

**UTRECHT  
MICROPALAEONTOLOGICAL  
BULLETINS**

F.J. JORISSEN

**BENTHIC FORAMINIFERA FROM THE ADRIATIC SEA;  
PRINCIPLES OF PHENOTYPIC VARIATION**

**37**

## UTRECHT MICROPALAEONTOLOGICAL BULLETINS

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BENTHIC FORAMINIFERA FROM THE ADRIATIC SEA;  
PRINCIPLES OF PHENOTYPIC VARIATION

F.J. JORISSEN

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## CONTENTS

	Page
Abstract .....	5
Chapter I. Introduction .....	7
I.1. Purpose of the investigation .....	7
I.2. Environmental parameters .....	7
I.3. Methods of faunal analysis .....	12
I.4. Acknowledgements .....	13
Chapter II. General distribution of benthic foraminifera in the Adriatic Sea .....	15
Chapter III. Distribution of benthic foraminifera in biofacial units II and IV .....	29
III.1. Introduction .....	29
III.2. Material .....	30
III.3. Results .....	31
III.4. Discussion .....	36
Chapter IV. Phenotypic variation .....	41
IV.1. Introduction .....	41
IV.2. Genus <i>Ammonia</i> Brünnich, 1771 .....	42
IV.2.1. Introduction .....	42
IV.2.2. Distribution .....	43
IV.2.2.1. <i>Ammonia beccarii</i> (Linnaeus, 1758) .....	43
IV.2.2.2. <i>Ammonia parkinsoniana</i> (D'Orbigny, 1839) .	46
IV.2.2.3. <i>Ammonia perlucida</i> (Heron-Allen and Earland, 1913) .....	51
IV.2.2.4. <i>Pseudoeponides falsobeccarii</i> Rouvillois, 1974 .	51
IV.2.3. Taxonomy .....	52
IV.3. Genus <i>Bulimina</i> D'Orbigny, 1826 .....	66
IV.3.1. Introduction .....	66
IV.3.2. Distribution .....	67
IV.3.3. Discussion .....	71
IV.3.4. Taxonomy .....	75
IV.4. Genus <i>Elphidium</i> Montfort, 1808 .....	84
IV.4.1. Introduction .....	84
IV.4.2. <i>Elphidium granosum</i> (D'Orbigny, 1846) .....	85
IV.4.2.1. General distribution .....	85
IV.4.2.2. Geographical variation .....	86
IV.4.2.3. Discussion .....	92

IV.4.3. <i>Elphidium poeyanum</i> (D'Orbigny, 1839) .....	95
IV.4.3.1. General distribution .....	95
IV.4.3.2. Geographical variation .....	96
IV.4.3.3. Discussion .....	101
IV.4.4. <i>Elphidium advenum</i> (Cushman, 1922) .....	102
IV.4.5. <i>Elphidium crispum</i> (Linnaeus, 1758) .....	103
IV.4.6. <i>Elphidium margaritaceum</i> Cushman, 1930 .....	103
IV.4.7. Taxonomy .....	104
Chapter V. Life strategies in benthic foraminifera .....	125
V.1. Limiting factors .....	125
V.2. Microhabitat separation .....	126
V.2.1. Introduction .....	126
V.2.2. Niche separation in the Adriatic Sea .....	127
V.3. Principles behind intraspecific variation .....	130
V.3.1. Introduction .....	130
V.3.2. Discussion .....	132
V.4. Conclusion .....	138
Chapter VI. Applications .....	141
VI.1. Introduction .....	141
VI.2. Benthic productivity .....	142
VI.2.1. Introduction .....	142
VI.2.2. An example of paleo-ecological interpretation: core IN 68-23 .....	144
VI.2.3. Discussion .....	148
References .....	153
Appendix I .....	159
Appendix II .....	162
Appendix III .....	164
Appendix IV .....	172
Appendix V .....	174

## ABSTRACT

The distribution and morphology of the benthic foraminifera in the Adriatic Sea appear to be strongly dependent on two primary controlling environmental parameters, oxygen concentration and food availability. These factors are both governed by the runoff from the Po and other Italian rivers, and by the subsequent distribution of the fluvial discharge products by the system of surface currents.

The area most strongly influenced by runoff products, which is characterized by ample food availability and low oxygen concentrations at the bottom, is a strip parallel to the Italian coast at a water depth of between 20 and 60 m. In the present study we describe in detail the changes in the benthic foraminiferal faunas along transects perpendicular to this zone. The faunas along these transects react essentially in two different ways to the changes in environmental conditions. On the one hand we see qualitative and quantitative changes in the composition of the faunas, and on the other hand a number of species show a high degree of ecophenotypic variation.

Statistical analysis of the faunal patterns resulted in the recognition of eight faunal clusters. One of these clusters, occurring in the near-shore zone, is consisting of obviously reworked specimens. The other seven clusters are separated on the basis of differences in the tolerances for stressed conditions and in the preferences for particular feeding niches of the various taxa. In the centre of the zone influenced by run-off products the faunas are dominated by a cluster with *Bulimina marginata* forma *denudata* and *Nonionella turgida*. Obviously the taxa of this cluster have the greatest tolerance for the sometimes stressed conditions found in this area.

In the taxa *Ammonia parkinsoniana*, *Elphidium granosum* and *Elphidium poeyanum*, comparable successions of three fundamental morphologies are demonstrated. Compact morphotypes are typical for the near-shore, relatively nutrient-poor and oxygen-rich environment, in which there is a minimum influence of runoff products. In the somewhat deeper, food-enriched environment with lower oxygen concentrations, inflated morphologies occur. Still deeper, in the central part of the strip influenced by run-off products, where oxygen-poor conditions occur, these types are found with supplementary characteristics.

The study of the variation in *Bulimina marginata* suggests that in this taxon the morphology reflects the life position of the animal. On the basis of the distribution of different morphologies in this and in similar species, it is concluded that the degree of niche separation in benthic foraminifera is dependent

on the thickness of the oxygen-containing layer. If this thickness is minimal, the inbenthic microhabitat is ruled out, and only taxa adapted to an epibenthic microhabitat are found.

In the final chapter some possibilities to apply the results of our study are discussed. It is argued that the bathymetrical distribution of benthic foraminifera in the Adriatic Sea is largely influenced by variations in productivity. Although the Recent situation can be described in great detail, one should be careful about using these data for estimating paleo-depths in other basins and/or other time-slices.

Far more promising is the potential use of the present results for the interpretation of benthic foraminiferal faunas from deltaic environments in terms of productivity. It is demonstrated that not only variations in the productivity itself can be distilled, but also the source of such variations, such as variations in run-off, changes in circulation patterns and sea level fluctuations. It is suggested that benthic foraminifera should be used more often in pollution studies, because they can provide an accurate description of the distribution patterns of pollution phenomena in the bottom environments.

## Chapter I

### INTRODUCTION

#### I.1. PURPOSE OF THE INVESTIGATION

The Adriatic Sea plays an eminent role in the history of foraminiferology. Of the first foraminifera described formally in the 18th century, many originated from this region. In the first standard work on foraminiferal taxonomy by D'Orbigny (1826), a large number of the descriptions were based on material from the beach sands of Rimini. Therefore, a large number of currently widely used taxa have originated in the Adriatic Sea.

An earlier paper (Jorissen, 1987) reported the main results of a study on the distribution of benthic foraminifera in the taphocoenoses found in 285 grab samples and piston-core tops from the Adriatic Sea. The most important conclusions were that the benthic foraminiferal distribution patterns are determined to a great extent by the input of nutrients and suspension load from Italian rivers (mainly from the Po), and the subsequent transport and distribution of these products by surface currents to the bottom environments of the Adriatic Sea.

In the present paper we shall concentrate on the benthic foraminiferal associations from the areas where the influence of these factors is felt most strongly. Before doing this we shall give a short survey of the oceanographic conditions and sediment distribution pattern in the Adriatic Sea, and shall summarize the main results of our earlier investigation.

#### I.2. ENVIRONMENTAL PARAMETERS

An exhaustive review of the oceanographic parameters of the Adriatic Sea has been given by Buljan and Zore-Armanda (1976). In the present paper we shall discuss only those parameters which in our opinion are of importance for the distribution of benthic foraminifera. The maps of the sedimentological parameters which are presented here are based on the same set of samples as the one we are using for the study of the benthic foraminifera, and were made after Pigorini (1968), Van Straaten (1970) and Breman (1975, based on unpublished data from Van Straaten and Veenstra).

In figure 1 the locality of all grab samples and piston-core tops are plotted on a bathymetric map of the basin. In the Adriatic Sea three main bathymetric elements can be distinguished:



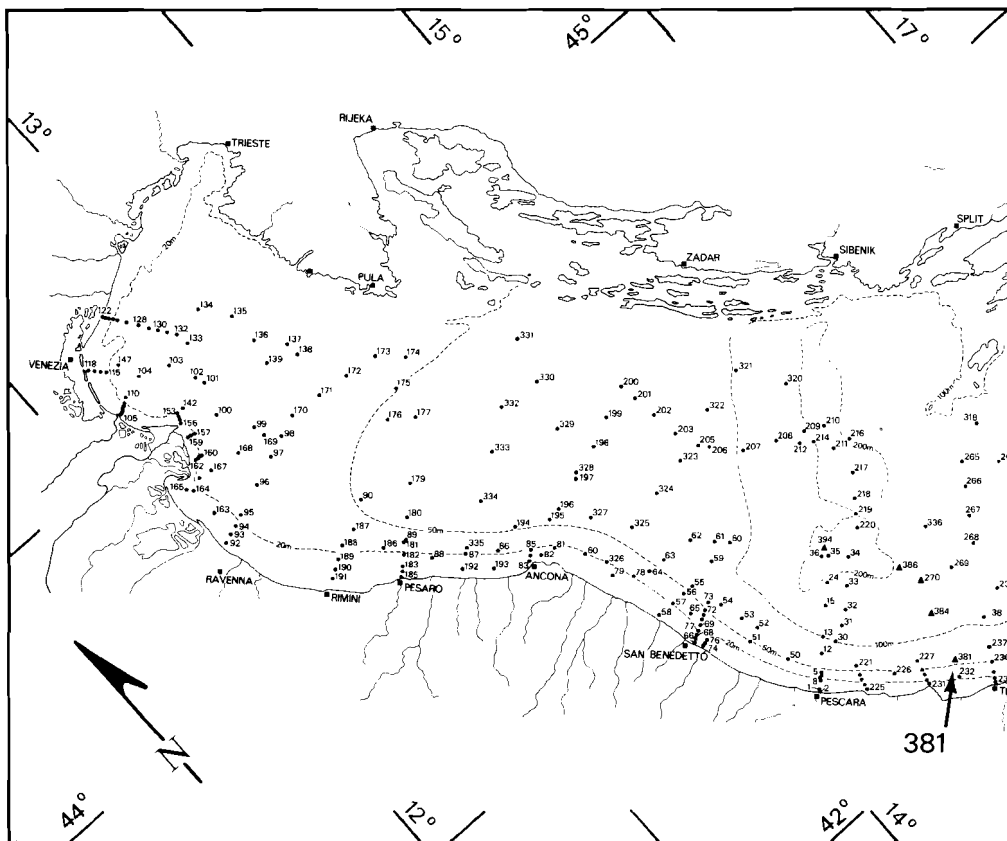
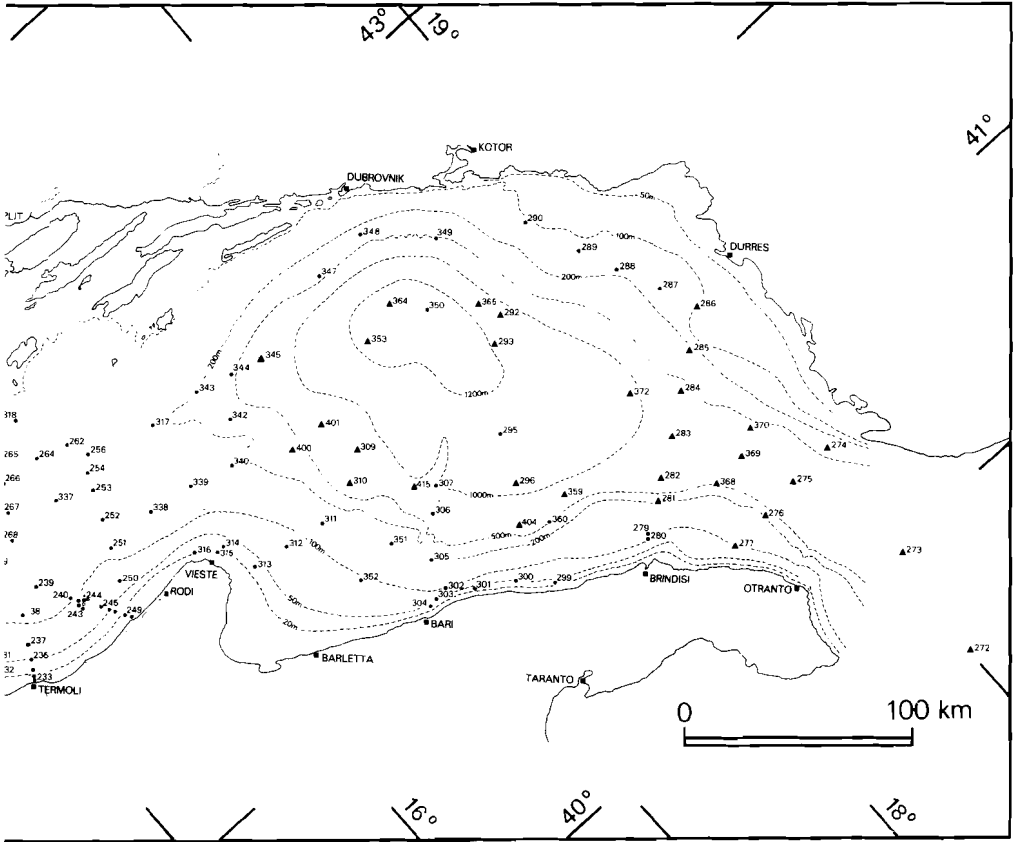


Fig. 1. Generalized bathymetric map of the Adriatic Sea, with the sample localities. Dots indicate grab samples, triangles denote core-tops (after Pigorini, 1968 and Breman, 1975, based on data from Van Straaten).

1) a relatively deep (down to some 1225 m) southern basin, situated between Dubrovnik and Bari, is separated from the Ionian Sea by a sill with a maximum depth of 750 m,

2) a shallow central basin (maximum depth some 270 m), called Jabuka Pit by Buljan and Zore-Armanda (1976), is situated between Sibenik and Pescara. It is separated from the southern basin by a platform with a maximum depth of some 160 m,

3) a gently sloping platform, which is deepening from 25 m east of Venezia to some 125 m north-west of the central basin. The zone separating the central and southern basins can be considered as a continuation of this platform.



A general survey of the water masses and circulation pattern in the Adriatic Sea was published by Zore-Armanda (1968). According to this paper three layers can be distinguished: a surface layer (0 - 40 m depth), an intermediate layer and a deep layer. The transition from the intermediate layer to the bottom layer takes place at about 150 m depth in the central basin and at about 500 m in the southern basin. Each of the three layers displays its own annual variation.

Most important for the distribution of the fluvial discharge products is the surface layer, which is characterized by an anti-clockwise circulation pattern. In figure 2 a simplified picture, averaged for the whole year, is given. In winter

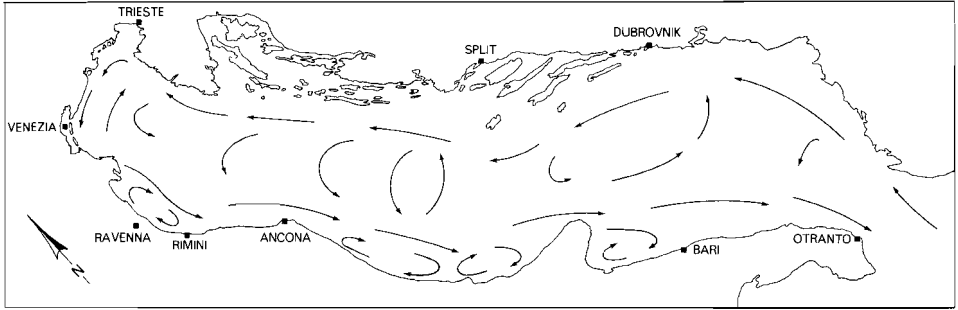


Fig. 2. Simplified surface current pattern, averaged for the whole year (after Zore-Armanda, 1968; Hesse et al., 1971; Nelson, 1972; Breman, 1975).

the SE-NW current along the Yugoslavian coast prevails, whereas in summer the NW-SE directed current along the Italian coast is the stronger one. In spring and autumn both currents are of equal strength. Local cells are present in a number of places; a very important one is active in spring and autumn in the Gulf of Trieste.

For the temperature and salinity distribution in the basin we refer to the work of Buljan and Zore-Armanda (1976). Both parameters show only minor variations at the sea bottom (beneath the thermocline), and are therefore probably of minor importance for the distribution of benthic foraminifera.

A sedimentological description of the sea-bottom has been given by Van Straaten (1965, 1970), Pigorini (1968) and Brambati et al. (1973). In appendix I the sedimentological parameters measured on our sample-set are listed. The grainsize distribution as found in our samples has been contoured in figure 3. A main bipartition is present between sandy and clayey bottoms. Sandy bottoms are found on the platform area and along the Italian coast, whereas clayey bottoms are present in the deep basins, and in a strip of intermediate water depth (20 - 60 m) parallel to the Italian coast (the so-called mud-belt of Van Straaten, 1965). According to Van Straaten (1965) sedimentation has been more or less continuous in the clay-belt, whereas the sandy substrates should be the result of winnowing of Pleistocene material and non-deposition during the Holocene. Therefore the foraminifera found in the clay-belt can be interpreted as (sub-)recent, whereas the bulk of the specimens found in associations from the sand platform are of Pleistocene age.

The distribution of calcium carbonate in the sediment (figure 4) is perfectly correlated with the grain-size; clayey samples are poor whereas sandy samples are rich in calcium carbonate.

% FRACTION >50 MICRONS

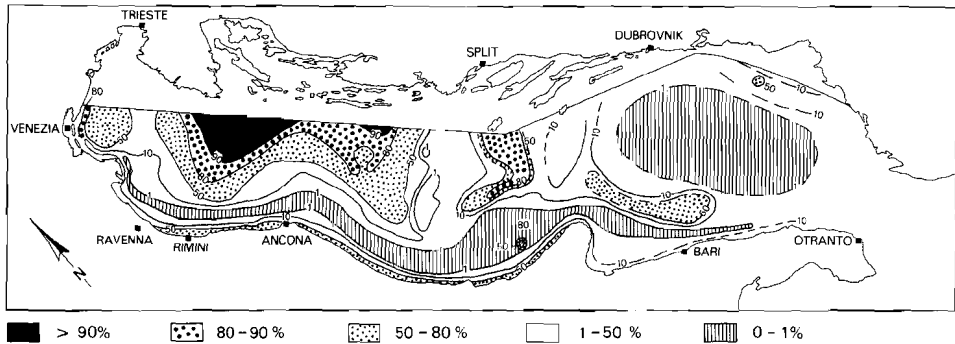


Fig. 3. Grainsize distribution in the samples indicated as percentage of the sand fraction (> 50 microns) (after Breman, 1975, based on data from Veenstra).

A negative relation can be observed between the grain-size distribution and the percentage of organic matter in the sediment (fig. 5). Together with the clay particles, large amounts of organic matter are supplied by the Po and other rivers, transported in suspension by the surface currents, and finally deposited together.

Gamulin-Brida (1967) studied the benthic macro-fauna of the Adriatic Sea. Her biogeographical zonation appears to be linked to the nature of the substratum and the presence of vegetation. Van Straaten (1970, 1985) and Breman (1975) studied the basin-wide distribution of molluscs and ostracods respectively. They used the same samples as we used for the present study on benthic foraminifera.

% CALCIUM CARBONATE

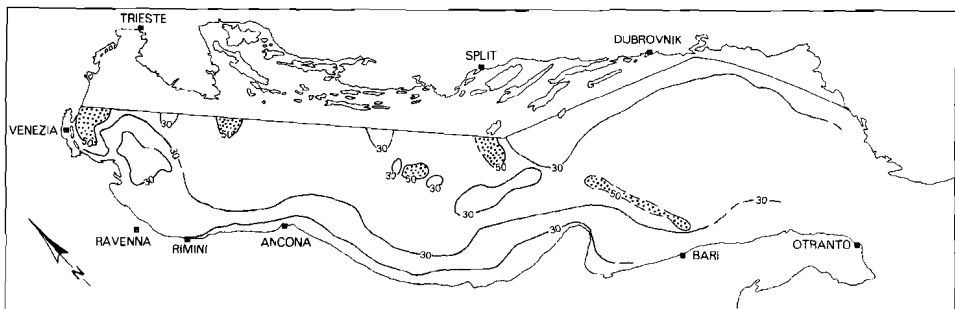


Fig. 4. Percentages of calcium carbonate in the sediment (after Breman, 1975, based on data from Veenstra). Dotted areas indicate sediments containing more than 50 % calcium carbonate.

## % ORGANIC MATTER

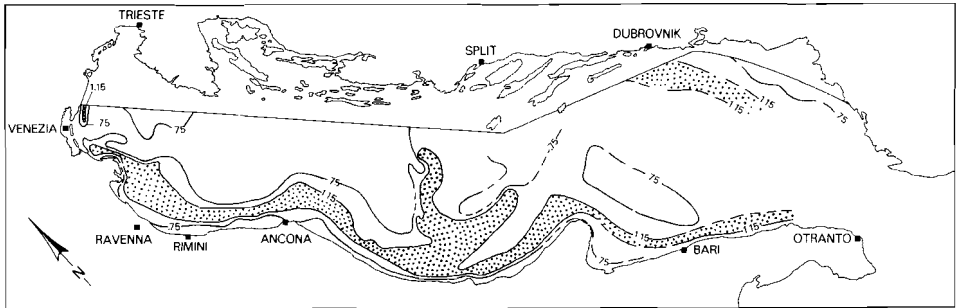


Fig. 5. Percentages of organic matter in the sediment (after Breman, 1975, based on data from Veenstra). Dotted areas indicate sediments containing more than 1.15 % organic matter.

### 1.3. METHODS OF FAUNAL ANALYSIS

A general description of the basin-wide distribution of benthic foraminifera in the Adriatic Sea was given by Jorissen (1987). The sample-set, which was collected in 1962, consisted of 285 grab samples and piston-core tops from all over the basin, with the exception of the Yugoslavian coastal area. These samples, which had largely been left untreated until 1983, were washed over a set of sieves with mesh-widths of 63, 150 and 595 microns respectively. Because the material had not been stained, no attempt could be made to distinguish between 'living' and fossil specimens; therefore our study is necessarily of a paleoecological nature.

Only the 150 micron fraction was used for the quantitative study. The wash residues were split with an Otto microsplitter, and complete splits were picked until a minimum of 250 benthic foraminifera was reached. These foraminifera were mounted in Chapman slides (deposited in the collection of the dept. stratigraphy/micropaleontology of the Rijksuniversiteit Utrecht), determined, and counted. Finely agglutinated taxa, which tend to decompose rapidly after burial (e.g. *Discammina compressa*, *Eggerella scabra*, *Reophax* spp., see Bizon and Bizon, 1985) were not incorporated in the quantitative analyses so that the counting results could better be used for a future comparison with core material.

For our taxonomy, a broad (assemblage) species concept was adopted, although lower categories were distinguished at a forma level. Whenever possible, the taxonomy of the comparatively recent papers of Parker (1958), D'Onofrio (1959) and Von Daniels (1970) was followed.



In the present paper some of the counting results are re-interpreted. Because lack of space precluded publication in our earlier paper (Jorissen, 1987) a list of all recognized taxa is reproduced in appendix II, and for all taxa used in our numerical analyses the relative frequencies are given in appendices III, IV and V.

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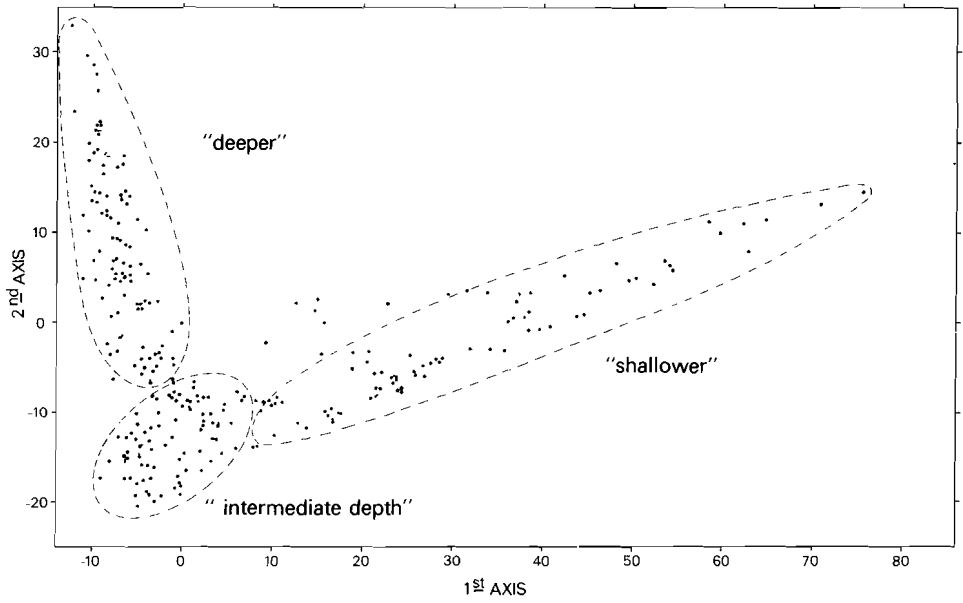


Fig. 6. Plot of the sample scores on the first two principal component axes (after Jorissen, 1987).

## Chapter II

### GENERAL DISTRIBUTION OF BENTHIC FORAMINIFERA IN THE ADRIATIC SEA

A principal components analysis was performed on the basis of the relative frequencies of the 50 most abundant taxa in all 285 samples studied (Jorissen, 1987). It was concluded that both the first and the second principal components are related to the bathymetry (fig. 6), whereas the third (probably still significant) component shows strong correlations with the sedimentary properties of the samples: the percentages of sand fraction (negative), calcium carbonate (negative) and organic matter (positive). In table I the factor loadings on the first three axes are reproduced for those taxa which have a significant correlation with at least one component.

	PCA I	PCA II	PCA III
<i>Textularia agglutinans</i>	-.061	<b>-.268</b>	-.050
<i>Quinquel. aspera/costata</i> group	-.009	-.052	<b>-.191</b>
<i>Bulimina marginata</i>	<b>-.191</b>	<b>-.264</b>	<b>.617</b>
<i>Uvigerina mediterranea</i>	<b>-.222</b>	<b>.673</b>	.139
<i>Uvigerina peregrina</i>	-.047	<b>.159</b>	.003
<i>Trifarina angulosa</i>	-.053	<b>.152</b>	.026
<i>Buccella granulata</i>	.011	-.117	<b>-.284</b>
<i>Valvulineria bradyana</i>	-.061	<b>-.248</b>	<b>.366</b>
<i>Asterigerinata mamilla</i>	-.018	-.069	<b>-.249</b>
<i>Ammonia parkinsoniana</i> **	<b>.911</b>	<b>.186</b>	<b>.194</b>
<i>Elphidium granosum</i>	.094	<b>-.225</b>	<b>-.152</b>
<i>Elphidium poeyanum</i>	.078	<b>-.177</b>	-.000
<i>Cibicides lobatulus</i>	-.066	-.030	<b>-.215</b>
<i>Nonionella turgida</i>	.059	<b>-.169</b>	<b>.264</b>

Table I. Factor loadings of the taxa on the first three principal component axes; only taxa with a significant correlation (95% confidence interval, in bold) with one of the axes have been reproduced.

\*\* In our earlier paper (Jorissen, 1987) *Ammonia parkinsoniana* was determined as *Ammonia beccarii tepida*.

By combining the sample scores on the first and third principal component axes, four sample clusters could be recognized (figure 7). These clusters were translated into four biofacial units, which are mapped in figure 8.

Biofacial unit I comprises all deep water samples (50 - 1225 m) from clayey substrata, having intermediate percentages of calcium carbonate and organic matter. Typical benthic foraminiferal inhabitants of this area are shown on plate 1.

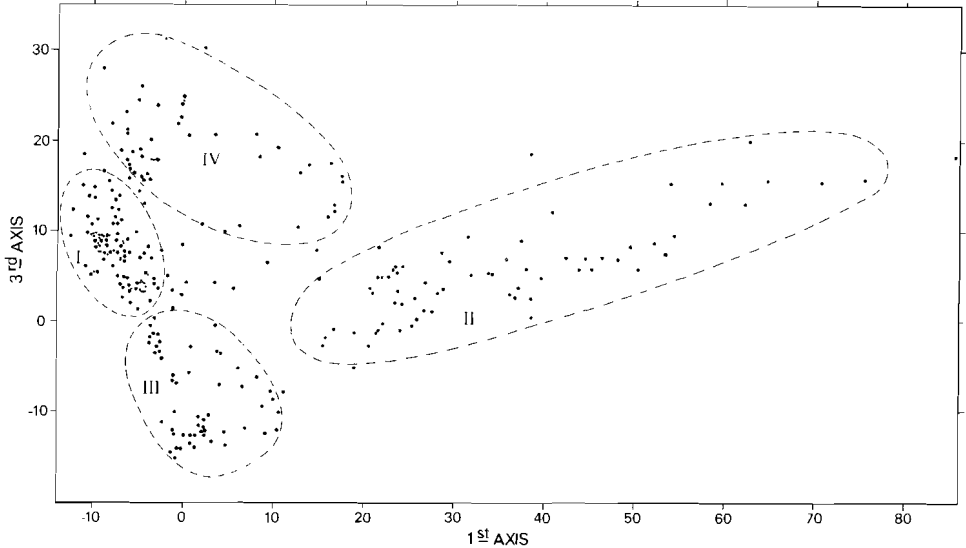


Fig. 7. Plot of the sample scores on the first and third principal component axes, in which four clusters are recognized (after Jorissen, 1987).

Biofacial unit II occupies the complete near-shore zone (7.5 - 25 m) parallel to the Italian coast, with coarse substrata rich in calcium carbonate and poor in organic matter. Typical representatives of the benthic faunas found in this zone are pictured on plate 2.

Biofacial unit III comprises all samples from the sand platform (20 - 100 m), which are enriched in calcium carbonate and extremely poor in organic matter. Typical (sometimes epiphytic) representatives of the associations found in this area are pictured in plate 3.

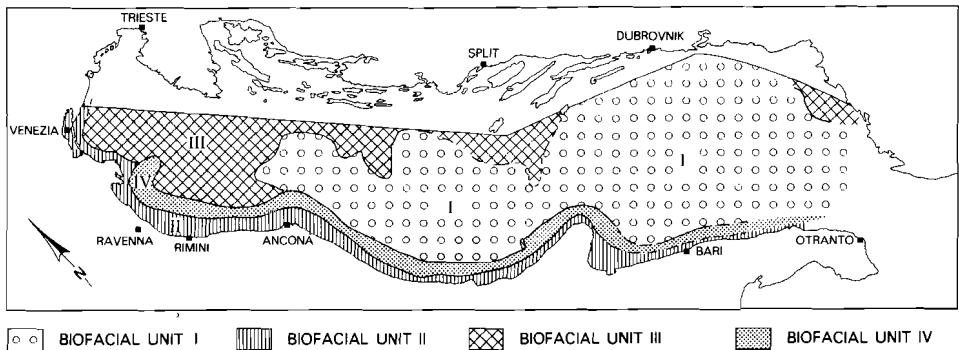


Fig. 8. Geographical distribution of the four biofacial units indicated in figure 7 (after Jorissen, 1987).

Biofacial unit IV finally comprises the samples found in the zone parallel to the Italian coast (20 - 100m), where the bulk of the runoff products is deposited. Consequently, these samples are clayey, poor in calcium carbonate and rich in organic matter. Typical elements of the associations found in this zone are pictured on plate 4.

In order to obtain more information about the benthic foraminiferal community structure, an R-mode cluster analysis was performed on the basis of the same data. The resulting dendrogram, in which eight faunal clusters could be recognized, is reproduced in figure 9.

In biofacial Unit I the faunal assemblages are dominated by taxa of clusters 1,2 and 3. It was concluded (Jorissen, 1987) that the frequencies of the three faunal clusters are mainly determined by factors relating to the bathymetry, one of these being almost certainly the percentage of organic matter (food availability).

In the shallow water biofacial unit II the associations are strongly dominated by representatives of cluster 4. Some of the taxa of this cluster display considerable morphological variation along transects penetrating into biofacial unit IV. A number of these morphological trends will be treated extensively in the present paper.

In biofacial unit III, the sand platform, clusters 5 and 6 are important faunal constituents. In both clusters, which appear to be separated on the basis of water depth, some elements have a test morphology that suggests an epiphythic life position. Others are assumed to live on the bottom, and may have a certain tolerance (or preference) for the input of small amounts of clay. It should be borne in mind that the associations found in biofacial unit III cannot be considered as a (sub-)recent fauna, because they consist of a mixture of Pleistocene and Holocene material.

Biofacial unit IV is strongly dominated by clusters 7 and 8. The cumulative frequencies of both clusters show strong positive correlations with the percentage of organic matter in the sediment. Because of the high sedimentation rate in this zone, and also because of the extremely low species variability observed in the samples, the associations are considered to be very similar to the (sub-) recent standing stock.

Both clusters appear to reflect conditions of enlarged food availability and suggest conditions of lowered oxygen concentration. Especially the taxa belonging to cluster 7, which are all strongly correlated with the third principal component axis, can reach extremely high (joint) frequencies in the centre of the clay-belt; this is also where maximum percentages of organic matter are found (compare figures 5 and 10). As the zone of clay-sedimentation gradually deepens from some 20 m in front of the Po delta to some 60 m in the southern



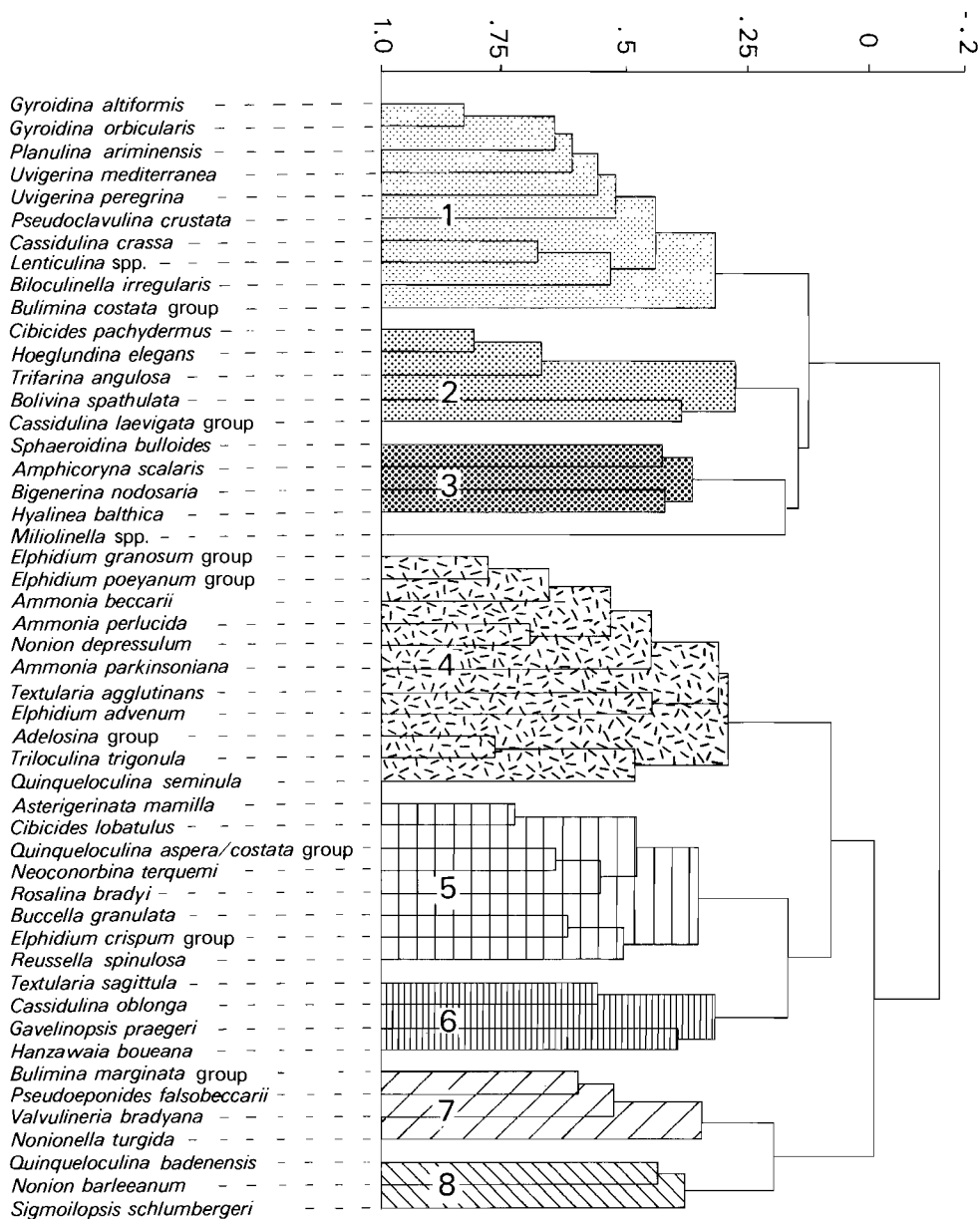


Fig. 9. Dendrogram of 50 taxa, based on an R-mode cluster analysis (after Jorissen, 1987).

part of the Adriatic Sea, a succession of peak occurrences of *Nonionella turgida*, *Bulimina marginata* forma *denudata* and *Valvulineria bradyana* can be observed.

One of the conclusions of our former paper (Jorissen, 1987) is that especially these three taxa can be considered as excellent markers for a large benthic productivity, which often goes hand in hand with environmental (low-oxygen) stress.

CLUSTER 7

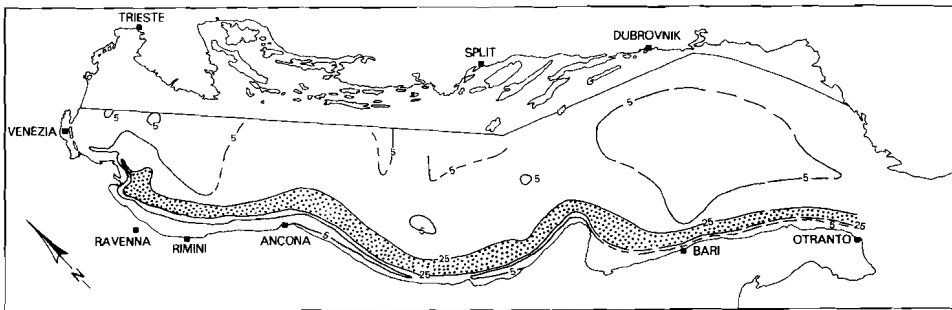


Fig. 10. Distribution map of the taxa belonging to faunal cluster 7 of Jorissen (1987). The cumulative frequencies of the *Bulimina marginata* group, *Pseudoeponides falsobeccarii*, *Valvulineria bradyana* and *Nonionella turgida* have been mapped; in dotted areas all samples have cumulative frequencies higher than 25 %.

As to the factors controlling the general distribution of benthic foraminifera in the Adriatic Sea two conclusions can be made:

- the most obvious faunal break at some 100 m water depth is probably determined by the depth of the photic zone. Below this depth epiphytic taxa, suggesting the presence of a vegetation cover, are no longer found in substantial amounts,

- at a water depth of less than 100 m, the distribution of benthic foraminifera is governed by a number of factors which are independent of the water depth. It was concluded that these factors, such as the nature of the substratum, food availability, oxygen concentration and presence of a vegetation cover, are all controlled by the combination of two parameters: the amount of river (mainly Po) discharge and the re-distribution of runoff products by the (surface) current pattern.

In the remaining part of this paper, we shall concentrate on the influence of the combined effect of these two factors on benthic foraminifera. By making a more detailed study of the faunal associations from biofacial units II and IV we shall try to obtain a better understanding of the mechanisms behind the observed quantitative as well as qualitative changes.

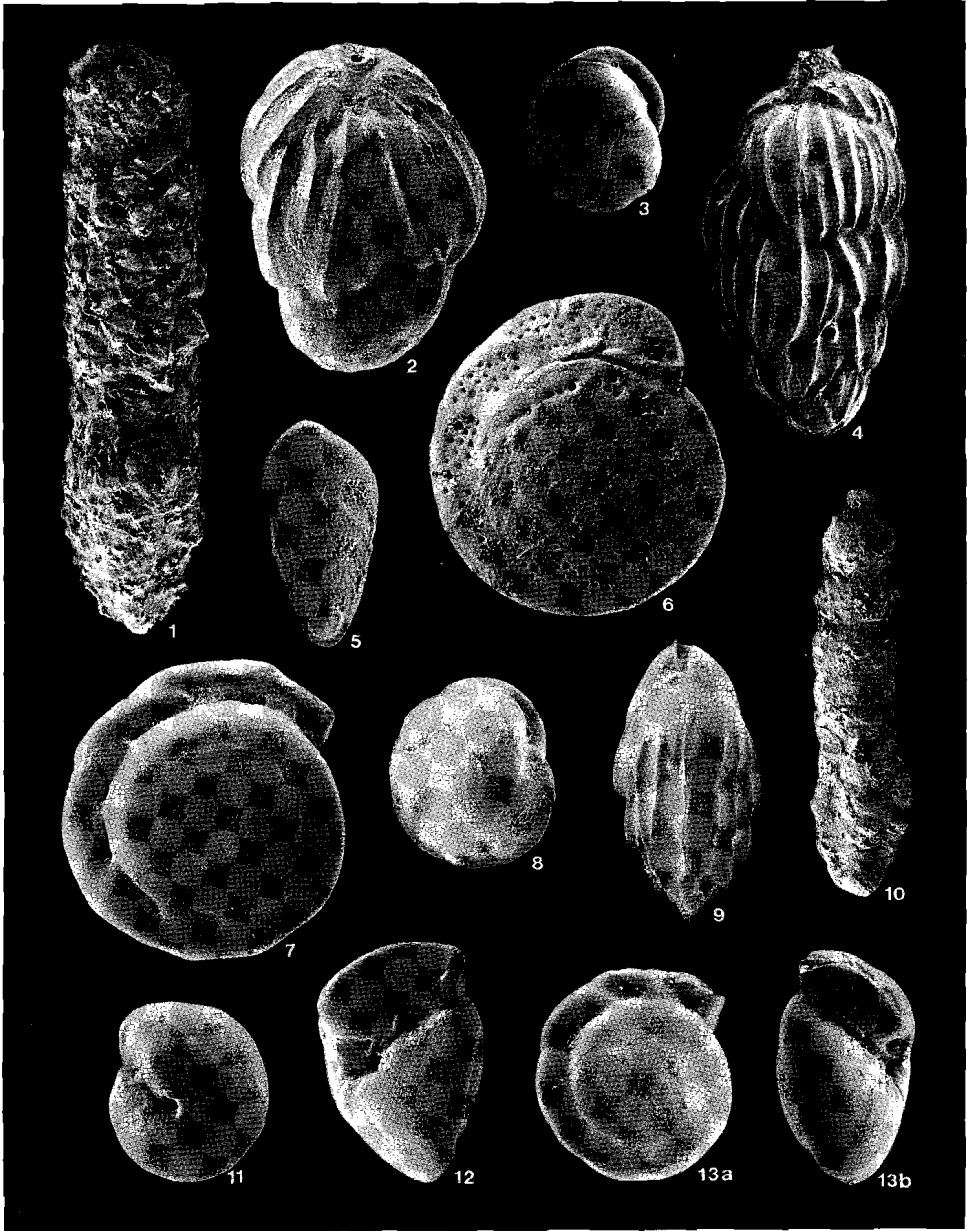
## Plate 1

(reproduced from Jorissen, 1987)

### Taxa characteristic for Biofacial Unit I

- Fig. 1: *Pseudoclavulina crustata* Cushman, sample 394 (water depth 252 m).  
Fig. 2: *Uvigerina mediterranea* Hofker, sample 369/2A, Holocene (water depth 868 m).  
Fig. 3: *Cassidulina crassa* D'Orbigny, sample 282 (744 m).  
Fig. 4: *Uvigerina peregrina bifurcata* D'Orbigny, sample 302 (91 m).  
Fig. 5: *Bolivina spathulata* (Williamson), sample 394 (252 m).  
Fig. 6: *Cibicides pachydermus* (Rzehak), dorsal side, sample 217 (247 m).  
Fig. 7: *Gyroidina altiformis* R.E. and K.C. Stewart, dorsal side, sample 369/2A, Holocene (water depth 868 m).  
Fig. 8: *Cassidulina laevigata carinata* Silvestri, sample 34 (220 m).  
Fig. 9: *Bulimina costata* D'Orbigny, sample 282 (744 m).  
Fig. 10: *Bigennerina nodosaria* D'Orbigny, sample 62 (80 m).  
Fig. 11: *Gyroidina altiformis* R.E. and K.C. Stewart, ventral side, sample 293 (1198 m).  
Fig. 12: *Gyroidina altiformis* R.E. and K.C. Stewart, apertural view, sample 296 (1063 m).  
Fig. 13a: *Gyroidina orbicularis* D'Orbigny, dorsal side, sample 282 (744 m).  
Fig. 13b: Same specimen, apertural view.

All magnifications X 80, except figures 1 (X 40), 10 (X 40) and 5 (X 60).



## Plate 2

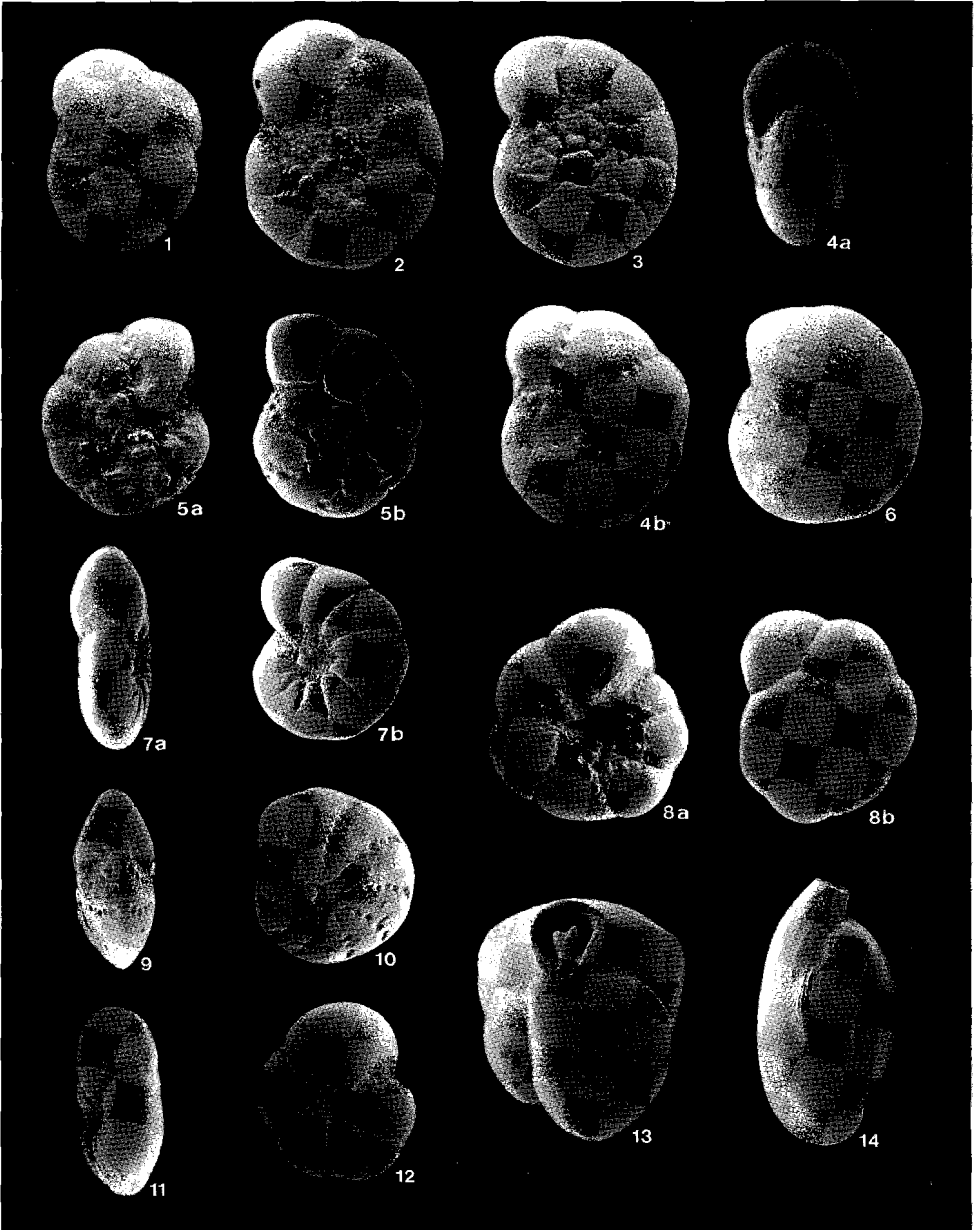
(reproduced from Jorissen, 1987)

### Taxa characteristic for Biofacial Unit II.

- Fig. 1: *Elphidium granosum* forma *granosum* (D'Orbigny), sample 126 (water depth 19 m).  
Fig. 2: *Elphidium granosum* forma *granosum* (D'Orbigny), morphotype intermediate with *E. granosum* forma *lidoense* Cushman, sample 123 (10 m).  
Fig. 3: *E. granosum* forma *lidoense* Cushman, sample 182 (16.5 m).  
Fig. 4a: *Elphidium poeyanum* forma *poeyanum* D'Orbigny, apertural view, piston-core 394, Upper Pleistocene (Recent water depth 252 m).  
Fig. 4b: same specimen, side view.  
Fig. 5a: *Ammonia beccarii* forma *beccarii* (Linnaeus), ventral side, sample 235 (23 m).  
Fig. 5b: same specimen, dorsal side.  
Fig. 6: *Elphidium poeyanum* forma *decipiens* (Costa), sample 126 (19 m).  
Fig. 7a: *Nonion depressulum* (Walker and Jacob), apertural view, sample 126 (19 m).  
Fig. 7b: same specimen, side view.  
Fig. 8a: *Ammonia parkinsoniana* forma *tepida* (Cushman), ventral side, sample 185 (10 m).  
Fig. 8b: same specimen, dorsal side.  
Fig. 9: *Elphidium advenum* (Cushman), apertural view, sample 315 (22 m).  
Fig. 10: *Elphidium advenum* (Cushman), sample 315 (22 m).  
Fig. 11: *Ammonia perlucida* (Heron-Allen and Earland), apertural view, sample 182 (16.5 m).  
Fig. 12: *Ammonia perlucida* (Heron-Allen and Earland), sample 65 (23 m).  
Fig. 13: *Triloculina trigonula* (Lamarck), sample 234 (17 m).  
Fig. 14: *Adelosina longirostra* (D'Orbigny), sample 123 (10 m).

All magnifications X 80.





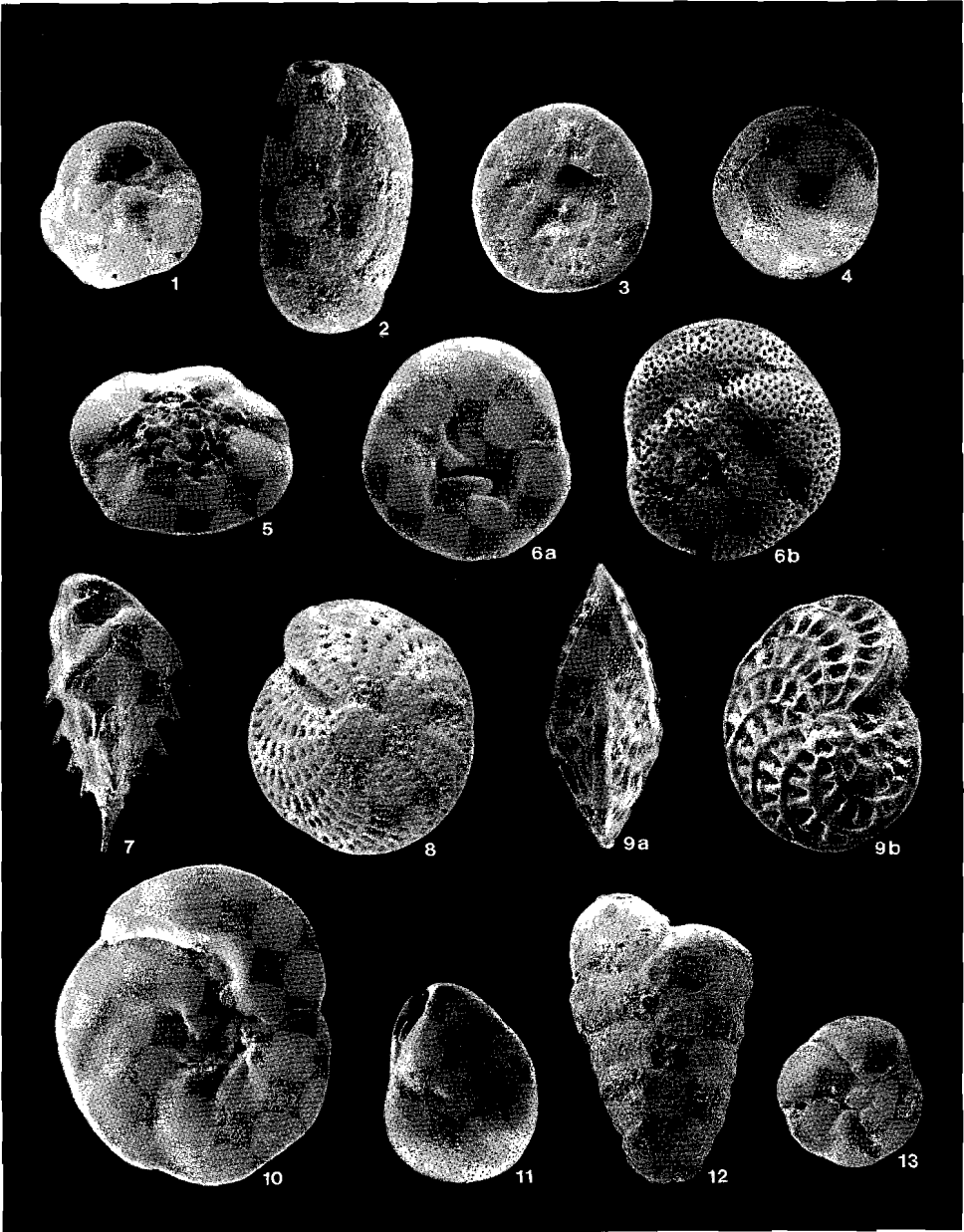
### Plate 3

(reproduced from Jorissen, 1987)

#### Taxa characteristic for Biofacial Unit III.

- Fig. 1: *Asterigerinata mamilla* (Williamson), ventral side, sample 171 (water depth 40 m).  
Fig. 2: *Quinqueloculina aspera* (D'Orbigny), sample 122 (8 m).  
Fig. 3: *Neoconorbina terquemi* (Rzehak), ventral side, sample 177 (58 m).  
Fig. 4: *Neoconorbina terquemi* (Rzehak), dorsal side, sample 171 (40 m).  
Fig. 5: *Buccella granulata* (Di Napoli Alliata), apertural view, sample 286 (99 m).  
Fig. 6a: *Rosalina bradyi* (Cushman), ventral side, piston-core 394, uppermost Pleistocene (Recent water depth 252 m).  
Fig. 6b: same specimen, dorsal side.  
Fig. 7: *Reussella spinulosa* (Reuss), sample 64 (40 m).  
Fig. 8: *Elphidium crispum* forma *crispum* (Linnaeus), sample 92 (8 m).  
Fig. 9a: *Elphidium crispum* forma *macellum* (Fichtel and Moll), apertural view, sample 182 (16.5 m).  
Fig. 9b: same specimen, side view.  
Fig. 10: *Hanzawaia boueana* (D'Orbigny), ventral side, sample 174 (45 m).  
Fig. 11: *Cassidulina oblonga* Reuss, sample 54 (70 m).  
Fig. 12: *Textularia sagittula* Defrance, sample 174 (45 m).  
Fig. 13: *Gavelinopsis praegeri* (Heron-Allen and Earland), ventral side, sample 171 (40 m).

All magnifications X 80, except fig. 8 (X 40).



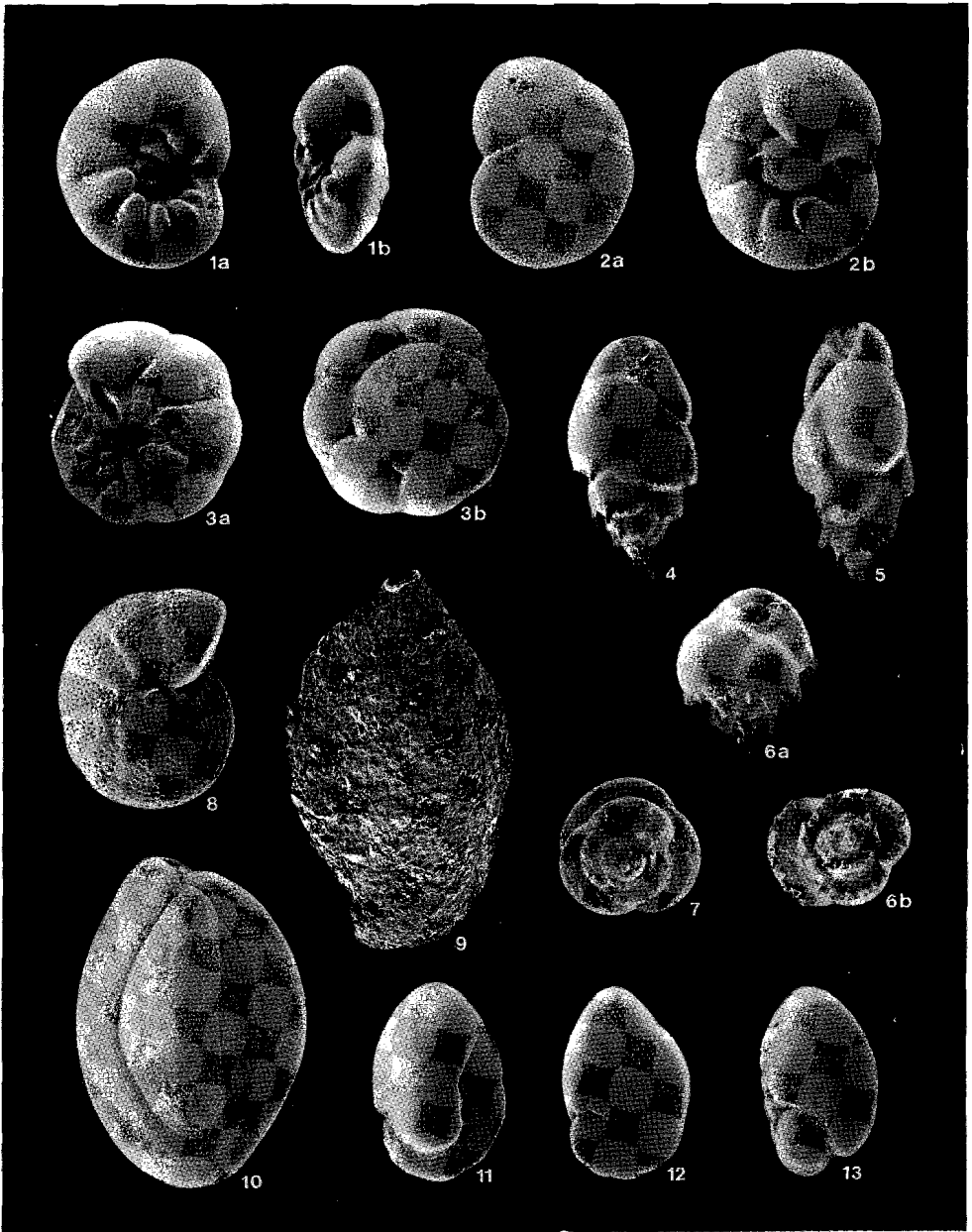
## Plate 4

(reproduced from Jorissen, 1987)

### Taxa characteristic for Biofacial Unit IV.

- Fig. 1a: *Valvulineria bradyana* (Fornasini), ventral side, umbilical chamber flaps broken off, sample 12 (water depth 80 m).  
Fig. 1b: same specimen, side view.  
Fig. 2a: *Valvulineria bradyana* (Fornasini), dorsal side, sample 12 (80 m).  
Fig. 2b: same specimen, ventral side, chamber flap of last chamber protruding into the umbilicus.  
Fig. 3a: *Pseudoeponides falsobeccarii* Rouvillois, ventral side, sample 99 (35 m).  
Fig. 3b: same specimen, dorsal side.  
Fig. 4: *Bulimina marginata* forma *denudata* Cushman and Parker, sample 195 (61 m).  
Fig. 5: *Bulimina marginata* forma *aculeata* D'Orbigny, sample 195 (61 m).  
Fig. 6a: *Bulimina marginata* forma *marginata* D'Orbigny, sample 282 (744 m).  
Fig. 6b: same specimen, bottom view.  
Fig. 7: *Bulimina marginata* forma *denudata* Cushman and Parker, bottom view, sample 195 (61 m).  
Fig. 8: *Nonion barleeianum* (Williamson), sample 245 (80 m).  
Fig. 9: *Sigmoilopsis schlumbergeri* (Silvestri), sample 169 (35 m).  
Fig. 10: *Quinqueloculina badenensis* D'Orbigny, sample 195 (61 m).  
Fig. 11: *Nonionella turgida* (Williamson), ventral side, sample 6 (40 m).  
Fig. 12: *Nonionella turgida* (Williamson), dorsal side, sample 186 (22 m).  
Fig. 13: *Nonionella turgida* (Williamson), side view, sample 6 (40 m).

