

# Studies on some *Miogypsinoïdes-Miogypsina* s.s. associations with special reference to morphological features

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Bock, J. F. de. Studies on some *Miogypsinoïdes-Miogypsina* s.s. associations with special reference to morphological features. Scripta Geol., 36 : 1-137, 61 figs., 44 pls., Leiden, August 1976.

The primary differentiation within the genus *Miogypsina* is based on features seen in vertical sections. The subgenus *Miogypsinoïdes* lacks lateral chambers and the equatorial plane is covered on each side by zones of massive laminae, whereas the subgenus *Miogypsina* has well-developed lateral chambers on each side of the equatorial layer. *Miogypsinoïdes* shows an intraseptal canal system, due to the presence of a toothplate and a septal flap which are not found in *Miogypsina* s.s. Several samples contained specimens which show the possible transition from *Miogypsinoïdes* to *Miogypsina* s.s. The disappearance of the septal flap and the toothplate in *Miogypsina* was probably simultaneous with the appearance of lateral chambers. It seems that the existence of lateral chambers precluded the presence of an intraseptal canal system.

The equatorial chambers of *Miogypsinoïdes* have a simple stolon system, whereas the equatorial chambers of *Miogypsina* show a more complex stolon system. With the appearance of the lateral chambers the stolon system became more complex. The diameter of the protoconch of *Miogypsinoïdes* is generally larger than that of *Miogypsina* s.s. This difference is less striking in the stratigraphically older samples.

Several morphological features and microstructures are described in detail, such as the canal systems, the stolon system, the protoconchal stolon, the growth of the equatorial chambers, and the free nucleoconches of *Miogypsinoïdes* and *Miogypsina* s.s.

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## Chapter I.

### INTRODUCTION

The differentiation between *Miogypsinoides* and *Miogypsina* s.s. as well as possible transitions forms the main subject of this thesis. Miogypsinidae were studied from six well-known localities. The samples come from Baron (Freudenthal, 1969), Christus (Drooger, Kaasschieter & Key, 1955), Estoti (Drooger, 1964) and Carry le Rouet, all in France. One sample from Larat (van der Vlerk, 1966) and some samples from Madura were used (van der Vlerk & Postuma, 1967; Drooger & Schipper, 1974).

The material from France included some early *Miogypsinoides-Miogypsina* s.s. associations of *M. formosensis* and *M. basraensis* as well as *M. bantamensis* and *M. gunteri*. Thus the material provided an opportunity to study various morphological features that accompanied the development of early representatives of *Miogypsina* s.s., and their relationships with the earlier *Miogypsinoides*. The material from Larat is known to contain *M. dehaartii* and *M. borneensis* with transitional forms showing the stages of development between *Miogypsinoides* and *Miogypsina* s.s. (van der Vlerk, 1966). The samples from Madura comprised an assemblage of younger *Miogypsina* – *M. antillea* (van der Vlerk & Postuma, 1967; Drooger & Schipper, 1974) – that resulted in a thorough investigation of the embryo, the stolon system and the growth of the test.

The samples from Madura and a sample from Estoti contained well-preserved nucleocoenoches of *Miogypsina* s.s. and *Miogypsinoides*. In morphological investigations of the Rotaliidea little attention has been paid as yet to the various morphological features which in general are different from those of Miogypsinidae. Smout (1954, 1955) gave only a simplified model of the test growth for Rotaliidea, and barely considered the Miogypsinidae. Reiss (1957-1967) compared the morphological description of various features within Rotaliidea with characteristics of Miogypsinidae known from the literature. A close look at the morphology and the microstructures of the test of Miogypsinidae may reveal the origin of various features of Miogypsinidae and as a result their possible relationship with rotaliid ancestors. Many authors have already stated that for taxonomy the microstructures as well as the way in which the animal grew are most important.

### *Acknowledgements*

The author is greatly indebted to the late Professor I. M. van der Vlerk, who stimulated this research almost to the end. The author is very grateful to Mr O'Herne for his interest and the valuable suggestions offered during many fruitful discussions in the course of the investigations as well as his critical reading of the manuscript. I wish to express my gratitude to Drs. A. C. van Ginkel, J. H. Germe-raad and D. S. N. Raju for correcting and discussing the manuscript. I am indebted to Professor C. W. Drooger, who kindly provided the excellent material from France.

Special thanks go to Messrs W. C. Laurijssen and W. A. M. Devillé for the excellent micrographs and to Messrs H. Kammaraat and F. P. van Sandij, the S.E.M. technicians at the Institute of Geology and Mineralogy, University of Leiden. The perfect drawings were made by Mr J. Bult. Last but not least I have

to thank many members of the technical and administrative staffs at the Institute of Geology and Mineralogy in Leiden as well as at the National Museum of Geology and Mineralogy.

#### PREPARATION TECHNIQUES

When possible at least 30 specimens per sample were investigated. The shape of each test was described and the thickness (T), diameter (D), width (d), and the distance from the apex to the thickest part (t) were measured (Fig. 5).

Three techniques were used to study the internal features: (1) microradiographs were taken of those specimens which had only a few layers of lateral chambers or no lateral chambers at all (see below), (2) specimens not suitable for radiographs were sectioned horizontally or vertically, (3) specimens which could be split with a needle were studied by scanning electron microscopy (S.E.M., Cambridge Instruments).

Some specimens from samples from Madura were exceptionally suitable for the study of the interior. The cavities in these specimens are completely filled with chamosite; when the test is dissolved in hydrochloric acid a perfect negative of the interior is obtained. The specimens which were radiographed horizontally were subsequently sectioned vertically to compare the vertical and the horizontal features.

A great advantage of the X-ray technique is that the internal features can be studied without damaging the specimen. Drawings of the embryonic apparatus were made by using the microradiographs and in case of thin sections by means of a camera lucida with a Leitz microscope. Half-sectioned specimens were not used because it is impossible to enlarge such a section more than 100 times. When specimens are recrystallized, or when the chambers are infilled with secondary calcareous material, it is practically impossible to determine the shape and position of the chambers.

#### *The X-ray technique*

Specimens which are suitable for microradiographs are either small, or without or with only a few lateral chambers. Moreover there should be little or no recrystallization and the cavities should not be filled with secondary material.

The microradiographs were made with a nonius G.P. camera (Enraf Instruments, Delft, Holland). For this study the camera was changed slightly (Fig. 1). A circular copper plate which fits with great precision in the camera was provided with two pillars in which the slide can be mounted between a copper plate with an opening and the photographic plate. The plane of the slide is perpendicular to the X-ray beam. The available area is about 225 mm<sup>2</sup>; the diameter of the opening in the copper plate is 17 mm.

A slide is prepared by mounting several specimens with cellotape on a piece of hard plastic (thickness 0.5 mm). Depending upon the size of specimens, up to 50 specimens can be 'photo-sectioned' at a time. The taped side of the slide is pressed against the photographic plate. The exposure time varies from three minutes for small specimens (0.5 mm) to 20 minutes for large specimens (3 mm). The thickness on the lateral sides of the test forms the main criterion for the exposure time. The photographic plate is developed in about two minutes. The sensitive layer is protected afterwards with permount and glass.

The advantages of this technique are the large number of sections available in a few minutes and the lack of damage to the specimens in the slide. The micro-radiographs show the presence of lateral chambers in *Miogypsina* s.s. (visible as thin lines covering the equatorial chambers) and the intraseptal canal system in *Miogypsinoidea* (Pls. 1, 2, 43).

For the explanation of the symbols used in the figures and plates, see the foldout page

#### TERMINOLOGY

The terms used most frequently are defined below, other terms are explained at the beginning of the appropriate chapter.

#### *Apex* (A, Fig. 4)

In specimens with an eccentric embryonic apparatus, the apex is generally the area where the embryonic apparatus is situated. Externally this is the pointed part of the usually trigonal test.

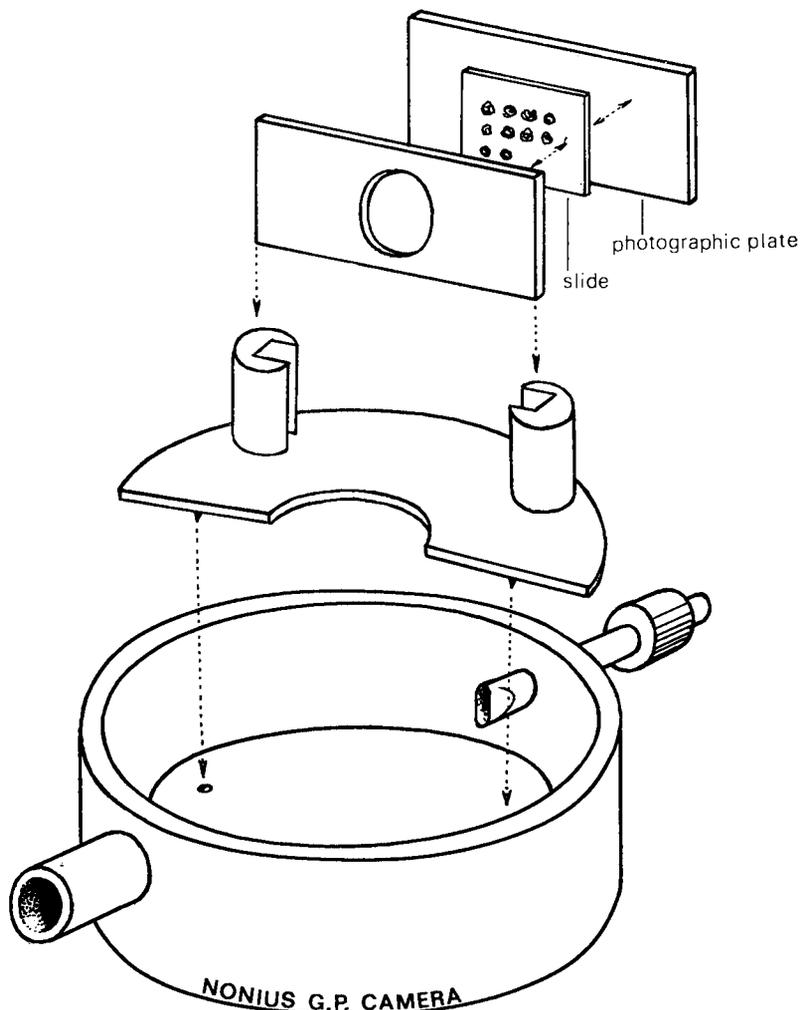


Fig. 1. The camera used to make the microradiographs.

*Marginal fringe* (MF. Fig. 3)

The marginal fringe is a zone of truncated cones at the apex of the test.

*Nucleoconch* (Pls. 15-18)

In macrospherical *Miogypsinidae*, the nucleoconch is restricted to the protoconch (I) and the deutoconch (II), i.e. the nucleoconch is bilocular. The study of the nucleoconch in microspheric *Miogypsinidae* was outside the scope of the present study.

*The first and the second primary auxiliary chamber* (PA-I and PA-II, Fig. 2)

In uniserial specimens PA-I is the first chamber formed after I and II. In biserial, triserial and quadriserial specimens a chamber is formed on either side of I and II: PA-I and PA-II. PA-II is situated near the protoconchal stolon (PS). Both auxiliary chambers lie in the equatorial plane.

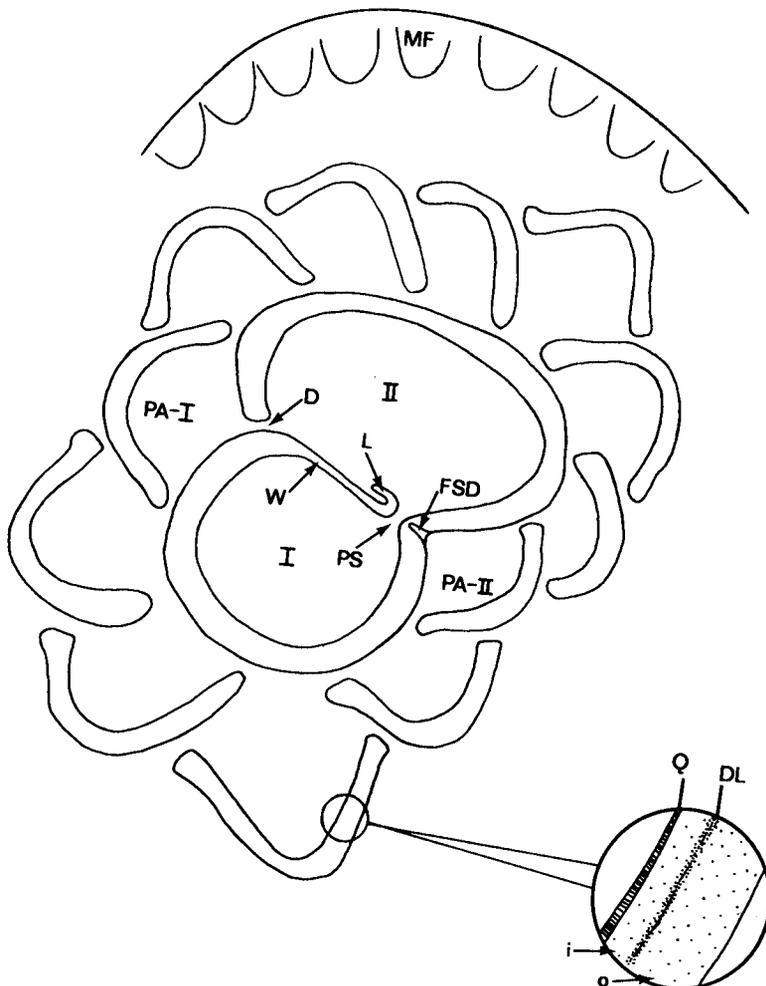


Fig. 2. A quadriserial embryonic-nepionic apparatus.

*Embryonic-nepionic apparatus* (juvenarium) (Figs. 2, 4)

This is a group of chambers at the centre, often at the apex of the megalospheric test; they differ in shape and arrangement. In the uniserial *Miogypsinidae* the embryonic-nepionic apparatus consists of the protoconch (I), the deuteroconch (II) and the row of peri-embryonic chambers starting from the first primary auxiliary chamber (PA-I). In the biserial, triserial and quadriserial *Miogypsinidae* the embryonic-nepionic apparatus consists of I, II, PA-I, PA-II and the two or more whorls which surround I and II and originate from PA-I and PA-II.

*Protoconchal stolon* (PS, Figs. 2, 4)

The protoconchal stolon is a stolon between I and II. In equatorial section the protoconchal stolon is not located in the centre of the wall (W) between I and II, but lies close to the PA-II. The stolon forms a lip (L).

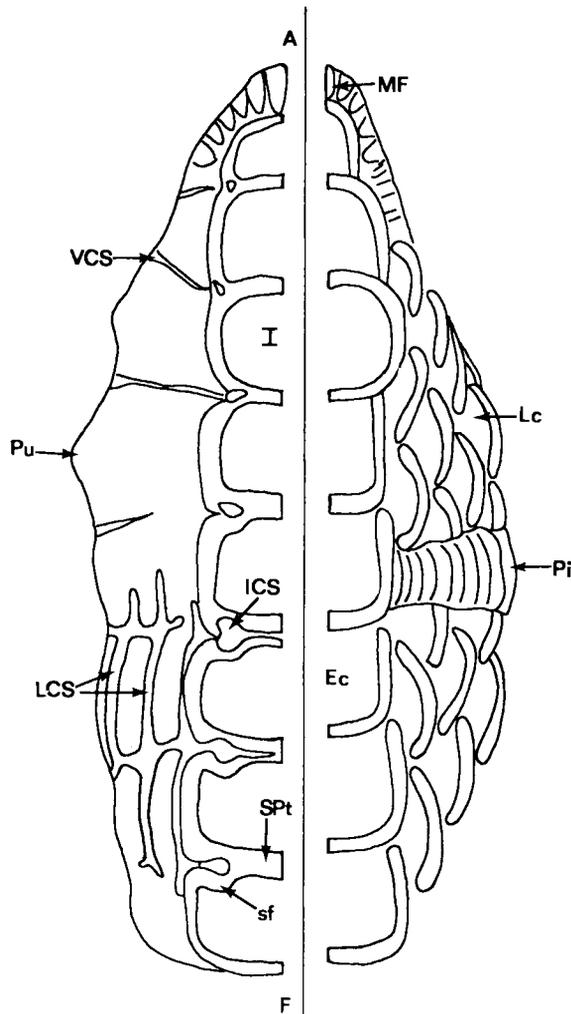


Fig. 3. Vertical section. Half of a *Miogypsinoides* and half of a *Miogypsina* s.s.

*Lip* (L, Figs. 2, 4)

An elevated 'collar' which completely surrounds the protoconchal stolon. This lip is not homologous to the apertural lips observed in several genera of the Rotaliidea.

*Funnel-shaped deutoconchal stolons* (FSD, Fig. 2)

Two funnel-shaped stolons extending from the deutoconch to PA-II on either side of the cylindrical protoconchal stolon (de Bock, 1973).

*Aperture* (Ap, Fig. 11)

The opening at the base of the apertural face. This term is strictly limited to the terminal chamber; a similar opening between two successive chambers is named the *intercameral foramen* or *stolon*.

*Proximal and distal stolon* (PSt and DSt, Fig. 4)

The proximal stolon (PSt) in the spiral chamber is the one at the base of the distal face, close to the protoconch; the distal stolon (DSt) lies between the distal chamber wall and the distal face of the preceding chamber.

*Pores* (P, Fig. 29)

Tubular cavities of small diameter perpendicular to the lamination (Chapter IV, p. 24); they are distinct from stolons, apertures and canals. As defined by Banner and Williams (1973) a pore is a tunnel in a calcareous test which connects the perforations on the external and internal surfaces.

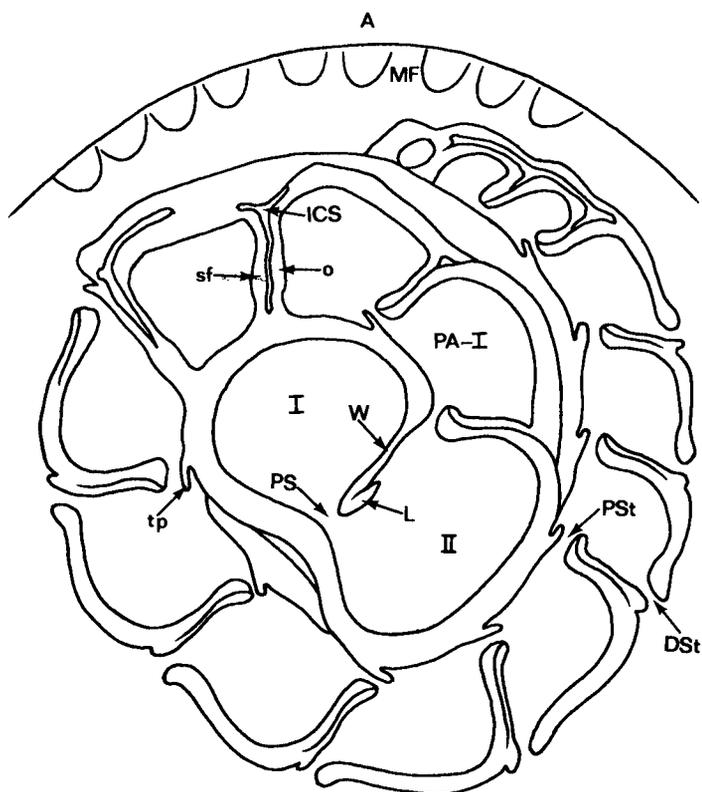


Fig. 4. An uniserial embryonic-nepionic apparatus.

*Perforations* (Fig. 29)

According to Banner and Williams (1973) the numerous openings covering the surface of the chamber walls should be named perforations. There are external and internal perforations.

*Tubules* (Tu, Pl. 37)

Each pore is coated with a discrete structure which forms an inner tube: the tubule.

*Transverse and vertical sections* (Fig. 2)

A vertical section in the present paper is an apical-frontal section through the protoconch perpendicular to the equatorial plane. Any other section perpendicular to the equatorial plane is a transverse section.

*Intraseptal, vertical and lateral canal systems* (ICS, VCS and LCS, Fig. 3)

The intraseptal canal system is formed only on one of the lateral sides, i.e. the ventral side of the equatorial chambers. The intraseptal canal system has vertical branches extending into the dorsal and the ventral side of the test: the vertical canal system. The intraseptal canal system is repeated several times, but only on the ventral side of the test, parallel to the intraseptal canal system. The repetitions are referred to as the lateral canal system.

*Ventral and dorsal side* (Ve and Do, Fig. 3)

As in the Rotaliidea, the lateral side of *Miogypsinoides* which contains the canal system is named the ventral side, the opposite is the dorsal side.

*Toothplate* (tp, Figs. 12, 22)

Toothplate (Reiss, 1963; 'axial plate' of Cifelli, 1962; 'umbilical plate' of Pervati, 1971; 'foraminal plate' of Hansen and Reiss, 1971). In *Miogypsinoides* the toothplate, sometimes highly developed, is an often elongated plate attached along the proximal side of the distal face, at the base of the distal face and at the base of the apertural face.

*Septal flap* (sf, Fig. 3)

Posterior element of the primary chamber wall. In this paper it is referred to as the imperforate extension of the toothplate along the apertural face of each chamber of *Miogypsinoides*, together with the primary wall forming the secondarily-doubled septum between the chambers.

*Dark line* (DL, Fig. 2)

In many Foraminifera belonging to the suborder Rotaliina a dark line is seen in the wall of the equatorial chambers. Many authors believe it to be a canal (see Chapter IV, p. 24. However this dark line, which can also be seen in vertical section, appears to be related to a phase of growth of the wall. It separates the inner lamella and the outer lamella (Reiss, 1963; Neumann, 1972).

*Coating* (Q, Fig. 2)

In thin sections the dark inner layer of the chamber wall proved to be a coating of microcrystalline material (de Bock, 1973, pl. 4)

## PARAMETERS

The classification of the Miogypsinidae in this paper is based mainly on internal features. For each specimen we noted the following specifications.

*External* (Fig. 5)

Before the specimens were sectioned, several features were described and the

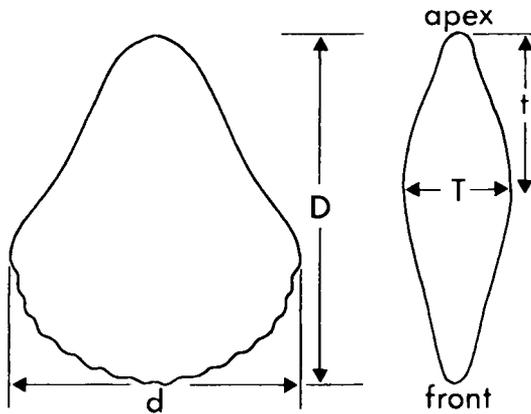


Fig. 5. External parameters.

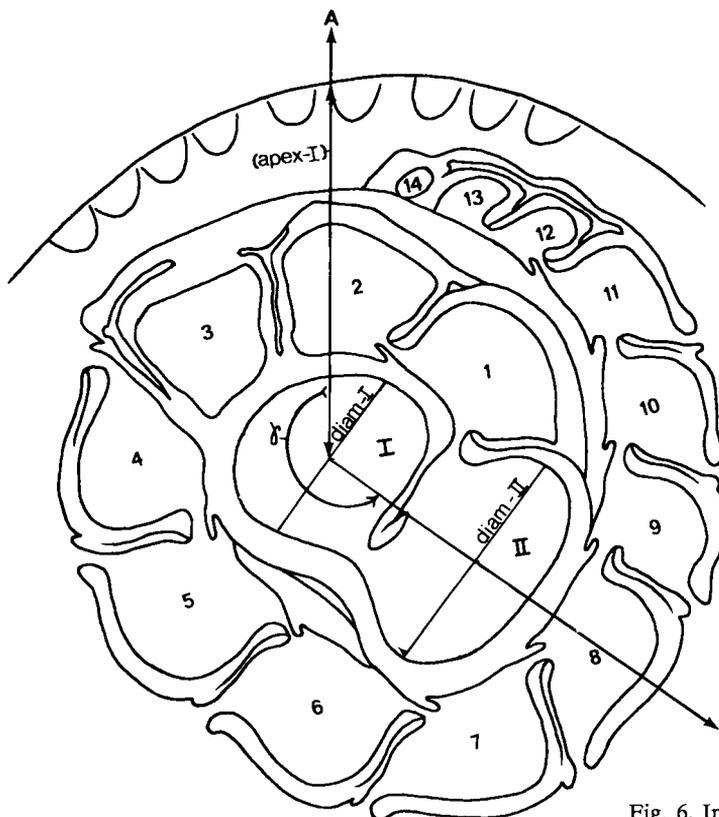


Fig. 6. Internal parameters.

following measurements were taken:

length (D) = the distance from the apex to the front,

width (d) = the greatest diameter perpendicular to D,

thickness (T) = the thickest part perpendicular to the equatorial plane,

(t) = the distance from the apex to the thickest part of the test (T).

*Internal* (Fig. 6)

X = the number of spiral chambers in the first whorl including PA-I.

Diam. I = the diameter of the protoconch; Diam. II = the diameter of the deuteroconch: actually the largest diameter of II that is parallel to the line taken as the diameter of the protoconch.

Apex-I = the distance from the apex to the centre of the protoconch.

$\gamma$  = the angle between the line from apex to front and the line connecting the centres of I and II (Drooger & Amato, 1969).

## Chapter II. Localities and samples

ESTOTI, FRANCE

### *Locality*

This is a locality in the southern part of the Aquitaine Basin, some 4 km NW of Saint-Paul-les-Dax. The abandoned quarry is situated on the right-hand side of the Herrere Valley, immediately south of the secondary road and below the farmhouse called Estoti; it is marked on the topographical map Mont-de-Marsan SO, 1 : 50 000. The material was collected by Drooger (see Drooger & Freudenthal, 1964).

FR1117 was taken from the most westerly outcrop. The other three samples were taken from a short succession of strata at an outcrop farther to the east. Stratigraphically FR1118 is approximately 1.0 m above FR1117; FR1119 is 1.9 m above FR1118 and FR1120 is 0.5 m above FR1119.

### *Material*

FR1117. The specimens are poorly preserved, often highly recrystallized; only a very few were suitable for microradiography. The specimens could be split into two different groups on the basis of external features. One group had well-preserved ornamentation on the outer surface, such as pustules and striae. The other group consisted of rounded specimens without ornamentation. The shape of the equatorial chambers is clearly visible in both groups. This difference in appearance may be due to transport.

*Nepionic arrangement* – uniserial. In *Miogypsinoides*  $X \leq 19$ ; in *Miogypsina* s.s.  $X \leq 17$ .

*Determination* – *Miogypsina* (*Miogypsinoides*) *bantamensis*, *Miogypsina* (*Miogypsina*) *septentrionalis*.

*Age* – Aquitanian.

FR1118. The specimens are well-preserved; only a few specimens show recrystallization. The thin and somewhat larger specimens show the position of all chambers and belong to *Miogypsinoides*. They could be separated from the smaller specimens which clearly show that the lateral chambers cover the equatorial chambers.

*Nepionic arrangement* – uniserial. In *Miogypsinoides*  $X \leq 22$ ; in *Miogypsina* s.s.  $X \leq 18$ .

*Determination* – *Miogypsina* (*Miogypsinoides*) *bantamensis*, *Miogypsina* (*Miogypsina*) *basraensis*.

*Age* – Aquitanian.

FR1119. This sample contained only very small and fragile specimens, which were suitable for microradiography.

*Nepionic arrangement* – uniserial. In *Miogypsinoides*  $X \leq 16$ ; in *Miogypsina* s.s.  $X \leq 17$ .

*Determination* – *Miogypsina* (*Miogypsinoides*) *bantamensis*, *Miogypsina* (*Miogypsina*) *gunteri*.

*Age* – Aquitanian.

#### CHRISTUS 1 AND 2, FRANCE

##### *Locality*

In the southern part of the Aquitaine Basin, Miogypsinidae were collected at Christus (near Dax) by Drooger, Christus 2 is 1.5 m above Christus 1. The age based on the content of smaller Foraminifera is at variance with the age based on Miogypsinidae (see Drooger, Kaasschieter & Key, 1955).

##### *Material*

The samples contained numerous well-preserved specimens, which could be split into *Miogypsinoides* and *Miogypsina* s.s.

*Nepionic arrangement* – uniserial. In *Miogypsinoides* from Christus 1,  $X \leq 25$ ; from Christus 2,  $X \leq 22$ . In *Miogypsina* s.s. from Christus 1,  $X \leq 21$  and from Christus 2,  $X \leq 20$ .

*Determination* – *Miogypsina* (*Miogypsinoides*) *formosensis*, *Miogypsina* (*Miogypsina*) *septentrionalis*.

*Age* – Burdigalian-Aquitanian.

#### BARON, FRANCE

##### *Locality*

Baron is a locality near Christus (see Drooger, Kaasschieter & Key, 1955; Freudenthal, 1969: sample A88).

##### *Material*

FR1121. The specimens are very small. The main spiral is probably not completely developed in all specimens. The specimens show distinct ornamentation and are suitable for microradiography. Specimens belonging to the subgenus *Miogypsina* were not found. Only the larger specimens were used.

*Nepionic arrangement* – uniserial. In *Miogypsinoides*  $X \leq 19$ .

*Determination* – *Miogypsina* (*Miogypsinoides*) *formosensis*.

*Age* – Chattian.

## CARRY LE ROUET, FRANCE

The sections (planches) mentioned in the description of the following samples are from the C.R. Ve Congrès du Néogène méditerranéen, vol. III (Bull. Recherches Géol. Minières, 2, 1, 1972).

*Locality*

West of Marseille along the coast near the small port of Carry le Rouet the Aquitanian deposits are rich in Bivalvia, Gastropoda, Cephalopoda, Bryozoa, Foraminifera, etc. From these deposits five samples were selected which contained some Miogypsinidae.

*Material* (Pls. 3-6)

The specimens are generally well-preserved, especially those of M64 and M75 which are suitable for scanning slides. As the chambers are free of secondary material, all specimens are suitable for microradiography. In all samples *Miogypsinoides* could be distinguished from *Miogypsina* s.s. Nearly all specimens are uniserial, with a spiral chamber or the first primary auxilliary chamber (PA-I) at the apex. In a few specimens the deuteroconch is at the apex.

Anse deï Bano (Section 1, op.cit.)

Samples M64 and M75 are from level 15 of section 16 (op.cit.): a level with large *Lepidocyclina*. The horizontal distance between the two samples is 20 m. Sample M61 was taken 70 cm above M64. Clay lenses intercalated in the hard rock contained many free specimens of *Lepidocyclina* and *Miogypsina*. The specimens are well-preserved (Pl. 5).

*Nepionic arrangement* – uniserial. In *Miogypsinoides*  $X \leq 14$ ; in *Miogypsina* s.s.  $X \leq 16$ .

*Determination* – *Miogypsina* (*Miogypsinoides*) *bantamensis*, *Miogypsina* (*Miogypsina*) *gunteri*.

*Age* – Late Aquitanian.

Cap de Nautes (Section 1, op. cit.)

Sample M81. The sample was taken east of Carry le Rouet and corresponds with level 9 of section 15 and 16 (op. cit.). Only a few *Lepidocyclina* and *Miogypsina* were found.

*Nepionic arrangement* – uniserial. In *Miogypsinoides*  $X \leq 16$ ; only two specimens of *Miogypsina* s.s.:  $X = 12$  and 18.

*Determination* – *Miogypsina* (*Miogypsinoides*) *bantamensis*.

*Age* – Middle Aquitanian.

Calanque de Petit Nid (section 1, op. cit.)

Sample M51. The sample was rich in large *Lepidocyclina*; it corresponds with level 8 (R1) of section 15 and 16 (op. cit.).

*Nepionic arrangement* – uniserial. In *Miogypsinoides*  $X \leq 17$ ; in *Miogypsina* s.s.,  $X \leq 16$ .

*Determination* – *Miogypsina* (*Miogypsinoides*) *bantamensis*, *Miogypsina* (*Miogypsina*) *gunteri*.

*Age* – Early Aquitanian.

## KOMBANGAN, MADURA, INDONESIA

*Locality*

From sections through Oligocene and Miocene sediments of East Java and Madura, both the *Lepidocyclus* and the planktonic Foraminifera were examined by van der Vlerk and Postuma (1967); additional data on *Cycloclypeus* and some *Miogypsinidae* were published by van der Vlerk and O'Herne (1971), and the *Miogypsina* have been described in detail by Drooger and Schipper (1973). The outcrops are situated along the northern coast of East Java and Madura (see van der Vlerk & Postuma, 1967, fig. 1). In this paper a few samples from the Kombang section were used.

*Material*

The samples examined contain a well-preserved fine fraction. All inner and outer features are distinct. Some of the specimens provided an exceptional opportunity to study the interior. The cavities of these specimens are filled with chamosite: when the test is dissolved in HCl a perfect negative of the interior remains (see also O'Herne, 1974). The samples from this locality were selected on the basis of the preservation of the specimens and the presence of free nucleocoches of *Miogypsina* s.s. Specimens which could be assigned to the subgenus *Miogypsinoides* were not found.

*Determination* – Drooger and Schipper, 1973, assigned the specimens to *Miogypsina* (*Miogypsina*) *cushmani* or *Miogypsina* (*Miogypsina*) *antillea*.

*Age* – Burdigalian.

Sample	N	X			N	$\gamma^\circ$			N	Diam. I	
		Range	Mean $\pm$ $\sigma$ m			Range	Mean $\pm$ $\sigma$ m			Range	Mean $\pm$ $\sigma$ m
M. 61	17	7-17	10.5 $\pm$ 0.6		15	-196- 0	-90.7 $\pm$ 15.7		14	146-260	192 $\pm$ 9.4
M. 75	26	7-13	9.5 $\pm$ 0.4		25	-194- 0	-71.6 $\pm$ 9.1		27	151-296	216 $\pm$ 6.2
M. 64	45	7-14	9.9 $\pm$ 0.3		44	-166- -15	-80.7 $\pm$ 6.5		41	124-297	203 $\pm$ 6.0
M. 81	14	8-16	12.1 $\pm$ 0.6		15	-308- -8	-130.4 $\pm$ 18.8		15	94-239	160 $\pm$ 8.9
M. 51	22	8-17	11.9 $\pm$ 0.4		18	-235- -44	-132.2 $\pm$ 12.1		20	73-198	133 $\pm$ 9.3
FR 1120	45	8-17	12.2 $\pm$ 0.3		44	-310- -25	-156.1 $\pm$ 10.5		44	74-208	126 $\pm$ 4.2
FR 1119	16	8-16	11.0 $\pm$ 0.6		15	-244- 0	-105.9 $\pm$ 19.0		15	94-244	135 $\pm$ 8.2
FR 1118	30	8-22	11.7 $\pm$ 0.5		29	-305- -31	-129.7 $\pm$ 10.3		23	104-198	138 $\pm$ 4.7
FR 1117	23	7-19	13.0 $\pm$ 0.6		21	-340- -77	-196.9 $\pm$ 16.5		23	47-213	110 $\pm$ 3.5
Christ 2	36	10-22	14.9 $\pm$ 0.4		36	-350- -112	-219.6 $\pm$ 10.6		36	94-182	130 $\pm$ 3.5
Christ 1	27	9-25	14.7 $\pm$ 0.6		16	-415- -46	-208.7 $\pm$ 15.0		27	89-198	136 $\pm$ 5.5
Baron	16	13-19	16.8 $\pm$ 0.5		27	-360- -163	-265.7 $\pm$ 15.7		16	68-135	92 $\pm$ 4.2

Sample	N	X			N	$\gamma^\circ$			N	Diam. I	
		Range	Mean $\pm$ $\sigma$ m			Range	Mean $\pm$ $\sigma$ m			Range	Mean $\pm$ $\sigma$ m
M. 61	11	7-13	10.3 $\pm$ 0.6		11	-250- -20	-94.6 $\pm$ 20.0		11	73-146	111 $\pm$ 6.8
M. 75	62	6-14	9.1 $\pm$ 0.3		63	-207- +7	-88.8 $\pm$ 0.6		63	84-198	105 $\pm$ 2.5
M. 64	71	6-16	10.5 $\pm$ 0.3		68	-208- -11	-105.1 $\pm$ 6.5		72	27-216	114 $\pm$ 3.4
M. 81	2	12+18	15.0 $\pm$ 3.0		2	-349+ -120	-234 $\pm$ 114.5		2	89+125	107 $\pm$ 18.8
M. 51	25	9-16	11.6 $\pm$ 0.4		22	-202- -90	-147.3 $\pm$ 8.1		18	73-151	106 $\pm$ 4.9
FR 1120	31	9-20	12.5 $\pm$ 0.5		31	-360- -90	-182.7 $\pm$ 13.4		31	57-140	91 $\pm$ 3.5
FR 1119	21	9-17	12.5 $\pm$ 0.6		21	-295- -46	-178 $\pm$ 13.7		21	52-120	83 $\pm$ 3.6
FR 1118	17	8-18	13.2 $\pm$ 0.8		15	-360- -100	-195 $\pm$ 20.0		15	63-115	88 $\pm$ 4.2
FR 1117	13	11-17	14.5 $\pm$ 0.5		13	-360- -90	-239.4 $\pm$ 18.9		13	57-99	80 $\pm$ 3.9
Christ 2	19	11-20	14.8 $\pm$ 0.6		19	-360- -126	-217.3 $\pm$ 16.5		19	65-120	90 $\pm$ 3.8
Christ 1	20	12-20	15.8 $\pm$ 0.5		20	-350- -146	-249.5 $\pm$ 13.5		20	68-104	89 $\pm$ 2.5
Baron	—	—	—		—	—	—		—	—	—

### Chapter III. Taxonomy

Family MIOGYPSINIDAE Vaughan, 1928  
 Genus *Miogypsina* Sacco, 1893  
 Subgenus *Miogypsinoidea* Yabe & Hanzawa, 1928

*Miogypsina (Miogypsinoidea) formosensis* Yabe & Hanzawa, 1928

- 1930 *Miogypsina (Miogypsinoidea)* Van der Vlerk var. *formosensis* Yabe and Hanzawa — Yabe and Hanzawa, pp. 32-33  
 1963 *Miogypsina (Miogypsinoidea) formosensis* Yabe and Hanzawa — Drooger, pp. 315-349.

*Locality and samples* – Baron FR1121, Christus 1 and 2.

*Diagnosis* – Populations of *Miogypsinoidea* with  $M_X$  between 17 and 13.

*Remarks* – Small specimens from Baron in which the first spiral is probably not completely developed are assumed to be *Miogypsinoidea formosensis*. The specimens from Baron and Christus do not show the distinct lateral thickening mentioned in the original description of *Miogypsinoidea formosensis* by Yabe and Hanzawa. Raju (1973) reported that no assemblage of *Miogypsinoidea formosensis* with  $M_X$  between 16 and 14 had been found until then. For the *Miogypsinoidea* from Christus 1 and 2 however  $M_X$  is between 16 and 14 (Christus 1:  $M_X = 14.7$ ; Christus 2:  $M_X = 14.9$ ).

*Miogypsina (Miogypsinoidea) bantamensis* Tan Sin Hok, 1936  
 Pls. 1-14, 26, 33, 41.

- 1936 *Miogypsinoidea complanata* forma *bantamensis* Tan Sin Hok — Tan, pp. 48-50.  
 1963 *Miogypsina (Miogypsinoidea) bantamensis* (Tan Sin Hok), — Drooger, pp. 315-349.

*Locality and samples* – Estoti FR1117, FR1118, FR1119, FR 1120; Carry le Rouet M51, M81, M61.

*Diagnosis* – Populations of *Miogypsinoidea* with  $M_X$  between 13 and 10.

*Remarks* – The specimens from the above-mentioned localities show only a slight thickening of the lateral walls of the test. The specimens from M81 may be considered as an assemblage intermediate between *Miogypsinoidea formosensis* and *Miogypsinoidea bantamensis* (compare Drooger, 1964). The specimens from FR1119 and M61 are assumed to be an assemblage intermediate between *Miogypsinoidea bantamensis* and *Miogypsinoidea dehaartii* (compare Drooger, 1963). The name *Miogypsina bantamensis-gunteri* has also been used by Drooger (1964) to suggest an assemblage intermediate between the subgenera *Miogypsina* and *Miogypsinoidea*.

*Miogypsina (Miogypsinoidea) dehaartii* van der Vlerk, 1924  
Pls. 30, 39, 40, 42, 43.

1924 *Miogypsina dehaartii* nov. spec. — van der Vlerk, p. 430.

1953 *Miogypsina dehaartii* van der Vlerk — Drooger, pp. 110-114.

1973 *Miogypsina (Miogypsinoidea) dehaartii* van der Vlerk — Raju, pp. 80-81.

*Locality and samples* — Carry le Rouet M64 and M75.

*Diagnosis* — Populations of *Miogypsinoidea* with  $M_X$  less than 10 and a negative  $\gamma$ . Conical variants may be present.

*Remarks* — Drooger (1963) described the species of this locality as an assemblage intermediate between *Miogypsinoidea bantamensis* and *Miogypsinoidea dehaartii*. In view of the double maxima of X (Fig. 7) it may be a mixture of *Miogypsinoidea bantamensis* and *Miogypsinoidea dehaartii*.

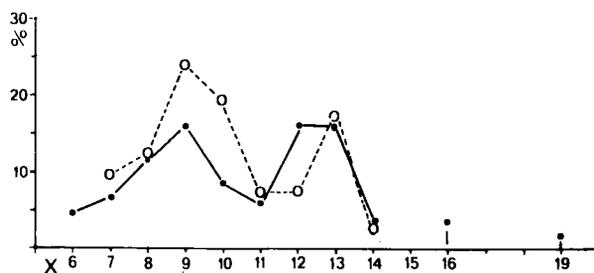


Fig. 7. The values of parameter X. Anse deï Bano, M64.

—•— = *Miogypsina gunteri*; o --- o = *Miogypsinoidea dehaartii* (N=45).

Subgenus *Miogypsina* Sacco, 1893

*Miogypsina (Miogypsina) septentrionalis* Drooger, 1960

1960 *Miogypsina (Miogypsina) septentrionalis* n.sp. — Drooger, pp. 41-45.

*Locality and samples* — Christus 1 and 2, Estoti FR1117.

*Diagnosis* — Populations of *Miogypsina* s.s. with  $M_X$  greater than 14

*Remarks* — In the sample from Christus 1 X ranges from 12 tot 21.

The assemblage may be considered as intermediate between *Miogypsina septentrionalis* and *Miogypsina basraensis*. Drooger interpreted specimens from a sample from Christus (A352a, Drooger, 1963) as an assemblage intermediate between *Miogypsinoidea formosensis* and *Miogypsinoidea bantamensis*; the occurrence of the subgenus *Miogypsina* in the same sample was not mentioned in Drooger's paper. Christus 2 and FR1117 which have a slightly higher  $M_X$  (= 14) may also be considered as an assemblage intermediate between *Miogypsina septentrionalis* and *Miogypsina basraensis*.

*Miogypsina (Miogypsina) basraensis* Brönnimann, 1940

- 1940 *Miogypsina (Miogypsina) basraensis* n.sp. — Brönnimann, pp. 1-113.  
 1952 *Miogypsina (Miogypsina) basraensis* (Brönnimann) — Drooger, p. 49.

*Locality and samples* – Estoti FR1118, and Carry le Rouet M81(?).

*Diagnosis* – Population of *Miogypsina* s.s. with  $M_x$  between 15 and 12.5.

*Remarks* – Drooger (1964) described the larger Foraminifera in a sample from Estoti as an assemblage intermediate between *Miogypsinoidea formosensis* and *Miogypsinoidea bantamensis*. The species name *M. basraensis* was used by Drooger because some transverse sections showed irregularly placed cavities in the side walls, suggesting the beginning of the development of lateral chambers. In sample FR1118 *Miogypsinoidea bantamensis* and *Miogypsina basraensis* are easily distinguished from each other. In M81 only two specimens of *Miogypsina* s.s. with  $X=12$  and  $X=18$  were present, therefore the specimens are not assigned to a species.

*Miogypsina (Miogypsina) gunteri* Cole, 1938  
Pl. 5.

- 1938 *Miogypsina gunteri* Cole — Cole, pp. 1-73.  
 1954 *Miogypsina (Miogypsina) gunteri* Cole — Drooger, pp. 227-249.

*Locality and samples* – Estoti FR1119, FR1120, Carry le Rouet M51, M61, M64 and M75.

*Diagnosis* – Populations of *Miogypsina* s.s. with  $M_x$  between 12.5 and 9.

*Remarks* – Drooger (1954, 1964) described several samples from Italy and France (Bordeaux) containing *Miogypsina gunteri*. He described (1964) an assemblage intermediate between *Miogypsinoidea bantamensis* and *Miogypsina gunteri* from Sausset (Marseille). After re-examination of the material from Sausset by the present author, it appeared possible to distinguish clearly between *Miogypsina gunteri* and *Miogypsinoidea bantamensis*. It seems justified to assign the specimens from M75 with  $M_x = 9.1 \pm 0.3$  to *Miogypsina gunteri* rather than to *Miogypsina tani*, in which  $M_x$  is less than 9.

#### Chapter IV. Morphological features and their development in *Miogypsinoidea* and *Miogypsina* s.s.

##### SIZE AND SHAPE OF THE TEST

Sample M64 from Carry le Rouet (and L20 from Larat in the Appendix) is used here to illustrate the difference in the shape and size of the tests of *Miogypsinoidea* and *Miogypsina* s.s.

The preservation of the specimens in sample M51, M61 and M81 is poor. In sample M81 only two specimens with lateral chambers have been observed. The specimens from sample M64 (and M75), however, are so well-preserved that *Miogypsinoidea* and *Miogypsina* s.s. could generally be distinguished even on the basis of external features only. This was verified in vertical sections.

Small (juvenile) to large (adult) specimens were found, the latter are approximately 3 x 4 mm (Fig. 8). At the apex the test forms a protruding knob in which the embryonic apparatus is located. The equatorial plane is often undulating or domeshaped. The pustules on the exterior of *Miogypsinoidea* lie immediately above the centres of the equatorial chambers; they become elongated towards the front. These specimens show little lateral thickening of the test. On both sides, ventral and dorsal, the position of the equatorial chambers remains visible from the outside. *Miogypsina* s.s. shows several layers of lateral chambers ornamented with pustules. The shape of the equatorial chambers is ogival to rhombic. In *Miogypsinoidea* the convex side of the test is considered as the ventral side, based on the position of the intraseptal canal system. Not a single specimen was found that showed a second primary auxiliary chamber (PA-II).

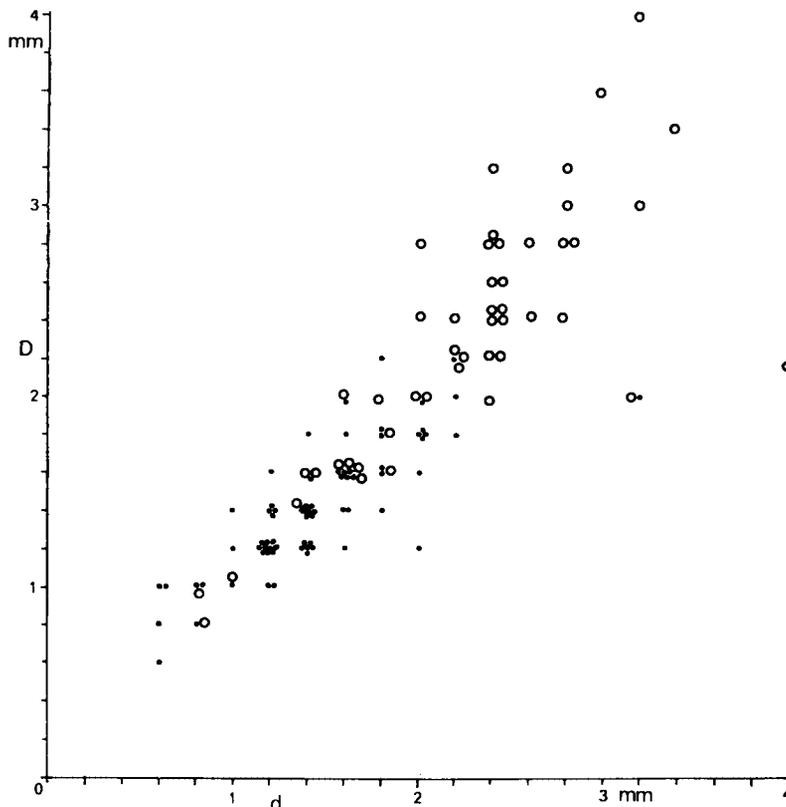


Fig. 8. Length (D) plotted against width (d). The relationship between D and d is fairly constant. The adult specimens of *Miogypsinoidea* are generally larger than those of *Miogypsina* s.s.

o = *Miogypsinoidea bantamensis* (N = 47); • = *Miogypsina gunteri* (N = 73)

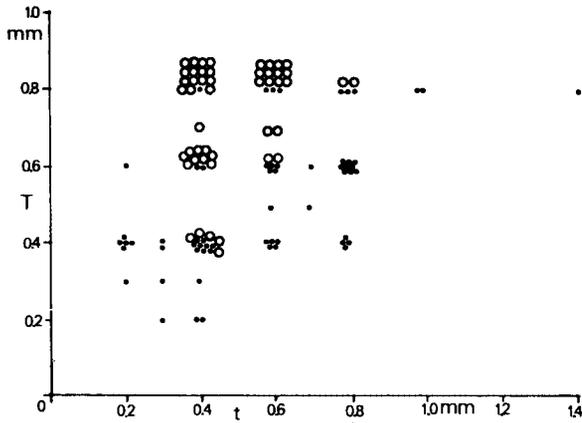


Fig. 9. Thickest part (T) plotted against the distance from the apex to the thickest part (t). Two types of lateral thickening may be distinguished: (1) Lateral chambers occur on both sides of the equatorial plane of *Miogypsina gunteri*. The lateral chambers grew from the frontal side towards the apical side (see Chapter IV, p. 62), so that the thickest part remains subcentral to central. (2) The specimens of *Miogypsinoidea bantamensis* show little or no secondary thickening of the lateral parts of the test. The shape and the position of the equatorial chambers in these specimens are visible on the exterior. The distance between apex and the thickest part of the test hardly changes. o = *Miogypsinoidea bantamensis* (N = 47); • = *Miogypsina gunteri* (N = 61).

