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T. FREUDENTHAL

**STRATIGRAPHY OF NEOGENE DEPOSITS
IN THE KHANIA PROVINCE, CRETE, WITH
SPECIAL REFERENCE TO FORAMINIFERA
OF THE FAMILY PLANORBULINIDAE AND
THE GENUS HETEROSTEGINA**

1

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STRATIGRAPHY OF NEOGENE DEPOSITS IN THE KHANIA
PROVINCE, CRETE, WITH SPECIAL REFERENCE TO FORAMINIFERA
OF THE FAMILY PLANORBULINIDAE AND THE GENUS
HETEROSTEGINA

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IN THE KHANIA PROVINCE, CRETE,
WITH SPECIAL REFERENCE TO
FORAMINIFERA OF THE FAMILY
PLANORBULINIDAE AND THE GENUS
HETEROSTEGINA

T. FREUDENTHAL

1969
SCHOTANUS & JENS INC.
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CONTENTS

	Page
SUMMARY	9
I. INTRODUCTION	11
II. LITHOSTRATIGRAPHY	27
1. Introduction	27
2. Description of the formations	29
2.1. Mesonisi Formation	29
2.2. Roka Formation	30
2.3. Koukounaras Formation	31
2.4. Kissamou Formation	33
2.5. Khairëtiana Formation	36
2.6. Khatzi Formation.	39
2.7. Tavronitis Formation	41
2.8. Ayios Yeoryios Formation	43
2.9. Akrotiri Formation	44
2.10. Soudha Formation	45
2.11. Keramia Formation	47
2.12. Gavdos Formation	48
3. Lithostratigraphic correlation	50
III. THE FAMILY PLANORBULINIDAE SCHWAGER, 1877.	53
1. Introduction, literature	53
2. The genus <i>Planorbulinella</i> CUSHMAN, 1927	57
2.1. Introduction	57
2.2. The genus <i>Planorbulinella</i> in the Mediterranean Neogene	59
2.2.1. Introduction	59
2.2.2. The genus <i>Planorbulinella</i> in the Neogene of Crete	59
2.2.2.1. Stratigraphic distribution	59
2.2.2.2. Material	60
2.2.2.3. External features	62
2.2.2.4. Measurements and counts of internal features	63
2.2.2.5. Internal features	64
2.2.2.6. Results of counts and measurements	67
2.2.2.7. Discussion of the results of counts and measurements; phylogeny	75
2.2.2.8. Systematics	76
III. 2.2.3. <i>Planorbulinella</i> in the Maltese and Italian Neogene	79
2.2.3.1. Introduction	79

	Page
2.2.3.2. <i>Planorbulinella</i> in the type Tortonian	79
2.2.3.3. <i>Planorbulinella</i> in the Neogene of Malta	80
2.2.3.4. <i>Planorbulinella</i> in the Neogene of Sicily	81
III. 2.3. <i>Planorbulinella larvata</i> (PARKER & JONES), 1860	82
2.3.1. Introduction	82
2.3.2. Material	82
2.3.3. External features	82
2.3.4. Internal features	83
III. 2.4. <i>Planorbulinella</i> in the Bodjonegoro I drill hole (Java)	84
2.4.1. Introduction, literature	84
2.4.2. External features	85
2.4.3. Internal features	86
III. 2.5. <i>Planorbulinella zelandica</i> FINLAY, 1947	86
2.5.1. Introduction, literature	86
2.5.2. Material	87
2.5.3. External features	88
2.5.4. Internal features	88
2.5.5. Remarks on the age of the <i>P. zelandica</i> populations	89
III. 2.6. <i>Planorbulinella trinitatensis</i> (NUTTALL), 1928	90
2.6.1. Introduction, literature	90
2.6.2. Material	90
2.6.3. External features	91
2.6.4. Internal features	91
2.6.5. Remarks on the age of the <i>P. trinitatensis</i> populations	92
III. 2.7. Conclusions	93
III. 3. The genus <i>Planolinderina</i> n.gen.	95
3.1. Introduction	95
3.2. Description of <i>Planolinderina</i> n.gen.	95
3.3. <i>Planolinderina</i> n.gen. in the Tertiary of the Aquitaine Basin	95
3.3.1. Introduction, literature	95
3.3.2. Material	96
3.3.3. External features	97
3.3.4. Internal features	97
3.3.5. Measurements and counts	97
3.3.6. Discussion of the results of counts and measurements; phylogeny	106
3.3.7. <i>Planolinderina escornebovensis</i> n.sp.	107
3.4. The genus <i>Planolinderina</i> in the Tertiary of the Indo-Pacific	108
3.4.1. Introduction, literature	108
3.4.2. Material	108
3.4.3. External features	110
3.4.4. Internal features	112
3.4.5. Counts and measurements	113
3.4.6. Discussion of the results of counts and measurements; phylogeny	115

	Page
3.5. Conclusions; phylogeny	116
III. 4. The genus <i>Linderina</i> SCHLUMBERGER, 1893	117
4.1. Introduction, literature	117
4.2. Material	118
4.3. External features	119
4.4. Internal features	120
4.5. Measurements and counts	121
4.6. Discussion of the results of counts and measurements; phylogeny.	123
4.7. Species distinction	124
III. 5. The genus <i>Hellenocyclina</i> REICHEL, 1950	126
5.1. Introduction, literature	126
5.2. Material	127
5.3. External features	128
5.4. Internal features	129
5.5. Measurements and counts	130
5.6. Discussion of the counts and measurements; phylogeny	132
5.7. <i>Hellenocyclina charentensis</i> n.sp.	134
III. 6. Conclusions, phylogeny, taxonomy, ecology	136
IV. THE GENUS HETEROSTEGINA IN THE NEOGENE OF EUROPE	141
1. Introduction, literature	141
2. Method of study, counts and measurements	143
3. Material	144
4. Results of the counts and measurements	147
5. Discussion of the results of counts and measurements; phylogeny	156
V. BIOSTRATIGRAPHY, CONCLUSIONS	159
1. Conclusions dealing with Xania Province, Crete	159
2. Biostratigraphic value of lineages outside Crete	160
APPENDIX I—X. Tables with the results of counts and measurements on Cretan <i>Planorbulinella</i> populations	162
PLATES	174
REFERENCES	179

S U M M A R Y

In this paper the stratigraphy of the Neogene deposits in the Khania Province, Crete, Greece, is described. Special attention is paid to the evolution and taxonomy of foraminiferal genera assigned previously to the family Planorbulinidae. This partial revision of the Planorbulinidae is based not only on our Cretan material, but also on samples from all over the world, in age ranging from Late Cretaceous to Recent. It is shown that at least part of the genera assigned to the Planorbulinidae probably have no relationship with *Planorbulina*, the nominal genus.

The following taxa are discussed:

Hellenocyclina REICHEL (Upper Cretaceous), with the species *H. beotica* REICHEL, *H. visserae* (HOFKER) and *H. charentensis* n.sp.;

Linderina SCHLUMBERGER (Middle Eocene, Upper Eocene), with the species *L. brugesi* SCHLUMBERGER, *L. buranensis* NUTTALL & BRIGHTON (= *L. bibilensis* SILVESTRI = *L. nuttalli* SILVESTRI), *L. rajasthanensis* SINGH (= *L. kirtharensis* SINGH = *L. bikanerensis* SINGH = *L. kolayatensis* SINGH), *L. paronai* OSIMO (? = *L. floridensis* COLE);

Planolinderina n.gen. (Upper Oligocene — Lower Miocene), with the species *P. escornebovensis* n.sp., *P. plana* (HERON-ALLEN & EARLAND) and *P. inaequilateralis* (HERON-ALLEN & EARLAND);

Planorbulinella CUSHMAN (Lower? Miocene — Recent), with the species *P. trinitatensis* (NUTTALL), *P. zelandica* FINLAY, *P. larvata* (PARKER & JONES), *P. rokae* n.sp., *P. astriki* n.sp., and *P. canaeae* n.sp.

The *Hellenocyclina* species probably belong to a single evolutionary lineage. The data on the age of our *Linderina* populations are rather controversial if a single lineage is assumed. The species placed in *Planolinderina* probably belong to two, more or less synchronously evolving, lineages. In the case of *Planorbulinella* it is assumed that there are three lineages, two of them being more or less parallel.

All of these lineages developed according to the principle of nepionic acceleration. Their evolution is shown on the basis of measurements and counts on the early chambers. The two most important parameters are the length of the early spiral and the size of the initial chambers.

However, both parameters show a negative correlation, and as a consequence

— if this correlation is very strong — random influences on the size of the early chambers will cause changes in the length of the spiral as well. Such influences may cause nepionic acceleration to become less distinct and less useful for stratigraphic correlation. This becomes most apparent in *Planolinderina*.

In *Planorbulinella* and *Hellenocyclus* nepionic development is furthermore complicated by the presence of recurrences of the one-aperture stage after orbital growth had started.

The results of these studies indicate that the family Planorbulinidae, as generally accepted nowadays, may comprise several completely unrelated genera. For the present it seems more correct to place each genus mentioned in a separate family. Hence, the following new families are proposed: Hellenocyclinidae, Linderinidae, Planolinderinidae, and Planorbulinellidae.

Apart from these "planorbulinellid" genera, attention is paid to the evolution of *Heterostegina* in the Neogene of Crete, SW France and Italy. Biometrical methods applied to features thought to change in the course of time do not yield satisfactory results. Evolutionary trends advanced by PAPP & KÜPPER (1954) and HOTTINGER (1966) are analyzed and partly rejected. The evolutionary pattern, though understood, does not allow a broad application of the genus to biostratigraphic correlations. Consequently, it cannot be used for an age determination of the Cretan Neogene deposits.

On the basis of the evolution of *Planorbulinella* it is shown that the marine sedimentation on Crete started during Tortonian time. Although not studied in detail and not described in this paper, the planktonic foraminifera indicate that a continuous marine sedimentation has gone on up into the Pliocene.

Chapter I

INTRODUCTION

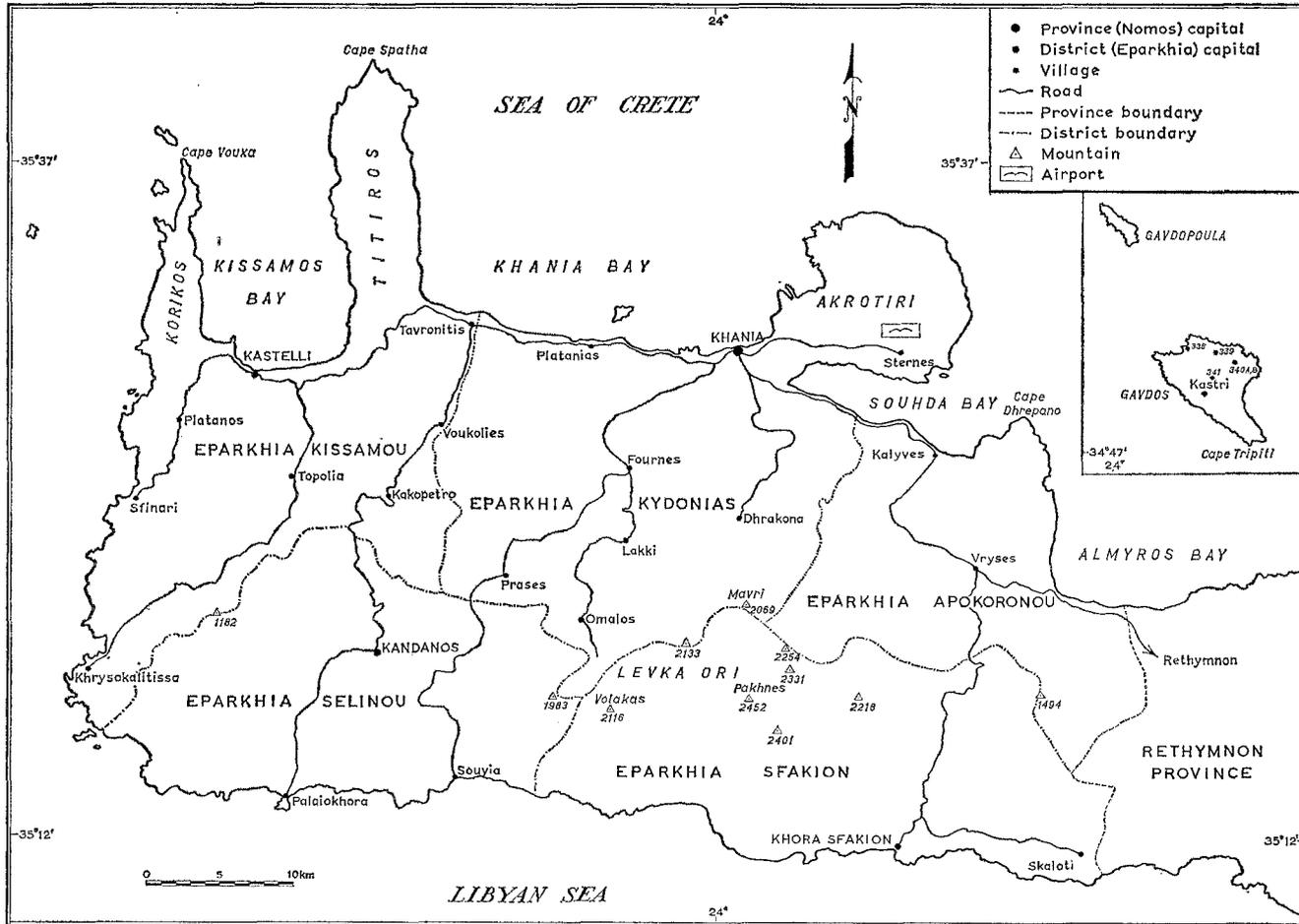
This paper deals with stratigraphy and micropaleontology of the Neogene deposits in the nomos Khania in Crete, the westernmost nomos (= province) of this island, named after its capital Khania. Khania has daily aeroplane and ferry boat connections with the Greek capital; it is linked with the other Cretan province capitals Rethymnon, Iraklion and Ayios Nikolaos by a metalled road running to the east along the northern coast of the island. To the west another road leads along the northern coast to Kastelli Kissamou. There are hardly any other metalled roads in the Khania province, but this situation has rapidly been improving during the last few years. The Khania province is subdivided into 5 eparkhias (= districts): Kydonias, Apokoronou, Kissamou, Selinou and Sfakion. Their geographic position is shown in fig. 1.

The province has a considerable revenue from citrus fruits (oranges, lemons) in the northern coastal plains. Other agricultural products are grapes, olives; potatoes are of minor importance. In the rocky Lefka Ori sheep farming and cheese making are the most important sources of income. Fishing is of less importance. Of late, tourism has become some source of income, but it is still insignificant compared with this industry in the Iraklion province because of the lack of excavated Minoan ruins.

In this paper village names will be accompanied by the name of the district in which they are situated. We have a special reason for doing so. In Crete, as well as in other parts of Greece, there seems to be a rather restricted stock of village names, thus often leading to the repeated use of the same name within a small area. Names like Neo Khorio (new village), Platanos (or Plantanias, or Platanes) (platan), Episkopi (outlook) and Vryses (well) are of common use and end up in considerable confusion if not the district, in which they are situated, is added. Therefore, village names are given in the following way: Vryses Apokoronou and Vryses Kydonias. Unless the district is completely clear from the context this procedure will be followed.

The confusion arising from identically named villages is certainly not a theoretical one. In the older literature it is often impossible to trace back whether the author is writing about the Khania or Iraklion province, a distance of about 150 km. But even if the province name has been given one may be up against the same difficulties.

Fig. 1. Schematic map of the Khania Province, Crete.



The Neogene deposits are found in the relatively low, hilly, coastal plains along the northern coast, nearly completely restricted to the districts of Apokoronou, Kydonias and Kissamou. To the south this hilly country changes into the steeply sloping mountain range of the Levka Ori (White Mountains); their highest peak is the Pakhnes (2452 m).

Field work was carried out during three summer months, in both 1962 and 1963; in the spring of 1965 the mapping was completed after another three months' field work. In September 1966 a short visit was made to take some additional samples and to clear up some minor points.

In chapter II a detailed description of the lithostratigraphy in the Khania province is given. The lateral extension of the formations is shown in the two accompanying maps (charts VII and VIII).

In the chapters III and IV attention is paid to some foraminiferal genera occurring abundantly in the Cretan Neogene: *Planorbulinella* and *Heterostegina*. In both cases we had to compare our material with that from other areas. In the case of *Planorbulinella* this study and comparison has grown out to a revision of the "family Planorbulinidae" of earlier authors. In the second case it was tried to test the evolutionary hypothesis advanced by PAPP & KÜPPER (1954). On the basis of these two genera an attempt has been made to get information on the age of the Neogene deposits in the Khania province, and the way in which the formations distinguished have to be correlated.

The author is greatly indebted to C. W. Drooger (Utrecht) for his help and criticism during the preparation of the manuscript. My thanks are also due to H. J. Mac Gillavry (Amsterdam) and P. Marks (Utrecht) for their reading of the typescript, and to J. E. Meulenkamp for his co-operation during the field work and our many discussions afterwards.

I should like to express my sincere gratitude to the following colleagues, who contributed to this paper by providing material for comparison and/or general information: A. Azzaroli (Florence), D. A. J. Batjes (Paris), D. J. Belford (Cannara), D. G. Brighton (Cambridge), W. S. Cole (Ithaca), C. W. Copeland (Alabama), N. Creutzburg (Freiburg i.B.), D. Curry (Northwood), R. Felix (Wageningen), J. E. van Hinte (Bordeaux), L. Hottinger (Basel), A. J. Key (Rijswijk), Li-Sho Chang (Taipei), Z. Reiss (Jerusalem), G. Salvatorini (Pisa), G. Sampo (Turin), G. H. Scott (Lower Hutt), Ruth Todd (Washington), T. Uchio (Tokyo) and Mary Wade (Adelaide).

The drawings and photographs were skillfully made by A. van Doorn, J. P. van der Linden and P. Hoonhout.

Much of the material was already present in the collections of the Geological Institute of Utrecht. Our described material is stored in the collections of that

institute (S 20767—S 22520). The same is true for the account of all measurements and counts.

Previous literature and maps.

Little is known of the stratigraphy and micropaleontology of the Neogene deposits of Crete. Only a few papers on these subjects have been published, and then mainly between 1861 and 1911. They hardly deal with stratigraphy; frequently they only contain lists of macrofaunas. One relatively recent paper (PAPP, 1947), has drawn attention to the fact that a continuous marine, Mio-Pliocene sedimentation might be found in Crete and since such continuous sections are not known to exist elsewhere in the Mediterranean area, it was considered of interest to gather more data concerning this problem. If PAPP's suggestion appears correct, there may be a possibility of indicating a Miocene — Pliocene boundary by means of foraminifera. For this the Mediterranean area is most appropriate, since the Late Miocene and Pliocene stages (e.g. Tortonian, Messinian, Tabianian, Plaisancian and Astian) have been established in this area.

RAULIN (1856, 1861, 1869) was the first to give details on the Cretan Neogene, dealing at the same time with many other topics, mainly of geographic and ethnographic nature, which are generally more interesting. He lists a number of localities from which he describes macrofossils. He considers the Neogene strata to be time equivalents of the "terrains subapennins"¹⁾ of Northern Italy. Moreover, he gives a fairly schematic geologic map (issued 1868).

SPRATT (1865) distinguished sediments of Miocene and Pliocene age; the Miocene strata are considered to be time equivalents of the Neogene sediments of the Maltese Islands (this conclusion is based on his study of the Neogene deposits of Gavdos Island). The accompanying schematic geologic map shows much less detail than that given by RAULIN (1868).

SIMONELLI (1894) gives the lithologic succession at several localities, partly in the Khania province (e.g. near Vryses Apokoronou, and on Gavdos Island). He lists some macrofossils and compares several lithologic units with the Italian Langhiano, Tortoniano and Elveziano; limnic sediments are considered to be of "Levantine" age.

BONARELLI (1901) distinguishes Middle Miocene, Pliocene (Astiano) and

¹⁾ RAULIN considers "subapennin" to be identical with Neogene, in this way misinterpreting d'ORBIGNY's (1852) "étage subapennin" (= Pliocene).

Levantinean sediments. Numerous macrofossils are mentioned, partly from the Khania province (Akrotiri Peninsula).

CAYEUX (1911 a, b), in two subsequent papers, gives an excellent outline of the Neogene deposits, although his age assignments seem to be incorrect from our point of view. In the Iraklion province thick detritical sediments at the base of the Neogene are considered to be of Helvetian age. In the Rethymnon province similar deposits (sand, sandstone, gravel, limestone) are said to contain *Ostrea crassissima* and *Operculina* (in reality *Heterostegina*). Comparable sediments are lacking in the Khania province, except for a small occurrence of clay with *O. crassissima* on Titiros Peninsula.

Overlying the coarse, detritical Helvetian sediments there are blue, in their upper part generally white, marls and marly limestones with macrofossils (for example, the well-known "index fossil" *Ancilla glandiformis*). Furthermore, gypsum masses, gravel and conglomerate beds are found interbedded within these marls and marly limestones. This lithologic unit is said to contain a rich mollusc fauna in the Rethymnon province, but it is thought to be absent in the Khania province. It is considered to be of Tortonian age.

During Sarmatian time sedimentation stopped, owing to a regressive phase.

The Pontian is considered to correspond to a transgressive phase, in which coarse or fine-grained, hard, yellow *Lithothamnium* bearing limestones, also containing *Pecten* and *Clypeaster*, are deposited. At its base this limestone is generally conglomeratic. In this limestone occasional *Heterostegina* or *Vermetus* concentrations may occur.

Pontian sediments are most widely distributed in the western part of Crete, e.g. the Khania province. They are said to be characterized by several *Pecten* species, for instance *P. vindoboniensis*, *P. dunkeri*, *P. latissimus*. In the same area the Pontian sediments are overlain by blue or yellow marls with *Ostrea cochlear*, about 300 m thick. Their age is thought to be Plaisancian. Their lithology strongly resembles that of the Tortonian sediments in the Rethymnon and Iraklion provinces, with which they were erroneously (according to CAYEUX) correlated by RAULIN. Locally gypsum masses and limestones are interbedded in these marls.

KOLIOPOULOS (1952), the first Greek student of our region, describes the stratigraphy and tectonics of the neighbourhood of Khania (including preneogene strata). Lithologic successions at three localities are given. At one locality (Psathi Hill, several km west of Khania) he traces the Miocene-Pliocene boundary, based on a change of the *Pecten* association. Another locality Trypes, in the eastern outskirts of Khania, with abundant *Heterostegina* cf. *complanata*, is considered to be of Pliocene age.

PAPP & KÜPPER (1954) described the latter *Heterostegina* as *H. complanata*

spiralis, which they considered to be of Late Miocene or Early Pliocene age.

MARTINI (1956), who mapped a part of the Khania province (Sheet Platánias), distinguishes from bottom to top:

(a) *Clypeaster*-Konglomerat, consisting of uncemented, cross-bedded gravel and sand, and well-rounded polymict conglomerates.

(b) *Clypeaster*-Kalk, consisting of yellow, bedded, often marly limestone.

(c) *Clypeaster*-Mergel, consisting of grey to greenish grey marls, with an interbedded member, the "Korallen-Kalk im *Clypeaster*-Mergel", consisting of greyish white, unbedded reefal limestone.

(d) Obere *Clypeaster*-Schichten, consisting of grey to greenish grey marl, alternating with platy marly limestones.

(e) Galatas-Schichten, consisting of grey to greenish grey marl, alternating with nodular, marly limestones.

(f) Platánias-Kalk, consisting of unbedded, dense to finely crystalline, sometimes marly, reefal limestone.

(g) Platánias-Konglomerat, consisting of uncemented gravel and sand, alternating with marls.

(h) Platánias-Mergel, consisting of whitish grey, soft marls, with some marly limestones and limestones in their upper part.

The unit a is considered to represent, at least partly, a fluvial environment; its age is not given. The units b—d are considered to be marine Tortonian. The unit e is marine as well, but it is probably of Sarmatian age. The units f—g are considered to be marine Pliocene. Reasons for these age assignments are not given.

CHRISTODOULOU (1963) gives an extensive account of the stratigraphy and micropaleontology of the Neogene of the whole island. In the Khania province the following lithologic succession is described by this author.

At the base thin conglomerates, overlain by breccious limestones and cemented or not-cemented sandy limestones with Pectinidae, *Clypeaster*, brachiopods, *Heterostegina*, *Neoalveolina* and *Orbulina suturalis*. These strata are considered to be of Helvetian age. They unconformably overlie preneogene rocks.

They are overlain by blue marls grading upward into variously coloured marls (yellow, green, ash-coloured). At the top marly limestones are present. Their total thickness varies between 50—150 m. Their age is considered to be Tortonian.

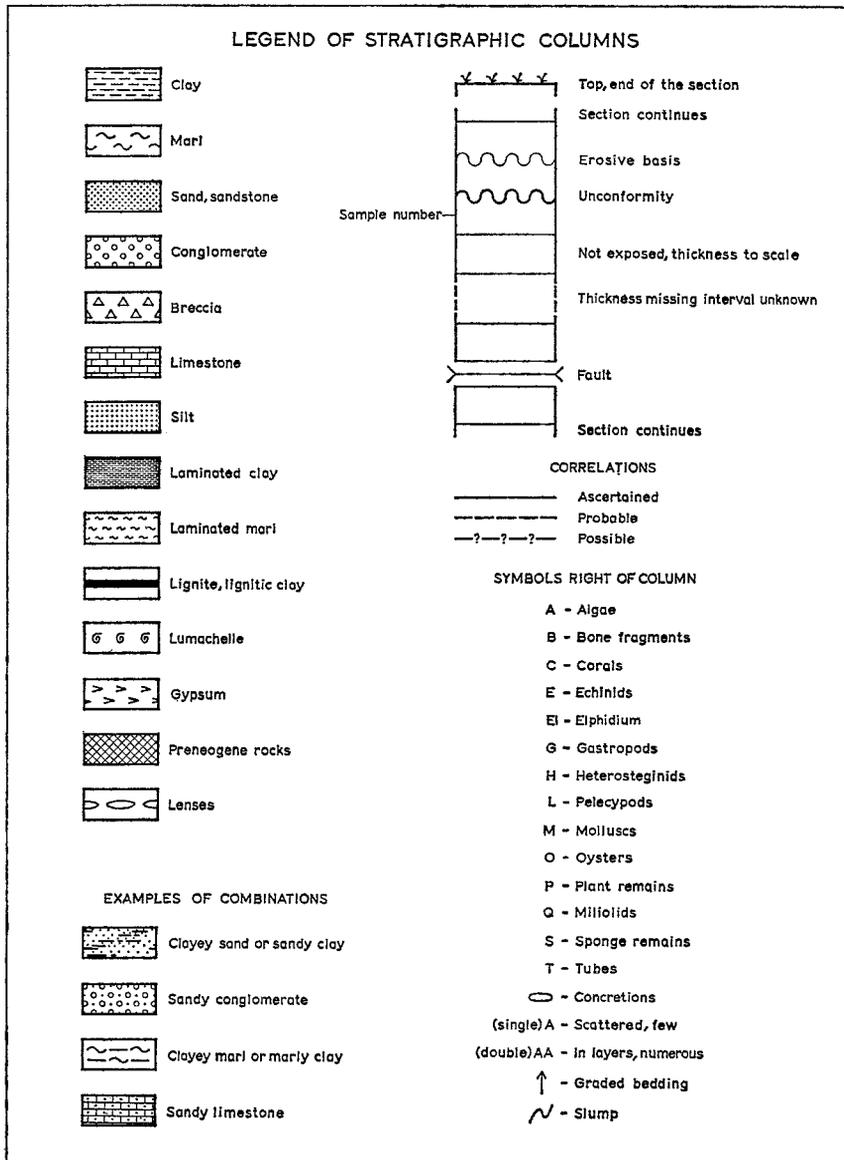
The complete succession of these strata he reports to be present in a section near the village of Episkopi Kissamou. A detailed review of the foraminiferal assemblages in this section is given in his table 6 (*op. cit.*). CHRISTODOULOU studied samples from Psathi Hill, a locality also referred to by KOLIOPOULOS

(1952), but he considers the entire section to be of Tortonian age. This age assignment, which excludes the Pliocene (of KOLIOPOULOS), is not based on paleontological evidence however, but on the absence of an unconformity, which, according to CHRISTODOULOU, characterizes the base of the Pliocene all over Crete.

The Sarmatian time is supposed to correspond to a tectonical uplift of the earlier sediments. In the same time fresh and brackish water sediments were formed in small, closed basins.

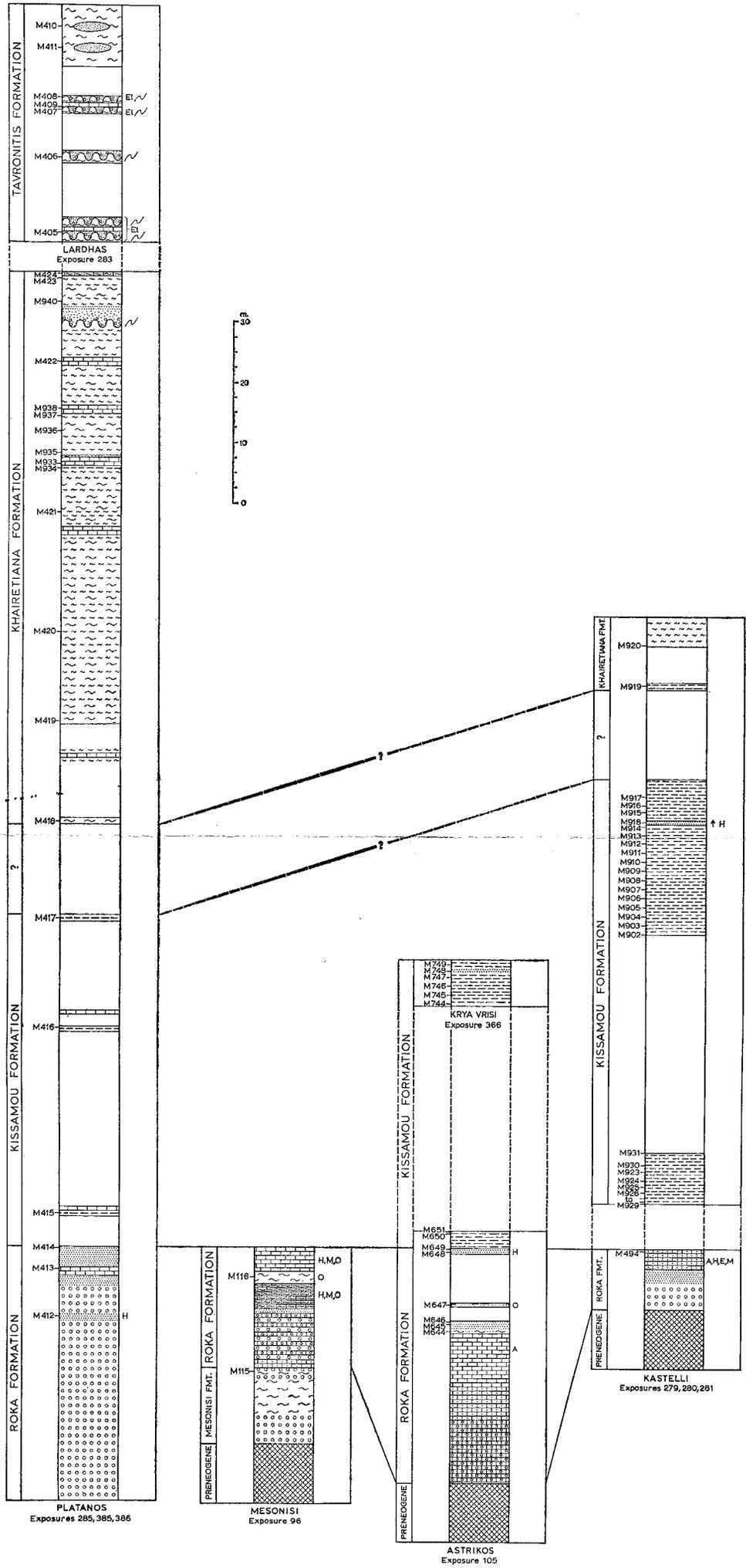
According to CHRISTODOULOU, the Pliocene corresponds to a transgressive phase in which yellow, sandy marls, changing upward into marly limestones, were formed. Locally the Pliocene starts with thin conglomerates, changing upward into cemented, sandy limestones with marly intercalations.

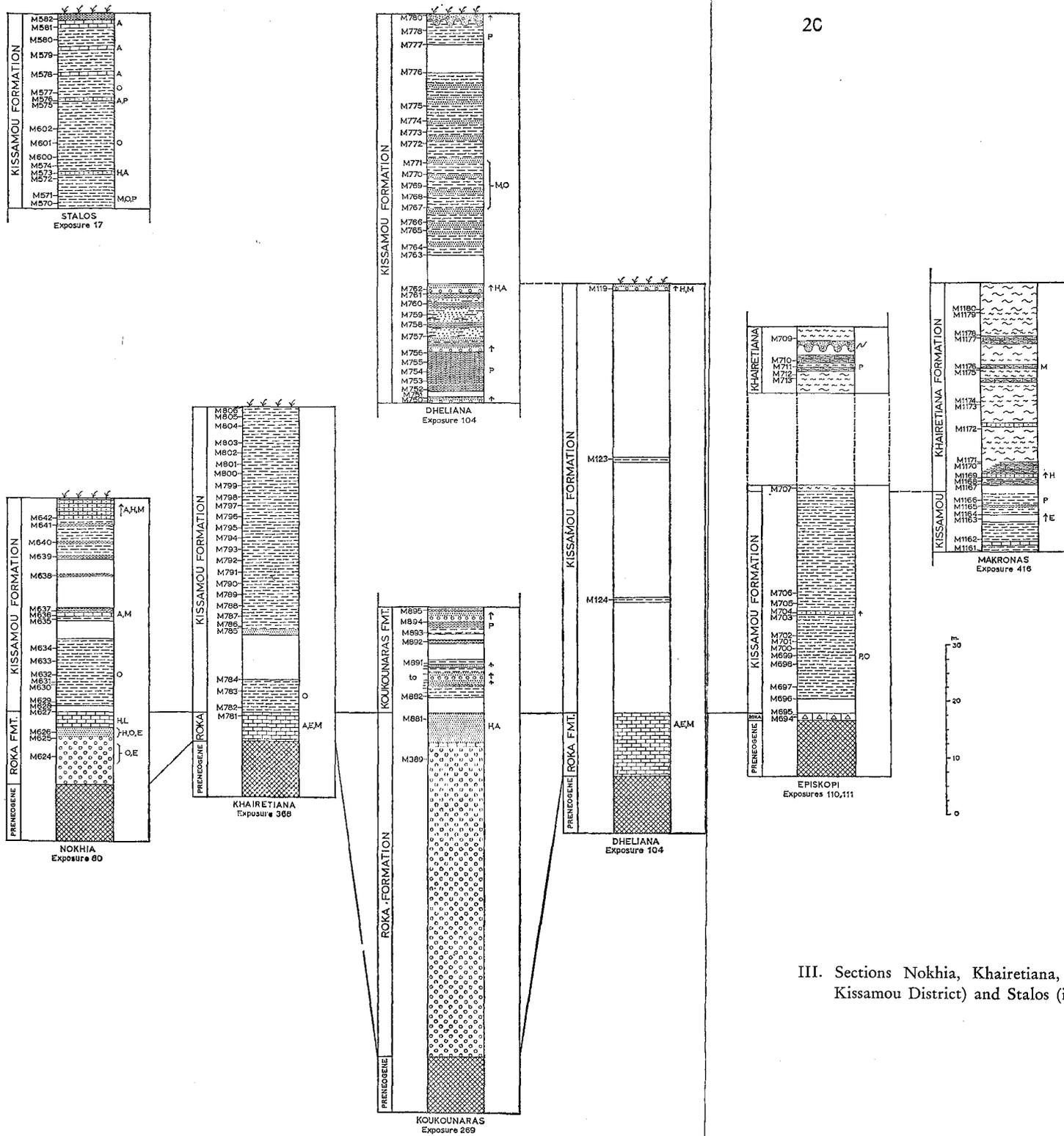
The lithologic succession described by CHRISTODOULOU roughly resembles that given by CAYEUX, but unlike that author, CHRISTODOULOU places the blue marls etc. in the Tortonian. The differences between both authors are mainly in their age assignments.



I. Legend of stratigraphic columns.

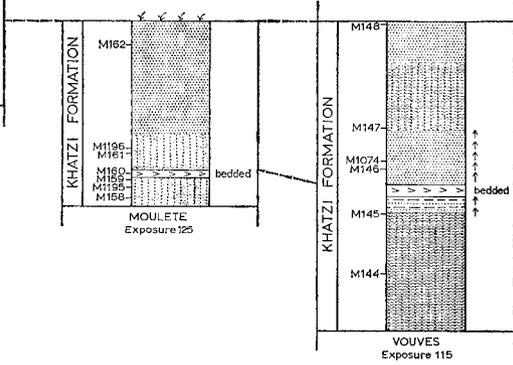
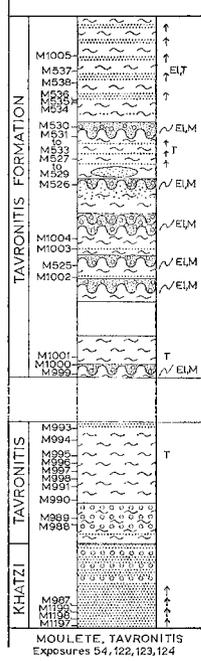
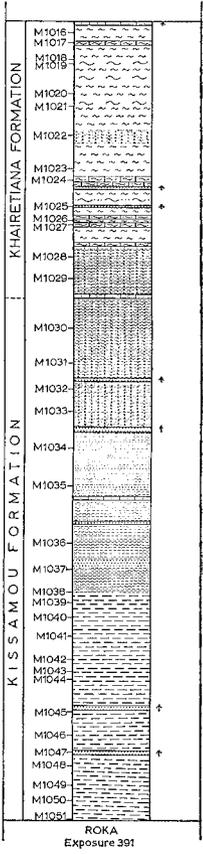
II. Sections Platanos, Mesonisi, Astrikos, and Kastelli (all in the Kissamou District).



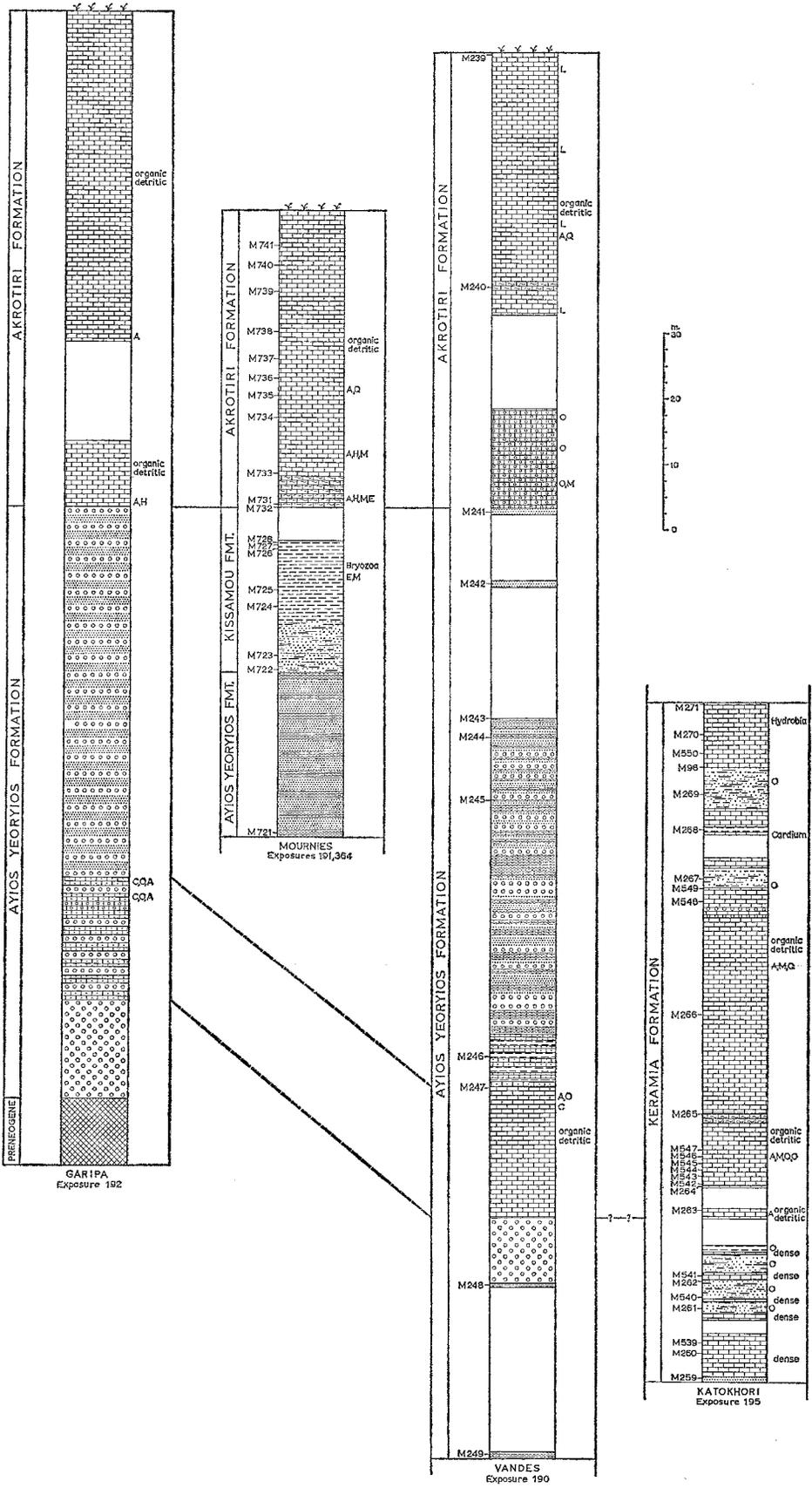


III. Sections Nokhia, Kharetiana, Koukounaras, Dheliana, Episkopi I, Makronas (in the Kissamou District) and Stalos (in the Kydonias District).

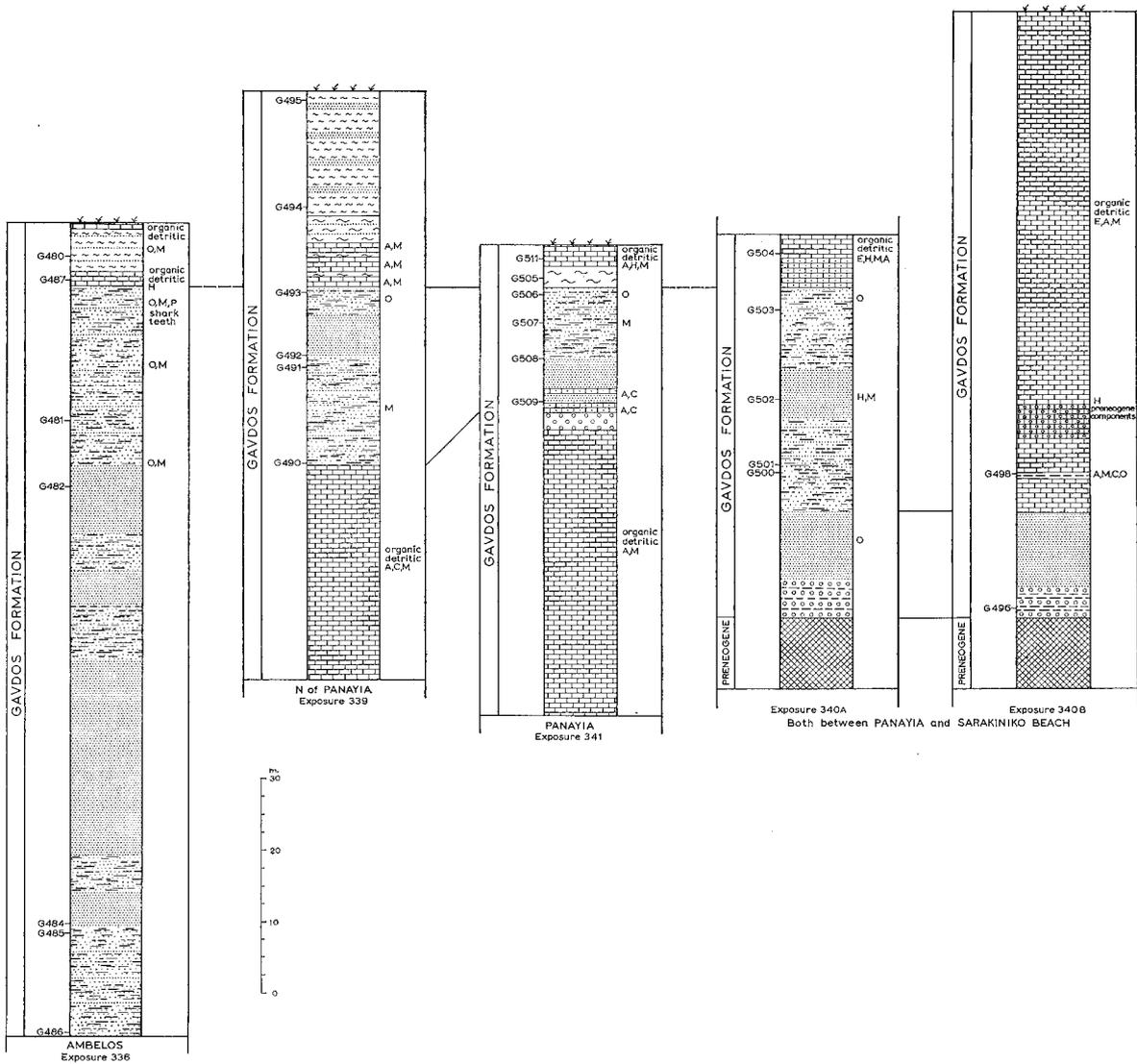
IV. Sections Roka, Potamidha, Moulere/Tavronitis, Moulere and Vouves (all in the Kissamou District, except for the Moulere/Tavronitis Section, which is situated in the Kydonias District).



V. Sections Garipa, Mournies, Vandes and Katokhori (all in the Kydonias District).



VI. Sections Ambelos, N. of Panayia, Panayia, and between Panayia and Sarakiniko Beach
(all on Gavdos Island).



KHANIA

BAY

KALATHA BAY

AKROTIRI PENINSULA

SOUDHA BAY

KHANIA

SOUDHA

PAL SOUDHA

SOUDHA ISL.

Garipa

Mournies

Malaxa

Kalam

KALYVES

Almyrida

Tsivaras

Armenoi

Gavalokhori

Vamos

Neo Khorio

Kaina

Ramni

Paidhokhori

Melidhoni

Pemonia

Fres

Tzilzifes

Vafes

Embrosneros

Alikambos

KERAMIA BASIN

YANDES

PLATI

Ay. Yeoryios

Katokhori

GEOLOGICAL MAP OF THE NEOGENE DEPOSITS IN THE KHANIA PROVINCE (CRETE), EASTERN PART. T. FREUDENTHAL.

LEGEND

-  Tavronitis Formation.
-  Khairitona Formation.
-  Akrotiri Formation.
-  Soudha Formation.
-  Kissamou Formation.
-  Ayios Yeoryios Formation.
-  Keramia Formation.
-  Preneogene Rocks.
-  Fault (certain).
-  Fault (uncertain).
-  Formation boundaries.
-  Exposure number.



Chapter II

LITHOSTRATIGRAPHY

II. 1. Introduction

Neogene sediments have a wide extension in the low, hilly, coastal plains in the northern part of the Khania province. To the south they are bordered by the steep mountain range of the Levka Ori (White Mountains), consisting of tectonically strongly disturbed strata of Triassic to Cretaceous age. In contrast, the Neogene strata have hardly been affected by tectonical movements.

Apart from their occurrence along the northern coast, Neogene deposits are also present on Gavdos Island in the Lybian Sea, approximately 25 km south of Palaiohora (fig. 1).

Within the body of Neogene deposits 11 formations are distinguished. The deposits of Gavdos Island are treated as a separate formation. Although lithologic similarities to other formations exist, the distance seems too big for any reliable lithostratigraphic correlation.

In describing the formations and their geographic distribution we will start in the Kissamou District in the west and gradually pass to the east (see fig. 2).

In the Kissamou District the preneogene rocks are unconformably overlain at one place by the Mesonisi Formation, and everywhere else by the Roka Formation. The latter is overlain in the south by the Koukounaras Formation and in the north by the Kissamou Formation. Both are overlain by the Khairitiana Formation, which is overlain in turn by the Tavronitis Formation in the westernmost part of the Kissamou District.

In the easternmost part of the Kissamou District the succession of the formations is slightly different. Here the Roka Formation is nearly absent. In the north the lowermost exposed Neogene strata belong to the Kissamou Formation. They are successively overlain by the Khatzi and Tavronitis Formations. In the south the lowermost strata, which unconformably overlie preneogene rocks, belong to the Khatzi Formation. They are overlain by the Khairitiana Formation, which is considered to be a lateral equivalent of the Tavronitis Formation in the north.

In the eastern part of the Kydonias District, in the vicinity of Khania, the Ayios Yeoryios Formation is found at the base of the Neogene. To the north it laterally passes into the Kissamou Formation. Both formations are conformably overlain by the Akrotiri Formation. To the south one finds an isolated occurrence of fresh water, brackish and marine deposits. They can hardly be correlated

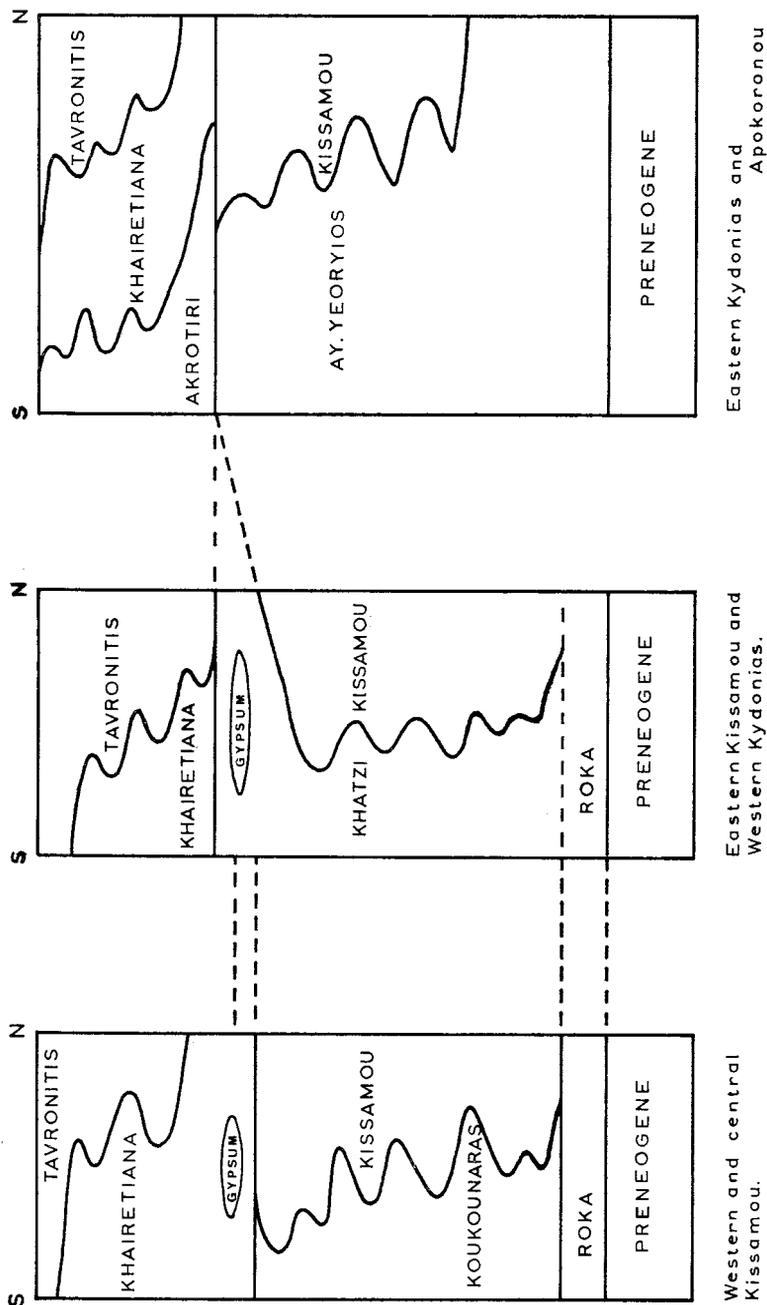


Fig. 2. Lateral transitions and lithostratigraphic correlations of the formations in several parts of the Khania Province, Crete.

with the other Neogene strata. They are therefore referred to as a separate formation, the Keramia Formation.

In the Apokoronou District, near Vryses, the lowermost Neogene strata belong to the Kissamou Formation. They are overlain by the Khairitiana Formation, which passes laterally in several directions, but mainly to the south, into the Akrotiri Formation.

Locally there are Neogene strata at the base of the Akrotiri Formation, which are lithologically well distinguishable from all other formations. They are separated as the Soudha Formation.

The Neogene strata of Gavdos Island are not subdivided into several formations. These deposits are described as Gavdos Formation, but it should be borne in mind that in this case the term formation is used in a much wider sense than has been done in the Neogene deposits along the Cretan north coast. It may denote at least two or even more lithologic units which we would consider as separate formations on Crete itself.

In the next pages we will give the succession and lateral transition of the formations, along with a detailed description. Their geographic extension is shown in the two accompanying geologic maps. The lithology and stratigraphic succession can be seen from the figured sections. Figured sections are marked with (x) in the text.

II. 2. Description of the formations.

II.2.1. MESONISI FORMATION

Diagnosis. The Mesonisi Formation consists of red conglomerates and yellow or grey marls.

Derivatio nominis. The name has been derived from the Mesonisi Church near Roka Kissamou.

Type section (x). In the vicinity of Roka near the church of Mesonisi, exposure 96.

Underlying Formation. The Mesonisi Formation unconformably overlies black, recrystallized, preneogene limestone.

Overlying Formation. The Mesonisi Formation is conformably overlain by the Roka Formation.

Geographic extension. The Mesonisi Formation is restricted to its type locality. It is not indicated on the geologic map.

Lithology. The Mesonisi Formation consists of red conglomerates, composed of preneogene, well rounded components, and yellow or grey marls. The conglomerates do not contain macrofossils. In the marls *Chara* sporangia occur frequently.

Discussion. The presence of *Chara* in the Mesonisi Formation points to a fresh water environment during sedimentation.

Literature. The beds concerned have not been mentioned by earlier authors.

Economic use. The Mesonisi Formation is of no economic value.

II.2.2. ROKA FORMATION

Diagnosis. The Roka Formation consists of conglomerates, *Heterostegina* bearing sands, and organic limestones.

Derivatio nominis. The name has been derived from the village of Roka Kissamou.

Type section. About 150 m E of the church of Roka, at the top of a steep canyon, exposure 390.