All magnifications X 80.



## DISTRIBUTION OF BENTHIC FORAMINIFERA IN BIOFACIAL UNITS II AND IV

### III.1. INTRODUCTION

In comparison with other marine basins, the Adriatic Sea shows some specific features which have considerable consequences for the environmental conditions at the bottom and thus for the benthic fauna. As indicated before, particularly the combination of two of these factors, the anti-clockwise surface current system (fig. 2; Zore-Armanda, 1968) and the vast quantity of river runoff, is not only perceptible in the upper part of the water-column, but has far-reaching consequences for the benthic ecosystem as well. The fluvial discharge comes almost exclusively from Italian rivers; of these the Po, with an average annual discharge volume of some 50 km<sup>3</sup> (Jerlov, 1958), is by far the most important. The riverine waters transport enormous quantities of suspended clay, organic detritus and dissolved nutrients into the Adriatic Sea. In the last decennium, eutrophication of the water column due to increased nutrient input has become a regular phenomenon (Degobbis et al., 1979; Stirn, 1969), especially in the northern Adriatic Sea where phytoplankton blooms have occurred repeatedly as a function of the Po discharge (Revelante and Gilmartin, 1977, 1980; Galliani et al., 1983; Gilmartin and Revelante, 1983; Malanotte Rizzoli and Bergamasco, 1983). Both the unconsumed particulate organic matter and a considerable part of the phytoplankton remains are carried away by the surface currents, and subsequently deposited in a relatively small part of the basin: the northernmost part of the Adriatic Sea and the narrow zone parallel to the Italian coast (Van Straaten, 1965, 1970; Brambati et al., 1973; Colantoni et al., 1978). After sedimentation, these products oxidize, leading to the (almost) complete consumption of the available oxygen, especially in summer when the stratification of the water column is at its maximum (Giordani and Angiolini, 1983). In extreme cases this can even lead to the total elimination of benthic life (Stefanon and Boldrin, 1980). Due to this system strong environmental changes develop over short distances; these changes profoundly affect the distribution of benthic foraminifera.

A comparison of figures 3, 5 and 8 shows that our biofacial unit IV conforms to the area where the larger part of the clay fraction (including most of the organic detritus) is deposited (Van Straaten, 1965). The low diversity, the typical species composition, and the sometimes poor preservation (dissolu-

tion?! of the benthic foraminifera found in this zone strongly suggest the presence of (at least periodically) stressed conditions, probably related to the high input of organic matter, in extreme cases leading to oxygen depletion.

As stated before, the aim of the present study is to consider this zone (biofacial unit IV) in more detail. We are particularly interested in the way in which the faunas respond to this type of environmental stress; our earlier study suggested that the faunas not only react by changes in their composition, but also by the occurrence of (eco-)phenotypic variation along the stress gradient.

In the present paper the faunal response to stressed conditions will be considered from three different points of view. In this chapter (III) we shall adopt a community approach. We will describe the quantitative and qualitative changes in the foraminiferal associations along the stress gradient and try to explain these in the light of the available environmental information. In chapter IV we shall consider the faunas at population level: the phenotypic variation in three of our morphologically most variable genera will be discussed. In chapter V we shall speculate on the principles behind these ecophenotypic changes, considering factors such as feeding strategy, microhabitat differentiation, functional morphology and seasonality. Finally, in chapter VI, we shall demonstrate some of the possible applications of the present study on the basis of the faunal variations found in a piston-core that was taken in the outer part of the clay-belt.

### III.2. MATERIAL

For the present study, basically the same sample-set (see fig. 1, sampled in 1962) has been used as for the construction of the general biofacial scheme (chapter II and Jorissen, 1987). We selected all samples belonging to biofacial units II and IV (fig. 8), and used the same counting results (appendix III), although for the present study taxonomic subdivision was carried through much further (appendix IV). The 124 samples employed were treated in a similar way as described in chapter I.3.

Also for the present study basically an assemblage species concept was used, but now a number of intraspecific varieties were determined and counted at a forma level as well. It should be emphasized that the distinction between morphotypes in gradual variations forced us more than once to make a highly subjective choice.

Although the samples were not stained, and the associations should in fact be considered as taphocoenoses, there are several arguments which convinced us that in most samples of biofacial units II and IV the faunas have not been displaced, and thus give a good (although not always complete) impression of the recent standing stock:

-- for most species, all size classes (juvenile as well as adult) are present in a given sample,

-- the diversity of the faunas is often very low, suggesting the absence of species added by displacement,

-- individual species tend to occur within a narrow depth range.

There are nevertheless three important reasons why the faunas are not fully comparable to the recent standing stocks:

-- a number of agglutinated taxa (e.g. *Reophax* spp., *Eggerella scabra*, *Discamina compressa*) are probably often underrepresented (or missing) due to rapid decomposition of the skeleton after death (Bizon and Bizon, 1985),

-- in some samples, mostly those close to the river Po outlets, strong signs of dissolution processes have been found. Particularly miliolids appear to be extremely vulnerable; sometimes only some extremely damaged, hardly determinable fragments are present (plate 25),

-- in some of the samples of the shallowest localities, obviously reworked specimens are present. The presence of reworked elements in a sample can be recognized not only from the poor preservation of the foraminifera, but also from a comparison with samples from the same water depth without reworked elements.

### III.3. RESULTS

On the basis of the 40 most frequent taxa an R-mode cluster analysis has been performed, using the computer programs BALANC (Drooger, 1982) and DENDRO. The program BALANC, based on the open covariance model, corrects for possible closed-sum (squeezing) effects. In our case, this is particularly relevant in view of the considerable fluctuations in the dominating faunal elements.

In the resulting dendrogram (fig. 11), eight clusters of benthic foraminifera can be recognized if a cut-off level of 0.190 is used. The frequencies of the taxa belonging to these clusters were summed, and the correlation between these cumulative frequencies and the values of four environmental parameters (directly measured on the same sample-set) were calculated. The results of these bivariate analyses are given in table II.



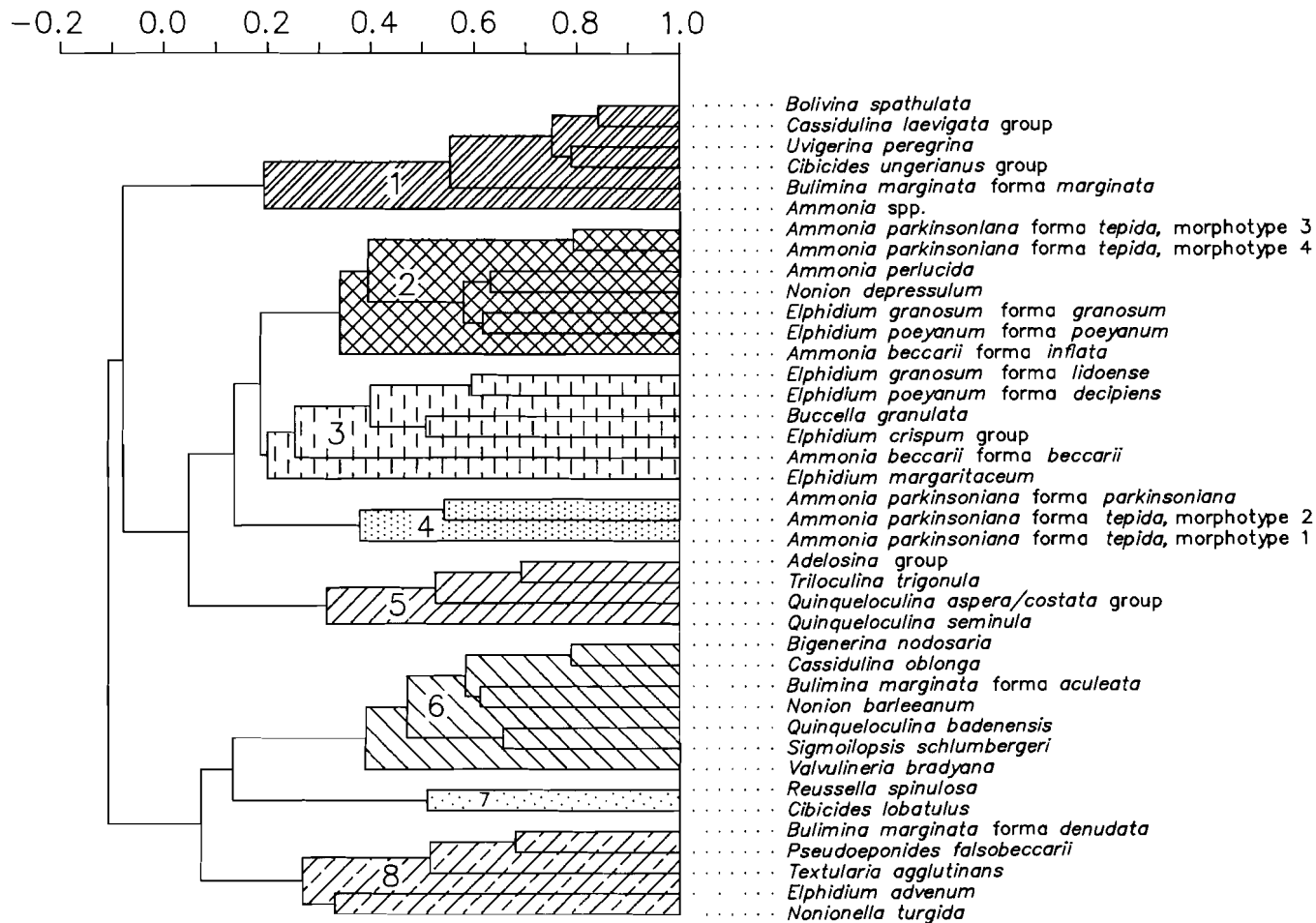


Fig. 11. Dendrogram based on an R-mode cluster analysis, and eight clusters recognized.

	Water Depth	Percentage fraction < 50 mu.	Percentage of CaCO <sub>3</sub>	Percentage of organic matter
Cluster 1	<b>-.167</b>	<b>.578</b>	.102	<b>-.398</b>
Cluster 2	<b>-.349</b>	<b>-.236</b>	.085	.114
Cluster 3	<b>-.425</b>	<b>.270</b>	<b>.327</b>	<b>-.418</b>
Cluster 4	<b>-.633</b>	<b>.325</b>	<b>-.023</b>	<b>-.391</b>
Cluster 5	<b>-.280</b>	<b>.487</b>	<b>.719</b>	<b>-.342</b>
Cluster 6	<b>.944</b>	<b>-.285</b>	<b>-.262</b>	<b>.301</b>
Cluster 7	<b>.301</b>	<b>.029</b>	<b>-.053</b>	<b>.064</b>
Cluster 8	<b>.407</b>	<b>-.523</b>	<b>-.347</b>	<b>.491</b>

Table II. Correlation coefficients between the cumulative frequencies of the taxa forming the eight clusters resulting from the R-mode analysis and some measured environmental parameters. Significant values (95 % confidence interval) are in bold.

To show the geographical distribution of the eight clusters, ten successive sample transects, all perpendicular to the coast, were selected from the original sample-set (fig. 12). The cumulative frequencies of the clusters have been plotted against the distance of the sample locality from the coast (fig. 13). This figure also includes curves for the water depth, the percentages of sand fraction, organic matter and calcium carbonate in the substratum, next to measures of foraminiferal diversity (number of species) and density (number of specimens per gram dry weight). These curves show that important environmental and faunal changes do indeed take place over short distances, not only along these transects, but also in a NW-SE direction, parallel to the Italian coast. The most important environmental and faunal changes are as follows:

- the continental shelf becomes steeper in south-eastern direction; a greater water depth is reached at a shorter distance from the coast. Coinciding with this, faunal changes take place over shorter distances and become more distinct.
- in most of the transects, the samples from the shallowest localities contain

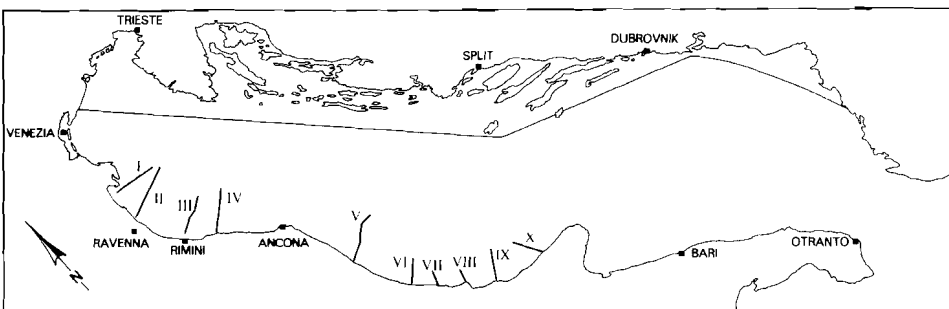


Fig. 12. Position of the ten sample transects perpendicular to the Italian coast (see also figure 13).

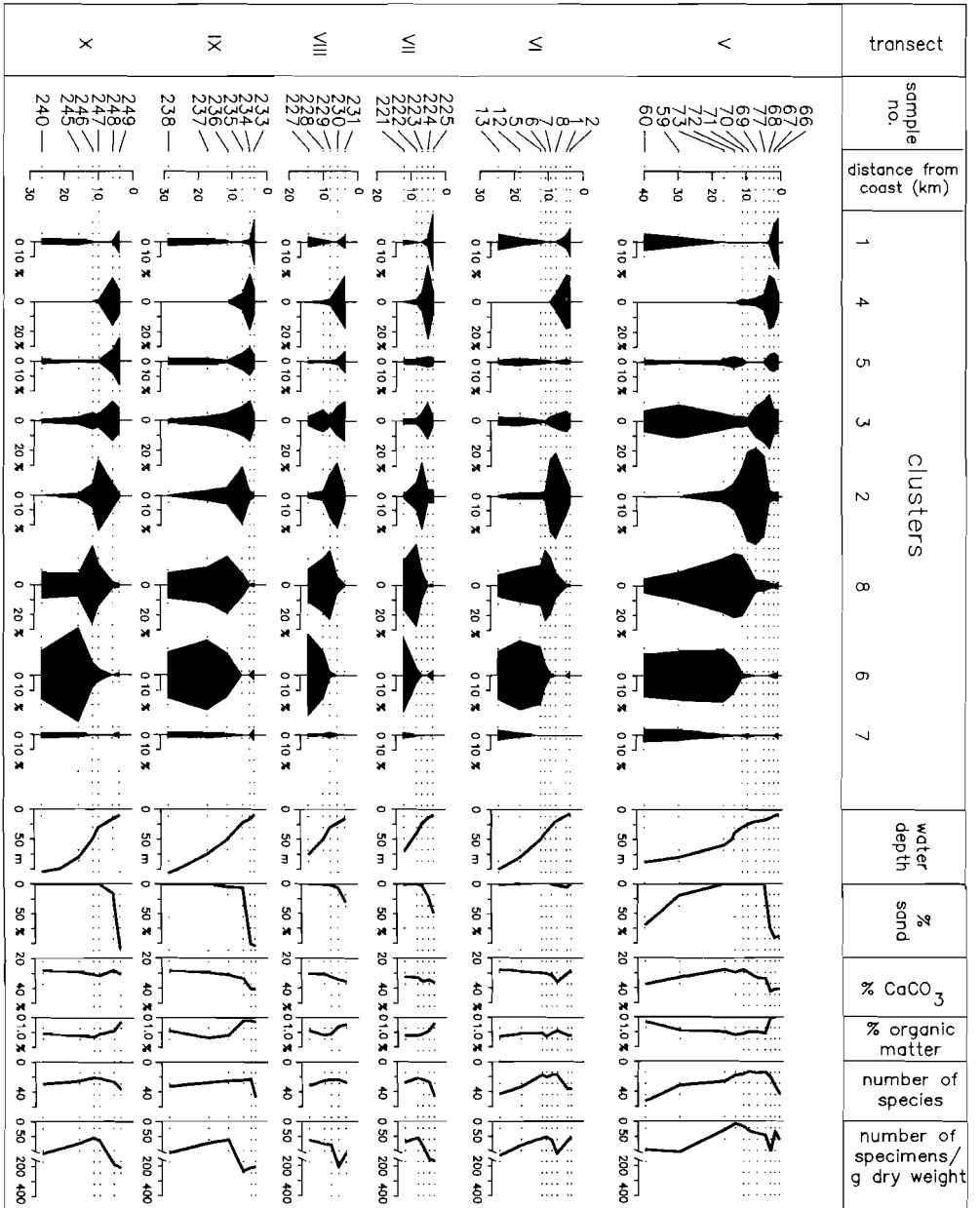
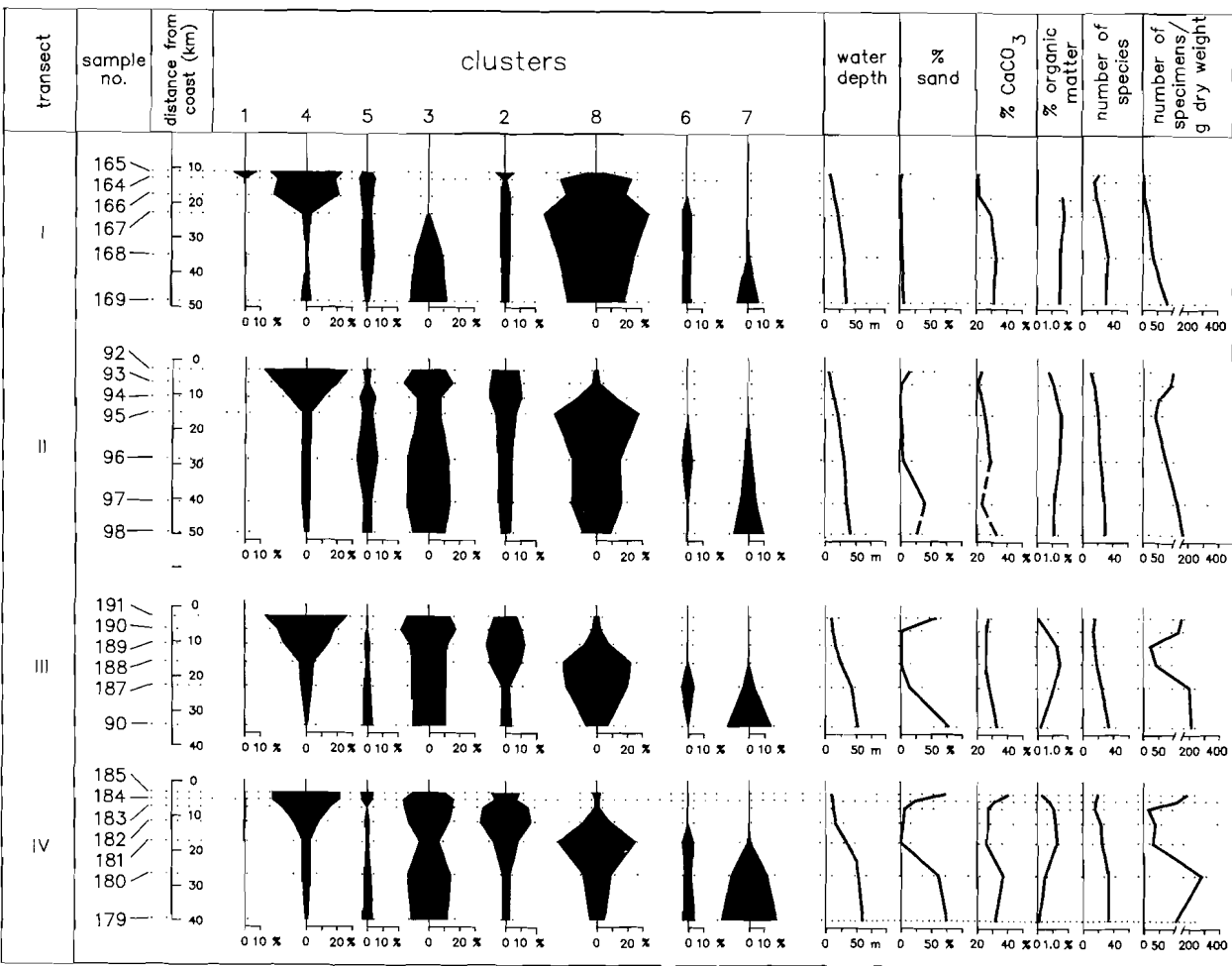


Fig. 13. Cumulative frequencies of the 8 clusters in the ten sample transects, together with some environmental and some other faunal parameters. All values have been plotted against the distance of the sample locality from the Italian coast.



a high percentage of sand (fig. 3), originating from coastal erosion and local runoff (Van Straaten, 1965). The sharp decrease in grain-size in the somewhat 'deeper' samples indicates the transition to the zone influenced by (Po-) runoff products deposited by the long-shore current system.

-- in the five northernmost transects, the sediment becomes sandier again in the samples from the deepest localities (compare fig. 3), which are located on the (Pleistocene) sandy part of the shelf (biofacial unit III in fig. 8). In the other five transects, the percentage of the sand fraction in the 'deeper' samples (belonging to biofacial unit I) remains below 1%.

-- in the two northernmost transects, located under the direct influence of the main Po outlets, suspended material is dispersed in a broad zone, and the percentage of organic matter in the sediments is relatively high ( $> 1\%$ ) in all samples (compare fig. 5). More southwards, sedimentation of suspended matter becomes more and more restricted to a relatively narrow zone that is characterized by maximum percentages of organic matter in the sediment. The depth of the zone of high contents of organic matter increases slightly in south-eastern direction; from 15 - 40 m in transects II and III to 40 - 80 m in the southernmost transects. In these last-mentioned transects the maximum percentages of organic matter are somewhat higher than in the more northern ones. Generally maximum percentages of organic matter roughly coincide with very low percentages of calcium carbonate. In the zone with highest percentages of organic matter, the number of taxa and the number of foraminifera per gram dry weight tend to reach minimum values.

#### III.4. DISCUSSION

On the basis of the rather meagre environmental information we have at our disposal, we can speculate about the ecological significance of the 8 clusters recognized. As can be seen from figure 11, they can be divided roughly into three groups: clusters 2 - 5, clusters 6 - 8 and the separate cluster 1. The separation into the two main groups (2-5 versus 6-8) corresponds to a difference in bathymetric distribution (table II). Clusters 2 - 5 comprise all relatively shallow-living taxa, whereas clusters 6 - 8 consist of relatively deep-living taxa.

The geographical distribution of cluster 1 is somewhat peculiar. Although it is mainly composed of species which are known as rather deep-living (*Bolivina spathulata*, *Cassidulina laevigata*, *Uvigerina peregrina*, *Bulimina marginata* forma *marginata* and biconvex morphotypes of *Cibicides*), maximum cumulative frequencies for this cluster are found in the most near-shore zone (7.5 - 12.5 m). Figure 13 and table II show that these maximum values coincide perfectly with high percentages of sand fraction. The most likely explanation for the presence

of these taxa in near-shore sediments is that they originate from reworking of Miocene and Pliocene deposits. The often poor preservation provides supporting evidence for this explanation. The near-shore samples that contain low numbers of cluster 1 give a better insight into the autochthonous standing stock. The increase of the cumulative frequencies of cluster 1 in the 'deepest' samples of the southernmost transects can be explained by the fact that at present taxa as *Cassidulina laevigata* forma *carinata* and *Bulimina marginata* forma *marginata* show a strong increase in frequency at about 80 m.

The group of relatively deep-living species is divided into three clusters. The two quantitatively most important clusters, 6 and 8, show a comparable pattern of correlation with the environmental parameters measured: significant negative correlations with the percentages of sand fraction and calcium carbonate and a significant positive correlation with the percentage of organic matter. As is shown in figure 13, in each transect cluster 8 dominates the faunal association in one or more samples; maximum frequencies are not so much dependent on water depth, but correspond roughly to maximum percentages of organic matter. In the two most north-western sample transects, under the direct influence of the main Po outlets, cluster 8 reaches highest values and dominates nearly all associations in the relatively broad geographic zone between 20 and 40 m water depth. More to the south the zone with a dominance of cluster 8 becomes much narrower, and maximum frequencies are found between 40 and 60 m in the southernmost transects. In contrast, the taxa of cluster 6 are nearly absent in transects I to IV, where the substratum is sandy in the 'deepest' samples. However, they are highly frequent in the more south-eastern transects between 60 and 80 m, in samples from clayey substrata.

Both clusters seem to comprise taxa which tolerate (or prefer) elevated concentrations of organic matter. There are however some distributional differences between the two clusters. The species of cluster 6 have a much stronger positive correlation with water depth than those of cluster 8 (table II), whereas the cumulative frequencies of the latter cluster have much stronger correlations with the percentages of sand fraction, calcium carbonate (both negative) and organic matter (positive). If for each of the two clusters we only consider those samples with cumulative frequencies higher than 10%, this pattern becomes even more enforced. The relation between cluster 8 and organic matter remains highly significant ( $r = .465$ ,  $n = 83$ ), whereas it reduces to insignificant values for cluster 6. The correlation between cluster 8 and water depth is no longer significant. From this we conclude that the distribution of the species constituting cluster 8 could be more dependent on high concentrations of organic matter (large food availability) than that of the species forming cluster 6. It is

then only a small step to the assumption that the species belonging to cluster 8 have somewhat more tolerance for (or are even relatively advantaged by) the stressed conditions, such as shortage of oxygen, which co-vary with the high concentrations of organic matter. In our opinion the taxa belonging to cluster 6, which seem to require a minimum water depth of 40 m, replace the taxa of cluster 8 as dominant elements in the faunas at the outer edge of the clay belt, where the decreased input of organic detritus no longer leads to periodically stressed conditions. Within cluster 6, *Valvulineria bradyana* seems to be the taxon with the highest tolerance for stressed conditions, as is indicated by its peak occurrences in the southern part of the Adriatic Sea (appendix III).

Cluster 7 consists of two species only: *Reussella spinulosa* and *Cibicides lobatulus*. As was concluded earlier (Jorissen, 1987), both species have some relation with the presence of a vegetation cover; possibly both have an epiphytic mode of life. For *Reussella spinulosa* a certain preference for a sandy substratum with a low input of clay was deduced (Jorissen, 1987). From fig. 13 it is clear that cluster 7 is found mainly on the outer edge of the clay belt and that the percentages diminish dramatically south-west of the sand platform.

In the group of shallow water clusters, a more or less similar correlation pattern with the content of organic matter can be observed, although the differences between the clusters are not as obvious. Clusters 3, 4 and 5 all show significant positive correlations with the percentage of the sand fraction, and significant negative correlations with the percentage of organic matter (table II). Cluster 2 however has a significant negative correlation with the percentage of the sand fraction and an almost significant positive correlation with the percentage of organic matter.

The taxa of cluster 2 are abundant in a shallow zone parallel to the coast, where high percentages of organic matter are still found. It is noteworthy that cluster 2 is relatively infrequent in the northernmost transect, but seems to increase at the expense of cluster 8 further southwards. The distribution of the taxa of cluster 3 is more balanced; they are present with more or less the same abundances in a relatively broad zone. Minimum frequencies are found in samples where cluster 2 reaches maximum values, viz. the shallowest samples with a high percentage of organic matter.

When interpreting the differences in distribution of clusters 2 and 3, it is useful to bear in mind that these clusters are largely composed of morphotypes belonging to the same few species. In chapter IV the distribution of these morphotypes will be discussed in further detail. For the moment we suggest that ecologically cluster 2 could be comparable to cluster 6; these taxa seem to prefer a relatively high percentage of organic matter (large food availability) as long

as this does not lead to severe shortage of oxygen. Unexpectedly, the closely related taxa of cluster 3 (partially belonging to the same species) do not show such a relation with the amount of organic matter, and seem to be even more intolerant of stressed conditions.

The distribution of clusters 4 and 5 is even more difficult to interpret. Cluster 4 is composed of three (uncoloured) morphotypes of *Ammonia parkinsoniana* (determined as *Ammonia beccarii tepida* in Jorissen, 1987). Numerically the cluster is strongly dominated by forma *parkinsoniana*. The cluster occurs in extremely high frequencies just in front of the main Po outlets and in fairly high numbers in a narrow zone parallel to the Italian coast, at a water depth of between 10 and 15 m. In the first area mentioned (which geographically is directly linked to a zone with maximum frequencies of the stress tolerant cluster 8, see figure 14) the preservation of the tests is often rather poor. *Ammonia parkinsoniana*, *Elphidium advenum* and especially in the miliolids show traces of dissolution (see pl. 25). If we consider only the samples with frequencies higher than 10 %, a strong negative correlation with the percentage of calcium carbonate is found ( $n = 64, r = -.408$ ) and the correlation with organic matter is no longer present. In chapter IV we shall conclude that *A. parkinsoniana* is tolerant of large fluctuations in a number of environmental parameters. The typical form (forma *parkinsoniana*), which strongly dominates cluster 4 numerically, might be especially tolerant of lowered salinities caused by local runoff. The way in which the morphology of the species changes in answer to these fluctuations will be treated in chapter IV.

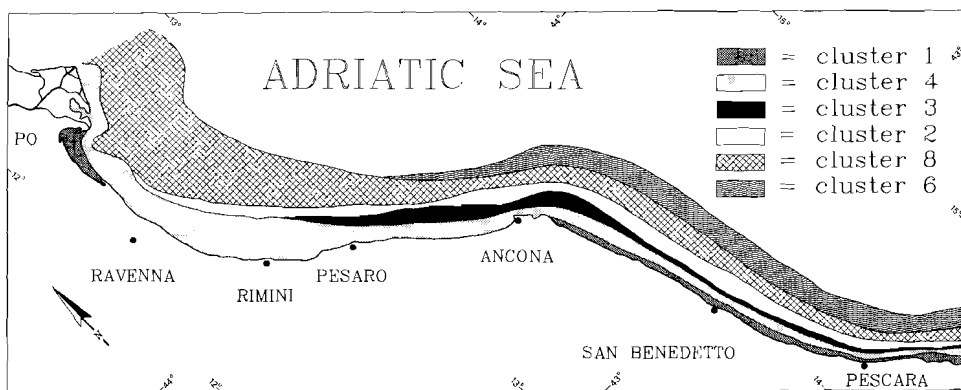


Fig. 14. Geographic distribution of the zones dominated by each of the six quantitatively most important clusters of figure 11.



Cluster 5 consists of miliolids only. The correlation with the percentage of  $\text{CaCO}_3$  is highly significant, even if only samples with high percentages (> 10%) of this cluster are considered ( $r = 0.67$ ,  $n = 23$ ). Maximum values are found in the north-eastern part of the Adriatic Sea (biofacial unit III of Jorissen, 1987) and in a comparatively small zone parallel to the coast, deepening slightly in southern direction. The strong correlation with the percentage of calcium carbonate suggests that the availability of calcium carbonate may act as a limiting factor for these species.

In transects IV, V and VI the percentages of cluster 5 are almost zero in the samples with maximum frequencies of clusters 2 and 8. In our opinion this points to a strong undersaturation of calcium carbonate in the bottom water at these localities. These low percentages of miliolids could even be caused by a periodical activity of dissolution processes in this zone characterized by high concentrations of organic matter. The bad preservation of the scarce miliolids found (pl. 25) and the fact that miliolids are more susceptible to dissolution processes than most other benthic foraminifera (Douglas and Woodruff, 1981) supports this speculation.

The geographical distribution of the six quantitatively most important clusters has been summarised in fig. 14; each sample is assigned to the cluster numerically dominating its fauna. The mapping of a number of clusters recognized on the basis of the first two axes of a principal components analysis (only the first of which was significant) yielded a more or less comparable picture. In figure 14, the zonation parallel to the coast is obvious, although it is more clearly developed in the south-eastern than in the north-western part of the Adriatic Sea. In our opinion this can be explained by an increasingly stable environment at a greater distance from the Po delta. Closer to the main outlets, the larger (partially seasonal) environmental fluctuations cause a much wider temporarily stressed zone (dominated by cluster 8) and prevent the establishment of a more complete faunal succession.

In our opinion the succession of the clusters 3,2,8 and 6 in the southern part of the Adriatic Sea can be seen as a function of one (complex of) primary factor(s) only; the taxa composing the latter three clusters (2, 8 and 6) seem to have a preference for an ample food availability, and it is their tolerance of stressed conditions that further determines their areal distribution. In the zone of maximum stress cluster 8 is dominant, whereas clusters 2 and 6 occupy parallel zones where stressed conditions are less (often) prevalent. Cluster 3 seems to occur outside the zone influenced by Po runoff, where stressed conditions usually are absent.

## Chapter IV

### PHENOTYPIC VARIATION

#### IV.1. INTRODUCTION

In the previous chapter we suggested that a faunal association has two different ways of coping with increasing environmental stress. On the one hand a part of the faunal association can be replaced by taxa having a greater tolerance for stressed conditions, and on the other hand taxa seem to react by adapting their morphology.

In benthic foraminifera ecophenotypic variation is a very common phenomenon; numerous examples have been described, especially for shallow-living taxa such as *Ammonia* and *Elphidium* (a.o. Feyling-Hansen, 1972; Schnitker, 1974; Wilkinson, 1979; Miller et al., 1982; Vénec-Peyré, 1983). As stated before, in our material too we observed strong morphological differences in a number of taxa along transects perpendicular to the coast. As these variations coincide with important environmental changes, they can well be interpreted as being of ecophenotypic nature. In some of these taxa, belonging to the genera *Ammonia*, *Bulimina* and *Elphidium*, the large morphological variation enabled us to recognize a number of morphotypes and to count these separately. These morphotypes proved to have a distinct geographical distribution, as is evident from their position in the clusters resulting from the R-mode analysis (fig. 11):

-- <i>Ammonia beccarii</i> :	forma <i>beccarii</i> -----	cluster 3
	forma <i>inflata</i> -----	cluster 2
-- <i>Ammonia parkinsoniana</i> :	forma <i>parkinsoniana</i> -----	cluster 4
	forma <i>tepida</i> , types 1-2 -----	cluster 4
	forma <i>tepida</i> , types 3-4 -----	cluster 2
-- <i>Elphidium granosum</i> :	forma <i>granosum</i> -----	cluster 2
	forma <i>lidoense</i> -----	cluster 3
-- <i>Elphidium poeyanum</i> :	forma <i>decipiens</i> -----	cluster 3
	forma <i>poeyanum</i> -----	cluster 2

-- <i>Bulimina marginata</i> :	forma <i>denudata</i> -----	cluster 8
	forma <i>aculeata</i> -----	cluster 6
	forma <i>marginata</i> -----	deep water, biof. unit I.

In each case one of the morphotypes is placed in a cluster influenced by Po runoff, whereas the other morphotype is found in a cluster characterized by taxa occurring under more sheltered conditions. This is precisely the situation one would expect if there is ecophenotypic adaptation along an environmental gradient, such as the one caused by the input and distribution of (primary and secondary) runoff products.

Ecophenotypic variation is observed not only in the species mentioned before, but also in the *Adelosina* group, *Quinqueloculina seminula*, *Triloculina trigonula*, *Elphidium crispum* and in *Textularia agglutinans*. In this chapter some of the best documented examples of phenotypic variation will be described in more detail, and an attempt will be made to explain the distribution of the various morphotypes as a function of the environmental changes.

## IV.2. GENUS AMMONIA BRÜNNICH, 1771

### IV.2.1. Introduction

Representatives of the 'beccarii-group' of the genus *Ammonia* are dominating elements in shallow water associations all over the world. In this respect the Adriatic Sea is no exception. Although the primary objective of the present study is certainly not a taxonomical one, and we therefore tend to neglect problems concerning the generic designation of the different species, the apparent relation between morphological variation and environmental parameters warrants a closer inspection of the taxonomical coherence between the various morphotypes observed in our associations.

In the last decennia, two main taxonomical concepts have been proposed for the 'beccarii-group':

1) a number of authors recognize a wide range of morphologically closely related forms, and determine these either as varieties/forms of *A. beccarii*, if considered to be the result of ecophenotypic variation (e.g. Chang & Kaesler, 1974; Schnitker, 1974), or as separate species (e.g. Hofker, 1971; Banner and Williams, 1973).

2) Bermudez (1952) was the first to consider the complex of South and Central-American morphotypes as being different from the typical (Mediterranean) *A. beccarii*. This concept was elaborated by Poag (1978), who concluded

that two different 'morphostocks' exist. *A. parkinsoniana* (D'Orbigny) is the oldest name available for the Western Atlantic morphostock, which does not include typical *A. beccarii*. To this stock belong morphotypes such as *batava* Hofker, *catesbyana* D'Orbigny, *flevensis* Hofker, *pauciloculata* Phleger and Parker, *sobrina* Shupack and *tepida* Cushman. *A. beccarii*, constituting the second (Mediterranean and Eastern Atlantic) morphostock, should include forms such as *inflata* Seguenza and *viennensis* D'Orbigny. Poag (1978) further noted the joint occurrence of representatives of the two groups in England and, citing Hofker (1960), in the Mediterranean.

The Adriatic Sea material strongly favours the second concept; two distinct morphogroups, with the characteristics as described by Poag, are present. Although each of these groups exhibits a wide range of morphological variation, a transition between the two was not observed. In our opinion this is sufficient reason to distinguish the two groups at the species level as *Ammonia beccarii* and *Ammonia parkinsoniana*. In this chapter we shall discuss not only these two species, but also the distribution of *Ammonia perlucida* (Heron-Allen and Earland) and of *Pseudoepionides falsobeccarii* Rouvillois, which seems to be closely related to *A. parkinsoniana*.

## IV.2.2 Distribution

### IV.2.2.1. *Ammonia beccarii* (Linnaeus, 1758)

The frequency distribution of *A. beccarii* is depicted in figure 15. Our material reveals a gradual transition between two extreme morphotypes; *A. beccarii* forma *beccarii* and *A. beccarii* forma *inflata*. Along the Italian coast, at water-depths of less than 20 m, forma *beccarii* dominates the *A. beccarii* populations (fig. 16). Highest abundances of *Ammonia beccarii* are found at a water depth of between 15 and 20 m, in samples with intermediate percentages of organic matter (0.8 - 1.1%), in which at least some sand fraction (> 2%) is present. The species is totally absent in the area directly in front of the main Po outlets (samples 153-167).

Populations dominated by forma *inflata* occur in two essentially different habitats. On the one hand highest abundances of this morphotype can be found in the northernmost part of the Adriatic Sea (biofacial unit IV, see figure 8), where a sandy substratum prevails and the percentages of organic matter are low (0.2 - 0.8%). On the other hand populations dominated by forma *inflata* are also present on the clayey substrata (less than 2% sand fraction) along the Italian coast, between 20 and 60 m water depth, where the percentage of organic matter in the sediment is relatively high ( $\geq 1\%$ ).

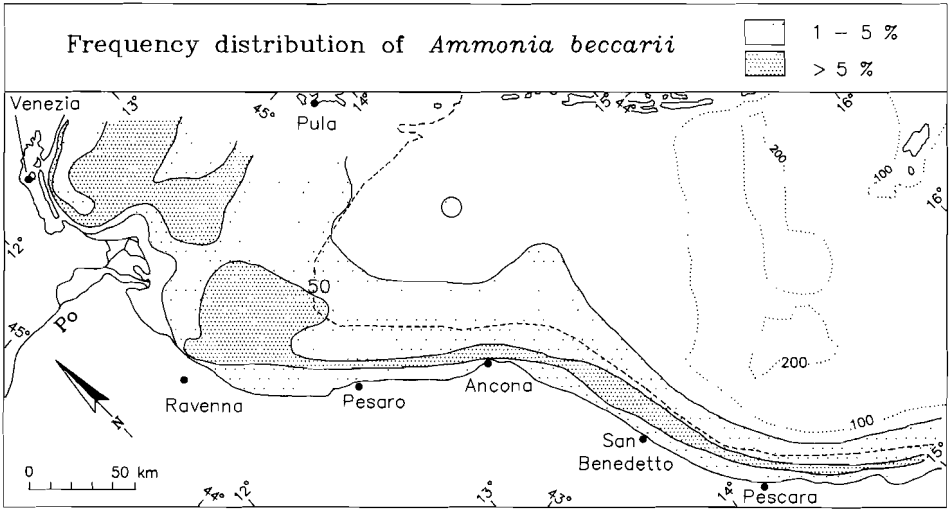


Fig. 15. Frequency distribution of *Ammonia beccarii*; the cumulative frequencies of both morphotypes have been mapped.

On the sandy substrata in the northern part of the Adriatic Sea, part of the *A. beccarii* populations consists of very large, heavily ornamented specimens, which do not occur on the clayey bottoms. Very characteristic for the faunas of this area are the high frequencies of *Buccella granulata* (up to 20%) and the relatively low frequencies of typical epiphytic taxa such as *Asterigerinata mamilla* and *Neoconorbina terquemi*.

In our opinion the food requirements of forma *inflata* are higher than those of forma *beccarii*, as is indicated by their respective positions in clusters 2 and 3 (fig. 11). The distribution of forma *beccarii* at the upper edge of the clay belt seems to indicate that its tolerance of stressed conditions is limited. In the central, more stressed part of the clay-belt, it is replaced by the somewhat more stress-tolerant forma *inflata*.

The apparent inconsistency in the distribution of forma *inflata*, which pertains to two different biotopes (i.e. sandy versus clayey substrata), has also been mentioned from other areas. Hageman (1979, p. 77), who reviewed relevant literature, interpreted the paradoxical distribution pattern of forma *inflata* as 'a preference for ill-defined clayey habitats with normal marine salinities in or in the vicinity of a vegetated area'. In the Ria de Arosa (Galicia, Spain; Van Voorthuysen, 1973) this morphotype also appears on clayey bottoms, which are food-enriched as a result of upwelling near the Galician coast occurring between March and November (Koldijk, 1968). As mentioned before, in the

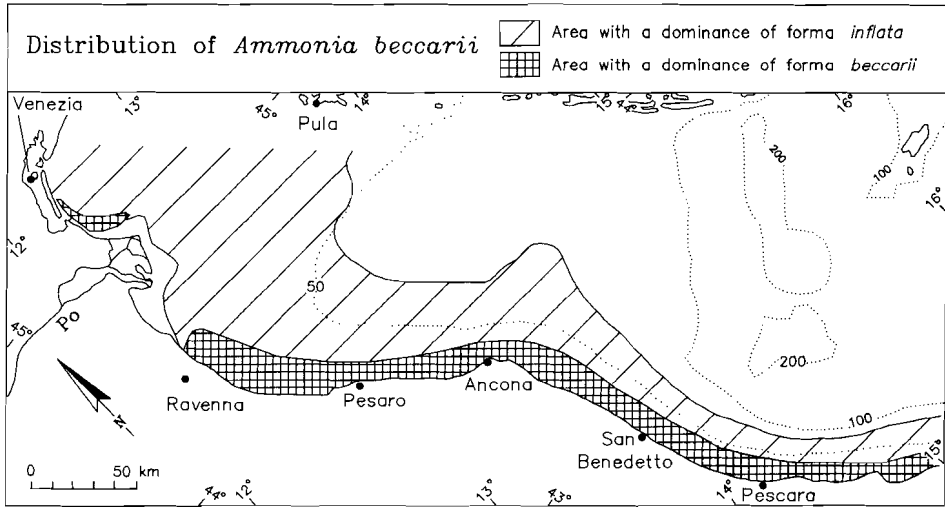


Fig. 16. Distribution of the morphotypes of *Ammonia beccarii*.

Adriatic Sea high phytoplankton standing stocks develop in autumn and spring under the influence of the input of nutrients by runoff, especially in the two zones where *forma inflata* occurs (Revelante and Gilmartin, 1977).

We think that *forma inflata* is quite independent of the type of substratum, but prefers an increased availability of some particular type of food. On clayey substrata (normally without vegetation) it is probably an epi-benthic deposit-feeder, whereas on the amply vegetated sandy substrata the larger and more ornamented forms could live and collect the same food elements on the vegetation cover. The definitely higher abundances reached in the well-vegetated northern Adriatic Sea could then be explained by the combination of a considerable increase in the dimensions of the niche and a much smaller influence of a shortage of oxygen at a greater distance from the actual bottom. A similar difference in the ornamentation (and inflatedness) between non-epiphytic and epiphytic morphotypes has also been described for *Amphistegina* (Larsen, 1976).

*Buccella granulata*, which also reaches much higher frequencies on the sandy deposits from the northern Adriatic than in the samples used for the present study, may have a similar ecological strategy.

The absence of a clear correlation between the distribution of *forma beccarii* and the influence of Po-runoff could indicate that this morphotype has adopted another feeding strategy, for instance feeding by means of symbiotic algae, which are claimed to occur in the genus *Ammonia* by Haynes (1965).

#### IV.2.2.2. *Ammonia parkinsoniana* (D'Orbigny, 1839)

The forms which in this study have been assigned to *A. parkinsoniana* are mainly morphotypes which in the past have often been labelled as *tepida*. Following Poag (1978), we are obliged to the use of the oldest name available, namely *parkinsoniana*. Since Le Calvez (1977) found no types of *Rotalia catesbyana* in the D'Orbigny collections, that name obviously is less suitable.

Although most of the Adriatic Sea material belongs to the lobate *tepida* type, the group is still extremely variable. Large differences in test morphology have been observed, but the extreme morphologies are always linked by intermediate associations and/or morphotypes. The most variable features are the lobate-ness of the test, the inflation of the chambers, the structure and ornamentation of the umbilical region, and finally the colour of the test. On the basis of these differences five morphotypes were distinguished:

*Morphotype 1*: white (uncoloured), thin-shelled, probably megalospheric morphotypes with extremely inflated chambers, a lobate outline, rounded pores, a large first chamber, with 6 - 7 chambers in the last whorl (pl. 7, fig. 1).

*Morphotype 2*: white (uncoloured), lobate morphotypes with a smaller first chamber, but otherwise being more or less similar to morphotype 1 (pl. 7, fig. 2-4, pl. 8, fig. 4-6).

*Morphotype 3*: brown (coloured), thin-shelled morphotypes with a lobate outline and 6 - 7 inflated chambers in the last whorl (pl. 10, fig. 1).

*Morphotype 4*: brown (coloured) morphotypes with a rounded outline and 7 - 9 chambers in the last whorl (pl. 10, fig. 2-3).

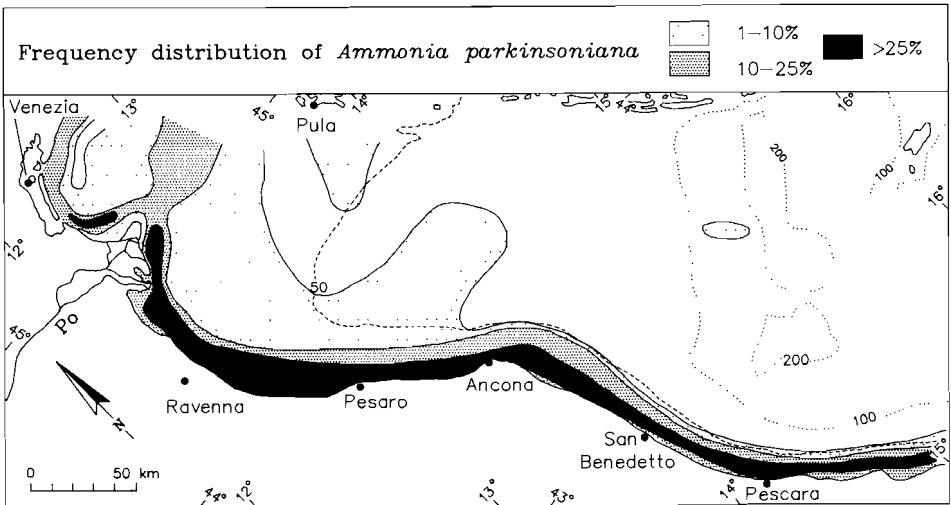


Fig. 17. Frequency distribution of *Ammonia parkinsoniana*; the relative frequencies of all (five) morphotypes have been summed and mapped together.

*Morphotype 5*: white (colourless), rounded, relatively large, thickly calcified morphotypes (pl. 9, fig. 1-4), with uninflated chambers, 8 - 9 in the last whorl, and a closed umbilicus in which a conspicuous umbilical knob may be present.

Unlike morphotypes 1 - 4, which are all assigned to *A. parkinsoniana* forma *tepida*, morphotype 5 more closely resembles the typical form, and is determined as *A. parkinsoniana* forma *parkinsoniana*. Extreme morphotypes of forma *parkinsoniana* with a very large umbilical boss (pl. 9, fig. 1) strongly resemble the *sobrino*-type (*Rotalia beccarii* var. *sobrino*, Shupack, 1934).

In figure 17 the cumulative frequencies of all five morphotypes together have been mapped. A closer inspection of the distribution of the individual morphotypes reveals that the distribution patterns of morphotypes 1 and 2, and also those of morphotypes 3 and 4, are more or less comparable. Therefore the frequencies of 1 and 2, and of 3 and 4, have been lumped for the construction of figure 18, which depicts the areal distribution of the populations dominated by the different morphotypes.

*A. parkinsoniana* forma *parkinsoniana* (morphotype 5), which strongly dominates our faunal cluster 4 numerically, is often very frequent in the shallowest faunal assemblages. All along the Italian coast between 10 and 20 m water depth it dominates the populations of *A. parkinsoniana*, apparently irrespective of substratum type and percentage of organic matter. On the sandy bottoms in the northern Adriatic Sea (fig. 8: biofacial unit III) it is the only morphotype of *A. parkinsoniana* that is present.

We agree with Seiglie (1975) that this morphotype is typical for relatively clean environments, although we think that its tolerance for the effects of in-

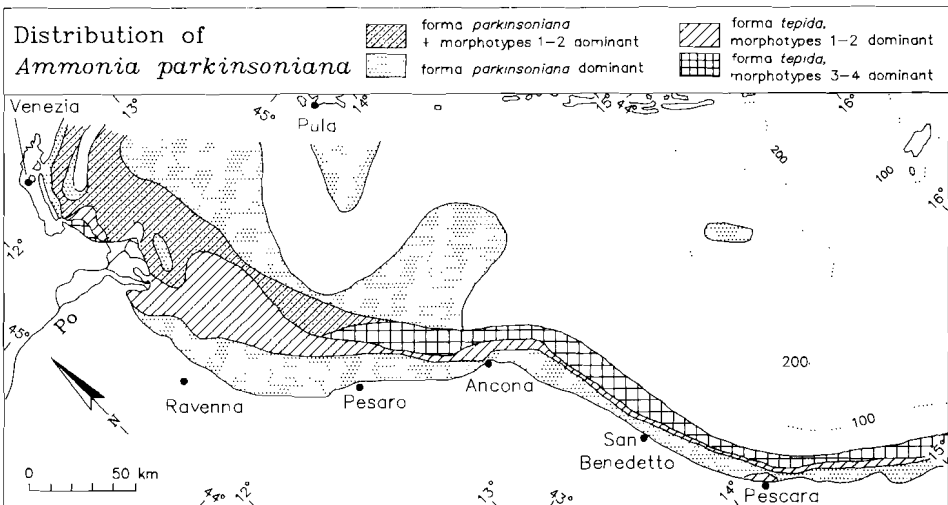


Fig. 18. Distribution of the morphotypes of *Ammonia parkinsoniana*.



creased nutrient supply could well be larger than for instance that of *A. beccarii* forma *beccarii*. The latter normally occurs in the same associations, but it is totally absent in front of the main Po outlets. In our opinion the factor which causes both forma *parkinsoniana* (morphotype 5) and the uncoloured morphotypes of forma *tepida* (1 and 2) to be joined in faunal cluster 4 can well be their tolerance of the lowered salinities found in the proximity of the river mouths.

Remarkable is the presence of *parkinsoniana*-types in samples 208 and 212 (water depth 121 and 130 m respectively), just north of the central Adriatic depression. According to Van Straaten (1965), the delta of the Po was situated in this area during the latest Pleistocene. The presence of the (obviously fossil) *parkinsoniana*-types in those samples is yet another argument in favour of a much shallower water depth in the past.

The distribution of forma *tepida* (morphotypes 1 - 4) appears to have a very close relation with the Po runoff system. Morphotypes 1 and 2, representing the uncoloured part of the variation, are dominating faunal elements in an aur-like zone around the Po delta, in samples with high percentages of organic matter ( $\geq 1\%$ ) and generally a low percentage of sand fraction. North and east of the Po delta their frequencies are comparable to those of forma *parkinsoniana*, leading to mixed populations. Directly south of the main Po outlets, in the zone most heavily influenced by runoff products, the populations become strongly dominated by the (probably megalospheric) morphotype 1. Chambers with an irregular chamber arrangement (compare Seiglie, 1975, pl. 4, fig. 11-15) are also present there.

As the water depth increases, forms belonging to morphotype 2 show a variation towards morphotypes in which the first chambers are coloured brown (pl. 10, fig. 1-3). Apart from a small area south of the lagoon of Venezia the coloured morphotypes 3 and 4 are restricted to a zone parallel to the Italian coast, at a water depth between 15 and 30 m. The sediment here contains high percentages of organic matter (0.9 - 2.1 %). In this 'coloured' group there is no variation towards extremely lobate or extremely rounded morphotypes. Relatively lobate morphotypes are dominant in the most shallow part, whereas more rounded morphotypes dominate the assemblages in deeper water.

In the literature forma *tepida* (our morphotypes 1-4) is known for its great tolerance for all kinds of stressed conditions (Bradshaw 1957, 1961). Morphotype 1, with its very fragile test and inflated first chamber, strongly resembles forms from Puerto Rico as figured by Seiglie (e.g. 1975; *A. catesbyana*, high-spired form, pl. 4, figs. 6-7, 11-15), although the test is not so typically high-spired. Cita and Premoli Silva recorded similar morphotypes from a boring in the lagoon of Venezia (1967, pl. 1, figs. 4-6, 11-14). According to Seiglie

this morphotype is characteristic for conditions of high organic pollution. In his opinion these megalospheric types can, by reproducing sexually, rapidly adapt to periodically changing environmental conditions such as shifts in the intensity of organic pollution.

We assume that the niche that forma *tepida* (morphotypes 1-4) occupies in the Adriatic Sea is more or less comparable to that described by Seiglie off Puerto Rico; forma *tepida* is quite unique in that it combines a certain preference for environments of organic pollution, and a tolerance for lowered salinities. If we compare the distribution of the coloured (morphotypes 3-4) and uncoloured (morphotypes 1-2) *tepida* types (fig. 18), the position of the uncoloured group in front of the Po delta appears to be linked to a certain tolerance for lowered salinities. The presence of teratological specimens further suggests that in this environment there is also some kind of chemical pollution. The dominance of morphotype 1 in some very shallow samples further south along the Italian coast, where it is replacing forma *parkinsoniana*, can then be explained by the presence of a local polluting effluent.

The deeper position (closer to the zone of maximum stress due to nutrient input) of the coloured group (morphotypes 3 and 4, belonging to cluster 2) seems to indicate some tolerance for low-oxygen stress. It is remarkable that in the deepest (relatively most stressed) part of this zone, there is a tendency for the organisms to develop a relatively broad imperforate zone along all sutures on the dorsal side (pl. 10, fig. 1d). Still deeper, in the zone of maximum stress, *Pseudoeponides falsobeccarii* (pl. 11, fig. 1-3) becomes an important faunal constituent. In this form, which in our opinion is morphologically close, secondary apertures have developed on the dorsal side, at the junction of the chamber and spiral sutures.

The distribution pattern described above leads us to some interesting conclusions:

-- It is remarkable that the transition from coloured (types 3 and 4) to uncoloured (types 1,2 and 5) morphotypes leads to a separation in the cluster analysis, but not the transition from forma *parkinsoniana* (type 5) to forma *tepida* (types 1-4); uncoloured tests are most numerous between 10 and 20 m whereas coloured tests occupy the 20 - 30 m depth zone. It should be noted that it is mainly the older chambers of the tests that are coloured. Boltovskoy and Wright (1976) suggest that the apparent colour of the test is a function of substrate chemistry; uncoloured tests can be the result of etching (compare Murray, 1967). This can be an explanation for the distribution of coloured and uncoloured morphotypes of *Elphidium granosum* and *Elphidium poeyanum*, but probably not for the distribution of *Ammonia*. The latter genus shows just the opposite distribution pattern of coloured and uncoloured morphotypes; in *Am-*

*monia parkinsoniana* the uncoloured morphotypes are generally present in the 10 - 20 m depth interval where the environment probably will be less reducing than it is at a lower depth.

- If we compare the morphological variation of *A. parkinsoniana* in the Adriatic Sea, which should be representative for the Mediterranean, with that in the Atlantic, it appears that the variation is less diverse in the Mediterranean. Highly ornamented forms are not present in our associations. The *batavus*-type, as it is used in the Atlantic (e.g. Murray, 1971, p. 150, figs. 1,4; Banner and Williams, 1973, pl. 1, figs. 1-2), with its depressed sutures on the dorsal side and pronounced ornamentation on the ventral side, falls completely outside our range of variation. If such morphotypes in the Atlantic do indeed belong to the variation of *A. parkinsoniana* (and not to *A. beccarii*, as we suspect), then it is clear that the *batavus*-types of this species in the Atlantic cover a part of the morphological variation which in the Mediterranean is covered by *A. beccarii*.

- Teratological specimens of *A. parkinsoniana*, which have often been reported, were also found in the Adriatic Sea. In our case these forms (pl. 8, figs. 1-3) are dwarfed, unlike the forms figured by Tufescu (1968, figs. 7-9) and Seiglie (1975, pl. 4, figs. 8-10), and show coiling anomalies from an early ontogenetic stage onwards. Explanations suggested are high variations in salinity (Tufescu, l.c.) or temperature (Seiglie, l.c.). In our opinion, the wall structure of these specimens shows clear signs of dissolution (pl. 8, fig. 1c), which suggests the influence of severe stress, possibly resulting from chemical pollution.

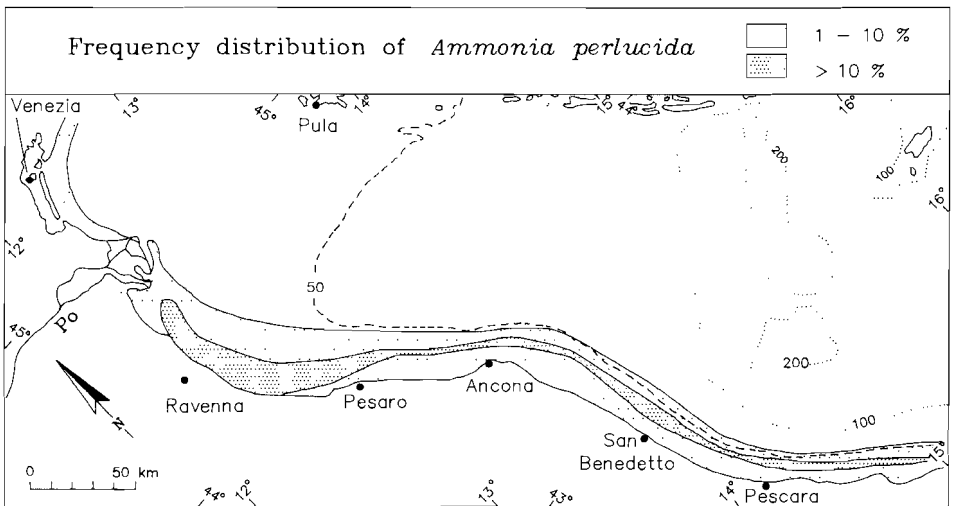


Fig. 19. Frequency distribution of *Ammonia perlucida*.

#### IV.2.2.3. *Ammonia perlucida* (Heron-Allen and Earland, 1913)

This species, which is morphologically quite different from the other *Ammonia*, is restricted to a very shallow zone (fig. 19). In front of the Po delta it is only present in small proportions, but directly south of this area and in a narrow strip along the Italian coast (around 20 m water depth) it reaches high frequencies. Its position in cluster 2 suggests a preference for environments with ample food availability and only a limited tolerance for shortage of oxygen. The presence of large numbers of specimens showing an irregular growth in the area south of the Po delta could indicate that this species too is influenced by chemical pollution.

Considerable variation was observed in the number and inflation of the chambers. Because no clear geographical trends were found, no further attempt was made to distinguish and/or quantify separate morphotypes.

