A comparison of *Lepidocyclina ferreroi* (Provale, 1909) and *Lepidocyclina multilobata* (Gerth, 1939)

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Foraminiferal collections from Java and Borneo stored in the Netherlands National Museum of Geology and Mineralogy in Leiden enables to study the range of variation in *Lepidocyclina ferreroi* and *L. multilobata.* Taken separately many features considered typical of *L. multilobata* and *L. ferreroi* are insufficient to identify the specimens. When typically developed both species are highly characteristic and easily distinguished. Transitional forms however cannot be classified with certainty. Possibly *L. multilobata* has evolved from *L. ferreroi* but too little is known about the ages of the two species, especially of *L. multilobata. L. crucifera* is probably a form of *L. ferreroi* with four rays distinguished by the development of more than one tubercle on each ray.

A questionable occurrence of *L. multilobata* in Madagascar is discussed.

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Introduction

Coleman (1963) considers *Lepidocyclina multilobata* (Gerth, 1939) and *Lepidocyclina crucifera* (Mohler, 1946) to be 'fringe species' of *Lepidocyclina ferreroi* (Provale, 1909); he states: 'whether or not these differences justify full specific separation depends on a more thorough knowledge of the range of variation in *L. (N.) ferreroi.*' The material found in the collections of the Rijksmuseum van Geologie en Mineralogie (National Museum of Geology and Mineralogy) in Leiden enables us to study the range of variation in *L.* cf. *ferreroi* and *L.* cf. *multilobata* to some extent. Classification remains tentative in many cases because of the variability of both species and the briefness of the original description of *L. ferreroi.* Several samples contained forms which seem to be transitional between the two species. With the exception of samples from Madura (Kombangan) and Java (Weber collection), most of the samples were rather small and did not contain more than ten specimens each.

In the description of the 'form groups' (F) and (M) means: considered to be characteristic of *L. ferreroi* or *L. multilobata,* respectively.

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SAMPLES

The following samples contain either *L.* cf. *ferreroi* or *L.* cf. *multilobata* and/or forms transitional between the two:

1. Samples Bg. 295-297 and Bg. 312-316 from the Middle Miocene of Kombangan, Madura (see van der Vlerk, 1967) with a rich fauna of *L.* cf. *ferreroi.*
2. Caudri's collection from the Tertiary f of Ngampel, East Java: *L. multilobata.* This type collection is stored at the Geological Institute of the University of Amsterdam (Caudri, 1939).
3. Rutten's specimens from the Lower Miocene of Bontang, Borneo (Rutten, 1914).
4. Rutten's specimens from the Lower Miocene of Sungei Blakin, Borneo (Rutten, 1914).
5. A collection of F. Weber:

a. Sample M.J. 289, south of Gunung Kapuan, about 2 km west of Dagangan, Middle Java; no age is given.
b. Sample M.J. 299, south of Watu Agar, southwest of Sebojo and Prantaän, Middle Java; no age is given.

6. Specimens from the Upper Tertiary e of Menjangau, Borneo.
7. Specimens from the Tertiary f of Santan, Borneo.
8. Specimens from the Tertiary e5-f1 of Balikpapan, Borneo.
9. Samples containing not more than 5 specimens per sample and originating

from Borneo: Balikpapan Lama (Tertiary e5-f2), Tarakan (Tertiary f1) and Wailawi (Tertiary f); Sumba: Praj Reha (Tertiary f1) and Nias Island (age unknown).

Discussion of the 'form groups' occurring in the samples

Samples from the Middle Miocene of Kombangan

External characteristics – The diameter of the test varies from 2.5-3.5 mm (F). The specimens show complete gradation from small to large (smooth) tubercles (F), and also from smooth tubercles to tubercles covered – partly or totally – with lateral chambers. Tubercles may also be absent altogether. Similarly specimens with pronounced radial costae (M) grade into specimens with faintly developed ridges or none at all (F). Of the 386 specimens taken at random from samples Bg. 295-297, 370 had 4 rays and 16 had 5 rays. In samples Bg. 312-316 the ratio was 30 specimens with 4 rays and 12 with 5 rays. (Pls. 1, 2).

Vertical sections (Pl. 6; Pl. 7, figs. 2, 3, 4; Pl. 8; Pl. 9, fig. 3). – The arrangement of the lateral chambers is variously irregular (F). The lateral chambers are spacious (F), subrectangular with rounded corners to lenticular. There are generally 5 or 6, sometimes 4 or 7 (F) layers of lateral chambers over the centre; the horizontal walls of the lateral chambers are slightly to markedly curved (F) but sometimes straight.

Equatorial sections (Pl. 7, figs. 1, 5). — The largest diameter of the deuteroconch is 160-530 μm with an average of 260 μm (F); the thickness of the wall of the nucleoconch is about 20-40 μm (average 29 μm). The equatorial chambers are hexagonal to spatulate, locally ogival. The radial length of the equatorial chambers is 60-110 μm (average 94 μm) within the rays and 40-70 μm (average 56 μm) in the interray areas (F). Most of the characteristics indicate *L. ferreroi;* the specimens with tubercles covered with lateral chambers would be characteristic of *L. multilobata.*

Caudri's type collection of L. multilobata

The collection consists of 45 specimens, 10 vertical sections and 17 horizontal sections.

External characteristics. – Compare Caudri, 1939. The 45 specimens, stored in 7 slides, show considerable variation:

1. Mahindu anticline : one half-sectioned specimen.
2. Mahindu anticline : 9 specimens, regular star-shaped forms with pronounced radial ridges but without tubercles.
3. Mahindu anticline : 2 specimens with pronounced tubercles.
4. Mahindu anticline : 18 specimens, irregular star-shaped to polygonal forms, no distinct radial costae or tubercles.
5. Tawun anticline : one specimen with pronounced tubercles, resembling Rutten's specimens from Bontang (Rutten, 1914).

6. Ngampel railway-cut : 7 specimens, see Caudri, 1939, pl. IX.
7. „ „ : 7 specimens, regular star-shaped forms with barely developed radial ridges or tubercles.

Vertical sections (Pls. 10, 11, 12, figs. 1, 2) – The arrangement of the lateral chambers, although variable, is generally regular. The horizontal walls of the lateral chambers are often slightly curved and are not as straight as Caudri's description would suggest. Likewise the lateral chambers, which are described as extremely narrow, are often quite spacious. The number of layers of lateral chambers in 8 vertical sections was 13, 10, 13, 7, 9, 9, 9, 11 (10-12 according to Caudri).

The outlines of the vertical sections suggest that they were prepared from specimens with indistinct tubercles which may be the reason that the 'Verfestigungssystem', as described by Caudri, is only visible in two of the sections (Caudri, pl. IX, fig. 71).

According to Caudri the vertical walls of the lateral chambers are thickened. A study of the 'Verfestigungssystem' in one of Caudri's vertical sections (Caudri, 1939, pl. IX, fig. 71) shows that the vertical walls are formed by the thickened parts of the horizontal walls and that small chambers occur where the horizontal walls become thinner (see also Pl. 12, fig. 1).

Equatorial sections – Compare also Caudri, 1939. The following measurements were made from Caudri's material: diameter of the nucleoconch: 340-730 μm, average 517 μm (600-700 μm according to Caudri); thickness of the wall of the nucleoconch: 30-40 μm (20-40 μm according to Caudri); radial length of the equatorial chambers in rays: 90-130 μ m, average 107μm (144 μm according to Caudri). Radial length of the equatorial chambers in the interray areas: 60-80 μm, average 76 μm. The shape of the equatorial chambers is hexagonal with rounded corners, becoming almost hexagonal or spatulate depending upon the roundness of the corners.

Rutten's specimens from the Lower Miocene of Bontang

The specimens were originally described by Rutten (1914) as *L. ferreroi* but were later assigned to *L. multilobata* by Caudri (1939) on the basis of the external characteristics. The present study demonstrates that it is often impossible to distinguish the two species by means of the exernal features. At present the specimens from Bontang are considered to be transitional between *L. ferreroi* and *L. multilobata*.

External characteristics (Pl. 5, figs. 1-6). – The diameter of the test is 3-4.5 mm (M). The development of the radial ridges and the tubercles varies (F, M).

The tubercles are usually covered with lateral chambers (M), which are often reduced (abraded?) to a more or less pronounced reticulate pattern formed by the thickened walls of the lateral chambers. This structure may cover the whole tubercle or be restricted to the margins leaving a smooth centre.

Vertical and tangential sections (Pl. 13, figs. 1-4; Pl. 14, figs. 1-4) – Vertical as well as tangential sections show that the vertical walls of the lateral chambers become progressively thicker towards the centre of the tubercles and the axes of the radial ridges, sometimes forming irregularly shaped massive patches or mas-

sive round pseudopillars (F). The pseudopillars are often bordered by a zone consisting of small lateral chambers which have thickened walls and are infiltrated with dark material (M). The same phenomenon may have formed dark isolated patches near the equatorial plane or near the nucleoconch (cf. Pl. 17, fig. 2; M?).

The number of layers of lateral chambers in 8 specimens was 4, 7, 6, 7, 7, 6, 9, 7 (F). The arrangement of the lateral chambers is predominantly irregular (F); the chambers are spacious, subrectangular to lenticular with straight to markedly curved horizontal walls (F, M).

Equatorial section (Pl. 14, fig. 5). – The following measurements were determined: diameter of the nucleoconch (1 spec.): 270 μm (F). Thickness of the wall of the nucleoconch 20 μm: the nucleoconch is nephrolepidine (F). Radial length of the equatorial chambers in rays: about 70 μm (F). Radial length of the equatorial chambers in interray areas: 40-50 μm (F). In many specimens from Bontang, *ferreroi* and *multilobata* characteristics occur side by side making identification difficult.

Rutten's specimens from the Lower Miocene of Sungei Blakin

These forms were assigned to *L. ferreroi* by both Rutten (1914) and Caudri (1939).

External characteristics (Pl. 4, figs. 13-18). – Small forms (2-3 mm) with small but prominent, sharply defined smooth pseudopillars (F). Radial costae are barely developed or absent (F).

Tangential sections (Pl. 15, fig. 2). – Pseudopillars of clear material (F) surrounded by a narrow dark zone consisting of small lateral chambers with thickened vertical walls. This zone varies in width and is comparable in structure to Caudri's 'Verfestigungssystem' (M).

Vertical sections (Pl. 15, fig. 3). – The lateral chambers are spacious, irregularly arranged (F). The pseudopillars are clear, not layered and not arranged in bundles. The number of layers of lateral chambers in 3 specimens was 6, 9, 10 (F, M?).

Equatorial sections (Pl. 15, fig. 4). – Measurements of one specimen: diameter of the nucleoconch 300 μm (F); the nucleoconch is nephrolepidine to trybliolepidine (F, M?). Radial length of the equatorial chambers in rays: 75-80 μm (F). Radial length of the equatorial chambers in the interray areas: 50-70 μm (F). Most features suggest *L. ferreroi,* the form is therefore indicated as *L.* cf. *ferreroi.*

Two samples of unknown age from Middle Java, collected by F. Weber

External characteristics (Pl. 3). – The diameter of the test varies from 2-4.5 mm (M). The radial ridges are usually well-developed (M). In most specimens the tubercles are covered with lateral chambers (M); some specimens show smooth but not pronounced pseudopillars which are elongated along the costae (Pl. 3, fig. 1; F).

Tangential sections (Pl. 18, figs. 1-5; Pl. 20, fig. 1). – More or less developed pseudopillars are surrounded by a wide dark zone of small lateral chambers with

thickened walls. The 'Verfestigungssystem' is sometimes developed as described by Caudri but may also form massive patches or heavy pillars in the central part of the 'system'. The pseudopillars seem to slope towards the centre of the test (Pl. 19, fig. 5).

Vertical sections (Pl. 16, 17, Pl. 19, fig. 3, Pl. 20, figs. 1, 2, Pls. 21, 22). – The pseudopillars are faintly layered and are surrounded by a dark zone which is comparable in structure to Caudri's 'Verfestigungssystem'. In some specimens no massive patches or pseudopillars have developed; these forms are identical to *L. multilobata* as described by Caudri.

The number of layers of lateral chambers in 12 specimens was 9, 8, 8, 8, 13, 11, 10, 10, 11, 7, 10 (M). The arrangement of the lateral chambers is generally regular (M), but is irregular in the juvenile stage (Pl. 16, figs. 1, 2, Pl. 19, fig. 3, Pl. 21, figs. 2, 3; F). In vertical sections two types may be distinguished: 1) Lenticular forms with a well-developed 'Verfestigungssystem' (M?). 2) Cigar to dumbbell-shaped forms, generally with distinct pseudopillars (F?). There is a complete intergradation between the two types, the shape being dependent mainly upon the development of the pseudopillars.

Furthermore the cigar or dumbbell-shaped forms agree in most other particulars with *L. multilobata.* All the specimens from the Weber samples are therefore assigned to *L.* cf. *multilobata.*

Equatorial sections (Pl. 19, figs. 1, 4, 5). – The following measurements were made: diameter of the nucleoconch: 500-680 μm (M).
Radial length of the equatorial chambers in rays: 90-120 μm (M).
Radial length of the equatorial chambers in interray areas: 70-100 μm (M).
The specimens from both Weber samples are practically identical although a distinct 'Verfestigungssystem' is found more often in the specimens from Watu Agar.

Specimens from the upper Tertiary e of Menjangau

External characteristics (Pl. 4, figs. 1-8). – These specimens are small (2.5-3 mm) with 4-5 rays (F) and small but prominent pillars (F). Radial ridges occur in some specimens.

Vertical and tangential sections (Pl. 23, Pl. 24, figs. 1-6). – In vertical and tangential sections the faintly layered pseudopillars appear to be surrounded by a narrow zone with infiltration of dark material. Within this zone very small lateral chambers may be observed locally. The zone becomes rather wide in some specimens and is then comparable in structure to Caudri's 'Verfestigungssystem' (Pl. 24, fig. 6; M). The number of layers of lateral chambers in 3 specimens was 8, 9, 8 (M?). The lateral chambers have distinctly curved horizontal walls (F); the arrangement is irregular (F). *L. ferreroi* characteristics predominate; those specimens with a wide zone of small lateral chambers around the pseudopillars are perhaps transitional to *L. multilobata.*

Specimens from the upper Tertiary f of Santan

Small forms with a maximum diameter of 3 mm (F) (Pl. 12, figs. 3, 4). The arrangement of the lateral chambers is irregular (F); the chambers are spacious (F).

The number of layers of lateral chambers in 3 specimens was 5, 5, 6 (F). There are no pronounced tubercules; an irregular 'Verfestigungssystem' is well-developed in some specimens (M) but shows no infiltration of dark material. Classification of the forms with *ferreroi* as well as *multilobata* characteristics is uncertain.

Some specimens from the Tertiary f of Balikpapan

These may be described as *L.* cf. *ferreroi* with some *multilobata* characteristics (Pl. 4, figs. 9-12, Pls. 25, 26).

Differences between *L. ferreroi* and *L. multilobata*

Determination of the differences between the two species remains tentative because the original description of *L. ferreroi* is incomplete.

Prior to 1939, when the original description of *L. multilobata* was published, all of these similar forms, including the latter species, were probably assigned to *L. ferreroi*. On the basis of the original descriptions and figures the following differences can be distinguished.

The maximum diameter of the test is 3 mm for *L. ferreroi* and 8 mm (usually 2.5 - 5 mm) for *L. multilobata*. The thickness of the test is 1 and 1.4 mm, respectively. *L. multilobata* should therefore generally be larger and flatter than *L. ferreroi*. However environmental factors seem to influence the development of the test: the tests from a given locality are usually about the same size.

The number of rays given for *L. ferreroi* is 3, 4, 5 (mainly 4) and for *L. multilobata* 5-6 (sometimes 4 or 7). The number of rays is an unreliable characteristic as was already noted by Caudri (1939, p. 225): 'An sich ist diese hohe Zahle nicht kennzeichnend für *L. multilobata*. Auf Ost-Sumba (Caudri 1934) würden Lepidocyclinen mit 6-7 Tuberkeln gefunden, die zweifellos *L. ferreroi* Prov. angehören.' Rutten made a similar observation (Rutten, 1914, p. 293): 'Es verdient Erwähnung dass die Variabilität an verschiedenen Fundorten recht verschieden zu sein scheint. Während in Balik Papan die Anzahl der Skeletpfeiler von 3-6 wechselte und die meisten Exemplare entweder 4 oder 5 Warzen aufwiesen (T. XXII, fig. 2), waren in einem grossen Material von Bontang fast alle Individuen mit 4 Warzen versehen.' It seems likely that the number of rays is dependent upon environmental conditions, compare also Cole (1961, p. 388). 'It should be recognized that in *Lepidocyclina* the stellate pattern is produced only by certain individuals, probably under the influence of ecological conditions and that this pattern is not genetically produced. Therefore, it does not have value as a specific character.'

The shape of the tubercles: on the exterior of *L. ferreroi* there should be large pronounced and smooth tubercles; in *L. multilobata* the tubercles are covered with lateral chambers. As mentioned in the descriptions of the specimens from Kombangan and from the Weber samples, all transitions are found from small to pronounced tubercles and from smooth tubercles to tubercles covered with lateral chambers. Smooth tubercles may however be the result of abrasion. In vertical sections *L. ferreroi* occasionally has fan-shaped bundles of pillars located under one tubercle. Caudri (1934, p. 107) described such pillars in *L. ferreroi* from

Sumba: 'There are no pillars in the shell, except at the angles, where they are collected in bundles under one great common tubercle.' In our material this type of pillar is found only in some specimens from Kombangan.

According to Caudri *L. multilobata* has no pillars but a 'Verfestigungssystem': a regular pattern formed by very small lateral chambers with thickened vertical walls and infiltrated by dark material. It is apparent from the Weber samples that locally the 'Verfestigungssystem' may form massive patches or even pronounced pseudopillars. In fact all gradations are found between a 'Verfestigungssystem' which tends to form pseudopillars (*multilobata* type) and pseudopillars which are surrounded by a zone varying in width and similar in structure to an irregular 'Verfestigungssystem' (*ferreroi* type). The analogy of the structures is also apparent in tangential sections.

The radial ridges, although described by Provale in *L. ferreroi,* are more pronounced in *L. multilobata* according to Caudri. Development of the ridges is highly variable; all transitional forms are generally found from specimens with faint ridges or none at all to specimens with pronounced radial costae. On the whole the ridges are more pronounced in the specimens from the Weber samples *(L.* cf. *multilobata)* than in the specimens from Kombangan *(L.* cf. *ferreroi).*

The shape of the nucleoconch. In *L. ferreroi* the deuteroconch embraces half of the protoconch (Provale, 1909). The nucleoconch of L. *multilobata* is described as nephrolepidine to trybliolepidine.

