid hydrospire-forming. Structures allied to reproductive system not observed.

Ambulacra lanceolate, slightly inclined, moderately depressed in sinuses. Low degree of inclination of ambulacra causes the sections to be at very small angle with the ambulacra, producing unusual form of sections in figs. 19.4–6. Lancets not parallel-sided; contact with peristomial ring shown figs. 19.1, 2, contact with radial body shown fig. 19.6. Lancet with inverted V-shaped outer surface, and concave inner surface, internally in contact with admedial hydrospire lamellae. Lateral surface of lancet nowhere in contact with R and D in sinus wall. Few side plates present in *D* ambulacrum (figs. 19.3, 4), situated at outer lateral surface of lancet. Side plates in aboral half of ambulacrum probably in lateral contact along median line of ambulacrum; lancet probably not exposed over aboral half of its length. Side plates not in lateral contact with R and D in sinus wall. Ambulacra appear to stand freely in ambulacral sinuses.

Hydrospires formed across full width of DR and RD growth sectors. Ten groups of hydrospires present. *C* and *D* anal hydrospires formed by wings of epideltoid and corresponding posterior radial limbs. Number of



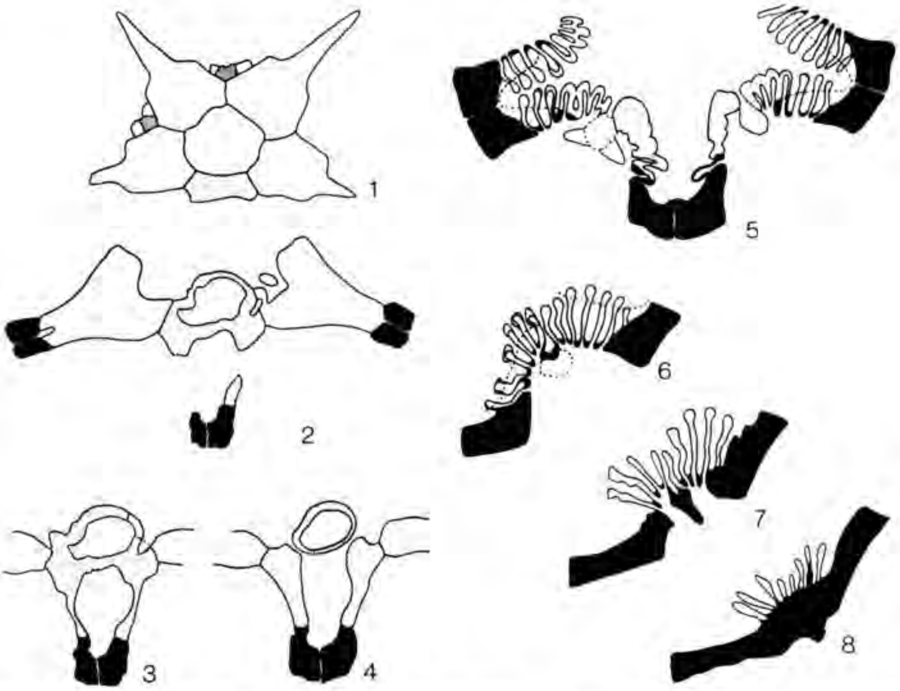
Textfig. 19. *Phaenoschisma gracillimum* (Rowley & Hare, 1891). Miss., Lower Burlington Fm., Louisiana, Missouri, USA; spec. Univ. Illinois, Rowley collec., RX-131L. Series of 6 transverse sections resp. from peels numbered 5, 10, 15, 18, 20, and 23, cut resp. 0.12, 0.27, 0.45, 0.59, 0.69, and 0.84 mm below top of theca. All figures × 15. (1) Peristome, complete section. (2–4) Composition of anal area; note presence of epideltoid and hypodeltoid; 2, note hypodeltoid. (4–6) Composition of ambulacral and hydrospire structures; note presence of hydrospires at *C* and *D* anal sides; 6, aboral end of lancet and hydrospires, *C* and *D* radials only. See textfig. 1 for further explanation.

hydrospires in regular fields is 5 or 6 in sectioned specimen, at *C* and *D* anal sides number of hydrospires reduced to 4 or 5 (figs. 19.4–6). Hydrospire slits situated in wall of ambulacral sinus, partly exposed when ambulacra intact. Entrance to hydrospires either direct or by way of wide hydrospire cleft between ambulacrum and sinus wall. Clefts extend over full length of ambulacra. Hydrospires functional over entire length. No secondary infilling of hydrospires observed.

Phaenoschisma laeviculum (Rowley, 1900)

Textfigure 20; Pl. III, figs. 26, 27; Pl. IV, figs. 19, 21

Total height of sectioned specimen 14.3 mm. Upper 4.98 mm, forming hydrospire-bearing vault, sectioned into 37 subsequent transverse peel sections at mean intervals of 0.13 mm. In textfigure 20 eight selected sections are shown.



Textfig. 20. *Phaenoschisma laeviculum* (Rowley, 1900). Miss., Upper Burlington Fm., Louisiana, Missouri, USA; spec. Univ. Illinois, Rowley collec. RX-94T. Series of 8 transverse sections resp. from peels numbered 15, 18, 19, 20, 22, 25, 31, and 34, cut resp. 0.99, 1.78, 1.91, 2.12, 2.70, 3.26, 4.21, and 4.89 mm below top of theca. All figures × 8. (1) Peristome, complete section. (2–5) Composition of anal area and structures allied to reproductive system; note presence of epi- and hypodeltoid; 2, 3, 4, note basis of gonoduct; 5, note hypodeltoid. (5–8) Composition of ambulacral and hydrospire structures in *C* and *D* ambulacra; note presence of hydrospires at *C* and *D* anal side; 6, 7, 8, *C* radial only; 8, aboral end of hydrospires. See textfig. 1 for further explanation.

Theca relatively thick-plated, with pentagonal cross section. Vault relatively high. Interambulacral pyramids present in all 5 interrays, remaining below peristome. Deltoid crest sloping downward (figs. 20.1, 2). Ambulacral sinuses well developed, steep-walled, with V-shaped cross section. Walls of sinus form angle of about 100°.

Deltoids relatively well developed. Peristomial ring composed of deltoid lips shown fig. 20.1. No canal systems observed in peristomial ring. Main bodies of deltoids extend downward internally to 3.26 mm below top of theca (fig. 20.6). Radial limbs relatively well developed, bend slightly inward. Only radial limbs sectioned.

At posterior side two anal deltoids: epideltoid and hypodeltoid. Epideltoid large, formed as two-winged plate, corresponding closely to regular deltoids. Hypodeltoid very small, rudimentary (fig. 20.5), overlapped by posterior radial limbs, without exposure on external surface of theca. Epideltoid hydrospire-forming. Gonopore not observed. Central portion of epideltoid produced into a tubelike structure internally (figs. 20.2–4), interpreted to be the gonoduct. Uncertain how and where the duct opened to exterior.

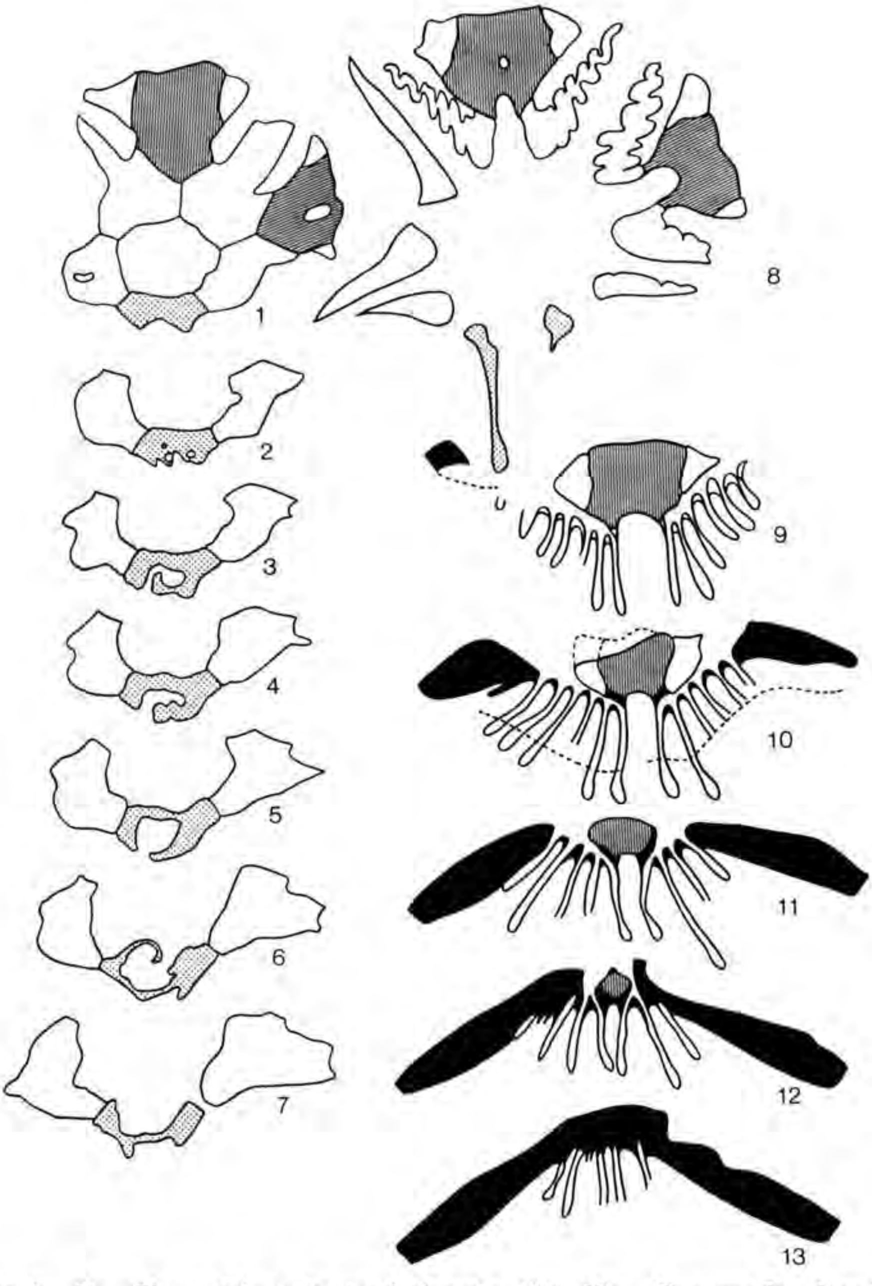
Ambulacra lanceolate, well inclined, slightly depressed in ambulacral sinuses. Ambulacra absent from sectioned specimen.

Hydrospires formed across full width of DR and RD growth sectors. In sections RD suture runs across hydrospire fields, represented in textfigures by broken line. Ten groups of hydrospires present. *C* and *D* anal hydrospires formed by epideltoid wings and corresponding posterior radial limbs. Number of hydrospires in regular groups is 7 or 8 in sectioned specimen, at *C* and *D* anal sides number of hydrospires reduced, observed to be 6 at *C* anal side (fig. 20.6). Hydrospires placed subparallel to one another, at acute angle to sinus wall. Hydrospire folds not extending deeply in thecal cavity, differentiated into hydrospire lamellae and inflated hydrospire ducts. Hydrospire slits situated in wall of ambulacral sinus, largely concealed by ambulacra when intact. Entrance to hydrospires largely by way of cleft between ambulacrum and sinus wall. Cleft inferred to extend over full length of ambulacra. Hydrospires functional over entire length. No secondary infilling of hydrospires observed.

Phaenoschisma chouteaui Macurda, 1964
Textfigure 21; Pl. III, figs. 16, 21, 23

Total height of sectioned specimen 8.3 mm. Upper 4.13 mm, forming hydrospire-bearing vault, sectioned into 32 subsequent transverse peel sections at mean intervals of 0.13 mm. In textfigure 21 thirteen selected sections are shown.

Theca relatively thick-walled, with decagonal cross section. Vault high. Interambulacral pyramids present in all 5 interrays, definitely remaining below peristome. Deltoid crest sloping downward (figs. 21.1–8). Ambulacral



Textfig. 21. *Phaenoschisma chouteaui* Macurda, 1964. Miss., Chouteau Ls., Providence, Missouri, USA; spec. USNM unregistered. Series of 13 transverse sections resp. from peels numbered 5, 6, 7, 8, 9, 10, 11, 12, 16, 22, 26, 28, and 29, cut resp. 0.12, 0.15, 0.18, 0.21, 0.24, 0.29, 0.33, 0.43, 0.73, 1.58, 2.48, 2.98, and 3.28 mm below top of theca. All figures × 13. (1) Peristome, complete section. (2–7) Composition of anal area and structures allied to reproductive system; note presence of single epideltoid; 2, note gonopore; 5, 6, note basis of gonoduct. (8) Complete section, note posterior limbs of epideltoid. (9–13) Composition of ambulacral and hydrospire structures in *A* ambulacrum; 12, aboral end of lancet; 13, aboral end of hydrospire folds. See textfig. 1 for further explanation.

sinuses well defined, steep-walled, with V-shaped cross section. Walls of ambulacral sinus form angle of about 100°.

Deltoids well developed. Peristomial ring composed of deltoid lips shown fig. 21.1. No canal systems observed in peristomial ring. Main bodies of deltoids extend internally to 1.58 mm below top of theca (fig. 21.10). Radial limbs moderately developed, bend slightly inward. Only radial limbs sectioned.

At posterior side only epideltoid observed (figs. 21.1–8), formed as two-winged plate, corresponding closely to regular deltoids. Epideltoid hydrospire-forming. Central portion of epideltoid produced into tubelike structure internally (figs. 21.5, 6), interpreted as part of gonoduct. Duct opens to exterior via lobed notch (figs. 21.3, 4) into pores situated around notch at aboral side of center part of epideltoid (fig. 21.2). All different parts, here interpreted as belonging to one epideltoid, in optical continuity.

Ambulacra lanceolate, well inclined, slightly depressed in ambulacral sinuses. Lancets not parallel-sided; contact with peristomial ring shown fig. 21.1, contact with radial body shown fig. 21.12. Lancet with flat outer surface and concave inner surface, internally in contact with admedial hydrospire lamellae. Lateral surface of lancet nowhere in contact with R and D in sinus wall. Side plates situated at outer lateral sides of lancet, not in lateral contact along median line of ambulacrum; lancet exposed over most of its length. Side plates not in contact with R and D in sinus wall. Ambulacra stand freely in ambulacral sinus.

Hydrospires formed across full width of DR and RD growth sectors. Ten groups of hydrospires present. *C* and *D* anal hydrospires observed to be formed by epideltoid, not shown in fig. 21 because of partial distortion of sectioned specimen. Number of hydrospires in a regular field is 6 in sectioned specimen. Hydrospire slits situated in wall of ambulacral sinus, largely concealed when ambulacra intact. Entrance to hydrospires largely by way of hydrospire cleft between ambulacrum and sinus wall. Clefts extend over full length of ambulacra (fig. 21.12). Hydrospires functional over entire length. No secondary infilling of hydrospires observed.

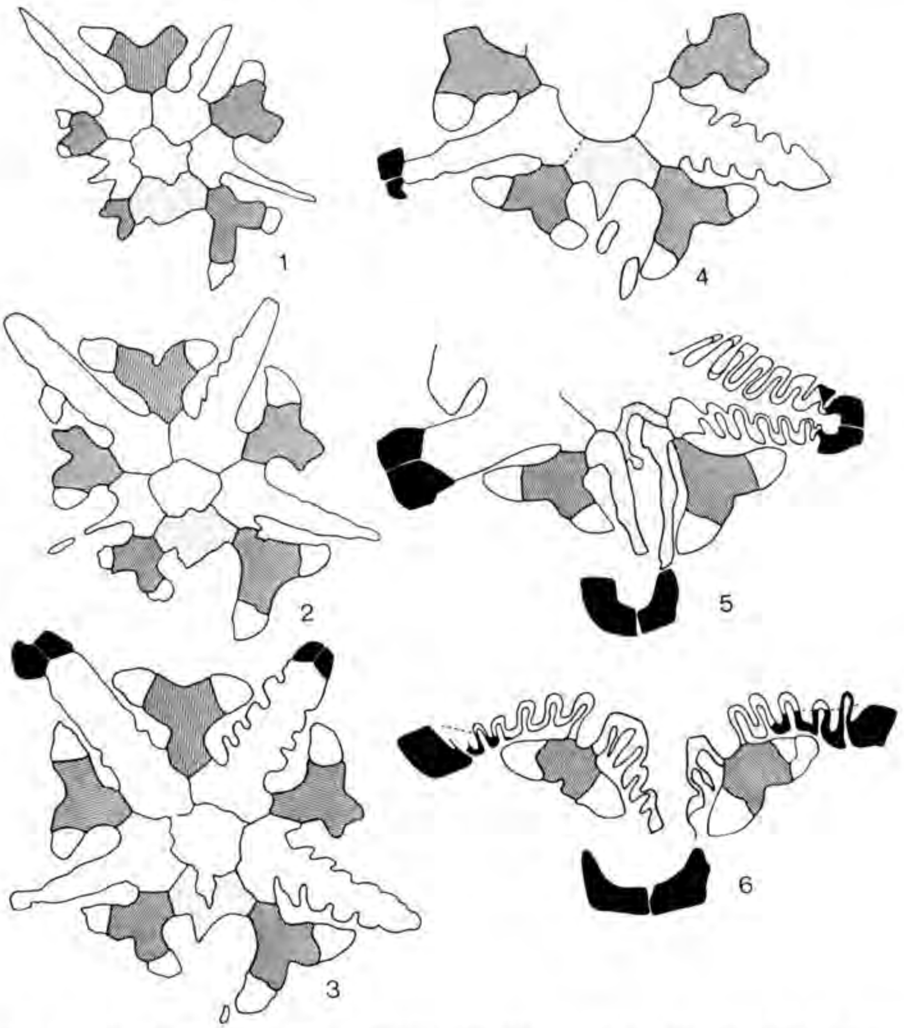
Phaenoblastus caryophyllatus (De Koninck & Le Hon, 1854)
Textfigure 22; Pl. IV, figs. 8, 12

Total height of sectioned specimen 9.8 mm. Upper 2.42 mm, forming part of hydrospire-bearing vault, sectioned into 28 subsequent transverse peel sections at mean intervals of 0.086 mm. In textfigure 22 six selected sections are shown.

Theca relatively thick-walled, with rounded pentagonal cross section. Vault prominent. Interambulacral pyramids present in all 5 interrays, remaining definitely below peristome. Deltoid crest subhorizontal. Ambulacral sinuses wide and shallow, with rounded cross section. Walls of ambulacral sinus form angle of about 100°.

Deltoids well developed. Peristomial ring composed of deltoid lips shown figs. 22.1–3. No canal systems observed in peristomial ring. Main bodies of deltoids extend internally to about 1.50 mm below top of theca. Radial limbs well developed, not bent inward. Only radial limbs sectioned.

At posterior side three anal deltoids observed: superdeltoid and two cryptodeltoids. Hypodeltoid not preserved, but inferred to be present



Textfig. 22. *Phaenoblastus caryophyllatus* (De Koninck & Le Hon, 1854). L. Carb., Tournaisian, Tournai, Belgium; spec. USNM unregistered. Series of 6 transverse sections resp. from peels numbered 4, 9, 14, 15, 19, and 21, cut resp. 0.10, 0.31, 0.55, 0.66, 0.92, and 1.22 mm below top of theca. All figures × 12. (1–3) Peristomial area, complete sections. (3–5) Composition of anal area; note presence of a super- and two cryptodeltoids. (4–6) Composition of ambulacral and hydrospire structures, posterior parts of sections only; 6, note presence of hydrospires at *C* and *D* anal sides. See textfig. 1 for further explanation.

during life as small, almost rudimentary plate at aboral side of anus, completely overlapped by radial limbs. Superdeltoid small, isometric, corresponding to deltoid lips of regular deltoids, forming part of peristomial ring (figs. 22.1–4). Two cryptodeltoids situated at lateral sides of anal opening, in contact with superdeltoid (fig. 22.5), do not meet laterally adoral from anus. Cryptodeltoids overlapped by posterior radial limbs, exposed laterally in *C* and *D* ambulacral sinuses. Skeletal structures allied to reproductive system not definitely observed.

Ambulacra petaloid, well inclined, slightly depressed in ambulacral sinuses. Lancets not parallel-sided; contact with peristomial ring shown figs. 22.1–3, contact with radial body not shown. Lancet with concave, broadly V-shaped external surface and flat to concave internal surface where bordering thecal cavity, internally in contact with admedial hydrospire lamellae. Lateral surface of lancet nowhere in contact with R and D in sinus wall. Side plates situated at oblique lateral sides of lancet, do not meet laterally along median line of ambulacra; lancet widely exposed over almost entire length. Side plates not in lateral contact with R and D in sinus wall. Ambulacra stand freely in ambulacral sinus.

Hydrospires formed across full width of DR and RD growth sectors. Ten hydrospire groups present. *C* and *D* anal hydrospires formed by two cryptodeltoids and corresponding posterior radial limbs (figs. 22.5, 6). Number of hydrospire folds in a regular group is 7 or 8 in sectioned specimen. Number of anal hydrospires in *C* and *D* anal fields reduced to 5 or 6. Hydrospire folds placed subparallel to one another, at acute angle to sinus wall, not extending deeply into thecal cavity, relatively thick-walled, without definite differentiation into hydrospire lamellae and hydrospire ducts. Hydrospire slits situated in wall of ambulacral sinus, largely concealed by wide ambulacra and overhanging side plates (fig. 22.6). Abmedial one or two slits completely exposed when ambulacra intact. Entrance to hydrospires largely by way of cleft between ambulacrum and sinus wall. Clefts extend over full length of ambulacrum. Hydrospires functional over entire length. No secondary infilling of hydrospires observed.

Kazachstanoblastus carinatus Arendt, Breimer, & Macurda, 1968

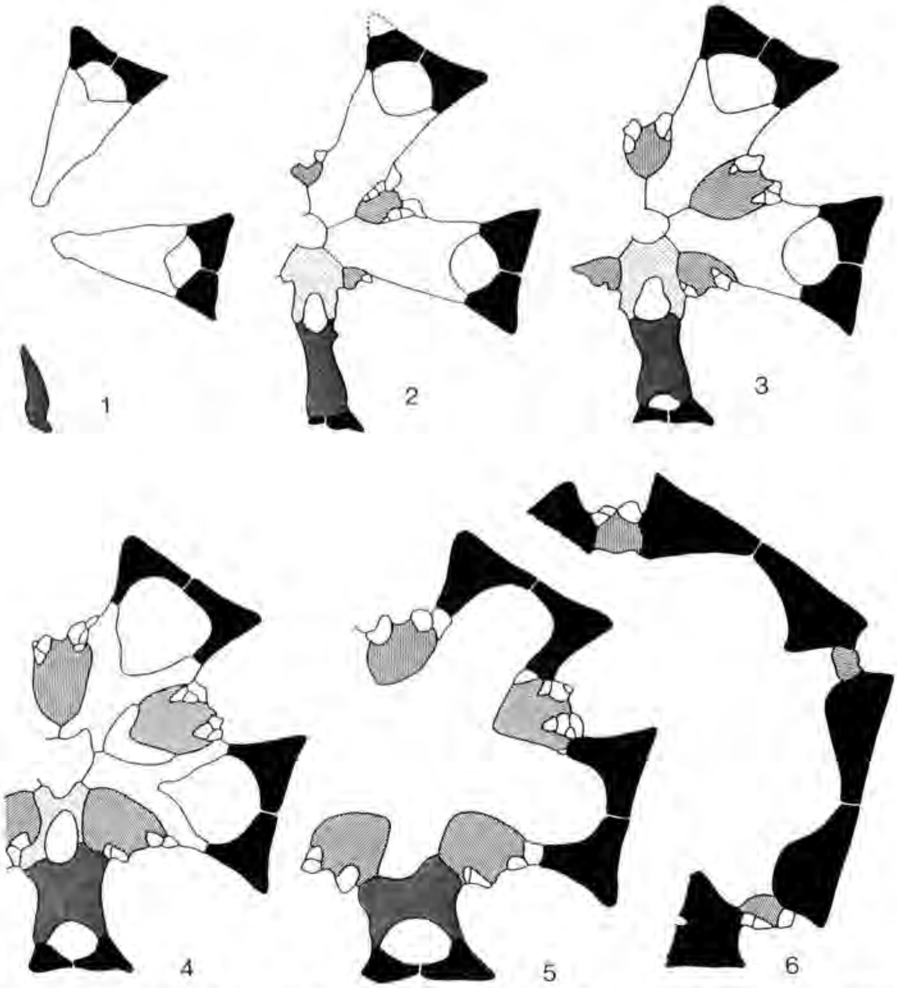
Textfigure 23; Pl. V, figs. 14, 16, 17

Total height of sectioned specimen 12 mm. Upper 4.63 mm, forming part of vault, sectioned into 43 subsequent transverse peel sections at mean intervals of 0.103 mm. In textfigure 23 six selected sections are shown.

Theca thick-walled, with pentagonal cross section. Vault prominent. Interambulacral pyramids prominent, present in all 5 interrays, rising 1.46 mm above peristome (figs. 23.1–3). Deltoid crest sloping upward. Ambulacral sinuses prominent, steep-walled with V-shaped cross section. Walls of ambulacral sinus form angle of 85°.

Deltoids weakly developed. Peristomial ring of deltoid lips shown figs. 23.2–4. No canal systems observed in peristomial ring. Main bodies of deltoids extend internally to about 2 mm below top of theca. Radial limbs strongly developed, bend moderately inward. Only radial limbs sectioned.

At posterior side two anal deltoids: epideltoid and hypodeltoid. Anus passes inbetween epi- and hypodeltoid (figs. 23.2–4). Epideltoid small, corresponding to deltoid lips of regular deltoids, forming part of peri-



Textfig. 23. *Kazachstanoblastus carinatus* Arendt, Breimer & Macurda, 1968. L. Carb., Lower Namurian, Tshan–Tshar, North Kazachstan, USSR; spec. Pal. Inst., Acad. Sci. USSR, nr. 1787/2. Series of 6 transverse sections resp. from peels numbered 10, 16, 21, 26, 29, and 39, cut resp. 0.88, 1.23, 1.46, 1.78, 2.08, and 3.48 mm below top of theca. All figures × 5.5. (1) Section above peristome. (2, 3) Peristome. (2–4) Composition of anal area, note presence of epi- and hypodeltoid. (2–6) Composition of ambulacral structures. See textfig. 1 for further explanation.

stomial ring (figs. 23.2, 3). Hypodeltoid relatively small, corresponding to deltoid bodies of regular deltoids, with exposure in walls of *C* and *D* ambulacral sinuses, not contributing to external body wall, completely overlapped by posterior radial limbs. Structures allied to reproductive system not observed.

Ambulacra sublanceolate, moderately inclined, strongly depressed in ambulacral sinuses. Lancets about parallel-sided. External surface of lancet grooved to receive side plates, with exposure along median line; internal surface of lancet strongly convex where bordering thecal cavity. Lancets laterally in contact with R and D in sinus wall (figs. 23.3–6). Side plates and outer side plates also in lateral contact with R and D in sinus wall.

Regular hydrospire structures absent.

2. Family OROPHOCRINIDAE

Serial sectioning of the orophocrinids has been fairly complete. All the known genera except *Acentrotremites* have received anatomical study through at least one species, if possible the type species. In the case of *Orophocrinus*, specimens of more than one species were available for sectioning.

Anatomical sections of the orophocrinids show differences if compared to anatomical sections of the phaenoschismatids. This is mainly caused by the different growth patterns for the deltoid DR sectors and the radial RD sectors.

The deltoids in the orophocrinids have incipient DD sectors, which build a narrow peristomial ring together with the superdeltoid or the epideltoid. This narrow peristomial ring is constructed in much the same way as in the phaenoschismatids. A major difference with the phaenoschismatids lies in the fact that orophocrinid deltoids expose their DR sectors on the external surface of the theca. This external exposure is present in all the sections of the orophocrinids given in textfigs. 24–32. In the separate descriptions of the several orophocrinid species this character is not further mentioned.

The orophocrinid DR and RD sectors are not involved in the formation of ambulacral sinuses and interambulacral pyramids, as in the phaenoschismatids. A sharp deltoid crest is absent and not seen in the sections. The deltoids do not rise above the peristome. The sections above the peristome in *Anthoblastus stelliformis* (textfig. 32) show that the deltoids of that species do rise above the peristome. This is due to the fact that in *Anthoblastus* there is deposition of secondary calcite on the outer surface of the deltoids. They are not to be mistaken for interambulacral pyramids as in the phaenoschismatids.

The growth pattern for deltoids and radials in the orophocrinids implies that the overall thecal shape is different from the phaenoschismatids.

In the orophocrinids the pelvis is broadly conical, and the vault is convex to hemispherical. Consequently, the transverse sections through the orophocrinid vault are rounded pentagonal or decagonal.

The radials are prominent plates, forming large parts of the external body wall. RD and RR sectors are both fully external.

The ambulacral structure of the orophocrinids is not essentially different from the phaenoschismatids. Ambulacra are elongate and not located in ambulacral sinuses; on the contrary they may even become somewhat conspicuous. Lancets are elongate and extend over the entire length of the ambulacrum. The oral end of the lancet abuts against the peristomial ring of deltoid lips; the aboral end is supported by the central part of the radial body. The ambulacrum is bordered by hydrospire clefts (except in *Brachyschisma*) through which the conjoined hydrospires communicate with the exterior. The hydrospire cleft becomes closed off phylogenetically, bringing the aboral parts of the ambulacra gradually in contact with the adjoining radials. This is performed by the secretion of secondary calcite, which also partly infills the aboral ends of the hydrospires. This secondary calcite is also present inbetween the hydrospires and under the lancet in some forms.

In each of the following specific descriptions of the anatomy of orophocrinid species, due attention is given to the structure of both ambulacral and hydrospire structures. They are the most variable characters which need the most attention.

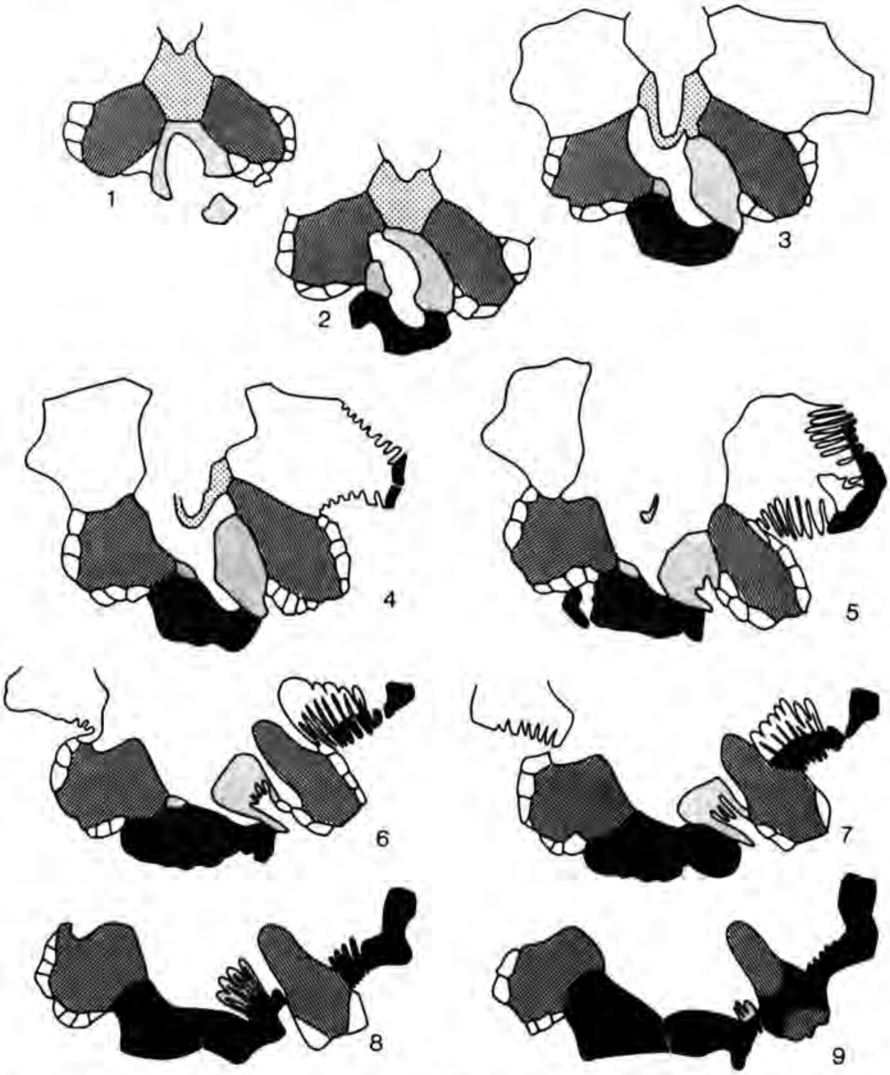
Brachyschisma corrugatum (Reimann, 1935)
Textfigure 24; Pl. VI, figs. 2, 5, 6, 15

Total height of sectioned specimen 8 mm. Upper 2.20 mm, forming hydrospire-bearing vault, sectioned into 32 subsequent transverse peel sections at mean intervals of 0.07 mm. In textfigure 24 nine selected sections are shown.

Theca thick-plated, decagonal in cross section. Vault low, hemispherical. Deltoids with fair DR sector, exposed at external side of theca (figs. 24.3, 4). DD sectors incipient, forming peristomial ring (figs. 24.1–3). No ring canals observed in peristomial ring. Main bodies of deltoids extend to 1.40 mm below top of theca. Radial limbs relatively well developed. RD and DR sectors form structures reminiscent of interambulacral pyramids and ambulacral sinuses in phaenoschismatids.

At posterior side 3 anal deltoids: superdeltoid, subdeltoid, and hypodeltoid. Superdeltoid small, corresponding to deltoid lips of regular deltoids, forming part of peristomial ring (figs. 24.1–4). Subdeltoid relatively small, asymmetrical, forming two limbs of unequal length, that on *C* anal side larger, forming hydrospires (figs. 24.6–9). Hypodeltoid well developed, with exposure on outer side of theca (figs. 24.2–5) and partly overlapped by posterior radial limbs (figs. 24.6–8). No gonopore observed in suture between super- and subdeltoid. Spoonlike projection of superdeltoid (figs. 24.3–5) interpreted as probably forming part of gonoduct.

Ambulacra lanceolate, conspicuous, slightly inclined, situated in faint and wide ambulacral sinuses. Lancets stout, almost parallel-sided; contact with peristomial ring shown figs. 24.1, 2, contact with radial body shown



Textfig. 24. *Brachyschisma corrugatum* (Reimann, 1935). M. Dev., Onondaga Ls., Williamsville, N.Y., USA. Spec. UMMP 26194. Series of 9 transverse sections resp. from peels numbered 11, 15, 21, 23, 26, 27, 28, 29, and 30, cut resp. 0.23, 0.45, 0.75, 0.90, 1.20, 1.30, 1.40, 1.60, and 1.80 mm below top of theca. All figures × 7, showing posterior half of sections, unless otherwise stated. Note presence of super-, sub- and hypodeltoid; presence of hydrospires at *C* anal side, and absence of hydrospires at *D* anal side; 1, 2, anal area only; 6, 7, 8, 9, *C* radial only. See textfig. 1 for further explanation.

fig. 24.9. Aboral part of lancet partly underlain by radial material. Internal surface of lancet concave where bordering thecal cavity. Lateral surface of lancets in contact with deltoids (figs. 24.4, 5), and radials (fig. 24.7). *D* lancet modified due to lack of *D* anal hydrospires, in contact with superdeltoid (fig. 24.1), subdeltoid (figs. 24.4–6) and corresponding radial limb (figs. 24.6–8). External surface of lancet broadly convex, completely concealed by side plates (fig. 24.8) except at adoralmost end. "Exposures" of lancets seen in sections due to partial weathering of sectioned specimen. Side plates and outer side plates present (fig. 24.8). Side plates in lateral contact along median line of ambulacrum. Side plates and outer side plates are in lateral contact with deltoid (figs. 24.3–5, DD sector), but not with radial, except at *D* anal side (figs. 24.6, 7).

Hydrospires formed across part of DR and RD growth sectors. In sections RD suture runs across hydrospire folds. Nine hydrospire groups present, that on *C* anal side formed by larger limb of subdeltoid and corresponding radial limb, that on *D* anal side absent (fig. 24.3–6). Number of hydrospire folds in a regular group is 7 or 8 in sectioned specimen (figs. 24.5–7); number of hydrospire folds in *C* anal field reduced to 4 (fig. 24.8). Hydrospire formation primitive. Hydrospire slits completely exposed, situated in faint ambulacral sinuses at both sides of the ambulacra. Hydrospire folds thick-walled, not placed parallel to one another but slightly conjoined, not differentiated into hydrospire lamellae and inflated hydrospire ducts, not extending deeply into thecal cavity but rather superficial structures. Entrance to hydrospire slits is entirely direct by way of exposed hydrospire slits.

Katoblastus püzos (Münster, 1843)
Textfigure 25; Pl. VI, figs. 9, 11, 14

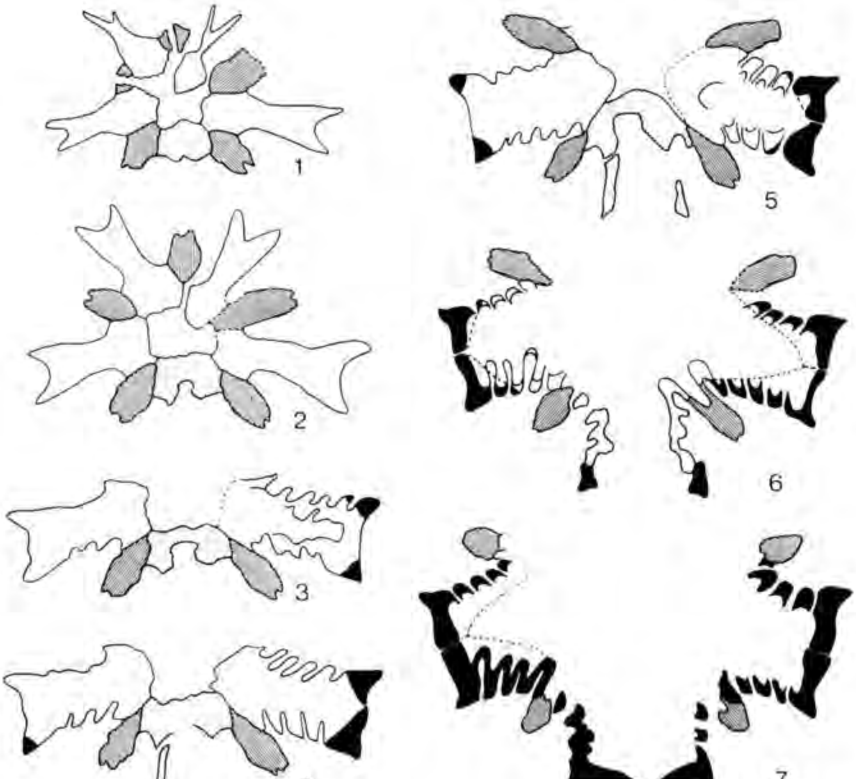
Total height of sectioned specimen 6.15 mm. Upper 2.58 mm, forming part of hydrospire-bearing vault, sectioned into 34 subsequent transverse peel sections at mean intervals of 0.076 mm. In textfigure 25 seven selected sections are shown.

Theca relatively thin-plated, with pentagonal cross section. Vault prominent, slightly convex. Deltoids with fair DR sector which is partly developed on external surface of theca (figs. 25.1–5), and partly in ambulacral sinuses bordering ambulacra (figs. 25.3–5). DD sectors incipient, forming peristomial ring (figs. 25.1, 2). No ring canals observed in peristomial ring. Main bodies of deltoids extend only to 1.19 mm below top of theca. Radial limbs well developed, overlapped by deltoid bodies (figs. 25.5, 6). RD and DR sectors form structures reminiscent of ambulacral sinuses in phaenoschismatids.

At posterior side 4 anal deltoids known: superdeltoid, two cryptodeltoids, and hypodeltoid. Superdeltoid small, corresponding to deltoid lips of regular deltoids, forming part of peristomial ring (figs. 25.1, 2).

Cryptodeltoids situated one at each side of anal cavity; adorally in contact with superdeltoid (fig. 25.5), but not meeting one another laterally along aboral edge of superdeltoid; aborally in contact with posterior radial limbs; cryptodeltoids form hydrospires. Hypodeltoid not preserved in sectioned specimen, but known to be present. Sections reveal that there is place for hypodeltoid contributing to external wall of theca (figs. 25.5, 6). No definite gonopore observed. Notch at aboral side of superdeltoid (figs. 25.2, 3) inferred to lodge gonopore. No traces of gonoduct observed. This is perhaps due to poor state of preservation of sectioned specimen.

Ambulacra linear, inclined, not conspicuous, flanked at both sides by depressions, which are reminiscent of phaenoschismatid ambulacral sinuses (figs. 25.5–7). Lancets elongate, relatively thin plates, parallel-sided; adorally in contact with deltoids in peristomial ring, and partly



Textfig. 25. *Katoblastus püzos* (Münster, 1843). L. Carb., Tournaisian; Tournai, Belgium. Spec. Musée Houiller, Louvain, Belgium, unregistered. Series of 7 transverse sections resp. from peels numbered 4, 8, 12, 14, 16, 20, and 24, cut resp. 0.15, 0.34, 0.51, 0.59, 0.68, 0.89, and 1.19 mm below top of theca. All figures × 12. (1, 2) Peristomial area, complete sections. (3–6) Composition of anal area, posterior part of section only; note presence of a super- and two cryptodeltoids. (4–7) Composition of hydrospire structures; note presence of hydrospires at *C* and *D* anal sides; posterior part of section only. See textfig. 1 for further explanation.

dividing deltoids (fig. 25.1); aborally in contact with radial body. Internal surface of lancet concave where bordering thecal cavity, in contact with admedial hydrospire lamellae (fig. 25.6, *C* amb.). Lateral surface of lancets not in lateral contact with deltoid and radial. Side plates and outer side plates not preserved in sectioned specimen. Lancet known to be exposed over $\frac{2}{3}$ of its length. Exposed part of external surface of lancet narrow, grooved.

Hydrospires formed across part of DR and RD growth sectors. In sections RD suture runs across hydrospire folds, represented in textfigure by broken line. Ten hydrospire groups present, those on *C* and *D* anal sides formed by two cryptodeltoids and corresponding posterior radial limbs (figs. 25.6, 7). Maximum number of hydrospire folds in a regular group is 5 in sectioned specimen; number of hydrospire folds in *C* and *D* anal groups not exactly known, due to poor state of preservation of the sectioned specimen, but probably reduced. Hydrospires primitive; thick-walled, especially in part formed by radial limbs, not differentiated into hydrospire lamellae and inflated hydrospire ducts; placed subparallel, not hanging deeply in thecal cavity. Hydrospire slits almost completely concealed when ambulacra intact. Entrance to hydrospires by way of hydrospire clefts bordering ambulacra and extending over full length of ambulacra. No infilling by secondary calcite observed at aboral end of hydrospires. No sublancetal secretion of calcite by radials known.

Mastoblastus ornatus Arendt, Breimer, & Macurda, 1968

Textfigure 26; Pl. X, figs. 1, 2, 6

Total height of sectioned specimen (figs. 26.1–6) is about 6 mm. Specimen sectioned into 49 subsequent transverse peel sections at mean intervals of 0.112 mm. In textfigure 26 (left hand column) six selected sections are shown to illustrate arrangement of thecal plates in posterior part of sections. In textfigure 26 (right hand column) six separate drawings are given to illustrate ambulacral and vestigial hydrospire structures.

Theca relatively thick-plated, with pentagonal cross section. Vault prominent, nearly hemispherical. Deltoids with relatively large DR sectors, completely exposed on external surface of theca (figs. 26.3, 4). DD sectors incipient, forming peristomial ring (figs. 26.2–4). No ring canals observed in peristomial ring. Radial limbs weakly developed, truncated at upper margins, not overlapping deltoid bodies. RD and DR sectors do not form ambulacral sinuses.

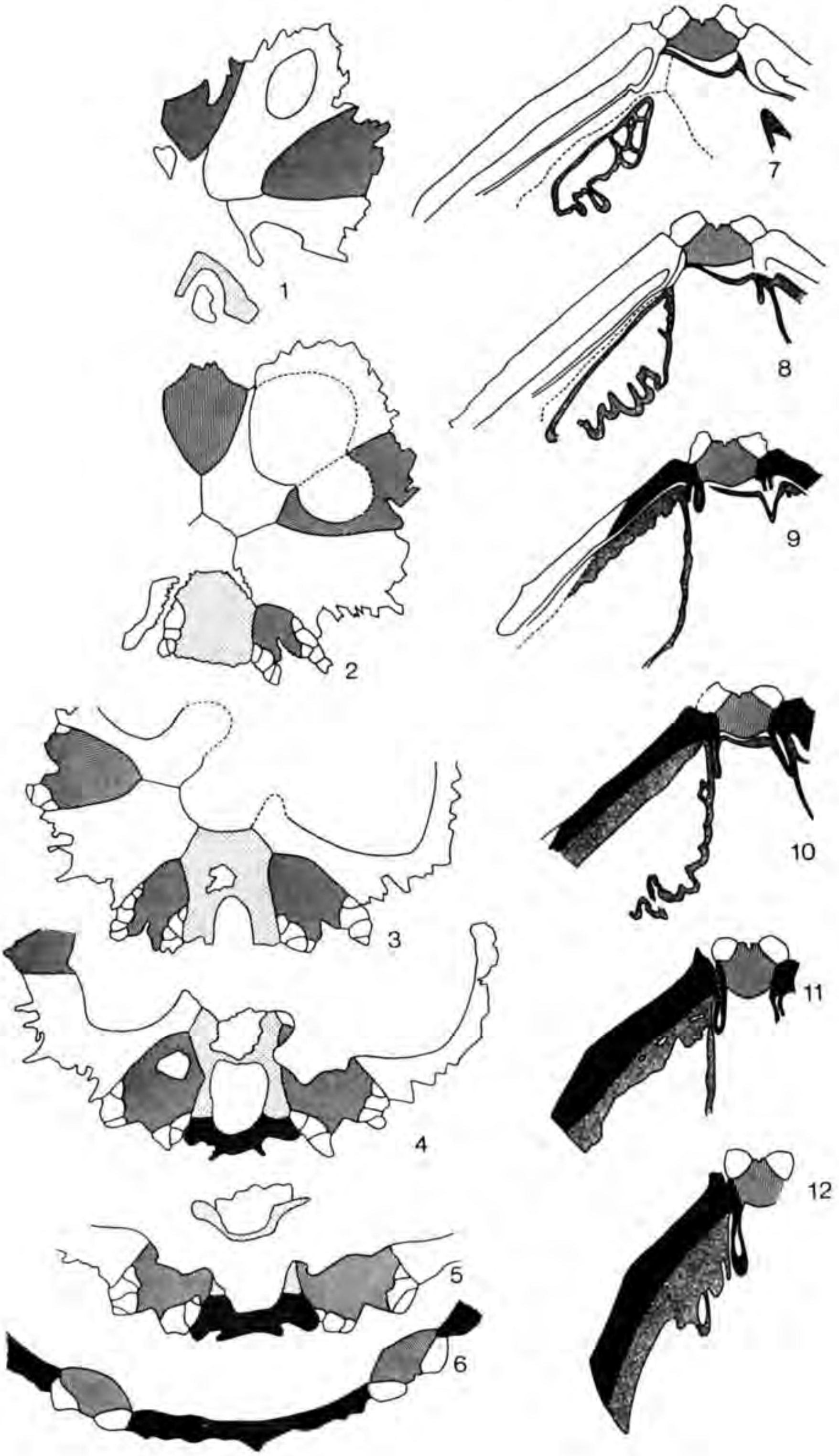
At posterior side 2 anal deltoids: an epideltoid and a hypodeltoid. Epideltoid small, corresponding to deltoid lips of regular deltoids, forming part of peristomial ring (figs. 26.2–5). Epideltoid has two limbs (fig. 26.4) which come in contact with hypodeltoid and *C* and *D* lancets. Epideltoid forms spoon-shaped extremity (fig. 26.5) which may be inferred to be part of the gonoduct. Gonoduct could possibly open in epideltoid by way of pore situated in opening on epideltoid shown fig. 26.3. Hypodeltoid relatively large, with exposure on external surface of theca (figs. 26.4–6), in contact with epideltoid limbs. Anus passes between epi- and hypodeltoid.

Ambulacra sublanceolate, conspicuous, not situated in ambulacral sinuses. Lancets elongate, almost parallel-sided; adorally in contact with deltoids in peristomial ring (figs. 26.1–4), aborally in contact with radial body. Internal surface of lancet slightly convex where bordering thecal cavity. Lateral surface of lancet may come in contact with radial and deltoid. Side plates and outer side plates present (figs. 26.2–6). Side plates do not meet laterally along median line of ambulacrum; lancet exposed (figs. 26.7–12). Exposed surface of lancet narrow, grooved. Side plates and outer side plates in contact with deltoid (figs. 26.7, 8) and radial (figs. 26.9–12).

Regular and well-developed hydrospires absent. One vestigial or rudimentary hydrospire fold present (figs. 26.9–12) along aboral half of ambulacrum, formed by radial material. Rudimentary hydrospire fold very small and short. It opens to exterior by means of a few interradial pores or a short slit (fig. 26.11).

Radial limbs involved in formation of interradially disposed sacs (figs. 26.7–12). Upper edges of sac situated about at RD suture. It is connected to the aboral edge of the deltoid by a calcified membrane, which optically belongs to the deltoid (figs. 26.7, 8). The deltoid itself takes no part in the formation of the sacs. The top part of the sac is lobed and projects freely into the thecal cavity. Aborally the sac first joins other lamellae (probably calcified flexible membranes) and at its aboral extremity it is connected with a more or less amorphous body of loose calcitic meshwork which lies against the inner edges of the radial limbs. The sacs occur over the same part of the ambulacra as do the rudimentary hydrospires. The exact distribution of these sacs is not known, but probably they did not occur in the posterior *CD* interray. It is not known whether or not the sacs of two adjoining radial limbs meet laterally to form one sac, which is bilobed at the top. No definite openings of the sacs with the external medium are found. Their function is puzzling.

Textfig. 26. *Mastoblastus ornatus* Arendt, Breimer & Macurda, 1968. L. Carb., Lower Namurian, Tshan–Tshar, North Kazachstan, USSR. Spec. 1788/321 Pal. Inst., Akad. Nauk, Moscow. Two series of transverse sections (shown fig. 1–6, and fig. 7–12 resp.). First series from peels numbered 6, 10, 15, 20, 22, and 36, cut resp. 0.15, 0.27, 0.45, 0.68, 0.75, and 2.10 mm below top of theca. Second series from peels numbered 44, 43, 41, 39, 30, and 24 through radio-deltoid region. All figures × 12. (1, 2) Peristome. (3–6) Composition of anal area and structures related to reproductive system; note presence of epi- and hypodeltoid; 5, note spoonshaped process of epideltoid; posterior parts of sections only. (7–12) Composition of ambulacral and hydrospire structures; note sac-like structure in radial position (grey); 9, 10, 11, 12, note incipient single hydrospire fold. See textfig. 1 for further explanation.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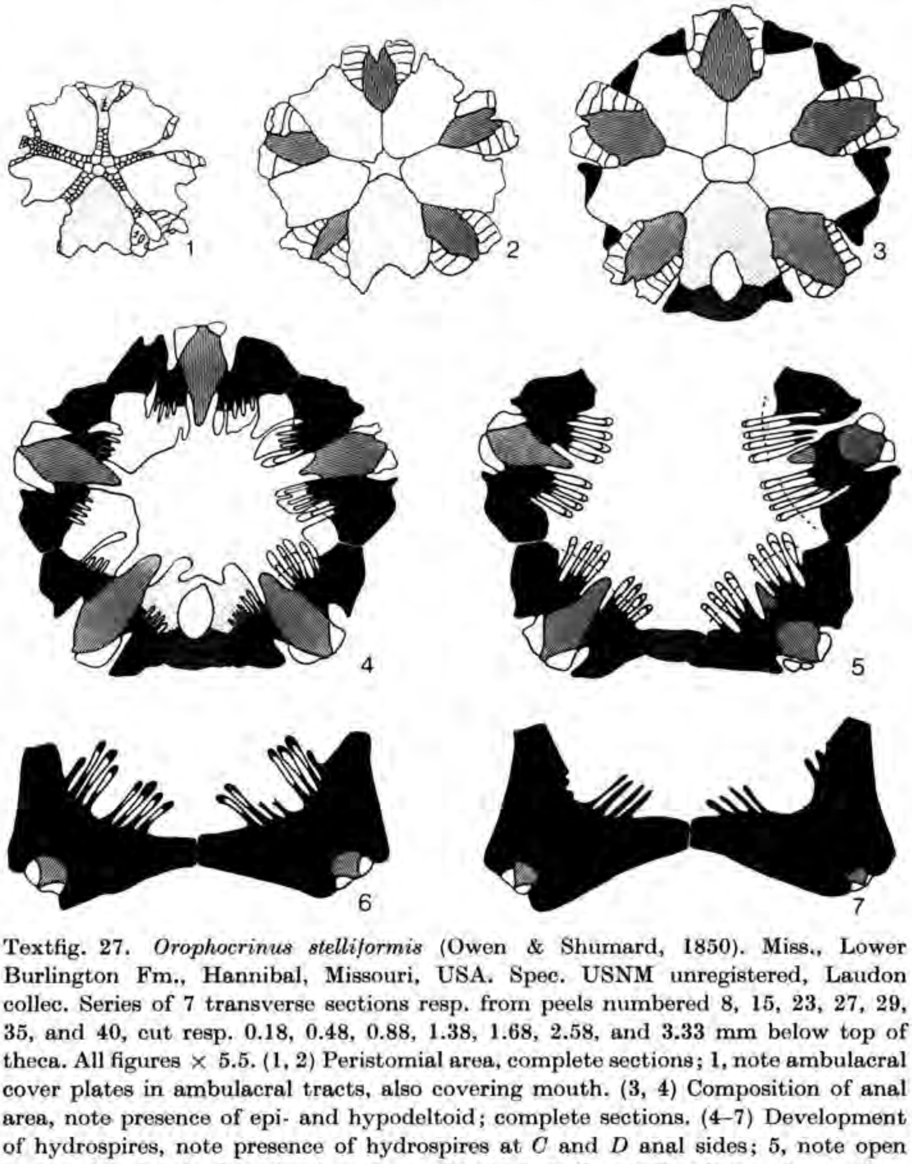
Orophocrinus stelliformis (Owen & Shumard, 1850)
Textfigure 27; Pl. VII, figs. 9–11

Total height of sectioned specimen 11.6 mm. Upper 3.48 mm, forming hydrospire-bearing vault, sectioned into 41 subsequent transverse peel sections at mean intervals of 0.084 mm. In textfigure 27 seven selected sections are shown.

Theca thick-plated, with pentalobate cross section. Vault well developed,



Textfig. 27. *Orophocrinus stelliformis* (Owen & Shumard, 1850). Miss., Lower Burlington Fm., Hannibal, Missouri, USA. Spec. USNM unregistered, Laudon collec. Series of 7 transverse sections resp. from peels numbered 8, 15, 23, 27, 29, 35, and 40, cut resp. 0.18, 0.48, 0.88, 1.38, 1.68, 2.58, and 3.33 mm below top of theca. All figures × 5.5. (1, 2) Peristomial area, complete sections; 1, note ambulacral cover plates in ambulacral tracts, also covering mouth. (3, 4) Composition of anal area, note presence of epi- and hypodeltoid; complete sections. (4–7) Development of hydrospires, note presence of hydrospires at *C* and *D* anal sides; 5, note open hydrospire cleft in *B* amb; *A* radius omitted; 6, 7, *C* and *D* radials only, sections below hydrospire cleft, note radial growth under lancet; 7, aboral tip of ambulacrum and lancet. See textfig. 1 for further explanation.

convex. Deltoids with fair DR sectors, which are exposed on external surface of theca (figs. 27.1–3). DD sectors relatively well developed with interdeltoid suture on external surface of theca, developed for lodging adoral end of ambulacral tracts. DD sectors form peristomial ring (figs. 27.2, 3). No ring canals observed in peristomial ring. Main bodies of deltoids extend internally to only 1.68 mm below top of theca (fig. 27.5). Radial limbs strongly developed, overlapping deltoid bodies (figs. 27.3, 4).

At posterior side two anal deltoids: epideltoid and hypodeltoid. Epideltoid well developed, forming part of peristomial ring (figs. 27.1–3). Epideltoid has two limbs which come in contact with hypodeltoid, *C* and *D* lancets, and posterior radial limbs (figs. 27.3, 4). Epideltoid hydrospire-forming, not observed to form structures allied to reproductive system. Hypodeltoid with exposure on external surface of theca, in contact with epideltoid limbs and posterior radial limbs (fig. 27.4). Anus passes between epi- and hypodeltoid (figs. 27.3, 4).

Ambulacra linear, conspicuous, not reaching peristome. Lancets elongate, parallel-sided; adorally in contact with deltoids in peristomial ring (figs. 27.2, 3), aborally in contact with radial body (figs. 27.6, 7). Internal surface of lancet convex where bordering thecal cavity (figs. 27.4, 5), and where underlain by radial material (fig. 27.6), flat at aboral tip (fig. 27.7). External surface of lancet inverted V-shape, with grooves along median line. Lateral surfaces of lancets in contact with radial along aboral part of ambulacrum (figs. 27.4, 5). Side plates and outer side plates present, but not reaching peristome (fig. 27.1). Side plates do not meet laterally along median line of ambulacrum; lancet exposed. At adoral extremity of ambulacrum the ambulacral tract is situated in a groove on interdeltoid suture. This groove is a continuation of the ambulacral tract on the groove in exposed median part of lancet. The groove is concealed by ambulacral cover plates in biserial arrangement (fig. 27.1), which also cover the mouth by means of five larger cover plates. Side plates are in lateral contact with deltoids (fig. 27.3) and with radials (figs. 27.5–7), along aboral part of ambulacrum, but otherwise separated from the radials by hydrospire clefts (fig. 27.5).

Hydrospires formed across DR and RD growth sectors. In sections RD sutures run across hydrospire folds, represented in textfigure by broken lines. Ten hydrospire groups present, those on *C* and *D* anal sides formed by epideltoid and corresponding posterior radial limbs (figs. 27.4, 5). Number of hydrospire folds in each of the ten groups is 4 in the sectioned specimen; number of anal hydrospires not reduced. Hydrospires placed subparallel, slightly conjoined in adoral half, not differentiated into hydrospire lamellae and inflated hydrospire ducts, not deeply pendent into thecal cavity. No external hydrospire slits. Entrance to hydrospires by way of restricted hydrospire cleft (fig. 27.5; *B*-amb.), extending along adoral half of ambulacrum. Along aboral half of ambulacrum hydrospire cleft is closed off by deposition of secondary calcite from the radial under the lancet. Aborally filled-in hydrospire cleft still observable as a groove bordering ambulacrum (figs. 27.4, 5). Aboral parts of hydrospires probably not functional, and probably filled in by secondary calcite from radial (figs. 27.6, 7).

Orophocrinus conicus Wachsmuth & Springer, 1888

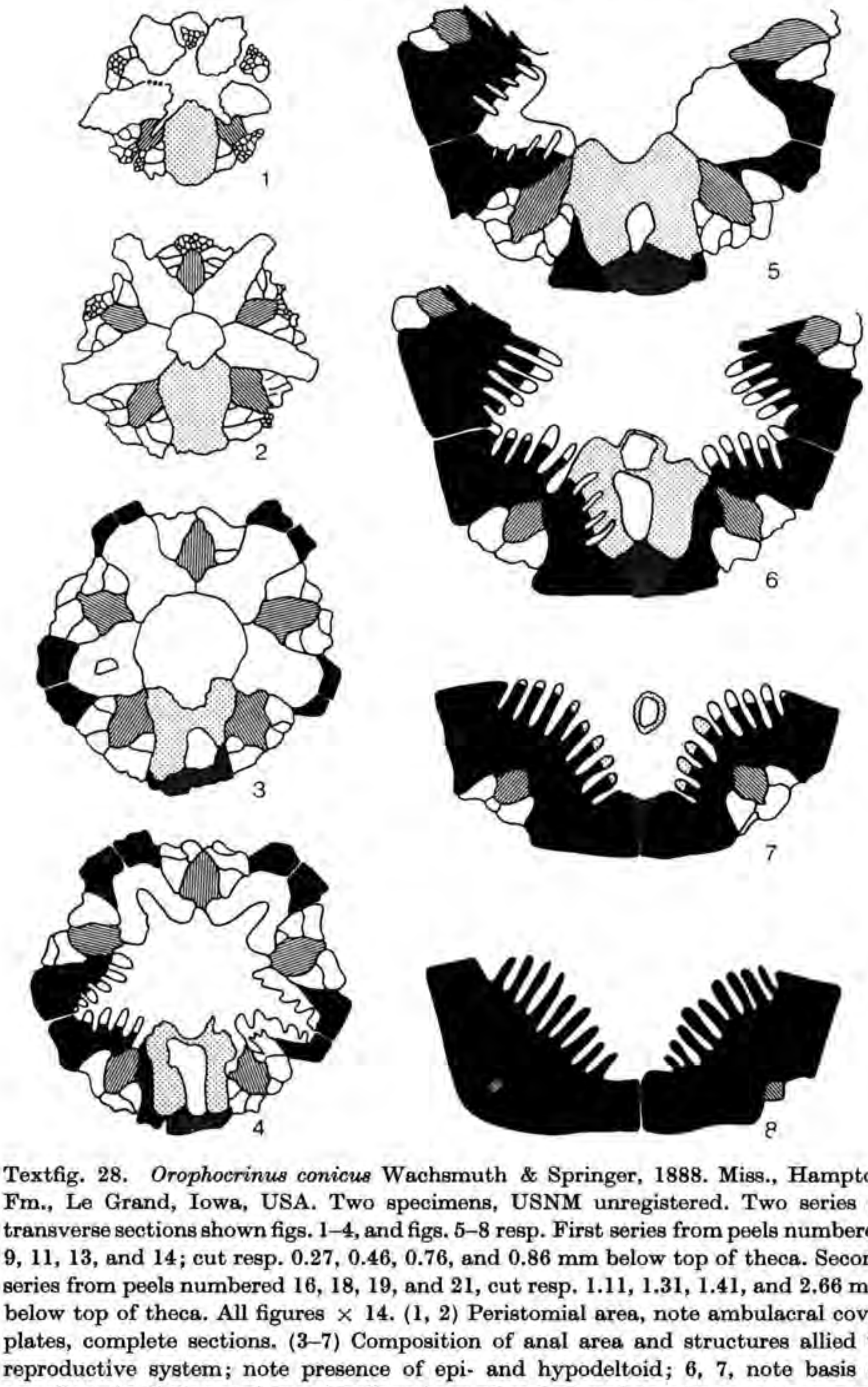
Textfigure 28; Pl. VII, figs. 1, 2, 4; Pl. IX, fig. 7

Two specimens sectioned, a juvenile specimen 4.7 mm high, and another specimen 7 mm high. Upper 1.16 mm of juvenile specimen sectioned into 16 transverse sections at mean intervals of 0.07 mm. In textfigure 28 (left hand column) four selected sections are shown. Upper 3.06 mm of larger specimen sectioned into 21 transverse sections at mean intervals of 0.07 mm. In textfigure 28 (right hand column) four selected sections are shown.

Theca thick-plated, with pentagonal cross section. Vault low, convex. Deltoids with fair DR sectors, which are exposed on external surface of theca (figs. 28.1, 2). DD sectors relatively well developed, with interdeltoid suture on external surface of theca, developed for lodging adoral end of ambulacral tracts. DD sectors form peristomial ring (fig. 28.2). No ring canals observed in peristomial ring. Radial limbs weakly developed, overlapping deltoid bodies (figs. 28.3, 4).

At posterior side two anal deltoids: epideltoid and hypodeltoid. Epideltoid well developed, forming part of peristomial ring (figs. 28.2, 3). Epideltoid has two limbs which come in contact with hypodeltoid, *C* and *D* lancets and side plates, and with posterior radial limbs (figs. 28.3–6). Epideltoid hydrospire-forming. Epideltoid produced into tubelike extension internally (figs. 28.6, 7), interpreted to be base of gonoduct. No external gonopore observed. Gonoduct inferred to open into anal cavity. Hypodeltoid with exposure on external surface of theca, in contact with epideltoid wings and posterior radial limbs (figs. 28.3–7). Anus passes between epi- and hypodeltoid (figs. 28.3, 5), covered by pavement of small cover plates.

Ambulacra sublanceolate, not conspicuous, not reaching peristome. Lancets elongate, almost parallel-sided; adorally in contact with deltoids in peristomial ring (figs. 28.1, 2), aborally in contact with radial body (fig. 28.8) and partly embedded in it. Internal surface of lancet V-shaped in adoral half, convex in aboral half. External surface of lancet convex. Lancets laterally in contact with radials and at aboral extremity underlain by radial material (figs. 28.6–8). Side plates and outer side plates present, but not reaching peristome (fig. 28.1). In aboral half of ambulacrum side plates meet laterally along median line of ambulacrum; lancets exposed over adoral half only. Side plates and outer side plates in lateral contact with radial and deltoid, with exception of length of hydrospire cleft. Ambulacral tract reaching peristome, in adoralmost part of ambulacra



Textfig. 28. *Orophocrinus conicus* Wachsmuth & Springer, 1888. Miss., Hampton Fm., Le Grand, Iowa, USA. Two specimens, USNM unregistered. Two series of transverse sections shown figs. 1–4, and figs. 5–8 resp. First series from peels numbered 9, 11, 13, and 14; cut resp. 0.27, 0.46, 0.76, and 0.86 mm below top of theca. Second series from peels numbered 16, 18, 19, and 21, cut resp. 1.11, 1.31, 1.41, and 2.66 mm below top of theca. All figures × 14. (1, 2) Peristomial area, note ambulacral cover plates, complete sections. (3–7) Composition of anal area and structures allied to reproductive system; note presence of epi- and hypodeltoid; 6, 7, note basis of gonoduct. (5–8) Composition of hydrospires and ambulacral structures, note presence of hydrospires at *C* and *D* anal sides; 7, note strong radial growth under lancet; 8, aboral end of lancet; posterior part of sections only. See textfig. 1 for further explanation.

situated on interdeltoid suture and coverd by ambulacral cover plates in biserial arrangement (figs. 28.1, 2).

Hydrospires formed across DR and RD growth fronts. In sections RD suture runs across hydrospire folds. Ten hydrospire groups present, those on *C* and *D* anal side formed by epideltoid and corresponding radial limbs. Number of hydrospire folds in each of the ten groups is 4 or 5 in the larger specimen (figs. 28.6–8); number of hydrospire folds in anal interarea not reduced. Hydrospires placed subparallel, not conjoined, not differentiated into hydrospire lamellae and inflated hydrospire ducts, not extending deeply into thecal cavity. No external hydrospire slits. Entrance to hydrospires by way of cleft (not shown in textfig. 28). Along aboral half of ambulacrum hydrospire cleft is closed off by deposition of secondary calcite from the radial under the lancet (figs. 28.6–8). Aboral parts of hydrospires probably not functional, and filled in by sceondary calcite from radial (figs. 28.7, 8).

Orophocrinus praelongus Bailey, 1886

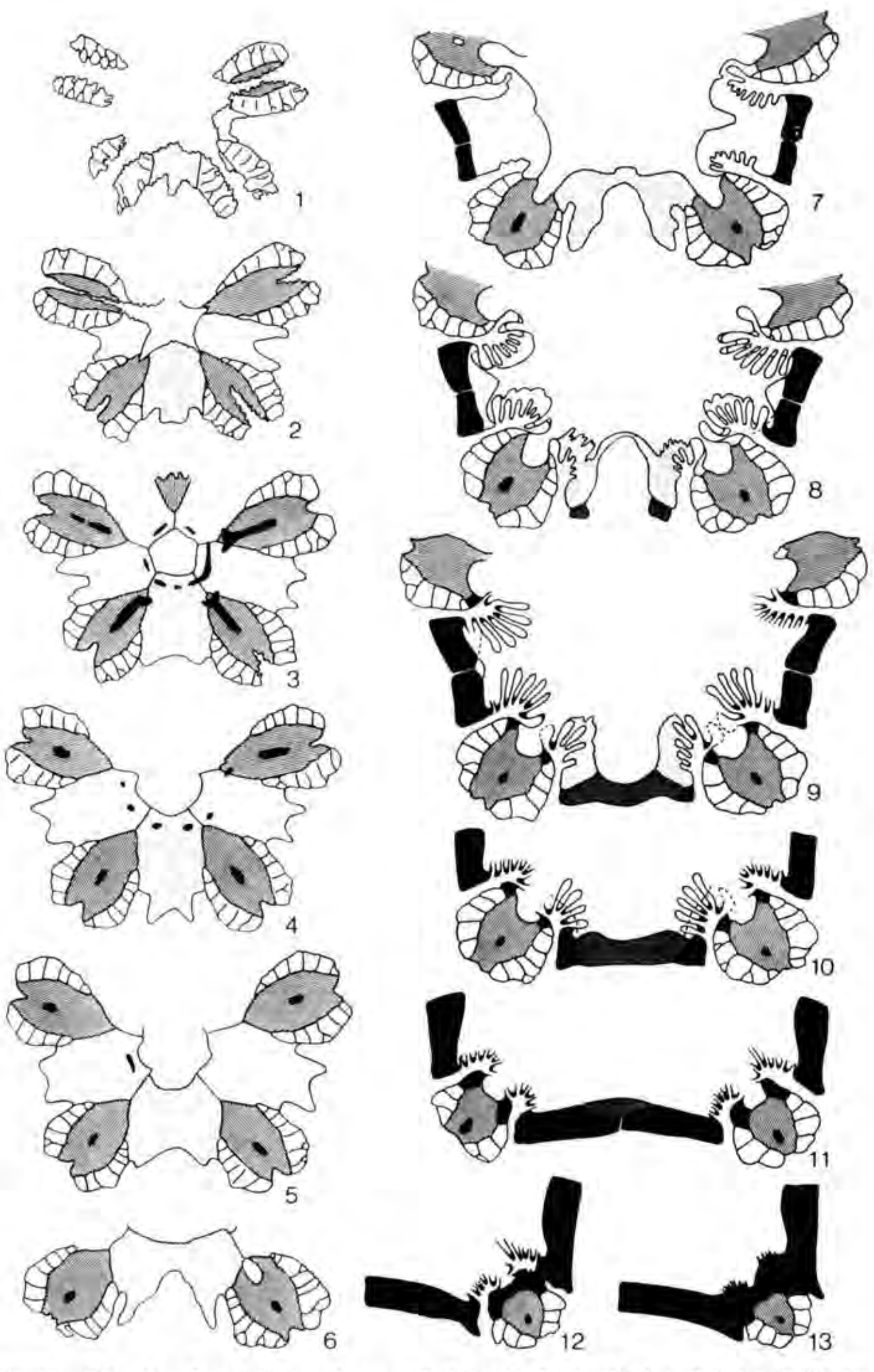
Textfigure 29; Pl. VIII, figs. 1, 3; Pl. IX, figs. 4, 5

Total height of sectioned specimen 18.85 mm. Upper 5.9 mm, forming hydrospire-bearing vault, sectioned into 52 subsequent transverse peel sections at mean intervals of 0.11 mm. In textfigure 29 thirteen selected sections are shown.

Theca relatively thin-plated, with pentagonal cross section. Vault low, convex. Deltoids with relatively large DR sectors, which are exposed on external surface of theca (figs. 29.2–5). DD sectors weakly developed, forming peristomial ring (fig. 29.3). Ring canals of oral nervous system preserved in peristomial ring, consisting of a pentagonal ring canal with angles at contacts with radial nerve canals in lancets, and chiasmas forming over interdeltoid suture (fig. 29.3). Main bodies of deltoids extend internally to 2.61 mm below top of theca (fig. 29.10). Radial limbs moderately developed, overlapping deltoids bodies (figs. 29.7, 8).

At posterior side two anal deltoids: epi- and hypodeltoid. Epideltoid large, forming part of peristomial ring (figs. 29.3, 4), corresponding to DD sectors of regular deltoids, carrying part of oral nervous system. Epideltoid has two limbs which come in contact with hypodeltoid and posterior radial limbs (fig. 29.9). Epideltoid hydrospire-forming (figs. 29.8, 9), but not observed to form structures allied to reproductive system. Hypodeltoid with exposure on external surface of theca, in contact with epideltoid wings and posterior radial limbs (figs. 29.9, 10); overlapped by posterior radial limbs (fig. 29.11). Anus passes between epi- and hypodeltoid.

Ambulacra sublanceolate, strongly conspicuous, reaching peristome (fig. 29.1). Lancets traversed by radial nerve canals of oral nervous system (figs. 28.3–13). Lancets elongate, parallel-sided; adorally in contact with



Textfig. 29. *Orophocrinus praelongus* Bailey, 1886. L. Carb., Feltrim Hill, Co. Dublin, Ireland. Spec. Trinity College, Dublin, nr. 7983. Series of 13 transverse sections resp. from peels numbered 5, 9, 14, 18, 21, 25, 30, 34, 37, 39, 43, 45, and 48, cut resp. 0.18, 0.38, 0.56, 0.74, 0.89, 1.45, 1.74, 1.99, 2.35, 2.61, 3.65, 4.20, and 4.58 mm below top of theca. All figures × 5.5. (1–3) Peristomial area; 3, note ring canal and radial canals of oral nervous system. (4–9) Composition of anal area, note presence of epi- and hypodeltoid; posterior parts of sections only. (7–13) Composition of hydrospires and ambulacral structures, note presence of hydrospires at *C* and *D* anal sides, note open hydrospire cleft; 12, 13, aboral end of ambulacrum, note closure of hydrospire cleft and weak radial growth under lancet, *C* and *D* radials only. See textfig. 1 for further explanation.

deltoids in peristomial ring (fig. 29.3), aborally in contact with radial body (fig. 29.13), and partly underlain by radial material (figs. 29.12, 13). Internal surface of lancets concave where bordering thecal cavity (figs. 29.7–10), or flat where underlain by radial (figs. 29.11–13). External surface of lancet inverted V-shape. Lancets not in contact with radial laterally. Side plates and outer side plates preserved. Side plates do not meet laterally along median line of ambulacrum, except at aboral extremity of ambulacrum; lancet exposed over most of its length, exposed surface of lancet grooved (figs. 29.3–8). Outer side plates placed at lateral periphery of ambulacra, alternating with side plates (figs. 29.2–5). Side plates and outer side plates in lateral contact with deltoid (figs. 29.2–7) and with radials at aboral end of ambulacra (figs. 29.12, 13), otherwise separated from radial by hydrospire cleft (figs. 29.7–11).

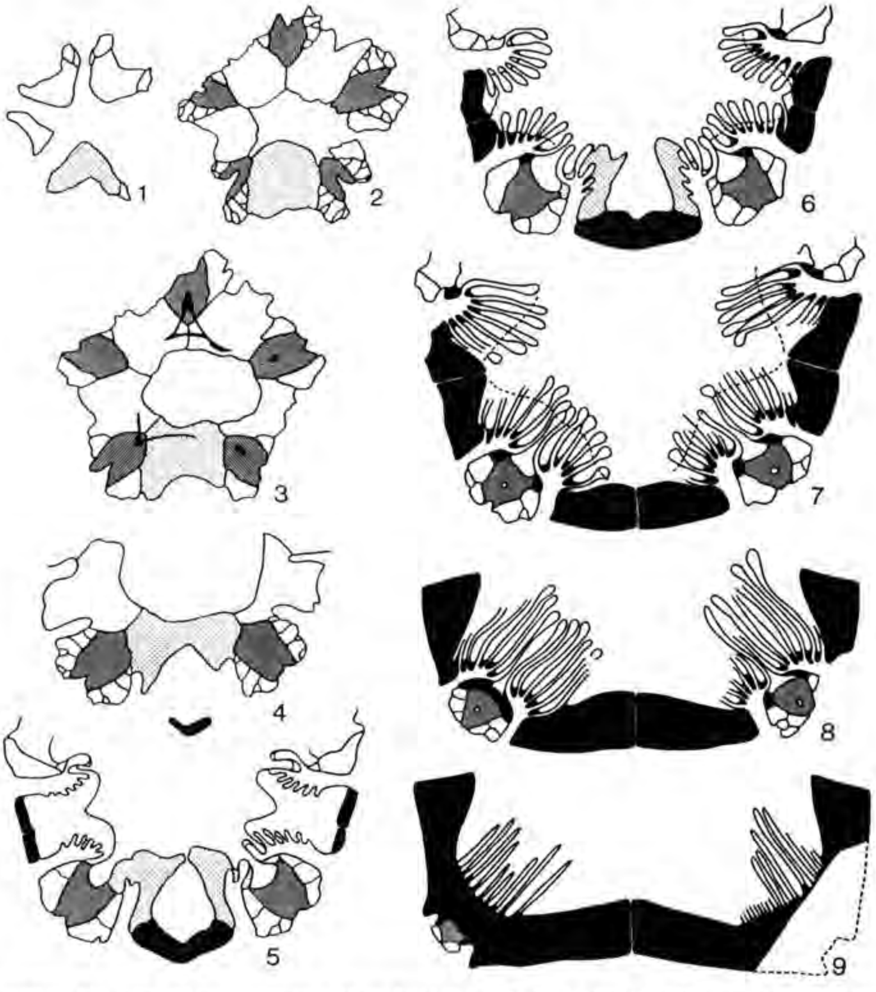
Hydrospires formed across DR and RD growth sectors. In sections RD sutures run across hydrospire folds, represented in textfigures by broken lines. Ten hydrospire groups present, those on *C* and *D* anal sides formed by epideltoid and corresponding posterior radial limbs (figs. 29.8, 9). Number of hydrospire folds in regular groups is 7 or 8 in sectioned specimen; at *C* anal side there are 6 hydrospire folds, and at *D* anal side 5; number of hydrospire folds in anal interareas slightly reduced. Hydrospires short, not extending deeply into thecal cavity, strongly conjoined over all of their length, weakly differentiated into thin hydrospire lamellae and inflated hydrospire ducts. No external hydrospire slits. Entrance to conjoined hydrospires by way of hydrospire clefts (figs. 29.7–12), separating radials from ambulacra, and extending over almost entire length of ambulacra. At aboral extremity of ambulacrum hydrospire cleft is closed off by deposition of secondary calcite from the radial under the lancet (figs. 29.12, 13). Filled-in hydrospire cleft still observable as a groove bordering ambulacrum (fig. 29.13).

Orophocrinus verus (Cumberland, 1826)
Textfigure 30; Pl. VIII, figs. 4, 6; Pl. X, fig. 7

Total height of sectioned specimen 14.5 mm. Upper 5.98 mm, forming hydrospire-bearing vault, sectioned into 34 subsequent transverse peel sections at mean intervals of 0.196 mm (variable from 0.03–0.40 mm). In textfigure 30 nine selected sections are shown.

Theca relatively thick-plated, with pentagonal cross section. Vault prominent, convex. Deltoids with small DR sectors, which are exposed on external surface of theca (figs. 30.2–4). DD sectors well developed, with interdeltoid suture on external surface of theca, forming peristomial ring (figs. 30.2–4). Ring canal of oral nervous system preserved in peristomial ring, consisting of pentagonal ring canal with angles at contacts with radial nerve canals in lancets, and chiasmas forming over interdeltoid sutures (fig. 30.3). Main bodies of deltoids extend internally to 2.78 mm below top of theca (fig. 30.7). Radial limbs strongly developed, overlapping deltoid bodies (figs. 30.5, 6).

At posterior side 2 anal deltoids: epideltoid and hypodeltoid. Epideltoid well developed, forming part of peristomial ring (fig. 30.3). Epideltoid has two limbs (figs. 30.5, 6), which come in contact with hypodeltoid (figs. 30.5, 6). Epideltoid hydrospire-forming (fig. 30.6), not observed to



Textfig. 30. *Orophocrinus verus* (Cumberland, 1826). L. Carb., Clitheroe, Yorkshire, England. Spec. collec. De Verneuil, Fac. des Sciences, Orsay, France. Series of 9 transverse sections resp. from peels numbered 3, 9, 12, 15, 20, 22, 25, 28, and 31, cut resp. 0.07, 0.28, 0.53, 1.08, 1.58, 1.98, 2.78, 3.78, and 4.98 mm below top of theca. All figures × 5.5 (1–3) Peristomial area; 3, note canals of nervous system; complete sections. (4–6) Composition of anal area; note presence of epi- and hypodeltoid; posterior parts of sections only. (5–9) Composition of hydrospires and ambulacral structures; note presence of hydrospires at *C* and *D* anal sides; note open hydrospire cleft; 13, strong radial growth under lancet, hydrospire cleft closed; posterior part of sections only. See textfig. 1 for further explanation.

form structures allied to reproductive system. Hypodeltoid with exposure on external surface of theca, in contact with epideltoid limbs (fig. 30.6) and posterior radial limbs. Anus passes between epi- and hypodeltoid (fig. 30.5).

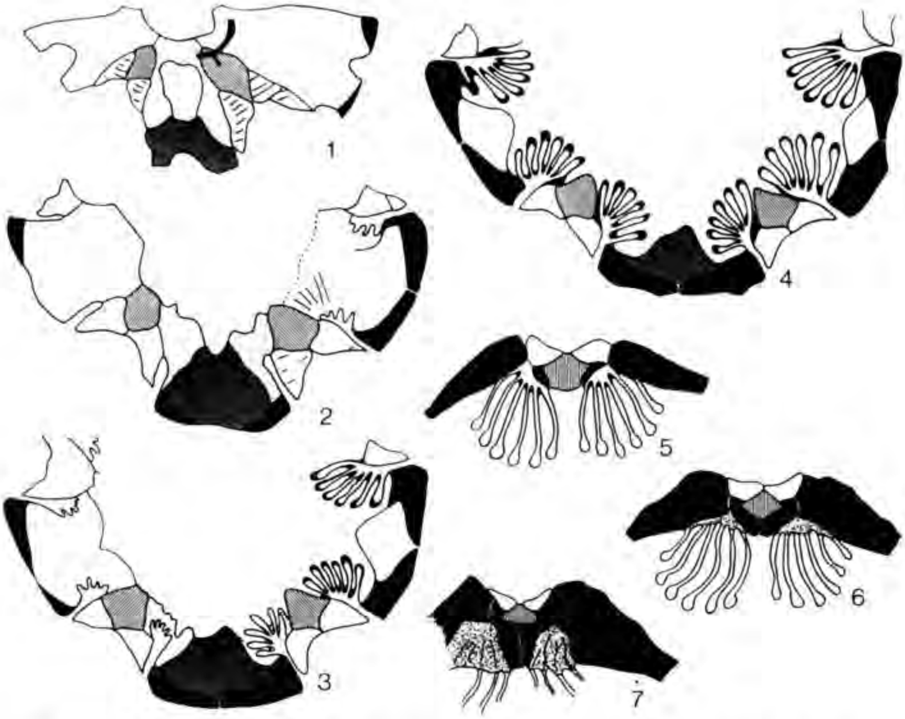
Ambulacra sublanceolate, slightly conspicuous, almost reaching peristome. Lancets elongate, parallel-sided, adorally in contact with deltoids in peristomial ring (figs. 30.2–4), aborally in contact with radial body (fig. 30.9) and partly underlain by radial material (fig. 30.8). Internal surface of lancet slightly concave where bordering thecal cavity (figs. 30.5–7), slightly convex where underlain by radial material (figs. 30.8, 9). External surface of lancet inverted V-shape, grooved along median line. Lancets laterally in contact with radial, except at aboral extremity of ambulacrum (fig. 30.9). Side plates and outer side plates present, but not reaching peristome (fig. 30.1). Side plates do not meet laterally along median line of ambulacrum, except at aboral extremity of ambulacrum (fig. 30.9); lancet exposed over most of its length. Outer side plates placed at lateral periphery of ambulacra, alternating with side plates (fig. 30.4). Side plates and outer side plates in lateral contact with deltoids (figs. 30.2–4), and with radials at aboral extremity of ambulacra (fig. 30.9), otherwise separated from radials by hydrospire cleft (figs. 30.5–8). At adoral extremity of ambulacrum the ambulacral tract is excavated in interdeltoid suture (fig. 30.1), thus being a continuation of the ambulacral tract on exposed surface of lancet.

Hydrospires formed across DR and RD growth sectors. In sections RD sutures run across hydrospire folds, represented in textfigure by broken lines. Ten hydrospire groups present, those on *C* and *D* anal sides formed by epideltoid and corresponding radial limbs (figs. 30.6, 7). Number of hydrospire folds in every one of the ten groups is 6 or 7 in sectioned specimen. Number of hydrospire folds in anal interarea not reduced. Hydrospires long, extending deeply into thecal cavity, strongly conjoined over all of their length, perfectly differentiated into thin hydrospire lamellae and inflated hydrospire ducts (fig. 30.7). No external hydrospire slits. Entrance to conjoined hydrospires by way of hydrospire clefts (figs. 30.5–8), separating radials from ambulacra, and extending over $\frac{2}{3}$ the length of ambulacra. At aboral extremity of ambulacrum hydrospire cleft is closed off by deposition of secondary calcite from the radial under the lancet (fig. 30.9). Infilled hydrospire cleft still observable as a groove bordering ambulacrum (fig. 30.9).

Pentablastus supracarbonicus Sieverts–Doreck, 1951
Textfigure 31; Pl. IX, figs. 10–21

Total height of sectioned specimen approximately 30 mm. Specimen sectioned in the way described by JOYSEY & BREIMER, 1963. For the sake of completeness the essential anatomic characters of the species are repeated here. The textfigures representing the sections are drawn up in the standard way as adopted for this monograph in order to allow easier and closer comparison with other species described.

Theca thick-plated, with depressed base and very prominent vault, pentagonal in plan view. Radial divided into inferradial bodies and superradial limbs. Deltoids with small DR sectors, which are partly exposed on external surface of theca (figs. 31.1, 2). DD sectors slightly developed, without substantial interdeltoid suture on external surface of theca, forming peristomial ring (fig. 31.1). Parts of ring canals of oral nervous system preserved in peristomial ring, consisting of part of pentagonal ring canal at junction with radial canal in lancet (fig. 31.1, *C*-lancet). Main bodies of deltoids extend internally to only 3.50 mm below top of



Textfig. 31. *Pentablastus supracarbonicus* Sieverts-Doreck, 1951. L. Carb., Namurian; Rabanal de los Caballeros, Palencia, Spain. Spec. 102455, Rijksmus. Geol. Mineral., Leiden, Netherlands. Series of 7 transverse sections resp. from sections numbered 2 (top), 4 (top), 5 (top), 6 (top), 8 (top), 10 (bottom), and 12 (top), cut resp. 0.70, 2.10, 2.80, 3.50, 4.90, 6.55, and 7.70 mm below top of theca. All figures × 4. (1–2) Composition of anal area; note presence of epi- and hypodeltoid; posterior part of sections only. (3–7) Composition of ambulacral and hydrospire structures; 3, 4, note presence of hydrospires at *C* and *D* anal side, hydrospires opening through hydrospire cleft; posterior part of sections only; 5, 6, 7, *D* radial only; 5, note hydrospire canal, 6, note strong radial growth under lancet, 7, note infilling of hydrospires. See textfig. 1 for furrher explanation.

theca (fig. 31.4). Superradial limbs strongly developed, overlapping deltoid bodies (figs. 31.3, 4).

At posterior side 2 anal deltoids: epideltoid and hypodeltoid. Epideltoid moderately developed, forming part of peristomial ring (fig. 31.1). Epideltoid has two limbs (figs. 31.1–3), which come in contact with hypodeltoid and side plates of *C* and *D* ambulacra. Epideltoid hydrospire-forming (fig. 31.3), not observed to form structures allied with reproductive system. Hypodeltoid relatively large, with exposure on external surface of theca, in contact with epideltoid limbs and posterior superradial limbs (figs. 31.2, 3), overlapped by posterior superradial limbs (fig. 31.4). Anus passes between epi- and hypodeltoid (fig. 31.1).

Ambulacra sublanceolate, not conspicuous, reaching peristome. Lancets elongate, parallel-sided; adorally in contact with deltoids in peristomial ring (fig. 31.1), aborally in acontact with inferradial body (fig. 31.7), and largely underlain by radial material (figs. 31.5–7). Internal surface of lancet V-shaped (figs. 31.4–6), but flat at aboral extremity (fig. 31.7). External surface of lancet in form of broad inverted V. Lancets laterally and internally in contact with superradial limbs or with secondary calcite secreted from these limbs (figs. 31.5–7), otherwise only separated from radial by hydrospire cleft (figs. 31.3, 4). Side plates and outer side plates present, reaching peristome. Side plates meet laterally along median line of ambulacrum (figs. 31.2–4, 6); lancet concealed over entire length except at adoralmost end. Side plates and outer side plates in lateral contact with deltoids (figs. 31.1, 2) and with superradial limbs at aboral half of ambulacrum (figs. 31.5–7), otherwise separated from superradial limb by hydrospire cleft (figs. 31.3, 4).

Hydrospires formed across RD suture, but built almost entirely by superradial limbs. RD suture crenulate, producing 'cedar tree effect' in sections (see JOYSEY & BREIMER, 1963). Ten hydrospire groups present, those on *C* and *D* anal sides formed by epideltoid (fig. 31.3) and posterior superradial limbs. Number of hydrospires in every one of the ten groups is 6. Number of hydrospire folds in anal interarea not reduced. Hydrospires moderately developed, strongly conjoined over all of their length, differentiated into thin hydrospire lamellae and inflated hydrospire ducts (figs. 31.5, 6). No external hydrospire slits. Entrance to conjoined hydrospires a restricted hydrospire cleft (figs. 31.3, 4), extending over $\frac{1}{3}$ the length of ambulacrum. Over lower $\frac{2}{3}$ the length of ambulacrum hydrospire cleft closed off by deposition of secondary calcite from the radial (figs. 31.5–7). Hydrospires towards aboral half of theca gradually filled in by secondary calcite until they become completely embedded in secondary radial calcite. Radial also built a strong deposition of calcite under the lancet, a structure formerly known as the 'sublancet' or as 'fused hydrospire plates', but now interpreted as being produced by secondary radial growth under the lancet and in between the hydrospires. This implies that aboral parts of hydrospires were gradually filled in during life of animal, and were no longer functional. In adult animals hydrospires believed to be functional over about the same length as the hydrospire cleft, through which they could communicate with the exterior.

Anthoblastus stelliformis Wanner, 1924b
Textfigure 32; Pl. XI, figs. 5, 6, 8, 9

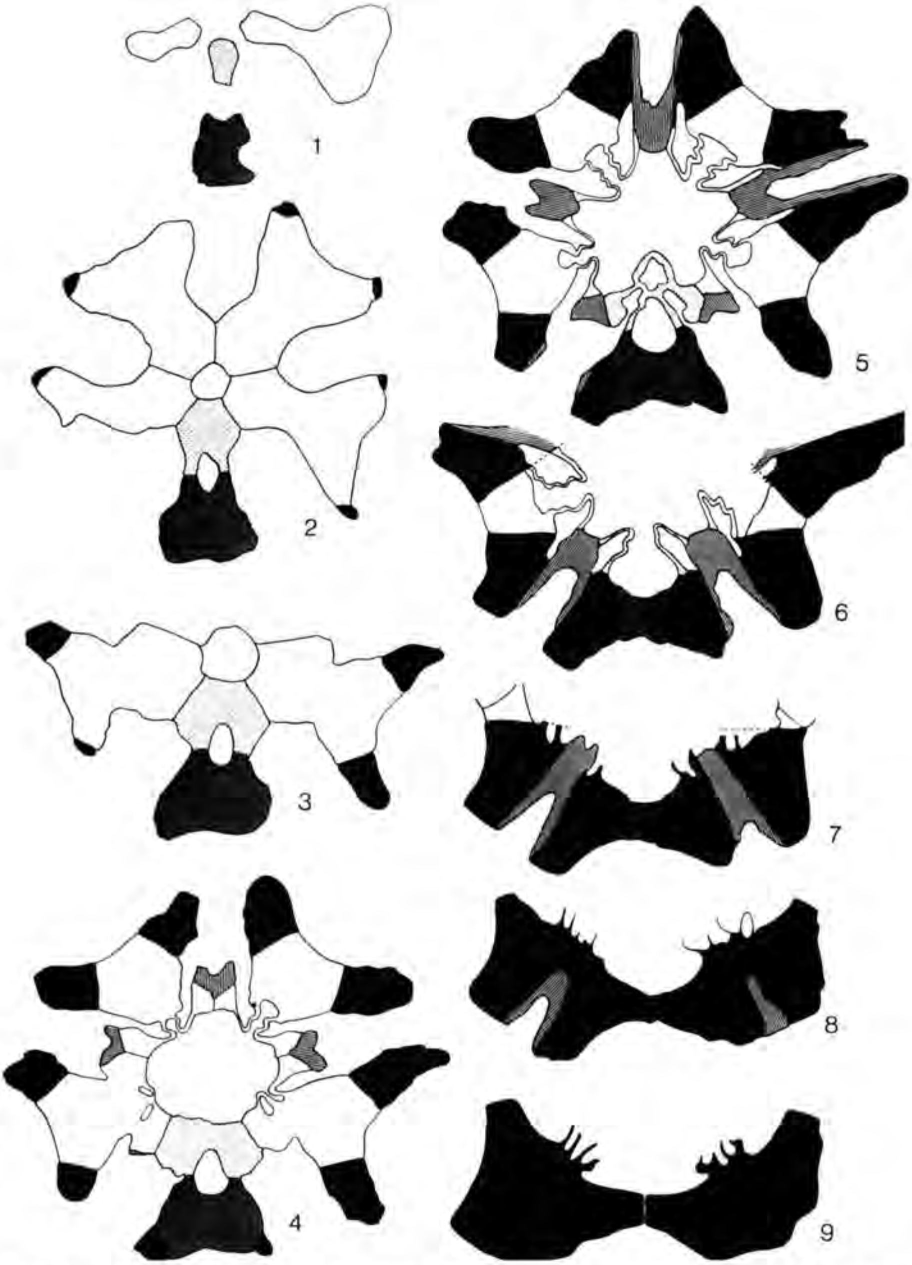
Total height of sectioned specimen 10.2 mm. Upper 4.4 mm, forming hydrospire-bearing vault, sectioned into 50 subsequent transverse peel sections at mean intervals of 0.088 mm. In textfigure 32 nine selected sections are shown.

Theca thick-plated, with pentalobate cross section. Vault high, broadly arcuate. Deltoids conspicuous, rising above peristome (fig. 32.1), with small DR sectors exposed on external surface of theca (fig. 32.2–4). DD sectors strongly developed with interdeltoid suture on external surface of theca, forming peristomial ring (fig. 32.2). No canal systems observed in peristomial ring. Main bodies of deltoids extend internally to 3.19 mm below top of theca (fig. 32.7), not overlapped by radial limbs.

At posterior side 2 anal deltoids: epi- and hypodeltoid. Epideltoid moderately developed, forming part of peristomial ring (figs. 32.2, 3). Epideltoid has two wings which come in contact with hypodeltoid (fig. 32.5) and with posterior radial limbs (fig. 32.6); epideltoid wings hydrospire-forming (figs. 32.5, 6). Body of epideltoid produced into tubelike extension internally (fig. 32.5) inferred to be part of gonoduct. Unknown how gonoduct opened to exterior, probably in anal cavity since external gonopore not observed. Hypodeltoid relatively large, with exposure on external surface of theca (figs. 32.4–8), in contact with epideltoid wings (fig. 32.5) and with posterior radial limbs (figs. 32.5–8), but not overlapped by these.

Ambulacra depressed, not reaching peristome, lanceolate. Lancets in form of elongated scoop, parallel-sided, adorally in contact with deltoids in peristomial ring (fig. 32.4), aborally in contact with radial body (fig. 33.8), and partly underlain by radial material. External surface of lancet strongly concave, produced by strong lateral outgrowth of lancet against radials; hence, lateral contacts of lancets and radials considerable (figs. 32.6–8). Side plates and outer side plates not preserved in sectioned specimen; lancet known to be completely exposed.

Hydrospire structures formed across DR and RD growth sectors. Ten hydrospire groups present, those on *C* and *D* anal sides formed by epideltoid (figs. 32.5, 6) and corresponding posterior radial limbs. No regular hydrospires are formed. In each position a hydrospire sac is formed, bi- or trilobed. Differentiation of sacs into definite hydrospires absent. Entrance to lobed hydrospire sacs by way of short cleft, mostly between deltoids and lancets (figs. 32.4, 5). Hydrospire sacs extend aborally over longer distance than hydrospire cleft does; cleft gradually closed off by secondary calcite. Secondary calcite also deposited by radial under lancet (fig. 32.8).



Textfig. 32. *Anthoblastus stelliformis* Wanner, 1924^{b}. Permian, Timor. Spec. L 8459, Geol. Inst., Univ. Amsterdam. Series of 9 transverse sections resp. from sections numbered 5, 10, 20, 25, 30, 35, 38, 41, and 48, cut resp. 0.95, 1.37, 1.95, 2.26, 2.55, 2.90, 3.19, 3.41, and 4.09 mm below top of theca. All figures × 6. (1) Section above peristome, through conspicuous deltoids. (2, 3) Peristome. (2–5) Composition of anal area; note presence of epi- and hypodeltoid; 5, note base of gonoduct on epideltoid. (4–9) Composition of ambulacral and hydrospire structures; 5, 6, note presence of hydrospires at *C* and *D* anal sides; 6, 7, note scoop-shaped lancet; 8, note radial growth under lancet; 9, aboral end of hydrospires; 7, 8, 9, *C* and *D* radials only. See textfig. 1 for further explanation.

3. Family NYMPHAEOBLASTIDAE

Owing to the lack of material no specimens of the nymphaeoblastids have been sectioned. Nymphaeoblastids are an extremely rare group of blastoids. Only a few species are known; none of these comprises more than a few specimens. Preservation of most all of the nymphaeoblastids is such that the calcitic skeletal material is no longer present. These circumstances have made it impossible to make an anatomical study of this interesting fissiculate family.

4. Family ASTROCRINIDAE

As a monotypic family the general and stable characters of the family cannot be distinguished from the generic characters. Therefore, no longer introductory statement to the anatomical sections of *Astrocrinus* is presented.

Astrocrinus tetragonus (Austin & Austin 1843)

Textfigure 33; Pl. XI, figs. 4, 7; Pl. XV, figs. 1, 3, 6

Total height of sectioned specimen 1.79 mm. Specimen sectioned into 35 subsequent transverse peel sections at mean intervals of 0.05 mm. In textfigure 33 sixteen selected sections are shown.

Thecal shape aberrant, developing both internal and external bilateral symmetry according to axis through *D* radius and *AB* interradius. Bilateral symmetry is secondary and produced by strong modifications at *D* radial side of body. Modifications include: (1) asymmetry of basals, placed in between *C* and *E* radial bodies; (2) reduction of posterior limbs of *C* and *E* radials; (3) reduction of *D* radial, sitting on top of posterior limbs of *C* and *E* radials; (4) modification of *DE* deltoid; and (5) reduction of *D* ambulacrum. Development of bilateral symmetry has produced a stalkless, tetralobed theca, without differentiation into vault and pelvis, in which the 4 regular ambulacra curve around the theca. Internally bilateral symmetry affects composition of hydrospire system and composition of anal area. The sections in textfigure 33 have been oriented in the usual echinoderm way, with *A* radius at upper side of each figure, and *CD* interradius at lower side.

Theca thick-plated with tetralobed cross section. Deltoids large, rhomboidal, with ample exposure on upper side of theca (figs. 33.1, 2). *DE* deltoid modified, with smaller external exposure than other deltoids (figs. 33.2, 3), but with larger internal extent than other deltoids. Deltoids have lips which together form a peristomial ring; interdeltoid suture developed on external surface of theca. Peristomial ring of deltoid lips preserves part of canal system of oral nervous system (figs. 33.3, 4), consisting of a pentagonal ring canal, with angles at contacts with radial nerve canals in lancets. No independent transverse commissures, forming chiasmas over interdeltoid sutures, seem to be present. The pentagonal ring canal and the radial nerve canals meet at the place where deltoids and lancets come in contact (figs. 33.3, 4). A radial nerve trunk is not observed in *D* lancet. Main bodies of deltoids extend internally to 0.70 mm below top of theca (fig. 33.9), except *DE* deltoid which extends to 1.20 mm below top of theca (fig. 33.14). Deltoids not overlapped by radial limbs.

At posterior side 4 anal deltoids: a superdeltoid, two cryptodeltoids, and a hypodeltoid (inferred to have been present). Superdeltoid (figs. 33.1–8) large, forming part of peristomial ring (figs. 33.2–4), bearing part of ring canal (fig. 33.3), forming a ring internally (figs. 33.5–8) inferred to be part of the gonoduct. No external gonopore observed; gonoduct inferred to have opened into anal cavity. Superdeltoid has prong for contact with *C* cryptodeltoid (fig. 33.5). Cryptodeltoids internal, asymmetrical, and of unequal development. *D* cryptodeltoid very small, almost rudimentary (figs. 33.7, 8); *C* cryptodeltoid large, extending to 1.02 mm below top of theca (fig. 33.13). Both cryptodeltoids adorally in contact with superdeltoid, but not meeting laterally along aboral edge of superdeltoid. *C* cryptodeltoid in contact with modified posterior limb of *C* radial, *D* cryptodeltoid in contact with prong of *D* radial (figs. 33.7, 8). Cryptodeltoids form hydrospires. Hypodeltoid not present, but inferred to have been present during life since there is place for one (figs. 33.3, 4). Anus passes externally between super- and hypodeltoid.

Radials five, of unequal development. *A* and *B* radials normally developed, *C* and *E* radials with reduced posterior limbs (figs. 33.9–14) which do not form hydrospires. *D* radial small, hydrospire-forming, in contact with elongate basal (figs. 33.14, 15), sitting on limbs of *C* and *E* radials.

Ambulacra five, four of which are regular and curving around theca; the fifth (*D* amb.) reduced in size, horizontal in position. Ambulacra not reaching peristome. Regular lancets curved lengthwise, parallel-sided, adorally in contact with deltoid lips in peristomial ring (figs. 33.2–4), aborally in contact with radial body (fig. 33.14). External surface of lancet strongly beveled for reception of side plates. Lateral surface of

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Textfig. 33. *Astrocrinus tetragonus* (Austin and Austin, 1843). L. Carb., Invertiel, Scotland. Spec. 2378 Royal Scottish Museum. Series of 16 transverse sections resp. from peels numbered 33, 31, 30, 28, 27, 26, 25, 24, 21, 20, 19, 18, 16, 14, 8, and 7, cut resp. 0.10, 0.21, 0.27, 0.37, 0.42, 0.47, 0.52, 0.57, 0.72, 0.77, 0.82, 0.87, 1.02, 1.17, 1.54, and 1.57 mm below top of theca. All figures × 15. (1–3) Peristomial area, complete sections; 3, note canals for nervous system. (4–8) Composition of anal area and structures allied to reproductive system; note presence of superdeltoid and two cryptodeltoids; 7, 8, posterior parts of sections only. (5–14) Composition of hydrospires and ambulacral structures; note two canals in lancets; 7, note simple hydrospire fold at *D* anal side; 9, 10, note single hydrospire fold at *C* anal side; 10, 11, posterior parts of sections only; 12, 13, 14, note *C* and *E* radials with modified posterior limbs, note small *D* radial. (15–16) Aboral parts of radials, showing one of the basals. See textfig. 1 for further explanation.


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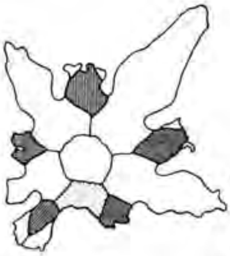
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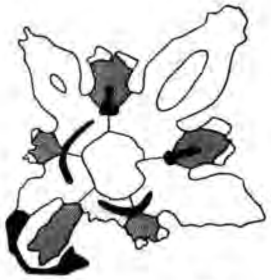
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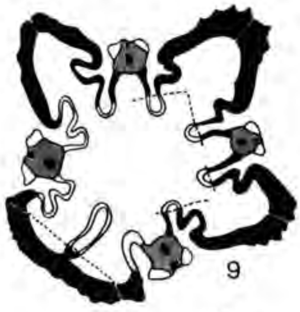
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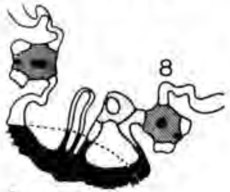
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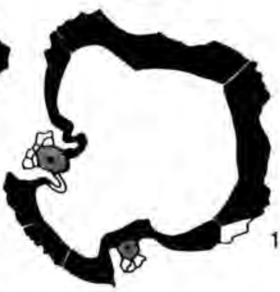
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lancet nowhere in contact with radials and deltoids (figs. 33.6–14). Internal surface of lancets flat to slightly convex where bordering thecal cavity, in contact with admedial hydrospires. *D* lancet reduced in size, straight, in horizontal position, resting on prong of *D* radial (fig. 33.4), with concave internal surface. Regular lancets bear radial nerve canals (figs. 33.4–14) in the center of the plates; a radial nerve canal is not observed in the *D* lancet (fig. 33.3). Regular lancets bear a second canal of smaller diameter than central nerve canal, and situated just beneath exposed median part of lancet. This canal is not observed in aboral part of lancet where side plates cover the lancet, (fig. 33.11–19). Termination of this canal in oral direction unknown. Canal interpreted to lodge part of radial water vessel.

Side plates and outer side plates present on all five ambulacra. In aboral part of ambulacra side plates are in lateral contact along median line of ambulacrum (figs. 33.13, 14). Lancet exposed over $\frac{2}{3}$ of its length except in *D* ambulacrum. Side plates and outer side plates not in lateral contact with radials and deltoids.

Regular hydrospires formed across RD sutures. Ten hydrospire groups present, those on *C* and *D* anal sides formed by cryptodeltoids (figs. 33.7–13). Regular groups have 2 hydrospire folds, but at *C* and *D* anal sides only one fold is present; number of anal hydrospires reduced. At left side of *D* lancet only one fold is present (figs. 33.5–10); number of hydrospires reduced at both sides of *D* ambulacrum which is affected by bilateral symmetry. Single *C* anal hydrospire well developed (figs. 33.7–13), entirely built up by *C* cryptodeltoid, without cooperation of modified posterior limb of *C* radial (fig. 33.13). Single *D* anal hydrospire very small, almost rudimentary (fig. 33.7), built up by *D* cryptodeltoid and two prongs from *D* radial. Single hydrospire fold at left side of *D* ambulacrum well developed, buit up by *DE* deltoid and two prongs from *D* radial. Modified *DE* deltoid is building two hydrospire folds at posterior side of *E* ambulacrum (figs. 33.9–13) without cooperation of modified posterior limb of *E* radial. Modified posterior limbs of *C* and *E* radials not hydrospire-forming; their function is taken over by *C* cryptodeltoid and modified *DE* deltoid. Hydrospires thick-walled, not differentiated into thin hydrospire lamellae and inflated hydrospire ducts. If two folds per group present, admedial fold better developed than abmedial one. Hydrospires conjoined Entrance to hydrospires by way of hydrospire clefts extending full length of ambulacra.

5. Family NEOSCHISMATIDAE

Serial sectioning of the neoschismatids has been incomplete, especially for the Permian genera from Australia. This is due to the fact that these genera are relatively rare, or composed of fragmentary material. Permian neoschismatid species are also fairly rare elsewhere. The only genera studied are *Hadroblastus* and *Timoroblastus*.

Anatomical sections of neoschismatids appear to be very different from those in the phaenoschismatids and the orophocrinids.

The deltoids are well developed in the neoschismatids, in near-horizontal position, fully exposed, and forming a large part of the upper or vault region of the theca. DD sectors are no longer incipient. This implies that these sectors no longer form a narrow peristomial ring with the epideltoid, such as in the phaenoschismatids and the orophocrinids. The total peristomial area formed by DD sectors is wide. Long interdeltoid sutures may be present. DR sectors of the deltoids are larger than the DD sectors.

The deltoids usually form a crest which slopes downward. But the deltoids typically do not rise above the peristome and are not involved in the formation of interambulacral pyramids. The sections above the peristome in *Timoroblastus coronatus* (textfig. 36) show that the deltoids of that species do rise above the peristome. This is due to the fact that in *Timoroblastus* there is deposition of calcite on the outer surface of the deltoids. The elevated deltoids are not to be mistaken for interambulacral pyramids as in the phaenoschismatids.

The radials of the neoschismatids are still large plates, forming mostly the sides of the theca. The RD sectors usually do not reach a large size.

The growth pattern for deltoids and radials in the neoschismatids implies that the form of the theca is cylindrical to cup-shaped, with a low vault. The transverse sections through the neoschismatids are either rounded or pentagonal.

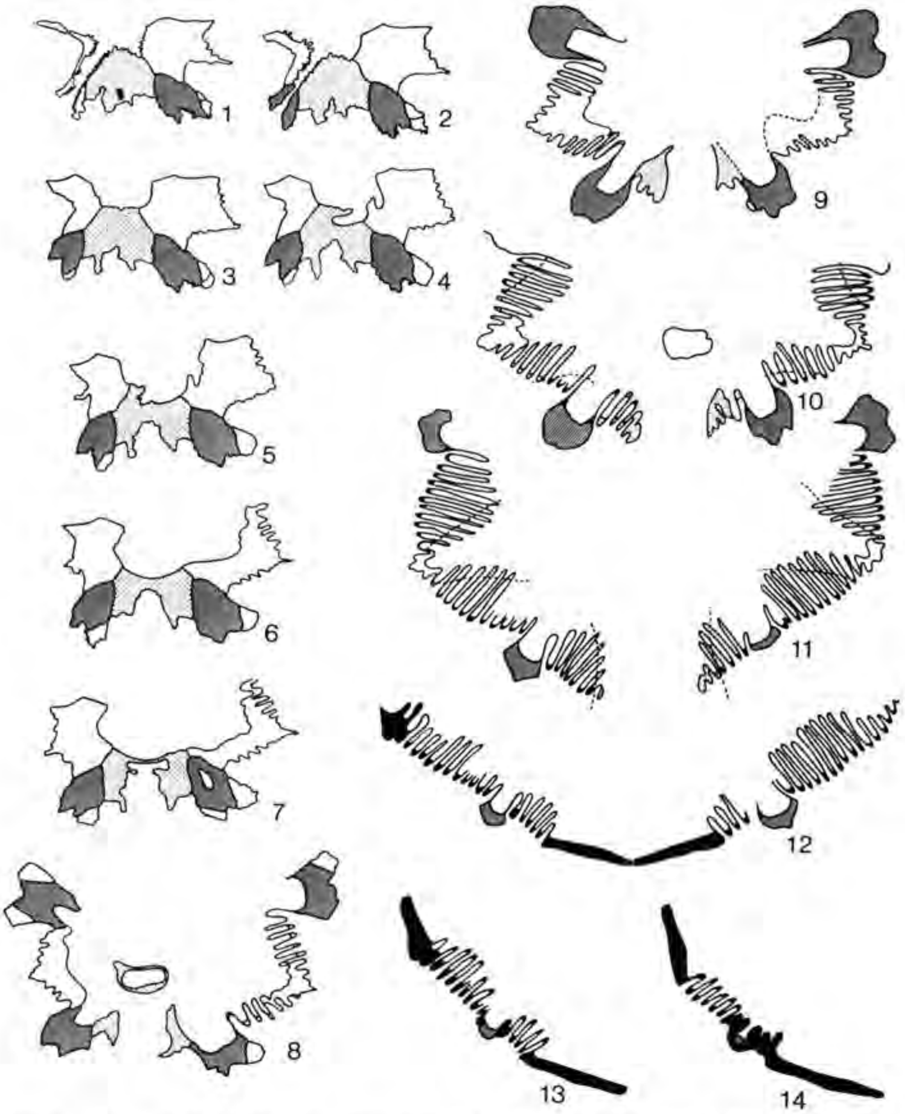
The ambulacral structure of the neoschismatids is not essentially different from other families. Ambulacra are linear to lanceolate, and may be removed from peristome in some later members. The ambulacra may lie in shallow depressions. Lancets are elongate and extend over the entire length of the ambulacrum. The oral end of the lancet abuts against the DD sectors, the aboral end is supported by the central part of the radial body.

Hydrospires in neoschismatids occur in ten groups (as so far known). The hydrospire folds are typically numerous, and occupy the full width of the RD suture. All the slits are exposed, but in some forms they are very short, suggesting that the ends of the slits have been gradually filled in by secondary calcite.

Hadroblastus convexus Fay, 1962
Textfigure 34; Pl. XVI, figs. 8, 10–13

Two specimens sectioned. Specimen illustrated figs. 34.1–8 is 10.7 mm high. Upper 4.95 mm sectioned into 58 subsequent transverse sections, eight of which are shown in textfigure 34, left hand column. Specimen illustrated figs. 34.9–14 is 12.3 mm high. Upper 5.55 mm sectioned into 33 subsequent transverse peel sections, six of which are shown in textfigure 34, right hand column.

Theca thin-plated, with broadly pentagonal cross section. Vault of about



Textfig. 34. *Hadroblastus convexus* Fay, 1962. Miss. Lake Valley Fm., Lake Valley, New Mexico, USA. Spec. USNM loc. 3027 (figs. 1–8), spec. USNM unregistered (figs. 9–14). First series of 8 transverse sections resp. from peels numbered 10, 11, 13, 14, 15, 17, 20, and 27, cut resp. 0.45, 0.50, 0.60, 0.65, 0.70, 0.80, 0.95, and 1.35 mm below top of theca. Second series of 6 transverse sections resp. from peels numbered 12, 14, 19, 24, 26, and 28, cut resp. 1.06, 1.64, 2.72, 3.85, 4.31, and 4.64 mm below top of theca. All figures × 5.5. (1–8) Composition of anal area and structures allied to reproductive system; note presence of epideltoid; posterior part of sections only; 1, note gonopore; 8, note base of gonoduct (compare with fig. 10). (9–14) Composition of ambulacral and hydrospire structures; note presence of hydrospires at *C* and *D* anal sides; 14, aboral end of hydrospires and lancet; 13, 14, *C* and *D* radials only. See textfig. 1 for further explanation.

equal height as pelvis. Wide and shallow ambulacral sinuses present.

