

Factors controlling the distribution of agglutinated foraminifera in Aalenian-Bajocian dysoxic facies (Pieniny Klippen Belt, Poland)

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ABSTRACT

Palaeoecological relationships between agglutinated foraminifera and environmental factors have been analysed in upper Aalenian-lower Bajocian black siltstones and mudstones (Skrzypny Formation) of the Pieniny Klippen Belt, Polish Carpathians. The formation represents isochronous and uniform deposition ranging from middle neritic to upper bathyal palaeobathymetric zones.

The lower portion of the Skrzypny Formation was deposited under anoxic to severely dysoxic conditions. The benthic microfauna is dominated by agglutinated foraminifera especially epibenthic *Trochammina* which thrived over the middle neritic to upper bathyal zone. The outer neritic was the only portion colonised by abundant endobenthic morphogroups including *Verneuilinella* and conical *Trochammina*.

The upper part of the formation is dominated by diverse calcareous foraminifera co-occurring with abundant ostracods, echinoderms, and gastropods. These associations indicate improved oxygenation of bottom water. In contrast to the lower part of the formation, the dominant agglutinated morphogroups are tubular forms such as astrophidites. The agglutinated endobenthic morphogroups were scarce and limited to *Ammobaculites fontinensis* (Terquem), which probably preferred better oxygenated conditions.

The distribution of foraminiferal assemblages and their comparison with sedimentological and palynological data suggest that agglutinated foraminifera responded primarily to bottom water oxygenation, the position of the redox potential discontinuity, and the quantity and quality of organic matter flux (nutrients for foraminifera). Finally, the agglutinated assemblages were also affected by dissolution of calcareous foraminifera, deposition rate, and the activity of macrofaunal bioturbators. All these factors were associated with the palaeotopography of the basin, its palaeogeographic position, water masses, eustatic sea level changes, and Jurassic climate.

INTRODUCTION

Previous investigations have revealed that environmental conditions play a major role in determining the distribution of benthic foraminifera. Ecological controlling factors are therefore of importance in reconstructing palaeo/ecological preferences. Unfortunately, palaeoecological interpretations of Jurassic foraminifera are hampered by a lack of direct modern analogues. There is a need, therefore, to integrate various sources of palaeoenvironmental information.

Benthic foraminifera are usually associated with various other organisms. Benthic organisms that share the same microhabitat respond in complex ways to different palaeoenvironmental change.

A comparison between the different responses to various parameters provides insight for palaeoecological studies.

Jurassic agglutinated foraminifera-dominated assemblages have been usually attributed to hypersaline and/or oxygen-deficient conditions (Gordon, 1970; Barnard *et al.*, 1981; Nagy & Johansen, 1991). The main objectives of this study are to evaluate factors controlling distribution of the Middle Jurassic foraminifera (primarily focused on agglutinated forms) in dysoxic/anoxic facies, to relate the benthic foraminiferal assemblages to palynological and ichnological data, and to compare these palaeoecological implications with modern and ancient examples.

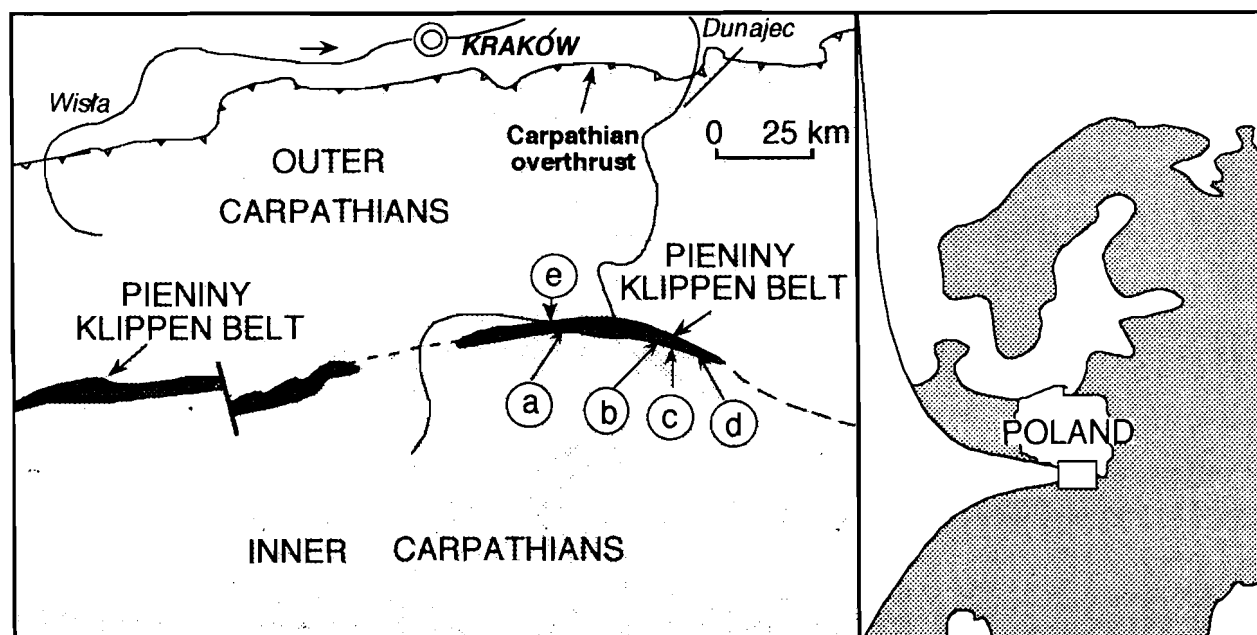


Figure 1. Location maps; localities: (a) Kapuśnica, (b) Krupianka, (c) Czajakowa Skała, (d) Biała Woda, (e) Harcygrund Valley.

MATERIAL AND METHODS

Geological outline

The upper Aalenian-lower Bajocian Skrzypny Shale Formation has been chosen for this investigation. The deposits studied crop out in the Polish part of the Pieniny Klippen Belt which constitutes an axial part of the Western Carpathians (Fig. 1). The Skrzypny Shale Formation is represented by black and dark grey claystones and mudstones containing mostly carbonaceous concretions (Birkenmajer, 1977). The mean thickness of the formation is approximately 10m, locally increasing up to 30m.

The deposits of the formation accumulated in the Pieniny Klippen Basin, which was a part of the Western Tethys (Birkenmajer, 1977). The basinal palaeobathymetric zones in the Klippen basin are represented by different depositional successions, such as the Czorsztyn, Niedzica, and Branisko successions (Fig. 2). The widespread palaeobathymetric distribution (from middle sublittoral to upper bathyal), synchronous deposition and generally uniform type of these deposits make them especially valuable for palaeoecological analysis.

Sampling and laboratory processing

A total of 33 surface samples from the Skrzypny Formation shales of the Czorsztyn Succession (17 samples; 2 locations), Niedzica Succession (7 samples; 2 locations), and Branisko Succession (9 samples; 1 location) have been collected for this study (Figs. 1, 2, 3). The sample processing consisted of drying, weighing out 250g samples, and disintegrating in a solution of sodium. The disintegrated samples were washed through sieves with mesh diameters of 105, 125, and 600 μm . The microfauna was picked from fractions 125–600 μm . The fraction 105–125 μm was tested revealing a little influence on

foraminiferal diversity and composition.

Methods of the analysis

Microfaunal analysis. For the quantitative analyses, all foraminifera were identified and counted at generic level (per 250g sample). For the morphogroup study and palaeoecological comparison, the percentage of each morphogroup has been calculated. Most of the specimens, excluding smooth-walled *Lenticulina*, have been determined at specific level for further studies.

Studies have shown that the test shape, mode of coiling, type of aperture and presence or absence of pores reflect different life positions and feeding strategies (e.g. Severin, 1983; Corliss, 1985; Jones & Charnock, 1985). Foraminiferal morphogroup analysis can be applied as a valuable tool for palaeoecological reconstructions. Moreover, all other comparative data, such as ostracods, gastropods, crinoidal and echinoidal remains, have been taken into account.

Palynofacies analysis. Benthic life is strongly linked to phytoplankton productivity. Phytoplankton remains are a main source of nutrition for benthic foraminifera (Gooday, 1988). To test foraminiferal response to the influx of phytoplankton remains, preliminary palynofacies data have been carried out. This is an analysis of the total amount of acid-resistant organic matter in sediments using palynological approach (normal transmitted light and reflected fluorescent light microscopy). Eight samples have been chosen for the analysis. These are the same samples collected for the foraminiferal analysis and represent all the depositional successions. Samples have been treated in HCl and HF acids and then washed through a 20 μm sieve.

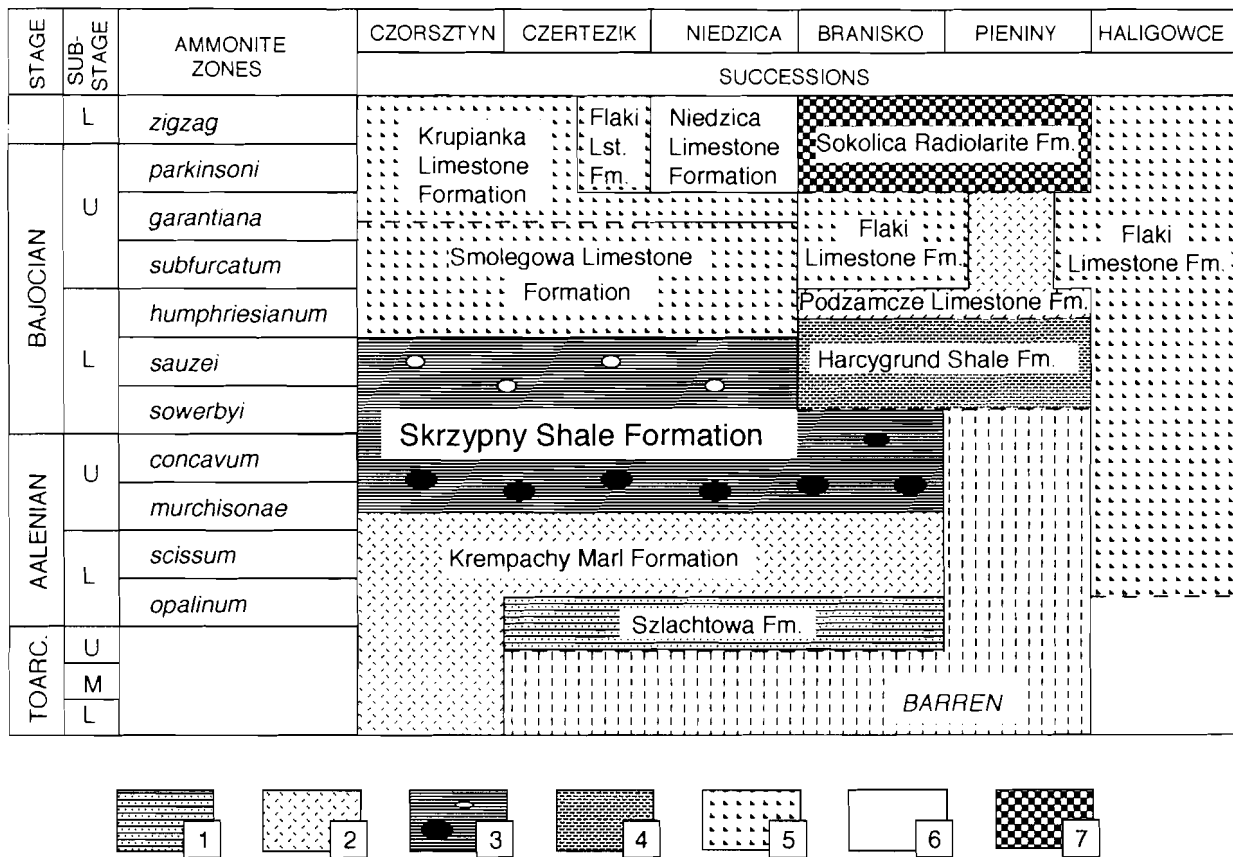


Figure 2. Lithostratigraphic units in the Pieniny Klippen Belt of Poland: Toarcian to lower Bathonian (after Birkenmajer, 1977; modified). 1. sandstones, mudstones; 2. spotted marlstones and limestones; 3. black claystones with carbonaceous (black pattern) and phosphatic (white pattern) concretions; 4. black marlstones and limestones; 5. crinoid limestones; 6. limestones; 7. radiolarites.

