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The foraminifera genus *Amphistegina* in the Korytnica Clays (Holy Cross Mts, Central Poland) and its significance in the Miocene of the Paratethys

ABSTRACT: Different populations of *Amphistegina* from the Central Paratethys have been studied and compared with the faunas of the Korytnica Basin, Central Poland. A biometrical computer analysis was used in order to solve the systematical problems of the species concept. The test shape and chamber development of the investigated species, taking in consideration relevant Recent species, demonstrated the phylogenetic relations and the differences between the species in question. Two main groups can be separated immediately. The first includes the species *Amphistegina mammilla* (FICHEL & MÖLL), *A. hauerina* D'ORBIGNY, and *A. radiata* (FICHEL & MÖLL), and is represented in the Miocene by only one species, namely *A. mammilla*. The Indo-Pacific origin of this fauna is proved by the close relation with *A. radiata*.

The *Amphistegina lessonii* D'ORBIGNY — species group is shown to have been represented by an independent species in the European Miocene, by *Amphistegina bohdanowiczi* BIEDA. It inhabited the Central Paratethys from the early Miocene to the early Badenian.

The Miocene forms were generally dextrally coiling. The existence of a subtropical climate during the Middle Miocene in Central Europe is supported. By means of the *Amphistegina* assemblages a biostratigraphic determination of the Korytnica Clays as early Badenian (corresponding the Lower Lagenidae Zone) was possible.

INTRODUCTION

The genus *Amphistegina* is one of the important foraminifera in the tropical/subtropical shallow water areas of today's oceans. These trochospirally coiled, relatively large foraminifera inhabit the carbonate productive belt and exhibit distinct distribution patterns in the different faunal provinces due to depth-dependent species. Therefore their occurrences in geological time represent important paleoecological and paleobiogeographical indicators.

The Middle Miocene Korytnica Clays in the Polish Fore-Carpathian Depression contain some larger foraminifera, e.g. *Amphistegina*, *Heterostegina*, and *Borelis*. In order to investigate the paleobiology of the fossil assemblages of

the Korytnica Basin, research on the genus *Amphistegina* was proposed by A. RADWAŃSKI. The paleogeographic and tectonic position of the area has been described by BAŁUK & RADWAŃSKI (1977a). The investigated samples originate from the northern slope of Mt. Lysa (BAŁUK & RADWAŃSKI 1977a, Fig. 2, section no. 2) and are numbered from the highest to the lowest position (Korytnica 1 to 6). The sediment is the basal gastropod-bearing clay. An additional sample comes from the *Heterostegina* sands of Chomentów, intercalated between the Korytnica Clays and the overlying *Lithothamnium* limestones.

Recently the systematics, stratigraphy and provincialism of *Amphistegina* has been reviewed by LARSEN (1976, 1978). Some problems concerning this group still remaining open, and a detailed analysis of the Miocene forms of the Central Paratethys was necessary. The establishment of the phylogenetic relationships of these Miocene species will enable a better understanding of the provincialism of Recent *Amphistegina* species.

In addition, a comparison of Recent species and the paleoenvironment of fossil forms in the Central Paratethys will allow an inference on the climate and circumstances of deposition. Throughout the Central Paratethys many shallow water deposits, whose exact stratigraphic position remained uncertain, yield these fossils. For this reason different assemblages are included in this investigation.

For systematical purposes certain Recent assemblages have also been investigated. A computer-based biometrical analysis has been used to solve the nomenclatorial problems.

The edition of this paper has been delayed for some years; only some minor changes have been added since. A preliminary poster presentation has been given therefore at the meeting of the Paleontological Society in Eggenburg (RÖGL & BRANDSTÄTTER 1991). The investigated material is deposited in the micropaleontological collection of the *Naturhistorisches Museum* in Vienna.

BIOMETRICAL ANALYSIS

Different morphotypes and some distinct species have been observed in the investigated assemblages of Miocene amphisteginas. In order to achieve a well-documented taxonomical solution of this problem, assemblages of different localities were grouped and measured. The main part stems from the Middle Miocene, Badenian stage, of the Central Paratethys. A preliminary investigation shows that two groups can be distinguished:

a) The *Amphistegina mammilla* stock. Two morphotypes, *A. mammilla* and *A. hauerina* have been separated by LARSEN (1978) according to the absence or presence of intersepta, and by PAPP & SCHMID (1985) based on the sharp angle of the spiral intercameral sutures in *A. hauerina*. Investigations of the different morphotypes reveal a third form with strongly lobate intercameral

sutures of the umbilical supplementary chambers. This form strongly resembles populations of *A. radiata*, and LARSEN (1976, p. 8) comments on the close relation to *A. radiata*. For this reason the different morphotypes have been measured separately and compared with Recent *A. radiata*.

b) The *Amphistegina lessonii* stock. In the Miocene of Europe the species name *A. lessonii* was predominantly used for amphisteginas with a strong asymmetric test and few large supplementary chambers. BIEDA (1936) created the new species *A. bohdanowiczi* for these forms and referred to the similarities with *A. lessonii*. Such forms are described from the Aquitanian and Burdigalian of southwestern France and from many localities of the Central Paratethys — from the Pannonian Basin to the Carpathian foredeep.

The same measurements have been carried out on both groups. These include largest and smallest diameters of the flat side of the test by means of a micrometer under the microscope; thickness of the test (+/-0.01 mm) by means of a special micrometer used to measure hair thickness. Chamber numbers were counted, in fossil specimens predominantly after embedding in water or alcohol for better transparency.

In the morphometrical analyses of amphisteginas, carried out by LARSEN (1976), LARSEN & DROOGER (1977), HALLOCK (1979), and HALLOCK & *al.* (1986) values of diameter and thickness, the so-called shape index was used. This approximation is useful in symmetric tests but does not consider the variability in forms changing from nearly planispiral to planoconvex forms, or take into consideration a strong protruding umbonal boss on one or both sides of the test. Therefore the number of chambers has been taken as a second important variable in this investigation, as chamber formation is a constant process in the life cycle.

Table 1

Morphometric properties: Average values of investigated *Amphistegina* populations
 M — *A. mamilla*, R — *A. radiata*, B — *A. bohdanowiczi*, L — *A. lessonii*
 (for abbreviations see text; n.d. = not determined)

	L	B	TH	CH	D	A	S	N	
WIEN/N1	2.31	2.15	0.70	25.90	2.23	0.54	3.20	24	M
WIEN/N2	2.28	2.14	0.69	26.50	2.21	0.52	3.20	24	
WIEN/N3	2.54	2.36	0.82	28.00	2.45	0.55	3.00	9	
WIEN/N4	1.74	1.61	0.53	21.10	1.67	0.49	3.20	24	
WIEN/N5	1.64	1.53	0.50	19.80	1.58	0.50	3.20	24	
BRUNN/1	1.96	1.82	0.65	23.90	1.89	0.50	2.97	24	
BRUNN/2	2.66	2.50	0.85	n.d.	2.58	n.d.	3.10	24	
STARO/1	1.84	1.73	0.69	23.60	1.78	0.47	2.62	24	
NL/1	2.25	2.13	0.74	26.20	2.19	0.53	3.00	24	
KOR/1	2.25	2.10	0.76	28.10	2.18	0.49	2.89	24	
KOR/2	1.89	1.81	0.62	24.60	1.85	0.47	3.00	24	
KOR/3	1.80	1.69	0.60	22.90	1.75	0.47	2.94	24	
KOR/4	1.65	1.56	0.52	21.30	1.60	0.46	3.10	24	

Table 1 (cont'd)

KOR/5	1.73	1.58	0.57	22.10	1.65	0.47	2.88	15	
KOR/6	1.66	1.56	0.56	22.00	1.61	0.44	2.97	8	
CHO/1	1.96	1.86	0.67	n.d.	1.91	n.d.	2.91	24	
JAVA/1	0.92	0.87	0.35	10.60	0.89	0.53	2.56	23	R
MAL/1	1.81	1.72	0.88	20.60	1.76	0.54	2.04	21	
KOS/1	1.24	1.13	0.57	14.40	1.18	0.52	2.07	24	B
KOR/1/1	0.83	0.77	0.39	10.00	0.80	0.49	2.08	3	
KOR/2/1	1.30	1.17	0.57	14.20	1.23	0.54	2.18	24	
KO3/3/1	1.31	1.18	0.56	13.50	1.24	0.57	2.24	24	
KOR/4/1	1.26	1.12	0.53	13.80	1.19	0.54	2.25	24	
KOR/5/1	1.10	1.01	0.51	13.30	1.05	0.50	2.11	18	
KOR/6/1	1.13	1.04	0.52	13.50	1.08	0.51	2.11	13	
LOC/1	1.45	1.32	0.60	14.80	1.38	0.59	2.31	24	
NL/1/1	1.47	1.33	0.66	14.70	1.40	0.60	2.13	24	
STARO2/2	1.23	1.12	0.55	14.50	1.17	0.51	2.14	24	
LEO2/1	1.35	1.23	0.56	13.10	1.29	0.63	2.31	16	
FUNA/1	1.46	1.34	0.65	11.20	1.40	0.79	2.16	20	
SETO/1	0.93	0.84	0.43	8.30	0.89	0.68	2.05	10	
SAF/1	1.01	0.93	0.42	9.60	0.97	0.64	2.32	7	
SAF/2	0.66	0.59	0.33	7.30	0.63	0.54	1.92	12	

An average diameter was calculated from the measured length and breadth; the number of chambers in the nearly circular test was transferred into the average arc length of the chamber periphery. All measurements of specimens calculated for mean values of populations are presented (Table 1).

Abbreviations used in the Tables:

L	maximum diameter
B	minimum diameter
D	average diameter = $(L+B) \cdot 0.5$
TH	thickness
CH	number of chambers in the final whorl
A	average arc length: = $2\pi D \cdot (CH)^{-1}$
S	shape index: = $D \cdot (TH)^{-1}$
N	number of specimens
XM	arithmetic mean of the X-values
YM	arithmetic mean of the Y-values

The morphological properties were studied by means of regression analysis. Regressions are given by the equation: $Y = d + k \cdot X$ where Y is the dependent, X the independent variable; r is the conventional correlation coefficient. The introduction of the arc length A makes it possible to compare the number of chambers CH with values in terms of length.

Amphistegina mammilla (FICHTEL & MOLL)

The first step involved investigating the different morphotypes of the *A. mammilla/A. hauerina* group existing in the Vienna Basin type localities. The regression parameters are given in Table 2A. The regression lines for the shape index of the populations fall into a narrow field, demonstrating that the different types belong to the same species (Text-fig. 1/4).

The specimens from the Korytnica assemblages are generally smaller. It should be mentioned that the specimens are worn and damaged. However, in the diagrams they have the same pattern as all other Middle Miocene Paratethys populations (Table 2A; Text-fig. 2/1-2; Text-fig. 2/5; Text-fig. 3A-3B). The population plots are in a linear arrangement.

The largest amphistegines observed were from the *Amphistegina* marl of Wien-Nussdorf, with a maximum diameter of 4.04 mm and a maximum thickness of 1.30 mm.

