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The late Eocene evolution of nummulitid foraminifer *Spiroclypeus* in the Western Tethys

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Megalospheric forms of Priabonian *Spiroclypeus* of the Western Tethys were morphometrically investigated. Based on the reduction of the average number of undivided, post-embryonic chambers, the investigated populations are grouped into two successive, phylogenetically linked species, *S. sirottii* sp. nov. and *S. carpaticus*. The evolution is also demonstrated by the increase of the number of secondary chamberlets in particular chambers, by the increase of the diameter of the first two whorls and by that of the size of the proloculus, although the latter turned out to be also ecologically controlled. This evolution is supported by the stratigraphic succession of populations in the Mossano section (N Italy) and by the change of accompanying fossils. Lacking in upper Bartonian beds, the first appearance of genus *Spiroclypeus* seems to be synchronous with the beginning of the late Eocene. The newly described *S. sirottii* is associated with *Heterostegina reticulata mossanensis* and orthophragmines containing forms of middle Eocene acme, both marking the lower part of the Priabonian. Meanwhile *S. carpaticus* co-occurs with *H. gracilis* and/or with orthophragmines characteristic of the upper part of the Priabonian. We suppose that the *Spiroclypeus sirottii*–*carpaticus* lineage is restricted to the Priabonian. Thus, *Spiroclypeus sirottii* is a zonal marker for the Shallow Benthic Zone (SBZ) 19 (early Priabonian) while *S. carpaticus* indicates the SBZ 20 (late Priabonian).

Key words: Foraminifera, Nummulitidae, *Spiroclypeus*, biometry, evolution, stratigraphy, Eocene.

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Introduction

The representatives of genus *Spiroclypeus* can be very frequently found in the upper Eocene larger foraminiferal assemblages of the Western Tethys. Two species, “*Spiroclypeus carpaticus*” and “*S. granulatus*” are mentioned alternatively; however, their relationship to each other is not clear.

The aim of this study is to elucidate the stratigraphic significance of species belonging to this genus within the Western Tethyan Eocene. This includes the comparative investigation of populations collected from different localities to determine whether they form a single evolutionary lineage and to recognize the stratigraphically controlled evolutionary trends that can lead to a more detailed subdivision of the genus and then, in turn, to a more well-established subdivision of the time-interval spanned by the studied samples. Based on joint occurrences with *Spiroclypeus*, the results of the paper by Less et al. (2008) on involute *Heterostegina* are widely used in this process in two respects. On the one hand, relying on their morphological similarity, the same methods used to investigate *Heterostegina* are applied to *Spiroclypeus*; on the other hand, the high-resolution heterosteginid scale serves for stratigraphical calibration of the spiroclypeid evolution.

No *Spiroclypeus* has been found in upper Bartonian localities containing *Heterostegina armenica* or the less ad-

vanced representatives of the *H. reticulata*-lineage with more than three undivided post-embryonic chambers in average. In four localities (Mossano, Verona—Castel San Felice, Úrhida, and Şarköy) the first occurrence of *Spiroclypeus* is linked to the presence of *H. reticulata mossanensis* marking the basal Priabonian. Thus, we can reasonably conclude that they appeared in the late Eocene. Data, seemingly contradicting this statement are discussed below. Because either involute Eocene *Heterostegina* or orthophragmines (both having become extinct at the end of the Eocene) are present in all the studied localities, our review is restricted to the Priabonian. The relationship between Priabonian and Oligocene–Miocene *Spiroclypeus* is discussed below.

The Indo-Pacific (e.g., Krijnen 1931; Tan 1937; Matsu-maru 1996) and Caribbean (Vaughan and Cole 1941) representatives of the genus *Spiroclypeus* are beyond the scope of our study, since they can be distinguished from the Western Tethyan late Eocene forms by their much looser spire and, therefore, no direct phylogenetic relationship can be reasonably supposed between them.

Institutional abbreviations.—ITU O, Istanbul Technical University, Özcan collection of the Geology Department; MÁFIE and O, Geological Institute of Hungary (Budapest), Eocene (E) and Oligocene (O) collection.

Abbreviations for biozones.—NP, Paleogene calcareous nannoplankton zones by Martini (1971); OZ, orthophragminid zones for the Mediterranean Paleocene and Eocene by Less (1998) with correlation to the SBZ zones; P, Paleogene planktic foraminiferal zones by Blow (1969) and updated by Berggren et al. (1995); SBZ, shallow benthic foraminiferal zones for the Tethyan Paleocene and Eocene (SBZ 1–20) by Serra-Kiel et al. (1998) and for the Oligocene and Miocene (SBZ 21–26) by Cahuzac and Poignant (1997) with correlation to the planktic and magnetic polarity zones.

Abbreviations for countries.—E, Spain; F, France; H, Hungary; I, Italy; TR, Turkey.

Historical background

Uhlig (1886) was the first to describe and figure identifiable *Spiroclypeus* under the name of *Heterostegina carpatica* from the flysch deposits of the Woła Łużańska (Polish Carpathians). The two drawings illustrating the equatorial section of A-forms give reliable information not only on the tightness of the spire (significant for Western Tethyan late Eocene *Spiroclypeus*) but also on the number of undivided neanic chambers that allow to quantify the evolutionary stage of the taxon. He listed also the associated fossils, among which the presence of orthophragmines assures the Eocene age of the type locality. At the same time *Nummulites tchihatcheffi* (corresponding to the megalospheric form of the *N. millicaput*-group) was also listed. This suggests a reworking of fossils in the type locality of *Spiroclypeus carpaticus*.

Douvillé (1905) introduced the genus *Spiroclypeus* from the Aquitanian beds of Borneo with a differential diagnosis that stresses the completely embracing nature of subsequent whorls as distinction from *Heterostegina*. Boussac (1906) emended the generic diagnosis by recognizing the presence of lateral chamberlets in not only the forms from Borneo but also in the material from Priabona. He introduced the name *Spiroclypeus granulatus* for these latter forms. In contrary to the good figures of the axial section, the equatorial section was rather poorly illustrated, a fact that hampers the recognition of the evolutionary stage of this species. Boussac (1906) distinguished his new species from Uhlig's (1886) "*carpatica*" by external features like the presence of the thin, undulated flange and also by the larger dimension and density of granules.

Bieda (1957, 1963) considered the presence of granules on the surface of *Spiroclypeus* as a generic feature and followed Boussac (1906) in distinguishing *S. carpaticus* and *S. granulatus* from each other by the quality of granulation. Internally, however, the two forms are quite different in the character of the spire; the one of *S. granulatus* being much more open. In our opinion these forms correspond to *Heterostegina gracilis* (more details see below).

Roveda's (1961) work from Priabona is very important in two respects. His published equatorial section of *Spiro-*

clypeus granulatus from the type-locality bears the same tight spire as *S. carpaticus* and it is very different from the spire characteristic for Bieda's (1957) *S. granulatus* (= *H. gracilis*, see above). Roveda (1961) declared the presence of the lateral chamberlets to be the most diagnostic feature of *Spiroclypeus*.

Hottinger (1977) provided the currently used definition of the genus and after a preliminary study (Hottinger 1964) proposed a single evolutionary lineage for the genus starting in the late Eocene with *Spiroclypeus granulatus* followed by the early Oligocene (?) *S. carpaticus*, by the late Oligocene *S. tidoenganensis* and terminating with the early Miocene *S. anghiarensis*. He also recognized the main evolutionary trends, the size increase of the proloculus, the opening of the spiral and the flattening of the test. By comparing the Eocene and post-Eocene forms, however, we do not suppose a direct phylogenetic continuity between them.

Herb (1978) introduced *H. gracilis* from Possagno (Italy), a taxon with granules on the surface but with no lateral chamberlets. Its internal features are practically identical with those of Bieda's (1957, 1963) and Grigoryan's (1986) *S. granulatus*, therefore these forms are not discussed below (see also in Less et al. 2008).

Fermont and Troelstra (1983) and Schiavinotto (1986) were the first to investigate *Spiroclypeus* populations and to characterize them biometrically. In our paper we adopt their system with some additions. Based on Schiavinotto's (1986) data on *S. granulatus* from Priabona, the type locality, this taxon in our opinion is a junior synonym of Uhlig's (1886) *S. carpaticus*.

Some figures of *Spiroclypeus* are presented in the works of Papazzoni (1994), Papazzoni and Sirotti (1995), Less (1999) and Özcan et al. (2007). These forms are described and discussed in more details below.

Terminology and concepts

The general architecture of *Spiroclypeus*.—According to Hottinger (1977), *Spiroclypeus* is a planispiral, lamellar, finely perforated, involute foraminifer belonging to the subfamily Nummulitinae. Its chambers become secondarily subdivided into regularly arranged secondary chamberlets (of very slightly hexagonal shape as seen in equatorial sections) by well-developed, complete secondary septa at different moments of their ontogeny. The spiral chambers never develop into annular ones as do those of *Cycloclypeus* or *Heterocyclina*. The diagnostic feature of *Spiroclypeus* that distinguishes it from *Heterostegina* is the presence of lateral chamberlets (Fig. 1), symmetrically on both sides of the spiral, formed by folding the walls of the alar prolongations and by piling the cavities between the folds from successive chambers to a chessboard-patterned construction. Externally (Fig. 1), the test is biconvex with a very slightly eccentric outline. Most of the surface is covered by granules; the network of chamberlets can be frequently seen on its very edge.