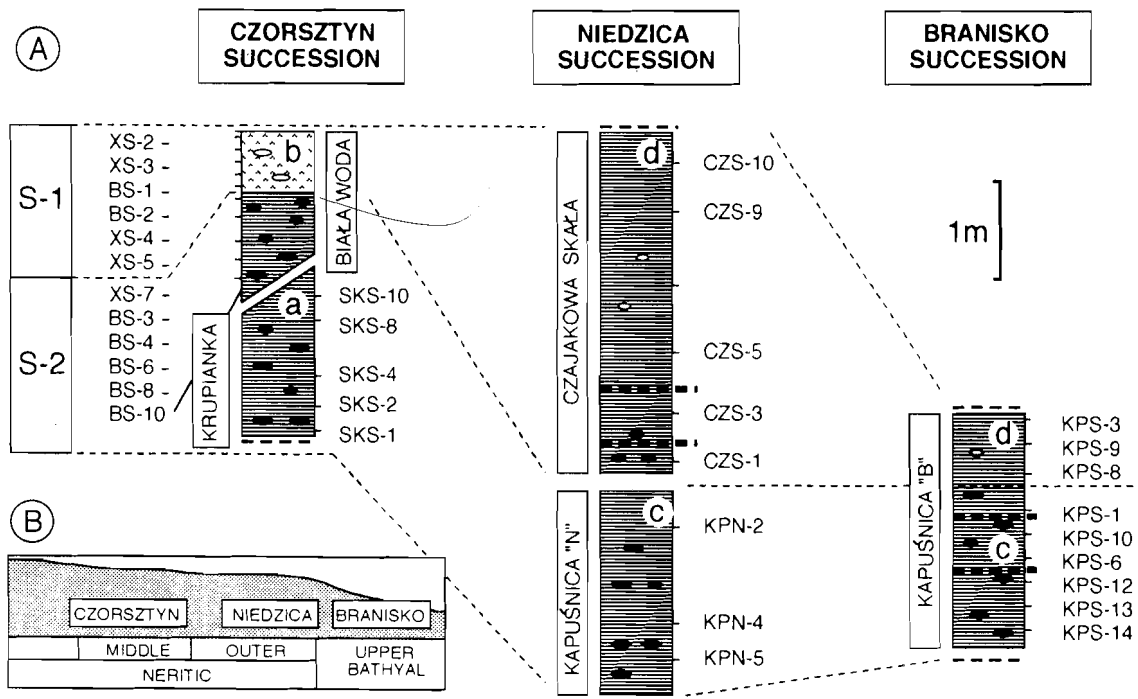


Figure 3. A. Lithostratigraphic columns of the Skrzypny Formation, localities, and samples collected (based on Tyszk, 1994b); a=black claystones with carbonaceous (mostly sideroplesite and calcite) concretions; b=grey spotted claystones and siltstones with phosphatic concretions; c=dark grey claystones with carbonaceous concretions; d=dark grey claystones with phosphate-carbonaceous concretions. Lower (S-1) and upper (S-2) part of the formation. B. Palaeobathymetric reconstruction of Pieniny Klippen Basin. Palaeobathymetric zones correspond to successions of Pieniny Klippen Belt (after Birkenmajer, 1977)

Smear slides have been prepared for the quantitative analysis of palynodebris. The simplified palynodebris classification of Brugman & Van Bergen (Van Bergen & Kerp, 1990) has been applied (Fig. 4).

Van Bergen & Kerp (1990)		This study
I	POLLEN GRAINS SPORES	POLLEN & SPORES
	UNICELLULAR ALGAE MULTICELLULAR ALGAE	ALGAE
II	WOOD REMAINS CUTICLES PLANT TISSUE	HIGHER PLANT REMAINS
III	TRANSPARENT S.O.M.	FLUORESCENT (ALGAL) A.O.M.
	YELLOW-BROWN S.O.M.	YELLOW A.O.M.
	BLACK-BROWN S.O.M.	BLACK-BROWN A.O.M.
		BLACK A.O.M.

Figure 4. Identified palynodebris categories in comparison to palynological classification; I=palynomorphs, II=structured palynodebris, III=structureless palynodebris (after Van Bergen & Kerp, 1990); S.O.M.=Structureless Organic Matter; A.O.M.=Amorphous Organic Matter.

Trace-fossil analysis. Subtle preparation methods, i.e. making small polished slabs of soft shaly sediment in the field, allowed to recognise burrow assemblages from the Czorsztyn Succession. Moreover, cutting slabs of the carbonaceous concretions completed the trace-fossil record. Comparison between foraminiferal, palynofacies, and trace-fossil data can provide considerable insight into the palaeoenvironment.

GENERAL DISTRIBUTION OF PALAEOENVIRONMENTAL INDICATORS

The shales of the Skrzypny Formation ("Murchisonae shales") have been previously attributed to a stagnant, oxygen-deficient palaeoenvironment based on the black coloration of the claystones and lack of macrobenthic fossils (Birkenmajer, 1963; Scheibnerova, 1965). In actuality, macro- and microfossil distribution patterns show a discrete complexity.

The Skrzypny Formation can be divided into two parts using lithological criteria (presence of concretions) and fossil associations, such as: trace fossils, crinoid fragments, ostracod abundance, foraminiferal abundance, and diversity (Figs. 6-8; see Tyszkka, 1994b). The lower part displays the presence of minute (0.2-0.5 mm in diameter) burrows and/or fine lamination (Ecozone S-1 sensu Tyszkka, 1994b). The foraminiferal assemblages dominated by agglutinated forms are poorly diversified and not abundant. Associated fossils are generally rare and are represented by ostracods.

By contrast, the upper part (at least 1-3m thick) contains diverse assemblages of relatively large burrows up to 15 mm in diameter (Ecozone S-2 sensu Tyszkka, 1994b). These trace fossils are represented by *Planolites*, *Thalassinoides*, *Zoophycos* and

Chondrites (Tyszkka, 1994b). The foraminiferal assemblages dominated by calcareous forms are much more diversified and relatively abundant. Associated fossils such as ostracods, small gastropods, crinoidal, echinoidal remains are much more numerous. Ammonites and the bivalve *Bositra buchii* (Roemer) are observed throughout the formation, comprising the nuclei of carbonaceous concretions.

In the lower part of the Skrzypny Formation in the Czorsztyn and Niedzica successions, numerous, large (up to 30-40 cm in diameter), spherical pelosiderite concretions occur. The upper part of the formation contains rare, small concretions (1-5 cm). Chemical analysis revealed that the concretions from the upper part of the formation are mostly phosphoritic. The phosphorus contents achieve highest values in the Czorsztyn Succession (6.80-9.40%), are intermediate in the Niedzica (4.60%), and lowest in the Branisko (1.10%). This geochemical pattern distinctly follows the palaeobathymetry of the Klippen Basin.

S [wt. %]

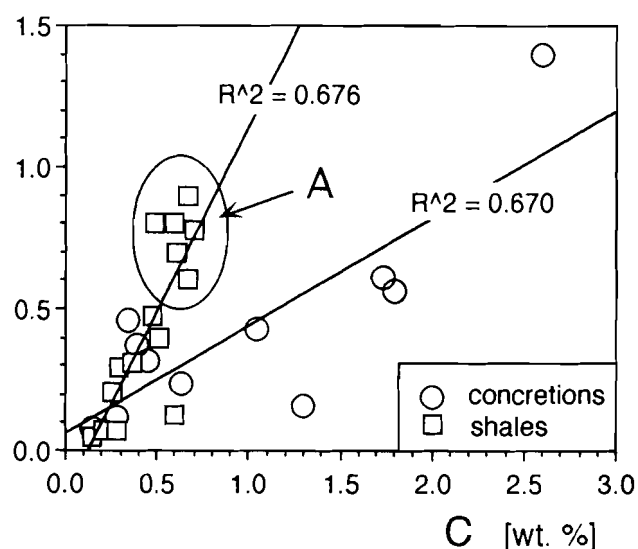


Figure 5. Plot of weight percent total organic carbon versus weight percent sulphur for shales and concretions of the Skrzypny Formation; A=cluster representing a higher pyrite content in the upper part of the formation (Czorsztyn Succession).

The organic carbon content of the shales varies from 0.15 to 0.71% also revealing the highest values within the Czorsztyn Succession (mean 0.57%). Mean organic carbon contents are similar in the Niedzica and Branisko successions - 0.21% and 0.24%, respectively. These values do not indicate anoxic benthic conditions because TOC values higher than 2% are usually believed to represent anoxicity. The shales are, however, overmature (dark brown palynomorphs with slight fluorescence), and their original TOC content may have been two to three times as high as measured. This is indicated by organic carbon values within the concretions, which varies from 0.24 to 2.60%. Moreover,

a regression analyses of TOC versus sulphur separately from shales and concretions displays a

reasonably good correlation, suggesting conditions very close to anoxia (Fig. 5; see Berner, 1984).

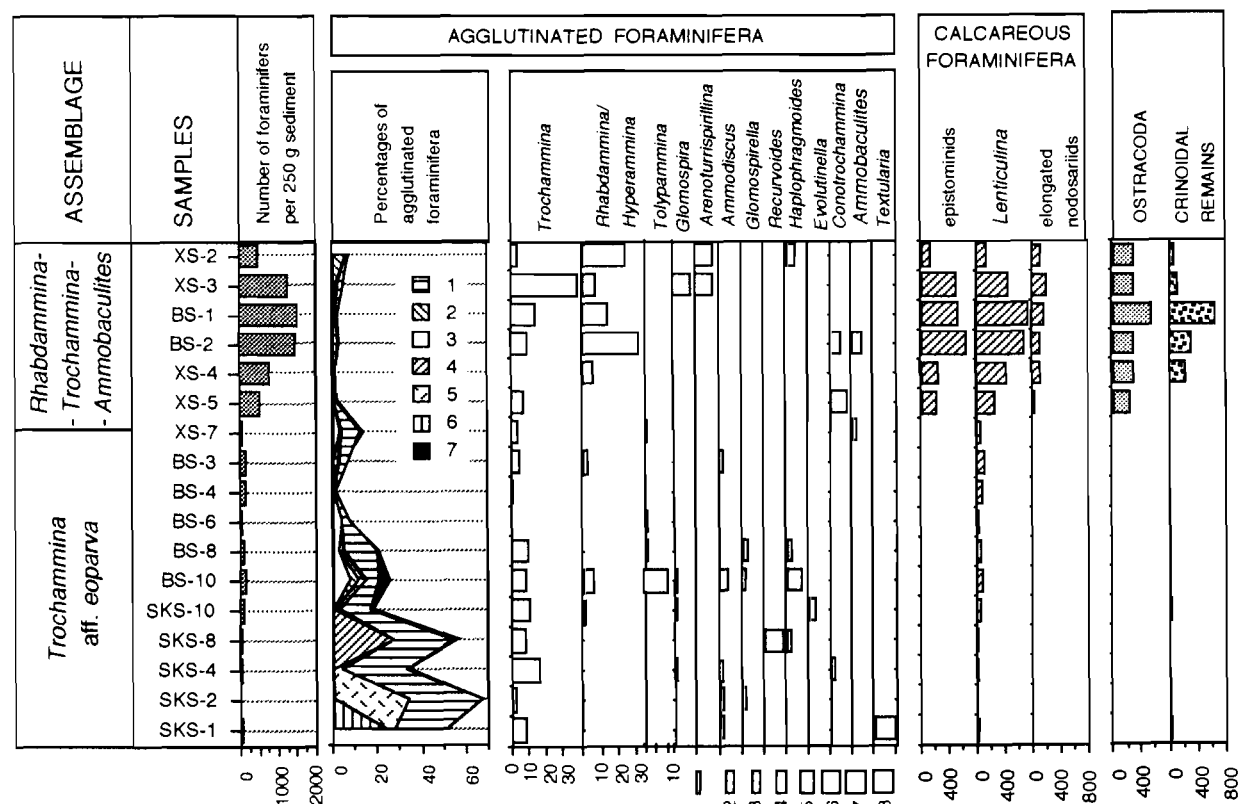


Figure 6. Distribution of agglutinated foraminifera versus calcareous foraminifera, abundances of ostracods and crinoid fragments in the Skrzypny Formation of the Czorsztyn Succession. Despite being plotted as percentage, all data are indicated in number of specimens per 250 g sample; 1=flat *Trochammina* spp., 2=*Rhabdammina*/*Hyperammina*, 3=*Haplophragmoides*, *Evolutinella*, 4=*Recurvoides*, 5=*Ammodiscus*, *Glomospirella*, 6=*Textularia*, 7=*Tolypammina*.