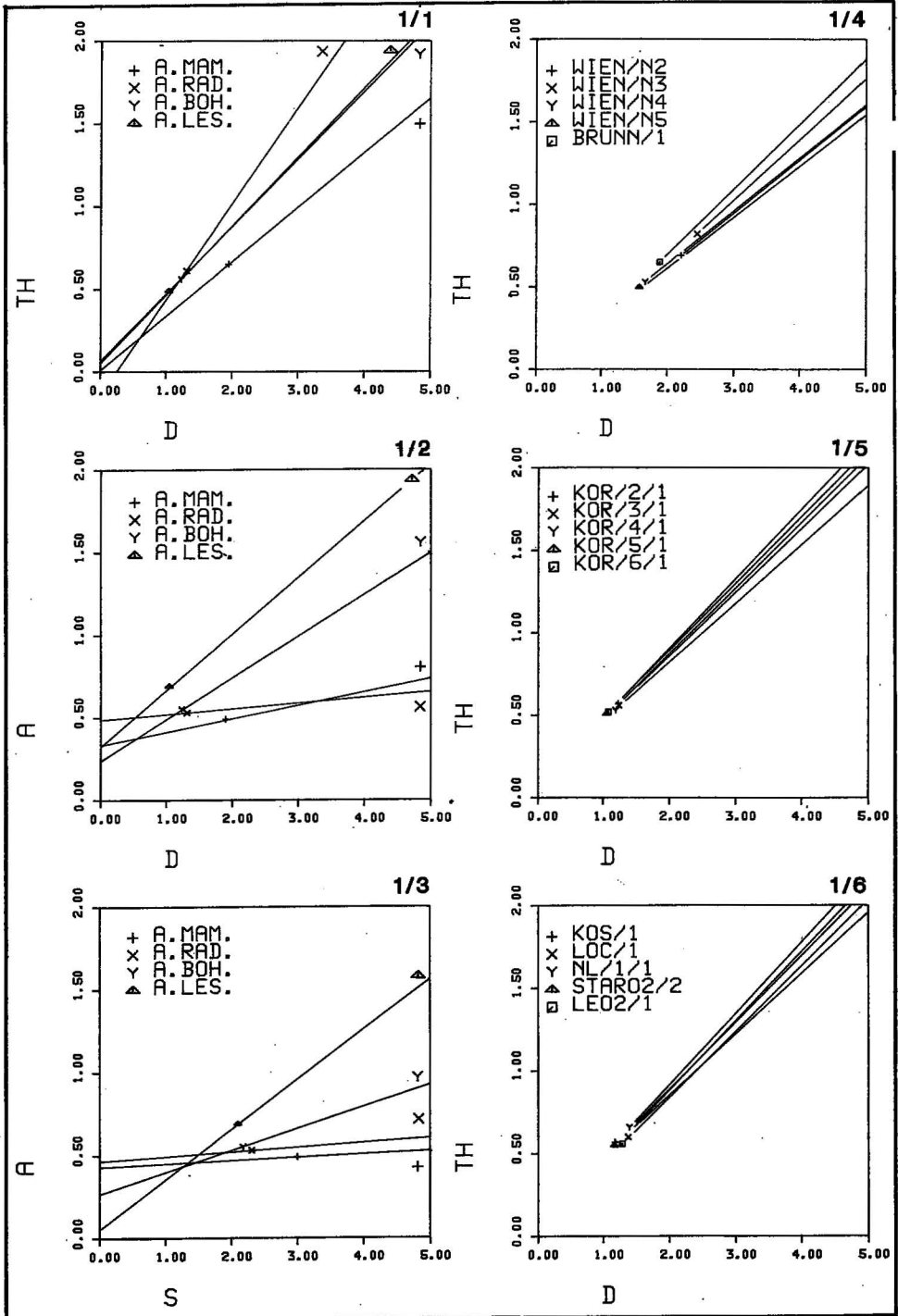
Amphistegina radiata (FICHTEL & MOLL)

To compare the phylogenetic relationship with *A. mammilla*, Recent populations of *A. radiata* were taken into consideration (see Tables 1 and 2A). In spite of the low number of available specimens a general trend separating the two species was observed. The shape index indicates a distinct difference between the large flat *A. mammilla* and the stout *A. radiata*, characterized by smaller diameters (Text-fig. 1/1). The phylogenetic relationship between the two forms is expressed clearly in the regression between the arc length and the shape index (Text-fig. 1/3). The chamber forming process in both species is very similar; this is demonstrated in the side views in Plates 1 and 2.

Amphistegina bohdanowiczi BIEDA and *A. lessonii* D'ORBIGNY

The differences to the Recent *A. lessonii* are rather difficult to define in a morphological description. Differences in the starlike arrangement of supplementary chambers have been mentioned by O'HERNE (1974) in stratigraphic successions. This has not been confirmed by the present study (compare Pl. 3, Figs 29-34). Regression analysis, however, reveals a distinction between the fossil and Recent species.

A very similar test shape in both species (Table 1) is reflected in the overlap of the regression lines (Text-fig. 1/1). In a comparison of the parameters of chamber growth to the diameters of tests and to the test shape, both species distinctly deviate in their regression (Text-fig. 1/2-3). As a certain degree of inaccuracy may exist because of the low number of Recent specimens



and the rather poor correlation of parameters, an additional calculation was carried out.

The regression parameters k and d (for $Y=D$, $X=A$) of the individual populations of *A. bohdanowiczi* and *A. lessonii* (Table 2B) significantly deviate from the corresponding k and d values calculated from the total number of both species (Table 3). If the above-mentioned k and d parameters from Table 2B are plotted in a d versus k diagram (Text-fig. 4), then a strong linear dependence between the slope k and the d value of the individual regression line is demonstrated. This regression of individual regression parameters gives correlation coefficients of -0.97 and -0.98 for the *A. bohdanowiczi* and *A. lessonii* populations respectively. Text-figure 4 also shows that the populations of the two species fall onto two distinct lines and hence can be regarded as two separate species.

A comparison between *A. bohdanowiczi* from Korytnica and the other localities, including the early Miocene of Leognan shows a good agreement in the correlation of test shape (Text-fig. 1/5-6). Scatter diagrams for the Korytnica samples are added in Text-figs 3A and 3B.

SYSTEMATIC ACCOUNT

In the following section the synonymy of the most important *Amphistegina* species of the Central Paratethys and the corresponding Recent forms is discussed.

Fig. 1

Regression lines for different parameters given in Table 3; position of the centres of mass (XM , YM) are indicated on the lines

1/1: Thickness versus diameters; Note the close relationship in the shape index of *A. bohdanowiczi* and *A. lessonii*, whereas *A. mammilla* and *A. radiata* diverge as based on relative thickness

1/2: Arc length versus diameter: in this correlation *A. mammilla* and *A. radiata* demonstrate a strong relation; whereas the other group deviates

1/3: Arc length versus shape index: the diagram shows that in the *A. mammilla/A. radiata* group the average arc length is almost independent of shape; in the first approximation the number of chambers increases linearly with test size; the phylogenetic relationship is expressed by the short distance between the regression lines; the *A. lessonii* group, strongly analogous in the parameters in Fig. 1/1, falls into two distinct species with these proportions

Regression lines for individual populations demonstrating near relationships; parameters given in Table 2A and 2B

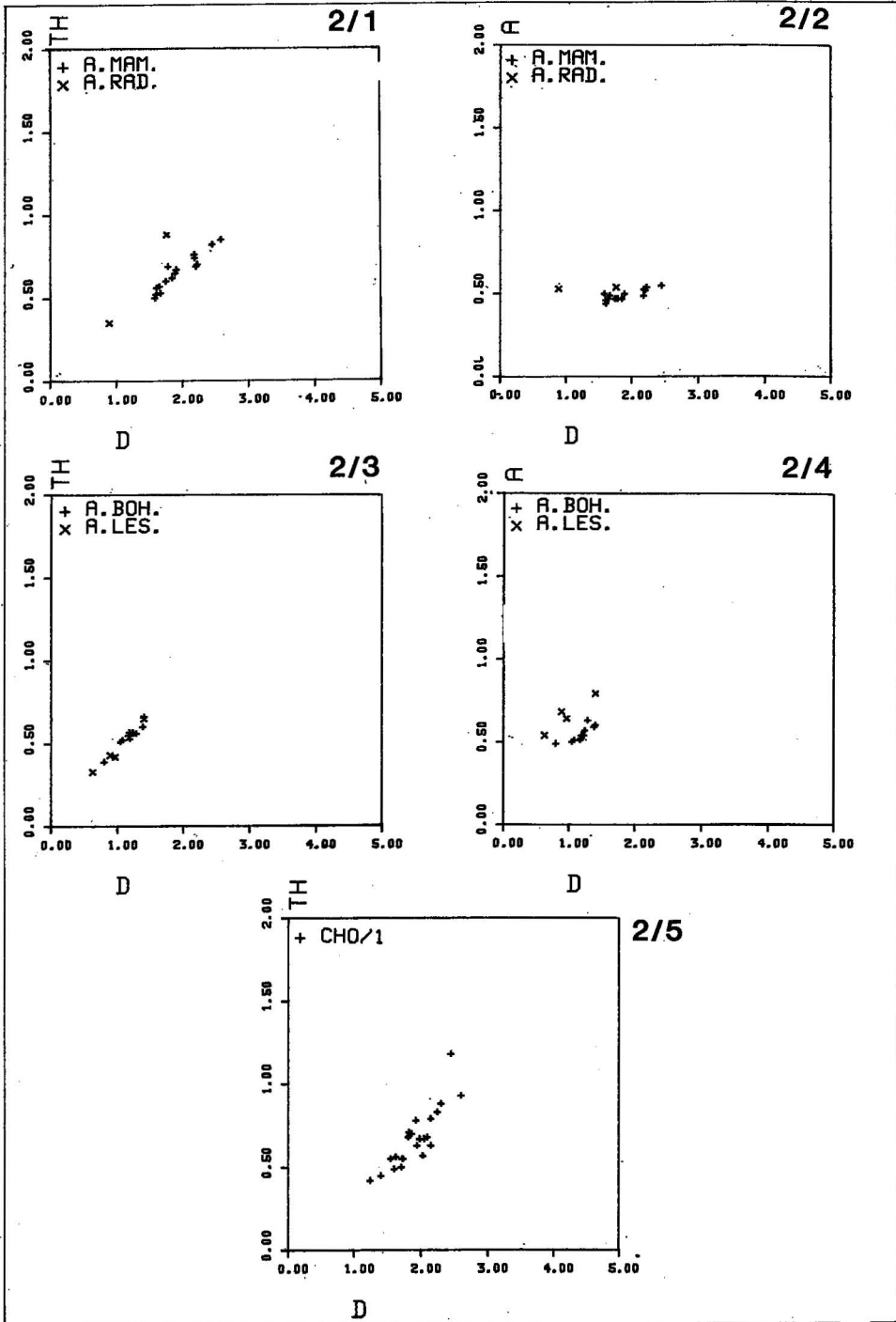
1/4: Relationship of test shape in *A. mammilla* topotypes: Brunn/1 — *A. mammilla* topotypes; Wien/N2 — type sample of *A. mammilla* neotype; Wien/N3 — *A. hauerina* morphotype from the same sample; Wien/N4 — morphotype with lobate intercameral sutures; Wien/N5 — morphotype intermediate between *A. hauerina* and *A. radiata*, with lobate umbilical sutures and intersepta

1/5: Relationship of test shape in the *A. bohdanowiczi* populations of the Korytnica section

1/6: Comparison of test shape of *A. bohdanowiczi* from different localities in Europe; all populations appear to belong to the same species

KOS/1 — Costei (= Kostej), Rumania, early Badenian; LOC/1 — Locatelliwald, Mailberg, Lower Austria, early Badenian; NL/1/1 — Niederleis, Lower Austria, early Badenian; STARO2/2 — Staropatica, Bulgaria, early Badenian; LEO2/1 — Leognan, France, *Heterostegina* sands, Burdigalian

All dimensions of TH , D , A in millimeters



Amphistegina mammilla (FICHEL & MOLL, 1798)

(Pl. 1, Figs 1–4; Pl. 2, Figs 7–8; Pl. 4, Figs 10–11; Pl. 5, Figs 1–3; Pl. 6, Fig. 2)

1798. *Nautilus mammilla*; FICHEL & MOLL, p. 53, Pl. 6, Figs a–d.
 1846. *Nummulina radiata*; D'ORBIGNY, p. 115, Pl. 5, Figs 23–24.
 1846. *Amphistegina hauerina*; D'ORBIGNY, p. 207, Pl. 12, Figs 3–5.
 1846. *Amphistegina mamillata*; D'ORBIGNY, p. 208, Pl. 12, Figs 6–8.
 1846. *Amphistegina rugosa*; D'ORBIGNY, p. 209, Pl. 12, Figs 9–11.
 1862. *Amphistegina haueri*; SUBSS, p. 144, Fig. 16/2.
 1876. *Amphistegina Haueri* D'ORB.; ZITTEL, p. 95, Fig. 34.
 1962. *Amphistegina hauerina* ORBIGNY subsp. *podolica* VENOLINSKI, p. 96, Pl. 12, Fig. 1c (*vide* DIDKOVSKI & SATANOVSKAYA 1970).
 1978. *A. mamilla* (FICHEL & MOLL, 1798); LARSEN, p. 224, Pl. 1, Figs 8–9, 11–12; Pl. 6, Fig. 3; Pl. 7, Fig. 4.
 1978. *A. hauerina* D'ORBIGNY, 1846; LARSEN, p. 224, Pl. 2, Figs 1, 4.
 1984. *Amphistegina mammilla* (FICHEL & MOLL, 1798); RÖGL & HANSEN, p. 41, Text-fig. 13; Pl. 10, Figs 1–3; Pl. 11, Figs 1–2.
 1985. *Amphistegina hauerina* D'ORBIGNY; PAPP & SCHMID, p. 75, Pl. 67, Figs 1–6.

Descriptions of this species have been given in detail by LARSEN (1978), RÖGL & HANSEN (1984), and PAPP & SCHMID (1985). Agreement has been reached on the synonymies of *A. hauerina* and the other species described by D'ORBIGNY (1846). In the present paper, biometrical analysis has proved that only one species of these different forms existed in the Middle Miocene of the Paratethys.