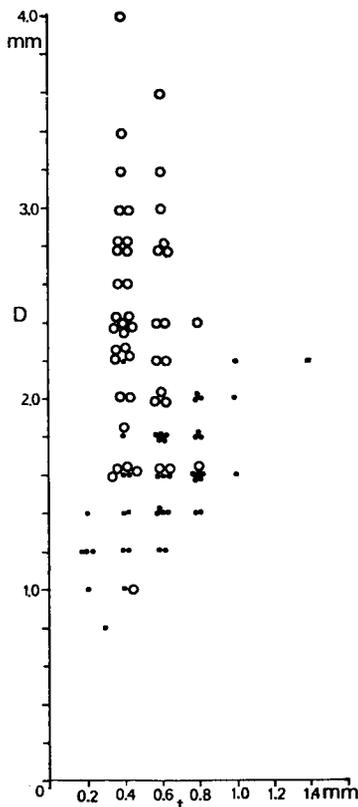


Fig. 10. The length (D) plotted against the distance from the apex to the thickest part of the test (t). In *Miogypsinoidea bantamensis* t remains fairly constant while D increases. The thickest part remains close to the apex. In *Miogypsinoidea gunteri* however the thickest part (T) moves from the apex as D increases due to the formation of the lateral chambers. o = *Miogypsinoidea bantamensis* (N=42); • = *Miogypsina gunteri* (N=47).

## TOOTHPLATE AND SEPTAL FLAP

*Terminology*

Before these structures are described some additional morphological terms are defined (Fig. 11).

*Posterior* – directed towards aperture of the spiral chamber; in direction of growth.

*Anterior* – directed away from aperture; opposite to posterior.

*Radial* – direction from pole or axis to any part of the outline of the test.

*Proximal* – towards the proloculus in the direction of growth.

*Distal* – away from the proloculus in the direction of growth.

*Apertural face* – frontal part of the last chamber formed.

*Distal face* – apertural face of the previously formed chambers.

*Base* – wall on which a chamber is built (axial wall or chamber wall).

*Ventral* – vertical, in direction of the intraseptal canal system.

*Dorsal* – vertical, opposite to ventral.

*Frontal* – direction of growth of the equatorial chambers.

*Apical* – opposite to frontal; in direction of the apex.

*Introduction*

In several genera belonging to the Rotaliidea the toothplate, the septal flap and the intraseptal passages or the ‘canal’ system have been recognized and described

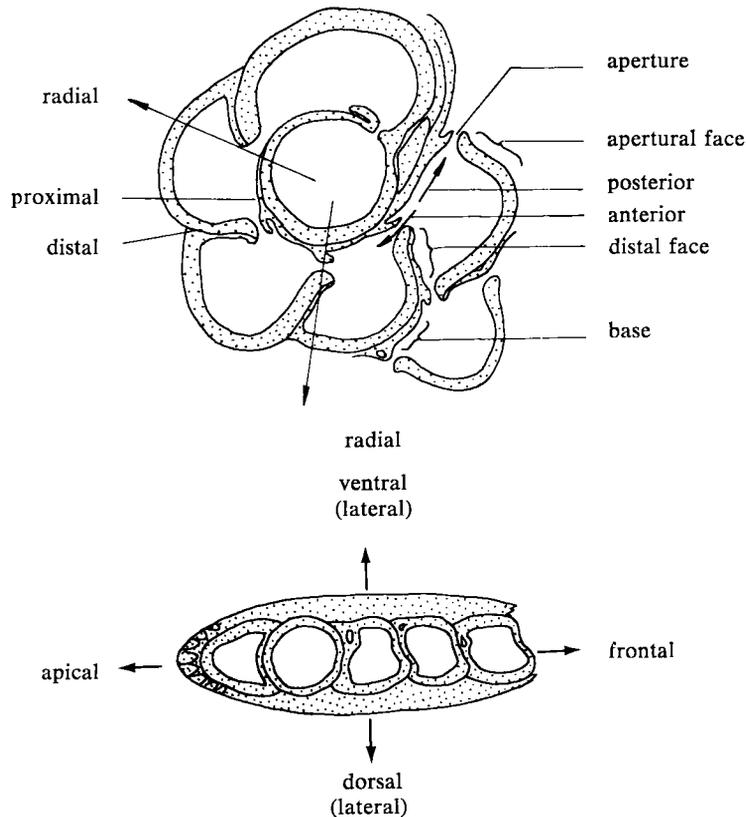


Fig. 11. A horizontal and a vertical section of *Miogypsinoidea*.

in detail. Although several authors have stated that Miogypsinidae possess comparable features these morphological features of the Miogypsinidae have never been studied properly.

Three structural patterns within the lamellar Foraminifera have been distinguished (e.g. Smout, 1954; Reiss, 1957-1963; Reiss, Hansen & Schneidermann, 1969).

a) A 'monolamellar' pattern, where each chamber wall is formed by a single-layered lamella (which also covers previously formed parts of the test). Therefore all septa and septal faces of the last chamber are single layered.

b) 'Bilamellar' pattern where in addition to the outer lamella, that forms the chamber wall and covers earlier parts of the test, an 'inner lining' of the same texture and composition as the outer lamella is secreted at each instar. This inner lining is confined to each chamber and coats its interior, resulting in primarily doubled septal faces and septa. In most bilamellar genera the inner lining is shown to wedge out at the previous septum and at the junction with the adjacent previous coil. In some forms, however, the inner lining also coats the previous septum, thereby leading to 'trilamellar' septa (Reiss, 1957, 1963, 1967; Glaesner & Wade, 1959; McGowran, 1966).

c) A 'rotaliid' pattern where extensions of the toothplate named 'septal flaps' (Smout, 1954; Reiss & Merling, 1958) are present in each chamber, secondarily forming double septa but leaving the septal face of the ontogenetically last chamber single-layered. The bilamellar structural pattern and especially the nature of the dark line separating the inner lining or the septal flap from the outer lamella were interpreted in different ways by various authors.

Hofker (1951) has defined the toothplate characteristic for his order Dentata as a 'peculiar inner structure, a more or less developed often contorted plate, running from a former, now septal foramen to the next one, through the chamber. The toothplate is formed together with the newly built chamber. . . .'. Reiss and Merling (1958, p. 7) gave a review of the toothplate in Rotaliidea. They wrote 'In the Rotaliidea a distinct toothplate is present in each chamber and is formed simultaneously with the latter. It runs from the intercameral foramen towards the cameral aperture, partly attached to the axial wall of the respective chamber as well as to its lateral walls. The toothplate of Rotaliidea is longitudinally folded and its distal end usually contorted. . . . the posterior part of the rotaliid toothplate near to the distal face of the previous chamber, bends "upwards" in a dorsal direction, covering the distal face of the previous chamber, and coalescing with the dorsal part of its own chamber wall, after having formed a more or less accentuated "forward" (in direction of growth) bend.' This description closely resembles that given for the toothplate and septal flap of *Miogypsinoidea*.

The elongated proximal part of the toothplate has a marked posterior direction and was referred to as the 'counterseptum' by Barker and Grimsdale (1936) and 'hook of the toothplate' by Hofker (1971). The toothplate is always absent in embryonic chambers (protoconch and deuterococonch) (Reiss, 1963).

Banner and Williams (1973) described a toothplate of *Ammonia bruennich* which is structurally continuous with the septal (rotaliid) flap; they also noted the presence of a basal calcareous lamella (basal anterior extension).

### *Toothplate and septal flap of Miogypsinoides*

The shape and position of the toothplate and septal flap are best understood with the help of figures and plates (Figs. 12, 22, 30; Pls. 9-13). The main characteristics of the toothplate and septal flap of the Rotaliidea can also be recognized in *Miogypsinoides*. In *Miogypsinoides* the toothplate and septal flap of the equatorial chambers are formed before each instar builds its 'own' chamber (Fig. 31; Pl. 33). Where the apertural face meets the base (or wall of the previously formed chamber) a toothplate is formed: it is a ventral-dorsal directed elongated structure narrowing in the dorsal direction and forming near the aperture a proximal part that points markedly in a posterior direction (the hook of the toothplate, Hofker, 1971). Ventral to this hook the toothplate bends away forming a curve which leads to the formation of a 'canal' or 'siphon'. In horizontal sections the hook of the toothplate in spiral chambers is distinctly visible (Pls. 10, 11). Under this hook is an opening that probably was the means of communication between the protoplasm of the chamber and the protoplasm of the canal system. Along the apertural face (or distal face) the toothplate forms an extension which parallels the distal face (septum) and merges with the dorsal and ventral walls of its own chamber (Pls. 9, 10). This extension is referred to as the septal flap. On the ventral side the septal flap bends, resulting in a horizontal canal from the proximal to the distal side along the apertural face. The canal is not always closed but may remain open during several instars, forming a deep groove or fissure. A second extension of the toothplate is formed along the base and is comparable to the basal anterior extension of *Ammonia bruennich* (see Banner & Williams, 1973). In this latter species this basal extension is perforated, whereas in *Miogypsinoides* it is imperforate. The texture of the basal extension is equal to that of the septal flap and toothplate (Pls. 10, 11). Only by its position it can be distinguished from the septal flap, just as with toothplate and septal flap. In *Ammonia bruennich* this basal extension is formed after the formation of the chamber, whereas in *Miogypsinoides* it develops before the new chamber is built.

The basal extension is not complete near the dorsal wall of the chamber. On the ventral side there is a bend in the basal extension in addition to the bend of the septal flap; together they complete a horizontal canal along the base or the proximal inner side of the chamber to be built. At the intersection is the vertical

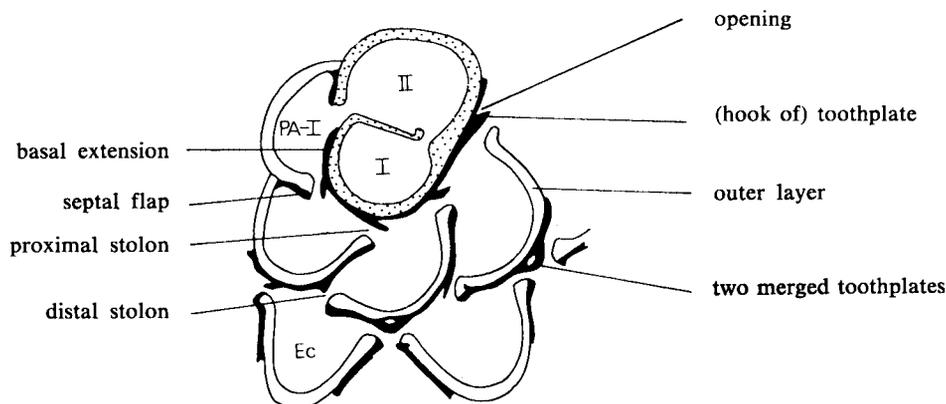


Fig. 12. Horizontal section of *Miogypsinoides*.

canal formed by the toothplate: a funnel-like 'canal' towards the dorsal side. In vertical as well as horizontal sections the double septa are visible. The toothplate and the basal extension often wedge out towards the dorsal side. Since the thicknesses of the apertural face (and distal face), the septal flap and basal extension hardly differ on the ventral side, they can be distinguished from each other only by their different positions. With the S.E.M. no line or parting between septal flap or basal extension and apertural face is seen, except at the level of the horizontal canal system (ICS). In specimens from Estoti the pores which are scattered sporadically over the vertical walls of the equatorial chambers terminate at the covering flap.

A spiral chamber with a proximal stolon (aperture) and a distal stolon (aperture) forms two toothplates. Both toothplates form a basal extension and a septal flap before the new chamber is built. Often equatorial chambers form two apertures of two different chambers that lie so close together that the respective toothplates merge to form a clear vertical canal (Pls. 7, 10, 12; Fig. 22). This canal penetrates into the dorsal wall where it forms a perforation at the outer surface. In contrast to the toothplates of the spiral chambers the toothplates of the equatorial chambers have no passage to the canal system. The gradual growth of the toothplate, septal flap and basal extension is described in Chapter IV, p. 48.

#### CANAL SYSTEMS

##### *Terminology*

Various terms are used for cavities and spaces inside the test of the Foraminifera which are formed by different structural elements (Fig. 14). As several authors have applied different terms to one and the same structure, a redefinition of the terms used in this paper for *Miogypsinidae* appears necessary. Reis (1957-1967) has discussed and redefined the terms used for *Rotaliidea*, and sometimes referred to corresponding structures in the *Miogypsinidae*; therefore references to his terminology are frequent here.

*Pore* (Fig. 14) – A tubular cavity of small diameter perpendicular to the lamination. Tubular cavities normal or parallel to the lamination have been named 'intra-

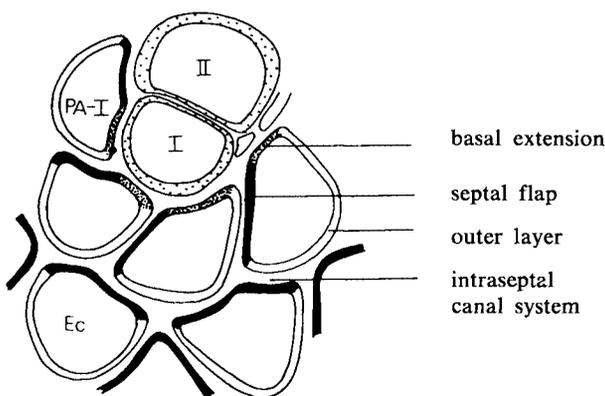


Fig. 13. Horizontal section at the level of the intraseptal canal system, showing the positions of the basal extension, septal flap and outer layer.

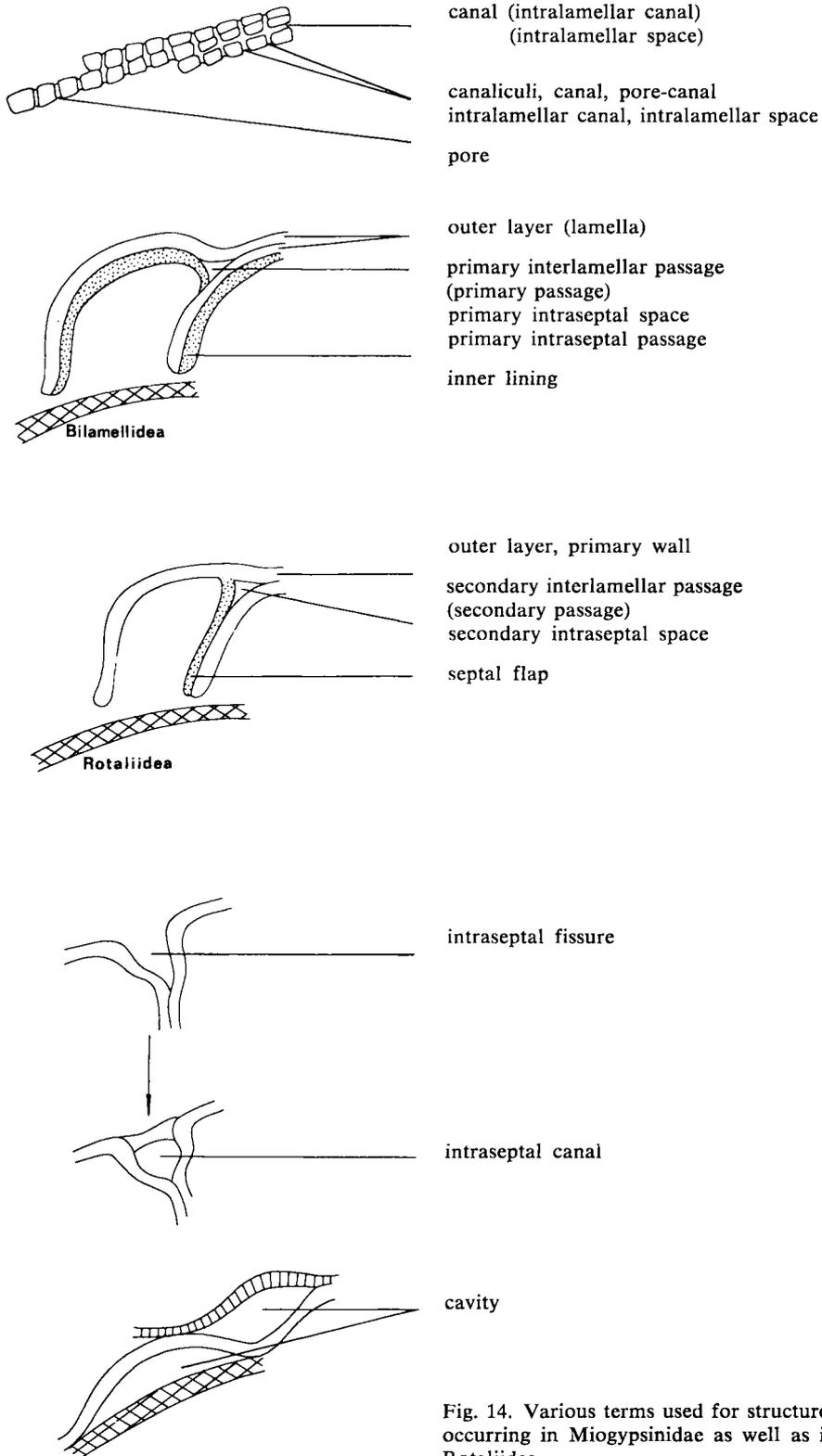


Fig. 14. Various terms used for structures occurring in Miogypsinoidea as well as in Rotaliidea.

lamellar canal' (Reiss & Merling, 1958; Reiss, 1963) or just "canals" (Smout, 1954) and when they perforate several subsequent and adhering lamellae, 'canaliculi' (Reichel, 1950) or 'connections' (Reiss, 1957, 1963, 1967) or 'pore-canal' (Reiss & Merling, 1958). These tubular cavities are considered true canals *sensu stricto* (Reiss & Merling, 1958; Reiss, 1963). Reiss (1958) stated that 'Canals are tubular cavities within the lamellae and provided probably passage ways for protoplasm'. *Primary interlamellar passage* (Fig. 14) – A space between two elements of one and the same chamber, the outer lamella and the inner lining (Reiss, 1963). Reiss and Merling (1958, p. 10) stated that 'no space between different structural elements of the same chamber or between different structural elements of subsequent chambers should be referred to as "canals"'. However in the same paper it is also noted that 'the intraseptal spaces of the Bilamellidea are primary formed and might be close to true canals, being enclosed within the chamber wall'. Thus this space within the septa of Bilamellidea was referred to as the primary intraseptal space or the primary intraseptal passage (Reiss & Merling, 1958).

*Vertical canal* – The funnel-shaped cavity between toothplate(s) and chamber wall (base or axial wall). This canal is not always developed. The extensions of the canal into the ventral and into the dorsal side of the test are also regarded as vertical canals. Reiss and Merling (1958, p. 8) stated 'In some families of Rotaliidea the interval defined by toothplate on one hand and axial (spiral chamber) wall (or vertical septa) is much smaller and in many planispiral (or nearly so) genera it is reduced to a pipe or funnel-like structure, to which the term canal or siphon often have been applied. Compare *Asterigina*, Reiss & Merling, 1959; pl. I, figs. 13, 14, Barker & Grimsdale, 1936'.

*Intraseptal canal* – This is a cavity formed by toothplate, septal flap and primary wall on the ventral side of the spiral chambers and the equatorial chambers. As mentioned above, Reiss and Merling do not consider these cavities to be canals: 'Spaces filled by protoplasm and formed between the toothplate and the chamber-walls of respective (own) chamber are not canals'. Because these spaces are secondarily formed, they were named 'secondary interlamellar passages' of 'secondary intraseptal spaces'. The intraseptal spaces characteristic for the Rotaliidea are secondarily formed; two instars are necessary for this formation. Reiss (1963) writes 'Various spaces formed in different genera have been regarded as "canal" or "siphons", particularly if having a funnel-like shape. The spaces formed by toothplates communicate with each other by openings left through incomplete attachment of the plate to the wall or by indentations formed by the plate. They communicate directly or indirectly through canals and the homologues'. The word 'passage' has been used for such interlamellar spaces, whereas a space is regarded to be intraseptal. This combination of terms is confusing. Drooger (1960) stated that the differentiation between canals and fissures might be impossible. Surface parts of the septal fissures (intraseptal fissures) may have been closed, forming intraseptal canals which generally open in sutural direction through ascending branches (Drooger, 1960). Thus buried fissures become canals.

In several genera of the Rotaliidea the spaces between the spiral chambers and the axial wall are often regarded as spiral canals. It is preferable to use the term 'canals' instead of passages for the continuously connected spaces formed by the septal flap of the spiral chamber and the equatorial chamber of *Miogypsinoides*, although one cannot speak of a distinct communication or connection with other parts of the protoplasmic body (except in the spiral chambers).

*Lateral canals* – Within the ventral part of the test, canals (formerly fissures) are formed at regular distances parallel to the intraseptal canals.

The term *cavity* or *chamberlet* generally is used for spaces between two subsequent laminae (Reiss & Merling, 1958; Reiss, 1963).

#### History

Yabe and Hanzawa (1928) suggested that *Miogypsinidae* which lack lateral chambers should be assigned to a separate group: the subgenus *Miogypsinoides*. Van der Vlerk and Wennekers (1929) objected because the absence of lateral chambers was not proven. Finally Tan Sin Hok (1936a) mentioned several reasons for separating *Miogypsinoides* from *Miogypsina* s.s., including the presence of an intraseptal canal system in the embryonic part as well as between the equatorial chambers. According to Tan the canal system in the *Miogypsinidae* is restricted to *Miogypsinoides*. However he also described a canal system for *Miogypsina* (*Miogypsina*) *borneensis*: a canal system which is intercalated between the lateral chambers. Regarding the canal system in *Miogypsinoides* Tan (1936) stated that the intraseptal canal system is connected with the exterior by vertical canals. It is not clear if these canals originate from cavities of the equatorial chambers or directly from the intraseptal canal system. The most accurate description of the intraseptal canal system in *Miogypsinidae* is given by Barker and Grimsdale (1937, p. 163): 'In the initial spire of the test a spiral canal can be recognized, from which spring offshoots passing into and along radial septa. At the distal termination of these septa, any one canal may (a) pass to the exterior, or (b) form a labyrinth

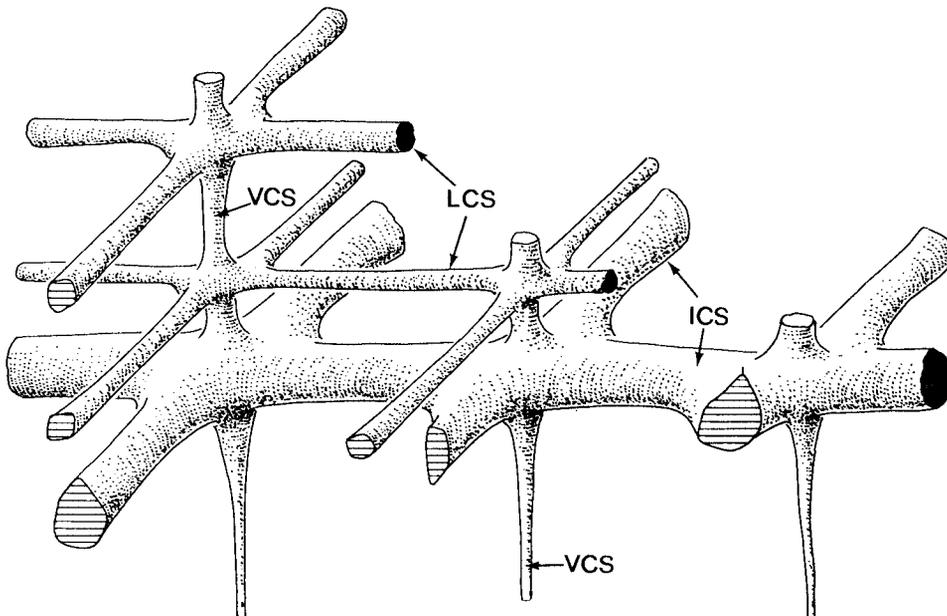


Fig. 15. Negative of part of the canal system in *Miogypsinoides*. In cross-section the intraseptal canal system is elongated to pear-shaped near the intersections. From the intersection the vertical and the lateral canal systems develop on the ventral side. On the dorsal side only the lateral canal system has developed. The first lateral canal system is found close to the intraseptal canal system.

of canals in the outer wall, or (c) bifurcate, the two branches entering either into the separate radial septa of the outer whorl, or into the septa of the equatorial net where they form an interwoven mesh with the branches from the septa'.

Several authors confused the presence of a canal system with the dark line; some authors even described the stolon system as a canal system (see Neumann, 1972).

### *Canal system in Miogypsinoides*

The shape and pattern of the canal systems will be described without constantly referring to the position of the toothplate and septal flap.

### *Shape and pattern of the intraseptal canal system*

In transverse sections the intraseptal canal system is elongated to somewhat pear-shaped near the intersections (Fig. 15). When the equatorial plane is cut obliquely, the resulting section cuts through the intersections of the intraseptal canal system and also bisects the vertical canal system (Fig. 16). Figure 16 shows an oblique section extending from the ventral (above) to the dorsal side (below) of the equatorial plane. When the intraseptal canal system on the ventral side is bisected (position 1-5 in Fig. 16), the resulting pattern is square to diamond-shaped. In the ventral-most section the perforated ventral (lateral) horizontal equatorial chamber wall (roof) is also cut. Position 5-9 in Fig. 16: the intraseptal canal system is cut at its largest diameter; the vertical equatorial chamber wall (septum) is rounded, its apical part consists of septal flap and toothplate, the frontal side is the primary wall (Pls. 7, 8, 10, 11). In position 9-11 in Fig. 16 the intraseptal canal system is bisected on the 'dorsal' side; it vanishes at the horizontal level where the stolons are situated. In thin sections as well as in S.E.M. slides the differentiation between septal flap and toothplate and primary wall is barely possible. In position 11-13 in Fig. 16 the stolons become visible; the intraseptal canal system is cut only locally. The vertical canal formed by the two merged toothplates at the base of the stolons is distinct (Pls. 7, 10). In position 13-14 dorsal to the stolon system the vertical equatorial chamber wall (septum) is thin, where the septal flap wedges out. The vertical canal in the frontal part of the septum, which penetrates into the dorsal wall of the test, is distinct (Pl. 10).

In *Miogypsinoides* the intraseptal canal system surrounds each embryonic, nepionic and equatorial chamber and also penetrates into the collar and into the marginal fringe of the apex. A thin section exactly through the intraseptal canal system shows all chambers as 'free' rings (Pls. 7, 10; Fig. 18).

The diameter of the intraseptal canal system is variable within one specimen as well as within a population. In general the diameter is smaller at the apex than near the front. Where the equatorial chambers are enlarged towards the front, the diameter of the intraseptal canal system is also greater. The intraseptal canal system shows branching perpendicular to the equatorial plane as well as parallel to it: the lateral and the vertical canal systems branch into the ventral side of the test which becomes porous, and the vertical canal system extends into the dorsal side of the test which remains rather "massive".

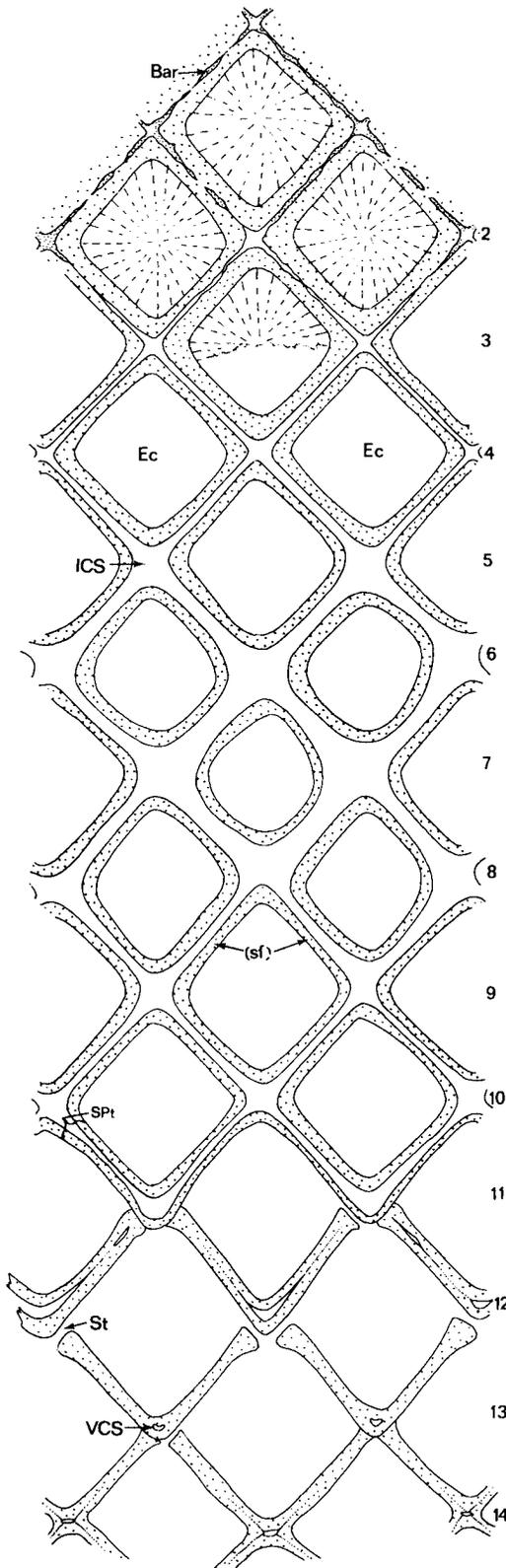
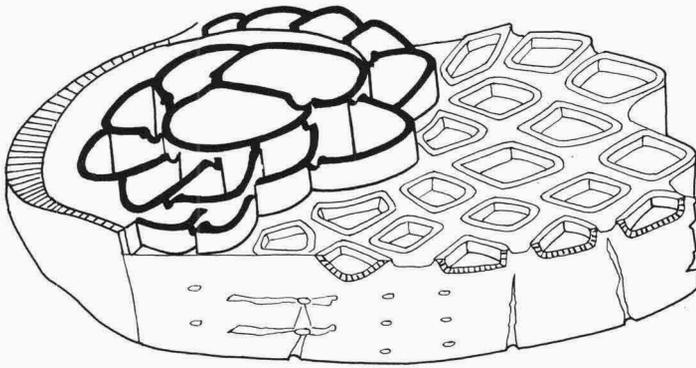
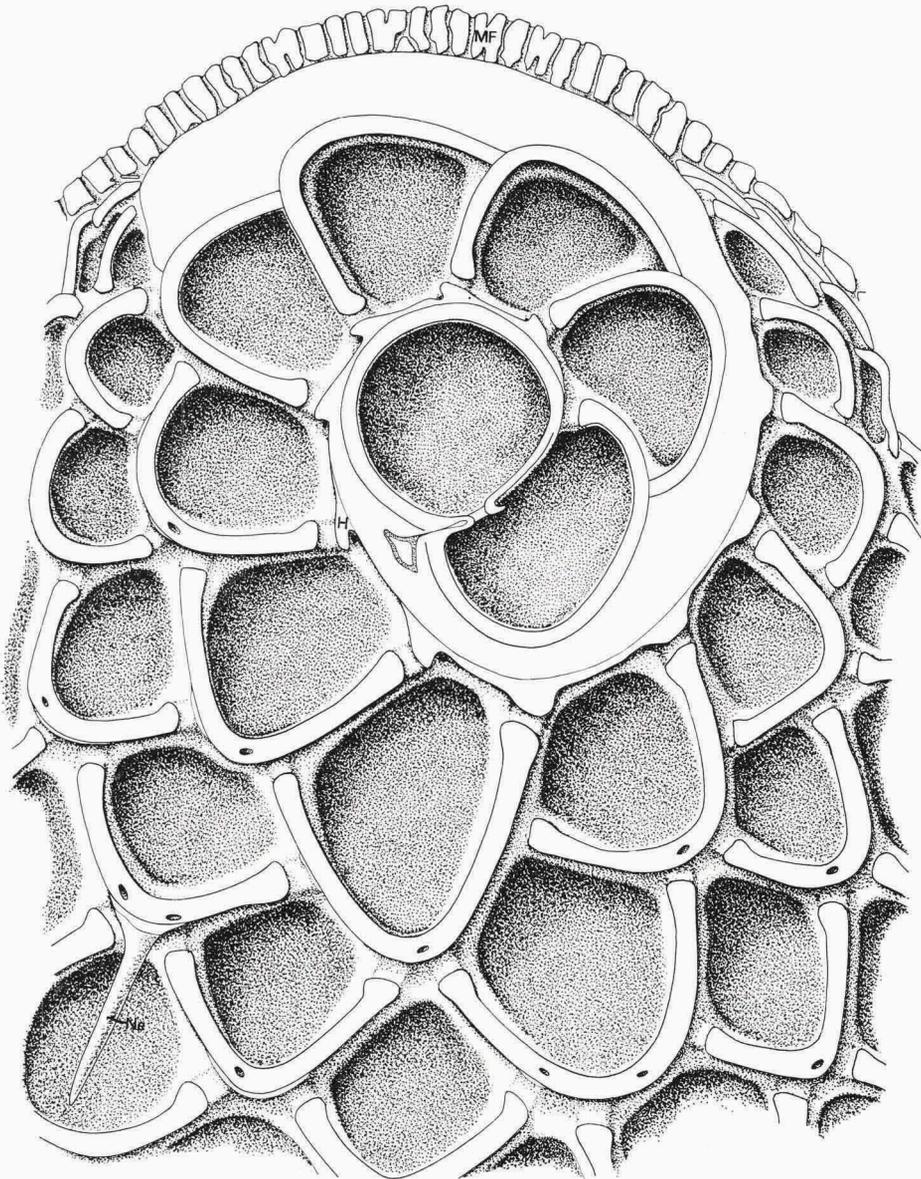


Fig. 16. A somewhat oblique horizontal section through the equatorial plane of *Miogypsinoides*. A part of the horizontal equatorial chamber wall is cut on the 'ventral' side. From here towards the middle of the equatorial plane the intra-septal canal system is cut. Near the middles of the equatorial plane the stolons become visible and the intra-septal canal system vanishes; only the vertical canal system is seen in the vertical wall of the equatorial chamber (septum).

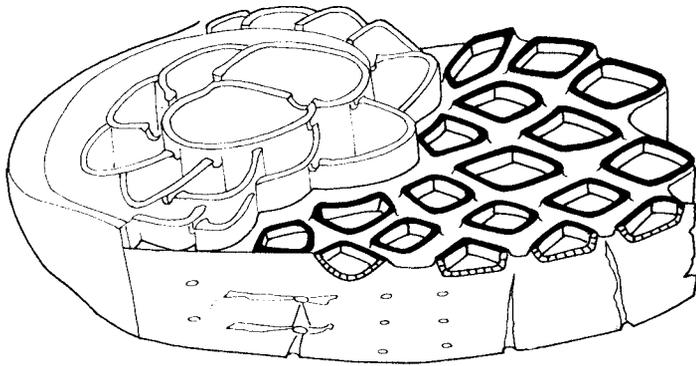
Fig. 17. A dorsal view of the equatorial plane of *Miogypsinoides*. A. the thick lines indicate the level of the section in Fig. 17B. B. At this level in the vertical walls (septa) of the spiral and equatorial chambers, the stolons and the vertical canal system are seen. Only the apical part of the intra-septal canal system is visible. The ICS is situated more ventrally in the thickened part of the septa of the spiral equatorial chambers (compare Fig. 18B).



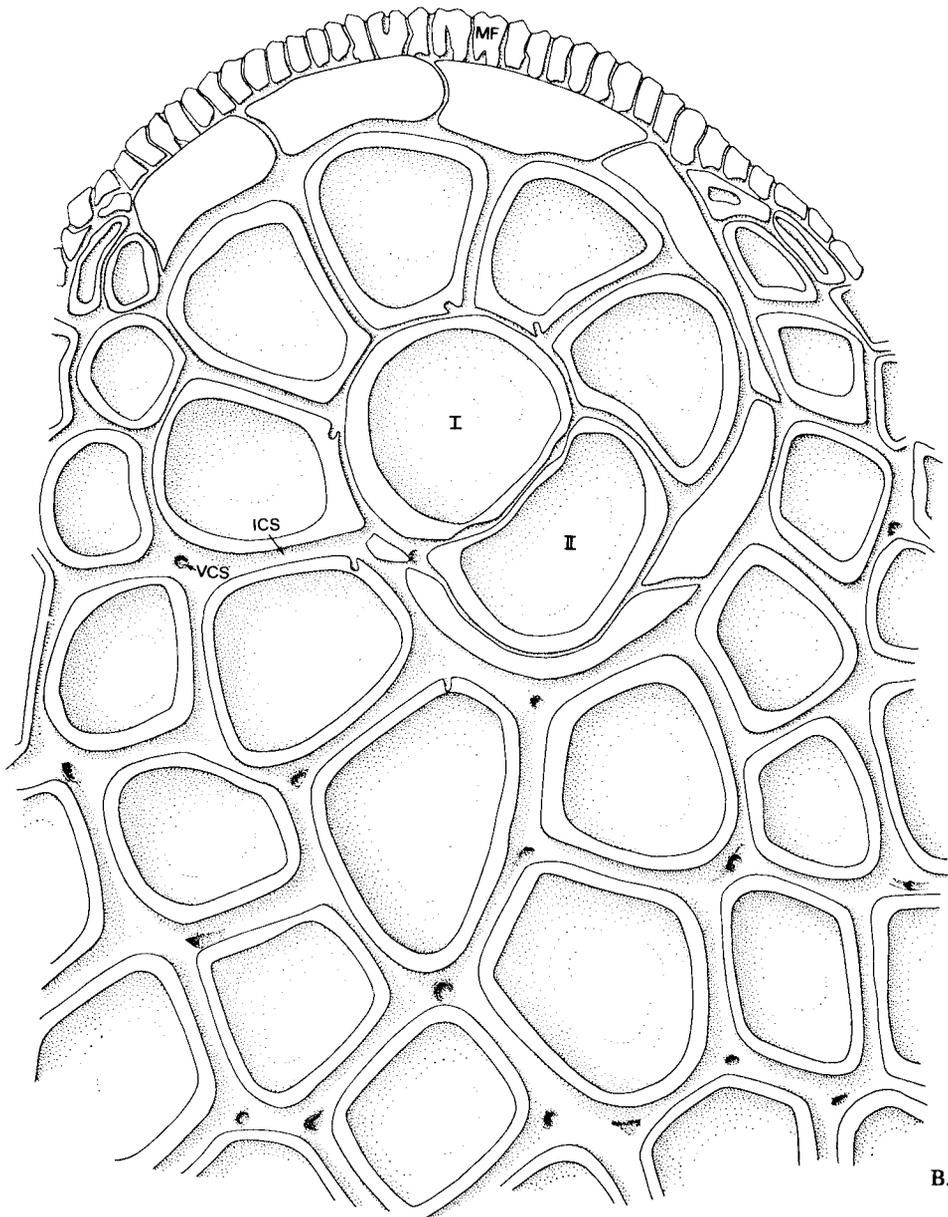
A.



B.



A.



B.

### *Lateral and vertical canal systems*

Vertical branching of the intraseptal canal system into the ventral and the dorsal sides of the test usually occurs from the intersections of the intraseptal canal system. The vertical canal penetrates from these intersections into the dorsal side of the test: the part of the vertical canal within the equatorial chamber is formed by the merger of the two toothplates at the base of the stolons (Figs. 22, 23, 31; Pls. 7, 10). Since the toothplate bends away from the chamber wall, the diameter of the canal is larger near the intersections on the ventral side than on the dorsal side of the equatorial chamber where it enters the dorsal wall. The vertical canal entering the dorsal wall often bifurcates (Fig. 23). On the ventral side of the test one or more repetitions of the intraseptal canal system occur at regular intervals. These parallel and similar lateral canal systems are interconnected by vertical branches: the ventral extensions of the vertical canal system. The lateral canal system is located immediately above the intraseptal canal system forming a repetition of the intraseptal canal system. The wall on the ventral (and the dorsal) side of the cavities of the embryonic, nepionic and equatorial chambers is only perforated by pores (Fig. 23; Pls. 13, 42). The pores may cross the lateral canal systems. The various levels of the lateral canal system are separated by dark-coloured material: bars (Pls. 9, 13). Probably the lateral canal system was first a system of fissures (sutural fissures) which were closed (buried) secondarily by this dark-coloured material, thus forming the canals (Fig. 21; Pl. 6). The canals between the intersections of the lateral canal system (i.e. the lateral canals) are somewhat convex when seen from the exterior (Pl. 13).

The vertical connections (branches) are not always perpendicular to the equatorial plane. At the apex the intraseptal canal system and the lateral canal system split into fine canals and cavities between the truncated cones of the marginal fringe. On the dorsal and the ventral sides of the test, the vertical canals have clear openings to the exterior; on the ventral side the bars open at irregular distances (Fig. 21; Pl. 13).

### *Communication between protoplasm of the intraseptal canal system and that in the spiral chambers*

Reiss and Merling (1958, p. 12) assumed that a system of passages existed for the protoplasm: 'In the Rotaliidea the intraseptal protoplasm communicates with the intralocular protoplasm of the remainder of the chamber through the space left between toothplate and umbilical (or lateral) chamber wall, which in turn is connected at least in many genera with the intralocular protoplasm of the remainder of the chamber through the space left by torsion of the toothplate as well as with the extralocular protoplasm either through apertures or through pore-canals or through both'.

Such an opening under the hook of the toothplate is also found in the spiral chambers of *Miogypsinoidea*; this opening is however more centrally situated than in most of the Rotaliidea. In the equatorial chambers where the toothplates have

- ◀ Fig. 18. A dorsal view of the equatorial plane of *Miogypsinoidea*.  
 A. The thick lines indicate the level of the section in Fig. 18B.  
 B. The intraseptal canal system (ICS) is cut here. From the intersections of the ICS the vertical canal system (VCS) penetrates the ventral wall. At the apex the ICS splits into small cavities between the truncated cones of the marginal fringe (MF).

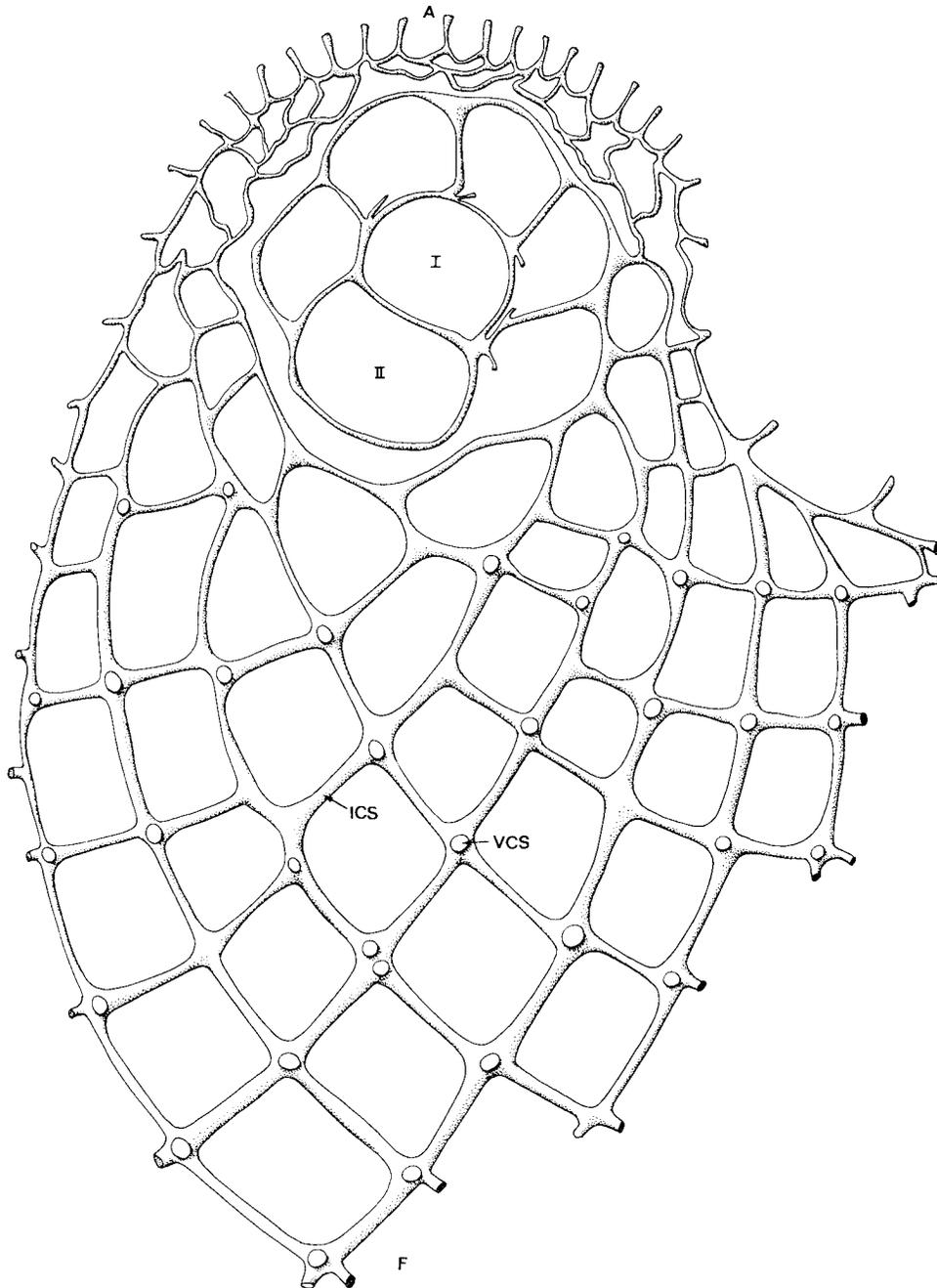


Fig. 19. Negative of the intraseptal canal system (ICS). The connection between the ICS and the first nepionic chambers is uncertain. The ICS splits into canals and cavities between the truncated cones of the marginal fringe (MF).

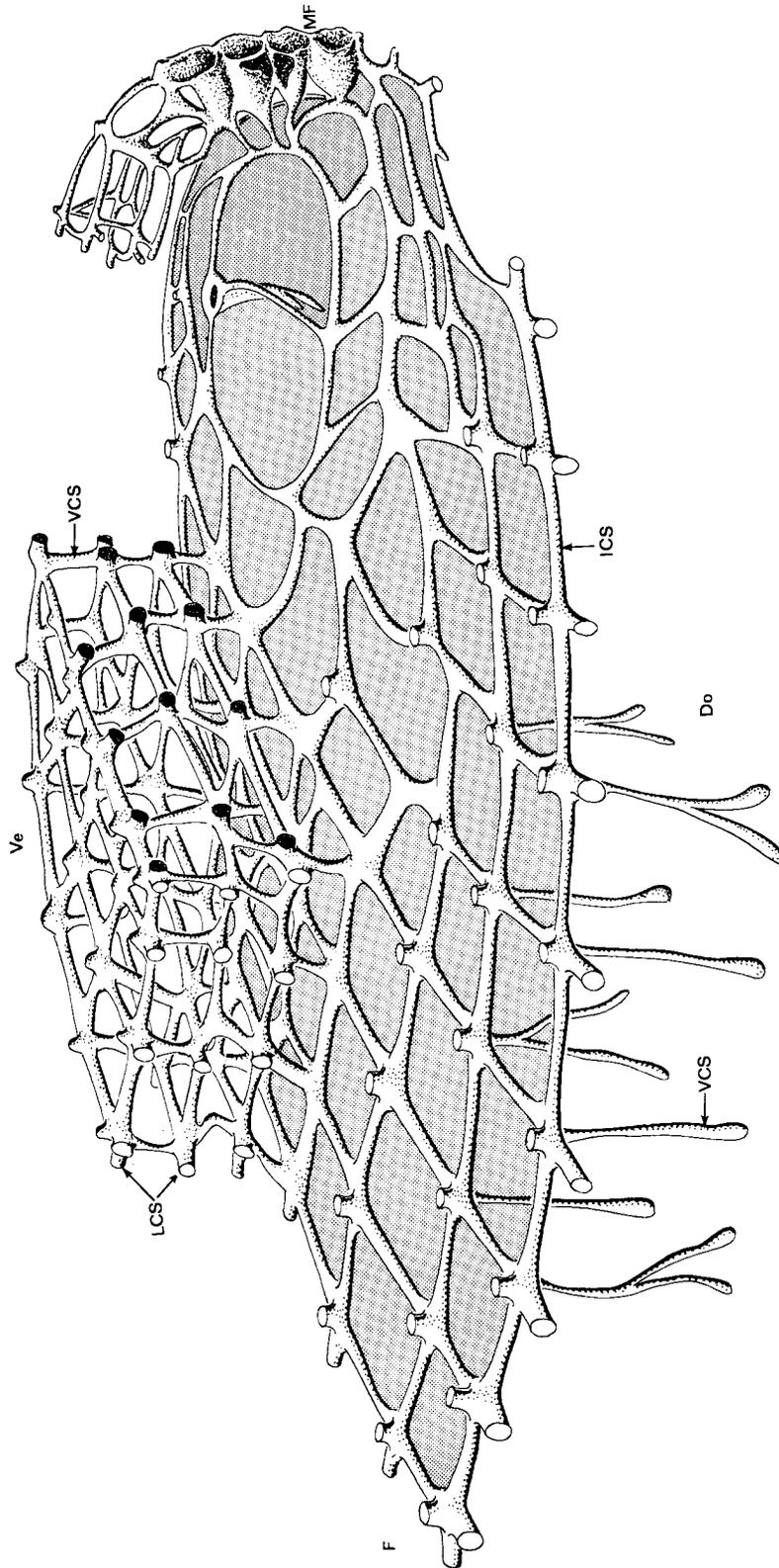


Fig. 20. Negative of the intraseptal (ICS), lateral (LCS) and vertical (VCS) canal systems in *Miogypsinoidea*.

merged, such an opening is not present. On the ventral side, the wall between I and II is double, probably due to the deep fissure between I and II (Pl. 15). In thin sections a tubular cavity of small diameter is sometimes seen on the 'PA-II' side, between the lip and the wall between I and II. This 'canal' may have acted as the first connection between the intralocular protoplasm and the protoplasm of the intraseptal canal system. There is no toothplate at the deuteroconchal stolon. In biserial *Miogypsina* s.s. two funnel-shaped deuteroconchal stolons have developed on the PA-II side, which may have provided the protoplasm with the inlet into PA-II (Chapter IV, p. 38). On the frontal side of the last equatorial chamber formed, the openings of the intraseptal canal system and the apertures are close together; this may have provided a connection between the intralocular protoplasm and that of the intraseptal canal system.

#### *Function of the canal system*

The function of the canal system is not clear: it may have been related either to growth (Smout, 1954) or to the metabolic system. Reiss and Merling (1958, p. 12) stated that 'No space in the endoskeleton of the Foraminifera is apparently ever left empty, with the possible exception of some "blind" canals or pores in which streaming has ceased in deeper parts of the skeleton. For this reason it must be assumed that the intraseptal spaces are always filled with protoplasm'.

