UTRECHT MICROPALEONTOLOGICAL BULLETINS

W. J. J. FERMONT

DISCOCYCLINIDAE FROM EIN AVEDAT (ISRAEL)

27

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Editor C. W. Drooger
Department of Stratigraphy and Paleontology
State University of Utrecht
Budapestlaan 4, Postbus 80.021
3508 TA Utrecht, Netherlands

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W. J. J. FERMONT

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ABSTRACT

Approximately 300 samples were collected from Lower to Middle Eocene sediments of the Avedat Plateau (Central Northern Negev, Israel). Fielddata, microfacies data – qualitative as well as quantitative with respect to P/B ratios and frequency distributions of larger foraminifera – and the analysis of some 30 samples with smaller benthonic foraminifera resulted in a detailed reconstruction of the northern foreslope of the Avedat Plateau with special reference to the paleo-bathymetry of autochthonous and allochthonous sediments.

Biometric data on the outer and inner morphology of *Asterocyclina* from about 30 samples and the inner morphology of *Discocyclina* from 17 samples were analysed.

The outer morphological data of *Asterocyclina* suggest an irregular increase of the test size in the course of the time combined with a relative flattening of the test.

The inner morphological data prove distinct heterogeneity in *Asterocyclina* and *Discocyclina.* In *Asterocyclina* two groups are recognized on the basis of the size of the embryon and the degree of enclosure of the embryonic chambers (R). The data suggest an increase in the course of the time of R and the size of the embryon. These parameters serve to subdivide the assemblages into biometric units: *A. taramellii* and *A. stella* in the group with a small embryon; *A. cuvillieri* and *A.* sp. in the group with a large embryon. Furthermore another "species" cf. *Asterophragmina pagoda* is separated on the basis of the reduction of radial chamber walls in the median layer. In *Discocyclina* three groups are recognized on the combinations of outer morphological characters and inner morphology. These are *D. varians* s.l., *D. archiaci* and *D.* sp. None of them shows evolutionary trends, but there are extreme differences in morphology between different samples.

The depth profile, the frequency distributions of the larger foraminifera and the morphological characters of *A. taramellii, A stella* and *D. varians* s.l. were compared. *Asterocyclina* shows a preference for the upper foreslope environment. *Discocyclina* is more frequent in the lower foreslope. The large overlap in depth range suggests a further niche segregation by means of other environmental parameters, possibly by means of substrate or vegetation dependency. In *Asterocyclina,* and possibly also in *Discocyclina* the test becomes more flattened with increasing depth.

The evolution within *Asterocyclina* is considered as an example of quantum speciation. The data suggest that with the change of *A. taramellii* to *A. stella* a change of habitat occurred. *D. varians* is considered as an "elastic" species,

which may adapt to widely different subenvironments and show corresponding morphological variation.

A hierarchy of morphological features is proposed, which may be used for discrimination on family, subfamily, genus and species level within the Discocyclinidae. Lower ranked features become increasingly environment controlled and may provide information on ecology.

The origin of the Discocyclinidae is discussed. It is suggested that they are derived from peripheral isolates of *Lepidorbitoides minor* and *L. socialis* which passed the Cretaceous-Tertiary boundary. A subsequent radiation, possibly via *A. taramellii* and *D. augustae* resulted in at least three different lineages in the subfamily Asterocyclininae and at least two in the subfamily Discocyclininae, each with its own rate of evolution.

Chapter I

INTRODUCTION

I.1 SCOPE OF THE INVESTIGATION

On the basis of the Eocene sediments of Ein Avedat (Israel) a detailed investigation has been carried out concerning the relations between the environment and the morphological characteristics of the orbitoidal foraminifera that belong to the family Discocyclinidae.

The aim of this study is to determine which changes in morphological characters have an ecological significance and which of them have an evolutionary value.

The Discocyclinidae are Early Tertiary highly evolved orbitoidal larger foraminifera the ancestral roots of which are poorly known. Either the Discocyclinidae arose during the Early Tertiary from an unknown ancestor, which implies a remarkably rapid radiation compared to other groups of orbitoidal larger foraminifera, or they are the continuations of (various?) groups of Late Cretaceous orbitoidal larger foraminifera that were already highly evolved at the beginning of the Tertiary. The only report of a "primitive" *Discocyclina* s.l. is by Caudri (1944, 1972). She described a discocyclinid form *Bontourina* (= *Hexagonocyclina*) from the Paleocene of the Caribbean, which has two equal-sized auxiliary chambers on either side of the embryon and four nepionic spirals.

All the Discocyclinidae have attained the ultimate stage of nepionic acceleration, at least in the megalospheric forms. As a consequence one is obliged to study the further development of this group in the morphology of the embryon.

As the differences are often very subtle it seemed advisable to make a statistical treatment of the data.

So far no-one has convincingly demonstrated evolutionary trends within the Discocyclinidae such as they are known from other groups of orbitoidal larger foraminifera, like the Lepidocyclinidae (Tan Sin Hok, 1933, 1936; Van der Vlerk, 1964; Van Vessem, 1978). Miogypsinidae (Drooger, 1963; Raju, 1974), *Helicorbitoides* and *Lepidorbitoides* (Van Gorsel, 1975), *Planorbulinella* and *Hellenocyclina* (Freudenthal, 1969) and the Pseudorbitoididae (Krijnen, 1972).

Already in the early literature on the Discocyclinidae it is repeatedly stated that this group shows no evolution at all (Oppenheim, 1901). The lack of distinct phyletic relationships has inevitably led to a confused taxonomical subdivision, based on outer morphology (most authors), axial sections (Neumann, 1958), equatorial chamber arrangement and size and shape of the embryon (Van der Weijden, 1940), arrangement of the microspheric nepiont (Brönnimann, 1945).

Our own species concept is based mainly on the configuration of the embryon. One might argue that many specific characters become visible only in an adult stage of the foraminifera but within a biometrical species concept one is obliged to work with parameters dependent on well-defined stages of the ontogeny.

It is well known that fluctuations superimposed on the assumedly phylogenetic trend of size increase of the embryon occur. These fluctuations are sometimes ascribed to environmental controls (Drooger & Raju, 1973; Van Gorsel, 1978; Drooger, Raju & Doeven, 1979). In this paper special attention is given to this kind of fluctuations.

The results of this paper may provide clues for the use of larger foraminifera in paleoecology, for a better understanding of the evolutionary pathways of larger foraminifera and, finally, it may lead to a better taxonomy of the Discocyclinidae as a group.

I.2 MATERIAL AND APPROACH

Samples were taken from the Lower and Lower-Middle Eocene of the Central Northern Negev (Israel). The surface distribution of the Eocene is shown in fig. 1. In the small but charming State Nature Reserve of the Ein Avedat Canyon the rock sequence is almost continuously exposed.

The Ein Avedat section was studied and the samples were collected in the years 1977–1979. The section consists of an alternation of chalks and calcarenites. Samples were taken from both.

Many beds are rich in larger foraminifera, notably *Asterocyclina, Discocyclina, Nummulites* and *Operculina.* Other genera, like *Cuvillierina* and *Assilina* are extremely rare. The genera *Asterocyclina* and *Discocyclina* are studied in detail, while the genera *Nummulites* and *Operculina* are only dealt with as groups.

The larger foraminifera are essentially allochthonous elements derived from the nearby Avedat platform (see chapter 2). Their sediments are intercalated in pelagic deposits which are considered to be autochthonous. Mixing between the two types of sediment occurs to a variable degree. Although the larger foraminifera were transported it was assumed that remains of the original community structure might still be preseved. Therefore a thorough analysis

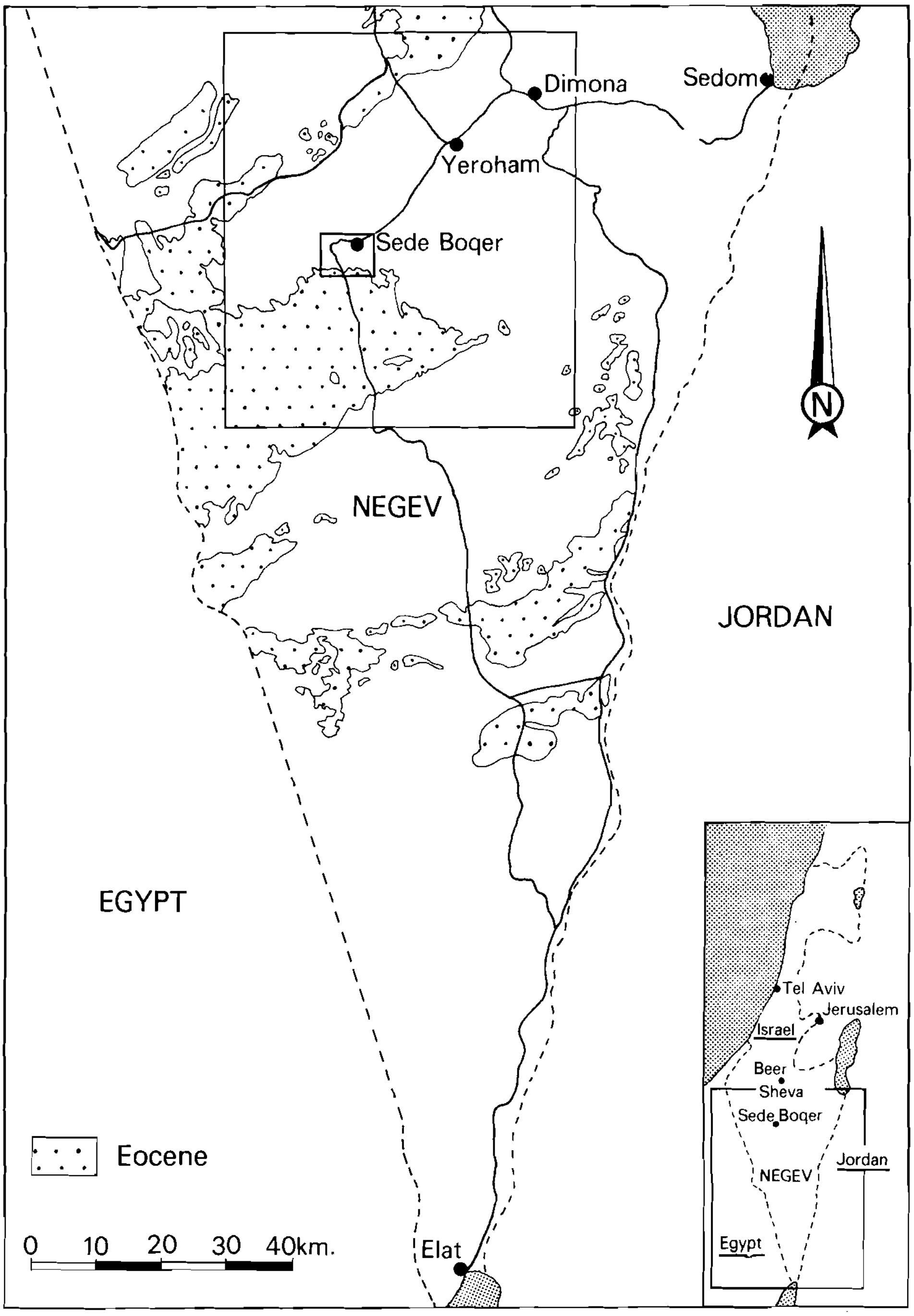

Fig. 1 Eocene outcrops in the Negev Desert, Israel (after Braun, 1967).

of the sedimentary history of the Ein Avedat section, based on field lithology, microfacies data, benthonic foraminifera and P/B ratios is presented in chapter 2.

We investigated several aspects of the larger foraminifera. The representatives of *Asterocyclina* received by far the most attention because they appeared to be the best preserved and most frequent.

For *Asterocyclina* we were able to measure characteristics of both the outer and inner morphology. The data are presented in chapter 3.

For *Discocyclina* we present mainly data concerning the inner morphology. The specimens were so often damaged that not enough specimens were available for us to make measurements on the outer morphology.

In chapter 4 we summarize all the data, and the patterns concerning the evolution and the ecology of the Discocyclinidae are discussed.

In the final chapter 5 the taxonomic consequences of our approach are considered.

The foraminifera and the thin sections are stored in the collections of the Department of Micropaleontology of the State University of Utrecht, coll. no. GFD 87–23 to GFD 98–50 and MF 1–1 to MF 2–95, respectively.

I.3 REGIONAL AND LOCAL SETTING OF THE AVEDAT SECTION

Eocene sediments form a prominent part of the surface of the Negev desert (fig. 1). These sediments form the final stages of a long history of repeated marine transgressions and regressions on the once continuous Afro-Arabic platform, the history of which began already in the Early Cambrian (Freund & Garfunkel, 1976). A major transgressive cycle started in Mid-Cretaceous time and ended in the Late Eocene. This cycle generated the deposition of a sequence consisting predominantly of carbonates. From the Late Eocene until today the platform was uplifted and there was subsequent erosion of the sedimentary cover. From then on mainly continental deposits came into being.

The Northern Negev shows a pattern of SW to NE striking anticlinal and synclinal structures belonging to the so-called Syrian arc (fig. 2). The folded belt is cut by high angle reverse faults striking EW. These structures were already present at the onset of the Tertiary (Bentor & Vroman, 1954; Arkin et al., 1972); they determined the realms of the various Eocene carbonate facies.

In the Central Northern Negev two structural areas are distinguished. In the South the Ramon anticline is the most pronounced structural unit. In the North there is a group of anticlinal structures the most important of which are Kevuda, Rekhme, Hatira and Hazera anticlines.

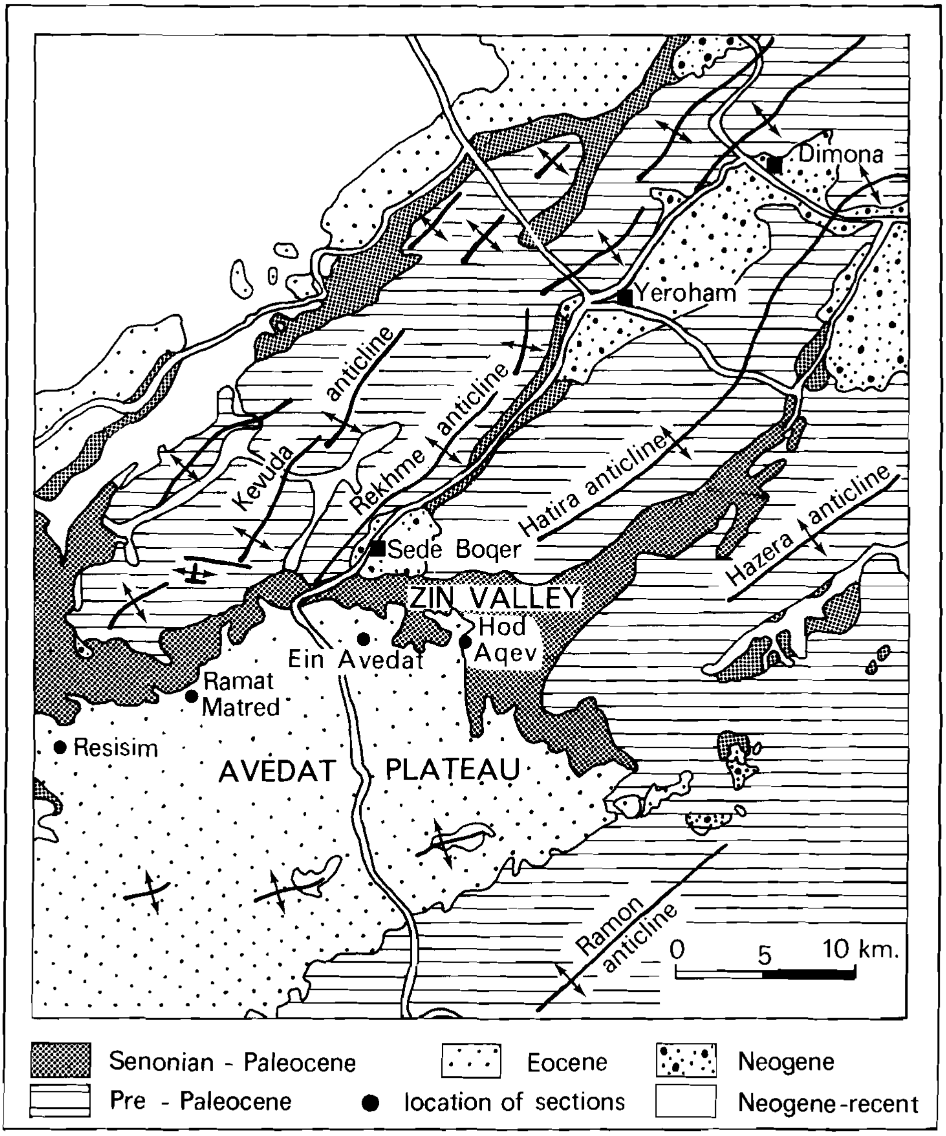

Fig. 2 Eocene outcrops and structural map of the Central Northern Negev (after Bentor et al., 1965; Arkin et al., 1972).

Both areas are separated by an EW trending flexure system.

The Northern limb of the Ramon anticline constitutes the sole of a carbonate ramp which developed during the Eocene (fig. 3). Its resistant limestones nowadays constitute a platform which is known as the Avedat Plateau. All the Eocene limestones diminish in thickness or wedge out towards the axis of the Ramon anticline. From the Ramon anticline to the North there is a general decrease in the degree of induration of the carbonates.

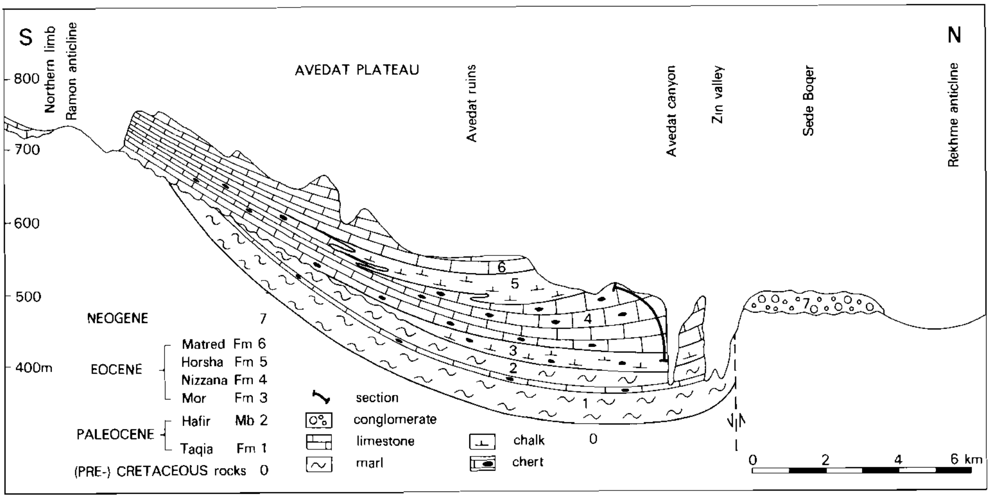

Fig. 3 Cross section through the Avedat Plateau. The vertical scale is greatly exaggerated. In the synclinal area the sedimentation is continuous from Cretaceous to Eocene. Towards the crest of the Ramon anticline the sedimentation is interrupted and the formations pinch out. Compilation of data after Bentor et al., 1965; Arkin et al., 1972; Benjamini, 1979, 1980; and the author's own observations.

In the anticlinal system north of Sede Boqer it is mainly Cretaceous rocks which are exposed. Eocene sediments are preserved only in the synclinal areas.

I.4 THE MOR AND NIZZANA FORMATIONS

The Eocene of the Northern Negev is subdivided into several formations (Bentor & Vroman, 1957; Braun, 1967; Benjamini, 1979). The lithostratigraphic subdivision is based partly on the degree of induration. The indurated calcarenites originated predominantly on or near the structurally high areas, whereas the more friable carbonates were deposited mainly in the synclinal areas.

In the immediate vicinity of the Ein Avedat Canyon four Eocene formations are recognized which from top to bottom are
Matred Formation
Horsha Formation
Nizzana Formation
Mor Formation

In the Canyon itself only the Mor and the Nizzana Formations are exposed.

The Mor Formation consists of well-bedded calcilutites and calcarenites with numerous chert levels. In the lower part of the formation dolomite rhombohedra and phosphate grains are common constituents and there are some bituminous intervals (Braun, 1967). Towards the top planktonic foraminifera wackestones become predominant. In the depressions the Mor Formation may conformably overlie the Upper Paleocene Taqia Formation. Towards the Ramon anticline the formation gradually pinches out and may unconformably overlie the Taqia Formation or pre-Tertiary rocks. The upper part of the formation may pass laterally into the Nizzana Formation.

The Nizzana Formation conformably overlies the Mor Formation but there are lateral passages as well. We define the base of the Nizzana Formation at the first bed containing numerous larger foraminifera. The formation consists

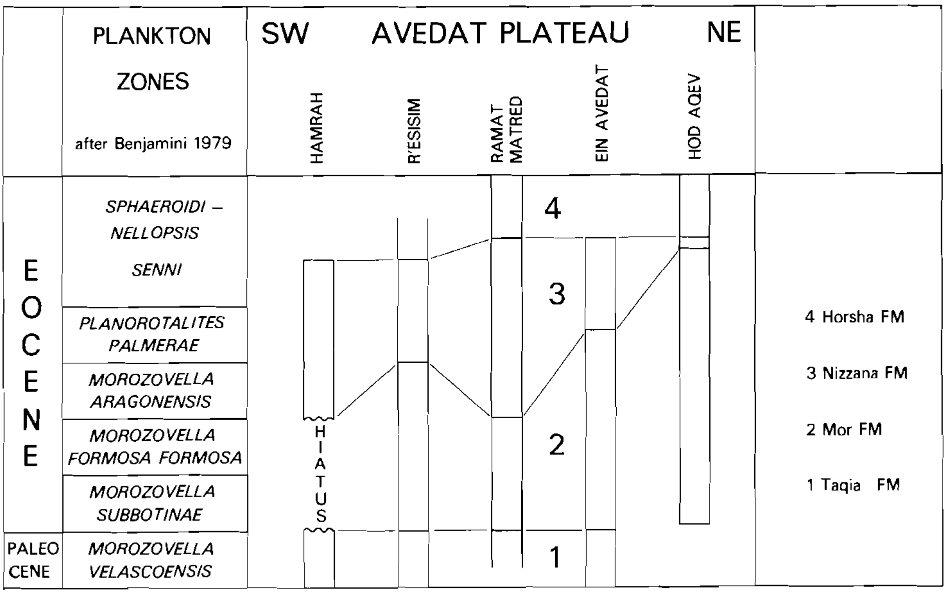

Fig. 4 Biostratigraphy of the Avedat area. The Mor and Nizzana Formations are partly time-equivalent (redrawn after data of Benjamini, 1979).

of horizontally and vertically irregular alternations – often chaotically arranged – of calcarenites and calcirudites. Chert levels occur predominantly in the finer grained sediments. Towards the Ramon anticline the formation gradually becomes thinner. Here it is overlain by the Horsha or the Matred Formation. Towards the north the Nizzana Formation pinches out rapidly. In the Avedat Canyon the formation reaches a thickness of more than 100 metres, while about 1 km. further at Hod Aqev, it has almost completely disappeared.

A zonation based on planktonic foraminifera has been presented for the Mor and Nizzana Formations by Benjamini (1979). According to this biozonation (fig. 4) it is obvious that the Mor and Nizzana Formations are partly time equivalent.

A detailed nannoplanktonic zonation of the Lower Tertiary was established by Romein (1979). The Nizzana Formation comprises the *Discoaster lodoensis* en *D. sublodoensis* Zone (fig. 5). The age of the Nizzana Formation ranges from the late Early Eocene to the early Middle Eocene (Martini, 1971; Bukry, 1975; Romein, 1979). According to the absolute time scale of Bukry (1975) the major part of the Nizzana Formation might have been deposited over a period of about one million years (fig. 5). The average rate of sedimentation was therefore approximately 10 cm./1000 years.

From these data a preliminary concept of the paleogeography can be reconstructed.

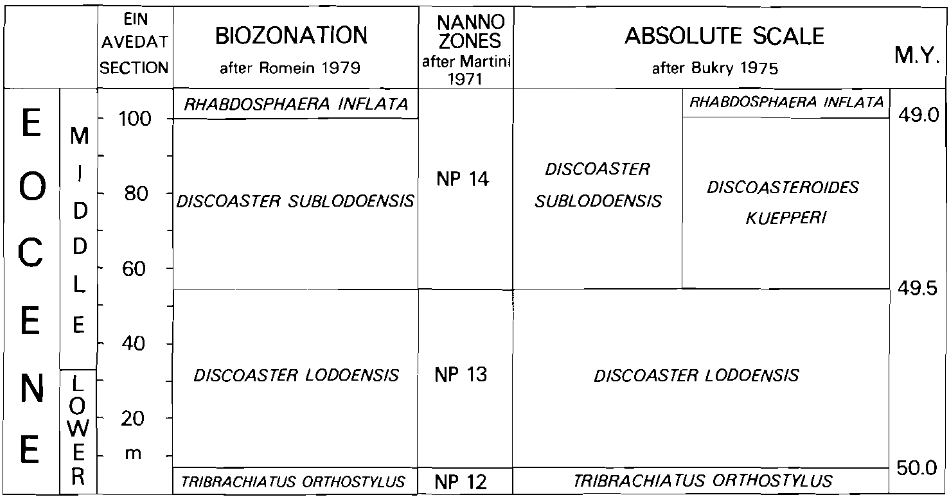

Fig. 5 A comparison of the nannoplankton zonation of Romein (1979) with the nannoplankton zonation of Martini (1971) and the absolute time-scale of Bukry (1975).

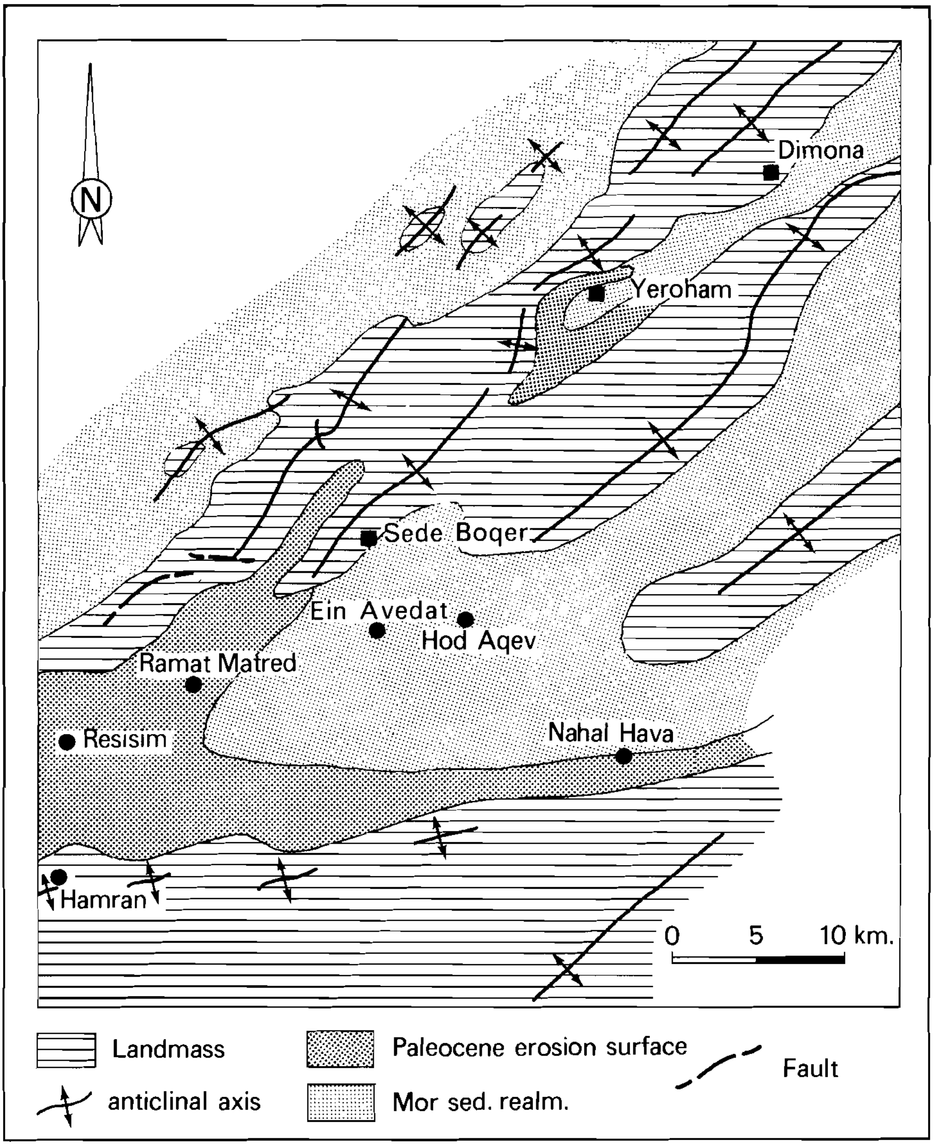

Fig. 6 Lowermost Eocene paleogeographic reconstruction of the Ein Avedat area with
1. a shallow marine semi-enclosed basin,
2. an area with eroded Upper Paleocene, and
3. older land mass
(after Arkin et al., 1972).

At the beginning of the Eocene the area of the Central Northern Negev had a low relief. In the depressions sedimentation was continuous from the Paleocene Taqia Formation across the Paleocene-Eocene boundary, which led to the development of the basal part of the Mor Formation (fig. 6). The sediments in these "restricted bays" (see also Arkin et al., 1972) are rich in dolomite, bituminous shales and phosphate, indicating rather stagnant water masses.

During the Early Eocene the sea covered much larger areas. In the depressions pelagic sediments became predominant. On and around the structural high of the Ramon anticline a carbonate ramp came into existence which consisted essentially of indurated limestones (the Nizzana Formation).

Continued tectonic instability caused the carbonate products to be transported downslope to the north where they interfinger with the pelagic sediments.

A more detailed description of the sedimentary history, based on the analyses of field-data, microfacies and faunal content is presented in the following chapter.

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This thesis is dedicated to my wife Josje.

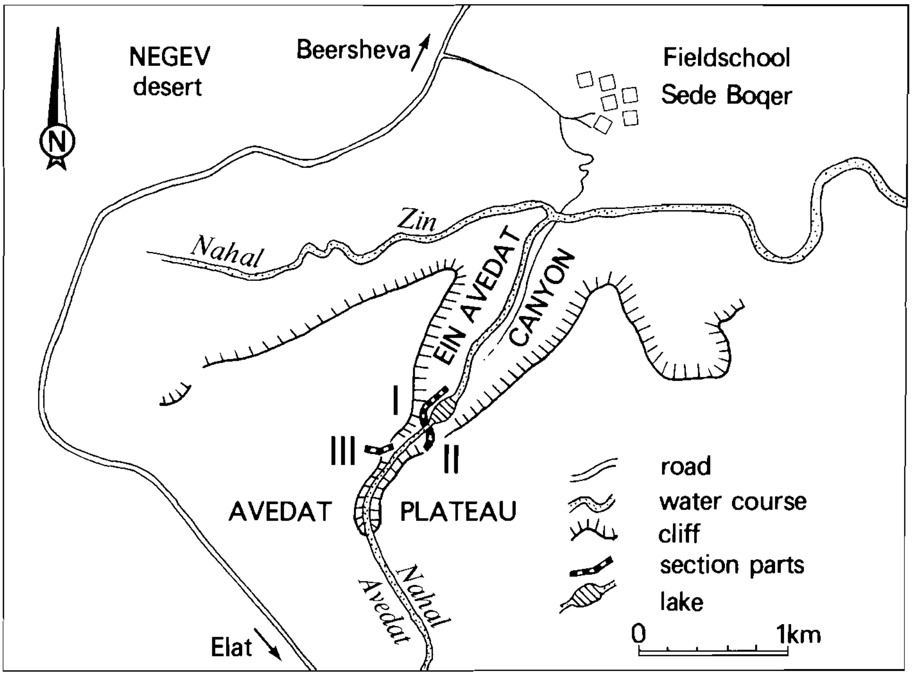


Fig. 7 The sample localities in the Ein Avedat Canyon.

Chapter II

THE SECTION OF EIN AVEDAT

II.1 INTRODUCTION

In our study of the Ein Avedat section our primary aim was to construct the paleo-environmental setting of the larger foraminifera in which we were interested. It soon appeared that the sediments of the Ein Avedat Canyon consist of a complicated and chaotic mixture of sediment types. This factor hampered the direct recognition of undisturbed faunal assemblages. Therefore we felt obliged to study the sediment features of the section in more detail.

Data were gathered concerning the field-lithology of the strata, the microfacies, the benthos associations of the smaller and the larger foraminifera and the P/B ratios. All these data together allow us to make a subdivision of the section into nine units, each of which has its own characteristics.

In fig. 10 the position of the samples, used for the analysis, is given.

In this chapter we present all these data. Then we discuss the combinations of features in each of the nine units. Finally a detailed environmental interpretation is given for the entire section with an emphasis on the paleobathymetry.

II.2 THE LOCALITY

The Ein Avedat Canyon in the Central Northern Negev is situated 3 km. SW of the fieldschool of Sede Boqer (fig. 7). The canyon is accessible via a dirt track from Sede Boqer. Between the entrance to the canyon and the Avedat plateau in the south there is only a footpath, which passess partly along steep stairs through the State Nature Reserve of Ein Avedat.

In the walls of the canyon the Mor and Nizzana Formations are almost continuously exposed. Our composite section consists of three parts. The lowermost 10 metres are situated along the stairs cut out in the western wall, close to the artificial lake. The second part of about 65 metres is in the eastern wall with its base on the platform above the lake and rises upwards to the base of the vertical cliff. The third interval is along the stairs leading to the Avedat plateau (fig. 7). The lithostratigraphic correlation of the three parts is easy because of the occurrence of prominent chert and "conglomerate" beds.

The overlying Horsha Formation is not exposed in the immediate vicinity of the Ein Avedat Canyon.

II.3 FIELD OBSERVATIONS IN THE EIN AVEDAT SECTION

II.3.1 **Introduction**

Our field classification of the various rock-types could be made more or less in accordance with the classification of carbonate rocks by Dunham (1962) and the amplifications of Embry & Klovan (1972). Owing to the wide variation in the lithological attributes such as texture, colour, faunal content, lithification and sedimentary structures, however, we had to make some modifications and refinements.

Previous authors described the carbonate sequence in the Ein Avedat region in terms of chalks and limestones (Braun, 1967; Benjamini, 1979); this subdivision is primarily an indication of the degree of induration. These authors already recognized that the chalks consist essentially of two types. The first one is a typical pelagic sediment, that fits in with the definition of chalk (Pettijohn, 1957), the other is a very fine-grained bioclastic packstone with a micritic matrix. The latter type may show a variable degree of microsparitization. If microsparitization has proceeded to a certain degree the rock will appear in the field as a limestone (indurated carbonate sediment), although there is no essential textural difference between this type of limestone and its non-indurated counterpart. In this paper we shall use the term chalk in the sense of Pettijohn for the planktonic foraminiferal pelagic sediments; this facies type is only recognizable in thin sections. For the field description of soft and hard carbonate sediments we shall use the prefixes indurated and non-indurated.

Our grouping on the basis of these fields observations brings together very different carbonate sediments. Furthermore it leads to discrepancies between the classifications made on the basis of the microfacies and those made on the basis of the field lithology.

II.3.2 **Rock** types

According to the grain size distribution of the sediments a subdivision could be made into four classes;

- mudstones: grains not visible with a hand-lens,
- fine-grained wackestones and packstones: grains visible but not determinable,

– coarse-grained packstones: individual grains determinable,
– floatstones: very coarse-grained with pebbles, cobbles and boulders.

Especially the subdivision in the finer grained rock types is not in good agreement with the classification of the microfacies types.

Additional features, like colour, thickness of the beds and internal structures of the sediment, allow us to make a further subdivision, which is presented below.

The vertical distribution of the rock types in the Ein Avedat Canyon is shown in fig. 8.

1. Cream-coloured mudstones

The thickness of the beds ranges from 5–40 cm., the colour from white to cream or light brown. The sediment is generally homogeneous with traces of burrowing near the contacts with the adjacent beds. Occasional platy chert levels have developed. The contacts with the adjacent beds are sharp. The beds may be indurated.

2. Brown-to-black mudstones and wackestones

The thickness of the beds ranges from 5 to 140 cm. The sediments in these beds consist of homogeneous to finely laminated dark brown carbonate deposits which are not indurated. The contacts with the underlying and the overlying beds are commonly sharp but they may be diffuse due to intensive burrowing. Black, clayey intervals are somtimes intercalated. Occasional lenses were found with well-sorted, very flat larger foraminifera, notably *Discocyclina* and *Asterocyclina.* At some levels vague indications of cross-bedding were observed. There are occasional nodular chert levels.

3. Homogeneous fine-grained packstones

The thickness ranges from 5 to 200 cm. The colour is white to light cream. Near the contacts with adjacent beds burrows are sporadically visible. The beds may show some degree of lithification: we found either small globular concretions up to 1 cm. in diameter or thin parallel veneers with a thickness of some mm. Some of the rocks are rich in glauconite. Occasionally fish remains were observed.

4. Fine-to-medium grained laminated-to-thin bedded packstones

The thickness of these strata ranges from 20 to 200 cm. but there are considerable lateral changes. The lamination in these cream coloured strata is subparallel with laminae and thin beds from 1 to 50 mm. The contacts with the adjacent beds are frequently disturbed by loadcasting. Flow structures are frequent. Locally the lamination is obscured by homogenization of the sediment due to burrowing. The beds contain variable amounts of glauconite.

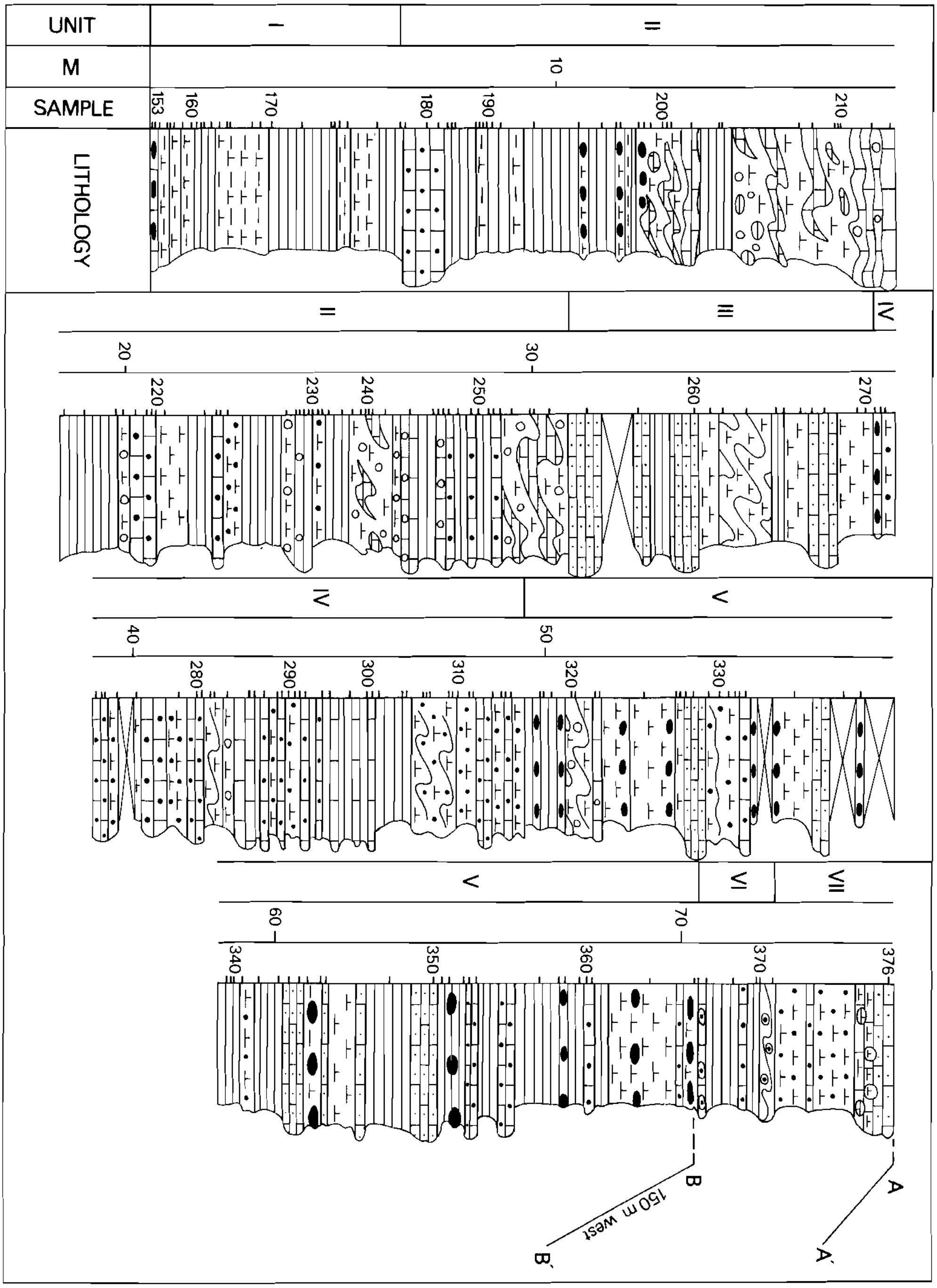


Fig. 8a The section of the Ein Avedat Canyon. Section parts I and II.

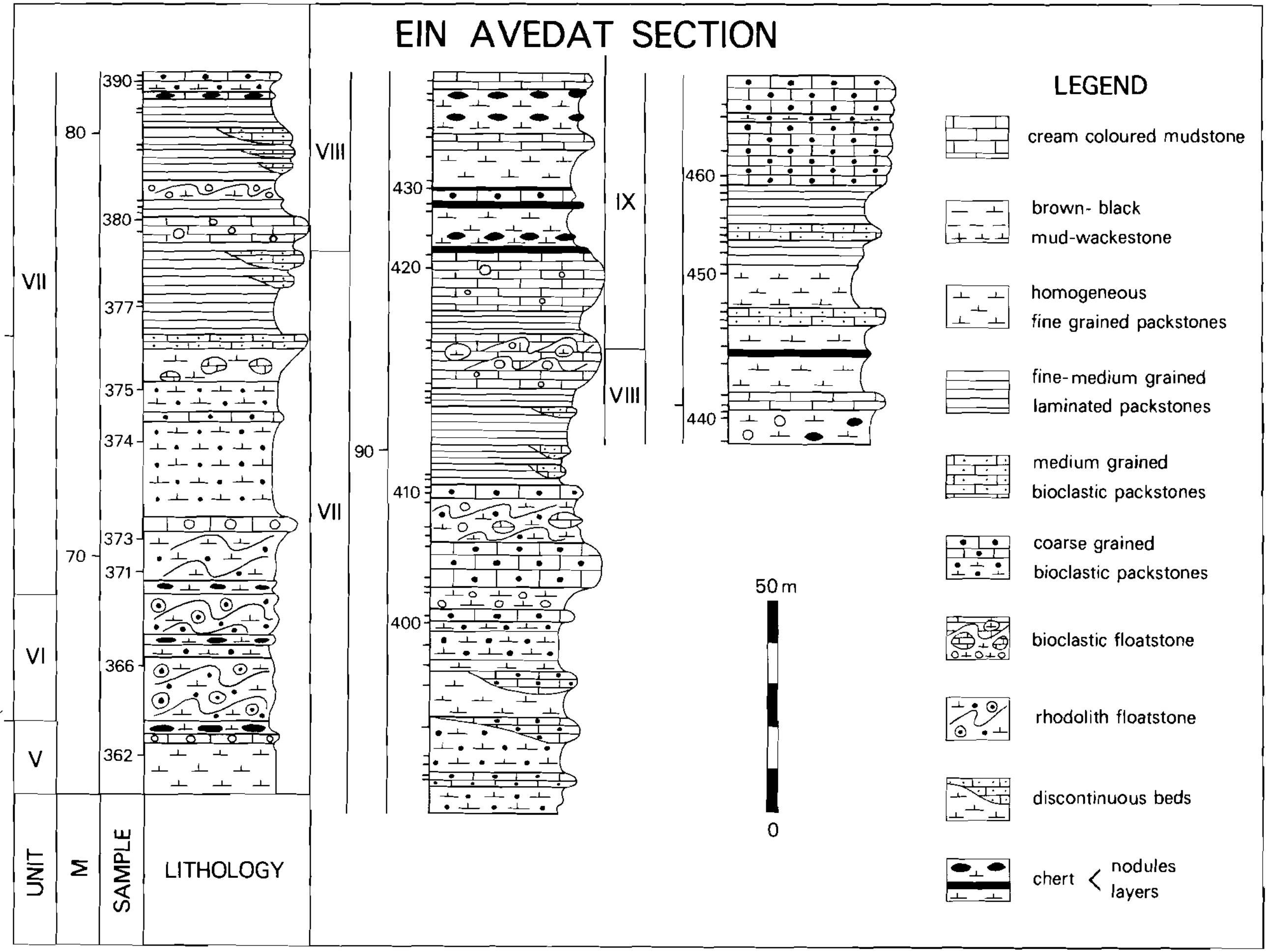


Fig. 8b The section of the Ein Avedat Canyon. Section part III (compare fig. 7). The columns are connected on the basis of very pronounced lithologies (A–A′ and B–B′).

In this type too globular concretions are observed.

It is sometimes difficult to distinguish between this type and the types 3 and 5. In this type laminae occur the lithology of which belongs either to the homogeneous fine-grained packstones of type 3 or to the medium-grained bioclastic packstones of type 5. We decided arbitrarily to refer to them as separate individual beds of the types 3 and 5 respectively whenever they had a thickness of 5 cm. or more.

5. Medium-grained bioclastic packstones

The thickness of the beds ranges from 5 to 100 cm. The usual colour is cream to light brown but sometimes it is yellow. The contacts with the adjoining beds are generally sharp. Some of the beds show small scale crossbedding, in others no internal structures were observed. Only minor quantities of larger foraminifera are present. On the basis of thickness three subtypes are recognized:

a. 5–10 cm. These are generally burrowed and occasionally show little irregular induration.
b. 10–30 cm. Burrowing is less frequent. The beds show more complete induration, but the lateral extension of the indurated rocks may be limited.
c. 30–100 cm. These beds only show burrows at the top. The beds are generally indurated and laterally continuous.

6. Coarse-grained bioclastic packstones

The thickness ranges from 20 to 200 cm., but may show considerable lateral variation. Occasionally the thickness may be much more than 2 metres. The colour varies from cream to light brown. The beds of type 6 may contain rapid alternations of two types of lithology, homogeneous fine-grained type 3 packstones and coarse-grained bioclastic packstones which are generally rich in larger foraminifera. The contacts with the adjacent beds are usually sharp and planar. However, disturbance due to loadcasting, to injection in overlying beds and to burrowing is frequent. Burrows in one type of sediment are frequently filled with sediment of the other and vice versa. The original lamination is sometimes completely destroyed by flow. The degree of induration is highly variable but is generally most pronounced in the top parts of the beds.

7. Very coarse floatstones

These beds are from 25 to 200 cm. thick and occasionally even thicker. The contact with the underlying beds may be highly disturbed by laod-casting or by slumping. The top parts of the beds frequently show intensive burrowing, or they may be disturbed by injection. The matrix varies from fine-grained to coarse-grained bioclastic packstones which may be indurated to a variable degree. Generally several of the sediment types mentioned before can be recognized. The lithoclasts range from well-rounded pebbles, cobbles and boulders to extremely flattened flakes. The individual lithoclasts can fairly easily be determined as belonging to one of the other lithologies described hitherto. The top of the beds is generally more indurated than the lower part. Burrows are very common in the uppermost 20 cm.

8. Rhodolith floatstones

The lithology of this type of sediment is essentially the same as that of the preceding one. The thickness of the beds shows large lateral variation. Over a distance of tens of metres the thickness may change from 30 cm. to more than 2 metres. Characteristic is the occurrence of numerous rhodoliths ranging in diameter from 0.5 to 4 cm.

II.3.3 Slumps

Slumps occur throughout the section, especially in the beds in which several types of lithology are observed. Owing to the steepness of the uppermost part of the outcrop, data are available for the lowermost 70 metres only. Although the variation in the 16 fold-axes measured is rather wide the axes indicate an average of the paleoslope towards the NNE.

II.4 MICROFACIES OF THE EIN AVEDAT SECTION

II.4.1 Introduction

The field characteristics did not provide a sound basis for a detailed discrimination of rock types, even after repeated detailed observations had been made along the section. In fact is was impossible to recognize a hierarchical pattern in the many features observed. The study of the microfacies provides us with a better insight into the sedimentary processes, and gives us a better understandig of most of the fieldobservations.

Oriented thin sections were prepared for 273 samples. The average surface of the thin sections is 8–10 cm^2. As far as possible oriented thin sections were made perpendicular to the bedding planes. In order to compare the wash-residues and the microfacies of rocks thin sections from soft rocks were prepared as well. These soft rocks were impregnated with Araldid D hardener under vacuum before sectioning. The samples were analysed qualitatively and quantitatively; the quantitative analyses concerned particularly the P/B ratios and the frequencies of the larger foraminifera.

Our classification is based on Dunham (1962) and the amplification of Embry and Klovan (1972). With this classification the whole spectrum of sediment-types can be described; essentially the sediment-types fall into two groups:

1. mudstones and wackestones,
2. packstones and floatstones.

The subdivision is primarily meant to be descriptive but there are distinct genetic implications. Group 1 consists predominantly of sediments that were deposited in situ, whereas the second group comprises mainly allochthonous sediments.

It is important to realize the scale at which these sediment types may still be recognized. In one thin section representatives of both groups often occur together in one of the following ways:

a. Alternations of laminae or thin beds,
b. Burrows in one of the types filled with sediment of another type,
c. Rock fragments of one group in the other group,
d. Homogenized intermediates.

Therefore the field observations which refer to a completely different scale are not directly comparable with the microfacies data. Microfacies types are referred to by letters in order to avoid confusion with the fieldtypes.

