

STUDIES ON THE GENUS ORBITOLINA
(FORAMINIFERIDA)

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ABSTRACT

The genus *Orbitolina* is described in detail and is shown to be represented by one species only: *Orbitolina lenticularis* (Blumenbach). This species can be subdivided into form-groups, based on the characteristics of the megalospheric embryonic apparatus. The evolution of the species is orthogenetic. The specimens probably lived with the apex of the cone pointed downward.

The microspheric test starts with a strepto-spiral, the megalospheric test with an embryonic apparatus consisting of a proloculus, a deuteroconch, and a varying number of epi-embryonic chambers. The embryonic apparatus is the only consistent feature on which the age of *Orbitolina* can be determined; the method applied will be described. The neanic chamber layers consist of tubular chamber passages; the chamber layers are interconnected by oblique, aligned stolons, placed alternately left and right of the chamber passages.

The contemporaneous allies *Coskinolinoidea texanus* Keijzer, *Dictyoconus walnutensis* (Carsey), *Orbitolinopsis kiliani* (Prever), *Dictyoconus floridanus* (Cole) subsp. *elongata* (Moullade) and *Simplorbitolina manasi* Ciry & Rat are described and some remarks are presented on the family Orbitolinidae.

CHAPTER I

INTRODUCTION

During field work in the southern spurs of the central Pyrenees, the author collected some samples of *Orbitolina*. Determination of species appeared to be almost impossible, as the literature on the subject is vague and contradictory.

However, the study of the samples from the Pyrenees and comparison of the data with those of samples from other regions, proved *Orbitolina* to be useful for stratigraphic purposes. This is very important, since many of the rocks in which *Orbitolina* is found are devoid of other fossils which are of stratigraphic use. In consequence, the study of *Orbitolina* was extended to all material the author was able to obtain from geographically and stratigraphically different localities; successive samples from sections were used for studying the evolution of *Orbitolina*.

The present paper is the result of these studies. The main purpose is to describe the internal structure of *Orbitolina* in detail, to revise the chaotic taxonomy and to outline the stratigraphic use of *Orbitolina*. Additional remarks are made on some related species.

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PREVIOUS STUDIES

Orbitolina is mentioned in most publications on the stratigraphy and palaeontology of deposits of Barremian to Cenomanian age in the Tethys province. The first mention, as far as known, is by De Saussure in 1799, when he described "la lenticulaire de la perte du Rhône" and considered it as a modification of a mineral. A Linnean name was assigned by Blumenbach (1805) when he described and illustrated "*Madreporites lenticularis*" from the Perte du Rhône. Lamarck (1816) assigned these forms to *Orbulites*, d'Archiac (1837) to *Orbitolites*. In 1850 d'Orbigny established the genus *Orbitolina* and in 1889 Martin established the family Orbitolinidae. Martin also was the first to describe the internal structure of *Orbitolina* and Egger (1899) was the first to depict the embryonic apparatus.

At that time *Orbitolina* was mainly classified using external characteristics: the shape of the test, the dimensions, etc. This was continued by Douvillé at the beginning of this century, but in addition he used the internal structure. This marked the beginning of including internal characteristics in the descriptions of species. The following papers are worth mentioning in this regard: Yabe & Hanzawa (1926), Silvestri (1932a), Davies (1939), Henson (1948), Sahni & Sastri (1957), Ayala-Castañares (1960), Douglass (1960a) and Schroeder (1962).

Henson (1948) was the first to analyse in detail the structure of the megalospheric embryonic apparatus, and he gave a detailed description of the structure of the neanic chamber layers. He was followed by Douglass (in 1957, in his then unpublished doctoral thesis) who gave graphical representations of some of the characteristics of the megalospheric embryonic apparatus for some species. Unfortunately, the stratigraphic range of *Orbitolina* in America is short, so that Douglass had little opportunity to observe changes in the shape of the embryonic apparatus; for distinguishing the forms he based his classification on characteristics which are considered to be highly influenced by ecological factors. Ayala-Castañares (1960) likewise used the characteristics of the megalospheric embryonic apparatus for taxonomic purposes. Schroeder (1962) stressed the importance of the internal structure of the test. He divided the genus *Orbitolina* into the subgenera *Orbitolina* and *Mesorbitolina*, which he based on the characteristics of the megalospheric embryonic apparatus.

CHAPTER II

LOCALITIES AND STRATIGRAPHY

Apart from samples collected by the author, many samples were received from other geologists and institutions. Most of these samples have been deposited at the Rijksmuseum van Geologie en Mineralogie, Leiden, Netherlands. Numbers 5891, 8115, 40018 and 115001–115176 are registration numbers of this museum. Samples on loan from other institutions are indicated as such.

In a study on the evolution of a group of organisms, it is a necessity to ascertain the relative geologic ages of the populations from which the samples are selected. These ages should be established by using other data than the relative development of the specimens of the studied group.

Sediments containing *Orbitolina* are generally devoid of planctonic foraminifera, ammonites, or other fossils which can be used for age-determinations. The ages attributed to these rocks consequently are not very accurate, and may be known only as "Albian" or even only as "Lower Cretaceous". The evolution of *Orbitolina* provides a useful calendar; however, only in a few places it could be connected with some accuracy to the geologic time-scale, because of lack of data. Consequently much work remains to be done to make the best possible use of *Orbitolina*.

The age of some samples could not be established by methods which are independent of *Orbitolina*. The age attributed to some formations in insufficiently studied regions may be different from the age found by using the evolution of *Orbitolina*. To enable the reader to form an opinion about the age determinations, brief discussions of determinations have been added and literature has been cited, when possible and necessary.

If the only available data on age are based on *Orbitolina*, or the age based on *Orbitolina* is different from or more accurate than the age based on other data, the *Orbitolina*-age is placed in brackets.

Latin numbers have been added to denote the form-group (discussed below) to which the megalospheric embryonic apparatus of the specimens belongs. In transitional samples from one form-group to another, both groups are indicated, e.g. III–IV. If in these transitions one group is represented by a minority of specimens, its number is placed in brackets, e.g. (II)–III.

Stratigraphic sections have been sampled by the author using a Jacob's staff for measuring. The stratigraphic columns in the present paper are simplified and only serve to illustrate the stratigraphic relations between the samples.

Samples are arranged according to countries and continents. For convenience a short list of samples has been added at the end of this paper.

EUROPE

France

The following eleven samples are from cuttings or cores of bore-holes in the Aquitaine Basin and were forwarded by Dr. J. Magné from the Esso REP, Bègles. For location of the bore-holes see text-fig. 1.

115122. Lugos 1, core 18, 1546 m. I.
 115123. Lugos 2, core 3, 1549.40 m. I.
 115124. Lugos 4, core 5, 1494.70 m. I.
 115125. Sanguinet 1, core 14, 3011.30 m. I.

These four samples are all of about the same age; the specimens of *Orbitolina* show about the same development, although 115125 seems to be slightly more primitive than the others (chart II). Sample 115122 contains also: *Lenticulina subalata* Reuss (= *L. cultrata* Montfort), *L. tricarinella* Reuss (= *L. crepidularis* Roemer), *L. (Marginulinopsis) striatocostata* Reuss, *L. bononiensis strictolipa* Tappan, *Globulina prisca* Reuss, *Pyrulina infracretacea* Bartenstein, *Tristix articulata* Reuss, *Verneuilinoides subfiliformis* Bartenstein, *Vaginulina*

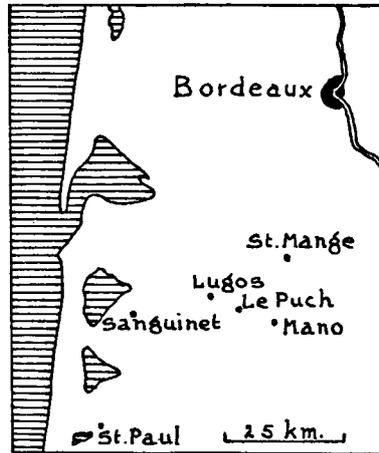


Fig. 1. Locations of boreholes in the Aquitaine Basin, France.

weigelti Bettenstaedt, *Voorthuysenia suturalis* (Ten Dam), *Cristellaria planiuscula* Reuss, *C. parallela* Reuss, *Gavelinella barremiana* Bettenstaedt, *Dentalina nana* Reuss, *D. siliqua* Reuss. This fauna as a whole indicates the age to be uppermost Barremian rather than Lower Aptian. A somewhat higher developed embryonic apparatus is present in specimens of *Orbitolina* from sample 115115, for which indications of an uppermost Barremian age have been found.

115127. St. Mange 1, 1236 m. I.
 115128. St. Mange 1, cores 14 & 15, 1079 m. I.
 115129. St. Mange 1, core 13, 1066.30 m. I.

These three samples are not much different in age. Sample 115129 contains also *Hiltermannia chapmanni* (Ten Dam), sample 115128 *Lenticulina roemeri* Reuss. *Choffatella* is also common in these samples. The specimens of *Orbitolina* are certainly less primitive than those in the preceding four samples. The conclusion that these samples are of Lower Aptian (Bedoulian) age corresponds with the opinion of Dr. Magné.

115130. Le Puch 1, core 9, 1399.50 m. All specimens are very small (largest diameter measured about 2 mm) and microspheric; Lower Albian.
 115134. St. Paul en Born 1, core 6, 1577.10 m. (Upper Aptian). II.
 115133. St. Paul en Born 1, core 1, 1253 m. (Lower Albian?). II?
 115136. Near Lasseube, S of Pau (Basses-Pyrénées). Received from Dr. Magné with the number BP 36. Flysch facies of the Lower Cenomanian. The embryonic apparatus of most specimens was found to be dissolved. IV.
 115025. Ballon (Sarthe), type locality of *O. concava* (Lam.). Just outside Ballon, at the first corner of the departmental road D 38 from St. Mars to Ponthouin, left side of the road; collected in soft greensand. Lower Cenomanian. IV.

115026. Same general locality as 115025, at the first corner, right side of the road, from a hard layer of calcareous greensand, which is regarded as the type level of *O. concava* (Lam.). Stratigraphically just below 115025. IV.
115027. Same general locality as 115025, 15 m past the first corner, on the right side of the road, stratigraphically about 2.5 m below 115026. Soft greensand. IV.
- Sample without registration number from the Muséum d'Histoire Naturelle, Genève. Type material of *O. concava* (Lamarck), from the Lower Cenomanian of Ballon, Sarthe. By courtesy of Dr. Lanterno it has been possible to detach and section one specimen from the largest of the two rock samples (pl. XVIII fig. 1). The section is deposited at the mentioned museum. IV.
115121. Col des Contrabandiers, about 3 km. E of Annecy (Hte. Savoie). The location is described by Moret & Deleau (1960). *Deshayesites weissii* and the development of *Orbitolina* point to Lower Aptian. I.
115120. Les Ravix, W of Villard de Lans (Isère). One of the type localities of *O. discoidea* Gras and *O. conoidea* Gras. From an outcrop in the brook; dark siltstone with some greensand, belonging to the "couches supérieures à Orbitolines". Base of the Upper Aptian (Jacob, 1906). I.
115119. Same general locality as 115120, in the soil on the trail along the brook. I.
115118. Rochers de la Ferrière, W of Villard de Lans (Isère), between La Martinière and the Centrale électrique de la Haute Bourne. Probably of the same age as 115120. I.
115117. About 50 m W of 115118 (probably separated by a fault) in dark-coloured marl intercalated in hard limestone. Contains also *Orbitolinopsis kiliani* (Prever). Probably transition from Barremian to Aptian. I.
115116. About 5 m below 115117, in soft limestone. I.
115115. Gorges de la Bourne, S of La Martinière and W of Villard de Lans (Isère), at about 840 m above sea-level. In marly bed in Urgonian limestone. Contains also *Dictyoconus floridanus* (Cole) subsp. *elongata* (Moullade), *Orbitolinopsis kiliani* (Prever). Belongs to the "couches inférieures à Orbitolines" which according to many authors (e.g. the Lexique Stratigraphique, fasc. 4a, vol. IV, p. 365; Thieuloy, 1959, p. 43) marks the end of the Barremian. I.
115142. Voreppe (Isère). Coll. Maync. (Base of the Upper Aptian). I.
8115. Perte du Rhône, E of Bellegarde (Ain). Type locality of *O. lenticularis* (Blum.). Specimens are abraded and some are filled with brown ferrous material. According to Jayet (1927) the *Orbitolina*-bearing beds at the Perte du Rhône lie at the transition from Lower to Upper Aptian.
- Sample without registration number from the Muséum d'Histoire Naturelle, Genève, from the Perte du Rhône (see 8115). Specimens are abraded but two of them are well preserved and show the megalospheric embryonic apparatus. This sample is probably from another level as 8115, as it does not contain any ferrous material; according to Jayet's description of the stratigraphy these samples cannot be much different in age. I.
- Sample without registration number from the Muséum d'Histoire Naturelle, Genève. From "Simiane, près de Marseille, Aptien" (Upper Aptian). II.
- Sample without registration number from the Institut Dolomieu, Grenoble. Coll. Kilian, from the road between Bourg-St.-Andéol and St. Rémyze (Ardèche). According to Kilian (see Douvillé, 1912, p. 3) it is of Upper Barremian age. (Base of Upper Aptian). I.
115114. Montagne de la Clape, E of Narbonne (Aude). About 50 m. N of the place where road D 68 (through Armisan) meets the road from Narbonne via Moujan to Narbonne Plage. In top-layers of the "calcaire à *Ostrea aquila*" of Cairol (1872, pp. 12, 14). Doncieux (1903, p. 115) places this limestone in the Bedoulian (Lower Aptian) and the superjacent limestone (the two limestones are separated by marls) in the Gargasian (Upper Aptian) (see text fig. 2). *Orbitolina* indicates that these marls form the base of the Upper Aptian. I.
115113. Along the road from Narbonne Plage to Narbonne, SE of the mountain top of 210 m, about 30 m W of the beginning of the road which runs to the farm NE of this top; in alternating sandy marls and thin sandy limestones. The stratigraphic relation to 115114 is shown in text fig. 2. Upper Aptian. I-II.
115090. Alternating sandy marls and limestones, directly N of the junction of the road Narbonne-Narbonne Plage and the road Narbonne Plage-Gruissan. (Upper Aptian). II.

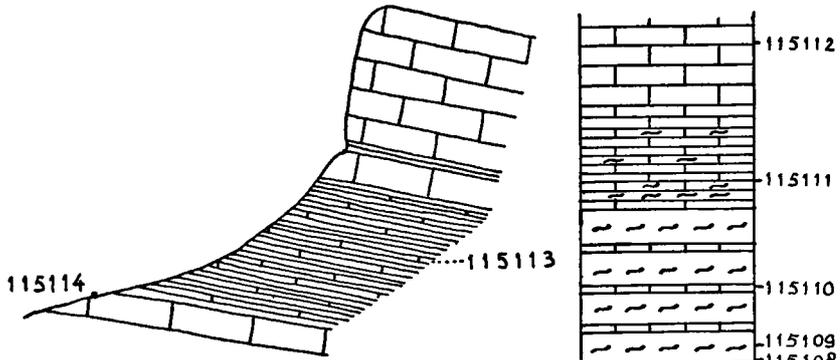


Fig. 2. Stratigraphic relations of samples 115113 and 115114, La Clape Mts., Aude, France. The sections shown in fig. 3 start stratigraphically just above the uppermost limestone of fig. 2.

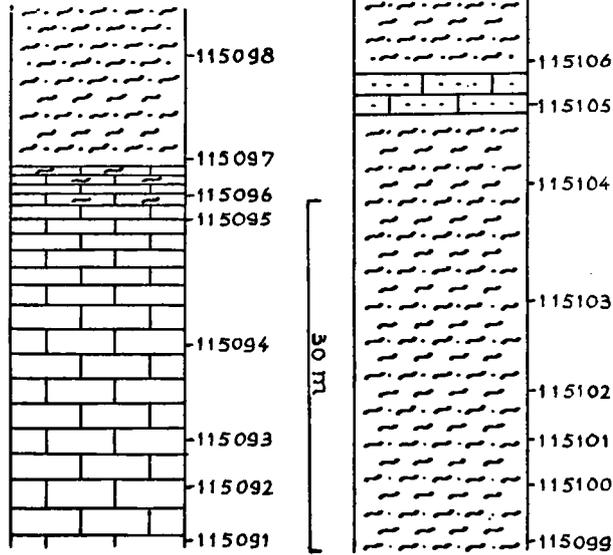


Fig. 3. Sections W of Narbonne Plage, Aude, France.

115089. Stratigraphically about 2 m. below 115090. II.
- 115091–115112. These samples are from two sections, probably partly overlapping (text fig. 3). The base of the lower section is found at the "Fontaine de Verre", about 50 m NW of the church of Narbonne Plage (Aude); the direction of this section is about W. Stratigraphically it begins at the top of the upper limestone shown in text fig. 2. The upper section begins about 25 m S of the top of the former section (115098) and probably partly overlaps this section, as the strike of the layers is about NE–SW. However, the limestones are cut off between these sections; due to the poor exposure, it could not be ascertained whether this is caused by a change in facies, by erosion, or by a fault. The charts of the properties of the embryonic apparatus of *Orbitolina* (charts III, IV) suggest a partly overlap of these sections. The upper section ends in the gully N of the holiday-centre Beau Soleil. According to Cairol (1872) and Doncieux (1903) the sections lie in rocks of Upper Gargasian (upper part of the Upper Aptian) age. All specimens of *Orbitolina* belong to form-group II; they are well preserved at the outside but have a somewhat recrystallised interior.
115143. La Clape, E of Narbonne (Aude). Coll. Maync. Upper Aptian. II.
115088. About 500 m. S of St-Paul-de-Fenouillet (Pyr. or.), on the side of road N 619 to Ansignan, in the transition of Aptian limestone to uppermost Aptian shales (according to the geological map), in sandy soft limestone. This is one of the two type localities of *O. lenticularis* mentioned by d'Orbigny (1850, vol. 2, p. 143). Specimens of *Orbitolina* are poorly preserved, but are higher developed than the specimens from Perte du Rhône. II.
115087. About 600 m. SSE of the Notre Dame de Laval, SE of Caudiès de Fenouillet (Pyr. or.). Roadside of D 9. Same stratigraphic position as 115088. II.

Spain

- 115038–115057. These samples are from the section shown in text fig. 4. Locality: Santa Fé de Orgaña, Lérida. The base of the section is situated at the SW-corner of the municipal water-basin. The section has been measured uphill towards the W. The upper part of the section covers the type locality of *O. mamillata* var. *subaperta* Astre. Astre (1930) considered the lower part of the section to be of Upper Aptian age and the upper part to be of Lower Albian age; Dalloni (1910) considered the rocks of the whole section to be of Lower Albian age. The stage of development of *Orbitolina* from samples near the base of the section indicates a lowermost Albian age. All samples show the transition of form-group II to form-group III; form-group II is represented by only a few specimens in the upper samples of the section.
115085. At the E-end of the municipal water-basin of Orgaña, Lérida. Stratigraphically about 30 m below 115038. II–III.
115033. About 150 m S of the barrage of Senterada, E-bank of the Flamisell river, NNW of Pobra de Segur, Lérida. Near top of Aptian (Urgonian) limestone. The sample contains also *Simplorbitolina manasi* Ciry & Rat, considered to be of lowermost Albian age. II–(III).
115034. Stratigraphically about 5 m above 115033, also with *Simplorbitolina manasi*. II–(III).
115032. About 1 km W of Bonansa, Huesca (WNW of Pont de Suert), at the roadside, in greensands between Aptian (Urgonian) and Cenomanian limestones. According to Dalloni (1910) the greensands are of Upper Albian age. IV.
115031. At the base of Cenomanian limestone, stratigraphically about 55 m above 115032. (Transition Albian-Cenomanian). IV.
115030. S of Pont de Suert, Lérida, on the side of the road to Aulet (see text fig. 5). On top of Aptian (Urgonian) limestone in sandy marls. II.
115029. Stratigraphically about 3 m above 115030. II.
115035. S-bank of brook, about 50 m N of Pallerol, Huesca (see text fig. 5). Below layers of lignite, in Urgonian limestone. Contains also *Simplorbitolina manasi* Ciry & Rat. Base of the Albian. II–III.
115036. About 1 km WNW of Pallerol, Huesca (see text fig. 5). In Urgonian limestone. The stratigraphic relations and the development of *Orbitolina* indicate the same age as 115035. II–III.

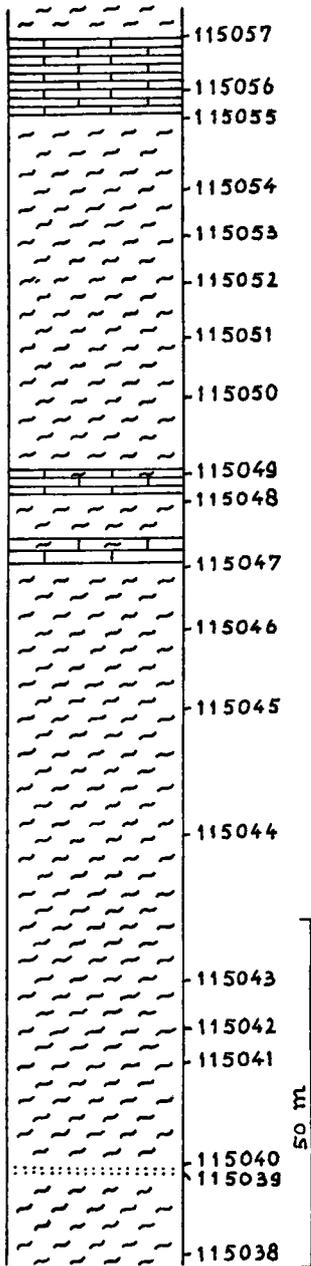


Fig. 4. Section W of Orgaña, Lérída, Spain.

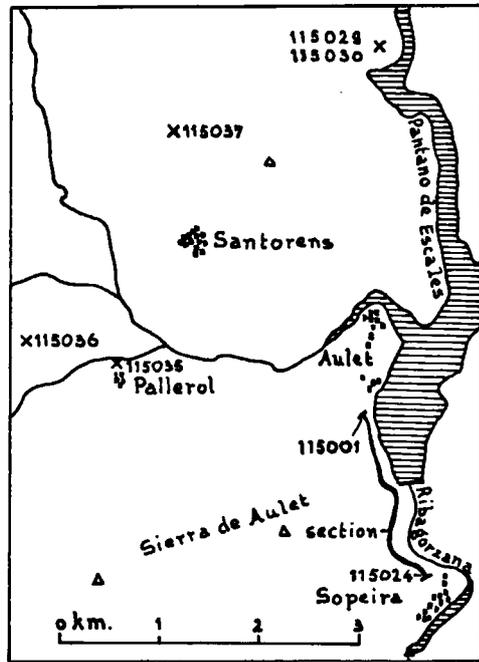


Fig. 5. Sketch-map of the localities near Aulet, Huesca, Spain.

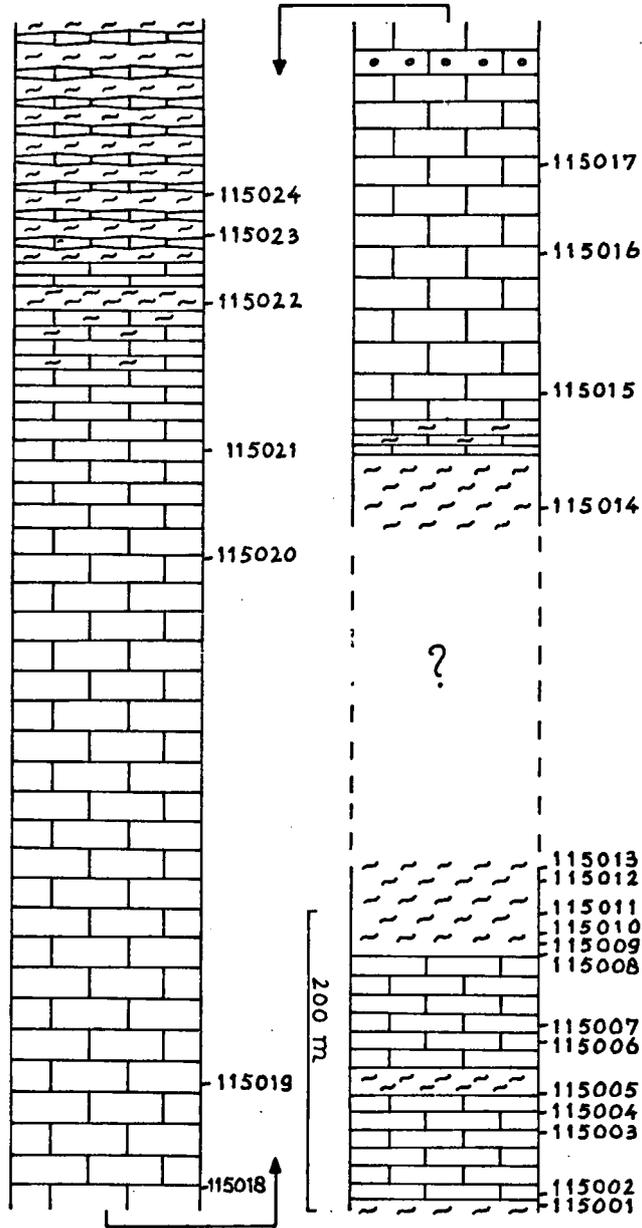


Fig. 6. Section between Aulet and Sopeira, Huesca, Spain.

115037. About 1 km N of Santorens, Huesca (see text fig. 5). In the transition of Albian sandstones and marls to Cenomanian 1st. IV.
- 115001–115024. These samples are from the section shown in text fig. 6, along the road from Aulet to Sopeira, Huesca (see text fig. 5). Sample 115001 is from the base of the first limestone bed one meets coming from Aulet. In the underlying clays and marls an Albian fauna was found by Dalloni (1910). Sample 115013 contains *Lenticulina orbiculina* (Reuss), *Sigmoilina antiqua* (Franke), *Globorotalites* cf. *subconicus* (Morrow), *Gavelinella baltica* (Brotzen), *Rotalipora evoluta* Sigal, *Planomalina buxtorfi* (Gandolfi), *Hiltermannia cretosa* (Ten Dam), *Brotzenia* cf. *spinulifera* (Reuss), *Patellina subcretacea* Cushman & Alexander, *Tritaxia pyramidata* (Reuss); this fauna points to Lower Cenomanian. About 200 m above sample 115024, a fauna typical of the uppermost Cenomanian has been found, with *Rotalipora montsalvensis* Monod, *R. turonica* Brotzen, *R. greenhornensis* (Morrow), *Præoglobotruncana stephani* (Gandolfi). Turonian has been demonstrated just above the level of this fauna. The boundary between Lower Cenomanian and Upper Cenomanian is not known with certainty; it lies probably near the top of the right part of the section of text fig. 6. Summarizing, it can be stated that the section begins at the transition from Albian to Cenomanian and ends in the Upper Cenomanian, not far from the Turonian. Specimens belonging to form-group IV are found throughout the section; from sample 115017 upward, specimens belonging to form-group V are also present.
115150. Mas de Ammurio, Alava. Coll. Colom. (Upper Albian?). IV?
115151. Dos Hermanas, Guipúzcoa. Coll. Colom. (Albian). III.
115152. Sabron, Alava. Coll. Colom. (Upper Aptian to Lower Albian). II.
115153. Cala Vadell, Ibiza, Balears. Coll. Colom. (Upper Aptian). II.
- Sample without registration number from the Institut Dolomieu, Grenoble, coll. Fallot. Villadelloges?, Ibiza, Balears. (Upper Aptian). II.
- Pa. 192/1935 (Dept. of Geology, Univ. of Utrecht). Urganian SW of Campvey, W.-Ibiza, Balears. (Upper Aptian). II.
115155. Topo-type specimens of *Simplorbitolina manasi* Ciry & Rat, from Gulina, Navarra. Coll. Rat. Transition Aptian-Albian.
115154. SW Infra, W of Zufia, 6 km W of Estella, Alava. Coll. Fricke. Dr. Fricke reports *Mortoniceras* (*Deiradoceras*) cf. *cycloceratoceras* Spath from the same level (pers. comm. H. Hiltermann). Upper Albian. IV.
115084. Road Solares-Ramales, km 11.8, about 18 km SE of Santander. Soft marly layer in hard *Orbitolina*-limestone. Contains also *Simplorbitolina manasi* Ciry & Rat. Lower Albian. II–III.
115156. Road Solares-Ramales, km 11.5. Specimens of *Simplorbitolina manasi* Ciry & Rat. Coll. Rat.
115176. Road Solares-Ramales, km 12. Hard limestone. Contains also *Simplorbitolina manasi* Ciry & Rat. Lower Albian. II–III.
115083. 3 m above 115176, in nodular limestone. Contains also *Simplorbitolina manasi* Ciry & Rat. Lower Albian. II–III.
115082. 5 m above 115176, in nodular limestone. Contains also *Simplorbitolina manasi* Ciry & Rat. Lower Albian. II–III.
- 115062–115081. These samples are from the three sections shown in text fig. 7; all sections have been measured to the N. Samples 115062–115072 are from a section which begins on the side of the road Solares-Ramales near the Puerto de Las Alisas, at km 22.5 (text fig. 7A). Samples 115073–115079 are from a section beginning at km 21.250 (text fig. 7B). The base of this section probably coincides with the top of the former section, but this is not certain, since the exposures between these sections are very poor and a fault might be present there. Samples 115080–115081 are from a section directly to the N of the former section (text fig. 7C); the base of the limestone of this section is separated stratigraphically from sample 115079 by about 80 m of coarse brownish and whitish sandstones. In sample 115062 *Coskinolinella daguini* Delmas & Deloffre has been found, which according to its authors (1961, p. 170) is characteristic of the extreme base of the Albian. In sections A and B, up to sample 115178, occasionally *Simplorbitolina manasi* Ciry & Rat has been found, which also marks the base of the Albian (Rat, 1959b, p. 315). Section C probably lies in rocks of middle Albian age; this is based on the stage of evolution of

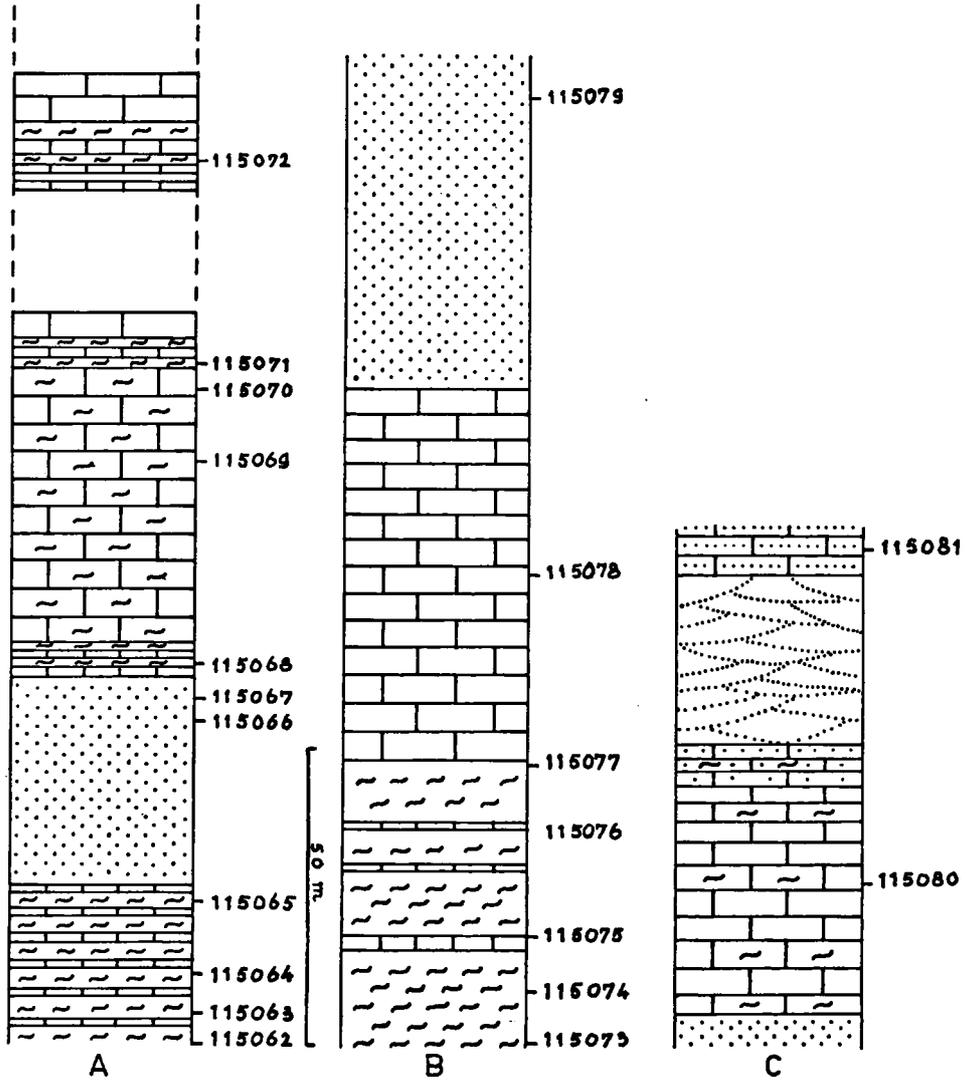


Fig. 7. Sections at the Puerto de Las Alisas, Santander, Spain.

Orbitolina and the stratigraphic relation to the other sections. Sections A and B contain specimens belonging to form-groups II–III, with only a few specimens of form-group II in the highest samples of section B; section C contains specimens belonging to form-group III only.

- 115058–115061. These samples are from a small section along the road Solares-Ramales, at km 25.9, just outside the village of Arredondo. Sample 115058 is from about 3 m N of the road, samples 115059, 115060 and 115061 lie resp. 3, 28 and 42 m above sample 115058. All samples contain also *Simplorbitolina manasi* Ciry & Rat; sample 115059 contains some specimens of *Coskinolinella daguini* Delmas & Deloffre. Base of the Albian. II–III.
115028. Las Barrietas, 7 km N of Valmaseda, 22 km W of Bilbao. Along the road which runs N of the village, about 75 from the village itself, about 25 m past the railway tunnel; level 2 of Rat (1959b, fig. 35, p. 274). (Transition Lower-Upper Aptian). I.
115126. About 3 km SW of Valmaseda, at the roadside, in the uppermost *Orbitolina*-level of Rat (1959b, fig. 22 III). The rock consists almost entirely of brownish micaceous material. Top of the Lower Cenomanian (Rat, 1959b, p. 333). IV.

Portugal

115157. Praia Pequena do Guincho, NW of Cascais, N-end of beach, from 2 m thick *Orbitolina*-marl. Coll. Herm. According to the geological map, this is Aptian-Albian. (Upper Aptian). II.

Italy

115147. Punto Orlando, near Castellammare di Stabia, about 8 km SE of Naples. Near base of quarry, from marl and marly limestone. Coll. Macfadyen. (Upper Aptian). II.
115146. Sta. Maria La Foca, NW of Sarno, NE of the Vesuvius. Sandy marl. Coll. Lazarri. (Upper Aptian). II.

Switzerland

115141. Road Weesen-Amnden am Walensee. Coll. Hagn. (Lower Aptian). I.
Sample without registration number from the Muséum d'Histoire Naturelle, Genève. From La Presta, Val de Travers (near Neuchâtel). (Lower Aptian). I.

Germany

115137. Roadside, W of Hölzelsau, N of Kufstein, Bavarian Alps. Brownish sandy marls. Coll. Hofker Sr. According to Hagn (1961) the exposure is of Cenomanian age. The sample contains also *Hedbergella washitensis* (Carsey), *Praeglobotruncana stephani* (Gandolfi), *Rotalipora greenhornensis* (Morrow) and *Lenticulina orbicula* (Reuss). Samples from deposits of nearby localities of the same age contain in addition to this fauna *Rotalipora cushmani* (Morrow), *R. reicheli* Mornod and *Praeglobotruncana delrioensis* (Plummer); these samples have been forwarded to the author by Dr. Hagn. Specimens of *Orbitolina* are generally poorly preserved; they are indicative of a middle Cenomanian age, whereas the micro-fauna indicates a probable Upper Cenomanian age. IV.
115138. Tennbodenbach, W of Margnardstein, Bavarian Alps. Coll. Herm. Upper Albian. No complete embryonic apparatus has been observed.
115139. Rosz und Buchstein, Tegernseer Berge, Bavarian Alps. Coll. Hagn. Cenomanian. No complete embryonic apparatus has been found.
115140. Lichtenstättgraben bei Ettal, Ammergauer Berge, Bavarian Alps. Coll. Hagn. Cenomanian. Only one poorly preserved embryonic apparatus has been found. IV?

Hungary

115144. Bakony Mts. Coll. Méhès. Dr. Méhès referred to this sample as material of *O. conica*. Albian-Cenomanian transition. IV.
115145. Zirc, Bakony Mts. Coll. Méhès. Dr. Méhès referred to this material as topo-type material of *O. lenticularis baconica* n. subsp. Upper Aptian to Lower Albian. II–III.

England

P 43429 (British Museum). Quarry at top of cliff, S of Dunscombe Farm, between Seaton and Sidmouth, Devon. Coll. Elliot. Upper Greensand. IV.

Tunisia

115148. Djebel Serdj. Coll. Maync. According to Dr. Maync there are indications for a Barremian-Aptian age of this sample, but the development of *Orbitolina* is indicative of a middle Albian age. III.

Algeria

115149. E-end of Sidi Rhgis, in quarry 1 km from main road, at Canrobert, 70 km SE of Constantine. Coll. Macfadyen. Upper Aptian. II.

Israel

115167. Heletz, borehole 2, core 15. Coll. Gerry. Lower Aptian (Grader & Reiss, 1958). I.

Lebanon

115175. E of Beirut, in Aptian green clays. Coll. Iraq Petrol. Co.; for exact locality see Henson, 1948, p. 111. Type locality of Henson's *O. cf. lenticularis* (Blum.). All specimens were abraded and none of them showed the embryonic apparatus.

115172. Mdereidj, above the "Falaise de Blanche". Coll. Iraq Petrol. Co.; for exact locality see Henson, 1948, p. 112. Type locality of *O. discoidea* Gras var. *libanica* Henson. Aptian (Upper). II.

Syria

115173. Wady N'Gara, Jabal Abd-el-Aziz. Coll. Iraq Petrol. Co.; for exact locality see Henson, 1948, p. 111. Type locality of Henson's *O. cf. discoidea* Gras. Aptian-Albian (Henson, 1948, p. 53). (Lower Aptian). I.

Arabia

115166. Dukhan no. 2 Well, Qatar Peninsula. Coll. Iraq Petrol Co.; for exact locality see Henson, 1948, p. 111. Type locality of *O. discoidea* Gras var. *delicata* Henson. Barremian? I.

115171. Dukhan no. 1 Well, Qatar Peninsula. Coll. Iraq Petrol. Co.; for exact locality see Henson, 1948, p. 111. Type locality of *O. concava* (Lam.) var. *qatarica* Henson. Lower Cenomanian. IV.

Iran

P 45080 (British Museum). Khamir, S-Iran. Coll. A. G. Davis. All specimens are microspheric.

P 45084 (British Museum). Pirazeh Stream, Kuh-i-khumi area, near Gach Saran oilfield, SW-Iran. Coll. A. N. Thomas. Aptian (Upper). II.

Birma

115086. Irrawaddy River, topo-types of *O. birmanica* Sahni. Coll. Geol. Survey of India. All specimens are somewhat abraded and the embryonic apparatus cannot be observed.

Borneo

8591. Seberoeang. Coll. Van Schelle. Probably type locality of *O. scutum-trochus* Fritsch. (Lower Aptian). I.

40018. "W-Borneo, Cenomanian". Coll. Wing Easton. (Lower Aptian). I.

P 43138 (British Museum). Headwaters of the Selang River, about 8 miles N of Bau, First Division, West Serawak. Rock slide.