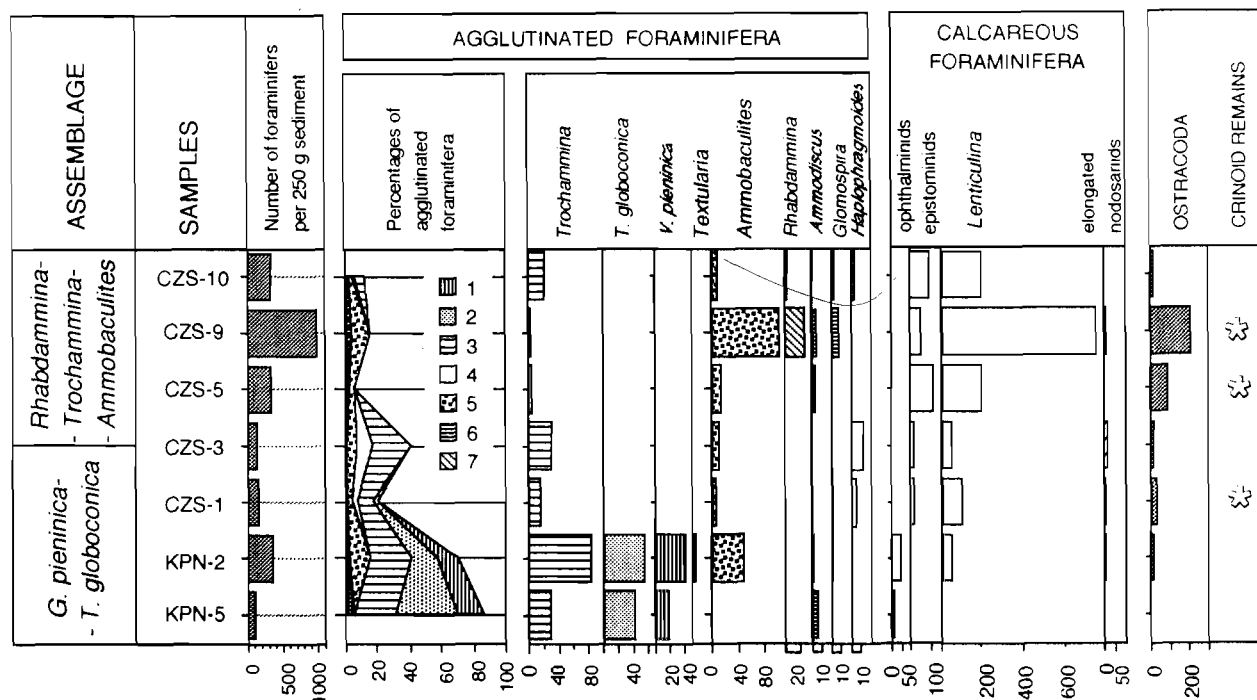


Figure 7. Distribution of agglutinated foraminifera versus calcareous foraminifera, abundances of ostracods and crinoid fragments in the Skrzypny Formation of the Niedzica Succession. Despite being plotted as percentage, all data are indicated in number of specimens per 250 g sample; (*) single occurrences of crinoidal fragments; 1=*Verneuilinella pieninica* sp.n., 2=*Trochammina globoconica* sp.n., 3=flat *Trochammina* spp., 4=*Haplophragmoides*, 5=*Ammobaculites*, 6=*Ammodiscus*, *Glomospirella*, 7=*Rhabdammina*.

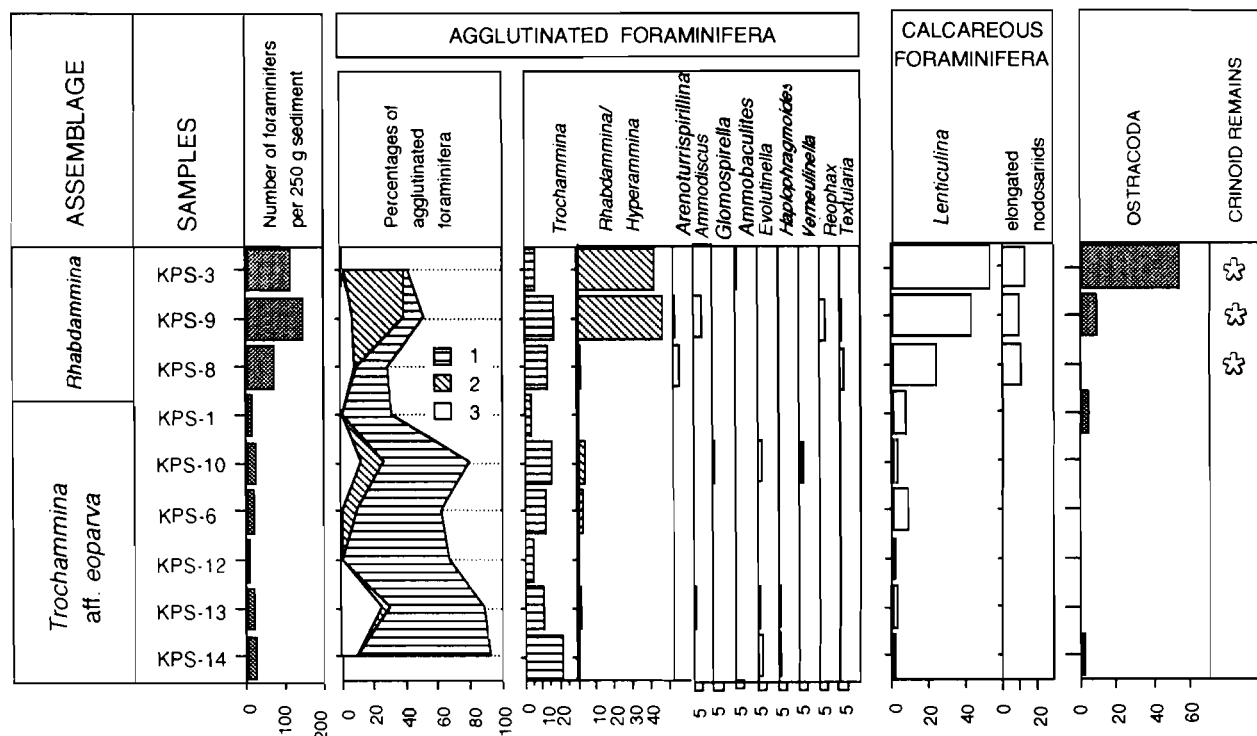


Figure 8. Distribution of agglutinated foraminifera versus calcareous foraminifera, abundances of ostracods and crinoid fragments in the Skrzypny Formation of the Branisko Succession; 1=flat *Trochammina* spp., 2=*Rhabdammina*/*Hyperammina*, 3= other agglutinated foraminifera; see Figure 7.

FORAMINIFERAL ASSOCIATIONS Lower part of the Skrzypny Formation

Trochammina aff. *eoparva* Assemblage

Samples: Czorsztyn Succession: SKS-1, -2, -4, -8, -10, BS-10, -8, -6, -4, -3, XS-7; Branisko Succession: KPS-14, -13, -12, -6, -10, -1.

The *Trochammina* aff. *eoparva* Assemblage is named after the characteristic species. The assemblage is characterised by very low abundances (10-30 specimens per 250g sample; Figs. 6, 8). The species diversity of agglutinated foraminifers is low to moderate. In addition to the typical *Trochammina* aff. *eoparva*, associated taxa in this assemblage are *T. pulchra*, *Ammodiscus*, *Recurvoides*, *Evolutinella*, *Haplophragmoides*, *Textularia*, *Tolypammina*.

This assemblage does not differ markedly between the two successions: *Tolypammina* occurs within the Czorsztyn Succession only, and *Rhabdammina* spp. and *Hyperammina* spp. are relatively more abundant within the Branisko Succession. Moreover, associated calcareous foraminifera are more abundant in the Czorsztyn succession. These differences can be related to the palaeobathymetry of the two zones (middle neritic and upper bathyal, respectively; see Tyszka, 1994b).

Calcareous Foraminifera. The associated calcareous foraminiferal assemblage displays relatively low abundance and diversity. It is dominated by smooth-walled *Lenticulina*, which plays a more important role within the palaeobathymetrically shallower Czorsztyn Succession. The latter area is also characterised by *Pseudonodosaria*, *Planularia*,

Nodosaria, *Spirillina*, and epistominids. Based on palaeoecological and taphonomical studies, these taxa are assumed to occupy epibenthic to shallow endobenthic microhabitats (Tyszka, 1994b).

Associated faunas. The associated fossil remains are extremely impoverished and consist of single smooth ostracods, echinoderm remains, and gastropods. The bivalve *Bositra buchi* is the only relatively abundant macrofossil. Small juvenile bivalves have also been found. These may be attributed to larval forms of *Bositra*. Birkenmajer (1963) and Myczyński (1973) have reported common ammonites found within the concretions. Moreover pyritized larval forms of ammonites have been occasionally recognised.

Trace Fossils. Associated trace fossil assemblages differ between the Czorsztyn and Branisko successions. The trace fossil assemblage of the Czorsztyn succession is represented by minute burrows up to 1 mm in diameter. Fine varve-like lamination has been recognised in the lowest part of the section (samples SKS-1, -2, -4) in the Krupianka Valley. Burrows of the Branisko Succession have been only recognised within the concretions and consist of a *Planolites-Chondrites* assemblage. Maximum burrow diameter measured on *Planolites* reaches 3-4 mm.

Palynofacies. The associated palynofacies (sample XS-7; Fig. 9) is characterised by an increased abundance of terrestrial higher plant remains (25-50%) and a lower amount of marine algae (0-4%), algal Amorphous Organic Matter (AOM) (0-8%), and yellow AOM (7-8%). By con-

trast, Sample SKS-4 is exceptional and reveals about 50% of yellow AOM. This relative increase in yellow AOM may be attributed to a different late diagenetical history. The higher fluorescence and lighter coloration of palynomorphs suggest the lower maturation of organic matter in the sample collected at the Krupianka locality. In fact this section represents another tectonic (Homole Block) unit within the Pieniny Klippen Belt (Birkenmajer, 1970) probably showing a different burial history.

***Verneuulinella pieninica* n.sp. - *Trochammina globoconica* n.sp. Assemblage**

Samples: Niedzica Succession: KPN-5, KPN-2.

This assemblage is named after taxa which almost exclusively occur in this association. The assemblage is characterised by high abundance (100-220 specimens per 250g sample) and moderate diversity of agglutinated foraminifera (Fig. 7). In fact, this is the only assemblage where agglutinates distinctly dominate over calcareous foraminifera.

In addition to *Verneuulinella pieninica* n.sp., and *Trochammina globoconica* n.sp., also *Trochammina* aff. *eoparva* is very abundant. Co-occurring species include *Ammobaculites fontinensis*, *Ammodiscus* spp., and *Textularia*.

Calcareous Foraminifera. An extremely poor calcareous assemblage is dominated by small ophthalminids and relatively rare *Lenticulina* spp. (Fig. 5). Other foraminifera are limited to single specimens of *Marginulinopsis*, *Pyramidulina*, *Lagena*, *Astacolus*, and *Pseudonodosaria* (Sample KPN-2).

Associated faunas. The associated microfauna is limited to 1-10 specimens of ostracods per 250g sample, pyritized juvenile ammonites, and micro-gastropods. Carbonate concretions consist of ammonites and *Bositra buchi*.

Trace Fossils. The trace fossil assemblage is represented by minute burrows up to 1-2 mm in diameter. Some of them may be classified as *Chondrites*. Fine varve-like lamination has not been observed.

Palynofacies. This palynofacies (Fig. 9) is enhanced in yellow AOM (50%) and impoverished in black-brown AOM. Higher plant remains and black AOM show equal percentages (20% each).

Upper part of the Skrzypny Formation

***Rhabdammina* - *Trochammina* - *Ammobaculites* Assemblage**

Samples: Czorsztyn Succession: XS-5, -4, BS-2, -1, XS-3, -2; Niedzica Succession: CZS-1, -3, -5, -9, -10.

This agglutinated foraminiferal assemblage is named after the dominant genera. The assemblage is characterised by variable abundances (10-150 specimens per 250g sample) and low species diversity of agglutinated foraminifera (Figs. 6, 8). In addition to the dominant *Trochammina* aff. *eoparva*, associated forms in this assemblage consist of *T. pulchra*, *Ammobaculites fontinensis*, *Glomospira*, *Recurvoides*, *Haplophragmoides*, *Conotrochammina*. All

these forms are overdominated by calcareous foraminifera (Figs. 6, 8).