The species itself is very variable in outline. The normal test is nearly planispiral and approaches a superficial symmetry. This is due to the very large supplementary chambers of the umbilical side, leaving only a small lobe of the primary chamber visible near the periphery in the alternating arrangement of the chambers. The peripheral position of the aperture, still interiomarginal-umbilical, intensifies this impression. During growth the asymmetric form becomes more prominent. Large adult specimens are commonly planoconvex with a flat umbilical or spiral side, in extreme cases becoming concaveconvex. There is also a tendency in large specimens for the chambers to grow somewhat irregularly, developing long alar projections, overgrowing older chambers. An evolute trend of the final whorl is also evident in such specimens. The umbonal bosses are normally more strongly developed on the umbilical side and are generally flush with the surface. Some protrude as tall cones.

In order to investigate ontogenetic development and changes in morphology, a few large specimens were opened. They have been embedded in water and the chambers have been removed one by one. The spiral intercameral sutures, forming a broad arc in the outer whorl, are increasingly angled in the inner whorl, and the intersepta are developed more distinctly. Similar changes occur at the umbilical side, demonstrating lobate-fringed intercameral sutures of the supplementary chambers in the juvenile stages of ontogeny. This corresponds principally to the results of biometrical measurements.

Fig. 2

Scattergrams of *Amphistegina* parameters

- 2/1: Test shape (diameter versus thickness) of averaged populations of Middle Miocene *A. mammilla* and Recent *A. radiata*
 2/2: Plot of arc length versus diameter of averaged Middle Miocene *A. mammilla* and Recent *A. radiata* populations
 2/3: Test shape (diameter versus thickness) of Miocene *A. bohdanowiczii* and Recent *A. lessonii* populations
 2/4: Relation of arc length to diameter in populations of Miocene *A. bohdanowiczii* and Recent *A. lessonii*
 2/5: *Amphistegina mammilla* from the *Heterostegina* sands of Chomentów, Poland; this fauna contains only one *Amphistegina* species

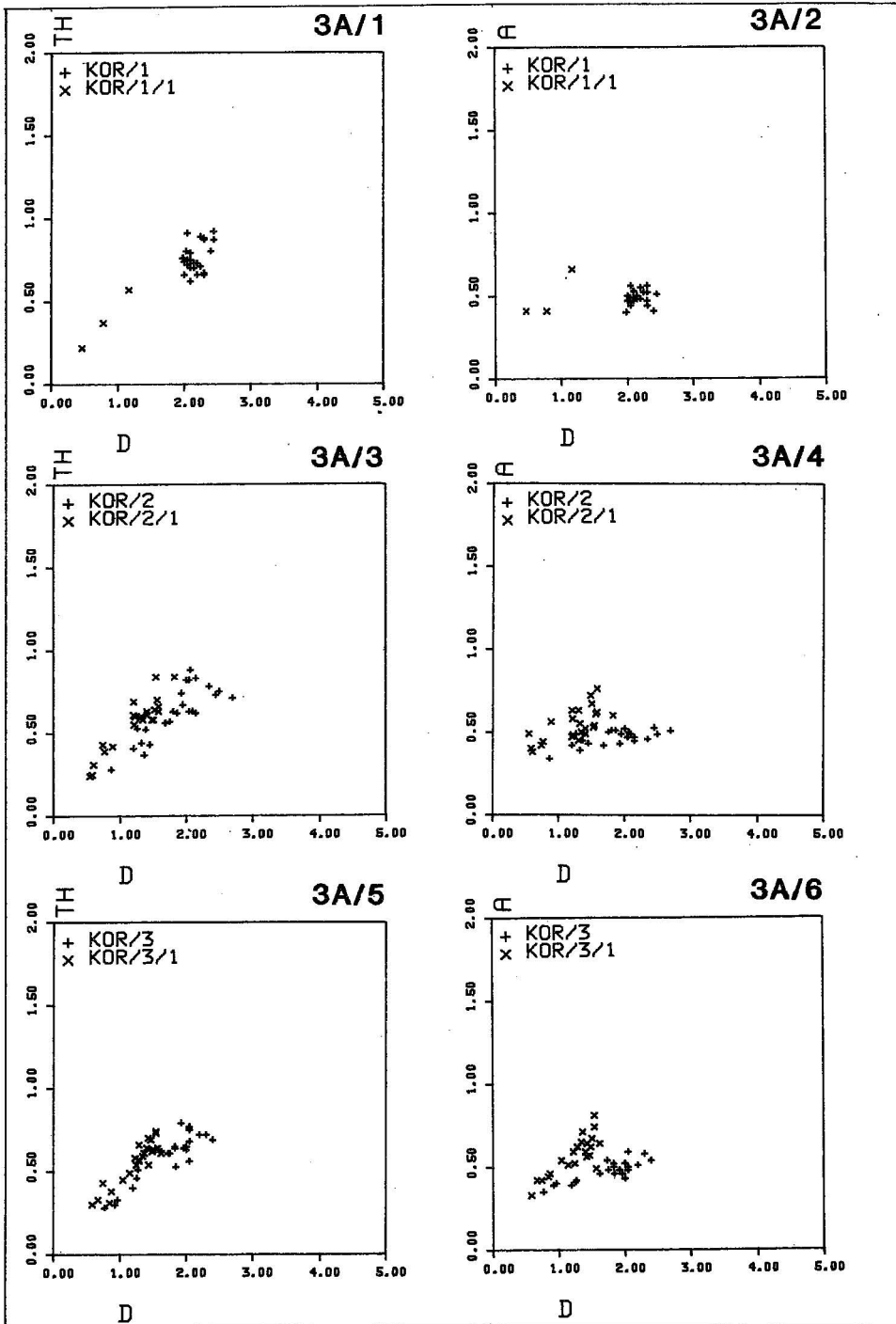


Fig. 3A. Scattergrams of the test shape relation and arc length versus diameter (chamber frequency in the final whorl against test size) for *A. mammilla* and *A. bohdanowiczi* in the Korytnica Basin, Poland. Samples numbered from highest to basal part of the section (KOR 1 to 6); both species are plotted in each diagram.

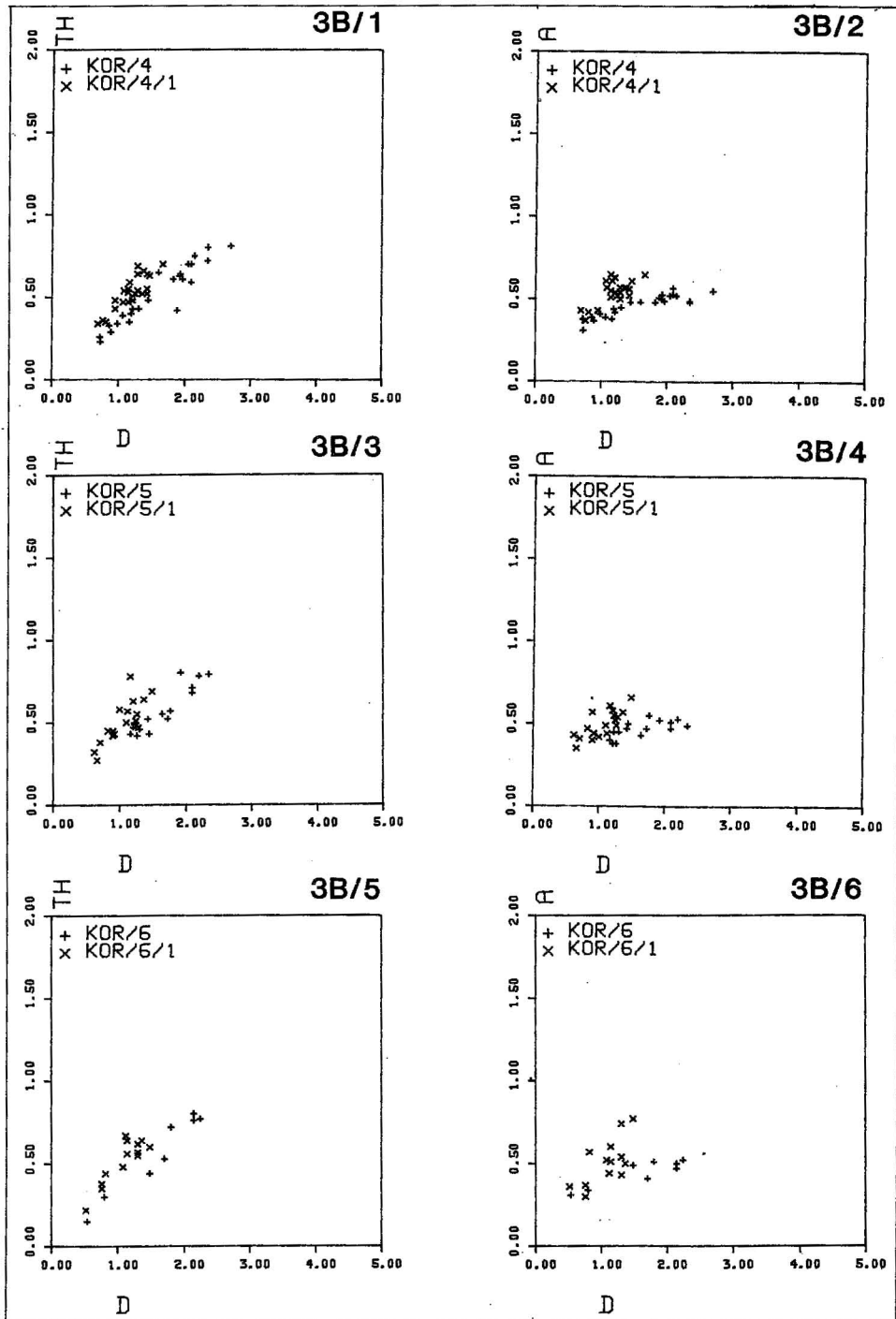


Fig. 3B. Relations of *A. mammilla* and *A. bohdanowiczi* in the Korytnica Basin, Poland (Fig. 3A continued)

Table 2A

Regression analysis of *Amphistegina mammilla* populations in comparison to Recent *A. radiata* (marked by *)
 Equation of regression line: $Y = d + kX$; r = correlation coefficient; XM , YM = arithmetic mean values

	X	Y	k	d	r	XM	YM
WIEN/N1	D	TH	0.30	0.04	0.85	2.23	0.70
	D	A	0.01	0.53	0.11	2.23	0.54
WIEN/N2	D	TH	0.31	0.01	0.81	2.21	0.69
	D	A	0.02	0.48	0.27	2.21	0.52
WIEN/N3	D	TH	0.37	-0.09	0.97	2.45	0.82
	D	A	0.04	0.44	0.67	2.45	0.55
WIEN/N4	D	TH	0.32	0.00	0.89	1.67	0.53
	D	A	0.12	0.29	0.87	1.67	0.49
WIEN/N5	D	TH	0.32	-0.01	0.92	1.58	0.50
	D	A	0.12	0.31	0.90	1.58	0.50
BRUNN/1	D	TH	0.39	-0.09	0.91	1.89	0.65
	D	A	0.04	0.43	0.38	1.89	0.50
BRUNN/2	D	TH	0.45	-0.31	0.71	2.58	0.85
	D	A	0.36	0.04	0.91	1.78	0.69
STARO/1	D	TH	0.36	0.04	0.91	1.78	0.69
	D	A	0.11	0.28	0.79	1.78	0.47
NL/1	D	TH	0.31	0.06	0.69	2.19	0.74
	D	A	0.03	0.47	0.20	2.19	0.53
KOR/1	D	TH	0.23	0.25	0.38	2.18	0.76
	D	A	0.05	0.39	0.16	2.18	0.49
KOR/2	D	TH	0.29	0.09	0.83	1.85	0.62
	D	A	0.06	0.35	0.63	1.85	0.47
KOR/3	D	TH	0.30	0.08	0.91	1.75	0.60
	D	A	0.11	0.28	0.83	1.75	0.47
KOR/4	D	TH	0.30	0.05	0.95	1.60	0.52
	D	A	0.10	0.30	0.90	1.60	0.46
KOR/5	D	TH	0.32	0.05	0.92	1.65	0.57
	D	A	0.09	0.32	0.70	1.65	0.47
KOR/6	D	TH	0.37	-0.04	0.97	1.61	0.56
	D	A	0.11	0.26	0.89	1.61	0.44
CHO/1	D	TH	0.46	-0.20	0.86	1.91	0.67
JAVA/1 *	D	TH	0.20	0.17	0.51	0.89	0.35
	D	A	0.14	0.40	0.35	0.89	0.53
MAL/1 *	D	TH	0.54	-0.07	0.92	1.76	0.88
	D	A	0.09	0.38	0.58	1.76	0.54