United States

115158. Cranes Mill-Fishers store road, Comal Cty., Texas. Glen Rose Limestone. Coll. Douglass (1960a, p. 9, coll. f 20101). Topo-type material of *O. minuta* Douglass. Upper Albian. IV.
115161. Cranes Mill-Fishers store road, 1.1 miles N of Guadalupe River, Comal Cty., Texas. About 200 ft. above the base of the Glen Rose Limestone. Coll. Barker. Albian. (II)–III.
115159. Comal Cty., Texas. Coll. Douglass. (Albian). III.
115160. Near Austin, Texas, top of slope on tributary stream of Onion Creek, 10 miles W of Dripping Springs, Wimberley Road, on Driftwood secondary road. Glen Rose Formation. Coll. Barker. (Uppermost Aptian or base of the Albian). II.
115164. Top of Mt. Barker, near Austin, Texas, 3 ft. above top of Walnut Clay, Comanche Peak Form. Coll. Barker. Topo-type material of *Dictyoconus walnutensis* (Carsey).
115165. Near top of Mt. Barker, near Austin, Texas. Walnut Clay, about 8–10 ft. below contact with Comanche Peak Limestone. Coll. Barker. Topo-type material of *Coskinolina adkinsi* Barker (= *Coskinolinoides texanus* Keijzer).
115132. Hood Springs Quad., Brewster Cty., Texas. Glen Rose Form. Coll. Douglass (1960a, p. 9, coll. f20124). Topo-type material of *O. pervia* Douglass. Rock fragments; no embryonic apparatus observed. Albian.
115135. Grant Cty., New Mexico. Broken Jug Limestone. Coll. Douglass (1960a, p. 11, coll. f20220). Topo-type material of *O. crassa* Douglass. Rock fragments; no embryonic apparatus observed. Albian.
115170. Grant Cty., New Mexico. Playas Peak Form. Coll. Douglass (1960a, p. 11, coll. f20228). Topo-type material of *O. parva* Douglass. Rock fragments; no embryonic apparatus observed. Albian.
115174. Grant Cty., New Mexico. Broken Jug Limestone. Coll. Douglass (1960a, p. 11, coll. f20211). Topo-type material of *O. gracilis* Douglass. Rock fragments; no embryonic apparatus observed. Albian.
115168. Grant Cty., New Mexico, Broken Jug Limestone. Coll. Douglass (1960a, p. 11, coll. f20218). Topo-type material of *O. grossa* Douglass. Rock fragments; no embryonic apparatus observed. Albian.
115169. Presidio Cty., Texas. Glen Rose Limestone. Coll. Douglass (1960a, p. 9, coll. f20144). Topo-type material of *O. oculata* Douglass. Rock fragments; no embryonic apparatus observed. Albian.

Mexico

115162. About 300 m N of Mal Paso, region of Huetamo, SE Michoacan. Morelos Formation. Coll. Ayala-Castañares (1960, p. 13). Topo-type material of *O. morelensis* Ayala-Castañares. Albian (base of the Albian). II–III.

Venezuela

115163. Upper Borracha Formation, Rio Punceres, E-Venezuela. Coll. Maync. Aptian-Albian transition (Rod & Maync, 1954). II–III.
115131. Trujillo State, road between Miton and Torococo, about 600 m from the small settlement El Halechal, coming from Miton. Roadside outcrop of limestone and calcareous shale; about in the middle part of the Aguardiente Formation. Coll. Bolli. Albian. III.

CHAPTER III

TECHNIQUES

Samples of *Orbitolina* were collected by the author following the usual method for other fossil foraminifera. Where possible, samples of soft rock were taken in order to obtain detached specimens. Together with single specimens also the very small specimens and the accompanying microfauna were collected. Poor samples were supplemented by collecting separate specimens from the same stratum.

After washing, the samples were divided in fractions smaller and larger than $1\frac{1}{2}$ –2 mm, depending on the size of the specimens found in the sample. This facilitated a rapid selection of useful specimens.

Instead of studying sectioned specimens in thin sections of rocks, it was preferred to section individual specimens for studying the structure of the test. Orientated thin sections of *Orbitolina* may be rapidly prepared after acquiring some skill. Thin sections of rocks have only been used for studying the relationship between *Orbitolina* and the enclosing sediment, for obtaining a large number of random sections, and for studying hard rock samples if no other material was available.

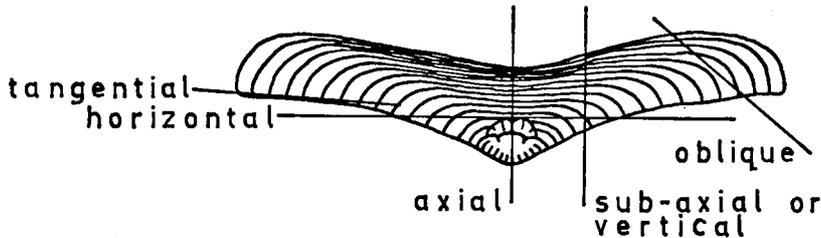


Fig. 8. Terminology of the orientation of sections.

The terminology used for orientation of the sections is given in text fig. 8. For making axial sections of single specimens, two techniques have been applied, depending on the size of the object. In both techniques the apex of the test was marked by a small dot of black ink, when the structure on the outside of the test is not clearly visible. This is done for relocating the proloculus.

Orientating the specimens and observing the result of the first stage of grinding is done by means of a microscope with direct illumination and low magnification. When the sections become thin enough to be translucent, a microscope with transmitted light is used. Dark field illumination proved to be helpful, especially when the sections are relatively thick; in this case the megalospheric embryonic apparatus may become visible as a more translucent area.

Specimens with diameters smaller than about 2 mm are placed on their margin in molten thermo-plastic on a glass slide; after cooling they are ground down on a fine carborundum stone wetted with castor-oil, until the ink dot is reached. Then the object is turned and grinding is repeated on the other side. When the ink dot is reached, further grinding is done on a fine honing stone (e.g. Arkansas oil-stone), until the proloculus is reached. The same is done again with the other side of the

specimen. Thus, by repeated turning and grinding, accurate sections through the proloculus, both megalospheric and microspheric, can be obtained. The frequency of the turning depends on the size of the proloculus and on the transparency of the specimen. In clear specimens the megalosphere may be sectioned already in the first run, so that the object has to be turned once only. For an accurate section through the microsphere the specimen must be turned repeatedly, and even then one may fail.

For making sections of larger specimens, the technique used by Douglass (1960a, p. 25) was slightly modified. The specimen is not mounted on a piece of plate glass, but on the standard glass slide, with slightly more than half of it extending beyond the edge of the slide. As a thin diamond blade was not available, multiple sections of one specimen could not be obtained as described by Douglass. The part of the test beyond the slide is ground down on a lap as far as close to the ink dot. Grinding is then continued on a honing stone. Since the specimen can be observed both parallel and (by holding the slide upright) at right angles to the plane of sectioning, grinding can be continued until the proloculus is reached. By keeping one corner of the slide on the grinding-stone, the cut becomes perfectly straight (fig. 9).

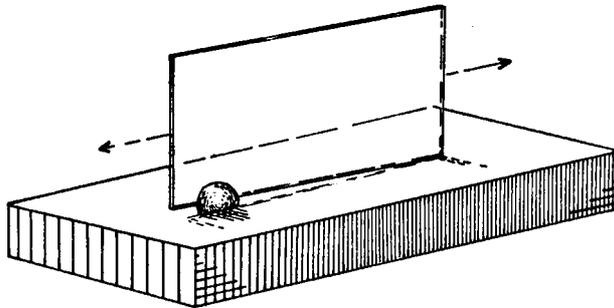


Fig. 9. Technique of preparing thin sections on a simple grinding stone. When one of the corners of the glass slide is kept on the stone, the cut will become perfectly straight.

When the proloculus is reached, the specimen is attached to its final place on the slide, with the ground side on the glass, and the other side is ground down. In some cases, the turning and grinding as described in the first technique is required for obtaining an accurate section through the proloculus.

The secondary filling of the originally open spaces in the tests of the specimens of some samples possesses a selective attraction to basic stains, such as methylene blue, malachite green, or a mixture of them, whereas the building material of the test remains uncoloured. Stain can be applied by immersing the specimens in the solution when they have some porosity, or by colouring the thin sections. In the latter case, the sections must be ground in water instead of using castor-oil. Applying some drops of a dilution of a photographic wetting-agent or a synthetic detergent is helpful.

Specimens which cannot be readily stained may be stained more easily after slight etching with diluted acetic acid. This acid, however, also weakens most of the thermo-plastics used for mounting the specimens, and it should be carefully applied. Care should also be taken to avoid penetration of the mounting material into the section; this can be achieved by heating the plastic as little as possible.

LIVING POSITION

The conical side of *Orbitolina* is generally covered with a smooth hyaline calcitic layer, whereas the distal side of the test is grooved; sediment particles may stick to this latter surface. Consequently it is not surprising that earlier authors considered the animal to live with its conical side upward, which was not contested by later authors. There are, however, some arguments in favour of a reverse position.

1. *Orbitolina* usually lived under conditions of rapid sedimentation. The cone surface of the test is imperforate and thus the individuals were poorly equipped to keep this surface clean. The test might easily be covered by deposited material; this would have resulted in burial and death of the animal in case the cone surface would have been turned upward.

2. The conical surface of the test is generally uneven, showing pits and other irregularities; these are not damages inflicted to the adult animal, since no parts of the test are absent. The distal surface on the contrary is nearly always regular. The irregularities were probably caused by relatively large particles of sediment. As these particles were in contact with the test long enough to affect the building process, it is not likely that they were resting upon the animal. The modification of the building process of the test suggests that the animal was growing against and around these particles. It cannot be assumed that the animal was growing below these particles and had to press them upward, as would be the logical conclusion when the apex of the test would be turned upwards.

In pl. XI fig. 4, part of a specimen is shown containing a mineral grain around which the marginal zone of the test was built. This seems to be possible only when the cone surface forms the bottom of the test and the particle was protruding from the sediment.

3. The tests containing quartz grains generally have a deeply concave distal side. If the apex had been pointed upward, the sand grains had to be lifted and kept in that position for some time to enable their building in the test; this is improbable.

4. In case the apex would be pointed upward, food and building material had to pass underneath the rim of the test, which would have required repeated lifting of the test, which particularly for the larger specimens can hardly be explained. It is true that the radial zone of some larger specimens curls toward the cone surface, but this is certainly not the rule. The author collected specimens from the Sierra de Aulet in the Spanish Pyrenees (sample 115011) with diameters up to 6.2 cm, which showed this feature only to a small extent. The curled shape might be explained by the fact that it enables a maximum lateral extension to the protoplasm. It is also an architectural consequence in building a nearly flat test with a large diameter.

It has been attempted to determine the position of the tests in the sediment. Small tests can be removed easily by stream or other actions upon the sediment. Experiments showed that tests, when thrown into water, descend with the conical side pointing downwards. Consequently, the presence in a sediment of a large number of tests with the conical side downward is no proof of this being the living position. Finding this side turned upward, however, may be taken as a fairly good indication of *Orbitolina* having lived in this position; this has not been observed by the author. The tests of the larger microspheric specimens might better be used for studying this problem. Both in the Sierra de Aulet (Spain) and Ballon (France), a definite orientation has not been found. Actually, these larger specimens were generally not oriented parallel to the bedding plane, and the observed positions probably did not reflect the living-position of the animal.

For the figures in the present paper it is assumed that the apex of the test is the lower part, just as in many other conical agglutinated foraminifera. The terminology is adapted accordingly.

LIFE CYCLE

Usually two types of tests are found in *Orbitolina*: one starting with a microsphere and one with a megalosphere. The microspheric tests are generally larger, less conical and fewer in number than the megalospheric tests. Consequently *Orbitolina* seems to be dimorphic in most cases.

In the Upper Cenomanian, however, the megalospheric forms can be subdivided in forms with a small megalosphere and relatively conical test, and forms with a larger megalosphere and a flatter test (text figs. 20, 21, 23, pl. XX figs. 7–15, pl. XXI figs. 1–4, 6, 13). A small number of morphologically transitional forms may be distinguished (chart IX). The stratigraphically uppermost sample (115024) contained about 450 specimens with a complete test; all of these are megalospheric, none microspheric. This cannot be considered as conclusive evidence that microspheric specimens were absent in the population, since they are nearly always in the minority. Nevertheless, *Orbitolina* might have become apogamous in the upper part of the Upper Cenomanian, at the conclusion of the gens.

In some samples trimorphism has been observed. The first stage of the case just mentioned is definitely trimorphic, but it has also been found at some other stratigraphic levels. The most evident case of trimorphism occurs in the transition of form-group II to form-group III, in material from the southern Pyrenees (e.g. samples 115047, 115051, 115035). Here the A_1 -generation consists of a small number of specimens belonging to form-group II, whereas the A_2 -generation shows only form-group III (charts I, V, pl. X figs. 10–14, pl. XIII figs. 7–10, pl. XIV figs. 11, 12). This trimorphism seems to be a local feature; contemporaneous material from other regions does not show such outspoken differences in the shapes and sizes of the embryonic apparatuses. The trimorphism in the Upper Cenomanian, however, seems to be more than a local feature; the material depicted by other authors (e.g. Henson, 1948, Schroeder, 1962) is also indicative of this trimorphism.

MEANS OF DISTRIBUTION

The megalospheric embryonic apparatus is relatively large, and this generation has probably not passed through a pelagic stage. Only in the most primitive specimens the volume of the embryonic apparatus is comparable to the volume of the tests of the largest known pelagic foraminifera. The embryonic apparatus of such forms might have been pelagic, but the specimens must have been benthonic after forming the first chamber layer, as detrital material has been found in later chambers.

In the B-generation, upon reaching the end of the spiral, the size of the test can be compared to that of the largest known pelagic foraminifera. Accordingly, the transition from spiral to conical test is supposed to mark the end of the pelagic stage of the microspheric specimens.

Consequently, it is likely that the B-generation, together with the gametes, is the means of distribution for *Orbitolina*. This is so effective, that panmixy is maintained during part of the stratigraphic occurrence in the entire Tethys province, from Japan to America.

When in the Upper Cenomanian *Orbitolina* probably became apogamous, these means of distribution disappeared, which resulted directly in a sharp decrease in number of specimens. Whether *Orbitolina* became truly extinct at that time, or developed into other species, is still unknown.

Sample 115130 indicates that the distribution took mainly place through the B-generation. In this sample only very small B-forms are present (largest diameter about 2 mm). The smallness indicates that the environmental conditions were unfavourable; the animals lived only a short time after deposition into the bio-coenose, and their life cycle was not completed.

CHAPTER IV

MORPHOLOGY

BUILDING MATERIAL

The septa in many specimens of *Orbitolina* consist of two parts, a hyaline layer and a microgranular, often opaque layer (text fig. 10). The hyaline layer lies at the outside of the septa and is known by a variety of names (see Douglass, 1960a, pp. 23, 24); the most common name is epidermis. The hyaline layer does not cover the entire septum, but generally only the cone surface, the marginal zone and the radial zone.

According to Douglass (1960a, p. 22) this layer consists of fine angular quartz grains in a calcareous cement. Henson (1948) stated that the epidermis is finely arenaceous; however, in Henson's opinion the epidermis forms not only the hyaline layer, but represents the whole wall of the cone surface. The present author has not found any traces of quartz in the hyaline layer; the layer appeared to consist of clear calcite only.

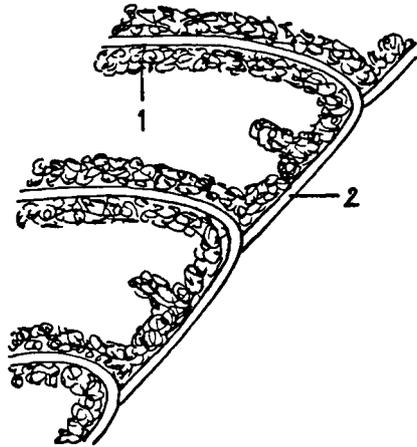


Fig. 10. Detail of vertical section of the marginal zone, showing the microgranular layer (1) and the hyaline layer (2).

Douglass (1960a, p. 22) considered this layer as a primary layer. Since it covers part of the septal face of the test, it should have been an obstacle to the accumulation of building material. The hyaline layer is present in places which are longer than usual exposed to environmental influences; it may be regarded just as well as a protective layer, formed after deposition of the microgranular layer.

The hyaline calcitic layer has not been observed in Barremian and Lower Aptian specimens of *Orbitolina*. It is possible that it was not present at that time, or it may be too thin to be noticeable.

Most walls only consist of microgranular calcitic material, often with agglutinate

detrital material. According to Henson (1948) the diameter of the granules is about 5–10 μ , but to the present author they appeared to be smaller, about 1 μ .

Many specimens have a large quantity of agglutinate material, consisting of mineral grains (mostly quartz), "calcite eyes", tests of other foraminifera or microfossils, mica flakes, sponge spicules, etc. Most of this material is found in the central complex, sometimes also in the radial zone, but it is invariably absent in the marginal zone. The amount and nature of this material is to a large degree independent of the bottom material. Stainforth (1952) drew the attention to the fact that arenaceous agglutination might be affected by the inability to secrete sufficient calcite from sea-water. This may have various causes: lack of light for photosynthesis (depth, or too much material suspended in the water), low temperature of the sea-water (populations living at the limit of their tropical biotope), too low or too high salinity. It may very well explain the occurrence of *Orbitolina* containing coarse quartz grains in limestones which are practically devoid of quartz, and of "clean" specimens in sandstones and arkoses (Henson, 1948, p. 45–46). It seems that *Orbitolina* selected angular quartz grains by pure necessity; if possible, it preferred the rounded "calcite eyes" which should have caused far less irritation to the protoplasm.

The degree of agglutination of the test does not seem to have much stratigraphic value, since all stages, from fine to coarse agglutination, occur at various stratigraphic levels. However, the occurrence of "calcite eyes" seems to be confined to strata of Upper Aptian to Upper Cenomanian age, and they are most frequently present in Albian specimens.

CALCITE EYES

In many specimens of *Orbitolina* rounded bodies of clear calcite are found, which are commonly called "calcite eyes". They occur most frequently in the central zone, and more scarcely in the radial zone. As far as known to the author, they are confined to specimens of *Orbitolina* of Upper Aptian to Upper Cenomanian age, and occur most abundantly in middle Albian specimens; in the latter case their abundance has led to the species *O. oculata* being established by Douglass (1960a).

Henson (1948, p. 46) considered these bodies to be of pathological or other secondary origin; Douglass (1960a, p. 23) concluded that they must have been open spaces during life, because they are filled with the same clear calcite as found in the radial passages; he drew the attention to the crystallisation of the calcite, which in many cases is radial and different from that found in the chamber passages. Thin sections revealed these bodies also in the sediment, which is a strong argument against the opinion that they were produced in *Orbitolina* itself.

Some of the calcite eyes are shown in pl. IX figs. 7–11, 14. Two types can be distinguished: a globular form with a nucleus and a slightly larger ovoid or kidney-shaped form without nucleus. The smaller ones generally consist of radially crystallized calcite crystals. They resemble very much the horizontal sections of *Nannocoelus* which were depicted by Brönnimann (1955, fig. 4); elongate sections have not been found, however, and the specimens might not belong to the species he depicted, but to a more globular form. According to Brönnimann some species of *Nannocoelus* are associated with *Orbitolina*; this is another indication of these small bodies probably being tests of *Nannocoelus*.

The majority of "calcite eyes" belongs to the larger type. In these forms radial crystallisation is seldom observed, and the calcite shows reticulate racks. These bodies are generally named *Oligostegina* or *Fissurina* (Galloway, 1933, Colom, 1955). The calcite eyes in *Orbitolina* can be distinguished from *Pithonella ovalis* (Kaufmann),

as described by Colom (1955, p. 121), by the absence of double-layered walls. The occurrence of "calcite eyes" in highly detrital sediments is in contrast with the typical occurrence of *Pithonella* in deep-sea sediments. However, the stratigraphic range of the "calcite eyes" corresponds with the range of *Pithonella* as given by Colom.

"Calcite eyes" show a remarkable resemblance to the statoliths of invertebrates, notably crustaceans and gastropods; the actual organisms by which the calcite eyes were secreted have not yet been recognized as such.

NEANIC PART OF THE TEST

In axial or other vertical sections the neanic part of the test of *Orbitolina* appears to consist of thin co-axial chamber layers, separated by septa which are visible as sutures on the outside of the test. The septum of each chamber turns back at the periphery of the test to join the previous septum. On the conical side of the test the septa may be nearly straight or rounded, so that this side of the test is smooth or ribbed. These changes in the roundness of the peripheral parts of the septa, just as well as the angle between the cone surface and the distal side of the test, are probably caused by changes in surface tension of the protoplasm, and thus, to some extent, by changes in the composition of both protoplasm and sea-water (see Rhumbler, 1914).

The parts of the septa which constitute the conical side of the test, are generally covered with a hyaline calcitic layer; this layer also covers part of the septal face of the chamber layers and gradually thins toward the centre of the test (text fig. 10, pl. XIX fig. 3). This layer was never found to cover the whole septum, and seems to be absent in the centre of the test.

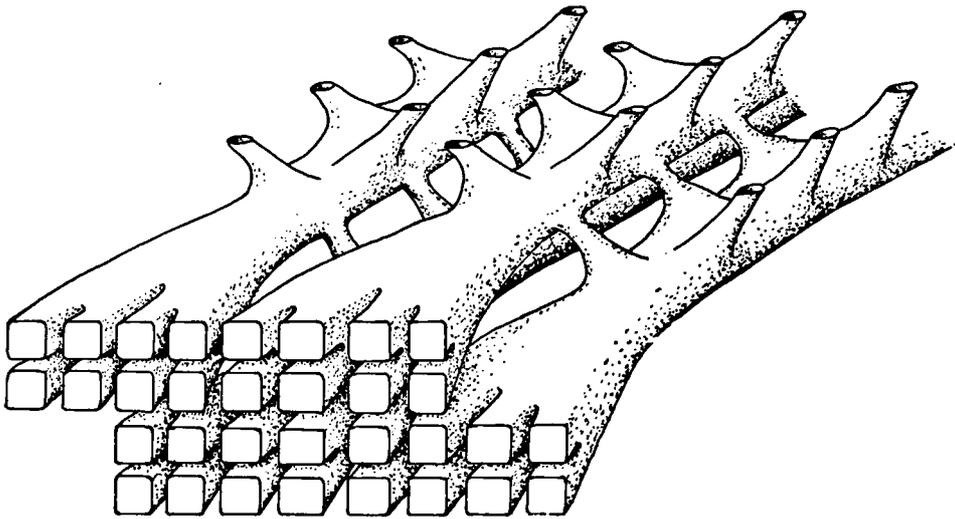


Fig. 11. Diagram of the chamber passages.

The chamber layers are basically a structure of chamber passages with agglutinate wall material between them. This system of passages is developed by leaving free grooves in the accumulating building material, as can be observed at the distal side of detached specimens. Text fig. 11 is a simplified drawing of these chamber

passages near the periphery of the test. Actually they are less regular, as shown in text fig. 12; these figures represent pyrite-filled specimens. A good impression of the structure can be obtained from the photographs of plate V, showing specimens, the passages of which are filled with pyrite.

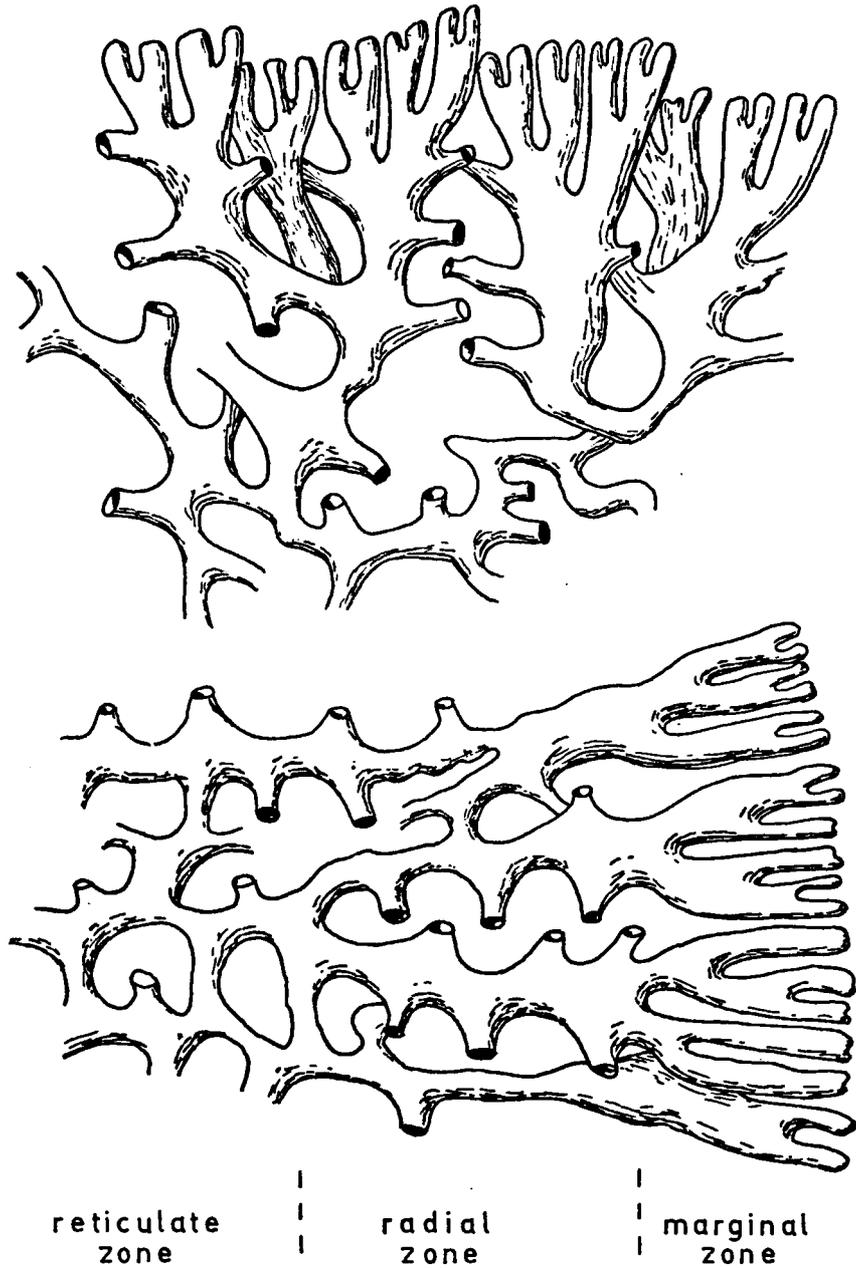


Fig. 12. Drawings of the system of chamber passages in two pyrite-filled specimens of sample 115122. 150 ×

The chamber passages are basically cylindrical. Alternately left and right of the passages stolons are placed, which penetrate the chamber septa and are located on one line with the stolons of adjoining chamber layers. As a result, the protoplasm is enabled a nearly straight passage through all chamber passages. The alternating position of the chamber passages in adjoining chamber layers causes the beautiful appearance of the surface of weathered specimens.

Although the chamber passages are basically cylindrical, they are generally triangular in cross-section. This is caused by sectioning the stolons on both sides of the passages in one and the same plane, or by the fact that in rather thick sections deeper located stolons are visible also (pl. V fig. 3, pl. IX fig. 4, pl. XI fig. 10, pl. XIX fig. 2). The zig-zag pattern visible on the distal side of detached specimens and in horizontal thin sections is also caused by these stolons (pl. V figs. 1, 2, 4-7, pl. IX fig. 5). To understand these structures, the open passages must be studied, not the more conspicuous "triangular main partitions" (see e.g. Davies, 1939 and Douglass, 1960a), which are no partitions at all, but merely the fillings with test material in the spaces not occupied by the passages and stolons. A comparison of pl. V fig. 1 and pl. IX fig. 5 distinctly shows the true nature of these "main partitions" and reveals that the chamber passages proper are not zig-zagging; this feature is caused by the stolons only.

Some authors (e.g. Martin, 1889, Douglass, 1960a) described "partitional pores" which would form interconnections between the passages of one chamber layer. The pyrite-filled specimens of plate V actually do not possess such pores and they have not been observed in other specimens either (see also Schroeder, 1962, p. 180).

In the neanic chamber layers, the system of chamber passages can be subdivided into three zones: the marginal zone, the radial zone, and the reticulate zone (or central complex) (Henson, 1948, p. 38). This can be observed in text fig. 12, pl. II fig. 5 and pl. V fig. 2.

The central complex is formed by the anastomosis of the chamber passages toward the centre of the test where they form an intricate reticulate pattern. In many specimens the alternating stolons are present in the reticulate zone, and the reticulate structure is primarily caused by lack of space. In the specimens of some samples, however, the central zone is less important to the living animal; the foramina are absent in the central complex, the zone is less thick and may even be completely absent, or it only exists as a filling in the centre of the radial zone (pl. XXI fig. 15). In this case, the chamber layers may become completely annular instead of discoid. As this is not related to geologic age, it may be ascribed to ecologic conditions.

The marginal and radial zones seem to be the most important parts of the test, since these zones are always present and form the best developed part of the neanic chamber layers. In the radial zone the chamber layers are nearly straight and always possess stolons for communication with adjoining chamber layers. A distinct boundary between the central complex and the radial zone has not been observed; the transition between these zones is gradual.

Towards the periphery the radial passages bifurcate; near the periphery itself the passages are widening and subdivided by plates, thus forming the cellules of the marginal zone. These zones are also transitional.

The function of the plates in the marginal zone may be a strengthening of the wall of the test, because more partitions are found when the thickness of the chamber layers increases.

Two types of partitions can be distinguished: the walls of the bifurcated passages (and the chamber septa) and the subdivisions in the passages. Partitions of the

first type are generally called main partitions (e.g. Davies, 1930, Henson, 1948, Douglass, 1960a). Partitions of the second type have been given various names, depending on their position; the horizontal and vertical primary plates dividing the spaces formed by the main partitions in four more or less equal parts; plates of lesser value (secondary, tertiary, etc.) again dividing these parts (pl. X fig. 7, pl. XIX fig. 2).

In the megalospheric specimens the marginal zone is usually subdivided by one horizontal and one vertical primary plate only, thus forming two rows of cellules in each main chamber. An exception must be made for the first chamber layer formed after the embryonic apparatus; because of the larger peripheral surface occupied, it generally contains three rows of cellules.

In the spiral part of the microspheric specimens the marginal zone (if one may call it thus at this stage) starts without primary plates. Only after the chamber layers have formed a complete disc, primary plates are formed. The number of plates in this generation increases with the diameter of the test. As many as seven rows of cellules have been found in the marginal zone of each chamber layer of extremely large specimens. Schroeder (1962, p. 179) reported even eight of these rows of cellules.

The vertical plates may be extending farther into the interior of the test than the horizontal plates, so that in tangential sections the cellules of the marginal zone may be elongate instead of square. This is also due to the fact that the chamber passages are seldom at right angles to the cone surface of the test; consequently tangential sections are not at right angles to these passages.

Schroeder (1962) stated that the chamber passages of some species are elongate rectangular in cross-section. He probably confused them with the cellules of the marginal zone, since the sections showing this shape are tangential sections. The section of a specimen from Ballon (Schroeder, 1962, pl. 21 fig. 6) definitely represents the marginal zone, because it does not show any trace of sand grains which at this locality are generally present in both the radial zone and the rudimentary reticulate zone. Fig. 2, pl. 21 of Schroeder (1962) shows a specimen with an "Ahnenrest" of chamber passages which are triangular in cross-section whereas the passages of the later chamber layers are elongate rectangular in section (1962, p. 192). The thickness of the "sub-epidermal layer" (Henson, 1948) increases with the diameter of the test. Consequently, the chance of tangential sections cutting the marginal zone of the first chamber layers is much smaller than cutting this zone in later chamber layers. This might explain this "Ahnenrest".

Pl. IX fig. 6 is a nearly tangential section in which the younger chamber layers of the specimen are cut deeper than the older ones. The transition from the finely subdivided periphery of the marginal zone via the elongate rectangular deeper parts toward the round chamber passages of the radial zone is visible, but in a sequence reverse to that in Schroeder's figure.

In the Upper Cenomanian the relative volume of the chamber passages increases and in vertical sections they become cellular. As the chamber layers maintain their normal thickness, the walls become unusually thin (pl. XX fig. 6). Horizontal sections show that the radial zone is very short and that the reticulate zone becomes more prominent (pl. XXI fig. 2; Schroeder, 1962, pl. 21 fig. 3). Moreover, the plates of the marginal zone become thicker. Tangential and vertical sections through the reticulate and radial zones show that the inclined stolons are still present, although they are short (pl. XXI fig. 1; Schroeder, 1962, pl. 21 fig. 7). In this way the chamber passages resemble those of *Iraqia*. The meaning of these changes in structure is not yet clear; they might be related to the change in life cycle and the approaching

extinction of *Orbitolina*. However, they have also been found occasionally in specimens from other stratigraphic levels; consequently, the appearance of these features does not justify the establishment of a new species.

The chamber passages of the first chamber layer following the megalospheric embryonic apparatus, are not interconnected. This first layer is actually annular and does not possess a central complex. The chamber passages in the layer have originated from separate foramina and the passages must be considered as true chambers. In later chamber layers the passages form an intricate pattern, especially in the central complex. Whether the passages in these chamber layers are all interconnected could not be established, even not in the pyrite-filled specimens. Consequently it is preferable to speak of chamber layers and not of chambers in denoting the cyclical additions to the test which are located between the septa.

MICROSPHERIC NEPIONIC CHAMBERS

In many microspheric specimens the initial part of the test is distinctly visible at the outside of the test, at the apex; it resembles a Phrygian cap (text fig. 13, pl. II figs. 1, 2). In the interior it is less distinct, due to its small size and the obliterating granules of the walls (e.g. pl. VI figs. 1-4). The study of carefully orientated axial sections parallel to the plane of symmetry of the Phrygian cap showed the outline of the whorl to be indistinct when the proloculus is cut and to be distinct when the section is located just beside the proloculus. In order to obtain a better understanding

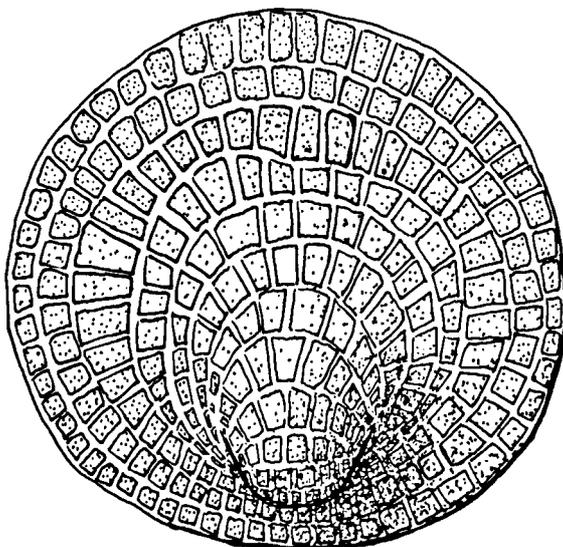


Fig. 13. Drawing of a very small microspheric specimen of sample 115124, showing the "Phrygian cap" formed by the last whorl of the strepto-spiral. 150 ×

of this problem, axial sections at right angles to the plane of symmetry of the Phrygian cap, and also horizontal sections were prepared. These sections show the initial part of the tests of the B-generation to be a strepto-spiral instead of a simple whorl.

Fortunately, in one sample (115122), received from Dr. Magné, part of the specimens is filled with pyrite. Pl. IV fig. 4 shows a horizontal section through one

of these specimens. The very small first whorl, which lies about horizontally, is distinctly visible. If correctly observed during sectioning, the proloculus lied somewhat nearer to the apex and is ground away. The diameter of the proloculus is about 5μ . The number of whorls in this specimen is about three, including the final one; this number may vary in other specimens, but to what extent is still unknown.

Each of the chambers of the first whorl is represented by only one small chamber passage, and resembles in section the chamber layers of the last whorl, as shown in pl. IV fig. 3. These chambers, which are interconnected by areal foramina, are fanning out and form the main chambers which are gradually containing more chamber passages. In the last whorl they can be subdivided into two parts, resembling the radial and marginal zones of the neanic chambers. No horizontal or vertical primary plates have been observed in the marginal zones of the chamber passages of the spiral. At the end of the spiral, the main chambers are becoming completely circular in outline (text fig. 13).

The evolution of the microspheric nepionic part of the test could not be traced completely, but it seems that the spiral decreases somewhat both in number of whorls and volume, and rises less far above the surface of the test in specimens from higher stratigraphic levels (compare pl. IV figs. 1, 3, 6 to pl. XIII figs. 11, 12).

MEGALOSPHERIC EMBRYONIC APPARATUS

The shape of the megalospheric embryonic apparatus of *Orbitolina* varies widely, but can be reduced to a basic form, consisting of a proloculus, a deuteroconch and a varying number of epi-embryonic chambers (text fig. 14).

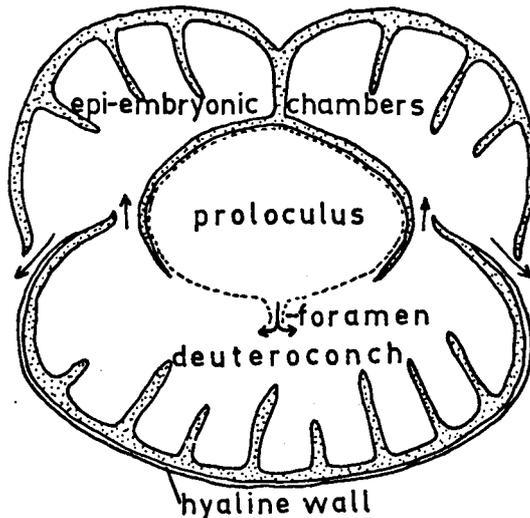


Fig. 14. Diagram of the megalospheric embryonic apparatus.

The proloculus of the geologically oldest forms consists of a globular body surrounded by a pseudochitinous wall. This wall is seldom preserved in its original shape. In many specimens it is seen as a crumpled brownish mass which suggests a spherical shape (pl. I figs. 11, 17, pl. VI figs. 11, 12). In only one case the proloculus of primitive *Orbitolina* has actually been observed to be spherical (pl. III fig. 4). This

specimen must have been filled immediately after death of the animal with dark green material; the proloculus is coloured slightly darker than the rest of the test.

In Upper Aptian and younger specimens the pseudochitinous wall of the proloculus is covered on the outside with a microgranular calcitic layer which facilitates the study of the proloculus. The shape is at first spherical, but in specimens from the Aptian-Albian transition and younger ones the proloculus has various shapes, depending on the geologic age (see text figs. 17–21, chart X).

The microgranular layer does not surround the proloculus completely; it is only partly present between the proloculus and the deuterocoench. Even in the most evolved forms it remains incomplete at this side. The pseudochitinous wall shrinks after death of the animal and may remain attached to the calcitic layer, but seldom at the side bordering the deuterocoench. Consequently, this side of the pseudochitinous wall is mostly found near the middle of the proloculus (pl. XIX fig. 13). In consequence, and also because the proloculus does not occupy the entire space left by the partitions of the deuterocoench (see below), Schroeder (1962, p. 177) assumed that the proloculus proper is subdivided into a protoconch and a deuterocoench. This was definitely not the case in the living animal.

The foramen of the proloculus cannot be easily located because of crumpling of the pseudochitinous wall, and also because the calcitic wall is not present at the place where it opens into the deuterocoench. In some specimens, in both axial and horizontal sections, the foramen has been found as a single undivided opening with the shape of a bottle neck (e.g. text fig. 15, pl. XIX fig. 1, pl. XX fig. 15).

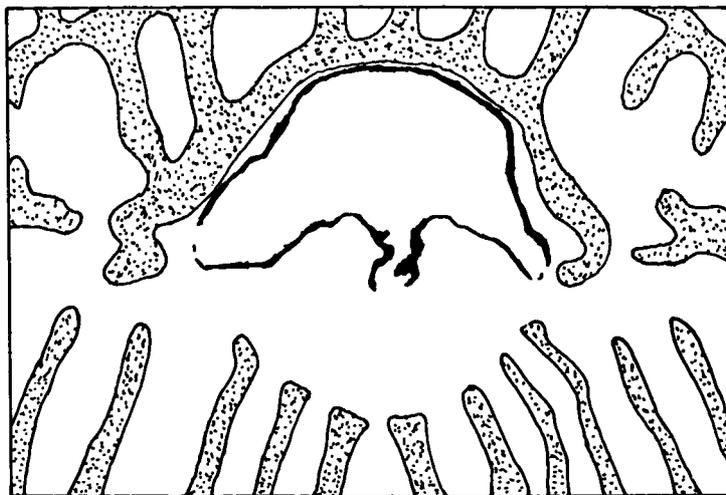


Fig. 15. Drawing of the central part of a megalospheric embryonic apparatus of a specimen of sample 115024, showing the somewhat crumpled pseudochitinous proloculus-wall and its foramen which is shaped like a bottle-neck. 200 ×.

The deuterocoench consists of a single chamber, partly subdivided by a reticulate structure of partitions which grow from the wall opposite the proloculus. On the outside of the test these partitions can be observed as a honeycomb structure within a circular area (pl. IV fig. 2, pl. XV fig. 4, pl. XVIII fig. 9). This area is called the supra-embryonic area by Henson (1948), but to avoid confusion with respect to the living position of the animal, the name embryonic area is preferred.

Douglass (1960a) for the first time stated that the deuteroconch is different from the proloculus and forms a distinct unit. He called the entire deuteroconch also the supra-embryonic area. The term deuteroconch must be preferred, however.

The partitions of the deuteroconch seldom reach the proloculus; this would obstruct the free passage of the protoplasm. This can be well observed in Albian or Lower Cenomanian specimens, in which the part of the proloculus-wall between proloculus and deuteroconch makes an acute angle with the rest of the wall (pl. XIII figs. 3, 4, 6, 8, 9, pl. XVIII figs. 1, 3, 5, 6). By drawing a line extending the wall (in an axial section) and thus completing the outline of the proloculus, it can be distinctly seen that only part of the space left by the partitions in the deuteroconch is occupied by the proloculus.