II.4.2 Microfacies types

Group 1

The microfacies types of this group are mud-supported. The matrix shows little or no sparitization. The micrite ranges in colour from yellow to dark brown. The grains consist predominantly of planktonic foraminifera, although occasionally radiolaria contribute significantly to the sediment. The sediment normally is intensively burrowed. Sometimes the laminae are composed of densely packed planktonic foraminifera, in which case the sediment is a packstone.

The associated grains are usually well preserved benthonic foraminifera. Fish remains are common. The sediment is often rich in glauconite. When radiolaria are abundant silicification hampers the recognition of other faunal elements.

Within this group three subtypes correspond to most of the sediments:

A. Radiolarian mudstones, which are partly silicified and rich in radiolaria, accompanied by small planktonic foraminifera.

B. Plankton mudstones containing small planktonic foraminifera associated with small buliminid benthonic foraminifera.

C. Plankton wackestones containing diverse faunas of large planktonic foraminifera which are often filled with glauconite. The associated benthos is well-diversified.

Group 2

The microfacies types of this group are grain-supported or matrix-supported. The sediment normally shows a high degree of sparitization of both the matrix and the grains. A further subdivision of this group can be made on the basis of textural properties and faunal composition. Because the major faunal elements fall into different size classes the subdivision based on the grain size correlates well with the subdivision based on faunal elements. Therefore we deviate somewhat from the size classification by Dunham (1962) and Embry & Klovan (1972).

D. Pteropod packstones. Very small pteropods form the major part of the recognizable grains. Microsparitization and silicification generally hamper the determination of other faunal elements. Minor quantities of crinoid fragments, sponge spicules, radiolaria and very fine shell debris could be recognized.

E. Fine grained bioclastic packstones. The grains are generally much smaller than 1 mm. These packstones are generally rich in fragments of larger foraminifera, echinoids, crinoids, smaller benthonic foraminifera like *Pararotalia,* agglutinants and biserially or triserially arranged species, algal fragments, pteropod fragments and indeterminable debris. Planktonic foraminifera are rare. The matrix consists of microsparitic micrite. Sometimes the sediment is intensively burrowed. Occasionally there is indistinct sorting.

F. *Pararotalia* packstones. This type has essentially the same composition as the previous one, but small *Pararotalia* specimens constitute a considerable part of the recognizable faunal elements. Larger foraminifera may be present as well.

G. Larger foraminiferal packstones. They show variable relative numbers of *Asterocyclina, Discocyclina, Nummulites* and *Operculina.* These faunas are generally associated with fragments of algae, echinoids, crinoid stems, smaller benthonic foraminifera and indeterminable bioclasts. In some thin sections the larger foraminifera show distinct orientation, in others none at all. The matrix is rich in partly microsparitic micrite. A further subdivision can be made on the basis of the dominance of one of the larger foraminiferal genera mentioned. This aspect will be described quantitatively and is not considered here.

H. Bioclastic floatstones. In the larger particles of this type, which may have a diameter of more than 10 cm., almost every type of lithology previously mentioned can be recognized. The aggregates are generally well

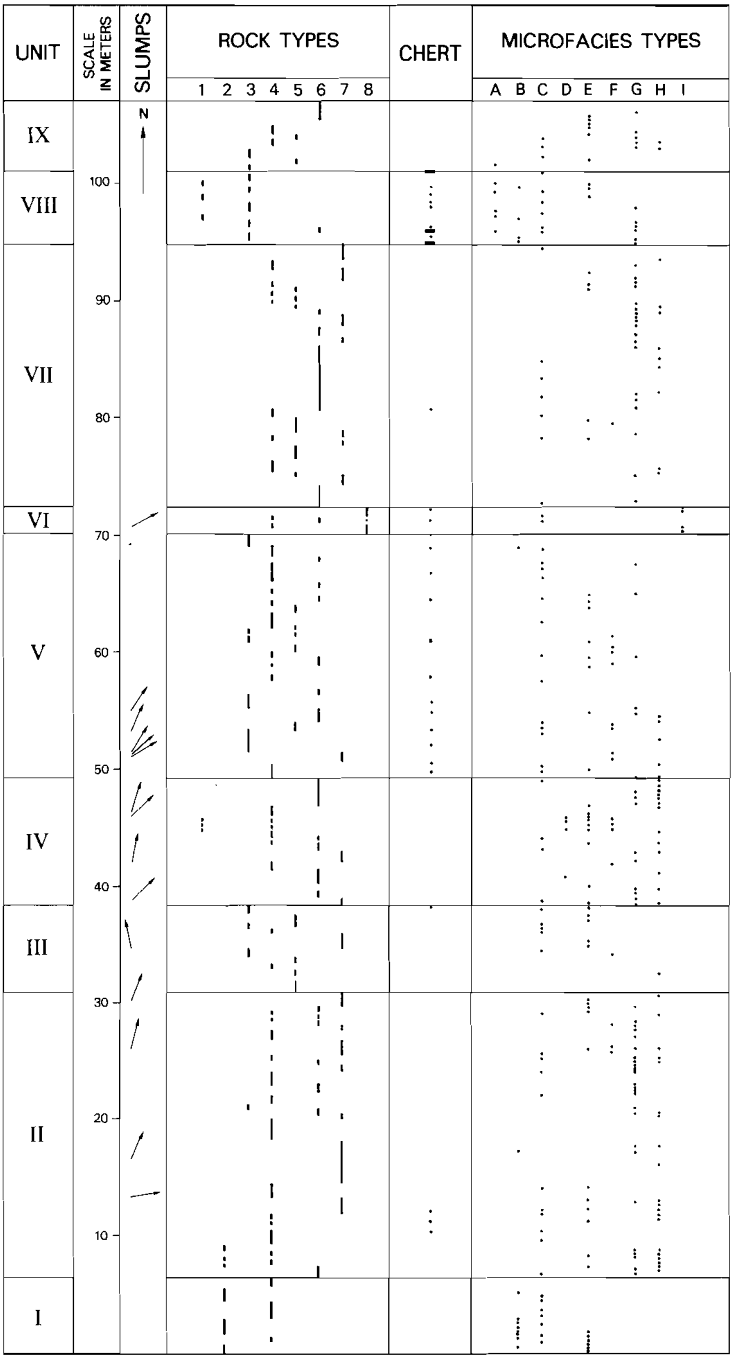


Fig. 9 A comparison between the vertical distribution of rock types and microfacies types in the sediments of the Ein Avedat Canyon.

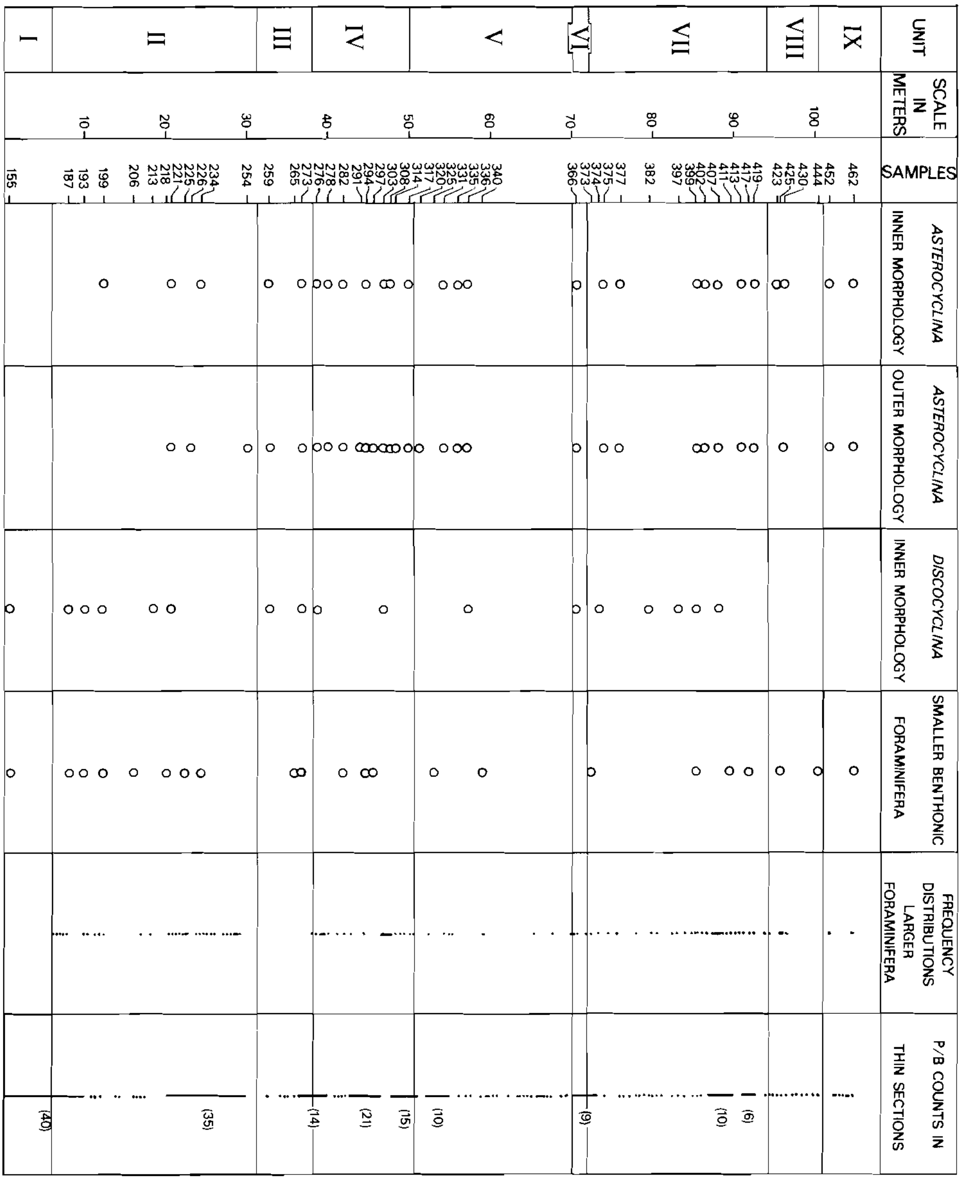


Fig. 10 Position of the samples used for the analysis of the inner and the outer morphology of *Asterocyclina*, the inner morphology of *Discocyclina*, the associations of smaller benthonic foraminifera, the frequency distributions of larger foraminifera in thin sections and the P/B counts in thin sections.

rounded and intensely sparitic. The matrix shows considerable variation and might be subdivided following the Dunham classification. However we restricted ourselves to the observation that the matrix generally consists of a mixture of the types mentioned before.

I. Rhodolith floatstones. Rhodoliths of *Archeolithothamnium* and *Lithophyllum* are occasionally found floating in a heterogeneous matrix consisting of many of the previously mentioned types. At the centre of the rhodoliths and between the successive laminae of the algae one occasionally finds representatives of *Asterocyclina, Pararotalia* and other smaller benthonic foraminifera. According to our classification these floatstones should be placed among the bioclastic floatstones of the previous group. The presence of this special growth form of the red algae warrants a separate treatment.

The vertical distribution of the microfacies types is presented in fig. 9. The position of the samples, used for the microfacies analysis, is shown in fig. 10.

II.5 COUNTS OF LARGER FORAMINIFERA IN THIN SECTIONS

Of the 273 thin sections available 103 were used to estimate the relative frequencies of the genera *Asterocyclina, Discocyclina, Nummulites* and *Operculina. Cuvillierina* and *Assilina* are so rare that they cannot cause essential changes in the relative frequencies of the other groups. We discriminated at the generic level only because species characters are frequently not recognizable in thin sections. We counted only those specimens of which more than half of the individual is preserved in the section. Counts were performed on thin sections containing at least 17 such specimens. Although we realize that counts of only 17 specimens are low, we assumed that they yielded sufficient information. Actually only a few thin sections contained such a low number of specimens. Most of the samples had more than 100 specimens per thin section (fig. 11). On average 140 specimens were counted per sample.

On the basis of the counts three associations are recognized which correspond predominantly to the larger foraminiferal packstones, but some belong to the rhodolith and bioclastic floatstones.

Most frequent are *Asterocyclina* packstones. This genus may represent up to 100% of the counted larger foraminifera.

Also *Nummulites* is sometimes very frequent but percentages and number of samples are lower than for *Asterocyclina.*

Occasional samples show a predominance of *Discocyclina.*

Operculina was never found as the most frequent genus but it occurs in small quantities in most of the samples.

The frequency distributions of the groups of larger foraminifera expressed in percentages are presented in fig. 12. The pattern shows large fluctuations throughout the section.

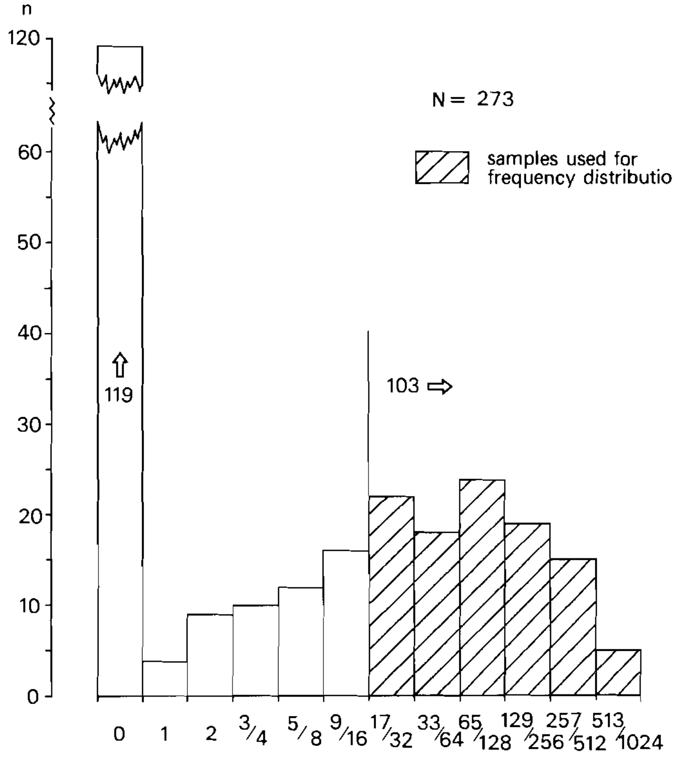


Fig. 11 Frequency distribution of the number of samples with specific numbers of larger foraminifera per thin section. The class 0 without larger foraminifera consists mainly of planktonic foraminiferal wackestones.

II.6 P/B RATIOS IN THIN SECTIONS

P/B ratios were calculated from counts performed on some 240 thin sections. The counts were carried out by moving the table of the microscope, on which the thin section was fixed, perpendicular to the ocular micrometer. Tracks of 500 μ width were scanned and benthonic and planktonic foraminifera were counted until a total of 200 had been reached. As far as possible, parts of the thin sections with homogeneous lithology were selected. Whenever sections with alternations of thin laminae of different lithologies were observed, tracks with one type of lithology were followed for the counting.

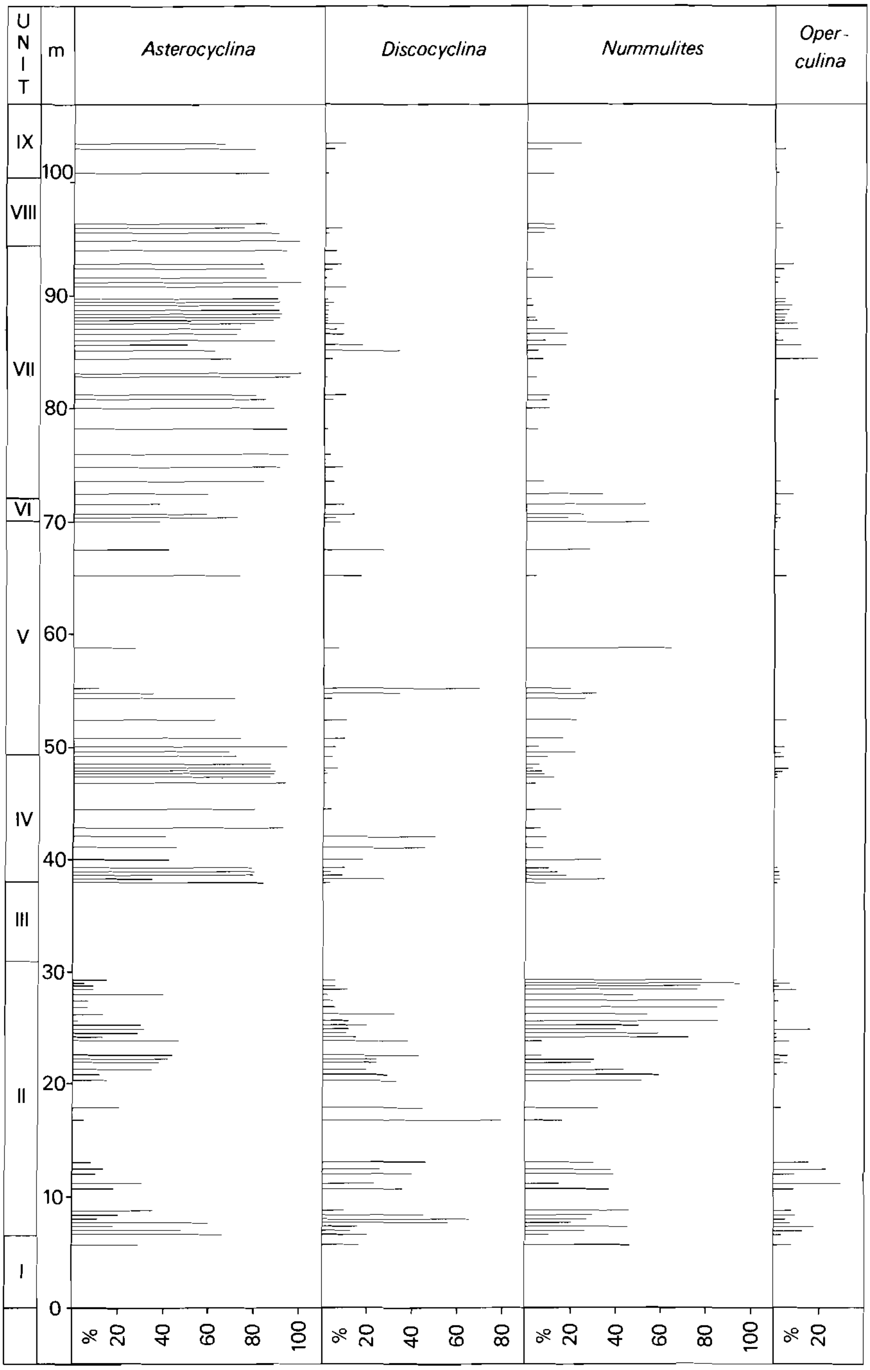


Fig. 12 Relative frequencies of larger foraminifera in thin sections.

This rapid alternation of facies is the reason why the results obtained from wash-residues, which on the average are from samples representative of a rock-column of approximately 10 cm., are generally not really comparable with the results obtained from the thin sections.

There are several major objections to the use of this method. First of all if the thin section is too thick, this hampers the recognition of the foraminifera, expecially the smaller ones. Secondly, the chance that the particles will be cut in the thin section depends on their size. This factor too is detrimental to the frequencies counted for the small foraminiferea. Therefore counts were performed excluding the larger foraminifera. Thirdly, sparitization of the particles may hamper the recognition. All these factors may cause selection and the calculated ratios may not be very reliable (especially in poorly preserved samples).

However, the fluctuations recorded are much wider than expected from statistical and procedural errors. Furthermore, the number of samples is so large that we may well be able to draw some conclusions.

During the counting it appeared that there was a systematic difference in the P/B ratios of the indurated and the non-indurated rocks. Therefore, on the basis of observations in the field and under the microscope, the thin sections were divided into two classes, non-indurated and indurated rocks; this subdivision correlates grosso modo with the subdivision in the microfacies of groups 1 and 2 respectively.

The results of the counts were calculated as ratios. The P/B ratios show fluctuations from 0.1 to 50. Therefore they are presented on a log-scale in fig. 13a.

In the indurated rock types the P/B ratios range from 0.1 to 8.0; the average is between 0.5 and 1.0.

In the non-indurated rocks the P/B ratios range from 0.3 to 50; the average ratio is approximately 6 to 10. The frequency distributions of the P/B ratios of both types are shown in fig. 13b.

II.7 SMALLER BENTHONIC FORAMINIFERA

II.7.1 Introduction

Species and even genus determination of smaller benthonic foraminifera is extremely difficult in thin sections. In order to obtain additional data concerning the composition of the foraminiferal associations we analyzed quantitatively the residues of 22 samples. Approximately 200 randomly collected benthonic specimens from the 125 to 500 μ fraction were determined. Species

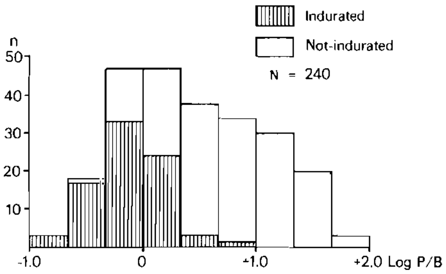


Fig. 13b The histogram shows the frequency distributions of the P/B ratios from both types of rocks.

diversity is given as the number of species per 200 benthonic specimens.

P/B ratios were calculated for the wash-residues from counts containing approximately a total of 200 planktonic and benthonic specimens.

Owing to the rapid alternations of different facies it is not possible to fully compare the counting data from wash-residues and thin sections. The wash-residues may show the average values of different associations, whereas the chance of coming across a pure association is much higher in thin sections. Furthermore, the size classes are well defined in the wash-residues, whereas the size of the specimens cut in the thin sections is largely a matter of chance.

The position of the samples used for the analyses of small benthonic foraminifera is shown in fig. 10.

II.7.2 Results

The results of the counts, i.e. the relative frequencies of the species, the P/B ratios, the numbers of species and specimens per count are listed in fig. 14.

P/B ratios

The P/B ratios vary considerably throughout the section. The lowermost P/B ratios with values of about one alternate with high P/B ratios all along the section.

Species diversity

The species diversity ranges from 16 to 54. No trend is visible. Well-diversified samples alternate irregularly with low-diversified samples.

Species groups

On the basis of resemblance in morphology and supposedly similar ecological behaviour (Wonders & van der Zwaan, 1980) several species groups were defined, which are described below.

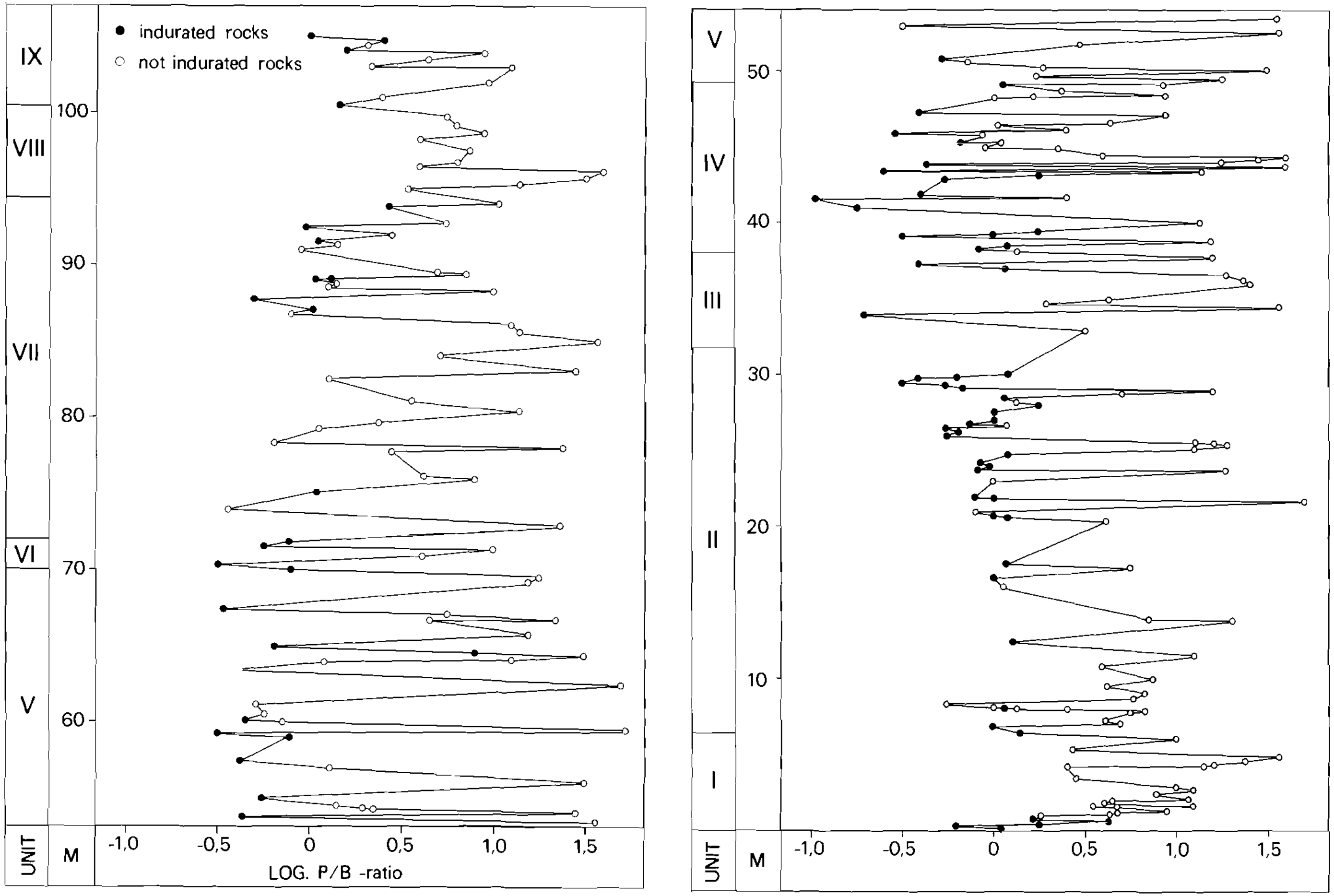


Fig. 13a Vertical distribution of the P/B ratios in thin sections. The P/B ratios are expressed on a log scale.

SAMPLE	157	187	193	199	206	218	225	234	265	273	282	294	297	325	340	373	399	411	417	425	444	462	GROUP
Nr. Specimens	197	209	213	214	195	190	171	191	184	203	181	226	208	191	204	200	200	194	216	201	201	182	
Nr. Species	35	34	34	29	30	39	30	32	44	32	24	34	16	44	20	22	54	41	29	37	28	35	
P/B Ratio	12	12	14	8.2	6.8	36	18	53	28.2	1.9	2.9	2.0	1.1	8.7	0.8	1.0	10	5.2	0.9	9.9	1.2	2.3	
Gaudryina piramidata	7	7	17	37	38	20	50	25	11	30	25	6		3	11	26	7	5	6	1	1	8	**1**
Spiroplectammina adamsi	1		3		1	4		1					1	2		1				1		1	
Spiroplectammina carinata		2	14	3	2	1		7	10			1		2			3	3		9			
Spiroplectammina sp		1	2						1								1	1		8			
Tritaxia tricarinata	8		2		2			1	1	1					2		1						
Glomospira involvens	2	2	1				2		1		1						2			1	8	3	
Gaudryina cf. *reynoldsi*	5		1	38	13	13	3		1	4	1	6	2	2	1	1	2						
Agglutinants spp	1		1	14	4	2	1	3	1	2			1	10	4		7	4		7		1	
Bulimina alsatica	17	4	13	4	4	4	8	4	2	2	4	4		5	1				29			1	**2**
Bulimina buchiana					5		4			1		2	10	1	9								
Bulimina inflata										2	3					3							
Bulimina aculeata											2												
Bulimina sp.1		18	2			6			1								1						
Globobulimina cf. *pacifica*				3			1		1								2						
Bulimina spp.									2									1	1	1	2	1	
Uvigerina urnula																		8					**3**
Uvigerina cf. *batjesi*	10	2				6	4	1	2	4		7						1	25			5	
Uvigerina hispidocostata												4											
Trifarina selseyensis	6	26	7	16	8	1	3	10	3		1	1				12							
Uvigerina spp.									1	1							3	1			4		
Bolivina tortuosa	9	6		3	8	4	3	11	18	1	9	17	22	6	24	37	6	30	81	7	80	23	**4**
Bolivina anglica	2					4	4		3	4	3	2	4		38	1	6	5	4	2	10		
Bolivina striatella																		10					
Bolivine cookei																						4	
Bolivina sp									2		1	1					5					4	
Asterigerina carinata	1		7	1	6	2	13	4	3	23	5	7		9	16	55	9	10	13	21	20	29	**5**
Pararotalia sp	3	2	2	3	23	10	30	4	30	58	98	106	158		82	41	14	6					**6**
Pararotalia cf. *debourle*									1	9													
Lenticulina intermedia	6	4	1		2	4		10	6					17			15	1	3	12			**7**
Lenticulina costata	1	2		1	2	9		2	1					1					1				
Lenticulina sp.	2		6	2		3	2	1			1	1		3	3		1		1		2	1	
Dentalina sp.	1													1				1				1	
Vaginulinopsis sp.				1	1																		
Astacolus cf. *decoratus*		1	1	1		2		1															
Nodosaria spp		1				5			2	3	2	1	1	14	1	1	4		5	11	2	4	
Lagenidae spp.														1			2					1	
Anomalinoides alazanensis	3	5	15	1	4			13	2		2	4		12	2		3	2	4				**8**
Hanzawaia boueana	8	10		4	3		2			4		4		1		1	4	4	2	3	5	7	
Hanzawaia producta	2	23	24	13	7	4	9	2	2	11		4				2	4	7		3			
Hanzawaia sp.	5	2	1	2			1	1	1	1		2		3		3	1		1				
Cibicides lobatulus	11		5	22	9	4	7	7	4	3		8		3	6		3	6	1	1		20	
Cibicides westi	1	18	12		11	1	5	5	14	21	6	10	1			7	16	32	14	5	38	51	
Cibicides spp.1			5	2								1		1		3	3	7	4		5	2	
Anomalina grosserugosa										2													**9**
Anomalina acuta	8	6	15	4	5	7		9	6		3	2		9		1	6	3		13	4		
Planulina sp.			3															1		5		2	
Planulina var. *tendami*	7	2		3	6	14		12	5	1	2	4		10	1		9				5		
Anomalinidae sp.		3		1	3	5			1				1	1	1	2		3	1	1			
Cibicides dutemplei	26	25	17	25	18	24	6	24	22	4	3	9	1	43		2	24	3	1	15	5	3	
Cibicides cf. *bradyi*														3		1		10		3	2	1	
Cibicides spp.2	3	17				2	2		4				1										
Globocassidulina subglobosa	17	7	12	2	2	4	1	20	6	2	1	2	1	1		2	7	12		43			**10**
Gyroidina spp.									2		2	3		2			4	6	1			2	
Gyroidinoides spp												1		6				2					
Pullenia quinqueloba		1												1			2	1		2			
Cancris auriculus	7	1	1	5		5	1		4	1				7				1	2	7		2	**11**
Cancris primitivus	4	2				1	3	7		2							9		1			2	
Valvulineria spp.	1		11	1	2	7			2									3	1	6	2		
Loxostoma applinae	2			1		3		1						3			3	1		6			**12**
Alabamina sp.					2	9	3				1						1		3			1	
Discorbis sp.					3		3		4	3	1	3					1						
Eponides umbonatus	9	5	2	2	1			4			4		1	5		2	1			6	1	1	
Eponides schreibersi	1	2	7				1	1					1				1	2	5		4		
Conorbina marginata			2							3							6					2	
Osangularia sp.		1	3						1			4	2		3	6	1	1	6	1	1	1	

Fig. 14 Range chart of smaller benthonic foraminifera, number of specimens per count, diversity and P/B.

1. Arenaceous forms

The specimens are generally poorly preserved. The most frequent species, *Gaudryina pyramidata*, is indicated separately in the frequency diagram. Less frequent, but present throughout are representatives of *Spiroplectammina,* notably *S. adamsi* and *S. carinata.* The relative frequencies of the arenaceous forms range from 5 to 45%.

2. *Bulimina* s.l.

The *Bulimina* group of species, including *Globobulimina* cf. *pacifica* occurs in frequencies of generally less than 8%. The most frequent species is *Bulimina alsatica,* which possibly covers several closely related species. Another common form is *Bulimina* sp. 1, which is small, compressed and almost triangular with well-developed striae. This species is poorly preserved.

3. *Uvigerina* s.l.

In the lower part of the section *Trifarina selseyensis* constitutes the major part of the group. *Uvigerina* cf. *batjesi* which is rather variable in our associations and which may include several closely related species, occurs throughout the section in variable numbers. This group also has frequencies which are generally below 8%.

4. *Bolivina* s.l.

From the base of the section onwards there is an irregular increase in the frequency of *Bolivina* specimens. This increase is mainly due to *B. tortuosa,* which is indicated separately in the diagram. Many of the specimens are damaged or otherwise poorly preserved. The only other species that contributes substantially is *B. anglica.* The *Bolivina* may form up to 40% of the assemblages.

5. *Asterigerina*

This group of planoconvex forms was separated from group 8 because the specimens are generally strongly recrystallized or damaged, frequently having the last whorl missing. In the upper part of the section *Asterigerina* is more frequent than in the lower part. The frequencies range up to 27%.

6. *Pararotalia* s.l.

The *Pararotalia* specimens are also generally poorly preserved. Many specimens had suffered severe recrystallization. The outer morphology of our *Pararotalia* sp. 1 closely resembles that of *P. manaensis* Wong (1975). The group plays a prominent role in part of the section. In the middle of the section a maximum of 75% is recorded.

In the lower and the upper parts of the section the group is scarce or absent. In one sample a form lacking an umbilical mass is found; this form closely resembles *P. debourlei* le Calvez.

7. Lagenidae

Lagenidae occur throughout the section in frequencies ranging from 1 to 12%. Only in one sample is the frequency as high as 24%. The group is rather diversified. Representatives of *Lenticulina* are the most common. Furthermore *Nodosaria* species are frequent; this group appeared to be very heterogeneous.

8. Planoconvex forms

In this group we brought together a rather diverse group of planoconvex forms on the basis of their supposedly epiphytic way of living. Most frequent are small specimens of *Cibicides lobatulus* (including *C. refulgens*), *C. westi, Hanzawaia boueana, H. producta* and *Anomalinoides alazanensis.* Representatives of *Discorbis* are rare and therefore they were included in the miscellaneous group. Planoconvex species are well represented throughout the section, but especially in the lower and the upper parts the proportions may exceed 25%. In the uppermost sample the percentage is even as high as 44%.

9. *Cibicides* s.l.

This heterogeneous group of biconvex species of supposedly non-epiphytic mode of life occurs in highly variable frequencies throughout the section. *Cibicides dutemplei* is the most frequent species. Only in one sample does it seem to be replaced by *C. bradyi.* The latter species occurs only in minor quantities in the upper part of the section. Other species recorded are *Anomalina acuta* and *Planulina burlingtonensis* var. *tendami.* The frequency pattern of this group is very irregular with percentages up to 34%.

10. Open marine calcareous spiral forms

This group too is based on similarities in overall characteristics of the test: tightly coiled and generally with fine pores. One might wonder, however, whether one is justified in grouping these species together. *Gyroidina, Gyroidinoides* and *Pullenia quinqueloba* occur in minor quantities in the middle part of the section, whereas *Globocassidulina subglobosa* is rather frequent in the lowermost part and in one of the topmost samples.

11. *Cancris/Valvulineria*

This group was formed also because of some similarity in test shape but especially because in other studies (Hageman, 1979) both genera seem to show a similar ecological behaviour. The group occurs in minor quantities with occasional frequencies up to 7%.

12. Miscellaneous

After the above groups had been formed the rather diverse remainder consists of representatives of various families. The individual species are generally represented by one or two specimens and only rarely by more. The group as a whole never exceeds 8%. The most frequent forms are *Eponides schreibersii, E. umbonatus,* while others, like *Loxostoma applinae, Conorbina* cf. *marginata, Osangularia* sp. and *Alabamina* sp. are rare.

Indeterminable

In almost every sample there are specimens that are indeterminable. As far as possible, they were grouped in the main groups described above. The remaining forms are generally not taken into account since there are only a few per sample. This means that they cannot markedly change the frequency patterns of the main groups (fig. 15).

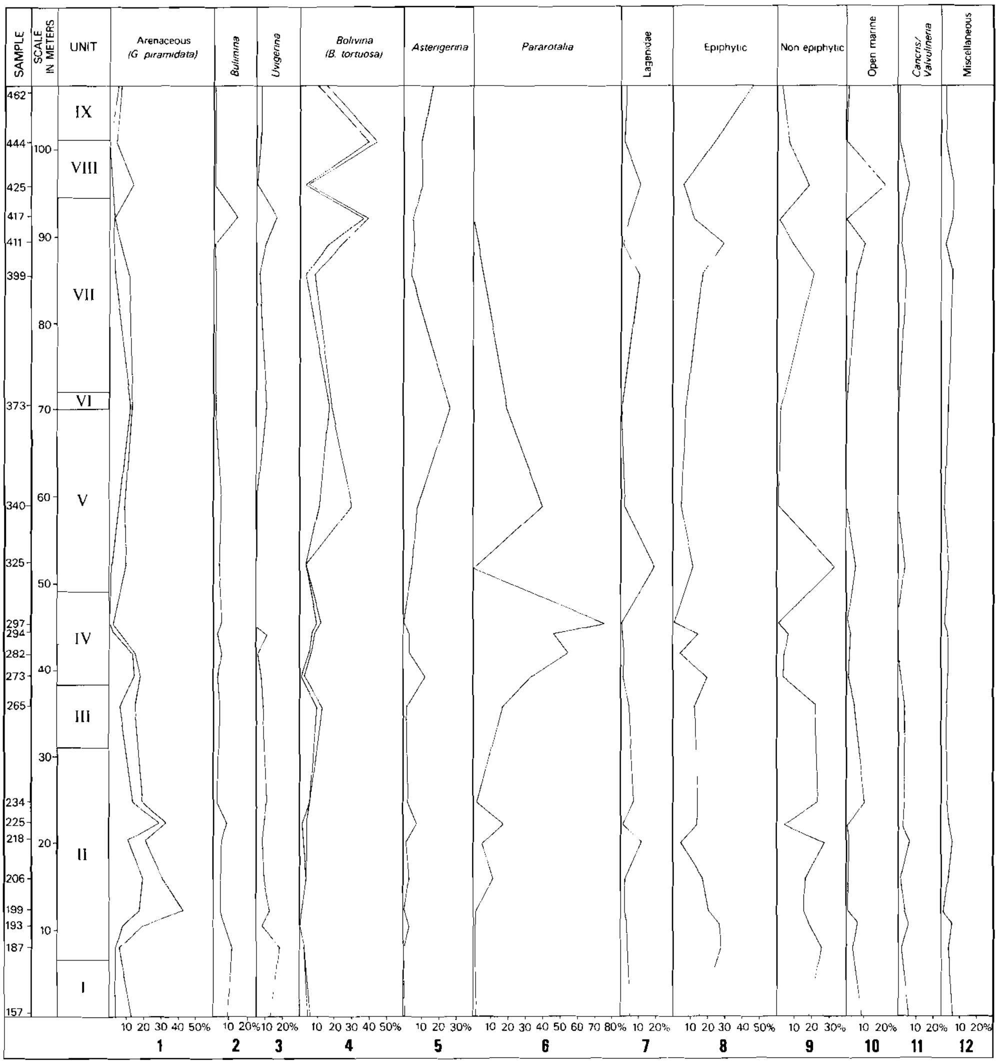


Fig. 15 Frequency distribution of the main groups of benthonic foraminifera.

Relations between species diversity and P/B ratios

The fluctuations in the P/B ratios and the species diversity are shown in fig. 16. There is a remarkable positive correlation between both characteristics. In the analysis of the thin sections we found that completely different assemblages alternate along the section, often in successive layers with a thickness no more than a few mm. One type of sediment is a planktonic foraminiferal wackestone with a well diversified benthonic foraminiferal association. The other extreme type contains bioclastic packstones with sometimes almost monotypic faunal associations like the *Pararotalia* packstones. Of course such differences of sediment types must also be recognized in the faunal associations of the wash-residues. An attractive explanation for the relation we found between the P/B ratio and the species-diversity might be that the correlation is caused by the repeated addition of a low-diversified shallow

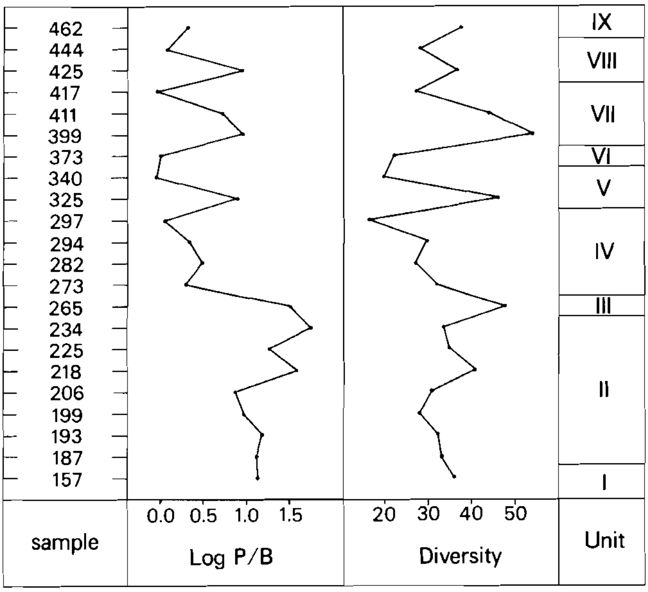


Fig. 16 Fluctuations in P/B (log scale) and diversity of the smaller benthonic foraminiferal associations.

water assemblage of allochthonous origin, to a more open marine authochthonous assemblage. In the following section some attention is paid to the possible composition of both groups.

Smaller benthonic foraminifera in the autochthonous and the allochthonous associations

During the counting in the thin sections we noted that there was a very distinct relation between the degree of induration of the sediment and the P/B ratios (fig. 13). Samples with a very low P/B value were generally more indurated, whereas samples with a high P/B were not. On the other hand one part of the fauna in the wash-residues showed distinct signs of recrystallization, whereas another part was generally well preserved. Since there is obviously a relation between the degree of induration of the sediment and the recrystallization of the benthonic foraminifera, we decided to make two species groups and to investigate how these groups are related to species diversity and the P/B ratio.

These groups are:

1. the poorly preserved group,

in which we include *Gaudryina pyramidata, Bolivina tortuosa* and group 5 and 6 with *Asterigerina* and *Pararotalia* respectively.

2. the well preserved group,

in which the foraminifera of the groups 7, 9, 10, 11 and 12 were included.

Several groups or parts of groups of species were not included in either group 1 or group 2. These percentages are not included in the comparison. They are the remaining arenaceous species, the groups 2 and 3, the remaining *Bolivina* species and group 8. They show no consistent pattern in the degree of preservation.

The percentages of the poorly preserved group are plotted against the log values of the P/B ratio and against the species diversity in fig. 17. In both cases there is a distinct negative correlation between the percentage values and the P/B ratios and the species diversities.

The percentages of the well preserved group are also plotted against the log P/B ratio and the species diversity in fig. 18. Again there are good correlations but now they are positive.

The values of the species diversity and the P/B ratio are also plotted against the percentages of both groups in fig. 19. Extrapolation of the scatter diagrams towards 100% of the poorly preserved group indicates that the species diversity of this group is less than 15 species per 200 specimens. If one bears in mind, however, that even small quantities of a highly diversified autochthonous group will strongly influence the species diversity positively, then the species diversity of a pure, allochthonous association may be much lower.

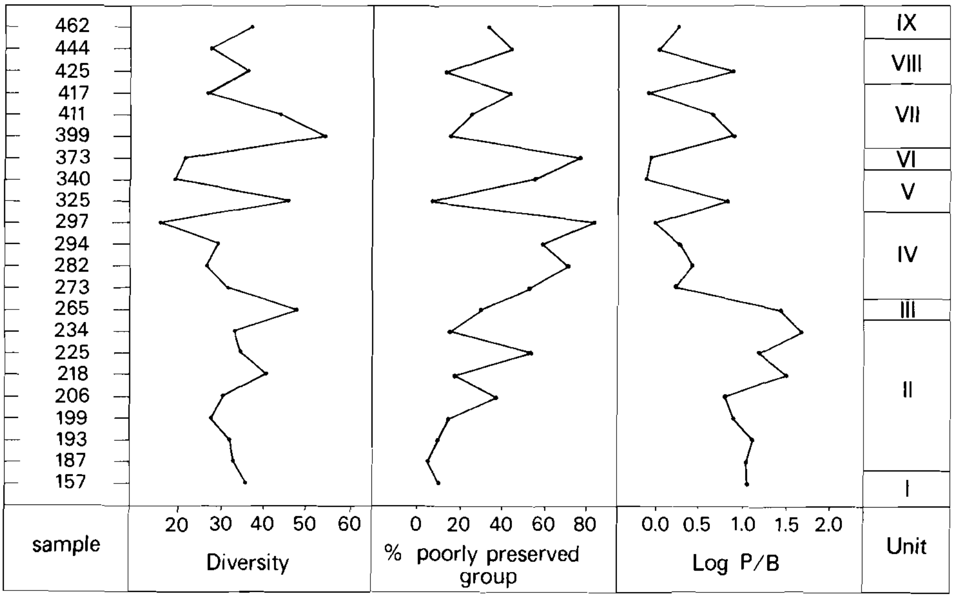


Fig. 17 Percentages of the poorly preserved groups, species diversity and log P/B.

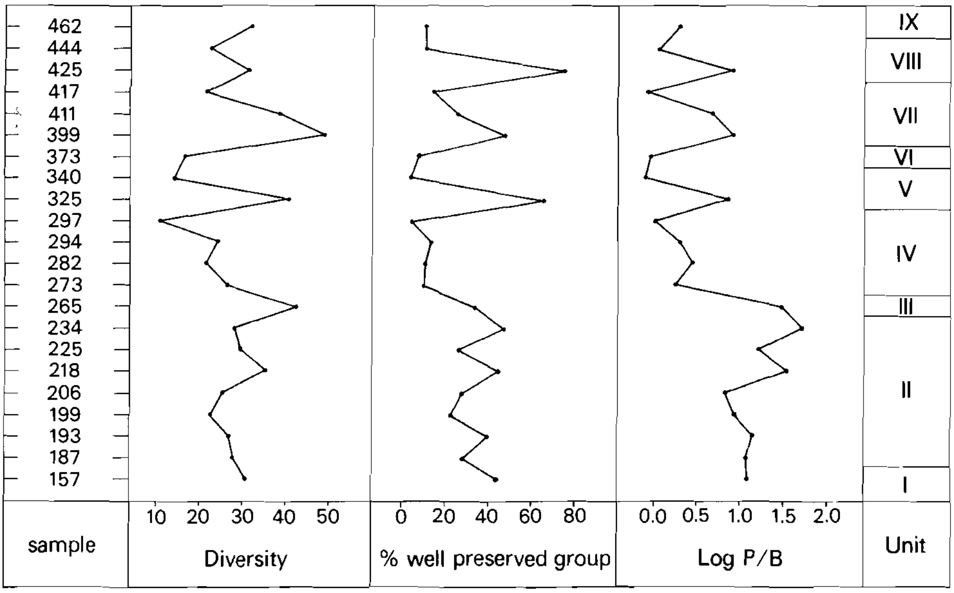


Fig. 18 Percentages of the well-preserved group, species diversity and log P/B.

The P/B ratios of such allochthonous associations are less than one. Extrapolation of the scatter diagram towards a 100% autochthonous association shows that this group is characterized by a species diversity of probably more than 40. The scatter diagram of the percentages of this group against the P/B ratios is more difficult to interpret. The scatter diagram suggests that in pure associations of the well preserved group the P/B value will be well over 10. To maintain that in this group the P/B ratios are constant may be too simple an assumption. Nevertheless some values are very high compared to the extrapolated P/B values for the poorly preserved group.

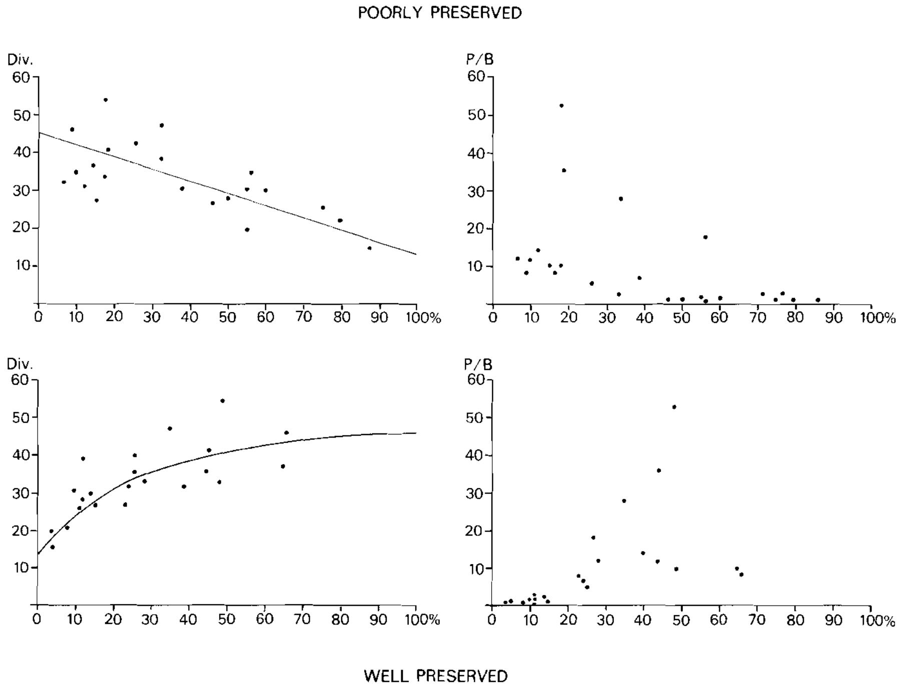


Fig. 19 Scatter diagrams of species diversity and of P/B against the percentages of the poorly preserved group and of the well-preserved group.

