

MIDDLE MIOCENE (EARLY BADENIAN) *AMPHISTEGINA* (FORAMINIFERIDA) FROM OLIMPÓW (CENTRAL PARATETHYS, POLAND)

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Gonera, M., 2012. Middle Miocene (Early Badenian) *Amphistegina* (Foraminiferida) from Olimpów (Central Paratethys, Poland). *Annales Societatis Geologorum Poloniae*, 82: 151–159.

Abstract: Specimens of Middle Miocene (Early Badenian) *Amphistegina* from the Polish Carpathians were examined. A section, sampled at the Olimpów quarry, displays chloralgal carbonates, rich in rhodolith nodules. Symbiont-bearing foraminifera (*Amphistegina*, *Elphidium* and *Asterigerinata*) constitute 15–57% of the total foraminifera assemblage. *Amphistegina hauerina* d'Orbigny, 1846 is the only species of the genus in the deposits studied.

The sensitivity of larger foraminifera to water turbulence and light availability was applied in a reconstruction of the community habitat. The diameter and thickness of the *Amphistegina* tests indicate that the habitat was a zone of low light penetration and weak energy – a palaeoenvironment, similar to that of the modern *A. radiata* (Hottinger *et al.*, 1993). Changes in the sphericity of the *Amphistegina* tests reflect a temporal drop of bathymetry in the middle part of the section. This is supported by other environmentally controlled features of the foraminiferal assemblage: the percentages of both planktonic and symbiont-bearing forms, as well as the proportions of robust and flat forms of *Elphidium*. It is possible that this variation in depth was due to eustatic changes in sea level, caused by Event Mi3 of the Middle Miocene climatic cooling. The spiral diameter of the test was at its lowest value then, indicating that maturity was reached at a faster rate. The period of shoaling offered the best life conditions for *Amphistegina* in this particular area.

Key words: Foraminifera, *Amphistegina*, Middle Miocene, Paratethys, Poland.

Manuscript received 16 August 2011, accepted 4 September 2012

INTRODUCTION

Amphistegina is a highly stenotopic, Recent representative of the foraminifera. Its occurrence is restricted to areas of carbonate sedimentation, at low latitudes and in waters of normal salinity (Murray, 1973; Larsen, 1976; Hallock, 1985). As a symbiont-bearing larger foraminifera, the genus is restricted to the euphotic zone (i.e. not deeper than ca. 100–120 m).

Amphistegina originated in the Eocene and spread as two main phylogenetic lineages (Larsen, 1978). *Amphistegina* could hold stratigraphic significance for the shallow-water facies of carbonate platforms, if the taxonomic changes in these evolutionary lineages (i.e., the morphological variants and their time ranges) were better defined. The facies of carbonate platforms are quite common in the Paratethys (Fig. 1A; Pisera, 1996) and contain *Amphistegina* at some locations. A comprehensive study of the genus in this area was presented by Rögl and Brandstätter (1993). The authors stressed the morphometric aspects of its taxonomy, considered the palaeogeographic seaways of this

larger foraminifera, and its applicability in stratigraphy. *Amphistegina* from Korytnica (a Middle Miocene site in the Polish part of Paratethys) was included in the study (location shown in Fig. 1B).

The present study deals with *Amphistegina* from the Olimpów Limestone (*Orbulina suturalis* Zone of the Middle Miocene). The research is intended as a contribution to the taxonomy and palaeogeographic significance of these larger foraminifera.

GEOLOGICAL BACKGROUND

In a palaeogeographic sense, the Olimpów Limestone occurs at the southern margin of the Carpathian Foredeep. The studied section constitutes a patch of the Middle Miocene cover, deposited in the Carpathians as piggy-back basin sediments. Affected by the syn- and post-depositional, structural evolution of the basement, as well as by later erosion and degradation processes, the cover has been preserved only as small, isolated fragments (Gonera, 1994a).