Deltoids with large DR sectors and hardly developed DD sectors, both exposed at upper side of vault. DD sectors with small interdeltoid suture on external surface of theca (figs. 34.1, 2), forming peristomial ring (figs. 34.3–7). No canal systems observed in peristomial ring. Main bodies of deltoids extend internally to 2.72 mm below top of theca (fig. 34.11), not overlapped by radial limbs. Radial limbs hardly developed, not bent inward.

At posterior side two anal deltoids: epideltoid and hypodeltoid. Latter not preserved in sectioned specimens, but known to be present in other specimens. Epideltoid large, forming part of peristomial ring (figs. 34.3–7). Epideltoid has two limbs which come in contact with hypodeltoid and with posterior radial limbs; epideltoid limbs hydrospire-forming (figs. 34.9–11). Body of epideltoid produced into tubelike extension internally (figs. 34.8, 10), inferred to be part of gonoduct. Gonoduct opening via gonopore in epideltoid (figs. 34.1, 2) Hypodeltoid not preserved, but has been present in open spot between epideltoid limbs in figs. 34.7–9, where it contributes to lateral wall of theca.

Ambulacra slightly inclined, sublanceolate, not reaching peristome, situated in slightly developed, wide and shallow ambulacral sinuses. Lancets not parallel-sided, narrowing in aboral direction; adorally in contact with deltoids in peristomial ring (figs. 34.1–7), aborally in contact with radial body (fig. 34.14), internally in contact with admedial hydrospire lamellae (fig. 34.10). External surface of lancet grooved (figs. 34.4–8), and strongly beveled for reception of side plates. Internal surface of lancets concave where bordering thecal cavity. Lancets not in lateral contact with radials and deltoids. Side plates present in specimen illustrated figs. 34.1–8. Side plates situated at outer lateral surface of lancet, not in contact laterally along median line of ambulacrum; lancet exposed. Median exposed surface of lancet bears ambulacral groove, which continues adorally on interdeltoid suture. Interdeltoid suture bears minor grooves of ambulacrum (figs. 34.1, 2). Side plates not in lateral contact with radials and deltoids.

Hydrospires formed across RD sutures. Ten hydrospire groups present, those on *C* and *D* anal sides formed by epideltoid (figs. 34.9–11) and corresponding posterior radial limbs (figs. 34.11–13). In regular groups number of hydrospires is variable from 12 to 15 (fig. 34.12) in sectioned specimen; in *C* and *D* anal fields number of hydrospires is 7 or 8. Number of anal hydrospires is reduced. Anal hydrospires of about equal length as regular hydrospires. Hydrospires short, not extending deeply into thecal cavity, placed parallel to one another, and parallel to longer axis of ambulacrum, not differentiated into hydrospire lamellae and inflated hydrospire ducts (figs. 34.11, 12). Hydrospire slits completely exposed on upper side of vault in shallow ambulacral sinuses. Entrance to hydrospires is completely direct by way of exposed hydrospire slits.

Hadroblastus whitei (Hall, 1861)

Textfigure 35; Pl. XVI, figs. 9, 14, 15; Pl. XVII, figs. 1–15

Total height of sectioned specimen 8.30 mm. Upper 3.61 mm, forming hydrospire-bearing vault, sectioned into 36 subsequent transverse peel sections at mean intervals of 0.10 mm. In textfigure 35 ten selected sections are shown.

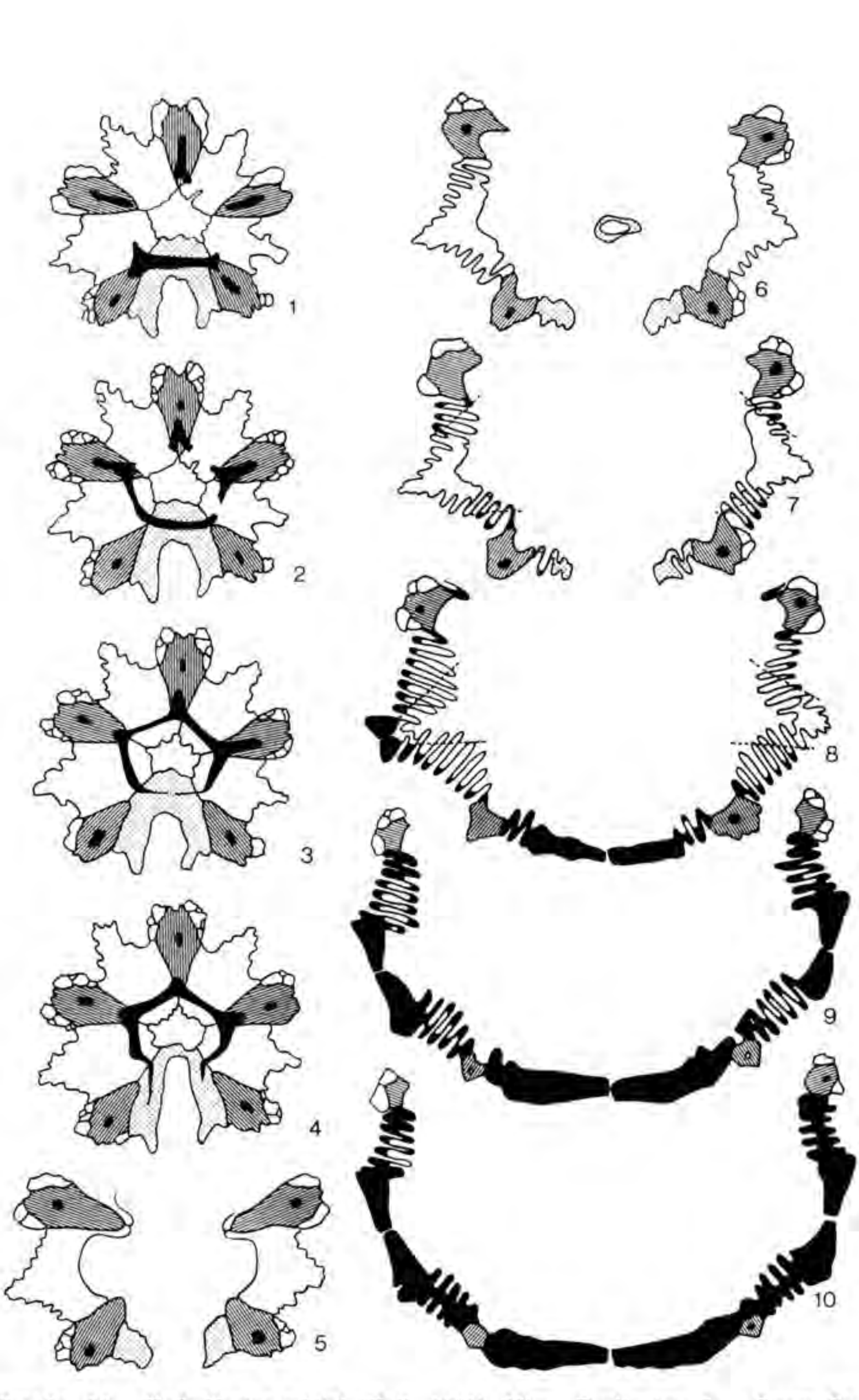
Theca relatively thick-plated, with decagonal to rounded cross section. Vault of about equal height as pelvis. Ambulacral sinuses present, but incipient.

Deltoids with moderately developed DR sectors and relatively well-developed DD sectors, both exposed on upper side of vault. DD sectors with short interdeltoid suture on external surface of theca, forming peristomial ring (figs. 35.1–4). Canal system of oral nervous system preserved in peristomial ring (figs. 35.1–4), consisting of pentagonal ring canal in deltoid lips with angles at contacts with radial nerve canals in lancet. No independent transverse commissures formed across interdeltoid sutures; no chiasmas present. Angles of ring canal situated at contacts of lancets with deltoids. At posterior side ring canal sends two short branches into epideltoid wings (fig. 35.4). Main bodies of deltoids extend internally to 2.15 mm below top of theca (fig. 35.8), not overlapped by radial limbs. Radial limbs moderately developed, not bent inward.

At posterior side two anal deltoids: epideltoid and hypodeltoid. Latter not preserved in sectioned specimen, but known to be present in other specimens. Epideltoid large, forming part of peristomial ring (figs. 35.1–4). Epideltoid has two limbs which come in contact with hypodeltoid and with posterior radial limbs; epideltoid limbs hydrospire-forming (fig. 35.7). Body of epideltoid produced into tubelike extension internally (fig. 35.6), inferred to be part of gonoduct. Uncertain how gonoduct opened into exterior; no gonopore observed. Hypodeltoid not preserved, but was present during life in open spot between epideltoid limbs (figs. 35.4–7), where it contributed to lateral wall of theca. Known from other specimens.

Ambulacra moderately inclined, lanceolate, not reaching peristome, situated in incipient ambulacral sinuses. Lancets not parallel-sided, narrowing in aboral direction; adorally in contact with deltoids in peristomial ring (figs. 35.1–4), aborally in contact with radial body (fig. 35.10), internally in contact with admedial hydrospire lamellae (figs. 35.7, 8). External surface of lancet strongly beveled for reception of side plates (figs. 35.5, 6). Internal surface of lancets concave where bordering thecal cavity. Lancets not in lateral contact with radials and deltoids. Radial nerve trunks of oral nervous system traverse full length of lancets (figs. 35.1–10).

Side plates and outer side plates present, situated at outer lateral surface of lancet; side plates not in lateral contact along median line of ambulacrum (figs. 35.2–8), except at aboral extremity (fig. 35.9); lancet



Textfig. 35. *Hadroblastus whitei* (Hall, 1861). Miss., Burlington Ls., Green Co., Missouri, USA. Spec. UMMP, Loc. 1966/M-88. Series of 10 transverse sections resp. from peels numbered 7, 8, 9, 10, 18, 24, 26, 29, 33, and 34, cut resp. 0.29, 0.33, 0.37, 0.40, 0.80, 1.30, 1.56, 2.15, 2,91, and 3.12 mm below top of theca. All figures × 7. (1–4) Composition of peristomial area, note presence of nerve canals (black) in deltoids and lancets; complete sections. (1–7) Composition of anal area and structures allied to reproductive system; note presence of epideltoid; 6, 7, note base of gonoduct; 5, 6, 7, posterior part of sections only. (6–10) Composition of ambulacral and hydrospire structures; note presence of hydrospires at C and D anal sides; 10, aboral end of hydrospires and lancets; posterior part of sections only. See textfig. 1 for further explanation.

exposed over most of its length. Side plates and outer side plates in lateral contact with deltoids (figs. 35.1–5), but not with radials.

Hydrospires formed across RD sutures. Sutures represented in textfigure 35 by broken line. Ten hydrospire groups present, those on *C* and *D* anal side formed by epideltoid (figs. 35.6, 7) and corresponding posterior radial limbs (fig. 35.8). In regular groups number of hydrospires is 7 or 8 in sectioned specimen (fig. 35.8); in *C* and *D* anal fields number of hydrospires is 2. Number of anal hydrospires strongly reduced. Anal hydrospires much shorter than regular hydrospires. Hydrospires short, not extending deeply into thecal cavity, placed parallel to one another, and parallel to longer axis of ambulacra. Hydrospires not differentiated into hydrospire lamellae and inflated hydrospire ducts (fig. 35.8). Hydrospire slits completely exposed on upper side of vault. Entrance to hydrospires is completely direct by way of exposed hydrospire slits.

Timoroblastus coronatus Wanner, 1924[a]

Textfigure 36; Pl. XXIII, figs. 2, 3, 5, 7; Pl. XXVI, figs. 1, 4, 5, 8–11; Pl. XXVII, figs. 1, 3–5, 9

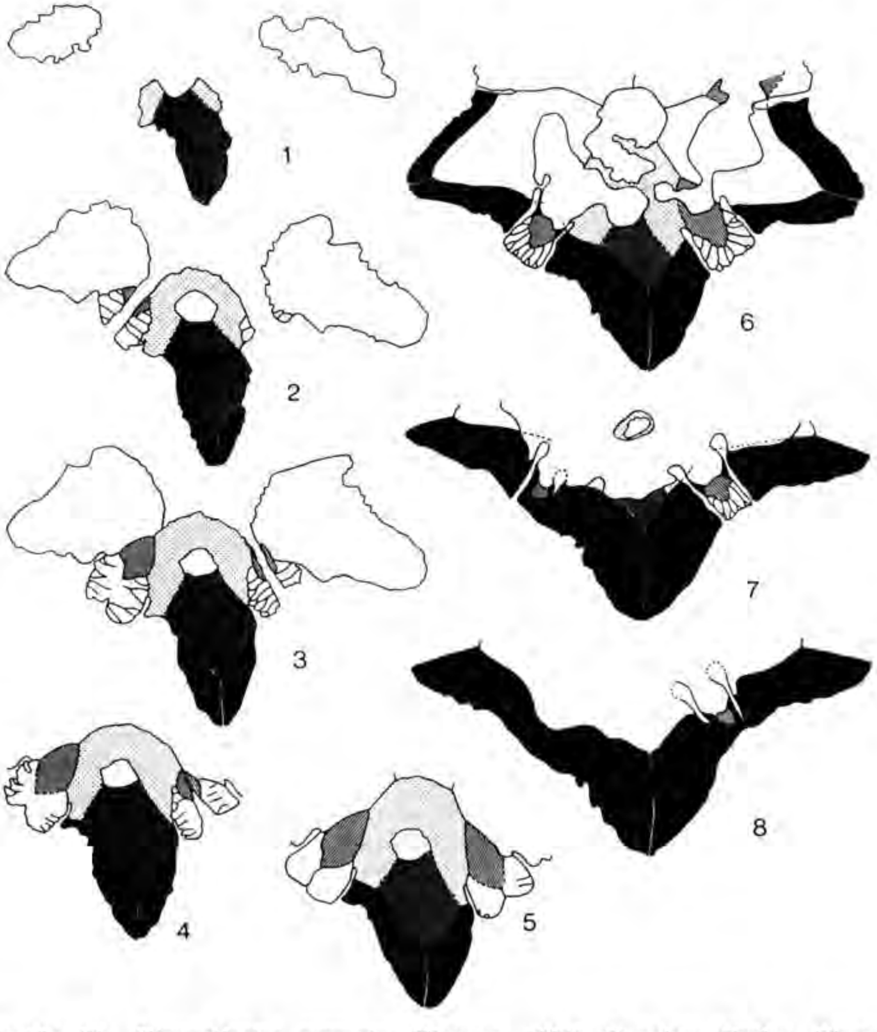
Total height of sectioned specimen 14.5 mm. Upper 4.64 mm sectioned into 36 subsequent transverse sections at mean intervals of 0.13 mm. In textfigure 36 eight selected sections are shown.

Theca boxlike, thick-plated, with bottom formed by basals, sides formed by radials and upper surface formed by deltoids. Cross sections of theca pentagonal, with angles of pentagon at interradial sutures.

Deltoids large, conspicuous, rising above peristome (figs. 36.1, 2), in near horizontal position, with subequal DD and DR sectors. DD sectors with interdeltoid suture on upper surface of theca, forming peristomial ring. No canal systems observed in peristomial ring. RD sutures sloping inward towards thecal cavity. Radials square, with small RD sectors placed at angle with RR sectors, forming an ill-defined ambulacral sinus with DD sectors.

At posterior side two anal deltoids: epideltoid and hypodeltoid. Epideltoid large, forming part of peristomial ring (figs. 36.3, 4). Epideltoid has two limbs which come in contact with hypodeltoid (figs. 36.1–6) and with posterior radial limbs (figs. 36.4–7); epideltoid limbs hydrospire-forming (fig. 36.6). Body of epideltoid produced into tubelike extension internally (figs. 36.6, 7), inferred to be part of gonoduct. Hypodeltoid large, in contact with epideltoid and posterior radial limbs. Suture between hypodeltoid and posterior radial limbs sloping inward towards thecal cavity. Hypodeltoid contributing to lateral wall of theca. Anus passes externally between epi- and hypodeltoid (figs. 36.2–5), but is mainly situated in notch on epideltoid. Anal cavity (fig. 36.6, lower cavity) internally separated from gonoduct (fig. 36.6, upper cavity) by septum. Gonoduct probably opened into rectum at level below anal opening.

Ambulacra small, petaloid, inclined, and removed from peristome (Pl. XXXIV, fig. 2). Lancets elongate rhombiform (fig. 36.4) with rounded aboral edge. Adoral parts of lancet in contact with deltoids (figs. 36.2–5), aboral part of lancet in contact with radial body (fig. 36.8), internally in contact with admedial hydrospire lamellae (figs. 36.6, 7). Lancets bordering thecal cavity only over relatively small area (figs. 36.6, 7).



Textfig. 36. *Timoroblastus coronatus* Wanner, 1924[a]. Permian, Basleo, Timor. Spec. Inst. Earth Sci., Free Ref. Univ., Amsterdam. Series of 8 transverse sections resp. from peels numbered 7, 9, 10, 12, 19, 26, 28, and 30, cut resp. 1.14, 1.74, 1.99, 2.09, 2.44, 3.04, 3.44, and 3.84 mm below top of theca. All figures × 4, showing posterior part of section, unless otherwise stated. (1–3) Above peristome, through deltoids. (4–5) Peristome, anal side and *C* and *D* ambulacra only. (1–7) Composition of anal area; note epi- and hypodeltoid; 7, note gonoduct. (2–6) Composition of ambulacral structures. (6–8) Composition of hydrospire structures, note *C* and *D* anal hydrospires. See textfig. 1 for further explanation.

Side plates and outer side plates present. One outer side plate per side plate, alternating with side plates. In smaller specimens side plates and outer side plates wedge-shaped, arrayed in a parabolic arc on aboral part of rhombic lancet. In larger specimens (such as the sectioned specimen) more side plates and outer side plates added, which, upon outgrowth of the lancet, come to rest on aboral part of lancet. In adoral part of ambulacrum side plates not in lateral contact along median line of ambulacrum (figs. 36.2–4), exposing adoral part of lancet in relatively deep ambulacral tract. Ambulacral tract continues adorally on interdeltoid suture. In aboral part of ambulacrum (figs. 36.6, 7) side plates and outer side plates completely cover lancet. Their wedge-shape and arrayment in parabolic arc is evident from fig. 36.6. Side plates are in lateral contact with deltoids (figs. 36.2–4), but not with radials (figs. 36 6, 7).

Hydrospires present across RD suture, but almost exclusively formed by RD growth sectors. Ten hydrospire groups present, those on *C* and *D* anal sides formed by epideltoid (fig. 36.6) and corresponding posterior radial limb (figs. 36.7, 8). Only one hydrospire fold present in every one of ten groups. Number of anal hydrospires not reduced. Anal hydrospires of equal development as regular hydrospires. Hydrospires extending full length of ambulacra, but not extending deeply into thecal cavity. Terminal hydrospire ducts differentiated, but their parallel hydrospire lamellae very short, or almost absent (figs. 36.7, 8). Communication of hydrospires with external medium by way of slits or clefts along both sides of ambulacrum, and separating ambulacra from radials. Clefts unite at aboral part of ambulacra. Adorally clefts separate adoral part of ambulacra from deltoids and may deviate from the ambulacra, being built exclusively of deltoid material.

6. Family Codasteridae

Serial sectioning of the codasterids has been fairly complete. With the exception of *Tympanoblastus*, all the known genera have received anatomical study.

Anatomical sections of the codasterids appear to be very different from those of the phaenoschismatids and the orophocrinids, and rather have some similarity to those of the neoschismatids.

The deltoids in the codasterids are well developed, in horizontal position, fully exposed, and forming a flat roof for the theca. DD sectors are large and may even be larger than the DR sectors. This implies that the DD area, surrounding the peristome, is very wide, and has long interdeltoid sutures on the upper surface of the theca. RD sectors of the deltoids are smaller than the DD sectors and may, in some cases, be very small indeed.

The deltoids may possess a subdued crest, but do not rise above the peristome. They are not involved in the formation of interambulacral pyramids and ambulacral sinuses. The sections above the peristome in *Nannoblastus pyramidatus* (textfig. 42) show that the deltoids do rise above the peristome. This is due to the fact that in *Nannoblastus* there is deposition of calcite on the outer surface of the deltoids. These elevated deltoids are not to be mistaken for interambulacral pyramids as in the phaenoschismatids.

The radials of codasterids are relatively large plates, mostly forming the sides of the theca. RD sectors are not highly developed, and an RA growth front may be present.

The growth pattern for deltoids and radials in the codasterids implies that the overall thecal form is cup-shaped with a flat roof. The transverse sections through codasterids are either rounded or pentagonal.

The ambulacral structures of the Permian codasterids are different from all other families. Ambulacra are removed from peristome, short, petaloid or rhombiform, with only a few side plates and brachioles. The lancet is exposed and rhombiform, and in *Pterotoblastus* does not support all the side plates. The plate is resting on facets in the interdeltoid suture, and on the central part of the radial body. It has only a small internal contact with the thecal cavity.

Hydrospire structures in codasterids are different from the phaenoschismatids and the orophocrinids, but have similarity with those in the neoschismatids. Typically there are only 8 groups of hydrospires. The hydrospires are few in number, and in later forms do not occupy the full width of the RD suture. All the slits are exposed. In later members, with reduced number of hydrospire slits, the slits need not be placed parallel to the longer axis of the ambulacrum.

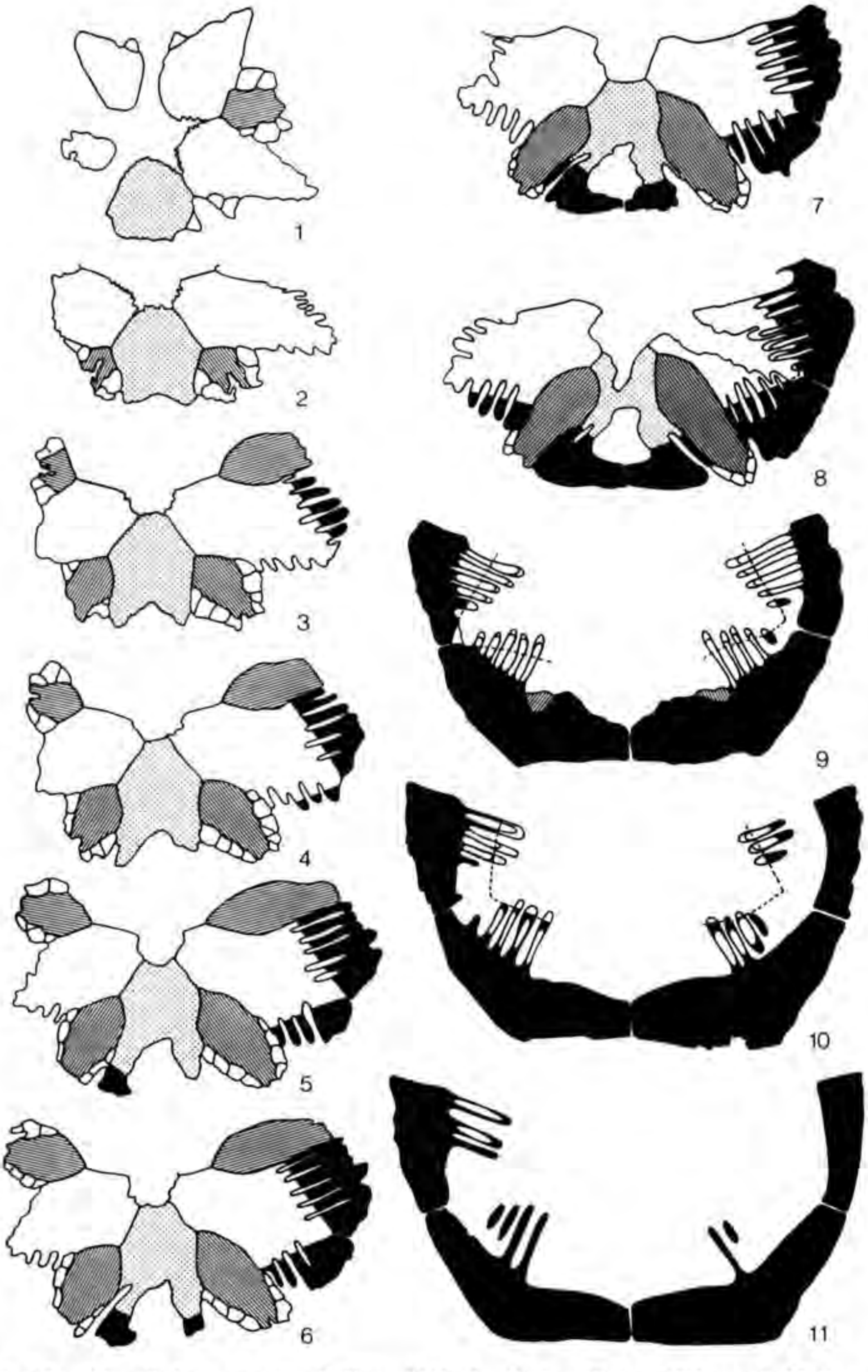
In *Codaster* the hydrospire slits are in a horizontal position, and the folds are hanging down in the thecal cavity in an almost vertical direction. This means that our horizontal transverse sections from top to bottom of theca, first cut the hydrospire slits and then the hydrospire folds. Only vertical longitudinal sections of *Codaster* would provide complete sections of the hydrospire folds in relation to the rest of the body wall. Transverse sectioning has been preferred however, in order to provide directly comparable information on overall body form, interrelations of main thecal elements, etc. Longitudinal sectioning would not have provided this sort of information.

Codaster acutus M'Coy, 1849

Textfigure 37; Pl. XXVI, figs. 2, 3, 6, 7; Pl. XXVII, figs. 2, 6–8;
Pl. XXVIII, figs. 1, 2, 4, 8, 9

Total height of sectioned specimen 11.3 mm. Upper 3.1 mm of theca sectioned into 32 subsequent transverse peel sections at mean intervals of 0.096 mm. In textfigure 37 eleven selected sections are shown.

Theca cup shaped, relatively thick-plated. Sides of theca formed mainly by radials; vault low to flat, formed mostly by deltoids, which are in subhorizontal position. Cross section of theca rounded pentagonal.



Textfig. 37. *Codaster acutus* M'Coy, 1849. L. Carb., Viséan (D2-zone), Malham, Yorkshire, England. Spec. Inst. Earth Sci., Free Ref. Univ., Amsterdam. Series of 11 transverse sections resp. from peels numbered, 6, 10, 12, 14, 16, 18, 20, 23, 26, 28, and 30, cut resp. 0.25, 0.45, 0.55, 0.65, 0.75, 0.85, 0.95, 1.12, 1.40, 2.00, and 2.43 mm below top of theca. All figures × 7, showing posterior parts of sections. (1–8) Composition of anal area; note presence of single epideltoid. (3–8) Composition of ambulacral structures; note exposure of lancet. (3–11) Composition of hydrospire system; 3, note hydrospire slits; 7, 8, note incipient hydrospire folds at *C* and *D* anal side; 9, note absence of regular hydrospire groups at *C* and *D* anal sides. See textfig. 1 for further explanation.

Deltoids completely exposed on upper surface of theca, with hexagonal outline in cross section (figs. 37.3, 4). Deltoids with faint crest and moderately developed DD sectors. Latter with short interdeltoid suture on external surface of theca (figs. 37.1, 2), separating ambulacra from peristome. DD sectors form larger peristomial area, but not a strict peristomial ring. No canal systems observed in peristomial area of deltoids. DR sectors well developed, broadly in contact with lancets and radials. Radial limbs slightly developed, not bent inward, not overlapping deltoids. RD suture sloping strongly inward toward thecal cavity.

At posterior side one anal deltoid: an epideltoid. Epideltoid large, with body and two short limbs. Epideltoid body forming part of larger peristomial area (figs. 37.2–6). Epideltoid limbs in contact with posterior radials (figs. 37.5–8), may be engaged in hydrospire formation. Epideltoid not observed to form any structures allied to reproductive system. Gonopore and gonoduct unknown. Hypodeltoid absent. Anus passes externally between posterior radial limbs and epideltoid (figs. 37.7, 8).

Ambulacra well developed, lanceolate, slightly removed from mouth, and in subhorizontal position. Lancets elongate rhombiform in plan view (figs. 37.6–8) with rounded aboral edge. Lancets adorally in contact with deltoids, aborally with radial bodies (fig. 37.9), bordering thecal cavity internally. External surface of lancet exposed (figs. 37.2–7), except at aboral extremity (fig. 37.8, *C* amb.). Side plates present, placed at outer lateral side of lancets, not in contact along median line of ambulacrum. Adorally side plates always in contact with deltoid (figs. 37.1–5); laterally they may come in contact with radials (figs. 37.6–8). Ambulacral tract situated in groove (figs. 37.6–8) on exposed surface of lancets, and extending over interdeltoid suture to contact mouth. Interdeltoid suture and adoral edge of deltoids provided with ambulacral lobe and furrow structure (fig. 37.1).

Hydrospires formed across full width of RD sutures. Eight regular hydrospire groups present, and single, incipient hydrospire folds at both *C* and *D* anal sides in sectioned specimen (figs. 37.7, 8). In regular groups number of hydrospires is 5 in sectioned specimen (figs. 37.7–9). Regular hydrospires placed parallel to one another, and subparallel to longer axis of ambulacra; differentiated into hydrospire lamellae (fig. 37.9), and inflated hydrospire ducts (fig. 37.10, note wider distance between sides of hydrospires than in fig. 37.9); descending to ca. 3 mm below top of theca, and hanging freely in thecal cavity. Hydrospires open through hydrospire slits (figs. 37.3, 8), all of which are completely exposed on upper side of theca. Hydrospire folds at *C* and *D* anal sides incipient, much shorter than regular hydrospires, not pendent in thecal cavity, but developed as superficial folding of thecal wall (compare *D* side of epideltoid in fig. 37.8 with corresponding place in fig. 37.9). Note complete absence of anal hydrospires at level of sections in figs. 37.9–11. Entrance to hydrospires is completely direct by way of exposed hydrospire slits.

Angioblastus variabilis Wanner, 1931

Textfigure 38; Pl. XXVIII, figs. 3, 6; Pl. XXIX, fig. 14; Pl. XXX, figs. 1–4, 6–9, 12

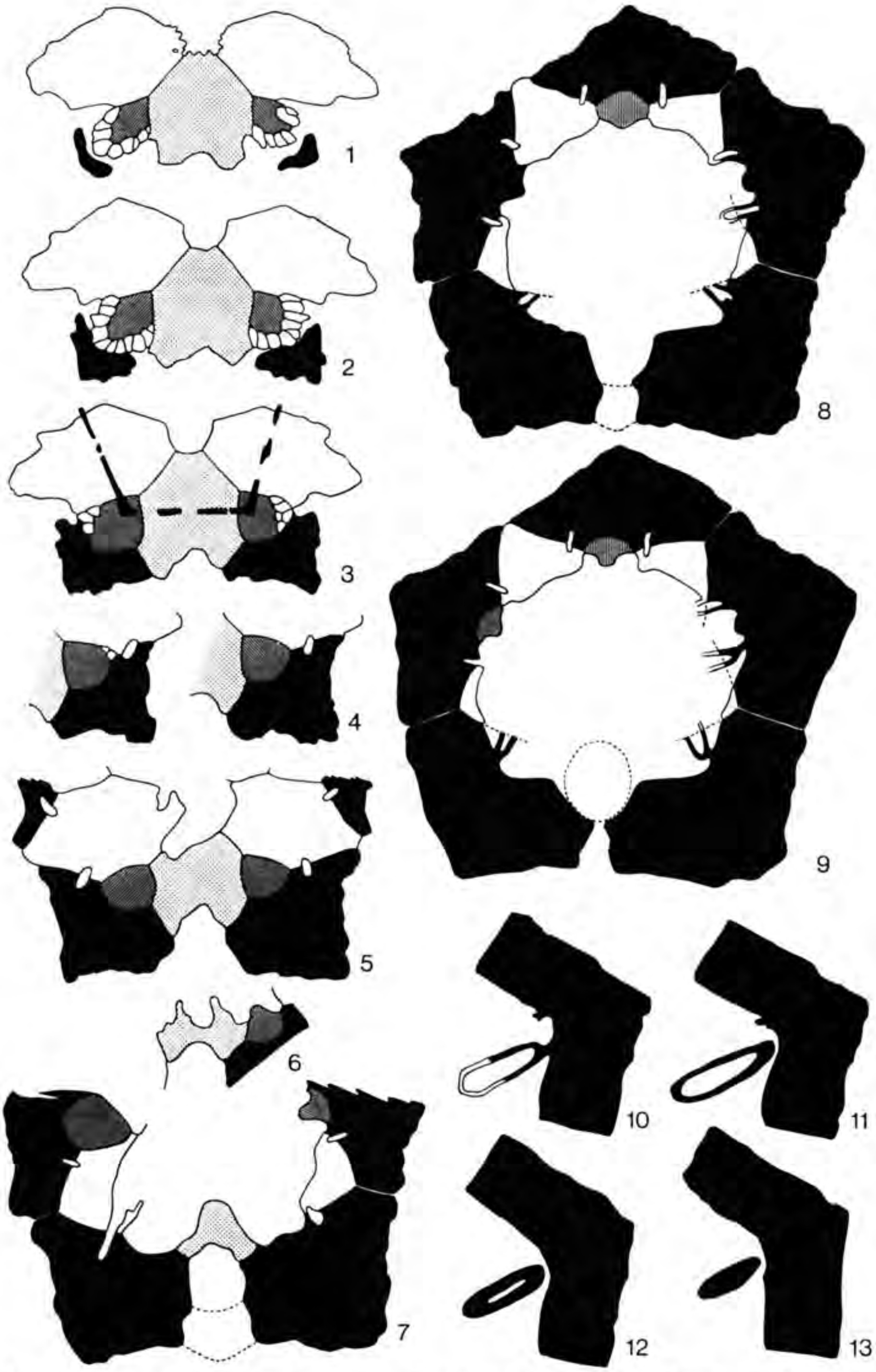
Total height of sectioned specimen 5.19 mm. Upper 1.99 mm of theca sectioned into 40 subsequent transverse peel sections at mean intervals of 0.05 mm. In textfigure 38 thirteen selected sections are shown.

Theca wide, cup shaped, thick-plated. Sides of theca swollen, formed by radials; vault low and flat, constricted, formed mainly by deltoids, which are in horizontal position. Cross section of theca pentagonal.

Deltoids completely exposed on upper side of theca, with hexagonal outline (figs. 38.1–3). Deltoids conspicuous, with subequal DD and DR sectors. DD sectors with long interdeltoid suture on external surface of theca (fig. 38.1), separating ambulacra from mouth. DD sectors form wide peristomial area in which a ring canal of oral nervous system is preserved (fig. 47.4). Ring canal (sections 15, 16) pentagonal with angles at contact with lancets. Transverse commissures over interdeltoid sutures not observed. DR sectors moderately developed, in contact with radials laterally (figs. 38.5–9). RD sutures sloping inward towards thecal cavity. Radial limbs not distinguishable, owing to presence of RA growth sector. RA growth sector conspicuous, curving around ambulacra (figs. 38.1, 2).

At posterior side two anal deltoids: epi- and hypodeltoid. Epideltoid large, with main body forming part of peristomial area (figs. 38.1–3), and with two short limbs, mostly internal, which come in contact with *C* and *D* radials (figs. 38.5–7), but not with hypodeltoid. Epideltoid has two little prongs projecting into thecal cavity (fig. 38.6) which are probably remnants of gonoduct insertion. Hypodeltoid small, not preserved in sectioned specimen, but its place indicated by broken lines in figs. 38. 7, 8, situated in notch between *C* and *D* radials, contributing to lateral wall of theca, not in contact with epideltoid. Anus situated almost at lateral side of theca, opening in upper part of suture between *C* and *D* radials. Adorally anus flanked by notch on epideltoid, aborally bordered by small hypodeltoid and laterally bordered by *C* and *D* radials. Tract for rectum internally excavated in suture between *C* and *D* radial (figs. 38.7–9, anal tract outlined in fig. 9).

Ambulacra small, rhombiform, well removed from mouth (figs. 38.1–3). Lancets rhombic, with rounded aboral edge. Lancets adorally in contact with deltoids (figs. 38.1–3), aborally with radial (figs. 38.3–8), only aboral portion bordering thecal cavity (figs. 38.7–9). External surface of lancet concealed by side plates, except central adoral end. Side plates and outer side plates present, placed in semicircle around aboral part of lancet (figs. 38.1–3). Adoral side plates come in contact with deltoid (fig. 38.2). Side plates are surrounded by, but not in contact with, raised edge of RA growth front (fig. 38.1). At lower level (figs. 38.2, 3) side plates revealed to rest directly on radial.



Textfig. 38. *Angioblastus variabilis* Wanner, 1931. Permian, Noko, Timor. Spec. Geol. Inst. Univ. Amsterdam, unregistered. Series of 13 transverse sections resp. from peels numbered 8, 10, 12, 13, 14, 16, 18, 20, 22, 23, 28, 29, 35, and 37, cut resp. 0.34, 0.45, 0.55, 0.60, 0.65, 0.75, 0.87, 1.09, 1.14, 1.37, 1.41, 1.68, and 1.80 mm below top of theca. All figures × 12. (1–3) Peristomial area, with small rhombiform ambulacra; 3, note nerve canals. (4–8) Composition of anal area, note presence of epideltoid, and loss of hypodeltoid; 4, 6, *C* ambulacrum only. (4–13) Composition of hydrospire structures; note absence of anal hydrospires; 4, short hydrospire slit; 10, 11, large hydrospire folds; 10, 11, 12, 13, *B* radial only. See textfig. 1 for further explanation.

Hydrospires formed across RD sutures. Eight hydrospire folds are formed, those on *C* and *D* anal sides absent (figs. 38,7–9). Externally there are short, exposed hydrospire slits (fig. 38.3) at the place where radial and deltoid meet. Hydrospire slit placed at angle with longer axis of ambulacrum. Internally hydrospire slit leads into a small tube in RD suture (figs. 38.4–7) which opens into a single, large hydrospire fold (figs. 38.8–13). Hydrospire folds thick-walled, formed equally by radials and deltoids, hanging freely in thecal cavity, extending to 1.80 mm below top of theca (fig. 38.13).

Angioblastus wanneri (Yakovlev, 1926^b)

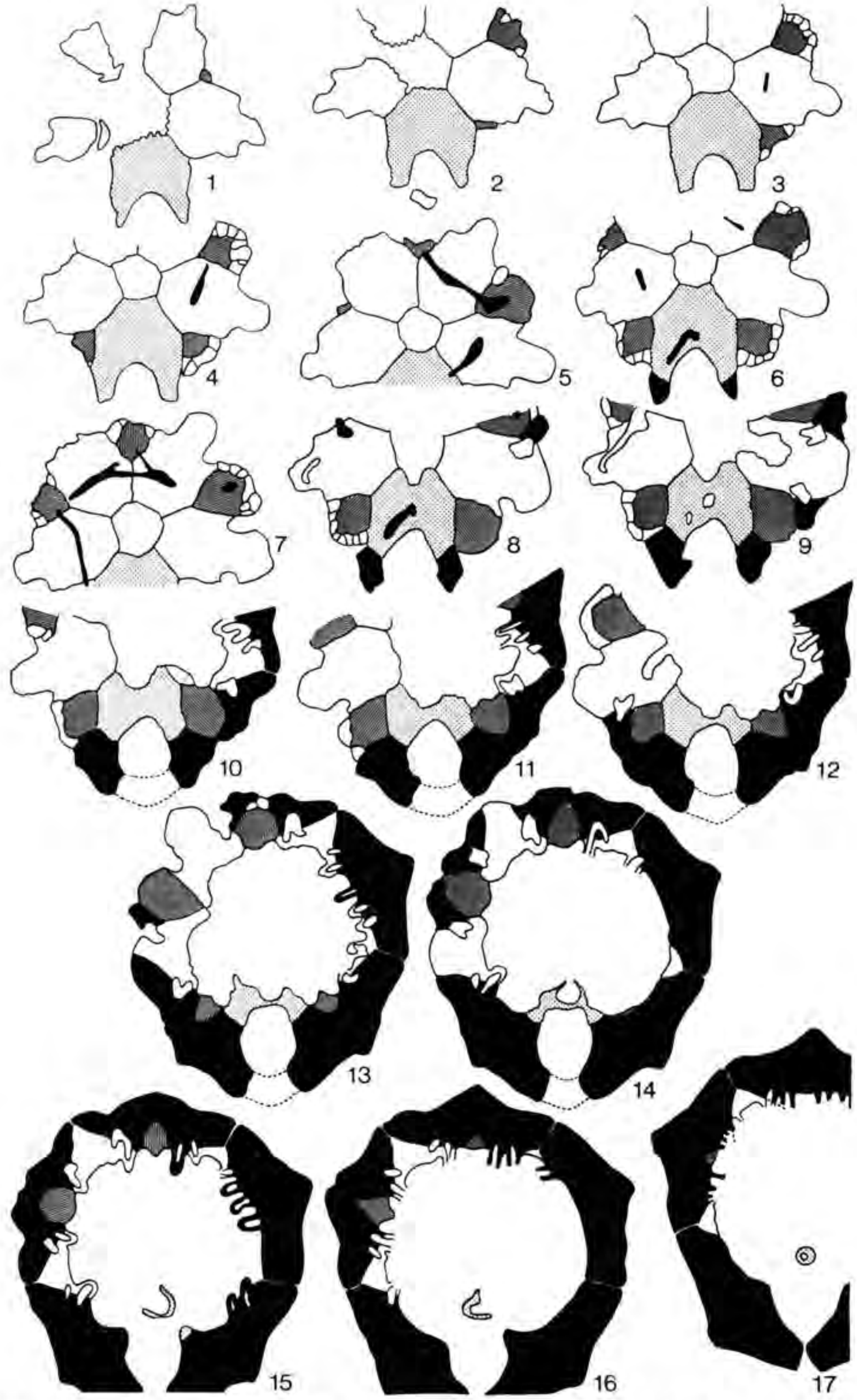
Textfigure 39; Pl. XXIX, figs. 7, 11–13, 15–18

Total height of sectioned specimen 8.6 mm. Upper 3.65 mm of theca sectioned into 28 transverse peel sections at mean intervals of 0.13 mm. In textfigure 39 seventeen selected sections are shown.

Theca cup shaped, thick-plated. Sides of theca formed by radials; vault low and flat, more or less constricted, formed mainly by deltoids, which are in horizontal position. Cross section of theca pentagonal.

Deltoids completely exposed on upper side of theca, with hexagonal outline (fig. 39.4). Deltoids conspicuous, with arrowlike elevations (fig. 39.1). Subequal DD and DR sectors. DD sectors with long interdeltoid suture on external surface of theca (fig. 39.2), separating ambulacra from mouth. DD sectors form wide peristomial area, in which a ring canal of oral nervous system is preserved (figs. 39.5–7). Ring canal pentagonal, with angles in adoral tips of deltoids. Transverse commissure is formed over interdeltoid suture (fig. 39.7). DR sectors moderately developed, internally in contact with radials (figs. 39.12–16). RD suture sloping inward towards thecal cavity. Radial limbs not distinguishable owing to presence of RA growth sector, which is not conspicuous.

At posterior side 2 anal deltoids: epideltoid and hypodeltoid. Epideltoid large, with main body forming part of peristomial region (figs. 39.4–7), and with two short limbs, mostly internal, which rest upon *C* and *D* radials (figs. 39.8–14). Epideltoid produced into tubelike extension internally (figs. 39.14–17) inferred to be part of gonoduct. Latter probably opened through gonopore on epideltoid (fig. 39.9). Epideltoid bears part of oral nervous system, and seems to have nerve canals descending into epideltoid limbs (figs. 39.6–8). Epideltoid not hydrospire-forming. Hypodeltoid small, not preserved in sectioned specimen (known from other specimens), but its place indicated by broken line in figs. 39.10–14, situated in notch between *C* and *D* radials, contributing to lateral wall of theca. Hypodeltoid probably not in contact with epideltoid limbs. Anus situated almost at lateral side of theca, opening in upper part of suture between *C* and *D* radials. Adorally anus flanked by notch on epideltoid (fig. 39.6) aborally bordered by small hypodeltoid (fig. 39.10) and laterally bordered



Textfig. 39. *Angioblastus wanneri* (Yakovlev, 1926^{b}). L. Permian, Krasnoufimsk, Ural Mts., USSR. Spec. UMMP 54890. Series of 17 transverse sections resp. from peels numbered 6–22, cut resp. 0.55, 0.65, 0.75, 0.85, 0.95, 1.05, 1.15, 1.25, 1.35, 1.45, 1.55, 1.65, 1.75, 1.85, 1.95, 2.05, and 2.15 mm below top of theca. All figures × 11. (1–2) Above peristome (partly), through arrow-like elevations of deltoids. (3–9) Vault region with ambulacra, note ring canal of oral nervous system. (10–17) Composition of anal area, note presence of epideltoid and loss of hypodeltoid; 14, 15, 16, 17, note gonoduct. Composition of hydrospire structures, note absence of anal hydrospires. See textfig. 1 for further explanation.

by *C* and *D* radials. Tract for rectum internally excavated in suture between *C* and *D* radial (figs. 39.13–17).

Ambulacra small, rhombiform, well removed from peristome (figs. 39.3–9). Lancets rhombic, with rounded aboral edge. Lancets bear very short radial nerve canals (fig. 39.7); nerves for side plates and brachioles depart directly from ring canal in lancet (section 13). Lancets adorally in contact with deltoids (figs. 39.3–12), aborally with radial (figs. 39.9–17), and only their aboral portions border thecal cavity (figs. 39.14–17). External surface of lancets concealed by side plates, except central adoral end. Side plates and outer side plates present, placed in semicircle around aboral part of lancet (figs. 39.6–8). Adoral side plates come in contact with deltoid (figs. 39.3–8). At posterior side the side plates may come in contact with *C* and *D* radials; in other ambulacra not observed to be in contact with radials.

Hydrospires formed over RD suture. Eight hydrospire groups present, those on *C* and *D* anal side absent (figs. 39.12–15). Externally there is one exposed hydrospire slit in sectioned specimen (figs. 39.6–8) indenting flank of DR sector, and placed at angle with longer axis of ambulacrum. Internally hydrospire slit leads into a small tube in RD suture (fig. 39.9) which soon becomes heart-shaped (fig. 39.10) or bilobed (figs. 39.10–12) and opens into two hydrospire folds (figs. 39.13–16). An incipient third fold is present at posterior side of *B* amb. in the sectioned specimen (figs. 39.11–13). Hydrospire folds short, thick-walled, not differentiated into hydrospire lamellae and inflated hydrospire ducts (fig. 39.15). Specimens of larger size than the sectioned one may have more hydrospire slits opening separately on upper surface of theca across DR suture, being fully exposed. This could imply that upon further growth the hydrospire folds gradually developed separate openings on upper surface of theca.

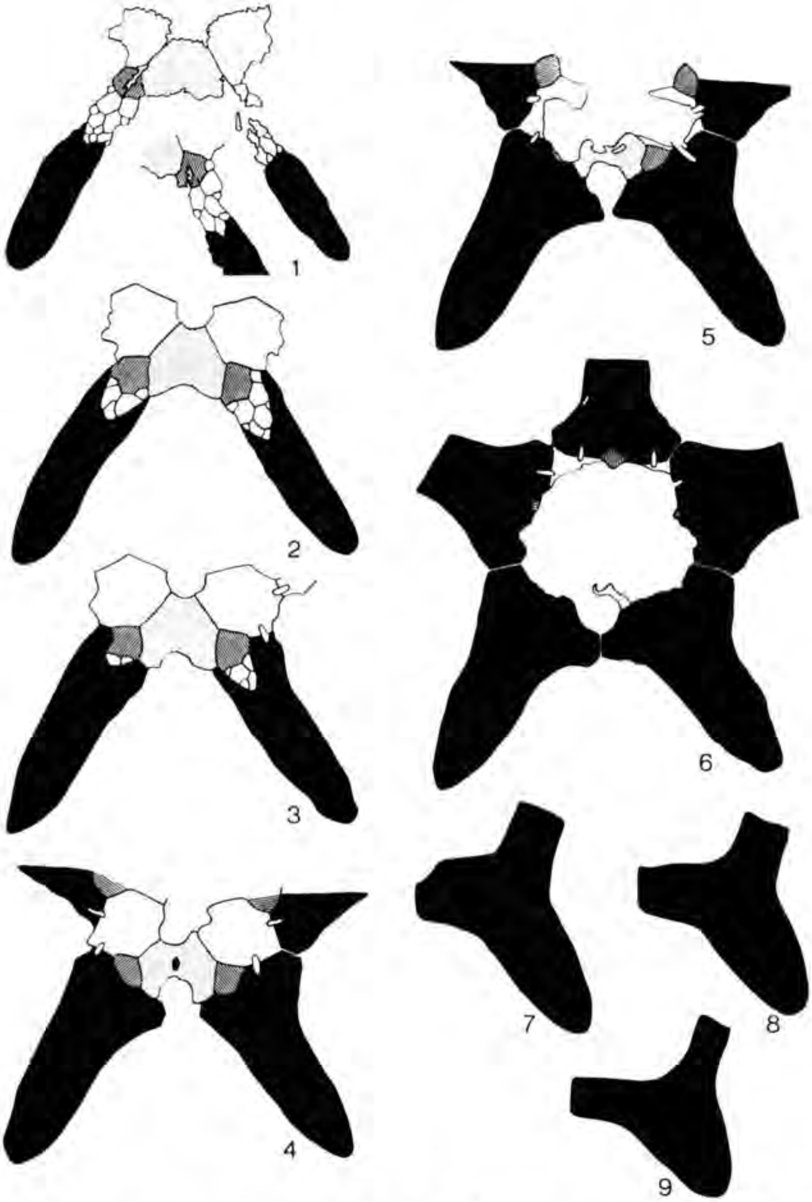
Pterotoblastus gracilis Wanner, 1924[a]

Textfigure 40; Pl. XXXI, figs. 11, 12; Pl. XXXII, figs. 3, 4, 6, 9, 10

Total height of sectioned specimen 7.2 mm. Upper 2.55 mm of theca sectioned into 37 transverse peel sections at mean intervals of 0.07 mm. In textfigure 40 nine selected sections are shown.

Theca cup shaped, very thick-walled, with only very small thecal cavity. Cross section stellate, due to strong development of prongs on radials; radial prongs bend upward, rising above peristome. Top of theca flat, constricted, formed mainly by deltoids, which are in horizontal position.

Deltoids completely exposed on upper side of theca, with unequal growth sectors, DD sector larger. DD sectors with long interdeltoid suture on external surface of theca (fig. 40.1), separating ambulacra from mouth. DD sectors form wide peristomial area. No ring canals of oral nervous system preserved. DR sectors weakly developed, in contact with radials



Textfig. 40. *Pterotoblastus gracilis* Wanner, 1924^{a}. Permian, Noko, Timor. Spec. Geol. Inst. Univ. Amsterdam, unregistered. Series of 9 transverse sections resp. from peels numbered 6 (7), 9, 12, 15, 18, 21, 24, 30, and 36, cut resp. 0.70 (0.75), 0.85, 1.00, 1.13, 1.24, 1.35, 1.50, 1.80, and 2.40 mm below top of theca. All figures × 7.5, showing posterior part of sections. (1) Peristome. (1–3) Ambulacral structures; note that lancet does not underlie side plates. (2–5) Composition of anal area, note presence of single epideltoid. (2–5) Composition of hydrospire system, note absence of hydrospires at C and D anal sides; 6, nearcomplete section; 7, 8, 9, *D* radials only. See textfig. 1 for further explanation.

laterally (figs. 40.2–6). RD suture sloping inward towards thecal cavity. Radial limbs not distinguishable owing to presence of radial prongs.

At posterior side one anal deltoid; an epideltoid. Epideltoid of equal form and proportion as regular deltoids, except embayment for anus along aboral edge (fig. 40.3). Internally epideltoid forms two short limbs (figs. 40.5, 6), which apparently form a bridge for support of gonoduct. Gonoduct opens through gonopore on epideltoid (fig. 40.4). No hypodeltoid ever observed in any known specimen. Anus passes externally between epideltoid and a notch in suture between *C* and *D* radials. Tract for rectum internally excavated in suture between *C* and *D* radials (figs. 40.5, 6).

Ambulacra elongate, removed from peristome (fig. 40.1). Lancets rhombic, with rounded aboral edge, adorally in contact with deltoids (figs. 40.1–5), aborally resting on radial (figs. 40.3–6), and only small aboral portion bordering thecal cavity (figs. 40.5, 6). External surface of lancet mostly exposed. Side plates and outer side plates present, large in size but small in number, placed in alternating order, with longer axis of plates at angle to longer axis of ambulacra (figs. 40.1–3). Adoral side plates in contact with lancet, all other side plates directly resting on radial prong, not underlain by lancet. Ambulacral tract continues on interdeltoid suture; tract known to be covered by cover plates in bilateral arrangement. Oral cover plates also known to occur.

Hydrospires formed across RD suture. Eight hydrospires present in sectioned specimen (compare fig. 40.4 to fig. 40.6), those on *C* and *D* anal sides absent (figs. 40.4, 5). Externally there is one exposed hydrospire slit (fig. 40.2) indenting flank of DR sector, and placed at angle with longer axis of ambulacrum. Internally hydrospire slit leads into a small tube in RD suture (figs. 40.2, 3), which opens into a single hydrospire fold. Exact characters of hydrospire folds unknown because they are broken off in sectioned specimen. Larger specimens than sectioned one may have more hydrospire slits per group, all of which open individually on upper surface of theca.

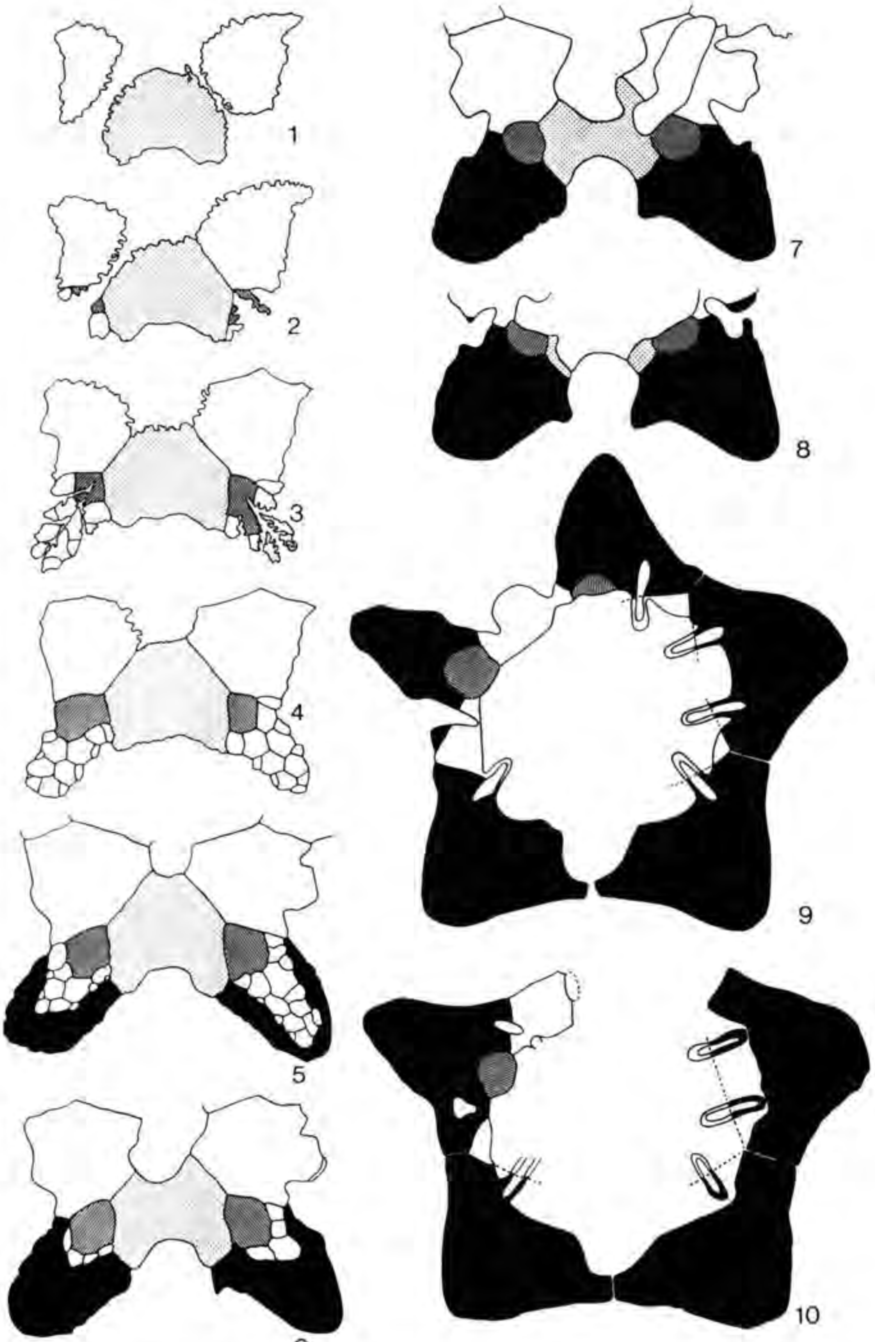
Pterotoblastus brevialatus Wanner, 1931

Textfigure 41; Pl. XXXI, figs. 2, 5, 7, 9, 13–15; Pl. XXXIII, fig. 8

Total height of sectioned specimen 4.7 mm. Upper 1.8 mm of theca sectioned into 36 transverse peel sections at mean intervals of 0.05 mm. In textfigure 41 ten selected sections are shown.

Theca cup shaped, very thick-plated, with relatively large thecal cavity. Cross section pronounced pentagonal due to slight development of blunt prongs on radials (fig. 41.6). Top of theca flat, constricted, formed mainly by deltoids, which are in horizontal position.

Deltoids completely exposed on upper side of theca, with unequal growth sectors, DD sector larger. DD sectors with long interdeltoid suture on external surface of theca (figs. 41.1, 2), separating ambulacra from



Textfig. 41. *Pterotoblastus brevialatus* Wanner, 1931. Permian, Noko, Timor. Spec. Geol. Inst. Univ. Amsterdam, unregistered. Series of 10 transverse sections resp. from peels numbered 8, 9, 10, 12, 17, 18, 20, 21, 24, and 26, cut resp. 0.29, 0.35, 0.40, 0.48, 0.72, 0.76, 0.84, 0.88, 1.05, and 1.15 mm below top of theca. All figures × 11.5, showing posterior parts of sections. (1–3) Peristome. (3–6) Composition of ambulacral structures; note that lancet does not underlie side plates. (6–10) Composition of anal area, note presence of single epideltoid. Composition of hydrospire system, note absence of hydrospires at *C* and *D* anal sides; 9, complete section. See textfig. 1 for further explanation.

mouth. DD sectors form wide peristomial area. No ring canals of oral nervous system preserved. DR sectors weakly developed, in contact with radials laterally (figs. 41.6–10). RD suture sloping inward towards thecal cavity. Radial limbs not distinguishable owing to presence of blunt radial prongs.

At posterior side one anal deltoid present: an epideltoid. Epideltoid of equal form and proportions as regular deltoids, except embayment for anus along aboral edge (figs. 41.6, 7). Internally epideltoid forms two short limbs (figs. 41.6, 7), which rest upon *C* and *D* radials. No structures allied to reproductive system found in sectioned specimen. Gonopore known to be present on epideltoid. No hypodeltoid ever observed in any known specimen. Anus passes externally between epideltoid and a notch in suture between *C* and *D* radials. Tract for rectum internally excavated in suture between *C* and *D* radials (figs. 41.9, 10).

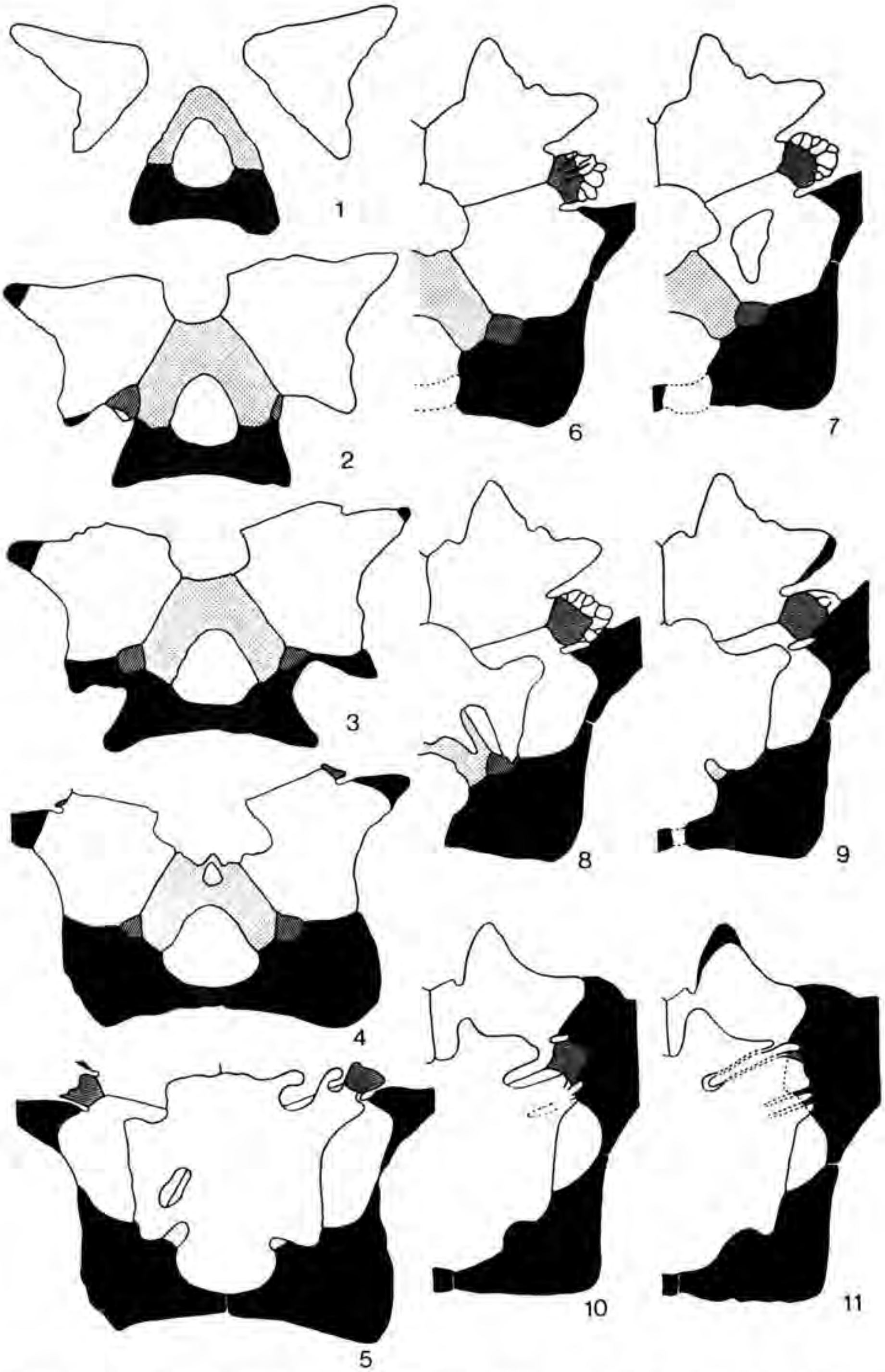
Ambulacra elongate, removed from peristome (figs. 41.1–3). Lancets rhombic, with rounded aboral edge, adorally in contact with deltoids (figs. 41.3–6), aborally resting on radials (figs. 41.7–9), and only a small aboral portion bordering thecal cavity (figs. 41.8–10). External surface of lancet mostly exposed. Side plates and outer side plates present, conspicuous, large in size but small in number, placed in alternating order (figs. 41.4, 5). Adoral side plates in contact with lancet, all other side plates resting directly on radial prong, not underlain by lancet (figs. 41.5–7). Ambulacral tract continues on interdeltoid suture, which is provided with minor lobe and groove structure (fig. 41.2) in the same way as developed on side plates (fig. 41.3).

Hydrospires formed across RD sutures. Eight hydrospires present, those on *C* and *D* anal sides absent (figs. 41.9, 10). Externally there is one exposed hydrospire slit in sectioned specimen (figs. 41.7, 8), right hand side of *C* amb.), indenting flank of DR sector, placed subparallel to longer axis of ambulacrum. Internally hydrospire slit leads into single hydrospire fold (figs. 41.9, 10). Hydrospire folds well developed, thick-walled, formed equally by radials and deltoids, not differentiated into hydrospire lamellae and inflated hydrospire ducts, hanging free in thecal cavity, extending to 1.15 mm below top of theca (fig. 41.10).

Nannoblastus pyramidatus Wanner, 1924b
Textfigure 42; Pl. XXXIII, figs. 1, 2, 5–7

Three specimens sectioned. In textfigure 42 sections have been presented from two specimens. Figures 1–5 are from specimen in the right hand side of the peels, figures 6–11 are from specimen in the middle of the peels. Both figured specimens about 4.8 mm high, and sections at mean intervals of 0.075 mm.

Theca thick-plated, with rhombic lateral profile, pentagonal or slightly pentalobate in cross section. Figs. 42.1–5 given for details of regular and



Textfig. 42. *Nannoblastus pyramidatus* Wanner, 1924b. Permian, Noko, Timor. Spec. Geol. Inst. Univ. Amsterdam, unregistered. Two series of transverse sections from two different specimens, illustrated figs. 1–5, and figs. 6–11 resp. First series from peels numbered 20, 23, 26, 28, and 31, cut resp. 0.69, 0.85, 0.95, 1.06, and 1.19 mm below top of theca. Second series from peels numbered 34–37, 39, 40, cut resp. 1.33, 1.37, 1.39, 1.46, 1.56, and 1.62 mm below top of theca. All figures × 11.5. (1–5) Right hand specimen to show composition of anal deltoids, note presence of epi- and hypodeltoid; 1, above peristome; 4, note opening for gonoduct. (6–11) Other specimen, showing composition of ambulacral and hydrospire structures, note absence of hydrospires at both sides of *C* amb. See textfig. 1 for further explanation.

anal deltoids. Deltoids occupying full upper surface of theca, very conspicuous by vertical build-up brought about by deposition of calcite on outer surface of deltoids. Regular deltoids building pyramidlike structures, separated from one another by deep ambulacral troughs (fig. 41.1). Pyramids rise to 0.7 mm above peristome. Sides of troughs inbetween deltoid pyramids subparallel. At anal side pyramidlike structure absent in sectioned specimen, but formed by hypodeltoid in other specimens. Sections through deltoids variable from trigonal (fig. 42.1) above peristome, to pentagonal (figs. 42.3, 4) near contact with radials. Deltoids have long interdeltoid suture at bottom of ambulacral trough, separating ambulacra from mouth. Deltoids form wide peristomial region. No ring canals observed in peristomial region of deltoids. Radiodeltoid suture subhorizontal externally, but internally sloping steeply towards thecal cavity. Radials have RA growth front which at upper surface of theca is embayed (fig. 42.3) for reception of ambulacra.

At posterior side two anal deltoids: epideltoid and hypodeltoid. Epideltoid not conspicuous, but provided with rim (fig. 42.1), smaller than regular deltoids, forming part of peristomial area. Internally epideltoid forms two short limbs (figs. 42.2–5), which rest on *C* and *D* radials. Epideltoid forms a tubelike structure (fig. 42.4) inferred to be part of gonoduct. No external gonopore observed. Hypodeltoid conspicuous, about as wide as high, situated aborally from anus at upper surface of theca, broadly in contact with *C* and *D* radials (figs. 42.2–4); epi-hypodeltoid suture short (figs. 42.1, 2). Anus located at upper surface of theca, passing between epi- and hypodeltoid.

Note absence of hydrospire structures at both sides of *C* and *D* ambulacra in figs. 42.2–5.

Figs. 42.6–11 given for detail of ambulacral and hydrospire structures. Ambulacra small, petaloid, removed from peristome (figs. 42.6, 7). Lancets rhombic, adorally in wide contact with deltoids (figs. 42.6–9), and aboral portion resting on RA growth front (fig. 42.10). Lancets hardly border thecal cavity. External surface of lancet mostly exposed. Side plates and outer side plates present, alternating with one another, few in number, placed in semicircle along aboral side of lancet. Side plates not in contact with deltoids (figs. 42.6–8), but aborally sitting on RA growth sector (figs. 42.8–9). Small nerve canals lead from center of lancet to side plates (fig. 42.6).

Hydrospires formed across RD sutures. In sectioned specimens only 6 hydrospires present, those on both sides of *C* and *D* ambulacra absent (figs. 42.3–5; 42.8–11). Externally there is a short hydrospire slit or cleft directly bordering ambulacra (figs. 42.6–9), both sides of *B* amb.) but not extending full length of ambulacra. Slit is aborally closed off by contact of side plates with RA growth sector (figs. 42.8, 9, at posterior side of *B* amb.). Slits lead internally to single hydrospire fold (fig. 42.11). Hydrospire folds well developed, thick-walled, formed equally by radials and deltoids, hanging freely in thecal cavity, extending to about 1.75 mm below top of theca. Differentiation of hydrospires into lamellae and ducts uncertain.

7. Family CERATOBLASTIDAE

As a monotypic family the general and stable characters of the family cannot be distinguished from the generic characters. Therefore no longer introductory statement to the anatomical sections of the genus *Ceratoblastus* is given.

Ceratoblastus nanus Wanner, 1940
Textfigure 43; Pl. XXXII, figs. 5, 11

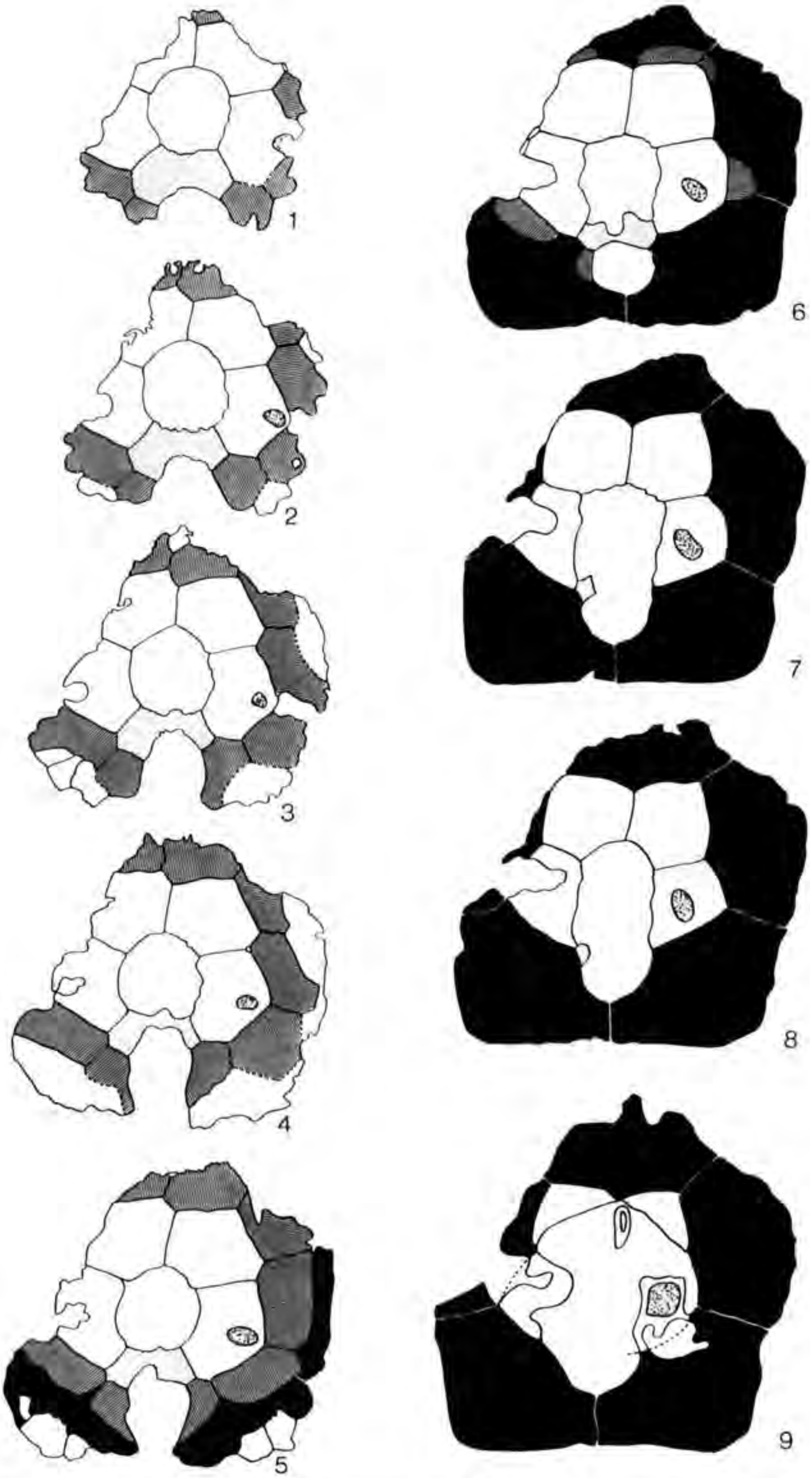
Total height of sectioned specimen 7.5 mm. Upper 1.4 mm, forming flat top of theca, sectioned into 35 subsequent transverse peel sections at mean intervals of 0.04 mm. In textfigure 43 nine selected sections are shown.

Theca thick-plated, horn-shaped, with flat restricted vault, pentagonal in cross section. Deltoids small, mostly confined to peristomial area, with broad hexagonal outline on upper surface of theca (figs. 43.1, 2). Ring canals of oral nervous system not observed on peristomial region of deltoids. Deltoids internally in contact with radials (figs. 6–9). RD suture sloping steeply toward thecal cavity. Posterior deltoid is epideltoid, smaller than four regular deltoids, embayed at aboral edge by anus, internally with two prongs (figs. 43.7, 8) in contact with *C* and *D* radials. Epideltoid not forming structures to be interpreted as part of reproductive system. Gonopore and gonoduct – such as in other fissiculate blastoids – not preserved. Anus passes externally between epideltoid and *C* and *D* radials. Tract for rectum internally excavated in suture between *C* and *D* radials (figs. 43.6–9).

Ambulacra relatively large, petaloid to rhombiform, occupying most of the space on upper surface of theca. Regular lancet plates absent. Instead ten plates are present in a circlet around the deltoids, and more or less alternating with these, lying directly on the radials (figs.43.4–6), and being very thin (0.25 mm). A pair of these plates belongs to one ambulacrum, and supports the ambulacral side tracts coming from the brachioles on the side plates. The two plates lying at *C* and *D* anal side are modified to form the lateral borders of anus (fig. 43.5). Side plates and outer side plates not observed beyond doubt. It is believed that side plates (and outer side plates?) are present in a zone bordering the pairs of plates along their aboral edge (the white areas in figs. 43.2–5, at periphery of drawing). These side plates would bear the brachiolar facets and support the brachioles.

Regular hydrospire structures absent.

Externally *BC* and *DE* deltoids possess a wide pore at their aboral



Textfig. 43. *Ceratoblastus nanus* Wanner, 1940, Permian, Noko, Timor. Spec. Geol. Inst. Univ. Amsterdam, unregistered. Series of 9 transverse sections, resp. from peels numbered 6, 8–15, cut resp. 0.15, 0.21, 0.24, 0.28, 0.32, 0.35, 0.38, and 0.45 mm below top of theca. All figures × 22. Note presence of single epideltoid (1–8), presence of ten larger plates underlying ambulacra (1–6), larger pores and canals in *BC* and *DE* deltoids (1–8) leading to sacs (9) hanging from same deltoids. See textfig. 1 for further explanation.

edge (figs. 43.1, 2). The pores give entrance to canals piercing the bodies of these two deltoids (figs. 43.3–8), which terminate in lobed sacs (figs. 43.9) formed by *BC* and *DE* deltoids. Function of these sacs unknown, but believed either respiratory or reproductive. A small fold has been observed in *A* radial position (fig. 43.9). It does not open to the exterior, it is unknown what plate the fold forms from, and it is unknown what its function is.

8. INCERTAE SEDIS

The Permian genus *Indoblastus* is the only genus of fissiculate blastoids which could not definitely be placed systematically in one of the families of fissiculate blastoids. The description of its anatomy is given here in an appendix to the descriptions per family.

Indoblastus granulatus Wanner, 1924[a]

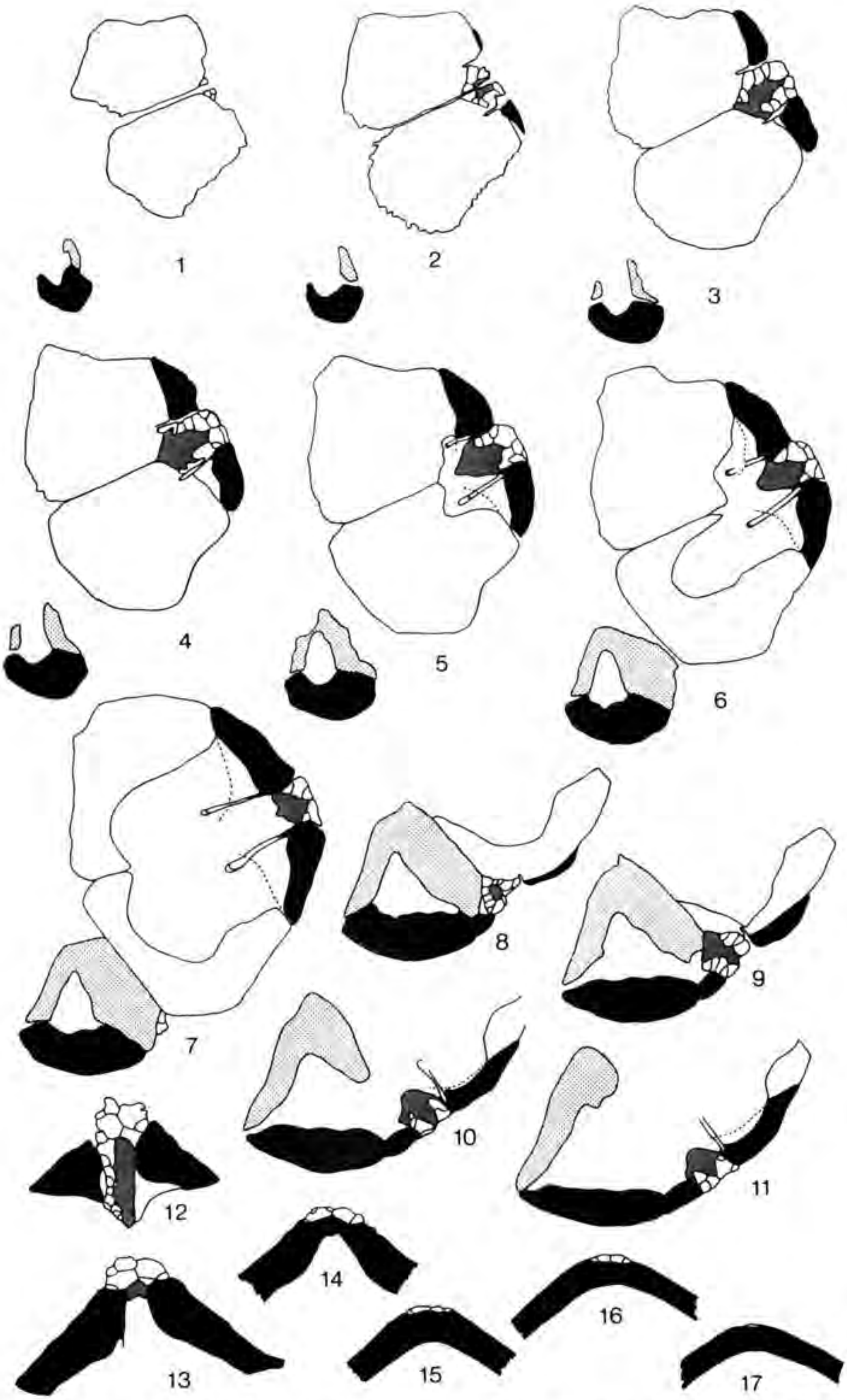
Textfigure 44; Pl. XXXII, fig. 2; Pl. XXXIII, fig. 4

Total height of sectioned specimen 22.3 mm. Specimen is slightly crushed, so that *AB* and *BC* deltoids and *B* ambulacrum have come to lie in a higher position than other deltoids. For that reason only right hand side of specimen is given in textfigures 44.1–11 (with omission of *B* radial in figs. 44.8–11). A total of 44 sections were made, covering upper 5.11 mm of specimen. Mean interval between sections is 0.15 mm.

Theca cup-shaped, with low vault, rounded pentagonal in plan view. Four regular deltoids rhombic, not conspicuous, without crest, and unequal sectors: DD sectors smaller than DR sectors. DD sectors form wide area around the mouth. No ring canals of oral nervous system found in peristomial part of deltoids. Deltoids form long interdeltoid sutures, separating ambulacra from mouth. Deltoids rest on radials, DR suture sloping inward to thecal cavity.

At posterior side two anal deltoids: epideltoid and hypodeltoid (figs. 44.1–11). Epideltoid small, corresponding to DD sectors of regular deltoids, forming part of peristomial area, not in contact with radials. Epideltoid not hydrospire-forming, not observed to form structures allied to reproductive system. Hypodeltoid larger than epideltoid, corresponding to DR sector of regular deltoids, in contact with *C* and *D* radials, contributing to external wall of theca. Anus passes externally between epi- and hypodeltoid.

Ambulacra lanceolate, conspicuous, removed from mouth (figs. 44.1–4), mostly situated on radials, and hardly extending on to deltoids. Lancets elongate, not extending full length of ambulacra. Adorally lancet in contact with deltoids (figs. 44.3, 4), aborally situated between radial limbs (figs. 44.6–11), internal surface bordering thecal cavity convex (figs. 44.5–11). Side plates and outer side plates present. Side plates in lateral contact along median line of ambulacrum; lancet concealed over entire length except at adoralmost end. Side plates fit in grooves on



Textfig. 44. *Indoblastus granulatus* Wanner, 1924^{a}. Permian, Noko, Timor. Spec. Geol. Inst. Univ. Amsterdam, unregistered. Series of 11 transverse sections resp. from peels numbered 6, 8, 10–13, 15, 17–20, cut resp. 0.18, 0.31, 0.44, 0.54, 0.64, 0.74, 0.94, 1.14, 1.24, 1.39, and 1.49 mm below highest point of *B* ambulacrum. Six additional sections through *A* ambulacrum given in figs. 12–17. All figures × 3. See textfig. 1 and text for further explanation.

lateral sides of lancet (figs. 44.5, 10, 11); external surface of lancet keeled along midline. Adoral side plates laterally separated from deltoids by short cleft or slit, which extends over a short distance inbetween side plates and radials (figs. 44.2–4); otherwise side plates in lateral contact with radial limbs (figs. 44.5–11). Aboral side plates of *A* ambulacrum (figs. 44.12–17) prove to lie directly on center part of radial body, not underlain by lancet. Outer side plates present, alternating with side plates (figs. 44.4, 12, 13).

Hydrospires formed across RD suture. Eight hydrospires present, those on *C* and *D* anal sides absent (figs. 44.8–11). A single hydrospire fold in every one of the regular groups. Hydrospires placed parallel to longer axis of ambulacra, formed mostly by radials, differentiated into thin hydrospire lamellae and inflated ducts (fig. 44.7), not extending deeply into thecal cavity. Entrance to hydrospire folds by way of short cleft or slit across RD suture, directly bordering ambulacrum (figs. 44.1–3, *B* amb.; figs. 44.8, 9, right hand side of *C* amb.), extending along short lateral contact of ambulacrum with deltoid and over same distance in aboral direction. No infilling of hydrospires observed.

9. APPENDIX

Transverse sections of a radial prong of *Thaumatoblastus longiramus* were made. This was done for the sole purpose of studying the extensions of the nervous system in the lancet and side plates, which were stated in blastoid literature to be different from other fissiculates.

Although we have definitely referred the genus *Thaumatoblastus* to the neoschismatids, it has been preferred to put the results of this study, being a special topic, in an appendix here.

Thaumatoblastus longiramus Wanner, 1924b

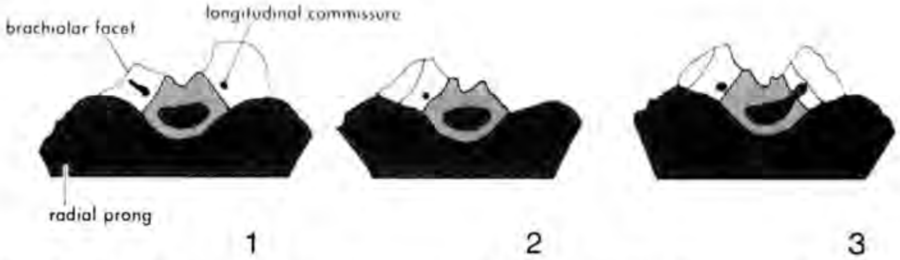
Textfigure 45; Pl. XXIV, fig. 2; Pl. XXV, figs. 1–8; Pl. XXVIII, fig. 5

Three transverse sections of a radial prong with ambulacral plates are presented. *Thaumatoblastus* is known only from radial plates, each of which is provided with an extremely well developed horizontal prong. The ambulacral areas are conspicuous, linear, and extremely elongated, extending over full length of the prong.

A lancet is present, extending the full length of the ambulacral area. Its internal surface is convex and is situated in a longitudinal depression of the radial prong. The external surface of the lancet is exposed over the full length of the ambulacral area. Along its outer midline there is an ambulacral groove. The side plates are situated on the inclined lateral surfaces of the lancet and rest on the radial prong. The central parts of the side plates are elevated (fig. 45.1, right hand side).

The lancets possess a very wide longitudinal canal, interpreted to be the radial nerve canal. Each series of side plates is shown to be pierced by a longitudinal canal. This canal is much smaller in diameter than the lancet canal. The two longitudinal canals are situated close to the lateral surfaces of the lancet, but are formed entirely within the side plates. The two canals are parallel to the lancet canal.

In one of the sections (nr. 2, fig. 45.3) a connective canal is shown to be present inbetween the radial nerve canal in the lancet and the longitudinal canal in the side plates. Another section (nr. 4, fig. 45.1) shows an offshoot from the longitudinal canal in the side plates, leading toward the brachiolar facet.



Textfig. 45. *Thaumatoblastus longiramus* Wanner, 1924b. Permian, Tubulopo, Timor. Spec. Rijksmus. Geol. Min., Leiden, unregd. Series of 3 transverse sections through radial prong with ambulacral plates. Wide radial nerve canal in lancet shown in all three sections. Note longitudinal canal in side plates, connecting with radial nerve canal (3), and giving offshoot to brachiolar facet (1); all figures × 7.

There is definite and conclusive evidence that the longitudinal canals in the side plates were interconnected with the radial nerve canal. Hence, the longitudinal canals in the side plates are interpreted to form part of the nervous system. They are held to have been longitudinal commissures inbetween the brachiolar nerves before they contacted the main radial nerve trunk.

COMPARATIVE ANATOMY

The aim of this section of the Anatomy Chapter is to provide comparative information on skeletal structures allied to the several different organ systems of the blastoids. The systems that have expressions in the skeleton are the genital system, the nervous system, and the ambulacral and watervascular systems. The information now available on each of these systems is dealt with in separate paragraphs below.

GENITAL SYSTEM

As a result of our anatomical studies of the fissiculate blastoids, some skeletal features of the blastoids are newly discovered and herein interpreted to belong to the genital system. The features involved are a pore in the anal interarea, which is internally connected with a canal or duct in the anal deltoids, which leads into a tube- or collar-shaped extension below the anal deltoids.

The pore has either an external or an internal position. If external it is formed in the sutures between the anal deltoids and situated between mouth and anus. This condition is present in certain primitive fissiculates with a complex arrangement of anal deltoids, including either a subdeltoid or two cryptodeltoids (figs. 46.1, 11). If internal the pore is found to open directly into the anal cavity. This condition is present in certain advanced fissiculates with a simplified arrangement of anal deltoids, excluding both subdeltoid and cryptodeltoids. The pore is then situated in the internal adanal surface of the epideltoid (figs. 46.2, 12).

The pore is here interpreted to be the external opening of the genital or reproductive system and to function as the *gonopore*. The duct or canal terminating in the pore is here interpreted as the *gonoduct*, connecting the gonad with the gonopore. This interpretation implies that the fissiculates are held to have had an internal gonad, fully enclosed within the thecal cavity, and opening to the exterior by way of gonoduct and gonopore.

The presence and configuration of gonopore and gonoduct in the several different fissiculate families is now briefly dealt with. A discussion of arguments why the pore and the duct are interpreted as belonging to the genital system is given at the end of this section.

In the phaenoschismatids, which are the main and ancestral stock of the fissiculate blastoids, an external gonopore is present and observed in the Silurian forms *Decaschisma pulchellum* (fig. 2.4), *Polydeltoideus enodatus* (fig. 3.3; 46.1), and the L. Dev. *Leptoschisma lorae* (fig. 4.4). In these cases the gonopore is located in the suture between the superdeltoid and the subdeltoid. In *Decaschisma pulchellum* a gonoduct is formed by the superdeltoid (fig. 2.9), but in *Polydeltoideus enodatus* and *Leptoschisma lorae* the gonoduct is formed by the subdeltoid (figs. 3.7, 8, and figs. 4.5, 6, resp.).

Lower Devonian phaenoschismatids other than *Leptoschisma* have provided less information on the genital system. In *Pleuroschisma verneuili* (fig. 11.6) the gonopore is found to lie externally in the suture between super- and cryptodeltoids. The gonoduct is formed by one of the cryptodeltoids. This condition still closely resembles that of the Silurian forms. The same is true for the Bohemian species *Caryoblastus bohemicus* which also has an external gonopore (fig. 5.3) in the suture between the superdeltoid and the larger cryptodeltoid; a gonoduct is not observed in this species. Neither a gonopore nor a gonoduct was found in the skeleton of the Spanish species of *Pentremitidea* and *Cryptoschisma*. In these genera the gonad probably opened in a lobed notch at the aboral edge of the superdeltoid.

Phaenoschismatids from the Middle Devonian have also provided information on the genital system. *Pleuroschisma lycorias* has an external gonopore (fig. 10.2) in the suture between superdeltoid and the cryptodeltoids. The gonoduct formed by the *C* cryptodeltoid (figs. 10.3–8) in the sectioned specimen, although one might think that in other specimens the other cryptodeltoid may form the gonoduct. In *Heteroschisma* the gonopore is only known from *H. alternatum* (fig. 14.4) and from *H. subtruncatum* (fig. 16.3), where it lies externally in the suture between the super- and the subdeltoid. The gonoduct in this genus is more widely known. It is present in *H. gracile* (figs. 12.4–6), *H. alatum* (figs. 13.3–6), *H. alternatum* (fig. 14.5), *H. canadense* (fig. 15.5), and *H. subtruncatum* (fig. 16.4). In all these species the gonoduct is formed by the subdeltoid.

No external gonopore was found in any Carboniferous (Mississippian) phaenoschismatids. The gonoduct is observed to be present in *Phaenoschisma acutum* (fig. 17.3). *P. conicum* (figs. 18.5, 6), *P. laeviculum* (figs. 20.2–4), and *P. chouteaui* (figs. 21.5, 6), in which species the gonoduct is formed by the epideltoid. No evidence of gonopore or gonoduct is found in *Phaenoblastus caryophyllatus.*

The Russian genera *Dolichoblastus* and *Kazachstanoblastus,* placed with a query mark in the phaenoschismatids, have not provided any information on structures belonging to the genital system.

Phaenoschismatids, as now listed above, prove to have an external gonopore in all such cases where the composition of the anal area is complex, and in which the superdeltoid is bordered aborally either by a

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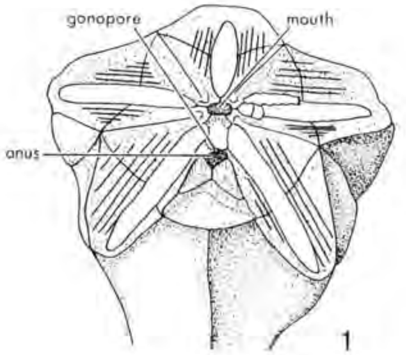
Textfig. 46. Morphology and anatomy of skeletal structures allied to the genital or reproductive system. (1) *Polydeltoideus enodatus* (Sil., Henryhouse Fm., Pontotoc Co., Okla., USA; spec. USNM 139567.) Specimen in oblique posterior view, showing external gonopore inbetween mouth and anus. (2) *Pterotoblastus brevialatus* (Perm., Timor, nr. 10 in growth series). Specimen in posterior view, showing gonopore in internal adanal surface of epideltoid. (3) *Polydeltoideus enodatus* (Sil., USA). Section of anal area (subdeltoid present) showing gonopore in suture between super- and subdeltoid. (4) *Pentremitidea pailletti* (L. Dev., Spain). Section of anal area (cryptodeltoids present, not reaching superdeltoid), with position of non-calcified external gonopore indicated. (5) *Pleuroschisma verneuili* (L. Dev., Spain). Section of anal area (cryptodeltoids present, reaching superdeltoid), with external gonopore in suture between super- and cryptodeltoids. Figures 3 and 5 to be compared with figure 11. (6) *Astrocrinus tetragonus* (L. Carb., Scotland). Section of anal area (cryptodeltoids present, reaching superdeltoid, but not joined admedially) with gonoduct in superdeltoid. (7) *Orophocrinus conicus* (Miss., USA). Section of anal area with gonoduct in epideltoid. (8) *Anthoblastus stelliformis* (Perm., Timor). Section of anal area with gonoduct in epideltoid. (9) *Phaenoschisma laeviculum* (Miss., USA). Section of anal area with gonoduct in epideltoid. (10) *Nannoblastus pyramidatus* (Perm., Timor). Section of anal area with gonoduct in epideltoid. Figures 7–10 to be compared with figure 12. (11) Longitudinal and median section through anal area of fissiculate blastoid with external gonopore in suture between superdeltoid and sub- or cryptodeltoid; compare with figs. 3 and 5. (12) Longitudinal and median section through anal area of fissiculate blastoid with gonopore in internal adanal surface of epideltoid; compare with figs. 7–10.



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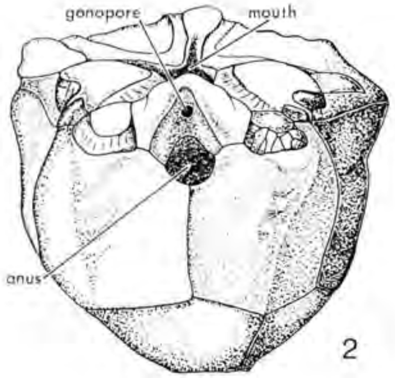

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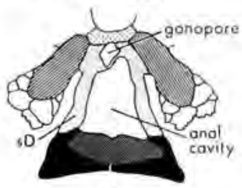
EXTERNAL GONOPORE IN SKELETON

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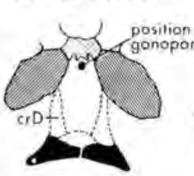
EXTERNAL GONOPORE OUTSIDE SKELETON

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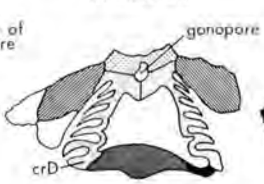
EXTERNAL GONOPORE IN SKELETON

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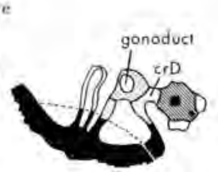

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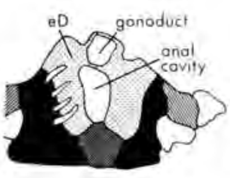
GONODUCT AND INTERNAL GONOPORE DEVELOPED BY EPIDELTOID



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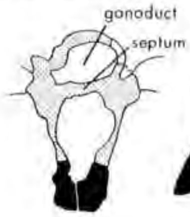

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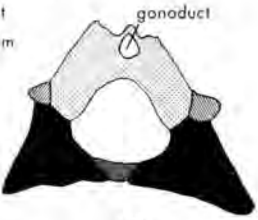

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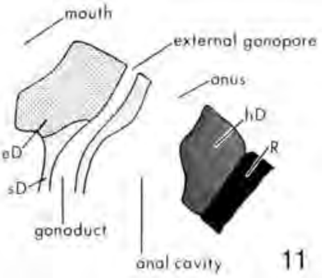

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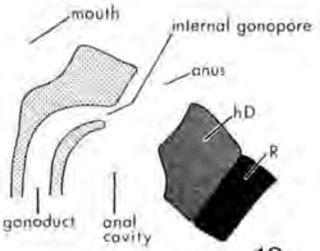


12

subdeltoid or by two cryptodeltoids *(Decaschisma, Polydeltoideus* (fig. 46.3), *Leptoschisma, Caryoblastus, Pleuroschisma, Heteroschisma).* This is apparently the primitive position of the gonopore; it is present in the oldest phaenoschismatids. It is probably highly significant that if cryptodeltoids do not meet laterally along the aboral edge of the superdeltoid (in *Pentremitidea* (fig. 46.4), *Cryptoschisma*, and *Phaenoblastus*) no gonopore is found in the skeleton. In such cases (and conspicuously so in *Pentremitidea*, fig. 46.4) the superdeltoid possesses, along its aboral edge, a semicircular rim which is produced aborally into two small prongs including a notch. It is this rimmed notch which is now believed to support the external opening of the gonoduct, which itself was not calcified as in the other phaenoschismatids.

Also, if the composition of the anal area is simple, and only an epideltoid is present *(Phaenoschisma)* no distinct gonopore is found externally. Such a pore should be expected to lie in the internal adanal surface of the epideltoid, opening into the anal cavity. The adanal surface of the epideltoid forms a notch in which the gonopore may be expected.

The gonoduct, as we have now interpreted it, is a small tube- or collar-like internal extension sent out by one of the anal deltoids (figs. 46.11, 12). Gonoducts have been found in all phaenoschismatids, except in *Pentremitidea, Cryptoschisma* and *Phaenoblastus* (in *Caryoblastus* not found either, but here probably due to state of preservation of the sectioned specimen). As a rule the gonoduct is formed by the subdeltoid (*Polydeltoideus* (fig. 46.3), *Leptoschisma, Heteroschisma*), or by the cryptodeltoids (*Caryoblastus, Pleuroschisma*, fig. 46.5). The only exception is *Decaschisma*, in which genus the gonoduct is formed by the superdeltoid. In case there is only an epideltoid (*Phaenoschisma*, figs. 46.9, 12) the gonoduct is formed by that plate. Here again, as with the gonopore, the gonoduct is found not to be calcified in forms where cryptodeltoids do not meet laterally along the aboral edge of the superdeltoid *(Pentremitidea, Cryptoschisma,* and *Phaenoblastus).*

Orophocrinids did not show an external gonopore. Remnants of gonoducts have been observed in *Brachyschisma corrugatum* (fig. 24.4) where it is formed by the superdeltoid, and in *Mastoblastus ornatus* (fig. 26.5), *Orophocrinus conicus* (figs. 28.6, 7; fig. 46.7), and *Anthoblastus stelliformis* (fig. 32.5; fig. 46.8) where it is formed by the epideltoid. It is surprising that an external gonopore has not been found in *Brachyschisma* where it could be expected to lie in the suture between the super- and the subdeltoid. Its absence may be due to the state of preservation of the sectioned specimen. It is not known with certainty how the gonoduct opened. In the case of *Katoblastus püzos* (with complex anal interarea: superdeltoid, two cryptodeltoids and hypodeltoid) where the cryptodeltoids do not meet laterally along the aboral edge of the superdeltoid, we find that the aboral edge of the superdeltoid possesses a notch which could have supported the gonopore in much the same way as in the phaenoschismatids

Cryptoschisma, *Pentremitidea*, and *Phaenoblastus*. In the case of *Mastoblastus ornatus* there could probably be a gonopore partly piercing the epideltoid. In all other cases the gonoduct is presumed to have opened in the anal cavity.

The astrocrinid *Astrocrinus tetragonus* did not show an external gonopore, but a gonoduct is present (figs. 33.5–8; fig. 46.6), formed by the superdeltoid. Here again, the gonoduct is presumed to have opened in the anal cavity.

The neoschismatids have received only partial anatomic study since many Permian forms have not provided sufficient material to allow sectioning of specimens. Only Carboniferous species of *Hadroblastus* and the Permian form *Timoroblastus* have been studied. In *Hadroblastus convexus* a gonopore is present (figs. 34.1, 2) in the central aboral part of the epideltoid. Gonoducts are found in *Hadroblastus convexus* (figs. 34.8, 10), *Hadroblastus whitei* (fig. 35.6), and *Timoroblastus coronatus* (fig. 36.7), in all three cases formed by epideltoid material.

The codasterids have provided definite and conclusive information on the presence of a gonopore. The pore is present in the internal adanal surface of the epideltoid of *Pterotoblastus gracilis* (fig. 40.4), and in *Pterotoblastus brevialatus* (fig. 46.2, specimen 10 of measured sample). In *Angioblastus wanneri* (fig. 39.9) a gonopore is probably also present on the epideltoid. Gonoducts are known from *Angioblastus wanneri* (figs. 39.14–17) and from *Nannoblastus pyramidatus* (fig. 42.5; fig. 46.10), in which cases it is formed by the epideltoid material.

Nothing could be determined for the nymphaeoblastids.

In textfigure 46 the skeletal structures belonging to the genital system have been shown comparatively. The external gonopore of *Polydeltoideus* is illustrated in fig. 46.1. The gonopore in the internal adanal surface of an epideltoid can be seen externally in forms with no hypodeltoid and which lost the anal cover plates. This is the case in the specimen of *Pterotoblastus brevialatus* illustrated fig. 46.2.

Figures 46.3–6 show four forms in which the anal area is complex and includes either a subdeltoid or two cryptodeltoids. In figs. 46.3–5 three primitive forms are presented with external gonopores. It should be noted again (as illustrated) that external gonopores only lie within the skeleton if the superdeltoid is bordered aborally either by a subdeltoid (fig. 46.3) or by two cryptodeltoids (fig. 46.5). A median longitudinal section through this region, representing this case, is shown in fig. 46.11. If there is no subdeltoid to border the superdeltoid, or if the cryptodeltoids do not meet one another along the aboral surface of the superdeltoid (as in fig. 46.4), neither gonopore nor gonoduct is found to lie within the skeleton. Apparently they were not calcified. The position of the gonopore is schematically indicated in fig. 46.4. It is supposed that in this case the gonopore was external. The astrocrinid position of the gonoduct (fig. 46.6), and the way it probably opened into the anal cavity is unusual for forms with complex anal deltoids.

Figures 46.7–10 show four different advanced forms in which the anal area is simplified and composed only of epi- and hypodeltoid. In these cases the gonoduct traverses the body of the epideltoid. The gonoduct is seen in the sections to be separated from the anal cavity by a short septum. The internal gonopore would appear in the sections as an interruption of this septum, bringing the gonoduct in open connection with the anal cavity. A median longitudinal section, representing this case, is shown in fig. 46.12.

It is, of course, necessary to present the arguments which led us to interpret the pore and the duct as the gonopore and the gonoduct. Theoretically there is only one alternative interpretation of the pore and the duct; namely, an interpretation of pore and duct belonging to the water-vascular system as the hydropore and the stone canal. The hydropore would then be exercising a madreporitelike function for replenishment of the water vessels. The duct or canal would be the stone canal, connecting the hydropore and the ring canal of the water-vascular system. This alternative interpretation is rejected because we think we have found expressions of the water-vascular system in other parts of the skeleton (see section on ambulacral and water-vascular system) and for the following further reasons:

First crinozoan hydropores, and notably in the cystoids, are known to be different in organization. Some of the hydropores are not simply one single opening, but rather a group of tiny openings, being a sievelike penetration of a thecal plate. Some others appear as short slitlike folds. This condition is not found within the fissiculates.

Second, the form, dimension, and arrangement of the duct are not in favor of an interpretation of the duct as the stone canal. Its diameter (up to 0.5 mm) far exceeds known diameters for crinozoan water vessels (0.1 mm). The form of the duct may be irregular, showing some folding, particularly in its innermost parts. This folding would rather correspond to irregular forms of a gonad than to a connection with a fine ring canal. Also the connection of the pore with the anal cavity, and notably the fact that in advanced fissiculates the duct is seen to open in the anal cavity (rectum), is strong evidence for its interpretation as a gonoduct.

Last, the configuration of pore and duct, as we have found it in the sections, would imply, on the basis of an alternative interpretation, a stone canal coming in from a posteriorly situated hydropore and penetrating freely and rather deeply into the thecal cavity. This would place the ring canal in a position somewhat removed from the mouth, detached from the peristomial epidermis, and lying freely within the thecal cavity. This position is highly unlikely for an echinoderm ring canal. This canal is always found associated with the mouth and to be attached to the peristomial epidermis. The ring canal would then be supported further by or hanging in strands and webs of connecting tissue, and the radial water vessels would have to freely traverse part of the thecal cavity and the peristomial opening in order to connect with the ambulacra on the outside of the theca. This is not held probable.

The main phylogenetic trends in the development of the genital system, as we have now defined, interpreted, and discussed it, are closely connected with the phylogenetic trends in the development of the composition of the anal deltoids. In order to keep all the information on phylogenetic trends together, the phylogeny of the genital system is further dealt with in the Chapter on Phylogeny.

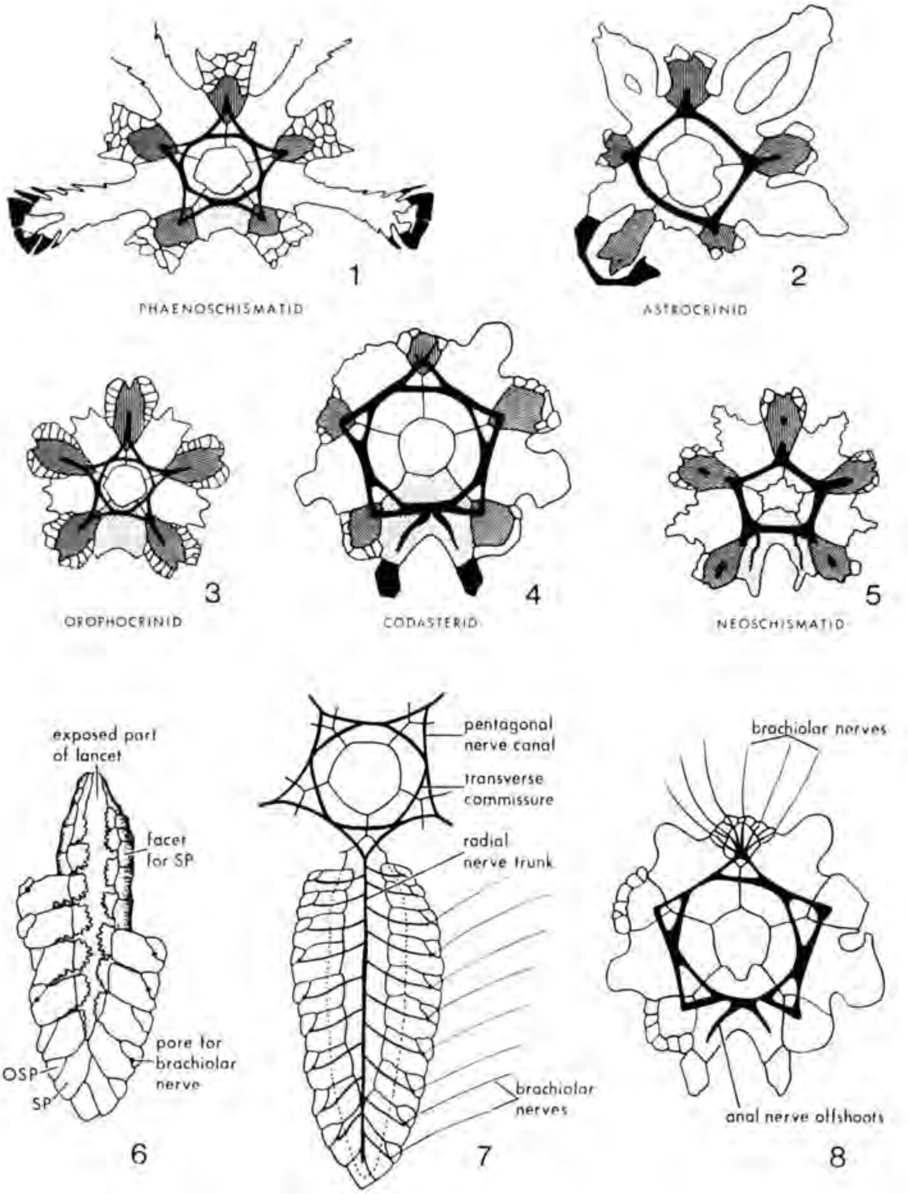
Nervous system

Blastoid nerve trunks are invariably lodged in canals within the skeletal mass, and, after fossilization, they are quite evident there. Information on the nervous system can only be obtained from specimens which are perfectly fossilized and preserve a detailed composition of their original inorganic skeletal calcitic structures. This implies that our knowledge on the composition of the nervous system in the fissiculate blastoids is scattered among representatives of the several different families. However, total information now available has led to a considerable improvement of our knowledge of the system.

The presence and configuration of elements of the nervous system in the several different fissiculate families is now briefly dealt with. A discussion on the total system is given at the end of this section.

The oldest known (Silurian and Lower Devonian) genera from the phaenoschismatids *(Decaschisma, Polydeltoideus, Leptoschisma, Caryoblastus, Pentremitidea, Cryptoschisma,* and *Pleuroschisma)* unfortunately have yielded no information on the composition of their nervous system. Only traces of radial nerve canals in the lancet (fig. 4.2; fig. 6.4; fig. 7.4; fig. 8.3) have been found.

On the contrary, the Middle Devonian phaenoschismatid genus *Heteroschisma* has provided splendid information on the composition of the ring canals of the oral nervous system. In *H. alternatum* (fig. 14.2), *H. canadense* (fig. 15.2; fig. 47.1) and *H. subtruncatum* (fig. 16.2) there is a pentagonal ring canal with the angles of the pentagon in the adoral tips of the lancets. The pentagonal canal crosses the lancet-deltoid (LD) sutures and traverses the deltoid lips. Transverse commissures are present over the interdeltoid sutures connecting with the pentagonal canal within the deltoid lips. At posterior side the pentagonal canal traverses the superdeltoid, and transverse commissures are sent out from the superdeltoid over its sutures with adjacent deltoids. The oral nervous system does not show any sign of differentiation at the posterior side. The radial nerve trunks traverse the lancets over their full length. They do not continue within the radial.



Textfig. 47. Anatomy of skeletal structures allied to nervous system. (1) Phaenoschismatid nervous system, drawn from *Heteroschisma canadense* (M. Dev., Ont.), slightly restored, compare with fig. 15.2 (2) Astrocrinid nervous system, drawn from *Astrocrinus tetragonus* (L. Carb., Scotland), slightly restored, compare with fig. 33.3. (3) Orophocrinid nervous system drawn from *Orophocrinus praelongus* (L. Carb., Ire.), slightly restored. (4) Codasterid nervous system, drawn from *Angioblastus wanneri* (L. Perm., USSR), restored. (5) Neoschismatid nervous system, drawn from *Hadroblastus whitei* (Miss., USA), slightly restored, compare with fig. 35.3. Note absence of transverse commissures in astrocrinid (2) and neoschismatid (5) nervous systems. Note presence of anal nerve offshoots in *CD* interray in codasterid (4) and neoschismatid (5) nervous systems. (6) *E* ambulacral area of holotype of *Phaenoschisma acutum* (L. Carb., Engl.), showing pores for nerve canals in sutures between side plates and outer side plates. (7) Reconstruction of phaenoschismatid nervous system, including central circumesophageal canals, radial nerve trunks, and offshoots leading to brachiolar nerves. (8) Reconstruction of codasterid nervous system, including central circum-esophageal canals and direct offshoots from these canals leading into the brachioles; note absence of radial nerve trunks.

The Carboniferous phaenoschismatid species *Phaenoschisma acutum* has provided a surprising result in the study of the oral nervous system. The type specimen of this species (BMNH E 8130, figured by G. B. Sowerby in 1834), shows a number of minute pores in the sutures between side plates and outer side plates in the *E* ambulacral field (fig. 47.6), situated in the middle of the brachiolar facets. The pores are interpreted as carrying a nerve extension coming from the radial nerve trunk in the lancet, and leading into the brachiole. This is the first time that any skeletal expression of the existence of such a brachiolar nerve has been found. From the position of the pores in the suture between side plates and outer side plates and in the center of the brachiolar facet, it is inferred that the brachiolar nerve was lying in the suture between the biserially arranged brachiolars, being enclosed *within* the brachiolar skeleton, (see also fig. 48.8).

(We have found two openings for brachiolar nerves in the spiraculate species *Deltoblastus verbeeki*, each lying in one half of the brachiolar facet. This would imply that each brachiolar possessed a separate brachiolar nerve.)

Phaenoschismatid fissiculates other than those mentioned above have yielded no information on the nervous system.

Knowledge of the orophocrinid nervous system is incomplete and scattered, preservation of the specimens being a major limiting factor. The best example of an oral nervous system in the orophocrinids has been found in *Orophocrinus praelongus* (fig. 29.3; fig. 47.3). As in the phaenoschismatids, the oral nervous system consists of a pentagonal canal with the angles of the pentagon in the adoral tops of the lancets. The pentagonal canal crosses the LD sutures and traverses the deltoid lips. Transverse commissures are present over interdeltoid sutures to connect with the pentagonal canal within the deltoid lips. The epideltoid carries part of the nervous system and there is no sign of differentiation of the nervous system at the posterior side of the organism. From the angles of the pentagonal canal five radial nerve trunks depart and traverse the lancet over its full length. The radial nerve ends in the aboral tip of the lancet.

In *Orophocrinus verus* (fig. 30.3) the oral nervous system is incompletely preserved; only some parts of the pentagonal ring canal and one transverse commissure have been observed. But this is, at least, further proof that the oral nervous system in orophocrinids is essentially similar to that of the phaenoschismatids.

In *Pentablastus supracarbonicus* (fig. 31.1) parts of the pentagonal canal have been observed, connecting the pentagonal canal with the radial canal in the lancet. No transverse commissure over interdeltoid sutures was observed.

The oral nervous system of the astrocrinid fissiculate *Astrocrinus tetragonus* (fig. 47.2) has a pentagonal canal of large diameter traversing the lips of the regular deltoids and the superdeltoid. The angles of the pentagon are situated at the points where LD and DD sutures meet. Independent transverse commissures formed over interdeltoid sutures seem to be absent. At least they are not observed, and it is unlikely that this should be due to state of preservation. Radial nerve trunks traverse the lancets over their full length. The radial nerves end at the aboral extremity of the lancets and are not continued into radial or basal material. A radial nerve trunk has not been observed in the modified *D* lancet and is believed to have been absent during life. As a result we may state that the oral nervous system of *Astrocrinus* underwent some modification, probably connected with its peculiar mode of life as a stalkless blastoid.