The shape of the equatorial chambers of *L. ferreroi* was described as small, subcircular to rhomboid by Provale and as hexagonal-spatulate by later authors. Caudri reports that the equatorial chambers of *L. multilobata* are large, hexagonal to spatulate. In our material all equatorial sections showed spatulate to hexagonal chambers with more or less rounded corners. The chambers may become almost hexagonal or spatulate, depending on the roundness of the corners. From Provale's original figures it appears that the equatorial chambers of *L. ferreroi* are smaller on the average than those of *L. multilobata.*

The form and arrangement of the lateral chambers in vertical sections. Caudri states that *L. multilobata* is characterized by an arrangement of very narrow chambers with straight walls in regular tiers. In the vertical sections of Caudri's type collection however specimens with rather spacious chambers and with slightly curved horizontal walls are not uncommon. *L. ferreroi* has an irregular arrangement of subrectangular chambers (Provale, 1909). Later authors generally described the lateral chambers of this species as spacious with rounded corners. The arrangement of the lateral chambers seems to be a useful characteristic, since it is definitely more regular in *L. multilobata* although an irregular arrangement occurs in the juvenile stage of this species.

The number of layers of lateral chambers recorded is 6-7 in *L. ferreroi* and 10-12 in *L. multilobata.* This appears to be one of the best means of distinguishing between the two species. In our samples the number of lateral chambers seemed to be consistent within each sample, being on the average either more than eight (9-12.5) or less than eight (5-7.5).

It follows from the above that several characteristics are useless for distinguishing between the species. In Table I the characteristics of *L. ferreroi* (original description and figures) and *L. multilobata* (Caudri's type collection) on the one hand are compared with those of *L.* cf. *ferreroi* (Kombangan) and *L.* cf. *multilobata* (Weber samples) on the other.

Table I. Measurements of horizontal sections and diameters of the test.

diameter of the nucleoconch		
Kombangan (160) - 200, 300 - (530) μm		average 260 μm
L. ferreroi	380-400 μm	
L. multilobata	340-730 μm	average 517 μm
Weber coll.	450-650 μm	average 557 μm
radial length of the equatorial chambers in the rays		
Kombangan	60-110 μm	average 94 μm
L. ferreroi	80-110 μm	
L. multilobata	90-130 μm	average 107 μm
Weber coll.	90-120 μm	average 101 μm
radial length of the equatorial chambers in interray areas		
Kombangan	40- 70 μm	average 56 μm
L. ferreroi	40- 50 μm	
L. multilobata	60- 80 μm	average 76 μm
Weber coll.	70-100 μm	average 85 μm
thickness of the wall of the nucleoconch		
Kombangan	20- 40 μm	
L. ferreroi	30- 40 μm	
L. multilobata	30- 40 μm	
Weber coll.	30- 40 μm	
Diameter of the test		
Kombangan	2.5-3.5 mm	
L. ferreroi	max. 3 mm	
L. multilobata	(2.5) -5, max. 8 mm	
Weber coll.	3-4.5 mm	

As surmised on the basis of other characteristics the specimens from Kombangan agree the most with *L. ferreroi* and those of the Weber samples with *L. multilobata.* On the whole *L. multilobata* has a larger nucleoconch and the radial length of the equatorial chambers is longer. The diameter of the test is somewhat larger for *L. multilobata;* the thickness of the wall of the nucleoconch is about the same for both species. Other possible differences between *L. ferreroi* and *L. multilobata* are: 1) Development of small patches of a dark 'Verfestigungssystem' near the equatorial plane of the nucleoconch was only encountered in *L. multilobata* in our material. 2) Infiltration of dark material, although not always present, is more common in *L. multilobata.* 3) The arrangement of the lateral chambers in the juvenile stage of *L. multilobata* is irregular (resembling the arrangement in *L. ferreroi)* in contrast with the more regular arrangement of the chambers formed later. There is no such contrast in *L. ferreroi.* In transitional forms the contrast is less distinct. 4) In vertical section *L. multilobata* is lenticular; *L. ferreroi* is cigar to dumbbell-shaped depending upon the development of the pseudopillars. The equatorial chambers often become higher near the tubercles and then decrease in height towards the margin. This feature is seen mainly in *L. ferreroi* as the development of pseudopillars is generally more pronounced in this species.

Besides being easy to determine, the number of layers of lateral chambers generally seems to be one of the most reliable distinctions between *L. multilobata* and *L. ferreroi.* Fig. 1 shows the frequency of various other characteristics in relation to the number of lateral chambers. Populations were classified according to the average number of lateral chambers, assuming that *ferreroi*-like forms will predominate in populations with an average of less than 8 layers of lateral chambers, whereas more than 8 layers will indicate that *multilobata*-like forms predom-

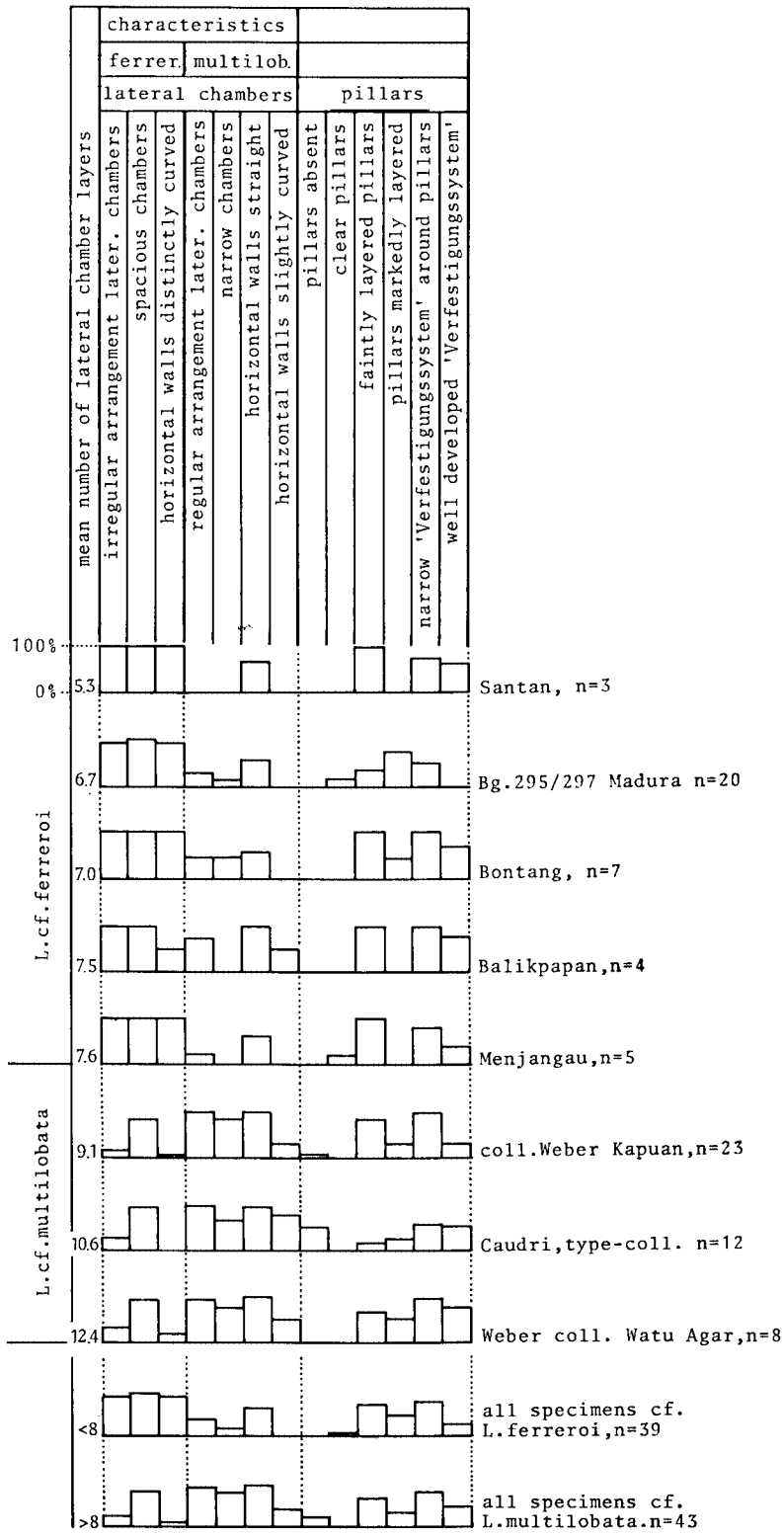

Fig. 1. Frequency of other characteristics in relation to the mean number of lateral chamber layers (per sample).
For: well developed 'Verfestigungssystem', read: more developed 'Verfestigungssystem'.

inate. It remains to be seen whether the frequencies of other characteristics corroborate this presumption. The following features seen in vertical sections are considered characteristic of either *L. ferreroi* or *L. multilobata: L. ferreroi:* an irregular arrangement of spacious lateral chambers with distinctly curved horizontal walls. *L. multilobata:* a fairly regular arrangement of narrow lateral chambers with straight or slightly curved horizontal walls.

The types of pseudopillars or tubercles seen in vertical sections are incorporated in the histograms. A distinction is made between: 1) Smooth clear pillars without layering, 2) Pillars with a faint layering, 3) Markedly layered pillars, 4) A 'Verfestigungssystem' which has developed as a narrow zone around pseudopillars, 5) A well-developed 'Verfestigungssystem' sensu Caudri.

It is apparent from the histograms that the populations with an average of less than 8 layers of lateral chambers show predominantly *ferreroi* characteristics and populations with an average of more than 8 lateral chambers agree the most with *L. multilobata.* Since the separate samples are small in many cases, the totals should be compared (Figs. 1, two lowermost histograms). The histograms may be unfavourable influenced by the presence of transitonial forms in many of the samples.

A comparison is therefore made between the populations of Kombangan, which agree the most with *L. ferreroi* and those of the Weber samples, which resemble *L. multilobata* (Fig. 2, two uppermost histograms). It is evident that in vertical sections the main differences are the arrangement of the lateral chambers and the curvature of the horizontal walls. Distinctly layered pseudopillars occur frequently in *L. ferreroi;* a well-developed 'Verfestigungssystem' is typical of *L. multilobata.*

Within the specimens from the Weber samples a comparison was made between forms with relatively few chambers (6-8 layers) and specimens with more than 8 layers of lateral chambers. The forms with few lateral chambers are generally more *ferreroi*-like in other characteristics as well. This could indicate that both species occur in the samples. There is however complete intergradation between the different forms and not one single specimen was found which could definitely be assigned to *L. ferreroi.* Here all the forms were identified as either *L. multilobata* or *L.* cf. *multilobata.*

In the Kombangan populations the histograms of the specimens with few lateral chambers (5, 6 layers) and those with more numerous lateral chambers (7, 8, 9 layers) are similar. This may indicate a homogeneous population which closely resembles *L. ferreroi.*

VARIATION AND INTERGRADATION

Specimens with characteristics of *L. ferreroi* and *L. multilobata* occur mainly in the samples from Menjangau, Bontang and Balikpapan and less frequently in the Weber samples. In these transitional forms *ferreroi* and *multilobata* characteristics occur in the same specimen. Such forms may, for instance, agree in most characteristics with *L. ferreroi* but possess many layers of lateral chambers or they may be *multilobata*-like with only a few such layers. In other specimens an irregular and a regular arrangement of the lateral chambers may be found side by side. Likewise a 'Verfestigungssystem' and pseudopillars may develop in one specimen.

Many features considered to be characteristic of *L. ferreroi* on the one hand

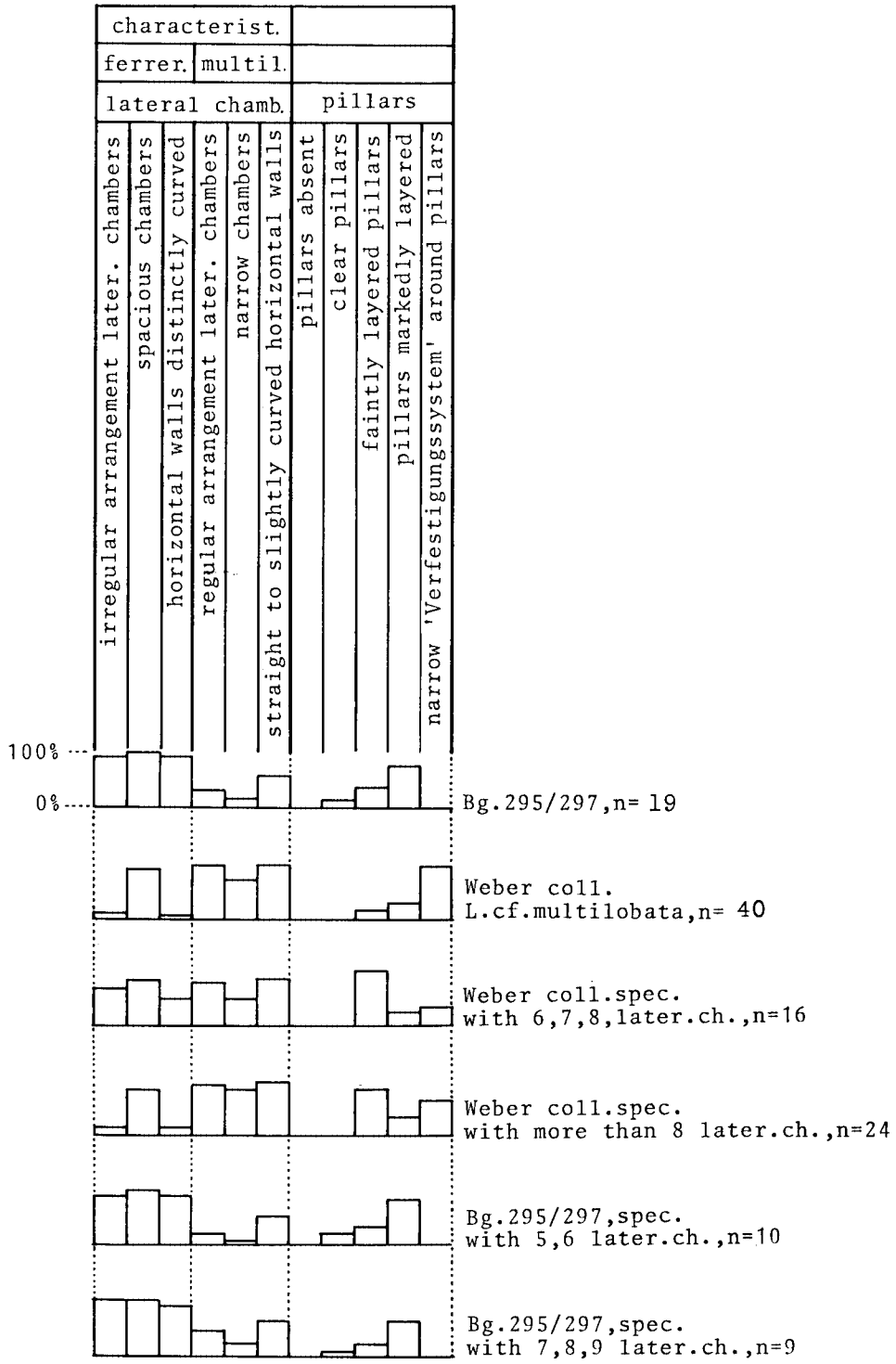

Fig. 2. Frequency of various characteristics in the samples from Kombangan and the Weber collection: histograms of total population and of populations divided according to the number of layers of lateral chambers.
For: narrow 'Verfestigungssystem' around pillars, read: 'Verfestigungssystem' sensu Caudri.

and *L. multilobata* on the other intergrade: 1) There is complete intergradation from smooth tubercles into tubercles covered with lateral chambers and from small to pronounced pillars (or pillars may be absent altogether). A similar intergradation may be seen in the development of the radial ridges which may be distinct, faint or absent. 2) There is often thickening of the vertical walls of the lateral chambers along the axes of the rays. In these parts of the test more than one tubercle may develop on one ray giving rise to *crucifera*-like forms. Although such forms were not uncommon in our material, no specimens were found which could definitely be assigned to *L. crucifera*. As the latter species agrees in most particulars with *L. ferreroi,* it is not unlikely that *L. crucifera* is simply a varietal form of *L. ferreroi* with 4 rays. 3) The width and arrangement of the lateral chambers is highly variable in both *L. ferreroi* and *L. multilobata* but on the whole *L. ferreroi* has more spacious chambers and a more irregular arrangement. 4) Finally all transition forms may be found between pillars with a narrow marginal zone, which is analogous in structure to Caudri's 'Verfestigungssystem' – with or without infiltration of dark material –, and a well-developed 'Verfestigungssystem' with or without massive patches or pseudopillars. Fig. 3 shows histograms of the frequency of specimens with a given number of lateral chamber layers in the various populations.

A questionable occurrence of *L. multilobata* in Madagascar (Republic of Malagasy)

The only reported occurrence of *L. multilobata* since Caudri's original description is from Madagascar (Beretti, 1973). This is a large eulepidine form from the Upper Stampian to Lower Aquitanian of that island.

Some measurements given by Beretti are: diameter of the specimens 3.6-11.8 mm, thickness of the specimens 1.6-4.5 mm, diameter of the nucleoconch 520-1050 μm, radial length of the equatorial chambers 90-158 μm.

According to Beretti the form has no tubercles but there is local thickening of the horizontal walls and an increase in the number of lateral chambers. Pl. 20, fig. 1 in Beretti (1973) however shows what seem to be distinct tubercles. She counted as many as 15 lateral chambers; this number decreased in the thinner parts of the test.

In the opinion of the present author the age and measurements of the Madagascar form deviate too much from Caudri's type specimens to justify classification as *L. multilobata,* although the specimens from Madagascar do sometimes show a striking resemblance to specimens in our material.

More probably they represent aberrant forms of *L. ephippoides* Jones & Chapman, 1900, a possibility also considered by Beretti.