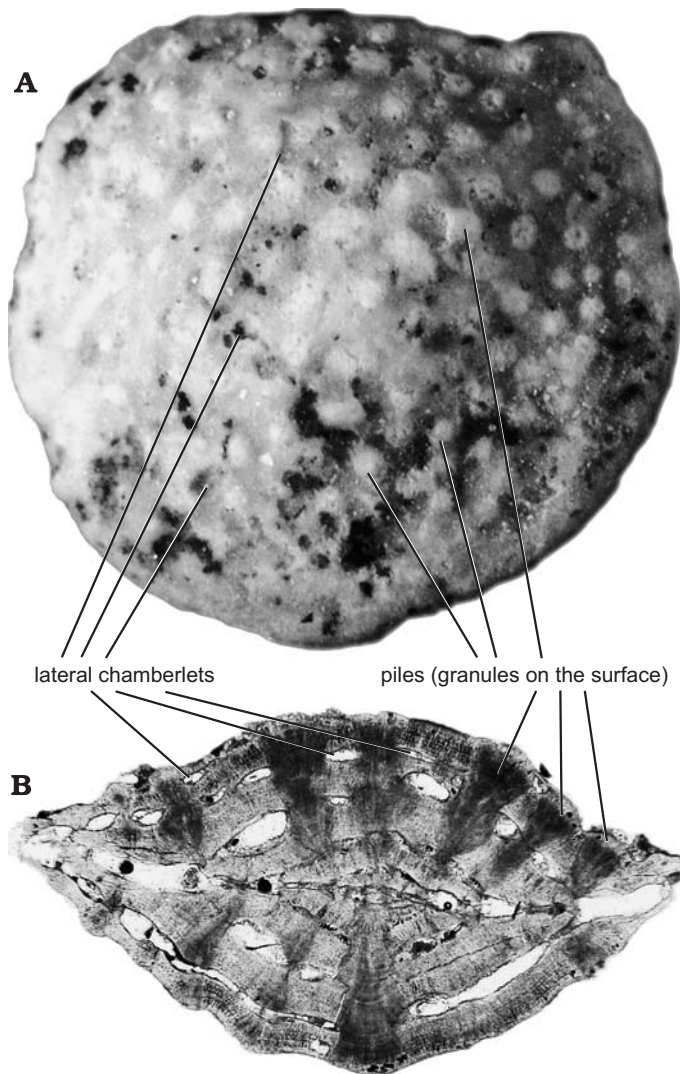


Fig. 1. Terminology for external and lateral features of *Spiroclypeus*: *Spiroclypeus carpaticus* (A) and *Spiroclypeus sirottii* (B).

Banner and Hodgkinson's (1991) interpretation of lateral chamberlets is somewhat different from that of Hottinger (1977, 2006). They mean by "true" lateral chamberlets in heterosteginids their alar prolongations subdivided into chamberlets. Hottinger (2006) suspects these "lateral chamberlets" to be undivided alar prolongations cut at an oblique angle in respect to the median line of the alae. Banner and Hodgkinson (1991) introduced the term "cubicula" for lateral chamberlets in our and Hottinger's (2006) interpretation. In order to avoid misunderstandings, in this work we follow Hottinger's (2006) concept on lateral chamberlets.

Spiroclypeus are assumed to have been symbiont-bearing. No particular size-difference of the adult shells between stratigraphically older and younger or between megalos- (A) and microspheric (B) forms can be observed. B-forms are rare, A-forms predominate. Axial sections are to be studied further. Therefore, we concentrate our investigations on the equatorial section of megalospheric forms.

Taxonomical concept.—We adopt the taxonomical concept and morphometric method based on Drooger (1993) and described in Less et al. (2008). *Spiroclypeus* from each sample appeared to form one single population both typologically and biometrically. Contrary to *Heterostegina reticulata* and *H. armenica* which were segmented into subspecies by Less et al. (2008), the supposed single lineage of Western Tethyan late Eocene *Spiroclypeus* is subdivided into (two) species because not only their populations but in most cases also their specimens can be distinguished from each other. The quite well recognizable differences in the axial sections of the two taxa also support their distinction in the specific level (see below).

Morphometry.—To apply the morphometric method, Eocene *Spiroclypeus* is described by nearly the same quantitative parameters that are measured and counted in the equatorial section of A-forms of *Heterostegina* by Less et al. (2008). One difference is the measurement of parameter D in the first two whorls. Five measurements and counts were executed as follows (see also Fig. 2):

P: The inner cross-diameter of the proloculus in μm . Wall-thickness is not measured.

X: the degree of "operculinid reduction" as reflected in the number of undivided, "operculinid" chambers before the appearance of the first subdivided, heterosteginid chamber, excluding the embryo (the first two initial chambers of megalospheric forms, see Hottinger 2006). Undivided chambers, reappearing after the first heterosteginid chamber, are not counted. In Fig. 2, $X = 2$.

S: the density of secondary chamberlets ("heterosteginid escalation") as reflected in the number of chamberlets in

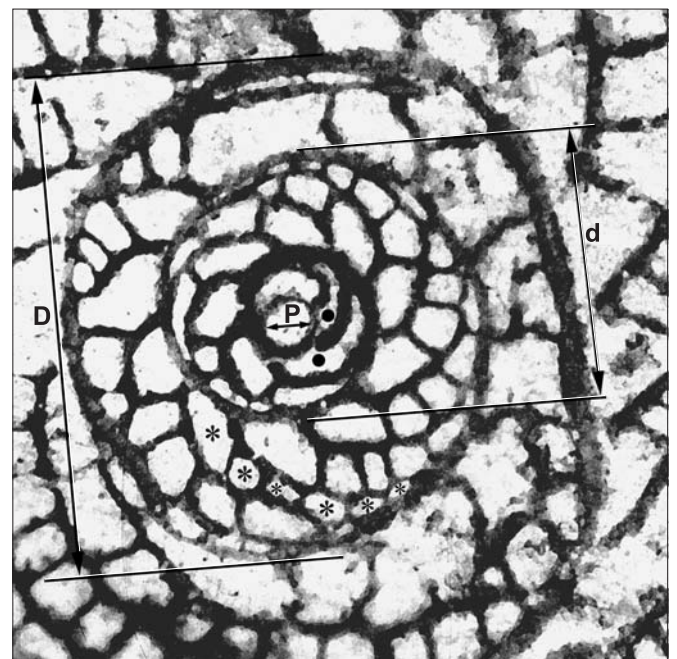


Fig. 2. The measurement system in the equatorial section of megalospheric *Spiroclypeus*. Pre-heterosteginid chambers (X) are marked by solid circles, secondary chamberlets in chamber 14 (S) by asterisks.

Table 1. Statistical data of *Spiroclypeus* populations. Abbreviations: n, number of measured specimens; aff. c., *Spiroclypeus* aff. *carpaticus*. * For D and K n = 18, for S n = 13. ** For S n = 7.