The neoschismatids have yielded relatively little information on the oral nervous system due to a lack of material. A regular case is known from *Hadroblastus whitei* (figs. 35.1–4; 47.5). It consists of a pentagonal canal of considerable diameter crossing the LD sutures and traversing the adoral tips of the regular deltoids and the epideltoid. The angles of the pentagon are situated at the points where LD and DD sutures meet. No independent transverse commissures crossing the DD sutures have been observed. At posterior side there are two short nerves lying in the limbs of the epideltoid. These nerves could probably have operated the anal opening. A radial nerve canal traverses the lancets over their full length. The radial nerves end at the aboral extremity of the lancets and do not continue into the radials.

In *Thaumatoblastus longiramus* (figs. 45.1–3; fig. 48.8) there is a very wide radial nerve trunk in the lancet. Longitudinal nerve commissures are found to run parallel to the radial nerve trunk and to traverse the bodies of the side plates. Connections between radial nerve and longitudinal commissures exist. An observed case is illustrated in fig. 45.3. Also, the longitudinal commissures send branches into the brachioles (fig. 45.1; fig. 48.8).

The codasterids have yielded more and partly unexpected information on the nervous system. In *Angioblastus variabilis* (fig. 38.3) there is a wide pentagonal canal of small diameter removed from the peristomial cavity with the angles of the pentagon in the adoral tips of the small rhombic lancets, crossing the LD sutures and traversing the regular deltoids and the epideltoid. No transverse commissures crossing DD sutures have been found. There is a chance, however, that this is due to preservation. In *Angioblastus wanneri* (figs. 39.4–8; fig. 47.4) an oral nervous system has been found with a pentagonal canal which is much the same as in *A. variabilis*. A transverse commissure over the DD suture has been found at *A* radial side (fig. 39.7), proving that the central part of the oral nervous system in codasterids is constructed in much the same way as in the phaenoschismatids and the orophocrinids. In *A. wanneri* there are probably offshoots from the pentagonal nerve canal in the limbs of the epideltoid, which, as in the neoschismatid *Hadroblastus whitei*, could have operated the anal opening.

A difference with the nervous system of other families is found in Permian codasterids. Radial nerve canals departing from the angles of pentagonal nerve canals seem to be absent in forms with a small rhombic lancet. In *Angioblastus wanneri* (section 13, unpublished) and in *Nannoblastus pyramidatus* (fig. 42.6) small nerve canals have been found coming from the adoral tip of the lancet and leading directly to the side plates and brachioles, which are placed in a semicircle around the aboral edge of the lancet. It is inferred that in such cases the brachiolar nerves departed independently from the angles of the pentagonal nerve canals (fig. 47.8).

Unfortunately, nothing has become known about the nervous system in *Pterotoblastus*. This would be especially desirable since this form has a short rhombic lancet, but the side plates are not placed in a semicircle around its aboral edge. The side plates are arranged in a longitudinal series and are sitting on the radial prong. The radial nerve could be lying in the radial prong, thus being the only case in which the radial would possess part of the nervous system.

In summary, the oral nervous system of the fissiculates is built according to a rather uniform pattern, showing only minor variations. For a better understanding of the matter two nervous systems have been reconstructed in fig. 47. The one case (fig. 47.7) represents the early phaenoschismatid development of the nervous system, the other case (fig. 47.8) represents the later Permian codasterid development of the system.

In all known cases a pentagonal nerve canal lies in the adoral parts of the regular deltoids and one of the anal deltoids (either superdeltoid or epideltoid). The sides of the pentagonal nerve canal traverse the deltoid lips, cross the LD sutures, and meet in the adoral tips of the lancets. With the exception of *Astrocrinus tetragonus* and *Hadroblastus whitei*, transverse commissures are present, formed over the DD sutures and connecting with the sides of the pentagonal nerve canal within the lips of the deltoids. If an elongate lancet with many side plates and brachioles is present (fig. 47.7), a radial nerve trunk is found to depart from the angle of the pentagonal canal and to traverse the full length of the lancet. In no case has any evidence been found that the radial nerve canal continued into the radial body, so as to connect with a possible other nervous system in the aboral part of the blastoid theca.

From the radial nerve trunk separate smaller nerves led to the brachioles. These brachiolar nerves traversed the sides of the lancet, and came to lie in the brachiole by way of a pore in the suturebetween side plates and outer side plates, as has been observed in *Phaenoschisma*. From there they probably ran the full length of the brachioles, enclosed within the brachiolar skeleton.

In the case of *Thaumatoblastus longiramus* there exists a pair of longitudinal commissures, running parallel to the radial nerve trunk in each of the two side plate series. The longitudinal commissures interconnected the offshoots for the brachiolar nerves.

If a short rhombic lancet with few side plates and brachioles is present (such as in the Permian codasterids, fig. 47.8) no radial nerve trunk is developed. The several different nerves leading to the brachioles depart separately from the angle of the pentagonal canal and lead independently into the side plates and brachioles.

We have now found that the main blastoid nervous system was the oral nervous system. An aboral nervous system, such as in the crinoids, is not developed or not known. The absence of knowledge of the blastoid aboral nervous system and the consequences it may have for the stalk and its flexibility, are dealt with later in the final section of this chapter.

The blastoid oral nervous system is interpreted to be the motor system. It is logical to suppose that the motor system was connected with and stimulated by a separate sensory system. One could think, in a good crinozoan fashion, of tube foot papillae with tactile function, passing received stimuli on to a hyponeural system, located just beneath the ambulacral epidermis. The motor system would pass stimuli to brachiolar muscles (if they existed), causing the brachioles to actively move; to tube foot muscles for contraction of tube feet and operation of movable cover plates; to anal muscles for opening and closure of the anus; and to muscular tissue around the mouth for opening and closure of the mouth (if it was not covered).

In order to keep all information of the phylogeny together, the phylogeny of the nervous system is dealt with in the Chapter on Phylogeny.

AMBULACRAL AND WATER-VASCULAR SYSTEMS

The ambulacral system of blastoids is mainly an external system and should receive due attention in morphological descriptions. However, anatomical studies of blastoids have now proved that in some cases parts of the ambulacral systems have come to lie within the skeleton. For the sake of clear morphological and anatomical description of these systems, it has been found necessary to redefine previous morphologic terms applied to the ambulacral system.

The terms *ambulacral field*, *ambulacral area*, or *ambulacrum* are used for description of blastoids to include the total structure composed of the ambulacral plates: lancet, side plates, and outer side plates. The brachioles are held not to be part of the ambulacral area, as in the definition of ambulacrum by BEAVER, FAY, & MOORE (1967). The ambulacral area bears the ambulacral tract.

The term *ambulacral tract* is completely new, and is introduced to help morphological descriptions to be more precise. It is a concave tract on the brachioles, ambulacral areas, and interdeltoid sutures, with ambulacral grooves in its bottom, and covered by ambulacral cover plates (figs. 48.2, 4, 5). The ambulacral tract consists of a *brachiolar tract*, present on the brachioles; of *side tracts*, situated on the sutures inbetween adjacent side plates; and a *main tract* along the median line of the ambulacral area (either on exposed lancet or, again, inbetween side plates), continuing on to the interdeltoid sutures. The five main tracts may join in a circumoral position (Pl. XXXIII, fig. 8). The entrance of the brachiolar tract on the ambulacral area is known as the brachiolar socket. From there it connects with the ambulacral side tracts (Pl. XXXIV, figs. 4–6).

The borders of the ambulacral tracts are easily observed in the blastoids. The side tracts inbetween adjacent side plates are separated by elevated central parts of side plates and/or by elevated transverse ridges on the central parts of exposed lancets (Pl. XXXIV, figs. 1, 5, 6); the main tract has a marked line near the interdeltoid suture (figs. 48.1, 2, 4, 5; Pl. XXXIV, fig. 2).

The ambulacral tract is always a concave tract. In some cases it is known to be covered with cover plates. Another type of structure, ambulacral spines, was described and illustrated by FAY & REIMANN (1962, textfig. 4) from *Hyperoblastus nuciformis*. If their interpretation is correct, cover plates were apparently absent. The ambulacral spines might have served the same function as the cover plates. Ambulacral side tracts of *Pentremites symmetricus* have been described by BEAVER (1967) as being covered by biserially arranged cover plates. The main tract in *P. symmetricus* is known to have been covered (at least in the adoral part) by a tegument enforced with many small irregular calcitic platelets. In our present study the main ambulacral tract on interdeltoid sutures of *Orophocrinus stelliformis* and *Pterotoblastus gracilis* (fig. 48.3) have been found to be covered by biserially arranged cover plates. Brachiolar tracts have been described in the literature as being covered by cover plates (SPRINKLE & GUTSCHICK, 1967).

The cover plates of the ambulacral tract system are known as *ambulacral cover plates*. The homologues of these plates in the crinoids are called ambulacral plates. However, in the blastoids this term would create confusion because the lancet, side plates, and outer side plates are regarded as ambulacral plates.

The ambulacral tract possesses an *ambulacral groove system*, situated in the bottom and the sides of the concave ambulacral tract. The grooves are present in the median line of the main ambulacral tracts and are termed *main ambulacral grooves*. They are also present in the median line of the ambulacral side tracts and termed *ambulacral side grooves* (Pl. XXXIII, fig. 8; Pl. XXXIV, figs. 1–6). They continue onto the brachioles and, consequently, are termed *brachiolar grooves*. All along their course on the ambulacra the ambulacral grooves send out *minor grooves* to the left and right in the walls of the ambulacral tract. In many cases the minor grooves at both sides of the ambulacral grooves are known to alternate with one another. The parts of the ambulacral tracts inbetween the minor grooves (known as minor lobes) may be somewhat thickened admedially (figs. 48.4, 5). Normally the minor grooves do not reach the outer edge of the tract but remain below that line, and entirely within the ambulacral tract. Two examples of ambulacral groove systems are illustrated in figs. 48.2 and 48.4.

What we have now defined as the ambulacral groove system has been interpreted in several ways in previous literature on the subject. The brachiolar, side, and main parts of the ambulacral groove system frequently have been interpreted as the "food groove", an interpretation we do not follow because we think that morphological and anatomical information now available can no longer support that view.

In past literature the minor grooves at both sides of the ambulacral groove have been termed "cover plate lobes and furrows". Recently Beaver (1967) interpreted them as "articulation grooves for ambulacral cover plates". We wish to modify this interpretation for the following reasons. Amongst the crinozoans the ambulacral cover plates do not have any particular articulatory structures expressed in the skeleton. In the blastoids the ambulacral cover plates (if present) are situated high up at the extreme edge of the ambulacral tract, whereas the minor grooves occupy the lower regions of the tract. If the minor grooves served the cover plates for articulatory purposes, the cover plates would reach far down in the tract and almost fill it. The purpose of the cover plates is rather to protect anything underneath them. Sections have shown that there is indeed an open space under the cover plates. Of course, we agree with Beaver that the ambulacral cover plates could open and close when biserially arranged. A possible mechanism for opening and closing these

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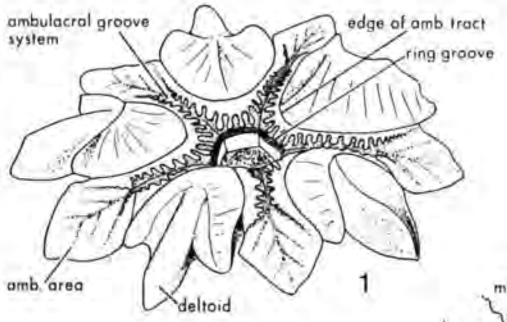
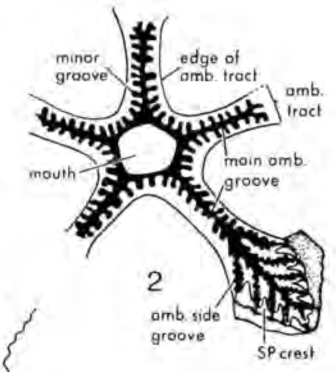
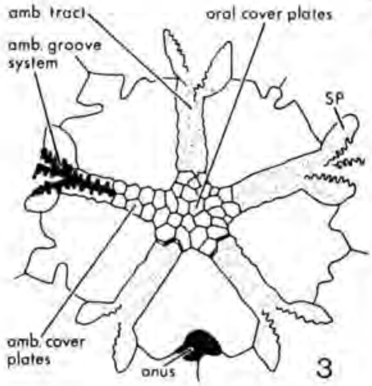
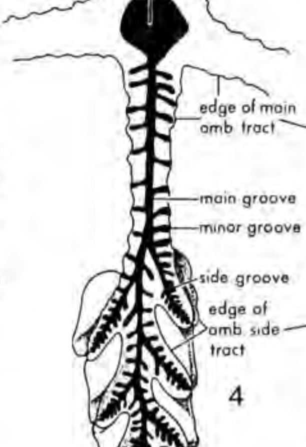
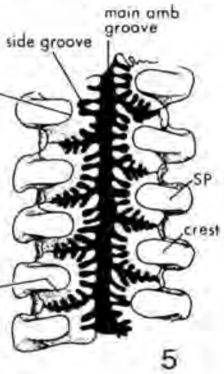
Textfig. 48. Morphology of skeletal structures allied to ambulacral and water-vascular systems. (1) *Angioblastus wanneri* (L. Perm., USSR). Oblique adoral view of ambulacral tract and groove systems to show impression of ring canal. (2) same, plan view, with detailed ambulacral tract and groove systems in *C* ambulacral area. (3) *Pterotoblastus gracilis* (Perm., Timor). Adoral plan view, showing ambulacral tracts; mouth covered by ambulacral cover plates. Ambulacral groove system drawn in *DE* tract. (4) same, with detailed ambulacral tract and groove systems on one ambulacral area. (5) *Thaumatoblastus longiramus* (Perm., Timor). Plan view of part of ambulacral area, showing detailed structure of ambulacral tract and groove systems. (6) same, side view, showing inclined brachiolar facets and position of ambulacral grooves. (7) Reconstruction of blastoid water-vascular system, including ring canal, radial water vessels and side vessels leading to brachiolar vessels; vessels provided with tube feet, but only partly shown. (8) Reconstruction of transverse section of ambulacral area (inspired by *Thaumatoblastus longiramus*), showing water vessels and tube feet in the ambulacral groove system, and ambulacral cover plates roofing over ambulacral tract. Nerve canal in lancet gives offshoots in brachiolar skeleton. Note longitudinal commissure in side plates. (9) Series of drawings to show progressive overgrowth of ambulacral groove system by lancet. (a) open groove; (b) partial overgrowth by lancet, restricted grooves with pores between thickened lobes, main groove restricted at external side; (c) complete overgrowth by lancet, groove is now duct lying in lancet, pores opening in ambulacral tract.

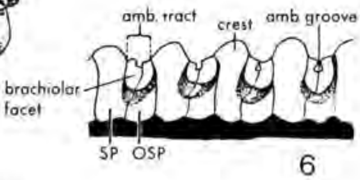

ambulacral groove system
edge of amb tract
ring groove
amb. area
deltoid
1

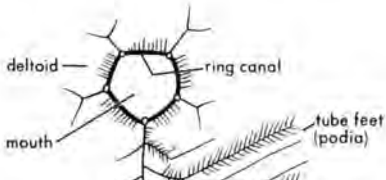

minor groove
edge of amb. tract
amb. tract
mouth
main amb. groove
2
amb. side groove
SP crest

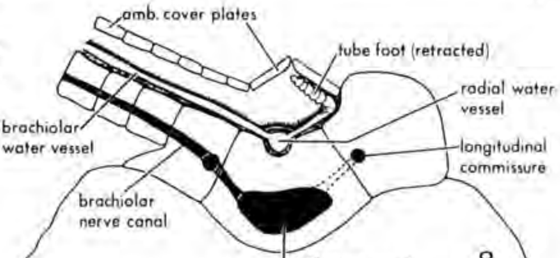

amb. tract
oral cover plates
amb. groove system
SP
amb. cover plates
anus
3

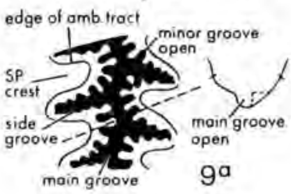

mouth
edge of main amb. tract
main groove
minor groove
side groove
edge of amb. side tract
4

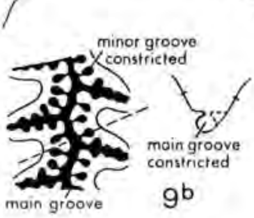

main amb groove
side groove
SP
crest
5

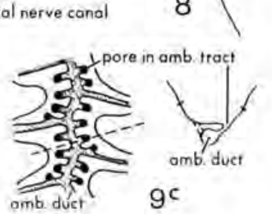

amb. tract
crest
amb groove
brachiolar facet
SP
OSP
6


deltoid
ring canal
mouth
tube feet (podia)
radial water vessel
7


amb. cover plates
tube foot (retracted)
radial water vessel
brachiolar water vessel
longitudinal commissure
brachiolar nerve canal
radial nerve canal
8


edge of amb tract
minor groove open
SP crest
side groove
main groove open
main groove
9a


minor groove constricted
main groove constricted
main groove
9b


pore in amb. tract
amb. duct
amb. duct
9c

is suggested below. We would like to suggest a new interpretation for the ambulacral tract and its ambulacral grooves than previously given. In this interpretation it is essential that we have distinguished between ambulacral tract and ambulacral groove. The ambulacral tracts come in from the brachioles, run over the ambulacral areas, and end in the mouth. It is generally accepted that the brachioles are the main food-gathering organs and that the food is conveyed by the ambulacral system to the mouth. A food-gathering and a food-conveying function may be attributed to the ambulacral tract. When functional the ambulacral cover plates were opened. Our interpretation of morphologic details within the ambulacral tracts starts from the assumption that the blastoid ambulacral tract was not essentially different from any other crinozoan ambulacral tract, and, consequently, it is felt legitimate to compare it with the ambulacral tract of the living crinoids.

The ambulacral tract of a living crinoid is a concave tract, the bottom of which is formed by a thick ambulacral epidermis, provided with long attenuated cells with cilia and with mucous-secreting cells. The tract is bordered by a series of lappets which may contain reinforcing calcareous deposits or even complete ambulacral cover plates. Within the crinoid ambulacral tract minute podia or tube feet are placed in triads in alternating order. The podia contain the terminal branches of the water-vascular system which directly join the radial water vessel. The crinoid radial water vessel immediately underlies the ambulacral epidermis and follows the median line of the ambulacral tract. The podia function in gathering food by spitting out a mucous net, and assist the cilia in conveying the food towards the mouth. The podia are muscular, able to protract by a pressure-regulation system in the water vessels, and to contract by their own musuclar activity. The podia are laterally connected with the lappets and they close the cover plates upon their contraction.

The uniformity of the ambulacral tract system in living crinoids suggests its use as a model for fossil and extant crinozoans. Therefore, the following interpretation of the blastoid ambulacral tract system is offered. The form of the tract and the form and arrangement of the ambulacral cover plates is directly comparable between blastoids and crinoids. The ambulacral grooves in the ambulacral tract of the blastoids are believed to have lodged the water-vascular system. The five main grooves of the ambulacral areas therefore lodged the five radial water vessels. From these, side vessels were given off to each side tract and ultimately on to the brachiolar tract. The minor grooves everywhere present along the ambulacral grooves are interpreted to have lodged the terminal vessels of the water-vascular system, which were leading into the tube feet or podia. Each minor groove is interpreted to have lodged one podium at least, if not a triad of podia. The podia are believed to have been responsible for opening and closing of the ambulacral cover plates (when in biserial arrangement). The entire width of the ambulacral tract can be thought of as being coated or lined with ambulacral epidermis. This makes the food-conveying capacity of the tract considerably larger than for the previously known "food groove". If anything should be compared to a food groove, it is the ambulacral tract.

One of the main points brought forward by the present interpretation is the supposition that the ambulacral groove system did indeed lodge a vascular system. We will consider now if there is any evidence from the blastoids themselves that (1) we are dealing with a vascular system, and (2) that the vascular system involved is indeed the water-vascular system.

(1) We have defined the ambulacral groove system as having minor grooves at both sides in alternating order. The parts of the tract inbetween the grooves may be thickened and appear as lobes. The alternation of grooves and lobes has sometimes been called the ambulacral lobes and furrows. It is known from blastoids (e.g., *Mesoblastus crenulatus*) that the lobes inbetween the grooves may be so thickened that they contact one another laterally. By so doing they constrict the terminal portion of the groove and convert it in a pore (fig. 48.9). In such cases the pore connects with a tubelet underneath the thickened lobes. These tubelets open into the main groove, which itself is now a bit constricted at its external side. We may speak in this case of a certain overgrowth of the lancet over the grooves. This tendency is even further developed in the orbitremitids, which recently received anatomical study by BREIMER & JOYSEY (1968). They found conclusive evidence for the presence of an ambulacral duct system just underneath the external surface of the lancet. The configuration of this ambulacral duct system is the same in every detail as for the ambulacral groove system. There is a main ambulacral duct along the median line of the ambulacral area; there are tributary or side ducts underlying the ambulacral side tracts; and lastly there are minor ducts which pierce the lancet and connect with the main ambulacral ducts. The minor ducts open with pores *in* the ambulacral tract. Breimer & Joysey have confined themselves to a purely morphological description of the ambulacral duct system of the orbitremitids and have waited to present a biological interpretation until the results of the present anatomical study (which was already in progress when they wrote their paper) would be available. Their work proved that the ambulacral duct system of the orbitremitids lodged a vascular system.

From the present work it has become known that *Astrocrinus tetragonus* is the only fissiculate blastoid which has an ambulacral duct system comparable to that in the orbitremitids.

It is clear from our reasoning that the ambulacral duct system of the orbitremitids is nothing else than the ambulacral groove system of other blastoids overgrown by lancet and side plate material (fig. 48.9). When the "groove" is situated within the lancet, it is a duct system. One might deduce from this that the ambulacral groove system, if open, also lodged a vascular system.

(2) If the ambulacral groove system did indeed lodge a vascular system, which of the several different crinozoan vascular systems could have possibly been lodged in or occupied the grooves?

The genital system must now be excluded as having been lodged in the blastoid ambulacral groove and duct systems. Good evidence has been presented earlier, that the blastoids had internal gonads fully enclosed within the thecal cavity, which opened externally via a gonoduct and a gonopore in the anal cavity (see section on Genital System, this Chapter). From this it is concluded that the genital system of the blastoids was unlike that of the crinoids and did not develop a system of genital canals leading into the brachioles. For this reason the ambulacral groove or duct system is not held to have lodged part of the genital system.

The blastoid oral nervous system is known to develop nerve canals within the skeleton. It is now fully established that the main blastoid nervous system was an oral nervous system lying in the deeper parts of brachioles, lancets, and deltoid DD sectors. No connection has been found between the nerve canals and the ambulacral groove or duct system. Other nervous systems that the blastoid may have had are not held to have been so greatly developed as to leave canals in the skeleton.

The hemal or pherihemal systems are not believed to be responsible for shaping the blastoid ambulacral groove or duct system. The crinozoan hemal system is lacunar rather than vascular. If it had vessels like the ones to be interpreted, they would be very highly differentiated and evolved, a condition which is held very unlikely for the blastoids. The perihemal system of the crinozoans is badly known. In part, its function is performed by the coelomic system.

The coelomic system in crinozoans is divided into an aboral or perivisceral coelom and an adoral or subambulacral coelom. The former surrounds the internal organs (digestive canal) in the theca of crinoids and is of a spongy nature.

The adoral coelom is differentiated as a canal system, everywhere underlying the ambulacral tract and the water vessels. Both the aboral and the adoral coelom send extensions into the arms and pinnules of crinoids. In the blastoids it is held impossible for the aboral or perivisceral coelom to have had extensions outside the theca on the ambulacral areas leading into the brachioles. There is never a direct connection of the brachioles with the thecal cavity. Hence, we exclude the possibility of the aboral coelom having occupied the ambulacral groove or duct system.

The adoral coelomic compartment in the blastoids can be thought to have been situated just beneath the mouth in the peristomial cavity. There is, theoretically at least, a possibility that the adoral coelomic compartment did indeed send adoral coelomic canals out on the ambulacral areas towards the brachioles to underlie the ambulacral epidermis. But as we will see below, we will exclude this possibility on the ground that the blastoid ambulacral tract is regarded as too narrow for lodging these relatively spacious coelomic canals.

The water-vascular system is left as the only possible crinozoan vascular system which could have occupied the blastoid ambulacral groove or duct systems. We hold that the ambulacral grooves exactly reflect the shape of the water-vascular system, and are nothing else than the impression of the water-vascular system in the skeleton. Indeed the ambulacral groove system fulfills every requirement which a crinozoan water-vascular system should have.

First the dimensions. The size, and mainly the diameter, of crinozoan water vessels are generally greatly overestimated. Measurements of the diameter of radial water vessels in anatomic preparations of a mature *Antedon* specimen showed that the diameter varies from 0.1–0.2 mm. The width of the open main ambulacral grooves or closed main ambulacral ducts in blastoids is exactly of the same order of magnitude. Also, the dimensions of the minor grooves closely correspond to the size of a crinoid tube foot. The width of an adoral coelomic canal in crinoids is up to 0.5 mm, which is too wide to have been situated in a blastoid ambulacral tract; the canal would almost fill it.

Second the form. If the ambulacral grooves or ducts were shaped by the water-vascular system, we should find at least a ring canal, radial water vessels, side vessels, and tube feet, sitting on either side of these canals. The main groove, in our interpretation, did accommodate the radial water vessel, the side grooves the side water vessels. The minor grooves are interpreted to have accommodated the direct offshoots from the water vessels, which led to the tube feet. The impressions of the ring canal can be seen in some forms (e.g., *Angioblastus wanneri*, figs. 48.1, 2; *Pterotoblastus brevialatus*, Pl. XXXIII, fig. 8). The edges of the deltoid DD sectors, bordering the peristomial cavity, are shown to possess a five-sided groove with minor grooves coming in from the adoral tips of the deltoids. This groove is interpreted to reflect the position of the ring canal and the labial podia.

In figure 48.7 we have tried to present a complete reconstruction of a blastoid water-vascular system, as reflected by the ambulacral groove system. Fig. 48.8 gives a reconstruction for *Thaumatoblastus longiramus*, showing the position of the radial water vessel in the main ambulacral groove covered with ambulacral epidermis. A tube foot is given off on the right hand side, and a side vessel is running to the left in the brachiole. The reconstruction is based on actual sections of *T. longiramus*, and closely takes into account morphological details shown in figs. 48.5, 6.

Our interpretation, as now presented, implies that we may indeed think in terms of typical crinozoan ambulacral and water-vascular systems as probably being present in all living and extinct crinozoans. This interpretation of the ambulacral groove or duct system being a reflection of the blastoid water-vascular system is preferred above previous interpretations in which the hydrospires are described as the blastoid water-vascular system (BEAVER, 1967).

We have not yet discussed the entrance to the water-vascular system as it could possibly have been organized in blastoids. An external madreporite or hydropore is absent. The single pore in the posterior interradius inbetween the anal deltoids is held to be the gonopore and not the hydropore for reasons set out elsewhere (see section on Genital System). No other pores in the body wall of blastoid thecal plates are known that could have been homologous to crinoid hydrospores, and function as inlets for the water-vascular system. This leaves the ring canal of the water-vascular system without a direct and obvious connection with the outside world, a condition also present in the crinoids. If again, a comparison with the crinoids may be made, we could infer that a blastoid water-vascular ring was provided with many fringelike "stone canals" for intake of water from one of the coelomic compartments as in the crinoids. The coelomic compartments, and primarily if not exclusively, the perivisceral coelom, have been in close contact with the hydrospires. One might speculate that the hydrospire lamellae, being very thin in many cases, were semipermeable to allow water to pass to the perivisceral coelom.

DIGESTIVE SYSTEM

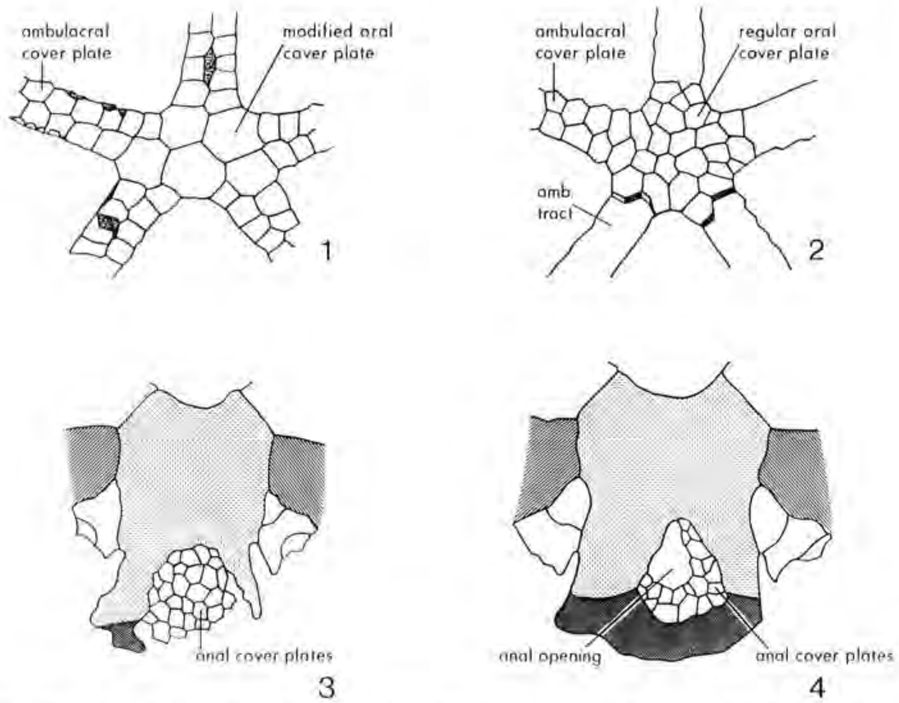
In the fissiculate blastoids only the entrance and exit of the digestive tube are known. The mouth is invariably situated at the free pole of the theca, and the anus is invariably located in the posterior or *CD* interray.

The *mouth*, in a number of cases, is known to be covered by cover plates. In *Orophocrinus stelliformis*, *O. conicus*, and *O. saltensis*, the mouth is covered by five larger plates in a more or less regular arrangement (fig. 27.1; figs. 28.1, 2; fig. 49.1). These five plates are in contact with the biserially arranged ambulacral cover plates which cover the five main ambulacral tracts on the interdeltoid sutures. In *Pterotoblastus gracilis* (fig. 48.3; fig. 49.2) the mouth is also covered, but now by many small plates in irregular arrangement. These plates are the continuation of the biserially arranged ambulacral cover plates covering the five main ambulacral tracts on the interdeltoid sutures.

These four cases (plus an undescribed phaenoschismatid from Montana) are the only ones known among the fissiculates. It is impossible from this to state that the mouth of the fissiculates was always covered by some sort of plated structure. Among spiraculates more examples of oral cover plates are known, proving that the four fissiculate cases mentioned above are not isolated. But it remains possible, at least theoretically, that in some of the fissiculates, and especially the primitive phaenoschismatids, the mouth was not covered by a plated structure.

A regular arrangement of five plates covering the mouth, such as

Orophocrinus, poses the question of a possible homology with oral plates in the crinoids. The five oral plates of the crinoids have an interradial position. In the blastoids, the five oral cover plates are in line with the deltoids and share the interradial position with them. Their topographic position would not detract from a possible homology with the crinoid orals. A more serious problem is posed by the fact that crinoid orals belong to the adoral skeleton and are formed in the vestibular roof of the embryo. No direct embryological evidence, of course, can be given for the blastoids.



Textfig. 49. Oral and anal cover plates in the fissiculate blastoids. (1) *Orophocrinus stelliformis* (Miss., USA). (2) *Pterotoblastus gracilis* (Perm., Timor). (3, 4) *Orophocrinus conicus* (Miss., USA). For further explanation see text.

However, there is another argument. From the arrangement in *O. stelliformis* (fig. 49.1) it can be seen that the five larger plates covering the mouth are the modified and enlarged cover plates of each of the five series of ambulacral tracts. In each ambulacral tract the oralmost cover plate in the right hand series is a larger one and helps to cover the mouth. The posterior one (in the *CD* interradius) is pushed a little in an anterior direction. From this arrangement it is deduced that the five plates are essentially normal cover plates. They are best identified as oral cover plates, rather than orals.

It is assumed that oral cover plates, if irregularly arranged, as in

Pterotoblastus, were not movable, and, consequently, covered the mouth permanently.

The *anus* in the fissiculates is known to be covered in *Orophocrinus conicus* and *O. stelliformis*. A group of small, polygonal, and irregularly arranged plates covers the anus (figs. 49.3, 4). Again, as with the mouth, it would not be justified to state that in all fissiculates the anus was always covered by a plated structure. This may or may not have been the case. Anal cover plates, by necessity, must have had such an organization that periodical opening remained assured.

HYDROSPIRE SYSTEM

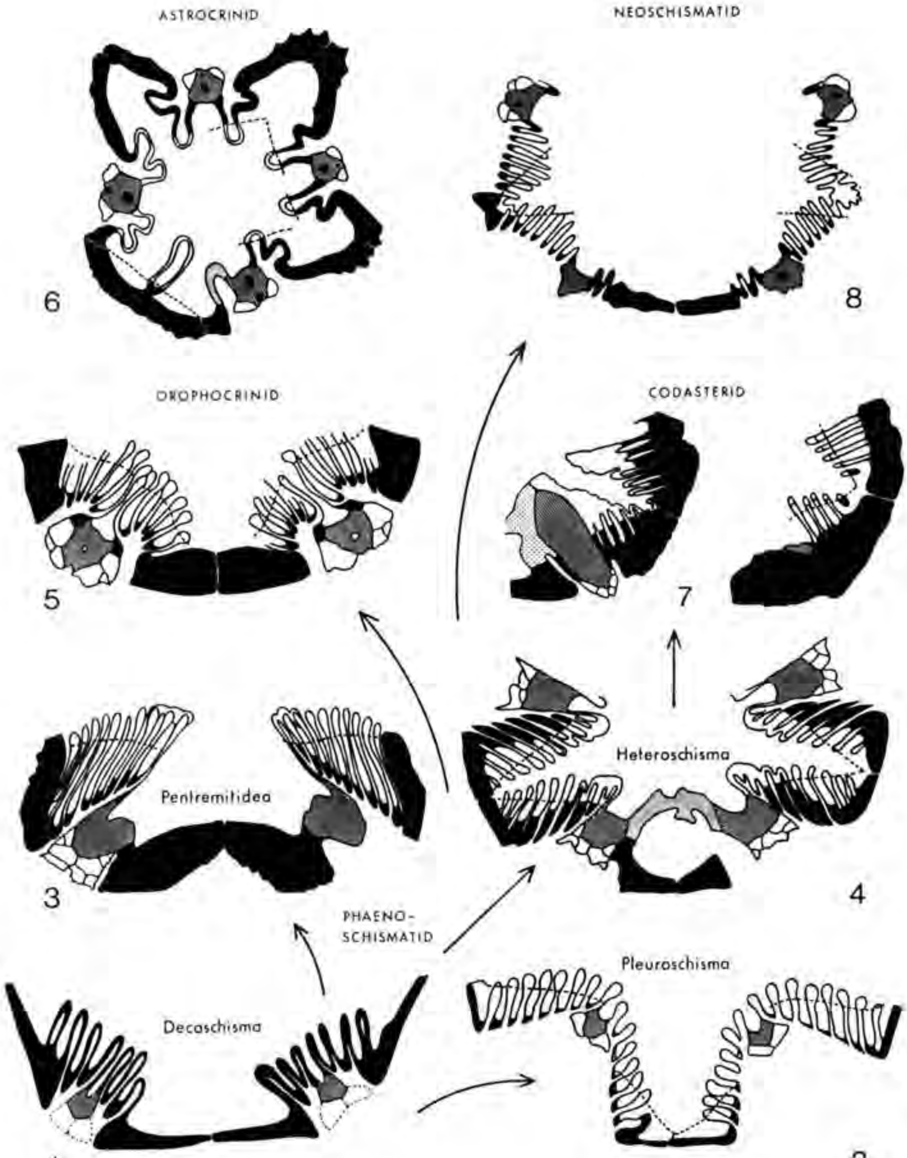
Comparative anatomy of the hydrospire system in fissiculate blastoids shows that hydrospires invariably are built across the RD sutures by radials, regular deltoids, and, sometimes, the anal deltoids. Invariably, the hydrospires are infoldings of the body wall, situated at both sides of an ambulacral area. The hydrospire folds communicate with the external medium through hydrospire slits. The slits may be either completely exposed on the external surface of the theca, or be completely concealed by the ambulacral plates; all possible intermediate situations of partially exposed hydrospire slits are known. In the latter case there is always a hydrospire cleft, separating the ambulacral plates (lancet, side plates, and outer side plates) from the sinus wall (formed by radials and deltoids in the phaenoschismatids). This character is taken as the prime distinctive feature for separating between fissiculates and non-fissiculates.

Hydrospire folds are generally thin-walled, and may show differentiation into parallel hydrospire lamellae and inflated hydrospire ducts or tubes. The hydrospires are generally placed at an angle with the sinus wall (in the phaenoschismatids), and are either placed parallel to one another (most phaenoschismatids, codasterids, and neoschismatids), or are conjoined (orophocrinids, astrocrinids).

The comparative anatomy of hydrospire structures has been illustrated in textfig. 50. Fig. 50.1 starts with one of the oldest phaenoschismatid species, *Decaschisma pulchellum* (Sil., USA; fig. 2.11), in which hydrospire folds are present in all ten available positions, few in number, thick-walled, and not differentiated into hydrospire lamellae and inflated hydrospire ducts. The total enlargement of the thecal wall by hydrospire folding is limited. Thick-walled hydrospires are not regarded as very effective in relation to their function.

Three other hydrospire constructions have been presented for the phaenoschismatids in figs. 50.2–4. These three cases are more or less representative for the morphological trends exhibited by the hydrospire structures in the phaenoschismatids.

The Middle Devonian species *Pleuroschisma lycorias* (M. Dev., Ontario; fig. 10.9; fig. 50.2), still shows ten hydrospire groups, but the hydrospire



Textfig. 50. Comparative anatomy of fissiculate hydrospire structures. (1) *Decaschisma pulchellum* (M. Sil., USA). (2) *Pleuroschisma lycorias* (M. Dev., Ontario). (3) *Pentremitidea archiaci* (L. Dev., Spain). (4) *Heteroschisma canadense* (M. Dev., Ontario). (5) *Orophocrinus verus* (L. Carb., Eng.). (6) *Astrocrinus tetragonus* (L. Carb., Scot.). (7) *Codaster acutus* (L. Carb., Eng.). (8) *Hadroblastus whitei* (Miss., USA). For further explanation see text.

slits are now completely exposed, and the hydrospire folds open individually and directly through their own slits. The folds are short and wide, thin-walled, and placed parallel to one another. A differentiation into hydrospire lamellae and hydrospire ducts is present.

In *Pentremitidea archiaci* (L. Dev., Spain; fig. 8.4; fig. 50.3), there are only eight hydrospire groups. The hydrospire slits are almost completely concealed by ambulacral plates. The entrance to the hydrospire slits is by way of a cleft separating the ambulacral plates from the sinus wall. The hydrospire folds are thin-walled, long, and show a slight differentiation into hydrospire lamellae and hydrospire ducts.

Heteroschisma canadense (M. Dev., Ontario; fig. 15.4; fig. 50.4) shows a tendency halfway inbetween *Pleuroschisma lycorias* and *Pentremitidea archiaci*. The hydrospires are only partly concealed by ambulacral plates. The entrance to the hydrospire slits is either direct (for exposed slits), or by way of a cleft separating the ambulacrum from the sinus wall. The hydrospire folds are thin-walled, and have a slight differentiation into lamellae and ducts.

Figs. 50.5 and 6 show the tendencies in, respectively, the orophocrinids and the astrocrinids, to bring the hydrospires into an internal position. The examples chosen are representative for the configuration of hydrospire structures in these families. The hydrospires in these families are internally conjoined and jointly communicate with the exterior through a hydrospire cleft, separating the ambulacral plates from the radial and deltoid plates. In *Orophocrinus verus* (L. Carb., Eng.; fig. 30.7; fig. 50.5) the hydrospire folds are large in number, long, thin-walled, and well differentiated into hydrospire lamellae and inflated hydrospire ducts. On the contrary, in *Astrocrinus tetragonus* (L. Carb., Scotland; fig. 33.9; fig. 50.6) the hydrospires are small in number, short, thick-walled, and poorly differentiated into hydrospire lamellae and hydrospire ducts.

Figs. 50.7 and 8 show the quite opposite morphological tendency in both the codasterids and the neoschismatids to bring the hydrospires into an external position. The examples are chosen as representative for the configuration of hydrospire structures in these families. Because of the large external development of the deltoids, the hydrospires in these families are on the upper surface of the theca and are fully exposed. The folds open individually through their own hydrospire slits. In *Codaster acutus* (L. Carb., England; figs. 37.8, 9; fig. 50.7), the hydrospires are long, thin-walled structures, with a differentiation into hydrospire lamellae and inflated hydrospire ducts. Fig. 50.7 shows the hydrospire slits in the left hand drawing, and the hydrospire lamellae in the right hand drawing. In *Hadroblastus whitei* (Miss., USA; fig. 35.8; fig. 50.8) the hydrospires are short, thin-walled structures, which lack a differentiation into lamellae and ducts.

A further and more complete treatment of the main phylogenetic trends in the fissiculate hydrospire structures are dealt with in the Chapter on

Phylogeny. It is felt logical to keep all the information on the phylogeny together in that chapter. We have here confined ourselves to the comparative anatomy of the hydrospire structures and their function.

In previous literature two functions have been proposed for the hydrospire system: a genital and a respiratory function. The supposed genital function was deduced from a morphologic comparison with the genital bursae of some modern asterozoans. Our finding of the gonopore and the gonoduct (see section on Genital system) in the blastoids is conclusive evidence that hydrospires cannot be considered any more as possible reproductive organs. The blastoid gonads are now believed to be intrathecal organs opening to the exterior by way of their own duct and pore in the posterior *CD* interradius. There are no skeletal connections between the hydrospires and the gonopore and gonoduct. This connection would be easily detectable in the posterior interray where anal hydrospires are in close proximity to the gonoduct and the gonopore. However, the complete and consistent separation of anal hydrospires and gonoduct/gonopore is further evidence that hydrospires were not part of the genital system.

This implies that the alternative interpretation of the hydrospires as specialized respiratory surfaces has gained new strength. Indeed, almost everything seems to be in favor of this interpretation. Hydrospires, as infoldings of the body wall, increase enormously the total surface of the body wall. This increased surface is everywhere in direct external contact with the surrounding medium (seawater), and in direct internal contact with the body cavity (probably perivisceral coelom). As very thin parts of the body wall they may, indeed, have been destined for skin-respiration, a widely used respiratory mechanism in modern echinoderms.

However, the respiratory function of the blastoid body wall may not have been limited to the hydrospire surface alone. It is held probably that respiration (oxygen intake) in blastoids may have been primarily exercised by the epithelial cells of the podia and the ambulacral epidermis. These epithelial surfaces are known in extant crinozoans to be responsible for a large percentage of total oxygen intake.

In order to be able to function as respiratory surfaces, the movement of water through the hydrospires is necessary. This movement should bring well-aerated water inbetween the hydrospire lamellae. Such water movements could be twofold. First, brachiolar movements should draw water toward the ambulacral areas to flow over the hydrospire slits (if exposed). Next, the water should be drawn within the hydrospires. This can only be performed by ciliary epithelium. Inward water movement can be thought to have taken place primarily at the aboral end of the slit and outward water movement at the adoral end of the slit. The inflated hydrospire duct or tube is held to be the main outflow canal for water. Respiration is thought to have taken place through the thin hydrospire lamellae, and discharge of water through the tube.

We have also suggested a possible excretory function for the hydrospires but this is speculative. No excretory organs as such are known at present from crinozoans. The *modus operandi* for excretion in living crinoids is poorly known. Saccules, brown bodies, specialized coelomocytes, and respiratory surfaces are all believed to be responsible for part of the excretion in crinoids. It seems logical, however, to suppose that the exchange of products through the hydrospire wall in blastoids was not limited to just oxygen intake. Rather, one could think of gaseous exchange as a whole, including oxygen and carbon dioxide diffusion, and excretion of soluble excretory products. The principal nitrogenous excretory products are ammonia and urea. The nitrogenous wastes are known in modern echinoderms to pass directly to the exterior via respiratory surfaces. It is perhaps not too much to suppose that hydrospire walls performed a similar excretory function in this way.

We have discussed earlier (section on water-vascular system) the possible role of the hydrospires in the function of the water-vascular system. No part of the blastoid thecal wall is known to possess any true hydropores (ciliated funnels) for intake of water into the coelomic and water-vascular systems. One could speculate that pores were present in the hydrospire lamellae. However, hypotheses of this type about the microstructure of hydrospire lamellae must await electron scanning microscope studies.

DOUBTFUL SYSTEMS

During the present anatomical study of the fissiculates, some internal skeletal structures have been found, which cannot at this moment be definitely allied to one of the organ systems described so far in this chapter. We refer to the five lobed sacs in interradial position in the thecal cavity of *Mastoblastus ornatus* (figs. 26.7–12) and to the two lobed sacs pending from the *BC* and *DE* deltoids in *Ceratoblastus nanus* (fig. 43.9).

An interpretation of the function of these sacs has to reckon with the fact that both in *Mastoblastus* and in *Ceratoblastus* hydrospires are either vestigial or completely absent. If, as we believe, the hydrospires have a respiratory function, there may be a possibility that the doubtful organs here under discussion are to be interpreted as respiratory organs. However, from their morphology one cannot exclude the possibility that we would be dealing here with genital organs.

The sacs of *Mastoblastus* are probably five in number, hanging from the deltoids in an interradial position. It is unknown whether or not these sacs opened to the exterior. A gonoduct is known to exist in *Mastoblastus*. We have not found a skeletal connection between the gonoduct and the internal lobed sacs. This is simply due to the fact that the gonoduct and lobed sacs are known from two different specimens, the one in which the sacs occur being fragmentary. It is very unfortunate that we have been unable to find this skeletal connection between sacs and gonopore. Such a connection would have proved that the sacs were indeed to be interpreted as the internal gonads. In such a case we also would have had the first definite record of the internal gonads in the blastoids. It is believed that, in any case, the sacs of *Mastoblastus* belong to visceral skeleton. An interpretation of these sacs as respiratory organs is again hampered by the fact that we do not know their connection with the external world. If they were indeed respiratory organs a large and wide connection with the exterior medium would be required.

The sacs of *Ceratoblastus nanus* are certainly two in number, hanging from the *BC* and *DE* deltoids. They open to the exterior by means of two large pores in the *BC* and *DE* deltoids. A gonopore in the posterior interray, such as in regular fissiculates, is absent. So, it could be that the sacs in *Ceratoblastus* are in fact genital organs, and their openings the gonopores. A difficulty, however, would be that these "gonopores" are in quite different positions, compared to all other fissiculate blastoids. One cannot exclude, in this case, that the sacs are interpretable as respiratory sacs, being analogues of the hydrospire systems of other fissiculates.

The result of our remarks on *Mastoblastus* and *Ceratoblastus* is, that we are dealing with organs of doubtful genital or respiratory function. Formerly, in blastoid literature the hydrospires were the organs with a questionable genital or respiratory function. We believe we have now solved that problem by definitely ascribing a respiratory function to the hydrospires. But, at the same time, we have now introduced in the blastoid literature a new set of organs with the same old problem of doubtful genital or respiratory function.

SUMMARY OF RESULTS

It is appropriate to present in this final section of the anatomy chapter a summary of the main results of our anatomical study, with an indication of their bearing upon the zoological affinities of the blastoids within their class of the crinozoan echinoderms.

(1) The fissiculate blastoids have a gonopore and a gonoduct. The pore is external in Silurian and Devonian forms, but internal (opening in anal cavity) in advanced Carboniferous and Permian forms. The pore is situated in the posterior interradius between mouth and anus. The gonopore and gonoduct were previously unknown in blastoids. It is concluded form their presence that blastoid gonads were intrathecal organs, fully enclosed within the thecal cavity. The possibility that the genital systems send out genital canals into the brachioles is excluded. The blastoid brachioles are held to be devoid of gonads.

Observations prove, that, insofar as the genital system is concerned, the blastoids have affinities with the cystoids, rather than with the crinoids. Cystoids and blastoids have a gonopore, and are held to have had intrathecal gonads. On the contrary, the crinoids lack a gonopore (even in their early larval stages of development), and their gonads are extrathecal pinnular organs, interconnected by a system of genital canals. Such canals are absent from blastoid brachioles.

(2) The main (motor) nervous system in the blastoids is an oral nervous system. It is composed of circum-esophageal canals in the deltoid lips, radial nerve canals in the lancets, and presumably brachiolar nerves in the brachiolar skeleton. The adoral position of the blastoid nervous system is in marked contrast with the crinoids. In the crinoids the main (motor) nervous system is the aboral nervous system. Its center lies in the basals, and the main nerve canals pass through the radials into the arms and pinnules. No evidence of an aboral nervous system in the blastoids was found during this study. One could deduce from this apparent difference with the crinoids, that the blastoid nervous system would have more affinities with the cystoid nervous system. One could speculate that in cystoids the oral nervous system is equally well developed as in the blastoids. This can be inferred from the fact that cystoid ambulacra and brachioles are extrathecal, as in the blastoids. We know, of course, far too little about the cystoid nervous system. It is hoped that future cystoid workers will appreciate that sectioning their specimens could be very rewarding.

(3) There is little evidence to suggest the nature of the coelomic system of the blastoids. There are never direct connections between the brachioles and the thecal cavity, which would have contained the main aboral or perivisceral coelom. Coelomic canals belonging to the adoral coelom (which is subambulacral in the crinoids) are not believed to have extended into the ambulacral tracts, and this would not have been present in blastoid brachioles. The coelomic canals would be too spacious for that. Here again, we would have a major difference with the crinoids, and probably another affinity with the cystoids.

From the results mentioned in points (1) through (3) it may be concluded that the blastoid brachiole (Pl. XXXII, fig. 1) has some fundamental differences from the crinoid pinnule. The crinoid pinnule (as the crinoid arm) is an evagination of the thecal cavity, carrying with it the coelomic, hemal, and genital systems. The blastoid brachiole is merely an extrathecal appendage. As such it is directly comparable to cystoid brachioles.

(4) The presence of hydrospires in blastoids points to another affinity with the cystoids. Recent crinoids lack any system which can possibly be compared to the blastoid hydrospire system. On the contrary, the rhombiferan dichopores are interpreted as organs comparable to the blastoid hydrospires. Both are believed to be specialized respiratory organs.

(5) The ambulacral and water-vascular systems of the blastoids are believed to have had the same organization as in the crinoids. It is believed that there is a typical crinozoan water-vascular system, present in all major crinozoan groups (cystoids, blastoids, and crinoids). A distinction has been made for the blastoids between the ambulacral tract and the

ambulacral groove. The ambulacral tract is rather wide and concave, either covered with movable, biserially arranged, ambulacral cover plates, many small irregular polygonal plates, or protected by ambulacral spines within the tract. The ambulacral groove lies in the bottom of the ambulacral tract, and was previously interpreted as the "food groove" or as "articulatory structure for the cover plates". However, the interpretation given here, holds that the ambulacral groove is nothing else than the impression of the water-vascular system with its podia (Pl. XXXIII, fig. 8). The ambulacral groove may undergo overgrowth by lancet and side plate material and come to lie within the lancet, just beneath its external surface. When overgrown by the lancet, the ambulacral grooves prove to be an ambulacral duct system, provided with short side canals opening with pores in the ambulacral tract. The pores contained the tube feet.

From the results mentioned in point (5) it is concluded that the blastoid brachiole, although devoid of extensions from the coelomic and hemal and genital systems, functioned in exactly the same way as a crinoid pinnule. The presence on the blastoid pinnule of an ambulacral tract and a water vessel with tube feet made it well adapted for food-gathering and respiration, two functions also performed by the crinoid pinnule.

As the main result of our antomic study of the fissiculates, we have found new evidence for the old belief that the blastoids are related to the cystoids. This idea is further elaborated in the chapter on phylogeny.

CHAPTER III

QUANTITATIVE ONTOGENY

INTRODUCTION

Blastoids provide an excellent opportunity to study growth in a group of fossil organisms. One of their most obvious ornamental features are the chevrons of growth lines on the radial and basal plates. The growth lines converge toward a point on a plate and it is thus possible to identify the origin. Since calcite was usually added only laterally to the edges of the plate (inferentially by mesodermal cells), the entire postmetamorphic ontogenetic development can be studied quantitatively. The radial plate is usually six-sided, with sutures bordering adjacent radials, basal(s), and two deltoids. The point of origin is at the aboral end of the ambulacrum, and the plate has grown outward toward the radiodeltoid (RD), interradial (RR) and radial-basal (RB) sutures. There are thus three directions of growth in the radial, each composed of a direction (an axis — from the origin to the suture) and a sutural area along which the new lateral increment of calcite is added (the front: RDF, etc.). An axis and its growth front (RD; RDF) define a sector of the plate. The origin of the basal is near its proximal end. In early blastoids, most growth occurred upward toward the radials (BR) but some lateral growth toward the other basals (BB) and stem area (BA) is also found. In more advanced blastoids, the origin of the basal is frequently obscured by secondary calcite secreted on top of an earlier-formed surface to effect a broader stem attachment area. The growth of the deltoids is more complex. Growth lines are usually not visible unless the aboral region of the deltoid lies in part outside the ambulacral sinuses. However, the origin usually lies near the adoral tip. Most growth is directed away from the mouth (DR), thereby creating more space for hydrospire formation and extension of the ambulacrum, but there is a small increment toward the interdeltoid (DD) suture as well, with consequent continued reformation of the ambulacral tract on the interdeltoid suture. The lancet, which is the principal plate of the ambulacrum, grows most rapidly at its aboral end. Space must usually be created for this by growth along the radiodeltoid suture which creates a void at the aboral end of the ambulacrum. This is the site of the generation of new side and outer side plates and, inferentially, new brachioles.

The growth of a blastoid can be thought of as involving several subproblems for the animal. The viscera were contained in a solid external shell of plates. (The plates themselves lay within the mesoderm and are thus an endoskeleton.) The visceral mass was roughly spherical or some deformed pentagonal-ellipsoidal departure from this. If it was to increase in size, the balloon of plates surrounding it had to increase. This was effected by the addition of calcite to the lateral edges of the basals, radial, and deltoids, which increased the volume of the interior, provided progressively larger openings for the oral opening and anus, and allowed the respiratory organs (hydrospires) to increase their surface area and number to keep up with the increased volume of the viscera. The second subproblem involves an increase in the number of brachioles which captured food. This increase was usually dependent on the formation of space at the aboral end of the ambulacrum by growth along the radiodeltoid suture as outlined above, but later blastoids found additional means of effecting this. The third subproblem involves the support of the theca by the stem. As the mass of the theca increased through growth, some change in the surface area of attachment was necessary to maintain stability. As mentioned above, early blastoids effected this by growth along a BA axis but later forms turned to secondary calcite or some other mechanism.

Since a blastoid is comprised of a limited number of plates, each with a limited number of sectors, it becomes possible to quantify the ontogeny of each plate and to study how growth rates varied within and between plates. To effect this, we measured between 50–55 variables for each specimen within a growth series, and then compared these measurements by a least squares regression program. If sufficient data was available, up to 80 equations were used to study the ontogeny of each species. In the following pages, we present illustrations of the interaction of 13 of the principal variables (textfigs. 51–95) for each fissiculate species (except where previously illustrated), and trace out their ontogenetic development and phylogenetic modification. Each line in the textfigures is based upon a regression equation in the form $y=a+bx$ where a is the y intercept and b is the regression coefficient; a is the first number, b the second number by each line in the textfigures. The rate of change between two parameters is described by b. None of our data was transformed to logarithms as all curves are apparently linear. Each line is fitted only to the interval for which we have data. The other principal statistic we have employed is the correlation coefficient (r). Its square (r^2, the coefficient of determination) is a measure of the degree of association or covariation of the variables under study. In blastoids, r is usually 0.8 or higher (many are >0.9) so that 64 percent or more of the total variation on the variables is described by their interrelationship. In our ontogenetic discussion, each of the 50–55 variables have been considered. A full table of the regression equations for each species will be published subsequently by Macurda in the publications of the Museum of Paleontology, University of Michigan.

In regression analysis, an optimum sample size is 20 or more specimens.

Due to the rarity of fissiculates, this is usually not attainable. In some instances, we could select from many specimens from a narrow interval at a single locality (e.g., *Heteroschisma alternatum*). In these instances, the procedure for inclusion in the growth series followed that of MACURDA, 1966. In other instances, we had to rely on the material available in collections from one formation in a district; individual specimens might not be well localized geographically except to the region (e.g., *Decaschisma pulchellum*). (A full list of the specimens utilized and their geographic, stratigraphic, and museum locations will be included subsequently with the aforementioned regression equations.) In some instances, our sample size is quite small (e.g., *Phaenoschisma conicum*: 5; *Pentremitidea lusitanica*: 6). We are well aware that the confidence interval around a regression line widens rapidly as sample size decreases and that statements concerning the statistical interrelationships of these species are correspondingly more suspect. We offer the following justifications for even attempting an analysis of these specimens. First, our experience has shown us that due to the high correlation coefficients (r) between parameters in blastoids, the addition of new specimens (e.g., from 10 to 20) does not materially affect the previously defined statistics; new points plot in the previously defined regions. Second, if there is a numerical spread of the values, this more clearly allows a determination of the regression coefficient b, than a large number of points with almost all the same values. Any regression solution tries to minimize the variation around the line. In some instances, we obtained negative regression coefficients between some variables in some species (e.g., *Anthoblastus stelliformis*, figs. 77.6–8). At face value, this would mean that when one variable increased, the other was thus decreasing and, hence, resorption was involved. This negative value is simply an artifact of the regression model and the clustering of the points near one value. Thirdly, we have scoured the museums and localities of five continents and our analysis includes all material known to us. We feel even a summary based on limited data is better than none as, in many instances, the number of available specimens will not increase materially in the near future.

There has been some criticism of the least squares regression model because of its assumption of dependency of one of the variables. We have compared the equations published earlier (MACURDA, 1967a) which were fitted by Barlett's line of best fit with those generated by a least squares computer regression program. Since the correlation coefficients are usually 0.9 or higher, the lines are approaching unity (i.e., a straight line through all the points at $r = 1.00$) and there is virtually no difference between the equations.

In our discussion of fissiculate ontogeny which follows, we compare the growth rates of axes (e.g., RD/RR) between different forms. As can be seen in the relevant textfigures, the y intercepts are rarely equal to 0. The regression coefficient, therefore, describes the relationship only for the interval for which we have data. The value of *b* would indicate one rate of growth but can be misleading when compared with another species if the spread of data points is not large. Therefore, our comments on growth are based upon both the regression equations and a direct overlay of relevant graphs on one another. All points had to start from zero; there is no such thing as a two-dimensional plate with a value of 2.0 mm in one direction and 0.0 mm in the other.

Certain aspects of fissiculate ontogeny (e.g., stems, cover plates, brachioles) have been described in previous studies (MACURDA, 1965b, 1966) and are not repeated here as the present study has not added to or modified these discussions. An in-depth description of the ontogeny of a fissiculate blastoid and the parameters measured which provided the model for this ontogenetic study can be found under MACURDA, 1966. Illustrations of growth axes, fronts, sectors, and secondary deposits are given in the Treatise (MACURDA, 1967b, p. S 356–369).

In describing the quantitative ontogeny for each of the species of fissiculate blastoids (as follows on p. 186–284), a standard way of illustrating the principal growth phenomena has been adopted. This includes the presentation of 8 standard drawings per species. Textfigure 51 is used in the following paragraphs as model for reading textfigures 51–95.

The first parameters which should be considered are the length and width of each specimen in the growth series (fig. 51.2). This most always indicates the known size range of the species. The subsequent figures illustrate the ontogenetic development of individual plates and compares them with each other for specimens of the growth series. The ontogenetic development of a single part (sector) of the radial is determined by measuring two parameters. The distance from the radial origin (at the aboral end of the ambulacrum) to a suture (e.g., the interradial) indicates the, amount of outward growth that has occurred in that direction (Pl. VII, fig. 6). The measurement of a suture indicates the width of the area along which calcite was added during the last growth increment. A comparison of the amount of outward growth with the width of the area where calcite was added for each of the three parts of the radial thus summarizes the amount of the development of each sector, as given in fig. 51.1. The relative development of each sector can be compared by plotting the length of the radial axes against one another, as in figs. 51.6, 8.

The growth of the basal can be portrayed in a manner similar to that of the radial. The origin is located near the lower, or proximal end and most growth has occurred toward the radio-basal suture (Pl. VII, fig. 5). Graphs can be made similar to those for the radial showing development within a sector and comparing growth between sectors but for reasons of space, we have chosen to summarize the growth of the basal by showing the relative development compared to the radial (RD and RB) and deltoid (figs. 51.3, 4).

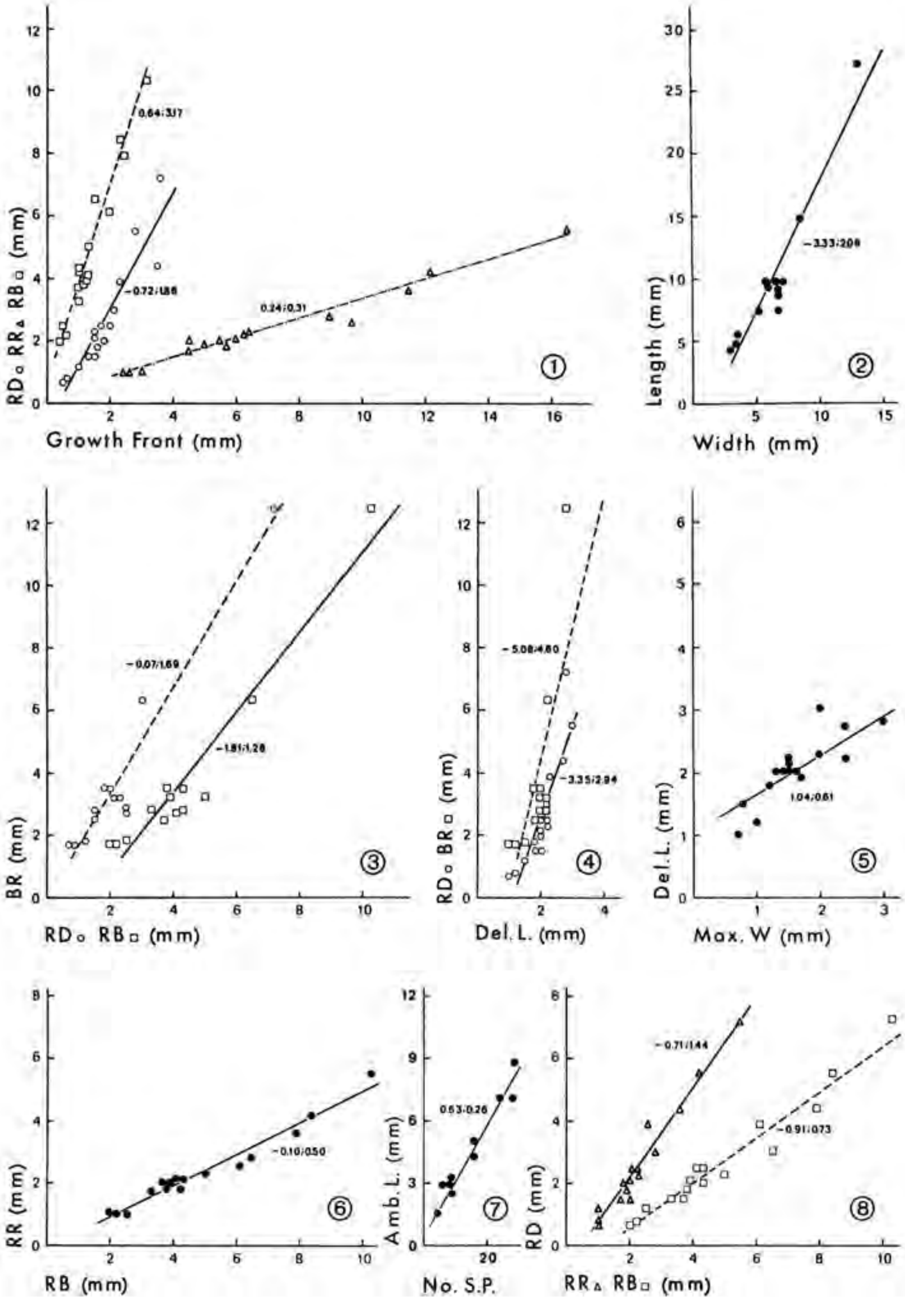
As indicated earlier, the growth of the deltoid is more complex. The origin is usually located near the adoral end (Pl. VII, fig. 7; Pl. XIX, fig. 2) and most growth has occurred outward toward the radiodeltoid suture (DR axis). In later forms, growth toward the interdeltoid suture becomes more prominent. We have studied these relations but again for reasons of space, have restricted our graphic portrayals to a comparison of deltoid length with its width (fig. 51.5) and compared relative deltoid development with the radials (RD) and basals (BR) as in fig. 51.4.

The space available for ambulacral growth is usually determined by radial and deltoid growth. The new plates are added at the aboral end of the ambulacrum as the lancet grew outward (Pl. VII, fig. 6). The development of the ambulacrum and the rate of addition of new side plates is shown by comparing the ambulacral length with the number of side plates present along one side as in fig. 51.7.

Family PHAENOSCHISMATIDAE

Silurian. The oldest known fissiculate is *Decaschisma pulchellum* (Pl. I, figs. 1–3). Its maximum size (fig. 51.2) is reasonably large as blastoids go and its tall narrow shape, with the ambulacra confined to the upper surface, is the prototype of the typical phaenoschismatid. The basals have a BA axis and form a conspicuous part of the theca, forming more than half of the pelvis. They are thus long and narrow. The BR axis grew faster than the RD axis and somewhat faster than the RB axis of the radial (fig. 51.3); it grew much faster than the deltoid (fig. 51.4). The diameter of the stem attachment area increases from 0.3 to 1.0 mm. The radials are conspicuous in the upper part of the theca, projecting above the oral opening. The highest rate of growth in the radial is to be found in the RB sector (figs. 51.6, 8); there is apparently a

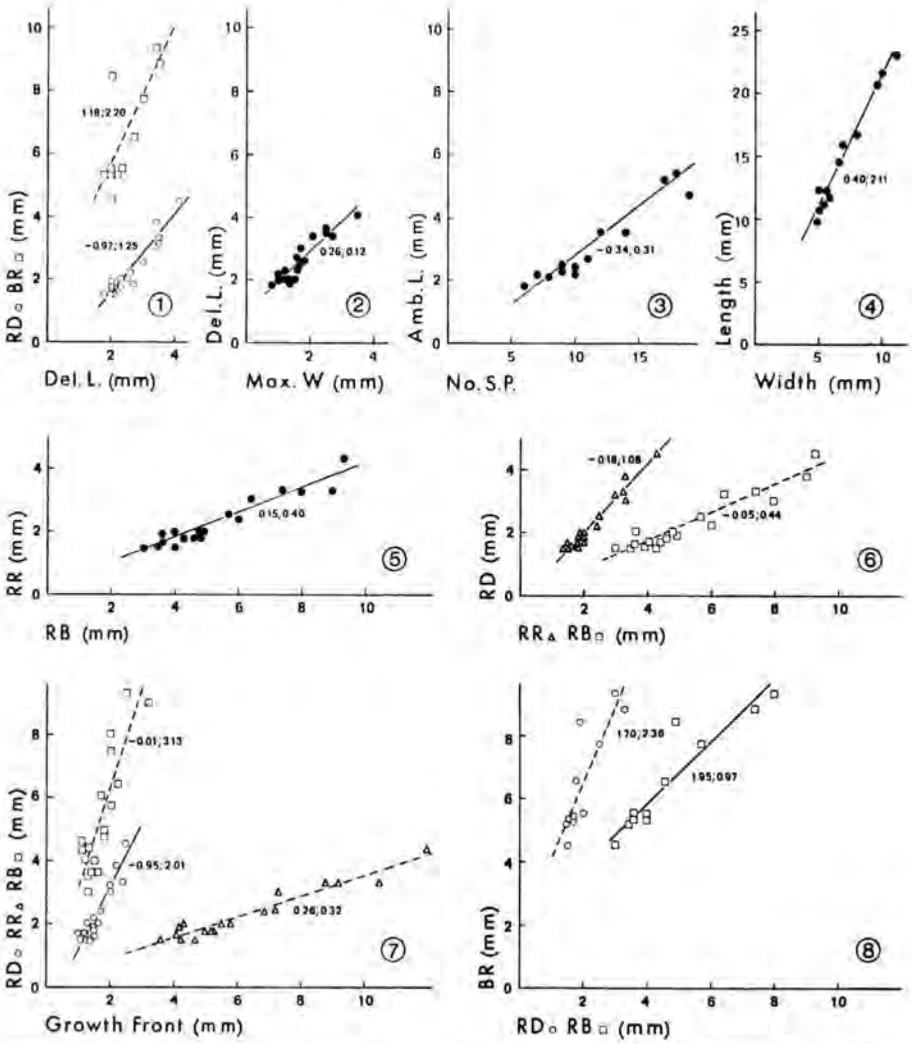
Textfig. 51. *Decaschisma pulchellum* (Miller and Dyer, 1878) Sil., Waldron Sh., Ind., USA. Ontogenetic development based upon 16 specimens. Lines fitted by least squares regression program with equation in form of $y = a + bx$. a is the y intercept of the resultant line, and b is the regression coefficient. These are given (a first) for each line in the textfigures. Symbols beginning with R apply to radials, B basals; second letters (as RD) indicate growth direction from origin of plate in question (R) toward radiodeltoid suture. Further explanation of position of growth axes and fronts given in text. Unless otherwise indicated, details and explanation of textfigs. 51–95 standard. Some individual plots, e.g. (2), may not contain as many points as other plots because of missing data due to incomplete preservation of specimens involved. Length of line plotted only for length where data exists. (1) Ontogenetic development of radial growth axes vs radial growth fronts. (2) Length of complete thecae in growth series vs their width. (3) BR growth axis vs development of RD and RB axes. (4) Ontogenetic development of RD and BR growth axes vs development of deltoid length. (5) Ontogenetic development of length of deltoid vs its greatest aboral width. (6) Ontogenetic development of RR growth axis vs development of RB growth axis. (7) Ambulacral length vs number of side plates along one side of ambulacrum for specimens in growth series. (8) Ontogenetic development of RD growth axis vs development of RR and RB growth axes.


①
RD○ RR△ RB□ (mm)
Growth Front (mm)
0.64/3.17
-0.72/1.86
0.24/0.31
②
Length (mm)
Width (mm)
-3.33/2.08
③
BR (mm)
RD○ RB□ (mm)
-0.07/1.69
-1.81/1.28
④
RD○ BR□ (mm)
Del. L. (mm)
-5.08/4.80
-3.35/2.94
⑤
Del. L. (mm)
Max. W (mm)
1.04/0.61
⑥
RR (mm)
RB (mm)
-0.10/0.50
⑦
Amb. L. (mm)
No. S.P.
0.53/0.26
⑧
RD (mm)
RR△ RB□ (mm)
-0.71/1.44
-0.91/0.73

slight acceleration in RD at the expense of RB in more mature specimens. Growth within each radial sector (fig. 51.1) follows a pattern in which the RD sector grew moderately outward on a somewhat narrow front, the RR sector less so but on a broad front, and the RB sector strongly outward on a somewhat narrow front. The deltoid is a relatively inconspicuous plate confined to the uppermost part of the theca; the crest grew upward. Deltoid length (fig. 51.1) is greater than the greatest deltoid width (unless otherwise indicated, this is always in the aboral part); the deltoid crest comprises the major part of the deltoid length. Both the greatest adoral and minimum width of the deltoid increase throughout the ontogenetic series (0.3–1.0 and 0.2–0.7 mm, respectively). The aboral rate of growth of the deltoid (as measured by deltoid length) was much less than that of RD (fig. 51.4), implying a faster rate of growth on one plate edge than the other. The space occupied by the anal deltoids is longer and wider than that of a regular deltoid. Within the anal deltoids, the superdeltoid undergoes almost no change in length once formed but does increase in width; the subdeltoid continues to lengthen; data for the width of the hypodeltoid suggests it is the most rapidly growing anal plate. The lancets are concealed within the ambulacra (except adoralmost) and are of moderate length; they occur in an ambulacral sinus. They lengthen throughout growth, adding new side plates (fig. 51.7), but the width is essentially constant. The distance from the adoral end of the ambulacrum to the oral center increases slightly. The number of regular hydrospires increases from 3 to 9 per group, but the latter appears to represent an upper limit that once reached, does not increase with increasing size. The correlation between the number of regular and anal hydrospire slits is random (0.07); the latter number from 2 to 4.

The other known Silurian fissiculate species are assigned to *Polydeltoideus*. The type species, *P. enodatus* (Pl. I, figs. 8, 12) is similar in its overall thecal shape to *Decaschisma*. It reaches approximately the same maximum size (fig. 52.4). There is a BA axis in the basals; the stem attachment area increases slightly (0.7–1.5 mm). The rate of growth of the narrow basals is again large with respect to the radial and deltoids, only RB approaching it (figs. 52.1, 8). The radials are again conspicuous, projecting above the oral opening. The highest rate of growth is found within the RB sector (figs. 52.5, 6); there is no apparent acceleration of any axis with time. Growth patterns within each radial sector are almost identical with those of *Decaschisma* (figs. 51.1; 52.7). The deltoid of *P. enodatus* is a more conspicuous plate; its relative length and growth rate have increased (figs. 52.1, 2). The crest slopes upward and forms the largest part of the plate. The greatest adoral width and minimum width increase only slightly (0.4–0.8 mm and 0.2–0.5 mm, respectively). Again the length of the area occupied by the anal deltoids is slightly larger but the width is almost the same. The anus increases slightly in size. The hypodeltoid is an actively growing plate. The ambulacra of *P. enodatus* are slightly shorter; new side plates are added at almost the same frequency (fig. 52.3). The distance from the oral center to the lancet is essentially constant. The number of regular hydrospires ranges from 5 to 10 throughout the ontogenetic series but is usually near 6 per group. The anal hydrospires usually number 3 per group.

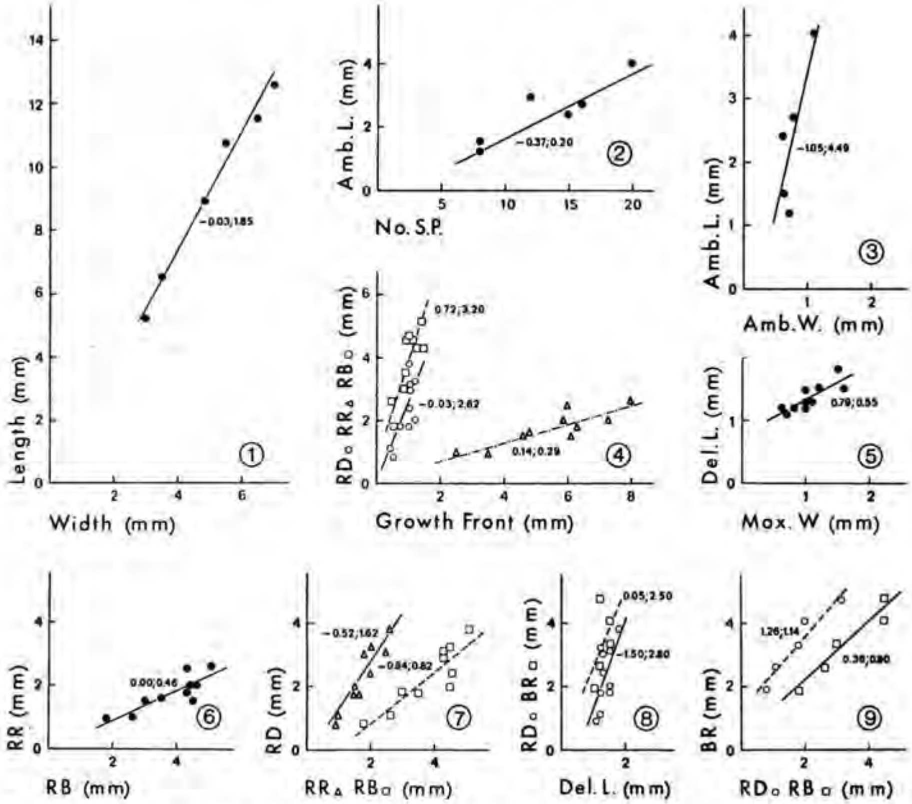
A Silurian fissiculate from Europe has been questionably assigned to *Polydeltoideus: P. ? plasovae*. The question mark stems from some uncertainty about the number of anal deltoids. There is only one known specimen, but its shape and the proportions of the plates suggest the species had an ontogenetic development which was very similar to that



Textfig. 52. *Polydeltoideus enodatus* Reimann and Fay, 1961. Sil., Henryhouse Fm., Pontotoc Co., Okla., USA. Ontogenetic development based upon 18 specimens. See textfig. 51 for further explanation.

of *P. enodatus*. The external form of this specimen is well shown by PROKOP (1962) but we further prepared the oral area to reveal details of the anal area.

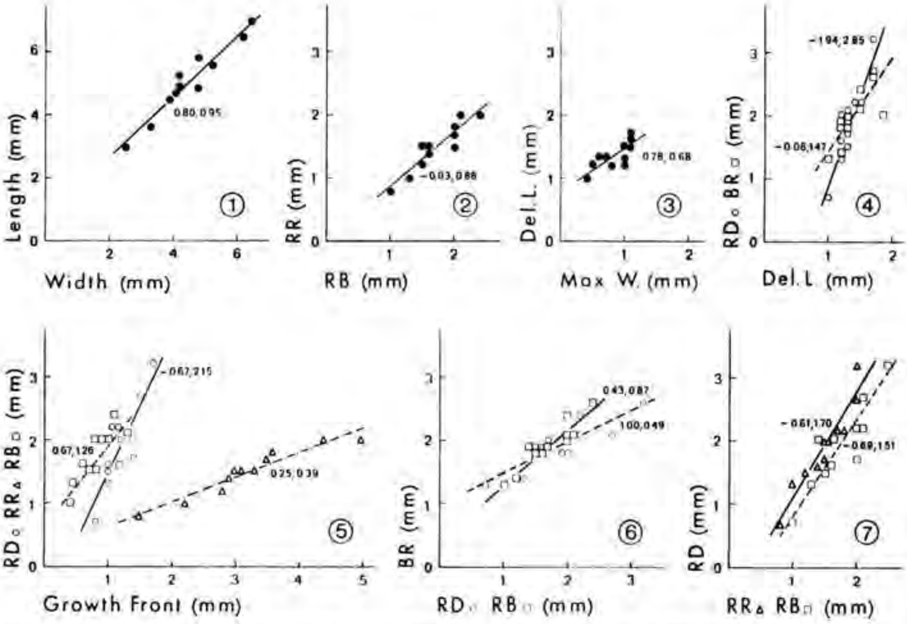
Devonian / Gedinnian. The earliest (and only Gedinnian) Devonian blastoid is *Leptoschisma lorae* (Pl. I, figs. 4–7). Its overall shape resembles that of *Decaschisma* more than *Polydeltoideus* but its overall form is very similar to both, with the ambulacra being confined to the upper surface. The maximum known size is only half that of the other two (fig. 53.1); the rate of increase of length to width is almost the same. The basals are long and narrow, have a small attachment area proximally (0.3–0.7 mm), a BA axis, and form a conspicuous part of the pelvis. The rate of growth, however, is slightly less with respect to the radial (fig. 53.9) than the two Silurian genera but about the same for the deltoid (fig. 53.8), still being much faster. The radials again project above the oral opening. RD grows at a faster rate with respect to the other two radial axes than in the previous two genera, more so to *Polydeltoideus* than *Decaschisma*,



Textfig. 53. *Leptoschisma lorae* (Dunbar, 1920). L. Dev., Birdsong Sh., Tenn., USA. Ontogenetic development based upon 18 specimens. (4) Ambulacral length vs ambulacral width. See textfig. 51 for further explanation.

but RR and RB remain the same (figs. 53.6, 7). RD accelerates slightly with respect to RB. Within the radial sectors, the rate of growth of the RD axis is faster with respect to its growth front but the RR and RB sectors are essentially identical to *Decaschisma* and *Polydeltoideus* (fig. 53.4). The deltoid is again small, being longer than wide (fig. 53.5). The crest, which slopes upward, forms the principal part of the plate, indicating the dominance internally of the DR axis. The rate with respect to the RD axis, however, is much less (fig. 53.8). The greatest adoral width and minimum width of the deltoid are essentially constant. The space occupied by the anal deltoids is longer and wider; the superdeltoid increases very slightly in width; the hypodeltoid expands its width. The narrow ambulacra are similar to the Silurian forms except there are more side plates per mm (figs. 53.2, 3). The distance from oral center to lancet is constant. The number of regular hydrospires increases from 3 to 8, the anal from 3 to 6 per group, but the correlation between them is low (0.47).

Emsian. Higher in the Devonian, a variety of fissiculate forms appear in the Emsian, some being quite similar in form to the genera discussed so far, others a departure. Perhaps the most pronounced example of the latter is *Caryoblastus bohemicus* (Pl. I, figs. 10, 11). Instead of having the conical shape seen before, *C. bohemicus* is bud-shaped. The upper part of the theca is essentially the same as the preceding genera and a comparison of oral views shows little obvious difference (Pl. I, figs. 4, 10); laterally, however, this is not the case. Length and width are subequal (fig. 54.1). The modification of form is caused by changes in the growth rates of the basals and RB sector. The basals are no more long and narrow but subequal; the rate of growth with respect to the RD axis and deltoid is substantially slowed (figs. 54.4, 6). The rate of growth of BR and RB remains essentially the same (fig. 54.6). A BA axis is no longer manifest, and is perhaps no longer present. (The diameter of the stem attachment area is 0.3–0.8 mm). The radials are again conspicuous, projecting above the oral opening. The rate of growth of the RB axis is no longer dominant, but is only slightly greater than RD and RR in the smallest specimens and is supplanted by RD as growth proceeds (figs. 54.2, 7). The relative growth rate of RD/RR remains nearly the same. Within the radial sectors, the only major departure is to be found in the RB sector in which the rate of forward growth is slowed relative to the front (fig. 54.5). The deltoid is still relatively inconspicuous, confined to the upper surface; the crest slopes steeply upward and dominates the plate. Deltoid length is greater than the width (fig. 54.3). The greatest adoral width increases only slightly; the minimum width is constant. The aboral rate of growth is much less than that of RD (fig. 54.4) as in *Decaschisma* and *Leptoschisma*. The area occupied by the anal deltoids is usually slightly longer and wider than that of a regular deltoid. The length of the superdeltoid is essentially constant but its width increases slightly. The cryptodeltoids increase in length and the hypodeltoid in width (insufficient data on length of latter). The width of the anus is essentially constant. The distance from the oral center to the adoral end of the ambulacrum increases very slightly with growth (0.1 mm). Ambulacral length increases from 0.7 to 3.5 mm within the growth series but there is insufficient data to characterize its width or the side plates. The number of regular hydrospires is apparently fixed at 3 per group (rarely 4); the number of anal hydrospires varies from 2–3; r between the two is 0.04. The full width of a regular RDF is not utilized for hydrospire formation.

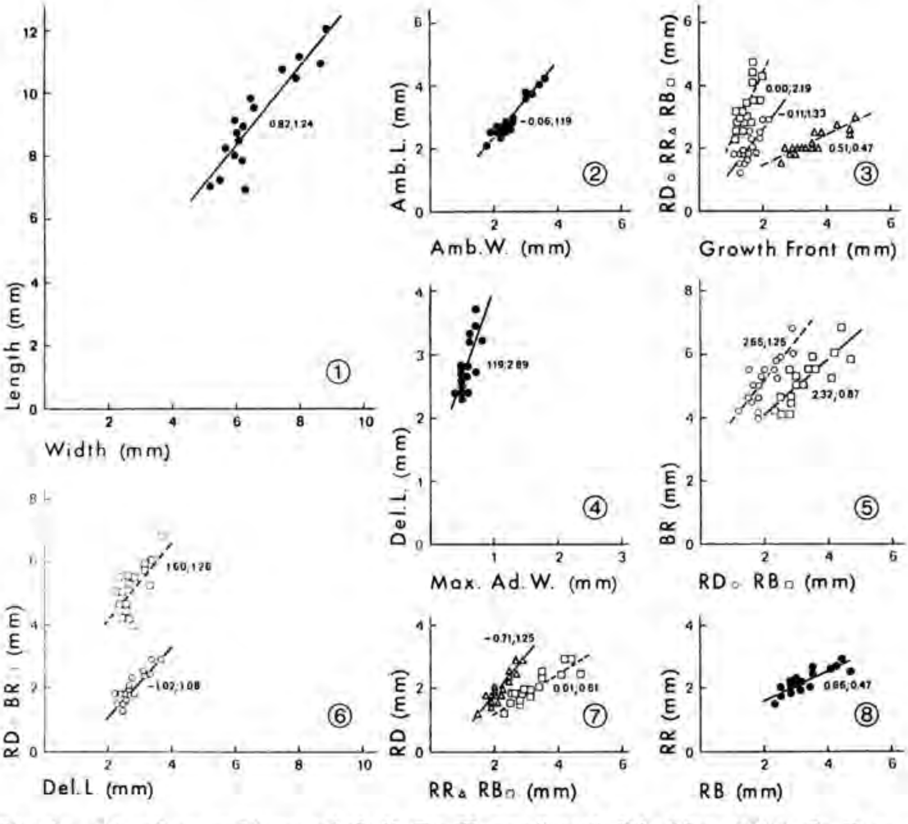


Textfig. 54. *Caryoblastus bohemicus* Breimer, Macurda, and Prokop, 1968. L. Dev., Slivenec Ls., Konvarka, Bohemia. Ontogenetic development based upon 11 specimens. Insufficient data for ambulacral length vs number of side plates. See textfig. 51 for further explanation.

A single specimen of a form which may be a *Caryoblastus* is found in Spain (Pl. I, figs. 15, 16). Its growth habits would apparently be very similar to that of *C. bohemicus*. The number of hydrospire slits per group is greater (7–8 in regular; 7 in anal) but the full width of RDF is not utilized for their formation.

Another departure from growth patterns seen previously is found in *Cryptoschisma schultzii* (Pl. I, figs. 9, 13, 17). The prominent deposits of secondary calcite on the basals and the much-flattened, slightly parabolic vault with the widened ambulacra immediately set it apart. Its maximum known length is intermediate and similar to *Leptoschisma*; its width, however, much more closely approaches the length (fig. 55.1). The diameter of the stem facet is quite large, increases ontogenetically (range

1.5–3.2 mm). The massive deposit of secondary calcite on the proximal part of the basals continues to increase in height (1.7 to 4.8 mm in the growth series), progressively obscuring more of the plate. Total growth of the basal has been faster with respect to RD and RB than in *Decaschisma*, *Leptoschisma*, and *Caryoblastus*. However, it is slower than the BR/RD of *Polydeltoideus* and equal to the latter's BR/RB, but is generally slowed with respect to the deltoid as in *Caryoblastus* (figs. 55.5, 6). The radial is not as prominent as in the previous genera, not reaching above the oral opening. The RB axis has the highest rate of growth and the rates of the three radial axes relative to one another are almost the same as in *Decaschisma*, *Polydeltoideus*, and *Leptoschisma*; there is no acceleration of the RD axes (figs. 55.7, 8). Within the sectors, rates of growth of RD/RDF (fig. 55.3) are similar with those of *Decaschisma* and *Polydeltoideus*, while RR is slightly accelerated relative to RRF and RB decelerated relative to RBF in these genera and *Leptoschisma*. The deltoid is more conspicuous and the crest (again the major part) grows directly outward, thereby considerably expanding the area of the vault. The rate of growth of the

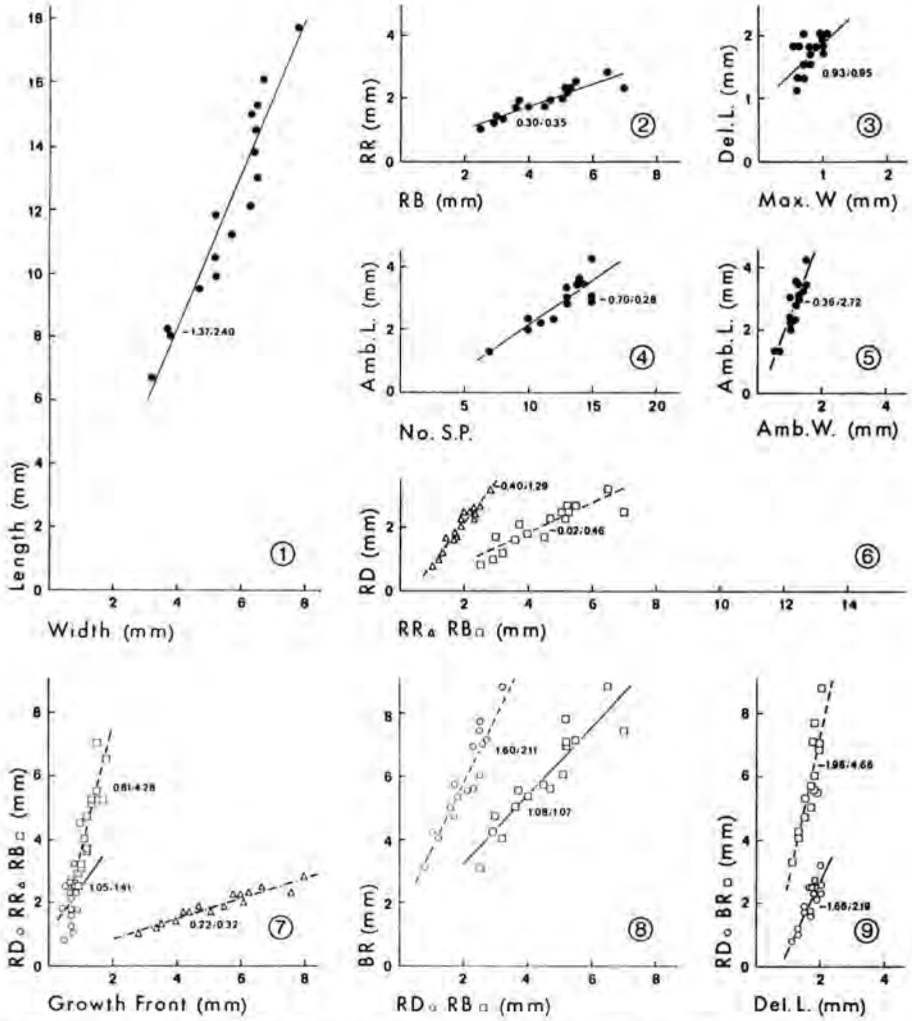


Textfig. 55. *Cryptoschisma schultzii* (De Verneuil and d'Archiac, 1845). L. Dev., La Vid Fm., Colle, León, Spain. Ontogenetic development based upon 17 specimens. (4) Deltoid length vs maximum *adoral* width. See textfig. 51 for further explanation.

deltoid with RD is almost equal (fig. 55.6); the exposed part of the deltoid is narrow because of the impingement of the side plates (fig. 55.4). The greatest adoral, minimum, and greatest aboral width of the deltoid increase slightly during growth. The superdeltoid increases in length and width and the anus in width. The crypto- and hypodeltoid are too rarely preserved to be able to comment on their ontogenetic development. The distance from the ambulacrum increases slightly during growth; the ambulacra are of modest length and quite wide (fig. 55.2), almost filling the ambulacral sinus. The number of side plates per mm is higher than in *Decaschisma* or *Polydeltoideus*. The lancet is widely exposed and increases in width ontogenetically (from 0.8 to 1.7 mm). The number of hydrospires increases from 4 to 7 but the full width of RDF is not utilized for their formation. Anal hydrospires are lacking.

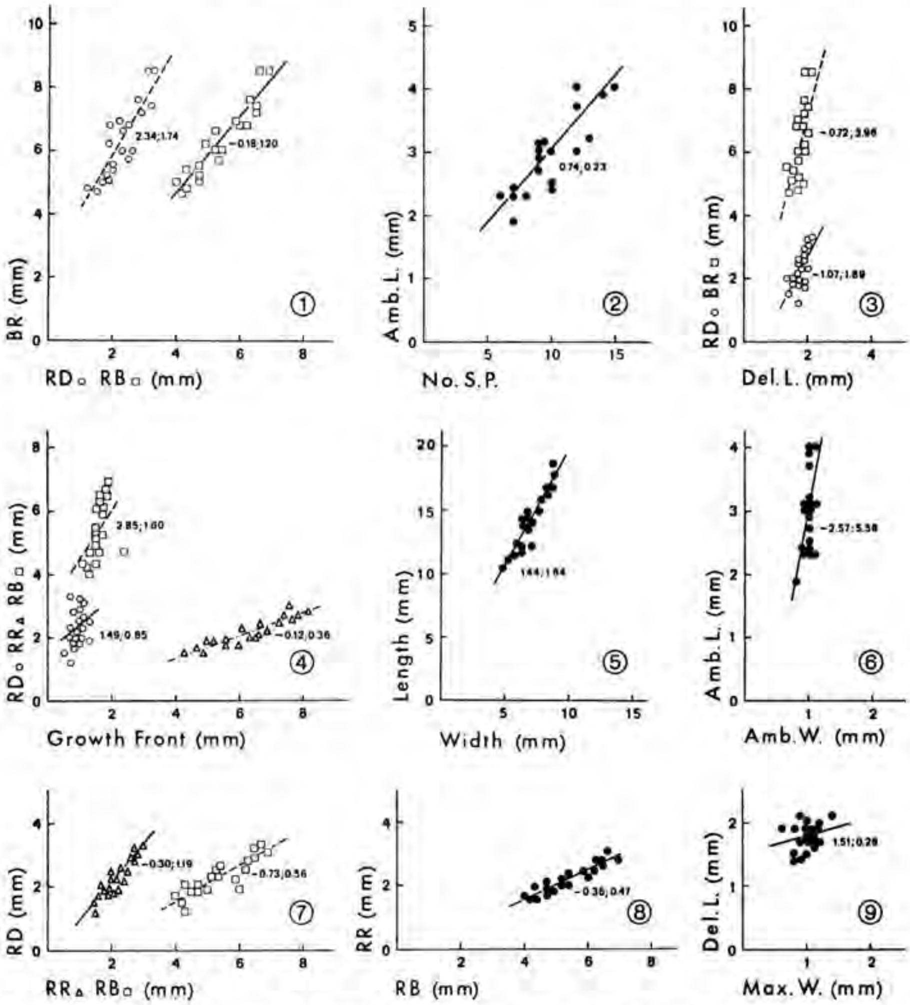
There are three species of *Pentremitidea* in the Emsian of Spain. They are similar in gross form but differences in growth rates in some parts contribute to their specific differentiation. *P. pailleti* (Pl. I, figs. 22–24) is tall and conical; it is the thinnest of the three species relatively (fig. 56.1). The vault is small and the ambulacra are confined to the upper surface. The basals have a BA axis, are long and narrow, and form a conspicuous part of the theca. The rates of growth of BR relative to RD and deltoid length is as high as or slightly higher than the Silurian genera *Decaschisma* and *Polydeltoideus* and, hence, faster than the Devonian genera discussed so far. BR to RB is the same for all (figs. 56.8, 9). The diameter of the base is narrow (0.5–1.3 mm). The radials are long and narrow, forming the upper part of the theca and extending slightly above the oral opening. The regression coefficients of the radial axes indicate the relative dominance of RB and lack of emphasis on RD as in most earlier forms (figs. 56.2, 6). There is no ontogenetic acceleration of the RD axis. Within the radial sectors the comparative rates of the axes and their fronts almost duplicate those of *Decaschisma* and *Polydeltoideus*, with the slight exception of an acceleration of RD relative to RDF (fig. 56.7). The high rate of RB to RBF reflects the narrowness of the theca. The small deltoid is slightly longer than broad (fig. 56.3); the crest dominates it and slopes upward from the origin; its rate of growth is less than that of the opposing RD axis (fig. 56.9). The greatest adoral width of the deltoid expands slightly; the minimum width is essentially constant. The area occupied by the anal deltoids is longer than that of the regular deltoids. The superdeltoid increases slightly in length and width; the width of the anus increases. The distance from the oral center to the adoral end of the ambulacrum increases very slightly as the ambulacrum lengthens and widens (fig. 56.5); the rate of addition of new side plates (fig. 56.4) is similar to that of *Decaschisma*, *Polydeltoideus*, and *Leptoschisma*. The lancet is concealed except at the adoral tip. Since the hydrospire slits are not developed across the full width of RDF and are concealed by the ambulacra, their ontogenetic behavior is not readily observable (there being 5 in a 9 mm specimen and 7 in a 15 mm specimen; the latter is about the maximum size). They are lacking in the anal interarea.

The second species of *Pentremitidea*, *P. archiaci* (Pl. I, figs. 14, 18–21) is very similar in its maximum size to *P. pailleti*, but somewhat wider (fig. 57.5); it is an intermediate size blastoid. The ambulacra and deltoids are again restricted. One of its very characteristic features is the relatively broad, flaring basal attachment area (1.9–2.9 mm) which is produced by growth on an outward-flaring, very pronounced BA axis. The area appears to reach a large size early in the growth of the organism as it is 1.9 mm in the smallest specimen in the growth series (length: 10 mm). The basals are tall and conical and have the same growth rates as in *P. pailleti* when



Textfig. 56. *Pentremitidea pailleti* (De Verneuil, 1844). L. Dev., Ferroñes, Asturias, Spain. Ontogenetic development based upon 16 specimens. See textfig. 51 for further explanation.

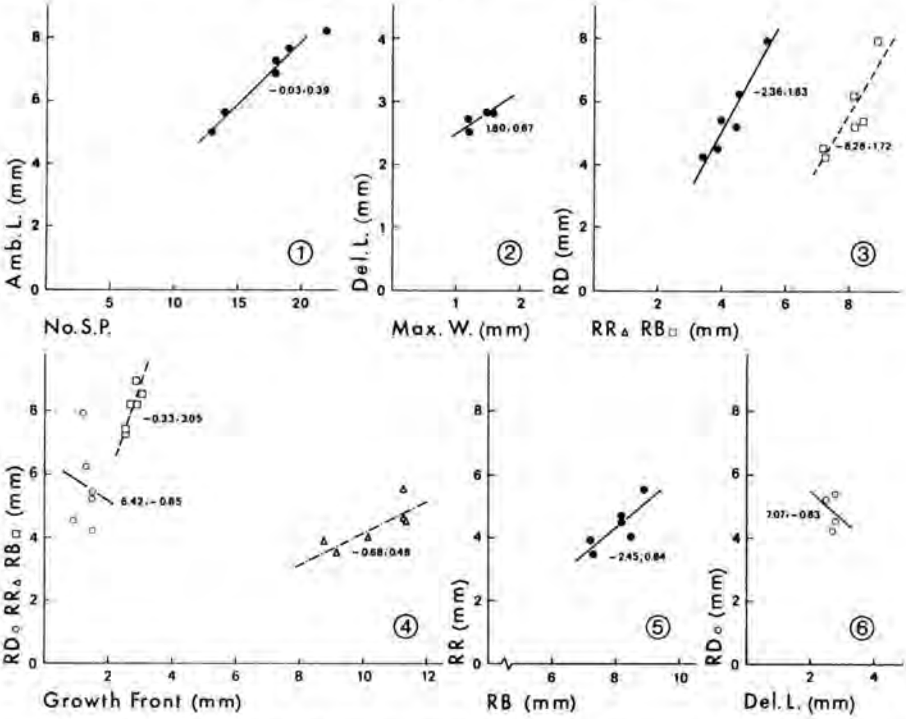
compared with the radials and deltoids (figs. 57.1, 3). The radials are somewhat more restricted in appearance. The comparative growths of the radial axes are also almost identical (figs. 57.7, 8). Again, there is no acceleration of RD. Growth rates are also very similar within the radial sectors (fig. 57.4). The deltoid is small, longer than wide (fig. 57.9), but apparently grows very slowly as its size varies little throughout the growth series. The crest dominates and slopes moderately upward. The greatest adoral width expands very slightly, the minimum width is essentially constant. RD grows somewhat more rapidly than Del. L. (fig. 57.3). The length and width of the area occupied by the anal deltoids increases slightly in size; the length is usually slightly greater than that



Textfig. 57. *Pentremitidea archiaci* (Etheridge and Carpenter, 1882). L. Dev., La Vid Fm., Colle, León, Spain. Ontogenetic development based upon 20 specimens. See textfig. 51 for further explanation.

of the deltoid. The superdeltoid increases very slightly in length and a bit more in width. The distance from the oral center to the adoral end of the ambulacrum remains almost constant; the lancet is concealed (except for the adoral tip). The ambulacrum is small as in *P. pailleti* but does increase in length, adding new side plates (fig. 57.2), about the same per unit distance as *P. pailleti*. The ambulacrum does not increase in width with growth (fig. 57.6), whereas it did in the latter. The number of hydrospire slits is 6–7 throughout the growth series. The full width of RDF is not utilized for hydrospire formation. Anal hydrospires are again lacking.

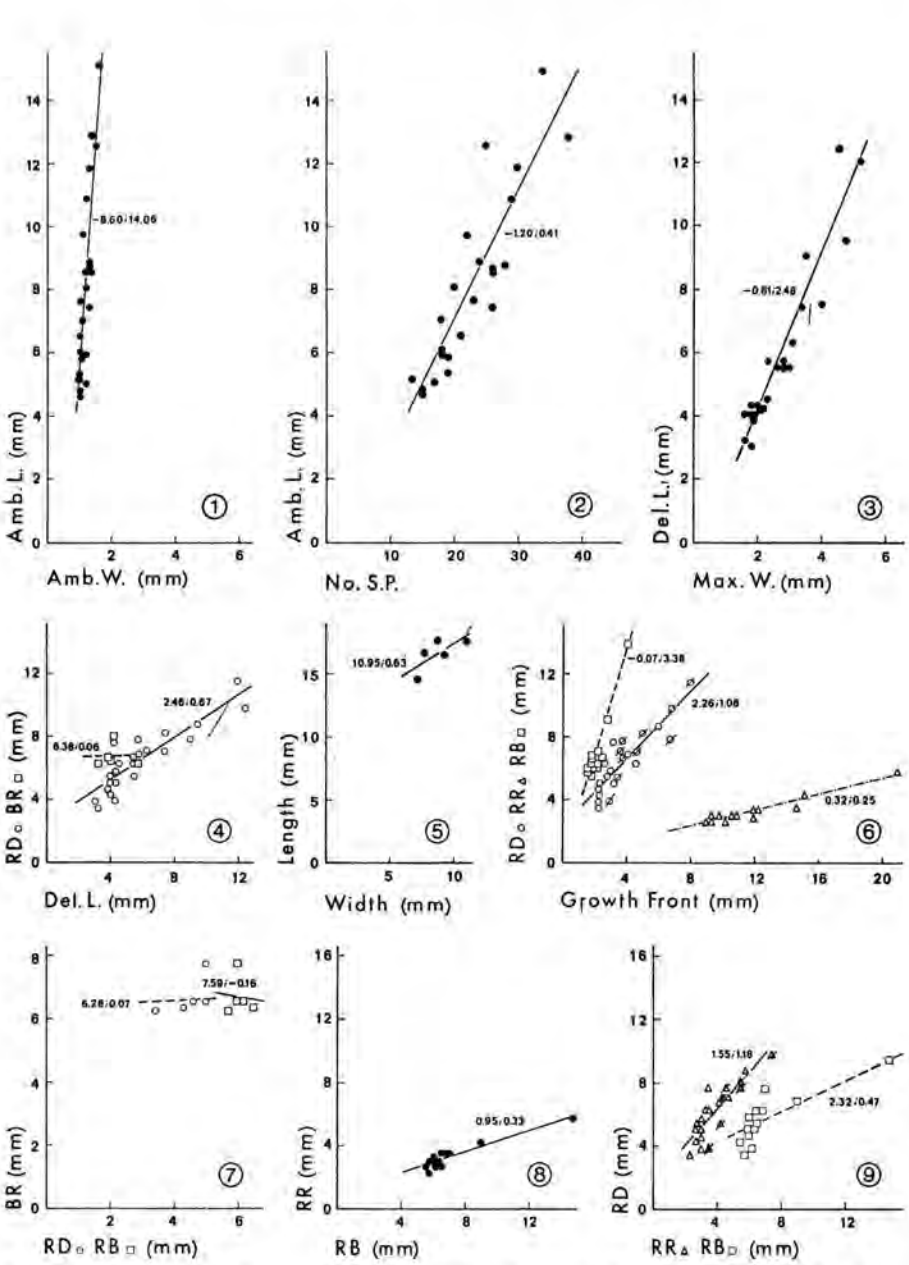
The third species of *Pentremitidea*, *P. lusitanica* (Pl. II, figs. 2, 3), is the rarest of the three. It reaches a greater size and is somewhat wider, the vault thereby appearing slightly expanded (there is inadequate data to portray L/W). The basals are usually damaged, but a BA axis is known to be present in one specimen and the stem attachment area is relatively narrow. The basals are conical; there is inadequate data to generate any quantitative comparisons but, if one plots two available points, the rate of growth of BR relative to RB and the deltoid appears to lie on a linear projection of the rates of *P. archiaci* but be quite different when compared with RD, the latter having accelerated. The radials are prominent in the upper part of the theca but project only very slightly above the peristome. The comparative growth rates of the radial axes differ from the other two species of *Pentremitidea*, reflecting a relative emphasis on RD and de-emphasis of RB (figs. 58.3, 5). There may be a slight acceleration of RD to RB during growth but more data is needed to substantiate this. Within the radial sectors, the rate of growth of RD/RDF is high, but the distribution of points led to a nonsensical regression solution (fig. 58.4). RR is slightly accelerated relative to RRF when compared to the other species of *Pentremitidea*. RB/RBF is apparently the same. The deltoid is very modest in its development; length is greater than width (fig. 58.2). The crest slopes moderately upward from its origin. There is insufficient data to discuss deltoid or anal deltoid ontogeny except to note that the length and width of the superdeltoid appear to increase as does the width of the area occupied by the anal deltoids. The RD appears to grow at a relatively much faster rate than the deltoid and faster than that of the other species of *Pentremitidea*, but the limited data generates a nonsensical regression solution (fig. 58.6). The distance from the oral center to the adoral end of the ambulacrum has apparently increased. Ambulacral length increases at a comparatively faster rate than in other species of *Pentremitidea* and new side plates are added at a slower rate (fig. 58.1). This rate is lower than in the forms discussed so far. Ambulacral width has also apparently expanded as the maximum width is 2.2 mm. Only the inner part of RDF is used for hydrospire formation. There is insufficient information to comment on the ontogenetic behavior of hydrospire development; there are apparently between 5 and 9. Again, anal hydrospires are lacking.



Textfig. 58. *Pentremitidea lusitanica* Etheridge and Carpenter, 1882. L. Dev., La Vid Fm., Colle, León, Spain. Ontogenetic development based upon 6 specimens. See textfig. 51 for further explanation.

There is one fissiculate found with *Caryoblastus bohemicus* in the Emsian of Czechoslovakia whose generic identity we cannot determine because of the poor preservation of the anal deltoids in the only known specimen (Pl. II, figs. 1, 6). Its tall narrow form and full use of RDF for hydrospire formation clearly indicate it is not cospecific with any other Emsian blastoid or, apparently, any other fissiculate. With one specimen, we obviously cannot produce a rigorous ontogenetic analysis, but inspection of the specimen in top and lateral views clearly suggest that more specimens would indicate a similarity with the earlier fissiculates. It has a BA axis, the basals are long and narrow; RB represents 58 percent of the total rate of growth in the radial, one of the highest known rates and very similar to *P. archiaci*. The deltoid is inconspicuous, and the crest slopes upward. The ambulacra are short. There are 10 hydrospire groups with approximately 7 in each regular group and about 3 in the anal interarea.

The other known Emsian blastoid, *Pleuroschisma verneuili* (Pl. II, figs. 5, 9, 11) is one of the largest Devonian fissiculates. Complete thecae are intermediate in size (fig. 59.5); the ratio of L/W at this size (1.75/1.0) suggests that a large incomplete theca with a width of 23.7 mm would have a length of slightly over 40 mm; an incomplete specimen is over

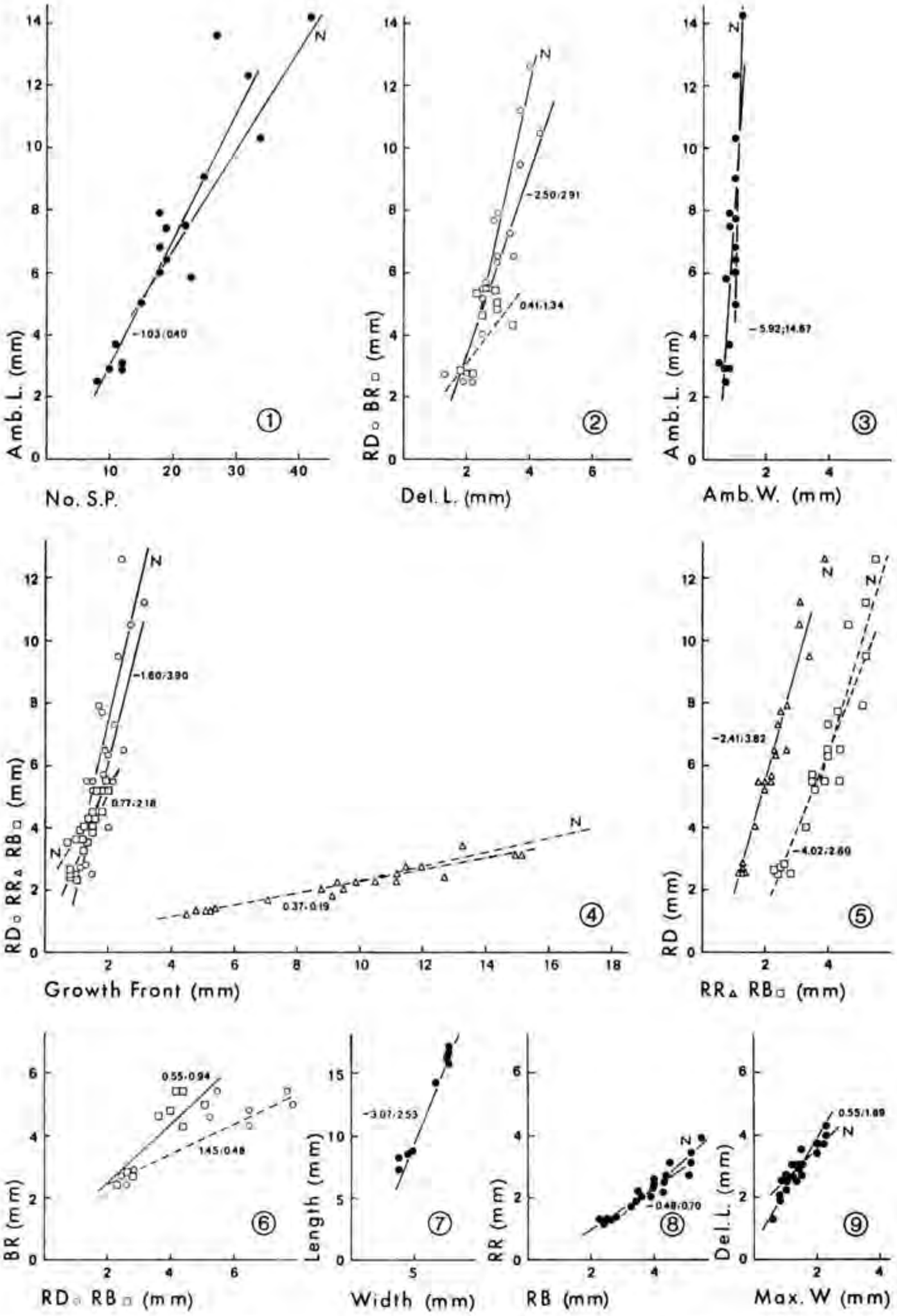


Textfig. 59. *Pleuroschisma verneuili* (Etheridge and Carpenter, 1882). L. Dev., Colle, León; Fenolleda, Ferroñes; Spain. Ontogenetic development based upon 23 specimens. (6,9) Specimens with incomplete data (i.e., not represented in other parts of the plot) have a diagonal line through the symbol. See textfig. 51 for further explanation.

36 mm in length. The pelvis is very similar in shape to most earlier forms (conical), suggesting similar growth habits, but the conspicuous deltoids have considerably expanded the vault. The ambulacra are still restricted to the upper part. The basals are conical and have a BA growth axis. Extremely limited data suggests a narrow stem attachment area. The limited data for the basals produces a nonsensical regression solution for basal growth (fig. 59.7), but if we project a line from the origin to the data points, it suggests that BR grows slightly faster than RB but only equals the growth rate of RD. The latter is in contrast with previous forms (except *Caryoblastus*). The solution for BR/Del. L. is again nonsensical (fig. 59.4), but the distribution suggests that BR grows at a somewhat faster rate than the deltoid. The radial is very conspicuous, projecting well above the peristome. A comparison of the growth of the radial axes shows that RB is still the predominant axis but RD approaches it; RR is somewhat slower relatively than in most previous forms (figs. 59.8, 9). There is no apparent ontogenetic accelaration of RD. Within the radial sectors, the radial axes and fronts have their usual growth relationships (fig. 59.6). The deltoid is a conspicuous plate, with a long crest rising above the peristome. It is long and narrow, reaches a large size, and is an actively growing plate (fig. 59.3). Both the greatest adoral and minimum width increase slightly. The rate of growth of the deltoid relative to RD is slightly faster (fig. 59.4), in contrast to most other previous forms. The higher rate of deltoid growth also expresses itself in being faster than that of the anal deltoids, a reversal of the usual. The superdeltoid is apparently a rather inactive plate once a length near 0.6 to 0.7 mm and a width near 1.0 mm is reached as it generally has very low correlation coefficients internally and with other parts of the anal interarea. The correlation of hypodeltoid length with the deltoid length ($r = 0.66$) is greater than that with superdeltoid length (0.52). The correlation of anus length and width is random (−0.01) but both dimensions appear to increase ontogenetically. Anus length is fairly well correlated with hypodeltoid length (0.79) but its width is less well correlated with hypodeltoid width (0.53). The hypodeltoid is an actively growing plate, increasing both in its length (0.7–3.0) and width (0.8–2.5); $r = 0.89$. The distance from the oral center to adoral end of the ambulacrum increases. Ambulacral length increases regularly to a large maximum, but its narrow width scarcely changes (fig. 59.1). Side plates are added (fig. 59.2) at a rate similar to that of *Pentremitidea lusitanica*, which it was noted earlier, is slower than most preceding forms. The lancet remains concealed except at the adoral tip. Hydrospires are extremely numerous in *Pleuroschisma verneuili*. Those in regular groups number from 11 to 32 in the growth series; anal hydrospires number from 5 to 12 in the same specimens ($r = 0.63$). The maximum known number of anal hydrospires is 21 in a specimen where the number of regular hydrospires is in excess of 23. *P. verneuili* has by far the largest maximum number of hydrospires of

any phaenoschismatid. This is brought about by using the full width of RDF for hydrospire formation, building a deep, steep-walled ambulacral sinus by the relative expansion of RDF, and accelarating the growth rate of RD relative to other axes.