Summarizing we can say that the values of species diversity and P/B ratio are determined for the most part by the mixing of two groups. The characteristics of these groups are:

1. the allochthonous group:
   - P/B ratios of approximately 1,
   - species diversity of less than 10,
   - major constituents of the faunal associations are *Pararotalia, Asterigerina, Bolivina, Gaudryina* and unspecified numbers of the other species groups.

2. the autochthonous group:
   - P/B ratios of 10 to 60,
   - species diversity of more than 40,
   - major constituents are the groups of the planoconvex species, Lagenidae, open marine forms, *Cancris/Valvulineria,* miscellaneous and unknown numbers of the remaining groups.

II.8 THE SUBDIVISION OF THE EIN AVEDAT SECTION

Field-data, qualitative and quantitative analyses of thin sections and the analysis of the associations of smaller benthonic foraminifera prove unequivocally that the Ein Avedat section contains a mixture of sediments of allochthonous and autochthonous origin. The field lithology in combination with microfacies data and faunal associations enabled us to subdivide the section of Ein Avedat into nine units, each of which has its own character. The units are outlined below.

Unit I 0–6.20 metres samples: Is 153–177

This unit is composed of well-bedded, vertically irregularly alternating mudstones and wackestones and finely laminated packstones. At the base of the unit there are some chert levels. The contacts between the beds are sometimes indistinct due to burrowing. Indistinct crossbedding occurs at some levels.

In the basal part of the unit fine-grained bioclastic packstones alternate with planktonic foraminiferal mudstones and wackestones. The microbioclastic packstones contain small fragments of larger foraminifera. The plankton mudstones and wackestones are rich in undersized specimens, while the associated benthos is rich in small bi- and tri-serially arranged foraminifera. Towards the top of the unit planktonic specimens gradually increase in size. Some of the beds contain laminae with well sorted planktonic foraminifera.

In the lowermost three metres the P/B ratio increases gradually from about 1 to 12. In the upper part of the unit even higher values are observed, but irregularly distributed low values occur as well.

No complete larger foraminifera were found, only small fragments.

This unit is considered to be the top of the Mor Formation.

Unit II 6.20–30.90 metres samples: Is 178–257

The unit is characterized by the frequent occurrence of coarse-grained bioclastic packstones, bioclastic floatstones and fine-to-medium grained bioclastic packstones. The coarse beds are rich in larger foraminifera. In the lowermost part of the unit some dark mudstones and wackstones were still observed. Here we found dark, irregular, clayey layers with extremely well sorted larger foraminifera. The latter are very flat and belong mainly to the genera *Asterocyclina* and *Discocyclina.* In the lower part there were indications of cross-lamination in the fine-to-medium grained packstones. The floatstones are generally more indurated at the top of the beds.

The unit shows a large variation in the types of microfacies. The planktonic foraminifera are generally larger than in the previous unit, while the associated benthos in the lower part of the unit is still rich in biserial and triserial species. Towards the top the benthos associations become more diverse. Some of the plankton wackestones show distinct sorting in thin laminae. In the fine-grained bioclastic packstones *Pararotalia* appears in the middle part of the unit, but only near the top of the unit can the beds be called *Pararotalia* packstones. The coarse-grained packstones are rich in larger foraminifera, which are sometimes oriented parallel to the bedding-planes. In some samples from the lower part of the unit the larger foraminifera are not only sorted according to size but they sometimes show very little intrageneric morphological variation.

The frequency distributions of the larger foraminifera show a threefold subdivision of the unit. In the lowermost two metres *Asterocyclina* is the most frequent genus, in the middle part *Discocyclina* is sometimes very abundant and near the top *Nummulites* packstones are frequent.

The P/B ratios of the indurated packstones and floatstones range from 0.5 to 1.5. In the non-indurated rocks they range from 1 to 63; the average P/B ratio is approximately 8.

In the lower part of the unit arenaceous species are frequent.

Unit II forms the basal part of the Nizzana Formation.

Unit III 30.90–38.40 metres samples: Is 258–270

Compared with the previous unit there is a distinct drop in the average grain-size. Homogeneous fine-grained packstones alternate with medium-grained bioclastic packstones. Only one bioclastic floatstone is found in the middle of the unit. The base of the unit is taken at the base of the first medium-grained packstone.

Of the microfacies types the planktonic foraminiferal wackestones and fine-grained bioclastic packstones are the most frequent. Only one *Pararotalia* packstone was found. Larger foraminifera are scarce. In the wackestones the benthonic fauna is very diverse.

The P/B ratios in the planktonic foraminiferal wackestones generally exceed 10, whereas in the bioclastic packstones they are approximately 1.

Unit IV 38.40–49.45 metres samples: Is 271–316

In this unit coarse-grained rocks are again frequent. Coarse-grained bioclastic packstones and floatstones alternate with fine-to-medium-grained laminated packstones, while in the middle part there are some cream coloured mudstones. Among the coarse-grained bioclastics there are numerous larger foraminifera locally oriented parallel to the bedding planes and sometimes concentrated in burrows. In some of the coarse-grained packstones the density of the larger foraminifera diminishes gradually upwards as does the degree of induration.

Planktonic foraminiferal wackestones are rare in this interval but, if present, they do not differ from those in the underlying unit. In the finer-grained bioclastic packstones *Pararotalia* is frequent and in some cases the layers can be described as *Pararotalia* packstones. In the coarse-grained bioclastic packstones and floatstones larger foraminifera are very frequent, although considerable numbers of *Pararotalia* and fragments of algae occur as well.

The frequency distribution of the larger foraminifera (fig. 12) shows that *Asterocyclina* is the most frequent genus. Only in the lower part of the unit are some samples encountered that show a predominance of *Discocyclina*.

The P/B ratios reach extremely low values, especially in the *Pararotalia*-rich packstones, whereas extremely high values are observed in the planktonic foraminiferal wackestones.

The frequent occurrence of *Pararotalia* is also reflected in the reduced numbers of other smaller foraminifera in the counts of the wash-residues.

Unit V 49.45–70.40 metres samples: Is 317–364

This unit consists predominantly of fine-grained sediments. Homogeneous fine-grained packstones alternate with fine-to-medium-grained packstones which are frequently laminated. Coarse-grained bioclastic packstones were found as well. Nodular chert beds are frequent. The first chert bed is taken as the base of the unit.

In thin sections the fine-grained sediments are invariably rich in *Pararotalia*. In many cases the latter are the main constituent grains and the rocks are described as *Pararotalia* packstones. *Pararotalia* has replaced the larger foraminifera almost completely; the latter are very scarce in the packstones. The planktonic foraminiferal wackestones are rich in glauconite and the accompanying benthonic fauna is well diversified. Alternations of laminae of planktonic foraminiferal wackestones and *Pararotalia* packstones are frequent. Silicification occurs predominantly in the fine-grained bioclastic packstones.

The scanty data on the larger foraminifera show that *Asterocyclina* is relatively less frequent in the associations than in the previous unit.

The more indurated bioclastic packstones show P/B ratios of approximately 0.5, whereas the wackestones have P/B ratios of 6 to 50.

Unit VI 70.40–72.30 metres samples: Is 365–372

Typical for this unit is the occurrence of several rhodolith floatstones; rhodoliths constitute a prominent part of the pebbles. The unit shows a considerable variation in thickness. Laterally, in a few tens of metres, the thickness may change from 2 to 4 metres. Slump features are obvious. Within the bioclastic floatstones clouds of fine-to-medium-grained laminated packstones are found. Some chert nodules are present.

The thin sections show that the rhodoliths float in a highly variable matrix of fine-to-coarse-grained bioclastic packstones and planktonic foraminiferal wackestones.

The P/B ratios in the matrix of bioclastic packstones are below 1, whereas values of 5 to 8 were found in the clouds of planktonic foraminiferal wackestones.

Unit VII 72.30–94.60 metres samples: Is 373–420

The unit shows a highly variable lithology. The greater part consists of coarse-grained bioclastic packstones and floatstones, alternating with fine-to-medium-grained sometimes laminated packstones. The beds show large undulations and slump features. This unit shows a considerable increase in thickness to the north. Many of the beds, especially above the 80 metre level, are extremely rich in larger foraminifera. The top parts of the floatstones are sometimes intensively burrowed and conspicuously more lithified. The base of the beds is sometimes disturbed by loadcasting. At 81 metres a single chert level is found. Above 83 metres many of the beds are crossed by numerous vertical joints with lithified rims. The strike of the joints is roughly NW-SE. At many places limestone nodules are present in levels, sometimes in pockets.

Occasional planktonic foraminiferal wackestones are found in the middle part of the unit. Fine-grained bioclastic packstones are rare. *Pararotalia* packstones were only found in the lower part of the unit. In the top part one sample is rich in biserial benthonic and in planktonic foraminifera.

The frequency distributions of the larger foraminifera show a distinct increase in the percentage of *Asterocyclina* from unit V to unit VII. In the middle of unit VII, at about 80 metres, there is a drop in the frequency of *Asterocyclina,* whereas in the upper part of the unit this genus is extremely frequent again, sometimes with percentages up to 100.

The P/B ratios of the indurated rocks are low but in the top part of the unit the values are one or more. The P/B ratios of the non-indurated rocks show a wide variation from less than 1 to more than 30.

The benthos-associations in the topmost layers are rich in *Bolivina,* especially *B. tortuosa.*

Unit VIII 94.60–101.25 metres samples: Is 421–444

Compared with the preceeding unit there is a distinct decrease in grain-size. Homogeneous fine-grained packstones and cream-coloured mudstones alternate irregularly. Chert levels are frequent and sometimes developed as beds of approximately 10 to 20 cm. thickness. The base of the unit is defined at the base of the first continuous chert bed. Only in one bed were larger foraminifera found, with an orientation parallel to the large scale crossbedding. In this unit too the beds are disturbed by slumps. The chert beds in some cases follow the slump structures. Some tops of the limestones show intensive burrowing. Again there are many vertical joints.

This interval is the only one with radiolarian mudstones which alternate with planktonic foraminiferal mudstones and wackestones. The radiolaria are poorly preserved and many of the beds show distinct silicification. The planktonic foraminiferal mudstones are rich in small specimens, while the associated benthonics are dominated by small biserial specimens, notably of *Bolivina.*

Only in the lower part of the unit were some poorly washed packstones found with larger foraminifera; again there was distinct orientation of the tests. These packstones are dominated by *Asterocyclina.*

The P/B ratios in this interval show values of 3 to 10. In two samples higher values were observed.

Among the wash-residues one sample appeared to be very rich in *Bolivina tortuosa.*

Unit IX 101.25–107 metres samples: Is 445–463

This unit roughly shows a coarsening upward sequence. In the lower part there are homogeneous fine-grained bioclastic packstones. In the middle part there are fine-to-medium-grained bioclastic packstones, in which small scale crossbedding was observed. In the upper part a thick bed of coarse-grained packstones forms the top of the section. This bed is rich in larger foraminifera.

The thin sections show that in the lowermost metres there are still some planktonic foraminiferal wackestones and these alternate with fine-grained bioclastic packstones. The fine-grained packstones are well-sorted but still contain a high mud-content. There are indications of cross-lamination, in which larger foraminifera are occasionally found in an oriented position. The coarse-grained unsorted bioclastic packstones at the top are sometimes rich in larger foraminifera.

Here too *Asterocyclina* is the most frequent genus.

The P/B ratios range from 1 to 10.

The topmost sample, of which the wash-residues were studied, is very rich in epiphytic benthonics.

II.9 THE RECONSTRUCTION OF THE SEDIMENTARY HISTORY OF THE EIN AVEDAT SECTION

II.9.1 Introduction

Wilson (1970, 1975) distinguished various types of carbonate facies and developed a general scheme of Standard Facies Belts ranging from 1 (basinal deposits) to 9 (platform evaporites). The deposits of the Mor and Nizzana Formation fit nicely into his model. The planktonic foraminiferal wackestones with their well diversified benthonic foraminiferal associations are typical for open shelf deposits (facies belt 2), whereas the ultimate sedimentary environments of the floatstones, slumps and chert levels are typical for toe-of-slope (facies belt 3) to foreslope (facies belt 4).

Subtle differences in the relative frequencies and composition of the various types of sediment distinguished in our paper, together with differences in the faunal associations and in the P/B ratios allow us to make a fairly good reconstruction of the dynamic equilibrium between subsidence history and progressive lateral and vertical outbuilding of the Avedat platform carbonates in the vicinity of the Ein Avedat Canyon.

II.9.2 Mechanisms of sedimentation

The sedimentary mechanisms are fairly constant throughout the history of the sequence of Ein Avedat, but the ultimate appearance of the rocks shows a considerable variation due to fluctuations in the rate of sedimentation.

We are dealing with two essentially different lithofacies. The first is of pelagic origin comprising the planktonic foraminiferal mudstones and wackestones and the radiolarian mudstones of rather variable thickness. These beds are interpreted as autochthonous because there is normally an absence of transport phenomena. The high P/B ratios and the well diversified benthonic faunas in the major part of the section are typical for open shelf deposits. The occurrence of thin laminae of well sorted planktonic foraminifera indicates that energy conditions were temporarily sufficiently high to cause winnowing. The second lithofacies of generally grain-supported rocks may still have a high mud-content. The sediments are rich in associations of larger foraminifera, *Pararotalia* and fragments of red algae. All these bioclasts are indicative of shallow water conditions.

The rapid alternation of layers with rich shallow water biota and other layers with an open shelf fauna proves that the shallow marine elements are in an allochthonous position. This is supported by the field evidence. Many of the "shallow" beds show signs of extremely rapid deposition; the watersoaked sediments evidently remained plastic for a while, which allowed the slumping of series of alternating autochthonous and allochthonous beds. Such series of beds collectively suffered syn-sedimentary and early diagenetic processes, which caused a variable overprint of the original configuration. Repeated scarcity of sediment supply gave bottom-dwelling organisms the opportunity to burrow into the sediment and eventually led to the formation of hardgrounds. Thin layers of (micro-)bioclastic packstones and bioclastic floatstones are generally intensively burrowed, but not indurated. Somewhat thicker beds of up to about 20 cm. also show burrowing and often distinct hardground development, whereas still thicker beds of mass-transported sediment frequently show burrowing at the top only, while induration is usually limited to the upper parts. The induration may affect the various lithofacies recognized in the thin sections.

The supply of allochthonous material varies throughout the section and determines the thickness of the individual autochthonous beds. The slump-directions indicate that the source area was continuously south of Ein Avedat.

II.9.3 Reconstruction of the paleo-environmental history

In this section a reconstruction of the paleoenvironment will be presented per unit of the section of Ein Avedat.

Unit I

The predominantly undersized planktonic foraminifera, together with a little-diversified buliminid fauna in the planktonic foraminiferal wackestones are thought to indicate restricted marine conditions. According to Boltovskoy (1976) such small planktonic foraminifera are typical for shelf waters, but they are generally scarce. The clayey intervals in this unit and the intensive burrowing suggest a low rate of sedimentation. If the shelves are wide the planktonic foraminifera may be very scarce or even absent in the inner parts of the shelf. The increase in the P/B ratio in the lower part of the section may then be explained by a transgression during the deposition of the top part of the Mor Formation. This concurs with the conclusions of earlier authors (Arkin et al., 1972; Benjamini, 1979) about the general transgressive character of the Mor Formation. Towards the top of the unit the planktonic foraminifera increase in size, indiciating more favourable conditions for the planktonic populations. According to Arkin et al. (1972, see also fig. 6) the Ein Avedat area was a semi-enclosed shallow marine basin during the time of the deposition of the Mor Formation. Subsidence of the area might have caused the entry of a more open marine water mass providing better living conditions for the planktonic foraminifera.

The intercalated fine-grained microbioclastic packstones with occasional vague indications of sorting may be explained in two ways. Primarily a somewhat increased vigour of bottom currents may have caused the winnowing of the sediment in situ, but the sorting may be a consequence of deposition in distal tongues of mass-transported sediment. The indication of sorting in the planktonic foraminiferal wackestones suggests that lateral displacement may have played a part. Since small fragments of larger foraminifrea were also recognized amongst the grains, we presume that at least part of the bioclastic packstones represent the distal tongues of mass-transported sediments, derived from an area colonized by larger foraminifera.

Unit II

The planktonic foraminiferal wackestones of this unit are again indicative of off-shore conditions at the place of deposition. The associated benthonics, which are still rich in biserial species in the lower part of the unit, become more diversified towards the top. This unit differs from the previous unit in that it possibly shows a development towards less restricted bottom conditions.

The relatively undisturbed clayey intervals at the base of the unit in which some levels occur with rather flat larger foraminifera, like *Discocyclina* and *Asterocyclina* cf. *lanceolata*, may be autochthonous. The slight morphological variation in these larger foraminifera may also point to relatively undisturbed thanatocoenoses. Larger foraminifera possess symbionts which are involved in their metabolism. Such symbionts, like zooxanthellae and diatoms (Lee, 1980) play an active role in photosynthesis and/or metabolism. This means that the lower depth limit of larger foraminifera is determined by the depth range of the photic zone. Furthermore, morphological changes with depth have been established for many larger foraminifera i.e. deeper living species or ecophenotypes are relatively flatter (Fermont, 1977a, b; Hottinger, 1977a; Larsen & Drooger, 1977; Muller, 1977). The combination of larger foraminifera and autochthonous planktonic foraminiferal wackestones suggests that the actual depth of the supposedly undisturbed thanatocoenoses of larger foraminifera must have been in the lower part of the photic zone, i.e. somewhere between 60 and 100 metres.

Beds with obvious signs of mass-transport are frequent in this unit. The thickness, frequency and grain-size of individual beds are considerable compared to the underlying unit. The sediments belong to a typical foreslope facies (Wilson, 1975). The difference in the grain-size of units I and II points to a progressive outbuilding of a nearby carbonate platform. The slump directions and the regional geology indicate that the carbonate platform must have been situated to the SSW. In contrast with the clayey intervals with larger foraminifera lower down in this unit these coarser beds generally contain larger foraminiferal associations rich in thicker *Asterocyclina* and *Nummulites* specimens. The relative thickness of these foraminifera and the allochthonous position of the strata in which they are found suggest that they were derived from shallower parts of the photic zone. The absence of biota of extremely shallow water points to a depth-range of approximately 20–60 metres for the source area of the allochthonous larger foraminiferal associations.

Unit III

The planktonic foraminiferal wackestones are not really different from the wackestones in the top part of the previous unit; they point to similar offshore conditions.

The distinct reduction in grain-size in the bioclastic packstones may be explained in two ways. Either the southern source area retreated due to an overall subsidence which was not counterbalanced by sufficient upgrowth and outbuilding of the carbonate platform; this would have led to a more distal character of the bioclastic packstones in the Ein Avedat area. Or changes in the distribution of specific environments in the source area diminished the supply of coarse-grained sediments. The more frequent occurrence of *Pararotalia* in this unit may point to such changes in paleogeography. However, the bioclasts are also rich in fragments of larger foraminifera, which supports the first explanation. Possibly both explanations have to be combined.

Unit IV

Planktonic foraminiferal wackestones are scarce in this interval but in so far as they are present they are comparable to those of the lower units II and III.

The fine-grained bioclastic packstones with their extremely low P/B ratios and the dominance of *Pararotalia* point to very restricted marine conditions at the place of origin. Wong (1976) reported associations of abundant *Pararotalia* with similar morphology from the Mana well in French Guyana. In his opinion these *Pararotalia* faunas were adapted to shallow marine conditions in a restricted (coastal-lagoonal?) environment with fluctuating salinity values.

Also the larger foraminiferal packstones, with abundant *Asterocyclina* and frequent fragments of rhodolith algae point to shallow marine environments in the source area, but not to otherwise restricted conditions.

Unit V

Planktonic foraminiferal wackestones are again frequent and no changes in composition are observed. Considering the sediment pile of about 70 metres from the base of our section to the top of unit V and the fairly constant presence of planktonic foraminiferal wackestones local subsidence must have been continuous with a total effect of at least 70 metres.

The frequent occurrence of *Pararotalia* packstones and the low P/B ratios, together with the diminished frequency of *Asterocyclina* packstones point to changes in the source area in which mainly *Pararotalia*-rich sediments were available for transport.

It is rather far fetched to attempt to reconstruct a detailed set of paleoenvironments in the source area on the basis of the characteristics of the allochthonous sediments, but in an upwards direction these allochthonous sediments seem to become more and more impoverished in their faunal content. From the supposedly autochthonous flat *Discocyclina* and *Asterocyclina* associations in the lower part of unit II, through the allochthonous associations of the units II to IV with the predominance of *Asterocyclina* in unit IV to the almost monotypical *Pararotalia* associations in unit V, there seems to be a logical continuation of a trend. It is attractive to explain such a trend by positioning these faunal associations along a depth cline. In view of the regional geology and the occurrence of slumps a depth cline must have been present. However, carbonate platforms are extremely complex in structure, in that superimposed on a general depth cline there may be a development of barriers, positive areas, lagoons and inlets which cause a lateral variation (Wilson, 1975). Nevertheless, in view of the vertical succession of faunal associations, the frequent slumping of sediments with *Asterocyclina* and algae (such as in the next higher unit) we assume that the *Asterocyclina* associations were produced somewhere in the top-part of the foreslope between an inner shelf area where *Pararotalia* flourished, and a deeper forslope area in which the flat *Discocyclina* and *Asterocyclina* and at least part of the *Nummulites* and *Operculina* thrived. As a consequence, after the initial general transgressive episode recognized in the top-part of the Mor Formation (unit I), there was a shallowing trend in the source area of the allochthonous sediments. Such a shallowing cannot be deduced from the autochthonous sediments.

Units VI and VII

Planktonic foraminiferal wackestones are scarce in these units. In unit VI and in the middle of unit VII they are still the same as in the previous units. At the top however one sample is observed to be very rich in biserial benthonics; the latter association would fit better into the next higher unit. The increase in the thickness of the unit towards the north and the mass-transport features point to a rapid outbuilding of the foreslope facies to the north.

The P/B ratios which show a distinct increase in their minimum values, and the disappearance of *Pararotalia* suggest a trend in the source area of allochthonous assemblages from unit V to the top of unit VII opposite to that from unit III to V, i.e. from a restricted *Pararotalia* environment to an upper foreslope facies with Rhodophyta and *Asterocyclina.*

The extremely rapid rate of sedimentation in this part of the section has almost certainly affected the depth of deposition of the uppermost sediments; this change is more strongly expressed in the next higher units.

Unit VIII

The planktonic foraminiferal wackestones and mudstones with their small planktonic foraminifera and blooms of biserial benthonics (predominantly *Bolivina tortuosa*) and the occurrence of radiolarian mudstones point to distinct changes in the paleoenvironment.

The general decrease in the maximum P/B values (except in one bed of bioclastic floatstones with clouds of planktonic foraminiferal wackestones with high P/B values, which may be of entirely allochthonous origin) and the occurrence of mega-crossbedding in one of the beds indicate a development towards a shallow shelf sea, where water conditions were favourable to radiolaria and relatively small planktonic foraminifera. Similar "radiolarian" basins are reported from the Eocene of the Gallilean foothills by Rabinovitch (1954, unpubl. report, fide Benjamini, 1979) and Benjamini (1979) in the northern part of the Hashefela syncline north of Beer Sheva. The blooms of radiolaria may be due to upwelling in front of shallow marine shelf seas. The abundant radiolaria present in this interval probably provided the material for the well-developed chert beds in the unit.

The gradual disappearance of the larger foraminifera in this unit simply indicates that the source area containing larger foraminifera was not available any more. The slumps in the planktonic foraminiferal wackestones and mudstones, in the bioclastic packstones and possibly in the radiolarian beds indicate that the mechanism of sedimentation had not changed. The increase in the P/B ratios of the bioclastic packstones, together with the occurrence of biserial benthonics and the disappearance of the larger foraminifera indicate that the difference between the autochthonous and the allochthonous material became reduced. In other words a levelling of the whole shelf area had taken place.

Unit IX

The disappearance of the planktonic wackestones, the presence of vague cross-laminations and the overall coarsening upwards in the unit witness to a sustained shallowing of the area. However, energy conditions must have remained low because all the samples studied still show a rather high mud-content that had not been removed by winnowing. In this unit the distinction between autochthonous and allochthonous sediments has become completely lost.

II.10 SUMMARY

The sediments of the Avedat plateau have been deposited in a shallow marine environment. The Ein Avedat section witnesses to a subtle equilibrium between the rate of subsidence and the rate of sediment accumulation.

From the top of the Mor Formation to the basal part of the Nizzana Formation we can conclude that there was a transgressive tendency during which the subsidence was not balanced by the rate of sedimentation.

In the lower part of unit II the flat larger foraminifera may have been deposited in situ. Because of the alternation of pelagic sediments and larger foraminiferal packstones we suppose that the sediments were deposited in a lower foreslope environment near the lower limit of the photic zone. The allochthonous beds of unit II witness to a progressive outbuilding of the Avedat plateau to the north. The sediments are probably derived from an upper slope environment.

In unit III the supply of allochthonous sediment ceased for a while, or nearly so. Probably this is – at least in part – explained by the subsidence of the whole area. The planktonic foraminiferal wackestones are indicative of an open shelf sea.

In unit IV and up to the lower part of unit V the larger foraminifera are gradually replaced by *Pararotalia* which is indicative for restricted inner shelf conditions. The sediments with shallow water foraminifera again alternate with pelagic sediments which proves their allochthonous origin. The increasing abundance of *Pararotalia* suggests a regressive tendency in the source area.

From unit V to the middle of unit VII the development was reversed. The *Pararotalia* packstones were replaced by larger foraminiferal packstones which might indicate a renewed transgressive episode in the source area, while the planktonic foraminiferal sediments remain unaltered. Towards the top of unit VII the accumulation of sediments of allochthonous origin was extremely rapid which reduced the depth of ultimate deposition: the autochthonous planktonic foraminiferal sediments gradually become impoverished.

This change culminated in the development of planktonic and radiolarian mudstones which are indicative of shallow shelf seas.

The regressive tendency continued in unit IX, in which sorting effects and sedimentary structures can be interpreted as a further shallowing of the area.

A tentative reconstruction of the relative paleobathymetry for the autochthonous and the allochthonous sediments of the Ein Avedat section is shown in fig. 20.

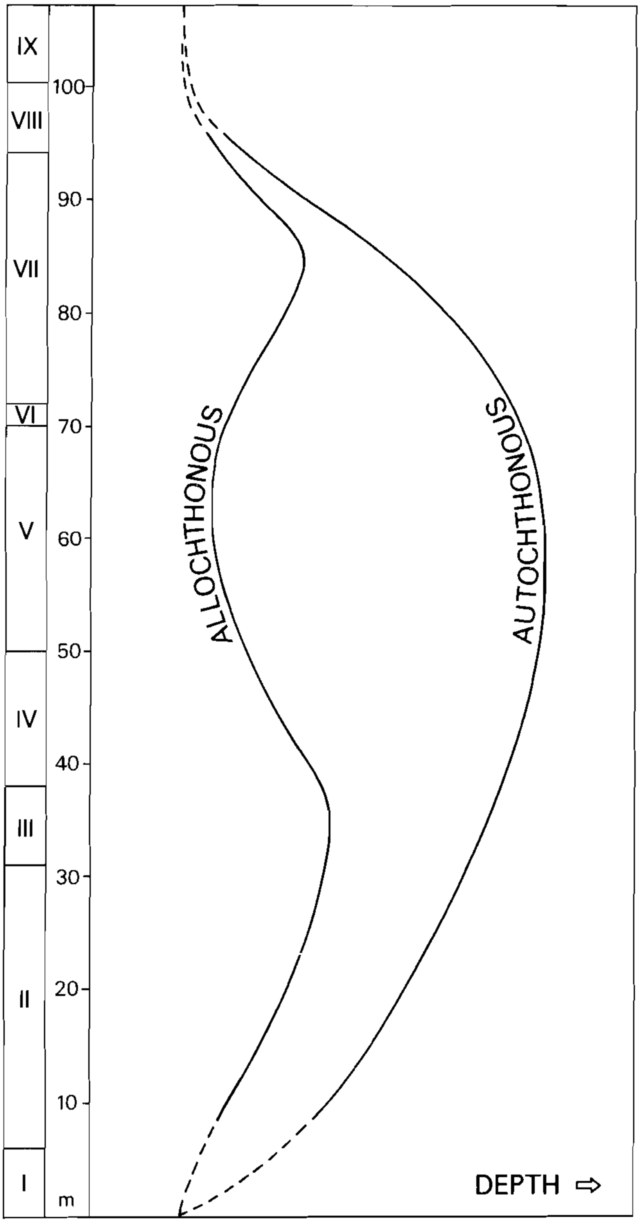


Fig. 20 Paleobathymetric reconstruction for the autochthonous and the allochthounous sediments of the Ein Avedat section.

Chapter III

THE DISCOCYCLINIDAE OF THE EIN AVEDAT SECTION

III.1 SOME REMARKS ABOUT THE HISTORY OF THE RESEARCH ON THE DISCOCYCLINIDAE

Rather than present an exhaustive review of the literature on the Discocyclinidae, we prefer to discuss the current state of our knowledge compared to our knowledge of other groups of larger foraminifera.

In several groups of orbitoidal foraminifera the recognition of distinct time-bound patterns has led to a fairly coherent picture of their phylogeny and generally to a considerable reduction of the number of species units required. Examples are the Miogypsinidae, Lepidocyclinidae, Orbitoididae, Lepidorbitoididae, Pseudorbitoididae. Once established, groups with a generally accepted phylogeny become the basic material for more advanced studies concerning provincialism, differential rates of evolution and ecophenotypic variation. Although the Discocyclinidae belong to the most highly evolved orbitoidal foraminifera, research about this complex group apparently proceeded very slowly in the course of the twentieth century. The actual state of knowledge is still at the level of describing species from all over the world, whereas there is no consensus at all about the systematic position of families, genera and species.

Gümbel (1868) was the first author who gave the discocyclinids a relatively fair systematic position. One of the genera of his family Nummulitidae was *Orbitoides*, which he subdivided into six sub-genera: *Orbitoides, Rhipidocyclina, Discocyclina, Asterocyclina, Actinocyclina* and *Lepidocyclina.* They were grouped together because of their median layer and lateral tissues.

Munier-Chalmas (1891) united all the forms with rectangular chambers in the equatorial layer in one genus, *Orthophragmina,* which he subdivided into four sub-genera: *Actinocyclina, Asterocyclina, Discocyclina* and *Rhipidocyclina.* On the basis of this subdivision Schlumberger (1903, 1904) was the first to recognize the importance of the structure of the embryon. His species concept was based on a combination of the outer morphology and the structure of the embryonic apparatus. H. Douvillé (1922) also followed the classification of Munier-Chalmas. His further subdivision at the species level is based mainly on details of the pustules and the lateral tissue.

Galloway (1928) created the subfamily Discocyclininae in which he placed the genera *Spiroclypeus* and *Discocyclina.* The latter genus is subdivided into the four subgenera of Munier-Chalmas. He maintained this classification in 1933 but then gave *Asterocyclina* and *Actinocyclina* a generic rank, and added the genus *Orthocyclina.*

Vaughan and Cole (1940) promoted the Discocyclininae to family rank and they separated the Discocyclinidae from the Cycloclypeidae. They subdivided the Discocyclinidae into two genera. *Discocyclina* and *Pseudophragmina* with the subgenera *Discocyclina* s.s., *Asterocyclina, Actinocyclina,* and *Pseudophragmina* s.s., *Proporocyclina* and *Athecocyclina* respectively. The latter genus is restricted to the American fauna province; its subdivision is based on the position of stolons and the more or less complete development of the radial walls of the equatorial chambers.

In the same year Van der Weijden (1940) approached the Discocyclinidae in a different way. Analogous to the successful subdivision of the genus *Lepidocyclina* by means of the morphology of the embryon he distinguished five subgenera in *Discocyclina.* This subdivision is rather artifical however and adds little to the understanding of the taxonomic relations in the group because there is no time-bound order for these subgenera.

Brönnimann (1945) presented a detailed study on the morphological differences between the genera *Asterocyclina, Discocyclina* and *Actinocyclina. Discocyclina* never has a stellate pattern, *Asterocyclina* has a stellate pattern in the median layer, and the radiate structure of *Actinocyclina* originates in the lateral tissue. The same author (Brönnimann, 1945b) studied the microspheric generations of the Discocyclinidae and he came to the conclusion that *Asterocyclina* and *Discocyclina* belong to two totally unrelated families. He subdivided the Discocyclinidae into two subfamilies, the Discocyclininae (in a sense completely different from Galloway, 1928) and the Orbitoclypeinae. His Discocyclininae are supposed to have annular chambers in the median layer, with a secondary subdivision into rectangular chamberlets, whereas the Orbitoclypeinae have true undivided chambers with an orbitoidal arrangement. Brönnimann's subfamily Discocyclininae includes the genera *Discocyclina, Actinocyclina, Proporocyclina, Pseudophragmina* and *Athecocyclina.* The subfamily Orbitoclypeinae consists of the genera *Orbitoclypeus* and *Asterocyclina.* As far as the Eurasian Discocyclinidae are concerned most of the subsequent authors follow Brönnimann's concept (Sigal, 1952; Schweighauser, 1953; Kecskeméti, 1959; Brolsma, 1973; Sirotti, 1978).

Neumann (1958) too agrees with the morphological subdivision of *Asterocyclina, Discocyclina* and *Actinocyclina* according to Brönnimann, but in her classification of the subfamily Orthophragmininae she adds *Pseudophragmina* and the commonly accepted name *Asterocyclina* is replaced by *Asterodiscus* Schafhäutl 1863.

Brönnimann's classification was further elaborated by Caudri (1972). She made a distinction between the European and American Discocyclinidae and erected several new genera. She raised the subfamilies of Brönnimann to family rank. The Discocyclinidae include the genera *Discocyclina, Actinocyclina, Proporocyclina, Athecocyclina* and *Asterophragmina.* In the family of the Orbitocyclinidae she puts the genera *Orbitoclypeus, Neodiscocyclina, Stenocyclina, Pseudophragmina, Asterocyclina* and *?Hexagonocyclina (= Bontourina* Caudri, 1948).

All the classifications mentioned above have several features in common. The first is that they all lack a convincing phylogenetic background. Secondly, all of them are based on more or less arbitrarily chosen features without any justification for the hierarchy of these features. Thirdly, species designations are generally based on a typological species concept in which normal variation is not or almost not recognized.

Brolsma (1973) analysed Lower Eocene Discocyclinidae from Gan (SW France). His biometrical data show that there is a close resemblance between his *Discocyclina augustae* and *Asterocyclina stellata,* whereas his *Discocyclina archiaci* is significantly different from the other two species in most of the internal parameters measured.

Little is known about the ecology of the Discocyclinidae. According to Kecskeméti (1959) *Actinocyclina, Asterocyclina* and relatively thick *Discocyclina* (*D. nummulitica, D. douvillei, D. chudeaui* amongst others) are most frequent near the Eocene coast-line in the Bakony mountains, whereas flat *Discocyclina* are more frequent in the deeper parts of the Eocene Bakony basin. Sirotti (1978) however suggested that the *Asterocyclina* beds of the Priabonian type section were deposited in deeper or at least more quiet water than the *Discocyclina* beds of the same section. His arguments for such a conclusion are not convincing however (see Setiawan, in prep.).

In this chapter we shall present detailed descriptions of the morphology of our Discocyclinidae. In the following chapter the ecology and evolution of the Discocyclinidae is discussed.

III.2 METHODS OF INVESTIGATION

III.2.1 The collecting of the specimens and the preparation methods

The specimens were collected from the 0.6 to 4.0 mm. sieve fraction of the wash-residues. Negligible numbers of specimens were found in the larger fraction and occasional broken specimens in the smaller fraction. In order to obtain statistically workable quantities some 25–30 specimens were picked at random. In some samples the number of specimens collected was less because of lack of material. When during the sectioning an abnormally wide variation was observed in the internal features of specimens from a single sample we picked additional specimens.

In the course of the investigation it appeared likely that the outer morphology (of *Asterocyclina*) might also provide information. Therefore a separate run was made to gather data on the outer morphology of *Asterocyclina.*

The specimens were mounted on glass plates and the median layer was made visible. Depending on the quality, half-sections were made by cutting the specimens along the median layer or by grinding away the lateral layers on one side, or thin sections were prepared by grinding away the lateral layers on both sides.

III.2.2 Measurements

Measurements were performed by means of a Leitz binocular microscope equipped with an ocular micrometer. The details of the morphology of the Discocyclinidae were measured with a calibrated micrometer. The measurement unit corresponds to 5.04 μ. In practice this value was rounded off to 5.0 μ, thus causing a systematic error of –1%, which is generally much less than the precision of half a measurement unit. The outer morphology was measured with the aid of a calibrated measurement unit of 0.10 mm.

III.2.3 Parameters

Eleven parameters were chosen. Eight describe the size and the configuration of the embryon and the first annulus in median sections, in accordance with the procedure followed by Brolsma (1973) with slight modifications and additions. One parameter was chosen for the number of ray-like prolongations in the median layer of *Asterocyclina.* Finally, two parameters are used for the outer morphology of *Asterocyclina.* All these parameters are shown in figs. 21 and 22. The internal size parameters include half the thickness of the wall on both sides.

D_1 = Diameter of the protoconch, measured perpendicular to the axis of symmetry of the embryon.

D_2 = Diameter of the deuteroconch, also measured perpendicular to the axis of symmetry of the embryon.

H_1 = Height of the protoconch, measured along the axis of symmetry.

H_2 = Height of the embryon, again measured along the axis of symmetry. There are two possibilities. If the protoconch is partly enclosed by the deuteroconch, H_2 is measured from the base of the protoconch to the top of the deuteroconch. If the protoconch is completely surrounded by the deuteroconch, which may be the case in *Discocyclina,* then H_2 is measured from the base of the deuteroconch to its top along the axis of symmetry.

H_c = Height of the "top-most" peri-embryonic chamber, which is cut by the axis of symmetry.
It should be realized that the height of this chamber is not always representative for the average height of the peri-embryonic chambers in a specimen.

R = $h/H_1 \times 100$ gives the degree to which the protoconch is enclosed by the deuteroconch.

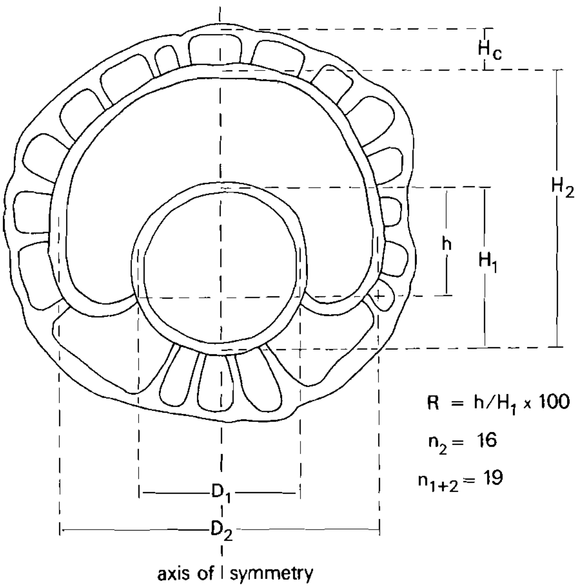


Fig. 21 Internal parameters of the Discocyclinidae.

h is measured along the axis of symmetry from the top of the protoconch to the line connecting the points where the deuteroconch wall touches the protoconch in the section. If the embracement is complete the lower boundary of h is taken in the middle of the wall of the deuteroconch.

n_2 = The number of peri-embryonic chambers on the deuteroconch, including the two principal auxiliary chambers.

n_{1+2} = The number of peri-embryonic chambers on the protoconch and the deuteroconch together. No difference is made between accessory auxiliary chambers, inter-auxiliary chambers and closing chambers, because in the bulk of the material such a differentiation appeared to be impossible. Only occasionally could such differences be observed in specimens of *Asterocyclina.*

r = The number of rays with more elongated chambers in the median layer. These rays correspond in general with the rays visible on the outside.

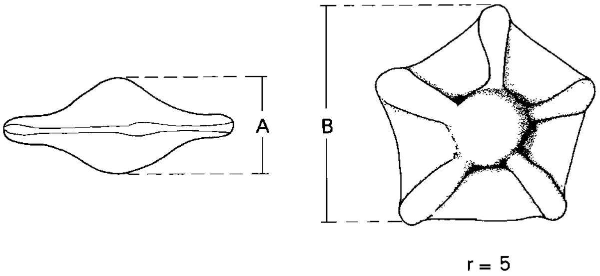


Fig. 22 External parameters of *Asterocyclina.*

In our material no *Actinocyclina* sensu Brönnimann (1945) were encountered. Occasionally equatorial rays are weakly developed without visible effects on the outer morphology.

A = The thickness of the specimen, measured perpendicular to the median layer.

B = The diameter of a specimen.

In *Asterocyclina* some problems may arise, due to the irregular outline of the specimens. B is measured along one ray, through the centre up to the intersection with the line connecting the ends of the two opposite rays.

III.3 *ASTEROCYCLINA*

III.3.1 Introduction

Today there is general agreement in the literature that *Asterocyclina* should be separated from the other Discocyclinidae on the basis of the presence of rays in the median layer. In our material there is no problem in making such a separation.

Stellate patterns are common features in larger foraminifera but as a general feature of the median layer they seem to be unique for *Asterocyclina.* In other genera, like *Orbitocyclina, Pseudorbitoides* and *Lepidocyclina* stellate "species" are also described separately, but they are commonly placed into the synonymy of non-stellate relatives (compare Van Gorsel, 1978; Van Vessem, 1978). In the European faunal province some ten species of *Astero-*

cyclina have been described (compare Van der Weijden, 1940; Schweighauser, 1953; Neumann, 1958; Sirotti, 1978). Many of the species, however, are discriminated on size, or size-dependent parameters. The variation in outer morphological characters is much less than in *Discocyclina.*

Representatives of *Asterocyclina* are frequent in the Ein Avedat section. The quality of the material appeared very good, which enabled us to collect data on the inner as well as the outer morphology.

The embryon of *Asterocyclina* invariably possesses the isodiscodine to nephrodiscodine configuration, which demonstrates that the variation in *Asterocyclina* is considerably less than in *Discocyclina* with respect to the inner morphological characters.

III.3.2 The building plan of *Asterocyclina*

The morphology of larger foraminifera is strikingly complex and representatives of *Asterocyclina* are no exception. The test comprises a median layer consisting of equatorial chambers and on both sides lateral layers consisting of lateral chambers.

The most important diagnostic features are recognized in the median layer which can only be studied in half-sections or in equatorial (= median) thin-sections.

In the centre of the median layer of *Asterocyclina* the embryon consists of a (sub-)circular protoconch and a kidney-shaped deuteroconch, which partly surrounds the protoconch (fig. 23). The embryon is almost invariably of the nephrodiscodine type (sensu van der Weijden, 1940), only occasionally are specimens of a more isodiscodine type. There are always two principal

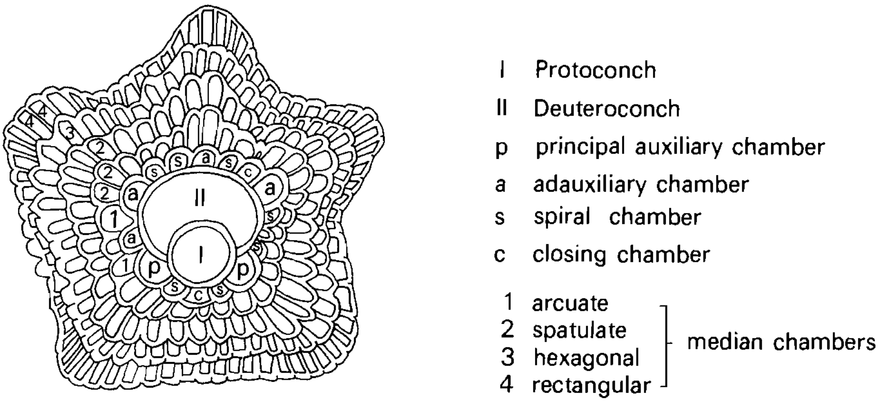


Fig. 23 Schematic drawing of a median section of *Asterocyclina.*

auxiliary chambers. They are generally somewhat larger than the other chambers in the first annulus.

The chambers of the first annulus are sometimes of variable size and shape. Especially in the lower part of the Ein Avedat section a differentiation can be made between accessory auxiliary chambers, interauxiliary spiral chambers and closing chambers. Such differentiation is too rare to be of practical value. Still, this differentiation is important because it can tell us something about the origin of *Asterocyclina* (see chapter 4). In fig. 23 we show a schematic drawing of such a primitive form.

A diagnostic feature of all Discocyclinidae is the rectangular shape of chambers in the median layer. In *Asterocyclina,* however, the first few annuli may contain chambers ranging in shape from arcuate to spatulate and hexagonal. The typical rectangular chambers are introduced gradually and they become dominant from the second to sixth annulus outward (fig. 23).

The rays in *Asterocyclina* are formed by relatively more elongated rectangular median chambers in definite positions relative to the embryon, which is not always the case with other foraminifera with stellate patterns (compare for instance Van Vessem, 1978, pls. 6, 7, 8). Normally five rays originate from the embryon. Two rays invariably originate from the principal auxiliary chambers. The others originate from the outer wall of the deuteroconch. When there are distinct size differences in the peri-embryonic chambers the rays generally originate from the larger ones. If there are more than five rays the additional ones start at a later ontogenetic stage in between the five rays already present (fig. 24). In fact, *Asterocyclina* does not reach radial symmetry but it remains fixed to some kind of bilateral symmetry, which is

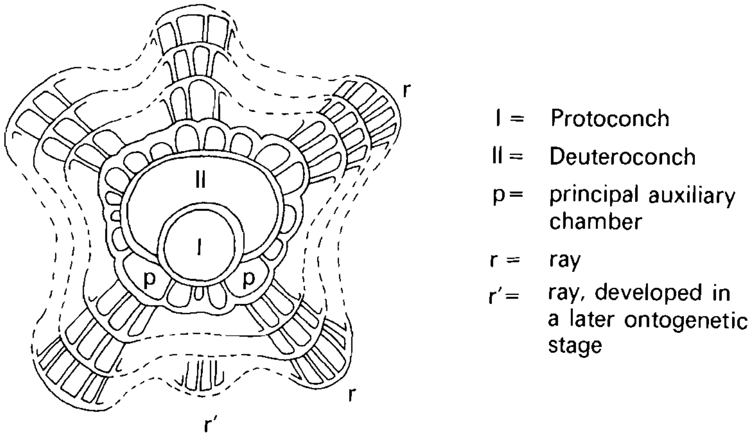


Fig. 24 Position of the rays of *Asterocyclina* relative to the embryon.

sometimes visible already from the outside. In pentagonal forms the angle between the rays originating from the principal auxiliary chambers is frequently somewhat larger than the angles between the other rays. Specimens with more than five rays, such as *A. lanceolata* (Schlumberger), are sometimes described as separate species.

The median layer of *Asterocyclina* thickens towards the periphery. In the interradial areas the median layer gradually increases in thickness but it generally remains single-layered. In the radial areas the median layer thickens more rapidly and it may become subdivided into more than one layer towards the periphery.

Occasional specimens were found in which annuli lacked the subdivision into chambers. These specimens start as an *Asterocyclina* but after the formation of the fifth or the sixth subdivided annulus extremely wide chambers are formed. In the literature such types are referred to as *Asterophragmina* Rao. In our material these specimens cannot be separated on the basis of morphological characters that concern the embryonic and the peri-embryonic parts of the test.

The lateral layers are strongly reduced in number towards the periphery. Perpendicular to the lateral layers there are calcite pillars, somewhat conical in shape; they are visible from the outside as relatively large pustules. The size of the pustules is dependent on the size of the test and therefore they are not very useful for discriminating different species.

The pustules at the surface are surrounded by rosettes of lateral walls, which may vary in number from five to nine.

There is no one-to-one relation between the number of annuli and the number of lateral layers. There are more annuli than lateral layers. In thin sections specimens were observed which already had three to four annuli, but lacked a lateral tissue. Large specimens may have bare and protruding peripheral parts of the median layers.

The generally high degree of recrystallization prevented us from carrying out a detailed analysis of fine structures like stolons.

III.3.3 The outer morphology of *Asterocyclina*

III.3.3.1 *Introduction*

So far most investigators have used the outer morphology of *Asterocyclina* to separate species (= morphogroups). In their species concepts they generally underestimate or disregard some aspects.

Many outer features of *Asterocyclina* are intrinsically connected with ontogeny. The conical pillars generally increase in number and surface expression during ontogeny. This makes the pustules an unsatisfactory characteristic for species discrimination, as thicker specimens, or thicker parts of the test will possess more and larger pustules. Also discrimination on the number of rays may be based on different ontogenetic stages of the same species. *Asterocyclina* starts with the construction of five rays. In the course of ontogeny the number may increase by addition of rays in the interradial areas or by bifurcation of existing rays.

The size of *Asterocyclina* has frequently been used to separate "species" because of entirely different size ranges; this has led to a rather confused taxonomic literature. H. Douvillé (1922) suggested already that *A. taramellii* might be a juvenile of *A. stellaris*. Van der Weijden (1940) remarked that *A. taramellii* might be a juvenile of *A. stella*. The latter author suggested a close relationship between *A. stella* and *A. stellaris*.

Little or no research has been done so far on the growth patterns of *Asterocyclina*; an investigation of this type will perhaps enable us to establish natural links between various species described in the literature.

The ecophenotypic variation is ignored even more within this group. As far as we know, no conclusions have been drawn yet on the variation in size and shape with respect to supposed environmental differences. Investigations on Recent larger foraminifera have revealed that such relations do exist, however. Especially unknown depth-controlled factors seem to play a prominent role in determining the relative thickness of larger foraminifera (Hottinger, 1977a; Larsen & Drooger, 1977; Muller, 1977).

The aim of this chapter is threefold. Firstly, we shall provide data concerning the size and shape of *Asterocyclina*. Secondly, we want to ascertain whether the size and shape show trends along the column of the Avedat sequence. Thirdly, we want to discuss whether the fluctuations found can possibly be ascribed to environmental changes.