#### IV.2.2.4. *Pseudoeponides falsobeccarii* Rouvillois, 1974

Although, strictly speaking, this species (of cluster 8) does not belong to the genus *Ammonia*, its morphology strongly resembles that of *A. parkinsoniana*. It is present (fig. 20) in a broad zone in front of the Po delta, and further southwards between 30 and 50 m water depth, on clayey substrata with high percentages of organic matter. Small numbers of this species on the sand platform and in samples from shallow water near the Italian coast are probably reworked. We are of the opinion that the secondary apertures on the dorsal side, which is the only feature that differentiates *Pseudoeponides falsobeccarii* substantially from *A. parkinsoniana*, could well be an adaptation which enables

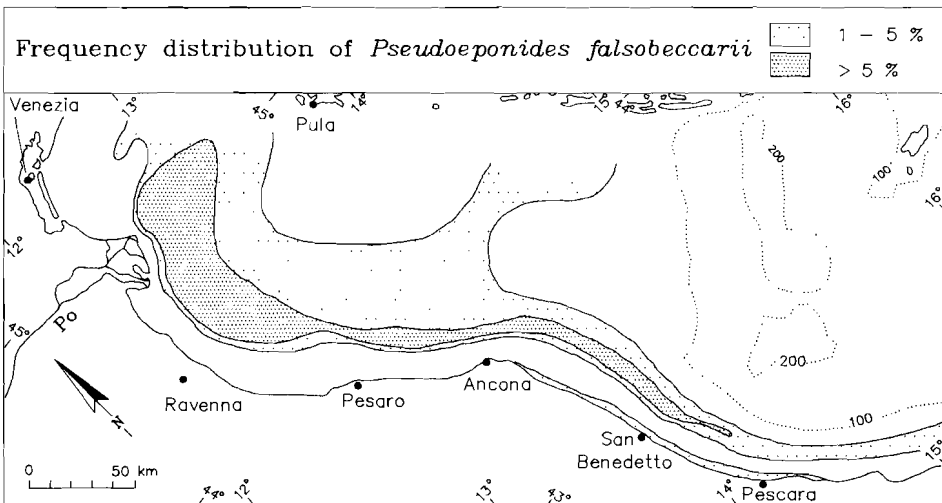


Fig. 20. Frequency distribution of *Pseudoeponides falsobeccarii*.

this species to cope with the more severe environmental stress in its distributional area.

#### IV.2.3. TAXONOMY

### **Ammonia beccarii** (Linnaeus, 1758)

Plate 2, fig. 5, plates 5 - 6

- 1758 *Nautilus beccarii* -- Linnaeus, *Systema naturae*, p. 710, pl. 1, fig. 1, pl. 19, figs. h,i.  
1862 *Rosalina inflata* -- Seguenza, *Atti Accad. Gioenia Sci. Nat.*, 18, p. 106, pl. 1, fig. 6.  
1967 *Ammonia beccarii* (Linné) -- Cita and Premoli Silva, *PARTIM, Mem. Biogeogr. Adriatica.*, 7, p. 48, fig. 9 (not figs. 3 b-d, not pl. 1).  
1970 *Ammonia beccarii* (Linné) -- Von Daniels, *PARTIM, Göttinger Arb. Geol. Paläont.*, 8, p. 86, pl. 7, fig. 5.  
1979 *Ammonia beccarii* (Linnaeus) var. *beccarii* (Linnaeus) -- Hageman, *Utrecht Micropal. Bull.*, 20, p. 87, pl. 1, fig. 1.  
1979 *Ammonia beccarii* (Linnaeus) var. *inflata* (Seguenza) -- Hageman, *Utrecht Micropal. Bull.*, 20, p. 88, pl. 1, fig. 2.  
1983 *Ammonia beccarii* (Linné) -- Vénéce-Peyré, *PARTIM, (Écophénotypes nos. 1,2 and 3, not no. 4), Cah. Micropal.*, 1983/2, pl. 1, figs. 1-5 (not fig. 6), pl. 2, figs. 1, 3-4 (not figs. 2, 5-6), pl. 3, fig. 4 (not figs. 1-3), pl. 5, fig. 1 (not fig. 4).  
1986 *Ammonia beccarii* (Linné) -- Rupp, *Beitr. Paläont. Österr.*, 12, p. 56, pl. 2, figs. 1-3.  
1987 *Ammonia beccarii beccarii* (Linnaeus) -- Jorissen, *Marine Micropal.*, 12, p. 47, pl. 2, fig. 5.

#### *Diagnosis*

In the Adriatic Sea *A. beccarii* can be distinguished from *A. parkinsoniana* by its larger dimensions, its deeply incised dorsal sutures in the last whorl and by its larger pores. Furthermore, *A. beccarii* is characterized by its pointed chamber flaps, the rectangular shape of the chambers on the dorsal side, the limbate sutures on the dorsal side in the older part of the test, and by the knob-by ornamentation on both sides of the test in adult specimens.

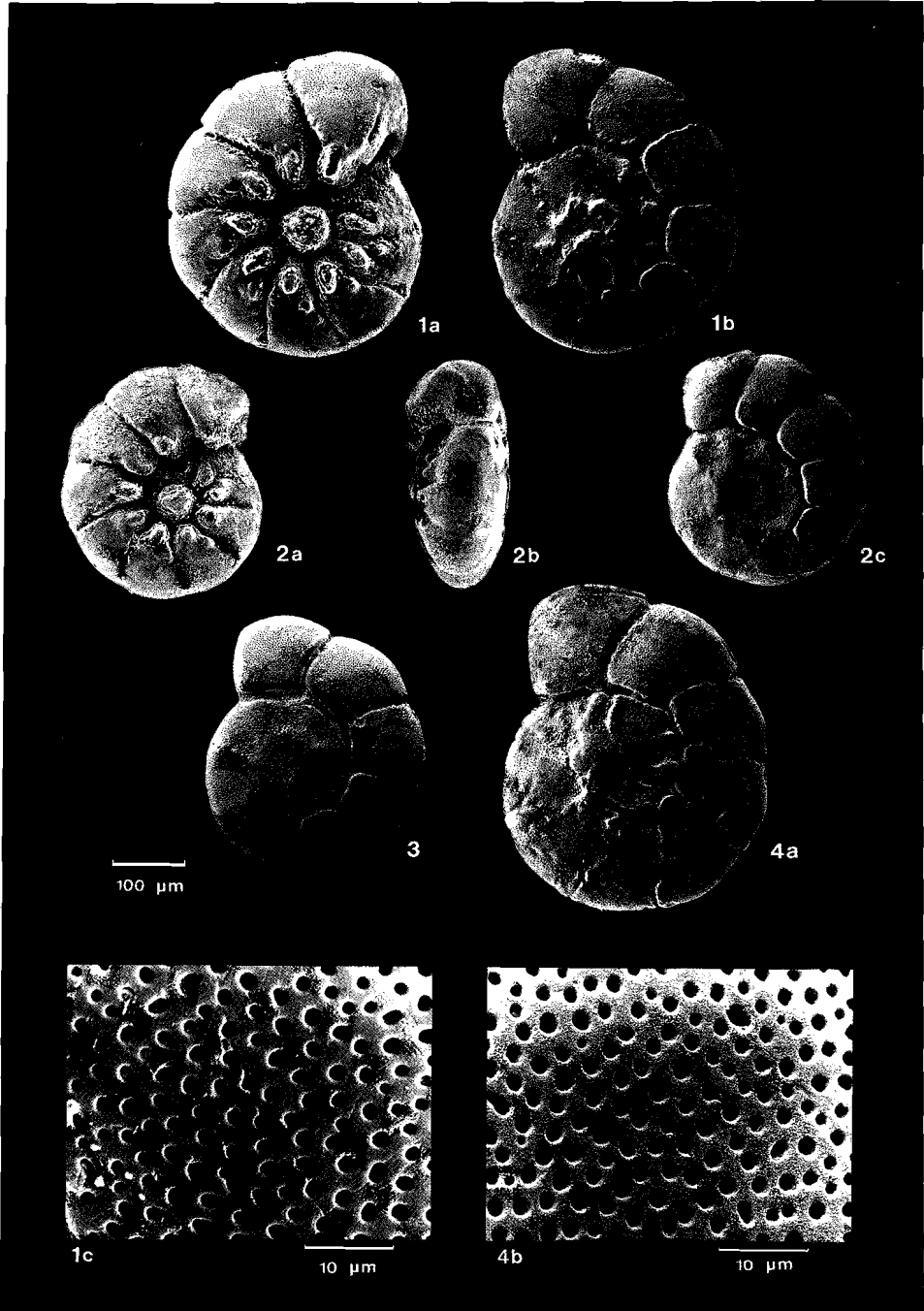
The diameter of the test ranges from 200 - 1000 microns; pore size from 1 - 2 microns.

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### Plate 5

#### *Ammonia beccarii* forma *beccarii*

- Fig. 1, sample 108; typical specimen, 1a: ventral side, 100 x, 1b: dorsal side, 100 x, 1c: pores, penultimate chamber, dorsal side, 1250 x.  
Fig. 2, sample 108; typical specimen, 2a: ventral side, 100 x, 2b: apertural view, 100 x, 2c: dorsal side, 100 x.  
Fig. 3, sample 78; transitional morphotype to *A. beccarii* forma *inflata*, dorsal side, 100 x.  
Fig. 4, sample 78; transitional morphotype to *A. beccarii* forma *inflata*; 4a: dorsal side, 100 x, 4b: pores, penultimate chamber, dorsal side, 1250 x.



### Remarks

In our material we notice a gradual transition between two extreme morphotypes;

-- typical forms (forma *beccarii*, pl. 5, fig. 1-2) are characterized by a flattened dorsal side, a well-developed umbilical knob, 9-10 chambers in the last whorl; the chambers are on the ventral side ending in an imperforate, flap-like projection into the umbilicus. The pores are extremely large (2 microns).

-- the other type (forma *inflata*, pl. 6, fig. 1-4) has a more convex dorsal side, on which the whorls are less embracing, so that more of the previous ones are visible. A well-developed umbilical knob is absent. There are 8 - 9 chambers in the last whorl. The umbilical region is obscured by the knobby ornamentation pattern.

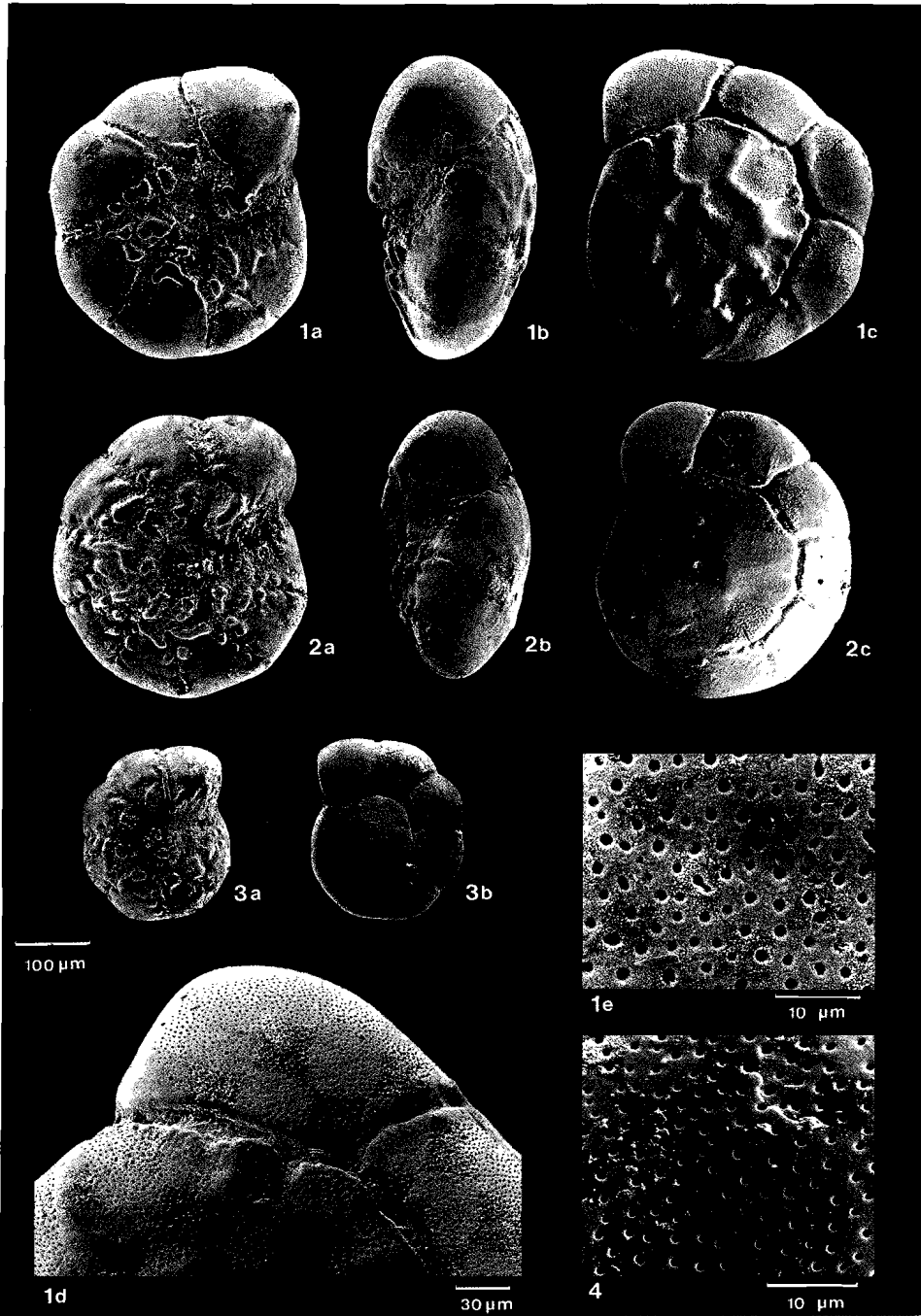
Although the latter morphotypes are by no means as spherical as those recognized by Hageman as *Ammonia beccarii* var. *inflata* (Seguenza) (1979, p. 88, pl. 1, fig. 2), they agree fairly well with the original description. Although intermediate morphotypes are often found we managed to make reproducible counts of the two morphotypes. In contrast with the observations of Vénec-Peyré, we never observed transitions from our forma *inflata* towards *Pseudoeponides falsobeccarii* Rouvillois (= *Ammonia beccarii*, forme 4 of Vénec-Peyré, 1983), which is characterized by the presence of secondary apertures on the dorsal side.

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## Plate 6

### *Ammonia beccarii* forma *inflata*

- Fig. 1, sample 72, typical specimen, 1a: ventral side, 100 x, 1b: apertural view, 100 x, 1c: dorsal side, 100 x, 1d: detail of last chambers, showing incised sutures, thickened sutures in earlier whorl and imperforate zones at the edge of the chambers, 250 x, 1e: pores, penultimate chamber, dorsal side, 1250 x.
- Fig. 2, sample 72, typical specimen, 2a: ventral side, 100 x, 2b: apertural view, 100 x, 2c: dorsal side, 100 x.
- Fig. 3, sample 72, juvenile specimen, 3a: ventral side, 100 x, 3b: dorsal side, 100 x.
- Fig. 4, sample 72, pores of unfigured specimen, penultimate chamber, dorsal side, 1250 x.





## Ammonia parkinsoniana (D'Orbigny, 1839)

Plates 2, fig. 8, plates 7 - 10

- 1839 *Rosalina parkinsoniana* -- D'Orbigny, Foram. de Cuba, p. 99, pl. 4, figs. 25-27.  
1926 *Rotalia beccarii* (Linnaeus) var. *tepida* -- Cushman, Carnegie Inst., Dept. Marine Biol., 23, Publ.no. 344, p. 79, pl. 1.  
1931 *Rotalia beccarii* (Linnaeus) var. *tepida* Cushman -- Cushman, U.S.Nat.Mus.Bull., 104, pt. 8, p. 61, pl. 13, fig. 3.  
1934 *Rotalia beccarii* (Linné) var. *sobrina* -- Shupack, Am. Mus. Nat. Hist., Novit., 737, p. 6, figs. 4a-c.  
1957 *Streblus beccarii* (Linné) var. *tepida* (Cushman) -- Bradshaw, J. Paleont., 31, text-fig. 1.  
1967 *Ammonia beccarii* (Linné) -- Cita and Premoli Silva, PARTIM, Mem. Biogeogr. Adriatica, 7, p. 34, figs. 3 b-d, pl. 1, figs. 1-6, 11-14 (not p. 48, fig. 9).  
1975 *Ammonia catesbyana* (D'Orbigny) -- Seiglie, Rev. Esp. Micropal., 7, p.471, pl. 2, fig. 21, pl. 4, figs. 1-15.  
1977 *Ammonia parkinsoniana* (D'Orbigny) -- Le Calvez, Cah. Micropal., 1977/2, p. 92, pl. 11, figs. 1-3.  
1978 *Ammonia parkinsoniana* (D'Orbigny) -- Poag, Trans. Gulf Coast Assoc. Geol. Soc., 28, p. 397, pl. 1, figs. 1-21.  
1979 *Ammonia beccarii* (Linnaeus) var. *tepida* (Cushman) -- Hageman, Utrecht Micropal. Bull., 20, p. 88, pl. 1, fig. 3.  
1985 *Ammonia parkinsoniana* (D'Orbigny) -- Kohl, Bull. Amer. Paleont., 88, no. 322, p. 81, pl. 28, fig. 4.  
1985 *Ammonia tepida* (Cushman) -- Kohl, Bull. Amer. Paleont., 88, no. 322, p. 81, pl. 28, fig. 3.  
1986 *Ammonia parkinsoniana* (D'Orbigny) -- Rupp, Beitr. Paläont. Österr., 12, p. 56, pl. 2, figs. 4-6.  
1986 *Ammonia tepida* (Cushman) -- Rupp, Beitr. Paläont. Österr., 12, p. 56, pl. 2, figs. 7-9.  
1987 *Ammonia beccarii tepida* (Cushman) -- Jorissen, Marine Micropal., 12, p. 47, pl. 2, fig. 8.

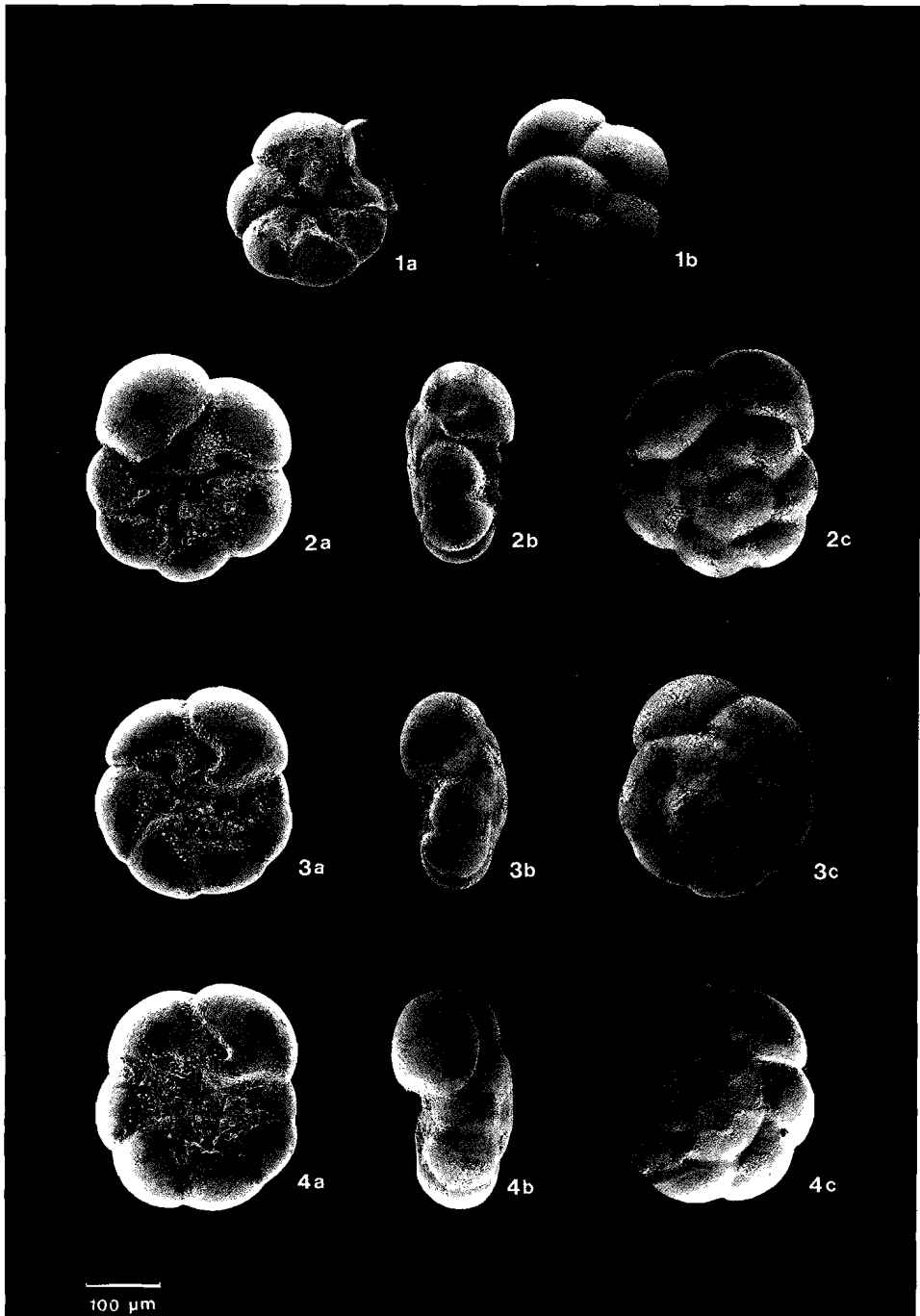
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### Plate 7

#### *Ammonia parkinsoniana* forma *tepida*

Uncoloured group; morphotypes 1 and 2; sample 164, figures 1 to 4 show the variation in the lobation of the test.

- Fig. 1, morphotype 1, extremely large, protruding first chamber, 1a: ventral side, 100 x, 1b: dorsal side, 100 x, pores figured on pl. 8, fig. 5.  
Fig. 2, morphotype 2, 2a: ventral side, 100 x, 2b: apertural view, 100 x, 2c: dorsal side, 100 x, pores figured on pl. 8, fig. 6.  
Fig. 3, morphotype 2, 3a: ventral side, 100 x, detail of umbilical structures figured on pl. 8, fig. 4, 3b: apertural view, 100 x, 3c: dorsal side, 100 x.  
Fig. 4, morphotype 2, 4a: ventral side, 100 x, 4b: apertural view, 100 x, 4c: dorsal side, 100 x.



### Diagnosis

Compared with *A. beccarii* the test of *A. parkinsoniana* is relatively small (< 300 microns), the sutures on the dorsal side are not incised but only depressed, the umbilical chamber flaps are relatively larger, the pores are definitely smaller (0.5 micron) and the dorsal side of the test is never ornamented with knobs.

Two extreme morphotypes are distinguished; forma *parkinsoniana* and forma *tepida*; these are linked by numerous intermediate morphotypes.

Forma *parkinsoniana* (pl. 9, figs. 1-4) is a relatively large, thickly calcified morphotype, with 8 - 9 uninflated chambers in the last whorl. The umbilicus is relatively closed, and provided with a conspicuous umbilical knob. The pores often have an irregular shape, especially on the dorsal side of the test (pl. 9, fig. 5). The position of the aperture is somewhat more extra-umbilical than it is in forma *tepida*.

Forma *tepida* (pl. 7, figs. 1-4, pl. 8, figs 4-6, pl. 10, figs. 1-3) is characterised by a more thin-walled test with always a somewhat lobate outline. The position of the aperture is more intra-umbilical, and generally an umbilical knob is not developed. Within forma *tepida* four morphotypes have been distinguished; morphotypes 1 and 2 (pl. 7, figs. 1-4) with uncoloured older chambers, and morphotypes 3 and 4 (pl. 10, figs 1-3) with (brown-)coloured first chambers.

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## Plate 8

### *Ammonia parkinsoniana* forma *tepida*, teratological morphotypes, sample 164

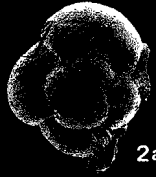
- Fig. 1, dwarfed specimen, 1a: dorsal side, 100 x, 1b: ventral side, 100 x, 1c: pores around spiral suture, dorsal side, 1250 x.  
Fig. 2, dwarfed specimen with coiling anomaly, 2a: dorsal side, 100 x, 2b: ventral side, 100 x.  
Fig. 3, dwarfed specimen with coiling anomaly, 3a: dorsal side, 100 x, 3b: ventral side, 100 x.

#### Details of specimens figured on plate 7:

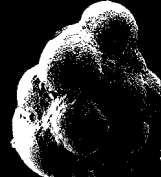
- Fig. 4, *A. parkinsoniana* forma *tepida*, morphotype 2, sample 164, specimen figured on pl. 7, fig. 3, detail of umbilical region of last chambers, showing incurving of chambers above chamber flaps and pearly ornamentation, 250 x.  
Fig. 5, *A. parkinsoniana* forma *tepida*, morphotype 1, sample 164, specimen figured on pl. 7, fig. 1, pores, dorsal side, penultimate chamber, 1250 x.  
Fig. 6, *A. parkinsoniana* forma *tepida*, morphotype 2, sample 164, specimen figured on pl. 7, fig. 2, pores, peripheral side, older chamber, 1250 x.



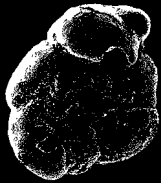
1a



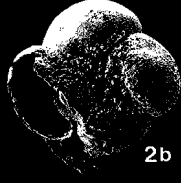
2a



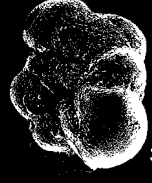
3a



1b

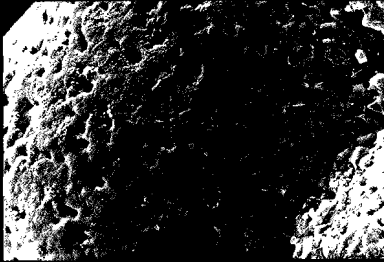


2b



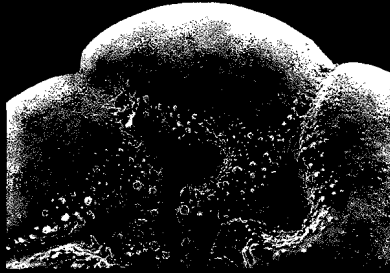
3b

100  $\mu$ m



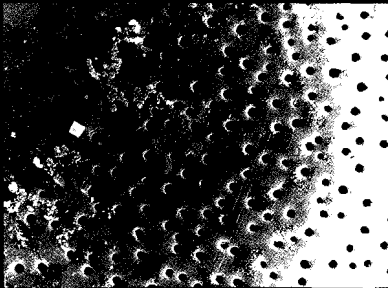
1c

10  $\mu$ m



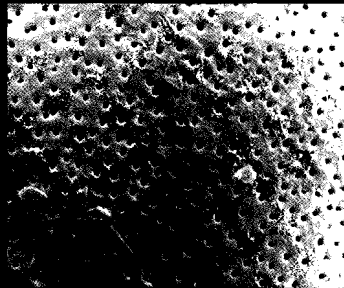
4

30  $\mu$ m



5

10  $\mu$ m



6

10  $\mu$ m

In the group with 'uncoloured' morphotypes there is a continuous variation from forms with inflated chambers, an extremely large protoconch, and a strongly lobate outline (morphotype 1, pl. 7, fig. 1) to morphotypes with less inflated chambers and a less lobate outline (morphotype 2, pl. 7, figs. 2-4, pl. 8, figs. 4-6). In both forms the intra-umbilical part of the aperture, an incurving of the last chamber under the well-developed flap-like projection (pl. 8, fig. 4), is clearly present. Along the chamber sutures on the ventral side the wall shows a pearly ornamentation. On the one hand this uncoloured group is linked by intermediate morphotypes to forma *parkinsoniana*, and on the other hand numerous transitional forms towards the 'coloured' group (morphotypes 3 and 4) are found.

Also in the group with (brown-)coloured initial chambers (morphotypes 3 and 4), there is variation in the inflation of the chambers and lobateness of the outline. The more lobate morphotype 3 (pl. 10, fig. 1) has inflated chambers (6 - 7 in the last whorl) and an intra-umbilical aperture positioned under a distinct flap-like projection. The less lobate morphotype 4 (pl. 10, figs. 2-3) has somewhat less inflated chambers, 7 - 9 in the last whorl; the intra-umbilical part of the aperture is more weakly developed, the chamber extensions are not so clear, and an umbilical knob may be present.

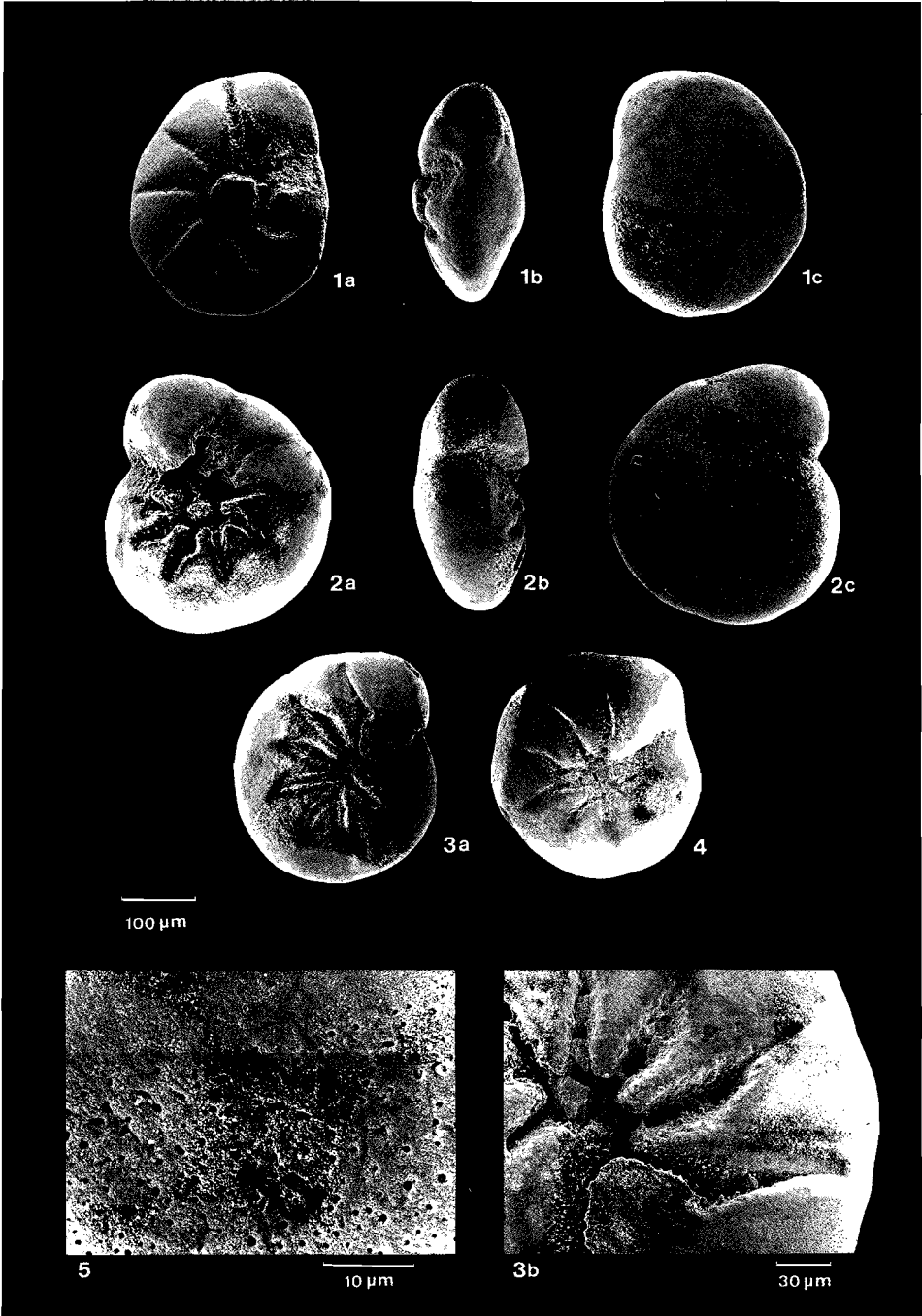
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## Plate 9

### *Ammonia parkinsoniana* forma *parkinsoniana*

Uncoloured group, morphotype 5, sample 76, specimens showing variation in the development of the umbilical knob.

- Fig. 1, extreme form (*sobrino*-type) with enormous umbilical knob, 1a: ventral side, 100 x, 1b: apertural view, 100 x, 1c: dorsal side, 100 x.  
Fig. 2, typical form, 2a: ventral side, 100 x, 2b: apertural view, 100 x, 1c: dorsal side, 100 x.  
Fig. 3, typical form, 3a: ventral side, 100 x, 3b: detail of umbilical region, showing exceptionally well developed chamber flap of last chamber, 250 x.  
Fig. 4, typical form without umbilical knob, ventral side, 100 x.  
Fig. 5, specimen not figured, pores in the penultimate chamber, dorsal side, 1250 x.



## **Ammonia perlucida** (Heron-Allen and Earland, 1913)

Pl. 2, fig. 11-12, pl. 11, fig. 4-5.

- 1913 *Rotalia perlucida* -- Heron-Allen and Earland, Proc. Roy. Irish Acad., 31, p. 139, pl. 13, figs. 7-9.  
1931 '*Rotalia*' *perlucida* Heron-Allen and Earland -- Cushman, U.S. Nat. Mus. Bull., 104, pt. 8, p. 63, pl. 13, fig. 4.  
1968 '*Rotalia*' *perlucida* Heron-Allen and Earland -- Albani, Contr. Cushman Found. Foram. Res., 19, p. 110, pl. 9, figs. 12, 16.  
1970 *Aubignyna mariei* -- Margerel, Rev. Micropal., 13, p. 58-64, fig. 1-2, pl. 1-2.  
1970 *Aubignyana* cf. *mariei* Margerel -- Von Daniels, Göttinger Arb. Geol. Paläont., 8, p. 85, fig. 60, pl. 7, fig. 6.  
1977 *Aubignyana* cf. *A. mariei* Margerel -- Haake, J. Foram. Res., 7, p. 65, pl. 1, fig. 13.  
1986 *Aubignyna perlucida* (Heron-Allen and Earland) -- Rupp, Beitr. Paläont. Österr., 12, p. 56, pl. 4, fig. 5-7.  
1987 *Ammonia perlucida* (Heron-Allen and Earland) -- Jorissen, Marine Micropal., 12, p. 47, pl. 2, figs. 11-12.

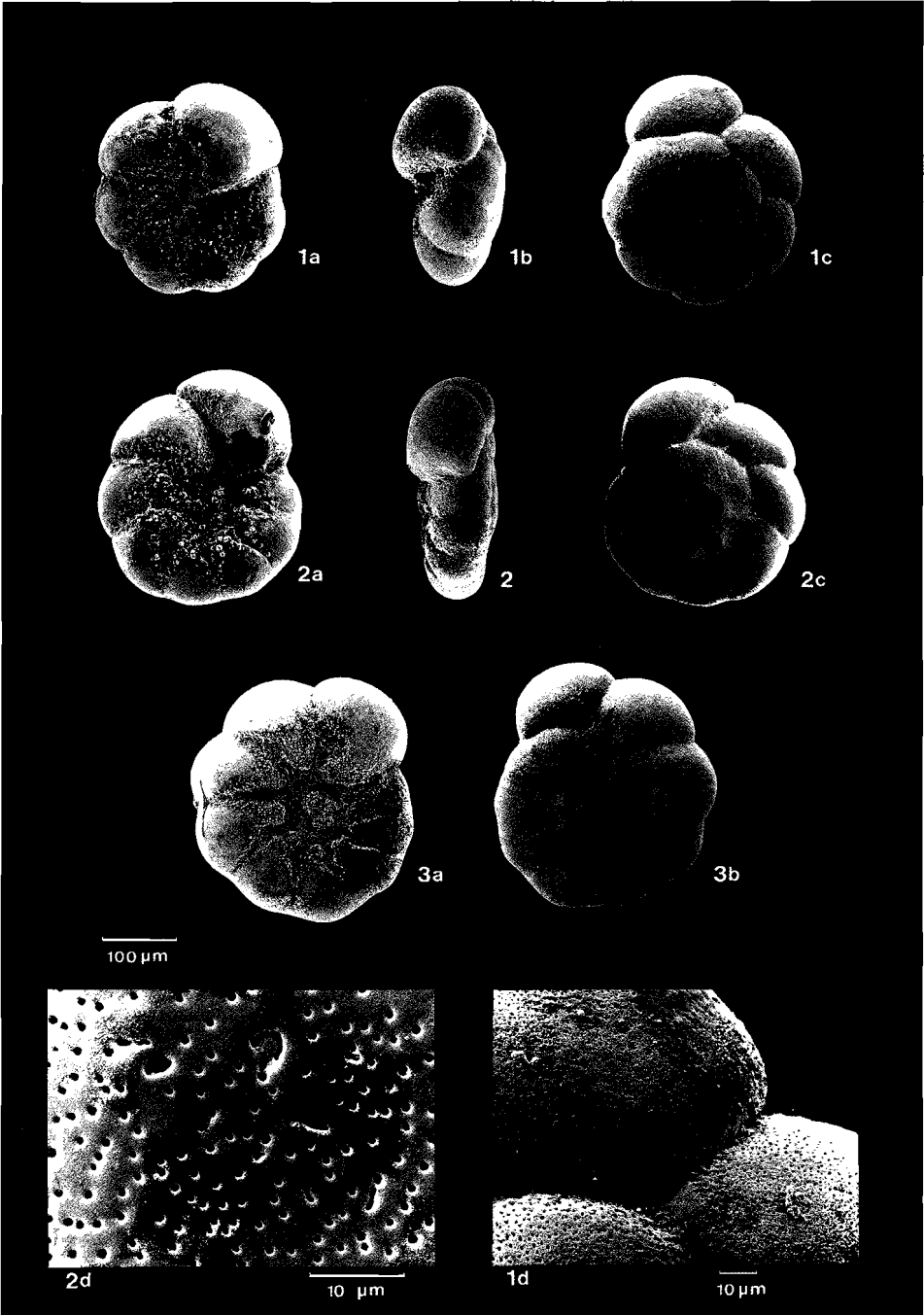
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## **Plate 10**

### *Ammonia parkinsoniana* forma *tepida*

Coloured group, morphotypes 3 and 4, sample 71, specimens showing variation in lobateness and umbilical structures.

- Fig. 1, morphotype 3, well-developed chamber flaps, 1a: ventral side, 100 x, 1b: apertural view, 100 x, 1c: dorsal side, 100 x. 1d: detail of last chamber on dorsal side, showing imperforate zone along the sutures, 500 x.  
Fig. 2, morphotype 4, umbilical region more open, with umbilical knob, chamber flaps less developed, 2a: ventral side, 100 x, 2b: apertural view, 100 x, 2c: dorsal side, 100 x. 2d: pores, dorsal side, penultimate chamber, 1250 x.  
Fig. 3, morphotype 4, 3a: ventral side, 100 x, 3b: dorsal side, 100 x.





***Pseudoeponides falsobeccarii* Rouvillois, 1974**  
Pl.4, fig. 3, pl. 11, figs. 1-3.

1974 *Pseudoeponides falsobeccarii* – Rouvillois, Cah. Micropal., 3, pl. 1, figs. 1-12.

1977 *Ammonia beccarii* (D'Orbigny) – Haake, PARTIM, J. Foram. Res., 7, pl. 1, figs. 1-2.

1983 *Ammonia beccarii* (D'Orbigny), écophénotype 4 – Vénec-Peyré, PARTIM (not écophénotypes 1,2 and 3), Cah. Micropal., 1983/2, pl. 1, figs. 1-6, pl. 2, figs. 2, 5-6 (not figs. 1, 3-4), pl. 3, figs. 1-3, pl. 5, fig. 4.

1987 *Pseudoeponides falsobeccarii* – Jorissen, Marine Micropal., 12, p. 47, pl. 4, fig. 3a,b.

*Remarks*

In contrast with the observations of Vénec-Peyré (1983), we never observed any continuous variation between this species and *A. beccarii* or *A. parkinsoniana*. In our opinion *Pseudoeponides falsobeccarii* morphologically is very close to *Ammonia parkinsoniana* forma *tepida*. The only structural difference is the presence of secondary openings on the dorsal side; these could be an adaptation to the more stressed conditions in its distributional area.

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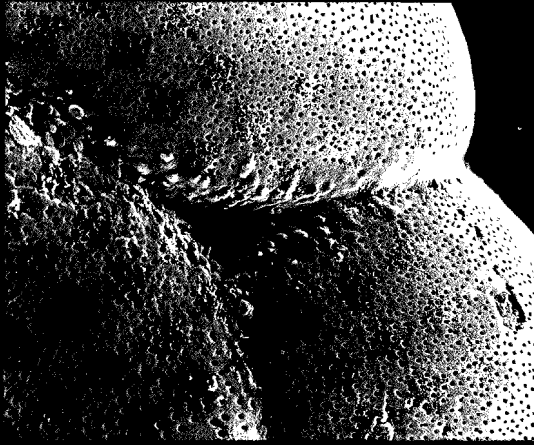
**Plate 11**

*Pseudoeponides falsobeccarii*

- Fig. 1: sample 72 (40 m), specimen not figured, detail of secondary aperture, enlargement 625 x.  
Fig. 2a: typical specimen, sample 167 (23 m), dorsal side, enlargement 100 x.  
Fig. 2b: same specimen, detail of pores in older chambers, enlargement 1200 x.  
Fig. 3: sample 167 (23 m), specimen not figured, detail of ventral side, enlargement 625 x.

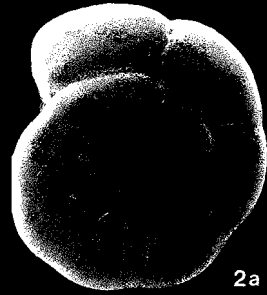
*Ammonia perlucida*

- Fig. 4: sample 182 (16.5 m), specimen not figured, detail of umbilical area, enlargement 400 x.  
Fig. 5: typical specimen, sample 57 (20 m), ventral side, enlargement 100 x.



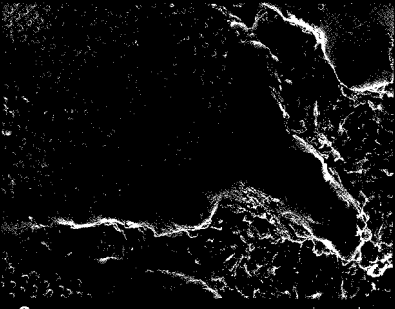
1

10  $\mu\text{m}$



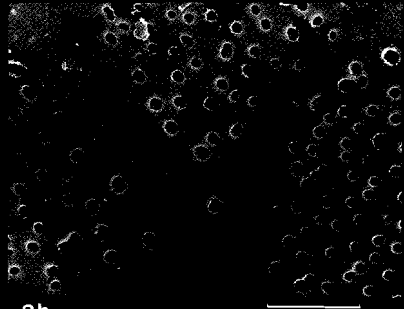
2a

100  $\mu\text{m}$



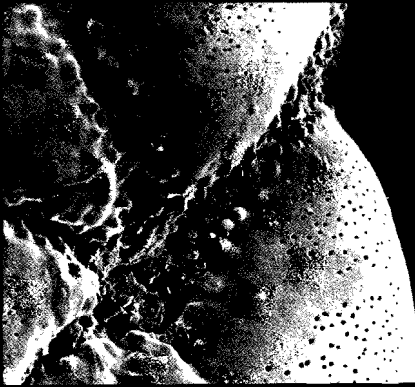
3

10  $\mu\text{m}$



2b

10  $\mu\text{m}$



4

30  $\mu\text{m}$



5

100  $\mu\text{m}$

### IV.3.1. Introduction

In the genus *Bulimina* two main groups of morphotypes can be recognized; these are characterized by costate and non-costate specimens respectively. These two groups show differences not only in the ornamentation pattern, but more importantly, also in their internal structures (Verhallen, 1986). Therefore, a subdivision at a higher than species-level could be considered.

Although it is generally agreed that the recent non-costate morphotypes form one group in a biological sense, the various taxonomical concepts employed in the literature show large differences. A number of workers (e.g. Höglund, 1947; Boltovskoy, 1959; Feyling-Hansen, 1964), mainly studying recent material, accept the ultimate consequence of the biological homogeneity of the group and recognize one species only, although sometimes they distinguish a number of formae. Other investigators, mostly working on fossil material, adopt a more typological approach and describe their material using a selection of the numerous species names available. In this way more than 10 different species of non-costate *Bulimina* are recognized in Italian Pleistocene associations (Agip S.p.A, 1982), which are indeed extremely variable.

Of course, the variation expressed by the different associations should be described in some way, in order to retain the maximum of paleoecological and biostratigraphical information. This is particularly so because buliminids are known for their tolerance of stressed conditions (e.g. Bandy et al., 1964; Van der Zwaan, 1982). Unfortunately, two entirely different concepts of differentiation in non-costate *Bulimina* are currently used. A number of authors consider the chamber form as the most suitable character for taxonomic separation, especially the absence or presence of the so-called undercuttings of the 'marginata' chamber-type. According to the second concept, originally developed by Fornasini (1901), the general outline and the degree of regularity of the chamber arrangement are the prime criteria to be used. The presence and nature of ornamentation in the older part of the test are then of minor importance and, although this is not a very elegant solution, a variety *marginata* is recognized in several species (e.g. D'Onofrio, 1981).

In our opinion both concepts are to some extent valuable. Indeed, the development of undercuttings is an essential character. In the Mediterranean, morphotypes showing this feature occurred only from the Late Pliocene onwards (Verhallen, 1987) and intermediate associations or morphotypes are rarely found after the *marginata*-type has completed its development. On the other hand, the 'marginata' chamber-type can be found in morphotypes which can exhibit considerable differences in other characters. In some cases there appears

to be no continuous variation between these morphotypes with 'marginata' chambers. Unfortunately, in most studies using fossil material a geographically, and also (paleo-)bathymetrically, limited area is considered, and this certainly leads to over-simplification. This can be demonstrated by our results using (sub-)recent material from the Adriatic Sea. If only relatively deep samples (deeper than 100 m) are considered, the picture that emerges is quite uncomplicated: two well separated groups of non-costate *Bulimina* are present. The *marginata*-group, with so-called undercuttings, is quite uniform in morphology, whereas the *aculeata*-group, without undercut chamber-margins shows a definitely higher morphological variability. Morphotypes intermediate between the two groups are not found. But the samples used for the present study (0-100 m water depth) suggest a completely different picture; the two groups are no longer clearly separable, but are linked by intermediate morphotypes, and the *marginata*-group exhibits a much larger morphological variability.

The apparent coherence of all non-costate morphotypes in associations from our shallow-water samples, compelled us, at least for the time being, to use the concept of one single species: *Bulimina marginata*.

Within *Bulimina marginata* three morphotypes were distinguished; two with undercut margins (forma *marginata* and forma *denudata*) and one without undercut margins (forma *aculeata*). Although it would have been easy to separate a larger number of morphotypes (especially within forma *aculeata*), we had the impression that this would not furnish more information, but would only complicate an already complex picture. Moreover, it should be emphasized that our differentiation into three morphotypes is only made for the present study on the nearshore clayey zone. In other geographical areas a further subdivision would perhaps be made in order to yield the maximum of (paleo-) environmental information.

#### IV.3.2. Distribution

In figure 21 the cumulative frequencies of the three morphotypes of *B. marginata* have been mapped, and in figure 22 the areas dominated by each of the morphotypes have been indicated.

Forma *marginata* is found on clayey substrata from 80 m depth downwards; deeper than 125 m it dominates the populations. In the central basin maximum frequencies are reached around 150 m and in the southern basin at a water depth of about 300 m. The presence of forma *marginata* in the shallow water zone south of Ancona is obviously the result of reworking of older material.

Between 60 and 100 m forma *marginata* is gradually replaced by forma *denudata*. The latter form, also with undercut margins, proliferates on clayey

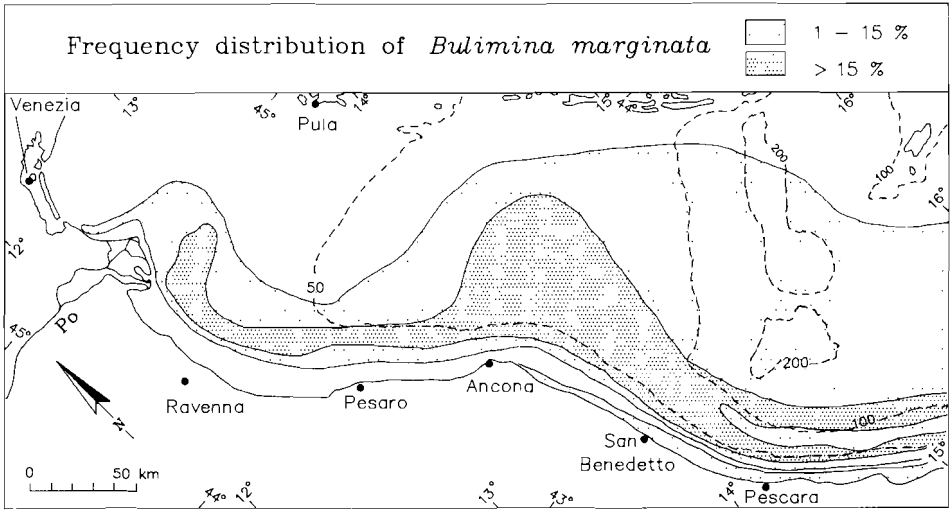


Fig. 21. Frequency distribution of *Bulimina marginata*; the cumulative frequencies of the three morphotypes have been mapped.

bottoms between 30 and 50 m depth (fig. 22). Around 50 m water depth it intergrades with forma *aculeata*, which lacks undercuttings.

Forma *aculeata* is present between 30 and 300 m water depth, not only in clayey, but also in more sandy samples. Between 70 and 125 m this morphotype dominates the *B. marginata* populations.

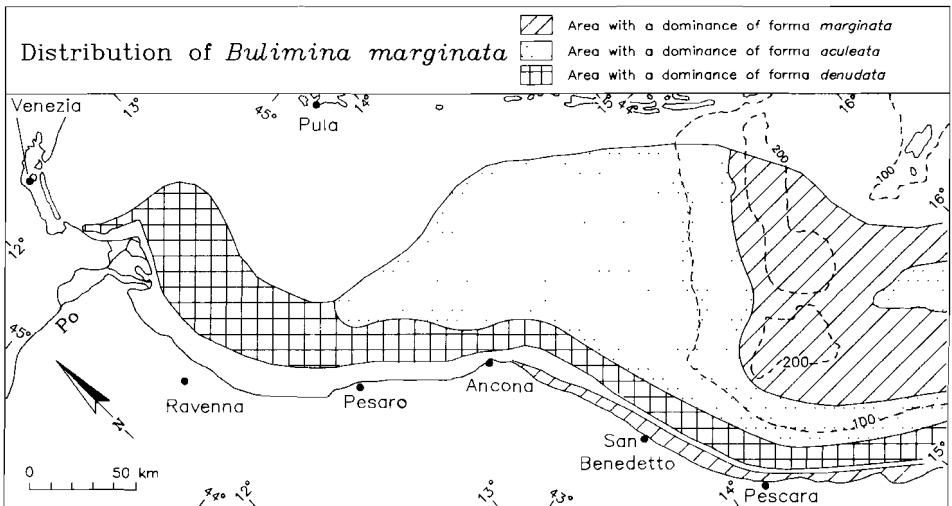


Fig. 22. Distribution of the morphotypes of *Bulimina marginata*.

To gain better insight into the distribution of the three morphotypes distinguished and the way they intergrade, we studied a succession of *Bulimina* populations from different water depths. The environmental parameters measured in these samples are listed in table III, together with the frequencies of the three morphotypes, the number of species per (250-)count and the number of foraminifera per gram dry weight.

Sample no.	depth (m)	% sand	% org. matter	% calc. carb.	No. of species /count	forams/ g dry weight	percentage <i>marginata</i>	percentage <i>denudata</i>	percentage <i>aculeata</i>
71	30	.5	1.1	27.7	17	18	-	14.4	1.9
7	30	.1	1.1	31.5	18	13	--	10.6	1.5
6	40	.1	1.3	30.4	21	3	--	21.3	1.9
5	50	.0	1.1	29.8	18	7	--	15.2	5.2
12	80	.1	1.1	28.7	34	61	- 7.5 -		4.1
30	100	.4	1.3	28.6	46	137	4.1	--	8.6
31	125	1.0	1.2	30.6	45	32	9.6	--	7.0
32	150	1.2	1.1	30.6	40	15	8.0	--	.4
33	180	2.2	1.2	32.4	35	22	4.0	--	.4
34	220	1.0	?	34.0	30	63	5.7	--	.8
282	744	?	?	?	55	15	10.9	--	1.5

Table III. Environmental and faunal data for ten samples used for the analysis of morphological patterns of *Bulimina*.

These samples were taken along a transect perpendicular to the Italian coast, near Pescara (transect VI in fig. 12); exceptions are sample 71 (taken from transect V, near San Benedetto) and sample 282 (taken in the southern Adriatic basin). All these samples were taken from clayey substrata with high percentages of organic matter. The slight increase of the sand fraction in samples 31 - 34 is caused by the pinching out of the Holocene clay-belt. Curzi and Tomadin (1986) mention an extremely thin cover (20 cm) of Holocene clay deposits at 130 m depth here. Pleistocene relict sands are thus barely covered, and mixing with the clays occurs by means of burrowing. Towards the bottom of the central basin, the thickness of the Holocene clay cover increases again to some 3 m (Curzi and Tomadin, op. cit.; Jorissen, in prep.).

The variation observed along this composite depth transect is figured in plates 12 - 14, using associations from samples 71, 5, 12, 31, 34 and 282. At 30 m water depth (sample 71) the assemblage is strongly dominated by typical representatives of forma *denudata* (pl. 12, fig. 1-4, pl. 13, figs. 1-2,6). The lower margins of the chambers are rounded, although the flattened area at the aboral

side of the chambers, being typical for the '*marginata*' chamber-type, is clearly present (pl. 13, figs. 1-2). The spinose ornamentation is very weakly developed. A small number of intermediate morphotypes (pl. 12, fig. 5, pl. 13, fig. 3), which have lost most of their undercuttings, form a link with some scarce specimens of forma *aculeata* (pl. 12, fig. 6, pl. 13, fig. 4, pl. 15, fig. 4), which is represented by elongated, scarcely ornamented types. A similar variation is found in samples 7 (30 m) and 6 (40 m).

At 50 m water depth (sample 5) the morphological variation has increased considerably, although forma *denudata* (pl. 12, figs. 8-10, pl. 13, fig. 6) is still the dominant morphotype. On the one hand the variation has shifted slightly in the direction of forma *marginata*. On the other hand, forma *denudata* is clearly linked by intermediate forms (pl. 12, fig. 11, pl. 13, fig. 7) with forma *aculeata* (pl. 12, figs. 12-13, pl. 13, figs. 8-9). Some individuals of forma *aculeata* and also some of the intermediate specimens still belong to the nearly unornamented, elongated type, but now more characteristic *aculeata*-types, with a spinose ornamentation at the aboral end of the test and with a somewhat tapering outline are also present.

The situation found at 80 m water depth (sample 12) differs essentially from that in shallower water. Although the percentage of morphotypes with '*marginata*' chamber-types has decreased, the morphological variation within this group has shifted substantially towards the typical forma *marginata*. The angle of the undercuttings is sharper and the ornamentation is better developed. However, the test is still elongated; in our opinion this population occupies an intermediate position. Forma *aculeata* is represented by typical specimens, with a tapering test and spinose ornamentation on the older chambers. Intermediate morphotypes between forma *aculeata* and the group with '*marginata*' chamber-types are now virtually absent; two distinct, and well separated morphogroups can be recognized.

This clear separation is found in all 'deeper' samples. At 125 m water depth (sample 31), the variation in the group with '*marginata*' chambers has again shifted somewhat further towards forma *marginata*. Although the length/width ratio is still somewhat high, all other characters suggest that this population should be determined as forma *marginata*. As in sample 30 (100 m water depth), forma *aculeata* is present with relatively high frequencies.

Between 150 and 220 m water depth (samples 32, 33 and 34) the length/width ratio of forma *marginata* is further reduced, and typical representatives of this forma dominate the *Bulimina* populations. Forma *aculeata* is no longer an important faunal constituent.

In the considerably deeper southern basin (sample 282, 744 m) typical morphotypes of forma *marginata* are found (pl. 14, figs. 9-11, pl. 13, fig. 15).

### IV.3.3. Discussion

The succession as described for the central Adriatic basin is depicted schematically in fig. 23. The change in variation between forma *denudata* and forma *marginata* takes place gradually over a relatively wide depth interval, and might therefore be linked to a gradual shift of environmental characteristics. However, the variation between forma *denudata* and forma *aculeata* is restricted to a much narrower depth interval, and might therefore be the result of a more abrupt environmental change.

In our opinion the environmental characteristics relevant for the interpretation of the variation in *Bulimina* are the following:

-- the geographical distribution of *Bulimina marginata* is clearly linked to sediment with high percentages of organic matter; this non-costate species seems to have a preference for a high food availability,

-- the substantial clay sedimentation in the 30 - 80 m depth zone, which is characterized by periodically stressed conditions, obviously has resulted in the establishment of a number of environmental gradients, to both shallower and deeper areas.

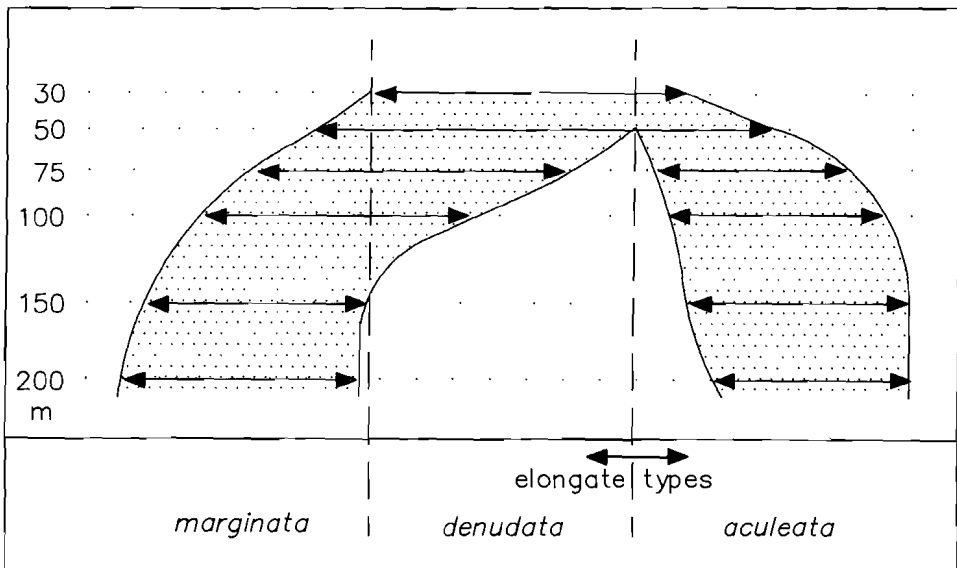


Fig. 23. Scheme indicating the range of morphological variation in *Bulimina marginata* as observed in different water depth intervals in the central Adriatic area.



If we try to define the morphological variation in the non-costate buliminids more concisely, we find that different morphological characters are involved in the two transitions observed. For the transition between the two main groups (*marginata* group and *aculeata* group) these are:

- presence/absence of undercuttings,
- position and degree of ornamentation; the ornamentation is at the lower margin of most of the chambers in *denudata*, but only on the basal part of the older chambers in *aculeata*,
- form of the test in transverse section; rounded in *denudata*, triangular in *aculeata*.

For the transition within the *marginata* group (*denudata* - *marginata*) these are:

- degree of ornamentation,
- length/width ratio,
- angularity of the lower margin and breadth of the undercuttings.

We cannot try to find causal relationships between the variation in these characters and environmental trends without speculating about the functional morphology of these characters. Unfortunately, this is without doubt the most remote corner in our knowledge of benthic foraminifera, and the subject cannot be discussed without adopting a number of ill-founded premises.

Lipps (1983) supposed that scavenging foraminifera are advantaged by having an elongate test, whereas active (epibenthic) herbivores mostly have trochoid, lenticular or flattened tests. Verhallen (1986, and in prep.) supposed that a habitat separation may have taken place during the evolution of non-costate *Bulimina*; morphotypes with '*marginata*' chamber-forms should have a sessile mode of life in or on the sediment top layer, whereas forms lacking this character (the *aculeata* group) should be specialized in burrowing activities deeper in the sediment. A similar habitat separation was suggested for different morphogroups of *Uvigerina* (Van der Zwaan et al., 1986).

We realise that the morphology of the flat surfaces underneath '*marginata*'-type chambers can be interpreted in a number of ways (e.g. increase of the surface/volume-ratio, areas with larger pores specialized for gas exchange), and could well be multi-functional. In our opinion the alignment of the stout triangular spines at the chamber margins could indicate that one of these functions is to stabilize, so that the animal can maintain an upright position in the sediment top layer, and live there as a (more or less passive) deposit feeder. The far more streamlined (screw-like) outline of forma *aculeata* suggests a more active way of life, presumably in the sediment, where the capacity of burrowing is indispensable.

In our opinion, a plausible explanation for the observed discontinuity in

variation between forma *marginata* and forma *aculeata* in deeper water (see fig. 23) is only possible if one accepts the possibility of a vertical microhabitat separation within the sediment. In the samples from deeper water, the two main morphogroups (forma *marginata* and forma *aculeata*), and probably also the two micro-habitats, are well separated. The relatively invariable environmental conditions enable the epibenthic forma *marginata* to live in and on the relatively stable sediment top-layer, where they increase their stability by means of their well developed spines and undercuttings. The inbenthic, deposit-feeding forma *aculeata* can lead a burrowing life within the sediment, as this will normally not be severely undersaturated in oxygen.