Underlying Formation. At its type locality the Roka Formation unconformably overlies black, unbedded, metamorphous limestones which are considered to be of Cretaceous age. However, at the type locality there is no clear evidence for this age assignment as fossils are completely lacking. At other localities lithologically similar limestones are known to contain fossils which point to a Cretaceous age.

Near Roka this formation conformably overlies the Mesonisi Formation (exposure 96^(x)). At other localities it unconformably overlies variously coloured shales, the age of which is unknown (exposures 269 near Koukounaras Kissamou^(x) and 279 near Kastelli Kissamou^(x)).

Overlying Formation. Not present at the type locality. In the northern part of the Kissamou District the Roka Formation is conformably overlain by the Kissamou Formation, in the southern part by the Koukounaras Formation.

Geographic extension. The Roka Formation is restricted to the Kissamou District.

Lithology. Three different, more or less successive lithologic units can be distinguished within the Roka Formation. Generally no more than one or two of these units are present at a single locality. They are from bottom to top: a) Coarse, angular, polymict, red or reddish brown conglomerates. Generally they become more finely grained in their upper part and may then contain molluscs (*Ostrea* near Nokhia, exposure 80^(x)). The thickness varies between 1 and 60 m, but generally it does not exceed a few meters. The conglomerates reach their greatest thickness between Koukounaras and Kharkhaliana (exposures 269^(x) and 369 respectively).

b) Coarse- or fine-grained, red or reddish brown sands. Locally they are cemented by calcareous matrix, giving rise to strongly indurated calcareous sandstones. At many localities macro- and microfossils are present in the sands, most frequently *Clypeaster*, *Pecten*, *Ostrea* and *Heterostegina*. Exposures with a good

macro- and microfauna are found near Nokhia (exposure 80^(x)), Afrata (exposure 334), Gourlia (exposure 322), Palaiokastro (exposure 274), Koukounaras (exposure 269^(x)), Platanos (exposure 285^(x)), and Kalathainai (exposure 378). The thickness ranges up to 30 m near Platanos (exposure 285^(x)). Cross-bedded sands are found near Gribeliana (exposure 73) and near Potamidha (exposure 259). At both localities fairly strongly dipping sand layers are cut off by more horizontal, overlying sands. Near Kalathainai (exposure 377), *Heterostegina* bearing sands laterally pass into beds which show slump phenomena.

c) Thick-bedded or unbedded, yellow or orange, weathering bluish, hard, organic limestone. Macrofossils and microfossils occur abundantly, amongst them *Pecten* and *Clypeaster* being most common; sometimes also *Heterostegina* is found. The thickness of the limestone varies between 0.5 and 50 m, but generally it does not exceed 10 m. The type section of the Roka Formation only comprises these limestones, of 8 m thickness. Limestones are present at nearly each locality where the Roka Formation is exposed, and locally they overlie the conglomerates (a), and sands (b). A nice example of the succession conglomerate — sand — limestone is found near Nokhia (exposure 80^(x)). It clearly shows a diminishing grain size from bottom to top.

In those exposures in which the limestones of the Roka Formation are directly overlying the Cretaceous(?) black limestones, the contact is often very irregular, the basal part consisting of angular black limestone boulders cemented by yellow or brown calcareous matrix; furthermore fissures and holes in the black limestone surface are filled up with yellow calcareous matter.

Discussion. As to its lithology and faunal contents the Roka Formation reflects a near-shore, shallow water environment. The cross-bedded sands may reflect a fluvatile sedimentation.

Literature. Strata belonging to the Roka Formation have been described by MARTINI (1956) as "*Clypeaster-Kalk*" and "*Clypeaster-Konglomerat*". The *Clypeaster*-limestone (= our limestones of unit c) are considered to be marine Upper Miocene (Tortonian?), the *Clypeaster* conglomerates are said to be (at least partly) fluvatile Upper Miocene. For example the cross-bedded sand layers near Gribeliana (exposure 73) are considered to be of fluvatile origin.

Economic use. The limestones of the Roka Formation are locally exploited for road metalling and house building. Near Roka and Panethymos houses were excavated in the limestones a long time ago.

II.2.3. KOUKOUNARAS FORMATION

Diagnosis. The Koukounaras Formation consists of graded beds with generally thin, interbedded, amorphous clays.

Derivatio nominis. The name has been derived from the village of Koukounaras Kissamou.

Type section ^(x). Escarpment along the road from Koukounaras Kissamou to Kalathainai Kissamou, about 50 m south of the church of Koukounaras (exposure 269).

Underlying Formation. At the type locality the Koukounaras Formation is underlain by the Roka Formation, the contact not being exposed. At other localities a similar superposition was observed, but in the south of its outcrop area the Koukounaras Formation unconformably overlies Cretaceous (?), black, metamorphous limestones.

Overlying Formation. The Koukounaras Formation may have been overlain by the Khairitiana Formation, but in that case this cover has been nearly completely removed. Only near Makronas Kissamou (exposure 389) is there a clear indication that it is really overlain by the Khairitiana Formation.

Geographic extension. The Koukounaras Formation is restricted to a quadrangle formed roughly by the villages of Koukounaras Kissamou, Makronas Kissamou, Malathyros Kissamou and the church of Ayios Paraskevi Kissamou.

Lithology. The exposures in the Koukounaras Formation are generally small, and long sections have not been found. For this reason it is rather difficult to get a good insight into the lithology and thickness of this formation. The best section known to us is that of the type locality.

The main body of the Koukounaras Formation consists of indurated graded beds; their thickness ranges between 0.5 and 2 m. To their tops the graded beds pass into laminated and amorphous blue clay, the thickness of which is variable, but seldom exceeds the thickness of the graded beds. From south to north the thickness of the graded beds decreases, whereas the thickness of the clays increases in that direction.

The basal parts of the graded beds generally consist of coarse limestone components, well rounded algal balls, and clay balls, the size of which ranges from a few centimeters to about 30 cm. Toward the top of the graded beds the grain size decreases and *Heterostegina* individuals appear, together with small algal debris and shell grit. The overlying laminated and amorphous blue clays contain some molluscs, especially *Amussium*.

The coarse basal parts of the graded beds often erode the underlying amorphous clays, giving rise to very irregular, undulating contacts.

In the southern part of its outcrop area, for example near the church of Ayios Paraskevi (exposure 377), clays are completely lacking. Here only coarse- to medium-grained, graded sandstones are present, of 50 m thickness. In the same locality it becomes difficult to differentiate the sands of the Roka Formation and those of the Koukounaras Formation. There, the algae and *Heterostegina*

bearing sands of the Roka Formation laterally pass into beds, which are composed of an irregular mixture of sand, gravel and clay balls, and which have undulating lower contacts. In northern direction the same beds show a clear grading.

In the greatest part of the outcrop area only the indurated, graded beds are exposed, and in most exposures the intercalated clays are invisible. The total thickness of this formation is probably over 200 m.

Discussion. A reasonable explanation of the alternation of graded beds and amorphous clays would be given by the mechanism of turbidity currents. In that way the coarse to fine-grained graded beds have to be regarded as displaced material originating (in this case) from a near-shore, shallow water environment, as indicated by the presence of algal balls and heterosteginids and redeposited in a deeper, off-shore environment. The intercalated, amorphous clays point to a fairly quiet environment, certainly not very shallow, as indicated by the scarcity of molluscs (mainly *Amussium*). These clays may be interpreted as the sediments which have been formed "en place".

Literature. No reference to this formation was found in the literature.

Economic use. The Koukounaras Formation is of no economic value.

II.2.4. KISSAMOU FORMATION

Diagnosis. The Kissamou Formation consists of amorphous, sometimes laminated clays with graded and non-graded clastic intercalations.

Derivatio nominis. The formation has been named after the Kissamou District.

Type section ^(x). In badlands 300 m E of the village of Potamidha Kissamou, immediately east of a concrete irrigation canal, exposure 212.

Underlying Formation. As the base of the Kissamou Formation is not exposed at the type locality, the underlying formation could not be observed. Everywhere else in the Kissamou District the Kissamou Formation conformably overlies the Roka Formation. In the Kydonias District, near Mournies (exposure 191 ^(x)), the Kissamou Formation is underlain by the Ayios Yeoryios Formation, but it is also a lateral equivalent of the top of the latter formation. Elsewhere the base of the Kissamou Formation is not exposed, neither near Vryses (exposure 184) nor in the isolated occurrences near Stalos and Dharmatokhori (exposures 17 and 116).

Overlying Formation. At the type locality the transition from Kissamou Formation to the overlying Khairtiana Formation is not exposed. This transition has been observed at two localities only, near Roka Kissamou (exposure 391 ^(x)) and Makronas Kissamou (exposure 416 ^(x)). Only near Makronas is the contact sharp, near Roka a boundary can hardly be drawn. In the eastern part of the

Kissamou District the Kissamou Formation is conformably overlain by the Khatzi Formation, for example near Kalami (exposure 395) and near Zymvragou (exposure 305) in the south and near Dharmatokhori in the north (exposure 116).

In the Kydonias District the Kissamou Formation is probably conformably overlain by the Tavronitis Formation between Ayia Marina and Khania, and it is conformably overlain by the Akrotiri Formation near Mournies (exposure 191^(x)).

In the Apokoronou District, the small, isolated occurrence of the Kissamou Formation near Vryses (exposure 184) is overlain by the Khairitiana Formation, but the contact is not exposed.

Geographic extension. The Kissamou Formation is nearly completely restricted to the Kissamou District, where it laterally passes into the Koukounaras Formation. Isolated occurrences one finds in the vicinity of Dharmatokhori Kissamou, Khania and Vryses Apokoronou.

Lithology. The main body of the Kissamou Formation consists of blue or purple amorphous clays, but locally these clays are laminated. Within these clays strongly indurated, graded and ungraded, sandstones, calcarenites and organic limestones occur at various stratigraphic levels. Three different types of lithology will be discussed below.

1. Blue or purple, generally amorphous, sometimes laminated clays. Macrofossils are present, but they are abundant at a few localities only, for example near Stalos Kydonias (exposure 17^(x)). From this locality numerous molluscs have been described KOLIOPOULOS (1952). Among them *Pycnodonta*, *Amussium* and *Ephippium* are the most common genera, *Dentalium*, *Arca*, *Cardium*, *Venus*, *Corbula*, *Chlamys*, *Spondylus* and *Ancilla* occur in smaller quantities. A similar mollusc fauna was found in the isolated occurrence of the Kissamou Formation near Vryses Apokoronou (exposure 184). In other fossiliferous localities *Amussium* is the most common mollusc, but it is never abundant.

Near Dheliana Kissamou (exposure 104^(x)) and near Ayia Marina Kydonias (exposure 21) the Kissamou Formation mainly consists of laminated, sandy clays. In both exposures we have to do with an alternation of thin sand and clay laminae. At other localities, for example near Roka Kissamou (exposure 391^(x)), the upper part of the Kissamou Formation consists of laminated clays, being transitional to the laminated clays and marls of the overlying Khairitiana Formation. The origin of this lamination is not known.

2. Graded, clastic intercalations.

In nearly all sections studied the main mass of blue and purple clays is interrupted by indurated coarse- to fine-grained graded beds at various stratigraphic levels. Their thickness ranges from 5 cm to 10 m. Because of their induration the graded beds often form caprocks, the softer, plastic clays having been eroded away.

Generally the basal parts of the graded beds consist of gravel, sometimes mixed with large clay balls derived from erosion of underlying clays. Algal balls and *Heterostegina* specimens are commonly present in the coarse basal parts. Towards the tops of the graded beds the grain size decreases and sand becomes dominant; *Heterostegina* and algal balls disappear. Occasionally there is a narrow, laminated transition between the sandy upper parts of the graded beds and the overlying amorphous clays.

Generally the thickness of the graded intercalations does not exceed 2 m, but it is much thicker (10 m) near Ligoriana Kissamou (exposure 372). Here the basal part is very coarse and consists of big calcareous boulders (amongst them coarse coral debris) up to 50 cm diameter.

A very fine example of a graded intercalation can be observed near Episkopi Kissamou (exposure 354). Here, within a 3 m thick caprock, several graded beds are overlying each other. Each one has a coarse basal part and the grain size decreases rapidly to their tops, which consist of finely laminated clay. The laminated clay shows convolute lamination which is cut off by the coarse basal part of the next, overlying graded bed. Sometimes overlying graded beds strongly erode the underlying beds in such a way that the laminated clay at the top of the underlying sequence has been completely eroded away (clay balls are still found in the coarse basal part of the overlying bed), and even part of the fine-grained top has been removed.

3. Non-graded sand, gravel and limestones.

At several localities sand or gravel layers, without any clear graded bedding, occur within the blue and purple amorphous clays at various stratigraphic levels. They are often indurated by calcareous matter. At the locality Psathi near Stalos Kydonias (exposure 17^(x)) several of these beds are present in the top of the Kissamou Formation. These beds consist of an irregular mixture of sand and medium-size calcareous (mainly algal) components. They contain also bryozoa, coral debris and *Heterostegina*.

Near Maredhiana Kissamou (exposure 276) the top of the Kissamou Formation consists of a 3 m thick, unbedded limestone. It is composed of an irregular mass of cemented *Serpula*, mollusc shell debris, as well as complete shells. Similar looking limestones are formed nowadays in the intertidal beach flat, for example at Livadhi Bay (exposure 387) and near the jetty of Georgioupolis Apokoronou, but in both cases a hard base rock is present (this is not the case near Maredhiana). We have probably to do here with material of similar origin, but displaced and cemented.

The total thickness of the Kissamou Formation amounts to 175 m.

Discussion. The blue and purple clays form the major part of the Kissamou Formation. Morphologically, however, the graded (and non-graded) intercala-

tions are much more striking than the clays, since they are often indurated and form caprocks which can be traced over considerable distances.

As to the origin of the graded beds we may refer to our discussion on the origin of the graded beds in the Koukounaras Formation. Also in this case we are of the opinion that shallow water, near-shore material (for example algae and *Heterostegina*) together with coarse to fine clastic material has been transported by turbidity currents into deeper, off-shore environments.

It may now be clear, if one compares the lithology of the Koukounaras and Kissamou Formations, that both formations do not differ essentially. They are clearly lateral equivalents. In practice the boundary between both formations is drawn where graded beds are dominating (Koukounaras Formation) or where amorphous clays are dominating (Kissamou Formation). Of course, this lateral transition is a gradual one and the boundary is not sharp.

Literature. The graded or ungraded caprocks MARTINI (1956) referred to as separate lithologic units: "Obere *Clypeaster*-Schichten" and "Korallen-Kalk im *Clypeaster*-Mergel". The amorphous clays are named "*Clypeaster*-Mergel", and in the vicinity of Khania they are referred to as "*Galatas*-Schichten".

The latter MARTINI considers to be of Sarmatian (?) age, the others are thought to be of Tortonian age. Since graded and non-graded intercalations may occur at many variable levels in the amorphous clays it is not useful to designate them by a special name.

Economic use. Near Ayia Marina Kydonias the amorphous clays are quarried for brick fabrication.

II.2.5. KHAIRETIANA FORMATION

Diagnosis. The Khairtiana Formation consists of alternating layers of amorphous marls and laminated marls or clay. Gypsum deposits are locally present in its lower part. Graded beds are rare.

Derivatio nominis. The formation has been named after the village of Khairtiana Kissamou.

Type section. ^(x) Escarpment along the recently (1964?) broadened road from Kaloudhiana Kissamou to Khairtiana Kissamou. The type section is exposed in three successive outcrops; the strata in between are not exposed, but the stratigraphic gaps are small (4 m and 1 m respectively). The church at the northern village entrance of Khairtiana has been built on the top of the type section (exposure 292).

Underlying Formation. At the type locality the Khairtiana Formation is underlain by the Kissamou Formation, but the transitional (probably gypsiferous) strata are not exposed. In the centre of the Kissamou District the Khairtiana

Formation is underlain by the Kissamou Formation in the north and by the Koukounaras Formation in the south. A clear contact with the Kissamou Formation is present only near Makronas (exposure 416^(x)).

In the eastern part of the Kissamou District the Khairëtiana Formation is underlain by the Khatzi Formation. The transition is a gradual one and is exposed near Voukolies (exposure 127) and near Panethymos (exposure 107 B).

In the Apokoronou District the Khairëtiana Formation is overlying the Kissamou Formation in the neighbourhood of Vryses (exposure 184). Furthermore, it is partly overlying and partly a lateral equivalent of the Akrotiri Formation. The same superposition and lateral transition is found on Akrotiri Peninsula.

Overlying Formation. At the type locality the Khairëtiana Formation forms the top of the Neogene strata. In the westernmost part of the Kissamou District, near Lardhas (exposure 283^(x)), it is overlain by the Tavronitis Formation.

In the Kydonias District the Khairëtiana Formation is partly overlain by the Tavronitis Formation, and it is partly a lateral equivalent of it (Khairëtiana Formation in the south, Tavronitis Formation in the north). In the Apokoronou District the Khairëtiana Formation is not overlain by other Neogene strata.

Geographic extension. The Khairëtiana Formation is most widely distributed in the Kissamou and Apokoronou Districts.

Lithology. The Khairëtiana Formation consists of numerous alternations of yellow to brown predominantly, laminated marls, clays or sandy clays, and yellow amorphous marls or marly limestones. Coarse, graded intercalations are rare.

The thickness of one sequence of laminated and amorphous layers generally does not exceed 5 m. Graded beds generally are 0.5 m thick or less.

The amorphous marls do contain scarce molluscs or other macrofossils, but microfossils occur abundantly, especially *Discospirina*, and other, smaller miliolids. These foraminifera were not found in the laminated clays and marls, which contain much plant debris. Moreover, sponge needles and diatoms are very common in the laminated layers.

The few, coarser graded beds show close resemblance to those in the Koukounaras and Kissamou Formations, but their basal part is generally less coarse. The biggest components do not exceed 1 cm in diameter. Marl or clay balls were not observed. *Heterostegina* specimens are found in the coarse lower parts, but they are never common and were observed at two localities only.

In the Kissamou District, along the north coast, between the villages of Dhrapanias and Papadhiana, gypsum deposits are present in the lowermost part of the Khairëtiana Formation. They are found in association with laminated marls, that contain fish remains (sometimes complete skeletons). RAULIN (1861) described these fishes as *Lebius* from the village of Kaleryiana (exposure 295).

In those exposures in which the gypsum is clearly bedded (for example

exposure 295), the thickness does not exceed 1.5 m. At other localities, where bedding planes are invisible, the thickness may amount to 50 m. Here, probably we have to do with squeezed out gypsum masses or solved gypsum masses, which have been secondarily crystallized. Such irregular gypsum masses were observed near Papadhiana (exposure 278) and near Kaloudhiana (exposures 297, 323).

In the Apokoronou District the Khairitiana Formation has a slightly different lithologic character. Here, laminated and amorphous white marls alternate with coarser, organic, detritic limestones, in which never any gradation could be observed. In the neighbourhood of Almyrida (exposure 422) the detritic beds wedge out in northern direction. Generally the amorphous marls and detritic beds are strongly indurated, whereas the laminated marls are soft. This difference led to a terraced character of the morphology.

At two localities near Kalyves Apokoronou (exposure 164 and 222) the laminated marls are of very light weight and devoid of plant remains. Sponge needles occur abundantly. These laminated marls alternate with thin (up to 15 cm) indurated limestone beds with numerous *Pycnodonta*. The marls show close resemblance to the Italian "tripoli" and Spanish "moronitas".

The maximal thickness of the Khairitiana Formation probably amounts to 100 m.

Discussion. In its lower part the Khairitiana Formation consists mainly of brown to white, laminated marls or clays. If it is borne in mind that the Khairitiana Formation is overlying the Kissamou Formation, its similarity to the upper part of that formation becomes clear. The transition from one to the other is gradual and a boundary between both formations can be drawn only arbitrarily.

The origin of the lamination in the upper part of the Kissamou Formation has not become clear from our field data, and the same is true for the laminated marls and clays of the Khairitiana Formation. Even for the alternation of laminated and amorphous marls no sound explanation can be given on the basis of the field observations.

Evidently, the plant debris which frequently occur in the laminated beds can provoke some kind of lamination, if deposited intermittently, but it is doubted whether such an explanation is justified for all the laminated layers.

Probably grain size alternations play a part in the origin of the lamination as well.

Literature. Sediments belonging to the Khairitiana Formation have not been designated by a special name by earlier authors.

Economic use. The Khairitiana Formation is exploited in small quarries near Gavalokhori Apokoronou for building stones.

II.2.6. KHATZI FORMATION

Diagnosis. In the Khatzi Formation two lithologic units are distinguished: a coarsely clastic one consisting of conglomerates and subordinate marls and clays, and a finely clastic one consisting of numerous thin graded beds and laminated clay. Gypsum deposits may be present in its upper part.

Derivatio nominis. The formation has been named after the village of Khatzi Kissamou.

Type section. On the western side of the road from Khatzi Kissamou to Fotokadhon Kissamou, in a wide hairpin curve (exposure 311 A). The type section has not been figured, as its lithology is laterally changing rapidly.

Underlying Formation. At the type locality, as well as along the southern border of the Neogene deposits, the Khatzi Formation unconformably overlies black, recrystallized (Cretaceous?) limestones. Everywhere else this formation is overlain by the Kissamou Formation.

Overlying Formation. In the type section the transition from the Khatzi Formation to the overlying Khairitiana Formation is not exposed. It is visible, however, near Voukolies Kissamou (exposure 127). In the southern part of its outcrop area the Khatzi Formation is overlain by the Khairitiana Formation, in the northern part it is overlain by the Tavronitis Formation. The Khairitiana and Tavronitis Formations are considered to be, at least partly, lateral equivalents of each other.

Geographic extension. Apart from a small, dubious occurrence near Platania Kydonias (exposure 198), the Khatzi Formation is restricted to the eastern part of the Kissamou District.

Lithology. Within the Khatzi Formation a rough subdivision into two lithologic units can be made, a coarsely clastic one and a predominantly finely clastic one, which units are lateral equivalents of each other. The last mentioned comprises the largest part of the formation's outcrop area.

The coarse, clastic sediments occur mainly along the southern border of the Neogene deposits, overlying preneogene, black limestones, between the villages of Fotokadhon Kissamou and Limni Kydonias. The type section is situated in this type of sediment. Its lithology is: well, to moderately well bedded, brown or grey, polymict conglomerates. The bedding planes are always strongly undulating. Components are badly rounded shale and quartzite, not exceeding 10 cm in diameter. Furthermore well rounded calcareous components occur. In the conglomerates macrofossils are present, for example *Pecten* and *Ostrea*.

In between the conglomerate layers thin, generally dark coloured, laminated sandy clays and sandy marls are present. Rarely dark, amorphous clays occur. Macrofossils are not found in the fine-grained, intercalated layers.

In the type section several sedimentary phenomena were observed. Coarse

conglomerates have eroded underlying laminated marls and clays, giving rise to irregular, undulating contacts. Balls of clay and marl are found between the shale, quartzite and calcareous components of the conglomerates. Furthermore, masses of coarse material slumped into fine-grained sediments were observed. Graded bedding was not seen. In the uppermost part of the Khatzi Formation, near Kato Kefala Kissamou (exposures 399, 400), limestones and sandy limestones with *Clypeaster*, *Pecten* and *Heterostegina* occur. They strongly remind us of the limestones of the Roka Formation. The thickness of this coarsely clastic unit of the Khatzi Formation amounts to 100 m maximally.

The finely clastic sediments mainly consist of thin graded beds. These beds are never coarse-grained in their basal parts. The size of the components does not exceed 0.5 cm. To their tops the grain size decreases rapidly and at their tops laminated, dark, blue or black clays are present. The coarser, basal parts of the graded beds are often indurated, whereas the upper, laminated parts are soft. In the laminated clays convolute lamination was observed at several localities. Macrofossils were not found in the graded beds, but plant debris was often present in the laminated clays.

Nice examples of graded beds can be observed near Moulete (exposure 124^(x)), Vouves (exposure 115^(x)), Kares (exposure 306) and Neo Khorio (exposure 317). In the last exposure the graded bedding becomes less clear to the top of the Khatzi Formation. Alternations of sand and clay are present, but there is no distinct graded bedding.

Toward the top of the formation thin calcareous beds occur in association with a gypsum layer of 1.5 m, which is well exposed near Neo Khorio (exposure 316). In the calcareous beds we found complete skeletons of fishes, which resemble those found in the laminated marls associated with a gypsum bed in the lowermost part of the Khairtiana Formation near Kaleryiana Kissamou (exposure 295). Gypsum layers in similar position are exposed also in the neighbourhood of Vouves (exposure 115^(x)), near Skafiotou (exposure 314), near Mothiana (exposure 149), and near Moulete (exposure 125^(x)). The colour of the clay, which overlies and underlies the gypsum bed may vary considerably; black, blue, green and red colours were observed.

At some localities, for example near Vouves (exposure 115^(x)) and near Moulete (exposure 124^(x)), the uppermost part of the Khatzi Formation is more coarsely developed. Here red sand and gravel beds are found at the top of the formation.

It is rather difficult to get a good insight into the thickness of this finely clastic unit of the Khatzi Formation on the basis of our field observations. The thickness diminishes from south to north, probably amounting to 80 m in the south, and to at least 40 m in the north (near Vouves, exposure 115^(x)).

Discussion. The region of the coarse, mainly conglomeratic sediments of the Khatzi Formation along the border of Neogene deposits in the south is considered to be a near-shore supply area of material which spread widely to the north. Slump structures in the type section for example point to a displacement in northern direction. The origin of the graded beds which dominate in the finely clastic sediments of the Khatzi Formation may be explained by turbidity currents, probably originating from the supply area in the south. Other sedimentary phenomena, like details of the convolute lamination, justify the assumption of a transport direction from south to north.

Literature. MARTINI (1956) erroneously included deposits near Dharmatokhori in the "Platanias Mergel", which is characterized by a completely different lithology.

Economic use. The gypsum beds near Neo Khorio were exploited during the second world war.

II.2.7. TAVRONITIS FORMATION

Diagnosis. The Tavronitis Formation consists of amorphous marls, which alternate in the upper part of the formation with many slightly graded beds. In the marls many slumps of coarse material occur.

Derivatio nominis. The formation has been named after the Tavronitis River.

Type section ^(x). The type section is situated in an escarpment along the road from the Maleme airstrip to Sirili Kissamou (exposure 54), along the eastern bank of the Tavronitis River.

Underlying Formation. At the type locality only the upper part of the Tavronitis Formation is exposed. Slightly farther to the south the lower part is exposed in outcrops along the road from Tavronitis Kissamou to Voukolies Kissamou. There, as well as in the whole eastern part of the Kissamou District the Tavronitis Formation conformably overlies the Khatzi Formation. In the western part of the Kissamou District near Lardhas the Tavronitis Formation overlies the Khairitiana Formation, which is its lateral equivalent in the eastern part of the Kissamou District.

Near Platanias Kydonias the Tavronitis Formation probably unconformably overlies preneogene rocks. Near Galatas Kydonias the Tavronitis Formation is underlain by the Kissamou Formation, but the contact is nowhere exposed.

Overlying Formation. The Tavronitis Formation is nowhere covered by other Neogene deposits.

Geographic extension. The Tavronitis Formation is restricted to the eastern and westernmost parts of the Kissamou District, and occurs in vast areas of the Kydonias District.

Lithology. In its lower part this formation consists mainly of white, amorphous marls. In its middle part it consists of gravel masses slumped into similar looking marls and in its upper part it consists of slightly grading sand beds alternating with amorphous marls.

The succession is well exposed along the eastern and western banks of the Tavronitis River, most other outcrops are small and give hardly any information about the lithological succession. Therefore, the following description is based mainly on the outcrops along the Tavronitis River.

a. The lower part of the Tavronitis Formation is exposed near Moulete Kissamou (exposures 124, 123^(x)). It consists of white, amorphous, unbedded marls without macrofossils. Many unoriented tubular worm tracks were observed. They have a slightly lighter colour than the surrounding marls. In the basal part several non-graded coarse gravel layers are interbedded. They contain well rounded shale and quartzite components. The contacts with the underlying and overlying marls are irregular and undulating. The gravel beds wedge out in northern direction.

b. The middle part of the Tavronitis Formation consists of white, amorphous, unbedded marls with numerous unoriented worm tracks. Large masses of coarse, macrofossil bearing material have slumped into these marls. They have eroded the underlying marls, giving rise to strongly undulating contacts. Big marl balls have been mixed with the other displaced material. The upper contact of the layers containing slumped masses with the overlying marls is generally straight, but some of the slumps were found to have eroded an underlying one. The slumped masses attain a thickness of maximally 3 m, which thickness decreases rapidly in a horizontal sense. The slumped material consists of sand, and in minor quantities of gravel. Large quantities of *Pecten* and *Elphidium* are present. No indication of graded bedding was observed. This middle part of the Tavronitis Formation is exposed near Moulete Kissamou (exposure 122^(x)) and in the lower part of the type section.

c. In the type section the marls with slump structures are overlain by well bedded, slightly grading, medium- to fine-grained, brown, soft sands of 25–50 cm, which alternate with indurated, amorphous white marls with numerous unoriented worm tracks. Furthermore, big vertically running tracks of 2 to 3 cm diameter are present within the marls. They are filled with sandy material of the overlying graded sequence. Probably they are burrows of crabs. In the graded beds macrofossils are nearly completely lacking, but occasional specimens of *Elphidium* were found.

The total thickness of the Tavronitis Formation in the Tavronitis River valley amounts to about 80 m.

Near Platania Kydonias the basal amorphous marls contain calcareous concretions.

Near Platanos Kissamou, in the westernmost part of the area investigated, the upper part of the Khairitiana Formation gradually changes into white marls with large slump structures, but these marls are clearly laminated (exposure 386^(x)). Near Lardhas (exposure 283^(x)) similar slump structures are found in amorphous white marls. They are clearly identical with the sediments of unit b. Marls without slumps were hardly observed in this area. The coarse displaced material contains numerous *Pecten* and *Elphidium*.

Discussion. In the type section there is a clear change in lithology from bottom to top. This change reflects important changes in the character of the sedimentation. The amorphous marls at the base may reflect a fairly continuous, quiet, off shore sedimentation, comparable with that of the clays of the Kissamou Formation. Probably the same sedimentary conditions prevailed throughout the time of sedimentation of the Tavronitis Formation, but to its top the influence of displaced material becomes stronger.

The slumps contain coarse material and representatives of *Elphidium*, which usually live in shallow near-shore water. They point to the transport of material from a near-shore supply area into deeper water. Since similar slumped masses are found in the vicinity of the supply area of displaced material in the Koukounaras Formation we may assume that the supply area in this case was not far away either.

The graded beds in the upper part of the type section point to a transport of material by means of turbidity currents. In this case we suppose that the supply area was farther away.

Literature. The Tavronitis Formation has been subdivided into two lithological units by MARTINI (1956): "Platania-Mergel" and "Platania-Konglomerat". "Platania-Mergel" is applicable to our unit a. of the type section; the "Platania-Konglomerat" comprises our units b. and c. They are considered as marine Pliocene by MARTINI ("Lower Plaisancian or Astian").

Economic use. The Tavronitis Formation is of no economic value.

II.2.8. AYIOS YEORYIOS FORMATION

Diagnosis. The formation consists of conglomerates, sands, clays and organic, detritic limestone.

Derivatio nominis. The formation is named after the village of Ayios Yeoryios Kydonias in the Varvara River valley.

Type section ^(x). The type section is situated along the western flank of the Varvara River valley, S of Vandes Mountain (exposure 190).

Underlying Formation. The Ayios Yeoryios Formation is underlain by preneogene shales and black, recrystallized limestones the age of which is unknown.

Overlying Formation. At the type locality the Ayios Yeoryios Formation is overlain by conglomeratic or sandy sediments of the Akrotiri Formation. In the northern part of the Varvara River valley it is overlain by the Kissamou Formation.

Geographic extension. The Ayios Yeoryios Formation is restricted to the Kydonias District, in a quadrangle formed roughly by the villages of Mournies, Ayios Yeoryios and Garipa and the Plati hill.

Lithology. It is hardly possible to give a short description of the lithology of the Ayios Yeoryios Formation, as it is highly variable and rapidly changing laterally. At its base generally medium-thinly bedded, brown or reddish brown, well rounded conglomerates are present. The components derived from the underlying preneogene rocks are polymict and their size rarely exceeds 5 cm. The thickness of the conglomerates amounts to 100 m or more. Locally the components are cemented with calcareous matter and contain coral fragments (exposure 192^(x)).

Toward their top, as well as laterally, the conglomerates pass into sands and sandy, laminated, brown or blue clays, which alternate in an irregular order. Fossils are rare. *Pecten*, *Ostrea* and ostracods were found. Graded beds were never observed. The type section of the Ayios Yeoryios Formation is situated in these fine-grained sediments. Laterally the upper part of the formation passes gradually into the Kissamou Formation.

In the basal part of the type section a 20 m thick, organic, detritic, well bedded limestone is present. It is nearly completely composed of *Pecten*, *Ostrea* and algal remains; also coral debris plays a part, though a subordinate one. Perhaps these limestones can be correlated with the coral detritus bearing level in conglomerates of exposure 192^(x) in the Therissiano Canyon.

Discussion. Little can be said about the sedimentary environment of this formation, but it is highly probable that we have to do with a near-shore equivalent of the Kissamou Formation.

Literature. No literature reference to this formation was found.

Economic use. The Ayios Yeoryios Formation is of no economic value.

II.2.9. AKROTIRI FORMATION

Diagnosis. The Akrotiri Formation consists of organic limestones, and subordinate conglomerates and *Heterostegina* bearing sands.

Derivatio nominis. The name has been derived from the Akrotiri Peninsula.

Type section^(x). Situated in the western bank of the Varvara River valley, south of Mournies Kydonias (exposures 191 and 364).

Underlying Formation. At the type locality the Akrotiri Formation is underlain by blue clays of the Kissamou Formation. Farther southward in the same valley the Akrotiri Formation is underlain by the Ayios Yeoryios Formation, which is, at least partly, a lateral equivalent of the Kissamou Formation. At most other localities, where the base of the Akrotiri Formation is exposed, it is overlying pre-neogene shales or black crystallized limestones. In a small occurrence along the southern flank of Soudha Bay the Akrotiri Formation is underlain by the Soudha Formation (exposure 239).

Overlying Formation. In the type section, as well as in other parts of the Kydonias District, the Akrotiri Formation is not overlain by other Neogene strata. In the Apokoronou District the Akrotiri Formation laterally passes into the Khairitiana Formation and it is also overlain by it.

Geographic extension. The Akrotiri Formation is restricted to the Apokoronou District and to the eastern part of the Kydonias District.

Lithology. The Akrotiri Formation nearly completely consists of organic, detritic and marly limestones. Its base may be conglomeratic or sandy.

In those places where the Akrotiri Formation overlies preneogene rocks generally coarse, well rounded conglomerates are found. The size of the components, derived mainly from the underlying preneogene rocks, but rarely exceeds 10 cm. The thickness of the conglomerates is usually less than 2 meters; near Pemonia Apokoronou the thickness amounts to 25 m.

At the other localities, where the Akrotiri Formation overlies Neogene strata, its basal part is generally developed as coarse- to medium-grained, brown, uncemented sands, but occasionally also with conglomerates. These sands contain a rich fauna of macro- and microfossils, amongst which *Ostrea*, *Pecten*, *Clypeaster* and *Heterostegina* are most abundant. This fauna very well resembles that of the sands of the Roka Formation, and that of limestones in the uppermost part of the Khatzi Formation. These sands are exposed in the Therissiano Canyon (1.5 km west of the Varvara River valley, exposure 193) and in the eastern outskirts of Khania, near the church of Ayios Kiriaki (exposure 15). They are maximally 10 m thick.

The major part of the Akrotiri Formation consists of unbedded and of thick, well bedded, white or yellow limestones or marly limestones. They are composed of organic detritus, mainly of algae and in minor quantity of shell debris or complete mollusc shells. In the basal part of these limestones *Heterostegina* occurs in the type section. At some localities the molluscs are excellently preserved, for example near Khorafakia Kydonias in the Akrotiri Peninsula (exposure 202). Here *Amussium*, *Pecten*, *Ostrea* and *Pholadomya* are abundant, in addition to very numerous brachiopods (*Terebratula*) and echinids.

At some localities, mainly along the southern flank of Soudha Bay (for

example at exposure 86), algae form irregular, often lens-shaped bodies of unbedded reefal limestone. They wedge out laterally within a few meters. The total thickness of the Akrotiri Formation amounts to 125 m (Akrotiri Peninsula).

Discussion. It is assumed that the Akrotiri Formation has been deposited in a shallow environment. Its fauna, for example the heterosteginids, clearly point to such an environment. Very similar algal limestones are formed at present in the intertidal zones of some Cretan beaches. They also occur all along the mediterranean coasts, forming rather extensive coastal platforms (the french "trottoirs").

Literature. The Akrotiri Formation is referred to as "pietra di Malta" by BONARELLI (1901).

Economic use. The Akrotiri Formation is exploited near Khania for making cement. At numerous places the limestones are used for house building.

II.2.10. SOUDHA FORMATION

Diagnosis. The Soudha Formation consists of thin-bedded, dense limestones.

Derivatio nominis. The formation derives its name from Soudha Bay.

Type section. The type section is situated in an escarpment along the road from Soudha Kydonias to Kalami Apokoronou, about 1.5 km from Kalami (exposure 87).

Underlying Formation. The Soudha Formation is underlain by brecciated, pre-neogene (Cretaceous?) crystallized black limestone.

Overlying Formation. The Soudha Formation is overlain by the limestones of the Akrotiri Formation (absent at the type locality).

Geographic extension. The Soudha Formation is restricted to a few outcrops along the road from Soudha Kydonias to Kalami Apokoronou (exposures 239 and 87).

Lithology. The formation consists of thin-bedded or platy, brown, yellow or white, dense limestones or slightly sandy limestones. Occasionally thin, sandy and marly layers were found interbedded. Neither macrofossils nor microfossils were found. A single observation was made of a layer of coarse sand eroding an underlying finer sand, giving rise to an undulating contact in between (exposure 239). It is difficult to get some idea of the thickness of this formation, because its strata are strongly affected by movements along the Soudha fault. Perhaps the thickness will amount to 75 m (11 m in the type section).

Discussion. Judging from the peculiar type of lithology, and the complete lack of fossils, we might have to do with fresh water deposits. SIMONELLI (1894) described fresh water molluscs from Kalami. They have probably been derived from the deposits concerned.

Literature. See discussion.

Economic use. The Soudha Formation is of no economic value.

II.2.11. KERAMIA FORMATION

Diagnosis. The Keramia Formation consists of dense, thin-bedded limestones, of thick-bedded organic limestones and of clays with oysters.

Derivatio nominis. The formation has been named after the Keramia depression.

Type section ^(x). The type section is situated in the Keramia depression, in an escarpment along the road from Malaxa to Katokhori Kydonias, about 7 km south from Khania (exposures 69 and 195).

Underlying Formation. The base of the Keramia Formation is never exposed.

However, it is highly probable that no other Neogene formation is underlying the Keramia Formation. It is assumed that it unconformably overlies preneogene shales and limestones.

Overlying Formation. The Keramia Formation is not overlain by other Neogene strata.

Geographic extension. The Keramia Formation is only well exposed at the type locality. Everywhere else in the Keramia depression, to which it is geographically restricted, the Keramia Formation is affected by a deep, red surface weathering, to such an extent that additional, small exposures are found only in deep erosion gullies.

Lithology. The formation consists of alternating brown clays with oysters and white, dense limestones generally without macrofossils. This alternation is interrupted in the middle of the formation by rather massive, thick-bedded organic limestones.

A short summary of the lithologic succession in the type section is given below.

At the base 1 m of reddish to brown sand is present. It is overlain by an alternation of thin-bedded, white, dense, often brecciated limestone without macrofossils and brown clays with *Ostrea* and *Crassostrea*. The limestones measure up to 6.50 m in thickness, the clays may attain a thickness of 3 m. The total of these alternating strata measures about 25 m. They are overlain by some 10 m of slightly bedded organic limestones, composed of mollusc shells (fragments and complete shells) and algal detritus. In the lowermost part *Ostrea* dominates. This limestone is overlain by 30 m of badly exposed, organic limestone, composed mainly of mollusc shells, with smaller quantities of algal remains. The organic material plays a far less important part in this limestone, the underterminable calcareous contents is much higher.

These limestones are overlain by white, dense, thin-bedded (up to 10 cm) limestones, which only in the top of the section contain clear casts of macrofossils (*Hydrobia*). They alternate with brown clays with *Ostrea* and *Crassostrea*. These alternating beds measure about 25 m.

The minimum thickness of the Keramia Formation is slightly more than 100 m.

Discussion. The middle portion of the formation consists of limestones which show a close resemblance to the organic limestones of the Akrotiri Formation. For this reason a similar environment is assumed. The oyster clays probably represent a more brackish environment. *Crassostrea* populations have been described from such an environment in the Rhone delta.

As to the dense limestones little can be concluded. It is assumed that they are of fresh water origin, but sound arguments are lacking. Their lithology rather strongly differs from that of the limestones of the Soudha Formation.

Literature. The sediments of the Keramia Formation have not been designated by a special name by any previous author.

Economic use. The sediments of the Keramia Formation are of no economic value.

II.2.12. GAVDOS FORMATION

Diagnosis. The Gavdos Formation consists of the complete succession of Neogene strata of Gavdos Island.

Derivatio nominis. The formation has been named after Gavdos Island.

Type section (*). Coastal cliff N of Ambelos village, exposure 336 (compare fig. 1).

Underlying Formation. The Gavdos Formation is underlain by various pre-neogene rocks.

Overlying Formation. The Gavdos Formation is not overlain by other Neogene strata.

Geographic extension. The Gavdos Formation is restricted to Gavdos Island.

Lithology. The lithology of the Gavdos Formation is very variable. Its strata are rather strongly affected by block faulting. Because of these factors and because of the lack of a topographic map no attempt was made to establish a detailed stratigraphy. The lithological succession and its lateral changes are discussed on the basis of a few figured sections.

The type section consists mainly of alternating brown, fine sands and blue, amorphous sandy clays. In the upper part of the section these clays contain numerous specimens of *Crassostrea* and few plant remains. Furthermore, rare shark teeth were found in this higher part of the section. The uppermost part of the section consists of yellow, organic, detritic, algal limestones, locally containing *Heterostegina*, and of yellow laminated marls, alternating with brown fine sands. To the southern and eastern part of the island the sands and clays, which predominate in the type section, wedge out. They are replaced by calcareous sediments, mainly organic, detritic limestones.

In the sections of exposures 339, 341 (*) near Panayia church (at the path

from Kastri to Karave Beach) the basal part of the Neogene consists of organic, detritic, algal limestones. These limestones are overlain by brown sands and blue or greenish clay containing *Crassostrea* in their upper part. The upper parts of the sections consist of marls and organic, detritic, algal limestones with heterosteginids. In the section of exposure 339 the marls are predominantly laminated. They resemble those of the Khairitiana Formation in the vicinity of Kalyves Apokoronou (compare p. 38).

In two exposures (340 A, B) ^(x) between Panayia and Sarakiniko Beach the basal Neogene strata consist of conglomerates. The components are well rounded preneogene serpentinites in a green clayey matrix. The conglomerates are overlain by sands with some intercalated *Crassostrea* beds. In exposure 340 B these sands are overlain by limestones built of cemented reefal material, changing upward into detritic, algal limestones. The lower part of the limestones passes laterally into sands and clays containing heterosteginids in their middle part and *Crassostrea* in their upper part (exposure 340 A). They are overlain by algal limestones which contain scarce *Clypeaster*.

It is difficult to get an insight into the thickness of the Gavdos Formation, because correlations based on the uppermost occurrence of *Crassostrea* are doubtful in many cases. It is assumed that the thickness is at least 150 m, but it may be considerably more.

Discussion. The major part of the Neogene sediments of Gavdos consists of shallow water sediments, e.g. organic, detritic limestones containing algae and heterosteginids. The lower part of the type section may represent deeper water deposits, as macrofossils are nearly completely lacking and planktonic foraminifera occur abundantly.

Literature. SPRATT (1865) compared the Neogene sediments of Gavdos (referred to as Gozzo by that author) with those of Malta on the basis of echinids and shark teeth. He did not designate them by a special name.

SIMONELLI (1894) gives a schematic outline of the stratigraphy of the Neogene of Gavdos. He distinguishes in descending order:

- d) Limestone with *Clypeaster altus*, *Ostrea crassissima* and heterosteginids,
- c) Grey marls with fish and plant remains (*Laurus*, *Cinnamomum*, *Callitris*),
- b) Blue marl with *Cleodora*, bryozoa and scattered selenite crystals,
- a) Grey sandy marl with plant remains.

The succession given hardly resembles that presented in our sections.

Economic use. All houses on Gavdos Island are built of Neogene organic, detritic, algal limestones.

II.3. Lithostratigraphic correlation.

In our description of the formations occasional remarks were already made about correlations and lateral transitions of formations. This point will be treated in more detail below. The most important correlations are shown in fig. 2.

In the Kissamou District the lowermost Neogene strata belong to the Mesonisi Formation. In that formation red conglomerates and sandy clays prevail; *Chara* is abundant. It clearly corresponds to a fresh water environment. The Mesonisi Formation is overlain by the Roka Formation, representing a shallow water environment, as indicated by its fossil contents, such as *Heterostegina*, *Ostrea*, *Clypeaster*. This lithostratigraphic unit can easily be recognized in the Kissamou District, and it is a reliable level for correlation.

The Roka Formation is overlain by two marine formations, the Koukounaras and Kissamou Formations, which are, at least partly, lateral equivalents. Within both formations correlation possibilities are rather restricted. Occasionally the strongly indurated graded beds can be used for correlation over considerable distances (maximally 2.5 km), but generally their thickness decreases so rapidly to the north that they are hardly useful for correlation. They often form caprocks.

In more complete sections, where the transition to the overlying formation is more or less clearly visible, for example near Kastelli Kissamou, Makronas Kissamou, Kalami Kissamou, Episkopi Kissamou, amorphous clays are still overlying the uppermost graded beds. The amorphous clays change at the top of the Kissamou Formation into laminated clays, which can hardly be differentiated from the laminated clays and sandy clays at the base of the overlying Khairetiana Formation. The boundary is arbitrarily drawn, and does *not* provide a reliable basis for lithostratigraphic correlation. As soon as marls appear in the Khairetiana Formation, the difference with the amorphous clays of the Kissamou Formation is very clear.

Fortunately these transitional strata between both formations are not thick, and in several localities they comprise a gypsum bed which belongs clearly to the basal part of the Khairetiana Formation, taking into account the associated thin laminated marls. Within the Khairetiana Formation there is no peculiar level that is useful for correlation, except for the gypsum bed near the base. This gypsum bed is correlated with the gypsum bed in the top of the Khatzi Formation in the eastern part of the Kissamou District. Since, in that area the Khairetiana Formation overlies the Khatzi Formation, it must be concluded that the lower part of the Khairetiana Formation in the centre of the Kissamou District corresponds to the upper part of the Khatzi Formation in eastern Kissamou.

Within the Khatzi Formation of eastern Kissamou there is hardly any possi-

bility for long distance correlation. Most of the graded beds rapidly wedge out in northern direction and they provide no reliable basis for correlation, as they sometimes do in the Kissamou Formation.

The gypsum layer is the only useful correlation level.

The Khatzi Formation is overlain by the Khairitiana Formation in the south and by the Tavronitis Formation in the north. In the field the lateral inter-relationship of both formations is not clear, but it is based on the fact that both are overlying the same formation and probably at about the same level (slightly above the gypsum bed).

The correlation farther to the east is based mainly on the isolated occurrences of the Kissamou Formation near Stalos Kydonias, Mournies Kydonias and Vryses Apokoronou. They are all correlated with the top of the Kissamou Formation in the Kissamou District. In the Varvara River valley near Mournies the Kissamou Formation is overlain by the Akrotiri Formation, which has a rich fauna in its base (*Heterostegina*, *Pecten*, *Clypeaster* and algae). This level is correlated with organic limestones occurring locally in the top of the Khatzi Formation.

Within the Akrotiri Formation the basal, *Heterostegina* bearing strata are the only reliable correlation level; they are indeed very useful in the field.

The lateral transition from Kissamou to Ayios Yeoryios Formation cannot be traced in the field, but must be inferred from the fact that both are overlain by the Akrotiri Formation at a distance of no more than one kilometer.

The organic limestones toward the base of the Ayios Yeoryios Formation may be correlated with similar limestones in the middle of the geographically isolated Keramia Formation.

In the Apokoronou District it can clearly be seen in the field that the Khairitiana Formation is a lateral equivalent of the Akrotiri Formation, and that it overlies the Kissamou Formation. This superposition is in good accordance with our findings in the Kissamou District.

Chapter III

THE FAMILY PLANORBULINIDAE SCHWAGER, 1877

III.1. Introduction, literature.

If one retraces the history of foraminiferal taxa in the literature sense and contents of a unit often appear to have changed in the course of time, depending on the opinions of authors. This is not only true for taxa of lower rank, like species, but especially for taxa of higher rank, like genera and families. In this respect the family Planorbulinidae is not an exception; changes have been considerable.

The family has been established by CUSHMAN (1927) ex subfamily Planorbulininae SCHWAGER, 1877. Its diagnosis reads (CUSHMAN, 1933, p. 275):

„Test in the early stages coiled, attached by the dorsal surface; chambers at least in the early stages in a spiral arrangement, later spreading in annular series, irregular, or piled up into a solid mass; wall calcareous, usually coarsely perforate, in the early stages with a thin chitinous inner layer; apertures one or two to each chamber, peripheral, or in the massive forms with the aperture formed by coarse pores of the wall”.

In this family CUSHMAN (1933) included the following genera: *Planorbulina*, *Planorbulinoides*, *Planorbulinella*, *Linderina*, *Acerovulina* and *Gypsina*.

Subsequent authors removed some of these genera from the family Planorbulinidae, whereas other genera were added. The history of the family Planorbulinidae is illustrated in figure 3. In that figure the classifications by CUSHMAN (1933), GALLOWAY (1933), CHAPMAN & PARR (1936), GLAESSNER (1945), SIGAL (1952), POKORNY (1958), ORLOV (1962), REISS (1963) and LOEBLICH & TAPPAN (1964) are shown side by side. The classifications of CUSHMAN, CHAPMAN & PARR, GLAESSNER, SIGAL, POKORNY and ORLOV resemble one another. CUSHMAN's classification differs from the others in that *Halkeyardia* is assigned to the Cymbaloporidae. The classification by CHAPMAN & PARR includes *Chapmanina* and *Vaughanina* in the Planorbulinidae. The classification by GLAESSNER includes *Chapmanina* in the (sub) family. These genera are excluded in the other classifications.

The classifications of GALLOWAY and of LOEBLICH & TAPPAN also resemble each other. They mainly differ in that the latter authors exclude *Cymbaloporella* and *Archaeocyclus* from the Planorbulinidae.

The classification by REISS strongly differs from all others. In that classification the difference between monolamellid and bilamellid wall structure is ap-

Fig. 3. Classifications of Planorbulinidae (or Planorbulininae) by earlier authors.

CUSHMAN 1933	GALLOWAY 1933	CHAPMAN & PARR 1936	GLAESSNER 1945	SIGAL 1952	POKORNY 1958	ORLOV 1962	REISS 1963	LOEBLICH & TAPPAN 1964
2a <i>Planorbulinoides</i>	1 <i>Planorbulinoides</i>	2a <i>Planorbulinoides</i>	2b	2a <i>Planorbulinoides</i>	2a	2a <i>Planorbulinoides</i>	2a <i>Planorbulinoides</i>	1 <i>Planorbulinoides</i>
<i>Planorbulina</i>	2b <i>Planorbulina</i>	<i>Planorbulina</i>	<i>Planorbulina</i>	<i>Planorbulina</i>	<i>Planorbulina</i>	<i>Planorbulina</i>	<i>Planorbulina</i>	2a <i>Planorbulina</i>
<i>Planorbulinella</i>	<i>Planorbulinella</i>	<i>Planorbulinella</i>	<i>Planorbulinella</i>	<i>Planorbulinella</i>	<i>Planorbulinella</i>	<i>Planorbulinella</i>	<i>Planorbulinella</i>	<i>Planorbulinella</i>
<i>Linderina</i>	<i>Linderina</i>	<i>Linderina</i> (8a?)	<i>Linderina</i>	<i>Linderina</i>	<i>Linderina</i>	<i>Linderina</i>	4 <i>Linderina</i>	<i>Linderina</i>
<i>Gypsina</i>	3b <i>Gypsina</i> <i>Sphaerogypsina</i> <i>Pseudogypsina</i>	<i>Gypsina</i>	<i>Gypsina</i>	<i>Gypsina</i>	<i>Gypsina</i>	8a? <i>Eoannularia</i> <i>Gypsina</i>	<i>Eoannularia</i> <i>Gypsina</i>	3a <i>Gypsina</i>
<i>Acervulina</i>	<i>Acervulina</i>	<i>Acervulina</i>		<i>Acervulina</i>	<i>Acervulina</i>	<i>Acervulina</i>	<i>Acervulina</i> ?	<i>Acervulina</i>
5a <i>Halkyardia</i>	6 <i>Halkyardia</i>	<i>Halkyardia</i> (8a?)	<i>Halkyardia</i>	<i>Halkyardia</i>	<i>Halkyardia</i>		<i>Halkyardia</i>	5a <i>Halkyardia</i>
<i>Cymbaloporella</i>	2b <i>Cymbaloporella</i> <i>Archaecyclus</i>	5b <i>Cymbaloporella</i>	5a <i>Cymbaloporella</i>	5a <i>Cymbaloporella</i>	5a <i>Cymbaloporella</i>	5c <i>Cymbaloporella</i> 8a? <i>Archaecyclus</i>	6c <i>Cymbaloporella</i>	<i>Cymbaloporella</i> <i>Archaecyclus</i>
<i>Chapmanina</i>	6a <i>Chapmanina</i>	2a <i>Chapmanina</i> (8a?) <i>Vaughanina</i> (8a?)	<i>Chapmanina</i> 8b <i>Vaughanina</i>	6b <i>Chapmanina</i> 7b <i>Vaughanina</i>	7a <i>Vaughanina</i>	6a <i>Chapmanina</i> 7b <i>Vaughanina</i>	6a <i>Chapmanina</i> 7a <i>Vaughanina</i>	6a <i>Chapmanina</i> 7a <i>Vaughanina</i>
				9b <i>Hellenocyclina</i>	9a <i>Hellenocyclina</i>	9b <i>Hellenocyclina</i>	9a <i>Hellenocyclina</i>	9a <i>Hellenocyclina</i>
1 Cibicidinae	3a Acervulinidae	5a Cymbaloporidae	6a Chapmaninidae	7b Pseudorbitoididae	9a Lepidorbitoididae			
2a Planorbulinidae	3b Acervulininae	5b Cymbaloporinae	6b Chapmanininae	8a Orbitoididae	9b Lepidorbitoidinae			
2b Planorbulininae	4 Gypsinidae	5c Cymbaloporettidae	7a Pseudorbitoididae	8b Orbitoidinae				

plied. The other authors used mainly morphological similarities and supposed phylogenetic relationships.

