

**UTRECHT
MICROPALAEONTOLOGICAL
BULLETINS**

A.F.B. WILDENBORG

**EVOLUTIONARY ASPECTS OF THE MIOGYPSINIDS IN
THE OLIGO-MIOCENE CARBONATES NEAR MINEO
(SICILY)**

41

UTRECHT MICROPALAEONTOLOGICAL BULLETINS

Editors C. W. Drooger and G.J. van der Zwaan
Department of Geology
State University of Utrecht
Budapestlaan 4, Postbus 80.021
3508 TA Utrecht, Netherlands

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OLIGO-MIOCENE CARBONATES NEAR MINEO (SICILY)

A.F.B. WILDENBORG

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ABSTRACT

The investigation is based on a well exposed sequence of 120 to 130 metres of bioclastic limestones, located at the northwestern edge of the Hyblean Plateau on Sicily, 2 to 4 km NE of the village of Mineo. The carbonates were deposited in a shallow, open marine environment during the Chattian to Burdigalian time interval. Tests of the larger foraminifera *Miogypsina* are abundant in the lower and upper parts of the carbonate succession. The internal morphology of these tests has been thoroughly investigated.

Biometric research reveals that both the oldest and the youngest species of the *Miogypsina* lineage known from the Mediterranean province, are present in the Mineo carbonates. These species are *M. complanata* and *M. mediterranea* respectively. The morphometric series of *Miogypsina* is not complete, however; sedimentary hiatuses and changes in the local environment caused breaks in the biorecord of the Miogypsinids. The absence of the globally widespread *M. globulina* is remarkable. Long records have been found for the Aquitanian *M. gunteri* and for the Burdigalian *M. intermedia* and *M. cushmani*.

The Early Miocene associations of *Miogypsina* s.s. are often accompanied by associations of *Miogypsinoides*. Most of these are close to *M. bantamensis*. On the basis of the mean embryo size two types of assemblages of *Miogypsinoides* could be distinguished in the Aquitanian sediments. Type I with the smaller embryo ($D_1 = 110-125 \mu\text{m}$) resembles associations reported from African localities and type II with the larger embryo ($D_1 = 210-230 \mu\text{m}$) conforms to associations known from the European *Miogypsinoides* stock. Type II is restricted to the Aquitanian, whereas the range of type I extends into the Burdigalian.

The data set for the main lineage of *Miogypsina* exhibits a distinct overall change in morphology of the nepiont, which change is in agreement with the 'principle of nepionic acceleration' as defined by Tan Sin Hok. Detailed information on the Burdigalian *Miogypsina* s.s. shows that this trend is not the result of a gradual unidirectional change, but that the course was staggered. In smaller stratigraphical intervals the nepionic variable \bar{V} may exhibit stasis or shifts opposite to the overall positive trend.

Part of the observed changes in the nepiont may have been caused by variations in sediment accumulation rates or in a variable degree of reworking of older faunal elements. No evidence has been found for a direct control of the environment on the configuration of the nepiont. There is no proof for a functional dependence of the nepionic variables on the changes in mean embryo size; in the literature the latter size is sometimes related to some depth-linked

environmental factor. A substantial part of the morphological changes in Burdigalian *Miogypsina* s.s. are associated with intervals, in which this subgenus is present in low relative frequencies. This suggests that the evolution of *Miogypsina* s.s. was controlled by bottlenecks in the size of the standing stock.

By contrast with *Miogypsina* s.s. no net change has been observed in the Burdigalian sequence of *Miogypsinoides* assemblages; stasis prevails in this subgenus.

Chapter I

INTRODUCTION

I.1 PURPOSE AND SCOPE OF THE INVESTIGATION

In the last three decades many groups of orbitoidal larger foraminifera have been investigated with the application of biometric methods. For many groups lineages have been established that are in accordance with the evolutionary 'principle of nepionic acceleration' (Tan Sin Hok, 1932; 1936; 1937; Brönnimann, 1940; Drooger, 1952; 1963). Originally the evolutionary courses were thought to have occurred along fairly gradual lines, which concept nowadays is called phyletic gradualism.

Recently another theory has become emphasized more strongly. It states that evolution shows a step-like pattern, i.e. instant changes are alternating with longer periods of stagnancy. In most recent papers the pattern is explained by the theory of punctuated equilibria (Eldredge & Gould, 1972).

As the data on orbitoidal foraminifera became more detailed neither of these two models could explain all observations; at least for *Planorbulinella* they could not (M.M. Drooger et al., 1979). In addition to the general trend of change in *Planorbulinella*, which is again in accordance with the concept of nepionic acceleration, conspicuous setbacks occurred superimposed on this overall trend. These 'negative' changes counteracting the adaptive trend, could not be fully explained by the existing models. The staggered course has been named the pulsating evolution pattern, for which recently a complex explanation model has been advanced (Drooger, 1984).

Wondering whether the last-mentioned pattern would appear in other taxa as well, two more groups of larger foraminifera have been examined: *Orbitoides* from the Aquitaine basin in France (Drooger & De Klerk, 1985) and *Miogypsina* from part of the Hyblean Plateau on Sicily. In the *Orbitoides* example there seems to be little more than a punctuation or pulse in accordance with the direction of nepionic acceleration. The *Miogypsina* example will be dealt with in this paper.

In the past the family Miogypsinidae has been thoroughly investigated from different areas all over the world (e.g. Drooger, 1963; Raju, 1974). This has resulted in a clear picture of the major evolutionary lineages of the Miogypsinid clade. As a consequence we have a good basis for our more detailed research.

The Oligo-Miocene calcarenites near Mineo in Sicily offer the potential to in-

investigate the details of a substantial part of the *Miogypsina* lineages. Information on the sedimentary facies and the biofacies are given in chapter II. The morphometric time series of our *Miogypsina* assemblages is described in chapter III. With additional biostratigraphical data on the carbonates this time series is used to discuss several aspects of the local history of the Miogypsiniids and to reconstruct the sedimentation history in the Mineo area (chapter IV). In chapter V we will try to deduce the role of different evolutionary processes, which had shaped the time series established for our Miogypsiniids.

I.2 LOCATION OF THE STUDY AREA AND DATA GATHERING

The area of our study is located in the southeastern part of Sicily, which region is named the Hyblean Plateau (Altipiano Ibleo). At the northwestern border of this topographical high, 2 to 4 km to the NE of the village of Mineo we investigated a well-exposed small inlier of predominantly Lower Miocene carbonates. The precise location of the sections, which have been investigated, is given in chapter II.

The carbonate outcrops near Mineo lie about 20 km to the north of the more or less continuously exposed Oligo-Miocene carbonate sequences in the central part of the Hyblean Plateau (fig. 2).

Sampling was carried out during the spring-times of the years 1980 to 1983. During the last two field campaigns lithostratigraphical correlations were verified and geological mapping of the study area was completed.

The carbonate samples have been prepared and analysed in the laboratories of the Institute for Earth Sciences of the State University of Utrecht. Thin-sections of whole-rock samples have been prepared for a microfacies study and thin-sections of individual Miogypsiniids have been made for the biometric research. The thin-sections of the carbonates and of the individual Miogypsiniids have been stored in the collections of the Department of Stratigraphy and Micropaleontology, coll. no. MF 3 to MF 4 and GFD 151 to GFD 182, respectively.

I.3 GEOLOGICAL SETTING

The investigated Eocene to Miocene carbonates near Mineo are exposed in a small inlier, situated at the northwestern periphery of the Hyblean Plateau and close to the southeastern border of the Caltanissetta Basin (figs. 1 and 2). The Hyblean Plateau in its turn is located at the eastern edge of the Pelagian

Block (fig. 1), which is part of the African continental plate (Burollet et al., 1978). To the east the Pelagian Block is bounded by the Sicily-Malta Escarpment separating this block from the Ionian Abyssal Plain more to the east.

The Pelagian Block constitutes the foreland with respect to the south verging nappes of the Apenninic-Maghrebian Chain to the north. The most external and youngest thrust sheet is the Gela Nappe, which was pushed over the north-western continuation of the Hyblean Plateau during the Plio-Pleistocene (Lentini et al., 1987; fig. 3). Between the axial zone of the Apenninic-Maghrebian Chain and the Hyblean Plateau lies the Caltanissetta Basin. The Mineo area is located in the transitional zone between the Caltanissetta Basin proper and the central Hyblean Plateau ('Altipiano calcareo' s.s.; Carbone et al., 1982a) and the investigated carbonates are visible in a small 'window' amongst younger

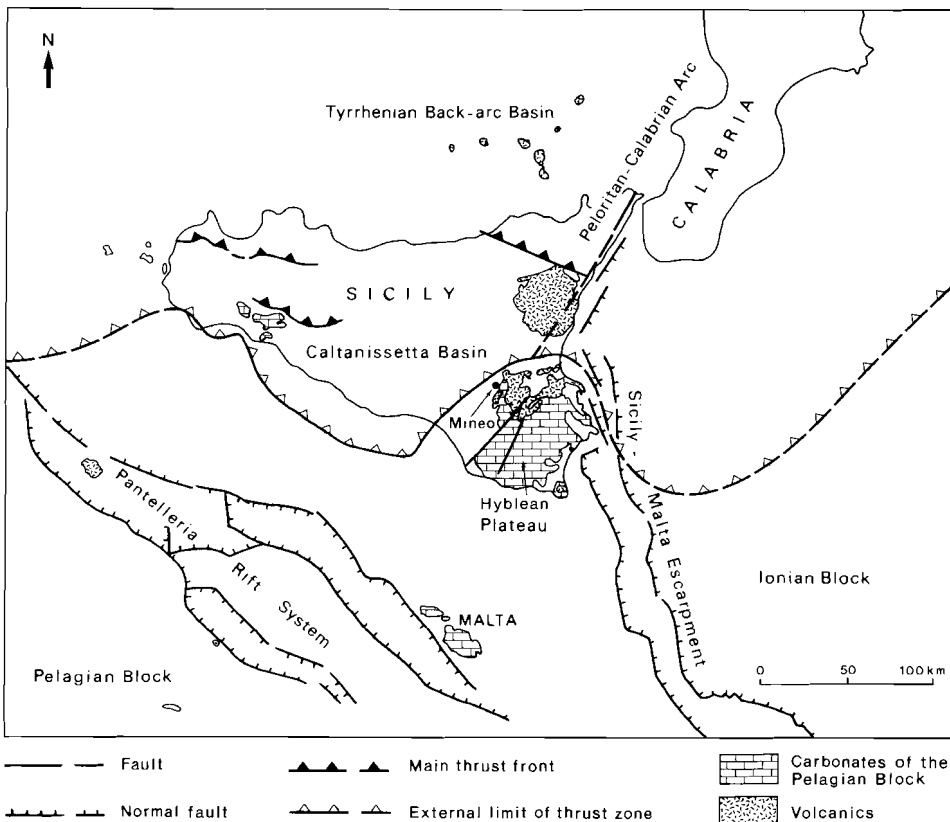


Fig. 1: Geological setting of Sicily in the central Mediterranean; the western NE-SW trending fault on the Hyblean Plateau marks the approximate position of the Comiso fault zone (modified after Boccaletti et al., 1984).

deposits (figs. 2 and 4). The boundary between the central plateau and the transitional zone is marked by the NE-SW trending Comiso fault zone.

On the relatively stable Hyblean Plateau we find an accumulation of about 5 to 10 km of Mesozoic and Cenozoic (and maybe also some Permian) sediments (Bianchi et al., 1989; Lentini et al., 1987), consisting predominantly of shallow marine carbonates and pelagic sediments with intercalations of

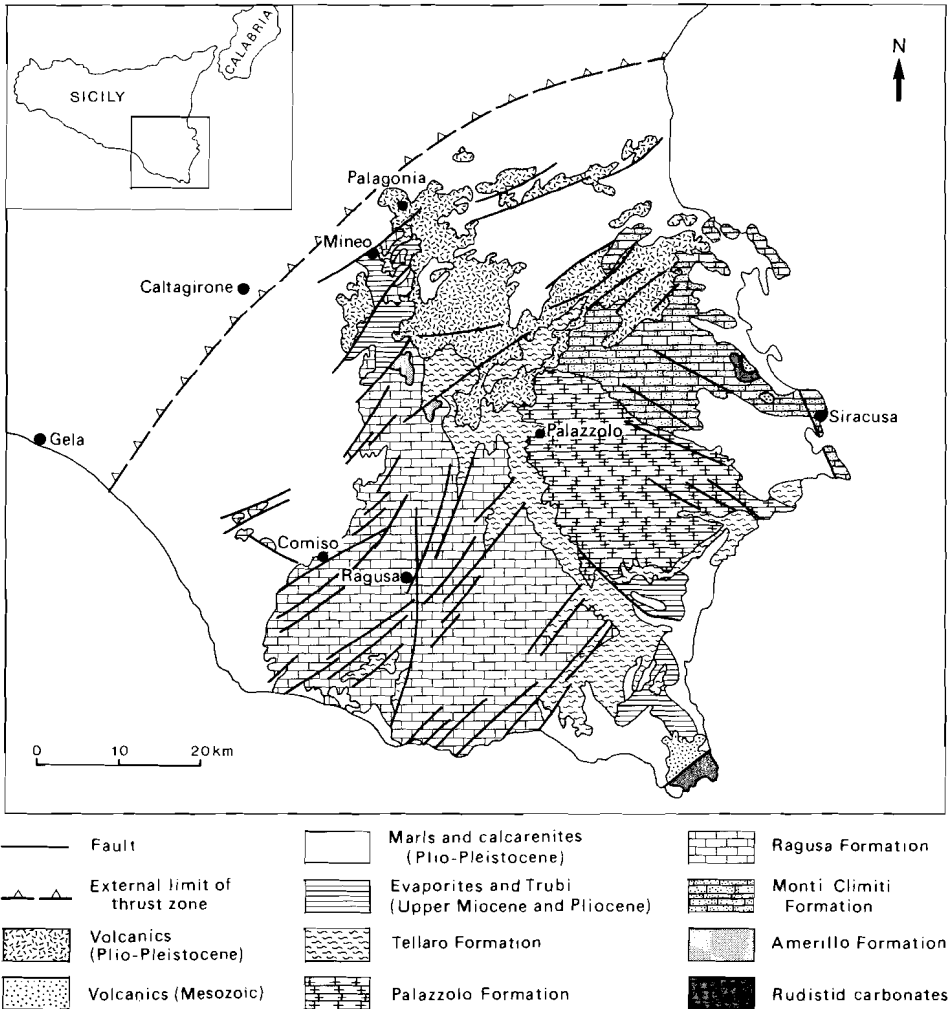


Fig. 2: Schematic geological map of the Hyblean Plateau; the area to the NW of the thrust front has not been mapped in this figure (modified after Ghisetti & Vezzani, 1980; Lentini et al., 1987; Courme & Mascle, 1988).

volcanites (Grasso et al., 1979; Pattaca et al., 1979). Knowledge of the Mesozoic strata is largely based on well data. Most outcrop data of the central plateau refer to sediments of the Upper Cretaceous and Tertiary (fig. 2).

In the central plateau area a northeastern and a southwestern sedimentation domain can be distinguished for the Tertiary (Grasso et al., 1979; Pedley, 1981; Grasso & Lentini, 1982). In the northeastern domain the sediments consist of a condensed sequence of Tertiary shallow marine carbonates with volcanites of Late Miocene to Recent age, whereas in the southwestern domain the Tertiary is represented by a less coarse and thicker sequence of carbonates, representing a deeper 'neritic' facies.

In the NE shallow marine carbonates of Oligo-Miocene age (Monti Climiti Formation: Pedley, 1981; Lentini et al., 1987) usually cover Upper Cretaceous volcanites or rudistid limestones (fig. 5). The Monti Climiti Formation is subdivided into the lower Mellili Member and the upper Siracusa Limestone Member, which are thought to be separated by a sedimentary hiatus in the most northeastern part of the central Hyblean Plateau. The upper member can be distinguished from the lower one by the presence of abundant rhodoliths and common specimens of the echinoid *Chypeaster*. The age relations within the Monti Climiti Formation are poorly known, so that a detailed chronostratigraphical correlation with the sediments in the southwestern domain of the central Hyblean Plateau and in the Mineo area is not possible. Volcanites with biohermal carbonates of presumably Tortonian Age (Carlentini Formation)

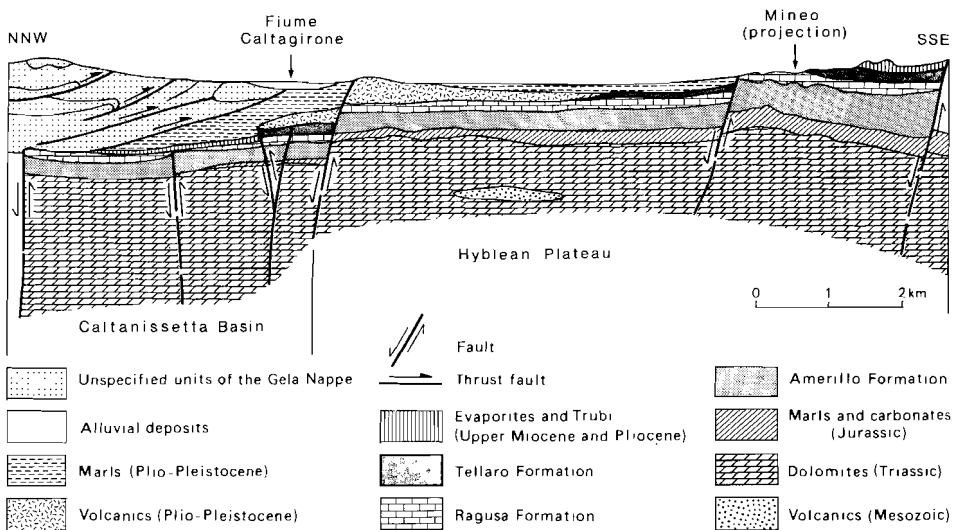


Fig. 3: Schematic profile across the area of investigation at the margin of the Hyblean Plateau and close to the Caltanissetta Basin (modified after Carbone et al., 1982b; Lentini et al., 1987).

overlie the Monti Climiti Formation (Grasso et al., 1982; fig. 5).

In the southwestern part of the plateau very fine white Eocene limestones with silicifications succeed Upper Cretaceous carbonates of about the same lithology (Amerillo Formation: Pieri, 1967; Pattaca et al., 1979). The basal part of the Eocene limestones is marked by breccias and slump structures. Fine to coarse, sometimes marly limestones of Oligo-Miocene age (Ragusa Formation: Rigo & Barbieri, 1959) overlie the Eocene deposits (fig. 5). In the upper part of the Ragusa Formation submarine channels and phosphorite horizons are

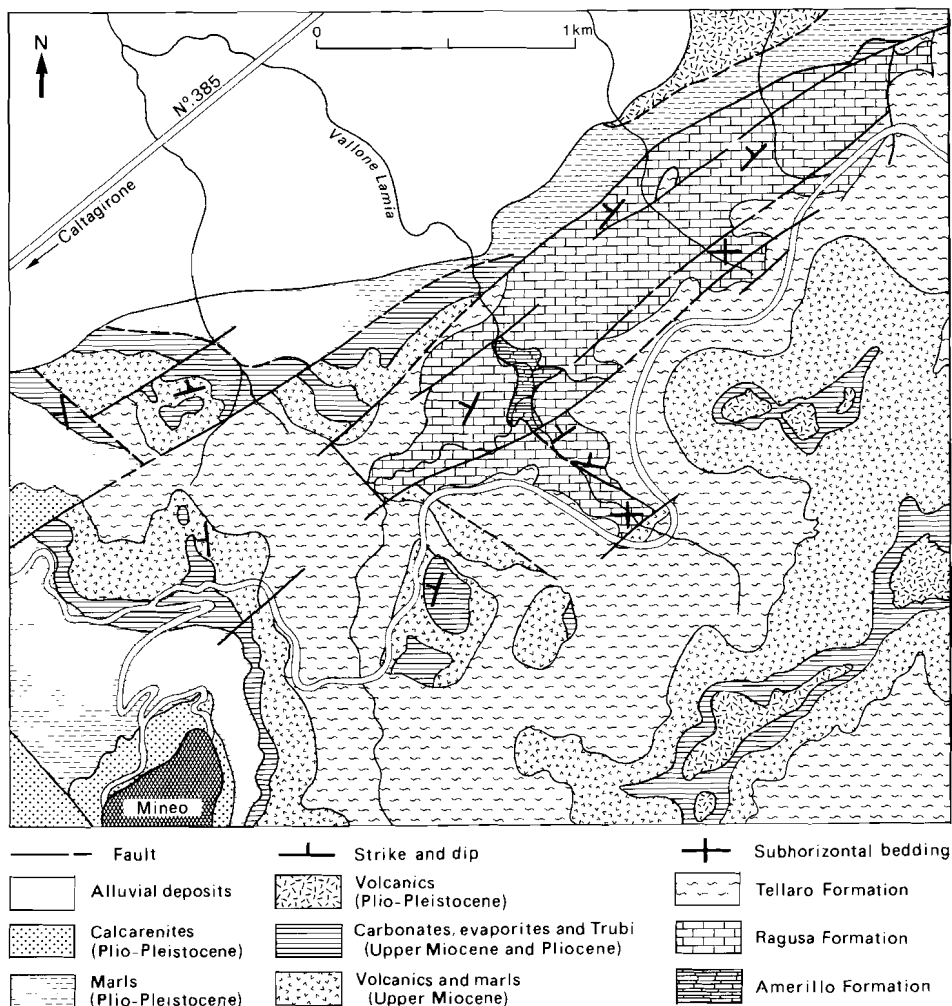


Fig. 4: Geological map of the area of investigation near Mineo.

present (Di Grande et al., 1979; Pedley, 1981). The sediments of the Ragusa Formation are overlain by the marls and subordinate fine limestones of the Tellaro Formation (Rigo & Barbieri, 1959; fig. 5). This formation of Middle to Late Miocene age passes upwards and laterally to the NE in the predominantly fine limestones of the Palazzolo Formation (Rigo & Barbieri, 1959). The Palazzolo and Ragusa Formations are in turn the lateral equivalents of the Monti Climiti Formation of the northeastern part of the central Hyblean Plateau (fig. 5).

The oldest carbonates exposed in the Mineo region are of Eocene age (see also chapter IV) and are very similar to the time-equivalent limestones of the central Hyblean Plateau (Amerillo Formation; figs. 4 and 5). The next higher lithostratigraphical units near Mineo consist of Oligocene and Lower Miocene carbonates. These sediments are of primary interest for our study, because many of them are rich in larger foraminifera, especially in Miogypsinids. This carbonate sequence shows some resemblance to the sediments of the Ragusa Formation in the central part of the Hyblean Plateau, but the succession in the Mineo region seems to contain a larger proportion of coarse carbonates than the corresponding sediments in the Ragusa area.

The age and thickness distributions of the Oligocene and Lower Miocene carbonates in both areas are quite different. In the type area of the Ragusa Forma-

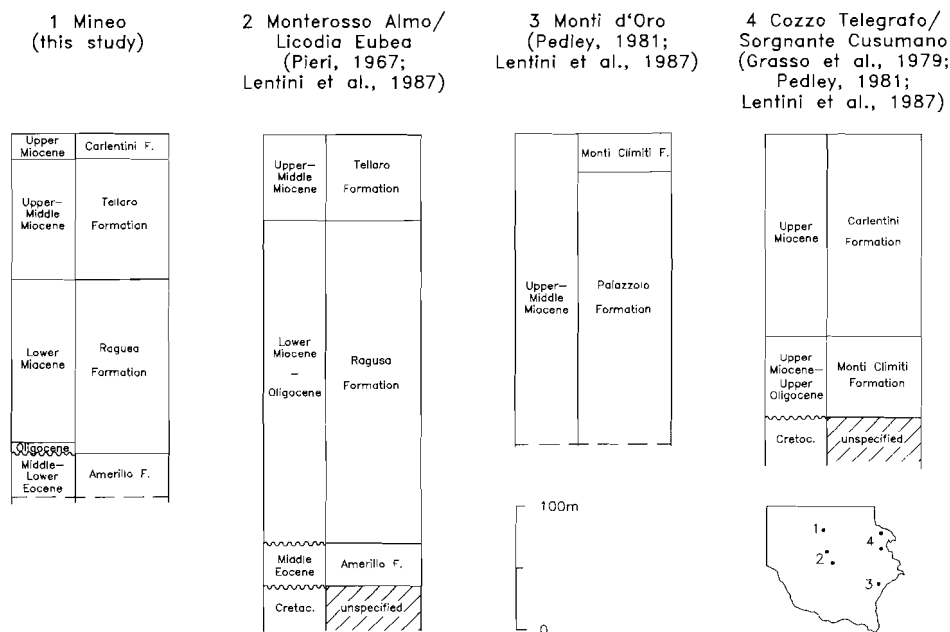


Fig. 5: Simplified composite stratigraphical columns of the Hyblean Plateau.

tion at least 130 metres are of Chattian Age and only some tens of metres are of Late Burdigalian Age; the Aquitanian and Early Burdigalian are represented by a hiatus (Working Group on the Palaeogene/Neogene Boundary, 1984). In the Mineo area on the other hand, only about 15 metres of Oligocene limestones are overlain by 120 to 130 metres of Aquitanian and Burdigalian limestones (see chapter IV).

In the Mineo region the carbonates are succeeded by Middle and Upper Miocene marls of the Tellaro Formation, in the upper part of which volcanic deposits are intercalated (figs. 4 and 5). The volcanites are sometimes covered by a relatively thin interval of bioclastic limestones. The lithostratigraphical position of the volcanites is similar to that of the Carlentini Formation in the northeastern part of the Hyblean Plateau. In the latest Miocene (Messinian) limestones of variable structure (laminated, brecciated, conglomeratic) and evaporites were deposited in the Mineo area. The Pliocene starts with white marls and marly limestones in Trubi facies, in the lower part of which calcareous breccias and volcanic components of variable size are present. The Trubi is covered by a succession of grey marls and calcarenites of Plio-Pleistocene age. In the Mineo area huge volcanic masses are present in this interval. The Plio-Pleistocene marls show a very distinct variation in thickness: from several metres in the area of investigation to a hundred metres or more to the west of Mineo.

The Mineo area is dissected by many faults, most of which have a SW-NE direction. The faults delimit blocks, which frequently show a tilt in north-western direction (figs. 4 and 8).

I.4 SYNOPSIS OF PREVIOUS RESEARCH ON MIOGYPSINA

For nearly a century now *Miogypsina* has been the subject of many micropaleontological investigations. The genus name was officially introduced by Sacco in 1893. The type species was described from a locality in northern Italy, known as the 'Colli di Torino'. In 1841 Michelotti had already described specimens of the same genus from the same general locality, but he classified them in Nummulitid genera.

In the early decades of the present century several descriptive studies on *Miogypsina* were published (among others by Schlumberger, 1900; Vaughan, 1924; Yabe & Hanzawa, 1928), which resulted in a large number of new species names. The taxonomy was entirely based on a typological species concept. At that time the phylogeny of this group of larger foraminifera was a topic of subordinate importance.

This changed when Tan Sin Hok (1936, 1937) recognized a time-dependent morphological trend in Indonesian *Miogypsina* on the basis of the nepionic

chamber arrangement, but Tan also used a typological species concept in his classification. From his research it appeared that in the course of geological time the initial spiral length had been reduced by the introduction of chambers with two apertures at continuously earlier ontogenetical stages. This process went on until the deuteroconch was equipped with two apertures, from which two chambers originated simultaneously, called the principal auxiliary chambers. In his later publication Tan recognized that these two chambers changed in phylogeny from strongly unequal in size to equality. Tan introduced the term nepionic acceleration for the time-bound sequence of morphotypes in *Miogypsina*. It meant that the onset of radial (orbitoidal) growth - or sectorial growth in *Miogypsina* - changed to earlier ontogenetical stages in the course of evolution.

The typological species concept in the taxonomical classification of *Miogypsina* was also applied by later authors (e.g. Brönnimann, 1940). A serious drawback of this approach is the introduction of a multitude of species names, which around 1950 had resulted in 60 to 70 different *Miogypsina* species. This practice naturally did not contribute to a transparent structure of the classification scheme for this genus.

Drooger (1952) in his thesis on American Miogypsinidae introduced the population concept for the classification. In this way the natural morphological variation within individual species was accounted for. In the period from 1953 until 1966 Drooger performed many biometric studies on *Miogypsina*, especially from European, North African and Indonesian localities. Other investigators, who studied *Miogypsina* with the same method are Souaya (1961; Egypt) and Raju (1974; India), but in the fifties and sixties micropaleontologists like Cole and Hanzawa continued to use the typological approach in the determination of the Miogypsinid species.

The biometric method appeared to be a useful tool in the study of the evolution of *Miogypsina* and of orbitoidal foraminifera in general. A thorough insight was built up in the evolution of the main lineage of *Miogypsina* and of its regional offshoots in the circum-Mediterranean, Indo-Pacific and central American bioprovinces; 20 to 30 species remained (Drooger, 1963), all based on nepionic chamber configurations. Some adjustments of the evolutionary scheme of *Miogypsina* in the Indo-Pacific realm resulted from the research of Raju (1974) and Drooger & Raju (1978).

The detailed research on the phylogeny of *Miogypsina* made this genus a very useful tool for chronostratigraphical correlations, especially on a regional scale (Drooger, 1956; Drooger & Laagland, 1986).

The biometric study of *Miogypsina* was not merely restricted to its nepionic characteristics; it also revealed a lot of data on the embryo size of the studied

assemblages. Drooger & Raju (1973) assumed that there is a positive relation in each *Miogypsina* species between the mean embryo size and latitude, which relation might reflect a dependence of the embryo size on light intensity. The authors further speculated that there could also be an increase of the mean embryo size with depth, which idea later on was substantiated indeed for several other groups of larger foraminifera, such as Recent *Heterostegina* and *Operculina* (Fermont, 1977a and b; Biekart et al., 1985). The authors found a more or less gradual increase of the mean embryo diameter with depth. Actually the depth-linked cline in embryo size seems to be of a more complex nature, as was shown for *Operculina* (Fermont et al., 1983). Embryo size would increase down to a certain depth limit, below which level the size is decreasing again.

In each lineage there is an irregular increase in embryo size, but in addition sudden drops have been documented. Large time-bound shifts in embryo size were found for *Miogypsina* as well, such as at the evolutionary level where *Miogypsina* s.s. originates from *Miogypsinoides* (Raju, 1974).

De Bock (1976) presented a detailed study of morphological features in *Miogypsina*. He found that *Miogypsinoides* possesses a well-developed canal system, whereas in *Miogypsina* s.s. such a system is lacking. On the other hand the latter has a more complex stolon system than the former.

I.5 ACKNOWLEDGEMENTS

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P. Hoonhout, T. van Hinte and J. Luteijn drew the figures and W.A. den

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Chapter II

THE CARBONATE SEDIMENTS

II.1 THE SECTIONS

The investigated carbonate exposures lie within an area of less than one square kilometre (fig. 6). Several small valleys with rather steep slopes - amongst others the Vallone Lamia and the Vallone Donna Ragusa - dissect the region of our research (fig. 8). At many places the valley walls are sufficiently well exposed for a meaningful description and sampling of the carbonate sediments.

The observations mainly refer to the section Lamia, the backbone of our investigation. Additional information was provided by the Donna Ragusa section and by a number of other sections in the Mineo carbonates (fig. 6).

The Lamia section consists of three parts, of which the lowest is situated in the NE-side of the Vallone Lamia (L_1); the middle part is in its western side

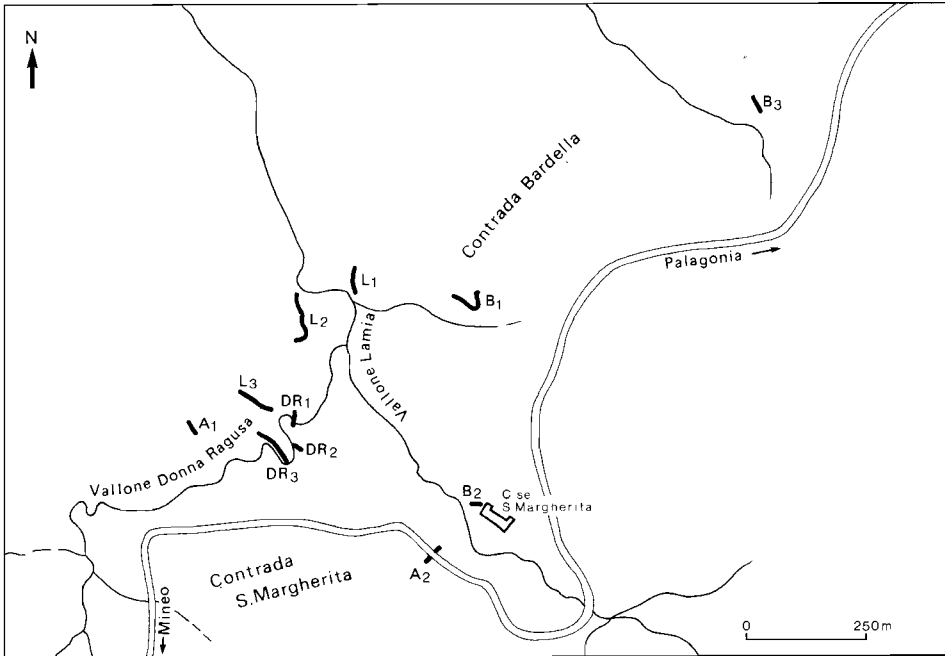


Fig. 6: Location of the investigated sections; L_1 , L_2 and L_3 = Section Lamia; DR_1 , DR_2 and DR_3 = Section Donna Ragusa; A_1 , A_2 , B_1 , B_2 and B_3 = Sections with additional information.

(L₂) and the top part is located in the NW slope of the Vallone Donna Ragusa (L₃). The middle part L₂ has a downthrow relative to the basal part L₁, caused by an easily recognizable fault running about parallel to the Vallone Lamia (compare figs. 6 and 7). The top of L₂ was correlated in the field with the base of L₃.

Close to the river bedding of the Vallone Donna Ragusa three exposures were combined (DR₁, DR₂ and DR₃), which together make up the section Donna Ragusa. This section corresponds with an interval in the L₂ part of the Lamia sedimentary succession. Lithostratigraphical columns of the sections Donna Ragusa and Lamia (the larger part of L₂ and L₃) are shown in fig. 9.

Additional information on the top part of the Mineo carbonates is provided by the sections A₁, A₂, B₁, B₂ and B₃ (fig. 6).

II.2 GENERAL REMARKS

Whole-rock thin-sections

In addition to the field observations, which concerned among other things grain size, sedimentary structures and the degree of induration, thin-sections of rock samples were investigated to acquire more detailed lithological and micropaleontological information. The thin-sections, which measure about 9 square centimetres, usually were made perpendicularly to the bedding-planes. This procedure was followed to level down the effect of small-scale vertical variations so that a representative picture of the entire rock sample could be furnished. In some cases additional thin-sections were cut parallel to the bedding-planes.

The lithological features microscopically investigated are the grain size, the type of grains and the texture. The proportion of coarse grains which measure more than 0.5 mm, provided a useful means for the definition of the coarseness of the sediment. The term 'fine' corresponds with 0 to 25% of coarse grains, 'coarse' means 25 to 60% of coarse grains and 'very coarse' refers to more than 60% of coarse grains.

For the classification of the carbonates the Dunham terminology (1962) was used, which was combined with the classification of Embry & Klovan (1971).

Next to the lithological characteristics of the limestones some quantitative foraminiferal aspects were studied in particular. The relative frequency of the planktonic foraminifera in the total associations of planktonic and smaller benthonic foraminifera ($= 100 P/(P + B)$) was established by scanning traverses in the thin-sections until a minimum number of 200 smaller foraminifera was reached.

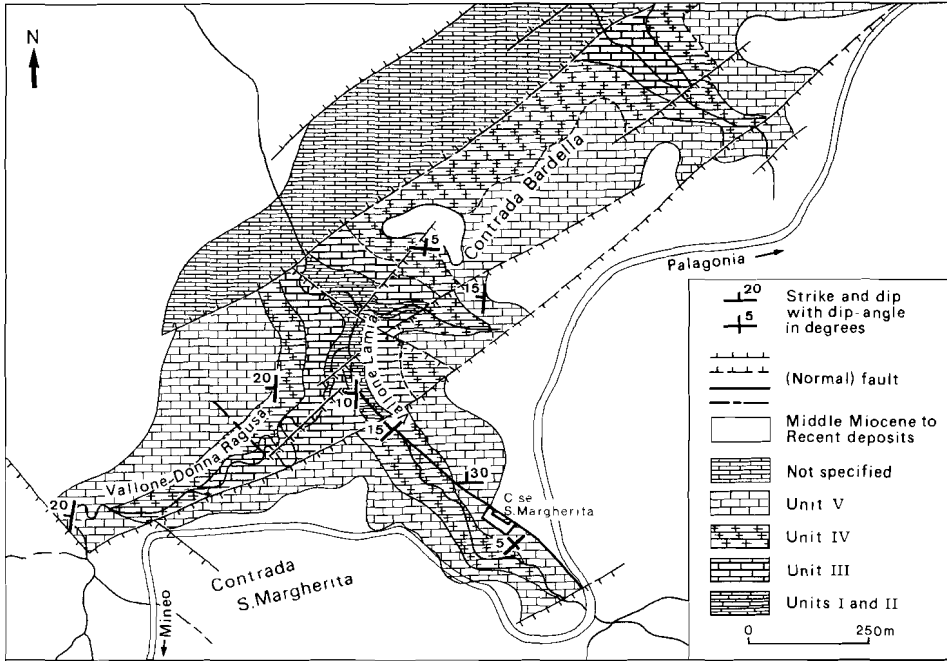


Fig. 7: Detailed geological map of the carbonate units in the area of investigation (Eocene- Lower Miocene).

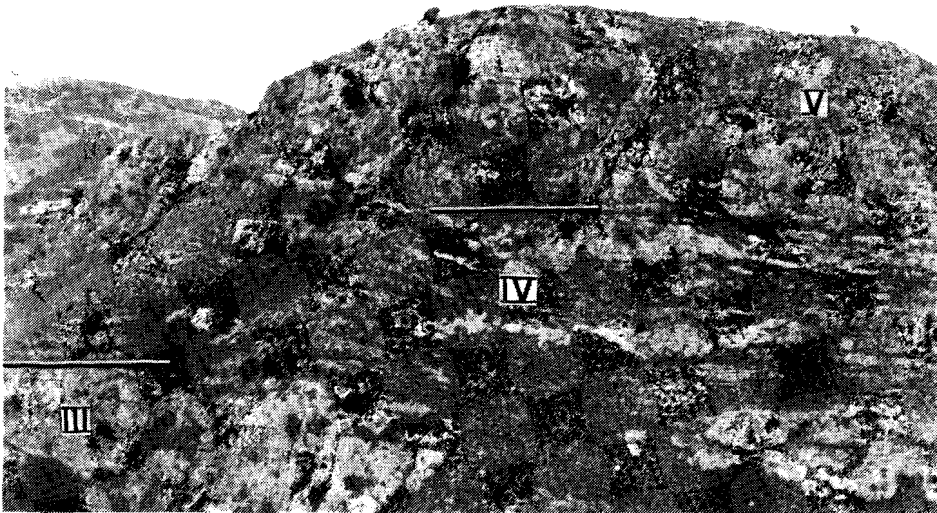


Fig. 8: View from the eastern side of Vallone Lamia to the west showing part of the investigated slopes of Vallone Donna Ragusa and Vallone Lamia; visible lithological units (III, IV and V) have been indicated.