Taxon	Parameter		Proloculus		Operculinid reduction		Heterosteginid escalation		1+2. whorl		Index of spiral opening	
			diameter				chamberlets in chamber 14		diameter			
			P (µm)		X		S		D (µm)		K = 100 × (D-d)/(D-P)	
Locality	n	range	mean ± s.e.	range	mean ± s.e.	range	mean ± s.e.	range	mean ± s.e.	range	mean ± s.e.	
<i>Spiroclypeus sirottii</i>	Verona, Castel S. Felice (I)	52	55–115	86.6 ± 2.0	2–10	4.52 ± 0.27	2–5	2.87 ± 0.11	550–1379	998 ± 22	38.3–59.3	50.9 ± 0.6
	<i>Villa Devoto</i>	19	55–110	86.8 ± 3.4	2–10	5.11 ± 0.50	2–4	2.79 ± 0.12	550–1238	974 ± 42	38.3–58.8	50.2 ± 1.4
	<i>Villa Le Are</i>	21	57–115	83.5 ± 3.3	2–8	4.33 ± 0.42	2–4	2.71 ± 0.17	760–1250	971 ± 26	46.5–59.3	51.1 ± 0.6
	<i>hairpin bend</i>	12	72–105	91.9 ± 3.2	2–6	3.92 ± 0.36	2–5	3.25 ± 0.28	832–1379	1082 ± 46	45.2–55.0	51.5 ± 0.8
	Mossano 5+6 (I)	25	72–150	92.5 ± 3.5	1–7	4.04 ± 0.34	2–4	2.62 ± 0.15	766–1300	1034 ± 27	42.3–60.3	52.3 ± 0.9
	<i>Mossano 5</i>	7	72–91	83.1 ± 2.9	2–7	4.43 ± 0.78	2–3	2.40 ± 0.24	920–1185	1020 ± 42	47.8–60.3	53.9 ± 1.8
	<i>Mossano 6</i>	18	75–150	96.2 ± 4.5	1–6	3.89 ± 0.37	2–4	2.69 ± 0.18	766–1300	1040 ± 35	42.3–57.1	51.7 ± 1.0
	Úrhida 10 (H)*	19	65–150	100.3 ± 4.3	1–7	3.74 ± 0.34	2–4	3.23 ± 0.20	860–1460	1075 ± 32	43.9–57.7	50.9 ± 0.8
Mossano 8 (I)	23	80–137	104.8 ± 3.7	1–7	3.39 ± 0.27	3–7	3.91 ± 0.21	884–1360	1115 ± 22	47.7–64.7	54.8 ± 0.9	
Şarköy (TR)	15	70–115	95.7 ± 3.0	1–5	3.07 ± 0.32	2–4	2.73 ± 0.15	765–1125	973 ± 28	47.0–57.3	51.6 ± 0.8	
<i>S. carpaticus</i>	Biarriz, Cachaou (F)**	8	82–145	104.5 ± 7.2	1–4	2.38 ± 0.32	3–7	4.57 ± 0.53	943–1820	1216 ± 100	42.8–60.9	54.2 ± 2.2
	Benidorm (E)	2	105–110	107.5	1–2	1.50	7–8	7.50	1210–1270	1240	58.8–62.1	60.5
	Possagno (I)	20	95–179	132.5 ± 5.2	1–4	1.50 ± 0.17	4–9	5.40 ± 0.28	1010–1562	1317 ± 32	38.5–63.0	56.4 ± 1.3
	<i>Possagno 1</i>	8	95–139	114.9 ± 5.6	1–4	1.50 ± 0.38	4–6	5.13 ± 0.30	1010–1341	1240 ± 43	38.5–61.7	55.4 ± 2.7
	<i>Possagno 2</i>	12	114–179	144.3 ± 5.8	1–2	1.50 ± 0.15	4–9	5.58 ± 0.43	1086–1562	1368 ± 41	49.0–63.0	57.1 ± 1.3
	Kisgyör, Remete 3 (H)	23	100–200	145.0 ± 4.7	1–3	1.48 ± 0.14	4–9	6.09 ± 0.27	1050–1720	1445 ± 40	50.0–60.8	56.3 ± 0.6
Priabona, blue clay (I)	30	97–210	137.8 ± 4.8	1–2	1.37 ± 0.09	3–9	5.57 ± 0.26	895–1720	1221 ± 34	42.0–70.4	53.7 ± 1.0	

Table 2. Most important characteristics of the localities investigated. * based on Less et al. (2008); ** orthofragmines and their zones are based on Less (1998) for Mossano, Less (1999) for Kisgyör, Less et al. (2000) for Úrhida, Özcan et al. (2007) for Şarköy, and on GL's unpublished data in the case of Verona and Priabona. Abbreviations: ↑ and ↓: above and below; ?: very rare occurrence.

Locality	Rock	Planktic foraminiferal zone (P)	Calcareous nannoplankton zone (NP)	Nummulites fabianii				Heterostegina *				<i>Spiroclypeus</i>	Orthofragmines**												Age and SBZ				
				typical	flatter ("N. retiatius")	reticulata	reticulata italica	gracilis	of middle Eocene acme		other forms										Orthofragminid zone (OZ)	early Priabonian - SBZ 19	late Priabonian - SBZ 20						
									<i>Discocyclina prati</i>	<i>Nemkovella strophiolata</i>	<i>Asterocyclina alticostata</i>		<i>A. kecskemetii</i>	<i>D. dispansa dispansa</i>	<i>D. trabayensis elazigensis</i>	<i>A. stellata stellaris</i>	<i>D. angustae</i>	<i>D. radians</i>	<i>D. nandori</i>	<i>Orbitoclypeus varians</i>				<i>A. stella</i>	<i>D. dispansa umbilicata</i>	<i>D. trabayensis</i>	<i>A. stellata buekensis</i>		
Priabona, blue clay	marly claystone	15–?17	19–20	↓	–	–	–	–	–	<i>carpaticus</i>	–	–	–	–	–	+	+	+	+	–	–	+	+	–	–	–	15	+	
Mossano 5+6	marl	15	18	?	–	+	–	–	–	<i>sirottii</i>	+	+	+	–	+	+	+	–	+	+	–	–	–	–	–	–	–	14	+
Mossano 8	marl	16	19–20	–	–	–	+	–	–	<i>sirottii</i>	–	–	+	–	–	+	+	+	+	–	+	–	–	–	–	–	–	14/15	+
Verona, Castel S. Felice	marl	–	–	+	–	+	–	–	–	<i>sirottii</i>	+	+	–	–	+	+	+	+	+	+	+	–	–	–	–	–	–	14	+
Possagno 1+2	marly limestone	16 (↑↓)	20 (↑↓)	+	+	–	+	+	+	<i>carpaticus</i>	not investigated												–	+					
Úrhida 10	marly limestone	–	–	–	–	+	–	–	–	<i>sirottii</i>	+	+	+	+	+	–	+	+	+	+	+	+	–	–	–	–	–	14	+
Kisgyör, Remete-kút 3	marly limestone	–	21	–	+	–	–	–	–	<i>carpaticus</i>	–	–	–	–	–	–	+	+	–	+	–	+	+	+	+	+	+	16	+
Benidorm	marl	–	–	–	–	–	–	–	+	<i>carpaticus</i>	not investigated												–	+					
Biarriz, (Lou) Cachaou	marl	16	19–20	–	–	–	–	–	+	aff. <i>carpaticus</i>	not investigated												–	+					
Şarköy	marly limestone	–	16–21	–	–	+	–	–	–	<i>sirottii</i>	+	–	+	–	+	+	+	+	+	+	+	+	+	–	–	–	–	14	+

the fourteenth chamber (including the embryo). In Fig. 2: S = 6.

d: The maximum diameter of the first whorl measured along the common symmetry axis of the first two chambers (in µm). This parameter is not tabulated in Table 1, but is used for calculating parameter K.

D: The maximum diameter of the first two whorls (in µm) measured in the same way as d.

From these direct parameters:

K: the index of spiral opening (independent from the size of the proloculus), is computed as:

$$K = 100 \times (D-d)/(D-P)$$

Five parameters (P, X, S, D and K) are evaluated statistically by standard methods per population. The results are summarized in Table 1. Bivariate plots and 95.44% confidence ellipses are generated in the same way as given in Less et al. (2008). For microspheric forms see the discussion in "Evaluation of parameters".



Fig. 3. Geographical distribution of the samples studied.

Material and methods

Localities

We tried to investigate material from a wide geographical (Fig. 3) and stratigraphical range. In describing our samples we start with Northern Italy where the most important paleontological sites are located. The most significant characteristics of the samples are summarized in Table 2 (the nomenclature of spiroclypeid populations is discussed later, specific names are listed here for the completeness of data). The information on the localities and the source of information on their fossil contents for Mossano, Verona, Possagno, Úrhida, Benidorm, Biarritz, and Şarköy are discussed in detail in Less et al. (2008). Additional comments on the samples are given below.

Northern Italy, Veneto area

Priabona.—The historical background of the Priabonian type section was extensively described recently by Bassi et al. (2000). Our sample was collected from the upper part of Via Centro (figured in Setiawan 1983) corresponding to about the boundary of the “*Discocyclina* beds” and “Blue claystone” of Hardenbol (1968) and Sirotti (1978). Relying on the description of the locality and on the similar faunal assemblage our sample has been taken very probably from the bed of sample Pr.55 by Setiawan (1983). This bed should be very close to the layers from where Boussac (1906), Roveda (1961) and Schiavinotto (1986) took their samples containing *Spiroclypeus*, since based on Sirotti (1978) and Setiawan (1983), the vertical range of the genus is rather restricted in the Priabona profile. Moreover, morphometrically our population (see Table 1) is very similar to that of Schiavinotto (1986), therefore it can be considered as topotypical for *Spiroclypeus granulatus* described by Boussac (1906) from here. At the same time in our opinion, its characteristics correspond to those of Uhlig’s

(1886) *S. carpaticus*, and therefore this latter name has to be used for specimens found at this site (more details see in the systematical part).

Sirotti’s (1978) and Setiawan’s (1983) orthophragminid materials were revised in Modena and Utrecht by GL (still unpublished). Nummulitids are listed based on Roveda (1961) and Sirotti (1978). Planktic foraminiferal and calcareous nannoplankton data are based on Barbin (1986, see in Brinkhuis 1994) and on Verhallen and Romein (1983), respectively.

Possagno.—Since *Spiroclypeus* are rather rare and morphometrically similar in the two samples (see Table 1), they are discussed together.

Mossano.—*Spiroclypeus* specimens occur only in the lower part of the Marne di Priabona starting immediately at the base. Samples Mossano 5 and 6 were taken from the two outcrops both representing the base of the Priabonian (see details in Less et al. 2008), and therefore, they are discussed together. In sample Mossano 7 *Spiroclypeus* is rather rare and poorly preserved. In sample Mossano 8 they are quite common, though again poorly preserved.