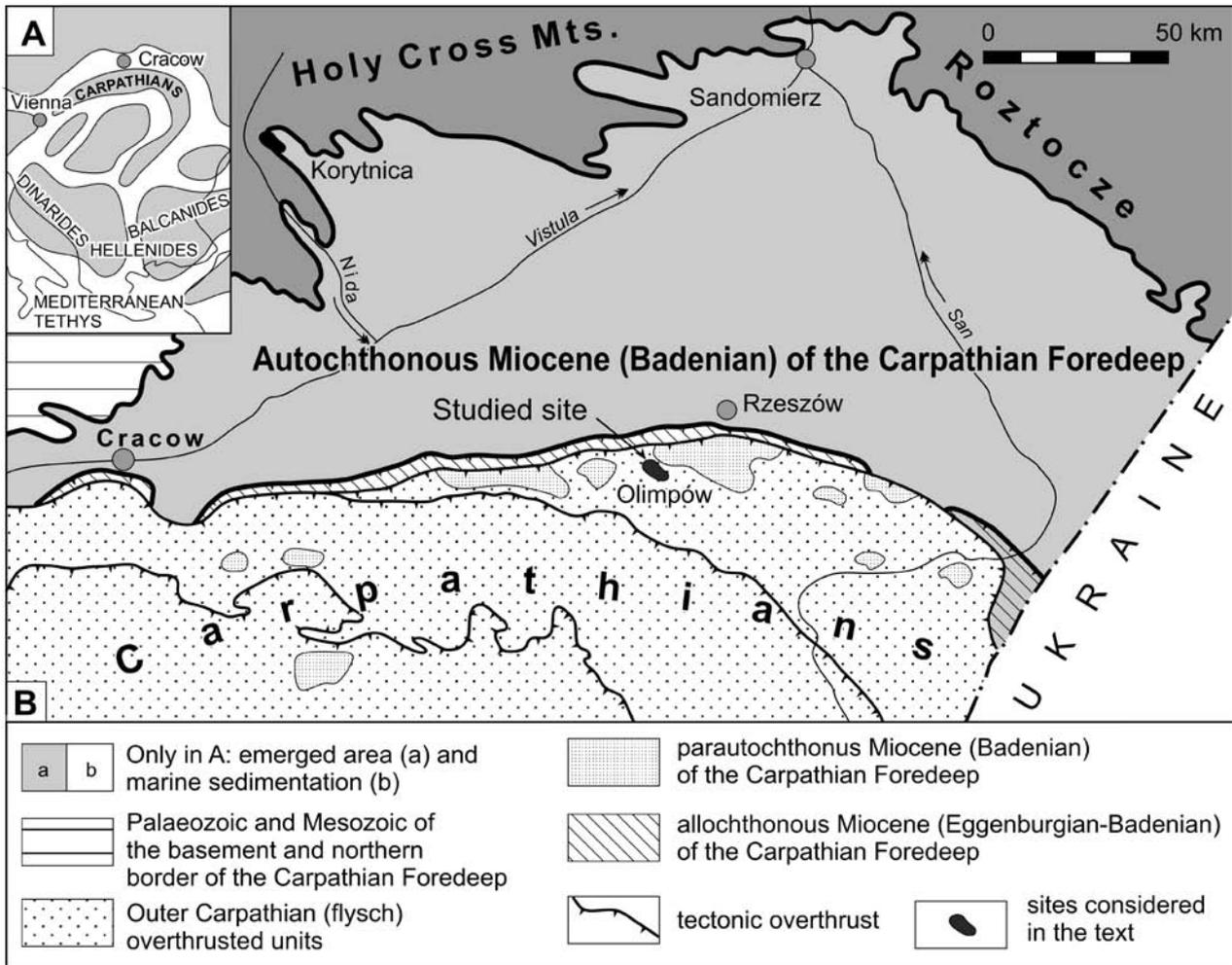


Fig. 1. Study area. **A** – Central Paratethys (after Rögl and Steininger, 1984) – Neogene, fringing basin of Mediterranean Tethys. **B** – Geological sketch map of Carpathian Foredeep and flysch overthrust zone in southern Poland (after Alexandrowicz, 1971)

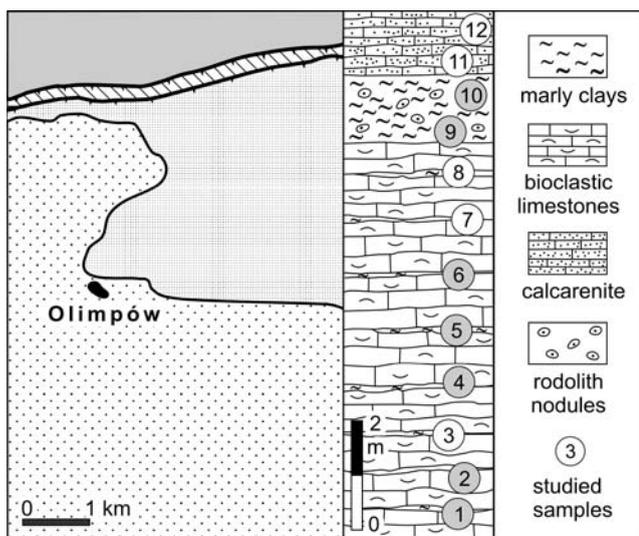


Fig. 2. Geological map of study area and section, showing location of deposits sampled (taxonomy in Gonera, 1994b); samples containing *Amphistegina* used in biometrical study are shaded. Explanations in the map as in Fig. 1

Carbonates are relatively scarce. At present, the Olimpów quarry provides the only accessible outcrop of these Miocene deposits. The section consists of algal wackstone facies of early Badenian age (Gonera, 1994b).

In the Olimpów quarry (GPS coordinates: N49°59' 47.34"; E21°43' 59.09"), bioclastic limestones are exposed. They are interbedded with layers of poorly consolidated carbonate mud and clays with siliciclastic content and calcareous algae nodules (Fig. 2). These soft intercalations were sampled for a study of the foraminifera. Besides red algae as the predominant rock-forming material, the residuum is made up of the rich, skeletal debris of chloralgal biotas. Although numerous, the fossils are monotonous, with respect to the taxonomic groups present. Apart from rodoliths, only foraminifera, bryozoans (Pouyet and Tarkowski, 1998) and ostracodes are represented. In the foraminifera assemblage, the following taxa are common: *Lobatula lobatula* (Walker and Jacob, 1798), *Textularia* sp. div., *Elphidium* sp. div., *Asterigerinata planorbis* (d'Orbigny, 1846), *Eponides haidingeri* (d'Orbigny, 1846), *Discorbis* sp. div., and *Amphistegina* (Gonera, 1994b). The *Amphistegina* content of the assemblage varies from 10–39% (Fig. 2: sample 7 and sample 4, respectively).