The total numbers of several groups of larger foraminifera were determined by counting them in the thin-sections. A specimen was included in the counting only if more than half of its test was preserved in the particular thin-section. The encrusting foraminifera were dealt with in a different way; they were counted only if their diameter in the thin-section exceeded the value of half a millimetre.

The total numbers of the larger foraminifera are figured logarithmically, because they fluctuate enormously, viz. between 0 and nearly 1000 specimens per thin-section. The thin-sections with zero or near-zero frequencies were not entered in the figures.

The absolute numbers of the separate taxa of larger foraminifera are not completely comparable, because they are slightly influenced by the variation in the scanning surface of the thin-sections and by the effects of sedimentary processes, such as sorting. These problems can partly be overcome by using the relative frequencies of the larger foraminiferal taxa. The major drawback of this procedure is that the percentages are interdependent. A high relative frequency of one group of foraminifera will squeeze the relative proportions of all other groups, which may result in distorted correlations between the various groups.

Subdivision of the larger foraminifera

The frequencies of seven, mainly generic groups of larger foraminifera were determined. These taxa are:

1. *Miogypsina* s.s.
2. *Miogypsinoides*.
3. *Amphistegina*.

This genus shows a large variation in the transverse outline and in the degree of trochospirality. The morphological diversity of this group probably indicates that it is polytypical or multispecific.

4. *Pararotalia*.

Two morphotypes can be distinguished, one with a smooth surface and the other with a pustulous outline.

5. *Lepidocyclina*.

This genus shows a distinct variation in size. Specimens with a relatively large diameter, i.e. larger than 2 mm, are present in the lowermost part of Unit III and in the lower interval of Unit IV (see description of the units in II.4). Individuals of relatively small size prevail in the upper part of Unit III.

6. Nummulitidae.

The Nummulitids comprise the following genera: *Heterostegina*, *Operculina* and *Spirochypeus*. Both evolute and partly involute specimens were lumped in *Heterostegina*. *Cyclochypeus* occurs at a few levels only.

7. Encrusting foraminifera.

This entity consists mainly of Acervulinid genera. Fragments of specimens which resemble *Victoriella* have also been included in this group.

Taxa of extremely low frequency have not been included in the countings. In Unit III these are *Sphaerogypsina* and Planorbulinids and in Unit V they are *Sphaerogypsina*, *Miolepidocyclina*, Nummulitids and questionable Discocyclinids. The relative number of unidentified individuals in Unit III varies between 0 and 8 percent. In Unit V the number of indeterminable specimens is next to nil.

II.3 SUBDIVISION OF THE CARBONATES

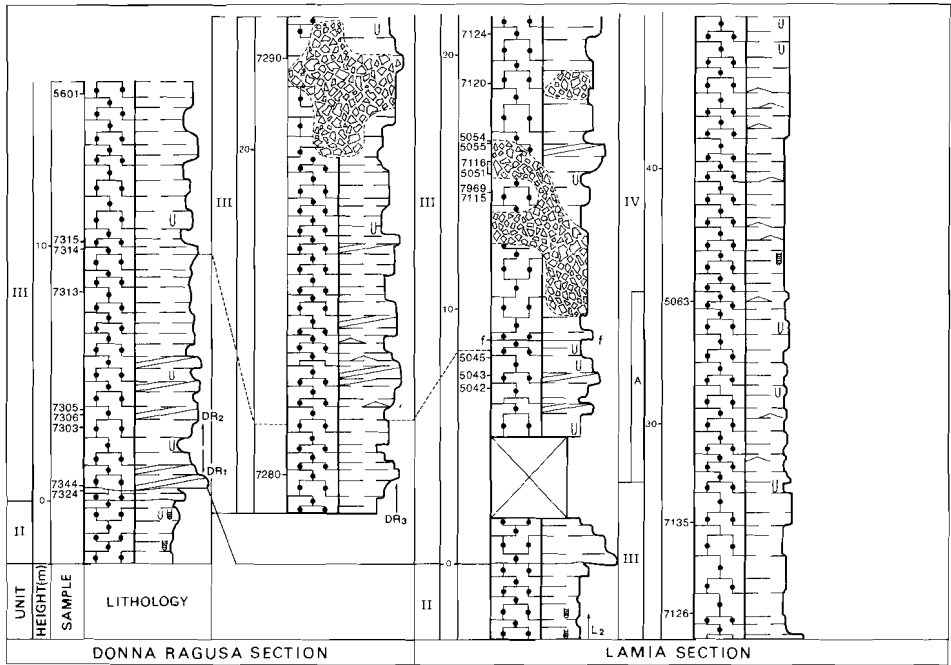
The Mineo limestone series (165 metres in Lamia) and the directly overlying marls were subdivided into the following six units from bottom to top (see also figs. 7 and 9):

Unit I: Very fine bioclastic smaller foraminiferal wackestones and packstones and interbedded thin marl layers. The larger part of the unit, of which about 36 metres are exposed in the Mineo area, is marked by the presence of silicifications of variable size, shape and colour.

Unit II: Very fine and fine bioclastic smaller foraminiferal packstones, which are marked by a diverse association of burrows. The thickness of the unit varies between 9 and 13 metres in the Mineo area.

Unit III: A sequence of fine to very coarse bioclastic larger foraminiferal packstones with a thickness ranging from 27 to 42 metres. Low-angle cross-bedding and burrows were observed. The fine fraction is composed of micrite, planktonic and smaller benthonic foraminifera and bioclastic hash. The coarse fraction, of which the grain size usually is smaller than one millimetre, is dominated by larger foraminiferal, echinoid and algal clasts.

Nine (sub)genera of larger foraminifera were met with in Unit III, of which *Miogypsina* s.s., *Miogypsinoides*, *Amphistegina* and *Pararotalia* may reach relative frequencies larger than 30 percent.



Unit IV: Fine bioclastic smaller foraminiferal packstones, which often show bioturbation. Sometimes there is wave-ripple lamination. The larger part of Unit IV, which has a total thickness between 45 and 50 metres, is devoid of larger bioclasts. At some levels in the lower part of the unit coarse bioclasts are present, of which the clasts of *Lepidocyclina* are very prominent. Their diameter ranges up to 1 cm.

Unit V: A succession of fine to very coarse bioclastic larger foraminiferal packstones, which sometimes grade into grainstones. Burrows and low-angle cross-bedding are common in this unit, the thickness of which varies between 42 and 50 metres.

The size of the grains is often more than one millimetre, but it never exceeds two millimetres. The large clasts belong to larger foraminifera, echinoids, algae, bryozoans and pelecypods.

Important (sub)genera of larger foraminifera in Unit V are *Miogypsina* s.s., *Miogypsinoides* and *Amphistegina*.

Unit VI: Whitish-grey marls overlying the carbonate series near Mineo. The stratigraphical contact between the marls and the limestones is marked by a hardground at the top of the latter.

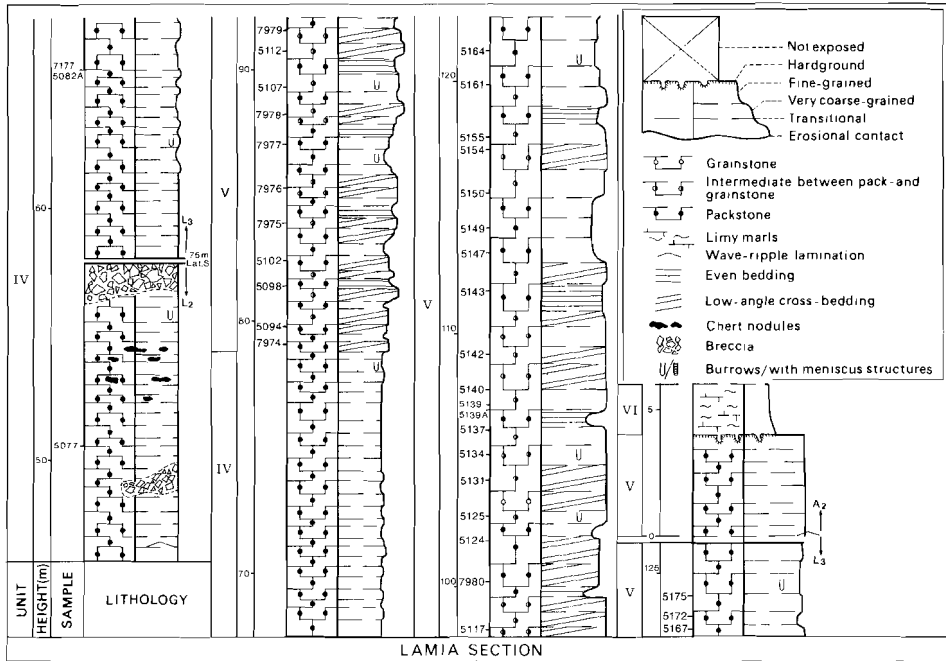


Fig. 9: Lithostratigraphical columns of the sections Donna Ragusa and Lamia. Note that the individual beds are not drawn to scale.

II.4 THE UNITS

Unit I: Very fine bioclastic smaller foraminiferal wackestones and packstones

The basal unit consists of very fine, white wackestones and packstones in beds with a thickness of 3 to 80 cm, which are separated by thin marl layers with an average thickness of less than one cm. The thickness of Unit I, exposed in the Lamia section (L_1 in fig. 6), is about 36 metres.

Burrows with a diameter of several millimetres to one centimetre or more are a common feature in these sediments. Occasionally wave-ripple lamination was observed.

The larger burrows sometimes are silicified. Usually silicifications are present as lenses, nodules and layers.

Microscopical investigation showed that the particles in the micrite matrix are planktonic and smaller benthonic foraminifera next to ostracodes and sponge spicules. Other components are phosphatic grains and bioclastic hash.

Interpretation

Deposition of the fine grained carbonates with wave-ripple lamination took place in a shallow 'neritic', open marine environment, possibly just below the photic zone.

Unit II: Fine and very fine bioclastic smaller foraminiferal packstones

This interval consists of grey to yellowish brown coloured beds of fine and very fine packstones, which beds vary in thickness between 20 cm and 1 m. The sediments are marked by a diverse association of burrows, some of which are of typical decapodan origin. In a few cases wave-ripple lamination was observed.

The total thickness of Unit II in the Mineo area varies between 9 and 13 m.

Planktonic and smaller benthonic foraminifera are common in the thin-sections, in addition to some subrounded algal fragments and bioclastic hash. The foraminiferal tests can be filled with glauconite, which also turns up as separate grains. Other components in the limestones are angular quartz fragments and black, opaque particles.

Interpretation

The environment, in which the carbonates of Unit II were deposited, is comparable to that of the depositional environment of Unit I. Probably the environment was shallower during the deposition of Unit II if one considers the absence of wackestones and marl intercalations and the presence of decapodan burrowing traces in this unit.

Unit III: Fine to very coarse bioclastic larger foraminiferal packstones (plate 1: figs. 7 and 8)

The lowermost interval in the Mineo carbonates, characterized by the presence of larger foraminifera, was distinguished as Unit III. This part of the succession consists of bedded, fine to very coarse packstones (fig. 9).

The thickness of the individual beds varies between 20 cm and 2 m. Usually a thin transitional zone is present in between the successive beds. Superimposed on the bedding we occasionally observed a small scale alternation of protruding and indenting layers with an average thickness of some centimetres.

The base of Unit III is very distinct, especially in the Donna Ragusa section (fig. 10). Here a bed of relatively coarse calcarenites cuts erosionally into the sediments of Unit II. This bed is succeeded by a second one with again an erosional lower bedding-plane. The basal part of this second layer is marked by an extremely coarse texture.

Incidentally the higher beds show sedimentary structures, viz. large scale burrows and low-angle cross-bedding. The height of the foresets amounts to 20 to 35 cm.

The thickness of Unit III, which amounts to about 27 m in the Lamia section, increases to about 42 m close to Donna Ragusa. Although distinct fluctuations in the average grain size occur throughout, Unit III as a whole shows a fining upward trend, which is especially distinct near Donna Ragusa.

The fine fraction is marked by planktonic and smaller benthonic foraminifera, bioclastic hash and micrite. Except for the latter component, the average size of the fine particles ranges from about 100 to 400 μm .

In the lower part of Unit III the relative frequency of the planktonic foraminifera in the associations of smaller foraminifera ($= P/(P+B)$) is variable with a peak value of 85 percent. Higher up the percentage increases regularly from about 35 to about 85 in Unit IV (fig. 11).

A general investigation of the smaller benthonics showed that the trochospiral and planispiral types clearly outnumber the serial ones. Arenaceous types usually are of minor importance and miliolids are next to absent.

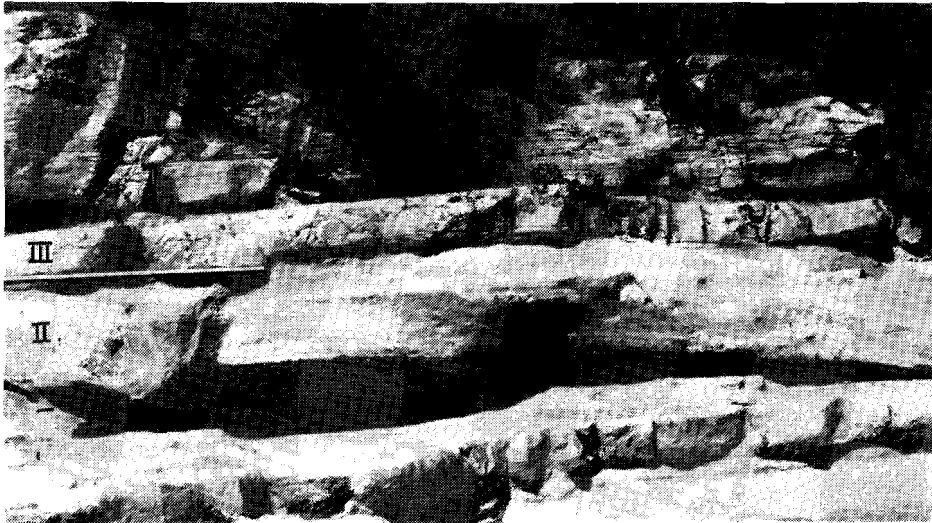


Fig. 10: Stratigraphical contact between the fine packstones of Unit II and the coarse to very coarse packstones of Unit III (section Donna Ragusa: DR₁). The lower bedding-planes of the two lowermost beds in Unit III are erosional. The thick upper bed (thickness = ± 1.5 m) is an important lithostratigraphical marker bed in the Mineo area.

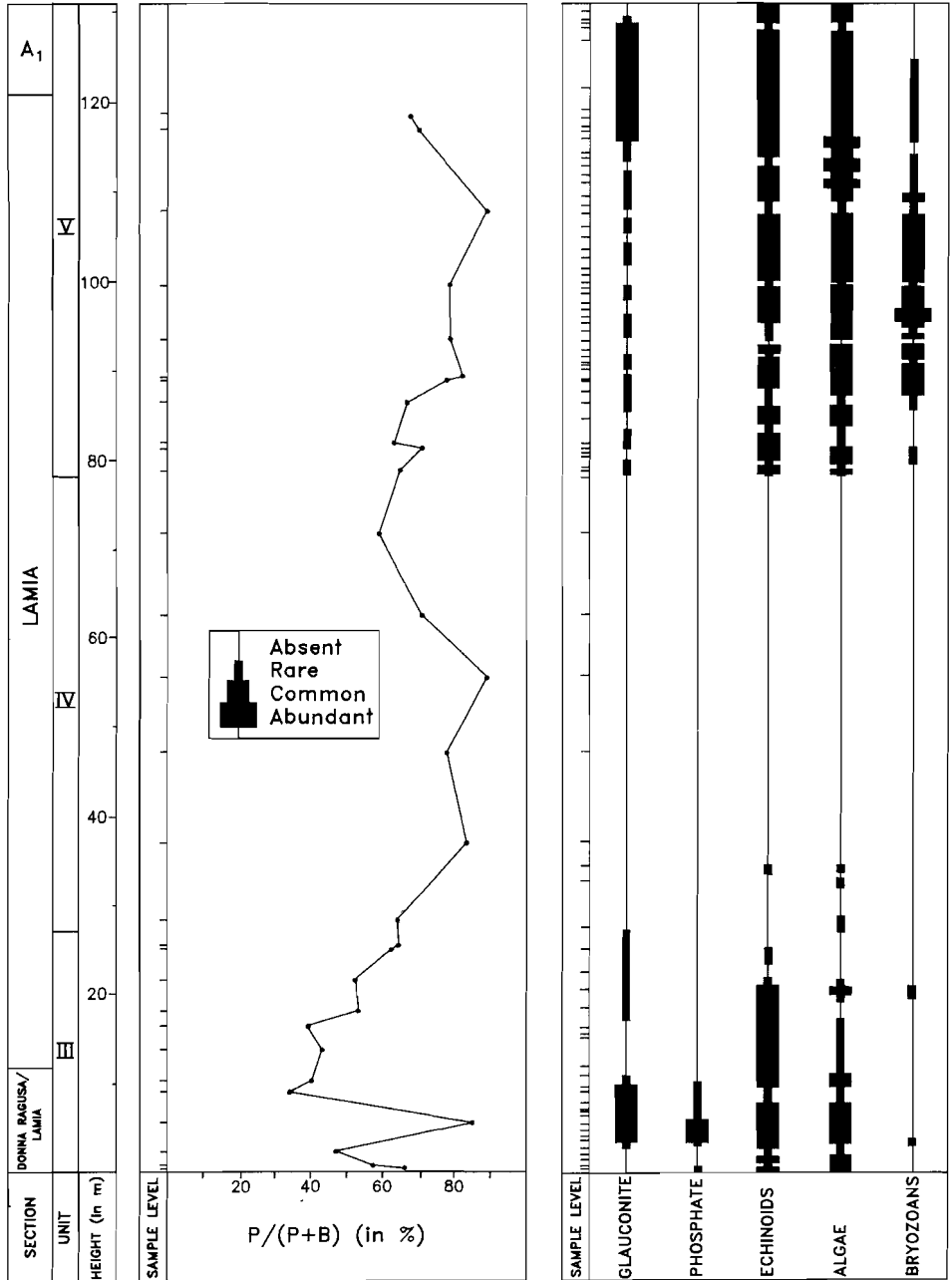


Fig. 11: P/(P+B)-ratio and overall distribution of the most important non-foraminiferal bioclasts (diameter of the grains > 0.5 mm) and of glauconite and phosphate in whole-rock thin-sections.

Usually the average grain size of the coarse part of the carbonate sediments is smaller than one millimetre. Only once, in the thin extremely coarse zone near the base of Unit III, this value is clearly exceeded, which makes this limestone to be intermediate between a packstone and a floatstone. The calcarenites are rarely well sorted; a preferred orientation of the grains was observed in but a few instances.

The coarse fraction of the packstones is dominated by larger foraminiferal, echinoid and algal bioclasts; especially the latter, which in most cases are of the Melobesioid type, generally have a subrounded shape. Locally some oyster fragments were observed. The proportion of the bryozoans is next to nil.

A common non-biogenic constituent in Unit III is glauconite, which is especially abundant in most of the basal part of the unit. The mineral turns up as separate particles and as fillings of foraminiferal tests. Phosphatic particles are present too, but they are less frequent than glauconite.

Larger foraminifera

In order to enlarge the data set for the basal part of Unit III, some thin-sections of the Donna Ragusa section were analysed in addition to the thin-sections of the Lamia section.

Preservation of the larger foraminifera varies from poor to moderately well; a substantial number is fragmented and some of the thick-walled types show microborings. The total number of the larger foraminifera in the analysed thin-sections varies between 16 and 264 specimens (fig. 12).

Miogypsina s.s. is the most prominent genus, except for the basal part of Unit III. Above this zone the relative proportion attains relatively high values between 27 and 80 percent. The largest proportions were found in the middle and upper parts of Unit III.

Miogypsinoides attains its highest relative frequencies in the lower part of this unit; once it exceeds 30 percent. In the upper part the proportion of this genus is 8 percent or less.

Another group of importance is *Amphistegina* with a percentage range from 5 to 51. The group of *Pararotalia*, which constitutes about 35% in the lowest sample of the Lamia section, rapidly disappears from the record. The Nummulitids are met with throughout Unit III in modest frequencies. Heterosteginid types (and *Cycloclypeus*) were only encountered in the samples of the lower part of Unit III, whereas in the upper part the Nummulitids are monopolized by the genus *Operculina*. The frequency of *Lepidocyclina* usually does not reach values above 5 percent; only in the lowermost metres of Unit III the proportion of this genus exceeds the 10 percent level.

Dissolution phenomena

Micro- and macroscopical voids and large breccia masses in the carbonates are probably the result of a diagenetical dissolution process. Large cavities in the form of fissures and caverns were observed in the field. At the other end of the size variation the carbonates often show small, irregular voids in thin-sections, which give the packstone locally the appearance of a grainstone (plate 1: fig. 8).

The vertical distribution of voids in Unit III is about the same as that of the breccias. In the section Lamia the breccias are present from the 10 m level in Unit III upwards. Undisturbed calcarenites grade laterally into intensively fissured sediments and subsequently into breccias. The latter usually form masses with a very irregular shape and a patchy distribution in the succession. Sometimes the horizontal dimensions of the breccia bodies clearly exceed their height.

The internal composition and texture of the breccia components are well comparable to those of the sediments, in which they are incorporated. The diameter of the individual elements varies between half a centimetre and 40 cm.

Interpretation

The types of bioclasts and the low-angle cross-bedding associated with high P/(P+B)-ratios, indicate that the sediments were deposited on a relatively shallow, open marine slope or platform. The sedimentation rate was low accor-

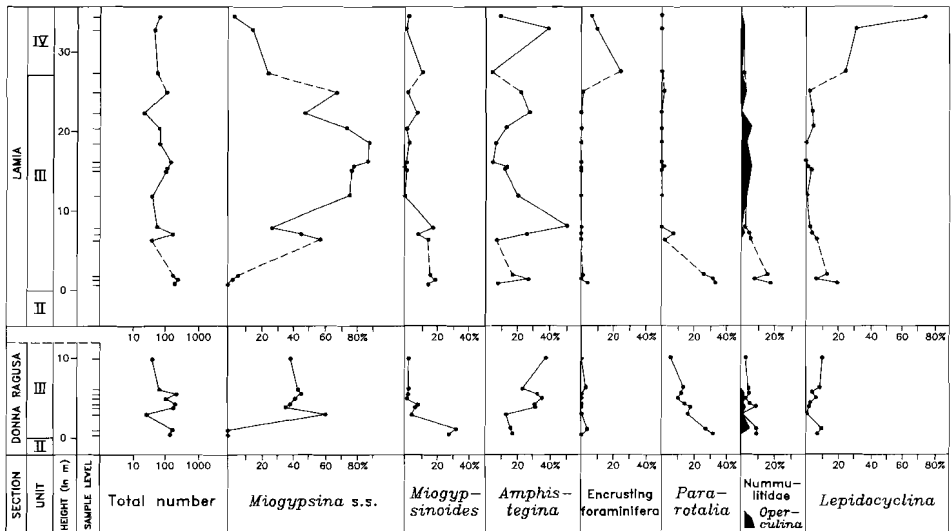


Fig. 12: Total numbers and relative frequencies of the larger foraminifera in thin-sections of Unit III and the lower part of Unit IV (Subunit A); data are from the sections Lamia and Donna Ragusa.

ding to the presence of glauconite and phosphatic particles. The fining upward trend in Unit III is probably related to a slight overall deepening of the environment or a shift to a more protected environment.

Unit IV: Fine bioclastic smaller foraminiferal packstones (plate 1: figs. 5 and 6)

This unit with a thickness of about 50 metres consists of vaguely bedded, fine and medium-fine packstones, in which larger bioclasts are very rare (figs. 9 and 11). The thickness of the individual beds varies between 4 cm and 35 cm.

Bioturbation is the most frequently observed sedimentary structure in Unit IV; both small-scale and large-scale burrows are present. At some places wave-ripple lamination was encountered. Half-way Unit IV rare siliceous nodules are present in the carbonates.

The average grain size does not change drastically from Unit III to Unit IV. The absence of glauconite in the latter gives a better distinction from Unit III. Geomorphologically the boundary between both intervals coincides with the abrupt decrease in steepness of the exposed valley side.

The lower 10 m of Unit IV are marked by a decrease of the grain size. Above this 10 m level the trend is reversed: fine packstones are replaced by medium-fine packstones, which are followed by coarse packstones in the top part of Unit IV.

For a short description of the fine fraction and of the group of smaller benthonic foraminifera in particular, we refer to the text of Unit III. In Unit IV the relative frequency of the planktonic foraminifera varies between 60 and 90 percent. A zone with relative frequencies greater than 70% is present in the lower-middle part of Unit IV (fig. 11).

Bioclasts larger than half a millimetre are not common in Unit IV. Occasionally dispersed, large bioclasts were met with in the basal part of Unit IV (Subunit A), which makes this sediment grading into a floatstone (plate 1: fig. 5). The large components are algal and echinoid fragments, rhodoliths with encrusting foraminifera, and larger foraminifera.

The larger part of Unit IV is devoid of large bioclasts. In the top part they reappear.

Larger foraminifera

With regard to Unit III the relative frequencies of *Lepidocyclina* and of the encrusting foraminifera are much higher in the lower part of Unit IV (Subunit A; figs. 9 and 12). The latter group, which is rare in Unit III, attains proportions between 5 and 25 percent. *Lepidocyclina* is a very characteristic element of Subunit A by its large relative frequencies between 25 and 75 percent and its

large diameter of up to one centimetre. *Miogypsina* s.s., *Miogypsinoides*, *Amphistegina* and the Nummulitids remain present in the lower part of Unit IV.

The association of Miogypsinids and Amphisteginids in the upper part of Unit IV resembles those of Unit V (fig. 14).

Interpretation

The disappearance of coarse bioclasts of shallow marine origin probably points to a (further) deepening during the deposition of the lower part of Unit IV. Renewed shallowing during the deposition of the upper part of Unit IV is suggested by the re-appearance of coarse shallow marine bioclasts.

Unit V: Fine to very coarse bioclastic larger foraminiferal packstones grading to grainstones (plate 1: figs. 1, 2, 3 and 4)

The uppermost unit in the Mineo carbonates consists of beds of fine to very coarse packstones, often grading into grainstones. Interbedded pure grainstones are rare (fig. 9).



Fig. 13: Low-angle cross-bedding in the coarse calcarenites of Unit V (section B₁).

The thickness of the individual beds ranges from 5 cm to 40 cm at the base and from 40 cm to 1 m at the top of Unit V. Commonly no sharp bedding-planes could be distinguished.

The burrows in Unit V are always of large-scale types with diameters varying between 2 and 3 cm. The sediments often show even bedding and low-angle cross-bedding (fig. 13). The sets comprise layers of 3 cm to 10 cm in thickness, which sometimes show a protruding and receding weathering profile. The sets higher than 25 cm dip in directions between 300°NW and 350°N.

A difference in the primary dip of the successive strata was observed at several locations (B₁, B₂ and B₃). While the lower beds of Unit V are subhorizontal in these places, they are slightly inclined - to about 10° - at higher levels in the carbonate series. On the average the inclined beds dip NW (B₂) to WSW (B₁ and B₃).

The transition from Unit IV to Unit V takes place according to a slow and staggering pattern. The coarsening upward trend in the top part of Unit IV is clearly continued in Unit V; coarse and very coarse calcarenites replace the medium fine calcarenites. Above the 35 m level of the unit the trend is waning; the very coarse calcarenites disappear from the record. Along with the increase of the average grain size the height of the foresets increases as well. At the base their height varies between 10 and 20 cm and higher up it can amount to more than 50 cm.

The thickness of Unit V in the Lamia section is 42 m, while close to the Donna Ragusa section it amounts to about 50 m. The transition to the next higher Unit VI is not present in these sections.

For a description of the composition of the fine fraction and of the group of smaller benthonic foraminifera we refer again to the text of Unit III. In Unit V the relative frequency of the planktonic foraminifera varies between 60 and 90 percent. A zone with large proportions of planktonic foraminifera is present in the middle-upper part of Unit V.

The thin-sections showed that the average grain size of the coarse fraction often exceeds the value of one millimetre, but it is never larger than two millimetres. The coarse grains are usually well rounded; angular and subangular, coarse grains are rare. Sorting is generally poor. The orientation of the bioclasts is variable, from random to parallel to the bedding-plane.

The coarse fraction of the sediments in Unit V consists of the clasts of larger foraminifera, echinoids, algae (dominantly *Melobesioids*), bryozoans and pelecypods, which are met with throughout Unit V. Between 10 and 30 m above the base level of Unit V bryozoan clasts are common, while in the rest of this sequence they are rare or lacking (fig. 11). In the uppermost part of the Lamia section oyster fragments are common; they are hardly present in the lower part of Unit V.

The larger foraminifera occasionally are filled with glauconite, which also can be present as individual grains. The glauconite content shows an increase towards the top of the Unit V. The microscopic voids in the carbonates are partly due to dissolution.

Larger foraminifera

Only four of the seven groups, which were found in the lower part of Unit III, reappear in distinct numbers in Unit V. These are *Miogypsina* s.s., *Miogypsinoides*, *Amphistegina* and the encrusting foraminifera, of which the latter are only of importance in a thin interval in the middle part of Unit V. Usually the foraminifera are well preserved.

The number of larger foraminifera in the thin-sections of Unit V is on the average much greater than in those of Unit III, sometimes approximating the value of 1000.

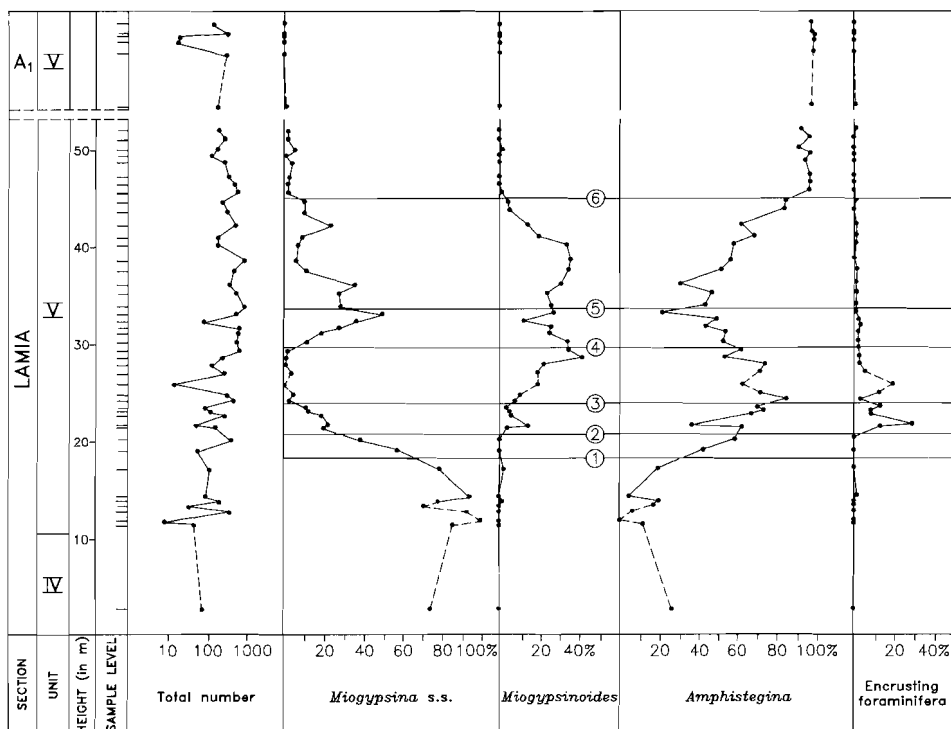


Fig. 14: Total numbers of larger foraminifera and relative frequencies of individual taxa in thin-sections of the upper part of Unit IV and Unit V; sections Lamia and A₁. The lines 1-6 mark changes in faunal composition.

To facilitate the description of the changes in the relative frequencies of the larger foraminifera, we marked some key levels in Unit V, numbered 1 to 6 (fig. 14).

Miogypsina s.s. dominates the assemblages in the upper sample of Unit IV and the lower ones of Unit V (plate 1: fig. 3). Its relative frequency varies between 70 and 100% up to level 1. *Amphistegina* complements these associations.

From level 1 to level 3 drastic changes are seen in the proportions of both genera. Close to horizon 3 *Amphistegina* attains a percentage of 85 and the frequency of *Miogypsina* s.s. drops to 5 percent. Simultaneously two other groups become relatively more important above level 2, viz. *Miogypsinoides* and the encrusting foraminifera.

The proportion of *Miogypsinoides* continues to increase in the zone of relatively low frequency of *Miogypsina* s.s. between the levels 3 and 4, while *Amphistegina* still dominates the assemblages. The proportion of the encrusting foraminifera drops to below 5 percent halfway between the levels 3 and 4.

Above horizon 4 the relative frequency of *Miogypsina* s.s. increases regularly to 50 percent close to level 5, which is partly reflected by a decline of the percentages of *Miogypsinoides* and *Amphistegina*.

Above the peak value of 50 percent *Miogypsina* s.s. shows a negative overall trend with several distinct fluctuations. The proportion of *Miogypsinoides* at first attains values, which were also observed close to horizon 4. Subsequently the percentage drops drastically, so that *Miogypsinoides* is next to absent in the upper part of Unit V. The relative frequency of *Amphistegina* increases to about 95 percent.

Above level 6 no conspicuous changes are apparent in the frequencies of the larger foraminifera anymore. In the youngest strata of Unit V (section A₁, fig. 14) the *Miogypsinids* have disappeared altogether, *Amphistegina* being the only genus to reach the top of the unit (plate 1: fig. 2).

Information from additional locations

In the area of investigation lateral changes in the grain size and the texture of the carbonates were noted. In section B₁ (fig. 6), which is about 500 metres to the NE of the upper part of our Lamia section, the grain size observed in the thin-sections may attain larger values than in Unit V of Lamia. Furthermore grainstones are more prominent in B₁.

The top of our section Lamia does not reach the top of the carbonate succession of Unit V. Two additional sections (fig. 6) yielded information on a still higher lithostratigraphical interval of Unit V (A₁) and on the stratigraphical contact between Unit V and the overlying marls (A₂).

In section A₁ a series of medium-fine and coarse calcarenites is present, of which the basal part overlaps the top part of Unit V in Lamia. Bryozoan par-

icles are next to absent in these upper beds in A₁. At about two metres below the top of the carbonate sequence a hardground is present as a 5 cm thick, brown to green coloured zone with a nodular upper surface. Glauconite, which is a common constituent of the calcarenites below the hardground, is of no importance above it.

In only one section (A₂) we were able to study the contact between the carbonates and the overlying marly sediments of Unit VI. The upper part of the carbonate succession in A₂, which consists of medium-fine and coarse calcarenites, is marked at the top by a hardground. It is a conspicuous, brown layer with a nodular upper surface, of which the thickness amounts to 3 to 5 cm. Several borings in the hardground are filled with limy marls of Unit VI (fig. 15).

It could not be verified whether the hardgrounds in the sections A₁ and A₂ belong stratigraphically to a continuous horizon. Their position relative to the carbonates suggests that they are not.

Interpretation

The shallowing trend for the upper part of Unit IV was distinctly prolonged during the deposition of the larger part of Unit V, as is indicated by the continuation of the coarsening upward trend and the appearance of low-angle

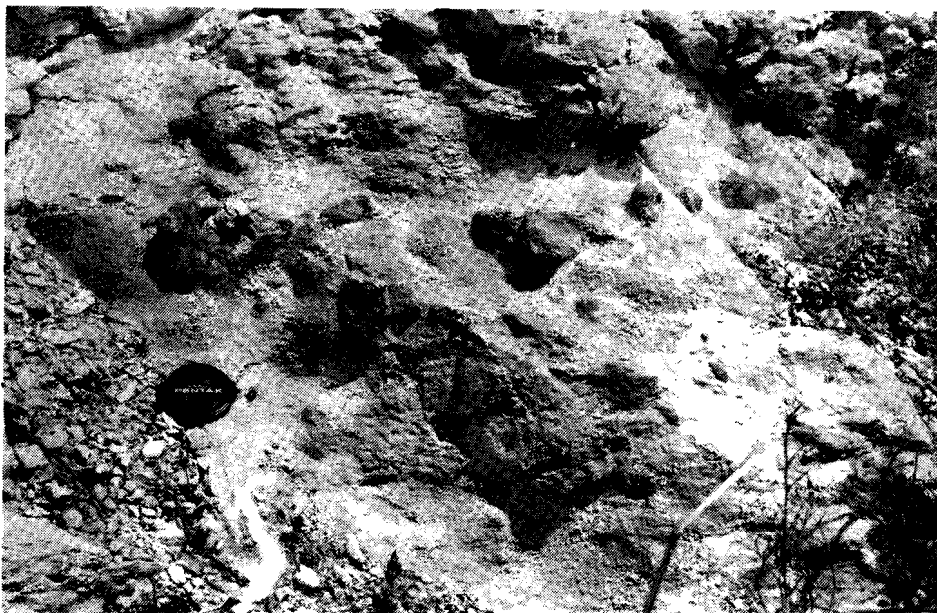


Fig. 15: Hardground at the boundary between Units V and VI (section A₂).

cross-bedded pack- and grainstones. The coarse grained carbonates accumulated in a shallow 'sublittoral', open marine environment. The high relative frequency of planktonic foraminifera suggests that the area was far from any coast line. In the upper part of Unit V the glauconite content increases and hardgrounds appear. Apparently, the sedimentation rate was lowered or periodically even ceased during the deposition of the upper part of Unit V.

Unit VI: Marls

The carbonate sequence near Mineo is covered by a sequence of grey, sometimes brownish marls and limy marls with a total thickness of about 100 m.

In section A₂ (fig. 6) brownish-white limy marls (2 m) and grey marls overlie the carbonates abruptly and unconformably. Wash residues (fraction > 595 μm) of the basal 5 metres of Unit VI still contain tests of *Amphistegina* and bioclastic material. Above this interval these components are of subordinate importance.

The P/(P+B)-ratio (fraction 150-595 μm) varies between 77 and 91% in the lowermost 2 metres of Unit VI, which range is comparable to that of Unit V. Between 2 and 8 metres above the top of Unit V the ratio has increased to values between 95 and 98%, which values are distinctly larger than those of Unit V.

Interpretation

After a period of non-deposition at the transition of Unit V to Unit VI, pelagic sediments were deposited in an open marine realm with a limited influx of shallow marine bioclastic material. Depth increased considerably as is indicated by the distinct increase of the P/(P+B)-ratio.

II.5 THE SEDIMENTARY ENVIRONMENT

Although of no immediate importance to our study of the larger foraminifera, some remarks can be made about the sediments of Units I and II. The occasional traces of wave action point to a shallow 'neritic' environment with frequent slow or non-deposition to explain the silicifications and large-size burrows. Considering the environmental analysis of the higher units we might well be dealing with an open marine carbonate slope or platform already, possibly just below the photic zone.

Most of the carbonates of Units III to V must have accumulated in a shallower, open marine environment, which is concluded from the presence of large-size burrows, low-angle cross-bedding, grainstones and numerous clasts of

organisms living in the photic zone. In such an environment it may be expected that bioclasts were laterally displaced, as is very likely to have been the case for the basal beds in Unit III with erosional lower bedding-planes and for the *Lepidocyclina* bearing floatstone in Unit IV.

Even in the cross-bedded, coarse grained sediments distinct quantities of fines are present. Apparently, complete winnowing did not happen in these sediments, because either the supply of fine material was too high and/or the level of hydrodynamic energy was still too low. Primarily well-sorted, fine and coarse sediments could well have been mixed by burrowing organisms, of which the sedimentary traces are abundantly present.

Planktonic foraminifera are very common in the fines throughout the carbonate sequence (fig. 11), which fact indicates that the sedimentation area was situated close to an 'oceanic' realm. It is much more likely that the Mineo area formed part of an isolated open marine slope or platform than that it was situated on a narrow shelf close to some continental coast line.