Population Mossano 8 differs from Mossano 5+6 (see also Table 1) in having (i) a somewhat smaller number of operculinid chambers (parameter X), (ii) a somewhat larger proloculus and (iii) some more chamberlets in chamber 14 (S). This trend is the same as observed in the case of the *Heterostegina reticulata* lineage in the same samples (Less et al. 2008). It is in accord with the stratigraphic position of the two populations and also with their slightly different accompanying fossils (Table 2). At the same time all the three parameters are much less advanced in both populations than for *Spiroclypeus carpaticus* in Priabona and Possagno. Therefore, a new species, *S. sirotti* is introduced in this paper for them with the type locality of the basal part of the Priabona marls in Mossano (sample Mossano 6).

Verona.—Since the morphometrical data from the three samples of Castel San Felice (Villa Le Are, Villa Devoto, and hair-pin bend) in which the genus is present are rather similar (see Table 1), the populations are discussed jointly below.

SE Spain

Benidorm.—One specimen of *Spiroclypeus* was found in the sample and another one has been measured based on Hottinger's (1964) pl. 7: 6.

France, SW Aquitaine

Biarritz, Lou Cachaou.—The biometrical data of the spiroclypeid population (see Table 1) show an intermediate position between those of typical *S. carpaticus* from Priabona and those of typical *S. sirottii* from population Mossano 5+6. Since the average number of post-embryonic pre-heterosteginid chambers ($X_{\text{mean}} = 2.38$) is closer to the value defining *S. carpaticus* ($X_{\text{mean}} < 2.7$) than to that of *S. sirottii* ($X_{\text{mean}} > 2.7$), the population is determined as *S. aff. carpaticus*, taking into account also the relatively small size of the proloculus.

Hungary

Úrhida (W Hungary).—*Spiroclypeus* only appear in the uppermost sample (Úrhida 10) associated to *Heterostegina reticulata mossanensis*, the most advanced representative of this lineage in this locality.

Kisgyőr, Remete-kút (NE Hungary).—Only one (Remete-kút 3) of the four samples described and figured in detail by Less (1999) and Less et al. (2000) from Kisgyőr contains a fairly rich population of well preserved *Spiroclypeus carpaticus* (*S. granulosus* in the two papers listed above). Planktic foraminifers have not been found in any of the four samples yet; however calcareous nannoplankton (determined by Mária Báldi-Beke) could be studied from samples Remete-kút 2 and 4. More details and the fossil list can be found in Less (1999) and Less et al. (2000) where other larger foraminifers (determined by GL) are also listed. According to our recent studies (unpublished data) *Nummulites retiatius* of the above two papers from Kisgyőr corresponds to *N. fabianii*.

Turkey (Thrace Basin)

Şarköy.—The genus *Spiroclypeus* was identified in all samples (Şarköy 2, 4, 9, and A) studied by Özcan et al. (2007) and Less et al. (2008); however, they are statistically investigated only from Şarköy 4.

Specimen preparation

We have studied isolated specimens mostly from marls and marly limestones. The axial sections from all localities and most equatorial sections from Şarköy have been exposed by thin-sectioning. In all the other cases we opened the equatorial section by splitting. In some cases (Priabona, Possagno) tests were heated before splitting. In other cases (Mossano, Verona, Úrhida, Kisgyőr) shells have been stained by violet

chemical ink. For the comparison of the splitting and the thin-sectioning see Less et al. (2008).

Evaluation of parameters

Contrary to genus *Heterostegina* (Less et al. 2008), Western Tethyan late Eocene *Spiroclypeus* seems to be nearly homogenous in their qualitative features like the surface of the test and the arrangement and shape of secondary chamberlets. Differences, however, may appear in the development of lateral chamberlets as observed in the axial sections. In specimens from samples with orthophragmines of middle Eocene acme (*Discocyclina pratti*, *Nemkovella strophiolata*, *Asterocyclina alticostata*, *A. kecskemetii*) lateral chamberlets are poorly developed (in Mossano, Verona, and Şarköy), whereas in specimens from samples containing *Heterostegina gracilis* but no orthophragmines of middle Eocene acme (Priabona, Kisgyőr) they are quite well-developed.

The statistical summary of quantitative features per population is given in Table 1. The greatest differences between populations are to be seen in the parameters X and S. Their mean values at the 95% confidence level are plotted in Fig. 4 (with the exception of the Benidorm population, which had too few specimens) from which the following conclusions can be drawn:

(i) The *Spiroclypeus* populations cluster in two groups. The upper left group corresponds to *Spiroclypeus sirottii*, the

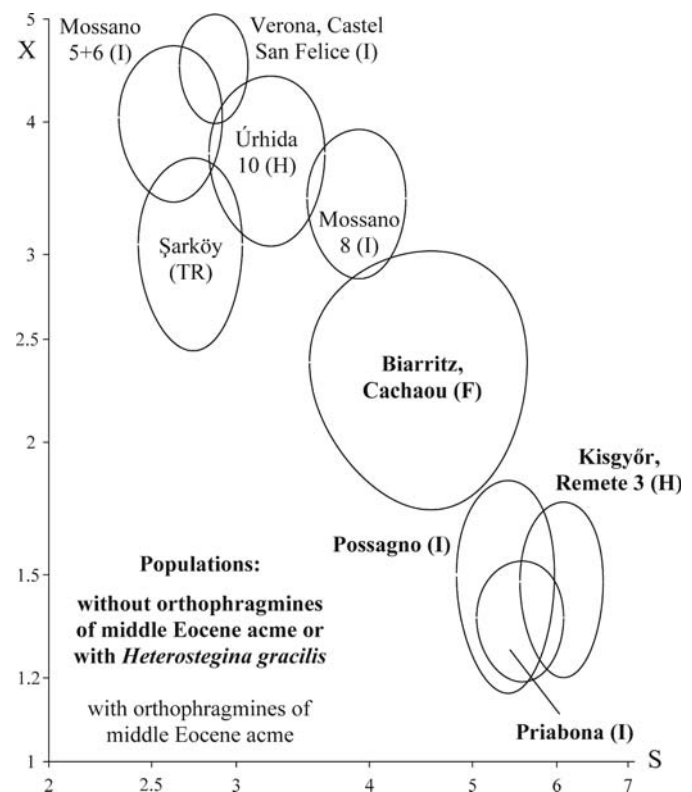


Fig. 4. Distribution of spiroclypeid populations (mean values at the 95.44% confidence level) on the S–X (heterosteginid escalation versus operculinid reduction) bivariate plot (both scales are logarithmic).

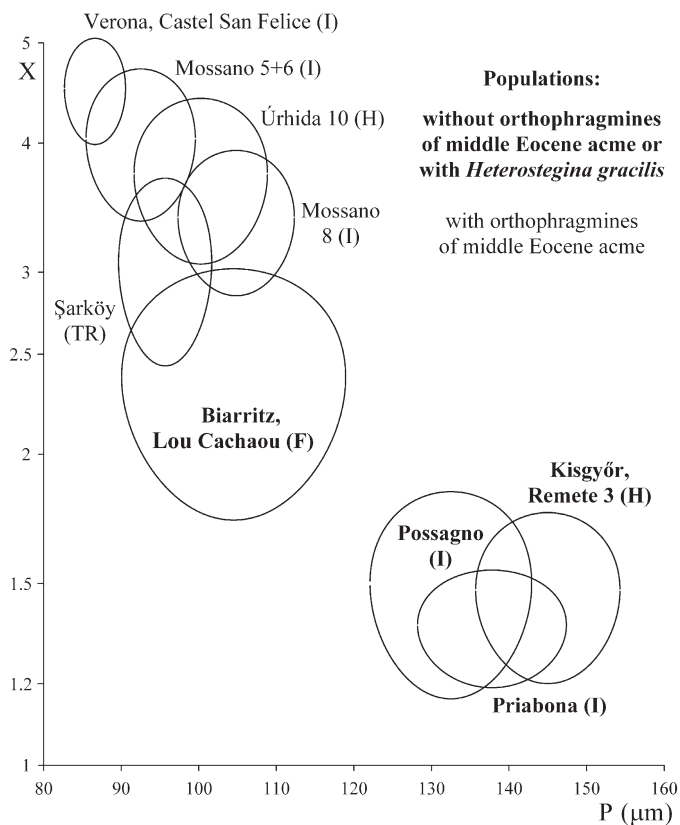


Fig. 5. Distribution of spiroclypeid populations (mean values at the 95.44% confidence level) on the P–X (proloculus diameter versus operculinid reduction) bivariate plot (X is on logarithmic scale).

lower right group to *S. carpaticus*. The population from Biarritz, Lou Cachaou (*S. aff. carpaticus*) takes an intermediate position between them.