MATERIALS AND METHODS

In order to appreciate the species of *Amphistegina* present, the approach to genus taxonomy, proposed by Larsen (1978), was applied. Accordingly, the following features were taken as species-diagnostic: the pattern of sutures, the complexity of the spiral side, the characteristics of the apertural face, the test-surface ornamentation and the form of the periphery. On the basis of observations on the living *Amphistegina*, some features have been inferred as reflecting intraspecific variation, depending on light availability and water turbulence (Larsen and Drooger, 1977), e.g. the shape of the test in profile (robust *versus* slim). The present paper follows this species concept for the genus. Actualistic principles and ecologic data on Recent *Amphistegina* have been applied to the palaeoenvironmental interpretation of the Olimpów samples.

The size of the foraminifera test and its sphericity and convexity are the basic morphometric features, applied to the reconstruction of habitat. Following this approach to palaeoenvironmental analysis, these measurements were gathered for the *Amphistegina* specimens from the Olimpów Limestone. The investigations were directed at the mudstone intercalations of the section (Fig. 2). Sufficient numbers of *Amphistegina* specimens, retrieved from seven soft-rock samples, yielded data that were summarized by means of general, statistical procedures (mean value, standard deviation and median calculated using Excel[®] Software). For each sample, about 300 specimens were measured.

RESULTS

Taxonomy

In the Olimpów section, only one morphotype of *Amphistegina* was detected (Fig. 3). The tests are low trochospiral, with 16 to 20 chambers at the last whorl. The aperture, as an interiomarginal slit on the umbilical side, is bordered by a lip. The apertural face is very low, with minute sculpting. The main chamber sutures of the ventral side are twisted backwards and forwards and also are bent backwards into a peripheral arch (Fig. 3). The toothplate extends from the apertural face to the previous septum; the chamber lumen is divided by this. The junctions of the toothplate with the wall define the star-shaped traces of additional sutures. The toothplate suture is rather short, restricted to the oral part of the main suture and the main chamber is sickle-shaped. The sutures on the dorsal side are relatively sharp-angled. Between the chamber sutures, there are short interseptae, with the shape of a simple line. Dextral coiling directions dominate in the specimens studied (Fig. 4).

This morphology is indicative of a phylogenetic phase, intermediate between *Amphistegina mamilla* (Fichtel and Moll, 1798) and *Amphistegina radiata* (Fichtel and Moll, 1798), a lineage inferred by Larsen (1978). The presence of interseptae only in some chambers indicates that the specimens examined belong to *Amphistegina hauerina* d'Orbigny, 1846. The tests display a coiling direction that is the same in both end members of the lineage.

Habitat

From considerations of ecology, the presence of *in situ* *Amphistegina* in a fossil community indicates a salinity of 30–45‰ and a warm-climate temperature as the basic, environmental conditions. Its distinctive morphotype reflects both a dynamic regime of water motion and the metabolic requirements of algal symbiosis (Hansen and Burchardt, 1977; Leutenegger, 1977; Lee *et al.*, 1979; Hallock and Glenn, 1986; Hallock *et al.*, 1991). As recent field studies have shown, CaCO₃ intensive secretion is indicative of both higher light intensity and increased water motion (Hallock, 1981; Kuile and Erez, 1984; Hallock *et al.*, 1986; Hallock *et al.*, 1991). According to these authors, the test shape of these larger foraminifers can be a useful tool for the recognition of these palaeoenvironmental conditions.

The application of *Amphistegina* for palaeoecological interpretation is justified by some of its biological characteristics. The sphericity (axial diameter to spiral diameter) of the test is a structural compromise between the hydrodynamic factors of habitat and the metabolic requirements of algal symbionts (Hallock, 1979; Röttger and Hallock, 1982; Hottinger, 1983). According to field observations and laboratory experiments on living *Amphistegina*, it has been documented that water motion is more important than light in producing an increased thickness of the test (sphericity > 0.5), whereas intermediate test thickness (0.4 < T/D < 0.5) is found in quiet environments, with a moderate to high level of light penetration (Hallock, 1979, 1981; Hallock and Glenn, 1986; Hallock *et al.*, 1986). Robust foraminiferal tests imply a current-swept environment, whereas thin, fragile tests indicate quiet, low-light environments (Brasier, 1975; Triffleman *et al.*, 1991). The relation of umbilical side thickness (L1) to spiral side thickness (L2) in test convexity denotes increased strength of the shell to resist being crushed (Wetmore and Plotnick, 1992). Living in favourable, environmental conditions, the foraminifera tend to mature in a minimal period of time and reproduce at a relatively small adult size, whereas those of stressed populations grow more slowly and mature at a larger size (Bradshaw, 1961; Hallock, 1974; Hallock *et al.*, 1986).

Considering the size-frequency distribution of the specimens, only those of samples 4, 5 and 6 are unimodal, representing a normal population structure (Fig. 4). In a foraminiferal population showing this kind of distribution, the empty tests in the sediment are of postreproduction origin. Therefore these three samples, located in the middle part of the Olimpów section, represent the gradual accumulation of post-reproductive shells over a longer period of time. On the other hand, in sample 2, all age-stages are equally frequent, which reflects the sudden death of all living specimens. The remaining three populations (samples 1, 9 and 10) exhibit bimodal distributions comprising two types of specimens, young and adult. The mortality of the young specimens was extremely high in the uppermost sample of the section. Apparently, the community stayed very close to lethal limits during this period. In view of the assumption that the mean diameter corresponds to reproductive maturity (Dodd and Stanton, 1981), the size-frequency diagrams indicate the most favourable conditions during sedimentation of sample