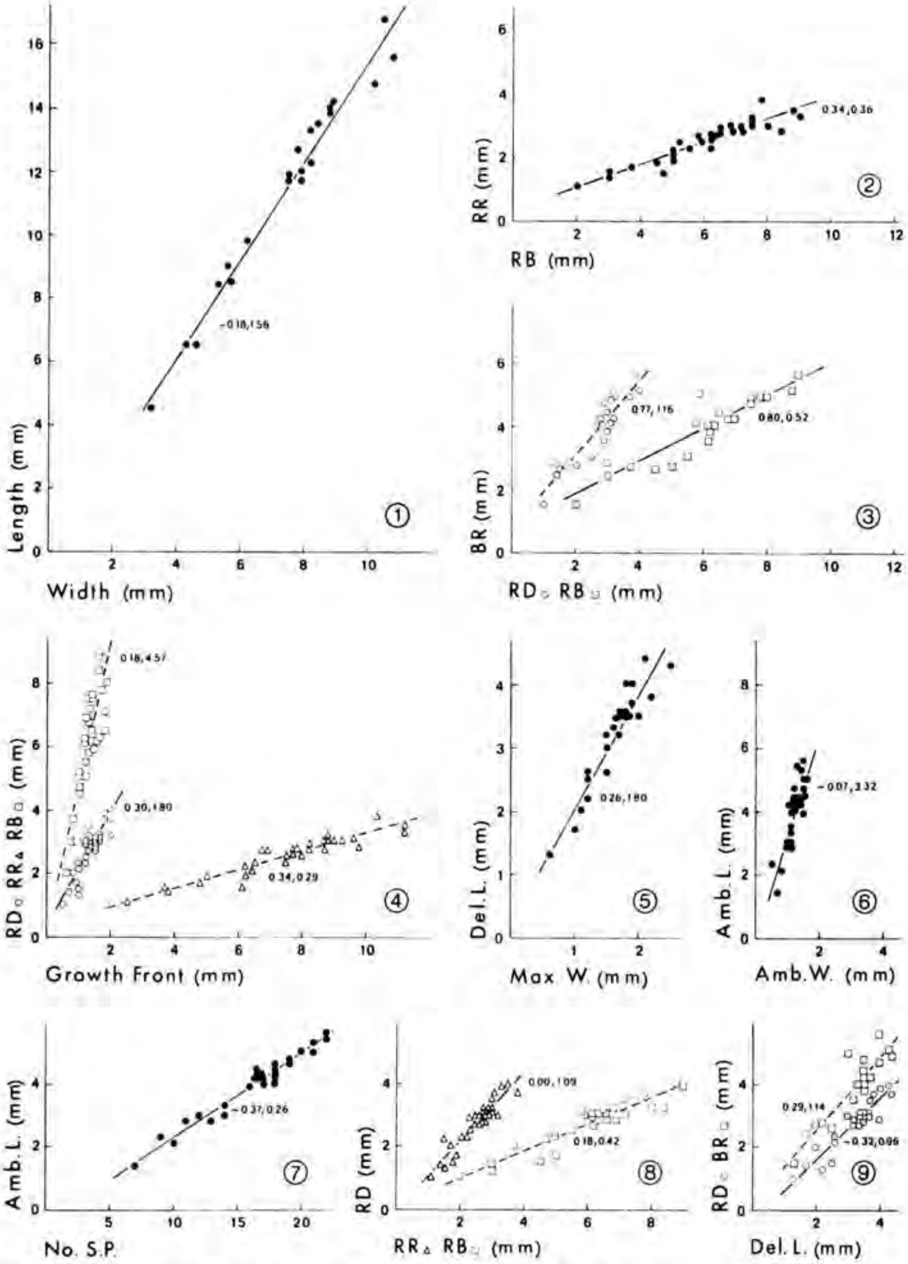
Eifelian-Givetian. *Pleuroschisma* is the most widely ranging Devonian phaenoschismatid; a second species, *P. lycorias* (Pl. II, figs. 4, 7, 8, 10) is found in the Givetian of eastern United States and Canada. Two populations of this species were available, one from western New York (the holotype came from here) and one from southwestern Ontario. The latter population was more complete so forms the basis for the following discussion of ontogeny; the regression lines for the New York population have also been plotted in textfigure 60 where available. They are indicated by N. *P. lycorias* apparently has a smaller maximum size than *P. verneuili*. The maximum size of a complete specimen of the former is intermediate in size (fig. 60.7); the largest incomplete specimens are over 22 mm in length but probably did not exceed 30 mm. A comparison of the lateral views of the *Pleuroschisma* species (Pl. II, figs. 8, 9) shows immediately that the vault of *P. lycorias* has been considerably enhanced and the relative rate of development of growth axes in the lower part of the theca reduced. The basals are still conical and have a BA axis. The stem attachment area is narrow (0.7–1.2 mm). The rate of growth of BR/RB is the same in the two species but the rate of growth of BR/RD is considerably accelerated toward the latter in *P. lycorias* (figs. 59.7; 60.6); the growth rate of BR/Del.L. is almost the same in the two species (figs. 59.4; 60.2). The radials are extremely prominent, forming at least two-thirds of the theca in lateral view and projecting above the peristome. RD has the highest rate of growth relative to RR and RB of any phaenoschismatid (fig. 60.5); some Mississippian phaenoschismatids closely approach it. RR is reduced to the lowest percentage of total radial growth found in any phaenoschismatid (see fig. 96.1). It still grows faster relative to RB than in *P. verneuili* (figs. 59.8; 60.8). There is a pronounced ontogenetic acceleration of RD, largely relative to RB. Within the radial sectors of *P. lycorias*, RR/RRF grows at relatively the same rate as in *P. verneuili* but RB is slightly slowed relative to RBF, and RD is greatly accelerated to RDF (fig. 60.4). The deltoid is less conspicuous than in *P. verneuili*; the crest, which forms the major portion of the deltoid, is originally directed upward but arcs downward aborally as an individual grows older. It is confined to the upper part of the theca. It does not lengthen as rapidly relative to its width (fig. 60.9) as in *P. verneuili*. The greatest adoral width and minimum width increase slightly during ontogeny. The anal deltoids are longer than the deltoid in *P. lycorias*, the reverse of that in *P. verneuili*. The superdeltoid is again a rather quiescent plate. The anus and hypodeltoid both appear to increase in width. The hypodeltoid is somewhat narrower relative to the length of the anal deltoids



Textfig. 60. *Pleuroschisma lycorias* (Hall, 1862). M. Dev., Moscow Shale, Western New York, USA, and Hungry Hollow Fm., Thedford and Arkona, Ont., Canada. Ontogenetic development of Western New York population based upon nine specimens, Ontario population upon ten. Points for both plotted jointly; separate regression lines plotted for each population (N = lines for New York specimens). Data for New York populations not as complete. (6) Lines for RD/RR coincident; N not drawn but would extend further upward as indicated by letter. See textfig. 51 for further explanation.

than in *P. verneuili*. The distance from the oral center to the adoral end of the ambulacrum is almost constant while the ambulacrum increases considerably in length; during this growth, the narrow width is essentially constant (fig. 60.3). The lancet remains concealed (except adorally). New side plates are added at almost the same rate as in *P. verneuili* (fig. 60.1). The maximum number of hydrospires is considerably reduced and compares closely with that of other Silurian and Devonian phaenoschismatids discussed thus far. The number increases ontogenetically from 2 to 8 per group, those in the anal area from 2 to 7 ($r = 0.92$). The full width of RDF is utilized.

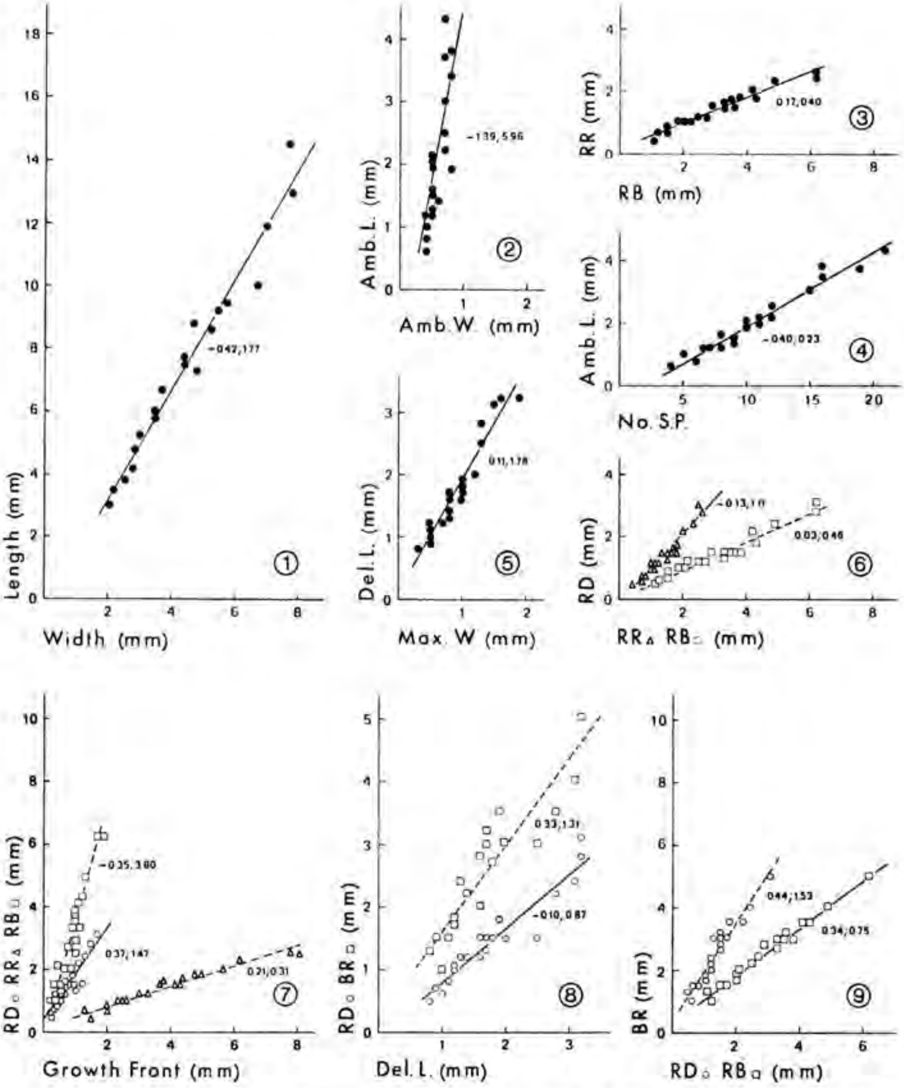
The remaining Devonian phaenoschismatid is *Heteroschisma*. It is widely distributed in the Eifelian and Givetian of the Eastern United States and Canada. The earliest species is *H. alternatum* (Pl. III, figs. 1, 2, 5, 6). It has a typical conical shape but the emphasis on the growth of the basals is obviously reduced compared to earlier forms and the vault altered to a broader, less angular profile. Maximum size is intermediate and length exceeds width by the usual magnitude (fig. 61.1). The presence of a BA axis is uncertain. The narrow stem attachment area increases in size ontogenetically. BR grows more slowly than RB and has the lowest relative rate of forms discussed so far. It grows somewhat more rapidly than RD (fig. 61.3) and the deltoid (fig. 61.9). The rate relative to the latter has usually been faster in previously discussed forms. The radials are prominent in lateral view, usually reaching just to the level of the oral opening. RB is the predominant radial axis (figs. 61.2, 8), usually comprising 50–55 percent of the total growth on radial axes; there is no ontogenetic deceleration of RB. The predominance of RB was seen in many of the earlier discussed forms; RD grows just a bit faster than RR (fig. 61.8). Within the radial sectors, the growth rates of axes relative to the fronts (fig. 61.4) are similar to that of forms such as *Decaschisma*, *Polydeltoideus*, and *Pentremitidea pailleti*. The deltoid is confined to the upper surface but is well developed; the crest is blunted and nearly horizontal. The deltoid continued to grow outward at a rate faster than the increase in width (fig. 61.5). The greatest adoral and minimum width continually increase. The deltoid grows at a slightly faster rate than RD (fig. 61.9), in contrast to most earlier forms. The anal deltoids are shorter than the regular deltoids because of the lack of a hypodeltoid. The superdeltoid, subdeltoid, and anus continually increase in size and regression coefficients between their lengths and width (both within and between entities) are between $r = 0.62$ to 0.86. As thecal size increases, the adoral end of the ambulacrum is continually displaced aborally from the oral center. Ambulacral length is modest; the width increases slightly with growth (fig. 61.6). The lancet remains concealed except at the adoral end. New side plates are added (fig. 61.7) at a rate similar to that of *Decaschisma*, *Polydeltoideus*, *Leptoschisma*, *Pentremitidea pailleti*, and *P. archiaci*. New hydrospires are added during growth in *H. alternatum*, utilizing the



Textfig. 61. *Heteroschisma alternatum* (Lyon, 1857). M. Dev., Jeffersonville Ls., Louisville, Ky., USA. Ontogenetic development based upon 31 specimens. See textfig. 51 for further explanation.

full width of RDF. The number increases from 3 to 11 in the growth series; a maximum of 12 per group are known. Anal hydrospires are lacking.

The oldest *Givetian* species of *Heteroschisma* is *H. canadense* (Pl. III, figs. 3, 4) from Southwestern Ontario. It retains a conical pelvis with a somewhat subdued vault; the ambulacra and deltoids are confined to the upper surface. Its length/width relationship (fig. 62.1) is almost the same as *H. alternatum*. The basals are conical and a small BA axis is present; the diameter of the base increases ontogenetically (0.3–1.2 mm). The rate

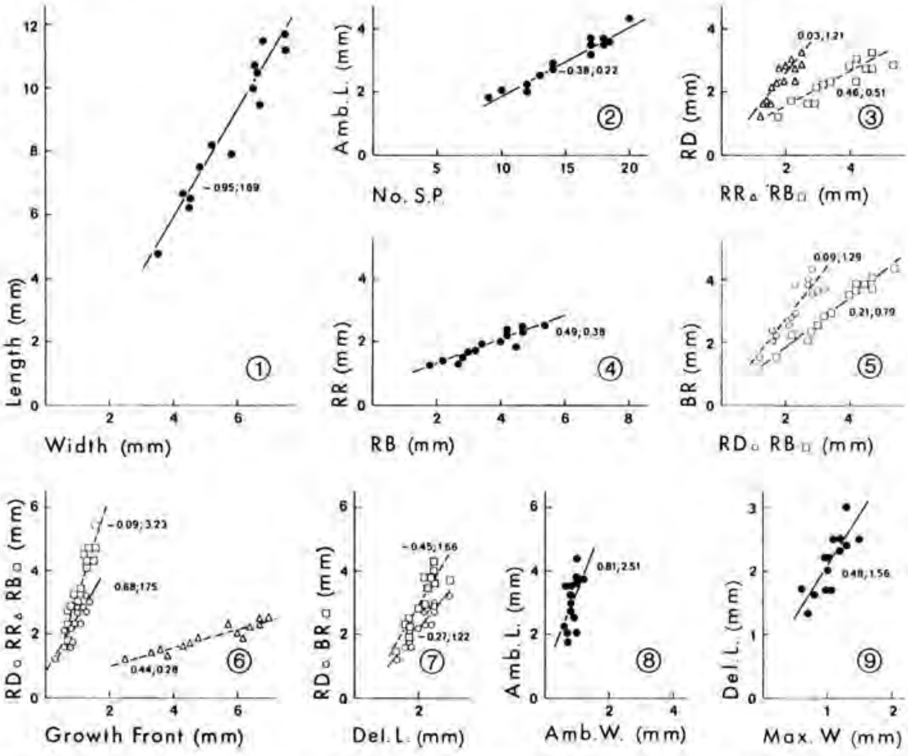


Textfig. 62. *Heteroschisma canadense* (Billings, 1869). M. Dev., Hungry Hollow Fm., Hungry Hollow, Arkona, Ont., Canada. Ontogenetic development based upon 20 specimens. See textfig. 51 for further explanation.

of growth of BR relative to RD, RB, and the deltoid is slightly faster than in *H. alternatum* (figs. 62.8, 9). The radials are prominent, extending to the level of the oral opening. The growth rates of the radial axes with one another and with their respective fronts are the same as in *H. alternatum* (figs. 62.3, 6, 7). There is no ontogenetic acceleration of RD. The deltoid has the same relative growth rates of its length and width (fig. 62.5) and with RD (fig. 62.8) as in *H. alternatum*. The deltoid crest, the dominant part of the plate, is usually directed almost straight out. The greatest adoral and minimum width increase slightly. The anal deltoids may be slightly longer in a few instances; the components of the anal deltoids (super-, subdeltoid) and anus increase ontogenetically and growth relations within and between these elements are highly correlated ($r=0.83$ to 0.92). The distance from oral center to the adoral end of the ambulacrum increases slightly as ambulacral length increases. The ambulacral width increases slightly (fig. 62.2); new side plates are added (fig. 62.4) at a very slightly higher rate than in *H. alternatum*. The lancet remains concealed (except adorally). New hydrospires are added ontogenetically (2–10 per group); the full width of RDF is utilized. Anal hydrospires are again lacking.

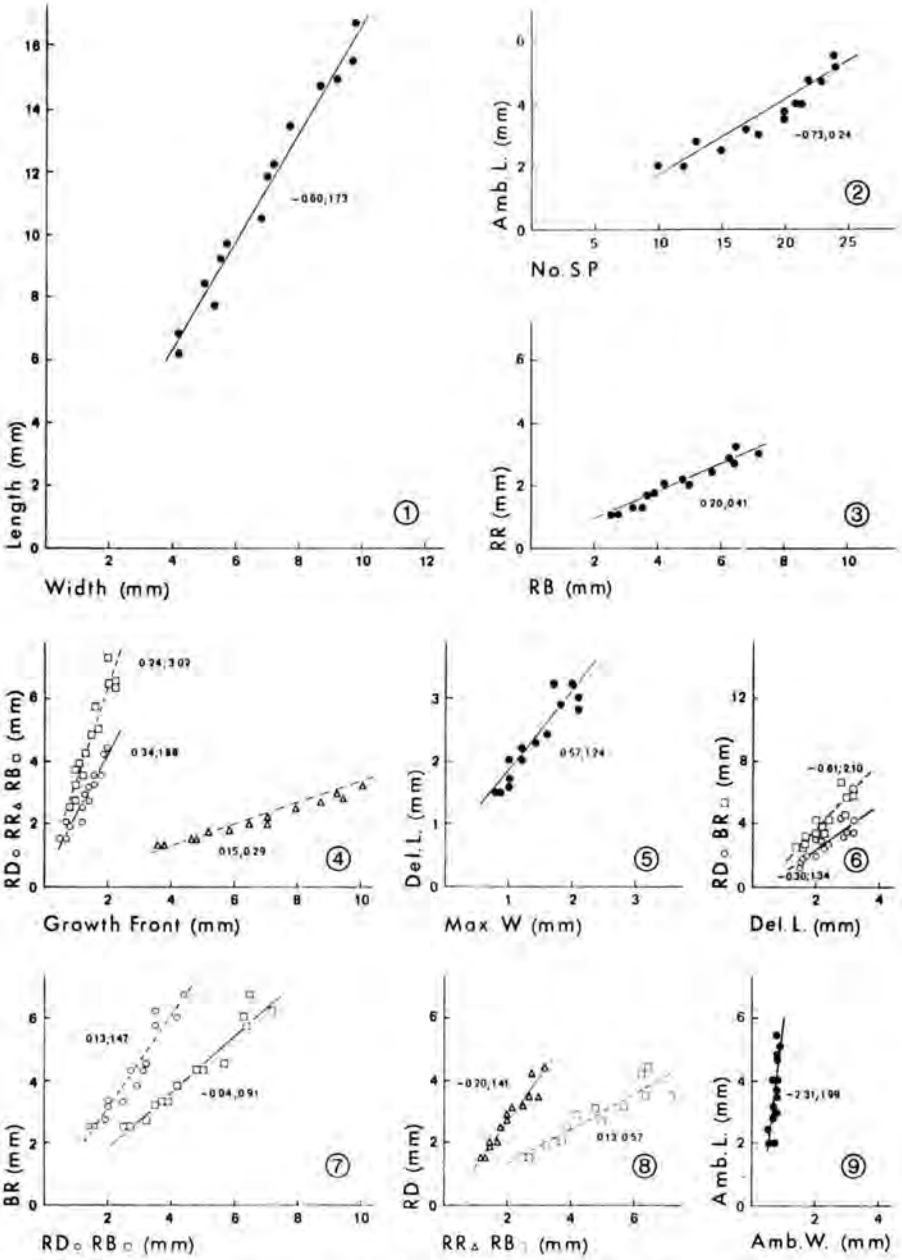
Heteroschisma alatum (Pl. III, figs. 7–9) is the next youngest Givetian species of this genus. Thecal shape is almost identical to the two previous species except for a slightly more angular vault; the deltoids and radials usually extend slightly above the oral opening. The relation between length and width is almost identical with that of the previous two species but the maximum known size is slightly smaller (fig. 63.1). A small BA axis is present in the conical basals; the diameter of the base increases slightly (0.8–1.3 mm). The growth rate of BR/RD is the same as for *H. alternatum*, of BR/RB and BR/Del.L. as for *H. canadense* (figs. 63.5, 7). The radials are perhaps not quite as prominent. RD grows at a slightly faster rate with respect to RR and RB (fig. 63.3) than in the previous two species while the rate of RR/RB remains the same (fig. 63.4). There is no ontogenetic acceleration of RD. Within the radial sectors only RD/RDF shows any difference from the previous two species, RD being a trifle accelerated (fig. 63.6). The crest of the deltoid usually slopes slightly upward, RD grows at a slightly faster rate than the deltoid (fig. 63.7). Otherwise, remarks made concerning the growth of the deltoid and anal deltoids in *H. canadense* apply here as well (fig. 63.9). Correlation coefficients amongst the elements of the anal deltoids are slightly lower ($r=0.48$ to 0.90). The ambulacrum reaches a slightly greater width than in *H. canadense* but the rate of addition of new side plates is the same (figs. 63.2, 8). The number of hydrospires in regular groups increase from 3 to 9; anal hydrospires are lacking.

The thecal shape of the youngest Givetian species of *Heteroschisma*, *H. gracile* (Pl. III, figs. 10, 11) contrasts with the preceding three species in having a much more angular vault. The deltoids and ambulacra are again confined to the upper surface. The relation between length and width (fig. 64.1) is the same as for the preceding species. No BA axis was positively identified in the conical basals; the diameter of the base increases from 0.7 to 1.4 mm. BR grows more rapidly with respect to RD than in *H. alternatum* and *H. alatum* and at the same rate as in *H. canadense*. The rate of BR to RB and the length of the deltoid is almost equal to that of *H. canadense* and *H. alatum* and faster than *H. alternatum* (figs. 64.6, 7). The radials are prominent, and extend above the oral opening. The comparative growth rates of the radial axes are the same as *H. alatum* (figs. 64.3, 8) as are the growth relationships within the sectors (fig. 64.4).



Textfig. 63. *Heteroschisma alatum* (Reimann, 1935). M. Dev., Potter Farm Fm., Alpena, Mich., USA. Ontogenetic development based upon 14 specimens. See textfig. 51 for further explanation.

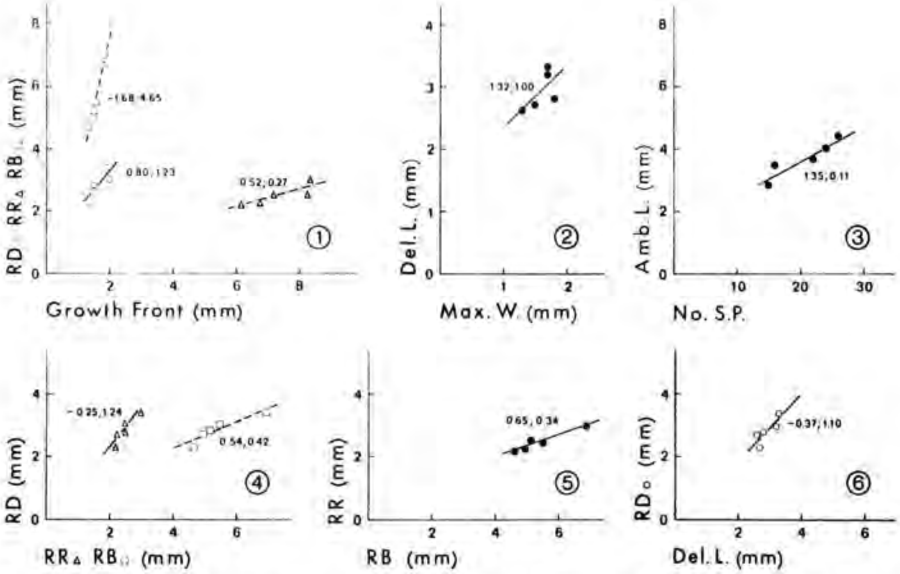
There is no ontogenetic acceleration of RD. The deltoid crest slopes more sharply upward than in the preceding species, and extends above the oral opening. The deltoid width is slightly greater than in *H. alatum* (fig. 64.5). The rate of growth of RD/Del.L. is the same as in *H. alatum* (fig. 64.6). Otherwise remarks concerning the growth of the deltoid and anal deltoids in *H. alatum* apply here as well except for Anus Length/Anus Width; it is poorly correlated ($r = 0.31$). The growth parameters of the ambulacra



Textfig. 64. *Heteroschisma gracile* Wachsmuth, 1883. M. Dev., Thunderbay Ls., Partridge Point, Alpena, Mich., USA. Ontogenetic development based upon 14 specimens. See textfig. 51 for further explanation.

(Amb. L./Amb. W. and Amb. L. (No. S. P.) are the same as for *H. canadense* (figs. 64.2, 9). The number of hydrospires in regular groups increases from 3 to 10; anal hydrospires are lacking.

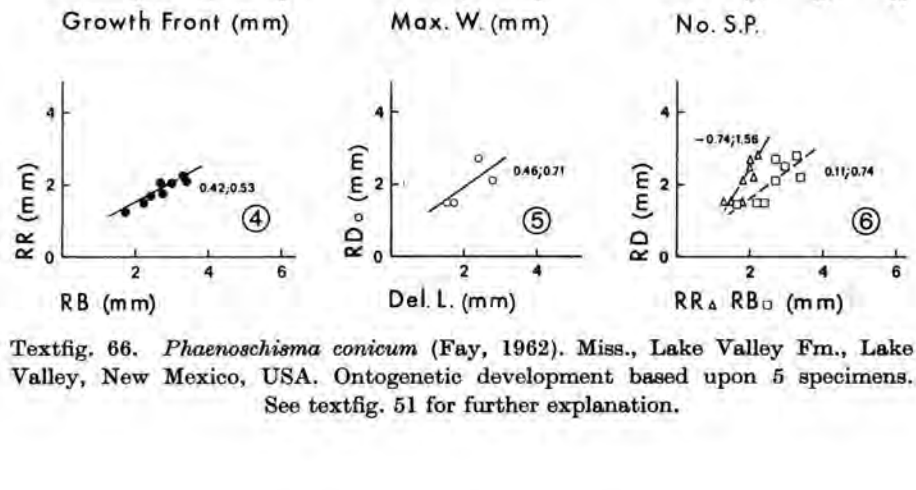
A fifth species of *Heteroschisma*, *H. subtruncatum*, (Pl. III, figs. 15, 20) occurs at a level approximately equal to that of *H. alatum* and *H. gracile*. Its thecal shape is very similar to *H. gracile*. Data for length and width are limited but available points would fall on the same line as for *H. gracile* (fig. 64.1). Data for the conical basals is also limited but they plot graphically in the same region as those of *H. gracile* suggesting very similar to identical relations for BR to RB, RD, and Del. L. The radials are prominent and extend above the peristome; the radial growth relationships are the same as for *H. gracile* (figs. 65.1, 4, 5). The deltoid crest slopes upward above the oral opening. The deltoid length/width (fig. 65.2) is the same as in *H. gracile* but it grew slightly faster relative to RD (fig. 65.6). Otherwise, remarks concerning the growth of the deltoid and anal deltoid in *H. gracile* apply here except for lower correlation coefficients. Ambulacral length increases but the width in the five cases known is constant. The rate of addition of new side plates is about as in *H. gracile* (fig. 65.3). The number of hydrospires per group in known specimens varies from 6 to 8; there are no anal hydrospires.



Textfig. 65. *Heteroschisma subtruncatum* (Hall, 1858). M. Dev., Cedar Valley Ls., Iowa, USA. Ontogenetic development based upon 5 specimens. See textfig. 51 for further explanation.

The specific identity of some other occurrences of *Heteroschisma* are not clear at present (Pl. III, figs. 12, 13).

Mississippian / Tournaisian - Visean. The genus *Phaenoschisma* is one of the most widely distributed phaenoschismatids. There is inadequate data to undertake an ontogenetic analysis of the earliest species, *P. chouteaui* (Pl. III, figs. 16, 21, 23). It is Kinderhookian. The next youngest species, *P. conicum* (Pl. III, figs. 18, 24, 25) is lowermost Osage. We do not have much data on L/W but the former is greater and exceeds 11 mm in the largest specimens. The thecal shape is still conical but the vault is rounded. The deltoids and ambulacra are still restricted to the upper surface. The conical basals have a short BA growth axis; the diameter of the base is narrow (0.4–0.5 mm). The data for basal growth is limited but the distribution of points on a graphic plot indicates they probably grew faster than RB, RD, and Del. L. The rate relative to RB is slightly slower than the other two. The radials are modest in their development and do not reach above the oral opening. RD grows at a slightly faster rate than slightly slower than RB (fig. 66.6); RB is slightly faster than RR (fig. 66.4). Thus the relative contribution of RB to radial growth is always equal to or greater than that of the other axes; this is similar to most previous forms but its percent relative contribution is less. There is no ontogenetic acceleration of RD. Growth relations within the radial sectors differ in that RB grows more slowly with respect to RBF than usual, resulting in a reversal of their usual position. RD/RDF and RR/RRF are about as usual (fig. 66.1). The deltoids are again longer than wide (fig. 66.2), slightly moreso than in *Heteroschisma alternatum*. The deltoid crest slopes

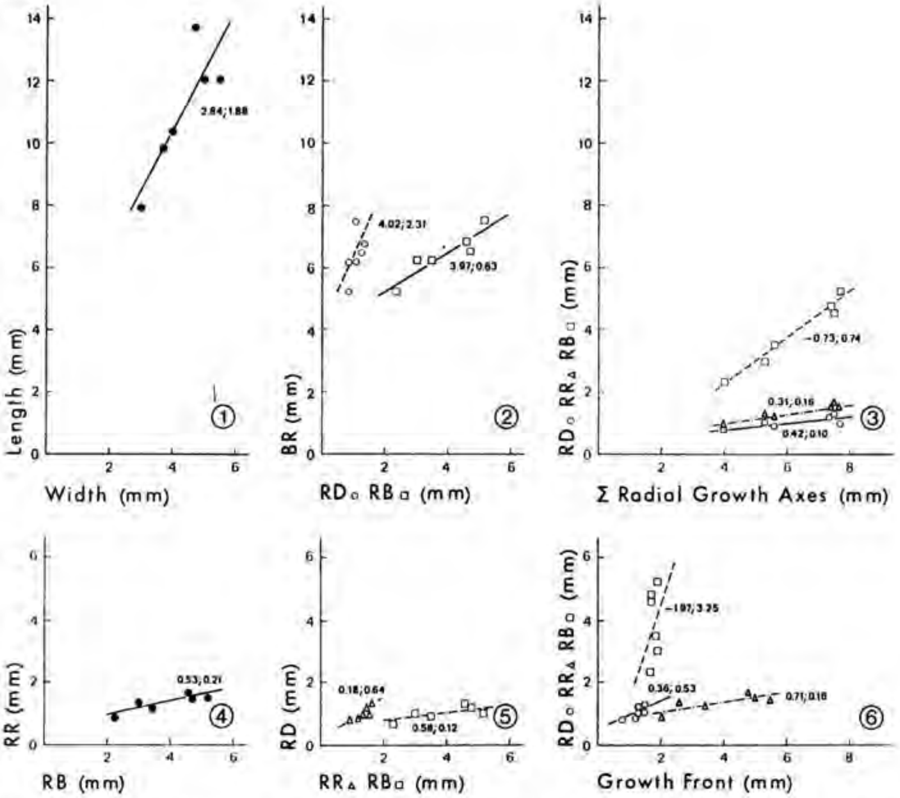


Textfig. 66. *Phaenoschisma conicum* (Fay, 1962). Miss., Lake Valley Fm., Lake Valley, New Mexico, USA. Ontogenetic development based upon 5 specimens. See textfig. 51 for further explanation.

clearly downward in *Phaenoschisma conicum* and is still the dominant part of the plate. The greatest adoral and minimum width increase ontogenetically. The deltoid grows as rapidly as RD (fig. 66.5), a situation approached but not equaled in some species of *Heteroschisma*. The growth of the deltoid and anal deltoids are about equal. In previous genera such as *Decaschisma*, *Polydeltoideus*, *Leptoschisma*, *Caryoblastus*, and *Pleuroschisma*, the hypodeltoid has been a plate which as a result of its growth patterns, formed part of the external thecal wall. There was an external RD sector in the anal interarea. Such a sector was also present in *Heteroschisma*, although here it formed a direct aboral border to the anus. In *Cryptoschisma* and *Pentremitidea*, this was changed and the hypodeltoid grew within the radial sinus. A similar situation pertains in all species of *Phaenoschisma* where the hypodeltoid becomes almost an afterthought at the tip of the anal interambulacral pyramid. In *Phaenoschisma conicum*, ambulacral length increases and widens. The lancet is exposed and there is a departure from linearity. New side plates are added at a somewhat slower rate than usual (fig. 66.3). The number of regular hydrospires per group varies from 5 to 7, the anal from 3 to 6.

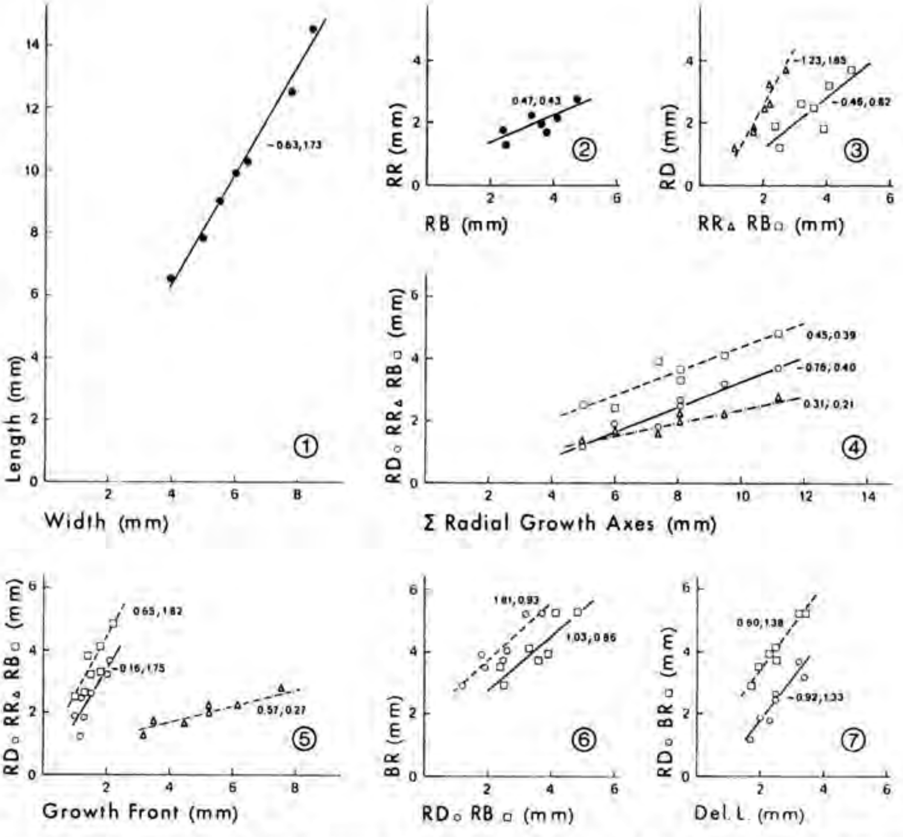
Another, slightly younger Osagean species of *Phaenoschisma* is *P. gracillimum* (Pl. III, figs. 14, 19). Its tall, narrow conical form, with a restricted vault, more closely resembles a Silurian or Devonian form than other Mississippian phaenoschismatids. Its width is the most narrow of any Mississippian fissiculate (fig. 67.1). The tall, narrow conical basals form a prominent part of the theca; the diameter of the stem plates (0.5–0.6) is narrower than that of the corresponding base (0.8–1.0). There is a prominent BA axis. The rate of growth of BR to RD and Del. L. is extremely rapid and one of the greatest differentials known; it also grows more rapidly than RB (fig. 67.2). The radials are prominent in lateral view, extending to about the level of the peristome. RB grows extremely rapidly compared with the other two radial axes (figs. 67.3, 4, 5); RB's percentage of the total radial growth is the highest of any phaenoschismatid and is approached by few other forms (fig. 96.1). There is apparently an ontogenetic acceleration of RB. Within the radial sectors, RD/RDF is unusual in being nearly equal; RR is slightly slower to RRF and RB slightly faster to RBF (fig. 67.6) than in *Phaenoschisma conicum*. The deltoid is an inconspicuous plate with relatively little development. The crest originates below but slopes upward aborally to near the level of the oral opening. The crest is the predominant part of the deltoid; the rate of growth of RD/Del. L. is nearly equal as in *P. conicum*. Deltoid and epideltoid length are approximately equal; the anus is longer than wide and increases in size ontogenetically. The ambulacra are small; they do increase in length and width. The lancet is exposed; new side plates are apparently added at a rate similar to that of *P. conicum*. The regular hydrospires number from 6 to 8 per group, anal from 5 to 6.

Phaenoschisma laeviculum (Pl. III, figs. 26, 27) appears at almost the



Textfig. 67. *Phaenoschisma gracillimum* (Rowley and Hare, 1891). Miss., Lower Burlington Ls., Louisiana, Missouri, USA. Ontogenetic development based upon 6 specimens. (3) Length of individual radial growth axes plotted against their sum for each specimen in the growth series, indicating the relative contribution of each to the total growth of the radial. See textfig. 51 for further explanation.

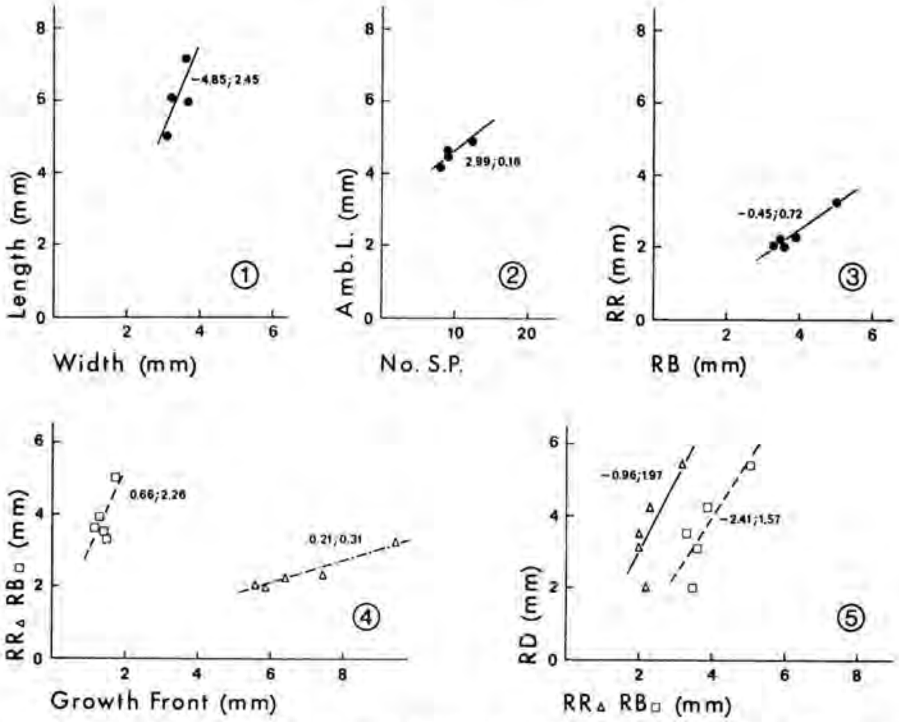
same stratigraphic level as *P. gracillimum*. The conical theca is broader than in *P. gracillimum* (fig. 68.1), L/W being very similar to *Heteroschisma alternatum*. The presence of a BA axis in the conical basals is uncertain; the base is narrow (0.6–1.1 mm). BR grows faster than RB, RD, and Del. L., the rate quickening from the former to the latter (figs. 68.6, 7). These rates are not as extreme as in *P. gracillimum*. The radials are prominent in lateral view, extending to about the level of the oral opening. The RB axis is the predominant one, but its relative rate of growth is less than in *P. gracillimum*; the relative rates of the axes is near *P. conicum*. RD grows at a slightly greater rate than RR and slower than RB; RR is slower than RB (figs. 68.2, 3, 4). RD/RR and RR/RB are as in *P. conicum*; RD is slightly slower with respect to RB. There is an ontogenetic acceleration of RD to RB. Growth relationships within the radial sectors show the usual disposition (fig. 68.5); RD and RB grow more rapidly than their fronts (moreso the latter); RR grows less slowly. RD/RDF is slower than in *P. conicum* but faster than in *P. gracillimum*; RR/RRF is slightly slower than in *P. conicum* and faster than *P. gracillimum*; RB/RBF is faster than in *P. conicum* and apparently slightly slower than in *P. gracillimum*. The deltoid is more conspicuous than in *P. gracillimum*; the crest is the dominant part and may slope slightly upward or downward. RD and Del. L. grow at almost the same rate (fig. 68.7) as in the two previous species of *Phaenoschisma*. The length of the epideltoid is the same or slightly less than that of the epideltoid. The anus increases slightly in size. The ambulacra are more prominent than in *P. gracillimum*, increasing in length throughout ontogeny (2.0–4.7 mm). New side plates (7–12) are apparently added at a faster rate than in *P. conicum*. The lancet is prominently exposed. There are 6–8 hydrospires per regular group, 5–6 in the anal interarea. Some specimens of *Phaenoschisma* from another formation appear to be assignable to *P. laeviculum* and reach the largest size of



Textfig. 68. *Phaenoschisma laeviculum* (Rowley, 1900). Miss., Upper Burlington Ls., Louisiana, Missouri, USA. Ontogenetic development based upon 7 specimens. (4) Length of individual radial growth axes plotted against their sum for each specimen in growth series, indicating the relative contribution of each to the total growth of radial. See textfig. 51 for further explanation.

all in this genus (Pl. IV, figs. 19, 21). These specimens were not included in the preceding ontogenetic analysis.

Phaenoschisma also occurs in the Visean of the British Isles. The type species, *P. acutum* (Pl. IV, figs. 3, 5) is represented by only a few specimens so the following discussion is based on limited data. Its form is conical; the vault is somewhat more expansive than previously. The maximum known size characterizes this species as moderate in size, similar to most previous forms. L/W (fig. 69.1) is almost identical to *P. laeviculum*.



Textfig. 69. *Phaenoschisma acutum* (Sowerby, 1834). L. Carb., Worston Shale Group, near Clitheroe, Lancashire, England. Ontogenetic development based upon 5 specimens. See textfig. 51 for further explanation.

It is unknown if there is a BA axis in the conical basals. There is insufficient data to run a regression analysis of BR growth but a scatterplot suggests that BR grows only slightly faster than RB and RD and a bit faster than Del. L. The radials are prominent in lateral view; they do not reach to the level of the oral opening. There is greater emphasis on the growth of RD than in previous species; it is faster than RR and equal to RB (fig. 69.5). RR/RB is almost identical to that of *P. laeviculum* (fig. 69.3). There is no acceleration of RD. Within the radial sectors, data for RD/RDF is limited, and no regression analysis was attempted; its distribution suggests it is similar to RB/RBF (fig. 69.4), where RB is faster than RBF.

RB is slightly faster to RBF than in *P. laeviculum*; RR/RRF is the same (fig. 69.4). The deltoid is fairly conspicuous; the crest is dominant and slopes downward. The plate is longer than wide but there is insufficient data to characterize its growth. The ambulacrum is broad when compared to the length; the rate of addition of new side plates is probably similar to other *Phaenoschisma* species but data is too clustered to be sure (fig. 69.2). There are 4 to 6 hydrospires per regular group; they are also present (in nearly equal number?) in the anal interarea. Larger specimens of *P. acutum* are found in Ireland (Pl. IV, figs. 10, 14). Other occurrences of *Phaenoschisma* are illustrated in Pl. IV, figs. 1, 2, 6, 7.

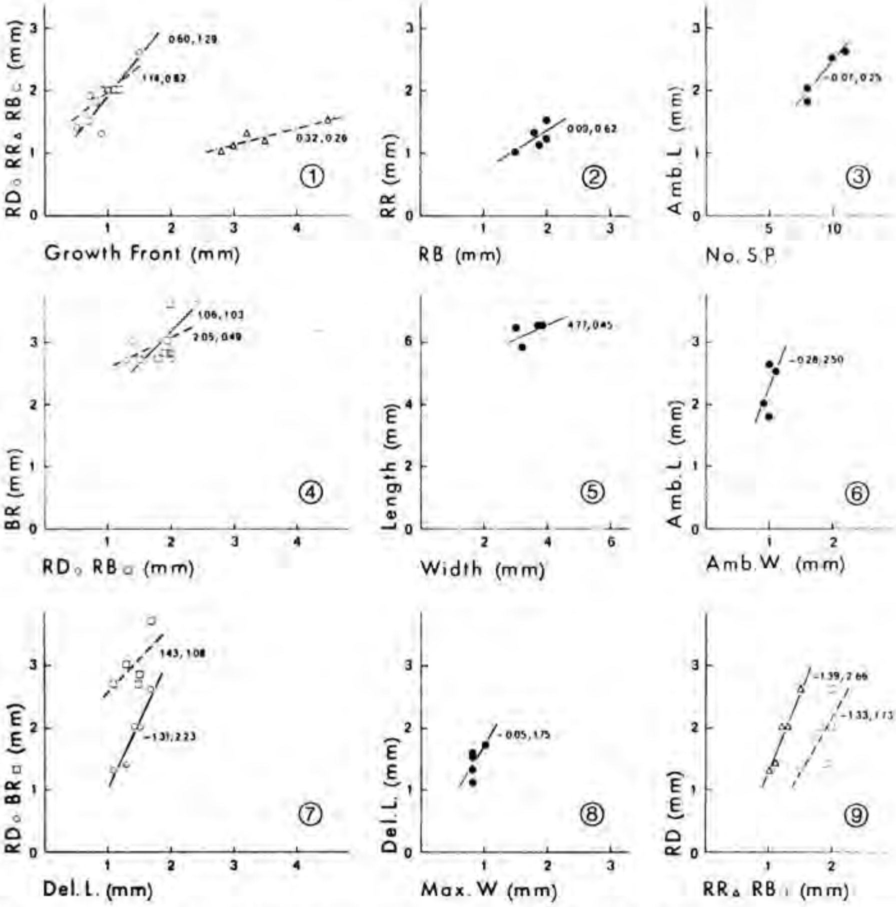
The genus *Phaenoblastus* is another phaenoschismatid which has a wide geographic distribution during the Tournaisian. The type species, *P. caryophyllatus* (Pl. IV, figs. 8, 12) was the subject of an earlier study in which its ontogenetic development was detailed. Therefore, it is only summarized here; textfigures are given in MACURDA 1967a. L/W is similar to *Phaenoschisma laeviculum*, but the vault is greatly expanded, the ambulacra being very prominent and extending downward on the theca. Maximum size is intermediate. The basals are conical, and have a BA growth axis. BR grew at a slightly faster rate than RB or Del. L., but RD grew much faster than BR. The radials are relatively conspicuous; initially, RB is the dominant axis with RD only slightly greater than RR. However, there is a very large acceleration of RD (from 30 to 50 percent of the total radial growth) with a slight decline in RR and large decline in RB. RR was about equal to RB. Within the radial sectors, the growth patterns were similar to *Phaenoschisma laeviculum* except for a faster rate of RD to RDF. The deltoid is conspicuous, and grew downward in an arc; the width more closely approaches the length. The hypodeltoid was quite small and did not contribute to the external wall of the theca. The ambulacra reach a much greater length than in *Phaenoschisma laeviculum*; side plates are added at about the same rate. The number of hydrospires in regular groups increases ontogenetically from 4 to 9, the anal from 3 to 6.

Another species of *Phaenoblastus* is found in the Kinderhookian of the USA. *P. pecki* (Pl. IV, figs. 11, 15, 18) is known to us from limited material so the following remarks are based largely upon a comparison of the distribution of data points on a graph when compared with similar graphs of *Phaenoschisma* and *Phaenoblastus*. The three complete specimens range between 7.5 to 11 mm in length, so the size of the specimens is similar to those with which they are being compared. L/W of *P. pecki* is slightly broader than *Phaenoschisma laeviculum* and *Phaenoblastus caryophyllatus*. The pelvis is conical but broad; the vault is conspicuous and the ambulacra reach well down toward the equator. The basals are conical; a BA axis does not appear to be present. The diameter of the base is narrow (0.8–0.9 mm). BR grows at a slightly faster rate to RB than it did in *Phaenoblastus caryophyllatus*. It is slightly slower, but still faster than RD and Del. L.;

in *Phaenoblastus caryophyllatus* RD was highly accelerated. The rate of BR to RB and RD is slightly less than that of *Phaenoschisma laeviculum*. Thus in *P. pecki*, BR grows most rapidly to RB, then RD and Del. L. The radials are somewhat reduced in prominence. Percentagewise, 37–42 percent of the total radial growth occurs in RD, while RR is 23–31 percent and RB is 28–35 percent (fig. 96.1). Thus, RD grows faster than any other axis, RB being reduced to near equality with RR. This relationship is different from any species of *Phaenoschisma* and is similar to *Phaenoblastus caryophyllatus*, but RR forms a greater part of the total in *P. pecki*. The pronounced acceleration of RD in *Phaenoblastus caryophyllatus* is apparently lacking in *P. pecki*. RD/RDF and RR/RRF are slightly faster than in *Phaenoschisma laeviculum* and *Phaenoblastus caryophyllatus*, while RB/RBF is slower. The deltoid crest slopes downward; its growth rate is probably similar to that of RD. There are 8 hydrospires per regular group and 4–8 in the anal interarea.

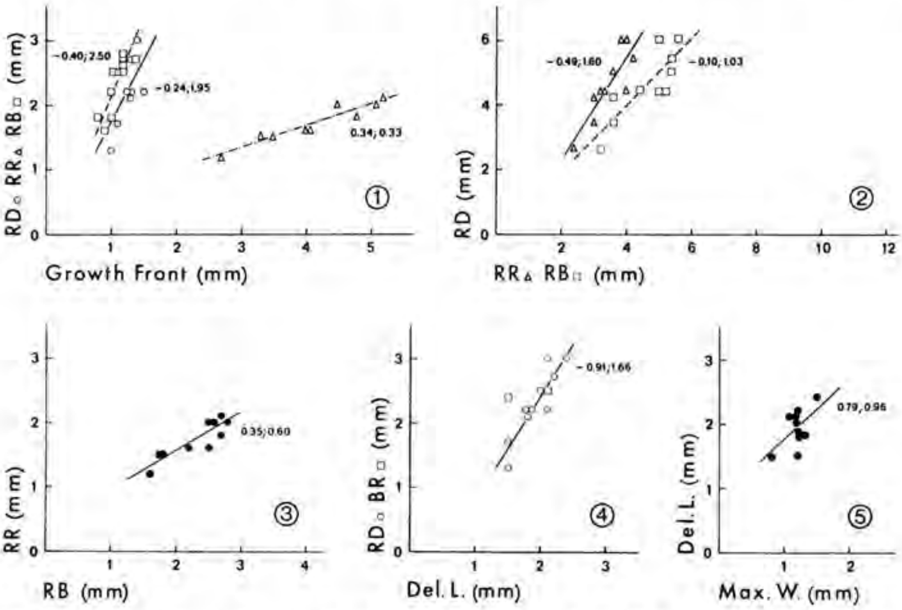
Pentremoblastus (USA; Kinderhookian) has been described as a spiraculate blastoid. Many characters of the type species *Pentremoblastus conicus* (Pl. IV, figs. 4, 9) resemble a *Phaenoschisma* or *Phaenoblastus*. Until we have studied it internally and the structure of a number of very closely related genera, we do not wish to modify its generic assignment. However, we suggest it may represent a phaenoschismatid in transition to a pentremitid. A second species, *Pentremoblastus subovalis*, (Pl. IV, figs. 13, 16) was described from the same locality. We present a figure showing the growth relationships of the type species, *P. conicus* (figs. 70.1–9) to show the similarities and differences with the species of *Phaenoschisma* and *Phaenoblastus*. The maximum size is small compared to other Mississippian species discussed thus far (fig. 70.5). The points lie between the lines of *Phaenoschisma gracillimum* and *P. laeviculum*. The theca is conical but the proportion of the vault is somewhat increased. A BA axis is present in the conical basals; the diameter of the base is quite narrow (0.3–0.4 mm). The rate of growth of BR is faster than that of RB and RD, having about the same rate with both (fig. 70.4); this rate is about equal to the BR/RB of *Phaenoschisma laeviculum* (we noted the rate of BR/RD was faster there). The rate of BR/Del.L. (fig. 70.7) is about equal to *Phaenoschisma laeviculum*. The rate of growth of RD is more rapid than RR and perhaps more rapid than RB (fig. 70.9); RR is less rapid than RB (fig. 70.2). RD is relatively more rapid than in *Phaenoschisma laeviculum*. The relative percentage of RD is greater than in this last named taxon and closest to but not as great as in *Phaenoblastus pecki*. There is no acceleration of RD. Growth within the radial sectors (fig. 70.1) is similar to *Phaenoschisma laeviculum* but the rate of increase of RD and RB to their front may be slightly slower. The deltoid of *Pentremoblastus conicus* is confined to the upper surface; the length is greater than the width (fig. 70.8). The crest forms the predominant part and slopes downward. There is no external hypodeltoid. The ambulacra are longer than wide with an exposed lancet (fig. 70.6); new side plates are added more rapidly than in *Phaenoschisma laeviculum* (fig. 70.3). There are 3–5 hydrospires in each regular group; 2–4 in the anal area. The full width of RDF is not utilized for hydrospire formation.

Late in the course of this study, after completion of the internal sectioning program and its drafting and interpretation, we were able to recognize and clarify the phaenoschismatids of the Lake Valley Ls., New Mexico, by further field work. One taxon from there is *Phaenoschisma conicum* (Pl. III, figs. 18, 24, 25) whose ontogeny was described above. However, there is a second taxon whose growth relationships appear to be important to an understanding of the temporal distribution of phaenoschismatid growth patterns. Until we have studied it internally, we do not wish to make a taxonomic assignment. Therefore, we will deal with its taxonomy in a subsequent paper but present a discussion of its growth



Textfig. 70. *Pentremoblastus conicus* Fay and Koenig, 1964. Miss., McCraney Fm., Seahorn Hollow, Adams Co., Illinois, USA. Ontogenetic development based upon 5 specimens. See textfig. 51 for further explanation.

as an aid to understanding the evolution of phaenoschismatid growth patterns. We will refer to it as UA (undescribed phaenoschismatid A; Pl. IV, figs. 17, 20; Pl. V, figs. 1, 2). There is insufficient data to plot L/W; the width does approach the length. The bud-like shape is different from previous Mississippian forms; it combines the somewhat attenuated base of *Phaenoblastus caryophyllatus* with the abrupt angular vault profile of a Silurian or Devonian phaenoschismatid. UA has conical basals but they are somewhat concave laterally; the base is narrow. It is unclear if there is a BA axis. The rate of growth of BR appears to be slightly greater than RB, RD, and Del.L. (fig. 71.4) but there is insufficient data to conduct regression analysis. The radial is prominent in lateral view, extending above the oral opening. RD grows more rapidly than RR but at the same rate as RB (fig. 71.2). RB grows slightly more rapidly than RR (fig. 71.3). The relative rate of the radial axes is intermediate between that of *Phaenoschisma laeviculum* and *Phaenoblastus caryophyllatus*. There is no ontogenetic shift of RD. Within the radial sectors, the growth relations are very similar to *Phaenoschisma laeviculum*, but RD and RB may be slightly quicker with respect to their front (fig. 71.1). The deltoid of UA is unique amongst Mississippian phaenoschismatids in how steeply the crest slopes upward, producing a deep ambulacral sinus. The crest is the predominant part of the plate. Deltoid length is greater than width (fig. 71.5); RD has a higher rate of growth (fig. 71.4). The greatest adoral

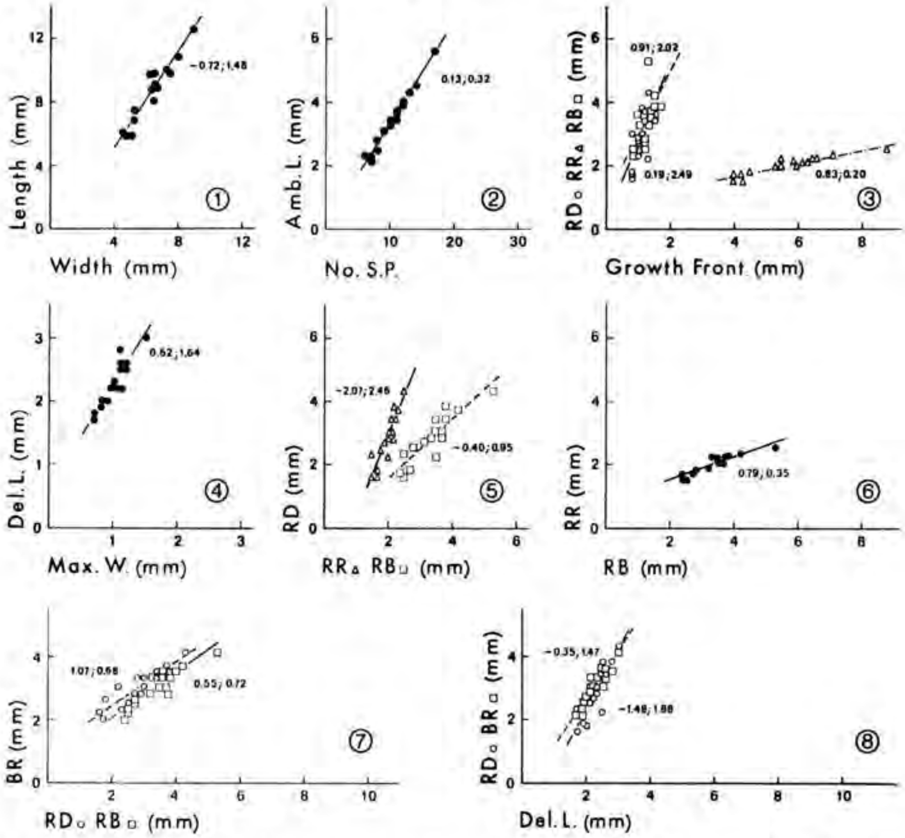


Textfig. 71. Phaenoschismatid, New Mexico. Miss., Lake Valley Fm., Lake Valley, New Mexico, USA. Ontogenetic development based upon 10 specimens. See textfig. 51 for further explanation.

and minimum width are rather constant. The anal deltoids are slightly longer than the regular deltoids but not always wider. There is an external growth front on the hypodeltoid. We cannot characterize the growth of the ambulacra; they are narrower than in *Phaenoschisma* and *Phaenoblastus* and apparently confined to the lower part of the ambulacral sinus. There is less exposure of the lancet. There are 4–6 hydrospires in each regular group, 2–3 in the anal interarea. The full width of RDF is not utilized for hydrospire formation.

Recently, J. Sprinkle and R. Gutschick have found a phaenoschismatid in the Mississippian Lodgepole Fm. (Tournaisian) of Montana (Phaenoschismatid n. gen. of textfig. 100). This form clearly is a new genus which they will describe in the near future. We are indebted to them for making it known to us for it is apparently an intermediate link between Devonian and Mississippian phaenoschismatids. We do not illustrate or describe it to preserve their priority but have studied the ontogenetic relationships of some of the principal growth components in order to understand the phylogeny of fissiculate growth. We will refer to it as "undescribed phaenoschismatid B" (UB). LW is slightly wider than in *Phaenoschisma laeviculum* (fig. 72.1). The maximum size places it in the intermediate size range; the vault has been expanded relative to the pelvis in comparison with Devonian phaenoschismatids, but the deltoids are restricted. The basals of UB are conical but appear truncated; there is no BA axis. The growth rate of BR to RB and RD is about equal; RB is just a bit faster (fig. 72.7). BR is faster than Del.L. (fig. 72.8). The radial is conspicuous in lateral view, extending to the level of the oral opening. RD grows more quickly than RR and just slightly slower than RB (fig. 72.5); RR is slower than RB (fig. 72.6). RB has the largest proportion of total radial growth but RD has a greater percentage than in most species of *Phaenoschisma* (e.g. *P. acutum*). RD has a greater relative rate of growth in the species of *Phaenoblastus*. The percentage of RD compares very closely with UA but RR is less. There is no acceleration of RD. Within the radial sectors, the rate of RR/RRF is the same as in *Phaenoschisma laeviculum* but both RD and RB grow more quickly with respect to their fronts; their relative rates are equal (fig. 72.3). The deltoid is relatively restricted, the crest is the dominant part and usually slopes slightly upward. Deltoid length is greater than width (fig. 72.4); RD grows more rapidly than Del. L. (fig. 72.8). There is an external hypodeltoid growth front as in "*Phaenoschisma*" *saharae* (see below). The ambulacra increase regularly in length to a greater relative size than in *Phaenoschisma laeviculum*; new side plates are added at the same rate (fig. 72.2). The number of regular hydrospires per group increases from 4 to 8, the anal from 3 to 6; $r=0.30$.

During the course of our study, specimens made available by Claude Pareyn from the Visean of Algeria have proved to belong to the same genus as that found by Sprinkle and Gutschick in the Tournaisian of



Textfig. 72. Phaenoschismatid, new genus, new species. Miss., Lodgepole Fm., Bandbox Mountain, Cascade Co., Montana, USA. Ontogenetic development based upon 16 specimens. See textfig. 51 for further explanation.

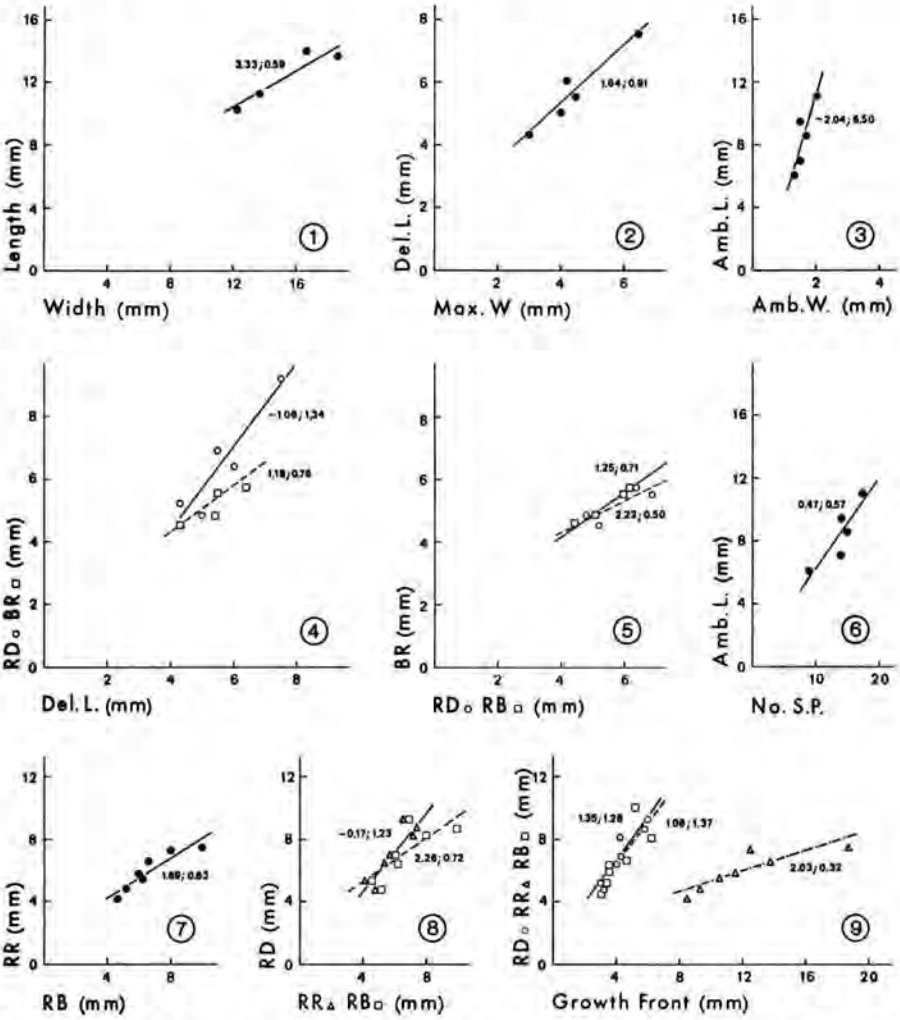
Montana. We have temporarily placed these in the genus *Phaenoschisma* as "*P.*" *saharae* but they do not belong to this genus; this species will be transferred by Sprinkle and Gutschick to their new genus. "*P.*" *saharae* (Pl. V, figs. 4, 5, 10) is known from only three specimens, so the following remarks were derived from an overlay of "*P.*" *saharae* data on UB graphs (figs. 72.1–8). The thecal shape of "*P.*" *saharae* is conical; the vault is less developed than UB and the deltoids are restricted. The theca is narrower and maximum size greater. The basals are conical; a BA axis is lacking. The rate of growth of BR to RD is faster (and thus different from UB); the rate of RB is probably slightly faster. BR is faster to Del.L. than it was in UB. The radials are prominent in lateral view, extending slightly above the peristome. Both RR and RB grow more rapidly with respect to RD than in UB; the rate of RR/RB is very similar. RB is the dominant part of radial growth (48–50 percent, fig. 96.1), while RD and RR are less (27–29 and 23 percent respectively). The relative percentage of RR remains the same in UB and "*P.*" *saharae*; the difference lies in the relative emphasis on RD in the former. The relative percentages of the radial axes in "*P.*" *saharae* are closer to UB than *Phaenoschisma gracillimum*. Within the radial sectors, RD/RDF is apparently the same, RR/RRF and RB/RBF are slightly faster but further data is needed. The deltoid is restricted and the deltoid crest slopes upward. It is relatively wider than in UB. Its rate of growth with RD appears very similar to UB. The hypodeltoid has an external growth sector. Because of its greater thecal size, the ambulacra reach a greater size than in UB but are the same width; side plates are added at the same rate. When there are 9 hydrospires in a regular group, there are 4 anal.

One phaenoschismatid (USA, Miss., Kinderhookian) whose deltoid growth relationships might have special phylogenetic significance is that illustrated in Pl. III, figs. 17, 22. At first glance, it looks similar to a *Phaenoschisma conicum* (Pl. III, figs. 18, 24, 25) but it is not because of differences in the deltoid crest and hypodeltoid. The basals are missing but they must have been a dominant part of the theca in lateral view because of their width at the broken lower edge of the theca and projected lateral profile. RB is the predominant radial axis. The deltoid crest originates flush with the adoral end of the deltoid instead of below it as in *P. conicum*; the crest slopes downward. This phaenoschismatid has a large hypodeltoid (in addition to the epideltoid) which contributes to the external wall of the theca; this condition is lacking in *Phaenoblastus* and *Phaenoschisma* and similar to that of UB. However, the ambulacral shape is different (petaloid vs. sublanceolate). Until further material is found, it is premature to make a generic assignment. There are 4 regular hydrospires per group; they are also present in the anal interarea.

Another Tournaisian-Visean phaenoschismatid whose generic position is unknown is illustrated in Pl. V, figs. 3, 6 (USA, Mo., Osage or Keokuk). This form is of interest because of its tall conical form, emphasis on BR and RB (latter is 44 percent of radial growth), small restricted deltoid with its upward sloping crest, narrow ambulacra in which the lancet is apparently largely concealed, and reduced number of hydrospires (4 per regular group, also present in anal interarea) due to a failure to utilize the full width of RDF for hydrospire formation. An understanding of its ontogeny and position in fissiculate evolution must await the discovery of additional material. Its relation to Miller's problematic "*Codaster*" *gratiosus* (Pl. V, figs. 7, 9), is unknown.

One other species has been assigned to *Phaenoschisma*: "*P.*" *benniei* (Visean) (Pl. V, figs. 8, 11, 13). This species definitely belongs to some other genus because of differences in the ambulacral sinus (apparently quite shallow) and a hypodeltoid with an external growth sector. We suggest it could be a neoschismatid similar to *Hadroblastus* but the available specimens are always squashed and the plates faulted. Therefore, we cannot suggest its proper generic assignment. The scarcity and mode of preservation precluded ontogenetic measurements but symmetry suggests an emphasis on growth in the vault region when compared with Devonian fissiculates.

Namurian. Kazachstanoblastus carinatus (Pl. V, figs. 14, 16, 17) from the Namurian presents an interesting contrast with earlier phaenoschismatids. Its theca is still conical but now much broader; the vault often approaches the size of the pelvis and length equals width for the first time (fig. 73.1). The ambulacra appear more expansive. The basals are conical but very broad and a BA axis is present. BR grows at the same rate as RD and RB (fig. 73.5), which is similar to UB. BR grows at the same rate as Del.L. (fig. 73.4). The radials are prominent in a lateral



Textfig. 73. *Kazachstanoblastus carinatus* Arendt, Breimer, and Macurda, 1968. L. Carb., Lower Namurian, Tshan–Tshar, North Kazachstan, USSR. Ontogenetic development based upon 7 specimens. See textfig. 51 for further explanation.

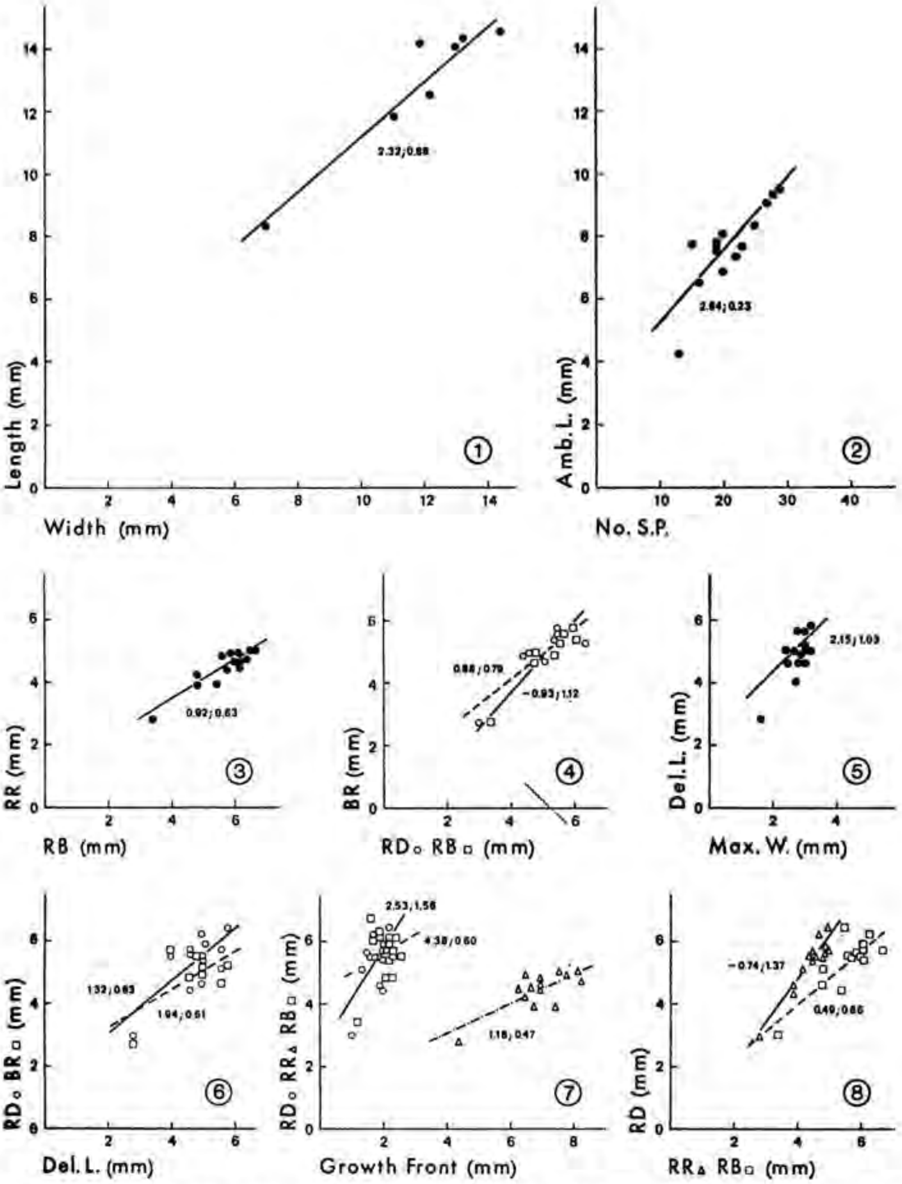
view, extending above the oral opening. RD and RB grow at almost the same rate with one another and they are only slightly faster than RR (figs. 73.7, 8). This near equality and the greater relative percentage of RR is almost unique amongst phaenoschismatids, only the Devonian *Caryoblastus bohemicus* being similar amongst those discussed so far. RD and RB both grow at the same rate with respect to their fronts within the radial sectors; they are faster to their fronts while RR is slower (fig. 73.9). The deltoid is a conspicuous plate, dominated by the crest which slopes upward. Del.L. is slightly greater than width (fig. 73.2); RD grows slightly more rapidly than Del.L. (fig. 73.4). The anal deltoids are about the same length as the deltoids; the anus is rather equidimensional. The hypodeltoid is extreme amongst the phaenoschismatids in its relative size, being larger than the epideltoid. It lacks an external growth front, instead forming an interambulacral pyramid. The ambulacra are prominent and width increases slowly in relation to length (fig. 73.3). New side plates are added at a slower rate than in most other forms (fig. 73.6). Hydrospires appear to be totally lacking in regular or anal areas; thus none of the broad RDF is used for hydrospire formation, which is unique in phaenoschismatids.

Another Namurian fissiculate which occurs with *Kazachstanoblastus carinatus* is *Phaenoschisma? rossica* (Pl. V, figs. 12, 15). This form is different from any other fissiculate but does not belong to *Phaenoschisma*. It is only known from a single specimen. Its conical profile appears pinched proximally; it has a low vault. There is a BA axis present in the basals; their rate of growth is greater than that of RB, RD, and Del.L. The radials are somewhat reduced in prominence; RD is the major radial axis (40 percent), as opposed to RR (29 percent) and RB (32 percent) (fig. 96.1). The deltoids are very restricted and grow quite slowly compared to RD. The deltoid crest is small and only slopes upward slightly. A hypodeltoid is apparently lacking. The ambulacra are short and the lancet is exposed only over half its length. The hydrospires are restricted in number (two per regular group, one per anal). The full width of RDF is not utilized for their formation.

Dolichoblastus shimanski (Pl. VI, figs. 1, 4) is a form which we have placed in the phaenoschismatids with reservation. It is large for a phaenoschismatid, over 21 mm in length. The pelvis is conical, the vault restricted but there are unusual "wings" along the interradial sutures, due to an increase of the thickness of lateral calcite deposited with growth; an increased rate produces an outward curvature of the RR axis. The basals are incomplete but large, and grew faster than RB, RD, and Del.L. The radials are reasonably prominent laterally, reaching to about the level of the oral opening. RB is the predominant axis (55 percent) compared to RD (19 percent) and RR (25 percent). The deltoid is small and it is unknown if it had a deltoid crest due to its preservation. The deltoid grew more rapidly than RD; the hypodeltoid was relatively small. The ambulacra are modest in size; the lancet is exposed only in the adoral half. The rate of addition of ambulacral plates was about normal. There were only eight hydrospire groups, with three per group. Their spacing was wider than in most all previous forms.

Family OROPHOCRINIDAE

Devonian. One of the first departures from the usual Devonian fissiculate growth patterns is found in the genus *Brachyschisma*. *B. corrugatum* (Pl. VI, figs. 2, 5, 6, 15), from the Eifelian, has a thecal shape which ranges from broadly conical to outflaring. Length is almost equaled by the width (fig. 74.1). Maximum size is intermediate. The vault is expanded and the ambulacra are quite prominent; the deltoids do not extend above the oral opening. The basals are conical, with a strong deposit of secondary calcite and relatively broad stem attachment (e.g., base 2.4 mm; stem plate diameter 2.0 mm). The rate of growth of BR is equaled by that of RB, RD, and Del.L. (figs. 74.4, 6), an unusual configuration in the Devonian. The radials are prominent in lateral view but do not extend above the oral opening; an ambulacral sinus is lacking. Both the radials and basals show prominent growth lines. RD grows slightly faster than RR, and at almost the same rate as RB (fig. 74.8). RR grows slightly more slowly than RB (fig. 74.3). The near equality of RD and RB differs from most all Devonian fissiculates. There is no ontogenetic acceleration of RD. Both RD and RR grow more rapidly than their fronts; their relative rates are equal. As usual, RR grows more slowly than RRF (fig. 74.7) but at a slightly faster rate than in most phaenoschismatids. The deltoid is unique amongst Devonian forms when compared to them. Instead of the sharp deltoid crest, the aboral part of the plate is broad and rather flat; there is apparently secondary deposition of calcite on the outer surface of this plate, producing an infilling of the hydrospires. The plate does project above the oral opening. Del.L. is greater than the maximum width (fig. 74.5); the rate of growth is only slightly less than RD (fig. 74.6). Both the greatest adoral and minimum width increase ontogenetically and are relatively broader than in phaenoschismatids. The length of the deltoids and anal deltoids are about equal; the widths are also about equal. The superdeltoid is an actively growing plate as is the subdeltoid, which is the larger of the three anal deltoid plates. Its unique asymmetry is not found elsewhere. The anus and hypodeltoid also increase in size ontogenetically. The distance from oral center to the adoral end of the ambulacrum is greater than in most Devonian fissiculates and increases ontogenetically. The ambulacra are much more prominent than most Silurian and Devonian forms, being elevated above the surrounding plates. They are of greater length than in most intermediate sized forms. The lancet remains concealed, except at the adoral tip. AmbW increases along with AmbL; new side plates are added at an average rate (fig. 74.2). The number of regular hydrospires per group ranges from 5 to 8, increasing ontogenetically. The outermost part of RDF is not used for hydrospire formation. There is only one anal group (D being missing); the number within it range from 2 to 5. The hydrospire groups of *B. corrugatum* differ in not being open to the origins of the plates but progressively closed off at the ends by secondary calcite.



Textfig. 74. *Brachyschisma corrugatum* (Reimann, 1935), M. Dev., Onondaga Ls., Williamsville, N.Y., USA. Ontogenetic development based upon 14 specimens. See textfig. 51 for further explanation.

At a slightly older horizon (Eifelian), there is a blastoid whose growth habit very closely resembles that of *B. corrugatum*. We have questionably placed it in *Brachyschisma* as *B? oostheizeni* (Pl. VI, figs. 3, 10, 13). Our data on it is limited but the close relationships of thecal form suggest similar growth patterns. The RB axis seems to be more dominant and the deltoids slightly narrower. The ambulacra are again elevated. The number of side plates per mm is about the same as is the range in number of regular hydrospires per group (5–8). We were unable to observe the anal interarea.

Two blastoid radials have been reported from the Eifelian of South America. They were illustrated by KNOD 1908, and appear very similar to those of a *Brachyschisma*. We have been unsuccessful in locating the original material and it is now apparently lost.

Mississippian / Tournaisian – Visean. In the Tournaisian we find the lowest stratigraphic occurrence of two genera, *Katoblastus* and *Orophocrinus*, in which there is a clearly defined external growth sector in the deltoid which is not involved in hydrospire formation. *Katoblastus* is restricted to the Tournaisian and represented by two species: *K. konincki* (Pl. VI, figs. 7, 8, 12) and *K. püzos* (Pl. VI, figs. 9, 11, 14). The ontogeny of these was detailed and illustrated graphically previously (MACURDA, 1967a); only a summary is presented here. *K. konincki* is relatively small and the length and width about subequal. The vault is slightly less than the pelvis; the ambulacra are restricted to the upper surface. The conical basals have a small deposit of secondary calcite at their proximal tip; the stem attachment area is narrow. Their rate of growth is equal to that of RD but slightly greater than that of RB and Del.L. The radials are somewhat reduced in prominence laterally. RD grows more rapidly than RR but only slightly more rapidly than RB. The last named grows slightly more rapidly than RR. There is no ontogenetic acceleration of RD. Within the radial sectors, RD grew most rapidly with respect to its front, RB less so. RR grew less rapidly than RRF. The deltoids are restricted to near the top; an external DR sector is present. The deltoid lengthened and increased in width ontogenetically; its rate of growth was less than that of RD. In both species of *Katoblastus*, the hypodeltoid has an external growth sector. The ambulacra of *K. konincki* are relatively short and narrow; the lancet is narrowly exposed. New side plates are added at a slightly higher rate than usual. Entrance to the hydrospires is via a hydrospire cleft, although part of the outermost slit is usually exposed; the cleft extends the full length of the ambulacrum. The adoral separation between adjacent clefts is very narrow. The number per group increases ontogenetically from 4 to 6; there is usually one less in the anal groups.

Katoblastus püzos (Pl. VI, figs. 9, 11, 14) differs from *K. konincki* in the greater expansion of the vault with the increased lengthening of the ambulacra. The vault may be greater than the pelvis. The maximum known size is 10 mm in length; it and the width are usually subequal. The conical basals have a large secondary calcite deposit (1.0–2.0 mm); the stem diameter is greater than in *K. konincki*. BR grows at the same rate as RB but much less rapidly than RD. It is slightly slower than Del.L. The radials are more prominent than in *K. konincki*; RD grows much more rapidly than RR and RB. These last two axes grow at an equal rate to one another. There is an ontogenetic acceleration of RD from 45 to 55 percent of the total radial growth. Within the radial sectors, RD and RB show similar relations in growth rates with their fronts as do *K. konincki* (except that RD reaches a greater total); RR grows more slowly with RRF. The deltoid is a bit more conspicuous but confined to the upper surface. It lengthened and widened ontogenetically; its rate of growth was much less than that of RD. The ambulacra lengthened fairly rapidly ontogenetically but were narrow; the lancet was narrowly exposed. The rate of addition of side plates was slightly faster than in *K. konincki*. There appears to be a maximum limit on the number of hydrospires in regular groups (5); those in the anal area are reduced in number. Entrance is via a hydrospire cleft which extends the full length of the ambulacrum; the outermost slit is exposed however. The adoral separation between adjacent clefts is very small.

The genus *Orophocrinus* contains the largest number of species recognized in any fissiculate blastoid, 10 in all. Five are found in the Tournaisian of North America, five in the Tournaisian and Visean of western Europe. The ontogeny of these 10 species has been the subject of previous discussions and illustrations by MACURDA (1965^b, 1966). In a few of the graphs accompanying the referenced articles, curvilinear relations between some variables were plotted. These lines were fitted visually as a suitable regression program was not available to Macurda at that time. Curvilinear relations between variables have not been found outside *Orophocrinus* during this study. Using our standard computer regression program on the original *Orophocrinus* data suggests most of the curvilinear relations are linear, with perhaps the exception of growth relations in the radials of some species as *O. stelliformis*.

Orophocrinus conicus (Pl. VII, figs. 1, 2, 4; Pl. IX, fig. 7) is the oldest North American species, being Kinderhookian in age. The theca is conical; the vault is less than the pelvis. Its maximum size is intermediate. The ambulacra are restricted to the upper surface. Length is slightly greater than width. The diameter of the stem plates varies from 1.5 to 2.5 mm. In *O. conicus* and other species, deposits of secondary calcite form the basal attachment area. In *O. conicus*, BR grows slightly faster than RB and a bit faster yet with respect to RD and Del.L. The radials are moderately prominent in lateral view; in none of the species do they extend up to the level of the oral opening. RB is the predominant radial axis in *O. conicus*, growing faster than RR and RB. There is an ontogenetic acceleration of RD and it comes to almost equal RB. RD is faster than RR. Within the radial sectors, RD grows rapidly with respect to its front, RB less so. RR grows more slowly than RRF. The deltoid in all species of *Orophocrinus* is restricted to the upper surface and has a larger separation between hydrospire clefts than in *Katoblastus*. There is a well developed external DR sector (this is also present in the hypodeltoid) and the deltoids grow out and down from the oral opening, lengthening at a greater rate than they widen in all species. Initially RD and Del.L. grow at approximately the same rate in *O. conicus* but RD becomes slightly faster ontogenetically. The ambulacra become fairly long compared to *Katoblastus* and widen as they grow. The lancet is exposed (as in all species of *Orophocrinus*). Side plates are numerous, being added more rapidly than in *Katoblastus*. Entrance to the ten hydrospire groups is via a hydrospire cleft in all species of *Orophocrinus*; it is partially closed at either end. In *O. conicus* it is one-half the ambulacral length. There are 4–5 hydrospires in each regular group with no anal reduction.

Orophocrinus gracilis (Pl. VII, figs. 5–7), which is apparently found in the late Kinderhookian as well as the Osagean, shows the greatest downward extension of the ambulacra on the theca of any form discussed so far; its thecal form is the most radical departure from the usual shape of an *Orophocrinus*. The theca is conoidal and the vault greater than the pelvis. The maximum size is intermediate. Length is slightly greater than width. The diameter of the flat base is relatively broad; the conical basals grow at about the same rate as RB and Del.L. but much more slowly than RD. The radials are prominent in lateral view. RD is the predominant radial axis, with an ontogenetic acceleration from 45 to 57 percent of the total radial growth (fig. 96.1), the largest percentage of any *Orophocrinus* species. RB grows slightly faster than RR. Within the radial sectors, RD grows very rapidly relative to its front; RR is slower relative to RRF than in *O. conicus*; RB/RBF is about the same. RD is faster to Del.L. than in *O. conicus*. Ambulacral length is relatively long; the rate of addition of new side plates is slower than in *O. conicus*. There are 4 hydrospires in the regular and anal groups; the hydrospire cleft extends along two-thirds of the ambulacral length.

Orophocrinus catactus (Pl. VIII, figs. 2, 5) is an Osagean species with a broadly conical pelvis and outward flaring vault; the former predominates. Maximum size approaches 30 mm; the width is usually slightly greater than the length. The flat base is relatively broad. RD and RB grow at a slightly faster rate than BR of the conical basals; their relative rates are equal. BR grows faster than Del.L. The radials are prominent in lateral view. Initially, RB is the predominant axis but there is a shift to RD; the relative rate of RD/RB is slightly faster than in *O. conicus*. Both RD and RB are slightly faster than RR. Again, RD is fast relative to its front, while RB is less so. RR is slightly faster to RRF than in *O. conicus*. RD is faster than Del.L.; the rate is the same as in *O. conicus*.

Ambulacral length is relatively long; the width increases ontogenetically. The rate of addition of new side plates is slower than in *O. gracilis*. There are 5–8 hydrospires per group; the hydrospire cleft extends along about one half the ambulacral length.

Orophocrinus stelliformis (Pl. VII, figs. 9–11), an Osagean species, represents one of the maxima in ambulacral development in *Orophocrinus*. Initially, the theca is conical but becomes parachute-shaped with growth. The width is almost always greater than the length; the vault becomes greater than the pelvis. Maximum size is large. Stem plates are up to 4.0 mm in diameter. The conical basals have a massive secondary calcite deposit. RB grows more rapidly than BR, RD even moreso. BR and Del.L. grow at an equal rate. The radials are prominent in lateral view. Initially RB is the predominant axis but there is a strong ontogenetic acceleration of RD from 30 to over 40 percent of the total radial growth with a corresponding deceleration of RB (fig. 96.1), RR maintains a constant percentage. Thus, RD nearly equals RR initially but accelerates away from it; RB declines to almost equal it. RD grows rapidly with respect to its front, RB slightly less so. RR is faster to RRF than in the preceding three species of *Orophocrinus*. RD grew relatively faster than Del.L.; the relative rate is comparable to that of *O. gracilis*. Ambulacral length is quite long (exceeding 26 mm) and the width increases ontogenetically. The rate of addition of new side plates is as rapid as in *O. conicus*; the maximum number exceeds 70 per side. There are 4–5 hydrospires in the regular and anal groups; the hydrospire cleft extends along one-third of the ambulacral length.

Orophocrinus saltensis (Pl. IX, figs. 8, 9; Pl. X, fig. 4) is another Osagean species which changes from a conical to parachute-shaped theca during growth. It is thus similar to *O. stelliformis*. Width becomes greater than length but the vault remains less or sub-equal to the pelvis. Maximum known size is intermediate. The maximum known diameter of a stem plate is 2.5 mm. The BR of the conical basals grows at a rate equal to that of RB but slower than RD. BR is very slightly faster than Del.L. In comparison to *O. stelliformis*, BR/RD is the same, BR/Del.L. is almost the same, while BR/RB is more different. The radials are prominent in lateral view. Growth relations between the radial axes show the same degree of shift of RD relative to RB; RB more nearly equals RR. RD/RDF, RR/RRF, and RB/RBF are very similar to *O. stelliformis*. RD is slightly slower to Del.L., however, than in *O. stelliformis*. Amb.L./No S.P. is almost the same; ambulacral width increases ontogenetically. There are 5 hydrospires in the regular and anal groups; the hydrospire cleft extends along one-third of the ambulacral length.

Orophocrinus orbignyanus (Pl. VII, figs. 3, 8) is a Tournaisian species from Europe. The theca is conical, the length greater than the width, the vault is not as prominent, and the ambulacra are restricted to the upper surface. Maximum size approaches 30 mm. The diameter of the crenellae exceeds 4 mm. The conical basals grow slightly more slowly than RB but slightly more rapidly than RD, a configuration different from the previous species. BR grows rather rapidly to Del.L. This rate is more rapid than in *O. catactus*. The radial is prominent in lateral view. RB has one of the larger percentages of total radial growth found within the genus; there is some shift toward RD but it never equals RB. RD grows at a more rapid rate than RR. RD grows rapidly relative to RDF while RB is less rapid to RBF. RR is slower than RRF, being only slightly faster relatively than the RR/RRF of *O. gracilis*, but slower than that of *O. conicus*. RD is fast with respect to Del.L., being similar to that of *O. saltensis*. It is slower than that of *O. gracilis* and *O. stelliformis*, faster than that of *O. catactus* and *O. conicus*. The maximum ambulacral length is slightly less than that of *O. catactus*; the rate of addition of new side plates is slightly more rapid but slower than most other species. There are 7–8 hydrospires per group, both regular and anal. The hydrospire cleft extends along slightly more than one-half of the ambulacral length.

Orophocrinus pentangularis (Pl. IX, figs. 3, 6) is a species which appears to occur in both the Tournaisian and Visean. It is conical, with a hemispherical vault which is always much less than that of the pelvis. The ambulacra curve part way down. Length is always greater than width and the maximum size large (35.0 mm). The diameter of the flat base is broad. BR of the conical basals grows at a slightly slower rate than RB but faster than RD as was seen in *O. orbignyanus*; RD is slightly slower to BR in *O. pentangularis*. BR grows faster than Del.L. The radials are prominent in lateral view. RB is the predominant radial axis (42–48 percent); there is scarcely any acceleration of RD. RD and RB are both faster than RR, the latter moreso. The rate of RD/RDF is quite high, that of RB/RBF less so. RR/RRF is one of the slowest rates found. RD/Del.L. is similar to *O. orbignyanus*. Because of the large size, ambulacral length reaches a relatively large dimension; the rate of addition of new side plates is as in *O. orbignyanus*. There are 7–8 hydrospires per group, both regular and anal; the hydrospire cleft extends along slightly more than one-half the ambulacral length.

The Visean species *Orophocrinus praelongus* (Pl. VIII, figs. 1, 3; Pl. IX, figs. 4, 5) is very similar to *O. pentangularis* and probably has very similar growth relationships.

Orophocrinus verus (Pl. VIII, figs. 4, 6; Pl. X, fig. 7), also from the Visean, is another example of highly developed ambulacra as in *O. stelliformis*. Thecal shape becomes parachute-shaped with growth; length and width are subequal. The vault becomes larger than the pelvis. Maximum size approaches 31 mm. The maximum known diameter of a stem plate is 3 mm. The conical basals grow more slowly than RB and much more slowly than RD. BR grows slightly more rapidly than the deltoid. The radials are prominent in lateral view. Within the growth series, RB was the major component of radial growth in the smallest specimen while

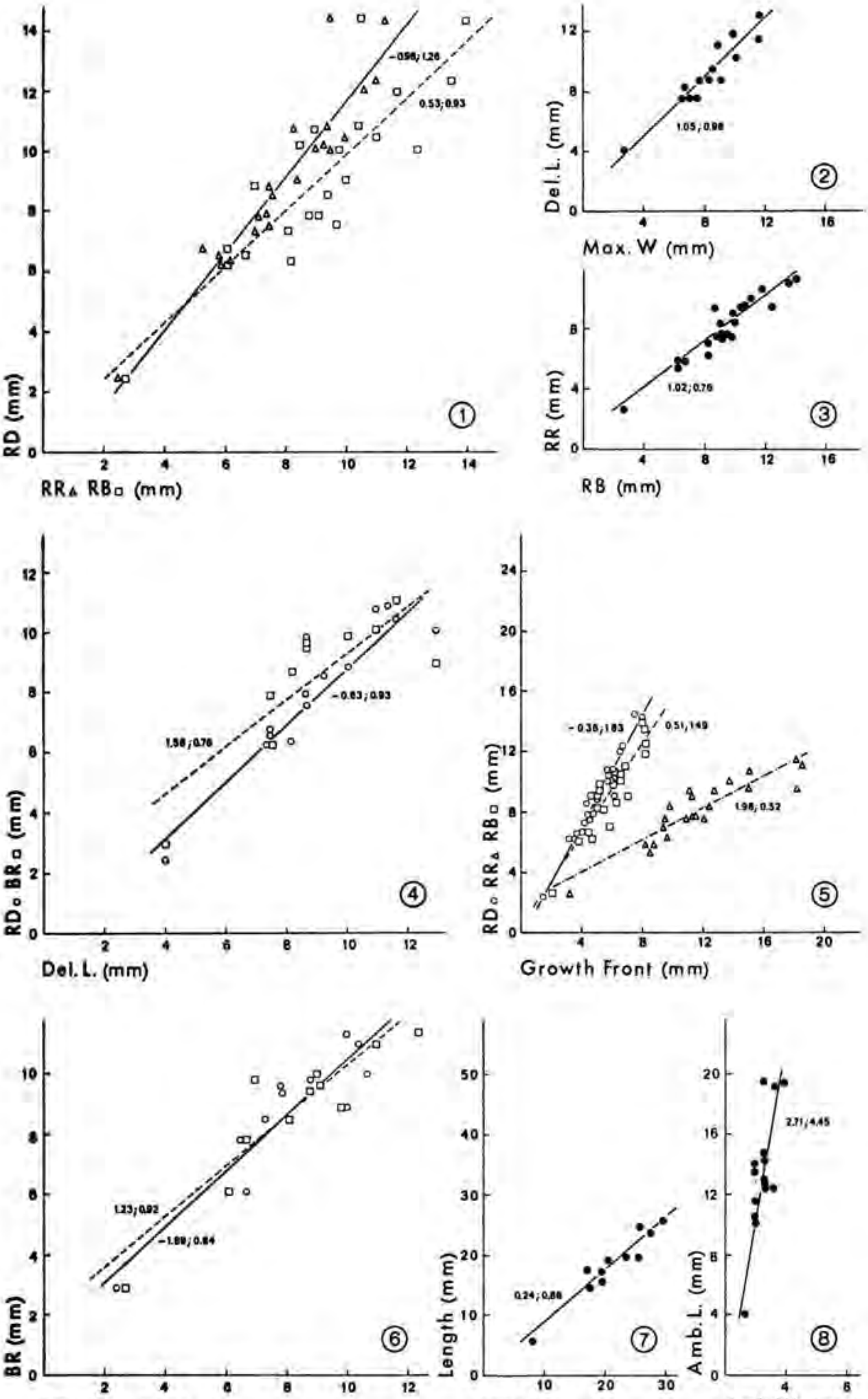
RD was less (36 and 42 percent respectively). With growth, RD increases to as high as 50 percent while RB declines to 25 percent (fig. 96.1). Thus there is a large acceleration of RD; its percentage is second only to that of *O. gracilis*. RD grows much more rapidly than RR, RB less so. RD grows very rapidly with respect to its front, RB less so. The rate of RR/RRF is very similar to *O. pentangularis*. RD grows much more rapidly than Del.L.; the differential is the highest of any *Orophocrinus* species. Ambulacral length is quite large, reaching as great a maximum as *O. stelliformis*. The rate of addition of new side plates is slower, however, being similar to *O. catactus*, so the maximum number is over one third less than in *O. stelliformis*. There are 6–8 hydrospires in the regular and anal groups; the hydrospire cleft extends along two-thirds of the ambulacral length.

Orophocrinus celticus (Pl. IX, figs. 1, 2), another Visean species, is a direct opposite to *O. verus*. It has the most slender, narrow, conical theca of any *Orophocrinus* species; its maximum size is 40 mm and the vault is much smaller than the pelvis. The base is narrower than other species (2.1 mm). RB grows more rapidly than BR of the conical basals but BR grows much more rapidly than RD and Del.L. The radials are prominent in lateral view. RB dominates the radial growth, 60 to 65 percent of the total (fig. 96.1) the largest of any species of *Orophocrinus*. RR is at its lowest relative percentage as is RD. There is no apparent ontogenetic acceleration. RD grows slightly more rapidly than RR. RB grows extremely rapidly to its front, RD much less so; this is the converse of other *Orophocrinus* species. RR grows quite slowly relative to RRF. RD grows more rapidly than Del.L. Ambulacral length is relatively shorter when compared to other *Orophocrinus* species; the rate of addition of new side plates is similar to *O. stelliformis*. There are about 9 hydrospires per group; the hydrospire cleft extends along about one-half the ambulacral length.

The maximum number of hydrospires known in *Orophocrinus* is eleven in a specimen from Ireland whose specific identity could not be established (MACURDA, 1965^{b}, p. 1086).

The other known Visean orophocrinid is *Acentrotremites ellipticus*. A discussion of its ontogeny follows that of the Namurian *Pentablastus suprcarabonicus* below.

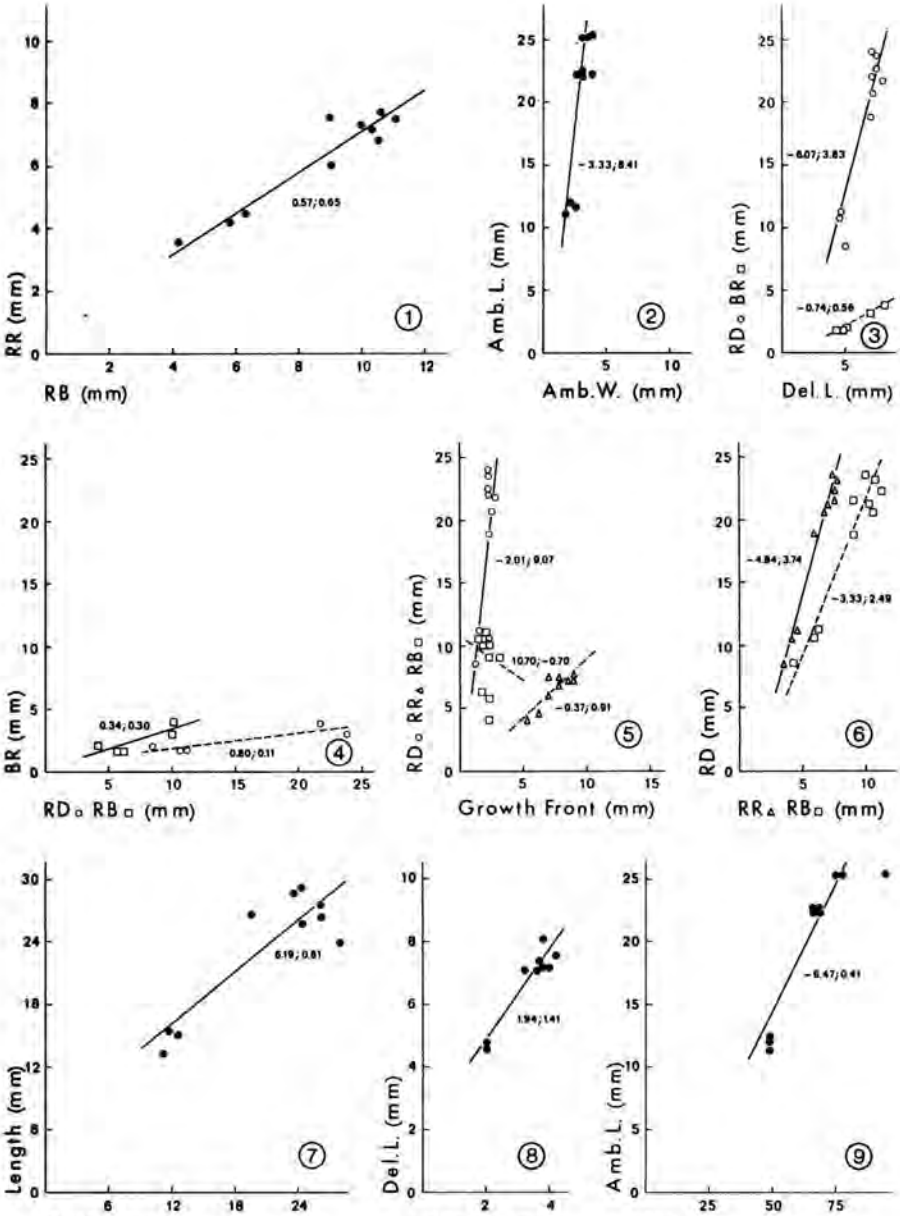
Namurian. In the Lower Namurian there is found a blastoid whose gross shape resembles an *Orophocrinus*. *Mastoblastus ornatus* (Pl. X, figs. 1, 2, 6) has a broadly conical pelvis and hemispherical vault; the latter is usually just slightly smaller. The ambulacra extend part way down the theca. Maximum thecal size is large, approaching 27–28 mm; length and width are subequal (fig. 75.7). The deltoids do not extend above the oral opening. The basals are broadly conical; the stem attachment area is formed from secondary calcite and is 1–2 mm in diameter. This is smaller than in *Orophocrinus*. BR grows at an equal rate with



Textfig. 75. *Mastoblastus ornatus* Arendt, Breimer, and Macurda, 1968. L. Carb., Lower Namurian, Tshan–Tshar, North Kazachstan, USSR. Ontogenetic development based upon 22 specimens. See textfig. 51 for further explanation.

RB and RD (fig. 75.6). It is approximately equal to Del. L. (fig. 75.4). The radials are prominent in lateral view but do not extend near the level of the oral opening. RD grows slightly faster than RR but at an equal rate with RB (fig. 75.1); RR is slightly slower than RB (fig. 75.3). The relative percentages of the three radial axes are very close to one another, only RR being slightly less. There is no apparent acceleration of RD. The slightly greater percentage of RR places the relative proportions of a *M. ornatus* radial closer to the RR pole of a triangular diagram (fig. 96.1) than those discussed before. Within the radial sectors, RD grows slightly more rapidly to its front than RB/RBF. RR is slower than RRF (fig. 75.5). The deltoid is prominent with a well developed external DR sector; it curves down from the oral opening. The deltoid reaches a large size and is wider than in *Orophocrinus* (fig. 75.2). It grows at an equal rate to RD (fig. 75.4). During growth both the greatest adoral and minimum width increase. The anal deltoids are equal or slightly longer than the regular deltoids. The hypodeltoid is the larger of the two plates by far and increases in both length and width. It has a broad external DR sector. The distance from the oral center to the adoral end of the ambulacrum increases ontogenetically; the lancet is exposed. The ambulacra reach a large length, widening during the process (fig. 75.8). The rate of addition of new side plates is as low or lower than that of any species of *Orophocrinus*. No clearcut hydrospires are present.

The Upper Namurian *Pentablastus supracarbonicus* (Pl. IX, figs. 10–12) represents another attempt to maximize the development of the ambulacra. The theca is elliptical to pear-shaped and the ambulacra reach well down toward the base. The vault is thus always much greater than the pelvis. The deltoid is restricted to the upper surface and does not project above the oral opening. The length is usually slightly greater than the width and the maximum size is large, approaching 30 mm (fig. 76.7). The basals are not visible in side view but confined to a basal concavity. Thus normal growth directions have been altered. The basal concavity increases in width and depth ontogenetically. The diameter of a stem plate approaches 3 mm. The growth rate of BR to RB or RD is the lowest we have thus far discussed with RD having almost an exponential rate by comparison (fig. 76.4). The deltoid also grows more rapidly than BR, but not quite as accelerated as the previous two (fig. 76.3). The radial is prominent in lateral view; it does not quite extend to the level of the oral opening. The radial is unique amongst fissiculates in actually being composed of two plates, an infer- and superradial. There are also secondary calcite deposits in the RD and RB sectors. The relative percentage of total radial growth of RD to RR and RB is the highest to be found in the orophocrinids, exceeding by one or two percent *Orophocrinus gracilis*. There is no acceleration of RD. Thus, RD grows much more rapidly than RR and RB (fig. 76.6) while RB grows more rapidly than RR (fig. 76.1). Within the radial sectors, RD increases extremely rapidly to RDF while



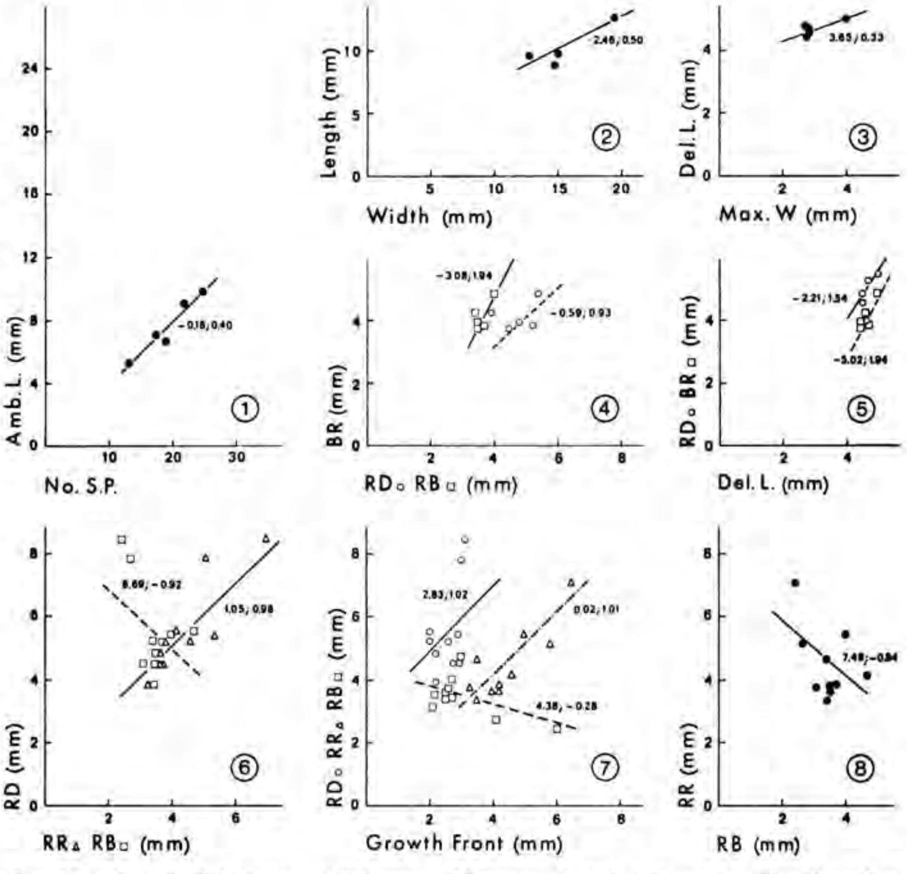
Textfig. 76. *Pentablastus supracarbonicus* Sieverts-Doreck, 1951. L. Carb., Namurian; Rabanal de los Caballeros, Palencia, Spain. Ontogenetic development based upon 10 specimens. See textfig. 51 for further explanation.

RB also grows rapidly to RBF. RR appears equal to RRF only because it has been plotted against the RRF of the inferradial and that of the superradial has not been included (fig. 76.5). If it had, RR would show its usual slow rate to RRF. The deltoid is directed mostly outward from the oral opening. It has a well developed DR sector. The deltoid is not as large as in *Mastoblastus* and it is narrower (fig. 76.8). The greatest adoral and minimum width increase. The anal deltoids are slightly longer than the regular deltoids and wider adorally and aborally. The epideltoid is the smaller of the two plates and grows slowly. The anus increases in size. The hypodeltoid increases fairly rapidly in size and has an external DR sector. The distance from oral center to the adoral end of the ambulacrum increases ontogenetically; the lancet is concealed except at the adoral tip. The ambulacrum increases in length to a quite large size, widening in the process (fig. 76.2). New side plates are added at a relatively rapid rate to reach a maximum greater than *O. stelliformis* (fig. 76.9). There are 5 to 6 hydrospires per group, an apparent ontogenetic increase of 1. Entrance to them is via a hydrospire cleft which extends along one-quarter to one-third the ambulacral length.

The discussion of the ontogeny of *Acentrotremites ellipticus,* Visean (Pl. X, figs. 3, 5) was postponed until here due to its resemblance to *Pentablastus. A. ellipticus* is very rare and its ontogeny is best understood by comparison with this latter genus. Its maximum size is very similar to *P. supracarbonicus,* approaching 30 mm. Its thecal shape is similar except that it is broader and has a flatter base. The ambulacra almost reach the base. The basals are confined to a basal concavity; their detailed structure is unknown. The stem attachment area is apparently broad. Growth relations of the radial axes are the same as *Pentablastus supracarbonicus*; the RDF may be slightly broader. The relative percentage of the radial axes is also the same as some *P. supracarbonicus.* The deltoid is apparently longer, growing at a faster rate to RD. The deltoids and anal deltoids are about equal; there is a large external hypodeltoid. The ambulacra extend all the way down the theca; the width increases through outgrowth of the side plates. The length of the ambulacrum is greater than in any specimen of *Pentablastus.* New side plates are apparently added at a slightly faster rate, producing the largest number of brachioles (100) along one side of an ambulacrum to be seen in any orophocrinid; this is about the maximum number known in any spiraculate (MACURDA, 1972). The principal point of difference from *P. supracarbonicus* besides a solid radial is the presence of a barred hydrospire cleft. Outgrowth of the radial produced a series of pore-like openings thus subdividing the hydrospire cleft.

Permian. The only post-Namurian orophocrinids belong to the genus *Anthoblastus* which is known from two species: *A. brouweri* (Asselian-Sakmarian) and *A. stelliformis* (Guadalupian). Since we have more data on the younger species, we will discuss it first.

In previous orophocrinids, most all of the growth has occurred on the lateral edges of the plates. This is changed in *Anthoblastus stelliformis* (Pl. XI, figs. 5, 6, 8, 9), where the liberal secondary deposition of calcite on the outer surface of each principal plate has produced a theca of markedly different form. Its closest analog is that of a broadly flaring flower. Maximum size is intermediate but because of the radial prongs, width exceeds length (fig. 77.2). The deltoids extend above the oral opening due to the secondary deposition and the vault and pelvis are about equal. The ambulacra are quite prominent. The basals are bulbous, with a stem attachment (if present) in a proximal concavity. BR grows more rapidly than RB and at an equal rate to RD (fig. 77.4). The deltoid apparently grows a bit more rapidly (fig. 77.5). The radials are prominent in lateral view; they extend to about the level of the oral opening. They are dominated by the scoop-shaped prong which is produced by secondary deposition to act as extension support for the ambulacrum. There is



Textfig. 77. *Anthoblastus stelliformis* Wanner, 1924^{b}. Permian, Guadalupian; Basleo District, Timor, Indonesia. Ontogenetic development based upon 10 specimens. See textfig. 51 for further explanation.

difficulty in obtaining growth data because of this deposit but RD appears slightly faster than RR and RB (fig. 77.6) while RR and RB are equal (fig. 77.8). RD grows most rapidly to its front, RB less so, and RR is equal to RRF (fig. 77.7). *A. stelliformis* has the greatest relative percentage of RR of any orophocrinid and the axes almost approach near equality. The deltoid is longer than wide (fig. 77.3) and has built a pyramid above the oral opening by secondary deposition. It is prominent but confined to the upper surface. It grows at the same rate as RD (fig. 77.5). The anal deltoids are slightly longer; the hypodeltoid is the larger of the two plates and forms an upward directed prong. The ambulacral length is increased considerably by the space made available by radial growth. The lancet grows in a most unusual manner both outward and upward, thereby producing a strongly concave cross section. The side plates are arrayed along its edges. New side plates are added at a slightly slower than usual rate (fig. 77.1). Ten hydrospire groups are present but regular hydrospires are lacking, their place being taken by a lobed sac.