III.3.3.2 *The data*

Thirty *Asterocyclina*-bearing samples were selected. We tried to choose samples for which data of the inner morphology were also available. Twenty-four of these samples appeared to contain a sufficiently large number of specimens for us to collect the second set for the measurement of the outer morphology (fig. 10). Random collections of some twenty-five specimens were made. Only in some samples the number of specimens was smaller, owing to lack of material. We measured A and B for 662 specimens. The contribution of *Asterocyclina cuvillieri* and *A.* sp. 1 (see chapter III.3.4) is considered negligible, because these forms are relatively scarce and furthermore they occur only in the lowermost part of the Ein Avedat section. As a consequence we think that we are dealing with (mainly) one species per sample.

$\bar{A}$, $\bar{B}$ and $\overline{A/B}$, their standard errors and the sample sizes are listed in table 1. The correlation coefficients $r_{A,B}$ are also given in this table. The distribution of the parameter means throughout the section is visualized in fig. 25.

The mean thickness $\bar{A}$ ranges from 0.56 mm. to 0.87 mm. There is an overall increase in $\bar{A}$ from the lower part to the top of the section, but deviations from the general trend are quite frequent.

The mean diameter $\bar{B}$ ranges from 1.10 mm. to 2.42 mm. $\bar{B}$ too shows an increase in average values from the bottom to the top of the section but deviations are again present. In the lower part of the section the average is below 1.5 mm., whereas in the upper part the $\bar{B}$ generally exceeds 2.0 mm.

An irregular trend with several coarse fluctuations is observed in $\overline{A/B}$. The ratios seem to decrease from well over 0.50 at the bottom to around 0.40 in the top part of the section.

No correlation with the rank number has been calculated for $\bar{A}$, $\bar{B}$ and $\overline{A/B}$, but the overall trends of size increase seem to be combined with a relative flattening of the test.

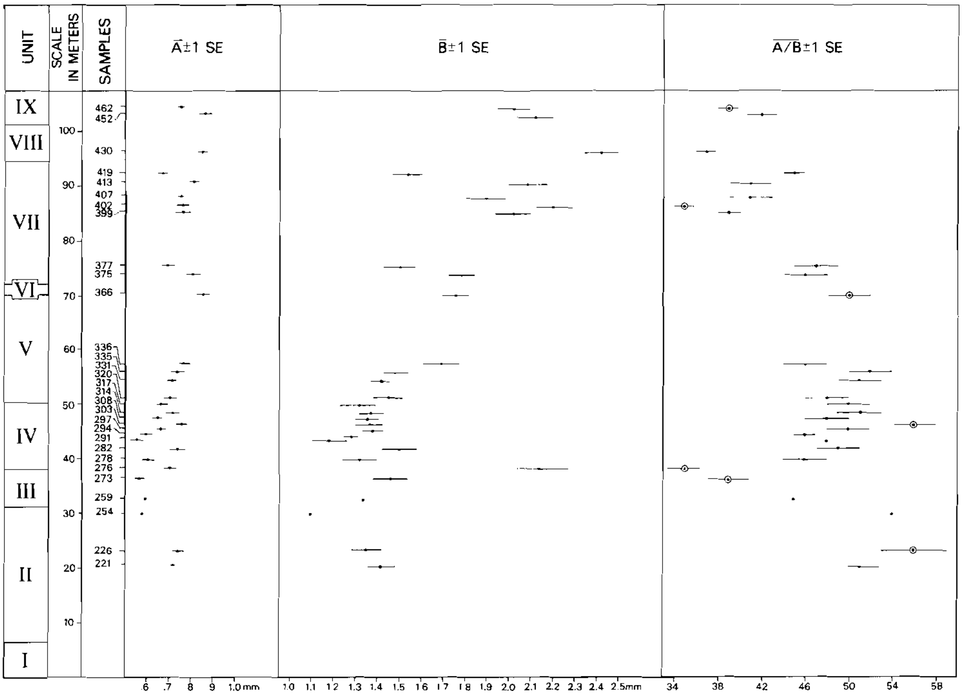


Fig. 25 Vertical distribution of the means (± 1 SE) of A, B and A/B in the *Asterocyclina* samples. The seven samples (compare fig. 27) with significantly deviating $\overline{A/B}$ values are indicated separately.

III.3.3.3 *Discussion*

It is impossible to establish a growth line in single individuals of extinct larger foraminifera with lateral chambers, because there is no one-to-one relation between the number of annuli observed in the median layer and the number of lateral layers. There are more annuli than lateral layers, which makes it impossible to establish the increase of thickness at each budding step of the median layer. The only data source at our disposal for establishing an average growth line is the size and shape of the individuals at their expiration. Two essential factors have to be considered in the analysis of such data:

1. the ontogenetic trajectory, and
2. the variation at a certain "age" (= size) interval in the population.

Larger foraminifera have no well-defined terminal ontogenetic stage and the sample means of the parameters A and B may be determined largely by the relative contribution of juvenile and "adult" specimens. However, because the life-time of "adult" larger foraminifera seems to be season-controlled (Ross, 1972; Muller, 1977) the majority of the specimens may be of comparable age. For this reason it was still considered meaningful to calculate the means and standard errors of these parameters.

If we compare the samples from a vertical succession of strata, two more factors are introduced which complicate the picture and which may thwart the drawing of conclusions. These factors are:

3. evolutionary trends, and
4. environmental changes which cause ecophenotypical variation.

There is yet another problem which complicates the analysis of our data of the outer morphology. Actually, the relation between the size parameters along the growth line is not linear but follows a rather complicated allometric pattern. Therefore the values of $\overline{A/B}$ have to be considered with caution.

In order to arrive at some approximation of an average growth line, we took the data of all samples together. In the cluster that resulted we calculated partial $\bar{B}$-values for the successive classes with a width of 0.4 mm. as well as the corresponding $\bar{A}$-values (table 2). The linear and the logistic regressions were calculated. Both these regressions are of little statistical value because they are arrived at by lumping data from markedly different samples. Nevertheless we assume that they may serve as some kind of reference with which the individual bivariate sample means can be compared.

From fig. 26 it is obvious that the linear regression line shows very little correspondence with the succession of partial means of A and B, although it should be realized that the partial means of the extreme classes are based on very few data. A comparison between the set of means of the successive classes

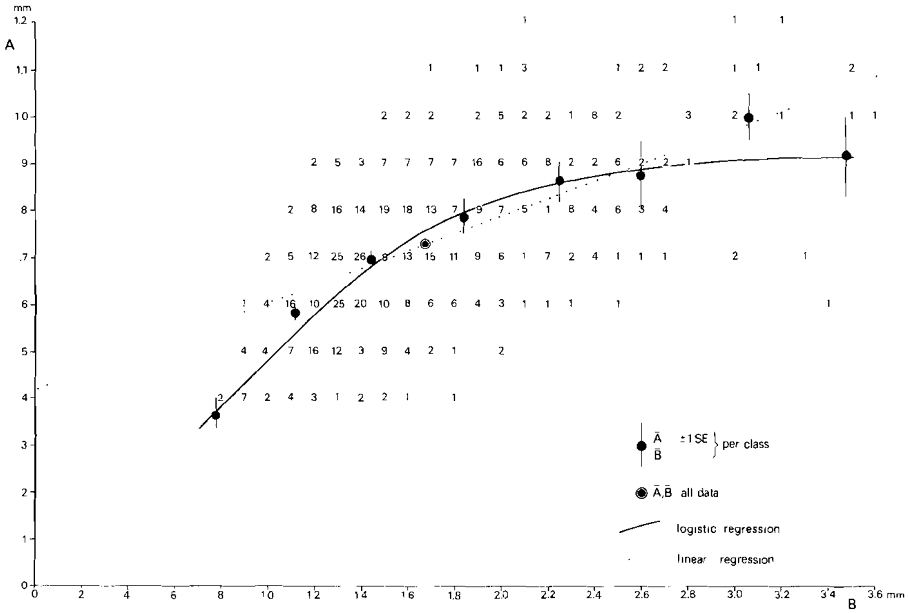


Fig. 26 Cluster of A against B of all *Asterocyclina* specimens, with the linear and logistic regression lines.

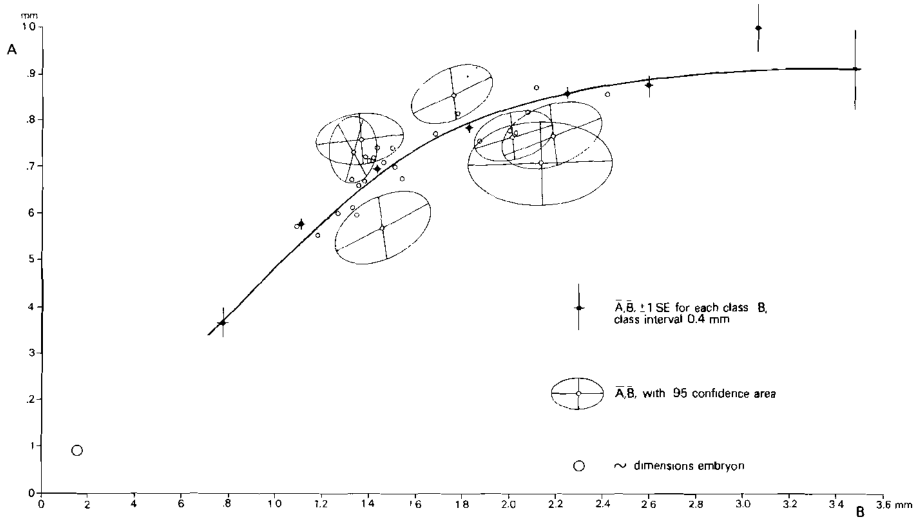


Fig. 27 Deviations from the reference line of fig. 26. Samples that deviate significantly from the reference line are indicated by their bivariate confidence areas.

and the linear and logistic regression lines reveals correlation coefficient values of 0.67 and 0.987, respectively, which are significant at the 0.95 and the 0.999 confidence levels in that order. Furthermore, whatever type of regression is used it must have its origin in the dimensions of the embryon. These dimensions are not exactly known, but the microfacies and inner morphology data yield values of approximately 0.090 and 0.150 mm. for A and B, respectively. From fig. 26 it is easily seen that a logistic regression has a better chance of fulfilling this requirement than the linear regression. For these reasons we preferred to use the logistic approximation for our comparison of the individual samples, although it is admitted that the actual growth pattern of the foraminiferal shell may be much more complex than suggested by the regression-lines.

Fig. 27 shows 0.95 confidence ellipses of the bivariate sample means (Sokal & Rohlf, 1969) of seven samples. Only those ellipses are figured that show no notable crossing of the best-fit-line of all data. Again, such a procedure is of little statistical value because the calculation of the confidence areas is based on the incorrect assumption that there is a linear relation between A and B. However we think that it is reasonable to conclude that the three samples with bivariate means above the reference line represent "populations" of relatively thick specimens, whereas the four samples below this line represent relatively thin "populations". The samples with relatively thick *Asterocyclina* are from bottom to top Is 226, 303 and 366, whereas the relatively thin specimens are from Is 273, 276, 402 and 462. It is interesting to note that these seven extreme samples do not completely correspond to the extreme values of $\overline{A/B}$ in table 1 and in fig. 25. The incomplete correspondence seems to be due to the differences in the position of the samples relative to the allometric "growth line".

If we use the seven samples mentioned above and with some care the $\overline{A/B}$ values of the other samples the following picture emerges concerning relatively thin and thick "populations".

Relatively thick specimens are found in the two samples in unit II. Extremely flat specimens are found at the transition of units III to IV. For units IV-VI the data suggest a fairly large relative thickness. From unit VI to the middle of unit VII the specimens become flatter again. From there to the top-most samples the values remain relatively low. The uppermost sample Is 462 belongs to the group of seven that deviate extremely from the reference line.

Finally, flat specimens with more than five rays were reported from the supposedly autochthonous assemblages in our lower part of the Nizzana Formation. This observation suggests that the acquisition of more than five rays might be an adaptation to deeper water circumstances. If such a relation with depth can be established it will provide an easy means for estimating relative paleo-depths. However, *Asterocyclina* specimens with more than five rays were also encountered in the allochthonous beds of unit II. If there is a relation between depth and the number of rays, then it must be concluded that the samples from the lower part of the Nizzana Formation contain heterogeneous assemblages. On the other hand we cannot disprove the possibility that reduction of the number of rays is an evolutionary trend in *Asterocyclina*, independent of ecology.

III.3.4 The inner morphology of *Asterocyclina*

III.3.4.1 *Introduction*

Twenty-eight samples containing *Asterocyclina* have been analysed biometrically. The samples cover the whole Nizzana Formation at irregular intervals (fig. 10). Some of the samples contained only few specimens. Altogether some 700 specimens have been measured.

The frequency distributions of D_1, D_2, R, n_{1+2} and r are shown in figures 28 en 29. For several of the parameters, notably the size parameters, D_1, D_2, H_1 and H_2, distinctly heterogeneous frequency distributions were observed in some of the samples, from the lowermost part of the Nizzana Formation. In the middle part of the formation we also found two samples, Is 336 and 366, containing single specimens with high D_1 and D_2 values. The coefficients of variability, which are given in fig. 28, show extremely high values. In the D_1-D_2 scatter diagrams, although not represented here, the heterogeneous samples can be split into two groups with only occasional specimens that occupy intermediate positions. Although we realized the possibility that an occasional individual might have been placed in the wrong group, we decided to split the *Asterocyclina* specimens into two groups, referred to as group 1 with the lower D_1 and D_2 values and group 2 with the higher D_1 and D_2 values. For the time being we cannot be sure about the biological meaning of both groups of megalospheres. At least for group 1 we suppose that the assemblages are homogeneous, i.e. belong to a single species.

After the sample splitting we calculated means and standard errors for each parameter and for all the samples in the separate groups.

In de following two sections the two groups are discussed separately.

III.3.4.2 *Asterocyclina of group 1*

Means

For the twenty-eight samples the means, standard errors and sample sizes

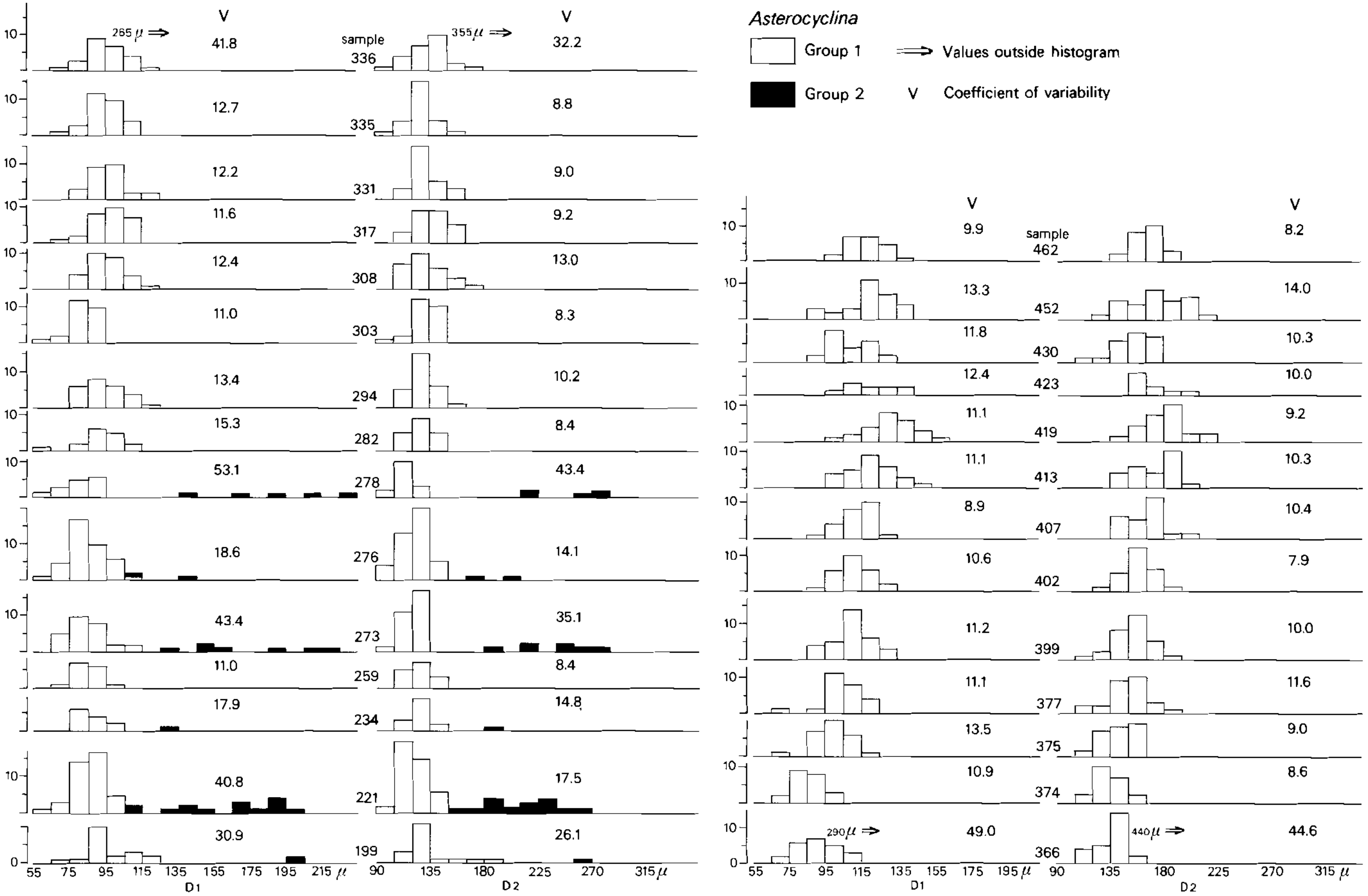


Fig. 28 Frequency distributions of D_1 and D_2 of *Asterocyclina*. The coefficients of variability, V, are also indicated.

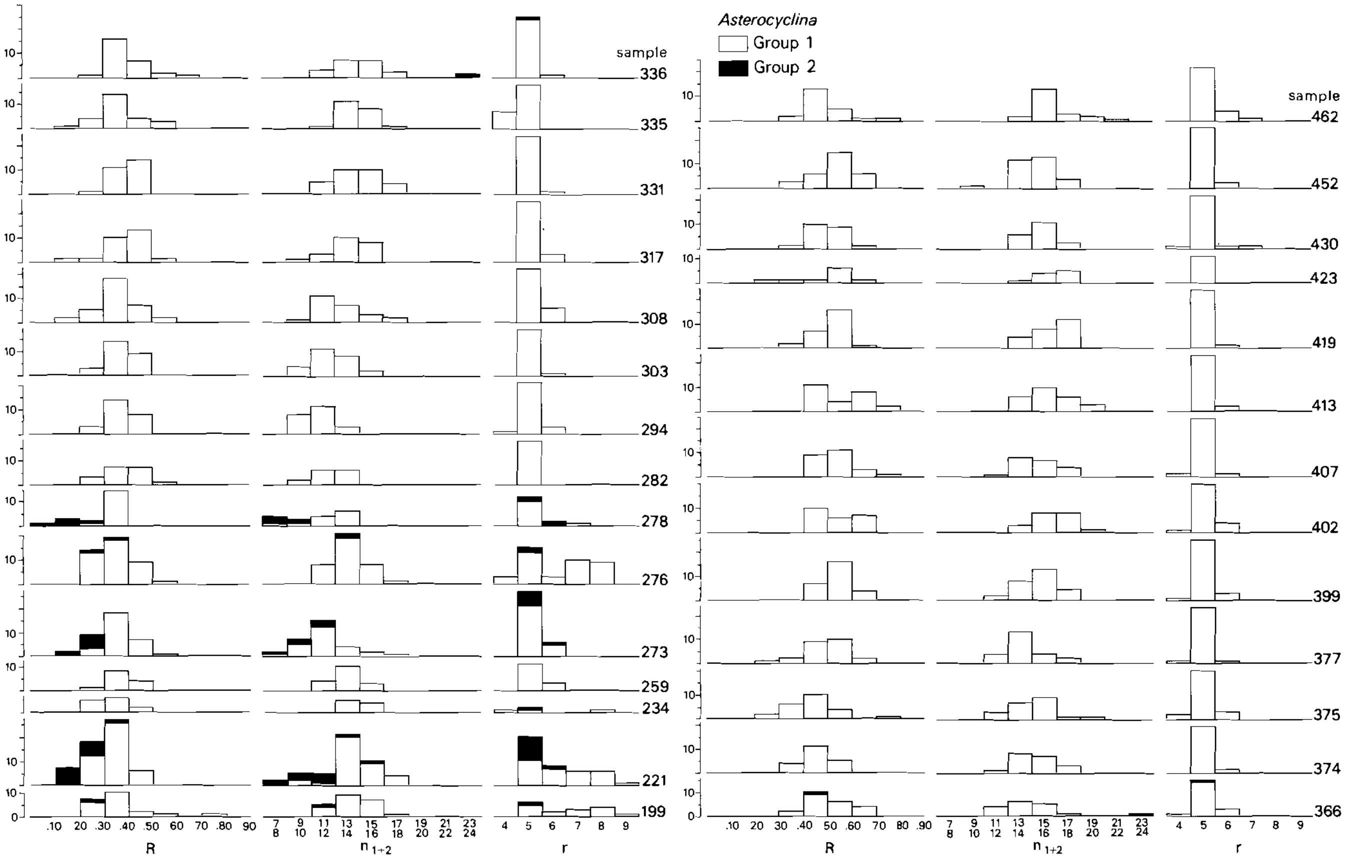


Fig. 29 Frequency distributions of R, n_{1+2} and r of *Asterocyclina*.

are given in table 3. The histograms of D_1 and D_2, and R, n_{1+2} and r are represented in figures 28 and 29, respectively. Because of the extreme similarity in distribution the histograms for the other parameters are not shown.

From the tables and the histograms we obtain the impression that most of the parameters show definite trends from the base to the top of the Nizzana Formation. In order to test the significance of these trends the samples were ranked from 1 to 28 and the correlations between rank number and parameter mean were calculated for each parameter (see M. M. Drooger et al., 1979), except for $\bar{r}$, because this parameter is almost constant throughout the section.

The hypothesis of no change was tested at the 0.001 probability level (26 df). The results for the test are

parameter	R	n_2	n_{1+2}	H_1	H_2	H_c	D_1	D_2
corr. coeff.	0.90	.78	.70	.88	.80	.88	.88	.89

For all the parameters tested the null hypothesis has to be rejected. Accordingly trends are thougt to be present for all the parameters. The fact that the existence of a trend has been proved does not mean that one has information about the pattern that has been followed in the course of time. The likelihood of a trend certainly is no proof of a sustained change (M. M. Drooger, 1982). Although all the parameter means show significant differences from bottom to top, the detailed patterns differ considerably from each other. For all the parameters significant fluctuations seem to be superimposed on the general trend.

The histograms presented (fig. 28 and 29) indicate fairly normal distributions. Without further testing one can reasonably assume that the frequency distributions of the parameters are normal; this allows us to apply the t-test for the testing of the differences between means.

Means ± 1 S.E. of the parameters are shown in fig. 30. In the following paragraphs the fluctuation patterns of the parameters will be discussed. $p = 0.05$ is taken as level of significance. The + of – signs indicate whether the suggested change is in accordance with or contrary to the overall trend direction, respectively. o indicates that the difference between a sample couplet when tested at the $p = 0.05$ level, is insufficient to reject the null hypothesis.

$\bar{R}$

The sample couplets that have been compared are listed below:

samples	t-value	df	direction
199–234	1.920	28	–
199–336	0.979	40	o
234–336	3.781	34	+
336–366	3.765	43	+
336–374	3.095	42	+
366–374	1.706	39	–
366–462	0.871	41	o
374–399	2.094	46	+

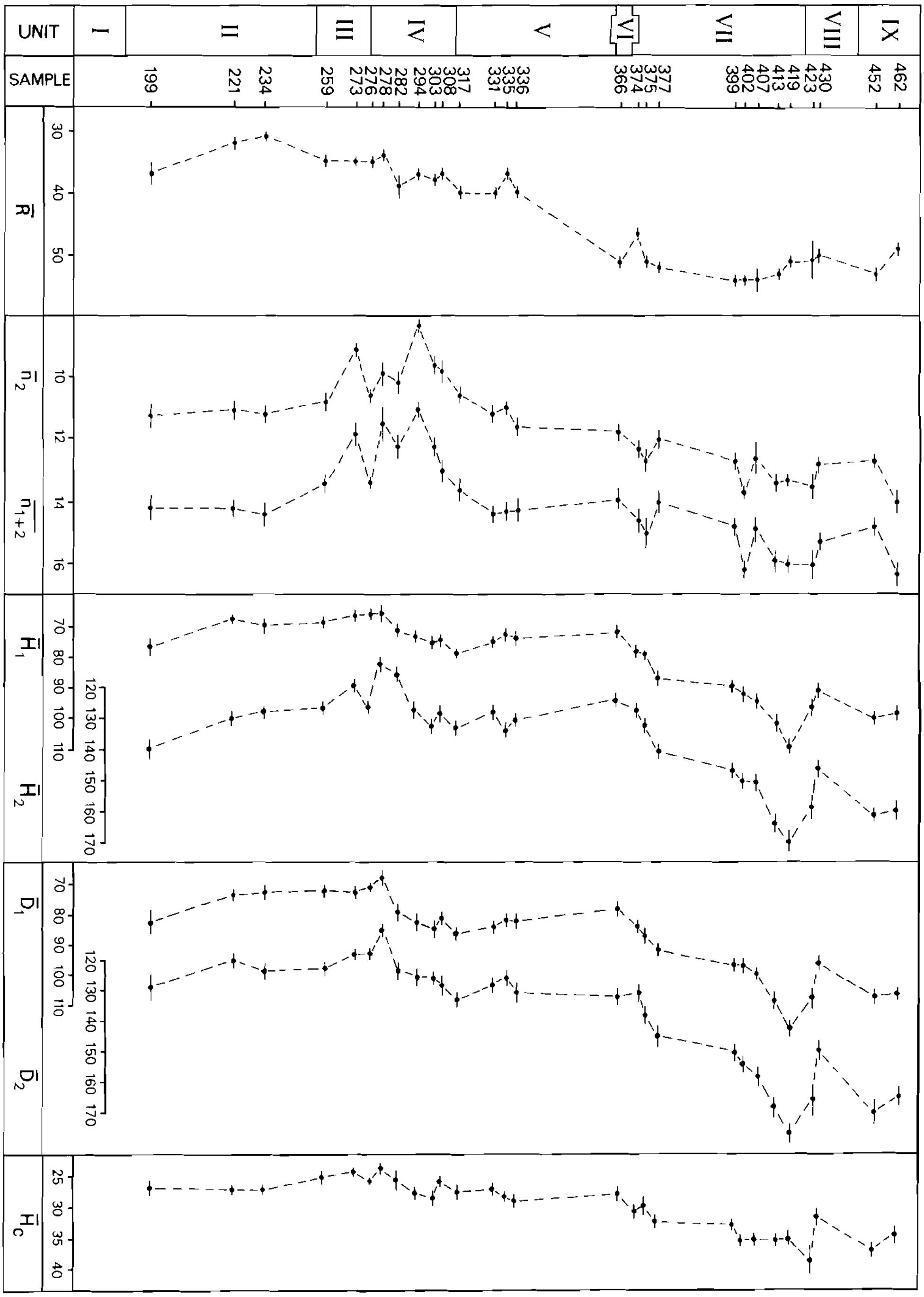


Fig. 30 Vertical distribution of the means and standard errors of the internal parameters of *Asterocyclina* of group 1.

The tests lead to several conclusions. In the lowermost samples, from Is 199 to 336 $\bar{R}$ ranges from 31 to 40. There is no net increase in $\bar{R}$ from the bottom to the top of this part of the section, but individual sample couplets show significant differences in both directions. A similar picture emerges for the samples of the upper part of the section (Is 366 to 462). However here the values of $\bar{R}$ range from 47 to 54. If one compares Is 374, which is the sample with the smallest $\bar{R}$ value in the upper part of the section, with Is 336, which has one of the highest $\bar{R}$ values in the lower part of the section, one finds a significant difference. There seems to be a gap in the $\bar{R}$ values between the lower and the upper part of the section, roughly corresponding to the upper half of unit V.

$\overline{n_{1+2}}$ and $\overline{n_2}$

The sequences of means of these parameters show very similar patterns because n_1, the number of peri-embryonic chambers on the protoconch, is relatively very small and fairly constant, ranging from 2 to 4, with a tendency to decrease in the course of the time. Only the parameter n_{1+2} will be discussed here.

Several critical sample couplets were tested by means of the t-test. Although the parameter is represented by integer values the t-test is supposed to be robust enough to be applied because of the large number of classes (compare M. M. Drooger et al., 1979). The results are:

samples	t-value	df	direction
199–294	6.558	38	–
294–336	7.175	39	+
366–462	4.152	37	+
402–452	3.148	48	–

Figure 30 shows that several of the other pulses to and from are significant as well. In the lower part of the section there is no net increase in $\overline{n_{1+2}}$ between the samples Is 199 and 336. However, there is a significant drop in the values in the interval between Is 259 and 317; this series of low values roughly corresponds with unit III and the lower part of unit IV. In contrast with the parameter R there is no notable change (less than one SE) between Is 336 and 366. In the upper part of the section there is a significant net increase in $\overline{n_{1+2}}$ between Is 366 and 462. But a significant setback may be observed between the samples Is 402 and 452.

$\overline{H_1}$ and $\overline{H_2}$

The parameters H_1 and H_2 are extremely well correlated (figures 30 and 31), and their means follow essentially the same pattern. Therefore, only the pattern of $\overline{H_1}$ will be discussed. Several sample pairs were tested. The results of the tests are:

samples	t-value	df	direction
199–336	0.569	42	o
199–278	3.213	32	–
278–317	5.219	39	+
317–335	2.155	49	–
366–377	5.428	46	+
399–419	6.331	52	+
419–430	5.544	45	–
430–462	2.418	42	+

The difference between Is 199 and 336 is not significant but in between these samples distinct fluctuations do occur. A maximum value occurs in Is 317 (top of unit IV) whereas in the range of unit V the values of $\overline{H_1}$ are normally significantly lower. There is no significant difference across the inforation-gap between the samples Is 336 and 366, as was observed for $\overline{R}$. In the upper part of the section, from unit VI to the upper part of unit VII, there is a significant increase in $\overline{H_1}$ from the sample Is 366 to 419, but the drop in $\overline{H_1}$ between the samples Is 419 and 430 at the transition from unit VII to unit VIII is significant as well. At the top of the Nizzana Formation the mean values are higher again.

$\overline{D_1}$ and $\overline{D_2}$

The parameters D_1 and D_2 are also extremely well correlated and the patterns of $\overline{D_1}$ and $\overline{D_2}$ are very similar (fig. 30 and 31). Therefore we discuss only one of the parameters (D_2). The differences between means that were tested are tabulated below.

samples	t-value	df	direction
199–336	1.380	37	o
199–278	2.140	39	–
278–317	2.615	35	+
336–366	0.683	39	o
366–462	4.240	40	+
399–423	1.940	37	+
423–430	2.246	30	–

$\bar{r}$

No t-tests were performed for the parameter r. In the majority of the samples the discrete values are distributed over one or two classes only. In the lower part of the section the distributions are wider but irregular. The frequency-diagrams show that the shift in the average values of r in the lower part of the section is caused by the disappearance of specimens with 7 or more rays (fig. 29).

Correlations

The correlation coefficients were calculated for each pair of parameters and for each sample. The significance of the r-values was tested at $p = 0.01$

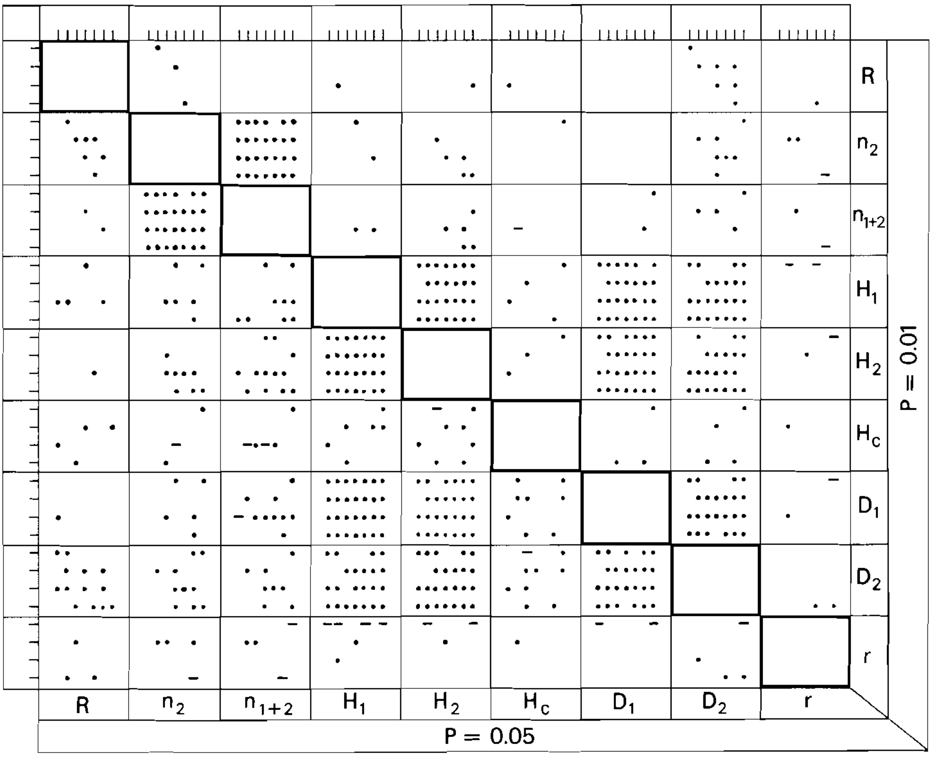


Fig. 31 Correlation matrix for the internal parameters of *Asterocyclina* of group 1.

and 0.05, respectively. The results are shown in fig. 31. Dots represent significant positive correlations, dashes significant negative correlations. Samples are ranked per cell in increasing stratigraphical order from left to right and from top to bottom.

The four size parameters of the embryon are almost invariably well correlated. The parameter H_c, the height of the peri-embryonic chambers, shows a much lower number of positive correlations with these size parameters. This is possibly due to the high variability of H_c.

The parameters n_2 and n_{1+2}, denoting the number of peri-embryonic chambers, show a moderate number of positive correlations with the size parameters of the embryon. Apparently the number of peri-embryonic chambers is partly size-dependent. The parameter n_2 shows occasional positive correlations with the degree of enclosure R.

This parameter R shows a fair number of positive ties with the size parameter D_2 and a smaller number with the parameter n_2.

The number of rays, r, does not show a distinct relation with any other parameter. However, it should be borne in mind that the variation in the number of rays is generally very low. Only in the samples of the lower part of the Nizzana Formation is the variation wider. It is interesting to note that the scarce significant negative correlations between r and the size parameters are generally found in this lower interval. Specimens with a small embryon tend to have a larger number of rays.

The plotting of pairs of parameter means for all 28 samples yields several types of clusters.

The combination of $\bar{R}$ with each of the other parameter means invariably yields a scatter diagram in which two separate clusters can be recognized. Two such diagrams are shown in fig. 32. The cluster with the lower $\bar{R}$-values corresponds to the samples from the lower part of the Nizzana Formation, Is 199 to 336, whereas the cluster with the higher $\bar{R}$-values consists of the samples from the upper part of the Nizzana Formation. It must be stressed again that $\bar{R}$ is the only parameter mean that shows a significant change across the information gap in unit V between the samples Is 336 and 366 (see also fig. 30). The correlation coefficient values between $\bar{R}$ and $\bar{D}_2$ and between $\bar{R}$ and $\bar{n}_2$ are very high when all samples are considered, but for the separate groups from the lower and the upper parts of the Nizzana Formation, respectively the correlation is weak or absent.

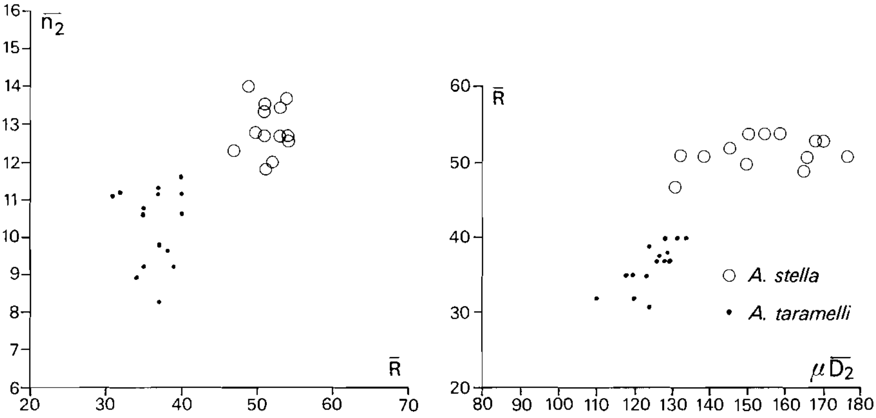


Fig. 32 Scatter diagrams of $\bar{R} - \bar{n}_2$ and $\bar{D}_2 - \bar{R}$ for *Asterocyclina* of group 1.

Because the twofold subdivision on the basis $\bar{R}$ is stratigraphically meaningful we maintained both sample groups for all other pairs of parameter means. The "lower" group is referred to as *Asterocyclina taramellii*, the "upper" group as *A. stella*.

The means of the size parameters of the embryon are invariably very well correlated. Some of the combinations are shown in fig. 33. The cluster of *A. taramellii* is relatively wide compared to the more elongate cluster of the pairs of parameter means in *A. stella.* On the basis of the dimensions of the embryon *A. taramellii* and *A. stella* cannot always be distinguished in single samples. The clusters of *A. taramellii* and *A. stella* in the diagrams of fig. 33 suggest that the ratios between the size parameters changed slightly at the transition from *A. taramellii* to *A. stella.*

In fig. 34 the relation between $\overline{H_c}$ and $\overline{D_2}$ is depicted. It was already noted that the parameter H_c is highly variable and this is also reflected in the rather

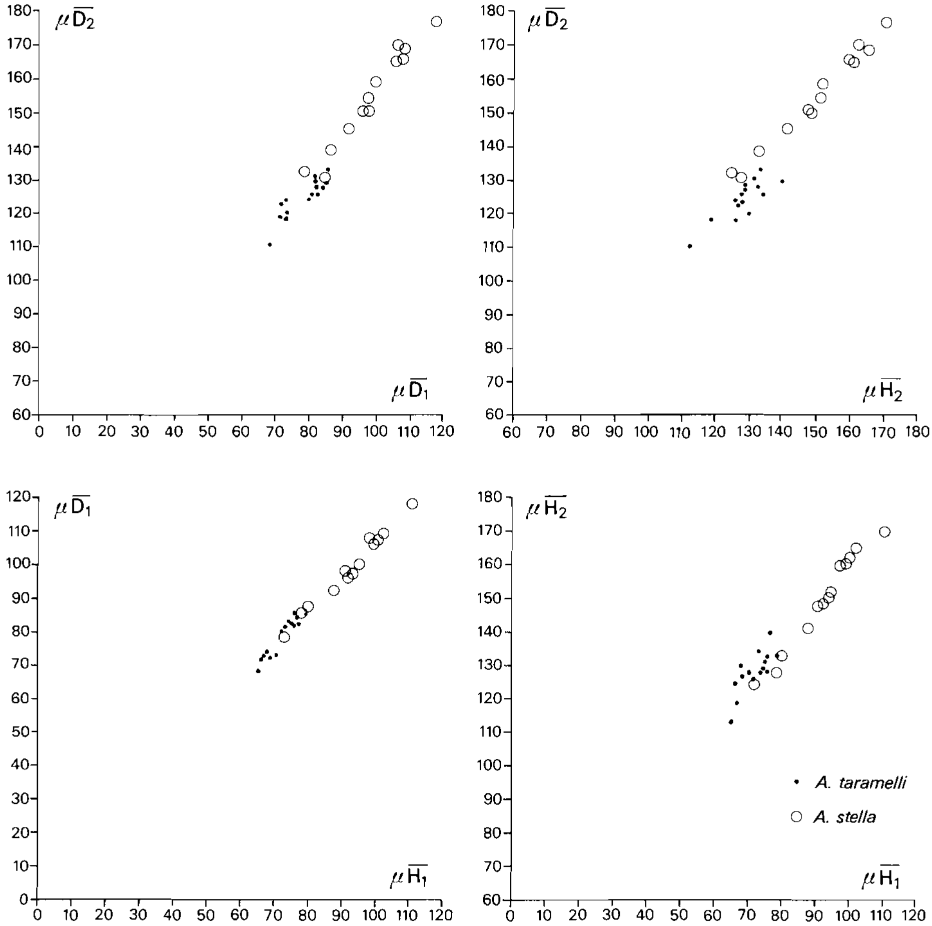


Fig. 33 Scatter diagrams of several pairs of parameter means for *Asterocyclina* of group 1.

wide scatter of both groups along a line of central tendency. For both species of *Asterocyclina* together there is a good correlation. The overlap between the clusters of *A. taramellii* and *A. stella* is small.

In fig. 35 finally some scatter diagrams are shown concerning the relations between the number of peri-embryonic chambers and $\overline{H_c}$ and $\overline{D_2}$. In both cases there is a good correlation when the groups are considered collectively. However, when the individual groups are considered they show wide clusters in which the positive correlation is poor.

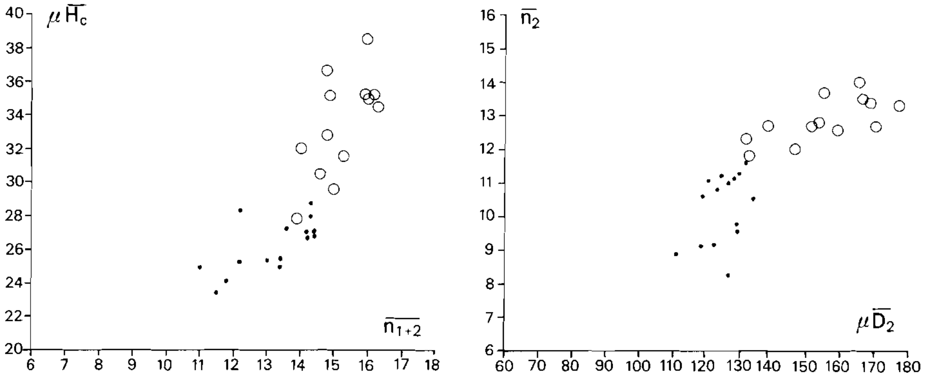


Fig. 34 Scatter diagram of $\overline{D_2} - \overline{H_c}$ for *Asterocyclina* of group 1.

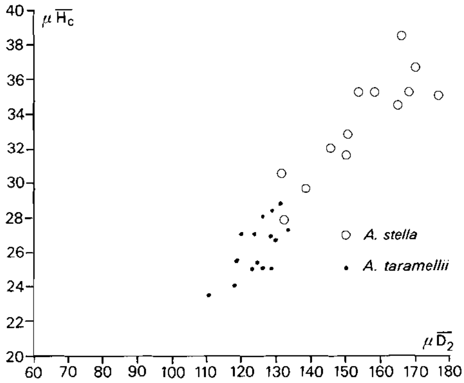


Fig. 35 Scatter diagram of $\overline{n_{1+2}} - \overline{H_c}$ and $\overline{D_2} - \overline{n_2}$ for *Asterocyclina* of group 1.

Morphological variation

Before the *Asterocyclina* associations were split into the two groups 1 and 2, the coefficients of variability appeared unacceptably high (fig. 28); in several samples the V-values were much higher than 20. After the splitting of the samples it was assumed that the samples of group 1 represented homogeneous populations. For the samples containing *A. taramellii* and for the samples with *A. stella* we calculated the separate $\bar{V}$-values with their standard errors for all the parameters. The differences in $\bar{V}$ in *A. taramellii* and *A. stella* were tested for each parameter by means of the t-test ($p = 0.05$). The results are:

R	n_2	n_{1+2}	H_1	H_2	H_c	D_1	D_2	r	
A. taramellii (Is 199–366, n = 15)									
18.90	13,49	11.91	12.05	9.32	17.09	12.99	9.73	11.65	$\bar{V}$
1.79	0.69	0.69	0.59	0.44	0.92	0.40	0.60	2.54	SE
A. stella (Is 366–462, n = 13)									
14.95	11.45	11.32	11.14	8.97	17.06	11.59	9.89	6.43	$\bar{V}$
0.95	0.69	0.64	0.27	0.34	0.92	0.45	0.44	0.82	SE
2.13	*2.09*	0.63	1.40	0.56	0.02	*2.33*	–0.22	*1.96*	t-value

The largest variation is observed in the parameters R and H_c. However, the former is a ratio of two linear measurements, while the latter represents the size of the peri-embryonic chambers, which is indeed highly variable.

The V-values are commonly lower in *A. stella;* for four parameters, namely R, n_2, D_1 and r the difference between the $\bar{V}$ of *A. stella* and of *A. taramellii* is significant. Apparently the range of morphological variation of *A. stella* populations is less than it is in the populations of *A. taramellii.*

III.3.4.3 *Asterocyclina of group 2*

Group 2 was discriminated from group 1 on the basis of the relatively larger size of the embryon. Only a few data on this group are available. Its occurrence is practically limited to the lower part of the Nizzana Formation, where it is scarce relative to group 1; in the middle part only two specimens were encountered. The results of counts and measurements are presented in table 4.

The frequency distribution of several parameters have been shown already in figures 28 and 29. Since in these figures the class intervals are based on the range of variation of the individuals of group 1 and because there are only a few data these distributions are irregular. Only samples Is 221, 273 and 278 yielded sufficient specimens for means and standard errors to be calculated. For these samples only the differences in the means of the parameters H_1, H_2 and H_c turned out to be significant but at rather a low level. They suggest an increase in the size of the embryon and the nepiont in the course of time.

We decided to lump all the data from the lower part of the Nizzana Formation. The two specimens from Is 336 and Is 366 were not included because they had high values for most of the parameters; some of these parameters are shown in the scatter diagrams of fig. 37.

	n_2	n_{1+2}	H_1	H_2	H_c	D_1	D_2	r
R								
n_2		+			–			
n_{1+2}					–			
H_1				+	+	+	+	+
H_2					+	+	+	+
H_c							+	+
D_1							+	
D_2								+

– + $p = 0.05$
– + $p = 0.01$

Fig. 36 Correlation matrix for *Asterocyclina* of group 2.

A correlation matrix was calculated for the specimens from Is 199 to 278 (fig. 36). There is a good correlation between the size parameters of the embryon. The parameter H_c shows a less pronounced positive relation with the size parameters of the embryon. There is a weak negative correlation between the number of peri-embryonic chambers and their height. The number of rays shows a 0.05 positive correlation with the size parameters, but not with D_1. No correlation was found between R and any of the other parameters. Some of these combinations are shown in the scatter diagrams of fig. 37.

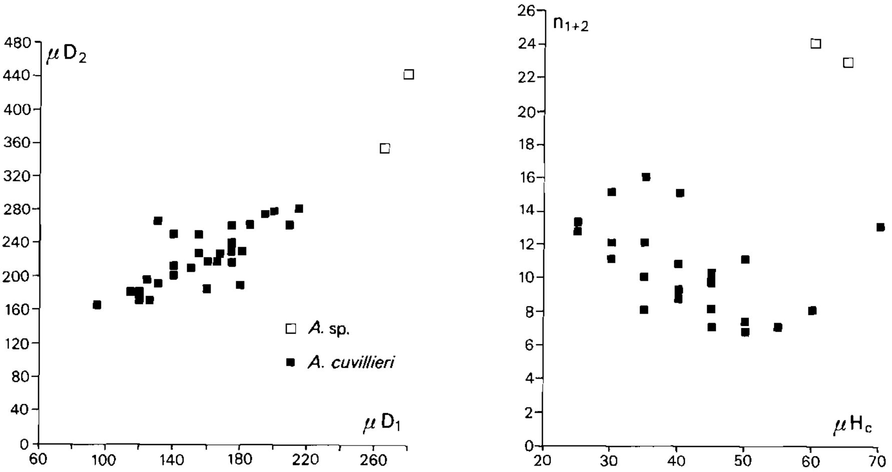


Fig. 37 Scatter diagram of $D_1 - D_2$ and $H_c - n_{1+2}$ for *Asterocyclina* of groups 2.

Although there is only a limited number of specimens the data suggest relations between the parameters similar to those found for group 1.

In the scatter diagrams the two specimens from Is 336 and 366 lie far outside the cluster of the other specimens. Just as we did with group 1 we split the specimens into two "clusters"; the one with the smaller-sized embryon is referred to as *A. cuvillieri*, the "cluster" of two specimens with giant embryons is referred to as *Asterocyclina* sp.

III.3.4.4 *Comparison between Asterocyclina of groups 1 and 2*

In group 1 a distinct increase in several parameters was observed. The increase in several parameters was observed. The increase in $\bar{R}$ is in accordance with the principle of embryonic acceleration. On the basis of the $\bar{R}$-values the data show two clusters which correspond to the lower part and the upper part of the Nizzana Formation. In view of the continuity of the other parameter means across our section unit V (fig. 30) we suggest that we are dealing with a single evolutionary lineage, i.e. that our *A. stella* evolved from *A. taramellii.*

There seems to be a similar relation in group 2 although only scanty data are available for *Asterocyclina* sp. Notwithstanding the limited number of data the differences in the R-values of *A. cuvillieri* and *A.* sp. seem to be in accordance with the principle of embryonic acceleration. Therefore we suggest that our *A.* sp. might have evolved from *A. cuvillieri.*

The scatter diagram of $\overline{D_2}$ versus $\overline{D_1}$ is shown in fig. 38. The figure suggests

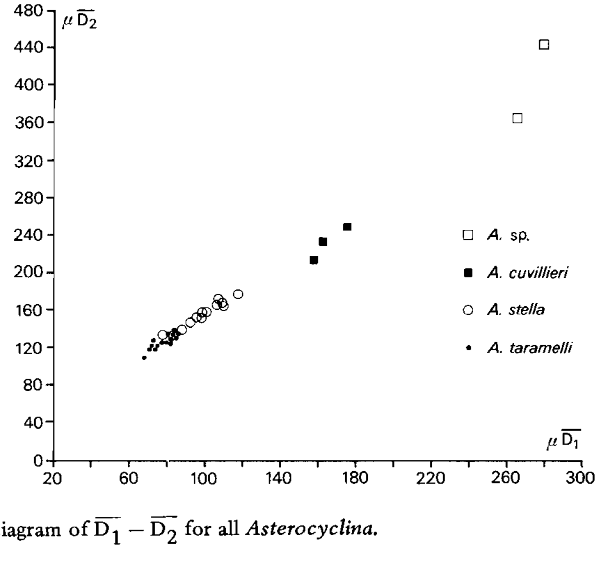


Fig. 38 Scatter diagram of $\overline{D_1} - \overline{D_2}$ for all *Asterocyclina.*

an almost perfect correlation between the parameter means when all four groups of *Asterocyclina* are considered collectively. (For *A.* sp. the data for the single specimens are given.)