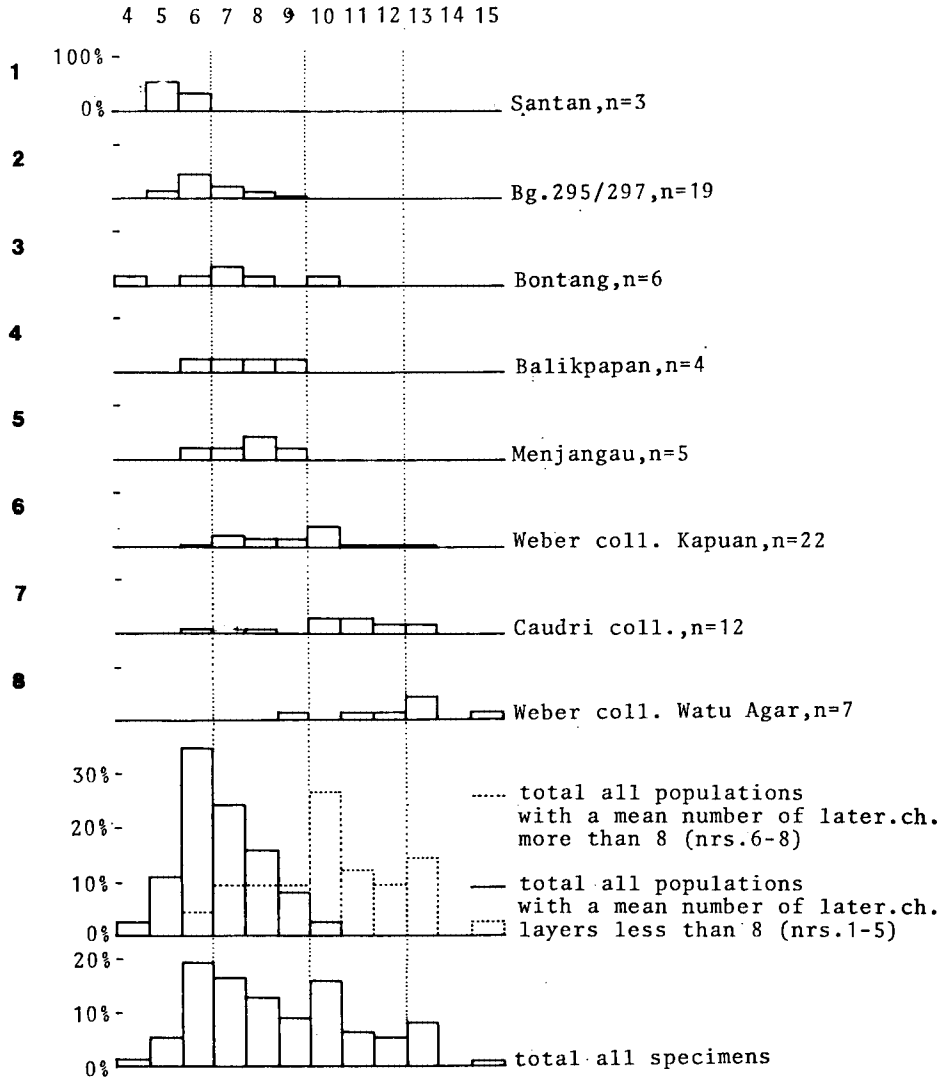

Fig. 3. Frequency of specimens with a given number of lateral chamber layers in the various populations.

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Plate 1

Lepidocyclina cf. *ferreroi* from the Middle Miocene of Kombangan, Madura. All figures are ca. 10 × enlarged.

Figs. 1-17. Specimens with pronounced, generally smooth, pseudopillars. Occasionally more than one tubercle has developed on the same ray (figs. 14, 15). Radial costae absent or barely developed; central part of the test generally depressed. Surface covered by a coarse reticulate mesh, compare *L. multilobata* (Pl. 3). RGM 210 080.
Figs. 18-37. Specimens from the same locality but the small pillars are not as well-developed. Rays rather distinct in some specimens (figs. 27, 32, 33). RGM 210 081. Compare also Pl. 2.

Plate 2

Lepidocyclina cf. *ferreroi* from the Middle Miocene of Kombangan, Madura (compare Pl. 1). All figures are 9 × enlarged.

Figs. 1-19. Pillars even less pronounced than in Pl. 1, figs. 18-37; radial costae on the other hand more developed. The tubercles are generally covered with lateral chambers. RGM 210 082.
Figs. 20-37. Specimens with tubercles which are even more poorly developed and *cruciferа*-like forms (figs. 21, 22, 24, 32, 37). The latter show a tendency to form more than one tubercle on the same ray. Radial ridges distinct in many of the specimens. RGM 210 083.

Plate 3

Lepidocyclina cf. *multilobata* from Kapuan and Watu Agar, Middle Java, age unknown (Weber collection). RGM 210 090. All figures are 10 × enlarged.

Figs. 1-19. The reticulate mesh on the surface is smoother than in the specimens from Kombangan (Pls. 1, 2). Radial costae are more highly developed. One specimen shows smooth but barely developed tubercles (fig. 1). The centre of the test is not as depressed as in *L.* cf. *ferreroi* from Kombangan (Pls. 1, 2).

Plate 4

All figures are 10 × enlarged.

Figs. 1-8. *Lepidocyclina* cf. *ferreroi* from the Tertiary e of Menjangau, Borneo; RGM 210 087. Pronounced, smooth tubercles in most specimens. Radial ridges often distinct but less wide and rounded than in *L. multilobata* (Pl. 3). More than one tubercle on the same ray in some specimens (figs. 1, 2).
Figs. 9-12. Large specimens from the Tertiary f of Balikpapan, Borneo; RGM 210 086. Tubercles partly or totally covered with a reticulate mesh formed by the thickened vertical walls of the lateral chambers. Occasionally smooth pillars occur (fig. 12); variation in the surface ornamentation of the test may result from abrasion. On the basis of the internal characteristics these forms from Balikpapan are assigned to *L.* cf. *ferreroi.*
Figs. 13-18. *L.* cf. *ferreroi* from the Lower Miocene of Sungei Blakin, Borneo; RGM 210 085. Pronounced and sharply defined smooth pillars. Radial ridges faint or absent, central part of the test depressed.

Plate 5

All figures are 10 × enlarged.

Figs. 1-6. Forms transitional between *Lepidocyclina ferreroi* and *L. multilobata* (?) from the Lower Miocene of Bontang, Borneo; RGM 210 088. Tubercles covered with a reticulate relict of lateral chambers.
Figs. 7-8. Some large specimens, also transitional between *L. ferreroi* and *L. multilobata,* from Balikpapan, Borneo; age unknown; RGM 210 089. Strongly developed rim, depressed centre of the test.

Plate 6

Lepodicyclina cf. *ferreroi* from the Middle Miocene of Kombangan, Madura. All figures are 150 × enlarged. Figs. 1, 3, 4 transmitted light, figs. 2, 5 reflected light.

Figs. 1, 2, 4. Markedly layered pillars, sometimes arranged in bundles; RGM 210 119, RGM 210 094 and RGM 210 118, respectively.
Fig. 3. Clear, barely layered pillar; RGM 210 091.
Fig. 5. Widening of the equatorial layer near the tubercles; RGM 210 095.

Plate 7

Lepidocyclina cf. *ferreroi* from the Middle Miocene of Kombangan, Madura. Reflected light, except fig. 5; fig. 5 × 55, other figs. × 36.

Figs. 1, 5. Sections through and near the equatorial plane. Thickening of the vertical walls of the lateral chambers along the axes of the rays.
Figs. 2, 3. (same specimen: RGM 210 094). Vertical sections showing the widening of the equatorial layer near the tubercles. Lateral chambers spacious with slightly curved horizontal walls. Locally small lateral chambers around and within the pillars (compare also fig. 4).
Figs. 1, 4, 5: RGM 210 102, RGM 210 096 and RGM 210 116, respectively.

Plate 8

Lepidocyclina cf. *ferreroi* from the Middle Miocene of Kombangan, Madura.
Figs. 1, 2 transmitted light, figs. 3-5 reflected light; fig. 1: × 55, fig. 2: × 15, figs. 3-5: × 36.

Fig. 1. Detail of Pl. 9, fig. 3.
Fig. 2. Detail of Pl. 8, fig. 5; RGM 210 095.
Figs. 1, 3, 4, 5. Variation in the arrangement of the lateral chambers; RGM 210 122, RGM 210 122, RGM 210 118 and RGM 210 095, respectively.
Fig. 5. Widening of the median layer near the tubercles.

Plate 9

Lepidocyclina cf. *ferreroi* from the Middle Miocene of Kombangan, Madura.
Figs. 1, 2, 4. reflected light; figs. 3, 5 transmitted light; figs. 1-4: × 36, fig. 5: × 55.

Figs. 1, 5. Tangential sections showing thickening of the vertical walls of the lateral chambers along the axes of the rays with local development of pillars; RGM 210 120 and RGM 210 097.
Fig. 2. Massive pillars at the ends of the rays; RGM 210 092.
Fig. 4. Tubercles formed by small lateral chambers with thickened vertical walls; RGM 210 130.
Fig. 3. Vertical section, compare Pl. 8, fig. 1; RGM 210 122.

Plates 10, 11

Lepidocyclina multilobata from the Tertiary f of Ngampel, E. Java (Caudri's type collection). Transmitted light; Pl. 10, figs. 1, 2: × 55, Pl. 10, figs. 3, 4, Pl. 11, figs. 1-4: × 36.

Fig. 1. Detail of Pl. 11, fig. 1.
Fig. 2. Detail of fig. 4. Compare also Pl. 12, figs. 1, 2.
Considerable variation is shown in the shape of the vertical sections, the shape of the lateral chambers and the curvature of the horizontal chamber walls. A 'Verfestigungssystem' is not present in all specimens. Infiltration of dark material is best seen in reflected light (light grey areas in specimens, see Pl. 12, figs. 1, 2).

Plate 12

Figs. 1, 2. *Lepidocyclina multilobata* from the Tertiary f of Ngampel, E. Java (Caudri's type collection). Reflected light; fig. 1: × 55, fig. 2: × 36; fig. 1 detail of Pl. 12, fig. 2.

Figs. 3, 4. Transitional specimen from the Tertiary f of Santan, Borneo, in reflected and transmitted light; × 36. Irregular arrangement of the lateral chambers with formation of irregular massive patches; RGM 210 135.

Plate 13

Transitional forms (?) from the Lower Miocene of Bontang, Borneo. Figs. 1, 5, transmitted light, figs. 2, 3, 4 reflected light; figs. 1, 5: × 150, figs. 2, 4: × 36, fig. 3: × 55.

Fig. 1. Irregular arrangement of the lateral chambers.
Figs. 2, 4. Tangential sections showing the development of the tubercles: irregular massive patches in fig. 2, small lateral chambers with markedly thickened vertical walls in fig. 4. Note infiltration of dark material (light grey in photographs).
Fig. 3. Pillars surrounded by a narrow zone resembling Caudri's 'Verfestigungssystem' with infiltration of dark material (light grey in photograph); spatulate equatorial chambers, sometimes becoming almost hexagonal (fig. 5).
Figs. 1-5: RGM 210 178, RGM 210 172, RGM 210 176, RGM 210 173 and RGM 210 174, respectively.

Plate 14

Transitional forms (?) from the Lower Miocene of Bontang, Borneo. Reflected light, except fig. 1; fig. 1: × 150, figs. 2-5: × 36.

Fig. 1. Detail of pillar with some small enclosed lateral chambers. RGM 210 181.
Figs. 2, 3, 4. Vertical sections showing the variation in shape and arrangement of the lateral chambers and the development of pseudopillars or 'Verfestigungssystem'. Arrangement rather regular in fig. 2. Note more irregular arrangement in the juvenile stage. RGM 210 179, RGM 210 182 and RGM 210 178, respectively.
Fig. 5. Section through and near the equatorial plane showing the thickening of the vertical chamber walls along the rays, spatulate-hexagonal equatorial chambers, nucleoconch nephrolepidine. RGM 210 174.

Plate 15

Lepidocyclina cf. *ferreroi* from the Lower Miocene of Sungei Blakin, Borneo. Reflected light, except fig. 5; figs. 1, 5: × 150, figs. 2-4: × 36.

Figs. 1, 5. Massive clear pillar without layering (same detail as fig. 1); RGM 210 138.
Figs. 2, 4. Tangential sections showing clearly defined massive pseudopillars surrounded by a narrow zone with infiltration of dark material (light grey in photograph). Within this zone small lateral chambers may be observed locally; RGM 210 137 and RGM 210 136.
Fig. 3. Vertical section (compare figs. 2, 4); RGM 210 138.

Plates 16, 17

Lepidocyclina cf. *multilobata* from Kapuan, Middle Java; age unknown (Weber collection). Reflected light, except Pl. 17, fig. 4. Pl. 16, figs. 1, 2, 4 and Pl. 17, figs. 1-4: × 36; Pl. 16, fig. 3: × 55.

Plates 16 and 17 show the variation in shape and arrangement of the lateral chambers and the development of pillars and/or 'Verfestigungssystem'. The latter is well-developed in the specimen from Pl. 17, fig. 1; most other sections show the development of massive patches or pillars within the 'system'. Arrangement of the lateral chambers is generally regular, the lateral chambers may be narrow (Pl. 16, fig. 1) or spacious (Pl. 17, fig. 4). Note irregular arrangement in the juvenile stage (Pl. 16, figs. 1, 2). Plate 17, fig. 2 shows infiltration of dark material around the pillars and near the nucleoconch (light grey in photograph).
Pl. 16, figs. 1-4: RGM 210 165, RGM 210 163, RGM 210 148 and RGM 210 160, respectively.
Pl. 17, figs. 1-4: RGM 210 190, RGM 210 156, RGM 210 166 and RGM 210 171, respectively.

Plate 18

Lepidocyclina cf. *multilobata* from Kapuan, Middle Java, age unknown (Weber collection). Reflected light, except fig. 4; figs. 1, 2, 3, 5: × 36; fig. 4: × 150; fig. 4 detail of fig. 2.

Tangential sections showing all transitions between massive pseudopillars (fig. 1) and tubercles formed by small lateral chambers with thickened vertical walls (compare 'Verfestigungssystem').
Figs. 1-5: RGM 210 203, RGM 210 154, RGM 210 205, RGM 210 154 and RGM 210 209, respectively.

Plate 19

Lepidocyclina cf. *multilobata* from Kapuan, Middle Java; age unknown (Weber collection). Figs. 1, 2 transmitted light, figs. 3-5 reflected light; figs. 1, 2: × 150; fig. 3: × 55; figs. 4, 5: × 15.

Fig. 1. Spatulate to hexagonal equatorial chambers; RGM 210 149.
Fig. 2. Detail of the 'Verfestigungssystem' (detail of Pl. 17, fig. 1); RGM 210 190.
Fig. 3. Faintly layered pillars, small lateral chambers occurring locally around and within the pillars. Irregular arrangement of lateral chambers in the juvenile stage; RGM 210 165.
Figs. 4, 5. Sections near and partly through the equatorial plane showing thickening of the vertical walls along the rays which may lead to the formation of pseudopillars; RGM 210 152 and RGM 210 149.

Plate 20

Lepidocyclina cf. *multilobata* from Watu Agar, Middle Java; age unknown (Weber collection). Reflected light; figs. 1, 2: × 55, fig. 3: × 150.

Fig. 1. Tangential section of a 'Verfestigungssystem'; RGM 210 218.
Fig. 2. Specimen with well-developed 'Verfestigungssystem' but with irregularly arranged spacious lateral chambers; RGM 210 219.
Fig. 3. Detail of pseudopillar with very regular layering (same detail also shown in transmitted light: Pl. 22, fig. 4); RGM 210 214.

Plate 21

Lepidocyclina cf. *multilobata* from Watu Agar, Middle Java; age unknown (Weber collection). Reflected light; figs. 1, 2: × 36, fig. 3: × 55. Compare also Pl. 20, fig. 2 and Pl. 22, figs 2, 3.

Vertical sections showing the variation in shape and arrangement of the lateral chambers and the development of pillars and/or 'Verfestigungssystem'. Irregular arrangement of the lateral chambers in the juvenile stage (figs. 2, 3). Figs. 1-3; RGM 210 220, RGM 210 221 and RGM 210 213, respectively.

Plate 22

Lepidocyclina cf. *multilobata* from Watu Agar, Middle Java; age unknown (Weber collection). Figs. 1, 2 reflected light; figs. 3, 4 transmitted light; fig. 1 × 55; figs. 2, 3: × 36; fig. 4: × 150.

Fig. 1. 'Verfestigungssystem'-like structure with pronounced tendency to form massive patches and pillars (detail of Pl. 21, fig. 3); RGM 210 213.
Figs. 2, 3. Compare Pl. 21; RGM 210 223 and RGM 210 214.
Fig. 4. Same detail as Pl. 20, fig. 3; RGM 210 214.

Plate 23

Lepidocyclina cf. *ferreroi* from the upper Tertiary e of Menjangau, Borneo. Figs. 1, 3 transmitted light; figs. 2, 4 reflected light; figs. 1, 2: × 150; figs. 3, 4: × 55. All photographs of the same specimen; RGM 210 131.

Faintly layered pillars with a local zone of small lateral chambers. For variation in shape and arrangement of the lateral chambers and the development of pillars compare Pl. 24, figs. 1, 2, 4.

Plate 24

Lepidocyclina cf. *ferreroi* from the upper Tertiary e of Menjangau, Borneo. Reflected light; fig. 4: × 55, other figs: × 36.

Figs. 1, 2, 4. Vertical sections, compare Pl. 23.
Figs. 3, 5, 6. Tangential sections. Small to large massive pillars surrounded by an irregular 'Verfestigungssystem'-like zone with infiltration of dark material (light grey on photographs). Figs. 1-6; RGM 210 132, RGM 210 127 RGM 210 123, RGM 210 128, RGM 210 126 and RGM 210 124, respectively.

Plate 25

Lepidocyclina cf. *ferreroi* from the Tertiary e5-f1 of Balikpapan, Borneo. Reflected light, except fig. 4; figs. 1, 3, 5: × 55, fig. 2: × 36, fig. 4: × 15.

Specimens with spacious lateral chambers, irregularly arranged. The development of pillars varies. Locally a zone with small lateral chambers and infiltration of dark material has developed; compare tangential section of fig. 4. Fig. 1 shows a detail of fig. 2.
Figs. 1, 2; RGM 210 185; figs. 3-5; RGM 210 184, RGM 210 183 and RGM 210 186, respectively.

Plate 26

Lepidocyclina cf. *ferreroi* from Java, exact locality and age unknown. Reflected light, except fig. 1; fig. 1: × 150, figs. 2, 3, 5: × 36, fig. 4: × 55.

Fig. 1. Detail of fig. 5: faintly layered pillars, locally small patches resembling a 'Verfestigungssystem'; RGM 210 141.
Fig. 2 and 4 vertical sections; RGM 210 140 and RGM 210 142.
Fig. 3. Tangential section; RGM 210 139.