Table 2B

Regression analysis of *Amphistegina bohdanowiczi* populations in comparison to Recent *A. lessonii* (marked by *); for explanations see Table 2A

	X	Y	k	d	r	XM	YM
KOS/1	D	TH	0.43	0.07	0.91	1.18	0.57
	D	A	0.28	0.19	0.76	1.18	0.52
KOR/2/1	D	TH	0.40	0.07	0.92	1.23	0.57
	D	A	0.19	0.32	0.67	1.23	0.54
KO3/3/1	D	TH	0.39	0.07	0.92	1.24	0.56
	D	A	0.30	0.20	0.81	1.24	0.57
KOR/4/1	D	TH	0.36	0.10	0.85	1.19	0.53
	D	A	0.23	0.26	0.71	1.19	0.54
KOR/5/1	D	TH	0.41	0.08	0.78	1.05	0.51
	D	A	0.26	0.22	0.77	1.05	0.50
KOR/6/1	D	TH	0.42	0.06	0.88	1.08	0.52
	D	A	0.33	0.15	0.68	1.08	0.51
LOC/1	D	TH	0.43	0.01	0.93	1.38	0.60
	D	A	0.16	0.37	0.66	1.38	0.59
NL/1/1	D	TH	0.38	0.13	0.89	1.40	0.66
	D	A	0.25	0.25	0.76	1.40	0.60
STARO2/2	D	TH	0.41	0.07	0.89	1.17	0.55
	D	A	0.24	0.22	0.78	1.17	0.51
LEO2/1	D	TH	0.40	0.04	0.79	1.29	0.56
	D	A	0.45	0.05	0.60	1.29	0.63
FUNA/1 *	D	TH	0.35	0.16	0.90	1.40	0.65
	D	A	0.28	0.40	0.53	1.40	0.79
SETO/1 *	D	TH	0.38	0.09	0.94	0.89	0.43
	D	A	0.66	0.09	0.90	0.89	0.68
SAF/1 *	D	TH	0.31	0.12	0.64	0.97	0.42
	D	A	0.39	0.26	0.71	0.97	0.64
SAF/2 *	D	TH	0.64	-0.07	0.94	0.63	0.33
	D	A	0.38	0.31	0.58	0.63	0.54

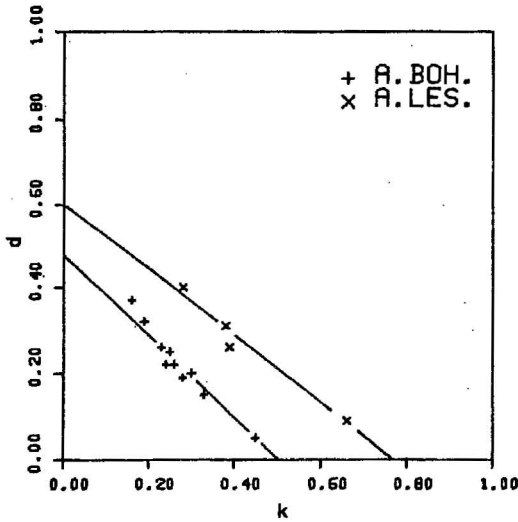


Fig. 4
Comparison of the regression parameters k and d for $Y = D$ and $X = A$ (Table 2B) for populations of *A. bohdanowiczi* and *A. lessonii*

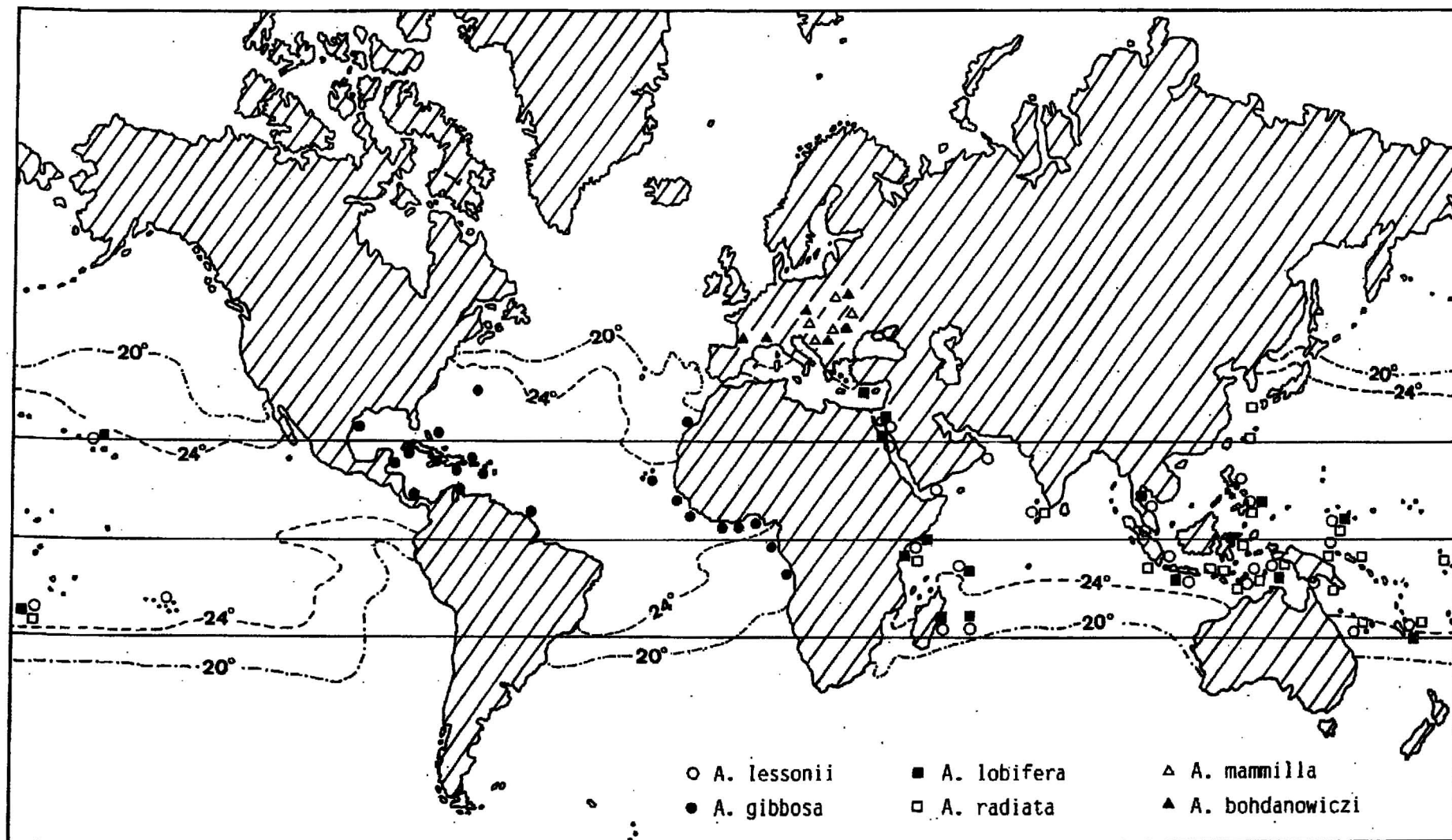
Table 3

Regression analysis for all investigated *Amphistegina* species calculated from all measured specimens (N)

A.MAM. — *Amphistegina mamilla*, A.RAD. — *Amphistegina radiata*, A.BOH. — *Amphistegina bohdanowiczi*, A.LES. — *Amphistegina lessonii*; for explanations see Table 2A

	X	Y	k	d	r	X_M	Y_M	N
A. MAM.	D	TH	0.33	0.02	0.89	1.95	0.65	344
	B	A	0.08	0.35	0.68	1.90	0.49	296
	S	A	0.02	0.44	0.10	3.00	0.49	296
A. RAD.	D	TH	0.58	-0.16	0.97	1.31	0.61	44
	D	A	0.03	0.49	0.32	1.31	0.53	44
	S	A	0.03	0.47	0.20	2.31	0.53	44
A. BOH.	D	TH	0.40	0.08	0.90	1.23	0.56	218
	D	A	0.25	0.24	0.73	1.23	0.55	218
	S	A	0.14	0.23	0.33	2.18	0.55	218
A. LES.	D	TH	0.41	0.07	0.96	1.04	0.49	49
	D	A	0.34	0.33	0.80	1.04	0.69	49
	S	A	0.30	0.05	0.45	2.10	0.69	49

The mean value of the diameter in the different populations ranges from 1.6 mm, with certain specimens having maximum values of up to 4 mm. The mean thickness varies between 0.5 and 0.8 mm, with a maximum value of 1.3 mm. The mean number of chambers in the last whorl lies between 20 and 28, reaching 47 in the largest specimens. For other values see Tables 1–3.

Distribution of *Amphistegina* species related to the present investigation

Recent provinces and distributions generally according to LARSEN (1978, Fig. 1); the 24° and 20°C summer isotherms, given according to the Rand McNally Atlas of the Oceans (BRAMWELL 1977), delimit the Recent assemblages

Amphistegina radiata (FICHEL & MOLL, 1798)

(Pl. 1, Figs 5–6; Pl. 2, Figs 9–11; Pl. 5, Figs 4–6; Pl. 6, Fig. 1)

1798. *Nautilus radiatus*; FICHEL & MOLL, p. 58, Pl. 8, Figs a–d.1826. *Amphistegina quoil*; D'ORBIGNY, p. 304, Pl. 17, Figs 1–4.1976. *Amphistegina radiata* (FICHEL & MOLL, 1798); LARSEN p. 7, Pl. 5, Figs 1–4; Pl. 6, Figs 1–2; Pl. 7, Fig. 5; Pl. 8, Fig. 5.1984. *Amphistegina radiata* (FICHEL & MOLL, 1798); ROGL & HANSEN, p. 43; Text-figs 15–16; Pl. 10, Figs 4–5.

This Recent species from the Indo-Pacific was revised by LARSEN (1976, 1978). The internal features, including the development of intersepta and supplementary chambers are figured in the above papers by internal moulds (shown for the first time by CARPENTER & *al.* 1862, Pl. 13; Fig. 29 for the spiral side). The main difference between *A. radiata* and *A. mammilla* is revealed in the shape index, demonstrating a much thicker test in the former species. The test of *A. radiata* is more symmetrically biconvex. Further distinctions include the more peripheral angle of the alar projections as well as the constant occurrence of intersepta, sometimes in two rows.

The close phylogenetic relationship to *A. mammilla* is indicated by the biometrical analysis (see Text-fig. 1/3), where a similar chamber-forming process is implied.

Amphistegina bohdanowiczi BIEDA, 1936

(Pl. 3, Figs 20–34; Pl. 4, Figs 1–6; Pl. 6, Figs 5–6)

1936. *Amphistegina bohdanowiczi* BIEDA, p. 266 (271), Pl. 8, Fig. 4a–c.1966. *Amphistegina lessonii* D'ORBIGNY, 1826; BUTT, p. 75, Pl. 4, Fig. 4.

This is a small species of *Amphistegina* with a mean diameter of 0.8 to 1.4 mm, specimens ranging up to 2.1 mm, and with a strong asymmetric test. It is biconvex to planoconvex, biumbonate, normally high-vaulted, with a mean thickness of 0.4 to 0.7 mm, and with maximum values of 1 mm. The aperture is distinctly umbilical in position, extending as an umbilical-extraumbilical, interiomarginal slit. The most distinct feature is the large pustulate area in front of the aperture, extending as a curved triangle between the umbilical umbo and the periphery. This pustulate area extends beyond the earlier chambers, giving an overall pustulate appearance of the umbilical side, if the chambers are broken in the final whorl. This is the case in the figured type specimen of BIEDA.

The spiral intercameral sutures are curved to sigmoidal or are angled. The umbilical side exhibits few rhomboidal supplementary chambers arranged in a star-like pattern, occasionally extending in a sickle-shaped fashion between the alternating primary chambers. The intercameral sutures of the supplementary chambers are slightly curved to lobate, normally showing a well-developed posterior lobe at the angle with the primary chamber. This pattern was used by O'HERNE (1974) for a stratigraphic evaluation during the Miocene, but has too large a variation to be used (*compare* Pl. 3, Figs 29–34).

The number of chambers within the last whorl averages between 10 and 15, with a maximum of 20.