The relation between $\overline{R}$ and $\overline{D_2}$ is shown in fig. 39. The samples of *A. taramellii* and *A. stella* are thought to fit to a single "evolutionary" line, whereas *A. cuvillieri* and *A.* sp. are different because of their low $\overline{R}$-values relative to their $\overline{D_2}$. Moreover, the $\overline{R}$-values of group 2 are smaller than those of contemporaneous group 1 assemblages. This leads us to the conclusion that we are dealing with different species.

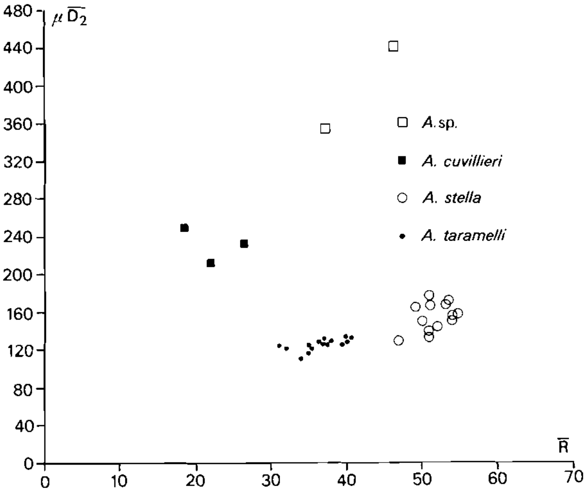


Fig. 39 Scatter diagram of $\overline{R} - \overline{D_2}$ for all *Asterocyclina.*

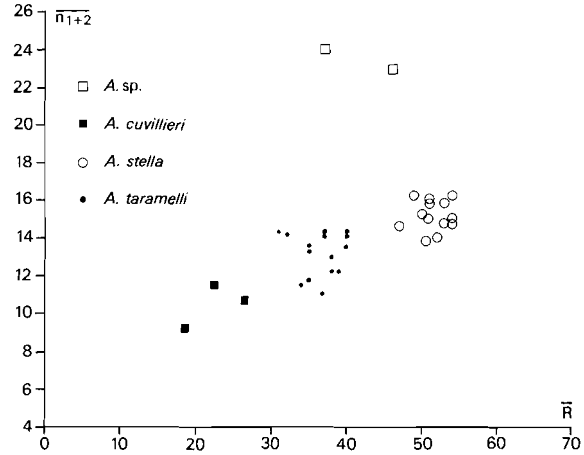


Fig. 40 Scatter diagram of $\overline{n_{1+2}} - \overline{R}$ for all *Asterocyclina.*

In fig. 40 we show the relations between the mean number of peri-embryonic chambers and the mean value for the degree of enclosure. If we were to draw a line of central tendency, e.g. the r.m.a., the group 1 line would pass through *A. cuvillieri,* whereas the two specimens of *A.* sp. are far away from this line. One could hypothesize there was another lineage from *A. cuvillieri* to these two specimens and therefore construct a much steeper $\overline{n_{1+2}}$-$\bar{R}$ line in fig. 40 for the second group.

If the patterns along which our *Asterocyclina* groups had evolved showed a correspondence with these lines it would be attractive to speculate about the origin of *Asterocyclina.* Either one group originated from the other or they had a common ancestor. The extrapolation of the lines and their intersections may provide information about the origin of *Asterocyclina.*

Figures 38, 39 and 40 suggest that a common ancestor might have had the features $\bar{R} = 20$, $\overline{D_2}/\overline{D_1} = 1.8$, $\overline{n_{1+2}} = 10$ and $\overline{D_2} = 100$.

III.3.5 Relations between the frequency patterns, the inner and the outer morphology and depth

For the comparison between the frequency patterns and the inner and outer morphology of *Asterocyclina* we have relative frequency data (%As) for 103 samples; these data were all derived from thin sections. We have data on test size parameters for 30 samples, and on internal morphology for 28 samples (fig. 10). The latter two categories are from wash-residues and sometimes from different samples. In fact we do not compare the data on relative frequency, test shape and internal features for the same samples.

Because the stratigraphic curves of all three categories show a fluctuating pattern with wide loops it may be permissible to compare these categories by projecting the individual mean data of the morphology on the frequency curve.

In order to reduce the staggered pattern of %As, which is based on too many samples, we constructed a smoother pattern by means of a five-points-moving average. Projections on this line are used as values for the calculations. If we suppose as a null hypothesis that the means of the morphology parameters and the %As are independent, then significant deviations of the correlation coefficient may suggest whether there might be interdependence; we can then try to translate this interdependence into paleontological interpretations.

The correlation coefficients of the %As and inner morphological parameters except r were calculated for the samples containing *Asterocyclina taramellii,* for those with *A. stella* and for both groups together. The results, tabulated below, give a confused picture.

parameter	*A. stella* (N = 11)	*A. taramelii* (N = 15)	together (N = 26)
$\overline{R}$	0.153	0.420	*0.630*
$\overline{n_2}$	0.480	*–0.592*	0.285
$\overline{n_{1+2}}$	0.520	*–0.584*	0.190
$\overline{H_1}$	*0.699*	0.267	*0.636*
$\overline{H_2}$	**0.674**	–0.125	*0.509*
$\overline{H_c}$	**0.592**	–0.139	*0.565*
$\overline{D_1}$	*0.685*	0.359	*0.623*
$\overline{D_2}$	**0.655**	0.133	*0.606*

(p = *0.01*)
(p = **0.05**)

When the two groups of samples are considered collectively it appears that the correlation coefficient values of %As and all the size parameters and $\overline{R}$ are significant at the 0.01 probability level. For these parameters the hypothesis of no correlation must be rejected. There is no significant relation between the %As and the number of peri-embryonic chambers.

If the two groups of samples are considered separately the picture is quite different. For *A. taramellii* none of the size parameters shows a significant correlation with the %As, whereas the number of peri-embryonic chambers shows a significant negative correlation with the %As when tested at $p = 0.01$. There is a weak positive correlation between $\overline{R}$ and %As ($p = 0.10$).

The correlation coefficients in the samples containing *A. stella* give a completely different picture. Modest r-values are found for the %As versus $\overline{H_2}$, $\overline{H_c}$ and $\overline{D_2}$ which are significant at $p = 0.05$, whereas the correlation coefficient values of the %As versus $\overline{H_1}$ and $\overline{D_1}$ are significant at the 0.01 level. Very weak positive correlations seem to exist between %As and the number of peri-embryonic chambers ($p = 0.10$) but there is no correlation between $\overline{R}$ and %As.

In fig. 41 scatter diagrams demonstrate the relations between %As and some of the parameter means. The $\overline{R}$ versus %As diagram shows that the overall positive correlation is caused by the relative position of the two clusters of *A. taramellii* and *A. stella*. The figures for the size parameters versus %As suggest the same, and moreover that the correlations calculated for *A. stella* are caused mainly by some one or two values.

On the other hand, a visual inspection of the patterns of %As versus the mean values of the size parameters of the embryon in figure 45 suggests comparable loops for *A. stella* when successive samples are connected, which seems to indicate that the significant correlations between the %As and the mean dimensions of the embryon have some meaning.

The clusters of *A. taramellii* show a peculiar arrangement. We connected the successive points according to their stratigraphic position. In the diagrams

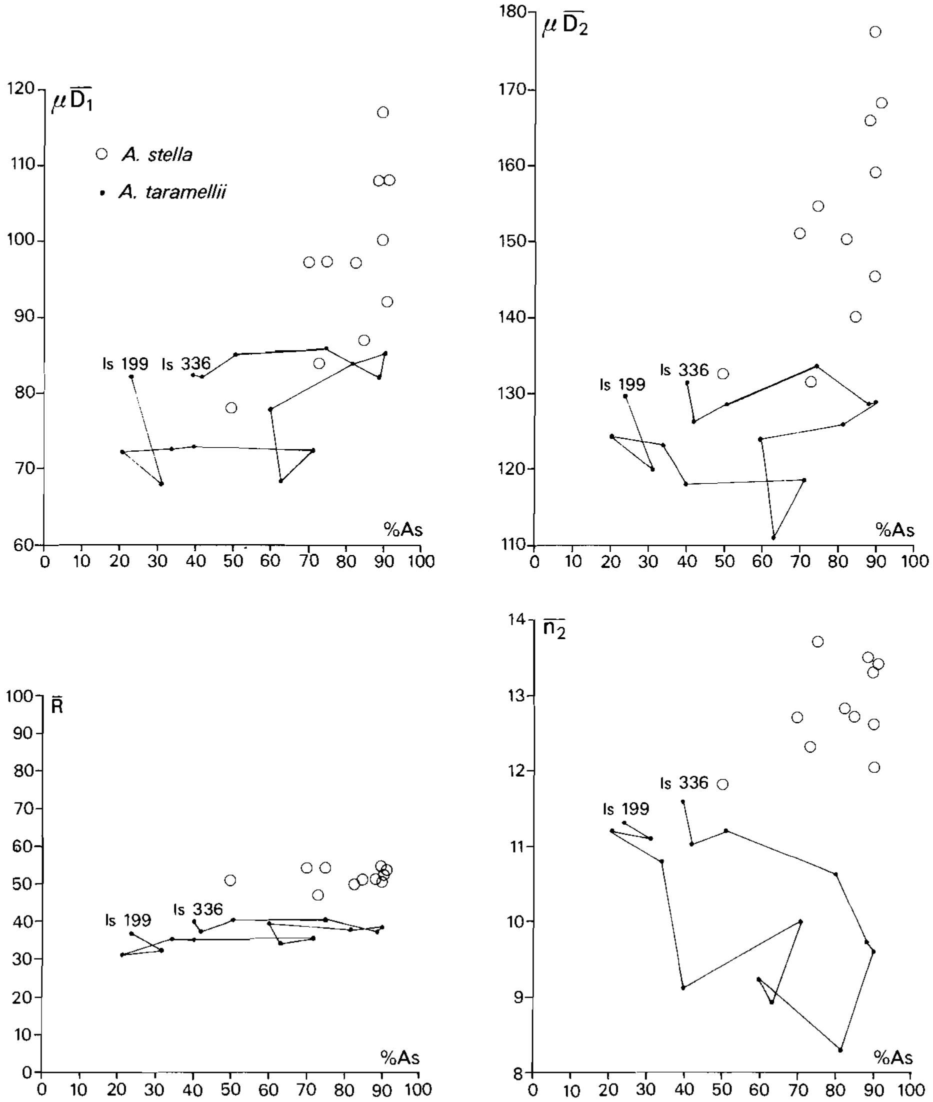


Fig. 41 Scatter diagrams of %As versus $\overline{D_1}$, $\overline{D_2}$, $\overline{n_2}$ and $\overline{R}$ for *Asterocyclina* of group 1.

of %As versus $\overline{D_1}$ and $\overline{D_2}$ the connecting lines follow a similar irregular path through the scatter field. Comparable patterns were found for the parameters $\overline{H_1}$ and $\overline{H_2}$ versus %As as well. The scatter diagrams give no indication of a positive correlation between the %As and the mean values of the size parameters of *A. taramellii.*

A similar explanation may be offered for %As and the mean numbers of peri-embryonic chambers. For *A. taramellii* we have an irregular path through the scatter field, which in this case results in a net negative correlation, whereas in the samples of *A. stella* the very weak positive correlation is caused by some one or two values.

Fig. 42 shows the relation between the parameters $\overline{D_1}$ and $\overline{n_2}$. Here too, the bivariate means of *A. taramelli* follow an irregular pattern through the scatter field, when connected in stratigraphic order. These patterns make no clear paleontological sense, unless we accept a random walk model or a time series effect for the various parameters.

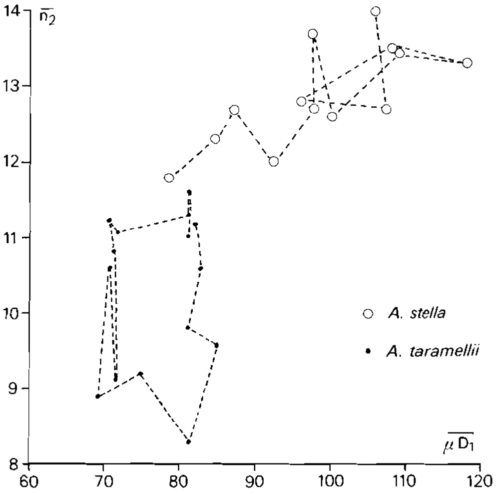


Fig. 42 Scatter diagram of $\overline{D_1} - \overline{n_2}$ for *Asterocyclina* of group 1.

The results of the correlation test on the outer morphological parameters and the %As are tabulated below:

	$\overline{A}$	$\overline{B}$	$\overline{A/B}$	(N)
A. stella	–0.498	–0.098	–0.199	9
A. taramellii	0.036	0.061	–0.060	19
together	–0.094	0.285	–0.281	28

No significant correlation is found between the %As and the means of the outer morphological parameters when the results are tested at the 0.05 probability level, neither when *A. taramellii* and *A. stella* are considered separately, nor when they are tested collectively. Two scatter diagrams, %As versus $\overline{B}$ and %As versus $\overline{A/B}$ are shown in fig. 43.

The correlation coefficients for pairs of inner and outer morphological parameter means were calculated to test whether there are significant relations between the inner and the outer morphology. Four parameters describing

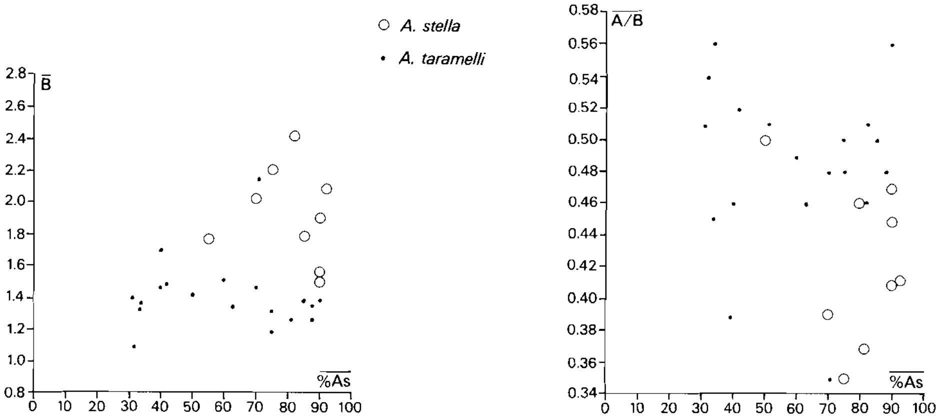


Fig. 43 Scatter diagrams of %As versus $\overline{B}$ and $\overline{A/B}$ for *Asterocyclina* of group 1.

the inner morphology were selected: $\overline{R}$, $\overline{n_{1+2}}$, $\overline{H_1}$ and $\overline{D_2}$. Because of the strong relation between the size parameters it was supposed that the other size parameters would yield comparable results. The results are listed below.

		$\overline{R}$	$\overline{n_{1+2}}$	$\overline{H_1}$	$\overline{D_2}$
A. stella	$\overline{A}$	−0.055	−0.218	−0.384	−0.293
(N = 11)	$\overline{B}$	0.094	0.376	0.120	0.113
	$\overline{A/B}$	−0.241	−0.403	−0.433	−0.368
A. taramellii	$\overline{A}$	**0.577**	**0.581**	0.357	0.449
(N = 13)	$\overline{B}$	−0.116	0.320	−0.323	−0.159
	$\overline{A/B}$	**0.558**	0.239	**0.511**	**0.494**
together	$\overline{A}$	***0.646***	0.339	***0.485***	***0.530***
(N = 24)	$\overline{B}$	***0.669***	***0.646***	***0.528***	***0.599***
	$\overline{A/B}$	−0.284	**−0.392**	**−0.418**	**−0.406**

(p = **0.05**)
(p = ***0.01***)

In *A. stella* the embryon size parameters show weak negative correlations with $\overline{A}$ and $\overline{A/B}$, none of which appeared significant when tested at the 0.05 probability level. There is no correlation between $\overline{B}$ and any of the inner morphological parameters.

In *A. taramellii* however, there are positive correlations between the inner morphological parameters and $\overline{A}$. These correlations are significant for $\overline{R}$ and $\overline{n_{1+2}}$ ($p = 0.05$) and for D_2 ($p = 0.10$). There are no significant correlations between $\overline{B}$ and the inner morphological parameters of *A. taramellii* whereas the correlations between $\overline{A/B}$ and $\overline{R}$, $\overline{H_1}$ and $\overline{D_2}$ are significant at $p = 0.05$.

When the correlations between the parameters are considered for the *A. taramellii* and the *A. stella* samples together, then the inner morphological parameters demonstrate significant positive correlations with $\overline{A}$ and $\overline{B}$ at $p = 0.01$, except for $\overline{n_{1+2}} - \overline{A}$, which is significant at the $p = 0.10$ level only.

The relations between the inner morphological parameters and $\overline{A/B}$ are all negative when tested at the 0.05 level, except for the combination $\overline{A/B} - \overline{R}$. This negative correlation appears to be significant only at the $p = 0.10$ level. In fig. 44 the relations between one of the embryon size parameters, $\overline{D_2}$, and the outer morphological parameters are depicted.

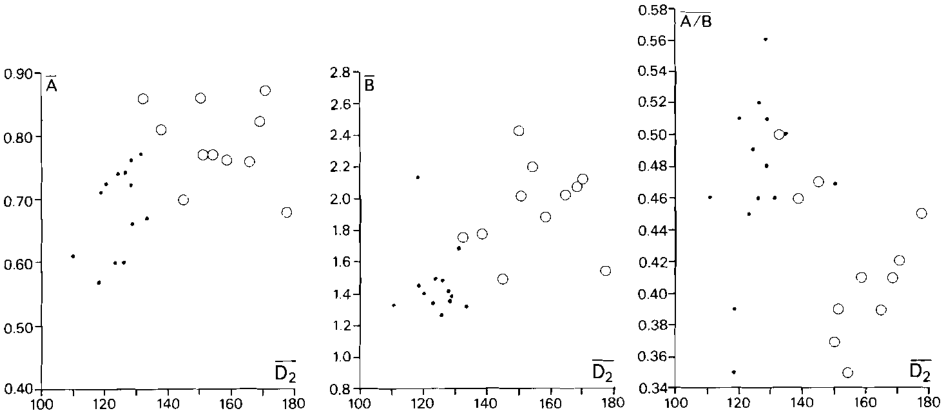


Fig. 44 Scatter diagrams of D_2 versus $\overline{A}$, $\overline{B}$ and $\overline{A/B}$ for *Asterocyclina* of group 1.

In order to assess whether there are relations between depth and any of the parameters the supposed depth profile of the allochthonous sediments was subdivided into nine relative depth classes (fig. 45) and these classes were compared with the various groups of parameters. Only the relation between the depth profile and the relative flatness of the test, $\overline{A/B}$, appeared significant ($p = 0.01$), i.e. groups of "deep" specimens are relatively flatter than groups of "shallow" specimens. Furthermore, at the base of the Nizzana Formations we found an alternation of autochthonous and allochthonous lager foraminifera-bearing strata. From the former group of strata no data on A and B were available due to the brittle state of preservation, but our field observations gave the impression that the specimens they contain are very flat. The allochthonous assemblages, which therefore come from shallower depths, contain relatively thick specimens of *Asterocyclina*.

Summarizing, our data suggest a correlation between increasing depth and decreasing relative thickness of the test of *Asterocyclina*. Similar relations have been reported for recent living larger foraminifera, like *Heterostegina* and *Operculina* (Hottinger, 1977a; Fermont, 1977a, b) and in *Amphistegina* (Larsen & Drooger, 1977); at the supraspecific level, too, flatter species replace thicker ones at greater depth (Muller, 1977, 1979; Hottinger, 1977a;

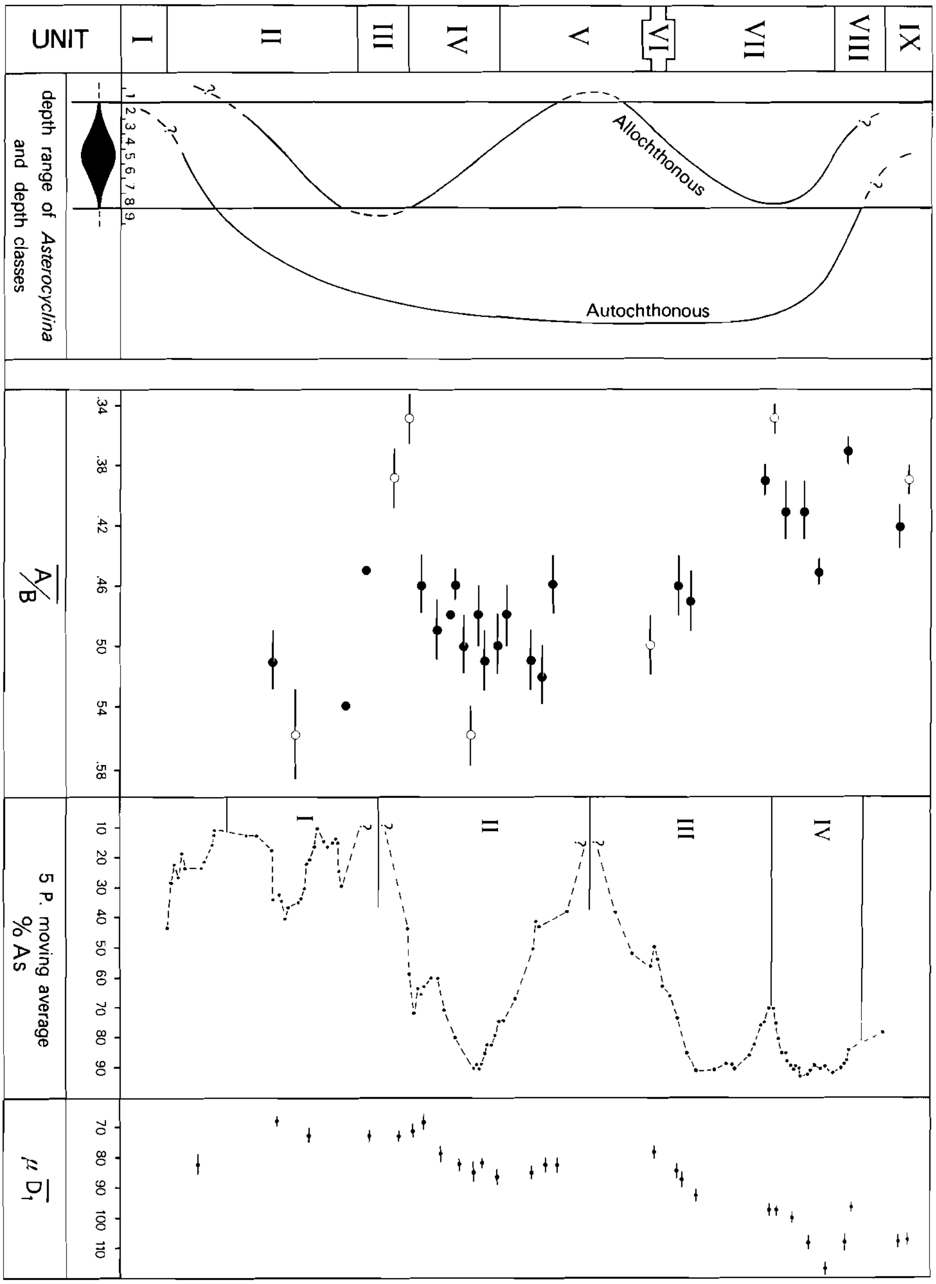


Fig. 45 A comparison between the depth profile and the patterns of the parameters $\overline{A/B}$, $\overline{\%As}$ and $\overline{D_1}$.

Larsen & Drooger, 1977). Such a relation may be a valuable tool for the estimate of relative depth fluctuations in successions of strata with shallow marine larger foraminifera. More sophisticated statistical methods will have to be developed, however, because the allometric growth also plays a role in the interpretation of the numerical data.

No linear relation was found between assumed depth and %As. However there seems to be another relation. Low values of the %As are found either in the shallowest parts or in the deepest parts of the depth trajectory, except in the basal part of unit II and the uppermost part of the section (unit IX). In the intermediate depth ranges four peak frequencies of the %As are observed (fig. 45).

Before this relation between depth and the %As can be interpreted some further discussion of the %As is necessary. The frequency distributions of larger foraminivera are based on only four groups. Analyses of the closed sums of such a small number of groups are dangerous, and in fact impossible unless we have additional data concerning the distribution of the separate groups of larger foraminifera. These data do indeed seem to be available. Relatively low values of the %As were found in units III, V and VIII; these intervals contain very few larger foraminifera. On the other hand relatively high to extremely high %As values were found at the base of unit II, at the top of unit II, in unit IV and in unit VII; these intervals are all extremely rich in larger foraminifera. The relations between the %As and the abundance of larger foraminifera in general suggest that the frequency patterns observed are caused mainly by fluctuations in the contribution of *Asterocyclina*, except perhaps in parts of unit II where rich associations were found with predominance of *Discocyclina* or *Nummulites*. If we accept that the major fluctuations in the frequency distributions of the larger foraminifera are caused mainly by the "squeezing" effect of *Asterocyclina*, then the consequence is that we must conclude that the relative frequencies of the remaining groups of larger foraminifera do not provide any realistic information. Therefore we cannot compare the relative frequencies and morphological characters of these remaining groups.

Apparently, if our reconstruction of the depth profile is correct at all, *Asterocyclina* shows a bell-shaped relative frequency distribution along the depth cline. This does not necessarily imply that depth controls the relative frequency of *Asterocyclina*. Other parameters controlling the habitat of *Asterocyclina* such as substrate composition or vegetation – which in turn may be depth dependent – might have yielded comparable results.

III.4 DISCOCYCLINA

III.4.1 Introduction

There is an astonishing amount of variation in this genus. Whatever morphological character of *Discocyclina* is chosen it seems to occur in combination with every other feature. On the basis of a typological species concept this variation has led to the designation of a multitude of species. In the European faunal province at least 30 species of *Discocyclina* have been described (cf. Van der Weijden, 1940, Schweighauser, 1953, Neumann, 1958; Kecskeméti, 1959; Sirotti, 1978). Yet, there is no convincing framework for the phylogenetic relations between the species recognized.

We are unable to clarify the phylogeny of the group because our own material, which was derived from one locality, represents a limited lapse of time. Therefore we aimed at recognizing relations between morphological characters in order to establish some kind of system in the variation within this group.

In contrast with *Asterocyclina* representatives of *Discocyclina* are scarce in the Ein Avedat section. Moreover, *Discocyclina* specimens are frequently damaged to such an extent that it is virtually impossible to establish growth patterns.

Extreme variation has also been observed in the shape of the embryonic part of the test. In one sample the configuration of the embryon may range from isodiscodine to eudiscodine; this makes te concept of evolution according to the principle of embryonic acceleration rather unlikely.

III.4.2 The building plan of *Discocyclina*

The building plan of *Discocyclina* is very complex, and shows a much wider variation than that of *Asterocyclina.*

The median layer consists of the embryon in the centre which is surrounded by annuli. The annuli are subdivided into chambers. The median layer is generally very thin.

Size and configuration of the embryonic chambers show considerable variation. There seems to be a rough correlation between the size of the embryon, the degree of enclosure and the number of chambers in the first annulus. Specimens having a small embryon generally have isodiscodine or nephrodiscodine configurations. There are generally fewer than 20 chambers in the first annulus. Intermediate-sized embryons show configurations ranging from nephrodiscodine to trybliodiscodine and eudiscodine. The number of periembryonic chambers is extremely variable. Specimens with a large embryon show configurations in which the protoconch is usually completely surrounded by the deuteroconch; there may be as many as 40 chambers in the first annulus.

The chambers in the first annulus are sometimes distinctly larger than those of the subsequent annuli. Their shape is regular and generally hexagonal to rectangular. Normally no differentiation can be made between accessory auxiliary chambers, spiral chambers and closing chambers. The principal auxiliary chambers are generally somewhat larger than the other chambers of the first annulus. They extend over the protoconchal wall, leaving little or no room for other chambers on the protoconch. For this reason we counted only the chambers attached to the deuteroconch. The hexagonal chamber type disappears during ontogeny, sometimes already in the second annulus but occasionally later, whereafter only the typical discocyclinid rectangular chambers are formed.

In contrast with *Asterocyclina* there are no rays in the median layer. However, a wavy development of the annuli was frequently observed. Closer inspection of such wavy annuli invariably revealed that they are cuased by regeneration over irregularly damaged subcircular specimens.

The lateral chambers also show considerable variation. The number of lateral layers decreases towards the periphery. In some specimens the lateral tissues are absent or nearly absent in the peripheral parts. In others the reduction is much less. The pillars are conical. The ultimate size of the pustules observed at the surface of the test is clearly dependent on the thickness of the individuals.

The pustules at the surface are surrounded by rosettes of lateral walls, which may vary in number from 5 to 14 or more. There is also a large variation in the distribution and size of the pustules.

III.4.3 The distinction of morphogroups on the basis of the outer morphology

On the basis of the outer morphology we recognized three essentially different groups of *Discocyclina.* We could only recognize these in "adult" specimens. The details of the inner morphology seem to confirm this threefold subdivision, so after sectioning we can extend the subdivision to the smaller specimens. It should therefore be realized that the subdivision of the *Discocyclina* specimens was partly based on a combination of features of the outer and inner morphology. The three groups will be discussed separately.

Group 1

In group 1 there is an extreme morphological variation. The specimens are generally small and may range in size from 1 to approximately 4 mm. At one end of the morphological variation the specimens are very flat and the tests are entirely covered with small pustules. Each pustule is surrounded by a rosette of 5–9 small lateral chambers. Such types are known in the literature by a variety of names like *Discocyclina augustae, D. augustae* var. *olianae, D. papyracea* and *D. trabayensis;* these names depend mainly on the presence, absence and size of the umbilical boss or on more or less pronounced pillars. At the other end of the variation range specimens are found which are relatively thick. The size ranges from 1–2 mm., the thickness from approximately 0.7–1.5 mm. These specimens generally have large pustules on the central part of the test. The pustules gradually diminish in size towards the periphery. Such types, with slight morphological differences, have been referred to as *D. douvillei, D. chudeaui, D. nummulitica* and *D. aspera.* In between these extreme morphotypes a continuous variation of intermediates is found. Such intermediates are also known by a variety of names, like *D. varians, D. andrusovi, D. seunesi* and *D. roberti.*

Generally there is a gliding variation in the outer morphology, but in the samples Is 193, 199 and 221 a discontinuity was observed. On the one hand there are extremely flat specimens of the *D. augustae* type. On the other hand there are relatively thick specimens of the *D. varians* type. In these samples these two groups were divided provisionally into the groups 1b and 1a, respectively. In the samples with a gliding morphological variation the flatter specimens of the *D. augustae* type are included in group 1a.

Although in most of the samples the morphological variation in group 1 is complete there are differences in what might be called the average type per sample. In the lowermost samples, from Is 157 to 259, flat to moderately thick specimens are most frequent. In samples Is 273 and 276 however, relatively thick specimens of the *D. varians* to *D. chudeaui* types predominate. In Is 303 to 374, specimens with moderate relative thickness are most frequent, thus resemblin the *D. varians* type. In Is 382 and 397 *D. augustae* types are dominant, whereas in the uppermost samples Is 399 and 407 the thicker types resembling *D. varians* and *D. chudeaui* become more frequent again.

Group 2

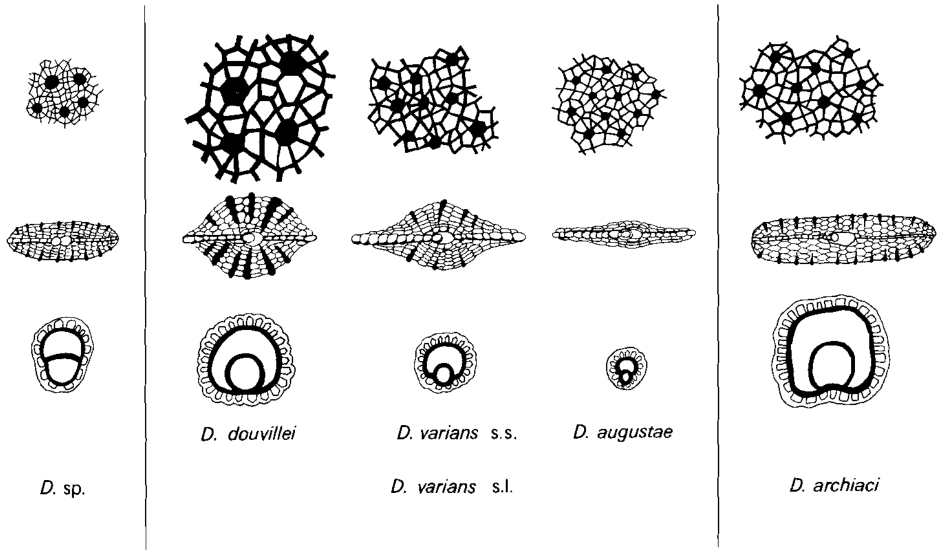
This group shows much less morphological variation than the previous group. Generally the specimens are larger than those of group 1. The surface of the test is generally covered with equally distributed pustules that diminish only slightly in size towards the periphery. The specimens lack the central boss which was observed in group 1. The pustules are surrounded by rosettes of 5–9 lateral chambers. Towards the periphery the thickness of the test is much less reduced than it is in group 1a. This type can be referred to as *D. archiaci.* In juvenile specimens it is extremely difficult to differentiate between groups 1 and 2 on the basis of outer morphology.

Group 3

Representatives of group 3 are scarce. They were found in two samples from the lower part of the Ein Avedat section, i.e. in Is 199 and 276. The features of their outer morphology permit their separation. The surface of the test is entirely covered by small pustules. The pustules are surrounded by rosettes of 10–14 lateral chambers. The specimens found are relatively small, approximately 1–1.5 mm., and relatively flat without an umbilical boss. The periphery is rounded and the peripheral part of the test is only slightly thinner than the central area. The literature names of this type are somewhat indistinct. On the basis of the outer morphological characters the specimens belong clearly to the group of "species" *D. scalaris, D. sella* and *D. discus,* all of which have relatively flat specimens covered with small pustules surrounded by rosettes of 10–14 lateral chambers. As is pointed out further on, the inner morphology is completely different. The embryon shows an isodiscodine configuration, which resembles that of *D. daguini.*

In this paper we shall refer to the groups mentioned by the following names:

group 1a	*D. varians*	*D. varians* s.l.
1b	*D. augustae*	
2	*D. archiaci*	
3	*D.* sp.	


D. douvillei *D. varians* s.s. *D. augustae*

D. sp. *D. varians* s.l. *D. archiaci*

Fig. 46 Schematic drawing of some of the structural elements of the various *Discocyclina* species. Above: lateral chambers arranged around the pustules. Middle: axial section with the embryon, median layer, lateral layers and conical pillars. Below: embryon configuration.

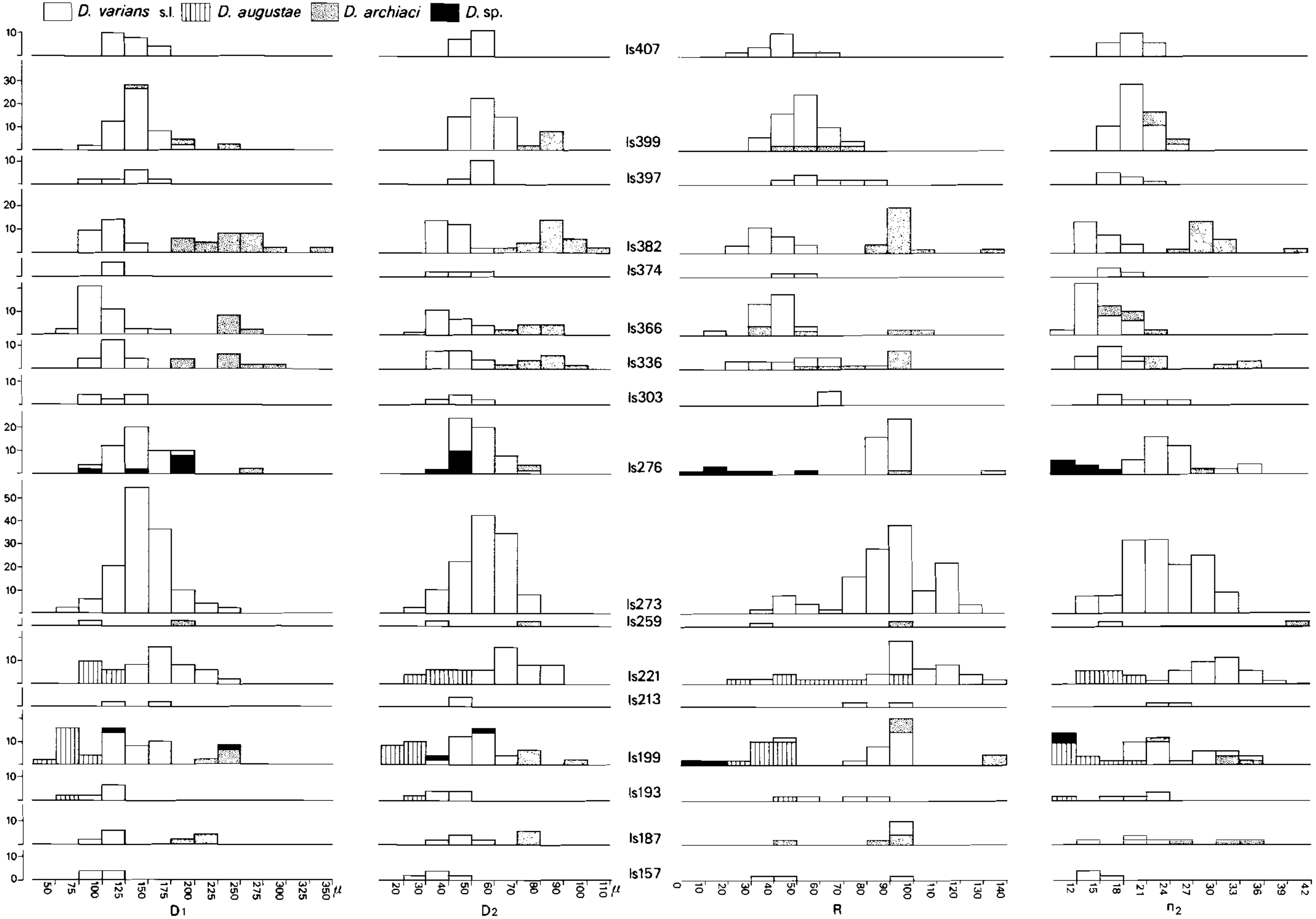


Fig. 47 Frequency distributions of D_1, D_2, R and n_2 of *Discocyclina*.

but we are well aware that a much wider variation is included in the "species" of our groups 1 and 2 than is normally thought acceptable in the literature on the Discocyclinidae. Some of the morphological features of *Discocyclina* are shown in fig. 46.

III.4.4 The inner morphology of *Discocyclina;* results of counts and measurements

III.4.4.1 *Introduction*

Altogether 17 samples containing *Discocyclina* were studied (fig. 10), some of which contained only a few specimens. In several samples the *Discocyclina* specimens were poorly preserved and after sectioning 289 specimens were eventually available for measurement.

Seven parameters were used: n_2, R, H_1, H_2, H_c, D_1 and D_2. For all these parameters distinctly heterogeneous frequency distributions were observed in some of the samples. The frequency distributions of the parameters D_1, D_2, R and n_2 are shown in fig. 47. The heterogeneity of most of the samples is also shown by the coefficients of variability (table 5), which are unacceptably high for most of the samples.

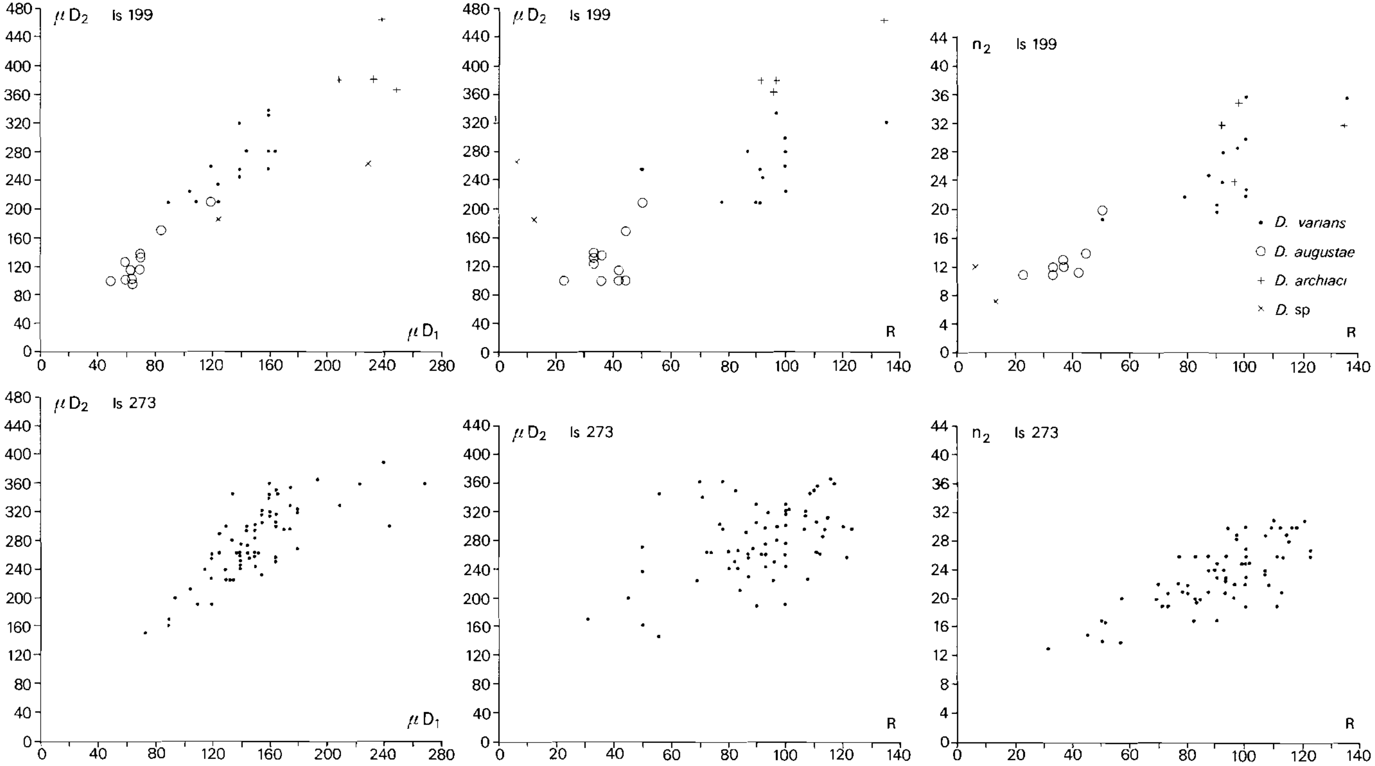
For several samples the scatter diagrams for pairs of parameters revealed distinct clusters, whereas in others the distributions do not point to heterogeneity. Some of the scatter diagrams for samples Is 199, 273 and 366 are shown in fig. 48. In these scatter diagrams the types recognized on the basis of outer morphological characteristics are indicated by different symbols.

In Is 199 there is a good agreement between the separation based on outer morphology and the separation based on D_1-D_2, except in the case of *D.* sp.

The scatter diagrams for Is 273 give an entirely different picture. This sample with continuous variation in *D. varians* s.l. shows a continuity for all parameters R, n_2, D_1 and D_2. There is no reason to subdivide the clusters.

The data for Is 366 evidently fall into two groups, corresponding to *D. varians* and *D. archiaci.*

Similar comparisons for the other samples revealed that the assemblages can generally be split into clusters that correspond to the groups of *D. varians* and/or *D. augustae, D. archiaci* and *D.* sp. For occasional individuals the relation is not clear or is in contradiction with the determination made on the basis of the exterior. Yet, accepting the possibility that a few specimens might have been placed in the wrong group, we treated the specimens which were thought to belong to the typological groups separately in our further calculations. The coefficients of variability of the separate groups, listed in table 5, are generally acceptable if homogeneity is assumed. The high values for R of


μD2 Is 199
μD1
μD2 Is 199
R
n2 Is 199
R
• D. varians
○ D. augustae
+ D. archiaci
× D. sp
μD2 Is 273
μD1
μD2 Is 273
R
n2 Is 273
R
0 40 80 120 160 200 240 280 320 360 400 440 480
0 40 80 120 160 200 240 280
0 20 40 60 80 100 120 140
0 4 8 12 16 20 24 28 32 36 40 44

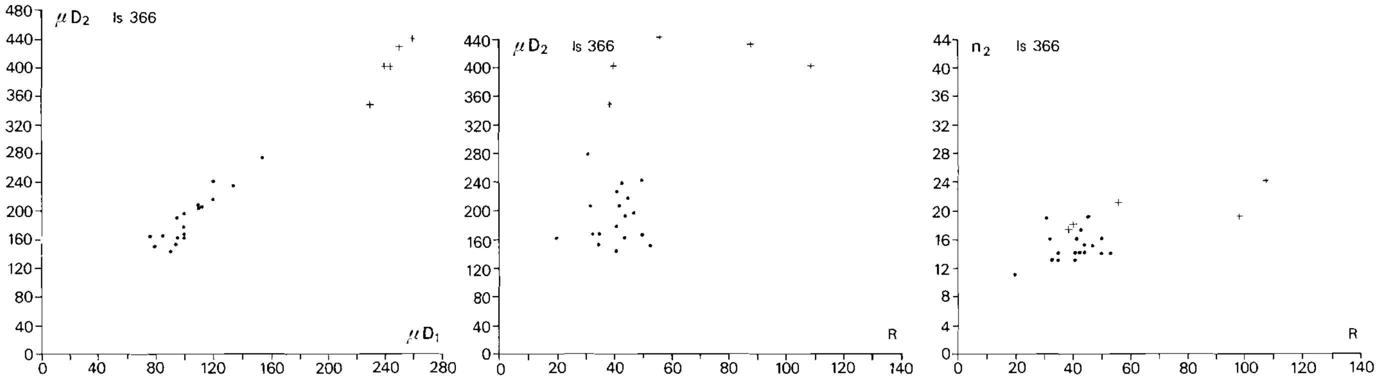


Fig. 48 Scatter diagrams of various pairs of parameters of *Discocyclina* from samples Is 199, 273 and 366.

D. varians s.l. may be due to the fact that R is a ratio between two measurements. The V-values of n_2, D_1 and D_2 have become reduced to acceptable values within this group, except for the V-values of n_2 in samples Is 303 and 199.

Although there are only a few specimens per sample in the other groups, the V-values do not reach extremely high values any more.

Assuming that the sample-splitting has led to fairly homogeneous groups we calculated means and standard errors for each parameter and for all the samples. The results are listed in table 6.

III.4.4.2 *Discocyclina augustae and D. varians*

It can be seen from table 6 and fig. 49 that there is no definite trend in any of the parameters in the section of Ein Avedat. Nevertheless the differences between sample means may be significant, resulting in a fluctuating pattern. For example, the average $\overline{D_2}$-value of the *D. varians* group is approximately 260 μ. Deviations of more than ± 60 μ occur for instance in samples Is 157, 221 and 366. These deviations are more than 8 times the corresponding standard error which is thought to be really significant. Deviations from the grand mean with a comparable magnitude are observed for the other parameters as well (fig 49).

The correlation coefficients were calculated for five pairs of parameters: R-n_2, n_2-D_2, H_1-H_2, D_1-D_2 and R-D_2. The significance of the r-values was tested at three levels of confidence. The results are listed in table 7. There is a fairly general positive correlation ($p = 0.01$) between the size parameters D_1-D_2 and H_1-H_2. Without further testing it was assumed that similar correlations existed for the other pairs of size parameters. In contrast with *Asterocyclina* there are positive correlations between the variables R and n_2 and between these variables and the size parameters in several samples. These correlations might be due to the occurrence of two clusters in a sample, whereas in single homogeneous clusters there would be no such correlation. However, neither the histograms nor the coefficients of variability contain indications for further heterogeneity within this group except in the case of *D. augustae* and *D. varians* s.s. which had been already recognized. Therefore it seems reasonable to assume that the *Discocylina* parameters n_2 and possibly R depend to a certain extent on the size of the embryon.