Sedimentation rates generally were low during the deposition of Units III to V inclusive, as is indicated by the intense bioturbation of the carbonates and the presence of glauconite in Units III and V. Hardgrounds in the top part of Unit V point to periods of non-deposition.

Unit III

The negative trend of the average grain size and the presence of cross-bedding in the lower part only, point to a decrease of the hydrodynamic energy and probably to a slight deepening or a more protected position on the slope or platform during the deposition of this interval.

The positive shift in the percentage of planktonic foraminifera in the upper part of Unit III, above JT7065, is compatible with the assumption of symsedimentary deepening. However, some observations of high relative planktonic frequencies in the lower part of the sequence, viz. up to 85%, may be contradictory to the idea of an overall deepening trend throughout the sedimentation of Unit III.

Redeposition with lateral displacement probably occurred during the sedimentation of the two basal layers with erosional lower contacts. The higher interval of Unit III underwent reworking, but probably without significant lateral displacement.

The presence of glauconite and phosphate, which have the highest concentrations in the lower part of Unit III, indicate a low average sedimentation rate for the carbonates in this unit.

Units IV and V

Our data suggest that the possible deepening trend during the deposition of Unit III continued during the sedimentation of the lower interval of Unit IV. This view is supported by the further increase of the relative frequency of planktonic foraminifera (fig. 11). Simultaneously the sedimentation of medium-fine packstones was replaced by accumulation of fine packstones. The large *Lepidocyclinids* in the lower part of Unit IV may have arrived by mass transport.

The absence of glauconite suggests that the sedimentation rate increased considerably.

Renewed shallowing is suggested for the upper part of Unit IV and the larger part of Unit V. This interpretation is based on the increase of the average grain size, the appearance of low-angle cross-bedding and of grainstones in Unit V and the massive return of the larger foraminifera and of other bioclasts, typical of the shallow marine realm. Remarkably high relative frequencies of the planktonic foraminifera in Unit V suggests that the carbonate buildup remained far from any coast line.

The upward decrease of the depositional depth is disputable for the uppermost part of Unit V in the Lamia section, in which the increase of the average grain size does not continue. However, in section B₁ (fig. 6) very coarse packstones dominate the carbonates up to the highest level in Unit V.

Laterally the average grain size and the proportion of grainstones increase towards the NE, i.e. from the Lamia section towards successively B₁ and B₃ (fig. 6). These lateral changes point to an increase of the hydrodynamic energy in this direction.

From the upper part of Unit V in section B₁ an increase of the depositional dip up to 10° is known, but such an increase was not observed in the Lamia section itself. The measurements of the depositional slope plead for a shallowing towards the ESE.

Judging from the relatively high glauconite content in the topmost two metres of the Lamia section, the sedimentation rate became very low. The hardgrounds near the top of the carbonate sequence (sections A₁ and A₂) indicate that deposition even ceased for a while.

Summarizing, the depositional environment of the Mineo carbonates can be characterized as a part of an isolated slope or platform area, where open marine conditions prevailed throughout. A better evaluation of the environmental history may be obtained when some time estimates can be linked to the lithostratigraphical units (see chapter IV).

Unit VI

The hardground at the boundary between the Units V and VI may represent the final expression of the shallowing trend during the deposition of Unit V or it may mark the onset of the eventual drowning of the carbonate slope or platform in the Mineo area. Pelagic sedimentation started to dominate the region, in which only some minor input of shallow-derived material took place. The increase of the P/(P+B)-ratio in the lower part of Unit VI pleads for a distinct deepening of the environment. The high ratios of 95 to 98% between 2 and 8 metres above the top of Unit V are indicative of depths of about 1000 m (Van der Zwaan, pers. comm. 1990).

II.6 PALEOECOLOGICAL CONSIDERATIONS

Before entering into paleoecological aspects of the larger foraminifera we have to evaluate the allochthony of part of the larger foraminiferal assemblages. Post-mortem transport of the larger foraminifera did occur. The carbonate sands were transported, which is shown by the roundness of the grains and by the presence of sedimentary structures like low-angle cross-bedding. There are but few indications in favour of mass-transport phenomena, however.

The rare, strongly recrystallized Miolepidocyclinids, that have been encountered in Unit V (chapter III), are thought to be reworked older specimens of Miogypsinids. Generally the internal structure of the larger foraminifera is well preserved. This suggests that post-mortem transport of the larger part of the larger foraminifera took place within a relatively short time interval and probably over relatively short distances.

Two aspects of the carbonate record will be considered in the paleoecological interpretation of the sequence of larger foraminiferal associations. These are depth and type of substrate. Because a rather good dataset is available for the upper part of the carbonate sequence, we will discuss this interval before the evaluation of Unit III and the basal part of Unit IV.

It has been suggested that the upper part of Unit IV and Unit V form a shallowing-upward sequence. Although the depth ranges of our taxonomical groups must have shown considerable overlap, some differentiation in their stratigraphical ranges is still visible. With respect to *Miogypsinoides* the range of *Miogypsina* s.s. extends with high frequencies into the deeper facies of Unit IV. *Amphistegina* frequencies show a negative correlation with those of *Miogypsina* s.s., from which it may be inferred that the former genus prefers shallower habitats.

If one considers the details of figure 14 depth apparently is not the only controlling factor in the distribution of the larger foraminifera.

During the deposition of the Mineo carbonates probably two types of substrate existed, on which the Miogypsinids thrived. One was an unstable sandy substrate, consisting of unconsolidated carbonate grains. On the other hand grains of crustose coralline algae, encrusting foraminifera and bryozoans indicate the existence of a solid substrate.

The frequency distribution of *Miogypsinoides* shows a positive relation with the semi-quantitative distribution of the bryozoans, which usually prefer a solid substrate (compare figs. 11 and 14). *Miogypsina* s.s. on the other hand is not preferentially associated with any kind of bioclast, typical for a solid substrate. No positive relation between this genus and the bryozoans or the encrusting foraminifera was found. From Unit V in section B₁ it appeared that no correlation exists between the presence of algal fragments and *Miogypsina* s.s. either. Probably *Miogypsina* s.s. was indifferent to the type of substrate or it might have preferred a sandy substrate of somewhat greater depth.

Relative to Unit V the thin-sections of Unit III and the lower part of Unit IV show low absolute numbers and a higher diversity of the foraminiferal assemblages (fig. 12). Bryozoans and encrusting foraminifera are nearly absent in Unit III (fig. 11). Encrusting algae are common in the lower part of this unit, but they are rare in most samples of the upper part. This change during the deposition of Unit III was accompanied by a deepening of the carbonate environment.

Pararotalia and the Heterosteginids are restricted to the shallowest basal part of Unit III. The deepening trend we suggested for the middle-upper part of Unit III is somehow corroborated by successive relative peaks of *Amphistegina* and *Miogypsina* s.s., followed by a *Lepidocyclina* maximum in the lower part of Unit IV. However, details of figure 12 suggest that history certainly was more complex.

Chapter III

BIOMETRIC ANALYSES OF THE MIOGYPSINIDAE

III.1 INTRODUCTION

In this chapter the morphometric data of the Miogypsinidae are discussed. Most investigated Miogypsinid associations were derived from the section Lamia. Samples from the Donna Ragusa section complement the record for the basal part of Unit III.

At many levels the sediments are too strongly indurated for us to isolate individual larger foraminifera. For this reason we sampled semi-weathered rock material, from which the larger foraminifera could be gathered easily. Although collecting of such material was carried out with the greatest care, we cannot guarantee that contamination with weathered material from the overlying calcarenites did not occur.

In the laboratory the samples were washed over a set of sieves. The wash-residues between 595 μm and 2 mm appeared to contain the bulk of the tests of the larger foraminifera. Only some of the Lepidocyclinids are present in the sieve-fraction larger than 2 mm.

Whenever possible, we picked a minimum number of 25 specimens from each sample. If two subgenera of *Miogypsina* were found to be present in one sample, we doubled the number of collected individuals. Sometimes lack of material forced us to be content with less specimens.

For the execution of our measurements we had to prepare median sections. For that purpose the specimens were mounted on glass plates, after which the individuals were grinded with another, rugged glass plate. This resulted in thin-sections or half-sections of *Miogypsina*, in which the median layer is distinctly visible. Because of the frequent scarcity of larger foraminifera in Unit III, we had to complete the data sets of *Miogypsina* with half-sections, found in the residues.

III.2 MEASUREMENTS - METHODS AND PARAMETERS

Following the definitions by Drooger (1952, 1963), several parameters of the juvenile apparatus of the Miogypsinidae were counted or measured.

The linear variables were measured in micrometers with a calibrated, ocular micrometer. The precision of the linear measurements is limited to about 5 μm . The angular parameters were measured in degrees with the help of another

ocular device, holding a revolving reticle and a fixed, graduated scale. The precision of the angular measurements is about 5 degrees.

The variables and their definition are listed below (see also fig. 16):

- X The total number of nepionic chambers in the initial spiral excluding the two embryonic chambers and including the closing chamber, if present.
- γ This angular parameter is a quantitative measure of the orientation of the nepiont in the foraminiferal test. A detailed description of the way of measuring γ was given by Amato & Drooger (1969).

Two line segments determine this variable. The first one starts at the centre of the protoconch and passes through the centre of the deuteroconch. The second line segment also starts at the centre of the protoconch and continues through the apex of the test, coinciding with the apical-frontal line. The zero of the γ -scale has been arbitrarily fixed at the configuration where both line segments coincide in individuals with one whorl or less.

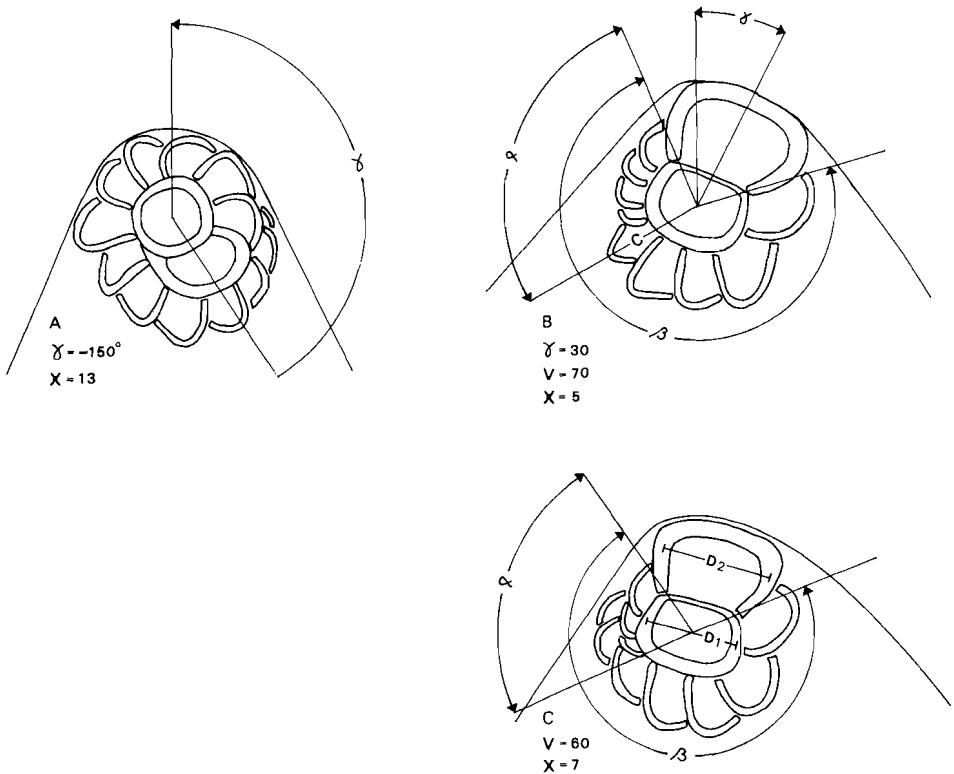


Fig. 16: Schematic drawings of nepionic configurations encountered in the Miogypsinids from Mineo, see text for the explanation of the symbols; c = closing chamber.

γ is positive if the first principal auxiliary chamber points to the frontal margin of the test. Otherwise γ is negative. In the latter case γ is measured by rotating the embryonic line segment in the direction of coiling towards the apical-frontal line segment.

V This parameter depends on two angular variables, α and β , in the following way: $V = 100\alpha/0.5\beta = 200\alpha/\beta$. The dimensionless ratio, which scale ranges from 0 to 100, indicates the degree of symmetry of the protoconchal spirals.

α is the arc length of the circumference of the protoconch underlying the shorter spiral and β is the arc length of the circumference of the protoconch underlying both protoconchal spirals.

D₁ The maximum diameter of the protoconch is measured perpendicular to the embryonic line (see γ) and includes half of the thickness of the walls.

D₂ This parameter represents the largest diameter of the deuteroconch, determined parallel to the measurement line of D₁.

The estimate of the exact number of chambers in the primary spiral (X) is rather difficult in individuals with long spirals. X may be estimated too low, because the ultimate chambers, which are very small, were not cut in the thin-section or half-section. On the other hand X may be estimated too high, because a lateral chamber was identified as the ultimate or penultimate spiral chamber. Furthermore, observations on X are hampered by a bad preservational state of the specimen.

The parameter V is not totally unambiguous with respect to the degree of symmetry of the protoconchal spirals. This small imperfection is caused by the absence or presence of a closing chamber between the protoconchal spirals (parameter C). In the specimens without a closing chamber the longer spiral overrides the shorter spiral. β in particular, does not take into account the part of the primary spiral, which overlies the chambers starting from the second principal auxiliary chamber (fig. 16c).

In addition to these parameters, which are generally used in the biometric research of the Miogypsinidae, we introduce some additional parameters for the associations of *Miogypsina* s.s.:

P Percentage of specimens with two principal auxiliary chambers (only for Unit III).

C Relative frequency of specimens, in which both protoconchal spirals end in the same closing chamber (only for Units IV and V); see also the discussion on parameter V.

CT Proportion of the individuals with a centripetal trend of the embryon. This phenomenon is said to be present if the nepiont is encircled by at least one annulus of neanic chambers.

III.3 THE MIOGYPSINIDAE IN UNIT III

III.3.1 Heterogeneity of the assemblages

The lowermost associations of *Miogypsina* in Unit III, JT7324 and JT7344, consist entirely of individuals with massive side walls. They all unmistakably belong to the subgenus *Miogypsinoidea*. The larger part of Unit III, however, is marked by the joint presence of types with lateral chambers and types without such chambers. The two groups correspond with the subgenera *Miogypsina* s.s. and *Miogypsinoidea*, respectively. The subgeneric identification of the Miogypsinids, which was carried out during the grinding process, was not successful for a small number of specimens, probably due to their bad state of preservation.

We might wonder whether the presence of both subgeneric groups can also be recognized in their biometric properties. The ranges of the parameter values

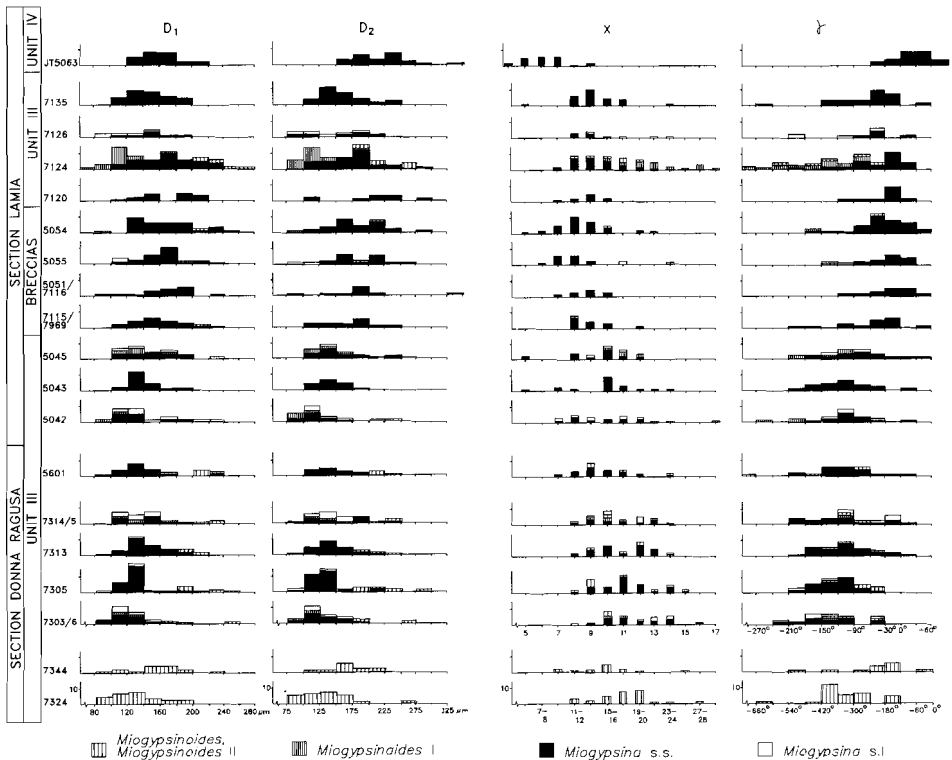


Fig. 17: Histograms of D_1 , D_2 , X and γ of *Miogypsina* in Unit III. The frequency distributions of JT5063 have been added to show the changes across the boundary between Units III and IV.

found for the *Miogypsina* s.s. and *Miogypsinoidea* individuals show a wide overlap in all parameters (fig. 17). Apparently both taxa are not mutually exclusive on the basis of individual, morphometric characteristics. Theoretically the presence of more than one biometric group might be recognized from the bimodal shape of the frequency distribution, from the large coefficient of variability for one or more parameters or from the patchiness of clusters in the scatter diagrams. However, the low relative frequencies of *Miogypsinoidea* in most samples seriously hamper the chance to recognize such mixture phenomena. The sample JT7124 is the only one, in which both subgenera are frequent.

In this association *Miogypsinoidea* and *Miogypsina* s.s. show distinctly different modal classes in the frequency distributions of the embryonic size parameters (fig. 17). The heterogeneity is also visible from the nepionic parameters, *Miogypsinoidea* being more primitive in both X and γ .

	V_{D1}	V_{D2}	V_X
<i>Miogypsina</i> (total association)	30	31	23
<i>Miogypsina</i> s.s.	21	23	16
<i>Miogypsinoidea</i> (total)	40	36	19
<i>Miogypsinoidea</i> I	18	21	16
<i>Miogypsinoidea</i> II	10	16	13

Table 1: Coefficients of variability for *Miogypsina* in sample JT7124.

In a way the coefficients of variability, which are shown in table 1, support the inhomogeneity of the assemblage in JT7124. In the Units IV and V, V_X and V_{D1} of the distinct *Miogypsina* s.s. and of the distinct *Miogypsinoidea* associations range from 10 to 25 (fig. 18). V_{D1} of 30 for the total association in JT7124 thus is rather high as compared with these 'normal' values. However, the separation into two subgeneric groups does not seem to result yet in two homogeneous entities. V_{D1} for *Miogypsina* s.s. in JT7124 is low ($V_{D1} = 21$), but V_{D1} for *Miogypsinoidea* in the same sample remains unacceptably high.

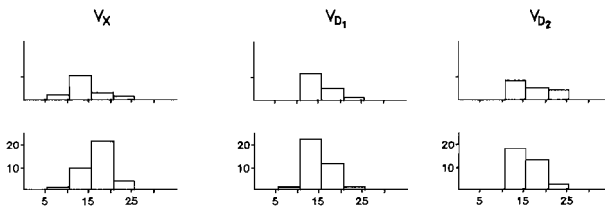


Fig. 18: Histograms of the coefficients of variability for X, D₁ and D₂ of *Miogypsinoidea* in Unit V (above) and *Miogypsina* s.s. in Units IV and V; N = number of samples.

This anomalous value of the coefficient of variability is understandable from the investigation of the scatter diagrams for the sample JT7124 (fig. 19), in which D_1 is plotted against X , γ and D_2 , respectively. In the D_1 - γ scatter it is clearly visible that the individuals of *Miogypsinoidea* fall apart into two clusters. The division in two groups is less distinctly reflected in the other two diagrams. It is likely that we are dealing with two different associations of *Miogypsinoidea* in JT7124.

The protoconchal diameter characterizes the two *Miogypsinoidea* groups best; group I consists of specimens with small protoconches and group II comprises

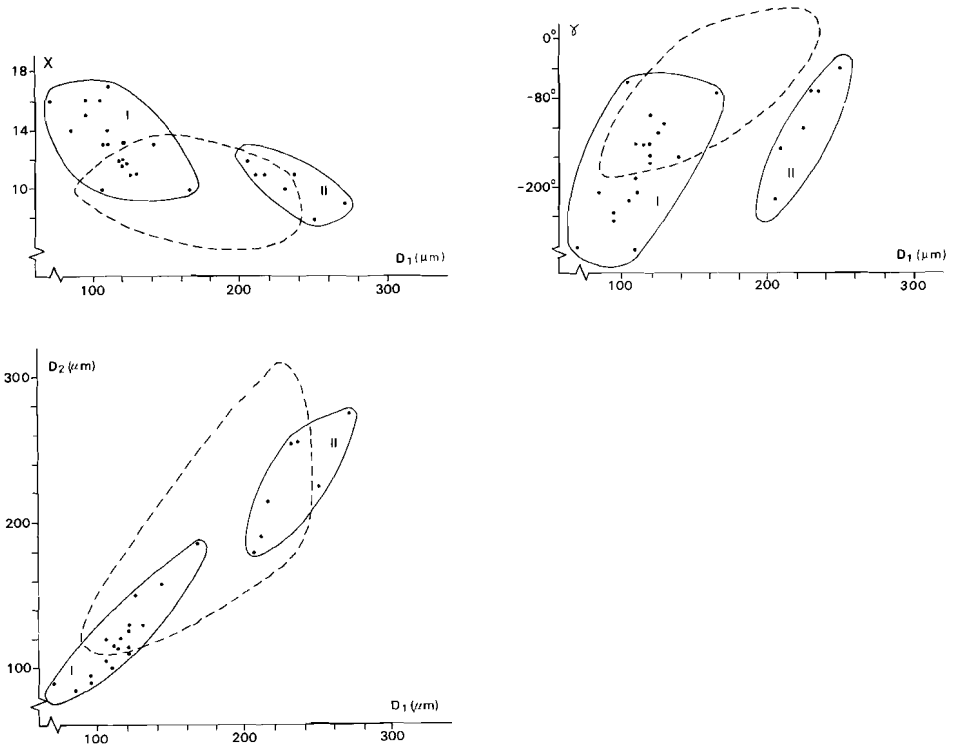


Fig. 19: D_1 - X , D_1 - γ and D_2 - D_1 scatter diagram of *Miogypsinoidea* in JT7124. Dashed line is scatter periphery of the accompanying *Miogypsina* s.s. individuals, solid lines scatter peripheries of *Miogypsinoidea* I and II individuals.

individuals with large protoconches.

In the scatter diagram of D_1 and γ it can be noted that group II is completely separated from the *Miogypsina* s.s. cluster, whereas group I shows an overlap with the latter. In the D_1 - X and D_1 - D_2 diagrams of JT7124 (fig. 19) the *Miogypsina* s.s. clouds show overlap with both groups of *Miogypsinoidea*.

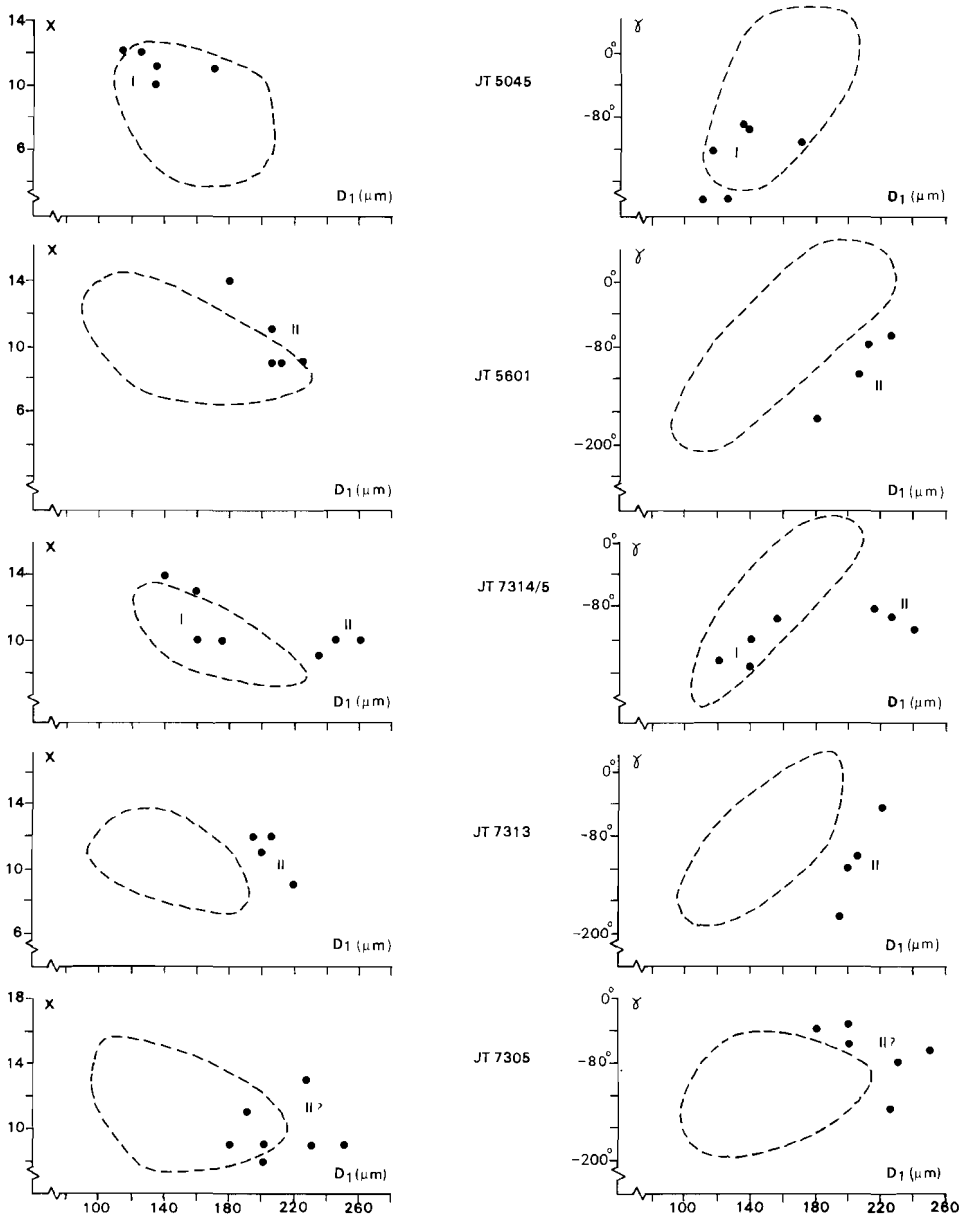


Fig. 20: X-D₁ and γ -D₁ scatter diagrams for *Miogypsinoides* in five samples of Unit III. Dashed line = scatter periphery of accompanying *Miogypsina* s.s.

Reviewing the data gathered from JT7124, we conclude that in this sample we are dealing with three biometric entities, viz. one of *Miogypsina* s.s. and two of *Miogypsinoides*.

With sample JT7124 as a reference we scanned the scatter diagrams of several other samples in Unit III (fig. 20). The *Miogypsinoides* 'clouds' in the samples JT7313 and JT5601, which show hardly any overlap with the *Miogypsina* s.s. clusters (fig. 20), can be classified in group II, marked by specimens with a large embryo. The *Miogypsinoides* in JT5045, which do overlap to a large extent the cloud of *Miogypsina* s.s., probably belong to the type with a small embryo. In JT7314/5 we may be dealing with another mixture of both types of *Miogypsinoides*, comparable to the assemblage in JT7124. The classification of the *Miogypsinoides* specimens in JT7305 is more problematic. The individuals with protoconchal diameters larger than 200 μm are close to the specimens of group II in the sample JT7124. The other *Miogypsinoides* individuals in JT7305 have an intermediate position between the two groups of *Miogypsinoides*, which were distinguished in JT7124. The total association of *Miogypsinoides* in JT7305 seems to be closest to group II in JT7124. The small size of the *Miogypsinoides* associations in Unit III sometimes hampered an unambiguous interpretation of the association in terms of the two *Miogypsinoides* groups in JT7124.

Because of the scarcity of *Miogypsinoides* in most individual samples we compiled all data on this subgenus in Unit III in some scatter diagrams (fig. 21). The data from the two lowermost samples in Unit III have not been entered in these diagrams. The resulting scatters are again interpreted in terms of the two types of *Miogypsinoides*, which have been distinguished in JT7124. The association of individuals with the smaller embryos will be referred to as *Miogypsinoides* I; the other will be named *Miogypsinoides* II. The critical value of D_1 to discriminate between both groups appeared to be 175 μm . It is clear from the scatter diagrams that both *Miogypsinoides* taxa cannot be separated on the basis of X and γ , notwithstanding the modal differences. The groups marked in figure 21 will also be used in the next paragraphs on *Miogypsinoides* of Unit III.

Summarizing, it can be stated that the biometric entities discerned in JT7124 can also be applied to other samples or groups of samples in the range of *Miogypsina* s.s. in Unit III. Solid proof for the existence of more than one biometric *Miogypsinoides* group is not furnished by most samples individually, because of the low relative frequencies.

III.3.2 Preliminary notes on analyses of individual lineages

With regard to the changes in the Miogypsinid time sequence, we have to comment on the spatial relationship of the investigated samples. The coverage with samples for Unit III was accomplished in two sections, the section Donna

Ragusa and the section Lamia. The former covers the basal part of Unit III and the latter the upper part. The amount of overlap between both sample suites could not be clearly established in the field.

However, some lithological and micropaleontological changes were observed during the microscopical investigation of the thin-sections, which have some correlation value. In both the Donna Ragusa and the Lamia sections a decrease in the numbers of glauconitic and phosphatic grains is present (fig. 11). On the basis of this change the sample couple JT7314/5 in the former section can be correlated with about the level of JT5045 in the latter. In both sections a distinct negative shift was also observed in the relative frequencies of

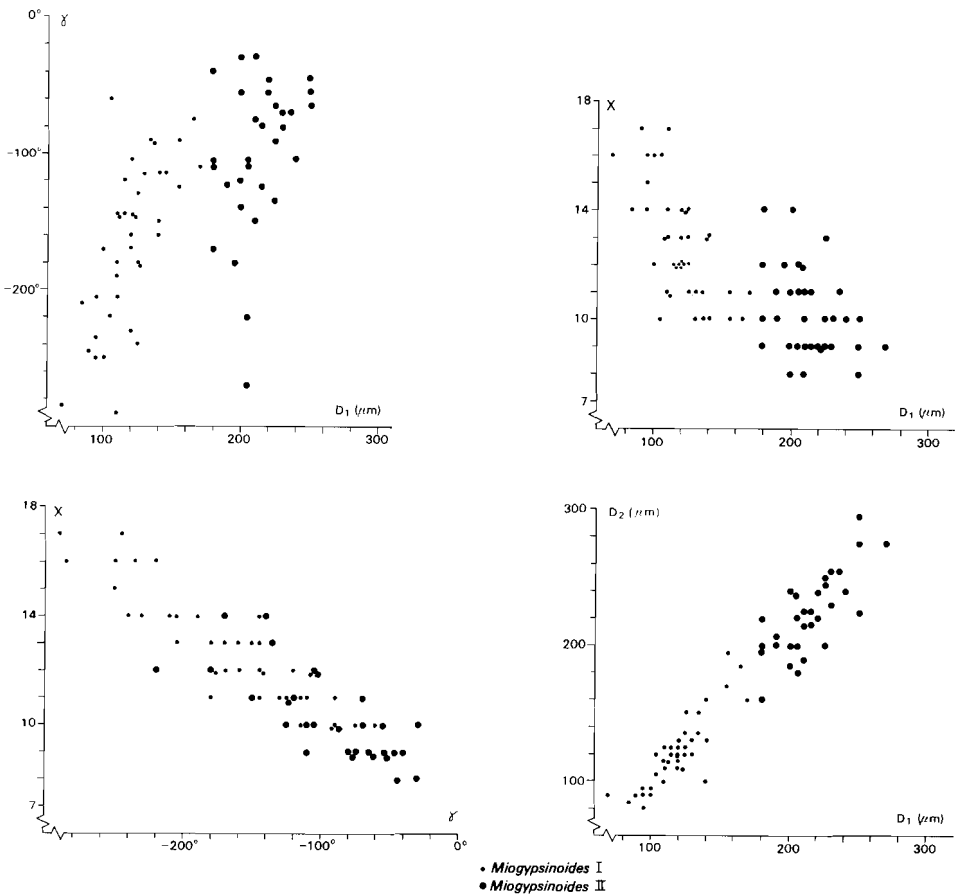
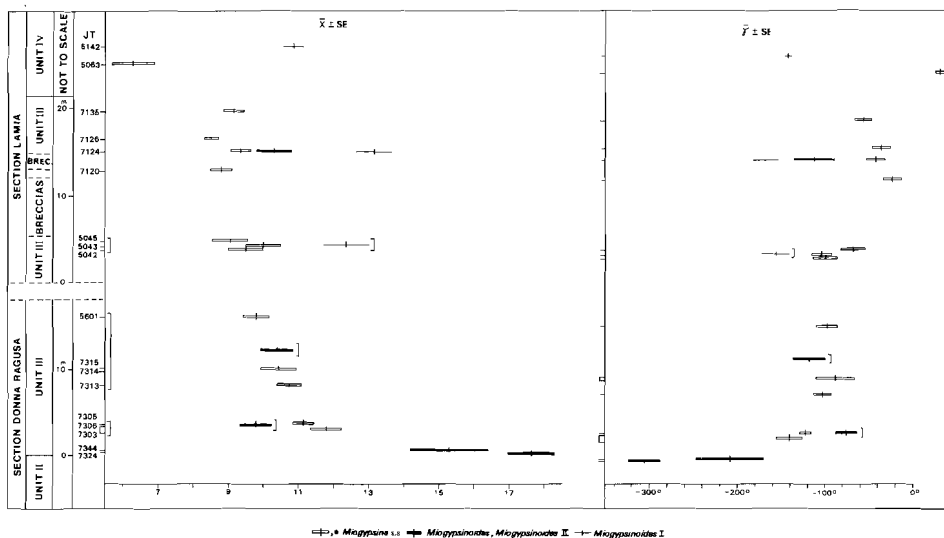


Fig. 21: γ - D_1 , X- D_1 , D_1 - D_2 and X- γ scatter diagrams of the *Miogypsinoidea* specimens co-occurring with *Miogypsina* s.s. in the samples of figure 17, including JT7280 and JT7290.



Pararotalia and *Spiroclypeus*, which resulted in a correlation of JT7314/5 in Donna Ragusa with sample JT5042 in Lamia; this sample level is about one metre and a half below JT5045 (fig. 12). The conclusion is that the amount of overlap of the sample suites of Donna Ragusa up to and including JT7315 and of Lamia is very small or even nil (fig. 9).

For this reason the trend analyses of the various parameters of *Miogypsina* in Unit III were carried out for the sample series in the Donna Ragusa section up to and including JT7315 and the successive sample suite in the Lamia section, but excluding the samples of the brecciated interval. This means that the following samples or sample pairs were not used in the trend analyses: JT5601, JT7280 and JT7290 from Donna Ragusa and JT7115/7969, JT5051/7116, JT5055 and JT5054 from the brecciated interval in Lamia.

The small-scale shifts and trends in the sample means will be termed positive, when they are in line with the literature data on the *Miogypsinidae* (e.g. Drooger, 1963; Raju, 1974). The outcomes of the tests will be labelled negative, when they are against the trends of overall changes, known from the earlier investigations. The tendencies, which we will consider in particular, are the principle of nepionic acceleration and the size increase of the embryo.

The differences between the sample means were checked with the t-test or with the Wilcoxon-test. The latter test was applied, when the frequency distributions of the variables involved deviate too much from the Gaussian curve. The degree of deviation was in turn tested with the help of the χ^2 -test. Only the parameter X needed testing with the Wilcoxon-test, because its data

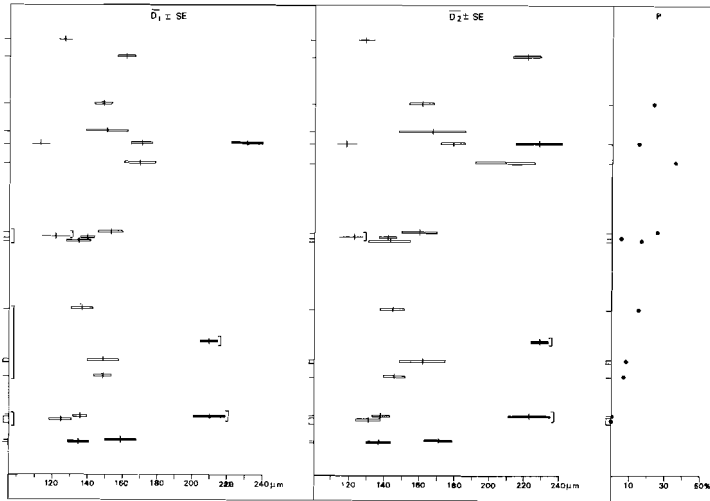


Fig. 22: \bar{X} , \bar{y} , \bar{D}_1 , $\bar{D}_2 (\pm 1 \text{ SE})$ and P of *Miogypsina* in the samples of Unit III. For the sake of convenience we added the means of two samples from Units IV and V. Horizontal bars equal two SE.

frequently appeared to be too skewed for the hypothesis of normal distributions.

Pairs of sample means were selected for the Wilcoxon- and the t-tests, to provide us with a good, overall picture of the small-scale changes, present in the time series of *Miogypsina*. The differences between samples at large stratigraphical distances were not given special attention, because the direction of the change is probably the same as the direction of the overall trend. If a significant shift was suspected to be present in one variable, all parameters of the sample couplet under consideration were tested. On the other hand no tests were applied to sample pairs, which do not show marked, visual differences in any variable.

III.3.3 *Miogypsinoidea*

Changes in the sample means

The two basal assemblages of *Miogypsinoidea*, which are not yet associated with *Miogypsina* s.s. specimens, show a distinct, positive shift in the nepionic and in the embryonic parameters (table 2).

These changes are not unequivocally continued in the younger series of *Miogypsinoidea* (fig. 22). Concerning the statistic \bar{X} , types I and II in the samples from JT7306 upwards seem to represent a more advanced stage of *Miogypsinoidea* with respect to the associations in JT7324 and JT7344. On the other

hand no further consistent significant change was observed in $\bar{\gamma}$ for the same set of associations of *Miogypsinoides*. The mean embryo diameters of the two types of *Miogypsinoides* in the younger samples show opposed changes relative to the assemblage in JT7344. *Miogypsinoides* I is marked by a drop in \bar{D}_1 and \bar{D}_2 , whereas these means increase significantly towards *Miogypsinoides* II (fig. 22, table 2). In the sequence of *Miogypsinoides* assemblages co-occurring with *Miogypsina* s.s. no distinct further changes are apparent; both in type I and in type II the differences between the parameter means are too small relative to the values of their standard errors to be of statistical significance (fig. 22).

Care must be taken in evaluating the above statements on the two *Miogypsinoides* types, because they may be biased by too low frequencies.