Although there is generally a strong correlation between the clay content, the content of organic matter and the percentage of deposit feeders (Purdy, 1964), Bader (1954) observed that the number of deposit feeding pelecypods strongly decreased as the percentage of organic matter exceeded a certain critical value. In his opinion this is probably the result of the accumulation of toxic decomposition products and/or the depletion of the available oxygen. As the oxygen concentration tends to decrease rapidly below the sediment surface (Jørgensen and Revsbech, 1985) taxa adapted to a burrowing way of life (as is our forma *aculeata*) are clearly not suited to live in the most stressed part of the near-shore claybelt, since there the oxygen-containing layer will periodically be extremely thin, if present at all. The strong frequency increase of forma *aculeata* at the outer edge of the clay-belt may well be the result of a rather sudden increase in the oxygen content. Especially the presence of assemblages dominated by forma *aculeata* between 75 and 125 m water depth, in samples with minor sand fraction percentages, suggests a relation with the higher oxygen content in these less well-sorted and more permeable substrata.

When the transects enter the shallower clay-belt, forma *marginata* is gradually replaced by forma *denudata*. Only in the most shallow part of the clay-belt these morphotypes with '*marginata*'-chambers show a continuous variation to atypical (elongated, nearly unornamented) representatives of forma *aculeata*, which is present there in much lower numbers than it is in deeper water (table III). In our opinion this suggests that the niches become less well separated, and that an inbenthic life position becomes disadvantageous.

The more or less intermediate morphology of forma *denudata* could be a response to the substantial seasonal and annual fluctuations in river runoff, which probably cause continuous shifts in important environmental variables, such as the thickness of the oxygen-containing top-layer. The enormous quantity of sediment deposited from suspension is a factor in itself; 1 - 3 m per 1000 years (Colantoni et al., 1980; Curzi and Tomadin 1986; Jorissen, in prep.)

means an average of 80 - 250 microns per month. In spring and autumn these values can probably be doubled at least. Obviously, also an epibenthic animal has to retain the possibility to correct its life position actively. Furthermore, the water saturation of the sediment top layer will be at a maximum (Curzi, pers. comm.) and as a consequence sediment stability will be minimal in a relatively broad zone. Therefore, epibenthic buliminids would on the one hand need the possibility to burrow actively, but would on the other hand also need stabilizing devices somewhat deeper in the sediment in order to maintain their upright position. In our opinion, both conditions imposed by these more gradually changing sedimentary characteristics are met by the increase of the length/width ratio in forma *denudata*. The same elongate form is described from a sewage outfall area in California, where similar environmental conditions can be expected (Bandy et al., 1964, *B. denudata*).

However, it is more difficult to explain the decrease in ornamentation that coincides with the transition from forma *marginata* towards forma *denudata*. A possible reason could be the much smaller availability of calcium carbonate due to the low pH in the clay-belt. Pictures of the ornamentation itself do not suggest that post-mortem dissolution processes play an important role.

Even without the aforementioned speculations, some final conclusions can be made:

-- non-marginate morphotypes of *Bulimina* have a definite preference for environments with high food availability. *Bulimina marginata* forma *denudata* is the morphotype that is most tolerant for a periodical presence of stressed conditions. Forma *aculeata*, possibly being an inbenthic deposit feeder, is advantaged by excess food availability as long as this does not lead to shortage of oxygen; forma *marginata*, possibly living in the sediment top-layer, seems to have similar limitations,

-- The transition between forma *marginata* and forma *denudata* seems to be linked to a gradual change in the environmental conditions, requiring a gradual adjustment of the morphology of the animal. The transition from forma *denudata* to forma *aculeata* seems to be related to a more abrupt change in the environment, which in this case could have been a rather sudden increase in the thickness of the oxygen-containing layer.

#### IV.3.4. TAXONOMY

##### ***Bulimina marginata* D'Orbigny 1826 forma *marginata***

D'Orbigny 1826

Pl. 4, fig. 6; pl. 12, figs. 7, 14-17; pl. 13, figs. 5, 10-11, 13-15; pl. 14, figs. 1-3, 7, 9-11; pl. 15, figs. 1-2, 5-6

1826 *Bulimina marginata* -- D'Orbigny, Tableau Méthod., p. 269, pl. 12, figs. 10-12.

1979 *Bulimina marginata* D'Orbigny -- Hageman, Utrecht Micropal. Bull., 20, p. 90, pl. 2, fig. 7.

1984 *Bulimina aculeata* -- Vénec-Peyré (not D'Orbigny), PARTIM, ECOMED, part N, pl. 6, fig. 2 (not figs. 1, 3).

1987 *Bulimina marginata* forma *marginata* D'Orbigny -- Jorissen, Marine Micropal., 12, p. 46, pl. 4, fig. 6a,b.

Typical specimens of forma *marginata* are characterized by the presence of broad, sharply angled undercuttings at the base of each chamber, and well-developed triangular spines aligned at the lower chamber margins. The length/width ratio is low (typical adult specimens: 1 - 1.5).

##### ***Bulimina marginata* D'Orbigny forma *denudata***

Cushman and Parker, 1938

Pl. 4, fig. 6; pl 12, figs. 1-4, 8-10; pl. 13, figs. 1-2, 6; pl. 15, fig. 3

1901 *Bulimina fusiformis* var. *marginata* -- Fornasini, Mem. R. Acc. Sc., ser. 5a, 9, p. 378, pl. O, figs. 24,45.

1938 *Bulimina pagoda* Cushman var. *denudata* -- Cushman and Parker, Contr. Cushman Lab. Foram. Res., 14, p. 57, pl. 10, figs. 1-2.

1977 *Bulimina* spp. -- Haake, PARTIM, J. Foram. Res., 7, p. 66, pl. 2, figs. 10-11. (not figs. 7-9).

1984 *Bulimina aculeata* -- Vénec-Peyré (not D'Orbigny), PARTIM, ECOMED, Part N, pl. 6, figs. 1,3 (not fig. 2).

1987 *Bulimina marginata* forma *denudata* Cushman and Parker -- Jorissen, Marine Micropal., 12, p. 46, pl. 4, figs. 4,7.

Forma *denudata* differs from the typical form in the rounded angles of its undercuts, its strongly reduced ornamentation and its larger length/width ratio (typical adult specimens: 1.7 - 2.0). In large specimens the undercuttings are not developed in the later chambers.

Although our forma *denudata* differs in some respects from the original description of *B. pagoda* var. *denudata* (the undercuttings are less extreme and not always present in the later chambers), the similarities (its reduced ornamentation and its larger length/width ratio) in our opinion justify the use of this name at a forma level. We judge the specimen figured by Bandy et al. (1964, p. 133, fig. 7D) to be close enough to our material to consider it synonymous. According to the taxonomical concept developed by Fornasini, our morphotypes could probably best be described as *B. fusiformis* var. *marginata*. However, we choose a different concept, and differentiate mainly on the basis of the chamber-form.

***Bulimina marginata* D'Orbigny forma *aculeata* D'Orbigny, 1826**  
Pl. 4, fig. 5; pl. 12, figs. 6, 12-13, 18-19; pl. 13, figs. 4, 8-9, 12, 16; pl. 14,  
figs. 4-6, 8, pl. 15, fig. 4.

1826 *Bulimina aculeata* -- D'Orbigny, Tableau Méthod., p. 269.

1901 *Bulimina fusiformis* -- Fornasini (not Williamson), Mem. R. Acc. Sc., ser. 5a, 9, p. 377-78, pl. O, figs. 1,3,4,6,9,16,18,21,23,27,36,40,41.

1970 *Bulimina aculeata* -- Von Daniels, Göttinger Arb. Geol. Paläont., 8, p. 82, pl. 5, fig. 8.

1979 *Bulimina elongata* D'Orbigny *subulata* Cushman and Parker -- Hageman, Utrecht Micropal. Bull., 20, p. 90, pl. 2, fig. 6.

1987 *Bulimina marginata* forma *aculeata* D'Orbigny -- Jorissen, Marine Micropal., 12, p. 46, pl. 4, fig. 5.

Forma *aculeata* is characterized by the absence of undercut margins of the chambers, a reduced and irregular ornamentation on the older part of the test, a comparatively large length/width ratio (typical adult specimens: 2.0 - 2.2) and sometimes a twisted appearance.

Forma *aculeata* comprises a number of morphotypes that have been separated previously on the basis of chamber outline and degree of ornamentation.

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**Plate 12**

*Bulimina marginata*

First row: specimens from sample 71 (30 m);

Figs. 1-4: forma *denudata*, typical representatives with rounded, but undercut chamber margins (see pl. 13) and weakly developed ornamentation.

Fig. 5: morphotype intermediate between forma *denudata* and forma *aculeata*. Clear undercuttings are no longer present (see pl. 13).

Fig. 6: forma *aculeata*, elongate, weakly ornamented morphotype.

Second row: specimens from sample 5 (50 m);

Fig. 7: morphotype intermediate between forma *denudata* and forma *marginata*; the almost complete absence of ornamentation is characteristic for the first-mentioned morphotype, whereas the angled undercuttings (see pl. 13) are typical for the latter.

Figs. 8-10: forma *denudata*, typical morphotypes.

Fig. 11: elongate morphotype, intermediate between forma *denudata* and forma *aculeata*.

Fig. 12: forma *aculeata*; elongate, nearly unornamented morphotype.

Fig. 13: forma *aculeata*, more typical morphotype with a basal spinose ornamentation and a somewhat tapering test.

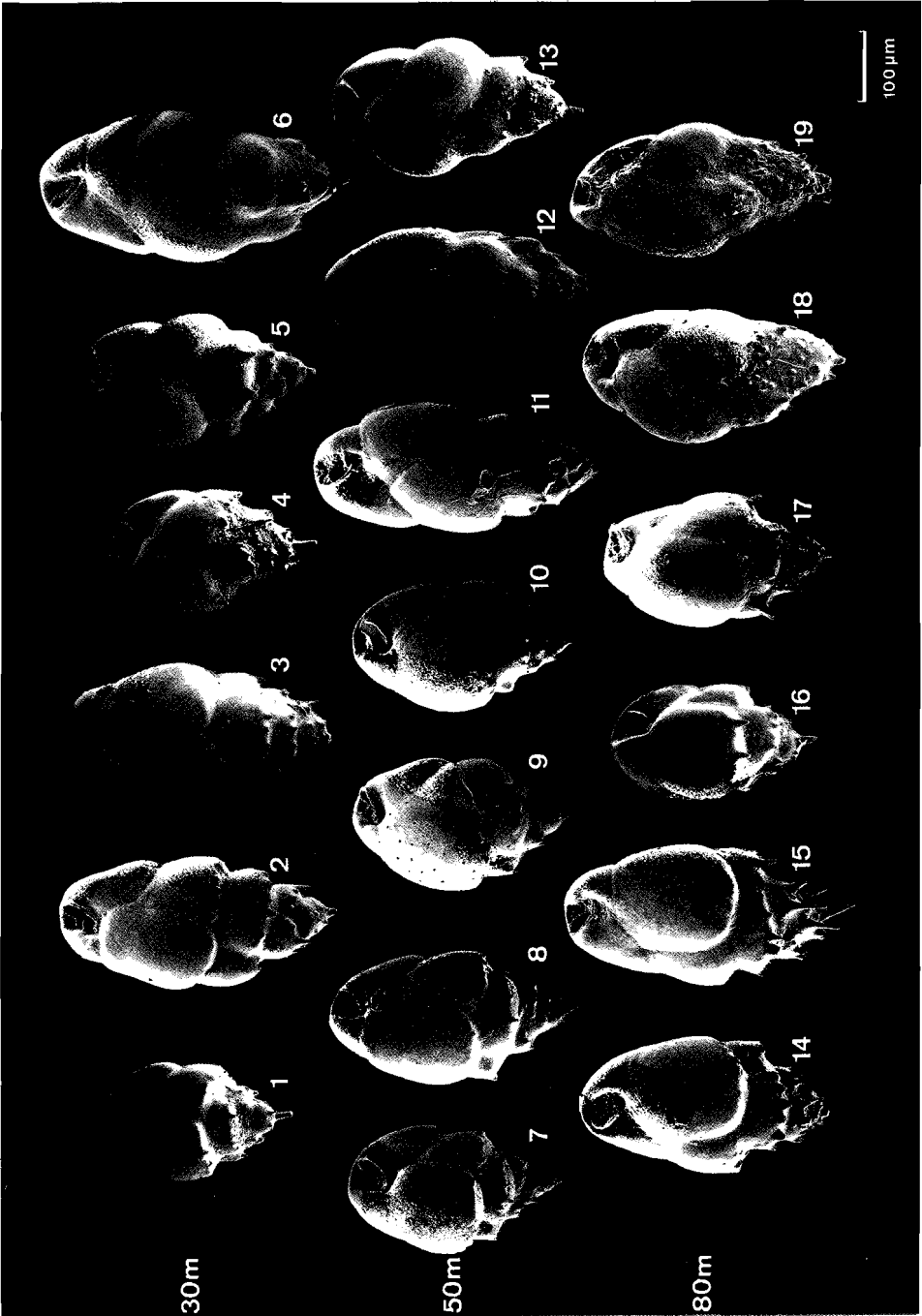
Third row: specimens from sample 12 (80 m);

Figs. 14-17: forma *marginata*; the chamber margins are definitely sharper than in shallower samples (see pl. 13), the ornamentation is better developed, but the test is still elongated.

Figs. 18-19: forma *aculeata*, typical morphotypes with a tapering test and spinose ornamentation on the older chamber.

Intermediate morphotypes are no longer present.

All enlargements 100 x.



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## Plate 13

### *Bulimina marginata*, viewed from below

First row: specimens from sample 71 (30 m);

- Fig. 1: forma *denudata*; detail of specimen pictured on pl. 12, fig. 1.  
Fig. 2: forma *denudata*; detail of specimen pictured on pl. 12, fig. 3.  
Fig. 3: morphotype intermediate between forma *denudata* and forma *aculeata*, detail of specimen pictured on pl. 12, fig. 5.  
Fig. 4: forma *aculeata*, elongate, weakly ornamented morphotype, detail of specimen pictured on pl. 12, fig. 6.

Second row: specimens from sample 5 (50 m);

- Fig. 5: morphotype intermediate between forma *denudata* and forma *marginata*, detail of specimen pictured on pl. 12, fig. 7.  
Fig. 6: forma *denudata*; detail of specimen pictured on pl. 12, fig. 10.  
Fig. 7: morphotype intermediate between forma *denudata* and forma *aculeata*, elongate, weakly ornamented morphotype; detail of specimen pictured on pl. 12, fig. 11.  
Fig. 8: forma *aculeata*, elongate, weakly ornamented morphotype, detail of specimen pictured on pl. 12, fig. 12.  
Fig. 9: forma *aculeata*, typical, detail of specimen pictured on pl. 12, fig. 13.

Third row: specimens from sample 12 (80 m);

- Fig. 10: forma *marginata*, elongate type, detail of specimen pictured on pl. 12, fig. 14.  
Fig. 11: forma *marginata*, elongate type, detail of specimen pictured on pl. 12, fig. 15.  
Fig. 12: forma *aculeata*, typical, detail of specimen pictured on pl. 12, fig. 19.

Fourth row: specimens from deeper samples;

- Fig. 13: forma *marginata*, elongate type, sample 31 (125 m), central basin, detail of specimen pictured on pl. 14, fig. 3.  
Fig. 14: forma *marginata*, typical, sample 34 (220 m), central basin, detail of specimen pictured on pl. 14, fig. 7.  
Fig. 15: forma *marginata*, typical, sample 282 (744 m), southern basin, detail of specimen pictured on pl. 14, fig. 9.  
Fig. 16: forma *aculeata*, typical, sample 31 (125 m), central basin, detail of specimen pictured on pl. 14, fig. 5.

All enlargements 150 x.





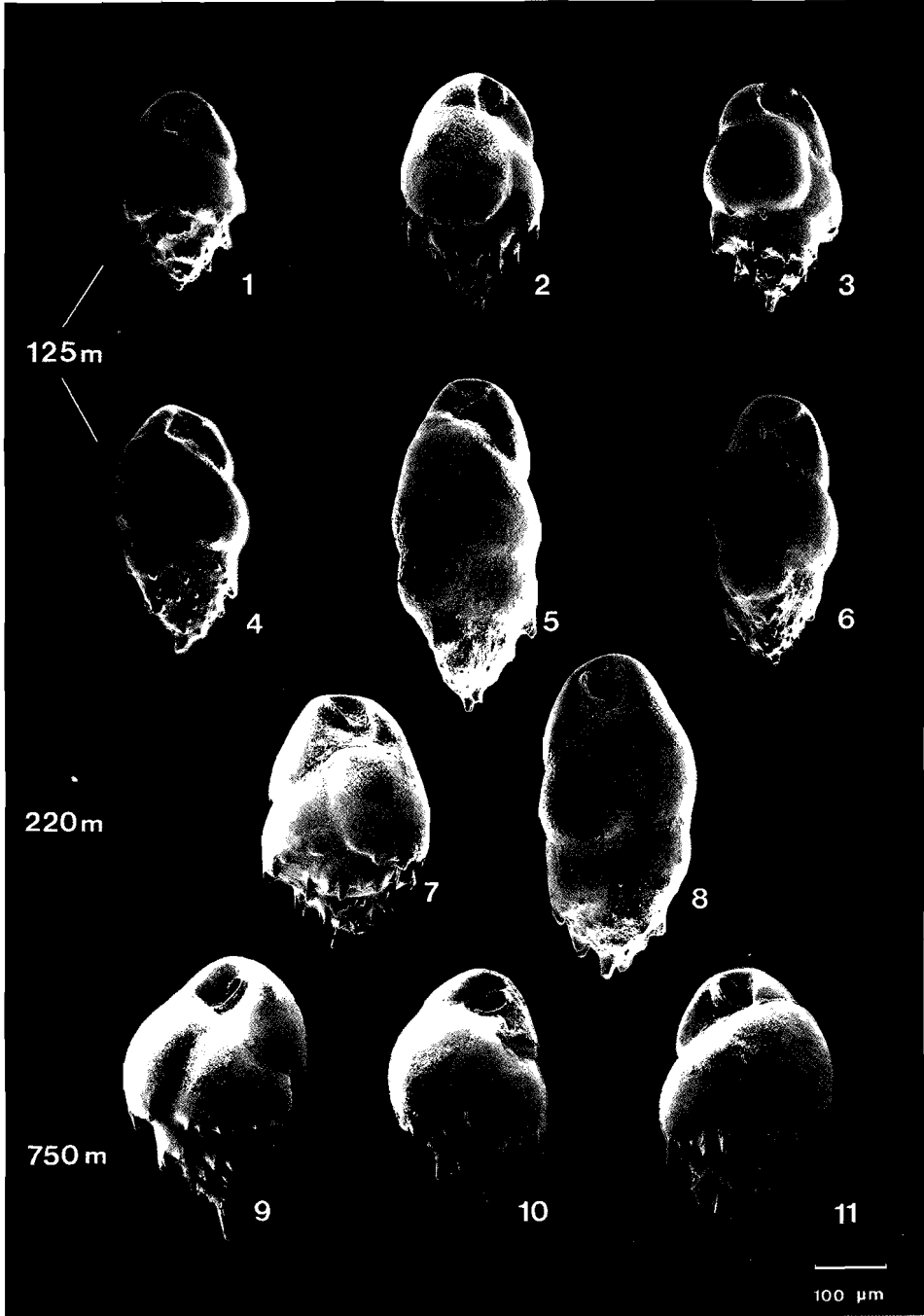
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## Plate 14

### *Bulimina marginata*

- Figs. 1-3:      forma *marginata*, sample 31 (125 m), central basin. Length/width ratio still somewhat high, further typical morphotypes.
- Figs. 4-6:      forma *aculeata*, typical morphotypes, sample 31 (125 m).
- Fig. 7:          forma *marginata*, typical morphotype, sample 34 (220 m), central basin.
- Fig. 8:          forma *aculeata*, typical morphotype, sample 34 (220 m).
- Figs. 9-11:     forma *marginata*, typical morphotypes, sample 282 (744 m), southern basin.

All enlargements 100 x.



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## Plate 15

### *Bulimina marginata*, details

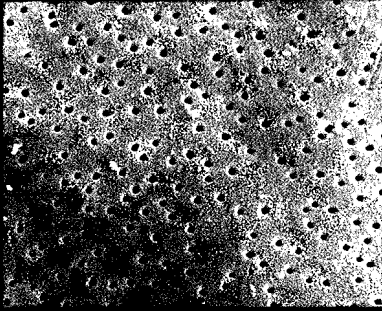
- Fig. 1: forma *marginata*, typical, detail of apertural structures, sample 282 (744 m), specimen pictured on pl. 14, fig. 10, enlargement 400 x.
- Fig. 2: forma *marginata*, typical, details of ornamentation and pores on the underside of the test, sample 282 (744 m), specimen pictured on pl. 14, fig. 9, enlargement 700 x.
- Fig. 3: forma *denudata*, pores, sample 71 (30 m), specimen pictured on pl. 12, fig. 1, enlargement 2500 x.
- Fig. 4: forma *aculeata*, *fusiformis*-type, pores, sample 71 (30 m), specimen pictured on pl. 12, fig. 6, enlargement 2500 x.
- Fig. 5: forma *marginata*, elongate type, pores, sample 12 (80 m), specimen pictured on pl. 12, fig. 15, enlargement 2500 x.
- Fig. 6: forma *marginata*, typical, pores, sample 282 (744 m), specimen not figured, enlargement 2500 x.



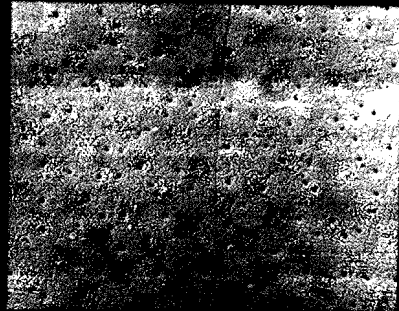
1 10  $\mu\text{m}$



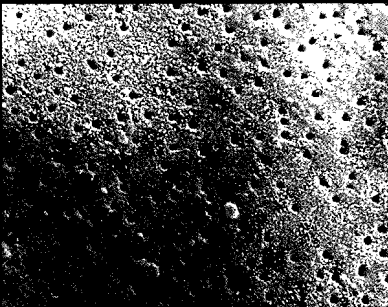
2 30  $\mu\text{m}$



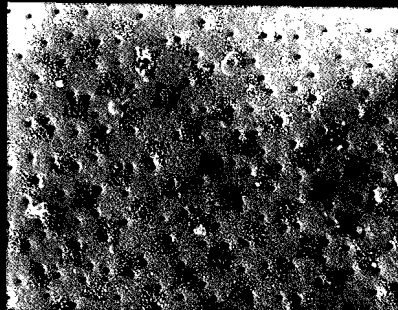
3 3  $\mu\text{m}$



4 3  $\mu\text{m}$



5 3  $\mu\text{m}$



6 3  $\mu\text{m}$

#### IV.4. GENUS *ELPHIDIUM* MONTFORT, 1808

##### IV.4.1. Introduction

During the last decennia, the number of papers on the genus *Elphidium* has increased enormously. An important contribution concerning the internal structures and the implications these have for generic designation was made by Hansen and Lykke-Andersen (1976). Furthermore, a number of studies dealing with intra- and inter-specific variation have appeared; some authors adopt a descriptive approach (Brodniewicz, 1972; Feyling-Hansen, 1972; Wilkinson, 1979; Miller et al., 1982), others a statistical/biometrical one (Buzas, 1966; Painter and Spencer, 1984; Buzas et al., 1985). The increased interest for this group can at least partially be explained by the fact that *Elphidium* appears to be highly sensitive to environmental variations in shallow marine habitats. Differences in environmental conditions are reflected in the morphology of the taxa, and therefore the various ecophenotypes seem to provide an important tool for (paleo-)ecological interpretation. Nearly all the afore-mentioned studies deal with Atlantic (or at least temperate) faunas. Interest seems to focus on the species *E. excavatum* (= *E. clavatum* as used by Wilkinson, 1979), in which some ten different formae have been recognized by the various authors.

Although some data have been published, the Mediterranean representatives of *Elphidium* are not nearly so well known as those from temperate regions. However, in our study concerning the general distribution of benthic foraminifera in the Adriatic Sea (Jorissen, 1987), it was suggested that the elphidiids could have a comparable (paleo-)ecological value in this subtropical region. Although they are less dominant in subtropical than in more temperate regions, representatives of the genus appear in substantial numbers on all types of bottoms in near-shore environments. The quantitatively most important species are *E. granosum* (D'Orbigny), *E. poeyanum* (D'Orbigny), *E. advenum* (Cushman), *E. crispum* (Linnaeus), and *E. margaritaceum* Cushman. Especially the two first mentioned show a high degree of intraspecific variability, which could be linked to variations in environmental parameters.

As can already be concluded from the enumeration of species that are important in the Adriatic Sea, our concept of the genus *Elphidium* is quite broad; it conforms to that of Hansen and Lykke-Andersen (1976), and comprises a number of taxa that have previously been assigned to *Criboelphidium* Cushman and Brönnimann, *Cribrononion* Thalmann, *Nonion* Montfort, or *Protelphidium* Haynes.

#### IV.4.2. *Elphidium granosum* (D'Orbigny, 1846)

##### IV.4.2.1. *General distribution*

Within *E. granosum*, there is a continuous variation between two extreme morphotypes: forma *granosum*, having a low number of chambers in the last whorl and an unfilled umbilicus, and forma *lidoense*, with a relatively high number of chambers in the last whorl and an umbilicus filled with imperforated knobs. A close relationship between *E. granosum* and *E. lidoense* was suggested earlier by Parker (1958), Brodniewicz (1972), Hageman (1979) and Rupp (1986).

The frequency distribution of *E. granosum* is depicted in figure 24, and in figure 25 the zones dominated by each of the two morphotypes are indicated. The highest frequencies of the species are found in the clay-belt parallel to the Italian coast. However, the species is also present in fair numbers (predominantly forma *lidoense*) on the sand platform. The typical form is the dominating one on clayey substrata with relatively high percentages of organic matter, whereas forma *lidoense* predominates on sandy substrata and on clayey bottoms with lower percentages of organic matter.

It is useful to bear in mind that in a continuous variation, forma designation is rather subjective. This is particularly true in the case of the 'deepest' samples considered in the present study, because there the two main distinctive criteria no longer co-vary. The number of chambers in the last whorl remains low, but the area covered by umbilical knobs increases strongly. Since our determinations were based on the last-mentioned criterion, a number of 'intermediate' morphotypes have been determined as forma *lidoense*.

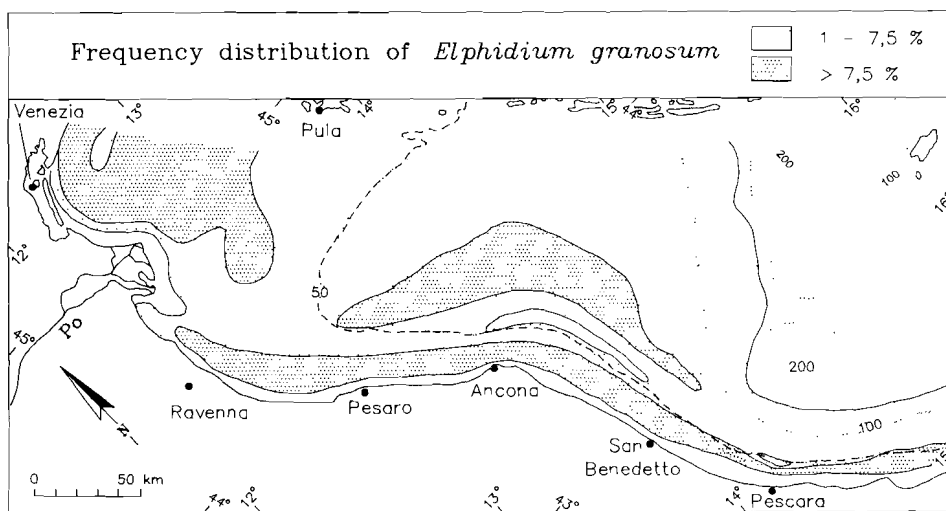


Fig. 24. Frequency distribution of *Elphidium granosum*; the two morphotypes taken together.

#### IV.4.2.2. Geographical variation

To obtain more insight into the precise distribution of the different morphotypes on clayey substrata, we have followed the variation in two transects: one (fig. 12: transect III, samples 191 - 90) located 75 km south of the Po delta, north-east of Pesaro and the second (fig. 12: transect V, samples 66 - 59) located some 125 km further southward, east of San Benedetto. In order to study the morphology in deeper water, we added two samples from transect VI (NE of Pesaro, samples 12 and 13). For all samples involved, the values of the known environmental parameters have been listed in table IV, together with the percentages of the two morphotypes, the number of species per (250-)count and the number of foraminifera per gram dry weight.

As can be seen in this table and figure 24, the cumulative frequencies of the two morphotypes of *E. granosum* in the most near-shore samples are relatively low. With increasing depth, the frequencies of *E. granosum* increase, until maximum percentages are reached at a water depth of about 20 m. In still deeper water, on clayey substrata the frequencies decrease to minimum values at some 40 m in transect III and at some 60 m in transect V. As soon as the transect enters the sand platform (samples 90 and 59), the percentages of *E. granosum* start to increase again. Typical representatives of forma *granosum* are only present in the clay-belt (fig. 25), in samples with maximum percentages for the species (around 20 m).

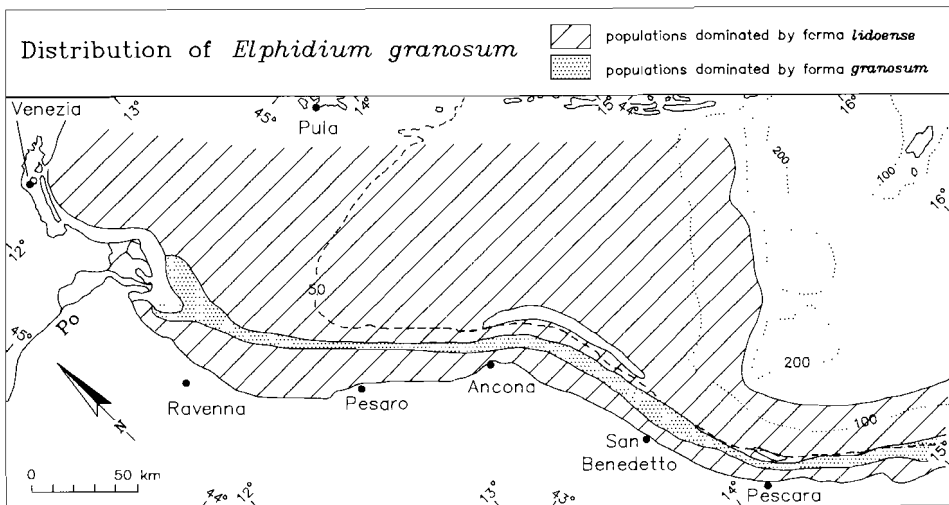


Fig. 25. Distribution of the two morphotypes of *Elphidium granosum*.

	Sample no.	depth (m)	% sand	% org. matter	% CaCO <sub>3</sub>	No. of species/ count	forams/ g dry weight	percentage <i>granosum</i>	percentage <i>lidoense</i>
Transect III	191	10.5	58.6	.1	27.8	17	215	.8	8.0
	190	13	2.4	.7	26.6	14	167	.0	10.6
	189	16.5	1.1	1.3	26.2	16	25	4.5	8.6
	188	26	.7	1.5	25.6	19	42	3.7	3.7
	187	42	14.6	1.1	28.2	25	307	.8	4.2
	90	52	78.6	.2	33.1	34	332	1.5	4.2
Transect V	66	8	88.2	.0	40.9	43	63	1.3	3.0
	67	11	91.4	.0	41.1	33	33	.4	7.5
	68	15	74.2	.1	42.7	21	108	.4	10.6
	77	17.5	.9	1.1	33.7	14	47	14.3	5.5
	69	20	.8	1.0	33.3	15	41	17.2	4.2
	70	25	.9	1.0	30.0	13	33	15.4	1.7
	71	30	.5	1.1	27.7	17	18	8.7	3.0
	72	40	.4	1.2	29.6	19	9	7.3	3.8
Transect VI	73	60	.4	1.0	27.6	27	29	1.2	1.6
	59	80	19.4	.9	33.0	32	766	.0	10.4
	12	80	.1	1.1	28.7	34	31	2.2	2.8
	13	100	.3	1.3	27.8	43	65	1.3	2.9

Table IV. Environmental parameters of samples used for the morphological analysis of *Elphidium granosum*.

The two transects show a comparable pattern of morphological variation; this has been visualised in plates 18 and 19, where in six successive rows the faunas of transect V (samples 67, 77, 70, 71 and 73), complemented by the fauna of sample 12, are figured. The morphological changes taking place in this transect are the following:

-- in the shallow-most samples forma *lidoense*, with well-developed umbilical knobs, strongly dominates the assemblages, whereas typical *granosum* morphotypes are not present (e.g. sample 67, pl. 18, first row).

-- a sharp faunal change takes place between 15 m (sample 68, comparable to sample 67) and 17.5 m water depth (sample 77, pl 18, second row). From 17.5 m downwards forma *granosum* strongly dominates the assemblages; typical representatives of forma *lidoense* are extremely scarce. The cumulative frequencies of the species show maximum values here.

-- it is obvious that the morphological variation changes much more gradually towards deeper water. At 30 m water depth (sample 71, pl. 19, first row), where the relative frequencies start to decrease, some of the *lidoense* characteristics return. Although the number of chambers in the last whorl remains low (typical for forma *granosum*), small umbilical knobs appear again.



-- this trend continues in still deeper water; at 60 m water depth (sample 73, pl. 19, second row), where the total abundance of the species is very low, nearly all the specimens show a prominent umbilical infill. At this depth a new morphological characteristic can be observed: on the *lidoense* (left) side of the variation the sutural ends (on the umbilical side) become deeply depressed, and look as if they are openings into the umbilical canal system (plate 19, fig. 8, enlarged on plate 17, fig. 5). The specimen figured by Von Daniels (1970, pl. 7, fig. 11) fits well into this association. We found no suitable name for such morphotypes.

More or less the same succession of associations is present in transect III, with the exception that samples with a strong dominance of typical forma *granosum* (as observed between 17.5 and 25 m) were not found.

It is obvious that the divergence in morphological characters observed in our deepest associations (number of chambers versus umbilical characters) causes problems with regard to morphotype designation. We decided to use the presence of umbilical knobs as the main criterion, so that a number of forms, which strictly speaking are intermediate (e.g. pl. 19, fig. 7-9, 13-14), were counted as forma *lidoense*. Of course this had consequences for the frequency analyses and distribution chart presented before (table IV, figs. 24-25).

	Sample	N	$\bar{k}$	$\bar{l}$	Depth
Transect III	191	20	9.03	307.4	10.5
	190	28	9.01	302.8	13
	189	26	8.70	310.4	16.5
	188	22	7.70	250.8	26
	187	10	8.05	276.9	42
	90	9	7.72	276.5	52
Transect V	66	36	8.69	283.3	8
	67	63	8.86	282.8	11
	68	58	8.97	287.2	15
	77	99	7.96	288.9	17.5
	69	96	8.03	276.2	20
	70	84	7.53	285.2	25
	71	46	7.72	269.9	30
	72	36	7.71	269.9	40
	73	23	7.50	265.7	60
	59	24	7.46	256.7	80
Transect VI	12	41	7.38	272.8	80
	13	40	7.21	266.0	100

Table V. Average values for the number of chambers in the last whorl ( $\bar{k}$ ) and maximum diameter ( $\bar{l}$ , in microns) of *E. granosum*.

In order to reduce this subjectivity, an attempt was made to describe the variation observed by simple biometrical methods. Therefore, for some 50 specimens (if present) from each sample the number of chambers in the last whorl and the maximum diameter of the test were determined. Because all samples yielded homogeneous populations of *E. granosum*, they can be characterized by the average values of the measured parameters, which are given in table V, and are plotted against water depth in figures 26 and 27.

As could be expected, in both transects the number of chambers in the last whorl shows a sharp drop at some 20 m water depth and very slowly decreases further with increasing depth. In the Pesaro transect (III), the reduction in the number of chambers is accompanied by an abrupt decrease in size. In the San Benedetto transect however, the average maximum diameter decreases more

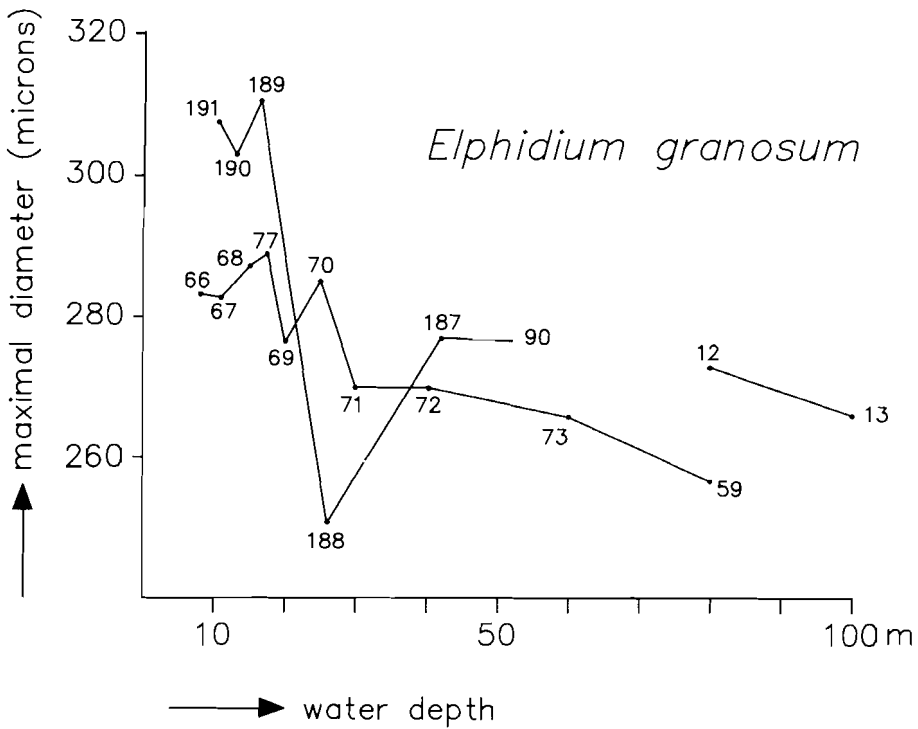


Fig. 26. Average values of the maximum diameter for specimens of *E. granosum* versus the water depth of their sample locality.

gradually from shallow to deeper habitats. Being aware of the possibility of post-mortem transport, we carefully re-examined the faunas of all samples of the Pesaro transect. Since a more or less complete size variation is present in a number of other taxa, we conclude that we are probably not dealing with a transport phenomenon.

In figure 28 the average number of chambers is plotted against the average maximum diameter. It should be remembered that these two parameters are interrelated by the growth curve of the animals. In both transects two clusters are found;

-- one characterized by a comparatively large number of chambers and a large diameter, corresponding to shallow-water samples dominated by extreme *lidoense*-types,

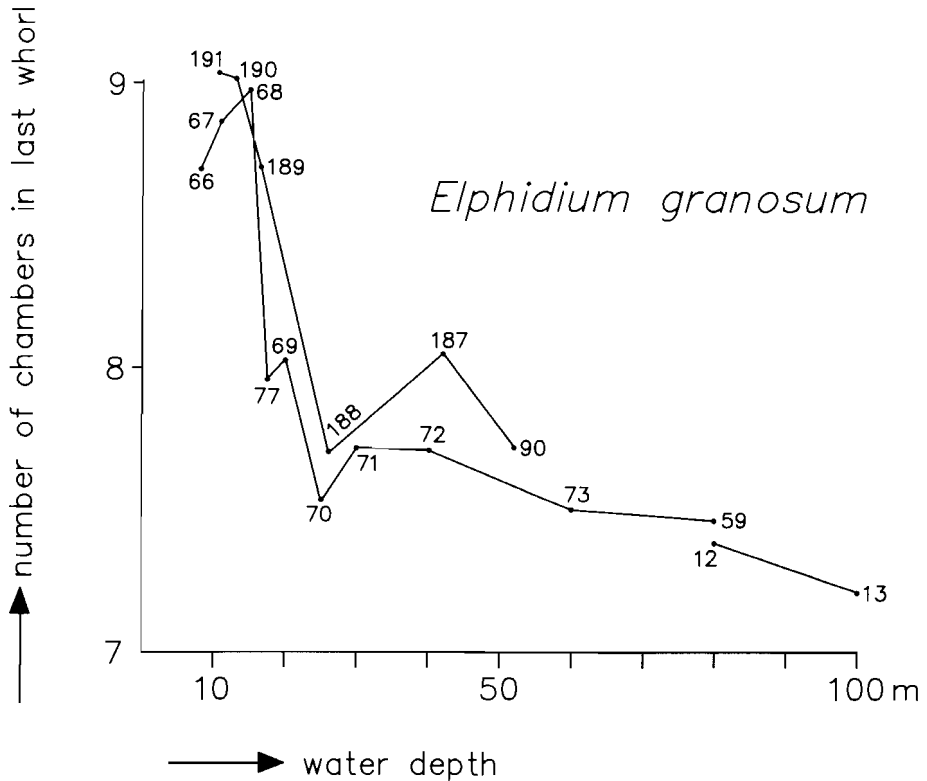


Fig. 27. Average values for the number of chambers in the last whorl of *E. granosum* versus the water depth of their sample locality.

– the other characterized by a small number of chambers and an intermediate or small diameter. In this second cluster two sub-groups can be recognized, one (IIa) having an intermediate number of chambers and an intermediate diameter (corresponding to rather shallow samples dominated by typical forma *granosum*) and another (IIb) with low values for both parameters (samples from relatively deep water), corresponding to the ‘intermediate’ associations.

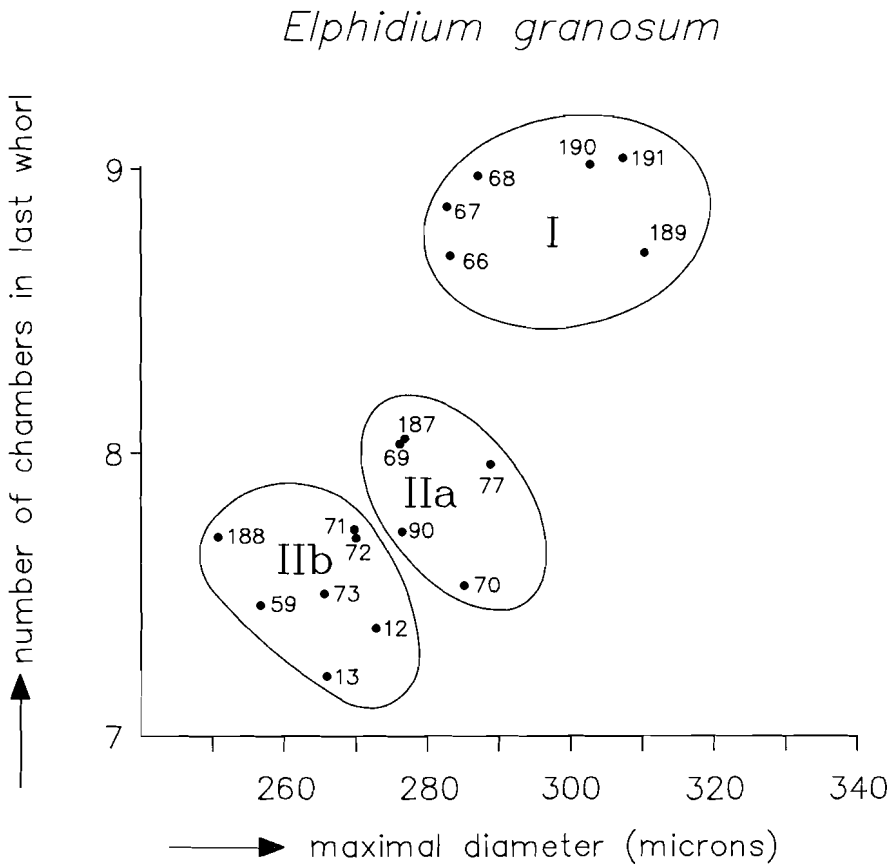


Fig. 28. Average number of chambers in the last whorl versus average maximum diameter in *Elphidium granosum*, for samples from transects III and V.

#### IV.4.2.3. Discussion

As we have seen, it seems to be possible to distinguish the three types of *E. granosum* populations on biometrical grounds. For the (clayey) San Benedetto transect V all available data, which have been entered in tables IV and V, are schematically summarized in figure 29. The complex of variation has been separated into seven elements: the maximum diameter, the number of chambers per whorl, the degree of inflation of the chambers, the outline of the test, the presence of umbilical knobs, the colour of the test and the relative abundance of the morphotype considered.

From this scheme, some of the relations between morphology and environment can be deduced. In transect V an abrupt change in parameters as well as in morphology takes place between samples 68 and 77 that come from water depths differing by only 2.5 m. The differences in environmental parameters are clearly the result of the upper limit of the influence of runoff products, which is obviously situated between these two samples and seems to be very sharp. The samples from the shallowest water (66-68) are sheltered from clay sedimentation, and conditions following from an increased nutrient input do not occur. In this 'unstressed' environment the populations are strongly dominated by the *lidoense* morphotype.

The outer zone influenced by fluvial runoff products is situated between 17.5 and 25 m water depth ( samples 77, 69-70). In our opinion, this zone can be characterized by a raised nutrient level, although periods of oxygen deficiency probably do not occur. The maximum frequencies indicate that *E. granosum*, and especially its forma *granosum*, has a marked preference for these conditions. Although the number of foraminifera per gram dry sediment is low, it is not unreasonable to assume that relatively high standing stocks are present here, if the dilution effect of the sedimentation of 0.1 - 0.3 cm per year is taken into consideration.

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Fig. 29. Scheme indicating the correlation between environmental parameters, general faunal data and the morphology of *E. granosum*.

## ENVIRONMENT

water depth	0 → 17.5 → 80m	
% sand	high	low
% organic matter	low	high
% calcium carbonate	high	low
oxygen availability	high	low → decrease → minimum

## FAUNAL PARAMETERS

diversity (number of species per 250 - count)	high	low → minimum → increase			
number of forams	high	low → minimum → increase			
prevailing cluster	1 / 3	2	6/2	6	8/6

## CHARACTERISTICS OF *Elphidium granosum*

morphological cluster	I	IIA → IIB
number of chambers	large	small
test size	large	small → minimum
chamber form	compact	inflated
outline test	rounded	lobate
umbilicus	filled with knobs	empty → filled
test colour	brown	colourless → brown
frequency	intermediate	high → low

Below 30 m water depth (samples 72-73, 12) the relative frequencies decrease to minimum values, and the intermediate morphotypes are predominant. The diameter of the test further decreases. It was concluded earlier that in this zone excess input of organic matter can periodically lead to oxygen shortage. The decreasing abundances of *E. granosum* suggest that this species does not have a large tolerance for such conditions. Probably the species is only capable of profiting from the high food supply as long as a certain (minimum) threshold value for oxygen is not exceeded.

In the light of this apparent relation between morphology and environment, we can speculate about the function of the various morphological changes. Types with a low number of inflated chambers appear under conditions of high food availability. This can well be the result of a more rapid increase of the protoplasm volume per growth step under such favourable conditions. Furthermore, it is common for the average diameter to decrease as 'environmental stress' increases or as the environment is extremely favourable. The species reaches reproductive maturity earlier so that it can profit optimally from the short periods with favourable conditions.

In our opinion, it is also possible to explain the somewhat different variation in the Pesaro transect III on the basis of the aforementioned assumptions. There the influence of the Po runoff has not yet crystallized and a fine-meshed succession of different environments, as is present further southward, is not yet established. The zone of periodically stressed conditions covers a wider area, and as a consequence faunal cluster 2 (fig. 11), characterized by taxa preferring unstressed, nutrient-rich conditions (such as *E. granosum* forma *granosum*), is hardly represented at all (fig. 14). For the variation in *E. granosum* this means that populations dominated by *lidoense* morphotypes are followed directly by associations dominated by intermediate morphotypes; populations strongly dominated by typical forma *granosum* are not found here.

The geographical distribution of the different umbilical characters is much more difficult to understand; very little is known about the function of umbilical knobs and chamber flaps. Umbilical knobs are often well developed in taxa with symbiotic algae. One could speculate that their function may be to store calcium carbonate and/or to concentrate light. In our forma *lidoense* symbionts may well be present, but in our 'intermediate' morphotypes, which live in a zone where the transparency of the water column will be extremely low due to the large quantity of suspended material, the presence of symbionts is highly improbable. We suppose that the more strongly developed umbilical features of the latter morphotypes (including the development of sutural openings) could point to a more intensive use of the canal system in this stressed

zone. Even more difficult to understand are the differences in test colour, which co-vary with the umbilical characters; tests with umbilical knobs are coloured, and tests without umbilical knobs are uncoloured.

A final remark must be made concerning the distribution of *E. granosum* on the sand platform. Here too the 'intermediate' morphotype dominates strongly, but the high abundances east of the present Po delta are in our opinion the result of reworking. The extremely poor preservation of most shallow mud-dwellers (*E. poeyanum* forma *decipiens* and *A. parkinsoniana* forma *tepida* are also abundant) strongly suggests that these forms are Pleistocene remnants testifying to a more eastern position for the former Po outlet.

#### IV.4.3. *Elphidium poeyanum* (D'Orbigny, 1839)

##### IV.4.3.1. General distribution

Within this species, a gradual variation between two extreme morphotypes can be observed: forma *poeyanum* with a comparatively small number of inflated chambers, depressed sutures and a relatively open umbilicus, and forma *decipiens* with a higher number of chambers, flush sutures and an umbilicus filled by glassy material. The relative frequencies of *E. poeyanum* are mapped in figure 30; the zone of samples with a substantial proportion of forma *poeyanum* (more than 25% of the morphotypes of *E. poeyanum*) is indicated separately.

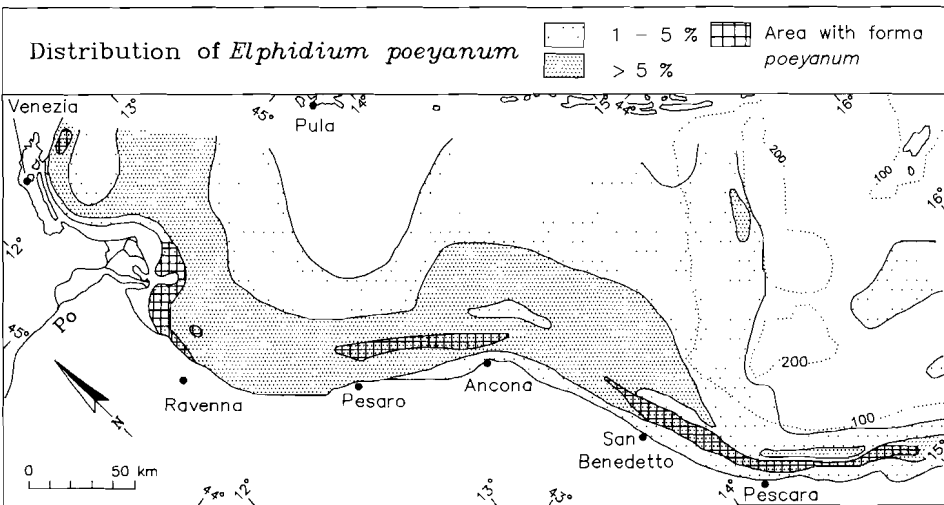


Fig. 30. (Frequency) distribution of the different morphotypes of *Elphidium poeyanum*. The area with a substantial amount of forma *poeyanum* (more than 25% of all specimens of *E. poeyanum*) is marked separately.



As for the distribution map of *E. granosum*, this figure too gives a very schematic picture. It is not always easy to distinguish between the two morphotypes, since the various morphological features involved do not always covary and additional features develop in deeper water.

#### IV.4.3.2. Geographical variation

To give a better picture of the distributional pattern, we show in plates 20 and 21 representatives of a number of populations found along sample transect V (perpendicular to the coast, east of San Benedetto), completed with the deepest samples of transect VI. The known environmental and faunal data of the various samples have been listed in table VI.

In the samples from the shallowest depths (66-68; pl. 20, first row), the *E. poeyanum* assemblages are strongly dominated by forma *decipiens*. On the poeyanum-side of the variation, the pore-size seems to be larger (pl. 20, fig. 5-6) and the flap-like chamber-projections become more distinct.

	Sample no.	depth (m)	% sand	% org. matter	% calc. carb.	No. of spec.	forams/ g dry weight	percentage <i>poeyanum</i>	percentage <i>decipiens</i>
Transect III	191	10.5	58.6	.1	27.8	17	215	.8	11.2
	190	13	2.4	.7	26.6	14	167	1.1	15.1
	189	16.5	1.1	1.3	26.2	16	25	1.0	7.6
	188	26	.7	1.5	25.6	19	42	1.1	12.9
	187	42	14.6	1.1	28.2	25	307	.8	13.5
Transect V	66	8	88.2	.0	40.9	43	63	1.3	3.3
	67	11	91.4	.0	41.1	33	33	.0	3.0
	68	15	74.2	.1	42.7	21	108	.4	6.0
	77	17.5	.9	1.1	33.7	14	47	2.6	5.5
	69	20	.8	1.0	33.3	15	41	3.4	8.8
	70	25	.9	1.0	30.0	13	33	7.2	3.1
	71	30	.5	1.1	27.7	17	18	2.7	4.2
	72	40	.4	1.2	29.6	19	9	.0	3.8
73	60	.4	1.0	27.6	27	29	1.2	9.0	
Transect VI	12	80	.1	1.1	28.7	34	31	0.7	1.9
	13	100	.3	1.3	27.8	43	65	.0	2.6
	31	125	1.0	1.2	30.6	45	61	.0	0.4
Transect VIII	231	16	30.6	.5	35.7	28	57	.8	5.0
	230	23	6.4	.6	34.3	24	109	5.8	8.2
	232	25	2.7	1.2	32.9	27	120	1.4	12.7
	229	30	1.9	1.1	32.5	24	28	4.0	3.2
	228	50	.4	1.2	30.7	23	25	.4	8.2

Table VI. Environmental and faunal parameters of samples used for the morphological analysis of *E. poeyanum*.

A notable change takes place between 15 and 17.5 m water depth (samples 68 and 77, pl. 20, second row): the variation strongly shifts in the direction of forma *poeyanum*. This coincides with an increase in the abundance of the species as a whole. Between 17.5 and 25 m (samples 77, 69-70) specimens with a complete umbilical infill, typical for forma *decipiens*, are quite rare. In typical representatives of forma *poeyanum* the test wall is rather thin, as can be seen from the presence of large numbers of broken final chambers (pl. 20, fig. 17-18).

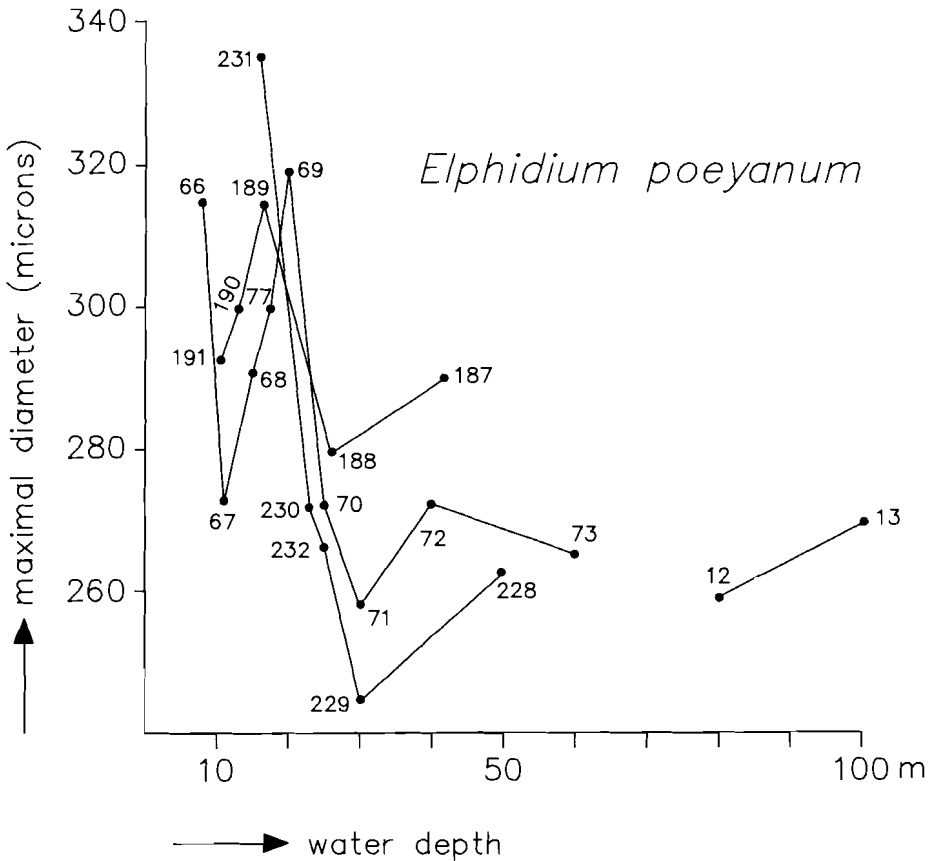


Fig. 31. Average values of the maximum diameter for specimens of *E. poeyanum* versus the water depth of their sample locality.

From 25 m downwards, a more gradual morphological shift takes place, incorporating the complete range of variation between the two morphotypes. At some 50 m water depth the chambers start to form imperforate zones adjacent to the umbilical region, at first (samples 71 - 73) mainly in forma *poeyanum* (pl. 21, fig. 6, pl. 23, fig. 2-3) but in still deeper samples (12-13, 31) also in forma *decipiens* (pl. 21, fig. 7-8, 13-17, pl. 23, fig. 4-5). Parallel to this trend, the number of retral processes tends to decrease and the pores become smaller.

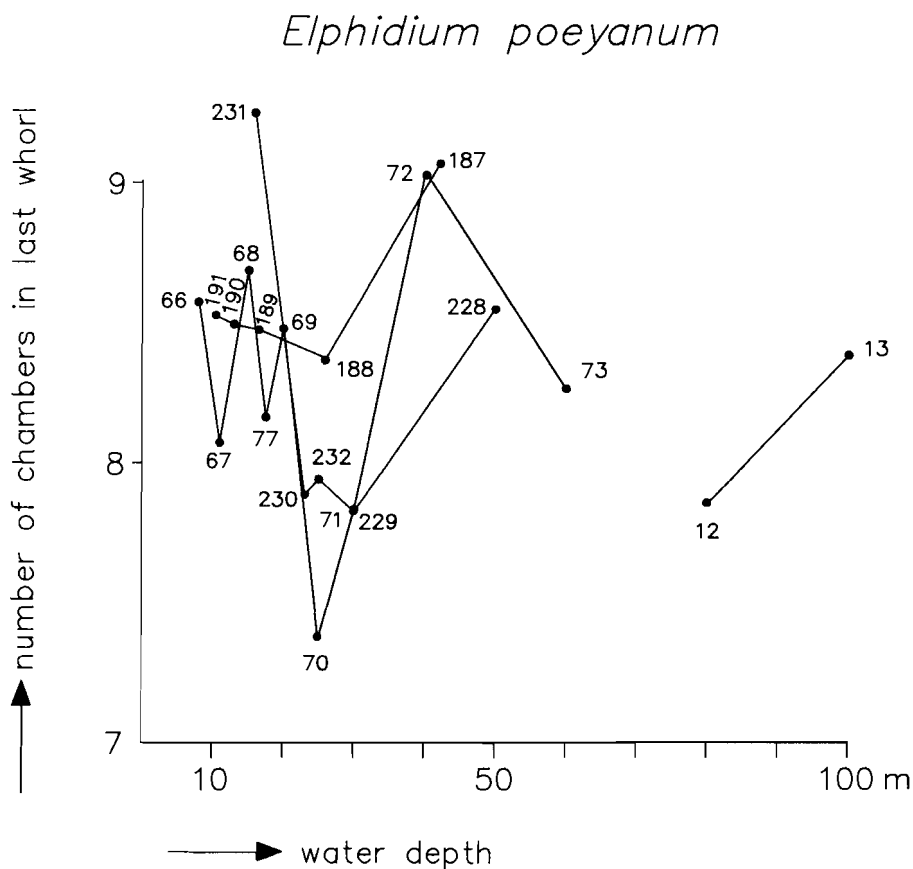


Fig. 32. Average values for the number of chambers in the last whorl of *E. poeyanum* versus the water depth of their sample locality.

For a number of samples, derived from four sample transects (fig. 12: transects III, V, VI and VIII) the number of chambers in the last whorl and the maximum diameter of the test have been established. Because all these samples yield homogeneous associations of *E. poeyanum*, the variation can be adequately described by the average values of these parameters, which are listed in table VII. In figures 31 and 32 the average values for each sample have been plotted against water depth, and in figure 33 they are plotted against each other.