Anthoblastus brouweri (Pl. XI, figs. 1–3) which is known from two specimens, is the older of the two known species. It shows similarities to *A. stelliformis* but uses less secondary calcite. Thecal shape is broadly ovoid, length being greater than width; the ambulacra are prominent and slightly extended; the deltoids are conspicuous by their secondary buildup but are confined to the upper surface. Maximum size is intermediate, with width greater than length; the vault is greater than the pelvis. The basals are broadly conical; the base is about 1.7 mm in diameter. BR grows at approximately an equal rate to RB but RD and Del.L. grow faster. The radials are prominent and extend to about the level of the oral opening. There is some deposition of secondary calcite to produce a swollen rim. RD has the predominant role in radial growth (44–45 percent) while RR (29–30 percent) and RB (25–27 percent) are less (fig. 96.1). Again, RR is higher than usual. Both RD and RB are faster than their fronts while RR is not. Secondary deposition produces a knob on the deltoid; its length is greater than its width. RD grows more rapidly than Del.L. The anal deltoids are longer than a regular deltoid; the hypodeltoid is the larger plate. The ambulacra are about as long as in *A. stelliformis* but wider; the rate of addition of new side plates is about the same. Hydrospire structure is unknown.

Family NYMPHAEOBLASTIDAE

Devonian. The nymphaeoblastids are one of the scarcest of all of the blastoid families. We could never obtain enough material to study their ontogeny by textfigures and regression analysis, but the preserved material we do have does afford some insight into the ontogeny of this family.

The oldest member of the nymphaeoblastids is *Pachyblastus dicki* (Pl. XII, figs. 1, 2; Pl. XIII, fig. 1) from the Emsian. Its form shows some harkening to the phaenoschismatids but is obviously different. Perhaps the easiest way to visualize the ontogenetic differences as far as the relative orientation of the growth axes is concerned is as follows: Imagine a large phaenoschismatid with an angular profile and relatively well-developed ambulacra. If this was like a collapsed balloon and one blew on it until one had all the growth axes on the same ellipsoidal-spherical surface, one would have a *Pachyblastus*. *P. dicki* is oblate spheroidal, with the ambulacra extending two-thirds to three-quarters of the length of the theca. The deltoids extend part way down the vault. The pelvis is broad and conical. Length is twice as great as width; maximum size is quite large, exceeding 40 mm in length. It is thus one of the largest Devonian fissiculates. The basals are conical; the stem is about 2 mm in diameter. It is unknown if there was a BA axis or secondary calcite. The basals grow at a slower rate than RB and much slower than RD. Data relative to Del.L. is unavailable. The radials are quite prominent in lateral view but do not extend to the level of the oral opening. RD is the predominant axis (64 percent), whereas RR (17 percent) and RB (19 percent) are much less (fig. 96.1). This percentage is amongst the lowest of any nymphaeoblastid but greater than that of any other fissiculate family. It is unknown if there was an ontogenetic acceleration of any radial axis. RD grew rapidly to RDF whereas RB was much less so; RR was much slower than RRF. Deltoids grow out and downward on the theca; they do not extend above the oral opening. A small rounded crest is present aborally. The deltoids are three times as long as wide and grow at approximately one-half the rate of RD. A small hypodeltoid is present; it has an external growth front. The ambulacra reach long lengths (in excess of 30 mm) and apparently widen during growth; the lancet is apparently narrowly exposed. With side plates being added at the relatively rapid rate of 4 per mm, the maximum number per ambulacral side approached 120, an extremely high number. Brachioles grew to more than 25 mm in length. The ten hydrospire groups are completely exposed. The full width of RDF is used for their formation. New hydrospires were apparently added ontogenetically as the maximum number known in a regular group is 9; there are 3 in an anal group when there are 7 in a regular. They are not secondarily infilled.

Mississippian. Pieces of *Xenoblastus decussatus* were first described in the 19th century but only recently with the discovery of a complete specimen by Barbara Conkin do we finally understand this species. *Xenoblastus decussatus*, Tournaisian (Pl. XIII, figs. 2–6, 8), is an ellipsoidal fissiculate in which the ambulacra reach almost to the base. The pelvis is small and almost flat. Maximum size exceeded 30 mm; length is always greater than width. The deltoids extend part way down the theca. The basals are small, lying in a horizontal plane on the base. The stem facet is formed from secondary calcite and is 1.8 mm in diameter. BR grows at the same rate as RB, but slower than the deltoid and much slower than RD. The radials are prominent in lateral view. RD reaches its greatest relative development of any fissiculate, being 77 percent of the total radial growth while RR is 13 percent and RB 10 percent (fig. 96.1). There may be an ontogenetic acceleration of RD. It grows quite rapidly relative to its front, RB at about an equal rate, and RR much slower than its front. The deltoid is conspicuous and curves out and downward; the length is twice the width and bumpy nodose ornament is found on the aboral part. RD grew about twice as fast as Del.L. The elongate ambulacra reach to the base of the theca and the ambulacrum continues to widen by lateral growth of the side plates. The lancet is not exposed along the radial. New side plates are added at a relatively slow rate (2 per mm). There are 10 hydrospire groups with 4 to 7 per regular group; the relative anal number is unknown. The full width of RDF is not utilized for hydrospire formation in large specimens. The aboral parts of hydrospire slits (and apparently the adoral ends on the deltoids) are secondarily infilled by calcite.

Another Tournaisian occurrence of a nymphaeoblastid that appears to be a *Xenoblastus* is illustrated in Pl. XIII, fig. 7.

Nymphaeoblastus is a widely ranging genus, being found in the Tournaisian and Visean throughout parts of Asia, Japan, and Australia. Its species are illustrated in Pl. XIV, figs. 1–6; Pl. XV, figs. 2, 8. The shape is ellipsoidal, the ambulacra extend to the very base. Length is greater than the width, and maximum size is large; over 30 mm in Australian specimens and over 70 mm in a Russian specimen. The deltoids extend down approximately one-third or more of the thecal length. The basals are confined to a concavity. Radials are prominent in lateral view; RD has the highest rate of growth, from 62 to 75 percent of the total radial; RB is the least (fig. 96.1). It is unknown if there is an ontogenetic shift. RD grows faster than RDF, RB less so; RR is slower than RRF. The deltoid grows out and downward at a relatively rapid rate, but is slightly slower than RD. Length exceeds width; occasionally there is a suggestion of a faint low crest aborally but nodose ornament predominates. Anal deltoids are usually slightly longer; a large hypodeltoid predominates. Very lengthy ambulacra may develop which also become quite wide; the rate of addition of new side plates (2–2.5/mm) is low but given the length, well over 100 side plates might be present in the largest specimen. The lancet is probably concealed. Hydrospire slits develop across the full width of RDF; up to 20 per group are known but 11 to 13 is more common. They are not reduced in number in the anal interarea. There is strong secondary infilling of the slits, particularly on the deltoid.

Permian. The only post-Mississippian nymphaeoblastid is a single specimen from the Permian of Timor: *Sphaeroschisma somoholense* (Pl. XV, figs. 4, 5, 7); it is Asselian-Sakmarian. This spheroidal form only reached about 10 mm in length and the width is slightly greater. The ambulacra reach almost to the base; the pelvis is very short. The deltoids are more confined to the upper surface than in previous genera, but still curve downward. The basals are almost flat. BR is about equal to RB but RD is greater; Del.L. is intermediate. RD is again the predominant radial axis (67 percent) while RB is the least (fig. 96.1). RD grows faster than RDF, RB equals RBF, and RR is slower than RRF. The deltoids are prominent orally, are longer than wide and grow more slowly than RD. There is a suggestion of a low, faint crest. The anal deltoids are about equal in length. The ambulacrum is quite convex, reaching almost to the base. The lancet is exposed. New side plates are added at a rapid rate (4/mm). There are ten hydrospire groups; some of the slits are partially concealed by the ambulacra. They do not occupy the full width of RDF; there are 1 to 3 per group; the anal groups have only 1.

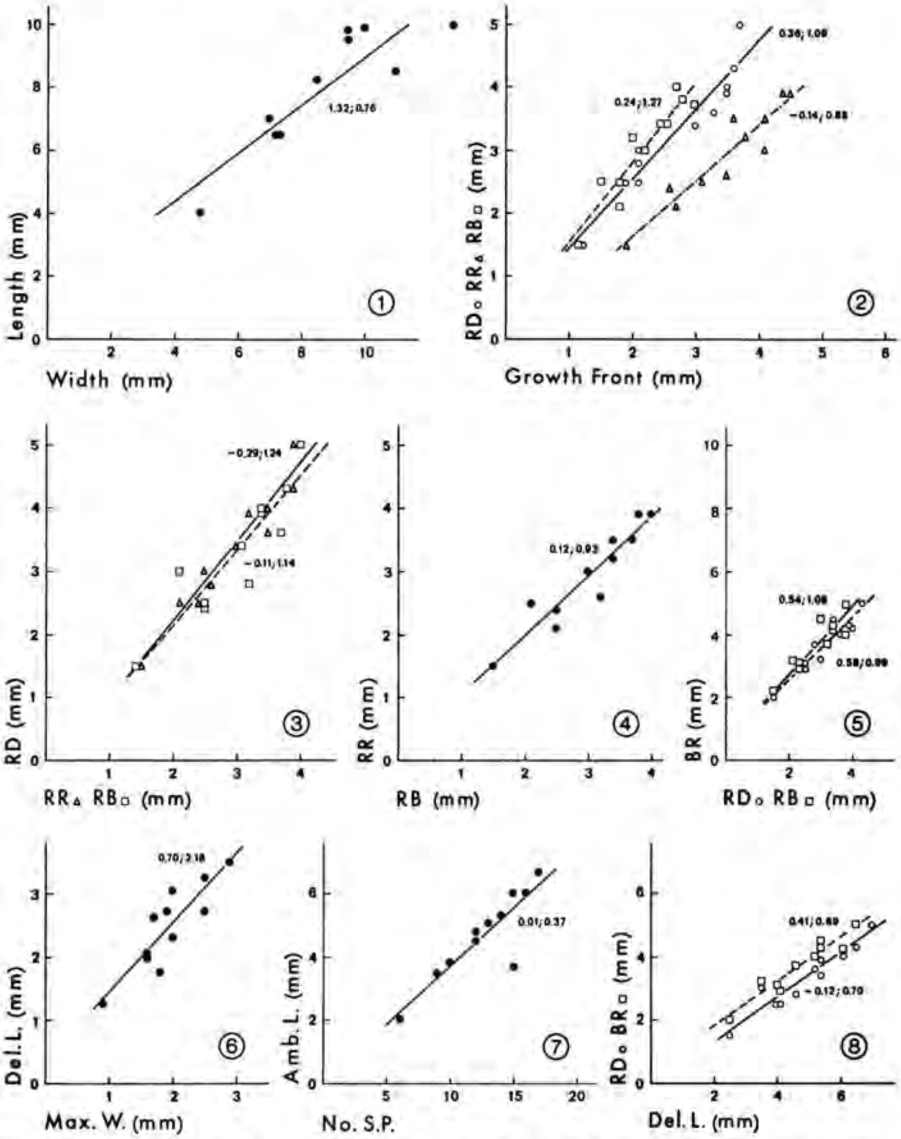
Family ASTROCRINIDAE

The fissiculate *Astrocrinus tetragonus* (Pl. XI, figs. 4, 7; Pl. XV, figs. 1, 3, 6) represents one of the most radical departures from the usual blastoid form. It has assumed a tetragonal symmetry and considerably modified the *D* side and basals. By these modifications, it could lie free on the sea bottom, never having developed a stem. We have described these changes in detail in the Anatomy chapter and textfigure 33. The available material does not lend itself readily to an ontogenetic analysis as most specimens are squashed and the plates faulted. In addition, the departure from normal plate arrangements and symmetry do not allow a direct comparison with other fissiculates. A size range of material is available, however, and certain features are worth comment. The maximum size of *A. tetragonus* is small, with lengths (or better heights) of 2.5–3.0 mm and maximum widths of 5.5–6.2 mm. The normal ambulacra are conspicuous, wrapping well down toward the base. The basals are pentagonal in outline, long and narrow, being in contact with all five radials, the four normal and an aberrant *D*. The contact with the *A* and *B* radials is narrow, that of the *C* and *E* radials broad, that with the *D* radial again short. Within the radials, RD is the most active sector. The deltoid has a comparatively rapid growth rate and is a conspicuous part of the theca. A crest is lacking. Four of the ambulacra are relatively large, and grow outward in a convex arc, reaching well down on the theca. New side plates are added at a much faster than usual rate (6/mm). The lancet is exposed in these ambulacra, whereas it is concealed (at least the aboral two-thirds) in the 5th shorter, aberrant ambulacrum (*D*). The surface of the plates are ornamented with discontinuous, linear ridges in the lower part of the theca; these ridges become small nodes on the upper surface. Their base is incised by a series of minute concave troughs. We do not know if this ornament results solely from the lateral addition of calcite to plate edges or whether there is addition on the free surface. ETHERIDGE and CARPENTER (1886, pp. 298–299, 302) believed some of these nodes bore spines and were perforate but we have not seen evidence of this.

Family NEOSCHISMATIDAE

Mississippian. The earliest neoschismatid genus *Hadroblastus* (Miss.) contrasts with the phaenoschismatids with which it occurs by the broad expansion of its vault and suppression of the interambulacral pyramids. The oldest species, *H. blairi* (Pl. XVI, figs. 1–6), is found in the Lower Tournaisian (Kinderhookian). It is known from limited material and will be discussed later.

The next youngest species of *Hadroblastus* from the Osagean, *H. convexus* (Pl. XVI, figs. 8, 10–13), is somewhat small and its length and width are equidimensional (fig. 78.1). The ambulacra are prominent. The vault is expanded but usually slightly less in length than the pelvis. The basals form a broad shallow cone with a small, narrow (0.6–1.2 mm) stem attachment area formed by secondary calcite deposition proximally. The rate of growth of BR is slightly greater than that of RD and RB (the relative rates are equal for the latter two: fig. 78.5) while BR is slower than the deltoid (fig. 78.8). The radials are moderately developed in lateral view, reaching almost to the level of the oral opening. An ambulacral sinus is lacking. The rate of growth of RD relative to RR and RB is slightly faster than and equal with respect to both axes, an unusual configuration heretofore (fig. 78.3). RR grows at an equal rate to RB (fig. 78.4); there is no acceleration of RD. RB and RD grow only slightly faster than their fronts, while RR nearly equals its front (fig. 78.2), a different configuration than in most previous fissiculates. The deltoid is a prominent plate, growing outward relatively rapidly to produce a moderately broad plate (fig. 78.6); the prominent crest arcs outward and downward with growth and forms most of the plate. The greatest adoral and minimum width of the deltoid increase ontogenetically. The deltoid grows more rapidly than RD (fig. 78.8). The anal deltoids are slightly shorter than the regular deltoids. Growth of the epideltoid gradually displaces the anus aborally. The hypodeltoid is also an actively growing plate, although slightly smaller than the epideltoid. As a result of the growth of the two anal deltoids, the size of the anus also increases ontogenetically. With growth along the interdeltoid suture, the ambulacra are displaced aborally from the oral opening (0.5–1.2 mm). Ambulacral length is intermediate; ambulacral width increases slightly ontogenetically but the width of the exposed lancet is almost constant. New side plates are added ontogenetically (fig. 78.7) at a rather average rate as compared to other fissiculates. The number of regular hydrospires per group increases from 4 to 13, the anal from 1 to 6 ($r = 0.88$). One specimen has 1 more anal hydrospire in one group (C) than the other anal group.

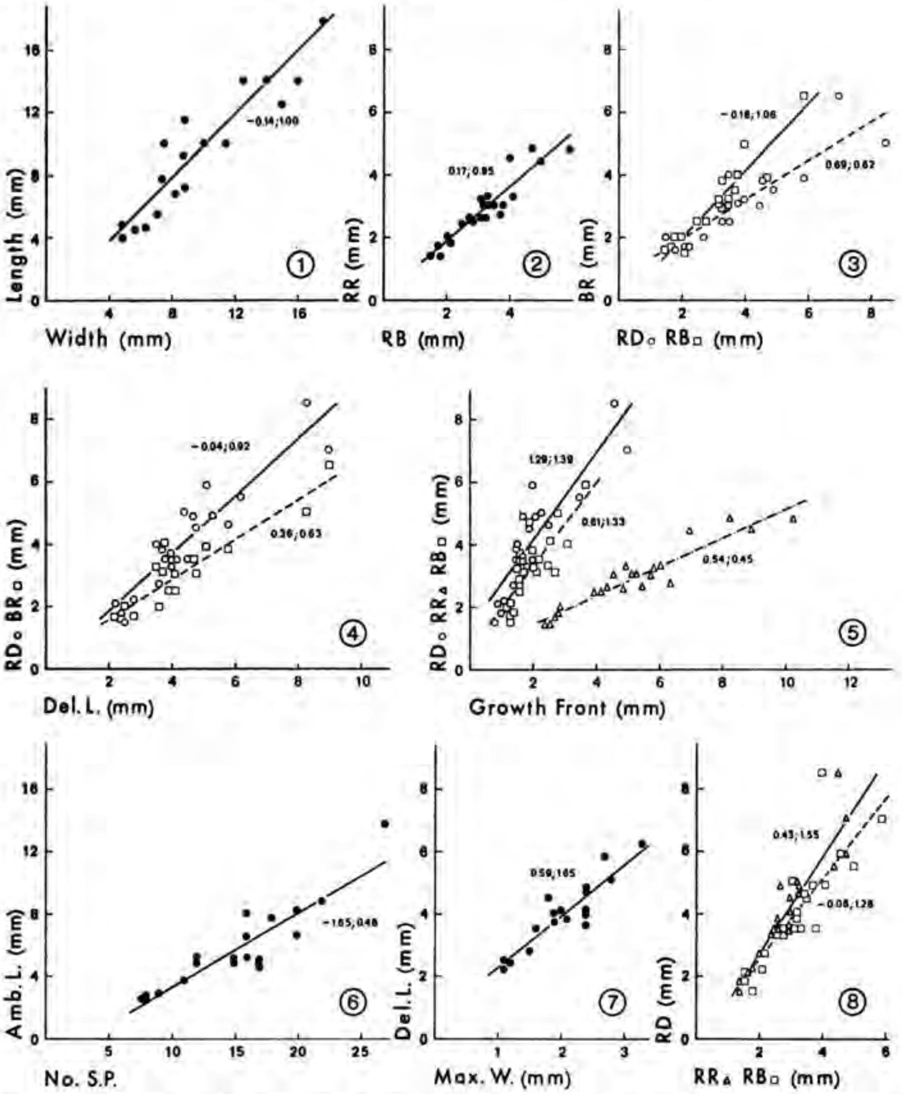


Textfig. 78. *Hadroblastus convexus* Fay, 1962. Miss., Lake Valley Fm., Nunn Mb., Lake Valley, New Mexico, USA. Ontogenetic development based upon 11 specimens. See textfig. 51 for further explanation.

Hadroblastus whitei (Pl. XVII, figs. 1–15) is a slightly younger but almost age equivalent Osagean species. This form is very rare when compared with the tens of thousands of echinoderms collected from the Burlington Limestone of Iowa and Missouri. Our growth series is comprised of small populations (subsets) from three areas along the 200 miles of outcrop belt in Missouri, plus the type specimen from Iowa and a few other isolated Burlington specimens. We have compared the three populations individually by regression analysis before combining them in textfig. 79. Certain shape differences are found in one of the subsets (e.g. Pl. XVII, figs. 7, 12, 15) but based upon our knowledge of variation in other blastoid species, we feel there is only one species of *Hadroblastus* represented by the specimens which we have called *H. whitei*. There is no sharp segregation of any characters within the growth series. *H. whitei*, as represented by the growth series, is intermediate in size (fig. 79.1), reaching toward a maximum of 20 mm. It should be noted that the fragmentary remains of one individual from northeastern Missouri (UMMP locality 1970, M-106) indicate the Burlington specimens approached size equality with the large St. Joe Ls. representatives (Pl. XVI, figs. 9, 14, 15) of *H. whitei*. In the Burlington representatives of this species, L/W are equal as in *H. convexus*. The vault may be greater or less than the pelvis; the relative prominence of the vault exceeds that of *H. convexus*. The basals form a convex, conical cup, with a narrow stem attachment area (usually 0.5–1.0 mm). BR grows at the same rate as RB as in *H. convexus* but in contrast RD grows more rapidly than BR (fig. 79.3). Del.L. grows faster than BR as in *H. convexus* (fig. 79.4). The radial is prominent laterally. RD grows faster than RR and RB (a bit moreso with the former; fig. 79.8); the relative rate of RD is a bit faster than in *H. convexus* and there is only partial overlap of the relative growth percentage of three radial axes. *H. whitei* has shifted toward RD. There may be an ontogenetic acceleration of RD. RR grows at an equal rate with RB as in *H. convexus* (fig. 79.2). Within the radial sectors, RD grows more rapidly than its front, RB is slightly slower, while RR is as usual slower than its front (fig. 79.5). Compared with *H. convexus*, RD is growing more rapidly with respect to its front while RR is slower; RB is the same. Again the deltoid is a conspicuous plate and has the same relative position as in *H. convexus*, and is slightly narrower (fig. 79.7); RD grows more rapidly with respect to Del.L. (fig. 79.4).

Growth within the deltoids and anal deltoids proceeds as in *H. convexus*. There is a tendency for the anal deltoids to be longer than the deltoids, the reverse of *H. convexus*. The ambulacrum is again gradually displaced aborally at the same time it increases in length. Maximum length of the ambulacrum is greater than in *H. convexus*; lancet exposure, increase in width, and rate of addition of new side plates (fig. 79.6) are almost as in *H. convexus*. The number of regular hydrospires per group ranges from 4 to 12, almost identical to *H. convexus*. Usually, the number of anal hydrospires per group is only one-third to one-half this (1 to 4), but larger specimens in the northeastern Missouri subset develop hydrospires across the hyporadial sutures, which may raise the number per side of the anal interarea to near equality or, in one instance, superiority. The presence of hyporadial hydrospires has not been seen in other families previously discussed. There may be some secondary infilling of the hydrospire slits.

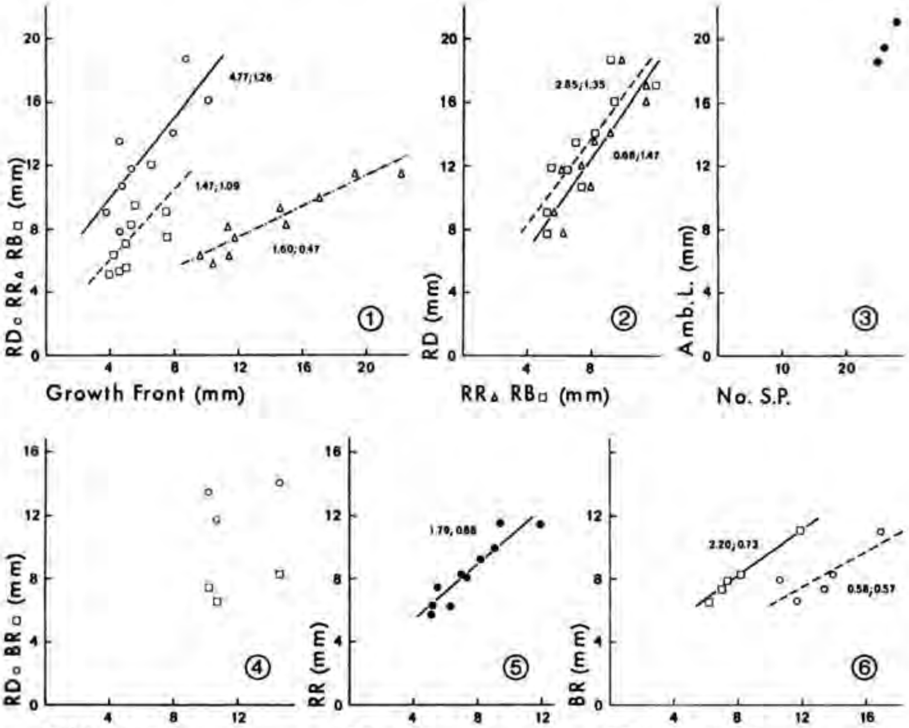
The specimens of *Hadroblastus* found in the St. Joe Ls. of Oklahoma



Textfig. 79. *Hadroblastus whitei* (Hall, 1861). Miss., Burlington Ls., Iowa and Missouri, USA. Ontogenetic development based upon 22 specimens. See text and textfig. 51 for further explanation.

and Missouri represent one of the largest known fissiculates and the maximum number of hydrospires found in any blastoid (up to 43 per regular group). There is an almost complete lack of size overlap when compared with Burlington Ls. specimens. However, one of the largest Burlington representatives (Pl. XVII, fig. 10) appears to clearly indicate the ontogenetic relationship between the two populations, and thus St. Joe representatives are assigned to *H. whitei* (Pl. XVI, figs. 9, 14, 15). We have illustrated the ontogenetic behavior of this population (textfig. 80) and the regression lines appear to be a continuation of those found in the

Burlington Ls. The largest complete specimens exceed 30 mm (MACURDA, 1965ᵃ, Pl. II, figs. 1, 3) and a projection based upon the largest known radial suggests a maximum dimension slightly in excess of 60 mm! Similar maximum dimensions amongst the fissiculates are seen only in *Nymphaeoblastus* and *Austroblastus* (the latter is a Permian neoschismatid). The basals come to lie in a flatter plane (Pl. XVI, figs. 14, 15) and the vault becomes extremely pronounced. The diameter of the stem attachment area is about 2.0 mm. BR grows at the same relative rate to RB, RR, and Del.L. (figs. 80.4, 6). The radials are quite prominent and do not reach the oral opening. The rate of RD/RR is equal but RD may be slightly faster to RB (fig. 80.2); RR is slightly faster than RB (fig. 80.5). This may be a consequence of the sampled size range. The relative percentages of the radial axes are nearly the same as those of the largest Burlington Ls. specimens and may represent an ontogenetic acceleration of RD. Within the radial sectors, RD and RB grow at the same rates to their fronts while RR is slightly faster (fig. 80.1). Growth relations within the deltoid are apparently the same; the deltoid grows at about the same rate with respect to RD although the latter may be slightly accelerated (fig. 80.4).



Textfig. 80. *Hadroblastus whitei* (Hall, 1861). Miss., St. Joe Fm., Oklahoma and Arkansas. Ontogenetic development based upon 10 specimens. (3, 4) Regression lines were not calculated due to a lack of data. See textfig. 51 for further explanation.

The number of side plates per mm is less (fig. 80.3). There is an indication in the largest Burlington specimens of a decrease in the rate of addition of new side plates. Instead, the side plates grow in length. The culmination of this trend is apparently seen in the St. Joe specimens where the spacing is less than 2/mm, whereas, that of the Burlington specimens is 2.5/mm. An increase in length of side plates after initial formation is quite unusual. The maximum number of side plates per ambulacral side probably approached 66 along the radial of the largest known specimen and by relative extrapolation, between 85 and 90 for the complete ambulacrum. This number is slightly exceeded in some nymphaeoblastids and orophocrinids. The number of hydrospires in regular groups of the St. Joe representatives of *H. whitei* increases regularly, following the same spacing as the Burlington representatives. Within the specimens included in text-fig. 80, the number increases from 7 to 28. The maximum number is found in the radial belonging to the 60 mm individual. MACURDA (1965[a]) earlier suggested that there were 60 per group but a more conservative figure is 43 (the middle of the group is obscured by matrix). The relative number of anal hydrospires in St. Joe specimens ranges from greater than one-half to equality. (They would again appear to be developed across the hyporadial suture but the relevant hypodeltoids are missing). Thus the 60 mm specimens had about 344 hydrospires in the eight regular groups and by extrapolation between 43 and 86 in the anal groups for a total number between 387 and 430. This is the maximum known in any blastoid, and only the giant *Austroblastus whitehousei* (Pl. XXIII, fig. 6) exceeds 300 (314). The presence of so many hydrospire slits raises interesting questions about respiratory physiology. As in the Burlington representatives of *H. whitei*, there may be some secondary infilling of the earlier formed parts of the hydrospire slits.

The St. Joe Ls. represents an unusual case of relative gigantism in blastoids. We have noted earlier the presence of the largest known *Phaenoschisma (P. laeviculum)* in this formation and this is true also for *Hadroblastus*. Spiraculates also reach large dimensions. An unusually large specimen of *Schizoblastus sayi* is known, *Dentiblastus sirius* is larger than elsewhere, and *Orbiblastus hoskynae* is a giant amongst the globose Mississippian spiraculates. The reasons for this relative gigantism are unclear.

The occurrence of an older species of *Hadroblastus*, *H. blairi* (Pl. XVI, figs. 1–6), was mentioned at the beginning of this section but a discussion of its ontogeny was deferred until here. It is known from only two specimens, one incomplete. The maximum known size is similar to *H. convexus*. The width is greater than the length, the vault and pelvis subequal. The growth relations of BR to RB, RD, and Del.L. appear to be as for *H. convexus*. Growth relations between radial axes and within the radial sectors are as for *H. convexus* as is Del.L./Max.W., RD/Del.L., and Amb.L./No S.P. The maximum number of known hydrospires is 9 per group; the number of anal hydrospires exceeds 6 here. The similarity in growth between *H. blairi* and *H. convexus* suggests they might be cospecific but there is insufficient material to definitely discern this; there is little change in *Hadroblastus* growth characteristics between the Kinderhookian and Lower Osagean.

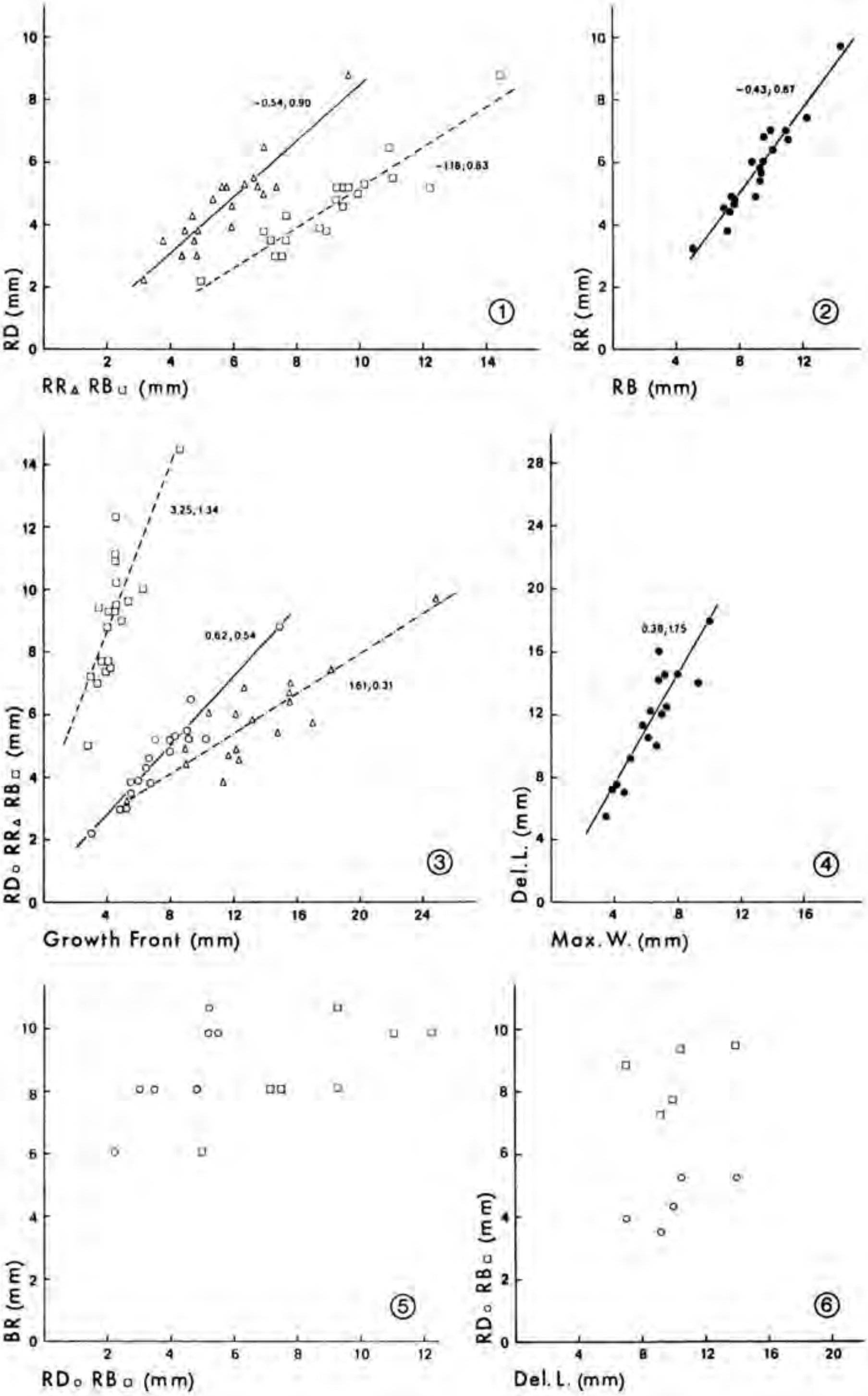
The fourth known species of *Hadroblastus* is *H. kentuckyensis*; it is apparently slightly younger than *H. whitei*. The holotype (Pl. XVIII, figs. 3, 5) represents another relative giant amongst fissiculates with a probable length of 35 mm and width of 45 mm. Based upon the radial profiles, the theca was more domed and the pelvis more produced and conical than in the large *H. whitei*. *H. kentuckyensis* is definitely represented only by the holotype and a large radial (Pl. XVIII, fig. 6). It is quite probable that three smaller specimens from the same stratigraphic level (e.g.: Pl. XVIII, figs. 7, 8) also represent this species but the dichotomy in sizes and localities does not provide a good basis for an ontogenetic analysis. Therefore our comments for *H. kentuckyensis* are confined to the holotype and radial; they are compared with the similar sized *H. whitei* from the St. Joe Fm. The stem attachment was of moderate diameter (2.0 mm). RD grows more rapidly with respect to BR but BR/RB and BR/Del.L. are the same as in *H. whitei*. The radial is very prominent laterally. RD grows more rapidly than RR and RB in the holotype; RD is subject to error in measurement in the radial but might have grown at the same rate as *H. whitei*. RR equals RB. RD appears to grow at the same rate to RDF as does RB/RBF, while RR may be slower to RRF. Del.L./Max.W. is similar and RD/Del.L. would appear to be as well. Amb.L./No S.P. would appear to lie on a projection of a line through the relevant points for *H. whitei*. The maximum number of hydrospires in a regular group is 23. While growth parameters are apparently similar to *H. whitei* except for RD, the spatial orientation of the axes produced a different thecal shape in *H. kentuckyensis*.

The more rapid growth of RD/BR is also found in the smaller specimens (Pl. XVIII, figs. 7, 8) provisionally assigned to *H. kentuckyensis* (when compared to similar sized *H. whitei*). RD again appears to grow more rapidly when compared to RR and RB. The relative percentage of the radial axes of these small specimens does not overlap a small *H. whitei*; they only compare with a large Burlington individual. Growth within radial sectors is similar. The deltoid is wider compared to its maximum width. RD is faster with respect to the deltoid. Amb.L./No S.P. is similar. The number of regular hydrospires is small (3–6); the number of anal ones is unknown.

The time of origin of new hydrospires into adjacent groups on a deltoid is usually simultaneous but one may be delayed relative to the other. Data for these large and small specimens suggest some ontogenetic differences with *H. whitei*, but we lack adequate material to substantiate this.

In the Lower Visean of Ireland there is a form, unfortunately incomplete, which may belong to *Hadroblastus* (Pl. XVIII, figs. 2,4). The form is about the size of an *H. convexus*, and the vault, while prominent, was exceeded by the pelvis. Length and width were about equal. The conical basals have a small attachment area (0.8 mm); the rate of growth of BR was a bit faster than that of RD and RB. The fastest growing radial axis was RB but it was closely followed by RD and then RR. The relative rates are similar to *H. convexus*. RD and RB grew more rapidly than their fronts while RR was slower. Only part of a deltoid is preserved; there are four hydrospire slits in a regular group. Other occurrences of *Hadroblastus* are illustrated in Pl. XVI, fig. 7 and Pl. XVIII, fig. 1). "*Phaenoschisma*" *benniei* (Pl. V, figs. 8, 11, 13) could represent another Visean neoschismatid but it is not well enough preserved to be sure.

Permian. There are no known Pennsylvanian neoschismatids but six genera are found in the Permian. One of the oldest of these is *Neoschisma australe* (Pl. XIX, figs. 1–4; 6–8; Asselian-Sakmarian). Only one partially complete crushed specimen is known but abundant individual plates have allowed us to reconstruct the ontogeny of this form. The theca was broadly conical with a wide rather flat top and tapered downward. The height of the vault was small and the ambulacra restricted. They were also removed from the oral opening. Length was probably greater than width and exceeded 35 mm. The basals were conical and had a broad stem attachment area which increased from 2.0 to 5.0 mm ontogenetically. Although complete specimens are lacking, it is possible to derive a comparison of radial and basal growth by matching plates with an equal RBF. This procedure, while not statistically exacting, demonstrates that BR grows much more rapidly than RD but is equaled by RB (fig. 81.5). In two cases, there were two equal radial values of RBF for one basal value; both were plotted). The radial is prominent in lateral view. Within the radial, RB is the dominant axis, comprising 44–51 percent of the total radial growth while RR is 26–32 percent and RD 19–27 percent (fig. 96.2). Compared with previous genera, it is unusual for RD to grow more slowly than RR (fig. 81.1); there is no acceleration of RD. RB is obviously faster than both RD and RR (figs. 81.1, 2). This contrasts strongly with *Hadroblastus*. Within the radial sectors, RD grew more slowly than its front, again unusual; RR is slower (as usual) while RB is faster (fig. 81.3). The deltoid is conspicuous orally, lacks a crest, and grows outward rapidly but broadens in doing so (fig. 81.4). There is a more prominent accentuation on growth in the adoral part of the plate than in previous genera. DD is a well-defined axis with a broad DDF, resulting in the adoral end of the ambulacrum being relatively far from the oral opening; it is further displaced ontogenetically. DD grows at one-third the rate of DR. Because of the many isolated plates which can be viewed both externally and internally, the origin of the deltoid can be pinpointed internally



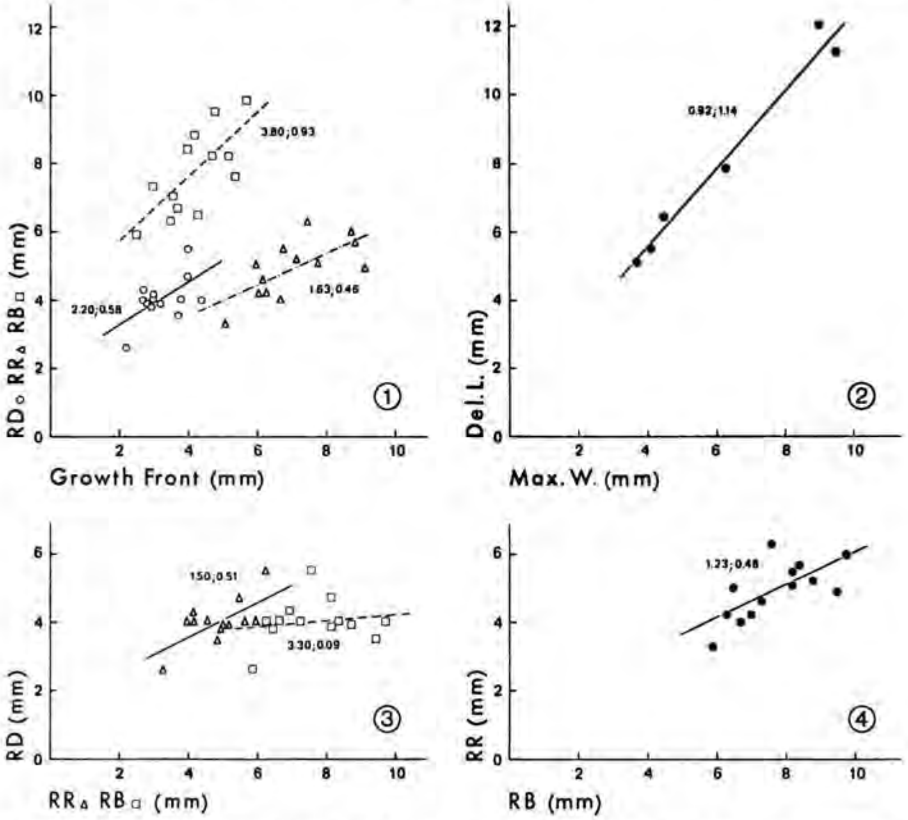
Textfig. 81. *Neoschisma australe* n. sp. Perm., Callytharra Fm., Callytharra Springs, Western Australia. Ontogenetic development based upon five isolated basals, twenty radials, and seventeen deltoids. (5, 6) Regression lines not calculated, see text. See textfig. 51 for further explanation.

(Pl. XIX, fig. 2). Thus the plate has actively grown outward from the origin toward the oral opening, resulting in the continued ontogenetic development of the adoral edge of the plate bordering the peristome. This edge remains narrow (0.7–1.5) and is not well correlated with deltoid length. An external groove is present on the adoral edge which we interpret as having borne the oral ring canal as in *Pterotoblastus brevialatus* (Pl. XXXIII, fig. 8); it thus would have been constantly shifted. The same is true of those parts of the water-vascular system lying along DDF. The greatest adoral width almost equals the greatest aboral width; they are close together because of the relatively shorter DAF. Again, the only way we can compare the growth of the deltoid with another plate (the radial) is to compare measurements for plates with an equal radiodeltoid suture. This has not been treated statistically but Del.L. obviously grows much more rapidly than RD (fig. 81.6). Since RB approximately equaled BR, it is here substituted for that parameter and thus suggests equality of growth for the basals and deltoids (fig. 81.6). Perhaps a better comparison of growth along the radiodeltoid suture is afforded by DR since Del.L. includes a larger than normal component of DD. Using the same five plates as in fig. 81.6, DR is usually about equal to RD but may exceed it. Knowledge of the epideltoid is limited to a very few plates but it was apparently large and actively growing; the hypodeltoid also reached considerable size (Pl. XIX, fig. 1). In the six *C* or *D* radials we have, it forms a prominent facet which ranges from 1.2–5.0 mm (Pl. XIX, figs. 3, 4). Correlation of this facet with RDF on the other side of the radial is 0.04. Ambulacra are seldom preserved but where seen, the lancet is exposed adorally. The relative length and width can be inferred from the radial sinus and DAF along the deltoid. The ambulacra were restricted, not reaching to the origin of the radial. The greatest length along a radial is 3.1 mm; along a slightly smaller deltoid it is 4.9. Thus in a specimen with a height approaching 35 mm and a width only a little less, ambulacral length would be slightly in excess of 8 mm. Width would be about 2 mm. Hydrospires are prominently developed but rapidly infilled secondarily, leaving only narrow, elongate ellipsoid openings across RDF; this configuration has not been seen in previously discussed forms but is quite prevalent in Permian neoschismatids and codasterids. In *N. stellaris*, the number of hydrospires increases ontogenetically from 7 to over 23. Anal hydrospires are developed across both the epiradial and hyporadial suture. When the number of regular slits here range from 8 to 17, the number of anal ranges from 0 to 11. (It is not known if anal hydrospires were completely lacking in this specimen as we have only the *D* side of the anal interarea. There are 16 in the regular group of this radial). In this group of six radials, the number of epiradial hydrospires varies from 0 to 4, the hyporadial from 0 to 7. Correlation of the subtotals or totals of the anal hydrospires with the regular number of hydrospires in these radials is essentially random. Spacing of hydrospire slits within all fields is highly correlated.

The two younger species of *Neoschisma* are known only from single specimens. *N. verrucosum* (Pl. XIX, fig. 5; Pl. XX, fig. 7) is Upper Artinskian. Its form is much more ovoid than *N. australe*; the ambulacra are again restricted and the vault has a small height. Length was greater than 16 mm; width approached 20 mm. Only parts of the basals are preserved but they were well-developed plates. The radials are prominent laterally. Growth relations between radial axes and within radial sectors apparently follow those of *N. australe* as does the relative percentage of the radial axes. The deltoids are prominent orally but incompletely preserved. They may be a bit wider than in *N. australe*. Growth of the deltoid relative to the radial is the same. The anal deltoids are large; the epideltoid is the larger of the two. The anus is of considerable size. Ambulacra are restricted; exposure of the lancet is small. Side plates number 3/mm. The number of hydrospires in a regular group is 17; there are 5 developed across the epiradial suture. None are developed on the hyporadial suture, probably because this suture lies outside a shallow ambulacral sinus and the hypodeltoid forms part of the external body wall which it does not in *N. australe*. Again there is strong secondary infilling of the hydrospire slits (maximum functional length 2.7 mm).

The gross form of the Guadalupian species of *Neoschisma*, *N. timorense* (Pl. XX, figs. 4, 8) appears to closely resemble that of *N. australe*. The vault is more scalloped, however, due to the rounded deltoids. It is again restricted in height and ambulacra are quite reduced, again not reaching to the origin of the radial. The size is intermediate. The conical basals have a prominent wide basal concavity proximally (width: 3.9 mm; depth: 3.0 mm), an unusual modification of the basals. The proximal stem plate was apparently quite broad for a theca this size. Growth of BR to RD and Del.L. was as for *N. australe* but RB was slower. The radial is prominent laterally. RD grows at the same rate as RR but is faster with respect to RB than in *N. australe* as is RR/RB. The relative percentage of RB is slightly reduced. RD/RDF and RR/RRF are as in *N. australe* while RB is slower to RBF. The deltoid is prominent orally; Del.L./Max.W. is as for *N. australe*, as is RD/Del.L. The epi- and hypodeltoid are prominent plates of about equal size; the latter did not contribute to the external thecal wall. The ambulacra are much reduced. Hydrospire slits number 6 to 7 in the regular fields; spacing is slightly irregular and they do not occupy the full width of RDF. There are apparently two across the epiradial suture, none across the hyporadial suture because of the massiveness of the plates along these sutures.

The genus *Notoblastus*, represented by four species, shows one of the prominent growth characteristics of Permian neoschismatids: the secretion of secondary calcite to form radial prongs. The earliest species, *N. stellaris* (Pl. XX, fig. 1; Pl. XXI, figs. 1, 2, 7, 8; Asselian-Sakmarian) occurs with *Neoschisma australe*. As with this latter species, only one somewhat crushed relatively complete specimen of *N. stellaris* is known but the presence of numerous isolated plates has allowed us to reconstruct its ontogeny. The theca is wider than high, cup-shaped, and the ambulacra are confined to the upper surface. Maximum thecal size is apparently intermediate. The illustrated specimen (Pl. XX, fig. 1; Pl. XXI, figs. 1, 7, 8) represents about the largest material known. The radials are characterized by short radial prongs which extend outward and upward. The convex basals lay in a much flatter plane than those of *Neoschisma australe*. The stem attachment area was intermediate in size (1.6–2.0 mm). Basal growth relative to other plates can only be inferred by comparing isolated plates with an equal RBF as in *Neoschisma australe*. The limited data suggests BR and RB had an equal rate of growth with one another while RD grew less rapidly than BR (faster, however, than in *Neoschisma australe*). The radials are prominent laterally; measurement of radial axes is not as exact as in previous genera because of the obscuring effects of secondary calcite on the radial. RD grew at a slightly less rapid rate than RR and more slowly than RB (fig. 82.3). RR was also slower than RB (fig. 82.4). The relative percentages of the three radial axes is similar to that of *Neoschisma australe*. RD grows more rapidly than its front; RR grows more slowly than its front, but is faster relatively than in *Neoschisma australe*, while RB/RBF is almost the same in both, RB being faster than its front (fig. 82.1). The secondary deposition of calcite forms a bladed radial prong with a somewhat serrated tip when preserved. The maximum prong length is 8.7 mm in one of the intermediate sized radials. The deltoids are conspicuous in their breadth; they also reach a relatively large size (fig. 82.2). There is prominent growth in the adoral part of the plate with a well-developed actively growing DD axis which about equals the DR axis. Observations made about the origin and adoral growth of the deltoid for *Neoschisma australe* apply here also. Secondary calcite forms a ridge which sharply sets off the adoral and aboral parts of the plate. The greatest adoral width of the plate almost equals the greatest aboral width and the two are relatively close together. A crest divides the plate aborally. Deltoid growth can only be compared with the radial by comparing plates with similar RDF and DRF. Limited data suggests that Del. L. is always greater than RD and less than RB (and by inference of its equality with BR, BR is also greater). DR, however, is almost always slightly less than RD. Fragments of the anal deltoids may be present in the crushed vault of the holotype (Pl. XXI, fig. 7) but, if so, are too badly preserved to be readily identifiable; they are unknown from isolated plates. The facets on the *C* and *D* radials indicate the presence of a large, broad hypodeltoid which contributes to the external thecal wall. The ambulacra are seldom preserved but their dimensions are indicated by the facets on the radials and deltoids. The lancet is exposed throughout its length, narrowing aborally; side plates number 2.5/mm. Ambulacral length appears to be relatively greater than in *Neoschisma australe*,

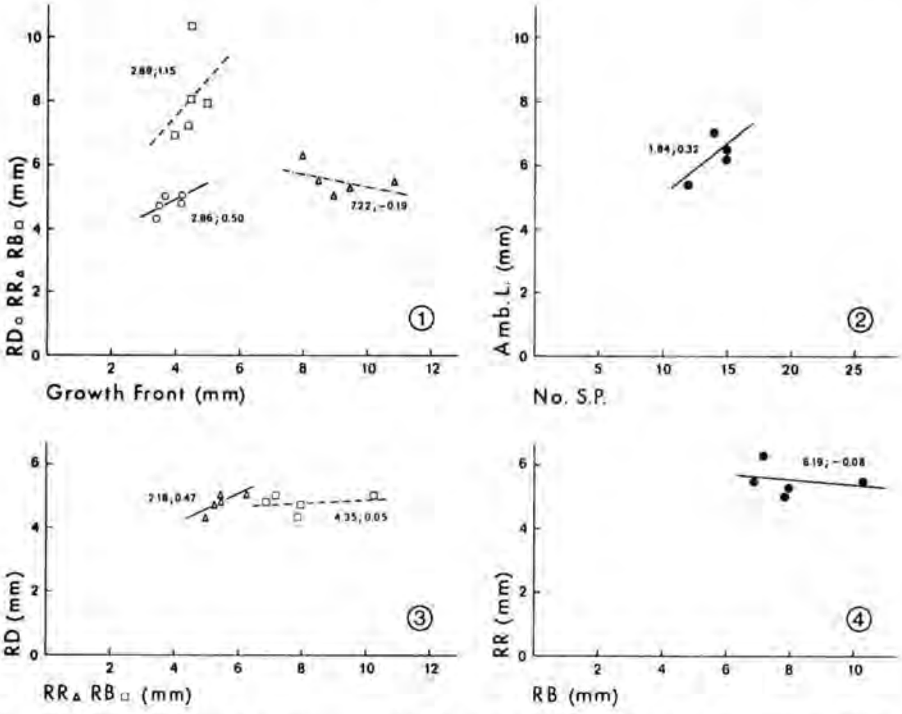


Textfig. 82. *Notoblastus stellaris* n. sp. Perm., Callytharra Fm., Callytharra Springs, Western Australia. Ontogenetic development based upon thirteen isolated radials and six deltoids. See textfig. 51 for further explanation.

being 5.3 mm in an intermediate sized specimen; it is also wider. Hydrospire slits are developed across the full width of RDF and are strongly infilled, both on the radial and deltoid. They increase in number ontogenetically (5 to 14 are known in the radials, up to 15 in the isolated deltoids). Hydrospire slits are also developed across the epiradial suture on both sides of the anal interarea. Here they number from 1 to 3; their number relative to regular groups appears highly variable, from 10:1 to 5:3 or 9:3. Hyporadial hydrospire slits are apparently not present. Spacing within the hydrospire fields is well coordinated.

At another locality (UMMP 1968/Pe-3) in the Callytharra Fm. in Western Australia, Macurda found isolated fissiculate plates that have a very long bladed secondary deposit on the radials which the ambulacrum extends well out onto (Pl. XXI, figs. 3–5, 9). Our first impression was that these might belong to *Thaumatoblastus* but the prong is bladed instead of round as in the latter and the structure of the ambulacrum is different, being the same as found in *Notoblastus stellaris*. The prongs are also serrated (Pl. XXI, fig. 9). *Neoschisma australe* and a species of *Rhopaloblastus* occur at both localities in question. Differences in size of the radial body do not appear responsible for the difference. At the first locality, the prong is short and the radial does not extend onto it. At the second they are all long and the ambulacra extend well out. Whether this growth difference represents a phenotypic or genotypic response is unclear but it does demonstrate the ability of these forms which we have called *Notoblastus* sp. to produce a long prong by secondary deposition and the ambulacrum to expand onto it.

In the Artinskian of Queensland is found a second species of *Notoblastus*, *N. cornutus* (Pl. XXII, figs. 4, 5). These occur as partially disarranged thecae. Their size was apparently intermediate and the length greater than the width. The vault was restricted to the upper surface. The basals are unknown; however, the RB sectors of the radials are concave (Pl. XXII, fig. 5), suggesting that the basals may have had some similarity to those of *Notoblastus brevispinus* in shape. They were wide plates, since the radials are almost as wide at the base as at the top. The radials are prominent laterally; there is a small rounded knob produced by secondary calcite deposition and a concave RB sector. Growth relations between radial axes and within radial sectors are as for *N. stellaris* (figs. 83.1, 3, 4).



Textfig. 83. *Notoblastus cornutus* (McKellar, 1969). Perm., Berserker Beds, Rockhampton, Queensland, Australia. Ontogenetic development based upon 5 specimens. See textfig. 51 for further explanation.

The form of the deltoid is also similar. It is slightly narrower, however. The plate may also be wider adorally. Del.L. is almost twice RD but the latter is greater than DR. The adoral sectors are prominent and separated from the DR sectors by a pronounced ridge. A crest bisects the latter sectors. Regular and anal deltoids are equal in length. The epideltoid is a good bit larger than the hypodeltoid. Ambulacral length increases ontogenetically; the lancet is exposed throughout its length. New side plates are added (fig. 83.2) at the same rate as in *N. stellaris*. 9–14 hydrospires are present in regular groups; 3 are present across the epiradial suture of the specimen with 14 regular slits. They are strongly secondarily infilled. Hyporadial hydrospire slits are lacking.

Notoblastus brevispinus (Pl. XXII, fig. 1; Artinskian) is known only from a single specimen. The theca has been flattened by crumpling in the middle of the radials. It was probably wider than high and intermediate in size. The ambulacra are prominently developed but confined to the upper surface. The basals are well developed with an intermediate sized stem cicatrix (1.8 mm). Because of the concavity in the RB sectors, their shape probably reflects the shape of those in *N. cornutus*. RD could again appear to be the least of the three radial axes. RDF and RBF appear to be broad relative to axis length. Other radial comparisons were not attempted because of plate distortion. The deltoid is a large prominent plate but its ornament has been largely removed by weathering. The DD sector would again appear to be well developed. The deltoid is similar in length to some of those of *N. cornutus* but relatively wider. The anal deltoids (an epi- and hypodeltoid) are longer than the regular deltoids; the epideltoid is the larger plate. The anus is large. Ambulacra are prominent with 2.2 side plates per mm. Hydrospire slits have been added across the full width of RDF and number 15 per group. There are 3–4 on the *C* epiradial suture but are apparently lacking (unless there is 1?) on the *D* side.

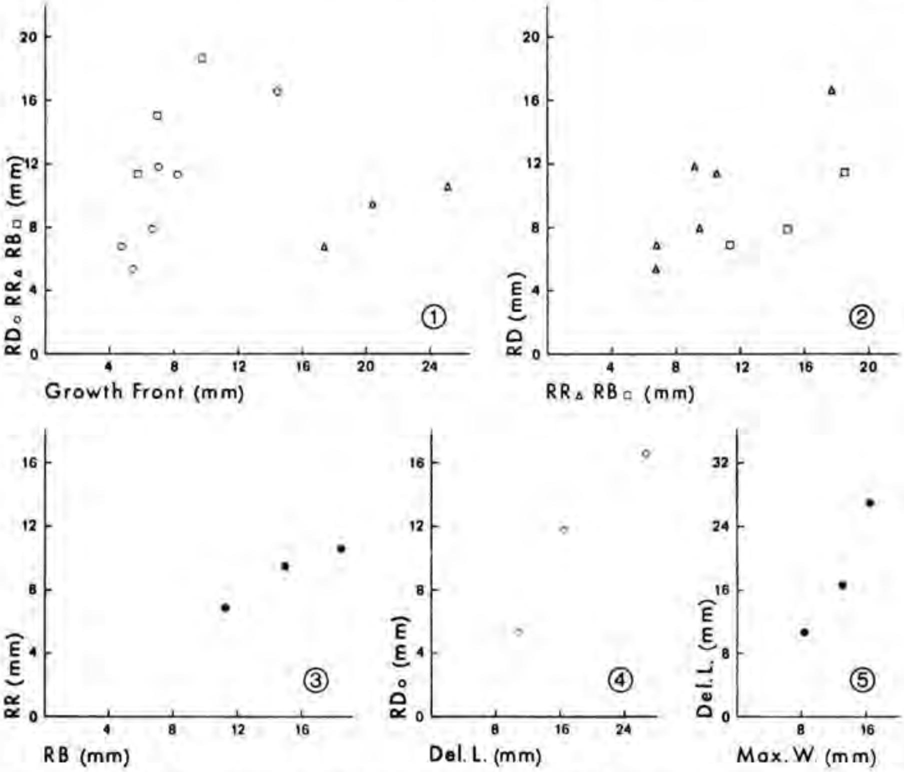
The fourth and youngest (Guadalupian) species of *Notoblastus*, *N. oyensi* (Pl. XX, figs. 3, 5, 6), resembles *N. stellaris* more than the other two species. It is known from a single specimen which is relatively small in size. The theca is lower than wide, the ambulacra are confined to the upper surface, and there were apparently small prongs on the deltoids. The basals are convex and lie in a relatively flat plane; there is a well-developed stem attachment area. The basals grew only slightly more rapidly than RD and slightly less rapidly than RB. RD finds greater relative development than in the other species of *Notoblastus*, being greater (31 percent) than RR (28 percent). RB (41 percent) is still dominant (fig. 96.2). RD appears faster to its front than in *N. stellaris* while the other radial sectors appear to be similar. The deltoid is not as prominent orally as in the other species. It is similar in shape to those of the other species but differs in having a less well-developed DD sector; the boundary between the DD and DR sectors is more subdued. Both BR and RD are greater than Del.L. The anal deltoids (an epi- and hypodeltoid) are the same length as a regular deltoid; the hypodeltoid is smaller. The ambulacra are not well preserved and were apparently small; side plates number 2/mm. There are seven hydrospires developed across the full width of RDF in a regular group. Three slits are present on the *D* epiradial suture. They are lacking on the *C* side; ornament suggests complete secondary infilling or recent atrophy.

An isolated deltoid originally described by WANNER (1940) as *Pterotoblastus* spec. nov. 1 (Pl. XX, fig. 2) appears to us to belong to *Notoblastus*. It may have come from a larger specimen of *N. oyensi*.

Austroblastus whitehousei (Pl. XXIII, figs. 1, 6, 8; Pl. XXIV, fig. 1) occurs with *Notoblastus cornutus* in the Artinskian. It is one of the largest of all fissiculates, exceeding 60 mm in diameter. It is known from disarranged and isolated plates but the two known basals and their associated radials, the shape of the radials, and the large deltoids suggest a thecal shape similar to that of *Notoblastus brevispinus*; i.e., massive and squat, being wider than tall. The ambulacra are confined to the upper surface. The basals probably lay in one plane; they grew at the same rate as RB and faster than RD. The radials are prominent in lateral view; there may be a slight concavity in the RB sectors. RD and RR grow at essentially equal rates with one another but RB is faster than both (figs. 84.2, 3). Within the radial sectors, RD grows faster than its front, RB slightly moreso, while RR is slower as usual (fig. 84.1). The deltoids are large, relatively wide plates (fig. 84.5), with moderate development of DD sectors but large DR sectors which are divided by a crest. Del.L. increases faster than RD (fig. 84.4); however, RD and DR are subequal. The two anal deltoids are of equal length to the regular deltoids. The epideltoid is slightly larger. The hypodeltoid reaches a large size (over 12 mm in the largest specimen). The anus has reached the largest known size within the fissiculates (L.: 6.5 mm; W.: 2.3 mm). Ambulacra reach a fair length (over 18 mm) but remain relatively narrow (less than 2.3 mm). The lancet is exposed and side plates are added at the rate of 2/mm. Hydrospires are added ontogenetically across the full width of RDF to a known maximum of 33; there is strong secondary infilling. The latter specimen has 25 anal hydrospire slits developed on both the epi- and hyporadial suture.

Along with *Austroblastus whitehousei* there occur two radials of similar shape but with a deep concavity in the RB sector. Numerous fingerlike spines extend out up to 7 to 8 mm from the surface of the RR sector. This type of feature is unique in blastoid radials. In *A. whitehousei*, there are several elevated ridges running parallel to RRF (Pl. XXIII, fig. 8). The ornament in the radials in Pl. XXIV, fig. 6 may represent variation within *A. whitehousei* or a second species of the genus.

A single isolated radial and ambulacrum (Pl. XXVIII, fig. 7) from the Upper Permian Oxtrack Fm. of Queensland appears to be a neoschismatid.



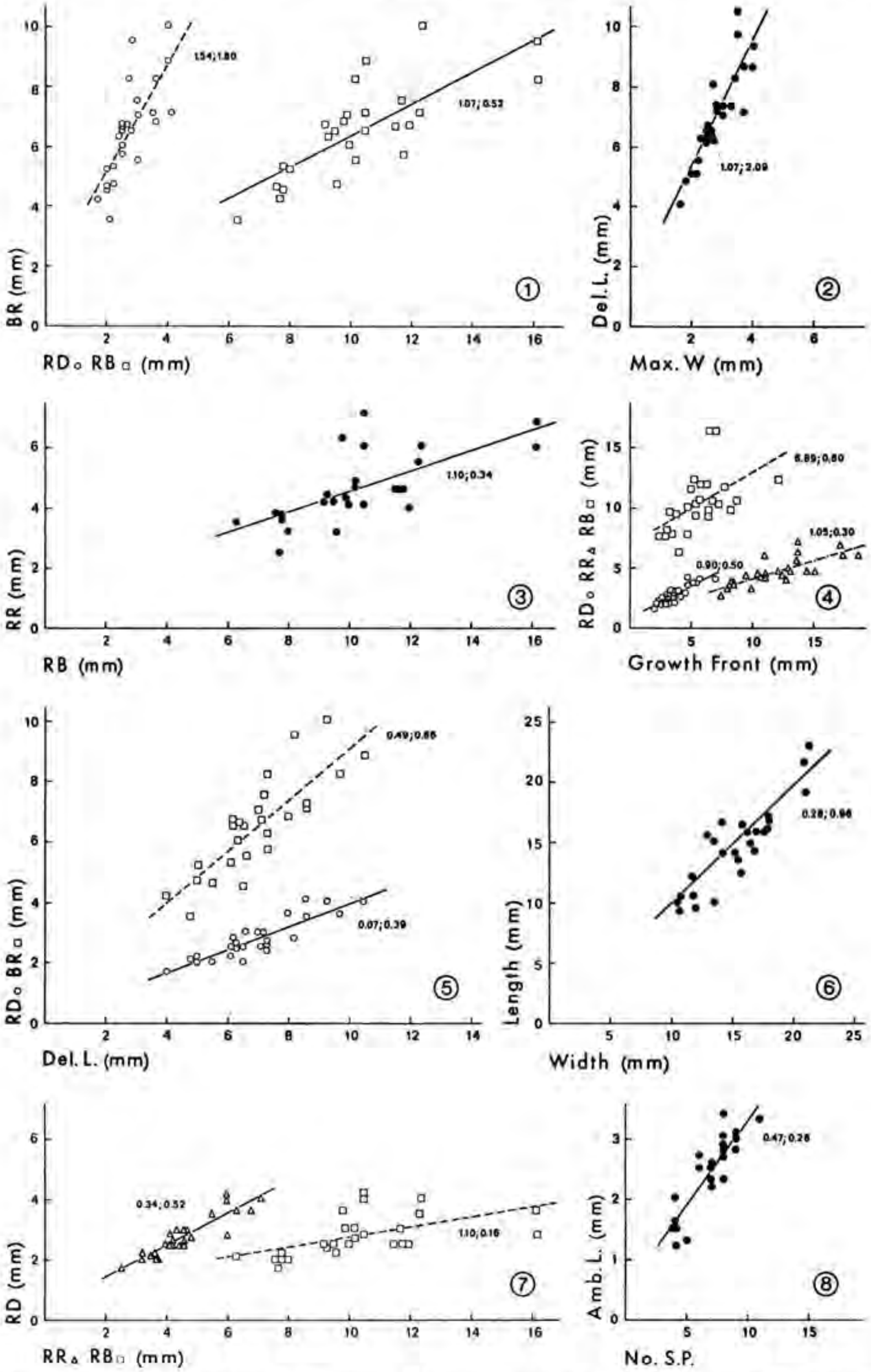
Textfig. 84. *Austroblastus whitehousei* McKellar, 1969. Perm., Berserker Beds, Rockhampton, Queensland, Australia. Ontogenetic development based upon 6 partial specimens. Regression lines not computed due to incomplete data. See textfig. 51 for further explanation.

The large radial with its numerous hydrospires is suggestive of an *Austroblastus*. The ambulacrum is of considerable size and width and would be one of the largest of any Permian neoschismatid. It appears to extend partially down on the radial.

Thaumatoblastus is known from the Artinskian (Pl. XXIV, fig. 2; Pl. XXV, figs. 4–7) and Guadalupian (Pl. XXV, figs. 1–3, 8; Pl. XXVIII, fig. 5). The Artinskian specimens are less numerous than the Guadalupian but appear cospecific within the limitations of the material. Therefore, our remarks are centered on the Guadalupian forms; all are known only from radial plates and prongs. Arranging five radials of *T. longiramus* (Pl. XXV, fig. 8; Pl. XXVIII, fig. 5) in a circle suggests a somewhat conical theca of intermediate to large size (radials of up to 25–30 mm height and width) with five extremely elongate radial prongs which have grown by secondary deposition. RDF was the narrowest of the three fronts, followed by RBF and RRF. RB was apparently the major axis, followed by RR and RD which would be about equal. Outward growth of the radials has produced very long prongs, circular in cross section, which bear the ambulacra on their upper surface. Prongs attached to radials of considerable length are known; the longest piece of prong is 55 mm and broken at both ends. Prongs terminate in a point and the ambulacrum carries almost to the end. The lancet actively grows outward, underlying the side plates which are added at the rate of 1.5/mm, a relatively slow rate. Brachioles are not preserved but they grew outward at a right angle to the prong. The number of hydrospires increases ontogenetically to 24; and hydrospires are developed only on the epi?-radial suture; ratios of 16/7 and 10/5 are known. *T. longiramus* represents the most extreme development of radial prongs of any blastoid and, by the immense spread of its arms, probably developed the largest filtration net (areawise) of any blastoid.

Dipteroblastus permicus (Pl. XXI, fig. 6; Pl. XXII, figs. 2, 3, 6; Pl. XXIII, fig. 4) represents one of the stranger combinations of growth characteristics to be found in a fissiculate. Two radials have grown out into prongs, a result of secondary calcite secretion. The associated ambulacra have also grown outward. The other three radials have no secondary calcite deposition and their ambulacra have remained quite small. This combination produces a pronounced bilateral symmetry. The size is intermediate and ambulacra face upward, none extending downward on the theca. The conical basals have a stem attachment area of 2.1 mm. BR grew at about the same rate as RB, faster than RD and Del.L. Each radial has its own growth pattern but RB was the predominant axis with RD the least. RDF was narrow, RRF wide, and RBF less so. Secondary growth in the *B* and *D* radials produced radial prongs. The deltoids have grown at different rates because of the thecal asymmetry; they are of moderate size with the DR sector forming the major portion of the plate; Del.L. grows slightly more rapidly than RD. A crest divides the DR sectors. The anal deltoids have grown asymmetrically; the hypodeltoid is smaller. Three ambulacra have grown only a slight amount; the other two are longer, extending onto prongs. The rate of addition of new side plates is slow. The number of hydrospires per group varies, dependent on the relative development of the plates. Up to 13 per group are known; strong, secondary infilling has occurred. Hydrospires are developed across the epiradial sutures and vary from 4(*C*) to 7(*D*) in number. Those on the *C* side have been infilled on the radial and are only functional on the deltoid.

The genus *Timoroblastus* is represented by two species but since the older, *T. weiensis* (Pl. XXIV, figs. 3–5; Upper Artinskian) is known from only one specimen, we will describe the ontogeny of the younger *T. coronatus* (Pl. XXIII, figs. 2, 3, 5, 7; Pl. XXVI, figs. 1, 4, 5, 8–11; Pl. XXVII, figs. 1, 3, 4, 5, 9; Guadalupian) first. The upper part of the theca of this species is fairly uniform but there is a great deal of variation in the lower part and this has led to the proposal of many subspecies. Our data described herein (textfig. 85) deals with one population from Tuniun Enu near Basleo,



Textfig. 85. *Timoroblastus coronatus* Wanner, 1924^{a}. Perm., Tuniun Enu, Basleo, Timor. Ontogenetic development based upon 26 specimens. See textfig. 51 for further explanation.

Timor. Members of this population show much of the known range of variation. However, another populations from Kampong Sebot (Pl. XXVI, figs. 1, 5; Pl. XXVII, fig. 9) shows much less variation in thecal form; its regression coefficients are similar to those given in textfig. 85. Another population from Noa, near Tuniun Enu, has developed the lower part of the theca into broad flaring props (Pl. XXVII, figs. 1,5). All members of these populations have a normal stem cicatrix. We have suggested a different life mode for *Timoroblastus*: that it rested on the bottom on its base and the stem was like a runner in a plant, not serving to support it. By this interpretation the variability in growth in the lower part of the theca would be a phenotypic response to different environmental conditions. The allochthonous nature of the Permian deposits of Basleo prevent any verification of these suggestions. It should be emphasized that these thecal differences result from normal lateral addition of calcite to the plate edges, not secondary calcite deposition. The different spatial relation of the basals to the radials has allowed this development.

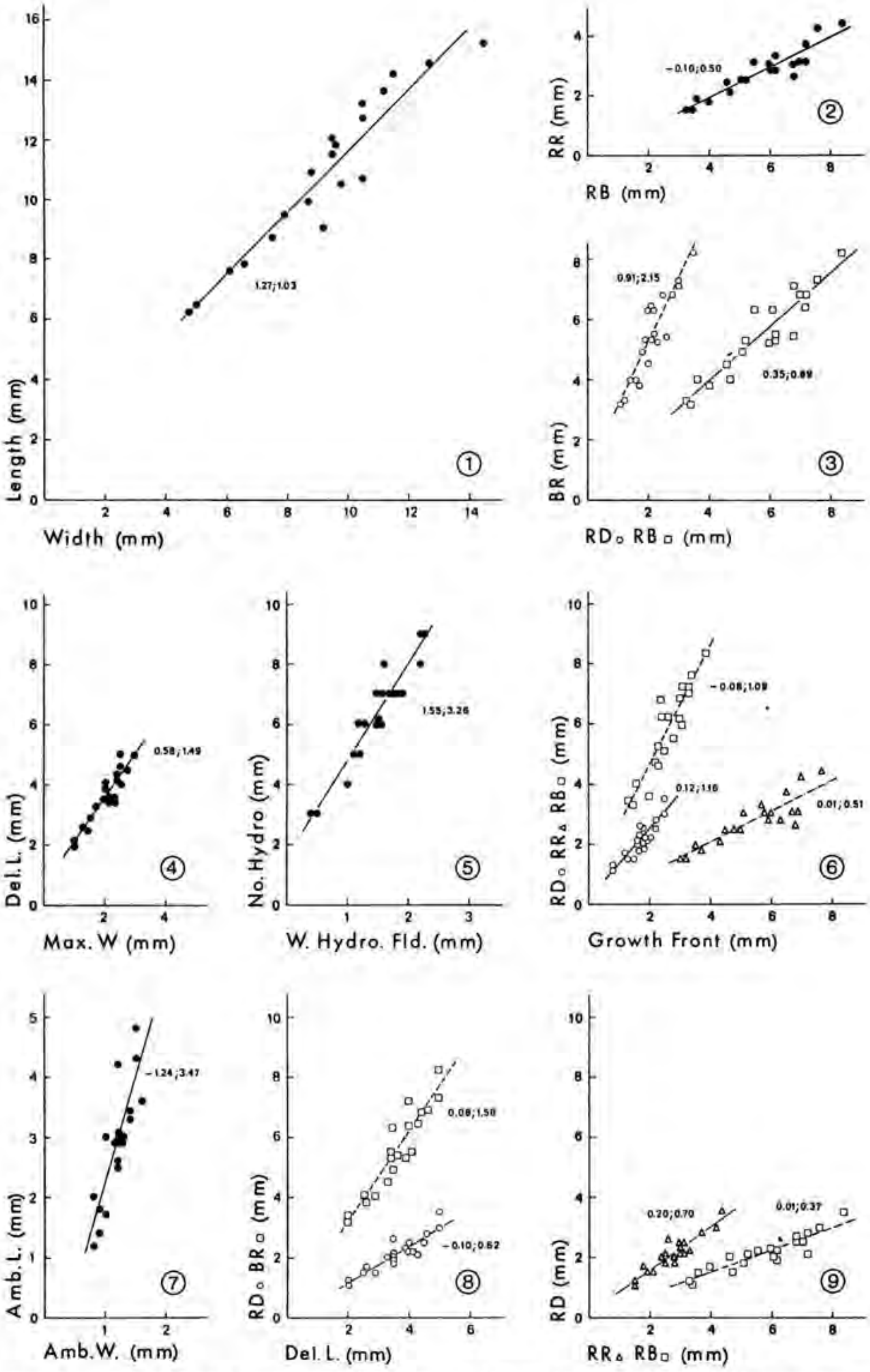
The specimens of *Timoroblastus coronatus* from Tuniun Enu (Pl. XXVI, figs. 4, 8–11; Pl. XXVII, figs. 3, 4) are mostly intermediate in size but a few exceed 20 mm in size (fig. 85.6). The ambulacra are short, confined to the upper surface; the pelvis is massive and boxy. The aboral part of the deltoid has been built up by secondary calcite secretion and projects above the oral opening. The basals are large and lie in a flat or concave plane (rarely convex). The stem attachment area increases in size ontogenetically from 1.0 to 2.0 mm. The basals may differentially accelerate their growth along the parts in contact with the basals to produce a star-shaped base in which the points are the widest part of the basal, a very unusual configuration (Pl. XXVI, fig. 9). BR grows more rapidly than RD but more slowly than RB (fig. 85.1); its rate of growth is equal to that of Del.L. (fig. 85.5). The radials are prominent in lateral view and RB is by far the dominant radial axis, comprising 43 to 64 percent of radial growth (average of 58 percent; fig. 96.2), the highest of any neoschismatid. RD is also reduced to its lowest value (minimum of 12 percent) and is always exceeded by RR which maintains a level comparable with other neoschismatids. Thus RB grows much more rapidly than RD or RR (figs. 85.3, 7) while RR grows more rapidly than RD (fig. 85.7). Within the radial sectors RD grows slightly more slowly than its front; RR shows its usual relationship, and RB is faster (fig. 85.4). The lateral parts of the radial-basal suture may accelerate relative to the central part to produce the flaring base. Thus the radial may be wider at its base than its top. The thickness of calcite along the lower part of RRF and outer part of RBF increases and broken cross sections of these prongs show that they are almost solid calcite, with a very small extension of the thecal cavity only into the uppermost part. Thus, despite apparent variations in thecal shape, the thecal cavity remains rather constant in its shape. The deltoid is a large, conspicuous plate that reaches a long length but also widens ontogenetically (fig. 85.2). There is some growth of a DD axis to produce a modest DD sector; the greatest adoral width almost exceeds the greatest aboral width plotted in fig. 85.2. The aboral part of the deltoid is dominated by a high ridge which is built up by secondary deposition; this becomes higher in larger specimens. The adoralmost edge of the plate bordering the peristome may increase in width slightly; all other edges are actively growing but the DR sector is the major one. Thus RD grows much more slowly than Del.L. (fig. 85.5). The anal deltoids may be slightly shorter, equal to, or longer than the regular deltoids. Both the epi- and hypodeltoid are actively growing plates and the hypodeltoid comes to exceed the epideltoid in size. The hypodeltoid is built up vertically to form the counterpart of the deltoid ridge; its aboral face may bear a ramp for the extension of the anus. The anus itself reaches large size, increasing in length from 0.9 to 3.2 mm and in width from 0.6 to 1.8 mm. Due to adoral growth in the deltoid, the distance from the oral center to the adoral end of the ambulacrum increases ontogenetically (from 1.7 to 3.6 mm). Ambulacral length is quite small relative to thecal size; it increases ontogenetically from 1.2–4.4 mm within the growth series. It does not reach to the origin of the radial. Growth along the adoral facing edge of the radial apparently displaced the ambulacrum with its lancet adorally relative to the radial origin. Ambulacral width also increases from 1.2 to 2.2 mm but the correlation of Amb.L./Amb.W. is low ($r=0.54$). The number of side plates increases from 4 to 11 (fig. 85.8). There is only one hydrospire slit per group and it is just adjacent to the ambulacrum. On occasion, radiodeltoid ornament is suggestive of the ability to build more hydrospires on RDF somewhere in their ancestry (Pl. XXVI, fig. 5).

The specimens of *T. coronatus* from Noa with the extremely large bases (Pl. XXVII, figs. 1, 5) represent the largest known size in this species. The development of these bases follows the steps outlined above as evidenced by the radial growth lines showing earlier stages. Thecal height is up to 20 mm, width to 40 mm. One specimen shows a much shorter ray in the *AB* interarea, and a notch at the ray end, as though this part of the specimen was in contact with or wedged against something and prevented from growing normally (Pl. XXVII, fig. 5).

The second species of *Timoroblastus*, *T. weiensis* (Pl. XXIV, figs. 3–5) is slightly older but known only from a single relatively small specimen. It is slightly wider than a *T. coronatus*. Growth relations within and between the plates appear to be very similar to those of *T. coronatus*. An RA axis is present in the radial (see ontogeny of *Angioblastus*). The principal difference is the development of more than one hydrospire per group across RDF (except in the anal interarea). These are more widely spaced relative to one another than normal neoschismatid hydrospire slits and are not developed on the aboralmost part of RDF.

Family Codasteridae

Mississippian. The earliest codasterid genus, *Codaster*, contrasts with Mississippian phaenoschismatids in the development of a cup-shaped theca and flattened vault. The ambulacra are restricted to the upper surface. The maximum size of the type species, *C. acutus* (Pl. XXVI, figs. 2, 3, 6, 7; Pl. XXVII, figs. 2, 6–8; Pl. XXVIII, figs. 1, 2, 4, 8, 9), is intermediate (fig. 86.1); length is slightly greater than width. The maximum known size is near 20 mm. The convex basals have a stem attachment area formed of secondary calcite; this increases from 0.5 to 1.4 mm in diameter. BR grew at the same rate as RB, more quickly than Del. L., and faster yet against RD (figs. 86.3, 8). The radial is prominent in lateral view. The RD sector is almost flat in lateral view. RB is the predominant axis, comprising 51 to 59 percent of the radial growth; whereas, RR is 22 to 29 percent and RD is only 17 to 23 percent (fig. 96.2). This is in contrast to the phaenoschismatids where RD was most always greater than RR. Thus, RB plots as the most rapid axis, and RR is slightly more rapid than RD (figs. 86.2, 9). There is no acceleration of RD. The disposition of the radial axes relative to their fronts is average except that RR is slightly faster relative to its front (fig. 86.6). The deltoids are prominent orally, flattened compared to phaenoschismatids, place a slightly greater emphasis on growth in the adoral part of the plate, and retain a flattened aboral crest. Del.L. exceeds Max.W. (fig. 86.4); the adoral edge of the plate bordering the peristome increases in width as do the maximum adoral and minimum width. The crest grows aborally and its width increases through some secondary infilling of hydrospire slits. Del.L. grows more rapidly than RD (fig. 86.8). There is only one anal deltoid, an epideltoid. The aboral margins of the anus are formed by the limbs of the radial as in *Heteroschisma*. Therefore, the epideltoid is usually shorter than the regular deltoid. The former is actively growing. Thus the anus increases in size due to the growth of the surrounding plates and is displaced aborally. The ambulacra are only moderately developed; their adoral end is shifted farther aborally during ontogeny. The lancet is exposed almost to the aboral end. Ambulacral length increases much more rapidly than width (fig. 86.7); side plates are added at the rather usual rate of 3/mm. Hydrospires are distributed across the full width of RDF, increasing ontogenetically from 3 to 9 (fig. 86.5). There is some secondary infilling at either end. The development of the anal hydrospires is more irregular. Within the growth series, there is usually only 1 on either side, regardless of thecal size. These slits are also much shorter. One specimen failed to develop any on one side; some have 2 on one side and 1 on the other. There is no predominance of one side over another. One specimen from another locality in Yorkshire has 4 anal hydrospires; this is the known maximum. Specimens from this second locality are also more likely to develop 2 per anal group.

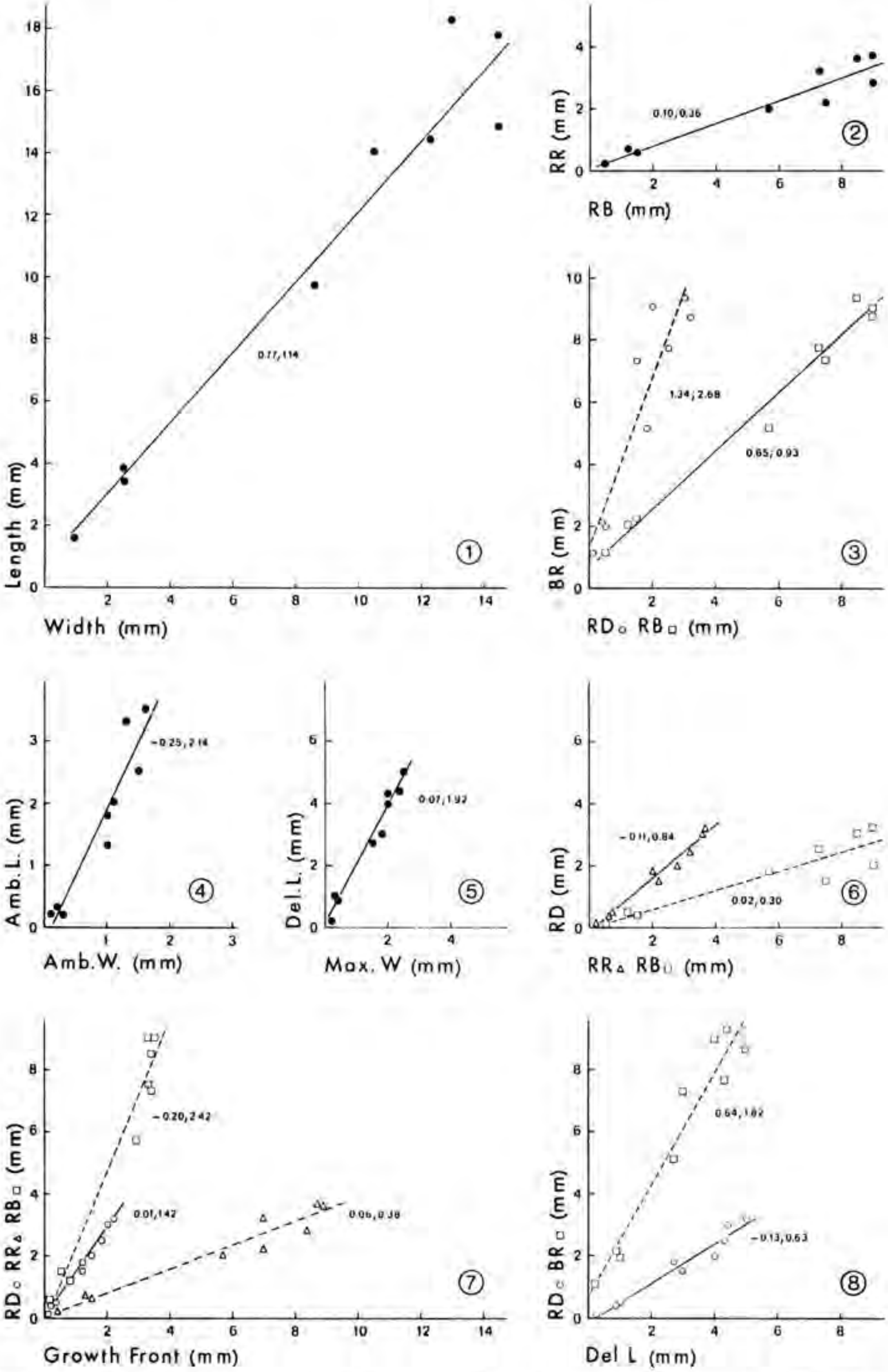


Textfig. 86. *Codaster acutus* M'Coy, 1849. L. Carb., Visean (D_2 zone), Grassington, Yorkshire, England. Ontogenetic development based upon 20 specimens. See textfig. 51 for further explanations.

Specimens of *Codaster* (Pl. XXVI, fig. 7; PL. XXVII, fig. 7; Pl. XXVIII, figs. 1, 2, 4, 8, 9) from Ireland include the smallest known immature fissiculates; these are particularly significant for interpreting growth relationships just after the beginning of skeletal secretion and filling in the always present data void near the origins of our graphs. We have reserved discussion of the earliest stages of ontogeny until the Phylogeny Chapter (see p. 351) because of its relevance to codasterid phylogeny. We have assigned the Irish representatives to *C. acutus* although a few differences may be noted in the growth of the upper part of the theca. Elements grow more slowly, producing a more restricted vault. This difference may be specifically distinct. The ontogeny of the Irish specimens is given in textfig. 87 for comparison. L/W and maximum size are the same (fig. 87.1). The rate of growth of BR to RB is almost identical but is slightly faster to RD and a bit more distinct relative to Del.L. (figs. 87.3, 8). RD is the same to RR but slightly slower to RB, and RR is slower to RB (figs. 87.2, 6). RD/RDF and RB/RBF are the same while RR is slightly slower relative to RRF (fig. 87.7). Internal deltoid growth and its growth relative to RD are the same (fig. 87.8). Ambulacral development follows the same pathway (fig. 87.4) except that relative size is slightly reduced due to less emphasis on the vault. The development of the hydrospires is the same except that we have been able to document the time of development of the first regular and anal hydrospire slits and the known numbers range from 0 to 8 and 0 to 1 respectively. See p. 351 for further discussion.

Pennsylvanian. As can be seen in textfig. 100, known Pennsylvanian fissiculates are about as common as the proverbial hen's tooth. Therefore, the genus *Angioblastus* assumes special significance: it ranges from Pennsylvanian through Permian and is now recognized on four continents in the eastern and western hemispheres, making it perhaps the most cosmopolitan of all blastoid genera.

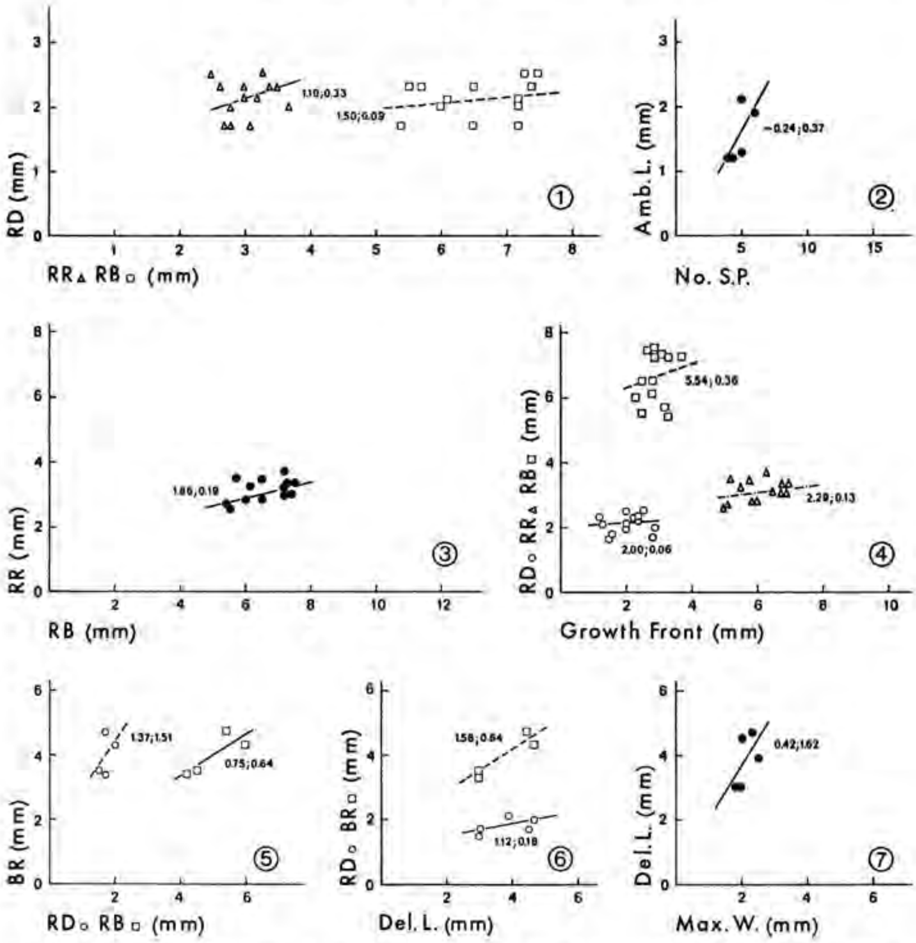
The earliest species of *Angioblastus*, *A. ellesmerensis* (Pl. XXIX, figs.6, 8–10; Bashkirian), is not represented by enough specimens to allow a formal regression analysis but the three relatively complete specimens do permit an ontogenetic comparison with *Codaster acutus* (textfig. 86). The theca is broad and cup-shaped just as in *C. acutus* but the deltoids project above the surface due to the deposition of secondary calcite. Length is slightly greater than width and would appear to follow the same line as for *C. acutus* (fig. 86.1). Maximum known size is intermediate (near 15 mm). The ambulacra are again confined to the upper surface of the theca. Basals are convex; the stem attachment area is formed of secondary calcite but not measurable. RB grew more rapidly than BR, in contrast to *C. acutus* where they were equal. RD and Del.L. also clearly grew more rapidly than in *C. acutus*. The radials are prominent in lateral view and the RD sector is nearly horizontal in lateral view. RB is again the



Textfig. 87. *Codaster acutus* M'Coy, 1849. L. Carb., Visean, Lisdowney, Co. Kilkenny, Ireland. Ontogenetic development based upon 9 specimens. See textfig. 51 for further explanation.

predominant radial axis (45–49 percent), whereas RR (26–29 percent) and RD (25–26 percent) are nearly equal (fig. 96.2). The growth of RD/RR and RR/RB closely follows that for *C. acutus* while RD is slightly faster to RB. Growth relations of the radial axes relative to their fronts follow *C. acutus*. Scattered small tubercles are developed on the surface of the earlier-formed parts of the radial. The deltoids are restricted to the upper surface. There is a greater emphasis on growth in the adoral part of the plate and it has come to be as wide adorally as aborally. There is a massive secondary deposit in the form of a curved ridge which separates the DD and DR sectors; a subdued crest extends aborally from its center. DDF and DAF appear to increase ontogenetically. RD is perhaps a bit faster relative to Del.L. than in *C. acutus*. A hypodeltoid is apparently lacking in this species. There is no trace of a hypodeltoid or facets for it in the three specimens where this is visible. A large rim, the counterpart to that of the regular deltoid, borders the anus adorally. The anus is relatively large and located on the upper outer edge of the theca. Ambulacral development is again relatively modest; side plates are added at 3/mm. Hydrospire slits occupy the full width of RDF and number 6–8. The functional length of the slit, however, is very short (0.3–0.4 mm). Anal hydrospires are developed in one specimen. Their presence or absence cannot really be clearly ascertained in the smallest specimen due to silicification. They appear to be absent in a second specimen, whereas in a third there are 3 on one side (*D*) and 1 on the other (*C*). This is the only species of *Angioblastus* to show the development of any anal hydrospires.

Angioblastus dotti (Pl. XXIX, figs. 1–5; Gzhelian-Orenburgian) is the other Pennsylvanian species of *Angioblastus*. It is usually disarticulated or flattened but enough complete specimens and isolated plates were available to conduct an ontogenetic analysis. Length exceeds width; maximum size is intermediate. Thecal shape is cup-shaped with apparently a flatter base than in the previously discussed codasterids. The ambulacra are rather modest and confined to the upper surface. The stem attachment area is small. BR grows more slowly than RB as in *A. ellesmerensis* while BR is comparatively faster to RD (fig. 88.5). BR/Del.L is apparently the same (fig. 88.6). The radials are prominent in lateral view and RB is the predominant axis, being between 50–60 percent of radial growth, whereas, RR is 24–30 percent and RD 14 to 22 percent. These differ from *A. ellesmerensis* and thus both RR and RB are faster to RD in *A. dotti*; RR/RB is the same (figs. 88.1, 3). RD is slower relative to RDF whereas RR/RRF and RB/RBF are the same (fig. 88.4). A small RA axis is present. (The ambulacrum does not quite reach to the radial origin; calcite is deposited around the aboral end of the ambulacrum in a concentric arc as growth proceeds in order to fill in this space.) The relative proportions of the deltoid are as in *A. ellesmerensis* (fig. 88.7), except that the plate has become wider adorally than aborally. A large secondary ridge again



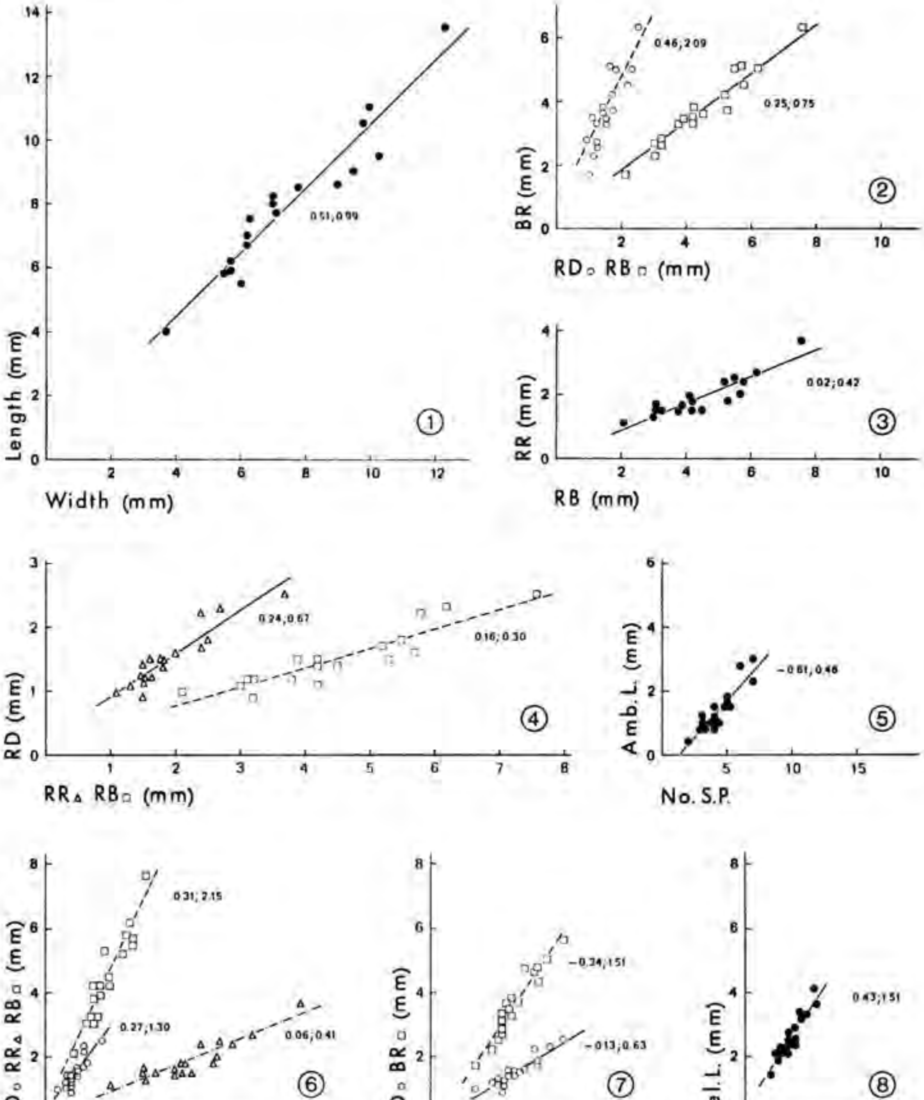
Textfig. 88. *Angioblastus dotti* (Moore and Strimple, 1942). Penn., Missourian, Hogshooter Fm., Ramona, Oklahoma, USA. Ontogenetic development based upon 13 specimens. (7) Maximum width of deltoid is in adoral part of plate. See textfig. 51 for further explanation.

divides the DD and DR sectors but an equally prominent keel now separates the adjacent DR sectors. RD grows more rapidly to Del.L. (fig. 88.6) than in *A. ellesmerensis*. The anus is rimmed adorally by a large collar; a hypodeltoid is present on the upper lateral wall of the theca. It is apparently not in contact with the epideltoid as in *A. variabilis*. Ambulacra are reduced in size compared to an equal sized *A. ellesmerensis*; the rate of addition of side plates is about 3/mm (fig. 88.2). The lancet is exposed over one-half the ambulacral length. New hydrospire slits are added ontogenetically, increasing from 4 to 9. Functional length is very short. They are lacking in the anal interarea.

Permian. Angioblastus is represented by 4 species in the Permian. The oldest of these, from the lowermost Permian of Bolivia, is *A. boliviensis*

(Pl. XXIX, figs. 19–21). Only one specimen was available to us; others may exist in private collections not currently accessible. Thecal shape is similar to *A. dotti*; the ambulacra are again restricted. Length exceeds width; the single specimen is near 10 mm in length. The convex basals lie in a relatively flat plane; the stem cicatrix is weathered. The growth of BR to RD, RB, and Del.L. is as for *A. dotti*. The relative percentage of the radial axes is as for *A. dotti* as are the growth relations between the radial axes and of each with its front. A massive secondary ridge divides the radial longitudinally. (As in those codasterids which have a wide base, the *C* and *E* radials are smaller than *A*, *B*, and *E* which must fill in the lower space of the theca; these latter plates are frequently wider proximally than distally, an unusual configuration. All radial comparisons are based upon *C* or *E*). The deltoid is very similar in its proportions to that of *A. dotti*. The secondary ridge dividing the DD and DR sectors is again present but subdued relative to the keel dividing adjacent DR sectors and the latter crosses it adorally. The anus is located in the same position as in *A. dotti* and rimmed adorally by a collar. Facets are present for a hypodeltoid. There are three hydrospire slits, occupying the full width of RDF; the functional length is quite short (0.3 mm). Slits are lacking in the anal interarea.

Angioblastus wanneri (Pl. XXIX, figs. 7, 11–13, 15–18) is a slightly younger species from the Lower Permian of the USSR. Its thecal shape resembles that of *A. dotti* and *A. boliviensis* but is a bit rounder and more swollen in the lower part. Maximum size is intermediate and the width almost equals length (fig. 89.1). The ambulacra, confined to the upper surface, are modest in their development. The convex basals form the broad thecal base; the diameter of the stem attachment area increases from 0.3 to 1.0 mm ontogenetically. BR has the same rate of growth with RD and RB as in *A. dotti* but grows more rapidly relative to Del.L. (figs. 89.2, 7). The radial is prominent laterally. RB is the predominant radial axis, comprising 50 to 62 percent of the radial growth while RR is 20 to 27 percent and RD 16 to 24 percent. These percentages are almost identical to those of *A. dotti* as shown by graphs of the radial axes (figs. 89.3, 4). RD grows more rapidly relative to its front while RR is a bit slower; RB/RBF is the same (fig. 89.6). An RA axis is present. The adoral part of the deltoid predominates; the plate is widest adorally. A secondary deposit again separates the DD from the DR sector; it extends into the DD sector. A strong keel separates the adjacent DR sectors, restricting the width of RDF available for hydrospire formation. Del.L. is greater than Max.W. (fig. 89.8); the adoralmost edge of the deltoid increases slightly in width during growth as do the other parts. The aboral part is perhaps the slowest growing (0.2 to 0.5 mm). The rate of growth of RD/Del.L. (fig. 89.7) is as in *A. dotti*. The length of the two anal deltoids is greater than that of the regular deltoids. The epideltoid is the larger plate; by its growth, the anus is shifted farther aborally. It forms an adoral

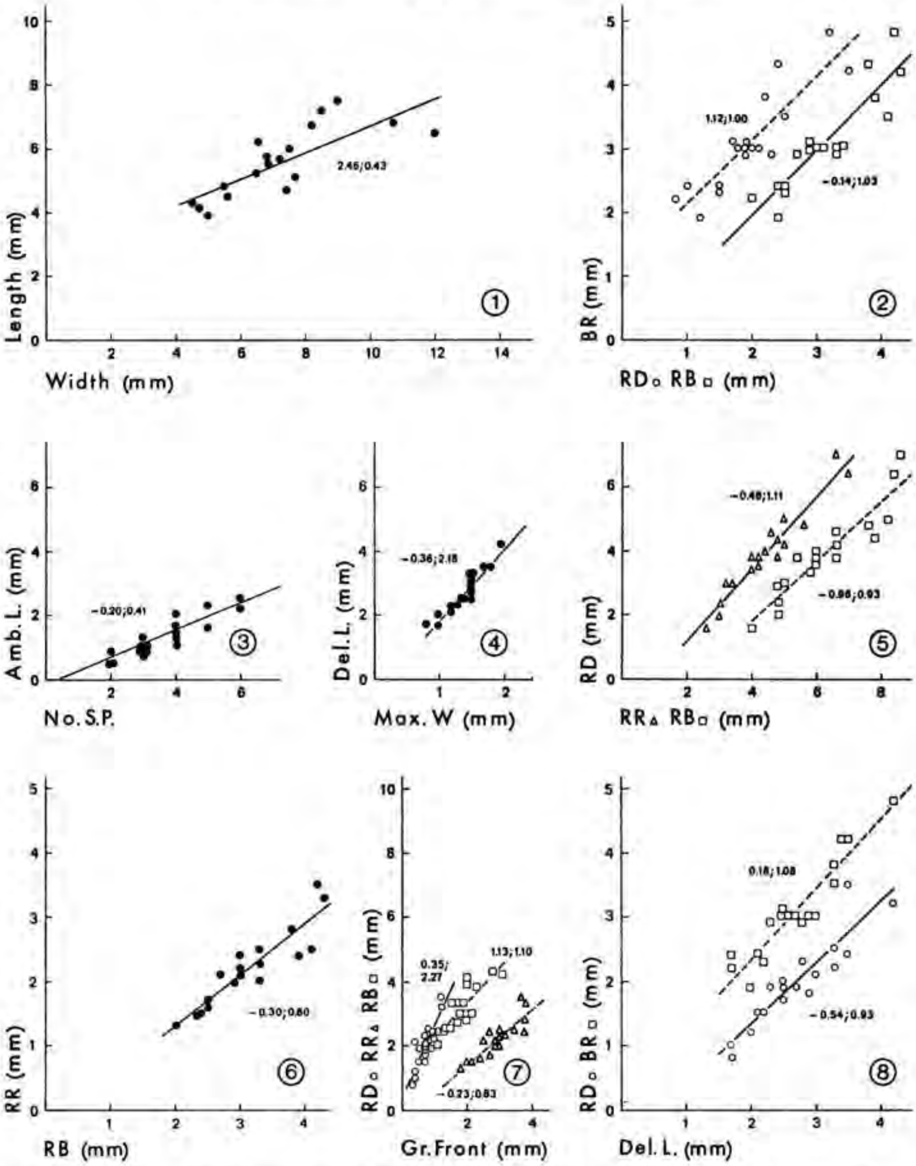


Textfig. 89. *Angioblastus wanneri* (Yakovlev, 1926[b]). L. Perm., Krasnoufimsk, Ural Mts., USSR. Ontogenetic development based upon 18 specimens. (8) Maximum width of deltoid is in adoral part of plate. See textfig. 51 for further explanation.

rim to the anus. The hypodeltoid is also an actively growing plate; as a consequence of their growth, the anus also increases in size. The ambulacrum is relatively small (fig. 89.5); its structure and rate of addition of new side plates is similar to that of other species of *Angioblastus*. Ambulacral width increases ontogenetically; the entire ambulacrum is shifted aborally from the oral center during growth (from 0.7 to 2.1 mm). The number of hydrospire slits is few (1–3) and the full width of RDF is not utilized for their formation. Functional length is short. There are no anal hydrospires developed.

Angioblastus miloradovitchi (Pl. XXX, figs. 10, 11), also from the Permian of the USSR, is very similar to *A. wanneri* in its shape. The only known specimen is slightly larger and relatively wider. BR grows at the same rate as RD and Del.L. of *A. wanneri* but its rate of growth is equal to RB whereas RB was faster in *A. wanneri*. The growth of the radial axes relative to one another and their fronts is as in *A. wanneri*. An RA axis is present. Deltoid shape is also very similar but the deltoid ornament differs and apparently there is a greater development of hydrospire slits on RDF, almost the full width being utilized. RD/Del.L. is the same as are the anal deltoids and ambulacral development. Hydrospire slits number six per group; we could not prove their presence or absence in the anal interarea. They are more highly developed on the radial than the deltoid and are infilled secondarily.

The youngest species of *Angioblastus*, *A. variabilis* (Pl. XXVIII, figs. 3, 6; Pl. XXIX, fig. 14; Pl. XXX, figs. 1–4, 6–9, 12; Guadalupian), is the only species of the genus in which width almost always exceeds the length (fig. 90.1); the maximum length is also less than 10 mm. The theca is more bowl-shaped and the ambulacra are modest and restricted. The convex basals lie in almost a flat plane and the radials almost appear as an overhang. The stem attachment area is small, not exceeding 1.2 mm. BR grows at an equal rate to RB and faster than RD and Del.L. (figs. 90.2, 8). The rate of BR to RD and Del.L. is less than in *A. wanneri*. The radials are quite prominent laterally. RB is still the predominant radial axis but less so than the other species of *Angioblastus*. It represents 37 to 49 percent of radial growth, while RR is 27 to 33 and RD is 20 to 32 percent (fig. 96.2). There is apparently an ontogenetic acceleration of RD. Thus, RD is equal to RR and slower than RB (fig. 90.5) but faster than in *A. wanneri*. While RB is faster than RR, its relative rate is slower than in *A. wanneri* (fig. 90.6). Within the radial sectors, RD is faster to its front than RB is to its (a reversal of the situation in *A. wanneri*) and RR grows more rapidly relative to RRF than in *A. wanneri* (fig. 90.7). An RA axis is present. Sharp ridges frequently radiate downward from the radial origin to the radial basal suture. The deltoid is similar in shape to *A. wanneri* but the ornament differs in being massive with the development of an aboral overhang over the radials. Greatest width is again adoral but is exceeded by Del.L. (fig. 90.4). The adoral edge bordering the peristome increases in width very slightly; all other parts of the deltoid are actively growing. The DD sector is large relative to the other sectors. RD and Del.L. grow at the same rate (fig. 90.8); in *A. wanneri*, Del.L. was faster. The anal deltoids almost always exceed the regular deltoids in length. The epideltoid is predominant but the hypodeltoid also increases,



Textfig. 90. *Angioblastus variabilis* Wanner, 1931. Perm., Noko, Timor. Ontogenetic development based upon 18 specimens. (4) Maximum width of deltoid is in adoral part of plate. See textfig. 51 for further explanation.

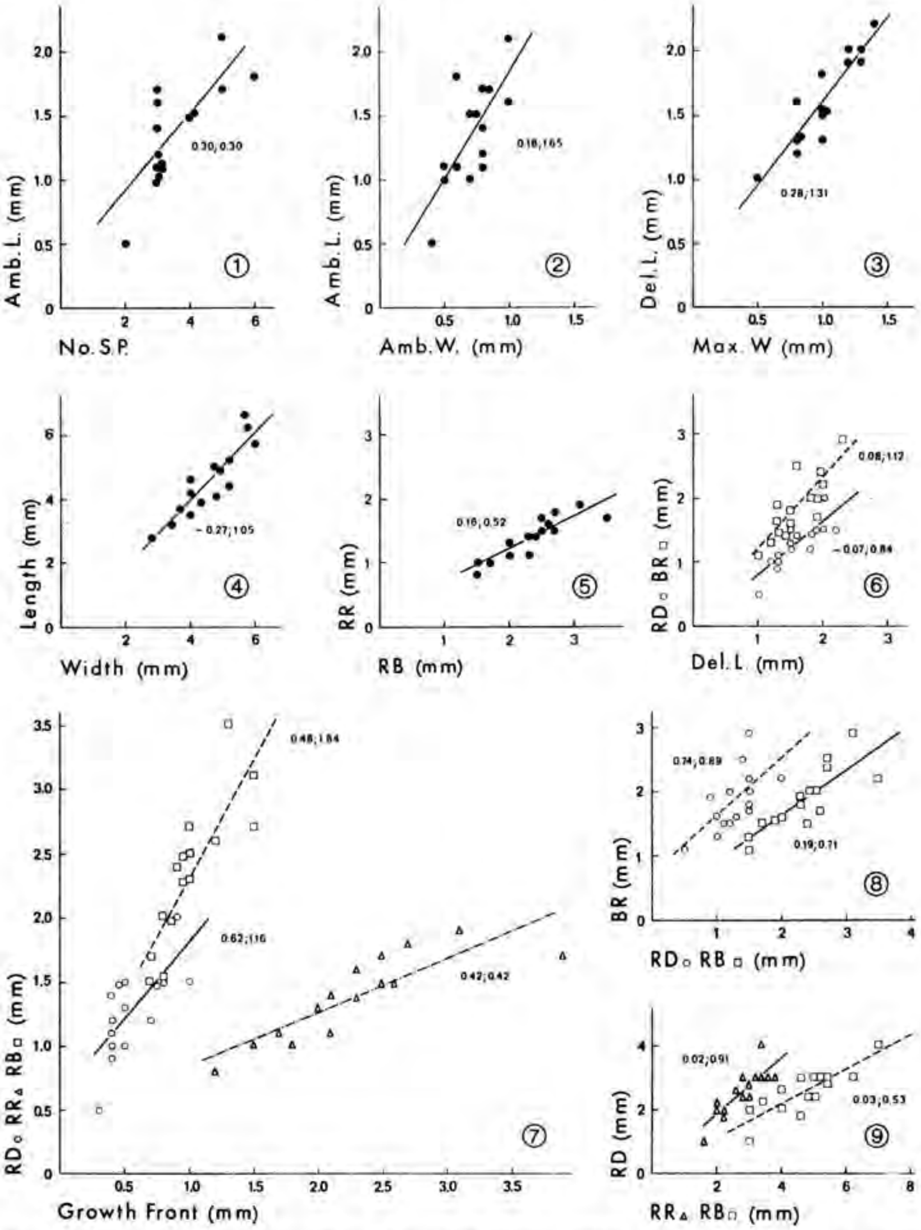
thus facilitating an increase in anal width from 0.5 to 1.0 mm. It is aborally displaced during growth. The hypodeltoid may not be in contact with the epideltoid. The ambulacra are rather small and the width either closely approaches or equals Amb.L. They are confined to the upper surface. New side plates are added at the same rate as *A. wanneri* (fig. 90.3). The adoral end of the ambulacrum is aborally displaced during ontogeny by deltoid growth. Hydrospires are found in eight interareas but anal ones are lacking. In only 2 of the 18 specimens (and not the largest) is there the development of 2 hydrospires per group. Functional length is again short.

Another codasterid found in the Lower Permian of the USSR is *Tympanoblastus pousirewskii* (Pl. XXX, figs. 5, 14; Pl. XXXI, figs. 3, 6). It is known to us from only two specimens but they are of different sizes and permit some observations on ontogenetic relationships. Length and width are almost equal and the maximum known size of the cup-shaped theca is intermediate. Ambulacra are restricted to the upper surface but find much greater expression than in *Angioblastus*. The basals are either conical or convex; the stem attachment area is relatively small. The radials are prominent laterally. RB grows more rapidly than BR; the latter is faster than RD and equal to Del.L. RB is the predominant axis as in all codasterids, being 50 to 54 percent of the radial growth while RR is 25–26 percent and RD is 20 to 23 percent (fig. 96.2). Thus, RR is slightly faster than RD and RB is much faster; RR is slower than RB. RD grows at the same rate to its front as is in *Angioblastus wanneri* but RR is clearly faster to RRF and RB may be slightly faster to RBF. The deltoid is a prominent plate, dominated by the DD sector with a bent-over, downward-growing smaller DR sector; a crest separates adjacent DR sectors. This downward bending of the DR sectors is unusual. Growth lines in the DD sector clearly indicate its adorally directed expansion, with the consequent continued reformation of the ambulacral tract along DDF and aboral shift of the ambulacra. All deltoid parts are actively growing. Del.L. is greater than RD but the rate of growth of DR is less than RD. The anal deltoids are about the same length as the regular deltoids; the epideltoid predominates. It is mostly formed by growth in the DD sectors. The anus is relatively large; the hypodeltoid is also actively growing. The ambulacra are prominent, reaching a greater length than in *Angioblastus* and also a greater width; they are unusually broad. Side ambulacral tracts have continually increased in length. Side plates are added at the rate of 2.5–3/mm. Hydrospire slits are developed across the full width of RDF and number six to eight in regular groups. They are more numerous and have a greater functional length than any Permian species of *Angioblastus*. The older parts of the hydrospire slits are apparently infilled on the radial. They are lacking in the anal interarea.

One of the largest of all codasterids is the single specimen described from the Lower Permian of the USSR as *Tympanoblastus elongatus* (Pl. XXX, fig. 13; Pl. XXXI, fig. 1). It approaches 20 mm in length; the latter is greater than the width. The theca is cup-shaped; the ambulacra are confined to the upper surface. The stem attachment area is small (1.0 mm) at the base of the convex basals. BR is slightly slower than RB, faster than RD and Del.L. RB is the predominant radial axis, 56 percent, while RR is 24 percent and RD 20 percent. Growth relations within the radial sectors are as for *A. wanneri*; a small RA axis is present. The deltoids are conspicuous and dominated by the DD sectors; the DR sectors are separated by a downward-sloping crest. The two anal deltoids are slightly larger than a regular deltoid; the epideltoid predominates. The hypodeltoid forms the aboral margin of an unusually large anus. Ambulacra are removed from the oral opening due to DD growth, of intermediate length, and side plates were added at 2/mm. The number of hydrospire slits is small, 2–3 per group, and their functional length short. They are lacking in the anal interarea.