Sample couple	Wilcoxon- test \bar{X}	$\bar{\gamma}$		t-test			
		$\bar{\gamma}$	df	\bar{D}_1	df	\bar{D}_2	df
JT7344-JT7124 (type II)	-2.87++	1.67	16	5.03	20++	3.79	17++
JT7344-JT7124 (type I)	-1.73+	1.13	30	-4.88	32--	-5.30	29--
JT7324-JT7344	-2.22+	2.75	40++	2.41	43+	2.86	40++

Table 2: Results of the t-test and the Wilcoxon-test of the observed differences between the samples of *Miogypsinoides*; levels of significance: P = 0.01 (+ + / - -), P = 0.05 (+ / -); degrees of freedom in t-test: df = N₁ + N₂ - 2; N₁ + N₂ = sum of observations in both samples.

Qualitative shifts in the morphotype composition

Before entering into details of the morphotype shifts in *Miogypsinoides*, we must point out a general aspect of the qualitative changes in the frequency distributions, which is of importance for our *Miogypsina* assemblages in general. The frequency of a morphotype just after its appearance or just before its disappearance in the biostratigraphical record is very low. The chance of an erratic loss of such a low-frequency type by sampling hazards is relatively large and consequently there is an influence on the precise determination of the entry or exit level of a specific morphotype.

In the following description we made no distinction between the two types of *Miogypsinoides*, which were introduced in paragraph III.3.1.

Alterations in the morphotype ranges are distinctly present in the nepionic variables (table 3), which correspond to the changes in the sample means (fig. 22). The changes in the ranges of the embryo diameters are much vaguer. With respect to the lowermost sample JT7324 the total range of morphotypes

in D₁ seems to expand both at the lower end and at the upper end of the variation, with one and four classes respectively, but there is very little change above the lowermost two samples. In D₂ we failed to show a clear change in the range.

	X	γ
Exits	28 - 18	-660° - -300°
Entries	10 - 8	-120° - 0°

Table 3: Entries and exits of X- and γ -morphotypes of *Miogypsinoides* in Unit III.

Biometric-taxonomical classification

For the classification scheme we refer to the compilation of Drooger (1963). The biometric species, we identified, are listed in table 4, together with the necessary data for the determinations.

The oldest association of *Miogypsinoides* was identified as *M. complanata*, which is succeeded by *M. formosensis* in JT7344. The determination of the assemblages, co-occurring with *Miogypsina* s.s., center around *M. bantamensis*. Type II assemblages are classified as *M. ex. interc. bantamensis-dehaartii* and those of type I are named *M. ex. interc. formosensis-bantamensis*.

Section	Sample/ sample suite	\bar{X}	SE	N	<i>Miogypsinoides</i> / <i>M. ex. interc.</i>
L	JT7124	10.3	0.52	7	(<i>bantamensis-dehaartii</i>)
A	(type II)				
M	JT7124	13.2	0.48	19	<i>formosensis-bantamensis</i>
I	(type I)				
A	JT5042/5 (type I)	12.3	0.71	9	(<i>formosensis-bantamensis</i>)
D R	JT7313/5/5601	10.4	0.47	12	<i>bantamensis-dehaartii</i>
O A	(type II)				
N G	JT7305/6	9.8	0.44	10	(<i>bantamensis-dehaartii</i>)
N U	(type II)				
A S	JT7344	15.3	1.08	14	<i>formosensis</i>
A	JT7324	17.63	0.63	30	<i>complanata</i>

Table 4: Species list of *Miogypsinoides* and pertinent, biometric data; N = number of observations on X in a sample or a sample suite; if N < 11 then the name is presented in parentheses.

Correlations in separate assemblages

The oldest assemblage of *Miogypsinoidea*, JT7324, reveals clearly significant correlations ($P = 0.01$) for all combinations of the parameters. In the next sample, JT7344, only D_1 - D_2 and X - γ are significantly correlated at the level of $P = 0.01$ (table 5, fig. 23). The other pairs of parameters covary more weakly in this association ($P = 0.05$) or are even devoid of significant correlation.

Usually the numbers of *Miogypsinoidea* specimens in the samples of the younger part of Unit III are too low to provide meaningful coefficients of correlation. Only *Miogypsinoidea* I in JT7124, in which sufficient individuals of this type are present, shows well correlated variables (table 5).

To have some notion of the association of the various couples of parameters in *Miogypsinoidea* I and II, we show several scatter diagrams, in which all specimens of both groups are presented (fig. 21). As usual, we see that X - γ and D_1 - D_2 are well correlated. The correlations between the nepionic and the embryonic parameters are not that obvious; type I shows weak covariations for the various combinations of nepionic and embryonic variables, whereas no such association is apparent for type II.

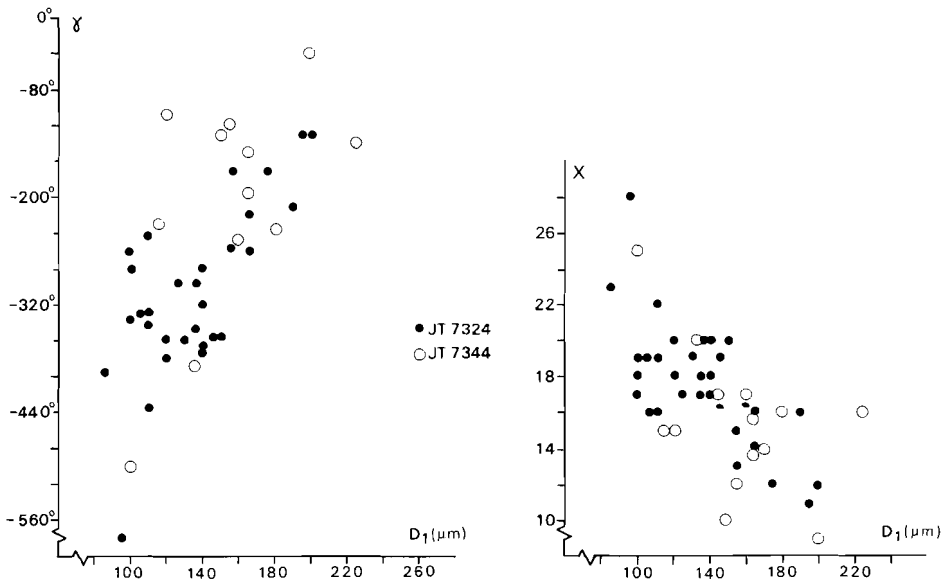


Fig. 23: Scatter diagrams of γ - D_1 and X - D_1 for *Miogypsinoidea* in the two lowermost samples of Unit III.

Sample		X- γ	X-D ₁	X-D ₂	γ -D ₁	γ -D ₂	D ₁ -D ₂
JT7324	r	-0.96	-0.71	-0.71	0.70	0.68	0.89
	N	30	30	30	30	30	30
		--	--	--	++	++	++
JT7344	r	-0.93	-0.49	-0.24	0.57	0.26	0.77
	N	12	14	11	12	11	12
		--	-		+		++
JT7124 (type I)	r	-0.95	-0.65	-0.72	0.67	0.70	0.92
	N	19	19	19	19	19	19
		--	--	--	++	++	++
JT7124 (type II)	r	-0.79	-0.83	-0.55	0.92	0.85	0.83
	N	6	7	7	6	6	7
		-	-		++	+	+

Table 5: Correlation of the parameters in single samples; $df = N - 2$; $N =$ pairs of observations; r-test is one-sided; $P = 0.01$ (+ + / - -), $P = 0.05$ (+ / -).

III.3.4 *Miogypsina s.s.*

Trends

Overall changes in the parameters of *Miogypsina s.s.* in Unit III (fig. 22) were determined by testing the correlation between the parameter means and the ranking numbers of the samples (cf. M.M. Drooger et al., 1979). The results of the r-test are listed in table 6.

All parameters show significant, positive trends, which means they are in line with the classical tendencies in the *Miogypsinids*: nepionic acceleration and embryonic size increase. \overline{D}_2 is the only statistic, which is not significantly correlated with the ranking number at a significance level of 0.01.

The partial trends in the upper part and the lower part of Unit III are not identical. In the section Donna Ragusa the trends are the same as the overall trends in Unit III, whereas in the section Lamia only $\overline{\gamma}$ still shows a significant trend in agreement with the overall change. Evidently, the significance of the overall trends is largely due to the data from the lower part of Unit III.

$\overline{D}_2/\overline{D}_1$, the ratio of the means of the embryonic diameters shows no distinct trend in Unit III ($r = 0.43$, $df = 9$, $P = 0.05$).

The overall changes in the values of P, the relative frequency of individuals with two principal auxiliary chambers, was not tested statistically. From the graph of P (rightmost column in fig. 22) we infer that this variable tends to increase upward in Unit III. The two lower assemblages of *Miogypsina s.s.* do not yet contain specimens with two P.A.C., whereas P attains values ranging from 15% to 36% in the upper part of Unit III.

Stratigraphic interval	N	\bar{X}	$\bar{\gamma}$	\bar{D}_1	\bar{D}_2
Total Unit III	11	-0.91 --	+0.89 ++	+0.69 ++	+0.65 +
Section Donna Ragusa	4	-0.98 -	+0.99 ++	+0.99 ++	+0.98 +
Section Lamia	7	-0.60	+0.73 +	+0.45	+0.41

Table 6: Trends in the various means of *Miogypsina* s.s. in Unit III tested with the t-test; df = N - 2; N = number of samples; test carried out one-sided; tested levels of significance: P = 0.01 (++/--), P = 0.05 (+/-).

Small-scale changes

In table 7 the results of the statistical tests are presented. All parameters are subject to positive shifts, which are most frequently shown by γ . Sometimes, setbacks occur as well, namely in the upper part of Unit III. Only for the embryonic size parameters the changes opposite to the overall trend attain a high significance level (P = 0.01). A significant change in a parameter is usually not accompanied by a significant shift in the other three variables of the same sample pair (table 7).

Qualitative shifts in the morphotype composition

For a general remark on changes in the morphotype composition, we refer to the previous description of *Miogypsinoïdes*.

The ranges of the morphotypes in *Miogypsina* s.s. were deduced from the histograms in figures 17 and 24. A recapitulation of the first and the last appearances in the nepionic variables X and γ is given in table 8.

The shifts in the ranges of X and γ are compatible with the overall trends of the sample means. The pattern of the successive entries and exits is not markedly systematic, which - as was explained earlier - may be due to the low relative frequencies of the types just after their origin or just before their real exit. The change in the variation of the diameters of the protoconch and the deuteroconch is not conspicuous. Both diameters are marked by a net gain and loss of one class of observations.

All frequency distributions of V in figure 24 represent samples from the upper part of Unit III in the section Lamia. In the lower part of Unit III there are no or very few individuals with a second nepionic spiral, viz. one per sample at a maximum in Donna Ragusa. Despite these low frequencies, the variation in the observational values is relatively large in the lower interval. In the

Sample couple	Wilcoxon-test		t-test				
	\bar{X}	$\bar{\gamma}$	df	\bar{D}_1	df	\bar{D}_2	df
JT7126-JT7135	1.23°	-0.82	31°	-0.21	36°	-0.37	30°
JT7124-JT7135	-0.29°	-0.92	53°	-2.84	63--	-1.79	54-
JT7120-JT7135	0.53°	-1.80	37-	-2.28	43-	-3.27	34--
JT7120-JT7124	0.78°	-1.11	38°	0.07	46°	-1.86	38-
JT5045-JT7124	0.07°	1.43	42°	1.62	48°	1.34	43°
JT5045-JT7120	-0.92°	2.34	26+	1.37	28°	2.52	23+
JT5043-JT7120	-2.25°	0.74	30++	3.42	32++	4.48	23++
JT5043-JT5045	-1.21°	2.06	34+	2.06	34+	1.67	28°
JT5042-JT7135	-0.41°	2.22	36+	1.63	41°	1.40	35°
JT5042-JT5045	-0.35°	1.58	25°	2.04	24+	1.15	24°
JT7314/5-JT5045	-1.53°	0.83	25°	0.54	27°	-0.04	23°
JT7314/5-JT5042	-1.26°	-0.44	20°	-1.28	23°	-1.06	19°
JT7313-JT5045	-2.40++	2.08	40+	1.36	44°	1.36	36°
JT7313-JT5601	-1.89+	0.29	44°	0.99	45°	-0.08	35°
JT7305-JT7314/5	-1.14°	1.98	38+	1.52	40°	2.01	37+
JT7305-JT7313	-0.67°	1.70	53+	1.31	55°	0.99	55°
JT7303/6-JT7313	-1.64°	2.23	41+	2.62	43++	1.68	37°
JT7303/6-JT7305	-0.93°	1.24	44°	1.52	44°	0.86	43°

Table 7: Significance of the observed differences between the sample means of *Miogypsina* s.s. in Unit III, tested by a one-sided t- or Wilcoxon-test; df for t-test = $N_1 + N_2 - 2$; $N_1 + N_2$ = sum of observations in both samples; significance levels; P = 0.01 (+ + / - -), P = 0.05 (+ / -); no significant result: (°).

	X	γ
Entries	8, 7, 6, 5	-30° - +60° (3 classes)
Exits	16, 15	--- ---
Dwindling frequencies	14, 13, 12	-270° - -150° (4 classes)

Table 8: Entries and exits of morphotypes in *Miogypsina* s.s. of Unit III.

associations up to JT5042 the classes in the range from 40 to 80 are already present. The next higher class, 80 - 90, appears in JT5045. While the range of V is large in Unit III, the relative frequencies of the various morphotypes remain low. (The samples from the breccia zone were left aside in the former statement.)

Biometric-taxonomical classification

The biometric classification scheme of the *Miogypsinids* of Drooger (1963) will be used to identify the assemblages of *Miogypsina* s.s. For more details on *M. socini*, which appeared to be present in the breccia zone, we refer to Drooger (1954a).

A review of the determinations is provided in table 9, which includes also the relevant, statistical data of the *Miogypsina* s.s. associations. The samples from the breccia zone are listed separately in the lower part of the table.

The dominant species of *Miogypsina* s.s. in Unit III is *M. gunteri*, which is transitional to *M. tani* in the upper part of the Lamia section.

Several, remarkable assemblages were derived from the breccia interval in the Lamia section. *Miogypsina* s.s. in sample JT7115/7969 is in good harmony with the determinations in the upper part of Unit III; it was identified as an intermediate of *M. gunteri* and *M. tani*. In the other samples from the breccias we met with *M. tani* (JT5055), *M. socini* (JT5054) and a transitional assemblage between these two species (JT5051/7116).

Miogypsina s.s. in JT5054 conforms very well to the diagnosis of *M. socini* (Drooger, 1954a; see also chapter VI). Unfortunately, we have no good idea of the original, stratigraphical position of the samples from the breccia zone. Anyhow, they are younger than the stratigraphical level of JT5045.

Section	Sample	\bar{X}	SE	N	P(%)	σ_p	N _{CT}	<i>Miogypsina</i> / <i>M. ex. interc.</i>
L	JT7135	9.2	0.31	26	23	7.6		<i>gunteri-tani</i>
	JT7126	8.5	0.22	6	29	17.1		(<i>gunteri-tani</i>)
A	JT7124	9.3	0.27	30	15	6.1		<i>gunteri</i>
M	JT7120	8.8	0.29	10	36	12.8		<i>gunteri-tani</i>
I	----- B R E C C I A Z O N E -----							
A	JT5045	9.1	0.50	16	26	11.0		<i>gunteri-tani</i>
	JT5043	10.0	0.51	19	5	4.9		<i>gunteri</i>
	JT5042	9.5	0.50	12	17	10.8		<i>gunteri</i>
D R	JT7290	9.9	0.47	25	8	4.7		<i>gunteri</i>
O A	JT7280	10.6	0.63	14	7	6.8		<i>gunteri</i>
N G	JT5601	9.8	0.37	20	15	8.0		<i>gunteri</i>
N U	JT7314/5	10.5	0.51	11	8	7.5		<i>gunteri</i>
A S	JT7313	10.8	0.33	24	7	4.8		<i>gunteri</i>
	JT7305	11.2	0.31	29	0	–		<i>gunteri</i>
	JT7303/6	11.8	0.46	17	0	–		<i>gunteri</i>
BRECCIA	JT5054	8.3	0.28	31	59	8.7	3	<i>socini</i>
	JT5055	7.7	0.22	16	39	10.2		<i>tani</i>
ZONE	JT5051/7116	8.7	0.29	13	44	12.4	2	<i>tani-socini</i>
	JT7115/7969	8.9	0.30	15	29	9.9		<i>gunteri-tani</i>

Table 9: List of identified, biometric species of *Miogypsina* s.s. and relevant, statistical data; N = number of observations on X in one sample; N_{CT} = number of specimens with a non-peripheral embryo; σ_p = standard deviation of P; if N < 11, the species name is printed in parentheses.

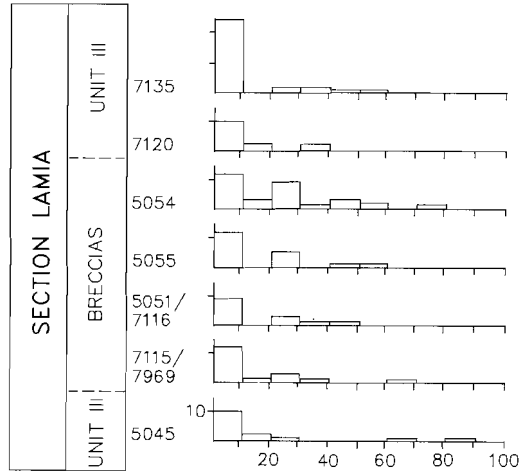


Fig. 24: Histograms of V for some samples of *Miogypsina* s.s. in Unit III.

Correlations

Both the X- γ and D₁-D₂ combinations of *Miogypsina* s.s. are distinctly correlated in about 80% and 100% of the total number of associations, negative and positive respectively (fig. 25). Less evident are the links between the nepionic and embryonic variables. A significant negative result of the r-test ($P = 0.01$) for X and D₁ or X and D₂ occurs in about 40% of the samples and about 60% of the associations have a distinct positive relation between γ and the diameters of the embryonic chambers.

A number of scatter diagrams in figure 27 illustrate the intensity of the covariation between X and D₁ and γ and D₁.

The correlation data from Donna Ragusa and from Lamia were also considered separately (table 10). Except for D₁-D₂, the relative number of significant correlations ($P = 0.05$) tends to be smaller in Lamia, the upper part of Unit III.

The sample means are without exception distinctly correlated at a significance level of 0.01 (fig. 26). A graphical presentation of the covariation between the means is provided in fig. 28. The individual correlation tests for the Donna Ragusa section and the Lamia section did not reveal largely different results, except for the couples $\overline{X-D_1}$ and $\overline{X-D_2}$, which are not correlated in Lamia (table 11).

P=0.05 P=0.01	X	γ	D ₁	D ₂
X	X	-80	-60	-70
γ	-80	X	+75	+75
D ₁	-40	+60	X	+100
D ₂	-35	+65	+100	X

Fig. 25: Percentage of significant correlation values ($P = 0.05$ or $P = 0.01$) of *Miogypsina* s.s. assemblages in Unit III. +75 means positive correlation in 75% of the samples; number of samples = 17.

Section	N	D ₁ -D ₂	X- γ	X-D ₁	X-D ₂	γ -D ₁	γ -D ₂
Lamia	10	10	7	4	6	7	6
Donna Ragusa	7	7	7	6	6	6	7

Table 10: Number of samples with a significant correlation ($P = 0.05$) for specific pairs of variables of *Miogypsina* s.s. in Unit III of the sections Donna Ragusa and Lamia.

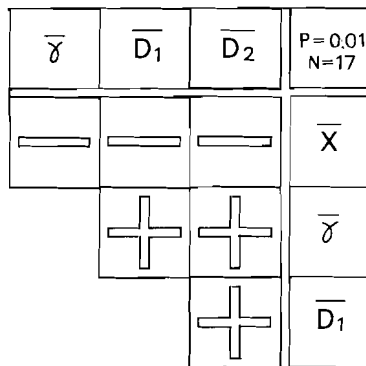


Fig. 26: Diagram showing the correlations between the various sample means of *Miogypsina* s.s. in Unit III.

Section	N	$\overline{X-\bar{\gamma}}$	$\overline{X-D_1}$	\overline{X}	$\overline{D_2}$	$\overline{\gamma-D_2}$	$\overline{D_1-D_2}$
Lamia	7	-	°	°	++	++	++
Donna Ragusa	4	--	--	-	++	+	+

Table 11: Correlation between the samples means of *Miogypsina* s.s. in Unit III of the Donna Ragusa section (JT7303-7315) and in the Lamia section (samples breccia zone excluded); $P = 0.01$ (+ + / - -), $P = 0.05$ (+ / -); r-test was executed one-sided; no significant correlation: (°).

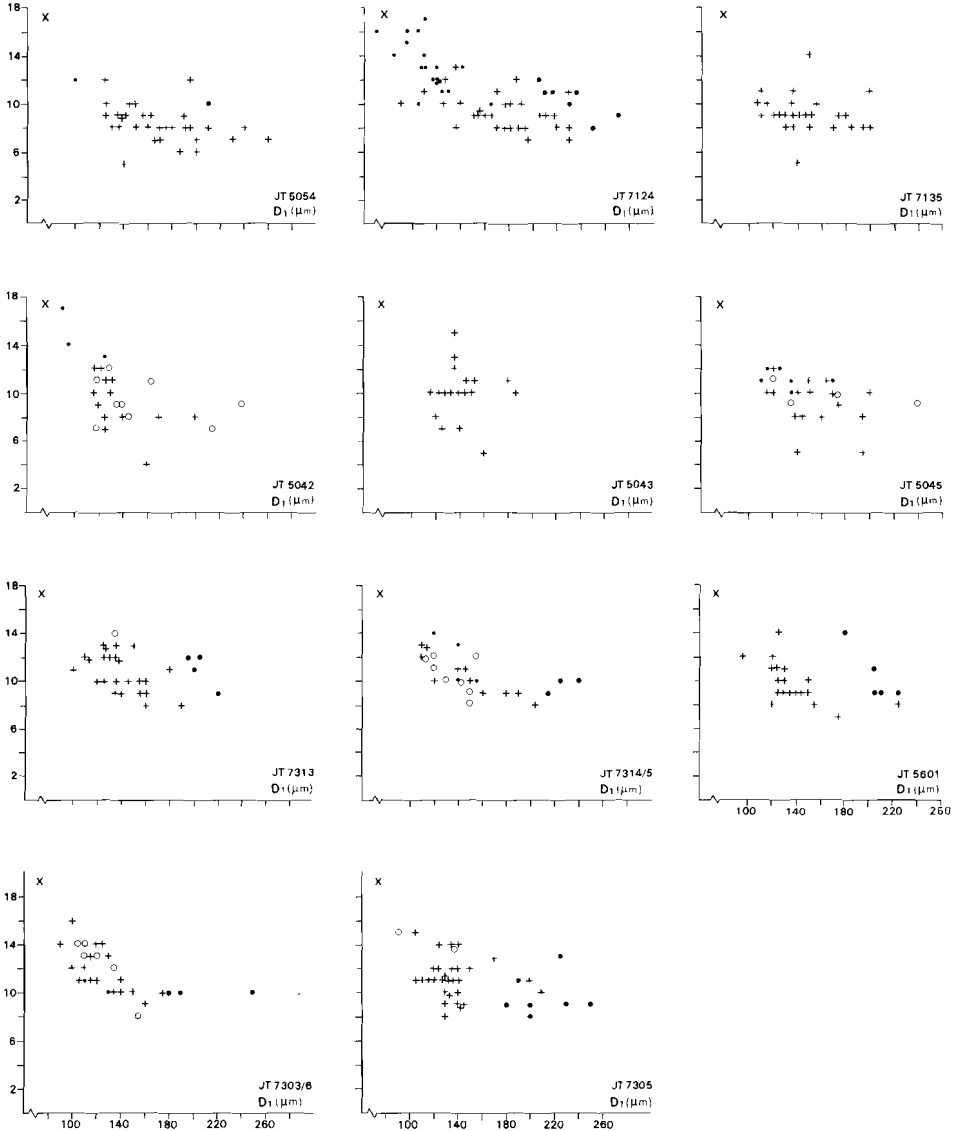
III.3.5 Comparison of the various biometric species units

Reviewing the analyses of the sample means, it becomes clear that the principle of nepionic acceleration is applicable to the total data set of Unit III. In fact only once a conflicting shift was noted, namely a negative one in $\bar{\gamma}$ of *Miogypsina* s.s. (table 7). The positive tendencies in $\overline{D_1}$ and $\overline{D_2}$ are not as straightforward as in \overline{X} and $\bar{\gamma}$. The embryonic diameters of *Miogypsina* s.s. in their lowermost associations and of *Miogypsinoidea* I in the same samples show a significant, negative shift with respect to *M. formosensis* in JT7344. By contrast, *Miogypsinoidea* II is marked by a positive change in these statistics. No distinct differences are apparent between $\overline{D_1}$ and $\overline{D_2}$ of *Miogypsinoidea* I and of *Miogypsina* s.s. from the lower part of the section.

The possibility of different development rates of \overline{X} and $\bar{\gamma}$ in the co-occurring *Miogypsina* s.s. and *Miogypsinoidea* is difficult to evaluate, because of too scanty information on the latter subgenus. Some statistical tests confirm the conclusion that may be gained from fig. 22. Both \overline{X} and $\bar{\gamma}$ of *Miogypsina* s.s. show a progressive trend, while the few data on *Miogypsinoidea* I and II suggest stability for both in the same interval. *Miogypsinoidea* I is always more primitive at comparable stratigraphical levels, whereas *Miogypsinoidea* II seems to shift from relatively somewhat more advanced than *Miogypsina* s.s. at the lowermost JT7305 level to more conservative in the JT7124 sample.

To gain more insight in the possible relationships between the four biometric entities, i.e. the primitive *Miogypsinoidea*, *Miogypsinoidea* I, *Miogypsinoidea* II and the co-occurring *Miogypsina* s.s., we made two scatter diagrams of $X-D_1$ and $\gamma-D_1$ (fig. 29), in which the variation of the four groups is illustrated by the individuals of selected samples. The diagrams show that the group of *Miogypsinoidea* II is in line with the longer axis of the cluster of the older *Miogypsinoidea* stock. The data cloud of the most primitive *Miogypsina gunteri* assemblage, JT7303/6, almost completely coincides with that of *Miogypsinoidea* I. The clusters of the older *Miogypsinoidea* and *Miogypsinoidea* II and those of *Miogypsina* s.s. and *Miogypsinoidea* I cover different, but parallel fields in the scatter diagrams with only a narrow zone of overlap.

The scatter diagrams of the means (fig. 28) show that all four taxa fit in with a single line for the embryonic ($\bar{D}_1-\bar{D}_2$) and the nepionic ($\bar{X}-\bar{\gamma}$) features. In the combinations ($\bar{X}-\bar{D}_1$ and $\bar{\gamma}-\bar{D}_2$) the two groups are apparent again. *Miogypsinoides* II could well be the regular continuation of *M. complanata* and *M. formosensis*, whereas the other two groups could have originated from such a line



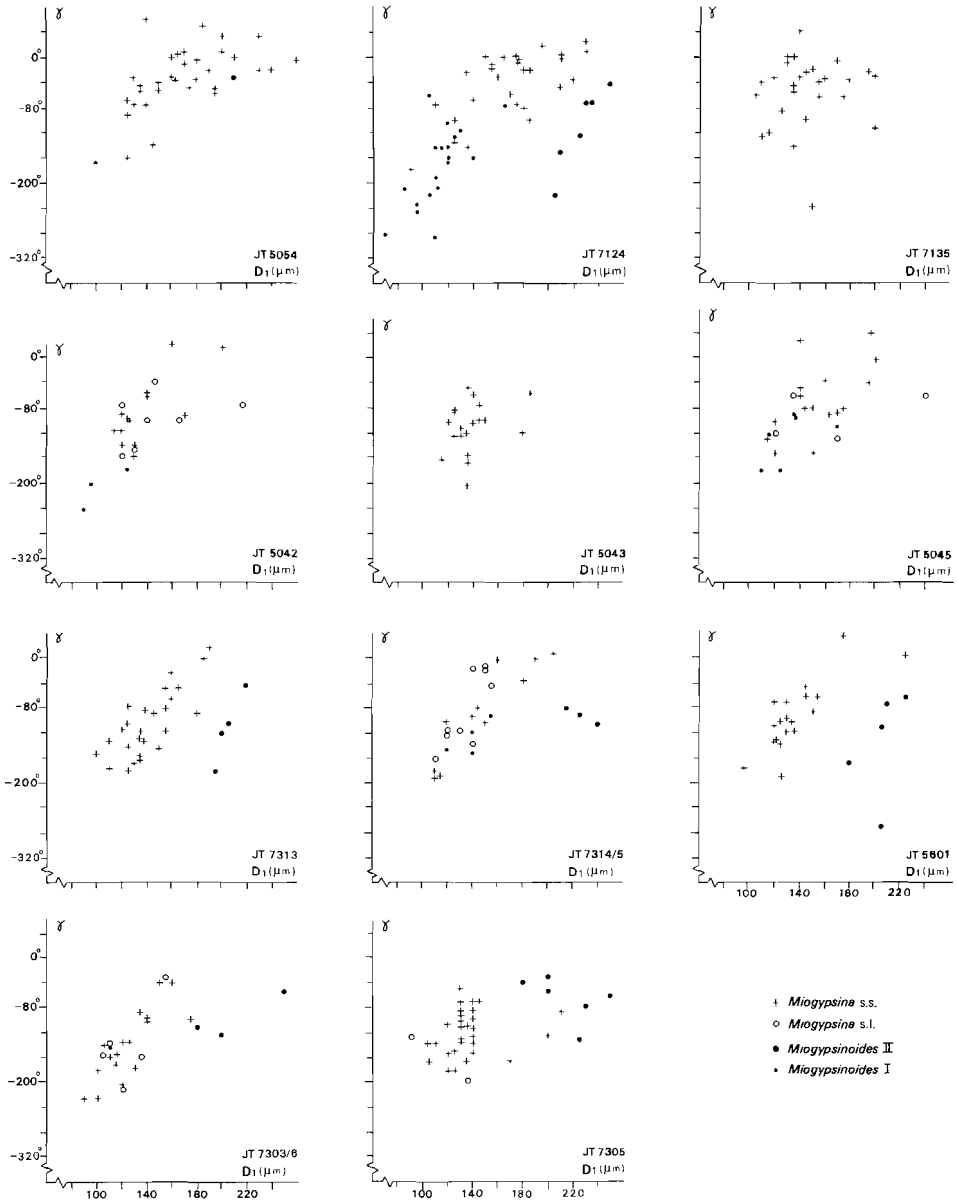


Fig. 27: Scatter diagrams of $X\text{-}D_1$ (left page) and $\gamma\text{-}D_1$ (right page) for various samples of *Miogypsina* in Unit III.

after a rapid drop in embryo size, each of the two following its own line of development afterwards.

It is the *Miogypsinoidea* I group which is new to the literature; the connections between the other three groups have been suggested before (Drooger & Raju, 1973).

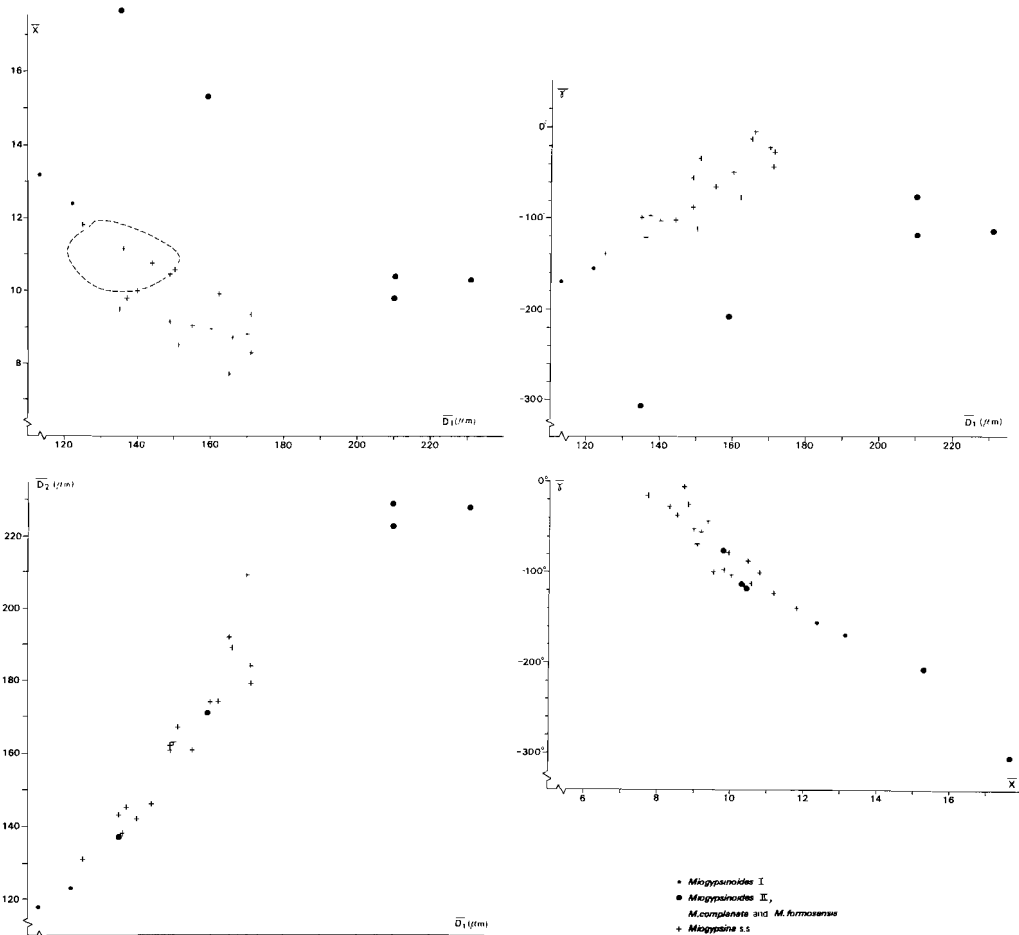


Fig. 28: $\bar{X}-\bar{D}_1$, $\bar{\gamma}-\bar{D}_1$, $\bar{D}_2-\bar{D}_1$ and $\bar{\gamma}-\bar{X}$ scatter diagrams of all *Miogypsina* assemblages of Unit III. Dashed line scatter periphery of *Miogypsinoidea* in Units IV and V.

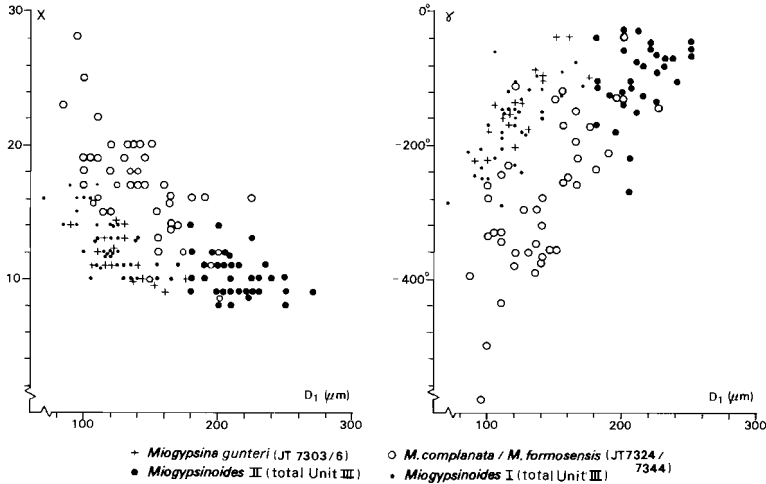


Fig. 29: X- D_1 and γ - D_1 scatter diagrams for selected samples of *M. complanata-formosensis*, *Miogypsinoides* II, *Miogypsinoides* I and *Miogypsina gunteri*.

III.4 THE MIOGYPSINIDAE IN UNITS IV AND V

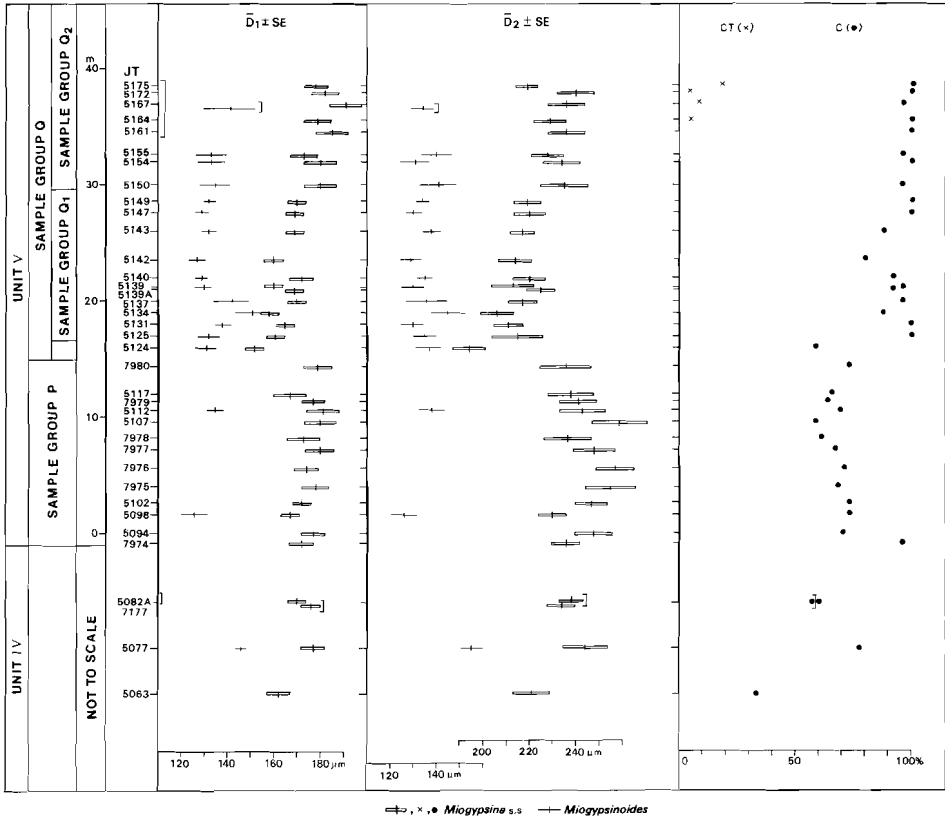
III.4.1 Introduction

The samples studied from the upper transgression-regression cycle were mainly derived from the upper coarse interval, our Unit V. A few are from Unit IV, amongst which only one sample represents the relatively thin somewhat coarser lower part of this unit.

As the separation of *Miogypsina* s.s. and *Miogypsinoides* in Unit V is evident both from the side-wall character and from the differences in the nepionic configuration, we will refrain from a preliminary discussion on the heterogeneity in the Miogypsinid assemblages.

Rare representatives of a third taxon, *Miolepidocyclina*, which appeared to have an aberrant, poor preservation of the test, were also encountered in some parts of Unit V. The specimens of this subgenus are always intensively recrystallized and for this reason they are interpreted as non-contemporaneous, reworked elements in the associations. All specimens of *Miolepidocyclina* possess a well-centered, nepionic apparatus, of which measurements point to an association in the range of *M. burdigalensis*. The individuals of this species will not be incorporated in the statistical data processing. The statistical procedure is about the same as that carried out for the Miogypsinids in Unit III.

First of all the trends in the subgenus under consideration will be analysed.



In the tests for overall changes we entered the actual, stratigraphical heights of the samples instead of using their ranking numbers, as was done for *Miogypsina s.s.* in Unit III. The position of the levels of sampling in the Units IV and V could be determined more accurately. Stratigraphically this method is a more realistic approach than the test with the ranking numbers. In addition, partial trends were computed for specific intervals of the *Miogypsina s.s.* time sequence.

