UTRECHT MICROPALEONTOLOGICAL BULLETINS

E. THOMAS

Project no. 1

DETAILS OF UVIGERINA DEVELOPMENT IN THE CRETAN MIO-PLIOCENE

23

UTRECHT MICROPALEONTOLOGICAL BULLETINS

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DETAILS OF UVIGERINA DEVELOPMENT IN THE CRETAN MIO-PLIOCENE

I.G.C.P. Project no. 1

E. THOMAS

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65 figures, 5 plates, 33 tables

ABSTRACT

Neogene uvigerinids with uniserial chambers were investigated biometrically. They were obtained from some 400 closely spaced samples from Upper Miocene and Lower Pliocene sediments in sections on the island of Crete (Greece). In each assemblage counts and measurements were carried out on a number of characteristics of the test of some fifty individuals. Five of these characteristics were believed to give the best information about the changes in the morphology in *Uvigerina.* These five are the total length and the maximum breadth of the test, the numbers of the uniserial and of the biserial chambers, and a factor describing the shape of the uniserial chambers, and a factor describing the shape of the uniserial chambers. In a few samples we also measured the diameter of the protoconch, and a number of specimens was dissolved stepwise to obtain data about the early growth stages.

Univariate, bivariate and multivariate statistical methods were applied to get more insight in the huge amount of data. For some samples we measured and calculated the oxygen and carbon isotopic ratios.

No obvious pattern of sustained change is observed for any of the parameters; instead we meet with large fluctuations and no consistent shift in the parameter mean values.

Two morphotypes could be separated, a thick and a thin one, but small numbers of intermediate individuals are present in many of the samples, and a group of samples in the lowermost Pliocene contains only intermediate morphotypes.

The separate groups of thick and thin uvigerinids show no sustained changes either, but a pattern of statistically significant fluctuations without a perceivable net change. In our opinion the morphotypes are ecophenotypes of a single species. The thick *Uvigerina* proliferates in laminated sediments in the Upper Miocene. These sediments are probably deposited under nutrient-rich and oxygen-minimum conditions in stagnant bottom waters in (semi-) isolated basins. The thin types are never numerous; they are the normal marine forms, which tolerate low nutrient levels. Both types are indifferent to high salinities.

In the Pliocene we only find the thin type in our lowermost samples. Higher in the sections these uvigerinids change fluctuatingly, but gradually into homeomorphs of the Miocene thick type, at about the level where the sediments change as well. Open marine marls pass gradually into an alternation of grey and brown clays. The latter clays were probably deposited under

oxygen-minimum conditions, comparable to those of the Upper Miocene laminated marls, and the thick type once again becomes very numerous. Still higher in the Pliocene sections the thick uvigerinids are replaced by thin ones, but it is not understood in which way this replacement took place. Whether there was a direct descendance in situ or a sudden immigration of the thin uvigerinids from other parts of the Mediterranean cannot be decided.

Morphologically the thin uvigerinids in the highest Pliocene samples are not different from those in the lowest Miocene sections. We have no good explanation for the large, statistically significant, fluctuations in the mean values of the parameters in the separate groups. An environmental control is likely. However, a contribution from random processes cannot be precluded; the staggered course of the development might be the result of a random walk of the succession of many asexual generations without correction by sufficient sexual interludes.

If the changes in the morphology of *Uvigerina* are primarily dependent upon the environment, they can be used for a facies correlation, which will have a limited value within separate basins only. Uvigerinids cannot be used for a time-bound zonation over larger distances.

Taxonomically we consider our thick and thin uvigerinids as subspecies of *Uvigerina cylindrica* (d'Orbigny). The thin type is named *Uvigerina cylindrica cylindrica* (d'Orbigny), the thick one *Uvigerina cylindrica gaudryinoides* Lipparini, and intermediate assemblages are given a hyphenated notation.

Chapter I

INTRODUCTION

I.1. GENERAL

Evolutionary lineages in many groups of foraminifera have been studied, especially in planktonic and larger foraminifera. Some groups of species of benthonic smaller foraminifera, notably species of *Uvigerina* also yielded well-documented lineages. Some species groups of *Uvigerina* have been extensively investigated. Biozonations based on evolutionary stages of different groups of *Uvigerina* have been proposed in North Western Germany (Von Daniels & Spiegler, 1977), the Vienna basin (Papp, 1953, 1963, 1964, Papp and Schmid, 1971), the Mediterranean region (Papp, 1963, Hottinger, 1966, Meulenkamp, 1969, Fortuin, 1974, 1977) and New Zealand (Vella, 1964).

Similar trends are described in ontogeny as well as in phylogeny for many unrelated groups of *Uvigerina*; trends from a triserial chamber arrangement towards a mainly biserial or mainly uniserial chamber arrangement.

From previous authors it is known that in the Neogene deposits of Crete huge numbers of well-preserved fossils of *Uvigerina* are found in closely spaced samples in many sections (Meulenkamp, 1969, Fortuin, 1977). The main points in the evolution of these *Uvigerina* were thought to be clear, though many problems remained unsolved. The Neogene paleogeography of Crete and the geological context of the sections are well known (Meulenkamp, 1969, Freudenthal, 1969, Fortuin, 1977, Meulenkamp, in prep. 1980). Within the scope of the I.G.C.P.-project nr. 74/I/1, "Accuracy in time" a detailed study of the Cretan uniserial uvigerinids seemed to us to be worthwhile, and was expected to give an idea of the reliability and accuracy of biozonations.

Our investigation aimed at getting more information concerning the progress in time of the morphological changes and the possible environment-dependence of such changes. If we know the pattern in time of the morphological changes we may get some insight into the resolution of the time correlations to be attained with the evolutionary stages of *Uvigerina*.

I.2. REVIEW OF PREVIOUS RESEARCH

Papp (1963, 1966) was the first to describe an evolutionary trend in

a group of uniserial uvigerinids he had sampled in Neogene deposits in the Rio Mazzapiedi valley, near Sant' Ágatha Fóssili (Piemonte basin, Northern Italy). *Uvigerina* specimens with up to three or four uniserial chambers are met with in the Tortonian blue clays, together with triserial *Uvigerina proboscidea* Schwager. Papp believed these uniserial uvigerinids to be intermediate forms between *U. proboscidea* and *Uvigerina gaudryinoides gaudryinoides* Lipparini. In the Messinian Papp reports the presence of two subspecies, *U. gaudryinoides gaudryinoides* and *Uvigerina gaudryinoides siphogenerinoides* Lipparini. The latter subspecies he considered more advanced; it has five or more uniserial chambers. In Pliocene deposits from Castell' Arquato, Asti and Piacenza Papp recognized another subspecies, *Uvigerina gaudryinoides arquatensis* Papp, which he considered as a highly evolved descendant from *U. gaudryinoides siphogenerinoides.*

Papp alleges that the uvigerinids constitute a beautiful evolutionary lineage. All transitional forms are found. The uvigerinids show a directional, rectilinear development from a wholly triserial to a mainly uniserial chamber arrangement. This author gives no explanation of the co-occurrence of *U. gaudryinoides gaudryinoides* and *U. gaudryinoides siphogenerinoides.*

Hottinger (1966) discovered the same lineage with the same taxonomic units in Morocco. He remarks that in the Messinian deposits very large specimens of *U. gaudryinoides gaudryinoides* are seen with "en crochet" sutures like *Uvigerina bononiensis* Fornasini.

Meulenkamp (1969) has revised the earlier work on uniserial uvigerinid lineages, and has made the first biometrical study of these uvigerinids. He does not agree with Papp that *U. proboscidea* is the ancestor of the uniserial uvigerinids, because of the differences between juvenile uniserial *Uvigerina* and *U. proboscidea.* He does not consider the co-occurrence of *U. gaudryinoides gaudryinoides* and *U. gaudryinoides siphogenerinoides* as typical for sediments of Messinian Age.

Meulenkamp distinguishes two different lineages of uniserial uvigerinids in the Mediterranean Neogene. Both lineages show the same sustained changes; an increase in the average number of uniserial chambers and a development towards a more regular arrangement of the uniserial chambers. He divided both lineages on the same criteria into four biometrical species, and considered it impossible to compromise between the typological approach of the taxa of the earlier authors and the results of his own biometrical analysis. Actually, every species of the literature might fit in with several of Meulenkamp's adjoining taxonomic units, so he preferred to coin new species names for almost all (seven out of eight) of his new species units. From the pre-existing names he made use only of *Uvigerina arquaten-*

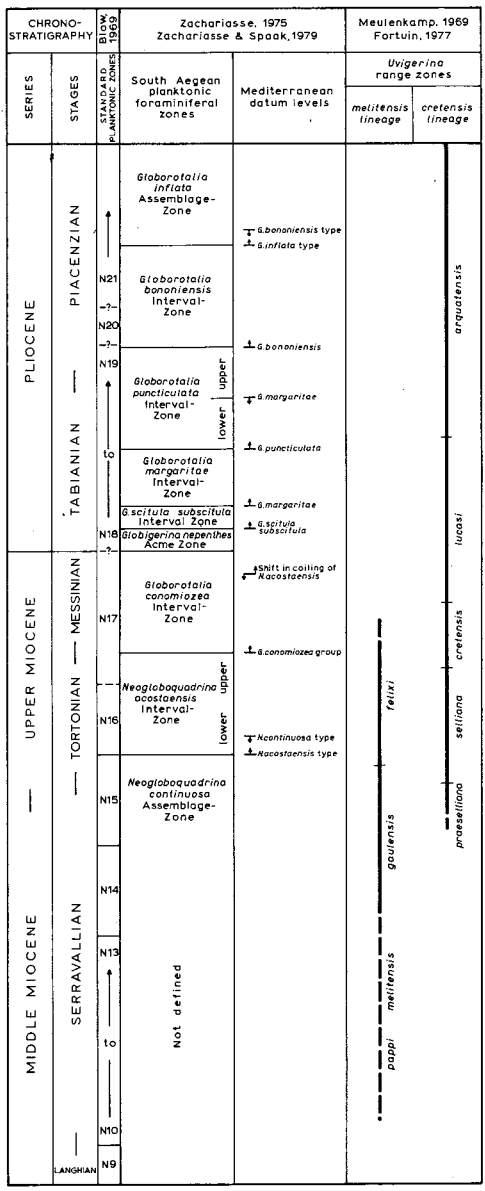

Fig. 1 The specific names of the Mediterranean uniserial uvigerinids after Meulenkamp (1969) and Fortuin (1977). The datum levels and the planktonic foraminiferal zonation are after Zachariasse (1975) and Zachariasse and Spaak (1979).

sis Papp for his youngest species after studying topotype material of this species (see fig. 1 for Meulenkamp's specific names).

The oldest of the two lineages ranges from Serravallian to Tortonian. Its three oldest representative species are known from Malta, the fourth species in this lineage is known from Crete. This lineage is called the *Uvigerina melitensis* one. The younger lineage ranges from the Late Tortonian into the Pliocene, and has representatives in Italy, Spain and on Crete. It is called the *Uvigerina cretensis* lineage. Meulenkamp regarded *Uvigerina bononiensis compressa* Cushman as the ancestor of the *U. melitensis* lineage. The ancestor of the *U. cretensis* lineage he did not know.

Felix (1973) has described foraminifera from the Oligo – Miocene deposits on Malta and Gozo. He made a calibration of the *U. melitensis* lineage versus a biozonation based on planktonic foraminifera and benthonic foraminifera other than *Uvigerina*. The oldest species, *Uvigerina pappi* Meulenkamp originated, according to Felix, in the lower part of his *Orbulina universa* Zone (N 9 – N 10), which ranges in age from Late Langhian to Early Serravallian. The next species, *Uvigerina melitensis* Meulenkamp probably came into existence in the Serravallian. Transitional samples between *U. melitensis* and the third species, *Uvigerina gaulensis* Meulenkamp Felix observed in Upper Serravallian deposits, in the top of the *O. universa* Zone (N 14). *U. gaulensis* appears in the *Neogloboquadrina continuosa* Zone (N 15). Felix envisages the beginning of the *U. melitensis* lineage somewhat earlier than Meulenkamp.

Zachariasse (1975) has made a study of planktonic foraminifera from the Mediterranean region and has made a calibration of planktonic foraminiferal versus uvigerinid zonations. The fit of the two zonations proved to be problematical between sections in Spain and those of Crete. The species boundary between the third species of the *U. cretensis* lineage, *Uvigerina lucasi* Meulenkamp and the fourth species of the same lineage, *Uvigerina arquatensis* Papp is located in Crete within the *Globorotalia margaritae* Interval Zone. In Spain *U. arquatensis* occurs together with Messinian planktonic assemblages, characterized by *Globorotalia dalii*. Zachariasse suggested that evolution in *Uvigerina* might have proceeded more rapidly in Spain.

Fortuin (1974, 1977) dates his formations on eastern Crete with the aid of Meulenkamp's biozonation. He used the same taxonomic units. In Serravallian deposits (his *N. continuosa* Oppel Zone) he found triserial to biserial forms, which he considered as the ancestors of the *U. cretensis* lineage. For these forms he created the new species *Uvigerina praeselliana*. According to Fortuin members of the first three species of the *U. melitensis* lineage, which were previously only known from Malta exist in the Serravallian de-

posits of eastern Crete. He noticed transitional forms between *U. pappi* and *U. melitensis* as well as *U. melitensis* and *U. gaulensis* in his Kalamavka Formation. In the upper part of this formation also *U. felixi* occurred, the youngest species of the *U. melitensis* lineage. The Kalamavka Formation as a whole is placed in the *N. continuosa* Zone. Fortuin gives no comment on the differences in calibration with the planktonic zonation of the Cretan and Maltese representatives of the *U. melitensis* lineage.

I.3. DEFINITION OF TERMS

1. Lithological sample: the amount of sediment taken at one level of a stratigraphic section.
2. Population: used in a statistical sense, any set of individuals or objects having some common observable characteristic. In our case all uvigerinids that may possibly form uniserial chambers and do not possess a flattened test constitute the population we are taking into consideration.
3. Assemblage: all uvigerinids that belong to the population, as they were living at one time and place. Time in this context has a duration corresponding with the thickness of the lithological sample. This concept of the assemblage corresponds to a local representation of a suite of biological populations.
4. Sample: a subset of the population and the assemblage. A sample consists in our work of all the specimens of uvigerinids picked from an aselect split of the residue of one lithological sample.

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Chapter II

PROVENANCE OF THE SAMPLES

II.1. INTRODUCTION

Uvigerina specimens were studied from four Miocene and three Pliocene sections, all located on Crete (fig. 2). In addition some samples from short sections at a few other Cretan localities were employed. The localities are also indicated in fig. 2.

The Miocene sections were chosen on the advice of Meulenkamp. The Pliocene sections are key-sections in the I.G.C.P.-project nr. 74/I/1. The benthonic and planktonic foraminifera from the Miocene sections are being examined by G. J. van der Zwaan. The planktonic foraminifera from the Pliocene sections are being investigated by P. Spaak, the benthonic foraminifera by H. A. Jonkers.

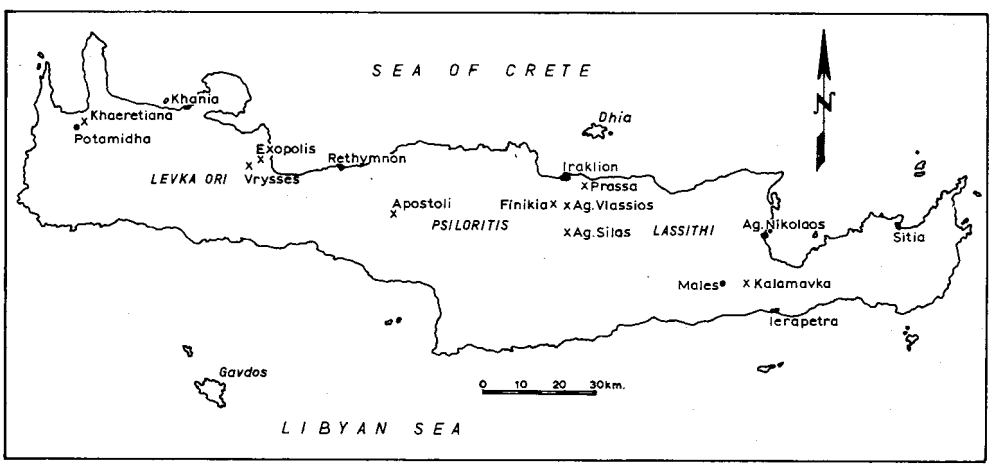


Fig. 2 Location of the Cretan sections.

II.2. THE SECTIONS

II.2.1. Section Apostoli

The section (fig. 3) is located in the Western part of Crete, in the province of Rethymnon. The section has been described by Meulenkamp (1969) and

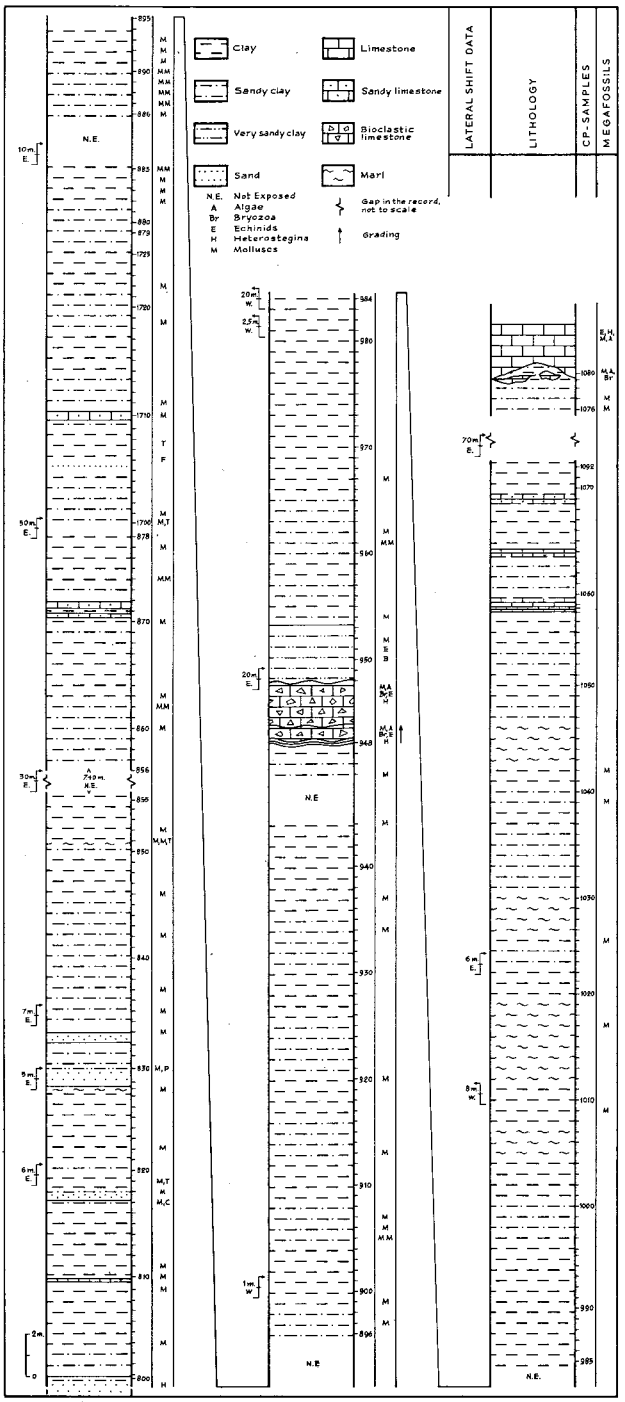


Fig. 3 Section Apostoli.

again by Meulenkamp (1979a). The section is in the steep side of a table mountain. Its stratigraphic height is about 165 m. On the whole 280 lithological samples were taken, most of them at mutual intervals of 50 cm. Of the 280 samples 35 contained a sufficient number of *Uvigerina.*

The section is the type section of the Apostoli Formation of Meulenkamp (1969).

Planktonic foraminifera from section Apostoli have been studied by Zachariasse (1979). Although there are some problems concerning the *Globorotalia conomiozea* entry level he is of the opinion that the sediments must be placed in the *Neogloboquadrina acostaensis* Zone.

Lithology

The section Apostoli consists of bluish-grey, often silty clays and marls. These overlie marine sands and conglomerates with *Heterostegina,* with oysters, *Pecten,* and other molluscs, and with echinids (*Clypeaster*). The sands are bioturbate and often contain concretions. The shallow-water, marine sands overlie fresh water deposits, sands and conglomerates.

In the lower part of the section the clays are often silty to sandy. There are some layers of sandstone. These sandstones consist of yellow sand, sometimes horizontally laminated, often burrowed. The sandstones sometimes contain shell debris and/or plant remains.

The clays are strongly bioturbate. At some levels they are very rich in molluscs, complete shells and fragments. Small solitary corals and burrows (*Serpula*?) may occur.

About half way the section there is a layer of bioclastic limestone of variable thickness. The layer may be subdivided into several thinner layers, which all show positive gradation and have sharp, irregular lower boundary planes. The limestone contains many remains of fossils, like *Heterostegina,* algae, bryozoans, molluscs (including *Pecten*) and brachiopods (including *Terebratula*). On top of the bioclastic limestone we observed a layer of very sandy marls, rich in the same fauna as the bioclastic limestone. In this layer we came across seacow-bones. It it strongly burrowed.

Higher in the section again bluish-grey clays were found, at first rather silty, but higher up less silty. Greyish-green marls are intercalated. In this higher part of the section there are less molluscs than in the lower part of the section. Strongly indurated marly beds can be observed, but no sandstones.

The clays and marls are overlain by bioclastic limestones of approximately 40 m thick. The limestones have a sharp, very irregular contact with the clays. The limestones contain *Heterostegina,* algae, molluscs (*Pecten*), bryozoans, and echinids (*Clypeaster*).

The upper part of the section is traversed by several small faults.

II.2.2. Section Exopolis

The section (fig. 4) is located in the Apokoronou district, Eastern Khania. The section has been described by Meulenkamp (1969). It consists of a roadside exposure and some gullies below, and a hillside exposure above the level of the road. The stratigraphic height of the section is about 18 m in the gullies, 12 m in the roadside exposure and 8 m in the hillside. We took 115 lithological samples, mainly at intervals of 25 cm. Twenty of them contained a sufficient number of specimens of *Uvigerina.*

Our samples cover only the upper part of the section as described by Meulenkamp. The lower part is no longer exposed. Meulenkamp (1969) places the lower part of the section, bluish-grey clays, in his Apostoli Formation. The limestone on top of the laminated and homogeneous marls in the uppermost part of the section he places at the base of his Mylopotamou Formation. This formation has recently been renamed Vrysses Formation, as belonging to the Vrysses Group (Meulenkamp, 1979b).

Planktonic foraminifera have been studied by Van der Zwaan. The *G. conomiozea* entry level is here also indistinct. The lower 10 m of the section he places in the *N. acostaensis* Zone, the higher parts of the section in the *G. conomiozea* Zone.

Lithology

The lower part of section Exopolis, below the road level, consists of bluish-grey clays with intercalations of bioclastic limestones. The clays overlie fresh water to shallow-marine deposits, consisting of sands, conglomerates and lignites (not shown in fig. 4). The clays are often silty and contain thin laminae of shell debris. Shell debris is also seen in pockets. We seldom met with plant remains. The clays are strongly burrowed, but slightly laminated intervals occur. The intercalated bioclastic limestones contain many molluscs, entire as well as fragmented, bryozoans, algae and *Heterostegina.*

The upper part of the section, above the road level, consists of an alternation of laminated and non laminated marls. The homogeneous layers start with bluish-grey and clayey marls. Higher in the section they become more indurated and grey-brown to very dark grey in colour. These beds are often burrowed and sometimes contain molluscs. The laminated layers are very neatly laminated and only occasionally slightly burrowed near the contact with the homogeneous sediments. The laminated marls vary in colour from grey to brown or even orange. They contain many plant remains, fish scales and teeth.

The laminated – non laminated alternation is overlain by bioclastic

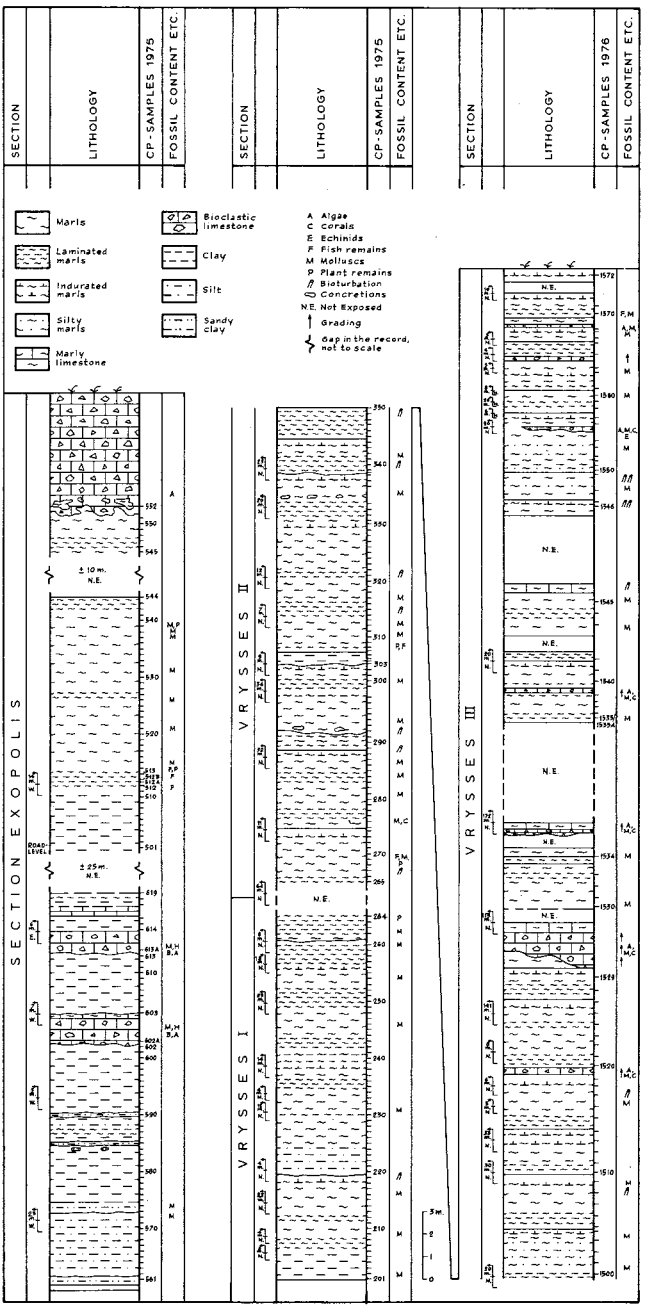


Fig. 4 Sections Exopolis and Vrysses.

limestones of approximately 5 m thickness, with a sharp, very irregular contact. The limestones contain molluscs, algae, bryozoans and *Heterostegina.*

II.2.3. Section Vrysses

The section (fig. 4) is located in the Apokoronou district, Eastern Khania and has been described by Meulenkamp (1969). The section consists of a series of road-side exposures with several gaps, especially in the upper part. The stratigraphic height of the section is about 85 m. The lower part of the section was sampled at 25 cm intervals, 250 samples were taken. The upper part of the section was sampled at 50 cm intervals. We took 72 samples. The lower part of the section is subdivided into sections Vrysses I and Vrysses II. Between these two subsections there is a major not exposed interval (± 64 m). The upper part of the section is named Vrysses III. In all, 124 samples of section Vrysses contained a sufficient number of *Uvigerina* (Vrysses I: 33; Vrysses II: 60; Vrysses III: 31). Meulenkamp's section Vrysses comprises only Vrysses I and II.

The sediments Meulenkamp (1969) placed in the Mylopotamou Formation, but recently Meulenkamp designated this section as the type section of the Vrysses Formation of the Vrysses Group (Meulenkamp, 1979b).

Planktonic foraminifera have been studied by Van der Zwaan. *G. conomiozea* occurs throughout the section, but never in large numbers. In the upper part of the section (sample CP 1542) he observes the shift in coiling direction in *N. acostaensis.* From sample CP 1537 upwards *Globigerina multiloba* occurs in large numbers. The section as a whole is placed in the *G. conomiozea* Zone.

Lithology

The section consists of an alternation of laminated and not laminated marls. In the lowest few meters of the section the homogeneous marls are bluish-grey, higher on they are greyish-brown to light yellowish-brown, often mottled with rust-coloured or violet spots. The marls are seldom silty. One frequently finds molluscs, whole or fragmented. In the upper part of the section oysters occur. Especially in the middle and higher parts of the section the top parts of the homogeneous beds are strongly indurated or contain calcareous concretions. The laminated marls are variable in colour, predominantly yellow to yellowish-brown, but also white, rose or orange. They often contain siliceous sponge spicules, fish scales and/or teeth and plant remains. Only occasionally do we meet with molluscs. Laminated marls often pass gradually upwards into homogeneous marls and

overlie with a sharp contact the indurated top part of a homogeneous layer. The laminated marls are often slightly burrowed near the upper contact with homogeneous marls. The thickness of the sequences varies greatly from about 50 cm to approximately 3 or 4 m. In the upper part of the section irregular layers and lenses of bioclastic limestones are intercalated. These have sharp, very irregular boundaries with the marls. The limestones contain molluscs, brachiopods, bryozoans and algae.

II.2.4. Section Khaeretiana

The section (fig. 5) is located in the Western part of Crete, province of Khania, and is described by Freudenthal (1969). The section consists of a series of roadside-exposures. The stratigraphic height of the section is

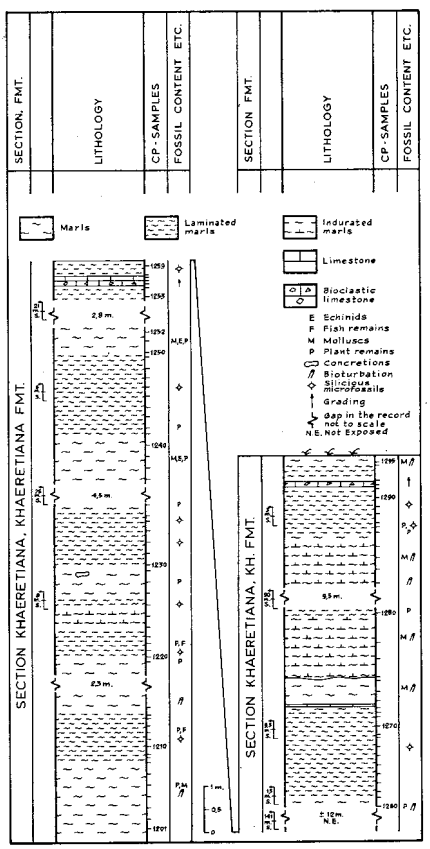


Fig. 5 Section Khaeretiana.

about 30 m, of which ± 12 m are not exposed. This section was sampled in great detail at intervals of 25 cm, often less. Of 95 lithological samples, 24 contained a sufficient number of *Uvigerina.*

G. conomiozea occurs throughout the section in small numbers (Van der Zwaan, pers. comm.). In sample CP 1245 *N. acostaensis* shifts its coiling direction; from sample CP 1230 upwards *G. multiloba* is present in large numbers.

The section is the type section of the Khaeretiana Formation as described by Freudenthal (1969). This formation Meulenkamp (1979b) places in the Vrysses Group.

Lithology

The section consists of an alternation of homogeneous and laminated marls. The homogeneous marls are yellow to brown, often mottled with black or violet spots. The marls are frequently burrowed and molluscs are often observed. Occasionally plant remains, *Discospirina* and echinids are met with. The marls are often indurated and contain calcareous concretions. The laminated marls vary in colour: yellow, white, greyish-white or even rose or orange. Plant remains are common, sometimes in large quantities. Fish scales and/or teeth, siliceous sponge spicules and porous, diatomaceous laminae are also frequently noted. Fairly regularly laminated marls pass gradually into homogeneous marls, upon which another layer of laminated marls lies with a sharp contact. The thickness of the sequences is variable, but does not exceed 4 to 5 m. A few thin, bioclastic limestone layers contain fragments of mollusc-shells and show positive gradation.

II.2.5. Review of the Miocene sections

The age relations between the Miocene sections are based on the planktonic foraminiferal data (fig. 6). There may be overlaps in time between the sections. Both in section Apostoli and in the lower part of section Exopolis we find problematical plankton-assemblages, which have been studied by Zachariasse (1979). In this interval there are frequent *G. conomiozea*-like individuals and transitional specimens between *G. conomiozea* and *Globorotalia menardii.* In the upper part of section Exopolis and in sections Vrysses and Khaeretiana one notices *G. conomiozea.* It is not known, whether a gap or an overlap in time exists between sections Exopolis and Vrysses. An overlap in time between the sections Vrysses and Khaeretiana is strongly indicated by the shift in coiling direction in *N. acostaensis* in both sections and the presence of large numbers of *G. multiloba.*

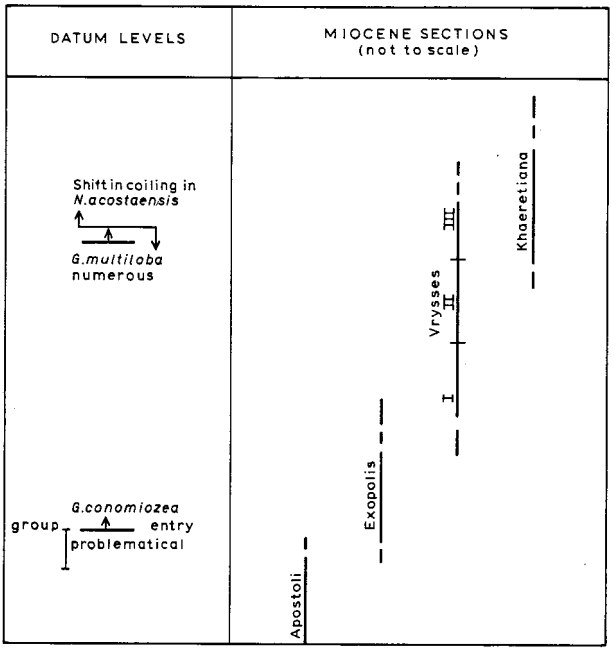


Fig. 6 The age relation of the Miocene sections based on planktonic foraminiferal data.

II.2.6. Section Prassa II

Section Prassa II (fig. 7) is located in the central part of Crete, province of Iraklion. The section is named Prassa II so as to distinguish it from the section Prassa, which has been described by Meulenkamp et al. (1978). The section consists of four roadside exposures, the mutual superposition of which is clear, but which are not continuously exposed. The stratigraphic height of these four exposures is about 10 m, 18 m, 2.5 m and 40 m. On the whole 144 lithological samples were taken, mainly at intervals of 50 cm, but partly at distances of 10 cm. Of these 58 contained sufficient numbers of *Uvigerina.*

The lowermost white, homogeneous marls are named Kourtes facies by Meulenkamp et al. (1979a); the alternation of brown and grey clays is named Finikia facies, and the alternation of beige marls and diatomaceous, laminated marls is called Stavromenos facies. All three types of lithology these authors include in the Finikia Formation.

Planktonic foraminifera have been studied by P. Spaak. Up to sample GR 1031 no *Globorotalia* were found, except for *Globorotalia subscitula.* From sample GR 1031 upwards *Globorotalia margaritae* occurs. From

sample GR 1074 upwards he observed both *G. margaritae* and *Globorotalia puncticulata.* A sandy layer contains hardly any keeled planktonic foraminifera and in the first diatomaceous marls, in sample GR 980, suddenly *Globorotalia bononiensis* appears. This suggests the presence of a considerable hiatus in the section, at the level of the sandy layer.

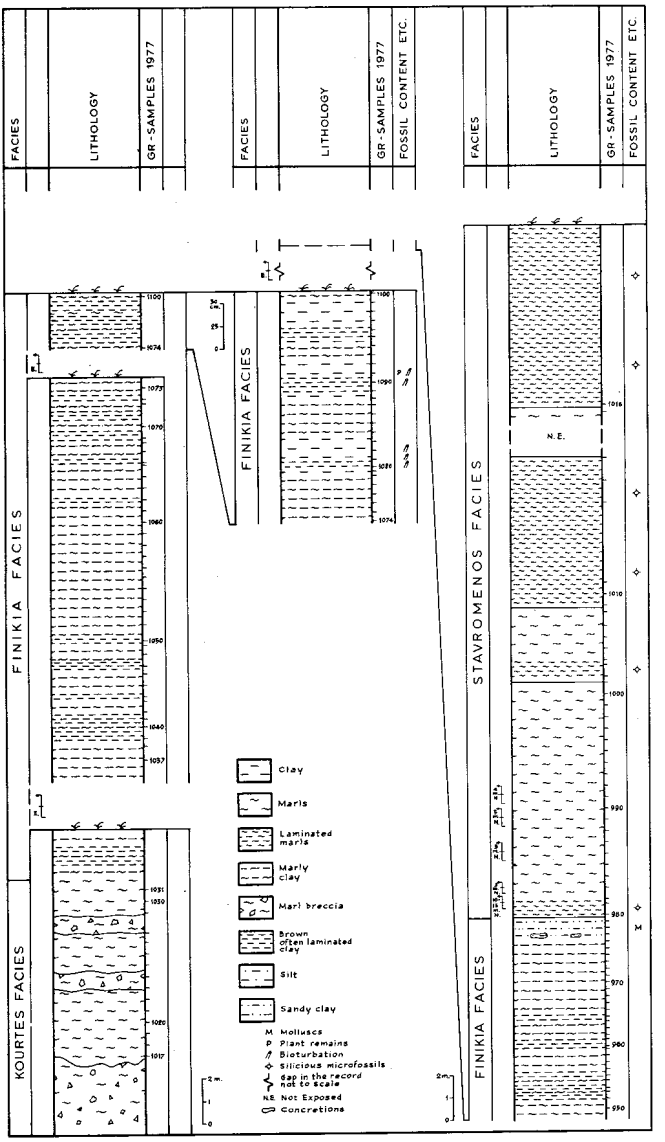


Fig. 7 Section Prassa II.

Lithology

The lower part of the section consists of white to beige, homogeneous marls. The marls overlie the irregular surface of marl breccias. In the marls two irregular layers of marl breccias are intercalated. These marl breccias contain pre-Neogene limestone and bioclastic limestones as components. The homogeneous marls resemble the Italian Trubi marls. Higher in the section the marls become gradually more clayey, and beige to grey in colour. Brown layers are intercalated in the grey clays. The brown layers are clays, often homogeneous, sometimes laminated with slight burrowing. The thickness of the brown layers is variable, from 10 to 60 cm. Above the alternation of brown and grey clays a layer of approximately 80 cm thick (samples GR 977 to GR 979) consists of fine, yellow sand, with irregularly shaped concretions and molluscs. On top of the sandy layer we observe an alternation of beige, homogeneous marls and laminated, white marls. The laminated marls contain much siliceous material, diatoms and sponge spicules. The thickness of the laminated marls varies from 10 cm to about 8 m.

II.2.7. Section Aghios Vlassios

The section (fig. 8) is located in the central part of Crete, province of Iraklion, and has been described by Meulenkamp et al. (1979a). We did not use the same set of samples, but the samples from a later sampling expedition, which cover the same stratigraphic interval and a somewhat higher interval. The section was sampled in a number of gullies. The stratigraphic height of the section is about 50 m. We collected 123 lithological samples, mainly at intervals of 50 cm, but partly at intervals of 25 cm. A sufficient number of *Uvigerina* was contained in 51 of these samples.

In section Aghios Vlassios sediments of the Kourtes facies are overlain by sediments of the Finikia facies, both placed within the Finikia Formation by Meulenkamp et al. (1979a).

The planktonic foraminifera have been studied by Spaak (in Meulenkamp et al., 1979a). In the second sample of the section *G. margaritae* is present already. In samples CP 2326 to 2332 *G. margaritae* and *G. puncticulata* occur together; in samples CP 2333 to CP 2356 *G. margaritae* was found alone. From sample CP 2357 upwards both *G. margaritae* and *G. puncticulata* are seen together, again up to sample CP 2243. From sample CP 2243 upwards only *G. puncticulata* remains.

Lithology

The lower part of the section consists of the homogeneous white marls of the Kourtes facies, which overlie a very irregular surface of marl breccias.

This part of the section is badly weathered. Higher in the section the Kourtes lithology changes gradually into the alternation of brown clays and grey clays of the Finikia facies. The thickness of the brown layers is variable, from 10 to about 70 cm.

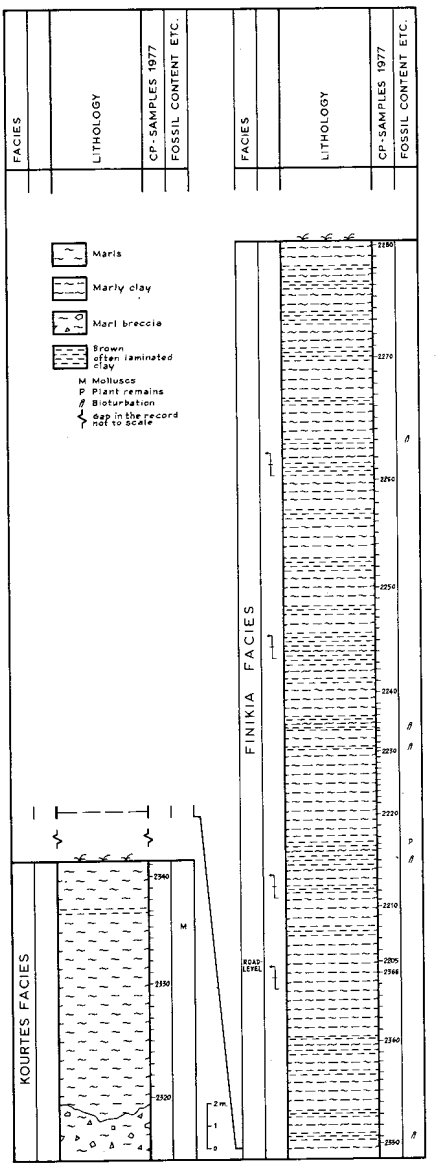


Fig. 8 Section Aghios Vlassios.

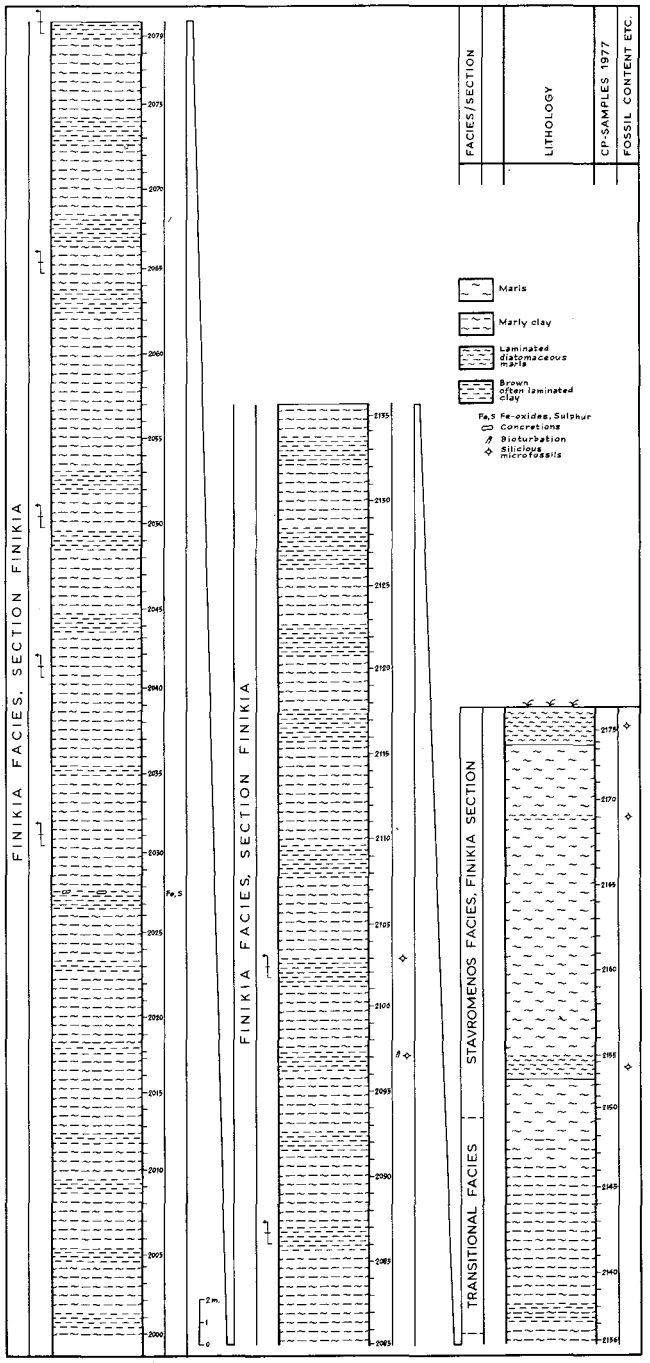


Fig. 9 Section Finikia.

II.2.8. Section Finikia

The section (fig. 9) is located in the central part of Crete, province of Iraklion. It has been described by Meulenkamp et al. (1979a). The section is found in a number of steep gullies. The stratigraphic height of the section is about 140 m. Lithological samples (175) were taken, mainly at intervals of 75 cm; 97 of these contained a sufficient number of *Uvigerina.*

The section is the type section of the Finikia Formation. The sediments are of the Finikia and Stavromenos facies.

The planktonic foraminifera have been studied by Spaak (in Meulenkamp et al., 1979a). In the lower part of the section, up to sample CP 2062 *G. puncticulata* occurs. Sample CP 2132 is the first sample that contains *G. bononiensis.*

Lithology

The lower part of the section consists of an alternation of grey and brown, often laminated, clays of the Finikia facies. Higher in the section this lithology changes gradually into beige-grey marls into which a few layers are intercalated of white, diatomaceous, laminated marls. These sediments are named Stavromenos facies by Meulenkamp et al., 1979. The thickness of the brown clays varies from about 10 cm to about 1.75 m. The thickness of the laminated, diatomaceous marls in this section does not exceed ± 1 m.

II.2.9. Review of the Pliocene sections

The age relations between the Pliocene sections, based on planktonic foraminiferal data are shown in fig. 10. The relations are rather complicated, due to the probable hiatus in section Prassa II. The lower part of section Prassa II is partly older than section Aghios Vlassios and partly of the same age. The upper part of section Prassa II is of the same age as the upper part of section Finikia or partly younger. The sections Aghios Vlassios, as represented by the new set of samples, and Finikia may overlap in time.

II.3. OTHER MATERIAL

Some samples were obtained from the Eastern part of Crete, province of Ierapetra. Because of tectonic complications in this region no long, undisturbed, sections are available. Thirty-six samples were obtained from section Kalamavka, which section has been described by Fortuin (1977). Eight of these samples contained sufficient *Uvigerina,* most of which are badly preserved, however. The samples were taken at irregular intervals of some

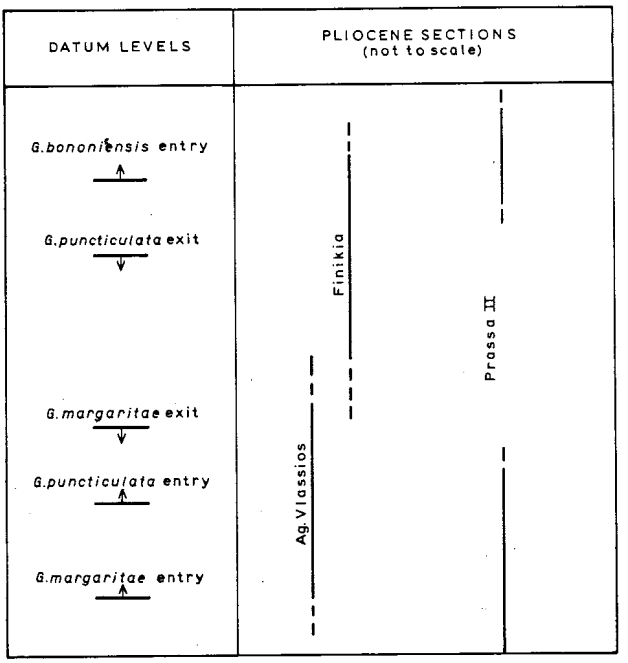


Fig. 10 The age relation of the Pliocene sections based on planktonic foraminiferal data.

meters (fig. 11). The sediments consist of alternating marls and calcareous sandstones of variable thickness. The section is the type section of Fortuin's Kalamavka Formation. In the lower part of the section planktonic foraminifera are scarce and of very bad preservation. In the higher part of the section, from sample GR 1952 upwards planktonic foraminiferal assemblages are better. The foraminifera have been studied by Spaak. From sample GR 1952 upwards *Neogloboquadrina continuosa* occurs.