In fig. 3 also the genus *Hellenocyclina* is taken into account, for reasons that will become clear farther on (see below). This genus has not been included in the Planorbulinidae by any of the authors mentioned.

From fig. 3 it can be seen that the following genera have been included at some time in the Planorbulinidae (or Planorbulininae):

Planorbulina, *Planorbulinoides*, *Planorbulinella*, *Linderina*, *Eoannularia*, *Gypsina*, *Sphaerogypsina*, *Acervulina*, *Cymbaloporella*, *Halkeyardia*, *Archaeocyclus*, *Chapmanina* and *Vaughanina*.

In all modern classifications the last two genera are excluded from the Planorbulinidae and we fully agree. However, the affinities of the other genera will have to be discussed more extensively.

Although (supposed) phylogenetic relationships have been applied in the classifications mentioned, it should be borne in mind that actually nothing is known of the phylogeny of the genera involved. Their evolution has not been investigated and for this reason any claim of phylogenetic classification has to be rejected.

As a consequence, only a classification on comparative morphology can be made.

An approach to such a morphological grouping is given below:

1. One-layered, flattened forms with a relatively long initial spiral, followed by irregular chamber growth. The initial chambers have one aperture, the later ones two. The apertures are peripheral slits extending to the dorsal side (compare *Cibicides*). To this group *Planorbulina* and *Planorbulinoides* belong.

2. One-layered, flattened forms with an initial spiral of variable length, followed by chambers with regular orbitoidal growth. The spiral chambers have one aperture, the later chambers two. The apertures are peripheral, not extending to the dorsal side. To this group *Planorbulinella*, *Eoannularia* and *Hellenocyclina* belong. *Archaeocyclus* may belong here as well, but the original description does not give sufficient evidence. The genera *Linderina* and *Planolinderina* n.gen. are also placed in this group, but their apertures differ from those of the preceding genera, as they consist of rows of rounded openings at the chambers' bases.

3. All kinds of spherical, conical and flat gypsinids. See MEULENKAMP (in preparation).

4. One-layered, conical forms with the initial chambers arranged in a spiral of variable length. The later chambers show regular orbitoidal growth. The

apertures are multiple, peripheral. *Halkyardia* and *Cymbaloporella* belong here.

In this review *Acervulina* is omitted. Its morphological characteristics are insufficiently known, not only to the present author, but also to earlier authors who tried to fit it into a classification.

Of course, this way of grouping does not imply any phylogenetic relationship, although it may exist at some places.

The apertural features of the genera included in group 1 resemble those of *Cibicides*. NYHOLM (1961) found *Planorbulina*-like resting schizonts in the life cycle of *Cibicides lobatulus*. Also studies by DUPEUBLE (1962) may indicate that *Planorbulina*-like individuals are merely variants of *Cibicides lobatulus*.

The chamber arrangement of the genera included in the groups 2 and 4 is identical with that of larger, orbitoidal foraminifera.

Orbitoidal chamber growth occurs in many completely unrelated larger foraminifera. In analogy we may assume that the genera, we are dealing with here, are unrelated. This is even more evident if we remember that all larger orbitoidal foraminifera in the beginning of their evolution had one-layered forms with an orbitoidal growth pattern of the chambers.

The relationships of the gypsinid foraminifera included in group 3 will be discussed by MEULENKAMP (in preparation).

Summarizing it may be stated that the family Planorbulinidae, such as presented in each of the classifications, is an artificial group of probably unrelated genera. This opinion will be substantiated in this chapter, in which the genera of group 2 will be treated.

This study was primarily based on the *Planorbulinella* populations occurring in the Cretan Neogene. To determine the Cretan material, we had to compare it with all other *Planorbulinella* species previously described. This has led us to the study of the other genera of group 2 as well. This became even more interesting, since it appeared from the literature, that several authors met difficulties in differentiating the genera *Planorbulinella*, *Linderina* and *Hellenocyclus* (for example HOFKER, 1958, 1966).

In this chapter a description is given of *Planorbulinella* populations from Recent deposits, and from the Neogene of Crete, Malta, Sicily, Northern Italy, Indonesia, New Zealand and the Caribbean region.

Planolinderina n.gen. populations are described from the Neogene of Indonesia and Australia and from the Paleogene and Neogene of France. *Linderina* populations are described from the Eocene of England, France, Somalia and Qatar. *Hellenocyclus* populations from the Upper Cretaceous of France and Holland are dealt with.

III.2. The genus *Planorbulinella* CUSHMAN, 1927.

III.2.1. INTRODUCTION, LITERATURE

Before proceeding to the description of the *Planorbulinella* populations studied, the literature bearing on the genus *Planorbulinella* and its type species, the Recent *P. larvata* will be reviewed. The generic diagnosis by CUSHMAN (1927) is:

„Test in the young attached and like *Planorbulina*, soon having the chambers developed about the periphery in annular series those of each series alternating with those of the adjacent ones, apertures two, one at each side of the chamber in the median line, test bilaterally symmetrical”.

CUSHMAN (1933), in the second edition of his classification, did not materially change this diagnosis, but added: "wall calcareous, usually coarsely perforate".

CUSHMAN (1927) designated *Planorbulina vulgaris* d'ORBIGNY var. *larvata* PARKER & JONES as type species of *Planorbulinella*, a species which was retained by most earlier authors in *Planorbulina*. In this respect it may be of interest to see which features caused CUSHMAN to create *Planorbulinella*, or rather, on which characteristics it can be distinguished from *Planorbulina*. If the diagnosis of both genera are compared, it appears that they differ only in the arrangement of the chambers. In *Planorbulina* (CUSHMAN, 1933) it reads: "very earliest chambers slightly trochoid, closely spiral, later in an irregular series of a single layer about the periphery". In *Planorbulinella* the later chambers have a more regular arrangement: "in annular series" and "alternating". However, differences in apertural characteristics have not been used by CUSHMAN.

The literature bearing on the type species *P. larvata* provides a basis for getting more data on the generic features of *Planorbulinella*.

The original description ¹⁾ by PARKER & JONES (1865) is:

"Fully developed forms; becoming concentric, with alternating chambers built over the apertures of the penultimate ring. In the seas of hot climates a large amount of exogenous granular matter is formed on the surface of the shell".

This description gives information neither about the aperture, nor about the internal features. However, the apertures are clearly visible in the accompanying figures. There are two, probably low, arch-like apertures at each side of the peripheral chambers. They are provided with small lips. The arrangement of the chambers looks quite regular.

¹⁾ Description after ELLIS & MESSINA. In reality PARKER & JONES did not give any clear description. The description by ELLIS & MESSINA is composed of scattered remarks on *P. larvata*, which apply to other species as well.

BRADY (1884, p. 92, pl. 92, figs. 5, 6) does not add essential new data on structure: "...characterized by the granular or tuberculate condition of the exterior". According to BRADY the species might be sessile; his fig. 5 shows an adherent specimen.

HOFKER (1927) extensively dealt with *P. larvata*.

„No trace of a canal system can be found. The apertures of the outer chambers are lipped”.

HOFKER recognized trimorphy on the basis of the internal features, which recognition needs some discussion. He distinguished an A1 generation, characterized by "initial chambers a short, somewhat irregular coil", an A2 generation in which "the first chambers form a raspberry" and a B generation with the "first set of chambers a close-coiled spiral".

Whatever the merit of the theory on trimorphism in foraminifera may be, it must be borne in mind that convincing statistical evidence has never been presented on the basis of morphology, neither by HOFKER, nor by any other author. According to these authors trimorphism might be demonstrated in two different ways, either by mere external differences, or by internal differences (e.g. size differences in protoconch or differences in chamber arrangement). The existence of the first type of trimorphism is subject to the personal opinions of authors. One author may distinguish three separate species, where the other sees three generations of the same species. Measurable protoconchal trimorphy should lead to a three-modal size distribution but this has never been sufficiently demonstrated. The same objections are true in the case of *P. larvata*. According to HOFKER a clear, externally visible trimorphy is certainly not present, but it should be present in the internal features. However, HOFKER's data are not convincing, primarily because of bad and/or incorrect drawings.

The close-coiled spiral in the B generation (his pl. 2, figs. 1, 4) can with some difficulty be retraced from his figures.

The A1 generation should be characterized by a short initial coil, but on p. 7 it reads: "... the first chambers, which build up an irregular heap ... in which one may distinguish a spiral with some connivance". However, the arrangement of the initial chambers of the figured specimens (pl. 2, figs. 5, 7) does not even show the slightest resemblance to a spiral.

The initial chambers of the A2 generation should form a "raspberry". Probably this is an arrangement of the first three chambers, which is not fully understood. The figures of specimens of this generation (pl. 2, figs. 3, 6) are completely puzzling.

NEUMANN (1954) considers the embryonic apparatus of *Planorbulinella* to be

multilocular. The meaning of "multilocular" is indistinct and we may in this respect refer to the comments on HOFKER's "raspberry". Both descriptive terms do not reflect the regularities in the configuration of the early chambers.

REISS (1963) described the arrangement of the embryonic chambers of *Planorbulinella larvata* as that of a protoconch and deutoconch, followed by a third, auxiliary chamber with two stolons. In addition, he considered the genus *Planorbulinella* to be bilamellid.

An emended diagnosis of *Planorbulinella*, mainly based on our own observations reads:

Test discoidal, planoconvex or slightly concavo-convex; wall calcareous, perforate. Chambers in one layer, early chambers in a trochoid spiral of variable length, or in a protoconch-deutoconch-auxiliary chamber(s) arrangement. Later chambers orbitoidally arranged, and provided with two arched apertures with a small imperforate lip each. There is no special thickening of the wall except for the subsequent lamellae formed at each instar over the whole test.

Planorbulina is different by the distinctly trochoid spiral of persistently considerable length, the *Cibicides*-like apertures, and the irregular growth of most later chambers.

Concluding from the literature data and our own observations the following species are within the limits of this description: *Planorbulinella larvata* (PARKER & JONES), *P. trinitatensis* (NUTTALL) and *P. zelandica* FINLAY.

III.2.2. THE GENUS PLANORBULINELLA IN THE MEDITERRANEAN NEOGENE.

pl. 1, figs. 1-6; pl. 2, figs. 1-6; pl. 3, figs. 1-7; pl. 4, figs. 1, 2; pl. 12, figs. 1-3b

III.2.2.1. *Introduction.*

The author is not aware of any earlier record of *Planorbulinella* in the Mediterranean Neogene. However, the genus proved to be rather common in the Cretan Neogene, and it is present also in Neogene deposits of Malta, Sicily, Northern Italy and Southern Spain (Guadalquivir Basin). Apparently it was widely distributed in the Mediterranean region. *Planorbulinella* populations from all these areas will be dealt with, except those from Southern Spain, which will be described by TjALSMA in a future paper on Neogene deposits of that area.

III.2.2.2. *The genus Planorbulinella in the Neogene of Crete.*

III.2.2.2.1. Stratigraphic distribution.

In the Khania Province occasional free specimens occur in marly intercalations of the Roka Formation. Moreover, scarce specimens have been observed in

random thin sections of the limestones of that formation. Free specimens occur most abundantly in the clays of the overlying Kissamou and Koukounaras Formations, which are lateral equivalents of each other. The strata of the lowermost part of the Khairitiana Formation occasionally contain scarce *Planorbulinella* specimens.

In the Rethymnon Province *Planorbulinella* is restricted mainly to the clays and marls of the Apostoli Formation. It occurs also in marly beds in the Rethymnon Formation, which is supposed to be a partly, lateral equivalent of the Apostoli Formation (see MEULENKAMP, in preparation).

From these data *Planorbulinella* appears to occur most frequently in clayey and marly sediments. Furthermore, it is restricted to the lower part of our Neogene succession. Possibly *Planorbulinella* disappeared because of a salinity change, as evaporites (gypsum) in the Khania Province are found at about the same level. The absence of evaporites in Eastern Khania and Rethymnon Provinces is — a priori — not inconsistent with this assumption. Salinity changes may be important enough to affect faunas without causing the formation of evaporites. The formation of evaporites may be strongly bound to more restricted geographic and topographic conditions locally present in the Khania Province, but which did probably not exist in the Eastern Khania and Rethymnon areas.

III.2.2.2.2. Material.

Planorbulinella specimens were available from about 1000 samples in both the Rethymnon and Khania Province. Only those in the Khania Province were gathered by the present author, the others were taken by J. E. Meulenkamp.

The washed residues of the samples investigated were subdivided into three size fractions by sieving. The size limits of the fractions are: > 1.0 mm, in between 1.0 and 0.250 mm and in between 0.250 mm and 0.125 mm. The number of *Planorbulinella* specimens per sample may vary strongly. In some samples only ten or even fewer specimens were present, in others 500 or 600 individuals.

Generally specimens from the middle size fraction were picked. In the coarser fraction they are nearly absent. In the finer fraction numerous specimens occur, but relatively less than in the middle fraction. In some samples, however, also specimens were picked from the finer fraction, when the number of specimens in the middle fraction was considered too small for a reliable conclusion about the population in relation to the importance of the sample's position.

A list of the sections studied is given below ¹⁾:

Section Kastelli Kissamou ^(x), samples M 929—M 925 and M 905—M 916,

¹⁾ Figured sections are marked with (x).

exposure 280. It comprises the Kissamou Formation, but the base of that formation is not exposed.

Section Koukounaras Kissamou ^(x), samples M 882—M 983, exposure 269. Type section of the Koukounaras Formation.

Section Dheliana Kissamou ^(x), samples M 759—M 774, exposure 104. Kissamou Formation; the base of the formation is not exposed.

Section Maredhiana Kissamou, samples M 809—M 820, exposure 369, 276. Kissamou Formation; its base is exposed.

Section Potamidha Kissamou ^(x), samples M 956, 955, M 1055—1063, M 950—M 943, exposure 212. Type section of the Kissamou Formation; the base of the formation is not exposed.

Section Roka Kissamou ^(x), samples M 1051—1035, exposure 391. Upper part of the Kissamou Formation.

Section Episkopi Kissamou I ^(x), samples M 696—705, exposure 110. Kissamou Formation; the base of the formation is exposed.

Section Episkopi Kissamou II, samples M 652—660, exposure 354. Kissamou Formation; the base of the formation is not exposed.

Section Episkopi Kissamou III, samples M 683—669, exposure 355. Kissamou Formation; the base of the formation is not exposed.

Section Khairitiana Kissamou ^(x), samples M 782—806, exposure 368. Kissamou Formation; the base of the formation is exposed.

Section Astrikos Kissamou ^(x), sample M 116 (Roka Formation, exposure 96), samples M 645—651 (transition from Roka to Kissamou Formation, exposure 105) and samples M 744—746 (Kissamou Formation, exposure 366).

Section Nokhia Kissamou ^(x), samples M 628—641, exposure 80. Kissamou Formation; the base of the formation is exposed.

Section Stalos Kydonias ^(x), samples M 570—580, exposure 17. Uppermost part of the Kissamou Formation.

Section Exopolis-Vryses, samples 850-D—Q and 846-P—A, exposures 850 and 846 (see MEULENKAMP, in preparation). Apostoli Formation and Mylopotamou Formation (846-A).

Section Prasses, samples 798-A and L, exposure 798 (see MEULENKAMP, in preparation). Lower part of the Rethymnon Formation.

Section Selli, samples 860-C to δ Z, exposure 860 (see MEULENKAMP, in preparation). Apostoli Formation (the base of the formation is exposed) and Rethymnon Formation.

Section Apostoli, samples 814-B—V, exposure 814 (see MEULENKAMP, in preparation). Apostoli Formation; the base of the formation is exposed.

III.2.2.2.3. External features.

Test small, discoidal, up to 1.4 mm, but in the majority of the specimens not exceeding 1.0 mm in diameter, both sides flat or one side slightly concave and the other slightly convex in the centre. Both sides are smooth. Generally all chambers are visible from both sides, but in the stratigraphically uppermost samples relatively big specimens occur which are strongly thickened by the subsequent laminae formed at each instar and therefore do not clearly show the early chambers. Generally the chambers are well separated from one another by depressed sutures. The periphery is rounded or acute, and lobate. The apertures are median, basal slits, two to each chamber, and each provided with an imperforate lip. The pore diameter ranges up to 13 μ .

III.2.2.2.4. Measurements and counts of internal features.

The early chambers of the individuals appear to be arranged in a trochoid spiral. The later chambers have a regular orbitoidal growth pattern. In macro-spheric specimens the initial spiral may be strongly reduced, resulting in a protoconch — deuteroconch — auxiliary chamber(s) arrangement of the early chambers. All these features strongly remind us of those known in other larger, orbitoidal foraminifera.

It has been known, since the studies by TAN SIN HOK on *Cycloclypeus* and *Miogypsina*, that in the course of time the number of chambers in the initial spiral may be reduced, giving rise to cyclical or annular chamber growth in increasingly earlier ontogenetic stages. This reduction in the number of spiral chambers TAN named nepionic acceleration. It has been investigated afterwards in several groups of larger foraminifera: *Cycloclypeus* (COSIJN, DROOGER, MAC GILLAVRY), *Helicolepidina* (VAN RAADSHOVEN), *Lepidocyclina* (GRIMSDALE, MOHLER, VAN DER VLERK, FREUDENTHAL), *Lepidorbitoides* (MAC GILLAVRY, PAPP) and *Miogypsina* (BRONNIMANN, DROOGER).

Several of these authors have applied mathematical methods for expressing the features of the early chambers, for example the number of chambers in the initial spiral. This procedure based on the statistical analysis of numerical data, enables one to make a more correct comparison of populations and more reliable decisions about similarities and differences. In *Miogypsina* the number of chambers in the nepionic spiral, in *Lepidorbitoides* and *Lepidocyclina* the number of (ad)auxiliary chambers have been successfully applied to unravel the evolution of these genera. Although the parameters used are different in these two groups, there is no difference in the feature they intend to express: the ontogenetic stage at which cyclical (orbitoidal) chamber growth starts.

The internal features of *Planorbulinella* can be measured and counted in a way similar to that used by DROOGER in his studies of miogypsinids. These meas-

urements and counts may provide a valuable basis for judging whether or not an evolution according to the principle of nepionic acceleration occurs in *Planorbulinella*.

For this purpose the following parameters were used (compare fig. 4):

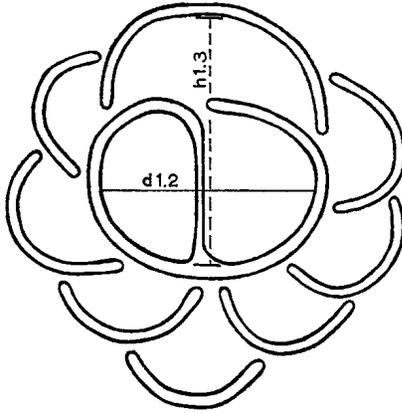


Fig. 4. The method of measuring $d1.2$ (diameter of the protoconch and the deutoconch) and $h1.3$ (diameter of the first three chambers together). In this example $Y=2$.

Y. The number of chambers in the initial spiral, which have a proximal stolon only, starting to count with the protoconch. The symbol Y was chosen in analogy with that used by DROOGER in miogypsinids but it differs in that also the protoconch and deutoconch are included in our Y . Theoretical investigations by MAC GILLAVRY (1965) favour our approach. For all populations the mean Y values (\bar{Y}) were calculated. The mean values are given along with their standard errors (σ). It must be remarked that an opening between protoconch and deutoconch is usually not visible.

d1.2. The diameter of the protoconch and deutoconch together, measured along a line through their imaginary centres, the wall thicknesses being excluded, except for the wall which separates protoconch and deutoconch. $d1.2$ measurements are expressed in μ . Mean values ($\bar{d1.2}$) were calculated for many populations.

The use of $d1.2$ is preferred to measuring the diameter of the protoconch and deutoconch separately, because in our material it is often difficult, or even impossible, to decide which one of both is the protoconch.

h1.3. The diameter of the first three chambers together measured along a line perpendicular to that of d1.2 and running through the imaginary centre of the third chamber. The measurements are given in a way similar to that of d1.2. There is no reason for preferring d1.2 to h1.3. Both are thought to give information on the size of the early chambers. Afterwards, however, d1.2 proved to be more useful, since h1.3 becomes of dubious value for comparison when the deuteroconch has two stolons, and consequently two chambers are formed at the third instar.

All measurements and counts apply to macrospheric specimens, which are highest in number in our *Planorbulinella* populations, commonly over 80 % of the total number. The measurements were made with a Leitz binocular microscope, ocular 12.5 and objective glass 12.0, with an accuracy of half a micrometer unit, which corresponds to 4.25μ (whole unit 8.5μ).

Since *Planorbulinella* consists of a single chamber layer the initial chambers are only covered by the successive laminae which envelop the whole test at each instar. Consequently, the initial chambers are commonly visible in transmitted light, especially so if the test is wetted with aniseed oil. Because of the slightly trochoid character of the initial spiral these chambers are generally better visible from one side than from the other. In the stratigraphically highest samples the tests are generally larger and with more chambers than in the lower ones. As a consequence, they are enveloped by more laminae and the arrangement of the initial chambers does not become clear in transmitted light. In these (few) cases equatorial thin sections were made.

A rough estimate of the number of specimens studied amounts to about 25.000. About 3/4 of them proved to be suitable for gathering data on the parameters mentioned above.

Although we intended to give a fair account of the *Planorbulinella* populations it would be impossible to treat separately all the samples investigated (about 450). The results of many of them, those taken from scattered exposures, will not be reported. They would not affect the final conclusions. Mainly the results of populations from the long, closely sampled sections will be recorded.

III.2.2.2.5. Internal features.

The length of the initial spiral may vary considerably. In microspheric specimens the number of chambers in the initial spiral with one opening ranges from 17—11. In macrospheric specimens the spiral (Y) consists of maximally 8 and minimally 2 chambers. Specimens with an initial spiral of 3 chambers are most common, those with $Y = 2$ are extremely scarce (0.0005 %).

In most orbitoidal foraminifera the chambers, which follow the first chamber with two stolons, have again two stolons each (compare for example fig. 4 and

fig. 5a, b, c). This is true in only part of our *Planorbulinella* specimens. If, for instance, the fourth chamber is the first that has two stolons ($Y = 3$), the following chambers may lack the second stolon again. The second stolon may be lacking in only one chamber of the fifth instar (fig. 5d), but it may be lacking also in both (fig. 5e, f); it may be lacking in only one chamber of the sixth instar (fig. 5g), but it may lack also in both chambers (fig. 5h) etc. In specimens with $Y = 3$ it was observed that chambers up to the seventh instar may lack this second stolon again. These types are indicated by 3/0, 3/1, 3/2, 3/3, 3/4, 3/5 and 3/6 respectively. In this designation the number behind the oblique line indicates the number of chambers lacking the second stolon after one chamber has acquired this feature; the number in front of the oblique line corresponds to Y . The same range of variation is present in each arbitrary Y type.

However, even more variants occur. For example, in a specimen with an $Y = 4$, only one chamber of the sixth, and only one chamber of the seventh instar may lack the second stolon (fig. 5l). Such an arrangement may occur in specimens with each arbitrary Y .

It is easily conceivable that there are even more possible variants on this basic pattern. They occur indeed, though not frequently.

There is, however, another, much more important variation in arrangement, which is discussed below. Generally, the two spirals originating from the first chamber with two stolons, are symmetrical and they commonly consist of three chambers each (apart from the closing chamber, which they have in common). Examples of such an arrangement are given in fig. 5a, d, e, g, h, k, l and n. However, these symmetrical spirals may consist also of two chambers only; this type is figured in fig. 5f.

Finally the spirals may be asymmetrical, consisting of an unequal number of chambers. Examples of this arrangement are shown in fig. 5b, c and m. They show specimens with spirals consisting of 2 and 3 chambers, spirals consisting of 2 and 4 chambers, and spirals consisting of 1 and 5 chambers respectively.

The symmetrical and asymmetrical types are designated by /a and /b respectively. In this way, for example the internal features of the specimen figured in fig. 5a are indicated by 3/0/a, which means: a specimen with three chambers with only one stolon; the following chambers all have two stolons each; the spirals originating from the fourth chamber are symmetrical.

In specimens with asymmetrical spirals the first chamber with two stolons is often asymmetrical as well, resembling a normal spiral chamber. One would expect the spiral with this direction to be the longer one, but this is true in only 50% of the specimens. From this seeming random distribution one may conclude that a change of coiling direction may be present in *Planorbulinella*. With respect to the single opening in the last one-aperture chamber similar random

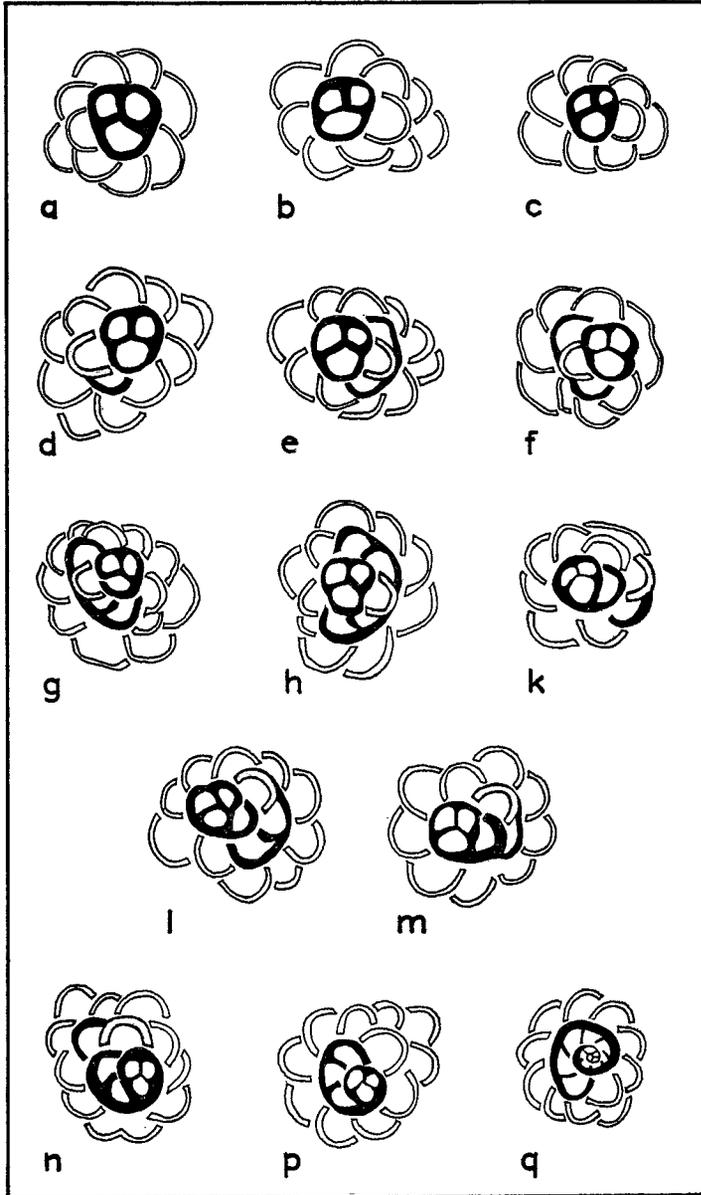


Fig. 5. Early chambers of Cretan *Planorbulinella*.

- | | | | |
|----------|----------|----------|--------------------------|
| a. 3/0/a | e. 3/2/a | k. 4/2/a | p. 6/0/a |
| b. 3/0/b | f. 3/2/a | l. 4/2/a | q. microspheric specimen |
| c. 3/0/a | g. 3/3/a | m. 4/1/b | |
| d. 3/1/a | h. 3/4/a | n. 5/1/a | |

distribution may be found in the relative lengths of the spirals. Even this single opening in the third chamber may be a misinterpretation of the original spiral because of the frequent difficulty to decide which of the first two chambers is the protoconch.

It seems of interest to note that similar features of early chambers exist also in other orbitoidal foraminifera. A "relapse of the one-aperture stage", following chambers with two apertures has been reported by MAC GILLAVRY (1963) in *Monolepidorbis*, *Omphalocyclus* and *Planorbulina*. In *Monolepidorbis* this relapse, and also a reversal of coiling direction, have been described by VAN HINTE (1966 b). The recurrence of the one-aperture stage has been observed by the present author (this paper) in *Hellenocyclina* as well.

In most of the *Planorbulinella* specimens the first three chambers are provided with a somewhat thickened wall (compare plates 1—4). An internal dark line has been frequently observed in the walls of the later chambers (pl. 3, figs. 4, 6).

III.2.2.2.6. Results of counts and measurements.

The results of Y counts (range and $\bar{Y} \pm \sigma$) and the number of individuals belonging to the 3/0, 3/1, 3/2, 3/3 and 3/4 ¹⁾ subclasses are presented in the appendix I—VIII. The samples are arranged in stratigraphic order. d1.2 values were calculated for 42 populations only; these values are given in the appendix IX—X along with the corresponding \bar{Y} . It is important to note that, owing to different numbers of observations, the \bar{Y} values given in the appendix IX—X may differ from those in the appendix I—VIII for the same sample.

Histograms of the Y distribution in successive samples of several sections are given. These sections are: Khairitiana (fig. 6, and App. I), Episkopi I (fig. 7, and App. I), Astrikos (fig. 8, and App. II), Nokhia (fig. 9, and App. II), Selli (fig. 10, and App. III) and Apostoli (fig. 11, and App. III).

From the histograms it is evident that there is an upward modal shift in the sections, which corresponds to a decrease of \bar{Y} in the same direction.

However, such a clear shift cannot be detected in the successive samples of the other sections, for which histograms are not given. These sections are: Kastelli (App. IV), Koukounaras (App. IV), Dheliana (App. V), Potamidha (App. VI), Roka (App. V), Episkopi II (App. VI), Episkopi III (App. VII), Stalos (App. VII), Exopolis-Vryses (App. VIII) and Prasses (App. VIII). It should be borne in mind, however, that the section Koukounaras represents only the lowermost part of the Koukounaras Formation, and furthermore, that in the other sections the lower part of the Kissamou (or Apostoli) Formation is not exposed.

¹⁾ 3/4 includes also 3/5 and 3/6 specimens.

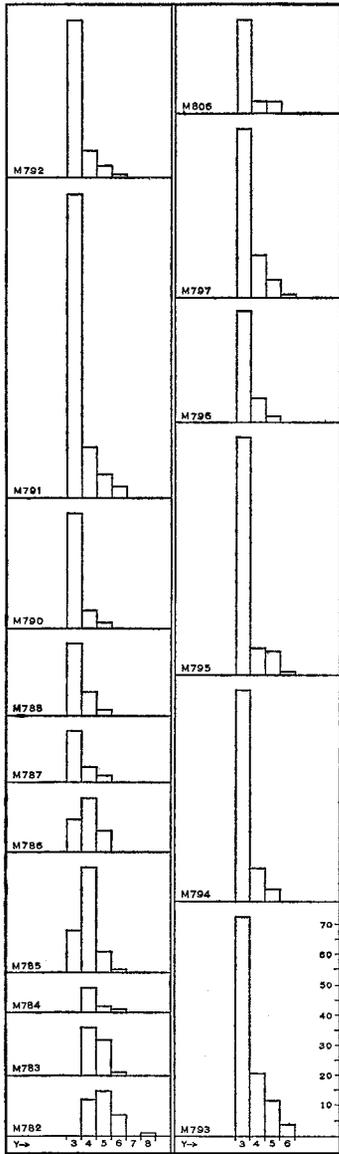


Fig. 6

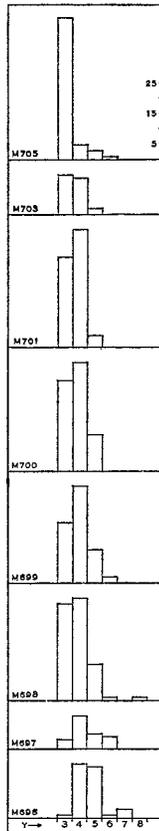


Fig. 7

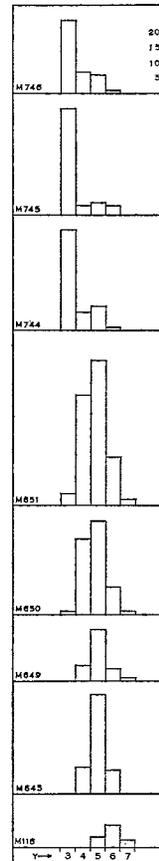


Fig. 8

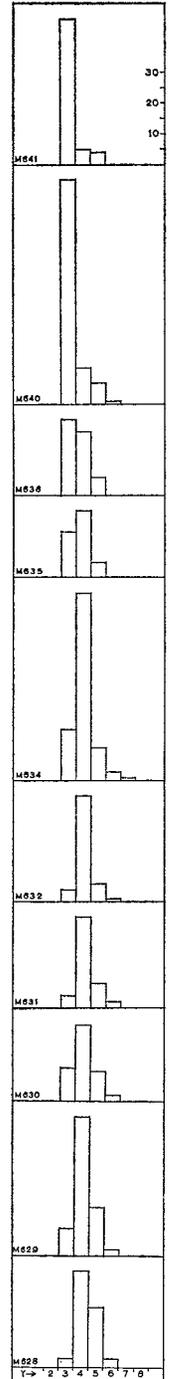


Fig. 9

In the section *Maredhiana* (App. VIII) there is a clear shift of \bar{Y} from bottom to top of the section, but this is not illustrated with histograms, because there is a big sampling gap between the lowermost sample and the stratigraphically higher ones.

From the data on \bar{Y} it is evident that the decrease in \bar{Y} in the sections is not a smooth one. Numerous setbacks (or jumps forward) occur, but they are never statistically significant.

From the Y histograms it is clear that the Y range of successive populations becomes smaller at increasingly higher levels. In the lower part of the figured sections the histograms reflect a normal distribution, but in the upper part the Y histograms become strongly skewed. There, nearly all individuals belong to the $Y = 3$ class. Few specimens have a longer initial spiral. It is remarkable that specimens with $Y = 2$ hardly occur in the Cretan material. Specimens showing this arrangement of the early chambers were found in a few sections only. They are: *Dheliana* (App. V), *Potamidha* (App. VI), *Stalos* (App. VII). Evidently there is some barrier which hampers the development of specimens with $Y = 2$. Because of the skewness of most Y distributions \bar{Y} values and their σ could not be used for our significance test. For this reason, in testing the significance of differences between the populations, a distribution-free test was used on the Y values: the Wilcoxon test¹⁾. The differences were considered significant for $u = 3.3$ or more. For $u = 3.3$ the probability that the samples could not have been derived from populations with the same Y distribution is 99.9%. If u is bigger than 3.3 this probability is even higher. The results of this significance test are also given in the appendix (I—VIII) in the way outlined below.

$$1) u = \frac{Q}{\sqrt{\frac{n_1 n_2 (n_1 + n_2 + 1)}{3}}}$$

in which u is the standardized normal deviate, Q gives the degree of difference between two populations, and n_1 and n_2 are the numbers of specimens in both populations.

- Fig. 6. Histograms showing the Y distribution of successive *Planorbulinella* populations in the section *Khairitiana Kissamou* (*Kissamou Formation*), *Khania Province*, *Crete*.
- Fig. 7. Histograms showing the Y distribution of successive *Planorbulinella* populations in the section *Episkopi Kissamou I* (*Kissamou Formation*), *Khania Province*, *Crete*.
- Fig. 8. Histograms showing the Y distribution of successive *Planorbulinella* populations in the section *Astrikos Kissamou* (*Roka and Kissamou Formation*), *Khania Province*, *Crete*.
- Fig. 9. Histograms showing the Y distribution of successive *Planorbulinella* populations in the section *Nokhia Kissamou* (*Kissamou Formation*), *Khania Province*, *Crete*.



Fig. 10

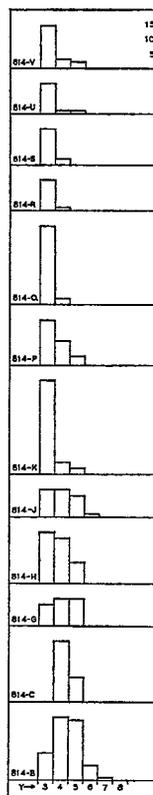


Fig. 11

Fig. 10. Histograms showing the Y distribution of successive *Planorbulinella* populations in the section Selli (Apostoli and Rethymnon Formations), Rethymnon Province, Crete.

Fig. 11. Histograms showing the Y distribution of successive *Planorbulinella* populations in the section Apostoli (Apostoli Formation), Rethymnon Province, Crete.

H In the example given A, B, C . . . H are the populations in stratigraphic order, A being the lowermost one. The successive, significantly different populations are in italics. Thus, in the example A differs significantly from C and from all higher populations. C again differs significantly from F and from all higher populations. F differs significantly from H. This way of reproducing the results of the significance tests enables one to recognize easily the number of significantly different successive steps in the population sequence.

From the data in the appendix (I—VIII) it appears that the number of such steps is:

3 in the sections Astrikos, Episkopi I and Khairitiana,
2 in the sections Selli, Apostoli, Nokhia and Maredhiana.

$\overline{d1.2}$ and $\overline{h1.3}$ values were calculated for the successive populations of only one complete section: Apostoli (App. IX). The other populations for which they were calculated were chosen more or less at random. $\overline{d1.2}$ and $\overline{h1.3}$ values and their standard errors were used for significance tests (Student's t-test).

Although there is a clear decrease of \overline{Y} from bottom to top in the Apostoli section, a distinct trend in the corresponding $\overline{d1.2}$ and $\overline{h1.3}$ is absent. If for example the $\overline{d1.2}$ and $\overline{h1.3}$ of the lowermost and highest populations are compared (see the corresponding σ) it appears that the differences are not statistically significant, although both populations are significantly different as to their \overline{Y} values (App. III).

Figs. 12, 13, 14 and 15 show scatter diagrams in which the \overline{Y} and $\overline{d1.2}$ observations of individuals of four populations were plotted. For each correlation coefficients (r)¹⁾ were calculated. They are:

sample	fig.	r	N ²⁾
814-B	12	-0.5029	52
M 651	13	-0.6269	40
M 786	14	-0.5592	32
M 911	15	-0.4829	47

$$1) r = \frac{\sum(x-\bar{x})(y-\bar{y})}{\sqrt{\sum(x-\bar{x})^2 \sum(y-\bar{y})^2}},$$

in which r is the correlation coefficient, x and y are two parameters, and \bar{x} and \bar{y} are the mean values of these parameters.

2) N = number of observations.

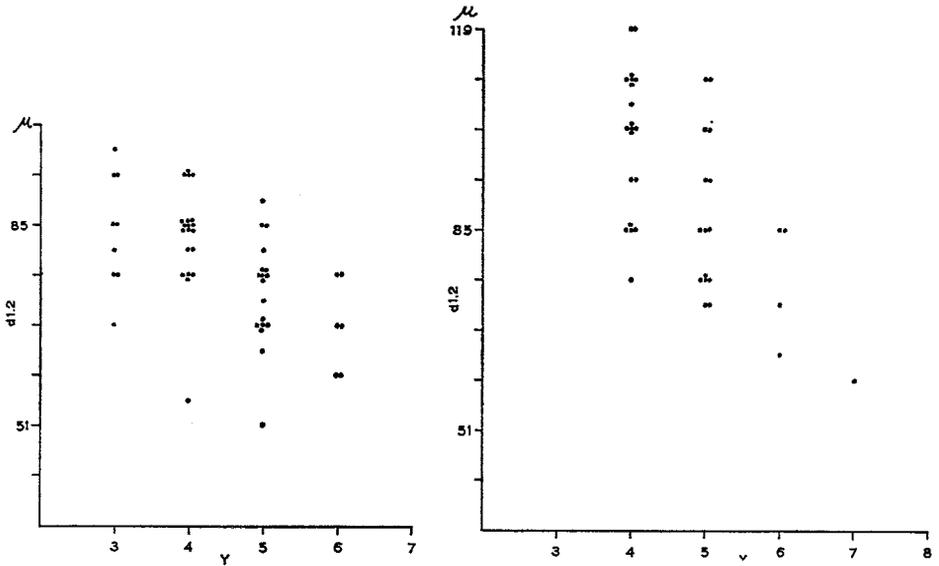


Fig. 12 (l.) $Y/d1.2$ scatter diagram of 52 *Planorbulinella* specimens from sample 814-B, section Apostoli, Rethymnon Province, Crete.

Fig. 13. (r.) $Y/d1.2$ scatter diagram of 40 *Planorbulinella* specimens from sample M 651, section Astrikos Kissamou, Khania Province, Crete.

These correlation coefficients indicate that there is, at a probability level of 99.9%, a significant negative correlation between both parameters in the examples given.

In fig. 16 the relationship between \bar{Y} and $\bar{d1.2}$ of 42 populations is shown. Calculation of the correlation coefficient yields $r = -0.6614$, which indicates a significant, negative correlation at a probability level of 99.9%.

The relationship between the parameters $d1.2$ and $h1.3$ is illustrated for one sample in fig. 17. This figure shows a scatter diagram in which 52 individuals of sample 814-B (section Apostoli) were plotted. For this population the correlation coefficient $r = +0.7420$, which corresponds at a probability level of 99.9% to a significant, positive correlation. In comparison with the correlation between Y and $d1.2$ of the same population (fig. 12), the correlation between both size parameters is stronger.

The relationship between $\bar{d1.2}$ and $\bar{h1.3}$ is shown in the scatter diagram of fig. 18. In this case $r = +0.9273$, which indicates a very strong positive correlation of both factors. The correlation is stronger than in the corresponding \bar{Y} and $\bar{d1.2}$ of the same populations (fig. 16).

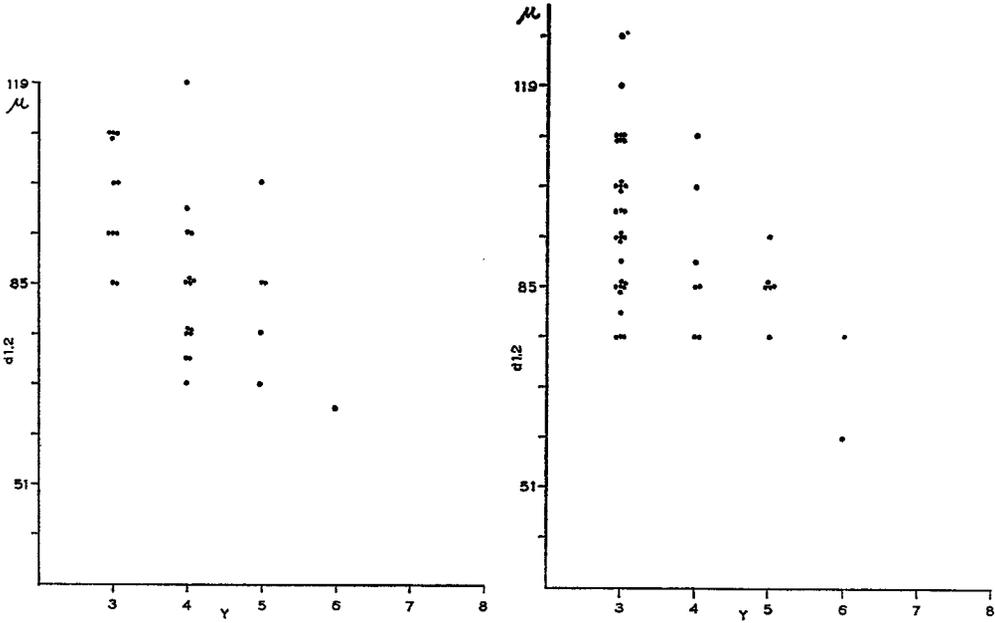


Fig. 14 (l.) $Y/d_{1.2}$ scatter diagram of 32 *Planorbulinella* individuals from sample M 786, section Khairitiana Kissamou, Khania Province, Crete.

Fig. 15 (r.) $Y/d_{1.2}$ scatter diagram of 47 *Planorbulinella* specimens from sample M 911, section Kastelli Kissamou, Khania Province, Crete.

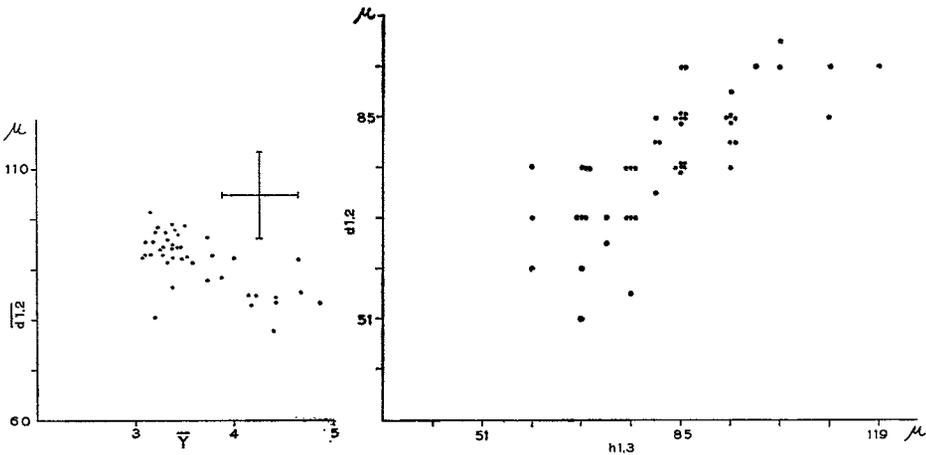


Fig. 16 (l.) Scatter diagram showing the relationship between $\overline{d_{1.2}}$ and \overline{Y} in 42 *Planorbulinella* populations from Crete. The cross gives average values of $\pm 3\sigma$.

Fig. 17 (r.) $h_{1.3}/d_{1.2}$ scatter diagram of 52 *Planorbulinella* specimens from sample 814-B, section Apostoli, Rethymnon Province, Crete.

Within a single population, M 905 (section Kastelli), partial $\overline{d1.2}$ values ¹⁾ were calculated separately for individuals belonging to the 3/0, 3/1, 3/2, 3/3 and 3/4 subclasses. These $\overline{\delta 1.2}$ values are given below. They indicate that there may be an increase of the mean size of the first two chambers corresponding to a decrease of the number of one-aperture chambers. Since the numbers of specimens (N) involved in each subclass are small, the standard errors of $\overline{\delta 1.2}$ are not given.

Y	N	$\overline{\delta 1.2}$
3/0	11	103.9
3/1	10	101.1
3/2	12	92.8
3/3	1	89.2
3/4	2	72.2

Because of the small number of specimens involved in this example, similar $\overline{\delta 1.2}$ calculations were made of the specimens of some 20 populations that were taken together. The 3/3 and 3/4 subclasses were omitted because of the very small numbers of specimens they contain. Apart from $\overline{\delta 1.2}$ data on the 3/0, 3/1 and 3/2 subclasses, also those on the Y = 4, 5 and 6 classes are given. The $\overline{d1.2}$ distribution within these (sub)classes is given in the histograms of fig. 19.

Y	N	$\overline{\delta 1.2}$
3/0	151	108.3 ± 1.0
3/1	169	100.6 ± 0.9
3/2	100	90.9 ± 1.0
4	196	87.9 ± 0.7
5	117	79.9 ± 0.9
6	22	71.7 ± 1.7

The mutual $\overline{\delta 1.2}$ differences between all Y (sub)classes are significant at a probability level of 99.9 %, except for the difference between the 3/2 and 4 (sub)classes. The results of the 3/0, 3/1 and 3/2 subclasses indicate that it is highly probable that there is an increase in the mean size of the first two chambers corresponding to a reduction in the number of recurrences of the one-aperture stage. It is reasonable to assume that this trend not only exists from the 3/2 to the 3/0 subclasses, but also from the 3/6 to the 3/2 subclasses. This assumption, however, cannot be checked because the numbers of specimens in the 3/6 to 3/3 subclasses are far too small.

¹⁾ Partial $\overline{d1.2}$ values will be given as $\overline{\delta 1.2}$.

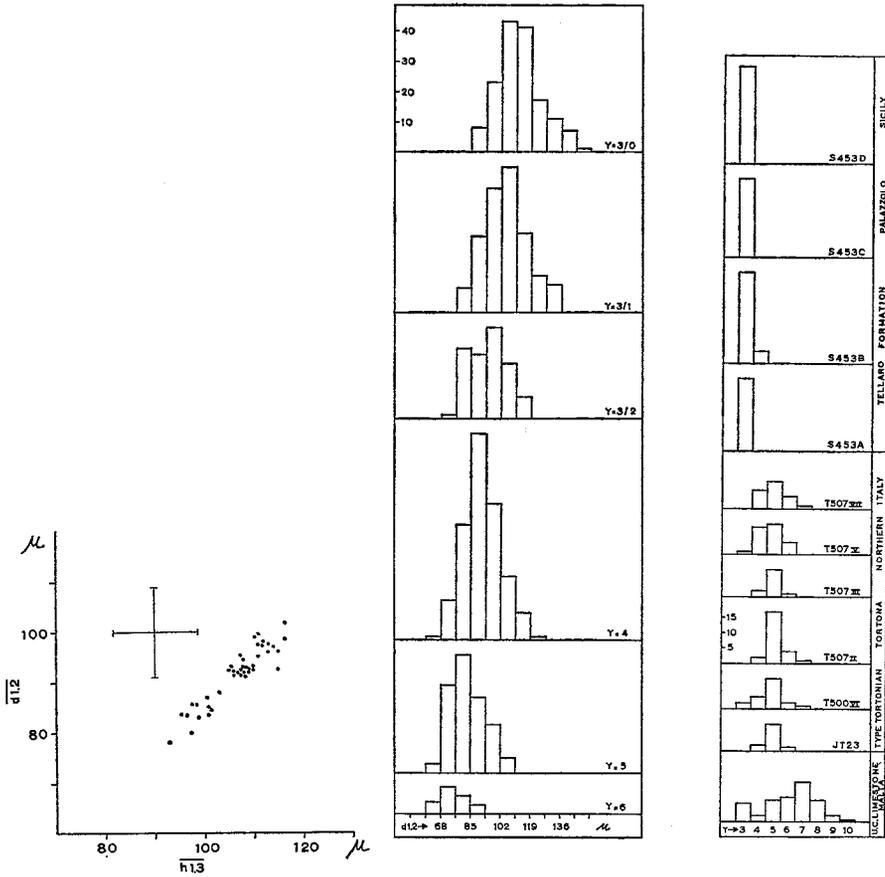


Fig. 18 (l.) Scatter diagram showing the relationship between $\overline{d1.2}$ and $\overline{h1.3}$ in 42 *Planorbulinella* populations from Crete. The cross gives average values of $\pm 3\sigma$.

Fig. 19 (m.) Histograms showing the distribution of $d1.2$ within selected Y classes. The interval of each histogram class is 8.5μ . The data were gathered from about 20 *Planorbulinella* populations from various stratigraphic levels in the Cretan Neogene.

Fig. 20 (r.) Histograms showing the Y distribution in Italian and Maltese *Planorbulinella* populations.

III.2.2.2.7. Discussion of the results of counts and measurements; phylogeny.

The reduction in the length of the initial spiral, which feature was observed in the subsequent populations of several sections, and which is illustrated in the histograms of figures 6—11, is in good accordance with the principle of nepionic acceleration advanced by TAN SIN HOK. From the bottom to the top of these sections several subsequent, significantly different populations can be distin-

guished. They have a smaller \bar{Y} at increasingly higher stratigraphic levels. The absence of this trend in the subsequent populations of other sections can be explained by the fact that they comprise only smaller parts of the stratigraphic succession in which *Planorbulinella* occurs in Crete.

A clear trend in the corresponding $\bar{d1.2}$ and $\bar{h1.3}$ was not observed. This seems rather remarkable since significant correlations exist between \bar{Y} and $\bar{d1.2}$, between \bar{Y} and $\bar{h1.3}$, and between $\bar{d1.2}$ and $\bar{h1.3}$. According to the negative correlation between $\bar{d1.2}$ and \bar{Y} one might expect that the clear decrease in \bar{Y} , observed in several sections, would correspond to an increase in $\bar{d1.2}$, but this is not true in the only section (Apostoli) for which it was checked.

Evidently the significant correlation between \bar{Y} and $\bar{d1.2}$, and between \bar{Y} and $\bar{d1.2}$ is not strong enough, that random or other effects on $\bar{d1.2}$ can influence the population's \bar{Y} . It is possible that the correlation is not so strong because of the presence of many individuals in which there are recurrences of the one-aperture stage. Since the size of the early chambers is correlated with the number of such recurrences, it might be assumed that these recurrences widen the $\bar{d1.2}$ range of individuals with a definite \bar{Y} . As a consequence, $\bar{d1.2}$ shows less change if compared with its average standard error, than does the corresponding \bar{Y} over the same stratigraphic interval.

The data presented justify the conclusion that there is an evolution according to the principle of nepionic acceleration in Cretan *Planorbulinella*. In the course of time the mean length of the initial spiral of subsequent populations decreases. This development enables us to distinguish species which follow each other in the course of time. The significance of differences in the length of the initial spiral of subsequent populations is of prime importance in judging the number of distinguishable species. In the sections studied maximally three significantly different, subsequent steps can be distinguished, but in the Neogene succession as a whole there are four steps. One might consider them as the boundaries of four subsequent species, but we preferred to widen the species limits amongst others because of the frequently skewed character of the \bar{Y} distribution. As a consequence, we have distinguished three species, the limits of which are drawn arbitrarily. These limits are:

$\bar{Y} = 6.49—5.25$: *Planorbulinella rokae* n.sp

$\bar{Y} = 5.24—4.00$: *Planorbulinella astriki* n.sp.

$\bar{Y} = 3.99—3.00$: *Planorbulinella canaeae* n.sp

These species are described below.

III.2.2.2.8. Systematics.

Planorbulinella rokae n.sp.; plate 12, fig. 1.

Etymology. The name is derived from the village of Roka Kissamou, Khania Province, Crete.

Holotype. Pl. 12, fig. 1, coll.nr. S20841.

Paratypes. 12 sectioned, macrospheric specimens.

Type level. Roka Formation, Miocene (Tortonian).

Type locality. In the vicinity of Mesonisi church near Roka Kissamou, Khania Province, Crete, sample M 116.

Diagnosis. A small *Planorbulinella* with a long initial spiral and very small initial chambers. The average \bar{Y} is between 6.49 and 5.25.

Description. Test small, discoidal, up to 1.0 mm in diameter, flat at both sides, smooth. At one side all chambers are visible, at the other side the early chambers cannot be seen. The periphery is rounded or acute, lobate. The apertures are median, basal slits, two to a chamber, and each provided with an imperforate lip. The pore diameter is about 10 μ .

The early chambers with proximal openings only are arranged in a trochoid spiral, consisting of a variable number of chambers (7—5 in the specimens of the type sample; mean 5.92 ± 0.20). The early chambers are small. The diameter of protoconch and deutoconch together ranges from 45 to 95 μ in the specimens of the type sample and the corresponding mean value is $73.0 \pm 4.9 \mu$.

A recurrence of the one-aperture stage is a common feature. The first three chambers are sometimes very prominent because they are thick-walled. The wall structure is bilamellid.

Remarks. *P. rokae* n.sp. differs from *P. astriki* n.sp. in the relatively longer initial spiral (mean number of chambers in the initial spiral in a population 6.49—5.25) and smaller size of the early chambers.