The main function of these partitions seems to be the strengthening of the outer wall of the deuteroconch which remains exposed during life. As the surface of the deuteroconch is enlarged during the evolution, the total number of partitions and the number of partitions per surface unit increase. In geologically younger forms, these partitions are longer than in the more primitive forms.

Schroeder (1962) subdivided the deuteroconch into a premarginal zone (opposite the proloculus) and a preradial zone (next to the epi-embryonic chambers).

In the lateral wall of the deuteroconch, near the contact with the proloculus, foramina are located in a circle (text fig. 16, pl. XV figs. 2, 5, 10). These foramina form lobes which surround the rest of the proloculus and meet at the middle of the

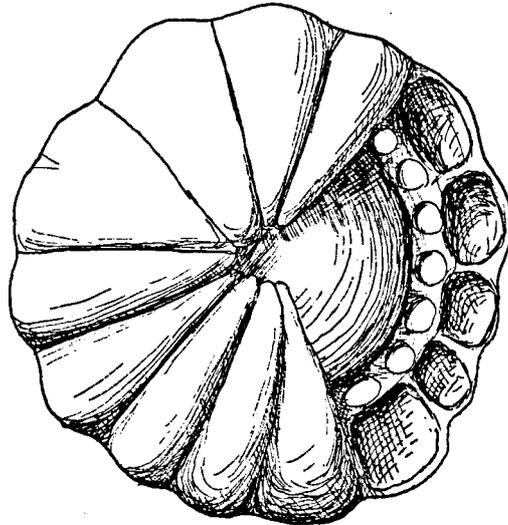


Fig. 16. Model of the embryonic apparatus of form-group II, seen from the side of the epi-embryonic chambers. To the right a part of the epi-embryonic chambers has not been drawn, to show the circle of foramina between the deuteroconch and the epi-embryonic chambers. Appr. 150 \times .

top. In axial sections of Barremian and Lower Aptian specimens of *Orbitolina*, these lobes cannot be easily distinguished from the proloculus, as the interjacent calcitic wall is not present and the pseudochitinous wall is generally poorly or not at all preserved.

Horizontal sections reveal the existence of the lobes in primitive *Orbitolina* by the notched structure of the outer wall. A brownish crumpled mass may be present in each of the lobes and is separated from the pseudochitinous wall of the proloculus (pl. VI fig. 6). In the middle of the top of the embryonic apparatus, where the lobes are meeting, a small pustule is attached to the proloculus in such a way, that the proloculus does not reach the outer wall of the embryonic apparatus.

In the Upper Aptian specimens appear with a microgranular calcitic layer between the proloculus and the lobes. In axial as well as horizontal sections, the lobes can be observed to be distinct chambers. The chambers which are visible in horizontal sections as a rosette around the proloculus, were called peri-embryonic chamberlets by Henson (1948, p. 46). He made no clear distinction between the lobes around the proloculus and the chamber passages of the first main chamber. As the lobes are not only peri-embryonic but also cover the top of the embryonic apparatus, it is preferred to call them epi-embryonic chambers, and to reserve this name for these lobes only. Each of the epi-embryonic chambers seems to originate from a varying number of foramina in the wall of the deuteroconch (e.g. pl. XV figs. 2, 10) and these chambers are interconnected via other parts of the test only. Consequently, they must be considered as chambers rather than as chamberlets. They are somewhat analogous to the primary auxiliary chambers of the Lepidocyclinidae.

The epi-embryonic chambers have the same position as the peri-embryonic chamber of Douglass (1960a) (although they do not reach the surface of the test), and the Subembryonale Zone of Schroeder (1962).

The epi-embryonic chambers proper are not subdivided when the calcitic wall is not present between these chambers and the proloculus. Simultaneously with the appearance of this calcitic layer (at the base of the Upper Aptian), partitions are formed, attached to the outer wall, probably to increase the strength. During evolution, the number of partitions increases; this leads to the original lobe-like structure to be obliterated in Cenomanian specimens; only a meshwork of interconnected cellules covers the proloculus and part of the deuteroconch at this stage. In horizontal sections located just above the foramina of the deuteroconch, this irregular structure can be seen to originate in a limited number of lobes (e.g. pl. XI figs. 3, 5, pl. XIX fig. 1, pl. XXI fig. 6).

The number of epi-embryonic chambers gradually increases from 5–8 in Upper Barremian or Lower Aptian specimens to 10–15 in Cenomanian specimens. The exact number cannot be easily ascertained, as horizontal sections may contain also the partitions of the deuteroconch, which is misleading (e.g. pl. XVII fig. 3).

In some specimens, the walls between part of the epi-embryonic chambers are absent; the chambers probably fused when being formed (pl. XI fig. 8). Because of the occasional absence of partitions in the epi-embryonic chambers, Schroeder (1962) established the species *O. pauletensis*, which according to him has only one saucer-shaped chamber with a few subdivisions, at the place where the epi-embryonic chambers are usually present. It is possible that the horizontal sections depicted by Schroeder are cut just below the foramina of the deuteroconch; the partitions in the deuteroconch seldom reach this far and they cannot be observed in horizontal sections of this kind (pl. XV fig. 5).

Schroeder (1962, p. 181) subdivided the Cenomanian representatives of the genus *Orbitolina* into the subgenera *Orbitolina* and *Mesorbitolina*, which he distinguished by the relative height of the epi-embryonic chambers. Although the relative height of the epi-embryonic chambers varies, considerable differences in height have only been observed in specimens from samples of different ages, and are of evolutionary significance only. It certainly does not justify the establishment of the two subgenera.

From the Lower Cenomanian or Upper Albian (where they would be present together) samples of the same age with specimens showing only "high" or "low" epi-embryonic chambers have never been collected; in samples of the same age, the same mean height and the same variation from "high" to "low" were measured.

Another indication that these subgenera are unnecessary and inapplicable for taxonomic purposes, is formed by Schroeder's diagrams for specimens from Noceco and Nava Ordunte (1962, p. 198, fig. 6) which show non-interrupted curves (Schroeder, 1962, p. 198, fig. 6). In each of the samples Schroeder distinguished three subspecies, belonging to two species which he assigned to different subgenera. The subspecies are transitional and obviously could not be distinctly separated; as even the members of the two subgenera cannot be distinguished, they should not be established at all.

In the outer wall of the epi-embryonic chambers, at the contact with the deuteroconch, foramina are present, connecting the epi-embryonic chambers with the chamber passages of the first main chamber (pl. IV fig. 11, 13, pl. V fig. 8, pl. XIV fig. 7). Each of these foramina seems to be connected with one chamber passage only. The number of these chamber passages of the first main chamber is about equal to the number of epi-embryonic chambers in the most primitive forms, but increases more rapidly during evolution than the number of epi-embryonic chambers. Consequently, the more evolved specimens have an irregular number of foramina per epi-embryonic chamber.

Except in the more primitive forms of *Orbitolina*, the outside of the test and part of the septa of the main chambers is covered with a hyaline layer. When this layer is present, it covers also the outside of the deuteroconch and in some cases even part of the outer wall of the epi-embryonic chambers (pl. VIII figs. 2-4). As can be seen for example in pl. VIII fig. 17, this part of the embryonic apparatus remains unprotected for some time, as it is not covered by the first chamber layers. The hyaline wall may be present at these places to protect these parts against external influences.

In an axial section of a megalospheric *Orbitolina*, the embryonic apparatus, consisting of proloculus, deuteroconch and epi-embryonic chambers, appears to be conspicuously open; the same applies to the first chamber layer, particularly in primitive forms (e.g. pl. II figs. 10, 15). Whether this chamber layer must be regarded as part of the embryonic apparatus, is difficult to decide. Barremian and Aptian samples did not contain specimens consisting of the three above mentioned components of the embryonic apparatus only. Specimens of that age were poorly supported by partitions in the embryonic apparatus and may easily have been destroyed. A study of twins (e.g. pl. II figs. 6-8, 11, 12) did not produce any evidence for or against this first chamber layer being formed in an embryonic stage; when the proloculi are close together it is still not possible to determine whether they are fused together in an embryonic or in a post-embryonic stage. In one Albian specimen, however, the first main chamber was absent; in this case, the first chamber layer must be regarded as post-embryonic (pl. XII fig. 15). In Barremian and Aptian specimens, the sides of the embryonic apparatus are nearly vertical. Considering that later main chambers are more or less horizontal, it is obvious that the first main chamber must be broad at the surface of the test in order to obtain a horizontal position for the later chamber layers. This may explain the larger volume of the first main chamber near the surface of the test, causing the open appearance.

Some authors (e.g. Douvillé, Henson) supposed that the megalospheric embryonic apparatus is spirally built, at least in the most primitive forms. A spiral has never been observed by the author; however, the structure of the microspheric test indicates, that the initial part of the ancestors of *Orbitolina* is probably a streptospiral.

CHAPTER V

TAXONOMY

Palaeontologic nomenclature should be based on biological and practical principles. The first is necessary on account of the use of the Linnean nomenclature, the second because fossils are used in the first place as a tool in stratigraphic studies.

The most important taxonomic group is the species, since it is the least artificial (Hiltermann, 1954).

A natural species can be defined as a group of organisms which possesses a gene-composition which, apart from sexual differences, can be distinctly distinguished from that of other groups of organisms. As it is not practicable to establish the gene-composition of each organism, biological definitions are not based on the gene-composition, but on the expression thereof in the constitution of the organism. Congenital reproduction between the members of the species is often included in these definitions as an important criterion; it is common in most species, but there are exceptions due to certain gene-combinations. Congenital reproduction is difficult to apply to establishing species, and is altogether useless in palaeontology. Consequently other characteristics expressed by the genes in the allelomorphs must be used. The species definition by Schindewolf (1962, p. 67) is more applicable in this regard: "Die Art ist eine Serie von Individuen, die in die Gesamtheit ihrer typischen Eigenschaften übereinstimmen und in ihren räumlich oder zeitlich aneinander anschliessenden Populationen eine meist nur geringfügige fließende Variabilität zeigen". This definition matches to a certain extent the definition by Simpson (1961, p. 153), who stated that the species is "a lineage evolving separately from others and with its own evolutionary role and tendencies".

The fact remains, that the establishment of a species is still determined by the "more or less arbitrary judgement of the taxonomists" (Gilmour, in Huxley, 1940, p. 469). By probing further, it should be possible to ascertain in most species the characteristics which are typical for the given gene-combinations and the characteristics which are irrelevant or not heritable, thus eliminating as much as possible the subjective touch of the student.

Another important advantage of Schindewolf's definition is the recognition of the vertical distribution of the species together with the horizontal one, which makes the species-concept more practicable for palaeontologists.

In palaeontology it is difficult to establish a "natural species". Fossilized "populations" may be represented by one or two specimens only, and in many cases the transitions between such populations are not present. Consequently, if the fossil records would be more complete, many species could be proved to represent stages of other species only. As foraminifera may occur in much larger numbers than other groups, the ideal species-concept as laid down in Schindewolf's definition, may be approximated to some extent. It is attempted to apply this to *Orbitolina*.

Many characteristics of the test of *Orbitolina* served the various authors for establishing species. Usually only external characteristics were used, as for example diameter of the test, relation height-diameter, shape of the test, number of chamber septa, a.o. Some relationship was found between these characteristics and geologic age: e.g. specimens with the largest diameter are found at the Albian-Cenomanian transition; the A₁-generation of the Upper Cenomanian is more conical than the

A-generation as a whole in the Lower Cenomanian; these cases are accidental and cannot be used for diagnosing species. Moreover, these characteristics are affected by ecologic conditions: unfavourable environments may reduce the possibility of reaching the full-grown size; high conical specimens have been found also in other than Cenomanian rocks, and they often appear to be ecophenotypes only. Since the shape of the test to some extent is dependent on the surface tension of the protoplasm (Rhumbler, 1914) and on the possibility of extracting calcite from the sea-water, it will be affected by changes in salinity and in temperature of the sea-water. Thus, as a whole, the shape of the test cannot be considered as of specific value.

Internal characteristics of the neanic parts of the test have been also used by authors for distinguishing species of *Orbitolina*, e.g. modes of agglutination and properties of the three zones. This also leads to confusion, since these properties are not only determined to a large degree by ecologic factors, but are overlapping each other considerably because of their heterogeneity. *O. oculata* Douglass was mainly defined on the basis of its large number of "calcite eyes"; a specimen of *O. parva* Douglass, defined on other characteristics, was reported by the same author as also containing a large number of these "calcite eyes". Even the partially dissolved condition of the test was used for establishing the genus *Birbalina* Sahní & Sastri (1957).

Apparently none of these single characteristics can be successfully used for defining the species of *Orbitolina*; even combinations are unreliable and not typical in the sense of Schindewolf's definition.

Only one part of the test remains to a large extent unaffected by ecologic conditions. This is the embryonic apparatus, which is formed in the protecting protoplasm of the microspheric generation.

The present author noticed that in each sample studied, the variation in shape of the embryonic apparatus is limited and that the same forms are found in contemporaneous samples from geographically different localities. Moreover, in the megalospheric embryonic apparatus a distinct evolution can be observed. Consequently, this apparatus can be best used as a taxonomic criterion in *Orbitolina*.

The volume of the megalospheric embryonic apparatus as a whole is steadily increasing, although some minor fluctuations may be observed. In its most primitive form, this apparatus basically consists of a chamber with a calcareous wall around it, and subdivided by pseudochitinous walls. The wall which remains exposed in the adult animal is strengthened by honeycomb partitions. It is easy to conceive that an increase in volume causes a weakening of the apparatus. The strengthening of the pseudochitinous wall by calcitic material thus seems a necessity and is not the effect of a sudden alteration of the gene-combination (or mutation). It is a gradual process which is accentuated by the appearance of the calcareous reinforcement. In sample 115113 all gradations between strengthened and unstrengthened forms occur; although two forms can be distinguished within the normal variation of the population, we certainly cannot speak of two species in this sample. When the sample is compared to a slightly older one (115114), it can be observed that the part of the population of sample 115114 with the larger embryonic apparatus (measured by the diameter of the deuteroconchs, chart IV) is not present in sample 115113; this group is replaced by specimens with the new form of embryonic apparatus. It might be considered the result of a mutation, but this can also be explained by assuming that for calcification of the walls the embryo had to reduce the volume of the embryonic apparatus in view of the obtainable quantity of calcite. This assumption is supported by the fact that sample 115114 contains specimens in which the calcification of the walls is faintly noticeable; these specimens have the largest

embryonic apparatuses of the sample (pl. VII figs. 4, 6). All these facts indicate that the covering of the pseudochitinous walls by calcitic material is a direct reaction to the steadily increasing volume of the embryonic apparatus; it is not a mutation as the transition is gradual. An alternation of the structure of the neanic part of the test and of the microspheric generation could not be observed, and the normal variation remains unchanged.

A neontologist, knowing these facts and asked to classify the population of sample 115113, would almost certainly consider the forms to belong to one single species. Likewise he would not see any reason to distinguish subspecies, since the forms do not occur in separate populations in different regions. So the Linnean nomenclature cannot be used to name the two forms.

Consequently, it must be concluded that before and after the calcification of the pseudochitinous walls in the megalospheric embryonic apparatus, the species remains the same, and that only non Linnean names can be assigned to these two members of the whole gens. The term "form-group" is proposed for these members. This term is artificial, although it is based on natural features of *Orbitolina*. Its main purpose is to divide the evolutionary stages of the *Orbitolina*-gens into useful units; it is closely related to the "forma"-concept of Boltovskoy (1958); however, as it is felt that these form-groups might be subdivided on other grounds into units which are equivalent to the "forma", this term will not be used. The form-groups will be indicated in this paper with latin numbers. When two successive forms occur in one sample, these stages are denoted by using both numbers.

The next important change in the shape of the megalospheric embryonic apparatus takes place when the globular proloculus changes into a proloculus with a flat distal wall (text fig. 19). This change may be explained as follows.

The embryonic apparatus in its most primitive stage must be regarded as composed of small drops of protoplasm, at first only separated by pseudochitinous walls, upon which calcitic material is secreted afterwards. Due to surface tension the protoplasm at first will be able to maintain a spherical shape; when the volume increases, gravitational forces will cause a flattening of the embryonic apparatus, if the structure is not reinforced. Not only the embryonic apparatus as a whole, but also the components become flattened. Most striking in this regard is the change in shape of the proloculus. At first it is spherical, but when the volume increases, it tends to model the distal wall, which forms the upper side, into two more or less straight parts shaped like a roof, to increase the strength (pl. XII figs. 3, 8, 12, 13). When the volume increases still further, this shape cannot be maintained, the roof collapses and the upper side of the proloculus becomes flattened; in some cases, when the volume is very large, it becomes concave (pl. XI fig. 1). In samples in which this change occurs, the larger proloculi show the new form, whereas the smaller proloculi maintain the primitive form. In sections in which the transition between these two forms can be observed (e.g. the sections in text fig. 7), it can be noticed that the higher the stratigraphic level of the sample, and thus the larger the mean volume of the embryonic apparatus, the more the number of specimens belonging to the primitive form decreases; these primitive forms generally have the smallest embryonic apparatus, so that it is likely, that the change in shape of the embryonic apparatus is primarily caused by the increase in volume. For the same reasons, discussed above for the first change in shape of the embryonic apparatus, it is improbable from a taxonomist's point of view, that the new form is a new species.

At this stage the partitions of the epi-embryonic chambers are not yet connected to the wall of the proloculus and only serve to strengthen the walls of the epi-embryonic chambers. In the next stage of evolution these partitions are connected

to the upper wall of the proloculus, thus giving this wall more strength and enabling this wall to become arched again. It seems that the shape of the outer wall of the epi-embryonic chambers did not provide sufficient strength, as in the new form each unit between the partitions of the epi-embryonic chambers becomes more or less globular, thus adding strength (pl. XX figs. 1, 5; text fig. 20). The volume of the epi-embryonic chambers is also reduced in order to decrease the weight upon the proloculus. The development of spherical cellules in the epi-embryonic chambers necessarily required a larger quantity of calcite. The decrease in volume of the embryonic apparatus after the transition is appreciable (chart X) and may not be explained solely by the need of more calcite, but another explanation cannot be offered. It probably will be better understood when some material becomes available in which this transition can be observed. Before and after the change, the structure of the other parts of the test and of the microspheric specimens remains essentially the same, only the shape of the epi-embryonic chambers and the volume of the whole apparatus have changed. Consequently, it seems likely that the change is not a mutation but a response to the steady increase in volume. Again there are apparently insufficient reasons to consider the new form as a new species.

The acute angle between the distal and proximal (or oral) walls of the proloculus in the older form is maintained in the initial stages of the new form-group (pl. XVIII figs. 1–6). At first the distal side remains flat, but eventually it becomes roof-shaped or arched to provide extra strength.

One other change can be observed in the evolution of *Orbitolina*: at about the middle of the Cenomanian two A-generations are being formed; at first transitional forms are present, but afterwards the generations become more distinct and the life cycle probably becomes apogamous. The A₂-generation is the continuation of the normal evolution of the embryonic apparatus; the embryonic apparatus of the A₁-generation is smaller. In samples from the Sierra de Aulet (Spain), the tests of the two generations are very small; in the A₂-generation 1–5 main chambers are added to the embryonic apparatus, in the A₁-generation 15–25. Apparently the A₁-generation lived longer than the A₂-generation. This might indicate that the continuous enlargement of the embryonic apparatus was detrimental and that the organism tried to avoid it by developing a smaller A₁-generation¹.

Thus, the changes in shape of the megalospheric embryonic apparatus can all be explained as architectonic necessities to cope with the progressive increase in volume; all transitions are gradual and are found to have the usual variation. The same reasoning as used for the first change can be followed also for the other changes, and it is obvious that the Linnean nomenclature cannot be used for the successive stages in the evolution of *Orbitolina*. In considering all evidence, it must be concluded that the genus *Orbitolina*, as known hitherto in literature, consists of one single species which can be subdivided into form-groups which are based on the shapes of the megalospheric embryonic apparatus. The only valid species name is *Orbitolina lenticularis* (Blumenbach), as this is the oldest, and the only one assigned to *Orbitolina* by d'Orbigny when he established the genus.

¹ Investigations carried out later have shown that in a sample, about 5 m above sample 115024 of the Aulet-section, only the A₁-generation is present. In the Upper Cenomanian of Navarrés and Ayora, Spain, this generation has developed into a more advanced form: *O. conulus* Douvillé (= *Dictyoconus valentinus* Almela). The results of these studies will be published in a future paper.

SYSTEMATIC DESCRIPTIONS

Order FORAMINIFERIDA

Family ORBITOLINIDAE Martin, 1889

Genus ORBITOLINA d'Orbigny, 1850

Type-species: Orbitolites lenticulata Lamarck, 1816 = *Madreporites lenticularis* Blumenbach, 1805.

Diagnosis: The same as the diagnosis of *O. lenticularis* (Blumenbach); see discussion.

Discussion: The genus *Orbitolina*, as known hitherto, consists of only one species (see preceding pages), which on morphological grounds can be subdivided into a number of form-groups.

According to Douglass (1960a, p. 28), the type species must be *Orbitolina lenticularis* (Blumenbach), since this is the only species assigned to the genus by d'Orbigny in 1850 in vol. 2, p. 143 of the *Prodrome de Paléontologie*, the entry of which reads:

Orbitolina, d'Orb., 1847. Ce sont des *Orbitolites* à cotés inégaux, l'un encroûté, l'autre avec des loges.

342. *lenticulata*, d'Orb., 1847. *Orbitolites lenticulata* Lamarck, 1816; Lamoureux, 1821, pl. 72, fig. 13-16. Perte du-Rhône (Ain), St.-Paul-de-Fenouillet (Aude).

1847 is the year in which the manuscript was finished; the year of publication was 1850. Examination of topo-type material showed that specimens from the Perte du Rhône belong to form-group I (pl. I fig. 9), whereas specimens from St.-Paul-de-Fenouillet belong to form-group II (pl. X figs. 1, 2). The species *O. plana*, *O. mamillata*, *O. concava* and *O. conica* were also mentioned by d'Orbigny, but on later pages of the *Prodrome* (pp. 184, 185); none of them can be regarded as the type-species, although many authors have done so.

Since *Orbitolina* is monospecific, the question arises whether the diagnosis of the genus is not too limited, as per definition a genus is an assemblage of closely allied species. It is probable that the diagnosis of the genus should be broadened, so as to include other forms, as *Simplorbitolina manasi* Ciry & Rat, *Dictyoconus arabicus* Henson and possibly also the genus *Iraqia*; as data on these groups are still incomplete, no attempt has been made to change the diagnosis.

Orbitolina lenticularis (Blumenbach)

(Plates I-XXI)

Synonymy: It is pointed out that the list of synonyms, as far as Linnean names are concerned, is rather complete; only the species established by Mamontova (1961) could not be listed, because the publication was not available. The number of papers in which species of *Orbitolina* are mentioned or described, amounts to close to a thousand. It proved to be an almost impossible task to check all of them, so the list of redescriptions is incomplete; only the most important ones are mentioned.

1805. *Madreporites lenticularis* Blumenbach, pl. 80 figs. 1-6.
 1816. *Orbulites concava* Lamarck, p. 197.
 Favre, 1912, pl. 1 fig. 6.
 1816. *Orbulites lenticulata* Lamarck, p. 197.
 Lamoureux, 1821, p. 45, pl. 72 figs. 13-16.
 1837. *Orbitolites conica* d'Archiac, p. 178.
 1837. *Orbitolites plana* d'Archiac, p. 178.
 1837. *Orbitolites mamillata* d'Archiac, p. 178.
 1840. *Orbitolites bulgarica* Boué, p. 239.
 1847. *Orbitolites concava* Defrance, Michelin, p. 28, pl. 7 fig. 9.
 1849. *Orbulites texanus* Roemer, p. 392.
 Roemer, 1852, p. 86, pl. X figs. 7a-d.
 1850. *Orbitolina lenticulata* (Lamarck), d'Orbigny, p. 143, no. 342.
 1850. *Orbitolina plana* d'Archiac, d'Orbigny, p. 184, no. 743.
 1850. *Orbitolina mamillata* d'Archiac, d'Orbigny, p. 184, no. 744.
 1850. *Orbitolina concava* (Lamarck), d'Orbigny, p. 185, no. 745.
 Martin, 1889, p. 211, pl. 24 figs. 1-13, pl. 25 figs. 14-20.
 Egger, 1899, p. 145, pl. XXII fig. 34, pl. XXIV figs. 38-40, pl. XXVI figs. 1-18.
 Douvillé, 1900, p. 226.
 Silvestri, 1932a, p. 171, pl. XI fig. 6, pl. XV figs. 1, 2.
 Davies, 1939, p. 787, pl. 2 fig. 15.
 Sahni & Sastri, 1957, p. 27, pl. III fig. 17.
 Douglass, 1960a, p. 32, pls. 2, 3.
 1850. *Orbitolina conica* d'Archiac, d'Orbigny, p. 185, no. 745.
 1852. *Orbitolina conoidea* Gras, pp. 34, 37, 52, pl. 1 figs. 4-6.
 Silvestri, 1932a, p. 182, pl. X fig. 4, pl. XI fig. 6, pl. XV figs. 5, 6, pl. XVI figs. 3, 4.
 Sahni & Sastri, 1957, p. 24, pl. IV figs. 4-7, text fig. 10.
 1852. *Orbitolina discoidea* Gras, pp. 37, 52, pl. 1 figs. 7-9.
 Silvestri, 1932a, p. 182, pl. XI fig. 6, pl. XVI figs. 5-7.
 Sahni & Sastri, 1957, p. 25, pl. III figs. 8-16, pl. IV figs. 1, 3, 8, 9, 10, text fig. 11.
 1854. *Orbitulites apertus* Erman, p. 603, pl. 23 figs. 1-3.
 1858. *Orbitolina lenticularis* (Lamarck), Pictet & Renevier, p. 1.
 1862. *Patellina concava* (Lamarck), Carpenter, Parker & Jones, p. 231.
 1866. *Orbitolina venezuelana* Karsten, p. 114, pl. VI fig. 6.
 1877. *Orbitolina (Patellina) lenticularis* (Blumenbach), Toula, p. 534, pl. VIII fig. 1.
 1877. *Orbitolina concava* Lin., Toula, p. 535, pl. VIII fig. 3.
 1877. *Orbitolina bulgarica* Deshayes, Toula, p. 535, pl. VIII fig. 2.
 Douvillé, 1915, pl. X figs. 2, 3, pl. XI fig. 1.
 Sahni & Sastri, 1957, p. 28, pl. IV fig. 2.
 1878. *Patellina scutum* Fritsch, p. 144, pl. XVIII fig. 15, pl. XIX figs. 2a-c.
 1878. *Patellina trochus* Fritsch, p. 145, pl. XVIII fig. 16, pl. XIX figs. 1a-c.
 1881. *Orbitolina sub-concava* Leymerie, p. 754, pl. E figs. 7, 8.
 Douvillé, 1940, pl. XVIII figs. 4-6.
 1891. *Orbitolina andraei* Martin, p. 59, pl. 2 figs. 1-14.
 1891. *Orbitolina texana* (Roemer), Taff, p. 727.
 Carsey, 1926, p. 22, pl. 6 figs. 6a-c.
 Hodson, 1926, p. 4, pl. 1 figs. 2, 4.
 Davies, 1939, p. 783, pl. 1 figs. 1, 3, 7, 9, 12.
 Douglass, 1960a, p. 34, pls. 4-6.
 1893. *Patellina texana* Hill, p. 20, pl. 1 figs. 2a-d.
 1902. *Orbitolina lenticularis* (Blumenbach), Egger, p. 579, pl. I figs. 1-9.
 Douglass, 1960a, p. 30, pl. I.
 1905. *Orbitolina choffati* Prever, pp. 469, 473.
 1905. *Orbitolina douvillei* Prever, p. 469.
 1905. *Orbitolina intermedia* Prever, p. 469.

1905. *Orbitolina paronai* Prever, p. 469.
Prever, 1906, pp. 163, 164.
Prever, 1908, pp. 323, 324.
Prever, 1909, p. 59, pl. I figs. 7-11.
1905. *Orbitolina polymorpha* Prever, p. 469.
Prever, 1908, pp. 323, 324.
Prever, 1909, p. 56, pl. I fig. 2.
1906. *Orbitolina boehmi* Prever, pp. 163, 164.
Prever, 1908, p. 323, 324.
Prever, 1909, p. 60, pl. I figs. 12-14.
1907. *Orbitolina michaelis* Silvestri, p. 168, footnote.
1908. *Orbitolina anomala* Prever, p. 323, 324.
1909. *Orbitolina polymorpha* var. *communis* Prever, p. 56.
1909. *Orbitolina polymorpha* var. *franca* Prever, p. 56.
1909. *Orbitolina polymorpha* var. *minima* Prever, p. 57.
1912. *Orbitolina bulgarica* (Boué), Douvillé, p. 3.
Elliot, 1952, p. 383.
- ?1912. *Orbitolina conulus* Douvillé, p. 3; 1904, pl. XVII figs. 2, 3a, 6. Douvillé, 1915, p. 146, pl. IX fig. 3.
1915. *Orbitolina* cf. *discoidea* Gras, Douvillé, pl. IX fig. 3, pl. X fig. 2, pl. XI fig. 1.
1924. *Orbitolina lenticularis* var. *venezuelana* Karsten, Dietrich, p. 183.
1925. *Orbitolina bulgarica* Deshayes var. *janeschi* Dietrich, p. 32, pl. IV, figs. 2, 3, 5.
1926. *Orbitolina discoidea-conoidea* Gras var. *ezoensis* Yabe & Hanzawa, p. 17, pl. III, figs. 18-20, pl. V figs. 4-17.
1926. *Orbitolina japonica* Yabe & Hanzawa, p. 18, pl. IV fig. 17.
1926. *Orbitolina japonica* var. *miyakoensis* Yabe & Hanzawa, p. 18, pl. IV, figs. 11-15, pl. V figs. 1-3.
1926. *Orbitolina planoconvexa* Yabe & Hanzawa, p. 19, pl. IV fig. 16, pl. VI figs. 1-7.
1926. *Orbitolina shikoensis* Yabe & Hanzawa, p. 19, pl. VI figs. 8-16.
1926. *Orbitolina trochus* (Fritsch), Yabe & Hanzawa, p. 19, pl. IV fig. 16, pl. VI figs. 1-7. Silvestri, 1932, p. 162, pl. IX fig. 3, pl. XI fig. 2, pl. XIII figs. 5-7, 9.
1926. *Orbitolina scutum* (Fritsch), Yabe & Hanzawa, pl. IV figs. 1, 2.
1926. *Orbitolina texana asaguana* Hodson, p. 5, pl. 1 figs. 6, 8.
1926. *Orbitolina texana monogasana* Hodson, p. 5, pl. 1 figs. 7, 9.
1926. *Orbitolina thompsoni* Hodson, p. 5, pl. 1 figs. 1, 5.
1926. *Orbitolina whitneyi* Carsey, p. 22, pl. 6 fig. 9.
1928. *Orbitolina pileus* Fossa Mancini, p. 197, pl. XXII fig. 4, pl. XXIII figs. 1, 2. Sahni & Sastri, 1957, p. 20, pl. II figs. 12, 13, text fig. 7.
1928. *Orbitolina parma* Fossa Mancini, p. 203, pl. XXII figs. 1-3, 5, 6, pl. XXIII figs. 3-6. Sahni & Sastri, 1957, pl. II figs. 11, 14, text fig. 8.
- non 1928. *Orbitolina gigantea* d'Orbigny, Cushman, p. 182.
1929. *Orbitolina tibetica* Cotter, p. 352, pl. XXVII figs. 1-12, pl. XXVIII, figs. 1-5. Sahni & Sastri, 1937, p. 23, pl. III figs. 1-7, text fig. 9.
1930. *Orbitolina mamillata* d'Archiac var. *subaperta* Astre, p. 306, figs. 1c, d.
1932. *Orbitolina concava* (Lamarck) var. *texana* (Roemer), Silvestri, p. 371, pl. 1 figs. 1-9, pl. 2 figs. 1, 2.
1937. *Orbitolina birmanica* Sahni, p. 365, pls. 29, 30, text fig. 1. Sahni & Sastri, 1957, p. 30, pl. IV figs. 12-19, pl. V figs. 1-11, text fig. 13.
1944. *Orbitolina concava texana* (Roemer), Barker, p. 207, pl. 35 figs. 10-16. Lozo, 1944, p. 553, pl. 5 figs. 1, 2. Stead, 1951, p. 594, pl. 2 figs. 29-30.
1945. *Orbitolinoides senni* Vaughan, p. 22, pl. 2.
1948. *Orbitolina kurdica* Henson, p. 48, pl. I figs. 9-15, text figs. 10a-c, 11a.
1948. *Orbitolina* cf. *discoidea* Gras, Henson, p. 50, pl. II figs. 1-9, text figs. 10d-i, 11b.
1948. *Orbitolina discoidea* Gras var. *delicata* Henson, p. 54, pl. II figs. 13, 14.
1948. *Orbitolina discoidea* Gras var. *libanica* Henson, p. 55, pl. II figs. 10, 12.
1948. *Orbitolina* cf. *bulgarica* (Deshayes), Henson, p. 56, pl. III figs. 1-4.

1948. *Orbitolina* cf. *lenticularis* (Blumenbach), Henson, p. 57, pl. III figs. 6–11.
 1948. *Orbitolina* cf. *trochus* (Fritsch), Henson, p. 60, pl. IV figs. 1–4.
 1948. *Orbitolina* cf. *concava* (Lamarck), Henson, p. 61, pl. IV figs. 5–10, text figs. 10j–r.
 1948. *Orbitolina concava* (Lamarck) var. *sefini* Henson, p. 64, pl. V figs. 1–4, 6.
 1948. *Orbitolina concava* (Lamarck) var. *qatarica* Henson, p. 66, pl. V figs. 7–11, text figs. 10s–y.
 Schroeder, 1962, p. 191, pl. 20 figs. 11, pl. 21 fig. 2.
 1949. *Orbitolina senni* (Vaughan), Henson, p. 176.
 Douglass, 1960b, pl. 4 figs. 14–18.
 Douglass, 1961, p. 478, pl. 66 figs. 5–9.
 1954. *Orbitolina texana* (Roemer) subsp. *texana* (Roemer), Frizzel, p. 80, pl. 7 figs. 32a–b.
 1954. *Orbitolina texana* (Roemer) var. *whitneyi* Carsey, Frizzel, p. 80, pl. 7 fig. 33.
 1957. *Orbitolina chitralensis* Sahni & Sastri, p. 16, pl. I figs. 1–3, text fig. 3.
 1957. *Orbitolina* cf. *chitralensis* Sahni & Sastri, p. 17, pl. I figs. 4–7, text fig. 4.
 1957. *Orbitolina kashmirica* Sahni & Sastri, p. 18, pl. I figs. 8–10, pl. II figs. 1–6, text fig. 5.
 1957. *Orbitolina kashmirica* var. *burzilensis* Sahni & Sastri, p. 19, pl. II figs. 7–9.
 1957. *Orbitolina obesa* Sahni & Sastri, p. 26, pl. IV fig. 11, text fig. 12.
 1957. *Birbalina pulchra* Sahni & Sastri, p. 28, pl. VI figs. 11, 12.
 1957. *Orbitolina birmanica* Sahni var. *kutaungensis* Sahni & Sastri, p. 32, pl. VI figs. 1–3.
 1957. *Orbitolina wadai* Sahni & Sastri, p. 33, pl. V figs. 12–16, text fig. 14.
 1957. *Orbitolina raoi* Sahni & Sastri, p. 34, pl. VI figs. 4–6.
 1957. *Orbitolina hukawngensis* Sahni & Sastri, p. 34, pl. VI figs. 7–10, text fig. 15.
 1960. *Orbitolina morelensis* Ayala-Castañares, p. 6, pls. 1–3.
 1960. *Orbitolina minuta* Douglass, 1960a, p. 36, pls. 7, 8.
 1960. *Orbitolina parva* Douglass, 1960a, p. 39, pl. 9.
 1960. *Orbitolina oculata* Douglass, 1960a, p. 39, pl. 10.
 1960. *Orbitolina pervia* Douglass, 1960a, p. 41, pl. 11.
 1960. *Orbitolina gracilis* Douglass, 1960a, p. 42, pl. 12.
 1960. *Orbitolina crassa* Douglass, 1960a, p. 43, pl. 13.
 1960. *Orbitolina grossa* Douglass, 1960a, p. 44, pl. 14.
 1962. *Orbitolina (Mesorbitolina) texana* (Roemer), Schroeder, p. 181.
 1962. *Orbitolina (Mesorbitolina) texana aperta* (Erman), Schroeder, p. 182, pl. 21 fig. 5, text fig. 5.
 1962. *Orbitolina (Orbitolina) concava concava* (Lamarck), Schroeder, p. 185, pl. 20 figs. 3–6, 8–10, pl. 21 fig. 6.
 1962. *Orbitolina (Orbitolina) concava pauletensis* Schroeder, p. 189, pl. 20 figs. 1, 2, 12.
 1962. *Orbitolina (Orbitolina) conica* (d'Archiac), Schroeder, p. 193, pl. 20 fig. 7, pl. 21 figs. 1, 3, 4, 7, 8.

Diagnosis: Test large (diameter up to about 6 cm but generally 1–10 mm), acute to flat conical, with many transitional forms. Dimorphic; microspheric test starting with a strepto-spiral; megalospheric embryonic apparatus consisting of a proloculus, a deuteroconch and a varying (usually 5–15) number of epi-embryonic chambers. In both generations the neanic part of the test consists of uniserially rectilinearly arranged discoidal chamber layers of increasing diameter. The chamber layers consist of a number of tubular chamber passages which are arranged in a marginal, a radial, and a reticulate zone; the space between these passages is filled with shell material. Communication between the chamber layers by aligned stolons, placed alternately left and right of the chamber passages. Cone surface imperforate, showing the circular sutures of the septa; marginal zone subdivided into cellules by horizontal and vertical plates; distal side grooved, convex, concave or of intermediate shape. Wall material agglutinate microgranular calcite with varying amounts of detrital material which usually is concentrated in the centre of the test; generally a hyaline calcitic layer covers the peripheral parts of the septa.

Description: see chapter on morphology.

Form-groups: The species *Orbitolina lenticularis* can be subdivided into form-groups by using the characteristics of the megalospheric embryonic apparatus. These form-groups are parts of the orthogenetic evolution and hence of stratigraphic significance.

Form-group I
(text figs. 17a & b)

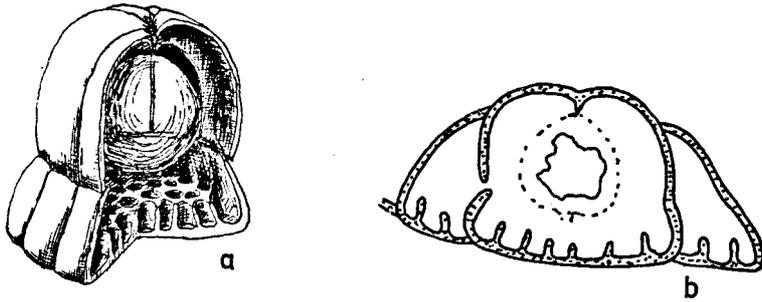


Fig. 17. The embryonic apparatus of form-group I; a: model, b: axial section. 150 ×

The embryonic apparatus consists of a globular proloculus, a deuteroconch, and undivided simple epi-embryonic chambers. No calcitic wall is present between these units, but a pseudochitinous proloculus wall has been observed in many specimens. The diameter of the deuteroconch in the most primitive specimens, measured at the surface of the test, ranges from 115 to 230 μ ; the diameter in the highest developed specimens of this form-group ranges from 200 to 340 μ . The lateral walls of the embryonic apparatus in primitive specimens are nearly straight (pl. I figs. 1-3); in younger specimens these walls are slightly bulging outward (pl. VII figs. 1-12). The most primitive forms have been found in the uppermost Barremian; the transition to form-group II is found at the base of the Upper Aptian.

Form-group II
(text figs. 18a & b)

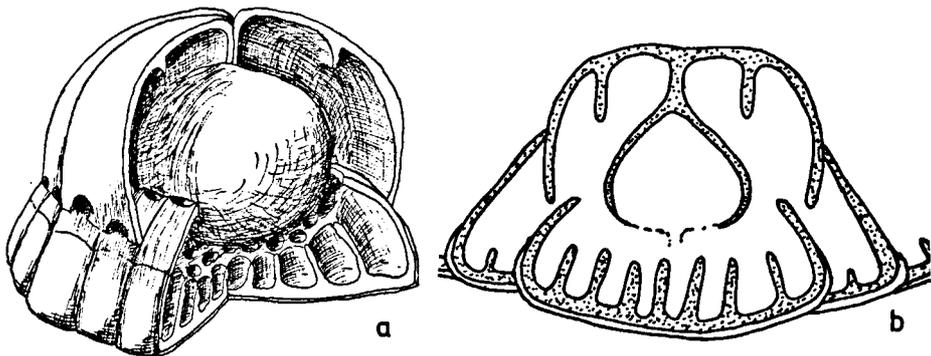


Fig. 18. The embryonic apparatus of form-group II; a: model, b: axial section. 150 ×.