Fortuin kindly put at our disposal a sample from the type locality of *U. praeselliana,* which is from sediments of the Prina Formation near the village of Males (sample Fo 719). This sample contains *N. continuosa.*

Some sample-rests of Freudenthal's samples from the island of Gavdos were washed. The relative stratigraphical positions of these samples are not clear. They are situated in different short sections, which cannot be correlated owing to many faults. No drawn section of these samples can be presented. All samples contain abundant planktonic foraminiferal assemblages, typical for the *N. continuosa* Zone (*N. continuosa, Globoquadrina dehiscens*). Seven of the Gavdos samples contained sufficient *Uvigerina.*

The Miocene sections of Apostoli, Exopolis, Vrysses and Khaeretiana are

all located in the Western part of Crete, while the Pliocene sections are all located in Central Crete. A study was made of some samples from the Miocene in the central region in the province of Iraklion. They are from the locality named Aghios Silas. Six samples were taken just below the gypsum deposits. Three of these contained sufficient *Uvigerina.*

Furthermore the collections of picked specimens of Meulenkamp and Fortuin were available, which are both stored in the Micropaleontological Collections of the Utrecht State University. Collection Meulenkamp is stored under the numbers CH 2175 – 2287 and T 277 – 290. Collection Fortuin is stored under the numbers T 65, T 66 and CH 5814 – 5905. The uvigerinids examined by Zachariasse (1975) were likewise at our disposal. These are stored in the same collection under the numbers CH 5906 – 5926.

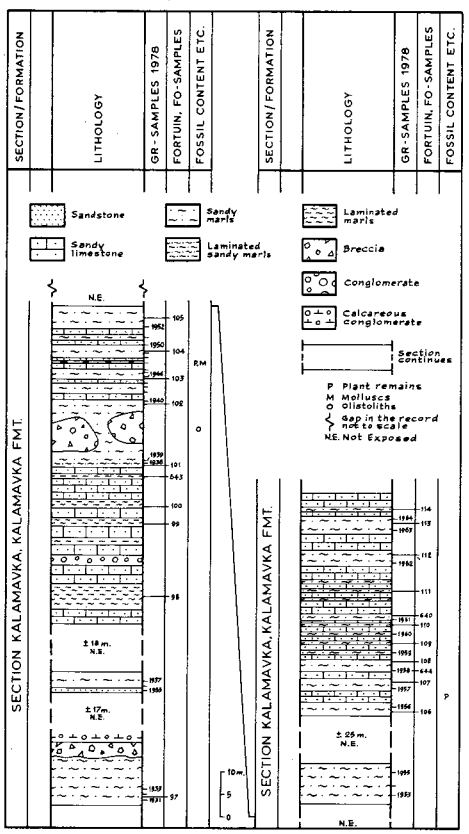


Fig. 11 Section Kalamavka, simplified after Fortuin (1977).

II.4. REMARKS ON THE REWORKING OF FAUNAS

In none of the sections were any indications found that faunas are reworked from older sediments: no markers from older zones have been identified. However, synsedimentary transport of faunas cannot be precluded. The presence of bioclastic limestones with algal fragments and often positive gradation in the sections Apostoli, Exopolis, Vrysses and Khaeretiana seems to indicate that such a transport of material from shallower to deeper parts of the basins did take place. In all these sections transport of foraminiferal faunas is quite conceivable. In sections Vrysses III and Khaeretiana large specimens of *Ammonia beccarii* and *Elphidium crispum* are present. These probably were transported from shallower parts of the basin.

In the lowermost Pliocene deposits of section Prassa II marl breccias are intercalated. Otherwise there are no indications for sediment-transport in the Pliocene sections.

Chapter III

METHODS OF INVESTIGATION

III.1. THE COLLECTING OF THE SPECIMENS

In our preliminary investigation the uvigerinids of individual samples turned out to have a large variation in all characteristics. For this reason we decided to pick fairly large numbers of specimens per sample; i.e. about 50 of the specimens with at least two uniserial chambers.

The number of specimens of *Uvigerina* in the residues varied considerably. The residues of the lithological samples were first scanned to make a rough guess at how much material we would need for an aselect collection of a sufficient number of individuals. Next splits were made with an Otto-sample splitter to obtain the estimated amount of material.

To scan the residues a quantity of material is spread on a picking-tray. This quantity is not an aselect part of the sample, but simply the first material to roll out of the sample-tube. Such an amount of material is called a strewing. Usually *Uvigerina* is enriched in a strewing relative to an aselect split of a comparable quantity of material (see table 1). Large specimens of *Uvigerina* tend to accumulate in the strewing on the picking-tray, whereas small specimens tend to remain behind in the sample-tube. Only samples containing at least ten specimens of *Uvigerina* in the scanned strewing were used. If an interval proved to be of special interest, samples with fewer

Samples	strewing	split	Samples	strewing	split	Samples	strewing	split
CP 561	24	12	CP 1505	49	35	CP 1521	36	30
CP 586	15	15	CP 1507	33	23	CP 1529	14	27
CP 613	24	20	CP 1509	36	27	CP 1530	10	9
CP 512B	17	8	CP 1510	12	8	CP 1531	16	33
CP 514	18	11	CP 1513	33	21	CP 1532	16	10
CP 530	33	23	CP 1515	36	19	CP 1536	26	11
CP 543	37	15	CP 1516	20	9	CP 1542	18	8
CP 547	25	20						
CP 549	54	21						
CP 550	23	20						
CP 552	17	10						

Table 1 Numbers of *Uvigerina* specimens in a strewing and in an aselect split of a comparable quantity of a residue.

Uvigerina-individuals were also made use of, and we made the attempt to obtain a sufficient number of specimens from such an *Uvigerina*-poor sample.

In all, more than 27,000 specimens of *Uvigerina* from more than 400 samples were investigated.

Linear measurements were made by means of an ocular micrometer. All measuring was done with a Leitz binocular microscope, ocular 16 and objective 12, with a precision of half a micrometer unit, corresponding to 5.4 μ. It should be realized that measured values are given in μ, though the inaccuracy range of individual measurements may run to about 5 μ.

All measured specimens were placed in Chapman-slides; they are stored in the Micropaleontological Collections of the Utrecht State University, collection numbers CH 5927 – 6023 and CH 6069 – 6108.

III.2. STUDY OF THE EARLY ONTOGENETIC STAGES

In order to study the early ontogenetic stages of *Uvigerina* a number of specimens was dissolved step by step. The chamberwalls were dissolved one by one, starting with the youngest chamber. To dissolve the calcareous wall dilute HCl (± 5% solution) was applied to the chamberwall with a thin brush. If the process of dissolution threatened to proceed too rapidly and/or too violently we put a concentrated solution of NaOH (± 40%) on the specimen.

The wall of *Uvigerina,* especially that of the older part of the test, appeared to contain much yellowish slime, insoluble in HCl, probably organic material. This slime, which interferes with the measurements, can be brushed away carefully with a thin brush and abundant water.

III.3. PARAMETERS

Counts and measurements were carried out on several features, viz. the length and breadth of the test, the number of uniserial chambers, the arrangement of the uniserial chambers and the relative length of the uniserial part of the test, all in accordance with Meulenkamp (1969). We also counted the number of biserial chambers. See fig. 12 for all parameters.

Length (L)

The length is the total length of the test, indicated by the symbol L. Neither the neck nor the occasionally present apical spine were included in the measurements of L.

Breadth (B)

The maximum breadth of the test is indicated by the symbol B and was

measured as shown in fig. 12. The ratio of L and B was calculated for all measured specimens and is indicated by L/B.

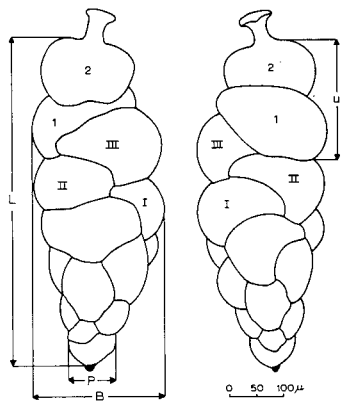


Fig. 12 Schematic drawings illustrating the measuring and counting of the parameters.

Length of the uniserial part of the test (u, R)

The parameter u is the maximum length of the uniserial part of the test. u is measured as shown in fig. 12. u is not used as a separate factor, but only for the calculation of the relative length of the uniserial part of the test. This relative length of the uniserial part of the test is indicated by the symbol R and calculated as follows: $R = u/L \times 100$.

Number of the uniserial chambers (A)

The symbol A indicates the number of uniserial chambers. A chamber is called uniserial when the next and the previous chamber are not in peripheral contact with each other. Only rarely do biserial chambers occur after the first uniserial chamber has been formed. These secondary biserial chambers were counted as uniserial.

There is a problem in differentiating between A = 0 and A = 1. We used Meulenkamp's method (1969), though this method is admittedly subjective. We draw a hypothetical line through the aperture and the initial end in such a way that the biserial character of the last chambers will show up quite clear. When the parts of the last chamber on both sides of the line are more or less of equal size this chamber is regarded as uniserial. An additional aid is found in the position of the neck. In specimens with two or more uniserial chambers there is only rarely a shallow depression at the base of the neck, which widens towards the lower suture. Final chambers with a marked depression are not considered as uniserial.

Number of biserial chambers (BI)

The symbol BI indicates the number of biserial chambers. A chamber is called biserial when the next and the previous chamber are in contact with each other, and the previous chamber is not in peripheral contact with the second next chamber. Problems will arise when a specimen has no uniserial and fewer than three biserial chambers. In such a case a chamber is called biserial if the angle between the central lines through a chamber and the previous one is more than 160° (estimated) in the plane at right angles to the longer axis of the individual (as viewed from above).

Arrangement of the uniserial chambers (s2)

If uniserial chambers are arranged in a staggered superposition they are called primitive uniserial chambers or y-chambers. The planes through the upper and lower sutural planes make a distinct angle with each other. If these planes are parallel to each other or nearly so the chamber is called a fully developed or x-chamber. According to Meulenkamp (1969) the angle between the sutural planes must be 20° or more if the chamber is to be called an y-chamber. This angle is usually not measured, but estimated, however.

Usually an x-chamber is followed only by other x-chambers. Occasionally y-chambers re-occur after the first x-chamber has been formed.

The number of y-chambers relative to the total number of uniserial chambers is indicated by the symbol S. S is calculated as follows: $S = y/A \times 100$.

The S-value for specimens in the ontogenetic stage A = 2 is indicated by the symbol s2. Likewise the S-value for specimens in the ontogenetic stage A = 3 is called s3. The s2-value can be estimated in all specimens that have at least two uniserial chambers.

The s2-value corresponds to a delimited ontogenetic stage of each individual. It should be borne in mind that s2 is in fact a binary parameter. As the first uniserial chamber is always an y-chamber, only values of 50 (one y-chamber, one x-chamber) and 100 (two y-chambers) can occur.

For a biometrical subdivision of his lineages Meulenkamp uses mean A-values in the more primitive parts of the lineages, when only few specimens have at least two uniserial chambers. For the more advanced parts of the lineages he makes use of mean s2-values. The species-boundaries for the lineages are defined as follows (Meulenkamp, 1969; Fortuin, 1974):

Uvigerina cretensis lineage	
U. arquatensis	$\bar{s}2 < 60$
U. lucasi	$60 \leqslant \bar{s}2 < 75$
U. cretensis	$\bar{s}2 \geqslant 75$ and $\bar{A} > 2.10$
U. selliana	$0.80 \leqslant \bar{A} \leqslant 2.10$
U. praeselliana	$\bar{A} < 0.80$
Uvigerina melitensis lineage	
U. felixi	$\bar{s}2 < 60$
U. gaulensis	$60 \leqslant \bar{s}2 < 75$
U. melitensis	$\bar{s}2 \geqslant 75$ and $\bar{A} > 2.10$
U. pappi	$0.50 \leqslant \bar{A} \leqslant 2.10$
U. bononiensis compressa	$\bar{A} < 0.50$

Protoconch-diameter (P)

In a few samples the diameter of the protoconch was measured, and is indicated by the symbol P. P is the largest diameter of the protoconch in the direction parallel to B. The walls of the protoconch are included in the measurement, but the ornamentation is not. In most of the samples P could be measured only after the application of a dilute solution of HCl to the oldest part of the test, so as to dissolve the often heavy ornamentation.

When the specimens are not heavily overgrown with secondary calcite, to distinguish between wall and ornamentation is easy. Between the costae the wall is visible because the pores are not covered by the ornamentation. The costae are dissolved carefully down to the level of the wall with pores.

Total number of chambers (N)

A number of specimens were dissolved chamber by chamber. Of these specimens the total number of chambers making up the test could be counted. This parameter is indicated by the symbol N, and includes triserial, biserial and uniserial chambers.

Lithology-parameter

In some of the sections alternations of laminated and homogeneous sediments occur, or alternations of grey and brown clays. In calculations of the correlation coefficients between the mean values of some of the parameters and the lithology the homogeneous and grey sediments are indicated by the value 0, laminated and brown sediments by the value 2. Weakly laminated sediments and slightly burrowed laminated sediments are indicated by the value 1.

III.4.1. Univariate and bivariate statistics

For each of the samples mean values were calculated for each of the parameters, together with the standard deviations (sd) and the standard errors of the mean (sem). Histograms were drawn of the distributions of some of the parameters for all of the samples. For eleven samples the histograms are given in section IV.2. In the selecting of these samples we took care that the extreme mean values of the parameters were represented together with intermediate values. From the respective groups of samples with high, low and intermediate parameter mean values we chose eleven samples.

For all samples scattergrams were drawn for the parameter combinations A-L, L-B and A-B. For the eleven samples mentioned above the scattergrams are presented in section IV.2. For these samples we calculated the correlation coefficients between the three parameter combinations. The correlation coefficient is indicated by the symbol r and is calculated as follows:

$$r = \frac{\Sigma\ (x_i - \bar{x}) \cdot (y_i - \bar{y})}{\sqrt{\Sigma\ (x_i - \bar{x})^2 \cdot \Sigma\ (y_i - \bar{y})^2}}$$

In this formula x_i and y_i are the i^{th} values of the parameters x and y respectively, and $\bar{x}$ and $\bar{y}$ are their mean values.

For each section we calculated the correlation coefficients between various combinations of parameter mean values.

The correlation coefficients were calculated also between the rank number of the samples and their parameter mean values. This correlation coefficient must be interpreted with reserve in a series of data of a fixed order, as samples in a stratigraphic succession are (Raup, 1977; Drooger, M. M. et al., 1979). Yet the correlation coefficient is thought to give us much information about the presence or absence of "trends", i.e. changes in parameter mean values along the stratigraphical column. A significant correlation coefficient had better not be interpreted heedlessly as having been caused by a sustained change due to evolutional or environmental stress. It should be noted that rank numbers are given to the samples disregarding the possible overlap in time of some of the sections.

For the Miocene samples and those of the Pliocene separately we calculated the correlation coefficients between the parameter mean values and the lithology parameter (possible values 0, 1, 2, see section III.3.).

For the continuous variables L and B a t-test was used to test the hypothesis, that pairs of samples belong to statistical populations with the same mean. It is not postulated, that the samples have also the same variances (Drooger, M. M. et al., 1979). In this t-test the value of t is calculated as follows:

$$t = \frac{(\bar{x}_1 - \bar{x}_2)}{\sqrt{(sem_1^2) + (sem_2^2)}}$$

In this formula $\bar{x}_1$ and $\bar{x}_2$ are the mean values of parameter x for the first and the second sample; sem_1 and sem_2 are their standard errors of the mean. In this test the number of degrees of freedom is approximately equal to the lower of both N values, minus 1.

A median test was used to verify the significance of the differences in the mean values of the binary parameter s2 (Drooger, M. M. et al., 1979). The application of the t-test and the median test to find out the significance of differences in the mean values of A and BI proved to give the same results, so we felt justified in using the t-test in most cases, though A and BI are discrete variables.

To decide on the assumption that a continuous variable can be considered to have a normal distribution we applied a goodness-of-fit test (Thomas, 1975). In this test the observed frequency distribution is compared with the ideal normal distribution with the same mean and the same standard deviation. If for the i^{th} class in the frequency distribution the observed frequency is f_i, the expected frequency is F_i and n is the number of classes, then:

$$\chi^2 = \sum_{i=1}^{i=n} (f_i - F_i)^2 / F_i$$

The number of degrees of freedom is equal to $(n - 3)$.

We calculated for all sections 5-points moving averages. From the samples 1 to 5 of a series of samples we computed the mean value of the 5 mean values. Next we did the same for the value of the mean value of samples 2 to 6, and so on. In this way all minor fluctuations are smoothed out and only more consistent changes remain.

Most of the calculations were carried out with a Canon Canola F 20 P calculator. The more elaborate calculations were made on the Cyber 73/28 computer of the Academic Computer Centre Utrecht. We used the statistical

programs of the Statistical Package for the Social Sciences, SPSS (Nie et al., 1977).

III.4.2. Multivariate statistics

Multivariate analysis is applied to find the structure of a set of data in a multidimensional space. We usually begin a multivariate analysis by calculating the correlation matrix displaying the relationships between all the variables. Next, we use several techniques which will reveal the information hidden in the correlation matrix in a condensed and simplified form.

In principal component analysis we make linear combinations of the original variables. The linear combination, which accounts for the largest part of the variance of the data is the first principal component; the linear combination, which is independent of the first principal component and accounts for the largest part of the variance, which is not accounted for by the first principal component, is the second principal component, etc. There are as many principal components as there are variables, but if the major part of the variance is accounted for by the first principal component we may disregard the rest. For each specimen in the analysis we can calculate a value, i.e. the score with respect to the principal component. This score is a linear combination of the original variables. If the first principal component accounts for the largest part of the variance the score on the first principal component of a specimen is a new variable, which combines most of the information of the original variables.

Discriminant analysis is used to examine the possibility to distinguish between groups of specimens. We place all the specimens in the analysis in groups. A discriminant function is a linear combination of the variables in such a way that the centroids of the groups are as far apart as possible. The significance of differences in the values of the discriminant function can be tested. The specimens can be allocated to the group in which they belong with the largest probability. This allocation of the specimens can be compared with the original grouping.

Cluster analysis can be defined as the attempt to find a natural grouping. It is reasonable to associate the idea of natural grouping with a multimodality of the multivariate distribution. Of the many possible techniques of cluster analysis we used Wishart's mode analysis, which method is a direct search for the modes in the distribution.

For more information, and an explanation of these multivariate methods, we refer to Blackith and Reyment (1971), Scott (1973), Sneath & Sokal (1973) and Marriot (1974).

III.5. REPRODUCIBILITY OF THE COUNTS AND MEASUREMENTS

To gain insight into the amount of subjectivity in counts and measurements some sets of specimens were counted and measured by different people. Some sets of specimens of Meulenkamp were counted and measured anew by us and some of our own samples were counted and measured by colleagues in Utrecht, G. de Man and C. P. Kok. Comparison of the results of various observations by different people can be made from the data of tables 2 and 3.

In 1979 we counted and measured some sets of specimens for the second time. These had been dealt with earlier in 1975 (table 4). The data obtained at different times show no large differences. The differences between the mean values are always less than two sem. The largest differences are observed in the $\overline{s2}$-values.

The comparison of the results as obtained by different authors gives a somewhat more depressing picture. The differences in mean values of L and B are mostly acceptable, i.e. less than two sem. The largest differences are observed between the values obtained by Meulenkamp and us. The differences are consistently in the same direction, i.e. our values are always larger,

Samples	$\overline{L}$ ± sem		$\overline{B}$ ± sem		$\overline{L/B}$ ± sem	
	Meul.	Thomas	Meul.	Thomas	Meul.	Thomas
437–30	534	559 ± 12	186	193 ± 3	2.88 ± 0.06	2.91 ± 0.06
437–27	531	544 ± 9	181	185 ± 3	2.94 ± 0.05	2.95 ± 0.05
437–25	531	543 ± 10	175	181 ± 2	3.04 ± 0.05	3.01 ± 0.06
437–24	540	552 ± 7	188	194 ± 3	2.88 ± 0.04	2.85 ± 0.04
437–15	487	501 ± 7	206	213 ± 2	2.36 ± 0.03	2.35 ± 0.03
437– 4	427	437 ± 5	188	193 ± 2	2.27 ± 0.03	2.26 ± 0.03

Samples	$\overline{A}$ ± sem		$\overline{s2}$ ± sem		$\overline{BI}$ ± sem
	Meul.	Thomas	Meul.	Thomas	Thomas
437–30	3.93 ± 0.13	3.83 ± 0.14	65	74.1 ± 4.7	2.31 ± 0.11
437–27	3.49 ± 0.13	3.53 ± 0.12	67	81.3 ± 4.3	2.25 ± 0.08
437–25	3.49 ± 0.14	3.47 ± 0.15	68	88.2 ± 3.7	2.21 ± 0.11
437–24	2.72 ± 0.15	2.59 ± 0.16	76	82.7 ± 4.7	3.28 ± 0.12
437–15	0.97 ± 0.13	0.87 ± 0.14	93	100 (n=7)	4.10 ± 0.18
437– 4	0.07 ± 0.05	0.21 ± 0.08	—	—	4.03 ± 0.12

Table 2 Mean values from measurements and counts by different people. Meul.: measured or counted by Meulenkamp. The mean values of BI were added, though this parameter has not been counted by Meulenkamp, because these will be referred to in section IV.4.3.

and they may have been caused by the use of different microscopes and different conversion factors of micrometer units into microns. Neither are the differences in mean values of A very large, mostly less than two sem. The only difference larger than two sem was observed in sample 437-4, as measured by Meulenkamp and us. This could be expected: the differentiation between A = 0 and A = 1 is very subjective. In this sample there were only a few specimens with A-values larger than 1.

The mean values of s2, however, are often more than 2 sem apart. We score consistently higher mean s2-values than both Meulenkamp and Kok did. The differences between our mean s2-values and those of De Man are not consistent, though frequently more than 2 sem.

The large differences between the mean s2-values of different authors have likely been caused by the fact that the angle between the sutural planes is not measured, but estimated, in combination with the fact that s2 is actually a binary parameter, which can only have one of two possible values. A difference between an angle of 19° and an angle of 21° is only very small, but it signifies the difference between the value 50 and the value 100 in the s2-factor. Several authors have evidently estimated an angle close to 20° differently, which gives rise to great differences in mean s2-values. In particular if specimens are not well preserved, and projections of the chambers cannot be clearly observed, such differences in estimates will occur.

Moreover, the value of 20° for the angle between the upper and lower sutural plane of the second uniserial chamber is somewhere near the mode of the distribution of the angles in most samples. It is not a low value between two modes of a bimodal distribution. This is illustrated in fig. 13, a histogram which shows the distribution of the angles between the sutural planes of the second uniserial chamber in 25 randomly picked specimens from sample CP 324.

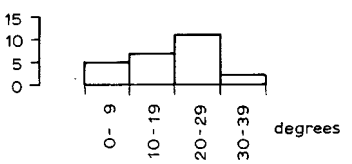


Fig. 13 Histogram of the angles between the upper and lower sutural planes of the second uniserial chamber in 25 randomly picked specimens from sample CP 324 (section Vrysses II).

Conclusions from mean values of s2, obtained by several authors should not be made too carelessly. The same can be said of the comparison of mean A-values, if there are many specimens with A = 0. The differences in such values may have been due to the subjectivity in the observations.

Samples	$\bar{L}$ ± sem		$\bar{B}$ ± sem		$\bar{s}2$ ± sem	
	De Man	Thomas	De Man	Thomas	De Man	Thomas
CP 1295	461 ± 10	465 ± 10	216 ± 4	218 ± 5	75 ± 3.5	76.5 ± 3.5
CP 1286	604 ± 10	602 ± 10	234 ± 4	231 ± 3	89 ± 3.2	96.6 ± 1.9
CP 1285	600 ± 14	583 ± 15	222 ± 4	222 ± 4	91 ± 3.0	89.0 ± 3.3
CP 1217	424 ± 10	426 ± 10	149 ± 2	146 ± 2	69 ± 3.5	63.3 ± 3.2
CP 1209	460 ± 8	458 ± 8	185 ± 3	184 ± 3	76 ± 3.8	92.1 ± 2.8
CP 1208	461 ± 9	454 ± 8	174 ± 3	175 ± 3	73 ± 3.4	73.3 ± 3.3
CP 1207	411 ± 7	411 ± 6	150 ± 2	147 ± 2	84 ± 3.3	73.5 ± 3.6
CP 1203	409 ± 6	407 ± 6	137 ± 2	136 ± 2	71 ± 3.5	64.5 ± 3.3
CP 1201	426 ± 14	409 ± 12	177 ± 6	174 ± 5	68 ± 3.4	72.0 ± 3.6

Samples	$\bar{A}$ ± sem		Samples	$\bar{A}$ ± sem	
	De Man	Thomas		Kok	Thomas
CP 1295	1.90 ± 0.13	1.74 ± 0.14	GR 966	3.24 ± 0.12	3.21 ± 0.12
CP 1286	1.79 ± 0.17	2.01 ± 0.19	GR 965	3.16 ± 0.11	4.18 ± 0.10
CP 1285	2.38 ± 0.21	2.49 ± 0.22	GR 964	3.20 ± 0.12	3.19 ± 0.11
CP 1217	3.40 ± 0.14	3.48 ± 0.15	GR 963	3.10 ± 0.10	3.15 ± 0.10
CP 1209	1.55 ± 0.12	1.65 ± 0.15	GR 962	3.26 ± 0.11	3.26 ± 0.11
CP 1208	1.70 ± 0.12	1.78 ± 0.14	GR 961	2.86 ± 0.12	2.89 ± 0.12
CP 1207	3.31 ± 0.14	3.31 ± 0.15	GR 960	3.18 ± 0.09	3.18 ± 0.09
CP 1203	3.64 ± 0.15	3.60 ± 0.17	GR 958	3.10 ± 0.15	3.08 ± 0.15
CP 1201	2.72 ± 0.17	2.71 ± 0.17	GR 957	3.20 ± 0.11	3.20 ± 0.11
			GR 956	3.04 ± 0.12	3.07 ± 0.10
			GR 955	3.72 ± 0.13	3.72 ± 0.13

Samples	$\bar{L}$ ± sem		$\bar{B}$ ± sem		$\bar{s}2$ ± sem	
	Kok	Thomas	Kok	Thomas	Kok	Thomas
GR 966	525 ± 10	538 ± 8	186 ± 2	190 ± 2	60 ± 2.9	73.2 ± 3.4
GR 965	507 ± 10	521 ± 7	182 ± 2	186 ± 2	68 ± 3.4	80.0 ± 3.3
GR 964	507 ± 10	522 ± 9	186 ± 2	189 ± 2	69 ± 3.5	77.4 ± 3.5
GR 963	510 ± 10	515 ± 7	178 ± 2	182 ± 2	65 ± 3.3	71.7 ± 3.4
GR 962	518 ± 10	528 ± 8	176 ± 2	180 ± 2	77 ± 3.6	85.6 ± 3.2
GR 961	530 ± 12	544 ± 11	194 ± 3	199 ± 2	77 ± 3.6	86.0 ± 3.2
GR 960	525 ± 8	534 ± 8	179 ± 2	183 ± 2	76 ± 3.6	84.3 ± 3.2
GR 958	495 ± 12	503 ± 11	165 ± 3	171 ± 3	78 ± 3.5	83.0 ± 3.5
GR 957	495 ± 10	502 ± 9	168 ± 3	167 ± 2	63 ± 3.1	80.2 ± 3.4
GR 956	500 ± 8	504 ± 9	163 ± 3	168 ± 2	74 ± 3.6	80.9 ± 3.3
GR 955	536 ± 8	543 ± 7	165 ± 2	168 ± 2	77 ± 3.5	80.0 ± 3.2

Table 3 Mean values from measurements and counts by different people.

Samples	$\bar{L}$ ± sem		$\bar{B}$ ± sem	
	1975	1979	1975	1979
CP 344	408 ± 5	405 ± 6	144 ± 2	145 ± 2
CP 324	482 ± 16	485 ± 18	199 ± 7	200 ± 8
CP 287	549 ± 18	550 ± 20	231 ± 8	231 ± 9
CP 278	606 ± 15	602 ± 14	258 ± 4	255 ± 5
CP 270	497 ± 20	497 ± 19	203 ± 8	207 ± 9
CP 211	438 ± 8	436 ± 7	162 ± 2	161 ± 2

Samples	$\bar{A}$ ± sem		$\bar{s}2$ ± sem	
	1975	1979	1975	1979
CP 344	3.87 ± 0.12	3.85 ± 0.11	56.0 ± 2.0	54.0 ± 2.6
CP 324	2.33 ± 0.18	2.30 ± 0.16	71.4 ± 3.6	67.5 ± 3.8
CP 287	2.17 ± 0.16	2.14 ± 0.15	75.0 ± 4.1	74.6 ± 3.8
CP 278	1.88 ± 0.14	1.92 ± 0.15	88.2 ± 3.0	90.0 ± 2.7
CP 270	2.53 ± 0.14	2.60 ± 0.11	65.9 ± 3.4	67.9 ± 4.0
CP 211	2.73 ± 0.15	2.70 ± 0.16	85.0 ± 2.0	87.2 ± 3.1

Table 4 Mean values from measurements and counts by the author at different moments.

III.6. STUDY OF LIGHT STABLE ISOTOPES

An analysis of the stable isotopes of carbon ($^{13}_{12}C$) and oxygen ($^{18}_{16}O$) was made on 47 samples.

The specimens of *Uvigerina* were crushed and heated at a temperature of 470°C for 30 minutes in a helium flow to destroy the organic matter. Uvigerinids proved to contain a relatively high percentage of organic matter. Next the carbonate was treated with 100% H_3PO_4 under vacuum at a temperature of 25.0°C for four hours to extract the CO_2. The CO_2-gas was passed through a trap placed in melting aceton at a temperature of −96°C to remove the water. The gas was collected in a liquid nitrogen-cooled trap at −196°C. The analysis of the samples was made with a Micromass 602C mass spectrometer. All analyzed samples contained at least several hundreds of specimens. They weighed from 1.5 to 40 mgr. As many individuals of *Uvigerina* were needed to make a reliable analysis, only samples with abundant *Uvigerina* could be used in the isotope analyses.

The results of the measurements are given in δ-values, in promille relative to PDB (a belemnite from the PeeDee Formation, used as a standard). Delta is equal to the isotope quotient in the sample, divided by the isotope quotient in the standard, minus 1 and multiplied by 10^3. The isotope quotient is $^{13}C/^{12}C$ or $^{18}O/^{16}O$.

The analyses yielded very reliable and reproducible results. The reproducibility of the values for oxygen and carbon isotopes is about 0.03‰.

All isotope measurements have been carried out by Van der Zwaan.

Chapter IV

RESULTS OF COUNTS AND MEASUREMENTS

IV.1. MEAN VALUES OF THE SAMPLES

Figures 14 and 15 contain the mean values of the parameters that were assumed to be the most relevant to illustrate the changes in the morphology in *Uvigerina*. The Miocene values are shown in fig. 14, the Pliocene values in fig. 15. The values of the samples from section Prassa are given in two parts, above and below the hiatus. The vertical lines in the mean A and mean s2 graphs represent the biometrical species boundary as have been defined by Meulenkamp (1969) and Fortuin (1974). The average range of the standard errors of the mean is indicated above each column. The samples are placed at equal distances, though the real distances between the samples are not equal because not all sections were sampled with the same interval between the lithological samples, and not all samples contained a sufficient amount of *Uvigerina*. For the real distances between the lithological samples see figs. 2 to 9 in chapter II.

In the graphs the groups of mean values representing the sections are placed above each other. This superposition in the figures is not meant to suggest a precise succession in time. There may be overlaps in time between some sections (see figs. 6 and 10, chapter II). Datum levels are indicated next to the graphs.

The mean values of the mean values per section are given in tabel 5, together with their standard errors of the mean. These data are also shown in fig. 16.

Figure 17 shows histograms of the frequency distributions of some mean values for all of the sections.

In table 6 the correlation coefficients are tabulated for some combinations of parameter mean values for all sections. Table 7 demonstrates the correlation coefficients between the rank numbers of the samples and the parameter mean values for all sections separately. In table 8 the correlation coefficients are tabulated between the parameter mean values and the sample rank numbers for all Miocene samples and for all Pliocene samples separately. The possible overlap in time between some of the sections is neglected in the assignment of rank numbers to the samples.

Table 9 shows the correlation coefficients between the lithology parameter and the mean values of some parameters for all Miocene values together, as well as for all Pliocene values.

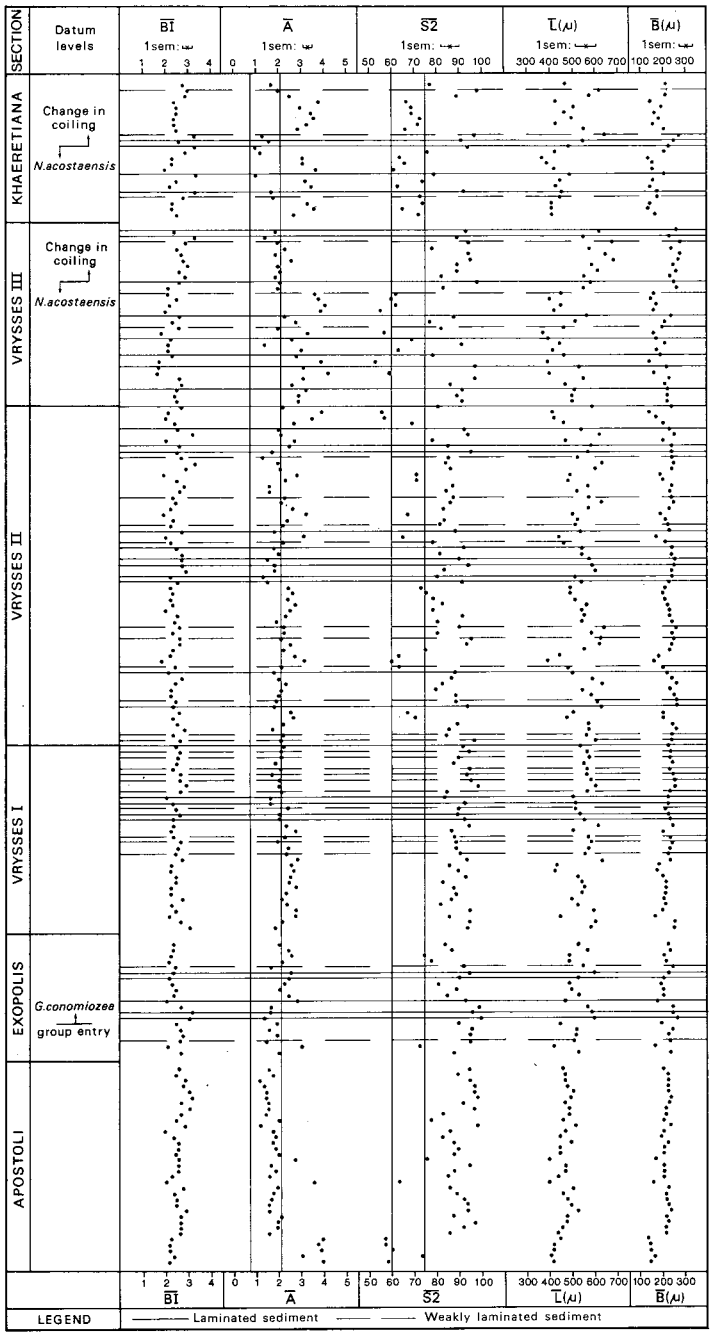


Fig. 14 The mean values of L, B, A, BI and s2 of all Miocene samples in stratigraphical succession. The average standard errors of the means are indicated above the columns. The vertical lines represent the species boundaries after Meulenkamp (1969) and Fortuin (1974).

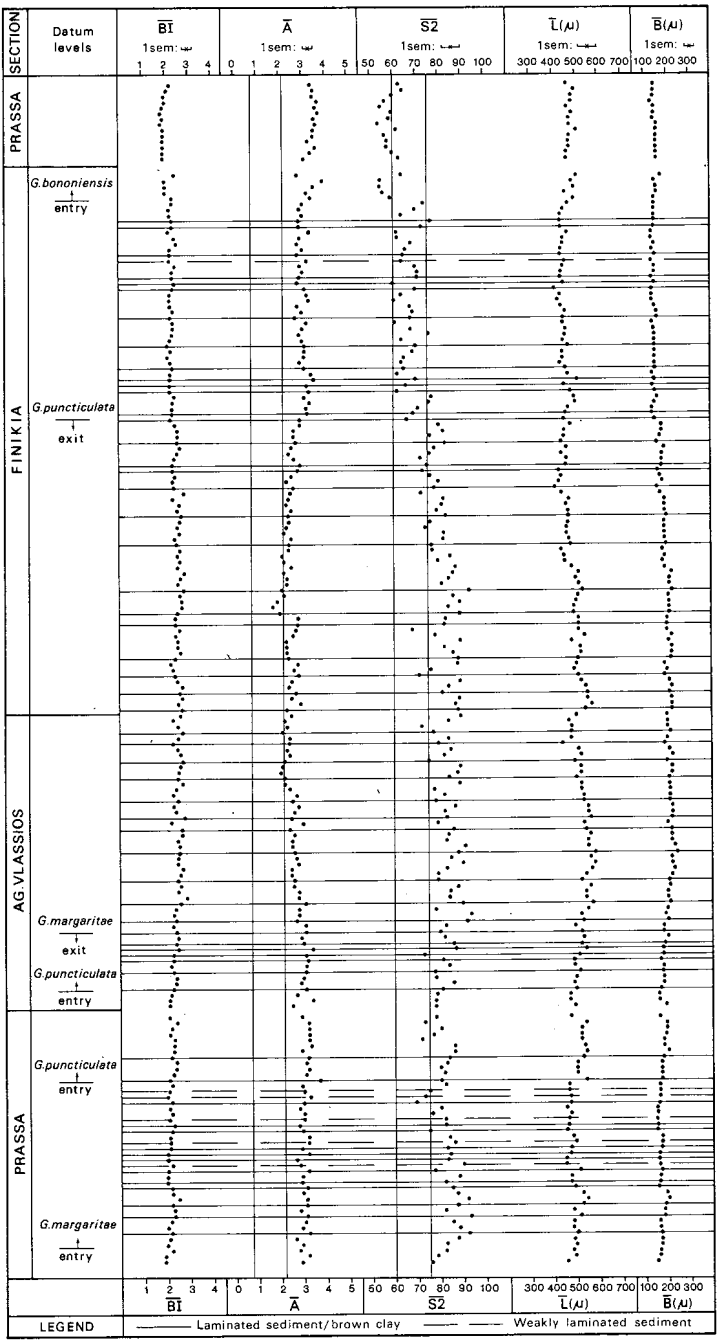


Fig. 15 The mean values of L, B, A, BI and s2 for all Pliocene samples in stratigraphical succession.

Sections	$\overline{L}$ ± sem	$\overline{B}$ ± sem	$\overline{A}$ ± sem	$\overline{BI}$ ± sem	$\overline{s2}$ ± sem
Prassa	483 ± 3	153 ± 2	3.49 ± 0.04	1.93 ± 0.03	59.2 ± 0.8
Finikia	473 ± 3	177 ± 4	2.74 ± 0.04	2.39 ± 0.02	74.6 ± 1.0
Ag. Vlassios	521 ± 4	202 ± 3	2.66 ± 0.05	2.46 ± 0.02	82.9 ± 0.7
Prassa	489 ± 4	167 ± 3	3.03 ± 0.03	2.16 ± 0.02	81.9 ± 0.8
Khaeretiana	475 ± 15	188 ± 8	2.59 ± 0.19	2.63 ± 0.08	76.6 ± 2.4
Vrysses III	510 ± 16	213 ± 7	2.47 ± 0.14	2.40 ± 0.06	80.3 ± 2.6
Vrysses II	540 ± 8	226 ± 3	2.22 ± 0.06	2.42 ± 0.04	81.3 ± 1.3
Vrysses I	542 ± 9	220 ± 4	2.21 ± 0.06	2.43 ± 0.04	89.4 ± 0.7
Exopolis	512 ± 11	213 ± 6	2.05 ± 0.10	2.42 ± 0.07	88.1 ± 1.7
Apostoli	454 ± 6	198 ± 5	1.99 ± 0.14	2.48 ± 0.05	84.4 ± 2.1

Table 5 Mean values of the mean values per section.

Sections	$\overline{A}$–$\overline{s2}$	$\overline{B}$–$\overline{s2}$	$\overline{s2}$–$\overline{s3}$	$\overline{A}$–$\overline{B}$	n
Prassa	–0.42	+0.06	**+0.74**	–0.49	14
Finikia	**–0.79**	**+0.82**	**+0.95**	**–0.78**	96
Ag. Vlassios	–0.04	+0.35	**+0.81**	**–0.63**	51
Prassa	–0.18	–0.21	**+0.92**	+0.29	44
Khaeretiana	**–0.80**	**+0.77**	**+0.97**	**–0.75**	24
Vrysses III	**–0.87**	**+0.88**	**+0.96**	**–0.76**	31
Vrysses II	**–0.72**	**+0.85**	**+0.94**	**–0.78**	60
Vrysses I	–0.17	**+0.49**	**+0.77**	**–0.62**	33
Exopolis	**–0.67**	**+0.65**	**+0.94**	**–0.85**	20
Apostoli	**–0.94**	**+0.93**	**+0.76**	**–0.95**	35
Sections	$\overline{A}$–$\overline{L}$	$\overline{L}$–$\overline{s2}$	$\overline{L}$–$\overline{B}$	$\overline{A}$–$\overline{BI}$	n
Prassa	+0.48	+0.21	–0.02	–0.03	14
Finikia	–0.13	**+0.46**	**+0.71**	**–0.80**	96
Ag. Vlassios	+0.04	**+0.48**	**+0.67**	**–0.46**	51
Prassa	**+0.64**	+0.17	**+0.87**	+10	44
Khaeretiana	*–0.45*	**+0.69**	**+0.87**	**–0.89**	24
Vrysses III	**–0.57**	*+0.43*	**+0.95**	**–0.62**	31
Vrysses II	**–0.53**	**+0.79**	**+0.92**	**–0.56**	60
Vrysses I	–0.18	**+0.56**	**+0.82**	*–0.35*	33
Exopolis	**–0.54**	**+0.64**	**+0.82**	**–0.81**	20
Apostoli	**–0.70**	**+0.70**	**+0.83**	**–0.63**	35

Table 6 Correlation coefficients between mean values.
bold $r \geqslant r_{0,995}$
italics $r \geqslant r_{0,975}$
n is the number of samples

Sections	$\overline{A}$	$\overline{BI}$	$\overline{s2}$	n
Prassa	+0.51	+0.73	+0.16	14
Finikia	+0.68	−0.70	−0.81	96
Ag. Vlassios	−0.82	+0.42	+0.15	51
Prassa	*+0.34*	+0.44	−0.43	44
Khaeretiana	−0.08	+0.17	+0.19	24
Vrysses III	−0.20	*+0.44*	+0.22	31
Vrysses II	+0.21	+0.13	−0.10	60
Vrysses I	−0.47	+0.10	+0.26	33
Exopolis	+0.28	*−0.45*	−0.23	20
Apostoli	−0.44	+0.45	+0.54	35

Sections	$\overline{L}$	$\overline{B}$	$\overline{L/B}$	n
Prassa	+0.32	−0.84	+0.84	14
Finikia	−0.60	−0.87	+0.80	96
Ag. Vlassios	−0.03	+0.64	−0.87	51
Prassa	*+0.31*	*+0.30*	−0.17	44
Khaeretiana	+0.55	*+0.46*	−0.19	24
Vrysses III	+0.65	+0.55	+0.04	31
Vrysses II	−0.15	*−0.25*	+0.10	60
Vrysses I	−0.18	*+0.42*	−0.50	33
Exopolis	+0.21	−0.06	+0.25	20
Apostoli	*+0.39*	+0.50	−0.46	35

Table 7 Correlation coefficients between sample rank-numbers and mean parameter values.
bold $r \geqslant r_{0,995}$
italics $r \geqslant r_{0,975}$
n is the number of samples

	$\overline{A}$	$\overline{BI}$	$\overline{s2}$	$\overline{L}$	$\overline{B}$	n
Pliocene	+0.14	−0.08	−0.70	−0.39	−0.27	205
Miocene	+0.24	+0.10	−0.26	+0.11	−0.02	203

Table 8 Correlation coefficients between mean values and the sample rank-numbers for all Miocene samples and for all Pliocene samples.
bold $r \geqslant r_{0,995}$
italics $r \geqslant r_{0,975}$
n is the number of samples

	$\overline{L}$	$\overline{B}$	$\overline{A}$	$\overline{s2}$	$\overline{BI}$	n
Pliocene	−0.04	−0.03	−0.01	+0.06	+0.11	205
Miocene	+0.21	+0.19	−0.18	+0.22	+0.22	203

Table 9 Correlation coefficients of the mean values and the lithology (0 = homogeneous, 1 = weakly laminated, 2 = laminated). A positive value of r signifies high mean values in laminated sediments, a negative value of r signifies low mean values in laminated sediments.
bold $r \geqslant r_{0,995}$
italics $r \geqslant r_{0,975}$
n is the number of samples

Evidently the existence of a directional, rather smooth trend in time is out of the question for all parameters. All parameters, including the s2 factor, which has been reported to "show a decrease without modal fluctuations of any importance" (Meulenkamp, 1969, p. 122) show a succession of small steps with large random fluctuations in all sections. Not only is it clearly impossible to place "scattered samples from small sections in the biostratigraphical succession" (Fortuin, 1974, p. 40), but it would be quite difficult to place even fairly long successions of samples in their proper place in the biostratigraphical sequence.

Even the mean values per section (fig. 16) show no evident sustained changes. The mean A value per section increases steadily in the Miocene up to the Lower Pliocene, but shows a decrease in the sections Ag. Vlassios and Finikia, only to increase again in the upper part of section Prassa.

The mean s2 value per section increases at first in the Miocene, shows a decrease in the higher Miocene sections, increases again in the lower part of section Prassa and in section Ag. Vlassios, and finally decreases strongly in the sections Finikia and in the upper part of section Prassa.

The mean values of the mean values of L and B per section show a fluctuating pattern resembling the pattern of the mean s2 values, that is, at first

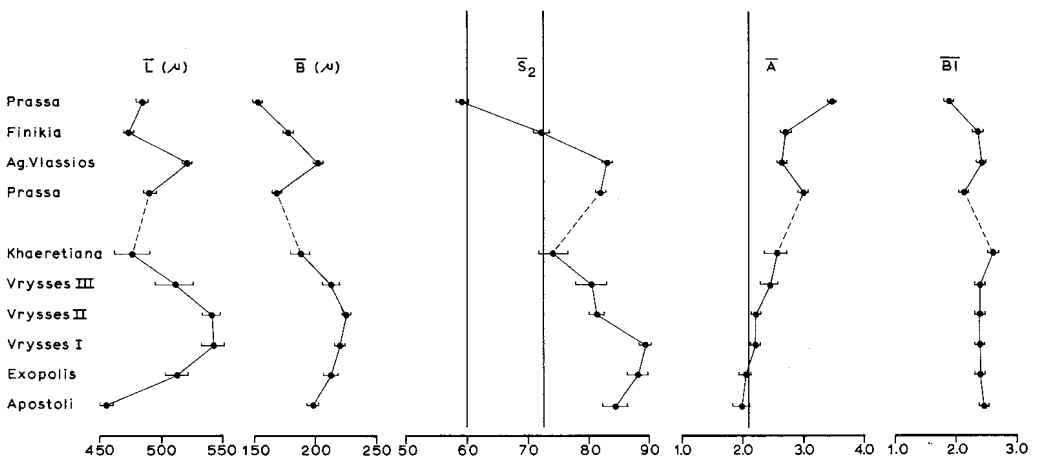


Fig. 16 The mean values of the mean values of L, B, A, BI and s2 per section.

an increase in the Miocene, followed by a decrease; in the Lower Pliocene again an increase, which in the mean values of L and B occurs somewhat higher in the stratigraphical column than the increase in the mean s2 values (in section Ag. Vlassios). In the Pliocene section Finikia and in the upper part of section Prassa the mean values per section of L and B decrease again.