Angell (1975) suggested that the septal and spiral canal in *Elphidiella hannai* function as channels for gaseous exchange with the surrounding water and not for the extrusion of pseudopodia. None of the living Foraminifera studied by Angell showed visible protoplasm in the canals.

For *Miogypsinoides* it seems reasonable to postulate that the canals were filled with protoplasm and that they were involved in the formation of the lateral sides of the test. This may be concluded from the regular pattern, the position of

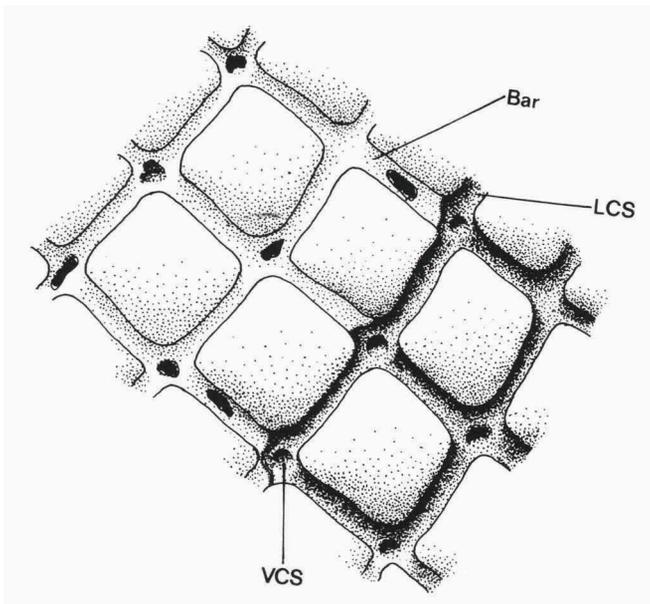


Fig. 21. At first the intraseptal canal system (and lateral canal system) is a system of fissures (sutural fissures) which later are secondarily closed (buried) by dark coloured material (bar), thus forming canals.

the canals and the fact that the inside of the canal system is often coated with a thin film of noncrystalline material. When the test of a specimen is bent (strongly in *Miogypsinoides dehaartii cupulaeformis*) the convex side is always the ventral side: this may be a result of the secretion of more shell material on the ventral side activated by the lateral canal system. Moreover, in its initial stage the lateral canal system is always visible as distinct fissures, indicating protoplasm streams (Smout, 1954; Reiss & Merling, 1958). In this way the protoplasm of the canal system may also have functioned as a feeding system, especially if the specimen was orientated with the ventral side up when living.

'Canals can sometimes function as foramina which initiate complexity of chambering' (Smout, 1954, p. 22). As the possibility is discussed that the canal system in *Miogypsinoides* gave rise to the formation of lateral chambers this may also be an argument for the presence of protoplasm in the canal system.

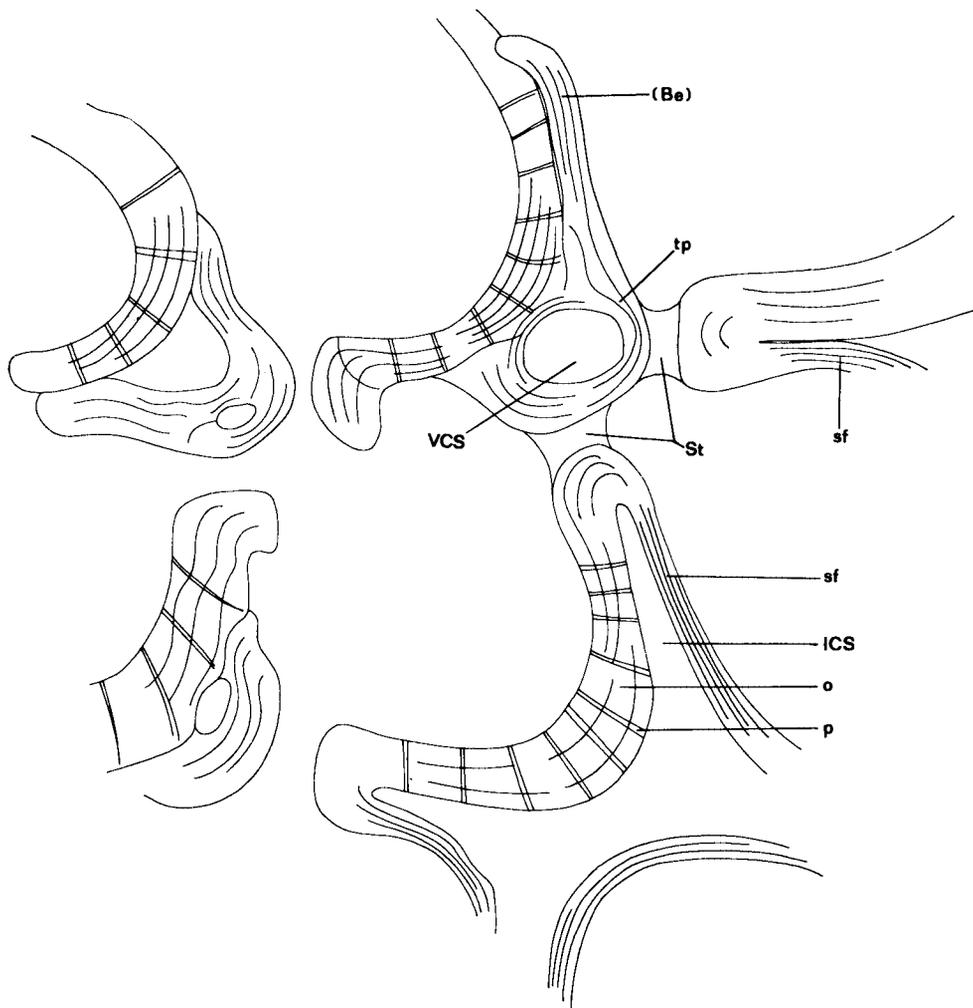


Fig. 22. The toothplates merge, forming a vertical canal from the ventral side towards the dorsal side. The pores of the primary wall terminate at the covering septal flap (sf) (or basal extension, Be) or in the intraseptal canal system.

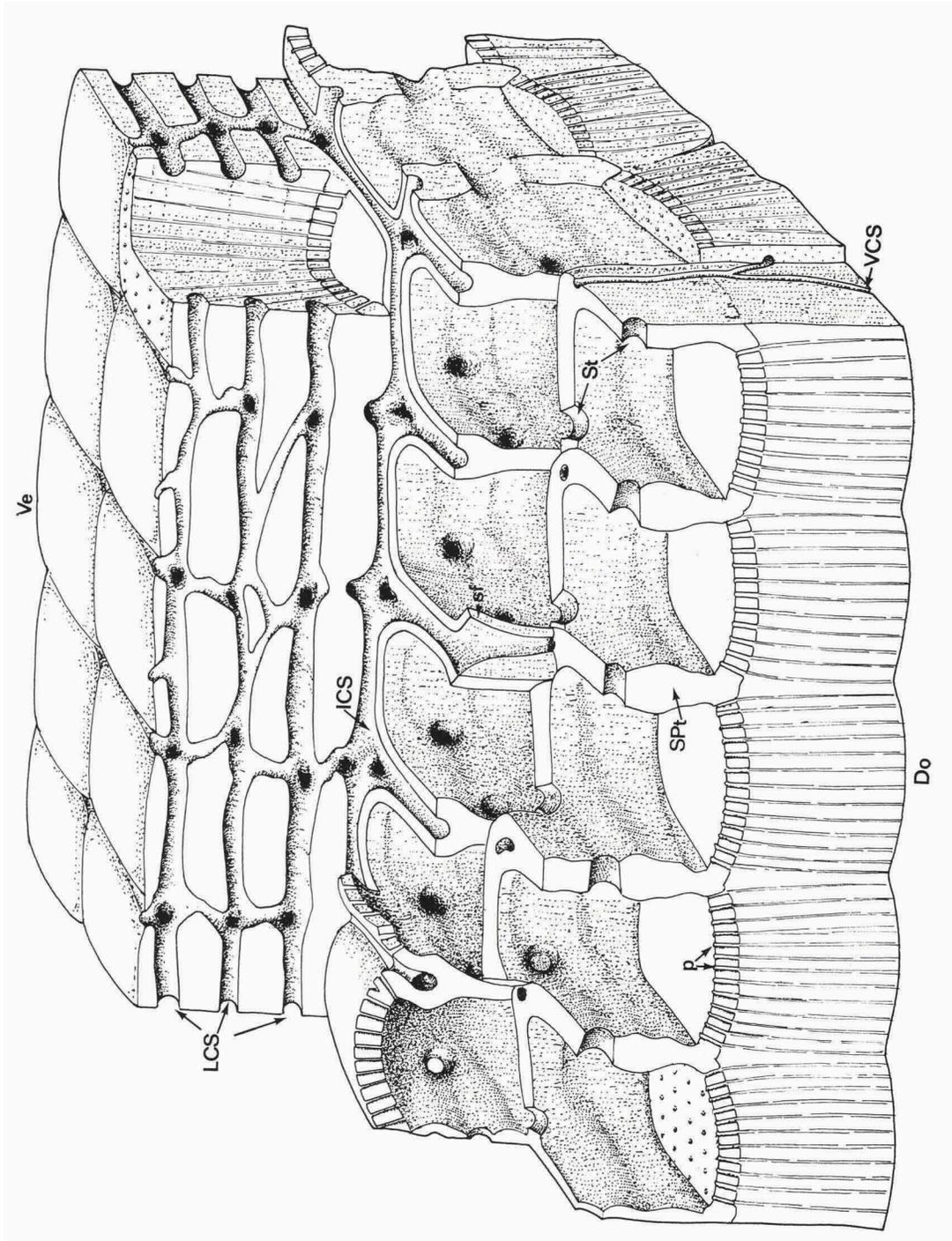


Fig. 23. Stereogram of the test of *Miogypsinoidea*. The intraseptal canal system (ICS) is on the ventral (Ve) side of the equatorial plane. The lateral canal system (LCS) is parallel to the intraseptal canal system and at regular distances from it. The vertical canal system (VCS) penetrates into the dorsal side of the test. Ventrally and dorsally of the cavities of the equatorial chambers the test is perforated by pores. The equatorial chambers have a simple stolon (St) system.

### *Disappearance of the canal system*

The presence of a canal system as well as the presence of a secondarily doubled septum necessarily coincides with the presence of a toothplate and a septal flap. In specimens which show a beginning of lateral chambers, the septal flap and toothplate (and therefore also a canal system) are absent. Consequently a dorsal and a ventral side can no longer be distinguished. Moreover as a result of the presence of an intraseptal canal system in *Miogypsinoidea*, the shape of the equatorial chambers also differs from that in *Miogypsina* s.s.

In *Miogypsina* s.s. the vertical and horizontal diameters of the equatorial chambers are almost equal, whereas the vertical diameter of the equatorial chambers in *Miogypsinoidea* is generally longer than the horizontal diameter. The equatorial chambers of *Miogypsinoidea* are asymmetrical in vertical section since the canal system occurs on the ventral side only and the dorsal part of the equatorial chamber protrudes towards the front (Fig. 31; Pls. 10, 33).

The equatorial chambers of *Miogypsina* s.s. show a thickening of septa towards the apex (the ridge of Chapter IV, p. 45) which lies at the centre of the septum. The chambers are symmetrical in vertical as well as in horizontal section.

As no intermediate forms between the secondarily doubled septa with canal system in *Miogypsinoidea* and the primarily double septa of *Miogypsina* s.s. (Chapter IV, p. 59) are found, these morphological features do not support the hypothesis that *Miogypsina* s.s. evolved from *Miogypsinoidea*.

#### NUCLEOCONCHES OF MIOGYPSINOIDEA AND MIOGYPSINA S.S.

### *Introduction*

Free nucleoconches of *Miogypsinoidea* were found in sample FR1120 from Estoti. Free nucleoconches of *Miogypsina* s.s. were found in the fine fraction of samples from East Java and Madura. These nucleoconches consist of two chambers: the protoconch and the deuteroconch. As a result of the examination of many juvenile specimens, these two chambers could be assigned with certainty to the most juvenile stages of both subgenera. Reiss (1963) stated that the bilocular nucleoconches apparently have been formed during the same instar, as the wall separating protoconch and deuteroconch is straight. He also noted that the protoconch and deuteroconch of bilocular nucleoconches of specimens with secondarily doubled septa are without toothplate and septal flap. Previous investigations (de Bock, 1973) indicate that the wall between protoconch and deuteroconch in *Miogypsina* (as well as in several other genera, a.o. *Lepidocyclina* (de Bock, 1976) is entirely different from all other walls formed in the test.

Recent studies of living *Heterostegina depressa* have shown the origin of the nucleoconches: outside the parent test meiosis takes place and initial chambers are formed which are primarily spherical (Röttger, 1974). They seem to consist of protoplasm only (with some symbiotic algae). The second chamber develops from the initial chamber by division, not by growth (Röttger, 1974). This explains the imperforate, straight and aberrant wall between protoconch and deuteroconch. The function and origin of the lip surrounding the protoconch stolon (Chapter IV, p. 38) however, remains questionable.

*The nucleoconch of Miogypsinoides* (Pl. 16)

The protoconch is an almost perfect sphere, consisting of a perforated wall. The wall between I and II is not perforated. No ornamentation is seen on the surface of the protoconch. The deuteroconch is kidney-shaped and perforated. There are fewer perforations on the vertical walls of the nucleoconch than on the lateral sides. (The vertical wall of the nucleoconch of *Miogypsina* s.s. is imperforate, see below.) The nucleoconch shown on Plate 15 has a well-developed septal flap, a toothplate and a basal extension on the PA-I side. The septal flap is curved on the ventral side, leaving a groove (or a fissure) along the deuteroconch. This fissure continues in the deep depression (fissure) between the protoconch and the deuteroconch. This is the initial canal system which surrounds the nucleoconch. The nucleoconch shows no deep fissure on the dorsal side. The deuteroconch of the specimen of Plate 15 has a hole on the dorsal side, the presence of which is not yet understood. The 'PA-II' side does not show any openings as would be expected, the sample contains only uniserial specimens.

*The nucleoconch of Miogypsina* s.s. (Pls. 15-18)

The nucleoconch of *Miogypsina* s.s. also consists of two chambers: the protoconch and the deuteroconch. The protoconch is cylindrical with convex lateral sides (Pls. 16, 17). The vertical walls (equatorial plane = horizontal) are not perforated in contrast to the horizontal (i.e. lateral) walls, a feature seen also in the equatorial chambers. The lateral walls show the external perforations of pores. Depending upon the growth stage of the specimen, the lateral walls show the development of pustules (Pls. 18, 34). The deuteroconch is kidney-shaped and is surrounded in the horizontal plane by a ridge (Pls. 16, 17). This ridge, small on the PA-I side, is accentuated on the apical side and bifurcates on the PA-II side. The ridge is also distinct on the inner surface (see the negative on Pl. 23). The PA-II side is recognized by the external openings of the two funnel-shaped deuteroconchal stolons (Chapter IV, p. 38; Pls. 17-19). The PA-I side shows the single opening of the deuteroconchal stolon, which forms the protoplasm inlet of PA-I. The ridge (part of the vertical wall) of the deuteroconch is not perforated by pores (Pl. 23). Most of the larger holes on the surface of the nucleoconch are the result of damage to the test. A stage consisting only of the protoconch has not been found; this may be an argument for the simultaneous growth of the protoconch and the deuteroconch. The shape of the free protoconches found in the sample differs in various respects from the protoconch of *Miogypsina* s.s. Another argument for the simultaneous origin may be the thin imperforate wall between I and II. This wall differs from all other walls of the test (Pl. 20), a feature also observed in the nucleoconch of *Lepidocyclina* (see de Bock, 1976).

PROTOCONCHAL STOLON WITH LIP

In an earlier paper concerning the embryonic structures of *Miogypsina*, the present author described a lip around the protoconchal stolon (de Bock, 1973). This description and the (slightly improved) figures are reproduced here. Horizontal sections, exactly through the middle of the embryonic chambers, show that the protoconchal stolon is situated on the PA-II side near the wall of the deuteroconch (Pls. 20-25; Figs. 24-27). This feature was already mentioned by Tan (1937).

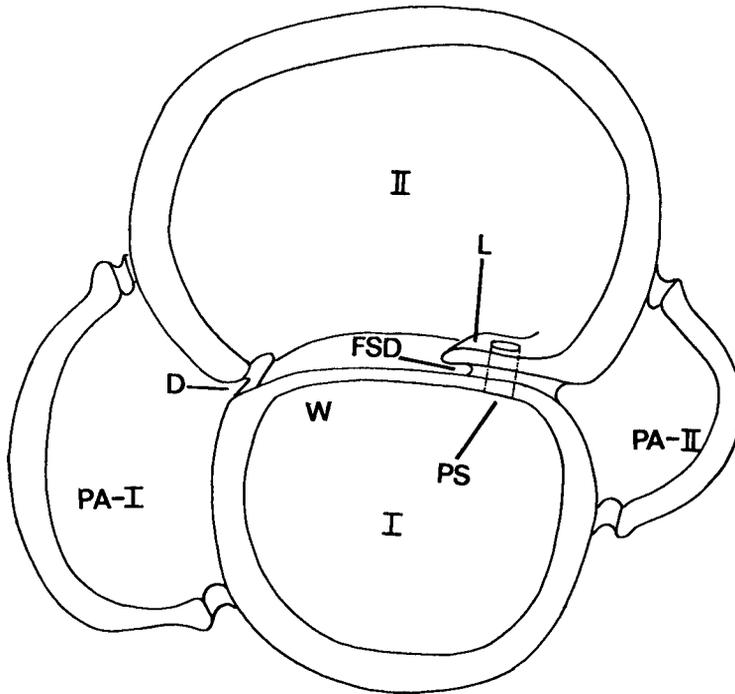


Fig. 24. A schematic drawing of the horizontal view of the embryonic apparatus of a biserial *Miogypsina*. The protoconchal stolon is situated near PA-II. It is difficult to determine whether the lip is part of the wall between I and II or part of the deuterostomal wall. Under this lip two funnel-shaped stolons extend to PA-II, one on each side of the cylindrical protoconchal stolon.

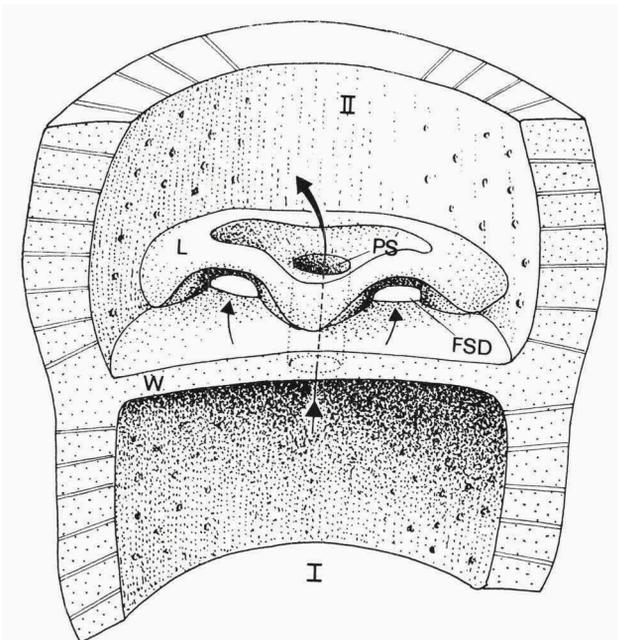


Fig. 25. Vertical view of the stolon system near PA-II. The narrow funnel-shaped deuterostomata (FS) are formed by the downward curve of the lip to the wall (W) between I and II. The arrows indicate the direction of the protoplasm stream.

He also described a funnel-shaped deuteroconchal stolon to PA-II. This complex stolon system on the PA-II side will be described here.

The protoconchal stolon is cylindrical and is elevated above the wall (W) between I and II (Figs. 23, 24). At the top is a 'collar' or a 'lip' since it protrudes somewhat (Fig. 25; Pl. 22). On the PA-II side, the lip is connected with the wall of the deuteroconch, which gave Tan the impression that the lip was formed by the deuteroconch. The possibility however that the lip forms part of the wall between I and II cannot be ignored.

Together with the wall between I and II the lip forms two openings which are the beginning of the two funnel-shaped deuteroconchal stolons. These two canals run on either side of the protoconchal stolon, forming a stolon system for the protoplasm stream to PA-II. Though not yet confirmed by precise measurements the diameter of the funnel-shaped deuteroconchal stolons seems to be directly proportional to the size of PA-II; the larger the diameter of the stolon, and thus the volume of the stream, the larger the resulting PA-II.

In thin sections the stolon system near PA-II may show different forms, depending upon the orientation of the section (Fig. 27). Many authors have mentioned the double wall between I and II near PA-II. This 'doubling' is encountered in sections on either side of the protoconchal and funnel-shaped stolons

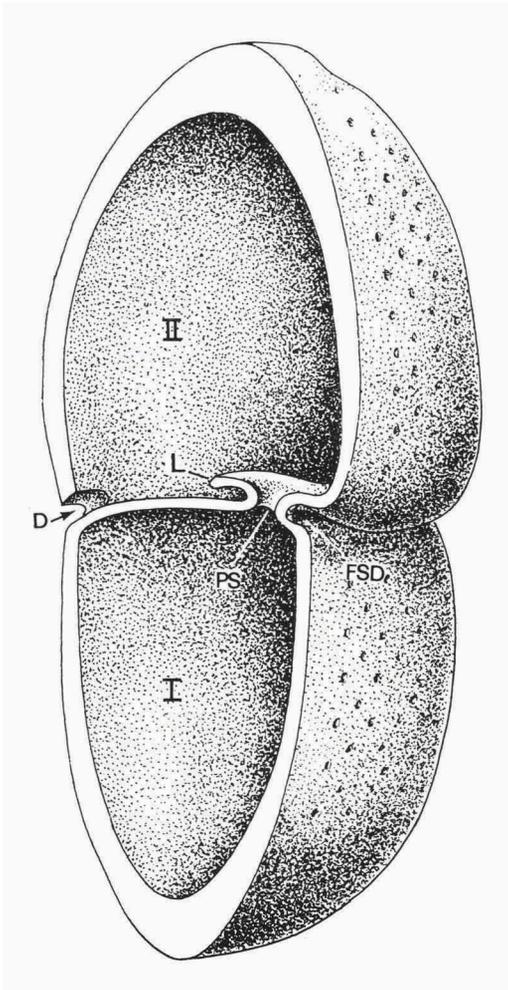


Fig. 26. A three-dimensional view of half a miogypsinid bilocular nucleconch, sectioned parallel to the equatorial plane and exactly through the protoconchal stolon (see also Pls. 20, 21). In this figure one of the funnel-shaped deuteroconchal stolons lies behind and around the cylindrical protoconchal stolon. (de Bock, 1973, fig. 3).

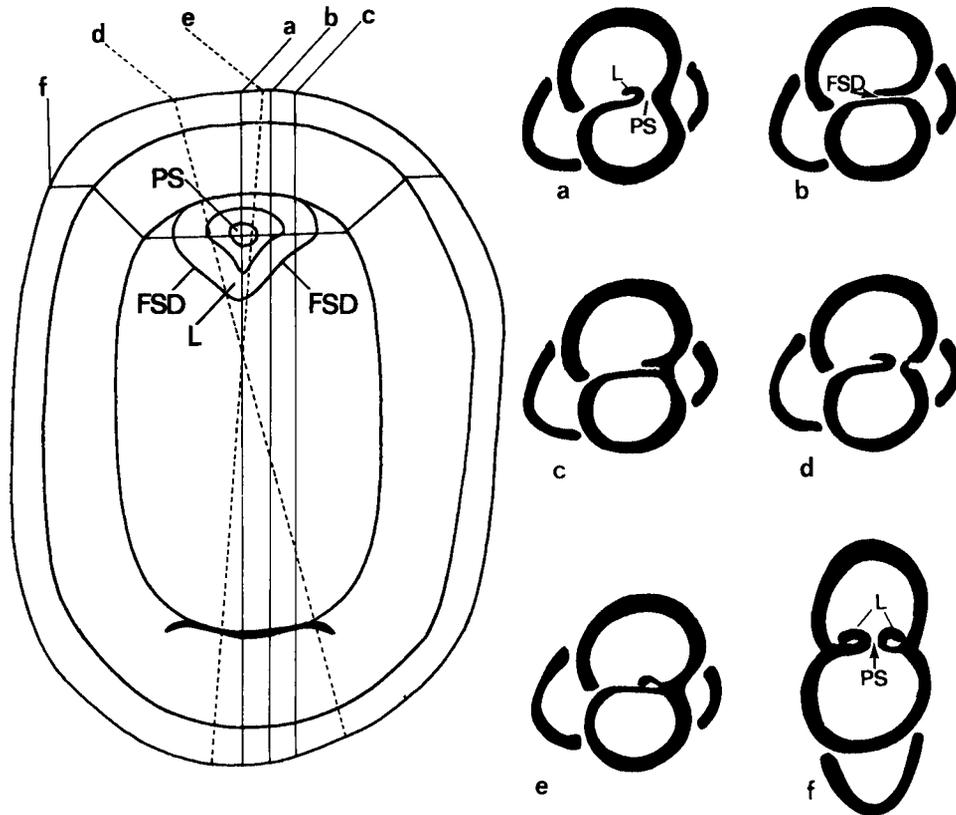


Fig. 27. Variously orientated thin sections through the embryonic apparatus of biserial *Miogypsina*. The funnel-shaped deutoconchal stolons run under the lip on either side of the protoconchal stolon (de Bock, 1973, fig. 4).

- a) Parallel to the equatorial plane and exactly through the middle of the protoconchal stolon. The funnel-shaped deutoconchal stolon is not visible.
- b) Parallel to the equatorial plane next to the protoconchal stolon. This section clearly shows the funnel-shaped deutoconchal stolon.
- c) Parallel to the equatorial plane and next to the funnel-shaped deutoconchal stolon. The lip touches the wall between I and II, causing 'doubling' of the wall.
- d) Oblique section through the protoconchal stolon. The opening of the funnel-shaped stolon is visible in the deutoconchal wall.
- e) Oblique section through the funnel-shaped deutoconchal stolon. This section often gives the impression that a little canal runs through the 'double' wall between I and II.
- f) A vertical section through the protoconchal stolon. Both sides of the lip bend downward thus forming the two funnel-shaped deutoconchal stolons.

(Fig. 27). From the specimens studied and from illustrations in other publications the presence of a lip could be established in all biserial species as well as in most of the uniserial species (compare also Ellis & Messina, 1965). The shape of the lip varies within the different species as well as within populations (Pls. 21, 24). In the earlier *Miogypsinidae*, i.e. the uniserial specimens, the lip is seen in the subgenus *Miogypsinoides* as well as in the subgenus *Miogypsina*. These specimens which have not developed a second primary chamber in general have a longer lip than the specimens with the two deutoconchal stolons. In some uniserial specimens

a narrow canal may be seen between the lip and the wall between I and II. This may have acted as a protoplasm inlet to the intraseptal canal system in *Miogypsinoides*.

#### STOLON SYSTEM

##### *Introduction*

In addition to the presence or absence of lateral chambers, another difference between these two subgenera is seen in the stolon system. Tan Sin Hok (1936b) already distinguished between two types of stolon systems:

- 1) The simple stolon system of *Miogypsinoides* with one stolon at the base of the chamber wall which gives rise to four stolons in each equatorial chamber.
- 2) The more complex stolon system of *Miogypsina* s.s.: at the base of the chamber wall there is a proximal stolon and a distal stolon (closer to the middle of the chamber). Tan also showed the presence of still another stolon: the concentric stolon, i.e. the open connection between two simultaneously formed equatorial chambers. Moreover Tan observed that the various stolons are located at different levels (Tan, 1936b). The stolon system will be described on the basis of a single equatorial chamber.

##### *Miogypsinoides* (Fig. 28; Pl. 26).

*Miogypsinoides* has a simple stolon system. Each equatorial chamber possesses four stolons: two for inflow and two for outflow. The two inflow stolons lie on the apical side and are close together. The two outflow stolons are opposite one another near the frontal side. All stolons are interconnected by a furrow on the apical side of the vertical wall (septa). On the frontal side, the furrow grades into a ridge. When two outflow stolons are very close they may grow together in the frontal direction, forming a single opening. The stolons possess a toothplate; together with the septal flap the toothplate forms a vertical canal with an opening under the hook of the toothplate in the spiral chambers. This canal connects the intraseptal canal system on the ventral side with the dorsal side, where the vertical canal continues towards the outer surface. The opening under the hook of the toothplate is sometimes absent; if present, a connection between the intralocular protoplasm and the protoplasm of the canal system was formed (see Chapter IV, p. 31).

##### *Miogypsina* s.s. (Fig. 29; Pls. 27, 28)

In *Miogypsina* s.s. the stolon system is more complicated. A schematic drawing of the stolon system is shown in Fig. 29. Two types of stolons can be distinguished: the horizontal stolons forming the inlet for protoplasm to equatorial chambers and the vertical stolons forming the inlet for protoplasm to lateral chambers. Generally each chamber has 12 horizontal stolons: 6 inflow stolons and 6 outflow stolons whereby the inflow stolons come from two different equatorial chambers and the outflow stolons lead to two different equatorial chambers. The horizontal stolons are arranged in groups of three. Each 'trio' is situated on a ridge (Fig. 29; Pl. 27). Two out of the three inflow stolons in a trio lie in furrows which connect two trios. Two trios are thus connected by two furrows provided the two trios are

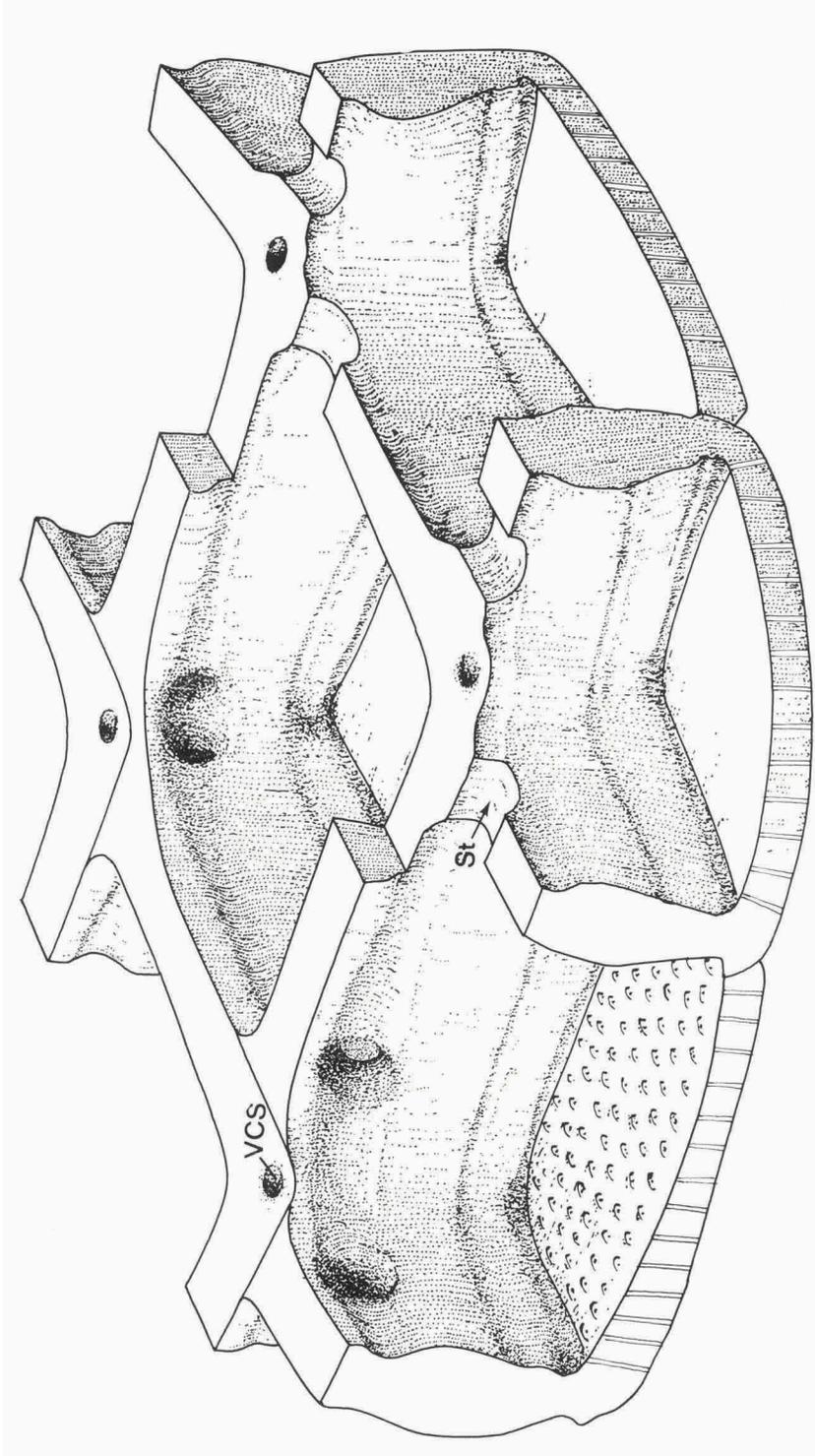


Fig. 28. The stolon system in *Miogypsinoidea* (septal flap and toothplate are not drawn). *Miogypsinoidea* has a simple stolon system. When two stolons are very close they form a single inflow opening. This figure shows two combinations of stolons in equatorial chambers sectioned at different levels. The vertical canal system is seen at the intersections of the vertical chamber walls (septa).

sufficiently far apart. A ridge is formed between the inflow and the outflow stolons and along the inner frontal side of the vertical chamber wall. The two stolons at the proximal end (base) of the septa of the equatorial chamber are already seen in the very early growth stages of an equatorial (or spiral) chamber (see Chapter IV, p. 48). The third distal stolon of each trio is formed when the vertical wall (septum) of the new equatorial chamber is made during an instar.

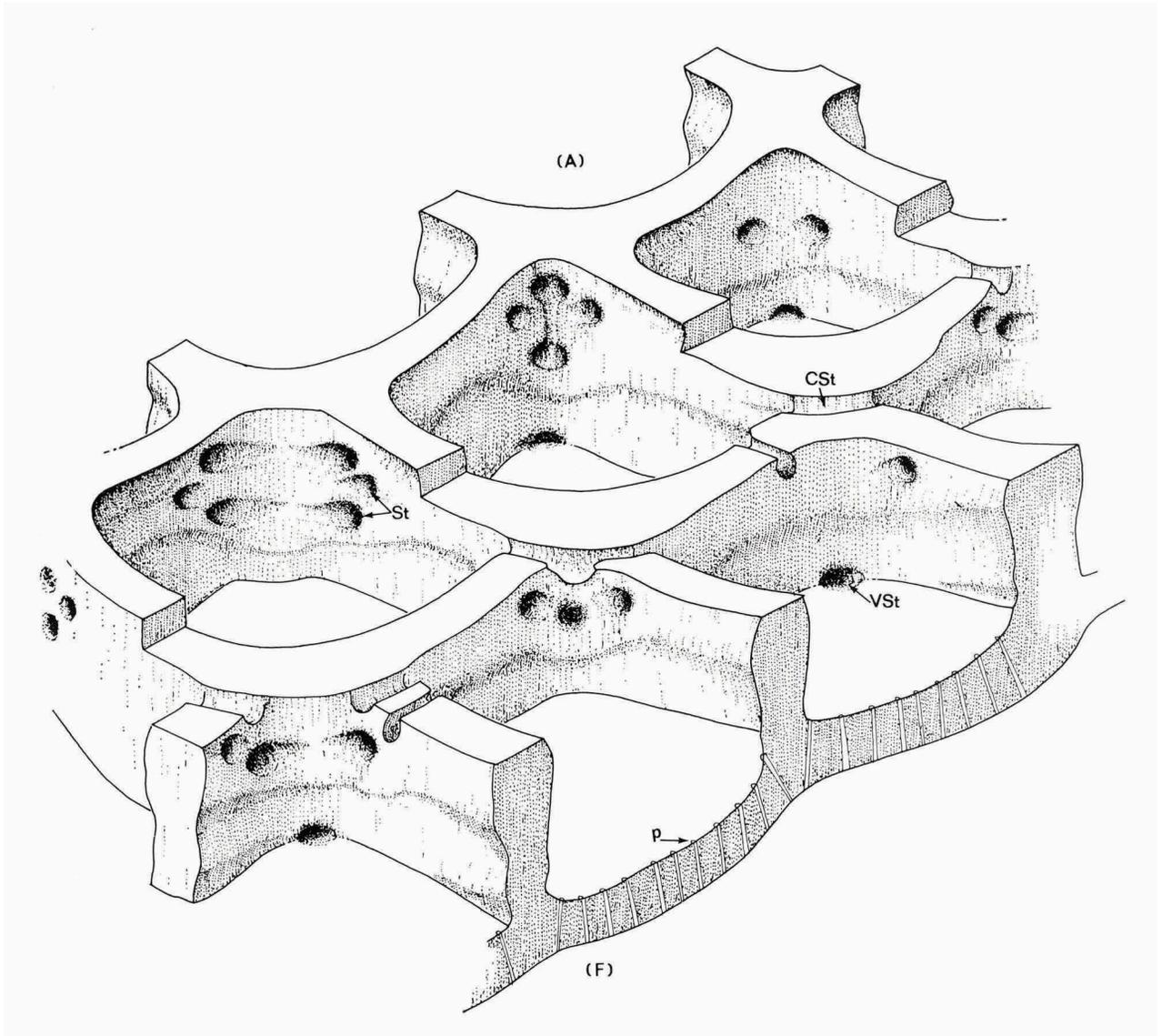


Fig. 29A. A schematic drawing of the stolon system in *Miogypsina* s.s.. One equatorial chamber possesses a maximum of 14 stolons: 12 horizontal stolons (6 inflow and 6 outflow) and 2 vertical stolons. The horizontal stolons form an inlet to the equatorial chambers, the vertical stolons form an inlet to the lateral chambers. Not every chamber has vertical stolons. The three pairs of equatorial chambers drawn one above the other have the same system.

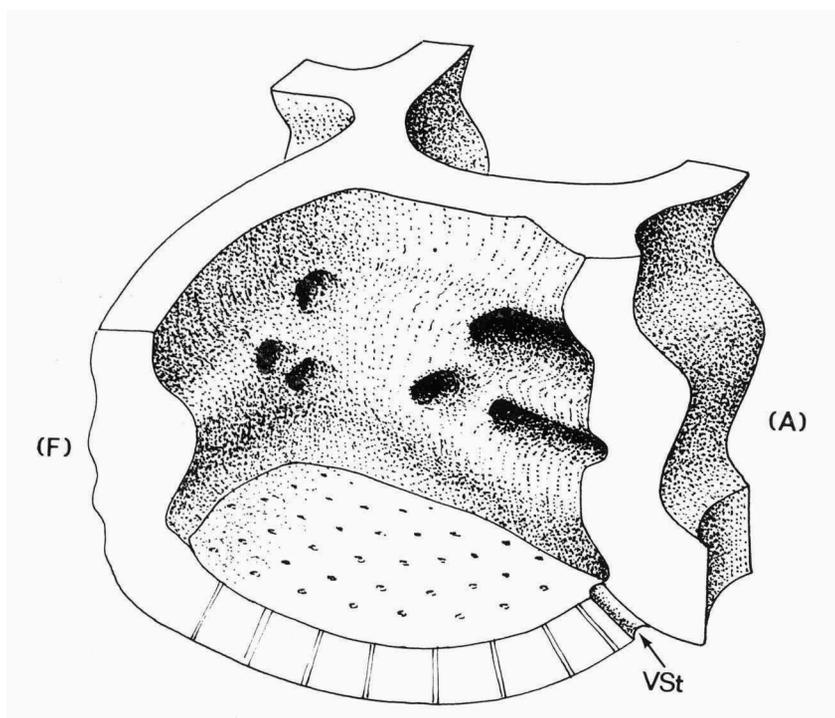


Fig. 29B. An apical-frontal view. To the right an inflow trio, to the left an outflow trio. The ridge on the frontal side in the equatorial chamber is visible.

When two inflow stolons are very close together they may grow together in several ways. The stolons of different trios may join forming a connection between two simultaneously formed equatorial chambers, i.e. Tan's concentric stolon (Pl. 27; Fig. 29). The third distal stolon of the trio serves as the inlet for protoplasm to the newly formed equatorial chamber. The process of growing together causes a decrease in the number of stolon openings.

In general two vertical stolons develop in one equatorial chamber. The vertical stolons are situated in opposite corners on the apical side of the equatorial chamber. Not all equatorial chambers have vertical stolons. The diameter of the vertical stolons is smaller than the diameter of the horizontal stolons (Pl. 28). The vertical stolons directed towards the apex form the inlet for protoplasm to lateral chambers which are located on the apical side of the corresponding equatorial chamber.

#### *Differentiation of stolon systems*

*Miogypsinoidea* shows the beginning of lateral chambers but does not yet have trios of stolons. However some equatorial chambers in some specimens have more than one stolon at the base of the septa; however a gradual and directional transition from the simple stolon type of *Miogypsinoidea* towards the complex stolon type of *Miogypsina* s.s. has not been encountered. The stolon system of *Miogypsina* s.s. as described in this paper was found in almost all specimens used in this study. Specimens of *Miogypsina* which have developed hexagonal chambers may possess an even more complicated, probably irregular system.

## LATERAL CHAMBERS

The secondary thickening (if present) of the lateral walls of the test in *Miogypsinoides* is lamellar, according to the model given by Smout, 1954. Tan assumed that the lateral chambers in Miogypsinidae could originate from the intraseptal canal system. In both cases it is assumed that the lateral chambers develop gradually.

A) *The lateral chambers originate from the vertical canal system*

Since the test of *Miogypsinoides* is asymmetrical (ventral and dorsal side) we might expect the origin of the lateral chambers on either side of the equatorial chambers to be different. As this is not the case we may assume that the disappearance of the septal flap and toothplate (i.e. canal system, see below) plays a major role in the formation of the lateral chambers; the disappearance causes a horizontal symmetry of the equatorial chambers. On the apical side of the equatorial chambers of *Miogypsinoides*, the vertical canal formed by toothplate and septal flap penetrates into the dorsal and the ventral sides of the test. When toothplate and septal flap disappear, two openings remain allowing a protoplasm stream to the lateral sides, i.e. two funnel-shaped connections (tubes) with a diameter larger than a pore are formed between the inner and outer protoplasm. As a result the openings become stolons and small lateral chambers are formed at the intersections of the septal walls of the equatorial chambers. The massive conical parts on both lateral sides of the equatorial chambers become smaller and between the pillars thus formed, the lateral chambers are arranged in regular tiers. The morphology of the stolon system of the lateral chambers during these stages is hard to trace.

B) *The lateral chambers originate from the horizontal lamination of the lateral part of the test*

The horizontal lamination seen in the test of *Miogypsinoides* is caused by the successive phases of growth. When a row of equatorial chambers is formed, the lateral test is probably thickened; then pillars develop as shown by Smout (1954, pp. 18, 19): the inflational or compound inflational-incised pillars. Strictly speaking we should distinguish between two possibilities here: (1) small cavities are formed between these pillars (i.e. in the vertical canal system, see also compound inflational residual pillars of Smout, 1954) or (2) they are formed in the pillars proper (i.e. the cavities are openings between the horizontal lamination; see Fig. 30; Pls. 30, 31, 32).

Regardless of these two possible developments the lateral chamber system would be much the same in A and B.

In rare specimens we find a lateral chamber system in the extreme lateral part of the test, i.e. it develops during a later stage of growth. These lateral chambers are formed by undulation of the lamina and are not assumed to have originated in a different way. These rare specimens, and those used for the hypotheses A and B which show the beginning of lateral chambers in a later stage, together provide morphological evidence for the theory that the subgenus *Miogypsina* has evolved from the subgenus *Miogypsinoides*.

The stages illustrated in Fig. 30 are all based on thin sections (Pls. 30-32); only the sequence is hypothetical.

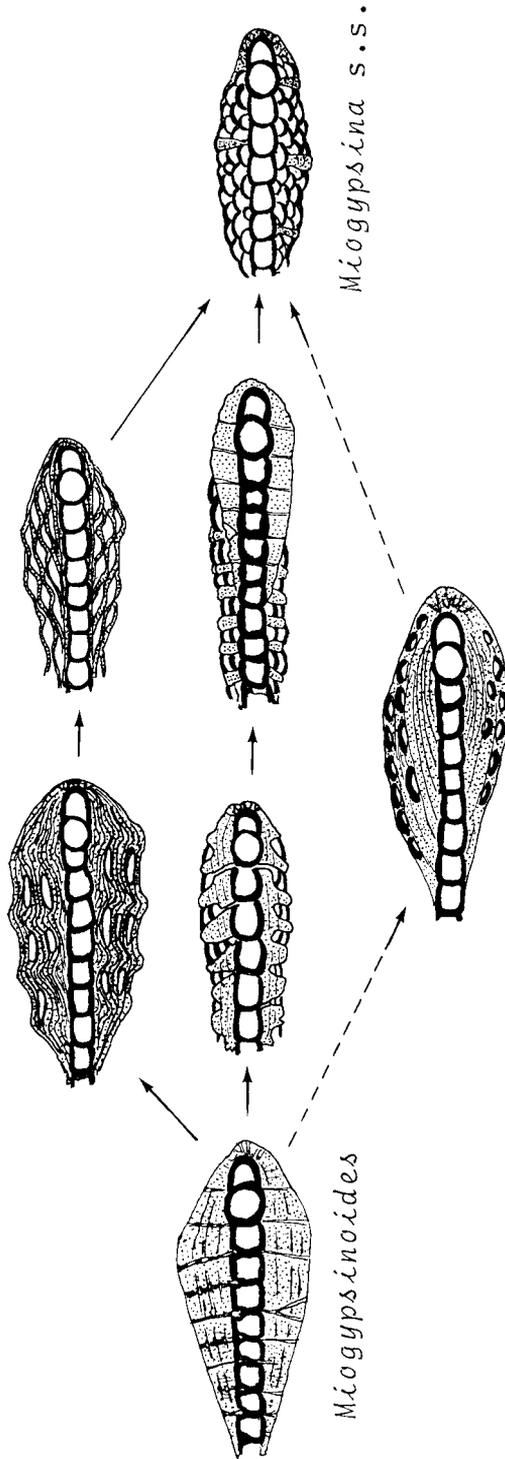


Fig. 30. Lateral chambers may originate from the vertical canal system (middle row) or from the horizontal lamination of the lateral part of the test (upper row). The specimens show the beginning of lateral chambers in a later stage of growth, and this may be morphological evidence for the theory that the subgenus *Miogypsina* evolved from the subgenus *Miogypsinoidea*. The sequence of the drawings is hypothetical.

## GROWTH OF THE EQUATORIAL CHAMBERS OF MIOGYPSINOIDES

Although we cannot study living specimens, we should be able to deduce the way of growth by examining abundant and well-preserved material. The sample of Estoti contains such specimens in which even the front of the last equatorial chamber formed is undamaged.

The S.E.M. micrographs clearly show the gradual growth of the septal flap on the outer side of the primary wall. It has been assumed that the septal flap was formed secondarily inside a chamber along the distal face of the preceding chamber. Figure 31 corresponds with Plate 33 and shows the gradual growth of the septal flap.

Fig. 31a shows two equatorial chambers with a perforated apertural face. In the recessed part between the two equatorial chambers the toothplate and the beginning of the septal flap are visible, as well as the apertures and the openings of the intraseptal canal system. The apertures are close together; between them the hooks of the two toothplates have merged. The apertures are surrounded by the rims of the toothplates, so that it looks as if there is only one opening. Ventral to the apertures the toothplate bends away from the primary wall. The two openings of the intraseptal canal system are seen. Towards the ventral side an opening is formed on the outside (not visible in this figure). Between the most ventral parts of the toothplates, the beginning of the perforated lateral side (roof) of the equatorial chambers is visible. Dorsal to the apertures the vertical canal (under the hook of the toothplate(s)) is open. Two extensions of the toothplate reach to the dorsal side of the equatorial chambers.

Fig. 31b shows that the imperforate septal flap grew gradually along the perforated distal faces of the equatorial chambers. The openings of the intraseptal canal system 'moved' towards the most frontal part of the equatorial chambers. The toothplates dorsal to the apertures merged and the vertical canal was lengthened.

Fig. 31c shows that the septal flap almost covers the entire apertural face of the equatorial chambers. The openings of the intraseptal canal system are located at the protruding parts of the equatorial chambers. The vertical canal is completed in the recessed part between the equatorial chambers, with an opening to the dorsal as well as to the ventral side of the test (not visible in this figure). Ventrally and dorsally parts of the perforated lateral walls of the equatorial chamber have already been formed.

Fig. 31d. The septal flaps are completed. Grooves along the face of the septal flap indicate the position of the apertures to be formed when the primary wall of the equatorial chamber is built. The hook of the toothplate has already formed a part of the vertical canal. The primary wall of the equatorial chamber to be formed is probably built during an instar, as no gradual growth of the chamber wall is seen.

## GROWTH STAGES OF MIOGYPSINA S.S.

Plates 17, 18, 34 and 35 show the various growth stages from the nucleoconch to the embryonic-nepionic apparatus.