The genus *Pterotoblastus* shows different ontogenetic patterns within the three species now recognized. The oldest of these, *P. ferrugineus* (Pl. XXXI, figs. 4, 8; Upper Artinskian), is known only from a single, small specimen. The bowl-shaped theca is wider than high; lateral prongs, resulting from secondary deposition on the radial, are present. The ambulacra are thus confined to the upper surface. BR appears to have grown less rapidly than RB, about the same rate as Del.L., and faster than RD. In comparison to *P. brevialatus* which follows, BR/RD and BR/Del.L. are the same, but RB is faster than in *P. brevialatus*. The radials are prominent laterally. Within the radial, RB was dominant, being 49 percent of the radial growth, while RR was 28 percent, and RD 23 percent (fig. 96.2). Both RD and RB grew more quickly than their fronts while RR was slower to its front. RD/RDF and RB/RBF apparently grew at the same relative rates as in *P. brevialatus* but RR was slightly faster to RRF. As in Permian species of *Angioblastus*, the deltoid is wider adorally than aborally due to accelerated growth in the DD sector. A small ridge separates the DD and DR sectors; a crest separates adjacent DR sectors. In contrast to other species of *Pterotoblastus*, there are two anal deltoids; the epideltoid predominates. The anal deltoids are of the same length as the regular deltoids. The ambulacra are moderately developed and appear to extend outward on the radial prong. In contrast to other fissiculate genera, the lancet is only developed at the adoral end of the ambulacrum; here it is in contact with the adoralmost side plates. Aboral to this, these rest directly on the radial. The ambulacrum is longer than wide. The hydrospire slits are developed across the full width of RDF but because of the relative development of the DR sector, there are only three per group. Their functional length is short (0.5 mm). The slits themselves appear slightly more widely spaced than usual. They are lacking in the anal interarea. There appears to have been secondary infilling of the earlier-formed parts of the slits.

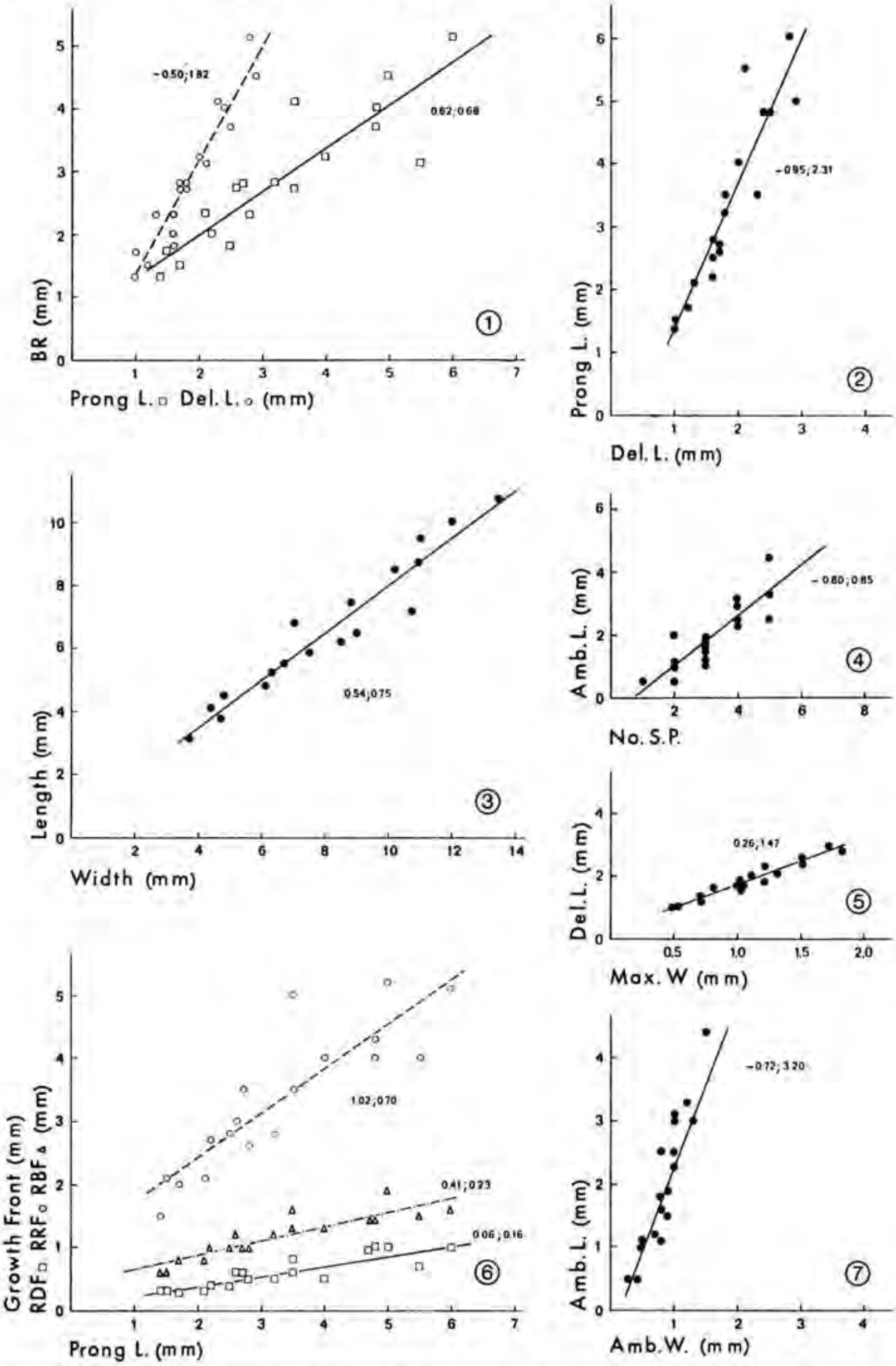
Pterotoblastus brevialatus (Pl. XXXI, figs. 2, 5, 7, 9, 13–15; Guadalupian) is a small fissiculate, not exceeding 7 mm. The length and width of the cup-shaped theca are about equal (fig. 91.4). The ambulacra are short and confined to the upper surface. Radial prongs are not developed. The diameter of the proximal stem plate varies from 0.5 to 1.0 mm. The basals form a broad convex base to the theca. BR grows slightly slower than RB but faster than RD and Del.L. (figs. 91.6, 8). The radials are



Textfig. 91. *Pterotoblastus brevialatus* Wanner, 1931. Perm., Noko, Timor. Ontogenetic development based upon 15 specimens. See textfig. 51 for further explanation.

prominent in lateral view and show the development of a small protuberance at the origin of the radial due to secondary calcite deposition. Its elevation varies from 0.0 to 0.9 mm. RB is again the dominant radial axes, being 43 to 54 percent of radial growth, while RR is 26 to 30 percent, and RD is 18 to 29 percent (fig. 96.2). These relations are almost the same as in other codasterids except that there is a bit more emphasis on RD and less on RB. There is no acceleration of RD. Thus RB grows more rapidly than RR and RD while the latter two are near equality (figs. 91.5, 9). Within the radial sectors, RB is fastest relative to its front while RD is slightly slower; RR is slower than its front, showing an average slope (fig. 91.7). Growth proportions within the deltoid are as for *P. ferrugineus*. The greatest width is adoral, usually being slightly greater than the greatest aboral width given in fig. 91.3. Del.L. grows slightly more rapidly than RD (fig. 91.6). There is only a single anal deltoid, the epideltoid; the aboral margins of the anus are formed by the radial limbs. As a result of epideltoid growth, the anus is displaced aborally at the same time it increases in size. The ambulacrum is also displaced aborally. It is usually rather short, longer than wide (fig. 91.2), with new side plates added at a rate of 2/mm (fig. 91.1). Ambulacral structure is as in *P. ferrugineus*. Hydrospire slits number one per group except in the largest of specimens where two with an incipient third are present. Again their functional length is short (0.1–0.4 mm); they are absent in the anal interarea.

Pterotoblastus gracilis (Pl. XXXI, figs. 11, 12; Pl. XXXII, figs. 3, 4, 6, 9, 10; Guadalupian) contains the largest known complete specimens of *Pterotoblastus* but these rarely exceed 10 mm in length. The theca is wider than high (fig. 92.3) because of the large radial prongs which are developed from the smallest individuals onward. The ambulacra extend onto the prongs and are therefore restricted to the upper surface. The basals are conical; the diameter of the attached proximal stem plate varies from 0.8 to 2.0 mm. Due to the dominance of the radial prong, direct measurement of radial axes is impossible but radial shape would indicate the dominance of RB as in other species of *Pterotoblastus*. Again by comparison of plate shapes, BR was probably about equal to RB and faster than RD; it is faster than Del.L. (fig. 92.1). The prong grew outward more rapidly than BR grew upward (fig. 92.1). The radial prong makes the radial very prominent in lateral view. Prong L. increases rapidly during ontogeny, increasing faster relatively than any radial front although RRF approaches it (fig. 92.6). The relative proportions of the deltoids are as in *P. brevialatus*, with the DD sectors again dominant and the DR sectors relatively small with a small crest separating adjacent sectors. The plate is only modest in size, and is again wider aborally than the maximum aboral width given in fig. 92.5. It grows much more slowly than the prong (fig. 92.2). The structure of the anal interarea and its growth is as in *P. brevialatus*. The ambulacrum is again displaced aborally by deltoid growth (from 0.5 to 2.2 mm); the ambulacral length exceeds the width (fig. 92.7) and side plates are slightly more numerous than 2/mm (fig. 92.4). Ambulacral structure is as in both *P. ferrugineus* and *P. brevialatus*. Growth occurs along the sutures between adoral side plates and the deltoid to increase the distance between adjacent brachiolar



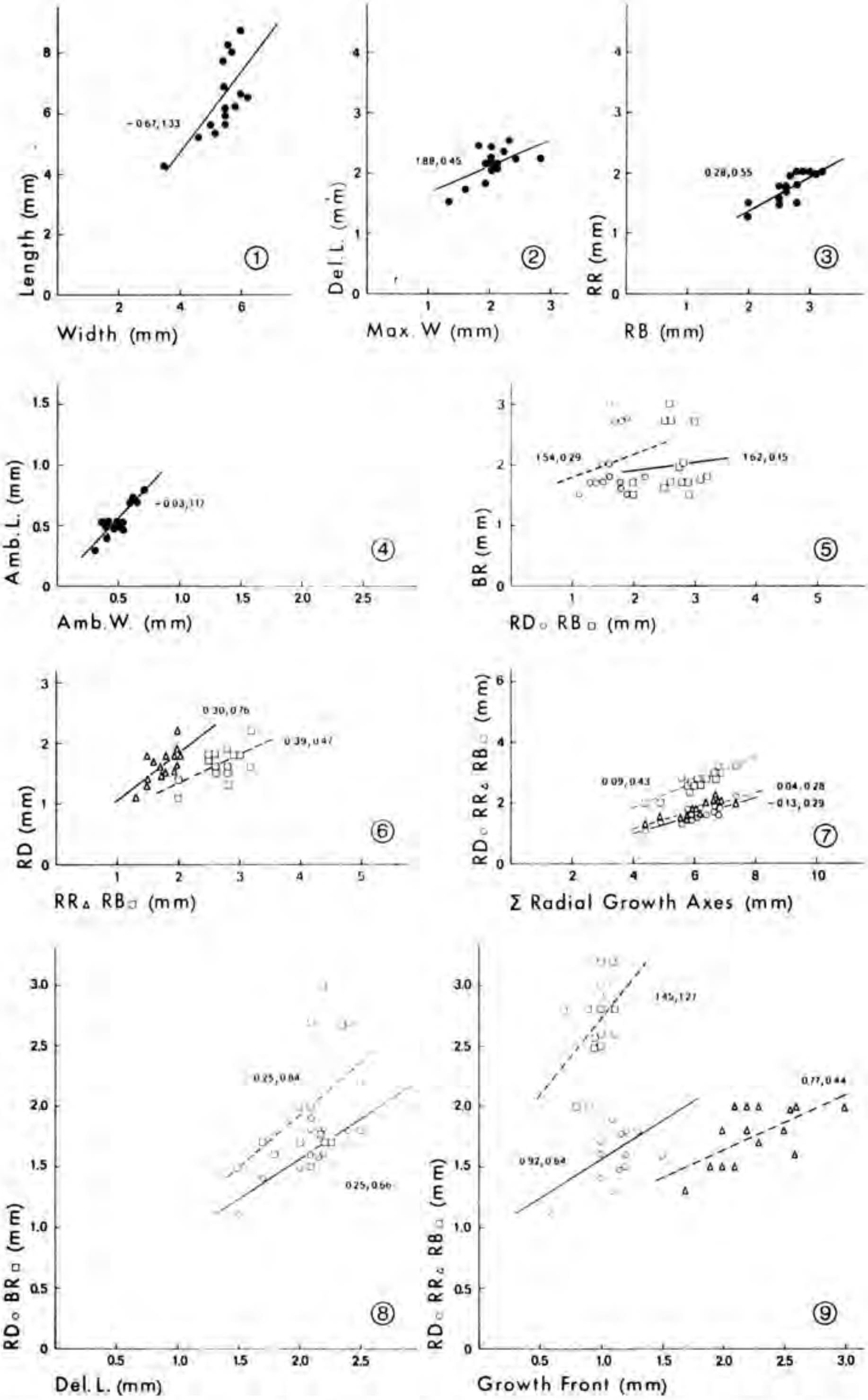
Textfig. 92. *Pterotoblastus gracilis* Wanner, 1924ª. Perm., Noko, Timor. Ontogenetic development based upon 18 specimens. Radial axes unmeasurable due to radial prong (see Pl. XXXII, fig. 9) formed of secondary calcite; therefore, it has been substituted for the radial axes and used as a measure of radial growth in (1), (2) and (6). See textfig. 51 for further explanation.

facets; this type of growth is unusual. Hydrospire slits gradually increase from 1 to 3 per group, developed across the full width of RDF. Their functional length is short.

WANNER (1940) described a single deltoid as belonging to "*Pterotoblastus* sp. no. 2" (Pl. XXXI, fig. 10). The plate alone is larger than any complete specimen of *Pterotoblastus* of any species. It differs from a typical *Pterotoblastus* plate in having a larger DR sector than DD sector. The hydrospire slits are wider than normal and their filled-in adoral ends meet in a zigzag pattern along the deltoid crest, which is also unusual. This can also be seen in *P. ferrugineus*. The slits are not numerous (only 6) so this deltoid may represent a plate of a *Pterotoblastus* sp. similar to *P. ferrugineus*.

The genus *Nannoblastus* differs in form from the typical codasterid because of the greater secondary deposition of calcite on the surfaces of the deltoids. Two species are known. The oldest, *Nannoblastus cuspidatus* (Pl. XXXII, figs. 7, 8; Asselian-Sakmarian), is only known from a single small, incomplete specimen. The basalia are missing; the radials are prominent in lateral view. RB is the dominant axis, 49 percent of radial growth, while RR is 26 percent and RD 25 percent. Relations between radial axes are as in *Nannoblastus pyramidatus* which follows but RD is slightly faster to its front, RR slower to its, and RB faster to its. The deltoid is small, nearly as wide as it is long; the ad- and aboral widths are equal. The deltoid has been built up vertically 1.0 mm. RD and Del.L. grew at an equal rate. The anal deltoids are slightly longer than a regular deltoid; the epideltoid is the larger plate. A facet indicates the former presence of a hypodeltoid. The side plates are missing. The lancet is small; it was partially exposed. Hydrospire structure is unknown.

The younger species of *Nannoblastus*, *N. pyramidatus* (Pl. XXXIII, figs. 1, 2, 5–7; Guadalupian), is represented by well-preserved material which details the ontogenetic development of the species. Thecae are small (less than 10 mm; fig. 93.1); length and width are about equal except for four members of the growth series which have unusually long basals and these segregate themselves and plot differently on measurements of BR (e.g., figs. 93.5, 8). The lower part of the theca is conical to broadly cup-shaped. The deposition of secondary calcite on the deltoids has produced high pinnacles above the oral opening. Some secondary calcite is also deposited over the origin of the radial. The ambulacra are quite restricted. The variation in growth of the basals produced a variety of pelvic forms; the diameter of the stem attachment area is narrow (0.4–0.6 mm). In general, BR has an equal rate to RD and Del.L. and grows more slowly than RB but on occasion may be accelerated relative to both (figs. 93.5, 8). The radial is moderately prominent in lateral view. RB is the major radial axis (fig. 93.7), being between 41 to 50 percent, while RR and RD are virtually equal, being between 26 to 31 percent and 23 to 31 percent respectively. RD grows at an equal rate to RR and is slower to RB;

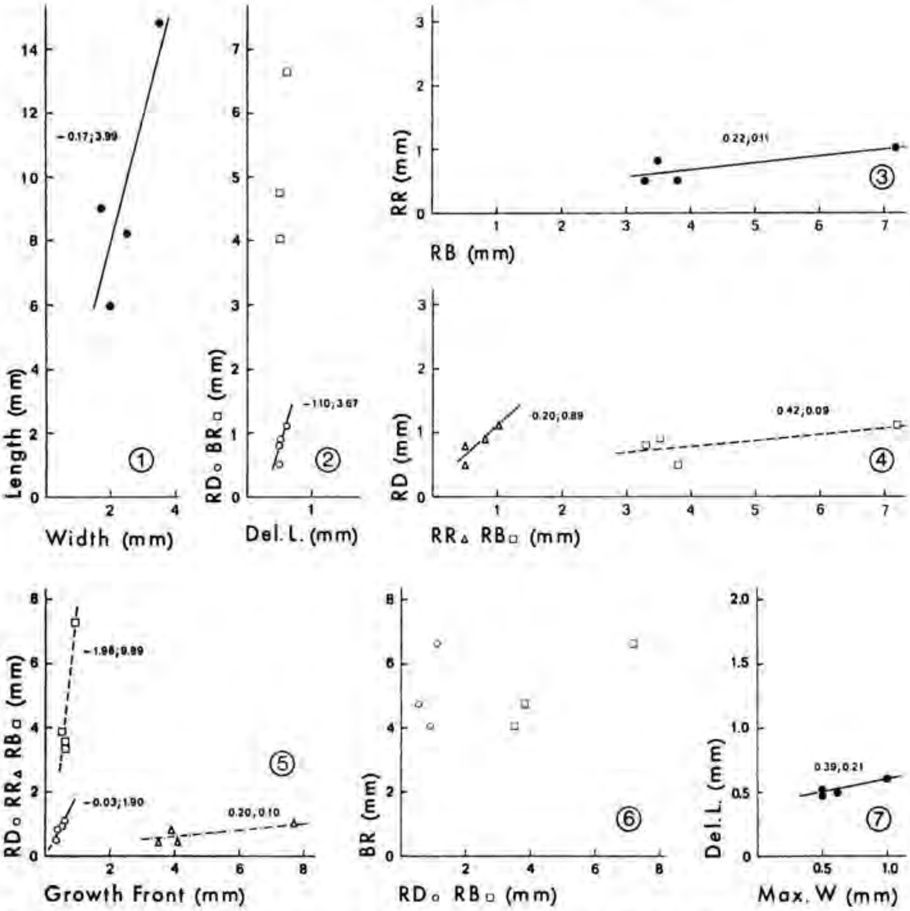


Textfig. 93. *Nannoblastus pyramidatus* Wanner, 1924^b. Perm., Noko, Timor. Ontogenetic development based upon 15 specimens. (2) Maximum width of deltoid is in adoral part of plate. See textfig. 51 for further explanation.

the same is true of RR to RB (figs. 93.3, 6). Within the radial sectors, RB is fast to its front, RD is less so, while RR is slightly slower than its front (fig. 93.9). A small radial lip is developed at the origin. The deltoid is an actively growing plate; apparently most horizontal growth occurred in the DD sector; the greatest width is adoral and is unusual in being equal to Del.L. (fig. 93.2). The width of the adoral edge bordering the oral opening remains constant. The deltoid pinnacle is progressively built upward from 0.8 to 2.7 mm. RD is slower than Del.L. (fig. 93.8). The anal deltoids are usually slightly longer than a regular deltoid. Once formed, there are limited changes in the epideltoid. The adoralmost edge bordering the oral opening remains constant in size; the adoral width expands. The distance from oral center to the adoral edge of the anus is also essentially constant as is anal size. The hypodeltoid is usually as wide as the epideltoid; its upper surface is built upward to form the counterpart to a deltoid pinnacle. The distance from the oral center to the adoral end of the ambulacrum increases very slightly. The ambulacra are quite small, and length and width are equal (fig. 93.4). The number of side plates does not exceed 2 per ambulacral side. No direct observations of the ontogeny of the hydrospire system were possible.

Family CERATOBLASTIDAE

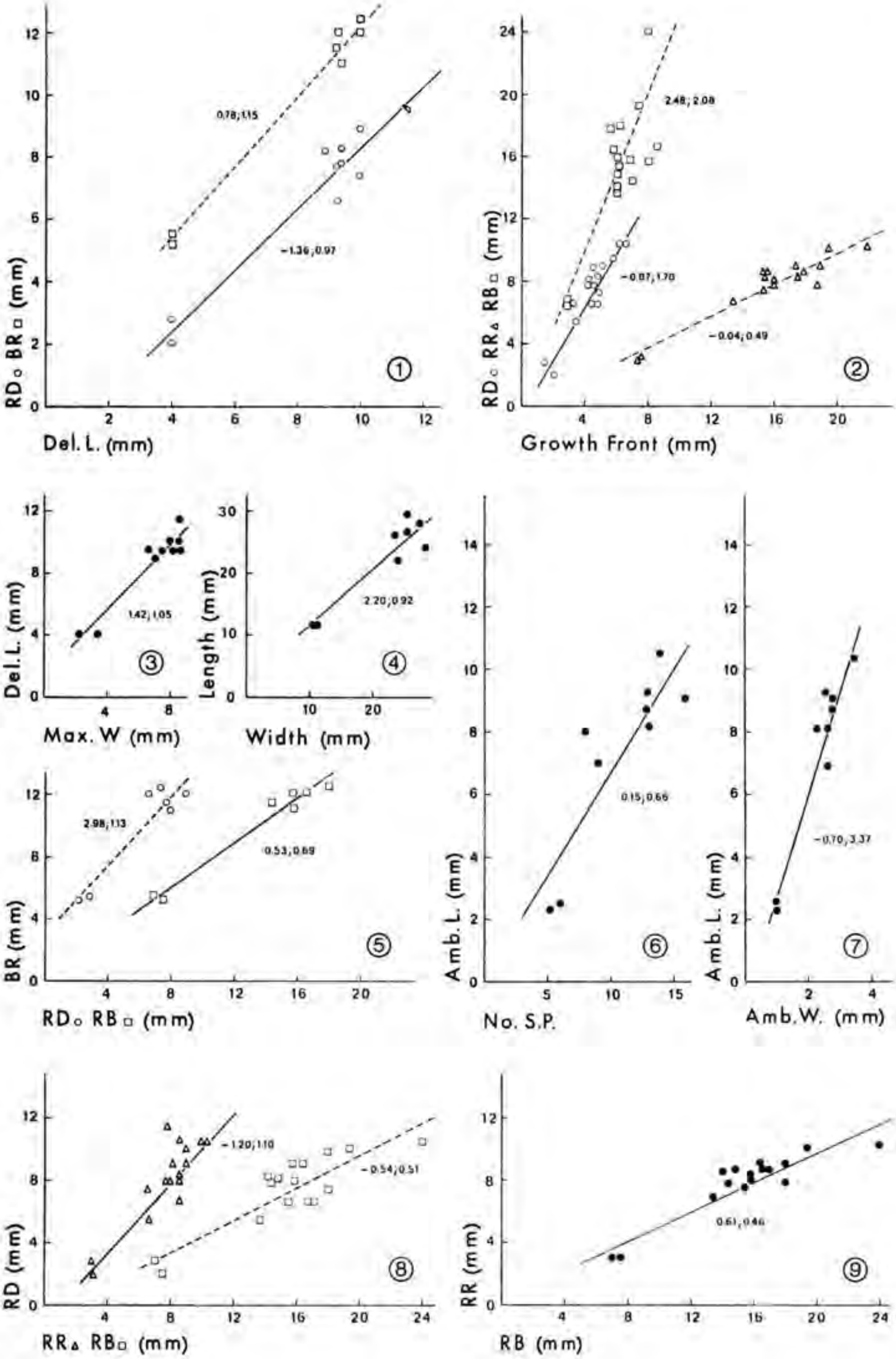
Permian. Ceratoblastus nanus (Pl. XXXII, figs. 5, 11; Guadalupian) is one of the most peculiar of the fissiculates. Its thecal shape is best likened to that of a small, slender pencil, with the ambulacra having a dendritic pattern on the upper, flat surface. The largest one reaches intermediate size; the width is extremely slender (fig. 94.1). The basals form a slender cylinder; preservation did not permit us to determine whether there was a stem attachment area. BR grows at an equal rate to RB; it is much faster than RD and Del.L. (figs. 94.2, 6). The radials are prominent in lateral view. RB reaches its maximum expression within any fissiculate, from 67 to 79 percent of the radial growth. RD is 10 to 17 percent, RR 10 to 15 percent (fig. 96.2). Thus RD and RR grow at nearly an equal rate, while RB is much faster than both (figs. 94.3, 4). Within the radial sectors, RB is extremely fast to its front, RD is somewhat faster than its front, while RR is very slow relative to its front (fig. 94.5). The deltoids are quite small, and their length is equal to or less than the width (fig. 94.7). RD grows faster than Del.L. (fig. 94.2). There is only a single anal deltoid, the epideltoid, which increases in width ontogenetically. The aboral margins of the anus are formed by the radial limbs; anal size is small. The ambulacral structure is quite unconventional and explained further in textfig. 43. The brachiolar facets are arrayed in a ring around the top of the theca and their number increases ontogenetically from 2 to 4. The length of the side food grooves also increases. Conventional hydrospire structures are absent.



Textfig. 94. *Ceratoblastus nanus* Wanner, 1940. Perm., Noko, Timor. Ontogenetic development based upon 4 specimens. (7) Maximum width of deltoid is in adoral part of plate. See textfig. 51 for further explanation.

INCERTAE SEDIS

Permian. The genus *Indoblastus* is represented by two species in the Guadalupian. The first, *I. granulatus* (Pl. XXXII, fig. 2; Pl. XXXIII, fig. 4), has a cup-shaped theca similar in form to that of a *Codaster*. They are a large form, reaching 30 mm in length; the width is usually slightly less than the length (fig. 95.4). The ambulacra are initially confined to the upper surface but later grow down slightly over the thecal edge. The diameter of the stem attachment area on the convex basals ranges from 0.8 to 1.9 mm in the growth series. BR grows more slowly than RB but more rapidly than RD (fig. 95.5); it is also slightly faster than Del.L. (fig. 95.1). The radials are prominent in lateral view. The RB axis is dominant as in the codasterids, being between 47 to 60 percent of radial growth, while RR is 22 to 27 percent and R is 16 to 27 percent. Thus the



Textfig. 95. *Indoblastus granulatus* Wanner, 1924ª. Perm., Basleo region, Timor. Ontogenetic development based upon 16 specimens. (3) Maximum width of deltoid is in adoral part of plate. See textfig. 51 for further explanation.

growth of RD and RR are equal while RB grows rapidly with respect to each (figs. 95.8, 9). Within the radial sectors, RB grows rapidly with respect to its front, RD slightly less so, and RR is slower than its front (fig. 95.2). The deltoid is a simple rhombic plate; it has moderately developed DD sectors but the DR sectors are larger. Its greatest width is adoral but does not equal the length (fig. 95.3). The plate grows outward in all directions, with the consequent reformation of the ambulacral tract along DDF. Del.L. grows faster than RD (fig. 95.1). The two anal deltoids are of about the same length as a regular deltoid. Both the epi- and hypodeltoid are relatively large plates, actively growing, with the consequent aboral displacement of the anus during growth. The anus increases in size to a relatively large dimension. The ambulacra are initially small but later grow down over the edge of the theca. The lancet is not involved in this; aborally the side plates rest directly on the radial. The lancet underlies only slightly more than half the ambulacral length; this is an unusual configuration and growth relationship. As ambulacral length increases, so does the width to a relatively broad dimension (fig. 95.7); new side plates are added at the rate of 3/mm (fig. 95.6). There is only a single hydrospire slit in each regular interarea, immediately adjacent to the ambulacra; the slit is short. None are present in the anal interarea.

The other Guadalupian species of *Indoblastus*, *I. weberi* (Pl. XXXIII, fig. 3), is represented by a single incomplete specimen. The length and width were probably near 20 mm; its outline was rounded laterally. The ambulacra are short and confined to the upper surface. The basals are not well preserved but were large. Exact measurement of the RB axis is not possible but it was obviously very dominant, approaching 69 percent as a minimum, while RR was near 20 percent and RD near 11 percent. RDF is about equal to RD while RRF increased much more rapidly than RR. The deltoids are small and confined to the upper surface. They are similar in shape to *I. granulatus*. They are wider aborally, almost

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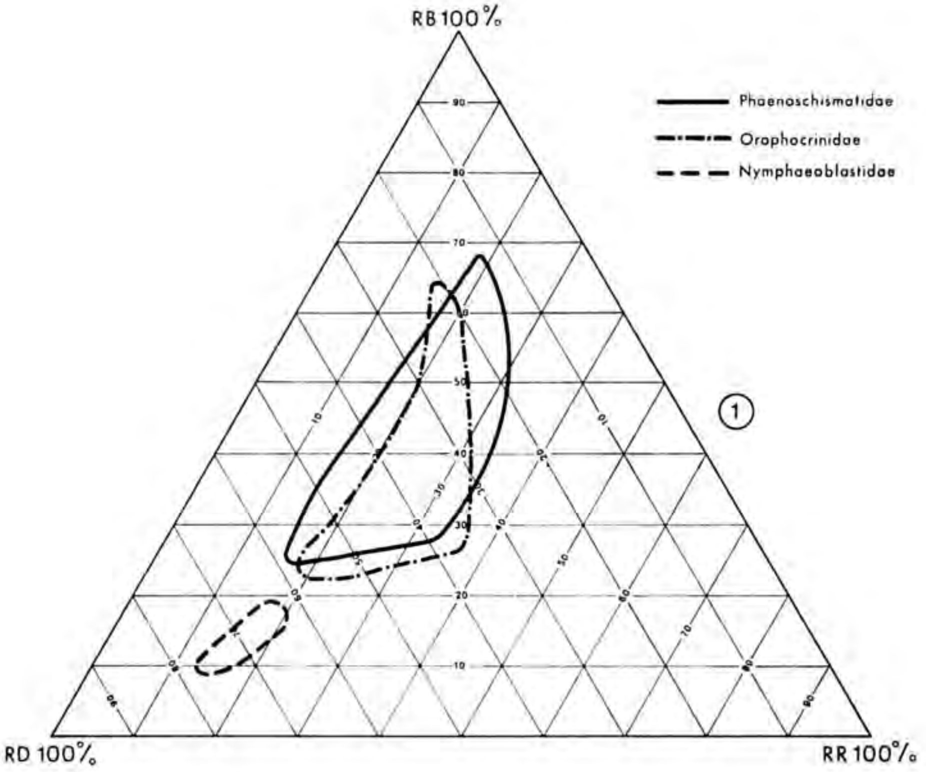
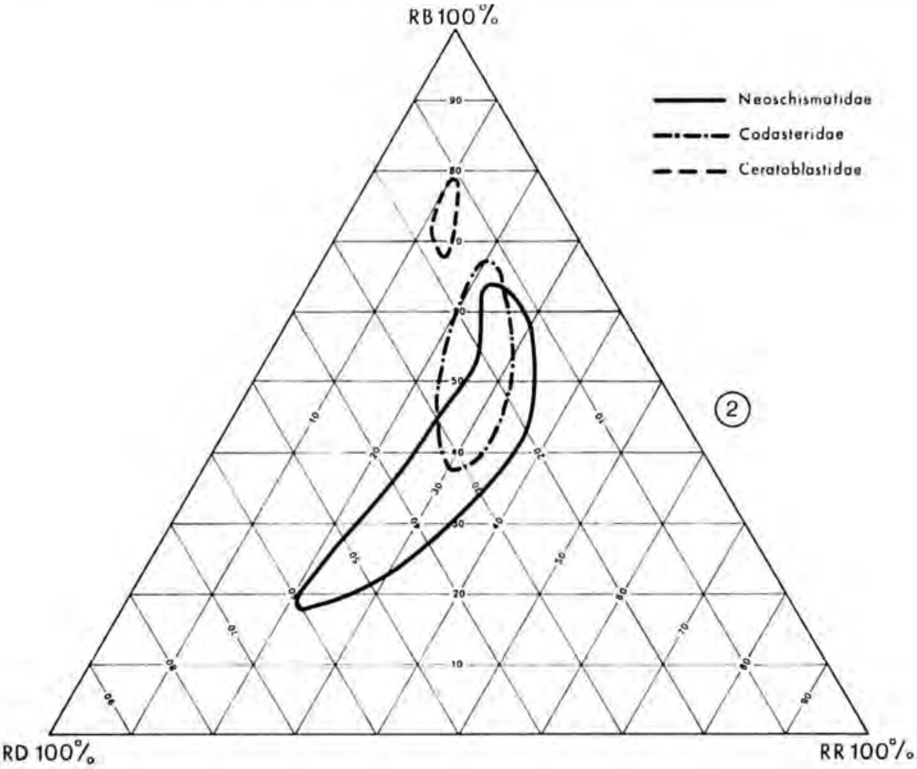
Textfig. 96. (1) Triangular diagram showing relative percentage of radial axes in those fissiculate families which are primarily Silurian through Mississippian in their occurrence. RD, RR, and RB are added to produce a sum for radial growth; each are then divided by the sum to give their relative percentage. Thus, all three are equal in the center of the diagram. Movement toward the lower left from this point indicates an increasing proportion of RD; moving upward indicates an increasing proportion of RB; moving toward the lower right indicates an increasing proportion of RR. The outlined oval, etc. for each family indicates the total region occupied by members of this family but does not indicate the density within the figure. (2) Triangular diagram showing relative percentage of radial axes in those fissiculate families which are primarily Permian in their occurrence. Lower left half region of neoschismatid distribution only occupied by Mississippian members of *Hadroblastus*. See text for further discussion.


RB 100%
RD 100%
RR 100%
Phaenoschismatidae
Orophocrinidae
Nymphaeoblastidae
10
20
30
40
50
60
70
80
90

①


RB 100%
RD 100%
RR 100%
Neoschismatidae
Codasteridae
Ceratoblastidae
10
20
30
40
50
60
70
80
90

②

equaling Del.L. They grew faster than RD. There are two anal deltoids which are longer than a regular deltoid. The anus is relatively large. The short ambulacra (length: 3.5 mm) are confined to the upper surface; new side plates were added at 3/mm. Hydrospire slits are as in *I. granulatus.*

CHAPTER IV

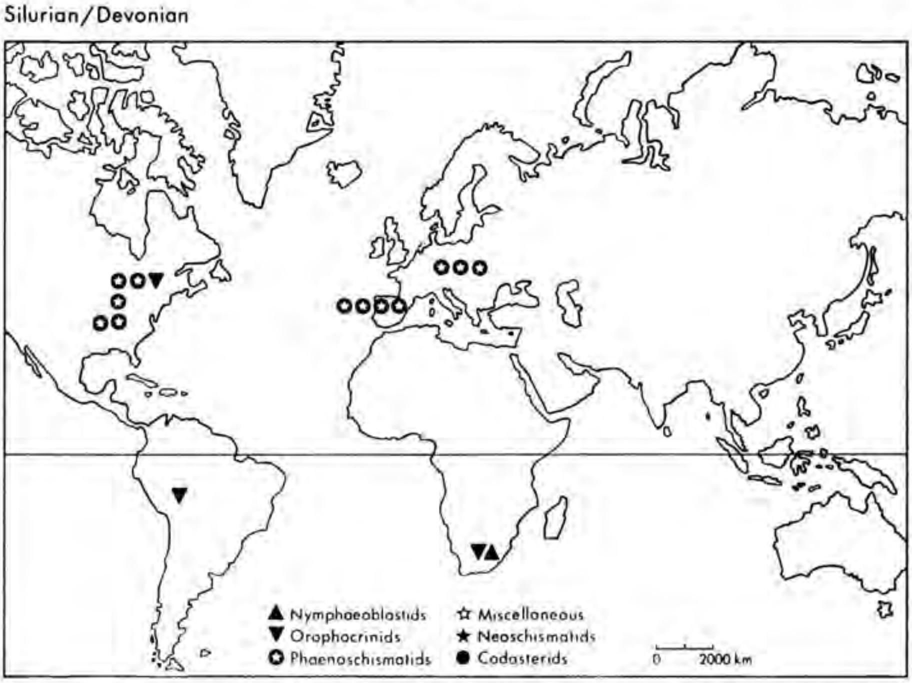
DISTRIBUTION AND PALEOECOLOGY

The fissiculate blastoids range through five geologic periods and have been found on every continent except Antarctica. During the course of this study one or both of us have had the opportunity to visit, study, and collect almost all the fissiculate localities (exceptions are noted). We would like to offer our observations on the sedimentary facies in which the blastoids were found, their relative abundance, and the diversity of the community in which they occur. Some remarks on the latter are derived from the literature referenced as are the stage citations. We do not intend this section to be a complete stratigraphic history of the formations involved, for that is beyond the scope of this study and available to readers in other reports.

DISTRIBUTION

The earliest known blastoids are found in the Silurian Wenlockian Laurel Limestone in Indiana (textfigs. 97, 100). These have been assigned to the spiraculate genus *Troosticrinus* which ranges into the Brownsport Formation (Ludlovian) of Tennessee, Bainbridge Formation of Missouri (Upper Wenlock, Lower Ludlow), and Devonian Bois d'Arc Formation (Gedinnian) of Oklahoma. It is also reported from the Silurian of Ohio, Illinois, and Kentucky. The 40′ Laurel Limestone is immediately succeeded by the thin 3–8′ Waldron Shale (Wenlockian) of Tennessee and Indiana which contains the earliest known fissiculate, *Decaschisma*; it is also known from the uppermost Laurel Ls. The Waldron is a gray calcareous shale with a typical diverse Silurian community. Some twenty other echinoderm genera are known from the Waldron, the most numerous being the crinoid *Eucalyptocrinites*. *Decaschisma* is a rare member of this community, only a few tens of specimens being known, in contrast to well over a thousand *Eucalyptocrinites*. In Indiana the invertebrates of the Waldron are found in patches, intervening areas being barren. The organisms formed small elevations on the sea floor. In Tennessee the large cup-shaped *Eucalyptocrinites* cups have been sedimented in an inverted position. The cups were used as a point of attachment for other stemmed echinoderms. Moderate current activity in a shallow-water environment is suggested for this formation.

The next youngest fissiculate occurrence is *Polydeltoideus enodatus* from the Henryhouse Formation (Early Ludlovian) of Oklahoma. *P. enodatus* is a rare member (between 20–30 specimens known) of a typical diverse



Textfig. 97. Geographic distribution of Silurian and Devonian fissiculates. Each symbol represents a generic occurrence. See text for discussion.

Silurian shelly fauna (brachiopods, ostracods, trilobites, small corals, bryozoa, etc.). The fauna of the Henryhouse Formation is dominated by brachiopods; in the area where *Polydeltoideus* is found, there are abundant specimens of the small crinoid *Pisocrinus*. Trilobites, bryozoa, and solitary corals also occur at this level. STRIMPLE (1963) listed 31 crinoid genera with 45 species from the Henryhouse Formation; most of these were represented by a relatively small number of specimens. The Henryhouse is a silty argillaceous calcilutite. AMSDEN (1960) concluded that the bottom was a mud composed of terrigenous and carbonate sediments, with quiet nonturbulent water, probably deposited in a zone corresponding to the outer neritic or outer sublittoral zone.

The only other known Silurian fissiculate is a single complete specimen of *Polydeltoideus ? plasovae* (plus some basals) from the uppermost part of the Přidoli Formation (Přidoli Stage) of Bohemia. PROKOP (1962) characterized the detrital limestones of the *Scyphocrinites* horizon of the Přidoli as representing shallow seas with strong currents. He called attention to the abundant Pisocrinidae. Our comparison of the Oklahoman and Bohemian occurrences suggests similar environments and a recurrence of similar echinoderm communities. In summary, *Decaschisma* and *Polydeltoideus* occurred in open water, relatively shallow environments with some current activity; they do not occur in any reef facies. They are found on marly or calcareous shale bottoms, in association with shelly faunas and other echinoderm genera.

The only Devonian Gedinnian fissiculate blastoid, *Leptoschisma lorae*, is found in the Birdsong Shale of western Tennesee (textfigs. 97, 100). *Leptoschisma* is a rare form, being known from only 10–15 specimens. The associated shelly fauna is dominated by brachiopods which occur in tremendous profusion in the interbedded limestones and shales. Some of the brachiopods are disarticulated. Moderately shallow-water environments are suggested.

At present we do not know of any fissiculate blastoids from the Siegenian but the Emsian is represented by a diverse fauna in Spain with occurrences in Bohemia as well. The Spanish occurrences are found in northern Spain. On the southern side of the Cantabrian Mountains in the Province of León, they are found in the upper part of the La Vid Fm. (Emsian). The middle part of the formation is a thick clastic unit (hundreds of meters); its upper part consists of interbedded red lenticular bioclastic marly limestones which are transitional into the Santa Lucia Fm. which is a massive carbonate. Here are found the fissiculates *Pleuroschisma verneuili*, *Cryptoschisma schultzii*, *Pentremitidea archiaci* and *P. lusitanica*, and *Caryoblastus ?* sp. *Cryptoschisma schultzii* and *Pentremitidea archiaci* are represented by several hundred specimens; *Pleuroschisma verneuili* by 25–30, *Pentremitidea lusitanica* approximately 10, and *Caryoblastus ?* sp. by one. The associated fauna is quite diverse, consisting of brachiopods, corals, occasional trilobites, bryozoans, stromatoporoids, and many crinoid genera. Here again we apparently are dealing with open, moderately shallow-water environments. To the north in the province of Asturias, *Pentremitidea pailleti* is found in Ferroñes where it occurred in the Ferroñes Fm. (Emsian); hundreds of specimens are known. *Cryptoschisma schultzii* and *Pentremitidea archiaci* are also known from the Ferroñes Fm. in Ferroñes but are rather uncommon. Specimens of these three forms have not been found recently at Ferroñes and we can offer no personal observations on their occurrence. Elsewhere in Asturias, *Pleuroschisma verneuili* is found in the Arnao Limestone at Arnao (several tens of specimens) and with *Pentremitidea lusitanica* (10–20) at Fenolleda (Arnao Fm.). At Arnao, the Arnao Ls. is a red encrinal limestone with some marly interbeds; the associated fauna includes specimens of the enormous camerate crinoid *Triblyocrinus flatheanus*. At Fenolleda the Arnao Fm. consists of thinly interbedded dark shales and limestones. This latter occurrence was characterized by higher rates of clastic sedimentation.

The Bohemian occurrences, *Caryoblastus bohemicus* (over 40) and an unnamed phaenoschismatid (1), are from the Slivenec Limestones (Pragian Stage). This stage was equated with the Emsian by BERRY, 1970, and with the Upper Siegenian and Lower Emsian by BOUCOT, et al., 1969. The Lower Devonian of Bohemia is characterized by a great variety of carbonate facies. The geologic setting and occurrence of the fissiculates was discussed by Prokop in BREIMER, MACURDA, and PROKOP, 1968. The fissiculates occurred with a diverse group of other echinoderms including the microcrinoid *Pygmaeocrinus kettneri*. It was concluded that the bottom was fairly solid and shallow, and characterized by mud and carbonate deposition.

The Spanish and Bohemian occurrences would belong to the Rhenish-Bohemian Provinces of BOUCOT, et al., 1969. In summary, the environments of the Gedinnian and Emsian occurrences discussed thus far appear similar to those of the Silurian genera discussed above.

The first record of fissiculate blastoids in the Southern Hemisphere is from the Bokkeveld Series (hundreds of meters) in the Republic of South Africa. Two genera, *Pachyblastus dicki* (10–12 specimens) and *Brachyschisma ? oostheizeni* (5 specimens) occur in greenish siltstones, along with brachiopods and trilobites. Coelenterates and bryozoa are conspicuous in their absence where the blastoids are found. Other echinoderms such as carpoids, asterozoa, and a few crinoids have been found in the same vertical sequence as some of the blastoids. There are no obvious sedimentary structures; the clastic bottom apparently precluded small planktonic feeders (coelenterates and bryozoans), suggesting a more turbid environment than those discussed previously. VILLIERS (1967) reviewed the history of the Bokkeveld and noted the north and northwestern sediment source area. The Bokkeveld Series is considered Lower Devonian; BOUCOT et al., 1969, in their review of early Devonian brachiopod zoogeography, recognized only early Emsian deposits in South Africa, belonging to the Malvinokaffric Province.

Two blastoid radials were described and illustrated by KNOD (1908) from the Devonian of Bolivia. Knod assigned them to *Codaster* (= *Heteroschisma*) aff. *pyramidatus* Shumard. KOZLOWSKI (1923, p. 109) listed the horizon as the Sicasica Fm. We have not seen the specimens in question, nor visited the locality, but based upon Knod's description and illustrations, the radials are somewhat pointed and have a sharp junction between the RD and RR sectors. This shape is more suggestive of a *Brachyschisma* than a *Heteroschisma*. DAVILA & RODRIGUEZ (1967) gave the age of the Sicasica Fm. as Eifelian – Givetian, making the Bolivian occurrence younger than the South African occurrence of *Brachyschisma?*, but the same age as the *Brachyschisma* of New York. The specimens were found as a cast and mold in a sandy calcarenite.

In North America Siegenian and Emsian fissiculate blastoids are lacking, but a rich and varied fauna begins with the Eifelian and extends through the Givetian. Two forms, *Brachyschisma corrugatum* and *Heteroschisma alternatum*, are found in the Eifelian Onondaga Ls. of New York, which is characterized by a large coral fauna. OLIVER (1966) has called attention to small bioherms or patch reefs in the Onondaga; *Brachyschisma* occurs on the edges of these. *Heteroschisma alternatum* is found in a fine-grained bioclastic limestone associated with echinoderm debris. Approximately

40 specimens of the former are known, 20 of the latter. *Heteroschisma alternatum* also occurs in the correlative Jeffersonville Ls. of Indiana and Kentucky, and the Columbus Ls. of Ohio. Approximately 200 specimens are known from the former area where they occur in the *Paraspirifer acuminatus* zone. The lithology of this zone is a grain-supported biomicrite and biosparite; according to PERKINS (1963), it represents a transgressive phase of the Jeffersonville. Brachiopods, bryozoans, solitary horn corals, and echinoderm debris, including that of several large camerate genera, constitute the dominant biotic material. An open marine environment with some current activity is suggested. We have no firsthand experience with the Columbus Ls. in Ohio; several tens of specimens are known from here.

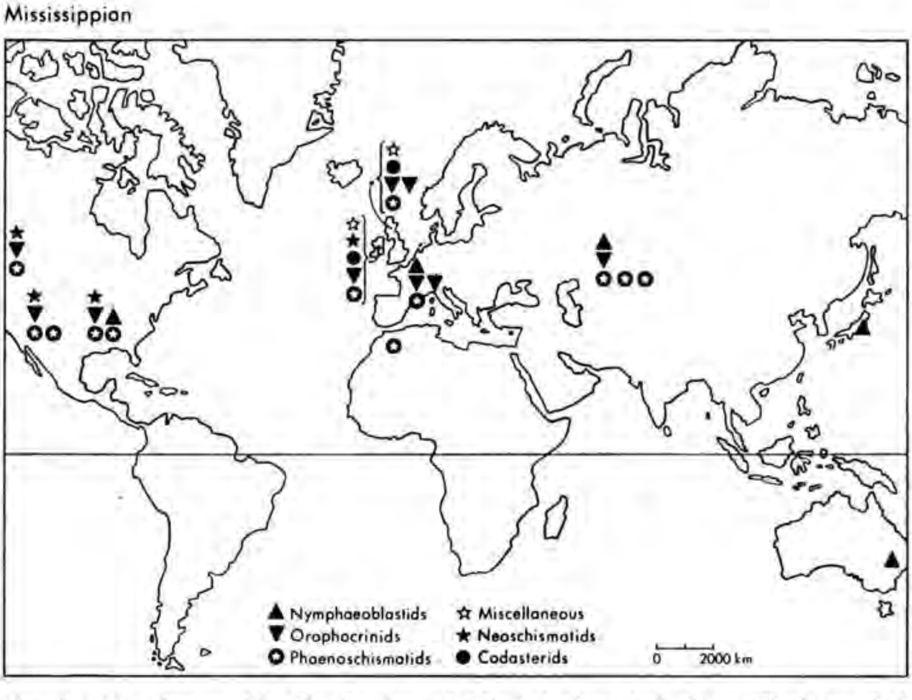
In New York, the Onondaga Ls. is succeeded by a thick complex series of interbedded limestones and calcareous shales which are assigned to Cazenovian and Tioughniagan stages of the North American standard; part of the former and all of the latter are equated to the Givetian. *Pleuroschisma lycorias*, an earlier species of which occurred in the Emsian of Spain, is found in the Centerfield Ls., Tichenor Ls., and Kashong Shale Mb. of the Moscow Shale, which belong to the Tioughniagan stage in New York. It preferred calcareous shales; between 10 and 20 specimens are known. *P. lycorias* is also known from the Hungry Hollow Fm. (Givetian) of Ontario with *Heteroschisma canadense* where they occur in a 3 ft. layer packed with horn corals. Small brachiopods, bryozoans, and many echinoderm genera are also known. This was a shallow-water, well-aerated environment. Further west in Michigan in the Givetian Traverse Group, are found the species *Heteroschisma alatum* (Potter Farm Fm., about 20 specimens) and *Heteroschisma gracile* (Petoskey Fm.?; Thunder Bay Fm., several hundred specimens). The former occurs with a typical shelly fauna in a calcareous shale; the latter is found in a greenish siltstone (Thunder Bay Fm.) with some bryozoans and brachiopods and other echinoderm genera. Open marine environments are suggested; *H. gracile* could exist in a region of clastic sedimentation. To the south, *Heteroschisma* sp. are found in the North Vernon Fm. (approximately 20 specimens) of Kentucky and Ohio (which is unconformably separated from the underlying Jeffersonville) and the Lingle Fm. (approximately ten specimens) of Illinois. These are Givetian and the lithologies are similar to the Jeffersonville occurrence, suggesting similar environments. Further west, *Heteroschisma subtruncatum* occurs in the Givetian Cedar Valley Ls. of Iowa, which is characterized by a diverse shelly fauna with many corals and other echinoderms. *H. subtruncatum* is quite rare, being represented by 5–6 specimens.

BARNES (1944) reported *Codaster* (=*Heteroschisma*) *gracilis* from the Middle Devonian of Missouri and REIMANN (1935) reported *Codaster* (=*Heteroschisma*) cf. *canadensis* from the Tichenor Ls. (Givetian) of New York, but we have not been able to verify these occurrences by inspection of any material.

In summary, three fissiculate genera are found in the Middle Devonian of north central and northeastern parts of the United States and Ontario. *Brachyschisma* (Eifelian) is associated with shallow-water patch reefs. *Heteroschisma* (Eifelian-Givetian) is wide ranging geographically, being found in shallow to moderately deep water, usually associated with shelly faunas with other echinoderms and corals, but occasionally in more clastic facies. *Pleuroschisma* (Givetian) occurs in fine-grained clastics and shallow-water environments, the latter with a diverse shelly fauna.

The Upper Devonian (Frasnian and Famennian Stages) are barren of fissiculate blastoids. The paucity of any blastoids from this interval is not understood; only two or three complete specimens of a spiraculate *(Hyperoblastus)* are known from Frasnian deposits in the United States; otherwise, blastoids are unknown from this interval on a worldwide scale.

The advent of the Mississippian saw the introduction of several new fissiculate genera, which are very widespread; no holdovers occur from the Devonian (textfigs. 98, 100). In North America, the earliest species of *Phaenoblastus (P. pecki)*, *Phaenoschisma (P. chouteaui)*, and *Hadroblastus (H. blairi)* are found in the Chouteau Ls. of Missouri. Only a few specimens of each are known. The Chouteau is usually a fine-grained micrite; the associated fauna includes brachiopods and other echinoderms. The fine-grained micrite and general lack of sedimentary structures suggest a nonturbulent environment. The Chouteau Ls. (Tournaisian) has been



Textfig. 98. Geographic distribution of Mississippian fissiculates. Each symbol represents a generic occurrence. See text for discussion.

equated to the K or Z zones of the British standard, and to the Cu IIa of Germany.

The problematic *Pentremoblastus conicus* (15–20) occurs in the fine-grained limestones of the McCraney Fm., and *Orophocrinus gracilis* (4) occurs in the clastic Northview Fm. in Missouri. These formations are approximately the same age as the Chouteau (Tournaisian), the former being slightly older. The first species of *Orophocrinus* (*O. conicus*, approximately 300 specimens) appears to the north in Iowa in the Hampton Fm. at approximately the same time. It was associated with other echinoderms in a shallow, moderately high energy environment.

The correlation of the Mississippian of the United States and the Lower Carboniferous of Europe has been uncertain until the conodont studies of the 1960's, primarily those of COLLINSON et al., 1962, and RHODES et al., 1969. Transatlantic age comparisons of the formations are based upon these works.

The Burlington Ls. of Iowa and Missouri is separated by a time gap from the underlying Chouteau and Hampton formations. It contains a diverse fauna of fissiculates: *Hadroblastus* (*H. whitei*, 25–30), *Orophocrinus* (*O. catactus*, 6–7; *O. gracilis*, 8–10; *O. stelliformis*, over 500), and *Phaenoschisma* (*P. gracillimum*, 6–8; *P. laeviculum*, 10–15). This formation is an encrinal limestone populated by over 70 echinoderm genera, and appears to represent a moderately high energy, extensive shallow-water bank deposits. The Burlington (Tournaisian) is correlated with the lower and upper parts of the C_1 subzone of England and upper Cu IIb–c and lowest Cu IId of Germany.

There is a biohermal facies developed in New Mexico, Oklahoma, and Arkansas which is equal to or slightly older than the Burlington Fm. Here again we find the same fissiculate genera (St. Joe Ls., Ark. and Okla.): *Hadroblastus whitei* (6–8), *Phaenoschisma laeviculum* (3), *Orophocrinus catactus* (3–4); Lake Valley Fm., New Mexico: *Hadroblastus convexus* (5), *Orophocrinus catactus* (6–7). The bioherms developed as local elevations on the sea floor and the diverse echinoderm community appears to have grown as a halo around the bioherms. In New Mexico, *Hadroblastus* and *Phaenoschisma* sp. also occur in a darker, probably deeper-water limestone. Further west in New Mexico in a nonbiohermal phase of the Lake Valley Fm., *H. convexus* (20–30), *Phaenoschisma conicum* (10), and an undescribed phaenoschismatid, UA (10), are found. Thousands of camerate crinoids and brachiopods dominate this fauna. *Orophocrinus saltensis* occurs in abundance locally (several hundreds) in a slightly muddy, fine-grained micritic to coarse-grained crinoidal phase of the Redwall Ls. in Arizona. This occurrence is approximately equivalent to the Burlington Ls. in age (Tournaisian). An undescribed phaenoschismatid genus (100+), *Hadroblastus* sp. (1), and *Orophocrinus* sp. (1?) are found in the Lower Mississippian of Montana. The undescribed phaenoschismatid occurs in the lower part of the Lodgepole Fm. in a micritic muddy limestone. A few have parts of the stem and oral cover plates attached. The associated fauna includes undistorted, almost complete fenestrate bryozoa in an upright position, brachiopods, and a few mollusks. This genus could apparently survive on a muddy bottom with fine-grained sediments as the occurrence is a biocoenose. We have no experience with the other two Montana occurrences.

In summary, the Mississippian fissiculates from the United States discussed thus far, appear to have inhabited several environments, ranging from the more shallow, turbulent Burlington type to the quieter water of the Chouteau to the halo type occurrence on bioherms. Some species occur in more than one environment. The associated faunas were usually dominated by camerate crinoids, plus brachiopods and fenestrate bryozoans.

In contrast to the above is the occurrence of *Hadroblastus kentuckyensis* and *Xenoblastus decussatus* in the New Providence Fm. of Indiana and Kentucky. These deposits are clastic, representing part of the Borden delta. The age is equal to or slightly younger than the Burlington (Tournaisian).

One of the oldest fissiculate occurrences in Western Europe is represented by *Katoblastus konincki* (7–8), *K. pūzos* (7–8), *Orophocrinus orbignyanus* (6–8), *Phaenoblastus caryophyllatus* (25–30), and *Xenoblastus* sp. (1), from the Tournaisian of Tournai, Belgium. Exact locality data is sketchy; that available was reviewed by MACURDA (1967^a). It was suggested that they came from strata numbered Tn 2a, Tn 3a or 3b in the Belgian sequence. In the British sequence these beds range from uppermost K, through Z to the lower part of the C_1 subzone of England. It thus corresponds with the interval containing the Chouteau to Burlington in the United States. MACURDA (1967^a) suggested the environment of the fissiculates at Tournai was probably fairly shallow water with a diverse community.

Orophocrinus is the only fissiculate blastoid genus from Tournai to be widely distributed elsewhere. Its occurrence in England and Ireland was detailed by MACURDA (1965^b). *O. celticus* (2), *O. orbignyanus* (2), *O. pentangularis* (15–20), *O. praelongus* (7–8), and *O. verus* (10–12) were recognized. They are most commonly associated with bioherms or reef knolls, although *O. pentangularis* is also found in black interbedded calcareous shales and limestones, part of an extensive shelly fauna containing other echinoderm genera. *Orophocrinus* starts in the Tournaisian; one species may range as high as the D zone.

Phaenoschisma acutum is another fissiculate from the British Isles. It is associated with reef knolls near Clitheroe, England (8–10), Dublin, Ireland (3), and Co. Fermanagh, No. Ireland (1). Another fissiculate, *Hadroblastus* sp.?, is found at the Dublin occurrence. The Clitheroe occurrences are C_2S_1, the Dublin C_2S_1, and the Fermanagh D, (possibly D_2).

Acentrotremites ellipticus is a rare form (3–4) from the Lower Carboniferous of England and Wales. According to PHILLIPS (1936), it occurs in the Middle Dibunophyllum Zone in Somerset and Kidwelly, Carmenthenshire.

The other Lower Carboniferous fissiculate species from northwestern Europe are *Astrocrinus tetragonus* (10–15) and *Codaster acutus* (350–400), which occur in the Middle Ls. in Yorkshire. Their age is D_2 in the English succession (Visean), Cu IIIc in the German. JOYSEY (1955) referred to the Grassington occurrence of *Codaster* as being associated with a crinoid-bank limestone, which was elevated a few feet above the sea floor. Here it occurs in profusion on one sloping bedding plane; it is almost unknown elsewhere in the Grassington occurrence. *Astrocrinus* is found further west at the Malham occurrence in a gray bioclastic limestone. In Ireland the two forms are found at Kilkenney: *C. acutus* (12–25), *A. tetragonus* (6) in a black limestone with occasional shale interbeds (Visean). *Astrocrinus tetragonus* is also known from a Visean D_1 occurrence in Co. Kerry, Western Ireland, where it occurs in a black limestone containing fragmental debris, apparently derived from a shallow-reef knoll. *Astrocrinus tetragonus* (several score) and "*Phaenoschisma*" *benniei* (6–7) occur in some calcareous shales and limestones in Scotland which belong to the D zone (Visean). Microcrinoids are also abundant. The sediments are shallow-water deposits, being immediately succeeded vertically in one locality by a cross-bedded beach deposit.

In summary, the Lower Carboniferous occurrences in the British Isles are often associated with biohermal or reef knoll development, but are also found in limestones with some calcareous shales. The environments probably varied in depth from near-shore to a deeper-shelf environment.

In the Lower Carboniferous (Tournaisian C_1, and Visean) of Kazachstan, USSR, the rare but widespread *Nymphaeoblastus miljukovi* (4–5) is found. We do not have firsthand knowledge of the field occurrence but the associated matrix is clastic. The form occurs in Central Asia and in Japan. The latter (6) occur as molds in tuff from the Kitakami Massif on Honshu; they are Tournaisian (C_1) in age. The only field occurrence of *Nymphaeoblastus* which we have studied is that of *N. bancrofti* from the uppermost Tellebang Fm. near Monto, Queensland in Australia. It is a rare (10–15) fossil, known only from one hillslope where it occurs as molds and casts in a gray, fine-grained siltstone. It is associated with a large brachiopod fauna. MCKELLAR (1964) suggested its age as Lower Visean. The type of sediments in which *Nymphaeoblastus* occurs suggests that it was adapted to an environment of clastic sedimentation; we do not know the depth at which it lived.

The most diverse Namurian fauna (E_1 subzone) is that from N. Kazachstan in the USSR where *Mastoblastus ornatus* (25), *Kazachstanoblastus carinatus* (6–10), *Dolichoblastus shimanski* (1), and "*Phaenoschisma*" *rossica* (1) are found. These occur in a dense, fine-grained limestone which is crammed with cephalopods (mostly nautiloids, but also goniatites), respresenting several tens of species. The echinoderms are the second most common element. Corals, bryozoans, gastropods, pelecypods, and crinoids also occur. We have not visited the locality; Arendt (in ARENDT, BREIMER, & MACURDA, 1968) concluded that there had been little transportation of the material and it occurred on a well-aerated bottom. So many species of cephalopods suggest to us a near-shore environment similar to what we have seen in the Lower Pennsylvanian of Arkansas, where *Pentremites* is found in strand-line bar deposits with many goniatites. The close association of so many cephalopods with blastoids is very unusual.

A phaenoschismatid *(Phaenoschisma ? saharae)* occurs in the Upper Visean and Lower Namurian of Western Algeria. The associated matrix is a crinoidal limestone; we have not visited the localities.

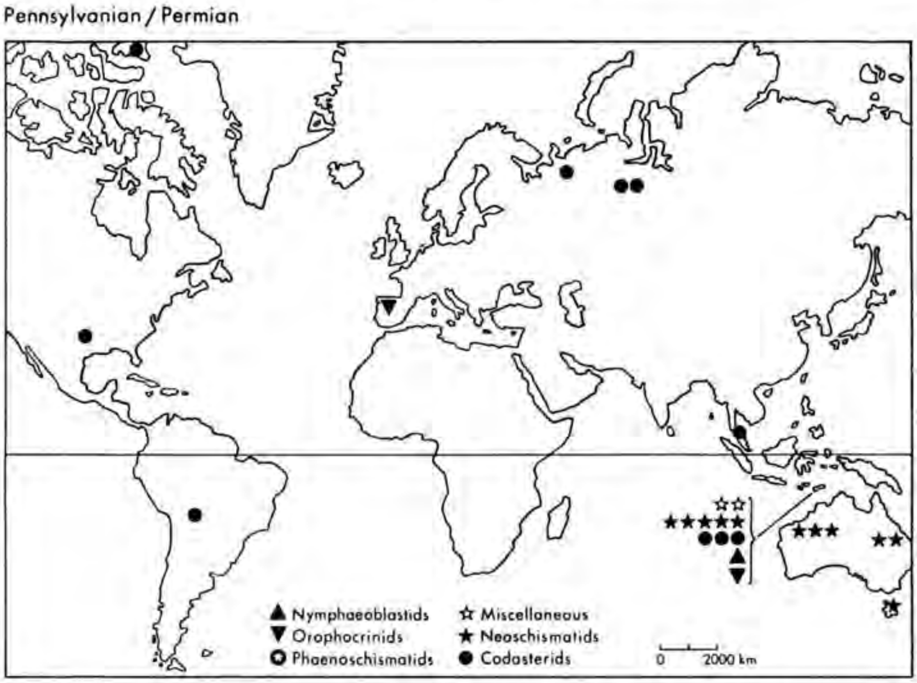
In Northern Spain at Rabanal de los Caballeros in the Rabanal Ls. is found the fissiculate *Pentablastus supracarbonicus* (30–35) of Upper Namurian age. It occurs in massive, black, somewhat lenticular limestones with black shale interbeds. The associated fauna of fusulinids, brachiopods, solitary corals, with some gastropods and crinoids, again suggests an open-shelf environment.

The Mississippian (and its equivalents elsewhere) is represented by diverse fissiculate faunas in North America, Europe, and to a lesser extent in Asia and Australia during the Tournaisian and the Visean. Only three Namurian occurrences are known. The spiraculates also underwent a decline in diversity and during the Pennsylvanian (and its equivalents elsewhere). During this 35–40 million years, blastoids are almost unknown on a worldwide scale.

The first species of the cosmopolitan genus *Angioblastus* in the Pennsylvanian *(A. ellesmerensis)* is found on Ellesmere Island in the Canadian Arctic (textfigs. 99, 100). According to Nassichuk (personal communication) the horizon is Atokan in age (=approximately Upper Bashkirian). Three or four other specimens of *Angioblastus ellesmerensis* also occur elsewhere in the Atokan of Ellesmere in a black crystalline limestone along with some inadunate crinoids. We cannot comment personally on the paleoecology of these occurrences.

The next youngest species of *Angioblastus* (*A. dotti*, 7–8 specimens, plus many scattered isolated plates), occurs in the Hogshooter Fm. at Ramona, Oklahoma. This occurrence is in the Missourian stage of the United States, approximately equal to the Lower Gzhelian of the USSR. The associated fauna includes mollusks, brachiopods, bryozoans, and algal fragments. According to CRONOBLE & MANKIN (1965), there are reefs built up laterally, dominated by algae and auloporoid corals. The rapid variations in facies suggest a well-aerated, moderate to high-energy, shallow-water environment. Thus, *Angioblastus dotti* and *A. ellesmerensis* are the only record of fissiculate blastoids for 35–40 millions of years, the total time span for the Pennsylvanian (Upper Carboniferous).

The only Permian fissiculate occurrence in the western hemisphere is



Textfig. 99. Geographic distribution of Pennsylvanian and Permian fissiculates. Each symbol represents a generic occurrence. See text for discussion.

that of *Angioblastus boliviensis* (1) in the marine Lower Permian near Zudanez, Bolivia (textfigs. 99, 100). Stehli (personal communication) suggests a Wolfcampian (Sakmarian) age. Some crinoids occur with it.

In the Lower Permian of the northern Ural Mts., USSR, several fissiculate species are found: *Angioblastus miloradovitchi* (1), *A. wanneri* (hundreds), *Tympanoblastus elongatus* (1), and *T. pousirewskii* (2). As with the South American occurrence, we have no firsthand experience. The enclosing sediment for *Angioblastus wanneri* is a marl. Goniatites are very rare to absent in this area (Furnish, personal communication, 1970).

The most extensive development of Permian fissiculates, 13 genera, occurs in SE Asia (Indonesian Timor, 12 genera) and Australia (4). The oldest occurrences in Timor are those at Somohole (Sakmarian) where *Anthoblastus brouweri* (1), *Nannoblastus cuspidatus* (1), and *Sphaeroschisma somoholense* (1) were found. The Permian stratigraphy of Timor must be deduced by a comparison of the faunas with other parts of the world for the Permian deposits are all allochthonous, occurring as isolated blocks in a Tertiary melange, which apparently came from the north. At Basleo, one of the principal occurrences, one finds Permian and Triassic blocks intermixed in stream beds. The Permian fossils weather from the blocks and occur as free specimens on a hillside. Thus the long list of localities each represent the fossils obtained from a separate block. Reconstruction of a detailed paleoecology is impossible. The environment, however, was favorable to the development of a diverse fauna of echinoderms, brachiopods, and cephalopods; other groups are found but are less common. The coelenterates and bryozoans seem to be relatively rare. The sediments which enclose the echinoderms often have a high percentage of volcanic material.

The Somohole occurrences are on the western end of the Island of Timor. About 150 km farther east, near the village of Basleo, is the principal collecting area for the Permian. Here, tens of thousands of Permian fossils have been collected from the allochthonous blocks over an area about 15 km long by 7–8 km wide. One species of *Timoroblastus*, *T. weiensis* (1), and *Pterotobastus*, *P. ferrugineus* (1), from Tai Wei occur in an area thought to be Upper Artinskian; the other occurrences near Basleo are generally regarded as lower Upper Permian (Guadalupian, Wordian) and thus the youngest known fissiculates. Here are found *Angioblastus variabilis* (several score), *Anthoblastus stelliformis* (10), *Ceratoblastus nanus* (4), *Dipteroblastus permicus* (1), *Indoblastus granulatus* (20–25), *Nannoblastus pyramidatus* (20–30), *Neoschisma timorense* (1), *Notoblastus oyensi* (1), *Pterotoblastus brevialatus* (several score), *P. decemcostis* (1?), *P. gracilis* (250–300), *Thaumatoblastus longiramus* (20–30), and *Timoroblastus coronatus* (several hundreds). *T. coronatus* is also found at Sebot, near Kapan. *Neoschisma verrucosum* (1) also occurs near Kapan (Bitauni: Upper Artinskian). *Indoblastus weberi* occurs at Hatu Dame in the Ramelau Mts., Portuguese Timor.

Some of the species found in Timor also occur in other areas. One example is *Pterotoblastus gracilis* (2), found in Thailand in a limestone block at the base of a seacliff with a rich brachiopod fauna.

The Permian of Australia contains several blastoid faunas which contain fissiculate blastoids. The oldest of these is the Callytharra Fm., Carnarvon Basin, W. Australia, (Upper Sakmarian): *Neoschisma australe* (several) and *Notoblastus stellaris* (several). The Callytharra is a crinoidal marlstone where the blastoids are found in association with crinoids and a rich brachiopod and bryozoan fauna. The disarticulated nature of most of the material and its abundance suggests a shallow, well-aerated environment. *Thaumatoblastus longiramus* itself is found in Australia, in the Noonkahbah Fm. (2–4 fragments) of the Fitzroy Basin and Coyrie Fm. (8–10 fragments) of the Carnarvon Basin of NW Australia (Upper Artinskian) and Berriedale Ls. (4–6 fragments) of Tasmania (Artinskian). We do not have firsthand experience with the first two locality; the enclosing matrix of one is a crinoidal marl. The Tasmanian occurrence is a silty, fine-grained limestone with small glacial erratics.

The type species of *Notoblastus*, *N. brevispinus* (1) is found in a silty limestone in the Branxton Fm. (Artinskian) of New South Wales. The exposure is a small isolated bedding plane adjacent to a stream and, except for a few other scattered brachiopods, little inference about paleoecology is possible.

To the north, near Rockhampton, Queensland, is found one of the giants of the fissiculates, *Austroblastus whitehousei* (several), accompanied by *Notoblastus cornutus* (several). The specimens occur as partially or wholly disarticulated molds and casts in a noncalcareous siltstone assigned to the Berserker Beds (Artinskian). A few brachiopods and bryozoans also occur. The enclosing matrix is rather featureless and does not show any obvious sedimentary structures.

The fragmentary remains of a neoschismatid have been found in the calcareous sediments of the U. Permian Oxtrack Fm. of the Bowen Basin, Queensland. Large numbers of brachiopods dominate the fauna.

In summary, it can be seen that *Angioblastus* was the most widely distributed Upper Paleozoic fissiculate, appearing in the Pennsylvanian of North America and the Permian of South America, the USSR and southeast Asia. It is found in a variety of matrices. Most other genera are endemic to a small area, although *Neoschisma*, *Notoblastus*, *Pterotoblastus*, and *Thaumatoblastus* occur in more than one area. Timor blastoids could apparently inhabit areas subject to volcanic ash falls. Some Australian forms could cope with clastics, and *Thaumatoblastus* appears to have even been able to penetrate into cold water.

SUMMARY OF GEOGRAPHIC DISTRIBUTION

The preceding discussion demonstrates that there is indeed a geographic pattern to the occurrence of the fissiculate blastoids (textfigs. 97–99). They arose in the Silurian in the Atlantic Basin, where they are represented by the phaenoschismatids. This family persisted until the Upper Mississippian, the last representative being found in Kazachstan. The orophocrinids appear to have arisen in the Devonian of North America (and South America and South Africa?), and developed into full flower in the Mississippian of the Atlantic Basin from western North America to the Urals; in the Permian they are found only on Timor. The rare nymphaeoblastids arose in South Africa in the Devonian, are found in clastic facies in eastern North America, Belgium, the Ural Mts., Central Asia, Japan, and Australia in the Mississippian, and are confined to the Island of Timor in the Permian. The neoschismatids arose in the Mississippian of the Atlantic Basin; in the Permian they are restricted to Timor and Australia. The codasterids are found in the Atlantic Basin during the Mississippian (England), Pennsylvanian (North America), and Permian (South America) but occur in greater profusion in the Permian of the Ural Mts. and southeast Asia.

SUMMARY OF STRATIGRAPHIC DISTRIBUTION

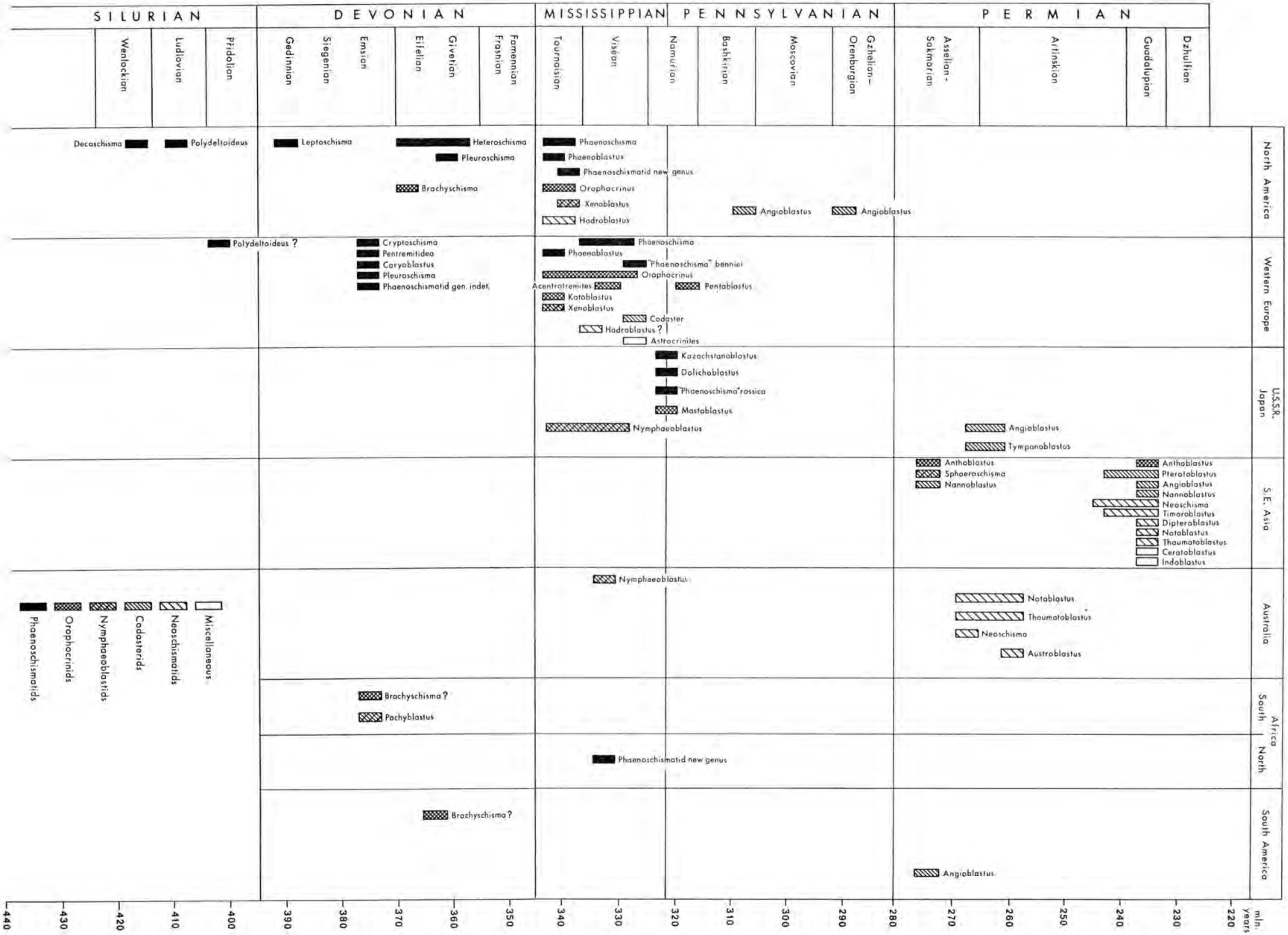
In textfigure 100, we have attempted to summarize the time-stratigraphic distribution of the fissiculate blastoids. The time scale used was that of the Geological Society of London (HARLAND, et al., eds., 1964).

This scale is a combination of radiometric dates and extrapolations based upon sediment thicknesses. Thus the dates assigned at system and stage boundaries and the length accorded each should be viewed somewhat plastically by the reader. STRACHAN (1964) attempted no time subdivisions of the Silurian; they are arbitrarily subdivided; stages follow BERRY (1970). FRIEND and HOUSE (1964, fig. 1) used a regression line to suggest subdivisions of the Devonian; stages follow OLIVER, et al., 1967. Three divisions are possible for the interval after the Devonian: Mississippian-Pennsylvanian (North American usage), Lower and Upper Carboniferous (Western Europe), or Lower, Middle, and Upper Carboniferous (USSR). We have used Mississippian and Pennsylvanian with European and Russian stage names, based upon the correlations of RHODES, et al., 1969, for the Mississippian, and FRANCIS and WOODLAND (1964) for the Pennsylvanian. The Permian stages are based upon GLENISTER and FURNISH (1961; personal communication, 1970). They subdivide the Lower Permian into the Asselian, Sakmarian, and Artinskian Stages. We have combined the first two because echinoderm-bearing localities have not been refined to this level. The Kungurian which is sometimes used for the uppermost Lower Permian is not used because it lacks official status (Glenister and Furnish, personal communication, 1970). In 1961 they used Guadalupian and Dzhulfian for the Upper Permian. In 1970 they recommended the recognition in the Guadalupian of three stages: Wordian, Capitanian, and Amarassian; we have used Guadalupian for simplicity in our chart. Time estimates for the stages follow SMITH (1964).

Within textfigure 100, we have plotted the occurrence of each fissiculate genus in seven geographic areas. An occurrence of a genus in one formation is indicated by a small bar; greater lengths were used if the genus was known to range through several formations or more than one stage. Lengths are not meant to represent the absolute existence in millions of years. Vertical offset of the bars in the same stage within or between areas, usually means an earlier or later time extent except in the Lower Mississippian and Permian of the USSR where our data is more general (i.e., "Tournaisian-Viséan" and "Lower Permian" respectively).

The fissiculate blastoids arose in the Silurian and survived until the end of the Permian. They are extremely scarce in the Silurian (3 species), but became more numerous in the Lower and Middle Devonian (11 and 7 species respectively). The Upper Devonian is barren of fissiculate blastoids (0 species). During the Mississippian fissiculate blastoid species are numerous (38 species). They declined during the Namurian (5 species) and the Pennsylvanian (2 species), but became more abundant again in the Permian (32 species; 17 Lower Permian, 16 Upper Permian; one species in both).

The stratigraphic record of the blastoids is incomplete, no blastoids being known from the following Devonian stages: Siegenian, Frasnian,



Textfig. 100. Stratigraphic distribution of fissiculate genera contrasted with geographic distribution. See text for explanation.

and Famennian. The lack of knowledge of these blastoids is viewed as an artifact. In Western Europe and North America the shallow, marly sediments, which the fissiculate blastoids preferred to live on, are not abundantly present in these stages. In other parts of the world they will become known if field work and collecting will progress further. It cannot precisely be predicted where these missing Devonian blastoid faunas will be found but South America, South Africa, Western Australia, and Antarctica should be the places to look for them.

Another major gap in the time stratigraphic distribution is the Pennsylvanian, only a few specimens of one fissiculate genus *(Angioblastus)* being known from the United States, and the Canadian Arctic (Ellesmere Island). The relative absence of blastoids from the Pennsylvanian is viewed as an artifact of preservation, not an evolutionary crisis. The Permian of Timor comprises many fissiculate genera, most all of which belong to genera/or families known before the Pennsylvanian. The phylogeny of Permian blastoids has shown (see Chapter on Phylogeny) that their trends can be traced from the Mississippian blastoids. They do not need to be regarded as the product of an evolutionary reradiation. This implies that there should be far more Pennsylvanian blastoids than are known today. Recent finds suggest that the Canadian Arctic may produce some of these, but the area is hardly accessible. The marine Pennsylvanian of China is probably a source for blastoids that age. Unfortunately to western paleontologists, China is even more inaccessible than the Canadian Arctic.

PALEOECOLOGY

BLASTOID SYNECOLOGY

The discussion on the distribution of fissiculate blastoids in relation to their physical and biological environment, as given above, allows us to draw several generalized conclusions with regard to the ecological conditions under which the fissiculate blastoids lived.

Blastoids are always part of marine, benthic communities, with no tolerance for salinity changes, as evidenced by their absence from littoral, lagoonal, estuarine, tidal flat, or other brackish water deposits. Typically, fissiculate blastoids also avoided true reefs; in only one case are they known to be even somewhat associated with deltaic deposits. Open marine waters of normal salinity apparently were an important ecological parameter to the blastoids.

Depth tolerance in blastoids is difficult to speculate on. Their absence from deeper-water geosynclinal facies, such as the Caledonian and Hercynian geosynclinal sediment belts, suggests that they did not occur in deeper water. Throughout their history they must have been confined to the shallower waters of the continental shelves.

Normally, the fissiculate blastoids are found on bottoms on which both lime and some mud have been deposited. In such cases the sediment is interpreted to have been deposited in shallow, open water, frequently under slight to moderate current activity. The normal faunal community to which the blastoids very generally belonged contained other echinoderms (mostly and predominantly crinoids), brachiopods, coelenterates, bryozoans; and to a lesser extent also trilobites and gastropods. These are faunal communities which mostly lived upon planktonic food sources. Blastoids are predominantly members of benthic filter-feeding communities; they typically do not inhabit a true reef environment.

Analysis of sedimentary features of the rocks in which blastoids occur proves that blastoids may indeed be regarded as moderate rheophile animals, living on muddy to limy bottoms, in shallow open water, and avoiding reefs. From a purely morphological point of view, we have concluded that most blastoids were predominantly rheophiles (Type I mode of life, as in *Orophocrinus conicus*; textfig. 101). Some of the blastoids, however, we have interpreted as being adapted to more rheophobe conditions. These blastoids (Type II mode of life, as in *Cryptoschisma schultzii*; textfig. 102) are in some cases occurring with rheophile camerate crinoids. The two modes of life for blastoids and crinoids are not conflicting, as it would seem at first glance. If there was any coherent community of larger, gregarious crinoids living under conditions of moderate current activity, the baffling effect of the crinoid canopy would have produced rather motionless waters near the bottom and inbetween the crinoids stems. Thus a micro-environment was created suitable for smaller, rheophobe animals. One may expect certain blastoid species (like *Cryptoschisma schultzii*) to have lived under moderate rheophobe conditions under a canopy of rheophile crinoids, forming an undergrowth with other rheophobe animals. This sort of condition is indeed present in the Lower Devonian of Spain. Microcrinoids and smaller crinoids (like, for example, the Pisocrinidae), might also be interpreted as rheophobe undergrowths.

Several deviations from the general blastoid mode of life and its ecological conditions are known. The nymphaeoblastoids throughout their history seem to have preferred to live on bottoms formed by fine-grained clastic sediments (clay to silts) derived from the continents. This may have meant living in very shallow waters. Their preference for fine-grained bottoms is quite outstanding and contrasts with other major blastoid groups.

There is nothing known with certainty about the occurrence of fissiculate blastoids in relation to climatic zones. If we plot the occurrences of Permian blastoids on a geographic map of the world with Permian climatic zones drawn in from a map after A. A. Ronov *, we see that all codasterid

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* Map in KAY & COLBERT, 1965, p. 467, fig. 19.12. The map involved is based on occurrences and interpretations of Permian fusulinids, corals, red beds, evaporites, tillites, etc., all of which indicate climatic conditions.

occurrences would fall within the tropical zones, and that most all neoschismatid occurrences would plot within the temperate zones. The Timor fauna would be about at the transition between the two climatic zones. We have already seen that *Thaumatoblastus longiramus* in Tasmania penetrated into colder water, as evidenced by its occurrence in a limestone with a few glacial erratics.

Only in a few cases do the blastoids show any relation to reef or bioherm formations. In Middle Devonian *(Brachyschisma)* we have an example of a blastoid associated with small patch reefs; in the Mississippian we have an example (St. Joe Fm., Lake Valley Fm.) of blastoids *(Hadroblastus, Orophocrinus, Phaenoschisma)* flanking smaller (10–200 m) biohermal elevations as a halo. In the Lower Carboniferous of the British Isles, blastoids have been found associated with reef knolls (or bioherms) *(Hadroblastus* sp. ?, *Orophocrinus, Phaenoschisma)*.

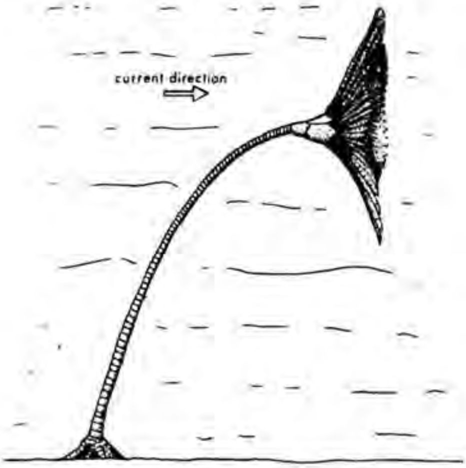
In only one case are the blastoids known to occur in (partly) volcanic marine sediments: Island of Timor, Republic of Indonesia. Part of the sediment is still carbonate; it may well be that blastoids there were adapted to living on lime and ash bottoms (as a variant to their usual lime and mud bottoms, which are similar). It is also conceivable that periodic heavy ashfalls were catastrophic, wiping out part of the benthic communities, to which the blastoids belonged.

BLASTOID AUTECOLOGY

Throughout their long history, the fissiculate blastoids appear to have normally inhabited a shallow to moderately deep sea, which would correspond to modern-day shelf environments. The evidence for this was presented in the previous section on fissiculate distribution and paleoecology. Their occurrence in marls and limestones suggests that they were only rarely well adapted to environments with moderate or high rates of clastic sedimentation. The reconstruction of a fissiculate blastoid's mode of life is usually subjective, for we do not know of any complete fissiculate stem-root systems and it is very rare to find a specimen with brachioles preserved; the theca has normally lain on the sea floor and behaved as a sedimentary particle prior to its ultimate burial. Nevertheless, we feel confident that we have enough data available to try to reconstruct several modes of life for the blastoids. The discussion of ecological relations of blastoids to the sediments in which they occurred, has suggested that blastoids are generally open-water animals, living under conditions of moderate current activity, and outside reef or lagoonal facies. A very general tendency for a rheophile (see BREIMER, 1969) mode of life may be assumed for many blastoids (see Type I below).

Type I. An example of the first mode of life in fissiculate blastoids is exemplified by *Orophocrinus conicus* (Miss., Iowa), and by *Pleuro-*

schisma lycorias (Dev., N.Y.; Pl. II, fig. 4; Pl. XXXII, fig. 1). It is one of the rare forms for which we know the stalk, theca, and brachioles (Pl. IX, fig. 7). The species possesses a long, somewhat flexible stalk, attached to a conical theca, and with long slender brachioles extending two or three times the height of the theca. We envision this animal as maintaining an elevated position a few centimeters above the sea floor during life. Spreading out the brachioles will produce a brachiolar funnel. The brachiolar funnel is thought to be effective in filtering planktonic food particles from a current. Any current will direct the theca and its brachiolar funnel in a manner as shown in textfig. 101. In order to exercise their function, the brachioles need to have elastic ligament fibers to counteract the water pressure when feeding. When not feeding, the brachioles were probably flexed in over the vault, and the elastic ligaments relaxed. This provided a mode of life for the blastoid very similar to that described by BREIMER (1969) for rheophile crinoids. We suggest that blastoids of the same organization as *O. conicus* are generally to be thought of as moderate rheophiles. This would not mean, however, that these blastoids could not live under rheophobe conditions at all. In the absence of current water they could probably direct the brachiolar funnel upward to collect food falling upon it from the plankton rain. Under rheophobe conditions they would probably have no difficulty to maintain the balanced elevated position; this could probably be effected by contraction of ligament fibers in the stem.

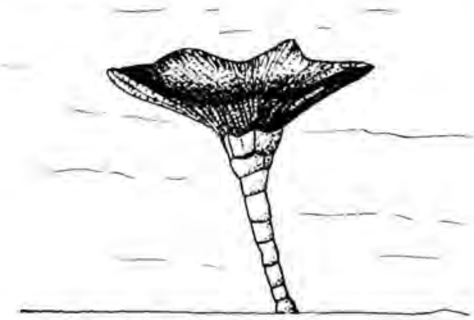


Textfig. 101. Type I mode of life, in which the blastoid has a long slender stem and brachioles and the latter are formed into a filtration fan. See text.

For discussion purposes, we will call the mode of life described above a Type I mode of life. Based upon a comparison of thecal shape, stem cicatrices and their diameter, stem plates where known, and ambulacral configurations, we suggest that the majority of the fissiculates had a

Type I mode of life. These blastoids possessed a normal pyramidal or cup-shaped theca with the ambulacra near the thecal top. Type I is viewed as the basic mode, its employment extending from Silurian to Permian.

Type II. A second mode of life in fissiculate blastoids is exemplified by *Cryptoschisma schultzii* (L. Dev., Spain). Only traces of brachioles are known, but the stalk is well preserved. It is different from the one in Type I blastoids. The stalk of *C. schultzii* consists of long cylindrical stem plates, which would not have provided the flexibility found in Type I. The apparent rigidity of the stalk suggests that it functioned more as a column, supporting the crown a short distance above the sea floor in a rigid position. *Cryptoschisma* is the first fissiculate blastoid to modify the normal BA growth axis of the early phaenoschismatids and to develop strong secondary calcite deposition, apparently to form a rigid attachment to the column. The theca and the brachiolar funnel of *Cryptoschisma* cannot ever have obtained a position in the water as has been drawn for *O. conicus*. We envision that *Cryptoschisma*, upon spreading out the brachioles, formed a brachiolar funnel that was directed upward. In this attitude it could passively collect food particles from the plankton rain. If it wanted to enlarge the food-collecting area of its funnel, it could spread out the brachioles even more, so as to form an almost two-dimensional fan to collect the food falling upon it. This mode of life suggests that the animal was more adapted to rheophobe conditions of life. If these tendencies were at all strong, it could create its own currents, in an active effort to bring food particles within its reach. Such currents could easily be created by expanding and contracting its brachiolar funnel. The only requirement for such brachiolar action would be that the brachiolars were provided with ligaments similar to the ones in *Antedon* cirrals. Our suggested rheophobe mode of life for *Cryptoschisma* would not mean that the animal would not and could not live under more



Textfig. 102. Type II mode of life, in which the currents are reduced, and the blastoid has a short stout stem. The brachioles form a cone. See text.

rheophile conditions. If under active current water, the brachiolar funnel could filter water for food. However, it was not able to transform its brachiolar funnel into a two-dimensional brachiolar filtration fan, and to direct that fan vertically against the current as in Type I feeders. The suggested mode of life for *Cryptoschisma* is given in textfig. 102. The bent thecae sometimes found in *Cryptoschisma* may be related to the rheophobe mode of life.

This Type II mode of life is not restricted to *Cryptoschisma schultzii*. In some other fissiculate blastoids we find a stem cicatrix with an abnormally large diameter in comparison to the size of the theca which is being supported. In a few instances the stem itself has been preserved and it has a different structure than in Type I. The other Devonian form which apparently employed Type II mode of life was *Pentremitidea archiaci* (Pl. I, fig. 14). It possesses a BA growth axis, but has modified it to form an extra-wide proximal attachment area whose edges curve downward over the top columnallike flanges. Again it has taller stem plates. We suggest that two Permian blastoids, *Neoschisma timorense* and *Pterotoblastus gracilis* also had a Type II mode of life. The former has an idented base; the proximal stem plate would have had an extremely large diameter (4.3 mm) for a blastoid. *Pterotoblastus gracilis* has stem plates which approach 2.0 mm in diameter on a relatively small theca; the latter is also frequently bent. This suggests a Type II mode of life. In the four cases described, the ambulacra are confined to the relatively flat upper surface of the theca. The development of wide petaloid ambulacra in *Cryptoschisma schultzii* could be a response to this mode of life.

Type III. In the chapter on fissiculate blastoid phylogeny, we noted that there is a tendency in many groups to elongate the ambulacra. Those with the greatest elongation, the nymphaeoblastids and some Mississippian orophocrinids, apparently could inhabit environments with a higher rate of sedimentation. The stem cicatrix in these forms appears to be normal, so we envision that they had a long, flexible stem, as for Type I. However, the expansion of the ambulacra over almost the entire circumference of the theca, meant that they could form a filtration apparatus which would have been much more complex, and a perhaps much more efficient baffling agent than those of a Type I form. The latter would have been more funnel-shaped with some lobations, due to the shape of the ambulacra. The filtration apparatus of the forms with expanded ambulacra (here designated Type III) could have been of much greater geometric complexity than Type I. Type III could be somewhat funnel-shaped but the funnel would be lobate. The increased number of arms would have provided a much greater baffling effect and the greater depth of this filtration apparatus would have provided an in-depth mechanism for food capture.

The first genus to develop long ambulacra was *Pachyblastus* (Pl. XII, fig. 1) which occurs in the clastic Bokkeveld Series of South Africa. It is also found in *Xenoblastus*, which is found in the New Providence Fm. (U.S.), part of the clastic sequence associated with the Borden Delta; *Nymphaeoblastus* which occurs in various clastic facies of Kazachstan, Central Asia, Japan, and Australia; and *Sphaeroschisma* which apparently occurred in a fine-grained clastic sediment in Timor.

The most pronounced examples of a Type III mode of life in the orophocrinids are *Acentrotremites*, *Orophocrinus verus*, and *Pentablastus* which have greatly expanded the ambulacra toward the base of the theca. These occur in more normal carbonate facies. (We frequently find echinoderms living in clusters or clumps. MEYER (1969, personal communication) reports observing *Nemaster grandis* and a basket star ophiuroid forming a common filtration fan on a coral reef in the Caribbean. Could it be that the clustering of the crinoids was an adaptive feature designed to form a more efficient filtration network, so that the baffling would be even more complete, such as the effect exerted by turtle grass in the Florida Bay region today?).

Type IV. In the Permian we find some blastoids whose thecal shape departs markedly from that of the earlier fissiculates. We believe some of these were adapted to living directly upon the bottom. One such form is *Timoroblastus*. The theca is box-shaped, the ambulacra are confined to the upper surface; it frequently expands the lower part of the theca into radiate, star-shaped extensions, and in extreme cases into spades. The stem diameter is apparently not of sufficient diameter to support a theca of the size involved. The expanded nature of the base suggests the animal sat directly upon the bottom, the expanded base helping to provide stability, and the greater amount of calcite also providing a lower center of gravity. The short ambulacra, confined to the upper surface, would thus not have been fouled by sediment as readily as longer ones. The stem cicatrix continues to expand in size as the thecal size increases, apparently indicating it remained attached. If our interpretation of *Timoroblastus* being a bottom dweller is correct, we do not know if it was so adapted throughout its entire life span, or whether it became bottom dwelling in its maturity. If it was elevated on a stem, the spade like basal extensions would have made it very unstable hydrodynamically.

Fissiculate blastoids which apparently dwell upon the bottom in this manner are designated Type IV. The large size, radial spines, and thecal shape of *Austroblastus* suggest it lived in a manner analogous to *Timoroblastus*. We suggest that the Permian crinoid *Calceolispongia* had a similar mode of life.

Anthoblastus stelliformis is apparently another example of a Type IV blastoid. It has long ambulacra which are scooplike (Pl. XI, fig. 6); the brachioles are attached along the upper edges of the scoop. They are restricted in how far they may bend downward at their base by the bordering radial or deltoid. The deltoids build five pyramid-shaped elevations. The basals of *A. stelliformis* are massive and bulbous, having been built by the deposition of free calcite on the surface. The diameter of the stem if present in large specimens would be small. We suggest that the massive basals lowered the center of gravity, that the spatulate radial prongs not only provided an increased area for ambulacra, but also supported the animal on the substrate. The brachioles could apparently only form an upward-directed collecting funnel. In times of stress they may have been folded downward, forming an umbrella over the scoop-shaped ambulacra; the tips of the brachioles may have lain in the area between the elevated areas of deltoid, thereby being afforded protection. It might have had shorter brachioles than a normal blastoid, analogous to *Blastoidocrinus*.

The only other fissiculate which adapted to a bottom-dwelling existence was the Mississippian genus *Astrocrinites*, which developed a bilateral symmetry and completely lost its stem.

Two Permian fissiculate genera *(Thaumatoblastus* and *Dipteroblastus)* are characterized by the development of extremely long radial prongs, which greatly expanded the number of brachioles. *Thaumatoblastus* is known only from its radials, but the lower part of the radial has a conical tapering profile, suggesting a cup-shaped theca similar to that of a Type I. The radial prongs (isolated segments greater than 55 mm) and the large number of brachioles attached along each side would have formed an enormous filtration or collection fan, which was flat and wheel-shaped, being two dimensional (Pl. XXV, fig. 8; Pl. XXVIII, fig. 5). It is interesting to note that the development of this enormous flat fan is analogous to the arm structure of the rhombiferan cystoid *Caryocrinites* (Silurian), and the camerate crinoids *Steganocrinus* and *Cytidiocrinus* (Mississippian). Each of these extended their food-gathering structures onto long prongs, thereby producing a greatly increased surface area by which currents could be baffled. These examples of homeomorphy occurred in the Silurian, Mississippian, and Permian. The other Permian blastoid with long radial prongs, *Dipteroblastus* (Pl. XXI, fig. 6; Pl. XXII, figs. 2, 3, 6; Pl. XXIII, fig. 4) has a rough bilateral symmetry, with three very short ambulacra, and two (*B* and *D*) which are almost opposite one another are extended onto radial prongs. Its filtration fan would have been more elongate, rectangular, with a gap in the center. Its stem cicatrix was large, suggesting it was elevated on a stem.

CONVERGENCE OR HOMEOMORPHY

Several features of blastoid morphology need special mention because of their possible importance for understanding the relation between ecological adaptations of the blastoids and their phylogenetic trends. Theoretically, one could expect ecology and phylogeny to interact in some way. Primarily, genotypic characters are involved in phylogenetic changes, but possibly also phenotypic characters. The latter are interpreted as those characters which demonstrate the adaptation of the animal to its specific environmental conditions. Parallel adaptational trends in blastoids may be expected wherever blastoids of different systematic affinities would occur together within the same ecologic niche. Beautiful examples of this phenomenon of convergence or homeomorphy can be presented for the fissiculate blastoids.

A first, and most striking example is found in the blastoids *Kazachstanoblastus* (Pl. V, figs. 14, 16, 17) and *Mastoblastus* (Pl. X, figs. 1, 2, 6) from the Lower Namurian of North Kazachstan. Although the two blastoids belong to different fissiculate families (phaenoschismatids and orophocrinids, respectively) they both lack hydrospire structures. Apparently, both forms show the same adaptation toward their environmental conditions, by complete (or nearly complete) reduction of their hydrospires. This provides an example of ecologic convergence or homeomorphy between the animals of different systematic affinity. We admit that this convergence is probably a phenotypic character and has little to do with the genotypic characters influencing the phylogenetic development of the systematic groups to which they belong or show affinity with. Reduction of hydrospires is clearly related to respiration. Apparently, both blastoids could switch from hydrospire respiration to brachiolar respiration, which their environment may have allowed equally for both forms. Phylogenetically, this could be without significance. Reduction of hydrospires in *Mastoblastus* occurs phylogenetically at a very early moment in the history of its family. Permian orophocrinids have hydrospires more highly developed than *Mastoblastus*. The environment in which several of our North Kazachstan blastoids lived must have been rather special to them. The accompanying fauna is unusual, consisting mostly of nautiloids. Their environment is a pure carbonate sediment, being highly fossiliferous, composed for a large part of animal remains.

Another example of convergence is taken from Lower Carboniferous deposits from the Boland district in Yorkshire, England. Involved is only one fissiculate genus *(Astrocrinus)*, and two spiraculate genera *(Orbitremites* and *Ellipticoblastus)*. Although the forms have different systematic affinities, they have developed the same ambulacral duct system through overgrowth by the lancet of the ambulacral groove system. This is a quite unique feature among the blastoids, so far as we now know. Only those genera mentioned possess the character. The fact that the ambulacral duct system uniformly occurs exclusively in one place and one time in different forms, is a possible hint toward seeking its explanation in similar environmental adaptation. However, in this particular case, it is hard to understand what the advantage or the significance of it is to the animals to have their radial water vessel buried in the lancet. It would certainly provide more protection for the vessel, but it is difficult to see what dangers the vessel was faced with. Was it parasitic feeding on the animals mucus stings in the ambulacral tracts? Or, was it connected with another, or more specialized, function of the water vessel?

A third example of convergence is provided by *Cryptoschisma schultzii* (Pl. I, figs. 9, 13, 17) and *Pentremitidea pailletti* (Pl. I, figs. 14, 18–20) in the Lower Devonian strata of Northern Spain. The two forms are systematically quite close (both are phaenoschismatids) but they differ in mode of life, the first being a more rheophobe food collector, the other being a more rheophile filter feeder. Yet the two forms show the same composition in anal area, a quite unique and unequaled situation. Both have the cryptodeltoids strongly reduced, leaving them without contact with the superdeltoid, and bringing the gonopore to lie outside the skeleton. This configuration of anal deltoids is unknown from outside Lower Devonian of Spain. Phylogenetically, this trend is probably without much meaning. Phylogenetic reduction of cryptodeltoids occurs in later Mississippian members of the phaenoschismatids, and is not as strong as it is in the Lower Devonian of Spain. Probably here also we have to seek our explanation in similar adaptations of the animals in their joint environmental conditions. Here it seems that the answer is to be found in the reproductive behavior of the animals, forced upon them by the environment.

More examples of convergent characters may be presented from those blastoids that are interpreted to have had a similar mode of life, although they lived far apart both in time and space. We now refer to *Cryptoschisma schultzii* (Pl. I, figs. 9, 13, 17; Lower Devonian, Spain) and *Pterotoblastus gracilis* (Pl. XXXII, figs. 3, 4, 6, 9, 10; Upper Permian, Timor), both of which have a Type II mode of life. The two forms show oblique growth in the theca, more calcite being added at one side; the stalk in both cases is stout with a wide stem cicatrix. From one specimen in *C. schultzii* we know that the rigid stalk was slightly oblique under the theca. In the characters mentioned, the two species show similar adaptations to environmental influences. These blastoids have grown obliquely, possibly as a response to crowding, irregular bottom topography, or external water pressure from one direction.

These examples given are to be taken into account when dealing with phylogeny of the group. One must, by necessity, subtract local and temporal adaptations to environments from phylogenetic inheritance and determination. Phylogeny deals primarily with genotypic characters, not with superficial phenotypic characters.

CHAPTER V

PHYLOGENY

PHYLOGENETIC DERIVATION OF THE BLASTOIDS

The derivation of the blastoids was probably monophyletic. This is suggested by the similarity in shape of the known Silurian fissiculate and spiraculate genera; by an apparent Silurian intermediate form between the two blastoid subclasses; and by a remarkably conservative thecal organization of the blastoids (in terms of number of major constituent elements) throughout their history from Silurian to Permian.

Several authors have speculated on the origins of the blastoids. These were reviewed by FAY (1967^{a}). Rhombiferan cystoids and edrioblastoids have been suggested as possible ancestors to the blastoids. We will refrain from trying to identify a specific genus, or even a group, as the blastoid ancestor. Rather, we would like to present several suggestions which may aid in the eventual identification of a blastoid ancestor.

It is our opinion that past practice to "evolve" a certain animal group from another such group is in many cases scarcely more than an exercise in logic and does not result in a valid statement on how things really went in nature. An example of such an exercise is Jaekel's 1918 "derivation" of the blastoids from *Cystoblastus*. We do not think of his "transformation" of thecal plates, "reduction" of pore rhombs, displacement of anus, and "transformation" of pore rhombs into hydrospires as valid. The blastoids are just one of the many echinoderm groups which have radiated from the main echinoderm stock during the Lower Paleozoic and were successful. The oldest known blastoid is a Middle Silurian (Wenlockian) genus from North America.

One can look for morphological and functional similarity of organ systems between blastoid and non-blastoid crinozoans. It then appears that there is no single group of Lower Paleozoic crinozoans resembling or approaching the total blastoid organization as a whole. If one were looking for a blastoid form and arrangement of thecal elements one would find this in the Stephanocrinidae (Coronata, Eocrinoidea; Ord.-Sil.), but these animals cannot possibly have been ancestral to the blastoids because of differences in ambulacral, brachiolar, and respiratory structures. If one were looking for similarity of ambulacral structures, one would find a very close resemblance in the Glyptocystitida (Rhombifera, Ord.-Sil.). If one were looking for the structure most close to the blastoid hydrospire system, one would find it in the early rhombiferan cystoids (like *Macrocystella*). But rhombiferan cystoids have a very different thecal form and composition, and should not be regarded as the direct ancestors of the blastoids. Blastoids have both eocrinoid and cystoid tendencies in their total organization.

Further, the polyphyletic origin of similar appearing respiratory structures, our lack of knowledge of the growth patterns, and ignorance of the detailed functional morphology of the possible blastoid precursors (which are under study by other workers), have caused us to refrain from trying to identify *the* blastoid ancestors.

We will now present the following suggestions with regard to the problem of the phylogenetic derivation of the blastoids. This is based primarily upon our present knowledge of early ontogenetic growth in blastoids, and upon the organization of primitive Mid-Silurian blastoids, which recently have become known (MACURDA & BREIMER, in preparation).

The thecal form of Silurian blastoids is a tall and slender conical pelvis with a restricted vault, narrow, relatively short ambulacra sited in an ambulacral sinus, with an upward opening anus surrounded by three anal deltoids. One of the apparent trends in blastoids and some other echinoderms is to increase the food gathering capacity. In the early eocrinoids the food gathering arms or brachioles are clustered around the oral pole as they are in the early rhombiferan glyptocystids. In later forms the ambulacral tract has been spread over the surface of the theca with more points for brachiolar attachment. Thus a *Cystoblastus* with its sphaeroidal shape and ambulacra which extend down towards the thecal equator would appear to be a relatively advanced evolutionary product. The Silurian blastoids in contrast have more restricted ambulacra and would appear to have been derived from a more primitive form with brachioles near the top. The lancet plate would appear to be a specialized blastoid development, perhaps related to the beginning of ambulacral expansion from an ancestor with brachioles clustered near the oral pole. Primitively the lancet does not support the main groove of the ambulacral tract except at the adoral end. Rather it acts as a support for side and outer side plates and surrounds the radial extension of the oral nervous system. Its development could have been a response to facilitate ambulacral growth and protect the nerve. (In rhombiferan cystoids with extensive ambulacra each ambulacral flooring plate must shift its position with respect to the thecal plate beneath it as the theca increases in size; in blastoids the side and outer side plates are fixed with respect to the lancet and only the latter must shift relative to the radial. See MACURDA, 1966, for further discussion of ambulacral growth).

We find a number of respiratory structures in rhombiferans, blastoids, and early crinoids whose structure is analogous but apparently not homologous. Thus, the respiratory nature of our blastoid ancestor may have been simple, being through a plate surface (à la *Macrocystella*) rather than a modified, restricted pore rhomb structure which extended over a large part of the theca as in early rhombiferans. We have found that the ontogenetic development of respiratory structures in the blastoid *Codaster* is a feature related to the development of the RD and DR sectors after the animal exceeds 1.5 mm in size. This occurs as a simple invagination across the radiodeltoid suture when sufficient area exists; new hydrospires are added as simple invaginations as greater area becomes available on the RD suture during growth.

The modes of growth in Paleozoic stemmed echinoderms strongly influenced the possibilities for experiments in new structures and modifications. In the early blastoids growth is by means of the lateral addition of calcite to the plate. Growth studies on other early echinoderms are not well advanced. Certain inferences can be made based upon ornament but need actual confirmation. For example, some of the thin-plated Cambrian eocrinoids such as *Acanthocystites*, *Lichenoides*, and *Akadocrinus* appear to have predominantly utilized the lateral method, and respiratory structures (epispires) were developed only at a certain size. *Macrocystella* (Rhombifera, Ord.) may have been similar.

Based upon the preceding discussion, it is suggested that the blastoids were derived from a relatively slender form with a relatively small number of plates. It may have been small, and the development of expanded ambulacra and their tube feet with a lancet and invaginated respiratory structures might be new structures developed in response to increasing size. The lancet may have also developed as a plate to fill a gap in the thecal plates where a plated integument formed a short ambulacrum. The form utilized the lateral secretion of calcite to form its theca. The stem was simple. The form possessed an oral nervous system and water vascular system whose ring canal lay external to the thecal plates, covered by cover plates.

We realize that this suggested derivation of the blastoids is highly speculative. It is offered only as an alternative to previous derivations. A better analysis of blastoid derivation must await the outcome of research on primitive Ordovician echinoderms.

SYSTEMATIC PHYLOGENY OF THE FISSICULATE BLASTOIDS

PHAENOSCHISMATID PHYLOGENY

The phaenoschismatids, as now grouped systematically on a phylogenetic basis, represent the main and ancestral stock of the fissiculate blastoids. The group arose during the Middle Silurian on both sides of the North Atlantic Basin (2 genera; USA, Eur.). During its development in Devonian times and until its extinction in late Mississippian times, it remained restricted in its occurrence to the Atlantic Basin. The family had its widest occurrence and development (in terms of numbers of genera) during the Devonian (6 genera) and remained widespread in the

North Atlantic Basin during the Mississippian (4, perhaps 6, genera). The family is the only fissiculate family not known to have survived into the Permian, nor to have migrated into other marine realms during its history.

Treatment of phylogenetic trends within the family of the phaenoschismatids will be done separately for several criteria in their order of phylogenetic importance. Distinct trends have been found for some morphological characters, while others have proved to have been essentially stable and conservative.

Distinct trends have been found in the composition of the anal area, the position of the gonopore in the anal area, the number of anal hydrospires and the structure of the ambulacral areas. The phylogenetic trends are briefly summarized here, and expanded upon below.

(1) The phaenoschismatids simplified the composition of the anal area. The original subdeltoid was first replaced by two cryptodeltoids, and these ultimately were replaced by a complex epideltoid. Simultaneously the hypodeltoid was first reduced and ultimately suppressed in some forms.

(2) There is a phylogenetic increase in the number of anal hydrospires connected with an accentuation of the anal interambulacral pyramid and the reduction of the hypodeltoid.

(3) Simplification of hydrospire-forming anal deltoids involved a phylogenetic change in position of the gonopore from external to internal.

(4) The ambulacral areas widened and gradually exposed the lancets.

The constant and conservative morphological characters in the evolution of the phaenoschismatids can be summarized as follows:

(1) The form of the theca has remained conical to biconical; the growth patterns for the main thecal elements have remained unchanged (but relative growth rates do change); interambulacral pyramids are always present and moderately developed, ambulacral sinuses are always present and have an angle varying from 60°-90°.

(2) The number of hydrospires in regular groups has remained constant (variable from 8–12).

(3) The number of side plates and brachioles per ambulacral area has remained constant.

Using the phylogenetic trends as summarized above, we have established a stock of phaenoschismatid genera in which the trends are most clearly observable. This stock of genera, arranged according to their age, is the following: *Decaschisma* (Pl. I, figs. 1–3), *Polydeltoideus* (Pl. I, figs. 8, 12), *Leptoschisma* (Pl. I, figs. 4–7), a Lower Devonian phaenoschismatid from Bohemia (Pl. II, figs. 1,6), *Pleuroschisma* (Pl. II, figs. 4, 5, 7–11), an undescribed phaenoschismatid from the Mississippian of Montana, *Phaenoblastus* (Pl. IV, figs. 8, 11, 12, 15, 18) and *Phaenoschisma* (Pl. III, figs. 14, 16, 18, 19, 21, 23–27; Pl. IV, figs. 3, 5, 10, 14, 19, 21). This group of genera is referred to below as the main phaenoschismatid stock. Other phaenoschismatid genera are regarded as offshoots from the main stock, either giving rise to other fissiculate lineages, or simply being radiant forms, not successful in leading to new fissiculate forms. The main time of evolutionary radiation in the phaenoschismatids is the Lower Devonian.

We will now try to further explain each of our provisional statements on the phylogeny of morphological characters in the family of the phaenoschismatids. This will be presented in order of the characters involved.

Thecal shape and growth patterns for main thecal elements. The maximum known size of Silurian phaenoschismatids (in terms of length) is about 25 mm. In the Lower Devonian, most species reach a maximum size between 10 and 20 mm; however, *Pentremitidea lusitanica* exceeded 20 mm and *Pleuroschisma verneuili* was the largest phaenoschismatid of any period, approaching 40 mm. Middle Devonian phaenoschismatids were also of intermediate length, between 10 and 20 mm, but *Pleuroschisma lycorias* reached a maximum between 25 and 30 mm. Most Mississippian phaenoschismatids were also of intermediate size, but *Phaenoschisma laeviculum* exceeded 20 mm. Thus from their inception in the Silurian, phaenoschismatids show relatively little variation in maximum size except for a very few species. The shape of the theca in the phaenoschismatids is a conservative character throughout the history of the group. Thecal shape has always remained conical to biconical, distinct ambulacral sinuses being present in between interambulacral pyramids.

In the main phaenoschismatid stock there is no trend either toward increase or decrease in the development of interambulacral pyramids. In all the genera belonging to the main stock, the interambulacral pyramids have only a moderate development. Also in these genera there is no trend toward widening or narrowing the ambulacral sinuses. The angle between sinus walls in the main stock varies from about 60° to 90°.

Several radiations from this constant growth pattern have occurred in the Devonian, when the phaenoschismatids underwent evolutionary radiation. *Pleuroschisma*, and notably *P. verneuili* (Pl. II, figs. 5, 9, 11), is aberrant in the sense that it has highly developed interambulacral pyramids, though not changing the angle of the ambulacral sinus. This strong development of interambulacral pyramids is related to, if not caused by, a tendency to strongly increase the number of hydrospire folds and to completely expose the hydrospire slits. Increase of the number of hydrospire folds is only possible if the length of the RD suture is increased. In its turn the RD suture can only be enlarged by stronger upbuilding of the interambulacral pyramid. The longer RD suture, by necessity, exposed the hydrospire slits formed across it.