Secondly, the small-scale changes in the sequences of means will be discussed. The Wilcoxon-test was applied to those variables, which appeared to be not normally distributed. Otherwise the t-test was used. The goodness-of-fit to a Gaussian distribution was again tested with the χ^2 -test. For *Miogypsina s.s.* the X-values usually deviate significantly from a normal distribution ($P = 0.01$). In *Miogypsinoidea* X and γ are the parameters that deviate relatively frequently. These parameters were always subjected to the Wilcoxon-test. The t-test was applied to the remainder of the variables. If in individual cases a distribution deviated too much from the Gaussian curve, the Wilcoxon-test was executed as well. This holds only for *Miogypsina s.s.*

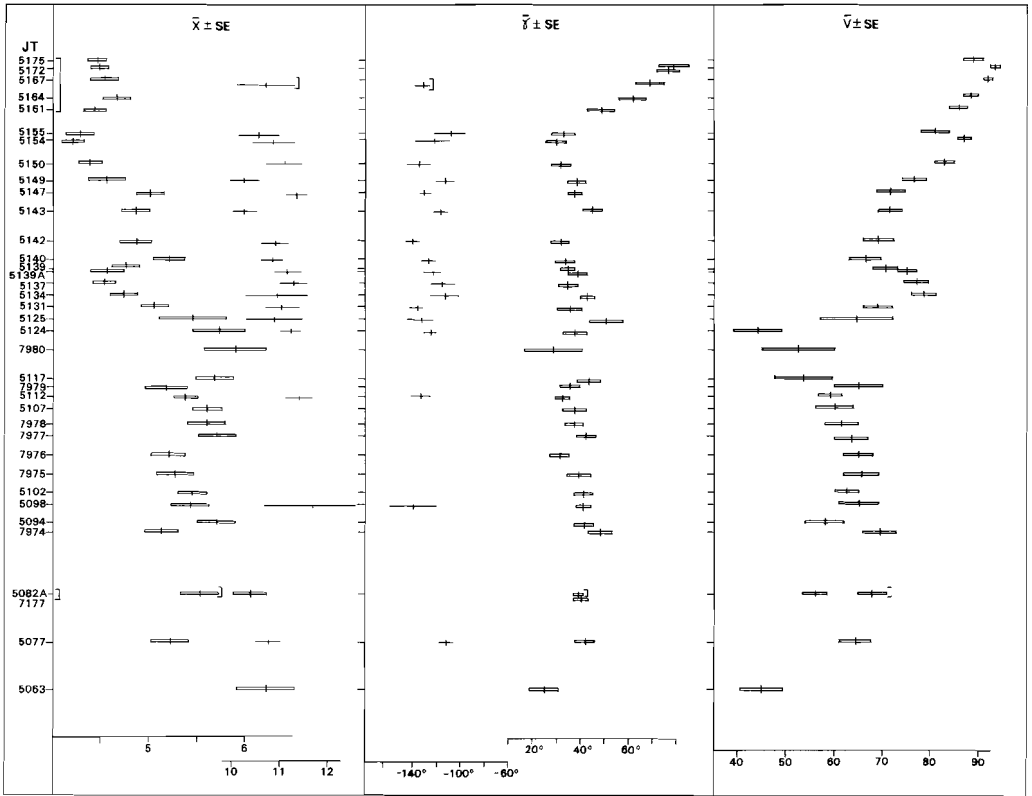


Fig. 30: \bar{X} , $\bar{\gamma}$, \bar{D}_1 and \bar{D}_2 (\pm SE) for *Miogypsina* s.s. and *Miogypsinoides* in Units IV and V of the section Lamia. For *Miogypsina* s.s. \bar{V} , CT and C have been figured too. Note that the samples in Unit IV have not been spaced relative to the stratigraphical distances.

III.4.2 Miogypsinoides

Trends

Distinct, overall changes are not present in *Miogypsinoides* (fig. 30, table 12). \bar{D}_2 is the only parameter, which exhibits a weak, negative trend ($P = 0.05$). This negative overall shift in \bar{D}_2 is probably caused by the relatively large value of \bar{D}_2 in the lowermost sample of *Miogypsinoides*, JT5077 (fig. 30).

Small-scale changes

Miogypsinoides in Units IV and V is distinctly smaller in \bar{X} than its counterpart in Unit III, referred to as *Miogypsinoides* I. No differences ($P = 0.01$) are

N	\bar{X}	$\bar{\gamma}$	\bar{D}_1	\bar{D}_2	\bar{D}_2/\bar{D}_1
18	-0.29 °	-0.08 °	-0.27 °	-0.49 -	-0.27 °

Table 12: Statistical significance of the trends in the means of *Miogypsinoides* in Units IV and V; N = number of samples; P = 0.05 (-), no significant result (°).

evident between the other variables of the associations of *Miogypsinoides* in Unit III (JT7124 as an example) and in Unit V (JT5142, bottom line in table 13).

Fluctuations (P = 0.01) in the nepionic variables were recorded from Unit V in the interval JT5137 to JT5149; once a shift was observed in $\bar{\gamma}$ and three times in X. The diameter of the protoconch shows a significant, upward decrease in the zone JT5134-JT5142 (P = 0.01). At this significant level there is no such a change in \bar{D}_2 . The comparison of the lowermost sample JT5077 and the upper samples JT5155 and JT5161/75 illustrates that no net shifts of importance occurred in the sample means of *Miogypsinoides*.

In addition, it appears from table 13 that a significant change in one parameter is usually not accompanied by a statistically distinct shift in another.

Qualitative shifts

Compared with *Miogypsinoides* I in Unit III two classes in X, γ and D_1 have disappeared from the range of *Miogypsinoides* in Units IV and V. Because the exact position of the morphometric boundary between *Miogypsinoides* I and II in Unit III is disputable, it is of little or no use to speculate on entries of morphotypes.

The morphological range of *Miogypsinoides* in the Units IV and V is variable, but there is no overall, qualitative shift (fig. 31).

Biometric determination of the species

In all samples (table 14) but two we found an association determinable as *M. bantamensis*. By strictly applying the rules, the assemblages in JT5143 and JT5149 are intermediate between the latter species and *M. dehaartii*, but biometrically they are not really different from the others.

Covariation

Both nepionic variables show significant correlations (P = 0.01) in most samples and so do both embryonic variables (fig. 32). Usually X is not clearly

Sample pair	\bar{X}	$\bar{\gamma}$	\bar{D}_1	df	\bar{D}_2	df
JT5155-JT5161/75	0.15	-0.81	0.61	18	-0.57	17
JT5149-JT5150	1.82-	-1.48	0.40	36	0.95	33
JT5147-JT5149	-2.60++	1.74+	0.71	42	0.87	40
JT5143-JT5147	2.45--	-1.57	-0.50	41	-1.53	41
JT5142-JT5143	-1.30	2.56++	0.95	44	1.44	44
JT5137-JT5143	-2.41++	0.40	-1.27	32	0.21	32
JT5134-JT5142	0.16	-1.61	-3.31	31--	-1.63	31
JT5134-JT5139A	0.36	-0.81	-2.93	32--	-1.53	31
JT5131-JT5134	-0.44	1.54	1.68	28	1.60	28
JT5124-JT5134	-0.53	0.83	2.19	35+	0.68	33
JT5124-JT5131	-0.21	-1.32	0.92	45	-0.94	43
JT5112-JT5140	-1.38	0.55	-1.11	34	-0.47	32
JT5077-JT5161/75	-0.38	-1.56	-0.63	32	-2.44	31-
JT5077-JT5155	-0.52	0.06	-1.93	36-	-1.89	34-
JT5077-JT5112	1.18	-1.77-	-1.89	36-	-2.15	34-
JT7124-JT5142*	-3.56++	1.38	2.34	40+	-1.36	40

* *Miogypsinoides* I in Unit III vs. *Miogypsinoides* in Unit V

Table 13: Outcomes of the t- and Wilcoxon-tests on the differences between the means of pairs of samples of *Miogypsinoides* in Units IV and V. $P = 0.01$ (+ + / - - -), $P = 0.05$ (+ / -), $df_t = N_1 + N_2 - 2$, $N_1 + N_2 =$ total number of observations.

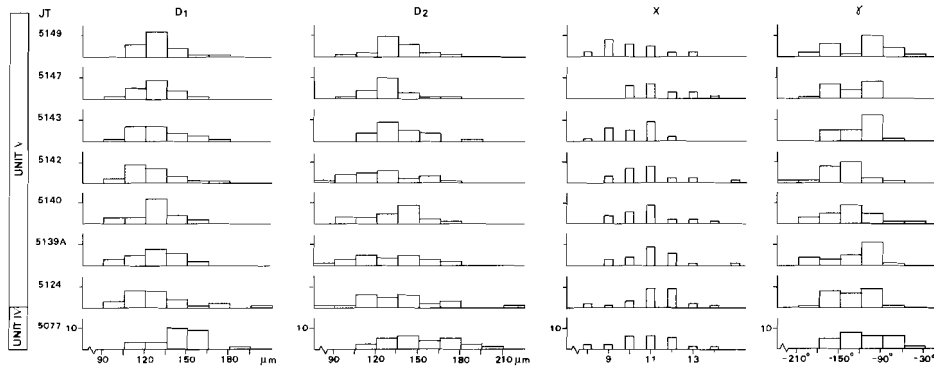


Fig. 31: Histograms of X , γ , D_1 and D_2 for *Miogypsinoides* in the samples of Units IV and V of the Lamia section.

associated with the embryonic parameters. γ is more frequently correlated with D_1 and D_2 (figs. 32 and 33).

The pairs of sample means \bar{D}_1 - \bar{D}_2 and $\bar{\gamma}$ - \bar{D}_2 are both well correlated. Less distinctly associated are \bar{X} - $\bar{\gamma}$ and $\bar{\gamma}$ - \bar{D}_1 . The other couplets of means did not yield significant r-values (figs. 34 and 35).

Sample	\bar{X}	SE	N	<i>Miogypsinoides</i> / <i>M. ex. interc.</i>
UNIT V				
JT5161/75	10.6	0.60	8	(<i>bantamensis</i>)
JT5155	10.5	0.44	12	<i>bantamensis</i>
JT5154	10.8	0.46	14	<i>bantamensis</i>
JT5150	11.1	0.40	14	<i>bantamensis</i>
JT5149	10.2	0.28	24	<i>bantamensis-dehaartii</i>
JT5147	11.3	0.27	20	<i>bantamensis</i>
JT5143	10.2	0.23	23	<i>bantamensis-dehaartii</i>
JT5142	10.9	0.30	23	<i>bantamensis</i>
JT5140	10.8	0.27	24	<i>bantamensis</i>
JT5139A	11.1	0.28	24	<i>bantamensis</i>
JT5137	11.3	0.30	11	<i>bantamensis</i>
JT5134	10.9	0.64	10	(<i>bantamensis</i>)
JT5131	11.0	0.35	19	<i>bantamensis</i>
JT5125	10.9	0.61	14	<i>bantamensis</i>
JT5124	11.2	0.27	27	<i>bantamensis</i>
JT5112	11.3	0.28	12	<i>bantamensis</i>
JT5098	11.6	1.00	8	(<i>bantamensis</i>)
UNIT IV				
JT5077	10.7	0.31	23	<i>bantamansis</i>

Table 14: Species names of *Miogypsinoides* in Units IV and V and the relevant biometric data; N = number of observations on X in one sample; if N < 11, the species name is in parentheses.

$P=0.01$	X	γ	D ₁	D ₂
$P=0.05$				
X		-80	-5	-5
γ	-85		+70	+35
D ₁	+5 -35	+85		+85
D ₂	-30	+70	+95	

Fig. 32: Relative frequency of the samples of *Miogypsinoides* in Units IV and V marked by a significant correlation between two variables ($P = 0.01$ or $P = 0.05$). Total number of samples is 18. -55 means 55% of the samples shows a significant negative correlation.

III.4.3 Relation between *Miogypsinoides* in Units III, IV and V

Concerning the mean diameters of the embryo *Miogypsinoides* in Units IV and V is closer to the type I group than to *Miogypsinoides* II in Unit III. The sample-mean clusters of the younger *Miogypsinoides* in fig. 35 partly cover the

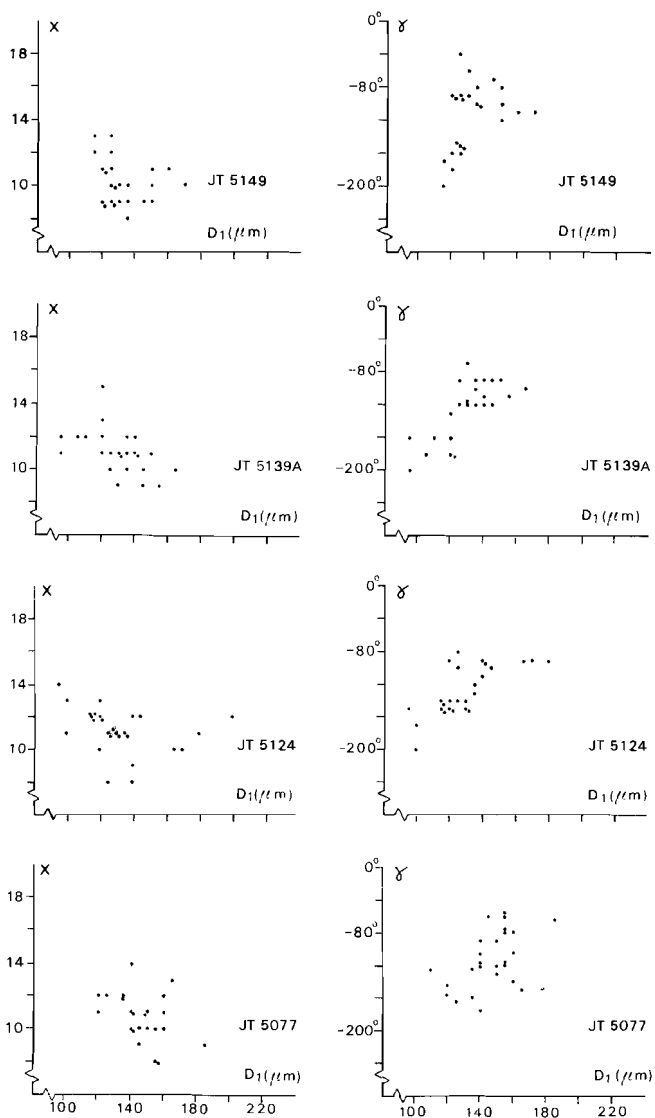


Fig. 33: Scatter diagrams of $X-D_1$ and $\gamma-D_1$ for *Miogypsinoides* in Units IV and V.

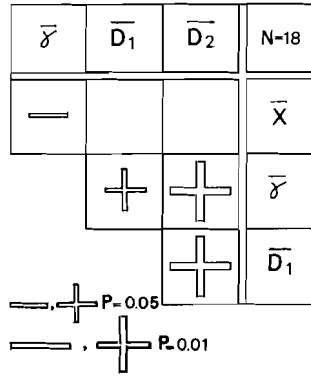


Fig. 34: Correlations of the sample means for *Miogypsinoidea* in Units IV and V. Total number of samples is 18.

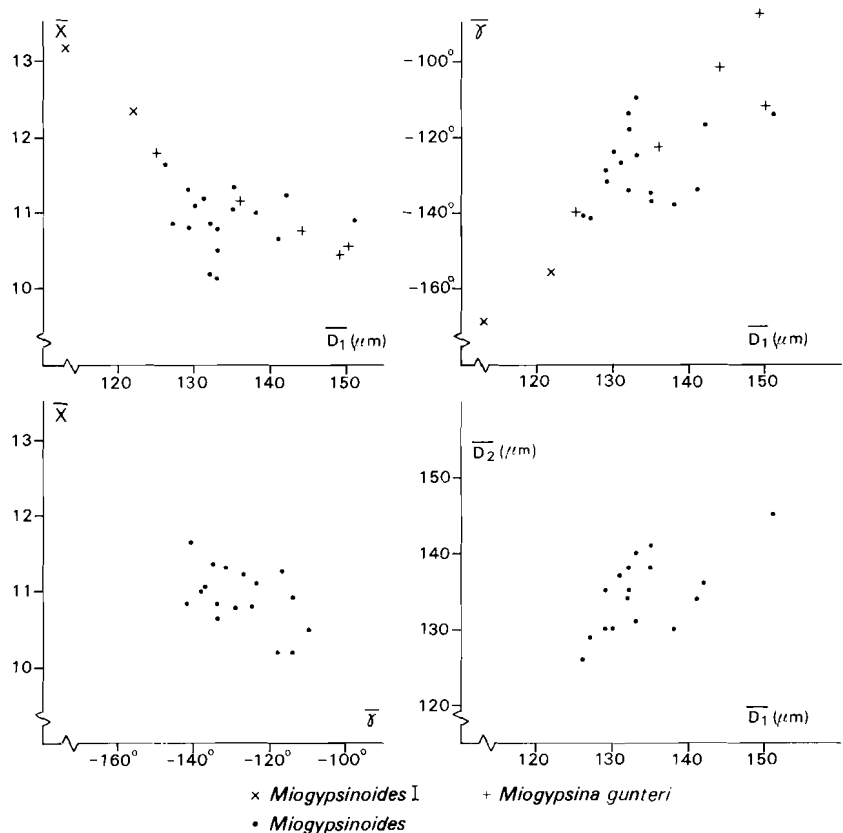


Fig. 35: Scatter diagrams of $\bar{X}-\bar{D}_1$, $\bar{\gamma}-\bar{D}_1$, $\bar{X}-\bar{\gamma}$ and $\bar{D}_2-\bar{D}_1$ for *Miogypsinoidea* in Units IV and V; data on *Miogypsinoidea* I and *Miogypsina* s.s. in selected samples of Unit III have been added to the diagrams of $\bar{X}-\bar{D}_1$ and $\bar{\gamma}-\bar{D}_1$.

developmental pathway of the *Miogypsina gunteri* group in Unit III.

To further delineate the relation between the various *Miogypsinoidea* groups, we plotted scatter diagrams of D_1 -X and D_1 - γ on the data from several samples in Units IV and V together with the outlines of the clusters of *Miogypsinoidea* I and II in Unit III (fig. 36). It appears that the stratigraphically higher *Miogypsinoidea* cluster largely overlaps the field of type I, whereas only a small fraction of the individuals lies within the scatter periphery of the cluster of type II.

The combined data make it very likely that *Miogypsinoidea* in the upper units is closely related to *Miogypsinoidea* I in Unit III.

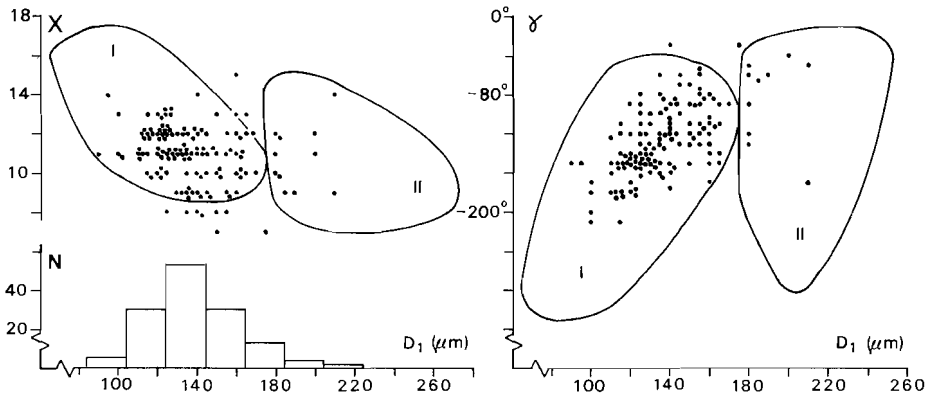


Fig. 36: Scatter diagrams of X- D_1 and γ - D_1 for *Miogypsinoidea* in Units IV and V and a histogram of D_1 . Included samples: JT5077, JT5124, JT5131, JT5134, JT5137, JT5150, JT5154, JT5155 and JT5175. The scatter peripheries of the *Miogypsinoidea* I and II clusters from Unit III have also been entered.

III.4.4 *Miogypsina* s.s.

Trends

For the total set of 37 samples \bar{X} and \bar{V} exhibit distinct overall trends at a significance level of $P = 0.01$, which trends both confirm the principle of neopionic acceleration (fig. 30, table 15). The overall change in $\bar{\gamma}$ is weaker ($P = 0.05$). The embryonic size parameters revealed no significant result of the r-test at all. Their ratio, \bar{D}_2/\bar{D}_1 , shows an upward tendency towards lower values ($P = 0.01$), however.

In figure 30 we see many discrepancies between the overall trends and various, partial trends in Unit V. In order to substantiate these deviations we tested the changes in several intervals of Unit V. The selected intervals are the

same as those to be dealt with in the section on covariation. The four intervals (P, Q, Q₁, Q₂) were chosen after visual inspection of figure 37, which shows remarkable patterns in the scatter diagrams of $\bar{V}-\bar{D}_1$ and $\bar{X}-\bar{D}_1$.

Hardly any overall change in the variables is obvious in the lower half of Unit V (table 15). Only \bar{V} and $\bar{\gamma}$ show significant trends, which are opposite

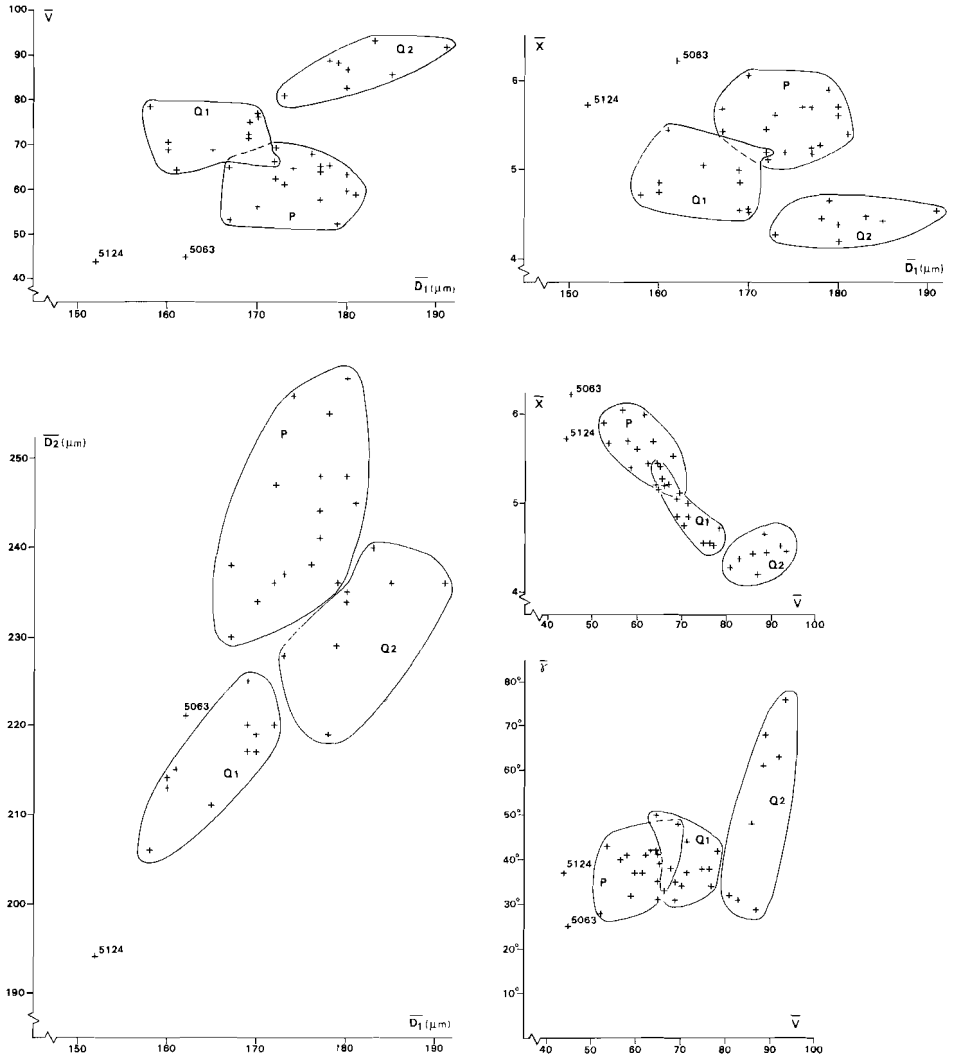


Fig. 37: Scatter diagrams of $\bar{X}-\bar{V}$, $\bar{\gamma}-\bar{V}$, $\bar{V}-\bar{D}_1$, $\bar{X}-\bar{D}_1$ and $\bar{D}_2-\bar{D}_1$ for *Miogypsina* s.s. in Units IV and V of the Lamia section; scatter peripheries of successive sample suites have been indicated (see text).

Stratigraphical interval	N	\bar{X}	$\bar{\gamma}$	\bar{V}	\bar{D}_1	\bar{D}_2	\bar{D}_2/\bar{D}_1
Total Units IV and V: JT5063–JT5175	37	-0.76 ++	0.38 +	0.72 ++	0.21	-0.27	-0.61 --
Lower Unit V: JT7974–JT7980 (P)	13	0.39	-0.64 --	-0.63 -	0.33	-0.04	-0.31
Upper Unit V: JT5124, JT5175 (Q)	20	-0.69 ++	0.60 ++	0.84 ++	0.87 ++	0.79 ++	-0.41 -
Lower upper Unit V: JT5125, JT5149 (Q ₁)	11	-0.31	-0.19	0.23	0.48	0.45	-0.20
Upper upper Unit V: JT5150–JT5175 (Q ₂)	8	0.62 -	0.95 ++	0.81 ++	0.35	-0.21	-0.62 -

Table 15: Statistical significance of trends in *Miogypsina* s.s. from Units IV and V; one-sided *t*-test; $df_r = N - 2$; N = number of sample pairs; P = 0.01 (++/-/-), P = 0.05 (+/-/-); + +/+ = in line with the principle of nepionic acceleration, γ -increase or embryonic size-increase; - -/- = in contradiction with these patterns. Note that sample JT5124 has not been included in sample group Q₁.

to the overall trends in the parameter means, however. A quite different picture arises from the tests on the associations of *Miogypsina* s.s. in the upper part of Unit V. Significant trends are present in all investigated parameters, which trends are parallel with those found for Units IV and V as a whole. Even the embryonic size parameters, which do not display an overall change, show a distinct positive trend in the upper half of Unit V.

Next, after splitting the upper half of Unit V into two successive intervals, Q₁ and Q₂, these parts were also tested for the presence of trends (the lower sample JT5124 of sample group Q has not been included in sample group Q₁). The results present a further modification of the general picture observed in the total sequence and in the upper half of Unit V. The sequence of *Miogypsina* s.s. associations in the lower interval Q₁ does not show any significant trend. On the other hand the tendencies in $\bar{\gamma}$ and \bar{V} of interval Q₂ are clearly compatible with the overall trends in Unit V, whereas the trend in \bar{X} appears to be opposite to the general direction of change. The embryonic parameter means are indifferent with respect to the stratigraphical height of the samples in this topmost interval.

Small-scale changes

Concerning the selection of sample pairs to be analysed, we put emphasis on those variations, which did not turn up in the trend analyses. This means that we preferred to check changes in the sample means, which occur on a smaller scale than the intervals tested for trends. In addition, it had to be plausible that

Sample pair	\bar{X}	\bar{y}	df	\bar{V}	df	\bar{D}_1	df	\bar{D}_2	df
JT5172-JT5175	-0.15	-1.11	50	-2.09	43-	-0.66	53	-2.12	47-
						(-0.42)			
JT5164-JT5172	-0.60	1.90	52+	2.94	51++	0.44	51	1.04	49
JT5161-JT5175	0.00	2.34	50+	1.16	44	-0.93	52	-1.66	48
						(-0.70)			
JT5155-JT5167	1.12	4.30	47++	3.27	47++	2.11	49+	0.74	45
				(2.96)	++				
JT5155-JT5164	1.73-	3.98	51++	2.28	51+	0.72	51	0.07	47
JT5154-JT5164	2.14-	4.67	51++	0.72	51	-0.15	51	-0.54	48
JT5154-JT5161	1.34	2.44	51++	-0.49	51	0.49	50	0.10	49
JT5154-JT5155	0.26	0.43	50	-1.77	50-	-0.81	50	-0.59	47
JT5149-JT5161	0.24	1.24	50	3.17	48++	1.88	50+	1.60	48
JT5149-JT5154	-0.86	-1.72	49-	3.74	47++	1.20	50	1.58	47
JT5147-JT5175	-2.38++	5.10	51++	4.54	43++	1.35	54	-0.15	44
						(0.95)			
JT5147-JT5154	-3.51++	-1.71	52-	4.67	50++	1.40	52	1.40	45
JT5143-JT5154	-2.70++	-2.56	51--	5.13	50++	1.35	51	1.93	49+
JT5142-JT5150	-1.86+	-0.03	48	4.03	46++	2.48	48++	1.68	43
JT5142-JT5143	0.13	2.30	50+	0.69	47	1.36	51	0.32	45
JT5140-JT5149	-2.40++	1.10	49	2.27	47+	-0.33	50	-0.07	44
JT5140-JT5142	-1.38	-0.40	49	0.52	47	-1.79	50-	-0.56	41
JT5139-JT5140	1.55	-0.26	51	-0.90	50	1.83	51+	0.56	45
JT5137-JT5140	2.67--	-0.20	52	-2.40	51-	0.31	51	0.30	45
JT5137-JT5139	1.25	0.03	53	-1.87	51-	-1.75	52-	-0.34	48
JT5134-JT5149	-1.10	-0.88	48	-0.52	46	2.19	50+	1.51	42
JT5134-JT5142	0.28	-2.43	48--	-2.42	46--	0.43	50	0.86	39
JT5134-JT5140	1.69-	-2.10	49-	-2.62	49--	2.31	50+	1.42	40
JT5134-JT5139A	-0.84	-0.82	51	-1.09	50	2.12	52+	2.07	42+
				(-1.03)					
JT5131-JT5175	-2.51++	4.43	48++	5.37	39++	1.80	50+	0.90	44
						(0.92)			
JT5131-JT5137	-2.34++	-0.14	51	2.08	47+	0.88	49	0.65	45
JT5131-JT5134	-1.30	1.36	48	2.35	45+	-1.33	48	-0.59	40
JT5125-JT5149	-2.05+	-1.74	34-	2.04	29+	1.17	35	0.36	31
JT5125-JT5131	-1.09	-1.85	34-	0.66	28	0.54	33	-0.30	29
JT5124-JT5167	-3.20++	2.94	32++	12.79	32++	3.72	34++	3.49	32++
		(2.95)	++						
JT5124-JT5137	-3.32++	-0.48	37	6.61	36++	2.79	36++	2.26	34+
JT5124-JT5131	-1.99+	-0.31	34	4.58	31++	1.94	33+	1.74	31+
JT5124-JT5125	-0.57	1.55	20	2.40	17+	1.22	20	1.69	18
JT7980-JT5124	-0.16	0.67	23	-0.95	20	-3.16	26--	-3.08	21--
						(-2.78)	--		
JT5117-JT5131	-1.74+	-0.84	29	2.40	26+	-0.15	28	-1.91	25
JT7979-JT5124	1.40	0.26	37	-2.52	34--	-3.15	37--	-3.69	31--
JT7979-JT5117	1.09	0.87	32	-1.07	29	-1.02	32	-0.16	25
JT5112-JT5117	0.87	1.59	32	-0.95	30	-0.98	32	-0.31	30
JT7977-JT7979	-1.55	-1.10	49	0.25	47	-0.34	51	-0.62	42
JT7977-JT5112	-0.68	-1.95	49-	-1.02	48	0.12	51	-0.24	47
JT7976-JT5112	1.13	0.19	54	-1.42	48	0.91	54	-0.86	44
JT7976-JT7978	1.48	1.14	46	-0.73	44	-0.11	52	-1.52	37

Sample pair	\bar{X}	\bar{y}	df	\bar{V}	df	\bar{D}_1	df	\bar{D}_2	df
JT7976-JT7977	1.57	1.95	49+	-0.30	46	0.81	51	-0.69	39
JT5098-JT7975	-0.67	-0.35 (-1.15)	52	0.10	50	1.61	54	2.20	41+
JT5098-JT5102	-0.12	0.05	49	-0.44	46	0.93	50	1.93	47+
JT5094-JT7976	-2.00+	-1.88 (-1.88)	51-	1.38	42	-0.46	50	0.78	38
JT5094-JT5098	-0.92	0.03 (0.30)	49	1.19	44	-1.51	49	-1.87	46-
JT7974-JT7976	0.16	-2.84	48--	-0.97	45	0.21	53	2.04	39+
JT7974-JT5094	2.07-	-1.22 (-1.30)	45	-2.24	41-	0.66	49	1.20	41
JT7177-JT7974	-3.05++	1.50	51	3.24	45++	0.42	57	0.19	48
JT5082A-JT7974	-1.27	1.87 (1.76)	46+	0.24	47	-0.53	53	-0.30	44
JT5077-JT5149	-2.27+	-0.67 (-0.67)	43	2.82	39++	-1.03	46	-2.55	40--
JT5077-JT7177	2.50--	-0.47 (0.09)	49	-2.03	40-	-1.12	52	-1.00	44
JT5077-JT5082A	0.82	-0.80 (-0.45)	44	0.71	42	-0.23	48	-0.66	40
JT5063-JT5125	-1.39	2.59 (2.63)	33++	2.19	29+	-0.05	34	-0.40	30
JT5063-JT5124	-0.94	1.29 (1.47)	33	-0.12	32	-1.28	34	-2.08	32-
JT5063-JT5077	-2.35++	2.27 (2.05)	42+	3.21	39++	2.18	45+	1.93	39+
JT5055-JT5063 (Unit III-IV)	-3.25++	4.10 (3.78)	37++	5.21	40++	-0.46	46	2.29	37+

Table 16: Statistical significance of the differences between the sample means of *Miogypsina* s.s. from Units IV and V; the tests were carried out with a one-sided t- or Wilcoxon-test. The latter was applied to \bar{X} and to the other variables in case they deviate too much from the Gaussian curve. df = $N_1 + N_2 - 2$, P = 0.01 (+ + / - -), P = 0.05 (+ / -).

the samples to be compared provided a significant result of the test in at least one variable. Notwithstanding these selection keys, we did not try to carry out a systematic search for all, small-scale changes. The only system in the whole procedure is that the t-test or the Wilcoxon-test was executed for all parameters of a specific sample pair, even if only a single variable was suspected to yield a significant outcome of the test.

A first glance at table 16 makes it clear that - apart from the positive shifts - significant, negative changes are present as well. From this table it can also be deduced that a significant increase or decrease in one variable, is often not accompanied by an equivalent shift in another parameter. In fact, only the statistics \bar{X} and \bar{V} frequently exhibit compatible changes (table 17).

Number of significant shifts in:					
	\bar{X}	$\bar{\gamma}$	\bar{V}	\bar{D}_1	\bar{D}_2
P = 0.05	23	25	33	15	16
P = 0.01	13	12	19	5	4
Shift directions in:					
	$\bar{X}-\bar{V}$	$\bar{\gamma}-\bar{V}$	$\bar{X}-\bar{D}_1$	$\bar{V}-\bar{D}_1$	$\bar{D}_1-\bar{D}_2$
P = 0.05					
Parallel	20	11	5	9	7
Opposite	1	4	1	1	0
P = 0.01					
Parallel	9	6	2	4	3
Opposite	0	1	0	0	0

Table 17: Number of significant shifts in the sample means of *Miogypsina* s.s. in Units IV and V, presented in table 16 and equivalent changes in various pairs of the sample means, parallel or opposite to the overall trends in the Miogypsinidae. Total number of tested sample couplets in table 16 = 58.

In the following paragraphs we will further pursue the successive changes in Units IV and V, to start with the description of the differences between the lowermost association from Unit IV (JT5063) and one of the most advanced assemblages from Unit III (JT5055). The tests indicate significant (P = 0.01), progressive shifts in all nepionic variables across the boundary between Units III and IV, which shifts are not associated with changes of comparable magnitude in the embryonic variables (table 16).

The difference between the assemblages of *Miogypsina* s.s. in Unit III and Units IV and V is also marked by the mutually exclusive ranges of \bar{D}_2/\bar{D}_1 . In the former interval the ratio varies between 1.00 and 1.20, whereas it ranges from 1.20 to 1.50 in the latter. This shift was not statistically analysed for individual sample pairs, however.

The positive difference between JT5063 and the majority of the higher samples of Units IV and V is not found for all samples, as is displayed by for instance the comparison of JT5063 and JT5124.

The means of *Miogypsina* s.s. in the upper part of Unit IV stay within the range of the parameter means found for the lower part of Unit V (fig. 30). The scanty data of Unit IV do not justify a more detailed discussion of this interval.

As to *Miogypsina* s.s. in Unit V, it is easily noticed that the intervals with major changes are not evenly distributed along the lithostratigraphical column (table 16, fig. 30). This means that notable shifts are restricted to certain intervals within Unit V. In the lower part of Unit V up to about sample JT7980,

i.e. interval P, almost no large fluctuations were detected in the parameters. $\bar{\gamma}$ once shows a negative change (JT7974-JT7976) at a significance level $P = 0.01$. The mean protoconch diameter seems to be the most invariable statistic in the basal strata of Unit V; not one pair of \bar{D}_1 values exhibits a distinct alteration at $P = 0.05$.

The rather stable pattern in the mean protoconch size is drastically cut off between JT7980 and JT5124, which stratigraphical levels are only 1.6 m distant from one another. Both embryonic parameter means attain distinctly lower values in JT5124. This considerable drop is succeeded by the positive trends in \bar{D}_1 and \bar{D}_2 for the Q part of Unit V. The nepionic statistic \bar{V} falls off more gradually from JT7979 to JT5124. Comparable, significant changes were not noted for \bar{X} and $\bar{\gamma}$.

A remarkable alteration of the percentage C, which change was not statistically tested, comes about between JT5124 and JT5125. C, which usually ranges from 59% to 73% in the lower part of Unit V, shifts to values between 80% and 100% in the top part of the sequence (fig. 30).

From JT5124 upwards \bar{V} and \bar{X} change considerably, but in a gradual way. \bar{V} increases up to JT5134 and \bar{X} decreases up to JT5137. The embryonic variables in this interval exhibit a less spectacular, but still distinct, positive change. In the next higher interval, which extends up to JT5140, the direction of change in \bar{X} and \bar{V} is reversed again, opposite to the overall trend. Alterations in both means with the same negative direction and magnitude are not present anymore in the higher part of Unit V. \bar{X} diminishes significantly between JT5140 and JT5149-JT5155 and stabilizes in the upper part of the succession. A large, progressive change is present in \bar{V} from JT5140 up to the top of Unit V, twice showing weak, negative shifts.

Fluctuations occur in $\bar{\gamma}$ up to JT5155 without resulting in a distinct net shift. Above JT5155 $\bar{\gamma}$ is marked by a series of positive changes, which are more or less well associated with significant increases of \bar{V} . The positive shift in $\bar{\gamma}$ near the top of Unit V is associated with the appearance of individuals, which possess a non-peripheral embryo (see CT in fig. 30). Four to eighteen per cent of the *Miogypsina* s.s. specimens in the upper four samples show such a non-peripheral position of the initial chambers.

Figure 30 and table 16 show that the above description of changes is not free from subjectivity. More and other minor shifts might be emphasized, but our enumeration certainly gives the major irregularities.

Summarizing the main changes in Units IV and V, we see in IV and the P part of V a fairly stable and staggering pattern in all parameters. The most important parameter \bar{V} shows an increase at the base and a return to about the same low value just across the top of the P interval. A rise and fall of \bar{V} values

in the lower part of Q_1 is followed by a fairly regular increase to the top of the section. The upper part of Q_2 shows the rapid positive change in $\bar{\gamma}$ in addition. The considerable drop in the embryonic size parameters at about the boundary between intervals P and Q and the subsequent renewed increase cause the peculiar pattern of the clusters in those scatter diagrams of figure 37, in which the embryonic and nepionic parameter means are combined.