The apparatus consists of a globular proloculus with a diameter between 50 and 175 μ , a deuteroconch with a diameter varying from 120 to 400 μ , and simple epi-

embryonic chambers with only a few partitions which seldom reach the proloculus. The walls of all these parts of the apparatus are calcitic. The stratigraphic range is from the lower part of the Upper Aptian to the lower part of the Lower Albian.

At the transition from Aptian to Albian, the larger specimens of populations belonging to form-group II have a proloculus which deviates from the spherical shape and tends to become flattened. These forms are the transitional forms to form-group III.

Form-group III
(text figs. 19a & b)

Proloculus with a flat, sometimes concave, distal wall, with a diameter ranging from 140 to 350 μ , a deuteroconch with a diameter ranging from 260 to 780 μ , and well-developed epi-embryonic chambers with an increasing number of partitions which seldom reach the wall of the proloculus. Stratigraphic range from the base of the Lower Albian to the lower part of the Upper Albian.

Form-group IV
(text figs. 20a & b)

The flat proloculus of form-group III is maintained for some time, but is gradually replaced by a proloculus which resembles in section a rounded triangle, or which may be arched. The diameter of the proloculus ranges from 85 to 455 μ , the diameter of the deuteroconch ranges from 245 to 1170 μ . The epi-embryonic chambers are complex and are subdivided into small interconnected cellules by short partitions which are also attached to the walls of proloculus or deuteroconch. The epi-embryonic chambers originate from a limited number of lobes, just as in the more primitive form-groups. The height of this layer of cellules is generally about half of the height of the deuteroconch (pl. XIX). Stratigraphic range from the lower part of the Upper Albian to the Upper Cenomanian.

Form-group V
(text fig. 21)

Proloculus nearly spherical or arched, with a diameter ranging from 65 to 260 μ . Outer wall of the deuteroconch rounded, causing the embryonic apparatus to be more or less globular. Diameter of the deuteroconch ranging from 200 to 650 μ . The epi-embryonic chambers have the same basic form as those of form-group IV, but may equal the height of the deuteroconch or are slightly lower. Upper Cenomanian.

Distribution: The geographic distribution of *Orbitolina* is discussed at length by Maync (1959, pp. 100–103, text fig. 3) and Douglass (1960a, pp. 28, 29, text fig. 29); the localities mentioned in the present paper can be added to their lists. In summary, *Orbitolina* is found in the entire Tethys province in the widest sense, which covers the region between the two Americas, South and Southwest Europe (including southern England), North Africa and the northern part of East Africa, the Near, Middle and Far East.

In the Americas *Orbitolina* is stratigraphically restricted to the Upper Aptian and the Albian. In the Old World the oldest reliable datings are Upper Barremian and the youngest are uppermost Cenomanian.

Ecology: The environments in which *Orbitolina* lived were fully discussed by Rat (1959) and Douglass (1960b), and the reader is referred to their papers. *Orbitolina*

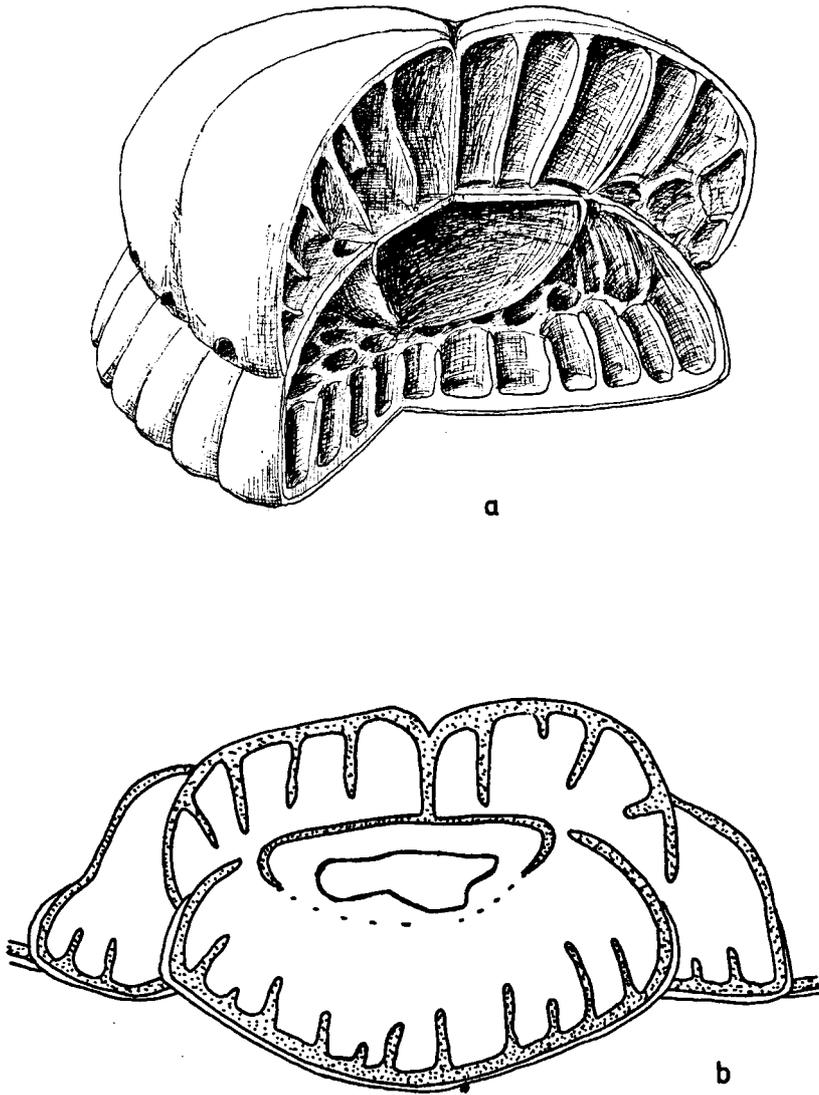


Fig. 19. The embryonic apparatus of form-group III; a: model, b: axial section. 150 \times .

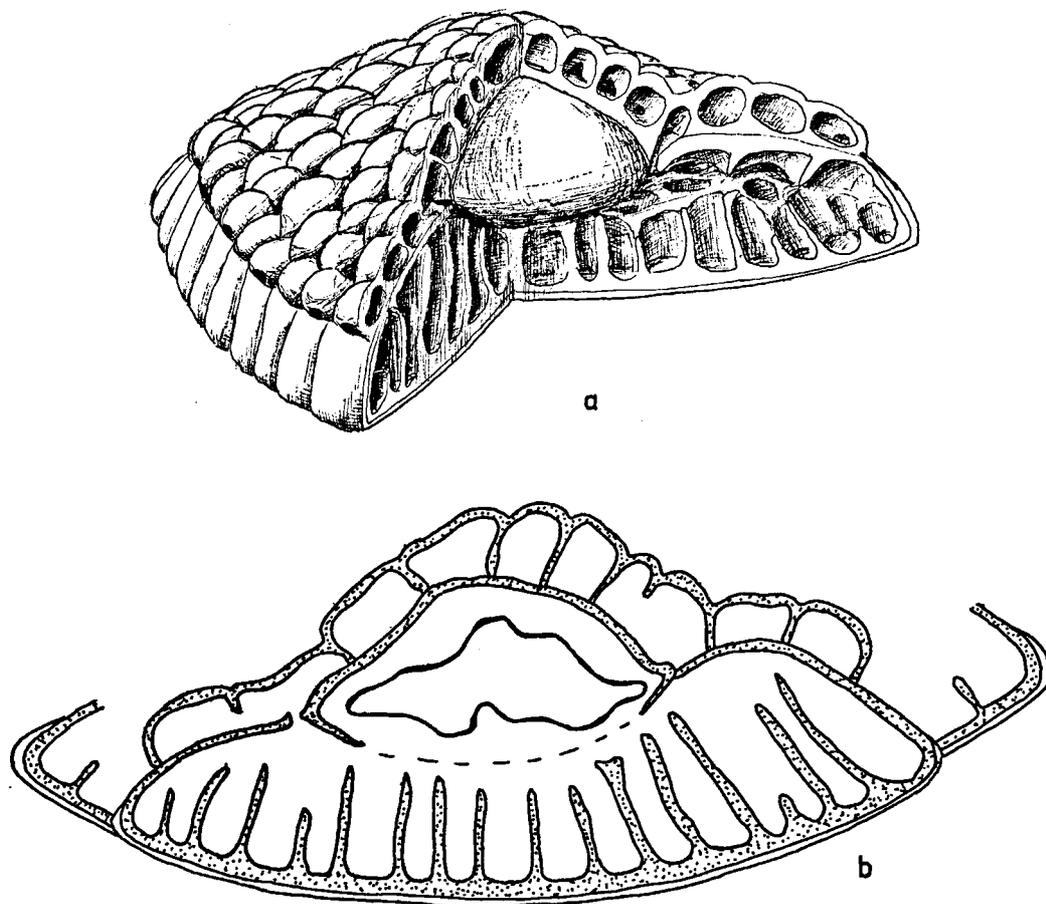


Fig. 20. The embryonic apparatus of form-group IV; a: model, b: axial section. 150 ×.

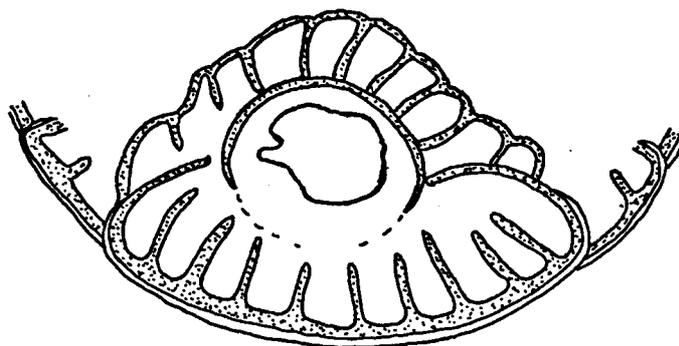


Fig. 21. Axial section of the embryonic apparatus of form-group V. 150 ×.

is generally found in a variety of sediments, but seems to be restricted to tropical or subtropical shallow marine deposits with a large quantity of detrital material; it is generally associated with biostromal or biohermal sediments. Douglass (1960b) concluded to a normal salinity of the waters in which *Orbitolina* lived. This applies to many deposits, especially to highly calcareous ones, in which the fauna is not appreciably different from the fauna generally found in shallow marine deposits. However, the accompanying fauna may often be limited and specialized. In such cases, the macrofauna is practically absent, whereas the microfauna is composed of fossils as *Choffatella*, small miliolids, and some species of ostracods. These microfaunas are generally limited in number of specimens and of species. Hiltermann (1949, after Remane) stated that the number of species in mesohaline waters (salinity 5–9 ‰) is distinctly smaller; it is suggested that *Orbitolina* occurred also in such environments instead of being limited to marine waters of normal salinity.

Discussion: For only a small number of species, subspecies, and varieties, placed in synonymy with *O. lenticularis*, it has been possible to determine to which form-groups they belong; topo-type material has been available of only a few. As other sources of information, the illustrations in literature have been used.

The synonyms for which the affinity to the form-groups has been ascertained, are listed below.

Form-group I

Madreporites lenticularis Blumenbach, 1805, = *Orbulites lenticulata* Lamarck, 1816, = *Orbitolina lenticulata* (Lamarck), d'Orbigny, 1850 (pars), = *Orbitolina lenticularis* (Blum.), Douglass, 1960a.

Topo-type material from the Perte du Rhône (Ain), France, contains form-group I (pl. I fig. 9). d'Orbigny mentioned also another type-locality, at St.-Paul-de-Fenouillet (Aude), France, the material of which belongs to form-group II (pl. X figs. 1, 2).

O. discoidea-conoidea Gras, 1852.

Topo-type material from one of the type localities (at Les Ravix, Isère, France) is shown in pl. III figs. 4, 5. According to Jacob (1929) the other type localities mentioned by Gras are of the same age; it may be assumed that the specimens from these localities also belong to the same form-group.

O. cf. discoidea Gras, Henson, 1948, pl. II figs. 1–3, text fig. 11b.

Topo-type material contains primitive specimens of form-group I (pl. I fig. 14).

O. discoidea Gras var. *delicata* Henson, 1948, pl. II fig. 13.

Topo-type material is shown in pl. I fig. 11 of the present paper.

?*O. scutum-trochus* Fritsch 1878. Sample 5891 from Seberoeang, Borneo is probably topo-type material of this species. Pl. VI fig. 7 shows an embryonic apparatus of this material.

Form-group II

O. lenticulata (Lam.), d'Orbigny, 1850, p. 143 (pars). See above.

?*O. bulgarica* (Boué), Douvillé, 1915, pl. X figs. 2, 3.

?*O. pileus* Fossa Mancini, 1928, pl. XXII fig. 4, pl. XXIII fig. 2. Pl. XXII fig. 4 is a simplified drawing, pl. XXIII fig. 2a horizontal section.

O. conoidea Gras, Silvestri, 1932a, pl. IX fig. 12, pl. XV figs. 5, 6.

O. conoidea Gras var. *libanica* Henson, 1948.

Topo-type specimens belong to form-group II (pl. VIII figs. 13–15).

- O. discoidea* Gras, Sahni & Sastri, 1957, pl. III fig. 13.
O. tibetica Cotter, Sahni & Sastri, 1957, pl. III figs. 3, 4, 6.
O. morelensis Ayala-Castañares (pars), 1960, pl. 3 figs. 1–11.
 Type material shows the transition of form-group II (1960, pl. 3 figs. 4–6, 10) to form-group III (1960, pl. 3 figs. 1–3, 7–9, 11).
 Topo-type material is shown in pl. XVI figs. 14, 15 of the present paper.
O. minuta Douglass (pars), 1960a, pl. 7 figs. 9, 25. It should be noted that this material is not from the locality of which the holo-type has been selected. Other material depicted by Douglass belongs to form-group III. Sixteen axial sections of specimens from the locality from which the holo-type has been selected belong all to form-group IV (pl. XVI figs. 16–18).
O. parva Douglass, 1960a, pl. 9 figs. 4, 8.
O. oculata Douglass, 1960a, pl. 10 figs. 13–15.
 ?*O. gracilis* Douglass, 1960a, pl. 12 figs. 12?, 14?
 ?*O. crassa* Douglass, 1960a, pl. 13 fig. 14?
 ?*O. grossa* Douglass, 1960a, pl. 14 figs. 6?, 7?

Form-group III

- O. mamillata* (d'Archiac) var. *subaperta* Astre, 1930.
 Topo-type material belongs to the transition from form-group II to form-group III, but form-group II forms a minority (pl. XI figs. 7, 8, pl. XIV figs. 5, 7, 9–13, pl. XV figs. 1–10).
 ?*O. concava* (Lam.), Sahni & Sastri, 1957, pl. III fig. 17.
 The figure is rather poor and the section is somewhat oblique; the distal side of the proloculus seems to be flat and the epi-embryonic chambers seem to be well-developed.
O. texana (Roemer), Douglass, 1960a, pl. 6 figs. 1, 3–6.
 As far as known, the embryonic apparatus of type-specimens has never been figured.
O. minuta Douglass (pars), 1960a, pl. 7 figs. 6, 7?, 8, 24 (see above).
O. pervia Douglass, 1960a, pl. 11 figs. 13, 15.
O. (Mesorbitolina) texana aperta (Erman), Schroeder, 1962, text fig. 6.

Form-group IV

- O. concava* (Lam.), from the type-locality at Ballon (Sarthe), France.
 A paratype specimen from the collection of Lamarck is shown in pl. XVIII fig. 1, and material from the type locality in pl. XVII figs. 15–18 and pl. XVIII figs. 2–9. Other topo-type material is depicted and described by Douglass (1960a, p. 32, pls. 2, 3) and Schroeder (1962, p. 185, pl. 20 figs. 3–6, 8–10).
 ?*O. concava* (Lam.), Egger, 1899, pl. XXVI figs. 2, 3.
 The figures are simplified drawings; the form-group to which they belong cannot be determined with certainty, but the figures indicate form-group IV.
O. concava (Lam.) var. *qatarica* Henson 1948, pl. V figs. 9, 11; Schroeder, 1962, pl. 20 fig. 11. Topo-type material is shown in pl. XVII figs. 11–13.
 ?*O. birmanica* Sahni, Sahni & Sastri, 1957, pl. V figs. 1–4, 6.
 None of these figures shows an axial section, but all sections are oblique. The epi-embryonic chambers appear to have a cellular structure, but this may be caused by the obliqueness of the sections. It is possible that the specimens belong to form-group III on account of the flat distal wall of the proloculus, but they might just as well belong to form-group IV.

- O. minuta* Douglass (pars). Topo-type material from the locality from which the holo-type has been selected belongs to form-group IV (see form-group II). Pl. XVI figs. 16–18.
- O. (Orbitolina) concava pauletensis* Schroeder, 1962, pl. 20 figs. 1, 2, 12.

Form-group V

- O. (Orbitolina) conica* (d'Arch.), Schroeder, 1962, pl. 20 fig. 7.

Henson (1948) found two forms, a conical and a flat one, in the Cenomanian samples containing *O. concava* (Lam.) var. *sefini* Henson. Judging from his figures, these forms might belong to the Upper Cenomanian A₁ and A₂ generations; it is possible that the conical forms belong to form-group V and the flat forms to form-group IV.

Material supplied by Dr. Méhès, and considered by him as *O. conica*, belongs to form-group IV (pl. XVIII fig. 12).

Material from Dr. Méhès, classified as *O. lenticularis baconica* nov. subsp., belongs to the upper part of form-group II (pl. IX figs. 12, 13). The paper in which these two forms are described had not been published when the present paper was prepared.

It has not been ascertained whether the specimen depicted by Douvillé (1904, pl. XVII fig. 2), which he mentioned later as the type for the species *O. conulus* Douvillé (1912), belongs to the species *O. lenticularis*. It seems more likely that it is a form closely related to *Iragia* or *Simplorbitolina*; also it is possible that it is identical with *Dictyoconus valentinus* Almela, as the type localities of the two species lie close together. The figured specimen is from Navarrés, Spain; *O. conulus* has been reported also from Orgon and Voreppe, both in France. The small conical forms from the last two localities probably belong to *Orbitolinopsis*¹.

Orbitolina gigantea d'Orbigny, Cusman's geno-type of *Orbitolina* (1928, p. 182), actually is a coral (Douvillé, 1933).

It has not been possible to ascertain where Blumenbach's type material is deposited. If this material cannot be located, it is suggested to select one of the two thin sections of topo-type material showing the embryonic apparatus, as lecto-type; the sections are deposited at the Muséum d'Histoire Naturelle, Genève.

Material: About 250 samples containing *Orbitolina* have been studied; about 190 samples contained specimens with an embryonic apparatus, or were important enough for other reasons to be included in the list of samples. About 2500 well orientated sections of detached specimens and about 450 thin sections of rocks have been prepared.

SOME CONTEMPORANEOUS ALLIES OF ORBITOLINA

Coskinoloides texanus Keijzer

(pl. XXIII figs. 3, 6)

1942. *Coskinoloides texanus* Keijzer, p. 1016, text figs. a–h.
Henson, 1949, p. 175.
Frizzel, 1954, p. 76, pl. 6 fig. 27.
Maync, 1955a, p. 89.
Maync, 1955b, p. 109, pl. 17 figs. 14, 15.
Douglass, 1960b, p. 258, pl. 6 figs. 7–13.
1944. *Coskinolina adkinsi* Barker, p. 206, pl. 35 figs. 1–4.
Lozo, 1944, p. 550, pl. 5 figs. 3–6.
Stead, 1951, p. 592, pl. 2 figs. 16–18.

¹ Comparison of material of these four localities proved these suppositions to be correct. The flat forms belong to form-group I. See foot-note 1. p. 39.

Description: An excellent description is given by Douglass (1960b) and reference is made to that paper for details.

Test small (diameter about 0.5 mm), conical; the height of the cone is generally slightly larger than the diameter of the base. Initial part of the test trochospiral, neanic chambers uniserial, discoidal, and subdivided at the periphery by simple radial partitions of varying length; in some cases with pillars in the central part of the last chambers. Cone often crooked. The septa can be observed at the outside of the test as circular depressed sutures. Apex pointed or slightly rounded. Base of the cone slightly concave. The aperture consists of a varying number of circular foramina located in the central part of the last-formed chamber septum. Wall material is microgranular calcite with little or no detrital material.

Discussion: *Coskinolinoides texanus* was originally assigned to the family Valvulinidae by Keijzer, and by later authors to the Orbitolinidae; it was considered as the phylogenetic ancestor of the whole family Orbitolinidae by Douglass (1960b, p. 255). Since the initial part of all other Orbitolinidae is or can be derived of a streptospiral, *Coskinolinoides* cannot be assigned to this family, and probably belongs to the Valvulinidae. This in spite of the analogy in structure with the chambers of the Orbitolinidae.

Dictyoconus walnutensis (Carsey)

(Pl. XXIII figs. 2, 5, 10)

1926. *Orbitolina walnutensis* Carsey, p. 23, pl. 7 figs. 11a–b, pl. 8 fig. 3.
 1928. *Coskinolina cooki* Moberg, p. 166, pl. 3 figs. 1–5, 7, 8.
 1932. *Orbitolina* (?) *walnutensis* Carsey, Vaughan, p. 609.
 1932. *Dictyoconus aegyptiensis* (Chapman) var. *walnutensis* (Carsey), Silvestri, 1932b, p. 377, pl. 1 figs. 10–12, pl. 2 figs. 3–5.
 1939. *Dictyoconus walnutensis* (Carsey), Davies, p. 775, pl. 1 figs. 4, 6.
 Cole, 1942, p. 25, pl. 4, figs. 6–7.
 Barker, 1944, p. 205, pl. 35 figs. 6–8.
 Lozo, 1944, pp. 5 figs. 7–11.
 Maync, 1955a, p. 85, pl. 13 figs. 1–7, pl. 14 figs. 1–8.
 Douglass, 1960b, p. 257, pl. 5 figs. 1–8.
 1941. *Dictyoconus cooki* (Moberg), Cole, p. 26, pl. 3 figs. 11–13, pl. 5 figs. 6–10, 12–13, pl. 6 figs. 1–8, pl. 18 fig. 12.
 Cole, 1942, p. 24, pl. 3 fig. 10, pl. 4 fig. 8.
 Cole, 1956, p. 214, pl. 25, figs. 6–7.

Description: Excellent descriptions have been given by Douglass (1960b) and Maync (1955a) and need not be repeated. The dimorphism, however, has never been mentioned as far as known.

Microspheric specimens are usually the largest. The nepionic part of the test of this generation could not be studied, because the pointed apex was found to be more or less damaged in all specimens which were probably microspheric. Some indications point to a strepto-spiral as in *Orbitolina*.

In megalospheric specimens the embryonic apparatus consists of a proloculus and a deuteroconch (pl. XXIII fig. 5). Together with the first chamber it forms a short spiral, the axis of which is at right angles to the axis of the later chambers. The plane of symmetry of the proloculus and deuteroconch does not coincide with that of the spiral; in horizontal sections the embryonic apparatus resembles the apparatus of *Simplorbitolina manasi* (pl. XXII fig. 4). Consequently the megalospheric generation of *D. walnutensis* starts with a streptospiral.

Discussion: According to Maync (1955b, pp. 91, 92) *D. walnutensis* has been recorded with certainty in the Aptian and the Albian; according to Douglass (1960b, p. 258) it occurs up to the middle Eocene.

The specimens described by Pfender (1938) and assigned to *D. walnutensis* certainly show affinities to this species, but the figures do not permit a confirmation of the determination. Moreover, some of this material is of Valanginian age and *D. walnutensis* has not yet been found with certainty in rocks older than Aptian.

Orbitolinopsis kiliani (Prever)

(Pl. XXIII figs. 1, 8, 9, 11)

1905. *Chapmania kiliani* Prever, p. 470.

1932. *Orbitolina* (?) *kiliani* (Prever), Silvestri, p. 159, text figs. 6 & 7, pl. IX figs. 14 & 15.

1932. *Orbitolinopsis kiliani* (Prever), Silvestri, p. 160, foot-note. Moullade, 1960, p. 190, pl. 3 figs. 6-12.

1955. *Coskinolina sunnilandensis* Maync (pars), pl. 17 fig. 12.

Description: Test small (generally less than 1.5 mm in diameter), conical. The diameter is generally slightly larger than the height. Apex of the cone generally rounded, base of the cone slightly convex. Initial chambers forming a strepto-spiral, later chambers uniserial, saucer-shaped. Neanic chambers subdivided near the periphery by radial vertical partitions; central zone reticulate (pl. XXIII fig. 9). No horizontal plates in the marginal zone. Wall material is microgranular calcite; in some specimens a very thin hyaline epidermis can be observed. Detrital material has not been observed.

Stratigraphic range: According to Moullade (1960, p. 190) this species is only found in the Barremian; it is present in samples 115115 and 115117 which are from the uppermost Barremian.

Dictyoconus floridanus (Cole) subsp. *elongata* (Moullade)

(Pl. XXIII figs. 4, 7)

1960. *Coskinolina sunnilandensis* Maync subsp. *elongata* Moullade, p. 189, pl. 1 figs. 10-14.

1961. *Coskinolina maynci* Chevallier, p. 31, pl. 1 figs. 6, 7.

Description: Test elongate conical; height up to 1.5 mm. Base of the cone slightly convex. The embryonic apparatus has not been observed, because the apices of all specimens were eroded to some extent. Neanic chambers saucer-shaped, uniserial, with a marginal zone subdivided by vertical plates only; pillars in the central zone. A number of foramina can be observed in the centre of each septum. Wall material is microgranular calcite without detrital material.

Discussion: *Coskinolina sunnilandensis* Maync is placed in synonymy with *Dictyoconus floridanus* (Cole) by Douglass (1960b, p. 258).

According to Moullade (1960, p. 189), the subspecies can only be distinguished from *Dictyoconus floridanus* (Cole) by the exceptional height of the test. Moullade suggested that *D. floridanus elongata* and *D. floridanus* are different generations of one species, but this could not be ascertained by the present author, as the available specimens were poorly preserved. Moullade stated that *D. floridanus elongata* is always accompanied by *D. floridanus*; however, sample 115115 only contains *D. floridanus elongata*.

The taxonomic position of *D. floridanus elongata* remains questionable since the term subspecies is reserved for morphologically different members of one species, which occur at geographically different localities separated by a barrier. Possibly it is nothing but a "forma" (Boltovskoy, 1958). Chevallier's reasons for establishing a distinct species cannot be accepted (1961, p. 31).

Distribution: *D. floridanus elongata* has been described from the Upper Barremian of Southern France and of the Swiss Alps (Moullade, 1960, Chevallier, 1961).

Simplorbitolina (?) *manasi* Ciry & Rat

(Pl. XXII figs. 1-9)

1951. *Dictyoconus* sp., Cuvillier & Sacal (pars), pl. 21 fig. 1.

1953. *Simplorbitolina manasi* Ciry & Rat, p. 85, pl. 1 figs. 1-6.

Douglass, 1961, p. 259, pl. 6 figs. 1-6.

Description: Test small (diameter generally less than 2 mm), conical, the height about equal to the diameter. Base of the cone slightly convex, apex rounded. Two forms can be distinguished. In one form the test starts with a strepto-spiral and a very small proloculus (pl. XXII figs. 7-9); very seldom horizontal plates are found in the marginal zones (Douglass, 1960b, p. 259, pl. 6 fig. 1). In the other form the test starts with an embryonic apparatus consisting of a proloculus and a deuteroconch, the plane of symmetry of which is about at right angles to the plane of symmetry of the rest of the initial spiral (pl. XXII fig. 4). In this form one set of horizontal plates is generally developed in the marginal zone of later chambers.

The structure of the neanic chambers resembles that of *Orbitolina lenticularis* (Blum.); in some specimens the horizontal plates are absent in the marginal zone.

Three zones can be distinguished in the neanic chambers: a marginal, a radial and a reticulate central zone (pl. XXII fig. 3), which are formed by modifications of the chamber passages. The chamber passages alternate in position in adjoining chamber layers. Passages are basically cylindrical, widening towards the periphery; here they are subdivided by vertical and in some specimens by horizontal plates which together form the cellules of the marginal zone. Towards the centre of the test the passages anastomose and form the reticulate or central zone. The chamber passages of adjoining chambers are connected by oblique stolons, placed alternately to the left and right of the passages in the radial and reticulate zones. These stolons are aligned in nearly straight rows (pl. XXII fig. 5).

The cone-surface and the peripheral parts of the septa are usually covered with a thin hyaline calcitic layer. Most of the wall material, however, consists of microgranular calcite, sometimes with a pseudo-chitinous layer inside the embryonic apparatus. No agglutinate material has been observed, but Douglass (1960b, p. 259) mentioned fine detrital material in the granular portion of the test.

Discussion: The two mentioned forms have not been found together in one sample. The first form, with the smaller proloculus, has been found in samples 115033, 115034, 115035 and in topo-type material forwarded by P. Rat (sample 115155). It is generally somewhat smaller than the other form which has been found in samples 115082-84, 115071, 115078, 115058-61 and in a sample from the same region, received from P. Rat (sample 115156). Although the forms have not been found together in one sample, it seems highly probable that they belong to different generations of one species. This is supported by their contemporaneous occurrence

(base of the Albian). Possibly this may be interpreted as in *O. lenticularis*, i.e. the intrusion into a biotope of very small microspheric specimens, followed, when possible, by an explosive development of chiefly megalospheric specimens. The specimens of the group with the largest proloculus are generally present in greater numbers than the specimens with the smaller proloculus. Among the specimens with the larger proloculus, however, only a minority was well enough preserved for studying the embryonic apparatus, and specimens with a smaller proloculus may also be present in these samples.

The resemblance between *Orbitolina lenticularis* and *Simplorbitolina manasi* is striking. Only the embryonic apparatus and the size of the test are different to some extent; horizontal plates are absent in only part of the specimens of *S. manasi*. It is suggested that these species belong to one single genus, *Orbitolina*. It is possible that other genera and species, as *Iraqia*, *Kilianina* and *Dictyoconus arabicus* Henson, belong to this genus also.

REMARKS ON THE FAMILY ORBITOLINIDAE MARTIN

Most of the foregoing species belong to the family Orbitolinidae. According to Douglass (1960b, pp. 254, 255) *Lituonella* and *Coskinolina* cannot be assigned to the Orbitolinidae, because of the keriothecal wall structure. In spite of their morphologic differences, the Orbitolinidae all seem to have had one common ancestor, as many transitional forms have been found.

The Orbitolinidae have some characteristics in common.

1. The initial part of the test is a strepto-spiral, or derived from this form. This can be best observed in microspheric specimens which, as usual in foraminifera, also have the most primitive features. Forms like the megalospheric embryonic apparatus in *O. lenticularis* (Blum.) may also be considered as derived from a strepto-spiral by reduction of the spiral to zero; however, this conclusion can only be made by studying the microspheric nepiont.
2. Adult tests are more or less conical, and formed by uniserial saucer-shaped chambers or chamber layers of increasing diameter.
3. These chambers or chamber layers are subdivided by partitions or pillars of varying intricate pattern. Their main function seems to be a strengthening of the chambers.
4. Chambers are interconnected by a varying number of round, often oblique, foramina which are mostly found in the centre of the chamber-septa.
5. The wall material is microgranular and calcitic, the cone-surface is imperforate. In some species an epidermis of hyaline calcite can be observed, but this is not of specific significance. Detrital material seems to be confined to some species only (notably *O. lenticularis*).

The megalospheric embryonic apparatus generally consists of at least a proloculus and a deuteroconch, but some forms seem to have a proloculus only (e.g. *Iraqia barremiana* Moullade, 1960, p. 191, pl. 3 figs. 13-16).

According to Douglass (1960b, p. 255), a form like *Coskinolinoides texanus* Keijzer must be regarded as the ancestor of the family. This seems to be primarily based on the assumption that the most simple form is also the most primitive. This need not necessarily be so. A simple form can also be the result of a process as degeneration or mutation. *C. texanus* starts with a trochoid spiral and consequently cannot be assigned to the Orbitolinidae, in spite of the slightly analogous structure of the

neanic chambers. Moreover, *C. texanus* is younger than most genera of the Orbitolinidae.

Orbitopsella has been mentioned as another ancestor of *Orbitolina*. Gignoux & Moret presented an ingenuous explanation of the evolution of *Orbitopsella* into *Orbitolina*, but since the initial part of the test of *Orbitopsella* is more or less planispiral, this explanation cannot be correct.

The most primitive genus assigned to the Orbitolinidae is *Kilianina* Pfender (Aurouze & Bizon, 1958, p. 68, pl. 1 figs. 1-12, pl. 2 fig. 8), described by Pfender (1936) and Aurouze & Bizon (loc. cit.) from the Bathonian of the French Alps. The depicted specimens appear to be poorly preserved, but the pictures show *Kilianina* basically to have the same structure of the chamber layers as *Orbitolina*, with radial passages and oblique, alternating, stolons, and three distinct zones. The nepionic part of the test has not been observed, but the resemblance of the neanic chambers to those of *Orbitolina* is considered sufficient to regard *Kilianina blancheti* Pfender as belonging to the family Orbitolinidae, and very likely as its ancestor.

Another genus of the same age, described by Aurouze & Bizon (1958, p. 72, pl. 2 figs. 1-7, pl. 3 fig. 3) is *Meyendorffina*. This genus, however, is closely related to *Haurania* Henson (1948, p. 11) and must be regarded as belonging to the *Lituolidae* on the basis of the structure of the neanic chambers and also because the nepionic part of the test forms a planispiral instead of a strepto-spiral.

Kilianina is probably derived from a Paleozoic endothyroid foraminifer, as the Orbitolinidae have a strepto-spiral. The resemblance between axial sections of microspheric specimens of *Orbitolina lenticularis* and *Paradoxiella pratti* Skinner & Garner (1955, see e.g. pl. 92 figs. 4-10) is striking; the latter is a Permian fusulinid, and the resemblance might be only coincidental.

The classification of the Orbitolinidae hitherto is based on formal grounds. Especially the types of subdivision in the chamber layers have been used as diagnostic characteristics for genera. Between most of these types transitions are present and it is generally difficult to assign a species to a certain genus exclusively on these characteristics.

As an example, *Orbitolina lenticularis* (Blum.) can only be distinguished from *Simplorbitolina manasi* Ciry & Rat on the basis of the embryonic apparatus; in some specimens of *S. manasi* only, horizontal plates are absent in the marginal zones of the youngest chamber layers.

Transitions have also been found in the structure of the neanic chambers of *Orbitolina* and *Dictyoconus* (see *Dictyoconus arabicus* Henson, 1948, p. 35, pl. I figs. 5-8, pl. XIV figs. 1-12), and between *Orbitolina* and *Iraqia* (see Bassoullet & Moullade, 1962, p. 106, 107, pls. 1-3 and form-group V of *O. lenticularis*, pl. XXI figs. 1, 2 of the present paper). It remains questionable, whether many of these characteristics of the neanic chambers are actually of generic significance; they might be considered as of specific value only (see also Douglass, 1960b, pp. 254, 258), or even as modifications (ecophenotypes for example) of one single species.

Consequently a thorough revision of the taxonomy of the family, based on characteristics of the neanic as well as the nepionic parts of the test, remains highly desirable. Likewise, the evolution of its members should be studied in detail.

CHAPTER VI

STRATIGRAPHIC USE OF ORBITOLINA

The shape and dimension of the megalospheric embryonic apparatus are considered the most useful diagnostic features in the evolution of *Orbitolina*. Other characteristics are of little or no use for stratigraphic purposes and are influenced by ecologic conditions to a large extent.

The shape and dimension of the test cannot be used, except for the large diameter (up to about 6 cm) of microspheric specimens from the Upper Albian and Lower Cenomanian. However, unfavourable circumstances will prevent specimens from attaining a maximum size.

It has been attempted to determine whether the relative size of each of the three zones in neanic tests shows an evolutionary trend. As these zones are transitional, it is difficult to ascertain which parts of the chamber layers actually belong to these zones. Such a trend has not been found; however, the radial zones in Upper Cenomanian specimens tend to become unusually short.

A feature which shows some change during time is the angle between the chamber floors and the cone-surface, measured near the periphery. In specimens of Barremian age this angle measures about 40–70°, in Lower Aptian specimens about 45–80°, in Upper Aptian ones 50–85°, in Albian ones 50–90° and in Cenomanian specimens 60–90°. Some correlations have also been found between these angles and the volume of the embryonic apparatus; in each sample, the specimens with the smaller angles are usually those with a smaller embryonic apparatus. As a whole, however, these angles are varying too much and the change from Barremian to Cenomanian specimens is too small to be practically used for stratigraphic purposes. These angles depend to some extent on the composition of protoplasm and of seawater (Rhumbler, 1914) and might be interesting in ecologic studies.

The agglutination depends on ecologic factors. Coarse quartz grains for example have been found in specimens from the Aptian to the Upper Cenomanian, and they may probably be present in Barremian specimens also. Calcite eyes, which are most abundant in the Albian, are of some importance, although they have been recorded from the Upper Aptian to the Upper Cenomanian.

The cellular appearance of the central and radial zones in axial sections of Upper Cenomanian specimens has been also observed in specimens from some samples from other stratigraphic levels.

As stated before, only in oriented sections the stage of evolution of the megalospheric embryonic apparatus can be fairly accurately determined; random sections may be misleading. In most cases it is easier to prepare sections of detached specimens than attempting to find an embryonic apparatus in thin rock sections. However, in Albian and Cenomanian specimens of *Orbitolina* it is generally possible to measure the size of the embryonic area on the outside of well preserved detached specimens and to obtain a good impression of the variation in diameter; in most cases it remains advisable to ascertain the form-group to which the specimens belong by means of axial sections, so as to avoid errors. For example Upper Cenomanian specimens of form-group V may be confused with Lower Cenomanian specimens of form-group IV or Lower Albian specimens of form-groups II–III, when only using the measurements of the embryonic area as diagnostic features (see chart X).

Charts I–IX show the diameters of the proloculi (in circles) and of the deuteroconchs (in dots) of a number of samples, together with the mean values (in crosses). These measurements were made on drawings of the embryonic apparatus, 150 times enlarged. The deuteroconchs have been measured at the surface of the test, in order to enable a comparison with the diameter of the embryonic area.

Charts III, IV, V, VII, VIII and IX are diagrams representing samples from stratigraphic sections; charts I, II and VI are diagrams of miscellaneous samples which are not much different in age. A composite diagram is given in chart X; it is based on samples with noticeably different measurements, and the stratigraphic position of which is fairly well known. Drawings of the embryonic apparatus of some specimens of each sample have been added to the chart X to show the variation in shape and to illustrate the form-group to which they belong. The stratigraphic range is indicated on the right, so that chart X shows the applicability of the evolution of *Orbitolina* for stratigraphic use.

As can be seen in the diagrams for successive samples collected from stratigraphic sections, the increase in diameter during time is generally not rectilinear, but may be fluctuating to some extent. These fluctuations may be caused by various factors. The most obvious of these is the shortness of the sections, causing the populations from which the samples were taken to be hardly different. Consequently, fluctuations caused by natural variation, errors and other subjective factors, studying insufficient numbers of specimens, amongst others, tend to obliterate the over-all increase in diameter.

As can be observed in the diagrams, particularly in those representing relatively long sections (e.g. charts VIII, IX), the increase in volume of the embryonic apparatus is obvious and can be best noticed by comparing the lowest samples with the highest.

From chart X it will be clear that a few axial sections of specimens belonging to the most primitive form-groups (form-group I and the lower part of form-group II) suffice to determine the age of the sample. Since the variation in these forms is small, appreciable differences in the mean values are apt to be caused by real changes in the mean values of whole populations, and thus by evolution, rather than by the secondary causes mentioned above.

Accurate age determinations of samples from Albian and Cenomanian strata are more difficult when only a few unselected axial sections are available, since the variation increases rapidly. A useful method is to select only three well preserved specimens, one with the smallest embryonic area, one with the largest and one with an intermediate embryonic area. The sections of these three specimens will give a good impression of the range in size and shape for the sample. Unselected specimens may give less reliable results. For example, some sections only showing forms as those on pl. X figs. 10–12 (sample 115035) indicate an Upper Aptian age. However, other sections of the same sample may show forms as those on pl. X figs. 13, 14 and the whole range of forms will indicate a Lower Albian age. These results are not much different, but errors like these may be avoided by using the proper techniques which can be easily applied.

In figs. 22, 23 and 24 the embryonic apparatus is shown of a number of specimens from resp. lowermost Albian, Upper Cenomanian and middle Cenomanian samples. These figures illustrate the increase of variation in the dimension as well as in the shape of the embryonic apparatus during evolution. As can be observed, the variation is gliding, except in sample 115024, in which the two A-generations can be distinguished.