A second radiation, but opposite in its direction, is found in *Cryptoschisma* (Pl. I, figs. 9, 13, 17). Here the interambulacral pyramids are far less developed than in contemporary main stock members, and the ambulacral sinuses are much wider (120°). On the basis of this morphologic character *Cryptoschisma* is to be placed off the main line of development in the phaenoschismatids.

Some species of *Heteroschisma* show the same radiation in thecal shape as *Cryptoschisma*. The ambulacral sinuses of most *Heteroschisma* species are still of the usual width and the interambulacral pyramids are of normal development. However, in *H. alternatum* (Pl. III, figs. 1, 2, 5, 6) the ambulacral sinuses have been distinctly widened (to 155°) and the interambulacral pyramids distinctly flattened, being only faintly developed. This development in *H. alternatum* is regarded as a very important character for understanding the phylogenetic derivation of the codasterids.

In the Silurian and most Devonian phaenoschismatids, the basals are long, narrow plates, which grow upward quite rapidly relative to the other plates; they are a main element of the theca. A BA growth axis is almost universally present and this must be regarded as the primitive condition. The only marked departure is known from *Cryptoschisma*, which has utilized extensive deposition of secondary calcite. This is probably due to the adaptation of a rheophobe mode of life. The growth rate of a basal (BR) remains relatively constant to its opposing axis in the radial (RB) during the Mississippian but the other parts of the radial and the deltoids assume greater importance, so the relative contribution of the basals to the theca is reduced. A BA growth axis is still present in many forms but secondary calcite deposition is utilized more extensively. The basals also become somewhat wider but still form a conical thecal base.

The shape of a radial is conservative in the Silurian and Devonian. Typically, it is a relatively elongate narrow plate with the origin of the plate resembling the apex of a pyramid. The RB sector is largest and the RD sector is confined to an ambulacral sinus. In a few Devonian and many Mississippian forms, there is a clear shift toward a much faster rate of growth in the RD sector and de-emphasis of the RB sector. Consequently, the ambulacra expand, enhancing the food-gathering capacity. Overall radial shape, however, remains much the same. The ontogenetic acceleration of RD with growth is present in six phaenoschismatid species; there is no selection toward this in later forms.

The shape of the deltoid also is basically stable. The plate is comprised of a small DD sector forming part of the peristomial ring and a crest which originates below the level of the DD sector and then slopes upward, rising above the oral opening. The sloping sides of the crest are filled with hydrospire slits. This configuration is maintained in most species; a few Devonian species have a horizontal crest and it slopes downward in a few Mississippian forms. The size of the deltoid increases relative to other plates.

Anal deltoids. The anal area of phaenoschismatids underwent distinct phylogenetic change during the evolutionary history of the group. Primitively, the anal area is of a complex composition, including a superdeltoid, a subdeltoid, and a hypodeltoid. (And even a pair of paradeltoids in *Polydeltoideus*).

The paradeltoids of *Polydeltoideus* are quite unique plates among the fissiculates, not being known from any other fissiculate genus. The plates are regarded as modified anal cover plates, perhaps contributing to a sort of anal chimney. They probably did not belong to the regular anal deltoids that phaenoschismatids normally have. They have played no role in the phylogeny of the anal area.

The presence of a subdeltoid is particularly noteworthy. The plate is only present in fissiculates, and is fully unknown in the spiraculates. In the fissiculates it only occurs in forms not younger than Middle Devonian. In the phaenoschismatids it is present exclusively in Silurian forms *(Polydeltoideus, Decaschisma)*. The Lower Devonian genus *Leptoschisma*, and the Middle Devonian genus *Heteroschisma*, also possess this plate. Possession of a subdeltoid is the primitive phaenoschismatid condition. Phylogenetically, the subdeltoid was not a persistent plate and was soon replaced by two cryptodeltoids.

Cryptodeltoids arose in the Lower Devonian in the fissiculates. All Lower Devonian phaenoschismatids (except *Leptoschisma*) possess a pair of cryptodeltoids. In *Caryoblastus* (textfig. 5.4; Pl. I, figs. 10, 11) and *Pleuroschisma* (textfigs. 10.2; 11.5–8) the cryptodeltoids meet laterally adoral to the anal cavity and border the superdeltoid. In *Pentremitidea* (textfigs. 7.3, 8.3; Pl. I, figs. 14, 18–24; Pl. II, figs. 2, 3) and *Cryptoschisma* (textfig. 6.4) the cryptodeltoids are restricted, and do not come in contact with the superdeltoid.

Cryptodeltoids are persistent in time. They range into the Mississippian where they are found in *Phaenoblastus*. They are the youngest cryptodeltoids we have definitely found in the fissiculates. As in some Lower Devonian forms the cryptodeltoids of *Phaenoblastus* are somewhat restricted adorally (textfig. 22.5). They do come in contact with the superdeltoid, but do not meet laterally adoral to the anus.

In Mississippian times, namely in *Phaenoschisma*, both the subdeltoid and the cryptodeltoids are absent. Instead, there is a large two-winged epideltoid (textfigs. 17.3, 4; 18.4; 20.2–4). The same condition is also found in *Dolichoblastus* (Pl. VI, figs. 1, 4) and *Kazachstanoblastus* (textfig. 23.2, 3; Pl. V, figs. 14, 16, 17), two Namurian probable end members of the phaenoschismatids. The large two-winged epideltoid is unknown in pre-Mississippian times.

The hypodeltoid of the phaenoschismatids is variably developed during the history of the group. In Silurian forms it is well developed, exposed on the external body wall and thus contributing to it. In Devonian genera the plate is moderately developed, and present in a horizontal position aboral to the anus. In *Cryptoschisma* the hypodeltoid is slightly aberrant because it is growing more inward (textfigs. 6.3–5); it has been eliminated in *Heteroschisma* (textfigs. 12.3, 4; 13.1; 14.4; 15.4, 5; 16.3). In many

Mississippian species the hypodeltoid is a small internal structure without exposure on the body wall (textfigs. 18.2; 19.2; 20.5). Ontogenetically, the plate is hardly growing at all, and is apparently suppressed. An undescribed phaenoschismatid genus from the Mississippian (Kinderhook) of Montana (UB) and Viséan-Namurian of North Africa (Pl. V, figs. 4, 5, 10) still preserves the primitive large hypodeltoid with ample exposure on the external surface of the theca.

Before we try to set out a main phylogenetic trend in the composition of the anal area, it is appropriate to discuss on the possible homology of anal deltoids in the phaenoschismatids. This discussion is based upon the function of the anal deltoids and their topographic position in the anal area of the animal.

The original function of the primitive Silurian and Lower Devonian subdeltoid in *Polydeltoideus*, *Decaschisma* and *Leptoschisma* is (1) to form hydrospires, and (2) to support and form the external gonopore. In order to exercise that function, the subdeltoid borders the anus topographically along its adoral and lateral sides. The plate is in contact with the superdeltoid and the posterior radial limbs. The external gonopore is formed in the suture between the super- and the subdeltoid, the hydrospires are formed across the suture between the subdeltoid and the posterior radial limbs.

Later in the phylogenetic development of the group the subdeltoid is replaced by two cryptodeltoids. If fully developed, these two plates have exactly the same topographic position as the one subdeltoid, and have exactly the same function. An external gonopore is built in the suture between cryptodeltoids and superdeltoid, and hydrospires are built across the sutures between the cryptodeltoids and the posterior radial limbs. It thus follows that the subdeltoid and the two cryptodeltoids are homologous.

It is particularly noteworthy that phylogenetically cryptodeltoids show incomplete and restricted development in L. Dev. genera *Pentremitidea* and *Cryptoschisma* (BREIMER, 1971), accompanied by loss of function of these plates. In *Pentremitidea* and *Cryptoschisma* the cryptodeltoids do not form hydrospires, and do not support a gonopore/gonoduct. A similar situation is found in the Mississippian genus *Phaenoblastus*. Here the cryptodeltoids are not restricted much as in *Pentremitidea* and *Cryptoschisma*. In *Phaenoblastus* the cryptodeltoids have lost the function of supporting an external gonopore (because they do not come in contact laterally adoral to anus), but they have retained the function of forming hydrospires.

The phylogenetic replacement of the subdeltoid by two cryptodeltoids suggests that the subdeltoid could be regarded as a result of the fusion of two elements developing separately in the early ontogeny of such a form, but undergoing early larval fusion to form a single subdeltoid plate. The subdeltoid is then explained as two fused cryptodeltoids. This would mean for the phylogeny of later forms that the original plate fusion of the two elements was not effectuated, so that they could appear as two fully developed cryptodeltoids, connected with a suture adorally from anus. The plates could phylogenetically have undergone further reduction, in which the common suture adoral to the anus (and the external gonopore!) was given up (e.g., *Phaenoblastus*). In an extreme case the two elements could remain as two small plates lateral from anus, even without forming hydrospires (e.g., *Pentremitidea*, *Cryptoschisma*).

The two-winged epideltoid of *Phaenoschisma* has the same two functions as the subdeltoid or the two cryptodeltoids. It is engaged in the formation of a gonopore, and in the formation of anal hydrospires. However, its topographic position in the anal area is not directly comparable. The two-winged epideltoid has the same position as the combination of a superdeltoid and two cryptodeltoids. The topographic position of the two-winged epideltoid in *Phaenoschisma* includes the position of the superdeltoid of other Mississippian phaenoschismatids.

Theoretically there could be two solutions to the possible homology of the plate. Either (1) cryptodeltoids have fused with the superdeltoid to form an epideltoid; or (2) cryptodeltoid elements have been fully reduced and suppressed during ontogeny, giving the superdeltoid element an opportunity to grow out and to occupy the position of the cryptodeltoids, thus forming an epideltoid. In the first case the phaenoschismatid epideltoid would be truly homologous to the combination of super- and cryptodeltoids. In the latter case the phaenoschismatid epideltoid would only be analogous to a super-cryptodeltoid combination, having a different ontogenetic origin, and being in fact homologous to the superdeltoid.

The problem of the homology of the phaenoschismatid epideltoid is difficult to solve. There is no complete phylogenetic trend line in time in which gradual phylogenetic reduction of cryptodeltoids occurs along with gradual phylogenetic emphasis on the superdeltoid replacing the cryptodeltoids. As we have seen, reduced cryptodeltoids do occur *(Pentremitidea, Cryptoschisma, Phaenoblastus)*. In the case of *Pentremitidea* and *Cryptoschisma* we do not see that the superdeltoid is enlarged, forming a two-winged structure to compensate for the loss of cryptodeltoid material. In *Phaenoblastus* the superdeltoid is indeed enlarged to partly compensate for the smaller cryptodeltoids. However, the available evidence is weak and not found to be conclusive. The true homologies of the phaenoschismatid epideltoid remain obscure. Only paleo-embryologic data could bring a definite answer, if such a science were at all possible.

There is a complication: the subdeltoid of *Heteroschisma*. The plate has the same position as in other phaenoschismatids, but has only one of the two usual functions, namely the formation of a gonopore. It does not form hydrospires. Apparently, *Heteroschisma* is to be regarded as an offshoot from the main stock of phaenoschismatids since it gave up one of the two original functions of the subdeltoid. As we will see later (Codasterid phylogeny) this soon meant giving up the whole plate.

We will now set out the main trend for the phylogenetic development of the anal area in the main phaenoschismatid stock. The main phylogenetic trend is simplification of the anal area by: (1) loss of the original Silurian subdeltoid; (2) replacement in Devonian times of the subdeltoid by two cryptodeltoids, plus starting a reduction of the hypodeltoid; (3) in Mississippian times either fusion of super- and cryptodeltoids to form an epideltoid, or the replacement of cryptodeltoids by the superdeltoid to form an epideltoid, frequently accompanied by a reduction of the hypodeltoid; (4) a change in position of the gonopore from external in primitive members with complex anal area, to internal in ultimate members with simplified anal areas.

Trends representing phylogenetic offshoots from the main phaenoschismatid stock are found (1) in *Cryptoschisma* and *Pentremitidea* where there is a very early (L. Dev.) reduction of the cryptodeltoids along with loss of both functions of these plates; and (2) in *Heteroschisma* with very late (M. Dev.) retention of the subdeltoid and loss of the hydrospire-forming function of the plate.

Hydrospires. We have distinguished a main phylogenetic lineage in the phaenoschismatids primarily based on the evolution of the anal area. A character immediately linked with this is the number of anal hydrospires.

Primitively, in the Silurian phaenoschismatid genera *Polydeltoideus* and *Decaschisma* the number of anal hydrospires is strongly reduced. In Lower Devonian times the development of the number of anal hydrospires is variable. In *Pleuroschisma* the number is still strongly reduced; in *Leptoschisma* it is generally reduced. *Caryoblastus* has the number of anal hydrospires most always reduced by one. The number of anal hydrospires in the Mississippian genera *Phaenoblastus* and *Phaenoschisma* is reduced and only slightly reduced respectively. Thus, in the main stock of phaenoschismatids there is a tendency to phylogenetically develop more anal hydrospires.

We have found that the number of hydrospires in regular fields is phylogenetically constant, not including offshoot trends. The following maximum number of hydrospire folds occurs in regular fields of mature specimens: *Polydeltoideus* 10, *Decaschisma* 9, *Leptoschisma* 8, *Pleuroschisma lycorias* 9, *Pentremitidea* 8 or 9, *Cryptoschisma* 8, most *Heteroschisma* species 10–12, *Phaenoblastus* 8, and *Phaenoschisma* 12–13. A distinct trend toward formation of more hydrospires in the regular fields is absent; the number is apparently a constant and conservative feature in the phylogeny of the family. Distinct offshoots from this main trend are *Caryoblastus* with only four hydrospire folds and *Pleuroschisma verneuili* with over thirty folds.

If the number of hydrospires in the regular fields is constant phylogenetically, it means that the number of anal hydrospires increases with time relative to the number of regular hydrospires.

It is interesting to try and find a relation between the phylogenetic increase of the number of anal hydrospires and the phylogenetic development of the anal deltoids that help form the anal hydrospires. At first glance one is inclined to believe that the Silurian and Lower Devonian subdeltoid was less able to form anal hydrospires than the Devonian and Mississippian cryptodeltoids were and that ultimately the Mississippian complex epideltoid was the most effective hydrospire-forming anal deltoid. However, there is a serious argument against such a hypothesis.

The number of anal hydrospires is determined by the effective length of the suture between sub- or cryptodeltoid and the posterior radial limb. The length of this suture is deeply influenced by the extent of the hypodeltoid. The larger the hypodeltoid, the shorter the suture between anal deltoid and posterior radial limb. This provides a good and conclusive clue that the phylogenetic increase in the number of anal hydrospires is in fact correlated with the phylogenetic reduction and ultimate suppression in some forms of the hypodeltoid and not with a weaker or stronger hydrospire-forming capability of sub-, crypto-, and epideltoid. This phylogenetic increase is also enhanced by the development of a truncated interambulacral pyramid in the *CD* interarea.

A phylogenetic trend shown by the hydrospires of the phaenoschismatids is a tendency for hydrospire folds to gradually differentiate into hydrospire lamellae and hydrospire ducts or tubes. Primitive hydrospire folds of *Decaschisma* are relatively thickwalled and lack any differentiation. Later members of the phaenoschismatids have developed more effective hydrospires by making them thinner-walled and by differentiating them into hydrospire lamellae and hydrospire tubes. The origins of the hydrospire tube may be entirely explained as a response of the hydrospire wall to the outflowing water current in the deepest parts of the hydrospire folds.

In the main stock of phaenoschismatid genera, hydrospire folds preserve a parallel arrangement. Conjunction of hydrospire folds occurs only in *Caryoblastus bohemicus* and *Pentremitidea lusitanica*.

In the main stock of phaenoschismatids there is no phylogenetic trend either toward further exposure of hydrospire slits, or, reversely, toward further concealment of hydrospire slits. Most genera in the main phaenoschismatid stock have the hydrospires partly exposed in the ambulacral sinus. Exceptions are *Pleuroschisma*, and notably *P. verneuili*, in which the hydrospires are nearly completely exposed, and *Caryoblastus*, *Pentremitidea* and *Cryptoschisma* in which they are completely or near-completely concealed.

The complete exposure of hydrospire slits in *Pleuroschisma verneuili* (Pl. II, fig. 11) is related to a strong development of interambulacral pyramids. In this character the species is to be placed off the main phylogenetic trend in the phaenoschismatids.

The mechanism of concealing hydrospire slits is variable and brought about by widely different methods, as exemplified by the genera discussed below.

Concealment of hydrospire slits in *Caryoblastus* (Pl. I, figs. 10, 11) is related to and brought about by developing prominent interambulacral pyramids and very narrow ambulacral sinuses (angle 35°), along with a reduction in the number of hydrospire folds which do not occupy the full width of RD suture.

In *Cryptoschisma* (Pl. I, figs. 9, 13, 17) the concealment of hydrospire slits is related to and brought about by a faint development of the interambulacral pyramids, by a widening of the ambulacral sinus (angle 120°) and by filling the ambulacral sinuses with wide petaloid ambulacra with fully exposed lancets. In addition, *Cryptoschisma* does not use the outermost part of the RD suture for hydrospire formation.

The complete concealment of hydrospire slits in *Pentremitidea* and notably in *P. lusitanica* (Pl. II, figs. 2, 3) is brought about by not using the complete RD suture for hydrospire formation and by bringing the ambulacral structures almost flush with the adjoining thecal plates while retaining the normal ambulacral pyramids, ambulacral sinuses, and lanceolate ambulacra.

Whereas in the first two cases of concealment of hydrospire slits the mechanism of concealment is really by specializing thecal structures, in the last case this has been done in a very unspecialized way. All of the three genera mentioned place themselves off the main phylogenetic stock of phaenoschismatid blastoids.

Ambulacral structure. In the early phaenoschismatids the ambulacral areas are linear, provided with many side plates in biserial arrangement, and completely covering the lancet except at the adoral tip. This form and composition of the ambulacral areas is the primitive phaenoschismatid condition. It is exclusively present in the Silurian genera *Polydeltoideus* and *Decaschisma*. The Lower Devonian genera *Leptoschisma*, *Caryoblastus*, and *Pleuroschisma* preserve the primitive linear ambulacra with the concealed lancet, but in *Heteroschisma* and *Pentremitidea* the ambulacra have become lanceolate, but the lancets are still concealed. An undescribed Mississippian (Kinderhook) genus from Montana (UB) still preserves the lanceolate ambulacrum, but *Phaenoschisma* already has lanceolate to petaloid ambulacra with an exposed lancet, and *Phaenoblastus* has petaloid ambulacra with an exposed lancet. Ambulacral forms are thus linear in the Silurian, linear to lanceolate in the Devonian, and lanceolate to petaloid in the Mississippian.

The main stock of phaenoschismatids shows a distinct phylogenetic trend by changing the ambulacral composition from linear with concealed lancets in early members to lanceolate and petaloid with exposed lancets in ultimate members. This means that genera of the main stock of phaenoschismatids gradually widened their ambulacral areas and exposed their lancets. There is no phylogenetic trend either toward reduction or toward increase in the number of side plates and brachioles per ambulacral area.

There is only one definite offshoot in ambulacral structures from the main trend in the phaenoschismatid stock. This is the Lower Devonian genus *Cryptoschisma*. Its ambulacral areas are widely petaloid and have widely exposed lancets. The ambulacral areas also have a reduced number of side plates. This composition of ambulacral area is distinctly unusual for Lower Devonian times. It places the genus *Cryptoschisma* off the main line of phaenoschismatid evolution.

Pentremitidea (L. Dev.) and *Heteroschisma* (M. Dev.) are not too far off the main trend in the development of ambulacral structures, and cannot really be treated as offshoots.

Discussion of other trends. So far we have discussed the main phylogenetic trends in the main stock of phaenoschismatid genera. We have done this for all available morphologic criteria, either constant or variable. In the discussion on each separate morphological criterion we have found genera which were to be regarded as displaying evolutionary trends that do not fit the trend in the main stock. Such forms were indicated as offshoots. The genera to be placed off the main phylogenetic line are *Caryoblastus* (L. Dev.), *Cryptoschisma* (L. Dev.), *Pentremitidea* (L. Dev.), and *Heteroschisma* (M. Dev.). This very clearly and evidently indicates that the phaenoschismatids underwent evolutionary radiation predominantly in Lower Devonian times. We will now discuss what evolutionary significance is to be attached to each of these offshoot genera in view of the possibility that they may have given rise to new and other stocks of fissiculate blastoids.

Caryoblastus (Pl. I, figs. 10, 11) has very significantly developed away from the main phaenoschismatid evolutionary pattern. It has done so primarily by the reduction of the number of hydrospires, but also by concealing the hydrospire slits in very narrow ambulacral sinuses inbetween very prominent interambulacral pyramids. As a result of concealing the hydrospire slits, the hydrospire folds show slight internal conjoining (textfigs. 5.6, 7) an unusual character for phaenoschismatids. The developmental trend in *Caryoblastus* is unique among the phaenoschismatids, though it does not lead the genus too far off the main stock. Almost every other essential character closely corresponds to those of genera in the main phaenoschismatid stock. The genus is interpreted as an early and specialized phaenoschismatid, not having given rise to any other groups of blastoids. It is an evolutionary end product at an early moment.

Cryptoschisma (Pl. I, figs. 9, 13, 17) is another example of a distinct developmental radiation of the early phaenoschismatids away from the main trends. The genus is a very specialized phaenoschismatid, differing in almost every important morphologic character from the genera in the main phaenoschismatid stock. *Cryptoschisma* has developed a flattened vault by reducing the height of the interambulacral pyramids and by widening and shallowing the ambulacral sinuses. Although it has preserved a regular number of hydrospires in each group, it has completely concealed the hydrospire slits by an extreme widening of the ambulacra. Widening the ambulacra involved a reduction of side plates and brachioles per ambulacral area. The genus has also reduced the cryptodeltoids (textfig. 6.4) and by so doing gave up both functions of those plates: forming anal hydrospires and forming an external gonopore. It has also developed strong secondary deposits of calcite on the basals. Only in a few characters has the genus not departed from the main developmental trends in the phaenoschismatids.

Cryptoschisma also is a direct end product of evolutionary radiation. The form was not successful in establishing a new lineage of fissiculate blastoids. However, some of the trends it shows have proved to be of phylogenetic importance. We refer specifically to its tendency to flatten the vault by suppression of the interambulacral pyramids. This has not been successful in *Cryptoschisma*, but it has in *Heteroschisma*, as pointed out below. Changing thecal shapes by flattening vaults may in itself be regarded as a successful phylogenetic change. But if it is accompanied by concealment of hydrospires by extreme widening of ambulacral areas (as in *Cryptoschisma*) no successful form results.

Pentremitidea is held to be an extremely important genus in blastoid evolution. It developed away from the main trend in the phaenoschismatids by reducing its cryptodeltoids (textfigs. 7.3; 8.3) and giving up both functions of the plate (forming anal hydrospires and forming an external gonopore). Its main phylogenetic significance lies in the fact that it has been able to conceal its hydrospire slits without going into building up a very specialized thecal form and specialized ambulacral areas, as *Cryptoschisma* did. *Pentremitidea* has retained its ambulacral sinuses, and its interambulacral pyramids The genus has changed the form of the ambulacral areas to lanceolate, and has brought the external surface of the ambulacral areas about flush with the adjoining radial and deltoid plates. By doing so it has almost filled the ambulacral sinuses with the ambulacra, giving up the depressed position of the ambulacra. These conditions have caused the hydrospires to slightly conjoin internally (notably in *P. lusitanica* (textfig. 9; Pl. II, figs. 2, 3). In this way a phaenoschismatid has evolved to be very close to a spiraculate blastoid. It is our opinion that *Pentremitidea* gave rise to a major stock of spiraculate blastoids. As stated by BREIMER, 1970, *Pentremitidea* is interpreted to have been directly ancestral to the pentremitid genus *Cordyloblastus*. The problems of the derivation of spiraculate blastoids from the fissiculates, and the polyphyletic origin of the spiraculates is further dealt with on p. 359. We would confine ourselves here to a short statement on transition of a *Pentremitidea*-like fissiculate into a pentremitid of *Cordyloblastus*-like appearance. In order to make the transition it would be necessary for the

Pentremitidea-like fissiculate to start spiracle formation (textfig. 9) and to develop hydrospire pores. It is very significant that *P. lusitanica* already has a crescentic rim on the deltoid lip so as to form a sort of proto-spiracle. If this crescentic rim could be completed by extending it onto the exposed tips of the lancets (as in *Cordyloblastus alejensis*), and ultimately grow out as a complete crescentic crest adoral to the deltoid body, a spiracle is built. Likewise, the formation of hydrospire pores is only a minor transition. The *Pentremitidea*-like fissiculate has its ambulacra bordered by hydrospire clefts, hydrospire pores being absent because the side plates and /or outer side plates do not come in lateral contact with R and D in the sinus wall. But, if the side plates and/or outer side plates do start making lateral contact with R and D in the sinus wall, thus partly bridging the hydrospire cleft, a hydrospire pore of the simplest possible type is built. This type of hydrospire pore is present in *Cordyloblastus alejensis*.

Heteroschisma is another offshoot from the phaenoschismatids. Its development is off the main trend in phaenoschismatid evolution, because the subdeltoid is not hydrospire-forming. We have seen already that the subdeltoid of *Heteroschisma* is the latest record of a subdeltoid, along with the subdeltoid of *Brachyschisma*. We regard the plate at that time as very late phylogenetically, being partly non-functional, and being in a state of suppression.

The former group of species now brought together as *Heteroschisma alternatum* (Pl. III, figs. 1, 2, 5, 6) is of considerable phylogenetic interest. *H. alternatum* has flattened the vault more so than other *Heteroschisma* species by reducing the height of its interambulacral pyramids and by widening the ambulacral sinuses. By so doing it completely exposed the hydrospire slits because it preserved the usual phaenoschismatid number of hydrospires and their parallel arrangement. It did not (as *Cryptoschisma* did) make an attempt to conceal the hydrospire slits by developing wide petaloid ambulacra.

The evolutionary trend developed in *Heteroschisma* has been successful and has given rise to the codasterid stock of fissiculate blastoids. Complete reduction of the subdeltoid of *Heteroschisma* would mean a transition from a phaenoschismatid into a codasterid. It is highly significant that the subdeltoid of *Heteroschisma alternatum* is decidedly smaller than the subdeltoids of other *Heteroschisma* species. It is concluded that *Heteroschisma alternatum* is at least the first definite phaenoschismatid radiation toward the codasterids, and probably even the direct forerunner of *Codaster*.

The same developmental trends as observed in *Heteroschisma* are also present later in *Dolichoblastus* (Pl. VI, figs. 1, 4). This genus has also flattened the vault by a faint development of the interambulacral pyramids and by a widening of the ambulacral sinuses, thus exposing the hydrospire slits. *Dolichoblastus* is in fact closer to the codasterids than *Heteroschisma* is because it has reduced the number of regular hydrospires, and because it has lost sub- or cryptodeltoids. The only phaenoschismatid characters *Dolichoblastus* has are the elongate conical pelvis and the interambulacral pyramids and the ambulacral sinuses.

Dolichoblastus is interpreted as a second phaenoschismatid radiation toward the codasterids. In fact it is possible to interpret *Dolichoblastus* as a true codasterid already. One could look to it as a codasterid genus having preserved in its later ontogenetic stages some phaenoschismatid-like characters. In our phylogenetic classification of the fissiculates (p. 21) we have placed *Dolichoblastus* in the phaenoschismatids with a query-mark. We could also have placed it with a query-mark in the codasterids.

There are two Lower Namurian forms *(Kazachstanoblastus carinatus* and "*Phaenoschisma*" *rossica)* which we have questionably assigned to the phaenoschismatids. *Kazachstanoblastus* (Pl. V, figs. 14, 16, 17) resembles other phaenoschismatids in its thecal shape, deep ambulacral sinuses, BA growth axis, and linear ambulacra. However, there is a complete lack of hydrospires. This may represent the parallel culmination of a trend seen in the orophocrinids toward the suppression of the hydrospires. Secondary infilling can be seen in the late Visean – upper Namurian "*Phaenoschisma*" *saharae* (Pl. V, figs. 4, 5, 10) from North Africa. This phenomenon is a very late development in the phaenoschismatids.

"*Phaenoschisma*" *rossica* (Pl. V, figs. 12, 15) is a form whose generic placement is in question because of uncertainties over the composition of the anal area. It does not belong to *Phaenoschisma* and probably represents a new genus. It has some phaenoschismatid characteristics (thecal form, ambulacral sinuses, lack of an external RD growth sector, and BA growth axis) but differs from other genera in its small number of hydrospire slits which are concealed, the entrance apparently being a cleft. In this character it resembles the orophocrinid *Katoblastus*. It combines both primitive and derivative features.

We will now try to very briefly summarize and evaluate the phylogenetic trends shown by offshoot genera during the evolutionary radiation in the Lower Devonian. We have seen that two efforts to conceal the hydrospire slits were not successful *(Caryoblastus* and *Cryptoschisma)*, and that the third *(Pentremitidea)* was successful. Comparison of the methods used to conceal the hydrospire slits should give an indication as to which method was the most adaptive. *Caryoblastus* reduced the number of hydrospire folds, but became extinct. *Cryptoschisma* changed the form of its ambulacra; it also became extinct. But the third, *Pentremitidea,* has found for the first time how to effectively conceal the hydrospire slits, namely by internally conjoining them and giving up the parallel arrangement of the folds.

The Lower Devonian phaenoschismatids underwent an evolutionary radiation, experimenting in ways of concealing hydrospire slits. Internal conjunction of hydrospire folds has been very important later in blastoid evolution (orophocrinids, spiraculates). We have seen two efforts to completely expose the hydrospire slits with retention of the parallel arrangement of the folds, one of them being unsuccessful *(Pleuroschisma verneuli)*, the other successful *(Heteroschisma alternatum)*. The latter has retained the usual phaenoschismatid number of hydrospires and flattened the vault, the first has exaggerated the vault in order to build more hydrospire folds. Flattening the vault has been a successful evolutionary change (codasterids, neoschismatids).

OROPHOCRINID PHYLOGENY

The orophocrinids as now grouped systematically on a phylogenetic basis represent a younger stock of fissiculate blastoids, derived from the phaenoschismatids. The group arose in the Devonian in the Atlantic Basin (1 genus, N. Am., South Africa?). During the Mississippian the group flourished (5 genera) and had spread over the Atlantic Basin (N. Am., Eur.), and even penetrated into Near Asia. The family survived into the Permian. By that time, and before its extinction, it had migrated to South East Asia (1 genus, Timor).

As for the phaenoschismatids, treatment of the phylogenetic trends within the family of the orophocrinids will be done separately for several criteria in their order of phylogenetic importance. Distinct trends have been found for some morphological characters, while others have proved to have been essentially stable and conservative.

Distinct trends have been found in the composition of the anal area, the position of the gonopore in the anal area, the structure of the ambulacral areas, but, most important, in the structure of the hydrospire system. The phylogenetic trends are briefly summarized here and expanded upon below.

(1) The orophocrinids simplified the composition of the anal area. The original subdeltoid was first replaced by two cryptodeltoids, and these ultimately were replaced by an epideltoid. Simplification of hydrospire-forming anal deltoids involved a phylogenetic change in position of the gonopore from external to internal.

(2) Orophocrinids have phylogenetically elongated the ambulacra and exposed the lancets, probably in an effort to increase the food gathering capacity by enlarging the number of side plates and brachioles. The elongation of ambulacra affected thecal form; vaults grew larger, inflated, or in some forms became stellate.

(3) Most important in orophocrinids is the trend toward concealment and, later, conjunction of hydrospire folds; followed by gradual closure of the hydrospire cleft by secondary radial calcite, limiting the effective area of hydrospires; and, finally, reduction of hydrospire structures.

The constant and conservative morphological characters in the evolution of the orophocrinids can be summarized as follows. (1) The basic thecal shape has essentially remained constant, conserving a conical pelvis and a convex vault. (2) The hypodeltoid was not reduced, probably leaving the number of anal hydrospires unchanged.

Using the phylogenetic trends summarized above, we have established a lineage of orophocrinid genera in which the trends are most clearly observable. This lineage of genera, arranged according to their age, is the following: *Katoblastus* (Pl. VI, figs. 7–9, 11, 12, 14), *Orophocrinus* (Pl. VII, figs. 1–11; Pl. VIII, figs. 1–6; Pl. IX, figs. 1–9; Pl. X, figs. 4, 7), *Pentablastus* (Pl. IX, figs. 10–12), *Anthoblastus*. This group of genera is referred to below as the main orophocrinid stock. *Brachyschisma* (Pl. VI, figs. 2, 5, 6, 15) is interpreted as an early orophocrinid, mainly by extrapolating backwards in time the trends in the main orophocrinid stock. *Mastoblastus* (Pl. X, figs. 1, 2, 6) and several characters of *Acentrotremites* (Pl. X, figs. 3, 5), *Pentablastus*, and *Anthoblastus* (Pl. XI, figs. 1–3, 5, 6, 8, 9) show radiant trends in orophocrinid evolution.

We will now try to further explain each of our provisional statements on the phylogeny of morphological characters in the family of the orophocrinids. Although we regard the evolution of the hydrospire system as the main evolutionary event in the history of the group, we will start by explaining the phylogeny of thecal shape, because it later elucidates phylogeny of the hydrospires.

Thecal shape and growth patterns for main thecal elements. The earliest orophocrinid, *Brachyschisma*, is intermediate in size, reaching a maximum length near 15 mm. *Katoblastus* never became large and early species of *Orophocrinus* are also intermediate in size. Most of the later species (7) reach a maximum length between 30 and 40 mm. Other Mississippian orophocrinid genera *(Acentrotremites, Mastoblastus,* and *Pentablastus)* also develop to a similar size, with a maximum length near 30 mm. The two Permian species of *Anthoblastus* are somewhat smaller. Beginning with the Devonian praecursor, there was a gradual increase in maximum size in the orophocrinids; Permian forms are not as large but display different growth characteristics.

The basic thecal shape in the orophocrinids is generally a conservative character throughout the history of the group. From the beginning of their history, orophocrinid thecae had a conical pelvis and a hemispherical vault. Thecal shape of orophocrinids is derivable from the phaenoschismatids, as suggested by the form of *Katoblastus* (Pl. VI, figs. 7–9, 11, 12, 14). This genus has a conical pelvis and a near-conical vault, thus still being close to a phaenoschismatid biconical thecal shape. Heights of vault and pelvis in *Katoblastus* are subequal. Also, *Katoblastus* still has its ambulacra situated in an ambulacral sinus, although interambulacral pyramids are no longer present. In as far as thecal shape is concerned *Katoblastus* could be regarded as a rather good intermediate between phaenoschismatids and orophocrinids.

As derivatives of the phaenoschismatids, the orophocrinids gave up the interambulacral pyramids and the distinct ambulacral sinuses. They are no longer present in typical orophocrinids. Thecal shape of the orophocrinids has evolved away from the phaenoschismatids mainly by a different growth pattern of its deltoids. These have typically developed part of their DR sectors on the outer or external surface of the theca. The plates are no longer completely overlapped by the radials and they are no longer crested and adapted to form an ambulacral pyramid with the radial limbs. In the phaenoschismatids the full length of the RD suture lies within the ambulacral sinuses, and its full width is most always used for hydrospire formation. The orophocrinids have developed part of the DR sector on the external surface of the theca, and this is no longer used for hydrospire formation. The other part of the DR sector is brought to an internal position by suppression of the ambulacral sinus, and is exclusively used for hydrospire formation. The exposure of part of the deltoid, along with suppression of interambulacral pyramids and ambulacral sinuses, results in a reduction of the effective length of the RD suture available for hydrospire formation.

The hemispherical orophocrinid vault is typically developed in *Brachyschisma* (Pl. VI, figs. 5, 15), *Orophocrinus* (Pls. VII–IX), *Mastoblastus* (Pl. X, fig. 2) and *Anthoblastus brouweri* (Pl. XI, fig. 3). Some *Orophocrinus* species (e.g. *O. conicus*, Pl. VII, fig. 4; *O. praelongus* Pl. VIII, fig. 3; and *O. pentangularis*, Pl. IX, fig. 3) are conservative in preserving a high conical pelvis and a low vault. Other *Orophocrinus* species (e.g. *O. stelliformis*, Pl. VII, fig. 9) have advanced and the vault has grown out at the expense of the pelvis.

There is a tendency in the later orophocrinids to accentuate the vault at the expense of the pelvis. This is very notably so in *Acentrotremites* (Pl. X, fig. 5) and *Pentablastus* (Pl. IX, fig. 10) where the base is depressed and formed by very small basals. In some cases (e.g. *Orophocrinus stelliformis*; *Anthoblastus stelliformis* Pl. XI, figs. 5, 6) expansion of the vault has produced a stellate thecal shape. We think the trend to develop the vault is caused by a tendency to elongate the ambulacra in an effort to increase the number of side plates and brachioles. The need for larger vaults was effected in different ways. In *Acentrotremites* and *Pentablastus* it has been brought about by inflation of the vault, in other forms by adding calcite on the external surfaces of thecal plates. Deposition of calcite on external surfaces has occurred in *Anthoblastus stelliformis* where it produced elevated deltoids and pronged radials for accommodation of the very elongate ambulacra.

The trend in the development in thecal shape in orophocrinid evolution is: changing thecal shape from nearly biconical with pelvis and vault of about equal height *(Katoblastus)* to a form with conical pelvis and convex vault *(Orophocrinus*; *Mastoblastus*; and *A. brouweri*, Pl. XI, fig. 1–3). Gradually less emphasis was placed on the development of the pelvis (extremely so in *Acentrotremites* and *Pentablastus*). Conservative trends are seen in some orophocrinid species which preserved the high conical pelvis (e.g., *O. conicus*, *O. pentangularis*, and *O. praelongus*) while others are highly advanced, having developed stellate theca (*O. stelliformis* and *Anthoblastus stelliformis*).

In the Devonian *Brachyschisma*, the basals have a conical form similar to many phaenoschismatids but a BA axis is lacking and secondary calcite was deposited. The basals become de-emphasized during the Mississippian. In the Tournaisian *Katoblastus*, they form only the lower part of the theca and there is strong deposition of secondary calcite in one species. They are usually conical in *Orophocrinus* but reduced in relative size and the lower portion is covered by secondary calcite. In two genera *(Acentrotremites* and *Pentablastus)* their outline is completely modified. Here they form part of a basal concavity and are quite small relative to the other plates. The earlier Permian species of *Anthoblastus*, *A. brouweri*, retains broadly conical basals but these are quite modified in the later *A. stelliformis* by the secondary deposition of calcite on the outer surface of the plate.

The radial of a Devonian *Brachyschisma* looks similar to that of a phaenoschismatid except that the RD sector has been flattened to lie in the same general plane as the ambulacrum and the origin is at the apex of a steeper pyramid. RB has been somewhat de-emphasized. In the Mississippian we find the development of an external growth sector for RD in *Katoblastus* and *Orophocrinus* and other later forms. The hydrospires lie in a hydrospire cleft. Much more emphasis is placed on RD and less on RB. The origin of the radial moves lower and lower on the theca relative to the oral opening with the consequent expansion of the ambulacrum and its number of brachioles. The maximum development of this is found in *Acentrotremites* and *Pentablastus* where the ambulacra reach almost to the base. Two Mississippian genera *(Katoblastus* and *Orophocrinus)* show an ontogenetic acceleration of RD in some or most of their species. The development of a super- and inferradial in *Pentablastus* is accompanied by deposition of secondary calcite on parts of the radial. In the Permian, secondary calcite deposition further modifies the radial shape, particularly in *Anthoblastus stelliformis*, where the radial is extended into a scoop-shaped prong.

The deltoid also undergoes modification. Its adoral breadth has increased in *Brachyschisma* while aborally it still somewhat resembles a crest. In the Mississippian all forms have an external DR sector. This is less developed in the earlier *Katoblastus* than the other genera. The deltoid remains confined to the upper surface of the theca but now forms part of the lateral thecal wall. The shape of the deltoid is further modified in the Permian *Anthoblastus* by the deposition of secondary calcite to form mound or pyramid-shaped elevations.

Hydrospires. Phylogenetic trends in the formation of hydrospires are exemplified by the genera *Katoblastus*, *Orophocrinus*, *Pentablastus*, and *Anthoblastus*, in which there are invariably 10 groups of hydrospires. We have defined them as the main orophocrinid stock. The evolutionary trends shown by them are important to an understanding of the phylogeny and systematics of the genus *Brachyschisma* (Pl. VI, figs. 2, 5, 6, 15).

Phylogenetic consideration of the hydrospire system in the orophocrinids should start with *Katoblastus*. With respect to hydrospire structure *Katoblastus* again shows the affinity of the orophocrinids with the phaenoschismatids from which they are derived. We have already seen that the ambulacral sinuses are still present in *Katoblastus*, and hence there is still space for a sub-parallel arrangement of the hydrospire folds in the sinus wall. The hydrospires of *Katoblastus* have a rather primitive construction: they are thick-walled and have no differentiation into hydrospire lamellae and hydrospire ducts. Conjunction of hydrospire folds has certainly not developed very much in *Katoblastus*; the folds are still arranged sub-parallel. The hydrospire slits of *Katoblastus* are nearly completely concealed; only occasionally is the abmedial hydrospire slit exposed. The hydrospires are functional over their full length. Entrance to the hydrospires is by way of hydrospire clefts at both sides of the ambulacra, extending the full length of the ambulacra. There is no infilling by seconary calcite from the radial underneath the lancet, nor in or in between the hydrospires.

The genus *Orophocrinus*, as now systematically defined, comprises a group of species which show essentially the same trends in the construction of the hydrospires. We have observed gradual differences in hydrospire construction between North American and European species. Unfortunately not all *Orophocrinus* species could be studied anatomically. One of these is *O. orbignyanus*, the oldest European species of *Orophocrinus*.

O. orbignyanus (Pl. VII, figs. 3, 8) is still primitive in having preserved a high conical pelvis, but is more advanced than *Katoblastus* in its complete concealment of hydrospire slits. It has left the hydrospire clefts completely open. Unfortunately, no statement can be made on the state of conjunction of its hydrospires, neither can this be done for the state of differentiation of hydrospires. The species is regarded as the most primitive *Orophocrinus* species now known.

The two European *Orophocrinus* species that could be studied anatomically are *O. praelongus* (Pl. VIII, figs. 1, 3) and *O. verus* (Pl. VIII, figs. 4, 6; Pl. X, fig. 7). The species differ in thecal shape: the first has preserved a primitive high conical pelvis, whereas the latter has developed a larger, convex vault. They have close affinity in the structure of the hydrospires and differ from their North American relatives. *O. praelongus* and *O. verus* both have the hydrospire slits completely concealed, and the hydrospires strongly conjoined (textfigs. 29.9; 30.7). The differentiation of hydrospire folds into hydrospire lamellae and hydrospire ducts is distinctly, although weakly, present in *O. praelongus* (textfig. 29.9) and it is perfectly developed in *O. verus* (textfig. 30.7). Both species are more advanced in conjunction and differentiation of hydrospires than their American relatives. However, they are less advanced in the closure of the hydrospire clefts. The clefts are still open over almost the entire length of the ambulacra in *O. praelongus*, and only the aboral extremity is closed off by deposition of secondary radial calcite. In *O. verus* closure of the hydrospire cleft is more advanced, about ⅓ of the total length being closed. Consequently the deposition of secondary radial calcite is stronger.

The two North American *Orophocrinus* species that could be studied anatomically are *O. conicus* and *O. stelliformis*. They do differ from their European relatives, but this is found to be only a matter of degree. They show the same phylogenetic tendencies. *O. conicus* and *O. stelliformis* – like their European relatives – mutually differ in thecal shape: the first has preserved a primitive high conical pelvis (Pl. VII, fig. 4), whereas the latter has developed a larger, convex vault (Pl. VII, fig. 9). They have close affinities in the structure of their hydrospires. *O. conicus* and *O. stelliformis*, like their European relatives, have completely concealed the hydrospire slits, but unlike the European relatives, the hydrospires are not strongly conjoined (textfigs. 27.5; 28.4–8) nor strongly differentiated into hydrospire lamellae and hydrospire ducts. In these respects the two species fall phylogenetically behind the European relatives. They are, however, more advanced in closure of the hydrospire cleft. In both American *Orophocrinus* species studied anatomically the aboral half of the hydrospire cleft is closed and the deposition of secondary radial calcite in the hydrospire cleft, under the lancet, and inbetween the hydrospires is stronger than in European *Orophocrinus* species.

Closure of the hydrospire cleft in *Orophocrinus* is further effectuated by infilling of deltoid material in the clefts along DR front.

All *Orophocrinus* species show further phylogenetic development than *Katoblastus* by: complete concealment of the hydrospire slits, gradual conjunction of hydrospire folds (along with differentiation into hydrospire lamellae and hydrospire ducts in some species), and gradual closure of the hydrospire cleft by infilling of secondary radial calcite inbetween the hydrospires and in the hydrospires, thus limiting the functional area of the hydrospires.

The phylogenetic trend in hydrospire structures found from *Katoblastus* to *Orophocrinus* is further developed in a direct line to *Pentablastus* (Pl. IX, figs. 10–12). In that genus the conjunction of hydrospire folds is complete, the closure of hydrospire cleft far advanced (only the adoral ⅓ is open) and deposition of radial calcite inbetween hydrospires and also under the lancet is extreme. The aboral parts of the hydrospire folds no longer hang freely in the thecal cavity, but are completely filled in, and enclosed by a body of secondary calcite that occupies a large volume of the aboral part of the thecal cavity. *Pentablastus* shows an extreme loss of function in the hydrospires; only the adoral parts are believed to have been functional.

The genus *Acentrotremites* (Pl. X, figs. 3, 5) has developed a thecal shape which is similar to that of *Pentablastus*. Access to the hydrospires is via a restricted hydrospire cleft which has been subdivided into a series of openings by a series of bars secreted by the radial. *Acentrotremites* is one of the rarest blastoids and the only information available on the internal structure is a paper by PHILLIPS (1936). Her figures (1936, figs. 4–10) show that the hydrospires are conjoined and differentiated into hydrospire lamellae and ducts.

Thus far, the main trend in orophocrinid hydrospire evolution has been to reduce their external accessibility by conjoining them, and partially closing them off by secondary infilling of hydrospire clefts. The latter has sometimes also involved an infilling of the hydrospires themselves. Reduction in size and number of hydrospire structures is a further possible step. This has occurred phylogenetically in both *Anthoblastus* and *Mastoblastus*. *Anthoblastus*, although much younger than *Mastoblastus*, is considered closer to the main phylogenetic stock, because reduction of the hydrospires is far less advanced than in *Mastoblastus*.

Anthoblastus (Pl. XI, figs. 5, 6) still preserves a very short hydrospire cleft (textfigs. 32.4, 5), mostly developed inbetween the deltoids and the ambulacra. Small bi- or trilobed hydrospire sacs are present over a slightly longer extent than the hydrospire cleft. The form of its hydrospires (bi- or trilobed sacs, textfigs. 32.5, 6) is seen phylogenetically as a further and extreme conjunction of individual hydrospire folds, and to be a simple continuation of earlier trends toward conjunction of hydrospires seen in Mississippian orophocrinids. Its very short hydrospire cleft is also seen as a continuation of a trend toward closure of hydrospire clefts in Mississippian orophocrinids. The only new character it has is the reduction in hydrospire-formation along the borders of the radials and the ambulacra. It has also given up deposition of secondary calcite within the theca. By reducing the hydrospires it shows a continuation of the tendency of Mississippian orophocrinids to reduce the functional area of the hydrospires.

Mastoblastus (Pl. X, figs. 1, 2, 6) has been shown to lack hydrospire clefts and to have only rudimentary hydrospire folds (textfigs. 26.9–11). The form is interpreted phylogenetically as having completed the trend toward closure of the hydrospire cleft and to have developed only rudimentary hydrospires. This means an almost complete reduction of hydrospires. The form is phylogenetically regarded as an offshoot, showing nearly complete reduction of hydrospires at an early moment (Lower Namurian).

The main phylogenetic trends in hydrospire structures in the orophocrinids can now be summarized as follows: (1) complete suppression of ambulacral sinuses and consequent concealment of hydrospire slits with conjunction of hydrospire folds later; (2) gradual closure of hydrospire clefts by infilling of secondary radial calcite and consequent limitation of the functional area of the hydrospires, especially in the aboral parts; (3) resultant reduction of hydrospires in ultimate members of the family. The phylogenetic trend in the orophocrinid hydrospire structures is the most important evolutionary trend during the history of the group.

By extrapolating our phylogenetic trend in hydrospire structures of the main orophocrinid stock backward in time, we could expect a Devonian orophocrinid to have more fully exposed hydrospire slits, sitting subparallel in structures like ambulacral sinuses. This condition is present in *Brachyschisma*, a form with a rather typical orophocrinid growth pattern for the main thecal plates. However, *Brachyschisma* has used full width of the RD suture for hydrospire-formation, but it has restricted them in functional length, probably by infilling of secondary calcite. This latter is a phenomenon also found in some latter Mississippian orophocrinids, and could be looked at as a primitive feature of the family. For the above reasons we have included *Brachyschisma* in the family of the orophocrinids in our phylogenetic classification.

Anal hydrospires. There is perhaps an early phylogenetic trend toward formation of more anal hydrospires. Mississippian members of the main orophocrinid stock almost always have an equal number of anal and regular hydrospire folds. One exception is *Orophocrinus praelongus*, where the number of anal hydrospires may be slightly reduced. The number of anal hydrospires of *Katoblastus pūzos* is generally slightly reduced. In *Brachyschisma* there are only nine hydrospire groups, the one at *D* anal side being absent. All this is – not too strong however – evidence for a phylogenetic increase in the number of anal hydrospires. This trend would be parallel to the same trend observed in the phaenoschismatids.

Anal deltoids. The phylogenetic development of anal deltoids in the orophocrinids shows a trend parallel to what has been demonstrated for the hydrospire-forming anal deltoids of the phaenoschismatids. Hydrospire-forming anal deltoids in the orophocrinids are the subdeltoid, the cryptodeltoids, or the epideltoid.

Brachyschisma (M. Dev.) preserves a subdeltoid (textfigs. 24.1–7). As we have seen earlier in the account of the phaenoschismatids, anal deltoids, we regard a subdeltoid of Middle Devonian age as a very late appearance of that plate. In fact the plate is unknown in post Middle Devonian times. We also believe that in Middle Devonian times the subdeltoid was being eliminated with consequent loss of its functions (hydrospire-formation and formation of an external gonopore). *Brachyschisma* is another good example of this same phenomenon. Its subdeltoid has reduced one of its limbs (*D* side) and lost the hydrospire-forming function there; the other limb (*C* side) of the plate is only moderately developed and has developed only a reduced number of anal hydrospires. The subdeltoid in *Brachyschisma* has retained the function of forming an external gonopore in the suture between the subdeltoid and the superdeltoid.

As in the phaenoschismatids, the subdeltoid is phylogenetically replaced by two cryptodeltoids. *Katoblastus* is the only known orophocrinid that definitely has cryptodeltoids (textfig. 25.6). The plates are incompletely developed, coming in contact with the superdeltoid, but not meeting laterally adoral from anus (textfig. 25.5). By not doing so the two cryptodeltoids have lost the function of forming an external gonopore (as in *Phaenoblastus*). The plates have only developed a reduced number of anal hydrospires.

All other orophocrinids (except perhaps *Acentrotremites*) possess an epideltoid, which is hydrospire-forming (textfigs. 27.4; 28.6; 29.9; 30.6; 31.3; 32.5). If an epideltoid is present the number of anal hydrospires is generally (with the exception of *Orophocrinus praelongus*) not reduced. The orophocrinid epideltoid forms an internal gonopore (textfig. 28.6).

The problem we discussed earlier on the homology of the phaenoschismatid epideltoid, also fully applies to the orophocrinid epideltoid.

The phylogenetic development of the orophocrinid hypodeltoid is conservative, not showing a distinct trend. The plate has always a growth front on the outer or external surface of the theca, and contributes to the outer body wall.

Concluding, we may state that the hydrospire-forming anal deltoids of the orophocrinids underwent the same phylogenetic change as the phaenoschismatids. This trend is simplification of the anal area by (1) loss of the subdeltoid, (2) replacement of the subdeltoid by two cryptodeltoids, and ultimately (3) replacement of two cryptodeltoids by an epideltoid. Along with simplification of the anal area, there is a change of position of the gonopore from external in early members to internal in later members. If there is an increase in the number of anal hydrospires, it cannot (as in the phaenoschismatids) be connected with a phylogenetic reduction of the hypodeltoid.

Ambulacral shape. The form of orophocrinid ambulacral areas is essentially a stable character during the history of the group. In all seven known genera now attributed to the family, the ambulacra are linear, sublanceolate or lanceolate, without showing a distinct trend to widen the ambulacra in time from linear to lanceolate. In fact we may conclude that the orophocrinids did not try to develop wider ambulacra. As far as we now know they never developed a wide petaloid ambulacral shape. As we will see below, there is a tendency for some later orophocrinids to elongate the ambulacra. Absence of phylogenetic widening of ambulacra, and presence of phylogenetic elongation of ambulacra will provide a good clue for understanding orophocrinid evolution (see Conclusions below).

There is a tendency in orophocrinid ambulacra to phylogenetically expose the lancet. By analogy with trends found in the phaenoschismatids, we take it that a concealed lancet is the primitive condition. This condition is indeed present in the oldest known orophocrinid genus *Brachyschisma*. Most Mississippian members have gradually exposed the lancet. *Katoblastus* has its lancet exposed over $\frac{2}{3}$ of its length and *Orophocrinus* and *Mastoblastus* have the lancet exposed over their entire lengths. *Acentrotremites* and *Pentablastus*, however, have retained the primitive condition of a concealed lancet.

Anthoblastus has developed one of the most extraordinary ambulacra now known among the fissiculates. The lancet in that genus is widely exposed. It is the only known example of a fissiculate lancet having developed considerable (obliquely outward directed) lateral growth fronts in the lancet, thus producing a scoop-like plate. The scoop of *Anthoblastus* is interpreted phylogenetically as having started from a normal, but exposed, orophocrinid lancet, having added, during growth, more calcite on its outer lateral surfaces, thus pushing the side plates upwards and forming a depressed central area in the ambulacral field. By developing lateral growth in the lancet, the genus *Anthoblastus* has certainly undertaken to introduce a new element in the phylogeny of the ambulacral structures. But it has done so on an essentially orophocrinid growth pattern.

A most important change in the ambulacra of the orophocrinids is a trend toward elongation of the ambulacra. This trend is not consistently present in all members of the main stock of the orophocrinids, rather they are scattered, but very significant examples of this phenomenon. Elongation of ambulacra is absent in *Brachyschisma*, *Katoblastus*, *Mastoblastus*, European species of *Orophocrinus* except *O. verus*, the American species *Orophocrinus conicus*, *O. catactus*. Elongation of ambulacra is distinctly present in *Orophocrinus stelliformis*, *O. saltensis*, *O. verus*, and in *Anthoblastus*, *Acentrotremites*, and *Pentablastus*. The trend toward elongation of ambulacra is directly correlated with the trend to inflate the vault in the same genera and species. We hold that elongation of ambulacra caused the forms to further accentuate the vaults in order to accommodate the longer ambulacra. The different consequences this had for thecal shape are discussed in the paragraph on thecal shape.

Orophocrinid elongation of ambulacra probably is an effort to develop more side plates and more brachioles on the ambulacra. This would be interpretable as a response for the need to enlarge the food-gathering capability of the total brachiolar area.

Conclusions. We believe that orophocrinids are derived phylogenetically from the phaenoschismatids, and more precisely from a member of the main phaenoschismatid stock. If we think of *Katoblastus* (L. Carb., Tournaisian) as an orophocrinid still preserving some phaenoschismatid-like features, it would appear that *Pleuroschisma* (and more precisely a Middle Devonian *lycorias* type of form) in the main phaenoschismatid stock most closely resembles *Katoblastus*. Both forms have a similar composition in the anal areas. *Pleuroschisma* also has the right age to be an approximate phaenoschismatid forerunner of the orophocrinids.

The changes involved in deriving an orophocrinid from the phaenoschismatids are: suppression of interambulacral pyramids and ambulacral sinuses, along with concealment, conjunction and final reduction of hydrospires, and elongation of ambulacra.

The orophocrinids are seen phylogenetically as a group of fissiculate blastoids which experimented with the hydrospire structures by bringing them into a completely internal position. Some members of the group have not preserved functional hydrospire structures. Bringing hydrospires into an internal position is not disadvantageous. We know from the spiraculates that fully internal hydrospires are effective structures, provided there are effective incurrent and excurrent structures. The spiraculates have developed both hydrospire pores and spiracles for that purpose. However, the orophocrinids have neither developed true hydrospire pores nor spiracles, and consequently reduced and/or gave up functional hydrospires. This interpretation of the evolution of the blastoids now suggests that fully internal hydrospires are not functionally advantageous unless hydrospire pores and spiracles are developed as effective structures for incurrent and excurrent water.

In this context we may find a key to understanding the seemingly strange and aberrant form *Acentrotremites*. This genus is now interpreted as having been the only orophocrinid form ever to have developed openings resembling hydrospire pores in an effort to create effective structures for directing incurrent water into the hydrospires. The genus, however, was not successful in establishing effective spiracles of which there are none. It has merely built openings by the indentation of the RD sector bordering the ambulacra. In this way it has partially bridged the hydrospire cleft. For the above reasons we have put *Acentrotremites* within the orophocrinids. In all other essential characters it very closely corresponds with the orophocrinids. We interpret the genus as an offshoot from the main orophocrinid stock attempting to retain effective hydrospires.

If we are right in attributing a respiratory function to the hydrospires, the phylogenetic decrease and final reduction of the hydrospires would have meant a decrease in hydrospire respiration. A compensation for this could have been an increase in the other blastoid respiratory surface: the ambulacral epidermis and the tube foot epidermis. This respiratory surface is mainly situated on the brachioles. We would indicate this as brachiolar respiration, as contrasted with hydrospire respiration. We could think of a physiological balance in total respiration between hydrospire respiration and brachiolar respiration. Probably the trend we observed to increase the ambulacral length had the effect of adding more brachioles and ambulacral tissue, thus increasing the effectiveness of brachiolar respiration to compensate for the phylogenetic loss of hydrospire respiration.

If orophocrinids phylogenetically shifted their respiratory method from hydrospiral to brachiolar, this may have been brought about by independent ecological needs to increase the food gathering surface, that is to increase the number of brachioles and tube feet. Once the animal has effectuated this, it found itself also provided with an effective means for brachiolar respiration, and consequently was able to gradually give up hydrospire respiration. We do not need to think of orophocrinids as unsuccessful. We have seen that the only way of preserving hydrospire respiration in fully internal hydrospires is to provide them with pores and spiracles. Only *Acentrotremites* experimented with this.

Other reasons can be suggested for the reduction of orophocrinid hydrospires. The use of long slits which open directly to the surrounding medium is found in the more primitive blastoids and rhombiferan cystoids. Forms using this type of respiratory structure do not persist in time. Internal hydrospires provided with pores and spiracles may have had a more efficient in- and excurrent mechanism, but modeling studies are needed to verify this.

NYMPHAEOBLASTID PHYLOGENY

The nymphaeoblastids as now grouped systematically on a phylogenetic basis represent, like the orophocrinids, a younger stock of fissiculate blastoids derived from the phaenoschismatids. The group arose in the Devonian at the eastern side of the Atlantic Basin (1 genus, S. Afr.). During the Mississippian the group spread over the Atlantic Basin (1 genus, N. Am. and Europe), and even penetrated into eastern Europe, Asia and Australia (1 genus). The family survived into the Permian. By that time, and before its extinction, it had restricted its occurrence to South East Asia (1 genus, Timor).

Distinct phylogenetic trends have been found for the thecal shape, the ambulacral structures, and the hydrospire system. The phylogenetic trends are briefly summarized here and expanded upon below.

(1) Thecal shape has changed from nearly biconical to ellipsoidal and spheroidal; the process involved emphasis on growth in the vault at the expense of the pelvis.

(2) Change in thecal shape is connected with, and probably caused by, a tendency to elongate the ambulacra.

(3) Functional hydrospire surfaces were reduced phylogenetically, either by infilling of hydrospire slits, or by not using the full width of the RD suture for hydrospire formation.

The constant and conservative morphological characters in the evolution of the nymphaeoblastids can be summarized as follows:

(1) The form and composition of the ambulacral areas is constant.

(2) The hypodeltoid was not reduced.

(3) The basic growth patterns for radials and deltoids were unchanged, although the relative rates were modified.

(4) The number of hydrospire groups remained constant.

Using the phylogenetic trends as summarized above, we will provisionally regard the lineage of the four known nymphaeoblastid genera *Pachyblastus* (Pl. XII, figs. 1, 2; Pl. XIII, fig. 1), *Xenoblastus* (Pl. XIII, figs. 2–8), *Nymphaeoblastus* (Pl. XIV, figs. 1–6; Pl. XV, figs. 2, 8), and *Sphaeroschisma* (Pl. XV, figs. 4, 5, 7) as the main nymphaeoblastid stock until more forms become available and anatomical studies can be made. The number of genera now included in the nymphaeoblastids is too small to be sure of real offshoot trends in each of the genera. Anatomical studies are badly needed since no serial sectioning of any of the known members could be done during this study. This limited our phylogenetic interpretations.

We will now try to further explain each of our provisional statements on the phylogeny of morphological characters in the family of the nymphaeoblastids. As for the orophocrinids we regard changes in thecal shape, ambulacral length, and hydrospire reduction to be interrelated and caused by the same principle agent(s).

Thecal shape and growth patterns for main thecal elements. The thecal size of the first nymphaeoblastid, *Pachyblastus* approaches 40 mm in length, making it one of the largest of all Devonian fissiculates. The genus *Xenoblastus* (Miss.) also was of similar size as were most representatives of *Nymphaeoblastus* (Miss.); one representative is one of the largest of all fissiculates (over 70 mm). In contrast, the Permian *Sphaeroschisma* is small. Thus, once developed, nymphaeoblastids maintained a large thecal size except in the Permian.

There is a distinct evolutionary trend in the development of the theca. The earliest nymphaeoblastid now known is *Pachyblastus* (Dev.; Pl. XII, figs. 1, 2; Pl. XIII, fig. 1). Its thecal shape is reminiscent of the biconical thecal shape of the phaenoschismatids. *Pachyblastus* still has a conical pelvis with upflaring basals; the vault is high and convex and has structures reminiscent of flattened out interambulacral pyramids. A subdued deltoid crest is present. Its cross-section is still pentagonal as in the phaenoschismatids.

Xenoblastus (Pl. XIII, figs. 2–8) and *Nymphaeoblastus* (Miss.; Pl. XIV, figs. 1–6; Pl. XV, figs. 2, 8) have a low pelvis and high vault, the thecal shape is essentially ellipsoidal with rounded pentagonal cross-section and low basals which are no longer upflaring, but are situated in near-horizontal bases. In *Sphaeroschisma* (Perm.; Pl. XV, figs. 4, 5, 7) the theca is spherical with small downflaring basals in a depressed base.

Nymphaeoblastids have phylogenetically changed their thecal shape from near-biconical through ellipsoidal to spherical, changed the cross-sections of thecae from pentagonal through rounded pentagonal to circular, and restricted the growth in the basals. A main trend is the emphasis the nymphaeoblastids placed on further outgrowth of the vault at the expense of the pelvis. This trend is also seen in some orophocrinids. As in that family, outgrowth of the vault is directly correlated with further elongation of the ambulacra.

The basals of the Devonian *Pachyblastus* are conical but much reduced in emphasis compared with the phaenoschismatids. In the Mississippian they are much de-emphasized, being almost flat in *Xenoblastus* or in a basal concavity in *Nymphaeoblastus*. The basals of the Permian *Sphaeroschisma* form a very broad cone, resembling those of *Xenoblastus*. In these three latter genera, the basals are extremely reduced compared to other plates.

Concomitant with the relative reduction of the basals, the RB sector is reduced to its smallest relative value in the nymphaeoblastids and the RD sector reaches its maximum expression. In this way the ambulacra come to reach all the way to the thecal base and the number of brachioles is considerably expanded when compared to a phaenoschismatid. The deltoid also increases in importance, becoming relatively larger and broader and forming part of the lateral thecal wall.

In all members of the nymphaeoblastids the DR sectors are fully exposed on the external surface of the theca. The DR sectors are growing downward from the origins of the plates. The transition from a phaenoschismatid ancestor into a nymphaeoblastid would require a suppression of the interambulacral pyramids by flattening them out and simultaneously subduing the deltoid crest. This can only be accomplished by downgrowth of the deltoids and bringing RD and RR sectors into the same plane. Only under these conditions can thecal integrity be preserved. By such a process the RD suture and all the hydrospire slits formed across it are exposed on the outer surface of the theca. The type of vault then obtained is present in *Pachyblastus*. We interpret this form as the "missing link" between the nymphaeoblastids and the phaenoschismatids, an interpretation enhanced by its Devonian age.

Ambulacral shape. The ambulacral shape of the nymphaeoblastids is a conservative character throughout the history of the group. Ambulacra have always remained linear or sublanceolate structures. There is not sufficient information to allow a statement on a possible phylogenetic exposure of the lancet, such as has indeed occurred in the phaenoschismatids and the orophocrinids. Also, no definite statement can be made whether ambulacra were conspicuous or not. *Pachyblastus* and *Xenoblastus* have conspicuous ambulacra, while they are not in the other two members. However, it is not clear if this reflects a true evolutionary trend in the groups.

All nymphaeoblastids have very elongate ambulacra. Compared to their phaenoschismatid ancestors, they have phylogenetically increased ambulacral length, adding more side plates and brachioles to the ambulacra. Also within the history of the group we see a further trend for elongation of the ambulacra. We believe that an effort to elongate the ambulacra caused the vault to further grow out. As in the orophocrinids we believe that the tendency to elongate the ambulacra is of prime importance for understanding the phylogenetic changes within the group.

In all nymphaeoblastids of the main stock, as provisionally defined above, there are invariably ten groups of hydrospires. There is no trend observable in this character. Hydrospires are, with the exception of *Sphaeroschisma*, placed parallel to one another, the slits being completely exposed on the external surface of the theca. This is believed to be the primitive nymphaeoblastid condition for the hydrospires.

In *Xenoblastus* the total functional area of the hydrospire slits is reduced by filling in both ends of each slit with secondary calcite. The full length of RD suture is not used for hydrospire formation. Consequently the number of hydrospire folds in regular groups is not large, but infilling is not strong.

The total functional area of the hydrospire slits is further reduced in *Nymphaeoblastus* by stronger infilling by secondary calcite, particularly in the deltoid region. The full width of the RD suture is still used for hydrospire formation. Consequently the number of hydrospire slits in *Nymphaeoblastus* is larger than in *Xenoblastus* but in *Nymphaeoblastus* the infilling of the hydrospire slits is much stronger. Both Mississippian nymphaeoblastid genera show a distinct phylogenetic trend to reduce the total functional area of the hydrospire slits by infilling. Only one of them *(Xenoblastus)* reduced the number of hydrospire folds by not using the full width of RD suture in hydrospire formation.

Sphaeroschisma shows a further continuation of the trend already started in *Xenoblastus*. It has further reduced the number of hydrospire folds by developing less hydrospires across the RD suture. In some of the ten positions only one hydrospire fold may be developed. If there are two or three per group, there may be a conjunction of the aboral parts of the hydrospire folds, using one common slit bordering the ambulacrum.

It has been very unfortunate that we have not been able to make anatomical studies of the nymphaeoblastids. Scarcity and mode of preservation has precluded this. All our statements on phylogeny of the hydrospire system are based upon what is observable from the external surface of the theca; this is hydrospire slits only. No general statement can be made on internal conjunction and differentiation of hydrospires, nor about internal deposits of secondary calcite in and inbetween hydrospire folds. Further research on new finds should clarify these points. We can only say that in the nymphaeoblastids there is a distinct phylogenetic trend toward reduction of the hydrospire system. Reduction is brought about either by infilling of hydrospire slits by secondary calcite, or by not using the full width of RD suture for hydrospire formation.

The reduction of the functional length of hydrospire slits is correlated with a trend to elongate the ambulacra in the nymphaeoblastids. This same correlation exists in the orophocrinids where phylogenetic reduction in the hydrospire system occurs with phylogenetic elongation of the ambulacra. It is very significant that the nymphaeoblastids now offer a second example of this same phenomenon. Here again, we suggest that the correlation between the two trends lies in respiration. Elongated nymphaeoblastid ambulacra had more side plates and brachioles, hence they had more ambulacral and tube foot epidermis available as a respiratory surface. Brachiolar respiration may possibly have been very effective, and to have allowed hydrospire respiration to decrease. The total respiration balance for the two respiratory surfaces might have remained unchanged.

Anal hydrospires and anal deltoids. The anal area of nymphaeoblastids is poorly known. Only in *Nymphaeoblastus* are we sure that there is an epi- and hypodeltoid. In all other members of the group there is a lack of information on the exact composition of the anal area. Available data suggest that a hypodeltoid is present throughout. The hypodeltoid does not form hydrospires in *Pachyblastus* and *Sphaeroschisma*, whereas it does in *Nymphaeoblastus*.

There is no information on a possible trend toward phylogenetic reduction of anal hydrospires. Rather, there is probably something to say in favor of more fully developing the anal hydrospires during phylogeny. In the primitive form *Pachyblastus* the number of anal hydrospires is reduced, whereas this is not the case in other members where known.

Increase in the number of anal hydrospires in the nymphaeoblastids would be a trend concurrent with the trends observed in the phaenoschismatids and the orophocrinids.

Conclusions. In our opinion the nymphaeoblastids were derived from a phaenoschismatid ancestor early in the Devonian. The group cannot logically be derived from one of the early phaenoschismatid offshoot genera known from the Lower Devonian, simply because they do not seem to have developed the right characters to derive a nymphaeoblastid from. The nymphaeoblastids seem to have radiated directly from the main phaenoschismatid stock.

The newly discovered genus *Pachyblastus* from the Devonian of South Africa is interpreted as a nymphaeoblastid preserving many phaenoschismatid-like characters, and still being close to its phaenoschismatid origin.

Evolution of the nymphaeoblastids, as now suggested by the organization of *Pachyblastus* must have been brought about by suppression of the phaenoschismatid interambulacral pyramids. As we have seen, this can only be accomplished by downgrowth of the DR sectors from the origin, and by bringing the DR, RD and RR sectors into one plane. If this is done the RD suture and its hydrospire slits come to lie in an exposed position on the external surface of the theca. A nymphaeoblastid thecal organization is now achieved.

Three important trends were shown in the evolution of the nymphaeoblastids: an expansion of the vault at the expense of the pelvis, a further elongation of the ambulacra and a decrease in functional hydrospire slit area. These three trends are parallel to the same trends in the orophocrinids. It is believed, as more fully discussed under Phylogeny of the orophocrinids that these three trends are interrelated and caused by a principle agent(s). Of prime importance is the trend toward further elongation of the ambulacra, adding more side plate and brachioles to the ambulacra, probably in an effort to increase food gathering capacity of the animal. Consequently vaults have to grow out in order to accommodate the longer ambulacra. Longer ambulacra, having more brachioles, would possess a larger respiratory surface, and would have been able to effect more efficient brachiolar respiration. If this condition was present, less emphasis had to be placed on hydrospire respiration. Consequently a reduction of the hydrospire surface followed.

Orophocrinids and nymphaeoblastids both have reduced the hydrospire system. The first group had to reduce fully internal hydrospires, the latter group fully exposed hydrospires. Both have used essentially similar methods for this reduction: infilling by secondary calcite and reduction of number of folds per group.

NEOSCHISMATID PHYLOGENY

The neoschismatidae as now grouped systematically on a phylogenetic basis, represent, like the orophocrinids and the nymphaeoblastids, a younger stock of fissiculate blastoids, derived from the phaenoschismatids. The group arose late in fissiculate evolution (probably in the Upper Devonian). The earliest known member is of Mississippian age, and occurred in the Atlantic Basin (N. Am., and probably Europe). The group is unknown from the Pennsylvanian. In Permian times it had its maximum development (6 genera) and occurred in South East Asia (Timor) and Australia.

Distinct phylogenetic trends have been found in ambulacral and hydrospire structures. The phylogenetic trends are briefly summarized here, and expanded upon below.

(1) There is a slight tendency for Permian neoschismatids to increase growth in the DD sectors, thus somewhat removing the ambulacra from the peristome.

(2) In Permian neoschismatids from Timor there is either a trend

toward further elongation of ambulacra, or, quite the opposite, toward reduction of ambulacra.

(3) In all Permian neoschismatids there is a tendency to decrease the functional area of hydrospires by infilling of the hydrospire slits.

The constant and conservative morphological characters in the evolution of the nymphaeoblastids can be summarized as follows:

(1) Neoschismatids have essentially preserved their original thecal shape. Only in case of elongation of ambulacra has the thecal form been modified. A deltoid crest is present, as are ambulacral sinuses.

(2) Composition of anal area has remained unchanged in neoschismatid phylogeny.

(3) Hydrospire structures of neoschismatids are essentially unchanged; there are always ten groups of hydrospires with fully exposed hydrospire slits, using full width of RD suture. There is no trend toward reduction of the number of hydrospire slits, neither in regular, nor in anal hydrospire groups.

(4) Form of neoschismatid ambulacra has remained elongate linear to lanceolate, with exposed lancet, throughout the history of the group.

It is difficult to set up an exact phylogenetic lineage of genera showing main phylogenetic trends, and arrange them in order of their relative ages. This is caused (1) by the fact that in many essential morphological characters neoschismatids have shown to be conservative rather than progressive, and (2) by the fact that, apart from *Hadroblastus*, all neoschismatids are of Permian age. As we will try to more fully discuss below, the neoschismatids from the Permian of Australia are considered to be phylogenetically closer to *Hadroblastus* than their Permian relatives from Timor. Australian neoschismatids are, broadly speaking, more conservative than the Timor ones. This may also be caused by the fact that Australian neoschismatids are, at least in part, slightly older than the Timor forms. The phylogenetic trends as outlined above, are more clearly shown by forms from the Permian of Timor. For practical purposes we will consider *Hadroblastus* (Pl. XVI, figs. 1–3; Pl. XVII, figs. 1–15; Pl. XVIII, figs. 1, 3, 5–8), *Austroblastus* (Pl. XXIII, figs. 1, 6, 8; Pl. XXIV, fig. 1), and the Australian species of *Neoschisma* (Pl. XIX, figs. 1–4, 6–8), and *Notoblastus* (Pl. XX, fig. 1; Pl. XXI, figs. 1, 2, 7, 8) as the main stock of neoschismatids. In this way the trends shown by Timor neoschismatids are most clearly visible and describable. Timor neoschismatids have produced some very specialized species, to be considered in part as representing late phylogenetic offshoots.

Although a relatively large number of Permian neoschismatids has become known, anatomical studies are incomplete. Australian neoschismatids are mostly known from isolated thecal plates, or from casts and molds. None of them could be studied anatomically for that reason. Timor neoschismatids are calcified, and could be studied anatomically, but some forms are extremely rare, belonging to species known only from one or two specimens. This has precluded serial sectioning.

We will now try to further explain each of our provisional statements on the phylogeny of morphological characters in the family of the neoschismatids. As we have seen for other families, trends in the development of hydrospires and the ambulacral structures are the most meaningful in phylogeny.

Thecal shape and growth patterns for main thecal elements. The earliest representatives of *Hadroblastus* (Miss.) are relatively small but some later forms have developed into one of the largest known fissiculates, between 40 and 60 mm in length. Only *Austroblastus* (Perm.) equals it in thecal size amongst the neoschismatids but the elongate radial prongs of *Thaumatoblastus* produce the greatest lateral expansion found in any blastoid. Other Permian neoschismatids were intermediate to large in size.

The thecal shape of the neoschismatids in the main stock is a conservative character. All members have preserved wide and broad thecae. A pentagonal cross-section of the thecae is also generally maintained during the history of the group. Some neoschismatids have changed thecal shape; however, in *Thaumatoblastus* (Pl. XXV, fig. 8; Pl. XXVIII, fig. 5) thecal shape is deeply influenced by a strong tendency to elongate the ambulacra. The genus has developed a cup-shaped pelvis and a strongly stellate vault. Thecal shape is also subject to change in *Timoroblastus* (Pl. XXIII, figs. 2, 3, 5, 7; Pl. XXVI, figs. 1, 4, 5, 8–11; Pl. XXVII, figs. 1, 3–5, 9). This is caused by a vertical buildup in the deltoids, and by formation of prongs or petals near the base of the cup. This change in thecal shape must have ecological significance, probably as an indicator of a special mode of life of *Timoroblastus*.

The basals of the earliest species of the Mississippian *Hadroblastus* are broadly conical; however, in some of the largest specimens these come to lie in an almost flat plane during growth (Pl. XVI). Those in the Lower Permian may be conical (as in *Neoschisma australe*) or form part of a broadly convex cup-shaped base *(Notoblastus stellaris)*. They are relatively prominent in most Permian species, having one of these two shapes. In *Neoschisma timorense* (Pl. XX, figs. 4, 8), they are modified to form a basal concavity and in *Timoroblastus*, they form part of a usually expanded base which was apparently used to stabilize the animal on the sea floor. In earlier forms the basals grew outward and upward; this is still found in some specimens of *Timoroblastus*, but they may also have been modified to grow outward and downward, forming a broadly convex base.

The radials of a Mississippian neoschismatid *(Hadroblastus)* are different than those of the Permian genera. In the Mississippian, the origin lies at the apex of a pyramid on the radial as in the phaenoschismatids. The RD sector is flattened to lie in the same plane as the ambulacra and is fully occupied by hydrospire slits. The relative percentage of the RD sector is large and the relative percentages of Mississippian and Permian radial axes do not overlap. There is an ontogenetic acceleration of RD in one *Hadroblastus* species. By way of contrast, the origin of the radial of a Permian neoschismatid such as *Austroblastus*, *Neoschisma*, or *Timoroblastus* has been changed to lie in a flat plane containing the RR and RB sectors; the RD sector is relatively reduced and at an angle to the RR sector. RB is the major growth axis. The radial may be strongly modified by the deposition of secondary calcite to form radial prongs as in *Notoblastus* and *Thaumaloblastus*; one peculiar asymmetrical genus, *Dipteroblastus* (Pl. XXI, fig. 6; Pl. XXII, figs. 2, 3, 6; Pl. XXIII, fig. 4), displays both types of radials. The radials of a form which may be *Austroblastus* (Pl. XXIV, fig. 6) develop peculiar horns on the outer surface of the radial due to secondary calcite deposition.

From the origin of the group there is some emphasis on further outgrowth of the DD sectors. These sectors were only slightly developed in *Hadroblastus*, but in all the Permian members they are moderately developed. So, from the origin of the group there is some emphasis on the development of DD sectors, which is somewhat enhanced in the Permian members. The effect of changing DD growth is to enlarge the exposed DD suture, and to remove somewhat the ambulacra from the peristome as seen in Permian neoschismatids.

Main stock members of the neoschismatids have preserved a deltoid crest. The crest is not directed upward but downward, caused by the downward growth of the deltoids. In the Timor neoschismatids the deltoid crest is far less developed than in their Australian relatives.

Main stock members of the neoschismatids have preserved an ambulacral sinus; this is particularly strong in *Austroblastus*. Again, Timor neoschismatids seem to have far less development of the ambulacral sinuses.

Thecal shape in the neoschismatids can only be derived from the phaenoschismatids. If we are right in interpreting *Hadroblastus* as a Mississippian neoschismatid, it would mean that the neoschismatid thecal shape developed from the phaenoschismatids through a *Hadroblastus*-like organization into the Permian neoschismatid thecal form. Neoschismatids have preserved the phaenoschismatid deltoid crest, but have developed it in a downward growing direction, and placed more emphasis on DD growth. Also the phaenoschismatid ambulacral sinuses are preserved, mainly in Australian neoschismatids. Downgrowth of the deltoid crest has prevented the forms from developing conspicuous interambulacral pyramids, which are, at least in Permian genera from Timor, distinctly reduced if compared to the phaenoschismatid situation.

The wide and broad neoschismatid pelvises are only derivable from the conical phaenoschismatid pelvises by a shift in relative proportions of different growth fronts in the radials. Notably, growth along the RR growth axis have been stressed, whereas growth along RD axis has diminished.

The form of the pelvis is cup-shaped in Mississippian and most Timor forms, but rather pyramidal in Australian forms.

Anal deltoids and anal hydrospires. The composition of the anal area in the neoschismatids has remained unchanged, both for Australian and for Timor forms, during the history of the group: an epi- and hypodeltoid is always present. The hypodeltoid always contributes to the external body wall. There is no trend toward further simplification of the anal area by further reduction of one of the two constituent elements. This is a further indication of a rather late derivation of the neoschismatids from the phaenoschismatids. In the Mississippian most phaenoschismatids had already simplified the anal area, having only an epideltoid and a hypodeltoid.

The gonopore is poorly known in the neoschismatids, and we cannot make a statement on its phylogeny. By analogy of other late fissiculates, it is expected that the gonopore of all neoschismatids has been in an internal position at the adanal surface of the epideltoid.

The number of anal hydrospires does not show a definite phylogenetic trend. The epideltoid always formed the anal hydrospires. The number of anal hydrospires is determined by the length of the suture between epideltoid and the posterior radial limbs. This suture is always shorter than the corresponding sutures between regular deltoids and the radial limbs. Only if the hypodeltoid forms anal hydrospires can the total number of anal hydrospires be equal to the number of regular hydrospires. Anal hydrospires formed by the hypodeltoid are known from the Mississippian species *Hadroblastus whitei* (Pl. XVII, figs. 2, 6), and the Australian species *Austroblastus whitehousei* (Pl. XXIII, figs. 1, 6) and *Neoschisma australe* (Pl. XIX, figs. 1, 3, 4, 8). It again shows the greater affinity of the Australian neoschismatids to their Mississippian forerunner. Hydrospires on the hypodeltoid are unknown from the Timor forms.

Hydrospires. Ten groups of hydrospires have always been present during neoschismatid phylogeny. There is no tendency to reduce one or more of the hydrospire groups. Even the number of anal hydrospires is not subject to phylogenetic reduction. The hydrospire slits in all ten groups of the neoschismatids are always and invariably exposed. There is no trend in this character.

In the main or conservative stock of neoschismatids, as defined above, the total width of DR sutures is always used for the formation of hydrospires. Hydrospire slits are numerous and placed parallel to one another. The number of hydrospire slits is large because the RD growth front is very wide, especially in Australian neoschismatids.

The Timor neoschismatids generally do not differ very much from this hydrospire pattern. Slits are numerous and built across full width of RD suture. A notable exception is *Timoroblastus*, where hydrospires are not formed over the full width of RD suture (3 slits present in *T. weiensis*: Pl. XXIV, fig. 4 and only 1 slit in *T. coronatus* Pl. XXVII, fig. 4). The latter sometimes shows features (Pl. XXVI, fig. 5) which may lead to the conclusion that more slits have been present but have gradually been completely filled in with secondary calcite, or, alternatively, it has reduced the number of hydrospire folds by not using the full width of RD suture.

In neoschismatids of the main stock, there is a phylogenetic trend toward limitation of the functional area of the hydrospire slits. This is exclusively brought about by infilling of secondary calcite at both ends of the hydrospire slits. This results in very short functional slits. Infilling by secondary calcite is not very much developed in *Hadroblastus*, but it is in most Australian neoschismatids. Therefore, we would suggest there is a progressive trend towards gradual infilling of hydrospire slits during phylogeny of the group.

The Timor neoschismatids also show the trend toward partial infilling of hydrospire slits by secondary calcite. This infilling is stronger in *Thaumatoblastus* (Pl. XXV, fig. 2) than it is in *Dipteroblastus* (Pl. XIII, fig. 4) and *Neoschisma* (Pl. XIX, fig. 5; Pl. XX, fig. 8). Perhaps we may interpret *Timoroblastus coronatus* as a form that has phylogenetically developed strong infilling by secondary calcite, closing the slits completely off, and retaining only the first formed, admedial slit. *Timoroblastus weiensis* (3 hydrospire slits) shows that *Timoroblastus* indeed had the capacity of forming more than one hydrospire in each of the ten groups. Also, in *Notoblastus oyensi* (Pl. XX, fig. 5) we see that hydrospire slits may become completely filled in: the *C* anal hydrospire slits in that species are fully closed off.

Ambulacral form. The genera and species in the main neoschismatid stock are characterized by stable and conservative features in their phylogeny. Again, most Timor forms show trends radiating from the organization in the main stock, and are regarded as offshoot or as specialized forms. The radiant trends shown in the Timor neoschismatids are most clearly observable with regard to ambulacral form and composition.

Primitively the neoschismatid ambulacral form, as preserved in *Hadroblastus*, is linear to lanceolate, of moderate length, and with a completely exposed lancet. In the members of the main neoschismatid stock the ambulacra have remained elongate structures with exposed lancets. The ambulacra have become slightly removed from the peristome by gradual phylogenetic emphasis on growth in the DD sectors. In some forms (*Notoblastus*; Pl. XXII, figs. 4, 5) the ambulacral form is rather rhombiform, but has principally remained an elongated ambulacrum of conservative length. The complete exposure of the lancet has been preserved, the number of side plates and brachioles has remained phylogenetically constant. In the Australian neoschismatids no offshoot trends (developing a different form of ambulacra) has been found apart from *Thaumatoblastus*.

On the contrary, in Timor neoschismatids there are very distinct offshoot trends in the ambulacral form, leading to very specialized forms. Two opposite trends are now known: a trend toward further, and extreme, elongation of the ambulacra; and an opposite trend toward reduction of the ambulacra.

The ambulacra of *Notoblastus oyensi* (Pl. XX, figs. 5, 6) are not preserved, but are estimated to have been of conservative length, not having been subject to reduction or to elongation. The ambulacra of *Neoschisma verrucosum* (Pl. XIX, fig. 5) are short, but not essentially different from the situation in the main neoschismatid stock. Inasfar as ambulacral structure is concerned, these two species do not show distinct trends away from the trends in the main neoschismatid stock.

Distinct reduction of ambulacra occurs in *Neoschisma timorense* (Pl. XX, figs. 4, 8), and in both species of *Timoroblastus*. Ambulacral shape is small, petaloid, with a few side plates and brachioles on a rhombic lancet. The ambulacra have not developed proportionally during the ontogeny of each of these species. They are believed to have maintained the juvenile composition and proportions of an ambulacrum in their later growth stages and during maturity. Thus they are an example of a neotenic trend in the phylogeny of the fissiculate blastoids. As we will see later in the account of the Timor codasterids and ceratoblastids, more examples of neoteny are known in Permian forms, mainly in the codasterids.

Elongation of the ambulacra has occurred in *Thaumatoblastus* and *Dipteroblastus*. In both cases it has produced specialized blastoids. *Thaumatoblastus longiramus* (Pl. XXV) is the most extreme example of elongation of ambulacra in the blastoids we now have. Such an elongation has already been discussed in the account of the orophocrinids where a similar, though less extreme, elongation occurs in *Anthoblastus stelliformis* (Pl. XI, figs. 5, 6, 8, 9). As in that orophocrinid, elongation of ambulacra has been brought about by deposition of calcite at the external surfaces of the radials. In that way a very pronounced stellate thecal form has developed. The number of side plates and brachioles in *Thaumatoblastus* has increased enormously.

The same elongation has occurred in *Dipteroblastus* (Pl. XXIII, fig. 4) although it is confined there to the *B* and *D* ambulacra (sitting on pronged *B* and *D* radials), the other three ambulacre being very much reduced. The reduced ambulacra of *Dipteroblastus* appear not to have developed proportionally during ontogeny, whereas the elongate ambulacra could be interpreted as their ontogenetic derivative. This would provide an example in one form of the tendency to reduce or elongate the ambulacra in the neoschismatids discussed above. Elongation of just two ambulacra in *Dipteroblastus* has produced a nearly bilaterally symmetrical thecal form. Here again we deal with a very specialized blastoid. We cannot very well see what advantage *Dipteroblastus* had with its peculiar mode of organization, unless we admit that it had changed its normal blastoid mode of life. The only other fissiculate blastoid developing bilateral symmetry, *Astrocrinus* (Pl. XI, fig. 7; Pl. XV, figs. 1, 3, 6) is a stalkless form, and an apparent direct bottom dweller. *Dipteroblastus* is not stalkless, but the function of its stalk is uncertain.

Conclusions. As we have already indicated, it is our interpretation that neoschismatids arose by evolutionary radiation from the phaenoschismatids. This probably would have happened in the Upper Devonian or Lower Mississippian because *Hadroblastus* is not greatly differentiated from a phaenoschismatid of the main stock.

A rather good intermediate between *Hadroblastus* and the phaenoschismatids would be a form with superdeltoid, two cryptodeltoids, and hypodeltoid contributing to the external wall of theca; having wide and shallow ambulacral areas and low interambulacral pyramids, not rising above peristome and a subhorizontal deltoid crest; with ten hydrospire groups; the number of hydrospire slits not or slightly reduced in the anal interarea, and completely or nearly completely exposed hydrospire slits; with wide and low pelvis. This organization is very much like what we know is realized in "*Phaenoschisma*" *benniei* (Pl. V, figs. 8, 11, 13) (L. Carb., Scotland), and in an undescribed genus from the lower Mississippian of Montana. The neoschismatid ancestor must have had an organization very much like these two species. It must, however, be of Upper Devonian or lowermost Mississippian age. It is very unfortunate that Upper Devonian fissiculate blastoids are unknown. Future findings of Upper Devonian blastoids will probably produce the neoschismatid ancestor or greatly contribute to understanding neoschismatid evolution from the phaenoschismatids.

Hadroblastus itself has several characters preserved which are distinctly phaenoschismatid: the deltoid crest, the ambulacral sinuses, and the parallel, exposed hydrospire slits in the sinuses. The composition of the anal arcs is similar to that of some phaenoschismatids of its age (Mississippian). It has radiated from the phaenoschismatids by changing its thecal shape to a wide, cup-shaped pelvis, and a convex vault. It has also started downgrowth of the deltoids and started to place more emphasis on growth in the DD sectors. Continuation of these trends could have given rise to the later Permian neoschismatids.

Evolutionary trends in the neoschismatids are mainly found in hydrospire and ambulacral structures. It is interesting to compare these trends with similar trends in other families. For orophocrinids and nymphaeoblastids we have concluded that a reduction of functional hydrospire surface is related to, and probably caused by, an increase in ambulacral length, or, in physiological terms, we have concluded that decrease in hydrospire respiration was made possible by an increase in brachiolar respiration. This has been said on the assumption that total respiratory demands were unchanged.

In the neoschismatids we also have examples of extreme elongation of ambulacra, as in *Thaumatoblastus*. This elongation of ambulacra seems also to be related to reduction of the hydrospire system. *Thaumatoblastus* hydrospire slits are more fully filled in than in other Timor neoschismatids, with the exception of *Timoroblastus coronatus*. However, *Dipteroblastus* with two extremely long ambulacra has not so greatly filled in the hydrospire slits. Anyhow, correlation between elongation of ambulacra and reduction of functional hydrospire surface seems to be weaker in the Timor neoschismatids than we observed it to be in the orophocrinids and the nymphaeoblastids.

This correlation is further complicated by the fact that in *Timoroblastus* (and notably in *T. coronatus*) we have a clear example of correlation between reduction of ambulacra and reduction of functional hydrospire surface, quite the opposite trend as observed elsewhere. We have already seen that the phylogenetic development of the ambulacra in *Timoroblastus* is a clear example of neoteny. We could also conclude that development of the hydrospire system in *Timoroblastus* is a case of neotenic development. It is a fact, as proved by anatomical studies of *T. coronatus*, that only the first formed hydrospire slit and fold is fully developed, and that further slits and folds, to be expected to have formed further on in the ontogeny of the species, have been omitted or suppressed. The one hydrospire fold of *Timoroblastus coronatus* is to be seen then as the preservation of an early ontogenetic feature during latter ontogenetic growth stages and during maturity. This is a neotenic trend. We will for these reasons consider *Timoroblastus* as a neotenic form within the Timor neoschismatids. As we will see later, in the account of the codasterids, neoteny played a major role in that family.

Timoroblastus is a distinct offshoot genus from the main neoschismatid patterns, not so much for the neotenic trends it demonstrates, but rather for its mode of life. We assume that *Timoroblastus* is one of the fissiculate forms that probably has experimented with its mode of life. This may be deduced from its peculiar and extremely variable thecal form. The thecal forms are unmistakably those of neoschismatids. Some specimens of *Timoroblastus* (and notably such forms as Wanner's varieties ungulatus and ingens) have developed anchor-like spades on the interradial and basiradial sutures. This form of theca suggests that specimens in the possession of such spades rested directly on the bottom (see section on Blastoid Autecology).

CODASTERID PHYLOGENY

The codasterids as now grouped systematically on a phylogenetic basis represent, like the neoschismatids, a younger stock of fissiculate blastoids derived from the phaenoschismatids. The lineage leading to the codasterids began in the Middle Devonian with *Heteroschisma*. The earliest member is of Lower Carboniferous age, and occurred in the Atlantic Basin (1 genus, Europe). In Pennsylvanian times the group had spread to North America and the Arctic regions (1 genus), and in Lower Permian times to South America (1 genus), and to the Urals (2 genera). In Permian times the group also migrated toward Southeast Asia (3 genera from Thailand and Timor). The group is unknown from Australia.

Derivation. Codasterids have been phylogenetically derived from the phaenoschismatids. The middle Devonian genus *Heteroschisma* is the direct precursor of *Codaster*, notably the species *Heteroschisma alternatum* which shows growth patterns which can be interpreted as leading directly toward *Codaster*.

Heteroschisma is a phaenoschismatid with a phylogenetically late subdeltoid, which has lost one of its normal functions (see section on phylogeny of phaenoschismatids). The subdeltoid does not form anal hydrospires, and it is only feebly developed, especially in *H. alternatum* (Pl. III, figs. 1, 2, 5, 6; textfig. 14.4), where it is even proportionally smaller than in other *Heteroschisma* species. In the transition from *H. alternatum* to *Codaster* (Pl. XXVI, figs. 2, 3, 6, 7; Pl. XXVII, figs. 2, 6–8; Pl. XXVIII, figs. 1, 2, 4, 8, 9) the subdeltoid was completely lost. The thecal shape and organization in *H. alternatum* is different from other *Heteroschisma* species, and definitely shows trends towards the codasterid thecal shape. *H. alternatum* has flattened its upper surface by making the interambulacral pyramids and the ambulacral sinuses very low, and the ambulacral sinuses very wide (155°). In the process it has completely exposed its eight groups of hydrospire slits. Thus a codasterid-like vault is already present in *H. alternatum*. The pelvis of *H. alternatum* is still conical and very phaenoschismatid. *H. alternatum* is the direct ancestor, thus probably providing the best example of a radiant form in the ancestral family which directly gave rise to a new family.

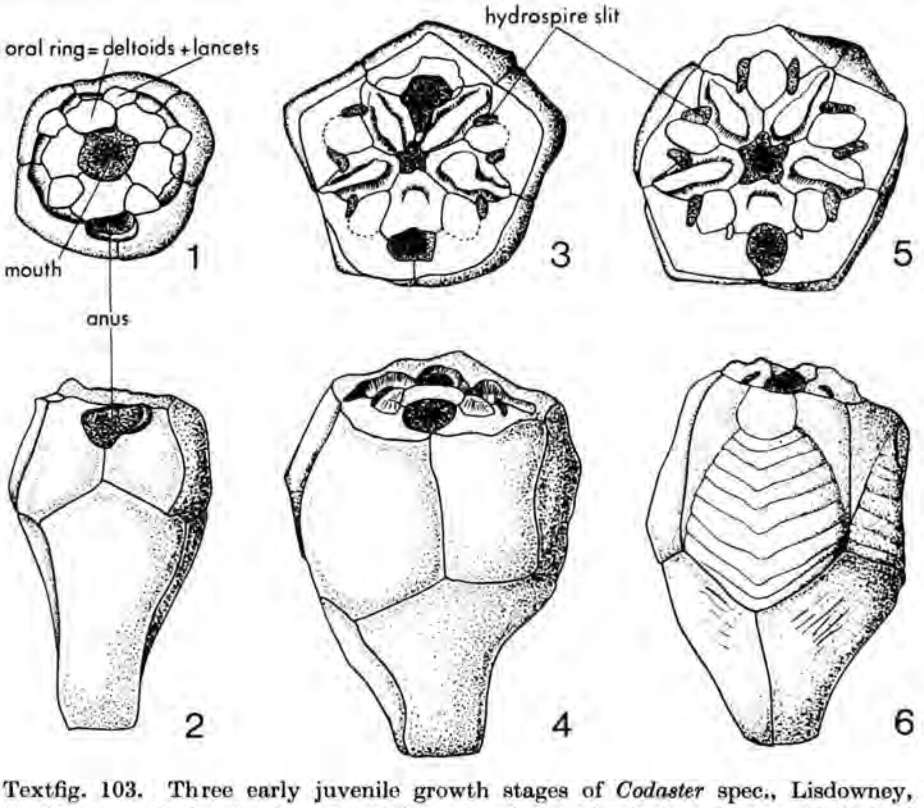
The phylogenetic changes from the phaenoschismatids to the codasterids are: (1) reduction, and final suppression of the subdeltoid and consequent loss of the anal hydrospires; (2) reduction of interambulacral pyramids and ambulacral sinuses by flattening these out; (3) consequently, complete exposure of the eight groups of hydrospire slits; (4) change in thecal form from biconical to cup-shaped.

The codasterid epideltoid is a non-hydrospire-forming plate in all later members of this family. Only in *Codaster* and the oldest species of *Angioblastus (A. ellesmerensis)* does it usually form rudimentary hydrospire folds. The plate is interpreted to be homologous with the phaenoschismatid superdeltoid, which is not hydrospire-forming either. The subdeltoid, with its hydrospireforming potentials, is regarded as having been completely reduced in phylogeny.

The phylogenetic trends in the codasterids will be dealt with in another way than has been done for the other families. This is done because the phylogeny of the codasterids shows only one dominant trend, which is not so markedly present in other fissiculate families. Codasterid phylogeny can only be understood as a clear and distinct case of neoteny. We have come to the conclusion that Permian codasterids have either retarded ontogenetic growth, or even have omitted part of the ontogenetic development that has been present in their ancestors *(Codaster)*.

Ontogeny of Codaster. Understanding codasterid phylogeny is impossible without understanding the ontogeny of *Codaster*. Very fortunately, some extremely significant finds of *Codaster* have been made by Dr. G. Sevastopulo, Trinity College, Dublin, in a quarry near Lisdowney, Co. Kilkenny, Ireland, from Lower Carboniferous sediments. The *Codaster* material involved comprises several specimens in a very early ontogenetic growth stage, ranging in height from 1.5 to 4.5 mm. These *Codaster* specimens are among the earliest ontogenetic growth stages known from any blastoid species. The most important growth features of these codasters will be briefly described here.

The youngest specimen (nr. 8067), 1.5 mm high (textfigs. 103.1, 2;



Textfig. 103. Three early juvenile growth stages of *Codaster* spec., Lisdowney, Co. Kilkenny, Ireland, collec. Dr. G. Sevastopulo, Trinity College, Dublin. (1, 2) Oral and lateral aspects of spec. nr. 8067; (3, 4) *idem*, spec. nr. 8017; (5, 6) *idem*, spec. nr. 8018. For explanation see text.

Pl. XXVI, fig. 7; Pl. XXVII, fig. 7; see also Pl. XXVIII, fig. 8) has a very high, rather narrow pelvis with strongly upflaring basals which are extremely large and occupy almost $\frac{2}{3}$ of the height of the pelvis. There are 3 basals and 5 radials. The radials are small and lack RD sectors. The theca has a flat upper surface. The anus is proportionally a very wide opening in a notch between the posterior radials at the upper lateral edge of the pelvis. The upper surface of the theca is restricted and smaller in diameter than the greatest width of the pelvis. It comprises a proportionally very wide mouth (width $\frac{2}{3}$ of total width restricted upper surface). The mouth is surrounded by a swollen peristomial ring, composed of nearly rectangular deltoids (DD sectors only). Very small, almost triangular ambulacra (probably lancet plates only) are present. They are about half the size of one deltoid (DD sector). The restricted upper surface is almost entirely formed by the mouth and the peristomial ring. No hydrospire structures have yet developed because DR and RD sectors have not yet developed on deltoids and radials respectively.

The larger specimens (nr. 8017, 3.5 mm high, textfig. 103.3, 4; and nr. 8018, 4.5 mm high, textfig. 103.5, 6) still have an elongate pelvis, but the basals occupy only half or less of the total height of the pelvis; radials have apparently now developed faster than the basals did. Radials have developed RD sectors on the (still flat) upper surface of the theca. The deltoids have changed their form to about hexagonal through outgrowth of the DR sectors and have become crested. In eight regular positions elongate depressions occur across the RD sutures, indicating that formation of the first hydrospires had just started. The ambulacra have changed their form from triangular to rhombic, having grown larger and apparently having added side plates. The mouth is proportionally smaller, as is the anus. The anus is now about at the upper surface of the theca, but still resting in a notch on the posterior radials.

Based upon this sequence of specimens, we would offer the following interpretation of early blastoid ontogeny.

(1) During ontogeny basals appeared first, followed by radials and deltoids. Radials and deltoids develop RD and DR sectors later in ontogeny.

(2) Mouth and anus are formed very early in ontogeny, probably at the moment when the primary evaginations of the hydrocoel developed; this is about at the time when deltoids initiated their DD growth sector.

(3) Lancets formed aboral from the primary evaginations of the hydrocoel, which came to lie externally on the lancet, thus starting ambulacral growth.

(4) Deltoids develop DR sectors, radials develop RD sectors, thus initiating hydrospire development in these sectors and providing space for expansion of the ambulacrum.

Apart from being of general importance for early blastoid ontogeny as a whole, the very juvenile codasters have an overwhelming importance for understanding codasterid phylogeny, hence for understanding Permian codasterids. Four important ontogenetic growth patterns in *Codaster* will be described, starting from the juvenile forms just described.

(1) The juvenile *Codaster* possesses small, petaloid ambulacra, with only a few side plates lying on a rhombic lancet. During further ontogenetic development the lancet grows out in a longitudinal (aboral) direction, thus obtaining its mature elongate lanceolate shape. In the process more side plates are added which come to lie in two series on both sides of the lancet, leaving its central part exposed. This is the adult form and composition of the ambulacra in *Codaster*. Ontogenetically, it changes its ambulacra from small petaloid with rhombic lancet and few side plates (juvenile) to lanceolate with many side plates (adult).

(2) The juvenile *Codaster* possesses hexagonal deltoids with DD sectors which are still larger than the DR sectors. During further ontogenetic development the deltoid grows out by gradually placing more emphasis on growth in the DR sectors. Thus in the adult *Codaster* the deltoid has obtained a nearly rhombic form with the DR sector becoming slightly larger than DD. Ontogenetically, *Codaster* changes the form of its deltoids from hexagonal with DD sector larger than DR sector (juvenile) to near-rhombic with the DR sector being slightly larger (adult).

(3) The juvenile *Codaster* possesses small DR and RD sectors which have grown less than the earlier formed DD and RR (RB) sectors. Hence, the total surface area for hydrospire formation is restricted and the number of hydrospires is very small: only one or two slits. During further ontogenetic development *Codaster* develops the DR and RD sectors, widens the RD suture and by so doing enlarges the surface area available for hydrospire formation. Consequently, more hydrospire folds and slits are added in ontogeny. Ontogenetically *Codaster* changes its potential hydrospire-bearing area (RD + DR sectors) from small and restricted with few hydrospire folds (juvenile) to larger and widened with many hydrospire folds (adult).

(4) The juvenile *Codaster* possesses a proportionally large anus lying in a notch in the posterior radials on the upper lateral edge of the theca. During ontogeny *Codaster* changes the position of the anus to the upper surface of the theca, no longer placing it in a notch in the posterior radials, and it becomes proportionally smaller. Ontogenetically *Codaster* changes the position of the anus and diminishes its relative size.

Each of these four ontogenetic growth tendencies in *Codaster* is interrelated with the others.

Codasterid phylogeny. Only by keeping in mind the juvenile form and composition of ambulacra, deltoids, hydrospires, and anus of *Codaster*, is the phylogeny of the Pennsylvanian and Permian codasterids easily understood.

Codaster is one of the largest of the codasterids, reaching a maximum size near 20 mm. Pennsylvanian species of *Angioblastus* (Pl. XXIX, figs. 1–6, 8–10) are slightly smaller than this as are the Permian species

(Pl. XXVIII, figs. 3, 6; Pl. XXIX, figs. 7, 11–21; Pl. XXX, figs. 1–4, 6–12); the youngest species, *A. variabilis*, is one of the smallest. The two species of *Tympanoblastus* (Perm; Pl. XXX, figs. 5, 13, 14; Pl. XXXI, figs. 1, 3, 6) approach 20 mm in length, whereas the species of *Pterotoblastus* (Perm; Pl. XXXI, figs. 2, 4, 5, 7–9, 11–15; Pl. XXXII, figs. 3, 4, 6, 9, 10) and *Nannoblastus* (Perm.; Pl. XXXII, figs. 7, 8; Pl. XXXIII, figs. 1, 2, 5–7) are small. Thus there is no tendency to build larger thecae, as was seen in the neoschismatids and orophocrinids.

The two most important genera in Pennsylvanian and Permian times are *Angioblastus* and *Tympanoblastus*. They will be dealt with first. *Pterotoblastus* shows a phylogenetic trend which differs from other Permian codasterids and will be dealt with separately.

Pennsylvanian and Permian specimens of *Angioblastus* and *Tympanoblastus* have preserved distinct, and conservative codasterid characters. They have preserved a cuplike pelvis, but may have restricted the flat upper surface of the theca, including deltoids, ambulacra, the hydrospire area, and mouth and anus. This trend is particularly strong in Permian specimens of *Angioblastus*. Phylogenetic development for the upper surface is now dealt with separately for each of the component parts.

Some adult Permian codasterids have small petaloid ambulacra, with a few side plates lying on the aboral side of a rhombic lancet. In contrast to *Codaster*, they have not ontogenetically grown out the ambulacra to form lanceolate structures with many side plates. They have maintained the juvenile form and composition of ambulacra in *Codaster* during later ontogenetic stages and during maturity, and have omitted the later part of ontogenetic development that has been present in their ancestors *(Codaster)*.

Adult Permian codasterids have hexagonal deltoids with DD sectors larger than DR sectors. In contrast to *Codaster* they have not ontogenetically grown out the DR sectors, changing their deltoid shape to near-rhombic. They have maintained in maturity the juvenile form of deltoids in *Codaster*, their ancestor.

They possess small DR and RD sectors, these having undergone less development than DD and RR (RB) sectors. The total surface area for hydrospire formation is restricted and the number of hydrospires is small: in many cases only one or two slits per group. In contrast to *Codaster* they have not ontogenetically developed the total DR + RD area and not much increased the number of hydrospires per group. They have maintained during maturity the juvenile proportion for the potential hydrospire-forming area in their ancestor, *Codaster*.

Adult Permian codasterids possess a proportionally large anus lying in a notch in the posterior radials at the upper lateral edge of the theca. In contrast to *Codaster* they have not ontogenetically changed the position of the anus to the upper surface, and have not diminished its relative size. They have maintained during maturity the juvenile position and proportion of the anus of the ancestral *Codaster*.

Concluding we see that adult Permian codasterids have maintained during maturity (1) the juvenile form of their deltoids; (2) the juvenile structure of their ambulacra; (3) the juvenile composition of their hydrospire-forming areas (DR + RD sectors); and (4) the juvenile proportion and position of their anus. In each of these four characters they have omitted part of the ontogenetic development that has been present in *Codaster*, their ancestor. This phylogenetic development is a very clear case of neoteny.

Angioblastus and *Tympanoblastus* are regarded as neotenic forms in the codasterids. This is particularly so for *Angioblastus*. Indeed, the organization of a mature *Angioblastus* is nothing else than the organization of a very juvenile *Codaster*. Looking at a mature *Angioblastus* is like looking at a very juvenile *Codaster*. *Angioblastus* is certainly a genus that has omitted a large part of the ontogenetic development *Codaster* underwent. This is perhaps not entirely true for *Tympanoblastus*. It may be that the genus has merely retarded ontogenetic growth. This can be deduced for example from the ambulacral structure. Ambulacra in *Tympanoblastus* may be more developed than in *Angioblastus*, having grown out to somewhat larger rhombiform ambulacra. The DR sectors in *Tympanoblastus*, on the contrary, may have stronger reduction than in *Angioblastus*; the sectors may be developed in a downward growth direction.

The thecal shape of the codasterids has remained a conservative feature throughout the history of the group. The pelvis of codasterids has remained unchanged and cup-shaped. The vault is almost exclusively formed by the deltoids. There is no trend toward developing another thecal shape in the codasterids. Some forms (*Angioblastus*, Pl. XXX, fig. 10; and *Nannoblastus*, Pl. XXXIII, fig. 2) have developed and RA growth sector in the radials. However, thecal shape may change if ambulacra become elongated *(Pterotoblastus gracilis)*; a stellate theca results in such a case.

Pterotoblastus shows a unique feature in fissiculate evolution. This is strongly so for *P. gracilis* (Pl. XXXII, figs. 3, 4, 6, 9, 10). It has the same neotenic trends for deltoids and hydrospire-forming area, as also for the lancet, but not for the side plates. The lancet has preserved a juvenile rhombic shape and it has not grown out to form an elongate shape. The number of side plates has remained small, but each of the individual side plates has grown out considerably in an effort to increase the total area for ambulacral tracts. The side plates have come to lie directly on a radial prong, and are not supported by the lancet. *Pterotoblastus* is the only example of a fissiculate blastoid which has increased the total functional length of the ambulacral tract system without any outward growth of the lancet.

Nannoblastus (Pl. XXXII, figs. 7, 8; Pl. XXXIII, figs. 1, 2, 5–7) is a form we have placed in the codasterids with a query mark. It shows features interpretable as neotenic codasterid characters: the juvenile-looking, small petaloid ambulacra on a rhombic lancet, the reduction of DR and RD sectors, and consequent reduction in hydrospire formation. Also the presence of an RA growth sector in the radials is known from Permian codasterids *(Angioblastus)*. The genus may in fact be another neotenic Permian codasterid.

Nannoblastus has some characters not known from other Permian codasterids. The shape of the pelvic area is five-sided pyramidal. The growth in the deltoids is not clear: it is suggestive of vertical upgrowth in a way comparable to *Timoroblastus coronatus* and *Anthoblastus stelliformis*. The genus has an hypodeltoid, which is atypical for Permian codasterids. The reduction of hydrospires in *Nannoblastus* is stronger than in typical Permian codasterids: only 6 hydrospires may be present, those on both sides of *C* and *D* ambulacra being absent (textfigs. 42.8–11).

Conclusions. Codasterids were derived from the main ancestral stock of fissiculate blastoids, the phaenoschismatids. *Heteroschisma* is considered to be the direct ancestor to *Codaster*. Derivation of codasterids from *Heteroschisma* involved a change in thecal growth from biconical to cup-shaped; a flattening of the vault by which the hydrospire slits became exposed; and by reduction of the subdeltoid.

Phylogenetic trends, in the sense of radiations toward new forms, were absent in the history of the codasterids. The family has remained essentially conservative throughout. The theca remained cup-shaped with a flattened upper surface; there has most always been only an epideltoid (apart from the hypodeltoid in *Pterotoblastus ferrugineus*, and most species of *Angioblastus*); there have most always been eight hydrospire groups (apart from rudimentary hydrospire folds on the epideltoid of *Codaster*, and *Angioblastus ellesmerensis*.

The dominant trend found in codasterid evolution is neoteny. The group may be limited by its strong neotenic tendencies, because it meant that possibilities for further ontogenetic development were no longer present. The space available for respiration, either ambulacral or hydrospiral, is reduced in contrast to other evolutionary lineages. Neoteny in the codasterids, particularly strong in Permian forms from Timor is also found in some Permian crinoids.

MINOR FAMILIES, INCERTAE SEDIS

The phylogenetic derivation of genera in the minor families, and those placed systematically as "incertae sedis", is briefly dealt with in this separate section of the Phylogeny Chapter.

Astrocrinidae. The genus *Astrocrinus* (Pl. XI, figs. 4, 7; Pl. XV, figs. 1, 3, 6) (L. Carb.: Engl., Scot.; Ireland) is a very specialized blastoid. Its extreme specialization is seen in the development of bilateral symmetry, and in its stalkless mode of life. As we have seen in the description of its anatomy (textfig. 33), the form has morphologically specialized and modified its *D* side. The form of its theca is unequalled among fissiculates. They do not show very much affinity to any other blastoid family with respect to thecal shape. The theca may have faint ambulacral sinuses and interambulacral pyramids, reminiscent of the phaenoschismatids. They suggest that phylogenetically *Astrocrinus* probably was derived from the phaenoschismatids. The genus would be a separate experiment in fissiculate evolution.

However, in some of its trends it shows affinities to the orophocrinids. The elongated ambulacra, the conjoined hydrospires, and the presence of hydrospire clefts bordering ambulacra, are trends distinctly parallel to trends in the orophocrinids. The composition of its ambulacral area (superdeltoid, two cryptodeltoids; and possibly a hypodeltoid) could be orophocrinid, but the same combination is also found in the anal area of some phaenoschismatids of the same age as *Astrocrinus*.

For the above reasons *Astrocrinus* is phylogenetically interpreted as either an early, but distant, offshoot from the orophocrinids, or a late offshoot from the phaenoschismatids, having partly developed trends parallel to the orophocrinids. In any case the genus is to be seen as a separate experiment in the evolution of the fissiculate blastoids, having developed trends unknown elsewhere.

Ceratoblastidae. The genus *Ceratoblastus* (Pl. XXXII, figs. 5, 11) (Permian, Timor) is not regarded as a specialized form. Rather we would think of this genus as another Permian form which exhibited neotenic trends in its ontogeny. This is evident in its thecal shape: the pelvis is very elongate, largely formed by prominent basals, being larger than the radials; the flat upper surface is restricted. This thecal shape is reminiscent of the thecal shape of a very juvenile *Codaster* (textfig. 103). The small and wide petaloid ambulacra with few side plates afford another example of a neotenic trend. This is also true for the proportionally large anus, situated in a notch on the posterior deltoids. Possibly, the fact that no hydrospires occur, is seen as a very strong neotenic trend.