The original material of BIEDA has been compared cordially by E. ŁUCZKOWSKA (Cracow). The species itself has been described as *Amphistegina lessonii* D'ORBIGNY in the European Miocene by many authors. A synonymy with *A. aucklandica* KARRER (1884), suspected by LARSEN (1976) is not existing. The latter species is very high conical, has a higher number of chambers in the final whorl, and a distinct smaller apertural pustulate area; the supplementary chambers are more irregularly outlined.

The species *A. bohdanowiczi* is known from the Oligocene (together with *Nummulites bouillei*), Aquitanian and Burdigalian of southern France (BUTT 1966; POIGNANI & PUJOL 1976, 1978); from the late Oligocene and Miocene (Tortonian) of Malta (FELIX 1973). In the Paratethys it is recorded from the early Miocene, Eggenburgian of the Bavarian Molasse Basin (WENGER 1987); from the early Badenian of the Central Paratethys: e.g. Pannonian Basin (KORECZ-LAKY & NAGY-GELLAI 1985), Carpathian foredeep (BIEDA 1936; ŁUCZKOWSKA 1964, 1967). Material has been observed during this study from the Burdigalian of Leognan (France); from the Eggenburgian of Eggenburg (Austria); from the Karpatian bryozoan limestones of Bantapuszta in Hungary; from the Langhian (NN5) of St. Martin de Hinx (Aquitaine Basin, France); from the early Badenian of the Molasse Basin north of the Danube in Austria and Moravia, and from the same age deposits in the Transylvanian Basin and Bulgaria.

Amphistegina lessonii D'ORBIGNY, 1843

(Pl. 2, Figs 15–16; Pl. 4, Figs 7–9; Pl. 6, Figs 3–4)

1826. *Amphistegina Lessonii* D'ORBIGNY, p. 304 (not Pl. 17, Figs 1–4): nomen nudum.

1843. *Amphistegina Lessonii* D'ORB.; D'ORBIGNY in GUERIN-MENEVILLE, p. 10, Pl. 3, Fig. 11a–b.

1976. *Amphistegina lessonii* D'ORBIGNY, 1826; LARSEN, p. 2, Pl. 1, Figs 1–5; Pl. 7, Fig. 1; Pl. 8, Fig. 1.

1977. *Amphistegina lessonii* D'ORBIGNY, 1826; LARSEN, p. 273, Pl. 1, Figs 1–9: neotype.

The nomenclatorial problems connected with this species have been discussed by LARSEN (1976). By a typographical error the reference to the type figure of *A. quooii* has been printed in the line of *A. lessonii*. The model no. 98 is in accordance with the general use of the species *A. lessonii*. The only comment that remains to be made concerns the year of publication. According to LARSEN's proposal to relate the figures of D'ORBIGNY (1826) to *Amphistegina quooii*, *Amphistegina lessonii* becomes a nomen nudum. The first publication after 1826 was in GUERIN-MENEVILLE (1843), who published D'ORBIGNY's original drawings „d'apres d'Orbigny” and „toutes de d'Orbigny”. In this case it seems acceptable to retain D'ORBIGNY as the author in the work of GUERIN-MENEVILLE.

In the description of LARSEN, outer morphology and internal structures have been explained. The chamber forms and internal partitions are well figured also by CARPENTER & al. (1862, Pl. 13, Figs 27–28) and by O'HERNE (1974) using internal moulds.

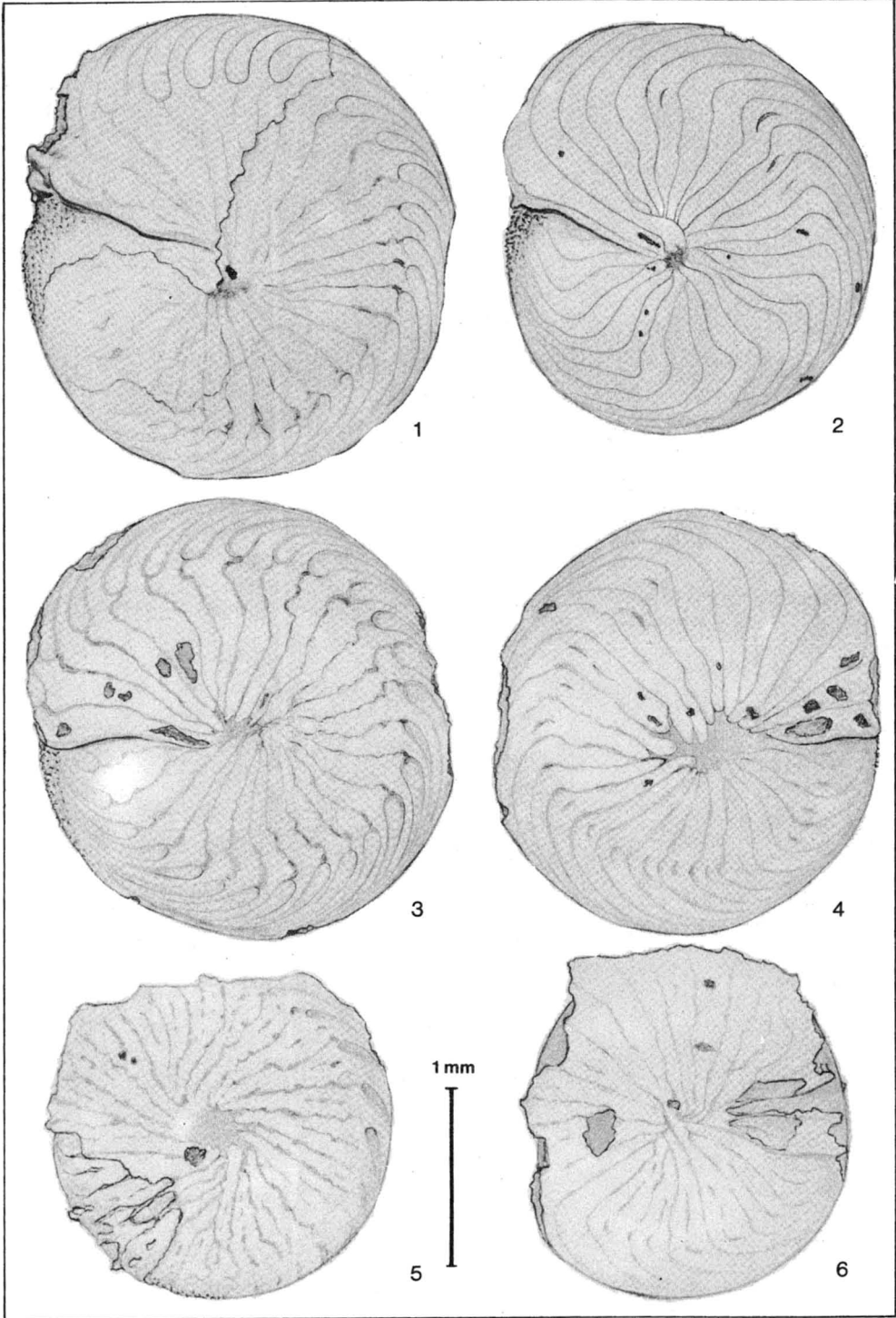
PLATE 1

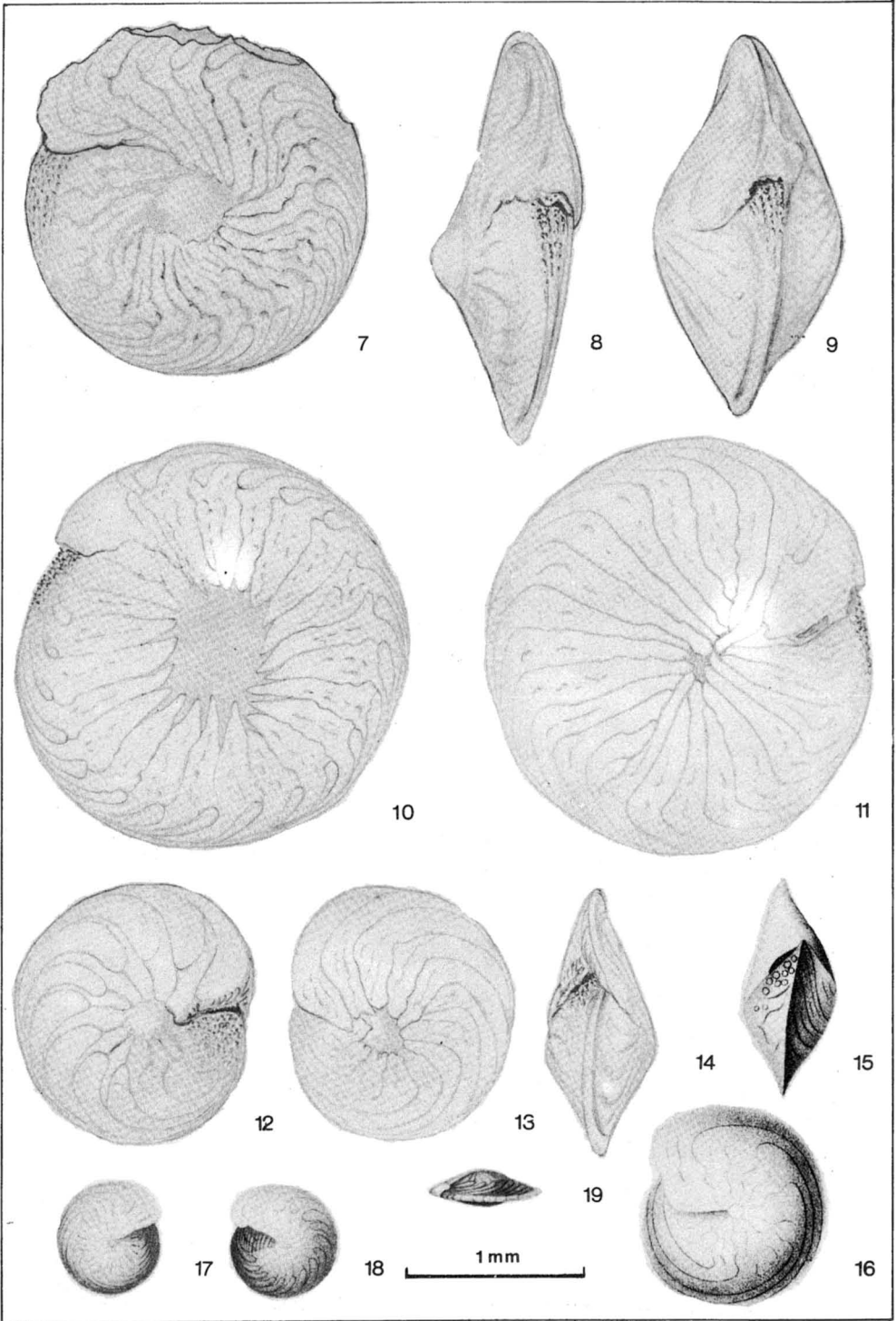
Amphistegina mammilla (FICHTEL & MOLL)

- 1 — Umbilical view, neotype: Wien-Nussdorf, Austria, Vienna Basin; Badenian, zone with agglutinated foraminifera (from RÖGL & HANSEN 1984, Fig. 13)
- 2 — Spiral view, showing sharply angled intercameral sutures and very scarce intersepta; Wien-Nussdorf, Austria, Vienna Basin; sample of the neotype
- 3 — Umbilical side with moderately lobate sutures of the supplementary chambers; Korytnica, Poland; sample no. 5; early Badenian
- 4 — Spiral side with intersepta as described in the morphotype *A. hauerina*; same specimen as in Fig. 3

Amphistegina radiata (FICHTEL & MOLL)

- 5 — Umbilical view of a sectioned specimen, lectotype; Recent, Indian Ocean (from RÖGL & HANSEN 1984, Fig. 15)
- 6 — Spiral view of a sectioned specimen, paratype; Recent, Indian Ocean (from RÖGL & HANSEN 1984, Fig. 16)





In a comparison with *Amphistegina bohdanowiczi*, differences are evident mainly in the number of chambers, which are fewer in *A. lessonii* (according to LARSEN, 1976, generally 12 at a 1 mm diameter). The test shape is very similar as demonstrated by the biometrical analysis. The species *Amphistegina gibbosa* D'ORBIGNY (1839) is flatter biconvex, has a distinctly larger number of chambers in the final whorl, and regularly developed intersepta, missing in *A. bohdanowiczi* (comp. Pl. 2, Figs 17–19).

Amphistegina gigantea KARRER, 1865

1865: *Amphistegina gigantea*; KARRER, p. 711, Pl. 2, Fig. 16.

MATERIAL: *Naturhistorisches Museum Wien*, Micropaleont. Collection No. MI-389.

A single specimen has been described from the Middle Miocene (Badenian) of Porstendorf, Moravia. The investigation of the original material showed this to be an *Assilina*, strongly worn and polished by erosion. Seven whorls are visible; diameter 8 mm. It is a reworked Eocene specimen.