The mean values per section of BI display a slight increase in the Miocene. The lowest Pliocene section has a lower mean BI value than the highest Miocene section. We observe an increase in the mean BI value in the Pliocene in the sections Ag. Vlassios and Finikia, and a decrease in the upper part of section Prassa.

The histograms of fig. 17 show no consistently shifting arrangement from the oldest to the youngest section, not for any of the parameters. If one considers the seemingly random fluctuations per section it is remarkable that the distributions of the means per section sometimes largely deviate from a normal distribution, particularly as regards the parameters B and s2 in the sections Apostoli, Exopolis, Vrysses II, Vrysses III, Khaeretiana and Finikia. Table 7 clearly shows that the correlation coefficients between the rank sample numbers and the mean values give no consistent picture for any parameter, in any of the sections. For all parameters both positive and negative values of r occur. Both significant increases and significant decreases are present in the succession of the mean values of all parameters.

If we consider the correlation coefficients between the sample rank numbers and the parameter mean values for all Miocene samples we see that the mean value of A increases significantly, whereas the mean value of s2 decreases significantly. These are the trends we expected to find. The other parameter mean values display no significant changes. Evidently one will have to consider a huge amount of samples to be able to show the presence of the expected trends, which are often (table 7) absent or even reversed in single sections.

In the Pliocene the correlation coefficients are significant for the mean values of s2, L and B, which all display a significant decrease. The decrease in the mean values of s2 is as expected; the mean values of A are not significantly correlated with the rank numbers of the samples.

Although the mean values of s2 show a significant decrease in both the Miocene and in the Pliocene the Lower Pliocene parameter mean values are not situated on the extrapolation of the Miocene trend, but are much higher.

Summarizing we may state that the expected trends can be demonstrated to exist only in a very general way. The fluctuations against the direction of the trends are comparatively enormous. Even a succession of as many as

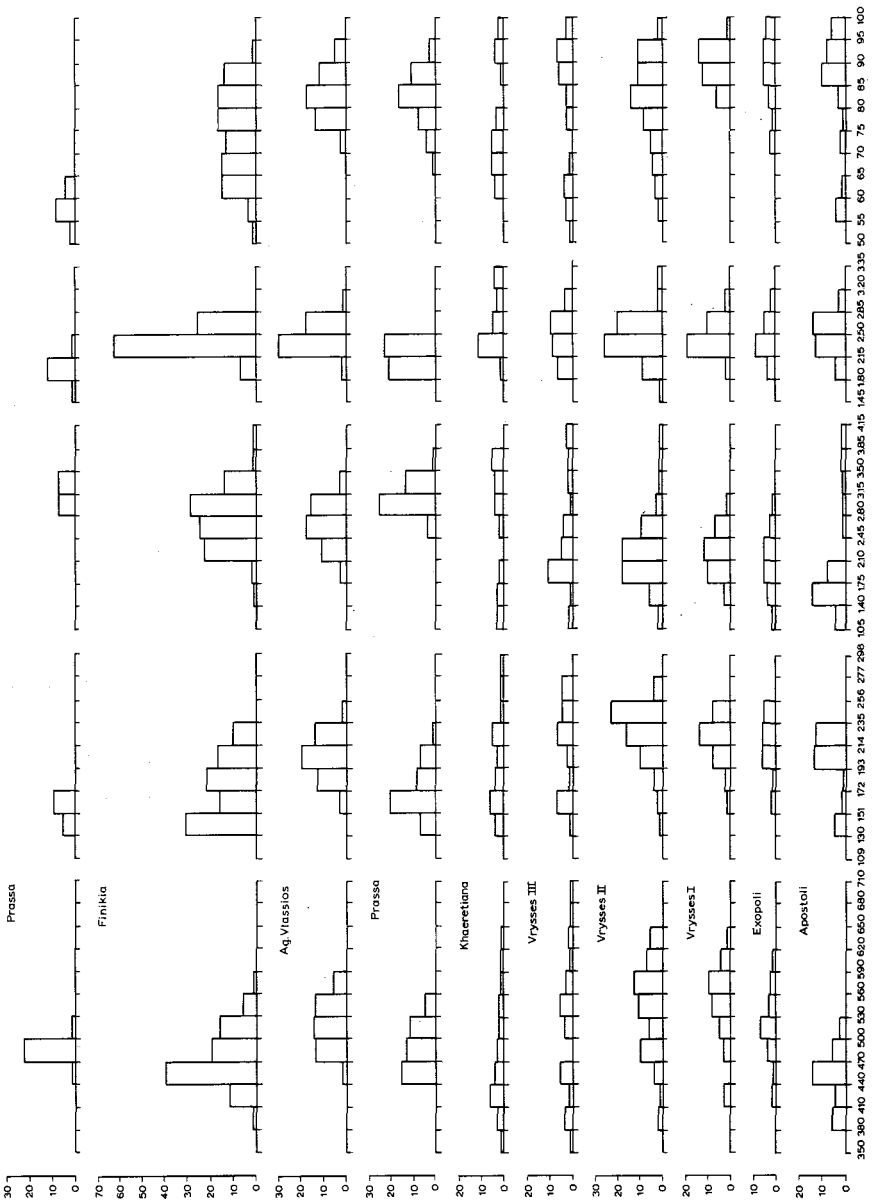


Fig. 17 Histograms of the mean values of L, B, A, BI and s2 per section.

50 samples (section Ag. Vlassios) shows a significant decrease in the mean values of A.

Table 6 and figs. 14 and 15 clearly indicate that most of the parameters pairwise show consistent significant correlations in many of the sections, even if the correlation does not seem to make sense considering the construction scheme of the uvigerinid test. For example, it seems reasonable to expect a positive correlation between mean A and mean L values. More often, however, a negative correlation is found. A correlation between mean L or B and the mean s2 value is not expected but does often occur.

There is a correlation between (almost) all the pairs of parameters in the sections Apostoli, Exopolis, Vrysses II and III, Khaeretiana and Finikia, i.e. the sections in which the distributions of the mean values of some parameters deviate largely from a normal distribution, as mentioned above.

The correlation of almost all pairs of mean parameter values gives a consistent picture. If there is a correlation it is always positive or always negative. The one exception to this rule is the correlation of mean A and mean L which is significantly positive in the lower part of section Prassa, but negative in all other sections where this correlation is significant.

The presence of many significant correlations between different pairs of mean parameter values means that samples that are extreme in one parameter are also extreme in other parameters. Likewise, "normal" samples are normal in all parameters. Extreme samples in opposite directions are different in all measured characteristics; i.e. they do not resemble each other at all.

Significant values of the correlation coefficients between lithology and mean parameter values have been found only in the Miocene, where all mean values, for which this correlation coefficient has been calculated, are significantly correlated with the lithological types. In laminated sediments L, B, BI and s2 have larger mean values and A has smaller mean values that in homogeneous sediments.

IV.2. THE DISTRIBUTION OF THE PARAMETER VALUES IN THE SAMPLES

The mean values of the successive samples display a pattern of large fluctuations superimposed on weak trends. This pattern does not suggest a clear-cut relation between the morphological changes in *Uvigerina* and time or sediment type. Only in the Miocene do some relations with the lithology seem to exist. The distributions of the parameter values within the samples appear to give more information.

The distributions were studied in all samples; the data are presented for only eleven. These samples were selected in such a way that high, low and intermediate mean values of the parameters are represented. As all parameters are either positively or negatively correlated with each other samples with an extreme mean value for one parameter have also extreme mean values of the other parameters.

The histograms for some parameters of the eleven Miocene and Pliocene samples are given in figs. 18 and 19. Table 10 tabulates the mean values and the standard errors of the mean of these samples. The distributions of the continuous variable B and sometimes also of L deviate strongly from a normal distribution for some of the samples (CP 2173, CP 2071, CP 324, CP 287, CP 270). A goodness-of-fit test was applied to the B-distributions of all eleven samples. We did not test the L-distributions. The results are given in table 11. All five samples enumerated above may indeed be considered to be not normally distributed as to B. The other samples do not deviate significantly from normality. In the histograms the non normal samples show a bimodal distribution of B. Most of the other samples have one mode

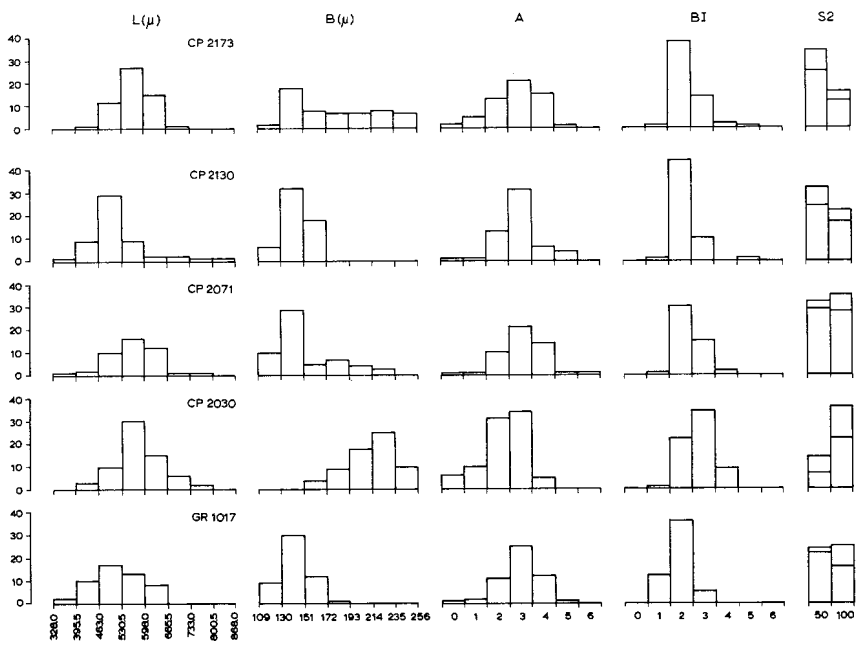


Fig. 18 Histograms of L, B, A, BI and s2 for five selected Pliocene samples. The lower line in the s2-histograms shows the number of specimens with A > 2.

corresponding in position with one or the other mode in the bimodal samples.

This seems to suggest the presence of two different groups of *Uvigerina,* one with small and the other with large values of B, or thin and thick *Uvigerina.* From the shape of the histograms it is evident that intermediate types do occur.

If we look at the shape of the chambers of the uvigerinids two different types can be observed also, one with scarcely depressed sutures, the other with bloated chambers. It should be noted that intermediate types are met with (fig. 20), but in most samples these are rare. Specimens like a and b in fig. 20, and like e and f constitute the major part of most samples. Specimens like c and d are found only in minor numbers in most of the samples. Some, however, as for instance CP 211 and GR 1017 consist predominantly of such specimens.

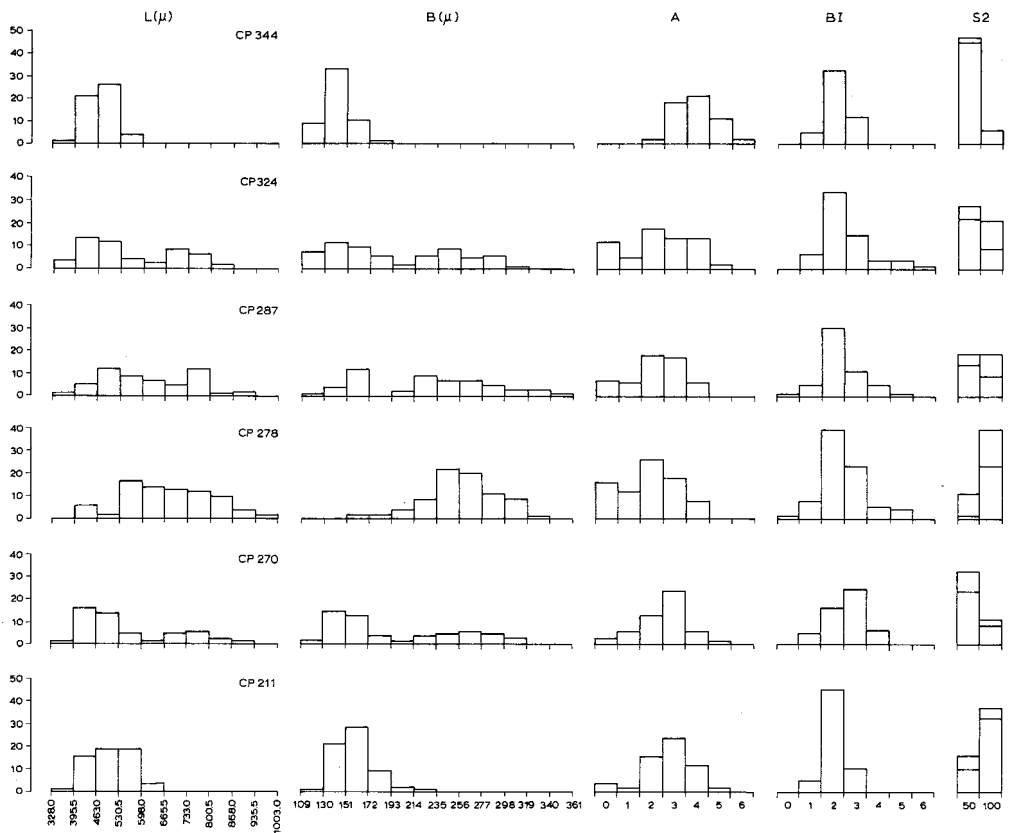


Fig. 19 Histograms of L, B, A, BI and s2 for six selected Miocene samples. The lower line in the s2-histograms shows the number of specimens with A > 2.

Samples	$\overline{L}$ ± sem	$\overline{B}$ ± sem	$\overline{A}$ ± sem	n
CP 2173	506 ± 7	182 ± 5	2.79 ± 0.14	57
CP 2130	452 ± 11	150 ± 2	2.93 ± 0.12	56
CP 2071	498 ± 11	157 ± 4	3.08 ± 0.15	49
CP 2030	514 ± 9	215 ± 3	2.18 ± 0.13	66
GR1017	454 ± 9	146 ± 2	2.92 ± 0.13	52
CP 344	408 ± 5	144 ± 2	3.87 ± 0.12	53
CP 324	482 ± 16	199 ± 7	2.33 ± 0.18	66
CP 287	549 ± 18	231 ± 8	2.17 ± 0.16	54
CP 278	606 ± 15	258 ± 4	1.88 ± 0.14	78
CP 270	497 ± 20	203 ± 8	2.53 ± 0.14	53
CP 211	438 ± 8	162 ± 2	2.73 ± 0.15	60

Samples	$\overline{BI}$ ± sem	$\overline{s2}$ ± sem	$\overline{L/B}$ ± sem	n
CP 2173	2.35 ± 0.12	63.9 ± 3.7	2.88 ± 0.08	57
CP 2130	2.21 ± 0.10	70.4 ± 3.4	3.01 ± 0.06	56
CP 2071	2.36 ± 0.13	76.6 ± 3.7	3.26 ± 0.12	49
CP 2030	2.77 ± 0.11	86.0 ± 3.2	2.40 ± 0.04	66
GR1017	1.87 ± 0.12	75.5 ± 3.6	3.13 ± 0.06	52
CP 344	2.09 ± 0.11	56.0 ± 2.0	2.84 ± 0.04	53
CP 324	2.50 ± 0.16	71.4 ± 3.6	2.47 ± 0.05	66
CP 287	2.32 ± 0.16	75.0 ± 4.1	2.41 ± 0.04	54
CP 278	2.43 ± 0.14	88.2 ± 3.0	2.34 ± 0.04	78
CP 270	2.60 ± 0.14	65.9 ± 3.4	2.46 ± 0.05	53
CP 211	2.09 ± 0.13	85.0 ± 2.0	2.71 ± 0.05	60

Table 10 Mean values and standard errors of the mean for eleven selected samples. n is the number of specimens in the sample. The number of specimens with 2 or more uniserial chambers is about 50.

The group of thin uvigerinids which can be recognized in the histograms proved to be about identical with the group with scarcely depressed sutures; the group of thick specimens with that with bloated chambers. The specimens intermediate in inflatedness of the chambers are often close to the thin group in value of B, but sometimes intermediate between the thin and the thick. Some samples contain the thin group, the intermediate group, or the thick group exclusively, other samples contain a mixture of both extreme groups with some intermediate specimens.

We tried to separate the specimens of the extreme groups. Intermediates play a role for calculations if they are the predominant element in the samples. The criterion of separating, admittedly subjective, is the degree

	f_i	F_i	$\frac{(f_i - F_i)^2}{F_i}$
CP 2173			
< 146.25	16	9.69	4.11
146.25 – 172.50	13	15.96	0.55
172.50 – 198.75	12	17.10	1.52
> 198.75	16	14.25	0.21 +
			χ^2 = 6.39
CP 2130			
< 131.25	7	7.84	0.09
131.25 – 142.50	18	17.92	0.00
142.50 – 153.75	18	19.04	0.06
> 153.75	13	11.20	0.29 +
			χ^2 = 0.44
CP 2071			
< 146.25	30	21.56	3.30
146.25 – 172.50	6	15.68	6.64
172.50 – 198.75	9	9.31	0.01
> 198.75	4	2.45	0.98 +
			χ^2 = 10.98
CP 2030			
< 181	11	8.58	0.68
181 – 206	20	22.44	0.27
206 – 231	27	24.42	0.27
> 231	8	10.56	0.62 +
			χ^2 = 1.84
GR 1017			
< 133.75	13	15.08	0.29
133.75 – 147.50	26	22.36	0.59
147.50 – 161.50	11	11.96	0.08
> 161.50	2	2.60	0.14 +
			χ^2 = 1.10
CP 344			
< 131	18	12.08	2.90
131 – 141	17	19.27	0.29
141 – 151	11	14.69	0.93
> 151	7	6.97	0.00 +
			χ^2 = 4.12
CP 324			
< 164	31	20.96	4.81
164 – 204	8	18.90	6.35
204 – 249	15	17.09	0.26
> 249	12	8.95	1.04 +
			χ^2 = 12.46
CP 287			
< 172	17	10.80	3.56
172 – 235	11	20.52	4.42
235 – 298	19	17.28	0.14
> 298	7	5.40	0.47 +
			χ^2 = 8.45
CP 278			
< 193.75	5	4.00	0.25
193.75 – 232.50	17	21.60	0.98
232.50 – 271.50	40	35.20	0.65
> 271.50	18	19.20	0.08 +
			χ^2 = 1.96
CP 270			
< 151	19	11.60	4.73
151 – 201	11	16.94	2.08
201 – 251	10	15.88	2.18
> 251	13	8.82	1.99 +
			χ^2 = 10.98
CP 211			
< 138.75	5	9.00	1.78
138.75 – 162.50	35	29.40	1.07
162.50 – 186.25	17	19.20	0.25
> 186.25	3	2.40	0.14 +
			χ^2 = 3.25

	$P_{97.5}$	$P_{99.0}$
χ^2:	5.02	6.64

The number of degrees of freedom is equal to 1

Table 11 χ^2-values for parameter B for the eleven selected samples of table 10.

of inflatedness of the chambers. The thick type (e and f in fig. 20) has bloated chambers, whereas in the thin type (a and b in fig. 20) the sutures are scarcely depressed. The thick specimens are thick-set and possess usually only a few uniserial chambers. Values of A = 4 or even A = 5 are found within this group, but very rarely; values of A = 2 and A = 3 are normal. The uniserial chambers are often arranged in a staggered series. The biserial part of the test is frequently twisted. In the literature these specimens are called "primitive". The thin specimens are small and slender and the chambers are not inflated. They usually possess from three to five uniserial chambers, which are arranged regularly. Thin uvigerinids are called "advanced" or "highly evolved" in the literature. The intermediate specimens (c and d in fig. 20) have a fairly slender test and slightly inflated chambers. They usually possess 2 to 4 uniserial chambers.

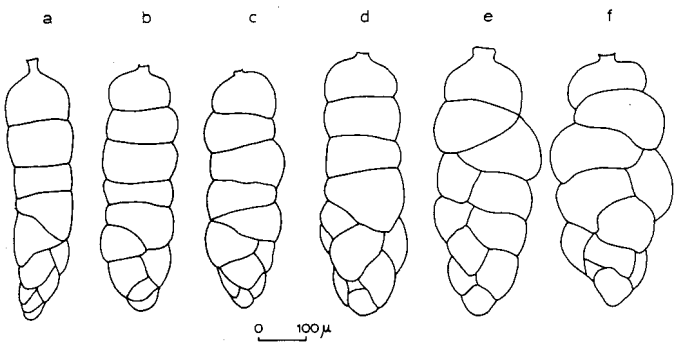


Fig. 20 Schematical drawings of some specimens from sample CP 324 (section Vrysses II) illustrating the inflatedness of the chambers.

It should be realized that up to the splitting of the uvigerinids into two (or three) groups reproducible procedures were made use of. We made aselect splits and the calculation of the means is an objective procedure. The demonstration that the distributions of the breadth is in some samples not a normal distribution is likewise wholly reproducible. But the splitting of the uvigerinids into groups, which separately we hopefully imagine to be homogeneous, is entirely subjective, as subjective in fact as a species determination by way of the resemblance of specimens to a figured holotype. We had to make the choice, however; it would have been absurd to use mean values as a centre-value for samples that clearly display a bimodal distribution, and to use statistical tests designed for samples with a normal distribution is likewise absurd.

In the calculation of the mean values for the extreme separate groups in the samples the small numbers of intermediate specimens were excluded. It should be realized that this exclusion will make the differences between the mean values of the groups apparently greater than they really are. However, samples with only thin uvigerinids or only thick ones do not show mean values that differ much from those of the groups obtained from samples with both groups after splitting. Probably the above mentioned effect of enlargement of the differences between the groups is negligeable.

We are well aware that the elaborate techniques described in section IV.6., implying the use of a computer, are no good at all if the separation into two groups might ever turn out to be spurious. In this respect it must be emphasized that there is a fair danger, once we consider the regular presence of the intermediate specimens throughout the Miocene and part of the Pliocene.

In the majority of the samples it appeared to be possible to separate both groups of *Uvigerina*. In the Miocene only a few specimens per sample proved to be intermediate. In a few Miocene samples (for instance sample CP 211 of which histograms are given in fig. 19) it was not possible to make this distinction. These samples contain homogeneous groups of specimens intermediate between thick and thin uvigerinids. No attempt was made to split these samples artificially into two groups, though some specimens might have been earmarked as either thick or thin.

In the Pliocene the situation presented more difficulties. In the lowest Pliocene more than 40 samples have characteristics intermediate between the thick and the thin type. These samples were all labelled intermediate. Higher in the Pliocene the two types are again easily distinguishable. Samples which contain about equal numbers of thick and thin specimens are quite common in the Miocene, but rare in the Pliocene.

More information about the mean values of the separate groups is given in section IV.3.

For the eleven samples for which histograms were given (figs. 18, 19) mean values were calculated for the separate groups (table 12). Scattergrams of all samples were made for the combinations of the parameters A and L, A and B, and L and B. For the eleven samples mentioned above these scattergrams are given in figs. 21–23. The correlation coefficients for these parameter combinations were calculated and are shown in table 13.

In the scattergrams the thick type and the thin type plot fairly well in separate clusters for the combinations L-B and A-B, but in most cases not so for the combination A-L. B evidently is the main discriminating parameter.

Samples	thick	$\overline{L}$ ± sem interm.	thin	thick	$\overline{B}$ ± sem interm.	thin
CP 2173	507 ± 10 (29)	— (2)	505 ± 11 (26)	213 ± 4		147 ± 2
CP 2130			452 ± 11 (56)			150 ± 2
CP 2071	482 ± 16 (18)	— (1)	511 ± 15 (30)	192 ± 5		136 ± 1
CP 2030	514 ± 9 (66)			215 ± 3		
GR1017		454 ± 9 (52)			146 ± 2	
CP 344			408 ± 5 (53)			144 ± 2
CP 324	540 ± 21 (40)	— (1)	395 ± 8 (25)	229 ± 8		142 ± 2
CP 287	614 ± 18 (37)		410 ± 8 (17)	264 ± 6		156 ± 3
CP 278	606 ± 15 (78)			258 ± 4		
CP 270	569 ± 26 (28)		397 ± 8 (23)	242 ± 9		146 ± 2
CP 211		438 ± 8 (60)			162 ± 2	

Samples	thick	$\overline{L/B}$ ± sem interm.	thin	thick	$\overline{A}$ ± sem interm.	thin
CP 2173	2.39 ± 0.06		3.42 ± 0.07	2.26 ± 0.20		3.41 ± 0.12
CP 2130			3.01 ± 0.06			2.93 ± 0.10
CP 2071	2.50 ± 0.07		3.76 ± 0.11	2.61 ± 0.20		3.38 ± 0.19
CP 2030	2.40 ± 0.03			2.18 ± 0.13		
GR1017		3.13 ± 0.06			2.92 ± 0.13	
CP 344			2.84 ± 0.04			3.87 ± 0.12
CP 324	2.29 ± 0.05		2.79 ± 0.06	1.55 ± 0.19		3.60 ± 0.18
CP 287	2.32 ± 0.04		2.65 ± 0.09	1.76 ± 0.18		3.20 ± 0.18
CP 278	2.34 ± 0.05			1.88 ± 0.14		
CP 270	2.34 ± 0.06		2.73 ± 0.07	2.06 ± 0.17		3.32 ± 0.17
CP 211		2.71 ± 0.05			2.73 ± 0.15	

Samples	thick	$\overline{BI}$ ± sem interm.	thin	thick	$\overline{s2}$ ± sem interm.	thin
CP 2173	2.58 ± 0.14		2.08 ± 0.08	75.0 ± 5.2 (24)		54.1 ± 4.4 (26)
CP 2130			2.21 ± 0.10			70.4 ± 3.4 (54)
CP 2071	2.58 ± 0.16		2.24 ± 0.09	— (8)		60.2 ± 5.6 (26)
CP 2030	2.77 ± 0.11			86.0 ± 3.2 (50)		
GR1017		1.87 ± 0.12			75.5 ± 3.6 (49)	
CP 344			2.09 ± 0.11			56.0 ± 2.0 (53)
CP 324	2.80 ± 0.19		2.04 ± 0.12	91.3 ± 4.0 (26)		52.0 ± 2.0 (21)
CP 287	2.42 ± 0.17		2.00 ± 0.14	88.6 ± 4.6 (20)		56.7 ± 4.5 (15)
CP 278	2.43 ± 0.14			88.2 ± 3.0 (51)		
CP 270	2.84 ± 0.14		2.28 ± 0.19	84.0 ± 5.1 (25)		50.0 (19)
CP 211		2.09 ± 0.13			85.0 ± 2.0 (53)	

Table 12 Mean values and standard errors of the mean for the separate groups in the eleven selected samples. The numbers between brackets are the numbers of specimens.

The significant, negative correlations within the samples between L and A and between B and A are evidently due to the mixing of the two types of *Uvigerina* because the significance disappears within the homogeneous groups. A significant positive correlation between L and B nearly always occurs within the thick group, and only rarely within the thin group. Of the two intermediate samples one displays this correlation, the other does not. A significant positive correlation between L and A is always found in the thin

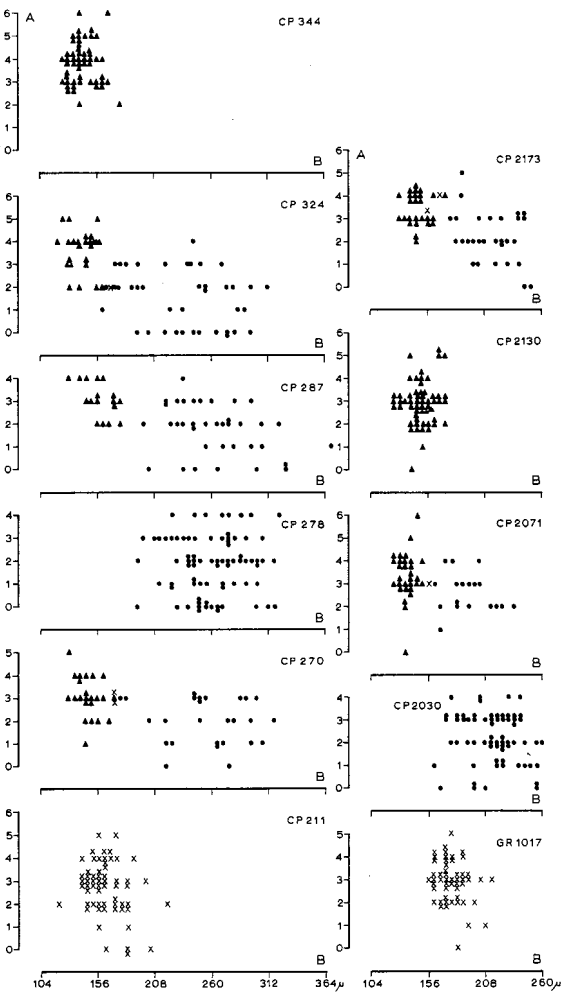


Fig. 21 Scattergrams of A versus B for eleven selected samples from the Miocene and Pliocene. Triangles represent thin type specimens, dots thick type specimens and crosses intermediate ones.

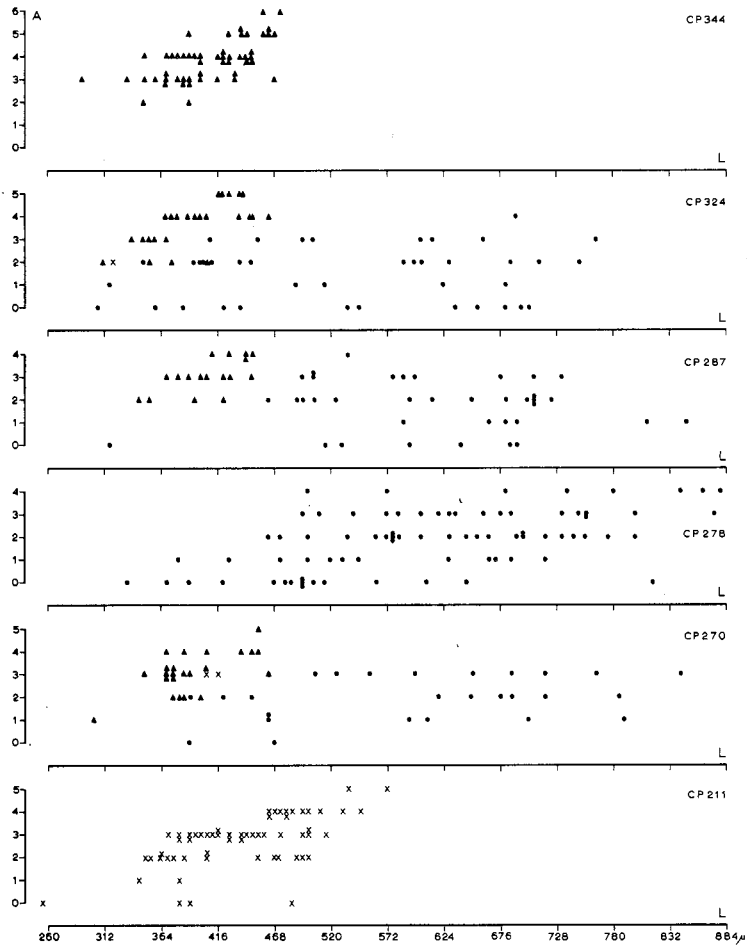


Fig. 22a Scattergrams of A versus L for six selected samples from the Miocene. Triangles: thin type; dots: thick type; crosses: intermediate type.

and intermediate groups, but not often within the thick group. A significant correlation between A and B is never met with in the homogeneous groups of all types.

The correlation coefficients within the samples were calculated for only the eleven samples. Scattergrams, however, were drawn for all samples, and these strongly suggest that the correlations as described above for the eleven samples may be considered representative for all samples.

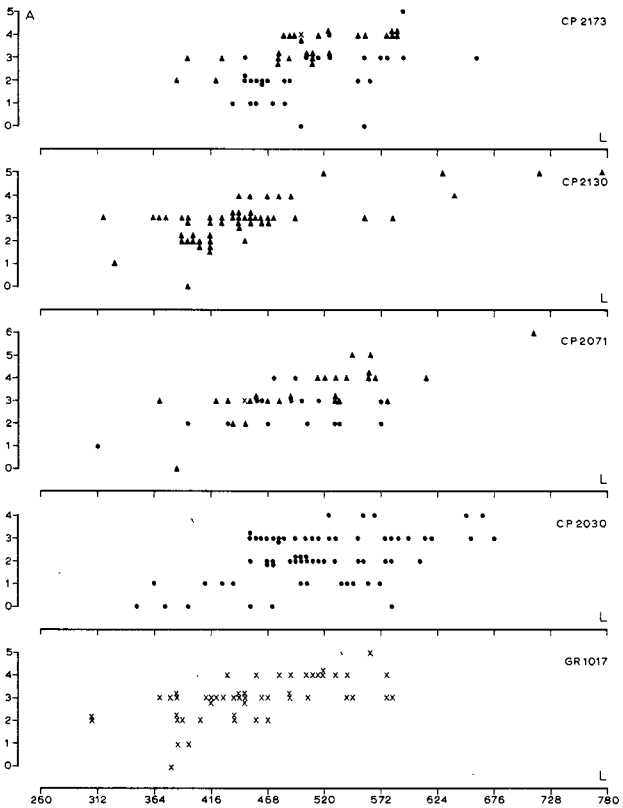


Fig. 22b Scattergrams of A versus L for five selected samples from the Pliocene. Triangles: thin type; dots: thick type; crosses: intermediate type.

IV.3. MEAN VALUES OF THE SAMPLES FOR THE SEPARATE GROUPS

IV.3.1. In general

The mean values and the standard errors of the mean were calculated for the separate morphotype groups (thick, thin, and intermediate) of *Uvigerina* for all the samples. The succession of these mean values is given in figs. 24 and 25 for the Miocene and Pliocene, respectively. The samples are placed at equal distances.

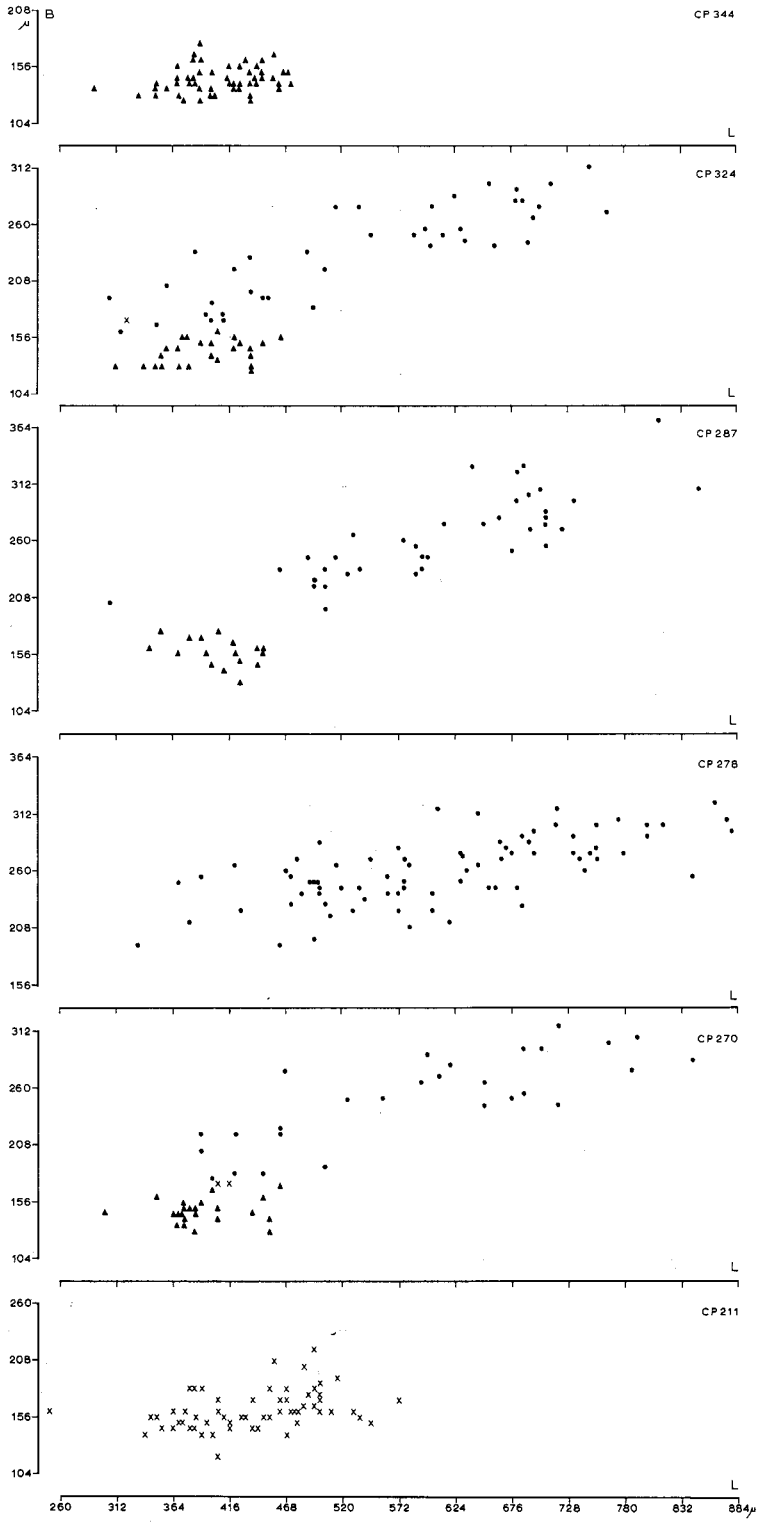


Fig. 23a Scattergrams of L versus B for six selected samples from the Miocene. Triangles: thin type; dots: thick type; crosses: intermediate type.

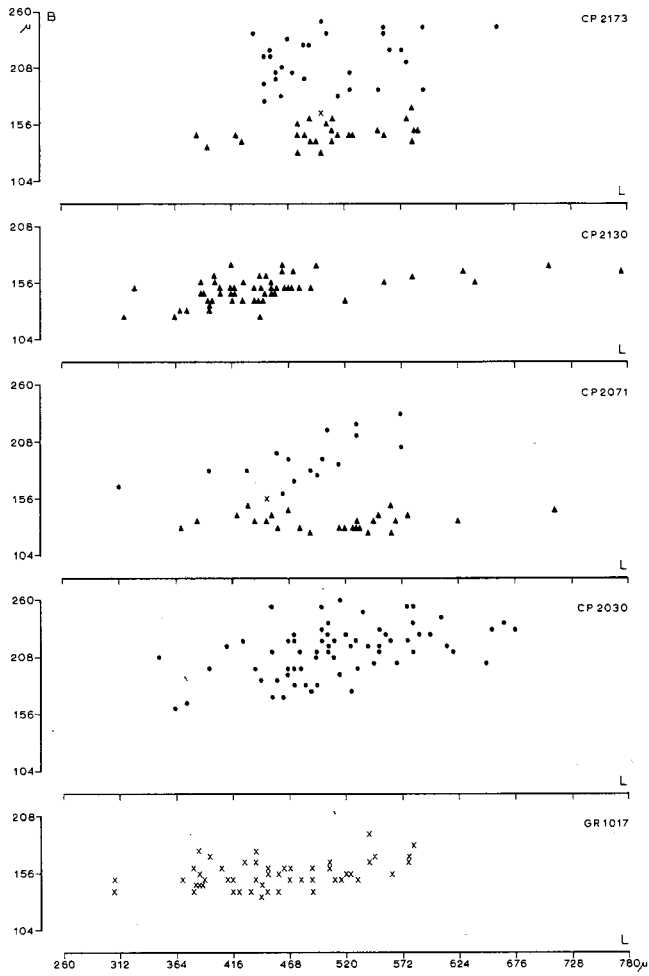


Fig. 23b Scattergrams of L versus B for five selected samples from the Pliocene. Triangles: thin type; dots: thick type; crosses: intermediate type.

A comparison with figs. 14 and 15, in which the mean values of the samples are given irrespective of the homogeneity of the samples clearly shows that the largest fluctuations in the mean values have disappeared; they were the result of the alternation of samples, that contain predominantly thick individuals with samples that consist mainly of thin specimens. But obviously not all fluctuations can be accounted for by mixing of different morphotypes; large fluctuations, significant at a probability level of 2.5% are also observed in the succession of the mean values of each of the groups. The

Samples	thick	Correlation L-B interm.	thin	mixed
CP 2173	+0.28 (29)		*+0.40* (26)	*+0.26* (57)
CP 2130			**+0.55** (56)	
CP 2071	**+0.62** (18)		+0.13 (30)	−0.00 (48)
CP 2030	**+0.48** (66)			
GR1017		**+0.42** (52)		
CP 344			+0.28 (53)	
CP 324	**+0.88** (40)		+0.36 (25)	**+0.87** (66)
CP 287	**+0.80** (37)		−0.30 (17)	**+0.89** (54)
CP 278	**+0.70** (78)			
CP 270	**+0.84** (28)		+0.17 (23)	**+0.88** (53)
CP 211		**+0.35** (60)		

Samples	thick	Correlation L-A interm.	thin	mixed
CP 2173	+0.11		**+0.73**	+0.22
CP 2130			**+0.68**	
CP 2071	+0.32		**+0.78**	**+0.67**
CP 2030	**+0.50**			
GR1017		**+0.66**		
CP 344			**+0.61**	
CP 324	+0.11		**+0.67**	*−0.26*
CP 287	+0.01		**+0.69**	*−0.31*
CP 278	**+0.55**			
CP 270	+0.11		*+0.53*	−0.19
CP 211		**+0.62**		

Samples	thick	Correlation A-B interm.	thin	mixed
CP 2173	−0.35		+0.04	**−0.61**
CP 2130			+0.14	
CP 2071	−0.17		+0.09	*−0.34*
CP 2030	−0.17			
GR1017		−0.21		
CP 344			−0.03	
CP 324	−0.24		−0.10	**−0.63**
CP 287	−0.31		−0.44	**−0.60**
CP 278	+0.02			
CP 270	−0.09		−0.28	**−0.50**
CP 211		*−0.28*		

Table 13 Correlation coefficients within the selected samples.
bold $r \geqslant r_{0,995}$
italics $r \geqslant r_{0,975}$
between brackets: the number of specimens.

Thick Sections	$\overline{A}$	$\overline{BI}$	$\overline{s2}$	$\overline{s3}$	$\overline{L}$	$\overline{B}$	$\overline{L/B}$	n
Prassa	—	—	—	—	—	—	—	—
Finikia	−0.07	−0.07	**−0.38**	***−0.28***	**−0.52**	**−0.42**	−0.04	51
Ag. Vlassios	**−0.83**	−0.02	−0.30	−0.12	**−0.68**	+0.06	**−0.89**	36
Prassa	—	—	—	—	—	—	—	—
Khaeretiana	−0.34	+0.01	−0.01	+0.14	+0.56	+0.46	−0.17	11
Vrysses III	−0.16	**+0.55**	+0.24	***+0.40***	**+0.56**	***+0.40***	+0.32	24
Vrysses II	−0.04	***+0.26***	+0.16	−0.02	−0.15	***−0.28***	+0.08	57
Vrysses I	**−0.47**	−0.02	+0.19	+0.22	+0.15	***+0.42***	**−0.50**	30
Exopolis	+0.35	***−0.55***	−0.38	+0.01	+0.27	+0.00	+0.29	19
Apostoli	**−0.53**	+0.29	+0.31	+0.18	+0.27	+0.29	−0.04	31
Thin Sections	$\overline{A}$	$\overline{BI}$	$\overline{s2}$	$\overline{s3}$	$\overline{L}$	$\overline{B}$	$\overline{L/B}$	n
Prassa	+0.22	**+0.77**	+0.45	+0.47	+0.32	**−0.73**	**+0.70**	14
Finikia	+0.02	−0.25	**−0.45**	**−0.48**	−0.02	**+0.40**	−0.17	47
Ag. Vlassios	—	—	—	—	—	—	—	—
Prassa	—	—	—	—	—	—	—	—
Khaeretiana	+0.14	−0.13	−0.24	−0.25	+0.45	**+0.65**	−0.20	16
Vrysses III	+0.46	−0.36	−0.17	−0.02	**+0.79**	**+0.75**	+0.08	16
Vrysses II	***+0.46***	−0.08	+0.20	−0.04	+0.32	+0.04	+0.24	25
Vrysses I	—	—	—	—	—	—	—	—
Exopolis	−0.93	+0.31	−0.39	−0.36	+0.77	***+0.98***	−0.87	4
Apostoli	***−0.81***	+0.45	+0.45	+0.65	***−0.81***	−0.29	−0.55	8
Intermediate Sections	$\overline{A}$	$\overline{BI}$	$\overline{s2}$	$\overline{s3}$	$\overline{L}$	$\overline{B}$	$\overline{L/B}$	n
Ag. Vlassios	+0.29	**+0.66**	+0.32	+0.44	**+0.75**	***+0.55***	+0.04	15
Prassa	***+0.34***	+0.44	**−0.43**	***−0.38***	***+0.31***	***+0.30***	−0.17	44

Table 14 Correlation coefficients between the sample rank-numbers and the mean values for the separate groups.
bold $r \geqslant r_{0,995}$
italics $r \geqslant r_{0,975}$
n is the number of samples

random fluctuations have the largest amplitude in the succession of mean values of thick type *Uvigerina* in the Miocene.

The lack of sustained changes proved to be not the result of the mixing of groups; in the separated, homogeneous groups, we can not distinguish gradual sustained changes either. Table 14 shows the correlation coefficients between the rank sample numbers and some parameter mean values for the different sections.

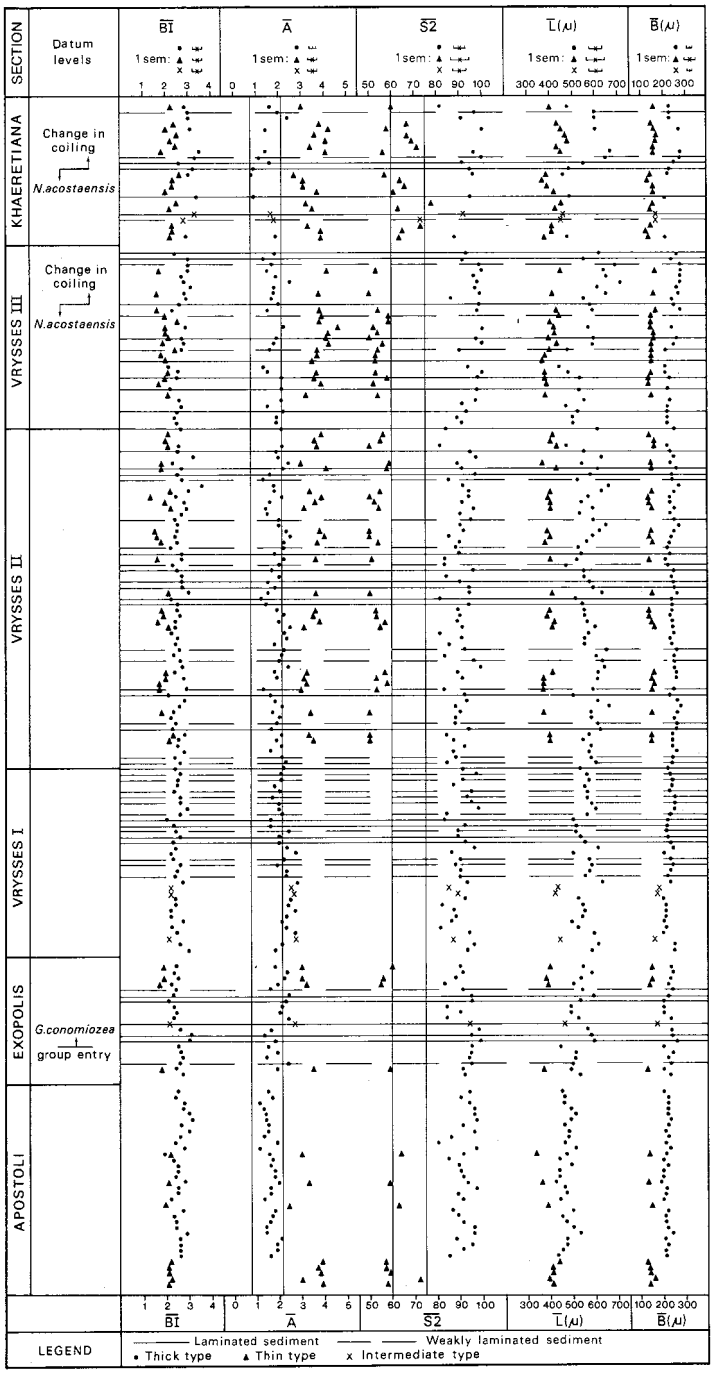


Fig. 24 The mean values of L, B, A, BI and s2 for the separate groups of all Miocene samples in stratigraphical succession.

