The middle to late Eocene evolution of nummulitid foraminifer *Heterostegina* in the Western Tethys

GYÖRGY LESS, ERCAN ÖZCAN, CESARE A. PAPAZZONI, and RUDOLF STOCKAR

Megalospheric forms of Western Tethyan late Bartonian to late Priabonian involute *Heterostegina* from numerous localities, marking different ecological conditions, were morphometrically investigated. They belong to three species, *H. armenica*, *H. reticulata*, and *H. gracilis* based on the presence/absence of granulation, on the chamberlet characteristics and on the relative size of proloculus. Within these species a very rapid evolution could be observed in the reduction of the number of operculinid chambers, in the increase of the number of chamberlets and partially in the increase of the proloculus size. This evolution is demonstrated by stratigraphic superpositions in several localities (especially in the Mossano section), and is supported also by the change of co-occurring fossils, starting with the disappearance of large-sized *Nummulites*, then followed by the appearance of the genus *Spiroclypeus* and then by the disappearance of orthophragmines of middle Eocene acme. Based on the reduction of operculinid chambers, two chronosubspecies of *Heterostegina armenica* and seven of *H. reticulata* are defined biometrically (four of them: *H. armenica tigrisensis*, *H. reticulata tronensis*, *H. r. hungarica*, and *H. r. mossanensis* are introduced here). This allows to subdivide the Shallow Benthic Zone (SBZ) 18 into three and SBZ 19 into two subzones. The extremely rapid evolution of *H. reticulata* allows to calibrate larger foraminiferal events around the middle/late Eocene boundary. The extinction of large-sized *Nummulites* seems to be heterochronous in the late Bartonian in having migrated eastward, while the first appearance of *Spiroclypeus* is shown to be synchronous at the base of the Priabonian. The middle/upper Eocene (= Bartonian/Priabonian) boundary is to be placed at the base of the Priabona marls in the Mossano section corresponding to the SBZ 18/19 limit, to the first appearance of genus *Spiroclypeus*, to that of *Nummulites fabianii* and of *Heterostegina reticulata mossanensis*. It falls into the upper part of both the P 15 and NP 18 planktic zones. The Western Tethyan Eocene involute *Heterostegina* became extinct, apparently with no Oligocene successors.

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

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Introduction

After a long-lasting period of simultaneous evolution of several phylogenetic lineages of alveolinids (Hottinger 1960), nummulitids (Schaub 1981; Hottinger 1977) and orthophragmines (Less 1987, 1998) in the early and middle Eocene, a major faunal change occurred in the Western Tethyan larger foraminiferal fauna in the vicinity of the middle/late Eocene boundary. Its most characteristic feature is the disappearance of large-sized *Nummulites*, *Assilina*, and *Alveolina* and simultaneously the appearance of some new nummulitid and other genera (e.g., *Heterostegina*, *Spiroclypeus*, *Pellatispira*, *Chapmanina*). In addition, some nummulitid lineages, which originated in the late middle Eocene, became dominant in the late Eocene (*Nummulites fabianii*, *N. chavannesi*, *N. incrassatus*, *Assilina alpina*, etc.). More details can be found in Papazzoni and Sirotti (1995) and in Romero et al. (1999).

The task to reconstruct the timetable of different faunistic events around the middle/late Eocene boundary is hampered very much by the almost entire absence of continuous profiles crossing the boundary in shallow-marine facies and containing both the disappearing old and appearing new forms. Such sections are well known only from NE Italy among which the Mossano section is the most useful (Fabiani 1915; Bassi 2005 with references) due to its continuity and mostly marly facies that facilitate isolating specimens of larger foraminifera. However, here too, a facies shift (sudden deepening) occurs at the boundary of shallow benthic zones (SBZ) 18 and 19 identified by Papazzoni (1994) and Serra-Kiel et al. (1998) with the middle/late Eocene boundary.

Therefore, we looked for indirect tools for detecting the chronology of larger foraminiferal events at the middle/late Eocene boundary with high resolution. Some evolutionary lineages (*Nummulites fabianii*, *Assilina alpina* and several orthophragminid lineages) cross the boundary but their evolutionary progress, which can be estimated most reasonably by the

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increasing size of their embryon (the two initial chambers of megalospheric forms; see Hottinger 2006), does not provide a resolution of less than one million years, which could be sufficiently precise for our purposes.

Fortunately, *Heterostegina* and *Spiroclypeus* give us another possibility because their evolution can also be followed through the decreasing number of undivided, operculinid chambers before the appearance of the first subdivided, heterosteginid chamber. Herb (1978), Papazzoni and Sirotti (1993), Less and Papazzoni (2000) and Less et al. (2000) suggested this strategy for Eocene *Heterostegina*, which would be in accord with the principle of nepionic acceleration introduced by Tan (1932) for Indonesian *Cycloclypeus* and then successfully applied to several Oligocene and Neogene larger foraminifera (for details see Drooger 1993). However, the genus *Spiroclypeus* seems to have appeared only at the very base of the SBZ 19 and can never be found together with the large-sized *Nummulites* (with test diameter of the B-forms over 15 mm). Its late Eocene evolution is described by Less and Özcan (2008). On the other hand, *Heterostegina* can first be found with the last large-sized *Nummulites* as shown by Papazzoni and Sirotti (1993) and Less et al. (2000), and then it can be followed through the whole Priabonian (Serra-Kiel et al. 1998). The relationship of Eocene and Oligocene *Heterostegina* is discussed below.

The aim of this paper is to biometrically describe and calibrate the evolution of Bartonian and Priabonian *Heterostegina* in the Western Tethys in order to provide a useful tool for high-resolution stratigraphy of this time-span.

Institutional abbreviations.—ITU O, Istanbul Technical University, Özcan collection of the Geology Department, Turkey; MÁFI E and O, Geological Institute of Hungary, Budapest, Eocene (E) and Oligocene (O) collection; MCSNL, Museo Cantonale di Storia Naturale in Lugano, Switzerland; NHMB, Naturhistorisches Museum Bern, Switzerland.

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), 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.—ARM, Armenia; CH, Switzerland; E, Spain; F, France; H, Hungary; I, Italy; TR, Turkey.

Historical background

The first species of Western Tethyan Eocene *Heterostegina* was described from the Helvetic nappes of Switzerland by Rütimeyer (1850) as "*reticulata*", then by Kaufmann (1867) as "*helvetica*". More details can be found in Herb (1978), who investigated these forms from their supposed type localities and assumed synonymy, preserving the name "*reticulata*" as having priority.

Bieda (1949) created the genus *Grzybowskia* for Eocene forms of the Polish Carpathians. Its diagnostic feature is the rhombic-hexagonal shape of secondary chamberlets differing from the regular, rectangular chamberlets of *Heterostegina*. The type of the new genus was his new species, *G. multifida*. Later he (Bieda 1957, 1963) described both "*multifida*" and "*reticulata*" as belonging to *Grzybowskia*. Köhler (1967) first suggested that these forms originated from involute *Operculina*.

The name *Grzybowskia* was widely used until Hottinger (1977) put them back into the genus *Heterostegina*, arguing that the generic features of *Grzybowskia* fall into the variation field of *Heterostegina depressa,* the type species. Hottinger (1977) gave also the currently used definition of *Heterostegina* and after a preliminary study (Hottinger 1964) proposed two parallel evolutionary lineages for involute forms, both having originated in the late Eocene. However, the establishment of these lineages (differing from each other in the tightness of the spire and in the density of subsequent chambers) is purely typological; moreover, the figured examples are coming from geographically remote areas. On the other hand, Hottinger (1977) clearly distinguished *Heterostegina* from involute *Operculina* (*O. bericensis*, *O. roselli*, *O. gomezi*) having sometimes randomly spaced secondary chamberlets with frequently incomplete secondary septa. These "anasteginid" forms could be observed in Spain in the same thanatocenosis with *O. gomezi* and, therefore were interpreted as intraspecific variations of the latter.

Herb (1978) revised *Heterostegina* from the Helvetic nappes of Switzerland and compared them with forms found in the Priabonian sections of Mossano and Possagno (Northern Italy). He found that in the Swiss localities a transition can be observed from involute *Operculina* (called *O. bericensis*) through anasteginid *O. gomezi* to real *Heterostegina*, first with numerous then with ever fewer operculinid chambers. This evolution could be followed in Mossano and Possagno where a more advanced form was found with a much reduced operculinid part. Herb put these forms of *Heterostegina* into a phylogenetic lineage called *H. reticulata* (corresponding to Hottinger's *H. helvetica*), starting with *H. reticulata multifida*, followed by *H. r. reticulata* and terminating with *H. r. italica*, a new taxon found in the material from Possagno. From the same sample he described a new species, *H. gracilis* (corresponding to Hottinger's *H. reticulata*), with granules on the surface of the test and having a more open spiral and more densely spaced subsequent chambers as compared to the *H. reticulata* lineage. In establishing this lineage, Herb (1978) was the first who—though in a typological basement—recognized the nepionic acceleration as driving the evolution of Eocene *Heterostegina*. From a stratigraphical point of view, he suggested that real *Heterostegina* appeared only in the Priabonian.

This idea was widely accepted: Bieda (1963) and Köhler (1967) believed that large-sized *Nummulites* (of the "*perforatus*" and "*millecaput*" groups) survived in the Northern Carpathians until the early Priabonian because they occur there together with *Heterostegina*. This phenomenon can be explained by the frequent reworking of different faunas in turbidite sediments. However, the co-occurrence of large-sized *Nummulites* and *Heterostegina* is also well known from Armenia (Krashenninikov et al. 1985; Grigoryan 1986), where the sedimenta-

tion is said to be free from turbidites. Grigoryan (1986) described and rather poorly figured two types of *Heterostegina* from sediments with large-sized *Nummulites*. She called one of them *Grzybowskia reticulata* (co-occurring with *Nummulites millecaput*); the other she described as a new species, *G. armenica*. The latter is a really primitive form with irregularly arranged secondary chamberlets that often have incomplete secondary septa. It co-occurs with *Nummulites gizehensis* (or rather *N. lyelli*) and shows some similarities with anasteginid *Operculina gomezi*; at the same time, we have found that its proloculus is surprisingly large (see below).

In their revisional work, Banner and Hodgkinson (1991) used the term *Heterostegina* only for their "maturoevolute" forms. They called the involute forms with subrectangular chamberlets *Heterostegina* (*Vlerkina*) or *Grzybowskia* if chamberlets were polygonal. Both types occur in our material with a wide variety of intermediates (see details later), so we cannot apply their classification.

The work of Papazzoni and Sirotti (1993) provided a big step forward in two respects. In studying the Mossano section, they observed the co-occurrence of *Heterostegina* with *Nummulites biedai* (one of the end-members of the rather complicated *N. perforatus*-group) in beds that have never been attributed to the Priabonian. Their findings prove that the evolution of Eocene *Heterostegina* started in the latest middle Eocene. In addition, they were the first to study *Heterostegina* biometrically and to evaluate their results statistically. By comparing the statistical results of different parameters of *Heterostegina* from three populations from the Mossano section in superposition, they recognized not only the strong decrease of the number of operculinid chambers marking the nepionic acceleration, but also the increasing size of the two initial (embryonic) chambers.

Romero et al. (1999) described *Heterostegina* from the Puig Aguilera section of the Igualada basin in NE Spain. On a typological basement, they distinguished two morphotypes within their *H. reticulata*, one with rather rhomboidal chamberlets and the other one with more regular, quadrangular to rectangular ones. Comparing their camera lucida drawings, the difference between the two morphotypes was not self-evident. The age of this profile was interpreted to be latest Bartonian despite of containing *Pellatispira* and *Biplanispira*, two genera that have never been previously reported in such relatively old rocks. Nevertheless, our studies have confirmed the latest Bartonian age of the *Pellatispira*-beds in Puig Aguilera (see below).
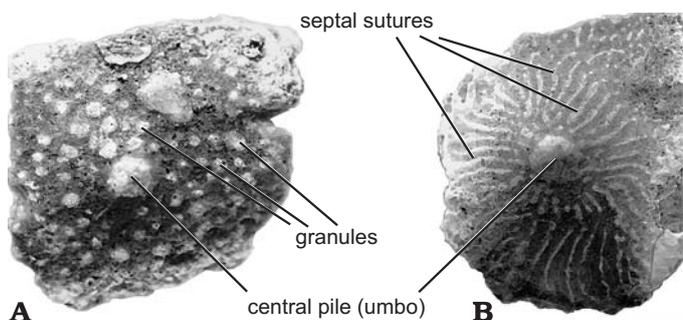
The recent papers of Stockar (1999), Less and Papazzoni (2000), and Less et al. (2000)—as more or less forerunners of our paper—are all based on statistically evaluated biometric studies. We build upon their main results. The main question we are addressing is whether Western Tethyan Eocene involute *Heterostegina* form one single lineage or multiple lineages. Thus, it is necessary to investigate the rate and stability of evolution within the lineage(s) to obtain a reasonable tool for characterizing larger foraminiferal events around the middle/late Eocene boundary.

Terminology and concepts

The general architecture of *Heterostegina*.—According to Hottinger (1977), the genus *Heterostegina* is defined by planispiral, lamellar, perforated shells with chambers subdivided into chamberlets that communicate with the chamberlets of the succeeding chamber by oblique, Y-shaped stolons. The genus *Heterostegina* belongs to the subfamily Nummulitinae because it exhibits a marginal cord.