Plate 17 shows a specimen which has not yet developed a first or a second primary auxiliary chamber. No secondary material can be observed on the test, so probably this is the earliest growth stage found in the present material. Compare

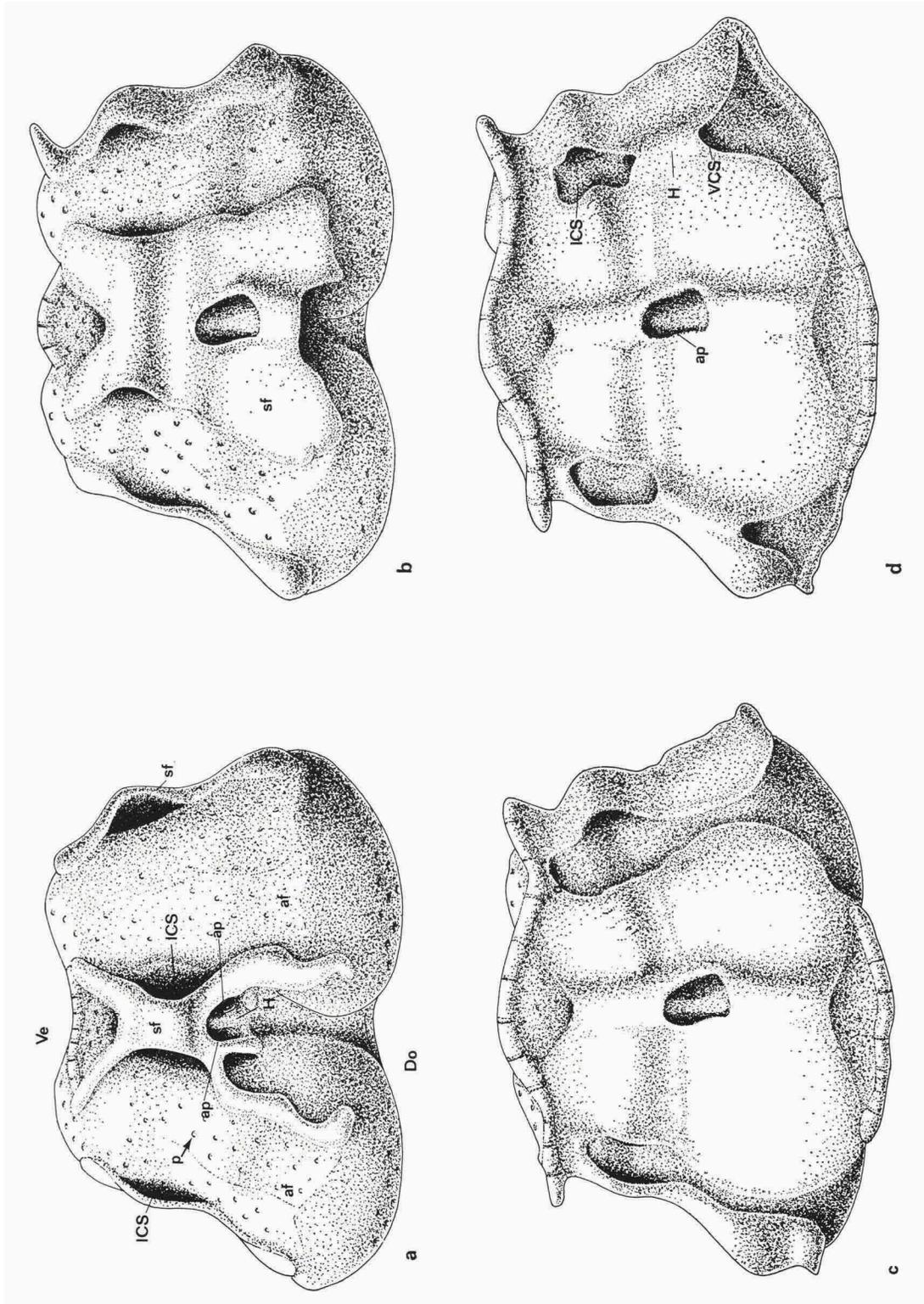


Fig. 31. The gradual growth of the septal flap (sf) along the apertural face (af) of the equatorial chambers of *Miogypsinoides*.

this with the two enlargements of the PA-II side (Pl. 19) which show the formation of secondary material (micrograph 2). The specimen on Plate 18 has not yet developed a PA-I or a PA-II, but already shows the beginning of the formation of the wall near the openings of the two deuteroconchal stolons. Furthermore the ornamentation of the lateral walls appears more distinct. This suggests the former existence of protoplasm at the outer surface of the test.

Plate 34 shows two specimens which have a first and a second primary auxiliary chamber. The marginal fringe is almost completely developed. The external ornamentation is even more accentuated. Small short 'needles' have been formed between the pores. The pores are more distinct than those seen in the specimen of Plate 17; in the second figure of Plate 34 the diameter of the external perforations of the pores near the apex is also larger. The latter specimen also shows the beginning of the development of the spiral chambers originating from PA-I and PA-II. The wall of the spiral chamber formed on the protoconch and on PA-I or PA-II is clearly visible. The initial formation of stolons, which are the inlets for the protoplasm to the next spiral chambers, can also be seen.

Plate 35 shows a complete embryonic-nepionic apparatus together with some equatorial chambers. The protoconch and the deuteroconch are still clearly visible since no lateral chambers have developed as yet. Two spirals originate from each auxiliary chamber, making the apparatus quadriserial. No embryonic-nepionic apparatus which shows the development of lateral chambers in this or earlier growth stages was found.

Most of the thin sections of *Miogypsina* s.s. show a dark line within the septa (Pl. 38). Near the centre of the equatorial layer this inner lining wedges out; thus in horizontal sections the dark line does not lie in the middle of the septa. Sometimes it is impossible to differentiate between the two layers of the septa. This may lead to the conclusion that *Miogypsina* s.s. is monolamellar. On the lateral sides of the equatorial chambers the dark line is distinct. The inner lining is connected to the 'roofs' of the equatorial chambers in such a way that interlamellar spaces are often formed. Therefore *Miogypsina* s.s. may possess primarily double septa (Pl. 38).

#### ORNAMENTATION

For a study of the ornamentation on the lateral walls of the Miogypsinidae the material should be well-preserved. The lateral walls of *Miogypsinoides* generally show a regular pattern of pustules or striae situated exactly above the cavities of the equatorial chambers. So the position of the spiral chambers and the equatorial chambers can already be seen from the outside. The lateral chambers and the equatorial chambers of *Miogypsina* s.s. show an irregular distribution of smaller pustules; one or more pustules are situated on the lateral walls of the chambers. On the outer surface between the external perforations of the pores in the lateral walls are small needles (Pl. 36). The difference in the ornamentation of well-preserved specimens is quite sufficient to distinguish *Miogypsinoides* from *Miogypsina* s.s.

Small juvenile specimens of *Miogypsina* s.s., in which lateral chambers have not yet developed, already show the fine scatter of pustules. A transition between the ornamentation of *Miogypsinoides* and *Miogypsina* s.s. has not been found.

### *Tubules*

The pores of *Miogypsina* s.s. (from East Java and Madura) contain tubules (Pl. 37) (Reiss, 1963, 1969; Banner & Williams, 1973). The tubules may be connected with the coating of the internal surface of the equatorial chambers (lateral chambers), i.e. the tubules may be the extensions of the coating from the internal surfaces. On the external surface the tubules are visible as ring-like ridges (Pl. 37).

### NEEDLES

Needles are often seen in equatorial chambers of *Miogypsinoides*. To the authors knowledge they have never been described before. The needles were observed in specimens from Larat, Anse deï Bano and Estoti, especially in specimens which were assigned to the subgenus *Miogypsinoides*. The needles may be short or long. A short needle is equal in length to the radius of the equatorial chamber. The longer needles may cross through as many as 7 of 8 rows of equatorial chambers and penetrate the dorsal wall of the equatorial chamber (Pl. 39). The needles grow from the apical side of the equatorial chamber towards the frontal side; generally the diameter of the needles increases towards the front (Pls. 39, 41). In one specimen a needle was found which had grown from the frontal side towards the apex (Pl. 41).

In reflected light the needles are transparent. In several thin sections the needles appear hollow, but the existence of a canal within the needles could not be ascertained. The needles may be highly recrystallized; notably this was observed in *Miogypsinoides dehaartii* (Pl. 40).

All needles were situated in the dorsal part of the equatorial chamber (Pls. 39, 40). The needles and the equatorial chamber appear to have grown independently because at the intersections of the equatorial chamber wall and the needles, no deformation of the wall or the needles is apparent.

It seems unlikely that needles only were formed in an environment rich in calcareous material; specimens with thin chamber walls show needles just as often as specimens with thick chamber walls. There is no regular pattern in the occurrence of needles in the equatorial chambers. The function as well as the origin of the needles is a complete mystery to the author.

### PROTOCONCH DIAMETER

#### *Introduction*

In general the adult specimens of *Miogypsinoides* have a larger test, thicker septa of the equatorial chambers, a larger diameter of the frontal equatorial chambers and a larger protoconch diameter as compared with *Miogypsina* s.s. In most of the diagrams (Figs. 35-46) the diameters of the protoconches of *Miogypsinoides* and *Miogypsina* s.s. overlap partly.

According to Drooger and Raju (1973) the difference in protoconch diameter between both subgenera increases during evolution. They described the general increase in protoconch diameter in the Miogypsinidae in three geographical regions, the American, Indo-pacific and Mediterranean regions. Although the general characters of *Miogypsinoides-Miogypsina* s.s. lineages is the same in all three regions, the development differs in detail from one region to another; more-

over within one region a certain differentiation into subregions is apparent. The wide scatter in the diagrams may be due to environmental influences (Drooger & Raju, 1973). Yet an indication of a substantial difference in environment is difficult to find in the sediments concerned and the possibility that assemblages have been mixed by transportation cannot be excluded. As long as there are not sufficient data about living Foraminifera in various environments, any explanation of the fluctuations in the diameter of the protoconch remains highly hypothetical.

A thorough study of a subregion may contribute to a better understanding of the changes in protoconch diameter of the *Miogypsinoides-Miogypsina* s.s. lineages. A good example is the study of protoconch diameter in the subregion India (Raju, 1974). Separate trends of the species from various subregions of the above-mentioned major region are conspicuous within the wide scatter diagram of Drooger and Raju (1973).

#### *Protoconch diameter and its relation to X and $\gamma$*

The trend in X,  $\gamma$  and diam. I for *Miogypsinoides* is only weakly reflected in *Miogypsina* s.s. If it could be shown that these weak parallel trends are significant in a statistical sense, then the deviations could be explained by differential reactions to the same environmental conditions. Then the material could be explained as a mixture of faunas from slightly different stratigraphical levels.

The difference in protoconch diameter between the samples is less distinct for *Miogypsina* s.s. than for *Miogypsinoides*. Comparison of Fig. 32a, b and c shows that the parameters X,  $\gamma$  and diam. I in *Miogypsina* s.s. might be inter-related; the same holds for *Miogypsinoides*. This seems especially so when comparing X and  $\gamma$  in *Miogypsinoides* which show the same fluctuations. In most of the localities (Fig. 32a) *Miogypsinoides* shows a slightly lower X, a less negative  $\gamma$  and a larger diam. I in comparison with *Miogypsina* s.s. The difference between the protoconch diameter of *Miogypsinoides* and that of *Miogypsina* s.s. barely increases; in the stratigraphically lower samples (FR1120 and M51) the difference even decreases. Above M51 the difference increases rapidly but decreases again in the uppermost sample (M61). The scatter diagrams X-diam. I (Fig. 35-46) often show considerable overlap in protoconch diameter with the exception of the samples Christus 1, M64, M75 and M61, which show a complete separation of the subgenera (Figs. 36, 44, 45, 46).

Figure 33 is the scatter diagram for the means of X and diam. I. The solid lines in this figure connect the sample of one section according to their stratigraphical position. The X-diam. I scatter diagram for *Miogypsinoides-Miogypsina* s.s. assemblages from the material studied in this paper, and the data from *Miogypsina intermedia* from Sardinia (Smit, 1974) and the data from the *Miogypsina* s.s. from N.W. Greece (Mulder, 1975), complete in some respects the diagram for the Mediterranean region (Fig. 34; Drooger & Raju, 1973, fig. 4).

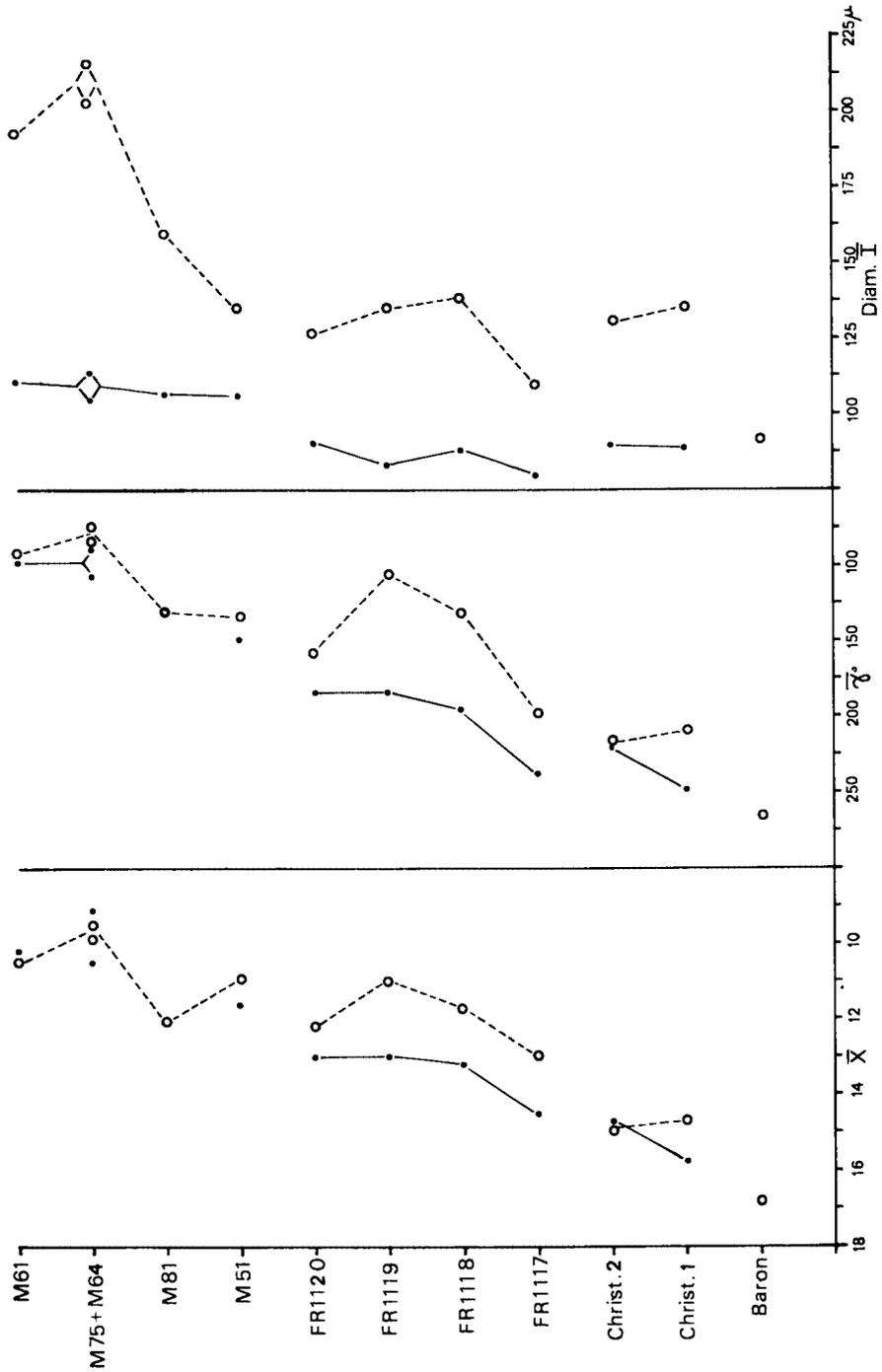


Fig. 32, a, b, c. The trend in parameters  $M_x$ ,  $M_\gamma$  and  $M_{diam. I}$ .

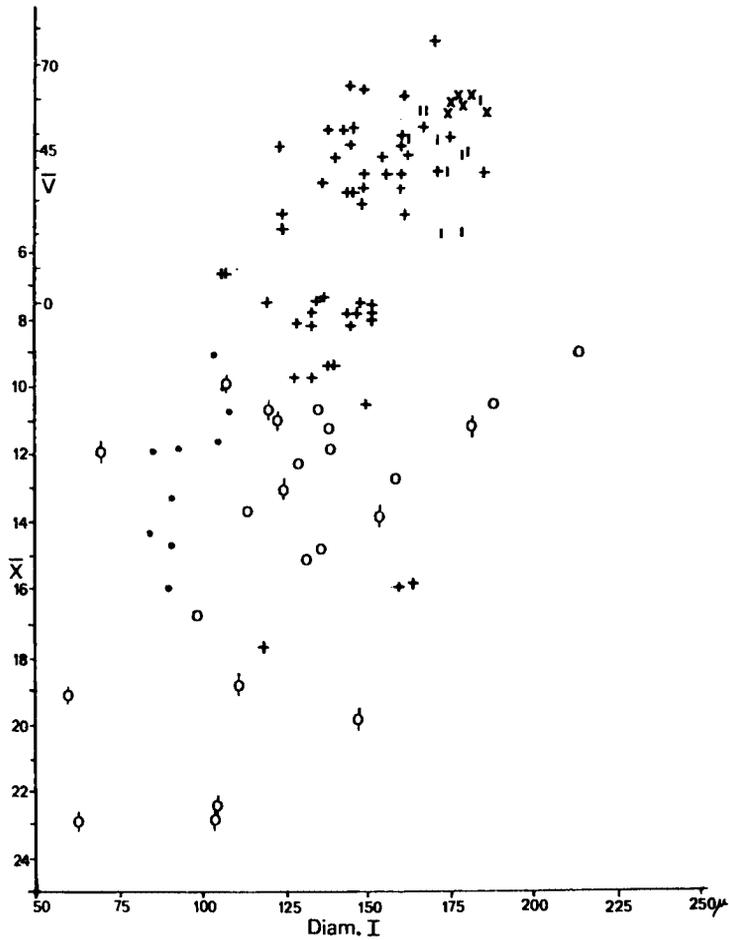


Fig. 33. Relation between mean protoconch diameter and values of the  $M_X$ - $M_Y$  scale in *Miogypsinoides-Miogypsina* s.s. assemblages of the Mediterranean region (including Africa and Europe, Drooger and Raju, 1973).

- $\phi$  = *Miogypsinoides* (Drooger & Raju, 1973)
- $o$  = *Miogypsinoides* (present study)
- $+$  = *Miogypsina* s.s. (Drooger & Raju, 1973)
- $\cdot$  = *Miogypsina* s.s. (present study)
- $\times$  = *Miogypsina intermedia* (Smit, 1974)
- $l$  = *Miogypsina* s.s. (Mulder, 1975)

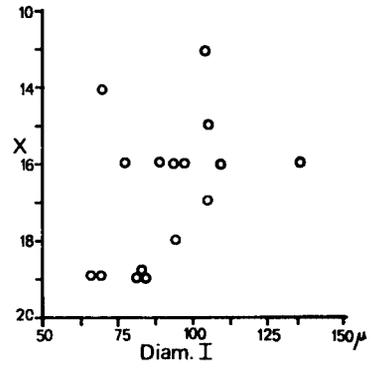
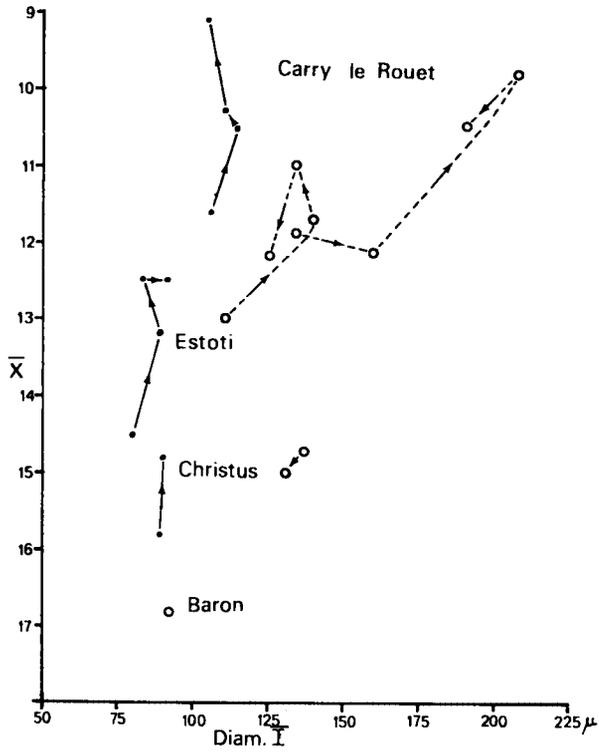


Fig. 35. Baron, X-diam. I.

Fig. 34. Diagram of  $M_X$  versus  $M_{diam. I}$ .

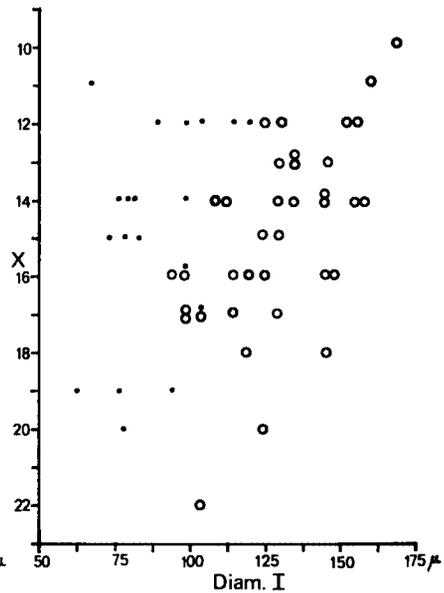
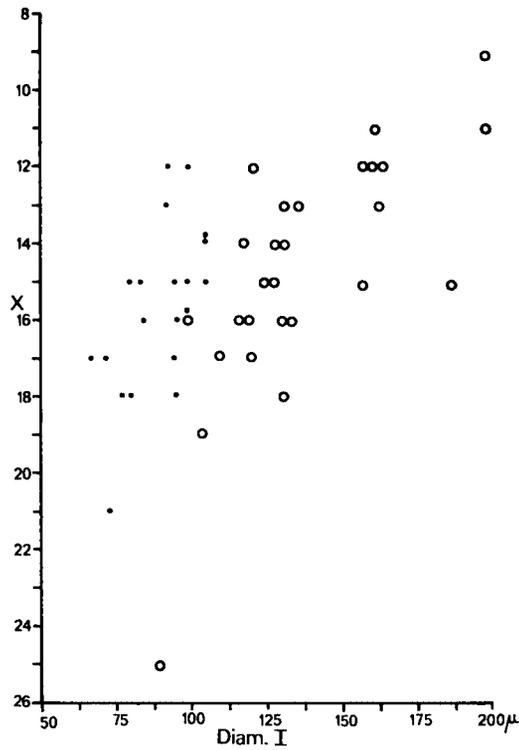


Fig. 36. Christus 1, X-diam. I.

Fig. 37. Christus 2, X-diam. I.

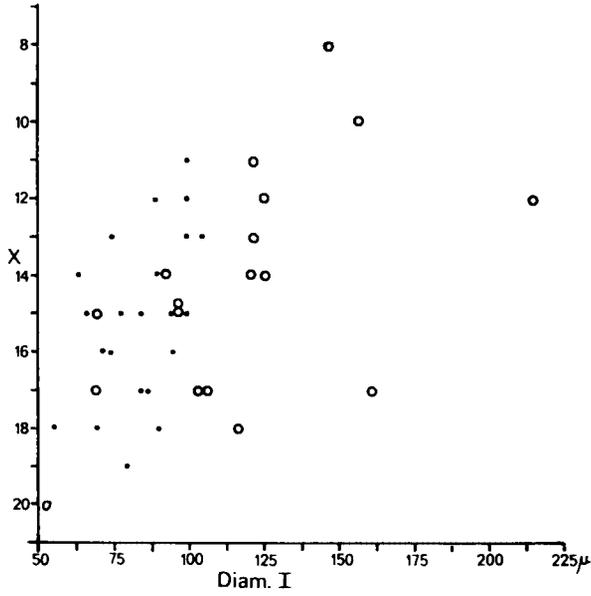


Fig. 38. Estoti FR1117, X-diam. I.

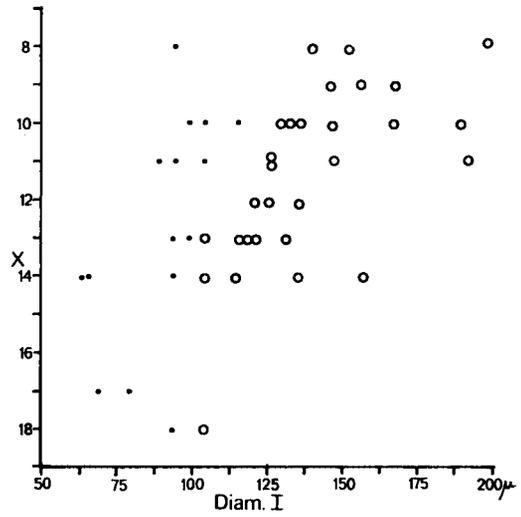


Fig. 39. Estoti FR1118, X-diam. I.

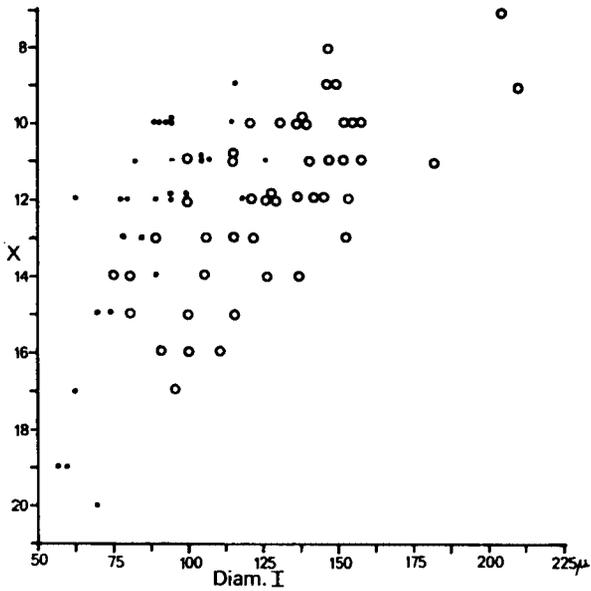


Fig. 40. Estoti FR1119, X-diam. I.

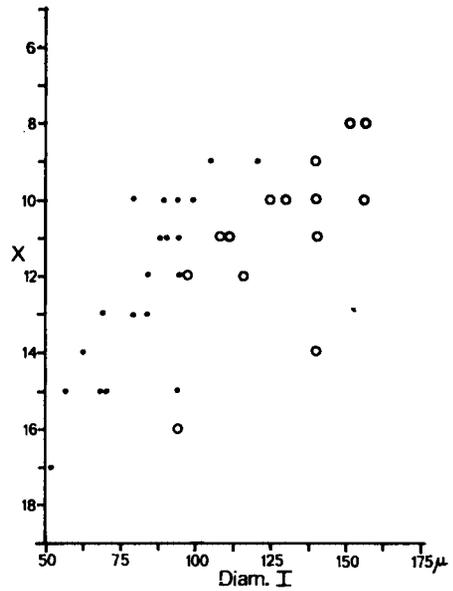


Fig. 41. Estoti FR1120, X-diam. I.

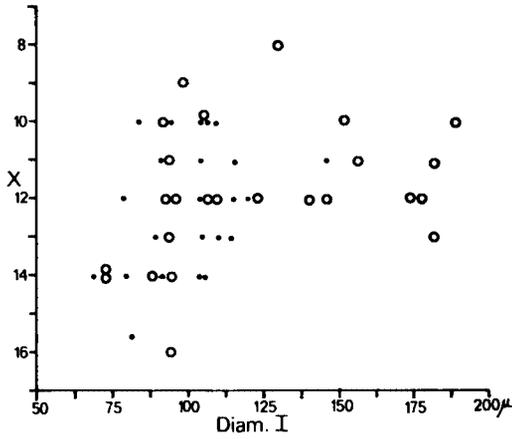


Fig. 42. M51, X-diam. I.

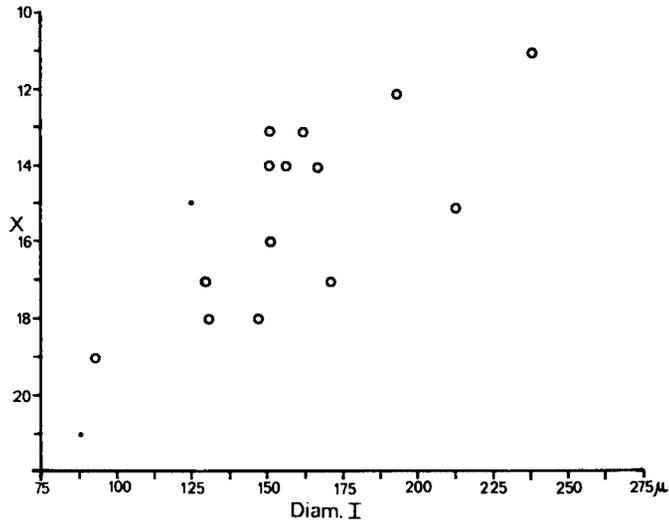
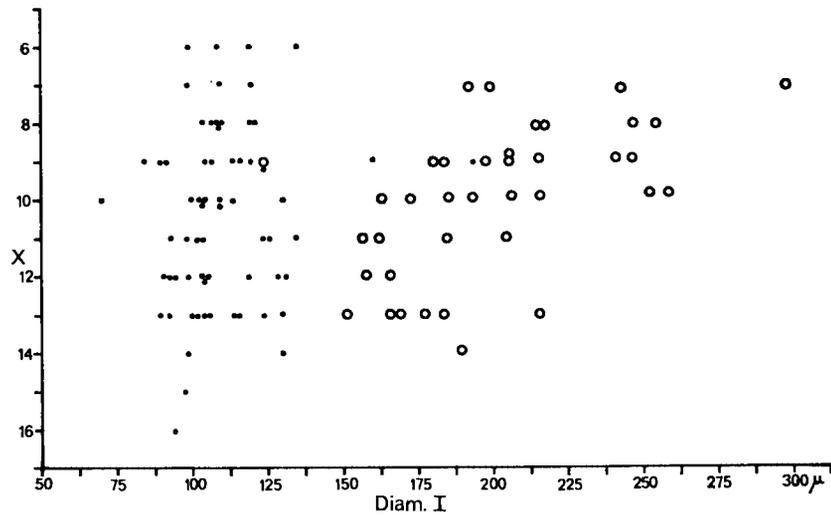


Fig. 43. M81, X-diam. I.

Fig. 44. M64, X-diam. I.



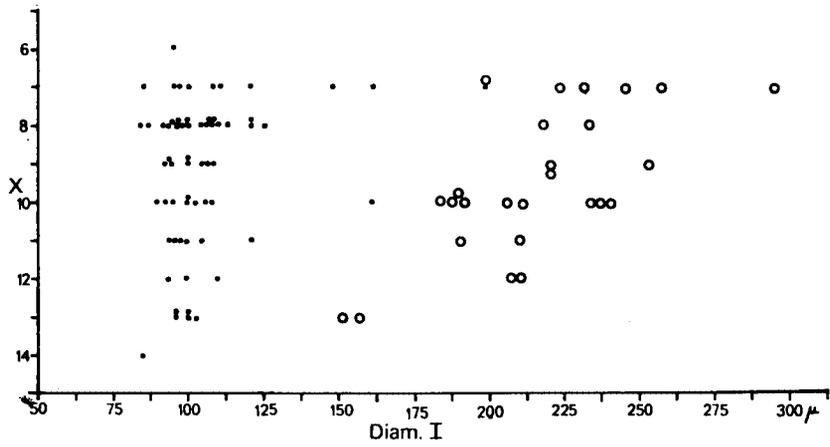


Fig. 45. M75, X-diam. I.

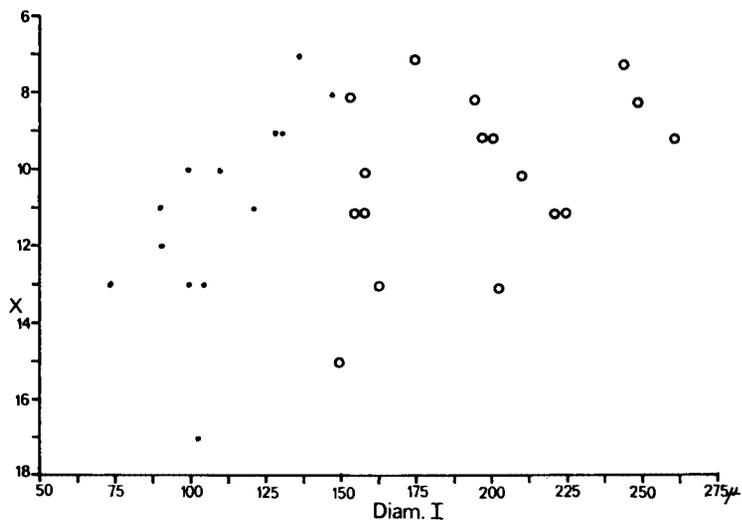


Fig. 46. M61, X-diam. I.

## Chapter V. Comparison between *Miogypsinoidea* and *Miogypsina* s.s.

### SUMMARY OF MORPHOLOGICAL DIFFERENCES

Table 2. Summary of morphological characteristics in *Miogypsinoidea* and *Miogypsina* s.s.

Characteristics	<i>Miogypsinoidea</i>	<i>Miogypsina</i> s.s.
Lateral chambers	absent	present
Canal system	present	absent
Toothplate and septal flap	present	absent
Ventral and dorsal side (recognizably differentiated)	present	absent
Doubling of the septa	secondarily	primarily(?)
Relative diameter of the protoconch	large	small
Number of stolons at base of septa (in the material studied)	one	three
Vertical stolon	absent	present
Adult specimens (generally)	large	small
Equatorial chambers	asymmetrical	symmetrical
Ornamentation	striae, large pustules, pillars	small pustules, pillars present

Lateral chambers, with the transitional forms shown in Chapter IV, p. 46, seem to occur in all samples in which *Miogypsinoidea* as well as *Miogypsina* s.s. has been found.

The canal system formed by toothplate, septal flap and primary wall (outer layer) in *Miogypsinoidea* is absent in *Miogypsina* s.s. In *Miogypsina* s.s. a dark line is recognized, separating outer layer and inner lining; often interlamellar spaces (or intraseptal passages, see Chapter IV, p. 23) have developed between these lamellar structures. This interlamellar space which is very narrow is formed by different structural elements in comparison with *Miogypsinoidea*; and therefore not similar to the intraseptal canal system of *Miogypsinoidea*.

A ventral and a dorsal side of the test cannot be established in this way for *Miogypsina* s.s. The doubling of the septa of the equatorial chambers (and spiral chambers) in *Miogypsinoidea* is obviously secondary, whereas the septa in *Miogypsina* s.s. are probably primarily doubled (the possibility of monolamellar septa in *Miogypsina* s.s. is not excluded).

The diameter of the protoconch is not a useful means of distinguishing between the two subgenera. Although the protoconch of *Miogypsinoidea* is generally larger than the protoconch of *Miogypsina* s.s. (Chapter IV, p. 51) it should be pointed out that in the other regions this difference is not necessarily present (Mulder, 1975). Furthermore the protoconch diameter seems to be highly influenced by environmental conditions.

The stolon system of both subgenera in the material studied is clearly different; gradual transitions between the stolon systems are not found. The development of lateral chambers coincides with the presence of a vertical stolon in the equatorial chambers which is absent in *Miogypsinoidea*.

In the material studied the adult specimens of *Miogypsinoidea* are generally larger than the adult specimens of *Miogypsina* s.s., in contrast to the dimension of adult microspheric specimens of these subgenera.

The shapes of the equatorial chambers in *Miogypsinoides* and in *Miogypsina* s.s. are different. This dissimilarity in shape is probably due to the difference in stolon system and the disappearance of the septal flap and toothplate. Distinct transitional forms between the two types of equatorial chambers are not found.

In all samples used in this study the difference in the ornamentation of well-preserved specimens was quite sufficient to distinguish between *Miogypsinoides* and *Miogypsina* s.s.

#### EVOLUTIONARY TREND AND PHYLOGENY

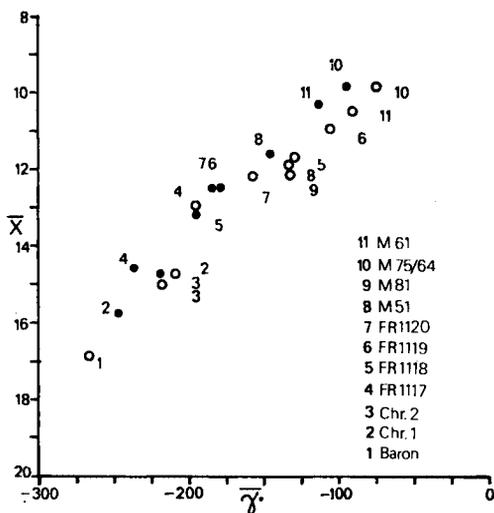
The 'nepionic acceleration', first described by Tan (1936, 1937) and later elaborately investigated by Drooger (1952, 1964), is beyond doubt a primary trend in the development of Miogypsinidae. However studies of Miogypsinidae in short stratigraphical intervals in various regions have revealed fluctuations in this development. The samples from Estoti and Carry le Rouet are from a single section; the data for these samples showed fluctuations in  $M_x$ ,  $M_\gamma$  and  $M_{diam. I}$  (Figs. 32, 33). This variation can be seen in the diagram  $M_x$  versus  $M_\gamma$  (Fig. 47). Nevertheless the 'nepionic acceleration' is satisfactorily confirmed for the larger stratigraphical units. The variable increases and decreases in diam. I prove that its taxonomic value should be considered small, as previously stated by Drooger (Drooger, Kaasschieter & Key, 1955).

The polyphyletic or monophyletic origin of the Miogypsinidae was discussed in detail by Drooger. Another problem is the development from *Miogypsinoides* to *Miogypsina* s.s. (Drooger, Kaasschieter & Key, 1955; Drooger, 1964).

The general morphological internal and external similarities such as the shape of the test and the size and arrangement of the embryonic, spiral and equatorial chambers indicate a close relationship between the two subgenera. The gradual origin of the lateral chambers and the stratigraphically later appearance of *Miogypsina* s.s. combined with the above-mentioned similarities suggested that *Miogypsina* s.s. has evolved from *Miogypsinoides*. Some arguments for different ancestors are however also present: not all morphological features in *Miogypsinoides* show a gradual change towards comparable characteristics in *Miogypsina* s.s. The question remains why no distinct transitional forms of septal flap and toothplate, canal system, stolon system and ornamentation have been found. Perhaps when the functions of the septal flap and toothplate and intraseptal canal system are understood, this problem will be solved.

Three possibilities exist:

- 1) *Miogypsinoides* and *Miogypsina* s.s. evolved from different rotaliid ancestors; however this seems unlikely.
- 2) Somewhere in a restricted span of time *Miogypsina* s.s. originated from *Miogypsinoides*: parallel evolution followed without any genetic relationship with *Miogypsinoides* which formed a separate stock. Migration (rafting in the embryonic stage) ensured the occurrence of *Miogypsina* s.s. in various geographical regions. The absence of transitional forms of the septal flap and toothplate supports this possibility.
- 3) *Miogypsina* s.s. evolved from *Miogypsinoides* when and where the necessary "favourable" conditions were present. This hypothesis, although it is contradicted by the overall development of Miogypsinidae, is supported by the observation of transitional forms of the features of the lateral chambers. The author of this paper favours this possibility.

Fig. 47. Scatter diagram of  $M_x$  versus  $M_\gamma$ .

#### ECOLOGY

Although a general trend in the parameters  $M_x$ ,  $M_\gamma$  and  $M_{diam. 1}$  is confirmed, minor variations disturb the trend within small stratigraphical intervals. These fluctuations may be due to reworking of earlier sediments or environmental conditions such as temperature, depth, salinity, turbulent or stagnant water or the amount of illumination available for the photosynthesis of the commensal algae (see Drooger & Raju, 1973). Unfortunately, data revealing the environmental conditions in sufficient detail are absent.

## Appendix

### DIFFERENTIATION BETWEEN MIOGYPSINOIDES AND MIOGYPSINA S.S. IN A SAMPLE FROM LARAT, MOLUCCA ISLANDS, INDONESIA

#### Introduction

The sample L20 from Larat is discussed here for the following reasons. The sample shows a differentiation between *Miogypsinoidea* and *Miogypsina* s.s. at a high stratigraphical level; the sample contains a fine and a coarse fraction; Dr R. A. Lagaay studied the bryozoan fauna which provided information on the environmental conditions; the stratigraphical position of the sample is well-known.

It is probable that the specimens belonging to the subgenus *Miogypsina*, referred to here as *Miogypsina borneensis*, are a mixture of *Miogypsina tani* and *Miogypsina globulina*. The conical form of *Miogypsinoidea* – *Miogypsinoidea dehaartii cupulaeformis* – was not included in the biometrical study, as it was impossible to acquire sections exactly through the embryonic apparatus. In the investigation of this sample the author was only concerned with the separation of the two subgenera on the basis of the presence or absence of lateral chambers.

### Locality and material

Four samples were available: L7, L14, L9 and L20. The sample studied (L20) is from the central part of the island Larat, 3.5 km south of Kalaan Lama; it consists of foraminiferal limestone. The assemblage was taken near the type locality Larat by Dr F. Weber (see also Drooger, 1953, van der Vlerk, 1966).

Environment: according to Lagaay (see Lagaay in van der Vlerk, 1966) the bryozoan fauna is typical for tropical waters and is classified as an assemblage of *Nellia*, *Vincularia* (s.s.), *Sertellidae* and *Margaretta*. Its depth is estimated to have been between 18 and 55 m. Preservation: unfortunately the specimens are recrystallized, cement has formed on the chamber walls and the finer structures are obscured.

### Classification

In this material it was possible to distinguish between the subgenus *Miogypsinoides*, referred to here as *Miogypsinoides dehaartii*, and the subgenus *Miogypsina*, referred to here as *Miogypsina borneensis* Tan Sin Hok, 1936a. A conical variety of *Miogypsinoides* is referred to as *Miogypsinoides dehaartii cupulaeformis*.

Tan (1936a, p. 53, pl. 1, figs. 18u, 19; pl. 2, fig. 1) described *Miogypsina borneensis* as an assemblage of uniserial specimens, with an incomplete spiral, one stolon in the first primary auxiliary chamber (PA-I) and equatorial chambers of arcuate, ogival or sometimes hexagonal shape. According to Tan no second primary auxiliary chamber (PA-II) is present in *Miogypsina borneensis*. Therefore Drooger (1952, p. 52) proposed the name *Miogypsina tani* for an assemblage in which less than 50% of the sample may have a second primary auxiliary chamber, with values of  $M_x$  below 9 and a negative  $M_\gamma$ . *Miogypsina tani* was originally described from Costa Rica and later from Italy and France.

Raju (1974) stated that *Miogypsina borneensis* is used now in the typological sense for widely different assemblages (including those with a positive  $M_\gamma$ ), and leads to confusion when using this name for assemblages defined numerically. An assemblage with a positive  $M_\gamma$  and a value of  $M_v$  (Drooger, 1952) between zero and 45 in which more than 50% of the sample possesses a second primary auxiliary chamber is named *Miogypsina globulina*.

Because it was found that in the sample from Larat a number of the individuals of the subgenus *Miogypsina* have a second primary auxiliary chamber and the values for  $M_\gamma$  were both highly negative and positive, the author maintained the species name *Miogypsina borneensis* to encompass all individuals belonging to the subgenus *Miogypsina* in the sample from Larat.

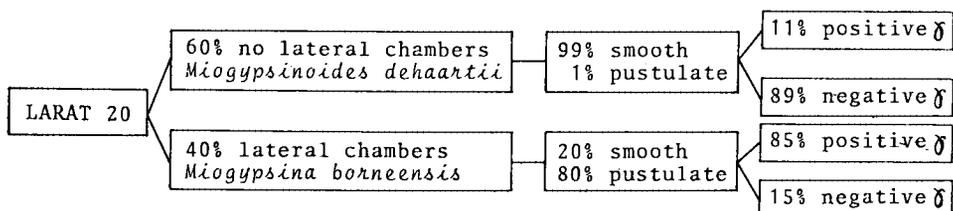


Fig. 48. Differentiation between *Miogypsinoides dehaartii* and *Miogypsina borneensis*.

*Comparison of Miogypsinoidea dehaartii and Miogypsina borneensis*

Van der Vlerk (1966) observed that the differentiation between *Miogypsinoidea dehaartii* and *Miogypsina borneensis* is quite difficult. At that time distinction was made on the basis of either a horizontal or a vertical section. Since the X-ray method provides both vertical and horizontal sections of the specimen and since the presence of an intraseptal canal system is used as an aid to identify these species, the distinction has become much easier.

For the description of *Miogypsinoidea dehaartii*, see van der Vlerk (1924, 1966) and Drooger (1953); for *Miogypsina borneensis*, see Tan Sin Hok (1936a). The description of *Miogypsinoidea dehaartii* may be summarized as follows:  $M_x$  up to 9,  $M_\gamma$  usually negative; surface smooth; no pillars or pustules; lateral wall lamellar; no lateral chambers.

The corresponding characteristics of *Miogypsina borneensis* are:  $M_x$  up to 9,  $M_\gamma$  usually positive; pillars and pustules present; lateral chambers present.

In general the deuteroconch in *Miogypsinoidea dehaartii* and *Miogypsina borneensis* is located at the apex; there are no spiral chambers or equatorial chambers between the deuteroconch and the apex. The equatorial chambers are oval to rhombic in shape. The main difference between *Miogypsinoidea dehaartii* and *Miogypsina borneensis* is that the latter has lateral chambers and no intraseptal canal system (Pl. 42).

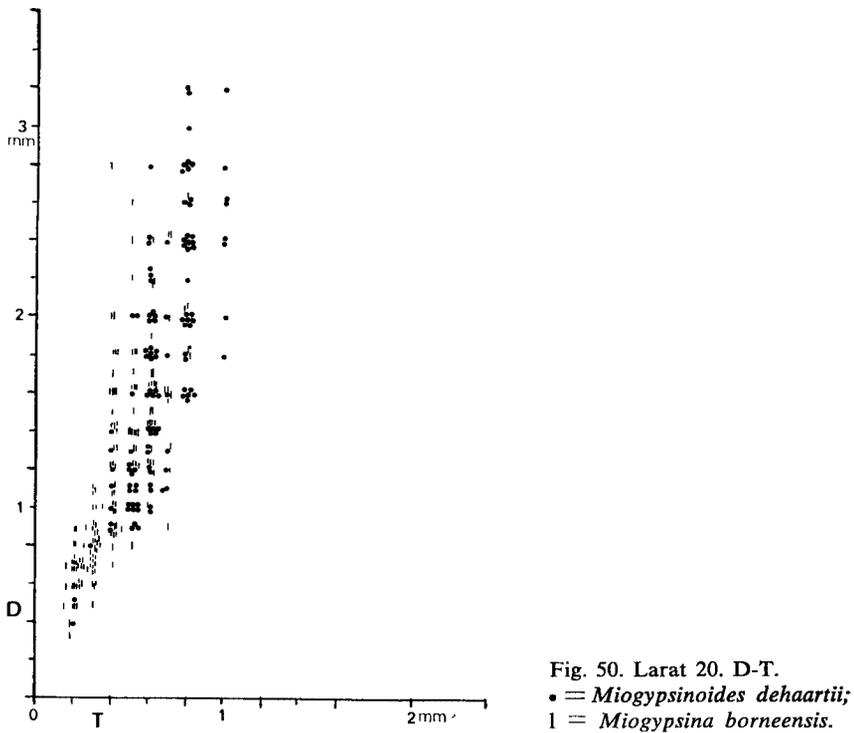
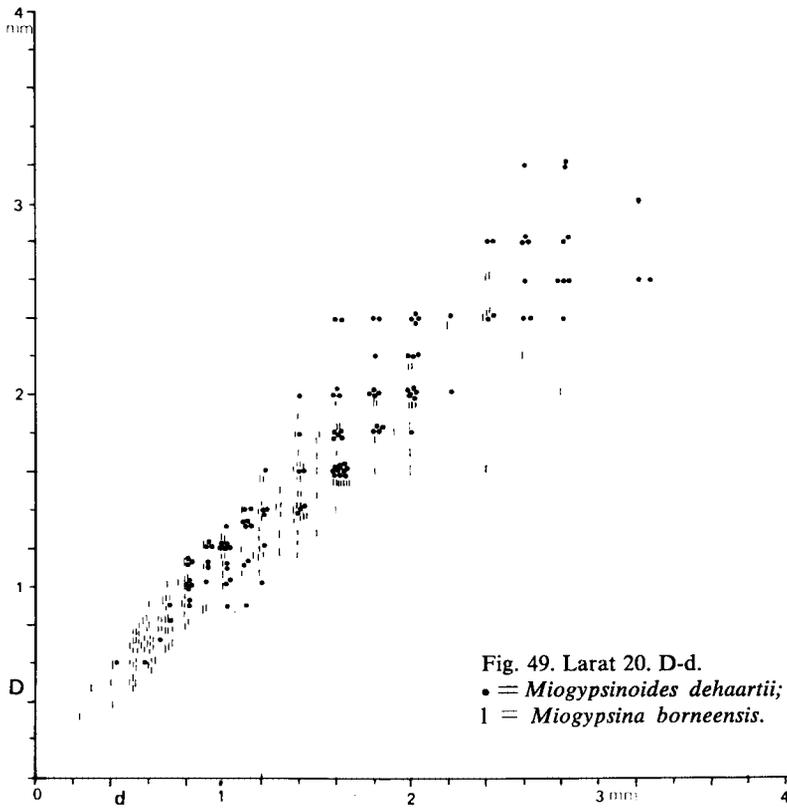
The assemblage of smooth and pustulate specimens has been split into two groups on the basis of the presence of lateral chambers: 60% showed no lateral chambers and have been assigned to *Miogypsinoidea dehaartii*; 40% showed the presence of lateral chambers and have been assigned to *Miogypsina borneensis* (Fig. 48). In *Miogypsinoidea dehaartii* 99% had a smooth outer surface; in *Miogypsina borneensis* 20% had a smooth outer surface. In *Miogypsinoidea dehaartii* the ratio between a positive  $\gamma$  and a negative  $\gamma$  was 11% to 89%; in *Miogypsina borneensis* the ratio between a positive  $\gamma$  and a negative  $\gamma$  was 85% to 15% (Fig. 48). The occurrence of intermediate forms makes it reasonable to assume that *Miogypsina borneensis* is closely related to *Miogypsinoidea dehaartii* and that one might have evolved from the other (see Chapter IV, Fig. 30; Chapter V, p. 60). Moreover, specimens which are transitional between *Miogypsinoidea dehaartii* with a flat test and *Miogypsinoidea dehaartii cupulaeformis* with a conical test also occur (Fig. 60).

*Size and shape of the test*

Figures 49, 50 and 51 show the growth of the tests of *Miogypsinoidea dehaartii* and *Miogypsina borneensis*. There is hardly any difference. The difference in lateral growth which is seen in the specimens from France is not visible here, due to the rather lamellar lateral growth of *Miogypsinoidea dehaartii* (Pls. 30, 31). The somewhat larger size of the test of the adult specimens of *Miogypsinoidea dehaartii* is the only minor difference.

The difference in the diam. I of the two subgenera (Fig. 55) is less distinct than in samples M64, M75 and M61 from France (Chapter VI, p. 71). Due to this slight difference in diam. I and the overlap for X, no clear separation is found in the scatter diagram diam. I versus X (Fig. 56).

Due to the more conspicuous difference in  $\gamma$ , the distinction between both subgenera is clear in the scatter diagram diam. I versus  $\gamma$  (Fig. 57).