Plate 1

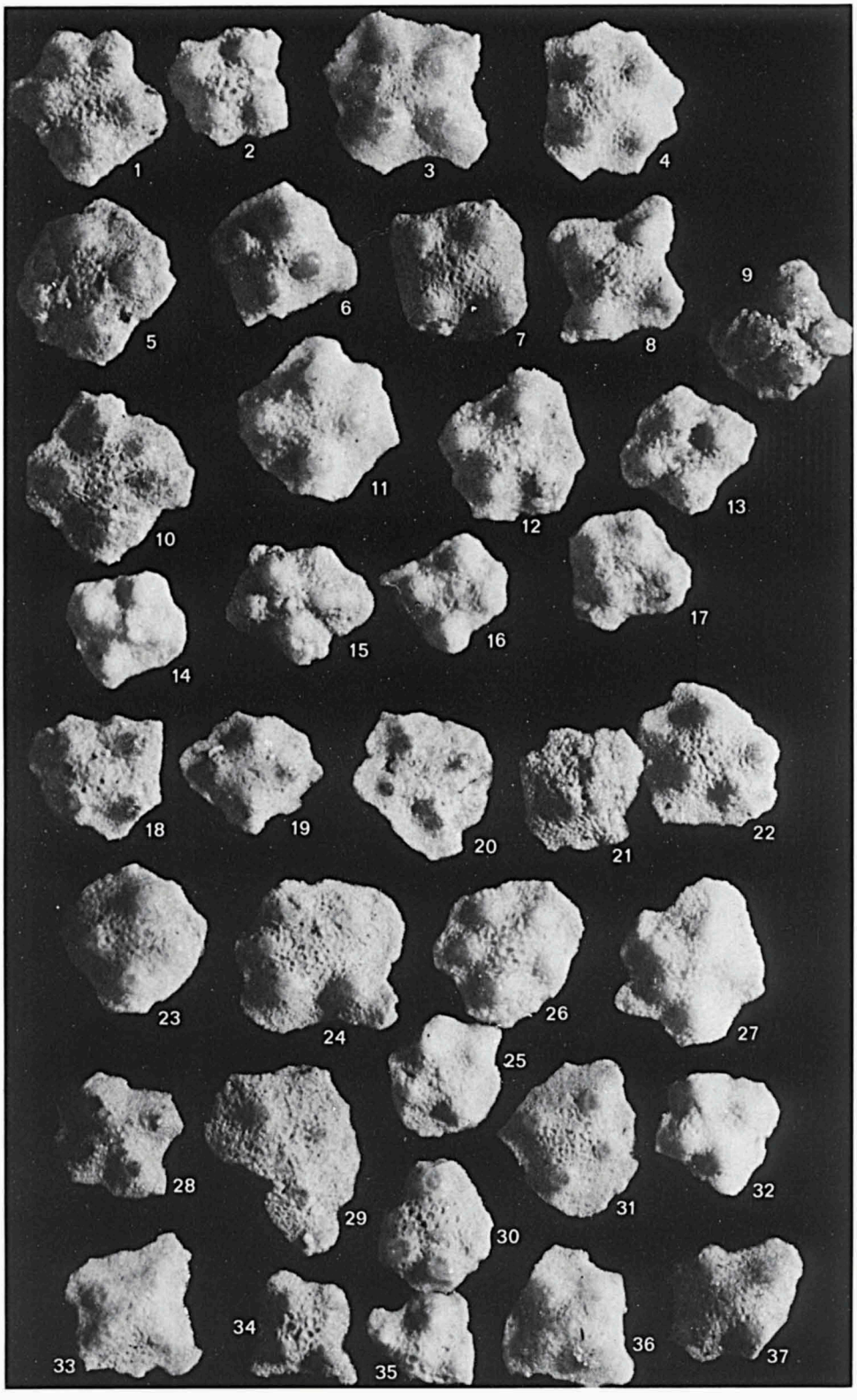
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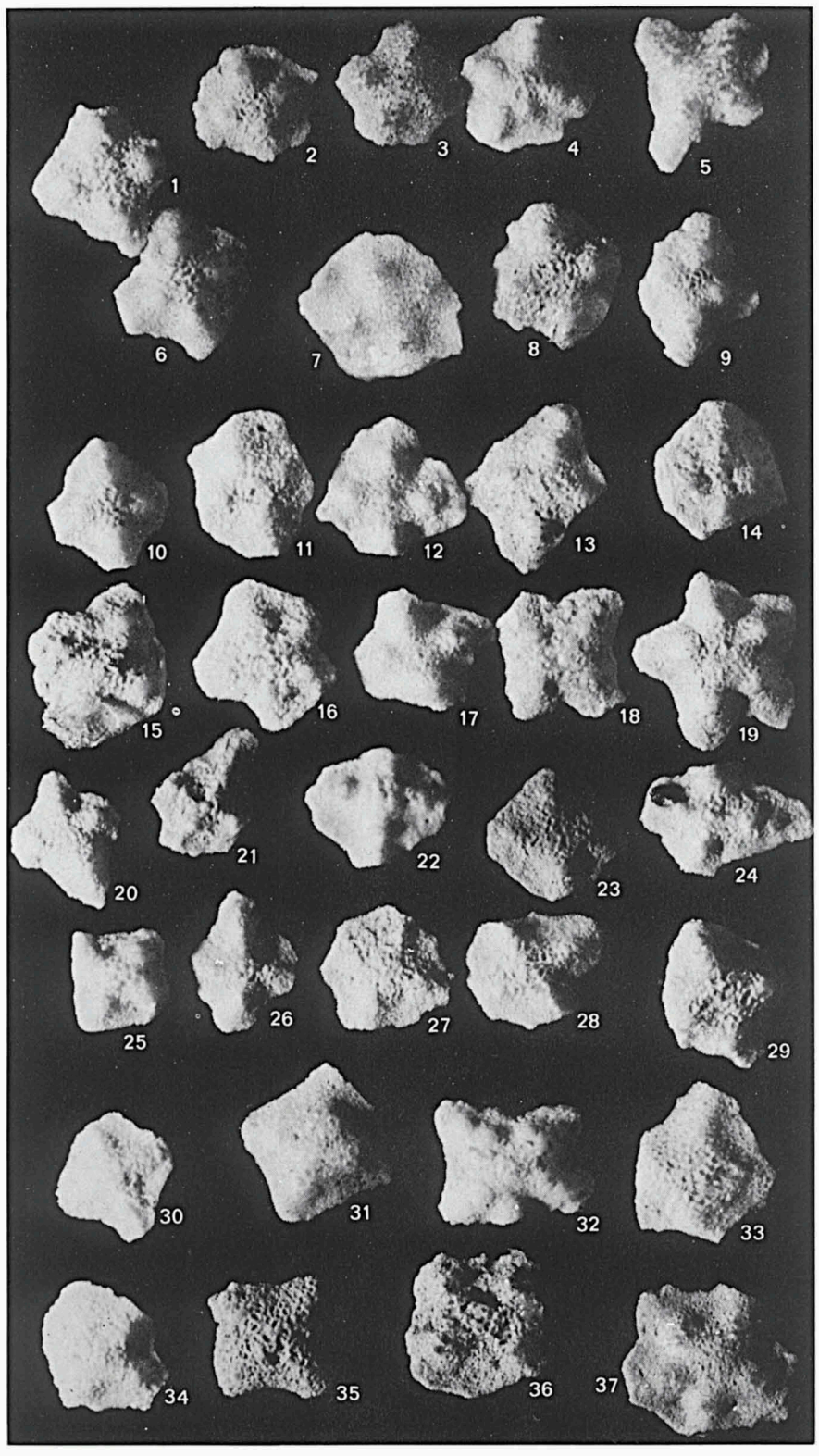
Plate 2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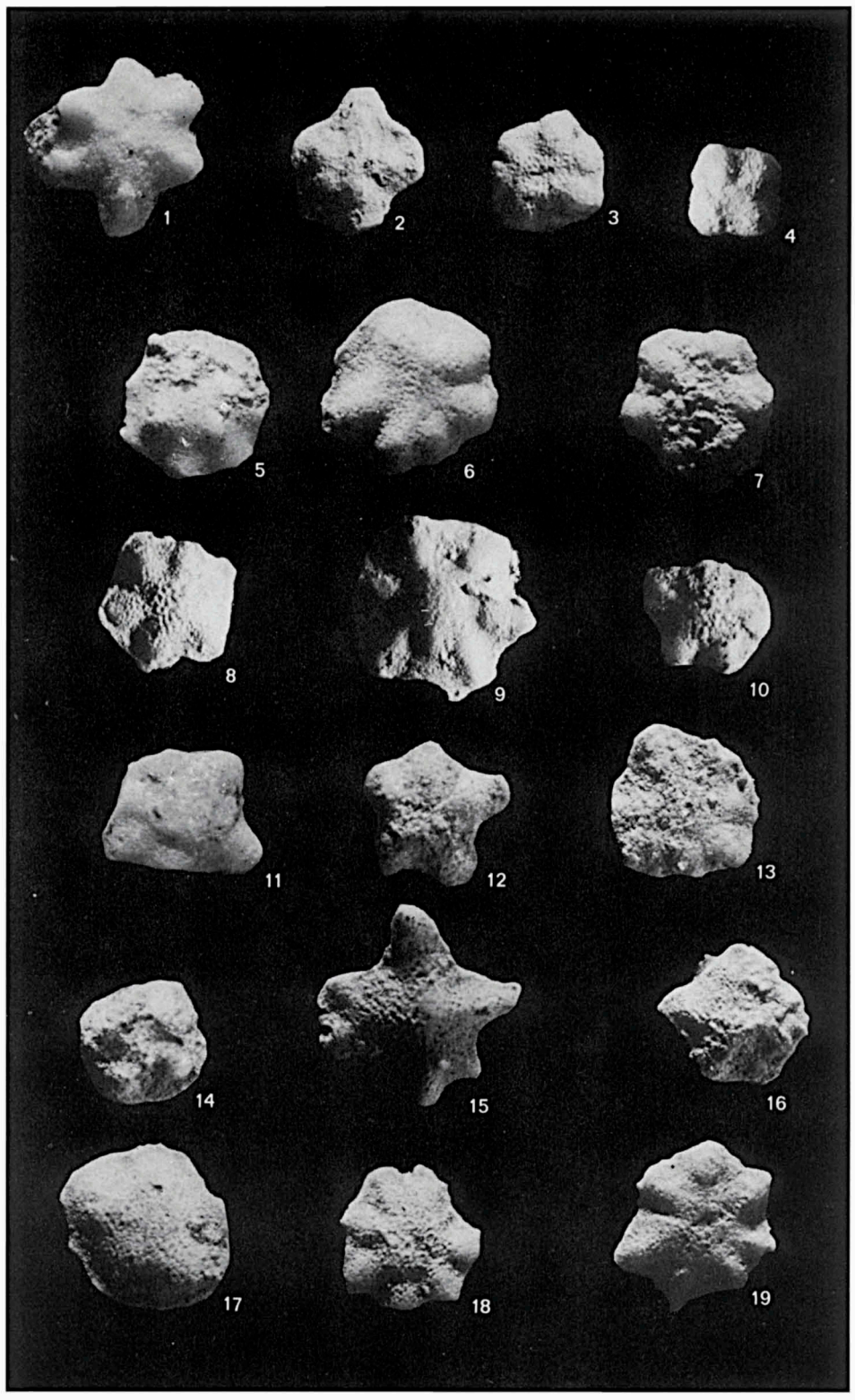

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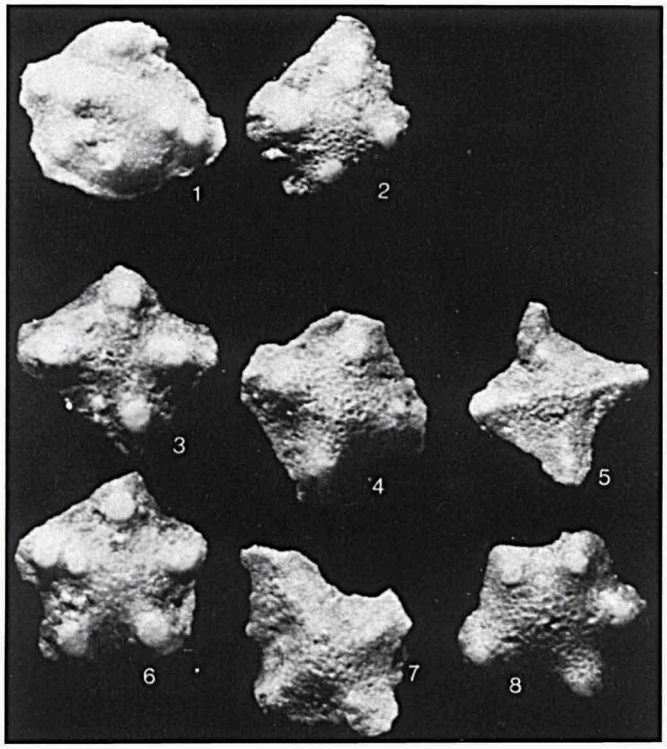

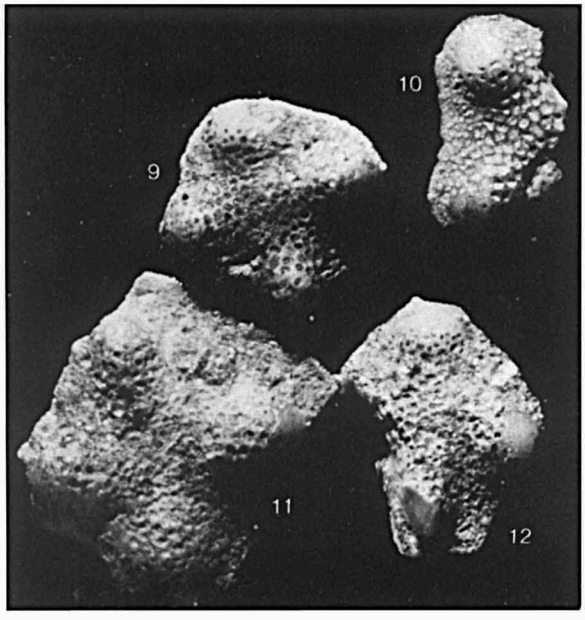

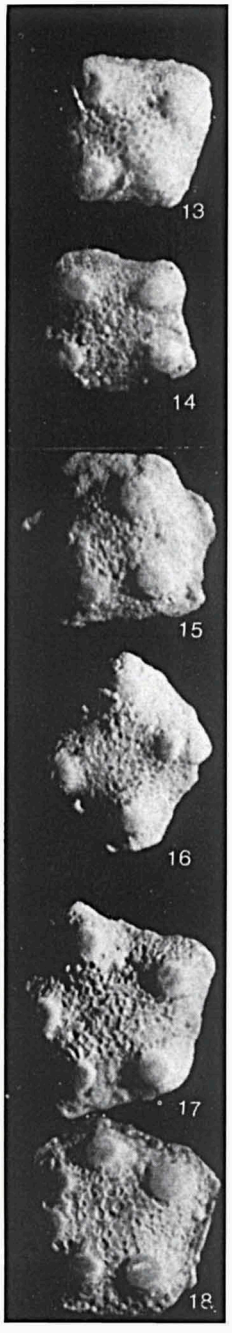

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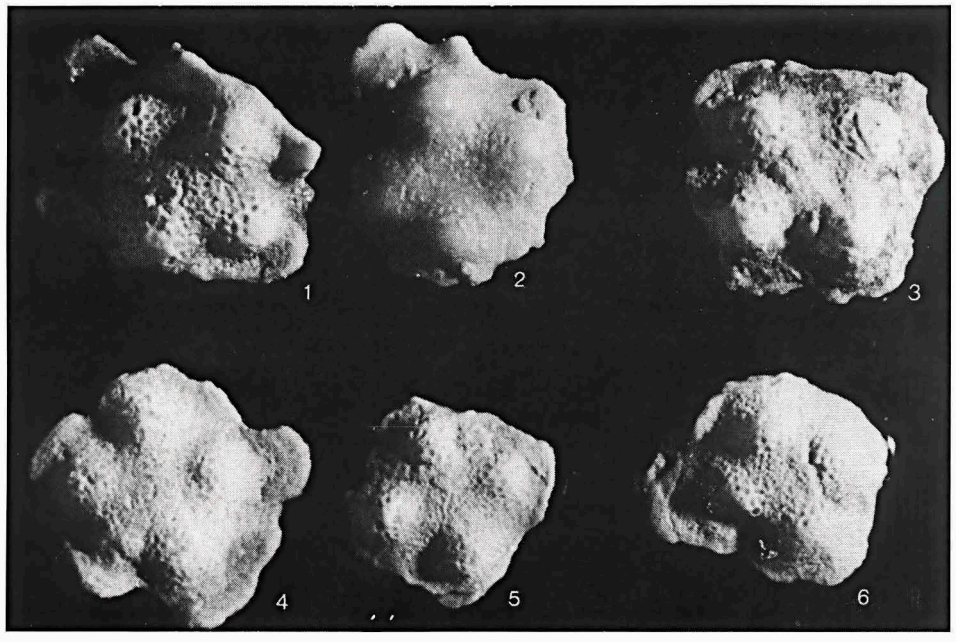

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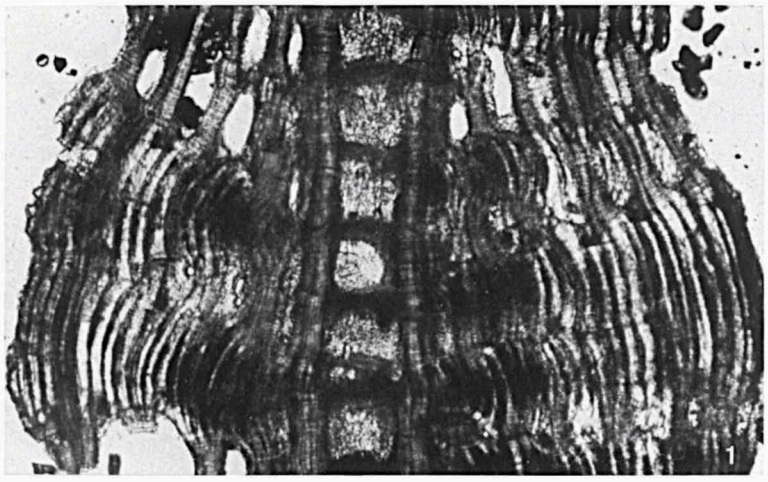

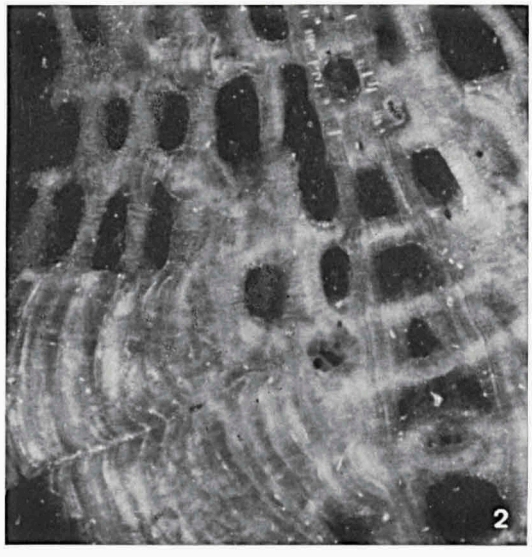

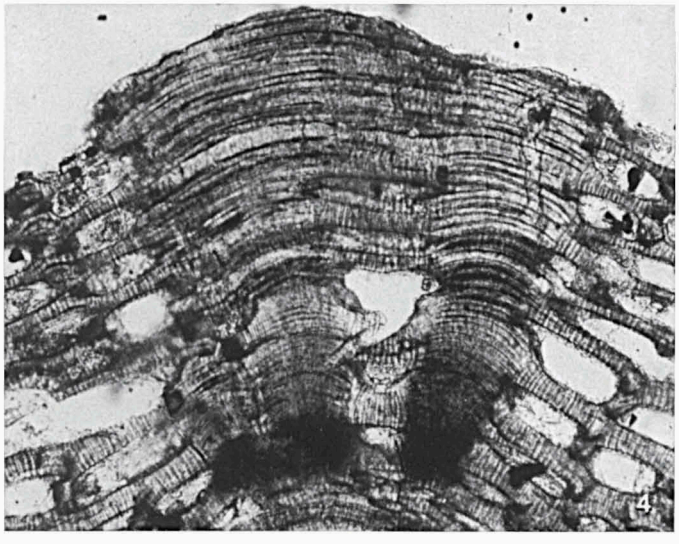

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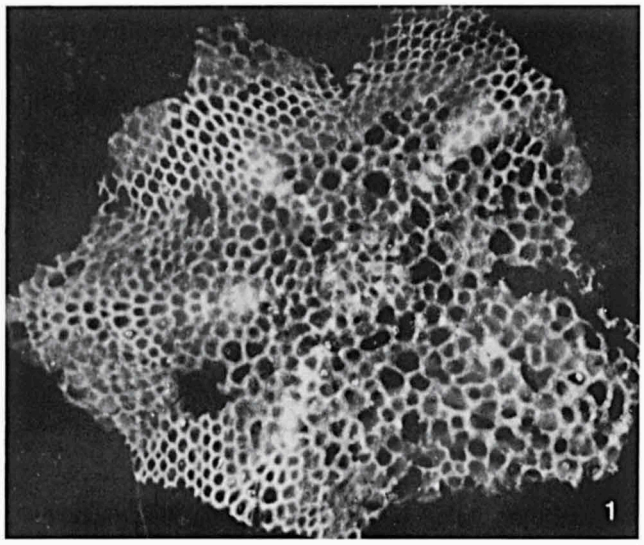