(ii) The populations are arranged in the plot according to their associated, age-determining larger foraminiferal fauna. Those without orthophragmines of middle Eocene acme or with *Heterostegina gracilis* are concentrated in the centre and in the bottom right whereas those with orthophragmines of middle Eocene acme in the upper left. It is worth noting that in this latter group not only the parameters of *Spiroclypeus* from particular populations but also those of *Heterostegina* are very similar to each other.

(iii) The stratigraphic superposition of the population Mossano 8 in respect to Mossano 5+6 that was directly observed in the field, is reflected also in their position in the plot.

(iv) The decrease of the number of undivided neanic chambers (X) and the increase of the number of chamberlets in chamber 14 (S) have a great stratigraphic significance. The strong negative correlation between the two parameters can also be read from Fig. 4.

Almost the same conclusions can be drawn from Fig. 5 where the mean values of the size of the proloculus (P) per population are plotted against those of X at the 95% confidence level. However, in this case the population from Biarritz, Lou Cachaou is closer to the group of *Spiroclypeus sirottii* associated with orthophragmines of middle Eocene

acme. This means that the general increase of the size of the proloculus is not only a far less rapid evolutionary trend than the change of X and S, but also far less reliable, probably because it is under an additional ecological control (for more details see Beavington-Penney and Racey 2004).

The diameter of the second whorl (D) is also quite useful in distinguishing the two species as shown in Fig. 6 where this parameter is plotted against X, once again at the 95% confidence level. From this plot the same consequences can be extracted as from the former two figures, almost with the same resolution power. The population from Biarritz, Lou Cachaou is again intermediate between the group of *Spiroclypeus carpaticus* and that of *S. sirottii*, as in Fig. 4.

The least diagnostic numerical parameter is K, the index of spiral opening that shows a very slow and rather uncertain increase, i.e., the spiral becomes generally looser in time. In general, there is a slight positive correlation between the size of the proloculus (P) and the laxity of the spiral.

As seen from the photos of Fig. 7, no real increase in the size of the test can be observed during the evolution of *Spiroclypeus* in the late Eocene. Moreover, no difference in the test size could be observed between the A- and B-forms, although the latter were rare. Parameter X (with the same meaning as in the A-forms) could be counted in four specimens. In sample Mossano 6, the X values were 18 and 22, in sample Mossano 7 it was 17 whereas in sample Kisgyőr,

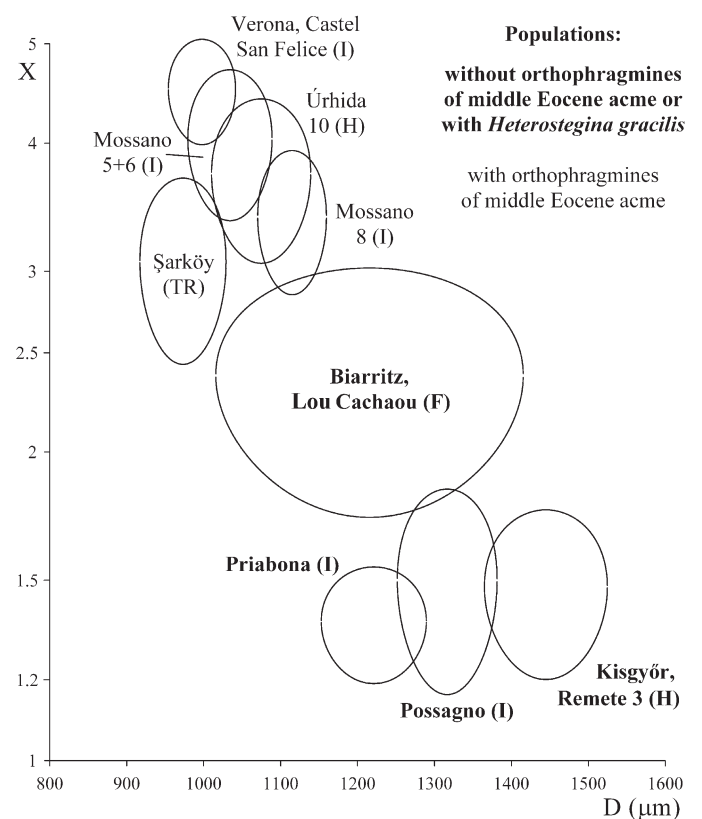


Fig. 6. Distribution of spiroclypeid populations (mean values at the 95.44% confidence level) on the D–X (second whorl diameter versus operculinid reduction) bivariate plot (X is on logarithmic scale).

Remete-kút 3 it was reduced to about 14. These data suggest that a reduction in the number of undivided neanic chambers also occurs in the microspheric forms, although the number of observations is too low to reach any firm conclusions.

Systematic paleontology

Order Foraminiferida Eichwald, 1830

Family Nummulitidae de Blainville, 1827

Genus *Spiroclypeus* Douvillé, 1905

Type species: Spiroclypeus orbitoideus Douvillé, 1905, late Aquitanian, river Tabalong, close to Tandjong (Borneo)

Remarks.—Based on the parameters evaluated above, Western Tethyan late Eocene *Spiroclypeus* can be grouped into two species. They can be discriminated using the number of the undivided neanic chambers (X). Based on our data (Table 1) $X_{\text{mean}} = 2.7$ is the most suitable value to separate *Spiroclypeus sirottii* with more undivided chambers from *S. carpaticus* with fewer. The classification of particular populations in the different taxa is reported in Table 1. Stratigraphical ranges of particular taxa are given in advance.

Spiroclypeus sirottii sp. nov.

Fig. 7A–N, P, Q, T.

1994 *Spiroclypeus granulatus* Boussac, 1906; Papazzoni 1994: pl. 2: 2.

1995 *Spiroclypeus carpaticus* (Uhlig, 1886); Papazzoni and Sirotti 1995: pl. 2: 11, 12.

2004 *Spiroclypeus sirottii* sp. nov.; Less and Gyalog 2004: pl. (black and white) 2: 4.

2007 *Spiroclypeus sirottii* sp. nov.; Özcan et al. 2007: pl. 1: 20.

Derivation of the name: In honor of the late Professor Achille Sirotti (Modena), an expert on larger Foraminifera.

Holotype: MÁFI E. 9591 (Fig. 7K), a megalospheric specimen split along the equatorial plane.

Type locality: Mossano (N Italy, Colli Berici), Marne di Priabona, sample Mossano 6.

Type horizon: Basal Priabonian, SBZ 19 A.

Material.—18 well-preserved megalospheric specimens split along the equatorial plane.

Diagnosis.—Involute, lense-shaped test with poorly developed lateral chamberlets. Most of the surface is covered by granules except at the shell's margin where usually a rectan-

gular sutural network can be seen. The proloculus is small; the coiling of the spiral is rather tight. The number of undivided postembryonic chambers (parameter X) is usually 2–7; its mean value exceeds 2.7 which distinguishes it from *Spiroclypeus carpaticus* (Uhlig, 1886). The secondary chamberlets are more or less regularly arranged, somewhat sparsely spaced and of very slightly hexagonal shape.

Description

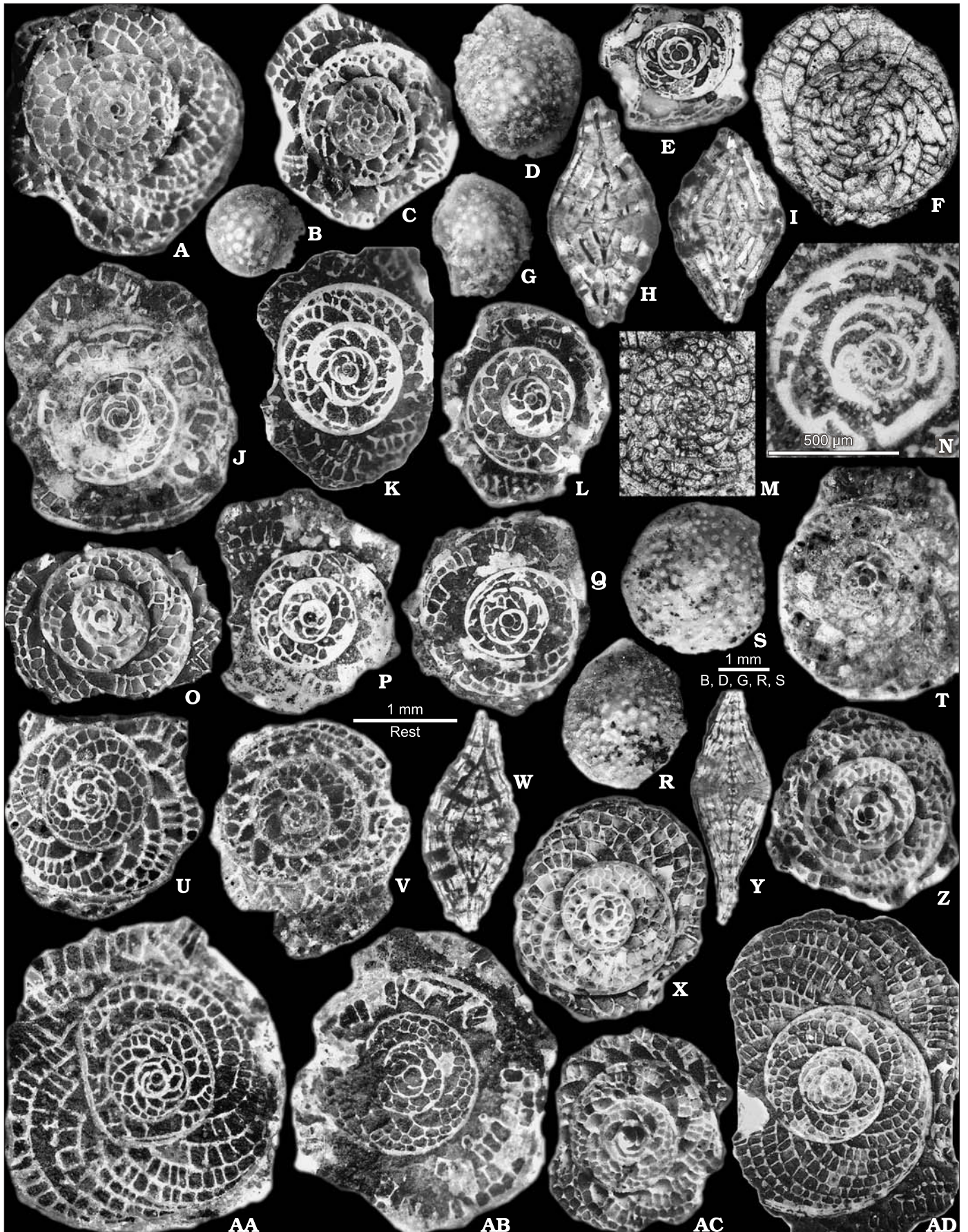
External features (Fig. 7B, D, G).—The test is small (1.5 to 4 mm in diameter), involute, biconvex, lense-shaped with a very slightly inflated, broad umbonal part occupying 70–90% of the test's diameter. It is covered by granules, which are very slightly larger in the centre than towards the shell's periphery where they are absent and where a regular, rectangular network of primary and secondary septa can sometimes be seen. No significant difference in size was recognized between A- and B-forms.