Stratigraphic distribution. Only found in one sample of the Roka Formation. Also occurring in the Upper Coralline Limestone of Malta (compare p. 81).

Planorbulinella astriki n.sp.; plate 12, figs. 3a, b.

Etymology. The name is derived from the village of Astrikos Kissamou, Khania Province, Crete.

Holotype. Pl. 12, figs. 3a, b, coll. nr. S 20842.

Paratypes. 108 macrospheric and 39 microspheric specimens.

Type level. Kissamou Formation (lowermost part), Miocene (Tortonian).

Type locality. Astrikos Kissamou, Khania Province, Crete, sample M 651.

Diagnosis. A small *Planorbulinella* with \bar{Y} between 5.24 and 4.00 and with small early chambers.

Description. Test small, discoidal, up to 1.00 mm in diameter, flat or slightly inflated in the centre at one side, slightly concave at the other side. Both sides are smooth. All chambers are visible from both sides, being accentuated by

relatively depressed sutures. The periphery is rounded or acute, lobate. The apertures are median, basal slits, two to each chamber, and each provided with an imperforate lip. The pore diameter is about 13μ .

The early chambers with one aperture are arranged in a slightly trochoid spiral, consisting of a variable number of chambers (7—3 in the macrospheric specimens of the type sample; mean value 4.75 ± 0.08 ; 16—10 in the microspheric ones). After the first chamber which has acquired a distal opening in addition to the proximal one, the subsequent chambers may lack this feature again. The initial chambers are small. The diameter of the protoconch and deuteroconch together ranges from 60 — 120μ in the type sample and the corresponding mean value is $92.2 \pm 2.4 \mu$ (calculated from 40 specimens). The first three chambers are somewhat differentiated from the later ones because they are thick-walled. The wall structure is bilamellid.

Remarks. *P. astriki* differs from *P. rokae* and *P. caneae* in having a smaller, respectively larger average number of one-aperture chambers in the initial spiral. It differs also in that the average size of the initial chambers is larger, respectively smaller.

Stratigraphic distribution. In Crete the species occurs in the topmost beds of the Roka Formation, and in the lower parts of the Koukounaras, Kissamou and Apostoli Formations. The species occurs also in the middle part of the Tortonian type section in Italy.

Planorbulinella caneae n.sp.; pl. 1, figs. 1—6; pl. 2, figs. 1—6; pl. 3, figs. 1—7; pl. 4, figs. 1, 2; pl. 12, figs. 2a, b.

Etymology. The name is derived from Canea, the mediaeval name for Khania, the capital of Crete.

Holotype. Pl. 12, figs. 2a, b, coll. nr. S 20843.

Paratypes. 37 macrospheric and 11 microspheric specimens.

Type level. Kissamou Formation (upper part), Miocene (Tortonian).

Type locality. Near Krya Vrisi Kissamou, Khania Province, Crete, sample M 746.

Diagnosis. A small *Planorbulinella* with \bar{Y} between 3.99 and 3.00, and with relatively big early chambers.

Description. Test small, discoidal, up to 1.4 mm, but generally less than 1.0 mm in diameter, almost flat, or slightly concave at one side and with a central inflation at the other side. Both surfaces are smooth. Generally all chambers are visible from both sides, but in big specimens with many chambers the side walls may be strongly thickened by the subsequent lamellae formed at each instar and then the initial chambers cannot be seen clearly from the outside. At both sides the chambers are accentuated by depressed sutures. The periphery is rounded

or acute, lobate. The apertures are median, basal slits, two to each chamber, and each provided with an imperforate lip. The diameter of the pores is about 13μ .

The early one-aperture chambers are arranged in a slightly trochoid spiral, consisting of a variable number of chambers (6—3 in the macrospheric specimens of the type sample, mean value 3.58 ± 0.14 ; 14—10 in the microspheric ones). Occasional specimens with $Y = 2$ occur in some samples. A relapse to the one-aperture stage is a very common feature. The initial chambers are relatively big. The diameter of the protoconch and deutoconch together ranges from 65—120 μ in the type specimens, and the corresponding mean value is $93.6 \pm 2.4 \mu$. The first three chambers are often well differentiated from the later ones because they are thick-walled. The wall structure is bilamellid.

Remarks. *P. canae* differs from *P. rokae* and *P. astriki* in having a more reduced initial spiral (mean values per population from 3.99—3.00) and in that the average size of the initial chambers is larger. Moreover, the test may be more strongly thickened and bigger than in the other two species. *P. canae* differs from the Recent *P. larvata* in its relatively longer initial spiral, in its smaller early chambers, in the smaller size (diameter) of the test, and in lacking a pustulate ornamentation.

Stratigraphic distribution. This species occurs in the middle and upper parts of the Kissamou, Koukounaras and Apostoli Formations. It is also present in the lowermost part of the Khairitiana Formation and in the Rethymnon Formation.

III.2.2.3. *Planorbulinella* in the Maltese and Italian Neogene.

III.2.2.3.1. Introduction.

To get information on the age of the Cretan Neogene deposits, it appeared to be of interest to gather data on *Planorbulinella* populations from deposits, the age of which is better known and/or fixed by definition (for example, type localities of stages). For this reason many samples of the whole Mediterranean area and of many different ages were investigated. *Planorbulinella* proved to be present in the type Tortonian, but it is apparently absent in the type Messinian (neotype), Tabianian, Plaisancian and Astian. It was found in Neogene deposits of Malta, Sicily and Southern Spain (Guadalquivir Basin).

III.2.2.3.2. *Planorbulinella* in the type Tortonian.

Most samples referred to have been taken by VERVLOET and have served that author for his study of the type Tortonian planktonic foraminifera. For the exact stratigraphic position of the samples one is referred to the paper by VERVLOET (1966). *Planorbulinella* populations were found in the following samples: T 500-VI, T 507-II, T 507-III, T 507-V and T 507-VII. Moreover,

Planorbulinella occurs in the sample JT 23, which has been taken by DROOGER and which has probably been derived from a level slightly lower than VERVLOET's sample T 500-VI. These samples comprise only the middle part of the type Tortonian (see also VERVLOET, 1966, p. 33, table V, Castellania Formation = type Tortonian). *Planorbulinella* was not found in the stratigraphically lower and upper parts of the type section.

It is of little use to give an extensive account of the external features of the *Planorbulinella* specimens. They closely resemble the Cretan ones. They are smooth, all chambers are visible from the outside, and there is no special thickening of the central portion. As to this last feature they differ only from specimens of the stratigraphically uppermost samples from Crete.

The results of counts and measurements are given below. The \bar{Y} distribution of all populations is furthermore given in histograms (fig. 20).

sample	N ₁	N ₂	Y					\bar{Y}	$\overline{d1.2}$	$\overline{h1.3}$
			7	6	5	4	3			
T 507-VII	20	19	1	4	9	6	—	5.00 ± 0.20	77.4 ± 3.4	80.5 ± 3.3
T 507-V	24	24	—	4	10	9	1	4.71 ± 0.16	79.7 ± 2.0	84.8 ± 2.7
T 507-III	12		—	1	9	2	—	4.92 ± 0.15		
T 507-II	24	22	1	4	17	2	—	5.16 ± 0.13	72.6 ± 2.2	75.1 ± 1.8
T 500-VI	19	17	1	2	10	4	2	4.79 ± 0.23	81.2 ± 2.3	87.7 ± 2.1
JT 23	12	8	—	1	9	2	—	4.92 ± 0.15	77.0 ± 5.6	84.5 ± 6.1

N₁ applies to the number of specimens involved in Y counts, N₂ applies to the number of specimens of which d1.2 and h1.3 measurements could be made.

From the above data the following conclusions can be drawn:

1. The mutual differences between the mean values for each parameter are insignificant (Wilcoxon-test, Student's t-test).

2. No clear trend is present, neither in \bar{Y} , nor in $\overline{d1.2}$ or $\overline{h1.3}$.

3. The populations have to be referred to *Planorbulinella astriki* n.sp. the \bar{Y} range of which is from 5.24—4.00. The size of the early chambers tends to be slightly larger in the Italian than in the Cretan populations, but the differences are insignificant.

4. At least part of the Cretan *Planorbulinella* populations is of Tortonian age.

III.2.2.3.3. *Planorbulinella* in the Neogene of Malta.

The sample studied (M 25) has been taken by R. FELIX, who kindly permitted the author to publish the results. It has been derived from the base of the Upper Coralline Limestone, 2.5 km W of Dingli (see R. FELIX in a future paper). The genus was not found in levels of the Maltese Neogene that are stratigraphically

lower. As to their outer appearance the Maltese specimens fully agree with the Cretan ones, but they are less well preserved, mainly because of exogenous matter, like calcareous and quartz grains, fixed to the outside of the tests. For this reason most specimens had to be sectioned for studying the early chambers. It is possible that, due to the difficulty to observe the apertural characteristics, some *Planorbulina* specimens were included.

The results of counts and measurements are given below. The Y distribution is also given in a histogram of fig. 20.

N	Y						\bar{Y}	$\overline{d1.2}$	$\overline{h1.3}$		
	10	9	8	7	6	5				4	3
46	1	2	7	13	8	7	2	6	6.20 ± 0.26	74.3 ± 3.0	74.2 ± 3.1

As to its \bar{Y} this population might be even more primitive than the lowermost Cretan one (M 116, from the Roka Formation at Mesonisi church near Roka Kissamou), but it does not differ significantly from it. However, it differs significantly from all other Cretan populations. For this reason it is referred to *Planorbulinella rokae* n.sp. the \bar{Y} range of which is from 6.49 to 5.25.

If compared with the population from Mesonisi, the Y range of the Maltese population is remarkably wide.

III.2.2.3.4. Planorbulinella in the Neogene of Sicily.

Planorbulinella populations were found in four consecutive samples of a single section in the Tellaro Formation near Palazzolo, Ragusa Platform, Sicily. The samples have been taken by R. FELIX. Their numbers are S 453 A, B, C and D, A being the lowermost one. The age of the strata involved is Later Miocene.

Most specimens are big and strongly thickened by consecutive laminae covering the test at each instar. Therefore the initial chambers can be seen from the outside in a few specimens only. In these respects the Sicilian specimens compare only with the stratigraphically higher ones of Crete, not with the lower ones.

The results of counts and measurements are given below. The Y distribution in the consecutive samples is shown also in the histograms of fig. 20.

sample	N	Y					\bar{Y}	$\overline{d1.2}$	$\overline{h1.3}$
		4	3	3/2	3/1	3/0			
S 453 D	32	—	32	3	6	23	3.00	117.0 ± 2.1	120.7 ± 2.3
S 453 C	26	—	26	3	7	16	3.00	110.3 ± 2.7	117.4 ± 3.2
S 453 B	34	4	30	5	9	16	3.12 ± 0.05	106.3 ± 2.6	113.8 ± 2.8
S 453 A	24	—	24	3	7	14	3.00	107.5 ± 2.7	112.6 ± 3.3

As to their \bar{Y} the Sicilian populations closely resemble the stratigraphically uppermost ones from Crete. However, the mean size of the initial chambers is larger in the Sicilian populations, especially so for the population of sample S 453 D which differs significantly from the Cretan populations both for $\bar{d}1.2$ and $\bar{h}1.3$.

Moreover, there seems to be a gradual size increase in $\bar{d}1.2$ and $\bar{h}1.3$ from bottom to top of the Palazzolo section. From these four populations only it is not possible to decide whether the bigger $\bar{d}1.2$ and $\bar{h}1.3$ are of taxonomic importance. They are provisionally referred to as *Planorbulinella* cf. *caneeae*, because the \bar{Y} values are on, or very close to, the upper limit of the species range.

III.2.3. PLANORBULINELLA LARVATA (PARKER & JONES), 1860.

pl. 4, figs. 3, 4; pl. 5, figs. 1, 2; pl. 6, fig. 4; pl. 12, figs. 4a, b, 5a, b.

III.2.3.1. Introduction.

Planorbulinella larvata is commonly found in coral sands of tropic and subtropic seas, especially so in the Indian and Pacific Oceans. Nearly all references of Recent populations concern these regions. The northernmost reported occurrence is from the Gulf of Eilat (Israel).

Many features of this species were recorded in the introduction to *Planorbulinella* (p. 57 etc.). Its external characteristics have been described sufficiently in the literature, but little is known of the arrangement of the early chambers.

III.2.3.2. Material.

The samples studied were derived from the following localities:

Yaene, Hachijo Island, Tokyo Prefecture. Recent beach sand (see also UCHIO, 1952). Donation T. UCHIO.

Keise, off Nawa, Okinawa, Ryukyu Islands, Japan. Recent calcareous sand, depth unknown (probably very shallow). Donation T. UCHIO.

D 5151, dredge sample of the Albatross Pacific Expedition, depth 24 fms, Sulu Archipel, Philippines ($5^{\circ}24'40''$ N; $27^{\circ}15''$ E). Donation Miss RUTH TODD.

Eilat, Israel, Rec. Station 23, no. 15210. Donation Z. REISS.

DD 53, dredge sample HMS Dampier Cruise 1963, South China Sea, off Borneo ($06^{\circ}40'$ N; $109^{\circ}36'$ E), depth 205 m. Donation A. J. KEIJ.

III.2.3.3. External features.

Since the specimens of the five populations studied resemble each other quite

well there is no use in describing the external characteristics for each population separately. The material of these samples fits well within the limits of the following description.

Test discoidal, diameter up to 2.5 mm maximally, flat at both sides, slightly concavo-convex or plano-convex. Both sides are provided with pustules, the diameter of which is 170μ maximally (in the Keise sample); the pustules are rounded, subrounded or U-shaped and they are not arranged in a special pattern. In the central portion the pustules may fuse to ridges, which are about 125μ broad and 5 to 7 times longer. They may be running radially, but they may show a more irregular, cerebral-like pattern also. The peripheral chambers are smooth (not provided with pustules) and they show clearly the coarse pores (diameter up to 13μ). The peripheral chambers have arched or slit-like peripheral apertures, two to each chamber, and each provided with a small imperforate lip. The periphery is rounded, lobate. The external features can be seen in two specimens figured on plate 12, figs. 4a, b and 5a, b.

III.2.3.4. *Internal features.*

The early chambers show a wide range of variation. Apart from the "normal" $Y = 1, 2, 3$ and 4 types, also a relapse to the one-aperture stage, similar to that found in the Mediterranean *Planorbulinella*, is present in many individuals. A specimen showing this relapse (3/3/a) is figured on pl. 5, fig. 1.

In some specimens (compare pl. 5, fig. 1), from Yaene, Keise and D 5151, the initial chambers are provided with a brown, chitinous "inner lining", which probably represents the original chambers' walls. In such specimens a dark line within the chambers' walls was never observed, whereas this feature was observed in specimens that are lacking this chitinous, brown "inner lining".

The apertures are clearly visible in the thin sections, except for those connecting the protoconch and deutoconch. Toward the periphery the diameter of the apertures increases slightly, being about 20μ in the peripheral chambers. In

sample	N	Y				\bar{Y}	$\overline{d1.2}$	$\overline{h1.3}$
		4	3	2	1			
Yaene	5	—	2	3	—	2.40	184.4	185.3
Keise	10 ¹⁾	1	2	6	1	2.30 ± 0.27	175.1 ± 10.1	181.0 ± 11.8
D 5151	4	—	2	2	—	2.50	148.7	162.6
Eilat	2	—	1	1	—	2.50	182.7	182.7
DD 53	2	—	—	2	—	2.00	170.0	174.2

¹⁾ The $\overline{h1.3}$ applies to 9 specimens only, because h1.3 cannot be measured in the specimen with $Y = 1$.

some specimens the first three chambers are clearly differentiated from the later ones because they are thick-walled.

The results of counts and measurements are given on p. 83. Because of the small number of specimens available in each sample the standard error of the mean is given for one population only. The individual measurements on all specimens are plotted in a $d_{1.2}/h_{1.3}$ scatter diagram (fig. 21).

The \bar{Y} results suggest that our populations differ from the Miocene Mediterranean ones. Because of the small numbers of observations differences between these populations are of small significance.

However, the $\bar{d}_{1.2}$ and $\bar{h}_{1.3}$ indicate that the Recent *P. larvata* populations differ strongly from the Mediterranean Miocene populations. This can easily be seen if a comparison with the uppermost Sicilian population is made. In that population $\bar{d}_{1.2} = 117.0 \pm 2.1$ and $\bar{h}_{1.3} = 120.7 \pm 2.3$.

To get a better insight into the differences between the Recent *P. larvata* and the Mediterranean Neogene populations, the results of counts and measurements of all specimens of the five populations were lumped. New mean values and corresponding standard errors were calculated and are given below. Moreover, the Y distribution is shown in the histogram of fig. 21.

N	Y				\bar{Y}	$\bar{d}_{1.2}$	$\bar{h}_{1.3}$ ¹⁾
	4	3	2	1			
23	1	7	14	1	2.35 ± 0.13	172.8 ± 5.4	178.3 ± 6.0

¹⁾ Calculated on 22 specimens only.

If these data are a better approximation of the internal features of the Recent *P. larvata*, this species can easily be differentiated from the Mediterranean Neogene species, especially so on the $\bar{d}_{1.2}$ and $\bar{h}_{1.3}$. Of course, to substantiate this assumption, in the future it will be necessary to gather data on Recent populations that contain more specimens.

III.2.4. PLANORBULINELLA IN THE BODJONEGORO I DRILL HOLE (JAVA).

III.2.4.1. Introduction, literature.

Specimens referred to as *P. larvata* (PARKER & JONES) have been described from the Bodjonegoro I drill hole by BOOMGAART (1949). The species has been recorded from depths of 412 and 419 m. The strata in which they occur BOOMGAART considers to be of Pliocene age. BOLLI (1966) considers them as Middle

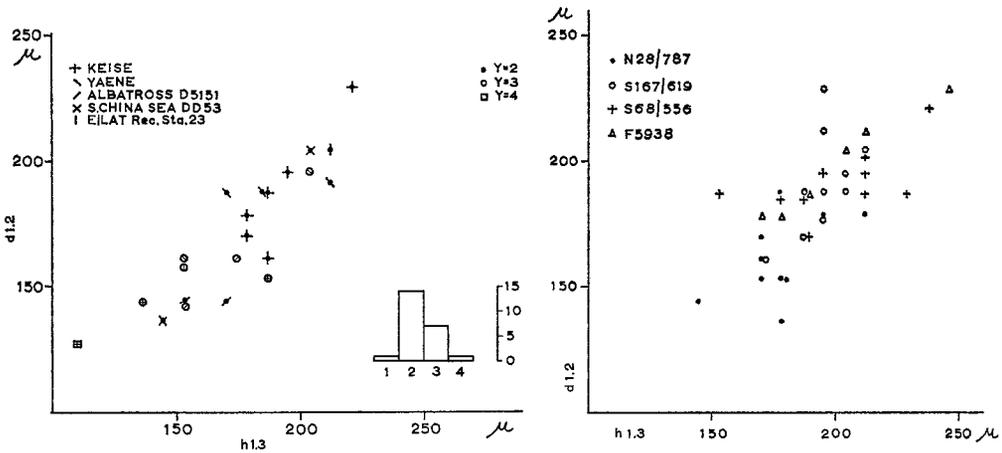


Fig. 21 (l.) $d_{1.2}/h_{1.3}$ scatter diagram of 22 *Planorbulinella larvata* specimens of five different samples. The histogram to the right shows the Y distribution in 23 specimens of these samples.

Fig. 22 (r.) Scatter diagram showing the relationship between $d_{1.2}$ and $h_{1.3}$ in 36 specimens of four *Planorbulinella zelandica* populations from New Zealand.

Miocene¹⁾. The material BOOMGAART studied is stored in the collection of the Geological Institute of the Utrecht State University and was available to the author. The material described below was derived from a depth of 419 m.

III.2.4.2. External features.

Test discoidal, diameter up to 1.5 mm maximally, flat or slightly concavo-convex. The plane of the equatorial chambers is not completely regular, but somewhat undulating. Both sides are strongly pustulate, the pustules covering nearly the whole surface, except for the peripheral chambers. The pustules are rounded or subrounded, and they do not fuse to ridges; their diameter generally does not exceed 85 μ , but occasionally it ranges up to 125 μ . The initial chambers are visible from the outside in a few specimens only, since the centre is generally thickened by calcareous laminae and pustules. The apertures are median low arches, two to each chamber, and each provided with a small imperforate lip.

Remarks. Externally the Bodjonegoro specimens do not differ essentially from

¹⁾ This age assignment may be doubted since stratigraphically higher zones (*Globorotalia margaritae* Zone, *G. crassaformis* Zone) BOLLI considered to belong to the Upper Miocene. These zones clearly represent the Pliocene in the Mediterranean Area. As a consequence a Late Miocene or Early Pliocene age seems to be more correct for our sample.

the Recent *P. larvata*, except for their smaller size and less strong, pustulate ornamentation. They differ strongly from the Mediterranean Neogene specimens in their larger size and in the presence of a pustulate ornamentation.

III.2.4.3. *Internal features.*

Also in the Bodjonegoro population a wide variation in the arrangement of the early chambers was observed. A recurrence of the one-aperture stage was frequently seen, but in the record of the Y distribution (below) the $Y = 3$ class was not subdivided in subclasses. The full results of counts and measurements are:

N	Y						\bar{Y}	$\overline{d1.2}$	$\overline{h1.3}$
	7	6	5	4	3	2			
30	2	2	—	3	11	12	3.16 ± 0.26	137.0 ± 7.4	142.1 ± 7.4

As to its \bar{Y} this assemblage is inside the range of variation of the Mediterranean populations. However, its $\overline{d1.2}$ and $\overline{h1.3}$ are bigger. As to the latter factors the differences with the Cretan populations are significant, but the differences with the Sicilian populations are not. Both factors differ significantly from those of the Recent *P. larvata* (if the $\overline{d1.2}$ and $\overline{h1.3}$ data of all *P. larvata* specimens of the 5 samples are taken together, compare p. 84). As to the length of the initial spiral the Bodjonegoro assemblage does not differ significantly (at a probability level of 99.9 %) from the Recent *P. larvata*.

There are some remarkable features in the Y distribution of the Bodjonegoro assemblage. It has a rather long tail and there are no specimens in the $Y = 5$ class. Although mere random effects cannot be excluded it might be a population mixed with reworked specimens, but this assumption cannot be substantiated because possible reworked specimens cannot be recognized by a different state of preservation.

As to the mean length of the early spiral the Bodjonegoro population is within the limits of *P. canaeae*. However, its $\overline{d1.2}$ and $\overline{h1.3}$ are bigger. For this reason this population is tentatively determined as *P. cf. canaeae*.

III.2.5. PLANORBULINELLA ZELANDICA (FINLAY), 1947.

pl. 5, figs. 3, 4; pl. 6, figs. 1, 6; pl. 12, figs. 6a, b, 7a, b.

III.2.5.1. *Introduction, literature.*

This species has been described originally from New Zealand in strata of

Altonian to Tongaporutuan age, which according to EAMES et al. (1962, fig. 4) corresponds to the time interval Late Aquitanian — Sarmatian in terms of European stratigraphy. According to JENKINS (1966) it corresponds to the Helvetian — Messinian interval. The original description of this species reads:

„Differs from *larvata* P. & J. and allied forms such as *inaequilateralis* H.-A. & E. and *trinitatensis* NUTTALL in much coarser and grosser structure and plano-convex shell, which is thick and solid. Ventral surface flat or slightly concave, dorsal strongly convex medially, flattening and often slightly excavate before reaching outer rim of chambers. Both surfaces cut up into prominent granules by irregular furrows, dorsal ones higher and smaller. A ring of larger sub-globular chambers on periphery, mostly alternating with smaller ones and projecting by half their size, with a conspicuous rimmed aperture on each side. Outer chambers coarsely perforate, perforations obscured by granulation, which is frequently finely wrinkled. Size 2 mm”.

Remarks on the internal features of this species have been made neither by FINLAY, nor by subsequent authors. As far as known to the present author *P. zelandica* has not been recorded from outside New Zealand.

III.2.5.2. *Material.*

The material studied has been kindly supplied by G. H. SCOTT.

F 5938, from Pourere, S. Hawkes Bay, South Island. Type locality of *P. zelandica*. Age: Waiauan.

S 68/556, from Weka Creek, N. Canterbury. Age: Awamoan — Altonian.

S 167/619, from the Upper Clifden Limestone, Clifden, South Island. Age: Awamoan or Altonian. This locality is also mentioned by FINLAY (1947).

N 28/787, Pakaurangi Point. Some of the specimens FINLAY figured have been derived from this locality (FINLAY, 1947, pl. 8, figs. 121—124). Age: Otaian. According to SCOTT this is our lowermost sample. According to FINLAY the species does not occur in beds older than Altonian, but SCOTT states (personal communication): "For some years the appearance of *P. zelandica* was taken to define the base of Altonian. However, other faunal evidence conflicted with this interpretation and we now think that N 28/787 is lower in terms of the standard sequence”.

The standard stage succession in New Zealand is:

Tongaporutuan
 Waiauan
 Lillburnian
 Clifdenian
 Altonian

Awamoan
Hutchinsonian
Otaian

If the age assignments of the samples are taken into account, it will appear that the samples cover nearly the whole time interval in which this species occurs in New Zealand. However, a sample from the Tongaporutuan was not available.

III.2.5.3. *External features.*

A redescription of this species on the basis of the topotypes is given below. Moreover, mention is made of the characteristics in which the specimens of the other samples differ from the topotypes.

Test discoidal, diameter up to 1.4 mm maximally, one side flat, the other slightly convex to conical. The ornamentation consists of irregular pustules, the diameter of which ranges up to 125 μ . The pustules fuse to irregular ridges in the central portion. The greater part of the flat side is ornamented with these ridges, whereas the other, convex to conical side, is mainly ornamented with isolated pustules. The peripheral chambers are smooth. They clearly show the pores, the diameter of which is about 17 μ . The apertures are median, basal slits, two to each chamber, and each with an imperforate lip. The periphery is rounded, lobate.

Remarks. As to their external features these specimens cannot be differentiated from *P. larvata* (compare also p. 83). The only difference is in the size of the pores, which feature is thought to be not of sufficient weight to justify their separation from *P. larvata*. The specimens of S 68/556 fully agree with this description. Those of S 167/619 are slightly bigger (up to 2.0 mm), the diameter of the pustules is larger (up to 170 μ), and the size of the pores is smaller (8—13 μ). The specimens of N 28/787 again closely resemble the topotypes, but they are somewhat bigger (up to 1.9 mm). The external features are illustrated by two figured specimens: pl. 12, figs. 6a, b and 7a, b.

III.2.5.4. *Internal features.*

A remarkable result of the study of the internal features is that all specimens have $Y = 2$, thus an arrangement of protoconch-deuteroconch and one principal auxiliary chamber. The spirals that originate from the third chamber and are running around the protoconch and deuteroconch generally consist of three chambers, the mutual closing chamber being excluded (compare pl. 5, figs. 3, 4; pl. 6, fig. 1). Both chambers of the fourth instar may be of unequal size. In that case the spirals originating from them are generally of unequal length.

A relapse to the one-aperture stage was observed in several specimens. A dark line is present within the walls of the chambers. The diameter of the apertures in the peripheral chambers is about 7μ in median sections. In one specimen we observed the stolon between protoconch and deuterococonch.

The results of counts and measurements are given below. The individual observations are plotted in a $d1.2/h1.3$ scatter diagram (fig. 22).

sample	N	\bar{Y}	$\overline{d1.2}$	$\overline{h1.3}$
F 5938	6	2.00	198.3 ± 9.2	199.7 ± 12.4
S 68/556	11 ¹⁾	2.00	192.1 ± 4.5	200.6 ± 8.4
S 167/619	10	2.00	191.2 ± 6.7	194.6 ± 3.8
N 28/787	10	2.00	161.5 ± 5.5	177.6 ± 5.9

¹⁾ $\overline{h1.3}$ and $\overline{d1.2}$ concern 10 specimens only.

In the table above the samples are arranged in the supposed stratigraphic order, F 5938 being the uppermost sample. From bottom to top there is a seeming size increase in $\overline{d1.2}$ and $\overline{h1.3}$, but from these four samples only it is difficult to draw a definite conclusion whether such a trend really exists in the New Zealand populations. Only $\overline{d1.2}$ of the lowermost population differs significantly from those of the stratigraphically higher ones.

As to the length of the early spiral the *P. zelandica* populations differ from the Recent *P. larvata* in that only specimens with $Y = 2$ are present. However, a differentiation on the basis of the size of the early chambers is not possible.

III.2.5.5. Remarks on the age of the *P. zelandica* populations.

In two of the samples studied other larger foraminifera occur as well. In sample N 28/787 *P. zelandica* is accompanied by miogypsinids, lepidocyclinids and heterosteginids, in sample F 5938 lepidocyclinids (*Trybliolepidina* according to FINLAY, 1947), heterosteginids and gypsinids occur. Since the evolution of *Lepidocyclina* and *Heterostegina* in the Indo-Pacific is still insufficiently known, attention was paid only to the miogypsinids.

All miogypsinids have two principal auxiliary chambers. An estimate of the $200 \frac{\alpha}{\beta}$ values made of 20 thin sections of *Miogypsina* indicates that the mean of this parameter is somewhere between 70 and 90, which corresponds to *Miogypsina cushmani* VAUGHAN.

Planktonic foraminifera occur in the N 28/787 sample only. They are mainly *Globigerina*, *Globigerinoides* and *Globoquadrina*. *Orbulina* was not observed.

From these data one might conclude a Late Burdigalian or Helvetian age for the N 28/787 sample, in terms of European stratigraphy.

III.2.6. PLANORBULINELLA TRINITATENSIS (NUTTALL) 1928.

pl. 6, figs. 2, 3, 5; pl. 13, figs. 1a, b, 4a, b, 5a, b.

III.2.6.1. *Introduction, literature.*

This species has been described originally as *Planorbulina larvata* PARKER & JONES var. *trinitatensis* from several formations of Trinidad. A type locality has not been designated by NUTTALL; as such we have to consider the locality from which the figured specimens have been derived: test well A, Tarouba Estate, Trinidad. As type level we have to consider the Amussium Clay, Lower Miocene or Upper Oligocene. The original description of *P. trinitatensis* reads:

"The exterior of the Trinidad forms differs from the typical by the former having no difference in the ornamentation or shape of the inferior or superior surfaces. Both flanks are considerably flattened, with a small central depression, and the amount of beaded shell-substance covering the exterior is variable, there being always sufficient to obscure the internal structure... In the majority of the specimens the peripheral chambers are broken, but when present exhibit the fine perforation and lipped apertures characteristic of the species. The average diameter of the test is 1.4 mm, and the average thickness 0.4 mm".

The species has been found and figured afterwards by other authors, who did not add essential new data to its structure (KEIJZER, 1945, p. 55; CUSHMAN & RENZ, 1947, p. 45, pl. 8, fig. 13; RENZ, 1948, p. 149; BERMUDEZ, 1949, p. 311, pl. 26, figs. 40, 41). Remarks on its internal features have been made neither by NUTTALL, nor by these subsequent authors. This species can morphologically clearly be distinguished from all other *Planorbulinella* species. It has not been reported from outside the Caribbean region.

III.2.6.2. *Material.*

The type material, which is stored in the Sedgwick Museum, Cambridge, was not available to the author. We therefore studied specimens that are morphologically very close to the type specimens, as figured by NUTTALL. Of course their assignment to *P. trinitatensis* is not completely certain. The specimens were derived from the following samples:

DB 324, Concord Silt, Tamana Formation, Mayo Quarry, Central Range, Trinidad (Late Miocene). Donation D. A. J. BATJES.

Ho 207, Point à Pierre, Upper Concord Marl, Trinidad (Miocene). Donation D. A. J. BATES.

T 1446, Banes, Eastern Oriente, Cuba (Oligocene). Coll. Keijzer, Utrecht; see also KEIJZER, 1945, geologic map.

R 246, \pm 4 km east of Banes Bay, Eastern Oriente, Cuba (Oligocene). Coll. Keijzer, Utrecht; see also KEIJZER, 1945, geologic map.

The age of the samples may be incorrect in modern sense.

III.2.6.3. *External features.*

The following description is based on the specimens of sample Ho 207.

Test discoidal, diameter up to 2.5 mm maximally, both sides flattened with a small depression in the centre. The ornamentation consists of U- or V-shaped pustules or ridges, the open side being oriented to the periphery. At the angular, peripheral chambers one can study how these pustules are being formed. The radial walls of two peripheral chambers as well as the tangential part of the wall of a previous chamber are coated with imperforate calcareous matter, which may even grow out beyond the periphery, forming small, imperforate, vertical lamellae, which have altogether a U- or V-shape in lateral view. After the next row of chambers has been added this ornamentation is visible only in lateral view. It may become more strongly developed, giving rise to U- or V-shaped pustules all over the lateral surfaces. In the central portion of the test the pustules fuse to a rosette-like pattern of radially running ridges, with a strong depression in the centre (compare pl. 6 fig. 5). The periphery has a ragged outline (compare also pl. 13, fig. 4). The apertures are median, basal slits or arches, two to each peripheral chamber, and each provided with a small imperforate lip.

Remarks. In the three other samples the specimens are generally smaller, but they do not differ essentially from the Ho 207 specimens.

Our *P. trinitatensis* material can easily be differentiated from all other *Planorbulinella* species on the basis of their external characteristics, especially so on the peculiar ornamentation and the ragged appearance of the periphery.

III.2.6.4. *Internal features.*

As in the New Zealand populations, also in those of *P. trinitatensis* all specimens have $Y = 2$ (= protoconch, deutoconch, and one principal auxiliary chamber, compare pl. 6, fig. 2). The nepionic spirals originating from the third chamber, which are running in opposite direction around the protoconch and deutoconch, generally consist of three chambers each, the mutual closing chamber being excluded. However, these spirals may consist of four chambers

also (compare pl. 6, fig. 2) and, when the chambers of the fourth budding are of unequal size, these spirals may be of unequal length. A relapse to the one-aperture stage was observed, but not frequently so. In some specimens a dark line within the chambers' walls is present.

The results of counts and measurements are given below. The populations are arranged according to upward increasing h1.3 values. The individual observations are plotted in a d1.2/h1.3 scatter diagram (fig. 23).

sample	N	\bar{Y}	$d\bar{1.2}$	$h\bar{1.3}$
Ho 207	10	2.00	150.4 ± 5.8	205.7 ± 10.7
DB 324	1	2.00	161.5	195.5
R 246	7	2.00	157.8 ± 9.8	178.5 ± 8.5
T 1446	5	2.00	139.4 ± 10.6	153.0 ± 10.4

On the basis of these numerical data it cannot be concluded that these populations really differ from one another. Only the h1.3 difference of T 1446 and Ho 207 is significant.

Furthermore, on their internal characteristics these populations cannot be differentiated from *Planorbulinella zelandica*. Such a differentiation is possible, however, on the basis of the external features (p. 91).

From a point of nepionic configuration *P. trinitatensis* might be slightly higher developed than *P. larvata*, since only specimens with $Y = 2$ are present.

III.2.6.5. Remarks on the age of the *P. trinitatensis* populations.

The accompanying fauna in the Trinidad samples is rather neutral; planktonic foraminifera occur scarcely (few *Globigerina* and *Globigerinoides*), larger foraminifera are absent. In the Cuban samples planktonic foraminifera are absent, but larger foraminifera are fairly frequent, amongst them miogypsinids and lepidocyclinids.

Only few *Miogypsina* specimens are available. They are badly worn and recrystallized. As a consequence, the sections made are very poor. Nevertheless they give some important information. All specimens have two principal auxiliary chambers. An estimate of the $200 \frac{\alpha}{\beta}$ values indicates that the mean $200 \frac{\alpha}{\beta}$ of the populations is somewhere in between 70 and 90, which corresponds to *Miogypsina cushmani* VAUGHAN. That species occurs in the Late Burdigalian or Helvetian time interval in terms of European stratigraphy.

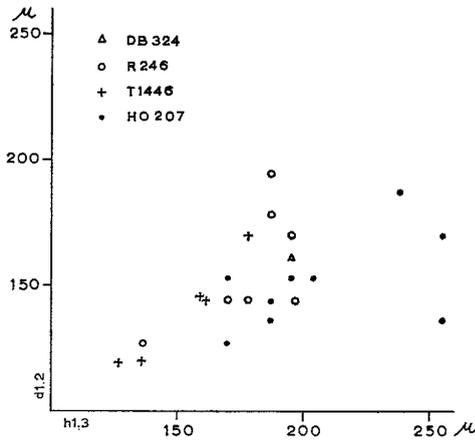


Fig. 23. Scatter diagram showing the relationship between $d1.2$ and $h1.3$ in 22 specimens of four *Planorbulinella trinitatis* populations from Cuba and Trinidad.

III.2.7. CONCLUSIONS

The results of Y counts of Cretan *Planorbulinella* populations indicate that there has been a reduction in \bar{Y} in the course of time. This reduction is in good accordance with the principle of nepionic acceleration. The Cretan populations belong to an evolutionary lineage, parts of which could be traced in other areas as well. Populations in the middle part of the type Tortonian are identical with those in the lower part of the Cretan Neogene. This indicates that at least part of the evolution took place during Tortonian time. A population of Malta may even be older than the Cretan ones on the basis of its \bar{Y} , and on the basis of the accompanying *Uvigerina* (see MEULENKAMP, in preparation) we may safely assume that it is really older. The populations of Sicily do not differ from the topmost Cretan ones, except in the larger mean size of the early chambers. From these data, alone it is not possible to conclude whether this larger size has some taxonomic or evolutionary importance, but again on the basis of the accompanying *Uvigerina* we may conclude that the Sicilian populations are younger than the uppermost Cretan ones, and still of Tortonian age. These findings show that in the course of time evolution in Y slowed down (also the progressing skewness of the Cretan populations and the near-absence of $Y = 2$ individuals in the Mediterranean Neogene supports this conclusion) and the size increase in the initial chambers became more important. The internal features of a Late Miocene or Early Pliocene population from Java and of the Recent *P. larvata* fit in with this trend. They illustrate that evolution continued up till Recent time. From the Late Tortonian onward evolution in Y nearly stopped, and size

increase in the initial chambers became a more important evolving character. For this reason the distinguishing of species in post-Tortonian *Planorbulinella* can only be based on the size of the initial chambers. However, before new species in this younger part of the lineage can be established, more data have to be gathered on Recent *P. larvata* populations in which $\overline{d1.2}$ (or $\overline{h1.3}$) can be measured on numerous specimens, in order to fix a lower $\overline{d1.2}$ (or $\overline{h1.3}$) boundary for this species.

From the data on the external features of the species belonging to this lineage, which will be named *larvata*-lineage, it appears that there has also been a change in external features in the course of time. Starting with small, unornamented specimens in the lower part of the Cretan Neogene, specimens become bigger and thicker in its upper part and in the Sicilian Neogene. The Bodjonegoro specimens are somewhat bigger and they have pustules also. The size of the Recent *P. larvata* specimens is still bigger and their ornamentation is coarser.

Planorbulinella zelandica can be differentiated from *P. larvata* on the basis of its peculiar Y distribution only (all individuals with $Y = 2$). More ample material of *P. larvata* will perhaps enable one to differentiate both species on the basis of $\overline{d1.2}$ as well. We tend to assume that the *P. zelandica* populations are more highly developed than *P. larvata* because only $Y = 2$ types were met. Within *P. larvata* also more primitive nepionic types occur. For this reason one might consider *P. zelandica* to be a descendant of *P. larvata*, but such a conclusion is in complete conflict with the time interval in which *P. zelandica* occurs, roughly Miocene. One cannot but conclude that *P. zelandica* belongs to another, older lineage, the ancestors of which are still unknown.

Planorbulinella trinitatensis can be differentiated from *P. zelandica* on its external characteristics only. Also, this species might be considered a descendant of *P. larvata*, if the time interval in which it occurs did not conflict with this interpretation. This time interval may be about equal for *P. trinitatensis* and *P. zelandica* (see also the remarks on the age of the samples studied), but our data are far too scarce for a definite decision. However, it is fairly certain that some populations of both species are of about the same age (on the basis of miogypsinids).

From these data on the age of both species and their highly similar internal features, one might say that they represent local adaptations (as to their outside features) of a single lineage, but they might just as well be parts of two completely independent lineages, which developed in geographically restricted areas.

Summarizing these data it may be inferred that the genus *Planorbulinella*, in the restricted sense as proposed in this paper, is polyphyletic. Lineages of *Planorbulinella*, as based on the generic diagnosis of p. 59, have evolved at least twice during the Tertiary (according to the principle of nepionic acceleration).

Whether the genus *Planorbulinella*, in our restricted sense, comprises completely unrelated groups cannot be decided, because the trochoid, spirally coiled ancestral foraminifera from which they originated, are still completely unknown.

III.3. The genus *Planolinderina* n.gen.

III.3.1. INTRODUCTION.

During our study of species previously assigned to *Planorbulinella* it appeared that the characteristics of two of them, *P. inaequilateralis* HERON-ALLEN & EARLAND and *P. plana* HERON-ALLEN & EARLAND, justify the establishment of a new genus, which is named *Planolinderina*. Apart from these two species, known from the South Pacific area only, we found numerous specimens belonging to the same genus in Oligocene-Miocene deposits of the Aquitaine Basin, France.

III.3.2. DESCRIPTION OF PLANOLINDERINA N.GEN.

Derivatio nominis. The name means: flat *Linderina*.

Type species. *Planolinderina escornebovensis* n.sp.

Diagnosis. A flat, discoidal, orbitoidal foraminifer without lateral chambers; apertures multiple.

Description. Test small, discoidal orbitoidal, without lateral chambers, flat on both sides, or plano-concave. The periphery is rounded, lobate, striate, parallel to the median plane. The peripheral chambers are provided with multiple apertures: two rows of rounded openings at the base of each chamber. Each opening is provided with a small, imperforate lip. The early chambers are arranged in a slightly trochoid spiral of variable length, or they show a protoconch-deuteroconch-principal auxiliary chamber(s) arrangement. The later chambers have orbitoidal growth. The wall structure is monolamellid.

Differential diagnosis. *Planolinderina* differs from *Planorbulinella* and *Hel-lenocyclina* in its multiple apertures. It differs from *Linderina* in lacking the pronounced, umbonal, lamellar thickening and it differs from *Halkeyardia* in its flat chamber layer and in its lack of umbilical pillars.

III.3.3. PLANOLINDERINA N.GEN. IN THE TERTIARY OF THE AQUITAINE BASIN.

pl. 7, figs. 1—7; pl. 8, figs. 1—3; pl. 14, fig. 2a, b.

III.3.3.1. *Introduction, literature.*

Specimens belonging to *Planolinderina* n.gen. have been rarely recorded from

the Aquitaine Basin. They have been referred to *Planorbulina mediterranensis* D'ORBIGNY by KAASSCHIETER (in DROOGER, KAASSCHIETER & KEIJ, 1955). Although he determined them as *P. mediterranensis*, he did compare them with *Planorbulinella larvata* (PARKER & JONES). Similar specimens have been referred to *Planorbulinella* cf. *larvata* (PARKER & JONES) by BUTT (1966). The latter author described the features in which his specimens derived from Escornebéou differ from the Recent *P. larvata*.

III.3.3.2. *Material.*

Planolinderina populations from 14 samples are described. According to the literature (DAGUIN, 1948; DROOGER, KAASSCHIETER & KEIJ, 1955; BUTT, 1966) their age ranges from Chattian to Aquitanian. The genus was not found in samples of Burdigalian age, neither in the type Burdigalian desposits, nor in other strata that are thought to be of Burdigalian age on the basis of miogypsinids (DROOGER, op. div.), apart from a few specimens in the samples A 364 and 365 from Pontonx. For comparison with the Aquitaine populations samples from the Doberg section near Astrup, NW Germany were investigated, because the Doberg strata are considered to be of Chattian age by all authors. Unfortunately *Planolinderina* is not present in these samples.

The populations studied were derived from the following samples of the Utrecht collections:

B-210-B, Lariey, type Aquitanian, Age: Late Aquitanian.

Fr-M-5, Fr-M-3, Moulin de l'Eglise, type Aquitanian. Age: Middle Aquitanian. The stratigraphic position of the samples is indicated by DROOGER in DROOGER, KAASSCHIETER & KEIJ (1955).

A 82, Cabanes near Saint Paul-les-Dax (see also DAGUIN, 1948, p. 109). Age: Aquitanian.

A 355, Listagnac near Saint Paul-les-Dax. Age: Aquitanian.

A 356, Estoti, some 4 km NW of Saint Paul-les-Dax and 11 km ENE of Escornebéou (see also DROOGER & FREUDENTHAL, 1965). Age: Chattian-Aquitanian.

A 353, Christus near Saint Paul-les-Dax (see also DAGUIN, 1948, p. 109; DROOGER, 1963). Age: Chattian-Aquitanian.

A 88, Baron near Saint Paul-les-Dax. Age: Chattian.

Aq 36, 29, 18, 25, 11, 9, Escornebéou. The same samples have been studied by BUTT (1966). They are listed here in stratigraphic order, Aq 9 being the lowermost one. Data on the miogypsinids and lepidocyclinids of the same locality have been given by DROOGER & FREUDENTHAL (1965) and by BUTT (1966). Age: Chattian.

II.3.3.3. *External features.*

Test small, discoidal, up to 1.0 mm in diameter, flat at one side, more or less strongly concave at the other side. Generally both surfaces are smooth, but the flat surface may be provided with fine, irregular, unoriented, imperforate ridges. Generally the chambers are visible in the peripheral portion only. The periphery is rounded, lobate and striate parallel to the median plane. The apertures are rows of some 3—6 lipped openings at the chambers bases. The diameter of the pores ranges up to 13 μ .

III.3.3.4. *Internal features.*

The number of chambers in the initial spiral (Y) ranges from 9 to 1. The spirals originating from the first chamber with two apertures are generally symmetrical (pl. 7, figs. 1, 2, 5, 7; pl. 8, fig. 1) but they may be asymmetrical as well (pl. 7, figs. 3, 4, 6). In symmetrical nepionts comparable spirals may consist of different numbers of chambers. For example, in the specimen of pl. 7, fig. 1 the spirals around the deuteroconch consist of two chambers each, the mutual closing chamber being excluded. In the specimen of plate 7, fig. 2 these spirals consist of three chambers each.

A recurrence of the one-aperture stage after one chamber has acquired a second, distal opening in addition to the proximal one, which feature is very common in *Planorbulinella*, was never observed, neither in the Aquitaine material, nor in the Indo-Pacific material, which will be described afterwards.

Furthermore, the first three chambers are never thick-walled, in the Aquitaine specimens. Also in this respect they differ from *Planorbulinella*.

A distinct, dark line within the chambers' walls was not observed.

III.3.3.5. *Measurements and counts.*

Because of the similarity in growth pattern with *Planorbulinella* the same parameters were counted and measured: Y and d1.2. In many specimens the deuteroconch has already acquired two stolons, giving rise to two chambers at the third instar. In such a chamber arrangement h1.3 become useless for comparison. Since the early chambers are invisible in transmitted light thin sections were made, about 20 for each population.

The results of counts and measurements are given below. The samples are arranged in their supposed stratigraphic order based on field evidence and nepionic development of miogypsinids. Furthermore, the samples are divided in three groups, each corresponding to a geographical vicinity of the samples included. They are from bottom to top: samples from the Escornebéou section, samples from the vicinity of Saint Paul-les-Dax, and samples from the type Aquitanian (Moulin de l'Eglise, Lariey). The Y distribution of all populations is

illustrated with histograms (figs. 24 and 25). In these figures the two columns to the right refer to the accompanying miogypsinids: the mean length of the nepionic spiral (\bar{X}) and the species determination (Det.). The data on the miogypsinids have been gathered by DROOGER (partly in DROOGER, KAASSCHIETER & KEIJ, 1955, partly unpublished), by DROOGER & FREUDENTHAL (1965) and by the present author (A 88, Baron).

sample	N	Y									\bar{Y}	$\overline{d1.2}$
		9	8	7	6	5	4	3	2	1		
B-210-B	23	—	—	—	—	—	2	12	7	2	2.61 ± 0.16	101.6 ± 4.4
Fr-M-5	20	—	—	—	—	—	3	4	10	3	2.35 ± 0.20	107.1 ± 5.1
Fr-M-3	24	—	—	—	—	—	1	8	10	5	2.21 ± 0.17	106.2 ± 4.3
A 82	20	—	—	—	—	—	3	9	4	4	2.55 ± 0.23	96.5 ± 6.1
A 355	20	—	—	—	—	—	2	13	2	3	2.70 ± 0.20	93.7 ± 4.8
A 356	20	—	—	—	—	2	5	7	5	1	3.10 ± 0.24	87.5 ± 6.5
A 353	20 ¹⁾	—	—	—	—	—	1	1	1	17	1.30 ± 0.18	128.8 ± 6.3
A 88	20	—	—	—	—	—	2	3	3	12	1.75 ± 0.24	107.5 ± 5.9
Aq 36	15	—	—	—	—	—	2	3	3	7	2.00 ± 0.30	93.5 ± 6.2
Aq 29	20	—	—	—	—	—	4	4	4	8	2.20 ± 0.27	91.4 ± 4.8
Aq 18	22	—	—	—	—	3	5	8	3	3	3.09 ± 0.26	82.9 ± 5.3
Aq 25	20 ¹⁾	—	—	—	—	4	5	6	3	2	3.30 ± 0.29	81.4 ± 4.9
Aq 11	20 ¹⁾	—	—	1	—	3	6	7	1	2	3.55 ± 0.32	78.1 ± 6.3
Aq 9	32	1	1	—	2	3	12	13	—	—	4.09 ± 0.25	64.5 ± 3.3

¹⁾ $\overline{d1.2}$ is based on one specimen less.

From the bottom to the top of the Escornebéou section there is a clear modal shift in the Y histograms (fig. 24), and a significant decrease in the length of the initial spiral. The corresponding $\overline{d1.2}$ increases significantly in the same direction. This trend seemingly reflects a development in accordance with the principle of nepionic acceleration.

In the Aquitanian type section there is a modal Y shift opposite to that present in the Escornebéou section (fig. 25), and an increase in \bar{Y} from bottom to top. However, this increase is not significant.

In the populations from the vicinity of Saint Paul-les-Dax, the stratigraphic order of which is based on the miogypsinids, there is also a reversed modal Y shift, similar to that in the Aquitanian type section. The \bar{Y} values show a jumping pattern.

If the stratigraphic order of the samples, as given above, is indeed correct, it will be evident that in the succession as a whole, from the

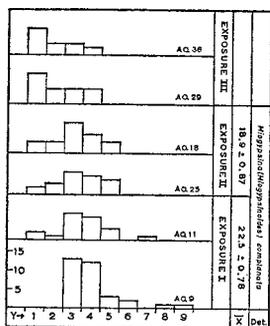
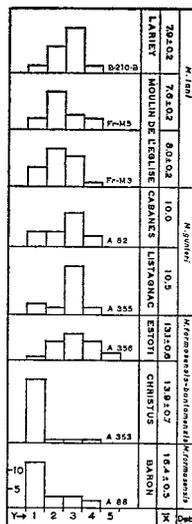


Fig. 24. (l.) Histograms showing the Y distribution in *Planolinderina* populations from Escornebéou, Aquitaine Basin, France. The columns to the right refer to the accompanying miogypsinids: the mean length of the nepionic spiral (x) and the species determination (Det.).

Fig. 25 (r.) Histograms showing the Y distribution in *Planolinderina* populations from the vicinity of Saint Paul-les-Dax and from the type Aquitanian. The columns to the right refer to the accompanying miogypsinids: the mean length of the nepionic spiral (x) and the species determination (Det.).



Escornebéou samples up to the type Aquitanian samples a distinct trend of decreasing \bar{Y} cannot be detected. An overall increase in d1.2 seems more likely. It was checked whether the jumping pattern in both parameters disappears if a four-paired trend test is made. This means that four successive samples give one mean, each time shifting one sample upward.

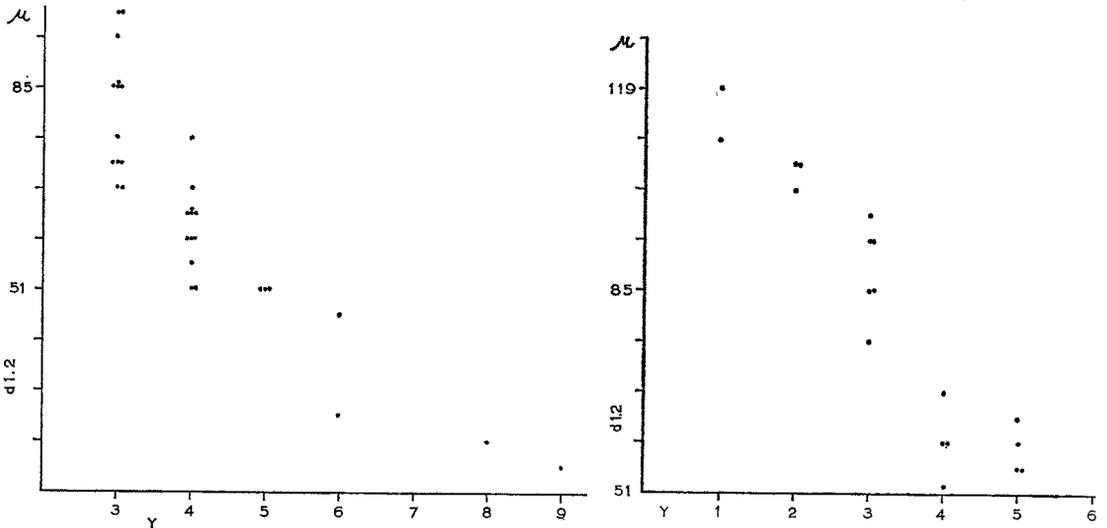


Fig. 26 (l.) Scatter diagram showing the relationship between Y and $d_{1.2}$ in 32 *Planolinderina* specimens of sample Aq 9, Escorneb  ou, Aquitaine Basin, France.

Fig. 27 (r.) Scatter diagram showing the relationship between Y and $d_{1.2}$ in 19 *Planolinderina* specimens of sample Aq 25, Escorneb  ou, Aquitaine Basin, France.

The results are given below:

\bar{Y}	$\bar{d}_{1.2}$
2.43	102.9
2.45	100.9
2.64	96.0
2.41	101.6
2.21	104.4
2.04	104.3
1.81	105.5
2.28	93.8
2.85	87.3
3.03	83.4
3.51	76.7

Although there is an overall decrease in \bar{Y} and an overall increase in $\bar{d}_{1.2}$ from bottom to top, the jumping pattern is still present. It is less prominent in $\bar{d}_{1.2}$ than in \bar{Y} . This unsatisfactory conclusion needs further investigation.