Qualitative changes in the frequency distributions

Several differences in the morphotype range of *Miogypsina* s.s. can be noted between the associations of Unit III and the base of Unit IV (JT5063). The shifts stand out most clearly in the parameters X and γ (table 18). No clear-cut change is present in the embryonic dimensions and alterations in the range of V do not occur at all across the boundary between Units III and IV.

Overall changes in the morphotype composition of *Miogypsina* s.s. in Units IV and V are distinct in X and V (fig. 38, table 18). The X-value 6, which often represents the modal class in the basal histograms, is only of subordinate importance in the upper distributions of Unit V. Just the reversed pattern has been found in class 4.

No distinct shift has been observed in the range of V up to JT7980. From this sample upwards the variation in V-morphotypes becomes distinctly reduced, which goes together with a tendency to shift the modal class towards larger values until the highest class is reached. At this stage the histograms of V are strongly asymmetric.

	V	X	$\gamma(^{\circ})$	$D_1(\mu\text{m})$	$D_2(\mu\text{m})$
Transition Unit III to IV:					
Entry	-	4	60 - 75	-	-
Exit	-	14 - 10	-150 - -60	80 - 100	90 - 120
Units IV and V:					
Entry	90 - 100	3	75 - 120 (120 - 165)	-	-
Exit	0 - 60	9 - 7,(6)	-45 - -15	-	-
Discontinuous record	-	-		100 - 120 200 - 280	270 - 390

Table 18: Changes in the morphotype range of *Miogypsina* s.s.

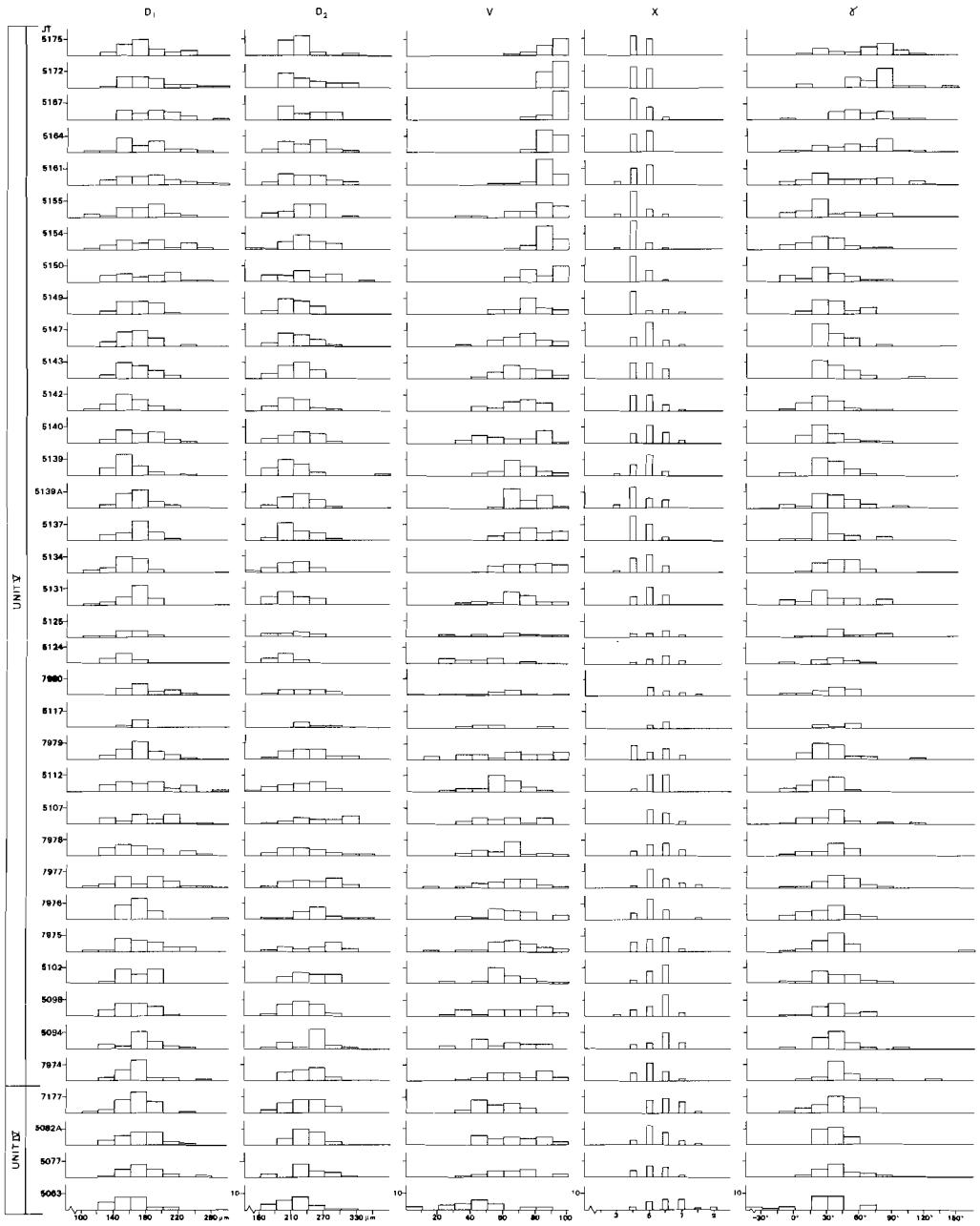


Fig. 38: Histograms for *Miogypsina s.s.* in the samples of Units IV and V of the Lamia section.

Sample	\bar{V}	SE	N	$\bar{\gamma}$	N _{CT}	<i>Miogypsina</i> / <i>M. ex. interc.</i>
UNIT V						
JT5175	89	2.03	19	68	5	<i>cushmani-mediterranea</i>
JT5172	93	1.04	26	76	1	<i>mediterranea</i>
JT5167	92	1.20	23	63	2	<i>mediterranea</i>
JT5164	88	1.31	27	61	1	<i>cushmani-mediterranea</i>
JT5161	86	1.75	27	48	0	<i>cushmani</i>
JT5155	81	3.06	26	32	0	<i>cushmani</i>
JT5154	87	1.53	26			<i>cushmani</i>
JT5150	83	2.11	25			<i>cushmani</i>
JT5149	77	2.38	23			<i>cushmani</i>
JT5147	72	2.88	26			<i>intermedia-cushmani</i>
JT5143	72	2.57	26			<i>intermedia-cushmani</i>
JT5142	69	2.81	23			<i>intermedia-cushmani</i>
JT5140	67	3.61	26			<i>intermedia-cushmani</i>
JT5139	71	2.43	26			<i>intermedia-cushmani</i>
JT5139A	75	1.92	27			<i>cushmani</i>
JT5137	77	2.48	27			<i>cushmani</i>
JT5134	79	2.77	25			<i>cushmani</i>
JT5131	69	2.96	22			<i>intermedia-cushmani</i>
JT5125	65	7.45	8			<i>(intermedia-cushmani)</i>
JT5124	44	4.88	11			<i>globulina-intermedia</i>
JT7980	53	7.36	11			<i>intermedia</i>
JT5117	54	5.94	6			<i>(intermedia)</i>
JT7979	65	5.03	25			<i>intermedia-cushmani</i>
JT5112	59	2.53	26			<i>intermedia</i>
JT5107	60	3.93	18			<i>intermedia</i>
JT7978	62	3.31	22			<i>intermedia</i>
JT7977	64	3.42	24			<i>intermedia</i>
JT7976	65	3.17	24			<i>intermedia</i>
JT7975	65	3.50	26			<i>intermedia</i>
JT5102	63	2.65	22			<i>intermedia</i>
JT5098	65	4.02	26			<i>intermedia</i>
JT5094	58	3.79	20			<i>intermedia</i>
JT7974	69	3.32	23			<i>intermedia-cushmani</i>
UNIT IV						
JT7177	56	2.35	24			<i>intermedia</i>
JT5082A	68	3.15	26			<i>intermedia-cushmani</i>
JT5077	65	3.68	18			<i>intermedia</i>
JT5063	45	4.59	23			<i>globulina-intermedia</i>

Table 19: List of species names of *Miogypsina* s.s. in Units IV and V; N = number of observations on V in one sample; N_{CT} = number of individuals with a centripetal trend of the embryo; if N < 11, the name is put between brackets.

γ -morphotypes ranging from 90° to 165° are already met with in the lower part of Unit V, but once present they do not tend to expand in the record. A more distinct incorporation of high-value classes in the variation of γ is shown by the uppermost associations, JT5161 to JT5175. In the same interval a shift is apparent in the position of the modal class of γ . Usually it lies between 15° and 45° , but in the upper assemblages the mode coincides with the class 75° - 90° .

The range of the embryonic variables contracts and expands without a net result. The fluctuations are well visible in the larger classes of the total range of D_1 and D_2 (table 18).

Biometric-taxonomical classification

The species name *Miogypsina mediterranea* as such or in an exemplum intercentrale construction was applied to assemblages, which - next to high \bar{V} values - attain high values of $\bar{\gamma}$ and possess one or more individuals with a centripetal trend of the embryo. With respect to \bar{V} this species is similar to *M. antillea*, which is the end-member of the *Miogypsina* s.s. stocks in the Indo-Pacific and American provinces.

In Units IV and V we found three successive biometric species, *M. intermedia*, *M. cushmani* and *M. mediterranea* and as many exemplum intercentrale categories (table 19). The intermediate assemblages are present in between the

$P=0,01$	X	γ	V	D_1	D_2
$P=0,05$					
X	X	+5 -5	-55	+5	-5
γ	+10 -10	γ	+5	-5	-5
V	-70	+10	V	+5	+10 -5
D_1	+20	+10 -5	+15	D_1	+85
D_2	+5 -10	+5 -5	+25 -5	+95	D_2

Fig. 39: Relative frequency of the samples of *Miogypsina* s.s. in Units IV and V marked by a significant correlation between two variables ($P = 0.01$ or $P = 0.05$). Total number of samples is 37. -55 means 55% of the samples shows a significant negative correlation.

individual ranges of the three biometric species or they may interrupt the range of the specific species, to which they are transitional.

The ranges of the two most common intercentral assemblages do not overlap. This does not hold for the *M. ex. interc. globulina-intermedia* category, which interrupts the record of more advanced taxa in JT5124.

Covariation

Usually the diameters of the protoconch and the deuteroconch are very well correlated in the individual samples. V and X show a negative correlation in

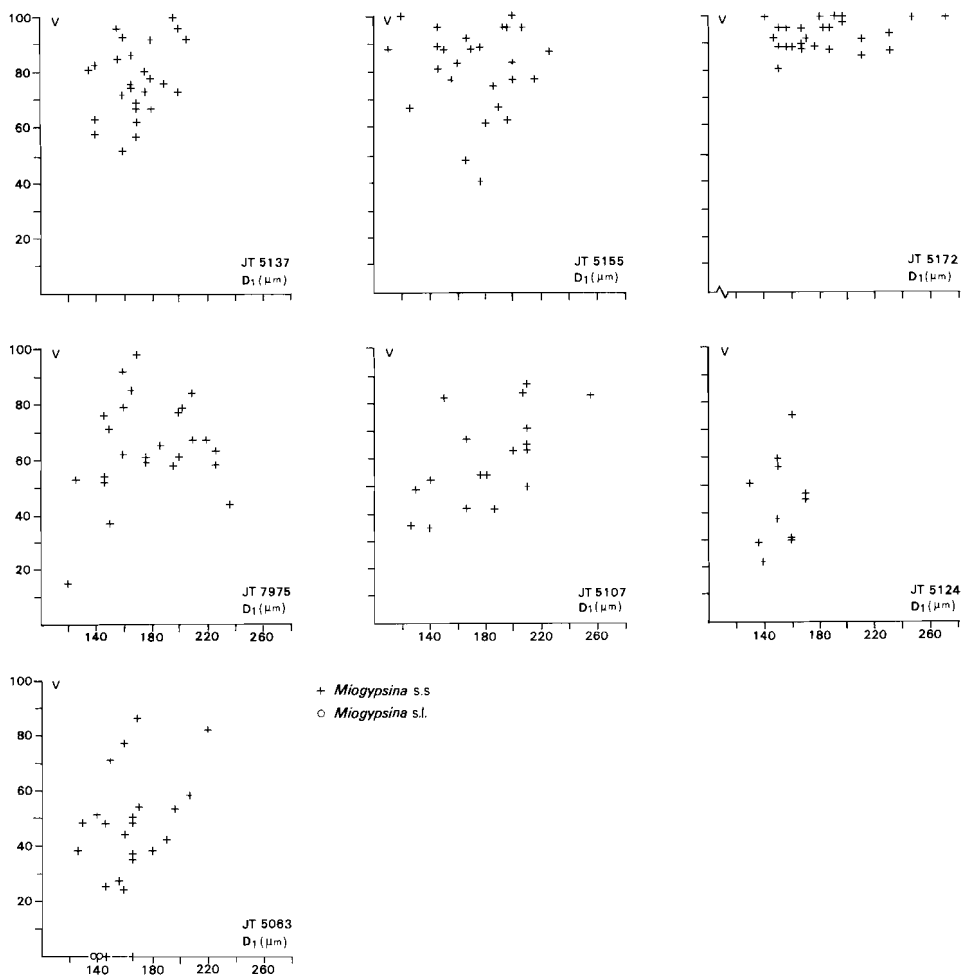


Fig. 40: Scatter diagrams of V-D₁ for selected samples of *Miogypsina* s.s. in Units IV and V.

more than half of the samples ($P = 0.01$). The combinations in the other sets of parameters barely ever result in a significant value of the correlation coefficient (figs. 39 and 40). With regard to Unit III the variables show fewer significant correlations in Units IV and V. An exception has to be made for D_1 and D_2 , which remain distinctly correlated throughout.

The sample means \bar{D}_1 and \bar{D}_2 and all the combinations with \bar{V} except $\bar{V}-\bar{D}_2$ are clearly associated at a significance level of $P = 0.01$. A weak covariation is apparent between $\bar{\gamma}$ and \bar{X} and between $\bar{\gamma}$ and \bar{D}_1 . The tests of the other pairs did not result in a significant outcome (figs. 37 and 41). This contrasts with the data of Unit III, which exhibit clear correlations between all combinations of parameter means.

$\bar{\gamma}$	\bar{V}	\bar{D}_1	\bar{D}_2	N=37
—	—			\bar{X}
	+	+		$\bar{\gamma}$
		+		\bar{V}
+, P=0.05	+		+	\bar{D}_1

Fig. 41: Correlations of the sample means for *Miogypsina* s.s. in Units IV and V.

The coefficient of correlation for a specific pair of sample means in the specific intervals of Units IV and V may deviate significantly from the r-value for the total sample suite in Units IV and V. In order to check this, r-tests were executed for the successive groups of samples in Unit V. It appears that the pairs of sample means in the four groups commonly are not covarying at $P = 0.01$; an exception is the entire upper interval Q (table 20).

	N	$\bar{X}-\bar{D}_1$	$\bar{X}-\bar{D}_2$	$\bar{V}-\bar{D}_1$	$\bar{V}-\bar{D}_2$	$\bar{X}-\bar{V}$	$\bar{\gamma}-\bar{V}$	$\bar{D}_1-\bar{D}_2$
P	13	0.17	-0.11	-0.10	0.11	-0.82-	0.39	0.55
Q	20	-0.69-	-0.74-	0.85+	0.83+	-0.87-	0.53+	0.91+
Q ₁	11	-0.16	-0.14	0.12	-0.05	-0.88-	-0.09	0.78+
Q ₂	8	0.38	-0.05	0.65	0.25	0.57	0.85+	0.59

Table 20: Results of the correlations tests of the sample means of *Miogypsina* s.s. in four intervals of Unit V; $P = 0.01$ (+/-); N = number of samples; r-tests have been executed one-sided. Note that JT5124 has been included in sample group Q₂, but not in group Q₁.

Chapter IV

BIOSTRATIGRAPHY AND GEOHISTORY

IV.1 BIOSTRATIGRAPHY

Planktonic foraminifera and calcareous nannoplankton appeared to provide useful index fossils in the basal Units I and II and in the marls overlying the carbonates (Unit VI). Although the planktonic foraminifera are very abundant in Units III up to V inclusive, their biostratigraphical resolution is smaller than that of the larger foraminifera. *Miogypsina*, *Lepidocyclina* and *Cycloclypeus* provide the species with biostratigraphical significance for these higher carbonate units.

Unit I

In general the nannoflora assemblages in the Units I and II are marked by an atypical composition. In sample JT7005 for example, *Discoaster* is strongly dominating; other types of nannoliths are rare. Adding to this the probable presence of reworked nannoflora specimens, our nannoplankton zonation of the Units I and II must be used with some caution.

The oldest investigated samples of Unit I, JT7005, JT7006 and JT7023A, are of Early Eocene age. The nannoflora in the basal interval of Unit I is characteristic of Zone NP13, the *Discoaster lodoensis* Zone. In addition to the nominate species *D. kuepperi*, *D. barbadiensis*, *D. saipanensis* and *Sphenolithus radians* were observed. The associations of planktonic foraminifera contain *Morozovella* cf. *aragonensis caucasica*, *M.* cf. *spinulosa*, *Acarinina bullbrookii* and *Globigerina senni*. This microfauna can be assigned to Zone P9 or P10.

The youngest sample in Unit I, JT7040, was interpreted on the basis of the nannoflora (NP15) to be of Middle Eocene age. The nannoflora consists of *D. saipanensis*, *Reticulofenestra dictyoda*, *R. scissura* and *Helicosphaera compacta*.

The planktonic foraminifera in sample JT7040 are represented by the *Globigerina eocenica* group, poorly preserved *G. senni* or *index* and *Turborotalia cerroazulensis*. The latter species ranges from Zone P10 up to and including Zone P16.

Unit II

The lower part of Unit II, which is represented by JT7077 and JT7366, probably was deposited in the Late Eocene. The co-occurrence of the planktonic foraminifera *Hantkenina alabamensis* and *Turborotalia cerroazulensis* s.s. in

these samples points to Zone P15 or P16.

The nannoflora assemblages in JT7366 and JT7077 are possibly indicative of the *Isthmolithus recurvus* Zone (NP19) and the *Sphenolithus pseudoradians* Zone (NP20), respectively. JT7366 contains *Isthmolithus recurvus*, *Sphenolithus predistentus*, *Cyclococcolithus formosus* and *Zygrablihus bijugatus*. In sample JT7077 *Sphenolithus predistentus*, *Ericsonia formosa* and *Reticulofenestra umbilica* were recognized.

If the biozonation on the basis of the nannoflora is correct, a large hiatus of about three nannoflora zones (NP16-18) is likely to be present at the boundary between the Units I and II (fig. 42).

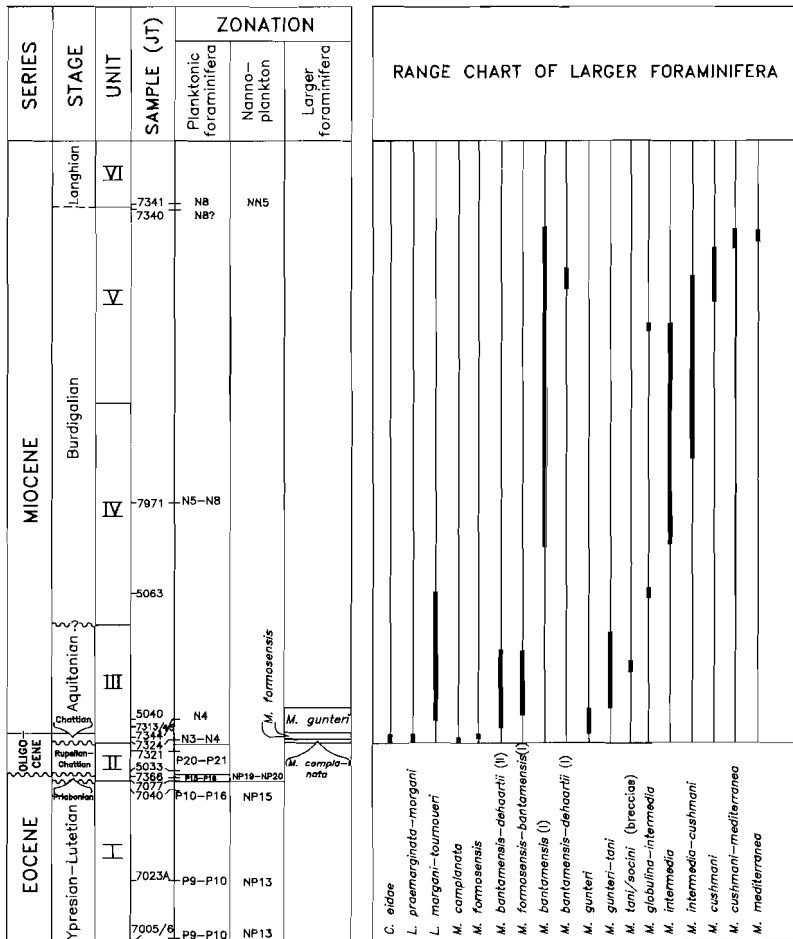


Fig. 42: Bio- and chronostratigraphical correlation of the Mineo carbonates with a range chart of the larger foraminiferal taxa. Planktonic foraminiferal zones according to Blow (1969) and Berggren (1972) and nannoflora zones according to Martini (1971). Oligocene biozones of larger foraminifers have been adopted from Drooger & Laagland (1986).

In the next younger samples of Unit II the nannoplankton is of no biostratigraphical value. The planktonic foraminifera in the upper part of Unit II (JT5033 and JT7321) indicate an Oligocene age, close to the Rupelian-Chattian boundary. JT5033 comprises *Neogloboquadrina opima opima*, *Globoquadrina galavisi* and *G. tripartita* and JT7321 is marked by *N. opima opima* and *N. opima nana*. Both samples can be assigned to Zone P20 or P21 (N1 or N2).

The carbonate sequence of Units I and II is much condensed or comprises gaps. Between JT7366 and JT5033 probably the Zones P18 and P19 are lacking (fig. 42).

Unit III

The oldest sample with larger foraminifera, which was studied biometrically (JT7324), contains *Miogypsina complanata*, *Lepidocyclina* ex. interc. *praemarginata-morgani* and *Cycloclypeus eidae*. For biometric data on the latter two species see table 21. Because of its relatively small embryo the association of *Cycloclypeus* in JT7324 is rather close to the Indonesian *C. eidae* (see Drooger & Roelofsen, 1982) and for that reason was identified as *C. eidae*. The co-occurrence of the three species of larger foraminifera in sample JT7324 points to a Chattian Age (Drooger, 1963; Felix, 1973; De Mulder, 1975). In the recent zonation of Drooger & Laagland (1986) the association would fit in their *M. complanata* Subzone, which is high in the Chattian. If this zonation is correct there might be another hiatus at the base of Unit III.

This oldest assemblage of larger foraminifera from the Mineo carbonates probably is slightly younger than the Maltese association of *Lepidocyclina*, *Miogypsinoidea* and *Cycloclypeus* from the upper part of the Lower Coralline Limestone, because in the latter deposit all three genera have a more primitive nepionic configuration with respect to their counterparts in our sample JT7324 (Felix, 1973; Drooger & Roelofsen, 1982).

The age determination of the planktonic foraminifera in our sample JT7324 is not in conflict with the dating on the basis of the larger foraminifera. The association of planktonic foraminifera in this sample contains *Neogloboquadrina opima nana*, *N. siakensis*, *Globoquadrina venezuelana* and *Globigerinoides primordius*, which can be assigned to Zone N3 or N4. Together these zones are thought to straddle the Chattian/Aquitania boundary.

The next higher sample in Unit III of the Mineo carbonates (JT7344) contains *Miogypsina formosensis*, which is thought to belong to the latest Oligocene subzone (Drooger & Laagland, 1986).

From the microscopical observations in the thin-sections (see chapter II) we learned that the first specimens of *Miogypsina* s.s. are present at a level, which

is about one metre above the base of Unit III in the section Lamia (fig. 11). At this level *Miogypsina* s.s. constitutes about 5% of the Miogypsinid association. Unfortunately, no biometric data are available on these Miogypsinids, so that they cannot be determined. Some of them do not yet show a fully developed complex of lateral chambers.

The most primitive association of *Miogypsina* s.s., which was identified, belongs to *M. gunteri* and was sampled from a level about 3 metres above the base of Unit III in the section Donna Ragusa. In Unit III of the section Lamia the same species is succeeded by *M. ex. interc. gunteri-tani*. From the breccia zone in the upper part of Unit III in Lamia associations of *M. tani*, *M. socini* and intermediates were derived. All three species are assigned to the Aquitanian, two of them on the basis of first-order correlation.

M. gunteri is associated with *Lepidocyclina* ex. interc. *morgani-tournoueri* (JT7313/4/5; table 21) and with *Globorotalia kugleri* (JT5040), which is characteristic of Zone N4. These data are in accordance with the conclusion of an Aquitanian Age (fig. 42).

In several samples of Unit III *Miogypsina* s.s. occurs together with *Miogypsinoides*, which is close to *Miogypsinoides bantamensis*.

Lower part of Unit IV

In the lowermost part of Unit IV (JT5063) an association of *Miogypsina* ex. interc. *globulina-intermedia* was determined, which is of Burdigalian Age on the basis of first-order correlation (Drooger, 1966a). Typical *M. globulina* is lacking in the carbonate sequence, which results in a large morphological shift in *Miogypsina* s.s. across the boundary interval between the Units III and IV, so that the possibility of a hiatus at the transition between both units cannot be excluded.

However, the change in *Lepidocyclina* across the boundary between the Units

Sample	<i>Lepidocyclina</i> ex. interc.	\bar{C}	SE	N	\bar{A}_1	SE	N
JT5063	<i>morgani-tournoueri</i>	5.3	0.34	22	49	1.2	25
JT7313/4/5	<i>morgani-tournoueri</i>	5.2	0.41	12	44	1.0	12
JT7324	<i>praemarginata-morgani</i>	3.4	0.26	26	40	0.8	25
	<i>Cycloclypeus</i>	\bar{X}	SE	N	\bar{D}_1	SE	N
JT7324	<i>eidae</i>	16.7	0.49	11	87	4.1	11

Table 21: Biometric-taxonomical data on *Cycloclypeus* and *Lepidocyclina* in Unit III and the basal part of Unit IV.

III and IV is far less impressive. In Unit IV *L. ex. interc. morgani-tournoueri* was identified, which is biometrically very close to the *Lepidocyclina* association accompanying *M. gunteri* in Unit III.

Some marly beds in the middle part of Unit IV (JT7971) yielded planktonic foraminifera, of which the most important species, *Globigerinoides altiaper-turus*, is mainly present in Burdigalian deposits (N5 to lower part of N8).

Upper part of Unit IV and Unit V

In the upper part of the carbonate sequence *Miogypsina intermedia*, *M. cushmani* and *M. mediterranea* and intermediate types are well represented. They are all of Burdigalian Age (Drooger, 1963; 1966a).

In a number of samples of Unit V *Miogypsina* s.s. is accompanied by *Miogyp-sinoides bantamensis* or *M. ex. interc. bantamensis-dehaartii* (fig. 42). The co-occurrence of *Miogypsina* s.s. and *Miogypsinoides* in Burdigalian deposits was reported from several localities in Africa (Morocco: Brönnimann, 1940; Drooger, 1954b; Egypt: Souaya, 1961; Nigeria: Brun & Wong, 1974), but at none of these places *Miogypsinoides* was found to range above the interval of *Miogypsina globulina/intermedia*.

In the topmost part of the carbonate sequence the *Miogypsinids* are not present anymore. A sample from these carbonates (JT7340) provided an association of planktonic foraminifera, which among other taxa contains *Globigerinoides* cf. *subquadratus* and *G. cf. sicanus* (lower part of Zone N8) and probably indicates a Late Burdigalian Age.

Unit VI (marls)

In the basal part of the marls, that cover the hardground at the top of the limestones, *Praeorbulina glomerosa* and *G. subquadratus* were encountered (JT7341). These planktonic foraminifera were assigned to the upper part of Zone N8, which is considered to be of Langhian Age. Apparently, the sedimentary hiatus at the top of the carbonate succession is not accompanied by a notable gap in the biostratigraphical record.

The nannoliths in the basal part of the marls point to the upper part of Zone NN5 (JT7341). Important constituents of the nannoflora in this sample are *Helicosphaera walbersdorfensis* and *H. waltrans*.

IV.2 LOCAL HISTORY OF THE MIOGYPSINIDAE

The Mineo carbonates have been found to contain both the first (*M. complanata*) and the last species (*M. mediterranea*) of the complete Mediterranean evolutionary succession (Drooger, 1963). Most of the species which are

theoretically in between have been found, but there is no smooth and continuous record.

M. complanata and *M. formosensis* are represented by single samples, lithostratigraphically close together; there are distinct morphometric gaps in between both assemblages and above to *M. bantamensis*. These data suggest a condensed sedimentary record or a record with considerable breaks.

The long stratigraphical record of the *M. bantamensis* group with little morphometric change is known from some places on the African continent as well. It is remarkable that we have found two morphometric groups that are very close to *M. bantamensis*, of which the one with the larger embryo seems to be the normal continuation of the earlier *Miogypsinoides* species. Whether the group with the smaller embryo is an offshoot and separate species from a different habitat like in the example of recent *Planorbulinella* (Thomas, 1977) is difficult to verify from our data. Anyway it is the form that lived longest, well up into the Burdigalian (see also V.2).

The *Miogypsina* s.s. lineage is well represented with its first species *M. gunteri* followed by a less good documentation of its normal Aquitanian successor *M. tani*, as well as by some indications of the North and Central Italian provincial successor *M. socini*. Our data are too few to understand the presence of both descendants at the same place. Maybe the Miocene Sicilian area had the usual development line of *M. gunteri* to *M. tani* with occasional waves of *M. socini* from the north.

The latter's descendant *M. burdigalensis*, which is known to have spread widely over and beyond the Mediterranean, probably lived in the Hyblean area, but we have found rare individuals only reworked in the upper part of our section (Unit V). We neither have an in situ record of *M. globulina*, the descendant of *M. tani* of the main lineage, which is the regular companion of *M. burdigalensis* elsewhere. We need not wonder that we have found no occasional reworked specimens of *M. globulina*; such individuals would easily form part of the variation range of the later species of the *Miogypsina* s.s. lineage. Our conclusion must be that during the life time of *M. burdigalensis* and *M. globulina* the sedimentary environment at and around Mineo was adverse for both species. Unpublished data of the Utrecht Department of Stratigraphy and Micropaleontology indicate that at least *M. globulina* lived in the eastern part of the Hyblean area, near Syracuse (Drooger, pers. comm. 1989).

The upper Unit V gives ample documentation of the last three *Miogypsina* species (*M. intermedia*, *M. cushmani* and *M. mediterranea*) up to the level of extinction of the entire lineage, which evidently took place before the carbonate sedimentation of Unit V came to an end.

IV.3 LOCAL SEDIMENTATION HISTORY

The relatively high percentages of planktonics throughout, the near-absence of terrigenous clastics, and the vast quantities of calcareous debris of organisms that must have lived in the photic zone characterize the general environment of the Oligocene and Early Miocene surroundings of the Mineo sites. We must think of a vast carbonate buildup or vast complex of buildups far from the influence of sediment supply of a more continental hinterland. We know that the Hyblean Plateau, also referred to as the Ragusa Platform, was part of the northern margin of the African plate (see also paragraph I.3).

The field data, microfacies study and overall foraminiferal contents have given various indications about the development of the sedimentary environments. Biostratigraphical dating by means of planktonics and the larger foraminifera give further evidence for the local sedimentary history.

Especially the *Miogypsinid* history is useful for a more detailed reconstruction of the sedimentation. If we assume that the successive morphometric species of the main lineage correspond to identical time ranges - which procedure is only thought warranted as a rough approximation - we may achieve an impression of sediment-accumulation rates.

From the Eocene up to some level in the Oligocene slow accumulation of carbonates with frequent interruptions resulted in the condensed series of Units I and II. They were deposited at relatively shallow depth, but possibly still below the photic zone since no larger forams have been found. The average sediment-accumulation rate is very low, in the order of less than 0.5 cm/ka, which means that the sequence is not only strongly condensed but likely to contain repeated non-depositional interruptions as is also indicated by the planktonic biostratigraphy. It is assumed that the Mineo area was part of an open carbonate shelf, receiving very little sediment, much of which was of biogenic origin. It probably was far from any substantial terrigenous supply. Wave action caused occasional winnowing.

The main change at the transition from Unit II to Unit III is the sudden onset of carbonate components that originated in the photic zone, which means that some further shallowing brought the area within reach of major benthonic carbonate producers of the slope or platform. The lowermost few metres of Unit III show that the supply to the Mineo area was sudden and probably spastic. Distinct erosional lower surfaces were observed and the single occurrences of two successive *Miogypsina* species on some 2 metres thickness suggest that we are dealing mainly with the occasional spill-over of detritus from the shallower part of the slope or platform, which probably was lying to the east. The net thickness of accumulated carbonates is very small for this part of the Chattian;

some 2 metres supposedly in 1 to 2 Ma. Considering the type of sedimentation, gaps must be more important than real deposition.

The major part of Unit III corresponds with the range of *M. gunteri* and *M. tani*, i.e. with the Aquitanian. Some 25 metres would correspond to some 2 Ma, which points to an average sediment-accumulation rate in the order of 1 cm/ka with much reworking by waves and organisms. Yet we think that carbonate producing organisms were living in and very close to the Mineo area.

There is a morphological gap between the youngest assemblage of *M. gunteritani* in Unit III and the oldest of *M. globulina-intermedia* in Unit IV, which pleads in favour of a sedimentary hiatus near the Aquitanian-Burdigalian boundary. We may be dealing with a hiatus as the final expression of a relative sea-level fall at the end of the Aquitanian. This assumption, however, is not corroborated by lithological and micropaleontological data; a drowning trend was thought to be more likely for the upper part of Unit III from the decrease in grain size and the increase in the relative frequency of the planktonic foraminifera.

Sedimentation seems to have changed drastically at the boundary of Units III and IV. Glauconite disappears abruptly and we face a 50 metres sequence of mainly very fine organic debris with only occasional presence of larger foraminifera. The rare data on the Miogypsinids suggest that this sequence corresponds largely to only part of the range of a single species (*M. intermedia*), whereas no data have been found pertaining to the earlier Burdigalian species *M. globulina*. Although not present, the range of this species might correspond to a minor sediment thickness at the base of Unit IV and/or the top of Unit III.

The average sediment-accumulation rate for Unit IV must have had a relatively very high value of some 5 cm/ka since assumedly less than one Ma corresponds to some 50 metres thickness.

The absence of *M. globulina* is remarkable since it is the most widely recorded species, frequently accompanying early Burdigalian onlap deposits (e.g. in the type area near Bordeaux, but also in the eastern part of the Hyblean Plateau near Syracuse).

Since there is no distinct proof for a relative sea-level fall and an emersion-event at the boundary between III and IV we tend to prefer another reconstruction of the environmental change. A rapid Burdigalian rise of sea level may have initially drowned the benthonic communities of the photic zone in and around the Mineo area causing a strong decrease of sediment supply. This means that the local range of *M. globulina* is hidden in a strongly condensed series, in the top part of Unit III and/or the basal part of Unit IV. The larger part of Unit IV would represent the subsequent massive progradation of the debris from renewed expansion of the productive carbonate slope or platform,

which probably still was mainly situated to the east.

In the upper part of Unit IV and in Unit V progressive shallowing evidently caused Miogypsinids to return to the Mineo area. Larger grain-size facies, burrowing and evidence of wave and current actions point to this shallowing, coinciding with a decrease of the sediment-accumulation rate to values of 2 to 3 cm/ka (40 to 50 metres of sediment in 2 to 3 Ma). It is likely that this trend continued for the topmost part of Unit V after the extinction of the Miogypsinidae, if one considers the increasing glauconite content and the hardgrounds near and at the top of Unit V.

The terminal hardground of Unit V reflects a short period of non-deposition near the Burdigalian-Langhian transition. The phase of sedimentary starvation may establish the final expression of the shallowing during the accumulation of Unit V or, on the other hand, it marks the onset of the drowning phase during the deposition of the overlying marls of Unit VI. With the deposition of the marls in the Early Langhian the carbonate buildups of the photic zone disappeared from the surroundings of Mineo. The area was rapidly drowned to depths of 500 to 1000 metres.

Chapter V

EVOLUTIONARY ASPECTS OF THE MIOGYPSINIDAE

V.1 INTRODUCTION

The succession of *Miogypsina* species in the Oligo-Miocene carbonates near Mineo provides us with unique proof for the general validity of the principle of nepionic acceleration (Tan Sin Hok, 1936) in the evolution of the Miogypsinidae. A major deviation from the earlier established evolution pattern in the Mediterranean realm consists of the contemporaneous, Aquitanian occurrences of two morphometric units close to *M. bantamensis*, instead of only one. They were named *Miogypsinoides* I and II. The former ranges well up into the Burdigalian. This divergence from the overall line of evolution will be discussed in paragraph V.2.

In paragraph V.3 the evolutionary patterns in our *Miogypsina* lineages will be dealt with in more detail, which actually was the main purpose of our investigation. The morphometric series will be compared with the results of earlier published detailed studies on other orbitoidal foraminifera and with current evolutionary theories.

V.2 THE DEVIATION FROM THE GENERAL DEVELOPMENT PATTERN

As has been shown in paragraph III.3 two groups of *Miogypsinoides* specimens, both close to *M. bantamensis*, are found to accompany *M. gunteri* in the Aquitanian carbonates near Mineo. The two biometric units, *Miogypsinoides* I and II, differ primarily in embryonic size and show relatively minor morphometric differences in nepionic configuration. The mean protoconch diameter of *Miogypsinoides* I varies from about 110 to 120 μm , whereas *Miogypsinoides* II is marked by a mean diameter of the protoconch of about 210 to 230 μm . The chronostratigraphical range of *Miogypsinoides* I continues into the Burdigalian, where it accompanies the successive species *Miogypsina intermedia*, *M. cushmani* and *M. mediterranea*. The Burdigalian *Miogypsinoides* I displays a small shift in its nepionic variables with respect to its Aquitanian ancestor; \bar{X} decreases from about 12 to 13 in the Aquitanian to about 10 to 11 in the Burdigalian. Apart from this shift that occurs close to the chronostratigraphical boundary, neither *Miogypsinoides* I nor *Miogypsinoides* II shows a significant net change in their nepionic variables. In both nepionic and embryonic characteristics *Miogypsinoides* I is very close to primitive *Miogypsina gunteri*.

Miogypsinoides II displays distinct morphological overlap with the older *M. complanata* and *M. formosensis* of the Mineo section.

So far, the simultaneous presence of two 'types' of *Miogypsinoides* in the Aquitanian is not known in the literature. Three hypotheses will be offered to explain the co-occurrence. First of all some remarks will be made on the habitats of both types on the basis of our own observations (chapter II).

In paragraph II.3 it has been suggested that the Burdigalian *Miogypsinoides bantamensis* (type I) probably preferred a hard substrate and somewhat shallower depths relative to *Miogypsina* s.s. For both Aquitanian *Miogypsinoides* the whole-rock thin-sections gave no reliable indications on the paleoenvironment, especially because of the low frequencies in this interval. The biometric data on *Miogypsinoides* I and II give possibly a clue to the relative position of the habitats of both units (paragraph III.3, fig. 17). In the successive samples of Unit III the frequency of type I relative to type II is largest in the upper part of the unit, which has been thought to represent the deeper facies of this interval. Thus *Miogypsinoides* II seems to have preferred shallower habitats with respect to *Miogypsinoides* I and so probably also with respect to *Miogypsina* s.s.