COILING DIRECTIONS

Changes in the coiling directions of foraminifera are used in the interpretation of stratigraphic successions and sometimes are considered to be

PLATE 2

Amphistegina mammilla (FICHEL & MOLL)

- 7 — Umbilical view with strongly lobate sutures of the supplementary chambers and irregular intersepta, resembling *A. radiata*; Niederleis, Lower Austria; Badenian, Lower Lagenidae Zone
8 — Apertural view of a specimen (presented in Pl. 1, Fig. 2) with an asymmetric test shape; short marginal aperture covered by an overhanging lip, and an elongate, flattened, pustulate area in front of it.

Amphistegina radiata (FICHEL & MOLL)

Recent, Maldives Islands, Helengeli, 32 m depth (coll. F. STERNBERG)

- 9 — Apertural view demonstrating the inflated biconvex test with a sharp peripheral angle and an aperture similar to *A. mammilla*; also with a small pustulate area
10 — Umbilical side with large glassy umbonal plug and irregular intersepta in each supplementary chamber
11 — Spiral side with small umbonal plug; sharp angle of intercameral sutures near the periphery; intersepta regularly arranged

Amphistegina lessonii D'ORBIGNY

Recent, Polynesia, Ellice Islands, Funafuti, 10 fathoms depth (Micropal. Collection, NHM Wien)

- 12 — Umbilical side demonstrating the star-like arrangement of sickle-shaped chambers and the large papillate area below the aperture
13 — Spiral side with primary chambers ending in finger-like projections in the glassy umbo; one or more intersepta per chamber are present
14 — Apertural view of the biconvex, sharply angled test; aperture forming an interiomarginal slit with a distinct lip

Amphistegina lessonii D'ORBIGNY

- 15-16 — Recent, Indian Ocean, Ile de France (= Mauritius); type figures in GUERIN-MENEVILLE (1843, Pl. 2, Fig. 11a–b)

Amphistegina gibbosa D'ORBIGNY

- 17-19 — Recent, Caribbean; type figures in R. DE LA SAGRA (1839, Pl. 8, Figs 1–3)

influenced by ecological properties. Using this method, o'HERNE (1974) studied the changes in amphisteginas of the Indonesian late Oligocene and Miocene.

The *Amphistegina lessonii* group starts with dextrally coiling forms in the Oligocene/early Miocene, changing to sinistral coiling during early Miocene, and returning to dextral coiling in the Middle Miocene. Recent populations are again predominantly sinistral coiling. The *Amphistegina quoyi* (= *A. radiata*) group is dextral coiling throughout. In the Japanese Miocene, MATSUMARU (1976) has also observed a dominance of dextrally coiling forms of *A. radiata* in the Miocene, decreasing in the Pleistocene.

The ecological aspects of coiling trends were investigated by HALLOCK & LARSEN (1979). Coiling trends are different on the species level but also change with regional distributions, as in *Amphistegina lobifera*. Age-dependent coiling changes and temperature-dependent deviations have also been observed.

Within the Miocene populations of the Central Paratethys dextrally coiling forms are generally dominant. Ninety-four percent of all counted *A. bohdanowiczi* (related to *A. lessonii*) are dextrally coiling specimens. Dextral coiling was registered in 89% of the total *Amphistegina mammilla* populations. Considering the stratigraphic development, however a decreasing tendency of dextrally coiling specimens from 92% in the early Badenian to 84% in the later Badenian was observed. The sinistral coiling mode is specially strong in typical forms of the *Amphistegina hauerina* morphotype. This Middle Miocene coiling trends are in agreement with the Indo-Pacific populations, and are probably influenced by the worldwide Middle Miocene warming for the dextrally coiling populations (compare MCGOWRAN 1979, 1986).

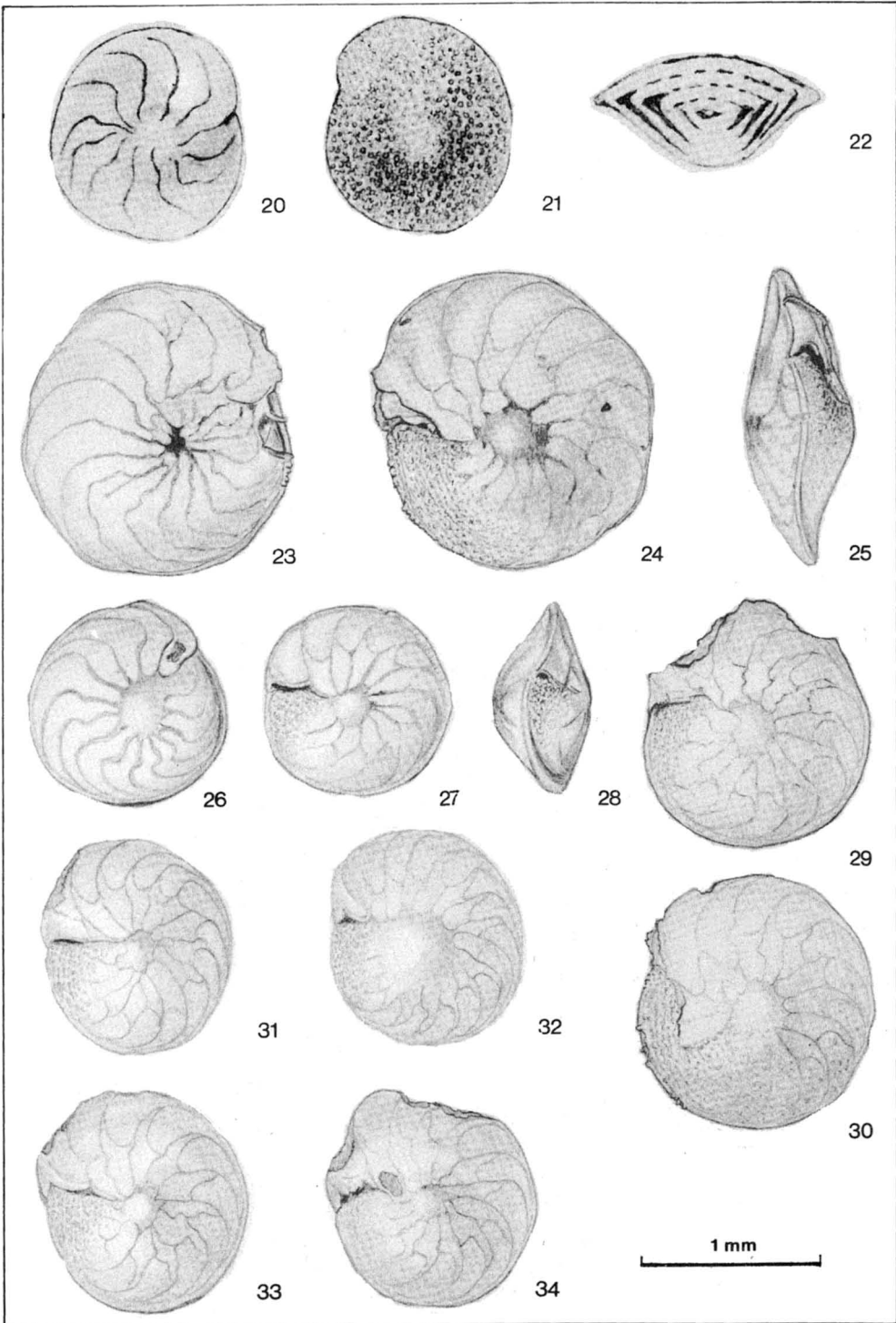
PLATE 3

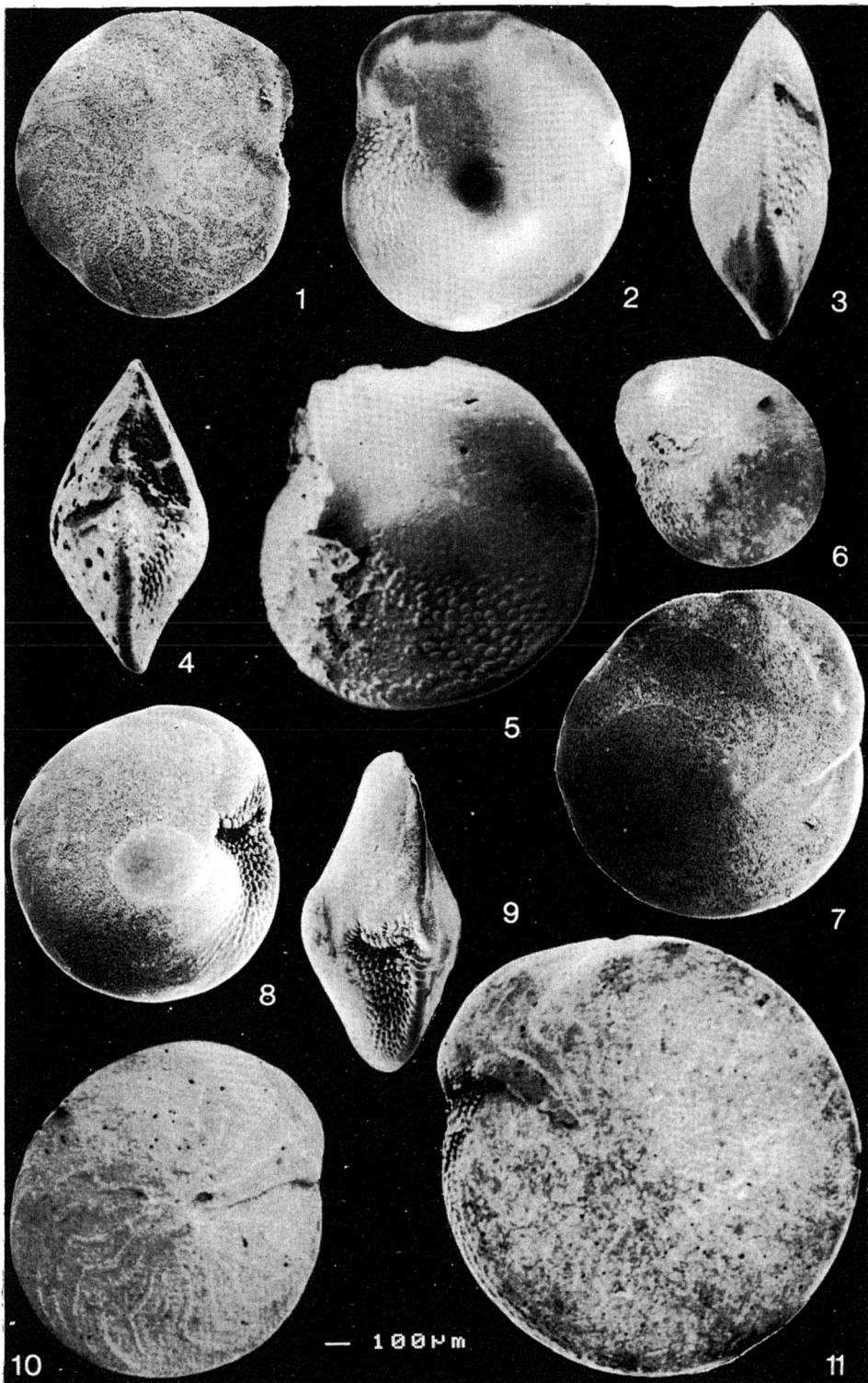
Amphistegina bohdanowiczi BIEDA

20-22 — Brzozowa, Poland, Middle Miocene; original figures of the holotype (from BIEDA 1936, Pl. 8, Fig. 4a-c)

Amphistegina bohdanowiczi BIEDA

- 23 — Spiral view of an adult specimen with tendency to evolute coiling; Korytnica, Poland, sample no. 2; early Badenian
- 24 — Umbilical side of the same specimen with large rhomboidal to sickle-shaped supplementary chambers, and a large pustulate area in front of the aperture
- 25 — Apertural view of the same specimen; test asymmetrically biconvex with keeled periphery; last chambers broken, the foramen in the wall of earlier chamber visible
- 26 — Spiral view; 27 — umbilical view; 28 — lateral view of a small specimen with sigmoid spiral intercameral sutures, and a slit-like aperture with a distinct lip; Costei (= Kostej), Timis district, Rumania, Transylvanian Basin; early Badenian
- 29-34 — Comparison of the umbilical sides of specimens from different localities; the variation in the outline of the supplementary chambers is large; the position of the posterior lobe of the suture halfway between umbo and periphery approximately constant; the pustulate area increases in size by the destruction of chambers of the final whorl;
- 29 — Korytnica, Poland, sample no. 3, early Badenian; 30 — Korytnica, Poland, sample no. 4, early Badenian; 31-32 — Niederleis, Lower Austria, early Badenian; 33-34 — Leognan, Aquitaine, France; *Heterostegina* sands, Burdigalian





ECOLOGY AND BIOPROVINCES OF *AMPHISTEGINA*

Ecological conditions governing the distribution of amphisteginas have been reviewed by LARSEN (1976), taking into consideration the publications since CUSHMAN (1921). The genus is an inhabitant of the tropical-subtropical belt and is dependent on symbionts; therefore it lives in shallow waters down to 70–80 m, occasionally somewhat deeper. A coarse correlation to the 14° winter isotherm of the surface waters is evident in the regional distribution. The correlation to summer temperatures is more accurate (Text-fig. 5).