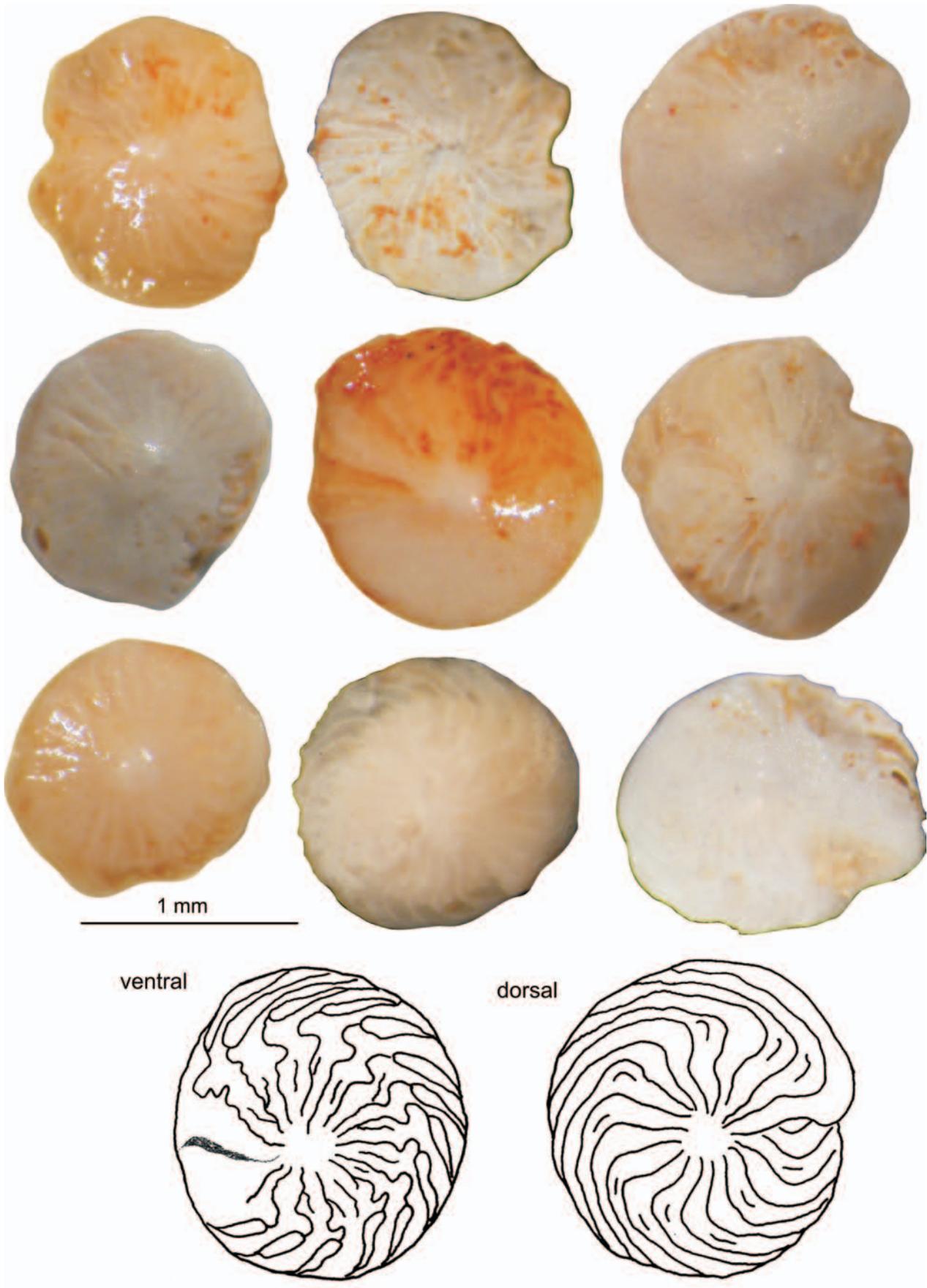


Fig. 3. Specimens of *Amphistegina* from Olimpów Limestone; tests were taken from the sample 9. Patterns of *Amphistegina* test sutures are provided below