The members of this genus can be either involute or evolute. The equatorial chamber lumen is secondarily subdivided into chamberlets, alar prolongations remain undivided. The secondary septa produced by folds of the inner lamella are progressively complete from proximal to distal within a spiral chamber in reaching the roof of the chamber. The adult chambers remain spiral throughout the ontogeny of the shell; they never develop into an annular stage, as in the case of *Cycloclypeus* or *Heterocyclina*. The lack of lateral chamberlets distinguishes *Heterostegina* from *Spiroclypeus*. For more details, including the stolon and canal systems, see Hottinger (1977).

Eocene *Heterostegina* are involute with no exception. Externally (Fig. 1), on the central part of the surface of the thin, biconvex test, either a central pile (umbo) or a fine granulation (rarely both) can be found. If granules are missing, the septal sutures depart from the umbo and transform into a reticulation at the periphery. This network can be observed also on specimens with granulation. Unfortunately, the external features are sometimes difficult to observe due to sticky encasing sediments adhering to the test surface.

Recent representatives of this genus are symbiont-bearing (Reiss and Hottinger 1984) and, we assume the Eocene forms to have been also. The enormous size-difference between megalo-(A) and microspheric (B) forms essential for recent *Heterostegina depressa* and large-sized *Nummulites* cannot be observed in Eocene *Heterostegina*. B-forms are rare, A-forms are normally about ten times more frequent. No consistent adult size differences between megalo- and microspheric or stratigraphically older and younger *Heterostegina* could be observed.

From previous research it is clear that the most characteristic specific/subspecific features of Eocene *Heterostegina* can be found in their equatorial section, the axial sections were of limited use for taxonomy. Therefore, we focus our investigations on equatorial sections of megalospheric *Heterostegina* that are more suitable for statistically evaluated biometric research, too.

Taxonomical concept.—We adopt a taxonomical concept based on qualitative differences—of yes/no character—on a

Fig. 1. Terminology for external features of *Heterostegina*: *Heterostegina gracilis* (**A**) and *Heterostegina armenica* (**B**).

higher and on numerical parameters extensively explained by Drooger (1993) on a lower level. Thus, in each sample the genus *Heterostegina* is treated as a single population that is discernable typologically and could also be proven by different bivariate plots of numerical parameters. Because of the lack of space these plots are not figured. However, in three cases (samples Possagno 1, 2 and Keçili 11) two different populations could be observed typologically and, in these cases, we tried to separate them graphically, too.

If a sequence of populations could be arranged into a stratigraphically controlled sequence with a definite evolutionary trend, it was considered to be a lineage. All members of a lineage are treated as a single species. The intraspecific evolution is characterized by rapidly evolving numerical parameters with whose help the species have been arbitrarily segmented into chronosubspecies. With this classification we save an important part of the notion of the species, i.e., individuals of one species are different from individuals of other species that is characteristic for the lineage but not for the segments, which can only be distinguished from each other at the population level. The process of segmentation is based on the principles of Drooger (1993) and described in detail in Less (1987, 1998) and Özcan et al. (2007). We also follow Drooger's (1993: 30) proposal in that the range of a segmented unit (chronosubspecies) should cover at least six times the average standard error of the means for the relevant parameter.

Morphometry.—In order to apply the morphometric method, we describe Eocene *Heterostegina* by using two qualitative features and five quantitative parameters. The first qualitative feature is the presence/absence of the central pile (umbo) and of the granulation on the test's surface. Either the umbo or the granulation is always present, very rarely both of them may occur. The second qualitative feature is the arrangement (irregular or regular) and shape (rhomboid, hexagonal or rectangular) of the secondary chamberlets. All the other characteristics are described quantitatively.

Based on the system introduced by Drooger and Roelofsen (1982), five measurements and counts were executed in the equatorial section of each megalospheric specimen (for microspheric forms, see the end of chapter "Evaluation of parameters"). These are (see also Fig. 2):

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

X: the number of undivided, "operculinid" chambers before the appearance of the first subdivided, heterosteginid chamber, excluding the embryon (the first two chambers) (degree of "operculinid reduction"). Undivided chambers, sometimes reappearing after the first heterosteginid chamber, are not counted. In Fig. 2, X = 4.

S: the number of chamberlets in the fourteenth chamber (including the embryon), reflecting the density of secondary chamberlets ("heterosteginid escalation"). If this chamber is not subdivided into chamberlets, S = 1. In Fig. 2, S = 4.

d: the maximum diameter of the shell in the first whorl as measured along the common symmetry axis of the embryon (the first two chambers) (in μm).
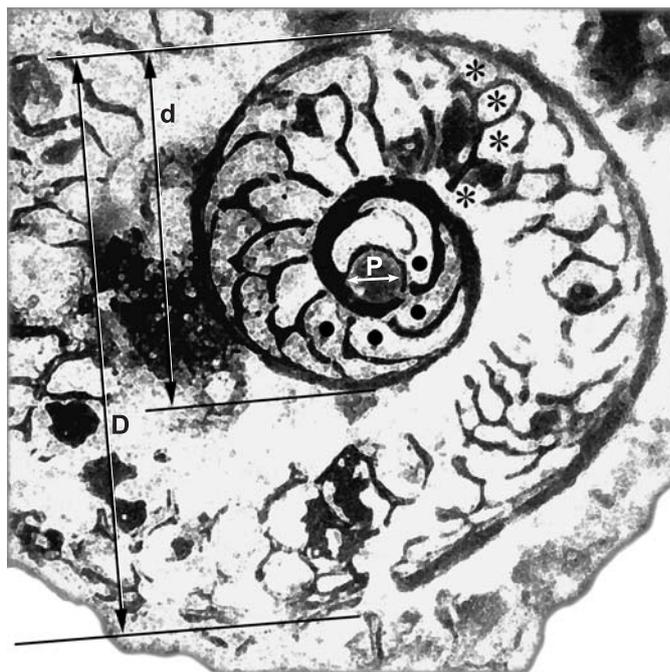
Fig. 2. The measurement system in the equatorial section of megalospheric *Heterostegina* (see also text). Pre-heterosteginid chambers (X) are marked by solid circles, secondary chamberlets in chamber 14 (S) by asterisks.

D: the maximum diameter of the first one and a half whorl (in μm) measured in the same way as d. Because of the lack of space this parameter is not tabulated in Table 1, however it is used to calculate parameter K.

From these direct parameters:

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

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

The 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 are drawn by the Graper (version 3.04) 2-D Graphing System (Golden Software Inc.). 95.44% confidence ellipses are generated by using the formulae (x changes between $x_{mean} - 2x_{s.e.}$ and $x_{mean} + 2x_{s.e.}$):

$$y = f(x) = y_{mean} + 2y_{s.e.} \times \{1-[(x-x_{mean})/2x_{s.e.}]^2\}^{0.5}$$
(upper half-ellipse)

and

$$y = f(x) = y_{mean} - 2y_{s.e.} \times \{1-[(x-x_{mean})/2x_{s.e.}]^2\}^{0.5}$$
(lower half-ellipse),

where x and y are the studied parameters in the horizontal and vertical axes, whereas x_{mean}, $x_{s.e.}$, y_{mean} and $y_{s.e.}$ are the mean and standard error (s.e.) values of the studied parameters for the actual population as given in Table 1.

Materials and methods

Localities

We tried to investigate material from a wide geographical (Fig. 3A) and stratigraphical range. In describing our samples we

Table 1. Statistical data of *Heterostegina* populations elaborated in this work with marking the presence/absence of the central pile (umbo) and of the granulation. Abbreviations: n, number of measured specimens; s.e., standard error.

Parameters: Proloculus diameter P (µm); Degree of operculinid reduction = number of undivided chambers X; "Heterosteginid escalation" = number of chamberlets in chamber 14 S; First whorl diameter d (µm); Index of spiral opening K=100×(D-d)/(D-P). Chamberlets shape columns: rhomboid (rh), hexagonal/rectangular (hr), small rectangular (sr); plus Incomplete septa (is).