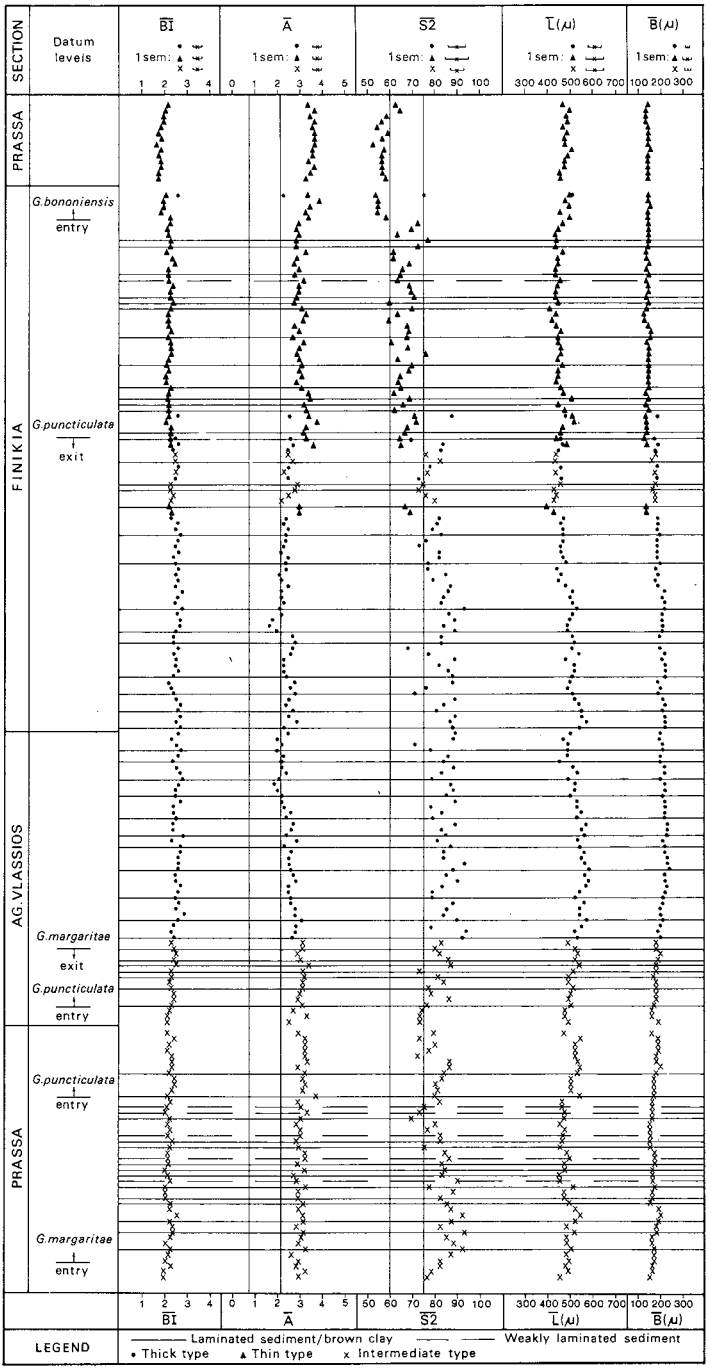


Fig. 25 The mean values of L, B, A, BI and s2 for the separate groups of all Pliocene samples in stratigraphical succession.

The mean A values for the thick uvigerinids are higher in the Pliocene than in the Miocene, but this is not the result of a gradual or staggered increase of A. The three significant correlation coefficients per section between rank sample numbers and mean A values are all negative, i.e. the mean A seems to decrease with time in the separate sections.

The mean BI values show both significant increases and decreases for the thick type. The mean s2 value decreases significantly only in section Finikia. The mean values of L and B increase significantly at a probability level of 2.5% in section Vrysses III, in the Upper Miocene. In the next higher sections L and B show no significant changes, but they decrease again in section Finikia. The mean ratio of L and B decreases significantly in section Vrysses III and in section Ag. Vlassios, and displays no significant changes in other sections.

In the Miocene the intermediate type is represented by six samples only. No correlation coefficients could be calculated. In the Lower Pliocene the intermediate type samples show a decrease in L, B and BI, significant at a 2.5% probability level. The mean value of A displays an increase in the lower part of section Prassa, while s2 mean values decrease. The L-B ratio demonstrates no significant changes.

In the thin uvigerinids we come across decreases and increases in mean A values, both significant at a 2.5% probability level. The mean values of BI increase significantly only in section Prassa (upper part). Only in section Finikia do the mean s2 values decrease significantly. The mean values of L and B both increase in section Vrysses, as in the thick group. The mean B values increase in some other Miocene sections and in the upper part of the Pliocene section Prassa. The mean ratios of L and B decrease in the upper part of Prassa.

We also calculated the correlation coefficients between the rank sample numbers (disregarding the possible overlaps in time between the sections) and the parameter mean values for all Miocene samples and for all Pliocene samples (see table 15). The mean values of L and B in the thick group increase significantly in the Miocene, and decrease in the Pliocene. The largest specimens occur in the topmost Miocene. It should be noticed that Hottinger (1966) has remarked upon the occurrence of exceptionally large *Uvigerina* specimens in the Messinian. These resemble our thick uvigerinids closely.

The mean s2 value of the thick type decreases in the Pliocene, but not in the Miocene. The mean values of BI increase in the Miocene and those of A decrease in the Pliocene. In no parameter can similar significant changes be observed in Miocene and Pliocene.

	$\overline{A}$	$\overline{BI}$	$\overline{s2}$	$\overline{L}$	$\overline{B}$	n
Thick						
Pliocene	−0.37	+0.08	*−0.29*	−0.73	−0.52	87
Miocene	+0.13	*+0.17*	+0.07	+0.33	+0.25	160
Intermediate						
Pliocene	−0.46	+0.56	−0.38	−0.38	*+0.27*	59
Thin						
Pliocene	**+0.40**	**−0.58**	**−0.56**	**+0.42**	**+0.36**	61
Miocene	*+0.26*	+0.03	−0.14	*+0.25*	**+0.41**	69

Table 15 Correlation coefficients of the rank sample numbers and the mean parameter values for the separate groups, for all Miocene and all Pliocene samples together.
bold $r \geqslant r_{0,995}$
italics $r \geqslant r_{0,975}$
n is the number of samples

The intermediate samples in the Lower Pliocene show an increase in the mean values of BI and B, and a decrease in the mean values of A, s2 and L.

The thin type uvigerinids display more consistency than the thick type. Both in the Pliocene and in the Miocene the mean values of A increase. However, this cannot be interpreted as a gradual change; the Miocene and Pliocene values have about the same range, but the lowest Pliocene values are fairly low as compared with the Miocene ones. The mean values of BI and of s2 show a significant decrease only in the Pliocene. The decrease in mean values of s2 in the Miocene is not significant. Again it should be borne in mind that there is no sustained change from the Miocene into the Pliocene; the Pliocene mean s2 values are much higher than the Miocene values, and decrease upwards in the Pliocene till they have about the same values as in the Miocene. The mean values of L and B increase in the Miocene as well as in the Pliocene.

The mean values of the mean values of some parameters per section per morphotype group are shown in table 16 and in fig. 26. These successions of means per section do not show a sustained change either.

Within the thick group the mean values of L, B and BI increase in the Miocene and decrease in the Pliocene. The mean values of A increase up to section Vrysses II, and after that they decrease up to and including section Khaeretiana. The Pliocene mean A values are higher than all Miocene values. The mean values of s2 decrease slightly up to section Vrysses II, and increase again higher in the Miocene. The Pliocene values are lower than all Miocene ones.

Sections	$\bar{L}$ ± sem			$\bar{B}$ ± sem		
	thick	interm.	thin	thick	interm.	thin
Prassa			482 ± 3 (14)			149 ± 1
Finikia	487 ± 5 (51)		458 ± 4 (47)	198 ± 2		145 ± 1
Ag. Vlassios	533 ± 5 (56)	501 ± 5 (15)		215 ± 2	179 ± 3	
Prassa		489 ± 4 (44)			167 ± 2	
Khaeretiana	553 ± 23 (11)		421 ± 8 (16)	241 ± 8		154 ± 2
Vrysses III	556 ± 14 (24)		405 ± 6 (16)	245 ± 5		153 ± 2
Vrysses II	576 ± 6 (57)		396 ± 4 (25)	245 ± 5		148 ± 1
Vrysses I	542 ± 9 (30)			220 ± 4		
Exopolis	524 ± 9 (19)		383 ± 5 (4)	221 ± 5		143 ± 4
Apostoli	465 ± 5 (31)		394 ± 11 (8)	210 ± 2		139 ± 2

Sections	$\bar{A}$ ± sem			$\bar{BI}$ ± sem		
	thick	interm.	thin	thick	interm.	thin
Prassa			3.57 ± 0.04			1.91 ± 0.03
Finikia	2.41 ± 0.04		3.13 ± 0.04	2.52 ± 0.04		2.23 ± 0.04
Ag. Vlassios	2.46 ± 0.05	3.03 ± 0.06		2.54 ± 0.05	2.31 ± 0.06	
Prassa		3.03 ± 0.03			2.16 ± 0.03	
Khaeretiana	1.45 ± 0.15		3.53 ± 0.12	3.06 ± 0.08		2.25 ± 0.05
Vrysses III	1.83 ± 0.06		3.86 ± 0.08	2.64 ± 0.06		1.95 ± 0.06
Vrysses II	1.92 ± 0.04		3.50 ± 0.07	2.57 ± 0.04		1.92 ± 0.08
Vrysses I	2.20 ± 0.06			2.46 ± 0.04		
Exopolis	1.95 ± 0.08		3.16 ± 0.11	2.49 ± 0.06		1.83 ± 0.04
Apostoli	1.64 ± 0.06		3.61 ± 0.11	2.56 ± 0.05		2.13 ± 0.03

Sections	$\bar{s2}$ ± sem		
	thick	interm.	thin
Prassa			58.0 ± 2.3
Finikia	81.7 ± 0.8		65.9 ± 0.8
Ag. Vlassios	84.7 ± 0.8	80.9 ± 1.0	
Prassa		81.9 ± 0.8	
Khaeretiana	93.6 ± 1.7		65.0 ± 1.1
Vrysses III	95.4 ± 0.8		53.9 ± 0.7
Vrysses II	89.7 ± 0.6		53.4 ± 0.6
Vrysses I	89.9 ± 0.8		
Exopolis	91.9 ± 1.0		57.5 ± 1.3
Apostoli	91.3 ± 0.8		58.5 ± 0.9

Table 16 Mean values of mean values and standard errors of the mean, per section, for the separate groups.

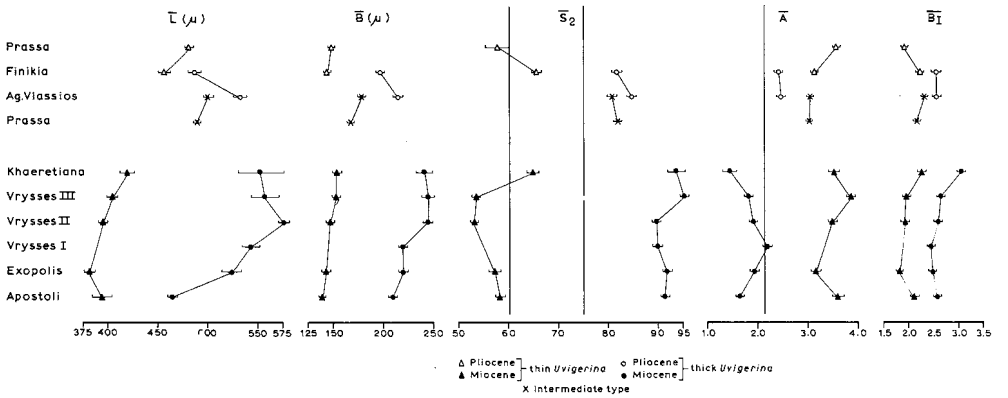


Fig. 26 The mean values of the mean values of L, B, A, BI and s2 for the separate groups per section.

In the intermediate group in the Pliocene the mean values of A and s2 do not change much, and the mean values of L, B and BI increase.

The thin group shows a slight increase in the mean values of L and B in the Miocene. The Pliocene mean values of L are higher than the Miocene ones, but the Pliocene mean B values are about the same as in section Vrysses II. The mean values of A, BI and s2 fluctuate. The highest mean values of s2 are found in the sections Khaeretiana and Finikia.

The histograms of the distributions of the mean values per section are shown in fig. 27. These histograms confirm that no sustained changes are found. There is no consistent shift in the series of sections that are arranged in the correct stratigraphic order.

Scattergrams were drawn for some combinations of parameter mean values for all the samples. The combinations are the mean values of A and L, the mean values of A and B, those of A and s2, those of L and B and the mean values of A and BI (see figs. 28 to 32). In all these scattergrams the thick and the thin type samples form different clusters, while the intermediate samples are situated somewhere in between these two clusters and overlap both. The best separation of the clusters is found in the scattergrams of the mean L values versus the mean B values, and of the mean A values versus the mean B values. The largest overlap appears in the scattergrams of the mean A values versus the mean BI values. It should be noted that the samples with low mean BI values in combination with low mean A values contain always relatively many triserial specimens and specimens with a few biserial chambers, not followed by uniserial ones. In these samples the

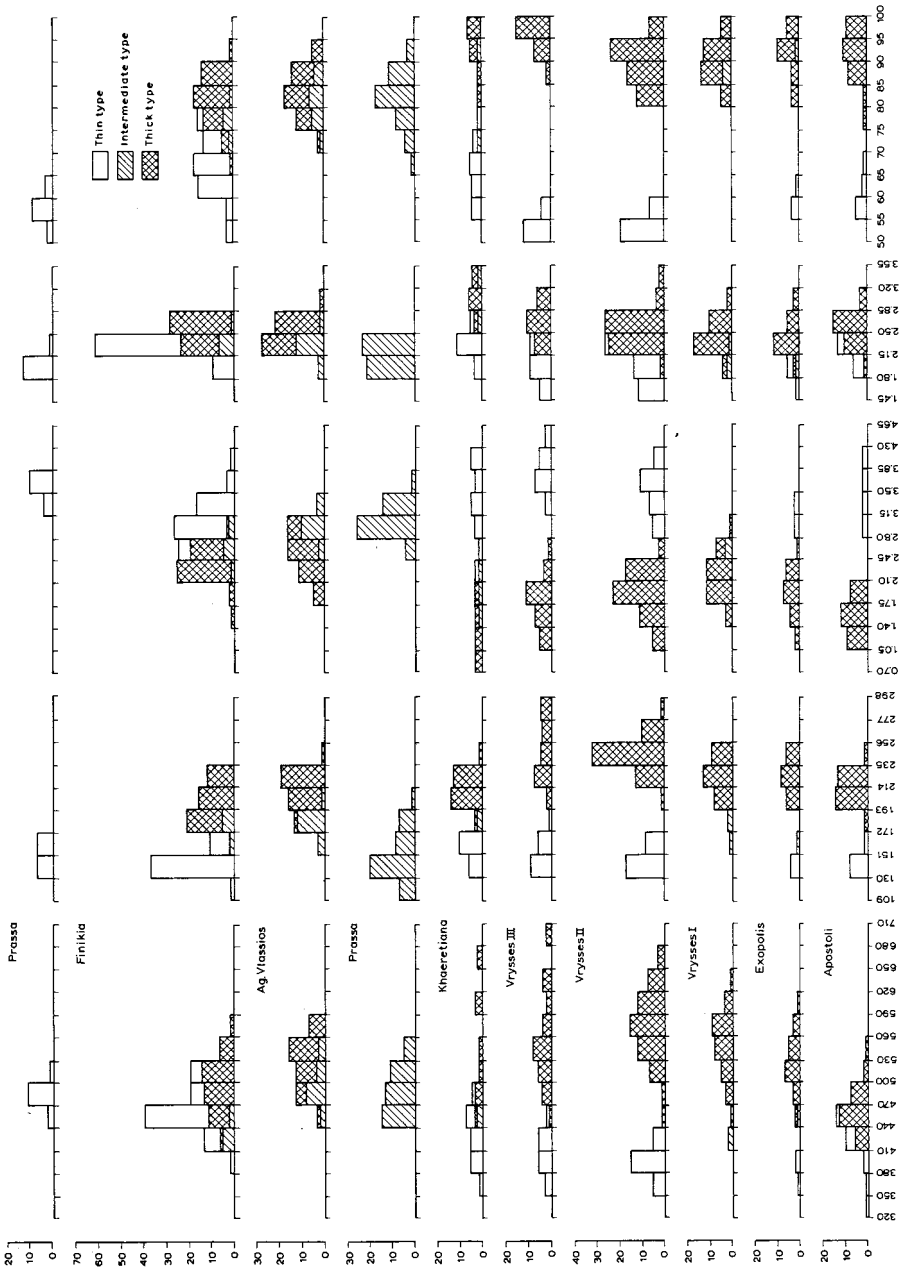


Fig. 27 Histograms of the mean values of L, B, A, BI and s2 for the separate groups per section.

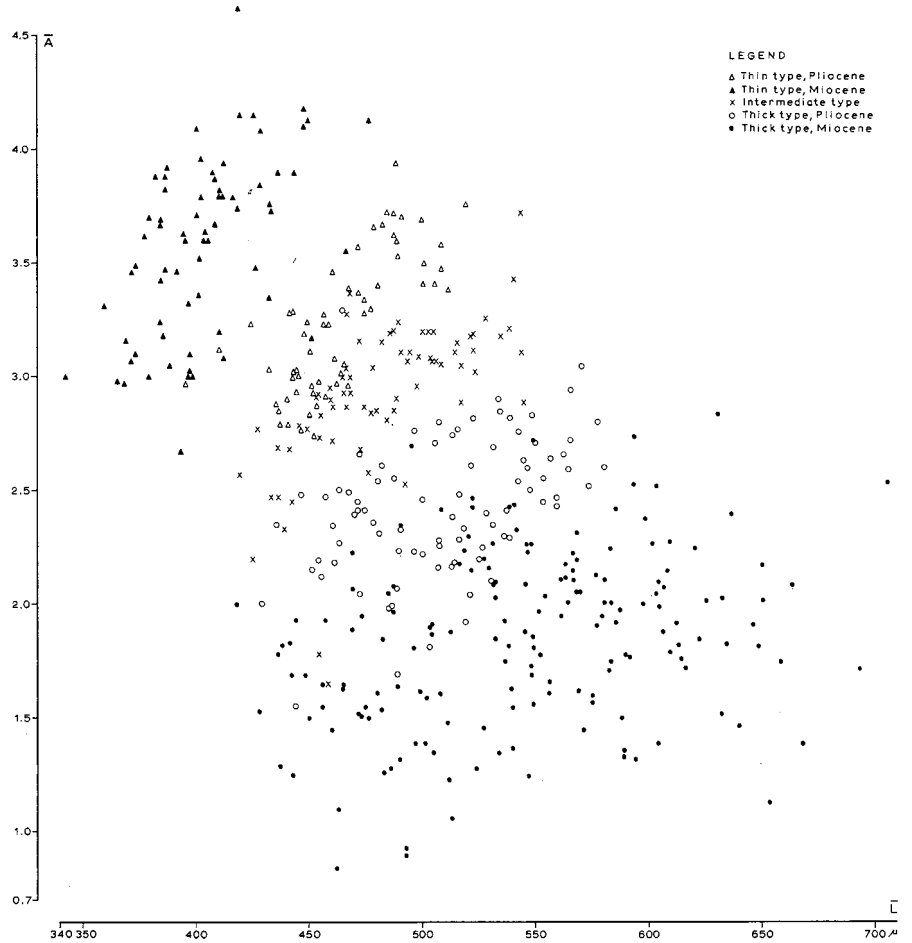


Fig. 28 Scattergram of the mean values of A versus those of L for the separate groups for all samples.

number of biserial chambers cannot be established in a delimited ontogenetic stage.

The Miocene and Pliocene sample groups of the same type usually cluster in somewhat different positions. In all scattergrams the cluster of the Pliocene thick type mean values overlaps partly the Miocene cluster, but lies closer to the thin type cluster. The clusters of the thin type for the Miocene and Pliocene overlap much more; only the mean L values of the Pliocene thin type samples are often larger than those of the Miocene thin type samples.

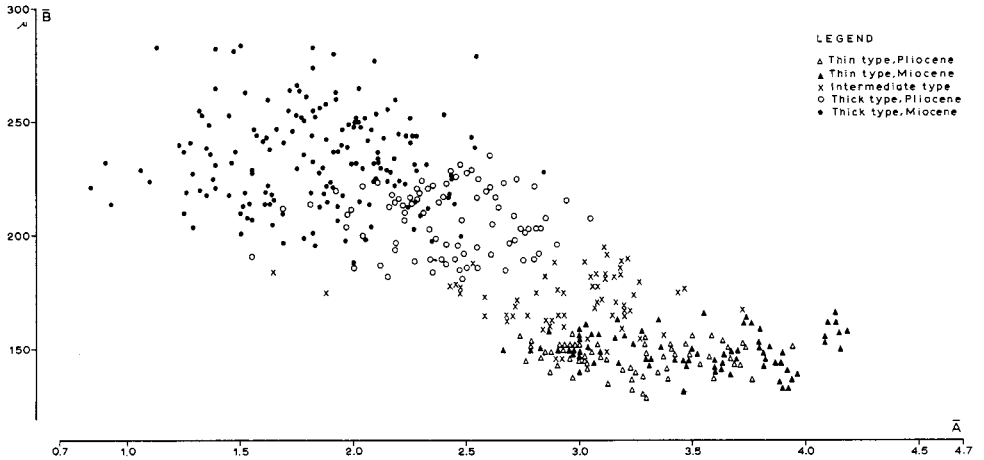


Fig. 29 Scattergram of the mean values of A versus those of B for the separate groups for all samples.

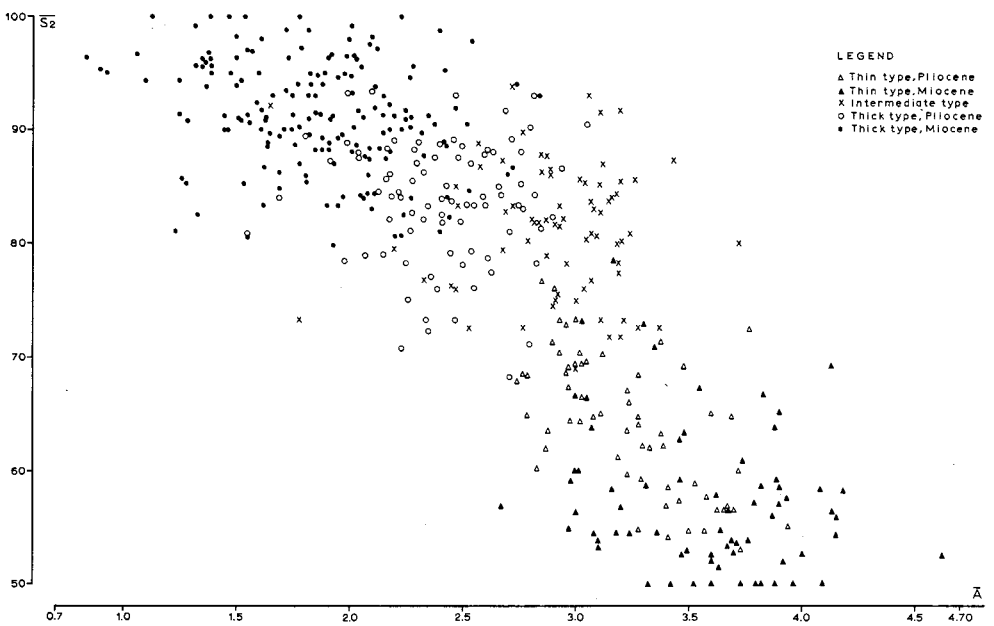


Fig. 30 Scattergram of the mean values of A versus those of s2 for the separate groups for all samples.

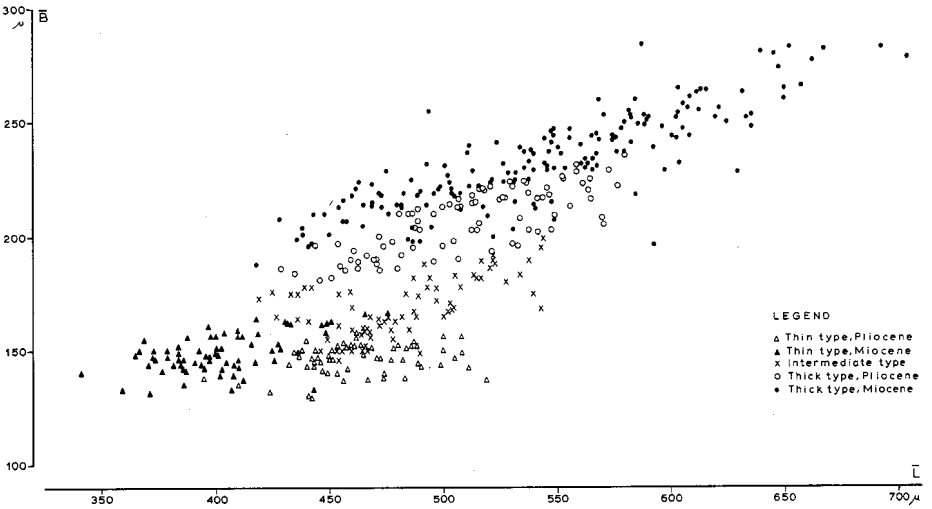


Fig. 31 Scattergram of the mean values of L versus those of B for the separate groups for all samples.

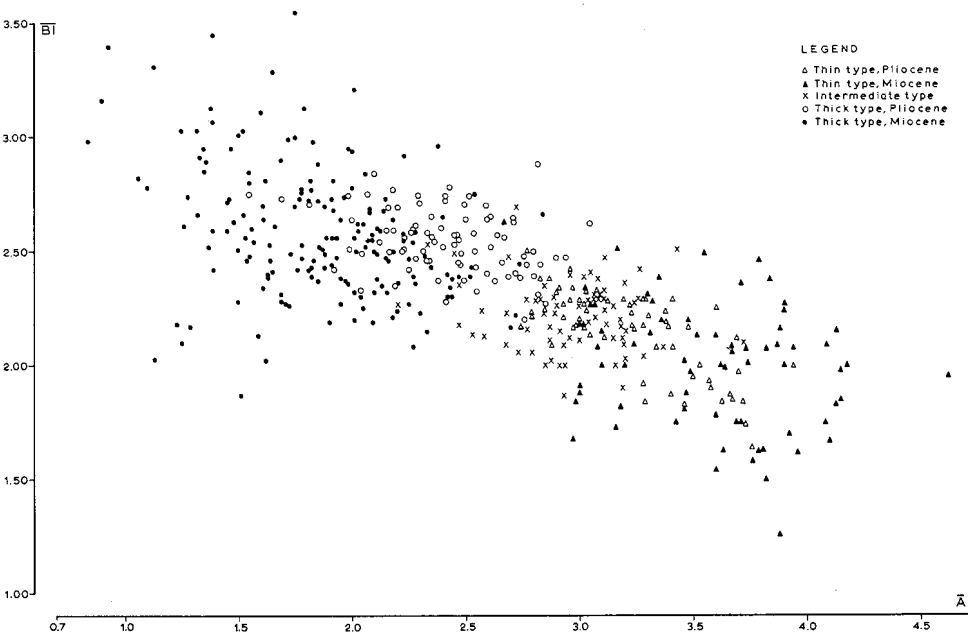


Fig. 32 Scattergram of the mean values of A versus those of BI for the separate groups for all samples.

Thick Sections	$\overline{A}$–$\overline{s2}$	$\overline{B}$–$\overline{s2}$	$\overline{s2}$–$\overline{s3}$	$\overline{A}$–$\overline{B}$	$\overline{A}$–$\overline{L}$	$\overline{L}$–$\overline{s2}$	$\overline{L}$–$\overline{B}$	$\overline{A}$–$\overline{BI}$	n
Prassa Finikia	*−0.34*	**+0.53**	**+0.82**	*−0.32*	+0.10	**+0.44**	**+0.87**	**−0.51**	51
Ag. Vlassios Prassa	+0.22	+0.10	**+0.72**	−0.09	**+0.68**	+0.30	**+0.62**	−0.15	36
Khaeretiana	−0.39	+0.51	**+0.80**	−0.11	+0.30	+0.52	**+0.84**	−0.27	11
Vrysses III	+0.30	**+0.56**	**+0.91**	+0.13	+0.34	**+0.56**	**+0.89**	−0.01	24
Vrysses II	−0.10	+0.20	**+0.71**	−0.16	+0.17	**+0.39**	**+0.85**	−0.24	57
Vrysses I	−0.17	**+0.50**	**+0.76**	**−0.63**	−0.18	**+0.57**	**+0.82**	−0.24	30
Exopolis	*−0.50*	+0.21	**+0.78**	**−0.67**	−0.22	+0.29	**+0.77**	**−0.67**	19
Apostoli	**−0.47**	*+0.41*	**+0.54**	−0.76	**−0.64**	**+0.50**	**+0.89**	−0.23	29

Thin Sections	$\overline{A}$–$\overline{s2}$	$\overline{B}$–$\overline{s2}$	$\overline{s2}$–$\overline{s3}$	$\overline{A}$–$\overline{B}$	$\overline{A}$–$\overline{L}$	$\overline{L}$–$\overline{s2}$	$\overline{L}$–$\overline{B}$	$\overline{A}$–$\overline{BI}$	n
Prassa	−0.25	−0.27	**+0.82**	−0.22	*+0.58*	+0.13	−0.08	−0.19	14
Finikia	**−0.44**	+0.00	**+0.89**	*−0.29*	**+0.63**	−0.23	+0.20	**−0.44**	47
Ag. Vlassios Prassa									
Khaeretiana	−0.14	+0.13	**+0.95**	+0.13	*+0.53*	+0.26	**+0.69**	**−0.66**	16
Vrysses III	−0.18	−0.26	**+0.71**	+0.07	*+0.60*	+0.09	**+0.63**	−0.17	16
Vrysses II	−0.23	*+0.43*	**+0.68**	−0.26	**+0.53**	+0.03	−0.30	**−0.66**	25
Vrysses I									
Exopolis	+0.13	−0.24	+0.25	+0.93	−0.73	+0.15	+0.78	−0.55	4
Apostoli	*−0.75*	+0.55	**+0.88**	−0.15	**+0.85**	−0.61	−0.13	−0.26	8

Intermediate Sections	$\overline{A}$–$\overline{s2}$	$\overline{B}$–$\overline{s2}$	$\overline{s2}$–$\overline{s3}$	$\overline{A}$–$\overline{B}$	$\overline{A}$–$\overline{L}$	$\overline{L}$–$\overline{s2}$	$\overline{L}$–$\overline{B}$	$\overline{A}$–$\overline{BI}$	n
Ag. Vlassios	+0.17	+0.17	**+0.78**	−0.36	+0.23	+0.32	**+0.66**	+0.18	15
Prassa	−0.18	+0.21	**+0.92**	+0.29	**+0.64**	−0.17	**+0.87**	+0.10	44

Table 17 Correlation coefficients between the mean values for the separate groups.
bold $r \geqslant r_{0,995}$
italics $r \geqslant r_{0,975}$
n is the number of samples.

The correlation coefficients for some combinations of parameter mean values were calculated (see table 17). The significant correlations between pairs of parameter mean values are only rarely consistent for all of the sections. The mean values of s2 and s3 are the only parameter mean values that are always significantly positively correlated. A significant correlation between mean values of A and B occurs sometimes, mostly in successions of thick type samples. If this correlation is found it is negative.

A positive correlation between the mean values of L and B was sometimes

observed in the thin type samples and always in the thick and intermediate types. A positive correlation between the mean values of B and s2 and between the mean values of L and s2 was often found in the thick type samples, but never in the intermediate and thin type samples. A positive correlation between the mean values of A and L is almost always present in the thin type samples, sometimes in the intermediate samples, but only rarely in the thick type samples. Only in section Apostoli was a negative correlation between the mean values of L and A found in the thick group. The correlation between the mean values of A and BI is seen sometimes in all types, and is negative if present. In all types a significant correlation between the mean values of A and s2 is rarely observed. When this correlation is observed it is negative.

The correlation coefficients between some combinations of mean values were also calculated for all Miocene samples and for all Pliocene samples for the different groups (table 18). A significant positive correlation is noticed between the mean values of L and B in all types in Miocene and Pliocene. A negative correlation between the mean values of A and BI is found in the thick and thin groups in the Miocene and Pliocene, but is not significant in the Pliocene intermediate type samples. A positive correlation between the mean values of A and L occurs in the thin type samples in the Miocene and Pliocene and in the intermediate samples. This positive correlation also appears in the Pliocene thick type samples, but not in the Miocene ones. This positive correlation is not present if many individuals have values A = 0. A negative correlation between the mean values of A and s2 is noticed in the

	$\bar{A}$–$\bar{s2}$	$\bar{A}$–$\bar{B}$	$\bar{A}$–$\bar{L}$	$\bar{L}$–$\bar{B}$	$\bar{A}$–$\bar{BI}$	n
Thick						
Pliocene	−0.04	−0.04	**+0.50**	**+0.80**	*−0.24*	87
Miocene	**−0.34**	−0.33	+0.08	**+0.86**	−0.49	160
Intermediate						
Pliocene	+0.08	+0.04	**+0.67**	**+0.64**	−0.16	59
Thin						
Pliocene	**−0.62**	−0.05	**+0.73**	*+0.27*	**−0.70**	61
Miocene	*−0.26*	+0.03	**+0.47**	**+0.56**	*−0.30*	69

Table 18 Correlation coefficients between the mean values for the separate groups, for all Miocene and all Pliocene samples together.
bold $r \geq r_{0,995}$
italics $r \geq r_{0,975}$
n is the number of samples.

thin type samples in the Miocene and Pliocene and in the Miocene thick type samples. A negative correlation between the mean values of A and B is met with only in the Miocene thick type samples.

Some of the correlations, as for instance the positive correlation between B- and s2-mean values in the thick type in some Miocene sections seem to make no sense in view of the construction scheme of the uvigerinid test. This suggests that several characteristics of the test form a strongly connected whole. Maybe all or the major part of the parameters are dependent on some unknown factor(s), which are probably environmental, but not on time.

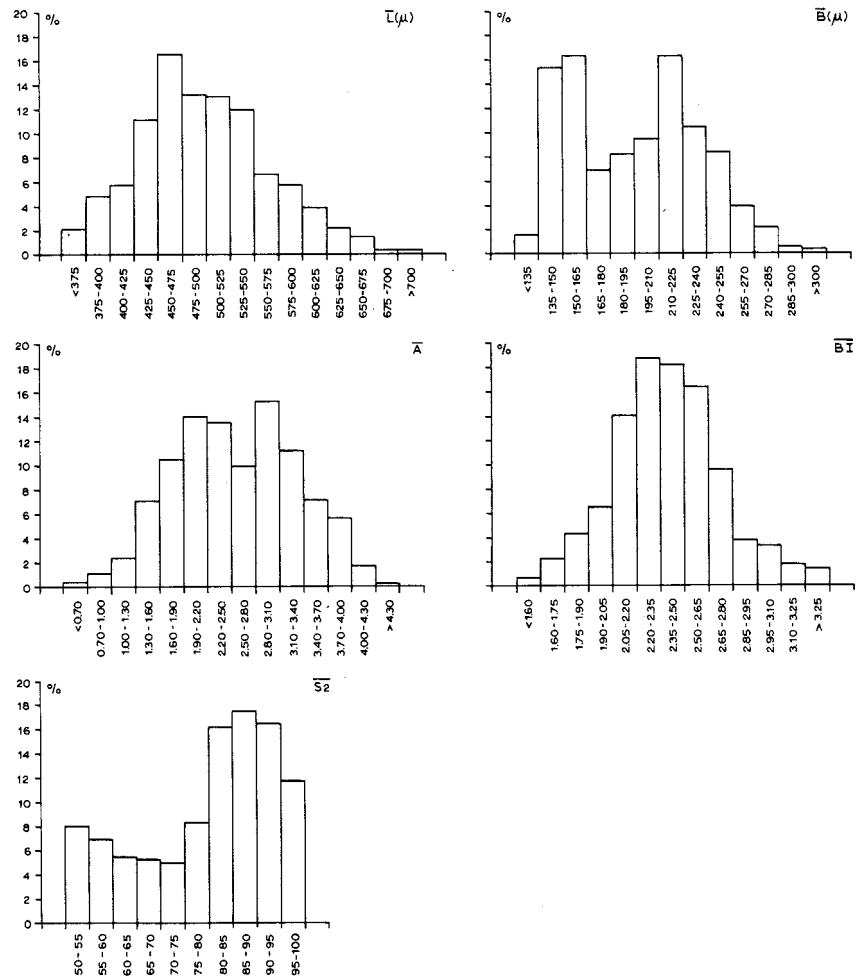


Fig. 33 Histograms of the mean values of L, B, A, BI and s2 for the separate groups for all samples together.

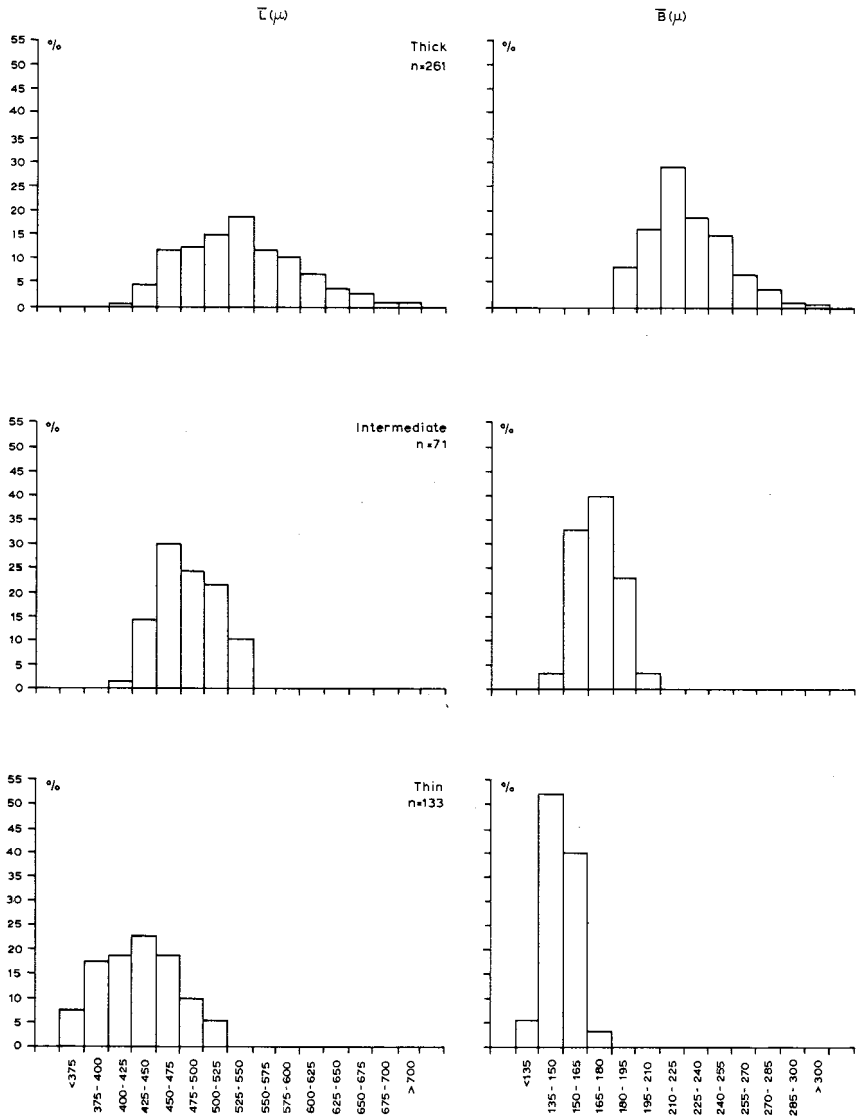


Fig. 34 Histograms of the mean values of L and B for the separate groups, per group.

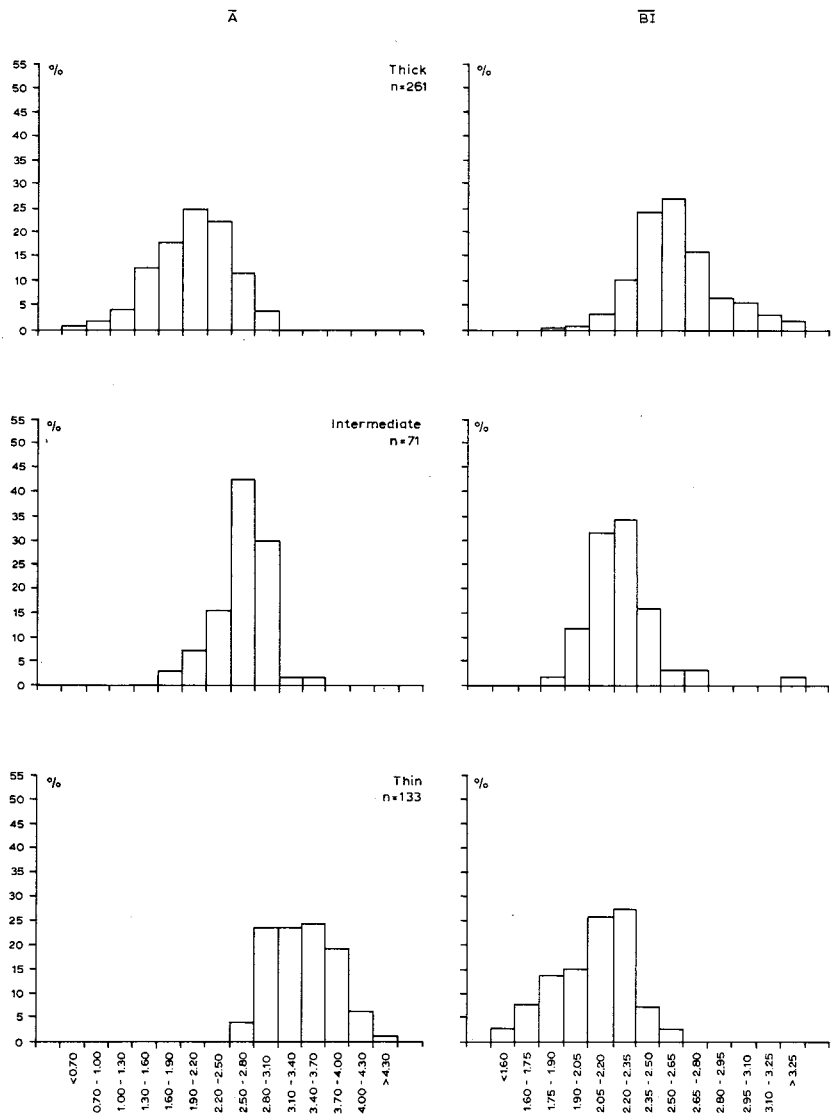


Fig. 35 Histograms of the mean values of A and BI for the separate groups, per group.

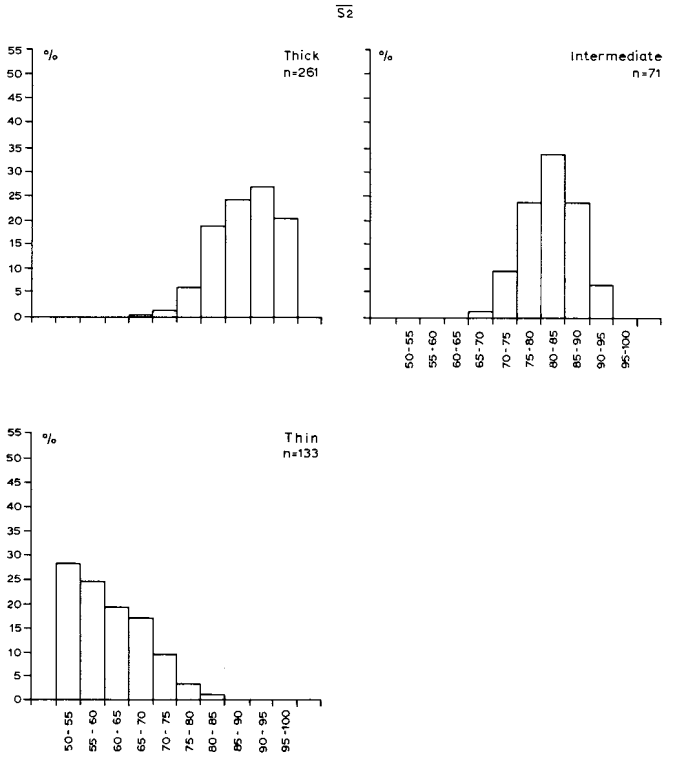


Fig. 36 Histograms of the mean values of s2 for the separate groups, per group.

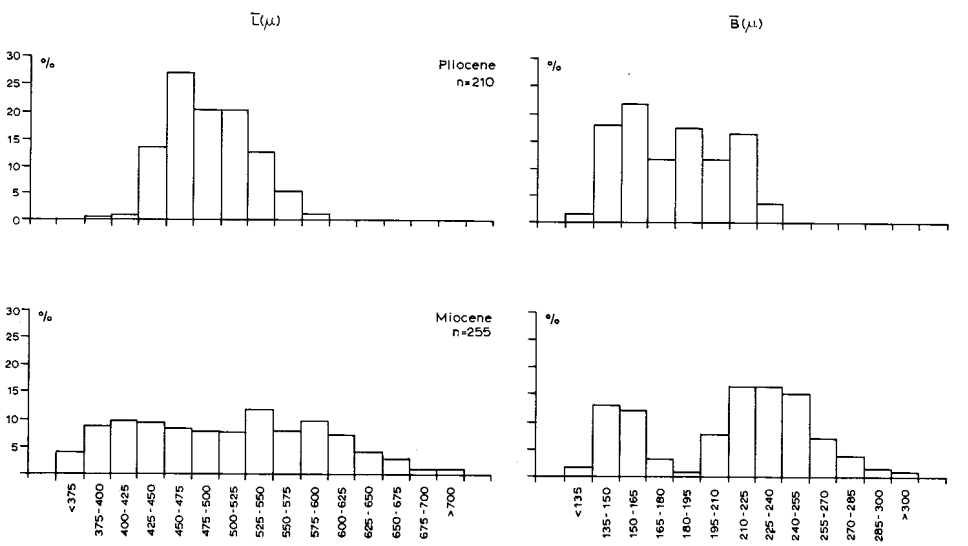


Fig. 37 Histograms of the mean values of L and B for the separate groups of the Miocene and Pliocene separately.