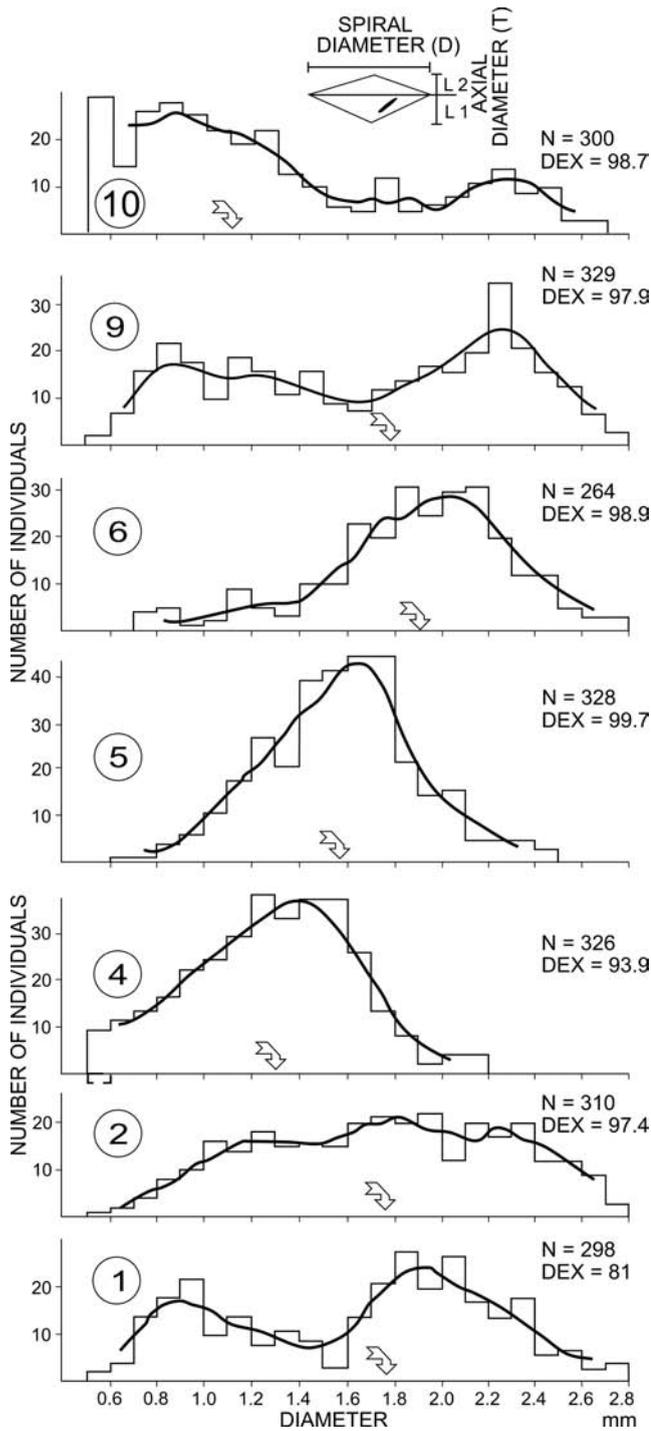


Fig. 4. Size-frequency data for *Amphistegina*, collected in Olimpów section (arrows indicate median value). N – total number of measured tests, DEX – percentage of dextrally coiled specimens

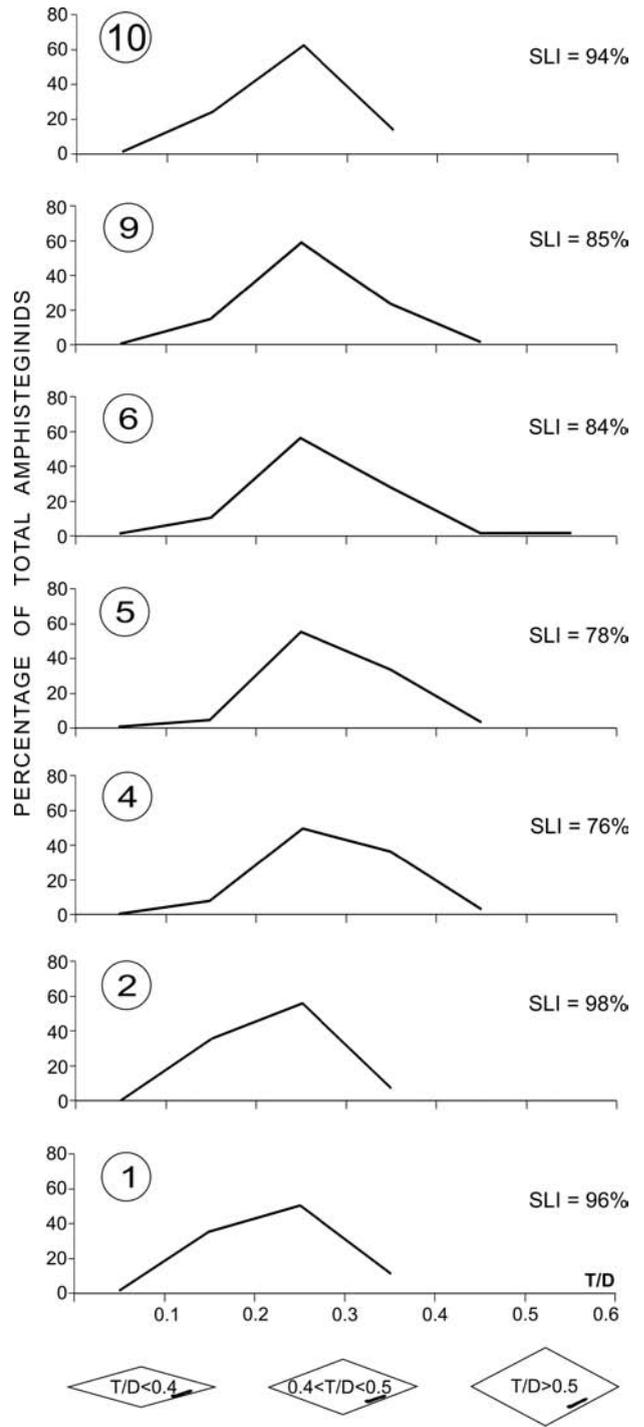


Fig. 5. Variation in T/D values (sphericity) of *Amphistegina* from Olimpów section. SLI – percentage of slender (T/D < 0.4) forms

4 and highly unfavourable conditions at the top of the deposits examined (sample 10).

The sphericity (T/D index) does not exceed 0.4 in the 76–98% of investigated tests of the *Amphistegina* (Fig. 5). Apparently, these specimens represent the thin-test morphotype. Such tests resulted from a quiet water habitat and low level of light. The examined tests of *Amphistegina* display

almost equally convex spiral and umbilical sides (Fig. 6); the predominance of spiral-side convexity is only slightly marked.