Taxon	Locality	P n	P mean ± s.e.	P range	X n	X mean ± s.e.	X range	S n	S mean ± s.e.	S range	d n	d mean ± s.e.	d range	K n	K mean ± s.e.	K range	Central pile	Granulation	rh	hr	sr	is
H. armenica *armenica* — Keçili 3 (TR)		12	151.9 ± 5.3	130 – 185	12	13.00 ± 1.06	7 – 19	12	1.58 ± 0.29	1 – 4	12	822 ± 33	670 – 1020	6	46.2 ± 0.5	45 – 48	+	−	+			+
armenica	Azatek (ARM)	11	155.9 ± 11.5	90 – 205	11	12.00 ± 2.22	2 – 23	11	2.00 ± 0.38	1 – 4	11	971 ± 83	490 – 1450	9	45.8 ± 1.5	38 – 53	+	−	+			+
tigrisensis	Keçili 11 (TR)	32	164.3 ± 4.9	114 – 225	32	6.75 ± 0.63	3 – 20	32	2.97 ± 0.19	1 – 5	31	891 ± 27	629 – 1295	29	45.5 ± 1.0	33 – 56	+	−	+			±
tronenesis — Keçili 11 (TR)		9	98.0 ± 4.1	78 – 110	9	24.11 ± 1.92	15 – 33	9	1.00 ± 0.00	1	9	617 ± 35	537 – 855	9	41.1 ± 2.0	31 – 47	+	−		+		−
tronenesis	Prella 5 (CH)	13	91.9 ± 4.3	72 – 120	13	20.46 ± 1.14	12 – 25	13	1.00 ± 0.00	1	13	529 ± 21	400 – 675	13	40.2 ± 1.7	32 – 54	+	−		+		−
tronenesis	Vic, La Trona (E)	62	99.4 ± 1.9	61 – 132	62	18.61 ± 0.65	9 – 31	62	1.11 ± 0.04	1 – 2	62	592 ± 15	286 – 914	62	44.6 ± 0.7	33 – 56	+	−		+		−
tronenesis	Úrhida 1 (H)	47	91.1 ± 3.1	44 – 140	47	17.87 ± 0.78	7 – 28	47	1.17 ± 0.06	1 – 3	47	592 ± 17	324 – 876	47	40.5 ± 0.7	30 – 50	+	−		+		−
hungarica	Siest (F)	9	87.2 ± 6.2	60 – 120	9	14.56 ± 1.26	10 – 23	9	1.22 ± 0.15	1 – 2	9	579 ± 30	460 – 750	9	40.8 ± 1.0	37 – 48	+	−		+		−
hungarica	Úrhida 2+3 (H)	39	98.9 ± 3.1	55 – 140	39	14.38 ± 0.75	6 – 25	39	1.26 ± 0.09	1 – 3	39	621 ± 17	415 – 880	39	40.5 ± 0.7	29 – 51	+	−		+		−
	Úrhida 2	26	102.3 ± 3.7	70 – 140	26	14.58 ± 0.89	7 – 23	26	1.27 ± 0.10	1 – 3	26	628 ± 22	440 – 880	26	40.5 ± 0.9	33 – 51	+	−		+		−
	Úrhida 3	13	92.1 ± 5.4	55 – 115	13	14.00 ± 1.45	6 – 25	13	1.23 ± 0.17	1 – 3	13	609 ± 30	415 – 785	13	40.5 ± 1.4	29 – 51	+	−		+		−
multifida	Puig Aguilera (E)	27	129.1 ± 4.0	91 – 171	27	9.30 ± 0.65	3 – 16	27	2.11 ± 0.15	1 – 4	27	742 ± 19	463 – 933	26	42.2 ± 0.9	30 – 49	+	−		+		−
multifida	Verona, M. Cavro (I)	28	91.2 ± 2.8	60 – 135	28	8.50 ± 0.57	4 – 17	28	2.00 ± 0.12	1 – 3	28	569 ± 15	442 – 760	28	38.6 ± 0.6	32 – 46	+	−		+		−
multifida	Mossano 2 (I)	15	87.2 ± 2.6	69 – 100	15	8.07 ± 0.57	4 – 12	15	2.00 ± 0.14	1 – 3	15	552 ± 19	438 – 740	15	41.2 ± 1.2	33 – 52	+	−		+		−
helvetica	Prella 4 (CH)	7	102.0 ± 6.1	80 – 120	7	6.43 ± 0.72	4 – 10	7	2.43 ± 0.20	2 – 3	7	629 ± 38	480 – 750	7	41.2 ± 2.6	32 – 50	+	−		+		−
helvetica	Úrhida 4+5 (H)	43	99.5 ± 2.8	55 – 150	43	6.05 ± 0.43	2 – 14	37	2.70 ± 0.14	1 – 4	42	637 ± 16	347 – 870	41	42.9 ± 0.6	34 – 50	+	−		+		−
	Úrhida 4	32	98.3 ± 3.6	55 – 150	32	6.09 ± 0.50	2 – 14	29	2.62 ± 0.16	1 – 4	32	644 ± 17	450 – 870	32	42.4 ± 0.7	34 – 50	+	−		+		−
	Úrhida 5	11	103.1 ± 3.2	84 – 120	11	5.91 ± 0.86	3 – 12	8	3.00 ± 0.27	2 – 4	10	616 ± 40	347 – 800	9	45.0 ± 0.6	42 – 49	+	−		+		−
helvetica	Gschwänt (CH)	43	119.0 ± 3.2	69 – 165	44	5.73 ± 0.35	1 – 12	43	2.72 ± 0.09	1 – 4	44	685 ± 19	427 – 1030	42	40.2 ± 0.7	32 – 54	+	−		+		−
helvetica	Úrhida 6 (H)	33	100.4 ± 2.6	70 – 140	33	5.48 ± 0.32	3 – 10	33	2.94 ± 0.13	2 – 4	33	662 ± 18	510 – 850	33	41.3 ± 1.0	25 – 51	+	−		+		−
helvetica	Úrhida 7 (H)	20	106.4 ± 4.7	80 – 150	20	5.30 ± 0.49	2 – 11	20	3.20 ± 0.19	2 – 5	20	731 ± 35	495 – 970	20	44.3 ± 1.5	25 – 56	+	−		+		−
helvetica	Biralu (ARM)	5	104.8 ± 7.2	84 – 124	5	5.00 ± 1.00	2 – 8	5	2.60 ± 0.24	2 – 3	5	572 ± 26	503 – 629	5	39.7 ± 1.3	36 – 44	+	−		+		−
helvetica	Úrhida 8 (H)	31	104.0 ± 2.7	85 – 155	31	4.74 ± 0.29	2 – 9	31	3.23 ± 0.21	2 – 7	31	640 ± 21	420 – 1000	31	41.7 ± 0.5	34 – 46	+	−		+		−
reticulata	Úrhida 9 (H)	52	122.9 ± 3.1	90 – 190	52	4.12 ± 0.19	2 – 8	52	3.38 ± 0.11	2 – 6	52	810 ± 24	510 – 1350	50	47.1 ± 0.8	35 – 57	+	−		+		−
reticulata	Oberbergli (CH)	13	121.9 ± 4.5	95 – 150	13	3.62 ± 0.40	1 – 6	13	3.00 ± 0.22	2 – 4	12	715 ± 43	505 – 1020	12	43.4 ± 0.8	39 – 48	+	−		+		−
reticulata	Mossano 3 (I)	28	101.6 ± 2.2	85 – 130	28	3.61 ± 0.24	1 – 6	28	3.43 ± 0.14	2 – 5	28	715 ± 25	520 – 1000	28	42.8 ± 0.8	35 – 51	+	−		+		−
reticulata	Vedi (ARM)	7	129.7 ± 8.0	101 – 160	7	3.29 ± 0.71	1 – 6	5	3.40 ± 0.24	3 – 4	5	731 ± 71	571 – 979	4	40.5 ± 2.7	33 – 45	+	−		+		−
mossanensis	Mossano 5+6 (I)	51	128.9 ± 3.6	90 – 240	51	2.49 ± 0.11	1 – 4	41	4.76 ± 0.16	3 – 7	48	854 ± 24	550 – 1320	41	45.0 ± 0.9	32 – 55	+	−			+	−
	Mossano 5	16	129.8 ± 8.7	95 – 240	16	2.50 ± 0.22	1 – 4	12	5.00 ± 0.37	3 – 7	15	880 ± 58	550 – 1320	10	45.5 ± 1.2	39 – 51	+	−			+	−
	Mossano 6	35	128.4 ± 3.5	90 – 185	35	2.49 ± 0.12	1 – 4	29	4.66 ± 0.17	3 – 6	33	842 ± 23	620 – 1160	31	44.8 ± 1.1	32 – 55	+	−			+	−
mossanensis	Şarköy (TR)	62	126.0 ± 3.1	70 – 230	62	2.37 ± 0.10	1 – 5	62	4.26 ± 0.11	3 – 6	62	751 ± 15	420 – 1010	62	44.4 ± 0.6	31 – 56	+	−			+	−
	Şarköy 2	17	133.2 ± 7.1	105 – 230	17	2.35 ± 0.24	1 – 5	17	4.24 ± 0.18	3 – 6	17	753 ± 22	625 – 1010	17	44.6 ± 1.4	34 – 56	+	−			+	−
	Şarköy 4	28	126.4 ± 4.4	70 – 165	28	2.36 ± 0.14	1 – 5	28	4.43 ± 0.16	3 – 6	28	766 ± 26	420 – 1000	28	45.0 ± 0.9	36 – 54	+	−			+	−
	Şarköy A	17	117.9 ± 5.1	90 – 160	17	2.41 ± 0.17	1 – 4	17	4.00 ± 0.24	3 – 6	17	724 ± 28	560 – 950	17	43.1 ± 1.2	31 – 50	+	−			+	−
mossanensis	Verona, C.S. Felice (I)	27	131.3 ± 4.8	90 – 185	27	2.26 ± 0.17	1 – 5	25	4.68 ± 0.19	3 – 6	26	862 ± 31	510 – 1200	24	45.5 ± 1.1	33 – 54	+	−			+	−
	Villa Le Are	16	127.2 ± 5.2	105 – 185	16	2.25 ± 0.23	1 – 5	16	4.50 ± 0.18	3 – 5	16	848 ± 28	710 – 1080	16	45.3 ± 1.4	33 – 54	+	−			+	−
	Villa Devoto	11	137.4 ± 9.2	90 – 185	11	2.27 ± 0.24	1 – 3	9	5.00 ± 0.41	3 – 6	10	885 ± 70	510 – 1200	8	45.9 ± 1.7	38 – 53	+	−			+	−
mossanensis	Úrhida 10 (H)	23	128.3 ± 4.0	85 – 160	23	2.26 ± 0.22	1 – 5	22	4.68 ± 0.21	3 – 6	23	822 ± 29	600 – 1160	23	47.5 ± 1.0	38 – 56	+	−			+	−
mossanensis	Verona, hairpin bend (I)	23	133.0 ± 3.9	100 – 160	23	1.96 ± 0.15	1 – 4	22	4.41 ± 0.18	3 – 6	22	832 ± 35	427 – 1120	19	45.2 ± 1.8	34 – 70	+	−			+	−
mossanensis	Mossano 7 (I)	27	132.8 ± 4.2	70 – 180	27	1.85 ± 0.14	1 – 4	17	4.88 ± 0.28	2 – 7	23	828 ± 37	485 – 1140	20	45.2 ± 1.0	38 – 57	+	−			+	−
italica	Mossano 8 (I)	34	136.9 ± 3.9	90 – 180	34	1.62 ± 0.09	1 – 3	33	5.06 ± 0.16	3 – 7	33	894 ± 23	670 – 1200	30	44.7 ± 1.1	31 – 58	+	−			+	−
italica	Possagno 1 (I)	26	143.0 ± 5.0	93 – 190	26	1.54 ± 0.10	1 – 2	26	5.50 ± 0.21	4 – 8	26	868 ± 23	617 – 1105	23	44.9 ± 0.9	36 – 54	+	−			+	−
italica	Possagno 2 (I)	18	173.1 ± 9.2	99 – 236	18	1.44 ± 0.18	1 – 4	18	6.72 ± 0.31	4 – 9	18	946 ± 45	579 – 1265	14	47.8 ± 1.2	40 – 57	+	−			+	−
italica	Noszvaj, Attila-kút (H)	26	170.1 ± 6.2	130 – 251	26	1.35 ± 0.10	1 – 2	26	5.35 ± 0.17	4 – 8	26	989 ± 34	594 – 1340	24	46.8 ± 1.1	36 – 57	+	−			+	−
H. gracilis	Possagno 1 (I)	14	169.8 ± 7.8	130 – 232	14	1.14 ± 0.10	1 – 2	14	11.50 ± 0.56	9 – 15	14	1148 ± 64	747 – 1646	8	57.4 ± 2.6	49 – 68	±	+			+	−
	Possagno 2 (I)	17	193.2 ± 7.1	135 – 250	17	1.12 ± 0.08	1 – 2	17	12.94 ± 0.64	9 – 18	17	1342 ± 75	952 – 2300	10	51.6 ± 1.7	38 – 57	±	+			+	−
	Biarritz, Cachaou (F)	26	205.6 ± 7.0	150 – 300	26	1.12 ± 0.06	1 – 2	25	13.96 ± 0.68	8 – 24	25	1386 ± 48	890 – 2100	4	53.9 ± 3.1	47 – 60	−	+			+	−
	Benidorm (E)	9	212.2 ± 14.0	155 – 290	9	1.11 ± 0.11	1 – 2	8	13.00 ± 1.55	7 – 19	8	1254 ± 84	950 – 1640	6	52.9 ± 0.7	50 – 55	−	+			+	−

start with Switzerland because of historical reasons, then follow with Italy and Hungary because the Mossano section (I) and Úrhida (H) play an outstanding role in establishing the heterosteginid evolution. The most important characteristics of the samples are summarized in Table 2 (the nomenclature of heterosteginid populations is discussed later, specific and subspecific names are listed here for the completeness of data). The composition of orthophragmine assemblages in samples Mossano 5+6 and 8, Verona, Castel San Felice, Úrhida 10 and Şarköy is tabulated in Table 2 of Less and Özcan (2008). Additional comments on some of the samples are given below.

Switzerland

Oberbergli.—This site is the type locality of Rütimeyer's (1850) *Heterostegina reticulata*. Based on Herb's (1978) description and co-ordinates RS easily found the locality in July 2005 (Fig. 4). Larger foraminifera cannot be isolated, however sometimes they naturally break along the equatorial plane. Unfortunately, Herb's specimens could not be found in the Natural History Museum of Bern, therefore only the four megalospheric forms illustrated in Herb's (1978: figs. 2–4 and 6) could be measured according to our system. Therefore, RS exposed natural equatorial sections on the site itself, and man-

Fig. 3. Locality maps. **A**. Geographical position of the samples studied. **B**. Detailed location of the Mossano samples (Italy) drawn after Papazzoni and Sirotti (1993). **C**. Detailed location of samples from Verona, Castel San Felice (Italy). **D**. Detailed location of the Úrhida samples (Hungary). **E**. Detailed location of the Şarköy samples (Turkey).

aged to obtain ten measurable *Heterostegina reticulata*. The altogether fourteen equatorial sections allow to identify the evolutionary degree of the population (Table 1) and to establish the subspecific characters of *H. reticulata reticulata*.

Gschwänt.—This site is the type locality of Kaufmann's (1867) *Heterostegina helvetica*. The co-ordinates are 655420/ 200720 (they are erroneously reported in Herb 1978) as observed by RS, who managed to find the locality in July 2005. Apart from our recently collected material, Herb's (1978) thin sections of *Heterostegina reticulata* from the site were also found and re-measured in the Natural History Museum of Bern. The less advanced evolutionary degree of *H. reticulata* from Gschwänt as compared to that from Oberbergli (Table 1) seems to be in contradiction with the relative stratigraphic position of the two

sites shown by Herb (1978). However, it can be explained by the redeposition of larger foraminifera of the Wängen Limestone in Gschwänt (thus, planktic data from the sandwiching *Globigerina* marls cannot be considered as relevant for their age) as opposed to their "in situ" position in Oberbergli.

Prella.—The studied samples of Eocene blocks and pebbles are redeposited from the Ternate Formation into Quaternary deposits of glacial origin.

Northern Italy

Our samples come from the Veneto area. We also tried to find *Heterostegina* in the Priabona type-section from where Roveda (1961), Sirotti (1978), and Setiawan (1983) mention them from the so-called *Asterocyclina* beds in the upper part of the

Priabonian. Unfortunately, all these forms turned out to be *Operculina gomezi* with no or no complete secondary septa as figured by Roveda (1961: pl. 18: 9), though under the name of *Heterostegina heterostegina*.

Mossano.—The Mossano section is almost the only one in the Western Tethys crossing the middle/upper Eocene boundary in shallow-marine facies (although a deepening event is recognizable between them). Therefore, it became a classical profile, which has been proposed as a possible "parastratotype" of the Priabonian (Cita 1969).

Just after the road was widened and all the outcrops were clean, Papazzoni and Sirotti (1993) noted two normal faults (Fig. 5) some ten meters before the cross-road to the Olivari locality that caused a repetition of the sequence. Therefore, the boundary between "Calcari nummulitici" and "Marne di Priabona" can be observed twice and our samples Mossano 5 and 6 represent the same basal layer of the Priabona marls containing absolutely the same fauna. Schweighauser (1953) and Herb and Hekel (1973) could not observe this repetition, and therefore, they put the samples Mossano 5 and 6 above each other. As a consequence, *Spiroclypeus* appearing exactly in the basal layer of Marne di Priabona was marked by Schweighauser (1953) already from his "Oberes Lutétien" in bed 31, which corresponds to our sample Mossano 5.

The location of our samples is shown in Fig. 3B. The left side of Fig. 6. shows a composite column from that part of the section, which contains samples Mossano 1 to 8. The middle and upper part of the Priabona marl are not drawn in the column because our samples Mossano 9 to 12 did not contain either *Heterostegina*, or *Spiroclypeus* although the presence of both was marked by Bassi et al. (2000) from their Stop 4 that corresponds to our sample Mossano 10. Here, as in Priabona, "*Heterostegina*" turned out to be *Operculina gomezi*.

Six samples (Mossano 2, 3, 5, 6, 7, and 8) were studied in detail especially for *Heterostegina* (Mossano 1 is represented by hard rock from which no isolated specimens could be obtained whereas Mossano 4 does not contain *Heterostegina*). The six studied samples represent five populations because Mossano 5 and 6 are identical (see above). The mean ±2 s.e. (standard error) of the parameters X, S, and P are figured in Fig. 6. The decrease of the first and the increase of the two others in stratigraphical order can be easily followed in the section. Thus, *Heterostegina* seem to have evolved through the Bartonian–Priabonian boundary very rapidly and were not too sensitive to facies changes in shallow-marine conditions.