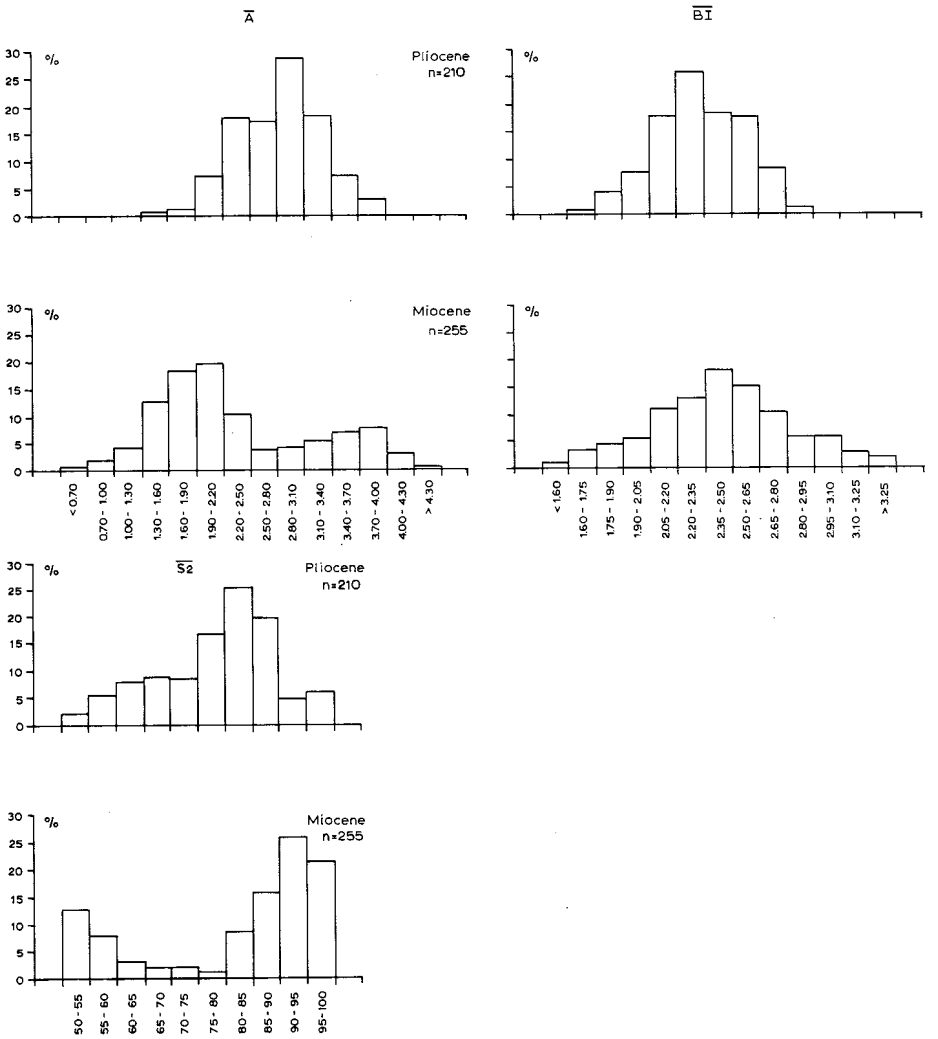


Fig. 38 Histograms of the mean values of A, BI and s2 for the separate groups for the Miocene and Pliocene separately.

In fig. 33 histograms for the mean values of all samples of all types combined are presented for only some of the parameters. The histograms of the distributions of the mean values of B, s2, and possibly of A indicate a bimodality in the distributions, whereas the distributions of the mean values of L and BI do not deviate from normal. The histograms together with the scattergrams of figs. 28 to 32 show that after the lumping of all samples irrespective of their position in the stratigraphical column the presence of several morphotypic groups is only evident for some parameters, notably the

mean values of B and s2. Yet in the majority of the samples the types are easy to separate. The mean values of all groups fluctuate irregularly. It is this fluctuation, which causes the poor separation of the mean values when all types are lumped together.

Figures 34 to 36 show histograms for all the mean values of the three types separately. All are unimodal.

In the figs. 37 and 38 histograms are given for all mean values of the Miocene together and for all those of the Pliocene together. They illustrate the presence of the intermediate samples in the Pliocene, especially the histogram of the mean values of B, which suggests the presence of three modes. Also the much wider range of the mean values of L and B in the Miocene as compared with the Pliocene is shown, the differences in the mean s2 values in the thin group in the Miocene and the Pliocene and the differences in the mean A values of the thick type in the Miocene and Pliocene.

Figure 39 illustrates the 5-points moving averages of all types in all sections. In this figure all the minor fluctuations are smoothed out, but we could not get rid of the fluctuating pattern. In these smoothed curves no overall trends are evident.

IV.3.2. Remarks on the groups in the Miocene

In fig. 40 the relative frequencies of the types are given in percentages. The minimum number of specimens per sample is 35. Since we collected per sample 50 specimens with at least two uniserial chambers, in samples with many individuals with A = 0 and/or A = 1 more than 50 specimens were picked, up to a maximum of 132.

In the lower samples of section Apostoli only thin type uvigerinids occur. This type is replaced abruptly by thick *Uvigerina.* In section Apostoli thick uvigerinids are a major constituent of the benthonic foraminiferal fauna in "blocks" of three to five samples. In between these "blocks" they are rare, in the more sandy to silty intervals. Higher in section Apostoli and in section Exopolis there are only a few samples with fair numbers of thin *Uvigerina.* In section Exopolis most samples with frequent thin uvigerinids are in the upper part of the section. In the laminated sediments thick *Uvigerina* are often numerous (up to 40% of the total benthonic foraminiferal fauna). In section Vrysses I the thick type is predominant, thin uvigerinids occur only as single specimens. In section Vrysses II the thick type remains the most frequent type, but mixed samples with about equal numbers of thick and thin individuals together with a few intermediate specimens are fairly common. In the sections Vrysses III and Khaeretiana more and more samples

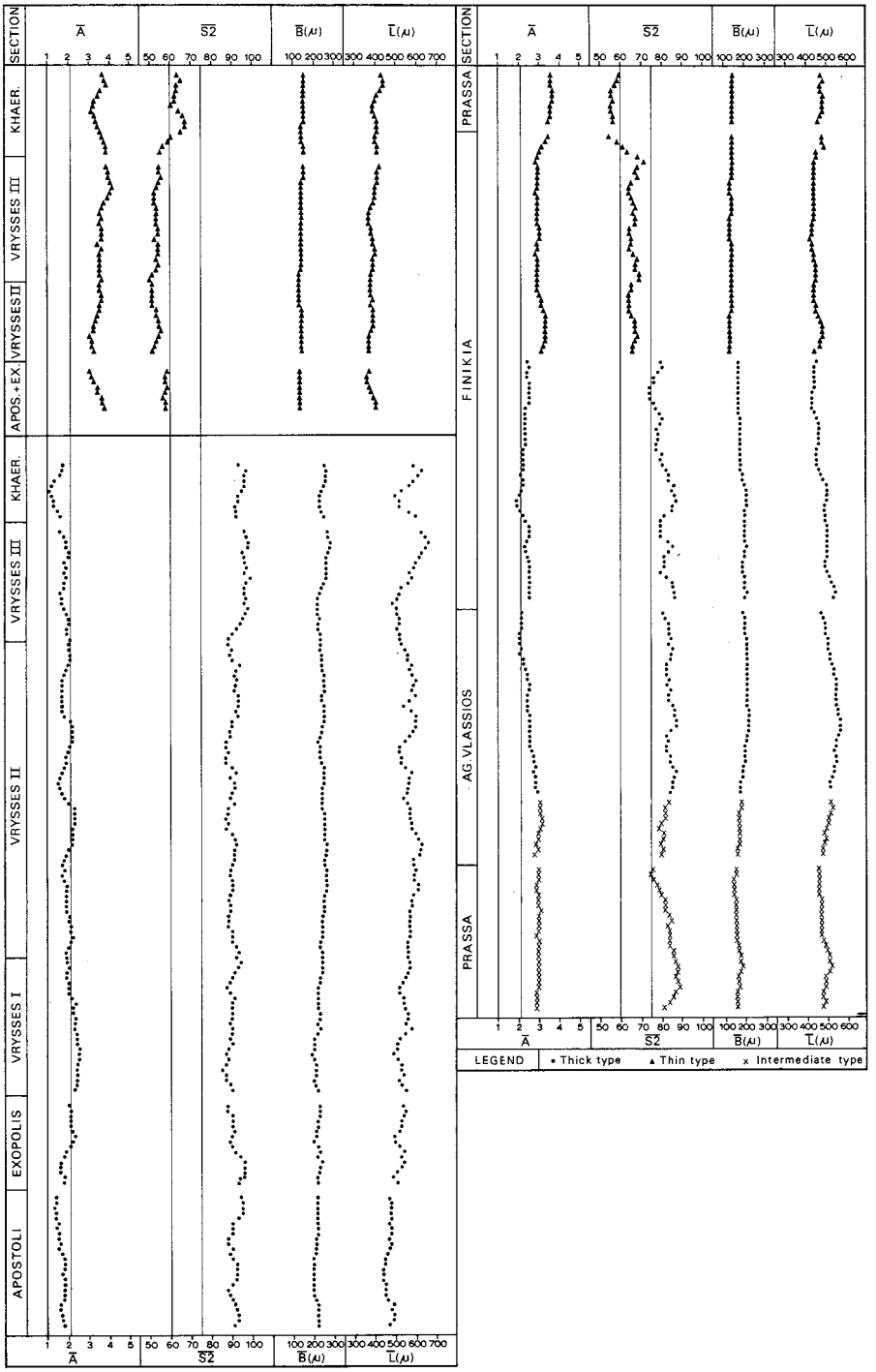


Fig. 39 Five-points moving averages of the means of L, B, A and s2 for the separate groups.

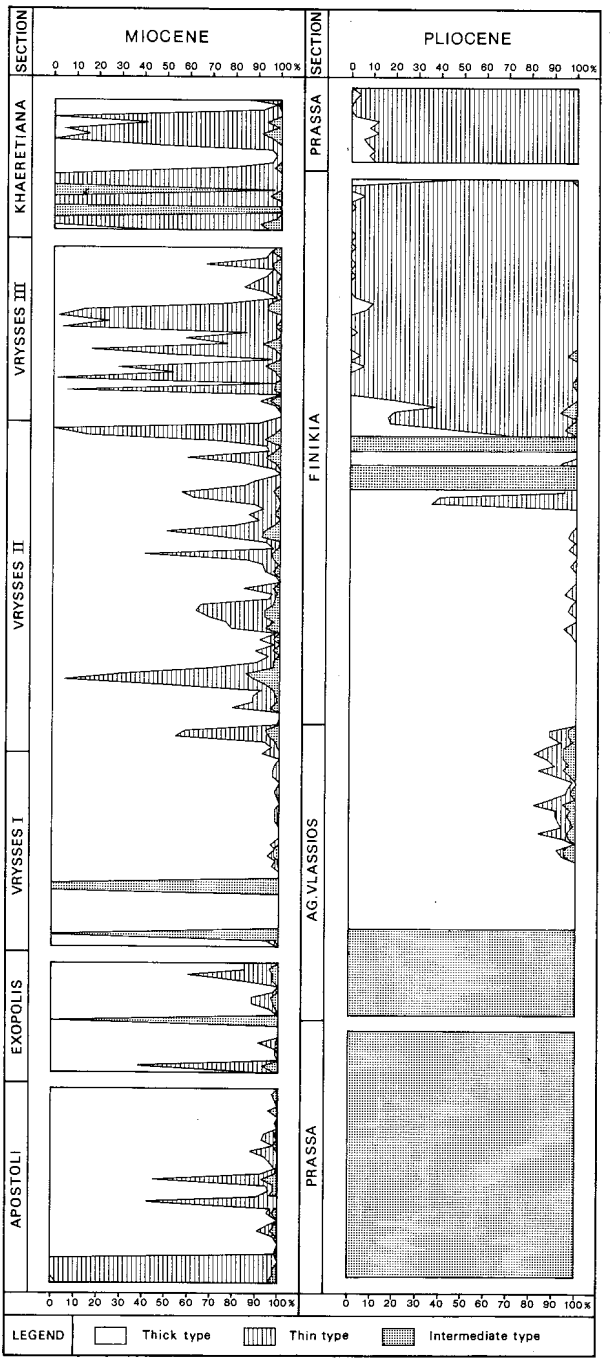


Fig. 40 Relative frequencies (in percentages) of the thick, intermediate and thin specimens in all samples.

with relatively many individuals of the thin type are found and the samples, dominated by thick type uvigerinids diminish in numbers. Here the types become more and more mutually exclusive and most samples contain either thick or thin uvigerinids. The intermediate specimens are observed in many samples throughout the Miocene sections, but they are rare. One sample in section Exopolis, three in section Vrysses I and two in section Khaeretiana were as a whole classified as intermediate type.

Short-time changes in morphotype dominance are obvious in the Miocene uvigerinids.

The thin type uvigerinids are never a fauna-dominating element. They never make up more than about 5 to 7% of the benthonic foraminiferal fauna. In contrast, the thick type is quite often a dominating element and comprises up to 60% of the benthonic foraminiferal fauna. These peak-values of thick *Uvigerina* are found mainly in the sections Vrysses I and II. The frequency and the amplitude of the peak-values decrease in the sections Vrysses III and Khaeretiana. The peaks are observed mainly in the laminated sediments. The intermediate type is never a fauna-dominating element. In the samples, which are classified as a whole as intermediate, they never exceed 5% of the total benthonic foraminiferal fauna. In the samples, where intermediate individuals occur together with those of other types, they are even rarer than 1% of the fauna.

We assigned to the occurrence of each homogeneous group of individuals for which mean values were calculated, a value of the parameter "type" (thick type = 0, intermediate type = 1, thin type = 2). This parameter shows a significant negative correlation with the parameter lithology (homogeneous sediment = 0, weakly laminated sediment = 1, laminated sediment = 2). The correlation coefficient is given in table 19a. This coefficient based on presence – absence data suggests for the Miocene a correlation of the thin type with homogeneous sediments and ipso facto of the thick type with the laminated sediments. The former correlation concurs with our general observations, the second may be partly the consequence of the statistical method.

Correlation coefficients between the parameter lithology and the mean values of the parameters for the morphotypes were also calculated (table 19). In none of the Miocene groups was a significant correlation found between the mean values and the lithology.

The significant correlations found earlier (table 7) between the mean values of the mixed samples from the Miocene (thick and thin type, with some intermediate specimens) and the parameter lithology are evidently a

consequence of the preference of the different groups for different types of lithology.

	$\overline{L}$	$\overline{B}$	$\overline{A}$	$\overline{s2}$	$\overline{BI}$	n
Thick						
Pliocene	+0.04	+0.07	−0.04	+0.11	+0.20	87
Miocene	+0.10	+0.02	+0.01	+0.07	−0.04	160
Intermediate						
Pliocene	+0.08	−0.00	+0.22	+0.02	+0.10	59
Thin						
Pliocene	**−0.31**	−0.07	**−0.34**	**+0.33**	***+0.27***	61
Miocene	+0.06	+0.16	+0.00	−0.13	−0.06	69

Table 19 Correlation coefficients between the mean values and the lithology for the separate groups. A positive value of r signifies high mean values in laminated sediments, a negative value of r signifies low mean values in laminated sediments.
bold $r \geqslant r_{0,995}$
italics $r \geqslant r_{0,975}$
n is the number of samples.

	r	n
Pliocene	+0.03	207
Miocene	**−0.21**	229

Table 19a Correlation coefficients of type (0, 1, 2) with lithology (0, 1, 2).

IV.3.3. Remarks on the groups in the Pliocene

We do not know the length of the time interval between the deposition of the highest lithological samples in section Khaeretiana (in the upper part of the *G. conomiozea* Zone) and the lowest ones in section Prassa (below the entry of *G. margaritae*). From this time interval no data on *Uvigerina* could be gathered.

The lowermost Pliocene samples pose some problems. The uvigerinids in these samples can not be identified as either thick type or thin type, and are classified as intermediate type. As to the mean values of A, B and BI these Lower Pliocene intermediate uvigerinids might be a continuation of the thin group of the Khaeretiana section. In the mean values of s2 and L they are somehow intermediate between the thin and the thick types of this topmost Miocene section; they would fit into neither one nor the other.

The intermediate uvigerinids change gradually, but with fluctuations, into almost perfect homeomorphs of the Miocene thick uvigerinids. The mean values of A of the Pliocene thick type as seen in the long succession of samples are higher than the mean A values in the Miocene, though incidentally mean A values as low as 1.30 were found. On the whole the mean s2 values in the Pliocene are somewhat lower than in the Miocene, in most cases between 80 and 90. The Pliocene thick *Uvigerina* never attain the extremely high mean values of L and B that occur in the highest Miocene, but they are very similar to the thick uvigerinids in section Vrysses I.

In the Pliocene sections we do not come across a long lasting co-occurrence of the thick and the thin morphotype. In the upper part of section Ag. Vlassios and fairly low in section Finikia single specimens of thin uvigerinids are found in otherwise thick type samples (see fig. 40 for the relative frequencies of the types in the Pliocene). Quite unexpectedly, about the *G. puncticulata* exit datum level the thick uvigerinids are replaced by thin ones, and only in a few samples unimodal distributions of the intermediate type were observed. The change is not gradual, however, because several samples in this stratigraphical interval contain bimodal distributions. In the higher parts of the sections thick uvigerinids occur as single specimens in otherwise thin type samples. Only sample CP 2173, the topmost sample of section Finikia does contain about equal amounts of thick and thin types. Intermediate specimens no longer appear in the upper part of the sections Finikia and Prassa.

In the samples with the intermediate type, *Uvigerina* is never a fauna-dominating element, and often rare, less than 1% of the total benthonic foraminiferal fauna. Thick *Uvigerina* is quite often a fauna-dominating element, in the Pliocene just as in the Miocene, and comprises up to about 40% of the benthonic foraminiferal fauna. The peak values of the thick type are found mainly in the brown clays, but this type is often numerous in the grey clays as well. Just before the thick type becomes replaced by the thin type the numbers of uvigerinids in the sediments decrease strongly. The thin type is never fauna-dominating in the Pliocene, just as in the Miocene. In the samples CP 2115 to CP 2130 these uvigerinids comprise up to about 5% of the benthonic foraminiferal fauna. In all other samples they are less numerous.

In the Pliocene no significant correlation is observed between the parameter "type" (values: thick type = 0, intermediate type = 1, thin type = 2) and the lithology parameter. It should be noted, however, that the change from the intermediate uvigerinids into the thick type occurs at the level

where the sediments of the Kourtes facies pass gradually into those of the Finikia facies.

In the thin type there is a significant correlation between the mean values of L, BI, A, s2 and the lithology. Low mean values of L and A, and high mean values of BI and s2 are correlated with "lithology 2", which includes in the Pliocene the brown clays of the Finikia facies and the diatomaceous marls of the Stavromenos facies. These correlations are not necessarily to be looked upon as a consequence of low mean values of A and L, and high ones of BI and s2 in the brown clays and diatomaceous marls, as compared with the homogeneous sediments between these layers. They result from the fact that the thin uvigerinids with comparatively high mean values of A and L, and low ones of BI and s2 are never found in the diatomaceous layers of the Stavromenos facies in sufficient numbers to study them. The relatively high mean values of A and L, and the relatively low mean values of BI and s2 from the homogeneous marls in the Stavromenos facies are compared with the few values from the brown clays in the Finikia facies, thus causing a correlation which might be stratigraphic rather than ecological.

IV.3.4. The data compared with those of previous authors

Many authors have distinguished two different types of uniserial uvigerinids in the Mediterranean Messinian deposits. They consider the two types as two subspecies, *U. gaudryinoides gaudryinoides* Lipparini and *U. gaudryinoides siphogenerinoides* Lipparini (Lipparini, 1932; di Napoli Alliata, 1951; Dieci, 1959; Dondi, 1963; Papp, 1963, 1966; Hottinger, 1966). All authors describe only one subspecies in the Pliocene. This subspecies is named *U. gaudryinoides siphogenerinoides* by the first four enumerated authors. Papp and Hottinger call the Pliocene uvigerinids *U. gaudryinoides arquatensis* Papp.

The two subspecies dealt with in the literature resemble our thick type (*U. gaudryinoides gaudryinoides*) and thin type (*U. gaudryinoides siphogenerinoides*), but the two types are not limited to the Messinian as was suggested by Papp and Hottinger. In the Cretan deposits they co-occur already in the sediments from the *N. acostaensis* Zone.

In our opinion the differences between *U. gaudryinoides siphogenerinoides* and Papp's Pliocene subspecies *U. gaudryinoides arquatensis* are trivial. This last subspecies also belongs to our thin type.

Meulenkamp (1969) and, following this author, Fortuin (1974, 1977) distinguish two different types of uniserial uvigerinids also, but their two types do not coincide with the two subspecies of the earlier authors. Meulen-

kamp interpretes his two different groups of *Uvigerina* as different lineages. Highly evolved members of the older lineage, belonging to the species *U. felixi* Meulenkamp co-existed with the most primitive members of the younger lineage. Meulenkamp thought *U. felixi* to become extinct before the entry of *G. conomiozea.* In our opinion *U. felixi* belongs to our thin type, but these uvigerinids did not become extinct at such a low stratigraphic level. Thin uvigerinids are found throughout the Messinian, though they may be (almost) absent in some sections, as for instance Vrysses I. For the sections Exopolis and Vrysses Meulenkamp has described a gradual, but staggered increase in the mean A values and a regular decrease in the mean s2 values in the younger (*U. cretensis*) lineage. In our opinion he was taken in by the increase in numbers of thin uvigerinids higher in section Vrysses II. Probably Meulenkamp has not observed the bimodality in the B-distributions and interpreted mixed assemblages of thick and thin individuals as evolved descendants of the stratigraphically lower assemblages of thick specimens. The type sample of *U. lucasi* Meulenkamp (sample 872 H of this author) suggests such a bimodal B-distribution. The "species" *U. lucasi* is not based on a homogeneous group. A histogram of the B-distribution of sample 872 H is given in fig. 41, the result of the goodness-of-fit test is shown in table 20.

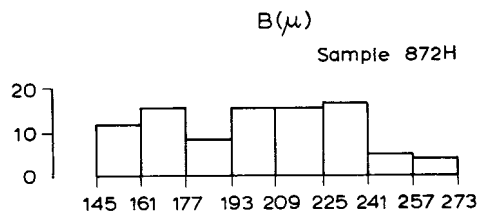


Fig. 41 Histogram of B in the type sample of *Uvigerina lucasi* Meulenkamp.

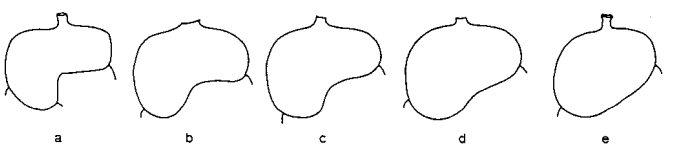
Classes	f_i	F_i	$\frac{(f_i - F_i)^2}{F_i}$
< 178	29	20.90	3.33
178 – 209	21	30.60	3.01
209 – 240	32	27.00	0.93
> 240	8	11.70	1.17 +
			$\chi^2 = 8.44$

Table 20 Goodness-of-fit test of the distribution of B in sample 872 H, the type sample of *U. lucasi.*

	$P_{97.5}$	$P_{99.0}$
χ^2:	5.02	6.63

Meulenkamp has given his "highly evolved" *Uvigerina* in the Miocene another species name than his "highly evolved" group in the Pliocene (*U. felixi* and *U. arquatensis* respectively), though he could "hardly differentiate both species as far as external morphology is concerned" (Meulenkamp, 1969, p. 144). Both groups are included in our thin type *Uvigerina.* For Meulenkamp it was a logical conclusion from his two lineage model that both "highly evolved" groups had to be distinguished; the end members of the lineages looked similar, but they were not related to each other. The "highly evolved" groups in the Miocene and in the Pliocene were considered as an example of parallel evolution.

A character on which a distinction between the older members of the lineages can be made is, according to Meulenkamp, the shape of the sutures in the non uniserial part of the test. Members of the *U. melitensis* lineage he said to have "en crochet" sutures like *U. bononiensis compressa* Cushman in contrast with specimens of the *U. cretensis* lineage. In our opinion this particular shape of the sutures is not reliable as a distinctive criterion. "En crochet" sutures is not actually a presence-absence character. Many intermediate shapes of the sutures are found. The text-figure shows the last



chambers of some specimens of sample CP 2251, section Ag. Vlassios. In many of the specimens, which according to Meulenkamp, belong to the *U. cretensis* lineage, "en crochet" sutures can be observed, as for instance in one of the paratypoids of *U. cretensis* (plate 5, fig. 1).

If we do not any longer believe in two uvigerinid lineages in the Cretan Neogene there does not seem to be any good reason to make a distinction between *U. felixi* and *U. arquatensis.*

IV.4. OTHER MATERIAL

IV.4.1. Scattered samples

In the samples from the section **Kalamavka**, which is older than the investigated sections dealt with in the previous pages and which is placed

in the *N. continuosa* Zone, the two types of *Uvigerina,* thick and thin, can be recognized as well. In the lowest two samples of this section, we find very large uvigerinids that resemble thick type *Uvigerina* closely in the overall shape of the test and in the shape of the chambers. Some differences are observed, however. These large uvigerinids have lower mean values of A (somewhat less than 0.50) and higher mean values of both L and B. The mean values of L and B are even higher than in the upper Miocene samples. Remarkably, in the samples studied earlier the size of the thick type seemed to increase fluctuatingly from the lowest section, Apostoli to the highest Miocene sections. The samples from section Apostoli, which is closest in time to section Kalamavka, contain the smallest thick type uvigerinids of all our samples.

For the time being we shall include the large individuals in our thick type.

Higher in the section Kalamavka the size of the thick uvigerinids decreases and the mean A values increase very fluctuatingly to obtain maximum values of about 1.30. The upper samples of the section cannot be distinguished from the later thick type samples. Thin type uvigerinids are found only in the upper samples of section Kalamavka. They have higher mean values of s2 than the younger thin type uvigerinids from the Miocene. They do not differ markedly in other aspects from the thin uvigerinids of higher stratigraphic levels (see table 21 for mean values of both types in section Kalamavka).

Because of the large size and the very low mean A values of the thick group the differences between the thick and the thin type are important. Intermediate specimens were not seen. Some histograms of a mixed sample are given in fig. 42, scattergrams of the same sample in fig. 43. The distinction between the two types is easier here than in the stratigraphically higher samples. The differences between both types diminish with time.

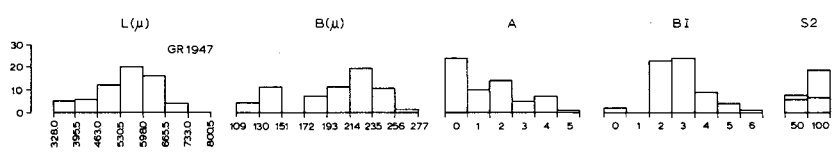


Fig. 42 Histograms of L, B, A, BI and s2 in sample GR 1947, section Kalamavka.

A sample from the type locality of *U. praeselliana* Fortuin (sample Fo 719, Prina Formation near Males) contains the same very large uvigerinids as were noted in the lower samples of section Kalamavka, and the mean A value is even lower.

The uvigerinids from some lithological samples from the island of **Gavdos** were also investigated. We used Freudenthal's material (1969). These samples

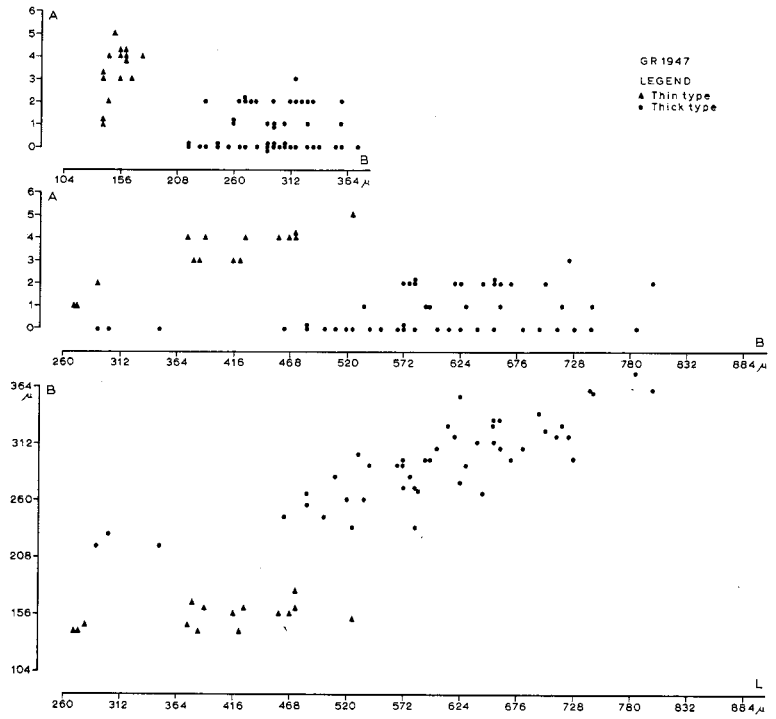


Fig. 43 Scattergrams of A versus B, A versus L, and L versus B in sample GR 1947, section Kalamavka.

contain abundant planktonic foraminifera. The samples can be placed in the *N. continuosa* Zone, but their relative stratigraphic position is not known, so no section can be given. In these samples the thick and the thin type of *Uvigerina* were noticed. The mean A values in the thick group are higher than in the thick group of section Kalamavka (the minimum is 0.77). One

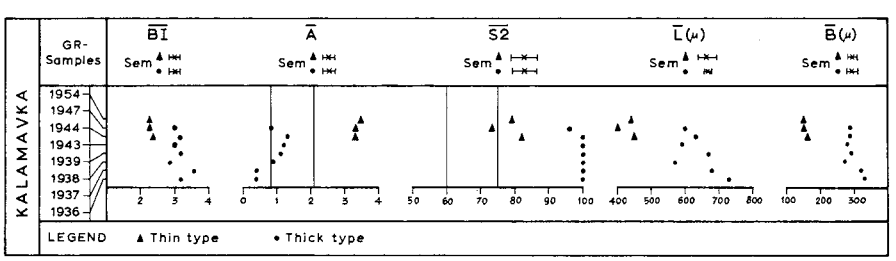


Fig. 44 The mean values of L, B, A, BI and s2 in section Kalamavka in stratigraphical succession.

Samples	$\bar{L}$ ± sem		$\bar{B}$ ± sem		$\bar{A}$ ± sem	
	thick	thin	thick	thin	thick	thin
			Section Kalamavka			
GR 1954		437 ± 10		151 ± 2		3.36 ± 0.13
GR 1947	601 ± 16	401 ± 16	294 ± 6	153 ± 3	0.77 ± 0.13	3.27 ± 0.30
GR 1944	629 ± 24	447 ± 11	288 ± 8	158 ± 3	1.30 ± 0.23	3.30 ± 0.22
GR 1943	593 ± 12		275 ± 5		1.18 ± 0.13	
GR 1939	673 ± 11		287 ± 4		1.07 ± 0.12	
GR 1938	572 ± 26		266 ± 7		0.91 ± 0.37	
GR 1937	679 ± 16		323 ± 3		0.39 ± 0.09	
GR 1936	729 ± 12		332 ± 4		0.41 ± 0.09	
Fo 719	697 ± 18		329 ± 4		0.09 ± 0.04	
			Gavdos			
G 507	524 ± 9		243 ± 4		1.36 ± 0.10	
G 503	564 ± 11	396 ± 6	262 ± 5	153 ± 2	1.30 ± 0.15	2.81 ± 0.11
G 500	597 ± 12		261 ± 3		0.96 ± 0.11	
G 491	581 ± 9		241 ± 2		2.41 ± 0.13	
G 490	588 ± 12	415 ± 17	265 ± 5	153 ± 3	0.73 ± 0.14	3.18 ± 0.26
G 485		461 ± 6		149 ± 1		3.58 ± 0.13
G 481	572 ± 11		243 ± 4		1.82 ± 0.13	

Samples	$\bar{BI}$ ± sem		$\bar{s2}$ ± sem		
	thick	thin	thick		thin
		Section Kalamavka			
GR 1954		2.28 ± 0.11			66.7 ± 4.8 (27)
GR 1947	3.04 ± 0.17	2.27 ± 0.12	100	(14)	73.1 ± 7.2 (15)
GR 1944	3.15 ± 0.21	2.35 ± 0.18	100	(10)	81.6 ± 5.7 (19)
GR 1943	3.00 ± 0.14		100	(21)	
GR 1939	3.23 ± 0.11		100	(22)	
GR 1938	2.91 ± 0.20		100	(3)	
GR 1937	3.63 ± 0.10		100	(4)	
GR 1936	3.64 ± 0.11		100	(4)	
Fo 719	3.27 ± 0.19		100	(1)	
		Gavdos			
G 507	2.86 ± 0.09		97.1 ± 1.6 (55)		
G 503	3.11 ± 0.13	2.16 ± 0.10	85.8 ± 2.9 (24)		66.1 ± 4.3 (31)
G 500	3.07 ± 0.16		97.6 ± 2.4 (21)		
G 491	2.53 ± 0.13		99.1 ± 0.9 (53)		
G 490	3.51 ± 0.16	2.18 ± 0.18	100	(8)	72.7 ± 7.9 (11)
G 485		2.25 ± 0.07			75.5 ± 3.5 (55)
G 481	2.62 ± 0.11		97.8 ± 1.6 (45)		

Table 21 Mean values and standard errors of the mean for the samples from Kalamavka, Gavdos and the sample from Males (Fo 719).

sample even has a mean A value of 2.41. The specimens are not as large as the specimens from the lower two samples of section Kalamavka.

The thin uvigerinids of Gavdos do not have as high mean s2 values as those of Kalamavka.

The mean values of the parameters of the samples from Kalamavka, Males and Gavdos are given in table 21. The succession of the mean values of the samples from Kalamavka is shown in fig. 44.

We investigated a few samples from the locality **Ag. Silas.** These samples were taken from just below the Messinian gypsum deposits, in the same central Cretan region where the Pliocene sections are located. These samples were studied to compare the Upper Miocene uvigerinids from central Crete with those from western Crete. The thick and the thin type were both observed, but thin specimens are rare. The mean values of some parameters of the thick type of Ag. Silas are given below.

Samples	$\overline{L}$ ± sem	$\overline{B}$ ± sem	$\overline{A}$ ± sem	$\overline{BI}$ ± sem	$\overline{s2}$ ± sem
AgS 4	550 ± 15	231 ± 8	2.17 ± 0.13	2.32 ± 0.11	97.7 ± 3.6
AgS 3	580 ± 12	248 ± 7	2.06 ± 0.15	2.56 ± 0.19	90.7 ± 6.3
AgS 2	622 ± 23	256 ± 8	1.85 ± 0.12	2.37 ± 0.09	93.0 ± 5.4

The uvigerinids do not show differences from these of the western Cretan sections.

IV.4.2. *Uvigerina bononiensis*

The taxonomy of *U. bononiensis* is somewhat confused. Fornasini (1888) has described the species from the Lower Pliocene marls near Bologna, Italy. In his original publication and in a later one (1898) he describes the species as an uvigerinid that is triserial in the older part of the test and later becomes biserial. Uniserial chambers he rarely observed. The test is compressed, especially in the biserial part of it. As ornamentation he observed longitudinal costae. The species resembles *U. parkeri* Karrer, but is distinct by the arrangement of the chambers (in what way he has not described).

Cushman (1925) describes *U. compressa* from sediments of the "Mediterranean-stufe" in the Vienna Basin. His type description bears a close resemblance to that of Fornasini's *U. bononiensis*. A differential diagnosis with the latter species is not given. Cushman mentions that his species resembles *U. parkeri* Karrer, but is distinct by "being more ornate".

Papp (1963) is of the opinion that the two names mentioned above should be used as names for two subspecies within one group, *U. bononiensis bononiensis* and *U. bononiensis compressa.* He gives no clear enumeration of the differences between these two subspecies. *U. bononiensis compressa* he assumed to be typical for the Badener series of the Vienna Basin, *U. bononiensis bononiensis* for the Pliocene, but it might be found as early as in the Tortonian. Both subspecies have according to Papp only a small triserial part of the test, which should be somewhat smaller in the nominate subspecies. In contrast with the names it should also be somewhat more compressed than *U. bononiensis compressa.*

In our opinion the two names should be considered as synonymous.

Meulenkamp (1969) considers *U. bononiensis compressa* as the ancestor of the older lineage of uniserial uvigerinids. Because of this supposed relationship we wanted to investigate some *U. bononiensis.* The species resembles our uniserial uvigerinids in many respects, e.g. it has a first, triserial part of the test, becomes later biserial, and rarely, even uniserial. The ornamentation is also similar. The most important difference between *U. bononiensis* and our uniserial uvigerinids is the compressed test in *U. bononiensis.* In our uvigerinids the test is round in transverse section, it is a flattened oval in *U. bononiensis.* In the latter group the chambers are distinctly longer in the direction parallel to the longer axis of the test than in the direction normal to this, in our uvigerinids the chambers are about equidimensional (the shape of the chambers in *U. bononiensis* is called "more long-drawn"). More trivial differences are the more marked "en crochet" shape of the sutures and the heavier ornamentation in *U. bononiensis.*

In most of our sections *U. bononiensis* is a rare constituent of the fauna.

In section Kalamavka we found large, thick specimens of *U. bononiensis,* often in the same samples as the uniserial uvigerinids. Fortuin (1977) has included in his species *U. praeselliana* many specimens, which show a distinct compression of the test, as for instance his figured specimens of pl. 1, figs. 1 to 4, sample Fo 460 T. In our opinion the individuals with a compressed test had better be placed in *U. bononiensis.* Fortuin (1974) gives no differential diagnosis between *U. praeselliana* and *U. bononiensis.* In our view to distinguish between both is not easy. According to their type description both species possess only rarely uniserial chambers, and many specimens from the type sample of *U. praeselliana* have sutures "en crochet". The only differences are the compression of the test in *U. bononiensis* and the more long-drawn shape of the chambers.

In other samples of section Kalamavka small specimens of *U. bononiensis*

were observed. These have somewhat more often a uniserial chamber than the thick *U. bononiensis.* They have about the same size as the thin type *Uvigerina,* but can be distinguished by the flattening of the test and the long-drawn shape of the chambers.

Fortuin (1977) reports the presence of *U.* ex. interc. *pappi-melitensis* from a sample in section Kalamavka (a mean A value of 1.98). These specimens belong to the thin type because of the non inflated chambers. We did not find thin type uvigerinids with such low mean A values, the lowest value is 2.40 in section Apostoli. The specimens of Fortuin are badly preserved and almost all are more or less deformed. It is difficult to see whether these specimens had originally flattened tests, but at least a number of them have long-drawn chambers. We do not believe that this sample contains a "primitive" group of thin uvigerinids, but it is a mixture of thin uniserial uvigerinids and thin *U. bononiensis.*

The mean values of *U. bononiensis* of two samples of section Kalamavka are given in table 22. The first of the samples contains thick *U. bononiensis,* the second thin ones. Histograms of the distributions of some parameters are given in fig. 45.

It is remarkable that we observe two types of *U. bononiensis* comparable with the groups, thick and thin, that we found in our uniserial uvigerinids.

In most of the Miocene sections *U. bononiensis* is not met with in large numbers, but in the upper parts of the Pliocene sections Finikia and Prassa they are often numerous. In these samples also two types of *U. bononiensis* could be distinguished, thick and thin ones. Sometimes both types are seen together. These samples display a bimodal distribution of B (goodness-of-

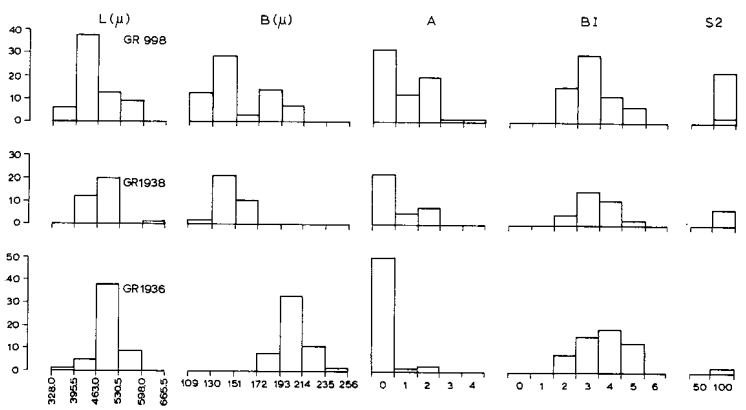


Fig. 45 Histograms of L, B, A, BI and s2 in *U. bononiensis* in three selected samples.

Samples	$\bar{L}$ ± sem		$\bar{B}$ ± sem	
	thick	thin	thick	thin
		Section Kalamavka		
GR 1938		428 ± 8 (35)		161 ± 3
GR 1936	558 ± 8 (55)		263 ± 3	
		Section Prassa		
GR 998	497 ± 13 (48)	363 ± 10 (15)	244 ± 5	148 ± 6

Samples	$\bar{A}$ ± sem		$\overline{BI}$ ± sem	
	thick	thin	thick	thin
		Section Kalamavka		
GR 1938		0.55 ± 0.15		4.30 ± 0.14
GR 1936	0.09 ± 0.06		3.66 ± 0.14	
		Section Prassa		
GR 998	0.13 ± 0.10	1.30 ± 0.15	3.87 ± 0.14	2.86 ± 0.14

Samples	$\overline{L/B}$ ± sem	
	thick	thin
		Section Kalamavka
GR 1938		2.67 ± 0.05
GR 1936	2.13 ± 0.03	
		Section Prassa
GR 998	2.05 ± 0.06	2.46 ± 0.04

Table 22 Mean values of *U. bononiensis* and standard errors of the mean. The numbers between brackets are the numbers of specimens.

Classes	f_i	F_i	$\frac{(f_i - F_i)^2}{F_i}$
< 158.75	40	25.08	8.88
158.75 – 197.50	3	20.46	14.92
197.50 – 236.50	13	13.86	0.05
> 236.50	10	6.60	1.75 +
			$\chi^2 = 25.60$

Table 23 Goodness-of-fit test of the distribution of B, in sample GR 998 (*U. bononiensis*).

	$P_{97,5}$	$P_{99,0}$
χ^2:	5.02	6.63

fit test in table 23; histograms in fig. 45; scattergram in fig. 46). The scattergrams of L versus B show two separate clusters. The two types are easily distinguished; intermediate specimens were not observed.

The thin *U. bononiensis* have slightly higher mean A values than the thick ones. Rare specimens with three or four uniserial chambers were noticed (pl. 2, fig. 3). Mean values for the groups in one sample are given in table 22. The situation is the same as in the thick and thin uniserial uvigerinids. There also the thin group has the highest mean A values.

It should be noted that in *U. bononiensis* the thick type is often a fauna-dominating element and comprises up to 40% of the benthonic foraminiferal fauna, just like the thick uniserial uvigerinids. The thin *U. bononiensis* are never fauna-dominating, again just as the thin uniserial uvigerinids.

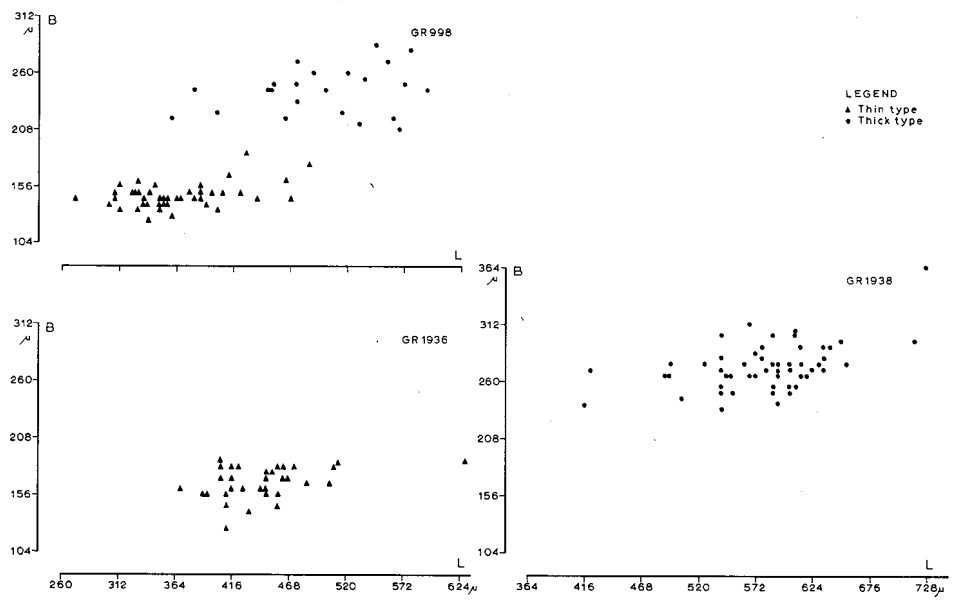


Fig. 46 Scattergrams of L versus B in *U. bononiensis* in three selected samples.

IV.4.3. The material in the collections

We studied the picked specimens in the collections of Meulenkamp (1969), Zachariasse (1975) and Fortuin (1974, 1977). In Meulenkamp's collection small, juvenile specimens are absent or rare in all samples.

Cretan material

In the Cretan material of all collections we did not observe differences

with our own material. We were able to distinguish the types thick, thin and intermediate in the collections. The mean values of all parameters are within the range of values obtained from ours. Especially samples, that had been identified as *U. lucasi* proved often to have a bimodal B-distribution.

In the Pliocene section Asteri (Meulenkamp, 1969; Zachariasse, 1975) we observed the replacement of the thick type in the Pliocene by the thin type at about the same stratigraphic level as in section Finikia (the exit of *G. puncticulata*). The same phenomenon is also seen in the samples of Fortuin's section Mirtos.

Spanish, Italian and Algerian material

From the small amount of Italian and Spanish material in the collections of Meulenkamp and Zachariasse only tentative conclusions may be drawn.

Meulenkamp has investigated four samples from the Spanish Carmona section, the type section of the Andalusian Stage. According to Perconig (1966) this stage corresponds to the Messinian. According to Verdenius (1970) the lowermost sample of Meulenkamp was taken from Tortonian deposits below the type Andalusian, the topmost sample from the Lower Pliocene deposits on top of the type Andalusian. In all these samples only thin type uvigerinids are found, which cannot be distinguished from our Cretan thin uvigerinids. In a sample from the Vera Basin (collection Zachariasse) again only thin type individuals are observed.

The time-discrepancy (Zachariasse, 1975) between the Spanish and the Cretan uvigerinids in the Upper Miocene needs not to exist, for the differences between the uvigerinids in both regions are due to the absence of the thick type in Spain, not to differences in mean values of parameters within one group.

In the Lower Messinian deposits from Northern Italy (section Rio Castellanía) both the thick type and the thin type, with intermediate specimens are found. In the Italian material the thick type is only observed below the gypsum deposits. Thin uvigerinids occur in the Pliocene deposits in the sections Rio Castellanía, Tabiano Bagni, Lugagnano-Castell' Arquato and Borzano. In the Pliocene neither thick type nor intermediate type uvigerinids were observed.

In a sample from the Chelif Basin, Northern Algeria from just below the gypsum deposits (Tauecchio and Marks, 1973) we could also identify the thick and the thin type with some intermediate specimens.

It should be noted that in the few samples from the Lower Pliocene in Spain and Italy no thick or intermediate type uvigerinids were met with, only thin type uvigerinids.

The *Uvigerina melitensis* lineage on Malta and Gozo

Meulenkamp has described two lineages of uniserial uvigerinids. The oldest of these, the *U. melitensis* lineage, should have developed mainly on Malta and Gozo, where he noticed the first three representative species. Meulenkamp believed he recognized a last species of this lineage in the Cretan *U. felixi.* The Cretan so-called representatives of the *U. melitensis* lineage can be identified with our thin type uvigerinids.

Fortuin describes from the Ierapetra region samples with higher mean s2 values and lower mean A values than *U. felixi.* He supposed these to be the older species of the *U. melitensis* lineage and to be identical to the Maltese species. As mentioned in section IV.4.2. the sample with the lowest mean A values is probably a mixture of *U. bononiensis* and our thin type, the other samples belong to our thin type.