The genus *Ceratoblastus* cannot be definitely linked phylogenetically with other families, because it developed quite extra-ordinary characters, unknown from other fissiculate families. The presence of ten larger ambulacral plates instead of the usual five lancets is unexplained phylogenetically. This is also true for the larger pores in the *BC* and *DE* deltoids leading to internal sacs (textfig. 43.9), the function of which is unknown.

The only likely family to link *Ceratoblastus* to is the codasterids, mainly because in that family neoteny has played a major role during the Permian.

Incertae sedis. The genus *Indoblastus* (Pl. XXXII, fig. 2; Pl. XXXIII, figs. 3, 4; Permian, Timor) is such a simple and unspecialized blastoid, that we cannot be sure of its phylogenetic affinities and derivation. It shows a slight reduction in the ambulacra (in which some aboral side plates lie directly on the radial), and strong reduction in the hydrospire system. These tendencies are known from all other families that have survived into the Permian and do not afford a conclusive clue towards its phylogenetic interpretation. Its thecal shape and composition of the anal area is such that we could think of either the codasterids or the neoschismatids as the two families which are, in some way or another related to the origin of *Indoblastus*. Certainly, *Indoblastus* is not related to the nymphaeoblastid and the orophocrinid lines of fissiculate evolution, but it, almost certainly, is related to the codasterid and neoschismatid lines of development. But its exact trends within that larger group is not understood.

SUMMARY OF PHYLOGENETIC TRENDS IN FISSICULATE BLASTOIDS

Following their appearance in the Silurian, the early fissiculate blastoids, the phaenoschismatids, radiated into several other families. We have considered each lineage separately in a previous discussion; consideration of all these families jointly suggests trends for several characters throughout the Middle and Upper Paleozoic.

The early theca was tall and conical and of moderate size in the Silurian. Some forms with this shape persist into the Mississippian but it is generally replaced during the Devonian and Mississippian by forms with cup-shaped thecae, forms with inflated vaults, spheroids, and box-like thecae. Once established these new forms were conservative; many provided space for larger ambulacra. A few forms exhibit a tendency to larger thecae.

In the early phaenoschismatids, the ambulacra were short to moderate in length, with a concealed lancet. In their derivatives, there is a broad tendency to expose the lancet and elongate the ambulacra thus adding more brachioles. The food-gathering capacity was thus enhanced. Those that show neoteny do not show this tendency.

The anal interarea of a fissiculate blastoid was the site of several functions: elimination, respiration (if anal hydrospires are present), and reproduction. Several modifications occurred which are related to each of these functions. In the anal area of the earliest fissiculates there were three anal deltoids: super-, sub-, and hypodeltoid. The subdeltoid was replaced by two cryptodeltoids; the hypodeltoid was sometimes suppressed, ultimately the anus was surrounded by the epi- and hypodeltoid or epideltoid and two radials (primarily neotenic forms), the number of anal hydrospires was small and there was a tendency to increase these. The relative number came to be almost equal or equal to the number of regular hydrospires except in neotenic forms where they were eliminated. The gonopore was external in primitive forms but, where known, it came to lie internally in later phaenoschismatids and their derivatives.

The hydrospires, via the hydrospire slits, were probably the principal respiratory structures in the early fissiculates. The number of these remained constant in many forms, but were increased in one group and reduced in a number of others, including the neotenic forms. The early forms had long, open slits, but there was a functional advantage to conceal, conjoin, and/or to infill the length of the functional slits until they were small ovoid openings across the radiodeltoid suture. This may have been related to a greater importance for ambulacral respiration, but this function is only inferred. Other environmental pressures may have induced this change.

The deltoids of early fissiculates possessed a small deltoid lip and sharp deltoid crest. With time, this was subdued, and in some forms replaced by an external deltoid body. The proportions of the parts of the plate also came to be modified by the increase in relative size of the DD sector in some, particularly the neotenic forms.

The shape of the radials was rather conservative throughout the history of the fissiculates. Proportions of the various sectors came to be modified, however, by an increase in the RD sectors to allow space for longer ambulacra. The RD sector also came to lie in an external position, no longer being within an ambulacral sinus.

The basal plates of the early fissiculates were tall and narrow; the stem attachment area was formed by BA growth sectors. There were apparently limitations to BA sectors for they were soon replaced by the secretion of secondary calcite or other means. In some groups the basals themselves came to be somewhat reduced in size and to lie in a horizontal plane or basal cavity.

The early fissiculates grew by the addition of calcite to the lateral edges of the plate. Almost without exception, the independently derived Permian fissiculate groups also add calcite to the free surface of a plate or plates. This apparently opened new environments to some.

Over a span of about 180 million years, the fissiculate blastoids were a rare but successful group. They originated in the North Atlantic Basin during the Silurian, began to migrate outward (primarily southward) during the Devonian, but were still primarily in the North Atlantic area in the Mississippian. With the advent of the Hercynian and Appalachian orogenies, these seas were denied to them. We have suggested that they continued to be present in relative abundance during the Pennsylvanian; when we can view them again in the Permian, they are primarily in southeast Asia and Australia. During that 180 million year span, the original conical fissiculate came to be modified into many different forms which changed form and modified functions of its components. We believe that the fissiculates have also given rise polyphyletically to the spiraculates. The first phaenoschismatid radiation to *Troosticrinus* and its apparent derivative genera such as *Schizotremites* (Dev.) (?) *Metablastus* (Miss.) and *Tricoelocrinus* (Miss.) occurred in the Silurian. The descendants of Lower Devonian *Pentremitidea* were modified into the spiraculates such as *Belocrinus* (Dev.), *Hyperoblastus* (Dev.), *Devonoblastus* (Dev.), and *Eleutherocrinus* (Dev.). In the latest Devonian or Early Mississippian yet another spiraculate group apparently sprang from the phaenoschismatids; these include *Petaloblastus*, *Pentremoblastus*, and *Pentremites*. Some of the first two groups may have survived into the Permian. Application of modern biological and paleontological principles has apparently resolved many phylogenetic questions in the blastoids, but the ultimate derivation of those many round blastoid genera of the Devonian and Mississippian remains to be solved.

COMPUTER SIMULATION OF FISSICULATE PHYLOGENY

The ultimate form in which a phylogenetic diagram is presented usually does not reflect the thought processes involved. We wished to completely reappraise the fissiculate blastoids so avoided any discussion or inferences until we had completely examined, described, and photographed all available material. We used this data to look at the time-distribution and association of approximately twenty characters in different forms. Certain groupings and distributions soon became apparent. Our evaluation of these led to the revision of the systematics given in Chapter I and the construction of a phylogeny given above. Like most phylogenies, ours is a statement of probability on the evolutionary interrelationships between these characters. We feel our phylogeny is closer to the actual record than previous efforts (e.g., FAY, 1967[a,b]) because of our opportunity to personally study all of the forms involved and the much greater amount of carefully determined data utilized.

After we had arrived at a phylogenetic history in the summer of 1969, another way of considering our data became available to us. KLUGE and FARRIS (1969) had developed a quantitative phyletic approach for inferring evolutionary relationships. This approach, called quantitative phyletics, is based upon the synthetic theory of evolution and is not synonymous with the phenetics of numerical taxonomy. It is based upon the Wagner method for producing the most parsimonious tree. The input data consists of coded data (presence or absence; configuration of a multistate character as type of anal deltoids; see Table I) for a series of characteristics for each taxon (genus in this case). One of these taxa is identified as being most primitive (A). The strategy utilized by the computer is to find that taxon (B) which most closely resembles the most primitive (A). Resemblance is based upon the least difference between the character states. B might differ from A in three characters of the twenty employed so B is plotted as being at a distance of three from A. If the difference occurs in a multistate character, this might have to change more than one level (0 to 2) so the distance given might be four but only three characters were involved. Thus the distance given between two taxa may be a sum of single changes in the level of a number of characters, a change of one character through more than one level, or a combination of these (textfig. 104). The printed output of the program shows which case applies. KLUGE and FARRIS (1969, p. 6–7) outlined the Wagner algorithm used in writing the quantitative phyletic program; it is paraphrased below.

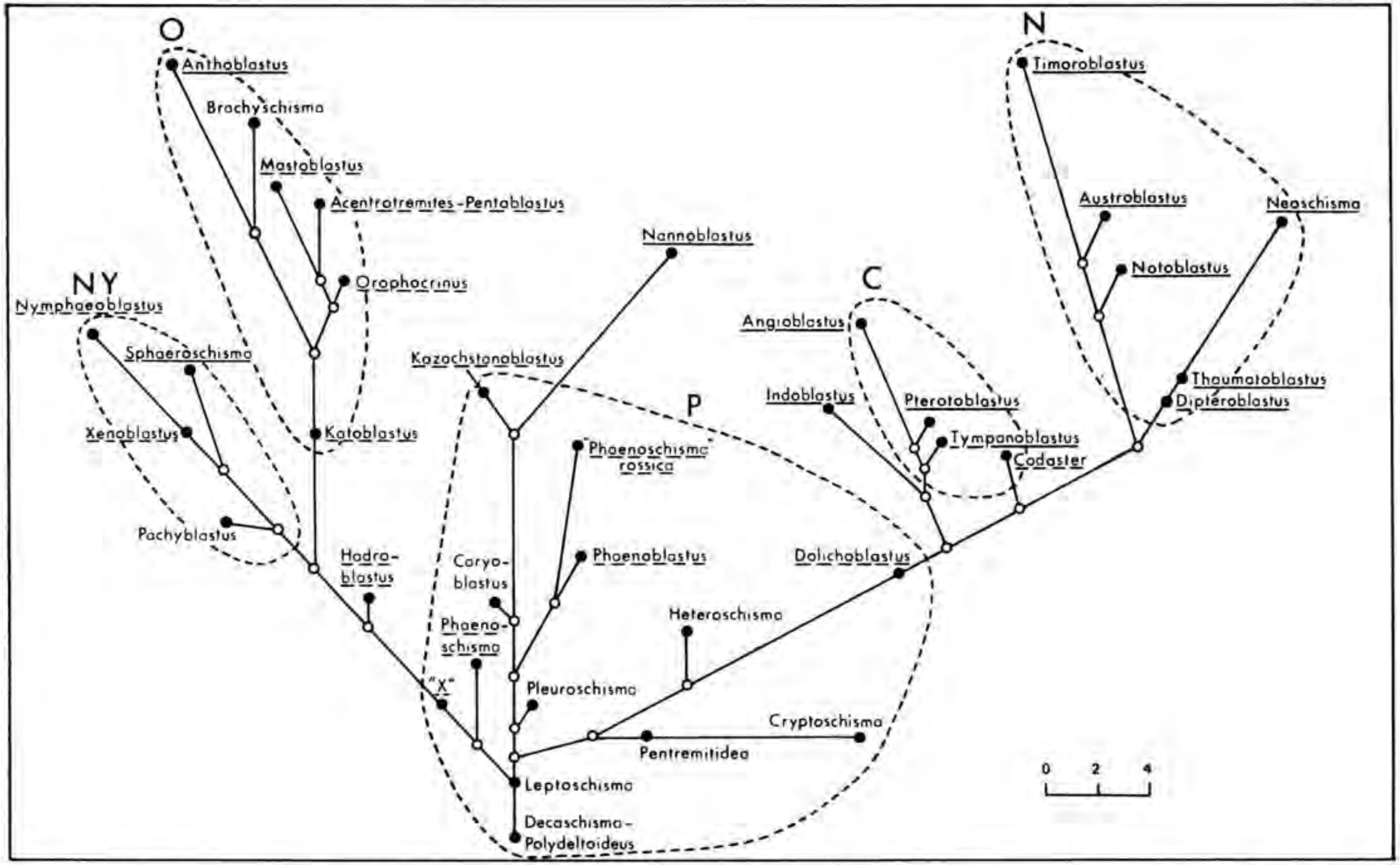
1. Choose an ancestor OTU (operational taxonomic unit). Go to 2.
2. Find the OTU that has the smallest difference (where the difference is the sum of the absolute difference in number of character states between the two OTU's involved). Connect it to the ancestor to form an interval. Go to 3.
3. Find the *unplaced* OTU A, that differs least from the ancestor. Go to 4.
4. Find the interval from which the OTU identified in 3 differs least.
5. Attach OTU A to the interval found in 4, denoted b. To do this construct an intermediate Y, and insert it into the tree.
6. If any OTU's remain unplaced, go to 3. Otherwise stop.

(Certain phrases outline computational procedures have been omitted).

The objective of the Wagner method is to form a network, or tree by connecting all of the original OTU's and realizing in the process a minimum number of changes on the tree.

The emphasis on parsimony produces the shortest possible linkage between the known taxa, given the constraint of one member being primitive. In order to link divergent forms, the program may have to produce several branches (only dual branchings are allowed at one time) and it thus may place several intermediates between known taxa. Those are not necessarily to be inferred as real entities or "missing links." The easiest way to visualize the finished product in a multi-dimensional framework is to look at an arborescent deciduous tree. (The elm is a good example). The trend is for continued splitting and divergence the higher one goes but some limbs may closely approach one another (convergence). A more detailed description of the theory and application of this approach may be found in KLUGE and FARRIS, 1969, and KLUGE, 1969.

We coded twenty characters (Tables I, II) for use in the quantitative phyletics computer program (Wagner program). These were the ones we had used for our previous considerations of taxonomy and phylogeny. The resulting diagram (textfig. 104) very closely parallels the overall evolutionary picture given earlier in this chapter. It should be reemphasized this textfigure was produced after the phylogeny we discussed earlier was constructed. Textfigure 104 does not prove that blastoids evolved in the way that we have discussed but it does confirm within the limitations of evolutionary theory and the Wagner method for producing evolutionary trees that we reached the most parsimonious solution to fissiculate phylogeny based upon the characteristics we considered important. (Obviously the use of different characters would produce a different diagram). We present textfigure 104 for comparison with our earlier



Textfig. 104. Quantitative phyletic diagram for fissiculate blastoids. Unlabeled points represent "intermediates." Geologic age of genera indicated by underlying: Sil., Dev. – blank; Miss. – dashed; Penn., Perm. – solid. Family designations indicated by large ovals. C = Codasteridae; N = Neoschismatidae; NY = Nymphaeoblastidae; O = Orophocrinidae; P = Phaenoschismatidae. Distance between points represents change in number of character states according to scale. Angles of branching and spatial proximity of different branches not significant. "X" is an undescribed phaeonoschismatid from Montana (UB). See text for discussion.

discussion. We do not wish to have statements made that genus A gave rise to genus B. We view the geological record of blastoids as being fragmentary and those which are available are but a limited sample of the totality. This limited sample shows the time distribution of characters but is too imperfect to permit exact statements on genus A & B, except in rare cases. We have tried to clearly indicate this in our discussion of fissiculate phylogeny given earlier. It should be noted that the data used for textfig. 104 counted time as but one twentieth of the total data but in only one instance is there time inversion of the derivation of genera when compared with their known stratigraphic distribution *(Brachyschisma)*. This strengthens our arguments that certain characters in blastoids have a limited time distribution and are interrelated.

Since we have tried to construct an evolutionary systematics, textfigure 104 is also a check on our family groupings. The groupings of genera found in the tree are as we have placed them in families with two exceptions. *Hadroblastus*, a Mississippian genus which we have placed in the neoschismatids lies between the phaenoschismatids and nymphaeoblastids and orophocrinids in textfigure 104. We suggest this is due to its recency of divergence from the phaenoschismatids. *Nannoblastus*, a form we placed in the codasterids, is shown as being at the top of a phaenoschismatid branch. It is the longest branch on the tree, differing in the most number of characters from any other taxon which may have resulted in difficulties in finding a place for it. It strongly employs secondary calcite. *Indoblastus*, a very generalized blastoid that we placed in *incertae sedis*, sorted out amongst the codasterids. *Astrocrinus* and *Ceratoblastus* were not included because many characters could not be encoded. *Decaschisma-Polydeltoideus* and *Acentrotremites-Pentablastus* plot at the same point because they are closely related and the characteristics we used to differentiate them are of local application and were not encoded. The coded values for each genus are given in Table II.

TABLE I

Character and character states for quantitative phyletics, fissiculate blastoids.

	Character	*Character state*	
I.	Thecal shape	0	Cup shaped to globose
		1	Biconical
		2	Ellipsoidal
		3	Pelvis Conical, Convex Vault
		4	Beaker-shaped
II.	Vault	1	Low
		2	Moderate
		3	Prominent
III.	Cross section	0	Pentagonal (Amb.)
		1	Rounded pentagonal
		2	Rounded
		3	Decagonal-stellate
		4	Pentagonal (Interamb.)
IV.	Basals	0	BA axis
		1	Secondary deposits
		2	Other
V	Deltoid	0	Large DR
		1	Subequal DR and DD
		2	Moderate DD
VI	Deltoid Crest	0	Prominent
		1	Reduced
		2	Absent
VII	Ambulacra	0	Long
		1	Medium
		2	Short
VIII	Ambulacral Shape	0	Rhombiform
		1	Lanceolate
		2	Linear
		3	Petaloid
IX.	Lancet	0	Exposed
		1	Concealed
		2	Widely exposed
X.	Ambulacral Sinus	0	Present
		1	Absent
XI.	No. Hydrospire Grps.	0	Eight
		1	Nine
		2	Ten
		3	<Eight
XII.	Hydrospire Slits Length	0	Short
		1	Medium
		2	Long
XIII.	Anal Hydrospire Reduction	0	Not present
		1	Slight
		2	Equal
XIV.	Hydrospire Slit Exposure	0	Exposed
		1	Partially concealed
		2	Concealed – absent
XV.	Hydrospire Slits on RD Suture	0	Full width
		1	Less than full width

TABLE 1 *Continued*

	Character	*Character state*	
XVI.	Anal Deltoids	0	Epi- or Epi-hypodeltoid
		1	Super-, sub-, hypodeltoid
		2	Super-, crypto-, hypodeltoid
XVII.	Hypodeltoid	0	Contributing to external wall
		1	Not contributing to external wall
		2	Absent
XVIII.	RA Growth Front	0	Present
		1	Absent
XIX.	Secondary Calcite Deposits	0	Yes
		1	No
XX.	Age	0	Silurian
		1	Devonian
		2	Mississippian
		3	Pennsylvanian-Permian

TABLE II

Character states for fissiculate genera. See Table I for explanation.

	Thecal-shape	Vault	Cross-section	Basals	Del	Del Crest	Amb	Amb Shape	Lanc	Amb Series	No Hydro Grps.	Hydro Sl.	Anal Reduc.	Hydro Sl. Exposure	Hy. Sl. Width	Anal Del.	Hypo. Contrib.	R. A. Gr. Front	2nd Calcite	Time
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Acentrotremites	2	2	0	2	0	2	0	1	1	1	2	1	2	2	1	0	0	1	1	2
Angioblastus	0	0	1	2	1	1	2	0	0	1	0	0	0	0	1	0	0	0	0	3
Anthoblastus	3	1	3	1	0	2	0	1	2	1	2	0	2	2	0	0	0	1	0	3
Austroblastus	4	1	4	2	2	0	1	1	0	1	2	0	2	0	0	0	0	1	0	3
Brachyschisma	3	2	3	1	0	2	1	1	1	1	1	1	1	0	0	1	0	1	1	1
Caryoblastus	3	2	0	0	0	0	1	2	1	0	2	2	2	2	1	2	0	1	1	1
Codaster	0	0	0	2	2	1	1	1	0	1	2	1	1	0	0	0	2	1	1	2
Cryptoschisma	3	0	0	1	0	0	1	3	2	1	0	2	0	2	1	2	1	1	1	1
Decaschisma	1	0	0	0	0	0	1	2	1	0	2	2	1	1	0	1	0	1	1	0
Dipteroblastus	0	0	2	2	2	1	0	2	0	1	2	0	1	0	0	0	0	1	0	3
Dolichoblastus	1	0	0	2	2	1	1	1	0	0	0	1	0	0	0	0	0	1	1	2
Hadroblastus	3	1	0	1	0	1	1	2	0	1	2	2	1	0	0	0	0	1	1	2
Heteroschisma	1	1	0	2	0	0	1	2	1	0	0	2	0	0	0	1	2	1	1	1
Indoblastus	0	0	1	2	2	2	1	1	0	1	0	0	0	2	1	0	0	1	1	3
Katoblastus	3	2	0	1	0	2	1	2	0	1	2	2	1	2	1	2	0	1	1	2
Kazachstanoblastus	3	2	0	0	0	0	1	1	0	0	3	0	0	2	1	0	0	1	1	2
Leptoschisma	1	1	0	0	0	0	1	2	1	0	2	2	1	1	0	1	0	1	1	1
Mastoblastus	3	2	0	2	0	2	1	1	0	1	3	0	0	2	1	0	0	1	1	2
Nannoblastus	1	2	0	0	1	2	2	3	1	1	3	0	0	2	1	0	0	0	0	3
Neoschisma	0	1	4	1	2	2	2	3	0	1	2	0	1	0	0	0	0	1	0	3
Notoblastus	4	0	3	2	2	1	1	1	2	1	2	0	1	0	0	0	0	1	0	3
Nymphaeoblastus	2	2	2	2	0	2	0	2	1	1	2	1	2	0	0	0	0	1	1	2
Orophocrinus	3	1	0	1	0	2	1	1	0	1	2	1	2	2	1	0	0	1	1	2
Pachyblastus	2	2	1	2	0	1	0	2	0	1	2	2	1	0	0	2	0	1	1	1
Pentablastus	2	2	0	2	0	2	0	1	1	1	2	1	2	2	1	0	0	1	1	2
Pentremitidea	1	0	0	0	0	0	1	2	1	0	0	2	0	1	1	2	0	1	1	1
Phaenoblastus	3	2	1	0	0	0	1	3	2	0	2	2	1	1	0	2	1	1	1	2
Phaenoschisma	1	1	0	0	0	0	1	1	2	0	2	2	1	1	0	0	1	1	1	2
Phaenoschisma rossica	3	2	1	2	0	0	1	2	0	0	2	2	1	2	1	2	2	1	1	2
Pleuroschisma	1	2	0	0	0	0	1	2	1	0	2	2	1	0	0	2	0	1	1	1
Polydeltoideus	1	0	0	0	0	0	1	2	1	0	2	2	1	1	0	1	0	1	1	0
Pterotoblastus	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	3
Sphaeroschisma	2	2	2	2	0	1	0	2	0	1	2	2	1	1	1	0	0	1	1	3
Thaumatoblastus	0	0	3	2	2	1	0	2	0	1	2	0	1	0	0	0	0	1	0	3
Timoroblastus	4	0	4	2	1	2	2	3	0	1	2	0	2	2	1	0	0	1	0	3
Tympanoblastus	0	0	0	2	1	1	1	0	0	1	0	0	0	0	0	0	0	1	1	3
Xenoblastus	2	2	0	2	0	1	0	2	1	1	2	1	1	0	1	0	0	1	1	2
"*X*"	1	1	0	1	0	0	1	2	0	0	2	2	1	1	0	0	0	1	1	2

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APPENDIX

Explanation of Museum Abbreviations used in Plate Legends.

Austr. Mus. = Australian Museum, Sydney
BMNH = British Museum (Natural History), London
BSNS = Buffalo Society of Natural Sciences, Buffalo Museum of Science
CGM = Central Geological Museum, Leningrad
GSC = Geological Survey of Canada
GSQ = Geological Survey of Queensland, Brisbane
IRSNB = Institute Royal des Sciences Naturelles de Belgique
MCZ = Museum of Comparative Zoology, Harvard Univ.
NMI = National Museum of Ireland
PIN = Palaeontological Institute, Academy of Sciences, Moscow
OU = University of Oklahoma, Norman
RSM = Royal Scottish Museum, Edinburgh
TCD = Trinity College, Dublin
THD = Technische Hogeschool, Delft
UCLA = University of California, Los Angeles
UI = University of Illinois, Urbana
UM = University of Missouri, Columbia
Univ. Ams. = University of Amsterdam, The Netherlands
UQ = University of Queensland, Brisbane
UMMP = University of Michigan, Museum of Paleontology
USNM = United States National Museum

The identity of the repository of some specimens is indicated in the plate legends by their number in the growth series to facilitate comparison between specimens. Most all of these are from the UMMP or USNM. A registry of all specimens in each growth series will be given by Macurda in the complementary species descriptions of these fissiculates to be published at UMMP.

EXPLANATION OF PLATES

PLATE I

Fig. 1. Oral view of *Decaschisma pulchellum* (Miller and Dyer, 1878), no. 14 in growth series. Anus at 6 o'clock in all oral views. Sil., Waldron Shale, Indiana, USA × 3.

Fig. 2. Lateral view (centered on B ambulacrum) of *Decaschisma pulchellum*, no. 12 in growth series. Horizon as above. × 3.

Fig. 3. Lateral (A) view of immature *Decaschisma pulchellum*. C.R.C. Paul collec., Cambridge Univ. Sil., Laurel Ls., Indiana, USA. × 7.5.

Fig. 4, 7. Oral and lateral (E) views of *Leptoschisma lorae* (Dunbar, 1920), no. 5 in growth series. Dev., Birdsong Shale, Tennessee, USA. × 3.

Figs. 5, 6. Lateral (E) and oral views of *Leptoschisma lorae*, no. 3 in growth series. Horizon as above. × 3.

Figs. 8, 12. Oral and lateral (D) views of *Polydeltoideus enodatus* Reimann and Fay, 1961, no. 10 in growth series. Sil., Henryhouse Fm., Oklahoma, USA. × 3.

Figs. 9, 13, 17. Oral, lateral (B), and basal views of *Cryptoschisma schultzii* (De Verneuil and d'Archiac, 1845), no. 13 in growth series. Anus at 6 o'clock in basal views. L. Dev., La Vid Fm., Colle, León, Spain. × 3.

Figs. 10, 11. Oral and lateral (A) views of *Caryoblastus bohemicus* Breimer, Macurda, and Prokop, 1968, no. 2 in growth series. L. Dev., Slivenec Ls., Konvarka, Bohemia, Czechoslovakia. × 7.8.

Fig. 14. Lateral (E) view of *Pentremitidea archiaci* (Etheridge and Carpenter, 1882) with stem columnals, no. 12 in growth series. L. Dev., La Vid Fm., Colle, Léon, Spain. × 3.

Figs. 15, 16. Oral and lateral (A) views of *Caryoblastus* sp.?. Inst. Earth Sci., Free Ref. Univ., Amsterdam. Horizon as above. × 3.

Figs. 18–20. Oral, basal, and lateral (E) views of *Pentremitidea archiaci*, no. 6 in growth series. Horizon as above. × 3.

Fig. 21. Oral view of *Pentremitidea archiaci*, BMNH E8033. L. Dev., Calcaire de Ferroñes, Ferroñes, Asturias, Spain. × 3.

Fig. 22. Oral view of *Pentremitidea pailleti* (De Verneuil, 1844), no. 12 in growth series. Horizon as above. × 3.

Figs. 23, 24. Oral and lateral (D) views of *Pentremitidea pailleti*, no. 14 in growth series. Horizon as above. × 3.

PLATE II

Figs. 1, 6. Oral and lateral (B) views of phaenoschismatid, genus and species indeterminate, Prokop collec., Geological Survey, Prague. L. Dev., Slivenec Ls., Konvarka, Bohemia, Czechoslovakia. × 7.8.

Figs. 2, 3. Oral and lateral (A) views of *Pentremitidea lusitanica* Etheridge and Carpenter, 1882, BMNH E789. L. Dev., Calcaire de Ferroñes, Asturias, Spain. × 3.

Fig. 4. Lateral (B) view of *Pleuroschisma lycorias* (Hall, 1862), BSNS E 11800, with columnals. M. Dev., Moscow Shale, New York, USA. × 3.

Figs. 5, 9. Oral and lateral (D) views of *Pleuroschisma verneuili* (Etheridge and Carpenter, 1882), Univ. Cal., Los Angeles 31680. L. Dev., Ferroñes? Spain, Chavan collec. (preservation atypical for this locality; apparently from La Vid Fm., Colle, León, Spain). × 3.

Fig. 7. Lateral (D) view of *Pleuroschisma lycorias*, Kopf collec., Univ. Cincinnati. M.Dev., Centerfield Ls., New York, USA. × 3.

Figs. 8, 10. Lateral (A) and oral views of *Pleuroschisma lycorias*, UMMP 56499. M.Dev., Hungry Hollow Fm., Ontario, Canada. × 3.

Fig. 11. Lateral (BC) view of *Pleuroschisma verneuili*, no. 19 in growth series. L.Dev., La Vid Fm., Colle, León, Spain. × 3.

PLATE III

Figs. 1, 2. Oral and lateral (A) views of *Heteroschisma alternatum* (Lyon, 1857), USNM S4586. M.Dev., Jeffersonville Ls., Louisville, Ken. area, USA. × 3.

Figs. 3, 4. Oral and lateral (B) views of *Heteroschisma canadense* (Billings, 1869), no. 18 in growth series. M.Dev., Hungry Hollow Fm., Hungry Hollow, Arkano, Ontario, Canada. × 3.

Figs. 5, 6. Lateral (B) and oral views of *Heteroschisma alternatum*, BSNS E21100. M. Dev., Onondaga Ls., Moorehouse Mb., LeRoy, N.Y. USA. × 4.

Figs. 7, 9. Oral and lateral views of *Heteroschisma alatum* (Reimann, 1935), no. 14 in growth series. M.Dev., Potter Farm Fm., Alpena, Mich., USA. × 3.

Fig. 8. Oral view of mutant *Heteroschisma alatum*, UMMP 58660. Horizon as above. × 3.

Figs. 10, 11. Oral and lateral (C) views of *Heteroschisma gracile* Wachsmuth, 1883, no. 11 in growth series. M.Dev., Thunderbay Ls., Partridge Pt., Alpena, Mich., USA. × 3.

Fig. 12. Lateral (E) view of *Heteroschisma* sp., UMMP 58661. M.Dev., North Vernon Fm., Beechwood Mb., Louisville Cement Co. Qy., Clark Grant, Clark Co., Ind., USA. (UMMP 1968/D–7). × 3.

Fig. 13. Oral view of *Heteroschisma* sp., UMMP 58662. Horizon as above. × 3.

Figs. 14, 19. Oral and lateral (B) views of *Phaenoschisma gracillimum* (Rowley and Hare, 1891), UI RX-131. Miss., Lower Burlington Ls., Louisiana, Mo., USA. Fig. 14 × 4; fig. 19 × 3.

Fig. 15. Lateral (C) view of *Heteroschisma subtruncatum* (Hall, 1858), no. 1 in growth series. M.Dev., Cedar Valley Ls., Linwood, Iowa, USA. × 3.

Figs. 16, 21, 23. Oral, basal, and lateral (B) views of *Phaenoschisma chouteaui* Macurda, 1964, UM 3573. Miss., Chouteau Ls., Providence, Mo., USA. × 4.

Figs. 17, 22. Lateral (D) and oral views of phaenoschismatid, UMMP 58663. Miss., Caballero Fm., Sacramento Mts., Alamogordo, N.M., USA. × 4.

Fig. 18. Lateral (AB) view of *Phaenoschisma conicum* (Fay, 1962), OU 4344. Miss., Lake Valley Ls., Nunn Mb., Lake Valley, N.M., USA. × 4.

Fig. 20. Oral view of *Heteroschisma subtruncatum*, no. 2 in growth series. M.Dev., Cedar Valley Ls., Iowa, USA. × 3.

Fig. 24. Oral view of *Phaenoschisma conicum*, UMMP 58664. Miss., Lake Valley Ls., Nunn Mb., Lake Valley, N.M., USA. (UMMP 1970/M-150). × 4.

Fig. 25. Lateral (E) view of *Phaenoschisma conicum*, USNM 160576. Miss., Lake Valley Ls., Nunn Mb., Apache Hill, Lake Valley, N.M., USA. × 4.

Figs. 26, 27. Oral and lateral (AB) views of *Phaenoschisma laeviculum* (Rowley, 1900). UI RX-94F. Miss., Upper Burlington Ls., Louisiana, Mo., USA. × 4.

PLATE IV

Figs. 1, 2. Oral and lateral (A) views of *Phaenoschisma* sp., USNM 160577. Miss., Shaly beds in Rockford Fm. (= Jacobs Chapel), Center Lot 62, Clark Grant, Floyd Co., Ind., USA. × 7.5.

Figs. 3, 5. Oral and lateral (C) views of *Phaenoschisma acutum* (Sowerby, 1834), UMMP 58664. L. Carb., Clitheroe Ls., Salt Hill Knoll., Clitheroe, England. × 4.

Figs. 4, 9. Oral and lateral (A) views of *Pentremoblastus conicus* Fay and Koenig, 1964, UM 15180. Miss., McCraney Fm., Seahorn Hollow, Adams Co., Ill., USA. × 4.

Figs. 6, 7. Lateral (B) and oral views of *Phaenoschisma* sp., USNM 160578. Miss., Shaly beds in Rockford Fm. (= Jacobs Chapel), Center Lot 62, Clark Grant, Floyd Co., Ind., USA. × 7.5.

Figs. 8, 12. Oral and lateral (A) views of *Phaenoblastus caryophyllatus* (De Koninck and Le Hon, 1854), Université de Mons, R.G. 10 (no. 7 in growth series, MACURDA, 1967[a]). L. Carb., Tournaisian, Tournai, Belgium. × 3.

Figs. 10, 14. Oral and lateral (A) views of *Phaenoschisma acutum*, TCD 7988. L.Carb., Visean, Feltrim Hill Knoll, Co. Dublin, Ireland. × 3.

Figs. 11, 15, 18. Oral, lateral (A), and basal views of *Phaenoblastus pecki* (Macurda, 1964), OU, unreg. spec. Miss., Chouteau Ls., Quarry west of Sedalia, Mo., USA. × 4.

Figs. 13, 16. Lateral (C) and oral views of *Pentremoblastus subovalis* Fay and Koenig, 1964, UM 15188. Miss., McCraney Fm., Seahorn Hollow, Adams Co., Ill., USA. × 4.

Fig. 17. Lateral (A) view of phaenoschismatid (UA), USNM 160579. Miss., Lake Valley Ls., Nunn Mb., Apache Hill, Lake Valley, N.M. × 4.

Figs. 19, 21. Oral and lateral (E) views of *Phaenoschisma laeviculum*, UMMP 58665. Miss., St. Joe Ls., roadcut, Whitewater Baptist Church, Delaware Co., Okla., USA. (UMMP 1965/M-142). × 4.

Fig. 20. Oral view of phaenoschismatid (UA), USNM 160580. Miss., Lake Valley Ls., Nunn Mb., Apache Hill, Lake Valley, N.M. × 4.

PLATE V

Figs. 1, 2. Oral and lateral (A) views of phaenoschismatid (UA), USNM 160581. Miss., Lake Valley Ls., Nunn Mb., Lake Valley, N.M., USA. × 4.

Figs. 3, 6. Oral and lateral (A) views of phaenoschismatid, USNM 160582. Miss., Osage or Keokuk (?), Mo., USA. × 4.

Figs. 4, 5. Oral and lateral (B) views of "*Phaenoschisma*" *saharae*, n. sp., Pareyn Collec., no. 437B. Univ. de Caen. L. Carb., Viséen supérieur, Fm. d'Akacha-Mazzer, Djebel Ioucha, Bechar, Algeria. × 3.

Figs. 7, 9. Lateral (A) and oral views of "*Codaster*" *gratiosus* Miller, 1880, Univ. Cincinnati 3814. Miss., Keokuk Ls., New Bloomfield, Mo., USA. × 4.

Fig. 8. Inclined oral view of "*Phaenoschisma*" *benniei* Etheridge and Carpenter, 1886, RSM 1958.1.2461. L.Carb., Visean, Carlops, Peebleshire, Scotland, U.K. × 7.5.

Fig. 10. Lateral (C) view of "*Phaenoschisma*" *saharae*, n. sp., Pareyn Collec., no. 437A. Univ. de Caen. L.Carb., Viséen supérieur, d'Akacha-Mazzer, Djebel Ioucha, Bechar, Algeria. × 3.

Fig. 11. Lateral view of a cotype of "*Phaenoschisma*" *benniei*, BMNH E666. L.Carb., Visean, Shale above no. 2 limestone, Kidlaw Quarries, near Gifford, Haddingtonshire, Scotland, U.K. × 8.7.

Figs. 12, 15. Oral and lateral (A) views of "*Phaenoschisma*" *rossica* Arendt, Breimer and Macurda, 1968, PIN 1788/8. L.Carb., L. Namurian, Tshan-Tshar, North Kazachstan, USSR. × 4.

Fig. 13. Lateral view of "*Phaenoschisma*" *benniei*, BMNH E30679. L. Carb., Visean, Scotland, U.K. × 8.7.

Figs. 14, 16, 17. Lateral (A), basal, and oral views of *Kazachstanoblastus carinatus* Arendt, Breimer and Macurda, 1968, PIN 1787/2. L.Carb., L.Namurian, Tshan-Tshar, North Kazachstan, USSR. × 3.

PLATE VI

Figs. 1, 4. Oral and lateral (E) views of *Dolichoblastus shimanski* (Arendt, Breimer and Macurda, 1968), PIN 1787/1. L.Carb., L.Namurian, Tshan-Tshar, North Kazachstan, USSR. × 3.

Figs. 2, 5, 6. Oral, lateral (B), and basal views of *Brachyschisma corrugatum* (Reimann, 1935), BSNS E16045. M.Dev., Onondaga Ls., Vogelsanger quarry, Williamsville, N.Y., USA. × 3.

Fig. 3. View from interior of oral view of external cast of *Brachyschisma ? oostheizeni* n. sp., Oostheizen collec., Zwartskraal, Prince Albert, S. Afr. Dev., Emsian, Bokkeveld Beds, road to Gamka Kloof from top of Zwartberg Pass, south of Prince Albert, S. Afr. × 3.

Figs. 7, 8, 12. Lateral (A), basal, and oral views of *Katoblastus konincki* Macurda, 1967^{a}, IRSNB, Collec. De Ryckholt in Collec. De Koninck, I.G. 34406. L.Carb., Tournaisian, Tournai, Belgium. × 4.

Figs. 9, 11, 14. Oral lateral (A), and basal views of *Katoblastus pilzos* (Münster, 1843), USNM S3230. L.Carb., Tournaisian, Tournai, Belgium. × 4.

Fig. 10. Lateral view from inside of exterior mold of two zygous basals and D (left) and E (right) radials of *Brachyschisma ? oostheizeni*, Oostheizen collec., Zwartskraal, Prince Albert, S. Afr. Dev., Emsian, Bokkeveld Beds, Gamka Poort at Gamka Poort Dam, southwest of Prince Albert, S. Afr. × 3.

Fig. 13. Lateral view of cast of interior of B radial of *Brachyschisma? oostheizeni*, Sedgwick Museum A 3045, Cambridge Univ. Dev., Bokkeveld Beds, Emsian, roadcut between De Doorns and Triangle, S. Afr. × 3.

Fig. 15. Lateral (D) view of *Brachyschisma corrugatum*, BSNS E12581. M.Dev., Onondaga Ls., Vogelsanger Quarry, Williamsville, N.Y., USA. × 3.

PLATE VII

Figs. 1, 2, 4. Oral, basal, and lateral (B) views of *Orophocrinus conicus* Wachsmuth and Springer, 1888, unregis. spec., Iowa State Dept. History and Archives, Des Moines (no. 17 of original growth series). L. Miss., Kinderhookian, Hampton Fm., LeGrand, Iowa. × 3.

Figs. 3, 8. Oral and lateral (EA) views of *Orophocrinus orbignyanus* (De Koninck, 1844), USNM S3229. L.Carb., Tournaisian, Tournai, Belgium. × 3.

Figs. 5, 6. Basal and lateral (B) views of *Orophocrinus gracilis* (Meek and Worthen, 1870), USNM S3228 (no. 1 of original growth series). L.Miss., Osagean, Lower Burlington Ls., Burlington, Iowa. × 3.

Fig. 7. Oral view of *Orophocrinus gracilis*, USNM S3228 (no. 2 of original growth series). Horizon as above. × 3.

Figs. 9–11. Lateral (B), basal, and oral views of *Orophocrinus stelliformis* (Owen and Shumard, 1850), Univ. of Iowa 3-289B (no. 29 of original growth series). L.Miss., Osagean, Lower Burlington Ls., Burlington, Iowa. × 2.

PLATE VIII

Figs. 1, 3. Oral and lateral (E) views of *Orophocrinus praelongus* Bailey, 1886, TCD 7420. L.Carb., Visean, Feltrim Hill Knoll, Co. Dublin, Ireland. × 2.25.

Figs. 2, 5. Lateral (D) and oral views of *Orophocrinus catactus* (Macurda, 1965^{b}), USNM, no. 8 of original growth series. L.Miss., Osagean, Lake Valley Ls., Indian Wells Canyon, Sacramento Mts., Alamogordo, N.M., USA. × 2.

Figs. 4, 6. Oral and lateral (A) views of plaster cast of *Orophocrinus verus* (Cumberland, 1826), BMNH E8139, L.Carb., Visean, near Whitwell, in Bolland, Lancashire, England, U.K. × 2.

PLATE IX

Figs. 1, 2. Lateral (E) and oral views of *Orophocrinus celticus* Macurda, 1965^{b}, NMI G.6. 1959/5. L.Carb., Visean, Carrickhill, Portmarnock, Co. Dublin, Ireland. × 2.

Figs. 3, 6. Lateral (B) and oral views of *Orophocrinus pentangularis* (Sowerby, 1834), RSM 1958.1.2392. L.Carb., Visean, Coplow Knoll, Clitheroe, England, U.K. × 2.

Figs. 4, 5. Oral and lateral (A) views of immature specimen of *Orophocrinus praelongus* Bailey, 1886, TCD, unregis. spec. Compare with Pl. VIII, figs. 1, 3. L.Carb., Visean, Feltrim Hill Knoll, Co. Dublin, Ireland. × 7.5.

Fig. 7. Lateral view of specimen of *Orophocrinus conicus* Wachsmuth and Springer, 1888, with brachioles and stem, USNM S3226. L.Miss., Kinderhookian, Hampton Fm., LeGrand, Iowa, USA. × 3.

Figs. 8, 9. Oral and lateral (B) views of *Orophocrinus saltensis* Macurda, 1965^{b}, USNM, no. 10 of original growth series. L.Miss., Osagean, Redwall Ls., Thunder Springs Mb., US Route 60, Salt River Canyon, Arizona, USA. × 2.

Figs. 10–12. Lateral (A), oral, and basal views of *Pentablastus supracarbonicus* Sieverts-Doreck, 1951, Leiden Univ., Rijksmuseum 102451. Carb., U.-Namurian, Rabanal Ls., Rabanal de los Caballeros, Prov. of Palencia, Spain. × 3.

PLATE X

Figs. 1, 2, 6. Oral, lateral (E), and basal views of ***Mastoblastus ornatus*** Arendt, Breimer and Macurda, 1968, PIN 1788/312. L.Carb., L.Namurian, Tshan-Tshar, North Kazachstan, USSR. × 3.

Figs. 3, 5. Oral and lateral (C) views of *Acentrotremites ellipticus* (Cumberland, 1826), BMNH E8256. L.Carb., Visean, Wrington, Somerset, England, U.K. × 3.

Fig. 4. Basal view of *Orophocrinus saltensis* Macurda, 1965b, USNM, no. 10 of original growth series. Compare with Pl. IX, figs. 8, 9. L.Miss., Osagean, Redwall Ls., Thunder Springs Mb., US Route 60, Salt River Canyon, Arizona, USA. × 2.

Fig. 7. Lateral (E) view of *Orophocrinus verus* (Cumberland, 1826), TCD, unregis. spec. L.Carb., Visean, Feltrim Hill Knoll, Co. Dublin, Ireland. × 2.

PLATE XI

Figs. 1-3. Oral, basal, and lateral (A) views of *Anthoblastus brouweri* Wanner, 1924b, THD 12264. L.Perm., Somohole, Timor, Indonesia. × 3.

Figs. 4, 7. Lateral (A) and oral views of *Astrocrinus tetragonus* (Austin & Austin, 1843), RSM 1958.1.2380. L.Carb., Visean, Carlops, Peebleshire, Scotland, U.K. × 7.5.

Figs. 5, 8. Oral and lateral (D) views of *Anthoblastus stelliformis* Wanner, 1924b, THD 12265. U.Perm., Sonnebait Series, Basleo, Timor, Indonesia. × 3.

Figs. 6, 9. Oral and basal views of *Anthoblastus stelliformis*, THD 12266. Horizon as above. × 3.

PLATE XII

Fig. 1. View of slab in siltstone with molds of several specimens of *Pachyblastus dicki* n. sp., R. I. Dick collec., Cape Town Univ., S. Afr. Note brachioles. Dev., Emsian, Bokkeveld Beds, Cape Province, S. Afr. × 1.

Fig. 2. Enlarged view of specimen in lower right corner of Pl. XII, fig. 1. × 3.

PLATE XIII

Fig. 1. Lateral view of cast of *Pachyblastus dicki*, n. sp., R. I. Dick collec., Cape Town Univ., S. Afr. Dev., Emsian, Bokkeveld Beds, Cape Province, S. Afr. × 3.

Figs. 2, 3, 5. Oral lateral (A) and basal views of *Xenoblastus decussatus* (Shumard, 1858), USNM 160583. L.Miss., New Providence Fm., Coral Ridge Mb., Bullitt Co., Ky. × 3.

Fig. 4. Lateral view of radial of *Xenoblastus decussatus*, USNM 160584. L.Miss., New Providence Fm., Button Mold Knob, south of Louisville, Ky. × 2.

Fig. 6. Lateral view of radial of *Xenoblastus decussatus*, USNM S3713. Horizon as above. × 3.

Fig. 7. Lateral view of radial and ambulacrum of *Xenoblastus* sp., Collec. Piret, IRSNB I.G. 9694. L.Carb., Tournaisian, Tournai, Belgium. × 7.5.

Fig. 8. Lateral view of radial of *Xenoblastus decussatus*, USNM S5462. L.Miss., New Providence Fm., Button Mold Knob, south of Louisville, Ky. × 3.

PLATE XIV

Fig. 1. Lateral (BC) view of plaster cast of *Nymphaeoblastus miljukovi* Von Peetz, 1907, CGM 4/1887. L.Carb., Tournaisian, Prov. d'Akmolinsk, N. Kazachstan, USSR. × 2.

Figs. 2, 3. Lateral (D) and oral views of *Nymphaeoblastus miljukovi*, PIN 2760/1. L.Carb., Central Asia, USSR. × 3.

Fig. 4. Lateral (DE) view of rubber cast of *Nymphaeoblastus miljukovi*, CGM 6163. L.Carb., C_1, Lake Chunkurul, N. Kazachstan, USSR. × 1.6.

Fig. 5. Lateral view of cast of *Nymphaeoblastus miljukovi*, Univ. Hokaido 16056. L.Carb., Do zone, Jumonji Stage, Arisu Series, Nasiosawas, Jumonji, Simoarisu-mura, Kitakami Massif, Kesen-gun, Iwate Prefecture, Northeast Honshu, Japan. × 3.

Fig. 6. Lateral (DE) view of *Nymphaeoblastus kazachstanensis* Yakovlev, 1941, CGM 6163. L.Carb., Visean C_1, Kyz-Dzhar, N. Kazachstan, USSR. × 1.

PLATE XV

Fig. 1. Oral view of *Astrocrinus tetragonus* (Austin & Austin, 1843), BMNH E850. L.Carb., Visean, Settle, Yorkshire, England, U.K. × 8.7.

Fig. 2. Inclined oral view of *Nymphaeoblastus bancrofti* McKellar, 1964, UQ F39410. L.Carb., Visean, Tellebang Fm., Portion 72, Parish of Cannindah, County of Yarrol, Queensland, Australia. × 3.

Fig. 3. Basal view of *Astrocrinus tetragonus*, BMNH 75995. L.Carb., Yorkshire, England, U.K. × 8.7.

Figs. 4, 5, 7. Oral, lateral (E), and basal views of *Sphaeroschisma somoholense* Wanner, 1924^b, THD. Specimen was sectioned by Wanner. L.Perm., Somohole, Timor, Indonesia. × 3.

Fig. 6. Oral view of *Astrocrinus tetragonus*, NMI G. 40:1965. L.Carb., Visean, D_1, foreshore Oyster Bay, Fenit, Co. Kerry, Ireland. × 3.

Fig. 8. Lateral view of *Nymphaeoblastus bancrofti*, UQ F39411A. L.Carb., Visean, Tellebang Fm., Portion 72, Parish of Cannindah, County of Yarrol, Queensland, Australia. × 3.

PLATE XVI

Figs. 1–3. Oral, lateral (E), and basal views of *Hadroblastus blairi* (Miller and Gurley, 1895), Univ. Cincinnati 3845. Miss., Chouteau Ls., Sedalia, Mo., USA. × 3.

Figs. 4–6. Basal, oral, and lateral (B) views of *Hadroblastus blairi* (Miller and Gurley, 1895), Univ. Cincinnati 3839. (Holotype of *Codaster jessieae* Miller and Gurley, 1896). Miss., Chouteau Ls., Sedalia, Mo., USA. × 3.

Fig. 7. Oral view of *Hadroblastus* sp., USNM 160585. Miss., Shaly beds in Rockford Fm. (= Jacobs Chapel), center Lot 62, Clark Grant, Floyd Co., Ind., USA. × 7.5.

Figs. 8, 12. Oral and lateral (A) views of *Hadroblastus convexus* Fay, 1962, no. 8 in growth series. Miss., Lake Valley Ls., Nunn Mb., Lake Valley, N.M., USA. × 3.

Figs. 9, 15. Oral and lateral (A) views of *Hadroblastus whitei* (Hall, 1861), USNM 160586. Miss., St. Joe Fm., 1½ mi. upstream from Grand River dam site, Pensacola Dam, Mayes Co., Okla., USA. × 2.

Figs. 10, 11. Lateral (A) and oral views of *Hadroblastus convexus*, no. 2 in growth series. Miss., Lake Valley Ls., Nunn Mb., Lake Valley, N.M., USA. × 3.

Fig. 13. Lateral (C) view of *Hadroblastus convexus*, no. 5 in growth series. Horizon as above. × 3.

Fig. 14. Basal view of *Hadroblastus whitei*, USNM 160587. Miss., St. Joe Fm., 1½ mi. upstream from Grand River dam site, Pensacola Dam, Mayes Co., Okla., USA. × 2.

PLATE XVII

Fig. 1. Oral view of *Hadroblastus whitei* (Hall, 1861), Sprinkle collec., MCZ 745. Miss., Burlington Ls., Rdcut on N side of I-44, 0.3 mi. E of Dry Branch Bridge, SW¼ SE¼ SE¼ sec. 26, T 29 N, R 25 W, Greene Co., Mo., USA. × 4.

Figs. 2, 6. Lateral (C) and oral views of internal chert cast of *Hadroblastus whitei*, UI RX-67A. Miss., Burlington Ls., near Curryville, Mo., USA. × 3.

Figs. 3, 4. Lateral (A) and oral views of *Hadroblastus whitei*, UI RX-67B. Miss., base of Upper Burlington Fm., Pratt's quarry, Louisiana, Mo., USA. × 4.

Fig. 5. Oral view of *Hadroblastus whitei*, UI RX-67C. Miss., Upper Burlington Ls., Louisiana, Mo., USA. × 4.

Figs. 7, 12, 15. Lateral (A), oral, and basal views of *Hadroblastus whitei*, UMMP 59712. Miss., Burlington Ls., Rdcuts, N and S sides of Rt. I-70, NW¼ sec. 13, T 48 N, R 19 W, Cooper Co., Mo., USA (UMMP 1966/M-45). × 4.

Figs. 8, 11. Lateral (A) and oral views of *Hadroblastus whitei*, Sprinkle collec., MCZ 746. Miss., Burlington Ls., Rdcut on N side of I-44, 0.3 mi. E of Dry Branch Bridge, SW¼ SE¼ SE¼ sec. 26, T 29 N, R 25 W, Greene Co., Mo., USA. × 4.

Fig. 9. Lateral (C) view of *Hadroblastus whitei*, Sprinkle collec., MCZ 747. Miss., Burlington Ls., roadcut, S side of Rt. I-70, NW¼ sec. 13, T 48 N, R 19 W, Cooper Co., Mo., USA. × 4.

Fig. 10. Lateral (A) view of *Hadroblastus whitei*, USNM 160588. Miss., Burlington Ls., Sweeney qy., Clifton City, Mo., USA. × 3.

Fig. 13. Lateral (A) view of *Hadroblastus whitei*, UMMP 59713. Miss., Burlington Ls., roadcut of N side of I-44, 0.3 mi. E of Dry Branch Bridge, SW¼ SE¼ SE¼ sec. 26, T 29 N, R 25 W, Greene Co., Mo., USA. × 4.

Fig. 14. Lateral view of cotype of *Hadroblastus whitei*, USNM S3238. Miss., Burlington Ls., Burlington, Ia., USA. × 3.

PLATE XVIII

Fig. 1. Lateral view of *Hadroblastus* sp., Sprinkle collec., MCZ 748. Miss., Lodgepole Fm., Standard Creek, Mont., USA. × 3.

Figs. 2, 4. Basal and lateral (A) views of *Hadroblastus* sp.?, TCD, unregis. spec. L. Carb., Visean, Feltrim Hill Knoll, Co. Dublin, Ireland. × 4.

Figs. 3, 5. Oral and lateral views of crushed holotype of *Hadroblastus kentuckyensis* (Shumard, 1858), USNM S3210. Fig. 3 oriented as in other oral views, with B ambulacrum in upper right center. B(right) and C(left) radials and zygous basal visible in fig. 4. Miss., New Providence Fm., Button Mold Knob, 7 mi. south of Louisville, Ky., USA. × 3.

Fig. 6. Lateral view of radial of *Hadroblastus kentuckyensis*, USNM 160589. Miss., New Providence Sh., first knob, 5 mi. south of Louisville, Ky., USA. × 3.

Fig. 7. Lateral (AB) view of *Hadroblastus kentuckyensis* (?), USNM 160590. Miss., New Providence Fm., top of knob one-fourth mile NW of Lebanon Junction, Ky., USA. × 3.

Fig. 8. Oral view of *Hadroblastus kentuckyensis* (?), Indiana Univ. no. 8266. Miss., Borden Grp., Monroe Reservoir, SE$\frac{1}{4}$ SE$\frac{1}{4}$ NE$\frac{1}{4}$ sec. 4, T 7 N, R 1 E, Monroe Co., Ind., USA. × 3.

PLATE XIX

Fig. 1. Oral view of reassembled isolated plates of *Neochisma australe* n. sp., showing oral outline before disarticulation. L. Perm., Callytharra Fm., Callytharra Springs, Western Australia. × 3.

Fig. 2. Internal view of isolated deltoid of *Neoschisma australe*, Univ. Western Australia F5714A. Horizon as above. × 3.

Figs. 3, 4. Lateral and inclined oral views of C radial of *Neoschisma australe*, Austr. Bur. Min. Res. GW137. Horizon as above. × 3.

Fig. 5. Oral view of *Neoschisma verrucosum* Wanner, 1924^{a}, THD 12254. Perm., 1 km. south of Kapan, Timor, Indonesia. × 3.

Figs. 6, 7. Lateral (CD) and oral views of holotype of *Neoschisma australe*, UMMP 58682. L. Perm., Callytharra Fm., Callytharra Springs, Western Australia. × 3.

Fig. 8. Lateral view of D radial of *Neoschisma australe*, Austr. Bur. Min. Res. GW137. Horizon as above. × 3.

PLATE XX

Fig. 1. Inclined oral view (centered on B) of holotype of *Notoblastus stellaris* n. sp., UMMP 58683. L. Perm., Callytharra Fm., Callytharra Springs, Western Australia. × 3.

Fig. 2. Oral view of deltoid of *Notoblastus* sp., Univ. Ams. Ge. 0.9927. U. Perm., Sonnebait Series, near Basleo, Timor, Indonesia. × 3.

Figs. 3, 5, 6. Basal, oral, and lateral (C) views of *Notoblastus oyensi* (Wanner, 1940), Univ. Ams. Ge. 0.9925. Perm., Sonnebait Series, Basleo, Timor, Indonesia. × 4.

Figs. 4, 8. Oral and lateral (A) views of *Neoschisma timorense* Wanner, 1940, Univ. Ams. Ge. 0.9993. Horizon as above. × 4.

Fig. 7. Lateral (D) view of *Neoschisma verrucosum* Wanner, 1924^{a}, THD 12254. Perm., 1 km. south of Kapan, Timor, Indonesia. × 3.

PLATE XXI

Figs. 1, 7, 8. Lateral (B), oral, and basal (rotated slightly counterclockwise) views of holotype of *Notoblastus stellaris* n. sp., UMMP 58683. L. Perm., Callytharra Fm., Callytharra Springs, Western Australia. × 3.

Fig. 2. Oral view of isolated deltoid of *Notoblastus stellaris*, Univ. Western Australia F5714E. Horizon as above. × 3.

Fig. 3. Oral view of radial prong of *Notoblastus* sp., UMMP 59726. L. Perm., Callytharra Fm., outcrop on west side of north-south wash, $\frac{1}{8}$ mi. south of Wooramel River, $\frac{1}{4}$ mi. SSE of junction of Wooramel River and Bilung Creek, 25°43′ S, 115°52.5′ E, Western Australia (UMMP 1968/Pe3). × 3.

Fig. 4. Oral view of radial with broken prong of *Notoblastus* sp., UMMP 59727. Horizon as above. × 3.

Fig. 5. Lateral view of radial prong of *Notoblastus* sp., UMMP 59728. Horizon as above. × 3.

Fig. 6. Lateral (C) view of *Dipteroblastus permicus* Wanner, 1940, Univ. Ams. Ge. 0.9939. U. Perm., Sonnebait Series, Tuniun Enu, Basleo, Timor, Indonesia. × 3.

Fig. 9. Lateral view of medial part of radial prong of *Notoblastus* sp., UMMP 59729. Horizon as for fig. 3. × 3.

PLATE XXII

Fig. 1. Oral view of *Notoblastus brevispinus* Brown, 1942, Austr. Mus. F. 39762. Perm., Upper Marine Series, Branxton Fm., Fenestella Sh., 4½ mi. S of Cessnock, N.S.W., Australia. × 3.

Figs. 2, 3, 6. Basal (rotated clockwise), lateral (EA), and lateral (B) views of *Dipteroblastus permicus* Wanner, 1940, Univ. Ams. Ge. 0.9939. U. Perm., Sonnebait Series, Tuniun Enu, Basleo, Timor, Indonesia. × 3.

Fig. 4. Oral view of *Notoblastus cornutus* (McKellar, 1969), GSQ F11385 (rubber cast of mold). L. Perm., Berserker Beds, Nerimbera Quarry, near Rockhampton, Queensland, Australia. × 3.

Fig. 5. Inclined oral view (centered on E) of *Notoblastus cornutus*, GSQ F11119 (rubber cast of mold). Horizon as above. × 3.

PLATE XXIII

Figs. 1, 6. Oral views of disarticulated and restored specimen of *Austroblastus whitehousei* McKellar, 1969, GSQ F11239 (rubber cast of mold; anus at 3 o'clock fig. 1, 6 o'clock fig. 6). L. Perm., Berserker Beds, Nerimbera Quarry, near Rockhampton, Queensland, Australia. × 1.5.

Figs. 2, 3, 5, 7. Basal, oral inclined oral (E), and lateral views of *Timoroblastus coronatus* Wanner, 1924ª, Univ. Ams. B6637. (Holotype of *Microblastus pocilliformis* Van Eykeren, 1942). U. Perm. Sonnebait Series, between Basleo and Noil Tonino, Timor, Indonesia. × 7.5.

Fig. 4. Oral view of *Dipteroblastus permicus* Wanner, 1940, Univ. Ams. Ge. 0.9939. U. Perm., Sonnebait Series, Tuniun Enu, Basleo, Timor, Indonesia. × 3.

Fig. 8. Lateral view of radial of *Austroblastus whitehousei*, GSQ F13533 (rubber cast of mold). L. Perm., Berserker Beds, Nerimbera Quarry, near Rockhampton, Queensland, Australia. × 2.

PLATE XXIV

Fig. 1. Inclined lateral view of disarticulated specimen of *Austroblastus whitehousei* McKellar, 1969, GSQ F11126 (rubber cast of mold). L. Perm., Berserker Beds, Nerimbera Quarry, near Rockhampton, Queensland, Australia. × 3.

Fig. 2. Oral view of isolated radial with part of prong of *Thaumatoblastus longiramus* Wanner, 1924ᵇ, Austr. Bur. Min. Res. KNF73. Perm., Noonkanbah Fm., 2.2 mi. bearing 288° from Bruten's old yard Cherrabun Station, Fitzroy Basin, Western Australia. × 3.

Figs. 3–5. Lateral (DE), oral, and basal views of *Timoroblastus weiensis* Wanner, 1940, Univ. Ams. Ge. 0.9931. Perm., Tai Wei, east of Basleo, Timor, Indonesia. × 3.

Fig. 6. Lateral view of isolated radial of *Austroblastus* sp. (?), GSQ F11197 (rubber cast of mold). L. Perm., Berserker Beds, Nerimbera Quarry, near Rockhampton, Queensland, Australia. × 3.

PLATE XXV

Figs. 1, 2. Lateral and oral views of radial and part of prong of *Thaumatoblastus longiramus* Wanner, 1924ᵇ, THD 12263. (Holotype of *T. longispinus* Wanner, 1924ᵇ). U. Perm., Sonnebait Series, Basleo, Timor, Indonesia. × 3.

Fig. 3. Lateral view of part of radial and prong of *Thaumatoblastus longiramus*, Free Ref. Univ., Amsterdam, unregistered. Horizon as above. × 3.

Fig. 4. Oral view of part of radial of *Thaumatoblastus longiramus*, Austr. Bur. Min. Res. ML87. L. Perm., Coyrie Fm., north bank of Lyndon River east of Mia Mia Homestead, 23°21′ S, 114°34′ W, Carnarvon Basin, Western Australia. × 3.

Fig. 5. Oral view of radial and part of prong of *Thaumatoblastus longiramus*, Austr. Bur. Min. Res. ML87. Horizon as above. × 3.

Fig. 6. Lateral view of radial and part of prong of *Thaumatoblastus longiramus*, Austr. Bur. Min. Res. ML87. Horizon as above. × 3.

Fig. 7. Oral view of part of radial prong of *Thaumatoblastus longiramus*, Univ. Tasmania 23193. L. Perm., Berriedale Ls., Maria Is., Tasmania, Australia. × 3.

Fig. 8. Lateral view of reassembled radials of *Thaumatoblastus longiramus*, Univ. Leiden collec. U. Perm., Soem Peh, Niki Niki, Basleo, Timor, Indonesia. × 2.4.

PLATE XXVI

Figs. 1, 5. Basal and lateral (CD) views of *Timoroblastus coronatus* Wanner, 1924ᵃ, no. 11 Kampong Sebot growth series. Perm., Kampong Sebot, Timor, Indonesia. × 3.

Fig. 2. Lateral (C) view of *Codaster acutus* M'Coy, 1849, no. 2 in growth series. L. Carb., Up. Visean, D_2 Subzone, Middle Ls., ¼ mi. S of Bare House, coor. SE007668, 1.8 mi. N of Grassington, England. × 3.

Fig. 3. Oral view of *Codaster acutus*, no. 4 in growth series. Horizon as above. × 3.

Fig. 4. Lateral (AB) view of *Timoroblastus coronatus*, no. 21 in Tuniun Enu growth series. U. Perm., Sonnebait Series, Tuniun Enu, Basleo, Timor, Indonesia. × 3.

Fig. 6. Oral view of *Codaster acutus*, no. 18 in growth series. Horizon as for fig. 2. × 3.

Fig. 7. Lateral (D) view of immature specimen of *Codaster acutus*, TCD 8067. L. Carb., Visean, quarry, 100 yds. W of Sean Delaney's Farm, Bally

Phillip, 0.8 mi. S of Lisdowney, which is 2½ mi. E of Ballyragget, Co. Kilkenny, Ireland. × 17.5

Figs. 8, 11. Lateral (B) and oral views of *Timoroblastus coronatus*, no. 11 in Tuniun Enu growth series. U. Perm., Sonnebait Series, Tuniun Enu, Basleo, Timor, Indonesia. × 3.

Figs. 9, 10. Basal and lateral (EA) views of *Timoroblastus coronatus*, no. 19 in Tuniun Enu growth series. Horizon as above. × 3.

PLATE XXVII

Fig. 1. Lateral (A) view of *Timoroblastus coronatus* Wanner, 1924^{a}, no. 1 in Noa growth series. U. Perm., Sonnebait Series, Noa, near Tuniun Enu, Basleo, Timor, Indonesia. × 2.5.

Fig. 2. Lateral (C) view of *Codaster acutus* M'Coy, 1849, no. 19 in growth series. L. Carb., Up. Visean, D_2 Subzone, Middle Ls., ¼ mi. S of Bare House, coor. SE007668, 1.8 mi. N of Grassington, England. × 3.

Fig. 3. Basal view of *Timoroblastus coronatus*, no. 12 in Tuniun Enu growth series. U. Perm., Sonnebait Series, Tuniun Enu, Basleo, Timor, Indonesia. × 3.

Fig. 4. Oral view of *Timoroblastus coronatus*, no. 19 in Tuniun Enu growth series. Horizon as above. × 3.

Fig. 5. Basal view of *Timoroblastus coronatus*, no. 2 in Noa growth series. U. Perm., Sonnebait Series, Noa, near Tuniun Enu, Basleo, Timor, Indonesia. × 2.25.

Figs. 6, 8. Lateral (A) and oral views of *Codaster acutus*, no. 7 in growth series. L. Carb., Up. Visean, D_2 Subzone, Middle Ls., ¼ mi. S of Bare House, coor. SE007668, 1.8 mi. N of Grassington, England. × 3.

Fig. 7. Oral view of immature specimen of *Codaster acutus*, TCD 8067. L. Carb., Visean, quarry, 100 yds. W of Sean Delaney's Farm, Bally Phillip, 0.8 mi. S of Lisdowney, which is 2½ mi. E of Ballyragget, Co. Kilkenny, Ireland. × 17.5.

Fig. 9. Oral view of *Timoroblastus coronatus*, no. 11 in Kampong Sebot growth series. Perm., Kampong Sebot, Timor, Indonesia. × 3.

PLATE XXVIII

Figs. 1, 2. Oral and lateral (C) views of *Codaster acutus* M'Coy, 1849, no. 8 in Lisdowney growth series. L. Carb., Visean, quarry, 100 yds. W of Sean Delaney's Farm, Bally Phillip, 0.8 mi. S of Lisdowney, which is 2½ mi. E of Ballyragget, Co. Kilkenny, Ireland. × 3.

Figs. 3, 6. Lateral (A) and oral views of *Angioblastus variabilis* Wanner, 1931, Univ. Ams. Ge. 0.9933. (Holotype of *Angioblastus depressus* WANNER, 1940). U. Perm., Nifu Muti, Timor, Indonesia. × 4.

Figs. 4, 9. Lateral (A) and oral views of *Codaster acutus*, no. 4 in Lisdowney growth series. L. Carb., Visean, quarry, 100 yds. W of Sean Delaney's Farm, Bally Phillip, 0.8 mi. S of Lisdowney, which is 2½ mi. E of Ballyragget, Co. Kilkenny, Ireland. × 3.

Fig. 5. Oral view of reassembled radials of *Thaumatoblastus longiramus* Wanner, 1924^{b}. Univ. Leiden collec. U. Perm., Soem Peh, Niki Niki, Basleo, Timor, Indonesia. × 2.

Fig. 7. Lateral view from interior of external cast of a neoschismatid radial and ambulacrum, GSQ, unregis. spec. Photograph courtesy R. McKellar.

U. Perm., Oxtrack Fm., Southeast Bowen Basin, Queensland, Australia. × 2.

Fig. 8. Lateral (D) view of immature specimen of *Codaster acutus*, TCD, unregis. spec. L. Carb., Visean, quarry, 100 yds. W of Sean Delaney's Farm, Bally Phillip, 0.8 mi. S of Lisdowney, which is 2½ mi. E of Ballyragget, Co. Kilkenny, Ireland. × 17.5.

PLATE XXIX

Figs. 1, 2. Lateral (C) and oral views of *Angioblastus dotti* (Moore and Strimple, 1942), USNM 111249. Penn., Hogshooter Ls., Ramona, Okla., USA. × 3.

Figs. 3, 4. Lateral (B) and oral views of *Angioblastus dotti*, USNM 160568. Horizon as above. × 3.

Fig. 5. Lateral (D) view of *Angioblastus dotti*, USNM 160569. Horizon as above. × 3.

Figs. 6, 9, 10. Oral, basal, and lateral (C) views of *Angioblastus ellesmerensis* n. sp., GSC 67261. Penn., Atokan, Ellesmere Is., Canadian Arctic. × 3.

Fig. 7. Oral view of *Angioblastus wanneri* (Yakovlev, 1926^b), no. 3 in growth series. L. Perm., Krasnoufimsk, Urals, USSR. × 3.

Fig. 8. Lateral (E) view of *Angioblastus ellesmerensis*, GSC, unregis. spec. Penn., Atokan, Hare Fiord, Ellesmere Is., Canadian Arctic. × 3.

Fig. 11. Lateral (E) view of *Angioblastus wanneri*, no. 9 in growth series. L. Perm., Krasnoufimsk, Urals, USSR. × 3.

Figs. 12, 13, 16. Oral, basal, and lateral (B) views of *Angioblastus wanneri*, no. 13 in growth series. Horizon as above. × 3.

Fig. 14. Basal view of *Angioblastus variabilis* Wanner, 1931, Univ. Ams. Ge. 0.9933. (Holotype of *Angioblastus depressus* WANNER, 1940). U. Perm., Nifu Muti, Timor, Indonesia. × 4.

Fig. 15. Basal view of *Angioblastus wanneri*, no. 10 in growth series. L. Perm., Krasnoufimsk, Urals, USSR. × 3.

Fig. 17. Oral view of *Angioblastus wanneri*, no. 17 in growth series. Horizon as above. × 3.

Fig. 18. Oral view of *Angioblastus wanneri*, no. 8 in growth series. Horizon as above. × 3.

Figs. 19–21. Lateral (C), oral, and basal views of *Angioblastus boliviensis* n. sp., USNM 160591. L. Perm., Zudanez syncline about 1 mi. S of village of Zudanez, Bolivia. × 4.

PLATE XXX

Figs. 1, 2. Oral and lateral (B) views of *Angioblastus variabilis* Wanner, 1931, no. 2 in growth series. U. Perm., Sonnebait Series, Noko, Basleo, Timor, Indonesia. × 4.

Figs. 3, 4. Lateral (A) and basal views of *Angioblastus variabilis*, no. 7 in growth series. Horizon as above. × 4.

Fig. 5. Oral view of *Tympanoblastus pousirewskii* (Stuckenberg, 1875), Mining Institute, Leningrad, 106/43. L. Perm., Timan tundra, Pechora Region, USSR. × 3.

Figs. 6, 12. Lateral (A) and oral views of *Angioblastus variabilis*, no. 10 in growth series. U. Perm., Sonnebait Series, Noko, Basleo, Timor, Indonesia. × 4.

Figs. 7, 9. Lateral (B) and oral views of *Angioblastus variabilis*, no. 14 in growth series. Horizon as above. × 4.

Fig. 8. Lateral (C) view of *Angioblastus variabilis*, no. 13 in growth series. Horizon as above. × 4.

Figs. 10, 11. Oral and lateral (D) views of *Angioblastus miloradovitchi* (Yakovlev 1940), CGM collec. 6324. L. Perm., Pechora Region, USSR. × 3.

Fig. 13. Oral view of *Tympanoblastus elongatus* (Yakovlev, 1937), CGM 8/6109. L. Perm., Ural Mts,. USSR. × 3.

Fig. 14. Oral view of *Tympanoblastus pousirewskii*, CGM collec. 7191. (Holotype of *Codaster barkhatovae* Yakovlev, 1941). L. Perm. Timan, USSR. × 3.

PLATE XXXI

Fig. 1. Lateral (D) view of *Tympanoblastus elongatus* (Yakovlev, 1937), CGM 8/6109. L. Perm., Ural Mts., USSR. × 3.

Fig. 2. Lateral (A) view of *Pterotoblastus brevialatus* Wanner, 1931, no. 7 in growth series. U. Perm., Sonnebait Series, Noko, Basleo, Timor, Indonesia. × 5.

Fig. 3. Lateral view of *Tympanoblastus pousirewskii*, CGM collec. 7191. (Holotype of *Codaster barkhatovae* Yakovlev, 1941). L. Perm., Timan, USSR. × 3.

Figs. 4, 8. Oral and lateral (A) views of *Pterotoblastus ferrugineus* Wanner, 1940, Univ. Ams. Ge. 0.9924. Perm., Tai Wei, east of Basleo, Timor, Indonesia. × 4.

Fig. 5. Lateral (A) view of *Pterotoblastus brevialatus*, no. 8 in growth series. U. Perm., Sonnebait Series, Noko, Basleo, Timor, Indonesia. × 5.

Fig. 6. Lateral (B) view of *Tympanoblastus pousirewskii* (Stuckenberg, 1875), Mining Institute, Leningrad, 106/43. L. Perm., Timan tundra, Pechora Region, USSR. × 3.

Figs. 7, 9. Lateral (A) view of *Pterotoblastus brevialatus*, no. 12 in growth series. U. Perm., Sonnebait Series, Noko, Basleo, Timor, Indonesia. × 5.

Fig. 10. Oral view of isolated deltoid of *Pterotoblastus* sp., Univ. Ams. Ge. 0.9926. (*Pterotoblastus* sp. no. 2, Wanner, 1940). U. Perm., Sonnebait Series. Nepo, Basleo, Timor, Indonesia. × 3.

Figs. 11, 12. Oral and lateral (A) views of *Pterotoblastus gracilis* Wanner, 1924^a, USNM 160592. Perm., Komuk, Thailand. × 3.

Fig. 13. Oral view of *Pterotoblastus brevialatus*, no. 13 in growth series. U. Perm., Sonnebait Series, Noko, Basleo, Timor, Indonesia. × 5.

Figs. 14, 15. Basal and lateral (A) views of *Pterotoblastus brevialatus*, no. 14 in growth series. Horizon as above. × 5.

PLATE XXXII

Fig. 1. Lateral view of basal part of brachioles of E ambulacrum of *Pleuroschisma lycorias* (Hall, 1862), BSNS E15987. M. Dev., Moscow Shale, Kashong Mb., salt shaft, Wadsworth, N.Y., USA. × 18.74.

Fig. 2. Oral view of *Indoblastus granulatus* Wanner, 1924ᵃ, BMNH E30688. Perm., Neoepantoekak, Timor, Indonesia. × 2.

Fig. 3. Basal view of *Pterotoblastus gracilis* Wanner, 1924ᵃ, no. 5 in growth series. U. Perm., Sonnebait Series, Noko, Basleo, Timor, Indonesia. × 4.

Fig. 4. Oral view of immature *Pterotoblastus gracilis*, no. 2 in growth series. Horizon as above. × 8.3.

Fig. 5. Lateral (B) view of *Ceratoblastus nanus* Wanner, 1940, Univ. Ams. Ge. 0.9934. Horizon as above. × 5.

Fig. 6. Oral view of *Pterotoblastus gracilis*, no. 8 in growth series. Horizon as above. × 4.

Figs. 7, 8. Oral and lateral (D) views of *Nannoblastus cuspidatus* Wanner, 1924ᵇ, THD 12270. Perm., Somohole, Timor, Indonesia. × 4.

Fig. 9. Lateral (B) view of *Pterotoblastus gracilis*, no. 15 in growth series. U. Perm., Sonnebait Series, Noko, Basleo, Timor, Indonesia. × 4.

Fig. 10. Oral view of *Pterotoblastus gracilis*, no. 12 in growth series. Horizon as above. × 4.

Fig. 11. Oral view of *Ceratoblastus nanus*, Univ. Ams. Ge. 0.9934 (Same specimen as fig. 5). Horizon as above. × 15.

PLATE XXXIII

Fig. 1. Oral view of *Nannoblastus pyramidatus* Wanner, 1924ᵇ, no. 6 in growth series. U. Perm., Sonnebait Series, Noko, Basleo, Timor, Indonesia. × 4.

Figs. 2, 6. Lateral (A) and oral views of *Nannoblastus pyramidatus*, no. 10 in growth series. Horizon as above. × 4.

Fig. 3. Inclined oral (C) view of *Indoblastus weberi* (Wanner, 1924ᵃ), collec. Geol.-Paläont. Instit., Friedrich-Wilhelm Univ. Bonn. Perm., Tuani, Niki Niki, Hatu Dame, Ramelau Mts., Portuguese Timor. × 3.

Fig. 4. Lateral (A) view of *Indoblastus granulatus* Wanner, 1924ᵃ, BMNH E30688. Perm., Neoepantoekak, Timor, Indonesia. × 2.

Fig. 5. Lateral (A) view of *Nannoblastus pyramidatus*, no. 13 in growth series. U. Perm., Sonnebait Series, Noko, Basleo, Timor, Indonesia. × 4.

Fig. 7. Lateral (B) views of *Nannoblastus pyramidatus*, no. 14 in growth series. Horizon as above. × 4.

Fig. 8. Enlarged view of oral opening with ring canal and ambulacra with minor lobes and furrows, *Pterotoblastus brevialatus* Wanner, 1931, no. 15 in growth series. Horizon as above. × 17.5.

PLATE XXXIV

Fig. 1. Enlarged view of left side of ambulacrum of *Xenoblastus decussatus* (Shumard, 1858), USNM S3713. L. Miss., New Providence Fm., Button Mold Knob, south of Louisville, Ky., USA. × 18.75.

Fig. 2. Enlarged view of C ambulacrum of *Timoroblastus coronatus* Wanner, 1924ᵃ, no. 22 in Tuniun Enu growth series. U. Perm., Sonnebait Series, Tuniun Enu, Basleo, Timor, Indonesia. × 17.5.

Fig. 3. Enlarged view of B ambulacrum of *Decaschisma pulchellum* (Miller and Dyer, 1878), no. 14 in growth series, Sil., Waldron Sh., Indiana, USA. × 17.5.

Fig. 4. Enlarged view of C ambulacrum of *Pleuroschisma lycorias* (Hall, 1862), UMMP 56499. M. Dev., Hungry Hollow Fm., Tile Yard, Thedford, Ontario, Canada. × 18.75.

Fig. 5. Enlarged view of E ambulacrum of *Heteroschisma alatum*, UMMP 58660. M. Dev., Potter Farm Fm., Alpena, Mich., USA. × 17.5.

Fig. 6. Enlarged view of B ambulacrum of *Hadroblastus whitei* (Hall, 1861), UMMP 59712. Miss., Burlington Ls., roadcuts, N and S sides of I-70, NW $\frac{1}{4}$ sec. 13, T 48 N, R 19 W, Cooper Co., Mo., USA. × 17.5.

PLATES I – XXXIV

PLATE I


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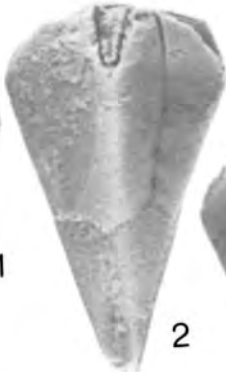
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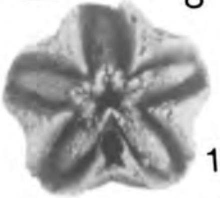
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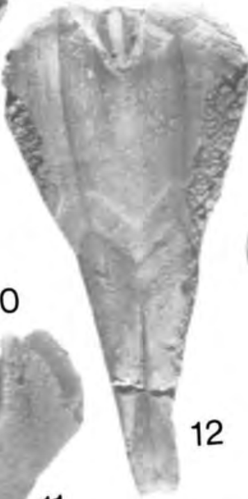
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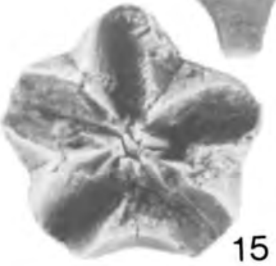
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PLATE II


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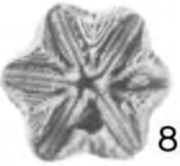
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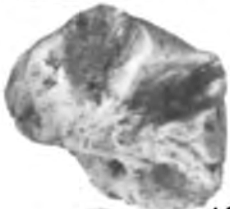
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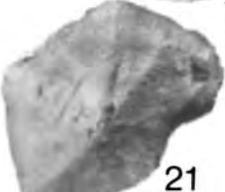
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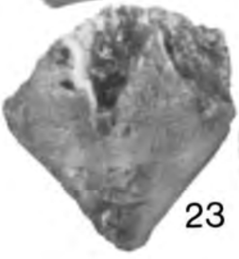
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PLATE IV


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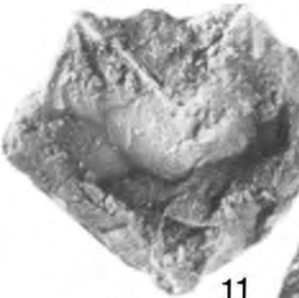
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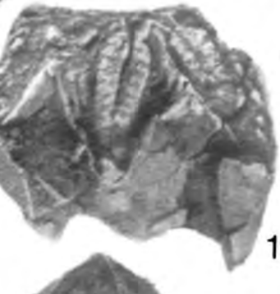
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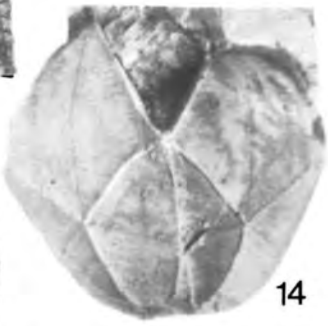
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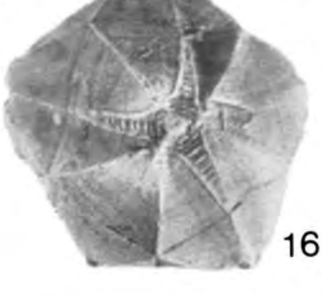
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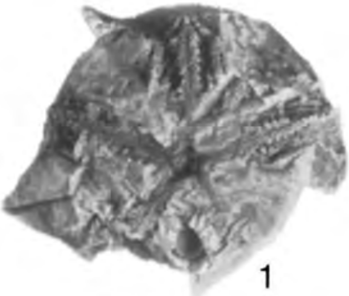
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PLATE VII


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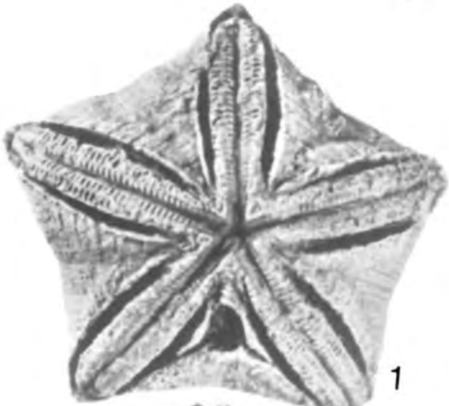
PLATE VIII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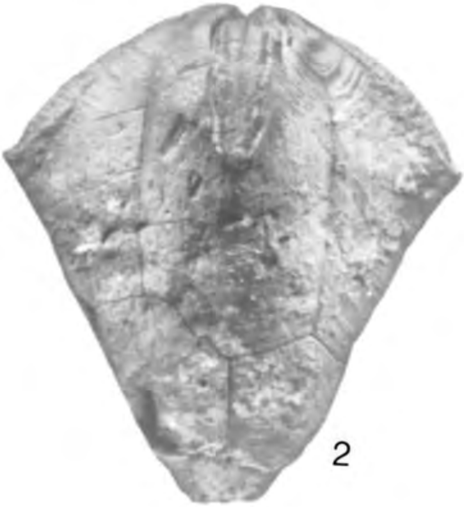
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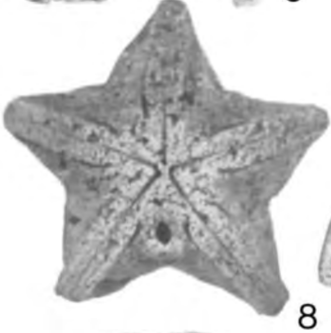
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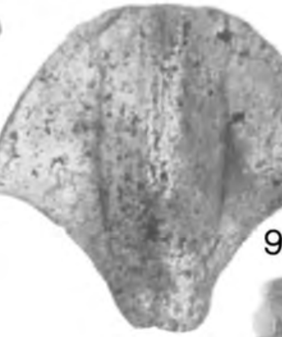
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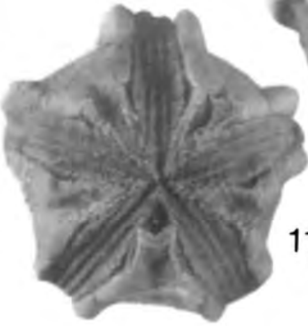
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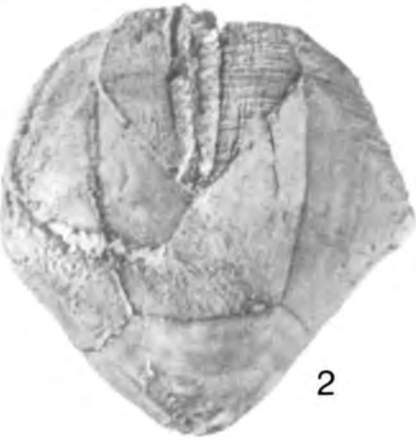
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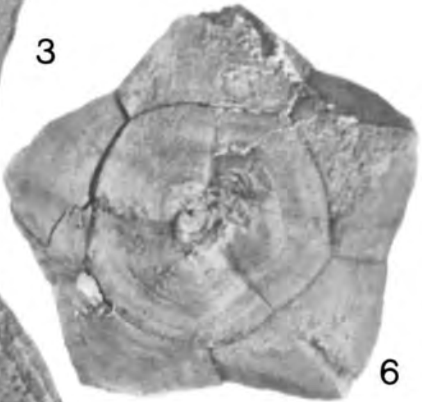
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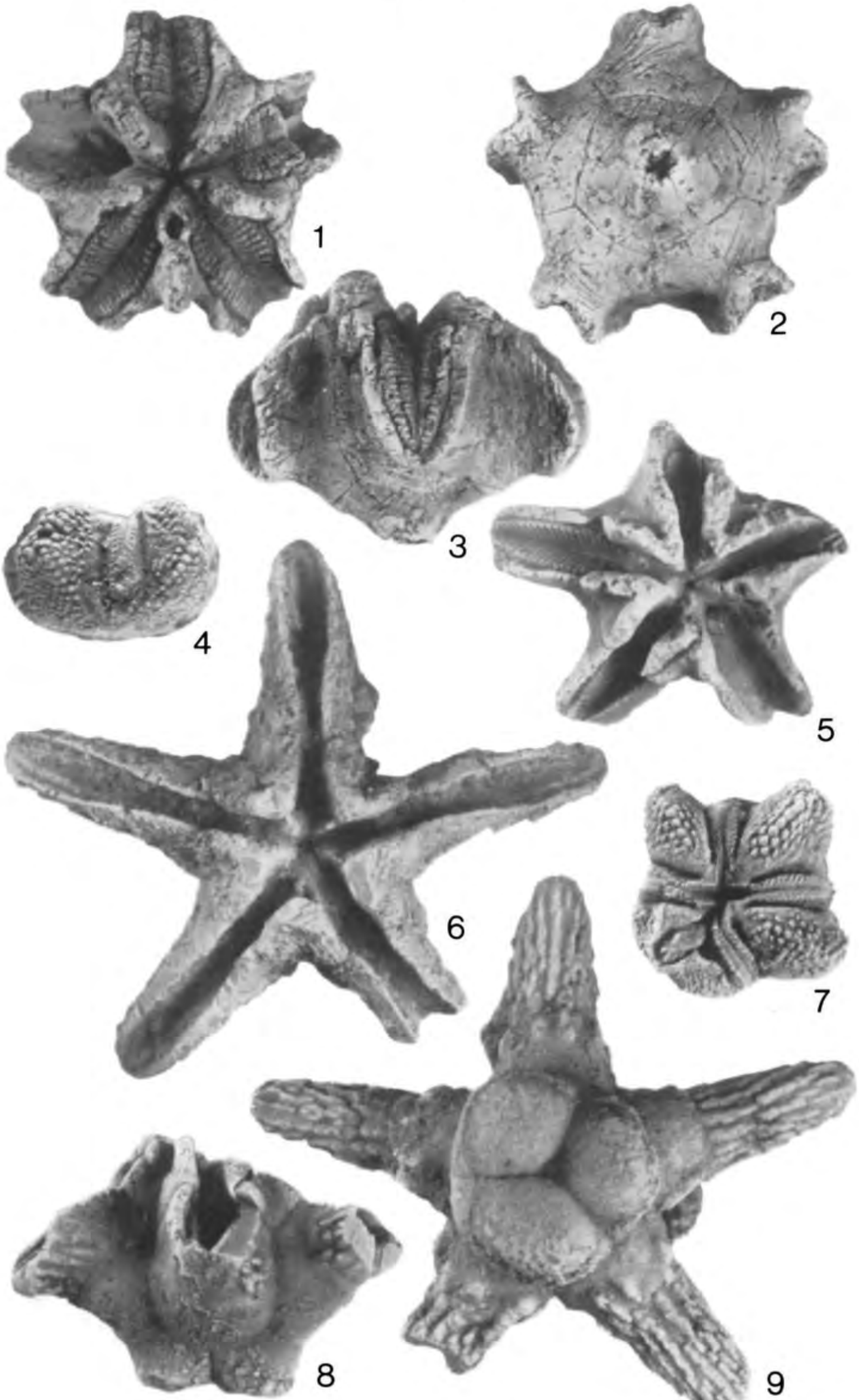

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PLATE XIII


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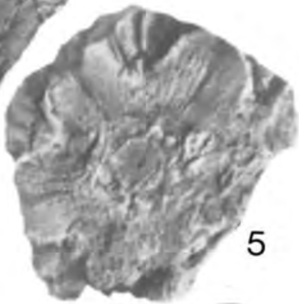
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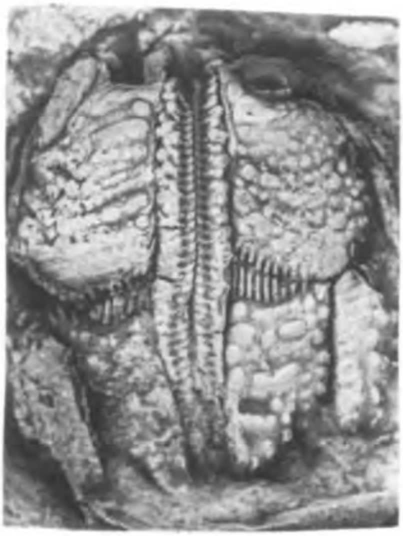
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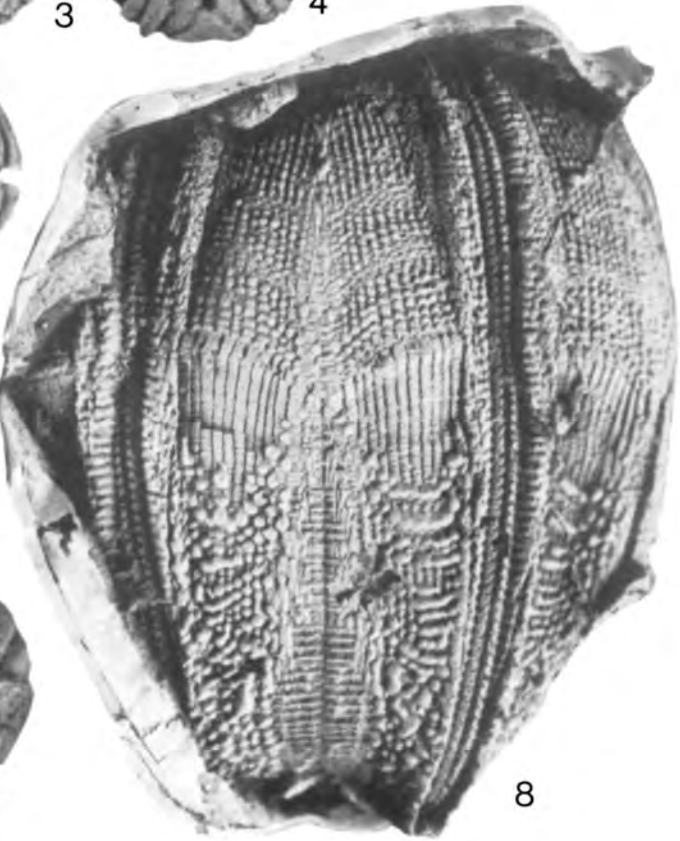
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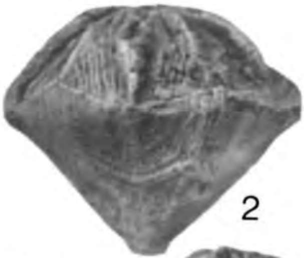
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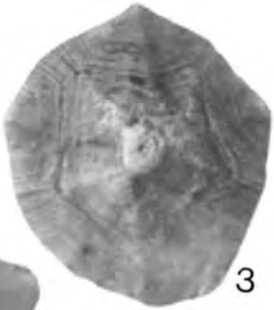
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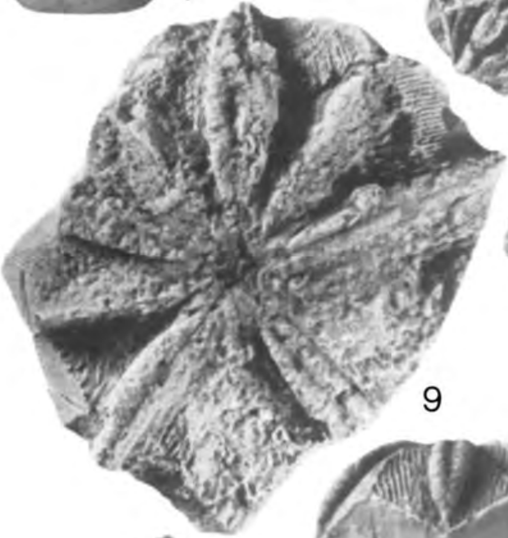
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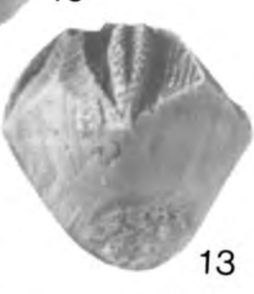
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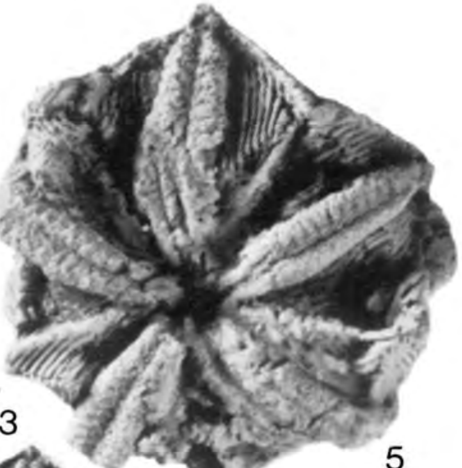
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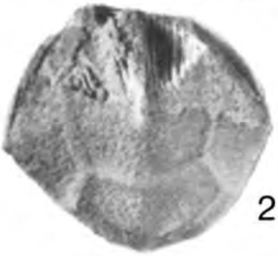
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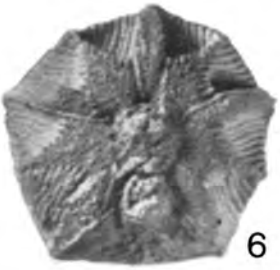
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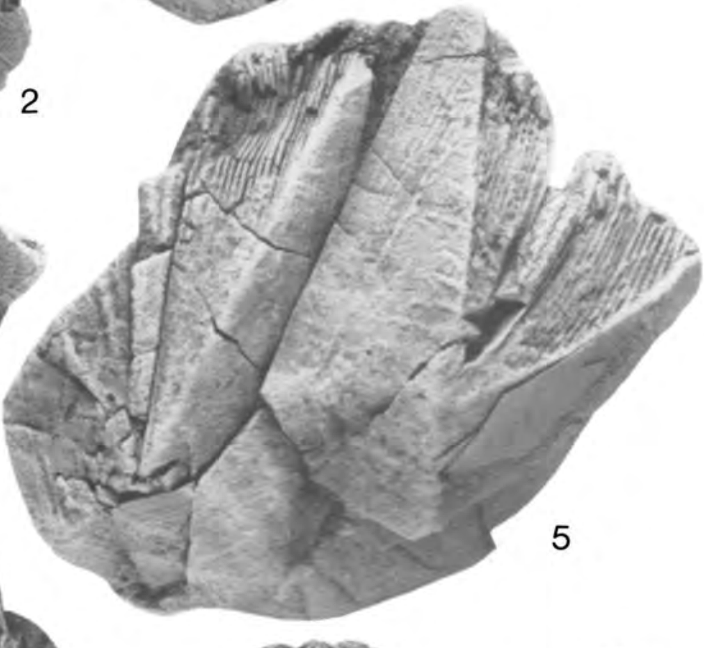
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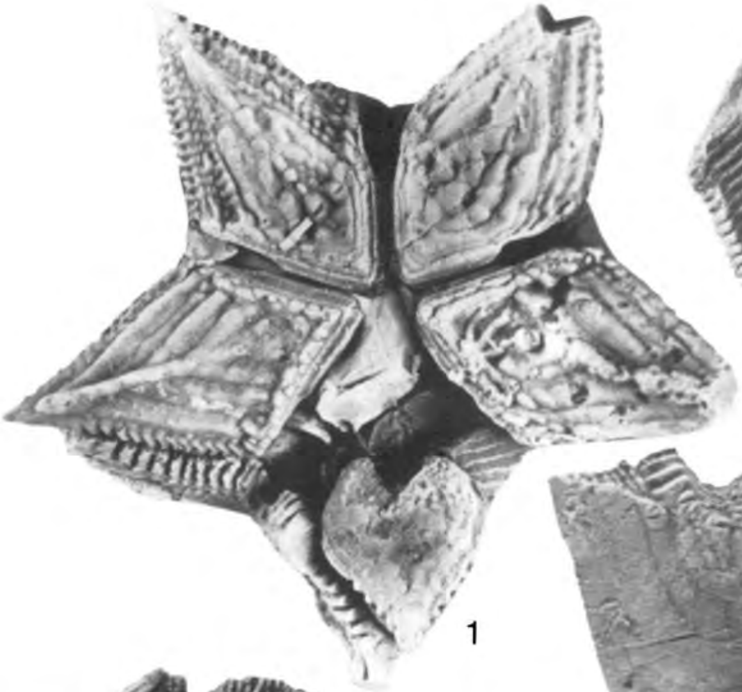

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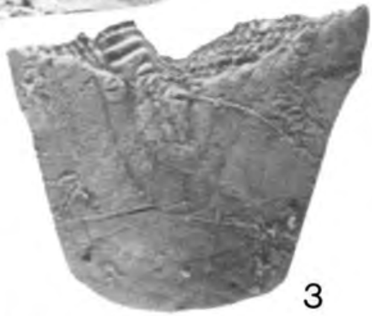

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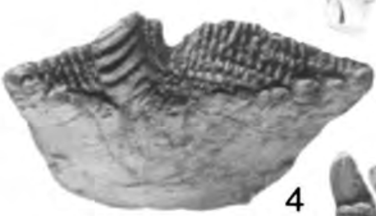

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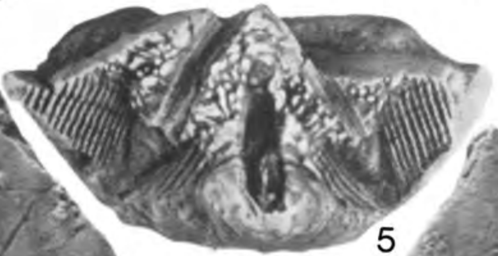

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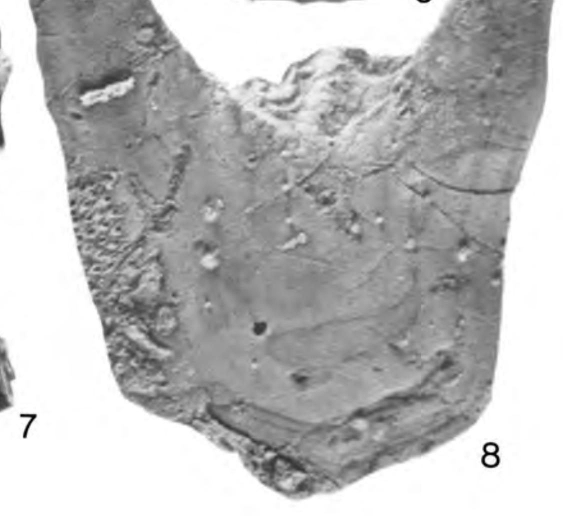

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PLATE XX

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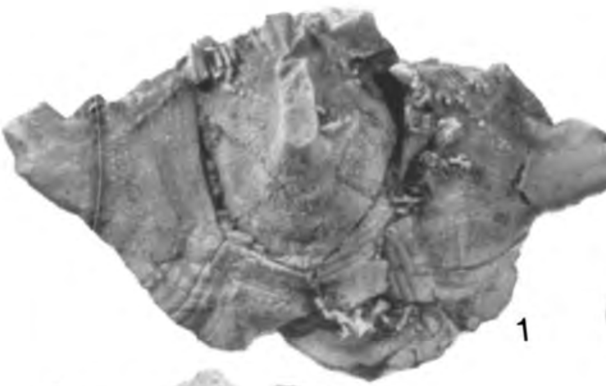
PLATE XXI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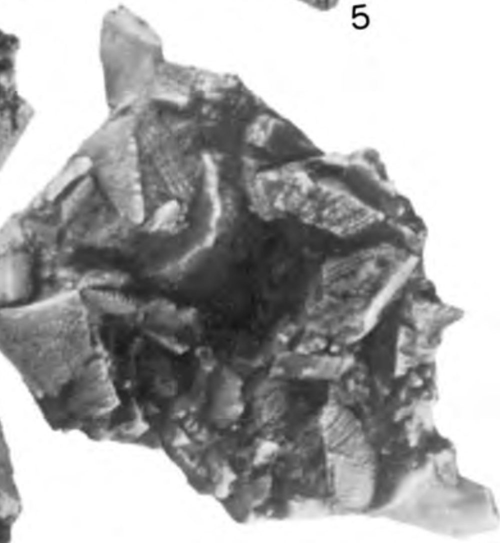
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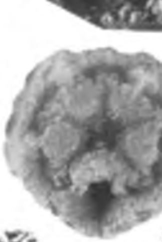
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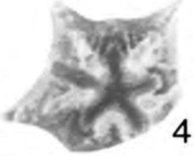

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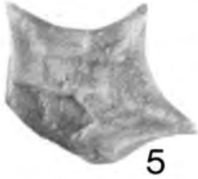

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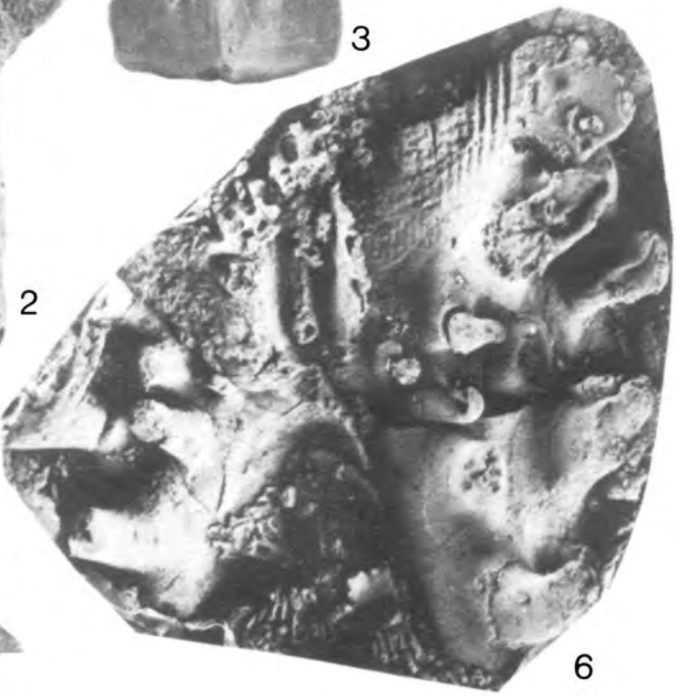

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PLATE XXV


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PLATE XXVI


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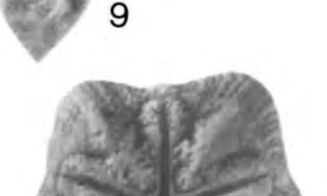
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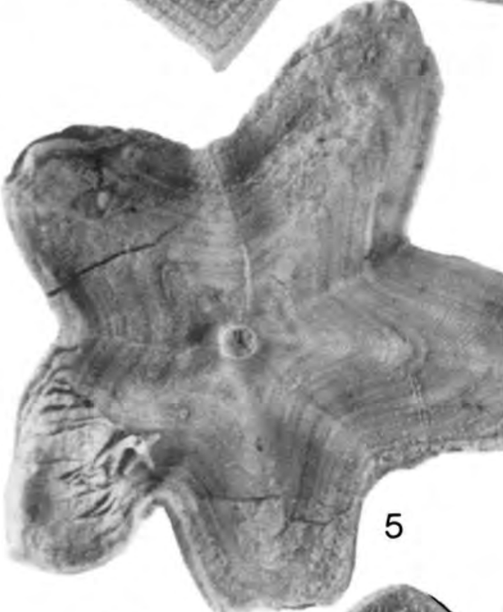
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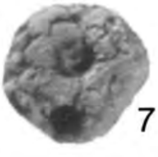
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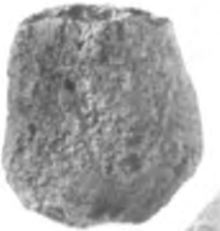
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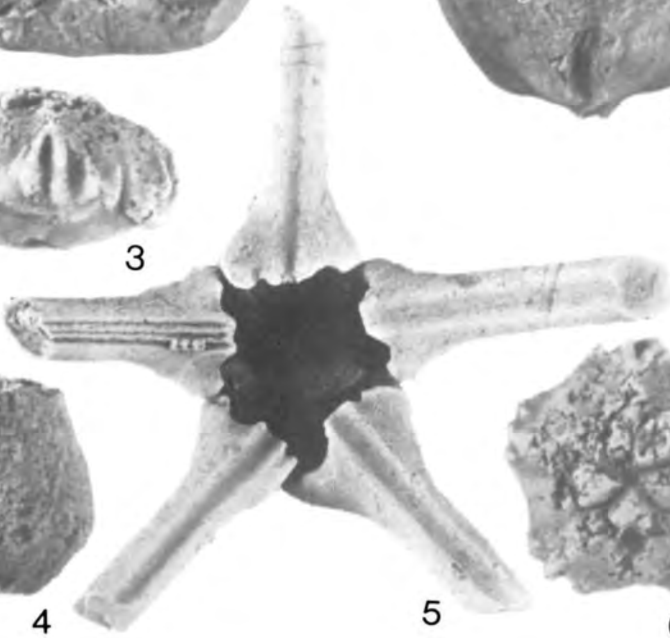
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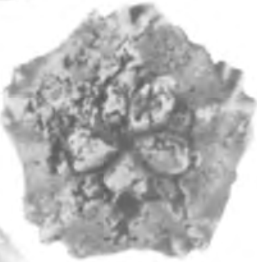
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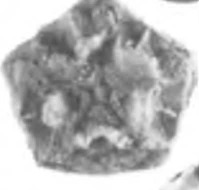
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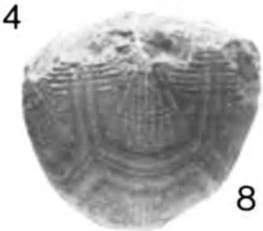
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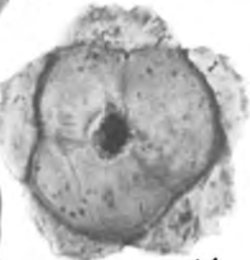
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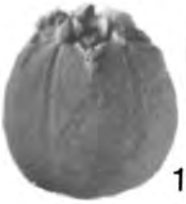
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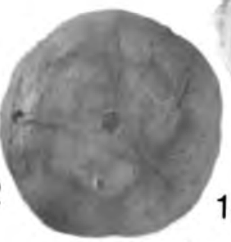
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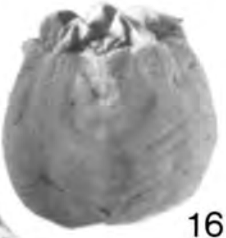
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PLATE XXX


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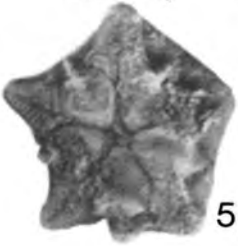
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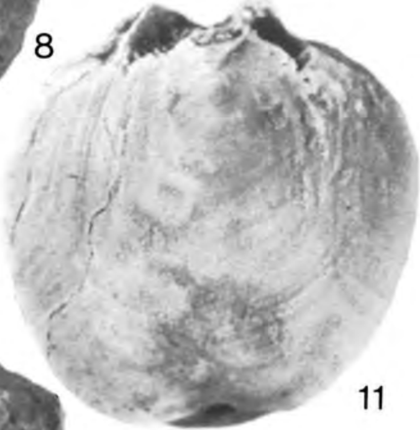
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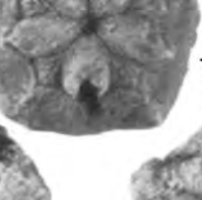
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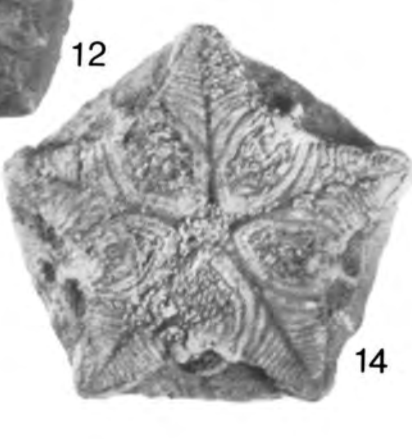
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PLATE XXXI


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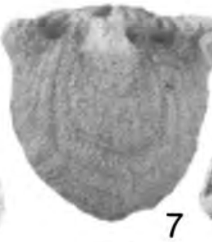
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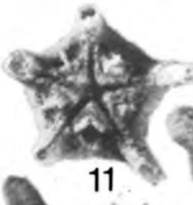
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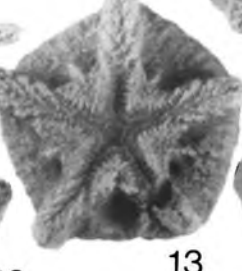
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PLATE XXXII


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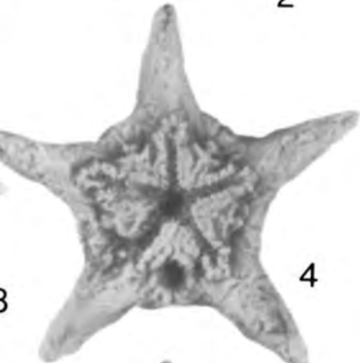
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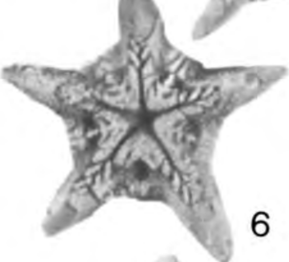
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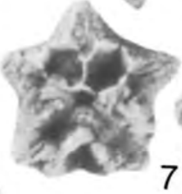
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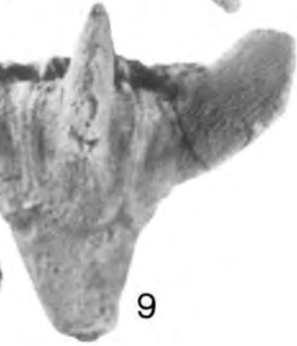
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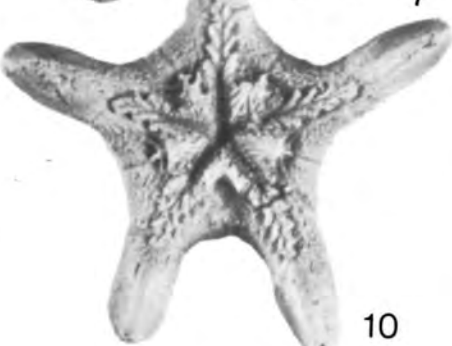
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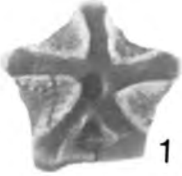
PLATE XXXIII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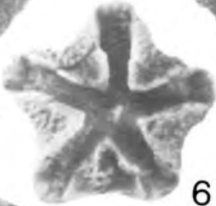
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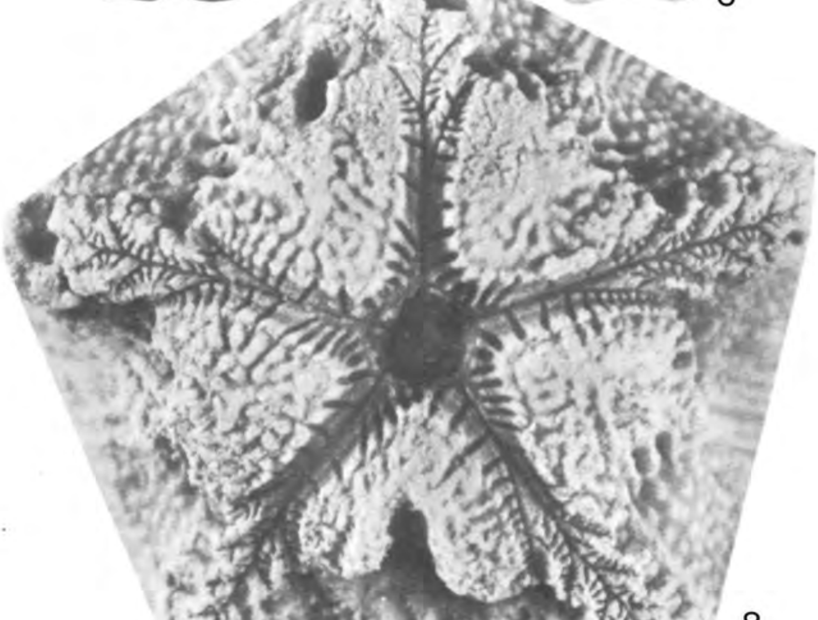
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PLATE XXXIV


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