This assemblage does not differ markedly between two successions. *Hyperammina* spp. is relatively more abundant within the Czorsztyn Succession. *Ammobaculites fontinensis* is more characteristic of the Niedzica Succession.

Calcareous Foraminifera. The associated calcareous foraminiferal assemblage displays a very high abundance and diversity (Figs. 6, 8). It is dominated by epistominids and diverse nodosariids. Episominids are represented by *Epistomina arcana* Antonova, *E. coronata* Terquem, and *E. semiornata* Terquem, and occasionally *Lamarckella* spp. The dominant nodosariid genera are smooth-walled *Lenticulina*, *Pseudonodosaria*, *Pyramidulina*, *Nodosaria*, *Marginulinopsis*, *Planularia*, *Vaginulinopsis*. The assemblage occasionally contains other foraminifera, such as *Ramulina*, *Spirillina*, *Spirophthalmidium*. Associated calcareous foraminifera are more abundant in the Czorsztyn Succession. This can be related to the palaeobathymetry of both zones. (middle to outer neritic). Based on palaeoecological and taphonomical studies, these taxa are assumed to occupy the whole range of microhabitats from epibenthic to deep endobenthic (Tyszk, 1994b).

Associated benthic faunas. Very abundant smooth-carapace ostracods, small gastropods, crinoidal fragments and echinoidal spines co-occur with foraminifera. Occasionally abundant beds with *Bositra buchi* have been found. Moreover juvenile bivalves and ammonites are very common. There is a trend in the abundance of the associated fauna, with samples from the Czorsztyn Succession displaying a higher abundance.

Trace Fossils. Associated trace fossils differ between both successions. The strongly bioturbated claystones and siltstones of the Czorsztyn Succession are dominated by the ichnotaxa *Thalassinoides*, *Planolites*, *Zoophycos*, *Chondrites*, and composite burrows. Maximum burrow diameter measured on *Thalassinoides* reaches 15 mm. All these burrows were produced preferentially at different depths within the substrate creating a tiering structure (see Werner & Wetzel, 1982). This tiering of burrows can be reconstructed applying cross-cutting relationships between various burrows. Thus *Thalassinoides* and *Planolites* are cross-cut by *Zoophycos*, *Chondrites* indicating that the last two represent the deepest tier within the substrata. The trace-fossil assemblage from the Niedzica Succession is not diverse and is represented by *Planolites* and *Chondrites*. The maximum burrow diameter is smaller, reaching just 5 mm.

Palynofacies. Black-brown AOM dominates (34-56%) within this biofacies. Moreover algal AOM, marine algae, and yellow AOM appear to be relatively increased (Fig. 9).

***Rhabdammina* Assemblage**

Samples: KPS-3, KPS-8, KPS-9.

This assemblage is named after the most abundant genus *Rhabdammina* (Fig. 8). Some of these forms should probably be attributed to *Hyperammina* spp. Low to moderate abundances (10–60 specimens per 250g sample) and moderate diversity characterise the assemblage. *Trochammina* aff. *eoparva* and *T. pulchra* are relatively abundant. Moreover, *Arenoturrspirillina*, *Ammodiscus*, and *Reophax* are present.

Calcareous Foraminifera. The co-occurring calcareous foraminifera are dominated by *Lenticulina* associated with *Spiroloculina*, *Spirillina*, *Laevidentalina*, *Pseudonodosaria*, and other single nodosariids.

Associated benthic faunas. Ostracods, pyritized casts of gastropods, single crinoidal fragments, and juvenile bivalves have been found. Ostracods are either lacking or are moderately common (up to 50 specimens per 250g sample).

Trace Fossils. The trace fossil assemblage is represented by *Planolites* and *Chondrites*. Maximum burrow diameter measured on *Planolites* ranges from 5 to 6 mm. Fine varve-like lamination has not been observed.

Palynofacies. This palynofacies (Fig. 9) is relatively enhanced in yellow AOM. Higher plant remains and black-brown AOM show equal percentages (a. 20%).

DISCUSSION.

FACTORS AFFECTING THE COMPOSITION OF BENTHIC FORAMINIFERAL ASSEMBLAGES

Oxygenation level vs. organic matter influx

Oxygenation level and organic matter influx have been recognised as a main controlling factor for foraminiferal distribution within black shale deposits (Bernhard, 1986; Koutsoukos *et al.*, 1990; Sjoerdsma & Van der Zwan, 1992; Jorissen *et al.*, 1992; Sen Gupta & Machain-Castillo, 1993). It can be assumed that the black claystones and siltstones studied represent oxygen-deficient facies. The extreme dysoxic, suboxic to episodically anoxic facies may be attributed to the lower part of the Skrzypny Formation. This is indicated by the lack of benthic macrofossils, appearance of fine varve-like lamination slightly disturbed by minute burrows, and generally small maximum burrow diameter within the bioturbated intervals (see Savrda & Bottjer, 1989). All these characteristics are especially typical for the palaeobathymetrically shallowest zone (Czorsztyn Succession). This facies is represented by the *Trochammina* aff. *eoparva* Assemblage which is characterised by very low abundances and diversity of agglutinated foraminifers associated with poor calcareous foraminifera dominated by *Lenticulina* spp.

On the other hand, the same assemblage has been found within the upper bathyal zone (in the Branisko Succession). This deeper facies does not exhibit any evidence of extended anoxia. The sedi-

ment is bioturbated by minute or small burrows, suggesting slightly better oxygenation i.e. suboxic to severe dysoxic conditions. This is also supported by organic carbon content which achieves twice to four times lower values in the Branisko Succession than in the Czorsztyn Succession. It therefore implies that neither oxygenation level alone, organic carbon values nor the depth governed this assemblage in different subenvironments.

The organic carbon content varies between successions, but shows similar palynofacies proportions i.e. both palynofacies display a relative increase in terrestrial plant remains and low proportions of amorphous organic matter and algae. These constituents may suggest that the bottom organic influx was depleted in algal remains. Most of the organic matter introduced into the bottom probably come from land. In fact, terrigenous organic remains are not as efficient as algal or bacterial organic matter which seem to be an easy-metabolizable source of nutrition for foraminifera.

Moreover, the *Trochammina* aff. *eoparva* Assemblage is numerically dominated by inferred epibenthic forms represented mainly by genus *Trochammina*. The palaeoecological and taphonomical study of associated *Lenticulina* spp. revealed that this form preferred shallow endobenthic to epibenthic microhabitat when co-occurring with *Trochammina* (Tyszkla, 1994b). The lack of deep infaunal morphotypes and impoverished burrowing activity point out that the redox potential boundary was located just beneath the sediment/ water interface. It seems likely that the coupling effect of extremely low oxygenation with a low influx of phytoplankton remains controlled the distribution of the *Trochammina* aff. *eoparva* Assemblage.

By contrast, *Verneuilinella pieninica* - *Trochammina globoconica* Assemblage attributed to the outer neritic zone completely differs in abundance, diversity, and composition. This assemblage is dominated by inferred endobenthic morphogroups (*Verneuilinella*, conical *Trochammina*, *Ammobaculites*). It is unlikely that the bottom water oxygenation was higher in the Niedzica palaeobathymetric zone. Ichtnologic and palaeontologic indicators imply suboxic to severe dysoxic conditions, thus, similar to the deeper part of the basin (Branisko Succession). Recent interpretations point out that assemblages with abundant and dominant endobenthic foraminifera reflect a higher organic-carbon flux (Corliss & Chen, 1988; Corliss & Fois, 1991; Herguera & Berger, 1991). If it could be applied in this study, we would expect a higher organic matter influx into the outer neritic zone. This is also suggested by a relative increase in yellow amorphous organic matter. Nevertheless, this increase is not coupled with an enhanced organic carbon content that may imply its syn- or postsedimentary utilisation. In fact, the concretions show a higher organic carbon content (ca. 1%) indicating its higher synsedimentary availability.

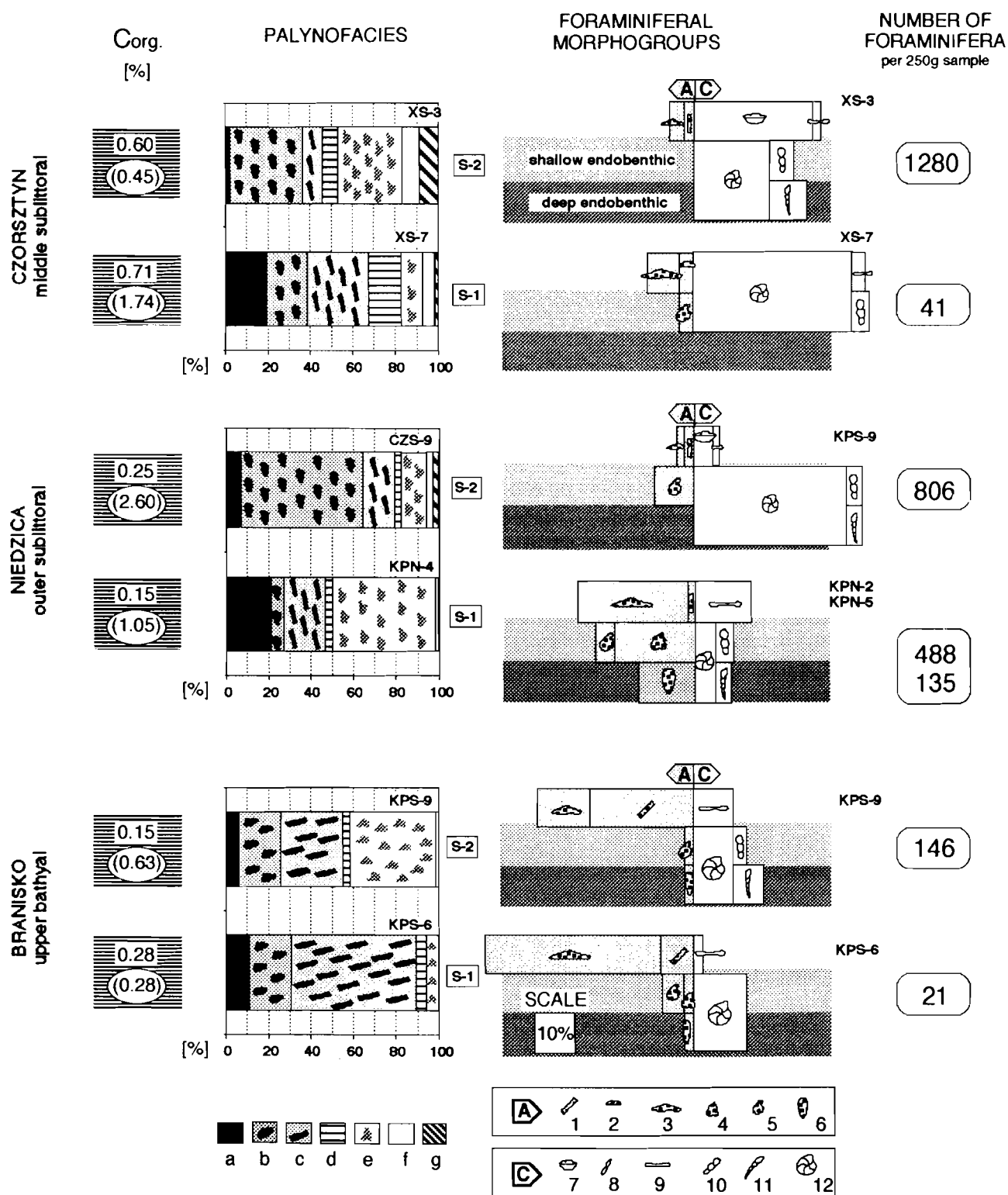


Figure 9. Comparison of organic carbon content within shales and concretions, palynofacies, foraminiferal morphogroups, and abundances of foraminifera within selected samples from the Skrzypny Formation. Organic matter types: a = black AOM, b = black-brown AOM, c = higher plant remains, d = pollen and spores, e = yellow AOM, f = fluorescent AOM, g = algae (mainly dinocysts). (S-1) = lower and (S-2) = upper part of the Skrzypny Formation. (A) Agglutinated foraminiferal morphogroups: 1 = tubular (*Rhabdammina*, *Hyperammina*), 2 = adherent (*Tolypammina*), 3 = planispiral and low-trochospiral (epibenthic), 4 = conical trochospiral, 5 = planispiral (epi-endobenthic), 6 = elongated; (B) calcareous foraminiferal morphogroups: 7 = planoconvex (epistominids), 8 = irregular, meandrine, 9 = planispiral, 10 = elongated, inflated (e.g. *Nodosaria*), 11 = elongated with straight periphery, 12 = lenticular.