Verona.—Both the upper Bartonian and lower Priabonian are outcropping in the vicinity of the city. The upper Bartonian can be found in Monte Cavro, whereas good lower Priabonian outcrops can be found in the northern periphery of the town, at the Castel San Felice (Fig. 3C). Since the Monte Cavro and Castel San Felice are only 3 km from each other, their Bartonian and Priabonian beds can be considered as belonging practically to the same section.

The three samples taken from the Castel San Felice contain almost the same fauna in which orthophragmines and "operculinids" are the main components. *Heterostegina* is practically identical in the two northern samples (Villa Le Are and
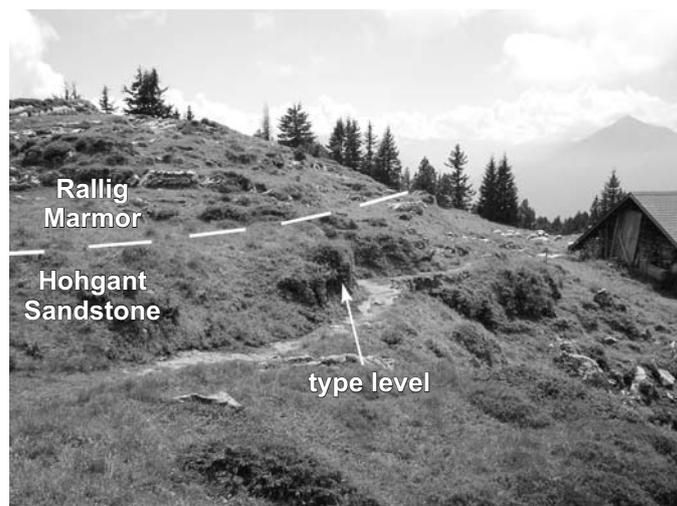
Fig. 4. The type locality of *Heterostegina reticulata* near the chalet Oberbergli (Switzerland). The uppermost Hohgant Sandstone includes here the transitional bed called *Discocyclina* Limestone. Photo: R. Stockar in 2005.

Fig. 5. Normal fault at the road from Mossano to Monte Stria just before the junction with the cross-road to Olivari. Marne di Priabona in the left, Calcari nummulitici in the right side. Photo: C.A. Papazzoni in 1989.

Villa Devoto), however, in the southern sample of the hairpin bend, the number of undivided chambers is somewhat lower. Therefore, in Table 1 the Villa Le Are and Villa Devoto localities are united as Castel San Felice and the hairpin bend sample is tabulated separately.

Possagno.—Sample Possagno 2 (which is stratigraphically about 8 m higher than Possagno 1) is from the type level of Herb's (1978) two new taxa (*Heterostegina reticulata italica*

Table 2. Most important characteristics of the localities investigated.

	Locality	Locality information	Comment in the text	Rock	Information on planktic foraminifera	Information on calcareous nannoplankton	Planktic foramini-feral zone (P)	Calcareous nanno-plankton zone (NP)
Switzerland	Oberbergli	Herb (1978); Fig. 4	+	sandy limestone	not known	Breitschmid (1978)	unknown	18 just above
	Gschwänt	Herb (1978)	+	allodapic limestone	Eckert (1963)	Eckert (1965)	15, not relevant	19, not relevant
	Prella 4	Stockar (1999)	+	bioclastic limestone	Herb (1976); Mancin et al. (2001)	not known	15 from matrix	unknown
	Prella 5							
Italy	Mossano 2	Bassi (2005) with references; Figs. 3B, 5, 6	+	nummulitic limestone	not known		unknown	
	Mossano 3							
	Mossano 5+6			marl	Luciani et al. (2002)		15	18
	Mossano 7							19–20
	Mossano 8						16	
	Verona — Monte Cavro 4	Papazzoni and Sirotti (1995)	+	limestone	not known		unknown	
	Verona — Castel S. Felice — Villa Devoto & Villa Le Are / hairpin bend	Fabiani (1915, 1919); Fig. 3C	+	marl	not known		unknown	
	Possagno 1	Cita (1975); Herb and Hekel (1975): samples 726 (Possagno 1) and 728b-c (Possagno 2)	+	marly limestone	Toumarkine and Bolli (1975)	Proto Decima et al. (1975)	16 (below and above)	20 (below and above)
	Possagno 2							
Hungary	Úrhida 1	Less et al. (2000): Stop 2; Less and Gyalog (2004); Fig. 3D, Table 3	+	marly limestone	not found	not found	unknown	
	Úrhida 2+3							
	Úrhida 4+5							
	Úrhida 6							
	Úrhida 7							
	Úrhida 8							
	Úrhida 9							
	Úrhida 10							
	Noszvaj, Attila-kút	Less et al. (2000): Stop 5	–	marly limestone	not known		unknown	
Spain	Vic, La Trona	Papazzoni and Sirotti (1995): Vic 2; Serra-Kiel et al. (2003): fig. 14, ? 4	–	calcareous siltstone	not known; magneto-stratigraphy: Burbank et al. (1992): C17.2n		~ 15 (lower part)	~ 17 (upper part)
	Puig Aguilera	Romero et al. (1999): PA-117	+	marl	Ferrer (1971)	not known	15	unknown
	Benidorm	Hottinger (1964)	+	marl	not known		unknown	
France	Siest	Less (1987): samples from Siest	–	marly limestone	Sztrákos et al. (1998)	not known	14 or 15	unknown
	Biarritz, (Lou) Cachaou	Boussac (1911): level 9	+	marl	Mathelin and Sztrákos (1993)		16	19–20
Armenia	Azatek	Krashenninikov et al. (1985): bed 9	+	tuffitic sandstone	Krashenninikov et al. (1985)		basal 15, indirect data	18 just below
	Biralu (Landzhar)	Krashenninikov et al. (1985): bed 8	–	marly limestone			15	18
	Vedi	Krashenninikov et al. (1985): bed 29	–	marly limestone			15	18
Turkey	Keçili 3	Özcan et al. (2007)	+	allodapic sandy limestone	Özcan et al. (2007)		14	16, ?reworked
	Keçili 11				not known		unknown	
	Şarköy	Özcan et al. (2007); Fig. 3E	+	marly limestone	Özcan et al. (2007)		unknown	16–21

and *H. gracilis*). He distinguished these two forms first of all by their different surface ornamentation. We have also recognized two surface types, one of them with a central pile and no granulation, characteristic for *H. reticulata italica*, and the other one mostly with no central pile (or sometimes with an indistinct umbo) but with a granulation diagnostic for *H. gracilis*. The internal morphology of the two forms could be distinguished typologically, too, by using the criteria described

Table 2—continued.

Locality	Information on *Nummulites*	Large-sized *Nummulites* (*N. perforatus-biedai, N. millecaput-maximus,* and *N. gizehensis-lyelli* groups)	Reticulate *Nummulites*	*Spiroclypeus* (Less and Özcan 2008)	Subspecies of *Heterostegina reticulata* (topotypes: bold)	Other *Heterostegina* (topotypes: bold)	Orthophragmind zone (OZ) (Less 1998; Less et al. 2000; Özcan et al. 2007; unpublished data)	late Bartonian - SBZ 18	early Priabonian - SBZ 19	late Priabonian - SBZ 20
Oberbergli	Herb (1978)	absent	absent	absent	**reticulata**	–	–	+		
Gschwänt	Herb (1978); own data	absent	absent	absent	**helvetica**	–	–	+		
Prella 4	own data	absent	absent	absent	*tronensis*	–	14	+		
Prella 5		absent	absent	absent	*helvetica*	–	14	+		
Mossano 2	Papazzoni and Sirotti (1995) and own data	*N. biedai*	*N. hormoensis*	absent	*multifida*	–		+		
Mossano 3					*reticulata*			+		
Mossano 5+6		absent	*N.* ex. gr. *fabianii,* very rare	*sirottii*	***mossanensis***	–	14		+	
Mossano 7					*mossanensis*				+	
Mossano 8					*italica*		14/15		+	
Verona — Monte Cavro 4	own data	*N. biedai* just below	*N. hormoensis*	absent	*multifida*	–	–	+		
Verona — Castel S. Felice — Villa Devoto & Le Are		absent	absent	*sirottii*	*mossanensis*	–	14		+	
Verona — Castel S. Felice — hairpin bend			*N. fabianii*		*mossanensis*	–			+	
Possagno 1	Herb and Hekel (1975)	absent	*N. fabianii* (not found by us)	*carpaticus*	*italica*	*gracilis*	–			+
Possagno 2					***italica***	***gracilis***	–			+
Úrhida 1	Less et al. (2000); Less and Gyalog (2004)	*N.* ex. gr. *millecaput-maximus*	absent	absent	*tronensis*	–	14	+		
Úrhida 2+3					***hungarica***	–		+		
Úrhida 4+5					*helvetica*	–		+		
Úrhida 6					*helvetica*	–		+		
Úrhida 7					*helvetica*	–		+		
Úrhida 8					*helvetica*	–		+		
Úrhida 9		absent			*reticulata*	–		+		
Úrhida 10				*sirottii*	*mossanensis*	–			+	
Noszvaj	Less et al. (2000, 2005)	absent	*N. fabianii*	only B-form	*italica*	–	–			+
Vic, La Trona	Papazzoni and Sirotti (1995)	*N. biedai* above	*N. hormoensis*	absent	***tronensis***	–	–	+		
Puig Aguilera	Romero et al. (1999)	absent	absent	absent	*multifida*	–	–	+		
Benidorm	not known	absent	absent	*carpaticus*	–	*gracilis*	–			+
Siest	Less (1987)	*N.* ex. gr. *perforatus*	rare ?*N. hormoensis*	absent	*hungarica*	–	14	+		
Biarritz, (Lou) Cachaou	Boussac (1911); Schaub (1981)	absent	absent	aff. *carpaticus*	–	*gracilis*	–			+
Azatek	Grigoryan (1986)	*N.* ex. gr. *gizehensis*	*N.* aff. *fabianii* (not found by us)	absent	–	***armenica armenica***	–	+		
Biralu (Landzhar)		*N.* ex. gr. *millecaput*		absent	*helvetica*	–	–	+		
Vedi	Grigoryan (1986) and own data		*N. hormoensis*	absent	*reticulata*	–	–	+		
Keçili 3	Özcan et al. (2007)	*N. millecaput, N. gizehensis*	*N. hormoensis*	absent	–	*armenica armenica*	14	+		
Keçili 11		*N. lyelli*		absent	*tronensis*	***armenica tigrisensis***	14	+		
Şarköy		absent	absent	*sirottii*	*mossanensis*	–	14		+	

by Herb (1978). *Heterostegina reticulata italica* bears a somewhat smaller proloculus, a tighter spiral with less dense chambers and rarer subdivisions. Instead, *H. gracilis* has a larger proloculus and a looser spiral with densely spaced chambers subdivided into numerous chamberlets. In its overall morphology *H. gracilis* is much more delicate ("graceful"). The two taxa co-occur also in sample Possagno 1, in which the specimens are much better preserved.
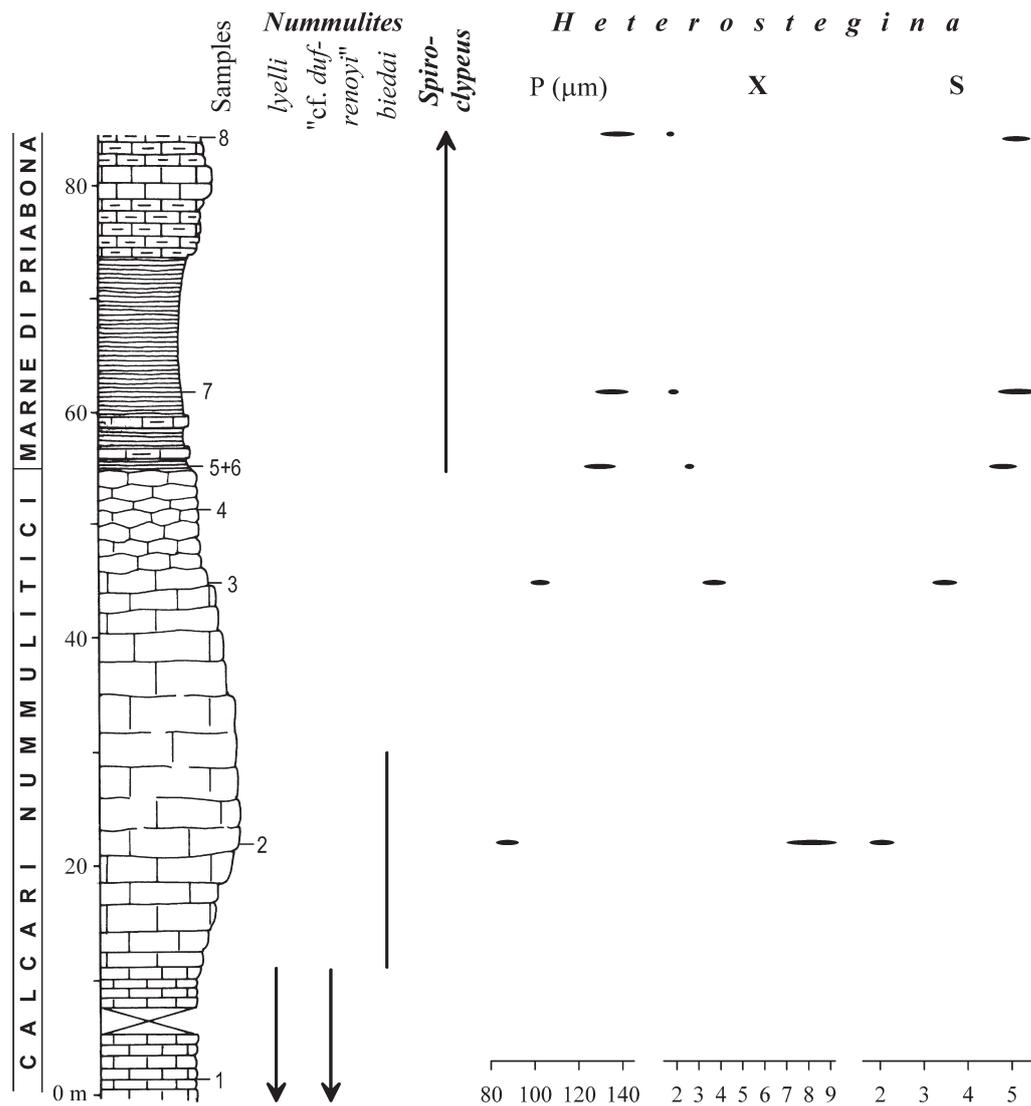
Fig. 6. The evolution of *Heterostegina reticulata* in the Mossano section (drawn after Papazzoni and Sirotti 1993) as reflected in the mean values (±2 s.e.) of three different parameters.