The question now arises whether the Maltese uvigerinids are also identifiable with our thin type. We could not obtain new samples from Malta and Gozo, but we had Meulenkamp's collection at our disposal. We re-measured six of his samples from Gozo (see table 2). Although our mean s2 values deviate from Meulenkamp's mean values the Gozo samples show a fairly consistent change. The mean values of A increase while the mean values of s2 decrease. The mean values of BI also decrease and the mean values of L increase. The mean values of B show no clear trend. There is no indication at all of heterogeneous samples. Unfortunately, only a short succession of samples illustrates this lineage which seems to be much better than the Cretan "lineage". In three samples the changes are completed, and the higher samples show no significant changes.

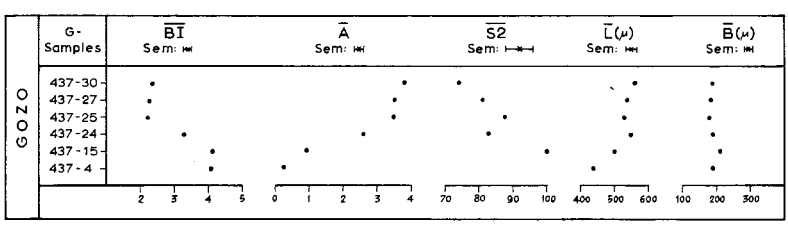


Fig. 47 The mean values of L, B, A, BI and s2 in the uvigerinids in section Tad Dabrani (437), Gozo.

Only a few samples have been described by Fortuin of the older species of the *U. melitensis* lineage from his Kalamavka Formation (*N. continuosa* Zone) and from the lower parts of his Makrilia and Ammoudhares Forma-

tions (top of the *N. continuosa* Zone and base of the *N. acostaensis* Zone). There seems to be a time discrepancy between the Cretan representatives and the Maltese ones, if one takes the planktonic zonations for granted. The Cretan *U. melitensis* lineage development must have been completed within the *N. continuosa* Zone, in which the most highly evolved species of the lineage occurs. This species continues up into the *N. acostaensis* Zone. But according to Felix (1973) the Maltese lineage starts earlier and has only reached the third species, *U. gaulensis,* in the *N. continuosa* Zone.

The mean values of A of the Maltese samples (table 2) are about the same as those of the thin uvigerinids from section Kalamavka (table 21), but differences are found in the other parameters. The mean values of L and B are greatly different for the Maltese and the Cretan groups, which should belong to one lineage. The Maltese mean values of L and B are intermediate between the values for the thick and the thin Cretan types. The Malta uvigerinids show a strong resemblance with our intermediate type. There are a few, not unequivocal differences, however. In the Maltese uvigerinids the shape of the sutures is more evidently "en crochet" and the chamber arrangement in the biserial part of the test is, as Meulenkamp has already described, more regular and less twisted (pl. 4, figs. 1–3).

In our opinion the Maltese *Uvigerina* should not be taken as really identical with the Cretan intermediate type because of these small differences, and, more importantly, because of the time discrepancy. The Maltese group seems to descend directly from *U. bononiensis,* as has been supposed by Meulenkamp. They appear to form a fairly good lineage, in which the changes are quickly completed. No relationship with the Cretan uniserial uvigerinids can be demonstrated to exist, since in the oldest known samples from Crete no intermediate individuals were found. Probably the Maltese uvigerinids can best be seen as a separate offshoot of *U. bononiensis* of which as yet no representatives have been observed outside the islands of Malta and Gozo.

IV.5. DATA FROM SCANNING ELECTRON MICROSCOPE PHOTOGRAPHS

The wall structure of both types of uniserial uvigerinids was studied with the aid of scanning electron microscope photographs. S.E.M.-photographs were also made of the wall structures of *U. bononiensis* and of the Maltese uvigerinids. In all these groups both striate and smooth chamberwalls were found. If we compare the size, shape and distribution of the pores we observe no differences between the groups: the wall structures are similar (plate 1, figs. 1–2, plate 2, figs. 1–7, plate 4, fig. 4). The shape of the pores is irregularly rounded to oval. The largest diameter of the pores is generally

between 0.60 and 1.10 μ. Hispid surfaces of the wall are covered with small, long-drawn tubercles which may coalesce into thin costae (plate 4, fig. 5). The ornamentations on the wall are between the pores. The pores are never closed by tubercles or costae, but remain open, even in the oldest part of the test with the heaviest ornamentation (plate 5, fig. 2).

All the groups, *U. bononiensis,* the Maltese uvigerinids and the thick and thin uvigerinids from Crete show a similar wall structure. However, one should not conclude that such a wall structure is common to all uvigerinids. The S.E.M.-photographs of the wall of some triserial uvigerinids (see pl. 3, figs. 1–3) are different. If we compare the wall structures of our uvigerinids with the photographs of Von Daniels and Spiegler (1977) the differences are also obvious, though the pore size in their *U. semiornata* group is in the same range as the pore size of our uvigerinids. In our opinion the similarity of the wall structure of all the uvigerinids we have studied possibly indicates a close relationship between all these groups.

IV.6. THE RESULTS OF THE MULTIVARIATE ANALYSES

IV.6.1. Principal component analysis

In the principal component analysis the mean values of L, B, A, BI and s2 were entered. We used all the homogeneous mean values of all samples. The samples of section Kalamavka were included, but not those of the samples from the collections.

	$\overline{L}$	$\overline{B}$	$\overline{A}$	$\overline{BI}$	$\overline{s2}$
$\overline{L}$	1.00	+0.85	−0.55	+0.62	+0.71
$\overline{B}$		1.00	−0.83	+0.72	+0.81
$\overline{A}$			1.00	−0.74	−0.81
$\overline{BI}$				1.00	+0.71
$\overline{s2}$					1.00

Table 24 Matrix of correlation coefficients.
$n = 465; r_{0,995} = 0.14$.

All the variables proved to be significantly ($r \geqslant r_{0,995}$) correlated as can be seen in table 24, which gives the matrix of the correlation coefficients. The clusters of the mean values in the multidimensional space are elongated ellipsoids owing to the existence of these correlations. A large percentage of the total variance in the multidimensional space is represented in the first

principal component (table 25). We can use the first principal component and disregard the rest, and thus reduce the dimensionality.

The loadings of the variables on the first three principal components are stated in table 26. All parameters are represented in the first principal component with about equal weight. In the literature (for instance Blackith and Reyment, 1971) the first component is often thought to be a size-factor in which only parameters of size have any weight. This is not the case in *Uvigerina*: all parameters and not only the size parameters L and B load on the first component with about the same weight. As the mean A value is negatively correlated with the mean values of all other parameters this parameter has a negative loading.

Princ. comp.	% of variance	cum. %
1	79.0	79.0
2	9.9	88.9
3	6.3	95.2
4	3.8	99.0
5	1.0	100.0

Table 25 The amount of the variance, accounted for by the principal components.

	P.C. 1	P.C. 2	P.C. 3
$\overline{L}$	+0.84	+0.52	+0.09
$\overline{B}$	+0.95	+0.15	+0.09
$\overline{A}$	−0.89	+0.35	+0.21
$\overline{BI}$	+0.85	−0.26	+0.46
$\overline{s2}$	+0.91	−0.06	+0.21

Table 26 The loadings on the most important principal components.

	P.C. 1	P.C. 2
$\overline{L}$	+0.21	+1.07
$\overline{B}$	+0.24	+0.31
$\overline{A}$	−0.23	+0.72
$\overline{BI}$	+0.22	−0.52
$\overline{s2}$	+0.23	−0.12

Table 27 The score on the first principal component is for each sample equal to: score = $0.21 \times \overline{L} + 0.24 \times \overline{B} - 0.23 \times \overline{A} + 0.22 \times \overline{BI} + 0.23 \times \overline{s2}$. For the variables standardized values must be used.

The second principal component is made up chiefly of the mean L and A, and the third component of the mean values of BI, A and s2. These components, however, account only for a low percentage of the total variance (table 25).

As the first principal component is situated in the direction of the largest variance we expect this component to transverse the clusters of our thick and thin type uvigerinids, if the variance between the groups is larger than the variance within the groups.

We calculated the scores for each sample on the first principal component, and the standardized coefficients of the variables, given in table 27. In fig. 48 the scores of all the samples are shown in the stratigraphical succession. Evidently these scores are different for the different types of *Uvigerina,* which means that the first principal component indeed transverses the clusters of the types.

The multivariate variable demonstrates the lack of sustained changes we had already expected from the figures for all variables separately (figs. 24, 25). The Lower Pliocene intermediate type samples are qua values of the multivariate variable close to the thin type samples. The scores change fluctuatingly higher in the Pliocene till they have attained multivariate scores close to the thick type samples. The Pliocene thick type samples have scores similar to those of the Miocene thick type samples in the sections Exopolis and Vrysses I. The samples from the topmost Miocene sections Vrysses III and Khaeretiana have very high scores, probably resulting from the large mean values of L and B of these samples.

On the whole, the principal component analysis yields the same results as the conventional statistics of all variables. The multivariate scores on the first principal component reflect the fluctuations in all parameters. One figure of these scores (fig. 48) can be used to show the morphological fluctuations in time, instead of the several figures of each of the parameters (figs. 24, 25). In the case of *Uvigerina* all the parameters are represented with about the same weight in the multivariate score on the first principal component (table 26).

IV.6.2. Discriminant analysis

In the discriminant analysis the mean values of the parameters L, B, A, BI and s2 were again used as variables. We made a discriminant analysis on the basis of two groups (thick type = 0; thin type = 2). The intermediate samples were not given a priori group membership and not entered as a separate category. The prior probabilities of belonging to one of the groups were given according to the percentages of thick and thin samples present.

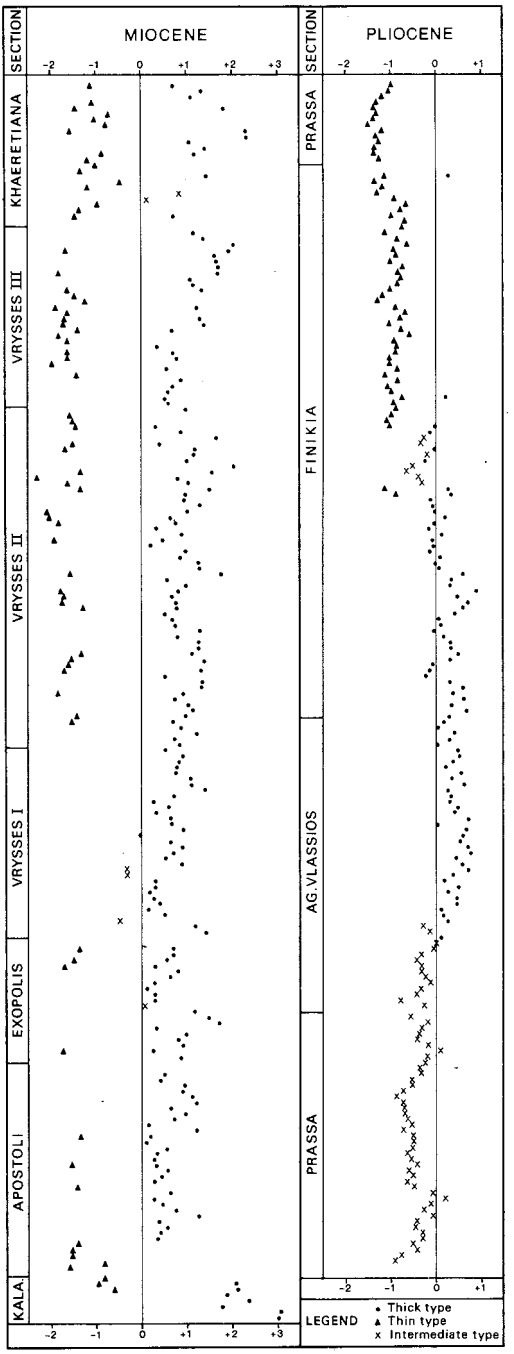


Fig. 48 The scores on the first principal component for all samples for the separate groups in stratigraphical succession.

In this rather simple type of discriminant analysis there is a snag, for the combined variances of all parameters for both groups are supposed to be equal. This is almost certainly not so for the uvigerinids, because the variances of all parameters are larger in the thick type than in the thin type. Yet this analysis is thought to give much information about the grouping of *Uvigerina*.

For each homogeneous set of specimens the value of the discriminant function was calculated as well as the probability of a sample to belong to one of the groups. The sample was then allocated in the group in which it belongs with the greatest probability, even if this probability is but 0.51. The grouping of the samples according to their discriminant scores was compared with the a priori grouping. All samples, which had been given no group membership, i.e. the intermediate samples, were also grouped.

	Coef.
$\overline{L}$	−0.73
$\overline{B}$	+1.77
$\overline{A}$	+0.09
$\overline{BI}$	−0.09
$\overline{s2}$	+1.62

Table 28 Discriminant analysis, standardized coefficients, 5 parameters.
Discriminant function: (unstandardized coefficients) $D = -0.01 \times \overline{L} + 0.04 \times \overline{B} + 0.11 \times \times \overline{A} - 0.25 \times \overline{BI} + 0.11 \times \overline{s2} - 11.56$.

From the standardized discriminant coefficients, given in table 28, it is obvious that the mean values of the parameters B and s2 are the best to discriminate between the two groups of *Uvigerina*, while L contributes but a little and A and BI hardly at all. Table 28 also shows the discriminant function with unstandardized coefficients. A sample will have about equal probabilities of belonging to either group if its value of the discriminant function is equal to −1.0. The probability that a discriminant score of −0.2 or less occurs within the statistical population of the discriminant scores of the thick type is less than 0.01. Likewise, the probability that a discriminant score of −1.6 or more occurs within the statistical population of the discriminant scores of the thin type is 0.01 or less. The region between the discriminant scores of −1.6 and −0.2 is called the undecided region.

Histograms of the values of the discriminant scores of all types are shown in fig. 49.

The results of the discriminant analysis are encouraging as regards the

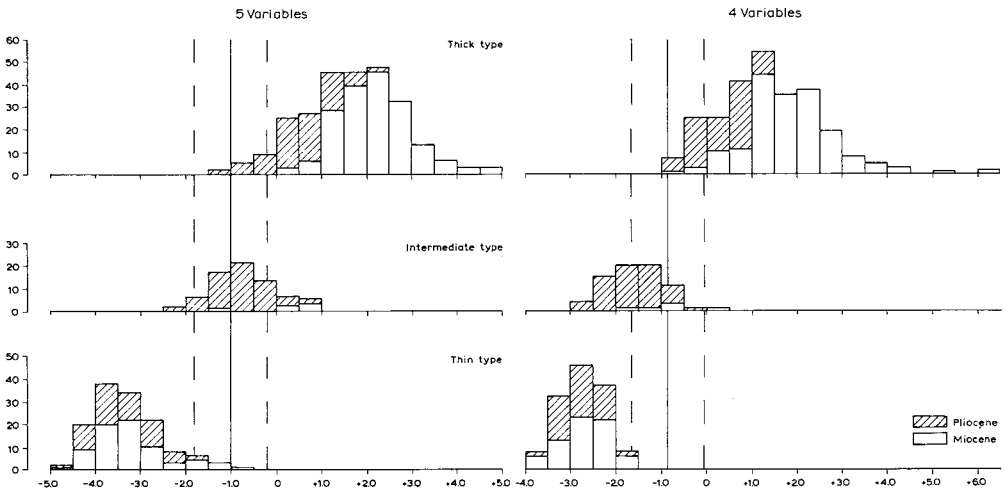


Fig. 49 Histograms of the discriminant scores for the separate groups. Left; analysis with L, B, A, BI and s2. Right; analysis with L, B, A and BI.

efficiency of the used grouping. Of all 465 samples used in the analysis, only two samples of the thick type and one of the thin type were "misplaced". The thin type sample, which according to its discriminant score would be closer to the thick type, is the oldest thin type sample from section Kalamavka with a high mean s2 value. The two thick type samples which according to their discriminant scores should be closer to the thin type, are Pliocene samples with extraordinarily low mean s2 values. The "misplaced" samples are all within the undecided region. The intermediate samples are partly grouped with the thick type samples, partly with the thin type. Many of these samples, however, are in the undecided region of discriminant scores. Only a few of them have discriminant scores of more than −0.2 or less than −1.6, and can be grouped with either type with a probability of more than 0.99.

This confirms again that the intermediate type samples are indeed intermediate in all the parameters. On the other hand, the lowermost Pliocene samples have discriminant scores of less than −1.6 and should belong to the thin group with a probability of more than 0.99. As has already been evident from the bivariate scattergrams the Pliocene thick type samples are somewhat closer to the thin type samples than the Miocene thick type samples. The majority of the Pliocene thick type samples is located outside the undecided region of discriminant scores, but some Pliocene thick type

samples and some Miocene thin type samples do have such undecided discriminant scores.

The discrepancies between our a priori grouping and the grouping based on the discriminant analysis are due to the presence of samples with "aberrant" mean s2 values, so it will be of interest to calculate a discriminant function, using only the mean values of L, B, A and BI as variables. This function is given in table 29 together with the standardized coefficients. The differences with the 5-variables discriminant analysis are evident. The mean value of B is still the best discriminating parameter, but the mean value of A is in the analysis with four variables of much greater importance. The mean values of L and BI are of less importance than in the 5-variables analysis. The equal-probability discriminant score is equal to −0.85, and the undecided region has boundaries at discriminant scores of −0.05 and −1.65. In this analysis no samples are "misplaced". The majority of the intermediate samples is now grouped with the thin type *Uvigerina* and much fewer of these samples are now within the undecided region as regards their discriminant score. But more Pliocene thick type samples are now located within the undecided region. Figure 49 shows histograms for the discriminant scores of all types.

	Coef.
$\overline{L}$	−0.33
$\overline{B}$	+1.82
$\overline{A}$	−0.65
$\overline{BI}$	+0.08

Table 29 Discriminant analysis, standardized coefficients, 4 parameters.
Discriminant function: (unstandardized coefficients) $D = -0.005 \times \overline{L} + 0.04 \times \overline{B} - 0.81 \times \overline{A} + 0.21 \times \overline{BI} - 4.76$.

The discriminant analysis appears to give good results. Our grouping, which was based on the inflatedness of the chambers proves to coincide with the best possible grouping on a linear combination of parameter mean values. The analysis with only four parameters (L, B, A and BI) fits in with the grouping on the basis of the inflatedness of the chambers somewhat better than does the analysis in which the s2 factor is added, but the differences are not large.

It is possible to place the discriminant scores of all samples in the stratigraphical succession. This was done in fig. 50 for the 5-variables analysis. This multivariate variable again gives a picture similar to the scores on the

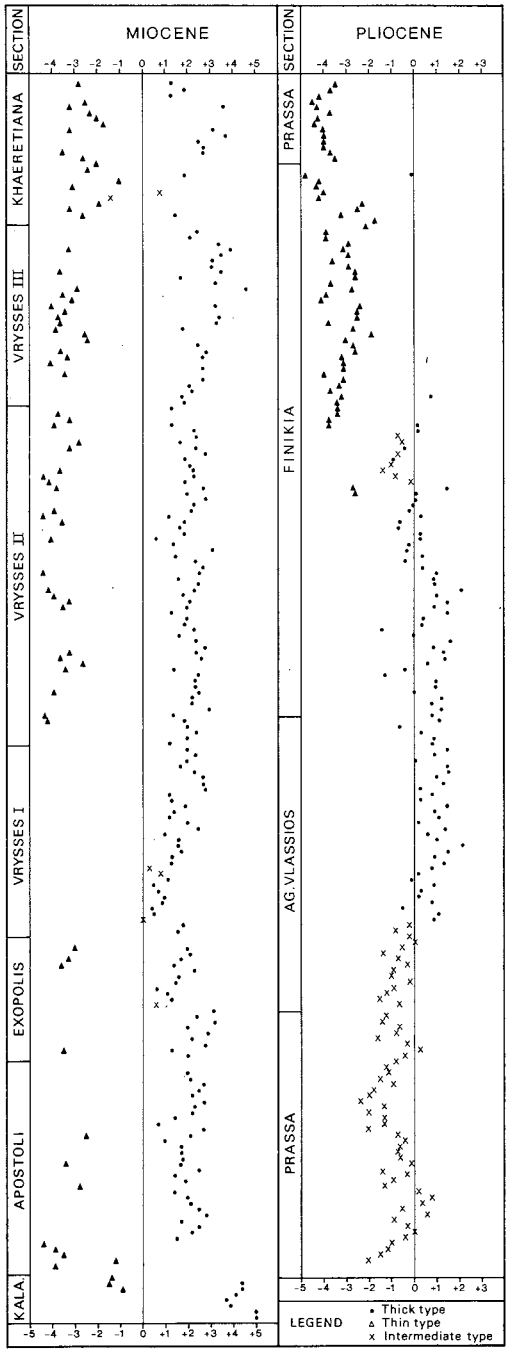


Fig. 50 The discriminant scores for the separate groups for all samples (analysis with five variables, L, B, A, BI, s2) in stratigraphical succession.

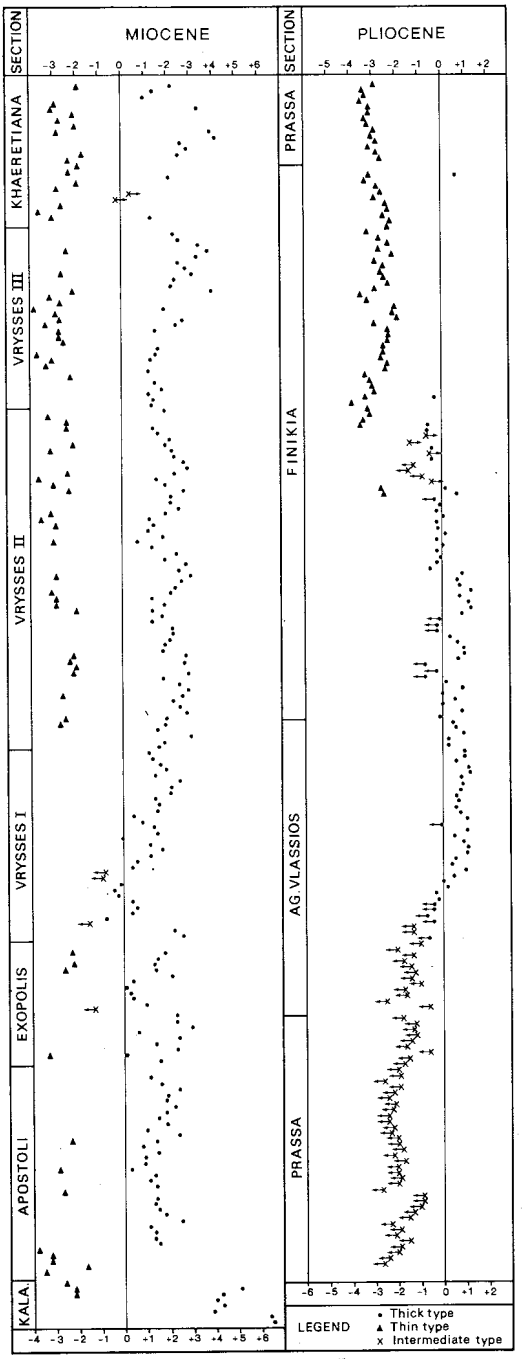


Fig. 51 The discriminant scores for the separate groups for all samples (analysis with four variables, L, B, A and BI). The results of the cluster analysis are shown as well. An arrow to the right signifies that the sample is included in the cluster, which contains predominantly thick type specimens. An arrow to the left signifies inclusion in the cluster which consists predominantly of thin type specimens. The arrows are only given for the intermediate type samples and for the samples that were included in a cluster, to which they do not belong according to the a priori grouping.

first principal component and all variables separately, i.e. no sustained changes. In this discriminant score, however, not all variables are equally weighted, for the mean values of B and s2 are the most important, whereas BI is scarcely represented.

In fig. 51 the discriminant scores of the 4-variables analysis are shown in the stratigraphical succession (in this figure the results of the cluster analysis, described below, were also entered). Figure 51 illustrates the now already familiar picture of fluctuations and no sustained changes. In this multivariate variable the mean values of B and A are the most important factors. The greatest difference with fig. 50 is the different allocation of the intermediate samples in the Lower Pliocene.

By using discriminant scores instead of the scores on the first principal component we introduced a hierarchy of the variables into the multivariate variable. The best discriminating variables have the highest place in this type of hierarchy.

IV.6.3. Cluster analysis

The discriminant analysis gave an answer to the question whether our grouping would be efficient. With cluster analysis we hoped to discover if our grouping of the uvigerinids is a "natural" one. We tried to get an answer to this question by means of Wishart's mode analysis. The mean values of L, B, A, BI and s2 were again made use of as the variables.

During the analysis the correlation coefficient we used as a distance-criterion decreased from 0.997 to 0.885. At this level all the samples are enclosed in one cluster. Just before this level is attained two clusters are found. One of these includes all the Miocene thick type samples, the majority of the Pliocene thick type samples, three intermediate type samples from the Miocene and four from the Pliocene. In the other cluster all the Miocene thin type samples are grouped, and all the Pliocene ones, together with three Miocene intermediate type samples and almost all Pliocene ones. Twelve Pliocene samples, which we consider to be thick type samples, were also included in this cluster.

The results of the cluster analysis are shown in fig. 51.

At a coefficient-level of 0.976 seventy-six % of all samples is placed in clusters. At this level three clusters are observed; one with thick type samples, another with thin type samples and a third one with intermediate type samples. Then the clusters with the thin and the intermediate type samples fuse. Later in the analysis some thick type samples from the Pliocene are included in this cluster, because of their resemblance to some of

the intermediate samples (the intermediate type uvigerinids pass gradually into thick type ones).

On the whole the cluster analysis seems to confirm the existence of different groups in *Uvigerina,* i.e. of several modes in the multivariate distribution. A classification based upon the inflatedness of the chambers coincides in the Miocene completely with the division into clusters according to the mean values of L, B, A, BI and s2. In the Pliocene the grouping is somewhat more problematical. The majority of the intermediate samples is placed in one cluster with the thin type samples. Some samples which we consider to belong to the thick type are also placed in this cluster.

IV.6.4. Discussion of the results of the multivariate analyses

The results of the multivariate analyses affirm the conclusions drawn from conventional statistics and from paleontological common sense. The existing problems cannot be solved by applying multivariate methods. The differences in the results of the discriminant analyses on four and five variables and the cluster analysis all concern the intermediate type samples in the Pliocene (and the few ones in the Miocene) so the multivariate analyses give no extra information exactly where problems are known to exist.

It is possible, however, to give a combined picture of the changes in five parameters with the aid of multivariate parameters. Naturally it is a disadvantage of these pictures that the parameters of the fossils themselves are no longer directly recognizable, but in our opinion such a simplified picture gives a good image of the changes in *Uvigerina.*

Our division into groups proves to work well, and is reproducible with discriminant analysis. Likewise, the cluster analysis shows the presence of two modes in the distribution of the parameters in the multidimensional space, which coincide fairly well with our groups. The discriminant analysis on four variables and the cluster analysis give the same results as regards the intermediate samples in the Lower Pliocene, the majority of them is grouped with the thin type. In view of this analysis and in accordance with the results from the conventional statistics the lowest Pliocene samples are considered as thin type uvigerinids, which change gradually, but by way of a few transitional samples into thick type uvigerinids.

It must be remembered (as has already been discussed in section IV.2.) that we used mean values of homogeneous groups in all the analyses. If our splitting of the samples into several groups would ever be shown to be wrong the later analyses will have no sense at all.

IV.7.1. The dissolved specimens

From the thick and the thin type of *Uvigerina* twenty specimens, picked from aselect splits of sample CP 300 (section Vrysses II), were dissolved chamber by chamber. Also two specimens from the topotype material of *U. praeselliana* (locality Males) were dissolved. After the removal of each chamber the L and B were measured. The total number of chambers was counted (N) and the diameter of the protoconch measured (P).

The histograms of P and N are given in fig. 52 and the five scattergrams of L and B versus N and P, and of P versus N are shown in fig. 53. The correlation coefficients for these combinations of parameters are tabulated in table 31. In table 30 the mean values and standard errors of the mean of P and N are given, together with the ranges. For one average specimen of the thin type, one of the thick type and one of the thick type from Males, figure 54 shows the L and the B at each budding step and L and B versus N.

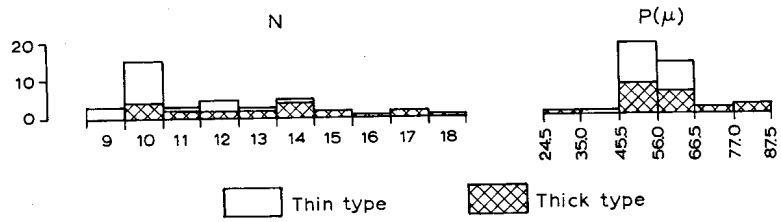


Fig. 52 Histograms of P and N in the dissolved specimens.

	$\bar{N} \pm$ sem	range	$\bar{P} \pm$ sem	range
thick	13.30 ± 0.57	10–18	57 ± 3	30–78
thin	10.55 ± 0.30	9–14	52 ± 1	35–62

Table 30 Mean values of P and N and standard errors of the mean in the dissolved specimens, with the ranges of P and N.

The range of P and N for the types overlap strongly, but ranges and mean values of both P and N are larger in the thick type. Evidently the types cannot be envisaged as distinct micro- and macrospheric generations. There is no bimodality in the distribution of all P values. Within each group a separation of different generations cannot be observed either.

In the thick uvigerinids P is correlated significantly ($r \geqslant r_{0.975}$) with both L and B; large, thick specimens have large protoconches. Short specimens with large protoconches are always typical juveniles (only triserial chambers). In the thin type uvigerinids the correlation between P, and L and B is not significant.

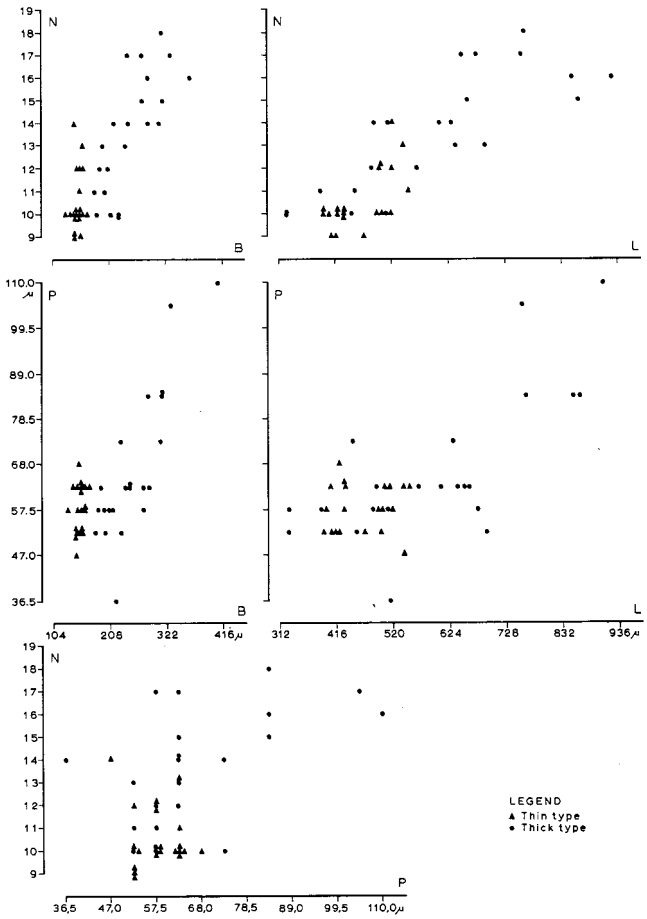


Fig. 53 Scattergrams of L and B versus N and P, and of N versus P for the dissolved specimens.

In both groups the total number of chambers is correlated significantly and positively with L. In the thick type a positive correlation between B and N is found, and P and N are significantly correlated ($r \geqslant r_{0.975}$).

On the average the growth of the test in the thick type proceeds by adding both to the length and the breadth of the test till from 8 to 15 chambers

have been formed. Later the breadth is about constant and only L increases further. In the thin type uvigerinids the breadth increases till from 6 to 10 chambers have been made. An increase in B during the formation of the 9th and 10th chamber sometimes occurs, but it is slight. The increase in B in the thick type continues during more budding steps than in the thin type.

	thick	thin
N–L	**+0.79**	**+0.70**
N–B	**+0.74**	+0.15
N–P	*+0.44*	–0.13
P–L	**+0.63**	+0.06
P–B	**+0.70**	+0.28

Table 31 Correlation coefficients of P and N versus L and B in the dissolved specimens.
bold $r \geqslant r_{0,995}$
italics $r \geqslant r_{0,975}$

The increase in L per added chamber is about the same in the thick as in the thin type. In fig. 54 the curves of L versus N greatly overlap. The differences in the size of a newly added chamber in the thick and the thin type are caused by differences in B.

Usually specimens of the thick type experience more budding steps than specimens of the thin type, though large overlaps in the values of N are observed. Specimens of the thick type retain during more budding steps the increase in B and L with each added chamber.

As far as these specimens can be considered to be representative for the entire groups the uniserial chambers add more to the length of the test than do the biserial chambers in the thin type, in which the uniserial chambers are arranged regularly. In the thick type uvigerinids, in which the uniserial chambers are arranged in a staggered series there is little or no difference between the length added by either uniserial or by biserial chambers. The length added by each chamber increases slowly and irregularly during the ontogeny.

IV.7.2. The protoconch sizes

The protoconch was measured in the eleven samples, of which histograms and scattergrams have been shown in section IV.2., and in *U. bononiensis* in sample GR 998, of which histograms are given in section IV.4.2. The diameter of the protoconches can be measured only in undamaged and well-preserved specimens. In each sample a number of specimens could not be used for P-measurements.

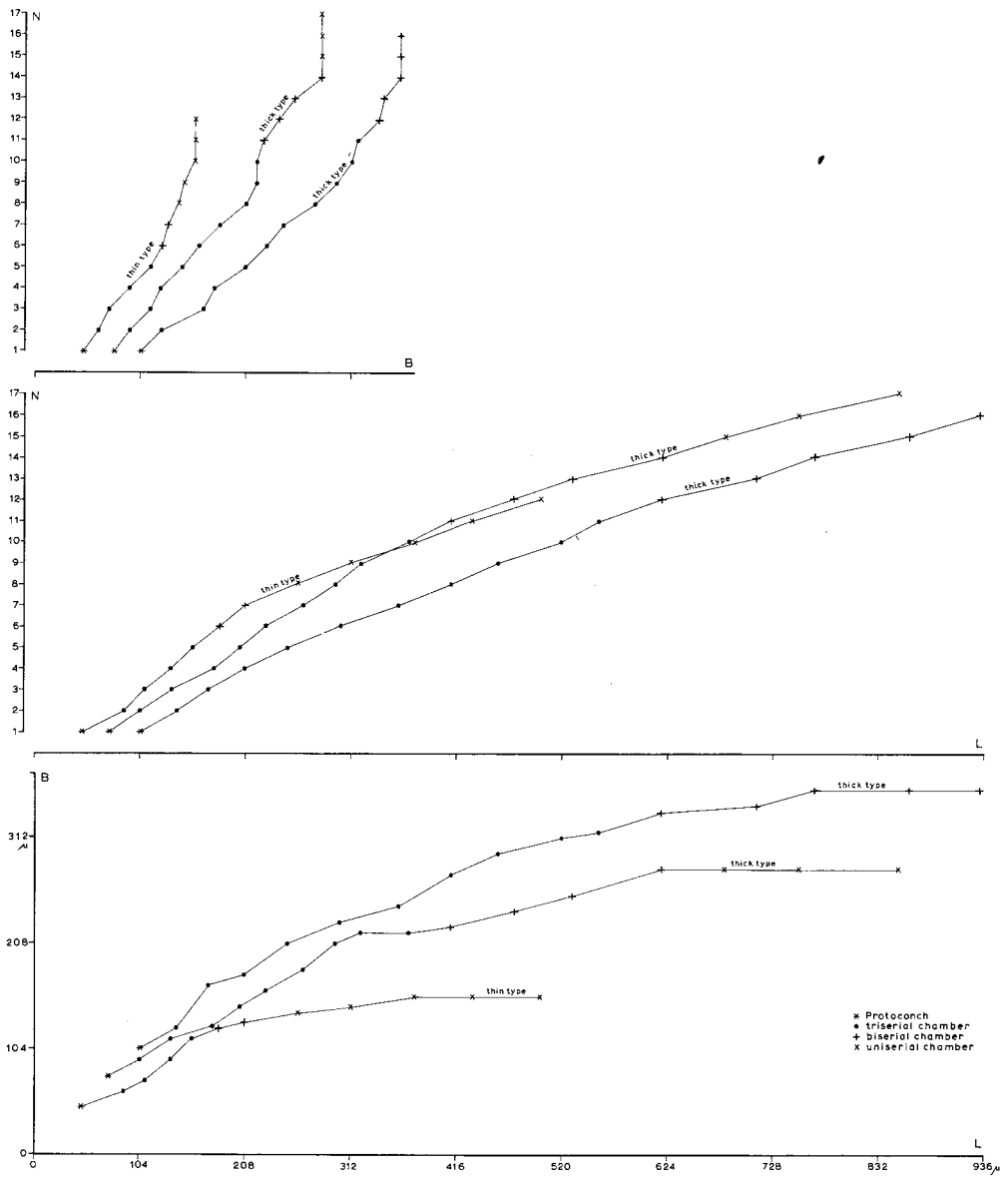


Fig. 54 Illustration of the growth stages in three selected specimens.

The mean values of P and their standard errors of the mean are given in table 32 for all types. Histograms are shown in fig. 55. The scattergrams of P versus L are seen in fig. 56.

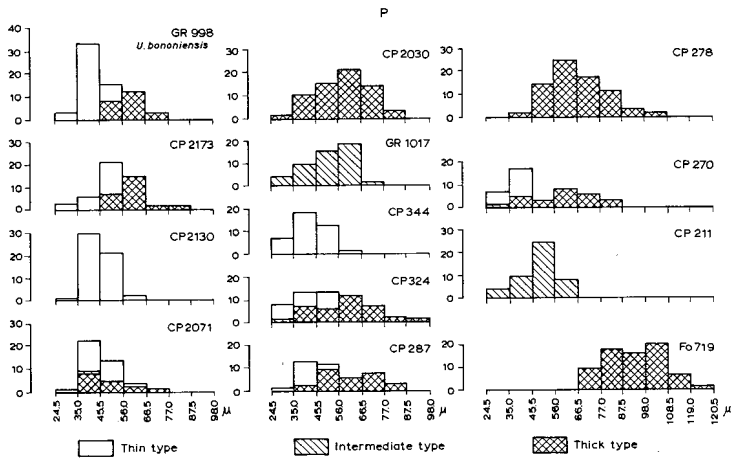


Fig. 55 Histograms of P for thirteen selected samples, one of which contains *U. bononiensis*.

Samples	thick	interm.	thin	*U. bononiensis* thick	*U. bononiensis* thin
GR 998				57 ± 1	40 ± 1
CP 2173	65 ± 2		48 ± 2		
CP 2130			48 ± 2		
CP 2071	51 ± 2		47 ± 1		
CP 2030	60 ± 2				
GR1017		55 ± 1			
CP 344			45 ± 1		
CP 324	63 ± 2		44 ± 1		
CP 287	64 ± 2		44 ± 1		
CP 278	69 ± 2				
CP 270	61 ± 3		41 ± 2		
		52 ± 1			
Fo 719	91 ± 2				

Table 32 Mean values and standard errors of the mean of the protoconch diameter in the selected samples.

Often the mean values of P for the thick type are significantly larger than those of the accompanying thin type uvigerinids, but the distributions of P display a large overlap. The individuals of sample Fo 719 (Males), the topotype material of *U. praeselliana,* are very large and have significantly greater protoconches than the other thick type uvigerinids. The thick type *U. bononiensis* have a mean value of P in the same range as the thick type *Uvigerina.* The mean value of P of the thin type *U. bononiensis* is slightly smaller than those of the thin type uniserial uvigerinids, and signifi-

Samples	thick	interm.	thin	*U. bononiensis*	
				thick	thin
		P and L			
GR 998				+0.09 (23)	**+0.41** (43)
CP 2173	***+0.43*** (26)		+0.18 (22)		
CP 2130			**+0.50** (53)		
CP 2071	+0.27 (16)		−0.13 (25)		
CP 2030	**+0.53** (64)				
GR1017		+0.07 (47)			
CP 344			−0.16 (38)		
CP 324	**+0.60** (35)		+0.32 (21)		
CP 287	**+0.61** (30)		−0.40 (14)		
CP 278	**+0.40** (71)				
CP 270	**+0.56** (26)		+0.08 (18)		
CP 211		***+0.30*** (49)			
Fo 719	+0.14 (69)				
		P and B			
GR 998				+0.41	+0.10
CP 2173	+0.37		**+0.47**		
CP 2130			**+0.51**		
CP 2071	+0.46		+0.13		
CP 2030	**+0.39**				
GR1017		−0.14			
CP 344			+0.08		
CP 324	+0.46		+0.03		
CP 287	+0.59		**+0.67**		
CP 278	***+0.27***				
CP 270	**+0.58**		+0.32		
CP 211		+0.24			
Fo 719	+0.10				

Table 33 Correlation coefficients between P and L and between P and B in the selected samples. The numbers between brackets are the numbers of specimens
bold $r \geqslant r_{0,995}$
italics $r \geqslant r_{0,975}$

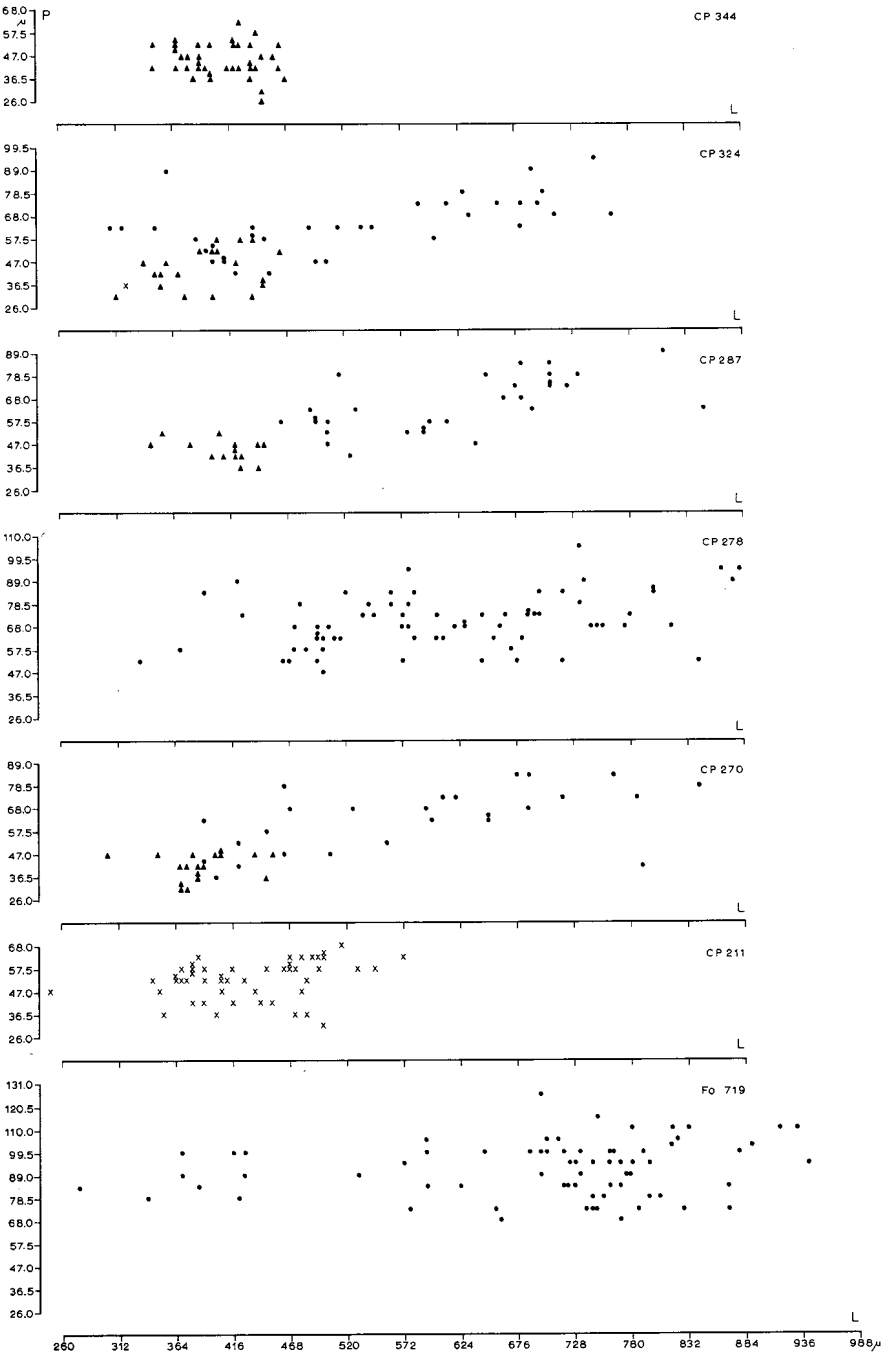


Fig. 56a Scattergrams of P versus L for seven selected samples from the Miocene. Triangles: thin type; dots: thick type; crosses: intermediate type.

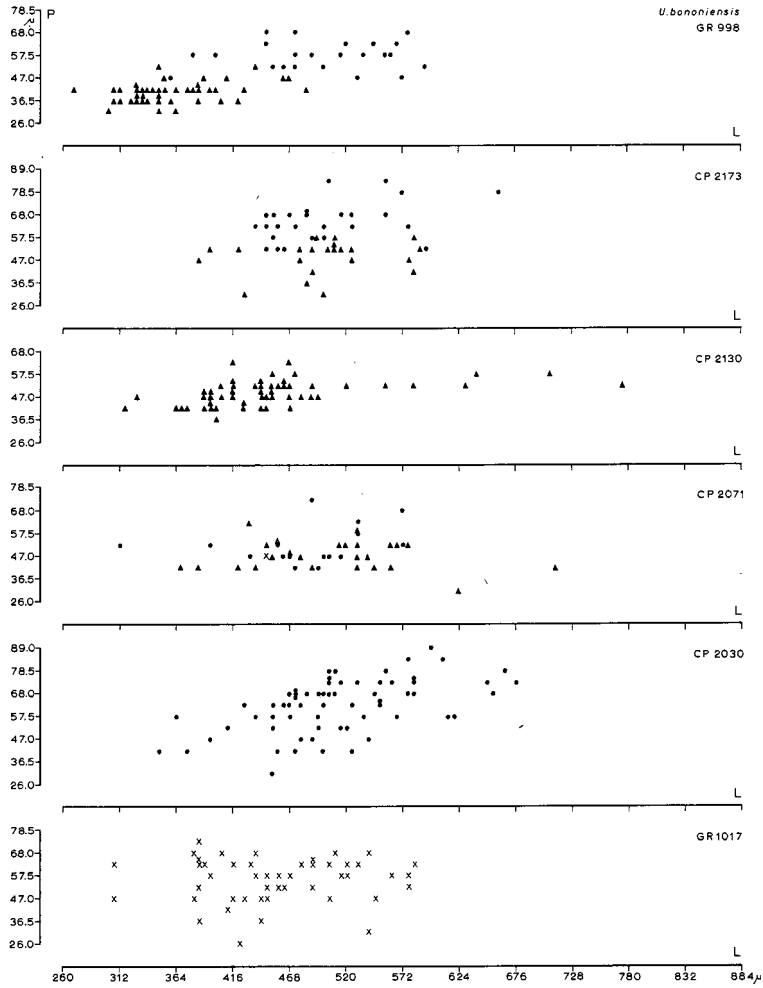


Fig. 56b Scattergrams of P versus L for six selected samples from the Pliocene, one of which contains *U. bononiensis*. Triangles: thin type; dots: thick type; crosses: intermediate type.

cantly (at a probability level of 1%) different from the mean value of P of the thick *U. bononiensis* in the same sample. The range of the protoconch-diameters in sample Fo 719 is 75 to 125 μ, in the thick type uvigerinids in the other samples 25 to 105 μ, and in the thin type samples 25 to 60 μ. The two intermediate type samples have protoconch-diameters in the range from 30 to 75 μ, the thick *U. bononiensis* from 48 to 75 μ, and the thin *U. bononiensis* from 25 to 55 μ.