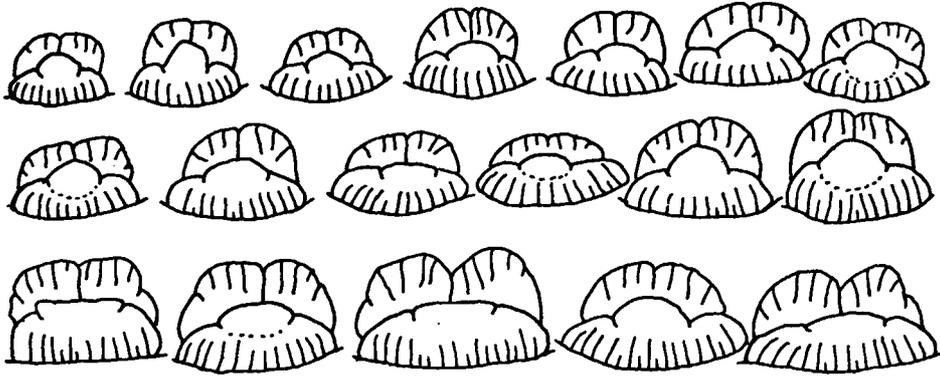


Fig. 22. Drawings of the embryonic apparatus of a number of specimens of sample 115059, illustrating the variation. 50 \times .

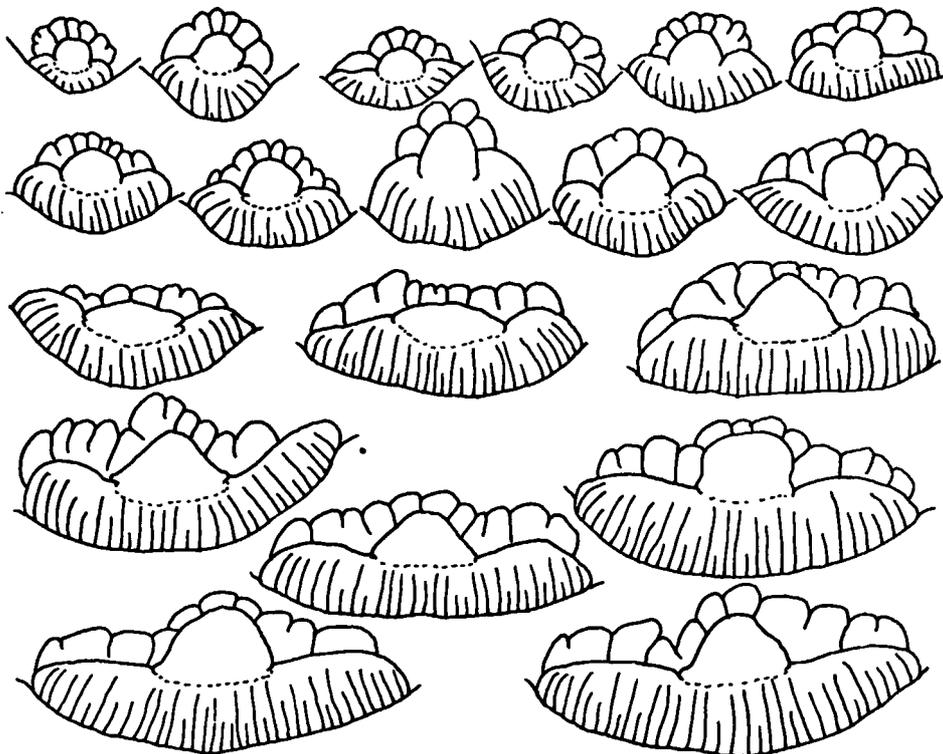


Fig. 23. Drawings of the embryonic apparatus of a number of specimens of sample 115024, illustrating the variation. 50 \times .

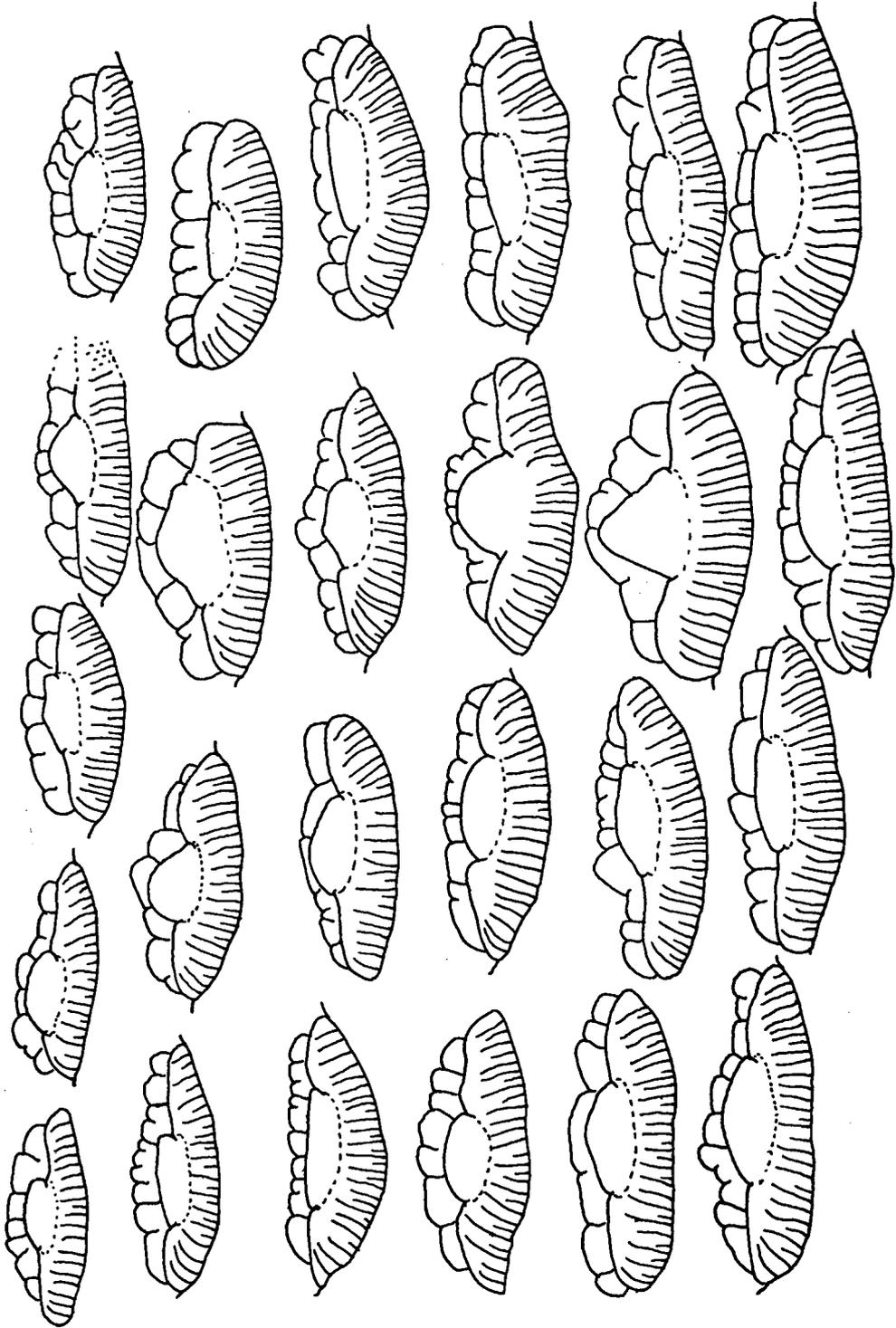


Fig. 24. Drawings of the embryonic apparatus of a number of specimens of sample 115025, illustrating the variation. 50 ×

Some age determinations based on the evolution of *Orbitolina* may appear to be dubious. This seems to be especially the case in samples of poorly preserved specimens, when some features cannot be properly distinguished. This has been found for sample 115137 (pl. IX figs. 15–17, chart VI). Specimens of this sample have an embryonic apparatus much resembling form-group II (compare e.g. with pl. XII figs. 8, 12, 13). The range in diameter of the deuteroconch is also in accordance with that of form-group II, except for two specimens which have an appreciably larger diameter. Closer observation shows the apex of the test of many specimens to be abraded to some extent, causing the diameter of the deuteroconch to be apparently smaller. Hence the mean diameter shown in chart VI (sample 115137) is smaller than the mean diameter of the original specimens. Some specimens distinctly show the cellular structure of the epi-embryonic chambers, typical of form-groups IV and V. Since specimens with a flat distal proloculus wall (diagnostic for primitive forms of form-group IV) are not present, and the two generations generally occurring in the Upper Cenomanian have not been found, the sample is probably from the upper part of the Lower Cenomanian. Hagn (1962, p. 166 and foot-note 10 on p. 170) concludes to an Upper Cenomanian age; however, the fauna is rather poor (see also list of localities) and the difference in the two determinations may actually be less significant.

As can be seen in chapter II, only a minority of the samples has been dated by using the evolution of *Orbitolina*; for most of these samples the data regarding localities and stratigraphy are insufficient to permit their dating on other grounds. The *Orbitolina*-datings of the other samples are in correspondence with other datings; the latter, however, are often not well substantiated and in most cases it is not possible to ascertain the relative stratigraphic position of samples of approximately the same age. The study of samples, the superposition of which was well established, shows that except for the minor fluctuations discussed above the volume is steadily increasing. Chart X is based on this observation. The approximate age of the samples mentioned in this chart has been established without using *Orbitolina*; the relative position of samples of approximately the same age has been established by also using the evolution of *Orbitolina*. Difficult also has been to establish the position of the boundaries of the time-units. *Orbitolina* has been reported by many authors from the Lower Barremian, but it could not be ascertained whether this concerns actually *O. lenticularis* or only related species. The stratigraphically lowermost sample collected by the author, which contains *Orbitolina*, is sample 115125, which is of Upper Barremian age. Sample 115115 seems to be of uppermost Barremian age (see chapter II); if the "couches inférieures à Orbitolines" throughout SE-France have the same age (as supposed by many authors), this might be correct, since the base of the Urgo-Aptian coincides with this level at the type-locality of Orgon. A Lower Aptian age has been demonstrated for sample 115128; thus the position of the Barremian-Aptian boundary seems to be well established.

The specimens of sample 115114 have an embryonic apparatus of approximately the same development as those of sample 115120 (type locality of *O. discoidea-conidea* Gras), which is of lowermost Upper Aptian age (see Jacob, 1906 and also Jayet, 1926, for the type locality of *O. lenticularis* at the Perte du Rhône). As sample 115113, which shows the transition of form-group I to II, lies close above 115114, this transition must be in the lower part of the Upper Aptian.

Sample 115104 is of Upper Aptian age (Cairol, 1872, Doncieux, 1903). Whether sample 115160 is Lower Albian or uppermost Aptian has not yet been ascertained, although stratigraphic data point to a Lower Albian age. The specimens of *Orbitolina* in this sample are more primitive than those in sample 115065; *Simplorbitolina manasi*

and *Coskinolinella daguini*, found in adjoining samples, indicate a lowermost Albian age for the latter sample. Consequently, the first specimens belonging to form-group III seem to appear at the base of the Albian or the top of the Aptian.

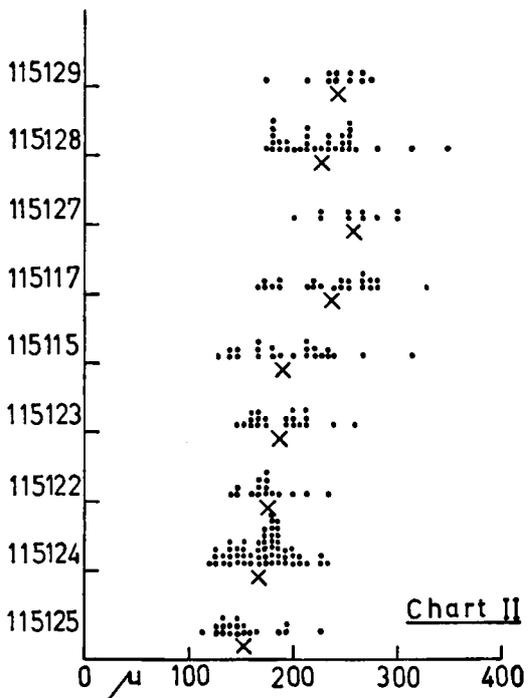
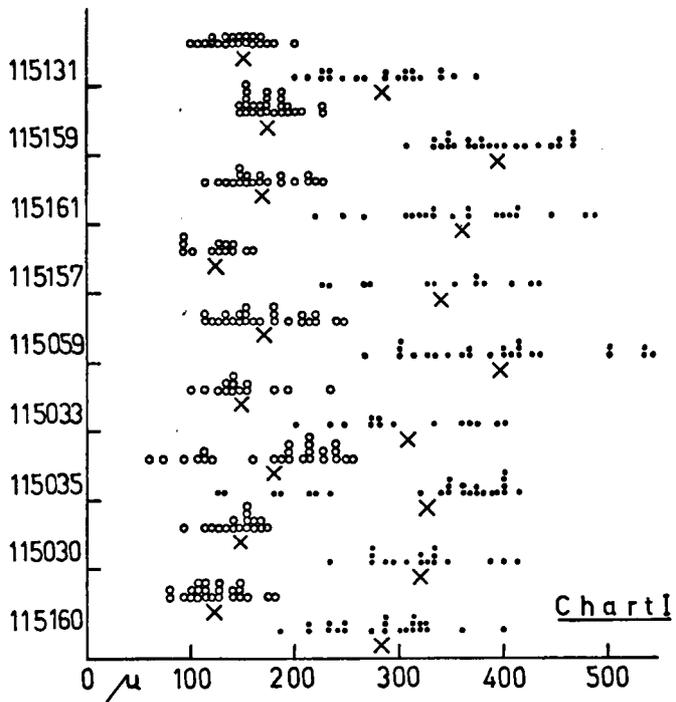
The position of the Lower Albian-Upper Albian boundary is still uncertain. Sample 115038, 115054, 115059, and 115076 all seem to be of Lower Albian age. Sample 115080 is stratigraphically appreciably higher than 115076, and may be of Upper Albian age. Sample 115158, however, is from the top of the Glen Rose Formation in Comal County, Texas, at the same level as the "Corbula" and "Salenia" beds. According to Douglass (1960a, p. 4), these beds are of Lower Albian age, but it is not certain that these beds provide reliable time-markers over large areas. Consequently, it is possible that the Lower Albian-Upper Albian boundary lies above sample 115158 and below sample 115032. The accurate stratigraphic position of the transition of form-group III to IV is also unknown; it must be located close to the Lower Albian-Upper Albian boundary.

Sample 115032 is of Upper Albian age (Dalloni, 1910), the microfauna of the beds of samples 115002 and 115005 points to a lowermost Cenomanian age; thus the Albian-Cenomanian boundary is well-established.

Sample 115025 (from the type locality of *O. concava* Lam.) is from the upper part of the Lower Cenomanian (Viennot, 1929, Schroeder, 1962); the stratigraphic position of sample 115024 points to an Upper Cenomanian age. Since sample 115025 only contains form-group IV, the transition to form-group V should be close to the Lower Cenomanian-Upper Cenomanian boundary. As samples from near this boundary are not available from a stratigraphically well-known region, it could not be ascertained whether the first appearance of specimens belonging to form-group V coincides with the Lower Cenomanian-Upper Cenomanian boundary.

Charts

- Chart I. Measurements of the embryonic apparatus of specimens of samples of Upper Aptian to middle Albian age.
- Chart II. Measurements of the embryonic apparatus of specimens of samples of Upper Barremian and Lower Aptian age.
- Chart III. Measurements of the embryonic apparatus of specimens of samples from a section near Narbonne Plage, France (see text fig. 3).
- Chart IV. Measurements of the embryonic apparatus of specimens of successive samples from the La Clape Mts., Aude, France (see text figs. 2 and 3).
- Chart V. Measurements of the embryonic apparatus of specimens of samples from a section near Orgaña, Lérida, Spain (see text fig. 4).
- Chart VI. Measurements of the embryonic apparatus of specimens of samples of Upper Albian and Lower Cenomanian age.
- Chart VII. Measurements of the embryonic apparatus of specimens of samples from a section at the Puerto de Las Alisas, Spain (text fig. 7A).
- Chart VIII. Measurements of the embryonic apparatus of specimens of samples from two successive sections at the Puerto de Las Alisas, Spain (see text figs. 7B & C).
- Chart IX. Measurements of the embryonic apparatus of specimens of samples from a section near Aulet, Spain (see text fig. 6).



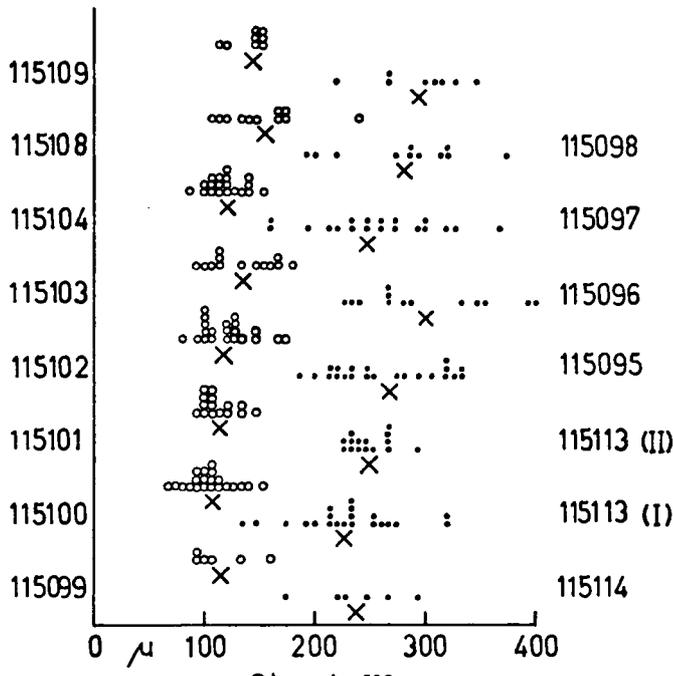


Chart III

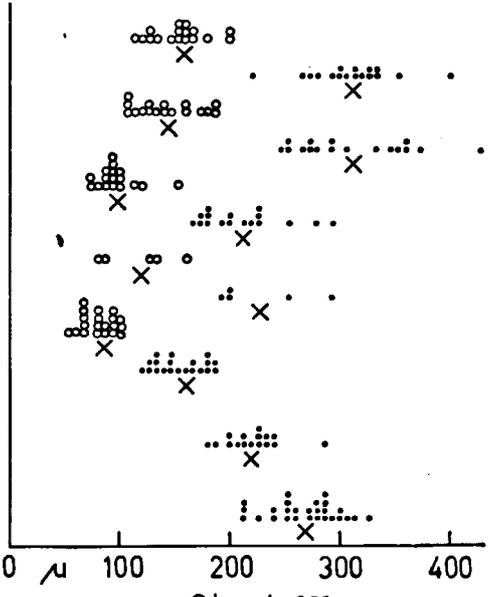


Chart IV

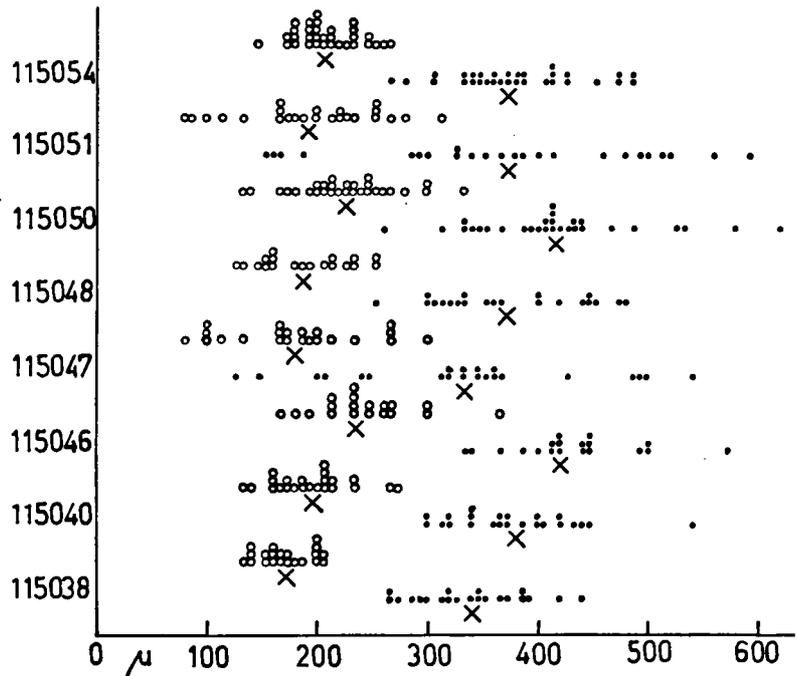
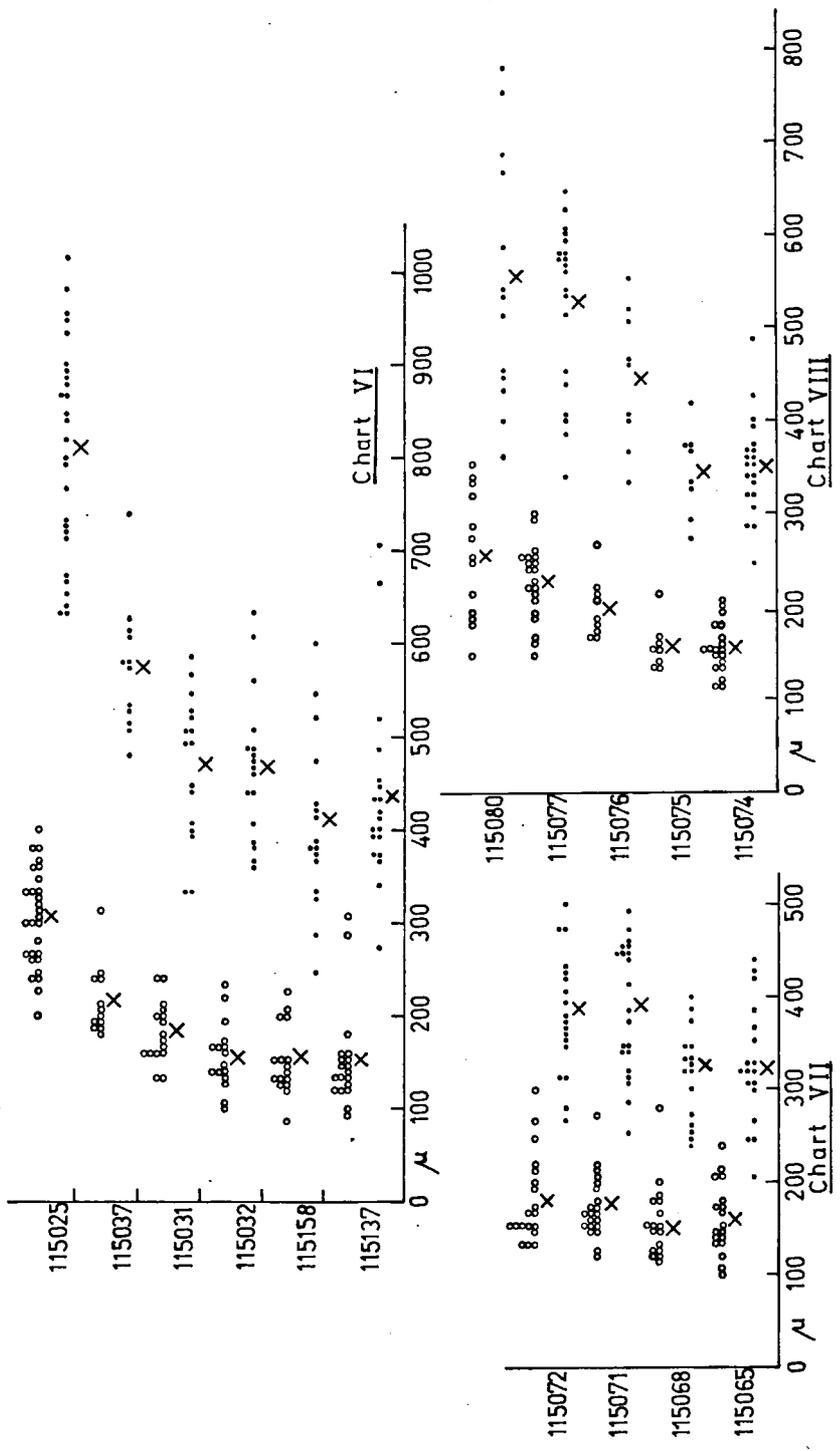


Chart V



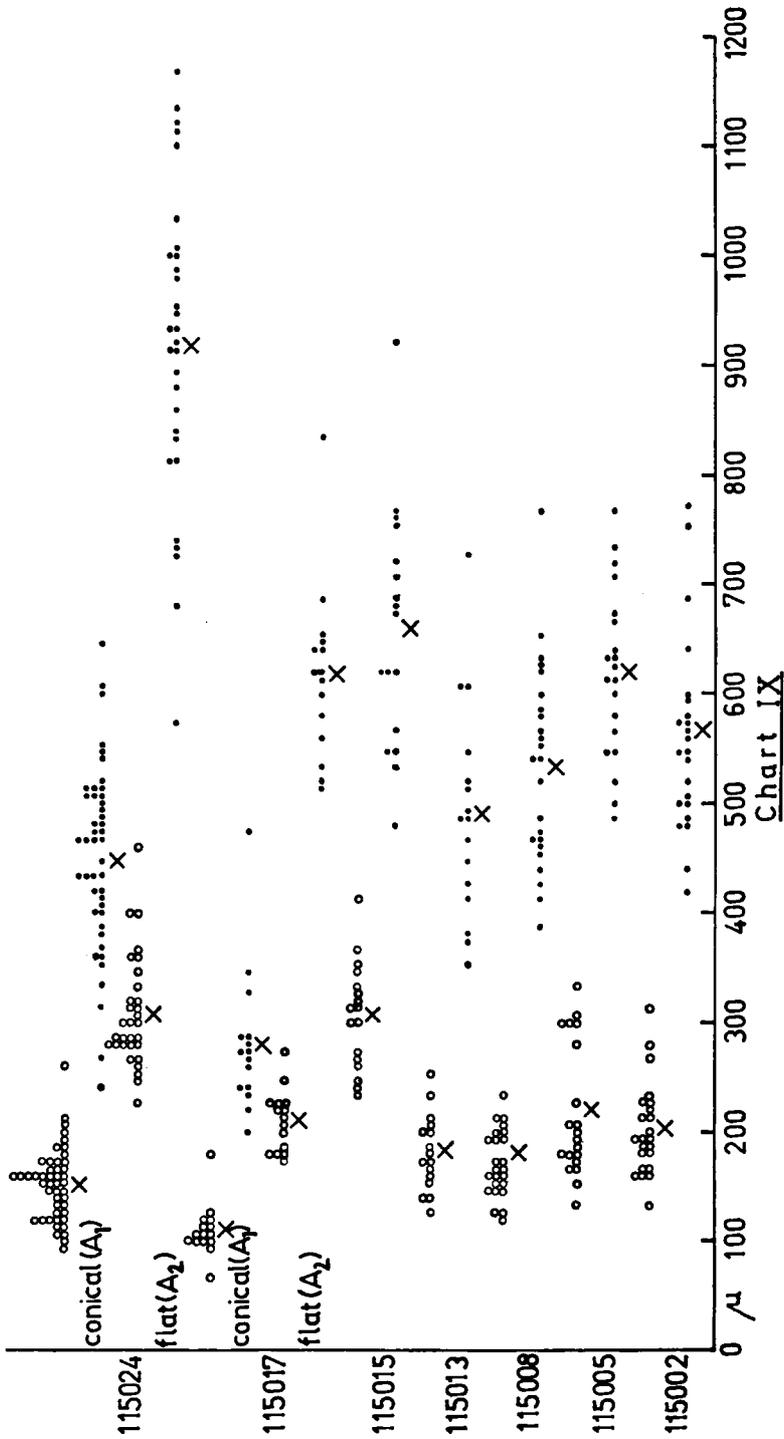
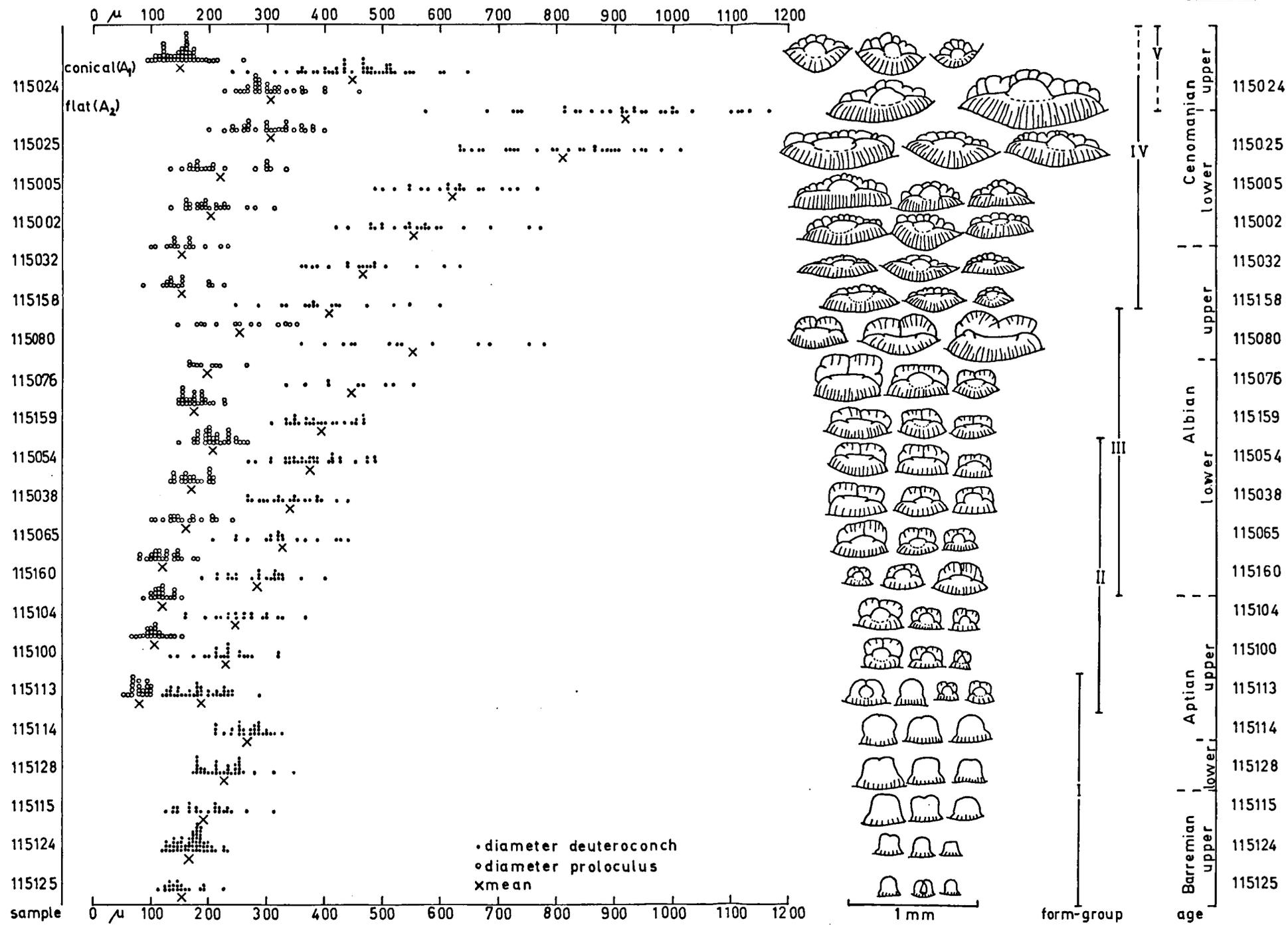


Chart X



SHORT LIST OF SAMPLES

Samples deposited at the Rijksmuseum van Geologie en Mineralogie, Leiden, Holland:

sample	locality:	plates:	page:
8591	Seberoeang, Borneo	VI	197
8115	Perte du Rhône, Ain, France	III	189
40018	West Borneo		197
115001-024	Sierra de Aulet, Huesca, Spain	IX, XI, XVII, XIX, XX, XXI	194
115025-027	Ballon, Sarthe, France	XVII, XVIII	188, 189
115028	Las Barrietas, Vizcaya, Spain	III	196
115029, 030	S of Pont de Suert, Lérida, Spain	VIII, IX	191
115031, 032	W of Orgaña, Huesca, Spain	XVII, XXI	191
115033, 034	NNW of Pobra de Segur, Lérida, Spain	X	191
115035	Pallerol, Huesca, Spain	X, XXII	191
115036	WNW of Pallerol, Huesca, Spain	X	191
115037	N of Santorens, Huesca, Spain	XVII, XXI	194
115038-057	W of Orgaña, Lérida, Spain	XI, XIII, XIV, XV, XXI	191
115058-061	Arredondo, Santander, Spain	IX, XXI, XXII	196
115062-084	Puerto de Las Alisas, Santander, Spain	XI, XII, XXI	194
115085	W of Orgaña, Lérida, Spain		191
115086	Irrawaddy River, Birma.		197
115087	SE of Caudiès de Fenouillet, Pyr. or., France		191
115088	S of St.-Paul-de-Fenouillet, Pyr. or., France	X	191
115089-114	Montagne de La Clape, Aude, France	VII, VIII, XXI	189, 191
115115-120	W of Villard de Lans, Isère, France	III, XXIII	189
115121	E of Annecy, Hte. Savoie, France	I	189
115122-124	Lugos, Aquitaine Basin, France	I, II, IV, V	188
115125	Sanguinet, Aquitaine Basin, France	I	188
115126	S of Valmaseda, Vizcaya, Spain	XI	196
115127-129	St. Magne, Aquitaine Basin, France	VI	188
115130	Le Puch, Aquitaine Basin, France	VI	188
115131	El Helechal, Trujillo State, Venezuela		198
115132	Hood Springs Quad., Texas, U.S.A.		198
115133, 134	St. Paul en Born, Aquitaine Basin, France	VIII	188
115135	Grant Cty., New Mexico, U.S.A.		198
115136	Lasseube, Basses-Pyr., France	XVIII	188
115137	W of Hölzelsau, Bavaria, Germany	IX, XI, XXI	196
115138	Tennbodenbach, Bavaria, Germany		196
115139	Rosz und Buchstein, Bavaria, Germany		196
115140	Lichtenstättgraben, Bavaria, Germany		196
115141	W of Weesen, St. Gallen, Switzerland		196
115142	Voreppe, Isère, France	I	189
115143	Montagne de La Clape, Aude, France		191
115144	Bakony Mts, Hungary	XVIII	196
115145	Zirc, Bakony Mts., Hungary	IX	196
115146	Sta. Maria La Foca, nr. Sarno, Italy	VIII	196
115147	Punte Orlando, nr. Naples, Italy	VIII	196
115148	Djebel Serdj, Tunisia		197
115149	Sidi Rhgis, Algeria	VIII	197
115150	Mas de Ammurio, Alava, Spain		194
115151	Dos Hermanas, Guipúzcoa, Spain		194
115152	Sabrón, Alava, Spain		194
115153	Cala Vadell, Ibiza, Spain		194
115154	SW Infra, Alava, Spain	XVIII	194

sample:	locality:	plates:	page:
115155	Gulina, Navarra, Spain	XXII	194
115156	Puerto de Las Alisas, Santander, Spain		194
115157	Cacais, Portugal	X	196
115158	N of Cranes Mill, Comal Cty., Texas, U.S.A.	XVI	198
115159	Comal Cty., Texas, U.S.A.	XVI, XXI	198
115160	W of Dripping Springs, Texas, U.S.A.	XVI	198
115161	N of Cranes Mill, Comal Cty., Texas, U.S.A.	XVI	198
115162	N of Mal Paso, Michoacán, Mexico	XI, XVI	198
115163	Rio Punceres, E Venezuela	XVI	198
115164-165	Mt. Barker, nr. Austin, Texas, U.S.A.	XXIII	198
115166	Dukhan no 2 Well, Qatar Peninsula, Arabia	I	197
115167	Borehole Heletz, Israel	I	197
115168	Grant Cty., New Mexico, U.S.A.		198
115169	Presidio Cty., Texas, U.S.A.		198
115170	Grant Cty., New Mexico, U.S.A.		198
115171	Dukhan no 1 Well, Qatar Peninsula, Arabia	XVII	197
115172	Mdereidj, nr. Beirut, Lebanon	VIII	197
115173	Wady N'Gara, Jabal, Syria	I	197
115174	Grant Cty., New Mexico, U.S.A.		198
115175	E of Beirut, Lebanon		197
115176	Puerto de Las Alisas, Santander, Spain		194

Samples from the British Museum:

P43138	Selang river, West Serawak, British Borneo	IX	197
P43429	Duncombe Farm, E of Sidmouth, England	XVII	197
P45080	Khamir, S-Iran		197
P45084	Pirazeh Stream, Kuh-i-khumi, SW-Iran	VIII	197

Samples from the Muséum d'Histoire Naturelle, Genève, Switzerland:

Sectioned specimen from Ballon, Sarthe, France	XVIII	189
Sample from Simiane, N of Marseille, France	VIII	189
Sample from La Presta, Val Travers, Switzerland	I	196
Sample from the Perte du Rhône, France	I	189

Samples from the Institut Dolomieu, Grenoble, France:

Sample from W of Bourg-St.-Andéol, Ardèche, France	I	189
Sample from Villadelloges, Ibiza, Spain	VIII	194

Sample from the Min.-Geol. Inst., University of Utrecht, Holland:

Pa 192/1935 SW of Campvey, Ibiza, Spain		194
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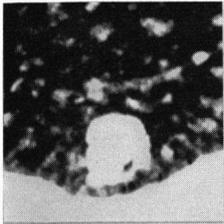
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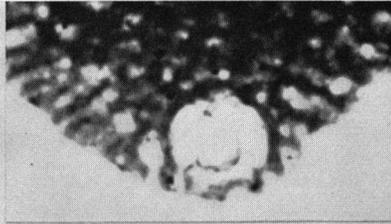
PLATES

PLATE I

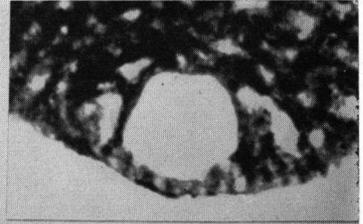
- Fig. 1 Sample 115125, slide 44. Axial section, 100 × .
- Fig. 2 Sample 115125, slide 1. Axial section, 100 × .
- Fig. 3 Sample 115125, slide 21. Axial section, 100 × .
- Fig. 4 Sample 115123, slide 1. Horizontal section through the embryonic apparatus, showing the lobes of the epi-embryonic chambers and the first set of chamber passages around them, 100 × .
- Fig. 5 Sample 115123, slide 20. Axial section through a pair of twins, 100 × .
- Fig. 6 Sample 115123, slide 35. Horizontal section through the embryonic apparatus, 100 × .
- Fig. 7 Sample 115123, slide 25. Axial section, 100 × .
- Fig. 8 Sample from La Presta, Switzerland (coll. Mus. Genève), slide 1. Axial section, 100 × .
- Fig. 9 Sample from the Perte du Rhône, Ain, France (coll. Mus. Genève), type locality of *O. lenticularis* (Blum.); slide 3. Axial section, 100 × .
- Fig. 10 Sample 115167, slide 1. Axial section, 150 × .
- Fig. 11 Sample 115166, slide 3. Axial section showing the well-preserved pseudochitinous walls of proloculus and epi-embryonic chambers, 100 × .
- Fig. 12 Sample 115142, slide 3. Axial section, 100 × .
- Fig. 13 Sample 115142, slide 4. Axial section, 100 × .
- Fig. 14 Sample 115173, slide 2. Axial section, 100 × .
- Fig. 15 Sample from the road between Bourg-St.-Andéol and St.-Remèze, Ardèche, France (coll. Kilian, Inst. Dolomieu, Grenoble); slide 1. Axial section, 100 × .
- Fig. 16 Sample 115121, slide 7. Axial section, 100 × .
- Fig. 17 Sample 115121, slide 3. Axial section, 100 × .