	Sample	N	$\bar{k}$	$\bar{l}$	Depth
Transect III	191	30	8.52	292.3	10.5
	190	41	8.49	299.4	13
	189	16	8.47	314.3	16.5
	188	38	8.37	279.4	26
	187	34	9.06	289.9	42
Transect V	66	37	8.57	314.5	8
	67	27	8.07	272.5	11
	68	33	8.68	290.6	15
	77	49	8.16	299.9	17.5
	69	45	8.48	318.9	20
	70	41	7.37	272.3	25
	71	28	7.83	257.9	30
	72	16	9.03	272.3	40
Transect VI	12	26	7.85	259.1	80
	13	25	8.38	269.4	100
Transect VIII	231	15	9.23	335.0	16
	230	39	7.88	271.6	23
	232	40	7.94	266.2	25
	229	17	7.82	244.4	30
	228	21	8.55	262.5	50

Table VII. Average values for the number of chambers in the last whorl ( $\bar{k}$ ) and maximum diameter ( $\bar{l}$ , in microns) in *E. poeyanum*.

At first sight these figures give rather a chaotic picture. The maximum diameter (fig. 31) tends to decrease with increasing water depth until minimum values are reached at some 30 m. In still deeper water the values remain low. However, on a more detailed scale considerable deviations from this trend are visible. Also the number of chambers in the last whorl shows minimum values between 20 and 30 m water depth. A closer inspection of figure 33 reveals that samples from ecologically similar areas seem to fall in three zones which show a similar relation between the number of chambers and maximum diameter:

-- a first group, which contains samples from 17.5 - 25 m water depth (69-70, 77, 230) , with substantial amounts of forma *poeyanum* (see table VI), is characterized by a low number of chambers in comparison with the diameter.

-- a second group contains all the samples from shallow water (66-68, 189-191, 231), which are strongly dominated by forma *decipiens*. These associations are characterized by an intermediate number of chambers in comparison with the diameter of the test.

-- a third group, containing all samples from depths below 25 m (12-13, 71-73, 187, 228-229, 232), is dominated by 'intermediate' morphotypes with imperforate zones. These associations have a high number of chambers in comparison with the diameter.

### *Elphidium poeyanum*

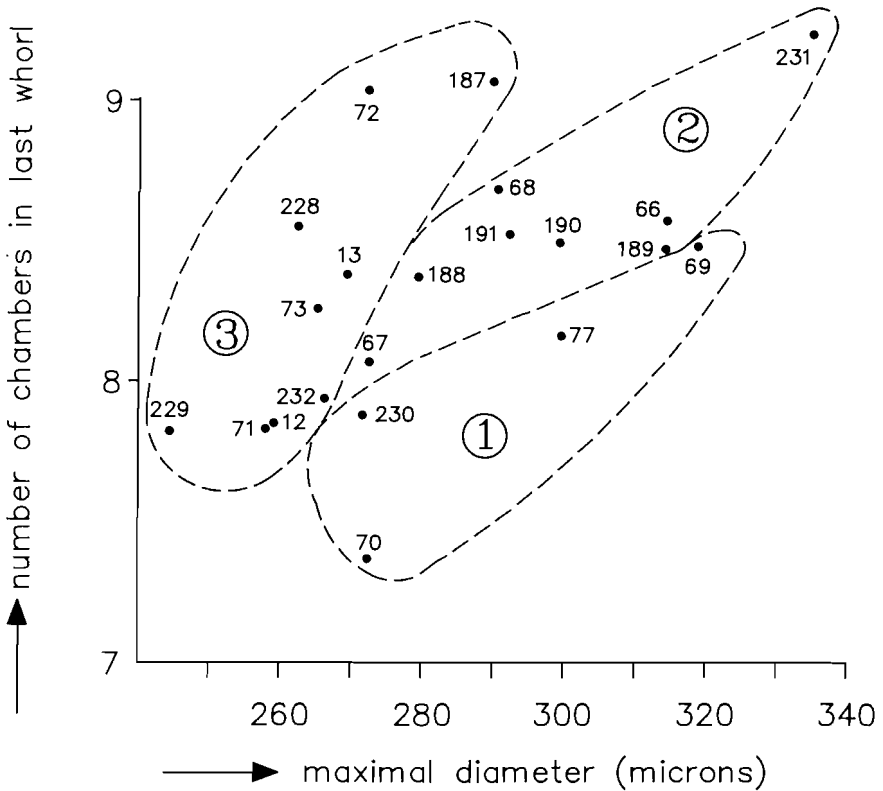


Fig. 33. *Elphidium poeyanum*, average number of chambers in the last whorl versus average maximum diameter, for samples of transects III, V, VI and VIII.

#### IV.4.3.3. Discussion

A tripartition in the populations can be recognized in *E. poeyanum* just as in *E. granosum*, although it is much more difficult to distinguish this on biometrical grounds. This tripartition is most distinct in the San Benedetto transect (V). In the samples from relatively shallow water (66-68) located outside the direct influence of Po runoff products, coming from localities with sandy substrata and a relatively low nutrient level, the assemblages are dominated by typical representatives of forma *decipiens*. One can conclude that this is the 'unstressed' morphotype of the species. In the next four samples (77, 69-71), located on the outer edge of the zone influenced by runoff, an important part of the populations consists of typical forma *poeyanum*. Within this zone, both the average diameter and the number of chambers in the final whorl decrease strongly. It was suggested before that this zone is characterized by high nutrient levels, but that there is no oxygen deficiency. It is likely that in this zone relatively high standing stocks of *E. poeyanum* are present, the low numbers of foraminifera per dry weight unit being caused by the strong dilution effect. In the relatively 'deep' samples (71-73, 12-13, 31) the test diameter remains about the same, but the number of chambers in comparison with the test diameter increases again. Furthermore, imperforate zones around the umbilical region are developed. Relative (and also absolute) abundances are low. It was concluded earlier that in the shallowest part of this zone (40 - 60 m), conditions of oxygen deficiency may be present periodically. *E. poeyanum* seems to have only little tolerance for such conditions.

A similar succession of morphotypes is found in the Termoli transect (VIII, 50 km southward). In the Pesaro transect (III), some 75 km south of the Po delta, a slightly different situation prevails. One finds no associations with large quantities of typical forma *poeyanum*, and there are no imperforate zones in the 'intermediate' morphotypes. It was suggested earlier (chapter IV.4.2.3) that closer to the Po delta, the environmental stability will be considerably lower, and therefore only stress-tolerant taxa will be present. For the same reason, it will be more difficult for the foraminifera to develop morphological adaptations (e.g. imperforate zones) to the variably stressed environment.

Although the morphological trends in *E. poeyanum* are less clear than in *E. granosum*, they can be explained in more or less the same way. Initially, in the zone with typical forma *poeyanum*, the number of chambers in the last whorl decreases as the food supply increases; this in our opinion is caused by a shortening of the reproduction cycle. The increased inflation of the test can be explained by a more rapid increase of the protoplasm volume per growth step, and the optimum use of the available amount of calcium carbonate. The relative increase in the number of chambers in deeper water can be explained

by a delaying of sexual maturity under stressed conditions. More difficult to understand is the development of imperforate zones in this stress zone. Although their function is not clear yet, a study of the literature shows that numerous taxa specialized to live in stressed environments (e.g. *Canceris*, *Nonionella*, *Valvulineria*) can develop similar imperforate wall portions.

#### IV.4.4. *Elphidium advenum* (Cushman, 1922)

Although *E. advenum* shows a high variability with respect to the lobateness of the periphery, the development of the keel and of an umbilical knob, no clear trends in these parameters were recognized. Therefore, separate morphotypes were not distinguished.

The distribution of *E. advenum* is depicted in figure 34. Maximum abundances are found in the northernmost part of the Adriatic Sea and in a narrow strip at about 25 m water depth along the Italian coast. This could be explained by a preference for ample food availability in combination with some tolerance for environmental stress. The peak frequencies just in front of the Po outlets (samples 157, 169 and 167) could point to a fair tolerance for the more local stress effects of the Po-effluents such as a lowered salinity or pollution by anorganic substances. The often clear indications for partial dissolution of the test (pl. 25) lend support to this idea. The presence of *E. advenum* in samples from the sand platform is in our opinion mainly the result of the reworking of older deposits.

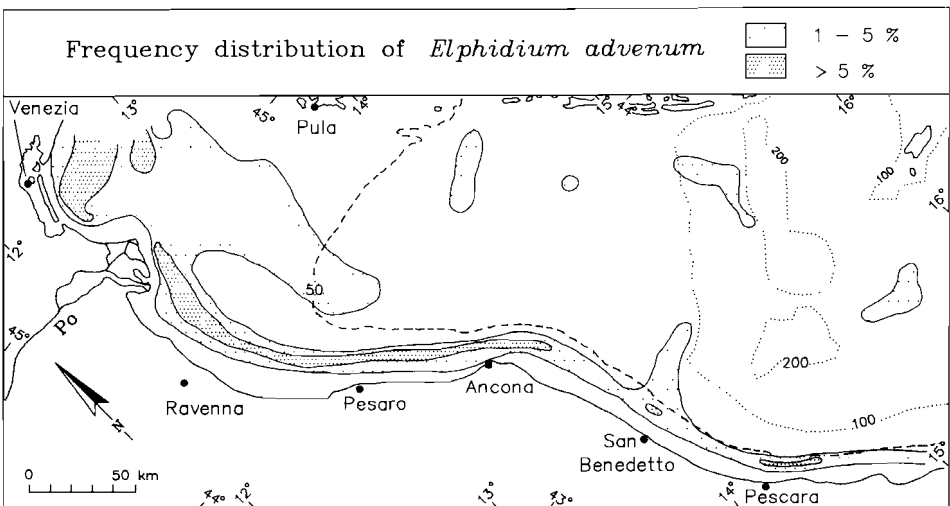


Fig. 34. Frequency distribution of *Elphidium advenum*.

#### IV.4.5. *Elphidium crispum* (Linnaeus, 1758)

The possible conspecificity of *E. crispum* and *E. macellum* is still a matter of dispute. Although it was often difficult, we counted the two forms separately. After studying the distribution in the Adriatic Sea, we have the impression that there is a continuous variation between the two types. This variation is mainly defined by ontogenetic changes in the umbilical properties and the number of chambers per whorl. The fact that no clear differences were found between the geographical distribution of the two (separately counted) taxa was an additional argument to consider both as morphotypes of *E. crispum*, and map their combined distribution (fig. 35). In this figure it can be seen that *E. crispum* occurs on all types of substrata. The highest frequencies in samples with slightly raised percentages of organic matter could indicate a certain preference for large food availability, but the scarcity in the zone most strongly influenced by Po runoff indicates that the species does not tolerate severely stressed conditions.

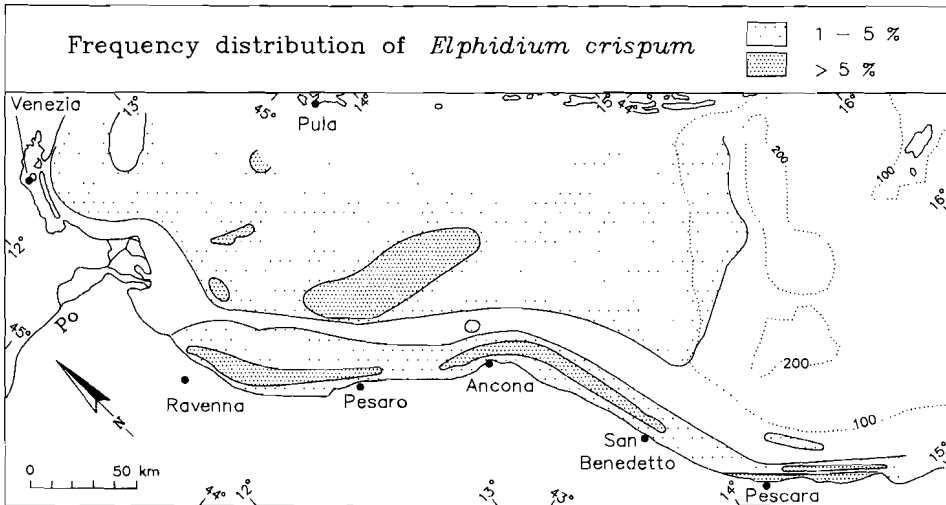


Fig. 35. Frequency distribution of *Elphidium crispum*.

#### IV.4.6. *Elphidium margaritaceum* Cushman, 1930

The distribution of *E. margaritaceum* has been depicted in figure 36. The species is only present in larger quantities in a narrow zone between Ravenna and Ancona, on the outer (upper) edge of the clay-belt, between 12.5 and 20 m water depth. Its preferences seem to be more or less the same as those of other constituents of faunal cluster 3 (fig. 11): raised food availability with no evidence of oxygen shortage.



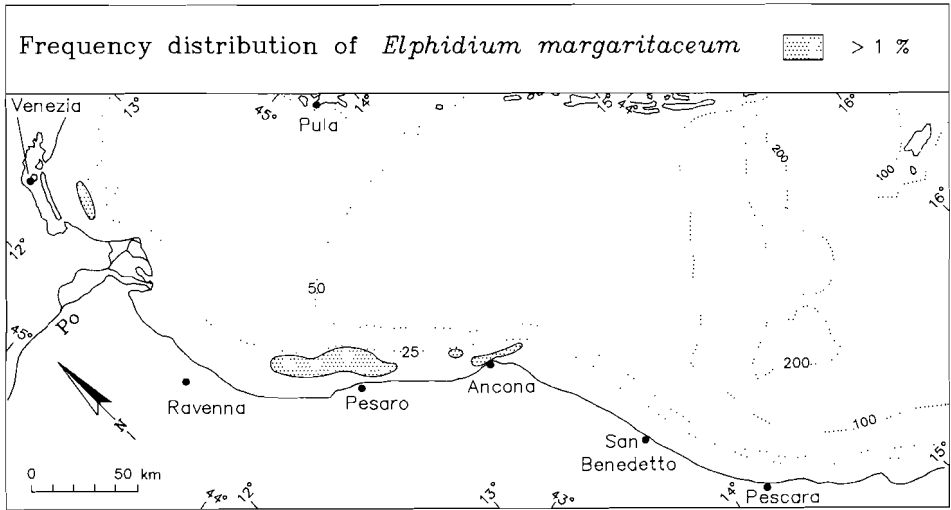


Fig. 36. Frequency distribution of *Elphidium margaritaceum*.

#### IV.4.7. TAXONOMY

### ***Elphidium granosum* (D'Orbigny, 1846)**

Plate 2, figs. 1-3, pl. 16 - 19

#### *Elphidium granosum* (D'Orbigny) forma *granosum* (D'Orbigny, 1846)

1826 *Nonionina granosa* -- D'Orbigny, Ann. Sci. Nat., 7, p. 294 (Nomen nudum).

1846 *Nonionina granosa* -- D'Orbigny, Foram. foss. Vienne, p. 110, pl. 5, figs. 19-20.

1951 *Nonion granosum* (D'Orbigny) -- Marks, Contr. Cushman Found. Foram. Res., 2, p. 48.

1972 *Protelphidium granosum* (D'Orbigny) -- Brodniewicz, PARTIM, Acta Paleont. Pol., 17, p. 484, fig. 27 (not 26), pl. 12, figs. 1-6, pl. 24, figs. 6-7 (not pl. 11, figs. 4-8, pl. 24, figs. 8, 11-12).

1979 *Elphidium granosum* (D'Orbigny) -- Hageman, PARTIM, Utrecht Micropal. Bull., 20, p. 95, pl. 6, figs. 3-4 (not figs. 5-7).

1986 *Elphidium granosum* (D'Orbigny) -- Rupp, PARTIM, Beitr. Paläont. Österr., 12, p. 60, pl. 16, figs. 3-4 (not figs. 1-2).

1986 *Elphidium excavatum* (Terquem) -- Wang and Lutze, PARTIM, J. Foram. Res., 16, p. 50, pl. 1, figs. 15-16, (not fig. 4/2, pl. 1, figs. 9-14).

1987 *Elphidium granosum* forma *granosum* (D'Orbigny) -- Jorissen, Marine Micropal., 12, p. 47, pl. 2, fig. 1.

#### *Diagnosis*

Compared with forma *lidoense*, the typical form is characterized by a relatively low (6.5 - 8) number of chambers in the last whorl, and the absence of glassy knobs in the umbilicus. Furthermore, the chambers are more inflated, resulting in a more lobate outline of the test. The sutures open clearly towards the umbilicus, giving rise to a wedge-like form; retral processes or sutural bridges are not developed. The test is flattened laterally. Most of the specimens are uncoloured.

## *Elphidium granosum* (D'Orbigny) forma *lidoense* Cushman, 1936

- 1936 *Elphidium lidoense* -- Cushman, Contr. Cushman Lab. Foram. Res., 12, p. 86, pl. 15, fig. 6.  
1955 *Elphidium lidoense* Cushman -- Kruit, Verh. Kon. Mijnbouwkw. Genootschap, Geol. Ser., 15, p. 471, pl. 2, fig. 8.  
1970 *Cribrononion excavatum* (Terquem) -- Von Daniels, Göttinger Arb. Geol. Paläont., 8, p. 87, pl. 7, fig. 11.  
1972 *Elphidium excavatum* (Terquem) forma *lidoensis* Cushman -- Feyling-Hansen, Micropaleontology, 18, p. 344, pl. 6, figs. 1-7.  
1972 *Protelphidium granosum* -- Brodniewicz, PARTIM, Acta Paleont. Pol., 17, p. 484, fig. 26 (not fig. 27), pl. 11, figs. 4-8, pl. 24, figs. 8, 11-12 (not pl. 12, figs. 1-6, pl. 24, figs. 6-7).  
1976 *Elphidium tuberculatum* (D'Orbigny) -- Hansen and Lykke-Andersen, Fossils and Strata, 10, p. 14, pl. 12, figs. 1-4.  
1979 *Elphidium granosum* (D'Orbigny) -- Hageman, PARTIM, Utrecht Micropal. Bull., 20, p. 95, pl. 6, figs. 5-6 (not figs. 3-4).  
1982 *Protelphidium granosum* (D'Orbigny) -- Agip S.p.A., pl. 21, fig. 2.  
1986 *Elphidium granosum* (D'Orbigny) -- Rupp, PARTIM, Beitr. Paläont. Österr., 12, p. 60, pl. 16, figs. 1-2 (not figs. 3-4).  
1986 *Elphidium excavatum* (Terquem) -- Wang and Lutze, PARTIM, J. Foram. Res., 16, p. 50, pl. 1, figs. 13-14 (not fig. 4/2, pl. 1, figs. 9-12, 15-16).  
1987 *Elphidium granosum* forma *lidoense* Cushman -- Jorissen, Marine Micropal., 12, p. 47, pl. 2, fig. 3.

### *Diagnosis*

Compared with the typical form, forma *lidoense* is characterized by a larger number of chambers in the last whorl (8-12) and the presence of a number of umbilical knobs. The chambers are less inflated, resulting in a less lobate outline of the test. The sutures do not open strongly towards the umbilicus; retral processes or sutural bridges are not present. The test has a biconvex shape. The specimens are usually coloured brown.

### *Remarks*

The use of the name *lidoense* at an intra-specific level in the Mediterranean species *E. granosum* (Hageman, 1979; Rupp, 1986; Jorissen, 1987 and present paper), as well as in the Atlantic species *E. excavatum* (Feyling-Hansen, 1972; Miller et al., 1982) and *E. clavatum* (Wilkinson, 1979) suggests a certain synonymy between these geographically separated forms. The discussion about whether *excavatum* or *clavatum* should be used as a species name is in our opinion an academic question. There are however some reasons which make us doubt that our forms and the Atlantic material are conspecific:

– in the Adriatic Sea material, retral processes or sutural bridges were never observed in *E. granosum*, either in the typical form, or in forma *lidoense*. In the Atlantic material, even in the most extreme morphotypes, some sutural bridges can always be recognized.

-- the range of variation as found in the Adriatic Sea does not show any morphological overlap with that described from the western North Atlantic. A comparison with material from the Canadian continental shelf convinced us that the North Atlantic morphotypes do not fit into our associations. In the morphotypes from the North Sea figured by Lévy et al. (1969, *Cribronionion lidoense*, pl. 1, fig. 9) it is not clear whether sutural bridges are present, but in a specimen from the Seine Bay (France, Atlantic coast) figured by Rosset-Moulinier (1972, *Cribroelphidium excavatum, lidoense*-type, pl. 17, figs. 1-4), tiny sutural bridges are clearly visible. Somewhat enigmatic however are the Baltic Sea faunas figured by Brodniewicz (1972); both in her forma A1 (and B, both similar to our forma *lidoense*) and A2 sutural bridges seem to be completely absent, but her forma A2 differs from our forma *granosum* by the presence of well-developed umbilical flaps.

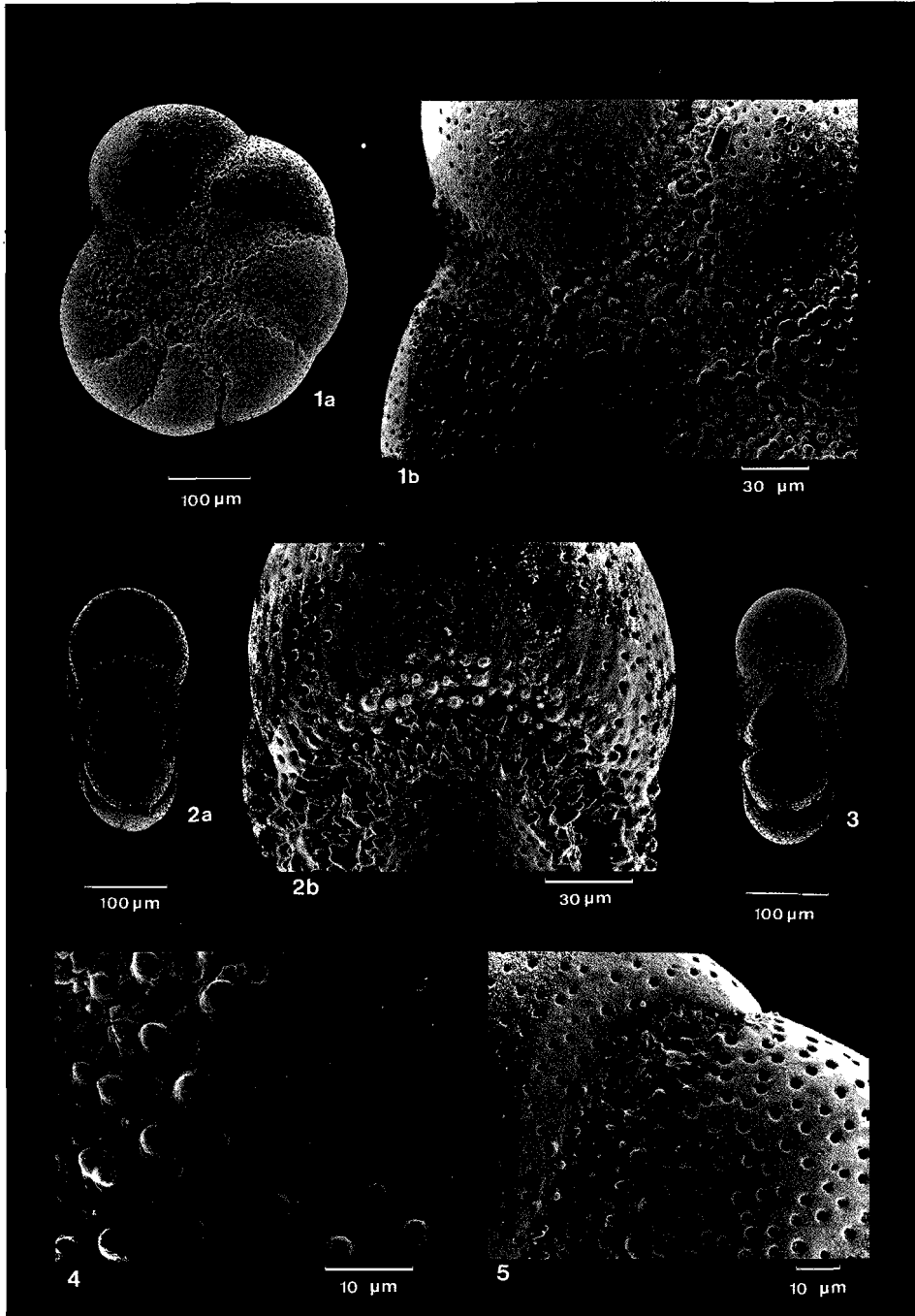
Although it seems impossible to solve this problem without comparing a large number of faunas, we think that for the moment it is advisable to consider the Mediterranean assemblages as belonging to a separate species. Unfortunately this has some far-reaching taxonomic consequences,

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## Plate 16

### *Elphidium granosum* forma *granosum*

- Fig. 1a: typical specimen, sample 70 (25 m), side view, enlargement 125 x.  
Fig. 1b: same specimen, detail of umbilical area, enlargement 250 x.  
Fig. 2a: typical specimen, sample 70 (25 m), apertural view of specimen pictured on pl. 18, fig. 10, enlargement 125 x.  
Fig. 2b: same specimen, detail of apertural area, enlargement 400 x.  
Fig. 3: 'intermediate' (deep water) morphotype, sample 73 (60 m), apertural view of specimen pictured in pl. 19, fig. 12, enlargement 125 x.  
Fig. 4: sample 77 (17.5 m), pores of specimen not figured, enlargement 1200 x.  
Fig. 5: sample 71 (30 m), specimen pictured on pl. 19, fig. 4, detail of pores and chamber suture, enlargement 600 x.



A study of topotypes of the Miocene species *E. granosum* (sampled and described by Prof. Marks, 1951) revealed that these forms are very close to the recent material, and that in the Miocene basically the same intraspecific variation existed as in the Recent. The material from the Miocene of the Vienna Basin depicted by Rupp (1986) confirms this picture. From the paper of Fornasini (1900) onwards, the species name *granosum* has been used correctly by Italian authors. In *E. lidoense*, described from the beach sands from Rimini, we have an excellent name for the part of the variation with umbilical knobs.

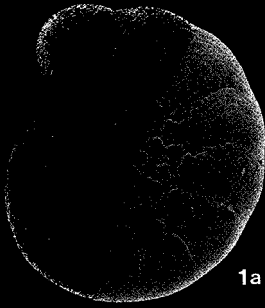
The taxonomic consequences are as follows: if our forma *lidoense* does indeed belong to a different species than do the *lidoense* morphotypes described from temperate regions, then the name should be restricted to Mediterranean material. If, however, the two morphotypes are conspecific, then the older name *E. granosum* has priority over *E. excavatum* also for the non-Mediterranean morphotypes.

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## Plate 17

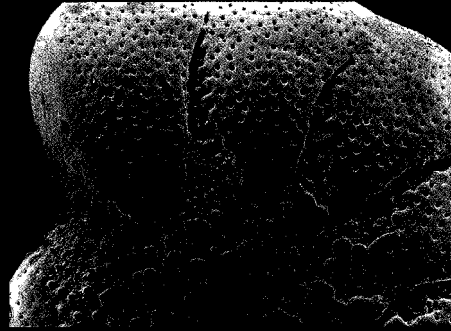
### *Elphidium granosum* forma *lidoense*

- Fig. 1a: typical specimen, sample 68 (15 m), enlargement 125 x. Fig. 1b: same specimen, detail of umbilical area, enlargement 250 x. Fig. 1c: same specimen, detail of pores, enlargement 1200 x.
- Fig. 2: sample 67 (11 m), apertural view of specimen pictured in pl. 18, fig. 3, enlargement 125 x.
- Fig. 3: sample 77 (17.5 m), specimen pictured on pl. 18, fig. 7, transitional type between forma *granosum* and forma *lidoense*, detail of aperture, enlargement 400 x.
- Fig. 4: sample 12 (80 m), apertural view of 'intermediate' (deep water) morphotype, specimen pictured on pl. 19, fig. 13, enlargement 125 x.
- Fig. 5: sample 73 (60 m), specimen pictured on pl. 19, fig. 8, detail of umbilical area showing openings of the umbilical canal system, enlargement 350 x.



1a

100  $\mu$ m



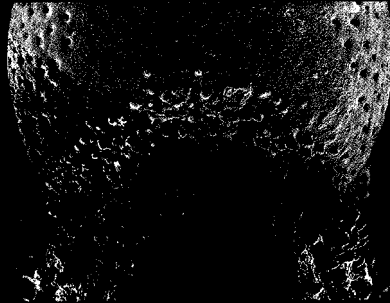
1b

30  $\mu$ m



2

100  $\mu$ m



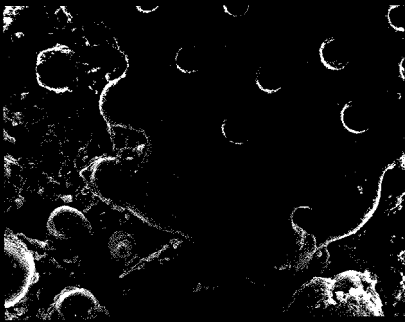
3

30  $\mu$ m



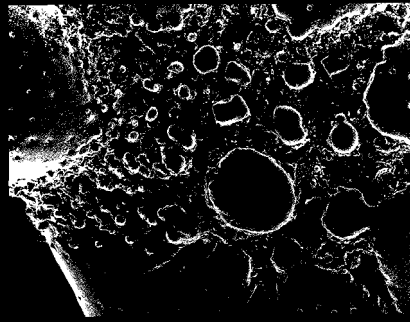
4

100  $\mu$ m



1c

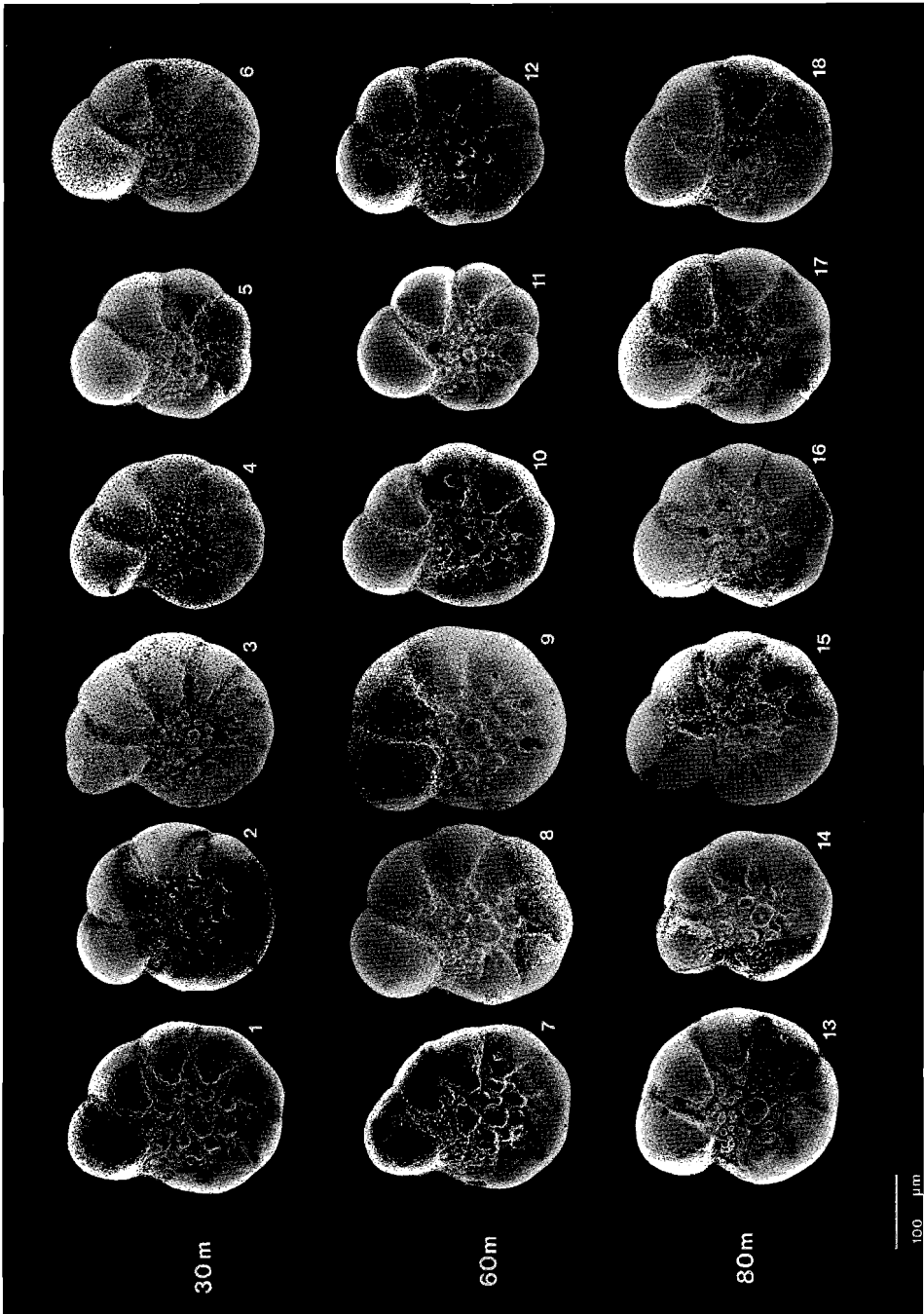
10  $\mu$ m



5

30  $\mu$ m







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Previous two pages:

**Plates 18 - 19**

*Elphidium granosum*

Morphological variation along transect V; for each sample, the specimens are grouped in the same way: the *lidoense*-side of the variation on the left, and the *granosum*-side on the right.

**Plate 18**

First row (figs. 1-6): sample 67, 11 m water depth; strong dominance of forma *lidoense*.

Second row (figs. 7-12): sample 77, 17.5 m water depth; strong dominance of forma *granosum*.

Third row (figs. 13-18): sample 70, 25 m water depth; strong dominance of forma *granosum*, fig. 13 (typical forma *lidoense*) seems to fall outside the variation.

All magnifications 100 x.

**Plate 19**

First row (figs. 1-6): sample 71, 30 m water depth; strong dominance of forma *granosum*, increase of umbilical ornamentation.

Second row (figs. 7-12): sample 73, 60 m water depth; 'intermediate' morphotypes with a low number of chambers, umbilical knobs and depressed sutural ends.

Third row (figs. 13-18): sample 12, 80 m water depth; 'intermediate' morphotypes.

All magnifications 100 x.

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Next two pages:

**Plates 20 - 21**

*Elphidium poeyanum*

Morphological variation along transect V. For each sample the specimens are grouped in the same way: the *decipiens*-side of the variation on the left, and the *poeyanum*-side on the right.

**Plate 20**

First row (figs. 1-6): sample 67, water depth 11 m; strong dominance of forma *decipiens*.

Second row (figs. 7-12): sample 77, water depth 17.5 m; the complete variation has shifted toward forma *poeyanum*.

Third row (figs. 13-18): sample 70, water depth 25 m; dominance of forma *poeyanum*.

All enlargements 100 x.

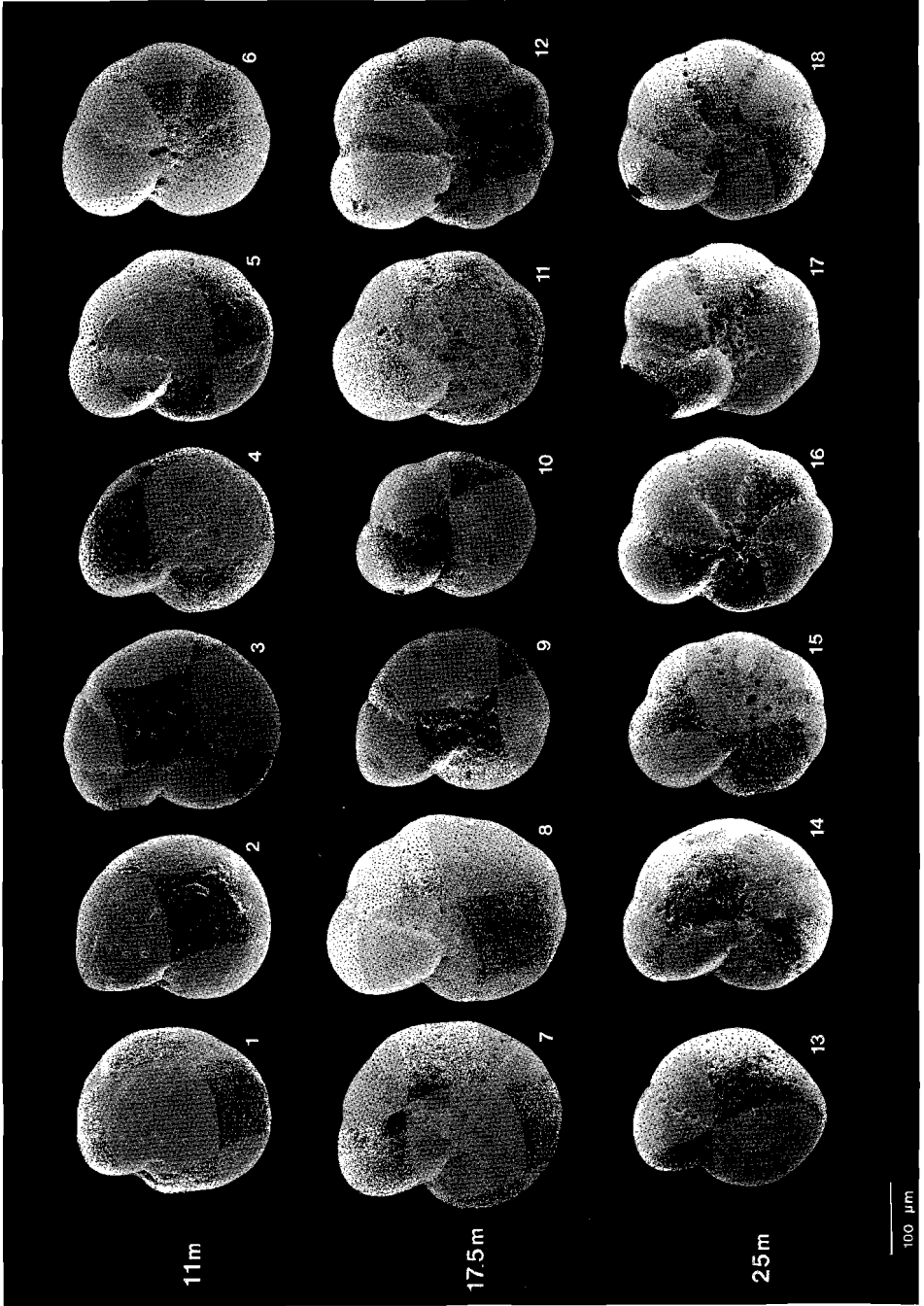
**Plate 21**

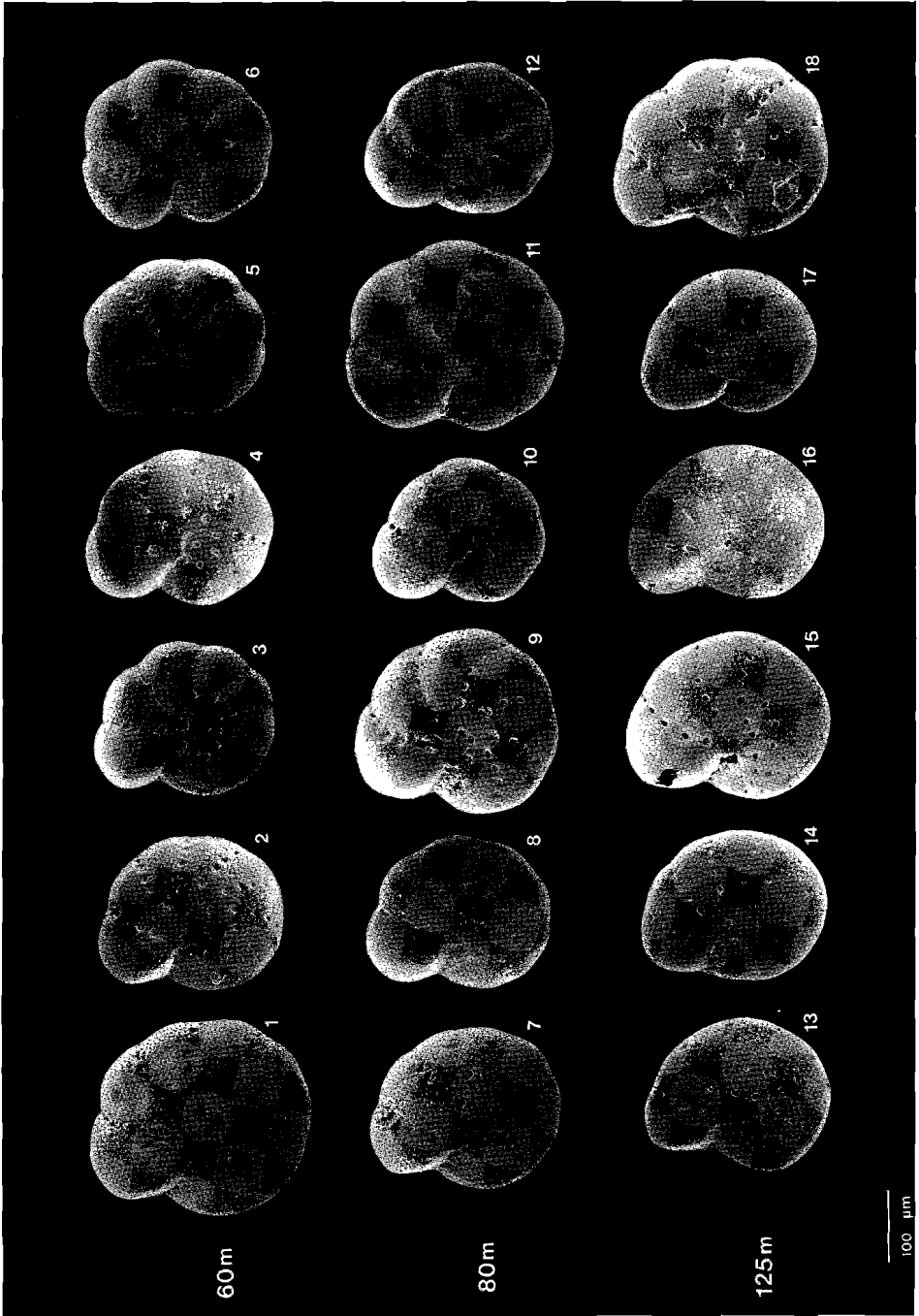
First row (figs. 1-6): sample 73, water depth 60 m; intermediate association, appearance of imperforate zones around the umbilicus and sutures.

Second row (figs. 7-12): sample 12, water depth 80 m; intermediate association, further development of imperforate zone (especially in *poeyanum*-types).

Third row (figs. 13-18): sample 31, water depth 125 m; intermediate association with large imperforate zones in all specimens.

All enlargements 100 x.





## **Elphidium poeyanum** (D'Orbigny, 1839)

Pl. 2, figs. 4,6; plates 20 - 23

### *Elphidium poeyanum* forma *poeyanum* (D'Orbigny, 1839)

- 1839 *Polystomella poeyana* -- D'Orbigny, Cuba, p. 55, pl. 6, figs. 25-26.  
1939 *Elphidium semistriatum* -- Cushman (not D'Orbigny), U.S.Geol.Surv. Prof. Pap., 191, p. 48, pl. 12, fig. 21.  
1939 *Elphidium poeyanum* (D'Orbigny) -- Cushman, U.S.Geol.Surv. Prof. Pap., 191, p. 54, pl. 14, figs. 25-26.  
1948 *Criboelphidium kugleri* -- Cushman and Bronnimann, Contr. Cushman Found. Foram. Res., 24, p. 18, pl. 4, fig. 4.  
1972 *Elphidium poeyanum* (D'Orbigny) -- Brodniewicz, Acta Palaeont. Polon., 17, p. 479, pl. 8, figs. 1-7, text-fig. 23.  
1974 *Criboelphidium poeyanum* (D'Orbigny) -- Seiglie, Caribb. Journ. Sci., 14, p. 29, pl. 1, figs. 10-12, pl. 5, figs. 74-75.  
1975 *Criboelphidium poeyanum* (D'Orbigny) -- Seiglie, Rev. Espan. Micropal., 7, p. 476, pl. 2, figs. 17-20.  
1976 *Elphidium kugleri* (Cushman and Bronnimann) -- Hansen and Lykke-Andersen, Fossils and Strata, 10, p. 12, pl. 9, figs. 4-8.  
1976 *Elphidium poeyanum* (D'Orbigny) -- Hansen and Lykke-Andersen, Fossils and Strata, 10, p. 13, pl. 9, figs. 9-12, pl. 10, figs. 1-5.  
1979 *Elphidium semistriatum* -- Hageman (not D'Orbigny), Utrecht Micropal. Bull., 20, p. 97, pl. 7, fig. 2.  
1985 *Elphidium poeyanum* (D'Orbigny) -- Kohl, Bull. Amer. Paleont., 88, no. 322, p. 84, pl. 28, fig. 7.  
1987 *Elphidium poeyanum* forma *poeyanum* (D'Orbigny) -- Jorissen, Marine Micropal., 12, p.47, pl. 2, fig. 4.

### *Diagnosis*

The typical form has a relatively low number of inflated chambers (6 - 8) in the last whorl, a lobate outline and depressed sutures. The umbilicus is not filled, but the chambers can form flap-like projections into it. The test is generally uncoloured and transparent.

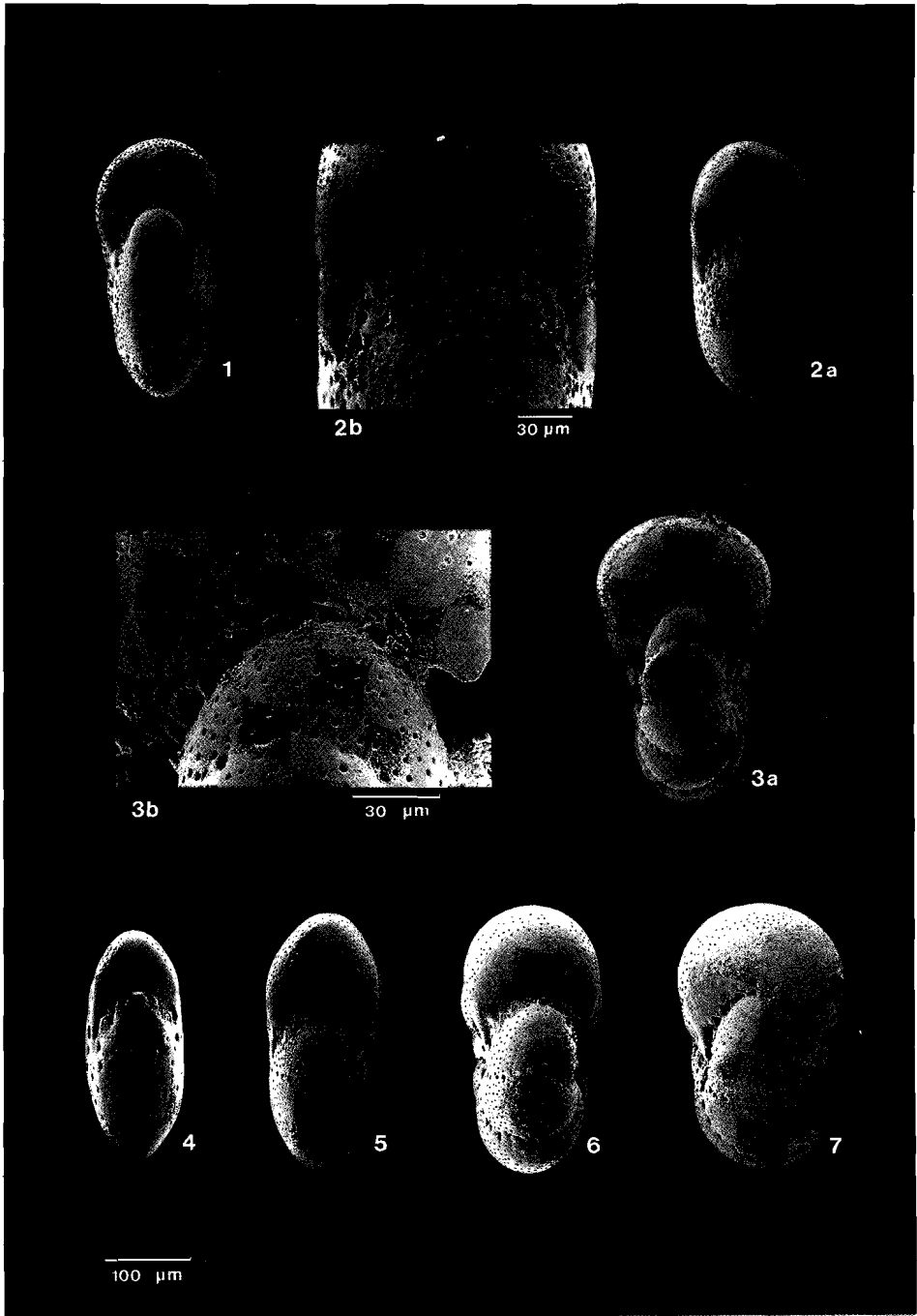
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## Plate 22

### *Elphidium poeyanum*, apertural views

- Fig. 1: forma *decipiens*, sample 67 (11 m), specimen pictured on pl. 20, fig. 6.  
Fig. 2a: forma *decipiens*, sample 67 (11 m), not figured specimen.  
Fig. 2b: same specimen, detail showing sealed openings of canal system.  
Fig. 3a: forma *poeyanum*, sample 77 (17.5 m), specimen figured on pl. 20, fig. 12.  
Fig. 3b: same specimen, detail of apertural face of penultimate chamber (last chamber broken off) showing central and lateral openings of canal system.  
Fig. 4: forma *decipiens*, sample 31 (125 m), specimen pictured on pl. 21, fig. 17.  
Fig. 5: forma *decipiens*, sample 77 (17.5 m), specimen not figured.  
Fig. 6: forma *poeyanum*, sample 70 (25 m), specimen pictured on pl. 20, fig. 16.  
Fig. 7: forma *poeyanum*, sample 77 (17.5 m), specimen figured on pl. 20, fig. 11, last chamber broken off.

Enlargements 125 x, except for figures 2b (250 x) and 3b (400 x).



## *Elphidium poeyanum* forma *decipiens* (Costa, 1856)

- 1856 *Polystomella decipiens* -- Costa, Atti Accad. Pont. Napoli, 7, p. 220, pl. 19, fig. 13.  
1856 *Nonionella rudis* -- Costa, Atti Accad. Pont. Napoli, 7, p. 205, pl. 20, fig. 2.  
1898 *Polystomella decipiens* Costa -- Fornasini, Rend. Real. Accad. Sc. Ist. Bologna, 2, p. 17, pl. 2, figs. 11-12.  
1900 *Polystomella decipiens* Costa -- Fornasini, Mem. Accad. Sc. Bologna, ser. 5a, 8, p. 400, fig. 50.  
1938 *Elphidium translucens* -- Natland, Bull. Scripps Inst. Oceanogr., Tech. Ser., 4, p. 144, pl. 5, figs. 3-4.  
1958 *Elphidium* cf. *E. minimum* (Seguenza) -- Parker, Rep. Swedish Deep Sea Exped., 8, p. 271, pl. 4, figs. 8-9.  
1966 *Elphidium cuvillieri* -- Lévy, Vie et Milieu, 17, p. 5, pl. 1, fig. 6.  
1969 *Cribrononion cuvillieri* (Lévy) -- Lévy et al., Revue Micropal., 12, p. 93, pl. 1, figs. 10-11.  
1970 *Cribrononion translucens* (Natland) -- Von Daniels, Göttinger Arb. Geol. Paläont., 8, p. 88, pl. 7, fig. 13.  
1972 *Cribroelphidium cuvillieri* (Lévy) -- Rosset-Moulinier, Trav. Lab. Geol., Ecole Norm. Sup., Paris, 6, p. 177, pl. 15, figs. 1-4.  
1976 *Elphidium translucens* Natland -- Hansen and Lykke-Andersen, Fossils and Strata, 10, p. 11, pl. 7, figs. 1-11.  
1977 *Elphidium translucens* Natland -- Haake, J. Foram. Res., 7, p. 66, pl. 2, fig. 3.  
1979 *Elphidium semistriatum* (D'Orbigny) var. *minimum* (Seguenza) -- Hageman, Utrecht Micropal. Bull., 20, p. 98, pl. 7, fig. 3.  
1982 *Cribroelphidium decipiens* (Costa) -- Agip S.p.A., pl. 22, fig. 2.  
1984 *Elphidium cuvillieri* Lévy -- Vénec-Peyré, ECOMED, part V, pl. 8, fig. 2.  
1987 *Elphidium poeyanum* forma *decipiens* (Costa) -- Jorissen, Marine Micropal., 12, p. 47, pl. 2, fig. 6.

### Diagnosis

Forma *decipiens* can be characterized by a relatively high number (8 - 11) of non-inflated chambers, a rounded outline and sutures that are flush with the surface. The test is flattened laterally (pl. 22). The umbilicus is completely filled with glassy material. The test is generally (cream-) coloured and less transparent than in the typical form.

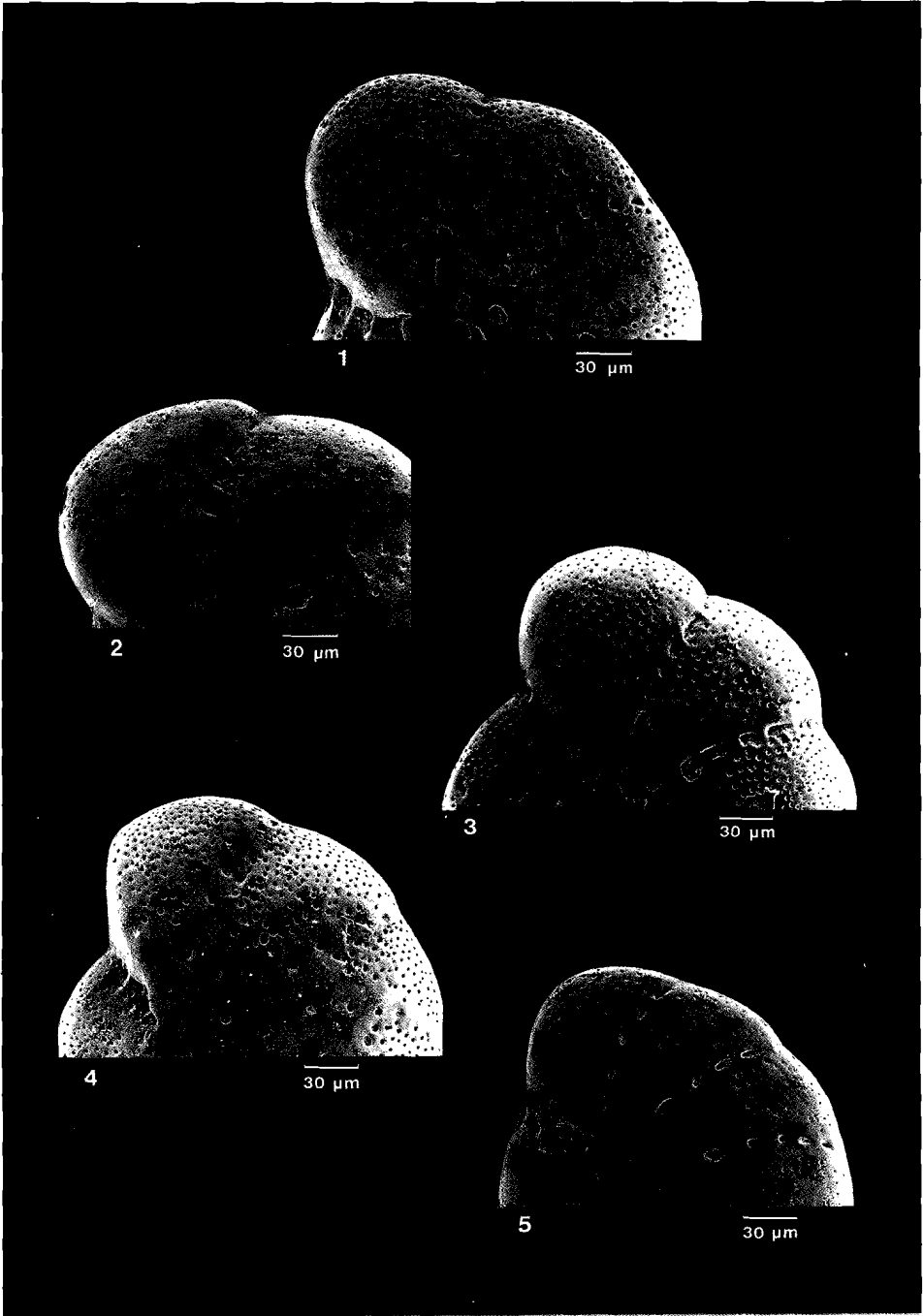
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## Plate 23

### *Elphidium poeyanum*, details of perforation

- Fig. 1: forma *decipiens*, sample 67 (11 m), specimen not figured, no imperforate zones developed.  
Fig. 2: intermediate morphotype, sample 73 (60 m), specimen pictured on pl. 21, fig. 3, small imperforate zones around umbilicus and along chamber sutures.  
Fig. 3: forma *poeyanum*, sample 73 (60 m), specimen pictured on pl. 21, fig. 6, large part of the chambers imperforate.  
Fig. 4: forma *decipiens*, sample 12 (80 m), specimen pictured on pl. 21, fig. 7, small imperforate zones around umbilicus and along chamber sutures.  
Fig. 5: forma *decipiens*, sample 31 (125 m), specimen pictured on pl. 21, fig. 14, large part of the chamber walls imperforate.

All enlargements 250 x.





### Remarks

Already in 1898 (and again in 1900) Fornasini noted the similarity between *P. poeyanum* and *P. decipiens*. Later, Brodniewicz (1972) also pointed to a continuous variation between the two species, and suggested that *E. cuvillieri* could be a synonym of *E. poeyanum*.

Although the species *Polystomella decipiens* was very inadequately figured by Costa, some specimens from his collections were excellently re-figured by Fornasini (1898). On the basis of the latter figures, the species has been used since by Italian investigators for the compact types of *E. poeyanum*. We have no doubt that the figures of Fornasini depict the same taxon as the species *E. translucens* and *E. cuvillieri*, which were described much later.

### **Elphidium advenum** (Cushman, 1922)

Pl. 2, figs. 9-10; pl. 24, fig. 3

1922 *Polystomella advena* – Cushman, Carnegie Inst. Publ., 311, p. 56, pl. 9, figs. 11-12.

1939 *Elphidium advenum* (Cushman) – Cushman, U.S. Geol. Surv., Prof. Pap., 191, p. 60, pl. 16, figs. 31-35.

1987 *Elphidium advenum* (Cushman) – Jorissen, Marine Micropal., 12, p. 47, pl. 2, figs. 9-10.

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## Plate 24

### *Elphidium crispum*

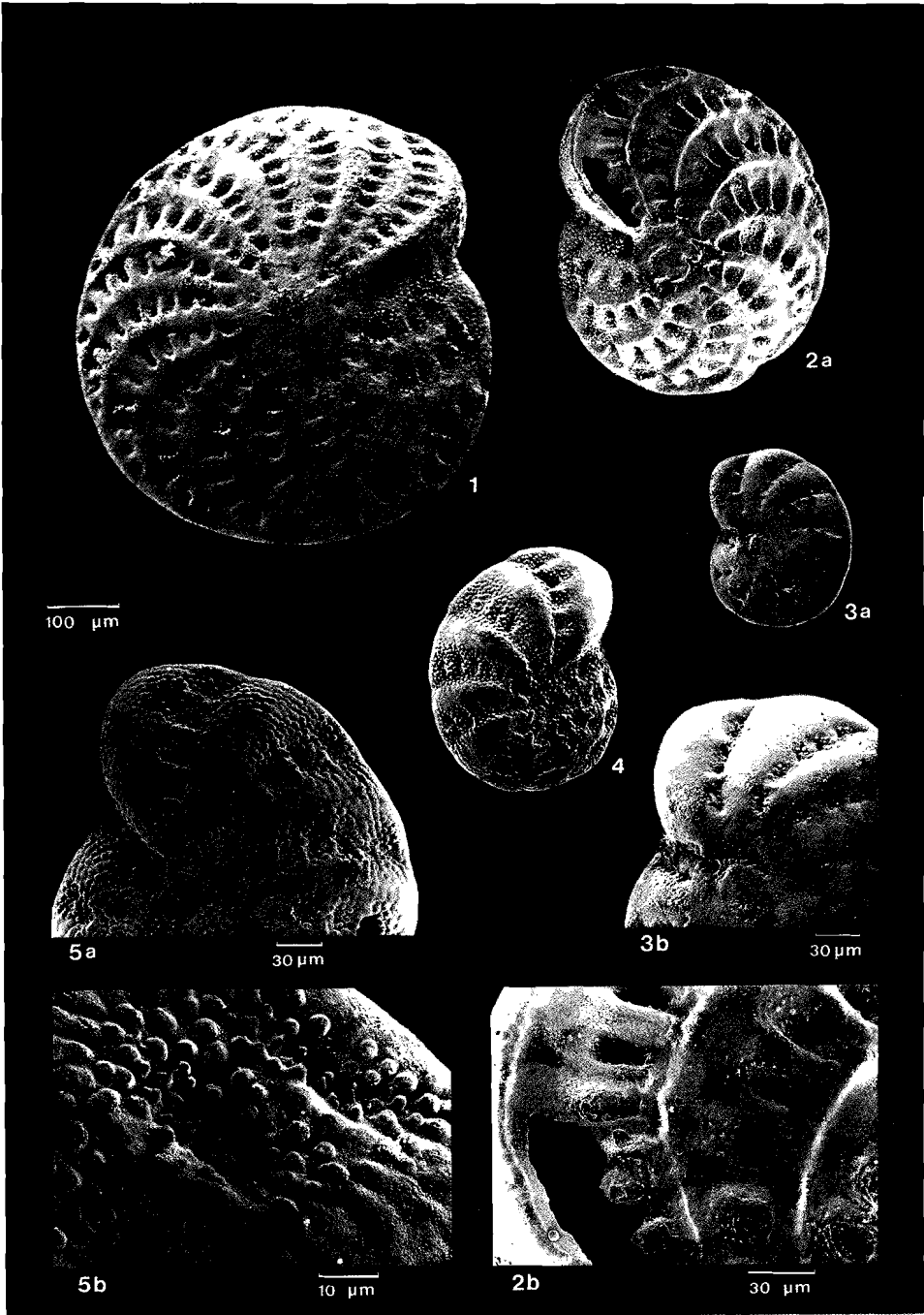
- Fig. 1: forma *crispum*, sample 93 (12 m), enlargement 100 x.  
Fig. 2a: forma *macellum*, sample 182 (16.5 m), enlargement 100 x.  
Fig. 2b: same specimen, detail of wall structure, enlargement 300 x.