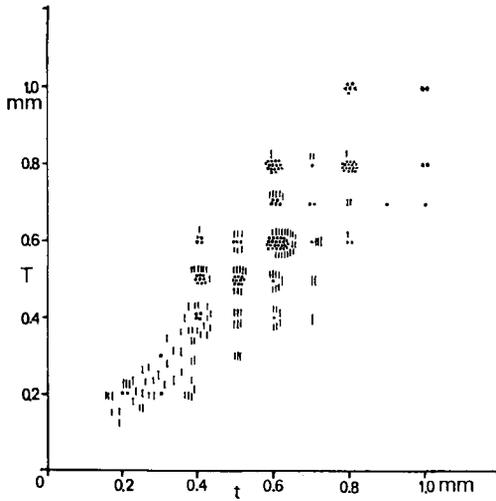


Fig. 51. Larat 20. T-t.  
 • = *Miogypsinoidea dehaartii*;  
 I = *Miogypsina borneensis*.

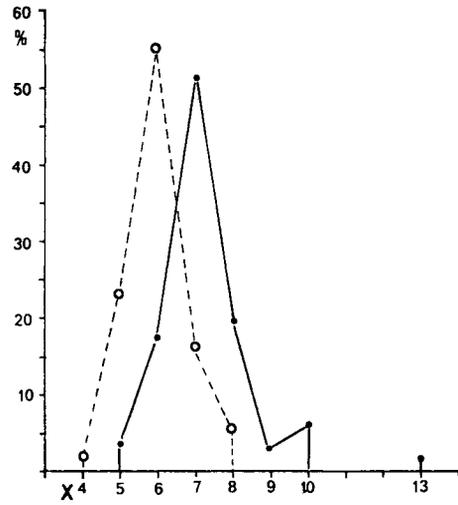


Fig. 52. Larat-20. The values for parameter X. The histogram shows an overlap. *Miogypsinoidea dehaartii* shows a maximum at X=7 and *Miogypsina borneensis* a maximum at X=6.  
 --- = *Miogypsina borneensis* (N=64);  
 — = *Miogypsinoidea dehaartii* (N=76).

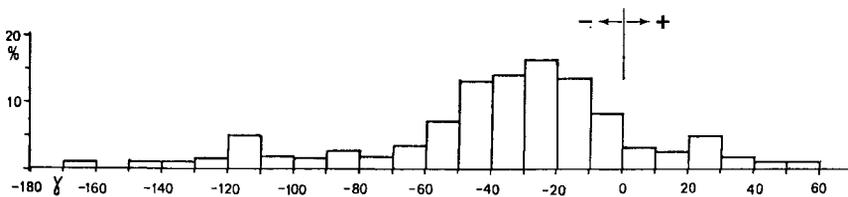
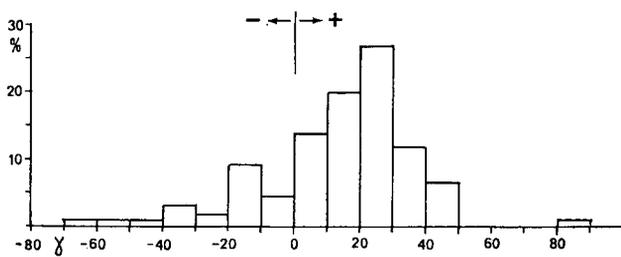


Fig. 53. Histogram of  $\gamma$  for *Miogypsina borneensis* and *Miogypsinoidea dehaartii*.  $\gamma$  is less variable in *Miogypsina borneensis* than in *Miogypsinoidea dehaartii*. Although there is an overlap, the difference in  $\gamma$  is distinct:  $\gamma$  for *Miogypsinoidea dehaartii* is mainly negative and  $\gamma$  for *Miogypsina borneensis* is mainly positive.

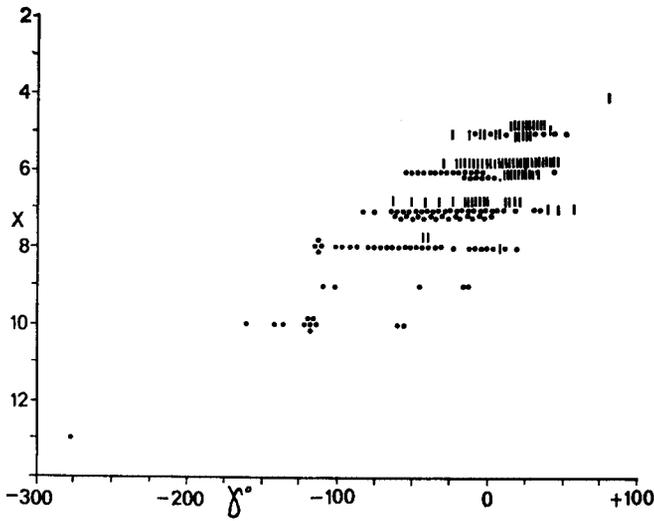


Fig. 54. Parameters X and  $\gamma$  show a correlation which represents the evolutionary trend in Miogypsinae; the scatter diagram of *Miogypsina borneensis* coincides in part with the diagram of *Miogypsinoidea dehaartii*. • = *Miogypsinoidea dehaartii*; | = *Miogypsina borneensis*.

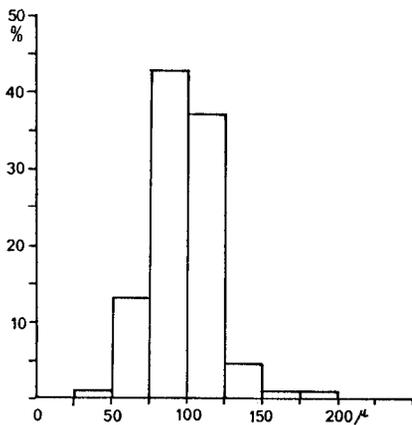
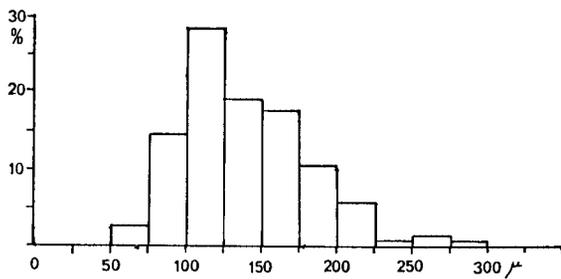


Fig. 55. Histograms of the diameter of the protoconch (I) of *Miogypsinoidea dehaartii* and *Miogypsina borneensis*. The difference is only slight.

As the diameter of the protoconch is included in the distance apex-I (p. 10) the strong correlation in this diagram is evident. The species show a clear overlap in the scatter diagram (apex-I) versus diam. I (Fig. 58). The separate areas found in the diagram diam. I versus  $\gamma$  (Fig. 57) are observed again in the diagram (apex-I) versus  $\gamma$  (Fig. 59). Some specimens of *Miogypsinoidea dehaartii* fall within the areas of *Miogypsina borneensis*.

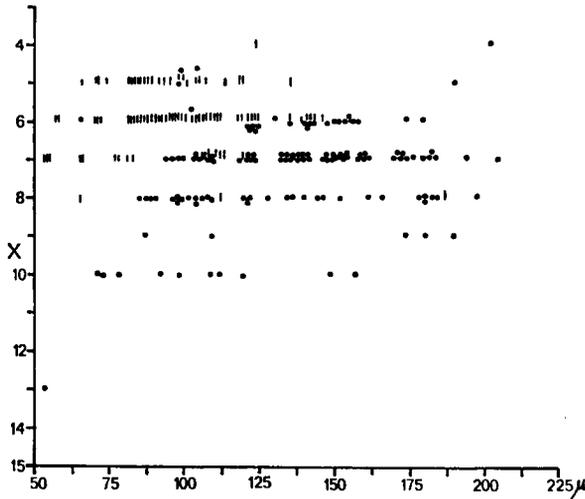


Fig. 56. Diam. I versus X. No clear distinction between the subgenera is found. • = *Miogypsinoidea dehaartii*; | = *Miogypsina borneensis*.

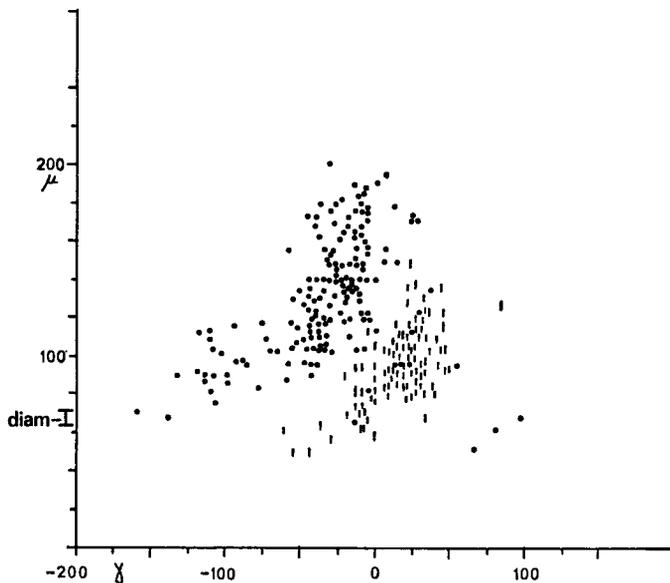


Fig. 57. Scatter diagram for diam. I versus  $\gamma$ . The plottings of the two subgenera lie almost in separate areas.

• = *Miogypsinoidea dehaartii*; | = *Miogypsina borneensis*.

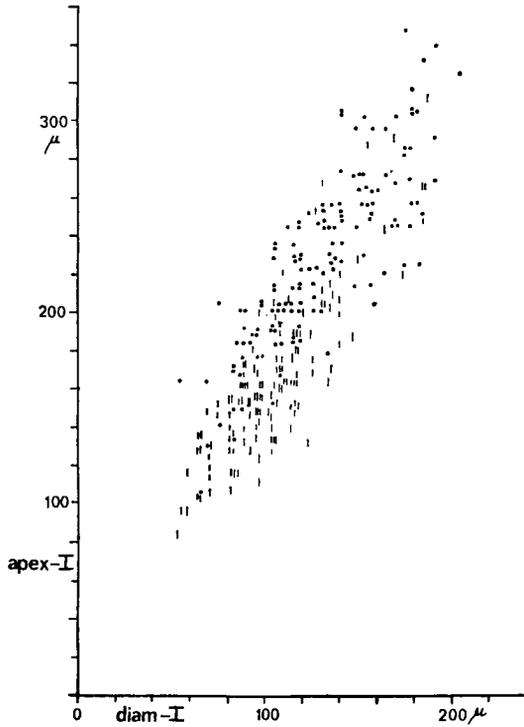


Fig. 58. A strong correlation is seen between (apex-I) and diam. I.  
 ● = *Miogypsinoides dehaartii*; I = *Miogypsina borneensis*.

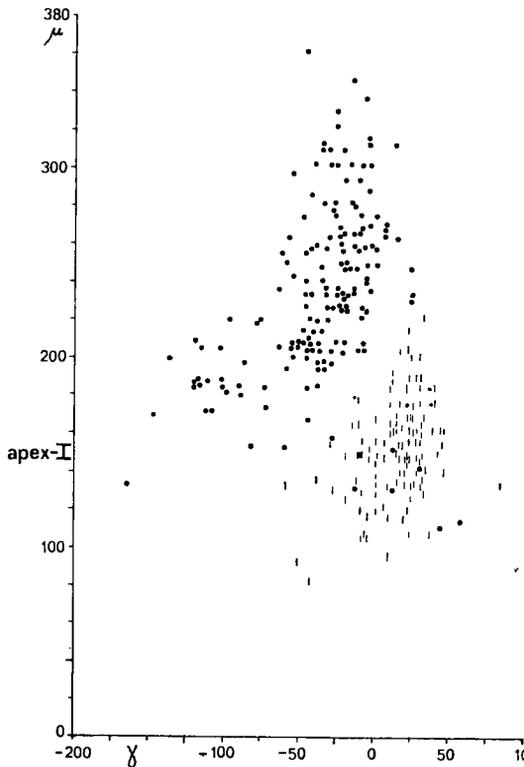


Fig. 59. (Apex-I) versus  $\gamma$ . The plottings are found in almost completely separated areas. The exceptions only occur in the distribution of *Miogypsinoides dehaartii*.  
 ● = *Miogypsinoides dehaartii*; I = *Miogypsina borneensis*.

## MORPHOLOGY OF MIOGYPSINA (MIOGYPSINOIDES) DEHAARTII CUPULAEFORMIS

*Miogypsina (Miogypsinoidea) dehaartii cupulaeformis* Zuffardi-Comerci, 1928

- 1928 *Miogypsina cupulaeformis* n.sp. — Zuffardi-Comerci, p. 142.  
 1936 *Miogypsina cupulaeformis* Zuffardi-Comerci — Tan, pp. 45-61, 84-98, 109-123.  
 1953 *Miogypsina dehaartii* Van der Vlerk var. *cupulaeformis* Zuffardi-Comerci — Drooger, pp. 104-123.  
 1954 *Miogypsina (Miogypsinoidea) cupulaeformis* Zuffardi-Comerci — Cole pp. 569-608.  
 1966 *Miogypsina (Miogypsinoidea) dehaartii* var. *cupulaeformis* Zuffardi-Comerci — van der Vlerk, pp. 421-429.

The species *M. cupulaeformis* may be considered as a subspecies of *Miogypsinoidea dehaartii*. Figure 60 shows the transition from the flat *M. dehaartii* test to the conical *M. cupulaeformis* test.

The cone is covered by a layer of equatorial chambers (Fig. 61). The surface of the cone is smooth, only sporadically ornamented with pustules. Sometimes pillars have developed. The sequence in Fig. 60 does not illustrate an ontogenetic development; all phases are already present in the juvenile stage.

The convex side is considered as the ventral side of the test in view of the position of the intraseptal canal system (Pl. 44; Fig. 62). The dorsal side of the test may be thick with a massive zone, or thin and hollow. Fig. 61 is a schematic drawing of the position of the embryonic-nepionic apparatus and the equatorial chambers in *Miogypsinoidea dehaartii cupulaeformis*.

A complete reconstruction is given in Fig. 62. In a vertical section through the embryonic apparatus the upper right-hand part of the section reminds us of the vertical section of the flat test of *Miogypsinoidea dehaartii*. The other half (left in Fig. 62) consists of a row of equatorial chambers; this is a vertical section through the curved layer of equatorial chambers of the conical wall. Above the embryonic apparatus the truncated cones of the marginal fringe may be seen. It may be assumed that I in Figure 61 is the protoconch in view of its spherical shape.

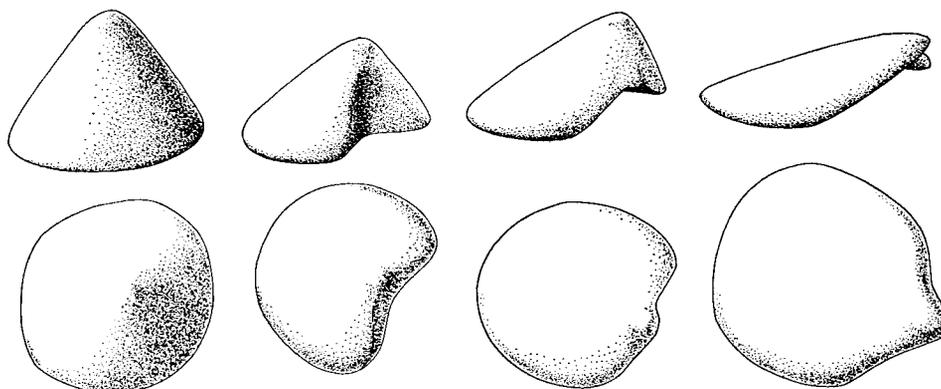


Fig. 60. The transition from the flat *M. dehaartii* test (right) to the conical *M. dehaartii cupulaeformis* test (left). The edges of the *M. dehaartii* type "curve" towards the dorsal side and at the same time the apex "moves" towards the centre of the test, so that the position of the embryonic apparatus becomes more central. Finally the cone is closed and the apex, containing the embryonic apparatus, is found at the "top" of the cone.

Generally the test is not perfectly conical. The embryonic apparatus occurs on the somewhat longer side of the cone. The intraseptal canal system lies in the exterior part of the cone (ventral side, see Pl. 44). The intraseptal canal system branches perpendicularly into the ventral and the dorsal side of the test (the vertical canal system). The vertical canals, branching into the dorsal side of the test, could not always be traced to the edge of the test probably because the course is irregular. The pores in the equatorial chamber walls continue on the ventral side to the ventral surface; on the dorsal side the pores bend 'down' and continue to the dorsal surface of the test (Pl. 44). Needles are fairly common.

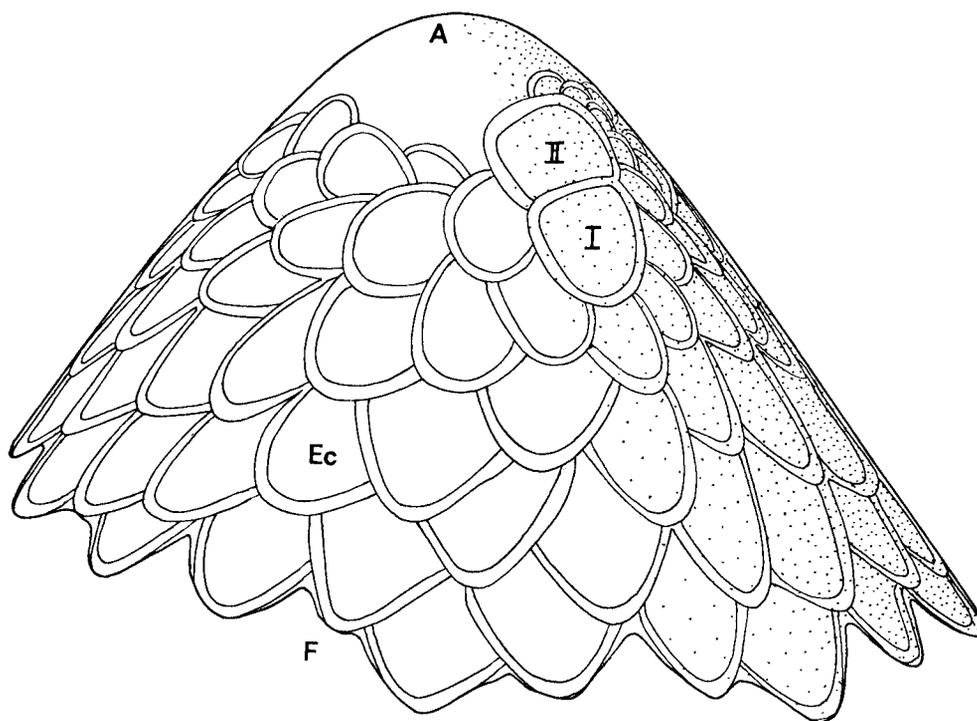


Fig. 61. A Schematic drawing of the position of the embryonic-nepionic apparatus and the equatorial chambers in *Miogypsinoides dehaartii cupulaeformis*.

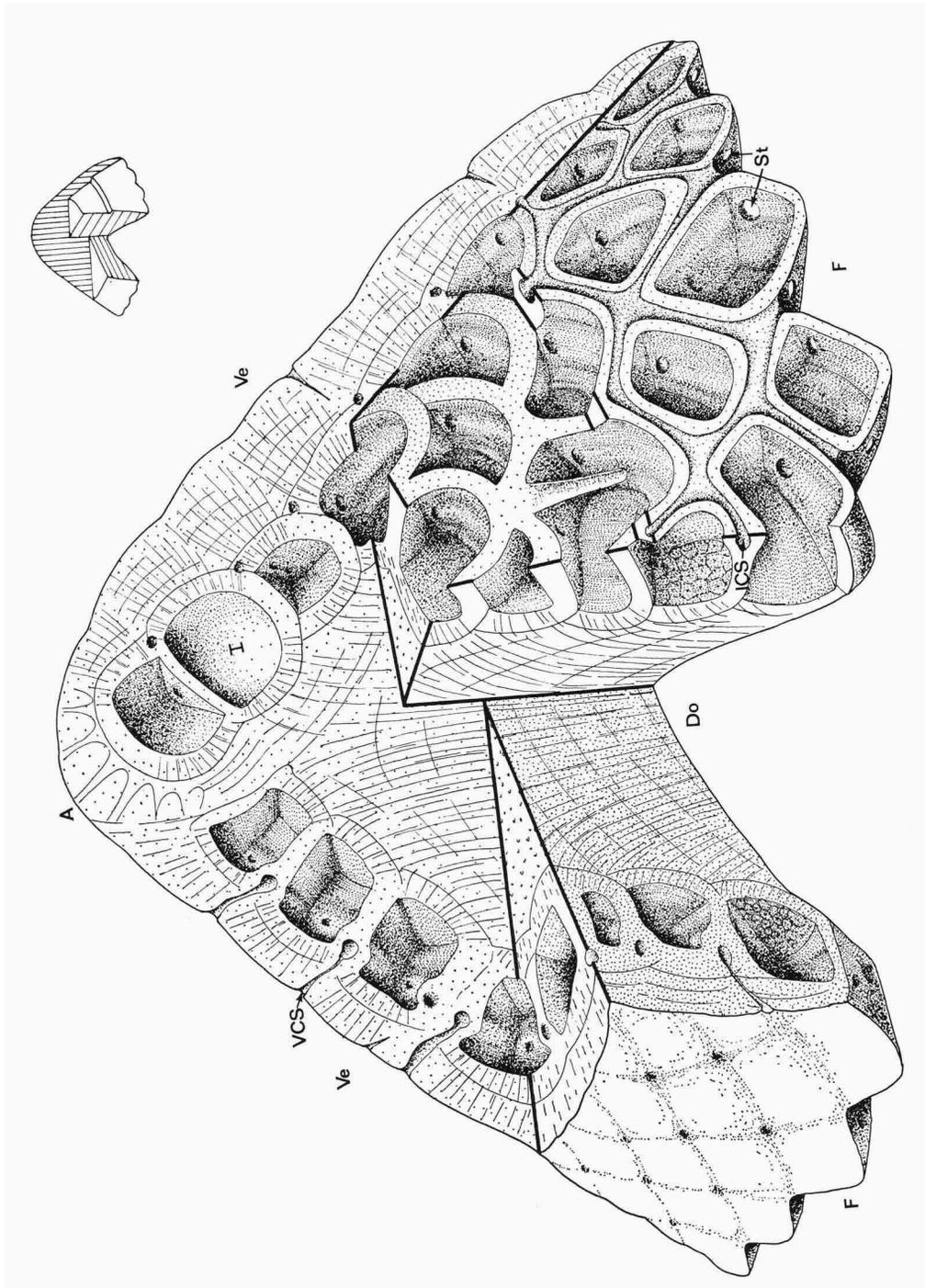


Fig. 62. A reconstruction of *Miogypsinoides dehaartii cupuleaformis*. The specimen is partly cut open to show the internal structures. The massive interior part of the cone is the dorsal side, the exterior part of the test is the ventral side which contains the intraseptal canal system. The embryonic apparatus is located at the top (apex) of the cone. In two equatorial chambers the cancellate structure containing the pores is shown.

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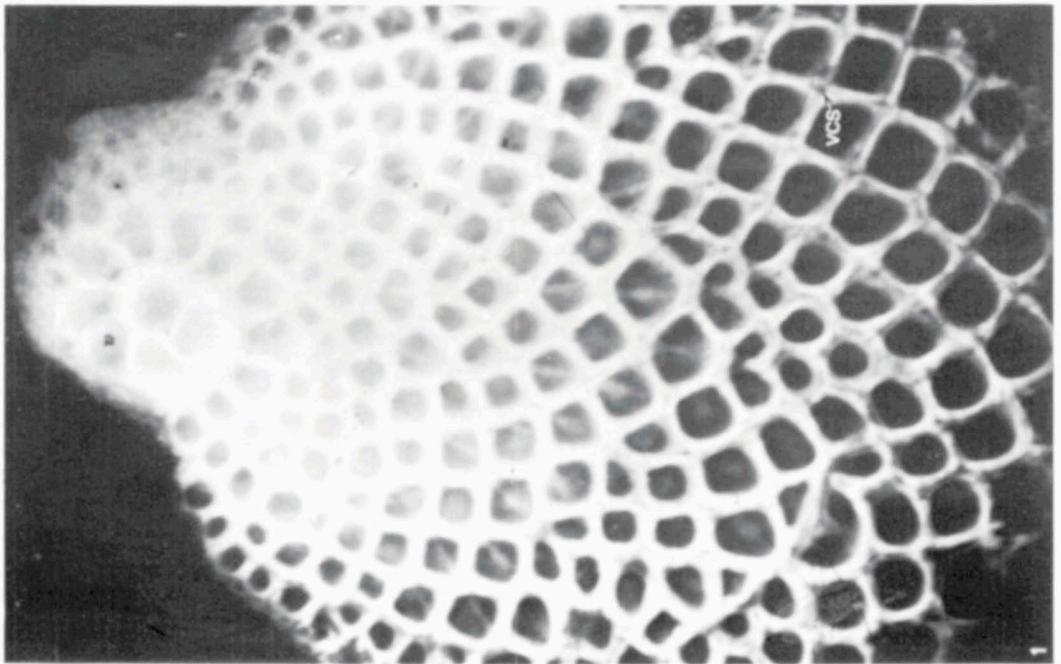
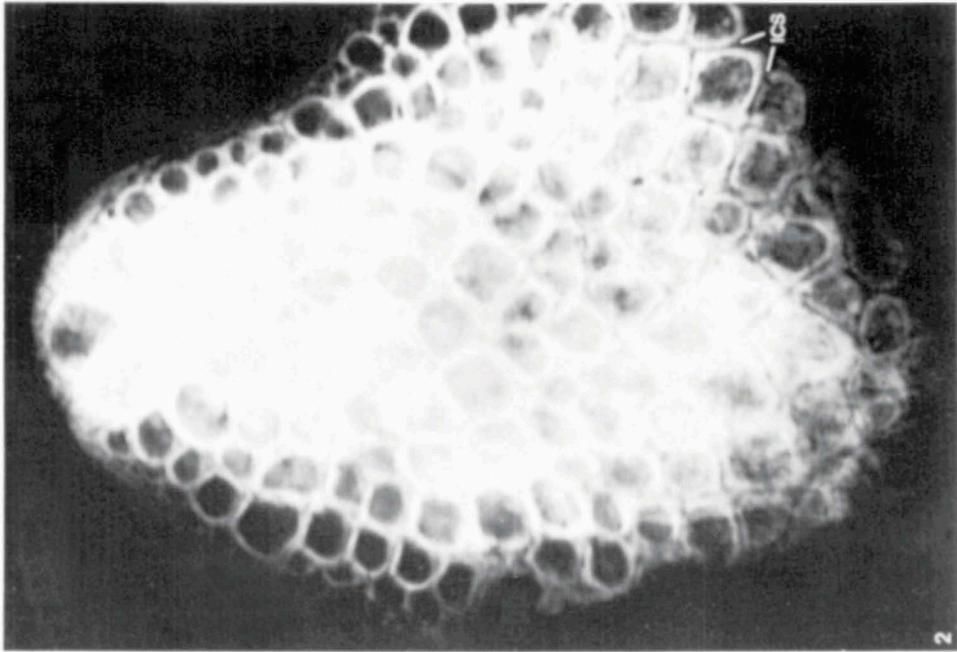
## Plate 1

Microradiographs of *Miogypsina (Miogypsinoides) bantamensis*, Anse deï Bano, M64, France.

Fig. 1. The microradiograph shows that the embryonic-nepionic apparatus is situated in the protruding part of the test.  $X = 12$ ,  $\gamma = -166^\circ$ . The spiral is broken on the left so that  $X$  is not certain. The intraseptal and the vertical canal system are clearly visible. In several equatorial chambers are needles. Specimen no. 2, RGM 230 446, x 25.

Fig. 2. The specimen has the first primary auxiliary chamber at the apex; no operculinid collar has developed. The intraseptal canal system is distinct.  $X = 8$ ,  $\gamma = -51^\circ$ . Specimen no. 75, RGM 230 412, x 25.

Plate 1

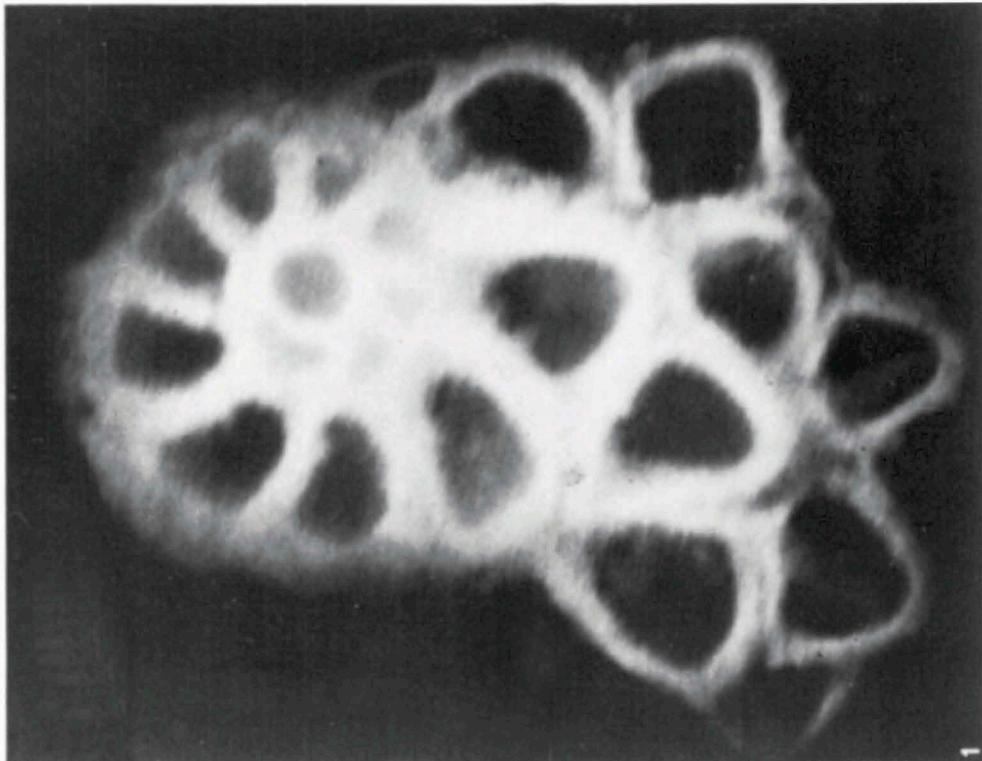
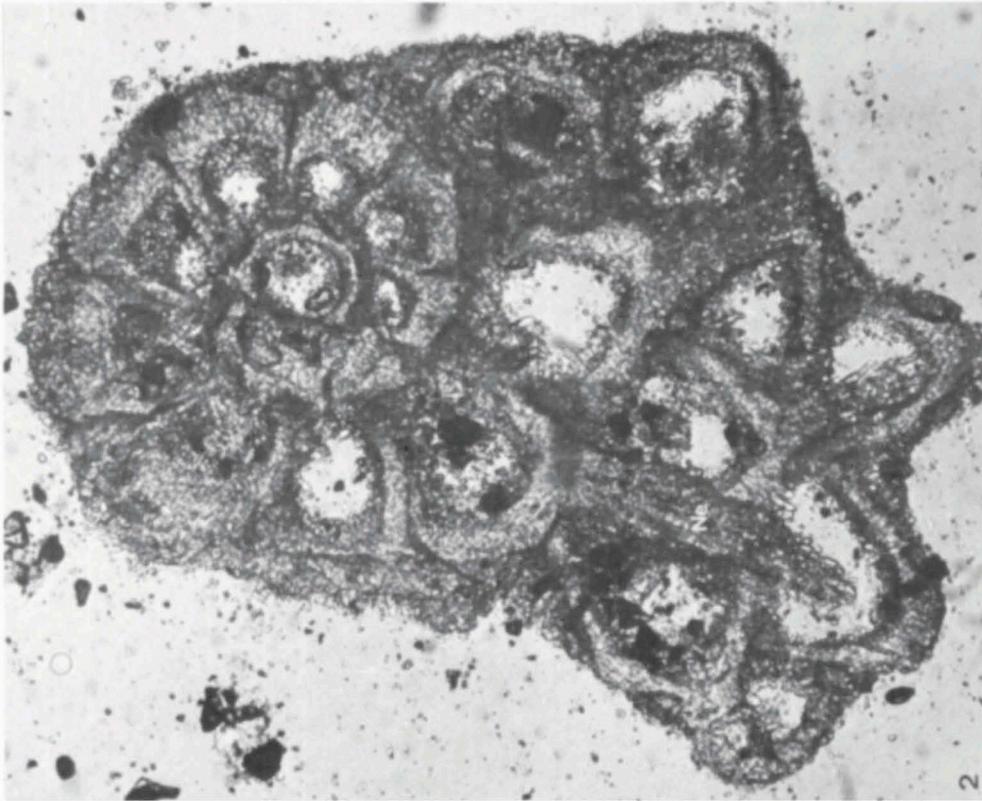


## Plate 2

*Miogypsina (Miogypsinoides) bantamensis*, Anse deï Bano, M64, France.

A thin section and a microradiograph of the same specimen. This specimen possesses a small protoconch,  $X = 13$ . A needle has developed from one of the spiral chambers. The intraseptal canal system is clearly visible in the thin section as well as in the microradiograph. Specimen no. 121, RGM 230 389, 230 358, x 100.

Plate 2



### Plate 3

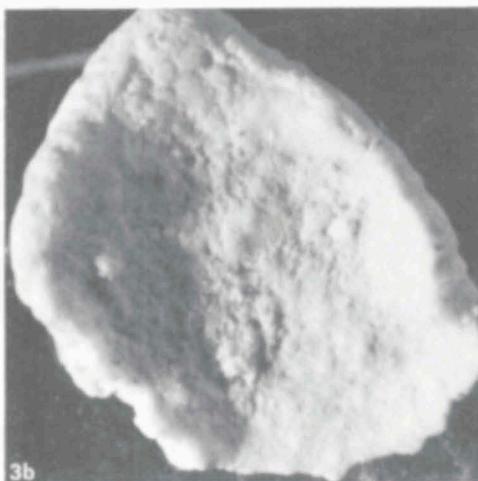
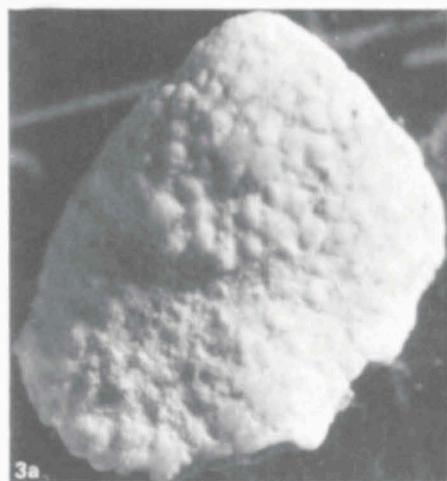
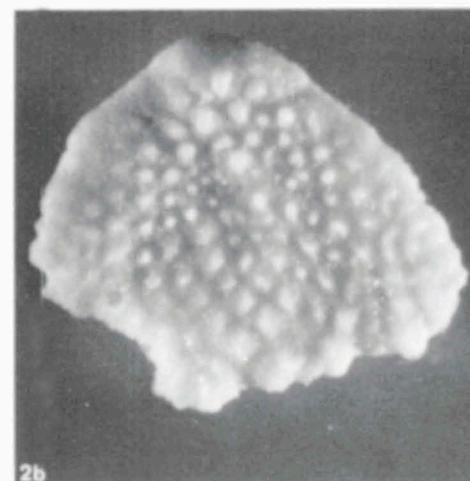
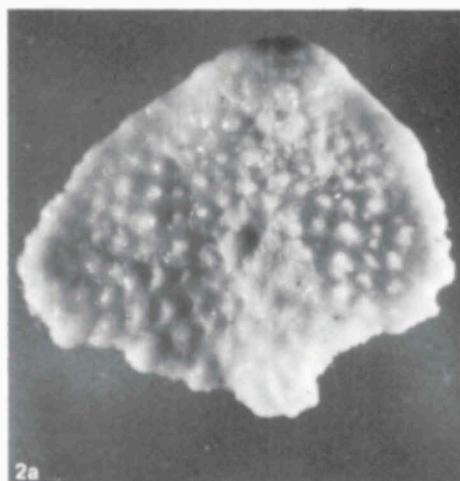
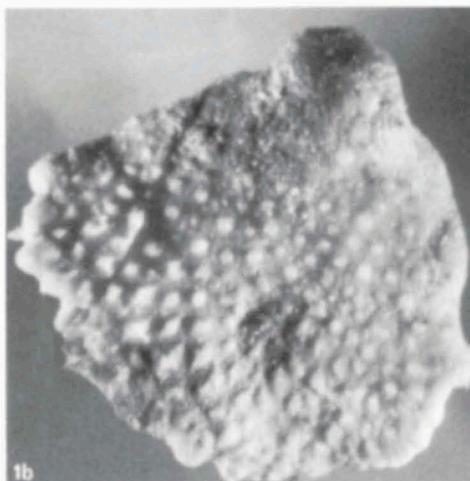
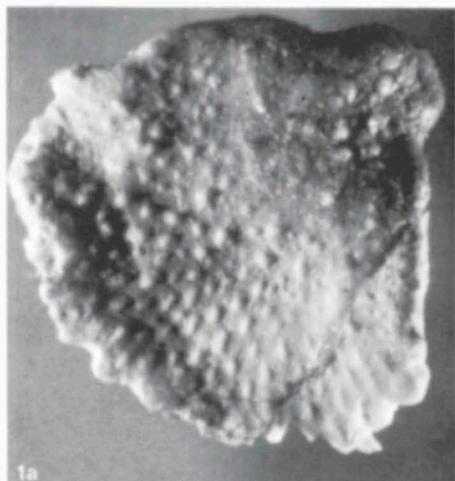
*Miogypsina (Miogypsinoïdes) bantamensis*, Anse deï Bano, M64, France.

Fig. 1a: dorsal side; fig. 1b: ventral side. The specimen corresponds with the microradiograph of Plate 1, fig. 1. The embryonic-nepionic apparatus is located in the protruding apical part of the test. The pustules are regularly scattered over the surface and are situated immediately above the centres of the lateral walls of the equatorial chambers. The pustules become elongated towards the front. There is hardly any secondary thickening of the lateral parts of the test. Specimen no. 2, RGM 230 446, x 22.

Fig. 2a: dorsal side; fig. 2b: ventral side. The equatorial plane is somewhat undulant. x 22.

Fig. 3a: ventral side; fig. 3b: dorsal side. A concavo-convex specimen. According to the position of the intraseptal canal system the convex side is the ventral side. x 22.

Plate 3

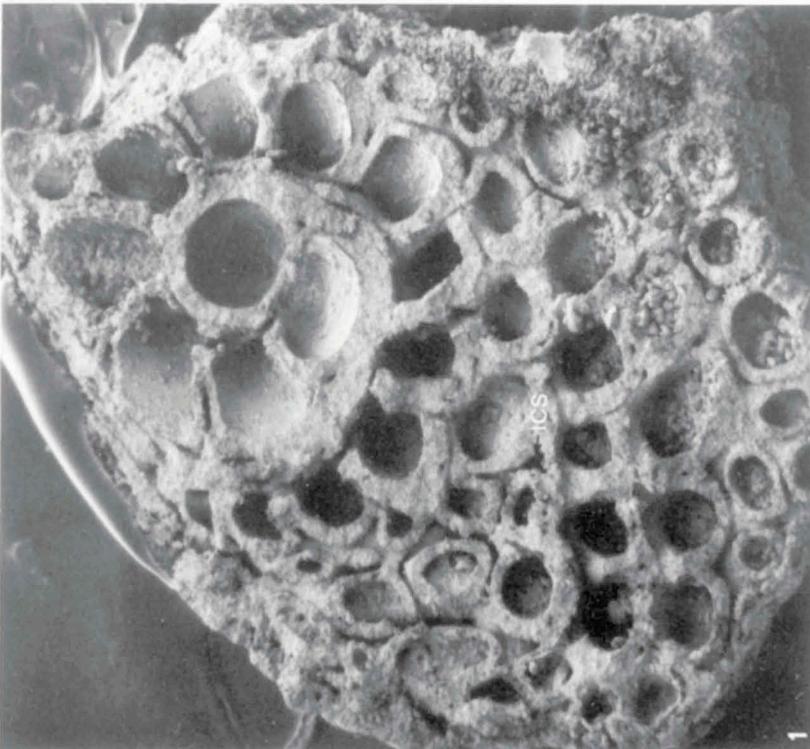
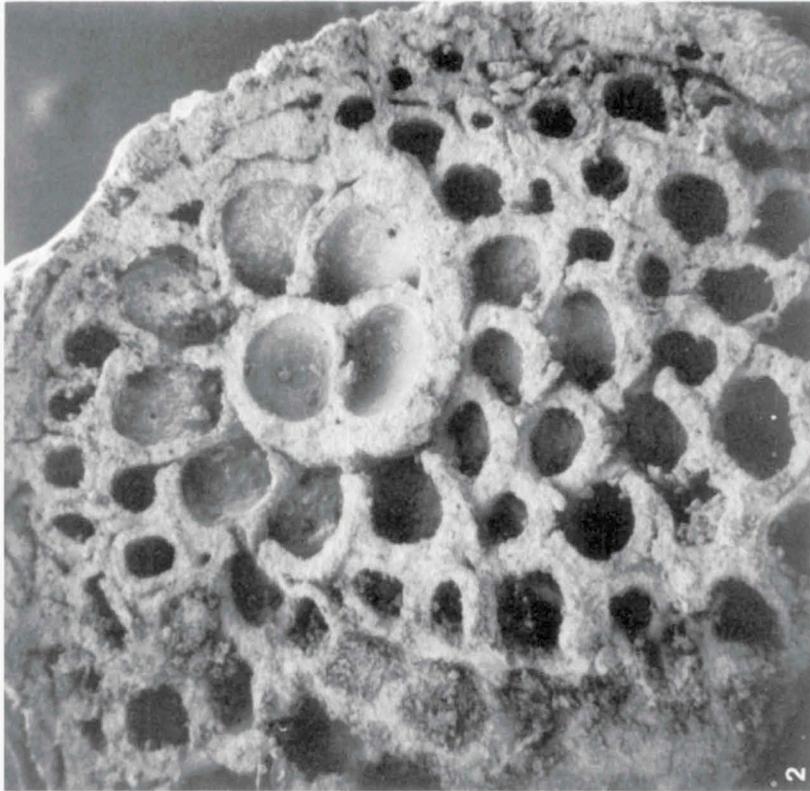


## Plate 4

*Miogypsina (Miogypsinoides) bantamensis*, Anse deï Bano, M64, France.

The specimen has been split into two halves. The intraseptal canal system is distinct. X = 14.  
RGM 230 817, x 100.

Plate 4



## Plate 5

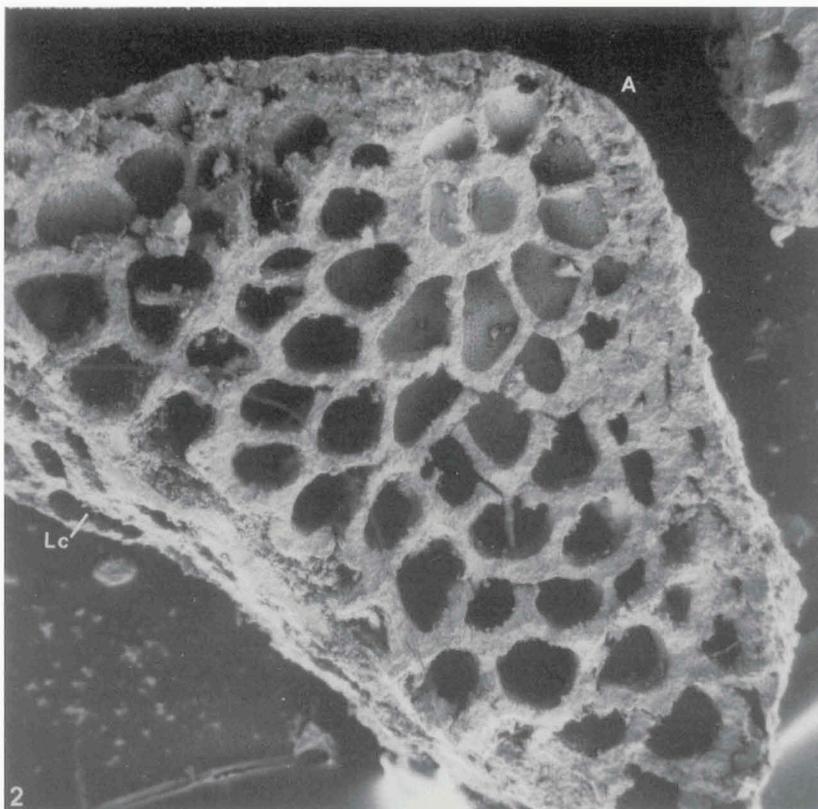
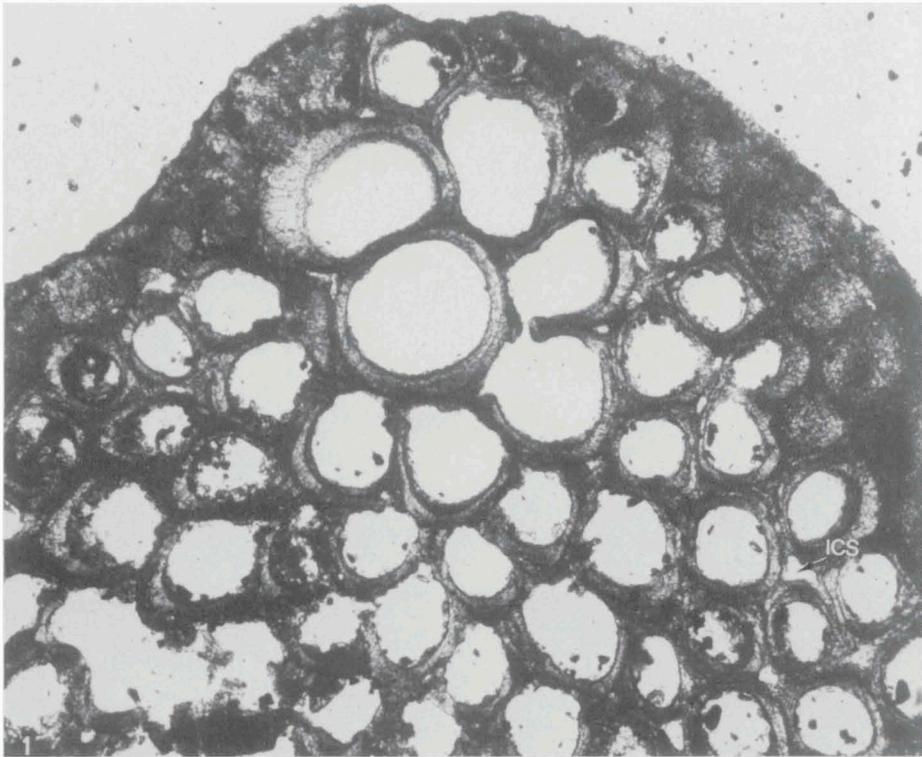
Fig. 1. *Miogypsina (Miogypsinoidea) bantamensis*, Anse deï Bano, M64, France.

This specimen shows the development of a second spiral out of the first primary auxiliary chamber (PA-I) around the deuteroconch (II). The intraseptal canal system (ICS) is distinct.  $X = 7$ ,  $\gamma = -30^\circ$ . Specimen no. 89, RGM 230 412, x 40.

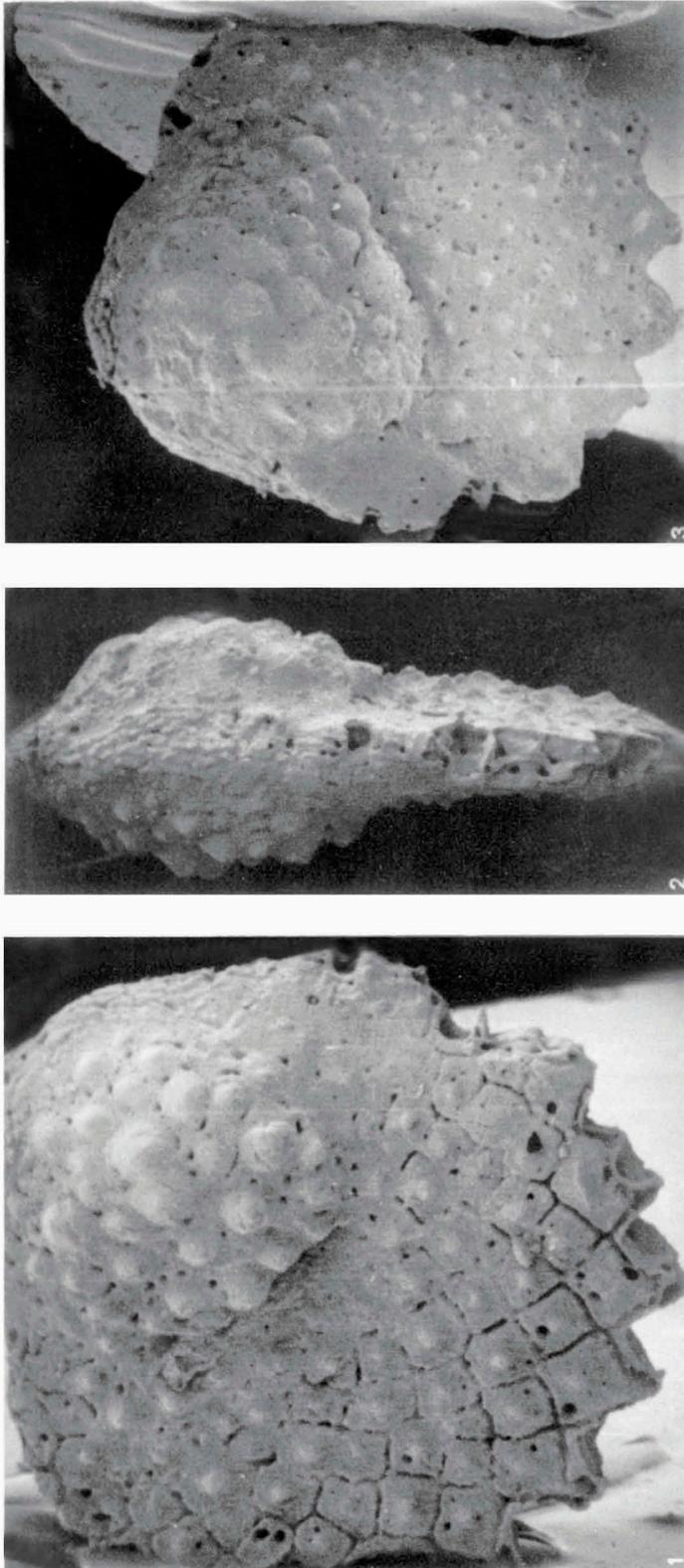
Fig. 2. *Miogypsina (Miogypsina) gunteri*, Anse deï Bano, M64, France.