The individual observations of four samples are plotted in $Y/d_{1.2}$ scatter

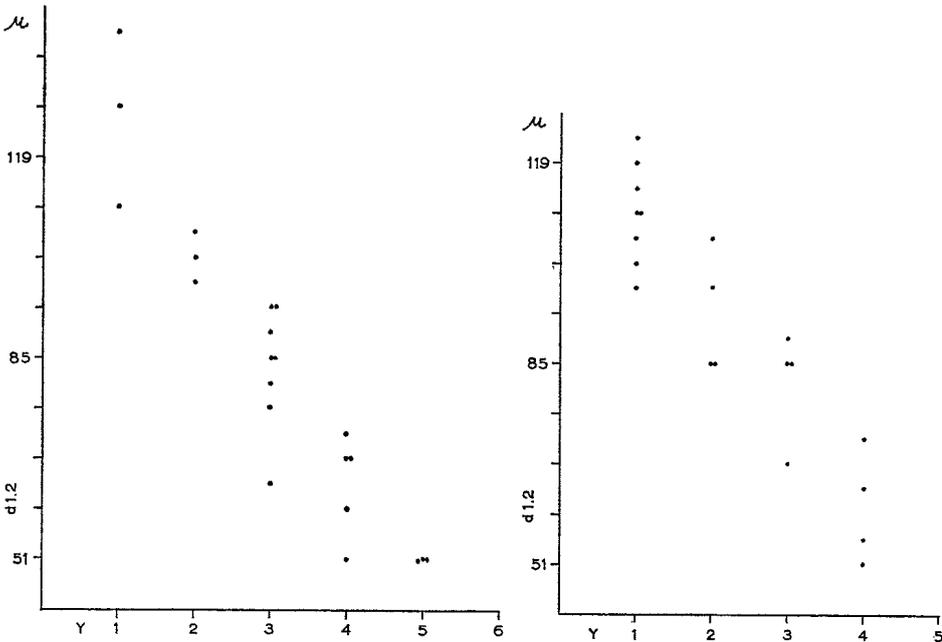


Fig. 28 (l.) Scatter diagram showing the relationship between Y and $d_{1.2}$ in 22 *Planolinderina* specimens of sample Aq 18, Escorneb eou, Aquitaine Basin, France.

Fig. 29 (r.) Scatter diagram showing the relationship between Y and $d_{1.2}$ in 20 *Planolinderina* specimens of sample Aq 29, Escorneb eou, Aquitaine Basin, France.

diagrams (figs. 26, 27, 28, 29). For these samples the corresponding correlation coefficients (r) were calculated.

sample	fig.	r	N
Aq 9	26	— 0.8557	32
Aq 25	27	— 0.9242	19
Aq 18	28	— 0.8833	22
Aq 29	29	— 0.8732	20

These correlation coefficients indicate that there is a strong, significant negative correlation (at a probability level of 99.9 %) between both parameters, or rather, that within a single sample specimens with a long initial spiral have small early chambers and reversed. This negative correlation is much stronger than it is in *Planorbulinella* (compare p. 71), and consequently of much greater influence on determination on the basis of \bar{Y} alone.

A similar result is obtained in scattering the \bar{Y} and $\overline{d_{1.2}}$ of the 14 populations

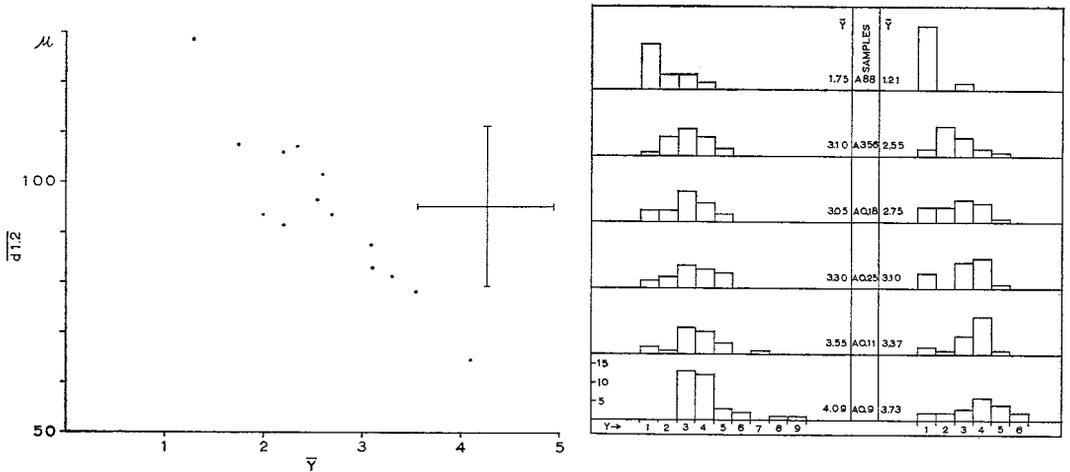


Fig. 30 (l.) Scatter diagram of \bar{Y} and $\bar{d1.2}$ of 14 *Planolinderrina* population from the Aquitaine Basin, France. The cross gives average values of $\pm 3 \sigma$.

Fig. 31 (r.) Histograms showing the Y distribution in several *Planolinderrina* populations from the Aquitaine Basin. The results in the left column apply to the second set of sections made one year after the first set, to which the right column applies.

studied (fig. 30). For these parameters $r = -0.8460$, a significant and again strong, negative correlation at a probability level of 99.9 %.

Bias

Because of the strong negative correlation between Y and $d1.2$ it was checked whether it may have influenced the final results on \bar{Y} and $\bar{d1.2}$. For several samples a first set of thin sections was made in 1964. At that time many sections had to be disregarded for counts and measurements, because they did not sufficiently show the early chambers. A year afterwards, for the same samples a new set of about 22 sections was made, after the author had improved his technique of sectioning to such a degree that a much lower percentage had to be discarded. The reasons for disregarding these were recrystallization and/or poor conservation.

The comparison of the Y histograms (fig. 31) and \bar{Y} of both sets leads to interesting conclusions. The \bar{Y} of the new set (left column, fig. 31) proved to be always higher than those of the former, the differences amounting to twice the average of the standard error of \bar{Y} . These results indicate that in the new set specimens with a long initial spiral were more often included. From the negative correlation between Y and $d1.2$ it is clear that also specimens with small early chambers were more often included in the second set.

Sample	Y									$\overline{M\delta 1.2}^1)$
	9	8	7	6	5	4	3	2	1	
B-210-B						(2) 82.9	(12) 91.0	(7) 119.0	(2) 127.5	104.8
Fr-M-5						(3) 79.3	(4) 95.6	(10) 118.4	(2) 134.6	105.3
Fr-M-3						(1) 76.5	(8) 87.6	(10) 109.2	(5) 136.0	102.3
A 82						(6) 68.7	(11) 80.7	(11) 108.2	(5) 136.0	98.4
A 355						(2) 72.2	(13) 86.6	(2) 97.7	(3) 136.0	98.1
A 356					(3) 59.5	(7) 69.2	(12) 82.7	(13) 107.2	(3) 138.8	91.4
A 353					(1) 59.5	(1) 59.5	(3) 82.7	(1) 106.2	(21) 132.9	88.1
A 88						(2) 63.7	(5) 86.7	(3) 89.2	(28) 121.4	90.3
Aq 36						(2) 57.4	(3) 80.7	(3) 82.7	(7) 114.1	83.6
Aq 29						(4) 60.6	(4) 81.8	(4) 93.5	(8) 110.5	86.6
Aq 18					(4) 49.9	(10) 67.1	(14) 82.9	(7) 102.6	(7) 131.7	86.8
Aq 25					(4) 56.9	(10) 59.5	(13) 85.0	(3) 104.8	(6) 114.0	84.0
Aq 11			(1) 25.5		(3) 51.0	(14) 64.3	(12) 83.6	(2) 95.6	(4) 120.0	73.3
Aq 9	(1) 21.4	(1) 25.5			(6) 47.9	(18) 58.8	(15) 80.4	(2) 106.2	(2) 125.3	63.5

$^1) \overline{M\delta 1.2} = \frac{\sum \delta 1.2}{n}$, in which n is the number of classes represented.

This result is quite well understandable if it is borne in mind that the author had got more experience in sectioning. It indicates that the 1964 results were biased.

This bias implies a warning for future studies on the genus *Planolinderina*. Results of measurements and counts should be accompanied by remarks on the percentage of discarded specimens, and on the reasons why they have been left out. Of course this warning applies to other groups of orbitoidal foraminifera as well, in which a strong correlation exists between the parameters used. The data given in the table (p. 98) apply only to the new set of sections.

In the next step, the $d_{1.2}$ observations of individuals with the same Y have been taken together for each population, and new $\overline{d_{1.2}}$ ¹⁾ were calculated for each Y class. The results are tabulated on p. 103. The numbers between brackets indicate the numbers of observations on which each $\overline{\delta_{1.2}}$ is based. The samples are arranged again according to the supposed stratigraphic order.

In the table given also specimens of the "first set of sections" were included to base the $\overline{\delta_{1.2}}$ on larger numbers of observations. However, most $\overline{\delta_{1.2}}$ values are still based on small or very small numbers of observations. Consequently they can be considered only as very rough estimates of the populations' $\overline{\delta_{1.2}}$. In all populations there is a clear increase in $\overline{\delta_{1.2}}$ from the left to the right, which corresponds to a decreasing Y. Similar results had already been obtained in the correlation tests. This table only illustrates the negative correlation of both parameters in another way.

If the $\overline{\delta_{1.2}}$ values of a certain Y class and for the "successive" populations are considered, there appears to be an overall increase in these $\overline{\delta_{1.2}}$ from bottom to top. This size increase, however, is certainly not a smooth one, neither is it of great magnitude. Numerous setbacks (or jumps forward) are present. They may be due to the small numbers of observations, but they may be real also. In order to avoid the influences of random or other effects, the $\overline{\delta_{1.2}}$ values of all Y classes of single samples were added. A new average was calculated by dividing this value by the number of classes represented. This parameter is indicated by $M\overline{\delta_{1.2}}$. Its values are given, for each population, to the right of the preceding table.

If the $M\overline{\delta_{1.2}}$ values of the population are regarded there appears to be a fairly constant increase in this parameter from bottom to top, but here too we have setbacks. As a whole, however, the increase is more smooth than for the Y classes separately. It is not possible to decide whether differences in $M\overline{\delta_{1.2}}$ are significant, since the parameter itself is meaningless from a statistical point of view.

As another check, partial \overline{Y} (\overline{y}) values were calculated of individuals that are within certain $d_{1.2}$ limits. Five size classes were distinguished. They are from: 186—153 μ , from 152—119 μ , from 118—85 μ , from 84—51 μ and from

¹⁾ These partial $\overline{d_{1.2}}$ are indicated again by $\overline{\delta_{1.2}}$.

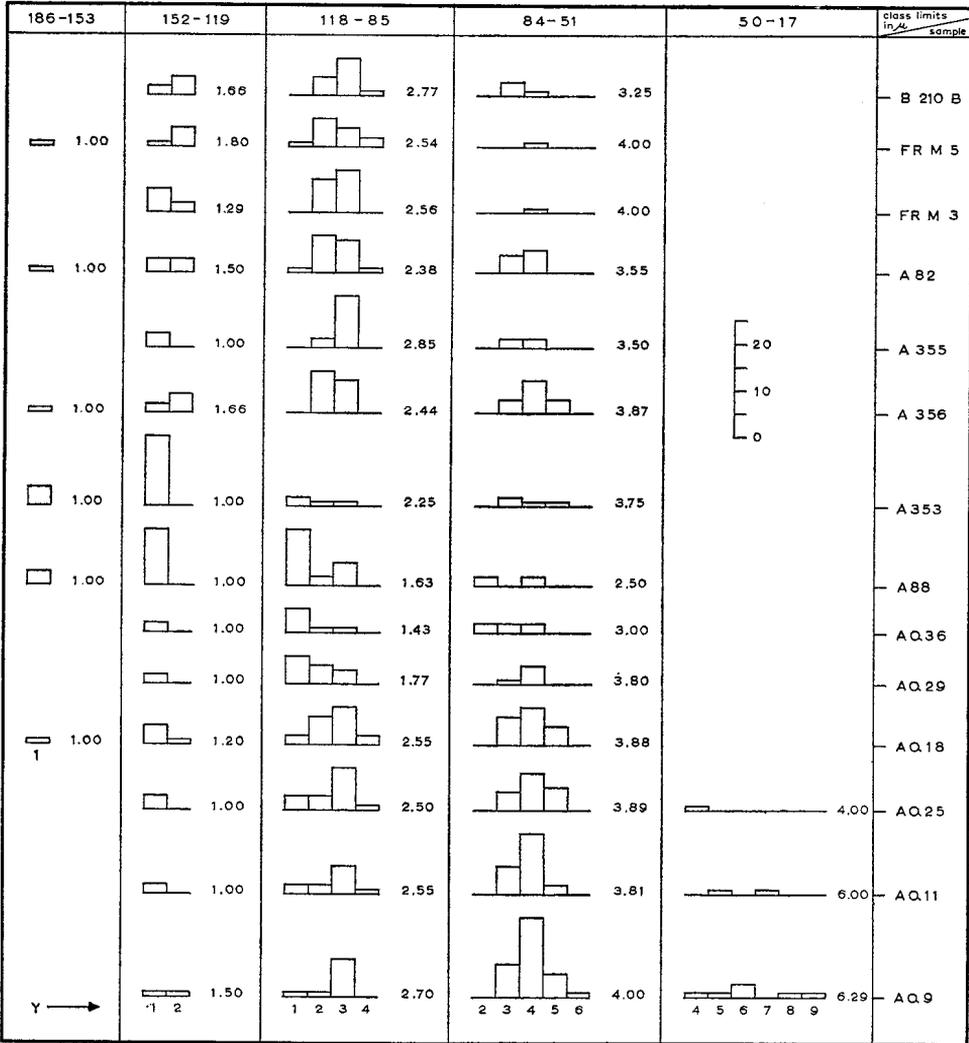


Fig. 32. Histograms showing the Y distribution within certain d1.2 limits of 14 Planolinderina populations from the Aquitaine Basin, France.

50—17 μ . The interval of each class is 35 μ . \bar{y} were calculated for all d1.2 size classes of each population. Moreover, the \bar{Y} distribution within each size interval is illustrated with histograms. Both, the \bar{y} and the histograms are given in fig. 32.

Within each sample there is \bar{y} decrease from the right to the left, which corresponds to d1.2 increase in the same direction. This is again another way of illustrating the negative correlation between Y and d1.2.

If the \bar{y} of "successive" populations within the same size intervals are considered, there is no distinct trend. However, the origin of this irregular pattern can be retraced from the accompanying histograms. In upward direction irregularities in numbers of low Y individuals, shifting to the next higher d1.2 class and of high values coming in at the other side, combined with too less numbers of observations, cause the jumping pattern.

III.3.3.6. *Discussion of the results of counts and measurements; phylogeny.*

Within the successive Escornebéou populations there is a clear \bar{Y} decrease at increasingly higher levels. This decrease, which is in good accordance with the principle of nepionic acceleration, coincides with an increase in $\bar{d}1.2$ in the same direction. However, in the stratigraphically higher populations these trends are seemingly absent and the picture becomes completely puzzling. These irregularities may be explained by environmental or other effects on d1.2. As a consequence of the strong, negative correlation between d1.2 and Y, such effects may cause considerable shifts in Y.

Apart from the trend in \bar{Y} , which is visible only in the successive Escornebéou populations, there is an overall, slow increase in $\bar{\delta}1.2$ of specimens with a same Y, but from subsequent higher populations. It means that specimens with a certain length of the early spiral tend to get bigger initial chambers at increasingly higher levels. Since the number of specimens of each Y class within single populations is generally small, the value of the $\bar{\delta}1.2$ is of dubious importance. Therefore an average of the $\bar{\delta}1.2$ of each population was calculated, the parameter $M\bar{\delta}1.2$. If the populations are arranged according to the field evidence and increasing $M\bar{\delta}1.2$, the succession of the populations is nearly completely the same as the order based on field evidence and miogypsinids. This is a fairly satisfactory result, since it might be expected, due to the similarity in growth pattern of planolinderinids and miogypsinids, that the development in both groups would be roughly parallel.

One might expect that the increase in $\bar{\delta}1.2$ within each Y class would correspond to a decrease in \bar{y} within certain d1.2 limits, but this is true only in the subsequent populations of Escornebéou. In the stratigraphically higher populations the \bar{y} even increases or may remain nearly constant. This irregular pattern may be explained by the fact that the $\bar{\delta}1.2$ increase within each Y value will cause low Y values to shift to the next higher d1.2 class, whereas high Y values come in from the other side.

Summarizing we reach the following conclusions:

1. There is a very strong negative correlation between the length of the initial spiral and the size of the first two chambers.

2. There is a general reduction in the length of the initial spiral from bottom to top.

3. There is a general size increase in the early chambers in the groups of specimens with a same number of chambers in the initial spiral of subsequent samples.

The second trend may be completely overshadowed by "random" fluctuations of $d_{1.2}$ and therefore it is not useful for the distinguishing of consecutive species.

The distinguishing of such species on the basis of the third trend is possible, but it is hampered by the generally, very low numbers of observations on which the $\delta_{1.2}$ are based. The parameter $M\delta_{1.2}$ which best shows the trend has the drawback that it cannot be used statistically. Consequently, different species cannot be based on $M\delta_{1.2}$. For this reason only one (new) species was established, *Planolinderina escornebovensis* n.sp., based on the lowermost population of Escornebéou. For this species upper and lower limits of \bar{Y} and of $d_{1.2}$ were not fixed.

III.3.3.7. *Planolinderina escornebovensis* n.sp.

pl. 7, figs. 1—7; pl. 8, figs. 1—3; pl. 14, fig. 2a, b.

Etymology. The name is derived from the locality Escornebéou.

Holotype. Plate 14, fig. 2a, b; coll.nr. S 20855.

Paratypes. 10 complete specimens, 51 horizontally sectioned specimens.

Type level. Escornebéou Beds ("faluns bleus"), Oligocene, Chattian.

Type locality. Escornebéou, SW France, Aquitaine Basin, exposure I, sample Aq 9 (see BUTT, 1966).

Diagnosis. A small *Planolinderina*, one side flat, the other slightly concave, with a relatively long nepionic spiral and small early chambers.

Description. Test small, discoidal, diameter up to 0.5 mm, flat at one side, and slightly concave at the other. Both surfaces are smooth and the chambers are visible from both sides, being accentuated by the relatively strongly depressed sutures. The periphery is rounded, lobate and striate parallel to the median plane. The multiple apertures are situated in rows at the chambers bases. These rows consist of some 3—6 small openings, each provided with a small imperforate lip. The openings are situated in between imperforate ridges that give the periphery its striate appearance. Pore diameter up to about 13 μ .

The early chambers are arranged in a slightly trochoid spiral of variable length (9—3 chambers in the specimens of the type sample), the later chambers show a regular, orbitoidal growth. The initial chambers are small. In the type sample the mean length of the initial spiral is 4.09 ± 0.25 , the mean diameter of the protoconch and deuteroconch together is $64.5 \pm 3.3 \mu$. Wall monolamellid.

Remarks. *P. escornebovensis* differs from *P. inaequilateralis* in the smaller

size of the test, in the less prominent plano-concave shape in vertical section, in the relatively longer initial spiral, and in the smaller size of the initial chambers. It differs from *P. plana* in the shape and size of the test, in the longer initial spiral and in the smaller size of the early chambers.

For the present the samples included have \bar{Y} values from 4.09—1.30, $\overline{d1.2}$ values from 64.5—128.8 μ , and $M\delta 1.2$ values from 63.5—105.3.

Stratigraphic distribution. Chattian — Aquitanian, Burdigalian (?), Aquitaine Basin, France.

III.3.4. THE GENUS PLANOLINDERINA IN THE TERTIARY OF THE INDOPACIFIC

pl. 8, figs. 4—6; pl. 9, figs. 1—6; pl. 14, figs. 1a, b, 3a, b, c, 6a, b.

III.3.4.1. *Introduction, literature.*

Two species, previously assigned to *Planorbulinella*, and originally described as *Planorbulina*, have the generic characteristics of *Planolinderina* n.gen. They are: *P. inaequilateralis* (HERON-ALLEN & EARLAND), 1924 and *P. plana* (HERON-ALLEN & EARLAND), 1924. The original description of *P. inaequilateralis* reads:

“... characterized by a convex superior surface and a concave inferior side. The inferior side often contains a small central boss, suggesting *Linderina*, but sections show that the boss consists of exogenous shell substance only, and it is confined to the concave side of the test, whereas in *Linderina* the thickening of the central portion of the test occurs on both faces of the shell.

The unequal development of the two faces of the test appears to be due to the fact that the individual chamberlets are pear-shaped, the broader end being on the upper surface of the test. The appearance of the test when mounted in balsam, and viewed from the inferior side, is very characteristic, the chambers appearing to be set in straight lines radiating from the primordial. The superior aspect does not show this feature, and is indistinguishable from typical *P. larvata*.

Both sides of the test are usually covered with exogenous shell substance, the layer being usually thickest on the concave inferior side, whereas in typical *P. larvata* the superior face is usually densely overlaid, while the inferior is comparatively smooth. ... An average specimen contains 6—8 concentric rings of chambers”.

According to CARTER (1964) the aperture consists of a pair of large pores at the base of each chamber in the median line. The early chambers show a protoconch- deuteroconch- two principal auxiliary chambers arrangement.

According to CARTER's specimen on pl. 13, fig. 270 the periphery is striate, as it is in the Aquitaine *Planolinderina* specimens.

The original description of *P. plana* is partly quoted below:

"Test free, discoidal, and highly compressed, consisting of numerous concentric annuli of small triquetrous chambers in one plane. Only the final annulus is distinguishable in opaque specimens, both faces of the test being evenly coated with a thin layer of shell matter deposited in very minute beads, which entirely obscure the sutural lines.

The species rarely grows to such dimensions as are attained by *P. larvata* or *P. larvata* var. *inaequilateralis* but specimens of 0.70—0.90 mm diameter occur. The smallest specimen measures only 0.33 mm, but it is typical. In a large specimen there may be as many as 12—15 annuli. The number of chamberlets in the final annulus sometimes exceeds 40".

According to CARTER (1958) a distinct aperture is not present. The early chambers show a protoconch- deuteroconch- two principal auxiliary chambers arrangement.

From these data and the figures given by the authors quoted both species seem to differ primarily in their diameter/thickness ratio and in the number of peripheral chambers.

Both species have originally been described from Filter Quarry, Moorabool River, Victoria, Australia. They concur also in many other localities in Victoria (CARTER, 1958, 1964). *P. plana* has been recorded also from New Zealand by HORNIBROOK (1961).

The stratigraphic range of both species has been given by CARTER (1964). They are of Miocene age, probably ranging from Aquitanian to Helvetian. *P. plana* appears slightly earlier than *P. inaequilateralis*. They disappear at the same level. According to EAMES et al. (1962) the stratigraphic interval, in which both species occur in Victoria, is of Aquitanian age. According to HORNIBROOK (1961) in New Zealand *P. plana* ranges from Upper Otaian or Awamoan — Waiauan (Upper Oligocene or Lower Miocene — Upper Middle Miocene) in terms of local stratigraphy. According to EAMES et al. (1962) this interval should correspond to Aquitanian — Tortonian in terms of European stratigraphy.

III.3.4.2. *Material.*

V—98, New Quarry, Batesford Limestone (middle part), Batesford, Victoria, Australia. Age: Burdigalian — Vindobonian according to CARTER (1964). Donation: Miss MARY WADE.

According to WADE (personal communication) "New Quarry is close to Filter Quarry, Moorabool, and in the same formation. Its material is generally

accepted as topotype material for HERON-ALLEN & EARLAND's Filter Quarry species, as Filter Quarry is flooded".

F-100, bryozoal limestone in the Fishing Point Clay; wave-cut platform at the southeast end of Castle Cove, Victoria, Australia. Age: probably Burdigalian according to CARTER (1964). Donation: Miss MARY WADE.

12737, McColl's Quarry, Longford Limestone, Parish of Glencoe, Gippsland, Victoria, Australia. The locality has been studied also by CARTER (1964) and is considered to be of Aquitanian age. Donation: D. J. BELFORD.

12732, Robertson's Quarry, Longford Limestone, Parish of Glencoe, Gippsland, Victoria, Australia. The locality has been studied also by CARTER (1964) (incorrectly quoted as Robinson's Quarry) and it is considered to be of Aquitanian age and to be slightly older than McColl's Quarry. Donation: D. J. BELFORD.

Mo-100, Sungei Tenging, Eastern Borneo, Indonesia. Age: T(ertiary)₁₁ which corresponds to the Burdigalian according to EAMES et al. (1962). For the exact location of the sample one is referred to DROOGER (1955). Collection Utrecht.

III.3.4.3. *External features.*

The external features of both species have been extensively discussed by CARTER (1958, 1964). It will be sufficient to review the most important features and to add some new data.

P. inaequilateralis has a relatively thick test, flat on one side and concave at the other; the apertures are multiple, each opening being provided with a small imperforate lip. The periphery is striate parallel to the median plane. The species most closely resembles the Aquitaine specimens, but in the latter the concavity is less prominent and the diameter of the test is generally smaller.

P. plana has a relatively compressed test, flat at both sides, but sometimes with a small inflation in the centre, corresponding to the initial chambers. It has also multiple apertures (each opening provided with a small imperforate lip) and a striate periphery. Individuals have relatively more peripheral chambers than *P. inaequilateralis* specimens with a same test diameter. These differences are illustrated by some drawn specimens (plate 14, figs. 1a, b, 3a, b, c, 6a, b).

In those samples in which both species occur together (all samples except for Mo-100 in which only *P. plana* occurs) they can easily be differentiated on the basis of the relationship between diameter and thickness, and the number of peripheral chambers. This relationship is illustrated for the specimens of sample 12732 from Robertson's Quarry. It will not be shown for the other samples, either because the number of individuals of one of both species is too small, or

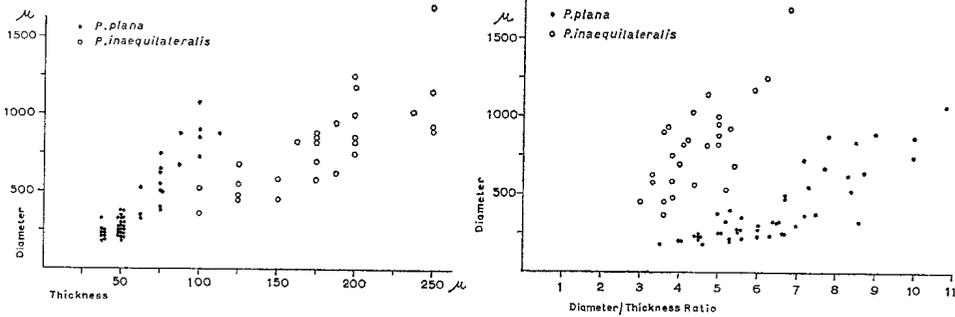


Fig. 33 (l.) Scatter diagram showing the relationship between diameter and thickness in specimens of *Planolinderina plana* and *P. inaequilateralis* from sample 12732, Robertson's Quarry, Parish of Glencoe, Victoria, Australia.

Fig. 34 (r.) Scatter diagram showing the relationship between diameter and diameter/thickness ratio in specimens of *Planolinderina plana* and *P. inaequilateralis* from sample 12732, Robertson's Quarry, Parish of Glence, Victoria, Australia.

because the specimens are badly worn and do not show the peripheral chambers sufficiently well.

Fig. 33 shows the relationship between the diameter and thickness of 27 *P. inaequilateralis* and 48 *P. plana* individuals from sample 12732. The specimens do not fall apart in two clearly separate clusters, but they have a separate distribution field. The same is true in fig. 34, in which the diameter of the same specimens is plotted against the diameter/thickness ratio.

Fig. 35 shows the relationship between the test diameter and half the number of peripheral chambers¹⁾ in 17 *P. inaequilateralis* and 36 *P. plana* specimens. In this figure the number of specimens used is smaller than in the preceding two, because the half-number of peripheral chambers cannot be ascertained but in part of the specimens. There is again no clear indication for two clusters, but the specimens of one species are not within the distribution field of the other. The same is true for the diagram of fig. 36, which shows the relationship between the thickness of the test and half the number of peripheral chambers.

Fig. 37 shows the interrelationship of diameter, thickness and half the number of peripheral chambers in a triangular diagram. 17 *P. inaequilateralis* and 36 *P. plana* individuals were plotted. In using these three features together the specimens of both species fall clearly apart in two separate clusters. It indicates that the external features, on which we have split the *Planolinderina* individuals

¹⁾ Half the number of peripheral chambers is preferred to counting the total number, because in many specimens a part of the periphery is broken away or worn.

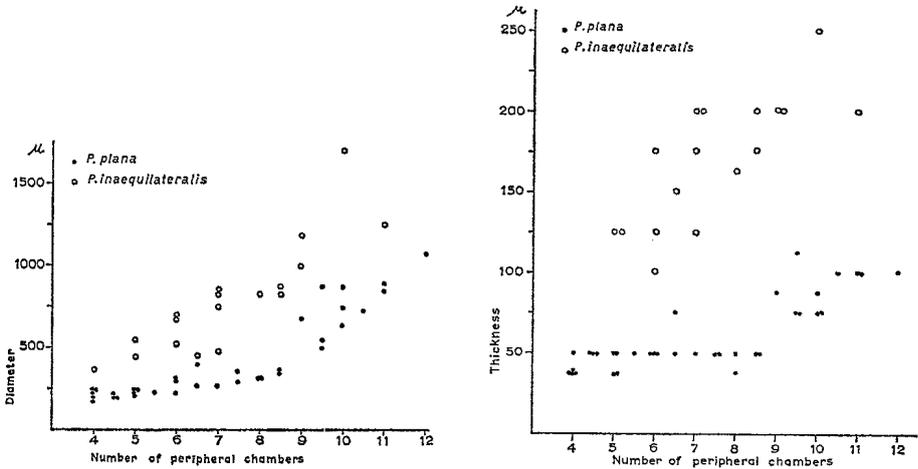


Fig. 35 (l.) Scatter diagram showing the relationship between diameter and (half) the number of peripheral chambers in specimens of *Planolinderina plana* and *P. inaequilateralis* from sample 12732, Robertson's Quarry, Parish of Glencoe, Victoria, Australia.

Fig. 36 (r.) Scatter diagram showing the relationship between thickness and (half) the number of peripheral chambers in specimens of *Planolinderina plana* and *P. inaequilateralis* from sample 12732, Robertson's Quarry, Parish of Glencoe, Victoria, Australia.

of the 12732 sample in two separate groups, justify the distinguishing of two species.

The diameter/thickness ratio is the only feature in which the populations studied can clearly be differentiated from each other. They are:

	<i>P. inaequilateralis</i>	N	<i>P. plana</i>	N
Mo-100			10.1 ± 0.3	37
V— 98			7.4 ± 0.3	34
F—100	4.8	5		
12737	4.4 ± 0.2	7	6.4 ± 0.2	39
12732	4.4 ± 0.2	27	6.4 ± 0.2	48

III.3.4.4. Internal features.

The internal features of the specimens of both species resemble those of the Aquitaine material. In all specimens of *P. inaequilateralis* and in most of *P. plana* the Y value is 1. In *P. plana* several specimens have a longer initial spiral, consisting of 5 chambers maximally. In several specimens of *P. plana* the 4 initial chambers are well differentiated from all other chambers, because they

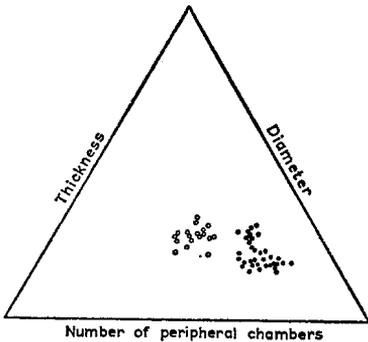


Fig. 37. Triangular diagram showing the relationship between (half the number of peripheral chambers, thickness and diameter in *Planolinderina plana* and *P. inaequilateralis* specimens from sample 12732, Robertson's Quarry, Parish of Glencoe, Gippsland, Victoria, Australia.

are thick-walled (plate 9, figs. 3, 4). This feature was observed neither in the *P. inaequilateralis* specimens, nor in the Aquitaine material of *Planolinderina*. In most cases the spirals originating from the principal auxiliary chambers are symmetrical. Generally, those around the protoconch consist of one chamber (the mutual closing chamber being excluded), and those around the deutoconch of two chambers each (pl. 9, figs. 1, 4; pl. 8, figs. 4, 5). Pl. 9, fig. 5 shows a *P. plana* specimen in which both spirals around the protoconch consist of two chambers each. The spirals around the deutoconch may be of unequal length, one consisting of one and the other of two or three chambers. The protoconchal spirals may be asymmetrical as well, one consisting of one, the other of two chambers (the mutual closing chamber always being excluded). These asymmetrical nepionts were observed in specimens of both species.

Pl. 9, fig. 2 shows a specimen in which only one spiral originates from one of the principal auxiliary chambers, thus being asymmetrical. This nepiont strongly reminds us of the relapse to the one-aperture stage, so well known in *Planorbulinella*. Whether it is really the same feature cannot be decided from this single observation only.

In the chambers' walls a dark line was never observed. Consequently, both species are probably monolamellid.

III.3.4.5. Counts and measurements.

The measurements and counts were made in a way similar to that applied in the Aquitaine planolinderinids. Hence, Y was counted and d1.2 was measured. Because of the fact that in the Indo-Pacific specimens the protoconch and deutoconch can easily be differentiated also the diameter of the protoconch and deutoconch were measured:

d1. The diameter of the protoconch, measured along a line perpendicular to

the line connecting the centres of protoconch and deutoconch (compare also fig. 4), the wall thicknesses being excluded.

d2. The diameter of the deutoconch, measured in the same way. The measurements of both features are expressed in μ . Their mean values ($\overline{d1}$ and $\overline{d2}$) are given along with the corresponding standard errors.

The results of counts and measurements on internal features of specimens of both species are recorded separately. In the table N_1 applies to \overline{Y} , and N_2 applies to $d1.2$, $\overline{d1}$ and $\overline{d2}$. The Australian populations are listed in the supposed stratigraphic order, the position of the Borneo population relative to the others is not certain.

Planolinderina plana

Sample	N_1	N_2	Y					\overline{Y}	$\overline{d1.2}$	$\overline{d1}$	$\overline{d2}$
			5	4	3	2	1				
Mo-100	31	28	—	—	—	—	31	1.00	105.4 ± 3.4	57.5 ± 1.7	69.2 ± 2.3
V 98	25	23	—	—	—	—	25	1.00	94.7 ± 4.4	56.2 ± 2.6	73.3 ± 3.5
12737	22	17	—	—	—	1	21	1.09	88.8 ± 4.2	53.5 ± 3.1	69.5 ± 3.7
12732	44	43	1	—	2	1	40	1.20	68.6 ± 2.7	38.7 ± 1.7	49.2 ± 2.4

Planolinderina inaequilateralis

Sample	N_1	N_2	Y	\overline{Y}	$\overline{d1.2}$	$\overline{d1}$	$\overline{d2}$
			1				
F-100	3	3	3	1.00	130.3	73.7	93.5
12732	17	16	17	1.00	122.0 ± 6.7	65.9 ± 4.4	78.0 ± 5.5

In the Australian populations of *P. plana* there seems to be an increase in the size of the initial chambers. As to all size parameters the lowermost population differs significantly from the other ones. There also seems to be a small decrease in \overline{Y} in the same direction. As to its size parameters the Mo-100 population differs significantly from the lowermost Australian one. As to the $\overline{d1.2}$ it differs also significantly (at a probability level of 99.9 %) from the population of sample 12737.

Little can be said about the *P. inaequilateralis* populations. As to its size parameters the population of sample 12732 differs significantly from the accompanying *P. plana* population, but the ranges of $\overline{d1.2}$, $\overline{d1}$ and $\overline{d2}$ of the specimens of both species are considerably overlapping each other. This is illustrated in figure 38, in which the histograms above the horizontal axis apply to *P. plana* and those below the axis to *P. inaequilateralis*.

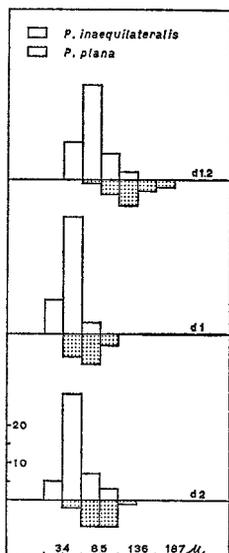


Fig. 38. Histograms of $d_{1.2}$, d_1 and d_2 populations of *Planolinderina plana* and *P. inaequilateralis* from sample 12732, Robertson's Quarry, Parish of Glencoe, Victoria, Australia.

III.3.4.6. Discussion of the results of counts and measurements; phylogeny.

If the seeming size increase of the initial chambers of the successive *P. plana* populations is credited with a stratigraphic and evolutionary value, its development strongly resembles that of the Aquitaine *Planolinderina* populations. Then, on the basis of the increasing $\bar{d}_{1.2}$, one might consider the Mo-100 population to be slightly higher evolved than those of 12737 and 12732, which is in accordance with the assumed age of the populations ("Burdigalian" in the former and "Aquitanian" in the latter). This trend might go together with an increase in the diameter/thickness ratio (p. 112), in such a way that specimens of populations at increasingly higher levels tend to get relatively more compressed tests.

On the basis of our few data it cannot be decided whether a similar trend is present in *P. inaequilateralis*.

Both Australian species can easily be differentiated on the basis of their diameter/thickness/number of peripheral chambers relationship. In that respect their ranges do not overlap. In the size of the initial chambers both differ significantly, but the ranges overlap considerably. As to their \bar{Y} a clear difference cannot be detected. This means that specimens of both species within a single sample can hardly be differentiated on the basis of internal features, whereas they can be differentiated externally.

It is hard to draw conclusions from these data. One might consider both species to be representatives of independent evolving lineages. They might be as well ecophenotypes of a single lineage, in which the size of the initial chambers

is connected in some way with the external characteristics, especially so because generally one of both species is nearly lacking in the individual samples. If so, one must conclude that in part of the samples studied faunas from different environments have been washed together.

III.3.5. CONCLUSIONS; PHYLOGENY.

In the Aquitaine planolinderinids there is a general \bar{Y} reduction from lower to higher stratigraphic levels, roughly from Chattian to Aquitanian. This reduction of \bar{Y} goes together with an increase in $\delta 1.2$ for specimens with the same length of the early spiral. The total effect of both trends is in accordance with the principle of nepionic acceleration, and roughly parallel to the evolutionary trend in the accompanying miogypsinids. The strong negative correlation of Y and $d1.2$, and of \bar{Y} and $\bar{d}1.2$, and the influence of unknown additional factors on $d1.2$, obscure the nepionic acceleration and hence the stratigraphic usefulness of the genus.

In the Indo-Pacific planolinderinids there may be a similar trend, but the few data hamper a definite conclusion. *P. inaequilateralis* differs from the Aquitaine material in possessing a slightly more prominent plano-concave test and a larger size. As to its initial spiral length it might be slightly higher developed than the Aquitaine populations (because only $Y = 1$ individuals are present), but as to its $\bar{d}1.2$ it fits in very well somewhere in the Aquitaine succession. These data are in good accordance with the age assigned to it (Aquitanian). However, the big geographic distance does not allow any correlation.

As to their \bar{Y} the *P. plana* populations are as highly or slightly higher evolved than the Aquitaine planolinderinids. However, the size of the early chambers is considerably smaller. Its position relative to *P. inaequilateralis* is still obscure: either separate lineage or ecophenotype. In the first case one may conclude that the genus *Planolinderina*, such as presented here, is polyphyletic, and in the second case it might be monophyletic. In the latter case some influence on $d1.2$ causing small early chambers, combined with the strongly reduced initial spiral, would suggest equivalence to the younger Aquitaine planolinderinids. The age in Australia is assumed to be Aquitanian, in Borneo even Burdigalian.

In this respect it is of interest to note that specimens which closely resemble *P. plana* have been found recently by V. AMATO in samples from Saint-Etienne — d'Orthe (Chattian) in the Aquitaine Basin (personal communication). The few specimens have a long initial spiral and very small early chambers. They might indicate that representatives of the *P. plana* lineage or comparably small ecophenotypes occur in the Aquitaine Basin as well.

III.4. The genus *Linderina* Schlumberger, 1893.

pl. 10, figs. 1—9; pl. 11, fig. 1; pl. 13, figs. 2a, b, 3a, b; pl. 15, figs. 1—3.

III.4.1. INTRODUCTION, LITERATURE.

The genus *Linderina* has been established by SCHLUMBERGER (1893) on material derived from the Eocene of Bruges (Gironde), France. The strata in which *Linderina* occur probably belong to the "Calcaire de Blaye", which is not exposed in surface outcrops near Bruges. The original description reads:

"Plasmostracum discoidal surépaissi au centre, composé d'un seul rang de nombreuses petites loges disposées circulairement autour d'une loge centrale et dans un même plan. Les parois de chaque série de loges se prolongent vers le milieu au-dessus des loges déjà formées. Cette enveloppe calcaire est traversée par de fortes perforations qui pénètrent directement jusqu'aux loges internes".

Linderina brugesi SCHLUMBERGER is the type species by monotypy. The depository of the type species has not been given, and according to NEUMANN (1954) the type material is probably lost.

Subsequent authors on *Linderina* have described additional species. A list of them is given below. We are well aware that it may be incomplete.

- L. paronai* OSIMO, 1908 (Upper Eocene, Celebes)
- L. chapmani* HALKYARD, 1918 (Bartonian, France)
- L. ovata* HALKYARD, 1918 (Bartonian, France)
- L. buranensis* NUTTALL & BRIGHTON, 1931 (Middle Eocene, Somalia)
- L. floridensis* COLE, 1942 (Lower Middle Eocene, Florida)
- L. bihilensis* SILVESTRI, 1948 (Middle Eocene, Somalia)
- L. nuttalli* SILVESTRI, 1948 (Middle Eocene, Somalia)
- L. rajasthanensis* SINGH, 1953 (Lutetian, India)
- L. bikanerensis* SINGH, 1953 (Lutetian, India)
- L. koyalatensis* SINGH, 1953 (Lutetian, India)
- L. kirtharensis* SINGH, 1953 (Lutetian, India)
- L. visserae* HOFKER, 1958 (Maastrichtian, Holland)

Two species have dubiously been referred to *Linderina*. They are:

- L. douvillei* SILVESTRI, 1910 (Upper Cretaceous, Campanian, France)
- L. baldacci* PREVER, 1912 (Eocene and Miocene, Italy)

In establishing these species their authors did not present essential new data on the generic features. The species have mainly been based on slight differences of the external characteristics in comparison with the type species *L. brugesi*. From

the literature it appears that the arrangement of the initial chambers is rather variable. In *L. paronai* and *L. floridensis* it is a spiral of variable length, in *L. buranensis*, *L. rajasthanensis*, *L. bikanerensis*, *L. kolayatensis* and *L. kirtharensis* the early chambers show a protoconch- deuterococonch- two principal auxiliary chambers arrangement.

Below we give a description of the genus based on our own observations.

Test discoidal, orbitoidal, without lateral chambers, biconvex, more or less strongly thickened in the central portion. Periphery rounded, lobate. The peripheral chambers are provided with two rows of some 4—7 rounded openings at the chambers' bases. The early chambers are arranged in a slightly trochoid spiral of variable length or they show a protoconch-deuterococonch-principal auxiliary chamber(s) arrangement. The later chambers show orbitoidal growth. The wall structure is monolamellid.

Of the species listed some are not within the limits of this description. *L. chapmani* belongs to *Halkeyardia*, *L. ovata* is probably a variant of *Cyclolocolina annulata* HERON-ALLEN & EARLAND. *L. visserae* belongs to *Hellenocyclina*. *L. douvillei* is an *Orbitoides* species (subgen. *Monolepidorbis*) (VAN HINTE, 1966a). The status of *L. baldacci* is completely obscure.

Of some *Linderina* species material is available, others will be discussed on the basis of the literature data.

III.4.2. MATERIAL.

Linderina specimens from the following localities were studied:

EG 189, Selsey Bill, Sussex, England. Upper Bracklesham Beds, Eocene (Auversian). Specimens of this locality have been referred to *L. brugesi* by HERON-ALLEN & EARLAND (1911) and CURRY (1960). Donation: D. CURRY.

Fr 1039, 1040, 1041 and 1043, Bois de Ronquerolles, Oise, France. Sables d'Auvers, Auversian, Paris Basin. Collection Utrecht.

Fr 564, 566, Auvers sur Oise, Seine et Oise, France. Sables d'Auvers, type Auversian, Paris Basin. Collection Utrecht.

Fr 1034, Le Ruel, Seine et Oise, France. Sables de Marines, Marinesian (Middle Bartonian), Paris Basin. Collection Utrecht.

Fr 1129, Daguerre farmhouse near Saint Pierre d'Irube, SE of Bayonne, Basses Pyrenées, Aquitaine Basin, France. Collection Utrecht. Lutetian according to NEUMANN (1954). She referred the *Linderina* specimens of this locality to *L. brugesi*.

Mt 12557, Wadi Dambarre, Western Midjurtinia, Somalia. Carcar Series (Carcar III), Upper Lutetian. The specimens of this sample AZZAROLI (1950, p. 107, locality I, horizon 12) assigned to *L. buranensis*. Donation: A. AZZAROLI.

A sample 4.5 km NNW of Sunto Trig. Station, Somalia (E 49°1'; N 10°39'30"); Middle Eocene. On the specimens of this sample NUTTALL & BRIGHTON (1931) established their *L. buranensis*. Donation: A. G. BRIGHTON.

A sample from Tug Buran, near Buran Pool, Somalia (E 48°47'; N 10°13'), Middle Eocene. The specimens of this sample NUTTALL & BRIGHTON (1931) assigned to *L. buranensis*. Donation: A. G. BRIGHTON.

Some specimens of Qatar, Lutetian, labeled *L. buranensis*. Donation: L. HOTTINGER.

Type specimens of *L. paronai* OSIMO, derived from Dongala, Celebes, Indonesia. Upper Eocene. Studied by courtesy of G. SAMPO.

Some *Linderina* specimens from Poulo Miang, Borneo, Indonesia; Eocene (Lutetian?). These specimens PROVALE (1909) determined as *L. paronai*. They are stored in the collections of the Geological Institute of the university of Turin, and they could be studied by courtesy of G. SAMPO.

III.4.3. EXTERNAL FEATURES.

On the basis of their external features the populations can be split in three more or less well distinguishable groups. The first comprises the populations from Selsey Bill and from the Paris Basin, the second group comprises the Daguerre and Mt 12557 population and the third one comprises the other Somalian populations and that from Qatar. For each group we give a description of the external characteristics.

1. Test small, discoidal, diameter up to 1.00 mm maximally, slightly asymmetrically biconvex. Both faces are strongly thickened in the centre by a glassy boss, generally being more prominent at one side than at the other (compare also HERON-ALLEN & EARLAND, 1911, pl. 12, fig. 7). The arcuate equatorial chambers are visible only near the periphery. They are coarsely perforate. The periphery is broad, rounded, lobate and sometimes striate parallel to the median plane (the latter applies to the Ronquerolles specimens). The peripheral chambers are provided with multiple apertures: median, basal rows of 3—5 rounded openings, two to each chamber.

The specimens from the Paris Basin and Selsey Bill are within the limits of this description. Those from the Paris Basin are generally somewhat smaller than those from Selsey Bill. The outer appearance of the Paris Basin specimens may be seen from the specimen on pl. 13, fig. 2a, b. Specimens from Selsey Bill have been figured by HERON-ALLEN & EARLAND (1911, pl. 12, figs. 1—5).

2. Test of moderate size, discoidal, diameter up to 3.5 mm maximally, bicon-

vex, only slightly inflated in the central portion. The central inflation may be provided with small (diameter up to $50\ \mu$) pustules. The arcuate equatorial chambers are visible in the peripheral portion only. The periphery is broad, rounded or acute, lobate. The peripheral chambers are provided with multiple apertures, two rows to each chamber, each one consisting of three or four large openings.

The specimens of Daguerre and Mt 12557 are within the limits of this description. They primarily differ from those in the first group by their larger size and less prominent central inflation.

For figures of specimens from Daguerre one is referred to NEUMANN (1954, pl. 5, figs. 1, 2).

3. Test large, discoidal, diameter up to 6.5 mm maximally, symmetrical or asymmetrical, biconvex. Both sides have a very strong central inflation with a heavy ornamentation of pustules or radially running ridges. The arcuate or ogival equatorial chambers are visible in the peripheral part of the test only. The periphery is broad, acute or rounded, lobate. The peripheral chambers are provided with multiple apertures, two rows to each chamber, each consisting of about four large openings.

The specimens of the Sunto, Tug Buran and Qatar populations are within the limits of this description. They primarily differ from both other groups by their larger size, more prominent central inflation and heavy, beaded ornamentation. A specimen from Sunto is figured on pl. 13, fig. 3.

III.4.4. INTERNAL FEATURES.

In our material the length of the initial spiral is variable, ranging from 5 to 1 chambers in macrospheric specimens, and from 15 to 8 in microspheric ones. A photograph of a microspheric specimen is given on pl. 10, fig. 6. The arrangement of the early chambers of macrospheric specimens is generally symmetrical. This is shown by several photographs. In specimens with $Y = 1$, the spirals originating from the principal auxiliary chambers may consist of one or two chambers each, the closing chamber being excluded. In the specimen figured on pl. 11, fig. 1 these spirals consist of one chamber each. In specimens with $Y = 2$, the spirals originating from the principal auxiliary chamber generally consist of three chambers each (compare pl. 10, figs. 1, 2, 3). They may be asymmetrical, consisting of 2 and 4 chambers (pl. 10, fig. 4). Also in specimens with a greater Y the spirals which originate from the first chamber with two apertures, generally consist of 3 chambers each (compare pl. 10, fig. 7; $Y = 3$).

The early chambers have no thickened wall as in *Planorbulinella*. Moreover,

a recurrence of the one-aperture stage was never observed. The wall structure is monolamellid.

III.4.5. MEASUREMENTS AND COUNTS.

Counts and measurements were made in a way similar to that used in *Planorbulinella* and *Planolinderina*. Data were gathered on the parameters d1.2 and Y. Since the tests are thickened in the central portion the internal characteristics had to be studied on thin sections.

The results of Y counts and d1.2 measurements are given on p. 122. The Y distribution of the populations is shown in the table, and also in the histograms of fig. 39. The order in which the samples are arranged does not necessarily reflect their real stratigraphic succession. Only the order of the samples of the Ronquerolles and Auvers sections is certain.

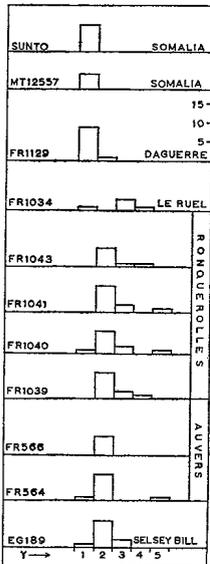


Fig. 39. Histograms showing the Y distribution in several *Linderina* populations from England, France and Somalia.

Moreover, the Y and d1.2 values of the type specimens of several *Linderina* species is given.

Sample	N	Y					\bar{Y}	$\overline{d1.2}$
		5	4	3	2	1		
Qatar	1	—	—	—	—	1	1.00	187
Mt 12557	4	—	—	—	—	4	1.00	182.7 ± 14.7
Sunto	7	—	—	—	—	7	1.00	175.1 ± 9.9
Tug Buran	2	—	—	—	—	2	1.00	178 and 159
Fr 1129	10	—	—	—	1	9	1.10 ± 0.10	126.2 ± 5.4
Fr 1034	5	—	1	3	—	1	2.80 ± 0.55	93.5 ± 15.6
Fr 1043	7	—	1	1	5	—	2.43 ± 0.32	98.3 ± 9.5
Fr 1041	10	1	—	2	7	—	2.50 ± 0.32	89.2 ± 8.3
Fr 1040	10	1	—	2	6	1	2.40 ± 0.36	105.4 ± 11.2
Fr 1039	10	—	1	2	7	—	2.40 ± 0.23	90.9 ± 6.1
Fr 566	5	—	—	—	5	—	2.00	129.2 ± 7.0
Fr 564	9	1	—	—	7	1	2.22 ± 0.38	101.5 ± 7.9
EG 189	10	—	—	2	7	1	2.10 ± 0.19	111.8 ± 9.5
<i>Linderina</i> species ¹⁾				Y				d1.2
<i>L. bikanerensis</i>				1				106
<i>L. kolayatensis</i>				1				95
<i>L. kirtharensis</i>				1				93
<i>L. rajasthanensis</i>				1				83
<i>L. floridensis</i>				3				100
<i>L. paronai</i>				4				116 (compare pl. 15, fig. 1)
<i>L. paronai</i> ²⁾				2				127 and 151 (compare pl. 15, figs. 2, 3)

¹⁾ All observations, except for *L. paronai*, are based on examinations of the figures of the types.

²⁾ Specimens figured by PROVALE (1909).

Little can be said about these data because of the low numbers of observations per sample, and especially so because the stratigraphic interrelationship of the populations studied is unknown. From the two sections studied, Auvers (Fr 564, 566) and Ronquerolles (Fr 1039—1043), one cannot decide whether there is a change in \bar{Y} or $\overline{d1.2}$ from bottom to top. In both cases the \bar{Y} and $\overline{d1.2}$ of populations of a single section do not differ significantly. If the populations of the two sections are compared mutually a statistically significant difference is found only between the $\overline{d1.2}$ of Fr 566 and Fr 1039 and Fr 1041.

The other population of the Paris Basin, from Le Ruel (Fr 1034), and that from Selsey Bill (EG 189) compare well with those from Auvers and Ronquerolles.

The populations from Daguerre and Somalia differ significantly in the length of the early spiral (probability 99.9 %) from those of the Paris Basin and Selsey Bill. The $\overline{d1.2}$ differences are significant in only part of the populations. Nevertheless, one gets the impression that a small \overline{Y} tends to coincide with a bigger $\overline{d1.2}$.

This may easily be seen if the populations are arranged according to a decreasing \overline{Y} from bottom to top. In this table the observations of the Qatar and Tug Buran populations are omitted, because of the very low numbers of observations, one and two respectively.

\overline{Y}	$\overline{d1.2}$	\overline{Y}	$\overline{d1.2}$
1.00	182.7	2.22	101.5
1.00	175.1	2.40	105.4
1.10	126.2	2.40	90.9
2.00	129.2	2.43	98.3
2.10	111.8	2.50	89.2
		2.80	93.5

Because of the low number of observations in each population it is difficult to get a good idea about this relationship. For the same reason $Y/d1.2$ scatter diagrams are not given. A calculation of the correlation coefficient (r) was made for one sample only, Fr 1040, because it has the widest Y range (from 5 to 1). In this case $r = -0.7235$, which is significant at a probability level of 99.0 %. The fact that the correlation is not highly significant may be due to the low number of observations.

For this reason the Y and $d1.2$ data of the four populations from Ronquerolles were taken together. For the 37 specimens of these four samples together $r = -0.6537$, which indicates a significant negative correlation of both parameters at a probability level of 99.9 %. There is a similar significant, negative correlation between the \overline{Y} and $\overline{d1.2}$ of the 11 populations studied (those from Qatar and Tug Buran being excluded). In that case $r = -0.8981$.