The test measurements indicate that the *Amphistegina* of the Olimpów Limestone is the morphotype, characteristic for low light and quiet waters, namely the deep, euphotic zone. The same depositional environment also was inferred

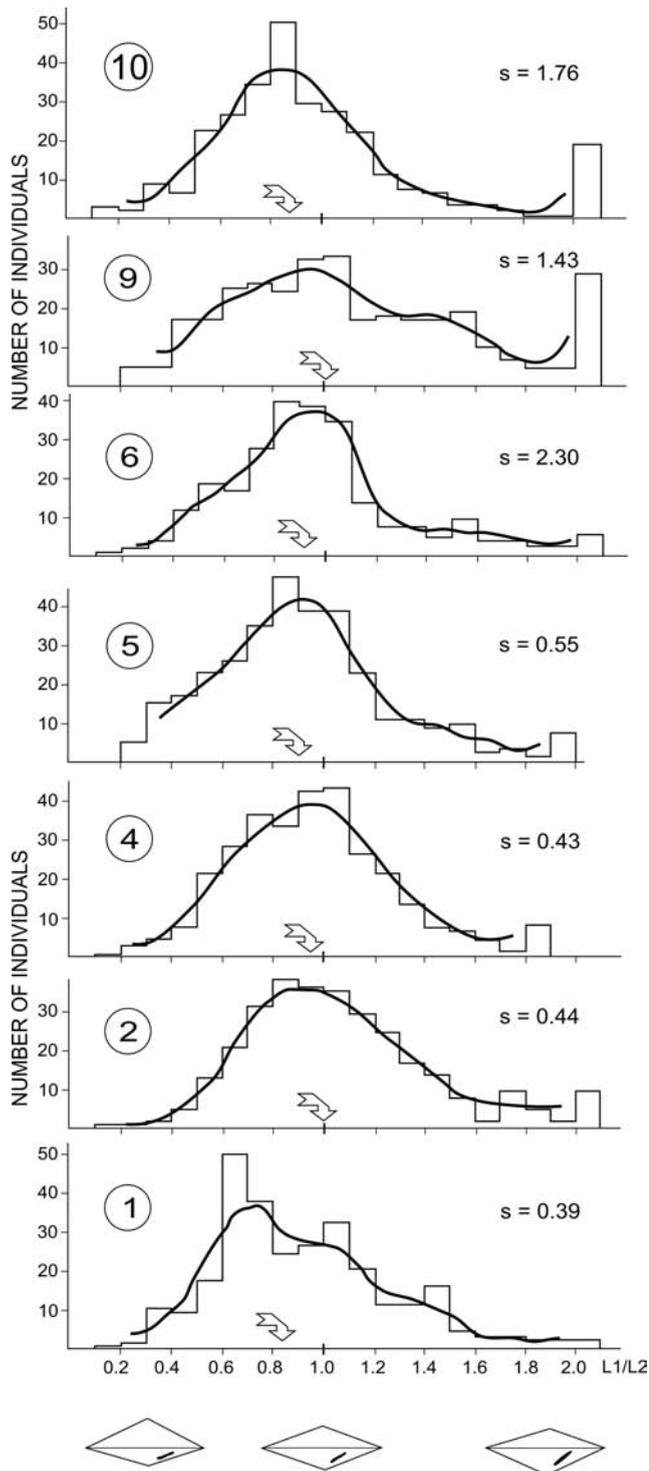


Fig. 6. Variation in convexity ($L1/L2$) in *Amphistegina* population from Olimpów section (arrows indicate median value)

for the Olimpów Limestone on the basis of bryozoa (Pouyet and Tarkowski, 1998). This indicates conditions very similar to those inhabited nowadays by *Amphistegina radiata* (Fichtel and Moll, 1798) (Hallock, 1984; Hottinger *et al.*, 1993), the taxon that is regarded as an end-member of the phylogenetic lineage considered.

DISCUSSION

The Olimpów *Amphistegina* displays structural characteristics, typical of the species *Amphistegina hauerina* d'Orbigny, 1846. The possession of interseptae in some of the chambers only is a prominent feature, distinguishing this morphospecies from both *A. mamilla* Fichtel and Moll, 1798 and *A. radiata* Fichtel and Moll, 1798; interseptae are absent in *A. mamilla*, whereas *A. radiata* has them in each chamber. However, there are differing views on such specimens, with regard to their species status. They are treated either as separate taxa (Larsen, 1978; Papp and Schmid, 1985), or lumped as synonyms of *A. mamilla* (Rögl and Hansen, 1984; Rögl and Brandstätter, 1993). The present account follows the former opinion.

Larsen (1978) considered *A. hauerina* to be the ancestor of *A. radiata* and, in some cases, as a descendant of *A. mamilla*. In this phylogenetic concept, the interseptae were highly evolving structures of the test. The other morphologic features seem to be conservative. The pattern of twisting of chamber sutures did not undergo a meaningful change in subsequent members of the phyletic lineage. These structures became more crooked in the younger representatives of the lineage (*A. hauerina* and *A. radiata*), by comparison with their ancestor (*A. mamilla*). The fundamental, evolutionary change proceeded through the increasing (advancing) complexity of the interseptae, as can be traced in the fossil record. Morphospecies, lacking these structures, do not exist at the present day (*A. mamilla* disappeared from the fossil record in the Middle Miocene). Instead, tests with a highly upgraded set of interseptae have developed. The interseptae were located in only some chambers at the initial stage. Their construction was as simple as a short, linear partition (*A. hauerina*). Later (*A. radiata*) interseptae were arranged in the advanced structures with the shape of a meandering arc. Along with the decrease in chamber number, complications occurred in the interseptae system. Moreover, on the umbilical side, additional, irregular branches formed along the chamber sutures. At the same time, the average number of chambers underwent a reduction: sixteen at *A. mamilla*, then fourteen at *A. radiata*. One can speculate that interseptae and the branches of the chamber suture took on the function of chamber sutures themselves – that is, the maintenance of the trochospiral structure of the shell. Were these additionally developed structures a more effective adaptation? Maybe the chambers became much more spaced and, through this, more suitable for the maintenance of symbiotic algae (Hallock, 1982, 1988; Hallock *et al.*, 1991). In this context, it is worth noting that the progression of interseptae is stronger on the spiral side of the tests – the one turned upward to the light source. The development of this feature as an adaptation must have a highly competitive meaning, because only this *Amphistegina* is present today; both *A. mamilla* and *A. hauerina* disappeared from biocoenoses in the geological past.