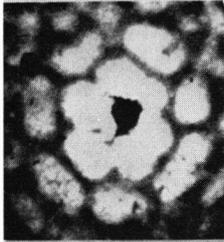
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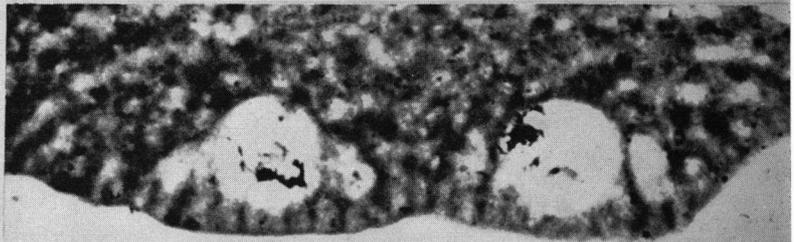
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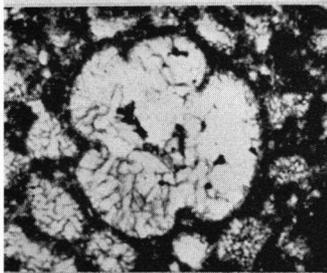
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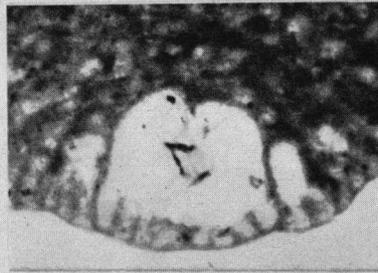
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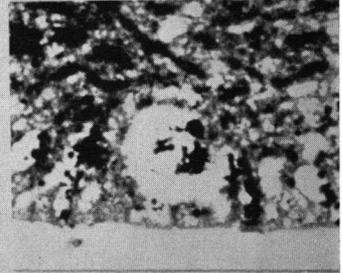
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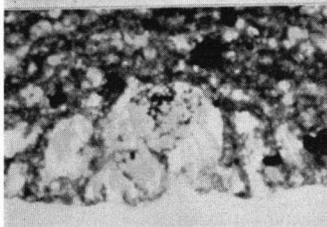
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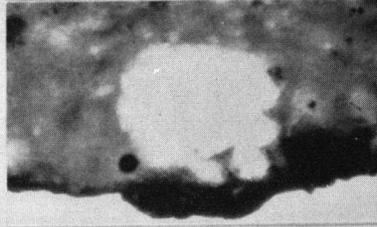
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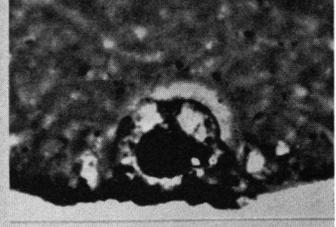
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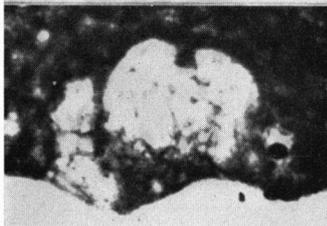
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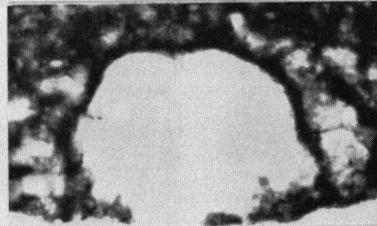
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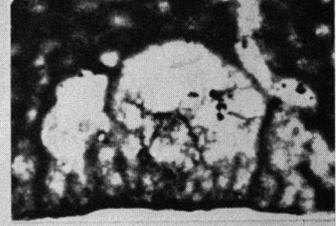
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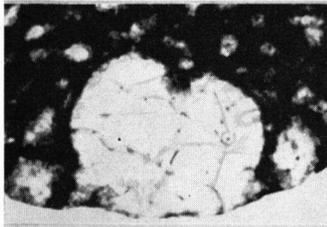
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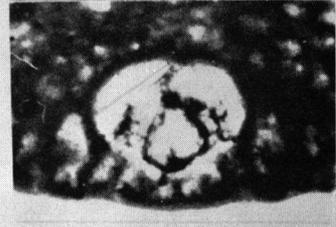
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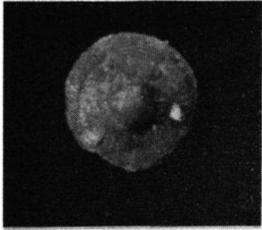


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PLATE II

All figures shown on this plate are of sample 115124.

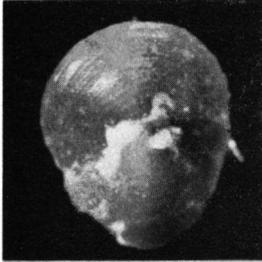
- Fig. 1 Microspheric specimen showing the Phrygian cap-like structure of the nepionic chambers, 20 × .
- Fig. 2 Microspheric specimen, 20 × .
- Fig. 3 Saddle-shaped twinned specimen, 20 × .
- Fig. 4 Horizontal section through the embryonic apparatus, with the passages of the first main chamber around it, slide 7, 100 × .
- Fig. 5 Slide 53. Horizontal section through a young specimen, showing the marginal, radial and reticulate zones, 50 × .
- Fig. 6 Slide 76. Axial section through a pair of twins which have grown together with part of their deuterocoenochs. The deuterocoenochs were visible at the outside of the test as a narrow elongate embryonic area, 50 × .
- Fig. 7 Slide 75. Axial sections through a pair of twins which have grown together with their deuterocoenochs. No embryonic area was visible at the outside of the test which resembled the test shown in fig. 3. On each side of each embryonic apparatus the first set of chamber passages can be seen distinctly. To the left, part of the test, just inside the marginal zone, has been dissolved, probably during fossilisation, 50 × .
- Fig. 8 Slide 80. Axial section through a pair of twins which have grown together with part of their deuterocoenochs, 100 × .
- Fig. 9 Slide 5. Horizontal section through the embryonic apparatus, showing the lobed epi-embryonic chambers and the passages of the first main chamber around them, 100 × .
- Fig. 10 Slide 1. Axial section, 100 × .
- Fig. 11 Slide 78. Axial section through a pair of twins, 75 × .
- Fig. 12 Slide 72. Axial section through a pair of twins, 75 × .
- Fig. 13 Slide 72. Axial section, 100 × .
- Fig. 14 Slide 16. Axial section, 100 × .
- Fig. 15 Slide 17. Axial section, 100 × .



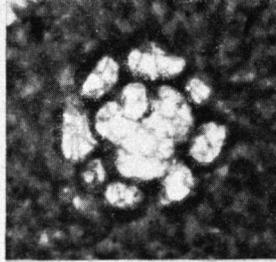
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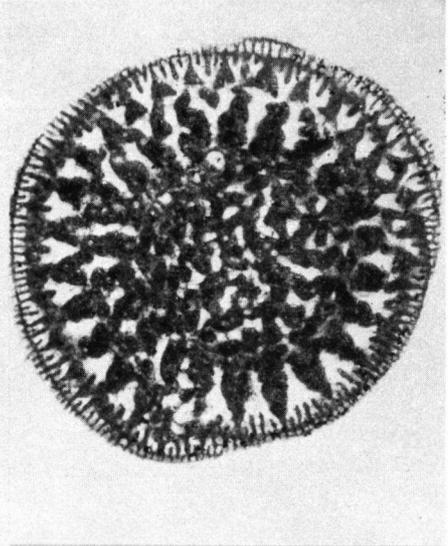
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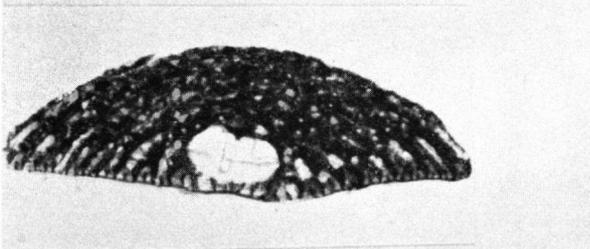
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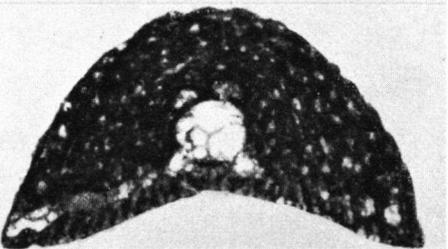
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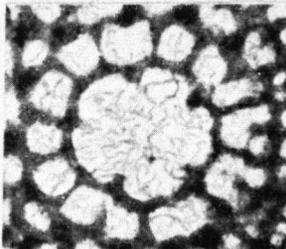
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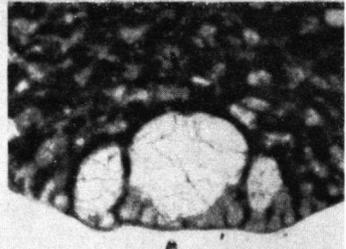
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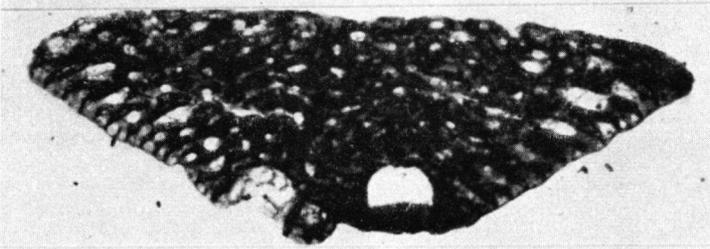
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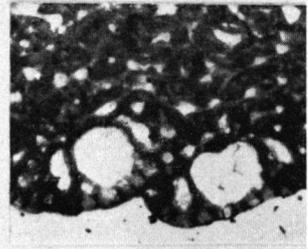
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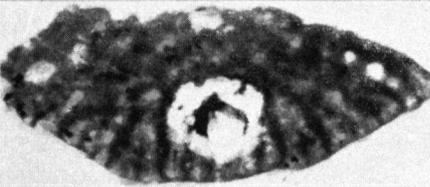
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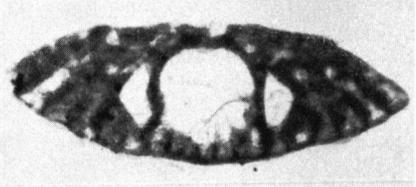
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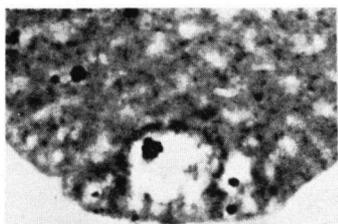
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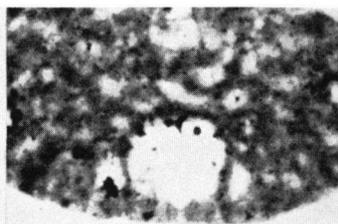
15

PLATE III

- Fig. 1 Sample 115115, slide 27. Axial section, 100 × .
- Fig. 2 Sample 115115, slide 29. Axial section, 100 × .
- Fig. 3 Sample 115115, slide 28. Axial section, 100 × .
- Fig. 4 Sample 115120, slide 8. Axial section, showing faintly the spherical proloculus which has been filled with slightly darker material than the rest of the test. Dark field illumination, 100 × .
- Fig. 5 Sample 115120, slide 7. Axial section. Embryonic apparatus filled with dark green material. Dark field illum., 100 × .
- Fig. 6 Sample 115115, slide 3. Axial section, 100 × .
- Fig. 7 Sample 115117, slide 32. Axial section, 100 × .
- Fig. 8 Sample 115117, slide 12. Axial section, 100 × .
- Fig. 9 Sample 115117, slide 8. Axial section, 100 × .
- Fig. 10 Sample 115116, slide 2. Axial section, 100 × .
- Fig. 11 Sample 115028, slide 2. Axial section, 100 × .
- Fig. 12 Sample 115028, slide 1. Horizontal section through the embryonic apparatus, with the lobed epi-embryonic chambers and the passages of the first main chamber around them, 100 × .
- Fig. 13 Sample 8115, slide 6. Sub-axial section, showing the chamber passages in cross-section and the stolons which interconnect them. Filled with dark brown material, 100 × .
- Fig. 14 Sample 8115, slide 1. Axial section, showing the filled chamber passages and stolons. Dark field illum., 75 × .
- Fig. 15 Sample 8115, slide 9. Oblique section showing the filled chamber passages and stolons. Dark field illumination, 50 × .



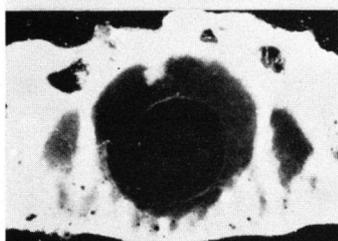
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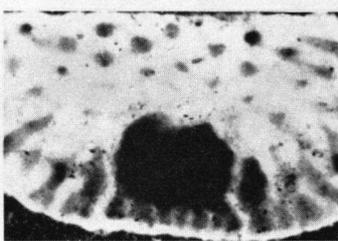
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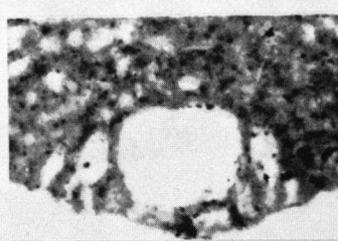
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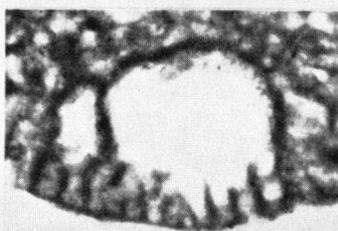
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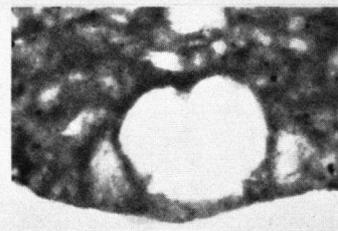
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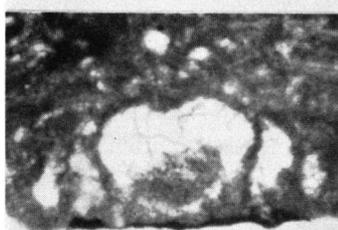
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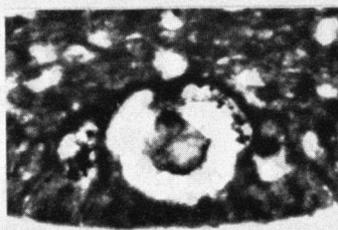
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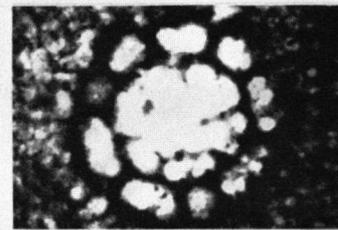
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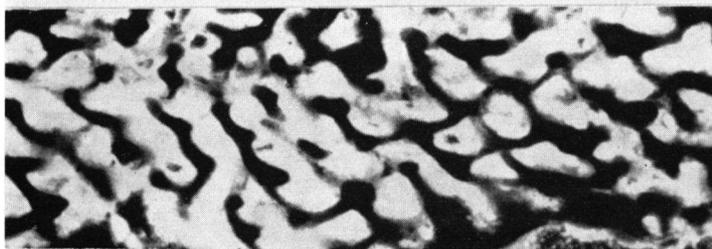
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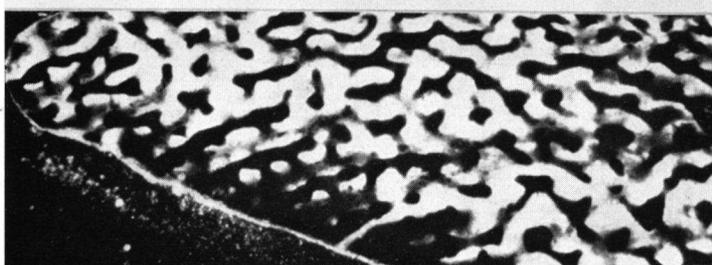
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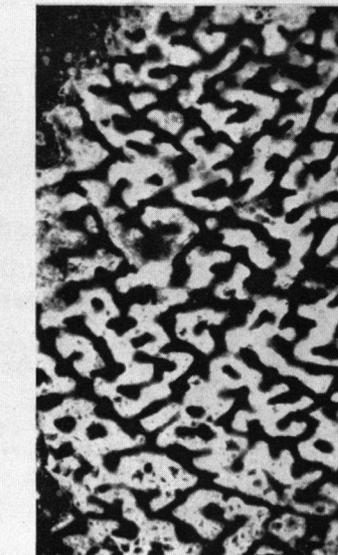
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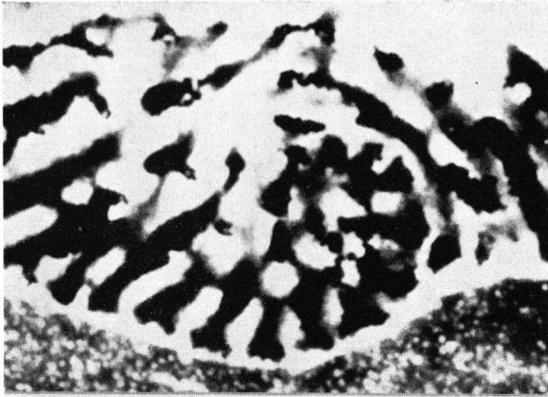


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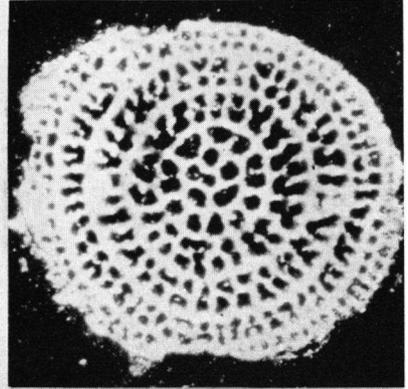
PLATE IV

All specimens shown on this plate are of sample 115122.

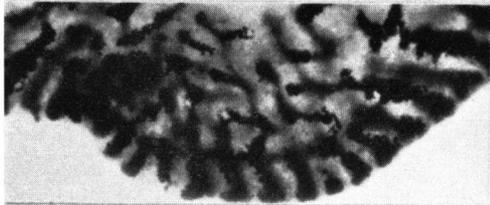
- Fig. 1 Slide 35. Axial section through the microspheric nepiont of a specimen filled with pyrite. The section lies in the plane of symmetry of the last whorl. Dark field illum., 200 \times .
- Fig. 2 Slide 5. Horizontal section through the deuteroconch of a megalospheric specimen, showing 18 cellules, which form the embryonic area. Filled with pyrite, dark field illum., 100 \times .
- Fig. 3 Slide 94. Axial section through a microspheric specimen, filled with pyrite, 100 \times .
- Fig. 4 Slide 100. Horizontal section through a pyrite-filled microspheric specimen, probably just above the proloculus. It can be seen clearly, that the initial whorls of the strepto-spiral do not lie in the plane of symmetry of the last whorl which lies in the SW-NE diagonal of the figure, at right angles to the plane of the photograph, 200 \times .
- Fig. 5 Slide 6. Axial section through a microspheric specimen, 150 \times .
- Fig. 6 Slide 92. Axial section through a microspheric specimen, partly filled with pyrite, 150 \times .
- Fig. 7 Slide 7. Horizontal section through the megalospheric embryonic apparatus, just above the partitions of the deuteroconch. In the middle of the embryonic apparatus the foramen of the proloculus in the pseudochitinous wall can be seen, 75 \times .
- Fig. 8 Slide 15. Axial section, incompletely filled with pyrite. The proloculus contains less pyrite than the rest of the embryonic apparatus, 150 \times .
- Fig. 9 Slide 40. Axial section, 75 \times .
- Fig. 10 Slide 82. Axial section through a pair of twins which have grown together with the deuteroconchs, 100 \times .
- Fig. 11 Slide 86. Axial section through a pyrite-filled specimen. In the wall of the embryonic apparatus the foramina to the first main chamber can be seen at both sides, 150 \times .
- Fig. 12 Slide 83. Axial section through a very small megalospheric specimen, 100 \times .
- Fig. 13 Slide 29. Axial section through a pyrite-filled specimen. Dark field illum., 100 \times .



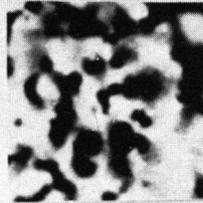
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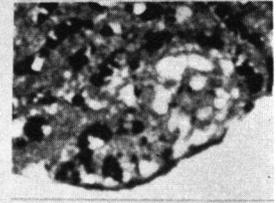
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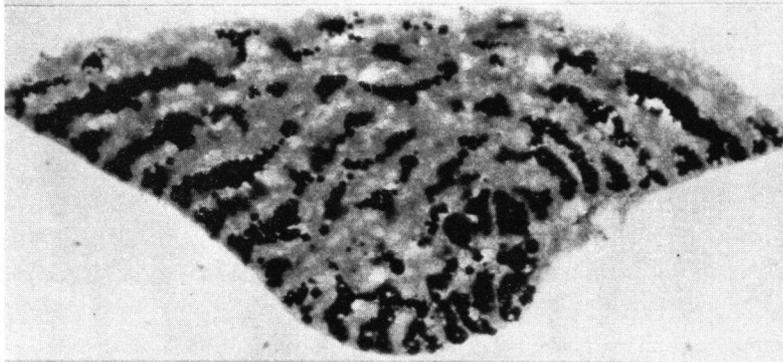
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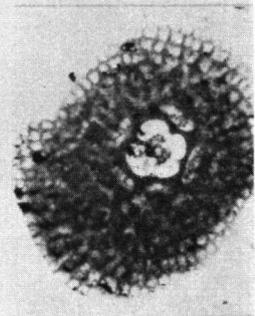
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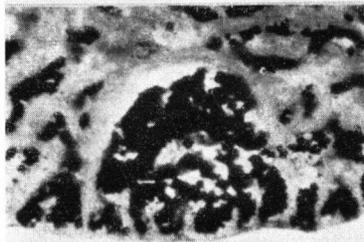
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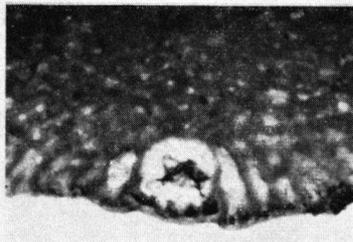
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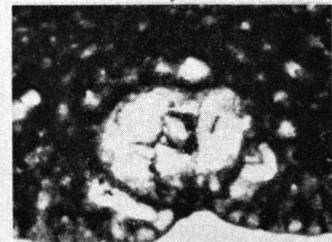
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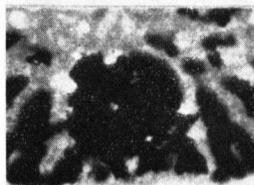
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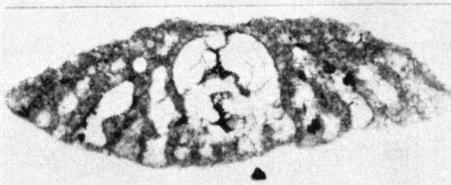
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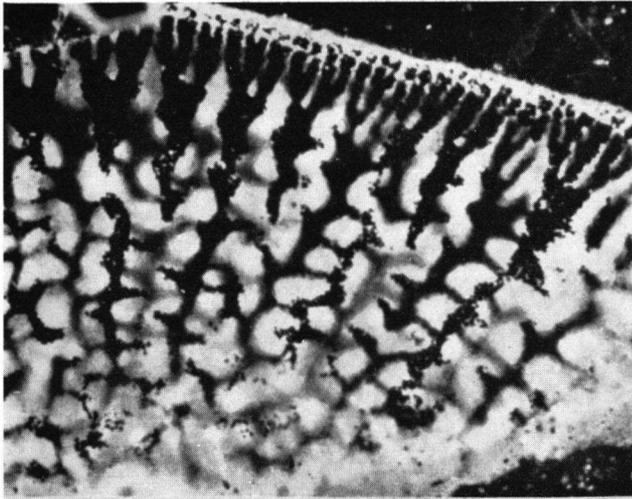


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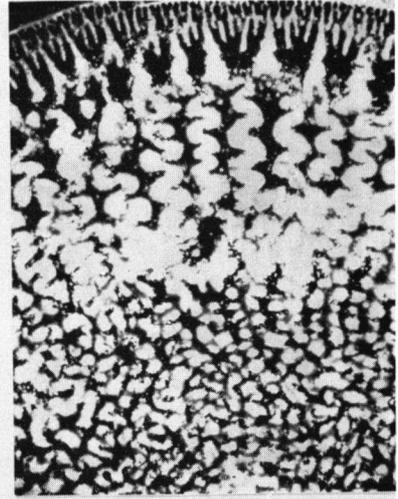
PLATE V

All figures on this plate show pyrite-filled specimens of sample 115122 and all except fig. 8 have been photographed using dark field illumination.

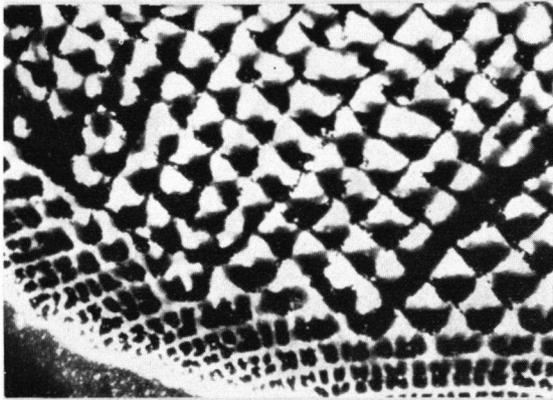
- Fig. 1 Slide 3. Oblique section parallel to the radial zone, showing the marginal zone and the radial passages with the stolons which interconnect them. It can be observed, that the zig-zagging is caused by the stolons, 100 ×.
- Fig. 2 Slide 85. Horizontal section, showing from above to below the marginal zone, the radial zone, and the reticulate zone, 50 ×.
- Fig. 3 Slide 58. Oblique tangential section, about at right angles to the chamber passages, showing the round sections of the passages and the stolons which interconnect them. The pattern of these stolons has given rise to the assumption, that the "main partitions" have a triangular cross-section, 75 ×.
- Fig. 4 Slide 1. Oblique section, about parallel to the radial zone. Enlarged portion of fig. 7, 100 ×.
- Fig. 5 Slide 4. Oblique section parallel to the radial zone, 100 ×.
- Fig. 6 Slide 80. Oblique section about parallel to the radial zone, 75 ×.
- Fig. 7 Slide 1. Oblique section, about parallel to the radial zone, 50 ×.
- Fig. 8 Slide 15. Horizontal section through the embryonic apparatus, 75 ×.



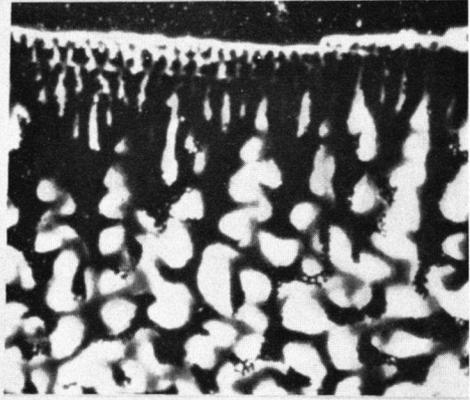
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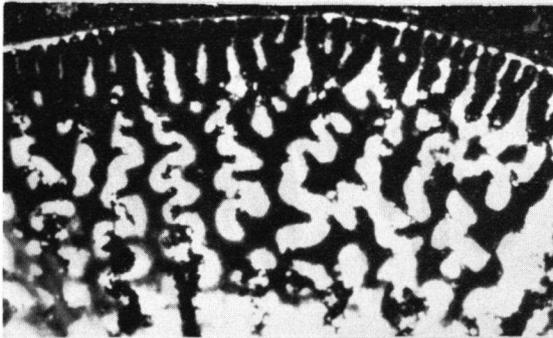
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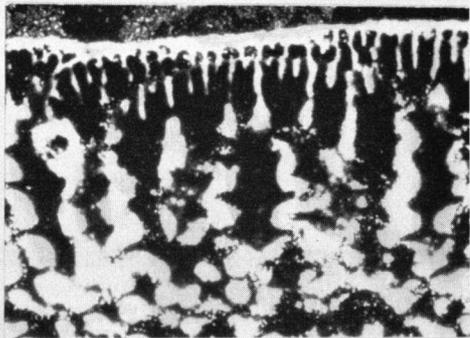
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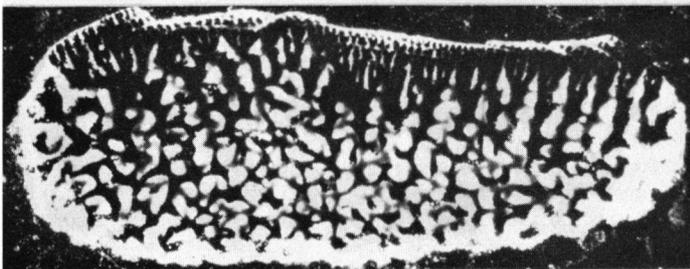
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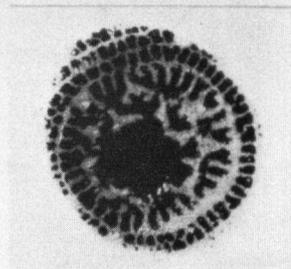
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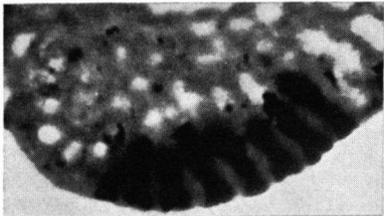
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8

PLATE VI

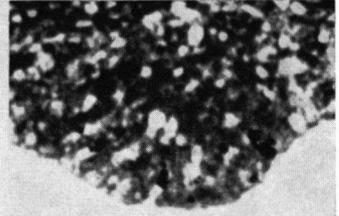
- Fig. 1 Sample 115130, slide 1. Axial section through a microspheric specimen, partly filled with pyrite, 150 × .
- Fig. 2 Sample 115128, slide 64. Axial section through a very small microspheric specimen, 100 × .
- Fig. 3 Sample 115128, slide 37. Axial section through a microspheric specimen, 100 × .
- Fig. 4 Sample 115130, slide 6. Axial section through a microspheric specimen, 150 × .
- Fig. 5 Sample 115128, slide 44. Horizontal section through a megalospheric embryonic apparatus, 100 × .
- Fig. 6 Sample 115128, slide 32. Horizontal section through a megalospheric embryonic apparatus. Each of the epi-embryonic chambers contains a crumpled brownish mass, which is clearly separated from the mass in the proloculus, 100 × .
- Fig. 7 Sample 5891, slide 1. Axial section, 150 × .
- Fig. 8 Sample 115127, slide 6. Axial section, 100 × .
- Fig. 9 Sample 115127, slide 13. Axial section, 100 × .
- Fig. 10 Sample 115129, slide 12. Axial section, 100 × .
- Fig. 11 Sample 115129, slide 5. Axial section, 100 × .
- Fig. 12 Sample 115129, slide 6. Axial section, showing the crumpled mass of the proloculus inside the embryonic apparatus, 100 × .
- Fig. 13 Sample 115128, slide 1. Oblique section of a specimen with dark brown filling, showing the marginal zone, the very short radial zone and part of the reticulate zone, 100 × .
- Fig. 14 Sample 115127, slide 8. Axial section, 100 × .
- Fig. 15 Sample 115128, slide 15. Axial section, 100 × .
- Fig. 16 Sample 115128, slide 7. Axial section through a small specimen, 100 × .
- Fig. 17 Sample 115128, slide 6. Axial section of a small specimen, 100 × .



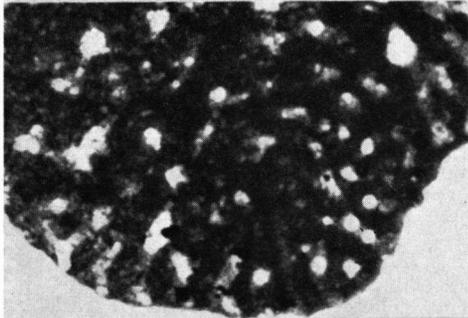
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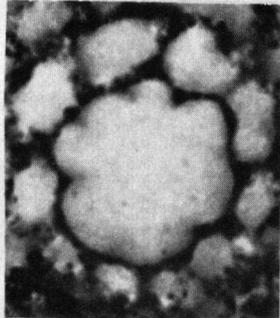
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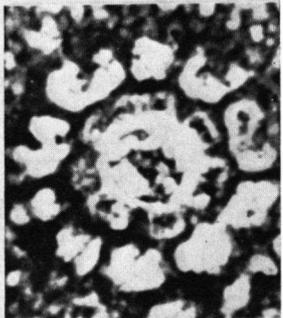
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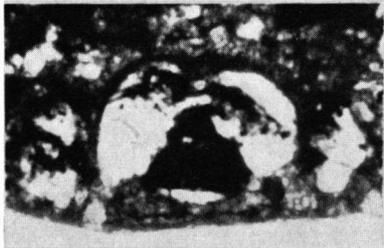
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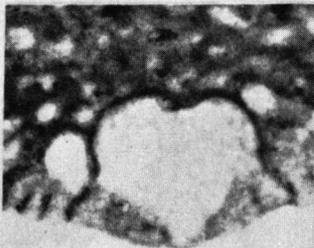
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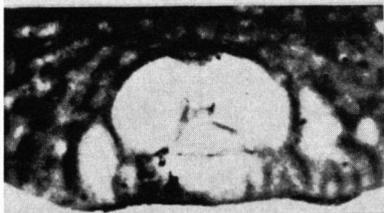
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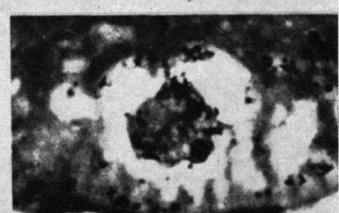
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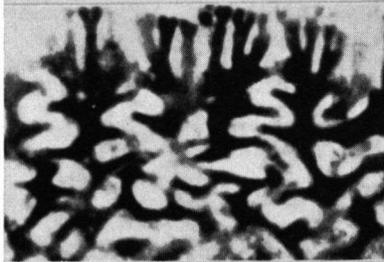
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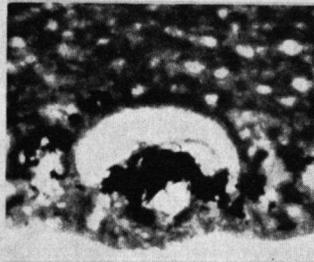
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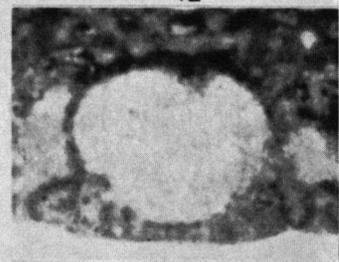
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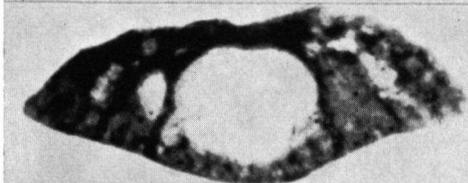
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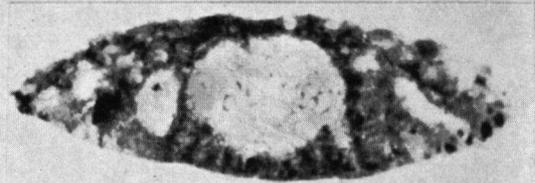
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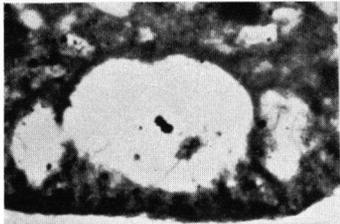
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PLATE VII

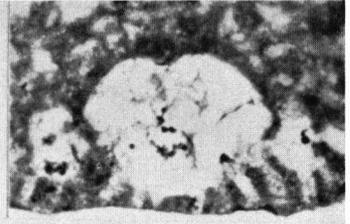
- Fig. 1 Sample 115114, slide 19. Axial section, 100 × .
- Fig. 2 Sample 115114, slide 34. Axial section, 100 × .
- Fig. 3 Sample 115114, slide 20. Axial section, 100 × .
- Fig. 4 Sample 115114, slide 14. Axial section, 100 × .
- Fig. 5 Sample 115114, slide 17. Axial section, 100 × .
- Fig. 6 Sample 115114, slide 31. Axial section, 100 × .
- Fig. 7 Sample 115113, slide 12. Axial section, 75 × .
- Fig. 8 Sample 115113, slide 33. Axial section, 150 × .
- Fig. 9 Sample 115113, slide 13. Axial section, 150 × .
- Fig. 10 Sample 115113, slide 30. Axial section, 150 × .
- Fig. 11 Sample 115113, slide 43. Axial section, 150 × .
- Fig. 12 Sample 115113, slide 34. Axial section, 150 × .
- Fig. 13 Sample 115113, slide 1. Axial section, 150 × .
- Fig. 14 Sample 115113, slide 45. Axial section, 150 × .
- Fig. 15 Sample 115113, slide 4. Axial section, 100 × .
- Fig. 16 Sample 115090, slide 3. Axial section, 75 × .
- Fig. 17 Sample 115095, slide 7. Axial section, 100 × .
- Fig. 18 Sample 115096, slide 2. Axial section, 100 × .



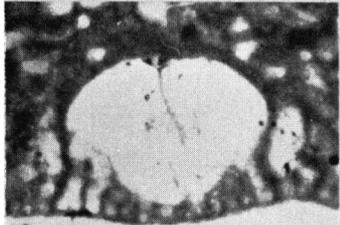
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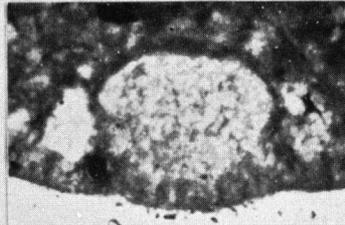
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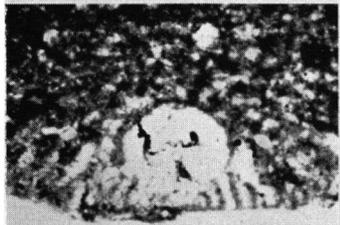
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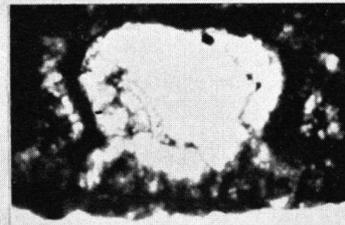
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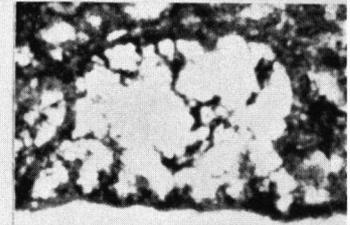
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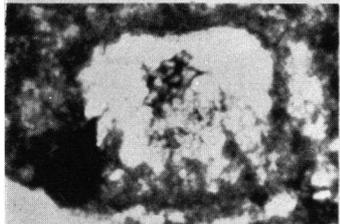
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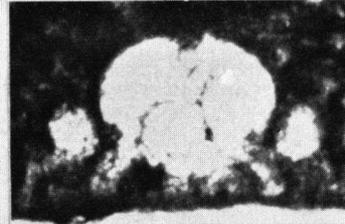
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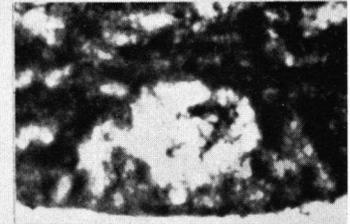
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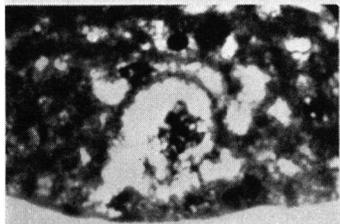
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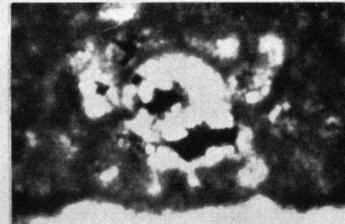
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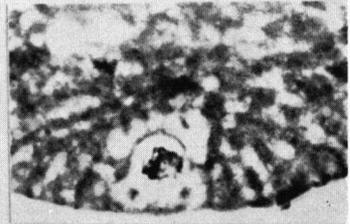
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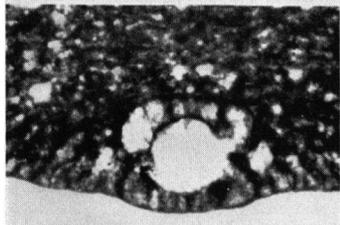
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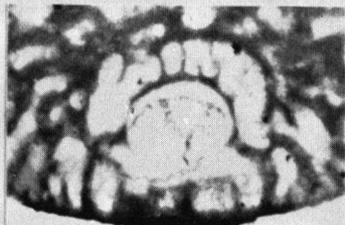
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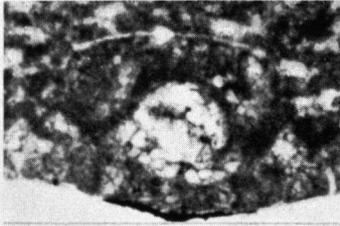
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PLATE VIII

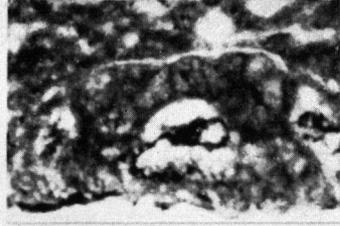
- Fig. 1 Sample 115098, slide 21. Axial section, 100 × .
- Fig. 2 Sample 115100, slide 20. Axial section, showing a thin hyaline layer covering the top of the embryonic apparatus, 100 × .
- Fig. 3 Sample 115102, slide 7. Axial section, showing a thin hyaline layer on top of the embryonic apparatus, 100 × .
- Fig. 4 Sample 115103, slide 11. Axial section, 100 × .
- Fig. 5 Sample 115133, slide 4. Axial section, 100 × .
- Fig. 6 Sample 115030, slide 1. Axial section, 100 × .
- Fig. 7 Sample from Simiane, near Marseille, France (coll. Mus. Genève), slide 1. Axial section, 100 × .
- Fig. 8 Sample 115134, slide 2. Axial section, 50 × .
- Fig. 9 Sample 115133, slide 2. Axial section, 100 × .
- Fig. 10 Sample P 45084, slide P 45086 (coll. British Museum). Axial section, 100 × .
- Fig. 11 Sample P 45084, slide P 45085 (coll. Brit. Mus.). Axial section, 100 × .
- Fig. 12 Sample from Villadelloges, Ibiza, Spain (coll. Fallot, Inst. Dolomieu, Grenoble), slide 3. Axial section, 100 × .
- Fig. 13 Sample 115172, slide 1. Axial section, 150 × .
- Fig. 14 Sample 115172, slide 3. Axial section, 150 × .
- Fig. 15 Sample 115172, slide 2. Axial section, 100 × .
- Fig. 16 Sample 115146, slide 9. Axial section, 100 × .
- Fig. 17 Sample 115149, slide 3. Axial section, 100 × .
- Fig. 18 Sample 115147, slide 5. Axial section, 150 × .