All the mean values of P are shown in fig. 57 versus the mean values of L, and B. The samples with high mean values of L and B also have high mean values of P. This positive correlation is often found in the individual samples, as can be seen in table 33. A positive correlation between P and L is observed in most of the thick type samples, but it is rare in the thin type samples. A positive correlation between P and B appears in some of the thick type and thin type samples. Of the two intermediate type samples one shows a positive correlation between P and L, none between P and B.

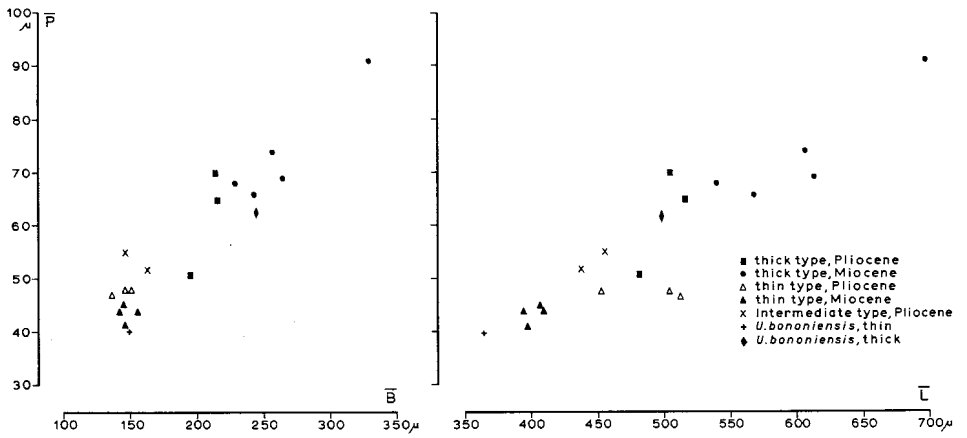


Fig. 57 Scattergrams of the mean values of P versus those of L and B for the thirteen samples, one of which contains *U. bononiensis*.

No clear distinction between two size groups of P values was observed. In a few samples, for example in sample CP 270, single large specimens were found with a comparatively small protoconch, but this protoconch has the same diameter as the protoconch of smaller specimens in the same sample. These large specimens might be microspheres; if so, microspheres are rare and no clear distinction between microspheres and macrospheres can be made on the basis of protoconch size.

IV.8. STABLE ISOTOPES

The complete results of the study of the stable isotopes will be published in the Proceedings of the Kon. Ned. Akad. Wetensch., ser. B, in a paper by Van der Zwaan and Thomas. We are discussing some preliminary results below in so far as they are relevant to the subject of this publication.

Figure 58 shows the isotopic values in the stratigraphic succession. A

staggered, but steady, increase in the δO^{18}-values is observed in the Miocene, and in section Khaeretiana we find very strong fluctuations. All measured δO^{18}-values except one (in section Khaeretiana) are positive. The differences in the δO^{18}-values are so large that to interpret these differences as being the result of only changes in the water temperature would lead to rather unlikely temperatures and temperature differences. Carbonate in equilibrium with normal seawater with a salinity of 35‰ and at a temperature of 25°C has an isotopic composition of 0‰ PDB. The isotopic values of the samples

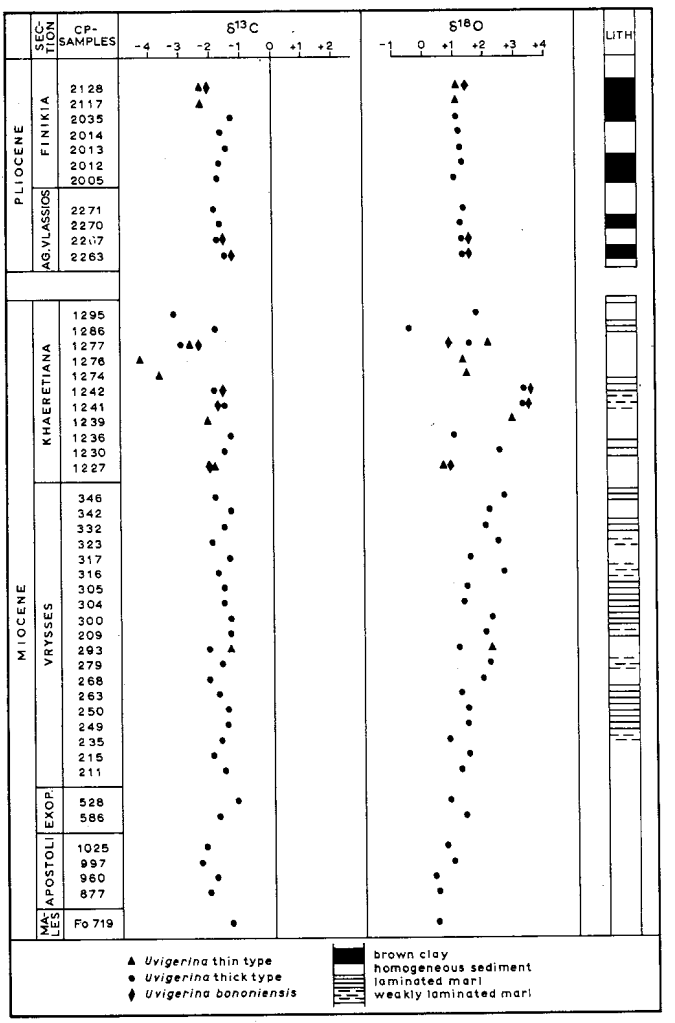


Fig. 58 Isotopic ratios of oxygen and carbon in some samples in the stratigraphic succession.

from section Khaeretiana indicate large aberrations from these conditions. Delta O^{18}-values from –0.5‰ to +3.4‰ were measured in this section. At constant salinities the maximum differences would signify temperature differences of about 15°C, which is obviously absurd for any reasonably large water mass. Changes in salinity offer a more likely explanation. The increase in the values of δO^{18} probably represents not a decrease of the temperature but an increase of the salinities in the bottom waters. These changes in salinity are not clearly related to the occurrence of the laminated sediments. The Pliocene δO^{18}-values are all about +1.2‰ and do not fluctuate much. These delta-values indicate water of a normal salinity of about 35‰ at a water temperature of about 15°C.

The δC^{13}-values are all negative. Section Khaeretiana shows values as low as –4.3‰. No trend can be seen in the values of δC^{13} in the Miocene sections. The largest fluctuations are found again in section Khaeretiana. The Pliocene values of δC^{13} hardly fluctuate, only the upper two samples have slightly lower values. In the literature interpretations of (changes in) δC^{13}-values are contradictory. We can not yet offer an explanation of the fluctuations in these isotopic values.

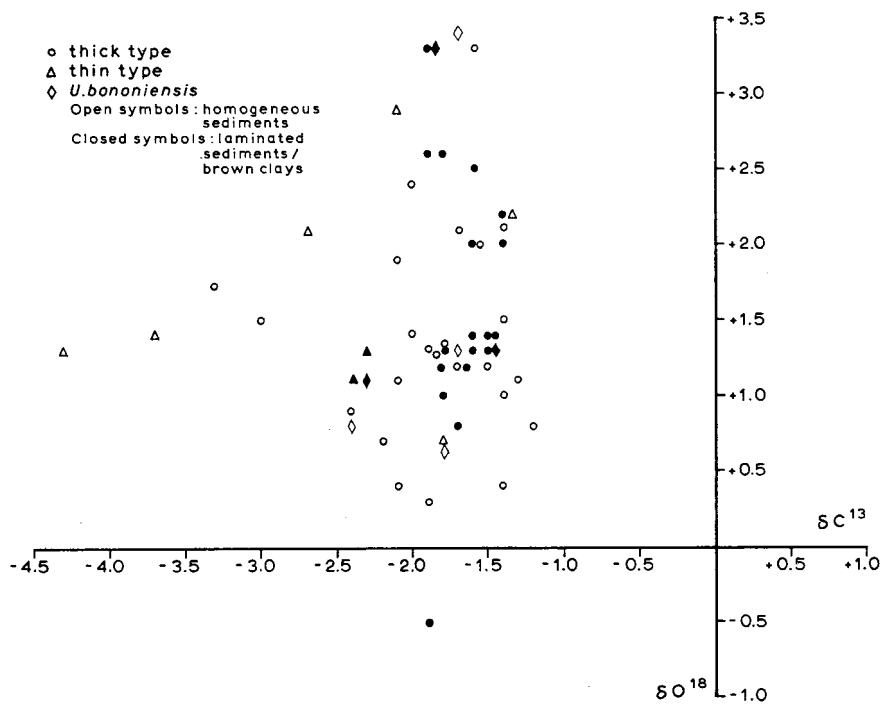


Fig. 59 Scattergram of the isotopic ratios of oxygen versus those of carbon.

A scattergram of the values of δO^{18} versus those of δC^{13} is presented in fig. 59. No linear relationship is observed between the values of δO^{18} and δC^{13}. A cluster with most of the samples is more or less parallel to the δO^{18} axis (variable δO^{18}-values and fairly constant δC^{13}-values). Only four samples are on a line more or less parallel to the δC^{13} axis.

In some samples the isotopic values were measured in *U. bononiensis,* and in either thick type or thin type *Uvigerina.* No meaningful differences were discovered between the values of these groups, which seems to suggest that no "vital effect" is involved in the secretion of the carbonate of the uvigerinid test. This is, however, contradicted by the data from the only two samples in which individuals of both the thick and the thin type could be analyzed. In all other samples it was not possible to gather a sufficient amount of thin type specimens. In one of these samples *U. bononiensis* was also analyzed. Both samples show unmistakable differences in the values of δO^{18} and δC^{13} in the two groups and in *U. bononiensis.*

Since only two samples could be analyzed, no interpretation of these differences can be given. As long as we cannot make certain that both groups lived at the same locality at the same time no conclusions regarding "vital effects" in *Uvigerina* can be made. The results might be interpreted as an indication that both groups did not live at the same place and/or time. They may represent assemblages that succeeded each other in time and/or assemblages from different depth-habitats brought together by synsedimentary transport.

Chapter V

DISCUSSION OF THE RESULTS

V.1. BIOZONATION IN *UVIGERINA*

On account of our data the biometrical species proposed by Meulenkamp (1969) evidently cannot be seen as successive taxonomical units. Meulenkamp's taxa are well recognizable, well defined statistical groups, but they are not successive. We observed a rapid alternation of different biometrical "species" along the stratigraphical column. In figs. 24 and 25 one observes that the vertical lines in the graphs of the mean A and s2 values, i.e. the boundaries of the biometrical species, are crossed again and again.

Evidently a biozonation considering the "evolutionary stages" in the uniserial uvigerinids is not reliable. Even a distinction between Miocene and Pliocene samples can only be made with reasonable certainty if one studies a long succession of samples.

The uvigerinids show large, significant, fluctuations in time in the interval we studied, but no net, perceivable, changes. In these uvigerinids and possibly also in other groups of smaller foraminifera (for instance bolivinids), the mean values of samples can be significantly different, whereas the changes are not irreversible. Possibly they are ecology-controlled and not genetic. If the fluctuating changes in the morphology of the uvigerinids are primarily dependent upon the environment (see section V.2.) no more than a correlation of environment, i.e. of facies, seems to be possible with the aid of the morphology of these uvigerinids. Such a correlation will have a limited value within a basin and cannot be used for time-bound correlations over larger distances.

V.2. THE TYPES OF *UVIGERINA*; WHAT DO THEY REPRESENT?

The two extreme types of *Uvigerina* often occur together in the Miocene samples and in a few of the Pliocene ones. Do these types represent different species or units at an infra-specific level? There is no unequivocal definition possible for species of the fossil record and certainly not in a group of fossils which probably reproduced at least partly asexually. We assume a species to be a morphologically homogeneous group that can be distinguished from other likewise homogeneous groups. Our two extreme groups of *Uvigerina* can be distinguished from each other in many samples and might

be considered to represent two species. We hesitate, however, to allocate our groups to two species because of the following considerations.

In many samples some intermediate individuals occur. Some samples as a whole can neither be assigned to the thick type nor to the thin type; they are intermediate in their characteristics.

In the Early Pliocene the so-called intermediate uvigerinids resemble the thin type in most of their parameters. They change gradually, but fluctuatingly, into homeomorphs of the thick uvigerinids from the Miocene. So it seems possible that thin type uvigerinids gradually changed into the thick type. The reverse was not observed; higher in the Pliocene sections the thick uvigerinids are replaced by thin ones with heterogeneous, mixed samples in between.

The Miocene uvigerinids

Thin type uvigerinids are never an important constituent of the benthonic foraminiferal faunas. They are found in the upper samples of section Kalamavka, together with a fairly diverse plankton fauna and an open marine benthos association. They occur as the only uvigerinids in the lower samples from section Apostoli in shallow marine sediments. In section Exopolis the thin types are observed mainly in the upper samples of this regressive sequence. In section Vrysses I they appear only as rare, single specimens. In section Vrysses II, Vrysses III and Khaeretiana they are more frequent (fig. 39). In Khaeretiana more samples contain thin uvigerinids than contain thick ones. The thin uvigerinids are commonly found in the non laminated sediments; they are rare-to-absent in the laminated marls.

It should be remembered that the Mediterranean Upper Neogene is thought to show a regressive trend. During the deposition of the sediments of the sections Exopolis, Vrysses I, II, III and Khaeretiana the salinity of the bottom waters probably increased (isotope data, section IV.8.).

The thick type uvigerinids are often a dominant constituent of the benthonic foraminiferal faunas. They are particularly numerous in the lower samples of section Kalamavka, where plankton is rare or absent, and the rest of the benthonic foraminiferal fauna is poor as well. In section Apostoli the thick types are relatively small. They replace the thin type fairly abruptly. In this section thick uvigerinids occur in large amounts in groups of three to five samples; in between these groups they are absent or nearly absent. Thick *Uvigerina* are rare in the blue clays of section Exopolis with the diverse, open marine faunas; they abound in the laminated sediments only. In section Vrysses I the thick type are almost the only representatives

of the uniserial uvigerinids, and often very abundant. In the sections Vrysses I and II the thick uvigerinids are the most abundant of all Miocene sections. They have peak-values up to about 60% of the total benthonic foraminiferal faunas. These peak-values are found in the laminated sediments. In the sections Vrysses III and Khaeretiana the thick uvigerinids start to decline. Peak-values still occur in the laminated sediments, but the peaks decrease in number and amplitude.

The intermediate type uvigerinids are always rare. In many samples we find only a few individuals. In the six wholly intermediate samples (in sections Exopolis, Vrysses I and Khaeretiana) they are not a faunadominating element.

In general, thick uvigerinids seem to proliferate under circumstances deviating from normal, open marine. In the laminated sediments the benthonic foraminiferal faunas are often dominated by a few species (as the thick *Uvigerina, Bolivina dilatata, Bolivina spathulata*). These sediments have not been burrowed. Presumably life was difficult for most benthonic organisms during the deposition of the laminated marls. Considering the results of the study of the oxygen isotopes the salinity increased probably throughout the Upper Miocene, but the laminated sediments do not represent periods of increased salinity as compared with the non laminated sediments.

According to Van der Zwaan and Thomas (in prep., 1980) in the Messinian Cretan basins the deposition of the laminated sediments took place while a strong stratification in the water column existed. In such a stratified water column the vertical water circulation will be interrupted. A total or partial absence of vertical circulation will have brought about the phenomenon that the oxygen in the bottom waters, after having been used up by the fauna, would not have been replenished by oxygen from the upper water layers, where the phytoplankton was living and producing oxygen. In the relatively small, Miocene, Cretan "isolated" basins the oxygen may have been nearly depleted in the bottom layers of the water. There would be abundant nutrients available for the organisms that were able to cope with the low oxygen levels. The water stratification in these basins was probably often interrupted, making the circulation start again, and bringing oxygenated waters to the bottom. But as time proceeded toward the Late Messinian the stratification in the basins got more severe, possibly as a consequence of the increasing overall salinities; the circulation of the water masses could not be fully restored. As the overall circulation diminished, less and less nutrients would have been available to the fauna.

If this model is valid we may envisage the thick *Uvigerina* as a phenotype

that is successful under conditions of an oxygen minimum. The thick uvigerinids needed the abundant nutrients under these adverse circumstances, then being able to proliferate. They possibly were indifferent to fluctuating and high salinities.

Thin uvigerinids did not have the possibility to "bloom". They are the "normal" phenotype, found in small numbers in diverse, open marine associations. They probably possessed a large tolerance for increased salinities and especially for low nutrient levels. They are still met with when the thick type starts to decline, high in the sections Vrysses III and Khaeretiana.

Lutze (1964) has described the existence of different ecophenotypes with a similar morphologic break with different oxygen content of the water in which the foraminifera were living, in the species *Bolivina argentea* Cushman in the basins off the coast of California.

If the above described model is valid all measured and counted parameters (i.e. the overall shape of the test in *Uvigerina*) will be strongly dependent on the environment.

The co-occurrence of the two extreme types of uvigerinids can be explained in several ways. It should be remembered that each sample has a 5 to 25 cm thickness of the sediments. The sediments of a large number of years were sampled together. When the environment changed rapidly within this period sediments deposited in different environments may be included in one sample. The intermediate specimens could have lived in the transitional time interval when the conditions were changing.

Alternatively the habitats of the types might have had an overlap. The intermediate type may then be interpreted as individuals living in an intermediate habitat (Lutze reports fairly rare intermediate bolivinid assemblages from the slopes in the Californian basins). Possibly the uvigerinids lived at different depths at the same time, and material from shallow water was transported to greater depths. An oxygen depletion will start in the deeper parts of the basin. If so, thick *Uvigerina* might have lived in the deeper parts of the basins, whereas the thin uvigerinids lived in the aerated, shallower water. The intermediate type may have lived in a transitional habitat somewhere on the slopes of the basins.

In the Upper Miocene Ecija Formation of the Spanish Carmona Section only thin uvigerinids are found. This formation was probably deposited under open marine conditions, and no indications for oxygen-minima are observed, hence the absence of thick *Uvigerina*.

In the Messinian deposits of Northern Africa and Northern Italy (Papp, 1963, Hottinger, 1966, collection Meulenkamp) both types of uvigerinids

occur together with intermediate specimens just below the gypsum deposits. Many authors (e.g. Dondi, 1963) describe faunas dominated by uvigerinids which show a close resemblance with our thick *Uvigerina.* These disappear somewhat below the gypsum, whereas *Uvigerina* identical to or similar to our thin type are observed in the Upper Miocene, below, between, above the gypsum, and in the Lower Pliocene.

The Pliocene uvigerinids

In the Lower Pliocene deposits of the Kourtes facies *Uvigerina* very similar to the Miocene thin type are met with. Meulenkamp et al. (1979a) are of the opinion that the Kourtes marls have been deposited under open marine conditions in a relatively large basin. Possibly the thin uvigerinids had undergone slight morphological changes in the time interval from which we have no information. This idea is supported by the fact that the thin type from the highest Miocene section, Khaeretiana, have a closer resemblance to the Lower Pliocene uvigerinids (for instance in the comparatively high mean values of s2) than the other Miocene thin uvigerinids.

The lowest Pliocene uvigerinids change into thick ones just where the sediments of the Kourtes facies change into those of the Finikia facies. The terrigenous clastic supply increased and the Finikia sediments were deposited in elongate, graben-like depressions (Meulenkamp et al., 1979a). In such a paleogeographic configuration stagnancy in the basins could occur, comparable to the water stratification in the Miocene. The brown, often laminated, clays of the Pliocene were probably deposited under oxygen minimum conditions in the bottom waters. The data from the oxygen isotopes (section IV.8.) indicate that the salinity did not deviate from normal, in contrast to the Miocene circumstances.

As the oxygen minimum conditions recur the thick *Uvigerina,* the phenotype thought to be in favour under such circumstances, reappears. The intermediate type uvigerinids are supposed to have lived under conditions that are transitional between those of the deposition of the Kourtes and Finikia facies.

The changes in the morphology of *Uvigerina* run parallel to changes in the benthonic and planktonic foraminiferal faunas and in the nannoplankton floras (Meulenkamp et al., 1979a). In the sediments of the Finikia facies the thick uvigerinids are often fauna-dominating elements in the brown clays.

The replacement of the thick type by the thin type is observed at about the level of the exit of *G. puncticulata,* the transition of interval II to interval III in Meulenkamp et al. This replacement in the section is not fully

understood. No changes in the lithology are evident, but the microfauna as a whole shows large shifts in the average relative frequencies of several taxa; some taxa disappear altogether. Although there seems to be no alteration in the paleogeographical configuration the different composition of the fauna suggests a change in the environment. The thick uvigerinids decline in numbers, and show some modifications in morphology just before they are replaced, viz. they show a tendency to resemble thin uvigerinids. At this level intermediate uvigerinids are found. Meulenkamp et al. suggest that changes in the Mediterranean circulation pattern may have occurred.

Possibly the Pliocene thin uvigerinids did not evolve on Crete from thick ones but migrated from more westerly parts of the Mediterranean, where the type is known to have existed throughout the Pliocene. Such a migration is conceivable in a time of changing circulation patterns, but this kind of explanation is thought not to be necessary.

Higher in the sections thick uvigerinids appear only incidentally. There could have been limited (in time and/or place) circumstances favourable for the thick type, or these rare individuals may have been reworked, though the sediments do not indicate reworking.

In these higher parts of the sections (Stavromenos facies) we came across the thick and thin *U. bononiensis*. The thick *U. bononiensis* is often a fauna-dominating element and has peak values in the diatomaceous marls. This seems to suggest that a "niche" for the thick type *Uvigerina* still existed and was filled by the thick *U. bononiensis* in the absence of the thick "uniserial" *Uvigerina*. The disappearance of the thick uvigerinids is not well understood. If the sediments of the Stavromenos facies were deposited under conditions of severe isolation of the basins the nutrient supply may have become too low for the thick type.

The Cretan development of thick uvigerinids in the Pliocene in contrast with the presumably constant presence of only thin ones in the Pliocene deposits in Spain, Morocco and Italy, can be understood. In the latter areas normal marine conditions reigned and no small, (semi-isolated) basins developed. The phenotype for aberrant, oxygen minimum conditions did not reappear. On Crete such conditions did occur and the phenotype is manifest.

The uvigerinids from Kalamavka

The presence of very large specimens of thick *Uvigerina* in the lowermost samples of section Kalamavka and in Males cannot be interpreted as an effect of time. Thick uvigerinids in the upper part of Vrysses III and Khaeretiana are also very large and have often also low mean values of A. The uvigerinids from Gavdos, from the same planktonic zone as those from Kalamavka, are

much smaller and have higher mean A values.

The large uvigerinids in Kalamavka become gradually but fluctuatingly smaller and get higher mean A values higher in the section where more diverse planktonic and benthonic associations are observed.

The formation of exceptionally large tests seems to be an answer to some environmental requirement. Unfortunately, not many data on these large uvigerinids and the progress of the change into more "normal" thick uvigerinids are available.

Concluding, we may say that the correlation between the types of *Uvigerina* and the inferred environment suggests that they are ecophenotypes. The existencne of similar types in *U. bononiensis* indicates that the dominance or prevalence of the types are a response to the environment.

It should be noted that the co-occurrence of the two ecophenotypes probably points to the existence of "aberrant" conditions as well as normal conditions. The co-occurrence of the two types is not typical for the Messinian Age, as has been suggested by Papp (1963), but it is indicative of the aberrant conditions, prevailing in the Mediterranean in this time. Likewise, the large size of thick uniserial uvigerinids is not characteristic for a Messinian Age as is suggested by Hottinger (1966), but is probably representative for the environmental conditions, locally realized in the Messinian.

Indeed we return to old theories if we suggest that the types of uvigerinids are ecophenotypes. Already Lipparini (1932, pp. 67, 68) assumed that the differences in the morphology of the uvigerinids were caused by ecological factors, related to the aberrant conditions during the Messinian.

V.3. REPRODUCTION AND GROWTH

The protoconch diameter of our uvigerinids shows no evident separation into two or more (three?) groups. Often the diameter of the protoconch is correlated with L, and in the thick type often also with B. The large, thick uvigerinids from Kalamavka and Males have extremely large protoconches. The thick *U. bononiensis* has protoconches in the same range as the thick *Uvigerina,* whereas the thin *U. bononiensis* has protoconches in the same range as the thin *Uvigerina.*

There seems to be an overall positive correlation between the size of the protoconch and the final size of the test, though this correlation is not always found within one sample.

The biological basis for the determination of the size of the protoconch we do not know. There could be some kind of environmental influence.

Probably only specimens with large protoconches have the capacity to attain a large test size, while it depends on other (environmental?) factors whether the large size is actually obtained. Specimens with a small protoconch may be unable to become large.

In the group of totally dissolved specimens only one individual was found with a comparatively small protoconch for its large size (fig. 53). This specimen is situated somewhat outside the cluster of the other specimens in the P versus N scattergram. In some of the samples in which protoconches were measured without total dissolution a few large specimens with comparatively small protoconches are observed, for instance, in sample CP 270 (fig. 56). If these specimens are microspheres there will be no clear difference in protoconch size between microspheres and macrospheres, and microspheres must be rare among the thick uvigerinids. Specimens with an intermediate protoconch size are numerous.

Sliter (1970) reports that dimorphism is found in natural assemblages of *Bolivina doniezi* Cushman. This dimorphism he no longer observed in his laboratory assemblages after some generations of clone forming. Both in natural and in laboratory assemblages this *Bolivina* shows a positive correlation between the size of the protoconch and the total length of the test, like our *Uvigerina,* but in the bolivinids the total number of chambers is negatively correlated with the size of the protoconch, in contrast with what we found in *Uvigerina.*

If the large specimens with the comparatively small protoconches are really microspheres, then reproduction in thick *Uvigerina* must have proceeded mainly asexually. One has assumed a predominantly asexual reproduction in many groups, in which a successful phenotype that is adapted to environmental circumstances will multiply quickly, as possibly happened during the proliferation of the thick uvigerinids (Dobzhansky et al., 1977, Mayr, 1974). We do not know how the reproduction took place in the thin and intermediate types. We found no signs of dimorphism. The protoconch measurements suggest a single generation, probably the asexual, macrospheric one.

V.4. THE DESCENT OF THE MEDITERRANEAN UNISERIAL UVIGERINIDS

After the counting and measuring of some 27,000 individuals of uniserial uvigerinids the descent of the group did not become any clearer. We can but add some speculations to those already existing.

Papp (1963) thought that *U. proboscidea* Schwager was the ancestor of the uniserial uvigerinids. We agree with Meulenkamp (1969) that *U. pro-*

boscidea does not resemble the juveniles of the uniserial uvigerinids at all. Moreover, S.E.M.-photographs show that the wall structure of *U. proboscidea* is different from the wall structure in our uvigerinids. Meulenkamp considers *U. bononiensis compressa* as the ancestor of his *U. melitensis* lineage and he could not find the ancestor of his *U. cretensis* lineage. Fortuin (1974) supposes his new species *U. praeselliana* to be this ancestor.

In our opinion *U. bononiensis*, the Maltese uvigerinids and the Cretan, Spanish, Italian and North African uniserial uvigerinids are all closely related. The wall structures of all these groups are very similar as to pore shape and size and to ornamentation. Both the uniserial uvigerinids (with the exception of the Maltese forms) and *U. bononiensis* show a large variation in their characteristics and may be present in two morphotypes, i.e. a larger, thick morphotype and a smaller, slender morphotype. All the groups have a similar, simple, internal toothplate without wings.

In our opinion the Maltese uvigerinids are probably not the ancestors of the thin Cretan uvigerinids, *U. felixi* of Meulenkamp and Fortuin, because of the differences in morphology described in section IV.4.3d. The Maltese group probably descended from *U. bononiensis* to which species they show a close resemblance, as Meulenkamp has suggested, though we think they are a separate offshoot.

Both Cretan groups may have originated from *U. bononiensis* independent of the Maltese stock. Together with the oldest known Cretan representatives of the thick and thin type uvigerinids thick and thin types of *U. bononiensis* occurred, which are similar to the uniserial uvigerinids in shape of the test. Figures 60 and 61 show the mean values of some parameters of the Cretan uvigerinids from the *N. continuosa* Zone together with the mean values of the Maltese uvigerinids and Cretan *U. bononiensis* of the same zone.

The large *Uvigerina* is very similar to the thick *U. bononiensis*. The differences are the compressed test in *U. bononiensis,* as well as the long-drawn shape of the chambers and a slightly heavier ornamentation. The thin *U. bononiensis* and thin uniserial *Uvigerina* are easier to distinguish because in most specimens there is a lack of uniserial chambers in the thin *U. bononiensis*. They are nearly equal in the dimensions of the test, but the test of thin *U. bononiensis* is compressed, and its ornamentation somewhat heavier than in the thin uniserial uvigerinid. We did not find actual transitional specimens between the thin uvigerinids and *U. bononiensis*; the so-called primitive members of the *U. melitensis* lineage, described by Fortuin, are in our view a mixture of thin *U. bononiensis* and our thin type.

We assume that *U. bononiensis* had the possibility of forming two different morphotypes, dependent on environmental circumstances. We further

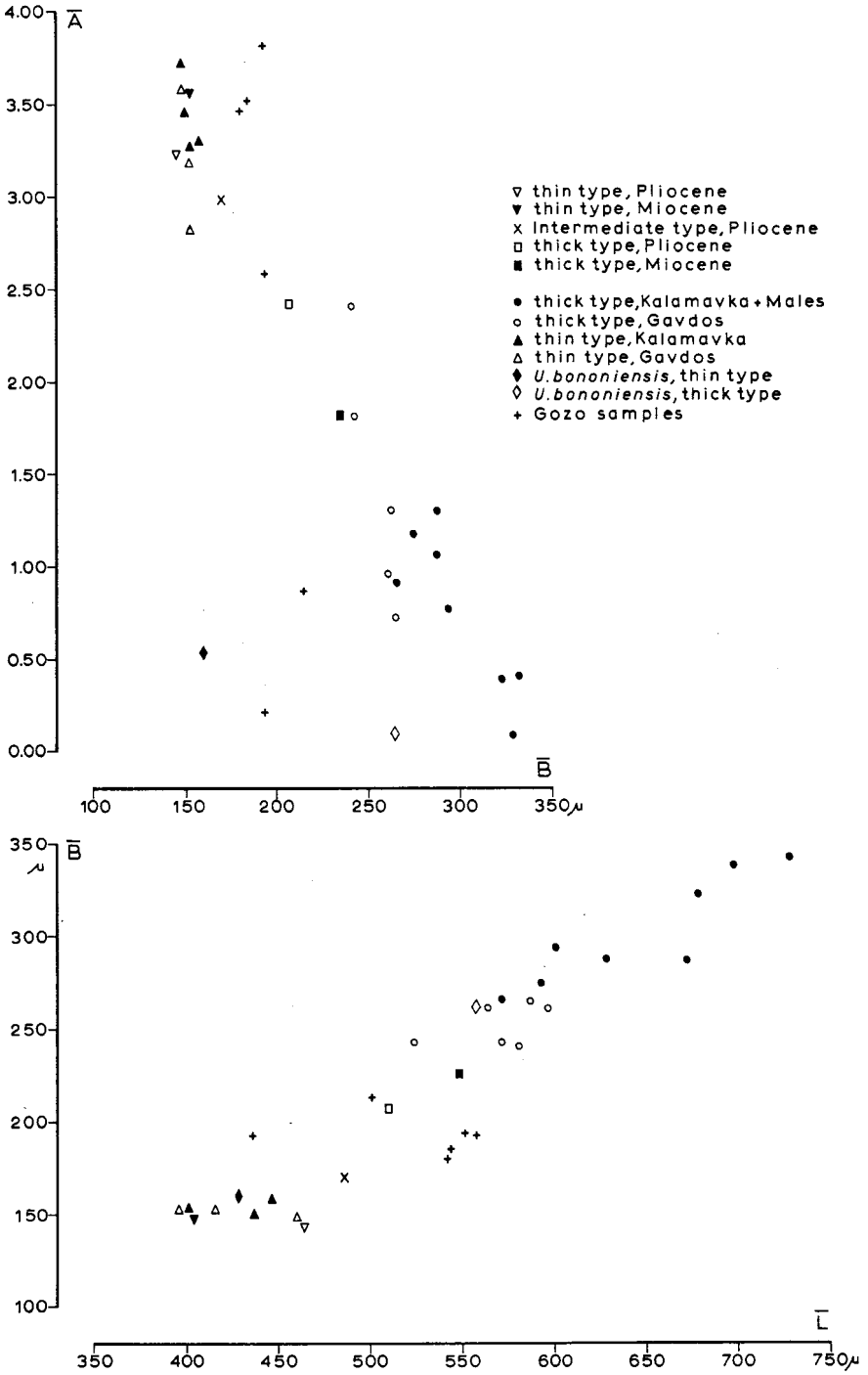


Fig. 60 Scattergrams of the mean values of A versus those of B, and of the mean values of L versus those of B of the samples from the *N. continuosa* Zone. The mean values of the samples from Gozo are included, and also the mean values of all younger Miocene samples and of all Pliocene samples.

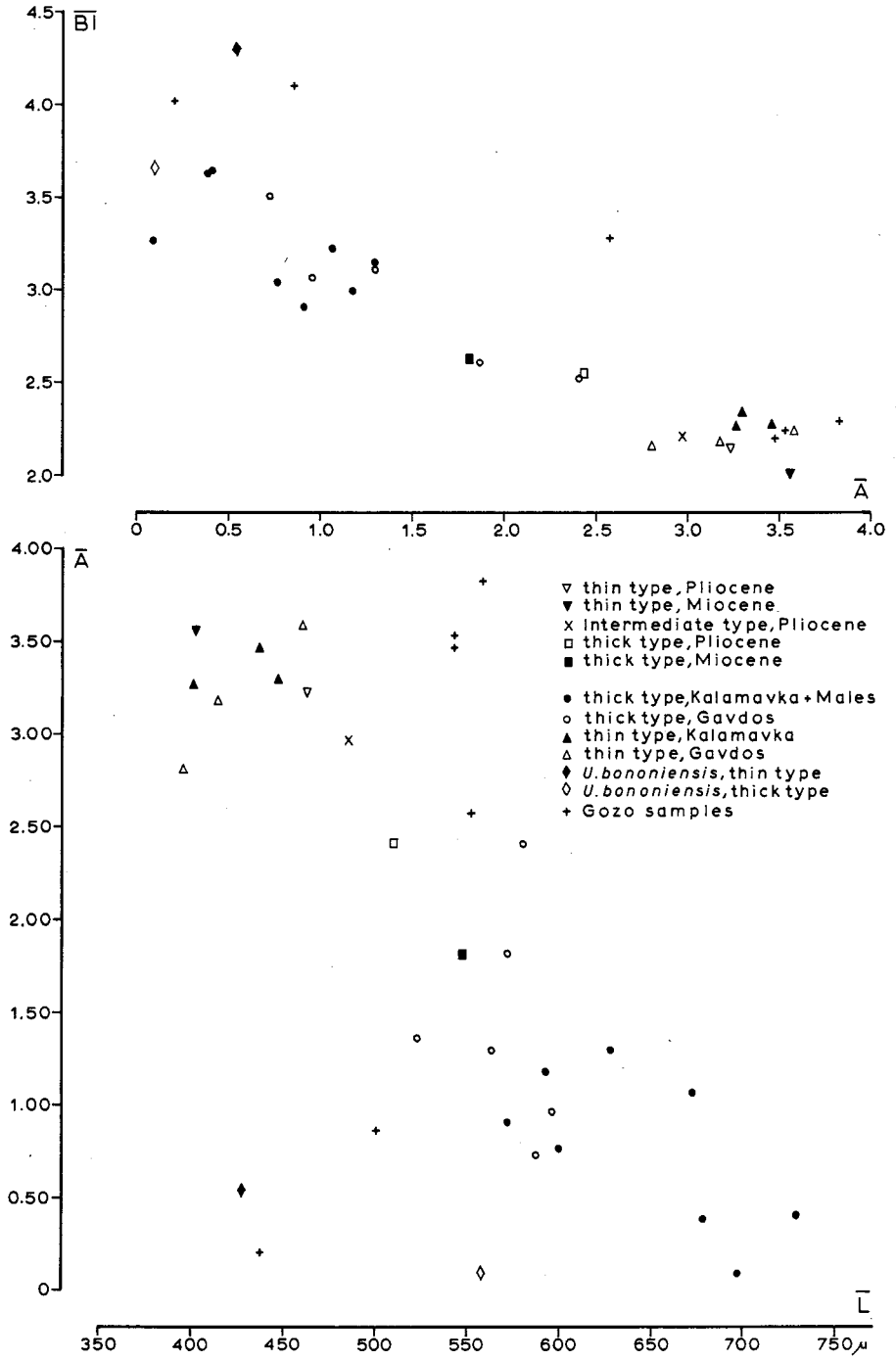


Fig. 61 Scattergrams of the mean values of A versus those of L, and of the mean values of A versus those of BI for the samples from the *N. continuosa* Zone. The mean values of the samples from Gozo are included, and also the mean values of all younger Miocene and of all Pliocene samples.

suppose that in the descendant uniserial *Uvigerina* the capacity of forming two morphotypes was maintained. One of the descendant morphotypes changed externally fairly much and quickly by adding uniserial chambers and forming a rounded test, which is our thin type. The other did not change so much, adding only a few uniserial chambers, and it became also rounded instead of flattened, our thick type. These forms acquired very slowly and fluctuatingly more uniserial chambers (from section Kalamavka to section Vrysses I), but higher in the sections they lost these extra uniserial chambers again. The two uniserial uvigerinid groups are thought to be very closely related and had not become isolated genetically.

We suppose that the thick phenotype disappeared somewhere in the Messinian. The Pliocene thick type is, as we see it, no direct continuation from the Miocene thick type, but from the thin group. This group had the possibility of forming the thick phenotype again when the environmental conditions required it.

We do not want to suggest that the origin of the uniserial uvigerinids from *U. bononiensis* must have taken place on Eastern Crete in the *N. continuosa* Zone. The seemingly "primitive" characteristics of the uvigerinids in Males and Kalamavka is probably not genuinely primitive, but a response to the environment, similar to the development observed in the Upper Messinian, when very low mean values of A are found again. An indication that the Kalamavka uvigerinids are not "primitive" can be found in the fact that the thick uvigerinids of Gavdos of the same planktonic zone have, in general, more uniserial chambers.

Probably the development from *U. bononiensis* into our uniserial uvigerinids had taken place already at the beginning of the *N. continuosa* Zone or earlier, since on Gavdos uniserial uvigerinids of both types with comparatively many uniserial chambers already coexisted in this zone. The two types of uvigerinids in section Kalamavka probably do not co-occur with their direct ancestors, but with the unchanged descendants of their ancestors.

V.5. THE CHOICE OF PARAMETERS

In case our theories concerning the environment-dependency of the types of uvigerinids are valid, all our measured or counted variables are in some degree environment-dependent, possibly the number of biserial chambers the least so. The diameter of the protoconch (a delimited ontogenetic stage) may be as much environment-dependent as the number of uniserial chambers. This size parameter has been considered as obviously environment-dependent

and thus unreliable in biozonation.

The mean values of the maximum breadth proved to be the best parameter for separating the types. This might signify that B is the parameter to be most influenced by the environment. It does not change much after a comparatively early stage in the ontogeny. Even in the thick *Uvigerina,* in which B increases for more budding steps than it does in the thin type, the maximum breadth is usually reached before the second uniserial chamber is formed, i.e. before the ontogenetic stage is attained at which the s2-value can be observed.

We have no reason to believe that the s2-factor is environment-independent, as has been suggested by Meulenkamp (1969, p. 62). It shows fluctuations of a comparable amplitude with those of the other parameters. We assume that not only the ontogenetic stage ultimately reached by an individual depends on the environment, but that also the values of all parameters of the individual in each delimited ontogenetic stage are considerably influenced by the environment, because we find large fluctuations in the mean values of the parameters of comparable ontogenetic stages. To choose delimited ontogenetic stages in the tests of foraminifera like our uvigerinids does not greatly help in our search for environment-independent variables. The parameters at comparable ontogenetic stages (P, BI and s2) appear to be just as variable and hence just as environment-dependent as those which depend clearly on the final ontogenetic stage reached by the individual (L, B and A).

Characteristics like the shape of the aperture in *Uvigerina* do not change at all in our samples, and may be environment-independent. Unfortunately, such stable characteristics do not change for long periods, and are of no use in biozonation.

There is no simple hierarchy of characteristics. Stable characteristics have a high rank in the hierarchy, and are used for distinguishing at a generic level. But it is difficult to give an order to the other parameters. Parameters like A and s2 have been given a higher rank than the others, because they were stated to reflect a sustained change. Taxonomic units like genera are probably best defined by stable characteristics, but if our lower taxonomic units (species and subspecies) prove to be dependent on the environment as to their shape, those units might be best defined by the most environment-dependent parameters. In our uvigerinids B will thus get a high rank in the hierarchy, because it is the best parameter for distinguishing the types.

V.6. EVOLUTION

Our investigation aimed first of all at getting information about how morphological changes proceed in time, and how evolution proceeds in a group of fossils, when studied in many closely spaced samples. Thousands of specimens were studied from a time interval of about eight million years, and the question is no longer how evolution proceeded, but whether evolution occurred at all in this interval in this group of fossils.

Evidently no sustained changes are present. Trends are found for some periods of time, but may, at another time, be absent or reversed in direction. We observed many fluctuations of a large amplitude as compared with the net result of the partial trends. Significant differences are often seen between adjacent samples of the same group. Two groups of phenotypes are met with together, or they succeed each other in time, but the thin *Uvigerina* from our highest samples in the *G. bononiensis* Zone of the Pliocene are very similar to those from our lowermost samples from the Miocene *N. acostaensis* Zone.

Whether the changes in the morphology of the uvigerinids may be called evolution depends upon the definition of this term. Some definitions of evolution are very comprehensive. For instance, the glossary of geology by Gary et al. (1977) gives the following definition: "Evolution is the development of an organism toward perfect or complete adaptation to environmental conditions, to which it has been exposed with the passage of time". Hotton (1968) says: "Evolution is that process, by which the structure of plants and animals changes with the passage of time". According to these definitions all the changes in the morphology of *Uvigerina* must be considered as evolution. However, some specialists in the study of evolution give less comprehensive definitions. Dobzhansky et al. (1977) state: "Organic evolution is a series of partial or complete and irreversible transformations of the genetic composition of populations, based principally upon altered interactions with their environment". Eldredge and Gould (1977) likewise emphasize that evolution is an irreversible process, and they define evolution as follows: "The modification through time of genes and gene frequencies. What we see, of course, is the phenotypic expression of the genes, since selection acts on the phenotype in any case; our fundamental source of information about any organism is its morphology".

These definitions stress the importance of genetic changes and irreversibility. Both groups of authors wish to include all amplitudes of irreversible genetic changes, also those below the species level. Naturally we cannot observe genetic differences in assemblages of fossils, and it is doubtful

whether we may draw conclusions about genetics from the morphology of the phenotypes of our uvigerinids.

Another problem is the meaning of the words irreversible and irreversibility. Some authors, for instance Romer (1949) maintain that evolution must only be irreversible as far as the gain or loss of complex structures or organs is concerned, and that evolution in all other instances can be and often is reversible. What we should include in "complex structures" in fossil protozoans is not al all clear. We might translate this condition as the gain or loss of new morphotypes and/or the loss of older ones in the course of time.

As regards the (ir)reversibility of the changes in the morphology in our uvigerinids, the supposed change from the thick and thin *U. bononiensis* couple into the thick and thin uniserial *Uvigerina* was probably irreversible, but it cannot be proved to have taken place. It probably happened prior to the stratigraphic interval we investigated.

A shift from thin *Uvigerina* into the thick type in the Lower Pliocene did occur, but it is not certain whether this is an irreversible change. Actually the thin type reappears higher in the Pliocene, but in this case we might be dealing with an immigration wave. If the immigration is not true we immediately lose the argument for an irreversible change in the Lower Pliocene.

In the higher Pliocene samples, some time after the thick type had disappeared, we find again in some samples a few specimens of the thick type. This might indicate that the capacity of the species of forming the thick phenotype did still exist in the later Pliocene. However, these thick individuals might have been reworked, though we observed no indications for reworking in the sediments. All the changes observed in our uvigerinids seem to be reversible.

From Pleistocene sections on Sicily (Decima, 1963) only uniserial uvigerinids similar to our thin type have been described. There is no evidence that their stock was no longer able to produce the thick phenotype; the circumstances might not have required it.

A direct consequence of the conclusion that irreversible changes in the morphology of *Uvigerina* cannot be demonstrated to have taken place unequivocally, is that we cannot accept evolution in the sense of Dobzhansky et al., or Eldredge and Gould.

Following the line of the semantics we may consider all the obviously reversible changes in the morphology of *Uvigerina* as not worthy of the name of evolution. Then the part of the history of the uvigerinids we studied must be envisaged as a stagnancy in evolution. Our uvigerinids might represent a

segment of an equilibrium phase in a punctuated equilibrium evolution model as is proposed by Eldredge and Gould (1972, 1977), but in that case we can only assume one instance of punctuation (the supposed descent of our uniserial uvigerinids from *U. bononiensis*) and a long time of equilibrium. The attempt to compromise our data with this recent evolution model seems to be fairly far-fetched, since, as an addition to the theory, we have to include in the term "equilibrium" the significant fluctuations in mean values with no net results. If we want to restrict the law of irreversibility of evolution to the gain or loss of complex structures (Romer, 1949) we may include all the reversible changes in *Uvigerina* in the concept of evolution, and the fluctuations can be seen as an illustration of the so-called zig-zag evolution of Henningsmoen (1964).

A fluctuating pattern of mean values with significant deviations has also been observed by M. M. Drooger et al. (1979) in the Cretan *Planorbulinella* from the sections Apostoli and Potamidha. The latter section is near to Khaeretiana, but comprises a lower stratigraphic interval. The time interval and the variation in the lithology in these two sections are much smaller than in the sum of our sections.

In these Cretan *Planorbulinella* no heterogeneity in the assemblages could be demonstrated. The fluctuations in the mean values of the parameters in *Planorbulinella* are of the same order of magnitude as those in the separate groups of Uvigerina. In contrast with Uvigerina there seems to be some net result of the changes in *Planorbulinella* in section Apostoli.

The trend expected in *Planorbulinella* is one of nepionic acceleration, which has been observed in many unrelated groups of orbitoidal larger foraminifera. The trend we expected to find in *Uvigerina* is one toward "lower seriality" (from a triserial chamber arrangement to a uniserial chamber arrangement), which has been said to exist in many unrelated groups of benthonic smaller foraminifera (Scott, 1974).

There has been much discussion about the "sense" in these trends. C. W. Drooger (1956, 1974) attributed the often observed nepionic acceleration to selective advantages of the attaining of radial growth in an early ontogenetic stage. No such theory has been elaborated for the supposed trends toward lower seriality. Several authors (for instance Scott, 1974) suggested that trends toward a lower seriality are caused by a selective advantage of a rapid increase in the length of the shell, i.e. of getting a more slender test at an early ontogenetic stage, the animals possibly being able to burrow more easily through the muddy sediments. Although it is known that uvigerinids are always most common in muddy sediments, it is, unfortunately,

not known whether they are actually infauna, so this hypothesis has no firm basis.

In *Uvigerina* as well as in *Planorbulinella* there are large fluctuations in the composition of the samples, whereas no new variants are introduced. For instance, we did never find uvigerinids with more than six uniserial chambers (though very rare specimens with as many as eleven have been reported by Lipparini, 1932). Specimens with six uniserial chambers were found already in our lowermost sections.

M. M. Drooger et al. (1979) rejected a random walk model (Raup, 1977) in which any mean value of a parameter is established by adding a random component to the previous value, and mere chance is the dominating factor. They accepted the nepionic acceleration model for the net change they observed, though not on the strength of their own data on *Planorbulinella,* but because this trend had been demonstrated to exist in so many other orbitoidal foraminifera. Because of the lack of a net result in the changes in our data we cannot accept the existence of a trend toward lower seriality. We cannot permit ourselves to reject a random walk model in *Uvigerina,* because the trends toward lower seriality in other groups are often not well documented either and only claimed to exist without decisive arguments, but on ontogenetic considerations alone.