Internal features.—The equatorial section of A-forms: The proloculus is small ($P = 50\text{--}150\ \mu\text{m}$, P_{mean} of different populations varies between 80 and 115 μm) and (after a kidney-shaped deuteroconch of similar size) is followed by a rather tightly coiled spiral comprising 2.5 to 4 whorls ($d = 350\text{--}720\ \mu\text{m}$, $d_{\text{mean}} = 490\text{--}650\ \mu\text{m}$; $D = 700\text{--}1350\ \mu\text{m}$, $D_{\text{mean}} = 920\text{--}1160\ \mu\text{m}$; $K = 38\text{--}61$, $K_{\text{mean}} = 49\text{--}56$). The chambers are very high; the primary septa are very strongly curved backward. After a few undivided (operculinid) postembryonic chambers ($X = 2\text{--}7$, very rarely 1 or 8 to 10; $X_{\text{mean}} = 2.7\text{--}5.5$) all the successive chambers are subdivided into secondary chamberlets that are rather regularly arranged, somewhat sparsely spaced ($S = 2\text{--}5$, very rarely 6 or 7; $S_{\text{mean}} = 2.3\text{--}4.3$) and of very slightly hexagonal shape.

The equatorial section of B-forms (Fig. 7N): Based on three specimens from samples Mossano 6 and 7, the size of the proloculus is 10–15 μm . It is followed by 17–22 undivided (operculinid) chambers before the appearance of the first subdivided chamber after which some undivided chambers may reappear in a few specimens. The arrangement and shape of chamberlets in the adult stage do not differ from those of the A-forms.

Axial section (Fig. 7H, I): The test is inflated, involute and biconvex. Piles are well visible, lateral chamberlets are visible but poorly developed.

Fig. 7. Priabonian *Spiroclypeus* from different European localities. A–N, P, Q, T. *Spiroclypeus sirottii* sp. nov., early Priabonian, SBZ 19. A–D, G, I. Verona (N Italy), Castel San Felice, Villa Le Are. A, C. A-form, equatorial sections, MÁFI E. 9586 (A), MÁFI E. 9587 (C). B, D, G. External views, (B) MÁFI E. 07.1, MÁFI E. 07.3 (D), MÁFI E. 07.2 (G). I. A-form, axial section, MÁFI E. 08.2. E, F, M. Şarköy 4 (NW Turkey). E, F, M. A-form, equatorial sections, MÁFI E. 9589 (E), ITU O/ŞAR.4-71 (F), ITU O/ŞAR.4-86 (M). H, K, L, N. Mossano 6 (N Italy). H. Paratype, A-form, axial section, MÁFI E. 08.1. K, L, N. Equatorial sections. K. Holotype, MÁFI E. 9591, A-form. L. Paratype, MÁFI E. 9590, A-form. N. Paratype, MÁFI E. 9592, B-form. J. Verona (N Italy), Castel San Felice, hairpin bend, MÁFI E. 9588, A-form, equatorial section. P, Q. Úrhida 10 (Hungary), A-form, equatorial sections, MÁFI E. 9594 (P), MÁFI E. 9593 (Q). T. Mossano 8 (N Italy), MÁFI E. 9595, A-form, equatorial section. O. *Spiroclypeus* aff. *carpaticus* (Uhlig, 1886), late Priabonian, SBZ 20, Biarritz (SW France), Lou Cachaou, MÁFI E. 9596, A-form, equatorial section. R, S, U–Z, AA–AD. *Spiroclypeus carpaticus* (Uhlig, 1886), late Priabonian, SBZ 20. R, S, W–Z, AC, AD. Kisgyőr (Hungary), Remete 3. R, S. External views, MÁFI E. 07.4 (R), MÁFI E. 07.5 (S). W, Y. A-form, axial sections, MÁFI E. 07.6 (W), MÁFI E. 07.7 (Y). X, Z, AC. A-form, equatorial sections, MÁFI E. 9195 (X), MÁFI E. 9502 (Z), MÁFI E. 9599 (AC). AD. MÁFI E. 9196, B-form, equatorial section. U, V. Possagno 1 (N Italy), A-form, equatorial sections, MÁFI E. 9597 (U), MÁFI E. 9598 (V). AA, AB. Priabona (N Italy), A-form, equatorial sections, MÁFI E. 9600 (AA), MÁFI E. 9601 (AB).



Remarks.—The name *Spiroclypeus sirotti* was informally used by Less and Gyalog (2004) for the population from sample Úrhida 10 and by Özcan et al. (2007) for the population from sample Şarköy 4, although no description was provided, so the taxon is introduced formally herein. The figures of Papazzoni (1994) and Papazzoni and Sirotti (1995) cited in the synonymy list illustrate specimens from nearby samples Mossano 5 to 7. These populations were re-evaluated in this paper and placed in synonymy with the present species.

Spiroclypeus sirotti can be confused only with *S. carpaticus*, however, the mean value of the post-embryonic pre-heterosteginid chambers (parameter X) for the A-forms is above 2.7 for *S. sirotti*. The other discriminative parameters are the mean value of the number of chamberlets in chamber 14 (parameter S) which is below 4.3 and that of the diameter of the first two whorls which is below 1160 µm. In axial section the rather poorly developed lateral chamberlets also help discriminate the two taxa.

In accord with Hottinger (1977) we suppose that *Spiroclypeus* (and consequently *S. sirotti*, the first representative of the genus known so far) evolved from involute *Heterostegina*, very probably from *H. reticulata* since it has a similar structure in equatorial section, but lacks lateral chamberlets and appeared in stratigraphically lower horizons. At the same time there can be little doubt on the derivation of *S. carpaticus* from *S. sirotti*. The identical structure of their equatorial sections, the more advanced numerical characteristics of *S. carpaticus* compared to *S. sirotti* (see Table 1 and Figs. 4–6), and the presence of well-developed lateral chamberlets at *S. carpaticus* and of course the relative stratigraphic position of the two taxa suggests *S. carpaticus* evolved from *S. sirotti*.

Geographic and stratigraphic distribution.—Early Priabonian (SBZ 19) of N Italy (Mossano, samples 5, 6 and 8; Verona, Castel San Felice: Villa Le Are, Villa Devoto and the outcrop of the hairpin bend), W Hungary (Úrhida, sample 10), NW Turkey (Şarköy).

Spiroclypeus carpaticus (Uhlig, 1886)

Fig. 7R, S, U–Z, AA–AD.