### *Elphidium advenum*

- Fig. 3a: typical specimen, sample 182 (16.5 m), enlargement 100 x.  
Fig. 3b: same specimen, detail of last chambers, enlargement 200 x.

### *Elphidium margaritaceum*

- Fig. 4: sample 182 (16.5 m), enlargement 100 x.  
Fig. 5a: sample 182 (16.5 m), enlargement 200 x.  
Fig. 5b: same specimen, detail of wall structure, enlargement 800 x.



## **Elphidium crispum** (Linnaeus, 1758)

Pl. 3, figs. 8-9: pl. 24, figs. 1-2

- 1758 *Nautilus crispus* – Linnaeus, Syst. Nat., Ed. 10, p. 709, pl. 19, fig. 1-d.  
1798 *Nautilus macellus* var. alpha, beta. – Fichtel and Moll, Test. Micr., p. 66, pl. 10, figs. e-k.  
1939 *Elphidium crispum* (Linné) – Cushman, U.S. Geol. Surv., Prof. Pap., 191, p. 50, pl. 13, figs. 17-21.  
1939 *Elphidium macellum* (Fichtel and Moll) – Cushman, U.S. Geol. Surv., Prof. Pap., 191, p. 51, pl. 14, figs. 1-3, pl. 15, figs. 9-10.  
1953 *Elphidium crispum* (Linné) – Phleger, Parker and Peirson, Rep. Swed. Deep Sea Exped., 7, no. 1, p. 31, pl. 6, fig. 17.  
1987 *Elphidium crispum* (Linnaeus) – Jorissen, Marine Micropal., 12, p. 47, pl. 3, figs. 8-9.

### *Remark*

Although the two morphotypes were lumped together for our quantitative analyses, we did distinguish forma *crispum* and forma *macellum* in our associations.

## **Elphidium margaritaceum** Cushman, 1930

Pl. 24, figs. 4-5

- 1930 *Elphidium advenum* (Cushman) var. *margaritaceum* – Cushman, Bull. U.S. Nat. Mus., 104, pt. 7, p. 25, pl. 10, fig. 3.  
1976 *Elphidium margaritaceum* Cushman – Hansen and Lykke-Andersen, Fossils and Strata, 10, p. 8, pl. 3, figs. 2-6.

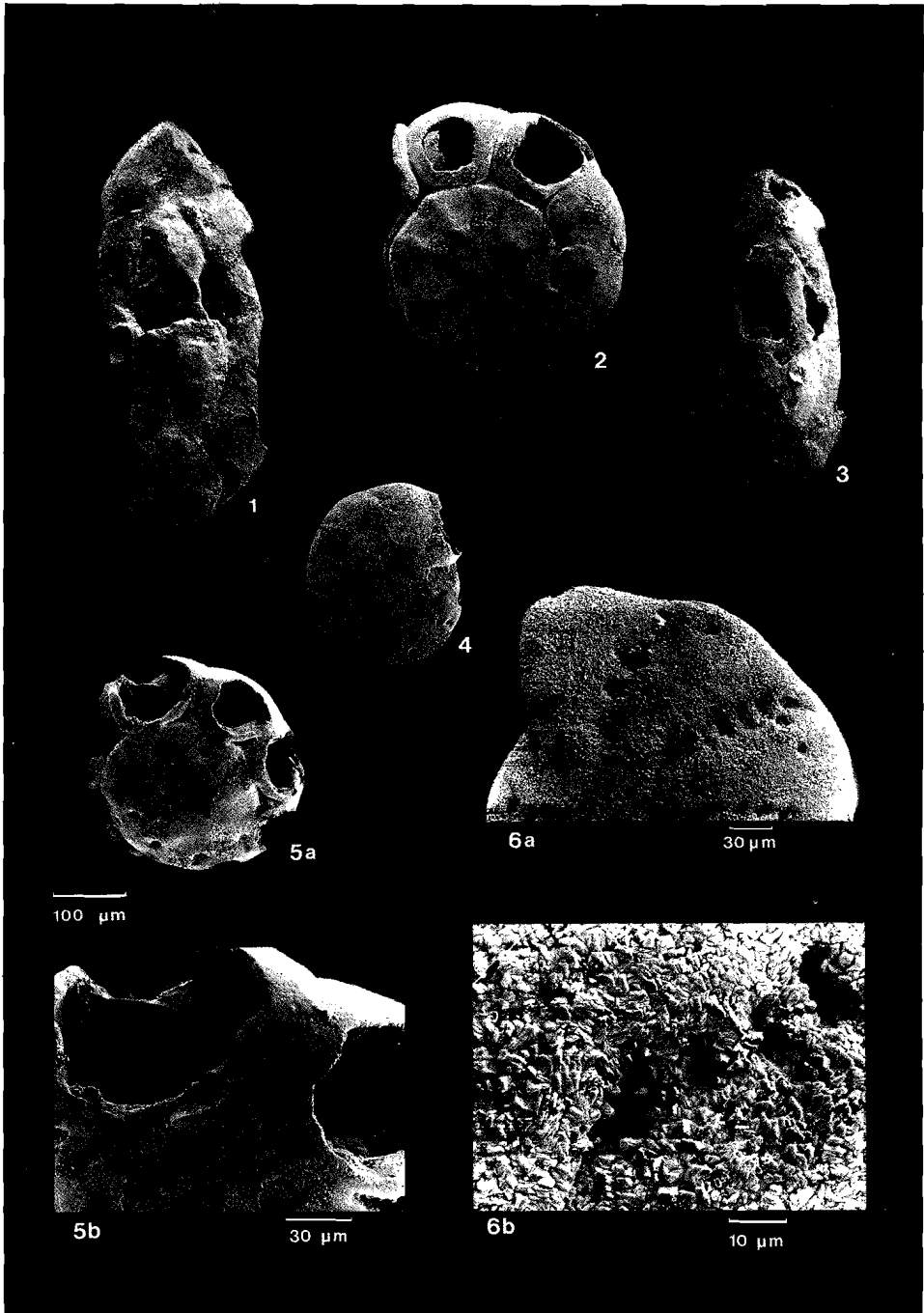
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## **Plate 25**

### **Dissolution phenomena**

- Fig. 1: *Quinqueloculina seminula*, sample 57 (20 m).  
Fig. 2: *Ammonia beccarii*, sample 157 (20 m).  
Fig. 3: *Quinqueloculina seminula*, sample 157 (20 m).  
Fig. 4: *Elphidium advenum*, sample 157 (20 m).  
Fig. 5a: *Pseudoepionides falsobeccarii*, sample 157 (20 m).  
Fig. 5b: same specimen, detail.  
Fig. 6a: *Elphidium advenum*, sample 157 (20 m).  
Fig. 6b: same specimen, detail of surface covered with gypsum crystals.

Enlargements 100 x, except figures 5b (300 x), 6a (200 x) and 6b (800 x).



## Chapter V

### LIFE STRATEGIES IN BENTHIC FORAMINIFERA

#### V.1. LIMITING FACTORS

In the previous chapters we discussed the benthic foraminiferal faunas from the clay-belt parallel to the Italian Adriatic coast (fig. 8: biofacial units II and IV). Ecologically, this zone is characterized not only by its clayey substratum, but also by its overall large food availability. This food availability arises from the input of considerable quantities of (particulate and dissolved) organic substances, in part directly from the fluvial discharge, but also as a result of relatively high primary production in the water column. At the bottom large standing stocks of algae, diatoms and bacteria provide a wide variety of nutritional elements for the benthic foraminifera. Our faunas demonstrate fairly conclusively that oxidation of these large quantities of organic matter at the bottom periodically leads to lowered oxygen concentrations.

In our opinion the amount of available food and oxygen are the two most important limiting factors for the benthic foraminifera in our biofacial units II and IV, and these factors are probably largely responsible for the differences observed between our faunas there. The nature of the substratum is also of importance, but this parameter shows only minor variations within the clay-belt. Only on the outer (lower) edge of our biofacial unit IV, where the thickness of the Holocene clay-cover strongly diminishes, are the underlying (Pleistocene) sands mixed with the clays. This probably results in a thickening of the oxygen-containing sediment top-layer. Other factors of importance are salinity, chemical (anorganic) pollution (both only in the direct vicinity of fluvial outlets) and light penetration. In our biofacial unit IV the light intensity at the bottom is probably strongly reduced as a result of the large amounts of organic detritus suspended in the overlying water column. Therefore it is highly unlikely that the benthic foraminifera living in this zone have a symbiotic feeding-strategy.

It should be noted that the influence of all the aforementioned ecological factors is largely determined by the combination of fluvial discharge mainly from the Po (but also from other Italian rivers) and the surface current system. Although some of the parameters show a trend perpendicular to the coast, water depth itself apparently is not a primary limiting factor in our area of investigation.

## V.2. MICROHABITAT SEPARATION

### V.2.1. Introduction

In this chapter we shall discuss our faunas in terms of microhabitat, life position and feeding strategies. In order to prevent confusion we begin by giving our definition of these expressions:

-- by **microhabitat** we mean a certain micro-environment; a specific location in or on the sediment,

-- by **life position** we mean the position of the organism with respect to the substratum; numerous terms can be used to describe the life position, e.g.: in-benthic, epibenthic, attached, epiphytic,

-- by **feeding strategy** we mean the way in which the animal gathers food, e.g.: suspension-feeding, deposit-feeding, scavenging.

Together these three terms more or less describe the feeding niche of the animal.

In the literature it has been stated that the benthic faunas in clay-rich environments are usually strongly dominated by deposit-feeding organisms (Sanders, 1958, 1960; Scott, 1978). In these environments, suspension feeders are scarce; this is not only because such a feeding strategy is unnecessary in view of the large food availability at and below the sediment-water interface (Walker and Bambach, 1974), but possibly also because their settling and the maintenance of their vertical life position are hampered by the instability of the sediment top-layer (Rhoads and Young, 1970). Although not immediately relevant to our faunas it is worth mentioning the study of Jones and Charnock (1985), who concluded that agglutinated benthic foraminiferal faunas in the shelf environment can be characterized by the presence of three different morphogroups, which have different feeding strategies and life positions. In order of abundance these are:

- 1) infaunal detritic/bacterial scavengers, often with an elongated test,
- 2) epifaunal (active) herbivores, detritivores and omnivores, mostly with a planispiral or trochospiral test,
- 3) epifaunal (attached, often epiphytic) herbivores, mostly with a trochospiral (conical) test.

It is far from easy to determine to what degree our faunas correspond with this feeding-niche separation. Data on the life position of individual taxa are extremely scarce and often contradictory. Even in the same area large differences have been observed in the life position of a single taxon (Von Daniels, 1970: *Nonionella turgida*; Ellison 1972: *Ammonia beccarii*). In our opinion the am-

biguity of the available data can be explained by the fact that most taxa are rather opportunistic in their choice of microhabitat.

It has been suggested in the literature (Lipps, 1983; Jones and Charnock, 1986) that infaunal detritus feeders should be characterized by an elongated shape. By a reduction of the cross-sectional area their burrowing capacity would be raised. However, a number of foraminifera observed in an inbenthic habitat do not have such an elongated test form (examples in Corliss, 1985).

Below the sediment-water interface, the oxygen tension tends to decrease rapidly (e.g. Jørgensen and Revsback, 1985). Therefore, an indispensable requirement for inbenthic faunal life is a certain tolerance for lowered oxygen concentrations. This could explain why a number of (not elongated) taxa, which are typical for low oxygen environments, have been observed in an inbenthic life position under better oxygen conditions (Bernhard, 1986). In a box-core from the western North Atlantic, maximum numbers of *Chilostomella oolina* and *Globobulimina affinis* were found between 7 and 9 cm depth within the sediment (Corliss, 1985); in the Mediterranean closely related taxa are found associated with sapropelitic layers (Van der Zwaan, 1980, 1983; Mullineaux and Lohmann, 1981; Jorissen, in prep.). We suppose that the microhabitat of these not typically elongated taxa could be largely a function of the oxygen profile; with high oxygen concentrations they will choose an inbenthic life position whereas they can still live in the sediment top-layer under more stressed conditions.

### V.2.2. Niche separation in the Adriatic Sea

In fig. 37 the cumulative percentages of the eight faunal clusters in the samples from transect V (east of San Benedetto) have been plotted against water depth, together with some of the environmental parameters. This sample transect shows the typical faunal succession perpendicular to the Italian coast. As concluded before, the boundary between the clay-belt (biofacial unit IV) and the near-shore zone (biofacial unit II) is much sharper than the transition towards unit I (deep water), which is more gradual.

The clay-belt (biofacial unit IV) is inhabited mainly by taxa belonging to faunal clusters 2, 8 and 6. Only in cluster 6 taxa with an elongated test, which suggests some specialization for a microhabitat within the sediment, are present (*Bigenerina nodosaria* and *Bulimina marginata* forma *aculeata*). However, an inbenthic life position has been observed (*Nonion barleeaanum*, Corliss, 1985; Gooday, 1986) or has been suggested (*Sigmoilopsis schlumbergeri*, Haynes, 1984, reported in Jones and Charnock, 1986) for some of the other (not elongated) taxa of cluster 6 too. It was concluded earlier that the test-form of the other

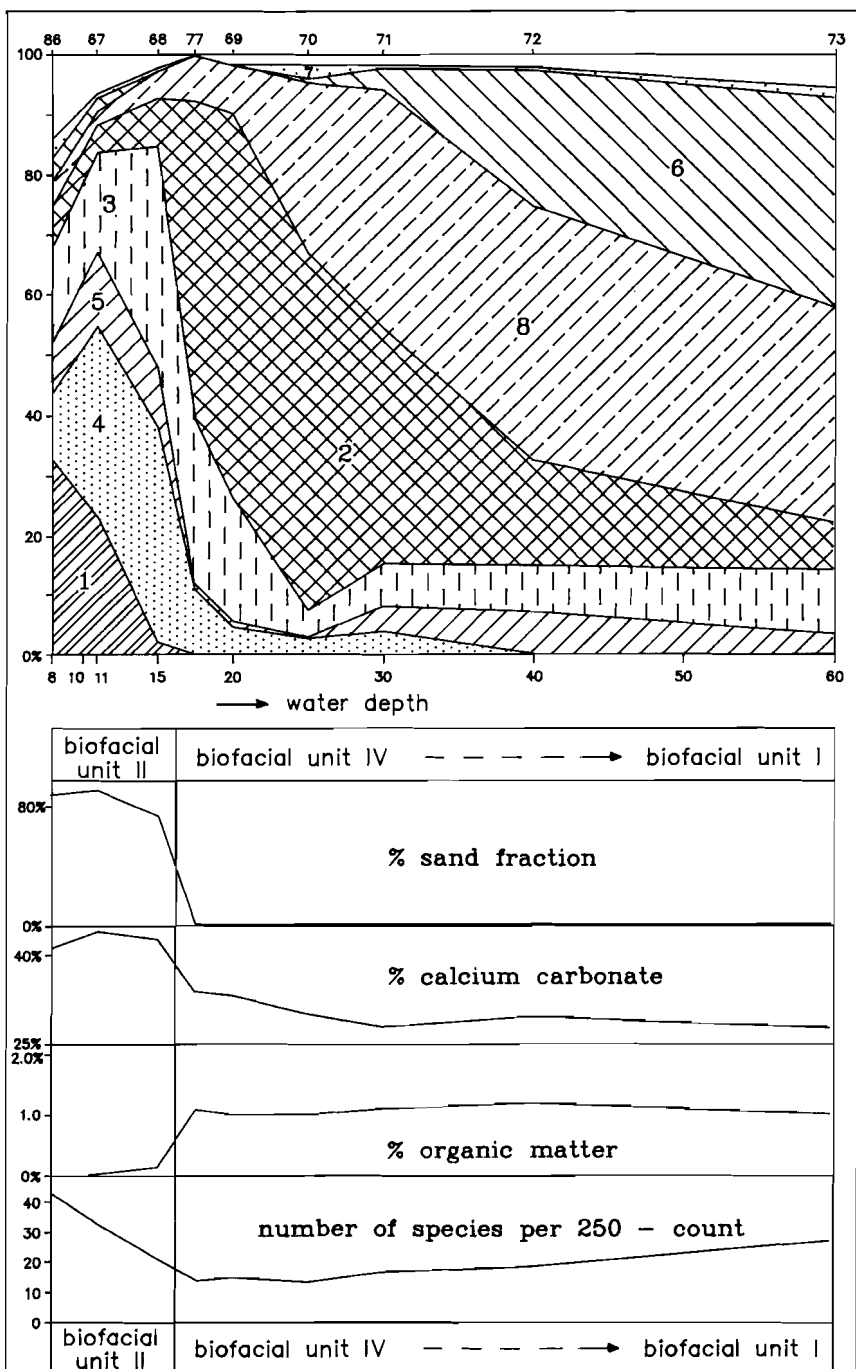


Fig. 37. Quantitative distribution of the eight faunal clusters in sample transect V together with some other faunal and environmental parameters, plotted against water depth.



morphotypes of *Bulimina marginata* (forma *denudata* and forma *marginata*) suggests a microhabitat in the sediment top-layer.

The more stress-tolerant cluster 8 contains no taxa with the elongated test shape which suggests an inbenthic habitat; only *Nonionella turgida* has been observed living within the sediment (Von Daniels, 1970). In the shallower water cluster 2, taxa, for which an inbenthic habitat has been described, are completely absent.

It can be concluded that the clay-belt is mainly inhabited by deposit-feeders that dwell in the sediment-top layer; taxa clearly specialized for a burrowing way of life are only present in the deepest part of the clay-belt, and epiphytic elements (cluster 7) are only present with low abundances. The increase in burrowing taxa towards deeper water (biofacial unit III) can be attributed to the combination of two factors. On the one hand the decreasing food availability could enlarge intraspecific competition, leading to microhabitat separation (Schoener, 1974; Levinton, 1979), and on the other hand the inbenthic niche could be made accessible by a thickening of the oxygen-containing layer, due to admixture of (reworked Pleistocene) coarser grained sediments. The scarcity of epiphytic elements is possibly a result of the (near-)absence of a vegetation cover on clayey substrata (Gamulin-Brida, 1967).

In the near-shore (more sandy) samples of biofacial unit II, clusters 1,4,5 and 3 dominate the faunas. It was concluded before that cluster 1 contains only reworked elements.

In the autochthonous assemblages, cluster 4, with its three morphotypes of *Ammonia parkinsoniana*, is the dominant constituent in the shallowest zone. The relatively numerous observations concerning the life position of this taxon, which has often been determined erroneously as *A. beccarii*, are not very consistent:

Brooks (1967): *A. beccarii*; top 3 cm.

Atkinson (1969): *A. beccarii*; epiphytic.

Ellison (1972): *A. beccarii*; maximum frequencies in sediment top in one core, and between 6 and 9 cm in a second core.

Matera and Lee (1972): *A. beccarii*; sediment top.

Dobson and Haynes (1973): *A. batava*; on hydroids.

Seiglie (1973): *A. tepida*; inbenthic.

Haward and Haynes (1976): *A. batava*; on *Chlamys*.

Collison (1980): *A. batavus*; sediment top.

In the case of the English material (*A. batavus* and *A. beccarii* of Atkinson) it is not clear whether these morphotypes belong to our *A. parkinsoniana* or

are more closely related to *A. beccarii* as used in this paper (see chapter IV.2).

Cluster 5 contains only miliolid taxa. For miliolids a similar diversity of life positions has been described or suggested:

Atkinson (1969): numerous epiphytic taxa.

Marszalek et al. (1969): *Quinqueloculina* (like numerous miliolids) upright, with the aperture downward to the substrate (in cultures).

Ellison (1972): *Miliammina fusca*; infaunal.

Matera and Lee (1972): *Q. seminula*: top three cm.

Dobson and Haynes (1973); numerous taxa on hydroids.

Haward and Haynes (1976); numerous taxa on *Chlamys*.

Buzas (1977): *Quinqueloculina*: infaunal.

Collison (1980): *Quinqueloculina*, mostly *Q. seminulum*; sediment top.

Severin et al. (1982): *Q. impressa*; to some extent infaunal.

Cluster 3 contains only trochospiral and planispiral taxa, for none of which an inbenthic life position has been described.

From these data it can be concluded that none of the taxa belonging to clusters 4, 5 and 3 are clearly specialized for a burrowing way of life. If there is any microhabitat separation, then it must take place in the sediment top-layer, but this has not been noted so far. In our opinion the most likely explanation for the absence of specialized infaunal elements is that most of the supply of nutritional elements is already consumed in the sediment top-layer (Walker and Bambach, 1974), and only minor portions are preserved within the sediment.

The main conclusion from the foregoing discussion is that in the faunas of our biofacial units II and IV there are no indications for a highly developed feeding-niche and microhabitat separation. This is probably the result of the overall large food availability, which results in the dominance of opportunistic (unspecialized) taxa. The existence of inbenthic elements seems to be largely precluded; either because the oxygen-containing layer is too thin, or because there are too few buried nutritional elements. These two factors evidently have a negative correlation.

### V.3. PRINCIPLES BEHIND INTRASPECIFIC VARIATION

#### V.3.1. Introduction

In the previous paragraph it was suggested that microhabitat separation takes place only in the deepest part of the clay-belt and that some of the taxa living

there, are adapted to a burrowing way of life. Earlier (chapter IV.3.3) it was concluded that the morphological differences observed in *B. marginata* could possibly be explained by such a microhabitat separation. However, for the extremely variable taxa *A. parkinsoniana*, *E. granosum*, and *E. poeyanum* no arguments could be found to support microhabitat separation between the various morphotypes. Therefore, there must be another explanation for the morphological changes in these taxa.

Both Poag (1978) and Wang and Lutze (1986) presented a substantially new concept for the interpretation of intraspecific variation in benthic foraminifera. Poag (1978) introduced the principle of paired ecophenotypy; in a number of species two distinct phenotypes can be found, which are linked by intermediates. The distribution of the two phenotypes is directly correlated with certain environmental factors, which in San Antonio Bay (California) are salinity and temperature. In Poag's opinion, smaller, thinly calcified morphotypes with fewer chambers are the result of reproductive acceleration, and are found particularly under (near-)optimum conditions. Likewise, larger, thickly calcified morphotypes with numerous chambers should be the result of a delayed reproductive maturity, and are characteristic for environments that are closer to the minimum requirements of the species. These minimum tolerances are refined (Poag, op. cit., p. 408) as 'environmental conditions that either exceed, or fall short of the optimum range' for the given species. In this context Poag thinks essentially in terms of salinity and temperature.

Wang and Lutze (1986) argued that in a number of benthic foraminifera there are two distinct ontogenetic stages; an early stage with compactly built, thick-walled chambers, and a later stage with inflated, thinner-walled chambers. In their opinion paired ecophenotypy as defined by Poag (1978) is the result of differences in the moment at which the change from the compact to the inflated chamber type takes place. This moment would depend on environmental conditions. According to Wang and Lutze compact morphotypes are dominant in more open marine waters, whereas inflated morphotypes are characteristic of more marginal environments.

The apparent contradiction between these two concepts is largely semantic. In the sense of Poag the term 'optimum' is used for an individual taxon; an optimum environment for a given species can be recognized by an accelerated reproductive maturity, and often by high frequencies. For other taxa these environments can easily be stressful. Wang and Lutze describe environmental conditions in a general (physical) way; a marginal environment is the opposite of an open marine environment, and can well be an optimum environment in the sense of Poag.

### V.3.2. Discussion

We think that the examples of phenotypic variation we described from the Adriatic Sea reveal somewhat more about the reasons of ecophenotypic variation. It is likely that the variation observed in *A. parkinsoniana*, *E. granosum* and *E. poeyanum* is comparable to that described in the papers of Poag and of Wang and Lutze. Although a sharp transition between two ontogenetic stages is rarely visible, the differences between the two morphotypes recognized in each of these species could well be the result of such a shift in a very early ontogenetic stage. The differences between our compact and inflated morphotypes are very similar to those described by Wang and Lutze (op. cit.). However, we did not explain the observed variation in terms of salinity and temperature, parameters that hardly show any variation in the studied area (Picotti, 1960; Nelson, 1970), but in terms of food and oxygen availability. Variations in these factors result from differences in the influence of runoff.

In figure 38 the distribution of the various morphotypes of the three species discussed is schematized. It should of course be borne in mind that this is the situation as found in time-averaged grab-samples. In the areas studied by Wang and Lutze (1986), compact morphotypes are characteristic for more open marine environments. The situation in the Adriatic Sea is comparable to that

locality	samples in front of Po delta	nearshore env.	15 – 30 m water depth	30 – 70 m water depth
environment	Po-influence large stressed env.	Po-influence minimal	Po-influence large no oxygen stress	Po-influence large oxygen stress
prevailing cluster	cluster 4	cluster 3	cluster 2	cluster 6
dominant morphotypes	<i>A. parkinsoniana</i> f. <i>tepida</i> , mt. 1–2 (inflated)	<i>A. parkinsoniana</i> f. <i>parkinsoniana</i> (compact)	<i>A. parkinsoniana</i> f. <i>tepida</i> , mt. 3–4 (inflated)	( <i>pseudoeponides falsobeccarii</i> ) (inflated)
	—	<i>E. granosum</i> f. <i>lidoense</i> (compact)	<i>E. granosum</i> f. <i>granosum</i> (inflated)	intermediate morphotypes (inflated)
	—	<i>E. poeyanum</i> f. <i>decipiens</i> (compact)	<i>E. poeyanum</i> f. <i>poeyanum</i> (inflated)	intermediate morphotypes (compact)

Fig. 38. Morphotypes of the morphologically highly variable species discussed in the text in relation with the environmental parameters.

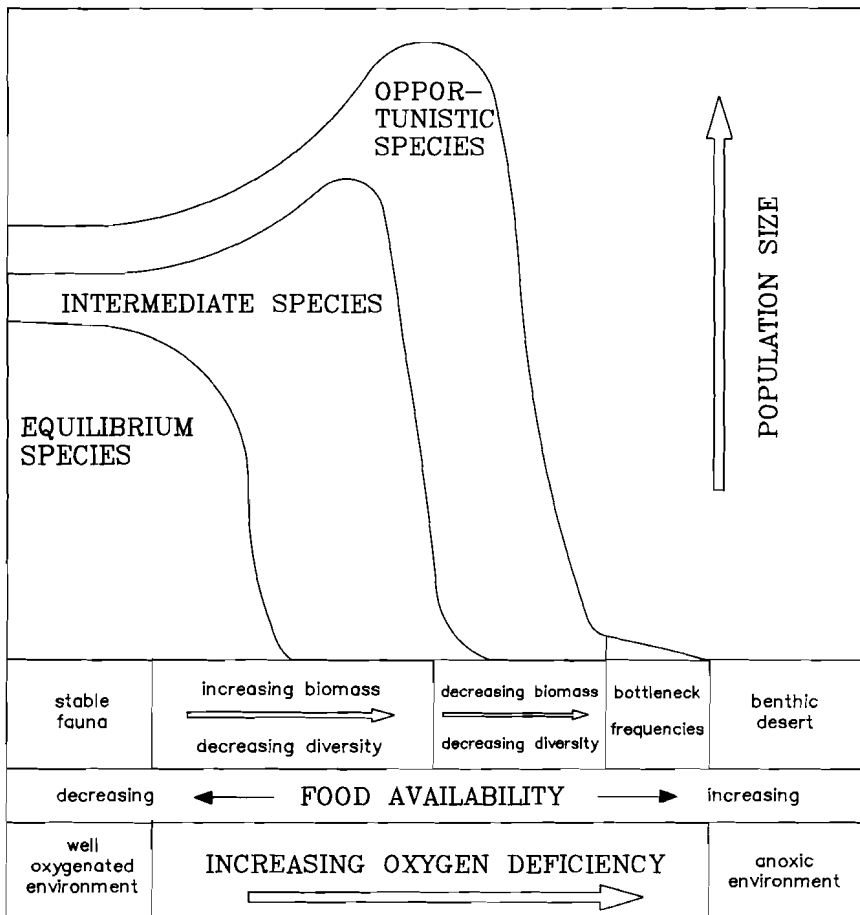


Fig. 39. Faunal density and life strategy as a function of food availability and oxygen concentration in the benthic environment (modified after Verhallen, 1987).

in San Antonio Basin (Poag, 1978), because the more open marine environments can be found in the most nearshore zone (with the exception of the direct surroundings of the Po delta), where the influence of Po-runoff is low.

Recently, in a discussion on the evolution of non-costate *Bulimina*, Verhallen (1987) suggested that for a given opportunistic species optimum conditions can be very close to stressed conditions (fig. 39). Although our species of *Ammonia* and *Elphidium* do not fully satisfy the criteria proposed by Levinton (1970) and Pianka (1970) for the recognition of r-strategists, they show some characteristics because of which they can be considered as such and certainly not as equilibrium (K-selected) species. These characteristics are:

- an initial rise in frequency with increasing stress,
- the possibility to dominate the assemblages (*A. parkinsoniana*),
- the tendency to be restricted to a certain (small) size- group under stressed conditions (which restriction is not caused by sorting effects),
- the eurytopic nature of their distribution,
- the tendency to decrease body-size, and presumably also to shorten the length of the reproductive cycle.

In our opinion the small difference between optimum and stressed conditions can be explained by the interplay of two counteracting environmental factors; i.e. an increase in biomass (and thus food availability), which normally co-varies with a decrease in oxygen concentration. Until a certain critical level is reached, an opportunistic species will benefit from the combination of increased food availability and concomitant decreased faunal competition pressure. This results in the high standing stocks often found in polluted environments. When the critical (minimum) level of the limiting factor (i.e. oxygen) is exceeded, then the positive influence of the increased food availability rapidly becomes subordinate to the stronger negative influence of oxygen depletion.

With this two-parameter model, three different environmental zones can be distinguished (fig. 40):

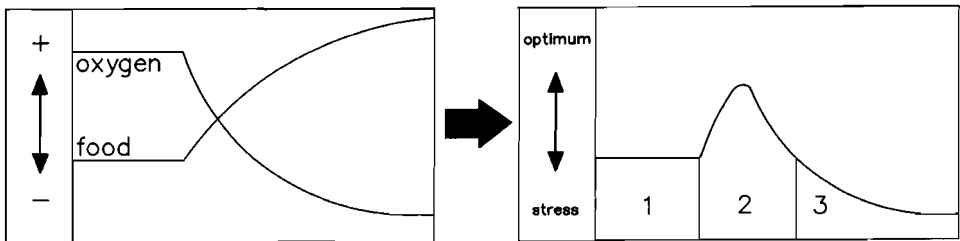


Fig. 40. Hypothetical ecological zonation resulting from the involvement of two contrasting environmental factors.

- 1) a zone where the optimum conditions of the species are not reached, but where also there is no question of stress;
- 2) a zone where the food availability causes optimum conditions for the given taxon; the oxygen shortage, although beginning, is not yet felt as a limiting factor;
- 3) a zone where the continued reduction of oxygen availability is rapidly becoming a limiting factor.

The first zone is characterized by the presence of compact morphotypes. In the Adriatic Sea, *A. parkinsoniana* forma *parkinsoniana*, *E. granosum* forma *li-doense* and *E. poeyanum* forma *decipiens* dominate the associations in the most near-shore zone, with the exception of the area directly in front of the Po-delta. Their morphology testifies to a slow increase of the protoplasm volume and presumably to a delayed reproductive maturity.

For the *Elphidium* morphotypes the second zone is positioned in the shallowest part of the clay-belt (between 15 and 30 m water depth). The inflated morphotypes, which are typical for near-optimum conditions (*A. parkinsoniana* forma *tepida*, *E. granosum* forma *granosum* and *E. poeyanum* forma *poeyanum*), dominate the assemblages, and high abundances are reached. The inflated morphology can be explained as being the result of a more rapid increase in protoplasm volume and an earlier attainment of reproductive maturation.

If the environment shifts towards the stressed conditions of the third zone (for the *Elphidium* morphotypes 30 - 70 m water depth, at a somewhat shallower depth for *Ammonia*), the abundances strongly decrease and the few remaining specimens show unexpected combinations of morphocharacters.

The way in which the various morphological characteristics generally co-vary with a compact or inflated chamber-type (depicted in table 2 of Wang and Lutze, 1986) also applies to the three examples from the Adriatic Sea. However, in zone 3 (30 - 70 m depth zone) some of these characteristics no longer co-vary. In *E. granosum* the test size and the number of chambers remain low, but the umbilical ornamentation increases, and we have the impression that the outlets of the canal system at the umbilical end of the chamber sutures become better developed. In *E. poeyanum* a similar diverging trend can be observed. The test size decreases, but the number of chambers increases again, and here a new morphological feature develops: imperforate fields are formed in the chamber walls around the umbilical area. A similar trend in perforation can also be found in samples from the deepest water where *A. parkinsoniana* forma *tepida* is present.

The presence of imperforate fields can be observed in a number of foraminifera specialized to live in stressed environments. The enlargement of the canal outlets can perhaps be considered as being indicative of a more intensive use of the canal system or of related internal structures (compare for instance the function of the internal tube in *Bulimina marginata* as suggested by Verhallen, 1986). The appearance of *Pseudoeponides falsobeccarii* in this zone, a species with an *Ammonia* morphology but provided with supplementary openings of the canal system at the dorsal side, reflects the same trend.

Although the presence of two ontogenetic stages has been convincingly demonstrated in a number of species, Wang and Lutze (1986) fail to indicate

why the (often abrupt) transition between the two stages takes place. In our view the examples of phenotypic variation from the Adriatic Sea can in many cases indeed be the result of an early ontogenetic break. We shall try to explain this break as a response to variations in the food and oxygen availability. Both factors are strongly influenced by fluvial runoff, which is a seasonal phenomenon. Spring and autumn maxima (Nelson, 1970) correspond to instantaneous phytoplankton blooms (Revelante and Gilmartin, 1976a,b). Even short periods of heavy rainfall, which result in high Po runoff, are followed by algal blooms (Malanotte Rizzoli and Bergamasco, 1983). Oxygen shortage, which occurs mainly in summer and autumn due to a temperature stratification of the water column, is also a seasonal phenomenon.

If the variation between compact and inflated morphotypes is indeed (partially) the result of an early ontogenetic shift in the growth pattern, then the impulse for such a shift may well be given by the seasonality of the controlling environmental parameters. A relation between seasonal changes in environmental parameters and standing stocks of benthic foraminifera has often been observed. In a number of these studies (Myers, 1943; Buzas, 1966; Lee et al., 1969; Erskian, reported in Lipps, 1983) it could be demonstrated that faunal reproduction is linked to seasonal changes in food availability. A seasonal triggering of reproduction is in accordance with the relatively short generation time (1-3 months) which has been observed in a large number of shallow mud-dwellers (e.g. Bradshaw, 1957; Boltovskoy and Lena, 1969; Von Daniels, 1970).

The two main factors controlling the distribution of benthic foraminifera, food availability and oxygen concentration, are both strongly influenced by seasonal shifts in (Po-) runoff. However, as the distance from the fluvial outlets increases, the input of nutrients will be less variable as a result of the averaging effect of the longer period needed for their transport. In our opinion, in comparison with the near-shore zone not influenced by Po-runoff, the clay-belt is food-enriched throughout the year. The variations in oxygen concentration will be definitely more variable, because these are also strongly influenced by the seasonal shifts in temperature. The high summer temperatures in the shallow water of the clay-belt cause a stratification that in the late summer and autumn can lead to oxygen shortage.

The oxygen crises which have been observed a number of times in the last decennium suggest that *Ammonia parkinsoniana*, *Elphidium granosum* and *Elphidium poeyanum*, which have only a limited tolerance of oxygen stress, are not able to live in the clay-belt throughout the year. Probably, in the period of the year with the lowest oxygen concentration (late summer and autumn), they only persist in the near-shore zone, outside the influence of Po runoff. Under the relatively nutrient-poor conditions found there, chambers are added at a slow rate, leading to compact morphotypes.



When the circulation in the water column is renewed in winter, the oxygen concentration will rise considerably, and the clay-belt will probably be invaded by juvenile (compact) specimens spreading from their near-shore refugium. As soon as these specimens have settled, they probably react to the still high food availability (in any case considerably higher than in the near-shore zone) by a strong increase of the rate of chamber addition as well as of the protoplasm volume per growth step. This leads to a shift very early in the ontogeny, the development of inflated chambers in the adult morphotypes, and an earlier attainment of reproductive maturation. It is likely that the foraminifera reproduce (and die) before the end of this advantageous period. Of course the newly formed foraminifera will miss the compact juvenile stage, and will be inflated throughout their ontogeny. If the environment becomes more stressed (because of the lowering of oxygen concentrations) growth (and reproduction) stops abruptly, and most foraminifera will die. This is the reason why species with a relapse from an inflated to a compact stage are hardly ever observed.

The same type of variation between compact and inflated morphotypes can be found in a number of other species (e.g. *Ammonia perlucida*, *Elphidium advenum*, *Elphidium crispum* (*crispum* versus *macellum* morphotypes) and *Nonionella turgida*) which have not been discussed in detail.

If the morphological transition indeed coincides with great differences in food availability, then it is not illogical to assume that the morphological transition could be connected with a change in feeding strategy. In our opinion the transition from compact to inflated morphotypes (geographically as well as ontogenetically) could well reflect a change from a passive to an active feeding strategy. In our examples this could be a change from a feeding by means of symbiotic algae to a more direct food uptake mechanism.

If this speculation should prove to be true than the difference between compact and inflated morphotypes can be explained theoretically as a difference in foraging tactics determined by the trophic resource availability. More precisely, this would mean that the compact morphotypes (or juvenile stages) act as K-strategists, whereas the inflated morphotypes (or the adult stages) of the same species have adopted an r-strategy. A theoretical discussion on the appearance of r- and K-selected morphotypes in relation to seasonality was given by Boyce (1979) and Boyce and Daley (1980).

Finally we would stress again that our hypothesis is highly speculative, and should be tested by a detailed sample campaign over a long period, for instance as was done by Von Daniels (1970) in the Limski Canal (north-eastern Adria). Unfortunately, the influence of the Po-runoff and other seasonal parameters is minimal in that environment, which is probably more sheltered, and clear

seasonal changes in frequency in the opportunistic species *Nonionella opima* could not be demonstrated.

#### V.4. CONCLUSION

The main conclusion from the previous discussions is that the claybelt-environment influenced by the Po-runoff is delimited in two essentially different ways. Towards deeper water, the environmental characters change very gradually, whereas there seems to be a sharp break towards shallower water. The inferred changes in the two most important parameters for benthic foraminifera, oxygen saturation and food availability, have been schematized in figure 41. Each of the two types of confinement yields a specific faunal response.

Entering the claybelt from deeper water, the faunas change very gradually. Probably as a result of the thinning of the oxygen-containing zone, the number of niches decreases; this is reflected in the much lower faunal diversity. Exclusively infaunal elements are no longer found, and only the most stress-resistant species remain; these eventually gradually develop a morphology that is adapted to a life position very close to the sediment-water interface.

Following the sample transects from shallow water into the claybelt, there is no gradual transition, but instead there is a sharp break in faunal composition. A number of taxa which are present on both sides of this break display

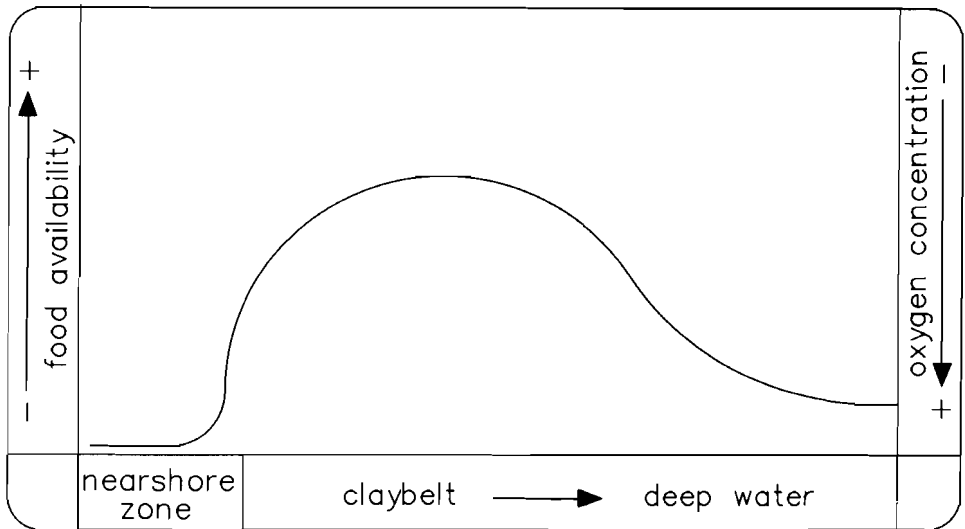


Fig. 41. Inferred variations in oxygen and food availability with water depth.

an abrupt morphological change over a very short distance. In our opinion this morphological change could well reflect a change in life strategy, namely from a relative K-strategy (feeding by means of symbionts) to a relative r-strategy. We think that a number of taxa found in the shallowest part of the clay-belt are not selected by their ability to persist in hostile environments, but are the result of immigrations from the near-shore zone during seasonal periods of relatively high oxygen concentration. In a juvenile (compressed) stage the foraminifera migrate into the clay-belt; upon arrived there the juvenile forms drastically change their feeding habits, and develop the more inflated adult morphology.

In this paper, two main types of morphological variation are distinguished:

- 1) gradual phenotypic changes along environmental gradients, e.g. the transition from *granosum*-types to 'intermediate' types in *Elphidium granosum*,
- 2) more abrupt changes due to differences in life strategy, not only in species populations (e.g. the transition from compact to inflated types in *E. granosum* and *E. poeyanum* populations), but probably also in individual specimens, although the latter has not been conclusively proved.

In our opinion a similar distinction between these two kinds of ecophenotypic changes could be made for a number of other organisms, and could provide important (paleo-)environmental information. The two types of information are complementary: intraspecific differences in life strategy could indicate a large influence of seasonality in some given factor, whereas gradual variation could give a clue to the intensity of the factor considered. It is clear that this kind of information can be extremely useful for the monitoring of eutrofication and pollution in the near-shore marine reach.

## Chapter VI

### APPLICATIONS

#### VI.1. INTRODUCTION

In the preceding chapters we discussed the (paleo-)ecology of shallow-water benthic foraminifera living on clayey substrata in some detail. If one were to adopt an actualistic approach, the results of such a (paleo-)ecological study could be used to interpret paleo-environments in terms of bathymetry, salinity, temperature, oxygen availability and benthic productivity.

In chapter I.2 it was concluded that in the Adriatic Sea temperature variations at the sea-bottom are minimal (below the thermocline), and that therefore the direct influence of this parameter on the benthic foraminifera is probably negligible. Furthermore, it was concluded that salinity variations are probably only of importance in the direct vicinity of the fluvial outlets. However, temperature and salinity variations do have an important indirect influence on the benthic ecosystem because they are responsible for the stratification of the water column, and in this way have an impact on the oxygen content of the bottom waters.

In figure 42 the (sub-)recent bathymetrical distribution of the most frequent taxa of benthic foraminifera in the Adriatic Sea is summarized. The distributional data for each taxon have only been incorporated if the frequency exceeds a certain minimum value. This minimum frequency (in figure 42 indicated separately for each taxon) is chosen on the basis of the maximum frequency values observed. A disadvantage of our data set is the fact that the depth range between 300 and 800 m is covered by relatively few samples which, moreover, often show a mixture of Holocene and Late Pleistocene material.

In shallow water (10 - 100 m) a very regular succession of taxa is found with increasing water depth (fig. 42). For a sample of unknown water depth, a reasonably accurate estimate (in the order of plus or minus 25 %) can thus be given on the basis of the faunal content. However, the depth zonation is not controlled primarily by bathymetry itself, but it is determined much more strongly by food and oxygen availability. Although these factors tend to have rather a constant relation with the bathymetry in the recent situation, it is obvious that this relation may have been different in the past. In a future paper (Jorissen et al., in prep.) it will be argued that the recent strong anti-clockwise surface current system, which governs the nutrient distribution, was established as late as the middle of the Holocene. This implies that the nutrient distribu-

tion was different before that time. Therefore, the detailed bathymetrical faunal succession found today in shallow water was probably already different during the earlier part of the Holocene.

A very important factor to be used for paleo-bathymetrical reconstructions is the lower limit of the photic zone, which is believed to account for the major faunal break found at some 100 m water depth (Jorissen, 1987; present paper, fig. 42). However, the water transparency and light penetration are also influenced by changes in the circulation pattern, and as a consequence so is the bathymetrical distribution of sensitive taxa.

Also for water deeper than 100 m there are strong indications that benthic productivity is the controlling factor for a great number of taxa. Even between the central and southern Adriatic basins important differences in the frequency distribution of a number of taxa are found at the same water depth. Productivity fluctuations may also explain why some taxa which at present are found in fairly deep water (e.g. *Cassidulina crassa*) were living at a much shallower depth during the latest Glacial.

The fact that the bathymetrical zonation at present in the Adriatic Sea is to a great extent dependent on the bottom and surface fertility implies that this zonation should only be used with great caution to determine the paleo-depth of material from other localities and/or time-slices. Additional evidence could perhaps be furnished by the P/B-ratio, which in the Adriatic Sea shows rather a good correlation with water depth. But this tool too can be used only if corrections are made for fluctuations in productivity, both in the water column and in the benthic ecosystem.

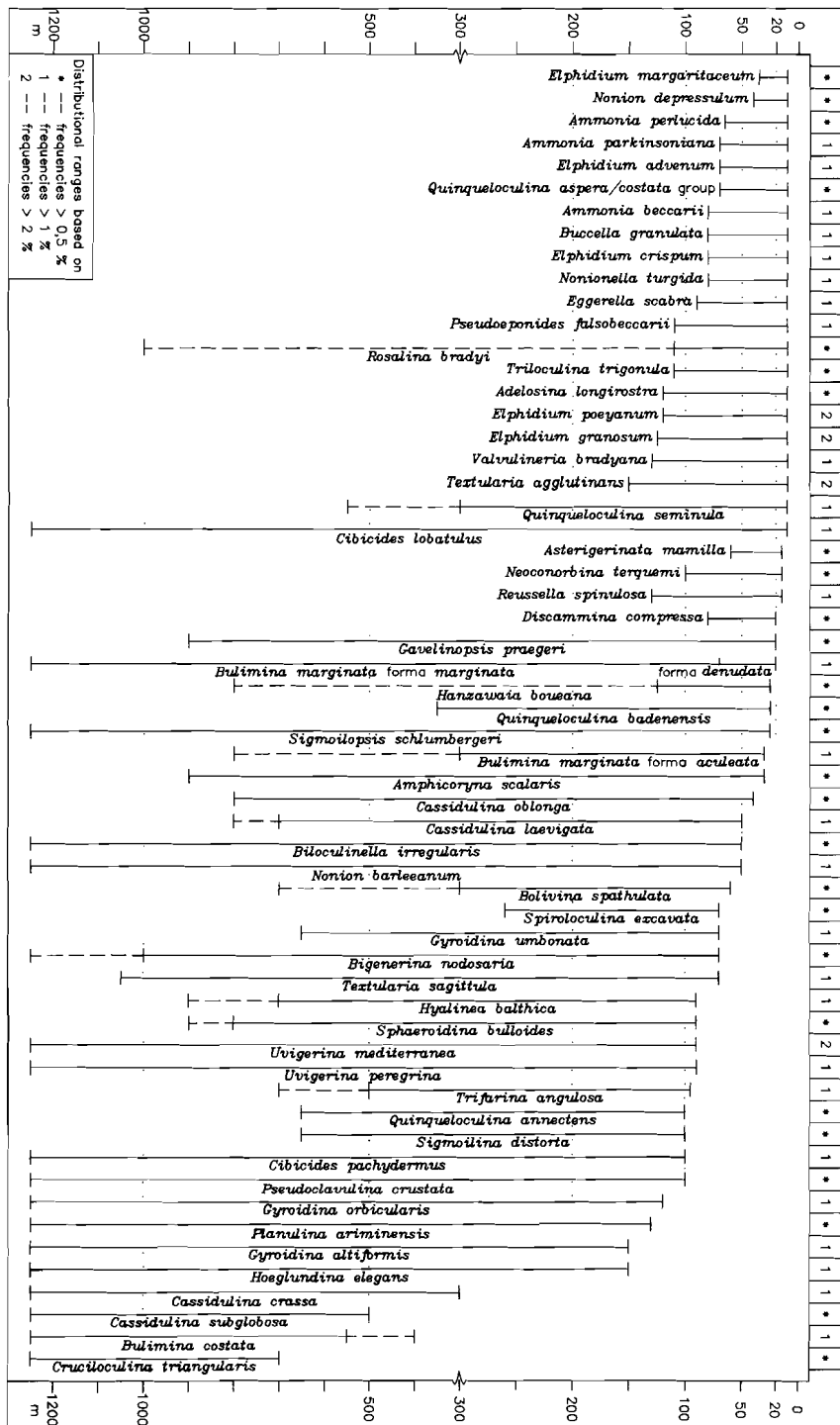
## VI.2. BENTHIC PRODUCTIVITY

### VI.2.1. Introduction

In the previous chapters it has been demonstrated that the combination of food availability and oxygen concentration, which determines the level of benthic productivity, is the most important controlling factor for a large number of the benthic foraminiferal taxa in the Adriatic Sea. Therefore fossil faunas

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Fig. 42. Bathymetrical distribution of the quantitatively most important taxa in the Adriatic Sea. The bathymetrical ranges are based on all observations where the specific taxon exceeds an arbitrary minimum value chosen on the basis of the maximal frequency observed for the taxon. Some rather inconsistent data have been entered by dashed lines.



from comparable settings should preferably be interpreted in terms of this controlling factor. This can be useful for:

- the recognition of basin-wide productivity changes,
- the recognition of oxygen-poor environments with an enlarged possibility of preservation of organic matter (e.g. oil source rocks),
- the reconstruction of circulation patterns,
- the interpretation of P/B-ratios (paleo-bathymetry, see above).

In this sub-chapter, some of these possibilities will be further illustrated by the interpretation of a piston-core from the Adriatic Sea.

### **VI.2.2. An example of paleo-ecological interpretation: core IN 68-23**

Core IN 68-23 was sampled in 1968 at locality 381, north of Termoli (fig. 1). The piston-core was taken at a water depth of 64 m and has a length of 411 cm. The core locality is situated in our biofacial unit IV (fig. 8), characterized by a clayey substratum, poor in calcium carbonate and rich in organic matter. It is located at the seaward edge of the clay-belt, in the strip dominated by faunal cluster 6 (fig. 14). Data on the mollusc fauna of the core were published by Van Straaten (1985).

The sediment consists entirely of grey homogeneous clays, with the exception of the topmost 4 cm which have a more yellow colour, probably due to oxidation (Colantoni and Gallignani, 1977). Within the core 17 levels were sampled; these samples were treated in the way described in chapter I.3.

A first inventory of the wash residues (> 150 microns) revealed substantial amounts of gypsum in samples 1 - 3 (0 - 50 cm), in which a number of the foraminifera show clear signs of dissolution. In samples 8 -10 (165 - 220 cm) both pyrite and gypsum were found; samples 12 - 13 (270 - 300 cm) and 16 (351 - 355 cm) contain a large quantity of ash fragments. Numerous sponge spicules and bryozoans were found in samples 14 and 15 (320 - 340 cm).

Sample	Level	Age (years BP)
381 - 1A	0 - 2 cm	Recent
381 - 1B	0 - 2 cm	400 (+ or - 90)
381 - 3	41 - 46 cm	1000 (+ or - 70)
381 - 6	116 - 121 cm	2160 (+ or - 70)
381 - 10	216 - 221 cm	2670 (+ or - 150)
381 - 17	376 - 381 cm	4590 (+ or - 100)

Table VIII. Radiocarbon datings made on the basis of plant material (sample 381 - 1A) or mollusc fragments (all others). More detailed information about the datings is available at the Robert J. Van der Graaff laboratorium of the Rijksuniversiteit Utrecht.

For each of the 17 samples at least 250 benthic foraminifera were determined and counted per taxon. The relative frequencies of the most important taxa are given in appendix V, and are shown in figure 43. For five samples radiocarbon datings were obtained, the results of which are given in table VIII. For the top-most sample one dating was made on plant material that originated mainly from the algal layer at the top of the core (age: Recent), whereas the second dating was obtained on the basis of mollusc fragments (age: 400 BP) The difference between the two datings can be explained by a mixing of recent and older mollusc fragments by means of burrowing. We suppose that upward and downward contamination are balanced deeper in the core, and we decided therefore to use the Recent date for the top, and to maintain the uncorrected radiocarbon datings for the other core-levels.

On the basis of these radiocarbon dates, sedimentation rates can be calculated; for the four successive intervals these are:

- samples 1 - 3 (1000 BP - Recent): 45 cm/ka,
- samples 3 - 6 (2160 - 1000 BP): 65 cm/ka,
- samples 6 - 10 (2670 - 2160 BP): 195 cm/ka,
- samples 10 - 17 (4590 - 2670 BP): 85 cm/ka.

The frequency curves in figure 43 show that no sharp faunal breaks are present. Throughout the core the taxa of faunal clusters 6, 3 and 8 (fig. 11) dominate the assemblages. Considering the environmental preferences of the recent representatives of these taxa it is evident that the larger part of the core sediments was deposited in a muddy realm in which the food supply was ample and reduced concentrations of oxygen could occur periodically. Therefore we decided to enlarge our data set by adding the frequency data of all (26) recent (grab-)samples from clayey substrata between 50 and 80 m water depth. This mixed and artificial data set is of sufficiently large size for a principal com-





ponents analysis. It is considered a correct basis for a comparison and interpretation of the down-core faunal variations.

For the total set of 43 samples a principal components analysis was performed on the basis of the computer program of Davis (1973). This analysis resulted in one significant factor only, which accounted for 53.65 % of the total variation. The taxa with the highest positive loadings on this axis are *Valvulineria bradyana* (.68), *Bulimina marginata* forma *denudata* (.39) and *Nonionella turgida* (.26), whereas *Bulimina marginata* forma *aculeata* (-.34) and *Elphidium*

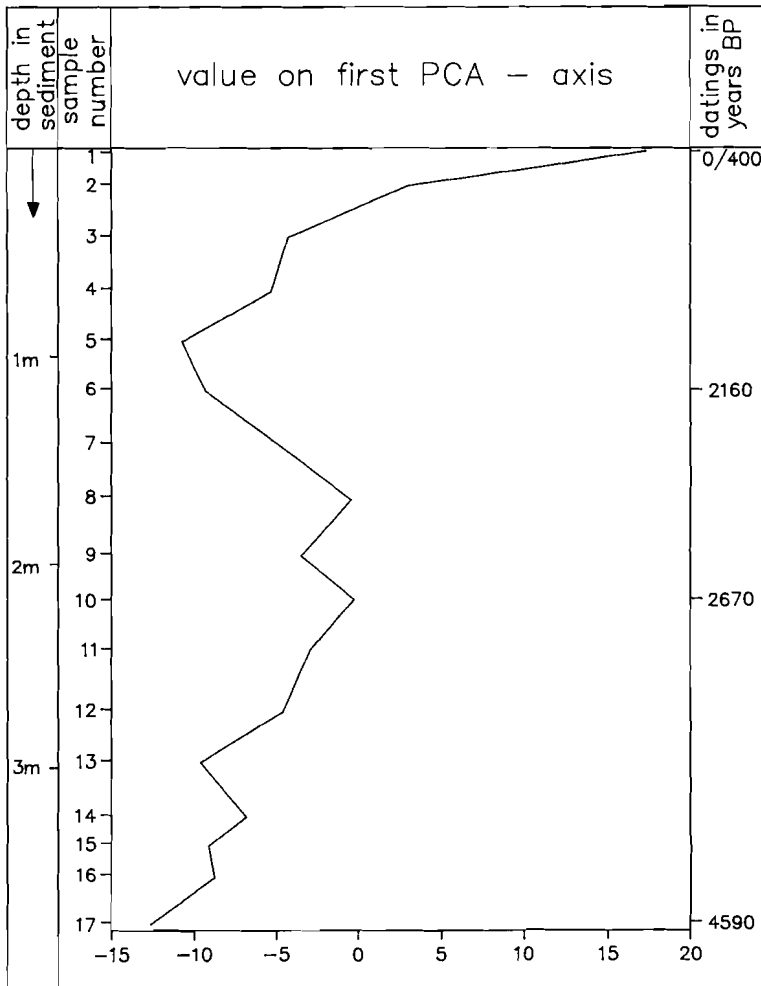


Fig. 44. Core In 68-23; sample scores on the first principal component axis, versus depth in the sediment.

*poeyanum* forma *decipiens* (-.25) have the highest negative loadings. For the individual samples of core IN 68 - 23 the scores on the first axis are depicted in figure 44.

### VI.2.3. Discussion

At present the zone between 50 and 80 m water depth can be considered as a zone of high productivity. It was suggested earlier (Jorissen, 1987) that the zone of maximum stress (characterized by a periodical shortage of oxygen) can be found around 30 m water depth in front of the Po delta and gradually deepens to some 60 m in the most southern part of the Adriatic Sea. In this direction along the clay-belt a succession of peak frequencies of *Nonionella turgida*, *Bulimina marginata* forma *denudata* and *Valvulineria bradyana* was observed (Jorissen, 1987). This succession is evidently caused by a depth factor superimposed on the food-balance. It is precisely these three species that dominate the positive side of the first principal components axis. We therefore conclude that high scores on this axis can be considered as indicative for high benthic productivity and in extreme cases for environmental stress (oxygen shortage). This conclusion is further supported by the fact that the samples with the highest loadings on this axis (1-3, 8-10) are all enriched in pyrite and/or gypsum. Van Straaten (1985) tried to explain the absence of pyrite in the top of the core (where the highest scores are reached) by the slowness of the pyrite-forming process.

In figure 45 the loadings on the first axis have been mapped for the 26 (Re-

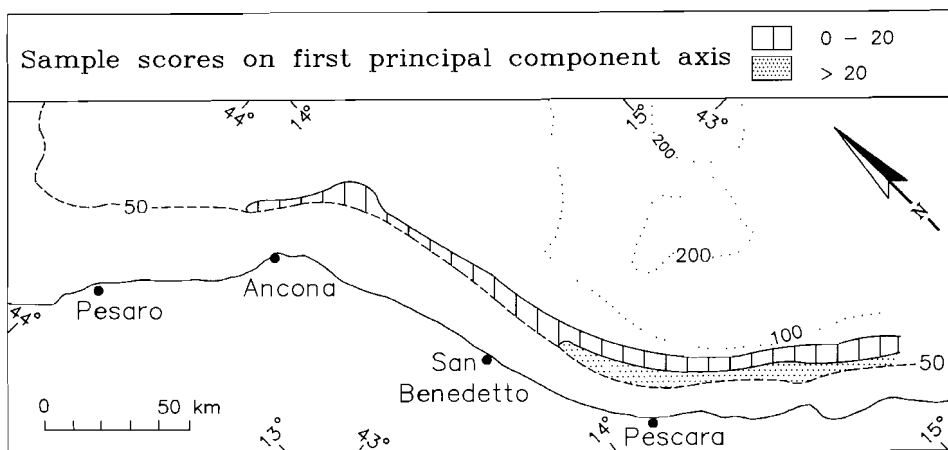


Fig. 45. A map of the sample scores on the first PCA-axis, used for a comparison with the samples of piston-core IN 68-23.

cent) grab-samples. It can be seen that for the same water depth increasing loadings are found in south-eastern direction. As was already indicated by the succession of the three productivity markers, the zone of maximum benthic productivity appears to deepen slightly in that direction.

A closer inspection of the samples of core IN 68 - 23 with the surface samples reveals a number of consistent differences in faunal contents:

- in core IN 68 - 23 *Ammonia parkinsoniana* is virtually absent, whereas it is present in a number of the grab- samples.

- in a large part of the core *Valvulineria bradyana* is present in much lower frequencies than in the grab-samples.