III.4.6. DISCUSSION OF THE RESULTS OF COUNTS AND MEASUREMENTS; PHYLOGENY.

The numerical data of the successive *Linderina* populations of two sections, Auvers and Ronquerolles, do not show a clear decrease of \overline{Y} from bottom to top. As a consequence there is no distinct indication for a development in accordance with the principle of nepionic acceleration. The populations of these sections, as well as those from Le Ruel and Selsey Bill seemingly form a fairly homogeneous

group. They cannot be differentiated on the basis of \bar{Y} . However, some populations differ significantly from one another on the basis of $\bar{d}1.2$.

The other populations, from Daguerre, Somalia and Qatar, are more highly developed than those of the former group as to their nepionic configuration. From this fact one might draw the conclusion that nepionic development exists in *Linderina*, but the age assignments are not consistent with this assumption. From the literature data the latter populations are considered to be of Lutetian age, the former ones of Bartonian (Auversian and Marinesian) age. However, especially for the samples outside the Paris Basin and England, these age assignments may be incorrect. If correct, the alternative explanation must be that the negative $\bar{Y}/\bar{d}1.2$ correlation completely obscures nepionic acceleration by "haphazard" fluctuations in $\bar{d}1.2$.

Because of the similarity in growth pattern with *Planorbulinella*, *Planolinderina* and other, larger, orbitoidal foraminifera it is reasonable to assume that a nepionic development existed in *Linderina*. The way in which *Linderina* developed cannot be seen from our data. *Linderina* most closely resembles *Planolinderina*, not only internally but also externally. Internally the first chambers are not thick-walled, a recurrence of the one-aperture stage is absent or nearly completely absent, and there is a negative correlation between the \bar{Y} and the $\bar{d}1.2$. From these analogies one may conclude that the evolution in *Linderina* is characterized by an \bar{Y} decrease, combined with a $\bar{d}1.2$ increase in the course of time.

III.4.7. SPECIES DISTINCTION.

In orbitoidal foraminifera in which there is a nepionic development species should be based on the internal characteristics, preferably numerically expressed. However, the *Linderina* species that have been established up till now have mainly been based on slight external differences with the type species *L. brugesi*. Since the type material of this species has probably got lost, and since its internal features have insufficiently been described by SCHLUMBERGER, it is impossible to decide whether the name *L. brugesi* is applicable to any of our populations. Especially so, while our single sample of the Aquitaine Basin (Daguerre) is different from those of northern France.

Type material of *L. buranensis* from Sunto was available to the author. It provided a sound basis for a comparison with other populations. The populations from Tug Buran, Mt 12557 and Qatar cannot be differentiated from it, neither on their \bar{Y} , nor on their $\bar{d}1.2$. They all are named *L. buranensis*. SILVESTRI (1948) described *L. nuttalli* and *L. bibilensis* from Somalia. The type material of both species was destroyed during the last world war (G. SALVATO-

RINI, personal communication). Both species were created because of slight external differences from *L. buranensis*. Part of the specimens from Sunto, figured by NUTTALL & BRIGHTON (1931), were included in *L. bibilensis* by SILVESTRI (1948). AZZAROLI (1950) considered both species to be synonyms of *L. buranensis*. He considered the external differences to be of insufficient weight for the distinguishing of separate species. In this respect we fully agree with AZZAROLI. Our data on the internal features of the topotypes of *L. buranensis* indicate that only one species can be distinguished in that population. Differences in the outside features do not correspond to internal differences. From these data, and from the fact that SILVESTRI's material was derived from about the same stratigraphic level as the types of *L. buranensis*, it is highly probable that *L. nuttalli* and *L. bibilensis* have to be considered to be synonyms of *L. buranensis*.

The status of the other *Linderina* species is rather obscure. The type specimens of *L. rajasthanensis*, *L. bikanerensis*, *L. koyalatensis* and *L. kirtharensis* have the same arrangement of the early chambers ($Y = 1$). The size of the early chambers is hardly different in the specimens (106, 95, 93 and 83 μ respectively). Such a range of $d_{1.2}$ variation is usual within a single population. Although SINGH (1953) did not give any indication about the samples from which his specimens were derived, it is clear that they were all taken from the same area (WSW of Marh village near Kolayat, Rajasthan, India) and from the same stratigraphic level (Kirthar Beds, "Lutetian"). From these data it is probable that these four "species" belong to a single species only, which should be named *L. rajasthanensis*.

It is interesting to note that the Upper Part of the Kirthar beds has been correlated with the Carcar III of Somalia (AZZAROLI, 1950). Their lower and middle part should be older. Our Mt 12557 population (*L. buranensis*) has been derived from the Carcar III. It is more highly developed (bigger $d_{1.2}$) than *L. rajasthanensis*.

The types of the Kirthar "species" are well within the $d_{1.2}$ range of the Daguerre population. Although they tend to fall at its lower side, it is not possible to differentiate them from that population. From these data the Daguerre population had best be named *L. cf. rajasthanensis*, the cf. being added to indicate that a decision in this question can be made only after a re-examination of the Indian "species" and *L. brugesi*.

The type specimens of *L. floridensis* and *L. paronai* are within the Y range of the populations of the Paris Basin and Selsey Bill ($Y = 3$ and 4 respectively). Two specimens assigned to *L. paronai* by PROVALE (1909) differ from the type in that they both have Y values of 2. Also these specimens are well within the Y range of the material of the Paris Basin and Selsey Bill. However, all specimens have a bigger $d_{1.2}$ than specimens with corresponding Y values in the material

from the Paris Basin and Selsey Bill. From a point of evolution they might be more highly evolved than the latter, but these few specimens do not justify any conclusion in this respect. We can only remark that the populations from the Paris Basin and Selsey Bill might be named *L. paronai* (or *L. floridensis*) on the basis of our present knowledge. These populations probably represent the most primitive linderinids known at the moment. Since they occur in the type Auver-sian (Bartonian) the age assignment of many other populations ("Lutetian") that are more highly evolved will have to be reconsidered.

III.5. The genus *Hellenocyclina* Reichel, 1950.

pl. 11, figs. 2-14; pl. 14, fig. 5; pl. 15, fig. 4.

III.5.1. INTRODUCTION, LITERATURE.

The genus *Hellenocyclina* has been established by REICHEL (1950) for small, orbitoidal foraminifera without lateral chambers, found in random thin sections of Cretaceous rocks near Iliki Lake, 90 km N of Athens, Greece. The original description of the genus reads:

"Foraminifère libre à test vitrocalcaire perforé; forme lenticulaire, accroissement concentrique, loges équatoriales de type arqué (ogival subabaissé) à 4 stolons, pas de loges latérales, mais test des faces supérieure et inférieure fortement épaissi. Embryon multiloculaire formé, chez le type, de 6 loges disposées en croix et autour desquelles on compte 4 spires de loges auxiliaires".

Hellenocyclina beotica REICHEL is the type species by monotypy. In this description the arrangement of the early chambers is not clear. MAC GILLAVRY (1963) re-examined the type specimens of *H. beotica* and gave an alternative explanation of this arrangement, but he states:

"An examination of the original material did not confirm this interpretation, but the situation is not clear in any case".

The present author also examined the original material (compare pl. 15, fig. 4). He cannot but agree with MAC GILLAVRY. Numerous additional thin sections made of rock samples from the type locality of *H. beotica* did not yield any good horizontal section through the early chambers. So for the moment the arrangement of the initial chambers of *H. beotica* will remain obscure.

H. beotica has been mentioned afterwards by NEUMANN & CUVILLIER (1950), by NEUMANN (1958) and by DUPEUBLE (1964) from the Cretaceous of France. Details on the arrangement of the early chambers were not presented by these authors.

MAC GILLAVRY (1963) gave details about a second European species, *H. visserae* (HOFKER). This species has been assigned to *Linderina* by HOFKER (1958, 1966). The arrangement of the early chambers of specimens belonging to this species are well known. MAC GILLAVRY (1963, pl. 7, figs. 1, 2) figured specimens with one principal auxiliary chamber from the Upper Cretaceous of Haute Garonne, France. HOFKER (1966, figs. 1, 2) figured specimens with an initial spiral of three chambers from the Upper Cretaceous of Limburg, Holland. From these figures it appears that the three early chambers have a thickened wall, and that a change of coiling direction may occur.

Below we give a description of the genus based on the literature and our own observations.

Test small, discoidal, orbitoidal, without lateral chambers, distinctly conical to almost flat. Periphery rounded, lobate. The peripheral chambers are provided with small, median, basal, slit-like apertures, two to each chamber. The (small) early chambers are arranged in a trochoid spiral of variable length, or in a protoconch-deuteroconch-principal auxiliary chamber(s) arrangement. The later chambers show orbitoidal growth. The first three chambers may have a thickened wall. A relapse to the one-aperture stage may be present. The wall structure is bilamellid.

Remarks. *Hellenocyclina* differs from *Planorbulinella* in the small size of the equatorial chambers and in the generally conical shape. It differs from *Planolinderina* and *Linderina* in the small size of the equatorial chambers, in its apertural characteristics, in showing relapse to the one-aperture stage, and in that the early chambers have a thickened wall. It differs from *Monolepidorbis* in the arrangement of the early chambers, and in the size of these chambers ¹⁾.

III.5.2. MATERIAL.

The populations studied were derived from the following samples, all in the Utrecht collections:

NL 16, 14, 15, Maastricht, Limburg, Holland. Type Maastrichtian (levels Mc and Md). The samples are listed in stratigraphic order, NL 16 being the lowermost one. Type locality of *Hellenocyclina visserae* (HOFKER).

Fr 955, 953, 954, Saint Marcet, Haute Garonne, France. Age: Maastrichtian. The samples are arranged in stratigraphic order, Fr 955 being the lowermost one. Fr 955 corresponds to sampling point 122 of MAC GILLAVRY (1955).

¹⁾ According to VAN HINTE (1966b) the arrangement of the early chambers of *Monolepidorbis* is fairly variable: it may be either spiral, or biserial. Nevertheless *Monolepidorbis* specimens with a definite Y can easily be differentiated from *Hellenocyclina* individuals with the same Y value on the basis of their considerably bigger d1.2.

Fr 418, Carrière du Chateau, Dumes, Landes, France. Age: Maastrichtian, according to NEUMANN (1958). A description of the locality has been given in the Excursion Guide to the Micropaleontological Colloquium, Bordeaux, 1957.

Fr 522, 521, 520, 823, 824, 825, Aubeterre, Charente, France. The samples are listed in stratigraphic order, Fr 522 being the lowermost one. The detailed stratigraphic position of the samples has been given by VAN HINTE (1965a). The samples Fr 522—823 have been taken from the type Campanian, the other two from the type Dordonian.

Fr 619, Talmont, Charente-Maritime, France. The sample has been taken in the coastal cliff under the roman church. Age: Late Campanian-Maastrichtian according to NEUMANN (1958, p. 62).

Fr 457, Plage des Nonnes, Meschers, Charente-Maritime, France. Age: Maastrichtian according to NEUMANN (1958).

III.5.3. EXTERNAL FEATURES.

As to their external features our material can be divided into three groups: 1. the specimens from Aubeterre, Talmont and Meschers, 2. those from Dumes and Maastricht, and 3. those from Saint Marcet. Below we give a description of the morphological features of these groups.

1. Test very small, diameter up to 0.4 mm, discoidal, one side more or less concave, the other slightly convex, but never becoming conical. In the centre there is often a small, prominent thickening of vitreous, calcareous matter. Both sides are finely perforate. The periphery is rounded, lobate. The peripheral chambers are provided with slit-like apertures, two to each chamber. All equatorial chambers are visible from both sides, the early chambers being arranged in a long spiral, the later chambers showing orbitoidal growth.

The populations from Aubeterre, Talmont and Meschers are within the limits of this description. A specimen from Aubeterre is figured on pl. 14, fig. 5.

2. Test small, discoidal, diameter up to 2.0 mm, one side flat or slightly concave, the other side convex to conical. Both sides are strongly thickened by calcareous matter. Periphery rounded, lobate. The peripheral chambers are provided with slit-like apertures, two to each chamber. The finely perforate equatorial chambers are visible in the peripheral portion only.

The populations from Maastricht and Dumes are within the limits of this description. They differ from those of group 1 in the more conical shape of the test, and in that the early chambers are not visible from the outside. A specimen from Maastricht is figured on pl. 14, fig. 4.

3. Test small, discoidal, diameter up to 2.0 mm, one side flat, the other

slightly convex. Periphery rounded or acute, lobate. Both sides are thickened by calcareous matter. The finely perforate equatorial chambers are visible over a great part of both sides as a regular meshwork of small rhomboids.

The populations from Saint Marcet are within the limits of this description. They mainly differ from those of group 2 in the less conical shape and in the better visibility of the equatorial chambers.

III.5.4. INTERNAL FEATURES.

The length of the initial spiral in our populations varies from 13 to 1 chamber in macrospheric specimens. In specimens with a high Y value the spirals originating from the first chamber with two stolons consist generally of five chambers each, the mutual closing chamber being excluded (compare pl. 11, figs. 3 and 6). These spirals may be of unequal length also, but this arrangement is not figured. In specimens with a short initial spiral, the spirals originating from the first chamber with two stolons are generally shorter, consisting of 3 or 4 chambers each, being symmetrical in most cases (compare MAC GILLAVRY, 1963, pl. 7, figs. 1, 2). A recurrence of the one-aperture stage was frequently observed, but this feature is not as common as it is in *Planorbulinella*. The first three chambers are clearly differentiated from the later ones, because their walls are more strongly thickened, especially so in short-spined individuals. In this respect the early chambers resemble those of *Planorbulinella*. According to drawings by HOFKER (1966, figs. 1, 2) there may be a reversal of the coiling direction, but we did not observe this feature in our individuals. The wall structure is bilamellid.

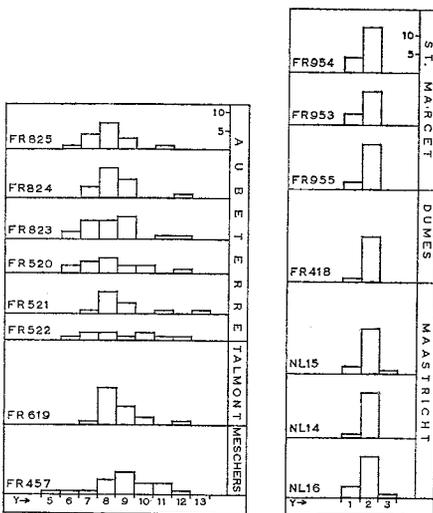


Fig. 40 (l.) Histograms showing the Y distribution in several French populations of *Hellenocyclina charentensis n.sp.*

Fig. 41 (r.) Histograms showing the Y distributions in several populations of *Hellenocyclina visserae (Hofker)*.

III.5.5. MEASUREMENTS AND COUNTS.

Measurement and counts were made in a way similar to those applied in *Planorbulinella*, *Planolinderina* and *Linderina*. Data were gathered on the parameters \bar{Y} and $\overline{d1.2}$. For the study of the internal features in most cases thin sections had to be made. In the Aubeterre, Talmont and Meschers specimens the initial spiral can clearly be seen from the outside, but because of the very small size of the early chambers these specimens had to be sectioned also for a reliable measuring of $\overline{d1.2}$.

In the following table we give the results of counts and measurements. The \bar{Y} distribution is shown also in the histograms of figs. 40 and 41.

Sample	N	Y											\bar{Y}	$\overline{d1.2}$	
		13	12	11	10	9	8	7	6	5	3	2			1
Fr 954	16	—	—	—	—	—	—	—	—	—	—	12	4	1.75 ± 0.11	65.1 ± 2.5
Fr 953	12	—	—	—	—	—	—	—	—	—	—	9	3	1.75 ± 0.13	57.7 ± 5.2
Fr 955	15	—	—	—	—	—	—	—	—	—	1	12	2	1.93 ± 0.12	60.1 ± 4.1
NL 15	15	—	—	—	—	—	—	—	—	—	1	12	2	1.93 ± 0.12	59.2 ± 2.9
NL 14	13	—	—	—	—	—	—	—	—	—	—	12	1	1.92 ± 0.08	51.0 ± 3.0
NL 16	15	—	—	—	—	—	—	—	—	—	1	12	2	1.93 ± 0.12	58.1 ± 3.8
Fr 418	12	—	—	—	—	—	—	—	—	—	—	11	1	1.92 ± 0.09	59.5 ± 6.6
Fr 825	16	—	—	1	—	3	7	4	1	—	—	—	—	8.00 ± 0.32	28.7 ± 1.5
Fr 824	17	—	1	—	—	5	8	8	—	—	—	—	—	8.35 ± 0.29	30.1 ± 1.7
Fr 823	20	—	1	1	—	6	5	5	2	—	—	—	—	8.20 ± 0.34	31.6 ± 1.4
Fr 520	14	—	1	—	2	2	4	3	2	—	—	—	—	8.21 ± 0.46	30.9 ± 2.1
Fr 521	12	1	—	1	—	3	6	1	—	—	—	—	—	8.83 ± 0.49	30.5 ± 1.7
Fr 522	10	—	1	1	2	1	2	2	1	—	—	—	—	8.80 ± 0.64	29.2 ± 2.6
Fr 619	19	—	1	—	2	5	10	1	—	—	—	—	—	8.63 ± 0.26	23.5 ± 0.9
Fr 457	20	—	1	3	6	4	1	1	1	1	—	—	—	8.95 ± 0.40	31.5 ± 1.5

The \bar{Y} and $\overline{d1.2}$ of the populations are plotted in the scatter diagram of fig. 42. From the data in the table and from the figures 40, 41 and 42 it is evident that our populations fall apart in two well separated clusters. These clusters consist of populations from Maastricht, Saint Marcet and Dumes on the one hand, and those from Aubeterre, Meschers and Talmont on the other hand. The populations belonging to a single cluster cannot be differentiated, neither by their \bar{Y} , nor on the basis of $\overline{d1.2}$. However, the populations from the two clusters

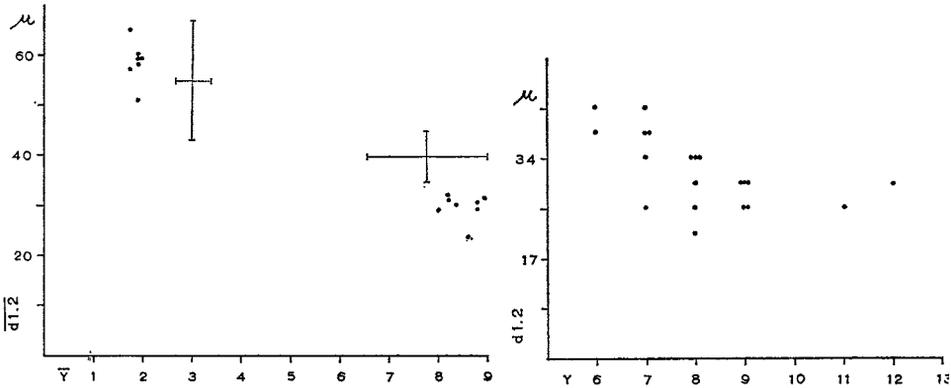


Fig. 42 (l.) $\bar{Y}/\bar{d1.2}$ scatter diagram of 15 *Hellenocyclina* populations from the Campanian, Dordonian and Maastrichtian of Western Europe. The crosses give average values of $\pm 3\sigma$.

Fig. 43 (r.) $Y/d1.2$ scatter diagram of 20 *Hellenocyclina* specimens of sample Fr 283, Aubeterre (type Campanian), Charente, France.

differ from one another significantly, both in the length of the initial spiral and in $\bar{d1.2}$.

Within the populations of the Aubeterre section there may be a decrease in \bar{Y} from bottom to top, but it is certainly not of great magnitude. This possible \bar{Y} decrease does not correspond to an increase in $\bar{d1.2}$.

The relationship between \bar{Y} and $\bar{d1.2}$ can be seen from the scatter diagram of fig. 43, in which the observations on 20 specimens from sample Fr 823 (Aubeterre) are plotted. In that population the correlation coefficient of both parameters is -0.604 , which indicates that there is a significant negative correlation, at a probability level of 99.0%. The specimens of two other French samples show also, at a probability level of 99.0%, a significant negative correlation between both parameters. They are:

Sample	N	r
Fr 824	16	-0.650
Fr 520	14	-0.811

In the other populations a negative correlation significant at a probability level of 99.0% is not present.

From these correlation coefficients it appears that the negative correlation between both parameters is less distinct than it is in *Planorbulinella* and *Planolinderina* populations. It is possible that this difference is caused by the lower numbers of observations.

The $\overline{d1.2}$ and \overline{Y} of the populations studied are scattered in the diagram of fig. 42. If the open field in between both clusters would contain the intermediate populations, there would be a significant negative correlation between both factors.

Since the number of observations in each sample separately is low, the relationship between Y and $\overline{\delta 1.2}$ is shown on the basis of all specimens of the Aubeterre, Talmont and Meschers populations. In calculating the $d1.2$ separately for each Y class ($= \delta 1.2$), we get the following result:

Y	N	$\overline{\delta 1.2}$
5	1	38.2
6	7	40.1 ± 2.1
7	20	33.8 ± 1.2
8	45	29.5 ± 0.7
9	29	26.5 ± 1.1
10	7	27.3 ± 1.7
11	7	29.1 ± 1.5
12	6	21.2 ± 2.1
13	1	25.5

From this table a decreasing Y seems to correspond to an increasing $\overline{\delta 1.2}$, but this increase is not a smooth one. Several setbacks (or jumps forward) occur. They may be due to the low numbers of observations in several Y classes.

The significance of mutual $\overline{\delta 1.2}$ differences between the Y classes was tested (Student's t-test):

Y	12	11	10	9	8	7
6	<i>6.356</i>	<i>4.263</i>	<i>4.738</i>	<i>5.738</i>	<i>4.789</i>	2.605
7	<i>5.210</i>	<i>2.447</i>	<i>3.125</i>	<i>4.486</i>	<i>3.095</i>	
8	<i>3.750</i>	<i>0.241</i>	<i>1.196</i>	<i>2.302</i>		
9	<i>2.236</i>	<i>1.397</i>	<i>0.395</i>			
10	<i>2.258</i>	<i>0.794</i>				
11	<i>3.062</i>					

In this table significant differences are in italics. It appears that $\overline{\delta 1.2}$ differences of successive Y classes are not significant. In some cases, however, classes which are farther apart from one another differ significantly.

III.5.6. DISCUSSION OF THE COUNTS AND MEASUREMENTS; PHYLOGENY.

The data presented indicate that on the basis of the internal features our

populations are well apart in two separate clusters. The populations of one cluster have a long initial spiral and small early chambers, whereas in the other populations these chambers are relatively large and the initial spiral is strongly reduced.

These data indicate that nepionic acceleration may have occurred in *Hellenocyclina*. It is possible that environmental or other effects on d1.2 influence \bar{Y} (owing to the negative correlation between \bar{Y} and d1.2), but it is assumed that such influences will not be very strong. This assumption is based on the fact that the correlation between \bar{Y} and d1.2 is not very strong and the mutual δ 1.2 differences between successive \bar{Y} classes are insignificant. As in *Planorbullinella*, in *Hellenocyclina* a relapse to the one-aperture stage occurs. Whether this feature is correlated in some way with the size of early chambers cannot be decided on the basis of our restricted material.

It is assumed that the populations of both clusters cannot be ecophenotypical expressions of a single species caused by random or other effects on d1.2, for example environmental influences. The populations of Aubeterre, Meschers and Talmont have to be considered as the ancestors of those of Maastricht, Dumes and Saint Marcet. This conclusion is in accordance with investigations by VAN HINTE (1966a) on *Orbitoides*. Also in that genus the Aubeterre populations are much more primitive than those of Maastricht and can clearly be differentiated from them. The more highly developed *Hellenocyclina* (from Maastricht, Dumes and Saint Marcet) are determined as *H. visserae* (HOFKER), the more primitive ones are named *H. charentensis* n.sp. This new species is described below. One of both species may be a junior synonym of *H. beotica* (REICHEL). Future research of the internal characteristics of the latter species, based on material from its type locality, may enable a decision about this problem.

In the French literature the age of the strata from which our *H. charentensis* populations were derived is generally given as Maastrichtian. This age assignment is the result of the incorrect assumption of many French micropaleontologists that the first appearance of *Orbitoides* coincides with the base of the Maastrichtian. However, *Orbitoides* occurs already in the type Campanian (Aubeterre section), together with *H. charentensis*. Consequently, also the strata of Talmont and Meschers are considered here to be of Campanian age.

In contrast with the opinion of other authors, for example EAMES in VAN HINTE (1966c) we agree with VAN HINTE that the Campanian and Maastrichtian are clearly separable stages. His opinion, based on the evolution of *Orbitoides*, is substantiated by the nepionic development of *Hellenocyclina*.

III.5.7. HELLENOCYCLINA CHARENTENSIS n.sp.

plate 11, figs. 2—14; plate 14, fig. 5.

Etymology. The name is derived from the Charente, France.

Holotype. Plate 14, fig. 5; coll.nr. S 20858.

Paratypes. Ten complete and 20 horizontally sectioned, macrospheric specimens.

Type level. "Craie tendre à *Ostrea vesicularis* LAMARCK, etc.", Cretaceous, type Campanian.

Type locality. Aubeterre, Charente, France; bed C, sample Fr 823 (see VAN HINTE, 1965a).

Diagnosis. A relatively flat *Hellenocyclus* with a long initial spiral and very small early chambers.

Description. Test small, discoidal, diameter up to 0.4 mm, one side more or less concave, the other side slightly convex, but never becoming conical.

In the centre there is often a small, prominent inflation of vitreous, calcareous matter. Both sides are finely perforate. The periphery is rounded, lobate. Each peripheral chamber is provided with two, small, median slit-like apertures. All equatorial chambers are visible from both sides. The early chambers are arranged in a trochoid spiral of variable length, 12—7 in the macrospheric specimens of the type sample, mean 8.20 ± 0.34 . The later chambers show regular, orbitoidal growth. A recurrence of the one-aperture stage frequently occurs. The initial chambers are very small. The size of the protoconch and deutoconch together ranges from 21—42 μ in the macrospheric specimens of the type sample; the corresponding mean is $31.6 \pm 1.4 \mu$. No distinct microspheric individuals were observed. The wall structure is bilamellid.

Remarks. *H. charentensis* n.sp. differs from *H. visserae* (HOFKER) in its less conical shape, the smaller early chambers and the longer initial spiral. In the populations assigned to *H. charentensis* n.sp. the mean length of the initial spiral ranges from 8.95 to 8.00. In the same populations the mean size of the protoconch and deutoconch together ranges from 23.5 to 31.6 μ . The species should best be defined on an upper and lower limit of the mean length of the initial spiral. However, such a delimitation is postponed for the present because the populations form only a small part of a still very incompletely known evolutionary lineage. Nevertheless it is possible to indicate where these limits will probably be drawn in the future: the mean value of the type population $\pm 4 \sigma$ ¹⁾. This means that the species limits will be about at 9.50 and 7.00.

Occurrence. Campanian of Talmont, Meschers and Aubeterre, France.

¹⁾ The standard errors of \bar{Y} can be used in this part of the lineage because the Y distributions are not skewed.

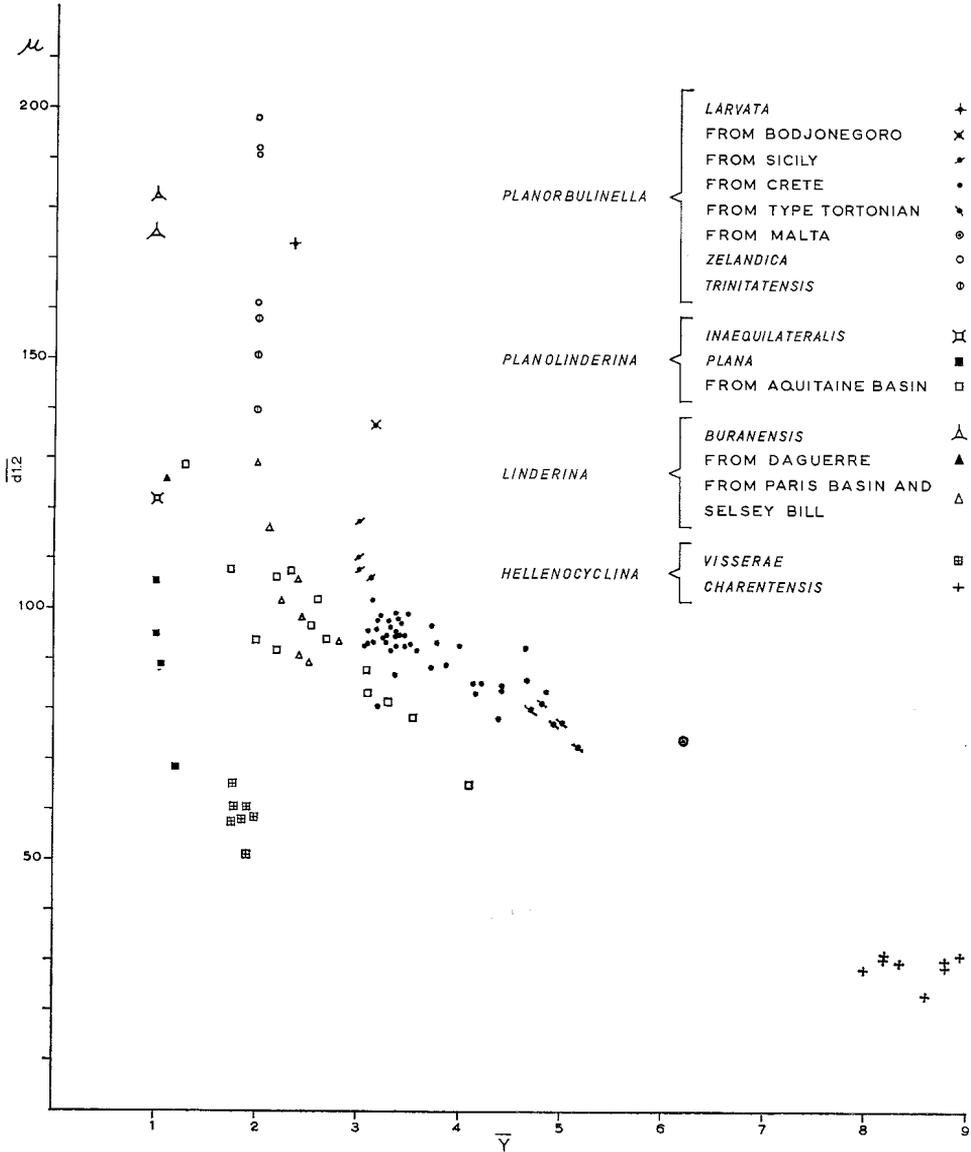


Fig. 44. $\bar{Y}/\bar{d}1.2$ scatter diagram of *Planorbulinella*, *Planolinderina*, *Linderina* and *Hellenocyclina* populations.

III.6. Conclusions, phylogeny, taxonomy, ecology

The results of the Y counts and d1.2 measurements of the populations of *Planorbulinella*, *Planolinderina*, *Linderina* and *Hellenocyclina* are given in the $\bar{Y}/d1.2$ scatter diagram of figure 44. The present knowledge of the time-stratigraphic distribution of the four genera is summarized in figure 45. From the latter figure these genera appear to be more or less consecutive in time. Only part of the range of *Planorbulinella* may overlap that of *Planolinderina*.

The evolutionary pattern in the four genera appears to be roughly the same. In the course of time there is a decrease in the number of chambers of the initial spiral, which trend is combined with a size increase in the early chambers. From the data presented it is plausible to assume that the reduction in the initial spiral is the most important trend in the early part of each evolving lineage, whereas the size increase in the first chambers becomes more prominent in their later parts. This assumption is mainly based on the hyperbole-like distribution of the populations of the *Planorbulinella larvata*-lineage in the $\bar{Y}/d1.2$ scatter diagram of fig. 44.

The highest level of evolution known to exist in specimens of these four genera is the protoconch-deuteroconch- two principal auxiliary chambers arrangement of the early chambers. Apparently the populations did not acquire additional "evolutionary possibilities" like lateral chambers, and/or additional auxiliary chambers. In this respect they differ from the other larger orbitoidal foraminifera, in which these features enabled them to develop much farther.

The four genera such as presented in this paper can be distinguished on the basis of the following features: (1) the shape of the test, (2) the lateral wall, (3) the aperture, (4) the size of the early chambers, (5) the wall of the early cham-

					RECENT
					PLIOCENE
					MIOCENE
					OLIGOCENE
					EOCENE
					PALEOCENE
					L.CRETACEOUS
HELLENOCYCLINA	LINDERINA	AQUITAINE BASIN PLANA INAEQUILATERALIS	LARVATA LINEAGE ZELANDICA TRINITATENSIS	GENUS OR SPECIES	AGE
		PLANOLINDERINA	PLANORBULINELLA		

Fig. 45. Time stratigraphic distribution of *Hellenocyclina*, *Linderina*, *Planolinderina* and *Planorbulinella*.

bers, (6) the relapse to the one-aperture stage, and (7) the wall structure. In the following table the numbers refer to the features mentioned.

<i>Hellenocyclina</i>	<i>Planorbulinella</i>	<i>Linderina</i>	<i>Planolinderina</i>
1. conical-flat	flat	biconvex	flat
2. thickened	unthickened	thickened	unthickened
3. simple	simple	multiple	multiple
4. small	moderate-large	moderate-large	moderate
5. generally thickened			generally unthickened
6. present	present	absent	absent
7. bilamellid	bilamellid	monolamellid	monolamellid

As to their external shape *Linderina* and *Hellenocyclina* on the one hand, and *Planorbulinella* and *Planolinderina* on the other hand resemble each other very closely. On the basis of the apertural characteristics and the internal features, however, *Linderina* resembles *Planolinderina*, and *Hellenocyclina* resembles *Planorbulinella*. It is doubted whether these features are of sufficient weight to assume a mutual relationship between *Linderina* and *Planolinderina*, and between *Hellenocyclina* and *Planorbulinella*. For instance, multiple apertures occur in many completely unrelated orbitoidal foraminifera: *Halkyardia*, *Lepidocyclina* and *Orbitoides*. Multiple apertures may have been acquired in the course of evolution. It should be borne in mind that for the present nothing is known about the ancestral, trochoid foraminifera from which these four genera have evolved. Such a knowledge is considered to be obligatory for statements about generic relationships. Moreover, at least *Planorbulinella* and possibly *Planolinderina* as well are each polyphyletic. Both genera may have evolved several times during geologic history from the same ancestor, like for example *Heterostegina* originated from *Operculina*, but they may have evolved convergently from unrelated ancestors as well.

From these data it appears that previous statements in the literature about the taxonomic position of the genera involved (compare also fig. 3) can neither be accepted nor rejected. We have to admit that our present knowledge is still far too poor to justify any definite conclusion in this respect. If we keep these genera together with *Planorbulina*, which rather belongs to the Cibicididae, we get a very artificial, complex higher unit. For the present it is more useful to accept the following classification into families.

Family Hellenocyclinidae n.fam.

Genus *Hellenocyclina* (REICHEL), 1950.

Type species: *H. beotica* REICHEL. Additional species are: *H. visserae* (HOFKER) and *H. charentensis* n.sp. One of the latter two species may be a junior synonym

of the type species, the internal characteristics of which are still unknown. All species probably belong to a single evolutionary lineage.

Occurrence: *H. charentensis* is restricted to the (type) Campanian and *H. visserae* is restricted to the (type) Maastrichtian. The genus is not known to occur outside Europe.

Family Linderinidae n.fam.

Genus *Linderina* SCHLUMBERGER, 1893.

Type species: *L. brugesi* SCHLUMBERGER. Additional species are: *L. buranensis* NUTTALL & BRIGHTON (= *L. bibilensis* SILVESTRI = *L. nuttalli* SILVESTRI), *L. rajasthanensis* SINGH (= *L. kirtharensis* SINGH = *L. bikanerensis* SINGH = *L. koyalatensis* SINGH), *L. paronai* OSIMO and *L. floridensis* COLE. It is possible that the latter species is a junior synonym of *L. paronai*, but a definite conclusion cannot be made because the available material of *L. paronai* is too restricted and because material of *L. floridensis* is not available. Furthermore one of the species listed may be a junior synonym of *L. brugesi*, the internal characteristics of which are completely unknown. The species may belong to a single evolutionary lineage, but the age assignments do not support this conclusion. A re-consideration of many age assignments of *Linderina* populations is necessary, as well as a re-study of the evolutionary development on the basis of long, closely sampled sections.

Occurrence: Lutetian?, (type) Marinesian, (type) Auversian; world wide.

Family Planolinderinidae n.fam.

Genus: *Planolinderina* n.gen.

Type species: *P. escornebovensis* n.sp. Additional species are: *P. inaequilateralis* (HERON-ALLEN & EARLAND) and *P. plana* (HERON-ALLEN & EARLAND). *P. escornebovensis* and *P. inaequilateralis* may belong to a single evolutionary lineage, but this assumption cannot be substantiated owing to the wide geographic distance of both species (Aquitaine Basin, France and Victoria, Australia respectively). *P. plana*, from Victoria and Borneo, may belong to a separate lineage. It is possible that this lineage is present in the Aquitaine Basin as well (Saint Etienne d'Orthe).

Occurrence: Chattian — Aquitanian, Burdigalian (?) of France, Australia and Indonesia.

Family Planorbulinellidae n.fam.

Genus: *Planorbulinella* CUSHMAN, 1927.

Type species: *P. larvata* (PARKER & JONES). Additional species are: *P. rokae* n.sp., *P. astriki* n.sp., *P. canaeae* n.sp., *P. zelandica* FINLAY and *P. trinitatensis* (NUTTALL). The latter two species may belong to separate evolutionary lineages,

which developed geographically far apart (in the New Zealand and Caribbean regions respectively), but at about the same time. The other four species belong to a single, younger lineage, the *larvata*-lineage, the Recent representatives of which are restricted to the Pacific and Indian Oceans.

Occurrence: Aquitanian ?, Burdigalian ?, Helvetian-Recent; world wide.

If the classification by REISS (1963) is adopted *Linderina* and *Planolinderina* have to be placed in the superfamily Monolamellidea and *Planorbulinella* and *Hellenocyclina* in the Bilamellidea. However, the present author does not agree with REISS in considering the "difference" between both superfamilies of taxonomic importance. Here the so-called dark internal line is considered to correspond to the original chitinous chamber wall. This original wall may be covered by lime at the outside, but also at the inside of the chambers. In the second case the wall will seem to be double (bilamellid), in the first case it suggests to have been built of a single layer only. This assumption is substantiated by the internal structure of several *P. larvata* specimens, in which the chitinous chamber walls are still clearly present in the early chambers. In these specimens the wall of the early chambers is "monolamellid", that of the later chambers "bilamellid".

Some remarks on the ecology of the four genera treated can be made. The Recent *P. larvata* is generally recorded from shallow water deposits of tropical or subtropical seas, for example in coral sands and reefs. The depth at which this species occurs according to the literature is very variable. BRADY (1884) reports it from about 10—420 m depth. It is reported from 36 and 100 m depth by CUSHMAN (1924). HOFKER (1927) reports specimens from 16—118 m depth. According to GRAHAM & MILITANTE (1959) the species is common at depths between 20 and 25 m, and rare at shallower depth. The common occurrences are reported from fore reef material and from a mid-channel between reefs. SAID (1949) records the species to be common in the coral reef areas of the Red Sea. In that region its depth range is said to be from 92—941 m. TODD (1965) mentions this species from two stations with a depth of about 35 and 40 m.

Most authors appear to give similar data on the environmental position of this species: shallow water in the vicinity of coral reefs. Records from greater depths probably apply to specimens washed downward.

In comparison with the environment in which the Recent *P. larvata* is living, that of the Cretan populations of the *larvata*-lineage is different. In most of the samples studied *Planorbulinella* is accompanied by a plankton-dominated fauna, which reflects an open water, off-shore environment. So, it is probable that the ancestors of *P. larvata* lived under different environmental conditions. It is unlikely that the Cretan populations have been displaced. For example,

in clays of the Cretan Kissamou Formation, in which *Planorbulinella* is very common, many graded beds are intercalated. They contain coarse shallow water material. However, in these graded beds *Planorbulinella* was not observed.

The faunas which accompany *P. zelandica* and *P. trinitatis* again reflect a shallow water, environment, as indicated, by the association with gypsinids, miogypsinids, heterosteginids and lepidocyclinids.

For *Planolinderina* in the Aquitaine Basin the data on the environment largely resemble those of *Planorbulinella*. The most primitive planolinderinids (from Escorneb eu) occur in clays which may reflect an off-shore sedimentation (according to BUTT, 1966). Interbedded layers with miogypsinids and lepidocyclinids, which may be slipped-off masses of unconsolidated barrier material, do not contain planolinderinids. However, more highly evolved *Planolinderina* populations from the Aquitaine Basin are always found in association with larger foraminifera, mainly *Miogypsina*.

The Pacific *Planolinderina* are accompanied either by associations of bryozoa, *Amphistegina* and planktonic foraminifera, or by faunas which contain bryozoa, *Rotalia* and few planktonics. In the Borneo sample also *Cycloclypeus* was found.

The data available on the ecology of *Linderina* indicate roughly a similar environment for all the populations studied. The linderinids are always accompanied by larger foraminifera, mainly *Nummulites*. This genus points to a shallow water environment.

The data on the ecology of *Hellenocyclina* are nearly identical with those on *Linderina*. In all samples larger foraminifera occur frequently, mainly *Orbitoides*. Planktonic foraminifera are absent or nearly completely so.

Summarizing these data on the ecology of the four genera it may be concluded that they are (or were) generally living in shallow water environments. However, for the older part of some of the lineages we get the impression that their representatives were living in a quieter, deeper environment. From these results there is a similarity with the assumed evolutionary development of *Orbitoides*, which genus should originate from the off-shore, planktonic *Planoglobulina* (according to VAN HINTE, 1965 b).

Chapter IV

THE GENUS *HETEROSTEGINA* IN THE NEOGENE OF EUROPE

IV.1. Introduction, literature.

From 1954 onward several authors have paid considerable attention to the evolution of Neogene heterosteginids. PAPP & KÜPPER (1954) started these studies in describing the morphology and evolutionary history of European Neogene heterosteginids. Their method of study and their most important results are summarized below

"All the morphological features that could be observed were taken into consideration. Two different processes, however, were necessary:

a. Determination of shape and ornamentation of the surface of at least 40—50 specimens.

b. Study of median sections, at least 15—20 in every population. The combination of both processes results in a definition of the morphogenetic stage of development of each population".

The general evolutionary trend, recognized by PAPP & KÜPPER (1954) and by PAPP (1963), has been summarized by TJALSMA (1966):

"The group of *Heterostegina* is thought to have developed from *Operculina complanata* (DEFRANCE). During phylogeny there is a trend towards an increased subdivision of the elongate chambers. Per individual secondary septa increase in number and length during ontogeny, and furthermore, there is a similar increase per chamber from the periphery inwards. Another trend consists of a shifting of the beginning development of the secondary septa towards earlier ontogenetic stages. These trends are primarily based on macrospheric specimens".

Contrary to these internal characteristics, there is no clear evolutionary change in the ornamentation. As to the general evolutionary trends some additional remarks have been made by HOTTINGER (1966). In addition to the length increase of the secondary septa there should be a size increase in the adult test and a slight increase in the relative height of the whorls. The size increase in the protoconch is not considered to be an important evolutionary trend. Moreover, the ornamentation is considered to be neither of stratigraphic nor of taxonomic value.

According to PAPP & KÜPPER (1954) and PAPP (1963) several species groups

can be distinguished amongst the Neogene heterosteginids. The distinction between these groups is not made very clear.

1. Evolute heterosteginids.

1a. The *costata*-group, known from the "Aquitainian" of the Aquitaine Basin (Saint Paul-les-Dax) to the "Tortonian" of the Vienna Basin. This species group occurs mainly in Central Europe. Its evolution is the best known.

1b. The *complanata*-group, known from the Mediterranean Tortonian and/or Pliocene. The representatives of this group are regarded as a substitute of the *costata*-group in the Mediterranean area, although it is probable that they are younger and phylogenetically related.

1c. The *granulatesta*-group, known from the "Helvetian" of the Aquitaine Basin (Orthez) and from the "Tortonian" of the Vienna Basin. The species of this group are "characterized by their special shape of the test and their granulate ornamentation". They are contemporaneous with at least part of the *costata*-group.

2. Involute heterosteginids.

This group comprises only *H. involutiformis* PAPP & KÜPPER, which is known from the Burdigalian of the Aquitaine Basin (Saucats).

HOTTINGER (1966) recognized the same species groups in the Neogene of Morocco, but the *granulatesta*-group is not known from that region. In Morocco similar evolutionary trends are found. However, from HOTTINGER's data the *complanata*-group appears to be contemporaneous with the *costata*-group. This is in sharp contrast to the stratigraphic distribution and supposed phylogenetic relationship of both groups given by PAPP & KÜPPER (1954) and PAPP (1963). The characteristics which enable HOTTINGER to distinguish the representatives of both groups are quoted below:

The species group of *H. costata* "est caractérisé par leur mégalosphère relativement petite et leur type de spire particulière, relativement serrée. L'insertion des septa secondaires ainsi que l'allure et l'espacement des septa primaires sont toujours remarquablement irréguliers".

According to the same author the species of the *H. complanata*-group "possèdent une mégalosphère plus grande, une spire moins enroulée et un bâti plus régulier et plus grossier que l'on en observe dans le group voisin. Le nombre des septa secondaires dans une loge d'un stade ontogénétique donné est toujours plus élevé par rapport à celui d'une forme du même âge du groupe *costata*".

WISSINK (1956) recognized representatives of the *costata*-group (sensu PAPP & KÜPPER) in the Miocene of Angola. He presented some details on measured

characteristics, for instance the size of the protoconch, the diameter of the second and third whorl, and the number of chambers in the second and third whorl.

Neither PAPP & KÜPPER, nor PAPP, nor HOTTINGER give detailed information about measurable features, although from their account on the evolutionary trends in heterosteginids it is clear that at least part of these evolutionary changes can be expressed numerically. PAPP & KÜPPER (1954) only give the "predominant number of smooth (operculine) septa in the species group of *H. costata* s.l." at various stratigraphic levels.

In this study it was tried to give an outline of the evolution in European Neogene *Heterostegina*, based on measurements and counts of characteristics thought to change in the course of evolution.

IV.2. Method of study, counts and measurements.

In studying the heterosteginids no special attention was paid to the shape of the test and its ornamentation. These outside features have been used by PAPP & KÜPPER (1954) and by PAPP (1963) to distinguish species and species groups, but their usefulness for stratigraphy and taxonomy has been rejected by HOTTINGER (1966). In this respect we fully agree with HOTTINGER. In the Cretan Neogene deposits for example, the outer appearance of the heterosteginids appears to be correlated with the type of sediment in which they occur. In limestones and sandy limestones the individuals have thick walls that are nearly smooth or only very slightly ornamented with small knobs. In coarse- to medium-grained sands and sandstones the ornamentation becomes more pronounced; most individuals have a more or less granulate test. In clays and sandy clays the ornamentation becomes even stronger, but the walls are thinnest. These data clearly point to an environmental influence on the ornamentation of heterosteginids. To avoid these apparent environmental influences, only the internal features were studied. It was tried to study at least 15—20 median sections of macrospheric specimens of each sample. Microspheric specimens occur, but they are very rare (ratio macrospheric/microspheric is about 250/1).

The following features were measured or counted (compare fig. 46):

d1. The diameter of the protoconch, measured along a line perpendicular to the line connecting the imaginary midpoints of the protoconch and deuteroconch. The measurements are expressed in μ . They do not include the wall's thickness.

h1. The height of the first whorl, measured along a line through the imaginary midpoints of the protoconch and deuteroconch. This measurement is also expressed in μ and it does not comprise the thickness of the marginal cord.

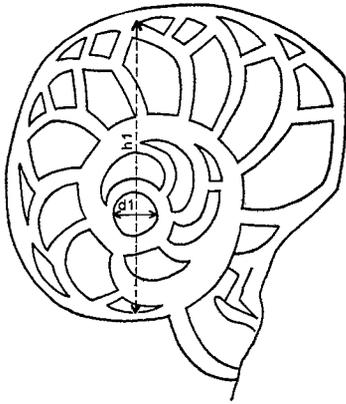


Fig. 46. The way of measuring the internal features of *Heterostegina*: $d1$ = diameter of the protoconch; $h1$ = height of the first whorl. In this example the number of operculine chambers (X) is 2, and the number of secondary septa in the 10th chamber (S_{10}) is 2.

X. The number of operculine chambers, starting to count with the protoconch.

Sn. The number of secondary septa (complete as well as incomplete) in the n -th chamber.

According to PAPP & KÜPPER (1954) the factor X might yield most reliable information about the level of evolution of heterosteginids. The factor $h1$ has been stressed by HOTTINGER (1966) as another feature changing in the course of evolution. The same author, however, does not consider $d1$ to be of importance in the evolutionary development. According to HOTTINGER (1966) $d1$, $h1$ and S_n may be useful for the distinguishing of the *complanata* and *costata* groups.

It has been observed by PAPP & KÜPPER (1954) that the length of the secondary septa increases in the course of evolution (compare also p. 141). In the older populations they are said to be incomplete or even hardly developed, in younger populations they should be fully developed and complete. We did not succeed in finding any suitable parameter for expressing the difference between complete and incomplete septa, and therefore we did not consider this feature. It is assumed, however, that disregarding this feature can hardly affect our final conclusions about the evolutionary history of the heterosteginids.

IV.3. Material.

Below we give a list of the samples investigated (all Utrecht collections):

JT 67, Croce Berton near Turin, Northern Italy. Type locality of *Heterostegina heterostegina heterostegina* (SILVESTRI), which species has been originally described as *Operculina complanata heterostegina* SILVESTRI (1907). Miogypsinids occurring in this sample have been referred to *Miogypsina globulina*

intermedia by DROOGER (1954). On the basis of the miogypsinids the age of this sample is considered to be Late Burdigalian.

Fr 12b, Pontpourquey, near the bridge over the Saint Jean-d'Etampes, Saucats, Aquitaine Basin, France. The miogypsinids of this sample have been determined as *Miogypsina intermedia* by DROOGER in DROOGER, KAASSCHIETER & KEIJ (1955). The age of this sample is considered to be Late Burdigalian.

Fr 16b, Cazenave, Aquitaine Basin, France. Age: Late Burdigalian.

Fr 17b, Saucats, Aquitaine Basin, France. The general name Saucats is given for the type locality of *Heterostegina involutiformis* PAPP & KÜPPER. Moreover, PAPP & KÜPPER (1954) described *H. heterostegina heterostegina* (SILVESTRI) from this locality. However, it is unlikely that our sample was taken at the same spot as that of PAPP & KÜPPER. The accompanying *Miogypsina globulina* (= *M. irregularis*) in our sample points to a Burdigalian age (see DROOGER in DROOGER, KAASSCHIETER & KEIJ, 1955).

Fr 31, Moulin de Lagus, Saucats, Aquitaine Basin, France. The same sample is referred to by DROOGER in DROOGER, KAASSCHIETER & KEIJ (1955). Its age is considered to be Middle Burdigalian.

Fr 474, 475, Sallespisse, Orthez, Aquitaine Basin, France. Both samples have been taken from the same stratigraphic level. Type locality of *Heterostegina granulatesta praeformis* PAPP & KÜPPER. The age of these samples is traditionally considered to be Helvetian (Sallomacian would be better).

The distribution of the genus *Heterostegina* in the Neogene of the Khania Province is summarized below. The heterosteginids are mainly restricted to two stratigraphic levels: the top of the Roka Formation and the base of the Akrotiri Formation. The latter level can probably be correlated with *Heterostegina* bearing beds at the top of the Khatzi and Koukounaras Formations. Moreover, *Heterostegina* occurs in graded beds intercalated in the Kissamou, Koukounaras and Khairitiana Formations. In the following list the investigated *Heterostegina* bearing samples were grouped corresponding to the formation from which they were taken.

1. Roka Formation

- M 106, organic limestone near Kamara Kissamou, exposure 82.
- M 114, medium-grained sand near Karthiana Kissamou, exposure 92.
- M 128, coarse sand near Kalami Kissamou, exposure 107A.
- M 300, organic, detritic limestone near Potamidha Kissamou, exposure 212.
- M 384, coarse sand near Roka Kissamou, exposure 254.
- M 396, coarse sand near Kato Palaiokastros Kissamou, exposure 274.
- M 404, sandy, organic limestone near Kastelli Kissamou, exposure 281.
- M 412, medium-grained sand, near Platanos Kissamou, exposure 285.

- M 463, organic, marly limestone near Gourlia Kissamou, exposure 322.
 M 474, marly, organic limestone near Afrata Kissamou, exposure 334.
 M 626, medium-grained sand near Nokhia Kissamou, exposure 80.
 M 648, medium-grained sand near Astrikos Kissamou, exposure 105.
 M 881, coarse sand near Koukounaras Kissamou, exposure 269.
 M 1187, coarse sand near Kalathainai Kissamou, exposure 377.
 M 1300, coarse sand near Khatzi Kissamou, exposure 55.
2. Kissamou Formation
- 2a. Graded intercalations in the Kissamou Formation
- M 402, graded, calcareous sandstone near Kastelli Kissamou, exposure 280.
 M 667, graded, indurated, calcareous sandstone (caprock) near Episkopi Kissamou, exposure 354.
 M 730, graded, calcareous sandstone near the byzantine church of Episkopi Kissamou, exposure 110.
- 2b. Non-graded, mainly calcareous intercalations in the Kissamou Formation.
- M 49, organic limestone near Stalos Kydonias, exposure 39 (top of the Kissamou Formation).
 M 471, organic, detritic limestone with abundant coral and bryozoa debris near Kamara Kissamou, exposure 329 (top of the Kissamou Formation).
 M 573, mixture of clay and algal balls in the hill Psathi near Stalos Kydonias, exposure 17 (top of the Kissamou Formation).
3. Koukounaras Formation (graded intercalations only)
- M 888, in the coarse base of a graded bed near Koukounaras Kissamou, exposure 269 (base of the Koukounaras Formation).
 M 469, calcareous sandstone near Voulgaro Kissamou, exposure 327.
4. Akrotiri Formation
- M 9, coarse-grained sand near the church of Ayios Kiriaki in the eastern outskirts of Khania, exposure 6. Type locality of *Heterostegina complanata spiralis* PAPP & KÜPPER.
 M 730, organic, detritic limestone near Mournies Kydonias, exposure 191.
5. Gavdos Formation
- G 487, organic, detritic limestone near Ambelos, exposure 337.
 G 502, coarse-grained sand near the Panayia church, Kastri, exposure 340.
- S 22.3, This sample has been taken by R. C. Tjalsma in the vicinity of Kouneni, S of Siteia, Lassithi Province, Crete. It was taken from

strata which in that area represent the base of the Neogene. It was included here only because the specimens it contains could easily be split horizontally by heating and subsequent cooling. In this case numerical data could be gathered on many more specimens than in the other Cretan samples, the individuals of which had to be sectioned.