- 1886 *Heterostegina carpatica* sp. nov.; Uhlig 1886: 201–202, pl. 2: 14–15; text-fig. 10.
 1906 *Spiroclypeus granulosus* sp. nov.; Boussac 1906: 96–97, pl. 2: 15–18; pl. 3: 19.
 1957 *Spiroclypeus carpaticus* (Uhlig, 1886); Bieda 1957: 208, 224–225, pl. 12: 3, 5, 6.
 1961 *Spiroclypeus granulosus* Boussac, 1906; Roveda 1961: 195–201, pl. 16: 13–16; pl. 17: 1–3; pl. 18: 7, 8; pl. 19: 12, 13.
 1963 *Spiroclypeus carpaticus* (Uhlig, 1886); Bieda 1963: 106, pl. 17: 12, 13 (?).
 1964 *Spiroclypeus carpaticus* (Uhlig, 1886); Hottinger 1964: pl. 7: 6.
 1977 *Spiroclypeus granulosus* Boussac, 1906; Hottinger 1977: text-fig. 48G, H.
 1986 *Spiroclypeus granulosus* Boussac, 1906; Schiavinotto 1986: pl. 1: 1–4; pl. 2: 1–5.
 1999 *Spiroclypeus granulosus* Boussac, 1906; Less 1999: 356, pl. 2: 3, 4.
 2005 *Spiroclypeus carpaticus* (Uhlig, 1886); Less et al. 2005: 98, photo 101/18.

Diagnosis.—Involute, disc-shaped test with well-developed lateral chamberlets. Most of the surface is covered by granules except the peripheries where usually a rectangular septal network can be seen. The proloculus is small to medium-sized; the coiling of the spiral is moderately tight. The number of pre-heterosteginid postembryonic chambers (parameter X) is usually 1–2, rarely 3; its mean value is less than 2.7, which distinguishes it from *Spiroclypeus sirotti* sp. nov. The secondary chamberlets are quite regularly arranged and densely spaced and of nearly rectangular shape.

Description

External features (Fig. 7R, S).—The test is small (1.5 to 4 mm in diameter), involute, biconvex, disc-shaped with a very slightly inflated, broad umbonal part occupying 60–90% of the test's diameter. It is covered by granules, which are slightly larger in the centre than towards the shell's periphery where they are absent and where a regular, rectangular network of primary and secondary septal sutures may often develop. No significant difference in adult shell size can be recognized between A- and B-forms.

Internal features.—The equatorial section of A-forms: The proloculus is small to medium-sized ($P = 100\text{--}200\ \mu\text{m}$, $P_{\text{mean}} = 115\text{--}155\ \mu\text{m}$) and (after a kidney-shaped second chamber of similar size) followed by a moderately tightly coiled spiral with 2.5 to 4 whorls ($d = 450\text{--}950\ \mu\text{m}$, $d_{\text{mean}} = 600\text{--}750\ \mu\text{m}$; $D = 950\text{--}1700\ \mu\text{m}$, $D_{\text{mean}} = 1150\text{--}1550\ \mu\text{m}$; $K = 40\text{--}63$, $K_{\text{mean}} = 51\text{--}60$). The chambers are very high; the primary septa are very strongly curved backwards. After a very few undivided (operculinid) postembryonic chambers ($X = 1\text{--}3$, very rarely 4; $X_{\text{mean}} = 1.2\text{--}2.7$) all the successive chambers are subdivided into chamberlets that are quite regularly arranged and densely spaced ($S = 4\text{--}9$, very rarely 3; $S_{\text{mean}} = 4.3\text{--}7$) and of nearly rectangular shape.

The equatorial section of B-forms (Fig. 7AD): The single specimen from sample Kisgyőr, Remete-kút 3, exhibits a microsphere of 15 µm in diameter. It is followed by about 14 undivided (operculinid) chambers before the appearance of the first subdivided chamber after which undivided chambers can rarely reappear. The arrangement and shape of chamberlets in the adult stage do not differ from those of the A-forms.

Axial section (Fig. 7W, Y): Relying also on Boussac's (1906: pl. 3: 19) and Roveda's (1961: pl. 17: 1–3; pl. 19: 12, 13) figures and descriptions, the test is slightly inflated, involute and biconvex. Lateral chamberlets are well developed, piles are well visible.

Remarks.—Uhlig (1886: text-fig. 10) provided two good figures of the equatorial section of A-forms when introducing the name "*carpatica*" for specimens from Woła Łużańska (Poland). In both sections the number of post-embryonic undivided chambers (parameter X) is 2 and in the upper figure the number of chamberlets in chamber 14 (parameter S) is 7. These parameters correspond well to our material, therefore the name *Spiroclypeus carpaticus* can be applied to them. Based on Roveda's (1961), Schiavinotto's (1986) and our

data and the figures of Boussac's (1906) *S. granulatus* from Priabona we conclude that Uhlig's (1886) *S. carpaticus* is synonymous but has priority making *S. granulatus* invalid. Moreover, the name "*granulosus*" was confusingly used previously for *Heterostegina gracilis* (see Less et al. 2008).

The figures of Boussac (1906), Roveda (1961), Hottinger (1977) and Schiavinotto (1986) cited in the synonymy illustrate specimens from the very close vicinity of our sample from Priabona, while Hottinger's (1964) form from Benidorm and Less' (1999) specimens from Kisgyőr come from the same samples which we have studied.

The distinction between *S. siroittii* and *S. carpaticus* is discussed under the description of the former. According to the figures of Western Tethyan upper Oligocene and lowermost Miocene *Spiroclypeus* by Henson (1937), Cahuzac and Poinignant (1997), and also based on our unpublished data, it seems that they differ from *S. carpaticus* in having a much looser spire, and a larger proloculus (compare them also in Figs. 7 and 8). Since no *Spiroclypeus* have been found in the Western Tethyan lower Oligocene and also because the above differences between *S. carpaticus* and the upper Oligocene and lowermost Miocene forms do not allow to directly link them phylogenetically, we suppose that *S. carpaticus* became extinct with no successors at the very end of the Priabonian.

Geographic and stratigraphic distribution.—Late Priabonian (SBZ 20) of the Polish (Wola Łużańska, Bukowiec) and Slovakian (Raslavice) Carpathians, of N Italy (Priabona, blue claystone; Possagno, Calcare di Santa Giustina, samples Possagno 1 and 2), NE Hungary (Kisgyőr, sample Remete-kút 3), SE Spain (Benidorm).

Spiroclypeus aff. *carpaticus* (Uhlig, 1886)

Fig. 7O.

The few specimens found in the sample from Biarritz, Lou Cachaou have intermediate numerical characteristics between those of *Spiroclypeus siroittii* and *S. carpaticus* (see Table 1 and Figs. 4–6). Because of the scarcity of the material the axial section could not be investigated. Based on the associated *Heterostegina gracilis* marking the late Priabonian and according to the average number of undivided chambers ($X_{\text{mean}} = 2.38$) that is closer to the value defining *S. carpaticus* than to that of *S. siroittii*, the population from Biarritz is determined as *S. aff. carpaticus*, taking into account also the relatively small size of the proloculus.

Discussion

Correlation with other fossil groups.—In Table 3 we summarize the age data based on the various fossil groups and discuss them in detail under the description of the various localities.

The boundary between the P 15 and 16 Planktic Foraminiferal Zones falls within the range of *Spiroclypeus siroittii*. The P16 Zone extends into the range of *S. carpaticus*. The P 16/17 boundary cannot be detected in our material.

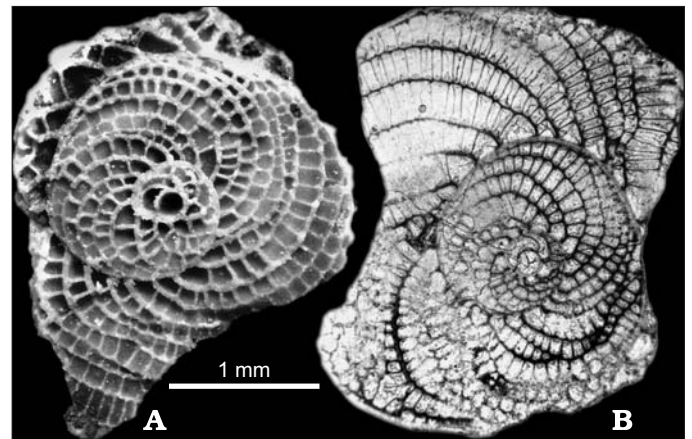


Fig. 8. Equatorial sections of megalospheric upper Oligocene and lowermost Miocene *Spiroclypeus blanckenhorni* Henson, 1937 from Turkey. **A.** Upper Chattian, SBZ 23, Kelereşdere (E Turkey), sample KEL 29, MÁFI O. 08.3. **B.** Lower Aquitanian, SBZ 24, Tuzlagözü (Central Turkey), sample TUZ 1, ITU O/TUZ.1-42.

The basal beds of the Priabona marl in Mossano (samples 5 and 6) with *S. siroittii* belong to the NP 18 Calcareous Nannoplankton Zone, however, the range of the species extends into the NP 19–20 Zone. *S. carpaticus* can also be found in this latter zone as well as in NP 21, marking the very top of the whole Eocene, since according to Berggren et al. (1995) the Eocene/Oligocene boundary is located within this latter zone.