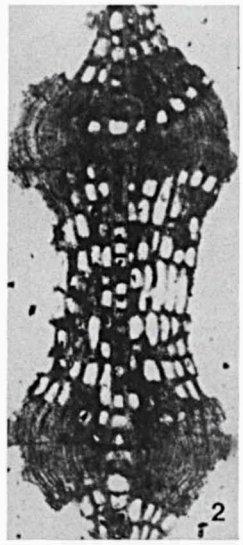

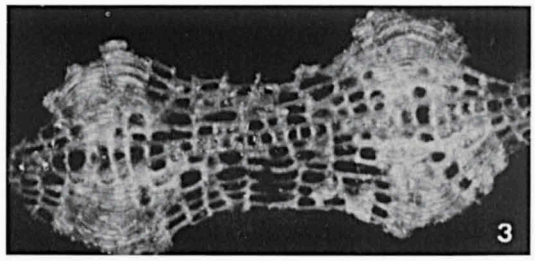

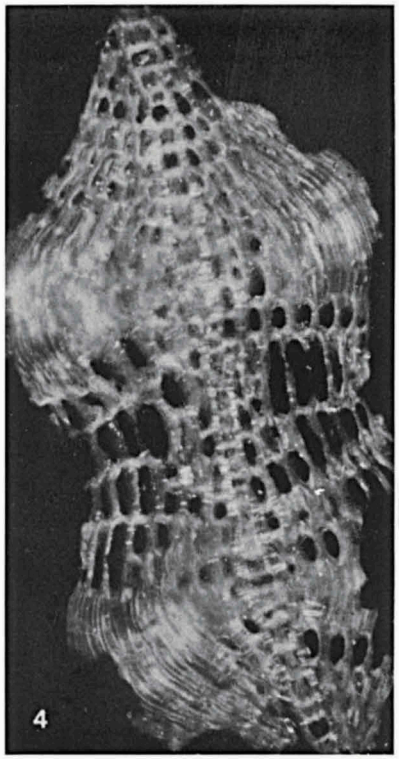

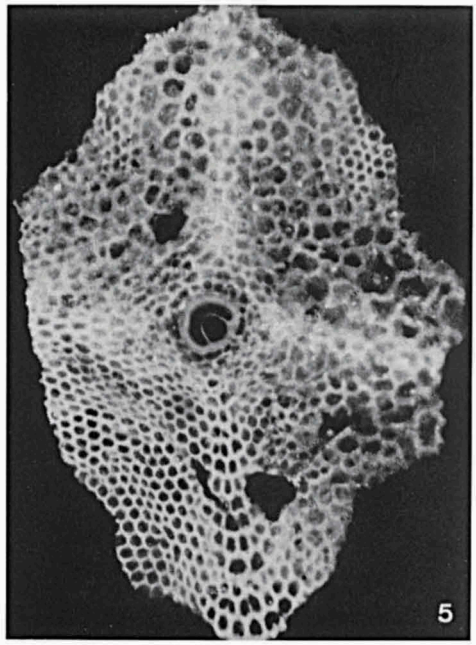

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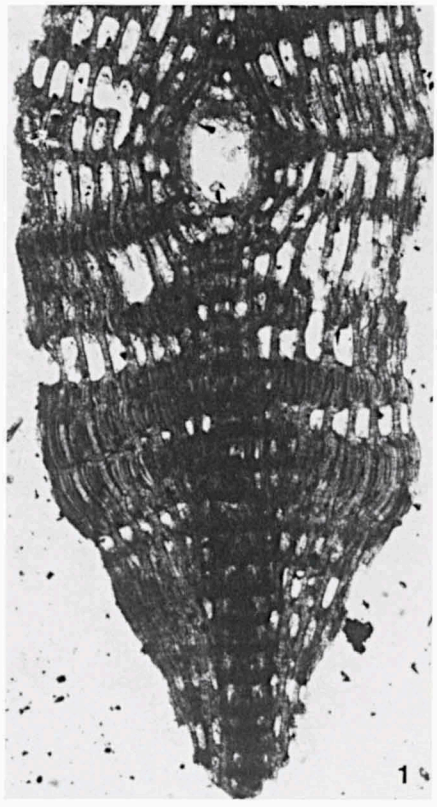
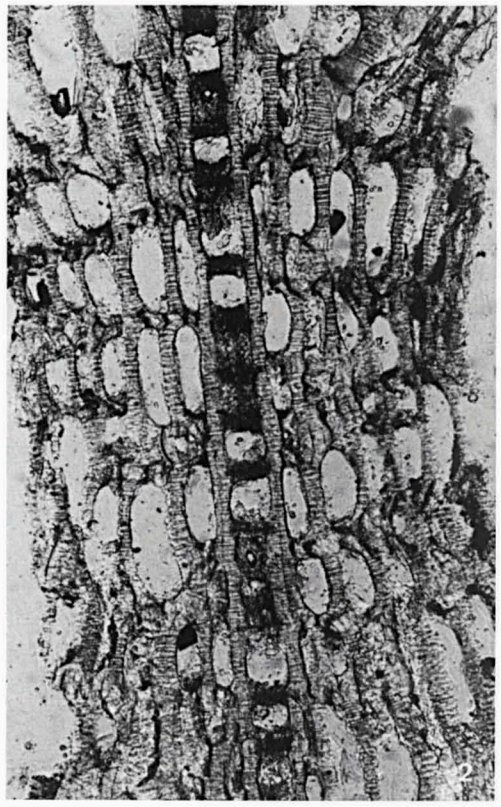
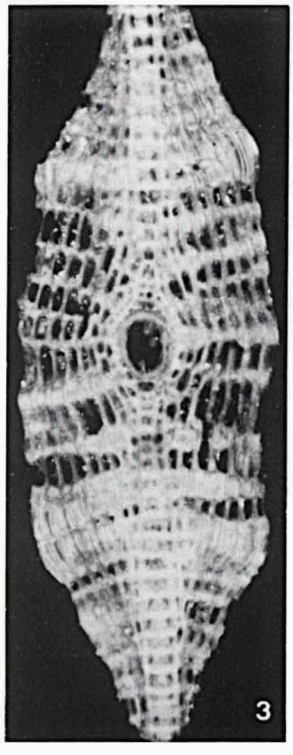
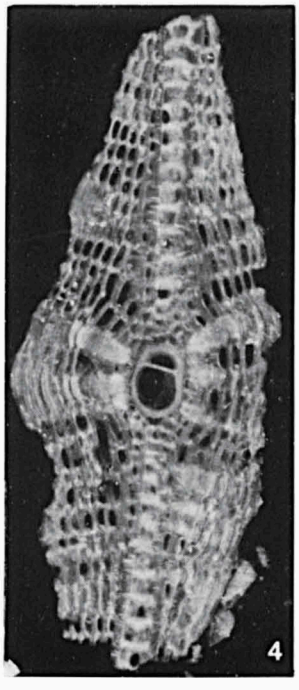








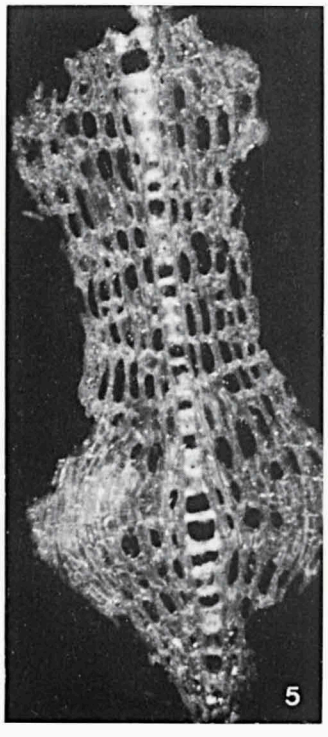
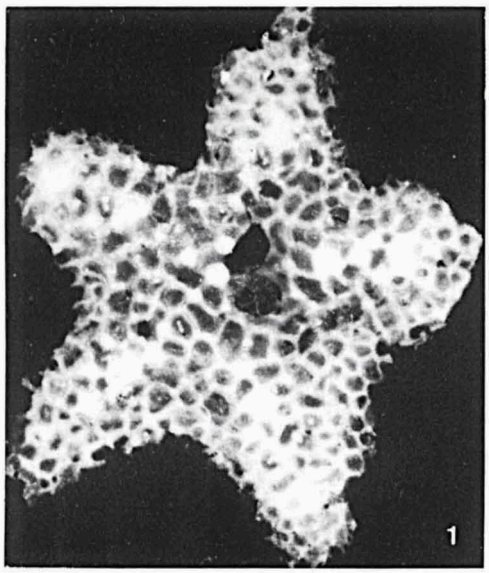
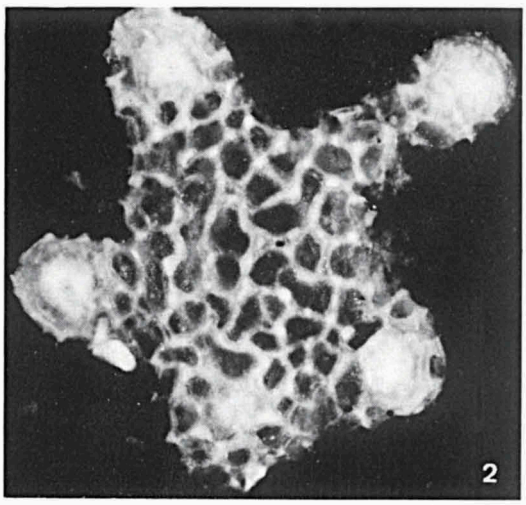
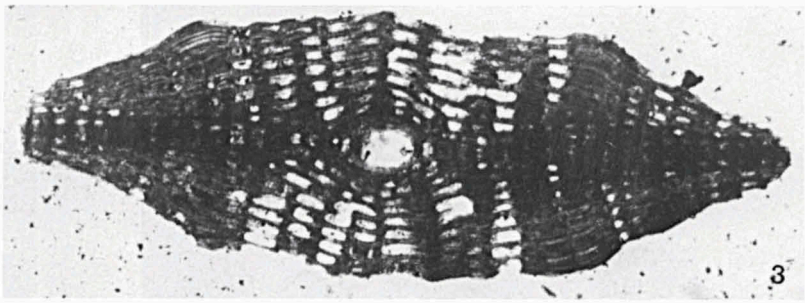
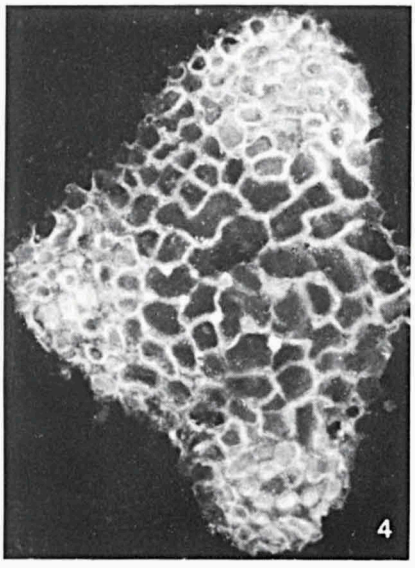


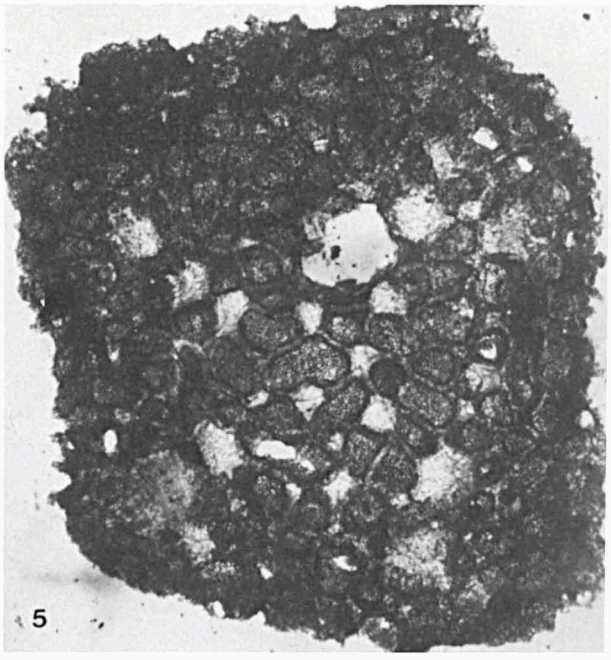
Plate 9











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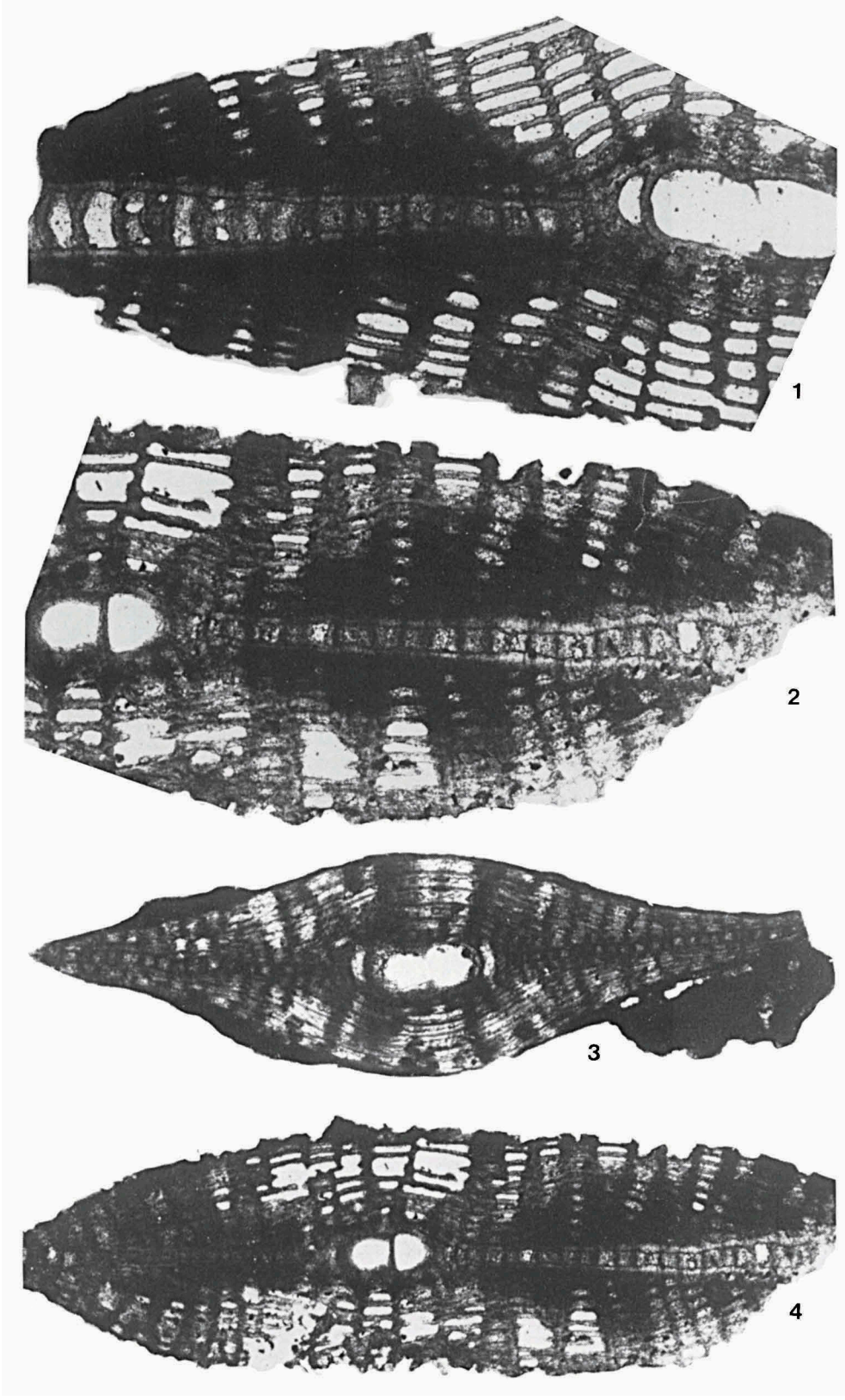

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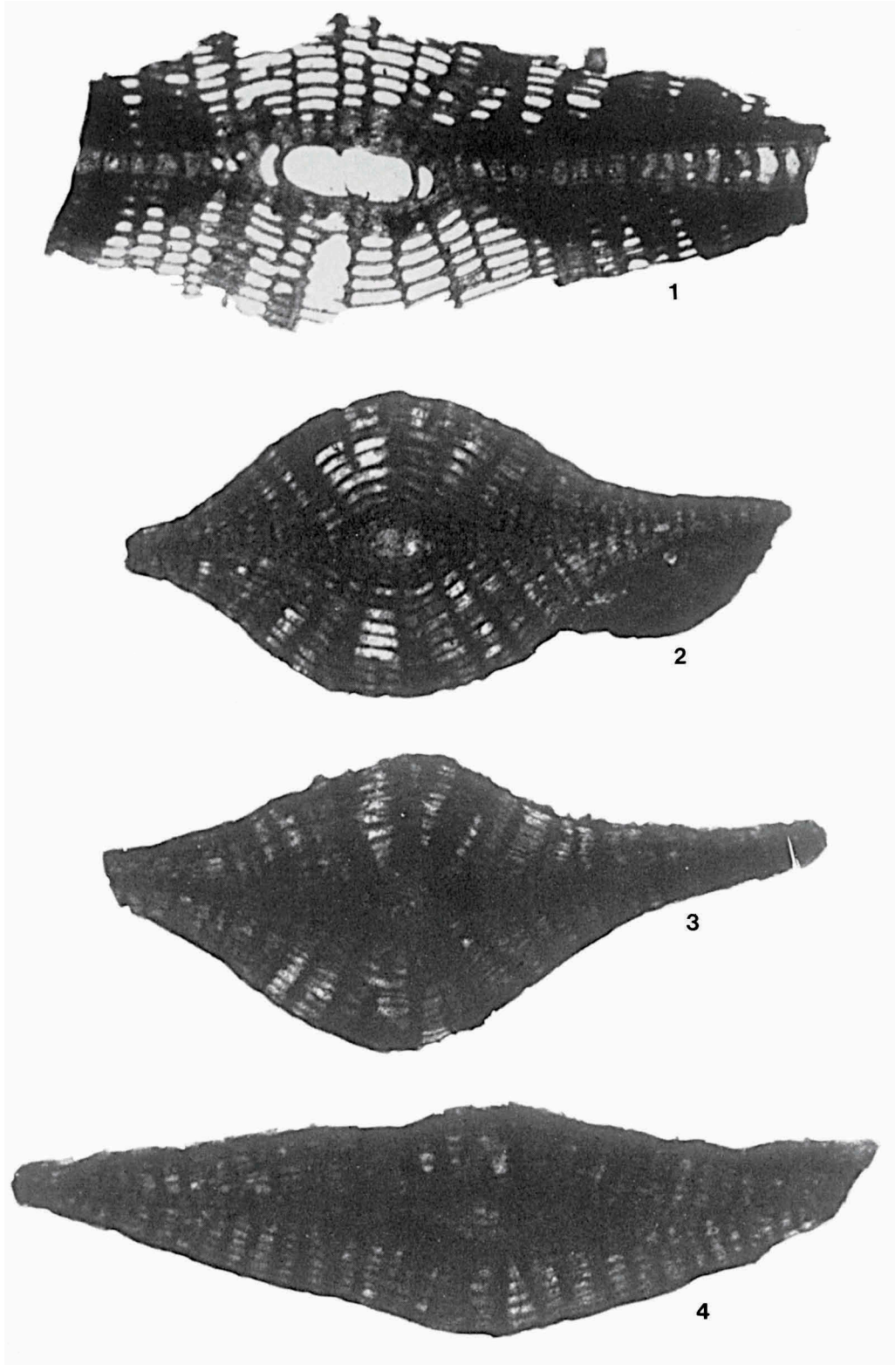