- in the core *Bulimina marginata* forma *denudata* is present almost only in the topmost three samples. Every grab-sample contains at least 2 % of this taxon. The mollusc *Turritella communis* shows exactly the same down-core distribution (Van Straaten, 1985),

- in the core much higher frequencies are found for *Reussella spinulosa*, *Buccella granulata*, *Elphidium crispum* and *Elphidium poeyanum* forma *decipiens*. All of these are forms which have some association with a coarser substratum.

On the basis of the scores on the first principal components axis (fig. 44) three zones are distinguished; these have been indicated in figure 46, where the samples have been plotted on the vertical scale according to their calibrated age.

Zone I extends from the bottom of the core up to sample 10 (220 cm) and covers the time interval between 5000 and 2670 BP. The sedimentation rate is intermediate, the productivity, as indicated by the sample scores on the first PCA-axis, increases regularly. In this interval the percentages of *Reussella spinulosa* and *Cibicides lobatulus*, both having some relation with a vegetation cover, and thus with a coarser substratum, decrease (see figure 43).

A second zone (II) extends from sample 10 up to sample 6 (220 - 120 cm, 2670 - 2160 BP). The sedimentation rate is extremely high; the productivity reaches high values in the lower part of the zone (samples 10 - 8) and later strongly decreases.

Zone III extends from sample 6 up to the top of the core (2160 BP - Recent). The sedimentation is low (45 - 65 cm/Ka), whereas the productivity, which is low in the basal part, shows an accelerated increase, leading to a maximum value in the topmost sample. Remarkable is the entry of *Bulimina marginata* forma *denudata* in sample 3 (41 - 46 cm).

The transition from zone I to zone II roughly corresponds in time with the transition from the Sub-Boreal, which had a warm and dry climate, to the Sub-Atlantic, characterized by a warm and humid climate.

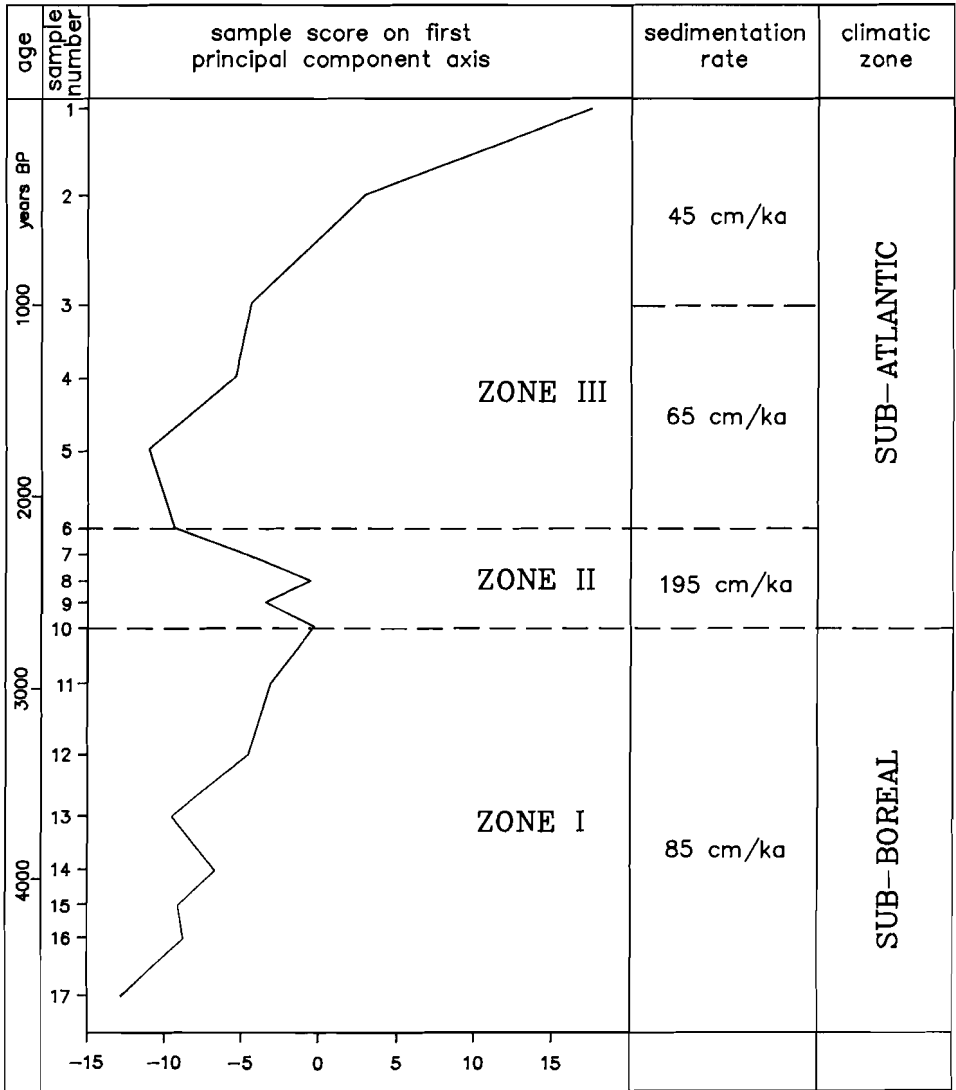


Fig. 46. Core In 68-23, water depth 64 m; sample scores on the first principal component axis versus the absolute age, calibrated on the basis of radiocarbon datings. Apart from the three faunal zones recognized, also the calculated sedimentation rates, general productivity trends and climatic zones have been indicated.

The problem that remains to be solved is whether the observed changes in productivity in the core near Termoli were caused by basin-wide changes, such as alterations of the circulation pattern or sea-level fluctuations. In the recent situation, in the Adriatic Sea clay-belt high productivity is correlated with a high sedimentation rate. In the largest part of the core this relation seems to be the same; in zone II, where high values on the first PCA-axis are found in samples 8 - 10, the sedimentation rate is two to three times higher than it is in the rest of the core. Only the strong increase in the sample scores in the top-most samples is not accompanied by a similar increase in the sedimentation rate. If we can trust the age estimates of samples 1 and 3, the sedimentation rate would even be decreasing here.

In a number of studies (Fontes and Bortolami, 1973; Bortolami et al., 1977; Colantoni, Galignani and Lenaz, 1979, 1980) it is argued that at 6000 BP the sea level was still some 25 m lower than today, and that maximum values (slightly higher than at present) were reached around 2000 BP. In our core clear bathymetric trends are not observed. The virtual absence of the most common shallow-water species *Ammonia parkinsoniana* suggests that the water depth was not less than 50 m in any part of the core. However, the sea-level changes claimed by most Italian authors should certainly not be rejected on the basis of our data, since the distribution of all taxa found in the clay-belt is primarily controlled by food and oxygen availability.

The increase in productivity values in zone I, leading to maximum values in sample 8 - 10, can be explained in two ways. One solution would be to explain it as the reflection of a basin-wide productivity increase. This would agree with the transition at this level from the Sub-Boreal towards the more humid Sub-Atlantic. However, with this model it is very difficult to give an explanation for the rapid drop in productivity we find at 2000 BP.

Therefore, we prefer a model which incorporates the sea-level changes claimed in the literature to explain the observed productivity fluctuations. With a rise of sea-level, the zone of clay sedimentation, which is identical to the zone of high benthic productivity, probably shifted in coast-ward (south-western) direction. We think that around 4500 BP (corresponding to the bottom of the core), when the sea-level was some 20 m lower than today, the belt of clay sedimentation was located seawards (north-east) of our site IN 68-23. With rising sea-level, this sedimentation zone approached our core locality, which resulted in an increase both in sedimentation rate and in productivity. The decreasing productivity during the following 500 years could then suggest that the sea-level rose still further until a maximum sea-level stand was reached around 2000 BP. The centre of the clay sedimentation zone would have shifted more or less to its recent position, i.e. south-west of our core locality.

From 2000 BP until Recent the sea-level stand was more or less constant. Therefore the productivity increase during this interval should be attributed to another mechanism. This increase has no positive correlation with an increase in sedimentation rate. The entry of *Bulimina marginata* forma *denudata* and the combined decrease of *Bulimina marginata* forma *aculeata* nevertheless strongly suggests the onset of more stressed conditions. It should be noted that the observed entry of *Bulimina marginata* forma *denudata* in sample 3 (41 - 46 cm) is probably situated somewhat too low, because of downward mixing.

In our opinion the onset of the stressed conditions registered in the top part of the core can only be explained by an increase in the human population in the Adriatic Sea hinterland. This population increase probably started in the late Middle Ages, and culminated in the heavy organic (and chemical) pollution which has developed in the Adriatic Sea during the last few decades.

The discussion of core In 68 - 23 shows that estimates of bottom productivity at one locality only can give insight into the Holocene development of the complete basin. Although our conclusions may seem to be somewhat speculative, in a future paper they will be supported by data for a larger number of cores taken from all over the basin. It appears that the study of productivity patterns by means of benthic foraminifera can not only make a valuable contribution to paleo-environmental investigations, but can also be used to determine the influence of pollution in the benthic ecosystem.

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Appendix I. Sedimentological (after Breman, 1975, based on data from Van Straaten and Veenstra) and general faunal data of the 285 samples studied:

- A -- sample number,
- B -- water depth (in meters),
- C -- percentage of sand fraction (> 50 microns),
- D -- percentage of calcium carbonate,
- E -- percentage of organic matter,
- F -- foraminiferal number (number of foraminifera per gram dry weight),
- G -- p/b-ratio (ratio of planktonic versus benthonic foraminifera).

A	B	C	D	E	F	G	A	B	C	D	E	F	G
1	10	5.9	30.3	1.2	18	0.10	73	60	0.4	27.6	1.0	29	0.02
2	7.5	1.3	28.4	1.2	3	0.11	74	8	92.6	33.9	0.1	30	0.00
5	50	0.0	29.8	1.1	7	0.01	75	12	85.6	37.1	0.1	32	0.00
6	40	0.1	30.4	1.3	3	0.01	76	15	78.8	38.3	0.3	127	0.00
7	30	0.1	31.5	1.1	13	0.00	77	17.5	0.9	33.7	1.1	47	0.00
8	20	3.0	36.0	0.9	135	0.00	78	20	2.2	30.4	1.0	21	0.00
12	80	0.1	28.7	1.1	31	0.03	79	15	39.8	44.8	0.4	40	0.13
13	100	0.3	27.8	1.3	65	0.07	80	20	5.1	33.8	0.9	44	0.10
15	150	15.5	39.5	1.0	535	0.23	81	18	2.9	29.9	1.1	50	0.00
24	197	1.2	33.6	1.2	215	0.17	82	18	7.2	32.1	0.9	41	0.08
30	100	0.4	28.6	1.3	47	0.07	83	17	15.9	35.9	1.3	42	0.00
31	125	1.0	30.6	1.2	61	0.11	84	18	8.6	32.6	0.8	58	0.00
32	150	1.2	32.4	1.1	174	0.19	85	21	0.5	29.2	1.0	47	0.00
33	180	2.2	34.0	1.2	289	0.20	86	22	2.2	28.5	0.7	68	0.00
34	220	1.0	31.3	---	302	0.24	87	20	2.0	28.8	0.9	32	0.00
35	253	0.4	27.1	1.1	84	0.18	88	18	11.2	31.2	0.5	26	0.01
36	260	0.6	31.1	1.3	114	0.25	89	33	0.7	25.1	1.4	14	0.00
50	50	0.3	29.4	1.3	6	0.01	90	52	78.6	33.1	0.2	332	0.00
51	50	0.4	27.9	1.2	14	0.00	92	8	15.2	23.3	0.8	111	0.00
52	77	0.4	27.8	1.3	26	0.06	93	12	1.7	20.7	1.1	95	0.00
53	75	0.4	27.9	1.1	30	0.03	94	17	0.5	23.5	1.3	54	0.00
54	70	0.4	27.5	1.3	35	0.04	95	22	0.7	25.3	1.6	42	0.00
55	60	0.5	27.4	1.1	17	0.01	96	32	5.8	29.4	1.5	77	0.00
56	40	0.4	27.0	1.3	12	0.01	97	35	40.4	23.2	1.1	157	0.00
57	20	0.7	31.5	1.0	31	0.00	98	40	26.4	33.1	1.1	222	0.00
58	10	93.7	40.5	---	39	0.02	99	35	2.7	35.8	0.4	36	0.00
59	80	19.9	33.0	0.9	766	0.04	100	31	17.6	35.3	0.5	105	0.01
60	88	69.6	37.5	0.3	734	0.09	101	31	38.6	33.2	0.3	349	0.00
61	82	40.4	33.7	0.8	1079	0.06	102	30	70.4	32.6	0.5	362	0.00
62	80	4.0	28.9	1.1	137	0.02	103	28	87.0	21.7	0.5	291	0.01
63	60	0.3	26.9	1.2	32	0.02	104	25	79.2	48.6	0.7	482	0.00
64	40	0.4	27.1	1.2	15	0.02	106	12.5	7.0	28.4	1.8	17	0.00
65	23	0.9	30.0	1.1	22	0.00	107	14	6.8	35.2	2.1	39	0.00
66	8	88.2	40.9	0.0	63	0.03	108	16	3.0	34.2	1.8	13	0.00
67	11	91.4	41.1	0.0	33	0.01	109	19	1.9	42.3	1.6	21	0.00
68	15	74.2	42.7	0.1	108	0.02	110	22	48.8	48.9	0.8	406	0.00
69	20	0.8	33.3	1.0	41	0.00	115	17	72.8	60.5	0.3	263	0.00
70	25	0.9	30.0	1.0	33	0.00	116	14	34.4	63.8	0.3	154	0.00
71	30	0.5	27.7	1.1	18	0.00	117	12.5	40.6	65.5	0.3	140	0.00
72	40	0.4	29.6	1.2	9	0.02	122	8	80.8	73.0	0.3	172	0.00

Appendix I, continued.

A	B	C	D	E	F	G	A	B	C	D	E	F	G
123	10	57.2	64.3	0.7	218	0.00	191	10.5	58.6	27.8	0.1	215	0.01
124	13	28.4	62.9	1.1	290	0.00	192	12	36.6	39.2	0.3	43	0.05
125	15	7.6	57.4	1.4	176	0.00	193	13.5	69.1	48.0	0.1	113	0.00
126	19	76.4	61.3	0.5	476	0.00	194	52	0.8	26.2	1.3	26	0.02
127	23	95.0	59.1	0.2	317	0.00	195	61	0.4	26.6	1.2	9	0.01
128	23	91.6	57.6	0.2	237	0.00	196	69	0.4	26.5	1.5	23	0.03
129	24	97.4	55.1	0.2	89	0.00	198	74	47.8	32.9	0.6	657	0.06
130	28	73.4	46.8	0.5	275	0.00	199	72	74.4	35.8	0.0	390	0.05
131	30	72.6	39.4	0.5	371	0.00	200	70	87.8	35.3	0.5	590	0.12
132	31	57.6	32.8	0.9	108	0.00	201	72	88.2	33.2	0.3	535	0.09
133	30	72.6	24.7	0.6	449	0.00	202	79	85.6	32.6	0.5	602	0.12
134	32	49.2	33.0	0.8	427	0.00	203	86	78.6	33.5	0.3	466	0.16
135	35	31.2	33.5	0.8	551	0.00	205	90	61.4	37.7	0.5	467	0.14
136	36	31.2	33.3	0.9	223	0.00	206	92	84.2	39.4	0.2	898	0.20
137	38	74.8	23.1	1.0	284	0.00	207	101	74.9	----	----	570	0.23
138	38	60.8	33.7	0.8	559	0.00	208	121	68.8	24.5	0.4	1301	0.25
139	38	68.0	31.2	0.6	823	0.00	209	144	65.0	----	----	6511	0.36
142	27	19.4	35.6	0.6	84	0.00	210	222	0.6	31.3	1.4	121	0.27
147	23	89.7	61.0	0.3	273	0.00	211	198	27.6	51.9	0.7	1514	0.15
157	20	0.2	24.8	----	2	0.00	212	130	49.6	63.7	0.5	4622	0.30
158	15	0.7	25.1	----	9	0.03	214	164	16.5	50.1	0.7	1524	0.25
159	9	1.6	20.4	----	28	0.02	216	188	3.0	35.1	1.3	586	0.29
160	20	0.7	25.9	----	15	0.00	217	247	0.5	29.8	1.2	103	0.24
161	15	2.6	21.5	----	3	0.07	218	220	0.7	31.9	1.3	156	0.24
162	10	14.4	20.1	----	22	0.62	219	180	11.3	40.0	0.9	1619	0.17
163	13	0.7	22.2	----	59	0.00	220	208	0.8	31.1	1.0	179	0.22
164	13	1.8	21.4	----	5	0.00	221	70	0.9	32.2	1.2	20	0.03
165	10	5.1	20.7	----	1	0.14	222	40	0.4	32.7	1.2	5	0.01
166	16.5	1.1	22.0	1.7	5	0.00	223	24	3.6	35.5	1.1	36	0.02
167	23	2.2	29.6	1.8	19	0.00	224	15	21.2	34.3	0.9	77	0.04
168	32	3.5	32.9	1.5	34	0.00	225	9	49.1	36.2	0.4	84	0.05
169	35	7.0	31.5	1.5	83	0.00	226	41	0.4	31.3	1.2	14	0.01
170	40	67.6	25.5	0.7	335	0.00	227	75	0.3	30.4	0.9	18	0.03
171	40	53.3	32.3	0.4	952	0.00	228	50	0.4	30.7	1.2	25	0.01
172	43	84.5	45.7	0.3	803	0.01	229	30	1.9	32.5	1.1	28	0.01
173	40	95.6	40.0	0.1	766	0.00	230	23	6.4	34.3	0.6	109	0.05
174	45	90.6	49.9	0.4	736	0.00	231	16	30.6	35.7	0.5	57	0.12
175	45	95.0	37.4	0.3	758	0.01	232	25	2.7	32.9	1.2	120	0.00
176	50	95.4	34.7	0.2	719	0.01	233	10	80.0	40.6	0.3	118	0.15
177	58	90.8	34.2	0.2	907	0.02	234	17	76.2	40.9	0.2	128	0.03
179	60	74.4	31.7	0.1	217	0.01	235	23	7.3	33.6	0.2	171	0.02
180	53	61.2	37.1	0.5	471	0.01	236	50	0.4	31.0	1.2	12	0.04
181	34	0.5	26.2	1.3	33	0.00	237	75	0.6	29.4	1.4	23	0.03
182	16.5	4.1	27.2	1.2	38	0.02	238	107	0.4	28.1	0.9	55	0.07
183	13	6.6	27.1	1.1	17	0.01	239	130	0.6	28.7	1.1	105	0.15
184	12.5	23.8	31.9	0.8	141	0.01	240	105	0.5	27.9	1.1	58	0.08
185	10	73.3	40.6	0.3	277	0.07	241	95	0.5	28.4	1.1	141	0.08
186	22	0.8	25.9	1.1	11	0.01	242	70	23.2	33.1	1.1	680	0.01
187	42	14.6	28.2	1.1	307	0.01	243a	35	0.7	----	----	15	0.00
188	26	0.7	25.6	1.5	42	0.00	243b	35	92.4	41.0	1.2	612	0.02
189	16.5	1.1	26.2	1.3	25	0.01	245	80	0.3	28.9	1.2	24	0.05
190	13	2.4	26.6	0.7	167	0.00	246	50	0.4	31.0	1.3	6	0.01

Appendix I, continued.

A	B	C	D	E	F	G	A	B	C	D	E	F	G
247	30	0.5	31.6	1.1	16	0.01	314	35	0.4	28.1	1.1	7	0.01
248	16	16.3	28.0	0.9	95	0.12	315	22	1.4	27.2	1.0	28	0.00
249	10	79.0	30.7	0.3	128	0.00	316	22	2.3	27.7	0.9	71	0.00
250	78	0.3	29.8	1.3	15	0.06	317	194	5.6	29.0	0.9	1384	0.27
251	118	0.6	28.2	1.1	125	0.08	318	99	88.8	89.8	0.5	194	0.17
252	123	5.0	32.4	1.1	679	0.21	320	141	70.2	38.8	0.3	1147	0.33
254	120	87.0	79.1	0.2	1786	0.15	321	101	93.2	29.0	0.5	1330	0.18
256	158	88.8	57.0	0.3	5882	0.28	322	91	72.6	35.4	0.5	797	0.16
262	175	46.2	49.0	0.7	2976	0.22	323	84	83.0	35.1	0.3	543	0.21
264	152	30.8	46.6	0.9	3949	0.29	324	88	21.6	34.0	1.0	488	0.10
265	158	4.2	37.2	1.0	608	0.24	325	68	0.4	26.6	1.2	30	0.03
266	138	49.4	55.3	1.0	6530	0.13	326	20	4.3	31.8	0.7	62	0.07
267	107	83.4	59.7	0.7	3066	0.14	327	68	0.5	26.8	1.3	21	0.02
268	145	1.0	34.2	1.3	277	0.11	328	77	7.4	33.3	1.1	204	0.03
269	150	0.5	29.6	1.4	152	0.10	329	71	70.0	39.8	0.3	291	0.03
270	170	1.2	30.6	1.4	269	0.15	330	71	61.6	32.5	0.4	282	0.05
272	843	----	----	----	118	0.01	331	64	94.2	45.5	0.4	919	0.02
273	957	----	----	----	3	2.71	332	68	70.6	37.1	0.3	218	0.04
274	293	----	----	----	58	0.73	333	71	48.6	29.5	0.4	310	0.02
275	819	----	----	----	46	2.03	334	68	44.8	33.8	0.4	275	0.01
276	384	----	----	----	130	0.16	335	26	0.2	25.3	1.2	14	0.00
277	102	----	----	----	51	0.08	336	137	60.8	52.5	0.6	3571	0.14
279	110	2.0	23.0	1.0	99	0.09	337	132	11.6	37.6	1.2	1442	0.20
280	112	5.5	22.2	1.4	46	0.11	338	128	10.8	32.6	1.2	865	0.16
281	302	13.2	27.1	0.8	152	0.14	339	132	20.0	40.8	0.9	2003	0.26
282	744	----	----	----	15	2.77	340	179	64.4	59.2	0.4	4114	0.26
283	875	----	----	----	2	5.88	342	249	10.0	34.4	0.7	1330	0.16
284	699	----	----	----	48	2.23	343	199	3.6	29.5	1.1	257	0.63
285	207	----	----	----	1574	0.33	344	355	16.2	33.3	0.8	1326	0.79
286	99	31.9	32.5	0.8	956	0.16	345	823	----	----	----	4	12.83
287	132	30.8	36.0	0.7	1492	0.19	347	311	1.5	26.8	1.1	137	0.80
288	165	9.8	28.6	1.1	1128	0.42	348	267	6.8	26.5	1.2	466	0.62
289	110	64.4	36.0	0.5	819	0.23	349	547	1.2	28.5	1.6	213	1.47
290	122	15.0	22.3	1.2	336	0.26	350	1216	0.9	32.2	1.1	13	11.06
292	1152	----	----	----	13	5.84	351	141	56.2	44.6	0.6	3892	0.20
293	1198	0.4	31.5	1.1	11	10.96	352	97	0.9	26.0	0.9	79	0.17
295	1161	1.2	31.6	0.8	16	9.76	359	885	----	----	----	777	0.42
296	1063	0.3	30.0	1.0	12	5.82	360	550	1.1	27.0	1.0	93	0.68
299	36	53.6	62.3	1.1	1935	0.00	365	1120	----	----	----	27	6.86
300	69	0.5	19.2	1.5	29	0.04	367	528	----	----	----	18	3.58
301	48	0.6	19.5	1.4	26	0.00	369	868	----	----	----	19	4.30
302	91	0.5	21.7	1.2	30	0.08	370	628	----	----	----	55	2.27
303	66	0.9	20.6	1.2	36	0.02	372	1030	----	----	----	7	7.21
304	48	1.9	20.1	1.2	36	0.00	381	64	----	----	----	18	0.01
305	152	68.2	55.9	0.6	2826	0.18	384	129	----	----	----	45	0.20
306	706	70.6	----	----	271	0.24	394	252	----	----	----	121	0.27
307	896	6.2	31.0	0.8	132	2.29	400	396	----	----	----	162	1.08
310	615	----	----	----	1143	0.28	401	797	----	----	----	43	5.91
311	136	66.8	48.9	0.6	5239	0.13	404	716	----	----	----	85	0.92
312	91	0.6	26.3	1.4	53	0.13	415	696	----	----	----	52	4.05
313	36	0.3	26.1	1.1	15	0.00							

Appendix II. List of (partially informal) taxonomical categories observed in grab-samples and core-tops from the Adriatic Sea.

- Ammodiacus* spp.  
*Glomospira charoidea*  
*Ammolagena* sp. A  
*Hormosira* spp.  
*Proteonina atlantica*  
*Reophax* sp. A  
*Reophax* spp.  
*Nouria polymorphinoides*  
*Adercotryma glomerata*  
*Adercotryma* sp. A  
*Haplophragmoides* sp. A  
*Haplophragmoides* sp. B  
*Haplophragmoides* sp. C  
*Haplophragmoides* spp.  
*Discammina compressa*  
*Trochammina* spp.  
*Ammoscalaria* sp. A  
*Ammoscalaria* spp.  
*Spiroplectammina* spp.  
*Textularia agglutinans*  
*Textularia conica*  
*Textularia sagittula*  
*Textularia trochoidea*  
*Textularia* spp.  
*Bigenerina nodosaria*  
*Siphonotextularia affinis*  
*Siphonotextularia concava*  
*Trochammina macroscoens*  
*Trochammina* spp.  
*Gaudryina flintii*  
*Tritaxia?* spp.  
*Eggerella scabra*  
*Eggerella scabra* forma A (black minerals)  
*Eggerella* sp. A (deep)  
*Eggerella* spp.  
*Pseudoclavulina crustata*  
*Martinotiella* spp.  
 Spec. (agglutinated, sessile) indet.  
 Spec. (agglutinated) indet.  
 Spec. (miliolid, agglutinated externally) indet. A  
 Spec. (miliolid, agglutinated externally) indet. B  
*Cyclogyra* spp.  
*Gordiospira?* spp.  
*Ophthalmidium acutimargo*  
*Ophthalmidium acutimargo concava*  
*Quinqueloculina (Massilina) bicornis*  
*Quinqueloculina (Massilina) secans*  
*Spiroloculina depressa*  
*Spiroloculina excavata*  
*Spiroloculina tenuiseptata*  
*Spiroloculina* spp.  
*Discospirina* spp.  
*Cruciloculina triangularis*  
*Quinqueloculina annectens*  
*Quinqueloculina aspera* forma *aspera*  
*Quinqueloculina aspera* forma *berthelotiana*  
*Quinqueloculina aspera* forma *quadrata*  
*Quinqueloculina aspera* forma *rugosa*  
*Quinqueloculina badenensis*  
*Quinqueloculina costata* forma *berthelotiana*  
*Quinqueloculina costata* forma *costata*  
*Quinqueloculina costata* forma *limbata*  
*Quinqueloculina costata* forma *lucida*  
*Quinqueloculina costata* forma *rugosa*  
*Quinqueloculina* cf. *Q. elegans* (sensu Kruit, 1954)  
*Quinqueloculina seminula*
- Quinqueloculina seminula* forma *longa*  
*Quinqueloculina stalkerii*  
*Quinqueloculina tenuicollis*  
*Quinqueloculina undulata*  
*Quinqueloculina* sp. A (smooth)  
*Quinqueloculina* sp. B (long, slender)  
*Quinqueloculina* spp.  
*Adelosina elegans* forma *brogniartii*  
*Adelosina elegans* forma *elegans*  
*Adelosina elegans* forma *partschii*  
*Adelosina ferrusaci* forma *ferrusaci*  
*Adelosina ferrusaci* forma *polygona*  
*Adelosina longirostra* forma *longirostra*  
*Adelosina longirostra* forma *striata*  
*Adelosina pulchella*  
*Pyrgo depressa*  
*Pyrgo elongata*  
*Pyrgo murrhyna*  
*Pyrgo subsphaerica*  
*Pyrgoella sphaera*  
*Sigmoilina distorta*  
*Sigmoilina grata*  
*Sigmoilina sellii*  
*Sigmoilina tenuis*  
*Sigmoilina* sp. A  
*Miliolinella oblonga*  
*Miliolinella subrotunda*  
*Miliolinella subrotunda* forma *labiosa*  
*Miliolinella* sp. A  
*Miliolinella* spp.  
*Sigmoilepsis schlumbergeri*  
*Triloculina affinis costata*  
*Triloculina gibba angusteoralis*  
*Triloculina triacarinata*  
*Triloculina trigonula*, short, with keel  
*Triloculina trigonula*, short, no keel  
*Triloculina trigonula*, long  
*Triloculina trigonula*, quinqueloculine form  
*Triloculina trigonula*, other morphotypes  
*Triloculina* sp. A (smooth)  
*Triloculina* sp. B (elongate aperture)  
*Triloculina* spp.  
*Biloculinella cryptella*  
*Biloculinella cylindrica*  
*Biloculinella elongata*  
*Biloculinella* cf. *B. globulus*  
*Biloculinella inflata*  
*Biloculinella irregularis*  
*Biloculinella labiata*  
*Biloculinella* spp.  
*Nummoloculina contraria*  
*Scutuloris* sp. A  
*Scutuloris* spp.  
*Articulina tubulosa*  
*Feneroplis* spp.  
 Miliolacea indet.  
*Nodosaria* spp.  
*Amphicoryna scalaris*, megalospheric  
*Amphicoryna scalaris*, microspheric  
*Dentalina* spp.  
*Lagena sulcata*  
*Lagena* sp. A (deep, sacculiform)  
*Lagena* spp.  
*Lenticulina peregrina*  
*Lenticulina* spp.  
*Margulinula* spp.



Appendix II, continued.

- Globulina myristiformis*  
*Glandulina rotundata*  
 Polymorphinidae/Glandulinidae spp.  
*Fissurina annectens* forma *pseudostaphyllearia*  
*Fissurina apiculata*  
*Fissurina kerguelensis*  
*Fissurina orbignyana*  
*Fissurina* spp.  
*Oolina hexagona*  
*Oolina squamosa*  
*Oolina* spp.  
*Buliminella* spp.  
*Sphaeroidina bulloides*  
*Bolivinita quadrilatera*  
*Bolivina aenariensis*  
*Bolivina alata*  
*Bolivina albatrossi*  
*Bolivina dilatata*  
*Bolivina pseudoplicata*  
*Bolivina spathulata*  
*Bolivina spathulata* forma *dilatatissima*  
*Bolivina striatula*  
*Bolivina* spp.  
*Cassidulionides* spp.  
*Bulimina costata* forma *costata*  
*Bulimina costata* forma *inflata*  
*Bulimina marginata* forma *aculeata*  
*Bulimina marginata* forma *aculeata*, *gibba*-type  
*Bulimina marginata* forma *denudata*  
*Bulimina marginata* forma *marginata*  
*Bulimina marginata*, shallow (*elongata*-)type  
*Bulimina marginata*, other morphotypes  
*Bulimina* spp.  
*Globobulimina pyrula*  
*Globobulimina* sp. A  
*Stilostomella* spp.  
*Stainforthia concava*  
*Stainforthia fusiformis*  
*Stainforthia* spp.  
*Reussella spinulosa*  
*Reussella* spp.  
*Uvigerina mediterranea*  
*Uvigerina peregrina*  
*Uvigerina phlegeri*  
*Uvigerina* spp.  
*Trifarina angulosa*  
*Trifarina angulosa* forma *pauperata*  
*Trifarina* spp.  
*Buccella granulata*  
*Epistominella* spp.  
*Gavelinopsis praegeri*  
*Neoconorbina terquemi*  
*Neoconorbina* sp. A  
*Neoconorbina* spp.  
*Planorbisorbis rarescens*  
*Rosalina bradyi*  
*Rosalina* cf. *R. columbiensis*  
*Rosalina* cf. *R. globularis*  
*Rosalina* sp. A (deep)  
*Rosalina* spp.  
*Rotamorphina involuta*  
*Valvulineria bradyana*  
*Valvulineria* spp.  
*Glabratella* spp.  
*Siphonina reticulata*  
*Asterigerinata adriatica*  
*Asterigerinata mamilla*  
*Pseudopionides falsobeccarii*  
*Spirillina vivipara*
- Ammonia beccarii* forma *bassleri*  
*Ammonia beccarii* forma *beccarii*  
*Ammonia beccarii* forma *inflata*  
*Ammonia parkinsoniana* forma *parkinsoniana* (mt. 1)  
*Ammonia parkinsoniana* forma *tepida*, morphotype 2  
*Ammonia parkinsoniana* forma *tepida*, morphotype 3  
*Ammonia parkinsoniana* forma *tepida*, morphotype 4  
*Ammonia parkinsoniana* forma *tepida*, morphotype 5  
*Ammonia perlucida*  
*Ammonia* spp.  
*Elphidium advenum*  
*Elphidium* cf. *E. clavatum*  
*Elphidium crispum* forma *aculeata*  
*Elphidium crispum* forma *crispum*  
*Elphidium crispum* forma *macellum*  
*Elphidium crispum* forma A  
*Elphidium* cf. *excavatum*  
*Elphidium fichtelianum*  
*Elphidium granosum* forma *granosum*  
*Elphidium granosum* forma *lidoense*  
*Elphidium margaritaceum*  
*Elphidium poeyanum* forma *decepiens*  
*Elphidium poeyanum* forma *poeyanum*  
*Elphidium* cf. *pulverum*  
*Elphidium* spp.  
*Parallina verruculata*  
*Eponides repandus*  
*Eponides* sp. A  
*Hyalinea balthica*  
*Planulina ariminensis*  
*Planulina* spp.  
*Cibicides lobatulus*, flat type  
*Cibicides lobatulus*, *refugens*-type  
*Cibicides pachydermus*  
*Cibicides uellerstorfi*  
*Cibicides* spp. (*ungerianus*-group)  
*Planorbulina mediterraneensis*  
*Gypsina* spp.  
*Hemigypsina* spp.  
*Cassidulina crassa*  
*Cassidulina crassa rossensis*  
*Cassidulina laevigata* forma *carinata*  
*Cassidulina laevigata* forma *laevigata*  
*Cassidulina oblonga*  
*Cassidulina subglobosa*  
*Chilostomella cziaeki*  
*Astronotium* sp. A  
*Astronotium* spp.  
*Nonion barleeanum*  
*Nonion boueanaum*  
*Nonion depressulum*  
*Nonion* sp. A  
*Nonion* spp.  
*Nonionella turgida*  
*Nonionella* spp.  
*Pullentia quinqueloba*  
*Pullentia* spp.  
*Gyroldina altiformis*  
*Gyroldina orbicularis*  
*Gyroldina umbonata*  
*Gyroldina* spp.  
*Oridorsalis* spp.  
*Hanzawaia boueana*  
*Hanzawaia* spp.  
*Paromalina coronata*  
*Hoeglundina elegans*  
*Stomatorbina concentrica*  
*Robertinoidea* spp.  
*Spec. indet.*

Appendix III. List of relative frequencies (percentages) of the most common taxa of benthic foraminifera in the grab-samples and core-tops.

first column: sample number  
 next columns: relative frequencies per taxon (percentages)  
 numbers in heading indicate:

- 1 -- *Textularia agglutinans*
- 2 -- *Textularia sagittula*
- 3 -- *Bigenerina nodosaria*
- 4 -- *Pseudoclavulina erustata*
- 5 -- *Quinqueloculina aspera/costata* group
- 6 -- *Quinqueloculina badenensis*
- 7 -- *Quinqueloculina seminula*
- 8 -- *Adelosina* group
- 9 -- *Sigmoilopsis schlumbergeri*
- 10 -- *Triloculina trigonula*
- 11 -- *Miliolinella* spp.
- 12 -- *Biloculinella irregularis*
- 13 -- *Amphicooryna scalaris*
- 14 -- *Lenticulina* spp.
- 15 -- *Sphaeroidina bulloides*
- 16 -- *Bolivina spathulata*
- 17 -- *Bulimina costata* group
- 18 -- *Bulimina marginata* group
- 19 -- *Reussella spinulosa*
- 20 -- *Uvigerina mediterranea*
- 21 -- *Uvigerina peregrina*
- 22 -- *Trifarina angulosa*
- 23 -- *Buccella granulata*
- 24 -- *Gavelinopsis praegeri*
- 25 -- *Neocoronbina terquemii*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	0.4	0.0	0.0	0.0	0.4	0.0	0.8	1.6	0.0	0.4	0.0	0.0	0.0	0.0	1.6	0.4	4.3	0.0	0.0	1.6	0.0	0.8	0.0	0.0	
2	0.0	0.8	0.4	0.0	1.2	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	1.6	0.8	5.1	0.4	0.0	1.2	0.0	0.0	0.4	0.4
5	2.6	0.0	0.0	0.0	0.0	0.0	2.2	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	20.4	0.0	0.0	0.0	0.0	0.0	0.4	0.0
6	2.4	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.5	0.0	0.0	0.0	0.5	0.0	0.5	0.0	23.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
7	0.4	0.0	0.0	0.0	0.0	0.0	1.1	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	12.2	0.0	0.0	0.0	0.0	1.1	0.0	0.0
8	3.5	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.8	0.0	0.0	0.0	1.2	0.0	1.2	0.0	0.0
12	9.3	0.4	2.2	0.0	0.0	0.4	0.7	1.9	1.9	2.2	0.0	0.4	3.4	0.0	0.0	0.4	0.0	11.6	1.1	0.0	0.0	0.0	0.0	0.4	0.0
13	8.7	1.3	3.9	1.0	0.0	1.0	1.6	1.0	1.0	0.3	0.6	1.9	0.0	0.0	0.0	3.5	0.0	16.7	2.6	8.0	1.9	1.0	0.0	1.0	0.0
15	5.1	5.1	6.1	1.6	0.0	0.6	0.6	0.3	2.6	0.0	1.0	0.6	0.0	0.0	2.9	0.0	0.6	8.4	0.0	15.7	3.8	7.4	0.0	1.0	0.0
24	1.2	0.0	1.4	0.9	0.0	0.3	2.9	0.0	3.2	0.0	0.3	0.6	0.0	0.3	0.6	1.4	0.0	4.9	0.0	21.0	0.6	10.1	0.0	0.0	0.0
30	7.1	1.9	10.2	0.4	0.0	1.9	1.9	0.4	1.5	0.4	0.4	0.0	1.9	0.0	0.4	3.8	0.0	12.8	1.5	11.3	0.0	0.4	0.0	0.8	0.0
31	5.8	3.1	6.2	1.2	0.0	1.2	3.1	0.0	2.3	0.0	0.4	0.4	0.4	0.4	0.0	4.2	0.0	16.5	0.8	23.8	0.0	2.3	0.0	0.4	0.0
32	2.8	1.2	3.6	1.6	0.0	0.8	3.6	0.4	1.2	0.0	1.2	0.8	0.4	0.4	2.0	0.8	0.0	8.4	0.4	28.4	0.8	6.4	0.0	0.0	0.0
33	2.0	0.0	1.2	3.2	0.0	0.8	4.0	0.0	2.4	0.0	1.2	0.8	0.0	0.8	0.8	2.8	0.0	4.5	0.0	26.3	0.4	13.8	0.0	0.0	0.0
34	0.4	0.0	0.0	0.8	0.0	0.8	3.4	0.0	0.8	0.0	0.8	0.8	0.4	0.4	0.0	1.9	0.0	6.4	0.0	24.9	1.1	7.5	0.0	0.0	0.0
35	0.0	0.0	2.6	0.7	0.0	1.1	7.9	0.0	2.6	0.0	0.4	0.0	0.0	0.0	0.0	0.4	0.0	4.9	0.0	26.2	0.7	12.0	0.0	0.0	0.0
36	0.9	0.0	0.3	0.3	0.0	0.3	4.1	0.0	1.5	0.0	0.0	0.3	0.0	0.3	0.0	0.3	0.0	4.4	0.0	25.9	0.9	6.4	0.0	0.3	0.0
50	5.3	0.0	0.0	0.0	0.0	0.8	4.5	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	18.6	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
51	6.5	0.0	0.0	0.0	0.0	1.0	3.0	0.3	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	19.6	0.8	0.0	0.3	0.0	0.0	0.0	0.0
52	10.7	0.4	3.7	0.0	0.0	0.7	3.0	0.4	3.0	0.4	0.0	0.0	0.7	0.0	0.0	0.7	0.0	20.3	2.2	0.0	0.0	0.0	0.0	0.7	0.0
53	10.3	0.0	3.8	0.0	0.0	0.8	4.2	1.5	3.0	0.0	0.0	0.0	1.1	0.0	0.0	0.4	0.0	19.0	0.8	1.5	0.0	0.0	0.0	0.4	0.0
54	11.7	0.7	1.7	0.0	0.0	2.7	2.3	2.7	2.7	2.7	0.0	0.0	2.3	0.0	0.0	0.0	0.0	18.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0
55	16.3	0.0	0.0	0.0	0.0	0.4	1.2	0.0	3.1	0.8	0.0	0.0	0.4	0.4	0.0	0.4	0.0	19.4	1.6	0.4	0.0	0.0	0.0	0.0	0.0
56	8.4	0.0	0.0	0.0	0.0	1.1	4.4	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	30.5	0.7	0.0	0.0	0.0	0.0	0.0	0.0
57	1.7	0.0	0.0	0.0	0.3	0.0	0.7	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.0	1.0	0.0	0.0	0.0	0.0	0.7	0.0
58	1.0	0.3	0.0	0.0	1.7	0.0	1.0	4.5	0.0	2.4	0.0	0.0	0.3	0.0	0.0	1.7	1.0	3.1	0.0	0.0	3.4	0.3	0.7	0.0	0.0
59	16.0	1.1	4.8	0.0	0.4	1.1	0.0	0.7	1.1	0.0	1.1	0.0	0.0	0.0	0.0	1.1	0.0	20.1	5.2	1.1	0.0	0.0	5.2	0.7	0.0
60	7.5	7.7	5.3	0.0	0.2	0.5	1.7	0.6	1.7	0.9	0.9	0.7	0.0	0.0	0.0	1.0	0.0	13.2	4.1	2.7	0.0	0.0	3.9	2.2	0.5
61	13.4	3.0	4.4	0.0	0.3	1.0	2.0	1.7	2.0	0.3	3.4	0.0	0.0	0.0	0.0	0.3	0.0	18.1	4.4	0.7	0.0	0.0	3.4	0.7	0.0
62	10.3	1.6	4.4	0.0	0.0	2.8	2.0	0.8	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.9	4.0	0.8	0.4	0.4	1.6	0.8	0.0	
63	16.0	0.0	0.5	0.0	0.5	2.8	1.4	0.5	1.4	2.3	0.0	0.0	0.5	0.5	0.0	0.0	16.4	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
64	12.7	0.0	0.0	0.0	0.0	1.0	5.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	32.2	4.4	0.0	0.0	0.0	1.0	0.0	0.0	
65	1.3	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.7	1.3	0.0	0.0	0.0	0.5	0.0	0.0	
66	0.3	0.0	0.0	0.0	2.6	0.0	1.3	3.0	0.3	1.3	0.0	0.0	0.0	0.3	0.0	5.3	1.3	9.6	0.3	0.0	3.0	0.0	1.3	0.0	0.0
67	0.7	0.0	0.0	0.0	1.1	0.0	1.1	7.1	0.0	3.0	0.0	0.0	0.0	0.0	0.0	4.1	0.7	4.1	0.0	0.0	1.9	0.4	1.9	0.0	0.0
68	2.6	0.0	0.0	0.0	0.8	0.0	2.3	4.5	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.8	0.0	3.0	0.0	0.0	0.0
69	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8	0.0	0.0	0.0	0.0	2.3	0.0	0.0
70	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.8	2.4	0.0	0.0	0.0	0.0	0.0	0.0
71	4.2	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.7	0.8	0.0	0.0	0.0	0.0	0.0	0.0
72	13.2	0.0	0.0	0.0	0.0	0.9	6.0	0.0	1.3	1.3	0.0	0.0	0.0	0.4	0.0	0.0	0.0	23.5	0.4	0.0	0.0	0.0	0.0	0.0	0.0
73	12.9	0.0	0.0	0.0	0.0	1.2	1.6	1.2	1.2	0.8	0.0	0.0	0.8	0.0	0.0	0.0	0.0	16.9	1.2	0.0	0.0	0.0	0.0	0.4	0.0
74	0.0	0.4	0.0	0.0	0.0	0.0	0.0	1.6	0.4	0.4	0.0	0.0	0.0	0.0	0.8	3.9	0.0	6.6	0.0	0.0	2.7	0.0	1.2	0.0	0.0

Appendix III, continued.

first column: sample number  
 next columns: relative frequencies per taxon (percentages)  
 numbers in heading indicate:

- 26 -- *Rosalina bradyi*
- 27 -- *Valvulineria bradyana*
- 28 -- *Asterigerinata mamilla*
- 29 -- *Ammonia beccarii*
- 30 -- *Pseudoeponides falsobeccarii*
- 31 -- *Ammonia parkinsoniana*
- 32 -- *Ammonia perlucida*
- 33 -- *Elphidium advenum*
- 34 -- *Elphidium crispum* group
- 35 -- *Elphidium granosum* group
- 36 -- *Elphidium poeyanum* group
- 37 -- *Hyalinea balthica*
- 38 -- *Planulina arminensis*
- 39 -- *Cibicides lobatulus*
- 40 -- *Cibicides pachydermus*
- 41 -- *Cassidulina crassa*
- 42 -- *Cassidulina laevigata* group
- 43 -- *Cassidulina oblonga*
- 44 -- *Nonion barleeaanum*
- 45 -- *Nonion depressulum*
- 46 -- *Nonionella turgida*
- 47 -- *Gyroldina altiformis*
- 48 -- *Gyroldina orbicularis*
- 49 -- *Hanzawata boueana*
- 50 -- *Hoeglundina elegans*

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
1	0.0	0.0	0.0	1.6	0.4	39.0	12.2	1.2	4.3	4.7	9.8	0.0	0.4	0.0	0.0	0.0	4.3	0.0	0.4	0.4	0.0	0.4	0.0	0.0	0.0
2	0.0	1.6	0.0	2.8	1.2	35.1	4.7	0.0	0.4	7.5	3.6	0.0	0.0	0.0	0.0	0.0	11.8	1.2	0.4	0.0	0.0	0.0	0.0	0.8	0.0
5	2.2	32.3	0.0	1.5	1.1	2.2	0.0	0.7	0.0	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.5	27.1	0.0	0.0
6	0.0	14.2	0.0	1.4	2.8	5.7	0.0	2.8	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	37.9	0.0	0.0	0.0
7	0.4	1.1	0.0	9.1	0.0	15.6	9.9	6.5	0.8	12.2	4.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	19.4	0.0	0.0	0.0
8	0.0	0.0	0.0	3.1	0.0	35.0	9.2	1.5	1.2	18.1	7.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.1	10.0	0.0	0.0	0.0
12	0.0	22.4	0.0	1.5	0.7	0.0	0.0	0.0	1.1	4.9	2.6	0.0	0.0	1.5	0.0	0.0	4.5	8.6	6.3	0.0	4.1	0.0	0.0	1.1	0.0
13	0.6	4.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2	2.6	1.9	0.0	4.2	0.6	0.0	4.8	3.9	7.4	0.0	0.6	0.0	0.0	0.6	0.0
15	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	2.6	1.6	0.6	7.7	1.9	2.6	2.2	2.2	1.9	0.0	0.0	1.9	0.3	1.3	2.9
24	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	3.7	3.2	11.2	0.0	15.0	1.2	1.4	0.0	0.0	0.0	1.7	2.3	0.0
30	0.8	7.9	0.0	0.0	0.0	0.0	0.0	0.4	1.5	0.8	0.0	0.0	3.4	1.5	0.0	0.0	4.5	4.9	7.9	0.0	0.0	0.0	0.4	0.4	0.0
31	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.4	1.5	0.4	2.7	0.4	0.0	2.7	3.1	4.2	0.0	0.0	0.4	1.2	0.8	0.0
32	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	2.4	2.4	1.2	5.2	0.0	10.4	2.0	1.6	0.0	0.0	0.0	3.6	0.0	1.6
33	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	1.6	0.8	8.9	0.4	7.7	1.6	1.6	0.0	0.0	1.6	0.4	0.0	2.8	0.0
34	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	5.3	0.8	12.1	0.0	17.4	3.4	0.8	0.0	0.0	1.9	1.9	0.0	2.6	0.0
35	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	2.6	0.0	1.9	2.6	0.0	9.4	10.1	1.9	0.7	0.0	0.0	0.7	1.5	0.0
36	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	3.2	0.0	11.7	0.0	14.6	3.2	3.8	0.0	0.0	1.2	2.9	0.0	7.0
50	0.0	28.3	0.0	4.0	2.0	3.2	2.0	0.8	0.0	9.3	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	16.2	0.0	0.0	0.0	0.0
51	0.0	26.9	0.0	3.4	2.6	0.5	1.6	1.0	0.0	8.6	6.8	0.0	0.0	0.3	0.0	0.0	0.5	0.5	2.1	0.0	13.8	0.0	0.0	0.0	0.0
52	0.0	12.6	0.0	0.8	2.2	0.0	0.4	0.0	0.7	5.2	3.7	0.0	0.0	2.6	0.0	0.0	1.1	10.4	8.1	0.0	1.5	0.0	0.0	0.0	0.0
53	0.4	12.2	0.0	1.1	1.9	0.0	0.0	0.0	0.4	3.4	5.3	0.0	0.0	0.8	0.0	0.0	0.0	15.6	7.6	0.0	1.5	0.0	0.0	0.0	0.0
54	0.0	10.7	0.0	2.0	3.0	0.0	0.0	0.0	0.0	3.3	7.0	0.0	0.0	2.3	0.0	0.0	0.0	7.0	6.3	0.0	5.0	0.0	0.0	0.0	0.0
55	0.0	16.7	0.0	3.5	8.5	0.0	0.4	0.0	0.0	1.9	7.0	0.0	0.0	0.4	0.0	0.0	0.8	6.2	6.6	0.0	2.7	0.0	0.0	0.0	0.0
56	0.0	18.9	0.0	4.4	4.4	0.8	0.4	0.7	0.0	6.2	9.8	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	6.5	0.0	0.0	0.0	0.0	0.0
57	0.0	0.0	0.0	9.0	0.0	22.1	19.0	0.7	1.0	19.7	11.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	1.0	0.0	0.0	0.0	0.0
58	0.0	1.0	0.0	5.5	1.4	25.1	2.7	1.4	1.7	4.5	5.2	0.0	0.3	2.1	0.0	0.0	11.0	0.7	1.4	0.0	0.0	0.0	0.0	0.3	0.0
59	0.7	0.0	0.0	0.0	0.7	0.0	0.0	1.1	4.1	10.4	8.2	0.4	0.0	1.9	0.0	0.0	4.1	4.5	1.1	0.0	0.0	0.0	0.4	0.4	0.0
60	1.7	0.0	0.2	1.0	0.5	0.2	0.0	1.4	2.7	4.3	3.1	0.2	0.0	4.8	0.0	0.2	7.2	7.0	0.5	0.0	0.0	0.0	1.4	0.0	0.0
61	1.0	0.0	0.0	0.0	0.3	0.0	0.0	0.3	3.7	6.4	6.0	0.7	0.0	5.0	0.0	0.0	4.0	6.7	1.7	0.0	0.3	0.0	0.0	0.7	0.0
62	0.8	0.0	0.0	0.0	0.4	0.8	0.4	0.4	2.4	7.1	15.5	0.0	0.0	2.8	0.0	0.0	2.4	8.3	3.2	0.0	1.2	0.0	0.0	0.0	0.0
63	0.0	10.3	0.0	3.3	5.2	0.0	0.0	0.0	0.5	0.5	15.5	0.0	0.0	2.3	0.0	0.0	0.5	9.4	5.6	0.0	0.0	0.0	0.0	0.0	0.0
64	0.0	6.8	0.0	4.9	6.8	2.0	0.5	0.5	4.4	8.3	5.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	2.4	0.0	0.0	0.0	0.0
65	0.0	0.0	0.0	11.7	0.3	20.5	24.2	1.6	1.1	15.7	7.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.5	2.9	0.0	0.0	0.0	0.0
66	0.0	2.0	0.3	6.3	3.0	11.9	3.3	1.0	2.0	4.3	4.6	0.0	0.3	3.0	0.0	0.0	11.9	0.0	1.7	0.0	0.0	0.0	0.3	0.0	0.0
67	0.0	0.4	0.0	2.2	1.5	32.2	4.1	0.0	1.9	7.9	3.0	0.4	0.4	0.4	0.0	0.0	10.1	0.4	1.5	0.0	0.0	0.0	0.0	0.0	0.0
68	0.0	0.0	0.0	5.3	0.0	38.9	4.9	1.5	11.7	10.9	6.4	0.0	0.0	0.4	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
69	0.0	0.0	0.0	8.4	0.0	20.7	17.6	0.4	3.4	21.5	12.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2	1.9	0.0	0.0	0.0	0.0
70	0.0	0.3	0.0	6.2	0.3	15.8	17.5	4.8	0.0	17.1	10.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.9	0.0	0.0	0.0	0.0
71	0.0	1.5	0.0	5.7	6.1	19.3	5.7	3.4	0.0	11.7	6.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	12.1	0.0	0.0	0.0	0.0	0.0
72	0.4	14.1	0.0	8.5	7.3	0.4	1.3	0.9	0.0	11.1	3.8	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	3.4	0.0	0.0	0.0	0.0	0.0
73	0.0	14.9	0.0	4.3	3.1	0.0	1.2	0.8	0.0	2.7	10.2	0.0	0.0	0.4	0.0	0.0	0.0	3.1	6.3	0.0	10.6	0.0	0.0	0.0	0.0
74	0.0	2.7	0.0	2.3	1.9	18.3	0.4	1.2	0.0	4.7	3.5	0.0	1.6	1.2	0.0	0.0	15.2	0.4	1.6	0.8	0.4	0.0	1.2	0.0	0.0



Appendix III, continued.