It remains uncertain what kind of nutrition influenced the expansion of the *Verneuilinella pieninica* - *Trochammina globiconica* Assemblage. We speculate that enhanced appearance of benthic bacteria favoured thriving of the foraminifers. Moreover it may have been related to the "edge effect" which has recently been recognised at the upper boundary of the Central California Oxygen Minimum Zone (Thompson *et al.*, 1985; Vercoutere *et al.*, 1987). Passing through extreme and severe dysoxic conditions (about 0.5 ml/l sensu Tyson & Pearson, 1991) causes the appearance of bacterial mats and an increase in faunal density. It is likely that benthic bacterial mats created a nutrition-rich subenvironment for this assemblage. It may be also speculated from the co-occurrence with abundant tiny ophthalminiids which have been previously reported in association with stromatolites in Callovian strata (Olszewska & Wieczorek, 1988).

The organic matter and oxygen control on foraminiferal associations is even more manifested in the upper part of the formation. Here a major change in foraminiferal assemblages is observed. Calcareous foraminifera took over the areas previously dominated by the agglutinates. Rare agglutinated foraminifera were represented by the *Rhabdammina* - *Trochammina* - *Ammobaculites* Assemblage in the middle and outer neritic zone, and the *Rhabdammina* Assemblage in the upper bathyal part of the basin.

Reasons for this faunal turnover should be apparent in the sedimentary record. The association of the early diagenetical sideritic concretions with black claystones was replaced by an association with small phosphatic concretions. The sediment associated with phosphatic concretions can be attributed to a fertile upwelling zone (Heckel, 1977; Sandberg & Gutschick, 1984). It seems likely that the increase in endobenthic and epibenthic foraminifera were linked to phytoplankton blooms that supplied rich nutrition. These blooms may have caused episodic or periodic anoxic conditions usually associated with upwelling areas (Kaminski *et al.*, this volume). The sediment was therefore rich in reactive organic matter which controlled sulfate reduction and pyrite formation (Berner, 1984). This is indicated by the positive correlation between the sulphur content and organic carbon in the samples from the Skrzypny Formation (Fig. 5). The higher pyrite content within shales (cluster A - Fig. 5) may be related to a higher availability of the reactive organic matter in the Oxygen Minimum Zone during deposition of the upper part of the formation.

Blooms may have caused periodic anoxicity of the bottom water. However, this is in disagreement with trace fossil and microfaunal data because larger maximum diameters of burrows and abundant calcareous benthic microfauna suggest a better oxygenation conditions (see Barnard *et al.*, 1981; Savrda & Bottjer, 1989). In fact both indicators fit when we

imply periodicity of upwelling and blooms. This periodicity first caused blooms and associated anoxicity of the shelf, then gradual oxygenation. This allowed the sediment to be successively recolonised by benthic fauna covering up primary sedimentary structures.

The *Rhabdammina* Assemblage shows a higher proportion of agglutinates dominated by tubular forms. An associated increase in amorphous organic matter (AOM) suggests a higher influx of metabolizable organic matter (Figure 9). This appears to be consistent with the inferred reasons of the faunal turnover in the shallower zones. Furthermore, upwelling over the sublittoral part of the basin could have been connected with the hydrodynamic conditions along the basin slope. This may have favoured increased numbers of suspension-feeding tubular foraminifera (see Altenbach *et al.*, 1988; Thies, 1993).

Macrobioturbators.

Studying the relationships between various groups of benthic organisms is extremely difficult in the fossil record. Nevertheless, there is no doubt that macrofaunal organisms influence the distribution of microfauna. Dayton (1984) remarked that large infauna (endobenthos) produce niches for small species and create biologically-induced heterogeneity of the habitat. There are several different relationships between benthic organisms. Experiments by Buzas *et al.* (1989) have shown that macrofaunal predation significantly reduces foraminiferal densities.

If predation alone controls foraminiferal densities, we should therefore expect impoverished foraminiferal assemblages within highly bioturbated sediments. In fact, there is an opposite trend in the deposits studied i.e. strongly bioturbated strata contain very abundant and diverse foraminifers. It is more likely that oxygenation and organic carbon influx controlled both macrofaunal and microfaunal palaeocommunities.

Furthermore, foraminiferal assemblages dominated by epibenthic and shallow endobenthic morphogroups (*Trochammina*, tubular forms) show a distinctive distribution related to shallow burrow tiering. An increase in foraminiferal abundances, and in deep endobenthic foraminiferal (mostly calcareous) morphogroups characterised by elongated shape and flush sutures co-occurs with extensive bioturbation and deep burrow tiering. Thus foraminifers shared the same microhabitat interacting with macrobioturbators. Perhaps foraminifera profited from bioturbating activity by feeding on enhanced amounts of bacteria which thrived on mucus and waste products. Moreover, macrobioturbators extended the niche space oxygenating the deeper substrate and trapping fresh metabolizable nutrients from the surface in their burrows (see Aller & Aller, 1986; Langer *et al.*, 1989).

Deposition rate and eustatic sea-level changes

Surface productivity (organic carbon flux) is correlated with benthic foraminifera abundance (Herguera & Berger, 1991). On the other hand, Gradstein (1983) pointed out that an "increase" in the number of tests per unit volume of sediment can be caused by a slower sedimentation rate. It is therefore essential to consider changes in the flux of terrigenous sediments when interpreting foraminiferal abundances. The appearance of *Zoophycos* in the upper part of the formation and a relatively strong increase in number of foraminifera reflects a lower sedimentation rate despite the foraminiferal response to organic carbon influx. Subsequent findings of phosphatic concretions, which are usually associated with condensed horizons, also supported this suggestion. Such concretions are reported as sequences of sea-level rise interpreted to be caused by eustatic rise (e.g. Heckel, 1977) or platform drowning (Föllmi, 1989).

Moreover, a sea-level rise may be indicated by "floods" of epistominids, an increase in numeric abundance of foraminifera enriched in uncoiled

nodosariids and small-size coiled *Lenticulina* spp. (see Tyska, 1994b). This is in agreement with previous studies. Flood occurrences of epistominids (Robertinidae) were previously found to be associated with the Early Jurassic transgressions (Copestake & Johnson, 1991). Likewise, Rey *et al.* (1993) analyzed various system tracts and concluded that transgressive system tracts correlate with an abundance of different species, small-size *Lenticulina* and the presence and development of certain rectilinear or uncoiled nodosariids.

There is little doubt that eustatic sea-level changes influenced palaeoenvironmental conditions in the semi-enclosed Klippen Basin. Sea-level lowstands represented by the lower part of the Skrzypny Formation caused stratification of the water column and stagnation of the bottom water. The water masses were changed during a transgressive phase bringing about mixing of the water via sills and upwelling nutrient-rich water to the neritic part of the basin. All these factors controlled the distribution of agglutinated foraminifera and other benthic organisms (Fig. 10).

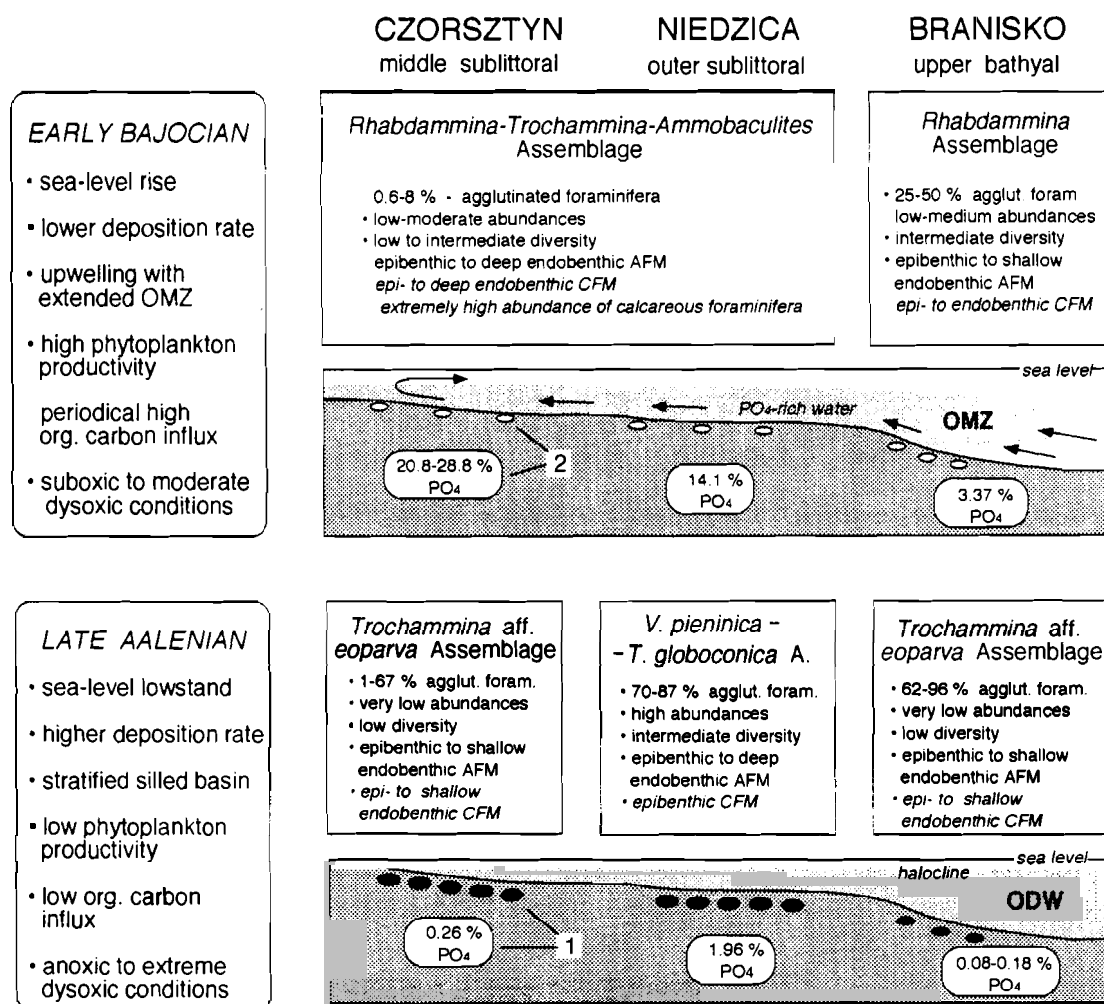


Figure 10. General characteristics of foraminiferal assemblages compared with palaeoenvironmental reconstruction of the Pieniny Klippen Basin in the late Aalenian and the early Bajocian. ODW - Oxygen Depleted Water; OMZ - Oxygen Minimum Zone; (1) carbonaceous concretions and (2) phosphate concretions with PO₄ content; variable vertical scale.

PALAEOECOLOGICAL IMPLICATIONS

The comparison of morphogroup analysis with previous studies of Jurassic benthic foraminifera provides new insight into the palaeoecological preferences of selected taxonomic groups.

Rhabdammina/Hyperammina. These tubular forms have been reported as abyssal-oceanic forms from the Atlantic part of the Tethys by Luterbacher (1972), Kuznetsova (1974), and Gradstein (1983) in agreement with their modern distribution (see Brady, 1884). Their very common abundance in deeper environments may be attributed to their suspension-feeding strategy and point to a low sedimentation rate and moderate hydrodynamic energy (Jones & Charnock, 1985; Altenbach *et al.*, 1988; Thies, 1993). On the other hand, Buzas *et al.* (1993) based on a statistical evaluation of recent data from various sources stated that tubular forms prefer a shallow to deep infaunal microhabitat.

The results of this study and previous studies support the idea that this group preferred the deep abyssal and bathyal depths, where they often comprise 90 percent of the foraminiferal assemblage (Tyszka, 1994a). *Hyperammina* and *Rhabdammina* could have survived in poorly oxygenated conditions related to the strongly dysaerobic biofacies.

It is curious that tubular forms have also been found in the Czorsztyn Succession, which represents a neritic environment (see Figs. 6, 10). This may be connected with a temporary low sedimentation rate and/or with the morphology of this shallow basin floor (Tyszka, 1994b).