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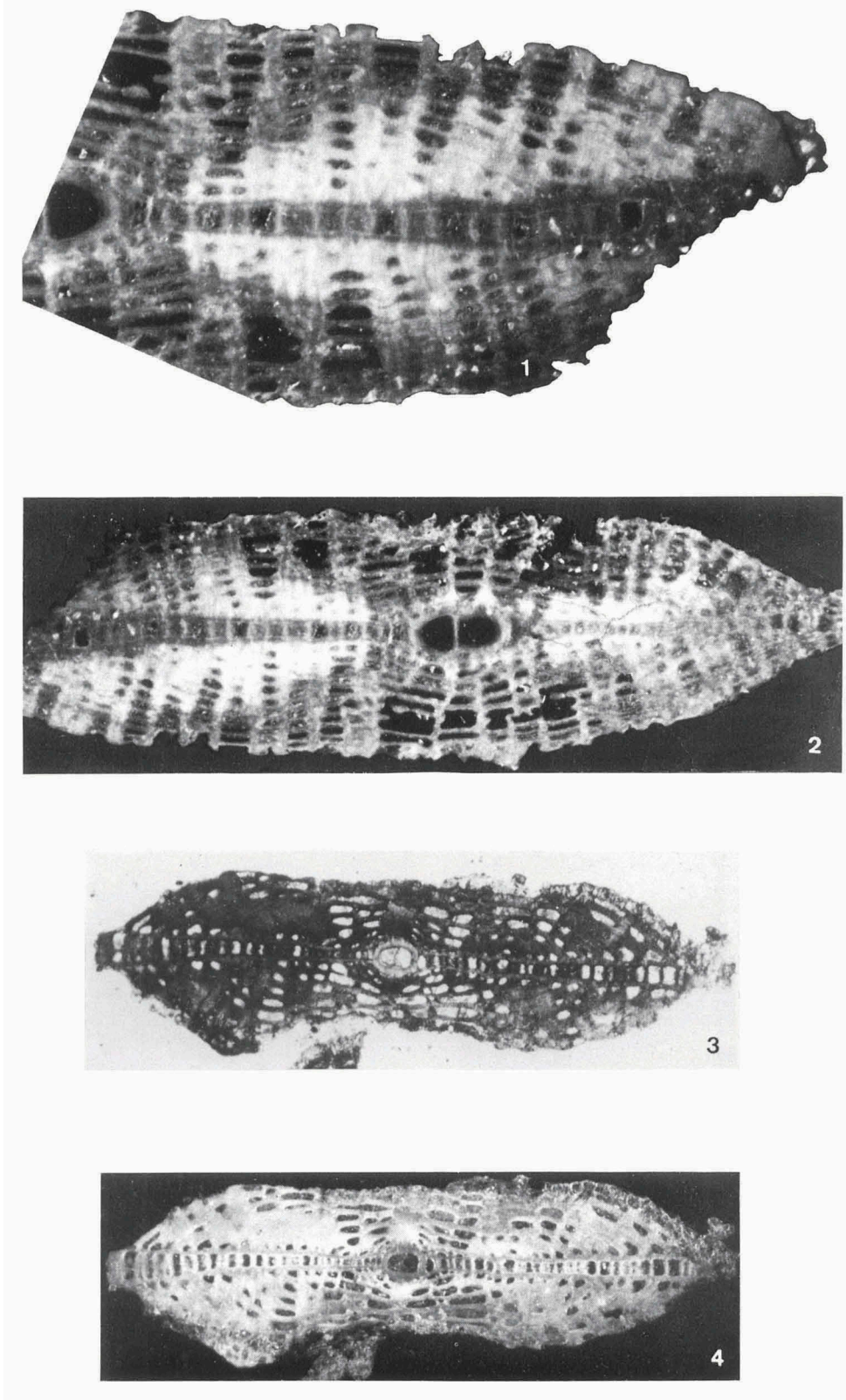
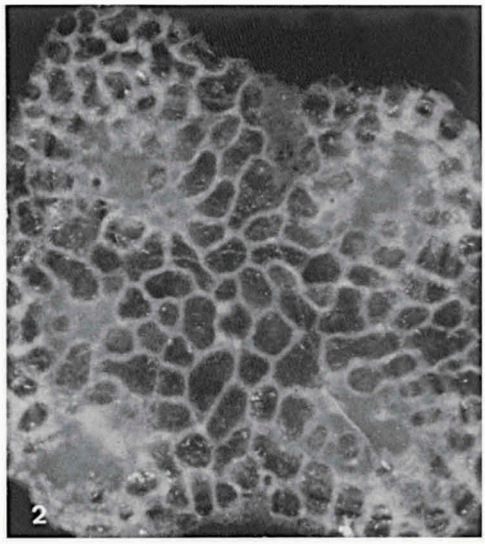
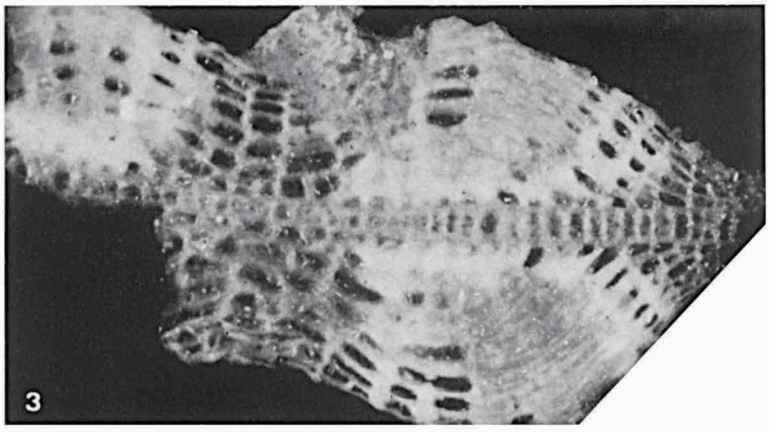
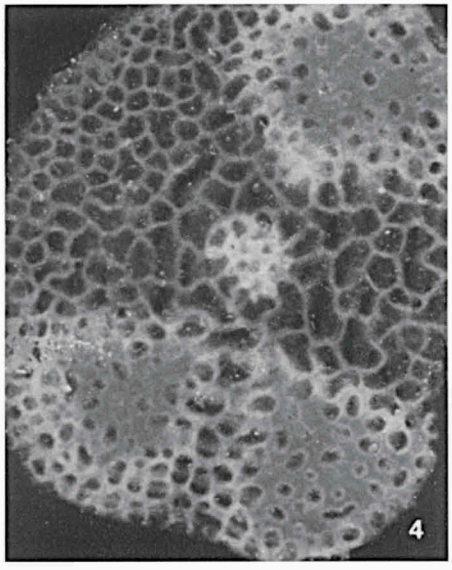


Plate 13







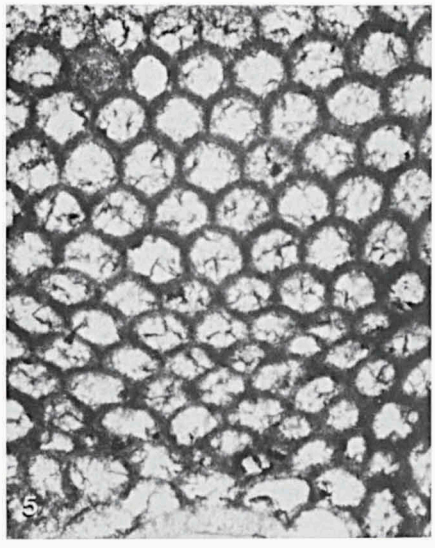
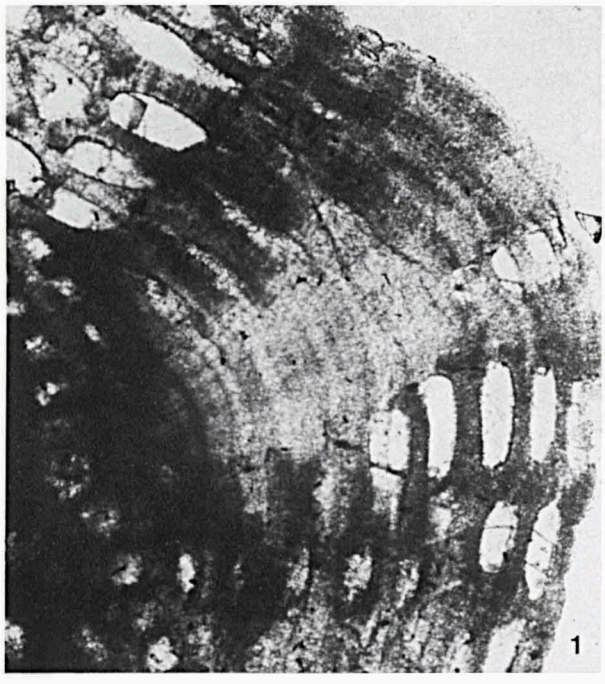
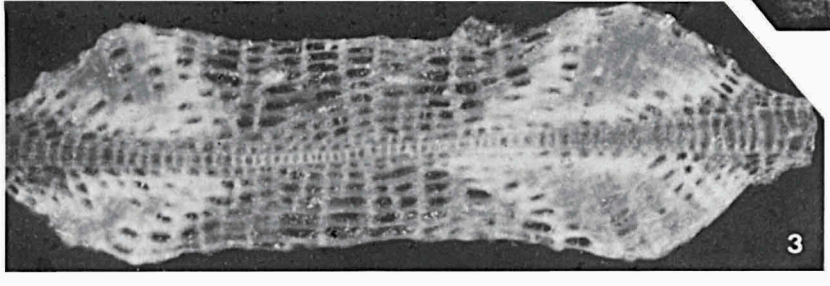
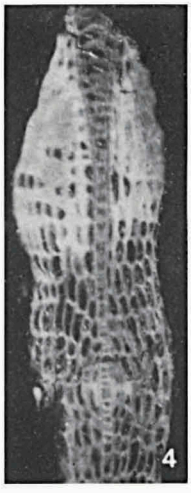
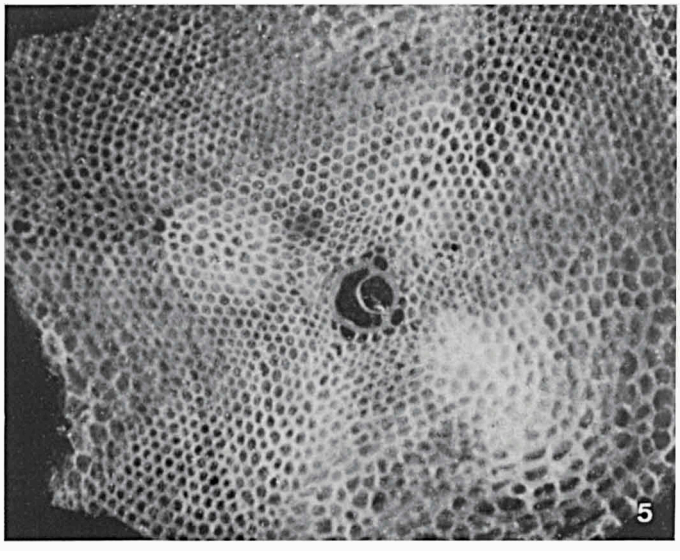


Plate 14









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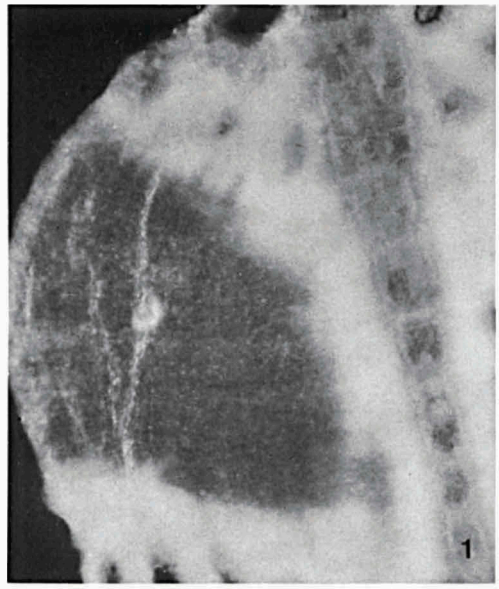
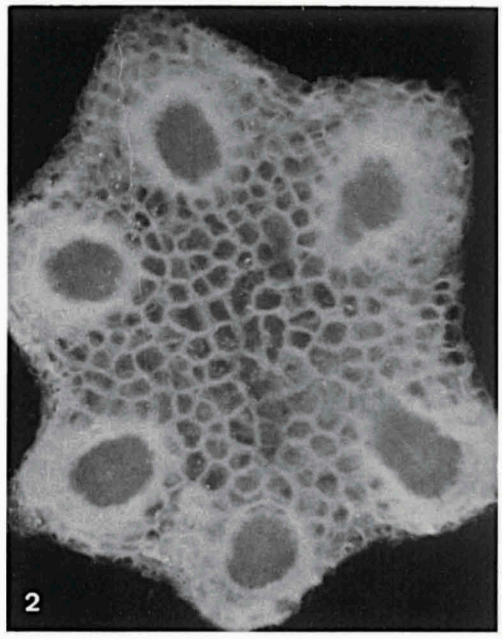
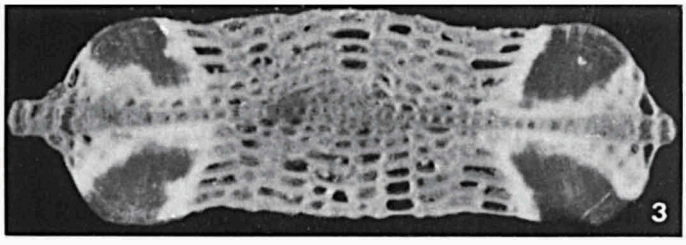