If we disregard *Miogypsinoides* I for a moment, the sequence of our *Miogypsina* populations in the Chattian and Early Aquitanian shows an excellent analogue of the differentiation in *Miogypsinoides* and *Miogypsina* s.s. in the Indo-Pacific realm, described by Raju (1974). As in the Indo-Pacific early *Miogypsinoides* in the Mineo region possibly split into two branches, one with lateral chamber complexes (*Miogypsina* s.s.) and the other preserving the massive side walls of *Miogypsinoides*. Simultaneously, the *Miogypsina* s.s. branch underwent a reduction of the mean embryo size with respect to *Miogypsinoides* II, the latter still showing distinct increase of embryo size with respect to the supposedly ancestral *M. complanata* and *M. formosensis*. This splitting into two branches could well represent the adaptation to specific habitats, if one considers the supposed preference of *Miogypsina* s.s. for habitats deeper than those of *Miogypsinoides* II. It follows from this reasoning that it is the addition of *Miogypsinoides* I to the faunal associations that remains to be explained.

There is a close resemblance between the embryos and nepionts of *Miogypsinoides* I and the most primitive *Miogypsina* s.s. (*M. gunteri*) in the Mineo region. This brings us to the first hypothesis to explain the presence of *Miogypsinoides* I in the region of Mineo. Both taxa with small embryos would belong to one monophyletic group. Taking into account the probable difference in preference for the type of substrate, we may assume a case of different adaptive evolution; *Miogypsinoides* I would have adapted to a hard substrate, whereas *Miogypsina* s.s. preferred a sandy substrate of somewhat greater depth.

However, we do not know of any parallel in the literature to support this first hypothesis.

Evaluating the biometric data of our *Miogypsinidae* in a broader regional scope, it appears that most Mineo species are morphologically very close to their counterparts in the northern part of the Mediterranean province (Drooger, 1963; Drooger & Raju, 1973). In the $\bar{X}-D_1$ scatter of figure 43 it can be seen that our associations of early *Miogypsinoides*, *Miogypsinoides* II and of *Miogypsina gunteri* fit rather well within the ranges of the *Miogypsina* data from the French and Italian localities. They differ from the more southern occurrences in having on the whole larger mean protoconch sizes. However, the Aquitanian-Burdigalian *Miogypsinoides* I is close to the *Miogypsinoides* associations from localities in Africa. So far Burdigalian *M. bantamensis* has been reported exclusively from African localities, viz. Egypt (Souaya, 1961), Morocco (Brönnimann, 1940; Drooger, 1954b), Cameroon (Küpper, 1960; Drooger, 1966b) and Nigeria (Brun & Wong, 1974). In embryo size and stratigraphical range of *M. bantamensis* Africa and Europe can be regarded as separate subprovinces of the Mediterranean *Miogypsinid* province (fig. 43).

The concept of two Mediterranean subprovinces leads to our second hypothesis, in which *Miogypsinoides* I is considered to be an immigrant in Sicily. In this context the Mineo region must be seen as part of the northern subprovince with its early *Miogypsinoides* evolution and the subsequent splitting of the lineage into the two branches of *M. gunteri* and *Miogypsinoides* II. Affinity with the European region is also expressed by the presence of *M. socini*, which was described from northern and central Italian localities (Drooger, 1954a; Schüttenhelm, 1976; Schiavinotto, 1979). *Miogypsinoides* I thus must have arrived in the Mineo area by migration from the nearby African subprovince during the Early Aquitanian.

Up to now we discussed two options for the explanation of the simultaneous occurrence of two biometric units of *Miogypsinoides* in the Aquitanian carbonates near Mineo. In one hypothesis immigration of *Miogypsinoides* I is suggested and in the other *Miogypsinoides* I is regarded as a local deviation of *M. gunteri*. In the third hypothesis the two Aquitanian *Miogypsinoides* are thought to be related to one another and to have evolved by 'in situ' cladogenesis from the same ancestral *Miogypsinoides* stock.

Some circumstantial evidence on the two Aquitanian *Miogypsinoides* seems to indicate a habitat difference linked to water depth. The type with the relatively small embryo, *Miogypsinoides* I, seems to have preferred deeper habitats than *Miogypsinoides* II, the type with the relatively large embryo. A well documented example of the same type of relation between habitat depth and embryo size was described for the two Recent *Planorbulinella* species in the

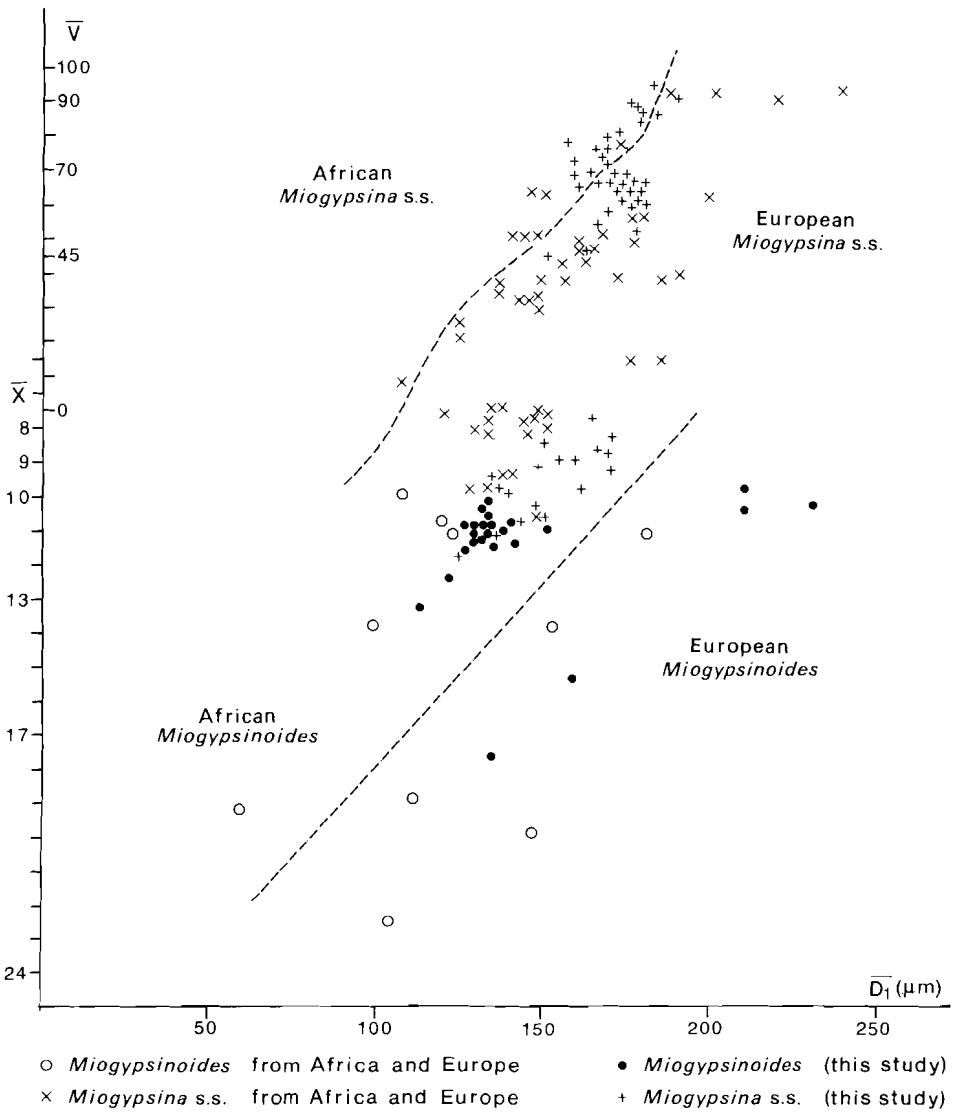


Fig. 43: \bar{D}_1 - \bar{X}/\bar{V} diagram of Miogypsinids in the Mediterranean province. Dashed lines separate European assemblages of *Miogypsina* from assemblages of African origin (literature data from Drooger & Raju, 1973; Brun & Wong, 1974; De Mulder, 1975).

Gulf of Elat (Thomas, 1977). And a similar relation was suggested for the separation of *Miogypsinoides* (large embryon) and *Miogypsina* s.s. (small embryon) in Aquitanian deposits of India (Raju, 1974; Drooger, 1983). Other examples of an intraspecific decrease of embryon size at greater depth were assumed for Recent *Operculina* from the Gulf of Elat (Fermont et al., 1983) and for Eocene *Discocyclus* *varians* s.l. from Israel (Fermont, 1982). As a further complication, the data on the latter two taxa indicate an additional, opposite morphocline, i.e. the increase of the embryon size with increasing depth for the shallowest part of the habitat gradient. The differentiation in embryon size for *Miogypsinoides* I and II thus might be seen as an in situ separation of two parts of a morphocline at considerable depth. The supposition of fair depth for our *Miogypsinoides* is rather unlikely, however.

In the preceding discussion three alternatives have been presented to explain the presence of two types of *Miogypsinoides* in addition to *Miogypsina* s.s. in the Sicilian Aquitanian. A local origin of all three taxa would invoke a rather complicated evolutionary event or series of events in a time interval close to the Chattian-Aquitanian boundary. Unfortunately, our record for this period is far from complete.

We prefer the hypothesis of immigration of *Miogypsinoides* I from a southern Mediterranean subprovince. There are good arguments to defend the postulate that the Mediterranean bioprovince was split into a northern and a southern subprovince. The Mineo region then was part of the European realm with its specific evolution of *Miogypsina*. At some time during the Early Aquitanian *Miogypsinoides* I, a typical form of the African subprovince, migrated to the Mineo area.

One might argue against such a hypothesis because the Mineo area was part of the African block anyway, and thus migration was rather unlikely. However, being part of the African block does not necessarily mean that the shallow domain was continuous in southward direction. We have seen that in Aquitanian time there was no *Miogypsina* record near Ragusa. And further south, in Malta and Gozo the Aquitanian *Globigerina* Limestone witnesses of marine conditions too deep for the Miogypsinidae. Although evidence is meagre because of lack of regional data, we prefer the migration hypothesis as the best choice.

V.3 PATTERN OF PHYLETIC EVOLUTION

V.3.1 Preliminary remarks

The main subject of our research is to establish and interpret the morphometric patterns of *Miogypsina* s.s. and *Miogypsinoides* for comparison with

various evolution theories. In this context it is of importance to know whether non-evolutionary factors influenced the observed patterns of morphometric changes in *Miogypsina*. Such factors may be of sedimentological or ecological nature. From the sedimentological point of view the morphological pattern may have been modified by sedimentary hiatuses, variable sedimentation rates and reworking of faunal elements.

In the preceding chapters various indications suggest that our *Miogypsina* record is interrupted by hiatuses. Sedimentary breaks are present in the record of the three *Miogypsinoidea* species and the oldest associations of *Miogypsina guntereri* in the lower part of Unit III. Furthermore, an interruption of the sedimentation may be present between the topmost association of *M. guntereritani* in Unit III and the association of *M. globulina-intermedia* in the basal part of Unit IV. On the other hand, highly variable sedimentation rates for Units III to V have been concluded from the vertical distribution of *Miogypsina* taxa and sediment properties (chapter IV).

From microfacies observations we know that the basal part of Unit III with respect to its upper part is rich in glauconite and phosphate, which suggests that the sedimentation rate for the lower part of Unit III is low in comparison with that for its upper part. This may partly explain the decrease in \bar{X} observed for *Miogypsina* s.s. in the older part of Unit III and the near-stasis of this mean in the younger part of this unit. In this reasoning it has been assumed that the rate of sustained evolution in *Miogypsina* s.s. is more or less constant.

In Unit V we see a more or less opposite pattern. The upward increase in glauconite content in Unit V and the presence of hardgrounds in its top part suggest a lowering of the sedimentation rate with time. This may partly explain the relatively thick lower interval of Unit V with near-stasis in \bar{V} and the distinct positive change in this variable for the upper part of the unit.

The presence of worn specimens of *Miolepidocyclina burdigalensis* in Unit V is probably the result of reworking of older Burdigalian sediments. A similar reworking of older specimens of *Miogypsina* s.s. might be held responsible for the backward pulses in \bar{V} that have been noticed for the sample pairs JT7979-JT5124 and JT5134-JT5140. Proof in favour of the presence of reworked elements in the *Miogypsina* s.s. assemblages of JT5124 or JT5140 has not been found. On the other hand, the presence of a worn specimen of *Miolepidocyclina burdigalensis* in JT5124 suggests that reworking of older faunal elements did take place for this sample interval.

For our evaluation of the evolutionary meaning of the observed morphometric patterns it is of great importance that we can rule out the effects of significant sedimentary breaks. Such a requirement is met best in the dataset gathered from Unit V. For this interval we must accept, however, that changes

in the sedimentation rate probably had an influence on the observed morphometric patterns for *Miogypsina* s.s. and that reworking of older faunal elements cannot be excluded.

The following discussion of the details of morphometric change in *Miogypsina* thus will be largely restricted to the Burdigalian Unit V because of its rather detailed dataset and the probable absence of notable sedimentary gaps.

V.3.2 Evolution in *Miogypsina* s.s.

In this and many earlier investigations it is the variable \bar{V} that has been used to describe the nepionic evolution of Burdigalian *Miogypsina* s.s. and to identify the successive biometric species. Our discussion will focus on the changes in this variable.

For the Burdigalian *Miogypsina* s.s. near Mineo \bar{V} shows a distinct positive trend with a net shift of about 3 ' $\bar{\sigma}$ ' ($\bar{\sigma}$ = average standard deviation). Looking in some more detail at the development of \bar{V} it is easily noticed that the changes are not gradual at all, intervals with stasis alternate with forward or backward pulses. The negative shifts in \bar{V} attain the maximum magnitude of 1.6 ' $\bar{\sigma}$ ' in the interval between JT7974 and JT5124; the value of 0.75 ' $\bar{\sigma}$ ' is found for the interval between JT5134 and JT5140.

The possible influence of variable sedimentation rates and of reworking on \bar{V} has been discussed already. It could not be excluded that they modified the time-bound pattern of \bar{V} . Another source of complications is whether or not and if so to what degree ecological factors might have controlled the changes in the variables, and especially in \bar{V} .

It has already been suggested that the diameter of the protoconch may change in relation to water depth or some depth-linked factor. According to theory (Drooger & Raju, 1973) protoconch diameter would increase towards greater depth. If furthermore some correlation would exist between embryonic size and nepionic parameters, such ecological factors could indirectly have affected the values of \bar{V} and \bar{D}_1 . An examination of the intra- and intersample correlations between the embryonic and nepionic variables is needed to evaluate this constraint.

\bar{V} - \bar{D}_1 is the only couple of embryonic and nepionic sample means, which shows a significant positive correlation at $P = 0.01$. This positive correlation for the entire Unit V is not found for its parts P, Q_1 and Q_2 . The \bar{V} - \bar{D}_1 correlation probably reflects no more than the long-term evolutionary trends of embryo and nepiont.

The shifts in \bar{V} and \bar{D}_1 from an older stratigraphical subunit to the next younger one are not parallel. The tendency of \bar{V} to increase from P to Q_1 (disregarding JT5124) and from Q_1 to Q_2 is not accompanied by unidirectional changes in \bar{D}_1 .

Our conclusion is that the positive correlation between \bar{V} and \bar{D}_1 probably is not the result of a functional relation between both statistics. If the mean size of the embryo was somehow determined by a depth-linked ecological factor, this effect probably was not reflected in parameter \bar{V} . On the contrary, the supposed shallowing during the deposition of Unit V would theoretically have caused a decrease in \bar{D}_1 instead of the general increase that we found. We think that we can rule out the effects of environment on the succession of \bar{V} values. This conclusion is in good harmony with the fact that intrasample V- D_1 correlations are hardly ever of statistical significance.

According to certain evolutionary theories (see below) we need low-frequency populations for rapid changes in morphology. As a check on such a possible relation we plotted the relative frequencies of *Miogypsina* s.s. from figure 14 in our figure 44, together with the means of V and D_1 . Conclusions to be drawn have a dubious value, however.

Because of the closed-sum effect, the changes in the relative frequency of *Miogypsina* s.s. do not necessarily reflect changes in the absolute numbers. The low relative frequencies of *Miogypsina* s.s. were concluded from the low total numbers (≤ 20 specimens/9 cm²) in thin-sections of samples that often are not the same as those from which the means were calculated. Furthermore the observed low-frequency zones for *Miogypsina* s.s. may be of local significance only because of the patchy distribution of the standing stock. A local low-frequency zone may be the result of a lateral shift of the larger foraminiferal populations and does not necessarily have a bearing on the regional frequency distribution in time.

In figure 44 three low-frequency zones of *Miogypsina* s.s. have been entered. The lowermost zone between levels 3 and 4, and straddling the P-Q boundary, is the most distinct one. Especially the middle one, based on three samples only, is very subjective. The uppermost zone in the top part of interval Q₂ is again more realistic.

The lowest \bar{V} values of Unit V are found in the low-frequency interval between levels 3 and 4 and correspond to a negative change followed by a leap forward at the top. We cannot exclude the possibility that reworking of older *Miogypsina* s.s. must be held responsible for the negative shift. Also \bar{D}_1 shows a set back halfway this lowermost zone of low relative numbers.

With increasing frequencies of *Miogypsina* s.s. across level 4, \bar{V} shows a notable increase, decrease and weak increase again into the middle low-frequency zone followed by a staggered increase across level 6 towards the top of Unit V.

Although significant fluctuations in \bar{V} seem to occur rather independently of

the low-frequency zones it must be admitted that following each of the two lower zones \bar{V} values are found to fluctuate at higher levels and also the \bar{D}_1 levels are different, though without a similar unidirectional pattern.

Apparently a significant part of the morphological changes in *Miogypsina* s.s. is associated with the intervals, in which this subgenus is present in low proportions. The lower and upper interval in Unit V with low relative frequencies of *Miogypsina* s.s. are preceded by distinct, but different changes in the overall composition of the larger foraminiferal assemblages (fig. 14). The middle low-frequency zone of *Miogypsina* s.s. does not stand out by a marked change in the overall composition of the assemblages of larger foraminifera. Evidently there is no uniform relation between the low-frequency zones of *Miogypsina* s.s. and overall faunal changes.

The morphometric changes in between the low-frequency zones seem to have

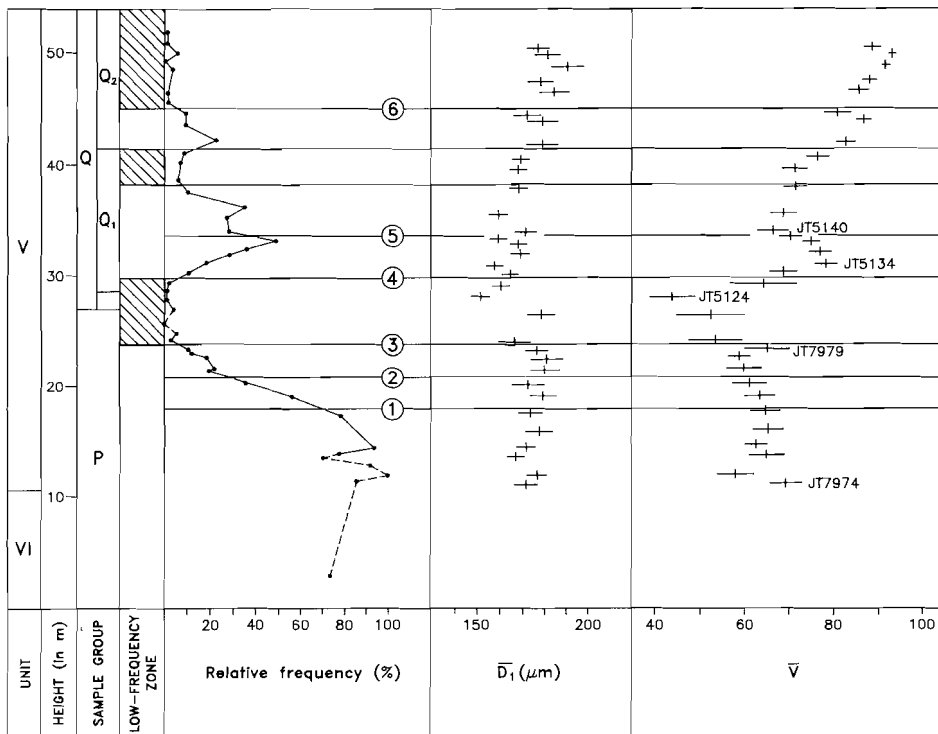


Fig. 44: Frequency of *Miogypsina* s.s. in Unit V and shifts in \bar{V} and \bar{D}_1 , illustrating the supposed relation between low-frequency zones and evolutionary changes. The lines 1-6 mark changes in faunal composition (see section II.4).

a random nature. \bar{V} shows a vague negative trend in the sample group P and in the sample group Q₁ no significant trend in this variable is present. The number of samples in Q₂ is too small to perform statistical tests for trends just below and within the upper low-frequency zone.

The variation in \bar{V} is limited for the successive sample groups bounded by the low-frequency zones. The total variation in \bar{V} for Unit V amounts to about 3 'σ', whereas it is about 0.7 'σ' in the sample group P and about 0.9 'σ' in Q₁ ('σ' = average standard deviation). The variation in \bar{V} for the sample set of Q₂ below the upper low-frequency zone is about 0.5 'σ' and in this topmost zone it equals about 0.7 'σ'.

In these upper sample groups the magnitude of the larger backward shifts in \bar{V} varies between 0.5 and 0.7 'σ'. These values are small relative to the value of about 1.6 'σ' for the maximum negative pulse to the \bar{V} in JT5124 in the lower low-frequency zone of Unit V.

Summarizing, we suggest that there was some link in the evolution of our Burdigalian *Miogypsina* s.s. to episodes with low frequencies of this subgenus. Evolutionary change seems to be of subordinate importance in the periods in between, when *Miogypsina* s.s. was relatively more frequent.

From the enumerated data it is apparent that the evolutionary model of phyletic gradualism can be discarded in the explanation of the changes in our *Miogypsina* s.s. A description in terms of pulsations or punctuations seems to be more appropriate.

The pattern in the succession of \bar{V} values for our *Miogypsina* s.s. in Unit V shows resemblance to the pattern of forward and backward changes observed in the Late Miocene *Planorbulinella* from Crete (M.M. Drooger et al., 1979). The variable \bar{V} of *Miogypsina* s.s. also displays some pulses or shifts which are opposed to the principle of nepionic acceleration. In both lineages the backward pulses do not exceed the morphometric range of single species. Nevertheless the negative shifts in our *Miogypsina* s.s. seem to be less impressive than in *Planorbulinella* because of the larger and more distinct overall change in line with the principle of nepionic acceleration. The evolutionary pattern in the Campanian *Orbitoides* from southwestern France (Drooger & De Klerk, 1985) is different in another way from our *Miogypsina* example. The *Orbitoides* show two stasis periods separated by a very distinct punctuation, which is in accordance with the principle of nepionic acceleration. The punctuation in *Orbitoides* is far more outstanding than the individual sample-to-sample progressive shifts in our *Miogypsina* s.s.

In the case study of *Planorbulinella* the term pulsating evolution was introduced to describe the pattern with both rapid backward and forward changes (M.M. Drooger et al., 1979). The concept of punctuated equilibria as

defined by Eldredge & Gould (1972) was considered to be inadequate because it originally pertained to rapid advantageous changes only. Afterwards Gould (1977) stated that speciation is stochastic with respect to long-term evolutionary trends, which in our opinion would mean that punctuations are not by definition unidirectional. For this reason we do not make a distinction between pulsations and punctuations in the characterization of the evolutionary changes in our *Miogypsina* s.s.

The pattern of evolutionary change observed in *Miogypsina* s.s. in Unit V can to some extent be described in terms of punctuations or of changes of limited duration alternating with periods of near-stasis. The punctuations seem to have a relation with the low-frequency zones of *Miogypsina* s.s. The intervals in between represent phases of near-stasis in \overline{D}_1 and \overline{V} , i.e. periods with relatively minor net changes, probably of random character.

In addition to the observed trends in the means of *Miogypsina* s.s. from the Mineo carbonates overall changes have been noticed in the corresponding morphotype ranges. In evaluating the changes in morphotype ranges it must be realized that sampling hazards hamper an accurate determination of the first or last occurrence of a specific morphotype. Furthermore, the real exit of a specific morphotype may be obscured by reworking phenomena.

Directing our attention to Unit V, we see that the total range of V-morphotypes is present in the lower part of this unit (sample group P) already. All V-morphotypes with the exception of the class 90-100 were already introduced in the Aquitanian *M. gunteri-tani*, but generally with very low frequencies. The range of V in Unit V is progressively reduced with in total 6 classes ($\overline{V} = 0-60$). Part of this reduction seems to coincide with the general shifts in \overline{V} in or across the low-frequency zones of *Miogypsina* s.s., but exits of V-morphotypes occur in the intervals between these zones as well.

One X-morphotype ($X = 3$) enters the *Miogypsina* s.s. record in Unit V, viz. in sample group P. Three morphotypes ($X = 8, 7$ and 6) disappear from the record in Unit V. These exits seem to be situated in the low-frequency zones of *Miogypsina* s.s.

Advanced γ -morphotypes ($90^\circ-165^\circ$) have been encountered in very low numbers in sample group P of Unit V. Two of these classes ($90^\circ-120^\circ$) become of more importance in the assemblages of the upper low-frequency zone in Unit V. One class of γ -morphotypes ($-15^\circ-0^\circ$) disappears in this zone.

The range of embryo-morphotypes does not display a distinct net shift throughout Unit V.

Although part of the morphotype shifts is associated with the intervals in which distinct changes in the corresponding mean values occur, they certainly

are not exclusive for these zones. When morphotypes of V and γ entered the record of *Miogypsina* s.s. they did not immediately expand in the assemblages.

The supposed relation between notable morphological changes and low frequencies of *Miogypsina* s.s. seems to be logical from the viewpoint of evolutionary theory. Several theories emphasize that evolutionary change occurs predominantly in small isolated populations. By contrast, evolutionary change is thought to be impossible in large populations with substantial gene flow. In the theory of punctuated equilibria (Eldredge & Gould, 1972) the small isolated populations are situated at the periphery of the main area of distribution. After the development to a better adapted species in such peripherally isolated populations the new forms are assumed to have migrated to the area of the unchanged main stock and to have replaced the ancestral forms.

Applying this theory to the changes of *Miogypsina* s.s. in the assumed low-frequency zones in Unit V would mean that the observed changes are not the reflection of in situ evolutionary processes, but merely the result of successive immigrations of populations which differ morphologically from the standing stock. In our opinion there is no compelling reason to accept beforehand the theory of faunal migrations to explain the changes in our time series of *Miogypsina* s.s.

For our case study we may just as well consider in situ evolutionary changes. The assumed low-frequency intervals in the sequence of *Miogypsina* s.s. assemblages possibly reflect local conditions, which would have promoted speciation in small populations. Such a theory of sympatric evolutionary change during frequency bottlenecks was elaborated by Drooger (1984) to explain the observed morphological changes in other orbitoidal foraminifera, like *Planorbulinella* and *Orbitoides*. The theory accounts for the occurrence of random changes as well as overall trends in the nepionic evolution of the orbitoidal foraminifera. One of the objections of this author against the theory of marginal isolation and subsequent migration concerns the poor chance of the small peripheral population to replace the large central ancestral one. The theory of frequency bottlenecks fits in with our conclusion that a substantial part of evolutionary changes in *Miogypsina* s.s. is linked to the assumed low-frequency zones.

However, the available data do not permit us to exclude the possibility of immigrations of *Miogypsina* s.s. in the Mineo area after periods of low frequency. Furthermore the theory of frequency bottlenecks does not offer an explanation for the introduction or disappearance of specific morphotypes in the *Miogypsina* record.

Chapter VI

REMARKS ON TAXONOMY

The taxonomical identification of the larger foraminifera is based on biometric criteria, the principles of which were defined by Drooger (1952). Additional taxonomical and morphological remarks will be presented below for the species of *Miogypsina*, *Cyclochypus* and *Lepidocyclina*.

Family MIOGYPSINIDAE

Genus *Miogypsina* Sacco, 1893

Subgenus *Miogypsinoides* Yabe & Hanzawa

Miogypsina (*Miogypsinoides*) *complanata* Schlumberger

Pl. 2, fig. 9, pl. 3, fig. 12, tabs. 4, II

Miogypsina complanata Schlumberger, 1900, p. 330, pl. 2, figs. 13-16; pl. 3, figs. 18-21.

Miogypsina (*Miogypsinoides*) *complanata* Schlumberger, Drooger, 1954a, pp. 230-232, only the assemblage from his locality 1: Villa Giuseppina.

Assemblages of this species are characterized by \bar{X} values larger than 17 (Drooger, 1963; Raju, 1974).

The trochoid character of the primary spiral is well recognizable in the specimens of the Mineo assemblage in sample JT7324. \bar{Y} , the mean number of spiral chambers with only one stolon, has the relatively high value of 9.5. As to the mean embryon size, the Mineo association is well comparable to those of the nominate species from north Italian and French localities.

Miogypsina (*Miogypsinoides*) *formosensis* Yabe & Hanzawa

Pl. 2, fig. 10, pl. 3, fig. 13, tabs. 4, II

Miogypsina (*Miogypsinoides*) *dehaartii* Van der Vlerk var. *formosensis* Yabe & Hanzawa, 1928, p. 534, figs. 1a-b.

Miogypsina (*Miogypsinoides*) *formosensis* Yabe & Hanzawa, De Bock, 1976, p. 15.

The assemblages of this species have \bar{X} values between 17 and 13 (Drooger, 1963; Raju, 1974).

In the association of sample JT7344, the mean number of spiral chambers with only one stolon (\bar{Y}) is 6. Considering the mean embryon size, this association shows some resemblance with *M. formosensis* reported from French localities.

Miogypsina (Miogypsinoidea) bantamensis (Tan Sin Hok)

Pl. 2, figs. 5-7, pl. 3, figs. 1-11, tabs. 4, 14, II, IV

Miogypsinoidea complanata forma *bantamensis* Tan Sin Hok, 1936, pp. 48-50, pl. 1, fig. 13.

Miogypsina (Miogypsinoidea) complanata Schlumberger, Drooger, 1954a, pp. 230-232, only the assemblage from his locality 2.

Miogypsina (Miogypsinoidea) complanata Schlumberger *mauretanicum* Brönnimann, Souaya, 1961, pp. 672-676, pl. 1, figs. 1-10, pl. 2, figs. 1-13.

Miogypsina (Miogypsinoidea) bantamensis Tan Sin Hok, De Bock, 1976, p. 15, pl. 1-4, pl. 5, fig. 1, pl. 6-14, 33, 41.

Populations of *Miogypsinoidea* with values of \bar{X} between 13 and 10 are determined as *M. bantamensis* (Drooger, 1963; Raju, 1974).

On the basis of embryon size, two groups of assemblages of *Miogypsinoidea* close to *M. bantamensis* can be recognized in Unit III. The Mineo assemblages that are marked by specimens with a relatively large embryon (type II), are in fact intermediates between *M. bantamensis* and *M. dehaartii*. The mean protoconch diameter in type II assemblages ranges from 210 to 230 μm . \bar{Y} , the mean number of chambers in the primary spiral with only one stolon, is about 2.5 in our samples. Type II assemblages are well comparable to the associations of *Miogypsinoidea* of European origin, e.g. from north Italy.

The associations of *Miogypsinoidea* that are marked by a relatively small embryon (type I), have a mean protoconch diameter of about 110 to 125 μm . The associations in Unit III are intermediate between *M. formosensis* and *M. bantamensis*. Their mean number of spiral chambers with one stolon (\bar{Y}) is about 5. In Unit V type I is represented by more distinct associations of *M. bantamensis*, which sometimes are transitional to *M. dehaartii*. D_1 varies between 125 and 150 μm in Unit V. Type I shows distinct resemblance with African assemblages, such as those from Nigeria and Egypt.

With future, larger data sets on the two types of Mediterranean *Miogypsinoidea*, one might become more certain about the concurrence of two distinct species.

Subgenus **Miogypsina** Sacco

Miogypsina (Miogypsina) gunteri Cole

Pl. 2, fig. 8, pl. 4, figs. 6-9, tabs. 19, I

Miogypsina gunteri Cole, 1938, p. 42, pl. 6, figs. 10-12, 14; pl. 8, figs. 1-9.

Miogypsina (Miogypsina) gunteri Cole, Drooger, 1954a, pp. 232-233, pl. 2, figs. 25-27; De Bock, 1976, p. 17, pl. 5, fig. 2.

Populations of *Miogypsina* with lateral chambers and values of \bar{X} between 12.5 and 9 are named *M. gunteri* (Drooger, 1952).

Typical assemblages of this species have been encountered in the lower part of Unit III (Lamia and Donna Ragusa sections). In the upper part of this unit (section Lamia) populations of *Miogypsina* s.s. are intermediate between *M. gunteri* and *M. tani*. Part of the specimens in the assemblages of *M. gunteri* have a second principal auxiliary chamber. They constitute up to 20% of the assemblages. The stage of development of the complex of lateral chambers shows considerable variation, as can be seen in the whole-rock thin-sections from the interval with *M. gunteri* (JT7303/6-JT5043). The morphology of the sidewalls in *Miogypsina* s.s. may range in one rock sample from partly massive with only a few lateral chambers to a fully developed complex of lateral chambers. Pillars of variable size are intercalated in the complex of lateral chambers in 5 to 40% of the specimens of *Miogypsina* s.s. that are cut in the whole-rock thin-sections.

***Miogypsina (Miogypsina) tani* Drooger**

Pl. 4, figs. 1, 2, tabs. 19, I

Miogypsina (Miogypsina) tani Drooger, 1952, pp. 26, 27, 51, 52, pl. 2, figs. 20-24; pl. 3, figs. 2a, b. Drooger et al., 1955, pp. 23, 24, pl. 1, figs. 11-15.

This species is characterized by \bar{X} values below 9 and by the presence of a second principal auxiliary chamber in less than half of the specimens per sample (Drooger, 1952; 1954a).

Typical *M. tani* has only been identified in sample JT5055. Quite a number of samples from the upper part of Unit III in the section Lamia contain associations of *M. ex. interc. gunteri-tani*. An assemblage intermediate between *M. tani* and *M. socini* was found once (JT5051/7116).

***Miogypsina (Miogypsina) socini* Drooger**

Pl. 4, figs. 4, 5, tabs. 19, I

Miogypsina (Miogypsina) socini Drooger, 1954a, pp. 233-235, fig. 2. Schüttenhelm, 1976, p. 64, pl. 1, figs. 1-5. Schiavinotto, 1979, pp. 259-261, figs. 1-5.

M. socini is marked by values of \bar{X} being larger than 7. At least 50 percent of the specimens per assemblage possess a second principal auxiliary chamber. Up to half of the specimens per assemblage have an embryo which is at a slight distance from the apical periphery of the test (Drooger, 1954a; Schüttenhelm, 1976).

Distinct *M. socini* has been identified in sample JT5054 from Unit III in the Lamia section. This assemblage conforms very well to the diagnosis of *M. socini* (Drooger, 1954a). Comparing our association with the one from the type locality in northern Italy, some small differences are apparent in the nepionic

parameters. The values of P and CT are about the same in both regions, but our Sicilian assemblage seems to have a somewhat more advanced, nepionic stage ($\bar{X} = 8.3 \pm 0.28$, $\bar{\gamma} = -29^\circ \pm 8.6^\circ$, $\bar{V} = 21 \pm 3.8$). The nepiont of *M. socini* in northern Italy is characterized by $\bar{X} = 9.1 \pm 0.34$, $\bar{\gamma} = -51^\circ \pm 8.0^\circ$ and $V = 14 \pm 2.7$.

Miogypsina (Miogypsina) intermedia Drooger

Pl. 2, fig. 3, pl. 5, figs. 4-8, tabs. 19, III

Miogypsina (Miogypsina) intermedia Drooger, 1952, pp. 35, 55, pl. 2, figs. 30-34; pl. 3, fig. 4; Souaya, 1961, p. 672, pl. 1, figs. 11-20; pl. 3, figs. 1, 2, 7, 10-12; pl. 4, figs. 1-12; Smit, 1974, pp. 433-436, fig. 1; Schüttenhelm, 1976, pp. 65, 66, pl. 3, figs. 7, 8. Schiavinotto, 1979, pp. 268-270, figs. 5, 6.

This species is characterized by \bar{V} values between 45 and 70. More than 50% of the specimens per sample possess a second principal auxiliary chamber (Drooger, 1952).

Typical assemblages of *M. intermedia* have been met with in samples from the upper part of Unit IV and the lower part of Unit V. Assemblages that are transitional to *M. cushmani* have been recognized as well. Associations intermediate between *M. globulina* and *M. intermedia* have been identified from the samples JT5063 and JT5124. Distinct assemblages of *M. globulina* are not known from the Mineo carbonates.

All specimens of our *M. intermedia* have a second principal auxiliary chamber. In 58 to 78% of the specimens per sample, the two protoconchal spirals end in a common closing chamber. Whole-rock thin-sections from the interval with *M. intermedia* (JT5094-JT5112) indicate that this species possesses a well-developed complex of lateral chambers. Pillars alternate with the lateral chambers in about 20 to 60% of the specimens per rock sample.

Miogypsina (Miogypsina) cushmani Vaughan

Pl. 2, fig. 4, pl. 6, figs. 7-12, tabs. 19, III

Miogypsina cushmani Vaughan, 1924, pp. 802, 813, pl. 36, figs. 4-6; Drooger, 1954b, pp. 586, 589.

Miogypsina (Miogypsina) cushmani Vaughan, Souaya, 1961, p. 671, pl. 1, figs. 21-30; pl. 3, figs. 3-6, 8, 9.

According to the original biometric definition, the assemblages of this species are marked by values of \bar{V} between 70 and 100. In more than half of the specimens per sample, V should be smaller than 90 (Drooger, 1952). Raju (1974) noted for his Indo-Pacific *M. cushmani* that \bar{V} is usually smaller than 90. In our investigation the biometric species has been applied to assemblages with \bar{V} values between 70 and 90.

Distinct *M. cushmani* has been identified in several samples from the middle and upper part of Unit V. Populations of *M. ex. interc. cushmani-mediterranea*

have been encountered in the upper part of Unit V. In 88 to 100% of the specimens in our assemblages of *M. cushmani* the protoconchal spirals end in a common closing chamber. Whole-rock thin-sections from the intervals with *M. cushmani* (JT5134-JT5139A, JT5149-JT5161) have revealed that 10 to 60% of the specimens per thin-section have pillars in the complexes of lateral chambers.

Miogypsina (Miogypsina) mediterranea Brönnimann

Pl. 2, figs. 1, 2, pl. 6, figs. 1-6, tabs. 19, III

Miogypsina mediterranea Brönnimann, 1940, pp. 94-97, pl. 6, figs. 5, 10, 11, pl. 8, figs. 23, 24, pl. 9, fig. 11, pl. 10, figs. 1-4, pl. 11, figs. 2, 3, 5-7; Drooger, 1954b, pp. 586, 587.

Miogypsina mediterranea var. *excentrica* Brönnimann, 1940, pp. 98-100, pl. 6, figs. 12-16, pl. 8, figs. 12, 25, pl. 9, figs. 3, 10, 12, pl. 10, figs. 5, 12.