This specimen has lateral chambers (Lc), therefore it is assigned to the subgenus *Miogypsina*. Several equatorial chambers show needles.  $X = 11$ . RGM 230 816, x 100.

Plate 5



## Plate 6

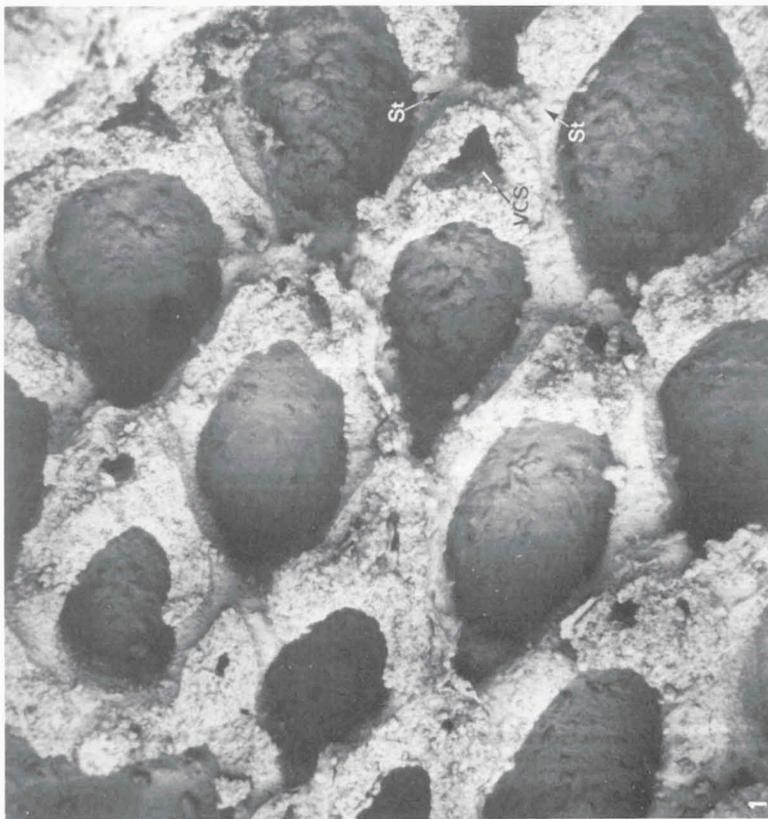
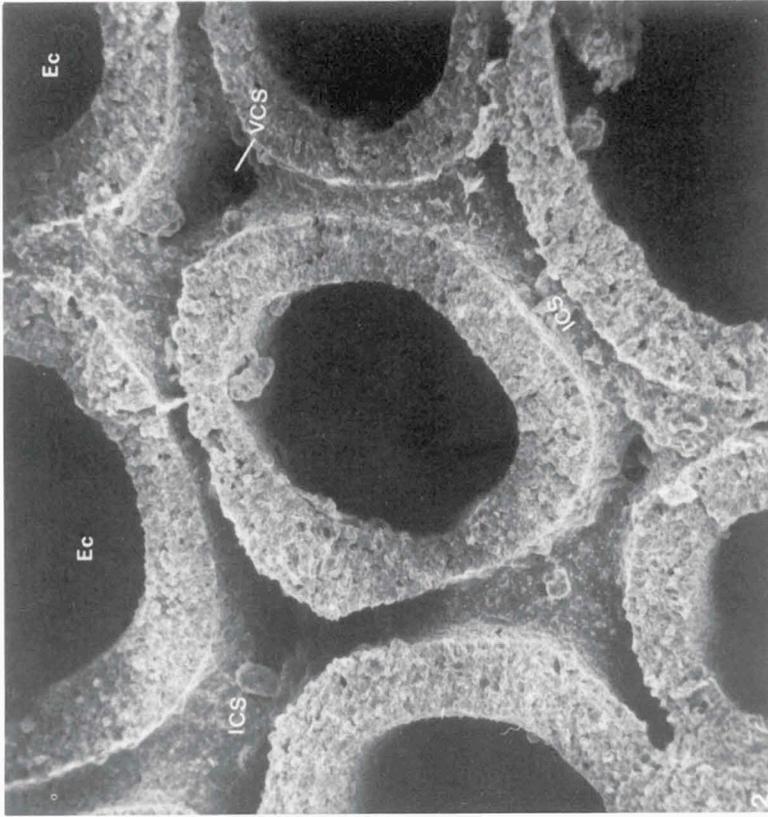


*Miogypsina (Miogypsinoides) bantamensis*, Anse dei Bano, M75, France: RGM 231 258.

Fig. 1. Ventral side of the test showing the lateral canal system. The fissures on the frontal side are in fact the first lateral canal system above the intra-septal canal system. Towards the apex the fissures are closed by material which in thin sections of the vertical canal system are visible. On the lateral wall of the equatorial chambers is one postule; x 58.

Fig. 2. Lateral view. The thickest part of the test is lateral to the embryonic-nepionic apparatus; x 55.

Fig. 3. Dorsal side of the test. The openings of the vertical canal system are distinct. One postule has developed on the lateral wall of each equatorial chamber; x 50.



Equatorial chambers of *Miogypsina (Miogypsinoidea) bantamensis*, Anse dei Bano, M54, France.

Fig. 1. The vertical canal system (VCS) passes through the septa of the equatorial chambers (Ec). RGM 230 823, x 220.

Fig. 2. Detail of the intraseptal canal system (ICS). The openings of the vertical canal system at the intersections of the intraseptal canal system are visible. RGM 230 813, x 500.

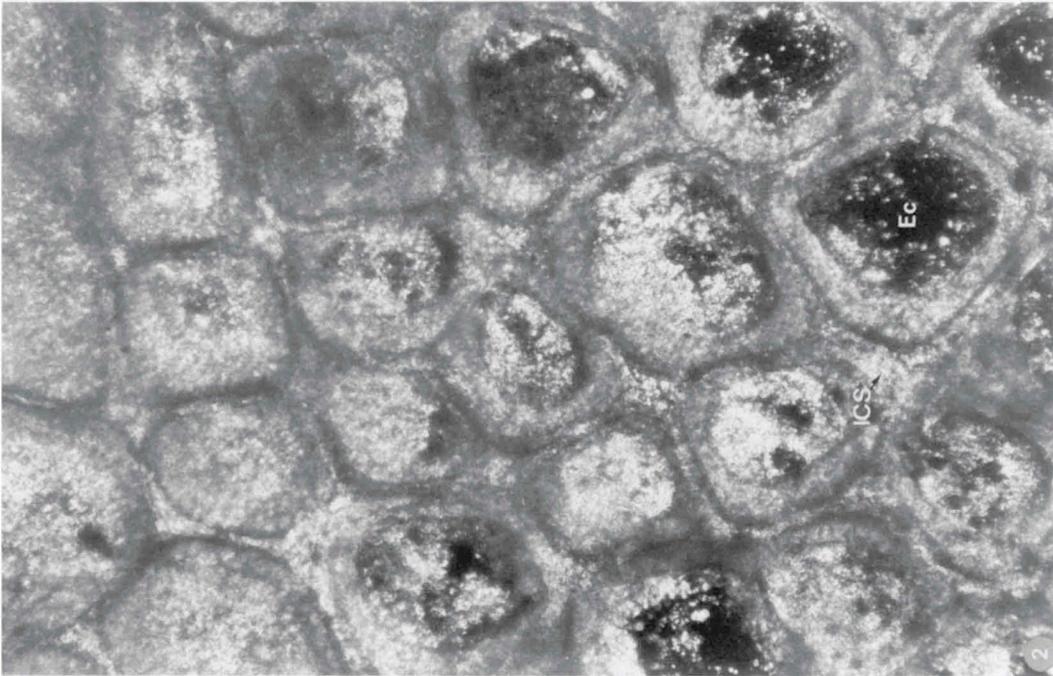
## Plate 8

*Miogypsina (Miogypsinoides) bantamensis*, Anse deï Bano, M64, France.

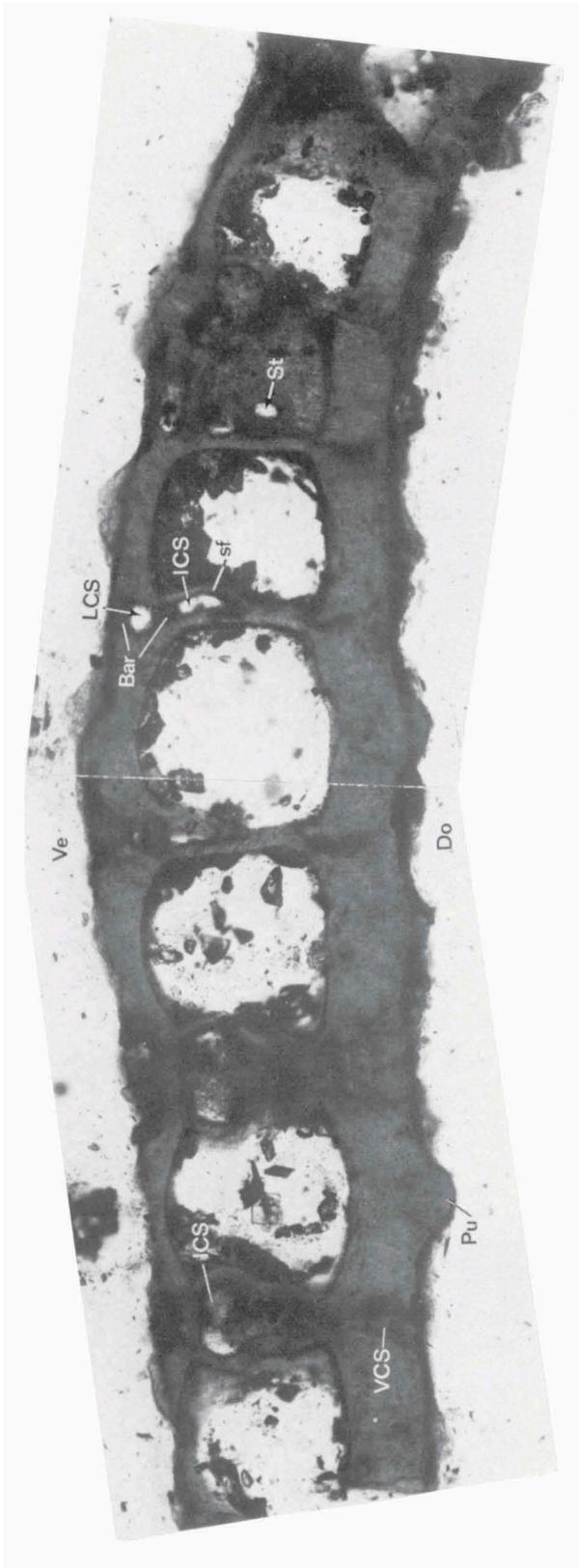
Fig. 1. Vertical section. The truncated cones of the marginal fringe (MF) are distinct. The cavities around these truncated cones are part of the intraseptal canal system. Specimen no. v17, RGM 230 318, x 100.

Fig. 2. A somewhat oblique horizontal section through the equatorial chambers, showing the shape of the intraseptal canal system (ICS): diamond-shaped when it is cut near the ventral side (upper part of the photograph) and rounded when it is cut through the centre of the canal system. RGM 230 481, x 50.

Plate 8

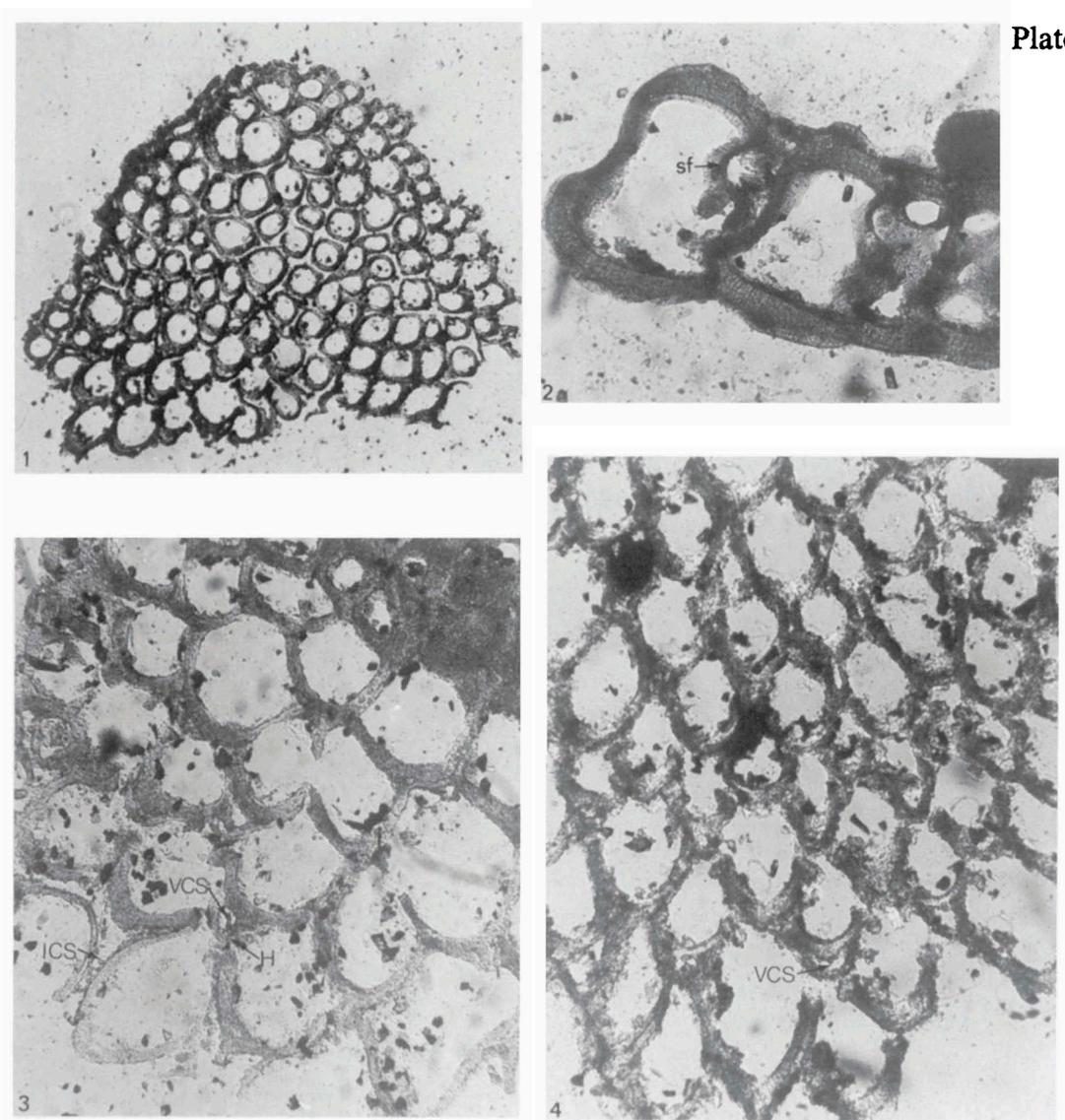


## Plate 9



Vertical section through *Miogypsina (Miogypsinoides) bantamensis*, Anse deï Bano, M64, France.

The septal flap (sf) bends inwards on the ventral side (Ve), thus giving rise to the intraseptal canal (ICS). The curved septal flap on the ventral side is not attached to the wall of the preceding chamber, but leaves an opening. This opening is closed (except at the intersections of the intraseptal canal system) by dark material (bar). The dark material is also found at certain intervals in the lateral canal system. The secondary doubled septa are clearly visible. Specimen no. v12, RGM 230 313, x 100.



*Miogypsina (Miogypsinoidea) bantamensis*, Estoti, FR1120, France.

Fig. 1. When the intraseptal canal system (ICS) is cut exactly through the centre, the equatorial chambers resemble 'free' rings. RGM 231 216, x 20.

Fig. 2. A vertical section through the equatorial chambers. The equatorial chambers are asymmetric: the dorsal part of the equatorial chambers protrudes towards the front; the septal flap (sf) bends away giving rise to the intraseptal canal system (ICS) on the ventral side. The septal flap and the lateral wall of the equatorial chamber are not attached to the preceding chamber wall. The opening in between is closed by dark material: the bar. RGM 231 223, x 50.

Fig. 3. Horizontal section through the equatorial chambers. The photograph corresponds with text-fig. 21 and shows the merged toothplates (tp) giving rise to the vertical canal system (VCS). RGM 231 229, x 40.

Fig. 4. Horizontal section through the equatorial chambers. The merged toothplates (tp) at the base of the stolons are clearly seen. RGM 231 215, x 40.

## Plate 11

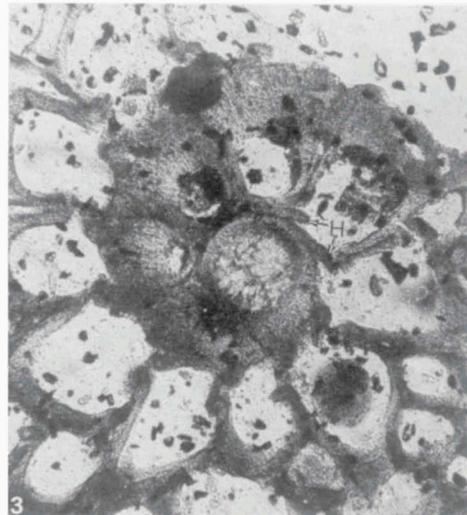
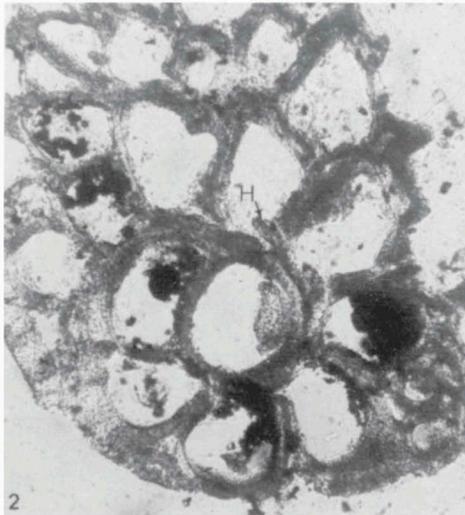
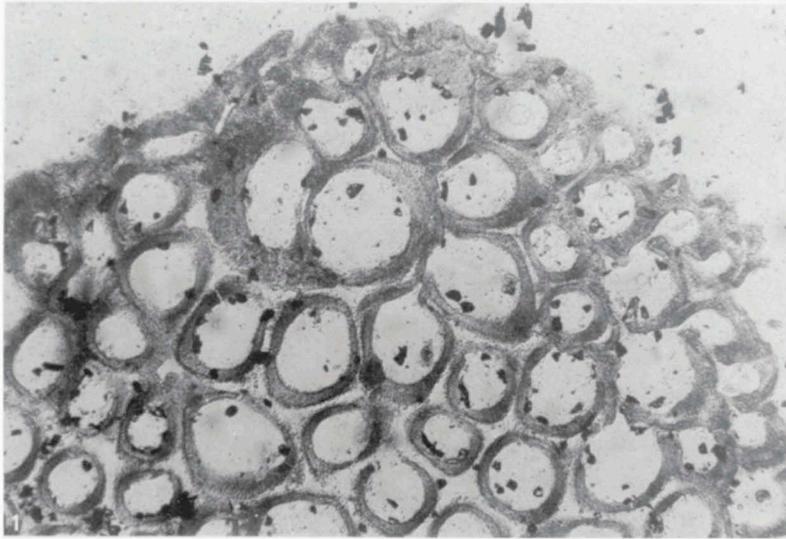
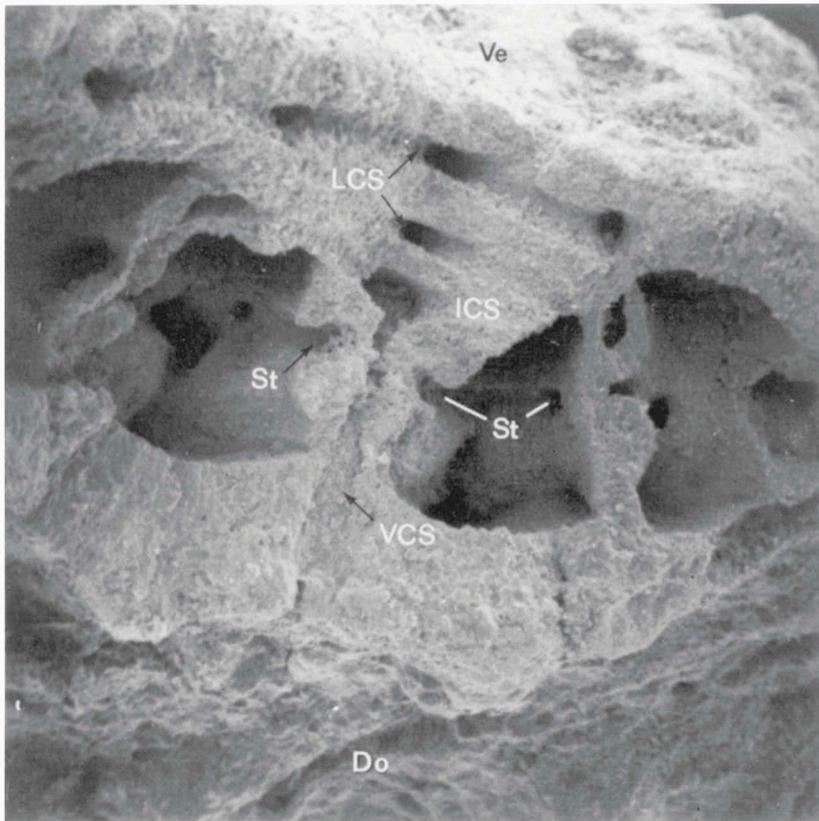
*Miogypsina (Miogypsinoidea) bantamensis.*

Fig. 1. The specimen is cut on the ventral side exactly through the centre of the intraseptal canal system (ICS); the equatorial chambers resemble 'free' rings. At the base of spiral chamber 3, 4 and 5 the connection between the vertical canal system under the toothplate (tp) and the intralocular protoplasm is seen. RGM 231 216, Estoti, FR1120, France, x 75, Figs. 2, 3. The embryonic-nepionic apparatus. At the base of the proximal stolon (PSt) of the spiral chambers the hook of the toothplate (H) is visible. The openings under this hook are the connections between the intralocular protoplasm and the vertical canal system. Fig. 2. RGM 231 224, Estoti, FR1120, France, x 75. Fig. 3. RGM 231 075, Christus-2, France, x 75.

Plate 12



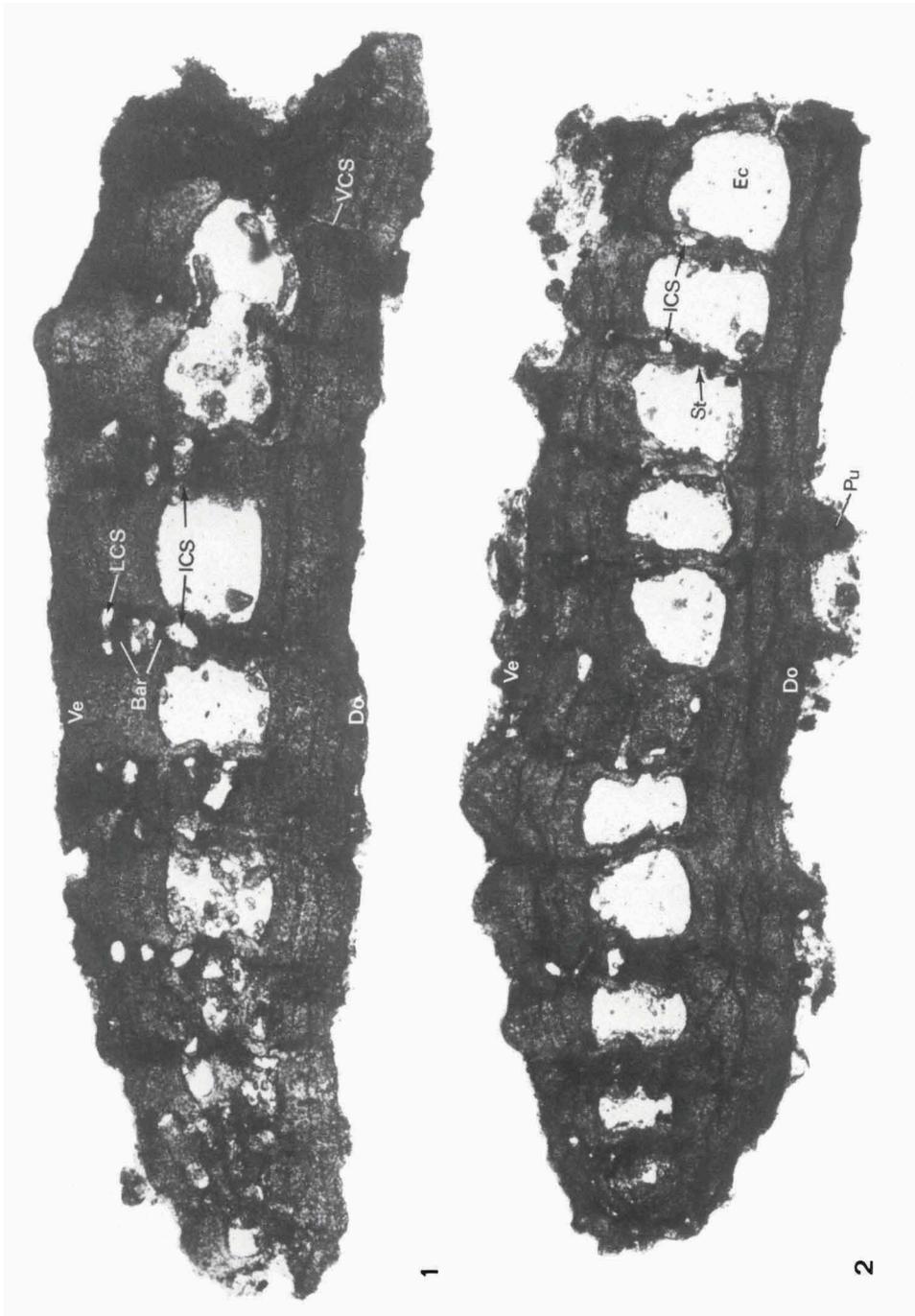
*Miogypsina (Miogypsinoides) bantamensis*, Anse deï Bano, M75, France.

The vertical canal system (VCS) extends from the ventral side, where it is connected with the intraseptal canal system (ICS), towards the dorsal side where it forms an opening at the surface. The vertical canal is formed between two merged toothplates (tp) of two closely adjacent stolons (St). The two stolons on either side of the vertical canal are distinct. RGM 231 257, x 200.

### Plate 13

Transverse sections of *Miogypsina (Miogypsinoides) bantamensis*, Anse dei Bano, M54, France. Figs. 1, 2. The intraseptal canal system (ICS) is found in the vertical wall of the equatorial chamber on the ventral side. The ventral part of the test contains the lateral canal system (LCS) and the vertical canal system (VCS). In the dorsal part of the test there is only the vertical canal system. Between the several layers of the lateral canal system the test is dark, as seen in vertical sections. The test on both lateral sides of the equatorial chambers is massive and is only perforated by pores. This part of the test frequently has pustules on the surface. Fig. 1. Specimen no. v11, RGM 230 312, x 40. Fig. 2. Specimen no. v14, RGM 230 315, x 40.

Plate 13



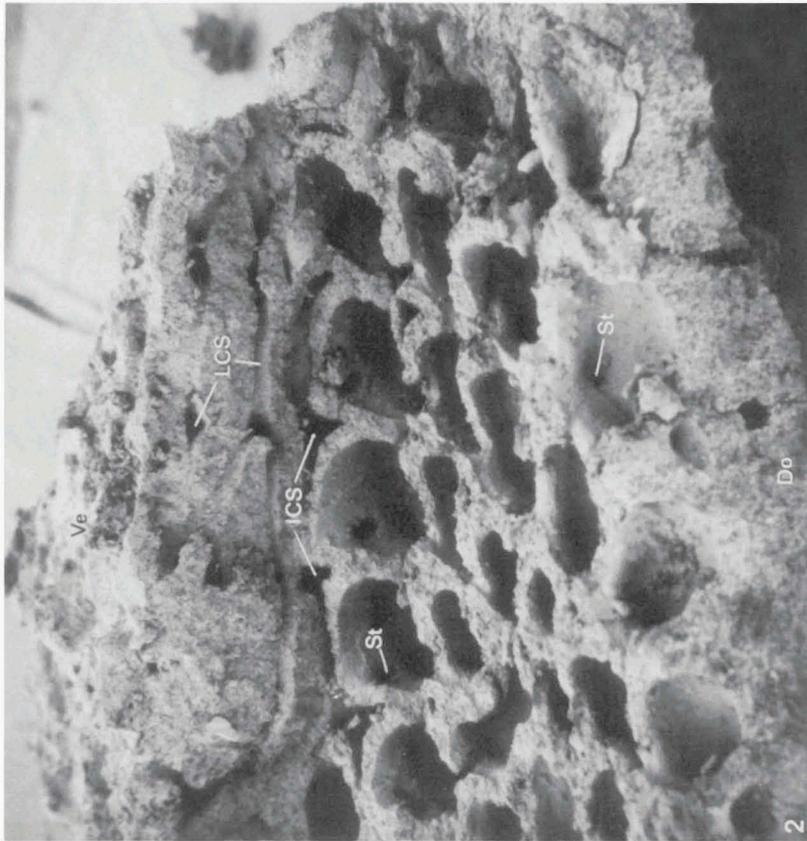
## Plate 14

*Miogypsina (Miogypsinoides) bantamensis*, Anse deï Bano, M64, France.

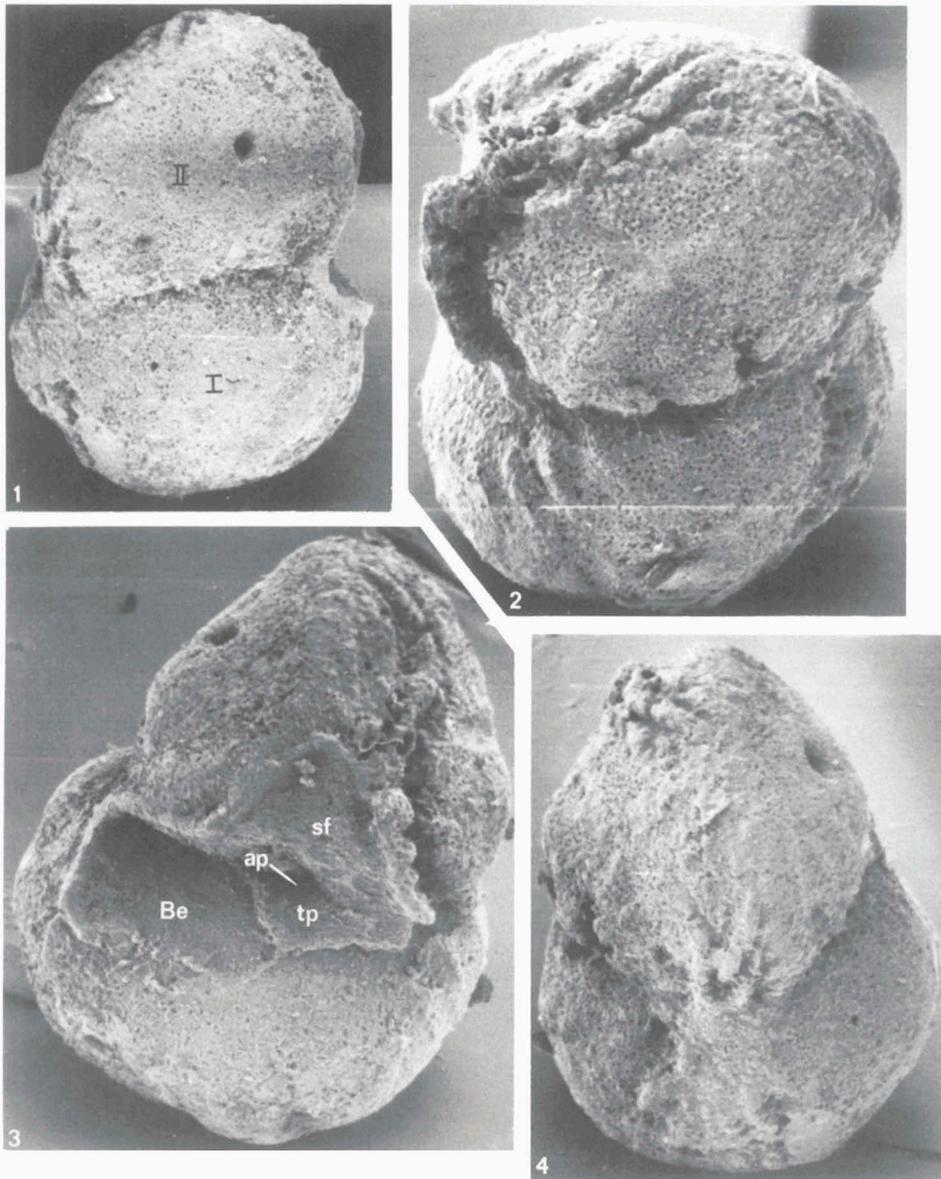
Fig. 1. Vertical view. The lateral side containing the intraseptal canal system (ICS) is called the ventral side (Ve) the opposite being the dorsal side (Do). The ventral part of the test contains the lateral canal system (LCS). The vertical canal system (VCS) penetrates through the vertical wall (septa) of the equatorial chambers into the massive dorsal wall. RGM 230 818, x 100.

Fig. 2. Equatorial chambers and ventral and dorsal part of the test. The ventral part (Ve) of the test contains the intraseptal canal system (ICS) and the lateral canal system (LCS), the dorsal part (Do) of the test only shows the vertical canal system (VCS). The lateral canal system is located immediately above the intraseptal canal system so that the wall above the chambers and between the canal system is massive and only perforated by pores. RGM 230 824, x 110.

Plate 14



## Plate 15



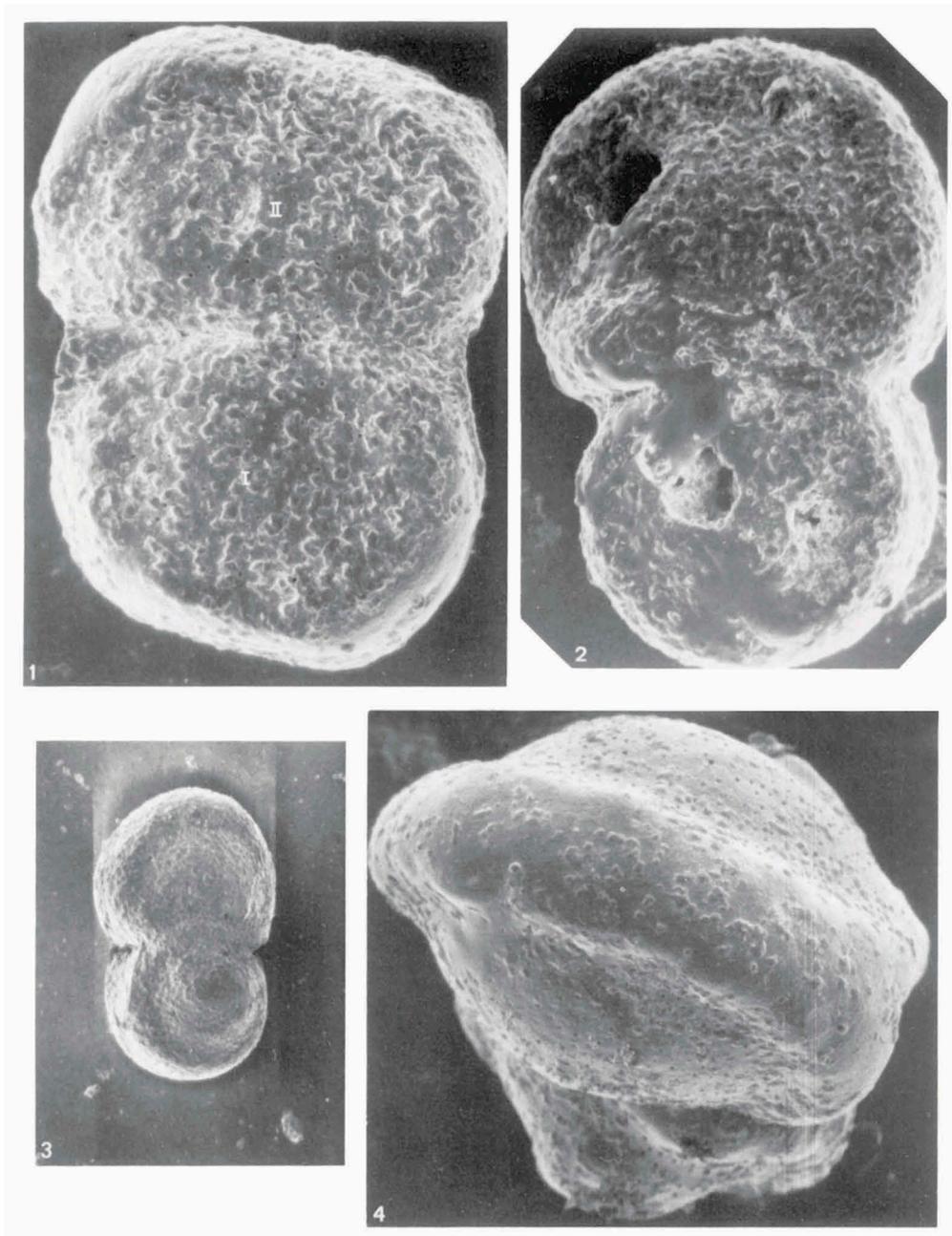
Bilocular nucleocoenoch of *Miogypsinoides*, Estoti, FR1120, France, RGM 231 259.

Fig. 1. Dorsal view; x 180.

Fig. 2. Ventral view. The deep fissure between protoconch (I) and deuterocoenoch (II) is visible, as well as the fissure formed by the septal flap (sf) and II, which is the beginning of the intraseptal canal system surrounding the nucleocoenoch. x 250.

Fig. 3. The PA-I side. Before the primary auxiliary chamber (PA-I) is built the toothplate (tp), septal flap (sf) and the basal extension (Be) are formed. The septal flap bends away giving rise to a fissure. The wall of the spherical protoconch is perforated; toothplate, septal flap and basal extension are imperforate. x 230.

Fig. 4. A view opposite to PA-I; x 200.



*Miogypsina* s.s., Kembangan, Bg.316, Indonesia, RGM 230 814.

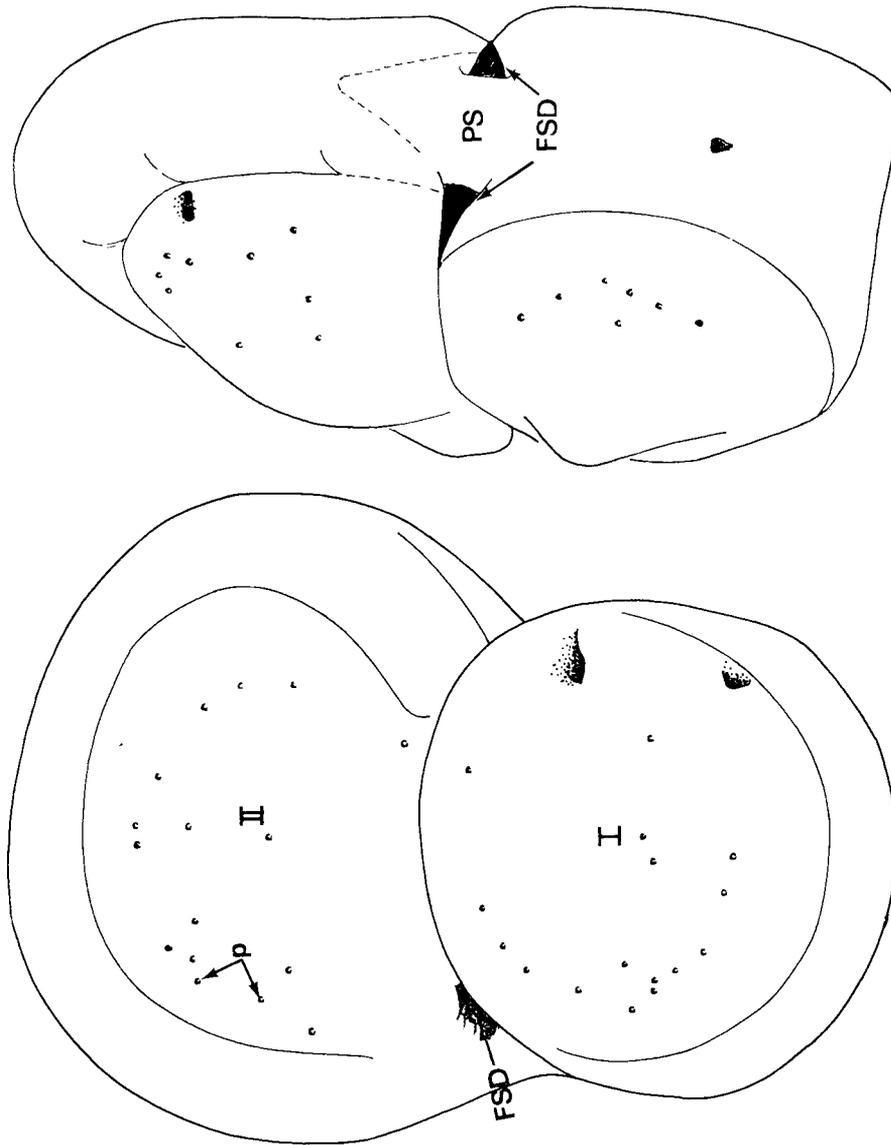
Four nucleocoenoches of *Miogypsina* s.s. These two chambers, the protoconch (I) and the deuteroconch (II), could be considered with certainty as the bilocular nucleocoenoches of *Miogypsina* s.s. Nucleocoenoches of different sizes and shapes were found.

Fig. 1. Lateral view, x 200.

Fig. 2. Lateral view, x 200.

Fig. 3. Lateral view, x 100.

Fig. 4. Apical view of a nucleocoenoch, showing distinctly the ridge around the deuteroconch; x 200.



### Plate 17

The nucleoconch of *Miogypsina* s.s., Kombangan, Bg.316, Indonesia, RGM 230 814.

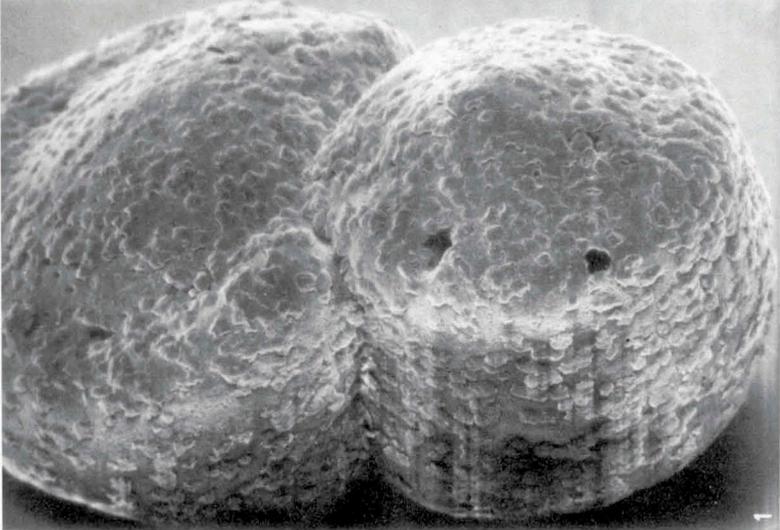
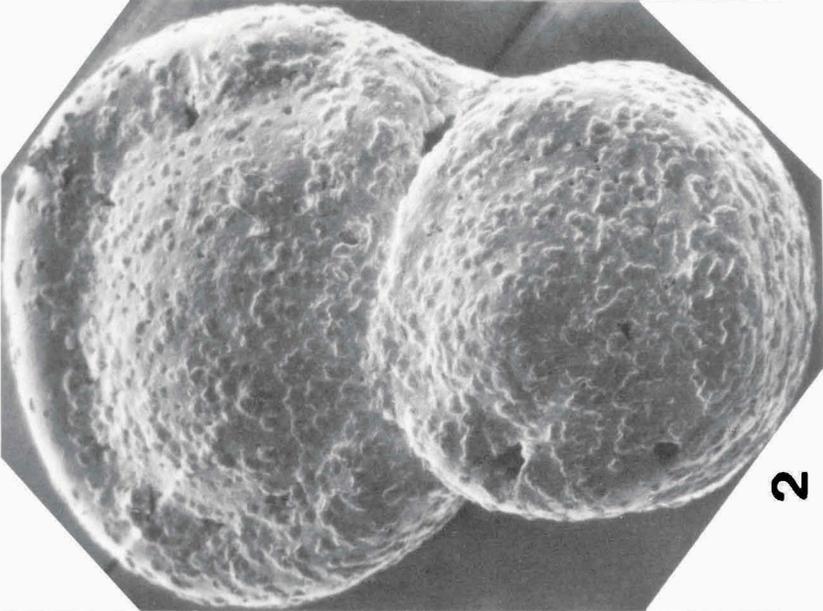
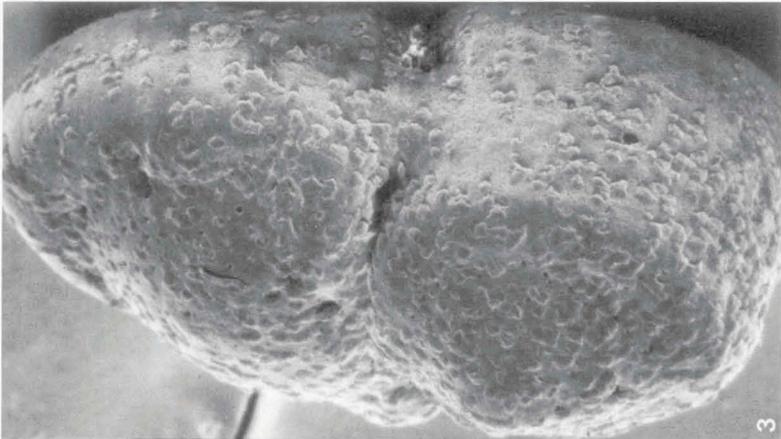
The protoconch (I) is cylindrical with convex lateral sides. The deutoconch (II) is kidney-shaped and is surrounded by a ridge. The PA-II side is recognized by the openings of the two funnel-shaped deutoconchal stolons. The PA-I side shows the single opening of the deutoconchal stolon (D).

Fig. 1. The PA-I side, x 200.

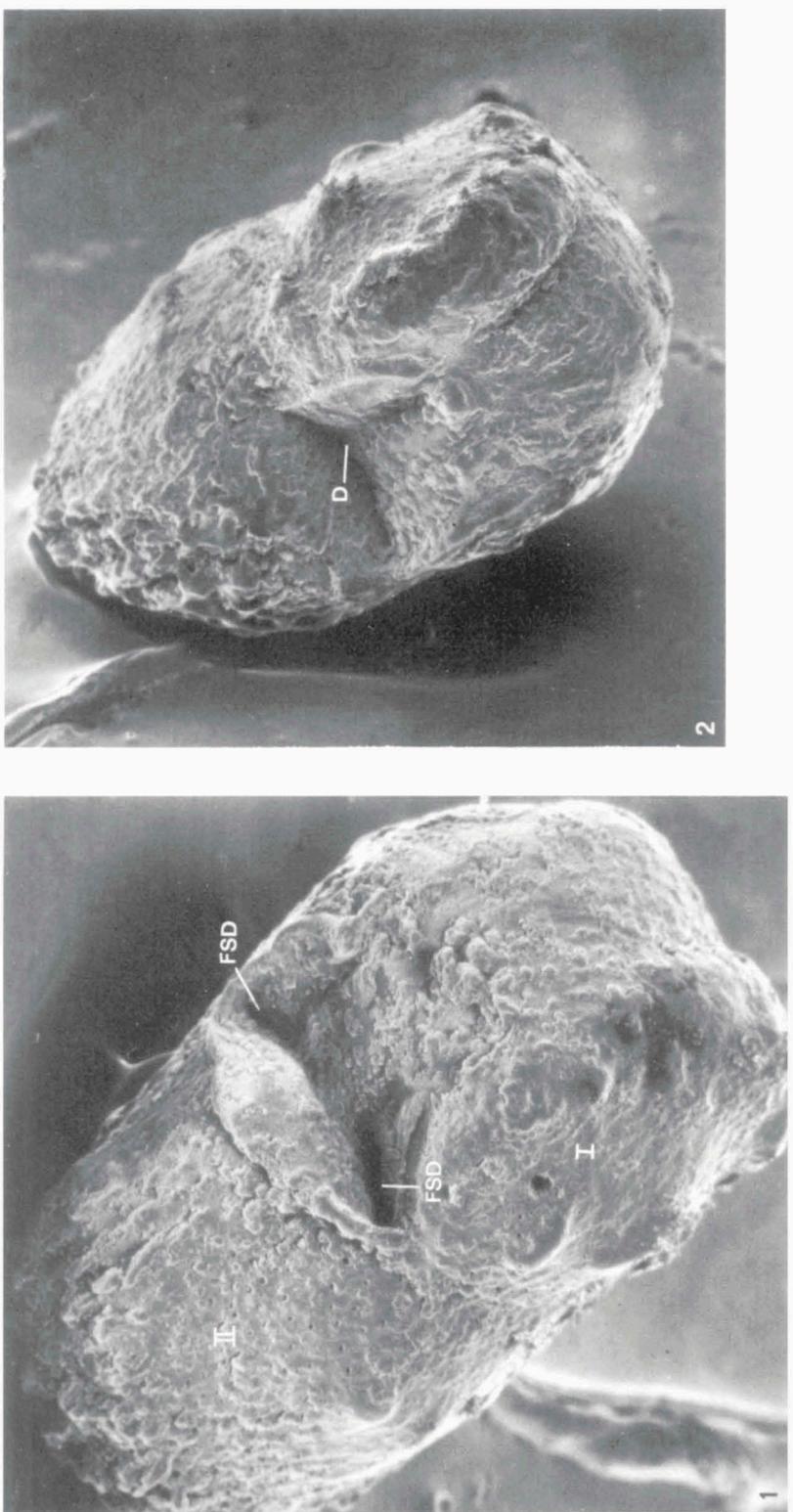
Fig. 2. Lateral view, x 200.