IV.4. Results of the counts and measurements.

In nearly all Cretan specimens already the fourth chamber has secondary septa ($X = 3$). In a few individuals, however, the fourth chamber is still operculine ($X = 4$) and the fifth chamber is the first one to have secondary septa. Consequently the mean number of operculine chambers (\bar{X}) is 3.0 or very close to this value. It was not calculated for the individual Cretan samples. Moreover, the mean value of secondary septa in a definite chamber (S_n) was calculated for a few populations only, primarily because it appeared impossible to make reliable counts in most sectioned specimens.

Generally, for each factor are given the number of observations (N), the range of variation, and the mean value \pm the standard error of the mean (σ) for each population. Size parameters are expressed in μ .

sample	N	d1		h1		X	
		range	mean	range	mean	range	mean
JT 67	20	100—175	127 \pm 6	525—1062	752 \pm 31	12—32	23.2 \pm 1.2
Fr 17b	28	87—187	146 \pm 5	562—1175	912 \pm 30	9—20	13.1 \pm 0.5
Fr 31	19	125—219	167	737—1287	989	7—21	12.4
Fr 12b	26	87—162	115 \pm 4	525— 975	775 \pm 22	14—35	24.1 \pm 1.0
Fr 16b	22	94—150	118 \pm 3	587—1062	794 \pm 27	18—32	22.5 \pm 0.7
Fr 375	66 ¹⁾	50—137	92 \pm 2	300— 875	565 \pm 13	3—11	6.0 \pm 0.2
Fr 374	38 ²⁾	62—125	91 \pm 2	287— 725	533 \pm 15	3—13	6.3 \pm 0.3

¹⁾ h1 measurements were made on 64 specimens. X counts were made on 63 specimens.

²⁾ h1 applies to 37 specimens.

Cretan samples					
sample	N	d1		h1	
		range	mean	range	mean
M 106	18	114—190	156 ± 4	660—1143	933 ± 30
M 114	23	108—279	158 ± 7	673—1524	927 ± 37
M 128	16; 15 ¹⁾	102—190	145 ± 7	584— 965	785 ± 36
M 300	20	127—190	154 ± 4	762—1270	938 ± 29
M 384	21; 20	102—190	143 ± 5	508—1270	874 ± 34
M 396	24	108—241	167 ± 7	571—1257	912 ± 40
M 404	20; 19	114—190	147 ± 5	673—1016	858 ± 22
M 412	24	76—216	165 ± 8	432—1232	905 ± 44
M 463	26	114—190	161 ± 4	597—1143	913 ± 27
M 474	21	102—178	149 ± 5	635—1245	905 ± 31
M 626	22; 21	89—229	141 ± 7	597—1448	864 ± 42
M 648	16; 15	102—203	143 ± 7	571—1041	848 ± 39
M 881	18; 17	102—229	167 ± 8	762—1397	1013 ± 50
M 1187	16; 15	89—190	144 ± 9	444—1270	900 ± 60
M 1300	20; 18	121—229	166 ± 7	800—1397	1017 ± 36
M 402	22; 20	165—317	211 ± 7	825—1549	1142 ± 50
M 667	19	102—254	191 ± 8	610 1397	1100 ± 43
M 730	20; 17	138—292	201 ± 8	737—1575	1144 ± 53
M 49	27; 26	138—254	204 ± 6	787—1549	1116 ± 41
M 471	23; 22	108—292	203 ± 9	610—1524	1065 ± 53
M 573	23	138—292	198 ± 7	914—1333	1129 ± 27
M 469	23; 22	82—241	171 ± 7	546—1232	1000 ± 33
M 888	19	63—190	152 ± 7	444—1333	904 ± 47
M 9		152—279	206	787—1778	1295
M 250	17	140—241	195 ± 8	762—1460	1079 ± 55
G 487	22	95—203	154 ± 6	610—1232	932 ± 35
G 502	15; 14	102—203	167 ± 8	737—1270	975 ± 49
S 22.3	58	100—225	161 ± 4	650—1375	1011 ± 23

¹⁾ If different, the first number applies to d1, and the second to h1.

sample	N	S 15		S 20		S 25	
		range	mean	range	mean	range	mean
S 22.3	38 ¹⁾	1—5	3.5 ± 0.2	3—9	5.6 ± 0.3	4—11	6.7 ± 0.4
Fr 374+375	56 ²⁾	1—4	2.1 ± 0.1	1—5	3.0 ± 0.2	2—9	5.4 ± 0.7
Fr 12b	22					0—7	1.7 ± 0.4
Fr 17b	18					0—8	4.8 ± 0.4

¹⁾ S 25 counts were made on 23 specimens only.

²⁾ S 20 counts were made on 29 specimens, and S 25 counts on 13 specimens.

If the samples are arranged according to their supposed stratigraphic order we find the following pattern in \bar{X} :

"Tortonian" of Crete	: 3.0 (or slightly more)
"Helvetian" of Sallespisse	: 6.0; 6.3
Late Burdigalian of Aquitaine Basin and Northern Italy:	24.1; 22.5; 23.2
Middle Burdigalian of Aquitaine Basin	: 13.1; 12.4

This pattern of \bar{X} is not in good accordance with the evolutionary hypothesis advanced by PAPP & KÜPPER. The anomalies in the Burdigalian populations are certainly not random, because the mutual differences between the Middle and Late Burdigalian populations are statistically highly significant (compare the standard errors of the means).

The relationship between d_1 and X is illustrated for several populations in the scatter diagrams of figs. 47 and 48. For all samples involved the correlation coefficients of both parameters were calculated. They are:

sample	N	r
Sallespisse (Fr 374 + 375)	101	-0.5831
Saucats (Fr 17b)	28	-0.1751
Moulin de Lagus (Fr 31)	19	-0.3714
Pontpourquey (Fr 12b)	26	-0.1054
Cazenave (Fr 16b)	22	-0.5064

These values indicate that, at a probability level of 99.9 %, there is only a significant, negative correlation between the X and d_1 of the specimens of the population Fr 374 + 375. The probability that a negative correlation between both parameters exists is only 99.0 % for the specimens of Fr 16b, 90.0 % for those of Fr 31, and even less for those of Fr 17b and Fr 12b.

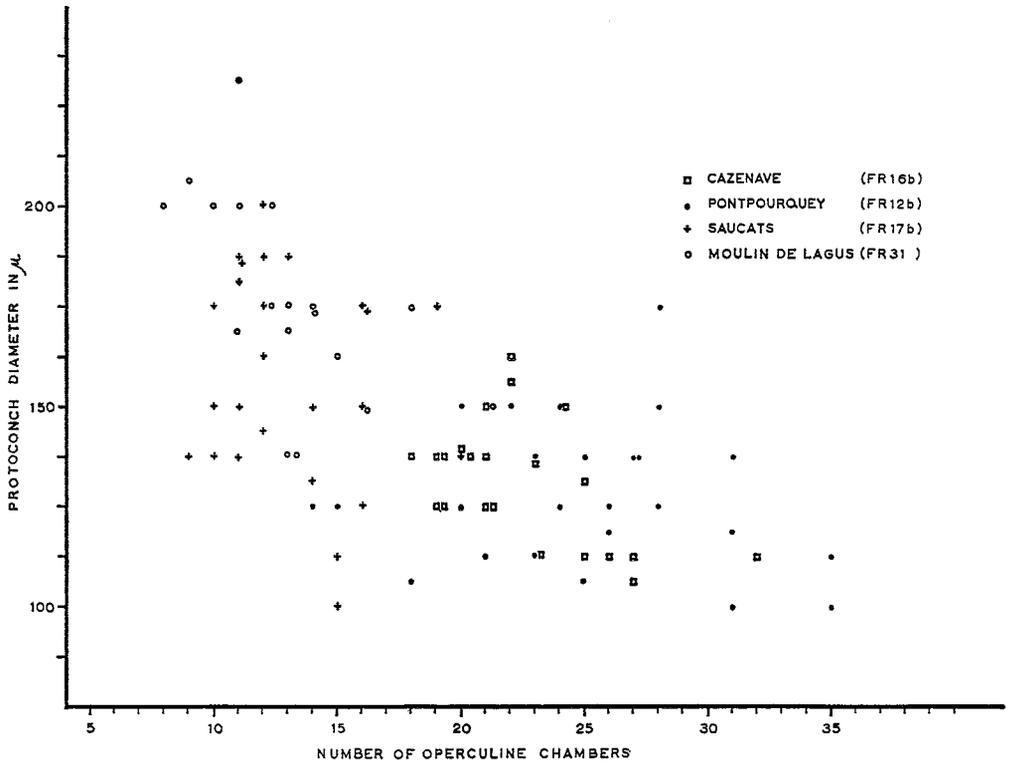


Fig. 47. $d1/X$ scatter diagram of *Heterostegina* individuals of four Burdigalian populations from the Aquitaine Basin, France.

In fig. 48 the size distribution of the protoconch of individuals from Sallespisse (Fr 374 + 375) is also illustrated by a histogram (classes of 12.5μ). This histogram is clearly unimodal. Although this $d1$ distribution is not figured for other populations, it is unimodal in all of them.

The relationship between $d1$ and $h1$ is shown in the scatter diagrams of figs. 49 and 50. In these diagrams are plotted the observations on specimens of the populations Fr 374 + 375 and S 22.3 respectively. From these figures a positive correlation between both parameters is evident. Calculation of the corresponding correlation coefficients yields:

sample	N	r
Fr 374 + 375	101	+0.8133
S 22.3	58	+0.8064

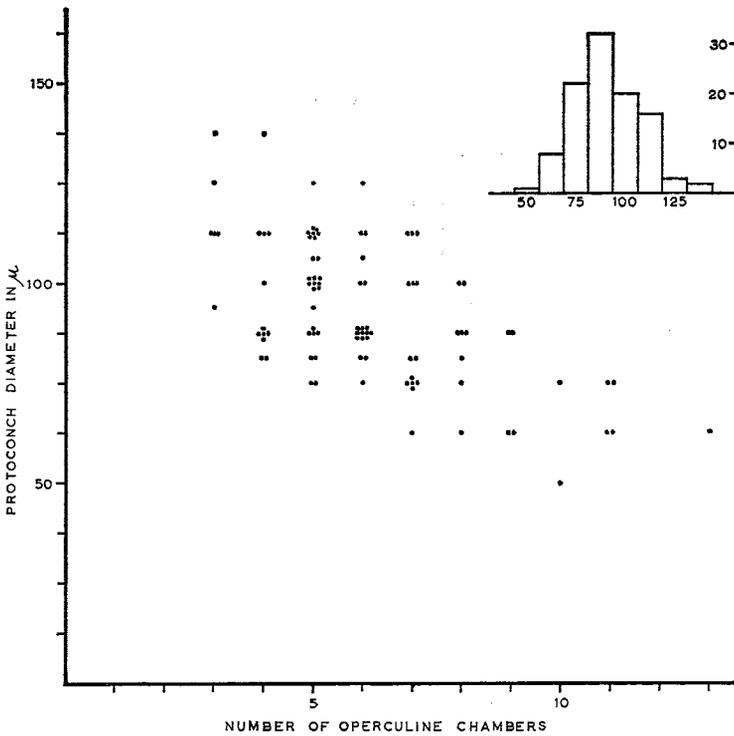


Fig. 48. $d1/X$ scatter diagram of *Heterostegina* specimens from Orthez (sample Fr 374 + 375), Aquitaine Basin, France. The histogram in the upper right angle shows the size distribution of the protoconch.

Both r values indicate that there is a significant positive correlation between both parameters at a probability level of 99.9 %.

For both populations the size distribution of the height of the first whorl is illustrated by histograms (figs. 49 and 50). In both examples, as well as in the other populations investigated, this distribution is unimodal.

The relationship between $\bar{d1}$ and $\bar{h1}$ of all populations studied is shown in fig. 51. Also in this case a positive correlation is evident. Calculation of the correlation coefficient yields: $r = +0.9541$ ($N = 35$). This value indicates that there is a significant positive correlation between both parameters, at a probability level of 99.9 %.

Data on the number of secondary septa in the 15th, 20th and 25th chamber are given for a few populations only (p. 149). If these populations are arranged according to their supposed stratigraphic order we get the following pattern for S 25:

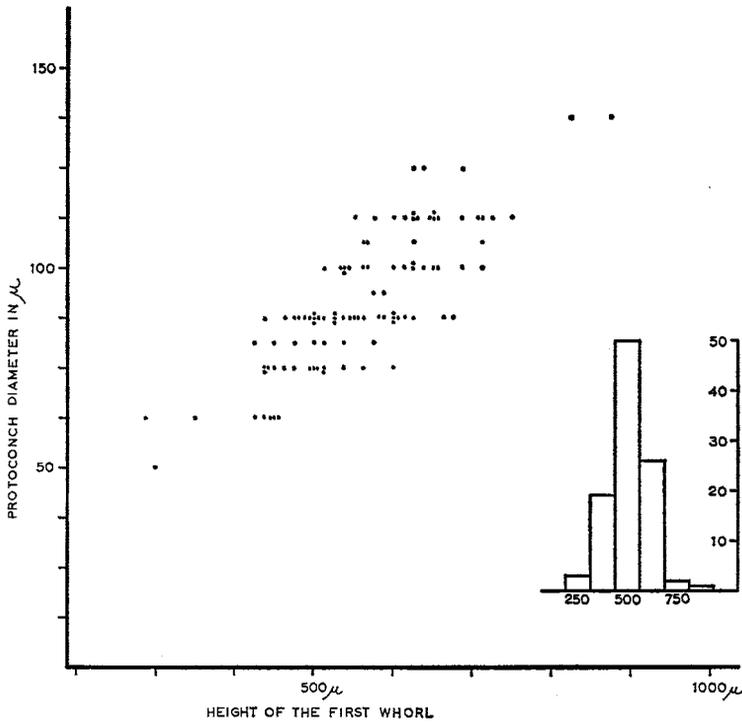


Fig. 49. d_1/h_1 scatter diagram of *Heterostegina* specimens from Orthez (sample Fr 374 + 375), Aquitaine Basin. The histogram in the lower right angle shows the size distribution of the height of the first whorl.

sample	$\overline{S\ 25}$
S 22.3 („Tortonian“)	6.7
Fr 374 + 375 („Helvetian“)	5.4
Fr 12b (Late Burdigalian)	1.7
Fr 17b (Middle Burdigalian)	4.8

These results are not in good accordance with the evolutionary changes postulated by PAPP & KÜPPER (1954) (compare p. 141, summary compiled by TjALSMA). Again, similar to the "trend" of reduction in the number of operculine chambers during phylogeny, the position of the Late Burdigalian population is anomalous with respect to the others. The anomalous low number of secondary septa relates to the fact that in many individuals the 25th chamber is still operculine ($\bar{X} = 24.1$) and the S 25 is zero consequently.

The relationship between S_n and d_1 was studied for all four populations. For

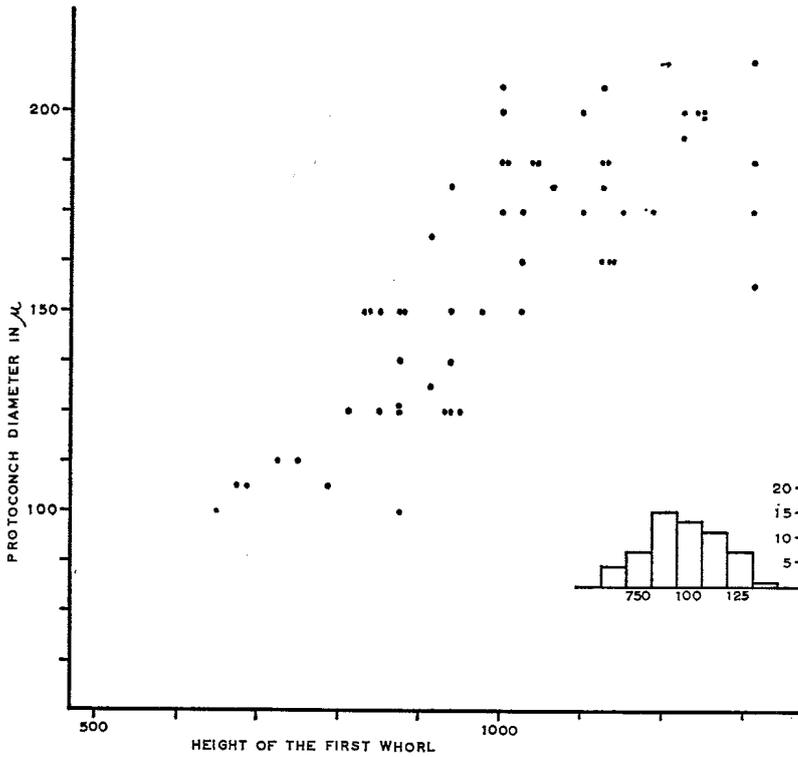


Fig. 50. $d1/b1$ scatter diagram of *Heterostegina* specimens from Kouneni, Crete (sample S 22.3). The histogram in the lower right angle shows the size distribution of the height of the first whorl.

certain $d1$ intervals partial $\overline{S_n}$ values were calculated. They are given in the following tables. It must be stressed that the numbers of specimens on which these

$d1$ ¹⁾	sample Fr 12b		sample Fr 17b	
	N	$\overline{S_{25}}$	N	$\overline{S_{25}}$
87.5	3	1.5	—	—
100.0	5	1.2	—	—
112.5	5	1.3	—	—
125.0	5	1.4	5	4.8
137.5	3	4.0	2	3.0
150.0	—	—	3	5.2
162.5	1	1.0	6	4.8
175.0	—	—	1	6.5
187.5	—	—	1	6.0

¹⁾ Protoconchal size given by the midpoints of the intervals μ .

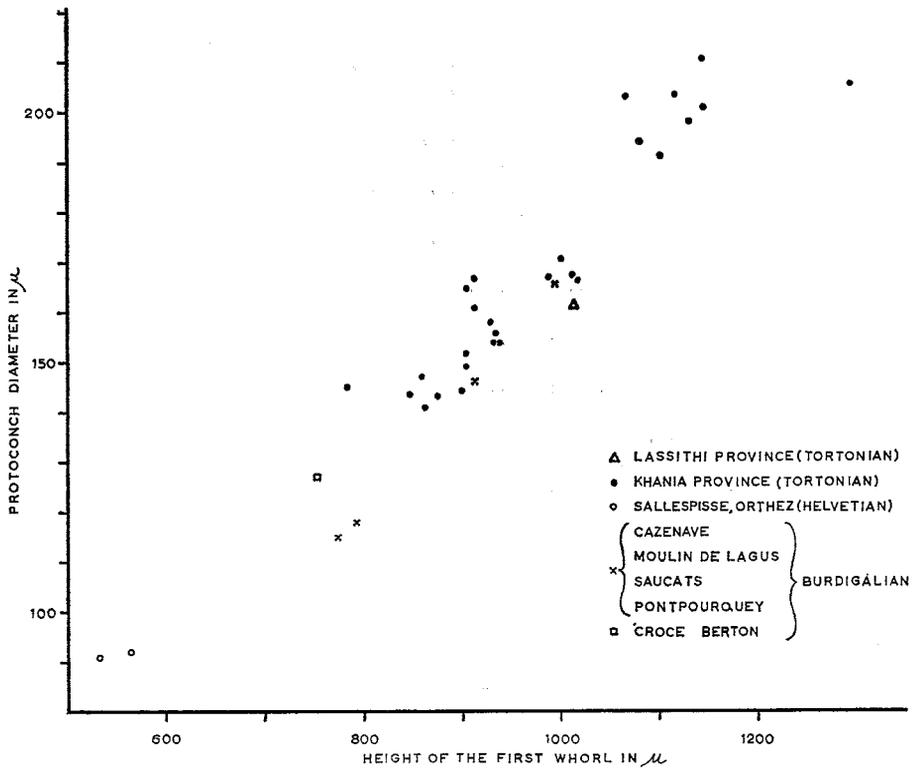


Fig. 51. $\overline{d1/h1}$ scatter diagram of several European *Heterostegina* populations. The cross gives average values of $\pm 3\sigma$.

$\overline{S_n}$ values are based generally are very low. As a consequence the significance of the individual partial $\overline{S_n}$ values is small.

Sample Fr 374 + 375, Sallespisse, Orthez, Aquitaine Basin.

$d1^1)$	N	$\overline{S_{15}}$	N	$\overline{S_{20}}$	N	$\overline{S_{25}}$
50.0	1	1.0	1	1.0	1	2.0
62.5	5	1.4	4	2.7	3	5.3
75.0	14	1.9	10	2.8	4	5.6
87.5	16	1.7	7	3.0	2	4.5
100.0	10	2.5	5	3.6	2	6.0
112.5	9	3.0	2	4.0	1	9.0
125.0	1	4.0	—	—	—	—

¹⁾ Protoconchal size given by the midpoints of the intervals/ μ .

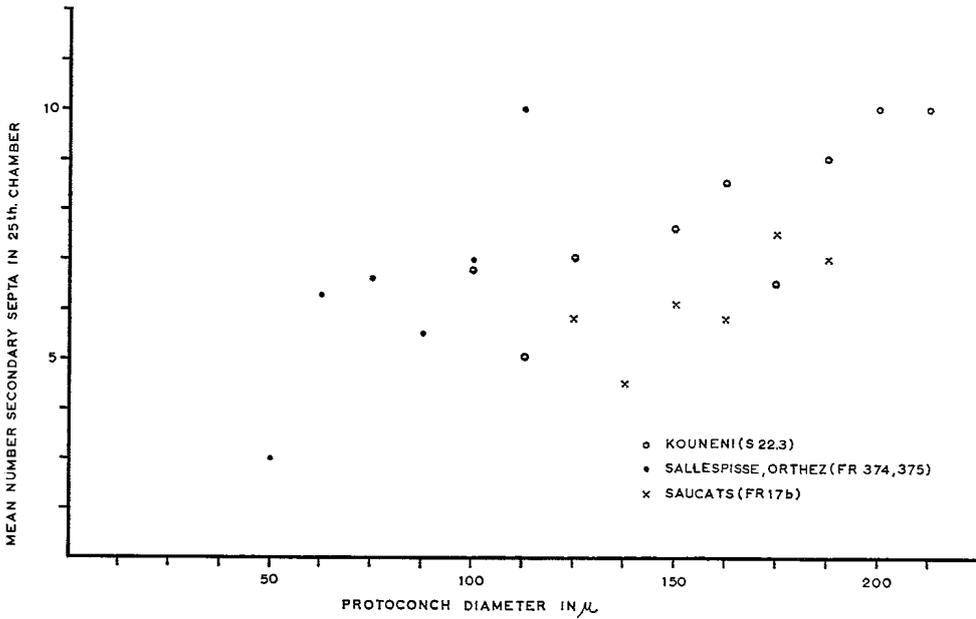


Fig. 52. Scatter diagram of $\overline{S 25}$ for successive $d1$ intervals of 12.5μ for three *Heterostegina* populations from Saucats, Sallespisse (Orthez) and Kouneni (Crete).

Sample S 22.3, Kouneni, Lassithi Province, Crete.

$d1^1)$	N	$\overline{S 15}$	N	$\overline{S 20}$	N	$\overline{S 25}$
100.0	4	2.0	4	5.2	5	5.8
112.5	1	3.0	5	4.0	1	4.0
125.0	6	3.1	—	—	4	6.0
137.5	1	4.0	4	5.2	—	—
150.0	5	3.4	1	5.0	4	6.6
162.5	3	3.8	5	4.4	2	7.5
175.0	7	4.2	5	5.6	2	5.5
187.5	5	4.2	5	7.0	1	8.0
200.0	4	3.0	6	6.7	3	9.0
212.5	1	4.0	1	7.0	1	9.0
225.0	1	4.0	1	9.0	—	—

¹⁾ Protoconchal size given by the midpoints of the intervals/ μ

From the data in the tables and figs. 52 and 53 it is reasonable to assume that within a single population at ontogenetically comparable stages individuals with larger initial chambers tend to have more secondary septa than individuals with smaller early chambers. Moreover, the number of secondary septa per chamber increases during ontogeny. The coefficient of correlation between the number

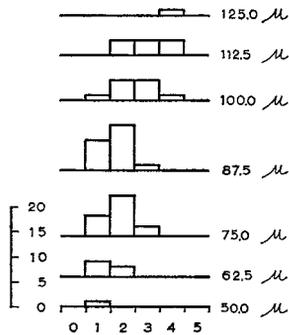


Fig. 53. Histograms of the number of septa in the 15th chamber for several d_1 classes (12.5μ) given by their midpoints, in the *Heterostegina* populations of sample Fr 374 + 375 from Sallespisse (Orthez), Aquitaine Basin, France.

of secondary septa in the 25th chamber and the size of the protoconch was calculated for four populations. The r values we give below:

sample	N	r
S 22.3	23	+0.6707
Fr 374 + 375	18	+0.4118
Fr 12b	22	+0.1388
Fr 17b	18	+0.1959

The r value of S 22.3 indicates that there is a positive correlation between both parameters at a probability level of 99.9%. For Fr 374 + 375 the probability that such a correlation exists is only 95%, and for the other populations this probability is less than 90%. These results resemble the data on the correlation between d_1 and X (compare also p. 149).

IV.5. Discussion of the counts and measurements, phylogeny.

Within single populations the size of the protoconch and the height of the first whorl were shown to be positively correlated. This means that individuals with small early chambers will have a relatively low spiral, and those with big initial chambers a relatively high one. Moreover, it was shown that within the populations studied the size distributions of the protoconch and those of the height of the first whorl are unimodal. This is not only true for the populations for which this feature is illustrated by means of histograms, but for *all* populations investigated. From these unimodal distributions it is concluded that they do not justify the distinguishing of more than one species within single populations.

The data presented on the relationship between the number of operculine chambers and the diameter of the protoconch are not fully conclusive. In some populations there is a distinct negative correlation between both parameters, whereas the probability that such a correlation exists in other populations is rather low. The same is true for the relationship between the number of secondary septa in a definite chamber and the size of the protoconch. In some populations it can be safely assumed that both parameters are positively correlated, whereas in others such a relation cannot be demonstrated. However, the possibility that the low significances of some correlation coefficients are the result of too low numbers of observations cannot be precluded.

If the \bar{X} and $\bar{d1}$ values of the Burdigalian populations are considered, there seems to exist a relationship between them (p. 147). A lower $\bar{d1}$ appears to correspond to higher \bar{X} values, and reversed. Although it cannot be proved on the basis of these few populations, that such a (negative) correlation really exists, it is assumed to be present. Such a correlation would explain the anomalous \bar{X} of the French and Italian Late Burdigalian populations with respect to the Middle Burdigalian ones, assuming the effect of influences on $\bar{d1}$ independent of a general evolution pattern. Evidently, mere \bar{X} values cannot be reliably applied to decisions on the age of randomly chosen populations.

The "Helvetian" and "Tortonian" populations do not show an anomalous \bar{X} (on the basis of the trend recognized by PAPP & KÜPPER), neither with respect to each other, nor with respect to the Burdigalian ones. Hence, there is no reason to believe that more than one group or lineage of Neogene *Heterostegina* is involved in our material. Our data do not allow to put the Burdigalian, "Helvetian" and "Tortonian" populations in separate lineages, as has been done by PAPP & KÜPPER and PAPP: *costata*-, *granulatesta*- and *complanata*-group.

It may be doubted whether the *granulatesta*-group can be statistically distinguished from the *costata*-group in the deposits of the Vienna Basin, in which they are said to occur together (PAPP & KÜPPER, and PAPP). For example, the figures of representatives of both groups derived from the same locality (Rauchstallbrunnen near Baden) given by PAPP & KÜPPER (1954, pl. 22, figs. 1, 2 and text plate 3, figs. 9, 10) hardly show any difference, apart from the more or less completeness of the secondary septa.

Already PAPP & KÜPPER (1954) suggest that the Mediterranean *complanata*-group might comprise descendants of the *costata*-group. This conclusion seems to be justified, since the Mediterranean (Cretan) heterosteginids have probably a lower \bar{X} (about 3.0) than the stratigraphically uppermost ones of the Vienna Basin (compare PAPP & KÜPPER, 1954, textplate 3, fig. 13: $X = 5$, fig. 14: $X = 6$, fig. 15: $X = 4$, fig. 16: $X = 4$). In our way of reasoning only one evolving group of heterosteginids exists in the European Neogene.

In this respect it is of interest to analyze the features which made HOTTINGER (1966) distinguish the *costata*- and *complanata*-group at the same stratigraphic level (see p. 142). The *costata*-group is said to be characterized by a small protoconch and relatively low spiral, the *complanata*-group by a big protoconch and relatively higher spiral. If these features are compared with our data on the correlation between d_1 and h_1 , it seems plausible that HOTTINGER separated the extreme individuals of single populations into "different groups". However, the homogeneity of our populations as to the size distribution of both features (unimodal curves) indicates that such an approach is not sound from a biological point of view. According to the same author the number of secondary septa in a certain chamber is higher in the *complanata*-group than it is in the *costata*-group. Also the differentiating value of this feature can be retraced on the basis of our numerical data. It was found in several populations that there is a clear relationship between the number of secondary septa and the size of the protoconch. The bigger the protoconch, the higher the number of secondary septa in a certain chamber will be. It means also that extreme values of d_1 and h_1 will correspond to extreme values of S_n . These data perfectly agree with the findings of HOTTINGER, but it is clear that we would not use them to distinguish species groups or lineages. Therefore HOTTINGER's approach, though understood and of quite common micropaleontological practice, is not followed.

In analyzing the evolution of heterosteginids in the European Neogene on the basis of the data presented in this paper we arrive at the following conclusions:

1. Only one lineage can be recognized amongst the European Neogene heterosteginids.
2. There is a more or less distinct negative correlation between the number of operculine chambers (X) and the size of the protoconch (d_1).
3. There is a more or less distinct positive correlation between the size of the protoconch (d_1) and the number of secondary septa in a randomly chosen later chamber (S_n).
4. There is an overall decrease in the number of operculine chambers (\bar{X}) in the course of time. This trend may be obscured by random effects on the average size of the protoconch (\bar{d}_1), owing to the negative correlation between d_1 and X .
5. The best way of expressing the evolution in the European Neogene heterosteginids probably would be calculating partial \bar{X} (or S_n) values for a definite d_1 interval. This means that only \bar{X} values of populations with a same or nearly identical \bar{d}_1 value can be compared with one another. However, this restriction greatly diminishes the stratigraphical usefulness of the genus.

Chapter V

BIOSTRATIGRAPHY, CONCLUSIONS

V.1. Conclusions dealing with Crete.

It was shown that the evolution of *Planorbulinella* in the Mediterranean area took place during Tortonian time. Consequently we consider the *Planorbulinella* bearing strata of Crete to be of Tortonian age. They comprise mainly the Roka, Koukounaras, Kissamou Formations and in the Rethymnon Province the Apostoli Formation. Since the Roka Formation comprises the lowermost marine strata it is concluded that the marine sedimentation started in the Tortonian. As to the age of the underlying fresh water deposits no definite conclusion can be made.

The possibilities for correlating Neogene Formations in the Khandia and Rethymnon Provinces by means of *Planorbulinella* are rather restricted. On the basis of this genus only one level can clearly be recognized: it comprises the lower parts of the Koukounaras, Kissamou and Apostoli Formations, which all contain *P. astriki* n.sp. The stratigraphic interval in which this species occurs generally measures only a few meters of sediment.

P. rokae n.sp. occurs at one exposure only, in the Roka Formation, and therefore does not provide a basis for correlation. *P. canaeae* n.sp. occurs throughout the Kissamou and Apostoli Formation, except for their basal parts. Hence, it cannot be used for a finer biostratigraphic subdivision.

Outside Crete, but still within the Mediterranean area, there are several possibilities for correlation by means of *Planorbulinella*.

1. The Roka Formation may be about equivalent to the Upper Coralline Limestone of Malta.

2. The basal beds of the Koukounaras, Kissamou and Apostoli Formations can be correlated with the middle part of the type Tortonian.

From the above data it is clear that the genus *Planorbulinella* offers only restricted possibilities for correlation, but the situation is worse in the case of *Heterostegina*. Although two more or less clearly developed *Heterostegina* levels can be traced in the field, the populations they contain cannot be differentiated on the basis of the measured internal features. Generally, the stratigraphically higher level contains populations with a larger average size of the protoconch than the lower ones, but exceptions occur, though not frequently. As another handicap for correlation, *Heterostegina* does not occur in the type sections of the Mediterranean stages.

On the basis of the literature, one might conclude that the lowermost Cretan populations are more highly developed than those from the Vienna Basin (higher \bar{X}), but it is possible that this conclusion is wrong, owing to changes in \bar{X} which may be caused by random effects on d_1 .

Apart from few, scattered (reworked?) *Planorbulinella* specimens in the basal strata of the Khairitiana Formation, and *Heterostegina* specimens occurring in the base of the Akrotiri Formation, these genera are absent in the stratigraphically higher part of the Neogene succession, mainly comprising the Khairitiana, Tavronitis and Akrotiri Formations. Hence, these genera cannot be used for an age determination of the formations mentioned.

However, planktonic foraminifera, though not studied in detail and not described in this paper, provide some information on their age. The Tavronitis and Khairitiana Formations contain abundant planktonic foraminifera, especially some *Globorotalia* species, which also occur in the type Plaisancian and Tabianian deposits of Northern Italy. They indicate that at least part of both formations are of Pliocene age.

Consequently, we may assume that the Mio-Pliocene boundary will approximately coincide with the boundary of the Kissamou — Tavronitis/Khairitiana Formations. At some localities the basal strata of the Khairitiana Formation contain gypsum deposits, pointing to changes of environmental conditions, but at other localities the transitional strata are fully marine. They indicate that continuous, marine sedimentation existed on Crete from the Miocene to the Pliocene.

V.2. Biostratigraphic value of the lineages outside Crete.

The results of counts and measurements on internal features of the orbitoidal genera *Hellenocyclina*, *Linderina*, *Planolinderina* and *Planorbulinella* show that these genera evolved according to the principle of nepionic acceleration.

In the case of *Planolinderina* this evolution proved to be a rather complex one, thus limiting the stratigraphic usefulness of the genus. Nevertheless, the parallel development in *Planolinderina* and the accompanying *Miogypsina* is an important result. It confirms and stresses stratigraphic conclusions and correlations based on the nepionic development of *Miogypsina*.

For the present *Linderina* does not offer possibilities for correlations, primarily because its evolution is still very incompletely known. It should be investigated on long closely sampled sections. Furthermore, the interrelationships of many Middle and Upper Eocene stages are so obscure, that it may be doubted whether the ages assigned to our samples reflect their real stratigraphic order.

For the moment, *Hellenocyclina* and *Planorbulinella* seem to be more suitable for long distance correlations. The nepionic development of *Hellenocyclina* is parallel with that of *Orbitoides*. Hence, it stresses correlations and stratigraphic conclusions based on the latter genus. For example, the type deposits of the Campanian and Maastrichtian stages can be clearly differentiated on the basis of *Hellenocyclina*.

Of the four orbitoidal genera studied, the evolution in *Planorbulinella* is the best known, especially so for the *larvata* lineage. This lineage offers good possibilities for long distance correlations (Mediterranean - Pacific). Older *Planorbulinella* lineages (*trinitatensis*, *zelandica*) are still too incompletely known for reliable biostratigraphic correlation. However, it is assumed that they may become very useful, if studied in more detail. Especially the *trinitatensis* lineage may become useful in clarifying part of the Caribbean stratigraphy.

The results of our studies on *Heterostegina* are not encouraging. For the present we are inclined to doubt stratigraphic conclusions based on the meandering evolutionary path of the Mio-Pliocene representatives of this genus.

Appendix I

In the Appendix I—VIII we give the results of Y counts on Cretan *Planorbulinella* populations. N applies to the numbers of specimens involved in each population. The Y columns give the Y distribution within each population. The Y = 3 class is subdivided into the 3/4, 3/3, 3/2, 3/1 and 3/0 subclasses. Y = 3/4 includes also specimens with Y = 3/6 and 3/5. The \bar{Y} column gives the mean Y values \pm the corresponding standard errors (σ). Sample numbers in italics refer to the results of the Wilcoxon significance test (compare p. 69). u values for significantly different successive steps (if present) are given for each section.

Section Khairtiana

sample	Y											\bar{Y}	
	N	8	7	6	5	4	3	3/4	3/3	3/2	3/1		3/0
M 806	39	—	—	—	4	4	31	—	5	13	6	7	3.31 \pm 0.10
M 797	77	—	—	1	6	14	56	—	2	18	12	24	3.38 \pm 0.08
M 796	47	—	—	—	2	8	37	2	—	9	16	10	3.25 \pm 0.08
M 795	97	—	—	1	8	9	79	—	2	21	25	31	3.29 \pm 0.07
<i>M 794</i>	85	—	—	—	4	11	70	—	1	17	20	32	3.22 \pm 0.06
M 793	110	—	—	4	12	21	73	—	1	22	29	21	3.52 \pm 0.08
M 792	66	—	—	1	4	9	52	1	—	12	15	24	3.30 \pm 0.08
M 791	130	—	—	4	8	17	101	1	—	25	34	41	3.35 \pm 0.06
M 790	46	—	—	—	2	6	38	—	2	12	14	10	3.22 \pm 0.07
M 788	34	—	—	—	2	8	24	—	—	8	4	12	3.35 \pm 0.10
M 787	24	—	—	—	2	5	17	—	—	2	4	11	3.37 \pm 0.13
M 786	36	—	—	—	7	18	11	—	—	1	4	6	3.89 \pm 0.12
<i>M 785</i>	57	—	—	1	7	35	14	—	—	3	4	7	3.91 \pm 0.09
M 784	11	—	—	1	2	8	—	—	—	—	—	—	4.36 \pm 0.21
M 783	29	—	—	1	12	16	—	—	—	—	—	—	4.48 \pm 0.10
<i>M 782</i>	35	1	—	7	15	12	—	—	—	—	—	—	4.94 \pm 0.15

Significance test. M 782—785: u = 4.9902

M 785—794: u = 5.7265

Section Episkopi I

sample	N	Y									\bar{Y}
		8	7	6	5	4	3	3/2	3/1	3/0	
<i>M</i> 705	56	—	—	1	3	5	47	9	13	25	3.25 ± 0.08
<i>M</i> 703	27	—	—	—	2	12	13	2	5	6	3.59 ± 0.12
<i>M</i> 701	73	—	—	—	4	39	30	3	11	16	3.64 ± 0.07
<i>M</i> 700	78	—	—	—	12	36	30	4	17	9	3.77 ± 0.08
<i>M</i> 699	65	—	—	2	11	32	20	1	8	11	3.92 ± 0.09
<i>M</i> 698	80	1	—	1	12	34	32	7	13	12	3.82 ± 0.10
<i>M</i> 697	23	—	—	4	5	11	3	—	1	2	4.43 ± 0.19
<i>M</i> 696	40	—	3	1	17	18	1	—	1	—	4.67 ± 0.13

Significance test. *M* 696—698: $u = 4.6623$

M 698—705: $u = 4.1940$

Appendix II

Section Astrikos

sample	N	Y										\bar{Y}
		7	6	5	4	3	3/4	3/3	3/2	3/1	3/0	
M 746	38	—	1	6	7	24	—	2	7	11	4	3.58 ± 0.14
M 745	45	—	3	4	3	35	—	4	8	14	9	3.44 ± 0.13
M 744	48	—	1	8	6	33	2	—	8	11	12	3.52 ± 0.12
M 651	109	2	16	48	39	4	—	—	1	1	2	4.75 ± 0.08
M 650	67	1	9	31	25	1	—	—	—	—	1	4.76 ± 0.09
M 649	27	1	4	17	5	—	—	—	—	—	—	5.04 ± 0.13
M 645	50	—	8	33	9	—	—	—	—	—	—	4.98 ± 0.08
M 116	12	2	7	3	—	—	—	—	—	—	—	5.92 ± 0.20

Significance test. M 116—645: $u = 3.5367$ (M 116—649: $u = 3.0276$)
 M 651—744: $u = 6.5346$

Section Nokhia

sample	N	Y										\bar{Y}
		7	6	5	4	3	3/4	3/3	3/2	3/1	3/0	
M 641	57	—	—	4	5	48	—	1	12	20	15	3.23 ± 0.07
M 640	94	—	1	7	12	74	1	1	20	22	30	3.31 ± 0.07
M 638	52	—	—	6	21	25	—	—	4	10	11	3.63 ± 0.09
M 635	42	—	—	5	22	15	—	—	—	9	6	3.76 ± 0.10
M 634	94	1	3	11	62	17	—	—	5	8	4	4.03 ± 0.07
M 632	46	—	1	6	35	4	—	1	3	—	—	4.09 ± 0.08
M 631	44	—	2	8	30	4	—	—	—	3	1	4.18 ± 0.10
M 630	48	—	2	10	25	11	—	—	1	5	5	4.06 ± 0.11
M 629	73	—	2	16	46	9	—	—	2	4	3	4.15 ± 0.07
M 628	58	—	3	20	32	3	—	—	—	3	—	4.40 ± 0.09

Significance test. M 628—635: $u = 3.9109$

Appendix III

Section Selli

sample	N	Y									\bar{Y}
		6	5	4	3	3/4	3/3	3/2	3/1	3/0	
860— δ Z	10	—	—	—	10	—	—	1	2	7	3.00
860—Z	62	1	1	5	55	—	—	16	13	26	3.16 \pm 0.06
860—U	30	—	1	3	26	—	—	6	9	11	3.17 \pm 0.08
860—T	48	—	4	11	33	—	—	14	14	5	3.39 \pm 0.09
860—S	42	1	7	2	32	—	—	6	11	15	3.45 \pm 0.13
860—Q	26	1	2	3	20	1	—	7	5	7	3.38 \pm 0.15
860—P	29	—	5	8	16	—	—	5	6	5	3.62 \pm 0.14
860—K	25	—	2	6	17	—	—	4	5	8	3.40 \pm 0.13
860—J	35	1	2	7	25	1	1	11	6	6	3.40 \pm 0.12
860—G	40	1	8	15	16	—	1	9	3	3	3.58 \pm 0.13
860—F	44	2	12	21	9	1	—	2	3	3	4.16 \pm 0.12
860—D	23	5	6	12	—	—	—	—	—	—	4.69 \pm 0.17
860—C	20	6	9	4	1	—	—	—	—	1	5.00 \pm 0.20

Significance test. 860—C — G: $u = 4.4534$

Section Apostoli

sample	N	Y									\bar{Y}	
		7	6	5	4	3	3/4	3/3	3/2	3/1		3/0
814—V	19	—	—	2	3	14	—	—	2	8	4	3.37 \pm 0.16
814—U	12	—	—	1	1	10	—	—	3	3	4	3.25 \pm 0.19
814—S	14	—	—	—	2	12	—	—	3	8	1	3.14 \pm 0.10
814—R	11	—	—	—	1	10	—	—	4	4	2	3.09 \pm 0.09
814—Q	28	—	—	—	2	26	—	—	6	8	12	3.07 \pm 0.05
814—P	26	—	—	3	8	15	—	—	4	5	6	3.54 \pm 0.13
814—K	37	—	—	2	4	31	1	—	9	9	12	3.22 \pm 0.09
814—J	26	—	1	7	9	9	—	1	2	3	3	4.00 \pm 0.17
814—H	39	—	—	7	15	17	—	—	4	4	9	3.74 \pm 0.12
814—G	25	—	—	9	9	7	—	1	—	4	2	4.08 \pm 0.16
814—C	28	—	—	8	20	—	—	—	—	—	—	4.28 \pm 0.08
814—B	56	1	5	20	21	9	—	—	3	3	3	4.43 \pm 0.12

Significance test. 814—B — K: $u = 5.7967$

Appendix IV

Section Kastelli

sample	N	Y									\bar{Y}
		6	5	4	3	3/4	3/3	3/2	3/1	3/0	
M 916	15	1	1	3	10	—	1	4	3	2	3.53 ± 0.24
M 915	23	—	1	5	17	—	—	8	6	3	3.30 ± 0.11
M 914	15	—	1	5	9	—	1	2	4	2	3.46 ± 0.17
M 913	32	—	1	5	26	—	—	5	10	11	3.22 ± 0.08
M 912	21	—	2	3	16	—	—	5	4	7	3.33 ± 0.14
M 911	47	2	6	7	32	—	1	9	16	6	3.53 ± 0.13
M 910	37	1	3	2	31	1	—	7	7	16	3.30 ± 0.12
M 909	25	1	3	5	16	—	—	9	6	1	3.56 ± 0.17
M 906	37	—	6	3	28	—	2	7	9	10	3.40 ± 0.12
M 905	55	1	8	6	40	2	1	14	10	13	3.45 ± 0.11
M 904	31	—	2	2	27	—	—	6	12	9	3.19 ± 0.09
M 925	22	—	2	5	15	—	—	1	10	4	3.41 ± 0.14
M 926	14	—	—	3	11	—	—	2	6	3	3.21 ± 0.12
M 928	24	1	3	5	15	—	1	1	8	5	3.58 ± 0.17
M 929	21	—	3	5	13	—	—	6	3	4	3.52 ± 0.16

Section Koukounaras

sample	N	Y								\bar{Y}
		7	6	5	4	3	3/2	3/1	3/0	
M 893	13	1	1	4	7	—	—	—	—	4.69 ± 0.27
M 891	13	—	2	6	3	2	1	1	—	4.61 ± 0.28
M 887	38	—	2	19	16	1	—	—	1	4.58 ± 0.10
M 884	17	—	2	11	4	—	—	—	—	4.88 ± 0.15
M 883	15	—	1	10	4	—	—	—	—	4.80 ± 0.15
M 882	40	—	7	21	11	1	—	1	—	4.85 ± 0.11

Appendix V

Section Dheliana

sample	N	Y										\bar{Y}
		6	5	4	3	2	3/4	3/3	3/2	3/1	3/0	
M 774	108	—	15	31	62	—	—	1	12	18	31	3.56 ± 0.07
M 773	17	—	2	3	12	—	—	—	6	3	3	3.41 ± 0.18
M 772	88	3	5	14	66	—	—	—	22	16	28	3.37 ± 0.08
M 771	40	1	4	11	24	—	—	—	8	6	10	3.55 ± 0.12
M 770	104	1	12	9	82	—	2	1	20	33	26	3.34 ± 0.07
M 769	27	1	3	7	16	—	—	1	4	5	6	3.59 ± 0.15
M 768	112	6	21	14	71	—	—	4	32	16	19	3.66 ± 0.09
M 767	26	—	2	3	20	1	—	—	2	7	11	3.23 ± 0.12
M 766	18	—	1	3	14	—	—	—	4	5	5	3.28 ± 0.14
M 765	58	1	3	13	41	—	2	—	11	12	16	3.38 ± 0.09
M 764	38	—	2	8	28	—	—	1	4	7	16	3.31 ± 0.09
M 763	56	—	4	12	40	—	1	2	12	7	18	3.36 ± 0.08
M 761	71	2	1	24	44	—	—	—	7	10	27	3.45 ± 0.08
M 759	30	—	3	14	13	—	—	—	3	2	8	3.67 ± 0.12

Section Roka

sample	N	Y										\bar{Y}
		6	5	4	3	3/4	3/3	3/2	3/1	3/0		
M 1035	21	—	1	1	19	—	—	—	6	3	10	3.14 ± 0.10
M 1040	32	—	2	6	24	—	—	—	7	9	8	3.31 ± 0.10
M 1041	40	—	2	10	28	—	—	—	8	14	6	3.35 ± 0.09
M 1045	27	1	2	3	21	—	—	—	7	7	7	3.37 ± 0.15
M 1046	45	—	6	5	34	1	—	—	7	10	16	3.37 ± 0.10
M 1047	28	—	1	8	19	—	—	—	6	8	5	3.36 ± 0.10
M 1048	27	—	2	2	23	—	—	—	2	9	12	3.22 ± 0.11
M 1049	14	—	2	2	10	—	—	—	1	4	5	3.43 ± 0.21
M 1050	26	1	1	5	19	—	1	—	3	7	8	3.38 ± 0.14
M 1051	25	—	2	2	21	—	—	—	6	7	8	3.24 ± 0.12

Appendix VI

Section Potamidha

sample	N	Y										\bar{Y}
		6	5	4	3	2	3/4	3/3	3/2	3/1	3/0	
M 943	91	2	4	13	72	—	1	5	26	20	20	3.29 ± 0.07
M 944	56	—	6	8	42	—	3	4	16	11	8	3.36 ± 0.09
M 945	75	4	9	13	49	—	2	3	25	9	10	3.57 ± 0.10
M 946	44	—	—	10	34	—	—	1	15	7	11	3.23 ± 0.06
M 950	131	2	12	16	101	1	—	3	23	28	46	3.35 ± 0.06
M 1063	38	—	2	4	31	1	—	3	11	7	10	3.18 ± 0.09
M 1062	27	—	3	4	20	—	—	1	5	9	5	3.37 ± 0.12
M 1061	72	2	7	12	51	—	3	3	12	22	11	3.44 ± 0.09
M 1060	66	1	4	11	50	—	5	2	11	21	11	3.33 ± 0.08
M 1059	78	2	5	16	55	—	1	3	25	13	13	3.41 ± 0.08
M 1058	57	—	7	16	34	—	—	2	12	10	10	3.53 ± 0.09
M 1057	45	1	—	17	27	—	1	—	13	5	8	3.44 ± 0.09
M 1056	30	1	8	6	15	—	—	1	5	6	3	3.83 ± 0.17
M 1055	23	—	5	1	17	—	1	—	8	3	5	3.48 ± 0.17
M 955	92	—	16	10	66	—	—	1	20	25	20	3.46 ± 0.08
M 956	12	1	2	4	5	—	—	—	—	3	2	3.92 ± 0.30

Section Episkopi II

sample	N	Y										\bar{Y}
		7	6	5	4	3	3/4	3/3	3/2	3/1	3/0	
M 660	66	—	2	11	7	46	1	1	18	12	14	3.53 ± 0.11
M 659	93	—	2	6	13	72	—	3	19	28	22	3.33 ± 0.07
M 658	133	1	—	12	24	96	2	5	31	23	35	3.39 ± 0.06
M 657	120	—	1	8	18	93	1	1	17	38	36	3.31 ± 0.06
M 655	121	—	2	15	15	89	3	3	36	29	18	3.42 ± 0.07
M 654	54	—	3	6	10	35	1	1	8	14	11	3.57 ± 0.12
M 653	42	—	—	8	8	26	2	1	6	10	7	3.57 ± 0.12
M 652	22	—	—	3	7	12	1	1	6	2	2	3.59 ± 0.15

Appendix VII

Section Episkopi III

sample	N	Y									\bar{Y}
		6	5	4	3	3/4	3/3	3/2	3/1	3/0	
M 669	28	—	1	4	23	—	3	11	3	6	3.21 ± 0.09
M 670	42	—	3	5	34	2	5	9	8	10	3.26 ± 0.09
M 671	151	2	12	24	113	1	4	49	28	31	3.36 ± 0.05
M 672	122	4	15	19	84	1	5	25	31	22	3.50 ± 0.07
M 675	48	4	7	8	29	1	2	13	8	5	3.71 ± 0.14
M 677	25	3	2	6	14	—	1	3	7	3	3.76 ± 0.21
M 678	22	2	3	4	13	1	1	4	4	3	3.73 ± 0.21
M 679	12	—	4	3	5	1	—	1	2	1	3.92 ± 0.27
M 680	54	4	13	12	25	1	—	10	10	4	3.92 ± 0.13
M 682	46	1	8	14	23	1	—	12	8	2	3.72 ± 0.12
M 683	86	—	18	28	40	1	1	9	21	8	3.74 ± 0.08

Section Stalos

	N	Y					\bar{Y}
		6	5	4	3	2	
M 580	91	—	1	2	87	1	3.03 ± 0.03
M 579	105	—	2	3	100	—	3.06 ± 0.03
M 575	30	—	—	—	30	—	3.00
M 574	90	—	3	4	83	—	3.11 ± 0.04
M 572	101	1	4	14	82	—	3.25 ± 0.06
M 571	93	—	12	14	67	—	3.41 ± 0.07
M 570	87	2	9	16	60	—	3.46 ± 0.08

Appendix VIII

Section Exopolis-Vryses

sample	N	Y										\bar{Y}
		7	6	5	4	3	3/4	3/3	3/2	3/1	3/0	
846—A	15	—	—	1	—	14	—	—	5	5	4	3.13 ± 0.14
846—O	47	—	—	—	—	47	—	—	12	18	17	3.00
846—P	10	—	—	1	—	9	—	—	3	2	4	3.20 ± 0.21
850—P	42	—	—	1	3	38	—	—	14	15	9	3.12 ± 0.06
850—O	27	—	—	3	7	17	—	—	8	4	5	3.48 ± 0.13
850—N	37	—	—	7	3	27	—	—	2	7	12	3.46 ± 0.13
850—M	52	—	—	2	4	46	—	—	14	19	13	3.15 ± 0.06
850—L	57	—	—	1	4	52	1	—	14	13	24	3.10 ± 0.05
850—J	67	—	—	1	5	61	—	—	5	18	38	3.10 ± 0.04
850—H	45	—	—	3	5	37	—	—	16	11	10	3.24 ± 0.08
850—F	39	—	—	1	4	34	—	1	4	14	15	3.15 ± 0.07
850—E	26	—	—	2	4	20	—	—	4	9	7	3.30 ± 0.12
850—D	73	1	—	12	11	49	—	—	20	21	8	3.53 ± 0.10

Section Prasses

sample	N	Y								\bar{Y}	
		6	5	4	3	3/4	3/3	3/2	3/1		3/0
798—L	22	—	1	—	21	—	—	6	9	6	3.09 ± 0.09
798—A	19	1	1	—	17	1	2	3	4	7	3.26 ± 0.19

Section Maredhiana

sample	N	Y							\bar{Y}	
		6	5	4	3	3/3	3/2	3/1		3/0
M 820	15	—	1	1	13	—	—	7	6	3.20 ± 0.15
M 819	17	—	1	1	15	—	2	6	7	3.18 ± 0.13
M 816	27	—	—	4	23	—	8	7	8	3.15 ± 0.07
M 814	45	—	5	8	32	—	6	16	10	3.40 ± 0.10
M 812	32	1	3	7	21	—	4	12	5	3.50 ± 0.14
M 809	30	—	8	19	3	1	—	—	2	4.17 ± 0.11

Significance test. M 809—812: $u = 3.6271$

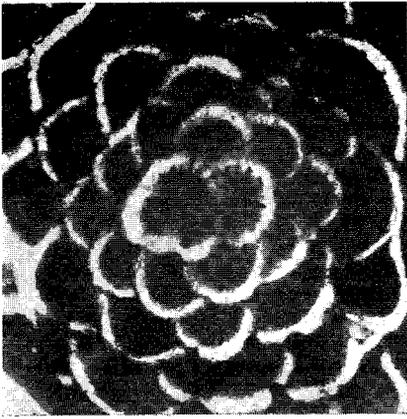
Appendix IX

In the appendix IX and X we give the mean size of the protoconch and deuterconch together ($\overline{d1.2}$) and the mean size of the first three chambers ($\overline{h1.3}$) together with their corresponding standard errors for 42 Cretan *Planorbulinella* populations. Moreover, we give the \overline{Y} of the same specimens on which $\overline{d1.2}$ and $\overline{h1.3}$ are based.