The difference between the two taxa is reflected also in their biometrical parameters (see Table 1 for both samples), especially in the case of S (the number of chamberlets in chamber 14). However, in plotting, e.g., the size of the proloculus (P) against parameter S (Fig. 7), the segregation of the two taxa is by far not self-evident, which indicates their close relationship. This is emphasized also by the usual presence of a central pile in the specimens from sample Possagno 1.

Comparing the evolutionary parameters of both *Heterostegina reticulata italica* and *H. gracilis* from the two samples, they (especially P and S) are clearly less advanced in sample Possagno 1 than in Possagno 2 (see also Table 1), well in accord with their relative position in the profile that is manifested also in the disappearance of the central pile of *H. gracilis* between the two levels.

Hungary

Úrhida (W Hungary).—Unfortunately, the outcrops in Úrhida are small and isolated, moreover, several of them were only temporarily exposed due to canalization and construction works and, therefore, most of them have already been lost. Faults are also very common in this area, and therefore, in most cases, the stratigraphic relationship between the outcrops is not directly visible. Nevertheless, the genus *Heterostegina* is abundant and very well preserved in Úrhida, several evolutionary stages are present and all the occurrences represent the same, outer shelf facies.

Ten samples have been studied from Úrhida; the localities are shown in Fig. 3D. They are numbered according to the evolutionary degree of their *Heterostegina* populations (Table 1). Since the parameters in samples Úrhida 2 and 3 and also in Úrhida 4 and 5 are very similar, these samples are jointly discussed. In Less et al. (2000) and in Less and Gyalog (2004) our samples bear different names, moreover the numbering of houses in the Petőfi Street changed in 2004. Therefore, in Table 3, we identify these different denominations with each other. The direct stratigraphic relationship could be observed

between samples Úrhida 1 and 3, the latter being about 1.5 m higher, and between Úrhida 7 and 9 where the last can be found approximately 2 m higher than Úrhida 7. Finally, sample Úrhida 8 lies about 1.5 m above Úrhida 6.

The rapid evolution of *Heterostegina reticulata* populations from sample 1 to 10 (Table 1), reflected in the evolutionary progress of the parameters X and S, is definitively in accord with the direct (the superpositions mentioned earlier) and indirect (see the faunal change in Table 2) stratigraphical data, and is synchronous with what is present in the Mossano section and in Verona. Especially, the appearance of *Spiroclypeus sirottii* of the same evolutionary degree (see Less and Özcan 2008) at the same evolutionary level of the *H. reticulata*-lineage in all these localities is really striking.

Spain

Puig Aguilera (NE Spain).—We could not distinguish the two morphotypes of *Heterostegina reticulata* indicated by Romero et al. (1999) from this locality and found a normal, homogenous population of *H. reticulata multifida*. The relatively large proloculus (see Table 1) is perhaps an effect of the relatively deeper depositional environment of the locality reflected also in the composition of the assemblage of larger foraminifera.

Benidorm (SE Spain).—Sample E 81 from where few *Heterostegina* have been studied was collected by Lukas Hottinger (Basel) in 1962 from the outcrop of the coastal road leading from Benidorm to Alicante. The detailed description of the outcrop is missing, since it had already disappeared few years later by the explosive development of the tourism along the coast. Because of the few specimens of *Heterostegina* available, we also measured Hottinger's (1977) figures, and these data are also used in the statistical summary of the sample tabulated in Table 1.

France, SW Aquitaine

Biarritz, Lou Cachaou.—We studied sample SCH 54123, which was collected by Hans Schaub and is stored in the Naturhistorisches Museum of Basel (Switzerland).

Table 3. Identification of different names and numberings with the location of the Úrhida samples.

Sample	Actual name	in Less and Gyalog (2004)	in Less and others (2000)
Úrhida 1	Kossuth Str. 60., lower	Kossuth Str. 60., lower	–
Úrhida 2	Kossuth Str. 50.	Kossuth Str. 50.	Other outcrop with *N.* "*millecaput*"
Úrhida 3	Kossuth Str. 60., upper	Kossuth Str. 60., upper	–
Úrhida 4	Petőfi Str. 102–104.	Petőfi Str. 42–44., lower	Stop 2A
Úrhida 5	Borehole Úrhida 1, 284–285 m	Úrhida Ú–1, 284.0–285.0 m	–
Úrhida 6	Petőfi Str. 120., lower	–	–
Úrhida 7	Petőfi Str. 106.	Petőfi Str. 42–44., middle	–
Úrhida 8	Petőfi Str. 120., upper	–	–
Úrhida 9	Petőfi Str. 108.	Petőfi Str. 42–44., upper	–
Úrhida 10	Jókai Str. 7.	Jókai Str. 7.	Stop 2B
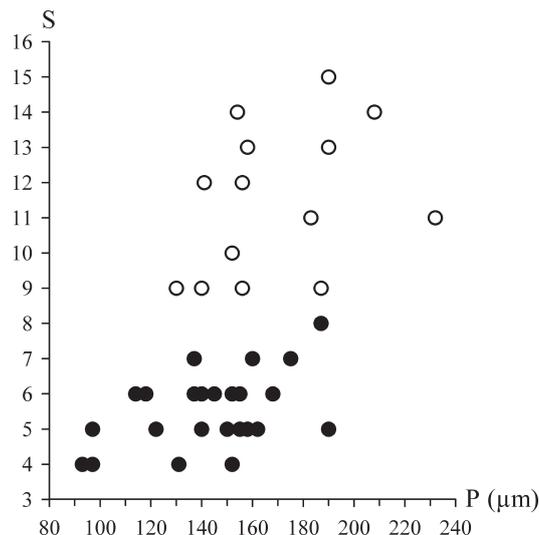
Fig. 7. Distribution of heterosteginid specimens from sample Possagno 1 on the P–S (proloculus diameter versus density of chamberlets in chamber 14) bivariate plot. Solid circles, *Heterostegina reticulata*; open circles, *H. gracilis*.

Armenia

Three samples containing *Heterostegina* have been collected by Susanna M. Grigoryan and Tibor Kecskeméti in 1989 from three different key-sections of Armenia.

Azatek.—The studied sample was collected from the type level of *Grzybowskia armenica*, a species introduced by Grigoryan (1986). These *Heterostegina* externally bear a central pile but lack granulation as *H. reticulata*, although they seem somewhat thinner than the latter. At the same time, internally they clearly differ from any of the evolutionary stages of this species found in the localities discussed above. Secondary chamberlets are strongly irregular, secondary septa are very often incomplete. In terms of the "*reticulata*"-lineage, they would correspond to the "*tronensis*" level. Meanwhile the evolutionary parameters (X and S, see Table 1) would refer it to the level between "*hungarica*" and "*multifida*" but the size of the proloculus would correspond to the level of "*italica*". Moreover, since we have found many specimens corresponding to Grigoryan's (1986) "*armenica*" also in the Keçili section (Turkey), this species can be considered as a valid one, different from *H. reticulata*. Nevertheless, in having accepted Hottinger's (1977) arguments on incorporating genus *Grzybowskia* into *Heterostegina*, it has to be called *H. armenica*. Since in the upper part of the Keçili section we have found a more advanced evolutionary stage of the species—above the representatives (from the middle part of the profile) similar to those from Azatek—it can be segmented into two chronosubspecies. Therefore, the less advanced one from Azatek is called *H. armenica armenica*.

Turkey

The localities are described in detail and figured by Özcan et al. (2007) where the complete list of fossils can also be found.

Keçili (Elazığ region, eastern Anatolia).—Larger foraminifera occur in the Bartonian part of the section. *Heterostegina* is still missing from its lower part belonging to the lower Bartonian

(SBZ 17 by Serra-Kiel et al. 1998 and OZ 13 by Less 1998), however *Operculina* ex. gr. *roselli–gomezi* is already present here. The *Nummulites fabianii*-group is represented here by *N. garganicus*.

Heterostegina occurs in all the samples of the middle and upper parts of the profile. They, however, have been examined in statistical quantity from two samples. The specimens from sample Keçili 3 (the middle part of the section) are very similar to those from Azatek by their rather thin tests, by the morphology of the chamberlets and by the biometrical parameters (see Table 1). Thus, the population can be determined as *H. armenica armenica*.

By their internal morphology, *Heterostegina* specimens from sample Keçili 11 (the upper part of the section) can be separated typologically into two groups. Most of the specimens belong to *H. armenica*, however with somewhat less irregular (than in Azatek and Keçili 3) chamberlets almost lacking incomplete secondary septa. The proloculus is also somewhat larger and the number of operculinid chambers is significantly less, than in the other two samples (see Table 1). Therefore, this form with a moderately thin test is considered as a more advanced form called *H. armenica tigrisensis*. At the same time a few specimens from Keçili 11 (externally similar to the others) have significantly smaller proloculi and many operculinid chambers before the appearance of the first subdivided chamber. The chamberlets are strongly polygonal but less irregular than those of the specimens belonging to *H. armenica*. No incomplete septa have been found. By all their characteristics (see Table 1) these specimens can be already placed into the *H. reticulata*-lineage as its least advanced member called *H. reticulata tronensis*. In the P–X bivariate plot (Fig. 8) the segregation of the two taxa is not unambiguous although their typological distinction is rather unproblematic in most cases.

Şarköy (Tekirdag region, Thrace Basin, Europe).—The genus *Heterostegina* has been found in all samples (Şarköy 2, 4, and 9) studied by Özcan et al. (2007), however they are examined in statistical quantity only from the first two samples. Later, we collected one more sample (Şarköy A) from the other side of the small valley (Fig. 3E). Since both the *Heterostegina* and the associated larger foraminifera are almost identical in all three samples (see Table 1) they can be jointly discussed. *Spiroclypeus sirottii* sp. nov. is associated in Şarköy with *Heterostegina reticulata* at the same evolutionary stage (*H. r. mossanensis*) as in the basal Priabonian of Mossano (samples 5 and 6), Verona (Castel San Felice and hairpin bend) and in sample Úrhida 10, all having the same age.

Preparation and photographing

We have studied isolated specimens (except the specimens from Oberbergli that were cut to expose the equatorial plane) collected mostly from marls and marly limestones. Thin sections were prepared by RS for specimens from Prella and by EÖ for specimens from Keçili and Şarköy and partly from Vic, La Trona, and Gschwänt. In most cases GL opened the equatorial section by the splitting method described for orthophragmines (Less 1981, 1987). The great advantage of this method is that these sections are perfectly oriented because they are broken
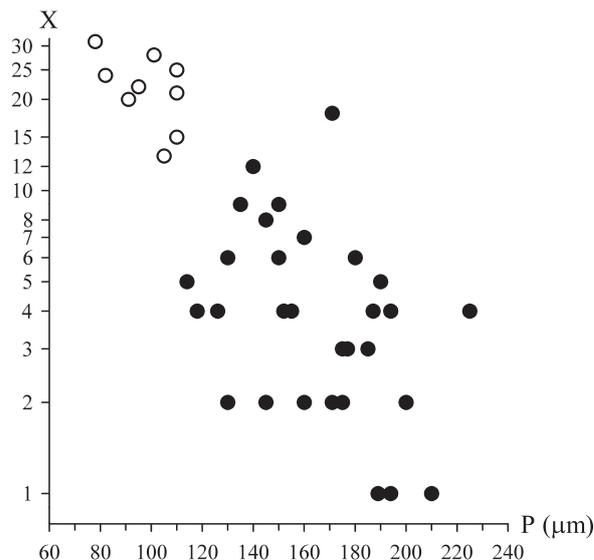
Fig. 8. Distribution of heterosteginid specimens from sample Keçili 11 on the P–X (proloculus diameter versus number of undivided post-embryonic chambers) bivariate plot (X is on logarithmic scale). Solid circles, *Heterostegina armenica*; open circles, *H. reticulata*.

along the weakest plane of the shell; thus the stolons are also exposed. Instead, thin-sections are not always perfectly oriented (also because the equatorial plane is often not a perfect one), therefore sometimes not all chamberlets are easily identifiable. This may cause some biases between the counts in split and thin-sectioned specimens from the same population.

Specimens were photographed mostly in incident light whereas photos of the thin-sections were made in transmitted light. In the six photoplates the enlargement is generally ×20 with two exceptions. The magnification of all the external views is ×10 whereas that of all the equatorial sections of B-forms is ×50.