Tolypammina. This adherent ammodiscid was reported by Munk (1980) from Upper Jurassic sediment deposited in the shallow epicontinental sea. This genus also represents a similar middle neritic environment in the Klippen Basin. *Tolypammina* has been found in sediment related to suboxic conditions. Its low abundance may be attributed to the unfavourable soupy substrate. Most likely, *Tolypammina* tests were attached to the shells of the bivalve *Bositra buchi*. Similar environmental preferences, i.e. a strong oxygen-deficiency and normal marine organic-rich facies, were reported from in the Upper Jurassic lower Nupra shales of Nepal (Nagy *et al.*, this volume).

Ammodiscus, Glomospirella. These genera are relatively rare in the studied material and co-occur with very low abundant and diverse assemblages attributed to the strongly dysaerobic biofacies. They were not restricted to a specific bathymetric zone but were relatively more common in the shallower environment which may have received a greater terrestrial supply. Nagy & Johansen (1991) reported common *Ammodiscus* in association with *Trochammina* from brackish deltaic facies with a high terrestrial impact.

Ammobaculites. *Ammobaculites fontinensis* occupied the whole bathymetric range from the middle neritic to upper bathyal or even abyssal depth. This probably shallow endobenthic genus preferred sed-

iment enriched in organic matter with relatively better oxygenated interstitial water. *A. fontinensis* achieved the highest abundance in the outer neritic zone and was associated with abundant and diversified calcareous foraminiferal assemblages. This species does not appear very opportunistic and it could be attributed to the intermediate taxa in the analysed environment. Morris (1982) reported another Jurassic species *A. coprolithiformis* as a less specialised form tolerant of phytal and non-phytal habitats.

Distinctly less abundant *Haplophragmoides* has revealed similar palaeoecological preferences. Another closely related evolute-planispiral genus *Evolutinella* occurred in a deeper environment attributed to the low oxygenated conditions.

Flat trochamminids. *Trochammina* seems to be the most cosmopolitan agglutinated foraminiferal taxon during the middle Jurassic. This genus has been described from shallow epicontinental to abyssal oceanic environments (Gradstein, 1983).

Assemblages with relatively common *Trochammina* represent the whole range of habitats from the shallow to the deep environment and from suboxic to moderate dysoxic conditions. However, this taxon played a more important role in extreme and severe dysoxic regimes represented by low abundant and diversified foraminiferal assemblages with a decreased calcareous foraminiferal and ostracod component.

Trochammina reveals an inverse distributional trend to tubular foraminifers and correlates with an increased abundance of terrestrial higher plant remains (Figs. 9, 10). Nagy & Johansen (1991) reported that a dominance of this taxon reflects a brackish, low oxygenated environment with a greater degree of terrestrial influence. The abundance of *Trochammina* is therefore related to the amount of higher plant influx from land. Modern trochaminids are usually passive or active herbivores and are common only in shallow environments (Jones & Charnock, 1985). Its different distributional pattern during the Early and Middle Jurassic indicates that this taxon had a different feeding strategy, and was not as specialised as it is today.

This taxon was more opportunistic than its younger successors in relation to stressed environments. Even the Late Jurassic trochamminids appear to be less tolerant to increasing dysoxia, giving way for more opportunistic infaunal morphogroups (Holbourn, 1992).

Verneuulinella pieninica - Trochammina globoconica. These species indicate a narrower range of preferences. They were common only in the outer shelf attributed to strongly and moderately dysaerobic biofacies (Niedzica Succession). Their high conical shape was probably suitable for an epibenthic to deep endobenthic organic-rich microhabitat. Higher frequencies of these inferred endobenthic forms point out to higher food availability. Perhaps "microaerophilic" bacterial

mats have been proposed as a source of nutrition for these taxa. This type of bacterial activity is typical of suboxic modern environments (Williams & Reimers, 1983).

Furthermore, these conical forms have been found in association with abundant ophthalminids, which are generally rare in other samples. Olszewska & Wiczeorek (1986) detected a peak in abundance of ophthalminids in a section associated with stromatolites on the Callovian North European Platform. Moreover, a similar assemblage with *Verneuilinella* and other numerous endobenthic agglutinated foraminifera have been found co-occurring with shamositic oncoides with stromatolite-like structures within a condensed section from the Flaki Formation (Fig. 2). All these records classify *V. pieninica* and *T. globoconica* as bacterial scavengers.

***Recurvoides*.** This is a rare genus in the Lower and Middle Jurassic. Nagy & Johansen (1991) have reported this genus in low or occasionally significant frequencies from Upper Jurassic prodeltaic sediments of the North Sea area. In our samples, *Recurvoides* has only been recognised in the lower part of the Skrzypny Formation (within Czorsztyn Seccession) thus from a shallow, oxygen-depleted palaeo-environment. In the Late Jurassic low oxygen environments this genus was much more common, occupying deeper habitat (Nagy *et al.*, this volume). During the Cretaceous, *Recurvoides* successfully colonised even the deepest abyssal environments comprising a major part of the flysch-type assemblage. This taxon represents reduced oxygen conditions (at least in the Jurassic), a relatively high sedimentation rate, with a tendency to invade deeper habitats through the time i.e. shallow in Early-Middle Jurassic to deep bathyal in the Cretaceous.

DISCUSSION AND CONCLUSIONS

Integration of various palaeoecological indicators revealed the complexity of factors associated with oxygen-deficiency in the studied facies. It seems obvious that oxygenation levels are not the only controlling factor. Organic matter enrichment appears to be an associated feature. Various authors have pointed out the influence of high epipelagic productivity on oxygen deficiency and nutrient availability (e.g. Koutsoukos *et al.*, 1990; Herguera & Berger, 1991) but the relation between the abundance of dysoxia-tolerant species and the quality of organic matter has not been explored (Sen Gupta & Machain-Castillo, 1993). This study demonstrates a direct relation between the quality of organic matter (palynofacies) and the distribution of benthic foraminifers.

Two different types of dysoxia-tolerant assemblages have been reported: (1) an opportunistic assemblage with abundant forms (Phleger & Soutar, 1973) and (2) a low abundance biofacies (Alve, 1990). The problem of two different distributional

trends has been pointed out by Sen Gupta & Machain-Castillo (1993) and is related to the tolerance to oxygen deficiency and preference for organic-rich sediment. The assemblages from the Klippen Basin reveal similar two reversal patterns: (1) relatively abundant assemblages dominated by either by agglutinated or calcareous endobenthic foraminifera, (2) relatively impoverished assemblages with low abundances, dominated by either epibenthic agglutinated foraminifera or coiled *Lenticulina* spp. These overall differences are attributed to the trophic structure and related to different organic matter inputs. Intensity, duration, and periodicity of anoxia may be other possible factors that had an impact on foraminiferal assemblages (Koutsoukos *et al.*, 1990). In general, following factors are likely to have governed the distribution of foraminifers in dysoxic conditions of the Skrzypny Formation:

- (a) oxygenation level
 - bottom water oxygenation,
 - interstitial oxygenation (depth of the redox potential discontinuity);
- (b) organic matter
 - quality (nature and origin of OM: whether it derives from terrestrial, phytoplankton, or benthic sources)
 - quantity of organic matter flux;
- (c) macrobioturbators
- (d) early diagenetic dissolution of foraminiferal tests
- (e) deposition rate (flux of terrigenous sediments).

It is considered that the type of the sediment (grain size; carbonate content) was not a controlling factor.

All these direct factors were related to primary factors (see Fig. 8):

- (a) water masses (strength of upwelling, stratification of water masses, physical characteristics);
- (b) nutrient availability;
- (c) palaeotopography of the basin;
- (d) palaeogeographic position;
- (e) eustatic sea-level changes;
- (f) climate;
- (g) evolutionary trends.

SYSTEMATIC DESCRIPTIONS

Order Foraminifera Eichwald, 1830

Suborder Textulariina Delage & Hérouard, 1896

Superfamily Astrorhizacea Brady, 1881

Family Bathysiphonidae Avnimelech, 1952

Genus *Rhabdammina* M. Sars, 1869

Rhabdammina spp.

Plate 1, Figs. 1-2

Remarks: This category includes all coarsely agglutinated tubular forms.

Genus *Rhizammina* Brady, 1879

Rhizammina sp.

Remarks. Specimens resemble *Rhabdammina* spp. but show branching tubular pattern.

Superfamily HIPPOCREPINACEA Rhumbler, 1895

Family HIPPOCREPINIDAE Rhumbler, 1895

Genus *Hyperammina* Brady, 1878

Hyperammina sp.

Plate 1, Fig. 3

Description. Tubular finely agglutinated forms; wall glassy in appearance; only single specimens show preserved proloculus.

Remarks. All finely agglutinated tubular forms were placed in this group.

Superfamily AMMODISCACEA Reuss, 1862

Family AMMODISCIDAE Reuss, 1862

Genus *Ammodiscus* Reuss, 1862

Ammodiscus spp.

Remarks. Specimens are poorly preserved.

Genus *Arenoturrspirillina* Tairov, 1956

Arenoturrspirillina sp. A

Plate 1, Fig. 4

Description. Test conical, trochospirally enrolled. Consists of a proloculus and a tubular second chamber of constant diameter. Umbilical side concave. Diameter of figured specimen 0.37 mm.

Genus *Tolypammina* Rhumbler, 1895

Tolypammina sp.

Plate 1, Figs. 5-6

Description. Test attached (preserved specimens separated from surface of attachment) planoconvex; proloculus not visible; second chamber winds irregularly; planar part distinctly flat revealing a meandering or somewhat irregular planispiral arrangement. Wall glassy, finely agglutinated; maximal diameter 0.4-0.5 mm.

Genus *Glomospira* Rzehak, 1885

Glomospira perplexa Franke, 1936

Plate 1, Fig. 7

Glomospira perplexa Franke, 1936, p. 18, pl. 1, fig. 12.

Glomospira perplexa Franke. - Tappan, 1955, p. 41, pl. 9, fig. 10.

Description. Test consists of a proloculus and irregularly coiled second undivided tubular chamber. Dense coiling does not follow any pattern. Wall finely agglutinated. Aperture at the open end of the second chamber. Maximal diameter of figured spec-

imen 0.42 mm, minimal 0.25 mm.

Remarks. Specimens are larger in size than the figured holotype (see Franke, 1936). Tappan (1955) pointed out that this genus is variable and the regularity of coiling could be nevertheless conspecific. Tappan's Early Jurassic forms are more regular in the spiral winding.

Genus *Glomospirella* Plummer, 1945

Glomospirella sp.

Description. Test small, initially streptospiral, later planispiral, finely agglutinated.

Superfamily HORMOSINACEA Haeckel, 1894

Family HORMOSINIDAE Haeckel, 1894

Genus *Reophax* de Montfort, 1808

Reophax sp.

Plate 1, Fig. 9

Description. An extremely coarse species with indistinctive chambers.

Family HAPLOPHRAGMOIDIDAE Maync, 1952

Genus *Evolutinella* Myatlyuk, 1971

Evolutinella sp. 1

Figure 11

Description. Test, planispiral, evolute, distinctly compressed; 2-3 whorl; 8-10 chambers in the last whorl; small globular chambers; periphery lobate; sutures flush; wall coarsely agglutinated.

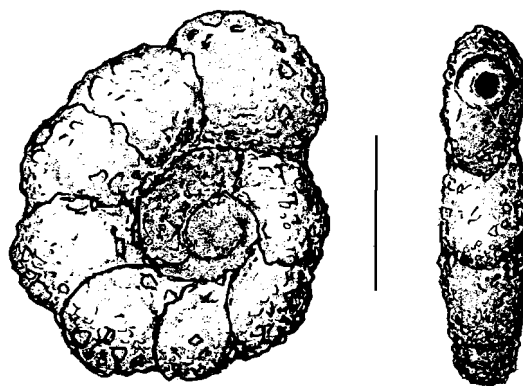


Figure 11. *Evolutinella* sp. 1, spiral and peripheral views, sample CZS-3; scale bar = 100 μ m.

Genus *Haplophragmoides* Cushman, 1910

Haplophragmoides globigerinoides (Haeusler, 1882)

Plate 1, Figs. 10-11

Trochammina globigerinoides Haeusler, 1882, p. 352, pl. 15, figs. 8, 9.

Haplophragmoides globigeriniformis (Haeusler)-Oesterle, 1968, p. 727, figs. 23, 24, 28b.