In *Uvigerina,* as opposed to *Planorbulinella* we only very rarely meet with individuals that may be considered microspheres. The reproduction was probably predominantly asexual and sexual generations were either absent or extremely rare for long periods of time. One might assume that there were random effects on the compositions of the successive clones within the assemblages. The changes may have been rapid and large, and thus might offer an "explanation" for the fluctuations. The predominance of certain clones might be influenced by environmental circumstances. In studies on recent organisms different clones appear to have slightly different environmental preferences (Suomolainen et al., 1976).

In *Planorbulinella* no environmental control could be pointed out. In *Uvigerina* the environment probably determines which of the two phenotypes is found (section V.2.), but little can be said about the ecological effect upon the fluctuations within the types. There seems to be some environmental influence; for instance, the extremely large tests in the thick type always occur in samples with aberrant benthonic faunas, which is not true for all the thick type samples.

In section Apostoli there was no possibility to compare the fluctuation-patterns in *Planorbulinella* and *Uvigerina.* The two genera are almost never met with in sufficient numbers in the same sample.

Concluding we may state that we discovered a fluctuating pattern of mean values with significant changes, but no net result. The nature of the fluctuations is not satisfactorily understood. Environmental effects seem observable, but their nature is not comprehended either. We are inclined not to apply the term evolution to fluctuating processes until it can be shown unequivocally that something irreversible took place, and new variants were introduced into the assemblages, and/or old ones were lost. Neither of the two can be proved in the uniserial uvigerinids in the time interval we studied.

Chapter VI

TAXONOMY

VI.1. TAXONOMY ON THE GENERIC LEVEL

We prefer the use of the generic name *Uvigerina* for uvigerinids that are able to form uniserial chambers. The application of the generic name *Hopkinsina* Howe and Wallace for uvigerinids that have a triserial chamber arrangement early in the ontogeny and a later biserial one, presents us with problems in the allocation of not fully developed, juvenile specimens as to their genus. We are up against the same difficulty with the generic name *Rectuvigerina* Mathews for uvigerinids with an early triserial stage, followed by a biserial and a uniserial chamber arrangement.

In our opinion the characteristic of a wholly triserial chamber arrangement against a partly triserial, partly biserial chamber arrangement, or to a partly triserial, partly biserial and partly uniserial chamber arrangement, is not suitable for distinguishing at the generic level in the uvigerinids. Mathews (1945) alleges that the triserial *Uvigerina* lack an internal toothplate in contrast with *Rectuvigerina.* It would therefore be possible to make the distinction between a juvenile *Rectuvigerina* and wholly triserial *Uvigerina.* The absence of an internal toothplate in a triserial *Uvigerina,* however, is not confirmed by Loeblich and Tappan (1964). We made some observations on partly dissolved specimens of our thin and thick type, on *U. bononiensis,* on *Uvigerina pygmea* d'Orbigny and on *Uvigerina mediterranea* Hofker. We found an internal toothplate in all these species, including *U. pygmea,* which is the type species of the genus *Uvigerina.* The presence or absence of a toothplate is no characteristic for defending the separation of the uvigerinids into three genera.

VI.2. TAXONOMY ON THE SPECIES LEVEL

There is plenty of confusion in the names for uniserial uvigerinids, even if we consider the names for the uvigerinids from the Mediterranean area only, and disregard the many names for the uniserial uvigerinids from California, the Gulf Coast and New Zealand.

The name *Clavulina cylindrica* was used by d'Orbigny as early as 1826 as a nomen nudum for a "fossile aux environs de Sienne". In 1852 d'Orbigny gave a very incomplete description of this species: "espèce finement striée

et long". Fornasini (1897) issued an unpublished drawing by d'Orbigny. This figure shows a specimen of *Uvigerina* with five uniserial chambers in a regular arrangement and with a striate test. Fornasini asserts that d'Orbigny's species is not an arenaceous form, and should not be assigned to the genus *Clavulina,* but to the genus *Sagrina* d'Orbigny. Fornasini believed *Sagrina cylindrica* to be identical with *Sagrina nodosa* Parker and Jones (1865). *Sagrina nodosa,* however, is not a species name from Parker and Jones. The latter erroneously called their specimens *Uvigerina (Sagrina) nodosa* d'Orbigny. *Uvigerina nodosa* d'Orbigny (1826), is a coarsely striate species. On the drawings it looks triserial to slightly biserial. No description is given. Parker and Jones describe and show a figure of a first triserial, later uniserial specimen, which is finely striate. The figured specimen has three uniserial chambers in a regular arrangement. Brady (1884) considered *Uvigerina nodosa* d'Orbigny as synonymous with *Uvigerina pygmea* d'Orbigny and erroneously credited Parker and Jones with the authorship of a species *Sagrina nodosa* Parker and Jones. Mathews (1945), the author of the genus *Rectuvigerina,* created a new species name for *Sagrina nodosa* Parker and Jones, not d'Orbigny. The new name is *Rectuvigerina nicoli,* and the holotype of this new species is the specimen of the drawing by Parker and Jones. All the figures of triserial to uniserial *Uvigerina* of d'Orbigny, Brady, and Parker and Jones are greatly similar and should, as we see it, be taken as belonging to one species, for which *Uvigerina cylindrica* (d'Orbigny) is the correct name.

Lipparini (1932) studied uniserial uvigerinids from Upper Miocene deposits near Bologna. He found triserial specimens, triserial and biserial specimens, and also triserial, biserial and uniserial ones. He thought these specimens to belong to one population, which would have to be placed in three genera according to their chamber arrangement. He wisely refused to split his population into three genera, and coined different variety names within the genus *Uvigerina.*

1) *Uvigerina tenuistriata* Reuss, for typical *Uvigerina,* i.e. wholly triserial specimens.
2) *Uvigerina tenuistriata* var. *gaudryinoides* Lipparini, for specimens with a triserial and biserial test. These have no uniserial chambers, are inflated, and not elongated.
3) *Uvigerina tenuistriata* var. *siphogenerinoides* Lipparini, for specimens with a uniserial final part of the test. These are slender and elongated; two to eleven uniserial chambers are shown in his figures.

All the specimens are finely striate. Lipparini states explicitly that all morphologically intermediate forms between his varieties can be observed. He supposes that the differences in the chamber arrangement and in the shape of

the test may have been due to ecological (physicochemical) factors under the aberrant conditions of the Late Miocene seas.

The names introduced by Lipparini have been widely used, especially by Italian authors, but often incorrectly. The name for the triserial species, *U. tenuistriata* Reuss is rather unfortunate. *Uvigerina tenuistriata* is an Oligocene species described by Reuss. Cushman and Edwards (1938) investigated topotype material of this species, and they decided that Reuss' figures and descriptions are obscure, and that *U. tenuistriata* must be placed in the genus *Angulogerina,* which was later assumed to be synonymous with the genus *Trifarina* (Loeblich and Tappan, 1964). Batjes (1958) looks upon *U. tenuistriata* as a subspecies of *Angulogerina gracilis* Reuss, and thus likewise places *"Uvigerina" tenuistriata* in the genus *Angulogerina.* Lipparini's varieties are no *Trifarina* and ought not to be placed in the species *T. tenuistriata.*

Giannini (1948) has described a new species, *Siphogenerina appenninica.* This is a triserial to uniserial uvigerinid, finely striate, with three to five uniserial chambers. He gives no differential diagnosis with *U. tenuistriata siphogenerinoides* and declares that his species resembles *Siphogenerina nodosa* Parker and Jones. *S. appenninica* is said to have more uniserial chambers than the latter species. By most later authors, e.g. Longinelli (1956) *S. appenninica* is considered as synonymous with *U. tenuistriata siphogenerinoides.*

Papp (1963, 1966) assigns the two subspecies not to the species *U. tenuistriata,* but to a species *U. gaudryinoides* Lipparini. He creates a new subspecific name, *U. gaudryinoides arquatensis.* This should be a Pliocene descendant of *U. gaudryinoides siphogenerinoides,* of which he supposed it to differ in being more slender and graceful, in having a smaller triserial part of the test and a more regular arrangement of the uniserial chambers. According to Papp the subspecies *U. gaudryinoides gaudryinoides* and *U. gaudryinoides siphogenerinoides* co-exist in the Messinian, and *U. gaudryinoides arquatensis* occurs in the Pliocene. Hottinger (1966) reported *U. gaudryinoides gaudryinoides* and *U. gaudryinoides siphogenerinoides* from the Messinian deposits of Morocco, and *U. gaudryinoides arquatensis* from the Pliocene deposits.

Christodoulou (1960) recognizes as many as four different taxa of uniserial uvigerinids; *Rectuvigerina* cf. *cylindrica* (d'Orbigny), *Rectuvigerina seriata* (Cushman and Jarvis), *Rectuvigerina tenuistriata gaudryinoides* (Lipparini) and *R. tenuistriata siphogenerinoides* (Lipparini). *R. seriata* is probably a misidentification. The holotype of Cushman and Jarvis is coarsely striate, with inflated chambers and uniserial chambers in a staggered

arrangement, whereas Christodoulou's figures show a finely striate specimen with its uniserial chambers in a regular arrangement. In our opinion these specimens should also be placed in the species *U. cylindrica* (d'Orbigny). Christodoulou uses both names *R. tenuistriata gaudryinoides* and *R. tenuistriata siphogenerinoides*, for thick-set uvigerinids with inflated chambers in a staggered arrangement, which is not in accordance with Lipparini's description.

Decima (1963) argues about yet another species name, *Rectuvigerina cylindroides* Moncharmont Zei (1961) as possibly synonymous with *R. tenuistriata siphogenerinoides.* We were not in a position to verify the original description by Moncharmont Zei. According to Decima the only differences between *R. cylindroides* and *R. tenuistriata siphogenerinoides* is the larger variability in the ornamentation in the former species. *R. cylindroides* should occur only in the Quaternary. Decima's figure has a close resemblance to *U. cylindrica* and should in our opinion be considered as identical with this species.

Salvatorini (1966) has introduced another new species name. His material comes from Messinian deposits near Radicondoli (Siena, Italy). Astoundingly, he chooses for his new species the same name that d'Orbigny (1826) thought fit for his uniserial uvigerinid from the environment of Siena, *Rectuvigerina cylindrica.* According to Salvatorini his species resembles *R. tenuistriata siphogenerinoides* closely, but it is distinguishable by its less lobate periphery and less depressed sutures. The chambers in *R. cylindrica* Salvatorini are reported to be higher and the neck shorter and more robust. In Salvatorini's figures the uniserial chambers are arranged slightly staggered. We think that these differences are trivial and that *Rectuvigerina cylindrica* should be considered not only as a homonym, but also as a synonym of *Uvigerina cylindrica* (d'Orbigny).

Meulenkamp (1969) has given a review of some names gives by earlier authors and concluded that he could not apply these names in his biometrical species-scheme, except for *Uvigerina arquatensis* Papp. He extended the description of this species to make it fit in his biometrical species; he introduced seven new species names founded on biometrical criteria, the number of the uniserial chambers and the shape of the uniserial chambers. Although the delimitation of Meulenkamp's species is based upon the incorrect assumption of sustained changes in two independent *Uvigerina* stocks, his species names have a valid base in the Linnean nomenclature. Fortuin (1974) made a new species name, likewise on biometrical criteria, *U. praeselliana.* This species he believed to be the ancestor of the youngest lineage of Meulenkamp.

In our view far too many names are found for the same, finely striate or hispid, slender uvigerinids with a comparatively small uniserial part of the test and a regular arrangement of the uniserial chambers, i.e. for our thin type *Uvigerina.* The correct name for this group is *U. cylindrica* (d'Orbigny). The type figure published by Fornasini is obviously identifiable with our thin type. We are seeing our two types of *Uvigerina* as subspecies within a single species, so our thin type is the nominate subspecies, and the name is *Uvigerina cylindrica cylindrica* (d'Orbigny).

The names *U. tenuistriata gaudryinoides* or *U. gaudryinoides gaudryinoides* have often been applied to our thick type *Uvigerina*; thick-set specimens with inflated chambers, and few or no uniserial chambers in a staggered arrangement (Papp, 1963, 1966; Hottinger, 1966; Dieci, 1959; Christodoulou, 1959). This application is in contradiction with Lipparini's type description. Other authors (e.g. di Napoli Alliata, 1951) use the name correctly only for specimens without uniserial chambers, and with biserial ones, and include all specimens with uniserial chambers in the subspecies *U. tenuistriata siphogenerinoides,* though they have inflated chambers.

In our view to base the division into two groups on the presence or absence of uniserial chambers is highly artificial. Lipparini gave two figures of *U. tenuistriata gaudryinoides* (plate 3, figs. 7, 8). He did not designate one of them as holotype. Both are identifiable with our thick type. The correct name for our thick type *Uvigerina* is *Uvigerina cylindrica gaudryinoides,* but the subspecies description must be emended to include also specimens with uniserial chambers.

We suggest to use the term *Uvigerina* ex. interc. *gaudryinoides-cylindrica* for the intermediate uvigerinids, though "ex. interc." was not intended for a situation such as we found in *Uvigerina.* The term "ex. interc." was coined for samples that cannot be located within one biometrical species, because they have a mean value of the parameter used for the delimitation of the species, close to the species boundary. Yet we think that this denotation is eminently suitable for our intermediate group.

For the time being we are including also the Maltese uvigerinids in this group. They resemble the Cretan intermediate group in the overall shape of the test, and in the mean values of the measured and counted parameters. We do not know enough of this group to be certain that it is not related to the other uvigerinids. So for the moment we are reluctant to give the Maltese uvigerinids another species name on vague phylogenetical grounds, while they are difficult to distinguish on morphological grounds.

Uvigerina cylindrica (d'Orbigny) subsp. cylindrica (d'Orbigny)

Clavulina cylindrica d'Orbigny, 1826, Ann. Sci. Nat., p. 268 (nomen nudum).
Clavulina cylindrica d'Orbigny, 1852, Prodr. Pal. Strat., vol. 3, p. 194.
Uvigerina (Sagrina) nodosa, Parker & Jones, not d'Orbigny, 1865, Roy. Soc. London, Philos. Trans., vol. 55, p. 363–364, pl. 114, fig. 15.
Sagrina nodosa "Parker & Jones", Brady, 1884, Rept. Voy. Chal., Zool., vol. 9, pt. 5, p. 583, pl. 114, fig. 18.
Sagrina cylindrica (d'Orbigny), Fornasini, 1897, Riv. Ital. Pal., vol. 3, p. 14, text-fig.
Uvigerina tenuistriata Reuss var. *siphogenerinoides* Lipparini, 1932, Giorn. Geol., ser. 2, vol. 7, p. 64, partim, pl. 3, figs. 5, 6 (not figs. 2, 3, 4).
Rectuvigerina nicoli Mathews, 1945, Journ. Pal., vol. 19, nr. 6, p. 593, pl. 81, fig. 2.
Uvigerina tenuistriata Reuss var. *siphogenerinoides* Lipparini, Di Napoli Alliata, 1951, Riv. Ital. Pal., vol. 57, partim, pl. 6, figs. 19, 27 (not figs. 20–23, 29, 33, 34).
Uvigerina tenuistriata Reuss var. *siphogenerinoides* Lipparini, Longinelli, 1956, Paleontogr. Ital., vol. 49, p. 164, pl. 13, fig. 21.
Uvigerina tenuistriata Reuss var. *siphogenerinoides* Lipparini, Dieci, 1959, Paleontogr. Ital., vol. 54, p. 72, pl. 6, fig. 9.
Rectuvigerina nicoli Mathews, Barker, 1960, Taxonomic notes etc., S.E.P.M. spec. publ. nr. 9, p. 235, pl. 114, fig. 18.
Rectuvigerina cf. *cylindrica* (d'Orbigny), Christodoulou, 1960, Paläont., Abt. A, vol. 115, p. 45, pl. 6, fig. 36.
Rectuvigerina seriata, Christodoulou, not Cushman & Jarvis, 1960, Paläont., Abt. A, vol. 115, p. 46, pl. 6, figs. 31, 32.
Rectuvigerina cylindroides Moncharmont Zei, Decima, 1963, Geol. Rom., vol. 2, p. 87, pl. 1, fig. 3.
Uvigerina gaudryinoides siphogenerinoides Lipparini, (transitional to *U. gaudryinoides gaudryinoides*), Papp, 1963, Mitt. Geol. Ges. Wien, vol. 56, p. 253, 254, pl. 6, figs. 9, 10.
Uvigerina gaudryinoides Lipparini subsp. *arquatensis* Papp, 1963, Mitt. Geol. Ges. Wien, vol. 56, p. 253, 254, pl. 6, figs. 11–15.
Uvigerina gaudryinoides siphogenerinoides Lipparini, Hottinger, 1966, Proc. 3d Sess. Comm. Med. Neog. Strat., Berne, p. 86, figs. 45–47.
Uvigerina gaudryinoides Lipparini subsp. *arquatensis* Papp, Hottinger, 1966, Proc. 3d Sess. Comm. Med. Neog. Strat., Berne, p. 86, figs. 37–41.
Rectuvigerina cylindrica Salvatorini, 1966, Atti Soc. Tosc. Sci. Nat., Mem., ser. A, vol. 73, p. 664, pl. 2, figs. 1–5.
Uvigerina felixi Meulenkamp, 1969, Utrecht Microp. Bull. 2, p. 138, pl. 2, figs. 23, 24, pl. 3, figs. 1, 2.
Uvigerina cretensis Meulenkamp, 1969, Utrecht Microp. Bull. 2, p. 141, partim, pl. 5, figs. 12–19 (not figs. 10, 11, not pl. 3, figs. 16–21).
Uvigerina lucasi Meulenkamp, 1969, Utrecht Microp. Bull. 2, p. 142, partim, pl. 4, figs. 5, 11–15, 19, 20 (not figs. 1–4, 6–10, 16–18), pl. 5, figs. 20–24, pl. 6, figs. 1–10, 16–18.
Uvigerina arquatensis Papp, Meulenkamp, 1969, Utrecht Microp. Bull. 2, p. 143, pl. 4, figs. 21–24, pl. 5, fig. 25, pl. 6, figs. 11–15, 19.

Remarks: See *Uvigerina cylindrica gaudryinoides.*

Uvigerina cylindrica (d'Orbigny) subsp. gaudryinoides Lipparini

Uvigerina tenuistriata Reuss var. *gaudryinoides* Lipparini, 1932, Giorn. Geol., ser. 2, vol. 7, p. 65, pl. 3, figs. 7, 8.
Uvigerina tenuistriata, Lipparini, 1932, not Reuss 1866, Giorn. Geol., ser. 2, vol. 7, pl. 6, fig. 1.

Uvigerina tenuistriata Reuss var. *siphogenerinoides* Lipparini, 1932, Giorn. Geol., ser. 2, vol. 7, p. 64, partim, pl. 6, figs. 2, 3, 4 (not figs. 5, 6).

Uvigerina tenuistriata Reuss var. *siphogenerinoides* Lipparini, Di Napoli Alliata, 1951, Riv. Ital. Pal., vol. 57, partim, pl. 6, figs. 20–23, 29, 33, 34 (not figs. 19, 27).

Uvigerina tenuistriata Reuss var. *gaudryinoides* Lipparini, Di Napoli Alliata, 1951, Riv. Ital. Pal., vol. 57, pl. 6, figs. 24–26, 30–32.

Uvigerina tenuistriata, Di Napoli Alliata, not Reuss, 1951, Riv. Ital. Pal., vol. 57, pl. 6, fig. 28.

Uvigerina tenuistriata Reuss var. *gaudryinoides* Lipparini, Dieci, 1959, p. 72, pl. 6, fig. 8.

Rectuvigerina tenuistriata gaudryinoides, Lipparini, Christodoulou, 1960, Paläont., Abt. A, vol. 115, p. 46, pl. 16, fig. 45.

Rectuvigerina tenuistriata siphogenerinoides Lipparini, Christodoulou, 1960, Paläont., Abt. A, vol. 115, p. 46, pl. 16, fig. 43.

Uvigerina gaudryinoides gaudryinoides Lipparini, Papp, 1963, Mitt. Geol. Ges. Wien, vol. 56, p. 253, pl. 6, figs. 7, 8.

Uvigerina proboscidea Papp, 1963, not Schwager, 1866 (transitional forms to *U. gaudryinoides gaudryinoides*), Mitt. Geol. Ges. Wien, vol. 56, p. 253, pl. 6, figs. 4, 5.

Uvigerina gaudryinoides gaudryinoides Lipparini, Hottinger, 1966, Proc. 3d Sess. Comm. Med. Neog. Strat., Berne, p. 86, figs. 42–44, 48–51.

Uvigerina selliana Meulenkamp, 1969, Utrecht Micropal. Bull. 2, p. 138, pl. 3, figs. 3–15, pl. 5, figs. 1–4.

Uvigerina cretensis Meulenkamp, 1969, Utrecht Micropal. Bull. 2, p. 141, partim, pl. 3, figs. 16–21, pl. 5, figs. 10, 11, (not figs. 12–19).

Uvigerina lucasi Meulenkamp, 1969, Utrecht Micropal. Bull. 2, p. 142, partim, pl. 4, figs. 1–4, 6–10, 16–18 (not figs. 5, 11–15, 19, 20, pl. 5, figs. 20–24, pl. 6, figs. 1–10, 16–18).

Uvigerina praeselliana Fortuin, 1974, Proc. Kon. Ned. Akad. Wetensch., ser. B, vol. 77, p. 40–45, pl. 1, figs. 1–6, text-fig. 2.

Remarks: The test is triserial in the early ontogenetic stages and may become biserial or biserial and uniserial in later stages. From 6 to 14 triserial chambers were observed, and up to 7 biserial chambers. The biserial part of the test is often twisted. Up to 5 uniserial chambers were met with, but specimens with more than 3 uniserial chambers are rare. In the Cretan material the mean values of the number of uniserial chambers are lower than 2.0 in most of the samples. In the Pliocene samples this mean value is often between 2.0 and 2.6. The mean number of uniserial chambers may be as low as 0.09, counted in one sample from the Miocene *N. continuosa* Zone. The uniserial chambers are arranged in a staggered series, rarely somewhat more regularly. The total number of chambers is between 9 and 19. The sutures are depressed, the chambers inflated. The sutures in the biserial part of the test are sometimes "en crochet". The test is rounded in transverse section. The aperture is round to slightly oval, terminal, with a neck and an internal toothplate connecting the apertures of the successive chambers. The internal toothplate has no wings and is of simple structure. The wall may be smooth, but is most often covered with fairly fine costae, which are continuous or discontinuous on the chamber, but are not continuous over the chamber sutures. The last-formed chamber is often smooth. Hispid ornamentation may occur. The short spines are discontinuous costae. The pores are irregularly round to oval in shape, and have usually a diameter of about 0.75 μ. The

range of the diameter of the pores is from about 0.60 to about 1.10 μ. The pores are not closed by the ornamentation. The diameter of the protoconch is between 30 and 125 μ. No clear dimorphism can be demonstrated. The diameter of the protoconch is often positively correlated with the total length and breadth of the test. Some large specimens with small protoconches may be microspheres. They are rare, less than 1 microsphere on 50 individuals.

The nominate subspecies has a much more slender test, usually higher mean values of the number of uniserial chambers and lower mean values of the number of biserial chambers. The uniserial chambers in the nominate subspecies are arranged more regularly. The ranges of the mean values of the two subspecies are shown in table 34. The nominate subspecies has only slightly depressed sutures, and its chambers are not inflated. *U. cylindrica gaudryinoides* shows a larger variation in all parameters than the nominate subspecies.

In most samples some intermediate specimens between the two subspecies can be observed. Some samples as a whole are intermediate between the subspecies. These samples we will give the name *U.* ex. interc. *gaudryinoides-cylindrica.*

Uvigerina ex. interc. gaudryinoides-cylindrica

Uvigerina pappi Meulenkamp, 1969, Utrecht Micropal. Bull. 2, pp. 135–136, pl. 2, figs. 3–11.
Uvigerina melitensis Meulenkamp, 1969, Utrecht Micropal. Bull. 2, pp. 136–137, pl. 2, figs. 12–15.
Uvigerina gaulensis Meulenkamp, 1969, Utrecht Micropal. Bull. 2, p. 137, pl. 2, figs. 16–22.

Remarks: In this group we placed all our uvigerinids, intermediate between the thick type, *U. cylindrica gaudryinoides* and *U. cylindrica cylindrica,* the thin type. These uvigerinids are in their mean values of the breadth of the test intermediate between the two subspecies, and the chambers are somewhat inflated. Morphologically the Maltese uvigerinids, as described by Meulenkamp, must be placed in this group, though their descent might be different from that of the Cretan intermediate uvigerinids.

	U. cylindrica cylindrica	*U. cylindrica gaudryinoides*
$\overline{L}$	342 – 519	418 – 729
$\overline{B}$	129 – 162	181 – 332
$\overline{A}$	2.67 – 4.62	0.09 – 3.05
$\overline{BI}$	1.26 – 2.63	1.87 – 3.63
$\overline{s2}$	50 – 81.6	68.2 – 100
	U. ex. interc. *gaudryinoides-cylindrica*	
$\overline{L}$	425 – 544	
$\overline{B}$	146 – 199	
$\overline{A}$	1.65 – 2.72	
$\overline{BI}$	1.87 – 3.29	
$\overline{s2}$	69.1 – 93.8	

Table 34 Ranges of the mean values.

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Plate 1

Fig. 1a — A specimen of *Uvigerina cylindrica cylindrica* (d'Orbigny) from sample CP 870, section Apostoli, X 90.

Fig. 1b — Detail of the wall of the last chamber of the specimen in fig. 1a, X 1300.

Fig. 1c — Detail of the wall of a costate chamber of the specimen in fig. 1a, X 1300.

Fig. 2a — A specimen of *Uvigerina cylindrica gaudryinoides* Lipparini from sample CP 870, section Apostoli, X 90.

Fig. 2b — Detail of the wall of the last chamber of the specimen in fig. 2a, X 1300.

Fig. 2c — Detail of the wall of a costate chamber of the specimen in fig. 2a, X 1200.

Plate 1

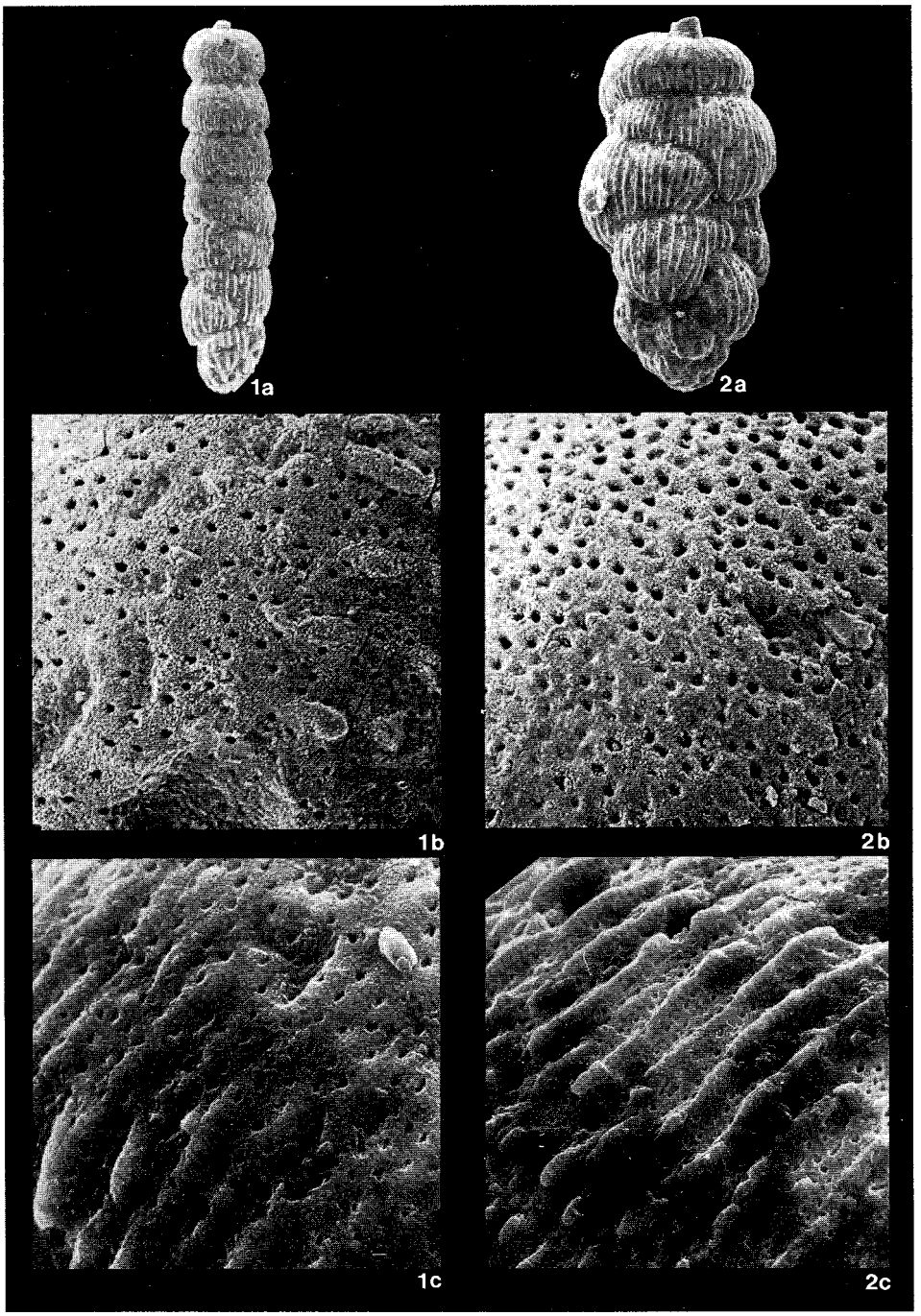


Plate 2

Fig. 1 A specimen of *Uvigerina bononiensis* Fornasini (thick type) from sample GR 998, section Prassa II, X 90.

Fig. 2 A specimen of *U. bononiensis* (thick type) from sample GR 998, section Prassa II, X 115.

Fig. 3 A specimen of *U. bononiensis* (thin type) from sample GR 998, section Prassa II, X 130. This specimen has four uniserial chambers, which is very rare.

Fig. 4 A specimen of *U. bononiensis* (thin type) from sample GR 998, section Prassa II, X 95.

Fig. 5 Detail of the wall of the last chamber of the specimen in fig. 2, X 1200.

Fig. 6 Detail of the wall of the last chamber of the specimen in fig. 1, X 1500.

Fig. 7 Detail of the wall of the last chamber of the specimen in fig. 3, X 1500.

Plate 2

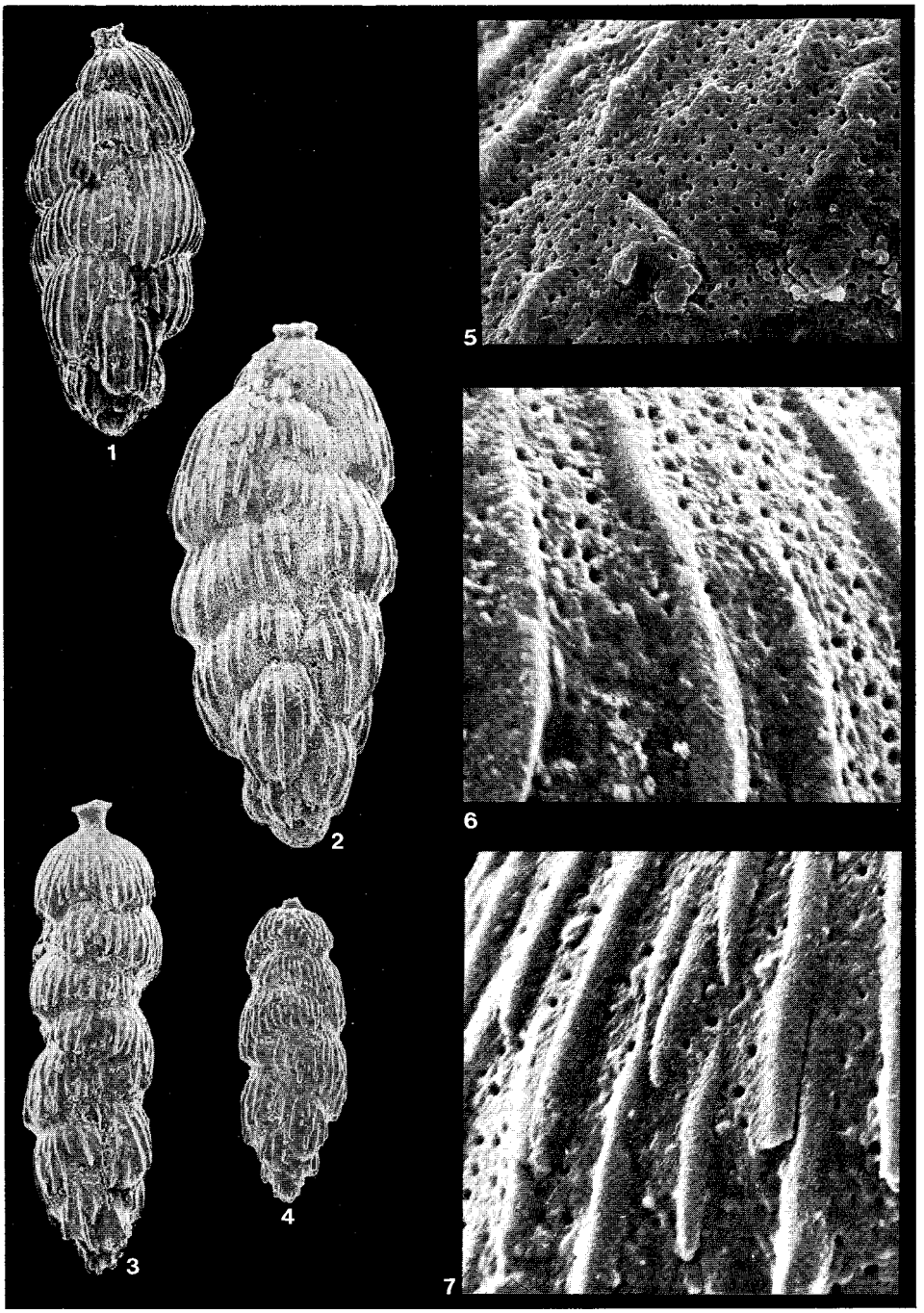


Plate 3

Fig. 1a — A specimen of the *Uvigerina rutila*-group from sample CP 212, section Vrysses I, X 70.

Fig. 1b — Detail of the wall of the last chamber of the specimen in fig. 1a, X 700.

Fig. 2a — A specimen of *Uvigerina proboscidea* from sample CP 567, section Exopolis, X 165.

Fig. 2b — Detail of the wall of the last chamber of the specimen in fig. 2a, X 835.

Fig. 3a — A specimen of *Uvigerina pygmea* from sample CP 567, section Exopolis, X 120.

Fig. 3b — Detail of the wall of the last chamber of the specimen in fig. 3a, X 600.

Plate 3

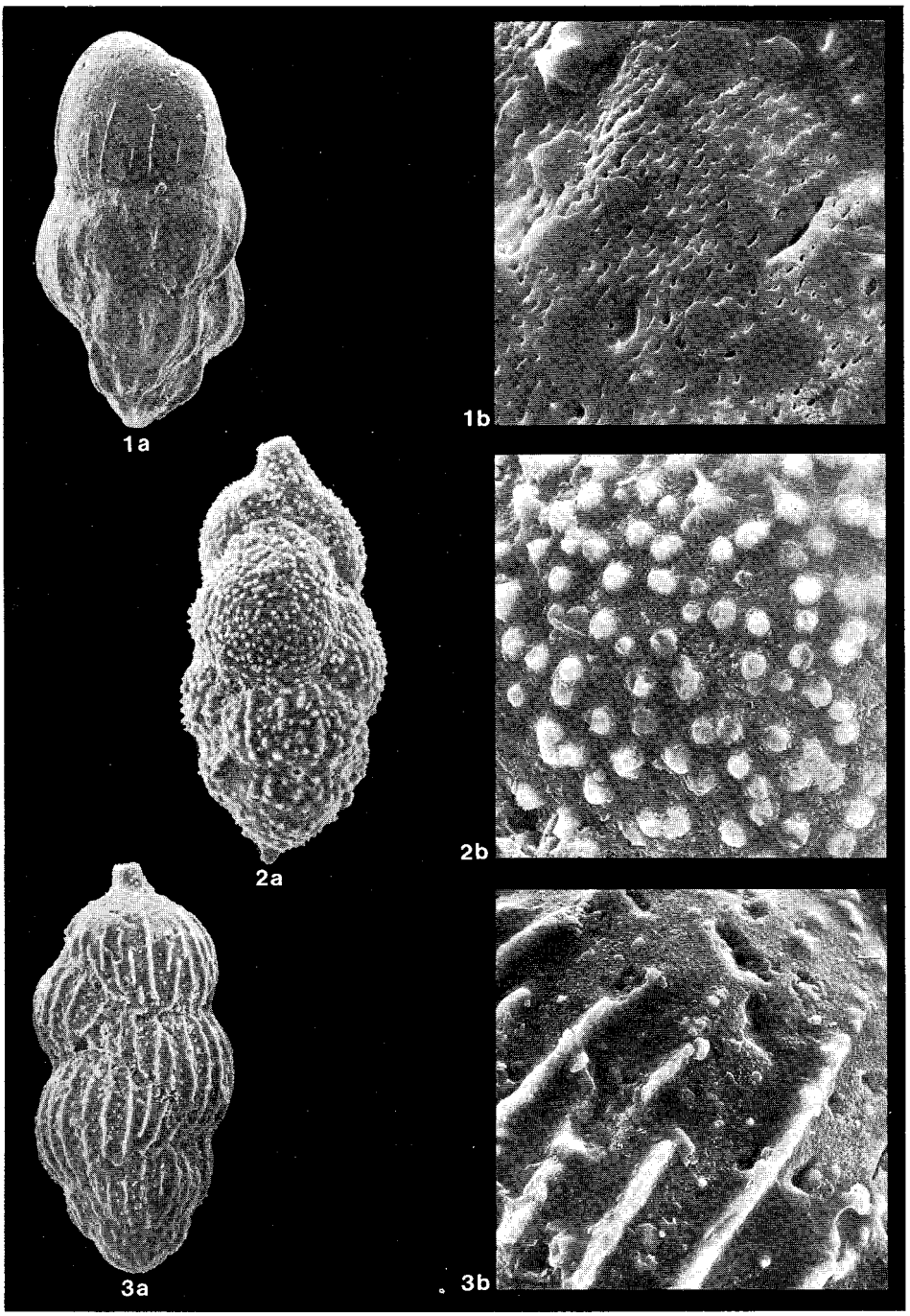


Plate 4

Fig. 1 Paratypoid of *Uvigerina pappi* Meulenkamp, sample G 437 – 15, section Tad Dabrani (437), Gozo, X 155.

Fig. 2 Paratypoid of *Uvigerina melitensis* Meulenkamp, sample M 356, section Gnejna Bay (356/357), Malta, X 110.

Fig. 3 Paratypoid of *Uvigerina gaulensis* Meulenkamp, sample G 437 – 27, section Tad Dabrani (437), Gozo, X 130.

Fig. 4 Detail of the wall of the last chamber of the specimen in fig. 3, X 700.

Fig. 5 Detail of the wall of a specimen of *U. cylindrica gaudryinoides* from sample CP 2267, section Ag. Vlassios, X 1500.

Fig. 6 Detail of the wall of a specimen of *U. cylindrica gaudryinoides* from sample CP 309, section Vrysses II, X 2800.

Plate 4

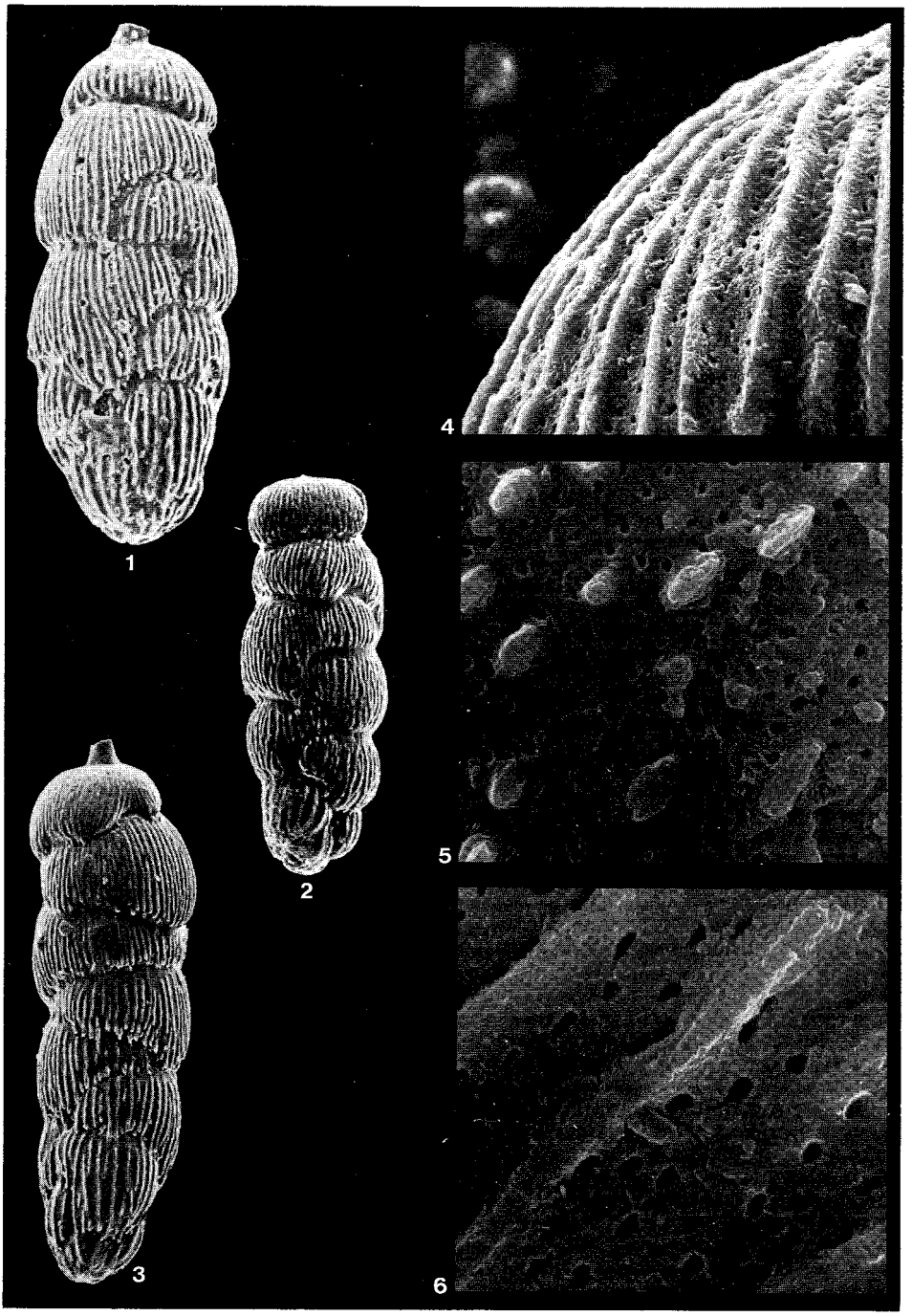


Plate 5

Fig. 1 Paratypoid of *Uvigerina cretensis* Meulenkamp, sample 850 Q, section Exopolis, X 100.

Fig. 2 Oldest part of the test of a specimen of *U. cylindrica gaudryinoides* from sample CP 249, section Vrysses I, X 250.

Fig. 3 A specimen of *U. cylindrica cylindrica* from sample CP 2117, section Finikia, X 95.

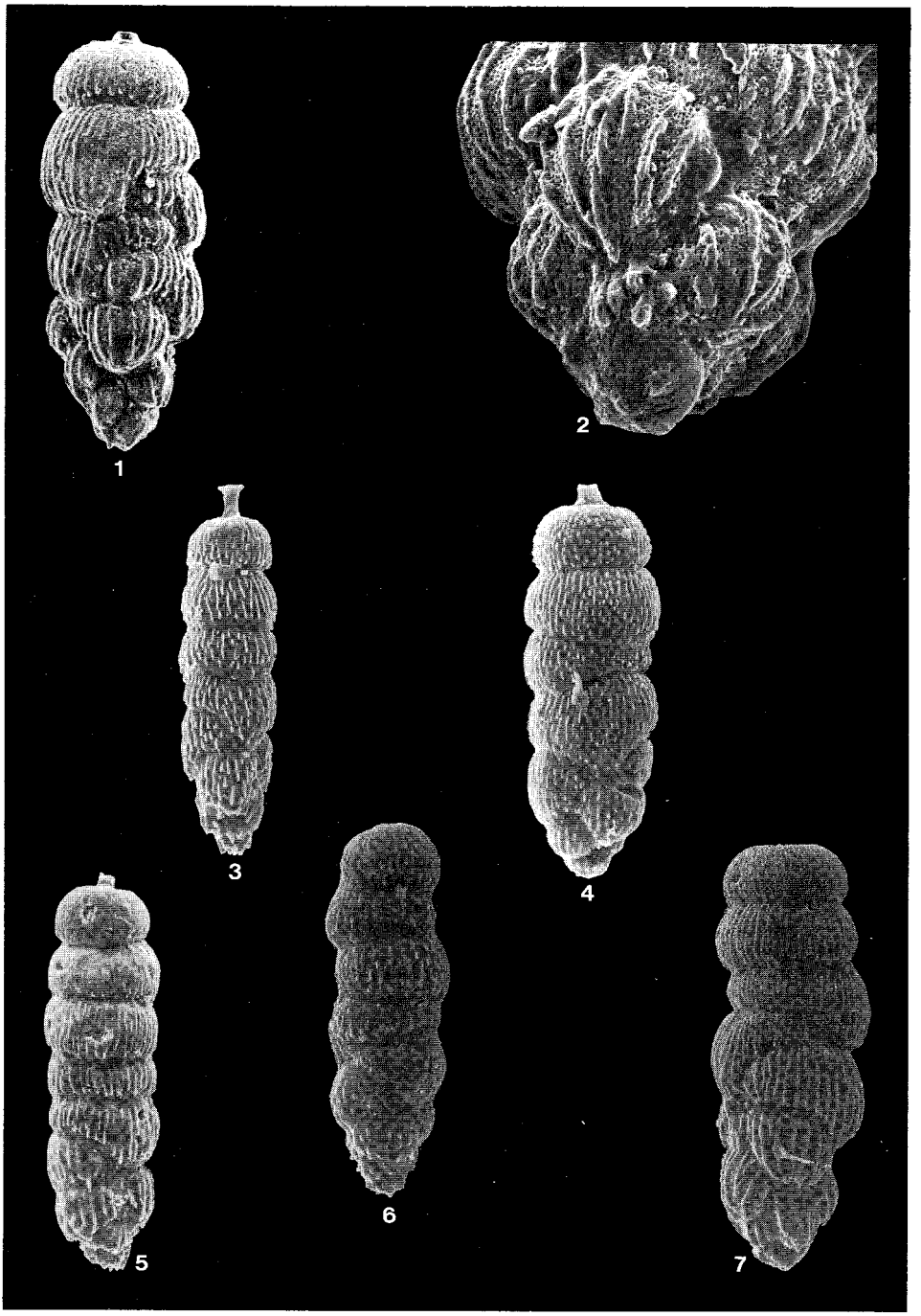
Fig. 4 A specimen of *U. cylindrica gaudryinoides* from sample CP 2005, section Finikia, X 95.

Fig. 5 A specimen of *U. cylindrica cylindrica* from sample CP 586, section Exopolis, X 115.

Fig. 6 A specimen of *U.* ex. interc. *cylindrica-gaudryinoides* from sample CP 586, section Exopolis, X 105.

Fig. 7 A specimen of *U. cylindrica gaudryinoides* from sample CP 586, section Exopolis, X 100.

Plate 5



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