Evaluation of parameters

The presence/absence of granulation proved to be an excellent qualitative feature in order to distinguish *Heterostegina gracilis* with granules from *H. reticulata* (and also *H. armenica*) lacking them as stated by Herb (1978). Central piles are diagnostic for *H. armenica* and *H. reticulata*. No central pile is present in *H. gracilis*, with the exception of sample Possagno 1, where this feature, observed in several cases, can be interpreted as a somewhat primitive stage of the species (reflected also in the numerical parameters as described below). This observation allows us to refine the diagnosis of this species as compared to Herb's (1978) strict statement on their absence.

The statistical summary of biometrical data per population (Table 1) shows that the greatest differences between populations can be found in parameters X and S. Their mean values at the 95% confidence level are plotted in Fig. 9. Five important consequences can be deduced.

(1) The populations of *Heterostegina gracilis* are clearly separate from those of *H. reticulata* and *H. armenica* using parameter S.
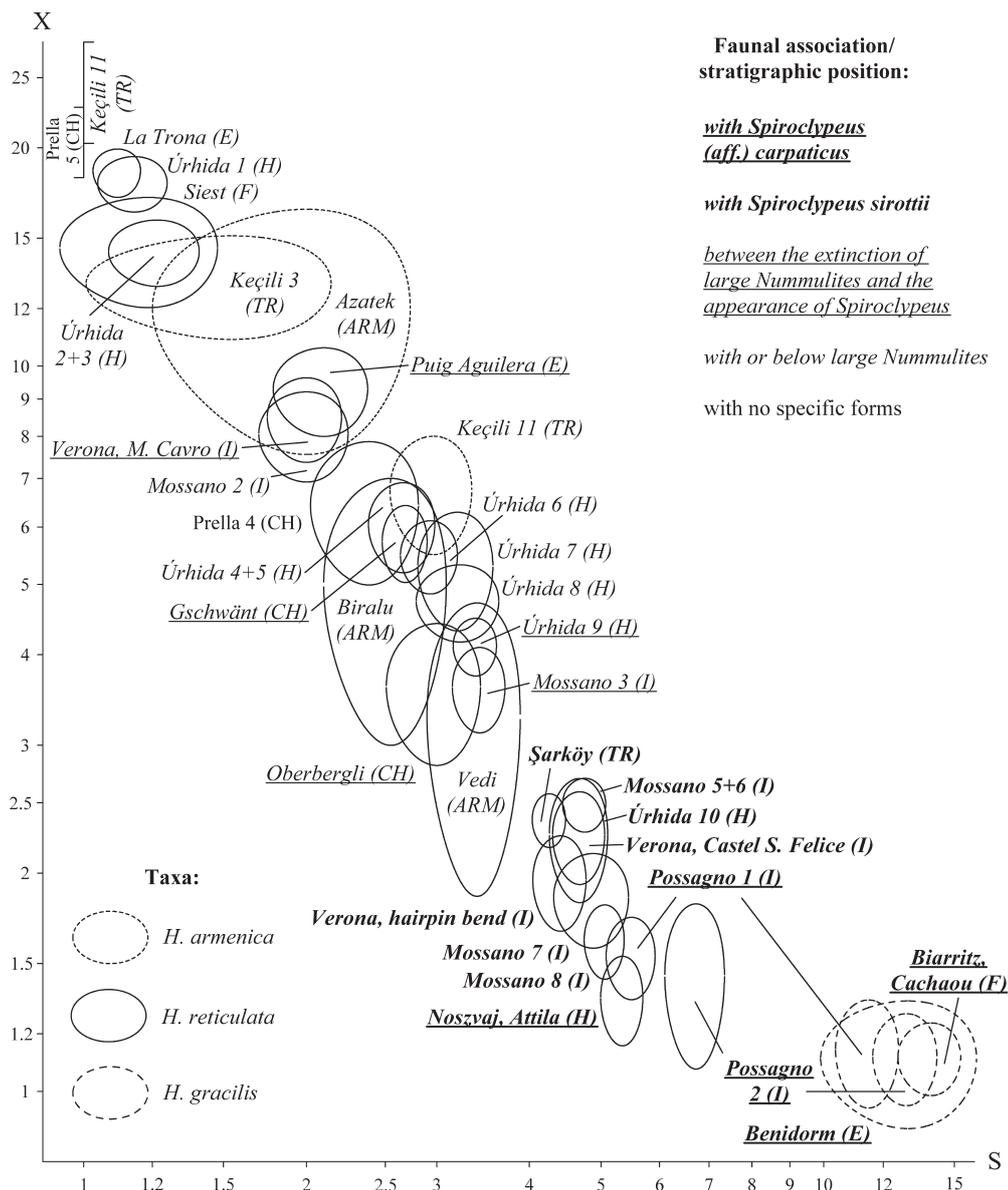
Fig. 9. Distribution of the Eocene heterosteginid populations (mean values at the 95.44% confidence level) on the S–X (density of chamberlets in chamber 14 versus number of undivided post-embryonic chambers) bivariate plot (both scales are logarithmic).

(2) The populations of both *H. reticulata* and *H. armenica* form a continuous chain each.

(3) The populations are arranged according to their associated, age-determining larger foraminiferal fauna. Those occurring with large-sized *Nummulites* (with test diameter of the B-forms over 15 mm) plot in the upper left quarter and in the centre of Fig. 9; those with neither large-sized *Nummulites*, nor *Spiroclypeus* in the centre; those with *Spiroclypeus sirottii* a little bit below and to the right of the centre. It is worth noting that the parameters of *Heterostegina*, as well as those of *Spiroclypeus*, are very consistent within populations. The *Heterostegina* populations occurring with *Spiroclypeus carpaticus* plot in the extreme lower right corner of Fig. 9.

(4) Populations from samples whose stratigraphic superposition can be directly observed in the field are arranged regularly in the plot, i.e., the "upper" populations can be found always below and to the right of the "lower" populations. These are the succession of samples Mossano 2, 3, 5+6, 7, and 9 in superposition, the couples of Possagno 1 and 2, Úrhida 1 and 3, 6 and 8, 7 and 9, and finally Keçili 3 and 11.

5. Thus, the decrease of the number of operculinid chambers (X) and the increase of the number of chamberlets in chamber 14 (S) have a great stratigraphic significance.

Nevertheless, the bivariate plot of Fig. 9 does not help in separating *Heterostegina armenica* from *H. reticulata*. Therefore, in Fig. 10 we plotted the mean values of X against those of the size of the proloculus (P) by population, once again at the 95% confidence level. In this bivariate plot *H. armenica* is distinguished from *H. reticulata* despite the closeness of the population from Puig Aguilera to the *H. armenica*-cluster. Based on the quite regular arrangement of secondary chamberlets, however, this population clearly belongs to *H. reticu-*
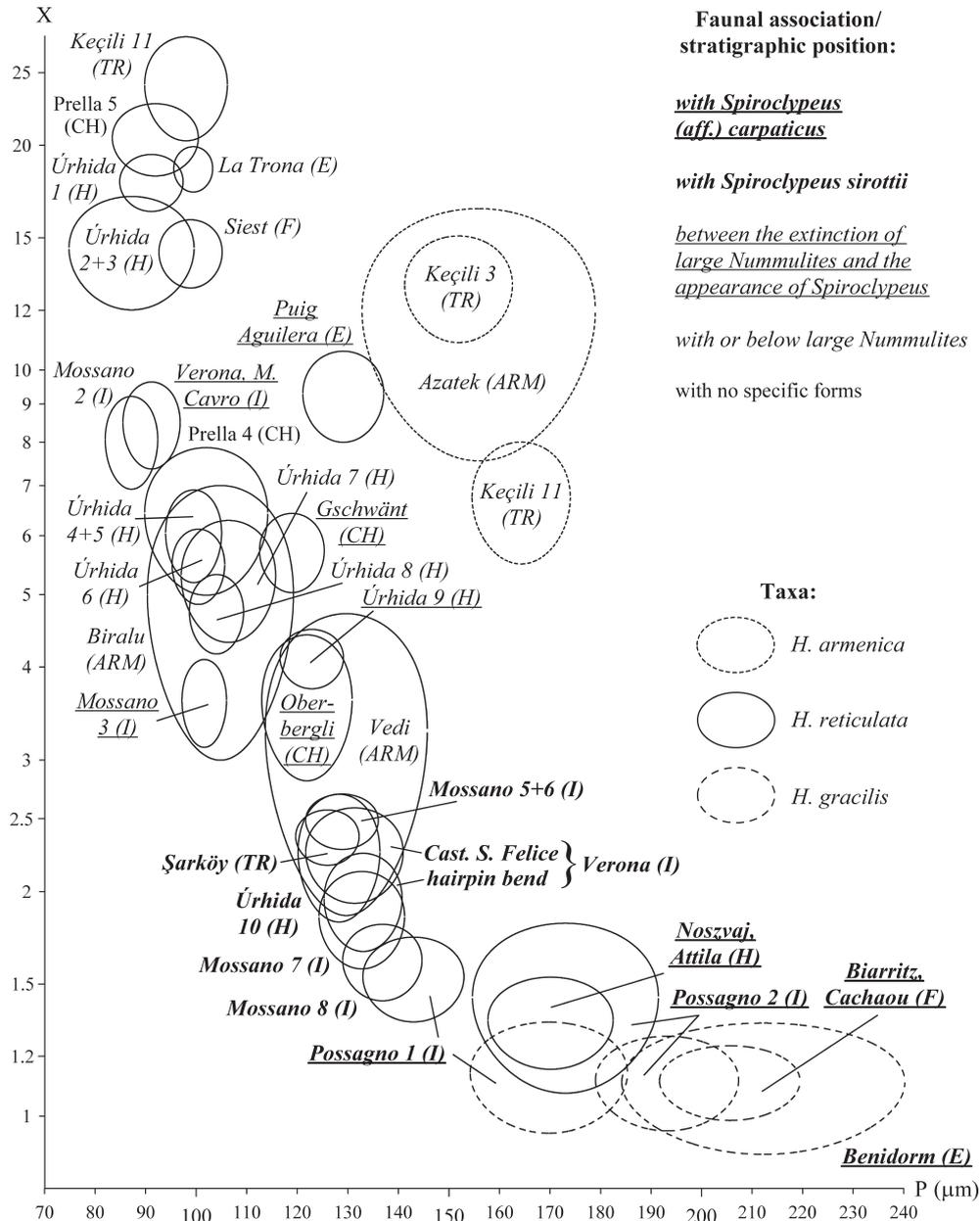
Fig. 10. Distribution of the Eocene heterosteginid populations (mean values at the 95.44% confidence level) on the P–X (proloculus diameter versus number of undivided post-embryonic chambers) bivariate plot (X is on logarithmic scale)

lata. At the same time, in this representation, the populations of *H. gracilis* are far less isolated from those of the most advanced *H. reticulata* than in Fig. 9.

From Fig. 10 almost the same consequences can be deduced as from Fig. 9, e.g., the almost continuous chain of the *H. reticulata*-populations, the regularity of the arrangement of populations according to their larger foraminiferal associations and the more advanced evolutionary degree of the populations coming from the "upper" samples as compared to those from the "lower" samples.

At the same time, it is clear from Fig. 10 (and also from Table 1) that the general increase of the size of the proloculus (P) of the *H. reticulata*-chain is a far less rapid and reliable evolutionary trend than the change in X and S. This difference is

even more valid for parameter d, the diameter of the first whorl, which is in strong positive correlation with P (see Table 1); however it can be measured less precisely. A good summary on the environmental and probably the biological control of the proloculus size of larger foraminifera with ample references can be found in Beavington-Penney and Racey (2004).

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 tends to become looser in time) within the *H. reticulata*-chain. The existence of two simultaneously running evolutionary lineages in the Priabonian— one with tightly coiled and another one with loose spiral—suggested by Hottinger (1977) could not be proven, however, *H. gracilis* has indeed a significantly looser spire as compared to *H.*

reticulata (see also Table 1). In general, there is a slight positive correlation between the size of the proloculus (P) and the laxity of the spiral.

Since parameters d and K are shown to be not really relevant in distinguishing species and characterizing their evolution, they (together with the measurement of parameter D) turned out to be unnecessary.

The arrangement and shape of the secondary chamberlets change quite reliably. The most primitive type with a quite irregular arrangement of rhomboid chamberlets, often with incomplete septa, is characteristic for *Heterostegina armenica*, especially for *H. a. armenica*, the more primitive subspecies from Keçili 3 and Azatek. A continuously improving regularity in the arrangement of the chamberlets, accompanied by the change of the shape from rhomboid to almost rectangular, can be recognized during the evolutionary track of *H. reticulata*. Finally, regularly arranged delicate rectangular chamberlets are characteristic for *H. gracilis*.

As visible from the photos of Figs. 11–15, no increase in the size of the adult test can be observed during the whole heterosteginid evolution. Moreover, *H. gracilis* is definitively smaller than the late Bartonian forms. No difference in the test size could be observed between the A- and B-forms, either, although the latter were seldom found. Parameter X (defined as for the A-forms) could be counted in six microspheric specimens from different samples. These specimens suggest a trend to the reduction in the number of undivided chambers (Table 4) also for the microspheric forms.

Systematic paleontology

Two of the three species of Western Tethyan Eocene involute *Heterostegina* are subdivided into chronosubspecies. To avoid repetitions only their common characteristics are discussed in the description of the species, while the partial features only in the subspecies description. The numerical characteristics of the equatorial section of the A-forms for each taxon are summarized in Table 5, parts of which are to be considered as belonging to their description. The classification of particular populations in the different taxa is reported in Table 1. Stratigraphical ranges of particular taxa are given in advance, in accord with the refined shallow benthic zonation (see below).