There are some indications that there is a relation between the inner morphology and the outer morphology. In Is 193, 199 and 221 very flat specimens of the *D. augustae* type could be treated as a separate group because of the morphological gaps observed. A comparison of the data of the co-occur-

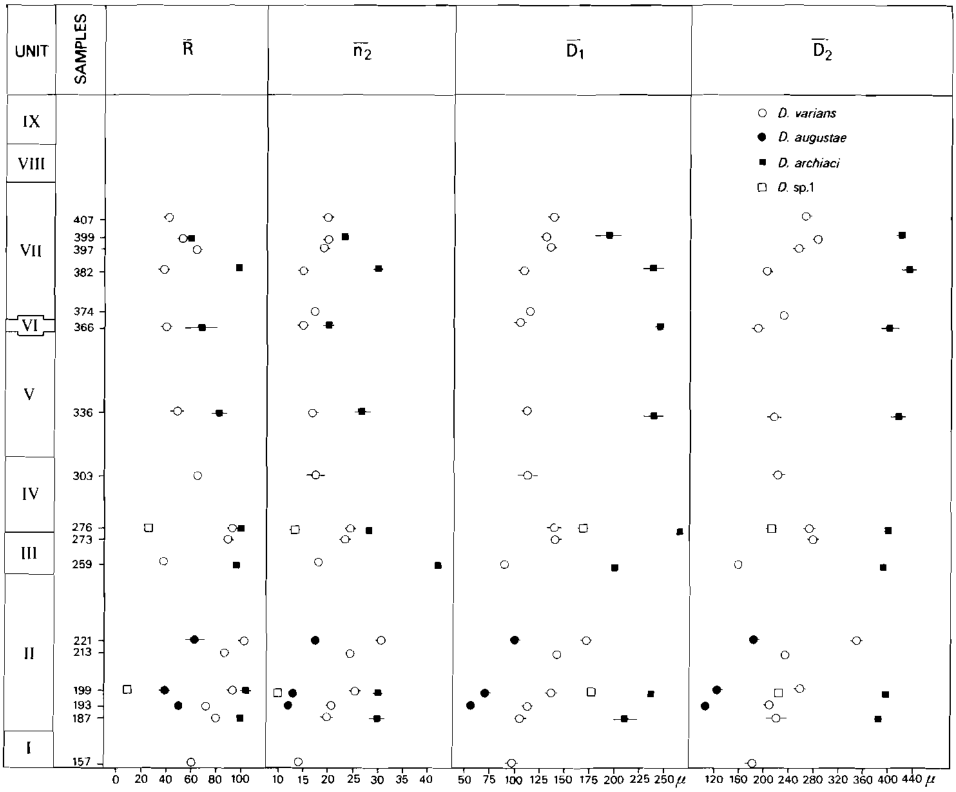


Fig. 49 Vertical distribution of some parameter means of *Discocyclina*.

ring groups of *D. augusta* and *D. varians* s.s. shows that the dimensions of the embryon in the former group are about half of those in the latter group which contains the thicker specimens.

A similar result was obtained for sample Is 273. In this sample no morphological break was observed between *D. augustae* and *D. varians* s.s. On the average the specimens are moderately thick. The specimens of this sample were subdivided into four groups corresponding to the types of *D. augustae*, *D. varians* and *D. douvillei*, in increasing order of relative thickness (compare fig. 46) and a fourth group of damaged or indeterminable specimens. The representatives of separate groups are indicated in the D_1-D_2 scatter diagram of Is 273 (fig. 50). There is a distinct relation between the dimensions of the embryon and the relative thickness of the test. *D. augustae* types invariably occur amongst the lower D_1-D_2 values, with one exception. The *D. varians* types are found in the central part of the cluster, whereas *D. douvillei* types occupy the highest part of the cluster with a large overlap with the *D. varians* types.

If this relation between the dimensions of the embryon and the relative thickness of the test has a more general value one might expect to find the highest $\overline{D_2}$-values in samples with relatively thick specimens and the lowest values in samples with relatively thin specimens. This is in fact what was found in some samples, like Is 273 and 276 with relatively thick specimens and high $\overline{D_2}$-values, and Is 157, 187, 193 and 382 with relatively flat specimens and low $\overline{D_2}$-values. However, in others, for instance Is 221 with no more than moderately thick specimens, $\overline{D_2}$ is extremely high. Apparently the relation between the inner and the outer morphology is more complex than is suggested by the data of Is 273.

III.4.4.3 *Discocyclina archiaci*

Far fewer data are available on *Discocyclina archiaci* than on *D. varians* s.l.; therefore only short comments will be made.

No trends can be seen in any of the parameters (fig. 49). The $\overline{D_2}$-values fluctuate around 400 μ and when the samples are compared none of the differences is really significant. A similar picture emerges for the other size parameters. Although there are some significant differences (for instance the $\overline{H_1}$-value of Is 399 is relatively low) the differences in the dimensions of the embryon are much less distinct than those observed in *D. varians* s.l. The para-

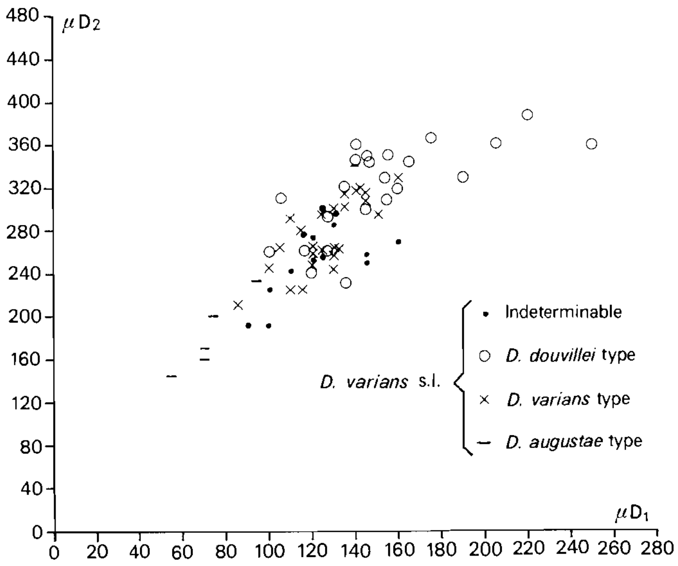


Fig. 50 Relation between the inner and the outer morphology of *Discocyclina varians* s.l. from Is 273.

meters $\overline{R}$ and $\overline{n_2}$ show some more significant differences but these parameter means show no trend either.

The parameters all show positive correlations (table 7). Owing to the small sample size they are of low significance in most cases. If all individuals are tested together, assuming that they come from the same population, all correlations turn out to be highly significant.

As in the specimens of *D. varians* s.l. a possible conclusion is that the parameters R, n_2 and H_c depend to a certain extent on the size of the embryon.

III.4.4.4 *Discocyclina sp.*

Only eight specimens are available from the samples Is 199 and 276 in the lowermost part of the section.

They have an embryon of the isodiscodine type. No further conclusions can be drawn owing to the small number of data.

III.4.4.5 *Comparison between D. varians s.l., D. archiaci and D. sp.*

The three groups we distinguished are different not only in their outer and inner morphology but also with respect to their vertical distribution in the Nizzana Formation.

D. varians s.l. is most frequent and occurs throughout the section. *D. archiaci* is present with relatively low frequencies throughout the section but in a considerably smaller number of samples than *D. varians*. The scarce *D.* sp. specimens occur in the lower part of the Nizzana Formation only.

With respect to $\overline{R}$, *D. varians* and *D. augustae* are intermediate between *D. archiaci* and *D.* sp. *D.* sp. has an isodiscodine embryon configuration, *D. augustae* a nephrodiscodine configuration, whereas in *D. varians* the configuration ranges from nephrodiscodine to eudiscodine. In *D. archiaci* the embryon shows a high degree of embracement ranging from umbilicodiscodine to eudiscodine.

The average n_2 in *D.* sp. is 12.5; in *D. varians* and *D. augustae* the averages are 24.6 and 15.1 respectively. In *D. archiaci* the average n_2 is 27.7.

In *D. varians* and *D. augustae* the $\overline{D_2}$-values are on average 260 and 150 μ respectively. In *D. archiaci* the average $\overline{D_2}$ amounts to 420 μ and in *D.* sp. to 220 μ.

In fig. 51 the relations between several combinations of parameter means are visualised.

The $\overline{D_2}$-$\overline{D_1}$-diagram demonstrates that the values for *D. varians* s.l. are well in line. *D. archiaci* is found at the upper extreme of the cluster. The means suggest a $\overline{D_2}/\overline{D_1}$ relation which is different from that of *D. varians* s.l. The mean values of D_1 and D_2 for *D.* sp. occupy extreme positions in the cluster.

The $\overline{D_2}$-$\overline{R}$ diagram shows a wide cluster. *D. archiaci* is found in the upper part, *D. augustae* in the lower part and *D. varians* in the central part of the cluster. *D.* sp. occupies an extreme position in the lower part of the cluster.

The scatter diagram of $\overline{n_2}$ versus $\overline{R}$ demonstrates the intermediate position of *D. varians.* Although the cluster is relatively wide the diagram shows that all data might fit to a single line of central tendency.

In summary, we seem to be justified in considering *D.* sp. and *D. archiaci* as discrete species. Because of the continuous variation in most of the samples we consider *D. varians* s.l. as a single species unit, notwithstanding the fact that there are extreme differences in average type per sample. There is even heterogeneity in some samples due to mixing of different subpopulations. The morphological fluctuations observed in *D. varians* s.l. are discussed in more detail in the following section.

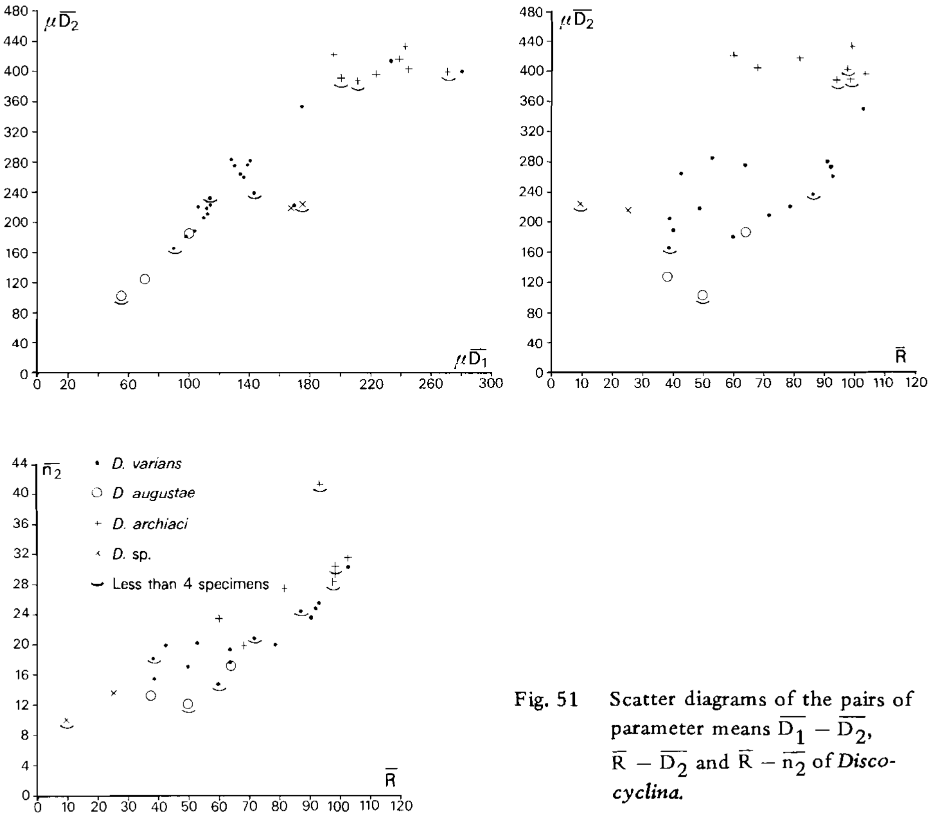


Fig. 51 Scatter diagrams of the pairs of parameter means $\overline{D_1}$ – $\overline{D_2}$, $\overline{R}$ – $\overline{D_2}$ and $\overline{R}$ – $\overline{n_2}$ of *Discocyclina.*

III.4.5 Relations between the fluctuations in the morphology of *Discocyclina* and trends in the sediments of Ein Avedat

The low number of observations on *D.* sp. and the fair constancy of the inner and the outer morphology of *D. archiaci* make it impossible to recognize any relation between the morphology and the sedimentary trends in the Ein Avedat section.

D. varians s.l. has the widest morphological variation in our material, so the data on *D. varians* s.l. allow for a more detailed comparison. As in the case of *Asterocyclina* the reconstructed depth profile was subdivided into nine relative classes of increasing depth. These classes were compared with the means of the internal morphological parameters of *D. varians.* Because of the low number of samples available we took the liberty of including the samples with a small number of data in the comparison. Samples with only one or two observations were not used. The correlation coefficients between the parameter means and the depth classes are tabulated below. For each comparison the sample size is 13.

parameter	$\overline{R}$	$\overline{n_2}$	$\overline{H_1}$	$\overline{H_2}$	$\overline{H_c}$	$\overline{D_1}$	$\overline{D_2}$
	−0.019	0.237	0.368	0.609	0.786	0.514	0.533
p	---	---	---	0.05	0.001	0.05	0.05

Although the positioning of the samples in the depth classes is entirely hypothetical and the statistical sample size is small, it is possible to draw some conclusions that make sense theoretically.

All the correlations between the internal size parameters and depth are positive, which means that specimens with a large embryon lived at greater depth. In fig. 52 the relations between depth and the inner morphological parameters are shown. The size of the peri-embryonic chambers seems to show the most extreme depth dependence. $\overline{H_2}$ and $\overline{D_2}$ are distinctly influenced by depth, and the dimensions of the protoconch seem to be influenced to a somewhat lesser degree. There seems to be no relation between $\overline{R}$ or $\overline{n_2}$ and depth, although there is a low positive r-value for the parameter $\overline{n_2}$. Evidently we are now faced with a contradiction. In the lower part of unit II a distinct discontinuity was observed in the morphological variation of *D. varians* s.l., for which reason we separated *D. augustae* from *D. varians* in samples Is 193, 199 and 221. The variation in the other samples appeared to be continuous. The lower part of unit II is the only interval where an alternation of autochthonous and allochthonous sediments bearing larger foraminifera was observed. The supposedly authochthonous *Discocyclina* specimens are extremely flat and apparently belong to the *D. augustae* type. Such well sorted flat specimens of *Discocyclina* were never found in the allochthonous assemblages. The deeper living flat *D. augustae* invariably have a small embryon relative to the allochthonous thicker *D. varians.*

A similar relation between the relative thickness of the test and the dimensions of the embryon was ascertained for sample Is 273, where there is a continuous variation from flat to thick specimens. The conclusion that the relatively flat *D. augustae* types lived at greater depth is compatible with data on Recent living larger foraminifera (compare Reiss et al., 1977, Muller, 1978). These data suggest that relatively flat, deep-living *Discocyclina* have a small embryon, whereas shallow-living, thicker specimens have a large embryon. According to this picture the relation is precisely the reverse of the relation we found from the comparison between the depth profile and the

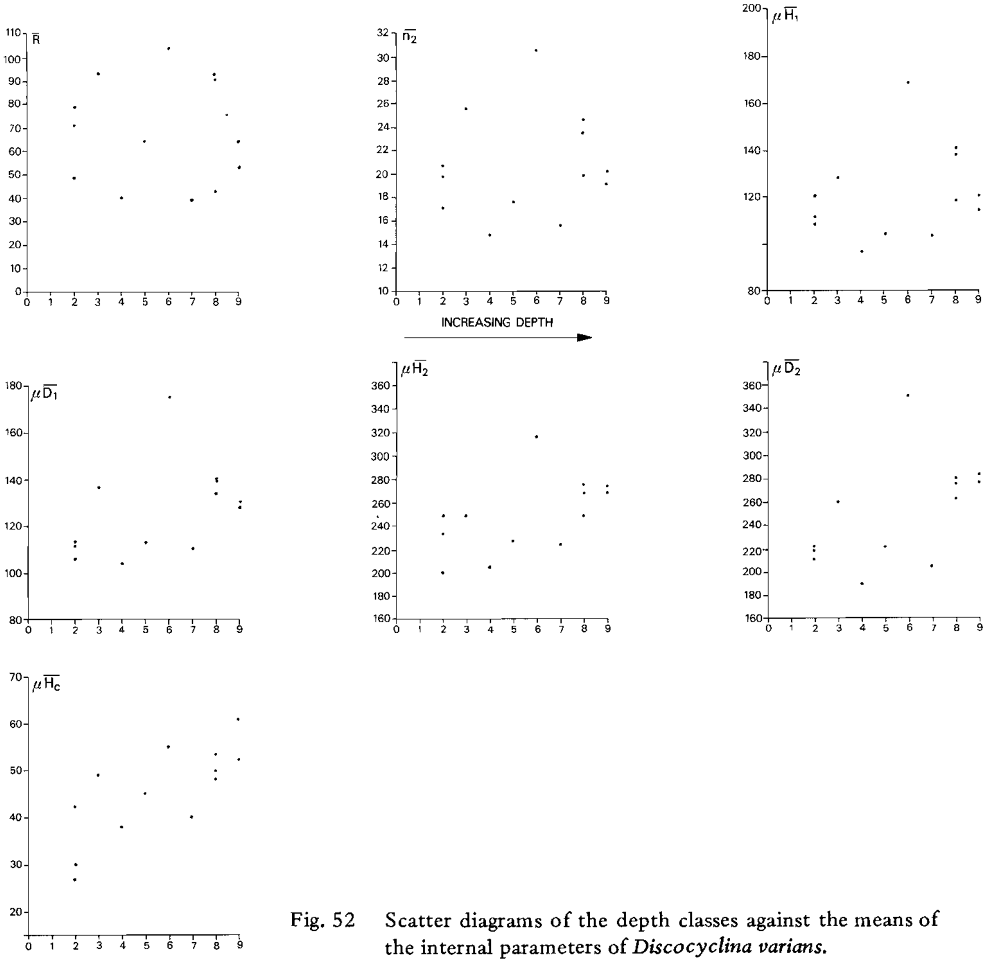


Fig. 52 Scatter diagrams of the depth classes against the means of the internal parameters of *Discocyclina varians.*

dimensions of the embryon, i.e. deeper living *Discocyclina* have a larger embryon.

We are forced to the conclusion that *D. augustae* is a separate species which lived at greater depth. The positive depth-embryon size correlation thus would be restricted to *D. varians* only. However, the continuous variation from *D. augustae* types to *D. varians* and *D. douvillei* types in most of the samples makes such a solution rather unlikely. Therefore we prefer the alternative hypothesis that *D. augustae* and *D. varians* belong to one species which shows an extremely wide morphological variation. Deep-living specimens are extremely flat and have a small embryon. Shallow-living specimens are on the average thicker. In the depth range of shallow-living populations there are differences in embryon size. The shallowest populations have smaller embryons than the populations at intermediate depths. However, if other environmental fluctuations played a role, our complex reconstruction, which is based on depth only, may be incorrect.

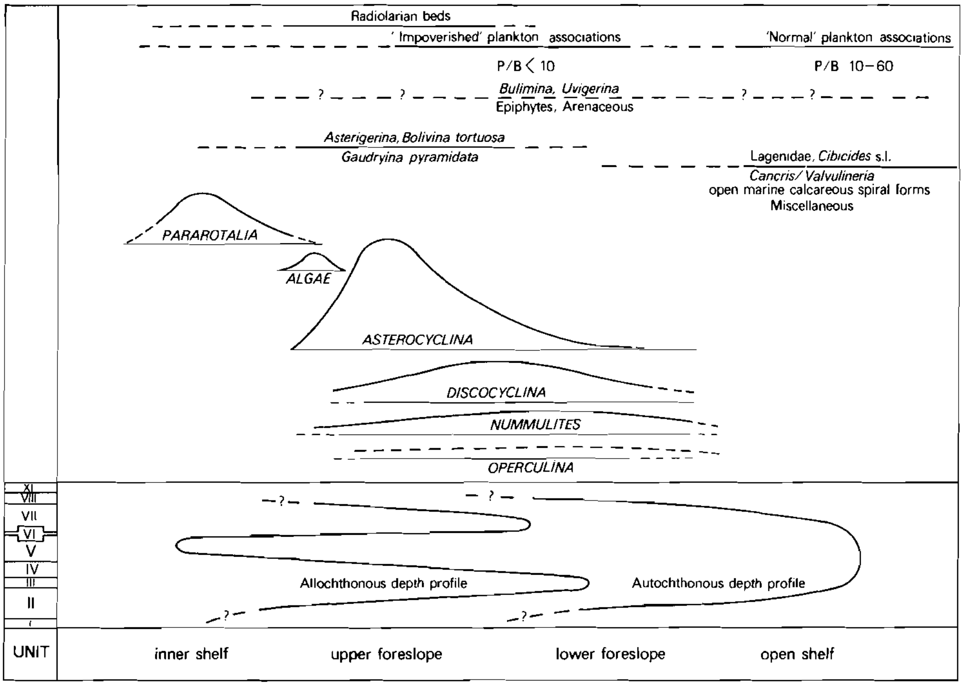


Fig. 53 Reconstruction of the foreslope faunal associations with emphasis on the larger foraminifera.

Chapter IV

SYNTHESIS

IV.1 FAUNAL DISTRIBUTIONS AND DEPTH

Fig. 53 shows our reconstruction of the original position of faunal associations along the depth cline of the north-dipping Avedat platform.

Such a reconstruction gives a simplified picture because other variables besides depth will also have shaped the faunal distribution pattern. For instance, the shallowing which we reconstructed for the allochthonous sediments in unit V was accompanied by a blooming of *Pararotalia* associations. The next higher shallowing in unit VIII was accompanied by radiolaria-rich beds which no longer contained any *Pararotalia.* In these cases other variables besides depth have played a considerable role. Furthermore it should be realized that our reconstruction does not involve a single time plane; it combines all faunas from a 100 metre vertical sequence. In the figure we plotted the supposedly shallow living *Asterigerina, Bolivina tortuosa* and *Gaudryina pyramidata* together, but in reality they have their high frequencies in different intervals of the section. Also the position of the genera of larger foraminifera should be considered with some caution; their niches may have changed in the course of the time, especially because we are dealing with different species in each genus.

In our reconstruction the inner shelf benthos is dominated by *Pararotalia.* Planktonic foraminifera are scarce and undersized, which is in agreement with Recent distributions (Lutze, 1974; Boltovskoy, 1976; Murray, 1976).

At the transition from the inner shelf to the upper slope algae are frequent; this is especially true of the units IV and VI. The algae are thought to separate the *Pararotalia* biotope from the biotope of the larger foraminifera.

The larger foraminifera are especially frequent in the foreslope environments. *Asterocyclina* is thought to have its peak frequencies in the upper foreslope area, whereas the *Discocyclina, Nummulites* and *Operculina* associations are situated in somewhat deeper habitats without further differentiation. In view of the co-occurrence of all genera of larger foraminifera in most of the samples their depth ranges must have overlapped to a great extent.

The niche separation between *Asterocyclina* and *Discocyclina* must also have been controlled by other variables besides depth. Closely related Recent larger foraminifera frequently show overlapping depth ranges (Reiss et al., 1977) and the separation of their niches is linked to differences in substrate or vegetation type. For instance, in the Gulf of Akaba *Amphistegina lessonii* and *A. lobifera* occur in the upper 70 metres in the same depth range as the sea plant *Halophila,* on which they live. *A. papillosa* and *A. bicirculata* are bottom dwelling species which are most frequent at a greater depth, but the depth ranges overlap (Hansen & Buchardt, 1977). According to Zohary et al. (1980) *Amphisorus hemrichi* and *Sorites orbiculus* live on the flat leaves and the stalks of *Halophila,* respectively; this niche separation is even more subtle. *Planorbulinella elatensis* and *P. larvata* have different depth ranges (Thomas, 1977). The latter species lives at the shallowest depth and is clearly epiphytic.

A similar explanation may be valid for our Eocene *Asterocyclina* and *Discocyclina. Asterocyclina* is assumed to have preferred shallower depths and its species were probably epiphytic, whereas *Discocyclina* species might have been living at a greater depth as bottom dwellers. If this assumption is correct, then the fluctuations observed in the frequencies of *Asterocyclina* are not necessarily controlled by depth but rather by the quality and the quantity of the vegetation. The "squeezing effect" of *Asterocyclina* could well be explained by fluctuations in vegetation which affected the abundance of *Asterocyclina* but did not affect the other species of larger foraminifera to a similar degree.

Our reconstruction of the deeper foreslope environment is mainly derived from the assumedly autochthonous sediments, in which the planktonics are larger and the high P/B ratios point to open marine water masses (Murray, 1976; Boltovskoy, 1976). The composition and diversity of the smaller benthonic foraminiferal faunas also point to open marine water masses in our foreslope environment. The occasional presence of supposedly autochthonous associations of larger foraminifera with flat *Discocyclina* and *Asterocyclina* indicates that the depth ranges of these genera extended to the lower limits of the photic zone, if we accept that all orbitoidal larger foraminifera have light-dependent symbionts (Lee, 1980, for references).

IV.2 ECOLOGY VERSUS EVOLUTION

A simplified summary of the correlations between the inner morphological parameters, the outer morphological parameters and the relative frequencies of *Asterocyclina* is shown in fig. 54.

No relation was found between the %As and the outer morphological parameters. This lack of correlation between %As and $\overline{A/B}$ is easily understood if we bear in mind that the $\overline{A/B}$ ratio shows an overall decrease with depth, whereas the %As is thought to have a bell-shaped frequency distribution along the depth cline. Both patterns are consistent with data on Recent foraminifera (Hansen & Buchardt, 1977; Hottinger, 1977; Fermont et al., 1982). The combinations of the inner parameters with %As and with the outer parameters give a confused picture. If the samples containing *Asterocyclina taramellii* and *A. stella* are considered together there are good to fair correlations between the various parameters except for the combinations %As – $\overline{n_{1+2}}$ and $\overline{A/B}$ – $\bar{R}$. For the data on the individual species such correlations are either completely absent, or they have a different sign, in which case only one of the species shows a correlation in accordance with the general pattern. There is a fairly simple explanation for these whole sequence correlations.

All *A. taramellii* samples together and all *A. stella* together differ in all grand means of parameter means. The younger species has distinctly higher values for all grand means except for the grand mean of the relative thickness of the test. In addition, values of 80–100 for %As are found mainly in the upper part of the section corresponding to the range of *A. stella.* Although *A. taramellii* oscillates once to similarly high values, its range shows %As values below 50. The frequent positive correlations for both groups together are thus selfevident. Yet it is hard to understand these correlations for the

	A. taramellii			*A. stella*			together		
	$\bar{R}$	$\overline{n_{1+2}}$	$\overline{D,H}$	$\bar{R}$	$\overline{n_{1+2}}$	$\overline{D,H}$	$\bar{R}$	$\overline{n_{1+2}}$	$\overline{D,H}$
$\bar{A}$	+ +	+ +	+	O	– O	– O	+ +	+	+ +
$\bar{B}$	O	+ O	– O	O	+ O	O	+ +	+ +	+ +
$\overline{A/B}$	+ +	+ O	+ +	– O	– O	– O	– O	– –	– –
%As	+ O	– –	O	O	+	+ +	+ +	O	+ +

	$\bar{A}$	$\bar{B}$	$\overline{A/B}$	$\bar{A}$	$\bar{B}$	$\overline{A/B}$	$\bar{A}$	$\bar{B}$	$\overline{A/B}$
%As	O	O	O	O	O	O	O	O	O

– – strong negative
– weak negative
+ O } possible correlations
– O }
O no correlation
+ + strong positive
+ weak positive

Fig. 54 Summary of the correlations found between %As, inner morphological parameters and outer morphological parameters for *A. taramellii, A. stella* and for the two species together.

whole sequence, because similar correlations for the separate species are either lacking, or contradict the general picture.

A first explanation for the differences between *A. taramellii* and *A. stella* might be that the change from one to the other was entirely ecology-controlled. If this was the case the differences in the parameter values for *A. taramellii* and *A. stella* might be explained by the hypothesis that we are dealing with separate parts of a morphocline along an undefined environmental gradient. This gradient cannot have been depth because none of the parameters except $\overline{A/B}$ shows a significant relation with depth. It is more likely that in this context the combination substrate-vegetation explains the differences between *A. taramellii* and *A. stella.*

A second explanation might be that the differences between *A. taramelli* and *A. stella* are entirely evolution-controlled. Because of the increase in $\overline{R}$ and in the size parameters of the initial stages we might be dealing with an adaptive response, which would correspond to the theories on parallel changes in orbitoidal larger foraminifera. The vertical suite of assemblages does not lead to a simple model, however.

When we started our investigation with four samples that covered the whole section at wide intervals (Is 221, 294, 375 and 452), all the parameters seemed to demonstrate a more or less regular increase, which could have supported the hypothesis of phyletic gradualism. However, as more data were collected this concept gradually became untenable.

Many of the details give the impression of a random walk (Raup, 1977) or of pulsating evolution (M. M. Drooger et al., 1979). In fig. 55 the differences between the mean values of $\overline{R}$ for successive pairs of samples of *Asterocyclina* (sample j and sample j+1) are shown in a frequency diagram. The class intervals correspond to approximately one average SE of the sample means. This diagram of $\overline{R_j} - \overline{R_{j+1}}$ shows a unimodal distribution around zero, which would be in good agreement with the random walk model. However, there is

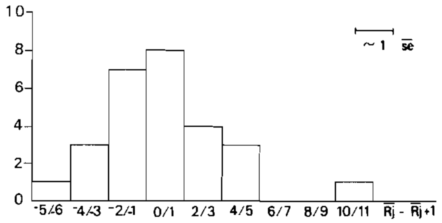


Fig. 55 Distributions of the values for the differences between all $\overline{R_j}$ and $\overline{R_{j+1}}$. j and j+1 are the rank numbers of successive *Asterocyclina* group 1 samples. The extreme value on the right-hand side represents the difference between Is 336 and 366.

one exception where the difference between two successive samples is unusually high ($p = 0.001$); this exception corresponds to the successive samples Is 336 and Is 366. In between is the interval where *Asterocyclina* had disappeared completely from the record and for which we concluded the culmination of a regressive episode. The significant difference in $\bar{R}$ for these two samples, the suggestion of a link with environmental changes and the fact that the direction of the change in $\bar{R}$ is in accordance with the "theory of embryonic acceleration", which has been proved to be valid in several other lineages, all seem to invalidate the random walk model for this exceptionally large morphological change.

If we take into account the duration of the deposition of the Nizzana Formation at Ein Avedat (approximately one my), it can be concluded that the increase in $\bar{R}$ must have occurred over a relatively short time interval. Moreover, we seem to be dealing with a new invasion of *Asterocyclina* in the area. The morphological change thus might be considered as a punctuated equilibrium (Eldredge & Gould, 1972) or as quantum evolution. Stanley (1979) defined quantum speciation as "a form of speciation (branching) that yields marked morphologic divergence, with this divergence taking place (1) within a small population and (2) during an interval that is brief with respect to the longevity of an average, fully established species of the higher taxon to which the new species belongs". In our opinion the transition from *A. taramellii* to *A. stella* may serve as an example of such quantum speciation.

A third explanation might be that the evolution and the ecology of *Asterocyclina* are interrelated. In an "evolution-ecology model" the evolution of *Asterocyclina* does not only pertain to its morphological changes but also to changes in its ecological niche (Pianka, 1978). The reduction in the range of the number of rays, the decrease in the V-values of the inner morphological parameters and the increase of the %As from *A. taramellii* to *A. stella*, together with the increase of the size parameters of the test and of the embryon might point to an increased specialization of *A. stella* relative to *A. taramellii*. These facts point to a narrower niche for *A. stella*, for instance with respect to its food requirement and/or symbiont composition.

It seems reasonable to suppose that a change of habitat for one species automatically influences the habitat of other species (Mac Arthur & Wilson, 1967). Therefore, in a model that supposes changes of habitat of a species in the course of the time the interaction between related species has to be considered as well. Representatives of *Asterocyclina cuvillieri* are relatively frequent in the lowermost part of the Nizzana Formation. In unit V two specimens of *A.* sp. were observed; they were no longer found in the upper part of the section. One could assume that the niches of both groups are not completely separated but overlap. The proliferation of *A. stella* in the upper part of the section might have dislodged *A.* sp. from its original niche. The result was either that *A.* sp. became extinct, or a complete niche separation occurred in which case the habitat of *A.* sp. was no longer represented in the samples. However, the disappearance of *A.* sp. may also be a "statistical extinction" due to the squeezing effect of *A. stella.*

In *Discocyclina* we did not find evolutionary trends in any of the species. *Discocyclina archiaci* showed minor fluctuations throughout the section and neither its occurrence nor its morphology could be related to depth. In *D. varians* s.l. there are distinct relations between the outer and the inner morphology and most of the morphological characters seem to be influenced by environmental gradients. Apparently the morphology of *D. varians* s.l. was very "elastic"; this property allowed this species to become adapted to a widely different set of subenvironments but such adaptions did not necessarily lead to speciation.

IV.3 PATTERNS OF HIERARCHY IN THE MORPHOLOGY OF THE DISCOCYCLINIDAE

One of the major problems concerning the group of the Discocyclinidae is that "evolutionary" trends like nepionic and embryonic acceleration, known from so many other groups of larger foraminifera (Drooger, 1956, 1974) do not seem to play a role. The Discocyclinidae belong to the most highly evolved larger foraminifera known. Yet, it seems unlikely that a group that persisted throughout the Paleocene and the Eocene evolved erratically.

Most of the taxonomic classifications proposed for the Discocyclinidae are based on postulations of the relative importance of morphological features. However, there is generally no proof of any hierarchy in morphological characters.

One of the aims of our investigation was to establish which parameters show evolution and which reflect environmental changes. In the following sections several morphological characters will be briefly discussed. They are ranked in decreasing order of the hierarchy: stability, evolution control, environmental susceptibility and ontogenetic dependence. Further investigations may prove that our ranking in some cases is incorrect. Moreover, we were unable to study all possible details of morphology. For instance, stolon systems were generally invisible owing to the varying degree of recrystallization. Axial sections were not studied systematically, but from the microfacies investigation we had the impression that these sections would not reveal evolving features or characteristics that would be otherwise important.

Chamber shape in the median layer

All Discocyclinidae have rectangular chambers in the equatorial layer. This is the dominant chamber type especially in *Discocyclina,* although sometimes, e.g. in *D. augustae,* arcuate to hexagonal chambers are present in the first annuli. In *Asterocyclina* a much wider variation is observed in the shape of the early median chambers of the test, which range from adauxiliary, spiral and closing chambers in the first annulus to arcuate and hexagonal chambers in the first four or more annuli. In this respect our few *Asterophragmina* specimens are of special interest. After the early ontogenetic development of the median chambers as in *Asterocyclina taramellii* the radial walls disappear and broad annular chambers develop. If such a chamber type indeed follows the rectangular chamber type in the course of the phylogeny, then the American Discocyclinidae may be linked to the European Discocyclinidae in a natural order, because in the American forms the absence of radial walls is a common feature, for instance in *Pseudophragmina* (*Athecocyclina*) (see Vaughan & Cole, 1941, 1948; Cole, 1964; Caudri, 1972).

Rays in the median layer

The number of rays appeared to be very constant in *Asterocyclina,* with a basic pattern of five radiating from the two principal auxiliary chambers and three larger adauxiliary chambers, or when such chambers cannot be recognized they radiate from the larger peri-embryonic chambers. Only in the lower part of our section were some more rays found intercalated between the basic pattern of five. We agree with Brönnimann about the high taxonomic value of the presence of rays. Vaughan (1945) reported complete intergradation between *Asterocyclina* and *Discocyclina* in American Discocyclinidae. Schweighauser (1953) too mentioned ray-like structures in *Discocyclina,* which become visible only in the later stages of ontogeny. However, from the figures of the latter author some of these structures are obviously due to regeneration. Nevertheless there is a possibility that *Discocyclina* stocks developed ray-like structures independently. In our material this was evidently not the case.

Number of lateral chambers around the pustules

The presence of lateral chambers is diagnostic for the Discocyclinidae as a whole, and therefore this character deserves a high rank in our hierarchy. The size of the lateral chambers is quite variable, but their arrangement around the pustules shows several consistent patterns. In *Asterocyclina, Discocyclina varians* s.l. and *D. archiaci* the number of lateral chambers around a pustule ranges from 5 to 9 or occasionally more, whereas in our *D.* sp. the number ranges from 10 to 14 or more. Such differences in lateral chamber structure were observed already by Douvillé (1922) and led him, and later Neumann (1958), to distinguish informal supraspecific groups. Van der Weijden (1940), however, reported a *Discocyclina nummulitica* with a variation from 5 to 18 in the number of lateral chambers around the pustules. Since he also included in this species specimens with ray-like structures we doubt whether his species grouping is correct. If future research justifies the discrimination of a group with a high number of lateral chambers around the pustules (*D. discus, D. marthae,* our *D.* sp. amongst others), then it will be of interest to find out whether there is embryonic acceleration in this group. Our *D.* sp. from the Lower Eocene has an isodiscodine chamber configuration, whereas other species in this group, commonly reported from the Middle and the Upper Eocene, have relatively large embryons with umbilicodiscodine to eudiscodine chamber configurations (Neumann, 1958).

The degree of enclosure

In our *Asterocyclina taramellii,* as well as in our *A. stella,* this parameter appeared to be relatively constant, but from the first to the second species the increase in $\bar{R}$ is in accordance with the embryonic acceleration model. An increase in $\bar{R}$ was also observed from *A. cuvillieri* to *A.* sp. No environmental influence for this parameter could be detected, either in the comparison with the depth profile, or in the relation with the relative frequency distribution. Also the correlations between R and the embryon size are very weak or absent. This parameter apparently has some evolutionary value.

In *Discocyclina* the picture is completely different. Large diffences were observed in $\bar{R}$ for *D. varians.* No direct environmental dependence could be detected but in several samples R showed a distinct correlation with the size parameters of the embryon: these in turn might have some relation with depth.

The number of peri-embryonic chambers

Drooger (1974) suggested that the number of peri-embryonic chambers might depend on the size of the embryon. Such dependence seems to exist in *D. varians* and to a lesser extent in *A. stella* but not in *A. taramellii.* In the latter species we even found a negative correlation between the means of the peri-embryonic chambers and the means of the embryon size parameters. If the correlations between these parameters can be translated as dependence of n on the embryon size, then this relation shows up only in the more advanced stocks of *A. stella* and *D. varians.* Van Gorsel (1975) came to a comparable conclusion in his study of the Late Cretaceous *Lepidorbitoides minor* and *L. socialis.* However, in the most advanced assemblages of *D. archiaci* no relation was found between n and D_2.

The dimensions of the embryon

The dimensions of the embryon generally show an increase in the course of the evolution of larger foraminifera, but deviations from the general trend are well known (Van Gorsel, 1975; M. M. Drooger et al., 1979). In our material too there are distinct fluctuations in the size of the embryon of *Asterocyclina taramellii, A. stella* and *D. varians* s.l. In *A. stella* these fluctuations show a positive correlation with the relative frequency of *Asterocyclina*. In *D. varians* they have a relation with depth. In both cases the dimensions of the embryon are evidently partly environment-controlled.

Dimensions of the peri-embryonic chambers

In *D. varians* it is this character that showed the best correlation with the depth profile, which suggests that the size of the peri-embryonic chambers is very sensitive to environmental changes. On the other hand, in *Asterocyclina* this character showed high V-values. Apparently this parameter should be assigned a low rank, although it has been used for the grouping of species in the Discocyclinidae (Bieda, 1963). It may be partly dependent on the size of the embryon, because in *Asterocyclina* there are occasional significant positive correlations between H_c and the size parameters of the embryon.

Test shape

The relative thickness of the test is perhaps the parameter which has been most frequently used to discriminate species within the Discocyclinidae. In *Asterocyclina* the relative thickness of the test was the only parameter which was found to have a distinct negative correlation with increase of depth. Furthermore the relative thickness shows a complex dependence on ontogeny. It is easy to understand why, if one comes across assemblages from different depths with completely different outer appearances, these are considered to be different species in a typological species concept. Because of its environmental dependence, which also may be deduced indirectly from the relation between relative thickness and embryon size in one of the *Discocyclina* samples, test shape is placed at a low level in our hierarchy.

Size of the pustules

The size of the pustules at the surface of the test has also been frequently used as an additional characteristic for species discrimination. However, pustule diameters are dependent on ontogeny and on the relative thickness of parts of the test; because of the conical structure of the pillars, the pustules will generally be larger in the umbilical area or on the elevated rays. Consequently their size is largely ecology-controlled.

Test size

The size of the test is also strongly controlled by environment. However, it cannot be denied that in the course of our succession the test size seems to increase, at least the maximum values do. Larger foraminifera have no well-defined final stage, and therefore this parameter purely described ontogeny. Accordingly, this parameter is placed at the lowermost level in our hierarchy.

IV.4 THE ORIGIN OF THE DISCOCYCLINIDAE

There is no consensus of opinion regarding the taxonomic position of the Discocyclinidae.

Vaughan (1933), Vaughan & Cole (1940, 1948) and Cole (1964) considered *Asterocyclina* and *Discocyclina* as closely related genera of true orbitoidal larger foraminifera.

Galloway (1933) on the other hand placed the genera in his family Cycloclypeidae which had directly evolved from the Camerinidae (= Nummulitidae).

Subsequent authors searched for morphological evidence to split the Discocyclinidae into two groups. On the basis of the configuration of the early chambers of the microspheres of the Discocyclinidae Brönnimann (1945) concluded that *Asterocyclina* and *Discocyclina* were totally unrelated. According to Brönnimann (1945) the former must have had a true orbitoidal origin, and the latter might have derived from a nummilitid ancestor. Brönnimann doubted this link in a later publication, however (Brönnimann, 1951). He proposed two subfamilies, the Orbitoclypeinae and the Discocyclininae; this subdivision was followed by most later authors (Kecskeméti, 1959; Caudri, 1972; Brolsma, 1973; Sirotti, 1978). Caudri (1972) even proposed to raise the Orbitoclypeinae and the Discocyclininae of Brönnimann (1945) to family rank.

The subdivision made by Galloway (1933) has some interesting consequences from an evolutionary point of view. The first Discocyclinidae are found already in the Middle Paleocene (Schweighauser, 1953; Neumann, 1958). The suggestion of a relationship between the Discocyclinidae and the contemporaneous Nummulitidae would imply that the evolution of the Discocyclinidae had been unusually rapid compared to the evolution in other groups of larger foraminifera, for which the rates of evolution are well established (Miogypsinidae, Lepidorbitoididae, Planorbulinellidae, etc.). The entire sequence of nepionic acceleration must have taken place during the early part of the Paleocene, which is an extremely short period indeed.

Alternatively, one might ask which of the many Late Cretaceous larger foraminifera (Van Gorsel, 1978) show a fair resemblance to the Discocyclinidae. At first glance it becomes clear that the Discocyclinidae show the closest resemblance to some of the Upper Cretaceous Lepidorbitoididae. Phylogenetic relations between Lepidorbitoididae and Discocyclinidae have already been suggested by several authors (Douvillé, 1916; Van der Weijden, 1940; Drooger, 1974; Van Gorsel, 1978). Because of the lack of detailed biometrical data however, it has been impossible to draw sound conclusions.

A brief comparison of our data with data for some *Lepidorbitoides* species from the uppermost Cretaceous, mainly after Van Gorsel (1975), is presented below.

Chamber shape in the median layer

Ogival to spatulate equatorial chambers are introduced in the peripheral part of *L. bisambergensis* and subsequently they appear in earlier ontogenetic stages of the younger species *L. minor* and *L. socialis*. *L. socialis* even has hexagonal chambers. In *Asterocyclina* ogival and spatulate to hexagonal chambers are found in the first annuli and the typical rectangular chambers are found in the later ontogenetic stages. In *Discocyclina augustae* spatulate to hexagonal chambers are found in the first annuli only.

Configuration of the embryon and the peri-embryonic chambers

No data are reported on the degree of enclosure in *Lepidorbitoides,* but a fair estimate of R can be made from the sections on the plates of Van Gorsel. In *L. minor* R is approximately 20 (Van Gorsel, 1975, pl. XII, XIII) and in *L. socialis* 30 (Van Gorsel, 1975, pl. XIV, XV). In the group of *A. taramellii* and *A. stella* there is an increase in $\bar{R}$ from approximately 35 to 50. Furthermore, we assumed that a common ancestor of both of our groups of *Asterocyclina* might have had an $\bar{R}$-value of approximately 20.

The $\bar{R}$-values in the extremely flat *D. augustae* are approximately 50 but separate individuals may have much lower R-values. In *D. varians* $\bar{R}$ shows a very wide variation. *D. archiaci* has R-values of 60 to more than 100. In *D.* sp. R-values are 25 or less.

In *L. minor* the number of adauxiliary chambers ranges from 1–3. There is a clear distinction between adauxiliary, spiral and closing chambers. In *L. socialis* the number of adauxiliary chambers ranges from 3 to 15 (Van Gorsel, 1975). Especially in variants with many adauxiliary chambers of equal size these chambers tend to be so close together that the lumen of the closing chambers frequently does not reach the deuteroconchal wall. The number of peri-embryonic chambers thus hardly exceeds the number of the adauxiliary chambers. In *D. augustae* n_{1+2} is 10 or more, which is thus comparable to the number of chambers in *L. socialis.*

In the lower part of the Nizzana Formation we found occasional *Astero-*

cyclina specimens with 3 adauxiliary chambers. Higher in the section it was impossible to distinguish such chambers from the other peri-embryonic chambers. In *D. varians* and *D. archiaci* there are sometimes more than 40 peri-embryonic chambers. In contrast, there are only 10 peri-embryonic chambers in our *D.* sp.

Van Gorsel reported an increase in the $\overline{D}_2/\overline{D}_1$-values from 1.07 in *Helicorbitoides voigti* to 1.6 in *L. minor* and 2.2 in *L. socialis*. The reduced major axis of $\overline{D}_2$-$\overline{D}_1$ is shown for *L. bisambergensis, L. minor* and *L. socialis* (calculated after data of Van Gorsel, 1975) in fig. 56 as well as those of our Disco-

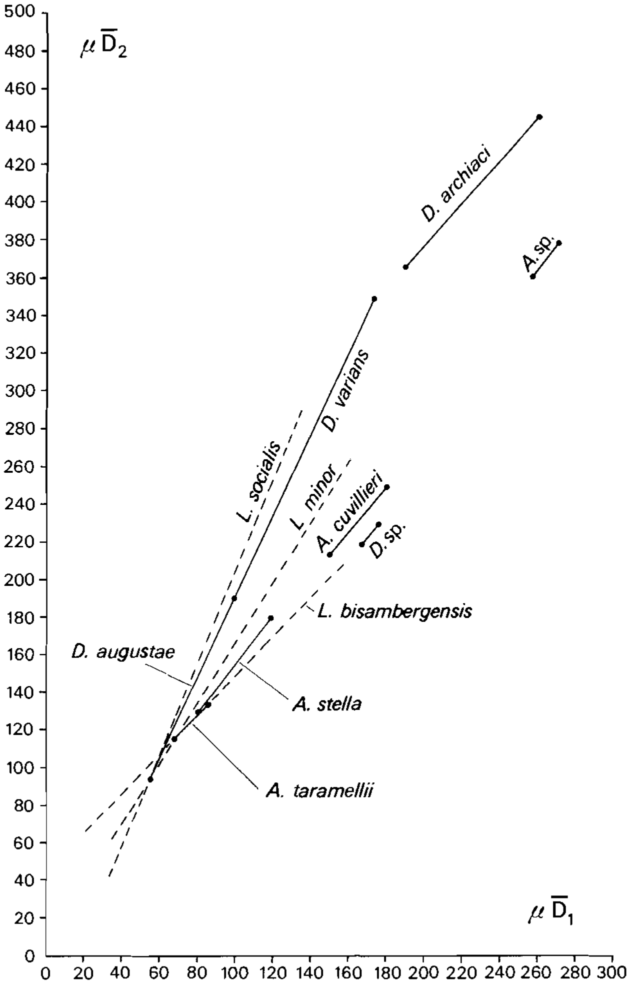


Fig. 56 Reduced major axes of $\overline{D}_2$—$\overline{D}_1$ of our *Discocyclina* and *Asterocyclina* species and of *Lepidorbitoides bisambergensis, L. minor* and *L. socialis* (after data of Van Gorsel, 1975).

cyclinidae taxa. There is a comparable position for the r.m.a. of *L. socialis* and *D. varians* s.l. The r.m.a. of *A. taramellii, A. stella* and *A. cuvillieri* are between the r.m.a. of *L. bisambergensis* and *L. minor.* The r.m.a. of *D.* sp. might belong to the group of *Asterocyclina,* whereas the r.m.a. of *D. archiaci* does not fit into the pattern.

Size of the embryon

In the *Helicorbitoides/Lepidorbitoides* lineage there is an irregular increase in the dimension of the embryon. In *H. voigti* the average mean value for the protoconch and deuteroconch are 75 and 80 μ respectively, in *L. minor* 105 and 170 μ, and in *L. socialis* 110 and 225 μ. In the most "primitive" *A. taramellii* these values are 75 and 120 μ, in *D. augustae* 80 and 120 μ, respectively. The values are much higher for the other Discocylinidae.

Test size

The upper Cretaceous *Helicorbitoides/Lepidorbitoides* lineage shows an increase in the test diameter from 2–3 mm. in *Helicorbitoides* to 5–10 mm. in *L. socialis.* In our material the test dimensions of *Asterocyclina* and *Discocyclina* do not exceed 4 mm.

Thickness of the median layer

According to the papers of Papp and Küpper (1953) and Van Gorsel (1973) *Helicorbitoides voigti* evolved from *Pseudosiderolites vidali;* the latter species has no lateral chambers but only a thick walled rotaliid spiral. In the course of time the rotaliid spiral became reduced in thickness relative to the lateral layers. In *Asterocyclina,* and especially in *Discocyclina,* the median layer is extremely thin, but not much thinner than in the last *Lepidorbitoides* species.

Discussion

Summarizing all these comparisons we can say that there seems to be a fair agreement in structure between *A. taramellii* and *L. minor* on the one hand and between *D. augustae* and *L. socialis* on the other. The chamber shape in the median layer might well be a continuation of the trend for new chamber types to shift from the periphery to earlier ontogenetic stages. The resemblance in the degree of enclosure, in the ratios of the diameters of deuteroconch and protoconch, in the number and structure of the peri-embryonic chambers and in the reduction of the height of the median layer, indicates that there can be little doubt that the Discocyclinidae evolved from the Late Cretaceous *Lepidorbitoides.* The data strongly suggest that *A. taramellii* evolved from *L. minor,* and *D. augustae* from *L. socialis.* If this is the case we have to admit that there was a reduction in protoconch size of approximately

30%, in deuteroconch size of about 30% and in test size of about 50%. In view of the low hierarchical level of these characters none of these changes is thought to be sufficiently important to invalidate our hypothesis.