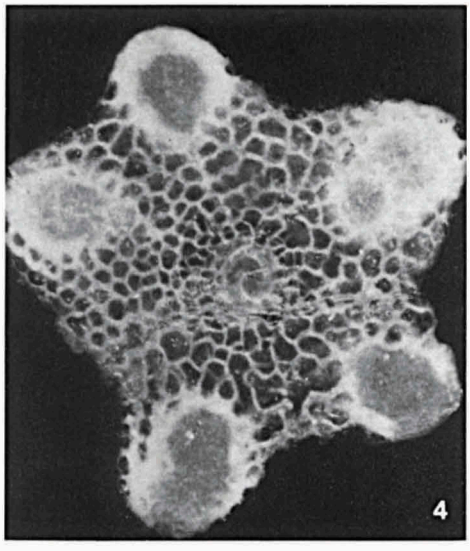


Plate 16

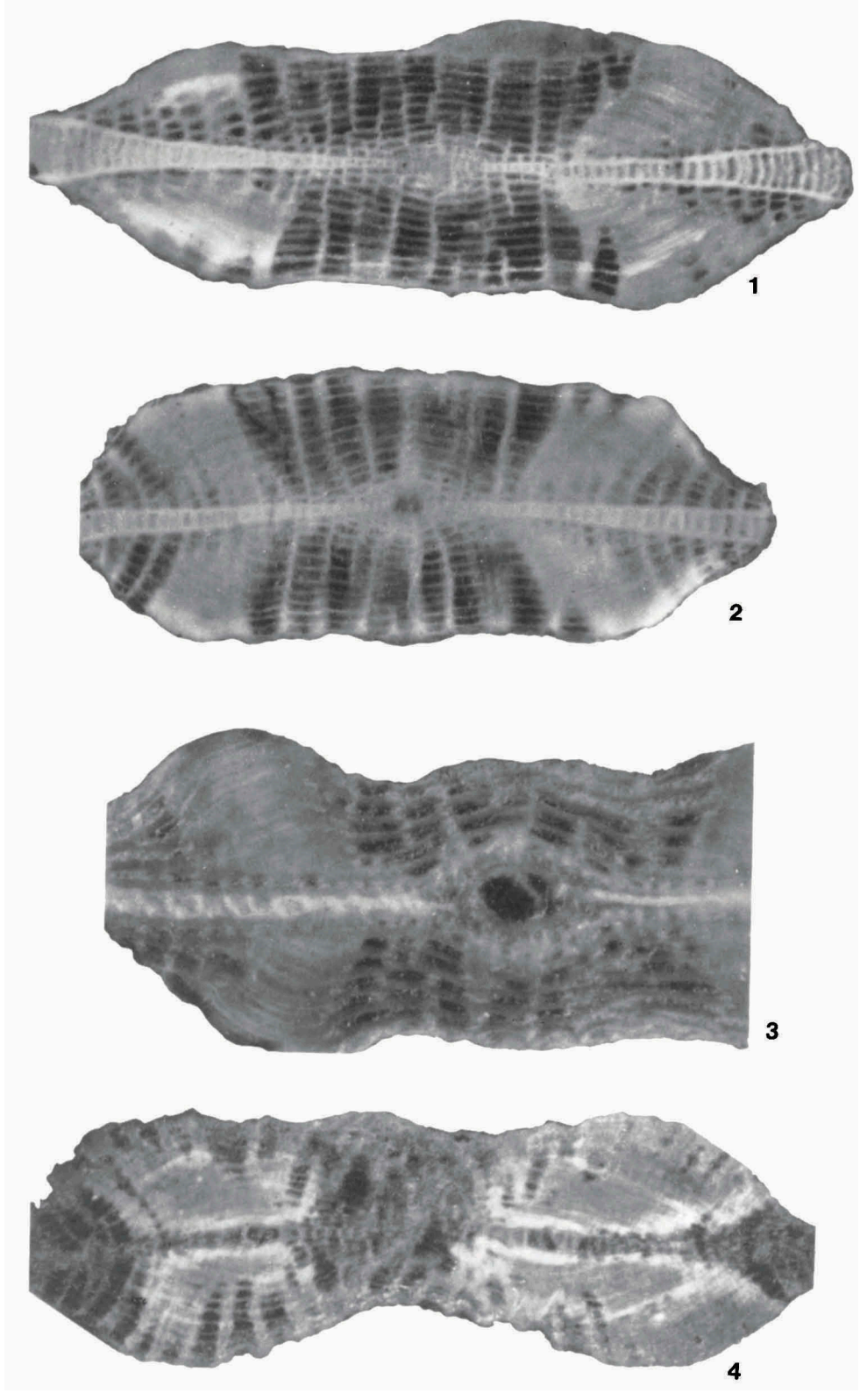


Plate 17

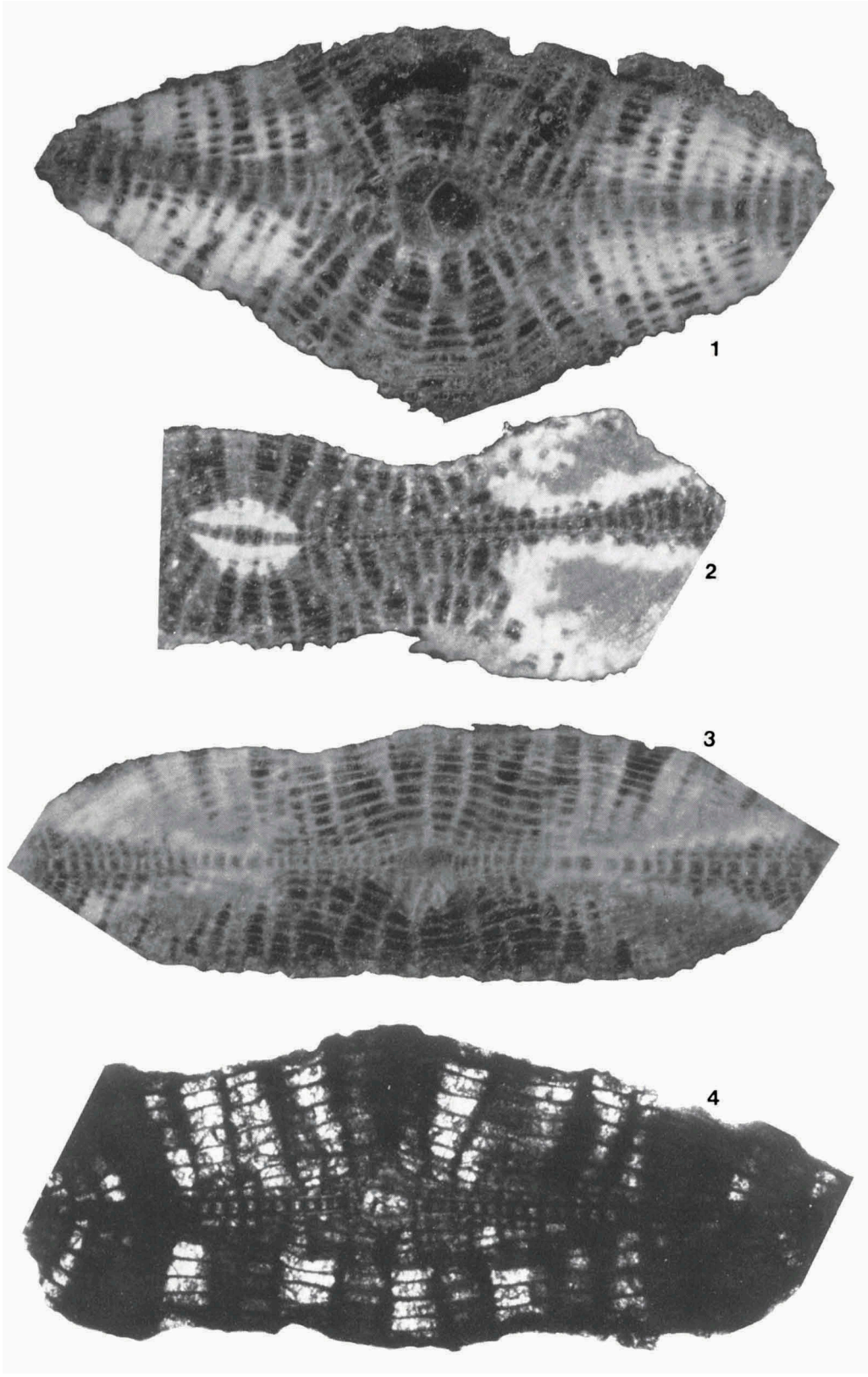
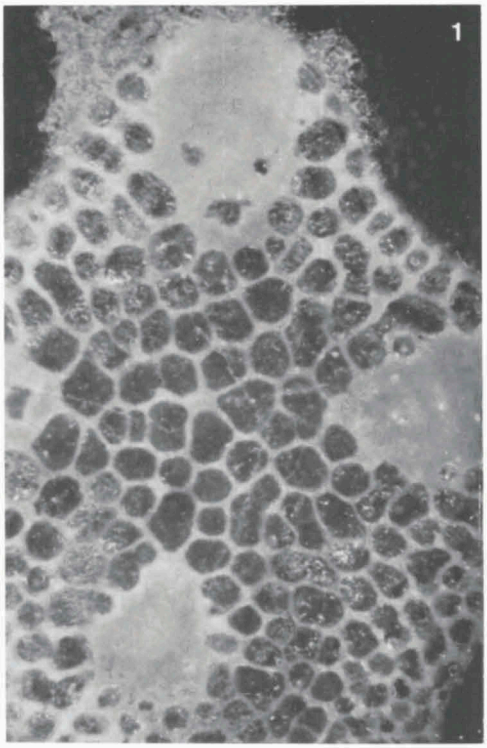
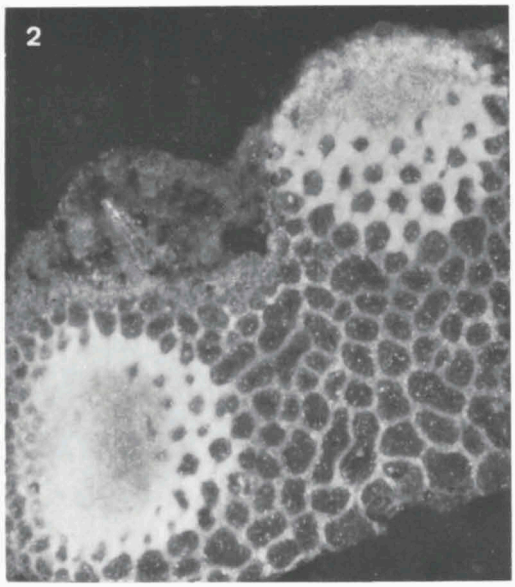
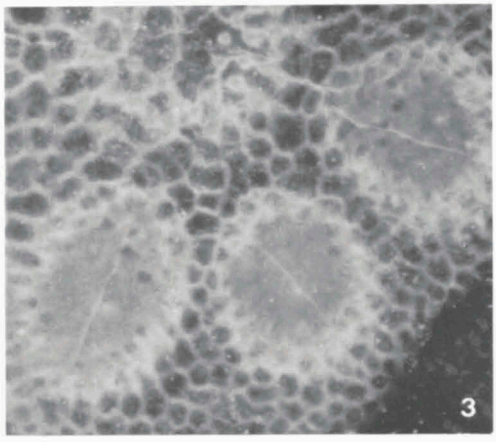
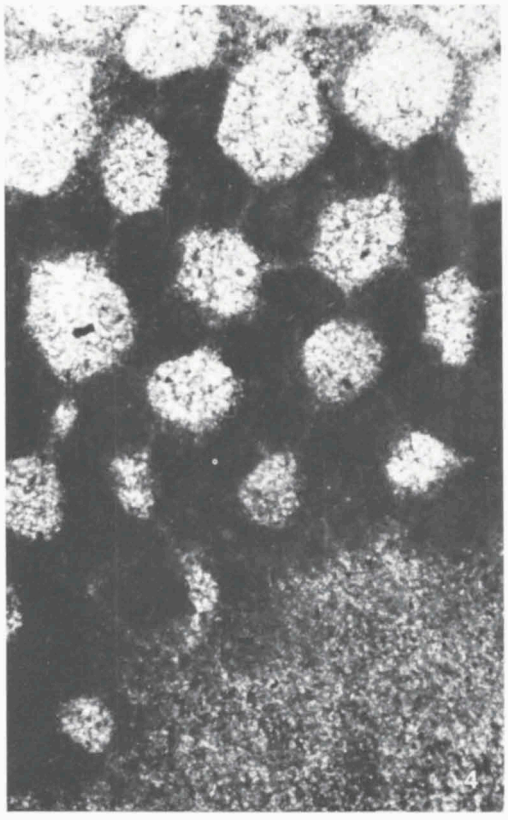


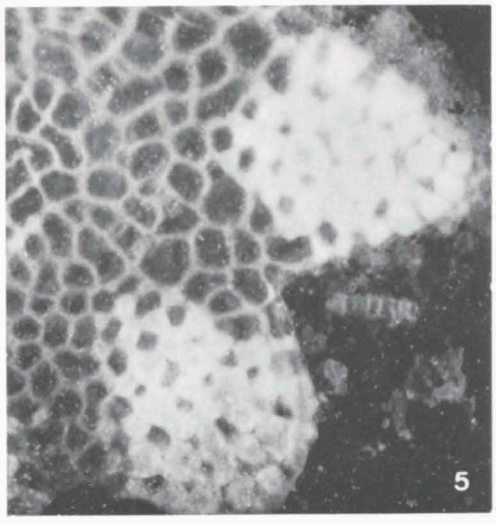
Plate 18











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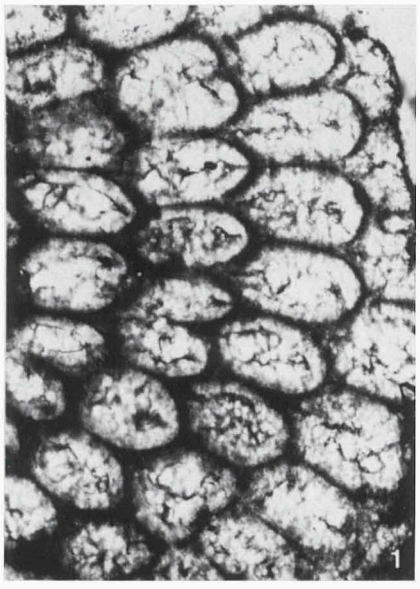
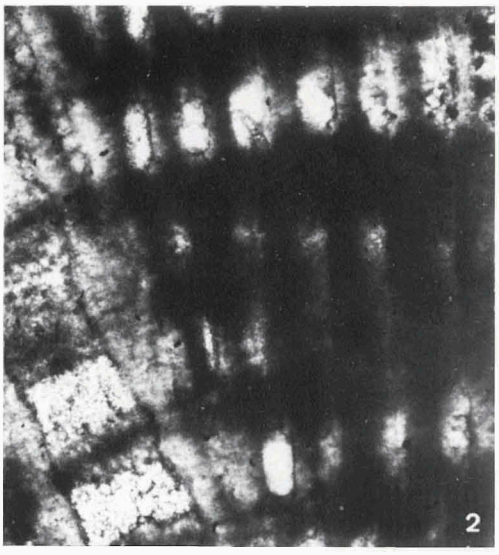
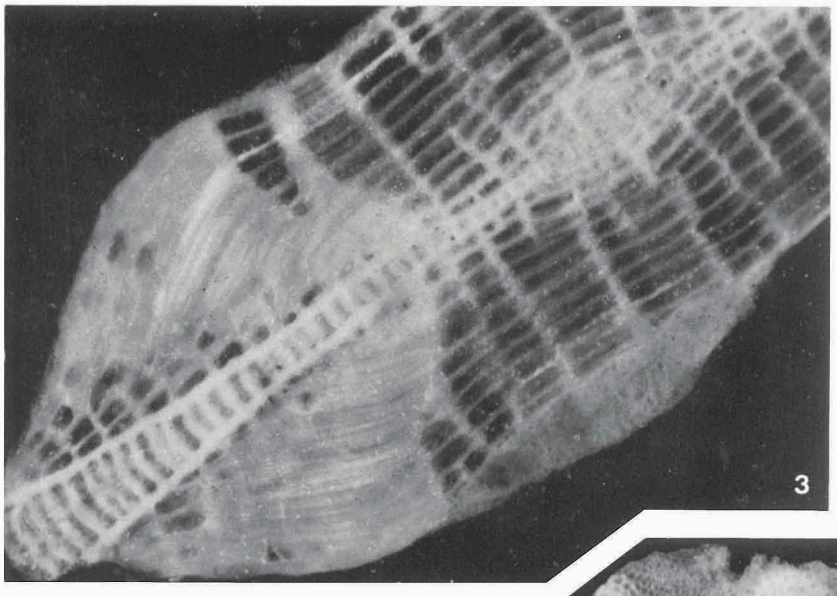
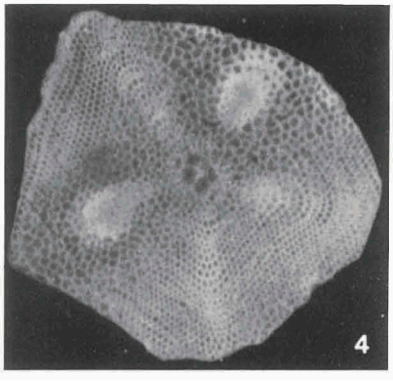








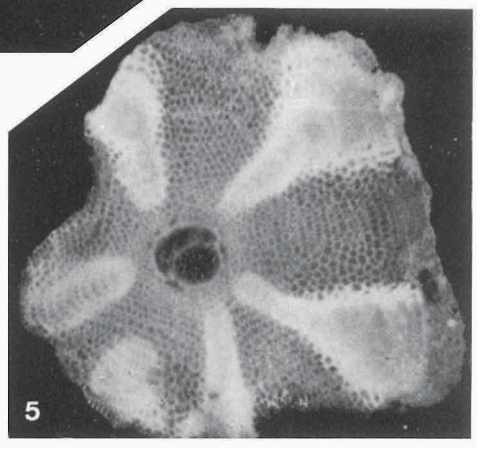
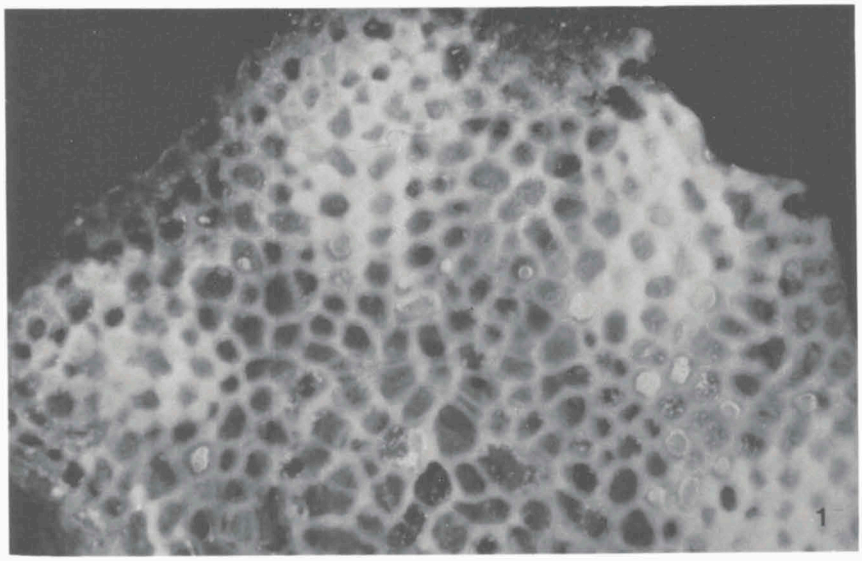
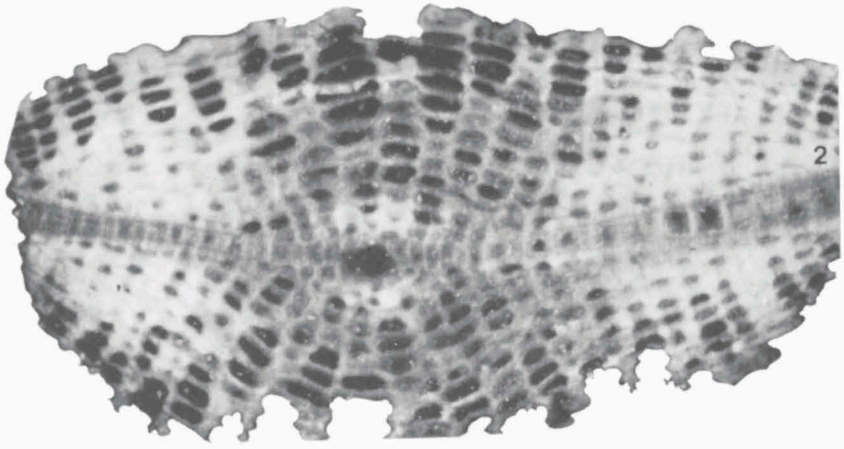