The Middle Miocene *Amphistegina hauerina* of the Olimpów Limestone is predominantly dextrally coiled (numerical data in Fig. 4). Also other members of the phylogenetic lineage display this direction: *A. mamilla* as *A. hauerina* ancestral and *A. radiata* as its recent descendant.

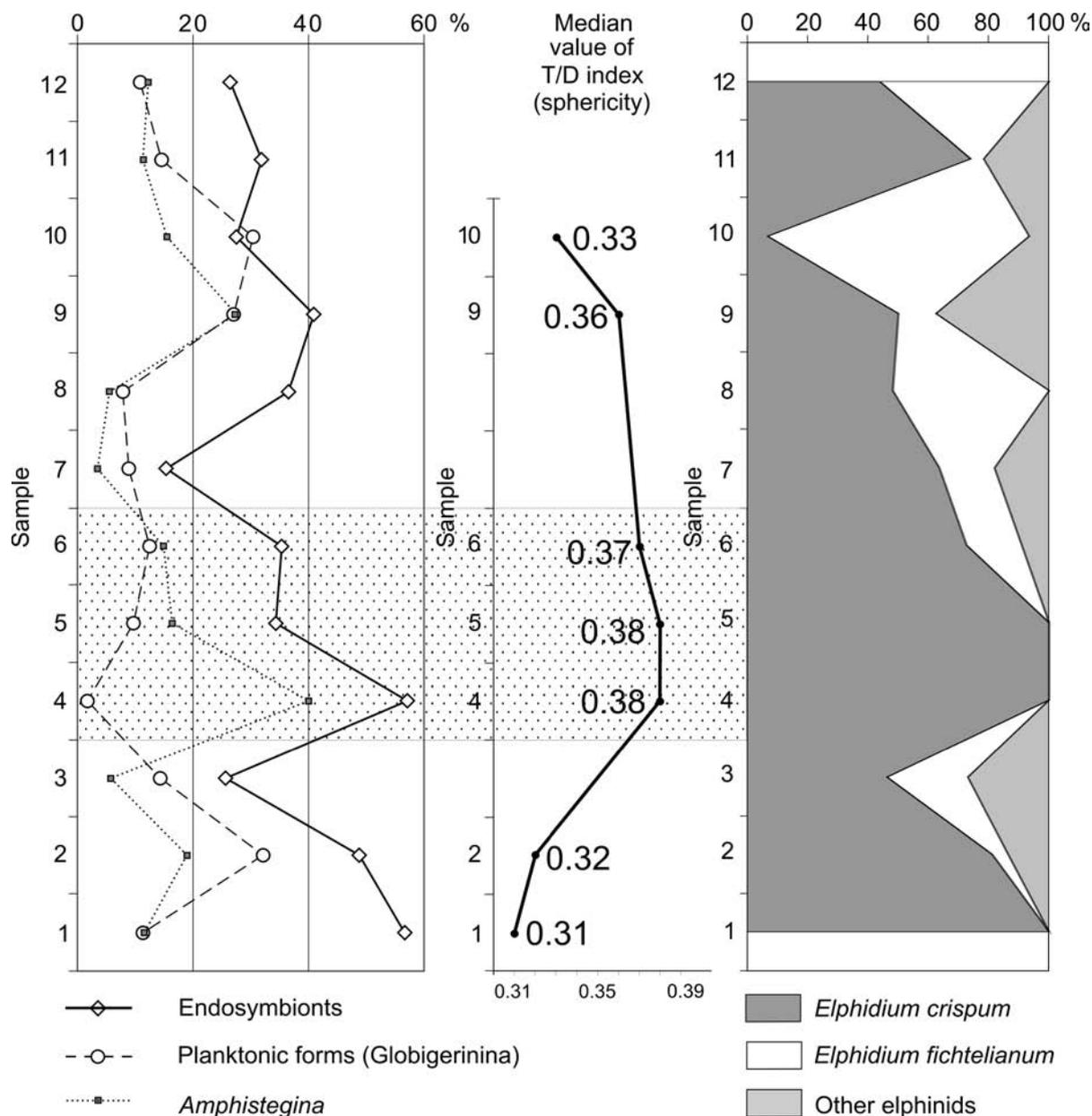


Fig. 7. Depth interpretation, based on test shape (sphericity) of *Amphistegina* and other foraminiferal indexes. Endosymbiont taxa considered in this chart for *Asterigerina*, *Elphidium* and *Amphistegina*. The dotted bar indicates the shoaling episode

However, sinistrality has been ascribed to the Miocene *A. hauerina* from both the Paratethys and Indo-Pacific regions (Larsen, 1978). The Middle Miocene *A. mamilla* (including *A. hauerina*) from the Paratethys was reported as being dextrally coiled (Rögl and Brandstätter, 1993). The apparent confusion is unclear. Nevertheless, differences in coiling direction is a phenomenon common in nature, but the reasons for this remain unknown. In spite of many investigations, there is a lack of general agreement: is it a genetically or environmentally conditioned process (Hallock and Larsen, 1979)?