The representatives of the *Nummulites fabianii*-group were found only in very few samples. Typical *Nummulites fabianii* occurs with both Eocene spiroclypeid species whilst the flatter form (= *N. "retiatius"*) was found only with *S. carpaticus*. Based on Serra-Kiel et al. (1998) *N. fabianii* marks the SBZ 19 Shallow Benthic Zone while *N. retiatius* indicates SBZ 20. Meanwhile Herb and Hekel (1973), Barbin (1988) and Trevisani and Papazzoni (1996) record *N. fabianii* with and sometimes above *N. retiatius* suggesting that their occurrence in upper Priabonian beds may be partly controlled by ecological factors. According to our recent studies (Less et al. 2006, unpublished data), typical *N. fabianii* occurs from the base of the Priabonian into the lower Oligocene. Meanwhile the flatter *N. fabianii* (formerly *N. retiatius*), having adapted to somewhat deeper marine environments, only occurs in the upper part of the Priabonian together with *S. carpaticus* as in the vicinity of Kisgyőr, Remete-kút (Less 1999; Less et al. 2000).

Our two spiroclypeid species can be correlated with the revised Eocene involute heterosteginid taxa (Less et al. 2008). *Spiroclypeus siroittii* from samples Mossano 5+6, Verona—Castel San Felice, Úrhida 10 and Şarköy 4 occurs with *Heterostegina reticulata mossanensis* marking the basal Priabonian (SBZ 19 A) and with *H. reticulata italica* (SBZ 19 B-20) in the more upper part of the Mossano profile (sample Mossano 8). *Spiroclypeus carpaticus* associates with *H. gracilis* indicating SBZ 20, in Possagno also with the simultaneously existing *H. reticulata italica*.

Spiroclypeus siroittii is found with orthofragmines of middle Eocene acme (*Discocyclina pratti*, *Nemkovella stro-*

Table 3. Assemblages of different fossil groups co-occurring with *Spiroclypeus* from particular localities that are ranged among shallow benthic subdivisions. Abbreviations: aff. c., aff. *carpaticus*; ↓ below; ? very rare occurrence.

Associated fossils		Taxa										
		<i>sirottii</i>				aff. c.	<i>carpaticus</i>					
		Samples	Mossano 5+6	Şarköy	Úrhida 10	Verona	Mossano 8	Biarritz, Cachaou	Priabona	Possagno	Benidorm	Kisgyőr
Planktic Foraminifera	P 15		●									
	P 16					●	●		●			
Calcareous nanno-plankton	NP 18		●									
	NP 19–20					●	●	●	●			
	NP 21											●
<i>Nummulites fabianii</i>	typical	?			●				↓	●		
	flatter									●		●
<i>Heterostegina reticulata</i>	<i>mossanensis</i>		●	●	●	●						
	<i>italica</i>					●				●		
	<i>gracilis</i>						●		●	●		
Ortho-phragmines	OZ 14		●	●	●	●	●					
	OZ 15								●			
	OZ 16											●
Shallow benthic zones	SBZ 19	A	A	A	A	B						
	SBZ 20						●	●	●	●	●	●

phiolata, *Asterocyclina alticostata*, and *A. kecskemetii*) whose last occurrence indicates the OZ 14 Orthophragminid Zone. The level of sample Mossano 8, where only rare *A. alticostata* was found, is placed at the limit of OZ 14/15. *Spiroclypeus carpaticus* does not associate with the above listed forms of middle Eocene acme, the orthophragminid fauna in the Priabona sample indicates OZ 15 while in Kisgyőr OZ 16 (the highest orthophragminid zone) is recorded.

Chronostratigraphic correlation.—The placement of the middle/late Eocene (= Bartonian/Priabonian) boundary is discussed in detail in Less et al. (2008). The base of the Priabona marls in the Mossano section is suggested to be the most suitable level for fixing this boundary. In this case the base of the Priabonian coincides with the first occurrence of three quite widespread larger Foraminifera: *Nummulites fabianii*, *Heterostegina reticulata mossanensis*, and *Spiroclypeus sirottii*, the latter also being the first representative of the genus itself, since it has not been found with the less advanced members of the *H. reticulata* lineage from the latest Bartonian (Less et al. 2008). The co-occurrence of *Spiroclypeus* with large-sized *Nummulites* (with test diameter of the B-forms exceeding 15 mm, belonging to the *N. perforatus-biedai*-, *N. millecaput-maximus*-, and *N. gizehensis-lyelli*-groups) having become extinct at the very end of the middle Eocene is unknown as well. However, the co-occurrence of *S. sirottii* with *H. reticulata mossanensis* in four different localities from three

quite remote areas (North Italy: Mossano and Verona; Hungary: Úrhida; NW Turkey: Şarköy) suggests that the first appearance of the genus *Spiroclypeus* was synchronous.

Bibliographic data on the presence of *Spiroclypeus* in the late middle Eocene can be disproved as follows: (i) The case of Schweighauser (1953) is discussed in the description of the Mossano locality in Less et al. (2008). (ii) Racey (1995: 81) indicates *Spiroclypeus* from one sample of the “Auversian” of Oman based on the presence of *Silvestriella tetrahedra*, *Fabiania cassis*, *Borelis vonderschmitti*, and *Calcarina* and on the absence of *Nummulites fabianii*. In our opinion, this accompanying assemblage may indicate both the late Bartonian and the Priabonian. (iii) Finally, Mohiuddin (2004) mentions *Spiroclypeus vermicularis* from the upper middle Eocene of Bangladesh that is in our opinion an erroneous determination according to his fig. 4B, which illustrates rather a *Nummulites*.

It is clear from Table 3 that the fossil assemblages associating with *S. sirottii* indicate the lower part of the Priabonian whereas those co-occurring with *S. carpaticus* indicate its upper part. Therefore, *S. sirottii* may be used as a zonal marker for the SBZ 19 Zone (early Priabonian) while *S. carpaticus* defines SBZ 20 (for details see also Table 8 in Less et al. 2008).

The further evolution of the genus in the early Oligocene is not recorded in the Western Tethys. Based on this and on the reasons discussed at the end of the chapter “Remarks” to the description of *S. carpaticus*, we can reasonably suppose that the *S. sirottii*–*carpaticus* lineage is restricted to the Priabonian.

Paleoecology

In almost all the investigated localities (with the exception of Benidorm from where we have no information), orthophragmines have been found in great quantity. They mark outer shelf conditions (Papazzoni 1994), thus we can reasonably suppose that *Spiroclypeus* are characteristic also for this environment, indicating a narrower paleoecological niche as compared to *Heterostegina* (Less et al. 2008). Nevertheless, their distribution from Spain to at least Oman (Racey 1995) provides potential for using *Spiroclypeus* in Western Tethyan stratigraphical correlation.

Conclusions

Based on the morphometrical study (especially on the statistical evaluation of the equatorial section of A-forms) of *Spiroclypeus* from ten European localities (extending from Spain to Turkey and covering the whole Priabonian) and also on the critical evaluation of bibliographic data we conclude that:

(i) Based on the reduction of the average number of undivided, post-embryonic chambers (parameter X), populations can be grouped into two successive, phylogenetically linked species, *Spiroclypeus sirottii* sp. nov. and *Spiroclypeus carpa-*

ticus (Uhlig, 1886). X_{mean} above 2.7 is diagnostic for the populations of the first species, whilst X_{mean} below 2.7 for those of the second one.

(ii) The evolution is also proven by the increase of the number of chamberlets in particular chambers (parameter S), by the increase of the diameter of the first two whorls (parameter D) and by that of the size of the proloculus (parameter P), although the latter turned out to be also ecologically controlled. Meanwhile the spire becomes only slightly looser (although this change—characterized by parameter K—is very uncertain) and the size of the test does not really increase in time. The morphological changes of the lateral chamberlets are to be studied further.

(iii) The evolution is supported by the stratigraphical succession of populations in the Mossano section (N Italy) and also by the change of the accompanying planktic foraminifera, the calcareous nannoplankton, the nummulitids (*Nummulites fabianii*-group and *Heterostegina*) and the orthophragmines.

(iv) Lacking in upper Bartonian beds, the first appearance of the genus *Spiroclypeus* in the Western Tethys seems to be synchronous with the beginning of the late Eocene.

(v) Based on the absence of the genus *Spiroclypeus* in the Western Tethyan lower Oligocene and on the significant morphological differences between the upper Eocene and upper Oligocene to lowermost Miocene forms, we suppose that the *Spiroclypeus sirottii*–*carpaticus* lineage is restricted to the Priabonian.

(vi) The newly described *Spiroclypeus sirottii* sp. nov. is associated with *Heterostegina reticulata mossanensis* and with orthophragmines containing still forms of middle Eocene acme, both marking the lower part of the Priabonian, thus it is a zonal marker for the SBZ 19 Zone.

(vii) Because *Spiroclypeus carpaticus* (Uhlig, 1886) co-occurs with *Heterostegina gracilis* but with no orthophragmines of middle Eocene acme (both phenomena characteristic for the upper part of the Priabonian), it characterizes the SBZ 20 Zone.

(viii) Based on the study of topotypical material, *Spiroclypeus granulatus* Boussac, 1906 is proven to be the junior synonym of *Spiroclypeus carpaticus* (Uhlig, 1886).

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