Description. Test small, planispiral, involute; final whorl consists of four chambers; chambers gradually increasing in size; periphery lobulate; sutures depressed, rounded; finely agglutinated with granulate surface.

Haplophragmoides sp. 1

Plate 1, Figs. 12-13

Description. Test, planispiral, involute, distinctly compressed; 6-7 chambers in the last whorl; chambers triangular; periphery non-lobate, rounded; sutures flush; wall finely agglutinated.

Family LITUOLIDAE de Blainville, 1827

Genus *Ammobaculites* Cushman, 1910

Ammobaculites fontinensis (Terquem, 1870)

Plate 1, Figs. 14-17

Haplophragmium fontinense Terquem, 1870, p. 337, pl. 24, figs. 29, 30a-b

Ammobaculites fontinensis (Terquem).- Franke, 1936, p. 127, pl. 12, fig. 24.

Description. Test planispiral becoming uniserial; the last whorl of the planispiral portion consists of 6-8 chamber; uniserial part short (1-3 chambers), rectilinear to curved, usually broken; wall built of coarse grains.

Remarks. The final uniserial part is usually not preserved (broken).

Superfamily HAPLOPHRAGMIACEA Eimer & Fickert, 1899

Family AMMOSPHAEROIDINIDAE Cushman, 1927

Subfamily RECURVOIDINAE Alekseychik-Mitskevich, 1973

Genus *Recurvoides* Earland, 1934

Recurvoides sp. 1

Plate 2, Figs. 1-2

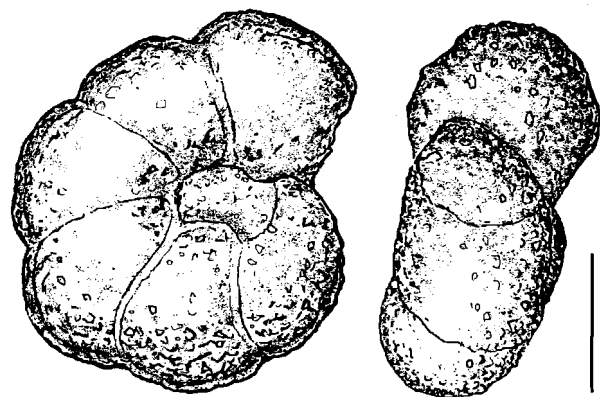


Figure 12. *Recurvoides* sp. 2, peripheral and spiral views, sample CZS-1; scale bar = 100 μ m.

Description. Test subglobular with globular-shaped, inflated chambers; chamber arrangement streptospiral with about 100 to 170° change in plane of volution; eight to ten chambers arranged in 2.5-3

whorls consisting of 2 to 3 chambers between abrupt changes in plane of coiling. Chambers are quite similar in size.

Recurvoides sp. 2

Figure 12

Description. Test subcircular in outline; 2-2.5 whorls; earliest chambers arranged streptospirally; the last whorl planispiral and consists of 4-5 chambers; wall thin, finely agglutinated; sutures usually depressed.

Superfamily TROCHAMMINACEA Schwager, 1877

Family TROCHAMMINIDAE Schwager, 1877

Subfamily TROCHAMMININAE Schwager, 1877

Genus *Trochammina* Parker & Jones, 1859

Trochammina aff. *eoparva* Nagy & Johansen, 1991

Figure 13; Plate 2, Figs. 3-4

Trochammina aff. *eoparva* Nagy & Johansen, 1991 p. 23-23, pl. 4, figs. 1-9.

Description. Test discoidal, low-spiral consisting of 2-3 whorls; spiral side slightly convex, umbilical somewhat concave; early spiral part almost ideally even, becoming lobate in the final whorl; sutures flush, inclined backward; wall finely arenaceous.

Remarks. This is the most common species of *Trochamminain* the studied material. The holotype was described from the Boreal lower Bajocian (Aalenian) of the North Sea area (Nagy & Johansen, 1991). Our specimens are similar in shape and the type coiling to the type species, but differ in possessing a lobate periphery. Both Boreal and Tethyan forms occur at the similar time interval, it is therefore likely that they were related.

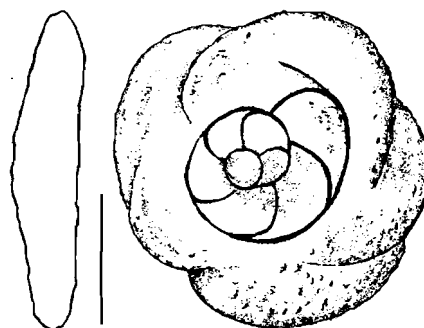


Figure 13. *Trochammina* aff. *eoparva*, outline of the cross-section and spiral view, sample KPN-2; scale bar = 100 μ m

Trochammina pulchra Ziegler, 1959

Plate 2, Fig. 5-7

Trochammina pulchra Ziegler, 1959, p. 94, pl. 2, figs. 6-8.

Trochammina pulchra Ziegler - Oesterle, 1968, p. 751, fig. 45f.

Description. Test discoidal, low-spiral consisting of about two whorls; spiral side slightly convex, umbilical concave; early spiral part with triangular increasing in size chambers; the final whorl consists

of 7-8 chambers; sutures depressed, straight to gently curved, inclined backward; periphery even or slightly lobate; wall finely agglutinated.

Remarks. This species differs from *Trochammina concava* Seibold & Seibold (1960) in having almost non-lobate periphery and more stable size of chambers in the last whorl. Chambers of *T. concava* distinctly increase in size as added in the last whorl.

***Trochammina globoconica* sp.n.**

Figures 14-15; Plate 2, Figs. 8-10

Conotrochammina sp. A Tyszkla 1994, pl. 3, figs. 1-3.

Derivation of name. From the conical and rounded, sub-globular shape of the test.

Diagnosis. A conical species with a rounded non-tapered periphery and sub-globular shape.

Holotype. Coll. A-II-109, Geological Museum, Institute of Geological Sciences, Polish Academy of Sciences, Kraków.

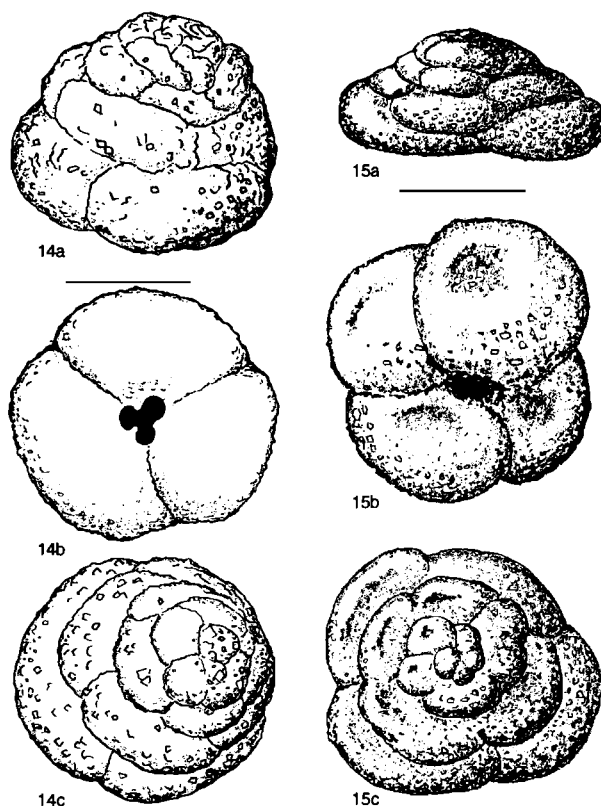
Material. Holotype (sample KPN-5) and paratypes (KPN-2, KPN-5). Additional specimens are housed at University College London, Micropalaeontology Unit.

Locality and horizon. Kapuśnica near Niedzica, Pieniny Klippen Belt, Polish Carpathians; Niedzica Succession; Skrzypny Formation; Aalenian-lower Bajocian.

Description. Test free, trochospiral, high conical with rounded non-tapered periphery, slightly lobate at spiral side; usually 4 to 5 whorls; chambers numerous from 4 to 5 per whorl, and reduced to 3-4 in the final whorl; chambers somewhat inflated; sutures slightly depressed, curving backwards; wall finely agglutinated, surface granular; aperture single, umbilical resembling a clover-like opening, usually poorly preserved; megalosphaeric and microsphaeric not recognized. Some specimens are squashed by compaction, appearing low conical in shape.

Dimensions. Greatest diameter of holotype: 0.21 mm, height of spire 0.18 mm.

Remarks. This form has been previously attributed to the genus *Conotrochammina*. In fact, careful examination of the same material has revealed an umbilical aperture located at the axial part. *Conotrochammina* shows a small areal opening about one-third the distance from the base of the chamber (Loeblich & Tappan, 1987). This species resembles *Trochammina topagorukensis* Tappan (1955) in the high spire and similar number of chambers per whorl, but differs in having a periphery that is rounded instead of subacute. Moreover *T. globoconica* is similar to *T. haeusleri* (Galloway), but differs in its more rounded, not tapered conical shape and different aperture, the latter reveals a slit-like aperture (see Cifelli, 1959; Kalantari, 1969).



Figures 14, 15. *Trochammina globoconica* sp.n., 14a-c. Holotype; 15a-c. Paratype. Peripheral, umbilical, and spiral views, sample KPN-5; scale bar = 100 µm.

Superfamily VERNEUILINACEA Cushman, 1911
Family CONOTROCHAMMINIDAE Saidova, 1981
Genus *Conotrochammina* Finlay, 1940

***Conotrochammina* ? sp. B**

Plate 2, Figs. 11-12

Conotrochammina sp. B, Tyszkla, 1994, Plate III, fig. 4.

Locality and horizon. Biała Woda Valley, Pieniny Klippen Belt, Polish Carpathians; Czorsztyn Succession; Skrzypny Formation; Aalenian-Lower Bajocian.

Description. Test free, trochospiral, "penta-serial", perfectly conical with subacute periphery (probably chambers in the last whorl are squashed showing a subacute shape of the periphery); five chambers per whorl, the final whorl exhibits five depressed (squashed) chambers with straight radial inflated sutures; sutures flush; wall finely agglutinated, surface granular; aperture not observed.

Dimensions. Greatest diameter 0.260 µm, height of spire 0.200 µm.

Remarks. Lack of preserved apertures and generally poor preservation make this identification tentative.

Superfamily ATAXOPHRAGMIACEA Schwager, 1877

Family GLOBOTEXTULARIIDAE Cushman, 1927

Genus *Verneuilinella* Tairov, 1956

Verneuiliella pieninica sp.n.

Figures 16-17; Plate 2, Figs. 13-15

Derivation of name. From the study area - The Pieniny Mts. (Western Carpathians).

Diagnosis. A conical highly trochospiral species with a regular quadriserial arrangement, clearly visible at the umbilical side, which distinguishes it from the triserial genus *Verneuilioides*.

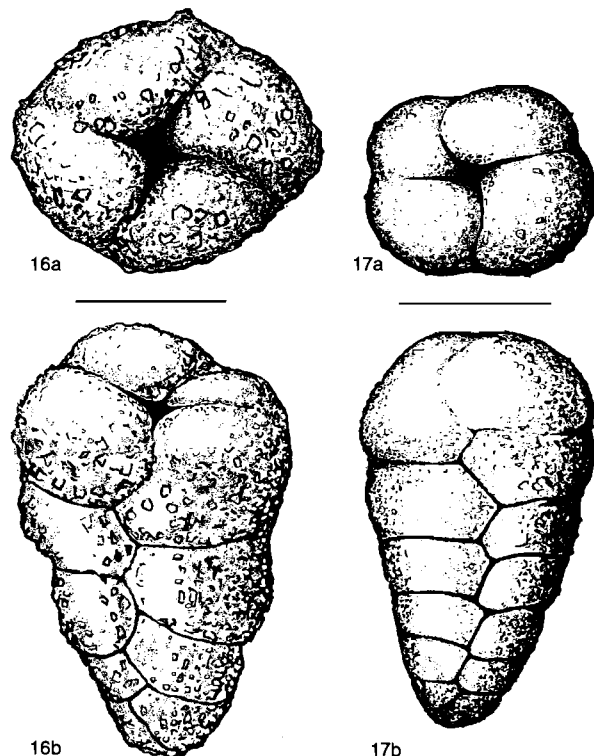


Figure 16-17. *Verneuiliella pieninica* sp.n. 16a,b. Holotype. 17a,b. Paratype. Umbilical, and peripheral views, sample KPN-2; scale bar = 100 μ m.