There is a need for elucidation of the stages of evolution, leading from *A. mamilla* to *A. radiate*, and for designation of the stratigraphic ranges of these stages. It is to be expected that the recognition and elucidation of the con-

secutive morphospecies would have useful stratigraphic applications. The issue is promising as such a tool in epicontinental and peripheral basins – such as the Paratethys. These applications are expected to be advantageous, as carbonate platform sediments are characteristically poor in orthostratigraphic markers (above all Globigerinina). In this case, good recognition of the phyletic stages of *Amphistegina* is expected to be a supporting – or even vital – tool for resolution to biostratigraphy (Hallock, 1982). It could be that the deposits containing both taxa (*A. mamilla* and *A. hauerina*) should be dated, as being older than the deposits, comprising solely *A. hauerina*. Currently, while it is unknown (not determined) if and when this divergence occurred, inferences on this problem are not possible. Tentatively only speculation is possible: it could be that the Olimpów Limestone

is younger than the deposits comprising only *A. mamilla* or both taxa of *Amphistegina*; the latter is the case of the Kozyńca Clay.

In the Central Paratethys, *Amphistegina* already is accepted as a meaningful stratigraphic marker. In the part of the Central Paratethys, situated north of the Carpathians (Fig. 1A), this foraminifera constitutes a useful tool for distinguishing the below-evaporite Badenian (e.g., Skawina Formation) from the younger Badenian (Alexandrowicz, 1997; Gonera *et al.*, 2000). Lithostratigraphic hiatuses occur in the Badenian salinity deposits (Wieliczka Formation). It is worth noting that in the southern areas of the Central Paratethys *Amphistegina* also persists in the younger part of the Badenian (Rögl, 1998). The retreat of this taxon above the saline deposits was due to remarkable environmental changes (Szczechura, 1982). This transformation now is interpreted as a process, driven by the Middle Miocene deterioration of climate (Gonera *et al.*, 2000; Gonera, 2001; Bicchi *et al.*, 2003). This crucial period has been correlated with the Mi3 Event of global climate cooling (standard scale according to Miller *et al.*, 1991). North of the Carpathians, the temperature in this earlier part of the Badenian ceased to be high enough for *Amphistegina*. Although conditions for carbonate sedimentations continued to exist, the biotas of these areas never again contained the thermophilous foraminifera, benthonic (i.e., *Amphistegina*, *Heterostegina*, *Borelis*) or planktonic (*Globigerinoides*), which had been present earlier.

In the middle part of the Olimpów section (samples 4, 5 and 6) the *Amphistegina* specimens display a higher sphericity than those of the lower and upper parts of the section. Does this apparent trend in sphericity indicate shoaling conditions, with intense water motion? To verify this hypothesis, additional, depth-controlled features of the foraminiferal community were investigated. The percentage of planktonic forms, the percentage of symbiont-bearing specimens and the proportions of robust and flat forms of *Elphidium* (*E. crispum* (Linne, 1758) and *E. fichtelianum* (d'Orbigny, 1846), respectively) were examined (Fig. 7). The data confirm that the depth of the sedimentary area decreased in this part of the section. The recorded trend in bathymetry was either due to tectonic movement (uplift of the sea bottom, followed by deepening in this particular area) or the shoaling of the sedimentary area, as a result of eustatic sea-level change (swing). In the second possibility, increased sphericity of the *Amphistegina* tests must have been a signal, corresponding to the Mi3 Event. If this was the case, the biometrical examination of larger foraminifera appears not only to be a precise method for the reconstruction of palaeoenvironment, but also a promising, ecostratigraphic tool.

CONCLUSIONS

1. Only one morphospecies of *Amphistegina* (*Amphistegina hauerina* d'Orbigny, 1846) appears in the Olimpów Limestone.
2. The habitat of *Amphistegina* from the Olimpów Limestone was the sea bottom of the deep, euphotic and low-energy zone.

3. There is an upward change in the sphericity of *Amphistegina* tests in the studied section. This indicates an ephemeral shoaling of the basin for the middle part of the section. The change in bathymetry was confirmed, on the basis of other members of the foraminiferal assemblage. The conclusion on shoaling in this part of the section is supported by planktonic forms, symbiont-bearing forms, and *Elphidium* morphotypes.

4. This shoaling episode corresponded to the best environmental conditions for *Amphistegina* in the area considered – the spiral diameter of the specimens is smallest and is an indication of rapid attainment of maturity. The population structure was unimodal in this interval, which indicates its normal population structure (gradual accumulation of post-reproductive tests in the sediment).

5. The biometric analysis of the test shape of the larger foraminifera, when used in palaeoenvironmental analysis, also appears to be an effective tool for ecostratigraphy. In the case studied, this method was used to trace pivotal events in global stratigraphy. This is especially valuable in epicontinental areas of sedimentation, devoid of planktonic foraminifera.

Acknowledgments

The author would like to thank Dr. Ewa Malata (Institute of Geological Sciences of the Jagiellonian University; Kraków, Poland), an Anonymous Reviewer for comments that helped to improve the manuscript, and Dr. Bogusław Kołodziej (Institute of Geological Sciences of the Jagiellonian University; Kraków, Poland) for help in taking the photographs for Fig. 3.

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