If we accept the hypothesis that the Discocyclinidae evolved along different lines from *Lepidorbitoides* species two questions immediately arise. The first concerns the mechanism that led to the separation of the *Asterocyclina* and the *Discocyclina* populations. The second is why the Discocyclinidae were the only orbitoidal group that crossed the Cretaceous-Tertiary boundary.

From his detailed investigation of *L. minor* from Maastricht and *L. socialis* from the Aquitaine basin McGillavry (1955, 1959) concluded that there were two independent trends which led to *L. minor* in a northern faunal province and *L. socialis* in a southern faunal province. Contemporaneity of both species was suggested by MacGillavry (1955), and by Drooger (1974) but was doubted by Van Gorsel (1975) who supposed that *L. minor* and *L. socialis* represent successive stages of a single lineage. If our assumption that *A. taramellii* evolved from *L. minor* and *D. augustae* from *L. socialis* is correct, then these Late Cretaceous species must have been contemporaneous. This conclusion supports the view that the populations from Maastricht and from France did indeed belong to different faunal provinces in which the Late Cretaceous evolution proceeded at different rates, unless the internal morphological characters varied along a geographic cline, with the more primitive *L. minor* in the peripheral northern province (compare Dilley, 1973, a, b) and the more advanced *L. socialis* towards the south.

Another point of interest is that *Asterocyclina* has been described from the Paleocene in Italy (Schweighauser, 1953). In the Indian subcontinent it seems to be restricted to the Eocene, especially the Middle and Upper Eocene (Samanta, 1965; Sen Gupta, 1963), although some of the age determinations are doubtful. In America *Asterocyclina* is restricted to the Middle and Upper Eocene (Vaughan, 1945). These data may indicate that *Asterocyclina* migrated from the European Boreal faunal province to the Mediterranean area and from there to the Indo Pacific and American faunal provinces, where *Discocyclina* was present already. Furthermore, the oldest European *Discocyclina* is *D. seunesi* from the Aquitaine basin, which is also the type area of *L. socialis*. *D. seunesi* is thought to be closely related to *D. augustae* (Douvillé, 1922; Schweighauser, 1953).

In conclusion we suggest that at least the European Discocyclinidae evolved from *Lepidorbitoides* stocks at the beginning of the Paleocene. The more primitive *L. minor* in the northern boreal province led to *Asterocyclina taramellii* from which in turn *A. cuvillieri* and *Asterophragmina* originated. The

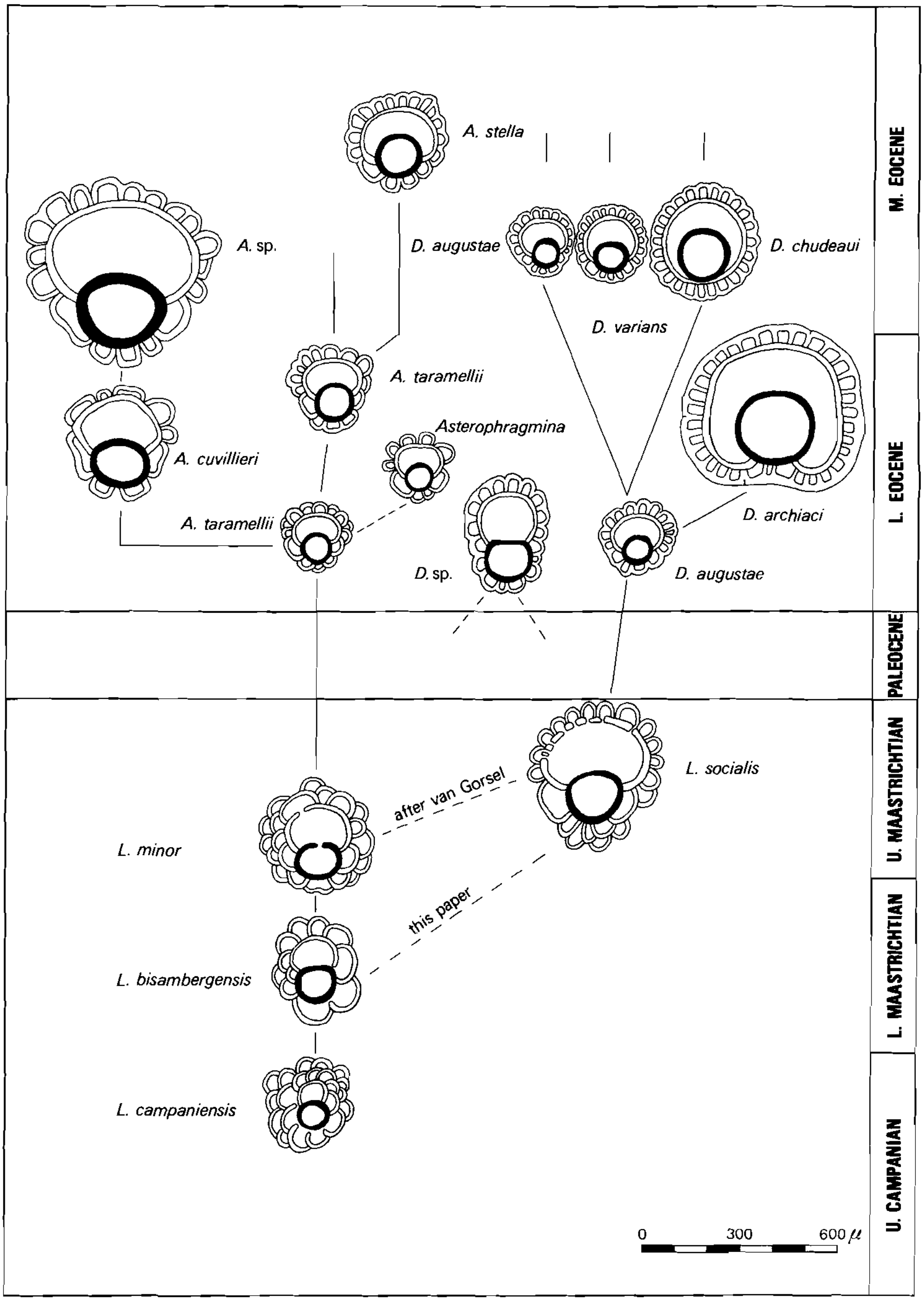


Fig. 57 Reconstruction of the phylogeny of the Discocyclinidae.

more advanced *L. socialis* led to *D. augustae. Lepidorbitoides polygonalis* from the Paleocene of Tibet (Douvillé, 1916) may belong to the group of transitional forms with hexagonal chambers. During the Eocene the morphological variation of *Discocyclina* increased enormously (compare Kecskeméti, 1959; Neumann, 1958; Schweighauser, 1953), leading to a considerable number of new typological species. As *D. archiaci* is more highly evolved than *D. varians* s.l. we suggest that these species originated from *D. augustae.* The phylogenetic position of *D.* sp. remains unclear. Fig. 57 shows a reconstruction of the phylogenetic relations between *Lepidorbitoides*, *Asterocyclina* and *Discocyclina.*

The Cretaceous-Tertiary boundary event affected more taxa than only the larger foraminifera. Other marine biota, such as planktonic foraminifera, corals, calcareous nannoplankton, as well as continental faunas, became extinct or rigorously reduced in diversity. The question of why these taxa became extinct may well be accompanied by the question of what was peculiar about those genera and species which did pass the Cretaceous-Tertiary boundary.

Several authors have mentioned that the Late Cretaceous larger foraminifera had different ecological preferences. Neumann (1958) reported a predominance of *Orbitoides* and *Omphalocyclus* along the southern border of the Aquitaine basin, whereas *Lepidorbitoides* and *Clypeorbis* are most common towards the centre of the basin. Radig (1963) described a predominance of *Orbitoides* and *Omphalocyclus* near the ancient coast in Northern Spain, whereas in the sediments deposited far from this coast *Lepidorbitoides* is more frequent. Van der Velde (1967, fide van Gorsel, 1975) reported *Lepidorbitoides* from fine-grained sediments and *Orbitoides* from coarse-grained sediments. *Orbitoides* is relatively thicker, with thicker walls than *Lepidorbitoides* (Van Gorsel, 1975). These observations led Van Gorsel to the suggestion that the distribution of the larger foraminifera may have been mainly determined by depth; this conclusion is compatible with faunal distribution in Recent environments (Reiss et al., 1977; Muller, 1977). According to Van Gorsel *Orbitoides* and *Omphalocyclus* might have lived at shallower depths, whereas *Lepidorbitoides* and *Clypeorbis* inhabited the deeper parts of the photic zone, with a large overlap in the range between the shallow and deep living species.

Amongst the Discocyclinidae of Ein Avedat there also seem to be depth relations, i.e. relatively thick specimens lived in shallower waters, whereas the flatter types preferred deeper habitats. If our conclusion that *Discocyclina* evolved from *Lepidorbitoides* is correct, then it becomes interesting to note that it evolved from a deeper living taxon. The primitive *Discocyclina* types which show the greatest resemblance to *L. socialis* are *D. hexagonalis* (Douvillé, 1916) and *D. augustae,* which are both extremely flat species. In this context it is also interesting to note that the oldest European species, *D. seunesi,* which is closely related (if not identical) to *D. augustae,* has been described from the central part of the Aquitaine basin (Neumann, 1958). Such flat types of *Discocyclina* must have lived in the deepest part of the photic zone. Although we lack data concerning the ecological preferences of other Upper Cretaceous larger foraminifera, the "species" or possibly rather the subpopulations that passed the Cretaceous-Tertiary boundary must have inhabited the deepest part of the photic zone.

It has already been suggested that *Asterocyclina* evolved from *Lepidorbitoides* of the Boreal realm, which is a peripheral province (Dilley, 1973, a, b) relative to the other Late Cretaceous larger foraminifera fauna provinces.

If all our supposed links are true, then the conclusion might tentatively be drawn that only peripheral populations of larger foraminifera from the Late Cretaceous passed the Cretaceous-Tertiary boundary. Peripheral here means peripheral with respect to depth and latitude.

Larger foraminifera depend on symbionts. Species are extremely specialized with respect to their symbiont flora (Lee, Reimer & McEnery, 1980; Lee, McEnery, Kahn & Schuster, 1978; for references see W. A. Muller, 1975, 1980). Most of the species investigated hitherto contain specific compositions of bacteria, algae, diatoms and zooxanthellae. On the other hand, as we know from biology, different species have different foraging tactics (Pianka, 1978). In peripheral parts of communities where the food supply is less, species must be less specialized in order to maintain themselves. Although no direct observations are available on differences in the foraging strategies of populations of larger foraminiferal species we assume that larger foraminifera are no exception to this rule.

If we apply the statements made above to the Discocyclinidae, then one might surmise that the Late Cretaceous larger foraminifera which became extinct were mainly the shallow living, highly specialized forms, whereas the parts of the deeper living *L. socialis* and the northernmost *L. minor,* which were supposedly less specialized, survived.

We would therefore suggest that, whatever happened at the Cretaceous-Tertiary boundary, it must have entailed a subtle biological process which affected the basal part of the food chain in almost the entire photic zone. This led to the extinction of the highly nutrient-specialized species (fig. 58).

The resulting ecological vacuum at the beginning of the Tertiary allowed a worldwide radiation of the Discocyclinidae which acquired several new features (e.g. rays), whereas other features like the embryonic enclosure, the introduction of new chamber types and the reduction of the height of the median layer evolved at different rates of evolution in different branches.

The reduction in the diameter of the embryon from *Lepidorbitoides* to the Discocyclinidae is another interesting conclusion that can be drawn from our hypothesis. Significant changes in the size of the embryon are known from Recent as well as from fossil larger foraminifera. In the case of the *Lepidorbitoides*-Discocyclinidae transition, species (or rather populations) with small-sized embryons were the only ones that survived. It is hypothesized that the size of the embryon is some kind of a measure for the degree of specialization. The supposed relation between embryon size and degree of specialization may be reflected in two essentially different time/space-bound patterns.

If a species – or a population – becomes less adapted to its environment we may distinguish two possible causes, either time-bound or space-bound. In the first case an unfavourable change of habitat in situ causes a reduction in embryon size. An example may be the reduction of the embryon size of

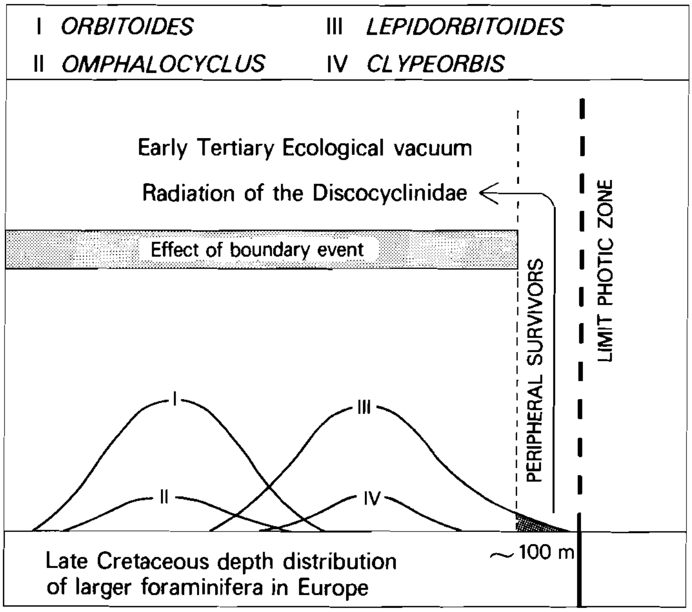


Fig. 58 Late Cretaceous depth distribution of orbitoidal larger foraminifera. The Cretaceous Tertiary boundary event destroyed most of the existing larger foraminifera. Only peripheral stocks – presumably the least specialized – survived. Only depth is indicated, but latitude is thought to show a similar pattern. The Early Tertiary ecological vacuum became filled by a radiation of the Discocyclinidae.

A. stella before its complete disappearance in unit VIII of the section of Ein Avedat. In the second case a species has migrated to a new environment where less suitable conditions appear to prevail. An example may be found in the distribution of Recent *Heterostegina* in the Indopacific and the Mediterranean. Recent *Heterostegina* are known in the Mediterranean off the Lebanon coast; they are closely related to the Indopacific *Heterostegina* species (Hottinger, 1977, b). The Mediterranean *Heterostegina* has a very small embryon relative to its Indopacific relatives. The only migration route seems to be from the Indopacific through the recent Suez-Canal; this makes this species of peculiar interest for future research.

If a species – or a population – becomes better adapted to its environment we may equally well distinguish two possibilities. The first is that changes of environment in situ produce new potential niches to which the species appears to be well adapted, with a subsequent increase of the embryon and genetic isolation from the parental stock. The other possibility is that the species migrates to new areas with better conditions. These areas are not necessarily depth- or latitude-bound, but may be characterized by different substrates or vegetation or even different food compositions. Here it may become adapted to these better conditions, which again may be reflected in an increase of the embryon size.

Examples of either of these mechanisms may be the descent of *A. cuvillieri* from *A. taramellii* or the radiation of several *Discocyclina* "species" with different embryon dimensions from a "primitive" *D. augustae.* Similar explanations may be offered for the origin of *Planorbulinella larvata* with a large embryon in the Recent environment of the Gulf of Elat from the *P. elatensis* stock which has a small embryon (Thomas, 1977).

However, it should be realized that in the case of our Ein Avedat study the real patterns in space and time cannot be deduced, because in our single section environmental differences and time are intrinsically interwoven.

Chapter IV

TAXONOMY

The twofold subdivision of the Discocyclinidae by Brönnimann (1945) was based on the structure of the nepiont of the microspheric generation. For the group of *Asterocyclina* Brönnimann chose *Orbitoclypeus* as the type genus, the type species of which, *Orbitoclypeus himerensis* Silvestri, however, turned out to be a *Discocyclina* species. Brönnimann remarked in 1951 that this (sub)family might be referred to as Asterocyclinidae, a suggestion which was not followed by subsequent authors (Kecskeméti, 1959; Schweighauser, 1953; Caudri, 1972; Brolsma, 1973; Sirotti, 1978).

As there is evidence, in our opinion, that *Asterocyclina* evolved from the Late Cretaceous *L. minor* via *A. taramellii* and *Discocyclina* from the Late Cretaceous *L. socialis* via *D. augustae* it would be possible to unite the Lepidorbitoididae (sensu Van Gorsel, 1978) and the Discocyclinidae into one natural family. We refrained from doing this for practical reasons and we shall continue to consider the Asterocyclininae and the Discocyclininae as two subfamilies that descended independentely from the Late Cretaceous *L. minor* and *L. socialis* respectively.

Further studies may eventually necessitate a revision of the American Discocyclinidae, which have obsolete or degenerate radial walls just like our *Asterophragmina.*

FAMILY DISOCYCLINIDAE

Subfamily Asterocyclininae

Genus **Asterocyclina** Gümbel, 1870
(type species *Asterodiscus pentagonalis* Schafhäutl, 1863)

Asterocyclina taramellii Munier Chalmas
(plate 4, figs. 1–6; plate 11, figs. 1–3)

Orthophragmina taramellii Munier Chalmas, 1904 in: Schlumberger 1904, Bull. Soc. Géol. France, sér. 4, 4, p. 131, pl. 6, figs. 41–46, 51–57.

Orthocyclina soeroeanensis van der Vlerk, 1923, Geol. Mijnb. Genootsch. Nederl. Kol., Geol. ser., 7, p. 93, pl. 1, fig. 1.

Asterocyclina taramellii (Munier Chalmas), Schweighauser, 1953, Schweiz. Pal. Abh. 70, p. 88–90, pl. 13, figs. 3, 11, text fig. 58.

Asterocyclina taramellii (Munier Chalmas), Neumann, 1958, Mém. Soc. Géol. France, 83, p. 118–119, pl. 28, figs. 7–10, pl. 29, figs. 1, 2, text fig. 39.

Diagnosis

The embryon is of the nephrodiscodine type. $\bar{R}$ is 40 or less. The mean diameter of the protoconch ranges from 60–100 μ, that of the deuteroconch from 100–160 μ. Amongst the peri-embryonic chambers three adauxiliary chambers are sometimes recognized.

Remarks

The species differs from *A. cuvillieri* in the larger degree of enclosure and the smaller size of the embryon. It differs from *A. stella* mainly in the smaller degree of enclosure.

A. taramellii is the oldest species of *Asterocyclina* reported in Europe, i.e. from the Middle Paleocene up to the Priabonian.

A. taramellii shows a fair resemblance to the Late Cretaceous *Lepidorbitoides minor*, from which it possibly derived. *A. taramellii* is considered to be the most primitive *Asterocyclina* from which other *Asterocyclina* and *Asterophragmina* stocks have branched off.

In our material the habitat of *A. taramellii* is preferentially the upper foreslope. It is possibly epiphytic, but populations may have lived at considerable depths towards the lower limits of the photic zone.

Asterocyclina stella (Gümbel)
(plate 5, figs. 1–6)

Orbitoides (Asterocyclina) stella Gümbel, 1868, Abh. K. Bay. Ak. Wiss. II, Cl. 10, 2, p. 138, pl. 2, 4.

Discocyclina (Discocyclina) stella (Gümbel), Van der Weijden, 1940, p. 50, pl. 8, figs. 1–4.

Asterocyclina stella (Gümbel), Schweighauser, 1953, Schweiz. Pal. Abh., 70, p. 90–91, pl. 13, figs. 6, 8.

Asterodiscus stella (Gümbel), Neumann, 1958, Mém. Soc. Géol. France, 83, p. 112–114, pl. 28, figs. 1–6, text fig. 36.

Diagnosis

The embryon is of the nephrodiscodine type. $\bar{R}$ is 40 or more. The mean diameter of the protoconch ranges from 80–120 μ; that of the deuteroconch from 120–180 μ.

Remarks

A. stella differs from *A. taramellii* in the larger degree of enclosure of the embryonic chambers. It is generally impossible to differentiate the peri-embryonic chambers into adauxiliary chambers, spiral chambers and closing chambers. The embryon is generally somewhat larger than that of *A. taramellii*, although there is a large overlap in the size of the embryons of the two species.

In the literature the separation between *A. stella*, *A. stellaris* and *A. stellata* is based mainly on outer morphological characters. It seems premature to define species limits based on R̄-values for *A. stella* before biometrical studies have been carried out on topotype material and on other *Asterocyclina* taxa like the species mentioned and species such as *A. mariannensis* (Cushman) and *A. furcata* (Rütimeyer). The latter two species seem to have an eudiscodine embryon configuration (Vaughan, 1945; Sirotti, 1978) and are thought to be typical for the Upper Eocene.

On the basis of our data it is assumed that *A. stella* flourished in an upper foreslope environment.

Asterocyclina cuvillieri (Neumann)
(plate 6, figs. 1–6)

Orthophragmina sp. Schlumberger, 1904, Bull. Soc. Géol. France, sér. 4,4, p. 133, pl. 3, fig. 8.
Asterodiscus cuvillieri Neumann 1958, Mém. Soc. Géol. France, 83, p. 119–121, pl. 31, figs. 1–8, pl. 32, fig. 5, text fig. 40.

Diagnosis

R̄ is 25 or less. The mean diameter of the protoconch ranges from 150 to 180 μ, that of the deuteroconch from 200 to 250 μ.

Remarks

This species has usually been included in other species. It is different from *A. taramellii* and *A. stella* because of its low degree of embryonic enclosure and the relatively large size of the embryon.

Comparison with the data of Neumann (1958) shows that our specimens generally have a somewhat smaller embryon. However there is good agreement with respect to the degree of embracement and the number of periembryonic chambers.

In our opinion *A. cuvillieri* either evolved from *A. taramellii*, or *A. taramellii* and *A. cuvillieri* had a Late Cretaceous ancestor in common, namely *Lepidorbitoides minor*.

Little is known about the habitat of this species. The fact that it is only found in the lower part of the Nizzana Formation may suggest that it has a relation with the autochthonous sediments, i.e. that it was a deeper living form.

Asterocyclina sp.
(plate 7 figs. 1–2)

Diagnosis

R̄ is larger than 25. The diameter of the protoconch is larger than 250 μ, that of the deuteroconch is larger than 350 μ.

Remarks

The two specimens found have a giant embryon. The scanty data do not allow for the definition of a new species. *Asterocyclina* sp. differs from *A. cuvillieri* in its higher degree of enclosure and the larger size of the embryon.

We suggest that it evolved from *A. cuvillieri.*

Genus **Asterophragmina** Rao, 1942

(type species *Pseudophragmina (Asterophragmina) pagoda* Rao, 1942)

Asterophragmina cf. **A. pagoda** (Rao)

(plate 7, figs. 3–5)

Discocyclina (Asterocyclina) sp. Rao, 1940, Curr. Sci., 9, p. 415–416, fig. 2.
Pseudophragmina (Asterophragmina) pagoda Rao, 1942, Geol. Surv. India, 77, prof. pap. 12, p. 1–17.

Diagnosis

With respect to its outer morphological characters and the structure of the early ontogenetic parts of the test this species is similar to *A. taramellii.* After the development of the normal rectangular chambers in the fourth to sixth annulus the radial walls disappear, leaving very broad annular chambers in the next annuli. In the radial areas the annular walls are considerably thicker.

Remarks

Rao (1942), following the classification of Vaughan & Cole (1940), considered his forms to be intermediate between *Asterocyclina* and *Athecocyclina* because of the combined occurrence of radiating costae (typical for *Asterocyclina*) and degenerate or obsolete radial septa (typical for *Athecocyclina*). This led him to the designation of the new subgenus *Pseudophragmina* (*Asterophragmina*). This subdivision was followed by most subsequent authors (Vaughan, 1945; Caudri, 1972). Our *Asterophragmina* specimens suggest a close relation with *Asterocyclina taramellii.* We consider our *Asterophragmina* to have derived from *A. taramellii.* In *Asterophragmina* the rectangular chamber type is followed by broad annular chambers. If this sequence of chamber types is confirmed by further investigations, then several genera of the American Discocyclinidae may be linked to the European genera in a natural order.

Since Rao based his species on microspheric specimens only, we apply a confer determination to our megalospheric individuals.

Subfamily Discocyclininae

Genus **Discocyclina** Gümbel, 1870

(type species: *Orbitolites pratti* Michelin, 1846)

Discocyclina varians (Kaufmann)
(plate 9, figs. 1–6, plate 10 figs. 1–4, plate 11, figs. 6–9)

Orbitoides varians Kaufmann, 1867, Beitr. Geol. Karte Schweiz, 5, p. 158, pl. 10, figs. 3, 5.
Orbitoides aspera Gümbel, 1868, Abh. K. Bay, Akad. Wiss., 10 (2), p. 298, pl. 3, figs. 13, 14, 32.
Orbitoides (Rhipidocyclina) nummulitica Gümbel, 1868, Abh. K. Bay. Akad. Wiss., 10 (2), p. 124, pl. 4, figs. 1–3, 16–18.
Orthophragmina chudeaui Schlumberger, 1903, Bull. Soc. Géol. Fr., sér. 4, 3, p. 282, fig. E, p. 283, pl. 9, figs. 18–20.
Orthophragmina douvillei Schlumberger, 1903, Bull. Soc. Géol. Fr., sér. 4, 3, p. 283, pl. 9, figs. 21–24.
Discocyclina varians (Kaufmann), Van der Weijden, 1940, p. 58, 59, pl. 10, figs. 1–5. Schweighauser, 1953, Schweiz. Pal. Abh. 70, p. 7 71–73, pl. 11, figs. 1, 4, 9, 12, pl. 12, fig. 6, text fig. 35, 52.
Discocyclina nummulitica (Gümbel), Van der Weijden, 1940, p. 35–37, pl. 4, figs. 4–6, 8. Neumann, 1958, Mém. Soc. Géol. France, 83, p. 99–100, pl. 18, figs. 1–7, pl. 25, fig. 5.
Discocyclina andrusovi de Cizancourt, Schweighauser, 1953, Schweiz. Pal. Abh. 70, p. 77–78, pl. 10, figs. 3, 6, 7, text figs. 17, 54.
Discocyclina seunesi Neumann, 1958 (not Douvillé 1922), Mém. Soc. Géol. France, 83, p. 109, 110, pl. 23, figs. 1–7, pl. 25, figs. 1–2, text fig. 34.

Diagnosis

The test shows an extreme variation in relative thickness. $\bar{R}$ ranges from 40 to 105. The mean diameter of the protoconch ranges from 90–175 μ, that of the deuteroconch from 180–350 μ.

Remarks

Because of the gliding variation observed in our samples we lumped in this group a considerable number of the typological species of the literature. Generally the types observed in our samples are somewhat smaller than those described in the literature.

We included *D. augustae* in *D. varians* s.l. in the samples with a continuous variation from *D. augustae* to *D. varians*. The morphological range in relative thickness of the test of these two extreme types is covered by *D. seunesi* Neumann 1958 (not Douvillé 1922). According to the original description of *D. seunesi* (Douvillé, 1922) it is an extremely flat species which shows resemblance to our *D. augustae*, with a degree of enclosure ranging from nephrodiscodine to eudiscodine, however.

D. varians differs from *D.* sp. in its higher degree of embryonic enclosure. It differs from *D. archiaci* in its relatively thicker test and its generally lower degree of enclosure. Because of the overlap in the ranges of these two characters of both species the determination of separate individuals is sometimes impossible.

D. varians inhabits the upper parts of the photic zone. The size of the embryon seems to be depth-dependent.

Discocyclina augustae van der Weijden
(plate 8, figs. 1–4)

Discocyclina (Discocyclina) augustae van der Weijden, 1940, p. 23–26, pl. 1, figs. 4–8, pl. 2, figs. 1–2.

Discocyclina augustae van der Weijden, Schweighauser, 1953, Schweiz. Pal. Abh., 70, p. 49–51, pl. 8, figs. 1–3, pl. 13, fig. 4.

Discocyclina augustae van der Weijden, Brolsma, 1973, Proc. Kon. Ned. Akad. Wet., Ser. B, 76, p. 417–418, pl. 1, figs. 5, 6, pl. 2, figs. 3–5.

Discocyclina applanata (Gümbel), Sirotti, 1978, Boll. Soc. Pal. Italiana, 17, p. 53–54, pl. 1, figs. 1–5.

Diagnosis

The test is extremely flat. The embryon has a nephrodiscodine configuration. The mean diameter of the protoconch does not exceed 100 μ, that of the deuteroconch ranges from 100 to 185 μ.

Remarks

This species differs from *D. varians* in its generally lower degree of enclosure of the embryonic chambers, its smaller embryon dimensions and its extremely thin test. In samples with a continuous morphological variation between *D. varians* and *D. augustae* types, those of *D. augustae* are included in *D. varians* s.l.

The species differs from *D. archiaci* in its much smaller embryon and in the lower degree of enclosure. It can be easily distinguished from *D.* sp. by its low number of lateral chambers surrounding the pustules.

This species has been known since the nineteenth century, but it was commonly included in other species like *D. applanata* (Gümbel), *D. papyracea* (Boubée) and *D. pratti* (Michelin) because of different taxonomic concepts. Van der Weijden (1940) was the first to give a detailed description that emphasized the embryonic structure.

D. augustae is related to the Late Cretaceous *Lepidorbitoides socialis* and we suggest that it was one of the founders of the Discocyclinidae, the immediate ancestor of which passed the Cretaceous-Tertiary boundary.

D. augustae types are known from the Lower Eocene (Neumann, 1958; Brolsma, 1973) to the Upper Eocene (Van der Weijden, 1940; Sirotti, 1978). This species has not yet been recorded from the Paleocene. However, Douvillé (1922) and Neumann (1958) reported from the Paleocene of the Aquitaine Basin in Southern France a paper-thin *Discocyclina seunesi* which is almost identical to *D. augustae* (see also Schweighauser, 1953).

Discocyclina archiaci (Schlumberger)
(plate 10, figs. 5, 6)

Orthophragmina archiaci Schlumberger, 1903, Bull. Soc. Géol. France, sér. 4,3, p. 277, pl. 8, figs. 5–7, 11, tf. c.

Discocyclina archiaci (Schlumberger), Schweighauser, 1953, Schweiz. Pal. Abh., 70, p. 57–60, pl. 10, figs. 1, 2, 5, 11, text figs. 13, 24, 25, 36.

Discocyclina archiaci (Schlumberger), Kecskeméti, 1959, Ann. Hist.-nat. Mus. Nat. Hungarici, 51, p. 49, 50, pl. 3, figs. 1, 2, 4, text fig. 12.

Discocyclina archiaci (Schlumberger), Brolsma, 1973, Proc. Kon. Ned. Akad. Wet., Ser. B, 76, p. 418. 419, pl. 1, figs. 1–4.

Diagnosis

The embryon configuration ranges from nephrodiscodine to eudiscodine with $\bar{R}$-values from 60 to 100 μ or more. The mean diameter of the protoconch ranges from 190–250 μ, that of the deuteroconch from 380–440 μ.

Remarks

D. archiaci differs from our *D.* sp. because of its smaller number of lateral chambers around the pustules (5–8) at the surface and in its embryon configuration, which is of the isodiscodine type in *D.* sp., whereas in *D. archiaci* the embryon enclosure is invariably high. The discrimination between *D. archiaci* and *D. varians* is more difficult. Flat representatives of *D. varians* (i.e. *D. augustae*) have a much lower degree of enclosure. The inner morphology of thick representatives of *D. varians* resembles that of *D. archiaci.* Such thick types are distinguished by their umbilical swell covered by relatively large pustules. In juvenile specimens it is sometimes difficult or even impossible to decide whether such specimens belong to *D. varians* or to *D. archiaci.*

No indications are found that the occurrence or the morphology of *D. archiaci* is depth-controlled.

Discocyclina sp.
(plate 8, figs. 5, 6)

Diagnosis

The embryon is of the isodiscodine type with $\bar{R}$-values of 25 or less. The diameter of the protoconch is about 175 μ, that of the deuteroconch approximately 220 μ.

Remarks

This species is easily recognized because of the high number (10–14) of lateral chambers surrounding the pustules and because of its isodiscodine embryon configuration. Douvillé (1922) already recognized an informal group of *Discocyclina* species with a high number of lateral chambers around the pustules, and most subsequent authors considered this as an important characteristic (compare Douvillé, 1922; Schweighauser, 1953; Neumann, 1958; Bieda, 1963). However, our *D.* sp. is different from other representatives of this informal species group because of its low degree of embryonic enclosure and its much smaller embryon. Species of this group are commonly reported from the Middle to Upper Eocene, e.g. *D. scalaris, D. discus* (Van der Weijden, 1940; Schweighauser, 1953; Neumann, 1958). If the species grouping according to the structure of the lateral chambers turns out to be correct, then the data suggest that we might be dealing with a separate lineage from *D.* sp. to *D. discus.*

In our material *D.* sp. specimens are found only in the lower part of the Nizzana Formation. *D.* sp. seems to belong to the deeper living groups because it was not found in the allochthonous assemblage of this part of the section.

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TABLES

sample	$\bar{A}$	se	$\bar{B}$	se	$\overline{A/B}$	se	$r_{A,B}$	n
Is 462	0.76	0.022	2.02	0.069	0.39	0.01	0.48	25
Is 452	0.87	0.029	2.12	0.093	0.42	0.01	0.63	25
Is 430	0.86	0.024	2.42	0.085	0.37	0.01	0.69	25
Is 419	0.68	0.027	1.54	0.067	0.45	0.01	0.67	25
Is 413	0.82	0.036	2.08	0.091	0.41	0.02	0.71	25
Is 407	0.76	0.019	1.89	0.091	0.41	0.02	0.42	25
Is 402	0.77	0.031	2.20	0.093	0.35	0.01	0.56	25
Is 399	0.77	0.034	2.02	0.093	0.39	0.01	0.73	25
Is 377	0.70	0.034	1.51	0.084	0.47	0.02	0.63	25
Is 375	0.81	0.029	1.78	0.071	0.46	0.02	0.34	25
Is 366	0.86	0.027	1.75	0.074	0.50	0.02	0.62	25
Is 336	0.77	0.034	1.69	0.084	0.46	0.02	0.57	25
Is 335	0.74	0.030	1.44	0.035	0.52	0.02	0.62	25
Is 331	0.72	0.026	1.42	0.043	0.51	0.02	0.08	25
Is 320	0.71	0.031	1.46	0.075	0.48	0.02	0.55	25
Is 317	0.67	0.033	1.32	0.75	0.50	0.02	0.53	25
Is 314	0.72	0.033	1.38	0.059	0.51	0.02	0.34	25
Is 308	0.66	0.024	1.36	0.036	0.48	0.02	0.34	25
Is 303	0.76	0.022	1.37	0.073	0.56	0.02	0.40	10
Is 297	0.67	0.027	1.38	0.048	0.50	0.02	0.61	25
Is 294	0.60	0.024	1.27	0.044	0.46	0.01	0.42	25
Is 291	0.56	0.024	1.18	0.090	0.48	0.03	0.62	5
Is 282	0.74	0.039	1.50	0.078	0.49	0.02	0.80	17
Is 278	0.61	0.023	1.34	0.078	0.46	0.02	0.52	29
Is 276	0.71	0.028	2.14	0.150	0.35	0.02	0.19	23
Is 273	0.57	0.027	1.46	0.079	0.39	0.02	0.65	30
Is 259	0.60	0.082	1.35	0.170	0.45	0.04	0.72	4
Is 254	0.58	0.012	1.10	0.100	0.54	0.11	0.69	3
Is 226	0.74	0.036	1.34	0.056	0.56	0.04	0.23	11
Is 221	0.72	0.021	1.41	0.066	0.51	0.02	0.30	30

table 1
Means, standard errors and sample sizes of the outer morphological parameters of <u>Asterocyclina</u> and the correlation coefficients for A - B.

class B mm	$\bar{A}$	se	$\bar{B}$	se	$\overline{A/B}$	se	n
0.5 - 0.8	0.367	0.033	0.767	0.033	0.476	0.027	3
0.9 - 1.2	0.580	0.012	1.114	0.010	0.496	0.010	109
1.3 - 1.6	0.696	0.008	1.432	0.007	0.485	0.005	274
1.7 - 2.0	0.775	0.012	1.865	0.009	0.421	0.008	151
2.1 - 2.4	0.851	0.012	2.245	0.014	0.373	0.020	70
2.5 - 2.8	0.874	0.025	2.597	0.018	0.347	0.021	39
2.9 - 3.2	1.000	0.055	3.070	0.027	0.330	0.018	10
3.3 - 3.6	0.917	0.096	3.475	0.025	0.263	0.105	6
0.5 - 3.6	0.728	0.004	1.668	0.019	0.436	-	662

table 2
Means, standard errors and sample sizes of the outer morphological parameters of <u>Asterocyclina</u> for each class B, and for all data together.

sample	$\overline{R}$	se	n	$\overline{n_2}$	se	n	$\overline{n_{1+2}}$	se	n	$\overline{H_1}$	se	n	$\overline{H_2}$	se	n	$\overline{H_c}$	se	n	$\overline{D_1}$	se	n	$\overline{D_2}$	se	n	$\overline{r}$	se	n
Is 462	49	1.5	22	14.0	0.36	22	16.3	0.40	22	99.5	2.25	22	160.9	3.12	22	34.5	1.23	22	106.6	2.24	22	165.2	2.89	22	5.2	0.11	25
Is 452	53	1.5	30	12.7	0.31	30	14.8	0.30	30	100.8	2.21	30	162.7	2.89	30	36.7	1.15	30	107.5	2.61	30	170.2	4.36	30	5.0	0.03	30
Is 430	50	1.3	21	12.8	0.26	20	15.3	0.26	20	91.8	2.33	22	148.5	3.24	23	31.6	1.29	22	96.3	2.38	23	150.4	3.21	23	5.1	0.12	20
Is 423	51	3.5	10	13.5	0.40	10	16.0	0.47	10	97.5	2.80	10	160.0	4.40	10	38.5	2.78	10	108.0	4.25	10	166.0	5.25	10	5.0	0.00	10
Is 419	51	1.0	25	13.3	0.22	25	16.0	0.26	25	111.0	2.54	25	170.8	3.44	25	35.0	0.95	25	118.4	2.62	25	177.4	3.26	25	5.0	0.04	25
Is 413	53	1.0	25	13.4	0.32	25	15.9	0.37	25	102.6	2.21	25	165.8	3.27	25	35.2	1.05	25	109.4	2.42	25	168.8	3.46	25	5.1	0.05	24
Is 407	54	1.9	22	12.6	0.46	20	14.9	0.40	20	95.2	2.40	22	152.0	3.01	23	35.2	1.10	21	100.0	1.91	23	158.9	3.51	23	5.0	0.09	20
Is 402	54	1.5	23	13.7	0.23	23	16.2	0.34	20	93.8	2.06	24	151.4	2.17	25	35.2	1.21	24	97.6	2.06	25	154.6	2.44	25	5.1	0.09	24
Is 399	54	1.0	28	12.7	0.30	29	14.8	0.33	29	90.8	1.92	29	147.9	2.40	29	32.8	0.95	29	97.8	2.03	29	150.9	2.80	29	5.1	0.07	28
Is 377	52	1.4	24	12.0	0.31	25	14.0	0.37	24	87.8	2.04	25	141.6	2.64	25	32.0	0.91	25	92.2	2.04	25	145.6	3.37	25	5.0	0.05	25
Is 375	51	1.7	22	12.7	0.37	23	15.0	0.52	22	80.4	1.84	25	133.4	2.30	25	29.6	1.47	24	87.2	2.34	25	138.8	2.48	25	5.0	0.09	25
Is 374	47	1.5	20	12.3	0.28	18	14.6	0.36	18	78.8	1.73	20	128.3	1.71	20	30.5	1.00	19	84.8	2.06	20	131.3	2.50	20	5.1	0.05	19
Is 366	51	1.7	21	11.8	0.25	20	13.9	0.40	17	72.6	1.91	23	125.0	2.47	23	27.8	0.98	20	78.7	2.45	23	132.7	2.58	22	5.1	0.10	18
Is 336	40	1.6	24	11.6	0.32	20	14.3	0.37	19	74.8	2.47	25	131.6	2.79	25	28.8	1.08	21	82.4	2.31	25	131.2	3.28	25	5.0	0.00	25
Is 335	37	1.6	25	11.0	0.24	24	14.3	0.29	23	73.6	2.11	25	134.4	2.45	25	28.0	0.76	25	82.2	2.08	25	126.2	2.20	25	4.7	0.09	24
Is 331	40	1.0	26	11.2	0.31	25	14.4	0.34	25	75.6	1.69	26	129.0	2.58	26	26.9	0.98	24	84.4	2.02	26	128.6	2.26	26	5.0	0.04	23
Is 317	40	1.4	26	10.6	0.29	21	13.6	0.40	20	79.2	1.53	26	133.7	2.59	26	27.3	0.99	24	85.6	1.94	26	133.5	2.39	26	5.1	0.06	27
Is 308	37	1.5	27	9.8	0.37	25	13.0	0.41	24	75.2	1.80	28	129.3	2.79	28	25.4	0.82	26	81.8	1.91	28	128.6	3.17	28	5.2	0.08	26
Is 303	38	1.2	25	9.6	0.26	23	12.2	0.32	23	75.8	1.65	26	133.1	2.28	26	28.4	1.34	25	85.0	1.84	26	128.8	2.12	25	5.1	0.05	19
Is 294	37	1.4	25	8.3	0.24	23	11.0	0.27	22	74.0	1.44	25	127.8	2.95	25	25.0	0.89	23	82.6	2.21	25	126.0	2.56	25	5.1	0.08	24
Is 282	39	2.1	15	9.2	0.39	15	12.2	0.36	14	71.9	2.23	16	125.9	2.33	16	25.3	1.58	15	79.7	3.03	16	124.1	2.58	16	5.0	0.00	16
Is 278	34	0.8	15	8.9	0.43	12	11.5	0.59	12	66.0	2.01	15	112.6	2.52	15	23.5	1.04	13	68.7	2.69	15	110.6	2.00	15	5.2	0.23	11
Is 276	35	1.3	40	10.6	0.22	36	13.4	0.22	36	66.4	1.36	40	125.8	1.28	41	25.5	0.60	36	71.5	1.36	41	118.6	1.70	41	6.3	0.16	37
Is 273	35	1.2	27	9.1	0.24	24	11.8	0.35	24	67.0	1.51	27	119.6	2.27	27	24.1	0.80	27	72.9	1.86	28	118.1	1.70	27	5.3	0.15	25
Is 259	35	1.8	15	10.8	0.33	14	13.4	0.27	14	69.0	1.30	15	127.3	2.48	15	25.0	1.19	15	72.3	2.05	15	123.0	2.66	15	5.2	0.12	13
Is 234	31	1.7	12	11.2	0.26	11	14.4	0.37	9	70.4	2.22	13	128.1	2.30	13	27.1	0.74	12	73.1	2.22	13	123.8	2.77	13	5.7	1.25	3
Is 221	32	0.8	41	11.1	0.25	35	14.2	0.26	35	67.8	1.24	41	130.2	2.26	41	27.1	0.68	39	73.8	1.62	41	120.1	2.07	41	6.2	0.25	26
Is 199	37	2.6	18	11.3	0.35	18	14.2	0.38	18	76.9	2.73	19	140.0	3.52	18	26.7	1.06	18	82.1	2.89	19	129.7	4.74	18	6.6	0.36	15

table 3

Means, standard errors and sample sizes of the internal parameters for *Asterocyclina* of group 1.

Asterocyclina taramellii: Is 199 - Is 336

Asterocyclina stella: Is 366 - Is 462

sample	$\bar{R}$	se	n	$\bar{n}_2$	se	n	$\bar{n}_{1+2}$	se	n	$\bar{H}_1$	se	n	$\bar{H}_2$	se	n	$\bar{H}_c$	se	n	$\bar{D}_1$	se	n	$\bar{D}_2$	se	n	$\bar{r}$	se	n
Is 366	46.0	-	1	17.0	-	1	23.0	-	1	215.0	-	1	405.0	-	1	65.0	-	1	280.0	-	1	440.0	-	1	6.0	-	1
Is 336	37.0	-	1	15.0	-	1	24.0	-	1	205.0	-	1	355.0	-	1	60.0	-	1	265.0	-	1	355.0	-	1	6.0	-	1
Is 278	18.6	2.5	5	6.2	0.7	5	9.2	1.2	5	165.0	9.5	5	291.0	4.5	5	54.0	4.3	5	175.0	14.6	5	249.0	14.1	5	5.5	0.3	4
Is 276	33.5	-	2	10.5	-	2	14.0	-	2	105.0	-	2	192.5	-	2	35.0	-	2	110.0	-	2	180.0	-	2	5.0	-	2
Is 273	26.4	4.0	7	8.0	1.1	5	10.6	1.5	5	133.6	11.3	7	262.9	18.8	7	37.9	3.5	7	162.1	13.2	7	232.1	12.6	7	5.2	0.2	6
Is 234	26.0	-	1	-	-	-	-	-	-	95.0	-	1	200.0	-	1	45.0	-	1	120.0	-	1	180.0	-	1	5.0	-	1
Is 221	22.3	2.4	13	7.6	0.6	11	11.4	1.3	11	122.3	3.9	13	232.4	6.1	13	38.8	2.8	13	157.5	4.6	13	210.8	7.7	13	5.1	0.1	11
Is 199	25.0	-	1	7.0	-	1	11.0	-	1	160.0	-	1	290.0	-	1	30.0	-	1	185.0	-	1	260.0	-	1	5.0	-	1

table 4

Means, standard errors and sample sizes of the internal parameters for *Asterocyclina* of group 2.