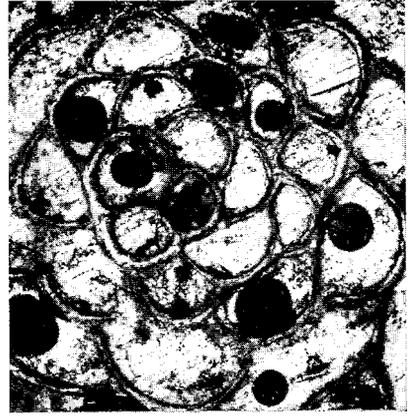
sample	N	\overline{Y}	$\overline{d1.2}$	$\overline{h1.3}$
Section Apostoli				
814—V	15	3.37 ± 0.18	86.7 ± 3.2	90.6 ± 3.3
814—U	11	3.27 ± 0.20	94.6 ± 4.4	98.1 ± 5.5
814—S	10	3.20 ± 0.14	80.3 ± 2.9	87.5 ± 3.3
814—R	10	3.10 ± 0.10	93.1 ± 3.2	97.7 ± 4.1
814—Q	27	3.07 ± 0.05	92.5 ± 2.7	104.8 ± 3.2
814—P	22	3.72 ± 0.15	88.1 ± 2.7	93.3 ± 2.4
814—O	9	3.11 ± 0.12	95.8 ± 5.1	104.8 ± 4.8
814—K	31	3.29 ± 0.10	92.9 ± 3.3	100.1 ± 3.5
814—J	26	4.00 ± 0.17	92.8 ± 3.1	98.1 ± 3.8
814—H	37	3.73 ± 0.12	96.8 ± 3.0	103.9 ± 3.4
814—G	21	4.19 ± 0.16	82.9 ± 2.5	89.0 ± 3.7
814—C	26	4.23 ± 0.08	85.0 ± 2.9	91.4 ± 2.7
814—B	51	4.42 ± 0.13	78.2 ± 1.5	82.7 ± 1.7
Section Kastelli				
M 904	31	3.19 ± 0.09	95.4 ± 2.5	101.0 ± 2.5
M 905	51	3.49 ± 0.11	92.3 ± 2.1	98.7 ± 2.2
M 906	32	3.41 ± 0.13	98.0 ± 2.1	102.4 ± 2.7
M 909	24	3.58 ± 0.17	91.5 ± 2.8	97.6 ± 3.5
M 910	35	3.31 ± 0.13	97.4 ± 2.6	102.8 ± 2.7
M 911	47	3.53 ± 0.13	92.7 ± 2.0	97.4 ± 2.1
M 912	21	3.33 ± 0.14	96.3 ± 3.3	103.2 ± 3.4
M 913	30	3.23 ± 0.09	98.7 ± 2.7	106.7 ± 3.1
Section Maredhiana				
M 809	30	4.16 ± 0.11	85.3 ± 2.8	88.7 ± 2.7
M 812	32	3.50 ± 0.14	99.3 ± 2.9	100.9 ± 2.9
M 814	42	3.43 ± 0.11	97.3 ± 2.5	101.3 ± 2.2
M 816	26	3.15 ± 0.07	93.0 ± 2.5	99.9 ± 3.3

Appendix X

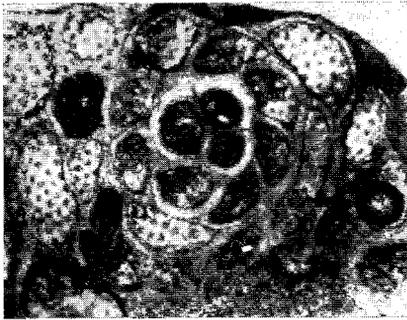
sample	N	\bar{Y}	$\overline{d1.2}$	$\overline{h1.3}$
Section Khairtiana				
M 782	32	4.87 ± 0.14	83.6 ± 1.9	85.5 ± 2.1
M 783	24	4.42 ± 0.12	83.7 ± 2.4	86.6 ± 2.2
M 785	48	3.79 ± 0.09	93.2 ± 2.2	95.6 ± 2.3
M 786	32	3.87 ± 0.13	88.7 ± 2.5	90.8 ± 2.7
Section Astrikos				
M 651	40	4.65 ± 0.12	92.2 ± 2.4	97.1 ± 2.8
Section Episkopi I				
M 696	40	4.67 ± 0.13	85.5 ± 1.9	90.7 ± 3.6
M 697	23	4.43 ± 0.19	84.4 ± 3.2	90.7 ± 3.6
Section Roka				
M 1035	15	3.20 ± 0.15	97.7 ± 4.9	101.4 ± 3.9
M 1040	29	3.34 ± 0.11	91.7 ± 2.3	96.1 ± 2.7
M 1042	38	3.37 ± 0.09	95.2 ± 2.3	97.5 ± 2.0
M 1045	26	3.37 ± 0.15	94.5 ± 2.8	98.9 ± 2.7
M 1046	43	3.39 ± 0.11	99.2 ± 2.4	101.2 ± 2.3
M 1047	27	3.37 ± 0.11	92.7 ± 2.8	95.4 ± 2.9
M 1048	25	3.16 ± 0.09	101.6 ± 2.6	106.6 ± 3.2
M 1049	13	3.46 ± 0.22	94.5 ± 4.0	98.7 ± 4.9
M 1050	24	3.42 ± 0.15	94.6 ± 2.5	98.1 ± 2.7
M 1051	23	3.26 ± 0.13	93.9 ± 2.9	96.1 ± 3.2



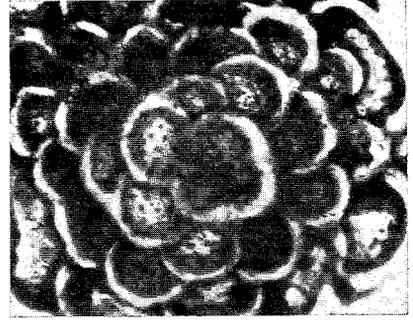
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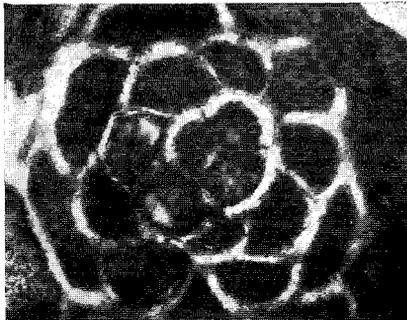
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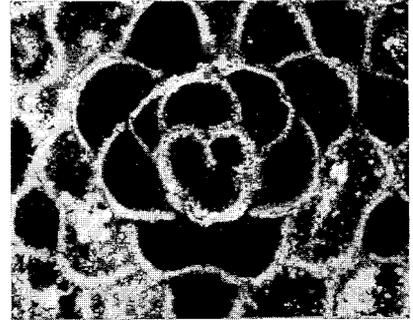
3.



4.



5.



6.

Plate 1

(all specimens X 145)

Figs. 1—6. *Planorbulinella canaeae* n.sp. from Crete.

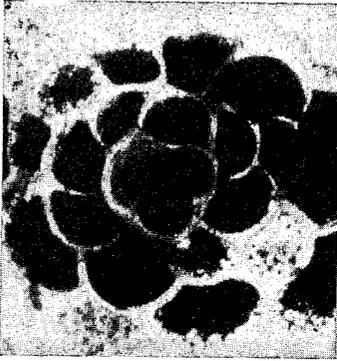
- 1) type 3/0/a, sample 548-F, Section Exopolis
- 2) type 3/0/a, sample 548-G-2, Section Exopolis
- 3) type 3/0/b, sample 548-E, Section Exopolis
- 4) type 3/1/a, sample M 816, Section Maredhiana
- 5) type 3/1/a, sample M 41 near Kamara Kissamou
- 6) type 3/2/a, same sample



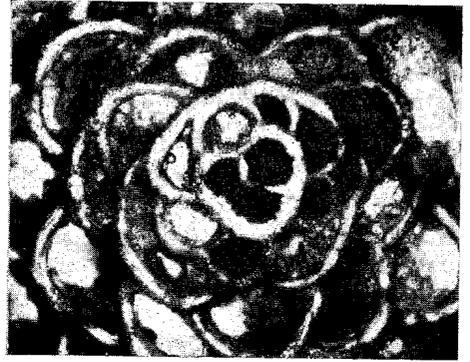
1.



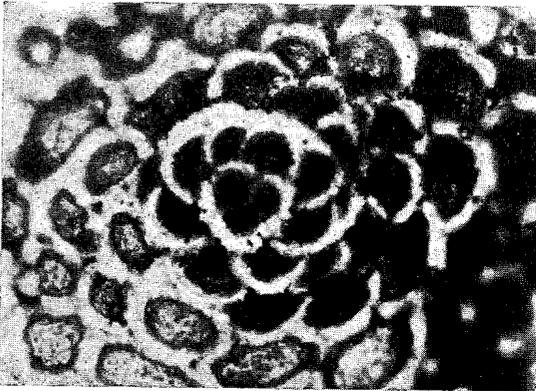
2.



3.



4.



5.



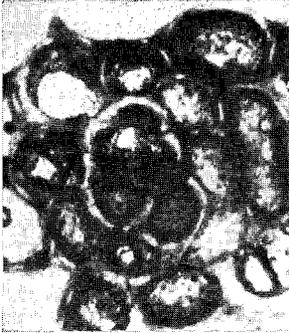
6.

Plate 2

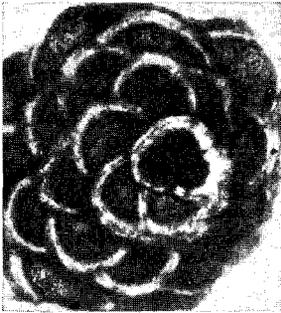
(all specimens X 145)

Figs. 1—6. *Planorbulinella canaeae* n.sp. from Crete.

- 1) type 3/2/a, sample M 227, Vryses (exposure 184)
- 2) idem
- 3) idem
- 4) type 3/3/a, sample 548-D, Section Exopolis
- 5) type 3/3/a, sample M 571, Section Stalos
- 6) type 4/0/a, sample M 574, Section Stalos



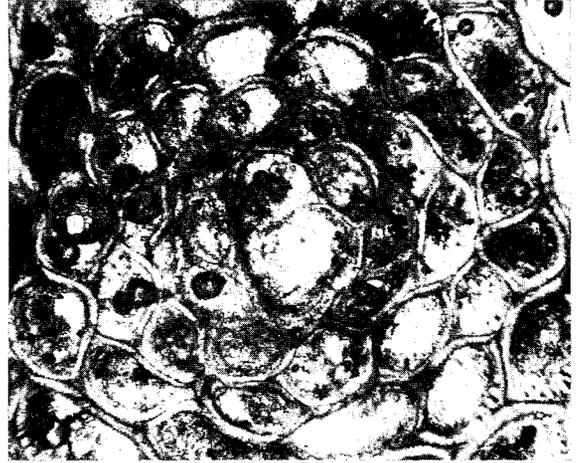
1.



2.



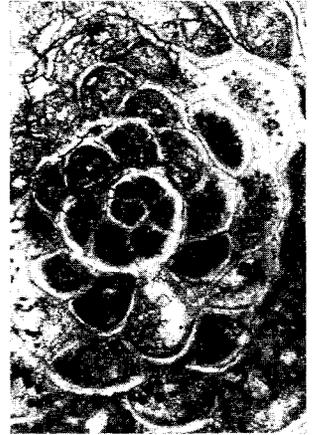
3.



4.



5.



6.



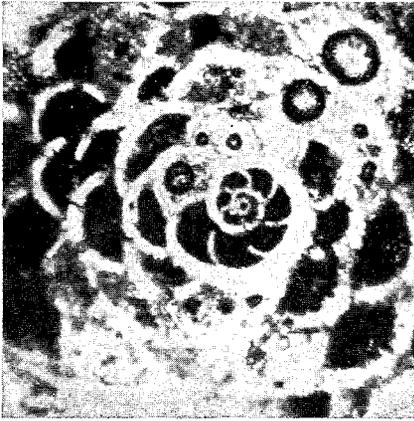
7.

Plate 3

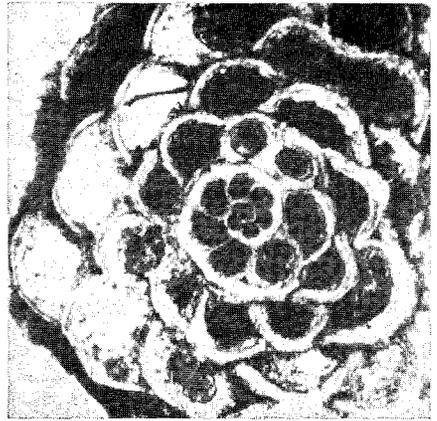
(all specimens X 145)

Figs. 1—7. *Planorbulinella canaeae* n.sp. from Crete.

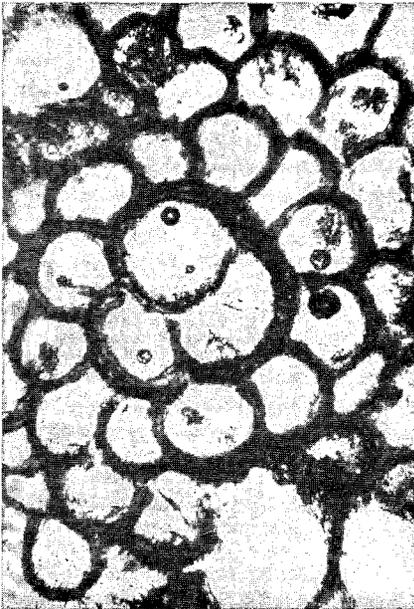
- 1) type 4/1/a, sample M 570, Section Stalos
- 2) type 5/1/a, sample 548-E, Section Exopolis
- 3) type 6/0/a, sample M 228, Vryses (exposure 184)
- 4) specimen showing the dark lines within the chambers walls, sample M 227, Vryses (exposure 184)
- 5) microspheric specimen, sample M 574, Section Stalos
- 6) microspheric specimen, sample M 572, Section Stalos
- 7) vertical section, sample M 552, Section Potamidha



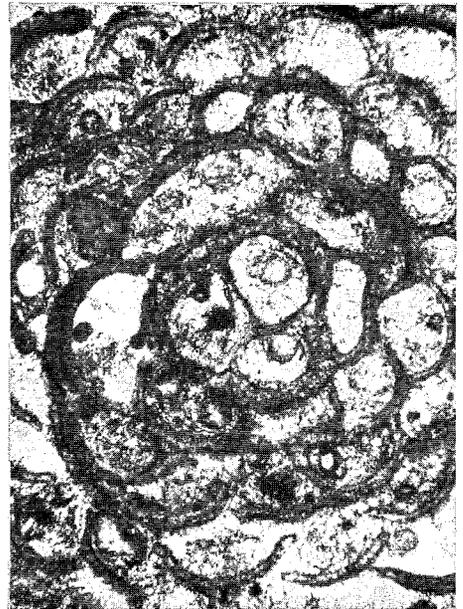
1.



2.



3.



4.

Plate 4

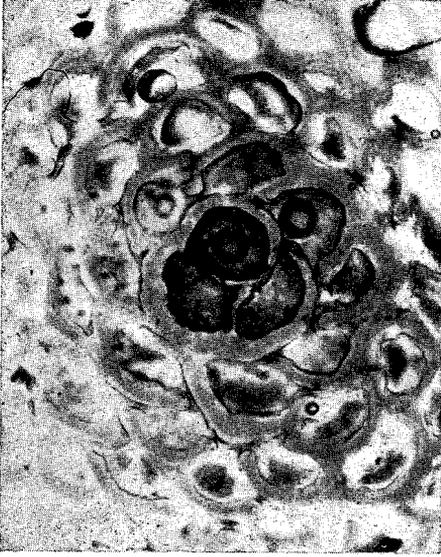
(all specimens X 145)

Figs. 1 and 2. *Planorbulinella canaeae* n.sp. from Crete.

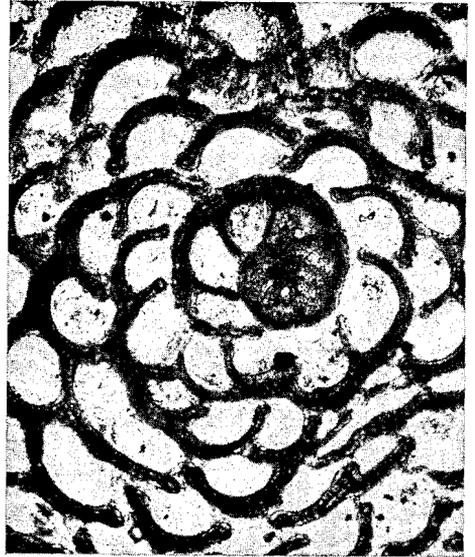
- 1) microspheric specimen, sample M 579, Section Stalos
- 2) microspheric specimen, sample M 572, Section Stalos

Figs. 3 and 4. *Planorbulinella larvata* (PARKER & JONES).

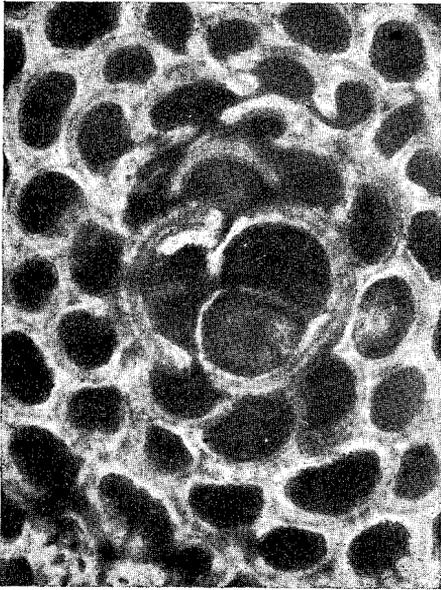
- 3) type 2/0/a, Eilat, Israel, Recent
- 4) type 2/0/a, Yaene, Hachijo Island, Tokyo Prefecture Japan, Recent



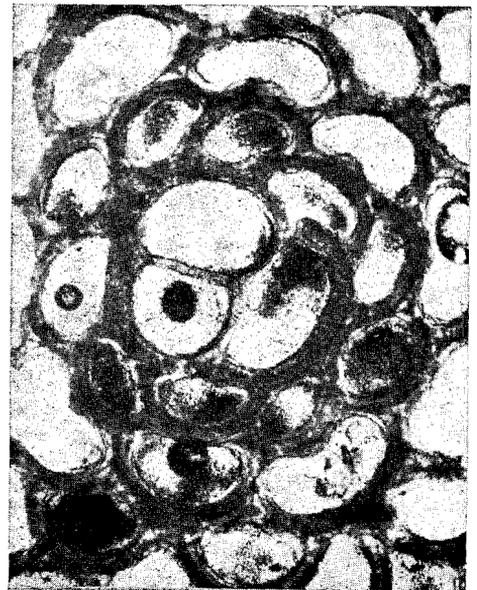
1.



2.



3.



4.

Plate 5

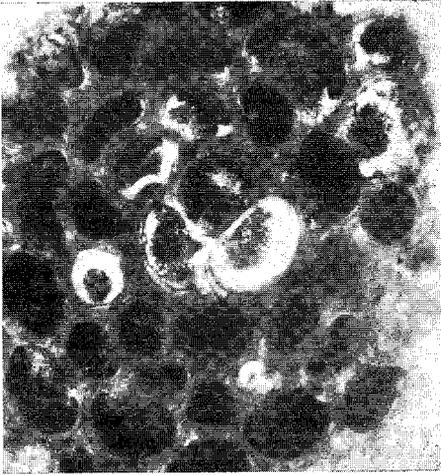
(all specimens X 145)

Figs. 1 and 2. *Planorbulinella larvata* (PARKER & JONES).

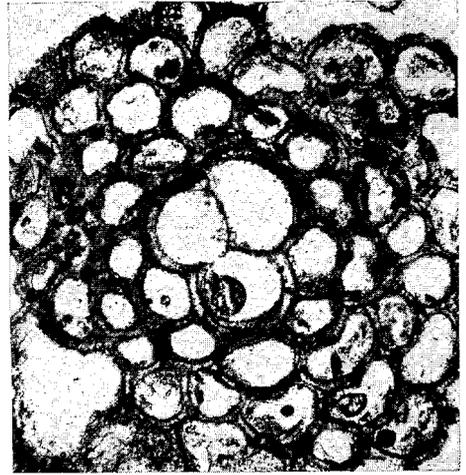
- 1) type 3/3/a, sample D 5151, Sulu Archipel, Philippines, Recent
- 2) microspheric specimen, idem

Figs. 3 and 4. *Planorbulinella zelandica* FINLAY.

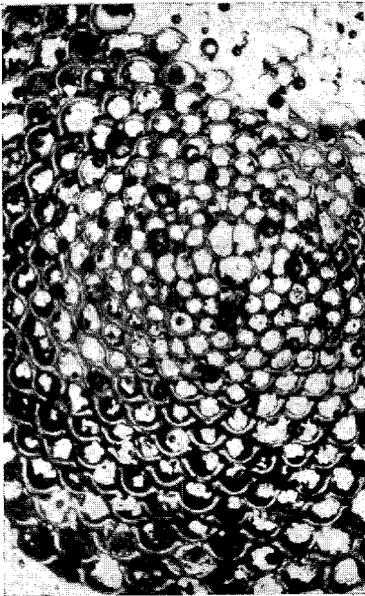
- 3) type 2/1/a, sample S 167/619, Clifden, South Island, New Zealand, Awamoan or Altonian
- 4) type 2/0/a, sample F 5938, Pourere, S. Hawkes Bay, South Island, New Zealand, Waiauan



1.



2.



3.



4.



5.



6.

Plate 6

(figs. 1—2, X 145; figs. 3—6, X 45)

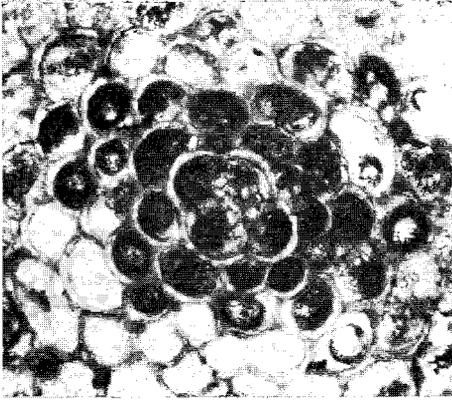
Figs. 1 and 6. *Planorbulinella zelandica* FINLAY.

- 1) type 2/0/b, sample N 28/787, Pakaurangi Point, New Zealand, Altonian (?)
- 6) vertical section, sample S 167/619, Clifden, South Island, New Zealand, Awamoan or Altonian

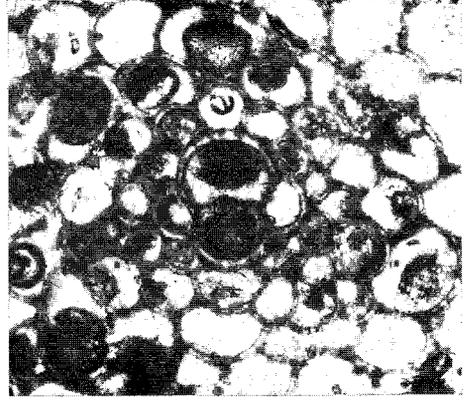
Figs. 2, 3 and 5. *Planorbulinella trinitatensis* (NUTTALL).

- 2) type 2/0/a, sample T 1446, Banes, Eastern Oriente, Cuba, "Oligocene"
- 3) type 2/0/a, sample Ho-207, Point à Pierre, Trinidad, Miocene
- 5) vertical section, same sample

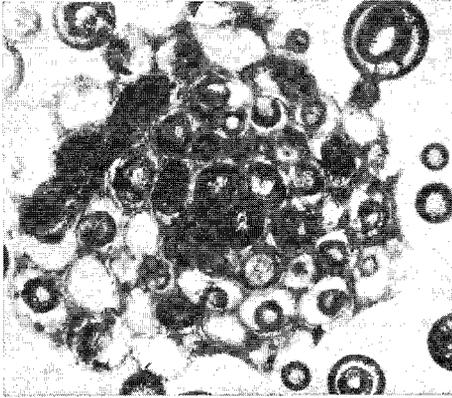
Fig. 4. *Planorbulinella larvata* (PARKER & JONES).
vertical section, sample D 5151, Sulu Archipel, Philippines, Recent



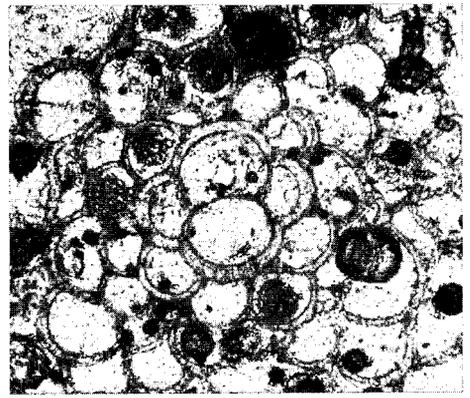
1.



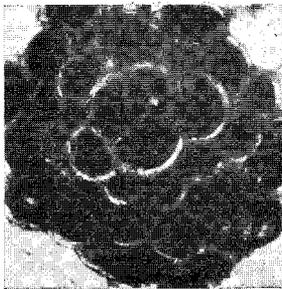
2.



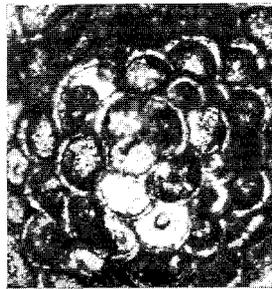
3.



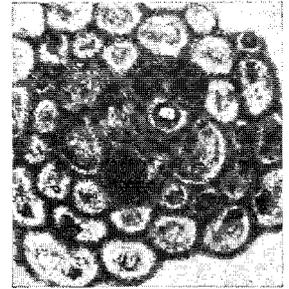
4.



5.



6.



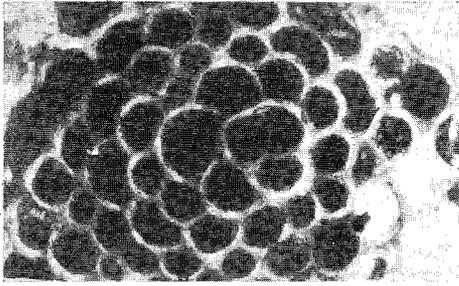
7.

Plate 7

(all specimens X 140)

Figs. 1—7. *Planolinderina escornebovensis* n.sp. from the Chattian-Aquitania of the Aquitaine Basin.

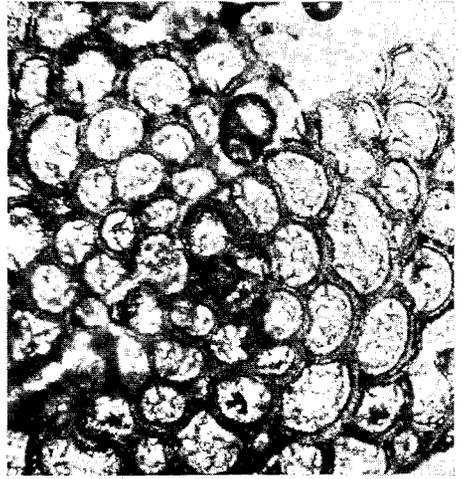
- 1) Y = 1, sample A 88, Baron, Chattian
- 2) Y = 1, sample A 356, Estoti, Chattian-Aquitania
- 3) Y = 1, sample A 88, Baron, Chattian
- 4) Y = 1, same sample
- 5) Y = 2, sample A 356, Estoti, Chattian-Aquitania
- 6) Y = 3, sample A 88, Baron, Chattian
- 7) Y = 4, sample A 355, Listagnac, Aquitania



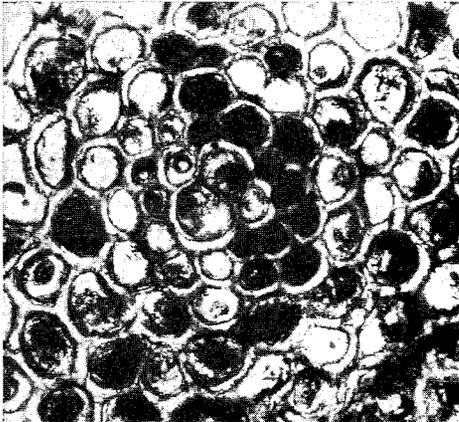
1.



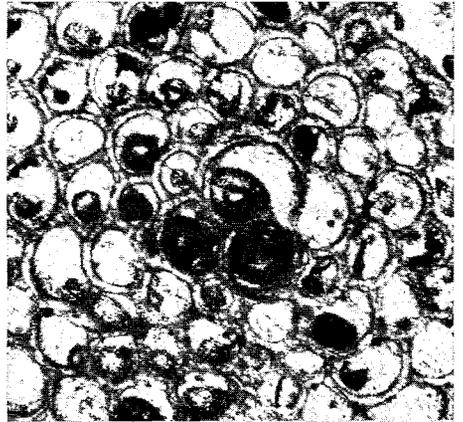
3.



2.



4.



5.



6.

Plate 8

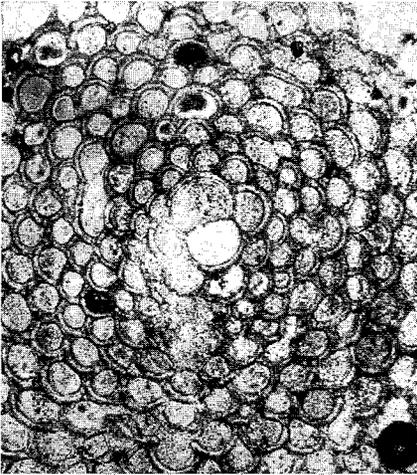
(all specimens X 140)

Figs. 1—3. *Planolinderina escornebovensis* n.sp. from the Chattian-Aquitania of the Aquitaine Basin.

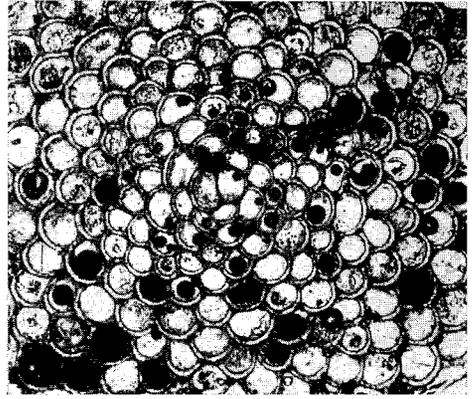
- 1) Y = 4, sample A 82, Cabanes, Aquitanian
- 2) Y = 5. sample Fr-M-3, Moulin de l'Eglise, type Aquitanian
- 3) vertical section, sample A 355, Listagnac, Aquitanian

Fig. 4—6. *Planolinderina inaequilateralis* (HERON-ALLEN & EARLAND) from Australia.

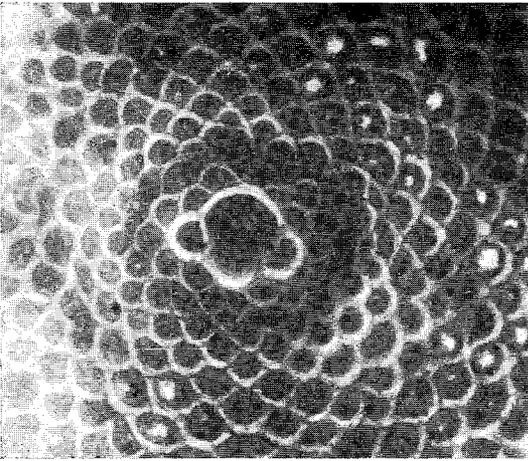
- 4) Y = 1, sample F-100, Castle Cove, Victoria, Burdigalian
- 5) Y = 1, sample 12732, Robertson's Quarry, Gippsland, Victoria, Aquitanian
- 6) vertical section, same sample



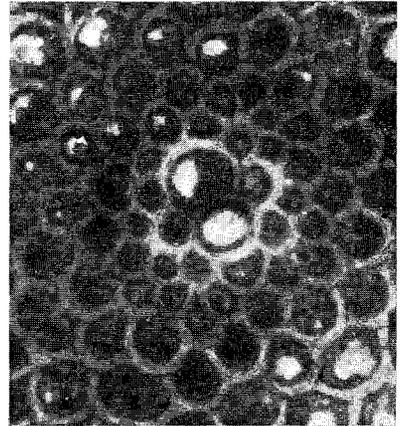
1.



2.



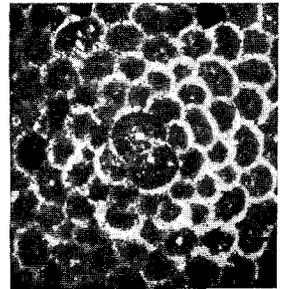
3.



4.



6.



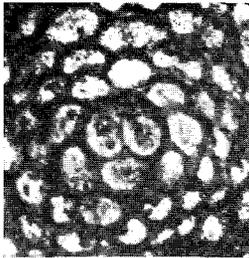
5.

Plate 9

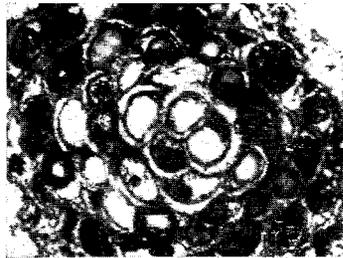
(all specimens X 145)

Figs. 1—6. *Planolinderina plana* (HERON-ALLEN & EARLAND)
from Australia and Borneo.

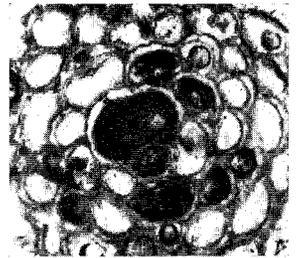
- 1) Y = 1, sample 12737, Mc Coll's Quarry, Gippsland, Victoria, Australia, Aquitanian
- 2) Y = 1, sample 12732, Robertson's Quarry, Gippsland, Australia, Aquitanian
- 3) Y = 1, sample V 98, Batesford, Victoria, Australia, type locality of *P. plana*, Burdigalian(?)
- 4) idem
- 5) Y = 1, sample Mo-100, Sungei Tenging, Borneo, Indonesia, "Burdigalian"
- 6) vertical section, sample 12732, Robertson's Quarry, Victoria, Australia, Aquitanian



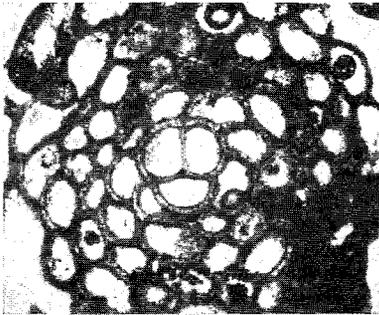
1.



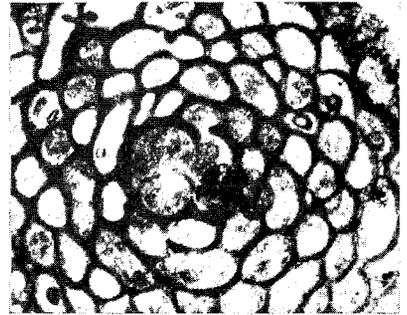
2.



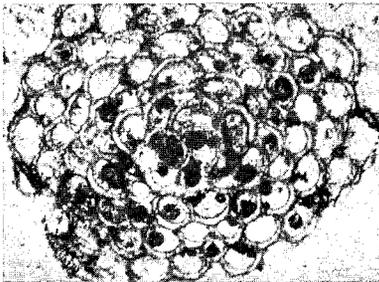
3.



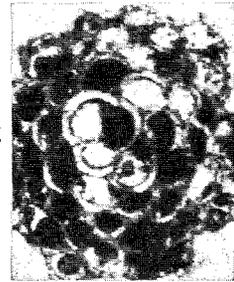
4.



5.



6.



7.



8.



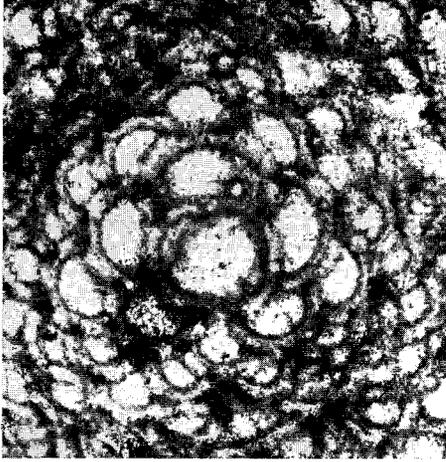
9.

Plate 10

(all specimens X 145)

Figs. 1—9. *Linderina* sp. cf. *L. paronai* OSIMO, all from the Upper Eocene of the Paris Basin.

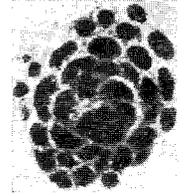
- 1) Y = 2, sample Fr 1041, Bois de Ronquerolles
- 2) Y = 2, sample Fr 1039, Bois de Ronquerolles
- 3) Y = 2, sample Fr 564, Auvers
- 4) Y = 2, sample Fr 1039, Bois de Ronquerolles
- 5) Y = 2, sample Fr 1041, Bois de Ronquerolles
- 6) microspheric specimen, sample Fr 1040, Bois de Ronquerolles
- 7) Y = 3, same sample
- 8 and 9) vertical sections, sample Fr 1041, Bois de Ronquerolles



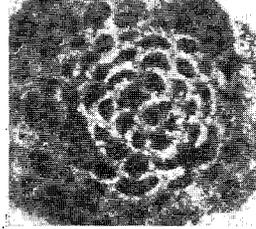
1.



2.



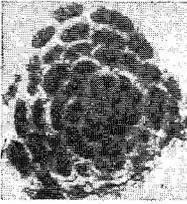
3.



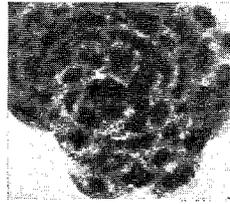
4.



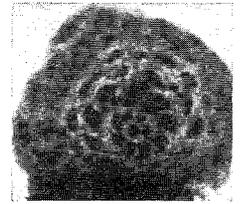
5.



6.



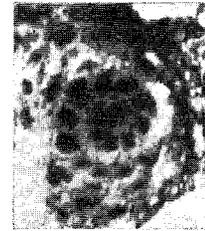
7.



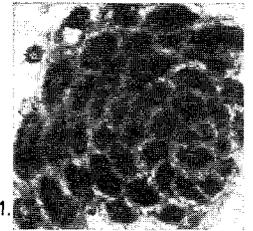
8.



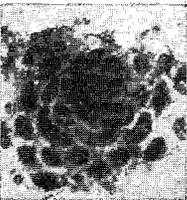
9.



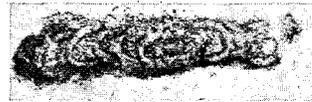
10.



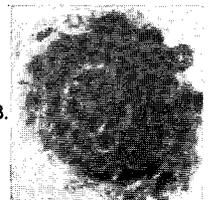
11.



12.



14.



13.

Plate 11

(all specimens X 145)

Fig. 1. *Linderina buranensis* (NUTTALL & BRIGHTON), Qatar, "Lutetian".

Figs. 2—14. *Hellenocyclina charentensis* n.sp., all from the Aubeterre Section, Charente, France, Campanian. Paratypes are those from sample Fr 823.

- 2) Y = 7, sample Fr 520
- 3) Y = 6, sample Fr 823
- 4) Y = 6, sample Fr 823
- 5) Y = 7, sample Fr 823
- 6) Y = 8, sample Fr 823
- 7) Y = 6, sample Fr 520
- 8) Y = 11, sample Fr 522
- 9) Y = 12, sample Fr 823
- 10) Y = 12, sample Fr 523
- 11) Y = 11, sample Fr 823
- 12) Y = 8, sample Fr 521
- 13) Y = 11, sample Fr 825
- 14) vertical section, sample Fr 523

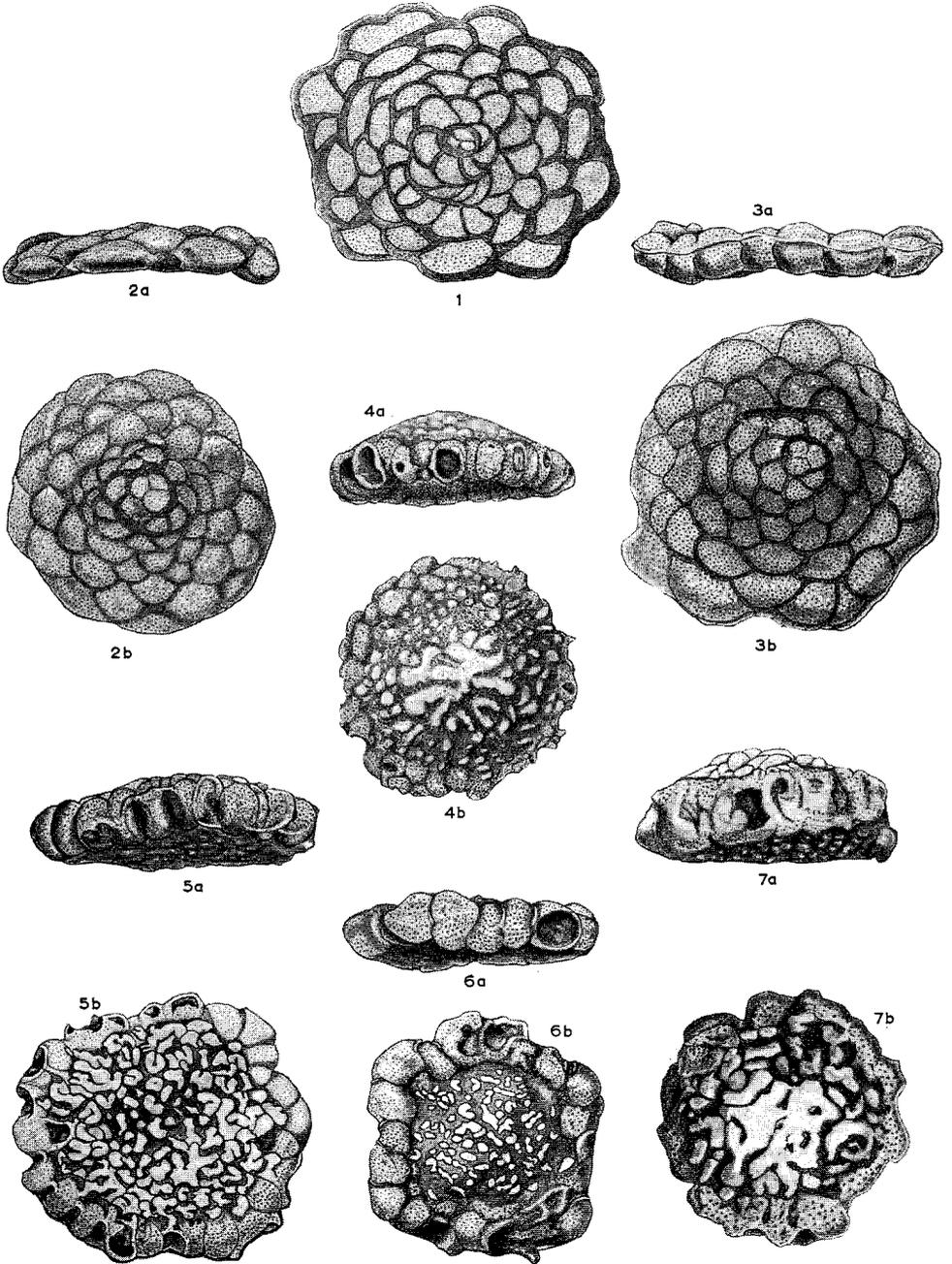
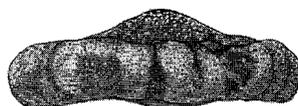


Plate 12

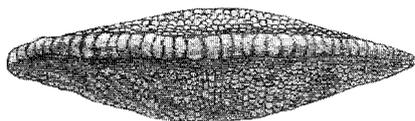
- Fig. 1. *Planorbulinella rokae* n.sp. Holotype. Sample M 116, Mesonisi church, Roka, Khania Province, Crete. Roka Formation. X 60
- Fig. 2a, b. *Planorbulinella canaeae* n.sp. Holotype. Sample M 746, Kria Vrisi, Khania Province, Crete. Top of the Kissamou Formation. X 60
- Fig. 3a, b. *Planorbulinella astriki* n.sp. Holotype. Sample 651, Astrikos, Khania Province, Crete. Base of the Kissamou Formation. X 60
- Figs. 4a, b and 5a, b. *Planorbulinella larvata* (PARKER & JONES).
4a, b) Keise, off Nawa, Okinawa, Ryukyu Islands, Japan, Recent. X 24
5a, b) Yaene, Hachijo Island, Tokyo Prefecture, Japan, Recent. X 24
- Figs. 6a, b and 7a, b. *Planorbulinella zelandica* FINLAY.
6a, b) Pakaurangi Point, New Zealand. Sample N 28/787, Altonian. X34.
7a, b) Topotype. Pourere, S. Hawkes Bay, South Island, New Zealand. Sample F 5938, Waiauan. X 34.



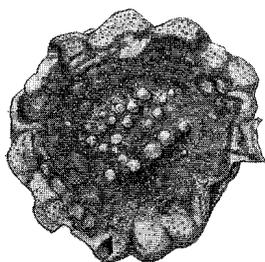
1a



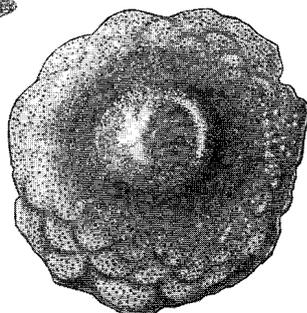
2a



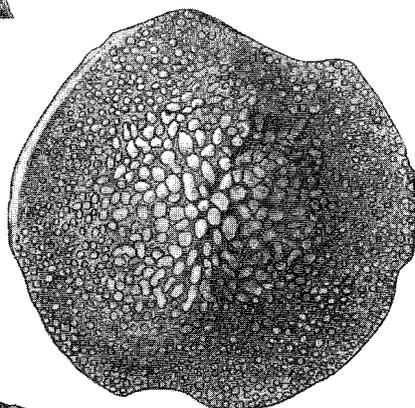
3a



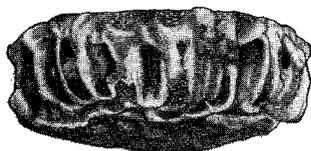
1b



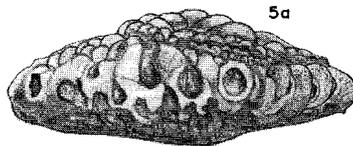
2b



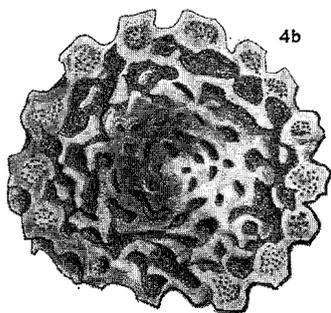
3b



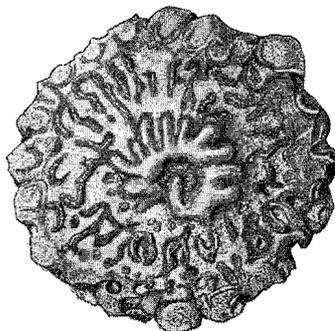
4a



5a



4b



5b

Plate 13

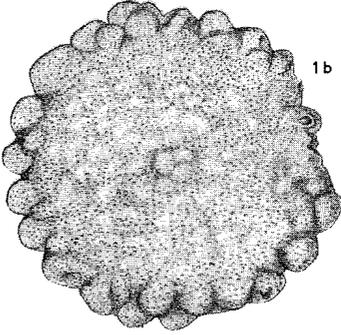
- Figs. 1a, b, 4a, b, 5a, b. *Planorbulinella trinitatensis* (NUTTALL)
1a, b) Sample T 1446, Banes, Eastern Oriente, Cuba,
"Oligocene". X 45
4a, b) Sample DB 324, Mayo Quarry, Central Range, Trinidad,
Late Miocene. X 60
5a, b) Sample Ho-207, Point à Pierre, Trinidad, Miocene. X 32
- Fig. 2a, b. *Linderina* sp. cf. *L. paronai* OSIMO. Sample Fr 1039, Bois de Ron-
querolles, Oise, France, Eocene (Auversian). X 90
- Fig. 3a, b. *Linderina buranensis* NUTTALL & BRIGHTON. Topotype. Sunto Trig.
Station, Somalia, "Lutetian". X 20



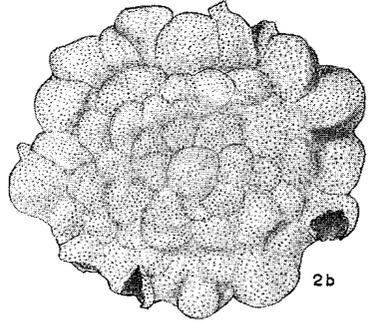
1a



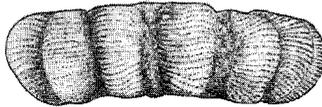
2a



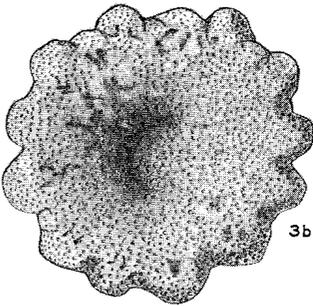
1b



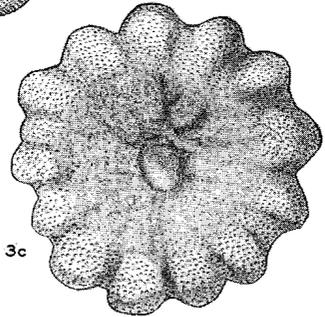
2b



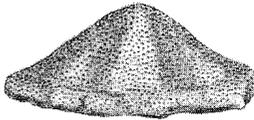
3a



3b



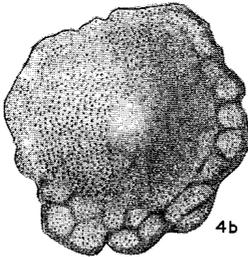
3c



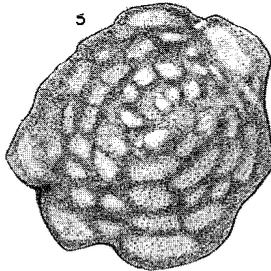
4a



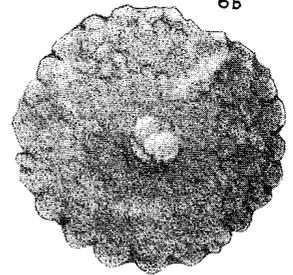
6a



4b



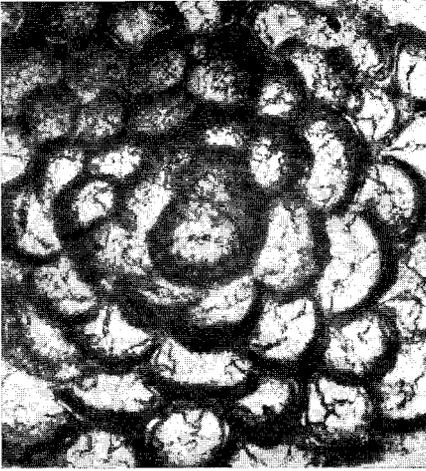
5



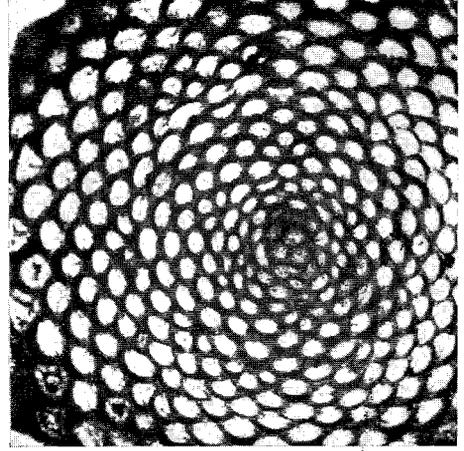
6b

Plate 14

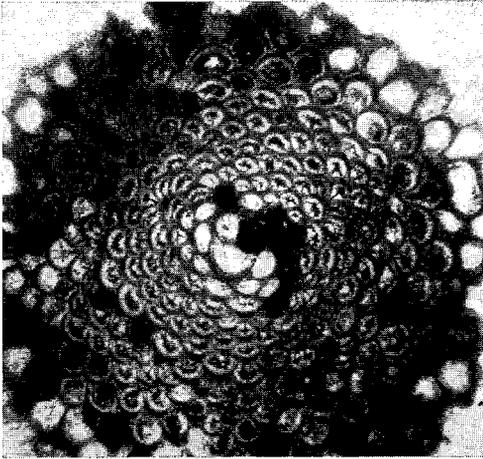
- Figs. 1a, b, 6a, b. *Planolinderina plana* (HERON-ALLEN & EARLAND)
1a, b) Sample 12732, Robertson's Quarry, Gippsland, Victoria, Australia, Aquitanian. X 54
6a, b) Sample Mo-100, Sungei Tenging, Borneo, Indonesia, "Burdigalian". X 54
- Fig. 2a, b. *Planolinderina escornebovensis* n.sp. Holotype. Sample Aq 9, Escornebéou, Aquitaine Basin, France, Chattian. X 145
- Fig. 3a, b, c. *Planolinderina inaequilateralis* (HERON-ALLEN & EARLAND). Sample 12732, Robertson's Quarry, Gippsland, Victoria, Australia, Aquitanian. X 70
- Fig. 4a, b. *Hellenocyclina visserae* (HOFKER). Topotype. Sample NL 16, Maas-tricht, Holland, Maastrichtian. X 145
- Fig. 5. *Hellenocyclina charentensis* n.sp. Holotype. Sample Fr 823, Aubeterre, Charente, France, Campanian. X 180



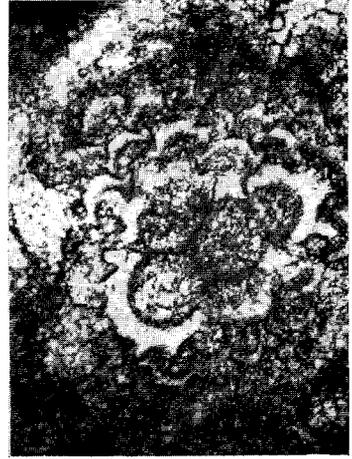
1.



2.



3.



4.

Plate 15

Figs. 1, 2, 3. *Linderina paronai* OSIMO.

- 1) Holotype, Y = 4, "Lutetian", Celebes. X 110
- 2) Specimen figured by PROVALE (1909), "Lutetian", Borneo.
Y = 2. X 60
- 3) idem. X 55

Fig. 4. *Hellenocyclina beotica* REICHEL. Horizontal section figured by REICHEL (1950). The arrangement of the early chambers is not clear. Upper Cretaceous, Greece. X 250

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