Order Foraminiferida Eichwald, 1830

Family Nummulitidae de Blainville, 1827

Genus *Heterostegina* d'Orbigny, 1826

Type species: *Heterostegina depressa* d'Orbigny, 1826, Recent, St. Helena Island.

Remarks.—Based on the qualitative and quantitative parameters evaluated above, the Western Tethyan late Bartonian to Priabonian *Heterostegina* can be grouped into three species. Due to the joint occurrence of the most advanced *H. armenica* and the most primitive *H. reticulata* in sample Keçili 11 and also to that of the most advanced *H. reticulata* and *H. gracilis* in samples Possagno 1 and 2, the stratigraphical succession of these species could be inferred.

Table 4. Number of undivided chambers (X) before the first segmented chamber in the B-forms of *Heterostegina reticulata* (the first two chambers are not counted).

Sample	Subspecies	Illustration	X
Siest	*hungarica*	Fig. 12E	37
Úrhida 9	*reticulata*	Fig. 13O	29
Mossano 3	*reticulata*	Fig. 14D	25
Mossano 6	*mossanensis*	Fig. 14J	20
Şarköy 4	*mossanensis*	not figured	21
Şarköy 4	*mossanensis*	not figured	18–20

Heterostegina armenica and especially *H. reticulata* form evolutionary lineages. Their intraspecific development can be characterized most effectively by the reduction of the undivided, post-embryonic chambers (X). Therefore they are subdivided into chronosubspecies by arbitrary limits of the mean values of this parameter. Table 6 illustrates the results of the t-test on parameter X in comparing the neighboring populations according to parameter X, in decreasing order. It demonstrates that the lineages are segmented at its weakest points, where p(t)-values are the lowest as compared to the neighboring values. The density of the segmentation is in accord with Drooger's (1993: 30) proposals.

Heterostegina armenica (Grigoryan, 1986)
Fig. 11A–I, M.

Emended diagnosis.—Involute, flat biconvex test with oval contour, central pile and slightly sigmoid septal sutures passing into an irregular sutural network in the edges. The proloculus is relatively large; the chamberlets (often with incomplete secondary septa) are rather irregularly arranged and characteristically polygonal. The number of undivided chambers is subjected to nepionic acceleration. Based on this, the species is subdivided into two chronosubspecies as follows:

H. armenica armenica $X_{mean} > 8$
H. armenica tigrisensis ssp. nov. $X_{mean} < 8$

Description

External features (Fig. 11A$_2$, M).—The test is involute, biconvex, flat and medium-sized (3–6 mm) with oval contour. The distinct central pile is somewhat eccentrically placed. Septal sutures are slightly sigmoid, passing into a rather irregular hexagonal network of primary and secondary septal sutures in the peripheral zone of the adult whorls.

Internal features.—The equatorial section of A-forms: The relatively large proloculus is followed by the second chamber of similar size and then by a loosely coiled spiral. The chambers are high, densely spaced and almost evenly arched. The first appearance of chamberlets is stratigraphically controlled; undivided chambers may often reappear in the neanic stage of growth. The arrangement of the chamberlets is characteristically irregular, though becoming more regular in both higher onto- and phylogenetic levels. Their shape is also irregularly polygonal; the secondary septa are often incomplete, especially in the early stage of phylogenesis. Numerical features are tabulated in Table 5.

Microspheric specimens have not been found yet.

Table 5. Numerical characteristics in the equatorial section of the A-forms of heterosteginid taxa. P_{mean}, X_{mean}, etc. indicate the mean values of the given parameter for particular populations.

Taxa / parameters		Diameter of proloculus		Number of undivided post-embryonic chambers		Number of chamberlets in chamber 14		Diameter of the first				Index of spiral opening $K=100\times(D-d)/(D-P)$	
								one whorl		1.5 whorls			
		P (μm)	P_{mean} (μm)	X	X_{mean}	S	S_{mean}	d (μm)	d_{mean} (μm)	D (μm)	D_{mean} (μm)	K	K_{mean}
Heterostegina	*armenica*	90–225	130→175	2–23	5.5←16	1–5	1→3.4	490–1450	750–1140	910–2200	1220–1750	33–56	43–48
	armenica armenica	90–205	130–175	2–23	8–16	1–4	1→2.8	490–1450	750–1140	910–1645	1220–1750	38–53	43–49
	armenica tigrisensis	115–225	155–175	3–20	5.5–8	1–5	2.6–3.4	630–1300	830–950	160–2200	1410–1630	33–56	43–48
	reticulata	45–250	75→190	1–33	1.1←28	1–9	1→7.2	325–1350	485→1060	500–2430	750→1830	25–60	37→50
	reticulata tronensis	45–140	80–105	7–33	17–28	1–2	1–1.25	285–915	485–625	500–1540	750–1115	30–56	37–47
	reticulata hungarica	55–140	75–105	6–25	11–17	1–3	1.05–1.6	415–880	520–655	680–1610	820–1055	29–51	39–43
	reticulata multifida	60–170	80–135	3–17	7.2–11	1–4	1.6–2.4	440–935	515–780	690–1470	820–1240	30–52	37–44
	reticulata helvetica	55–165	90–125	1–14	4.4–7.2	1–7	2–3.5	345–1030	540–800	570–1875	780–1400	25–56	37–47
	reticulata reticulata	85–190	95–140	1–8	2.8–4.4	2–6	2.6–3.9	505–1350	630–860	765–2430	970–1520	33–58	38–49
	reticulata mossanensis	70–240	120–140	1–5	1.7–2.8	3–7	3.9–5.1	420–1320	720–925	665–2300	1200–1600	31–60	43–49
	reticulata italica	90–250	130–190	1–4	1.1–1.7	3–9	4.7–7.2	580–1340	800–1060	100–2300	1360–1830	31–58	43–50
	gracilis	130–300	155–225	1–2	1–1.4	7–24	10–16	750–2300	1020–1480	1560–3600	1950–3300	38–68	48–60

Table 6. p[t]-values of parameter X in the case of *Heterostegina armenica* and *H. reticulata* and of parameter S in the case of *H. gracilis* for the most similar neighboring populations. Populations from samples Prella 4, Biralu and Vedi are not taken into consideration because of their very low number of specimens. Normal lettering for p[t] <0.05, underlined for p[t] = 0.05–0.20, bold for p[t] = 0.20–0.50, and bold underlined for p[t] >0.50.

Species	sub-species	sample	p[t(X)]
H. armenica	*armenica*	Keçili 3	**0.691**
		Azatek	0.043
	tigrisensis	Keçili 11	

Species	sub-species	sample	p[t(X)]
Heterostegina reticulata	*tronensis*	Keçili 11	0.125
		Prella 5	0.173
		La Trona	**0.469**
		Úrhida 1	0.041
	hungarica	Siest	**0.909**
		Úrhida 2+3	0.000
	multifida	P. Aguilera	**0.360**
		M. Cavro	**0.594**
		Mossano 2	0.008
	helvetica	Úrhida 4+5	**0.567**
		Gschwänt	**0.611**
		Úrhida 6	**0.754**
		Úrhida 7	

Species	sub-species	sample	p[t(X)]
Heterostegina reticulata	*helvetica*	Úrhida 7	**0.336**
		Úrhida 8	0.075
	reticulata	Úrhida 9	**0.289**
		Oberbergli	**0.987**
		Mossano 3	0.000
	mossanensis	Mossano 5+6	**0.417**
		Şarköy	**0.567**
		Verona, Felice	**0.995**
		Úrhida 10	**0.257**
		Verona, hairpin	**0.607**
		Mossano 7	0.168
	italica	Mossano 8	**0.567**
		Possagno 1	**0.658**
		Possagno 2	**0.640**
		Noszvaj	

Species	sample	p[t(S)]
H. gracilis	Possagno 1	0.103
	Possagno 2	**0.973**
	Benidorm	**0.583**
	Biarritz, Cachaou	

Axial section (Fig. 11E): The test is flat, biconvex and involute with a flaring last whorl. The central pile is distinct. The subdivision of the chambers into chamberlets is hardly visible.

Remarks.—The forms described above can be identified with Grigoryan's (1986) *Grzybowskia armenica* since we could investigate the material from Azatek, the type locality of this species. Its taxonomic validity is confirmed, since *Heterostegina armenica* differs from *H. reticulata* with similar degree of nepionic acceleration by the much less regular arrangement and shape of secondary chamberlets. The distinction is also confirmed by the significantly larger proloculus of *H. armenica* in comparison with the coeval *H. reticulata* (see also Fig. 10) as well as by the joint occurrence of the most advanced *H. armenica* (i.e., *H. a. tigrisensis*) with the most primitive *H. reticulata* (i.e., *H. r. tronensis*) in sample Keçili 11 where they could be separated biometrically (see also Fig. 8). Moreover, *H. armenica* is definitely flatter than *H. reticulata*.

Heterostegina armenica occurs together with the *Operculina gomezi*-group in all the localities known so far. The latter differs from *H. armenica* only in lacking complete secondary chamberlets and in having a significantly smaller (about 100 μm) proloculus. Since this involute *Operculina* appears first in lower stratigraphical levels than *H. armenica* (e.g., in the Keçili section, see Özcan et al. 2007), early members of the *O. gomezi* group may be considered as possible ancestors of *H. armenica*. The intraspecific evolution of *H. armenica* is expressed significantly in the decrease of parameter X and in the increasing density of the chamberlets (parameter S). The size of the proloculus (P) increases less distinctly. *H. armenica* either became extinct with no successors or gave rise to *H. reticulata*.

Fig. 11. Late Bartonian *Heterostegina* from different Western Tethyan localities (I). **A–F**. *Heterostegina armenica armenica* (Grigoryan, 1986), early late Bartonian, SBZ 18 A. **A**, **B**, **F**. Azatek (Armenia), A-form, topotypes. Equatorial sections (**A₁, B, F**), external view (**A₂**), MÁFI E. 9505 (**A**), MÁFI E. 9506 (**B**), MÁFI E. 9507 (**F**). **C–E**. Keçili 3 (E Turkey), A-forms. **C**, **D**. Equatorial sections, ITU O/KEÇ.3-73 (**C**), ITU O/KEÇ.3-64 (**D**). **E**. ITU O/KEÇ.3-67, axial section. **G–I**, **M**. *Heterostegina armenica tigrisensis* ssp. nov., Keçili 11 (E Turkey), middle late Bartonian, SBZ 18 B. **G–I**. A-form, equatorial →
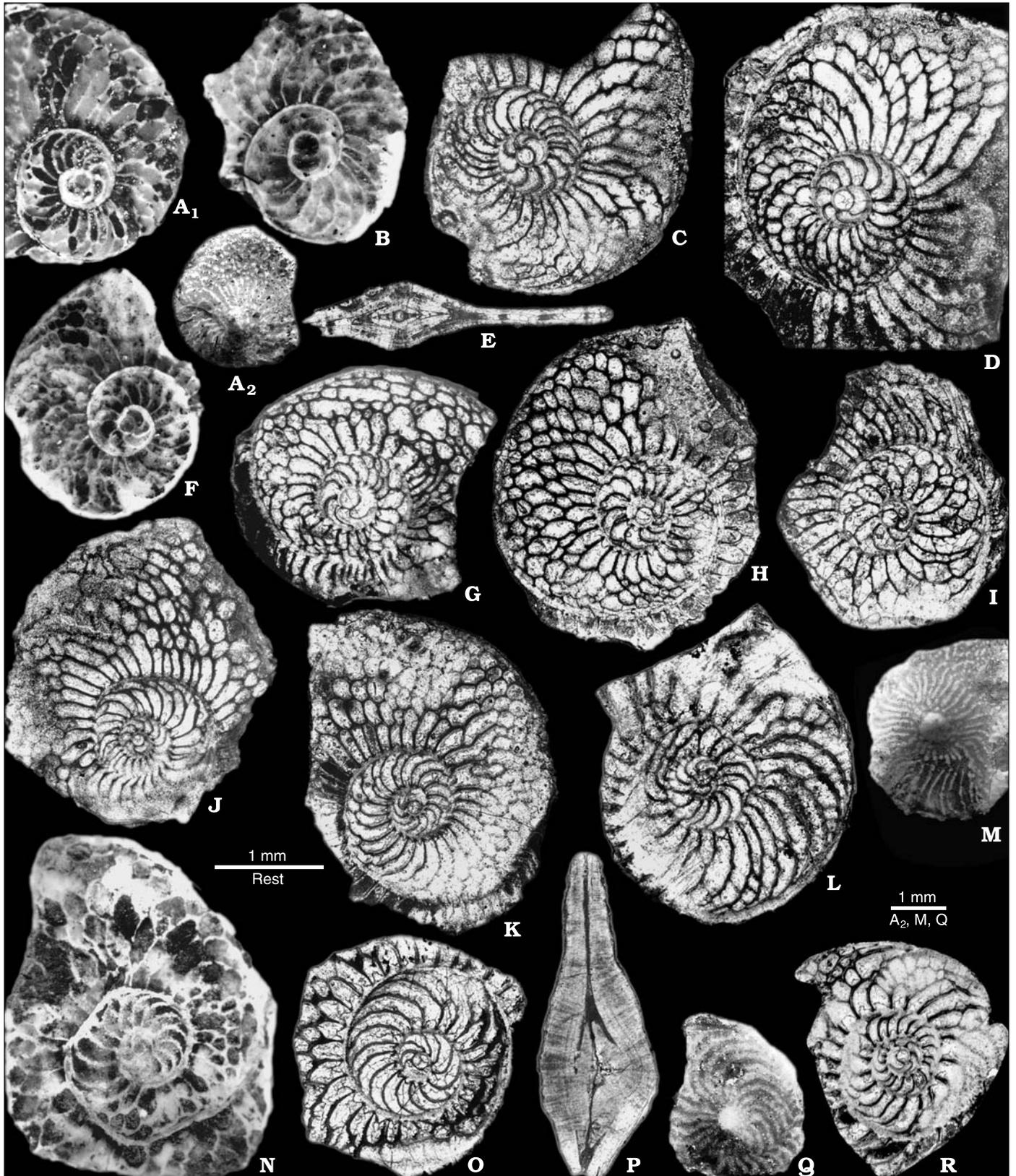
sections, paratype, ITU O/KEÇ.11-38 (**G**), holotype, ITU O/KEÇ 11-54 (**H**), paratype, ITU O/KEÇ.11-27 (**I**). **M**. Paratype, MÁFI E. 9508, A-form, axial section. **J–L**, **N–R**. *Heterostegina reticulata tronensis* ssp. nov., middle late Bartonian, SBZ 18 B. **J**, **K**. Keçili 11 (E Turkey), A-form, equatorial sections, ITU O/KEÇ.11-55 (**J**), ITU O/KEÇ.11-39 (**K**). **L**, **N–Q**. Vic (NE Spain), La Trona. **L**, **N**, **O**. A-form, equatorial sections, paratype, MÁFI E. 9509 (**L**), holotype, MÁFI E. 9510 (**N**), paratype, MÁFI E. 9511 (**O**). **P**. Paratype, MÁFI E. 9512, A-form, axial section. **Q**. Paratype, MÁFI E. 9513, external view. **R**. Prella 5 (Switzerland), MCSNL P5/β-3, A-form, equatorial section.