Normal to hypersaline seawater with a high CaCO₃ content is preferred. Commonly the genus is found in coarse substrates, but also inhabits lime mud. Some are reef species, while other prefer lagoons (REISS & HOTTINGER 1984).

A depth dependence of test shape and lamellar thickness was concluded by measurements and investigations of LARSEN & DROOGER (1977), HALLOCK & HANSEN (1979), and HALLOCK & *al.* (1986). These changes in wall thickness and test shape are connected to light penetration in the water column and to the specific requirements of symbionts. Amphisteginas host naked diatoms which are species-specific and probably responsible for the regional distribution, *e.g.* the absence of *Amphistegina radiata* from the Red Sea (LEUTENEGGER 1983, 1984; REISS & HOTTINGER 1984).

In the Gulf of Aqaba a distinct relationship between test shape and depth could be demonstrated (REISS & HOTTINGER 1984). The two subglobular,

PLATE 4

Amphistegina bohdanowiczi BIEDA

- 1 — Spiral view; 2 — Umbilical view of the same specimen; Opanec, Bulgaria; early Badenian
- 3 — Lateral view with slit-like interiomarginal aperture, bordered by a distinct lip; Niederleis, Lower Austria, Badenian, Lower Lagenidae Zone
- 4 — Lateral view of a specimen with broken final chamber; intercameral foramen and partition between primary and supplementary chambers visible; distinct peripheral keel; Korytnica, Poland, sample no. 2; early Badenian
- 5 — Umbilical side of a specimen with broken few last chambers; the large papillate area is extending below the last whorl in the apertural region; Costei (= Kostej), Timis district, Rumania, Transylvanian Basin; early Badenian
- 6 — Umbilical view of a small specimen; Korytnica, Poland, sample no. 2; early Badenian

Amphistegina lessonii D'ORBIGNY

- 7 — Spiral view; Recent, Polynesia, Samoa, Upolu, Apia harbor, 7-10 fathoms depth
- 8 — Umbilical view demonstrating the large umbonal boss and the pustulate area in front of the aperture; Recent, Polynesia, Ellice Islands, Funafuti, 10 fathoms depth
- 9 — Lateral view with an interiomarginal aperture, and a sharp keel; Recent, Funafuti (*as above*)

Amphistegina mammilla (FICHTEL & MOLL)

- 10 — Spiral side with strongly angled intercameral sutures; Wien-Nussdorf, Austria, Vienna Basin; Badenian, zone with agglutinated foraminifera
- 11 — Umbilical side with elongate narrow pustulate area in front of the aperture; Wien-Nussdorf (*as above*)

thick-walled species *A. lessonii* D'ORBIGNY and *A. lobifera* LARSEN occur in shallow waters and are epizoic on *Halophila* and other plants; they also inhabit hard substrates. The species *Amphistegina lobifera* prefers high-energy environments, *A. lessonii* quieter lagoons and channels. The deep water species *A. bicirculata* LARSEN and *A. papillosa* SAID live on the open shelf on soft and hard substrates between 80 and 130 m depth. Their tests are flat biconvex lenses with a planispiral tendency, and exhibit thin walls.

The Recent *Amphistegina* distribution is characterized by distinct faunal provinces (LARSEN 1978). The paleogeographic development of the provinces is as follows:

a) Atlantic — Caribbean province (including America):

Eocene	<i>A. cubensis</i> , <i>A. californica</i>
Oligocene	<i>A. angulata</i>
Miocene	<i>A. angulata</i> , <i>A. bowdenensis</i> , <i>A. floridana</i>
Pliocene	<i>A. angulata</i> , <i>A. bowdenensis</i> , <i>A. bicirculata</i> , <i>A. pulchra</i>
Recent	<i>A. gibbosa</i> , <i>A. papillosa</i>

b) Indo-Pacific province (including the Middle East):

Eocene	<i>A. eyrensis</i> , <i>A. waiareka</i>
Oligocene	<i>A. aucklandica</i> , <i>A. floridana</i> , <i>A. mammilla</i>
Miocene	<i>A. aucklandica</i> , <i>A. floridana</i> , <i>A. mammilla</i>
Pliocene	<i>A. lessonii</i> , <i>A. papillosa</i> , <i>A. radiata</i>
Recent	<i>A. lessonii</i> , <i>A. papillosa</i> , <i>A. radiata</i> , <i>A. bicirculata</i> , <i>A. lobifera</i>

c) Mediterranean province (including Europe):

Oligocene	<i>Amphistegina</i> sp., <i>A. choctawensis</i> ?
Miocene	<i>A. aucklandica</i> , <i>A. bokdanowiczi</i> (= <i>A. "lessonii"</i>), <i>A. mammilla</i> (incl. <i>A. "hauerina"</i>)
Pliocene	<i>A. bowdenensis</i> , <i>A. gibbosa</i> , <i>A. lessonii</i>
Recent	<i>A. lobifera</i>

Considering this ecological conditions and provincialism, the European Miocene amphisteginas fit into the paleogeographic development of the Mediterranean bioprovince (RÖGL & STEININGER 1984). At the end of the Oligocene and in the early Miocene a world-wide distribution of amphisteginas

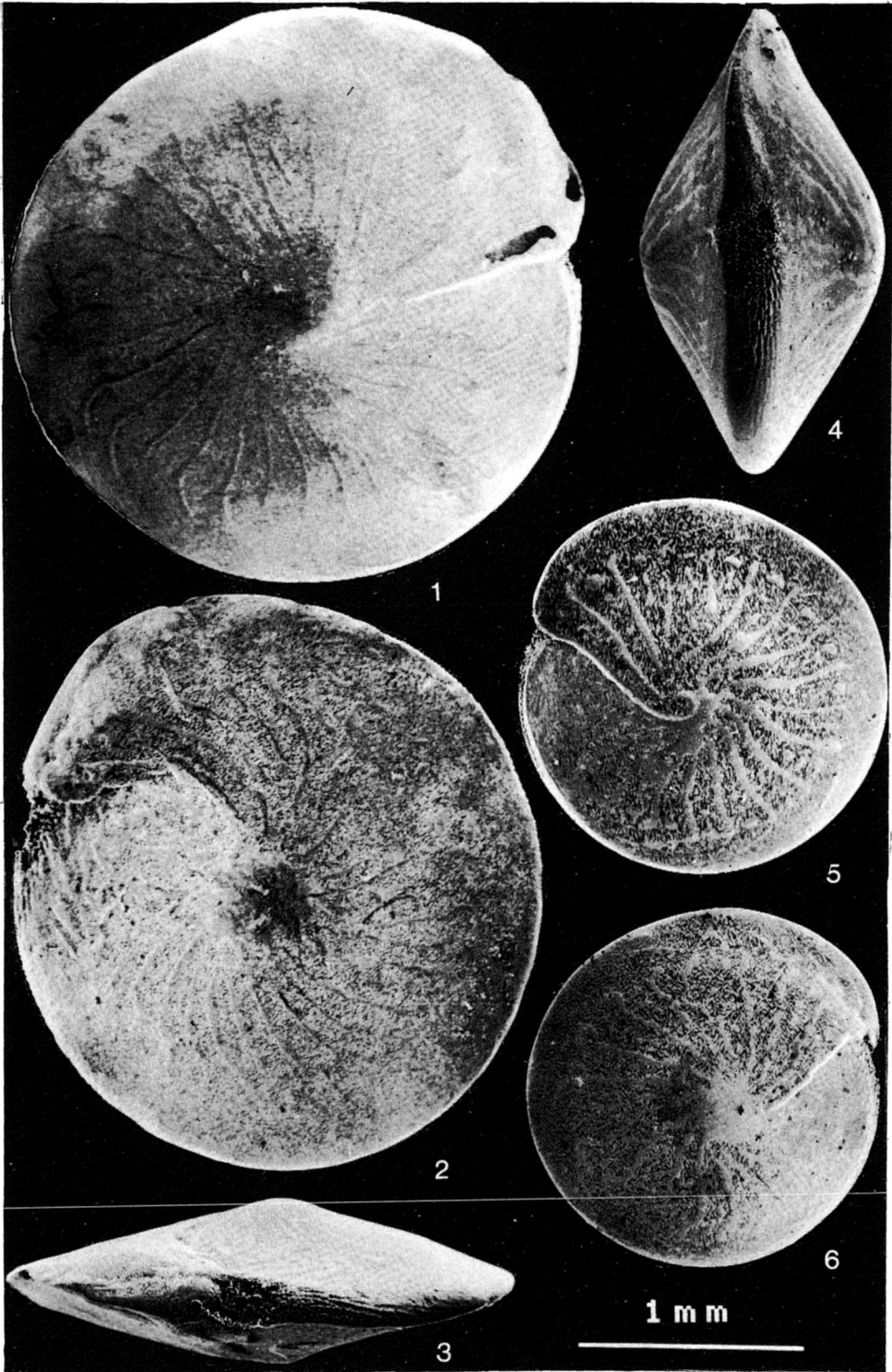
PLATE 5

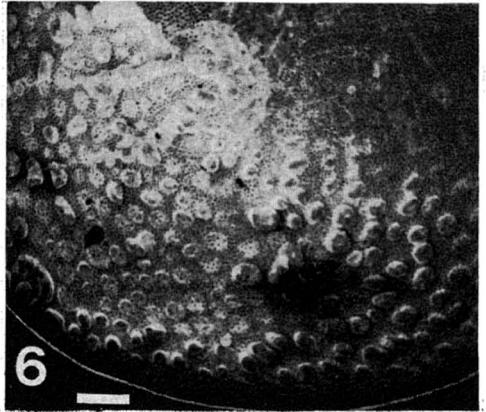
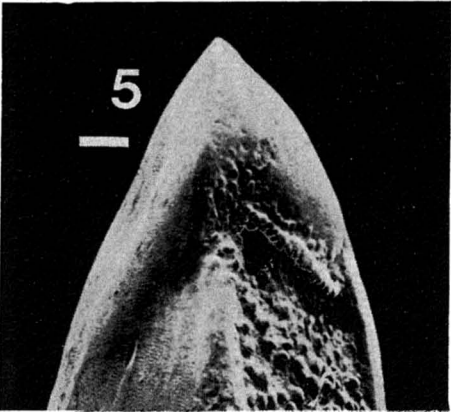
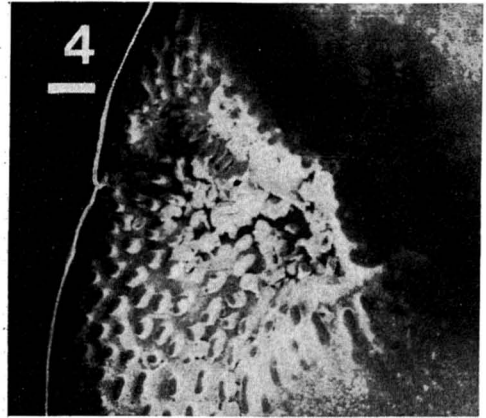
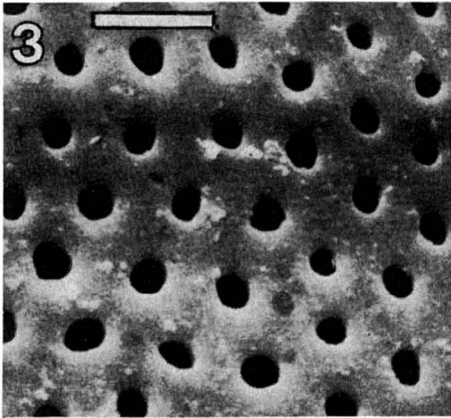
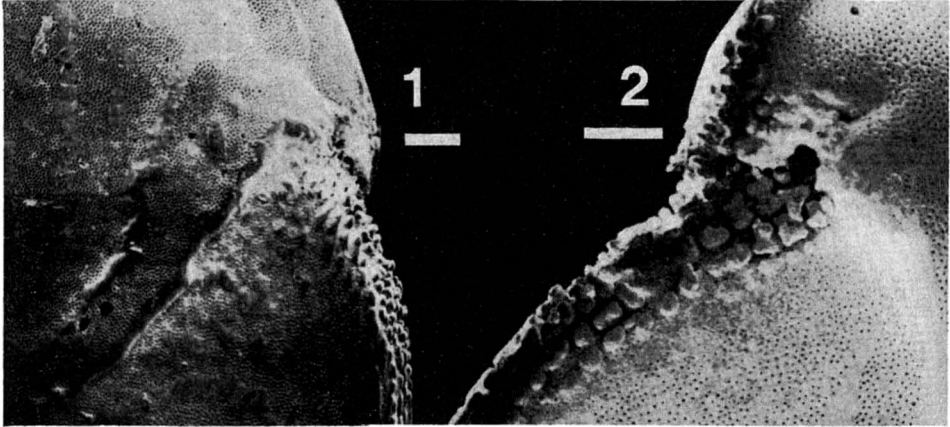
Amphistegina mammilla (FICHTEL & MOLL)