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
75	0.0	0.4	0.0	2.0	0.8	35.9	4.8	0.4	4.0	6.9	4.8	0.0	0.0	0.4	0.0	0.0	7.7	0.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0
76	0.0	0.0	0.0	5.9	0.4	57.0	1.6	0.0	7.8	8.2	0.8	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
77	0.0	0.0	0.0	4.8	0.0	21.6	23.8	1.1	8.1	19.8	8.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	3.3	0.0	0.0	0.0	0.0
78	0.0	0.0	0.0	19.8	0.0	23.3	2.5	3.5	7.9	9.9	7.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.5	0.0	0.0	0.0	0.0
79	0.0	0.0	0.0	3.4	0.0	36.9	3.0	2.1	5.2	10.7	8.2	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
80	0.0	0.0	0.0	4.5	0.0	24.3	16.0	1.1	6.0	11.9	13.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	1.5	0.0	0.0	0.0	0.0
81	0.0	0.0	0.0	7.3	0.0	27.2	7.3	5.0	5.0	12.3	8.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	5.3	0.0	0.0	0.0	0.0
82	0.0	0.0	0.0	13.4	0.0	26.2	6.4	2.0	8.4	13.4	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	3.7	0.0	0.0	0.0	0.0
83	0.0	0.0	0.0	3.7	0.4	44.5	5.9	0.0	1.8	4.4	4.4	0.0	0.0	1.5	0.0	0.0	1.5	0.0	0.4	0.7	1.5	0.0	0.0	0.0	0.0
84	0.0	0.0	0.0	13.1	0.0	19.7	4.5	1.6	5.7	15.2	10.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	2.5	0.0	0.0	0.0	0.0
85	0.0	0.0	0.0	9.8	0.0	22.2	12.4	3.8	3.0	8.1	9.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8	6.8	0.0	0.0	0.0	0.0
86	0.0	0.0	0.0	0.8	0.0	21.3	9.5	3.8	1.9	9.1	13.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4	10.3	0.0	0.0	0.0	0.0
87	0.0	0.0	0.0	4.2	0.0	13.7	11.0	5.3	3.8	18.6	13.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	3.4	0.0	0.0	0.0
88	0.0	0.0	0.0	6.4	0.0	22.2	8.1	3.4	5.1	20.9	9.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.4	0.0	0.0	0.0	0.0
89	0.0	6.6	0.0	3.0	6.6	4.2	10.8	0.6	0.6	6.0	7.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.8	5.4	0.0	0.0	0.0	0.0
90	0.0	0.0	8.8	5.4	1.9	1.1	0.0	1.1	5.0	5.7	1.5	0.0	0.0	15.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0
92	0.0	0.0	0.0	5.6	0.0	56.2	11.2	0.8	5.6	5.2	8.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0
93	0.0	0.0	0.0	7.1	0.0	43.4	15.4	0.4	2.0	13.0	10.6	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.4	0.4	0.0	0.0	0.0	0.0
94	0.0	0.0	0.0	1.3	0.0	25.8	9.2	2.5	0.0	14.6	8.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	10.0	0.0	0.0	0.0	0.0
95	0.0	0.0	0.0	5.8	6.2	8.9	2.3	7.3	1.2	2.7	12.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.6	0.0	0.0	0.0	0.0
96	0.0	0.0	0.4	6.4	7.2	6.4	0.4	0.4	6.0	7.2	11.2	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.8	0.8	0.0
97	0.4	0.0	2.0	5.5	5.1	5.5	0.8	0.4	2.0	7.8	4.7	0.0	0.0	4.7	0.0	0.0	0.0	0.0	0.0	0.4	2.3	0.0	0.0	1.6	0.0
98	0.0	0.0	9.7	4.3	1.6	2.7	0.0	1.2	0.8	10.5	3.1	0.0	0.0	5.8	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	3.1	0.0
99	0.0	1.1	0.7	8.8	8.0	2.6	0.4	0.4	4.0	3.3	10.6	0.0	0.0	2.6	0.0	0.0	0.0	0.0	0.0	0.0	3.6	0.0	0.7	0.7	0.0
100	1.1	0.0	5.3	11.4	5.3	3.8	0.0	2.3	2.7	9.1	8.3	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.4	0.4	0.0
101	0.4	0.0	6.7	10.7	5.2	11.1	0.0	2.6	1.9	9.6	5.6	0.0	0.0	4.8	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.7	0.0	0.4	0.0
102	1.0	0.0	5.9	5.6	5.2	8.0	0.0	3.5	4.8	16.0	5.2	0.0	0.0	4.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0
103	1.1	0.0	9.9	8.8	0.7	3.6	0.0	3.2	1.7	8.8	6.0	0.0	0.0	3.9	0.0	0.0	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0
104	7.2	0.0	4.3	5.7	0.0	2.2	0.0	3.0	1.8	9.3	1.8	0.0	0.0	4.3	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.4	0.4	0.0
106	0.0	0.0	0.0	5.3	0.0	77.1	3.7	0.0	0.4	0.4	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
107	0.0	0.0	0.0	5.6	0.0	82.4	1.7	0.7	0.0	0.3	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0
108	0.0	0.0	0.0	9.9	0.0	67.7	0.4	1.8	0.0	0.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.0	0.0	0.0	0.0
109	0.4	0.0	0.0	7.9	0.0	20.0	8.3	6.0	0.8	2.6	4.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8	5.7	0.0	0.0	0.0	0.0
110	4.2	0.0	2.3	4.2	0.0	4.9	0.8	3.0	2.3	8.0	6.8	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.4	0.8	0.0	0.0	0.4	0.0
115	3.4	0.0	0.8	1.9	0.0	7.3	1.5	5.7	2.7	8.8	8.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
116	1.3	0.0	0.0	3.2	0.0	17.3	4.5	3.2	3.8	6.7	8.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.3	0.0	0.0	0.0	0.0
117	0.0	0.0	0.0	4.8	0.4	13.2	4.4	1.2	6.0	7.6	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
122	0.0	0.0	0.4	9.0	0.0	18.0	5.6	0.9	3.4	12.9	9.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
123	1.2	0.0	0.0	1.6	0.0	23.1	8.9	1.2	2.0	16.2	10.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0
124	0.8	0.0	0.4	4.3	0.0	19.6	3.1	0.8	2.7	7.6	12.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0
125	1.8	0.0	0.4	1.8	0.0	20.4	6.5	3.3	3.3	11.3	17.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.1	0.0	0.0	0.0	0.0
126	2.6	0.0	1.1	8.6	0.0	7.9	0.0	5.2	3.1	10.1	7.5	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
127	3.0	0.0	2.6	14.3	0.0	0.4	0.0	6.0	4.8	12.4	1.5	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
128	6.6	0.0	6.6	9.8	0.0	1.2	0.0	7.8	2.9	5.7	1.2	0.0	0.0	4.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
129	4.7	0.0	3.1	9.8	0.0	2.0	0.0	4.7	2.4	5.9	0.4	0.0	0.0	5.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.8	0.0
130	2.6	0.0	8.6	9.4	0.6	2.9	0.0	5.7	8.6	12.5	3.7	0.0	0.0	6.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
131	1.2	0.0	9.6	16.2	2.3	7.3	0.0	3.8	8.0	9.2	5.8	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0
132	1.1	0.0	6.0	11.2	0.7	5.6	0.0	5.2	6.7	8.2	5.6	0.0	0.0	8.6	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	2.6	0.0	0.0
133	0.7	0.0	11.1	9.3	1.7	9.3	0.0	5.2	4.2	14.9	4.8	0.0	0.0	6.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.7	0.0
134	2.2	0.0	11.7	13.2	4.4	9.2	0.0	0.7	4.8	15.0	6.2	0.0	0.0	5.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.0	0.0
135	0.7	0.0	8.9	4.3	3.2	10.7	0.0	1.4	2.9	11.4	8.3	0.0	0.0	10.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0
136	0.0	0.0	7.1	3.8	5.6	20.3	0.0	1.5	4.1	9.0	6.4	0.0	0.0	8.6	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.8	0.0
137	1.1	0.0	10.3	6.6	1.5	3.0	0.0	0.4	4.1	10.7	4.0	0.0	0.0	9.6	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	2.2	0.0	0.0
138	0.7	0.0	15.4	4.5	1.5	1.5	0.0	1.5	5.6	5.2	3.0	0.0	0.0	9.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.6	0.0	0.0
139	0.4	0.0	7.5	5.7	2.2	2.5	0.0	1.4	2.2	11.1	4.0	0.0	0.0	8.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6	0.0	0.0
142	2.3	0.0	5.0	14.9	5.0	5.3	0.0	3.8	3.8	7.3	3.8	0.0	0.0	3.1	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.4	0.0	0.0
147	6.1	0.0	3.7	6.4	0.3	0.7	0.0	7.5	2.4	7.8</															

Appendix III, continued.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
182	4.5	0.0	0.0	0.0	0.3	0.0	1.4	0.8	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.6	1.4	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0
183	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.5
184	1.7	0.0	0.0	0.0	0.7	0.0	3.4	0.0	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0
185	4.7	0.0	0.0	0.0	0.0	0.0	2.4	2.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	2.4	0.0	0.0	0.0
186	0.0	0.0	0.0	0.0	0.0	0.0	4.1	0.4	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	4.9	1.2	0.0	0.0	0.0	2.4	0.0	0.0	0.0
187	16.2	0.0	0.0	0.0	0.4	0.0	2.3	0.4	3.5	1.2	0.0	0.0	0.0	0.0	0.0	0.0	15.8	5.0	0.0	0.0	0.0	3.5	1.5	1.2	1.2
188	4.4	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	24.3	0.0	0.0	0.0	0.0	2.6	0.0	0.0	0.0
189	7.1	0.0	0.0	0.0	0.5	0.0	0.5	1.5	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
190	4.5	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0
191	1.6	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
192	2.4	0.0	0.0	0.0	0.4	0.0	3.1	2.0	0.0	5.1	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	6.2	4.5	0.7	0.0	0.0	0.0	0.0
193	2.0	0.0	0.0	0.0	0.4	0.0	5.1	1.6	0.0	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
194	12.4	0.0	0.0	0.0	0.0	0.7	4.6	0.0	1.4	0.0	0.0	0.0	0.4	0.0	0.0	0.0	24.7	1.4	0.0	0.0	0.0	0.7	0.4	0.0	0.0
195	11.4	0.0	0.0	0.0	0.0	2.5	6.8	0.4	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	38.4	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
196	14.0	0.0	1.1	0.0	0.0	3.0	5.5	0.7	7.4	0.0	0.0	1.1	0.0	0.0	0.0	0.0	32.1	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
198	13.2	2.1	2.1	0.0	0.3	1.0	2.4	0.3	1.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	19.9	5.9	0.0	0.0	0.0	4.5	0.3	0.7	0.7
199	10.1	6.0	1.5	0.0	3.0	0.4	0.7	0.4	1.9	1.4	0.0	0.4	0.0	0.0	0.0	0.4	17.5	5.6	0.0	0.0	0.0	6.0	1.9	0.0	0.0
200	10.3	8.0	0.8	0.0	4.2	0.0	0.0	1.9	0.0	3.1	0.8	0.4	0.0	0.4	0.0	0.0	8.8	5.0	0.0	0.0	0.0	5.0	1.1	0.8	0.8
201	7.1	9.9	0.7	0.0	4.3	0.0	2.5	0.7	0.0	1.4	0.4	0.4	0.7	0.0	0.0	0.4	11.0	5.0	0.0	0.0	0.0	5.3	1.4	1.4	1.4
202	6.6	12.1	2.0	0.0	3.2	0.4	2.0	0.0	0.4	2.8	0.4	0.4	0.4	0.4	0.0	0.0	5.5	3.5	0.0	0.0	0.0	5.5	0.8	1.6	1.6
203	8.4	9.5	2.1	0.0	1.1	0.4	1.4	0.4	0.4	0.4	0.0	0.4	0.0	0.4	0.0	0.7	10.9	5.6	0.0	0.0	0.0	3.9	3.2	0.4	0.4
205	4.6	6.2	2.7	0.0	0.8	0.4	0.0	1.2	1.5	0.8	0.4	0.0	0.0	0.4	0.0	0.0	11.9	5.8	0.8	0.0	0.0	3.1	1.9	0.0	0.0
206	5.6	13.9	2.8	0.0	2.0	0.0	1.0	0.3	0.7	0.7	1.0	0.0	0.0	0.0	0.0	0.3	6.2	4.5	0.7	0.0	0.0	4.5	0.7	0.7	0.7
207	5.4	15.8	3.8	0.0	4.1	0.0	1.9	0.6	0.6	0.3	0.6	0.0	0.0	0.0	0.0	0.0	1.6	0.0	2.2	2.9	0.0	5.7	0.0	0.0	0.0
208	10.7	5.3	6.5	0.0	0.0	0.0	1.6	3.7	0.2	0.0	0.7	0.5	0.2	0.0	0.0	5.1	6.5	6.0	1.4	4.4	1.6	3.9	2.3	0.5	0.9
209	8.5	3.9	2.7	0.3	0.0	0.4	0.3	0.0	1.4	0.0	0.0	0.5	0.6	0.0	1.5	3.2	1.1	8.4	1.3	9.3	3.0	9.3	0.4	0.1	0.4
210	1.2	0.0	0.4	1.2	0.0	1.2	2.7	0.0	1.9	0.0	0.4	0.4	0.0	1.2	0.0	0.8	0.0	5.8	0.0	24.6	0.4	9.2	0.0	0.0	0.0
211	3.9	0.4	1.8	0.7	0.0	0.4	2.9	0.0	2.2	0.0	0.0	0.4	0.0	1.4	2.5	0.4	9.6	0.0	16.5	2.5	14.7	0.0	0.0	0.0	0.0
212	6.7	3.0	3.2	1.0	0.2	0.2	0.8	0.2	1.6	0.4	0.0	0.6	0.6	0.0	1.2	5.6	0.2	7.6	2.2	14.7	1.0	10.7	2.2	0.2	1.4
214	3.7	2.3	2.3	0.7	0.0	1.0	0.7	0.0	2.3	0.0	0.7	0.7	1.0	0.0	3.3	2.7	0.7	12.7	0.7	22.1	0.0	11.7	0.0	0.3	0.0
216	1.4	0.0	2.5	1.8	0.0	1.8	1.4	0.0	0.7	0.0	1.1	1.8	1.1	0.4	0.0	3.2	0.0	5.0	0.0	22.6	0.0	9.7	0.0	0.0	0.0
217	0.7	0.0	1.9	0.4	0.0	1.5	4.5	0.0	0.7	0.0	0.0	0.4	0.0	0.4	0.0	0.7	0.0	4.1	0.0	25.3	1.1	9.7	0.0	0.0	0.0
218	0.4	0.0	0.0	0.4	0.0	0.4	3.5	0.0	1.6	0.0	0.4	0.0	0.0	0.0	0.0	0.8	0.0	8.6	0.0	19.5	0.0	12.5	0.4	0.0	0.0
219	1.1	0.0	3.8	1.1	0.0	1.1	2.3	0.0	4.5	0.0	1.6	0.8	0.4	0.0	0.8	8.0	0.4	8.4	0.0	21.2	0.0	12.5	0.0	0.0	0.0
220	0.0	0.3	1.4	1.0	0.0	1.4	6.3	0.0	1.4	0.0	0.3	0.7	0.0	0.0	0.7	0.7	0.0	6.3	0.0	19.8	0.3	10.1	0.0	0.0	0.0
221	9.5	0.0	0.5	0.0	0.3	1.1	1.6	0.3	0.5	0.8	0.0	0.0	1.4	0.0	0.0	0.0	18.3	1.9	0.0	0.0	0.0	0.3	0.3	0.0	0.0
222	5.1	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	18.8	1.0	0.0	0.0	0.5	0.5	0.0	0.0
223	7.3	0.0	0.0	0.0	0.0	0.0	0.8	3.8	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.4	0.0	3.8	0.8	0.0	0.0	1.9	0.0	0.0	0.0
224	0.0	0.0	0.0	0.0	0.8	0.0	1.6	3.1	0.0	1.2	0.0	0.0	0.0	0.0	0.4	0.8	0.4	0.8	0.0	0.0	0.8	0.0	3.1	0.0	0.0
225	0.8	0.0	0.0	0.0	0.4	0.0	1.5	1.9	0.0	1.9	0.8	0.0	0.0	0.4	0.0	5.4	1.5	10.8	0.4	1.2	1.2	0.8	0.8	0.4	0.0
226	7.0	0.0	0.0	0.0	0.0	1.0	0.0	0.3	0.3	0.7	0.0	0.3	0.0	0.0	0.0	0.0	20.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
227	9.3	0.0	0.8	0.0	0.4	1.7	0.0	0.4	0.8	0.8	0.8	0.0	0.8	0.0	1.7	0.0	8.9	0.0	0.4	0.0	0.0	0.4	0.0	0.0	0.0
228	2.8	0.0	0.0	0.0	0.4	0.0	0.7	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17.7	1.1	0.0	0.0	0.0	0.7	0.0	0.0	0.0
229	2.8	0.0	0.0	0.0	0.0	0.0	0.4	0.8	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.4	0.0	13.9	3.6	0.0	0.0	0.0	0.8	0.0	0.0
230	2.7	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.7	0.0	0.0	0.0	0.0	0.3	0.3	0.0	1.7	1.0	0.0	0.0	1.4	0.0	0.3	0.3
231	1.1	0.0	0.0	0.0	2.3	0.0	1.1	4.6	0.0	6.1	0.0	0.0	0.0	0.0	0.0	0.0	0.4	1.9	0.0	0.4	0.4	0.0	6.9	0.0	0.4
232	1.4	0.0	0.0	0.0	0.0	0.0	1.7	1.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
233	0.3	0.0	0.3	0.0	2.1	0.0	1.8	3.6	0.3	1.8	0.0	0.0	0.0	0.3	0.3	1.8	2.7	4.5	0.0	0.0	4.5	0.6	0.9	0.0	0.0
234	0.0	0.0	0.0	0.0	3.4	0.0	3.0	5.7	0.0	6.5	0.0	0.0	0.0	0.0	0.4	0.4	0.0	0.8	0.0	0.4	0.0	17.9	0.0	0.0	0.0
235	7.0	0.0	0.0	0.0	0.0	0.0	2.1	3.6	0.0	4.8	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.6	0.0	0.0	0.0	4.8	0.0	0.0	0.0
236	6.3	0.0	0.0	0.0	0.0	0.0	0.0	1.6	1.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	18.2	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
237	9.5	0.0	1.4	0.0	0.0	0.0	1.0	1.6	2.7	1.7	0.0	0.0	0.0	0.7	0.0	0.0	14.9	2.0	0.7	0.0	0.0	0.0	0.3	0.0	0.0
238	6.2	0.4	7.0	0.0	0.0	1.5	2.9	1.2	0.7	0.0	0.7	0.7	0.0	0.0	0.4	1.5	0.0	23.8	0.7	19.8	1.1	0.4	0.0	0.4	0.0
239	2.3	0.4	1.5	1.5	0.0	1.5	2.3	0.0	1.9	0.0	0.8	0.8	0.8	1.2	0.8	0.0	11.2	0.0	36.3	0.8	2.7	0.0	0.0	0.0	0.0
240	11.2	0.6	7.6	0.0	0.0	1.2	3.5	0.0	1.2	0.0	0.0	2.4	0.0	0.6	0.6	1.2	0.0	16.5	1.2	18.2	0.6	0.0	0.0	0.0	0.0
241	9.4	0.8	9.1	0.4	0.0	2.0	3.1	2.4	0.0	0.4	0.0	0.0	0.0	0.4	0.8	2.0	0.0	13.0	0.4	15.4	0.8	0.4	0.4	0.4	0.0
242	6.1	1.9	2.6	0.0	0.9	0.6	0.0	1.0	0.6	0.0	0.3	0.0													



Appendix III, continued.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
276	4.0	1.5	4.0	0.4	0.0	0.7	1.5	0.4	1.1	1.1	0.4	1.1	2.2	0.4	0.0	3.3	6.3	8.8	0.7	3.7	2.9	0.4	2.2	1.1	4.4
277	5.0	1.5	3.1	0.8	0.0	1.2	1.5	1.2	1.9	1.2	6.2	0.0	0.8	0.0	0.0	0.8	0.0	12.4	0.8	3.1	0.0	0.0	0.0	2.3	0.0
279	7.4	9.6	6.3	0.0	0.0	0.7	2.6	1.1	2.2	0.4	0.0	2.6	1.1	0.0	0.4	0.7	0.4	11.4	2.2	6.6	1.5	0.0	0.0	0.4	0.0
280	2.7	2.7	2.2	0.0	0.0	0.5	2.2	2.7	1.1	0.5	0.5	1.6	1.1	0.0	0.0	0.5	0.0	21.1	0.0	7.6	1.6	0.0	0.0	2.2	0.0
281	0.0	0.0	1.9	0.4	0.0	1.5	3.0	0.0	1.5	0.4	0.7	1.5	1.1	0.7	0.4	0.0	2.3	8.6	0.7	3.7	4.1	3.0	0.4	1.5	4.1
282	0.0	1.1	2.3	0.0	0.0	0.4	0.0	0.0	2.6	0.0	0.0	0.4	1.5	3.4	0.4	2.3	1.9	12.4	0.0	13.2	10.9	0.0	0.0	1.1	0.4
283	0.0	0.6	0.0	1.2	0.0	0.0	0.6	0.0	0.6	0.0	0.6	3.5	0.0	1.8	0.0	0.0	2.3	1.2	0.0	20.3	15.7	0.0	0.0	0.6	0.0
284	0.0	0.0	0.0	0.7	0.0	0.0	0.3	0.0	3.6	0.0	0.0	2.6	0.7	1.7	1.0	0.0	5.6	6.3	0.0	21.7	16.1	1.0	0.0	0.0	0.0
285	6.9	2.8	2.4	1.0	1.0	0.0	0.3	0.0	1.4	0.3	1.0	2.4	1.7	0.7	0.7	0.0	7.0	6.2	0.3	8.3	10.8	0.7	0.0	3.1	1.7
286	9.3	7.5	6.1	0.4	0.4	0.0	0.0	0.7	0.7	2.5	0.0	0.4	0.7	0.7	0.4	0.0	0.0	2.9	5.0	0.7	0.4	0.0	5.4	0.7	0.0
287	10.7	2.0	7.9	2.0	1.2	0.4	0.4	0.0	1.6	0.4	1.2	0.4	1.6	0.8	1.2	2.8	0.8	9.9	3.2	3.2	2.4	0.0	0.8	0.4	1.6
288	9.2	1.1	7.0	1.8	0.0	0.7	2.9	0.4	0.7	0.0	0.7	0.4	2.9	0.7	2.2	0.4	5.9	17.6	0.0	5.5	4.4	0.7	0.4	0.7	0.0
289	12.3	2.4	9.5	0.4	0.8	0.0	0.4	1.2	2.0	0.4	0.0	0.0	2.0	0.8	0.0	0.8	0.8	10.7	2.4	1.6	2.8	0.0	2.4	0.8	0.0
290	9.7	2.7	8.4	1.7	0.0	0.0	1.3	0.3	0.3	0.3	1.0	0.3	1.7	0.7	0.7	0.3	0.3	24.0	2.7	2.7	1.4	0.0	0.0	0.7	0.0
292	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	1.5	0.0	1.9	1.9	0.0	0.8	0.0	0.0	1.5	1.9	0.0	32.6	17.4	0.0	0.0	0.0	0.0
293	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	2.9	0.0	1.5	0.0	0.0	2.4	0.0	0.0	22.4	5.2	0.0	0.0	0.0	0.0
295	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.4	0.0	1.6	0.0	0.0	0.0	1.6	0.0	38.8	15.7	0.0	0.0	0.0	0.0
296	0.0	0.8	1.9	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.8	2.7	0.4	2.2	0.0	0.0	2.3	3.1	0.0	21.0	14.5	0.4	0.0	0.4	0.0
299	7.6	0.0	0.0	0.0	7.0	0.0	0.0	5.0	0.0	6.7	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.6	0.0	0.0	4.2	0.0	4.6
300	10.0	0.0	1.1	0.0	0.0	2.9	3.6	3.2	0.7	5.0	0.0	0.0	2.1	0.0	0.0	0.0	0.4	24.3	1.1	0.4	0.0	0.0	0.0	0.0	0.0
301	6.9	0.0	0.0	0.0	1.8	0.0	0.4	2.9	1.1	6.9	0.4	0.0	0.4	0.0	0.0	0.4	0.0	13.9	2.2	0.0	0.0	0.0	4.7	0.0	0.4
302	7.8	0.7	6.7	0.0	0.0	1.4	1.8	2.2	4.2	0.7	0.0	0.0	0.7	0.0	0.0	0.0	0.0	21.2	0.0	0.7	0.0	0.0	0.0	0.4	0.0
303	6.6	0.0	0.4	0.0	0.0	0.0	0.7	0.0	0.4	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	27.6	1.8	0.0	0.0	0.0	1.8	0.0	0.0
304	9.7	0.0	0.0	0.0	1.0	0.0	0.5	4.1	2.6	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.2	4.1	0.0	0.0	0.0	4.1	0.0	1.0
305	9.2	7.1	5.2	0.3	0.3	0.0	1.3	0.8	0.8	0.0	1.3	0.8	1.0	1.3	3.4	1.6	1.6	4.2	0.5	9.9	11.3	2.6	0.3	0.0	0.0
306	5.4	8.1	0.4	0.0	5.0	0.0	0.0	0.8	0.8	5.4	1.5	0.0	1.2	0.0	0.0	0.4	0.8	0.4	5.0	0.0	0.0	0.0	5.8	2.3	2.7
307	1.2	1.6	1.2	1.6	0.0	0.0	0.0	0.0	3.2	0.0	0.0	2.0	0.0	0.4	0.8	0.0	3.6	3.6	0.4	15.7	10.8	4.8	0.0	2.0	0.4
310	6.1	4.8	0.3	0.0	0.0	0.3	0.6	0.0	1.9	0.0	2.2	0.0	0.6	1.6	1.0	0.6	1.6	8.3	0.0	2.2	2.5	1.1	0.3	0.0	0.0
311	6.9	5.0	3.5	0.9	0.0	0.3	0.3	0.3	0.9	0.3	0.6	1.3	0.6	0.0	1.9	7.6	1.3	11.6	0.6	10.1	7.6	1.3	0.6	0.3	0.9
312	8.5	0.5	7.7	0.3	0.0	1.1	3.6	2.2	0.5	1.1	0.3	0.5	0.0	0.0	0.8	1.4	0.0	22.1	1.4	9.3	1.1	0.0	0.0	1.1	0.0
313	11.1	0.0	0.0	0.0	0.0	0.0	4.8	1.8	0.0	0.9	0.0	0.0	0.0	0.9	0.0	0.0	0.0	24.2	0.0	0.0	0.0	0.0	1.8	0.0	0.0
314	12.3	0.0	0.0	0.0	0.0	0.0	3.4	1.7	1.4	0.7	0.0	0.0	0.0	0.3	0.0	0.0	0.0	27.4	0.0	0.0	0.0	0.0	0.7	0.0	0.0
315	1.2	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0
316	3.6	0.0	0.0	0.0	0.0	0.0	1.5	1.5	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.7	0.0	0.0	0.0	5.1	0.0	0.0
317	2.5	0.0	2.5	0.0	0.0	0.0	0.4	0.0	0.7	0.0	0.7	0.0	0.0	0.4	0.0	4.6	3.2	20.0	0.0	1.1	10.0	5.0	0.0	0.4	0.0
318	0.4	6.4	0.0	0.0	1.2	0.0	1.1	1.1	0.0	0.0	0.0	0.0	0.4	0.4	0.4	0.0	0.4	0.0	0.8	0.0	0.0	0.0	0.4	0.8	1.9
320	7.2	5.6	3.6	0.3	0.0	0.3	1.3	0.3	0.3	0.3	0.0	0.3	1.3	0.0	0.0	3.6	0.3	7.8	2.6	8.2	4.9	4.2	1.0	0.0	1.6
321	7.1	13.9	6.3	0.8	3.2	0.0	0.8	0.0	0.0	2.4	0.0	0.0	0.0	0.4	0.0	3.0	0.0	2.0	4.8	0.4	0.0	0.0	1.6	0.8	0.8
322	7.8	14.7	0.8	0.0	1.6	0.0	0.8	0.4	0.4	0.4	0.0	0.4	0.0	0.0	0.0	1.2	0.0	6.6	6.2	0.0	0.0	0.0	4.3	2.7	0.8
323	5.9	11.5	1.0	0.0	0.8	0.3	2.1	0.6	0.3	1.0	0.7	0.0	0.0	0.3	0.0	0.0	0.0	9.7	2.8	0.3	0.0	0.0	5.9	0.3	0.0
324	11.6	2.2	2.6	0.0	0.4	0.7	1.1	0.7	1.9	0.0	1.5	0.7	0.0	0.0	0.0	0.7	0.0	19.0	4.1	3.1	0.4	0.0	1.7	0.0	0.0
325	15.4	0.4	1.4	0.0	0.0	1.8	4.3	2.5	2.9	1.4	0.0	0.0	0.7	0.0	0.0	0.0	0.0	25.1	1.4	0.4	0.0	0.0	0.4	0.0	0.0
326	7.5	0.0	0.0	0.0	0.0	0.0	0.8	3.3	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2	2.1	0.0	0.0	0.0	0.8	0.0	0.0
327	9.8	0.0	0.9	0.0	0.4	2.1	3.4	1.3	5.1	0.4	0.0	0.0	0.4	0.0	0.0	0.0	0.4	22.6	0.4	0.0	0.0	0.0	0.0	0.0	0.0
328	17.0	0.4	4.5	0.0	0.0	1.5	1.1	0.4	2.3	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	15.8	7.5	0.0	0.0	0.0	4.5	1.1	0.4
329	9.5	2.7	1.5	0.0	2.7	0.4	0.8	1.5	2.3	1.5	0.8	0.8	0.0	0.0	0.0	0.0	0.0	18.2	4.2	0.0	0.0	0.0	7.2	1.1	0.8
330	15.4	2.9	0.4	0.0	2.5	0.0	1.1	0.4	0.7	1.4	0.0	0.4	0.4	0.0	0.0	0.0	0.0	8.2	11.8	0.0	0.0	0.0	5.0	3.2	1.0
331	8.5	13.1	0.0	0.0	6.2	0.0	0.7	1.1	0.0	1.4	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.0	0.0	0.0	4.6	0.7	4.3
332	7.4	4.4	0.3	0.0	4.7	0.3	1.0	0.7	0.3	1.7	0.3	0.3	0.3	0.0	0.0	0.0	0.0	11.8	6.8	0.0	0.0	0.0	14.9	0.3	0.7
333	16.1	2.6	0.7	0.0	1.2	0.7	2.2	0.4	1.5	1.5	0.4	0.4	0.0	0.0	0.0	0.0	0.0	14.0	6.7	0.0	0.0	0.0	7.9	1.5	0.4
334	11.2	0.3	0.3	0.0	1.7	0.3	1.0	1.7	2.0	1.7	1.7	0.0	0.0	0.7	0.0	0.0	0.0	10.5	8.8	0.0	0.0	0.0	7.1	2.0	0.3
335	7.0	0.0	0.0	0.0	0.0	0.0	2.5	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21.9	2.1	0.0	0.0	0.0	1.7	0.0	0.0
336	2.9	0.5	5.1	1.9	0.3	0.5	1.1	0.0	1.9	0.0	0.5	0.3	0.5	0.3	1.1	3.7	0.0	9.3	0.5	16.5	1.6	7.7	0.0	0.0	0.5
337	8.3	0.4	5.8	0.4	0.4	0.7	1.8	0.0	3.2	0.0	1.4	0.4	0.0	0.4	2.2	1.1	0.0	11.9	1.8	16.6	2.5	4.3	0.0	0.0	0.4
338	7.6	0.8	6.4	0.4	0.0	0.8	1.9	0.4	1.9	0.0	1.9	1.1	0.0	1.1	1.5	0.4	0.0	12.5	1.1	26.5	1.5	3.0	0.0	0.0	0.0
339	7.2	0.4	10.0	0.8	0.0	0.8	1.2	0.0	0.4	0.0	0.8	0.8	3.2	0.0	4.0	2.0	0.4	10.0	0.0	26.0	0.0	0.8	0.0	0.0	0.0
340	6.7	2.2	3.7	0.2	0.0	0.5	0.5	0.0	1.5	0.0	0														



Appendix III, continued.

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
276	0.0	0.4	4.0	0.7	0.0	2.9	1.5	2.2	0.7	2.9	2.9	0.4	1.1	4.8	0.7	0.4	3.3	3.7	2.6	0.4	0.4	0.0	1.1	0.4	0.4
277	0.0	1.9	0.0	0.0	3.9	0.0	0.0	0.0	0.8	3.1	3.1	0.0	0.0	3.9	0.0	0.0	5.0	3.9	18.5	0.0	0.8	0.0	0.0	0.0	0.0
279	1.1	3.8	0.0	0.0	0.4	0.0	0.0	0.0	0.0	1.5	0.7	2.2	0.0	4.8	0.0	0.0	4.1	4.4	12.9	0.0	0.4	0.0	0.0	0.0	0.0
280	2.2	3.8	0.0	0.0	2.2	0.0	0.0	0.0	0.0	1.1	1.1	0.0	0.0	7.6	0.0	0.0	5.9	3.8	13.0	0.0	0.5	0.0	0.0	0.0	0.0
281	0.4	0.0	1.5	0.0	0.4	0.4	0.4	0.0	1.5	3.7	4.1	0.7	0.7	3.7	0.7	0.0	13.5	5.2	3.4	0.0	0.0	0.0	0.7	0.7	0.4
282	0.8	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	2.3	0.8	1.5	7.2	5.7	1.1	0.8	0.0	0.0	1.5	2.6	1.1	0.0
283	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.5	2.3	1.2	11.0	0.0	0.0	3.5	0.0	0.0	4.7	5.8	0.0	0.0
284	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	5.3	1.3	4.6	1.0	1.6	0.0	1.0	0.0	0.0	4.6	4.3	0.0	1.0
285	0.0	0.7	0.3	0.0	0.0	0.0	0.0	0.3	0.0	0.0	1.4	1.7	1.1	6.3	0.0	1.4	5.2	3.1	2.1	0.0	0.0	0.7	0.0	2.4	0.3
286	0.4	0.0	0.0	0.0	0.0	0.4	0.4	0.4	1.8	3.2	1.1	1.1	0.0	10.4	0.0	0.4	6.8	1.8	0.0	0.0	0.0	0.0	0.0	0.4	0.0
287	0.0	0.8	0.4	0.8	0.0	0.8	0.0	1.2	0.4	0.8	2.0	1.6	0.0	6.0	0.4	0.4	6.0	3.6	0.0	0.0	0.0	0.4	0.0	4.4	0.8
288	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.7	1.1	3.3	0.0	2.6	1.5	1.1	1.5	2.9	2.2	0.0	0.0	1.1	1.1	1.8	0.0
289	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	2.4	3.2	1.6	1.2	0.0	6.3	0.0	0.0	5.9	2.0	0.8	0.0	0.0	0.0	0.0	5.9	0.0
290	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.7	4.3	0.0	5.7	0.3	0.0	7.7	2.3	0.7	0.0	0.3	0.0	0.7	2.0	0.0
292	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.9	3.0	0.8	1.5	0.0	0.0	1.1	0.0	0.0	7.2	4.9	0.4	0.4
293	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.8	4.8	1.9	3.3	0.0	0.0	1.9	0.0	0.0	11.0	10.5	0.0	2.9
295	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.9	3.5	0.4	1.6	0.0	0.0	1.2	0.0	0.0	12.5	4.7	0.0	0.0
296	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	3.1	2.3	1.9	3.1	0.4	0.0	3.1	0.0	0.0	5.0	5.7	0.4	0.0
299	6.3	0.4	17.6	1.8	0.7	0.0	0.0	1.1	0.8	13.0	4.9	0.0	0.0	4.6	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
300	0.7	15.7	0.0	2.1	5.7	0.0	0.4	1.4	0.4	1.8	2.5	0.0	0.0	0.0	0.0	1.1	2.5	6.8	0.0	1.4	0.0	0.0	0.0	0.0	0.0
301	1.1	6.2	7.3	2.2	4.4	0.0	0.3	3.7	10.9	5.1	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.7	2.2	0.0	2.6	0.0	0.0	0.0	0.0
302	0.4	15.2	0.0	0.7	4.9	0.0	0.0	0.4	0.0	3.2	1.1	0.0	0.0	3.2	0.0	0.0	1.8	7.8	8.5	0.0	0.0	0.0	0.0	0.0	0.0
303	0.7	22.4	0.0	3.3	6.6	1.1	0.4	0.7	0.0	5.1	8.5	0.0	0.0	0.7	0.0	0.0	0.7	1.5	3.7	0.0	2.6	0.0	0.0	0.0	0.0
304	1.5	5.6	5.6	5.6	6.6	1.0	2.6	3.1	1.0	9.7	6.6	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.5	0.0	6.1	0.0	0.0	0.0	0.0
305	0.3	0.0	0.3	0.0	0.0	0.0	0.0	1.0	0.5	0.5	1.8	1.8	1.0	7.3	0.0	1.0	2.1	4.7	2.3	0.0	0.0	0.3	0.3	1.3	0.3
306	0.4	0.0	0.4	0.0	0.0	0.0	0.0	0.8	2.7	3.5	1.2	0.0	0.0	5.0	0.0	0.4	5.0	3.1	0.0	0.0	0.0	0.0	0.0	3.8	0.0
307	0.8	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.8	2.8	4.0	5.2	1.6	1.2	8.8	0.8	2.4	0.0	0.0	1.6	0.8	0.0	0.0
310	0.6	0.0	0.6	0.0	0.0	0.6	0.3	0.3	0.9	0.3	1.3	2.2	6.1	10.5	1.3	1.6	11.1	2.9	1.6	0.0	0.0	0.0	0.6	0.3	0.0
311	0.0	0.0	0.6	0.0	0.0	0.0	0.0	1.3	0.3	0.6	3.8	3.8	0.0	3.8	0.9	1.6	1.3	2.8	2.2	0.0	0.0	0.3	0.3	2.2	2.0
312	0.6	0.0	1.1	1.1	0.0	0.0	0.3	0.3	4.6	2.7	3.6	0.0	0.0	4.1	0.0	0.0	3.6	5.7	4.4	0.0	0.3	0.0	0.0	0.0	0.0
313	0.0	11.0	0.0	6.6	9.7	0.0	0.0	6.6	0.0	8.8	5.3	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0
314	0.0	2.4	0.0	7.2	6.2	16.4	0.0	6.5	0.0	5.8	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0
315	0.0	0.0	0.0	8.3	0.0	18.3	12.7	11.5	1.6	12.7	12.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.9	0.0	0.0	0.0	0.0
316	0.0	0.0	0.0	7.3	0.0	26.9	9.8	8.4	3.3	6.2	15.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	7.6	0.0	0.0	0.0	0.0
317	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	1.4	0.0	2.1	18.1	0.4	0.0	1.1	0.0	18.2	2.1	1.4	0.0	0.0	0.0	1.1	0.4	0.0
318	0.0	0.0	21.4	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.4	0.0	0.0	22.2	0.0	0.4	1.1	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
320	0.6	0.0	0.3	0.3	0.3	0.3	0.3	2.0	1.3	3.6	4.9	0.6	0.6	4.6	1.0	2.6	3.9	2.0	2.0	0.0	1.0	0.0	3.3	1.0	0.0
321	0.4	0.0	2.8	0.0	0.0	0.0	0.0	1.2	1.2	4.4	0.8	0.0	0.0	4.8	0.0	0.0	9.5	14.3	0.0	0.0	0.0	0.0	0.0	1.2	0.0
322	0.8	0.0	0.0	0.0	0.8	0.4	0.0	0.8	1.9	2.3	2.7	0.0	0.4	8.5	0.0	0.4	10.5	7.8	0.4	0.0	0.8	0.0	0.0	2.7	0.0
323	0.7	0.0	0.3	0.0	0.7	0.0	0.0	1.7	3.8	4.5	3.8	0.0	0.0	8.4	0.0	0.0	9.1	10.1	0.0	0.0	0.0	0.0	0.0	1.4	0.0
324	0.7	0.0	0.4	0.0	0.0	0.0	0.4	1.5	11.9	9.0	0.4	0.0	1.9	0.0	0.0	4.1	6.7	1.5	0.0	0.7	0.0	0.0	1.5	0.0	0.0
325	0.4	3.9	0.0	2.2	3.2	0.0	0.0	0.4	1.1	1.8	8.6	0.0	0.0	3.9	0.0	0.0	0.7	7.2	4.7	0.0	1.4	0.0	0.0	0.4	0.0
326	0.0	0.4	0.0	7.1	0.0	23.0	7.1	0.8	3.3	9.6	11.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.4	7.1	0.0	0.0	0.0	0.0
327	0.0	16.2	0.0	3.4	1.3	0.0	0.0	0.0	0.0	0.4	6.8	0.0	0.0	1.7	0.0	0.0	0.0	1.7	15.4	0.0	2.1	0.0	0.0	0.0	0.0
328	0.8	0.0	0.0	1.1	0.0	0.4	0.0	0.0	3.4	9.1	8.3	0.0	0.0	4.9	0.0	0.0	1.1	7.2	2.3	0.0	1.1	0.0	0.0	0.8	0.0
329	0.4	0.0	0.0	0.8	0.8	1.1	0.0	0.4	1.5	8.7	3.8	0.0	0.0	9.8	0.0	0.0	3.0	6.4	0.8	0.0	0.0	0.0	1.1	0.0	0.0
330	1.8	0.0	0.0	0.7	1.1	0.4	0.0	0.7	3.2	5.4	4.3	0.0	0.0	6.8	0.0	0.0	7.2	2.2	0.0	0.0	0.4	0.0	0.0	2.5	0.0
331	2.1	0.0	15.2	0.0	0.7	0.4	0.0	1.1	2.8	3.9	1.1	0.0	0.0	11.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0
332	1.0	0.0	1.0	1.7	0.0	4.0	0.7	1.0	1.7	6.8	2.0	0.0	0.0	10.5	0.0	0.0	3.7	2.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
333	0.4	0.0	0.0	0.0	1.5	2.6	0.0	0.4	6.4	7.5	6.0	0.0	0.0	8.6	0.0	0.0	1.5	2.6	2.6	0.0	0.0	0.0	0.0	0.0	0.0
334	0.0	0.0	0.0	2.7	3.1	5.8	0.0	0.7	3.1	10.5	6.1	0.0	0.0	8.5	0.0	0.0	0.7	0.7	1.0	0.0	0.3	0.0	0.0	0.0	0.0
335	0.0	4.5	0.0	3.7	7.4	17.4	8.3	1.7	0.4	8.7	7.0	0.0	0.0	0.0	0.0	0.0	3.5	1.9	0.0	0.8	4.1	0.0	0.0	0.0	0.0
336	0.0	0.0	0.0	0.0	0.0	0.0	0.3	4.3	1.4	3.2	3.5	2.9	1.1	4.8	3.2	0.3	3.0	1.9	0.8	0.0	0.0	0.3	0.0	1.1	0.0
337	0.0	0.0	0.4	0.0	0.0	0.4	0.0	1.4	0.7	3.2	2.5	3.2	0.7	1.4	5.1	0.0	2.2	1.8	1.4	0.0	0.0	0.4	2.2	0.0	0.4
338	0.4	0.0	0.4	0.0	0.0	0.0	0.0	0.4	0.0	2.3	1.9	1.9	0.4	2.3	3.0	0.0	2.7	3.4	0.4	0.0	0.0	0.8	2.7	0.4	0.0
339	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.8	2.8	2.4	4.0	4.8	0.0	2.8	2.8	0.8	0.0	0.0	0.8	1.2	0.4	0.0
340	0.7	0.0	0.7	0.0	0.0	0.0	0.0	0.5	0.7	1.0	2.7	5.0	0.												

Appendix IV. List of relative frequencies (percentages) of subspecific categories used in the numerical analyses of the samples of biofacial units II and IV.

first column: sample number  
 next columns: relative frequencies per taxon (percentages)  
 numbers in heading indicate:

- 1 -- *Bulimina marginata* forma *aculeata*
- 2 -- *Bulimina marginata* forma *denudata*
- 3 -- *Bulimina marginata* forma *marginata*
- 4 -- *Ammonia beccarii* forma *beccarii*
- 5 -- *Ammonia beccarii* forma *inflata*
- 6 -- *Ammonia parkinsoniana* forma *parkinsoniana*
- 7 -- *Ammonia parkinsoniana* forma *tepida*, morphotype 2
- 8 -- *Ammonia parkinsoniana* forma *tepida*, morphotype 3
- 9 -- *Ammonia parkinsoniana* forma *tepida*, morphotype 4
- 10 -- *Ammonia parkinsoniana* forma *tepida*, morphotype 5
- 11 -- *Elphidium granosum* forma *granosum*
- 12 -- *Elphidium granosum* forma *lidoense*
- 13 -- *Elphidium poeyanum* forma *decipiens*
- 14 -- *Elphidium poeyanum* forma *poeyanum*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	0.0	0.0	3.9	1.6	0.0	19.3	16.1	0.8	0.8	2.0	2.0	2.8	3.5	6.3
2	0.0	0.0	4.7	2.8	0.0	12.2	21.3	1.2	0.4	0.0	5.1	2.4	2.4	1.2
5	5.2	15.2	0.0	0.4	1.1	0.0	0.4	0.0	0.0	1.9	1.1	1.5	0.0	0.0
6	1.9	21.3	0.0	0.9	0.5	0.9	0.0	0.0	0.5	4.3	0.5	0.5	0.0	0.0
7	1.5	10.6	0.0	2.7	6.5	0.0	1.1	0.4	9.9	4.2	11.8	0.4	1.5	3.4
8	0.4	1.5	0.0	2.3	0.8	4.2	4.2	3.1	16.9	6.5	16.5	1.5	3.1	4.2
12	4.1	7.5	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	2.2	2.6	1.9	0.7
50	2.0	16.6	0.0	1.6	2.4	0.4	0.0	0.0	0.4	2.4	2.4	6.9	2.4	0.4
51	3.9	15.7	0.0	0.0	3.4	0.0	0.0	0.0	0.0	0.5	1.0	7.6	6.5	0.3
52	15.9	4.4	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	1.5	3.7	3.3	0.4
53	14.8	4.2	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	2.3	1.1	5.3	0.0
54	14.0	4.7	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	1.0	2.3	6.7	0.3
55	13.2	6.2	0.0	0.0	3.5	0.0	0.0	0.0	0.0	0.0	0.4	1.6	6.6	0.4
56	1.5	29.1	0.0	0.0	4.4	0.0	0.4	0.0	0.0	0.4	1.5	4.7	9.1	0.7
57	0.0	9.0	0.0	5.2	3.8	1.0	4.8	1.7	3.1	11.4	18.0	1.7	9.7	2.1
58	0.3	0.0	2.4	5.5	0.0	20.3	4.1	0.0	0.0	0.7	1.0	3.4	4.8	0.3
64	2.9	28.8	0.0	0.0	4.9	0.0	0.0	0.0	1.0	1.0	5.9	2.4	5.4	0.5
65	0.3	7.4	0.0	0.5	11.2	0.0	2.9	0.0	3.5	14.1	12.8	2.9	4.8	2.4
66	0.0	0.0	4.3	6.3	0.0	7.6	3.6	0.0	0.0	0.7	1.3	3.0	3.3	1.3
67	0.0	0.0	2.6	2.2	0.0	27.3	3.7	0.7	0.0	0.4	0.4	7.5	3.0	0.0
68	0.0	0.0	0.0	5.3	0.0	29.4	5.3	1.5	0.8	1.9	0.4	10.6	6.0	0.4
69	0.0	3.4	0.0	2.3	6.1	1.9	1.9	1.1	11.5	4.2	17.2	4.2	8.8	3.4
70	1.4	15.4	0.0	0.0	6.2	0.7	2.1	0.0	7.5	5.5	15.4	1.7	3.1	7.2
71	1.9	14.4	0.0	0.0	5.7	0.8	0.8	2.3	9.8	5.7	8.7	3.0	4.2	2.7
72	5.6	17.9	0.0	0.0	8.5	0.0	0.0	0.0	0.0	0.4	7.3	3.8	3.8	0.0
73	8.2	8.6	0.0	0.0	4.3	0.0	0.0	0.0	0.0	0.0	1.2	1.6	9.0	1.2
74	0.0	0.0	2.7	2.3	0.0	17.1	0.0	0.0	0.4	0.8	0.8	3.9	3.5	0.0
75	0.0	0.0	0.8	2.0	0.0	30.6	2.0	1.2	0.4	1.6	1.6	5.2	4.0	0.8
76	0.0	0.0	0.4	3.5	2.3	50.4	3.9	0.8	0.4	1.6	0.4	7.8	0.8	0.0
77	0.0	0.7	0.0	4.8	0.0	4.4	4.8	1.8	5.1	5.5	14.3	5.5	5.5	2.6
78	0.0	5.0	0.0	19.8	0.0	2.5	2.5	3.0	6.4	8.9	6.4	3.5	6.9	1.0
79	0.0	0.0	0.0	3.4	0.0	23.2	3.4	4.3	2.6	3.4	2.1	8.6	7.3	0.9
80	0.0	0.0	0.0	3.4	1.1	12.3	7.1	2.6	1.5	0.7	3.7	8.2	12.7	0.7
81	0.0	1.3	0.0	4.0	3.3	8.6	11.3	3.3	1.7	2.3	4.0	8.3	8.0	0.7
82	0.0	0.7	0.0	12.1	1.3	11.7	9.1	1.7	2.7	1.0	4.7	8.7	5.4	0.7
83	0.0	0.0	0.4	3.3	0.4	22.1	18.8	2.9	0.0	0.7	0.4	4.0	4.4	0.0
84	0.0	0.4	0.0	11.9	1.2	5.3	9.4	2.0	1.2	1.6	2.0	13.1	9.4	1.2
85	0.0	5.6	0.0	6.0	3.8	3.0	8.1	3.0	4.7	3.4	6.4	1.7	3.8	6.0
86	0.0	8.0	0.0	0.8	0.0	2.7	3.4	1.5	8.7	4.9	5.7	3.4	8.0	5.7
87	0.0	1.5	0.0	1.9	2.3	1.5	3.8	1.5	1.5	3.3	0.4	18.3	14.4	1.1
88	0.0	1.7	0.0	4.7	1.7	12.8	5.6	0.0	0.0	3.8	0.9	20.1	8.1	1.3
89	1.2	27.1	0.0	0.0	3.0	0.0	1.2	1.2	1.8	0.0	4.8	1.2	7.2	0.0
92	0.0	0.0	0.0	5.6	0.0	48.6	5.2	0.4	0.0	2.0	0.4	4.8	5.2	3.6
93	0.0	0.0	0.0	7.1	0.0	28.0	10.6	1.6	0.4	2.8	0.4	12.6	9.8	0.8
94	0.0	0.0	0.0	1.3	0.0	11.3	9.2	2.9	0.4	2.1	6.3	8.3	5.8	2.5
95	0.0	15.8	0.0	0.0	5.8	4.6	0.8	0.0	0.0	3.5	0.8	1.9	11.2	0.8

Appendix IV, continued.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
96	0.0	9.2	0.0	0.0	6.4	1.6	2.0	2.0	0.0	0.8	0.4	6.8	10.4	0.8
99	0.0	17.2	0.0	0.0	8.8	0.7	0.0	1.8	0.0	0.0	0.0	3.3	10.2	0.4
106	0.0	0.0	0.0	5.3	0.0	16.3	2.4	10.2	26.5	21.6	0.4	0.0	0.4	0.4
107	0.0	0.0	0.0	4.7	1.0	15.0	7.0	5.0	39.5	15.9	0.0	0.3	1.3	0.0
108	0.0	0.0	0.0	9.9	0.0	25.1	2.2	7.6	18.4	14.3	0.4	0.0	0.4	0.0
109	0.0	0.0	0.0	0.0	7.9	6.4	2.6	2.3	4.5	4.2	0.4	2.3	4.2	0.4
116	0.0	0.0	0.0	0.3	2.9	5.4	2.9	3.2	3.8	1.9	1.3	5.4	7.7	0.6
117	0.0	0.0	0.0	2.4	2.4	4.4	1.6	2.4	3.6	1.2	0.4	7.2	4.4	1.2
122	0.0	0.0	0.0	1.7	7.3	7.7	2.6	1.3	3.0	3.4	2.1	10.7	6.9	2.1
123	0.0	0.0	0.0	0.0	1.6	7.3	6.5	1.2	3.6	4.5	4.9	11.3	8.1	2.8
124	0.0	0.0	0.4	0.0	4.3	8.6	4.7	2.0	2.0	2.4	7.8	9.8	9.0	3.1
125	0.0	0.0	0.0	0.0	1.8	7.6	3.6	3.6	3.3	2.2	4.0	7.3	12.4	4.7
136	0.0	0.4	0.0	0.0	3.8	17.3	0.8	1.9	0.0	0.4	0.4	8.6	6.0	0.4
157	0.0	0.0	0.0	0.0	1.4	56.0	2.8	6.0	0.5	6.5	0.0	0.0	0.0	0.0
158	0.0	0.4	0.0	0.0	1.5	30.1	26.3	6.4	2.6	1.9	0.8	0.0	0.4	0.4
159	0.0	0.0	0.0	0.0	0.0	48.5	39.2	4.6	0.3	1.6	0.0	0.3	0.5	0.3
160	0.0	1.0	0.0	0.0	0.5	13.0	1.9	7.2	0.5	1.9	2.4	1.0	1.0	0.5
161	0.5	1.4	0.0	0.0	0.5	26.5	5.2	23.7	0.5	3.3	0.9	0.0	1.9	0.9
162	0.0	0.0	0.0	0.0	0.0	32.0	25.4	4.9	0.0	2.0	0.4	0.0	2.9	0.8
163	0.0	0.1	0.0	1.1	2.1	26.8	11.3	3.2	0.8	2.1	0.7	10.8	12.0	1.2
164	0.0	0.0	0.0	0.0	0.0	11.4	6.4	19.5	0.5	0.0	0.0	0.0	0.5	0.9
165	0.0	0.0	0.8	0.8	0.0	16.8	9.2	20.2	1.7	5.9	1.7	0.0	0.0	0.0
166	0.0	0.0	0.0	0.0	1.0	16.7	8.4	17.2	0.5	2.0	0.0	0.0	0.5	2.0
167	2.9	12.9	0.0	0.0	2.5	3.3	0.0	2.5	0.0	0.4	1.7	0.8	0.0	0.0
168	0.0	28.5	0.0	0.0	2.0	0.0	0.0	0.8	0.0	0.0	2.4	3.6	8.8	0.4
169	0.0	13.6	0.0	0.0	2.9	2.9	0.7	2.6	0.0	0.0	0.4	7.3	6.2	0.4
181	1.5	26.4	0.0	0.0	1.0	2.0	0.5	2.5	2.0	1.0	3.0	2.5	5.6	0.5
182	0.0	1.4	0.0	0.0	3.4	9.6	2.8	3.9	3.7	1.1	3.9	11.0	9.6	3.9
183	0.0	0.5	0.0	2.1	0.5	20.3	9.1	2.1	1.1	4.3	1.6	8.0	11.8	2.7
184	0.0	0.0	0.0	9.8	1.3	35.4	5.1	3.4	0.3	2.0	0.0	5.7	5.1	1.3
185	0.0	0.0	0.0	2.0	0.0	32.8	6.7	4.3	0.8	3.2	0.4	4.3	8.3	0.4
186	0.0	4.9	0.0	2.0	0.0	3.7	3.3	3.3	1.2	1.6	2.8	4.5	8.5	3.7
187	2.3	13.5	0.0	0.0	1.5	3.1	1.2	2.7	0.0	0.4	0.8	4.2	13.5	0.8
188	0.4	23.9	0.0	0.0	2.9	2.6	2.9	4.0	0.4	0.4	3.7	3.7	12.9	1.1
189	0.0	1.5	0.0	4.5	3.5	17.2	5.1	6.6	3.0	2.0	4.5	8.6	7.6	1.0
190	0.0	0.0	0.0	1.9	1.1	29.8	3.0	4.2	0.4	1.1	0.0	10.6	15.1	1.1
191	0.0	0.4	0.0	1.6	0.0	47.0	0.4	5.6	0.4	0.4	0.8	8.0	11.2	0.8
192	0.0	0.0	0.4	1.6	0.8	37.0	6.3	4.3	0.8	3.1	1.6	5.5	7.5	1.2
193	0.0	0.0	0.0	2.3	0.0	46.1	4.3	0.4	0.4	2.0	0.0	9.0	4.7	0.0
194	16.3	8.1	0.0	0.0	4.2	0.0	0.0	0.4	0.0	0.0	3.2	0.7	11.7	0.4
195	27.4	11.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.8	0.0	3.0	0.0
196	22.5	9.6	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.4	1.1	3.7	0.0
221	3.5	14.7	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.5	1.1	0.3	0.5
222	0.5	17.8	0.0	0.0	2.0	1.0	0.5	2.0	4.1	3.0	7.6	2.0	0.5	0.0
223	0.4	3.4	0.0	0.0	6.5	5.7	3.8	3.4	11.5	3.4	7.6	1.5	3.8	3.8
224	0.0	0.0	0.4	5.5	1.6	39.1	5.9	4.3	1.2	0.8	1.2	2.7	2.3	0.4
225	1.5	0.0	8.9	1.2	0.4	7.3	1.9	5.4	0.4	2.3	1.2	1.9	1.9	0.0
226	3.7	16.7	0.0	3.0	0.0	0.3	0.0	1.3	1.0	0.3	4.0	3.0	0.0	0.3
227	3.4	5.5	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.4	3.8	1.3	0.0
228	1.4	16.3	0.0	0.0	1.4	1.4	0.0	0.4	0.4	1.1	2.5	5.7	8.2	0.4
229	0.0	13.9	0.0	0.0	1.2	2.8	0.4	0.8	4.8	5.2	6.3	2.0	3.2	4.0
230	0.0	1.4	0.0	1.7	3.1	4.8	7.2	6.5	7.9	4.1	8.2	1.7	8.2	5.8
231	0.4	0.0	1.5	2.3	0.0	30.3	4.2	0.0	1.1	3.4	1.5	7.3	5.0	0.8
232	0.7	2.1	0.0	0.0	4.8	0.7	3.1	2.4	7.5	5.1	11.3	7.5	12.7	1.4
233	0.3	0.0	3.0	0.3	0.3	17.3	0.3	0.3	0.3	0.6	0.0	3.6	0.9	0.0
234	0.0	0.4	0.4	0.0	2.3	35.7	1.1	0.8	0.0	3.4	0.0	3.8	1.9	0.0
235	0.0	0.9	0.0	0.0	6.1	1.5	7.0	2.1	12.1	2.1	7.9	2.7	7.9	6.7
236	2.1	16.1	0.0	0.0	3.1	0.0	0.5	0.0	0.0	2.1	5.2	3.1	7.8	0.5
237	7.5	7.5	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	4.1	1.7	2.4	0.0
243	0.0	18.3	0.0	0.0	2.3	1.9	0.5	0.5	9.9	5.2	6.6	4.2	5.2	0.5
245	9.1	2.9	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	1.4	2.4	2.4	0.0
246	3.2	22.7	0.0	0.0	9.2	0.4	0.0	0.0	1.2	2.4	1.6	0.8	9.6	0.8
247	6.3	10.0	0.0	0.0	11.8	2.2	0.0	0.4	10.3	5.2	8.5	0.4	7.0	2.2
248	0.0	0.0	0.0	1.6	3.2	18.7	9.1	4.4	3.2	1.6	2.4	6.3	9.1	1.2
249	0.0	0.0	0.4	4.7	0.0	15.8	0.0	0.4	0.0	0.4	0.0	4.3	0.8	0.4
250	9.7	6.0	0.0	0.0	2.2	0.0	0.0	0.0	0.0	0.0	2.2	0.7	1.5	0.4
300	16.8	7.5	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	1.8	2.5	0.0
302	18.7	2.5	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	2.1	1.1	1.1	0.0
303	11.4	14.7	0.0	0.0	3.3	0.0	0.0	0.0	1.1	0.0	1.1	4.0	8.1	0.4
313	5.7	18.5	0.0	0.0	6.6	0.0	0.0	0.0	2.6	2.2	4.4	4.4	4.8	0.4
314	8.6	18.8	0.0	7.2	0.0	2.4	0.3	2.1	3.4	8.2	4.5	1.4	2.7	0.7
315	0.4	1.6	0.0	0.0	8.3	3.2	1.2	0.8	7.1	6.0	9.5	3.2	11.5	0.8
316	0.0	0.4	0.0	0.0	7.3	8.4	2.5	0.0	9.1	6.9	3.3	2.9	13.8	1.8
325	19.7	5.4	0.0	0.0	2.2	0.0	0.0	0.0	0.0	0.0	1.8	8.6	0.0	0.0
326	0.0	4.2	0.0	0.0	7.1	2.5	7.5	0.8	8.4	3.8	6.7	2.9	10.0	1.7
327	0.0	5.6	0.0	0.0	3.4	0.0	0.0	0.0	0.0	0.4	0.0	6.8	0.0	0.0
335	5.4	16.1	0.0	0.0	3.7	2.5	0.8	4.5	5.4	4.1	4.5	4.1	4.1	2.9
381	4.2	3.8	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	2.8	8.4	0.7	0.0

Appendix V. Relative frequencies of the most common taxa of benthic foraminifera in piston-core 381 (IN 68-23).

first column: sample number  
 next columns: relative frequencies (percentages) per taxon  
 numbers in heading indicate:

- |  |   |
|--|---|
| 1 - <i>Textularia agglutinans</i>                            | 16 - <i>Ammonia perlucida</i>                         |
| 2 - <i>Bigenerina nodosaria</i>                              | 17 - <i>Ammonia parkinsoniana</i> forma <i>tepida</i> |
| 3 - <i>Quinqueloculina badenensis</i>                        | 18 - <i>Pseudoepionides falsobeccarii</i>             |
| 4 - <i>Quinqueloculina seminula</i>                          | 19 - <i>Elphidium advenum</i>                         |
| 5 - <i>Adelosina</i> group                                   | 20 - <i>Elphidium crispum</i>                         |
| 6 - <i>Sigmoilopsis schlumbergeri</i>                        | 21 - <i>Elphidium granosum</i> forma <i>granosum</i>  |
| 7 - <i>Triloculina trigonula</i>                             | 22 - <i>Elphidium granosum</i> forma <i>lidoense</i>  |
| 8 - <i>Bolivina spathulata</i>                               | 23 - <i>Elphidium poeyanum</i> forma <i>decepiens</i> |
| 9 - <i>Bulimina marginata</i> forma <i>aculeata</i>          | 24 - <i>Elphidium poeyanum</i> forma <i>poeyanum</i>  |
| 10 - <i>Bulimina marginata</i> forma <i>denudata</i>         | 25 - <i>Cibicides lobatulus</i>                       |
| 11 - <i>Reussella spinulosa</i>                              | 26 - <i>Cassidulina laevigata</i>                     |
| 12 - <i>Buccella granulata</i>                               | 27 - <i>Cassidulina oblonga</i>                       |
| 13 - <i>Valvulineria bradyana</i>                            | 28 - <i>Nonion barleeanum</i>                         |
| 14 - <i>Ammonia beccarii</i>                                 | 29 - <i>Nonionella turgida</i>                        |
| 15 - <i>Ammonia parkinsoniana</i> forma <i>parkinsoniana</i> |   |

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
381-1	6.9	0.3	0.7	1.7	0.3	1.4	1.0	0.0	4.2	3.8	0.7	0.7	30.9	0.0	0.0
381-2	10.5	2.2	0.4	0.7	0.9	0.4	0.4	0.0	5.9	3.9	3.7	2.2	14.4	1.5	0.0
381-3	11.3	2.1	0.3	0.3	0.7	0.7	0.0	0.0	11.3	2.1	3.1	6.5	9.2	0.7	0.0
381-4	6.9	2.1	0.6	1.2	1.5	1.2	1.2	0.0	15.9	0.0	2.7	6.3	9.3	1.5	0.0
381-5	11.9	1.7	1.0	2.0	0.7	1.4	0.0	0.0	10.9	0.0	4.1	7.5	3.1	1.0	0.0
381-6	10.7	3.7	1.1	1.5	2.2	1.1	1.9	0.0	15.4	0.0	3.3	2.9	3.7	2.2	0.0
381-7	9.1	1.6	0.7	1.0	0.3	0.3	2.3	0.0	11.7	0.0	1.0	5.9	8.8	0.0	0.0
381-8	7.9	0.8	0.8	0.8	0.8	0.8	0.4	0.0	12.2	0.0	2.8	2.8	14.2	0.4	0.0
381-9	10.1	0.4	0.0	0.8	1.6	0.0	0.4	0.0	14.0	0.0	1.6	0.4	11.7	0.4	0.0
381-10	7.0	0.4	0.7	1.5	0.7	0.7	1.9	0.0	16.2	0.0	0.7	1.1	15.4	1.5	0.0
381-11	7.4	1.1	0.4	0.7	1.1	0.4	0.7	0.0	13.3	0.4	3.0	2.6	12.2	0.7	0.0
381-12	12.1	2.3	1.1	0.0	1.5	1.9	0.4	0.0	8.3	0.4	1.9	0.8	7.2	2.7	0.0
381-13	11.1	1.7	1.2	0.4	2.1	2.1	1.2	0.4	11.6	0.0	2.5	3.7	2.1	0.4	0.0
381-14	12.0	1.2	0.0	0.4	0.4	2.0	0.4	0.0	13.2	0.0	5.6	3.6	6.8	1.6	0.0
381-15	9.2	2.8	0.4	0.4	0.8	2.0	0.4	0.0	12.4	0.0	3.2	2.4	3.2	2.0	0.0
381-16	12.3	1.1	0.7	1.5	0.4	1.5	0.4	0.0	15.2	0.4	5.6	2.2	4.5	0.7	0.0
381-17	16.1	1.1	0.7	0.7	0.7	0.7	0.0	0.0	13.2	0.0	7.3	3.7	0.0	0.4	0.0

	16	17	18	19	20	21	22	23	24	25	26	27	28	29
381-1	2.4	0.0	6.3	0.0	3.1	0.0	2.8	8.3	0.7	0.3	0.7	3.8	10.1	5.2
381-2	1.7	0.0	3.3	0.4	5.2	0.0	3.7	12.6	0.0	0.7	2.6	4.8	9.8	3.9
381-3	2.4	0.0	5.5	1.0	7.5	0.7	3.4	12.0	0.0	0.7	1.0	3.8	9.6	1.7
381-4	0.9	0.0	2.1	1.5	2.1	0.3	1.5	14.1	0.3	1.2	1.8	4.5	8.7	3.3
381-5	1.7	0.0	2.4	0.3	4.4	1.4	2.4	21.8	0.3	1.0	0.3	4.4	6.5	3.4
381-6	0.7	0.0	3.3	1.8	2.9	2.2	0.7	12.1	1.1	2.9	3.3	4.4	4.8	1.8
381-7	3.3	0.0	5.9	4.2	1.0	1.0	1.3	13.0	2.0	2.3	2.3	4.6	7.5	2.0
381-8	1.2	0.0	3.9	0.8	2.8	2.0	1.6	12.6	0.0	0.8	5.5	3.1	12.2	3.9
381-9	3.5	0.0	5.1	0.0	3.5	1.6	0.8	12.5	0.4	0.8	5.1	5.4	14.4	3.5
381-10	2.2	0.0	3.7	0.7	2.2	2.2	1.1	8.8	1.1	2.9	7.4	2.9	12.5	2.6
381-11	0.7	0.0	3.7	0.0	4.1	1.1	1.1	14.1	1.1	2.2	5.6	3.3	11.5	2.2
381-12	1.9	0.0	5.3	0.8	3.0	0.4	3.8	10.6	1.5	3.0	3.4	7.6	9.8	1.9
381-13	0.8	0.0	3.7	1.5	1.9	2.1	6.2	14.5	1.2	2.9	8.3	3.3	3.3	1.2
381-14	0.0	0.0	4.4	1.6	2.8	0.4	3.6	10.8	1.2	2.8	2.0	4.8	11.2	2.8
381-15	2.0	0.0	4.0	1.6	7.2	4.4	4.4	11.6	2.0	2.0	2.0	7.2	5.6	0.4
381-16	0.7	0.0	3.7	0.7	1.9	2.6	3.3	12.3	1.9	3.7	4.1	4.5	4.1	1.9
381-17	0.4	0.0	2.9	2.6	1.5	4.8	4.4	13.6	1.1	4.0	1.5	3.3	7.0	1.5

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