1



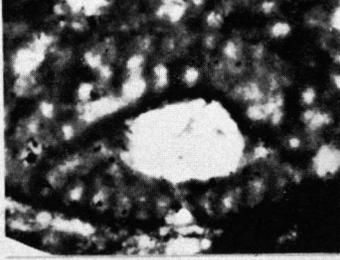
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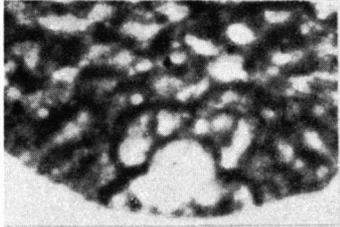
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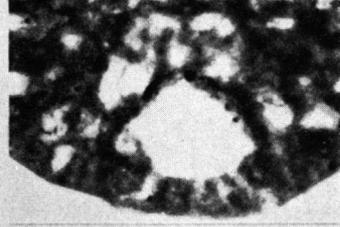
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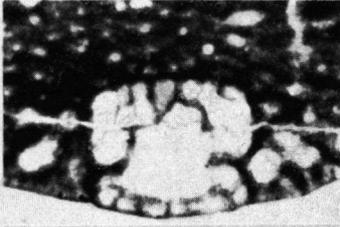
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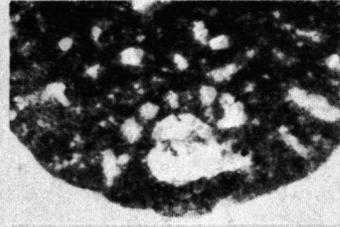
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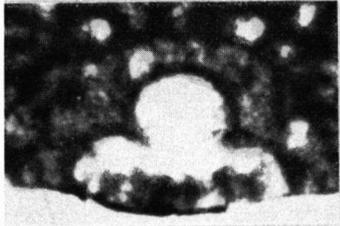
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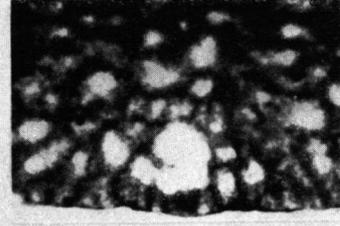
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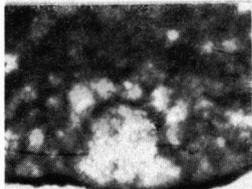
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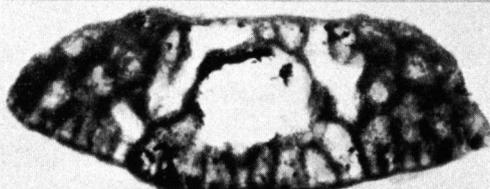
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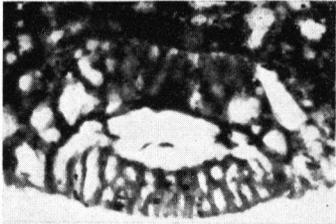
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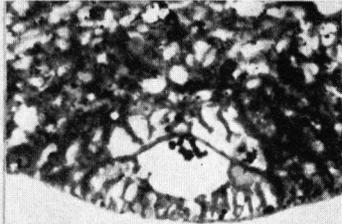
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PLATE IX

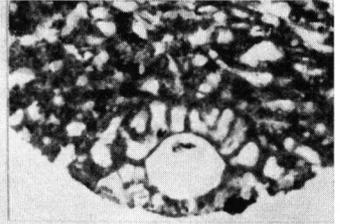
- Fig. 1 Sample 115059, slide 11. Axial section, 75 \times .
- Fig. 2 Sample 115059, slide 8. Axial section, 75 \times .
- Fig. 3 Sample 115059, slide 3. Axial section, 75 \times .
- Fig. 4 Sample 115059, slide 23. Subaxial section through the radial zone, showing the round sections of the radial passages and the stolons which interconnect them. The pattern of these stolons gives the impression, that triangular "main partitions" exist between the chamber passages, 75 \times .
- Fig. 5 Sample 115059, slide 34. Oblique section parallel to the radial zone of a chamber layer, showing from above to below the marginal zone, the radial zone and part of the reticulate zone. When one looks closely, it can be seen, that the zig-zagging of the radial passages is caused by the alternating stolons, 75 \times .
- Fig. 6 Sample P 43138, slide S 2274 (coll. British Museum). Tangential section cut progressively deeper. In the lower right corner the cellules of the marginal zone can be seen; to the left only the vertical main partitions and primary plates are present; this gives rise to an elongate cross-section; at the top the round and triangular sections of the radial passages can be seen, together with their stolons, 50 \times .
- Fig. 7 Sample P 43138, slide S 2274 (coll. British Museum). Calcite eyes in the central complex of a specimen of *Orbitolina*, 150 \times .
- Fig. 8 Sample 115059. Calcite eye in a specimen of *Orbitolina*, 150 \times .
- Fig. 9 Sample 115059. Calcite eyes with nucleus in a specimen of *Orbitolina*, 150 \times .
- Fig. 10 Sample P 43138, slide S 2274 (coll. British Museum). Calcite eye in a specimen of *Orbitolina*, 150 \times .
- Fig. 11 Sample 115029. Calcite eye with a nucleus in a specimen of *Orbitolina*, 150 \times .
- Fig. 12 Sample 115145, slide 1. Axial section, 100 \times .
- Fig. 13 Sample 115145, slide 2. Axial section, 100 \times .
- Fig. 14 Sample 115007. Calcite eyes in a specimen of *Orbitolina*, 100 \times .
- Fig. 15 Sample 115137, slide 36. Axial section, 100 \times .
- Fig. 16 Sample 115137, slide 5. Axial section, 100 \times .
- Fig. 17 Sample 115137, slide 12. Axial section, 100 \times .



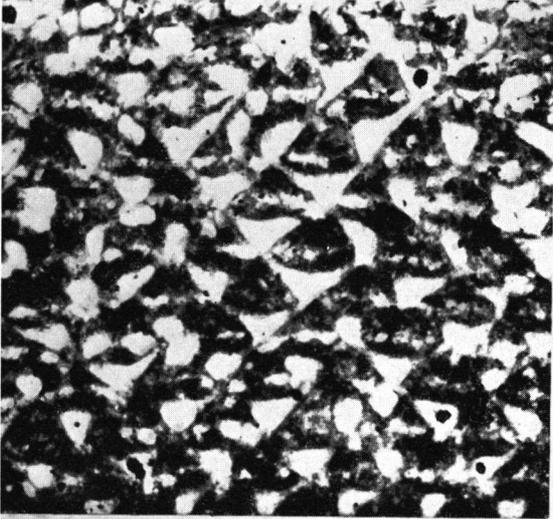
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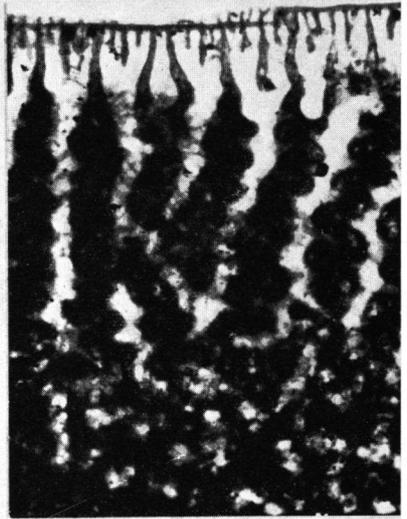
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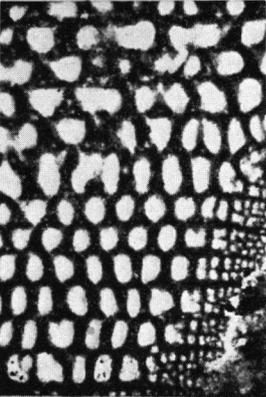
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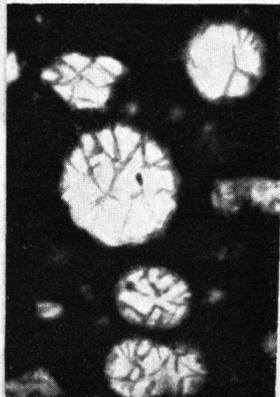
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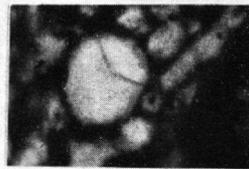
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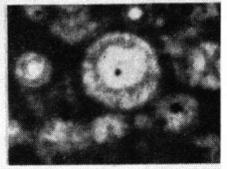
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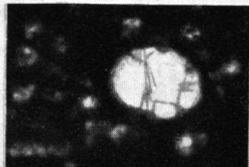
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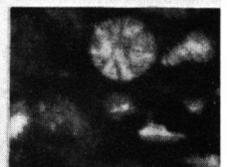
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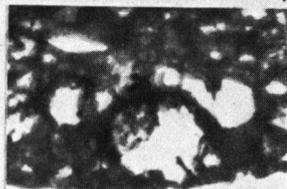
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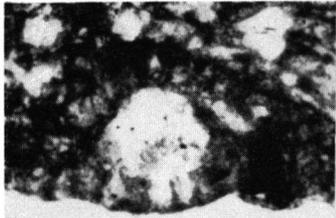
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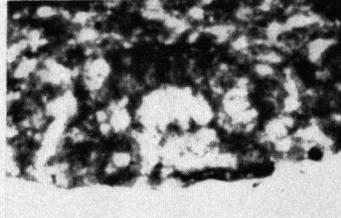
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PLATE X

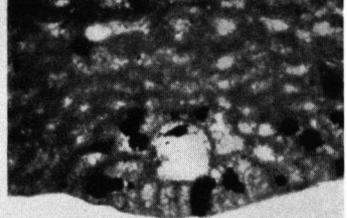
- Fig. 1 Sample 115088, slide 2. Axial section, 100 × .
- Fig. 2 Sample 115088, slide 1. Axial section, 100 × .
- Fig. 3 Sample 115157, slide 4. Axial section, 75 × .
- Fig. 4 Sample 115157, slide 10. Axial section, 75 × .
- Fig. 5 Sample 115033, slide 3. Axial section of a small specimen, 50 × .
- Fig. 6 Sample 115034, slide 2. Axial section of a small specimen, 50 × .
- Fig. 7 Sample 115036. Weathered surface of a specimen, showing the cellules of the marginal zone. Specimen is probably microspheric, 100 × .
- Fig. 8 Sample 115035, slide 5. Horizontal section through the megalospheric embryonic apparatus, 50 × .
- Fig. 9 Sample 115036, slide 4. Axial section, 100 × .
- Fig. 10 Sample 115035, slide 7. Axial section, 100 × .
- Fig. 11 Sample 115035, slide 15. Axial section, 100 × .
- Fig. 12 Sample 115035, slide 24. Axial section, 100 × .
- Fig. 13 Sample 115035, slide 3. Axial section, 100 × .
- Fig. 14 Sample 115035, slide 30. Axial section, 100 × .



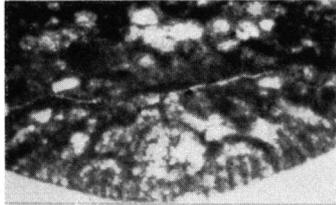
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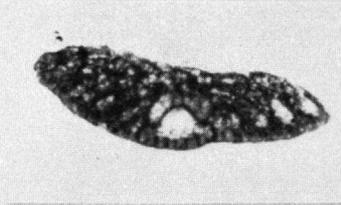
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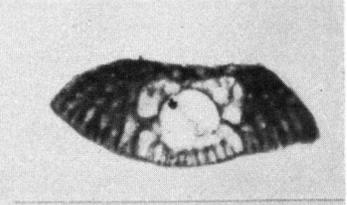
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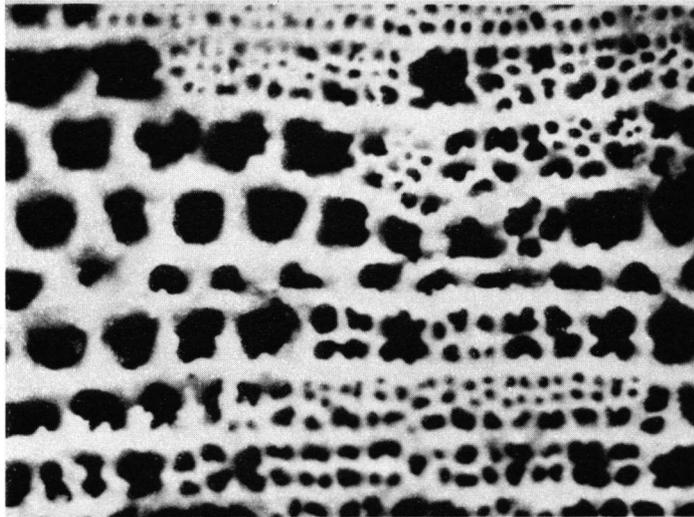
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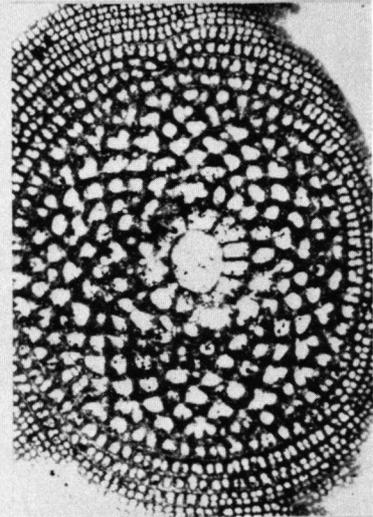
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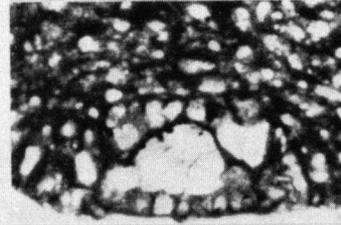
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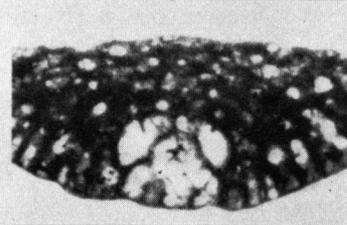
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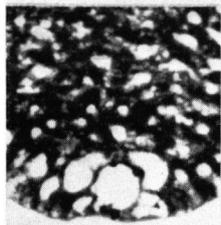
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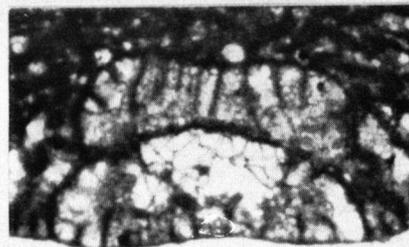
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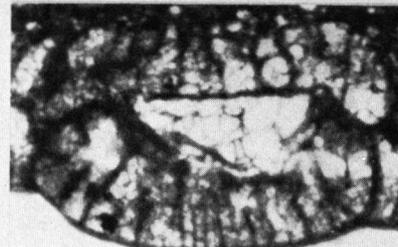
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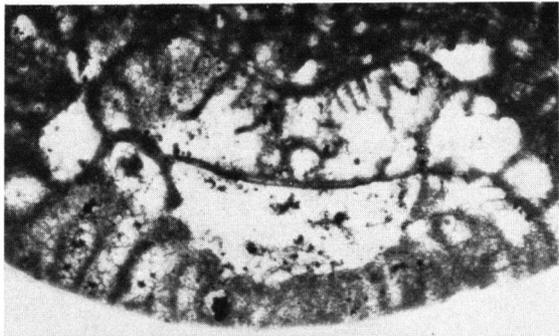
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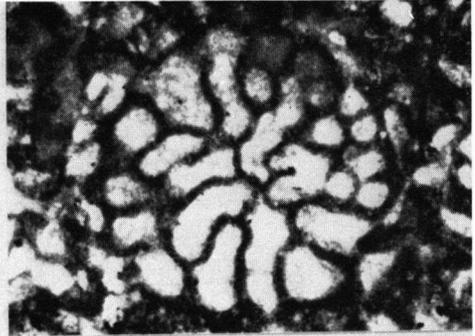
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PLATE XI

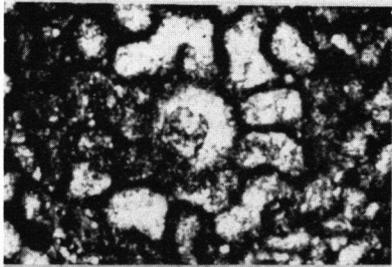
- Fig. 1 Sample 115080, slide 6. Axial section, 100 × .
- Fig. 2 Sample 115065, slide 25. Horizontal section through the epi-embryonic chambers, showing the partitions inside these chambers, 100 × .
- Fig. 3 Sample 115015, slide 31. Horizontal section, showing proloculus and epi-embryonic chambers, 100 × .
- Fig. 4 Sample 115162, slide 7. Axial section, showing a mineral particle around which the test has been built, 50 × .
- Fig. 5 Sample 115137, slide 39. Horizontal section, showing proloculus and epi-embryonic chambers, 100 × .
- Fig. 6 Sample 115065, slide 24. Horizontal section, showing proloculus and epi-embryonic chambers, 100 × .
- Fig. 7 Sample 115050, slide 57. Horizontal section through the epi-embryonic chambers, showing the walls of these chambers and some partitions in them, 100 × .
- Fig. 8 Sample 115050, slide 58. Horizontal section through proloculus and epi-embryonic chambers. Part of the walls of these chambers has disappeared, or did never exist because of a fusing of the chambers, 100 × .
- Fig. 9 Sample 115137, slide 9. Axial section showing abundant coarse quartz grains in reticulate and radial zones, 100 × .
- Fig. 10 Sample 115126, slide 4. Tangential section of a specimen with clear wall material and chamber passages coated with a thin layer of brownish material, showing the radial partitions and the stolons, 100 × .



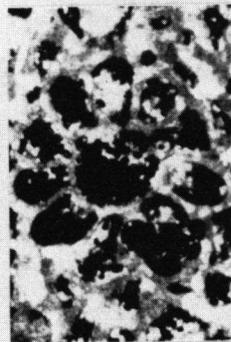
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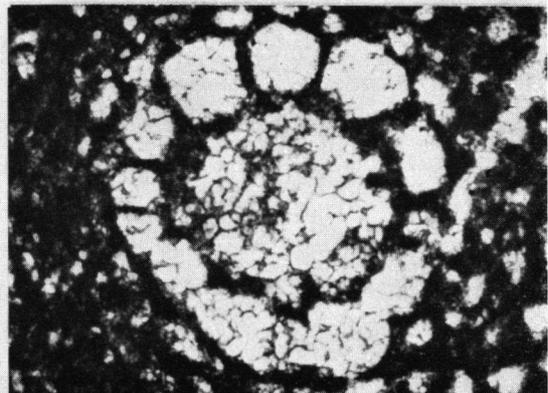
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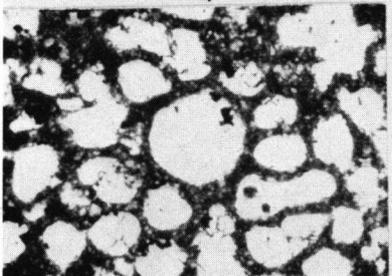
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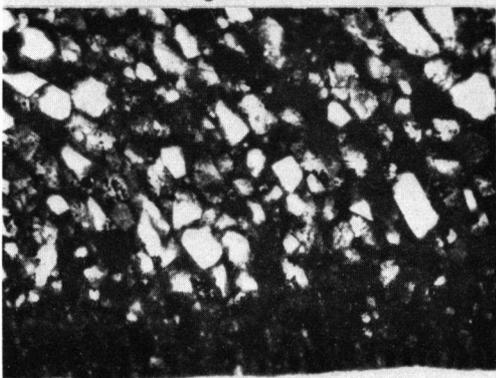
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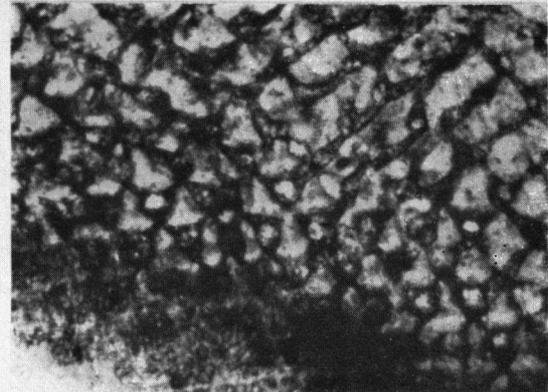
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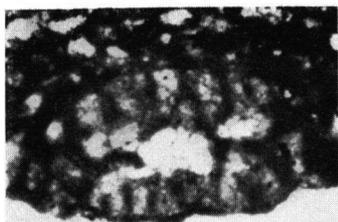
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PLATE XII

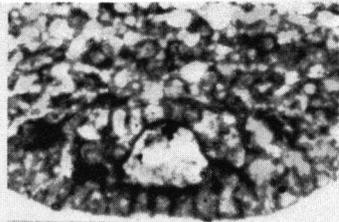
- Fig. 1 Sample 115063, slide 1. Axial section, 150 × .
- Fig. 2 Sample 115065, slide 5. Axial section, 150 × .
- Fig. 3 Sample 115065, slide 13. Axial section, 150 × .
- Fig. 4 Sample 115068, slide 3. Axial section, 150 × .
- Fig. 5 Sample 115071, slide 5. Axial section, 150 × .
- Fig. 6 Sample 115071, slide 3. Axial section, 150 × .
- Fig. 7 Sample 115071, slide 16. Axial section, 75 × .
- Fig. 8 Sample 115072, slide 9. Axial section, 150 × .
- Fig. 9 Sample 115073, slide 3. Axial section, 150 × .
- Fig. 10 Sample 115073, slide 18. Axial section, 150 × .
- Fig. 11 Sample 115074, slide 2. Axial section, 150 × .
- Fig. 12 Sample 115075, slide 4. Axial section, 150 × .
- Fig. 13 Sample 105076, slide 3. Axial section, 150 × .
- Fig. 14 Sample 115076, slide 17. Axial section, 150 × .
- Fig. 15 Sample 115078. Slightly oblique axial section, showing a specimen consisting of only the proloculus, deuteroconch, and epi-embryonic chambers. The epi-embryonic chambers show a cellular structure which is caused by the obliquity of the section, 50 × .
- Fig. 16 Sample 115080, slide 21. Axial section, 100 × .
- Fig. 17 Sample 115080, slide 14. Axial section, 100 × .



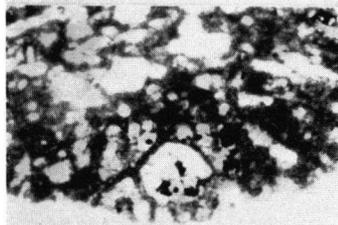
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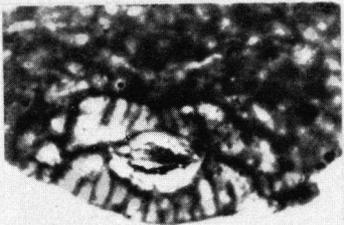
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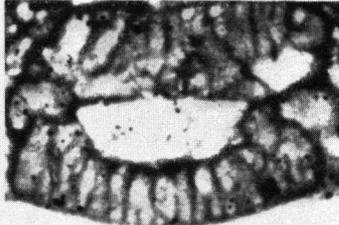
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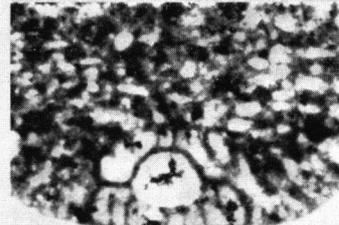
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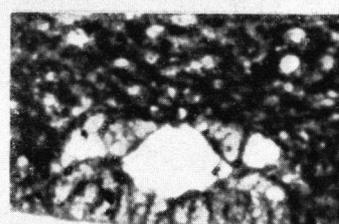
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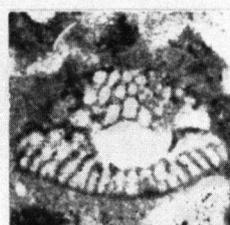
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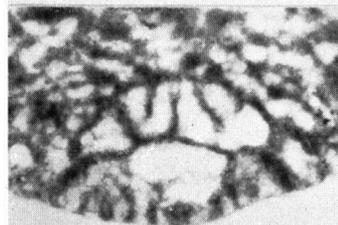
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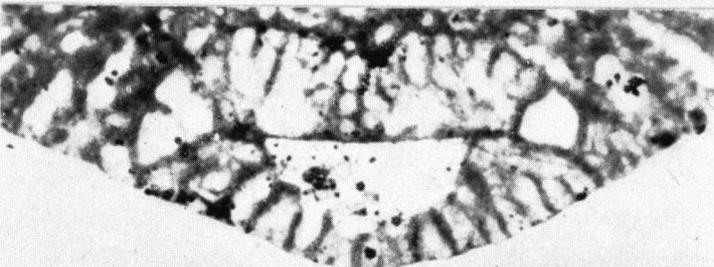
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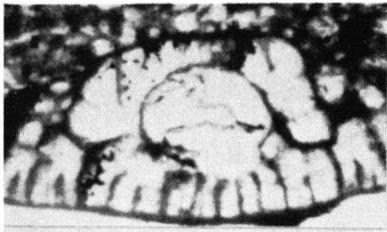
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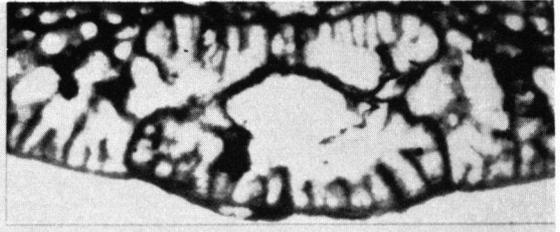
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PLATE XIII

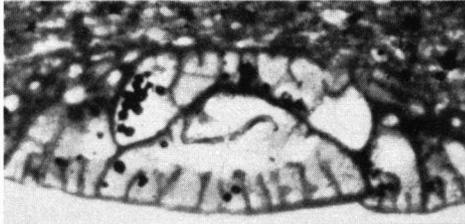
- Fig. 1 Sample 115038, slide 2. Axial section, 100 ×.
- Fig. 2 Sample 115038, slide 16. Axial section, 100 ×.
- Fig. 3 Sample 115038, slide 1. Axial section, 100 ×.
- Fig. 4 Sample 115040, slide 18. Axial section, 100 ×.
- Fig. 5 Sample 115040, slide 4. Axial section, 100 ×.
- Fig. 6 Sample 115046, slide 1. Axial section, 100 ×.
- Fig. 7 Sample 115047, slide 4. Axial section, 100 ×.
- Fig. 8 Sample 115047, slide 12. Axial section, 100 ×.
- Fig. 9 Sample 115047, slide 10. Axial section, 100 ×.
- Fig. 10 Sample 115047, slide 16. Axial section, 100 ×.
- Fig. 11 Sample 115047, slide 30. Axial section through a microspheric specimen. Faintly a very thin hyaline calcitic layer can be observed around the last whorl, 150 ×.
- Fig. 12 Sample 115047, slide 32. Axial section through a microspheric specimen, 150 ×.
- Fig. 13 Sample 115048, slide 2. Axial section, 75 ×.
- Fig. 14 Sample 115048, slide 18. Axial section, 50 ×.



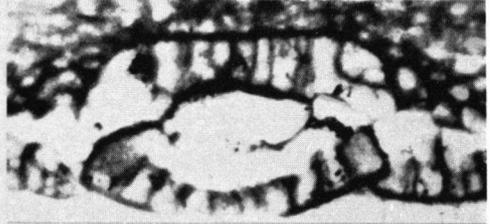
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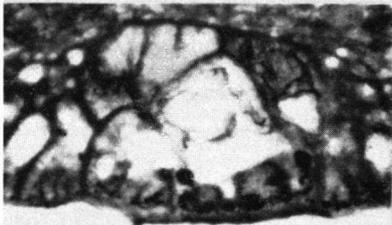
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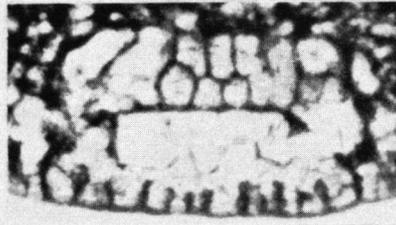
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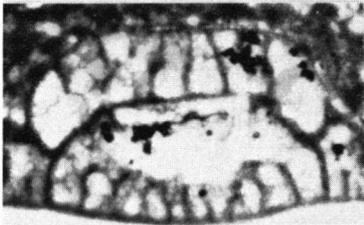
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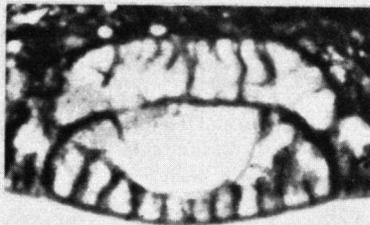
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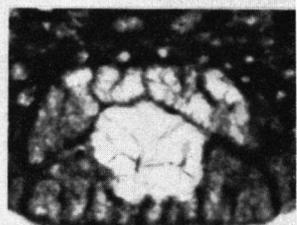
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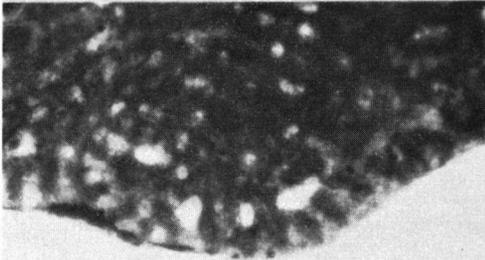
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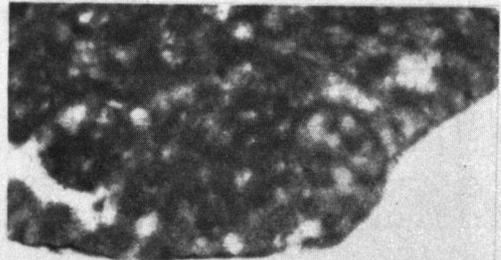
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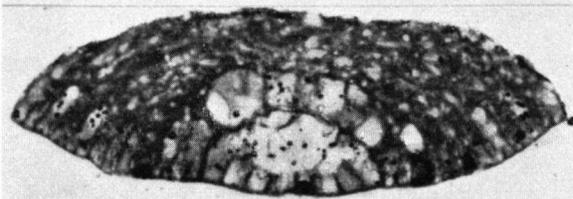
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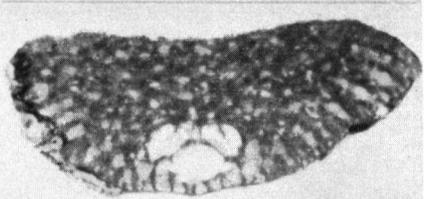
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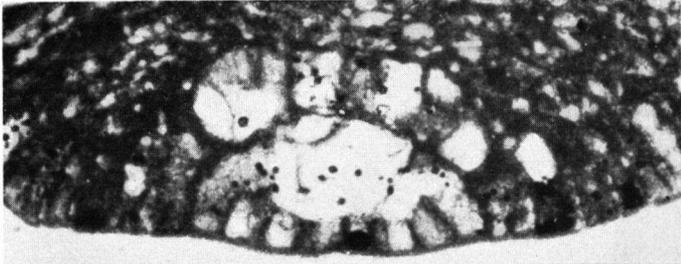
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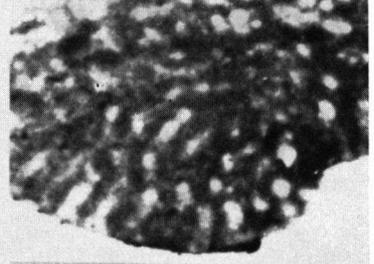
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PLATE XIV

- Fig. 1 Sample 115048, slide 2. Enlarged portion of fig. 13, pl. XIII Axial section, 100 × .
- Fig. 2 Sample 115048, slide 31. Axial section through a microspheric specimen, 100 × .
- Fig. 3 Sample 115048, slide 6. Axial section. To the right of the proloculus a foramen between the deuteroconch and an epi-embryonic chamber can be observed, 150 × .
- Fig. 4 Sample 115050, slide 56. Axial section through a microspheric specimen, 150 × .
- Fig. 5 Sample 115050, slide 15. Axial section, showing irregular epi-embryonic chambers, which hardly touch each other, 50 × .
- Fig. 6 Sample 115050, slide 34. Axial section through a microspheric specimen, 75 × .
- Fig. 7 Sample 115050, slide 40. Axial section. To the left a foramen can be seen between an epi-embryonic chamber and a chamber passage of the first chamber layer, 100 × .
- Fig. 8 Sample 115050, slide 55. Axial section through a microspheric specimen. Part of the last whorl has been broken off, 150 × .
- Fig. 9 Sample 115050, slide 4. Axial section. To the right growth of the animal seems to have been obstructed, and the animal has built its test around this obstruction, 50 × .
- Fig. 10 Sample 115050, slide 9. Axial section through a very small specimen, 50 × .
- Fig. 11 Sample 115051, slide 16. Axial section, 100 ×
- Fig. 12 Sample 115051, slide 20. Axial section, 75 × .
- Fig. 13 Sample 115054, slide 30. Axial section of an abnormal specimen, 100 × .



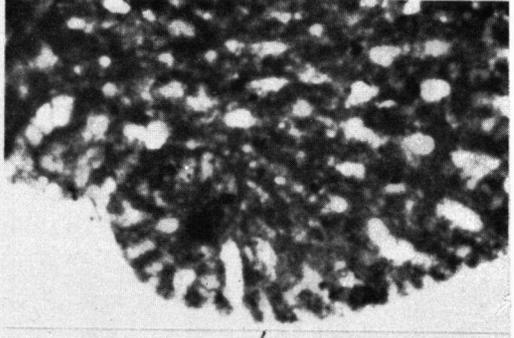
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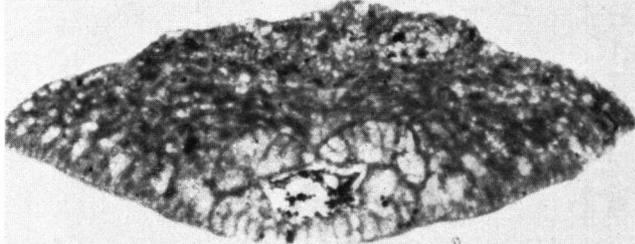
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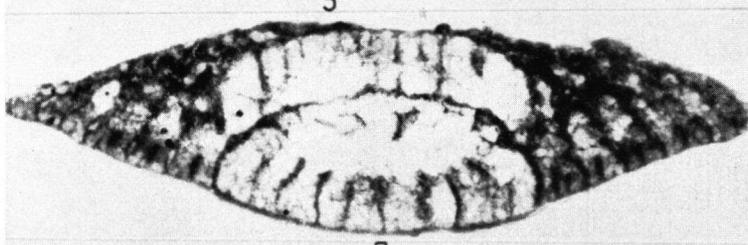
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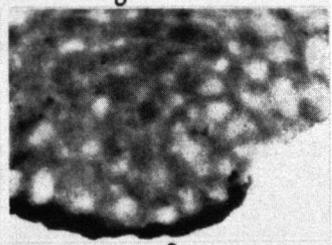
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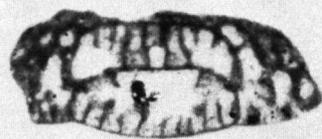
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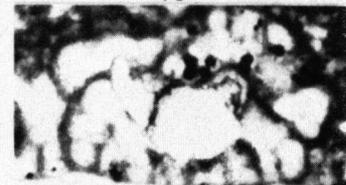
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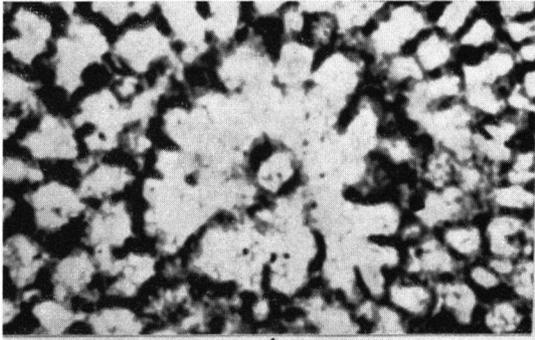
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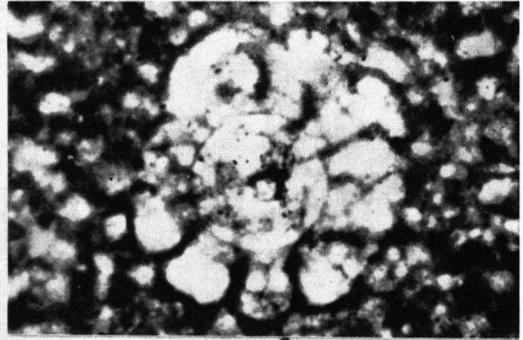
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PLATE XV

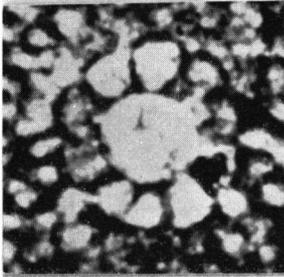
- Fig. 1 Sample 115051, slide 35. Horizontal section through the deuteroconch, close to the proloculus. In the middle the foramen in the pseudochitinous wall of the proloculus can be observed; the section cuts the foramen where it widens towards the deuteroconch, 100 \times .
- Fig. 2 Sample 115052, slide 3. Horizontal section through the proloculus, close to the deuteroconch. In the middle of the proloculus the foramen is visible, around the proloculus the walls of the epi-embryonic chambers and very faintly the circle of foramina between the deuteroconch and the epi-embryonic chambers can be observed, 100 \times .
- Fig. 3 Sample 115054, slide 57. Horizontal section through proloculus and epi-embryonic chambers, 100 \times .
- Fig. 4 Sample 115054, slide 58. Horizontal section through the deuteroconch, close to the surface, showing the cellules of the embryonic area, 50 \times .
- Fig. 5 Sample 115051, slide 29. Horizontal section through proloculus and deuteroconch, close to the epi-embryonic chambers, showing part of the circle of foramina, 100 \times .
- Fig. 6 Sample 115054, slide 42. Axial section, 150 \times .
- Fig. 7 Sample 115054, slide 63. Axial section of a twinned specimen, 50 \times .
- Fig. 8 Sample 115054, slide 56. Horizontal section through the epi-embryonic chambers, showing the subpartitions in them, 150 \times .
- Fig. 9 Sample 115054, slide 61. Axial section through a microspheric specimen, 200 \times .
- Fig. 10 Sample 115054, slide 53. Horizontal section through the epi-embryonic chambers, close to the proloculus, showing the walls of these chambers and faintly the circle of foramina between them and the deuteroconch, 100 \times .