Fig. 3. The PA-II side, x 200.

Plate 17



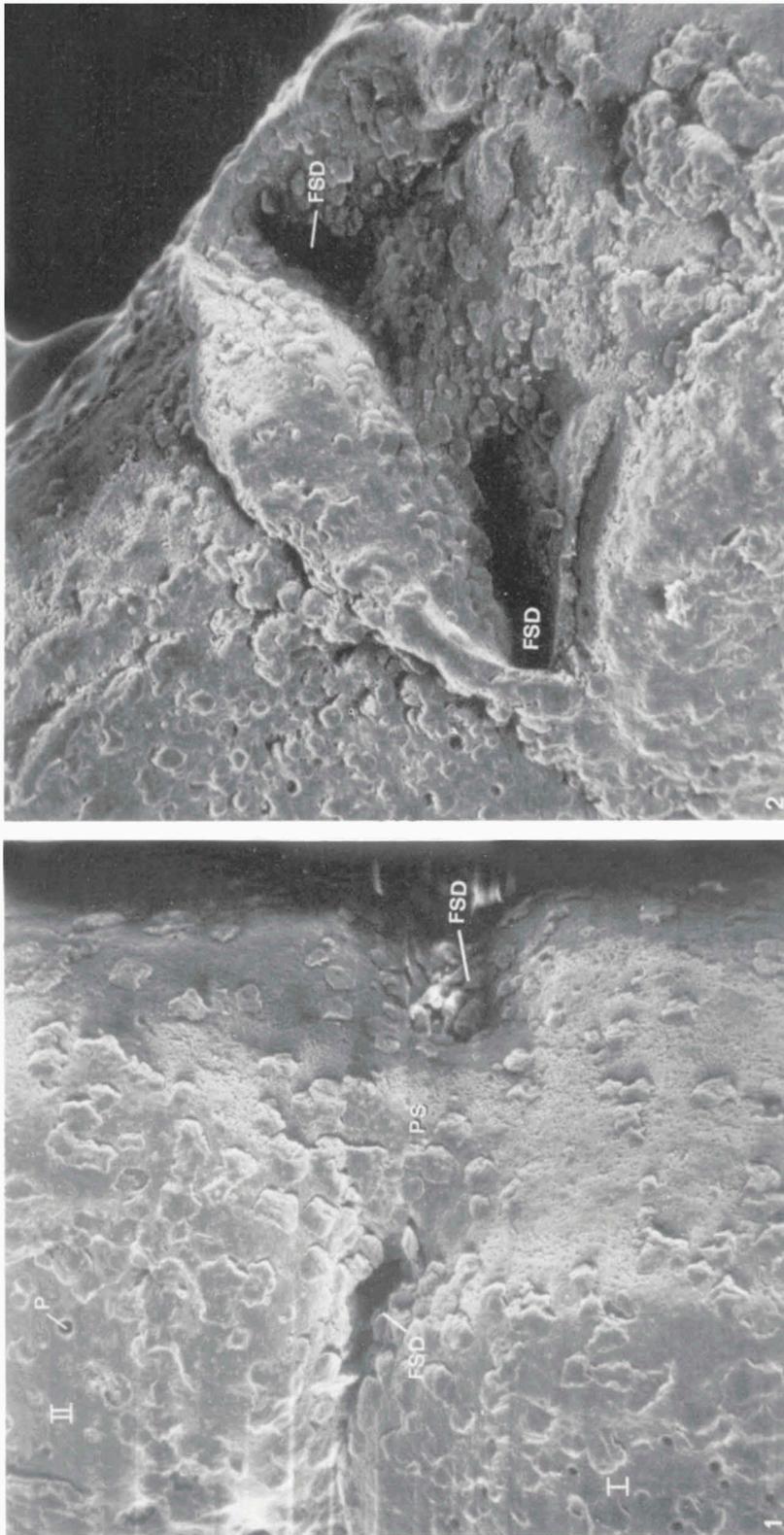
## Plate 18



The nucleocoenoch of *Miogypsina* s.s., Kombangan, Bg.316, Indonesia, RGM 230 814.

Fig. 1. The PA-II side. The openings of the two funnel-shaped deuterocoenochal stolens are distinct. The ornamentation on the surface is accentuated; the beginning of the wall of the second primary auxiliary chamber is visible. x 200.

Fig. 2. The PA-I side. This specimen has not yet developed a first nor a second primary auxiliary chamber (PA-I, PA-II). A marginal fringe has formed on the deuterocoenoch (II). x 175.



Two enlargements of the PA-II side of the specimens in Pls. 17, 18. In fig. 2 secondary material, which is the beginning of PA-II, is found around the openings of the two funnel-shaped deuteroconchal stolons. RGM 230 814, x 1000.

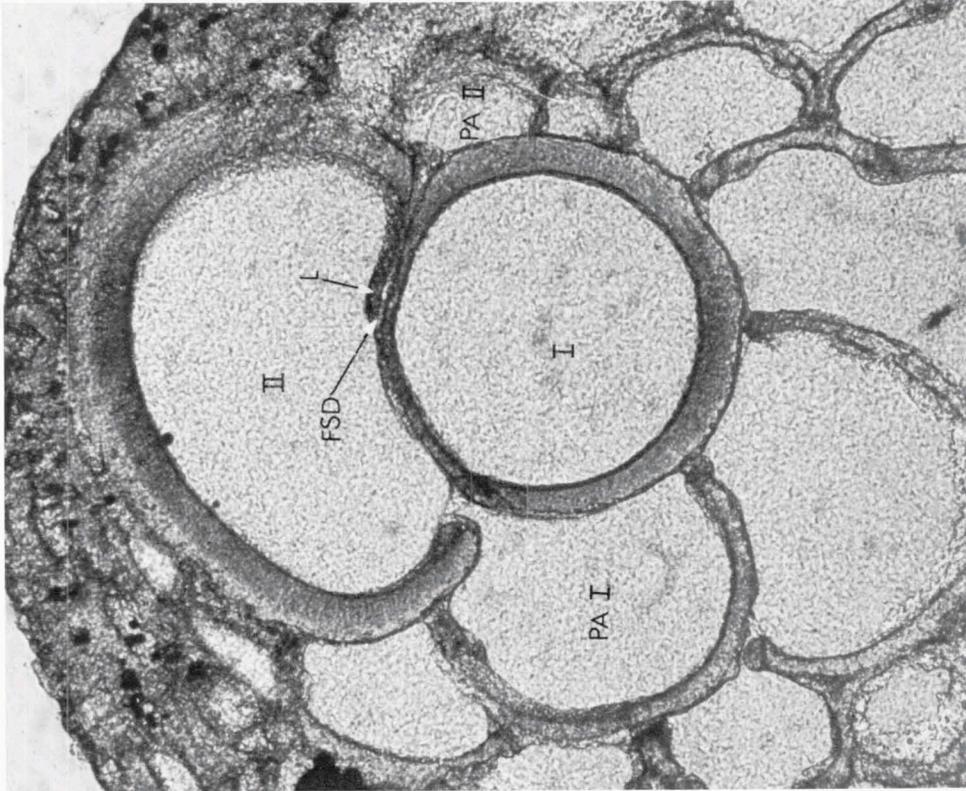
## Plate 20

*Miogypsina (Miogypsina) globulina*, Kombangan, Bg.315, Indonesia.

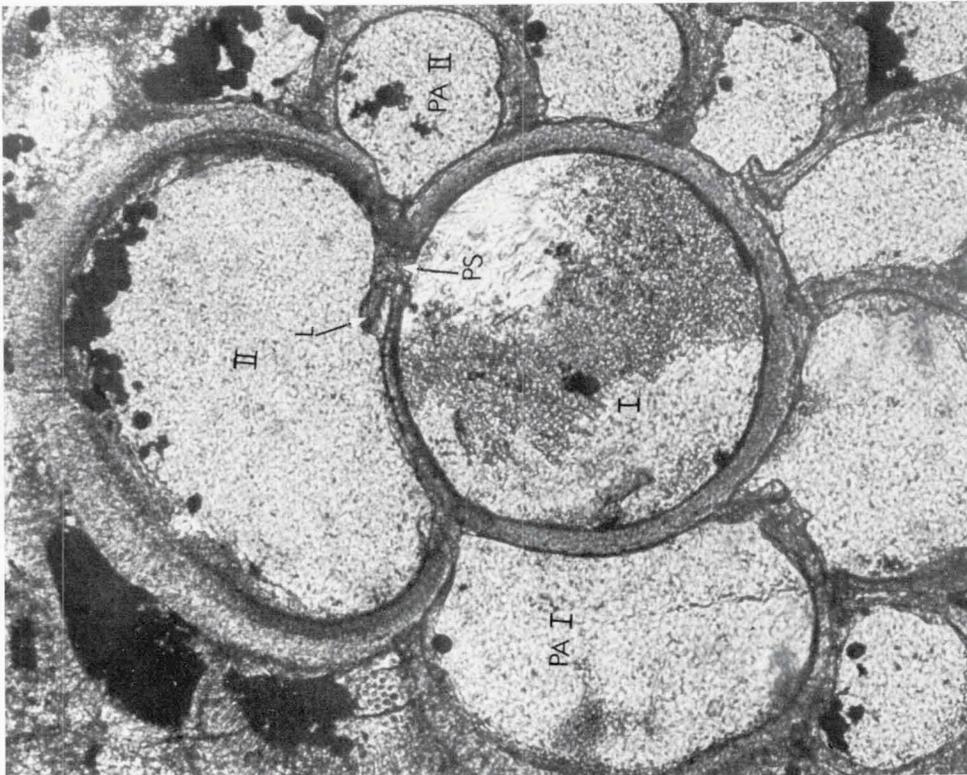
Fig. 1. Thin section parallel to the equatorial plane, exactly through the protoconchal stolon (PS). Because of the thickness of the thin section the cylindrical protoconchal stolon is visible. Specimen no. 7393, Coll. van der Vlerk, x 100.

Fig. 2. Horizontal section just next to the protoconchal stolon. The funnel-shaped deuteroconchal stolon (FSD) extends between the lip and the wall between protoconch (I) and deuteroconch (II). This stolon runs around the protoconchal stolon. Specimen no. 7325, Coll. van der Vlerk, x 100.

Plate 20



2



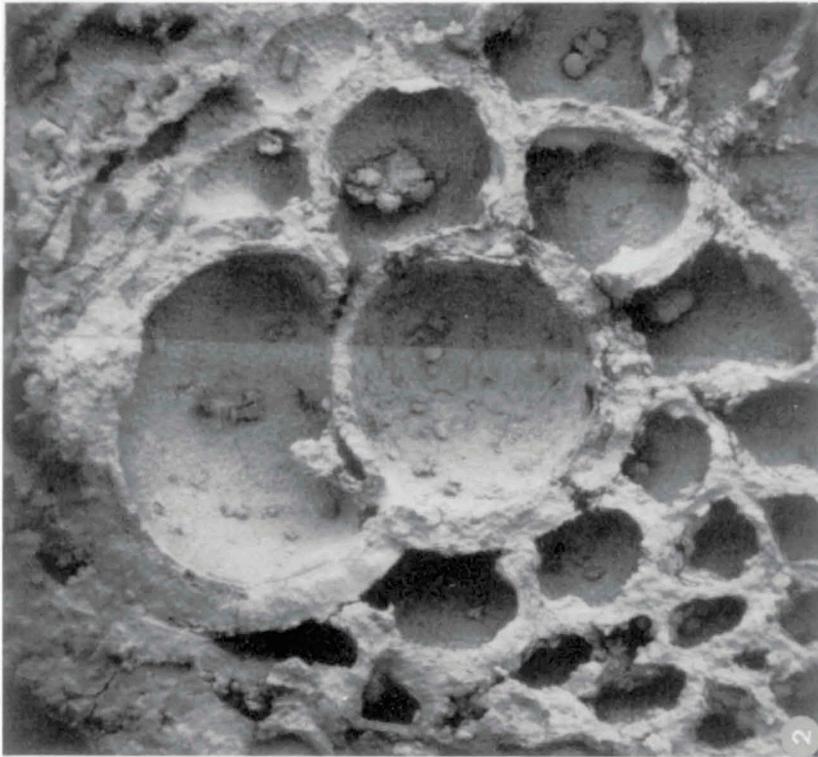
1

## Plate 21

*Miogypsina (Miogypsina) antillea*, Kombangan, Bg.312, Indonesia, RGM 230 812, x 210.

The specimen had been split in two halves exactly through the protoconchal stolon (PS). The protoconchal stolon lies on the PA-II side. The lip (L) points inwards, in the assumed direction of the protoplasm stream which formed the deuterocoel (II). Behind and around the protoconchal stolon between the lip and the wall (W) between I and II are the funnel-shaped deuterocoelal stolons (FSD).

Plate 21

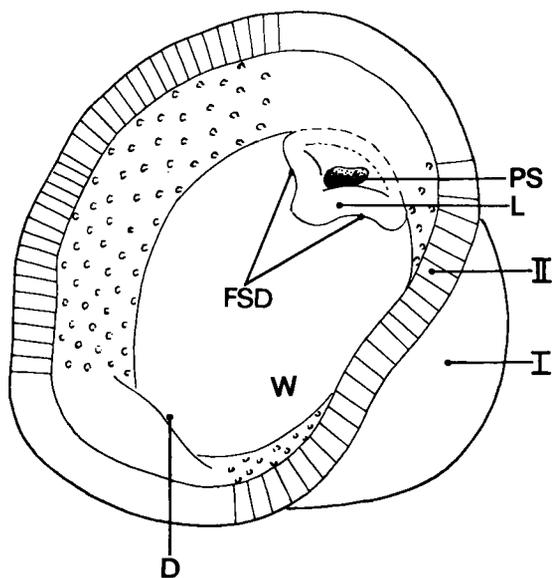


## Plate 22

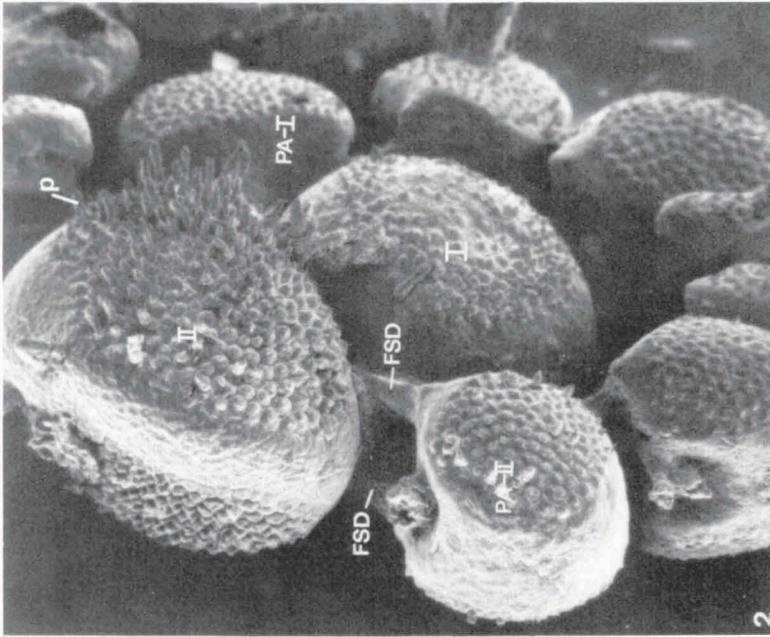
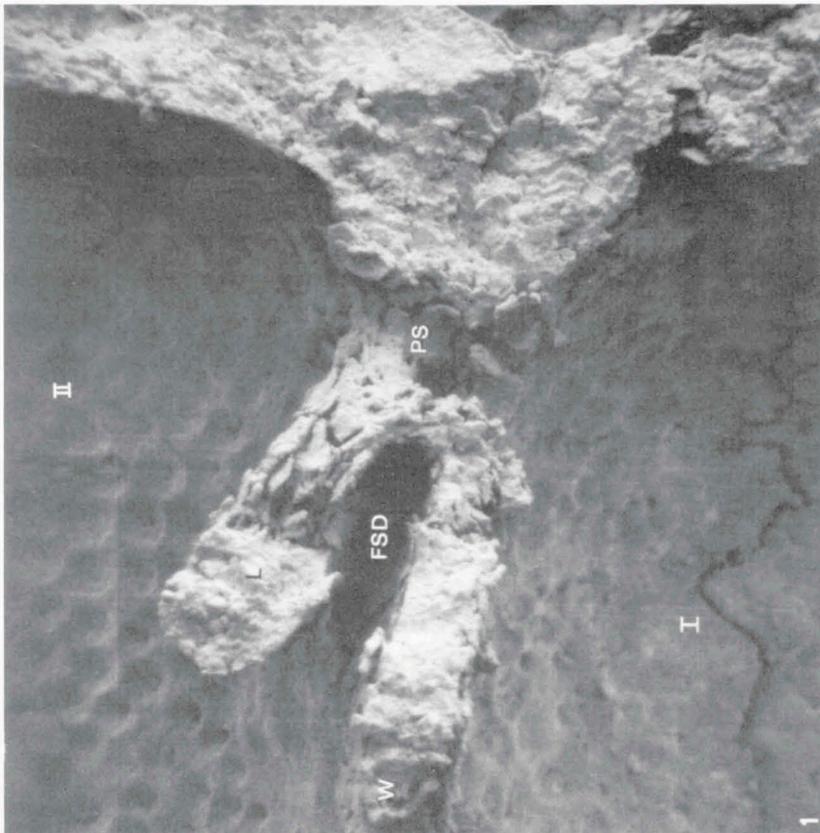
### *Miogypsina (Miogypsina) antillea.*

Sample L.393, N. Borneo (see van der Vlerk, 1925). Although this sample is not described in the present paper, this specimen is used to show the lip in the deuterocoel. The deuterocoel is open at the top and we can look into the deuterocoel at the wall (W) between I and II. The lip (L) is shaped like an arrow head. Under the lip, on either side of protoconchal stolon (PS), the two funnel-shaped deuterocoelal stolons (FSD) extend to PA-II.  
RGM 230 828, x 200.

Plate 22



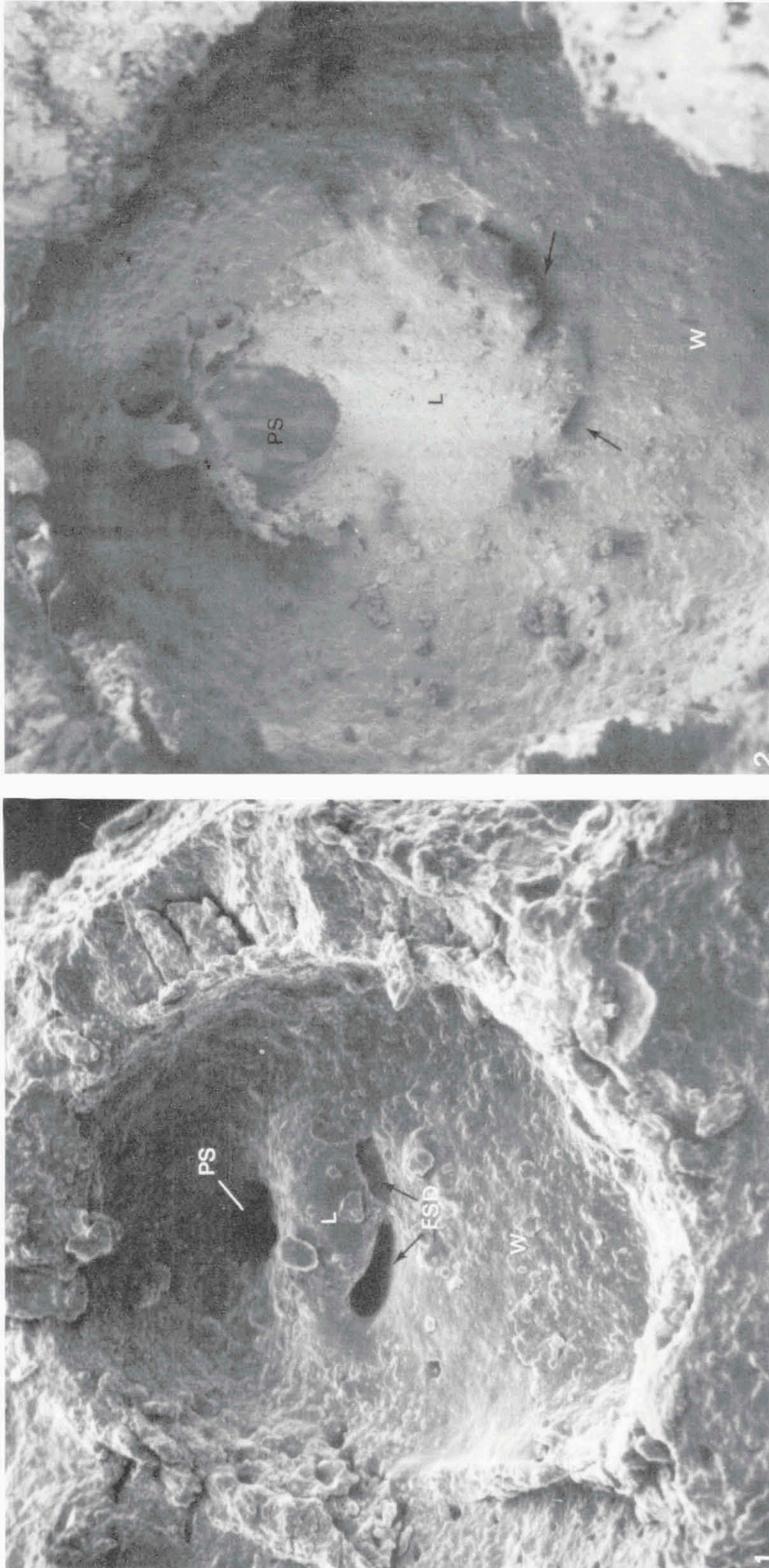
## Plate 23



*Miogypsina antillea*, Kombangan, Bg. 312, Indonesia.

Fig. 1. Detail of the protoconchal stolon and the lip on the PA-II side of the nucleoconch. On both sides around the protoconchal stolon (PS) two funnel-shaped deuterocoelal stolons (FSD) extend towards the second primary auxiliary chamber (PA-II), RGM 230 812, x 500.

Fig. 2. Negative chamosite mould of the embryonic apparatus. The two funnel-shaped deuterocoelal stolons (FSD) are distinct. The photograph shows that the ridge on the deuterocoelal (II) seen in free nucleoconches is not perforated by pores. Only the lateral sides of the chambers are perforated by pores (p). RGM 230 829, x 200.

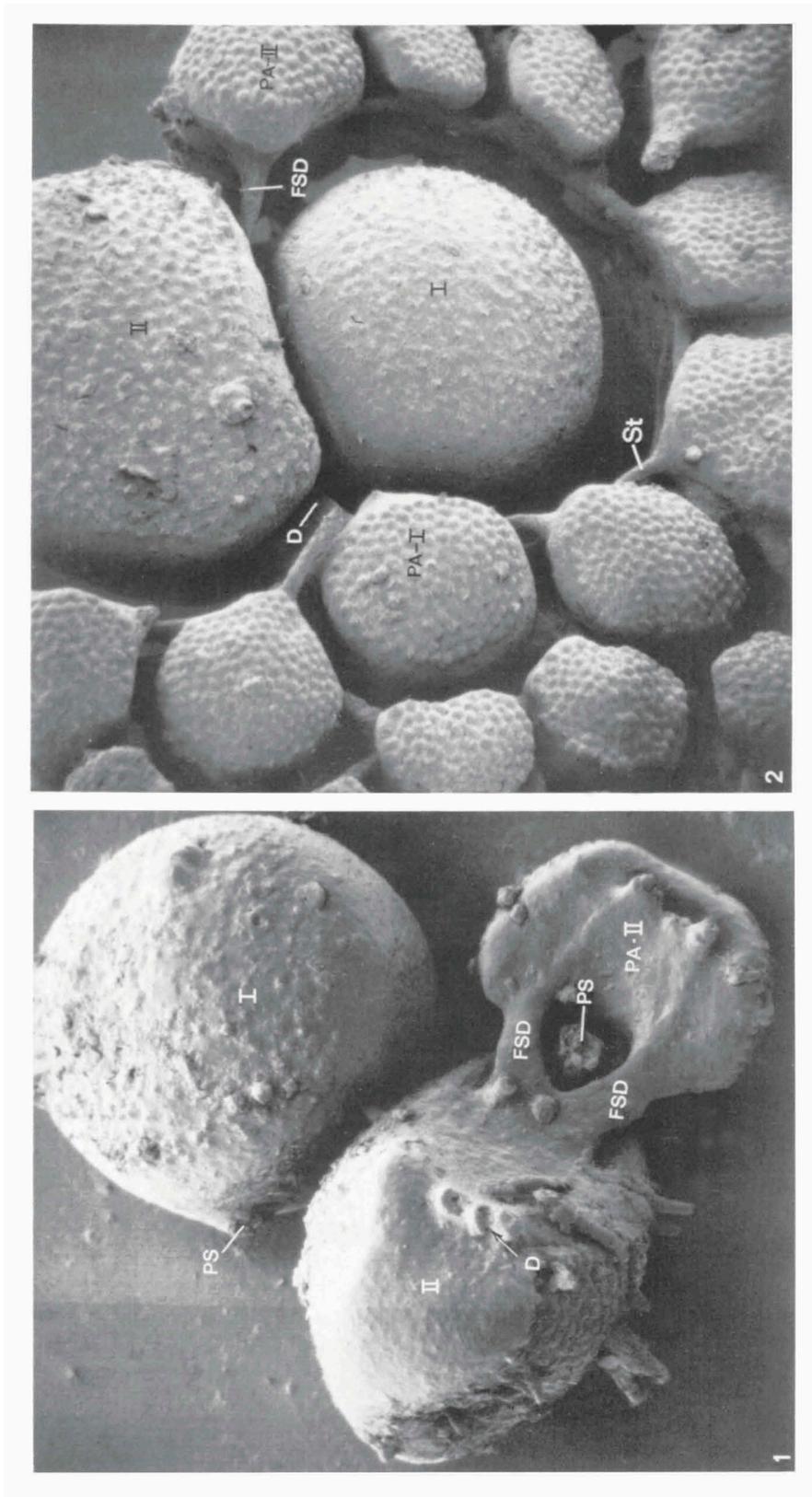


*Miogypsina* s.s., Kombangan, Bg.312, Indonesia.

Two different species of *Miogypsina* s.s. with a differently shaped lip around the protoconchal stolon.

Fig. 1. The two large openings of the funnel-shaped deutoconchal stolons (FSD) are distinct; the lip is short. This specimen possesses a large second primary auxiliary chamber, RGM 230 828, x 500.

Fig. 2. The openings of the funnel-shaped deutoconchal stolons are less distinct; the lip (L) is somewhat elongated. This specimen possesses a small second primary auxiliary chamber. RGM 230 828, x 500.



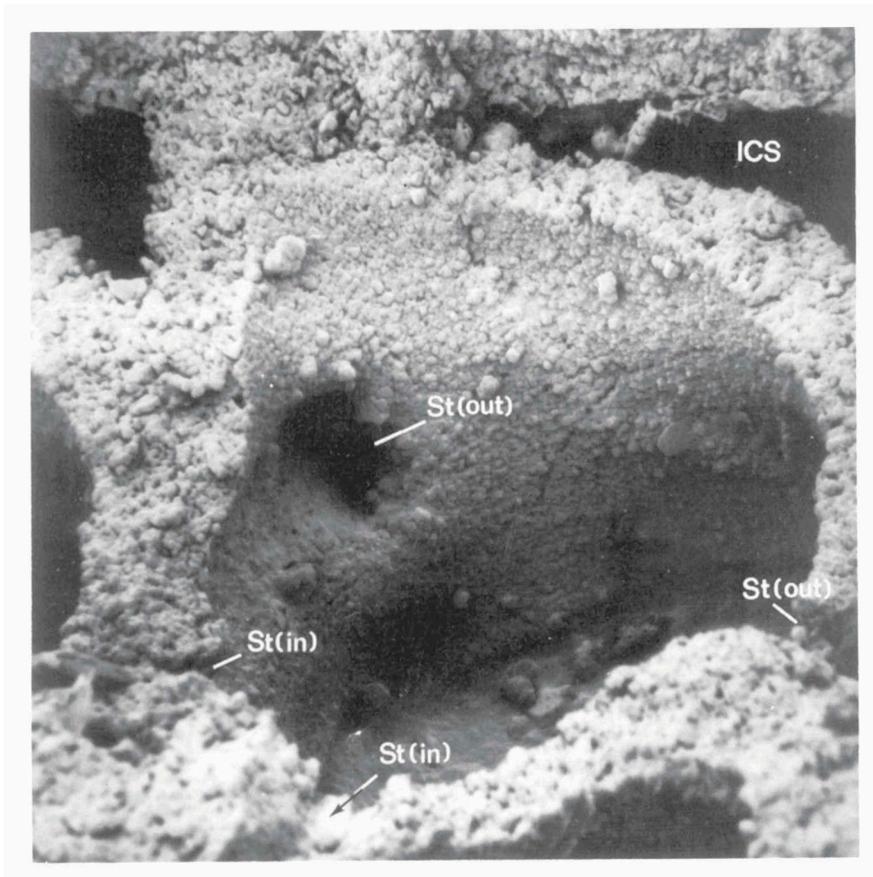


Plate 26

Plate 26

An equatorial chamber of *Miogypsina* (*Miogypsinoides*) *bantamensis*, showing the simple stolon system. The subgenus *Miogypsinoides* has a simple stolon system: each equatorial chamber possesses four stolons, two inflow stolons and two outflow stolons. All stolons are interconnected by a furrow situated on the apical side of the vertical chamber wall (septum). On the frontal side the furrow grades into a ridge.

Anse deï Bano, M64, France, RGM 230 825, x 200.

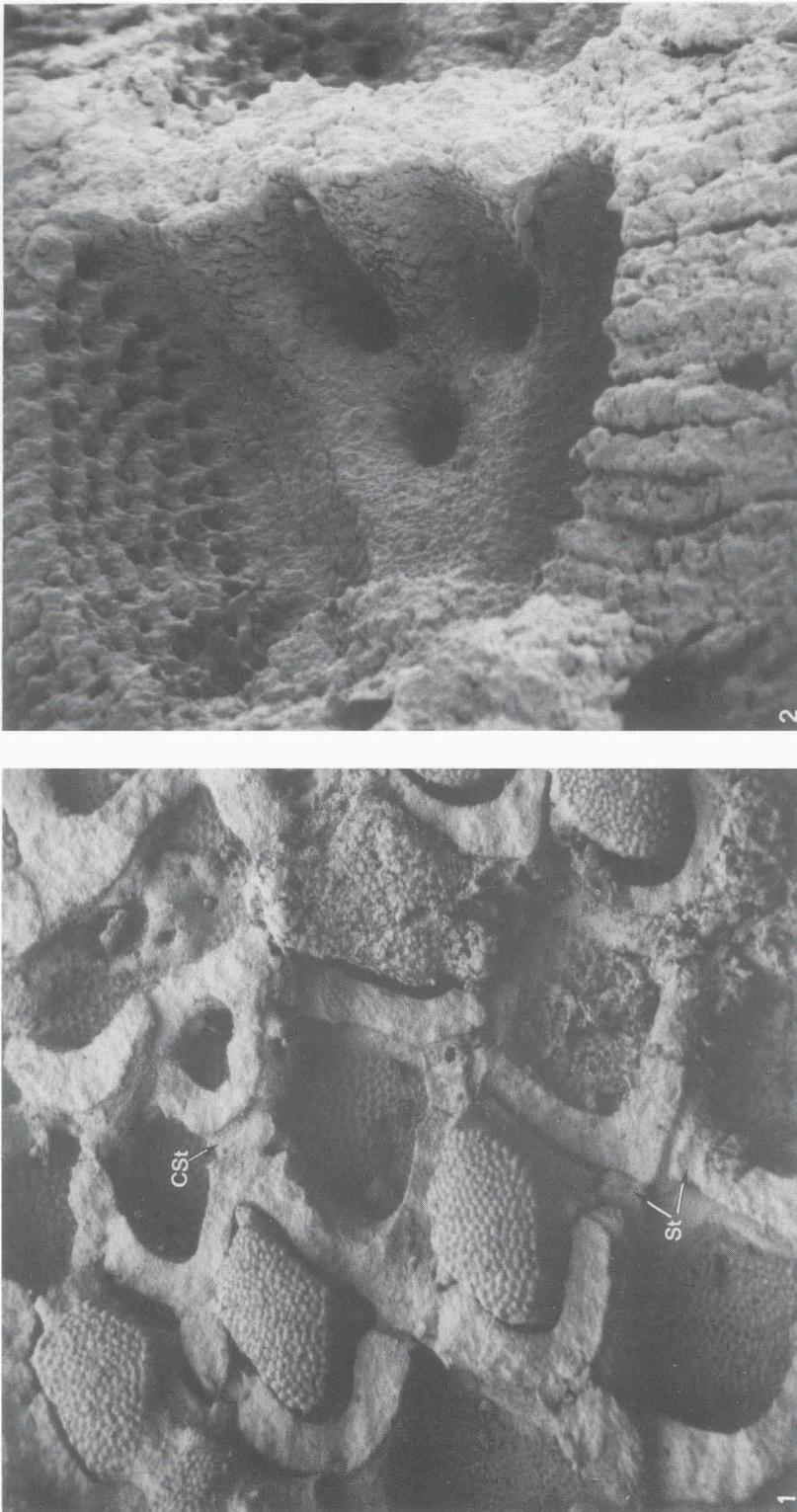
## ◀ Plate 25

Negative chamosite moulds of *Miogypsina antillea*, Kombangan, Bg.312, Indonesia.

Fig. 1. The two funnel-shaped deuteroconchal stolons (FSD) on both sides of the protoconchal stolon (PS) are distinct. The protoconch has broken off from the deuteroconch (II). RGM 230 822, x 200.

Fig. 2. The first and the second primary auxiliary chamber (PA-I and PA-II) are almost equal in size and shape. The several stolons connecting the spiral chambers are clearly visible. RGM 230 822, x 200.

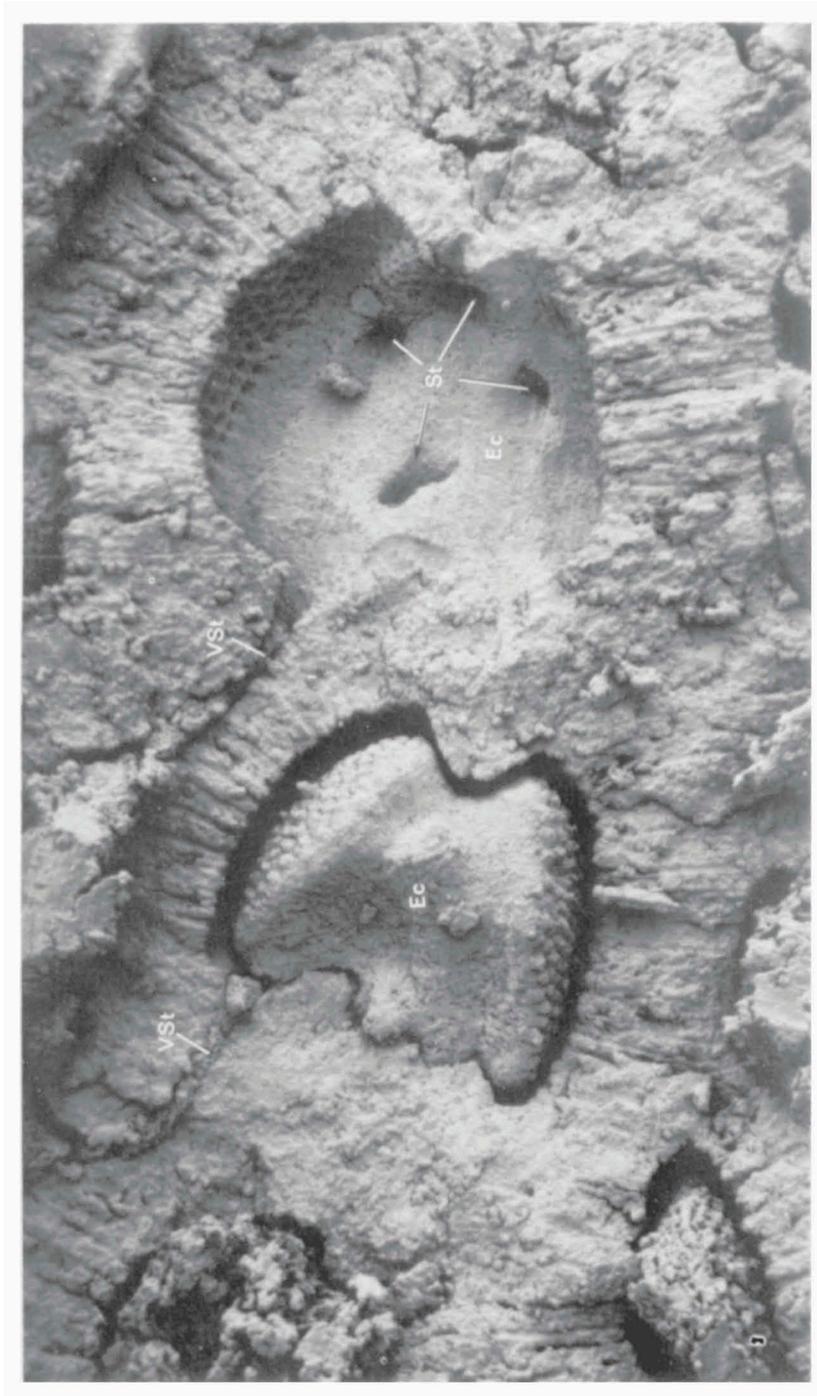
## Plate 27



Equatorial chamber of *Miogypsina* s.s., Anse d'ei Bano, France.

Fig. 1. When the stolons are close together, two stolons may merge forming a connection between two simultaneously formed equatorial chambers, i.e. Tan's concentric stolon (CSt.). RGM 230 820, x 200.

Fig. 2. In *Miogypsina* s.s. the stolon system is more complicated than in *Miogypsinoides*. Two types of stolons may be distinguished: the horizontal stolons forming the connection between equatorial chambers, and the vertical stolons (VSt) forming the connection between equatorial and lateral chambers. The horizontal stolons are arranged in groups of three. Each trio is situated on a ridge. Furrows interconnect the 'proximal' stolons of each trio. RGM 230 825, x 1000.



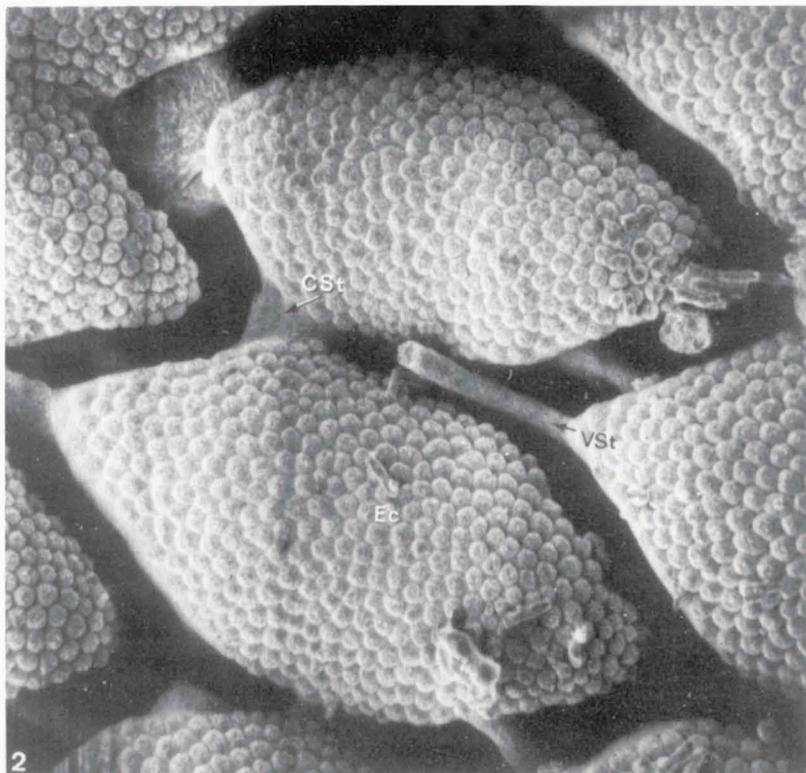
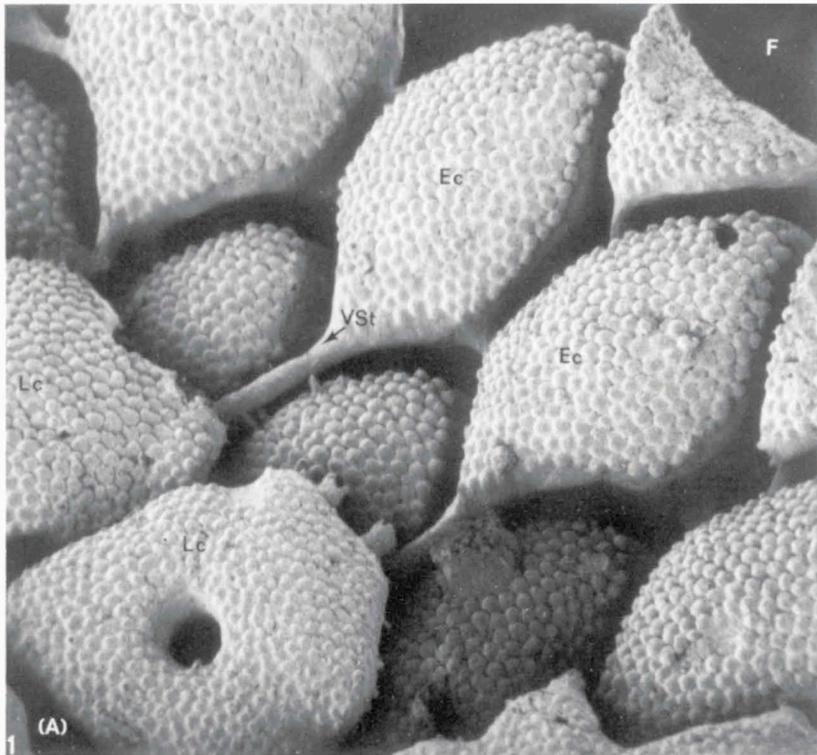
A vertical section through two equatorial chambers of *Miogypsina* s.s., Anse dei Bano, France. To the right in the photograph is a trio of 'horizontal' stolons (CSt) forming the connections with the lateral chambers are distinct. RGM 230 820, x 500.

## Plate 29

Two negative moulds of chamosite of the equatorial chambers in *Miogypsina thecideaformis* (hexagonal equatorial chambers, see Drooger & Schipper, 1973), Kombangan, Bg.316, Indonesia.

A vertical section through two equatorial chambers of *Miogypsina* s.s., Anse deï Bano, France. The vertical stolons (VSt) point towards the apex and form the connections with the lateral chambers (Lc). In fig. 2 one of the lateral chambers has an unexplained hole. Fig. 1. RGM 230 822, x 460. Fig. 2. RGM 230 819, x 550.

Plate 29



## Plate 30

Locality: Larat 20, Molucca Islands.

Fig. 1. *Miogypsina (Miogypsinoides) dehaartii* (after van der Vlerk, 1965, pl. 1). No lateral chambers have developed. The vertical canal system penetrates into the massive ventral and dorsal parts of the test. At the apex the marginal fringe with truncated cones is distinct. Coll. van der Vlerk, x 25.

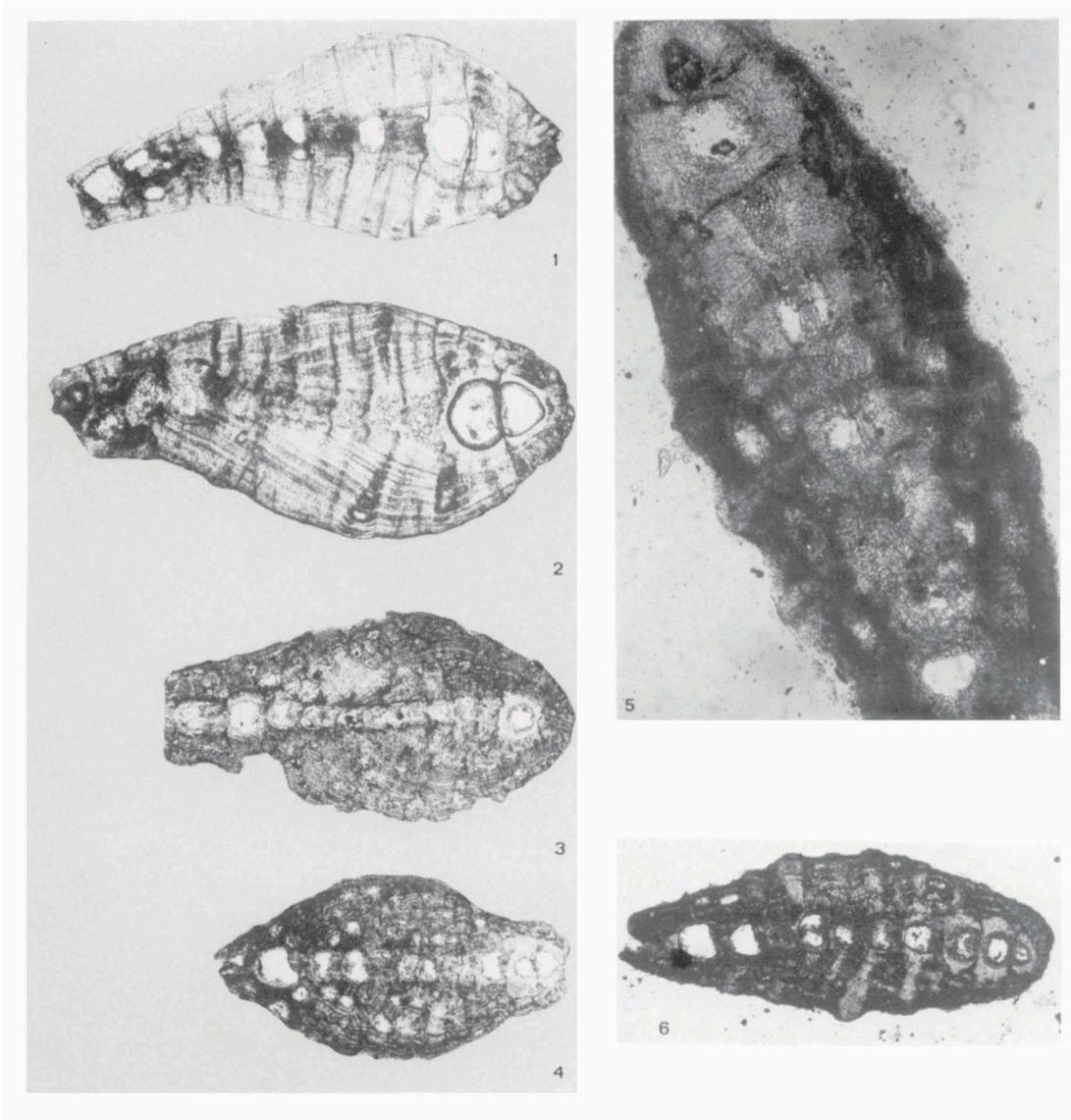
Fig. 2. *Miogypsina (Miogypsinoides) dehaartii* (after van der Vlerk, 1966, pl. 1). Within the horizontal lamination of the test are small cavities in pillar-like structures; this is one of the suggested possibilities for the origin of lateral chambers. The cavities lie in vertical rows. Coll. van der Vlerk, x 25.

Figs. 3, 4. Because of the absence of an intraseptal canal system and the development of lateral chambers, these specimens are assigned to *Miogypsina (Miogypsina) borneensis*. In horizontal rows in the lamination of the test are cavities which may also be the origin of lateral chambers (after van der Vlerk, 1966, pl. 1). Coll. van der Vlerk, x 25.

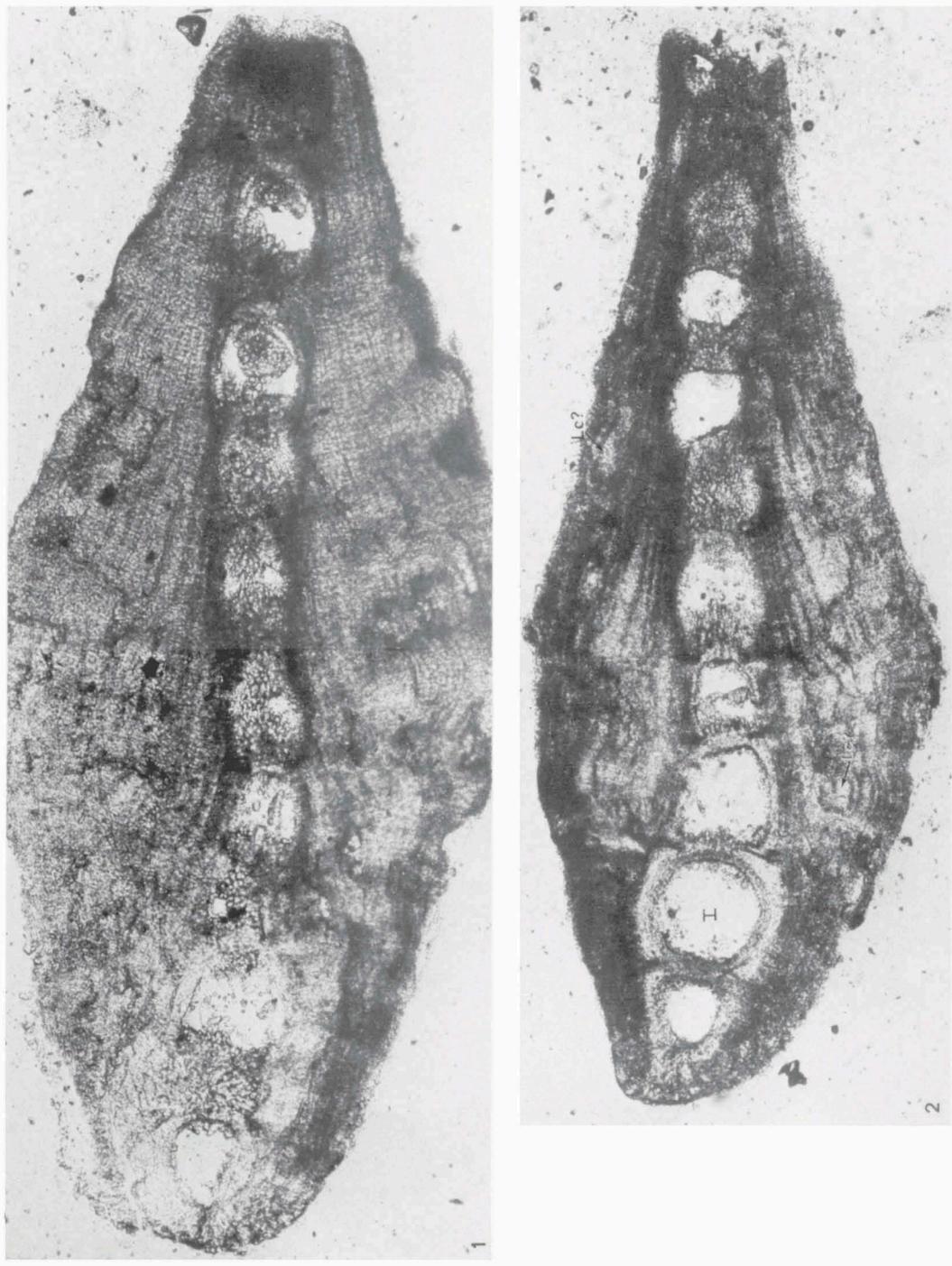
Fig. 5. *Miogypsina (Miogypsina) borneensis*, vertical section. In the juvenile stage there are no lateral chambers. In the more adult stages of growth the lateral chambers grow from the front towards the apex. Pillars develop from the equatorial chambers. RGM 230 534, x 50.