As to the configuration of the nepiont *M. mediterranea* is comparable to the American *M. antillea*. The assemblages of the former differ from those of the latter by a larger $\bar{\gamma}$ and by the presence of specimens with an embryo that is slightly removed from the periphery (Drooger, 1954b). *M. antillea* was defined on the basis of \bar{V} ranging from 70 to 100. Additionally, more than 50 percent of the specimens per sample should have a V value larger than 90 (Drooger, 1952; Raju, 1974). In our study the associations of *M. mediterranea* have been diagnosed on the basis of \bar{V} lying between 90 and 100 and the presence of specimens with a centripetal trend of the embryo.

Associations of *M. mediterranea* are present in the upper part of Unit V (JT5167 and JT5172). In the Mineo samples of this species $\bar{\gamma}$ appears to be distinctly larger than 50°, whereas in *M. antillea* $\bar{\gamma}$ is close to 0°. In 96 to 100% of the specimens per sample, the protoconchal spirals end in the closing chamber. A slight centripetal trend of the embryo is present in 4 to 18% of the specimens in the assemblages of *M. mediterranea* and *M. ex. interc. cushmani-mediterranea*.

Family NUMMULITIDAE

Genus *Cycloclypeus* Carpenter, 1856

Subgenus *Cycloclypeus* Carpenter

Cycloclypeus (Cycloclypeus) eidae Tan Sin Hok

Pl. 2, fig. 11, tabs. 21, V

Cycloclypeus eidae Tan Sin Hok, 1932, pp. 50-59, pl. 5, fig. 6, pl. 12, figs. 2, 3, pl. 13, figs. 1, 2, 4-6; Drooger & Roelofsen, 1982, pp. 206, 209, pl. 1, 2.

Cycloclypeus cf. *eidae* Tan Sin Hok, Felix, 1973, p. 68, pl. 2, fig. 9.

The Mineo assemblage of *Cycloclypeus* (JT7324) is morphologically close to the Indonesian *C. eidae* (Tan Sin Hok, 1932; Mac Gillavry, 1962). This species was also reported from Malta (Felix, 1973; Drooger & Roelofsen, 1982). The Maltese assemblage described by Drooger & Roelofsen has a smaller mean protoconch diameter ($\overline{D}_1 = 62 \mu\text{m}$) and a larger mean number of pre-annular chambers ($\overline{X} = 19.9$) than our Sicilian assemblage ($\overline{D}_1 = 87 \mu\text{m}$, $\overline{X} = 16.7$).

Family LEPIDOCYCLINIDAE

Genus **Lepidocyclina** Gümbel, 1868

Subgenus **Nephrolepidina** Douvillé
Tabs. 21, V

The embryonic and nepionic characteristics tabulated for our Lepidocyclinids fit very well into the European *Nephrolepidina* lineage (De Mulder, 1975; Drooger & Laagland, 1986). According to De Mulder's classification of European *Nephrolepidina* two types of exemplum intercentrale assemblages have been distinguished in the Mineo carbonates: *L. ex. interc. praemarginata-morgani* in sample JT7324 and *L. ex. interc. morgani-tournoueri* in JT7313-7315 and JT5063.

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Plate 1

Whole-rock thin-sections

- Fig. 1: Detail of very coarse grainstone grading into packstone with *Amphistegina*, *Miogypsina* s.s. and *Miogypsinoides*; just above level 5 in Unit V of the Lamia section (Burdigalian); sample JT7225, coll. no. MF3-181, appr. 20 \times .
- Fig. 2: Detail of coarse packstone grading into grainstone with *Amphistegina*; above level 6 in Unit V of section A₁ (Burdigalian); sample JT7069, coll. no. MF3-219, appr. 20 \times .
- Fig. 3: Detail of coarse packstone with *Miogypsina* s.s.; below level 1 in Unit V of the Lamia section (Burdigalian); sample JT7197, coll. no. MF3-153, appr. 20 \times .
- Fig. 4: Detail of very coarse grainstone grading into packstone with *Amphistegina* and *Miogypsinoides*; just below level 4 in Unit V of the Lamia section (Burdigalian); sample JT7218, coll. no. MF3-174, appr. 20 \times .
- Fig. 5: Detail of floatstone with *Lepidocyclina*, *Amphistegina*; lower part of Unit IV (Subunit A) of the Lamia section (Burdigalian); sample JT7143B, coll. no. MF3-99, appr. 7 \times .
- Fig. 6: Detail of very fine packstone with planktonic foraminifera and bioclastic hash; Unit IV of the Lamia section (Burdigalian); sample JT7145, coll. no. MF3-101, appr. 25 \times .
- Fig. 7: Detail of coarse packstone grading into floatstone with *Lepidocyclina*, *Pararotalia* and *Amphistegina*; lowermost part of Unit III of the Lamia section (Chattian); sample JT7052//, coll. no. MF3-55, appr. 6 \times .
- Fig. 8: Detail of coarse packstone with dissolution voids; both *Miogypsinoides* and *Miogypsina* s.s. are present; Unit III of the Donna Ragusa section (Aquitaniian); sample JT7308, coll. no. MF4-21, appr. 20 \times .

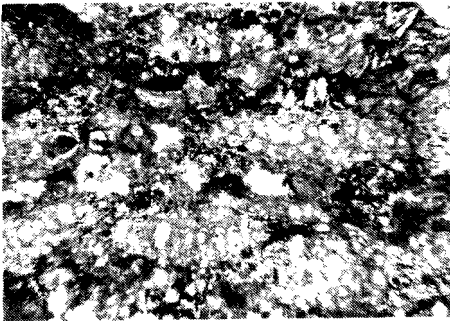
Plate 1



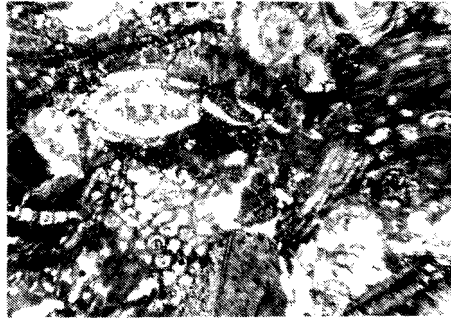
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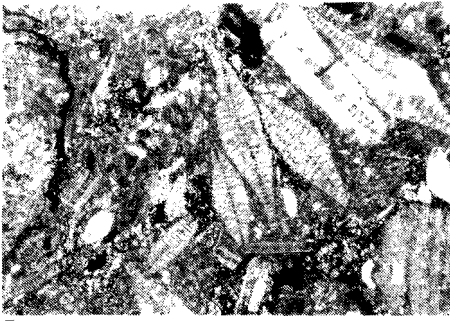
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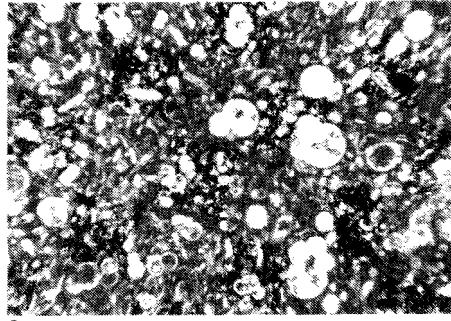
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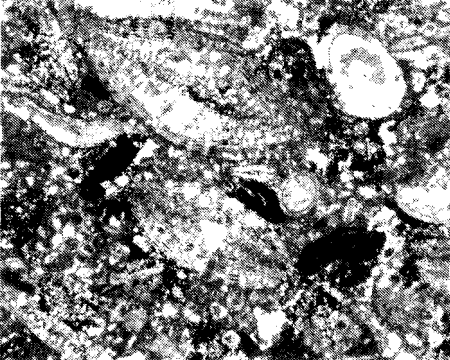
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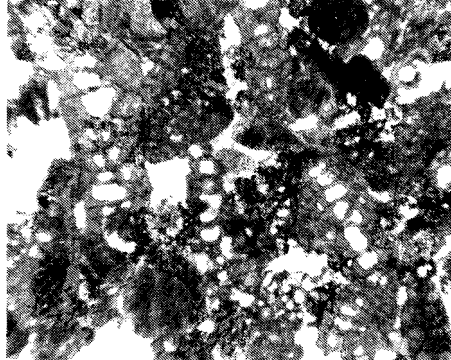
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Plate 2

Median sections of larger foraminiferal tests

- Figs. 1, 2: Morphotypes from *Miogypsina mediterranea* assemblages in Unit V of the Lamia section (Burdigalian); fig. 1: sample JT5172, coll. no. GFD166-23; fig. 2: sample JT5175, coll. no. GFD166-67.
- Fig. 3: Morphotype from *Miogypsina intermedia* assemblage in Unit V of the Lamia section (Burdigalian); sample JT5102, coll. no. GFD159-49.
- Fig. 4: Morphotype from *Miogypsina cushmani* assemblage in Unit V of the Lamia section (Burdigalian); sample JT5154, coll. no. GFD164-90.
- Fig. 5: Morphotype from *Miogypsinooides bantamensis* assemblage in Unit V of the Lamia section (Burdigalian); sample JT5140, coll. no. GFD168-37.
- Fig. 6: Morphotype from *Miogypsinooides ex. interc. bantamensis-dehaartii* assemblage (type II) in Unit III of the Lamia section (Aquitanian); sample JT7124, coll. no. GFD156-84.
- Fig. 7: Morphotype from *Miogypsinooides ex. interc. formosensis-bantamensis* assemblage (type I) in Unit III of the Lamia section (Aquitanian); sample JT7124, coll. no. GFD156-63.
- Fig. 8: Morphotype from *Miogypsina gunteri* assemblage in Unit III of the Donna Ragusa section (Aquitanian); sample JT5601, coll. no. GFD154-60.
- Fig. 9: Morphotype from *Miogypsinooides complanata* assemblage in Unit III of the Donna Ragusa section (Chatian); sample JT7324, coll. no. GFD151-93.
- Fig. 10: Morphotype from *Miogypsinooides formosensis* assemblage in Unit III of the Donna Ragusa section (Chatian); sample JT7344, coll. no. GFD152-16.
- Fig. 11: Morphotype from *Cycloclypeus eidae* assemblage in Unit III of the Donna Ragusa section (Chatian); sample JT7324, coll. no. GFD151-2.

Magnifications lie between 30 and 35×.

Plate 2

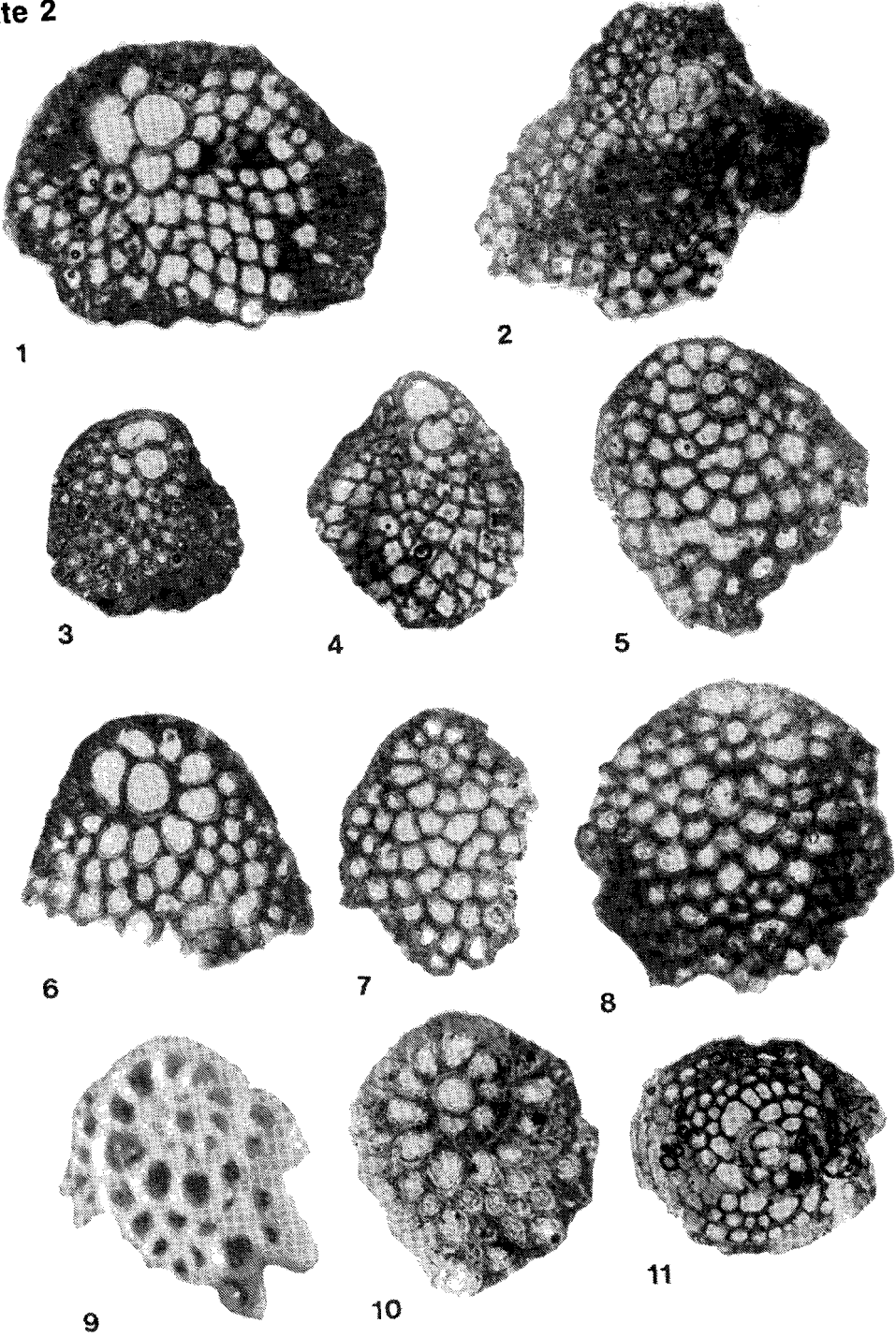


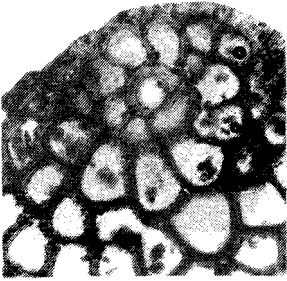
Plate 3

Embryonic-nepionic stages in median sections

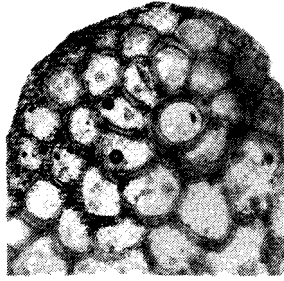
- Figs. 1-6: Various morphotypes from *Miogypsinoideaes bantamensis* assemblages in Unit V of the Lamia section (Burdigalian); figs. 1, 3, 6: sample JT5124, coll. no. GFD167-32, -45, -37, respectively; figs. 2, 4, 5: sample JT5140, coll. no. GFD168-44, -47, -37, respectively.
- Figs. 7-9: Various morphotypes from *Miogypsinoideaes ex. interc. formosensis-bantamensis* assemblage (type I) in Unit III of the Lamia section (Aquitanian); sample JT7124, coll. no. GFD156-64, -63, -76, respectively.
- Figs. 10, 11: Morphotypes from *Miogypsinoideaes ex. interc. bantamensis-dehaartii* assemblage (type II) in Unit III of the Lamia section (Aquitanian); sample JT7124, coll. no. GFD156-83, -84, respectively.
- Fig. 12: Morphotype from *Miogypsinoideaes complanata* assemblage in Unit III of the Donna Ragusa section (Chartian); sample JT7324, coll. no. GFD151-93.
- Fig. 13: Morphotype from *Miogypsinoideaes formosensis* assemblage in Unit III of the Donna Ragusa section (Chartian); sample JT7344, coll. no. GFD152-16.

The apical-frontal lines of the tests are oriented about perpendicular to the upper sides of the photos. Magnifications lie between 50 and 60 \times .

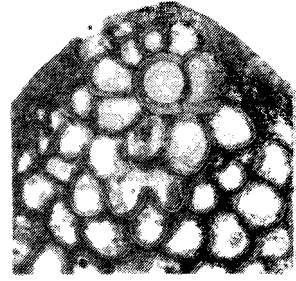
Plate 3



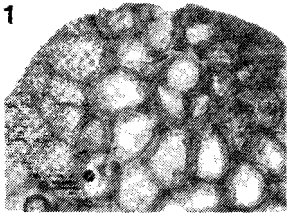
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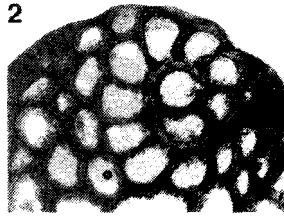
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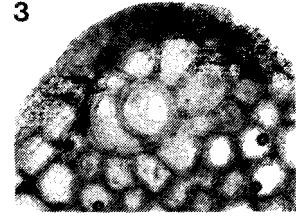
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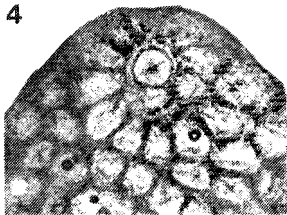
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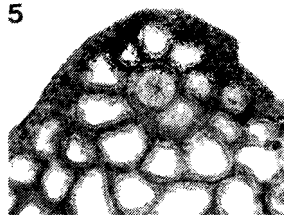
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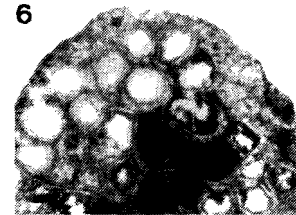
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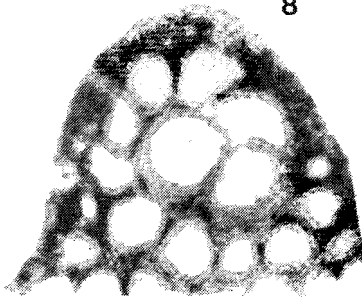
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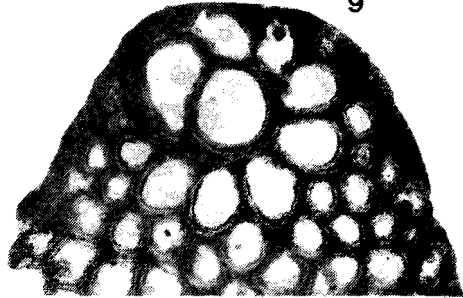
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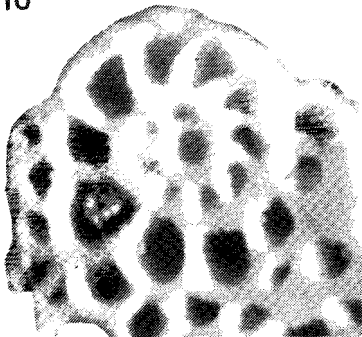
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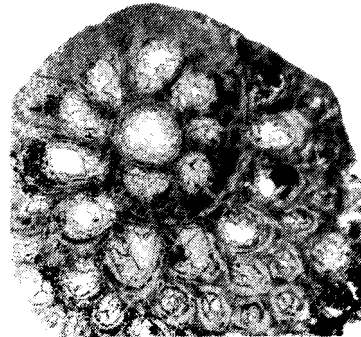
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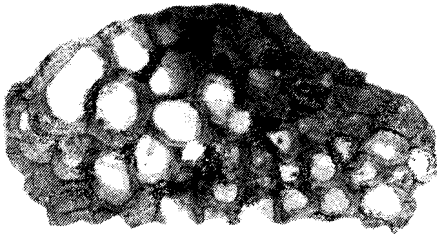
Plate 4

Embryonic-nepionic stages in median sections

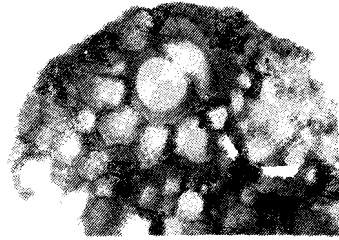
- Figs. 1, 2: Morphotypes from *Miogypsina tani* assemblage in Unit III (breccias) of the Lamia section (Aquitanian); sample JT5055, coll. no. GFD152-85, -69, respectively.
- Fig. 3: Morphotype from *Miogypsina* ex. interc. *tani-socini* assemblage in Unit III of the Lamia section (breccias; Aquitanian); sample JT5051, coll. no. GFD152-57.
- Figs. 4, 5: Morphotypes from *Miogypsina socini* assemblage in Unit III of the Lamia section (breccias; Aquitanian); sample JT5054, coll. no. GFD153-11, -16, respectively.
- Figs. 6-9: Various morphotypes from *Miogypsina gunteri* assemblages in Unit III (Aquitanian); figs. 6, 7, 8: Donna Ragusa section, sample JT7305, coll. no. GFD153-61, sample JT5601, coll. no. GFD154-60, sample JT7306, coll. no. GFD153-36, respectively; fig. 9: section Lamia, sample JT5042, coll. no. GFD155-46.

Magnifications lie between 50 and 60 \times .

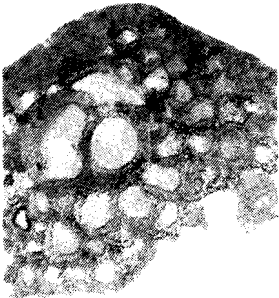
Plate 4



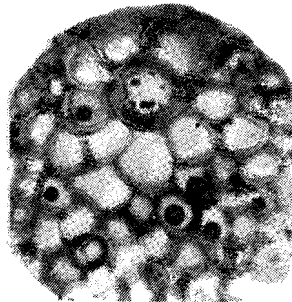
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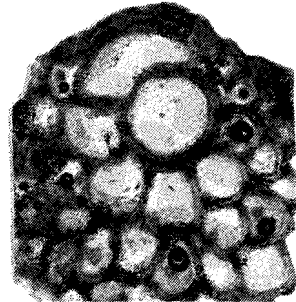
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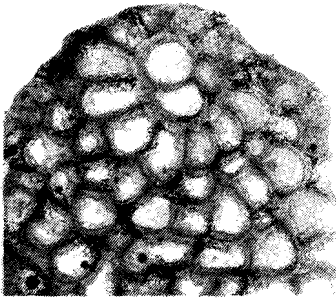
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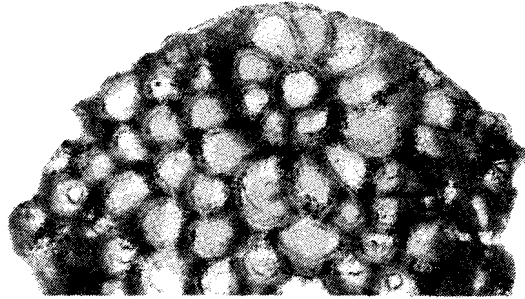
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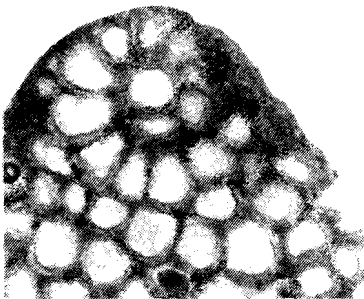
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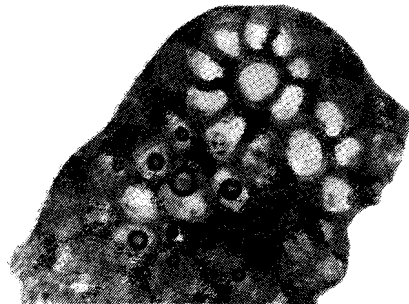
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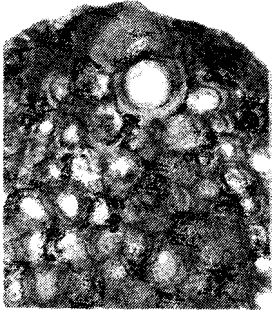
Plate 5

Embryonic-nepionic stages in median sections

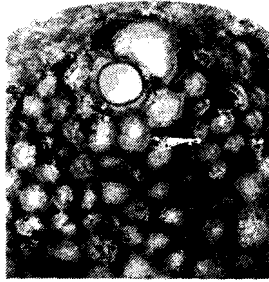
- Figs. 1-3: Various morphotypes from *Miogypsina ex. interc. globulina-intermedia* assemblage in Unit V of the Lamia section (Burdigalian); sample JT5124, coll. no. GFD161-68, -69, -67, respectively.
- Figs. 4-8: Various morphotypes from *Miogypsina intermedia* assemblages in Unit V of the Lamia section (Burdigalian); sample JT7975, coll. no. GFD159-56, sample JT5098, coll. no. GFD159-6, sample JT5102, coll. no. GFD159-49, sample JT5112, coll. no. GFD161-8, sample JT7977, coll. no. GFD160-30, respectively.
- Figs. 9-12: Various morphotypes from *Miogypsina ex. interc. globulina-intermedia* assemblage in the basal part of Unit IV of the Lamia section (Subunit A; Burdigalian); sample JT5063, coll. no. GFD157-46, -48, -37, -50, respectively.

Magnifications lie between 50 and 60 \times .

Plate 5



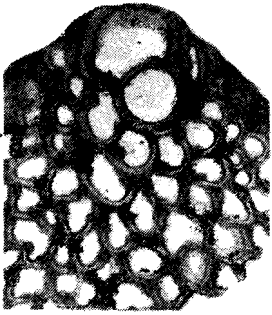
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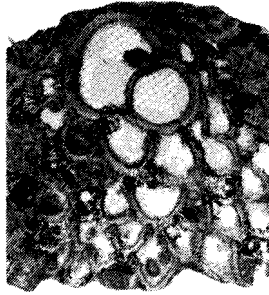
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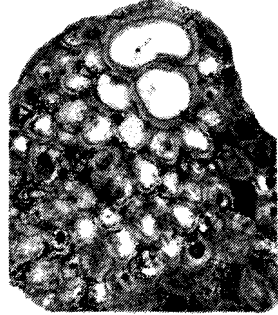
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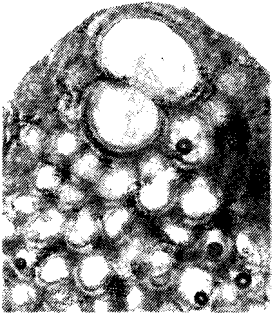
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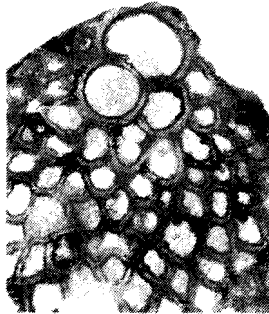
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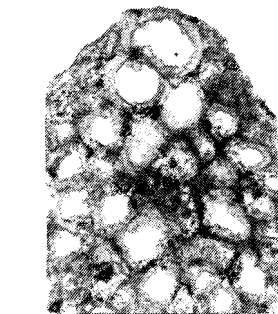
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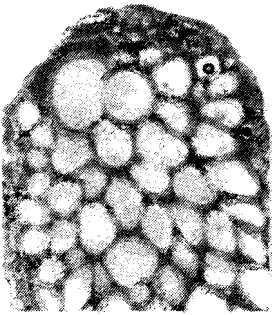
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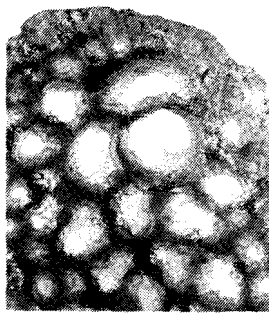
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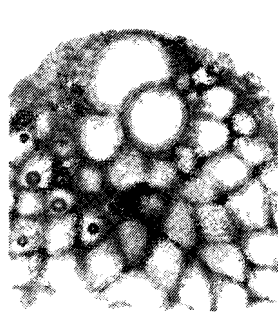
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Plate 6

Embryonic-nepionic stages in median sections

Figs. 1-6: Various morphotypes from *Miogypsina mediterranea* assemblages in Unit V of the Lamia section (Burdigalian); figs. 1-3: sample JT5175, coll. no. GFD166-59, -68, -67, respectively; figs. 4, 5: sample JT5172, coll. no. GFD166-36, -23, respectively; fig. 6: sample JT5167, coll. no. GFD165-92.

Figs. 7-12: Various morphotypes from *Miogypsina cushmani* assemblages in Unit V of the Lamia section (Burdigalian); figs. 7-9: sample JT5154, coll. no. GFD164-90, -95, -96, respectively; figs. 10, 11: sample JT5134, coll. no. GFD162-36, -28, respectively; fig. 12: sample JT5149, coll. no. GFD164-42.

Magnifications lie between 50 and 60 \times .

TABLES WITH STATISTICS ON THE
LARGER FORAMINIFERA
(I-V)

Table I: Basic statistics for *Miogypsina* s.s. in Unit III. σ = standard deviation of sample; N = number of observations in sample.

Sample	\bar{X}	σ	N	$\bar{\gamma}$	σ	N	$\overline{D_1}$ (μm)	σ	N	$\overline{D_2}$ (μm)	σ	N
Section Lamia												
JT7135	9.2	1.59	26	-56°	57.0°	27	149	26.5	31	161	33.3	26
JT7126	8.5	0.55	6	-37°	24.4°	6	151	30.5	7	167	47.0	6
JT7124	9.3	1.49	30	-43°	52.6°	28	171	35.4	34	179	41.0	30
JT7120	8.8	0.92	10	-25°	31.4°	12	170	34.3	14	209	52.6	10
JT5054	8.3	1.53	31	-29°	48.7°	32	171	36.3	32	184	41.5	27
JT5055	7.7	0.87	16	-15°	30.5°	15	165	28.4	23	192	36.9	16
JT5051/7116	8.7	1.03	13	-6°	53.8°	14	166	33.7	16	189	54.0	14
JT7115/7969	8.9	1.16	15	-51°	64.8°	15	160	33.5	21	174	37.2	13
JT5045	9.1	1.98	16	-67°	56.1°	16	155	26.9	16	161	40.9	15
JT5043	10.0	2.21	19	-104°	52.7°	20	140	18.1	20	142	20.3	15
JT5042	9.5	1.73	12	-100°	47.7°	11	135	25.3	12	143	40.6	11
Section Donna Ragusa												
JT7290	9.9	2.37	25	-78°	86.7°	23	162	38.8	33	174	48.6	29
JT7280	10.6	2.34	14	-112°	71.5°	13	150	44.0	14	163	53.3	13
JT5601	9.8	1.67	20	-98°	53.7°	20	137	27.2	19	145	25.0	14
JT7314/5	10.5	1.70	11	-88°	75.4°	11	149	31.2	13	162	42.4	10
JT7313	10.8	1.62	24	-102°	52.1°	26	144	24.0	28	146	28.6	23
JT7305	11.2	1.69	29	-123°	36.8°	29	136	23.4	29	138	28.0	29
JT7303/6	11.8	1.91	17	-140°	56.1°	17	125	22.7	17	131	26.3	16

Table II: Basic statistics for *Miogypsinoides* in Unit III.

Sample	Type	\bar{X}	σ	N	$\bar{\gamma}$	σ	N	\bar{D}_1 (μm)	σ	N	\bar{D}_2 (μm)	σ	N
Section Lamia													
JT7124	II	10.3	1.38	7	-113°	65.2°	6	231	23.4	7	228	35.6	7
JT7124	I	13.2	2.09	19	-169°	66.5°	20	113	20.4	19	118	25.2	19
JT5042/5	I	12.3	2.12	9	-156°	55.0°	9	122	24.0	9	123	25.5	9
Section Donna Ragusa													
JT7313/5/5601	II	10.4	1.62	12	-118°	62.0°	12	210	15.9	12	229	15.1	10
JT7305/6	II	9.8	1.40	10	-77°	37.8°	9	210	27.1	10	223	37.1	10
JT7344	--	15.3	4.05	14	-208°	128.3°	12	159	34.0	15	171	29.3	12
JT7324	--	17.6	3.47	30	-306°	94.3°	30	135	30.6	30	137	36.5	30

Table III: Basic statistics for *Miogypsina* s.s. in Units IV and V of the section Lamia.

Sample	\bar{V}	σ	N	\bar{X}	σ	N	$\bar{\gamma}$	σ	N	\bar{D}_1 (μm)	σ	N	\bar{D}_2 (μm)	σ	N
Unit V															
JT5175	89	8.9	19	4.5	0.51	22	68°	28.2°	25	178	26.8	28	219	26.5	24
JT5172	93	5.3	26	4.5	0.51	25	76°	28.0°	27	183	32.5	27	240	41.6	25
JT5167	92	5.8	23	4.5	0.67	23	63°	26.7°	23	191	33.5	25	236	36.5	23
JT5164	88	6.8	27	4.6	0.70	25	61°	29.2°	27	179	32.5	27	229	34.6	25
JT5161	86	9.1	27	4.4	0.65	24	48°	32.9°	27	185	35.4	26	236	42.5	26
JT5155	81	15.6	26	4.3	0.74	25	32°	24.7°	26	173	29.8	26	228	35.5	24
JT5154	87	7.8	26	4.2	0.59	24	29°	20.1°	26	180	37.9	26	234	38.5	25
JT5150	83	10.6	25	4.4	0.58	24	31°	22.2°	25	180	32.1	24	235	48.1	24
JT5149	77	11.4	23	4.6	0.95	20	38°	17.9°	25	170	21.0	26	219	28.0	24
JT5147	72	14.7	26	5.0	0.75	26	37°	13.5°	28	169	21.4	28	220	31.2	22
JT5143	72	13.1	26	4.9	0.78	26	44°	20.6°	27	169	22.8	27	217	25.1	26
JT5142	69	13.5	23	4.8	0.85	25	31°	19.1°	25	160	22.7	26	214	31.6	21
JT5140	67	18.4	26	5.2	0.90	26	33°	17.9°	26	172	25.2	26	220	32.7	22
JT5139	71	12.4	26	4.8	0.74	24	34°	15.0°	27	160	22.3	27	213	43.2	25
JT5139A	75	10.0	27	4.5	0.91	26	38°	21.6°	28	169	20.0	28	225	30.0	24
JT5137	77	12.9	27	4.5	0.64	27	34°	19.9°	28	170	19.7	27	217	30.3	25
JT5134	79	13.8	25	4.7	0.79	25	42°	14.2°	25	158	19.5	26	206	29.9	20
JT5131	69	13.9	22	5.1	0.72	22	35°	24.0°	25	165	20.5	24	211	29.0	22
JT5125	65	21.1	8	5.4	1.01	9	50°	21.7°	11	161	20.9	11	215	33.2	9
JT5124	44	16.2	11	5.7	0.91	11	37°	17.9°	11	152	13.3	11	194	21.9	11

Table III: (continued)

Sample	\bar{V}	σ	N	\bar{X}	σ	N	$\bar{\gamma}$	σ	N	\bar{D}_1 (μm)	σ	N	\bar{D}_2 (μm)	σ	N
JT7980	53	24.4	11	5.9	1.04	11	28°	43.4°	14	179	25.3	17	236	39.7	12
JT5117	54	14.6	6	5.7	0.52	6	43°	12.1°	6	167	6.8	6	238	22.8	5
JT7979	65	25.1	25	5.2	1.09	24	35°	21.6°	28	177	24.7	28	241	39.0	22
JT5112	59	12.9	26	5.4	0.64	26	32°	16.5°	28	181	35.0	28	245	50.6	27
JT5107	60	16.7	18	5.6	0.70	18	37°	25.4°	22	180	32.6	22	259	50.6	18
JT7978	62	15.5	22	5.6	0.96	22	37°	17.1°	20	173	33.1	26	237	44.8	20
JT7977	64	16.7	24	5.7	1.04	24	42°	19.4°	23	180	31.4	25	248	41.0	22
JT7976	65	15.5	24	5.2	0.88	24	31°	19.4°	28	174	24.5	28	257	36.1	19
JT7975	65	17.8	26	5.3	0.94	25	39°	27.5°	28	178	30.6	29	255	45.5	17
JT5102	63	12.4	22	5.5	0.67	22	41°	20.1°	25	172	18.9	25	247	32.3	23
JT5098	65	20.5	26	5.4	0.99	26	41°	17.6°	26	167	22.3	27	230	28.4	26
JT5094	58	16.9	20	5.7	0.96	21	41°	18.1°	25	177	24.1	24	248	36.3	21
JT7974	69	15.9	23	5.1	0.82	23	48°	23.2°	22	172	24.2	27	236	30.2	22
Unit IV															
JT7177	56	11.5	24	6.0	0.89	25	40°	18.7°	31	170	22.7	32	234	33.6	28
JT5082A	68	16.1	26	5.5	0.98	27	38°	11.9°	26	176	22.4	28	238	25.7	24
JT5077	65	15.6	18	5.2	0.88	18	42°	18.1°	20	177	25.0	22	244	36.3	18
JT5063	45	22.0	23	6.2	1.38	22	25°	29.0°	24	162	23.0	25	221	40.1	23

Table IV: Basis statistics for *Miogypsinoidea* in Units IV and V of the section Lamia.

Sample	\bar{X}	σ	N	$\bar{\gamma}$	σ	N	\bar{D}_1 (μm)	σ	N	\bar{D}_2 (μm)	σ	N
Unit V												
JT5161/75	10.6	1.69	8	-134°	19.2°	8	141	30.4	8	134	12.9	8
JT5155	10.5	1.51	12	-110°	47.5°	12	133	23.0	12	140	23.0	11
JT5154	10.8	1.72	14	-125°	52.7°	14	133	20.8	14	131	26.4	14
JT5150	11.1	1.49	14	-137°	45.5°	14	135	27.7	14	141	29.3	13
JT5149	10.2	1.35	24	-114°	41.3°	24	132	14.6	24	134	16.1	22
JT5147	11.3	1.22	20	-132°	27.0°	20	129	13.5	20	130	17.8	20
JT5143	10.2	1.09	23	-118°	28.8°	23	132	18.4	23	138	17.7	23
JT5142	10.9	1.42	23	-142°	32.3°	23	127	17.2	23	129	24.7	23
JT5140	10.8	1.32	24	-129°	33.4°	24	129	15.6	24	135	20.2	23
JT5139A	11.1	1.35	24	-124°	36.2°	24	130	17.4	24	130	24.6	23
JT5137	11.3	1.01	11	-117°	37.2°	11	142	27.4	11	136	29.1	11
JT5134	10.9	2.03	10	-114°	40.3°	10	151	23.8	10	145	26.3	10
JT5131	11.0	1.53	19	-138°	30.8°	20	138	19.1	20	130	21.2	20
JT5125	10.9	2.28	14	-134°	43.4°	14	132	17.6	14	135	16.1	13
JT5124	11.2	1.39	27	-127°	31.0°	26	131	24.1	27	137	28.4	25
JT5112	11.3	0.99	12	-135°	27.1°	12	135	15.0	12	138	19.4	11
JT5098	11.6	2.83	8	-141°	58.7°	8	126	16.8	8	126	18.3	8
Unit IV												
JT5077	10.7	1.48	23	-113°	34.6°	26	146	16.0	26	155	22.8	25

Table V: Some statistics for *Cycloclypeus* in Unit III and for *Lepidocyclus* in Units III and IV. Definition of parameters for *Cycloclypeus* according to Drooger & Roelofsens (1982) and for *Lepidocyclus* according to De Mulder (1975).

Cycloclypeus									
Sample	\bar{X}	σ	N	\bar{S}_{14}	σ	N	\bar{D}_1 (μm)	σ	N
JT7324	16.7	1.62	11	15.1	5.26	11	87	13.7	11

Lepidocyclus												
Sample	\bar{C}	σ	N	\bar{A}_1	σ	N	\bar{D}_1 (μm)	σ	N	\bar{D}_2 (μm)	σ	N
Unit IV												
JT5063	5.32	1.62	22	48.9	5.81	25	283	70.7	24	445	112.1	24
Unit III												
JT7313/4/5	5.25	1.42	12	44.3	3.65	12	298	77.7	12	480	114.8	12
JT7324	3.39	1.30	26	39.6	4.27	25	218	43.8	27	332	88.1	28

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