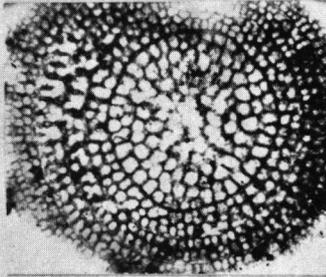
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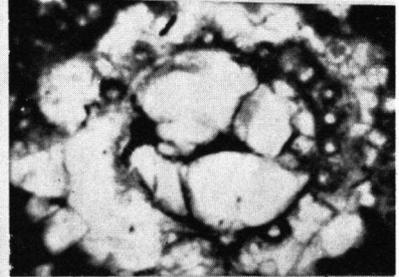
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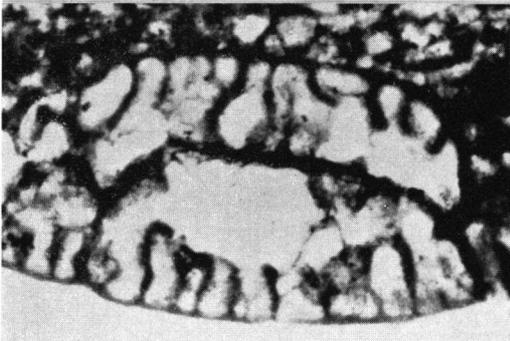
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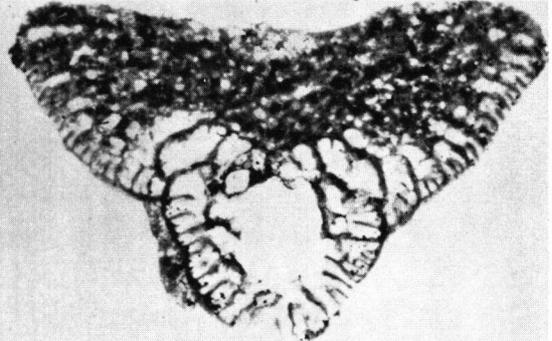
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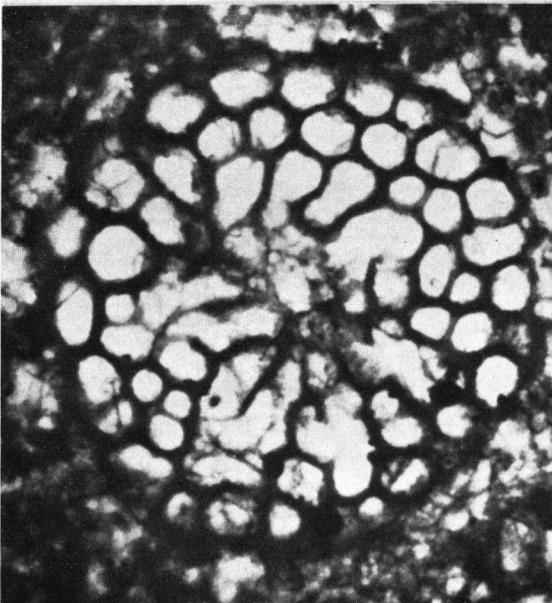
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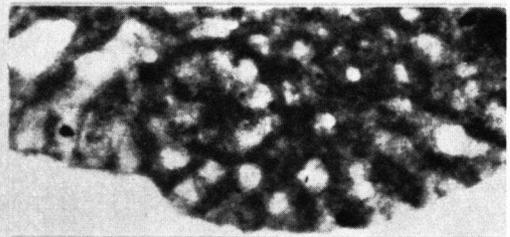
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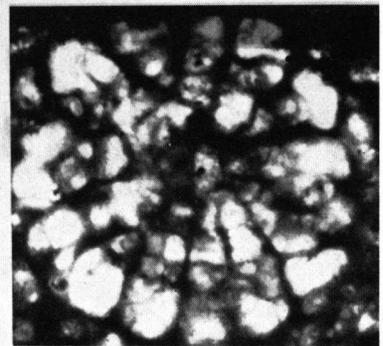
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PLATE XVI

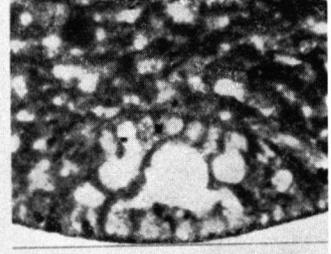
- Fig. 1 Sample 115160, slide 16. Axial section of a twinned specimen, 50 × .
- Fig. 2 Sample 115159, slide 3. Axial section, 150 × .
- Fig. 3 Sample 115160, slide 24. Axial section, 100 × .
- Fig. 4 Sample 115160, slide 18. Axial section, 100 × .
- Fig. 5 Sample 115160, slide 27. Axial section, 100 × .
- Fig. 6 Sample 115161, slide 13. Axial section, 100 × .
- Fig. 7 Sample 115161, slide 1. Axial section, 100 × .
- Fig. 8 Sample 115161, slide 3. Axial section, 100 × .
- Fig. 9 Sample 115163, slide 4. Axial section, 100 × .
- Fig. 10 Sample 115163, slide 1. Axial section, 100 × .
- Fig. 11 Sample 115159, slide 7. Axial section, 150 × .
- Fig. 12 Sample 115159, slide 21. Axial section, 150 × .
- Fig. 13 Sample 115159, slide 11. Axial section, 150 × .
- Fig. 14 Sample 115162, slide 7. Axial section, 100 × .
- Fig. 15 Sample 115162, slide 4. Axial section, 100 × .
- Fig. 16 Sample 115158, slide 25. Axial section, 100 × .
- Fig. 17 Sample 115158, slide 9. Axial section, 100 × .
- Fig. 18 Sample 115158, slide 5. Axial section, 100 × .



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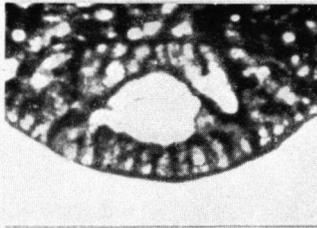
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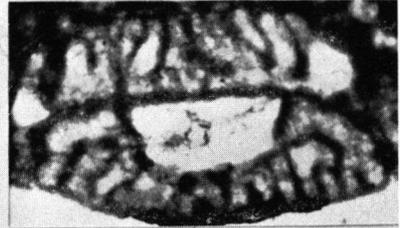
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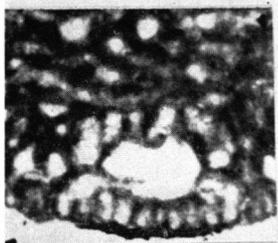
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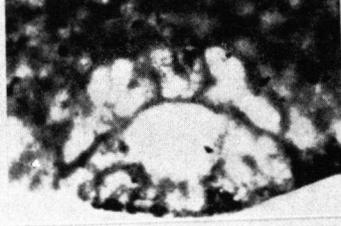
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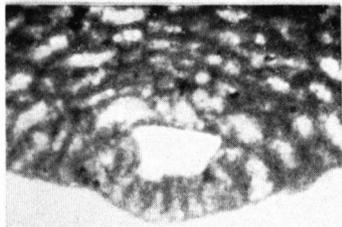
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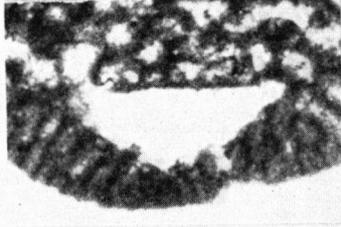
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PLATE XVII

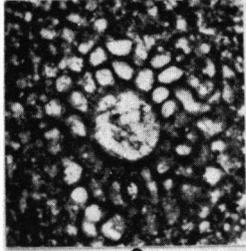
- Fig. 1 Sample 115032, slide 21. Axial section, 100 × .
- Fig. 2 Sample 115032, slide 6. Axial section, 100 × .
- Fig. 3 Sample 115032, slide 20. Horizontal section through proloculus and epi-embryonic chambers, 50 × .
- Fig. 4 Sample 115032, slide 9. Axial section, 100 × .
- Fig. 5 Sample 115015, slide 11. Slightly oblique horizontal section through proloculus and deuteroconch, 75 × .
- Fig. 6 Sample 115031, slide 12. Axial section, 75 × .
- Fig. 7 Sample 115031, slide 11. Axial section, 75 × .
- Fig. 8 Sample 115037, slide 14. Axial section, 75 × .
- Fig. 9 Sample 115037, slide 11. Axial section, 75 × .
- Fig. 10 Sample 115031, slide 16. Axial section of a small specimen, 75 × .
- Fig. 11 Sample 115171, slide 4. Axial section, 50 × .
- Fig. 12 Sample 115171, slide 2. Axial section, 50 × .
- Fig. 13 Sample 115171, slide 1. Axial section, 50 × .
- Fig. 14 Sample P 43429, slide P 45079 (coll. British Museum). Axial section, 50 × .
- Fig. 15 Sample 115025, slide 39. Axial section, 50 × .
- Fig. 16 Sample 115025, slide 44. Axial section, 50 × .
- Fig. 17 Sample 115025, slide 4. Axial section through a very young specimen which has added only the beginning of the first main chamber to the embryonic apparatus, 75 × .
- Fig. 18 Sample 115025, slide 5. Axial section, 50 × .



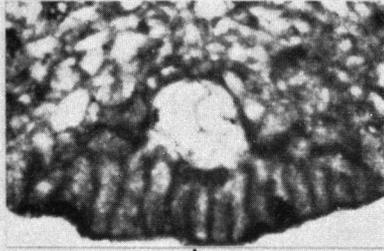
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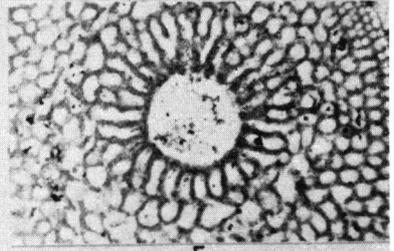
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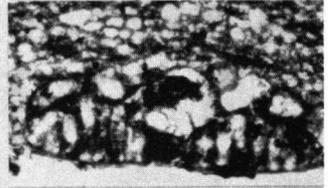
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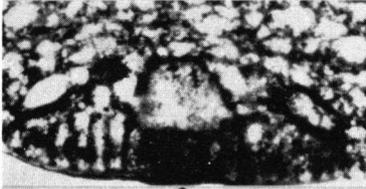
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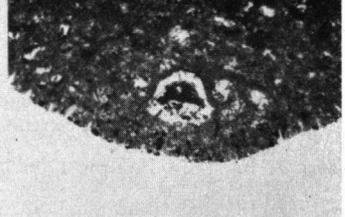
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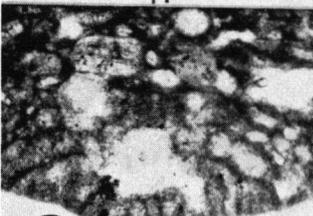
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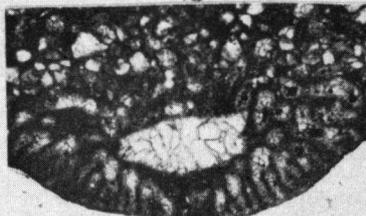
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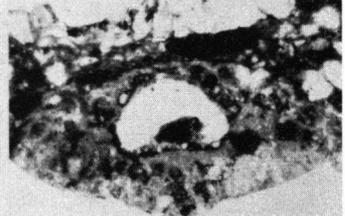
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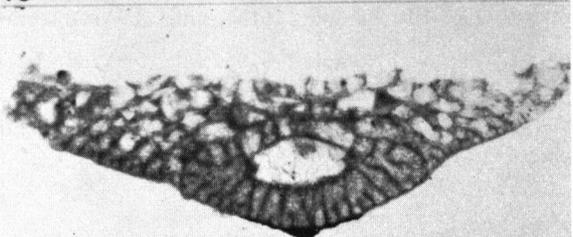
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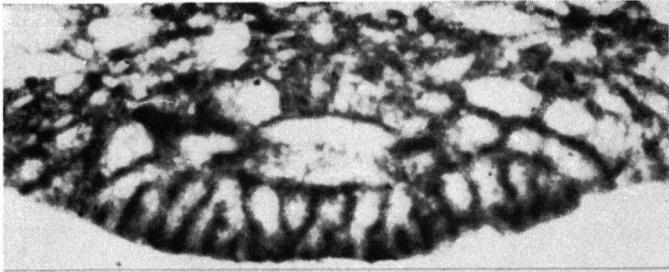
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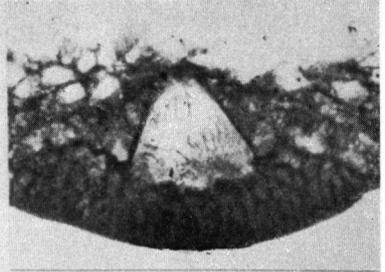
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PLATE XVIII

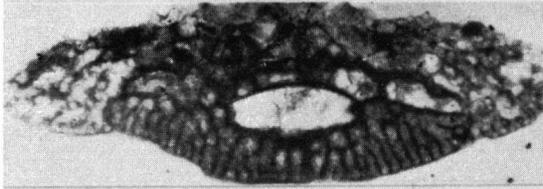
- Fig. 1 Axial section of a specimen of the type-material of *O. concava* (Lamarck), from Ballon, Sarthe, France (coll. Mus. Genève), 100 ×.
- Fig. 2 Sample 115025, slide 20. Axial section, 50 ×.
- Fig. 3 Sample 115025, slide 11. Axial section, 50 ×.
- Fig. 4 Sample 115025, slide 10. Axial section, 50 ×.
- Fig. 5 Sample 115025, slide 3. Axial section, 50 ×.
- Fig. 6 Sample 115025, slide 42. Axial section, 50 ×.
- Fig. 7 Sample 115025, slide 43. Axial section, 50 ×.
- Fig. 8 Sample 115025, slide 20. Axial section, 50 ×.
- Fig. 9 Sample 115025. Cone-surface of a specimen. In the middle the circular embryonic area can be observed, 15 ×.
- Fig. 10 Sample 115154, slide 4. Axial section, 50 ×.
- Fig. 11 Sample 115136, slide 5. Axial section showing a partly dissolved embryonic apparatus, 50 ×.
- Fig. 12 Sample 115144, slide 1. Axial section, 50 ×.



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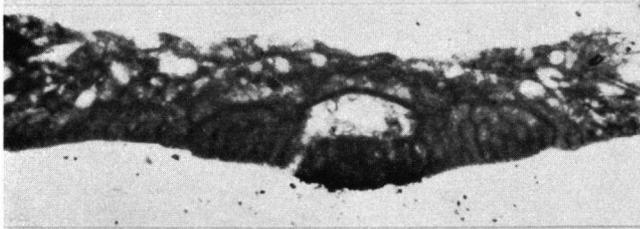
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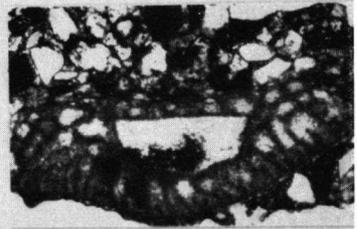
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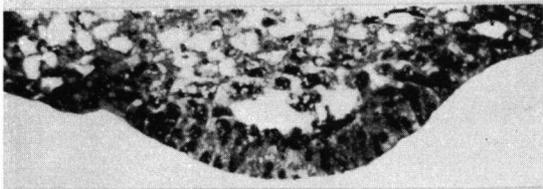
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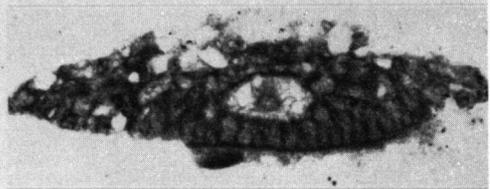
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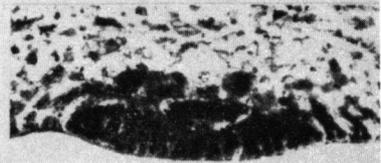
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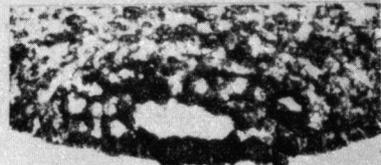
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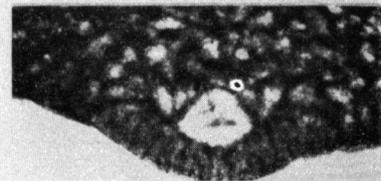
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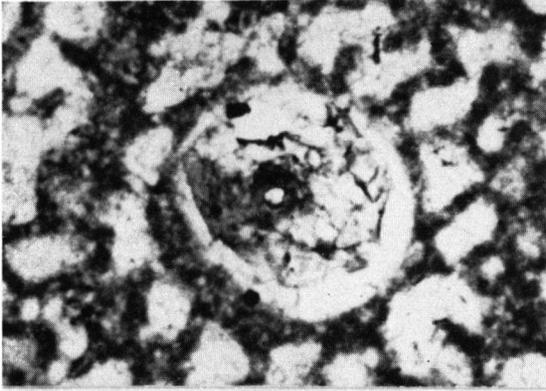
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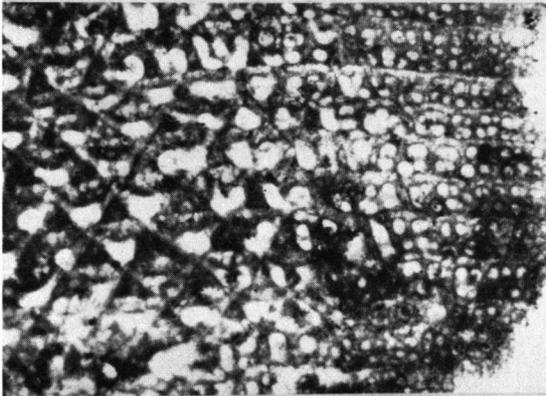
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PLATE XIX

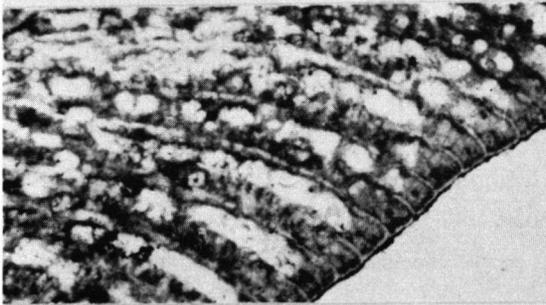
- Fig. 1 Sample 115001, slide 6. Horizontal section through proloculus and epi-embryonic chambers. In the middle the foramen in the pseudochitinous wall of the proloculus can be seen, 150 \times .
- Fig. 2 Sample 115002, slide 4. Tangential section cutting progressively deeper towards the left, and sectioning the marginal and radial zones, 50 \times .
- Fig. 3 Sample 115002, slide 37. Axial section. The hyaline calcitic epidermis can be observed, covering the cone-surface and a small portion of the septa, 75 \times .
- Fig. 4 Sample 115001, slide 4. Axial section, 75 \times .
- Fig. 5 Sample 115002, slide 1. Axial section, 100 \times .
- Fig. 6 Sample 115002, slide 37. Axial section, 75 \times .
- Fig. 7 Sample 115003, slide 2. Axial section, 75 \times .
- Fig. 8 Sample 115008, slide 11. Axial section, 75 \times .
- Fig. 9 Sample 115008, slide 4. Axial section, 75 \times .
- Fig. 10 Sample 115013, slide 29. Axial section, 75 \times .
- Fig. 11 Sample 115013, slide 15. Axial section of a specimen filled with black material, 100 \times .
- Fig. 12 Sample 115013, slide 32. Axial section, 75 \times .
- Fig. 13 Sample 115013, slide 27. Axial section. In the proloculus the shrunken pseudochitinous wall can be seen, 75 \times .
- Fig. 14 Sample 115013, slide 34. Axial section, 75 \times .



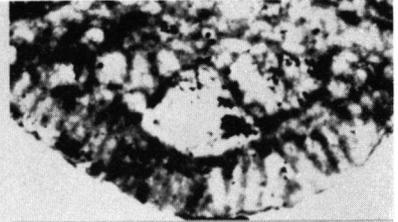
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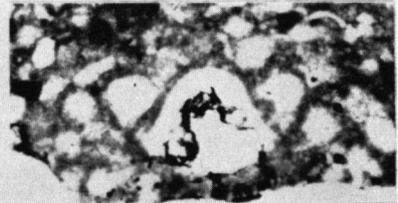
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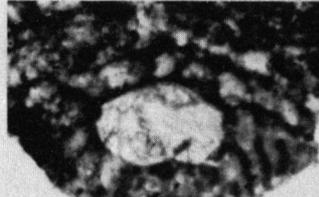
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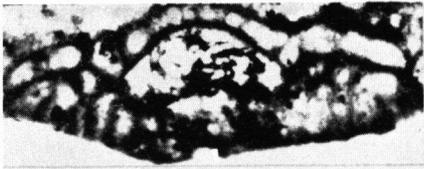
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PLATE XX

- Fig. 1 Sample 115011, slide 8. Axial section, 100 × .
- Fig. 2 Sample 115015, slide 30. Axial section, 50 × .
- Fig. 3 Sample 115012, slide 1. Axial section, 75 × .
- Fig. 4 Sample 115015, slide 27. Axial section, 50 ×
- Fig. 5 Sample 115015, slide 26. Axial section, 50 × .
- Fig. 6 Sample 115015, slide 27. Axial section; detail of marginal and radial zones, showing the cellular structure, 100 × .
- Fig. 7 Sample 115017, slide 3. Axial section, 100 × .
- Fig. 8 Sample 115017, slide 9. Axial section, 100 × .
- Fig. 9 Sample 115024, slide 5. Axial section, 75 × .
- Fig. 10 Sample 115024, slide 69. Axial section, 50 × .
- Fig. 11 Sample 115024, slide 1. Axial section, 100 × .
- Fig. 12 Sample 115024, slide 35. Axial section, 75 ×
- Fig. 13 Sample 115024. Conical specimen, 20 × .
- Fig. 14 Sample 115023, slide 1. Axial section, 150 × .
- Fig. 15 Sample 115024, slide 64. Axial section. In the proloculus the sectioned foramen in the pseudochitinous wall can be seen, 100 × .



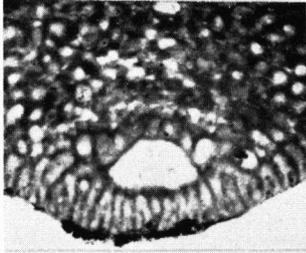
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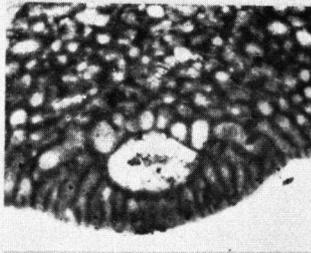
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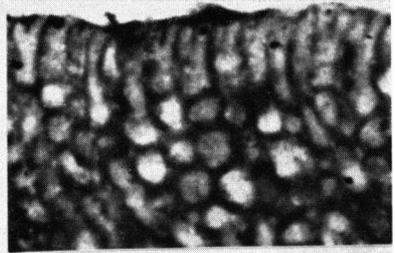
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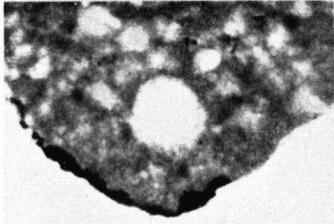
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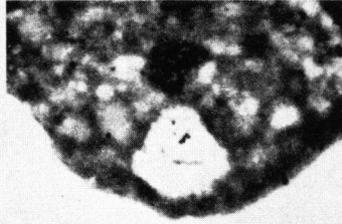
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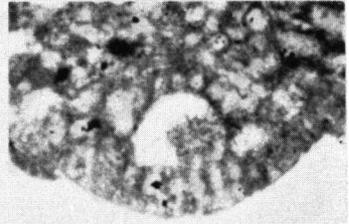
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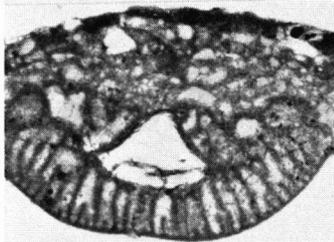
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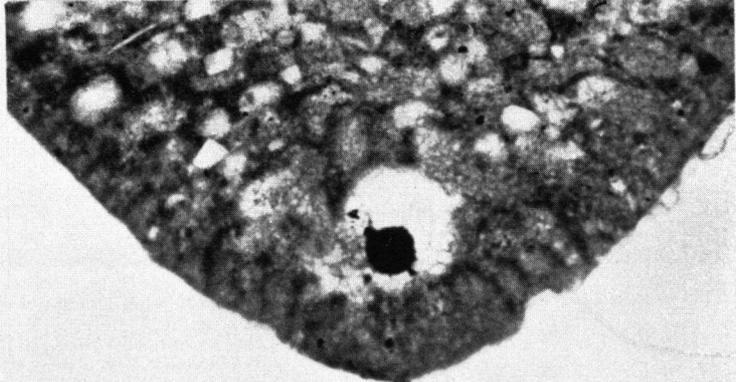
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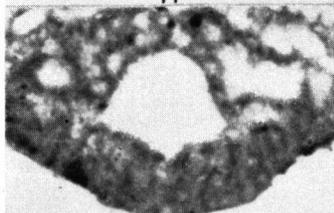
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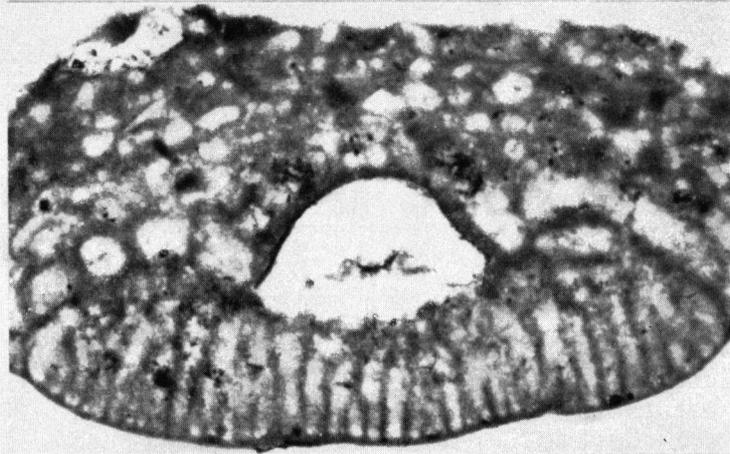
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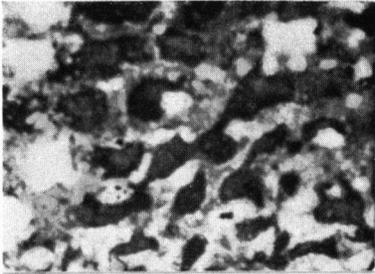
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PLATE XXI

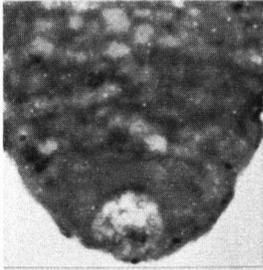
- Fig. 1 Sample 115024, slide 58. Axial section of a high-conical specimen of which the fillings have been coloured with methylene blue. Part of the reticulate zone; showing the cellular appearance of the main chambers and the short oblique foramina which interconnect the chamber passages, 100 ×.
- Fig. 2 Sample 115024, slide 60. Horizontal section of a high-conical specimen, coloured with methylene blue. The section is rather thick, so that the coloured fillings of other chamber layers are shining through. The partitions of the marginal zone are very thick and the radial zone is very short. The structure looks like *Iraqia*, rather than like typical *Orbitolina*, 75 ×.
- Fig. 3 Sample 115024, slide 78. Axial section of an eroded specimen, 100 ×.
- Fig. 4 Sample 115024, slide 13. Axial section, 100 ×.
- Fig. 5 Sample 115037, slide 11. Subaxial section of a megalospheric specimen, 10 ×.
- Fig. 6 Sample 115024, slide 100. Horizontal section through proloculus and epi-embryonic chambers of a conical specimen, 100 ×.
- Fig. 7 Sample 115059, slide 22. Axial section of megalospheric specimen, 10 ×.
- Fig. 8 Sample 115159, slide 9. Approximately axial section of a peculiarly twinned specimen, 10 ×.
- Fig. 9 Sample 115159, slide 8. Axial section of a twinned specimen, 10 ×.
- Fig. 10 Sample 115114, slide 10. Axial section of a megalospheric specimen, 10 ×.
- Fig. 11 Sample 115015, slide 3. Axial section of a megalospheric specimen, 10 ×.
- Fig. 12 Sample 115137, slide 23. Axial section of a megalospheric specimen, 10 ×.
- Fig. 13 Sample 115024, slide 78. Axial section of a megalospheric specimen, 10 ×.
- Fig. 14 Sample 115054, slide 59. Subaxial section of a microspheric specimen, 10 ×.
- Fig. 15 Sample 115002, slide 6. Axial section of a megalospheric specimen, 10 ×.
- Fig. 16 Sample 115001, slide 3. Axial section of a megalospheric specimen, 10 ×.
- Fig. 17 Sample 115059, slide 26. Axial section of a megalospheric specimen, 10 ×.
- Fig. 18 Sample 115074, slide 7. Axial section of a megalospheric specimen, 10 ×.
- Fig. 19 Sample 115032, slide 13. Axial section of a megalospheric specimen, 10 ×.
- Fig. 20 Sample 115114, slide 24. Axial section of a megalospheric specimen, 10 ×.
- Fig. 21 Sample 115114, slide 25. Axial section of a megalospheric specimen, 10 ×.



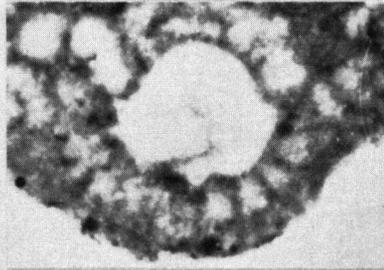
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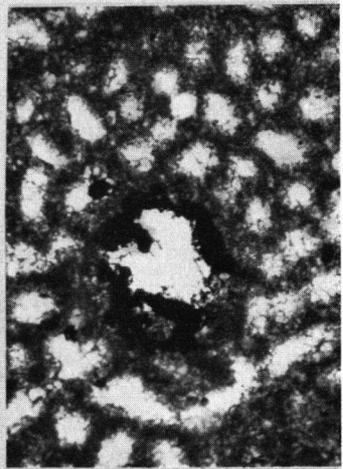
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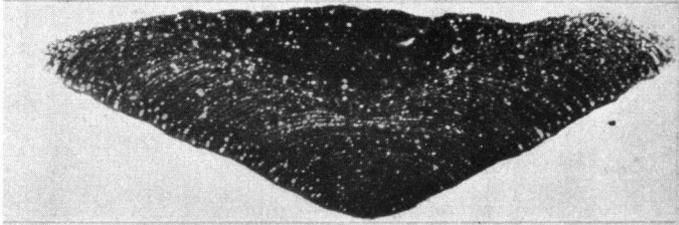
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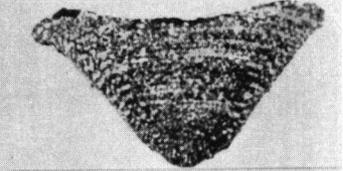
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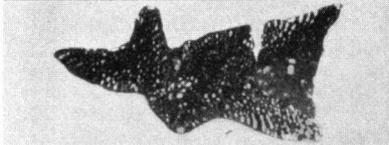
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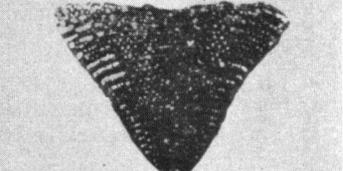
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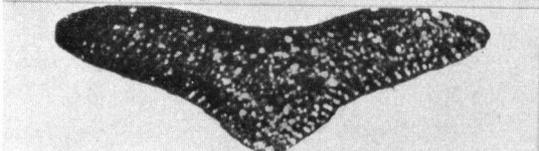
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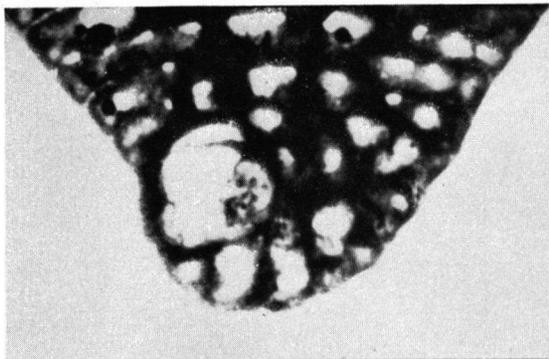


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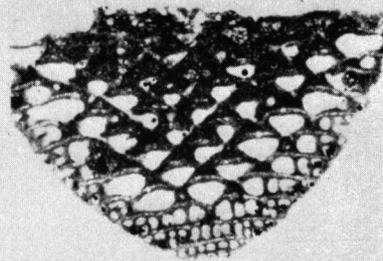
PLATE XXII

All figures are of *Simplorbitolina manasi* Ciry & Rat.

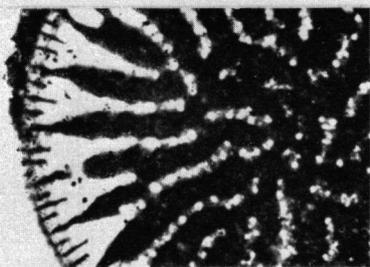
- Fig. 1 Sample 115059, slide XIII. Axial section of a specimen with large proloculus and deuteroconch, 150 \times .
- Fig. 2 Sample 115059, slide XIV. Oblique tangential section, showing the cellules of the marginal zone at the lower periphery, the round sections of the radial passages and the oblique aligned stolons. Also the hyaline calcitic layer can be observed, 50 \times .
- Fig. 3 Sample 115059, slide III. Horizontal section, showing from left to right the marginal zone, the radial zone and the reticulate zone. In the radial and central zone the cross-sections of the stolons can be observed, 50 \times .
- Fig. 4 Sample 115059, slide V. Horizontal section through the embryonic apparatus, showing proloculus and deuteroconch. The plane of symmetry of the initial spiral is about parallel to the SW-NE diagonal of the photograph, 150 \times .
- Fig. 5 Sample 115155, slide 3, topo-type. Horizontal section near the apex of the cone, showing a somewhat *Iraqia*-like structure, 50 \times .
- Fig. 6 Sample 115155, slide 1, topo-type. Axial section, showing detail of the neanic part of the test, 100 \times .
- Fig. 7 Sample 115155, slide 2, topo-type. Axial section, showing the initial part of the test with the small strepto-spiral, 150 \times .
- Fig. 8 Sample 115035, slide II. Axial section of relatively low-conical specimen, 100 \times .
- Fig. 9 Sample 115035, slide IV. Axial section, 100 \times .



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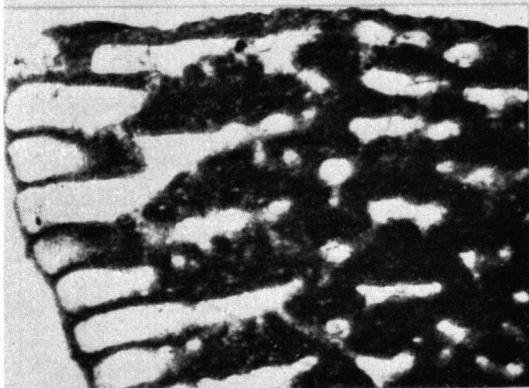
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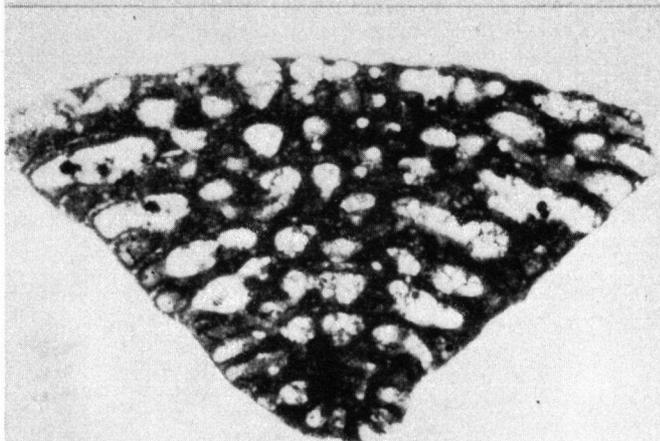
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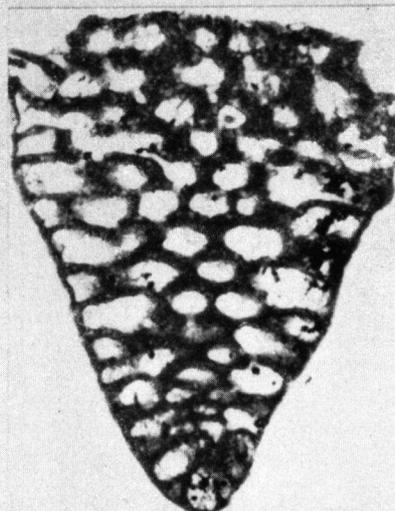
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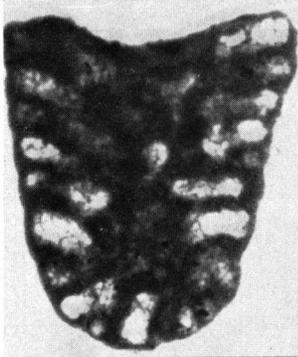
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PLATE XXIII

- Fig. 1 *Orbitolinopsis kiliani* (Prever). Sample 115115, slide XII. Axial section of a small specimen, 100 ×.
- Fig. 2 *Dictyoconus walnutensis* (Carsey). Sample 115164, slide 3, topo-type. Axial section showing detail of the neanic part of the test, 100 ×.
- Fig. 3 *Coskinolinoides texanus* Keijzer. Sample 115165, slide 1. Axial section, showing the simple partitions in the marginal zone. Black spots are secondary ferruginous fillings, 100 ×.
- Fig. 4 *Dictyoconus floridanus* (Cole) subsp. *elongata* (Moullade). Sample 115115, slide IX. Axial section, 50 ×.
- Fig. 5 *Dictyoconus walnutensis* (Carsey). Sample 115164, slide 15, topo-type. Axial section of a megalospheric specimen, showing proloculus and deuteroconch and the short horizontal plates in the marginal zones of the last chambers, 100 ×.
- Fig. 6 *Coskinolinoides texanus* Keijzer. Sample 115165, slide 6. Axial section, 150 ×.
- Fig. 7 *Dictyoconus floridanus* (Cole) subsp. *elongata* (Moullade). Sample 115115, slide IV. Horizontal section, 50 ×.
- Fig. 8 *Orbitolinopsis kiliani* (Prever). Sample 115115, slide XV. Axial section of a small specimen, 100 ×.
- Fig. 9 *Orbitolinopsis kiliani* (Prever). Sample 115115, slide XIII. Horizontal section, 100 ×.
- Fig. 10 *Dictyoconus walnutensis* (Carsey). Sample 115164, slide 2, topo-type. Horizontal section, 100 ×.
- Fig. 11 *Orbitolinopsis kiliani* (Prever). Sample 115115, slide X. Axial section of a small specimen, 100 ×.



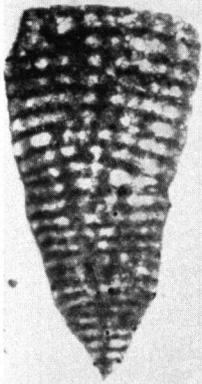
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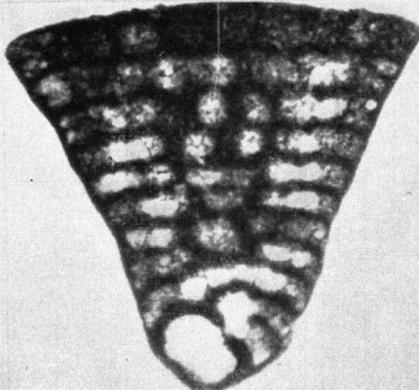
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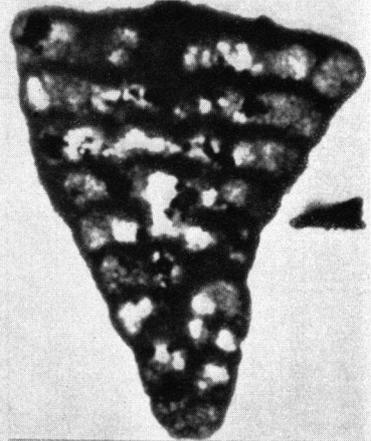
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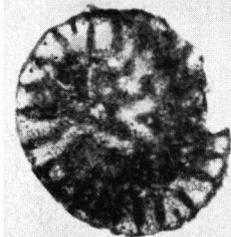
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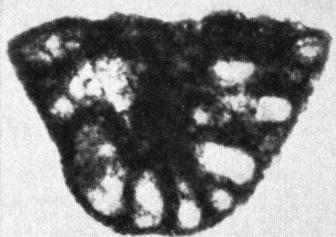
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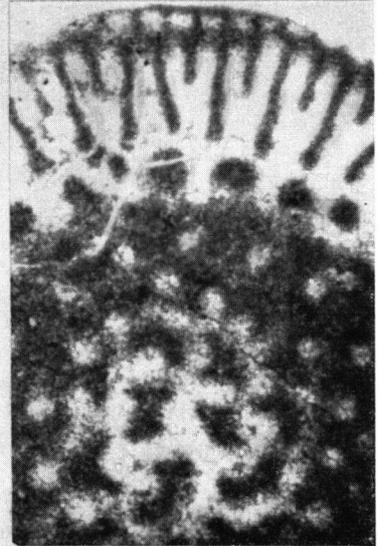
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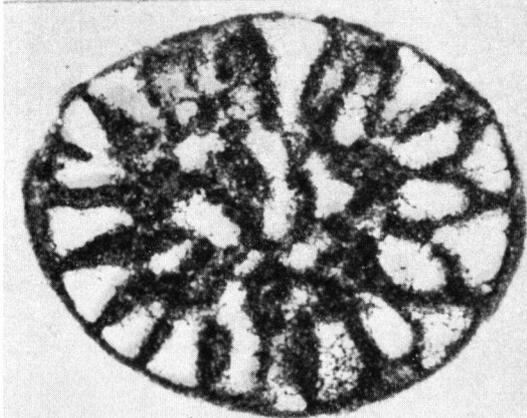
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