Fig. 6. *Miogypsina (Miogypsina) borneensis*. Lateral chambers have developed between the pillars arising from the lateral walls of the equatorial chambers. The pillars form tubercles on the surface. RGM 230 554, x 20.

Plate 30



## Plate 31

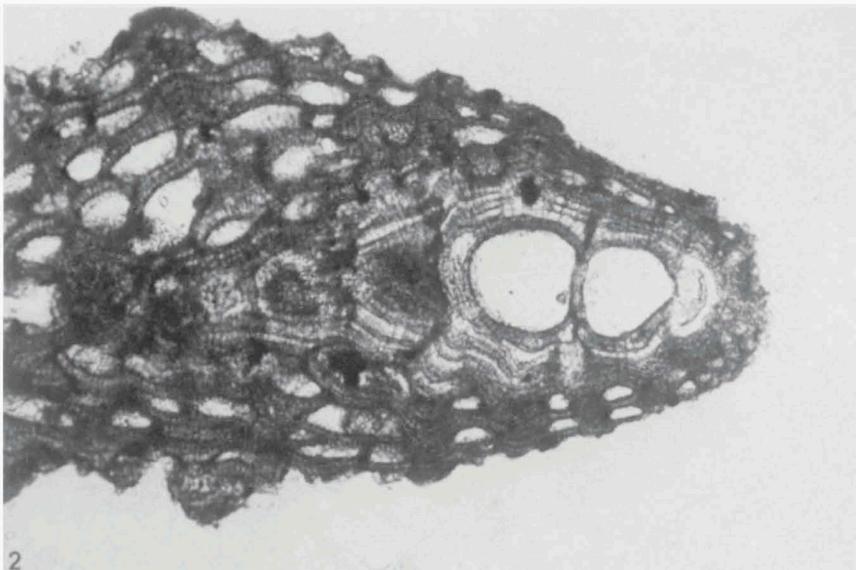
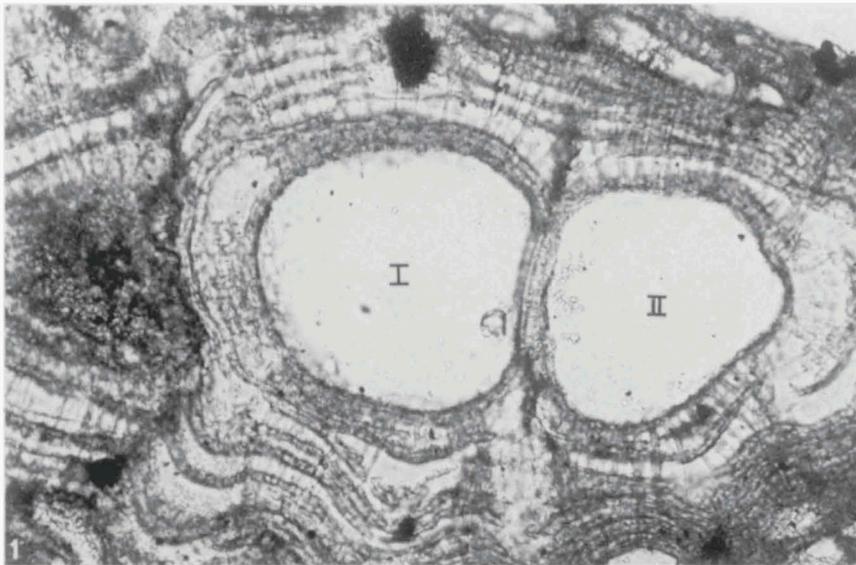


Two possible origins of lateral chambers; locality: Larat 20.

Fig. 1. On the lateral side of the equatorial chambers are pillars; the cavities between these pillars may be the beginnings of lateral chambers. RGM 230 670, x 80.

Fig. 2. In the horizontal layering of the lateral walls of the test are cavities which form the beginning of lateral chambers. Because no intraseptal canal system is seen, the specimen could be assigned to the subgenus *Miogypsina*: *Miogypsina borneensis*. RGM 230 504, x 90.

Plate 32



*Miogypsina* s.s., Kombangan, Indonesia.

The layers of lateral chambers grow from the frontal side towards the apex. In the juvenile stage cavities are formed between the lamellae of the lateral sides. This structure is comparable to the lamellar structure of *Miogypsinoidea*. Coll. van der Vlerk. Fig. 1, x 175. Fig. 2, x 80.

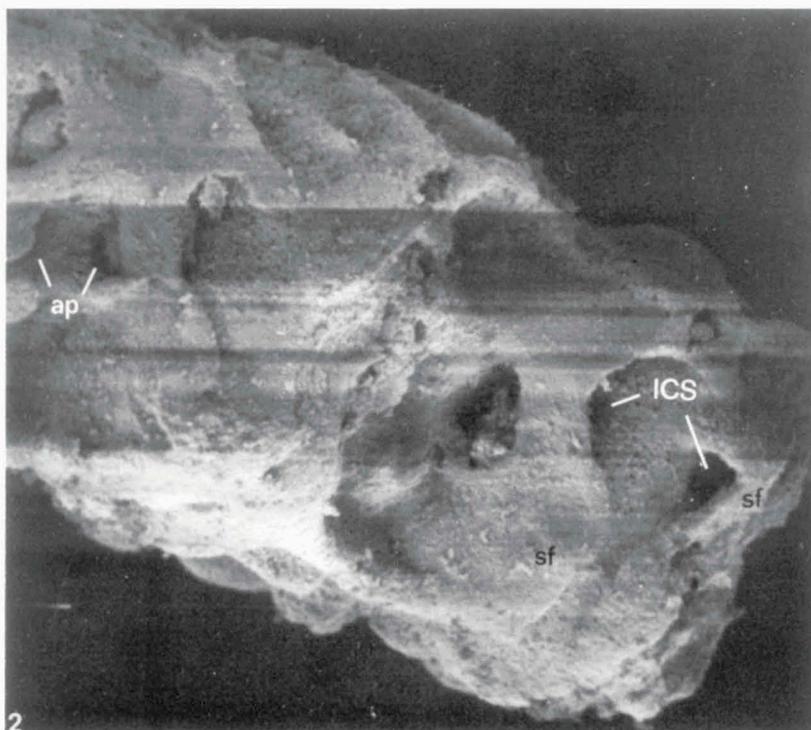
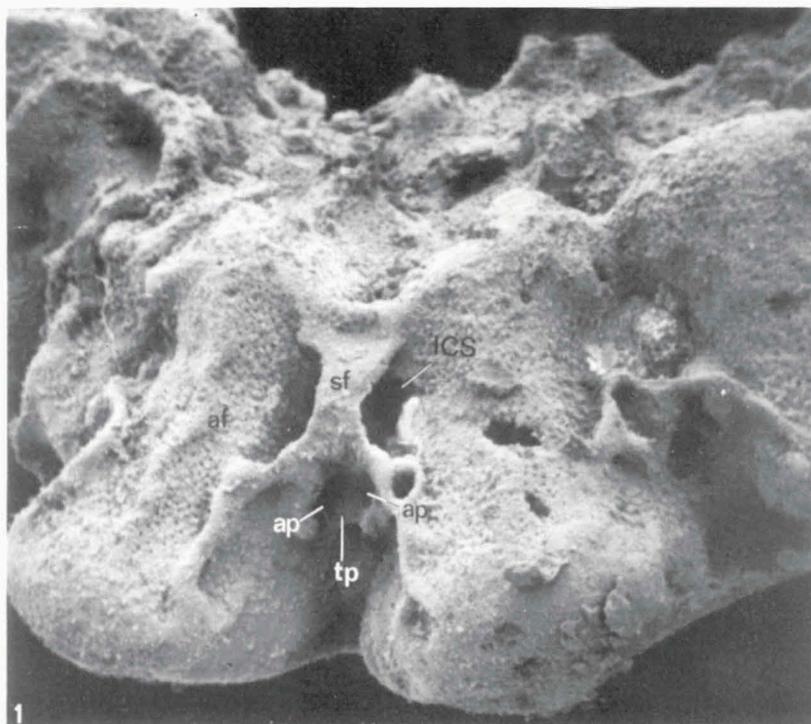
## Plate 33

*Miogypsinoidea bantamensis*, Estoti, FR1120, France.

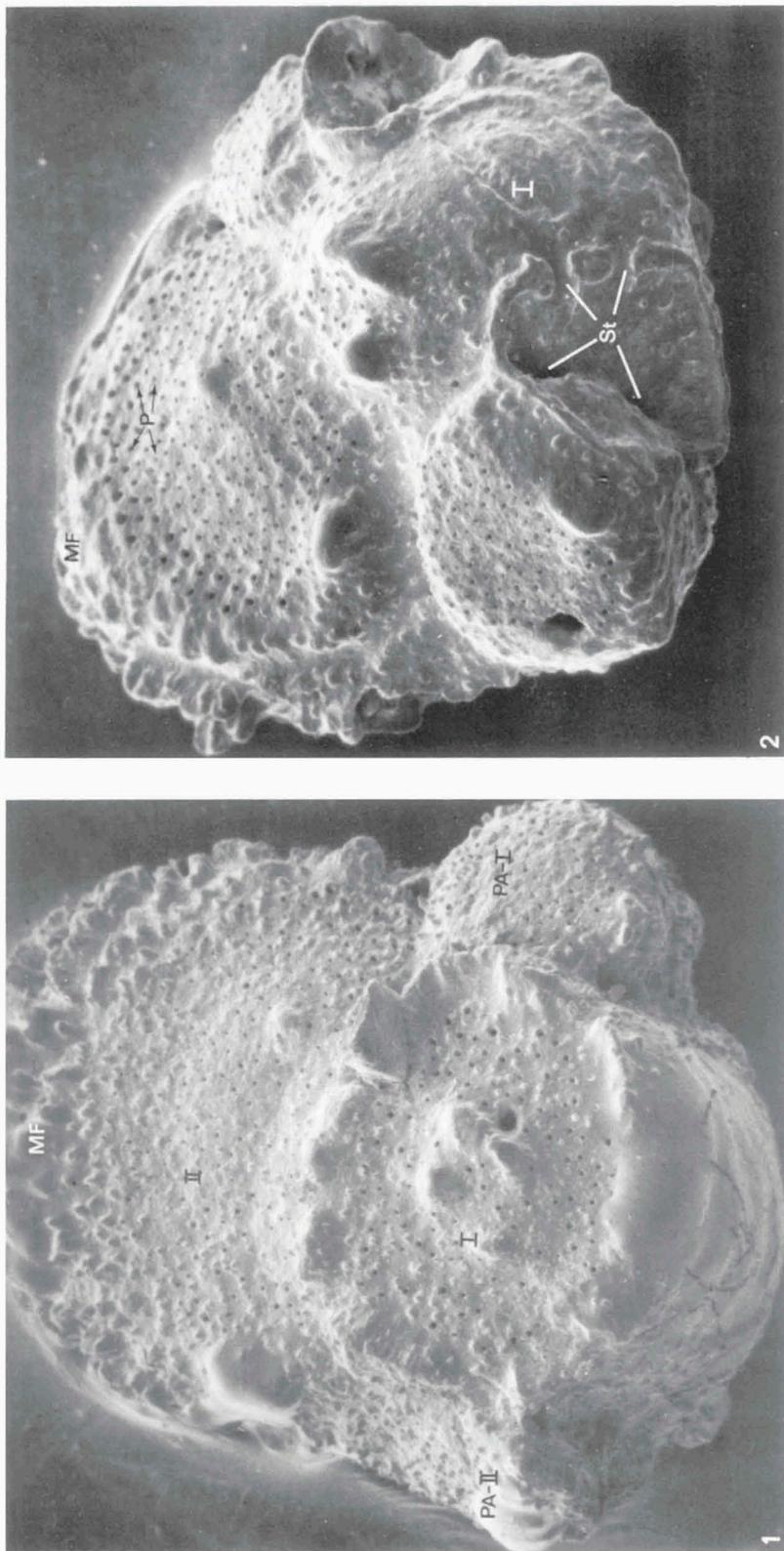
Fig. 1. Two equatorial chambers with a perforated apertural face (af). In the recessed part between the two equatorial chambers are the toothplate (tp) and the beginning of the septal flap (sf) as well as the apertures (ap) and the openings of the intraseptal canal system. The apertures are close together; between them are the two merged hooks of the toothplates. RGM 231 260, x 200.

Fig. 2. The septal flap (sf) almost covers the entire apertural face of the equatorial chambers. The openings of the intraseptal canal system (ICS) are situated on the protruding parts of the equatorial chamber. The vertical canal is completed in the recessed part between the equatorial chambers. Part of the ventral and dorsal 'roof' of the equatorial chambers is formed. RGM 231 260, x 200.

Plate 33

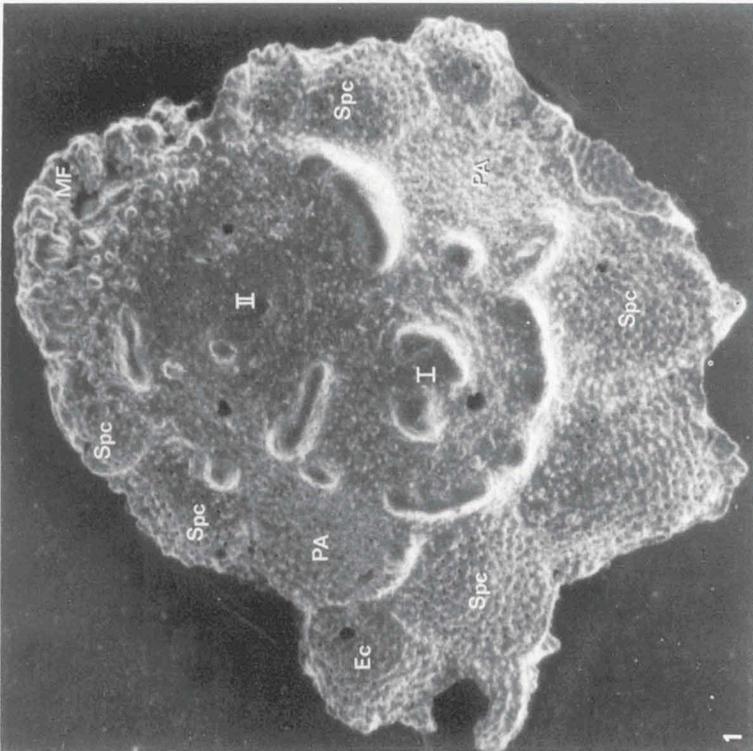
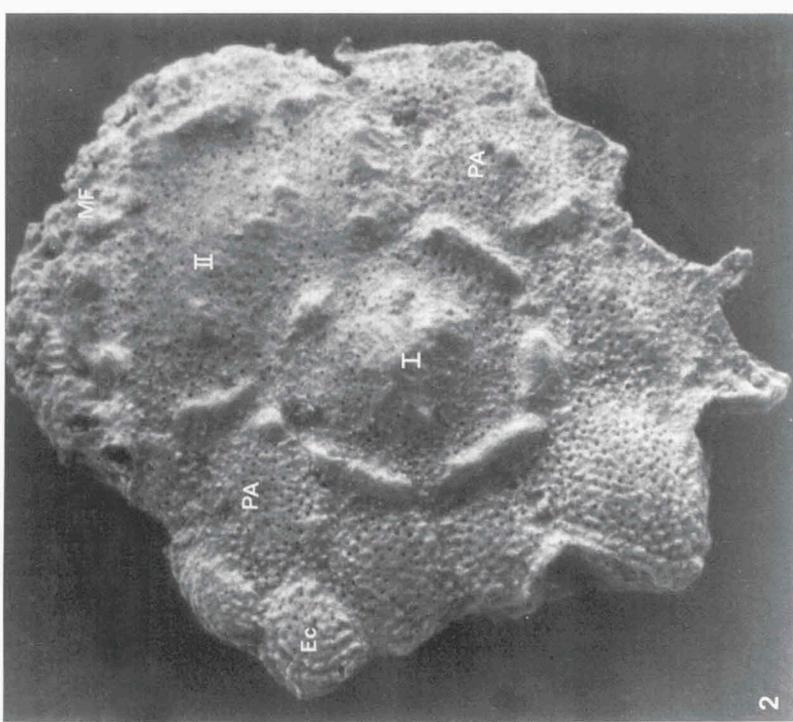


## Plate 34



*Miogypsina* s.s., Kombangan, Bg.316, Indonesia.

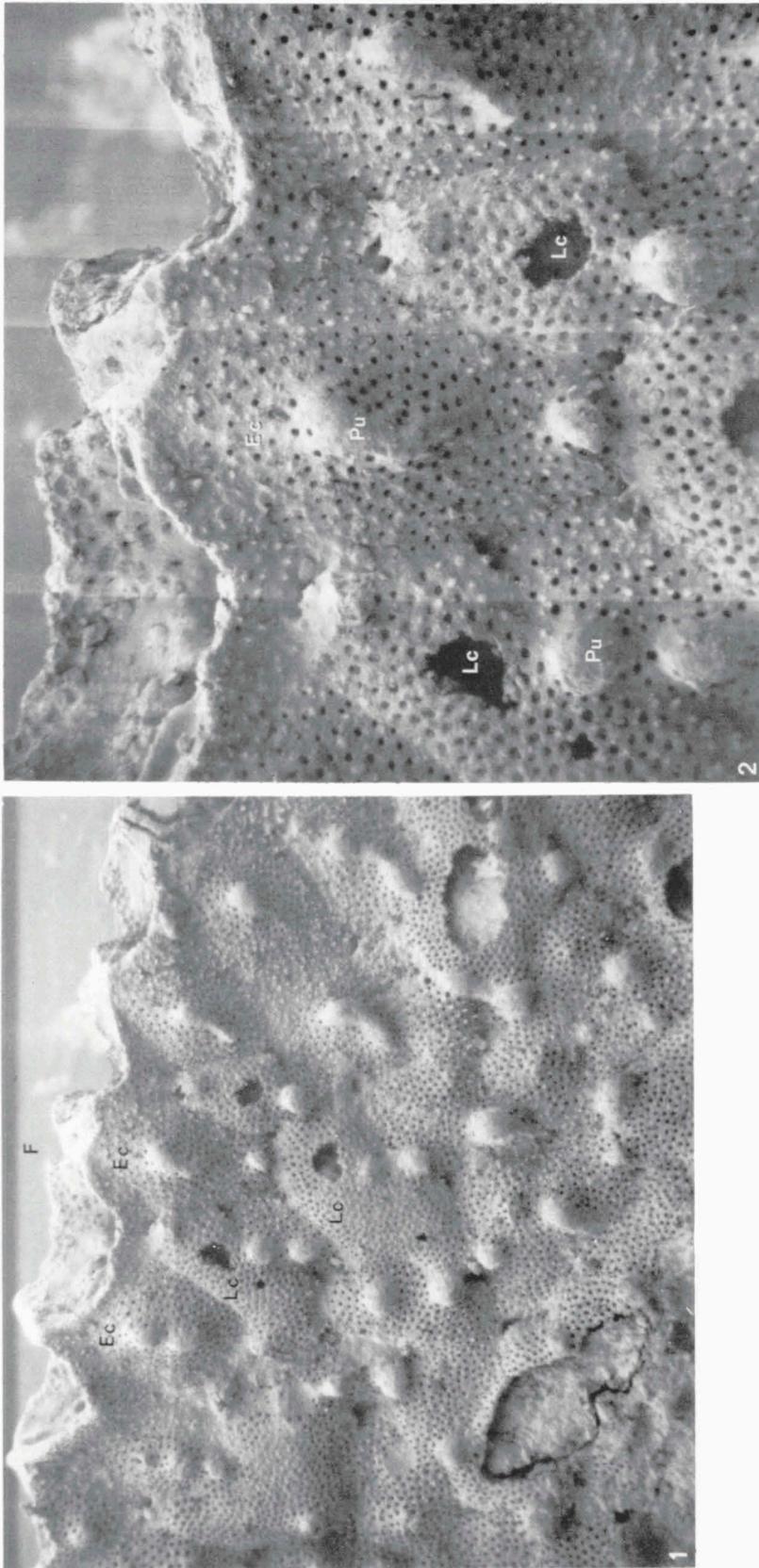
Two 'nucleoconches' which have developed a first and a second primary auxiliary chamber (PA-I and PA-II). The marginal fringe (MF) is almost completed. The external perforations of the pores are more distinct than in the earlier stages of growth. In fig. 2 the development of the spiral chambers is shown. The initial growth of the stolons (St) which will form the next chamber can also be seen. Fig. 1. RGM 230 816, x 200. Fig. 2. RGM 230 811, x 200.



*Miogypsina antillea*, Kombangan, Bg.316, Indonesia.

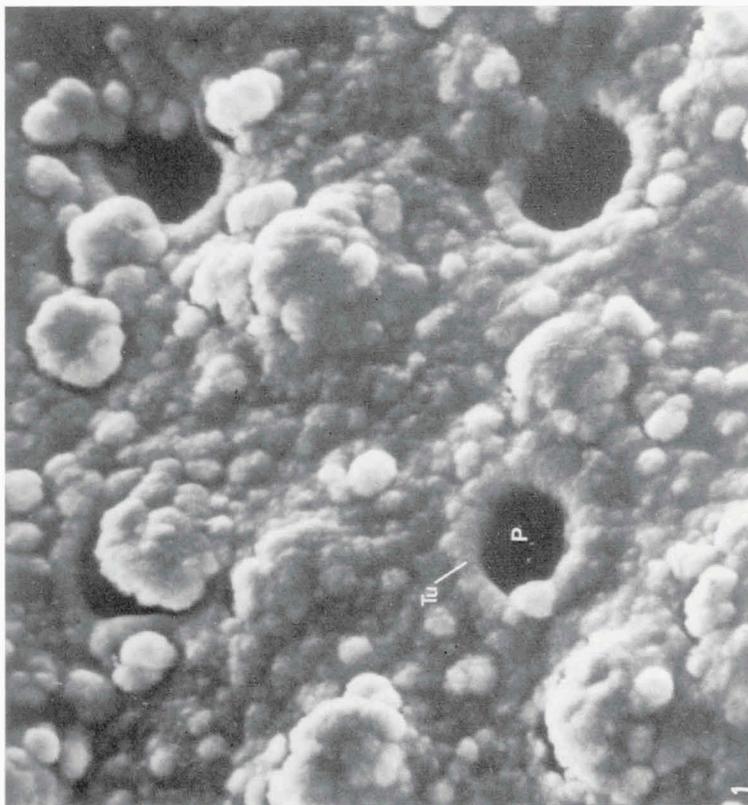
Two embryonic-nepionic apparatuses. The protoconch (I) and the deuteroconch (II) are still distinct since there are as yet no lateral chambers. Two spirals have originated out of each primary auxiliary chamber (PA-I, PA-II), making the embryonic-nepionic apparatus quadriserial. Fig. 1. RGM 230 810, x 200. Fig. 2 RGM 230 821, x 200.

## Plate 36



*Miogypsina antillea*, Bg.316, Kombangan, Indonesia, RGM 230 810.

Near the front the equatorial chambers (Ec) are clearly visible. At the centre of each equatorial chamber one or more pustules (pu) have developed. Pustules are also found on the lateral chambers (Lc). The pustules are not perforated by pores. There is no irregular arrangement of the lateral chambers. The surface is ornamented with small, short 'needles' between the pores. These needles are found over the equatorial chambers as well as the lateral chambers. Fig. 1. x 200. Fig. 2. x 500.



*Miogypsina antillea*, Kombangan, Bg.316, Indonesia.

Fig. 1. A vertical section through a pore (P) showing the tubule (Tu). RGM 230 821, x 50 000.

Fig. 2. The tubule (Tu) of the pore forms a ring-like ridge around the external perforations of the pore (P) (the surface is not etched). RGM 230 821, x 10 000.

## Plate 38

*Miogypsina globulina*, Bg.312, Kombangan, Indonesia, specimen no. 7598, Coll. van der Vlerk. Near the lateral sides of the equatorial chambers a dark line (Dl) is visible. On scanning photographs this dark line often proves to be an intralamellar space. This leads to the conclusion that the septa in *Miogypsina* s.s. are primarily doubled, although near the centre of the equatorial chambers a distinct separation between inner lining and outer layer can only be distinguished in a few cases.

The aberrant colour of the nucleoconch may indicate that the protoconch and the deutoconch originated by division without having calcified walls in that particular growth stage, as shown for *Heterostegina depressa* (compare Röttger, 1974).



Plate 38

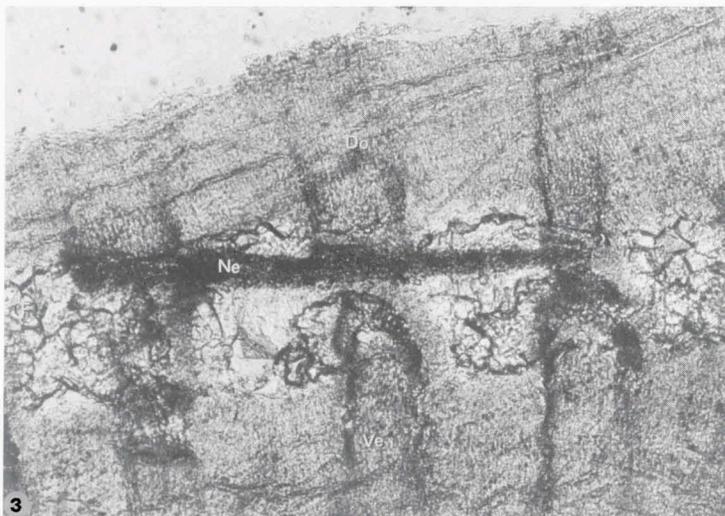
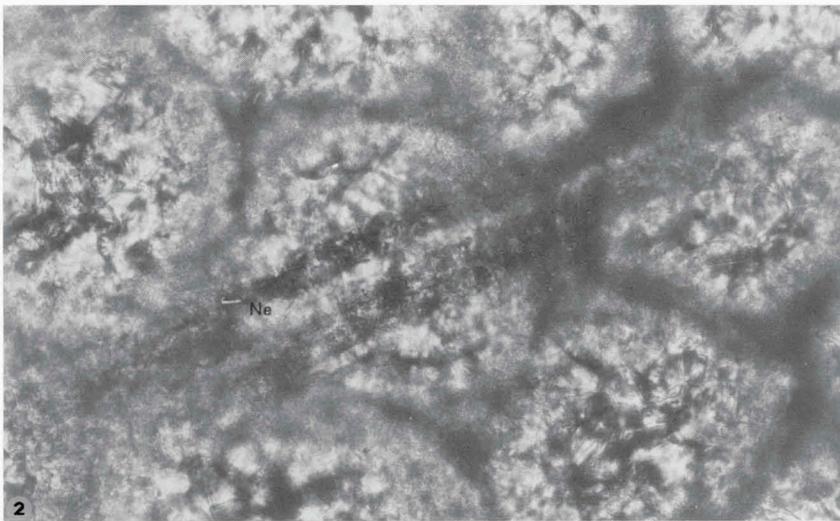
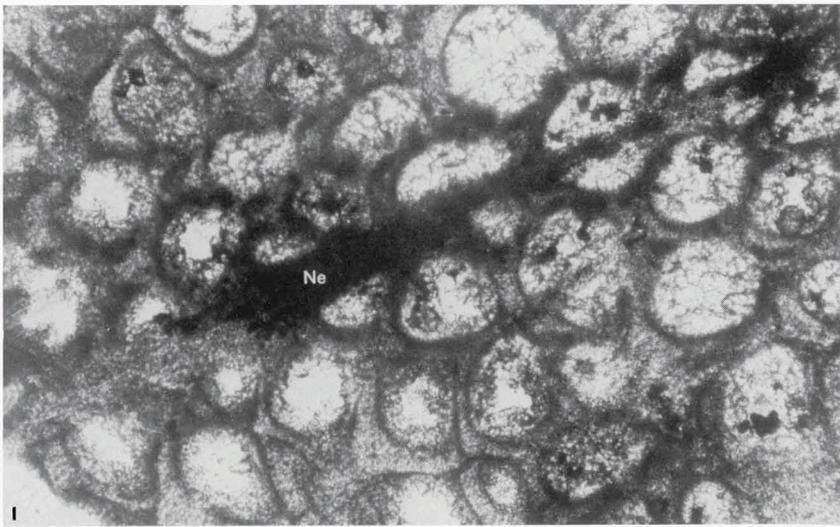
## Plate 39

Fig. 1. A needle in *Miogypsina (Miogypsinoidea) dehaartii cupulaeformis*, Larat 20, Molucca Islands. The diameter of the needle (Ne) increases towards the front. In this photograph the end of the needle becomes lighter in colour. The equatorial chambers and the needle appear to have grown independently. RGM 230 843, x 75.

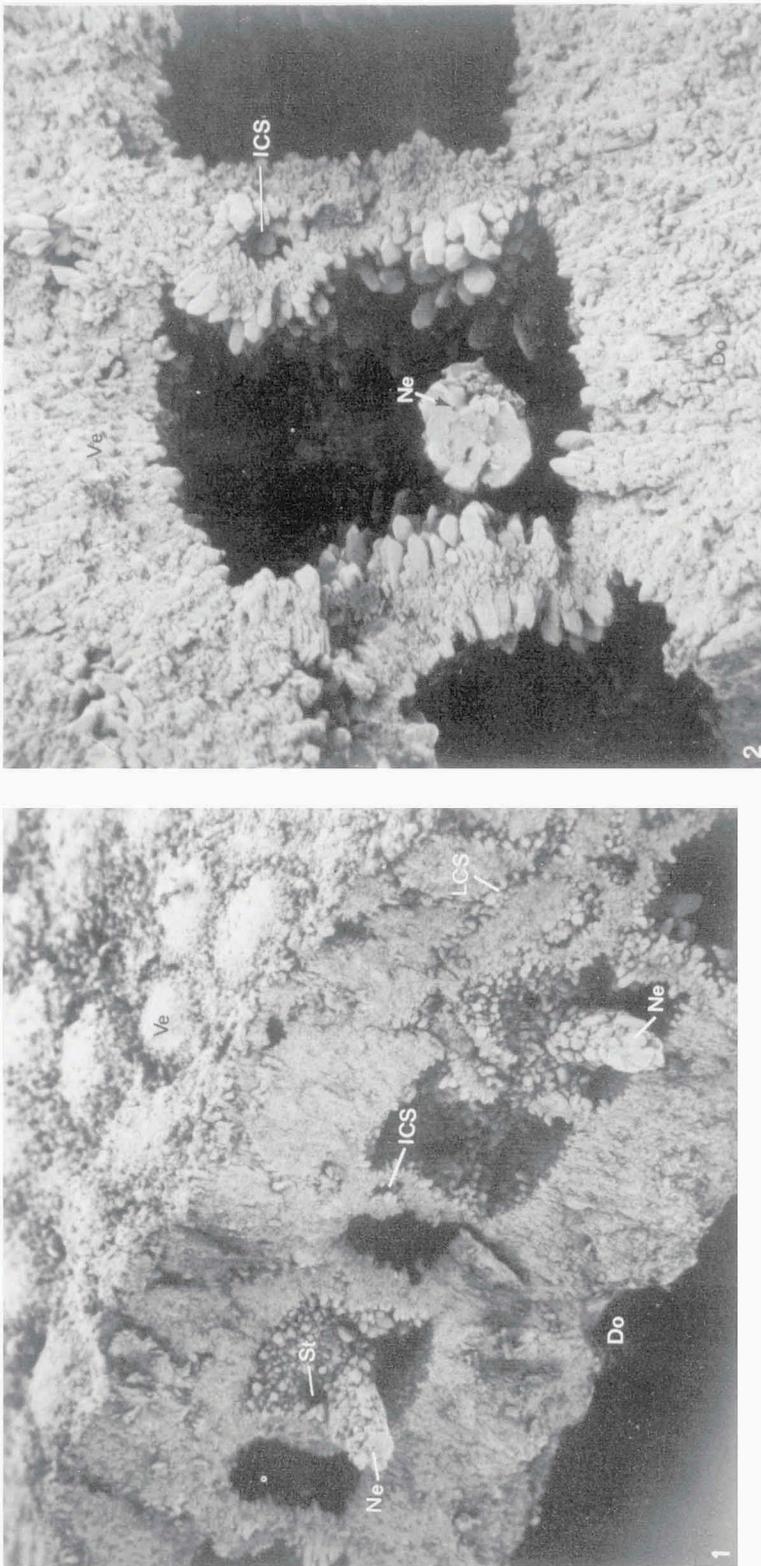
Fig. 2. A needle in *Miogypsina (Miogypsinoidea) dehaartii*, Larat 20, Molucca Islands. The needle appears to be hollow. Generally the needles are markedly recrystallized; it was therefore impossible to determine with any certainty whether the needles are in fact hollow. RGM 230 726, x 150.

Fig. 3. A needle in a vertical section of *Miogypsina (Miogypsinoidea) dehaartii*, Larat 20, Molucca Islands. The dark needle penetrates into the dorsal side of the test. RGM 230 705, x 75.

Plate 39



## Plate 40



Transverse section through the equatorial chambers of *Miogypsina (Miogypsinoidea) dehaartii*, Larat 20, Molucca Islands.  
 Fig. 1. Two needles (Ne) are shown; on both sides of the needles the inflow stolons of the simple stolon system are seen together with the intraseptal, the vertical and the lateral canal systems. RGM 230 830, x 200.

Fig. 2. Detail of the equatorial chambers with the position of the needles and the intraseptal canal system (ICS). RGM 230 824, x 590.

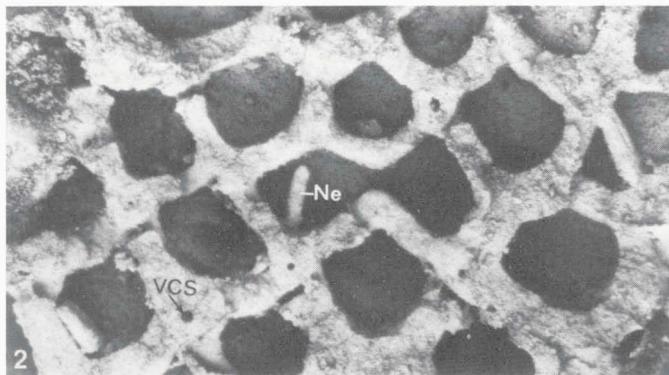
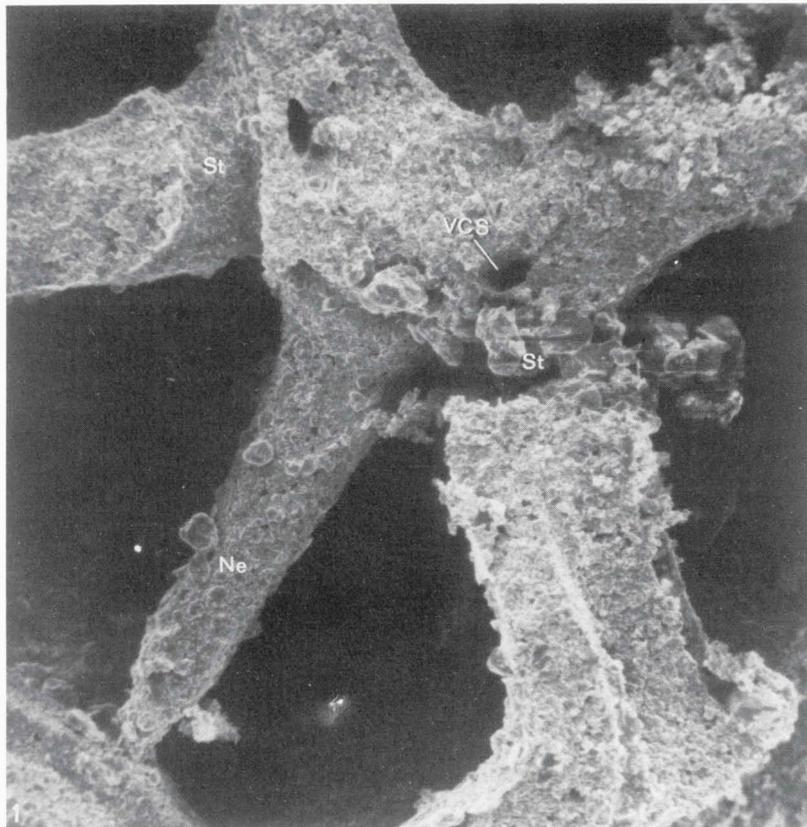


Plate 41

Plate 41

Equatorial chambers of *Miogypsina (Miogypsinoïdes) bantamensis*, Anse deï Bano, M64, France.

Fig. 1. A needle (Ne) with the length of one equatorial chamber. RGM 230 813, x 500.

Fig. 2. Generally the needles point towards the front. Only one needle was found pointing towards the apex. RGM 230 823, x 200.

## Plate 42

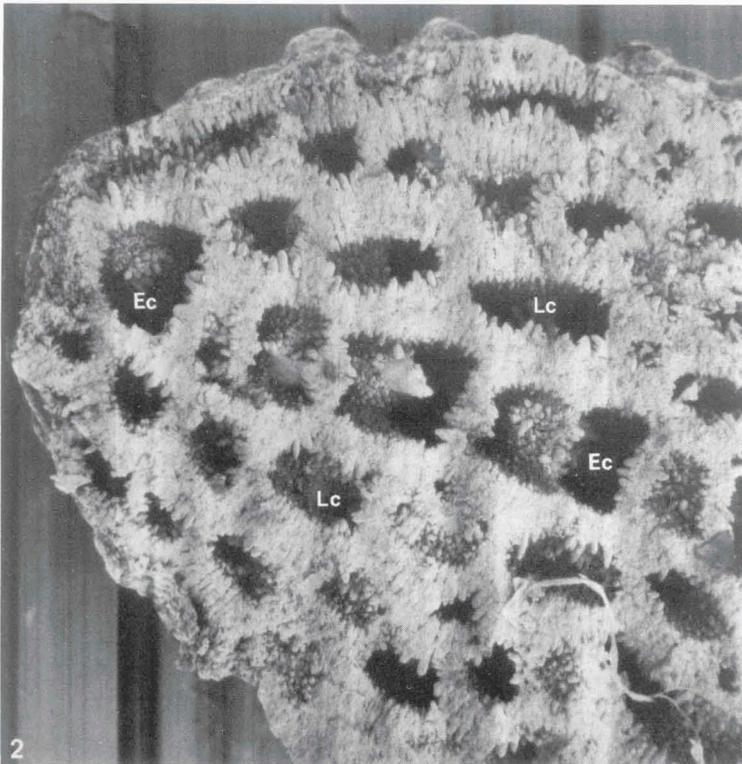
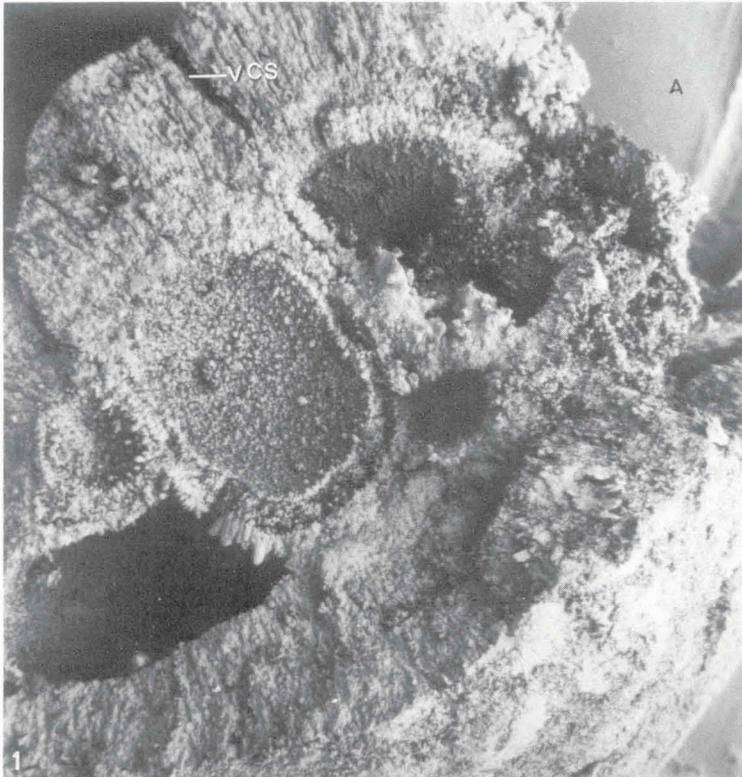
Fig. 1. Vertical section through the embryonic apparatus of *Miogypsina (Miogypsinoides) dehaartii*, Larat 20, Molucca Islands.

The lateral walls are perforated by pores; no lateral chambers have developed. RGM 230 824, x 200.

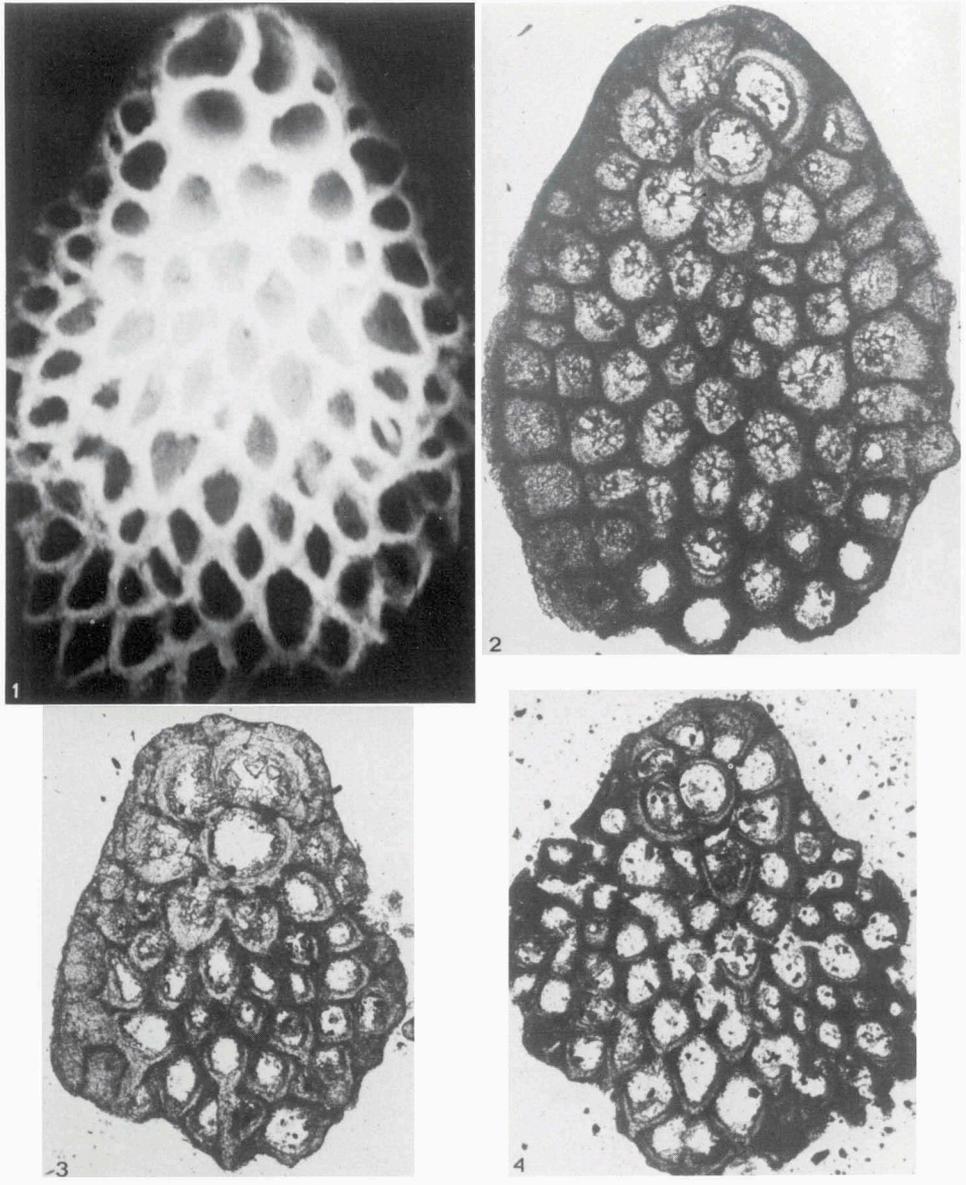
Fig. 2. Transverse section through *Miogypsina (Miogypsina) borneensis*, Larat 20, Molucca Islands.

The test is markedly recrystallized. Lateral chambers have developed with pustules on the surface. A needle can be seen in one of the equatorial chambers. RGM 230 824, x 200.

Plate 42

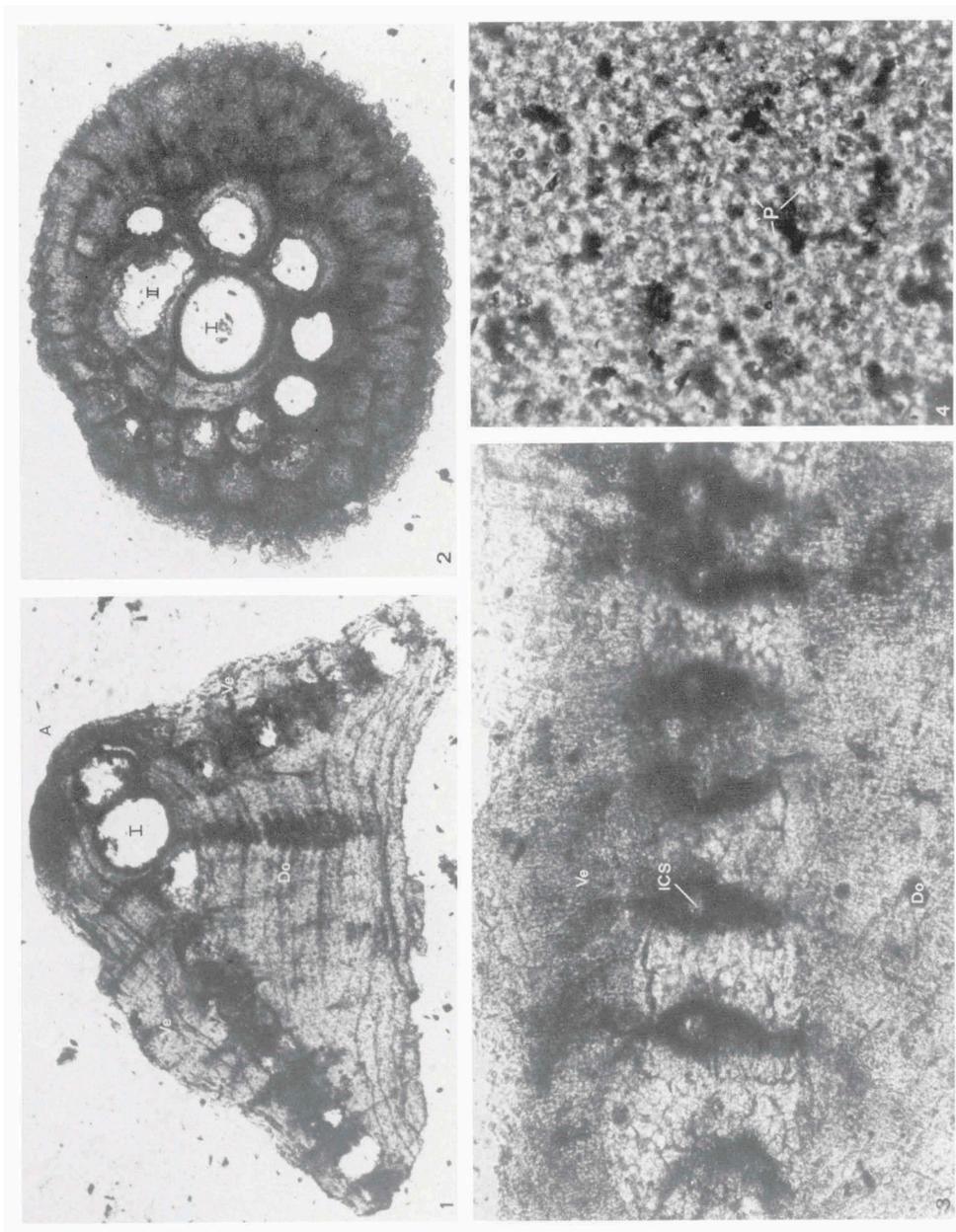


## Plate 43



Figs. 1-4. Three horizontal thin sections and a microradiograph of *Miogypsina* (*Miogypsinoidea*) *dehaartii*, Larat 20, Malucca Islands.

The specimens in figs. 1, 2 and 4 have the deuteroconch at the apex; in fig. 3. there is a spiral chamber at the apex. Fig. 1. RGM 230 645, x 40. Fig. 2. RGM 230 648, x 40. Fig. 3. RGM 230 688, x 40. Fig. 4 RGM 230 686, x 40.



*Miogypsina (Miogypsinoidea) dehaartii, cupulaeformis*, Larat 20, Molucca Islands.

Fig. 1. Vertical sections through the cone. The exterior is the ventral side, the interior cone is the dorsal side of the test. The embryonic-nepionic apparatus is situated at the top of the conical test. A pillar has developed in the dorsal wall. RGM 230 833, x 40.

Fig. 2. A section through the embryonic-nepionic apparatus at the top of the conical test. RGM 230 835, x 40.

Fig. 3. Vertical section through the equatorial chambers, showing the intraseptal canal system (ICS). RGM 230 852, x 100.

Fig. 4. A horizontal section through the dorsal side of the test, showing the porous dorsal wall. RGM 230 838, x 200.