- 1 — Spiral view of a large specimen with numerous chambers in the final whorl; the intercameral sutures are angled near the periphery; Kinberk (= Kienberg), Moravia; Middle Badenian
- 2 — Umbilical view with strongly lobate intercameral sutures of the supplementary chambers, and
- 3 — Lateral view of the same large flattened specimen; Kinberk (*as above*)

Amphistegina radiata (FICHTEL & MOLL)

- Recent, Indian Ocean, Maldives Islands, Helengeli, 32 m depth
- 4 — Apertural view of the nearly planispiral, strongly biconvex test
 - 5 — Spiral side with short intersepta, and 6 — Umbilical side of the same specimen





with relatively few chambers, strong asymmetric tests, and a large papillate umbilical area were noted (*compare* LARSEN 1978):

- A. cucklandica* — New Zealand, Middle East
A. angulata — Caribbean
A. floridana — Caribbean, Florida
A. bohdanowiczi — SW France, Central Paratethys

In the Middle Miocene, *Amphistegina mammilla* (including *A. hauerina* types) entered the Paratethys from the east. This species is already reported from the early Miocene of the Indo-Pacific province: New Zealand, South Africa, Indonesia, and also from the Oligocene of Israel (which seems to be questionable). During the Middle Miocene a faunal break occurred in the Paratethys, leaving only *A. mammilla* in the younger parts of the Badenian stage.

The Middle Miocene European occurrences fall in the warmest periods of the Tertiary after the Eocene, pointing to subtropical conditions. For the Korytnica Basin this is in agreement with the distribution of warm-water invertebrates (e.g. bryozoans, BALUK & RADWAŃSKI 1977b). These favorable conditions are also expressed by the large sizes of *A. mammilla* in the Central Paratethys (exceeding all Recent species). The subtropical warm water environment is further indicated by the common occurrences of Indo-Pacific foraminifera, e.g. *Borelis*, *Heterostegina*, *Sphaerogypsina*, as also pointed out by SZCZECURA (1985).

PLATE 6

1 — *Amphistegina radiata* (FICHEL & MOLL)

Spiral side, apertural region; the aperture does not extend onto the spiral side, and the papillate area is restricted to the keel; Recent, Maldives Islands, Helengeli, 32 m depth

2 — *Amphistegina mammilla* (FICHEL & MOLL)

Umbilical side, apertural region; restricted low and short aperture in a marginal position; apertural face and area in front of it are covered by coarse pustules arranged in rows; Wien-Nussdorf, Austria, Vienna Basin; Badenian, zone with agglutinated foraminifera

3 — *Amphistegina lessonii* D'ORBIGNY

Wall surface of the spiral side; Recent, Polynesia, Ellice Islands, Funafuti, 10 fathoms depth

4 — *Amphistegina lessonii* D'ORBIGNY

Umbilical side, apertural region with a narrow umbilical-extraumbilical aperture, covered by a thin lip; a large pustulate area is extending in front of it; Recent, Funafuti (*as above*)

5 — *Amphistegina bohdanowiczi* BIEDA

Lateral view with slit-like aperture, extending from the suture of the supplementary chamber to the periphery; bordered by a distinct lip, pustulate area in front of the aperture; Niederleis, Lower Austria; Badenian, Lower Lagenidae Zone

6 — *Amphistegina bohdanowiczi* BIEDA

Umbilical side; pustulate area in front of the aperture, extending in a triangular band between the periphery and the umbo; Costei (= Kostej), Timis district, Rumania, Transylvanian Basin; early Badenian

Scale bars: Figs 1-2, 4-6 = 100 microns; Fig. 3 = 10 microns

The provincialism of Recent species is explained by paleogeographic changes since the Miocene, mainly by the closure of the Mediterranean — Indian Ocean connection, as well as by the closure of the Panama gateway. The species of the *Amphistegina lessonii* group, including *A. gibbosa* and *A. bicirculata*, are still distributed world-wide. The *Amphistegina mammilla* group is restricted to the Indo-Pacific province in the form of its last descendent, *Amphistegina radiata* (see Text-fig. 5).

BIOSTRATIGRAPHIC ASPECTS AND THE AGE OF THE KORYTNIKA CLAYS

During the present study of the Central Paratethys *Amphistegina* populations, a distinct difference in the assemblages was noted. Some faunas contained both *Amphistegina mammilla* and *A. bohdanowiczi*, others only *A. mammilla*. The early Miocene faunas were nearly barren of amphisteginas, only scarcely represented by *A. bohdanowiczi*, in the Eggenburgian and Karpatian. This species, *A. bohdanowiczi*, otherwise is well represented in the Aquitanian of Escornebeou and the Burdigalian of Leognan in southwestern France.

In order to interpret these occurrences, the different localities were grouped according to their stratigraphic positions, as far as known in detail (Table 4). The occurrence of *A. bohdanowiczi* as the only appearing species is apparently restricted to the early Miocene. Beginning with the Middle Miocene (Badenian) a co-occurrence with *A. mammilla* and a strong increase in frequency is observed. Then during the early Badenian the faunal composition changes, and later *A. mammilla* exclusively is present. The change seems to have taken place between the Lower and the Upper Lagenidae Zone of the Vienna Basin biozonation.

With respect to the stratigraphic position of the Korytnica Basin sediments, the co-occurrence of *Amphistegina bohdanowiczi* and *A. mammilla* in the Korytnica Clays points to an early Badenian age, more specifically to the Lower Lagenidae Zone. Accordingly, the overlying *Heterostegina* sands at Chomentów, yielding only *A. mammilla*, would be determined as being at least Upper Lagenidae Zone.

To verify these determinations, a number of sediment samples from Korytnica have been investigated for their foraminifera fauna. The fauna is generally rich, but the larger foraminifera are worn, demonstrating a transport from shallower areas to the basin depth. The fauna contains sparse planktonics with the following species: *Globigerina diplostoma* REUSS, *Globigerinella regularis* (D'ORBIGNY), *Globigerinoides trilobus* (REUSS), *Praeorbulina glomerosa* (BLOW), as well as rare *Globorotalia transsylvanica* POPESCU. Some rare uvigerinas are present as *Uvigerina bononiensis compressa* CUSHMAN and *U. costai* ŁUCZKOWSKA. With respect to the stratigraphic investigations of the Middle Miocene of Poland, the deposition of the Korytnica Clays belongs to the early Badenian (Opolian), to the *Candorbulina universa* Zone of ŁUCZKOWSKA (1964)

or the *Amphistegina lessonii* Zone of ŁUCZKOWSKA (1967). The very rare occurrence of *U. costai* in one sample (KOR no. 5) is in agreement with the distribution of this species, ranging upwards from the upper part of the *Candorbulina universa* Zone.

Table 4

Stratigraphic occurrences of *Amphistegina mammilla* and *A. bohdanowiczi* in the Miocene of Europe, mainly the Central Paratethys

Abbreviations: ULZ — Lower Lagenidae Zone (early Badenian); OLZ — Upper Lagenidae Zone (early Badenian); SSZ — Zone with Agglutinated Foraminifera (Middle Badenian); BBZ — Zone with *Bulimina* and *Bolivina* (late Badenian)

LOCALITY	STRATIGRAPHY	<i>A. mamm.</i>	<i>A. bohdan.</i>
Escomebeou, France	Aquitanian		
Leognan, France	Burdigalian		
Eggenburg, Austria	Eggenburgian		
Traun section, Germany	Eggenburgian		
Varpalota, Hungary	Karpatian		
St. Martin, France	Langhian		
Korytnica, Poland ◁	early Badenian		
Costei, Rumania	early Badenian		
Staropatica, Bulgaria	early Badenian		
Porzteich near Sedlec, Moravia	early Badenian		
Immendorf, Austria	Badenian, ULZ		
Mailberg, Austria	Badenian, ULZ		
Niederleis, Austria	Badenian, ULZ		
Lysice (=Lissitz), Moravia	Badenian, OLZ		
Lapugiu de Sus, Rumania	Badenian, OLZ		
Baden - Sooss, Austria	Badenian, OLZ		
Baden, Rauchstall- brunngraben, Austria	Badenian, OLZ		
Vöslau, Austria	Badenian, OLZ		
Chomentów, Poland ◁	Badenian		
Uvaly near Valtice (=Garschental), Moravia	Badenian, OLZ/SSZ		
Podivin (=Kostel), Moravia	Badenian, OLZ/SSZ		
Steinabrunn, Austria	Badenian, OLZ/SSZ		
Gainfarn, Austria	Badenian, OLZ/SSZ		
Wien - Nussdorf, Austria	Badenian, SSZ		
Brunn am Steinfeld, Austria	Badenian, SSZ		
Forchtenau, Austria	Badenian, SSZ		
Sauerbrunn, deep-well, Austria	Badenian, SSZ		
Weissenegg near Wildon, Austria	Badenian, SSZ		
Freibüchl near Wildon, Austria	Badenian, SSZ		
Prinzendorf, Austria	Badenian, BBZ		
Mellach, power station, Austria	Badenian, BBZ		

The age determination of MARTINI (1977) is somewhat controversial. The argument of the missing *Helicosphaera ampliaperta*, a determination of *Discoaster ex gr. musicus*, and the occurrence of *Helicosphaera walbersdorfensis* (where the total range is unknown) does not enable a very precise age assignment. Therefore MARTINI'S determination of NN6 nannoplankton zone and a correlation to the Walbersdorf section (comp. RÖGL & MÜLLER 1976) is not in agreement with the biostratigraphic results obtained by foraminifera.

CONCLUSIONS

The investigation of the *Amphistegina* populations from the Korytnica Basin, Poland (Middle Miocene, Badanian) required that different problems concerning the systematics, phylogenetic relationships, bioprovincialism, paleoecology, and biostratigraphy be taken into consideration.

Two main groups can be distinguished within the Central Paratethys. The first is restricted to the species *Amphistegina mammilla* (FICHEL & MOLL), including morphotypes of *A. hauerina* D'ORBIGNY, which is the phylogenetic ancestor of *Amphistegina radiata* (FICHEL & MOLL). The second includes the species *Amphistegina bohdanowiczi* BIEDA, which is related to the Recent *Amphistegina lessonii* D'ORBIGNY. This species group had a world-wide distribution in the late Oligocene – early Miocene, extending partly into the Central Paratethys as well (compare LARSEN 1978). During the Middle Miocene, early Badanian, this form vanished from Central Europe and developed a strong provincialism up until Recent. The species *Amphistegina mammilla* appeared in the Central Paratethys at the beginning of the Middle Miocene, Badanian transgression, to be extinguished at the end of the marine phase at the Badanian/Sarmatian boundary. This group now has an Indo-Pacific distribution, surviving there as *Amphistegina radiata*.

From the paleoecological point of view, the occurrences of *Amphistegina* are related to warm, tropical-subtropical climatic phases; this is in agreement with the results obtained in other fossil groups. The presence of *A. mammilla* testifies to the ingression of Indian Ocean water in Central Europe.

The stratigraphic relevance of *Amphistegina* in the Miocene of the Central Paratethys is given by the different first and last occurrences of the above mentioned species. The early Miocene is defined by the occurrence of *A. bohdanowiczi* only. The first appearance of *A. mammilla* at the base of the Badanian and its co-occurrence with *A. bohdanowiczi* characterizes the earliest Badanian, Lower Lagenidae Zone. The later Badanian is yielding *A. mammilla* only. A biostratigraphic age determination for the Korytnica Basin is therefore possible: the Korytnica Clays belong to the early Badanian, Lower Lagenidae Zone, whereas the *Heterostegina* sands of Chomentów are the Upper Lagenidae Zone or younger.

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