Asterocyclina cuvillierri: Is 199 - Is 278

Asterocyclina sp.: Is 336 - Is 366

sample	V before splitting				V after splitting															
	Discocyclina s.l.				*D. varians*				*D. augustae*				*D. archiaci*				*D.* sp.			
	R	n_2	D_1	D_2	R	n_2	D_1	D_2	R	n_2	D_1	D_2	R	n_2	D_1	D_2	R	n_2	D_1	D_2
Is 407	29	9	12	10	26	9	12	10	–	–	–	–	–	–	–	–	–	–	–	–
Is 399	21	12	21	21	19	11	18	15	–	–	–	–	27	25	20	4	–	–	–	–
Is 397	20	14	17	8	20	14	17	8	–	–	–	–	–	–	–	–	–	–	–	–
Is 382	44	35	43	39	22	10	20	15	–	–	–	–	12	15	18	12	–	–	–	–
Is 366	43	18	49	37	20	14	19	19	–	–	–	–	48	14	5	9	–	–	–	–
Is 336	39	32	41	39	31	11	14	16	–	–	–	–	22	20	15	10	–	–	–	–
Is 303	4	29	18	10	4	29	18	10	–	–	–	–	–	–	–	–	–	–	–	–
Is 276	40	29	25	18	8	16	16	15	–	–	–	–	–	–	–	–	67	13	4	6
Is 273	22	19	20	19	22	19	20	19	–	–	–	–	–	–	–	–	–	–	–	–
Is 221	31	30	29	31	20	18	16	12	37	28	17	21	–	–	–	–	–	–	–	–
Is 213	17	9	26	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Is 199	50	37	47	45	20	23	17	15	20	23	28	27	11	9	–	–	–	–	–	–
Is 193	28	27	23	23	17	13	4	6	–	–	–	–	–	–	–	–	–	–	–	–
Is 187	22	30	36	30	–	20	10	18	–	–	–	–	2	13	11	4	–	–	–	–
Is 157	55	11	15	15	55	11	15	15	–	–	–	–	–	–	–	–	–	–	–	–

table 5

Coefficients of variability, V, of several parameters of *Discocyclina* before and after splitting of the samples.

sample	$\bar{R}$	se	n	$\bar{n}_2$	se	n	$\bar{H}_1$	se	n	$\bar{H}_2$	se	n	$\bar{H}_c$	se	n	$\bar{D}_1$	se	n	$\bar{D}_2$	se	n	
Is 407	42.7	3.56	10	19.8	0.53	10	118	4.0	10	249	5.5	10	50.0	2.2	9	135	5.1	10	264	8.2	10	*Discocyclina varians*
Is 399	53.0	1.98	27	20.1	0.42	27	120	3.5	27	274	6.5	27	60.6	2.6	27	128	4.4	27	284	8.0	27	
Is 397	64.2	5.14	6	19.2	1.12	6	117	3.1	6	268	3.6	6	52.5	2.8	6	130	8.8	6	278	8.4	6	
Is 382	39.0	2.31	14	15.5	0.45	11	104	3.2	13	224	6.2	13	40.4	1.5	11	110	5.9	14	205	8.4	14	
Is 374	-	-	-	17.3	-	3	102	-	3	220	-	3	32.5	-	2	113	-	3	233	-	3	
Is 366	40.4	1.92	18	14.8	0.49	18	96	3.4	18	205	8.4	18	38.1	1.8	18	105	4.6	18	190	8.8	18	
Is 336	48.9	5.40	8	17.0	0.66	8	111	6.3	11	248	10.6	11	42.7	3.3	11	113	5.0	10	219	11.4	10	
Is 303	64.4	1.50	3	17.5	2.50	4	104	8.3	5	226	10.5	5	45.0	-	2	113	9.0	5	221	11.5	4	
Is 276	92.7	1.60	20	24.5	0.89	20	138	5.3	21	268	7.3	21	47.9	1.7	21	139	4.9	22	275	9.2	22	
Is 273	91.1	2.44	67	23.4	0.55	67	140	4.6	67	276	6.3	67	53.5	1.2	66	140	3.4	68	281	6.4	68	
Is 259	38.9	-	1	18.0	-	1	90	-	1	185	-	1	30.0	-	1	90	-	1	165	-	1	
Is 221	103.5	4.69	20	30.5	1.20	20	169	5.9	20	317	8.2	20	55.0	2.4	20	175	6.2	20	352	9.3	20	
Is 213	86.5	-	2	24.5	-	2	120	-	2	233	-	2	50.0	-	2	143	-	2	238	-	2	
Is 199	93.1	5.13	13	25.6	1.61	13	128	4.9	17	249	9.8	17	49.2	3.0	13	137	6.0	15	260	10.3	15	
Is 193	72.0	7.00	3	20.7	1.30	4	120	2.9	3	234	12.5	4	30.0	-	3	113	2.5	4	211	5.8	4	
Is 187	79.6	-	4	19.8	2.00	4	108	8.8	4	200	7.1	4	26.7	1.7	3	106	5.5	4	223	19.7	4	
Is 157	60.0	17.80	3	14.3	0.90	3	93	4.3	4	194	7.2	4	26.7	1.7	3	99	7.2	4	181	13.1	4	
Is 221	64.3	8.49	8	17.6	1.73	8	90	7.5	8	187	10.8	8	36.9	4.5	8	101	5.9	8	186	13.8	8	*Discocyclina augustae*
Is 199	37.8	2.25	11	13.0	1.06	8	66	5.9	11	123	5.7	11	30.6	2.9	9	71	6.0	11	127	11.0	10	
Is 193	50.0	-	1	12.0	-	1	50	-	1	100	-	1	20.0	-	1	55	-	1	105	-	1	
Is 399	60.0	8.00	4	23.3	0.60	4	153	4.3	4	370	3.4	4	68.8	1.3	4	195	19.5	4	421	8.3	4	*Discocyclina archiaci*
Is 382	98.8	3.24	14	29.7	1.20	14	235	7.1	14	394	9.0	14	57.9	2.4	14	243	11.6	14	434	14.4	14	
Is 366	68.4	14.74	5	19.8	1.24	5	203	15.0	5	373	17.0	5	55.0	1.0	5	244	5.1	5	404	15.7	5	
Is 336	82.1	6.06	7	27.1	2.08	7	244	14.3	7	400	19.0	7	50.7	3.2	7	239	13.8	7	418	15.4	7	
Is 276	98.0	-	1	28.0	-	1	245	-	1	420	-	1	50.0	-	1	270	-	1	400	-	1	
Is 259	94.4	-	1	42.0	-	1	180	-	1	340	-	1	40.0	-	1	200	-	1	390	-	1	
Is 199	104.5	5.70	4	30.8	1.40	4	211	2.0	4	371	1.3	4	50.0	5.0	5	233	-	4	398	-	4	
Is 187	99.0	0.91	3	30.3	2.30	3	205	7.6	3	348	11.8	3	51.7	10.2	3	212	13.4	3	387	7.0	3	
Is 276	25.3	6.90	6	13.3	0.70	6	143	5.7	6	270	8.0	6	43.0	3.4	5	168	3.0	6	218	5.3	6	*Discocyclina* sp.
Is 199	9.5	-	2	10.0	-	2	148	-	2	307	-	2	35.0	-	2	178	-	2	225	-	2	

table 6

Means, standard errors and sample sizes of the internal parameters of *Discocyclina* species after splitting of the samples.

sample	r_{R-n_2}	n	s	$r_{n_2-D_2}$	n	s	$r_{H_1-H_2}$	n	s	$r_{D_1-D_2}$	n	s	r_{R-D_2}	n	s	
Is 407	0.476	10	0	0.410	10	0	0.780	10	3	0.569	10	1	0.000	10	0	*Discocyclina varians*
Is 399	0.210	27	0	0.676	27	3	0.768	27	3	0.416	27	2	0.415	27	2	
Is 397	0.242	6	0	0.409	6	0	0.911	6	3	0.640	6	0	0.665	6	0	
Is 382	0.692	11	3	0.686	11	2	0.828	13	3	0.598	14	2	0.423	14	0	
Is 374	–	3		–	3		–	3		–	3		–	3		
Is 366	0.248	18	0	0.271	18	0	0.945	18	3	0.903	18	3	0.060	18	0	
Is 336	0.800	8	3	0.393	8	0	0.627	8	1	0.838	10	3	0.690	10	2	
Is 303	–	3		–	3		0.519	5	0	0.760	4	0	–	3		
Is 276	0.309	20	0	0.771	20	3	0.827	20	3	0.723	22	3	0.374	22	1	
Is 273	0.733	67	3	0.640	66	3	0.675	67	3	0.557	68	3	0.269	67	2	
Is 259	–	1		–	1		–	1		–	1		–	1		
Is 221	0.558	20	3	0.605	20	3	0.798	20	3	0.788	20	3	0.195	20	0	
Is 213	–	2		–	2		–	2		–	2		–	2		
Is 199	0.707	13	3	0.595	15	3	0.878	17	3	0.778	15	3	0.449	13	0	
Is 193	–	3			4		–	3		–	3		–	3		
Is 187	–	4		–	4		–	4		–	4		–	4		
Is 157	–	4		–	4		–	4		–	3		–	4		
Is 221	0.915	8	3	0.856	8	3	0.844	8	3	0.874	8	3	0.708	8	2	*Discocyclina augustae*
Is 199	0.742	8	2	0.262	8	0	0.580	11	1	0.932	11	3	0.555	11	1	
Is 193	–	1		–	1		–	1		–	1		–	1		
Is 399	–	4		–	4		–	4		–	4		–	4		*Discocyclina archiaci*
Is 382	0.480	14	1	0.300	14	0	0.679	14	3	0.873	14	3	0.118	14	0	
Is 366	0.725	5	0	0.410	5	0	0.708	5	0	0.951	5	3	0.421	5	0	
Is 336	0.719	7	1	0.356	7	0	0.935	7	3	0.593	7	0	0.679	7	1	
Is 276	–	1		–	1		–	1		–	1		–	1		
Is 259	–	1		–	1		–	1		–	1		–	1		
Is 199	–	4		–	4		–	4		–	4		–	4		
Is 187	–	3		–	3		–	3		–	3		–	3		
Is 276	0.913	6	3	-0.416	6	0	0.845	6	2	0.839	6	2	-0.212	6	0	*Discocyclina* sp.
Is 199	–	2		–	2		–	2		–	2		–	2		

table 7

Correlation matrix of *Discocyclina* for levels of confidence:

s = 0 : p 0.050
s = 1 : p 0.050
s = 2 : p 0.025
s = 3 : p 0.010

Plate 1

Fig. 1	Radiolarian mudstone from unit VIII, sample IS 439 (coll. MF 2–70), X 25.
Fig. 2	Plankton mudstone from unit VIII, sample Is 433 (coll. MF 2–64). The specimens are relatively small, X 25.
Fig. 3	Plankton wackestone from unit VIII, sample Is 444 (coll. MF 2–75). The planktonic specimens are relatively small and accompanied by biserial benthonic foraminifera, X 25.
Fig. 4	Plankton wackestone from unit V, sample Is 325 (coll. MF 1–181). The planktonic specimens are of normal size. The associated benthos is diverse but relatively scarce, X 25.
Fig. 5	Pteropod packstone from unit II, sample IS 181 (coll. MF 1–31). The rock shows silicification which makes recognition of the smaller grains extremely difficult, X 10.
Fig. 6, 7	Fine-grained bioclastic packstones. Fig. 6, sample Is 454 from unit IX (coll. MF 2–85). The matrix consists of microsparitic micrite. Plankton is extremely scarce. Fig. 7, sample Is 358 (coll. MF 1–214) from unit V. Occasional *Pararotalia* specimens are recognizable. Both figures X 25.
Fig. 8	*Pararotalia* packstone from unit V, sample Is 344 (coll. MF 1–200). The benthos in these allochthonous assemblages is almost monotypic. X 25.

plate 1

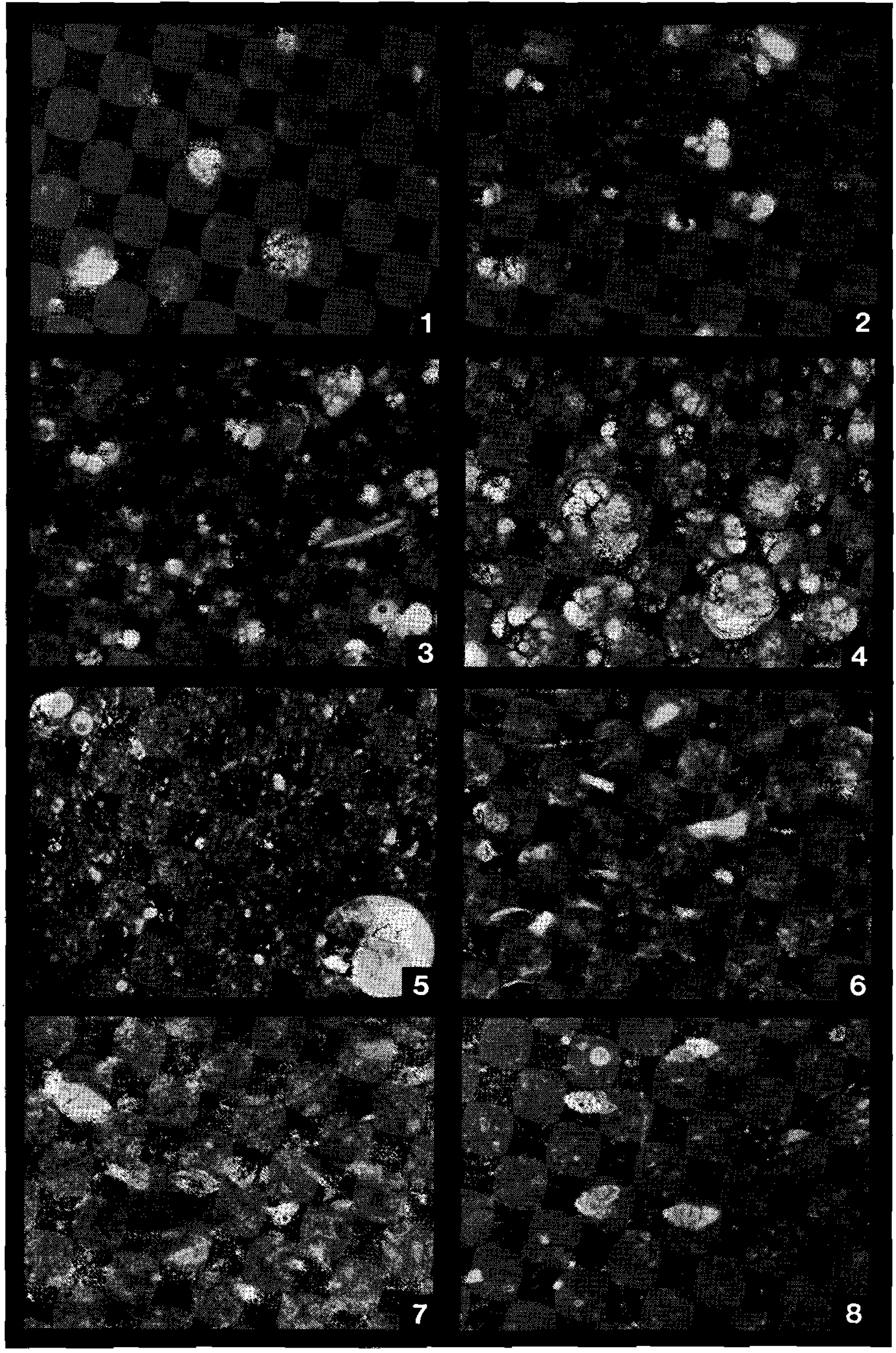


Plate 2

Fig. 1 Larger foraminiferal packstone from the base of unit II, sample Is 201 (coll. MF 1–54). *Asterocyclina* is the most frequent genus, × 25.

Fig. 2 Larger foraminiferal packstone from the top of unit II, sample Is 245 (coll. MF 1–99). *Nummulites* sp. is the major faunal element, × 10.

Fig. 3 Bioclastic floatstone from the top of unit V, sample Is 354 (coll. MF 1–210). The original layering of the autochthonous plankton wackestone and the allochthonous larger foraminiferal packstone has been completely disturbed by subsequent flow of the sediments, × 4.

Fig. 4 Allochthonous larger foraminiferal packstone (lower part) and autochthonous plankton wackestone (upper part) in sample Is 201 (coll. MF 1–54). The fragments of larger foraminifera in the latter have been transported as a result of burrowing, × 10.

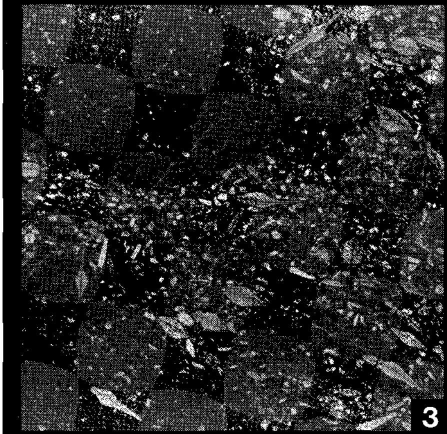
Fig. 5 Rhodolith floatstone from unit VI, sample Is 370 (coll. MF 2–1). In the centre of oncolith there are larger foraminifera as well as *Pararotalia*, × $2\frac{1}{2}$.

Fig. 6 Detail of the rhodolith floatstone of Is 370 with *Archeolithothamnium* and *Lithophyllum* with *Pararotalia* and some fragments of *Asterocyclina*, × 25.

plate 2


1


2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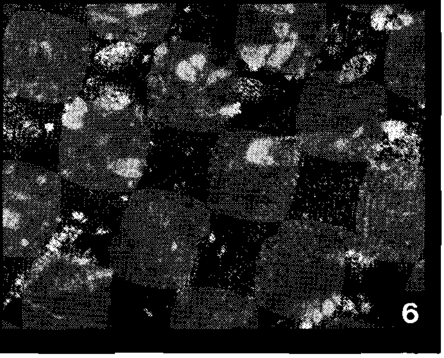
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Plate 3

Figs. 1–4	Morphological variation in *Asterocyclina* from Is 221 in the middle of unit II. The specimens are relatively thick.
Figs. 5, 6	Two extremely large and flat specimens of *Asterocyclina* from Is 276 at the transition of unit III to unit IV.
Figs. 7–10	Morphological variation in *Asterocyclina* from Is 320. The sample is from the base of unit V. The specimens are relatively small and thick.
Figs. 11, 12	*Asterocyclina* specimens of average size and shape in Is 382 from the lower part of unit VII.
Figs. 13, 14	Relatively large and flat specimens of *Asterocyclina* from Is 399 in the middle of unit VII.
Figs. 15–18	Morphological variation in *Asterocyclina* from Is 430. This samples has been taken from the base of unit VIII. The specimens are relatively thick.

The samples are arranged in stratigraphic order. All magnifications X 20.

plate 3

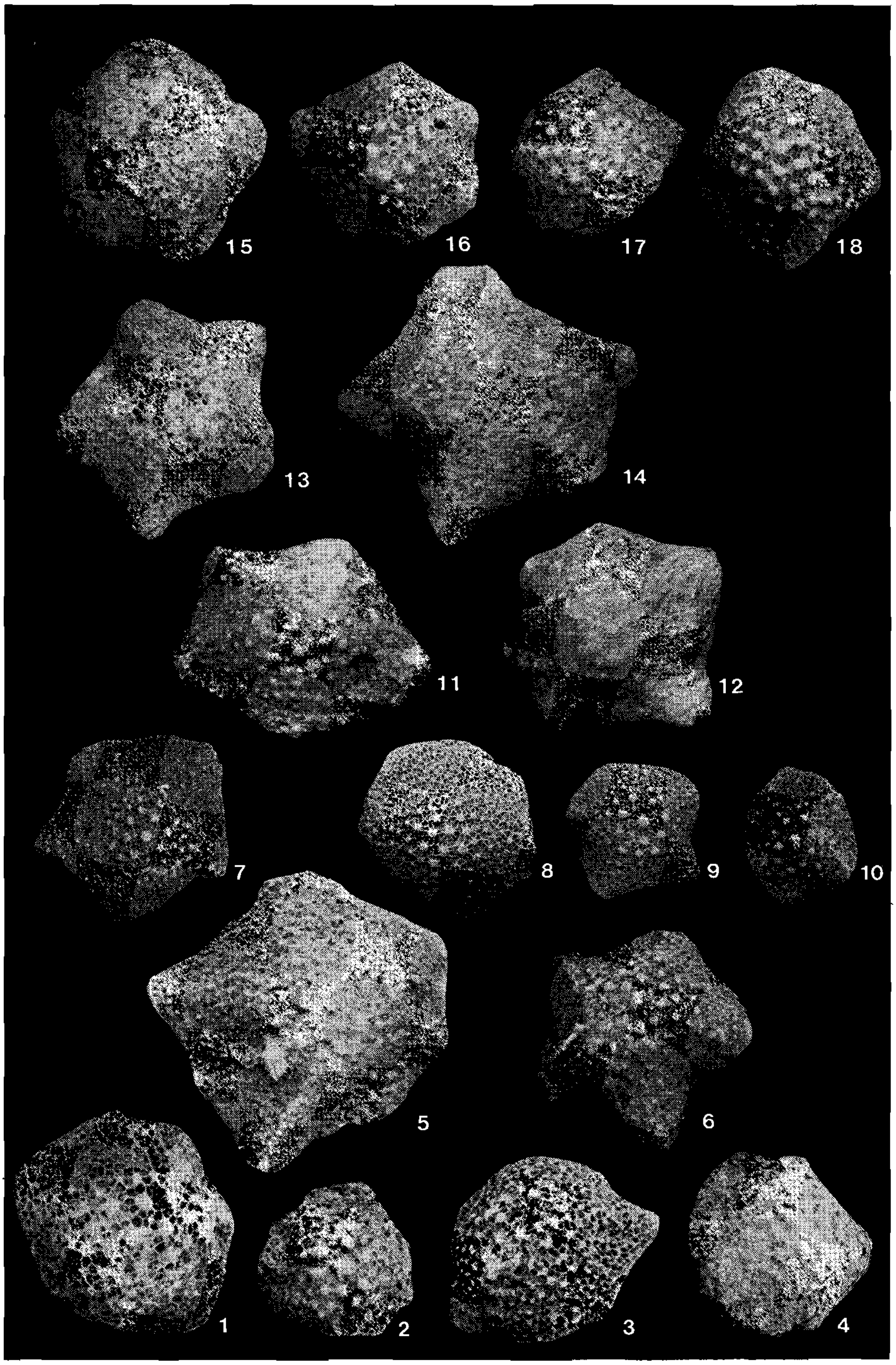


Plate 4

Fig. 1	*Asterocyclina taramellii,* sample Is 317, GFD 98–19. The typical rectangular chambers develop after the fifth annulus, × 50.
Fig. 2	Same specimen. At least two adauxiliary chambers can be recognized, × 200.
Fig. 3	*Asterocyclina taramellii,* sample Is 276, GFD 98–18. Six-rayed specimen with subcircular regeneration features. The typical rectangular chambers develop only in the youngest part of the test, × 50.
Fig. 4	Same specimen. Closing chambers and adauxiliary chambers are clearly visible. Compare *Lepidorbitoides minor* (Van Gorsel, 1975, pl. 12), × 200.
Fig. 5	*Asterocyclina taramellii,* sample Is 221, GFD 98–17, × 50.
Fig. 6	Same specimen, × 200. The test is severely recrystallized.

plate 4

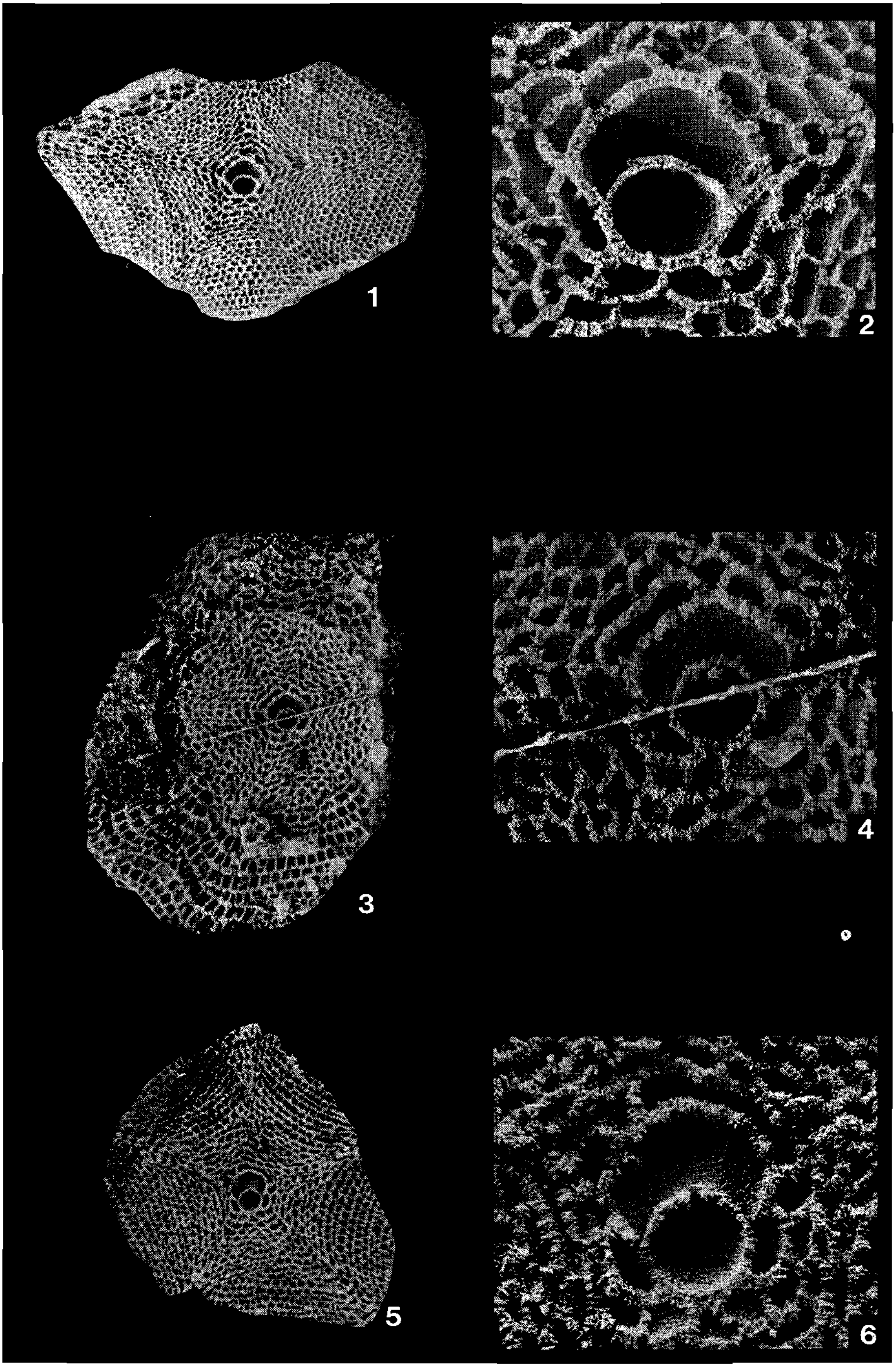


Plate 5

Fig. 1 *Asterocyclina stella,* sample Is 417, GFD 98–24, × 50.

Fig. 2 Same specimen, $n_2 = 14$, $n_{1+2} = 17$. No differentiation can be made between adauxiliary chambers and closing chambers except for those on the protoconch, × 300.

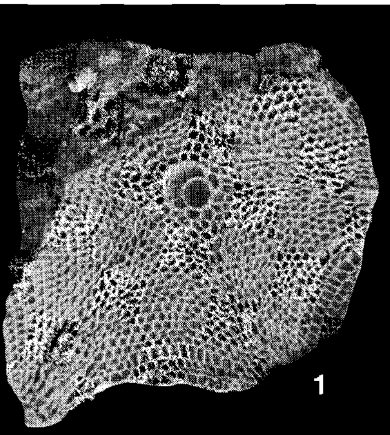
Fig. 3 *Asterocyclina stella,* sample Is 402, GFD 98–23. The broken specimen shows the equatorial layer and a part of the lateral layers. The equatorial layer shows approximately 20 "growth stepts", the lateral layer about 8, × 40.

Fig. 4 *Asterocyclina stella,* sample Is 402, GFD 98–21, × 40.

Fig. 5 *Asterocyclina stella,* sample Is 402, GFD 98–25, × 40.

Fig. 6 *Asterocyclina stella,* sample Is 419, GFD 93–17, × 100.

plate 5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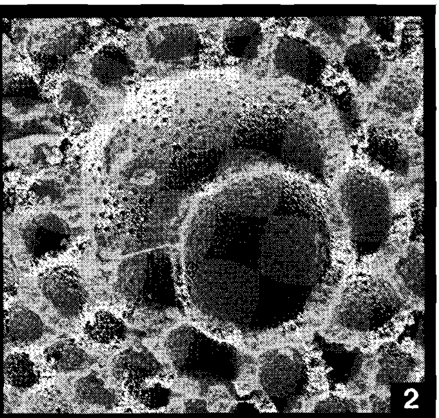
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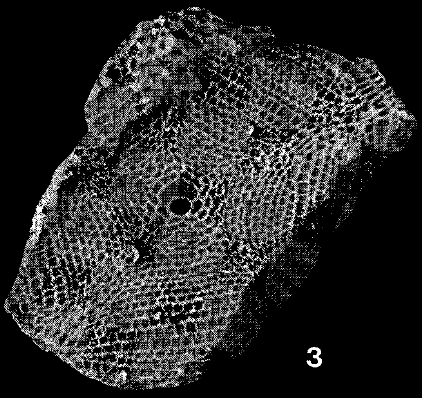
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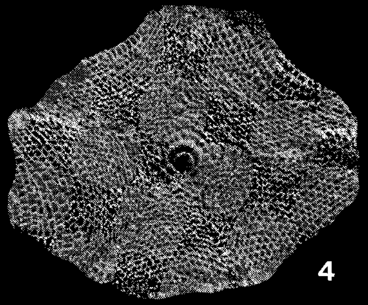
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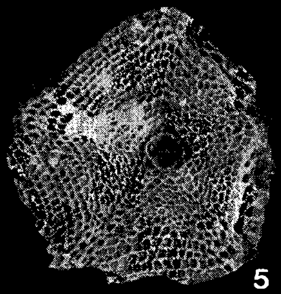
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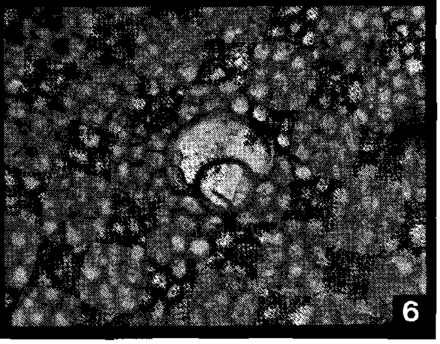
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Plate 6

Fig. 1 *Asterocyclina cuvillieri,* sample Is 199, GFD 98–30. Six-rayed specimen. Rectangular chambers are already present in the third annulus, X 50.

Fig. 2 Same specimen, X 175.

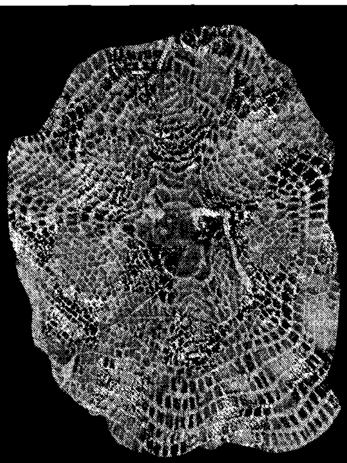
Fig. 3 *Asterocyclina cuvillieri,* sample Is 199, GFD 87–27, X 50.

Fig. 4 *Asterocyclina cuvillieri,* sample Is 221, GFD 98–29, X 50, Six-rayed specimen.

Fig. 5 *Asterocyclina cuvillieri,* sample Is 221, GFD 87–81, X 50.

Fig. 6 Same specimen, X 140.

plate 6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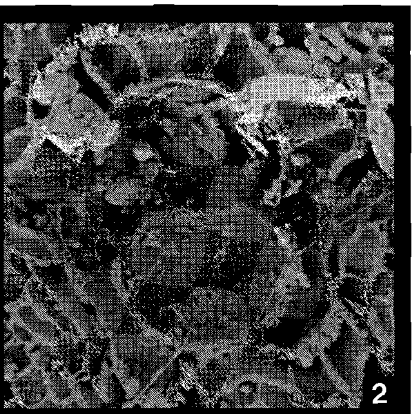
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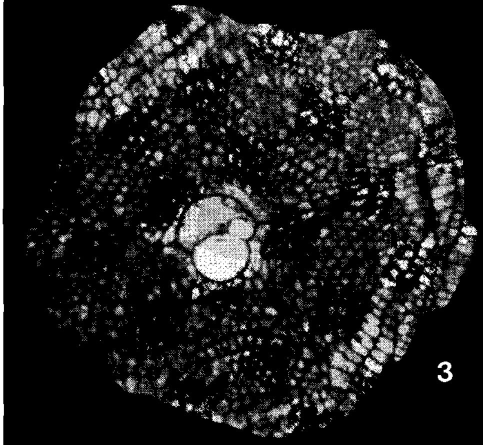
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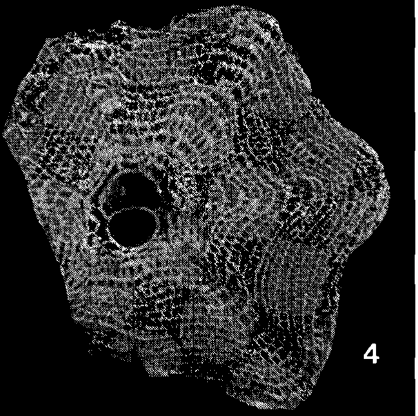
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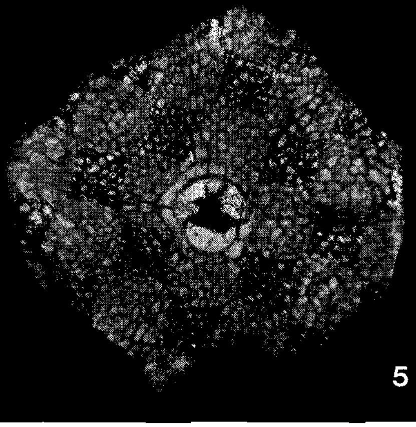
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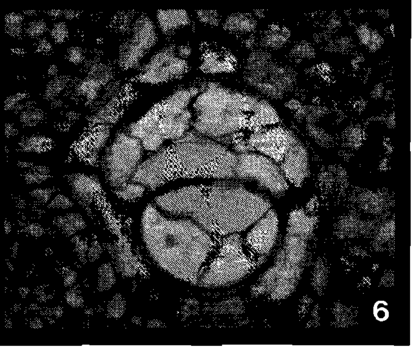
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Plate 7

Fig. 1	*Asterocyclina* sp., sample Is 336, GFD 91–46, X 50.
Fig. 2	*Asterocyclina* sp., sample Is 366, GFD 91–56, X 50.
Fig. 3	*Asterophragmina* cf *pagoda,* sample IS 335, GFD 98–31. Megalospheric specimen. Although the embryon is slightly damaged the neprodiscodine structure is still visible, X 50.
Fig. 4	Same specimen. The early ontogenetic part of the test closely resembles that of *Asterocyclina taramellii.* Radial walls disappear completely between the fifth and the ninth annulus, X 150.
Fig. 5	Same specimen. Peripheral part of the test. The chambers are very broad and lack radial elements. In the rays the walls are considerably thicker than in the interradial areas.

plate 7

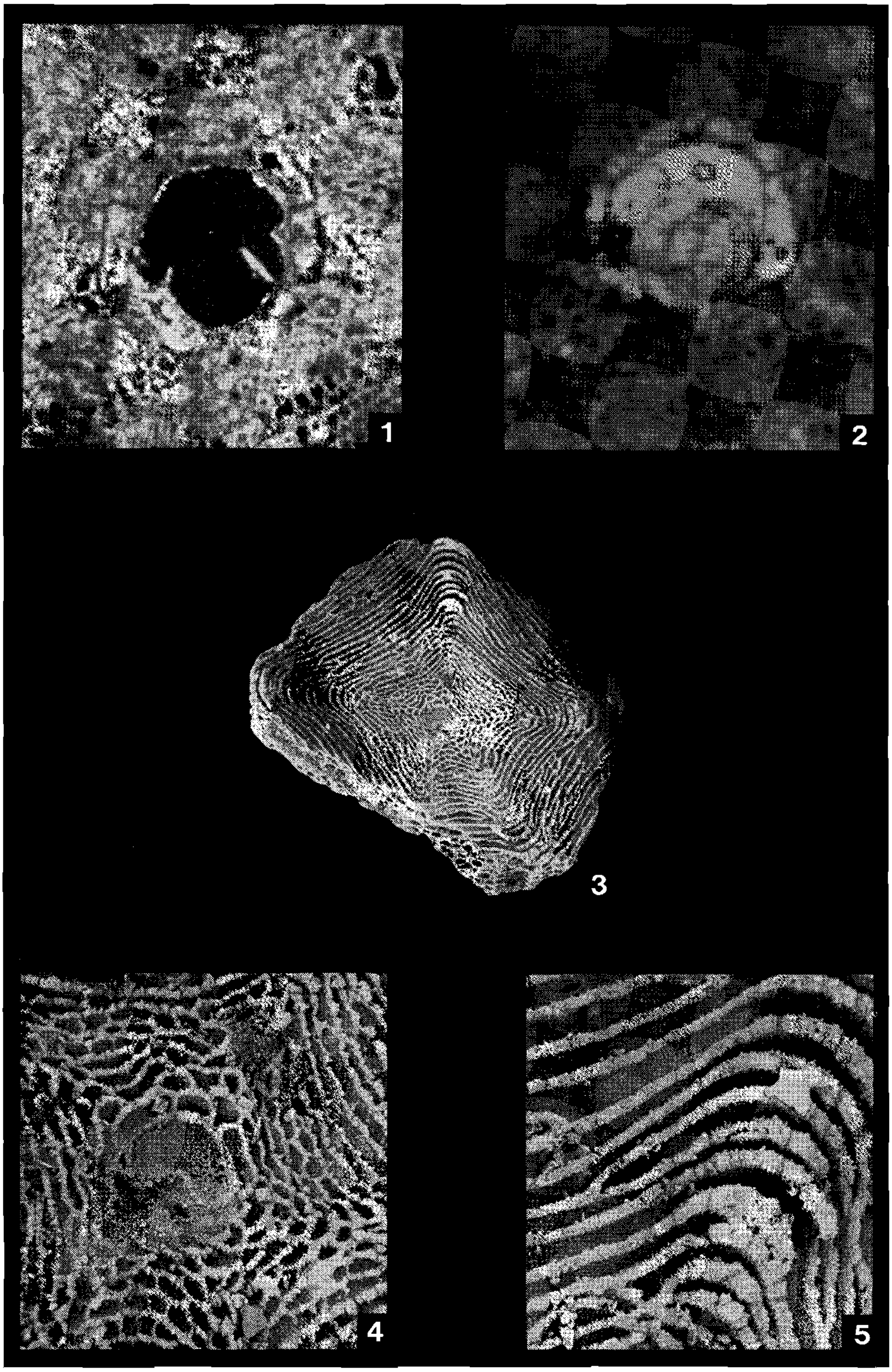
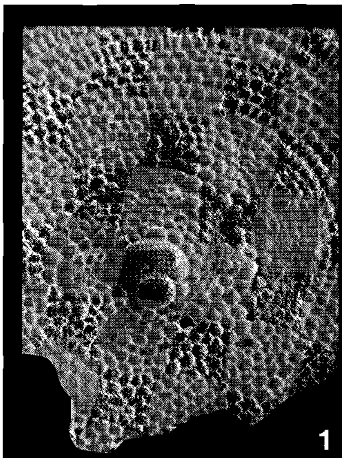


Plate 8

Fig. 1	*Discocyclina augustae,* sample Is 199, GFD 98–32. In this "primitive" specimen the early chambers of the equatorial layer are still arcuate, X 50.
Fig. 2	Same specimen. No clear differentiation can be made between adauxiliary, spiral and closing chambers. Apart from the thickness of the wall of the embryon this specimen is identical to *Lepidorbitoides socialis* (compare van Gorsel, 1975, pl. XIV, c, pl. XV, a), X 150.
Fig. 3	*Discocyclina augustae,* sample Is 221, GFD 98–33, X 20.
Fig. 4	Same sample. The first annulus contains hexagonal chambers the second annulus rectangular chambers, X 100.
Fig. 5	*Discocyclina* sp., sample Is 199, GFD 95–6, X 50.
Fig. 6	*Discocyclina* sp., sample Is 276, GFD 96–17, X 100.

plate 8



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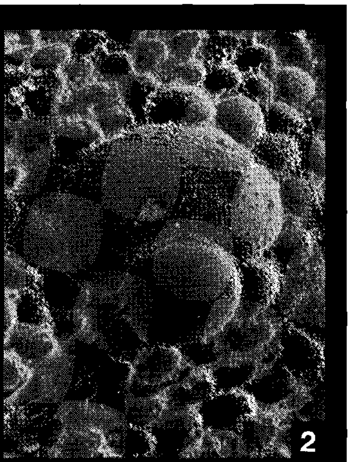

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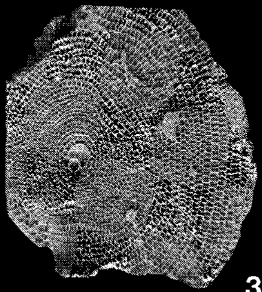

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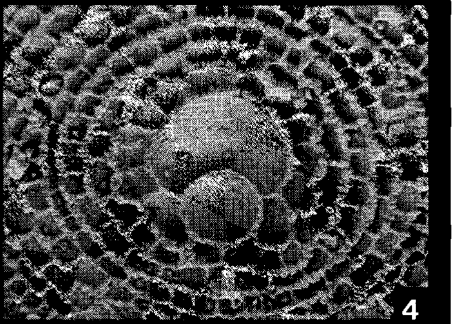

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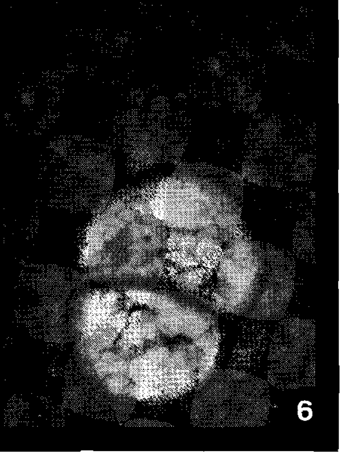

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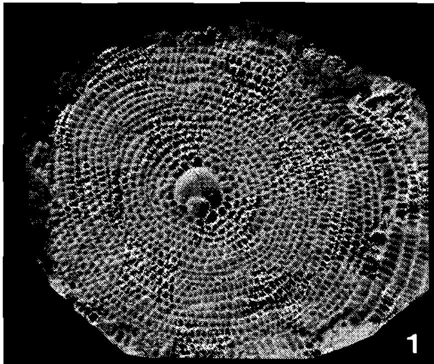
Plate 9

Fig. 1	*Discocyclina varians,* sample Is 273, GFD 98–34, × 30.
Fig. 2	Same specimen. The shape of the chambers in the first annuli ranges from hexagonal to rectangular. The embryon is of the nephrodiscodine type, × 120.
Fig. 3	*Discocyclina varians,* sample Is 273, GFD 98–36, × 30.
Fig. 4	Same specimen, × 90.
Fig. 5	*Discocyclina varians,* sample Is 273, GFD 98–36, × 30.
Fig. 6	Same specimen, × 90.

plate 9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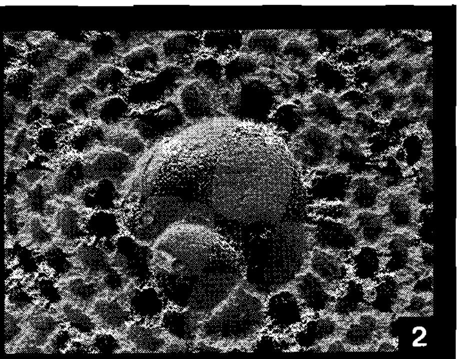
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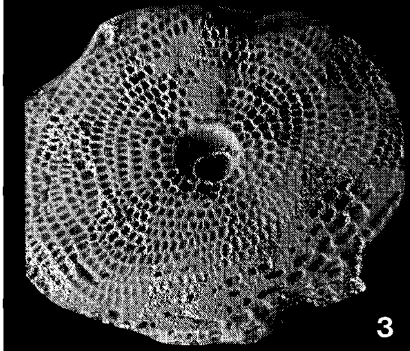
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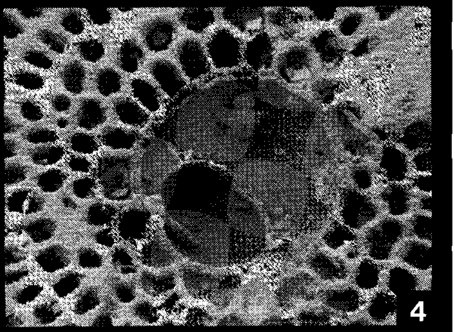
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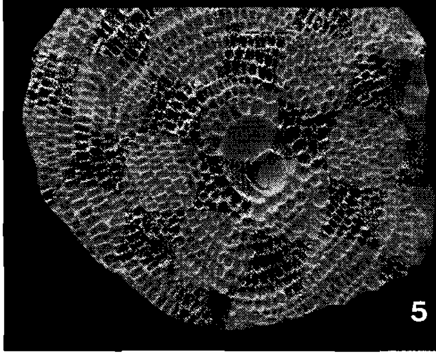
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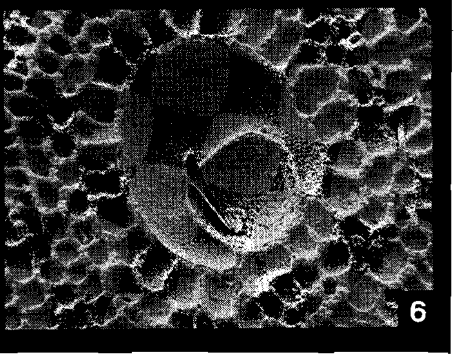
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Plate 10

Fig. 1 *Discocyclina varians,* sample Is 199, GFD 95–32, X 50.

Fig. 2 *Discocyclina varians,* sample Is 276, GFD 95–87. Note that chambers that are filled with calcite look as if they are hexagonal, whereas the empty chambers look rectangular, X 50.

Fig. 3 *Discocyclina varians,* sample Is 199, GFD 94–93, X 50.

Fig. 4 *Discocyclina varians,* sample Is 199, GFD 94–92, X 50.

Fig. 5 *Discocyclina archiaci,* sample Is 199, GFD 95–1. Note that there is no clear difference in the embryonic structure of this specimen and the previous one, X 100.

Fig. 6 *Discocyclina archiaci,* sample Is 199, GFD 94–89, X 100.

plate 10


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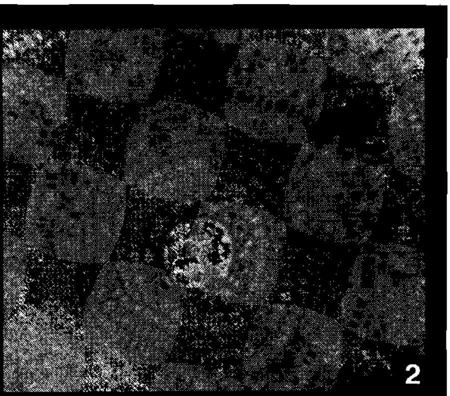
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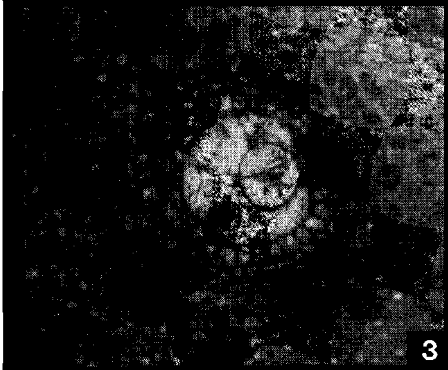
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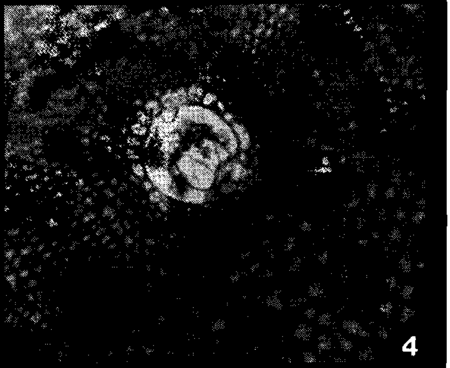
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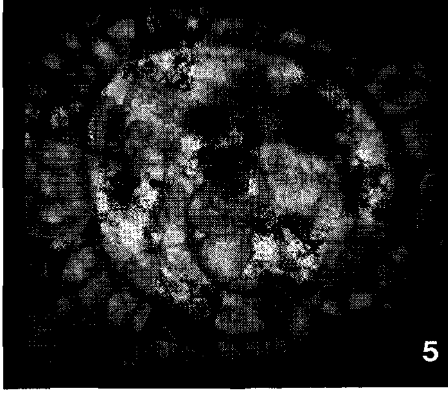
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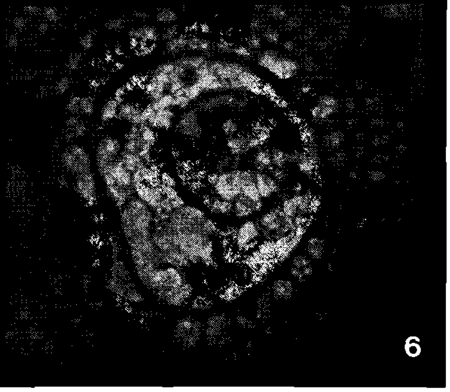
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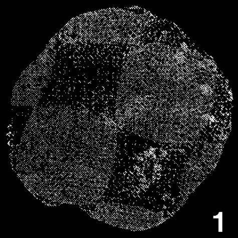
Plate 11

Fig. 1	*Asterocyclina taramellii,* sample Is 336, GFD 98–12. Microspheric specimen, X 20.
Fig. 2	Same specimen. The early chambers are not rectangular, X 85.
Fig. 3	Same specimen. Nepionic spiral of the microsphere. The (approximately) tenth chamber has two stolons, X 400.
Fig. 4	*Discocyclina* sp. sample Is 221, GFD 98–14. A very flat microspheric specimen (*D. augustae?*), X 20.
Fig. 5	Same specimen. Both the (approximately) seventh and the ninth chamber have two distally situated stolons from which two new chambers originate, X 265.
Fig. 6	*Discocyclina varians,* sample Is 273, GFD 98–15. Microspheric specimen. The test shows subcircular regeneration features, X 75.
Fig. 7	Same specimen, X 220.
Fig. 8	*Discocyclina varians,* sample Is 397, GFD 98–11. Microspheric specimen, X 135.
Fig. 9	Same specimen, X 365.

plate 11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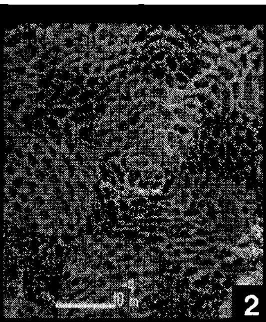
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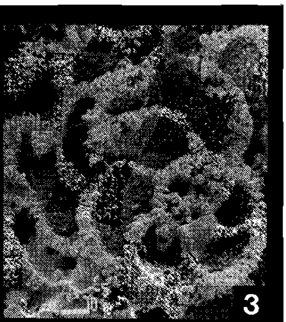
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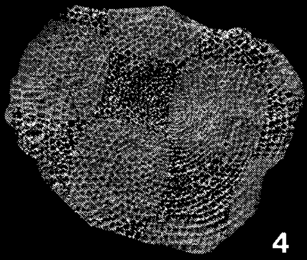
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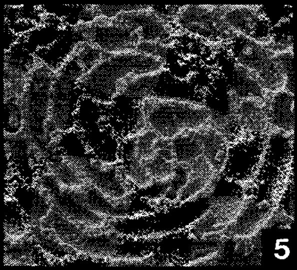
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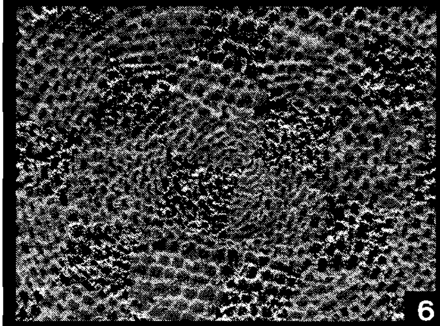
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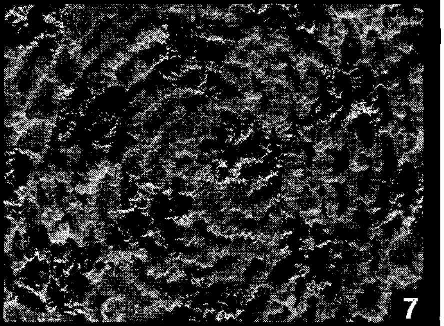
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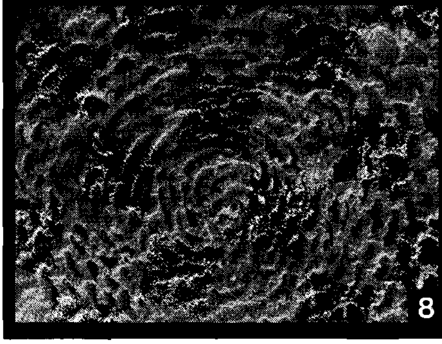
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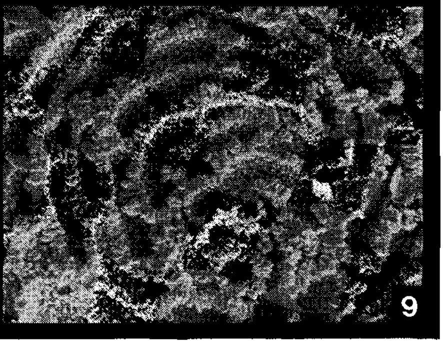
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