Plate 20





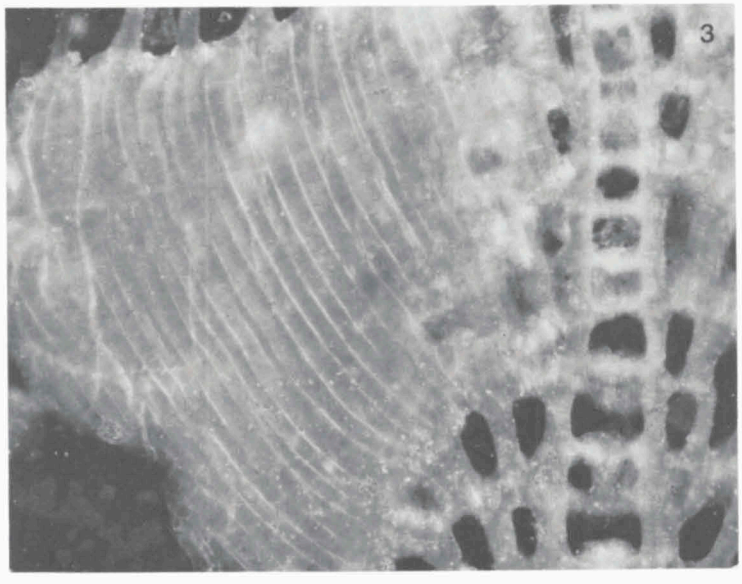


Plate 21

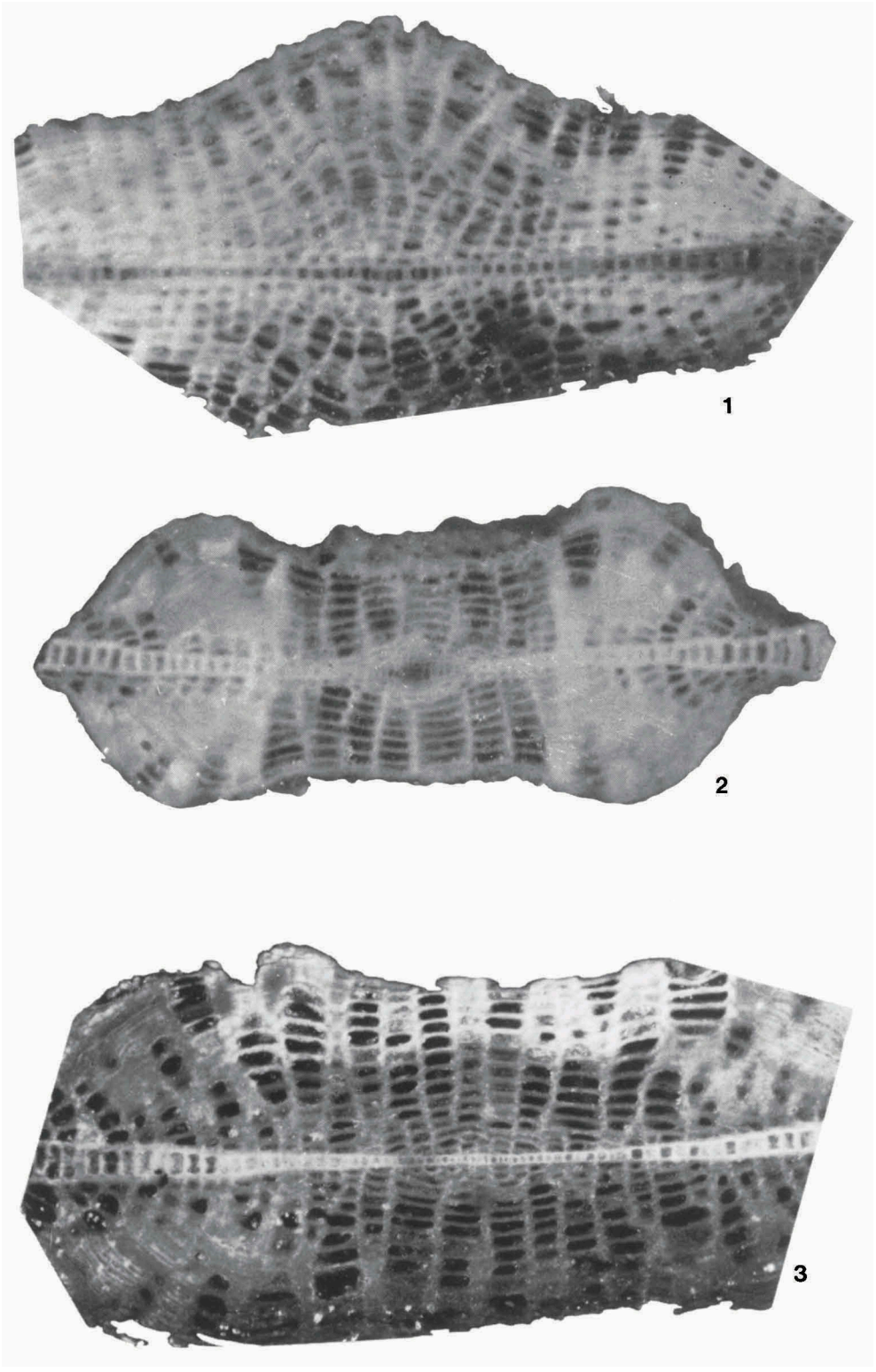
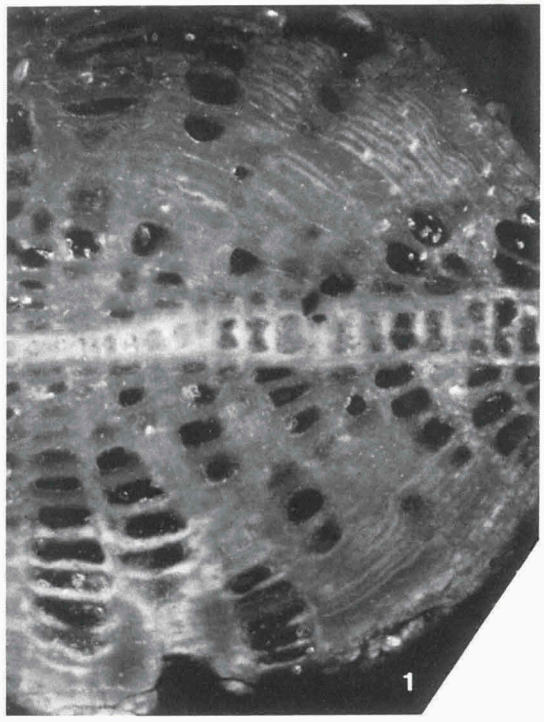
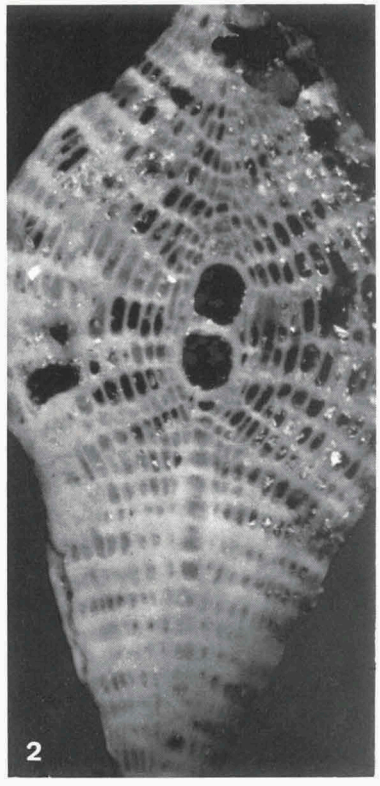
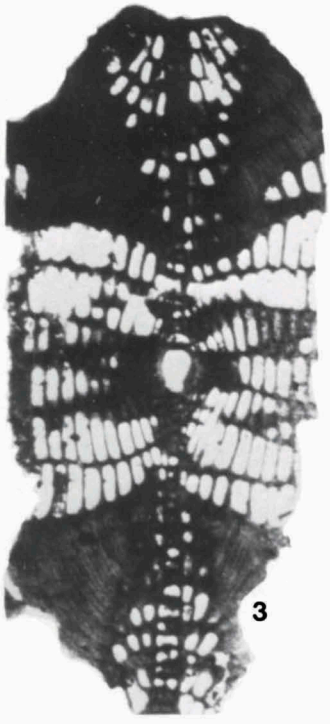


Plate 22







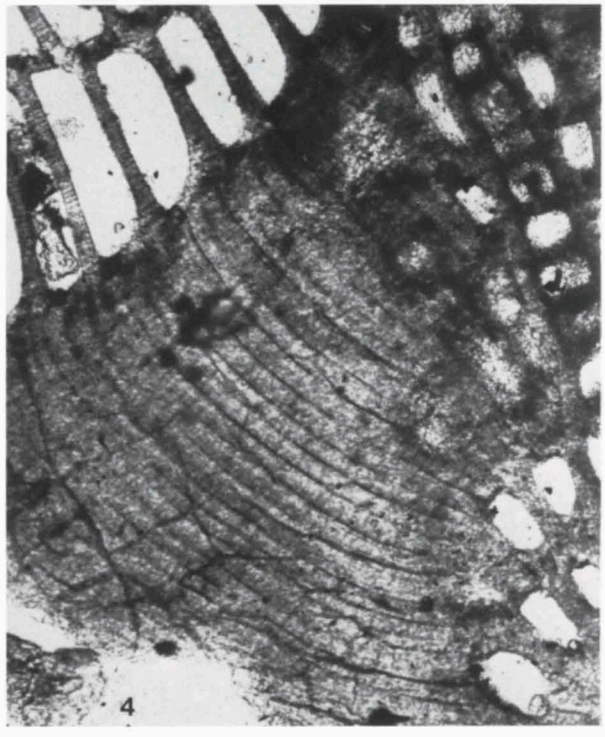
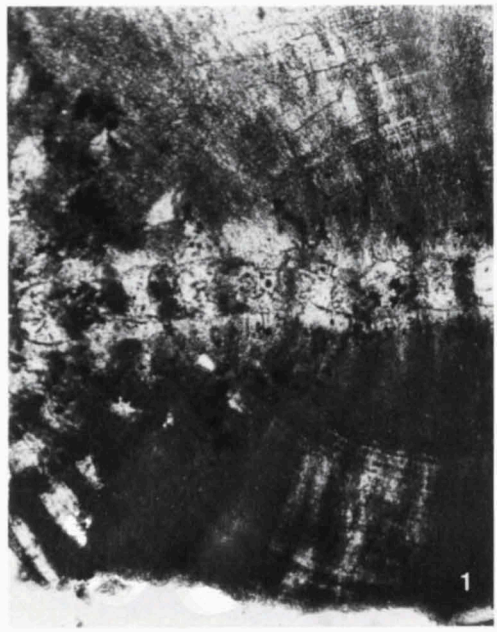
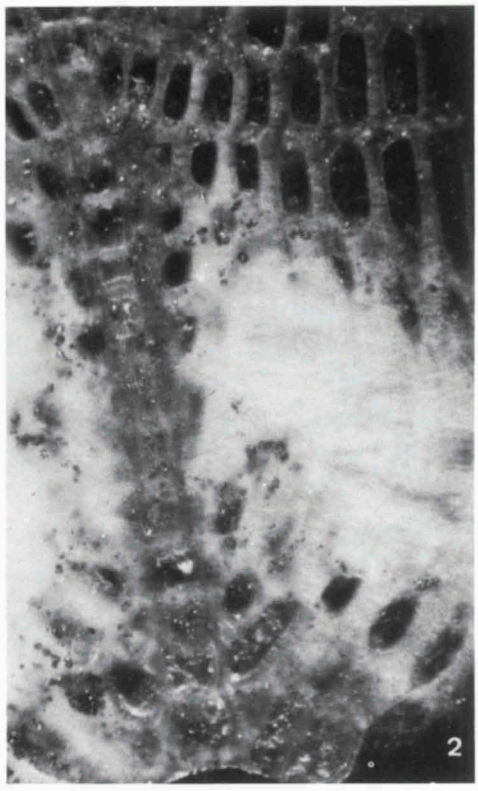
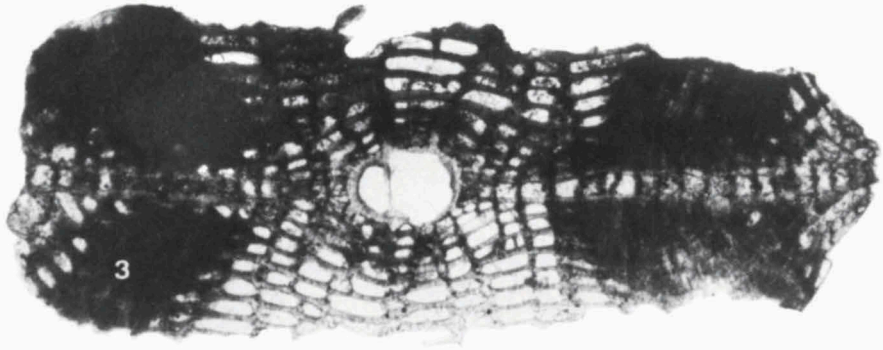


Plate 23







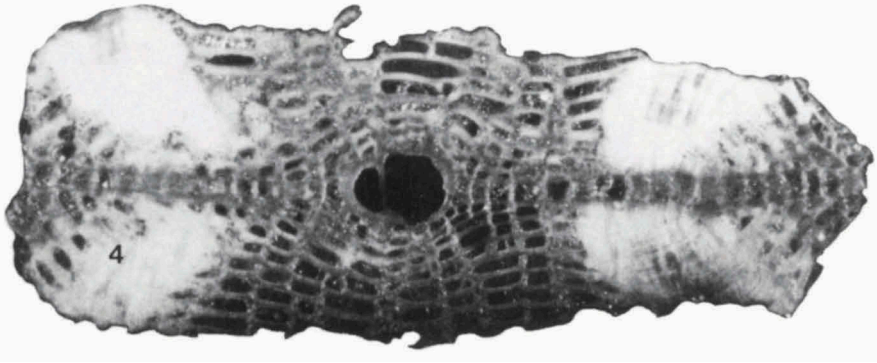


Plate 24

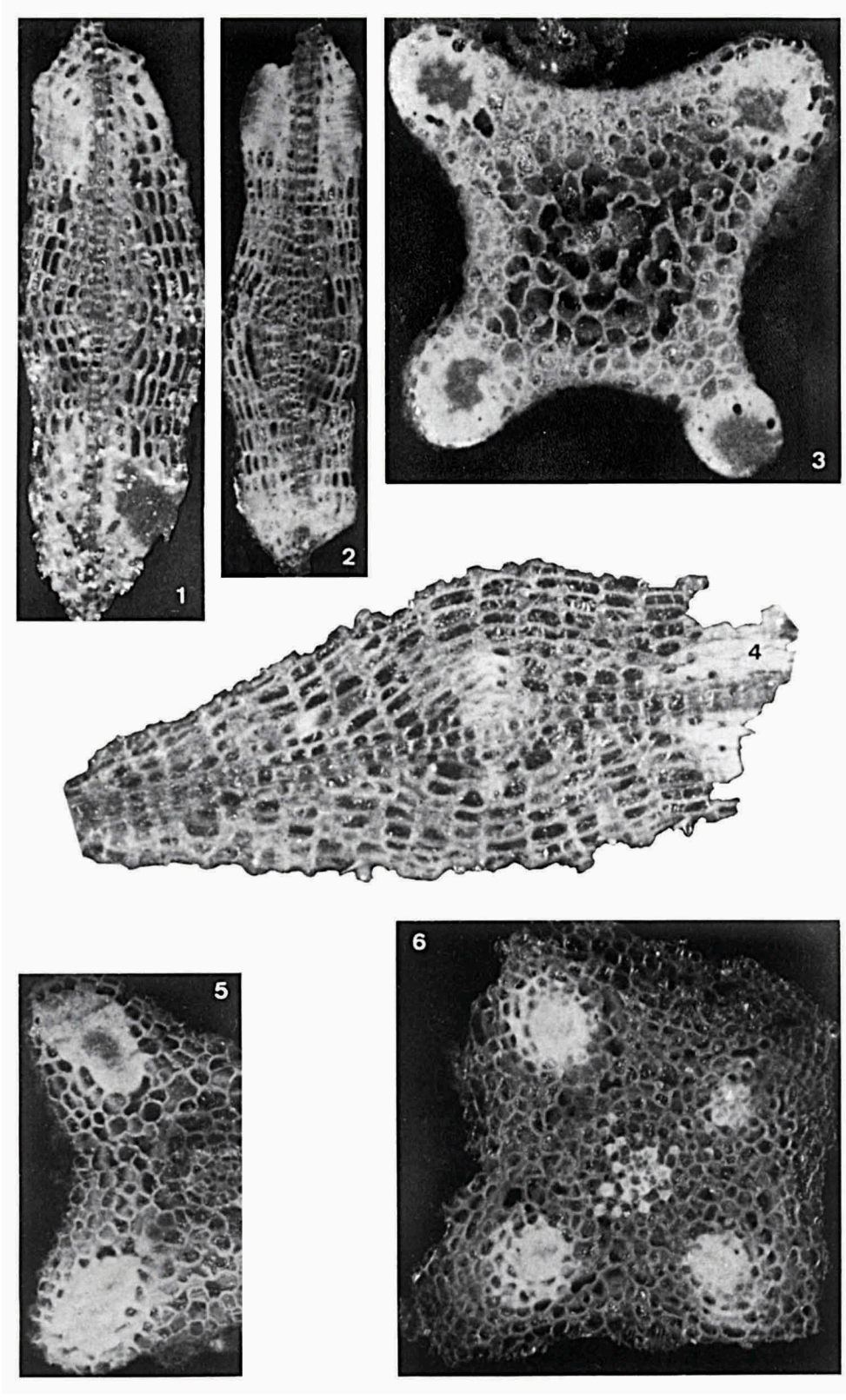
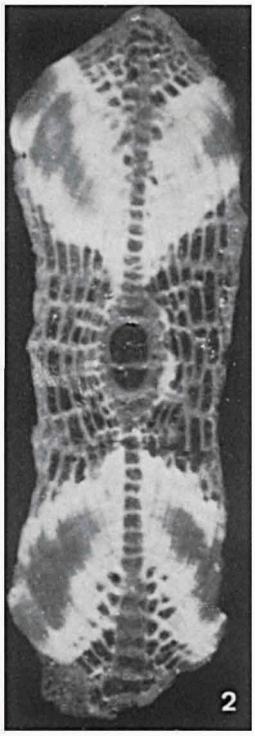
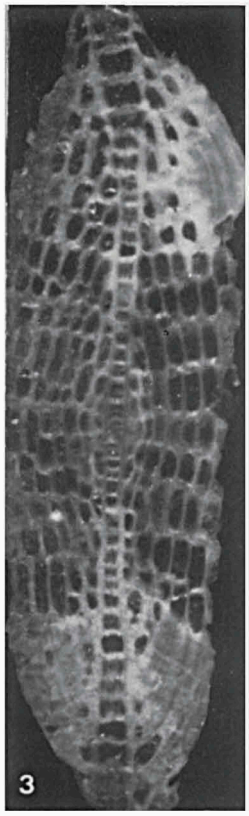
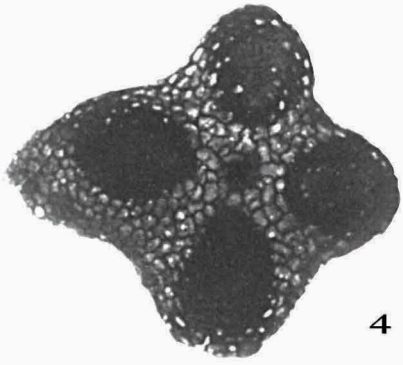


Plate 25







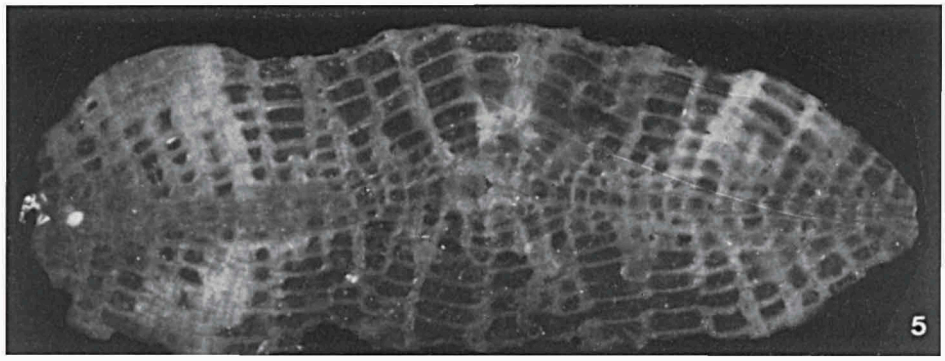


Plate 26