Holotype. Coll. A-II-109, Geological Museum, Institute of Geological Sciences, Polish Academy of Sciences, Kraków.

Material. Holotype (sample KPN-2) and paratypes (KPN-2, KPN-5). Additional specimens housed at University College London, Micropalaeontology Unit.

Locality and horizon. Kapuśnica near Niedzica, Pieniny Klippen Belt, Polish Carpathians; Niedzica Succession; Skrzypny Formation; Aalenian-Lower Bajocian.

Description. Test free, conical to subconical, trochospirally coiled constantly with four chambers per whorl, thus, forming regular vertical rows along axis of coiling; usually 6 to 9 whorls per test; chambers strongly overlap the earlier part of the test; sutures flush or slightly depressed; wall agglutinated from fine quartz grains; aperture invisible - most likely a small interiomarginal opening located

near the axis of coiling.

Dimensions. Holotype: high of spire 0.19 mm, greatest diameter 0.175 mm.

Remarks. This genus can be confused with triserial *Verneuilioides*. The last whorl shows clearly four chambers with quadriserial arrangement throughout. To our knowledge, this is the first report of *Verneuiliella* in the Jurassic. Loeblich & Tappan (1988) reported its range as Aptian to Turonian.

Superfamily TEXTULARIACEA Ehrenberg, 1838

Family TEXTULARIIDAE Ehrenberg, 1838

Subfamily TEXTULARIINAE Ehrenberg, 1838

Genus *Textularia* Defrance, 1824

Textularia haeusleri Kaptarenko, 1959

Figure 18

Textularia haeusleri Kaptarenko-Chernousova, 1959, p. 47, pl. 7, fig. 5-7.

Description. Test free, flattened, biserial and strongly elongated. Sutures flush, strongly oblique; early chambers not preserved; younger chambers slowly increasing in size as added; periphery almost parallel, straight to gently lobate; finely agglutinated; the last chamber forms a short neck with a terminal aperture.

Remarks. This species differs from *T. jurassica* Gümbel (1862) in having distinctly oblique sutures.

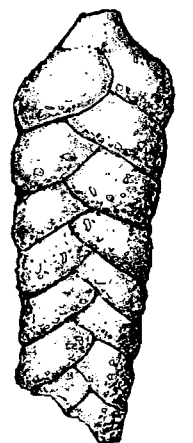


Figure 18. *Textularia haeusleri*, lateral view, sample KPN-2; scale bar = 100 μ m.

Textularia sp. 1

Description. Test free, flattened, biserial; sutures flush, somewhat oblique; early chambers increasing rapidly in breadth, younger chambers slightly increasing in size as added; periphery straight to gently lobate; finely agglutinated.

Remarks. This species shows broader test than *T. haeusleri* Kaptarenko-Chernousova (1959).

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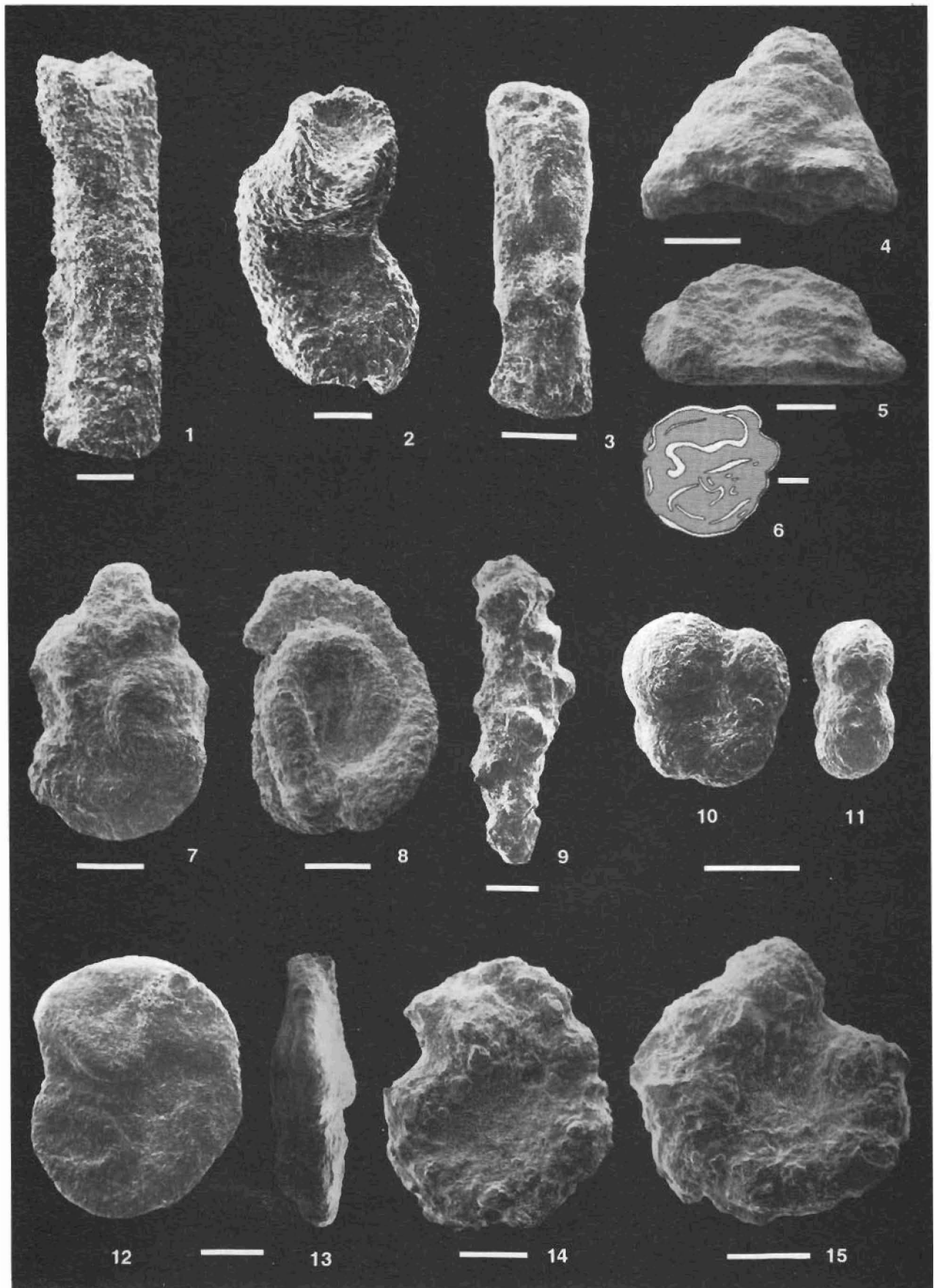


PLATE 1. 1. *Hyperammina* ? sp., sample SKS-9. 2. *Rhabdammina* sp., sample BS-2. 3. *Rhabdammina* sp., sample CZS-9. 4. *Arenaturrispirillina* sp., peripheral view, sample XS-3. 5, 6. *Tolypammina* sp., peripheral view, sample BS-10. 6. Drawing of the planar side. 7. *Glomospira perplexa* Franke, sample SKS-4. 8. *Glomospira* sp., sample CZS-9. 9. *Reophax* sp., sample KPS-9. 10, 11. *Haplophragmoides globigerinoides* (Haeusler), spiral view sample CZS-1. 11. Peripheral view. 12, 13. *Haplophragmoides* sp. 1, spiral view, sample KPS-14. 13. Peripheral view. 14, 15. *Ammobaculites fontinensis* (Terquem), 15. spiral view, sample CZS-1. 16. spiral view, sample BS-10. Scale bar = 100 μ m

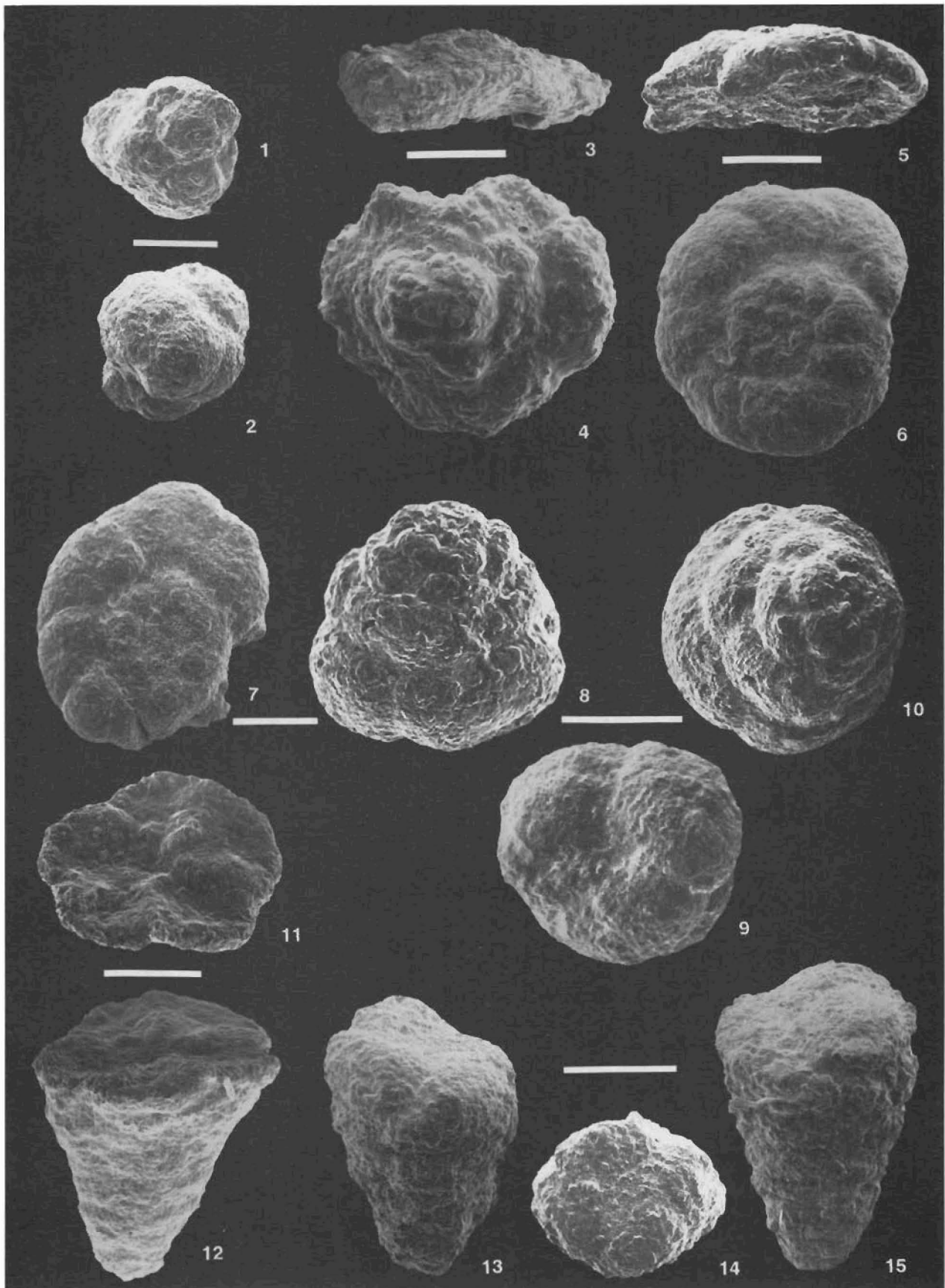


PLATE 2. 1. *Recurvoides* sp. 1, oblique view, sample CZS-1. 2. *Recurvoides* sp. 1, oblique view, sample CZS-1. 3, 4. *Trochammina* aff. *ceparva* Nagy & Johansen, peripheral view, sample CZS-1. 4. Spiral view. 5, 6. *Trochammina pulchra* Ziegler, peripheral view, sample SKS-10. 6. Spiral view. 7. *T. pulchra* Ziegler, spiral view, sample SKS-10. 8, 9, 10. *Trochammina globoconica* sp.n., holotype, peripheral view, sample KPN-5. 9 Umbilical view. 10. Spiral view. 11, 12. *Conotrochammina* sp. B, umbilical view, sample BS-2. 12. peripheral view. 13, 14. *Verneuiliella pieninica* sp.n., holotype, umbilical view, sample KPN-2. 14. Peripheral view. 15. *V. pieninica* sp.n., peripheral view, sample KPN-5. Scale bar = 100µm.