Geographic and stratigraphic distribution.—Early and middle late Bartonian (SBZ 18 A–B) of Armenia and Turkey (Eastern Anatolia) as detailed at the particular subspecies.

Heterostegina armenica armenica (Grigoryan, 1986)
Fig. 11A–F.

1986 *Grzybowskia armenica* sp. nov.; Grigoryan 1986: 120–121, pl. 37: 1–4, 7.

Diagnosis.—*Heterostegina armenica*-populations with X_{mean} exceeding 8.

The equatorial section of A-forms.—Secondary chamberlets are rather disorderedly arranged and of irregularly polygonal shape. The secondary septa are often incomplete. For numerical features see Table 5.

Remarks.—The biometrical parameters of the Azatek (the type locality of Grigoryan's 1986 *Grzybowskia armenica*) population indicate that they belong to the more primitive evolutionary stage of the species; therefore the subspecific name "*armenica*" is attributed to this stage.

Geographic and stratigraphic distribution.—Early late Bartonian (SBZ 18 A) of Armenia (Azatek) and Eastern Anatolia, Turkey (the middle larger foraminiferal horizon in Keçili, sample Keçili 3)

Heterostegina armenica tigrisensis ssp. nov.
Fig. 11G–I, M.

2007 *Heterostegina armenica* (Grigoryan, 1986); Özcan et al. 2007: pl. 1: 16.

Derivation of the name: Named after the river Tigris flowing close to the type locality.

Holotype: ITU O/KEÇ.11-54 (Fig. 11H), a megalospheric specimen sectioned along the equatorial plane.

Type locality: Keçili (eastern Anatolia), upper larger foraminiferal horizon, sample Keçili 11.

Type horizon: middle late Bartonian, SBZ 18 B.

Material.—32 well-preserved megalospheric specimens.

Diagnosis.—*Heterostegina armenica* populations with X_{mean} less than 8.

The equatorial section of A-forms.—The chamberlets are of somewhat irregularly polygonal shape. The secondary septa are occasionally incomplete. For numerical features see Table 5.

Geographic and stratigraphic distribution.—Middle late Bartonian (SBZ 18 B) of Eastern Anatolia, Turkey (the upper larger foraminiferal horizon in Keçili, sample Keçili 11).

Heterostegina reticulata Rütimeyer, 1850
Figs. 11J–L, N–R, 12–14, 15A–K.

Emended diagnosis.—Involute, biconvex test with central pile and slightly sigmoid septal sutures passing sooner or later into septal network towards the edges. The size of the proloculus is increasing in stratigraphic order from small to medium-sized, chamberlets (with no incomplete secondary septa) are changing simultaneously from rather irregularly arranged and rhomboid to regularly arranged and almost rectangular. Their number in chamber 14 (parameter S) also increases in stratigraphic

order but usually does not exceed 7–8. The number of operculinid (undivided) chambers is strongly reduced during the phylogenesis. Based on this, the species is subdivided into seven chronosubspecies as follows:

H. reticulata tronensis ssp. nov.	$X_{mean} > 17$
H. reticulata hungarica ssp. nov.	$X_{mean} = 11–17$
H. reticulata multifida	$X_{mean} = 7.2–11$
H. reticulata helvetica	$X_{mean} = 4.4–7.2$
H. reticulata reticulata	$X_{mean} = 2.8–4.4$
H. reticulata mossanensis ssp. nov.	$X_{mean} = 1.7–2.8$
H. reticulata italica	$X_{mean} < 1.7$

Description

External features (Figs. 11Q, 13B, 15I).—The test is involute, moderately thick, biconvex and medium-sized (3–6 mm) with oval contour. The distinct central pile is somewhat eccentrically placed. Septal sutures are slightly sigmoid, passing sooner or later into a hexagonal network of primary and secondary sutures towards the periphery of the whorls. No significant difference in adult size between the megalo- and microspheric forms could be observed.

Internal features.—The equatorial section of A-forms: The small to medium-sized proloculus is followed by the second chamber of similar size and then by a loosely coiled spiral. The chambers are high, densely spaced and almost evenly arched. The first appearance of chamberlets is stratigraphically controlled (see the diagnosis), undivided chambers may reappear only in the early stage of the phylogenetic development. The chamberlets (with fully developed secondary septa) are changing in stratigraphic order from rather irregularly arranged and rhomboid to regularly arranged and almost rectangular. Numerical features are tabulated in Table 5.

The equatorial section of B-forms (Figs. 12E, 13O, 14D, J): In the few microspheric forms listed in Table 4 the size of the proloculus is 10–15 μm. It is followed by 18–37 undivided chambers before the appearance of the first subdivided chamber after which operculinid chambers can rarely reappear. The reduction of parameter X in stratigraphical order can be reasonably supposed (see Table 4). The arrangement and shape of the chamberlets in the adult stage do not differ from those of the A-forms.

Axial section (Figs. 11P, 13A): Relying on our own, Herb's (1978: figs. 12, 13, 30), and Stockar's (1999: pl. 3: 6) preparations, the test is biconvex and involute with a wide last whorl and with a distinct central pile. The subdivision of the chambers into chamberlets is evident especially in the last whorl.

Remarks.—Four names, "*reticulata*", "*helvetica*", "*multifida*", and "*italica*" in historical order can be identified with the forms described above. They may correspond to different evolutionary stages of the species (see in detail at the description of the subspecies). Since "*reticulata*" is in priority among them, it is therefore the valid name for the species. To distinguish *Heterostegina reticulata* from *H. armenica* and *H. gracilis*, see our remarks in the description of the latter two forms. Their segregation is illustrated also in Figs. 7–10.

The early representatives of *H. reticulata* occur together with the *Operculina gomezi*-group in almost all the localities. The lat-

ter differs from *H. reticulata* only in lacking complete secondary chamberlets. Since this involute *Operculina* appears first in lower stratigraphical levels than *H. reticulata* (it can be directly observed in Keçili and also in Mossano where the San Pancrazio locality lacking *Heterostegina* contains *O. bericensis*), they can be considered as possible ancestors of the latter. The other possibility is an intermediate step between them represented by *H. armenica*. The intraspecific evolution is expressed significantly in the decrease of parameter X and in the increase of parameter S. The size of the proloculus (P) and that of the diameter of the first and first and a half whorls (d and D) also increase but with significant, probably ecologically-controlled deviations. The spiral becomes somewhat looser during the evolution of the species; however this change is the least evident.

Heterostegina reticulata gave rise to *H. gracilis* at about the middle of the Priabonian, then became extinct with no successors at the very end of the Eocene. Our preliminary studies on Oligocene involute *Heterostegina* (see in details below) suggest that they are not related directly to any of the Eocene forms. At the same time the derivation of genus *Spiroclypeus* from *Heterostegina reticulata* cannot be excluded since the former have a similar heterosteginid spiral but bear lateral chamberlets. Thus the *Spiroclypeus* morphology is more complex. Moreover, it appears in stratigraphically higher horizons than *H. reticulata*.

Geographic and stratigraphic distribution.—The middle late Bartonian to terminal Priabonian (SBZ 18 B-20) time-interval of the northern margin of the western Tethys, from Spain to Armenia (see in details at the particular subspecies).

Heterostegina reticulata tronensis ssp. nov.

Figs. 11J–L, N–R, 12A, B.

1999 *Heterostegina reticulata multifida* (Bieda, 1949); Stockar 1999: 6, pl. 1: 3; pl. 3: 7.
2007 *Heterostegina reticulata tronensis* ssp. nov.; Özcan et al. 2007: pl. 1: 15.

Derivation of the name: Named after the type locality of the taxon.

Holotype: MÁFI E. 9510 (Fig. 11N), a megalospheric specimen split along the equatorial plane.

Type locality: Vic (Spain), La Trona.

Type horizon: Middle late Bartonian, SBZ 18 B.

Material.—62 well-preserved megalospheric specimens.

Diagnosis.—*Heterostegina reticulata* populations with X_{mean} exceeding 17.

The equatorial section of A-forms.—The chamberlets are of rhomboid to polygonal shape; their arrangement is somewhat irregular. For numerical features see Table 5.

Remarks.—This name has been preliminarily used by Özcan et al. (2007) for the population from sample Keçili 11, however, with no description, so the taxon is introduced formally here. Stockar's (1999) figures illustrate the specimens from sample Prella 5. This population is re-evaluated in this paper and based on its parameters it is classified in synonymy with the present subspecies.

Geographic and stratigraphic distribution.—Middle late Bartonian (SBZ 18 B) of Spain (Vic, La Trona), Hungary (sample Úrhida 1), Eastern Anatolia, Turkey (the upper larger foraminiferal horizon in Keçili, sample Keçili 11), and Switzerland (sample Prella 5).

Heterostegina reticulata hungarica ssp. nov.

Fig. 12C–I.

2004 *Heterostegina reticulata hungarica* ssp. nov.; Less and Gyalog 2004: pl. (black and white) 1: 4.

Derivation of the name: Named after Hungary, the country of the type locality.

Holotype: MÁFI E. 9521 (Fig. 12H), a megalospheric specimen split along the equatorial plane.

Type locality: Úrhida (Hungary), sample Úrhida 2.

Type horizon: Middle late Bartonian, SBZ 18 B.

Material.—26 well-preserved megalospheric specimens.

Diagnosis.—*Heterostegina reticulata* populations with X_{mean} ranging from 11 to 17.

The equatorial section of A-forms.—The secondary chamberlets are of rhomboid to hexagonal shape; their arrangement is close to regular. For numerical features see Table 5.

Remarks.—This name has been preliminarily used by Less and Gyalog (2004) for the population from sample Úrhida 2, however, with no description, so the taxon is introduced formally here.

Geographic and stratigraphic distribution.—Middle late Bartonian (SBZ 18 B) of Hungary (samples Úrhida 2, 3), and SW France (Siest).

Heterostegina reticulata multifida (Bieda, 1949)

Fig. 12J–M, O–Q.

part 1949 *Grzybowskia multifida* sp. nov.; Bieda 1949: 153–158, 168–173, pl. 3: 1, 3, 7; pl. 4: 1. (non 2).
part 1978 *Heterostegina reticulata multifida* (Bieda, 1949); Herb 1978: 758, text-figs. 14–17 (non 11).
part 1993 *Heterostegina reticulata* Rütimeyer, 1850; Papazzoni and Sirotti 1993: 532, 535–536, pl. 1: 1; pl. 2: 1, 2.
1994 *Heterostegina reticulata* Rütimeyer, 1850; Papazzoni 1994: pl. 2: 1.
1999 *Heterostegina reticulata* Rütimeyer, 1850; Romero et al. 1999: 87, text-figs. 10–11.

Diagnosis.—*Heterostegina reticulata* populations with X_{mean} ranging from 7.2 to 11.

The equatorial section of A-forms.—The shape of the chamberlets is close to hexagonal; their arrangement is almost regular. For numerical features see Table 5.

Remarks.—According to Bieda (1949), the type locality of *Grzybowskia multifida* is a pebbly sandstone ("grès conglomeratique") intercalation in the Podhale flysch in Szaflary, in the northern slope of the Polish Tatras. It is associated with characteristic middle Eocene forms like large-sized *Nummulites* of the "*perforatus*", "*millecaput*", and "*brongniarti*" groups and *Assilina exponens* on the one hand and also with upper Eocene forms such as *Nummulites fabianii* and several small radiate *Nummulites*. Both the sedimentary features and the composition of the fossil assemblage indicate the mixing of the latter caused by redeposition. Bieda (1949) has provided

three good photos of the new species from the type locality. They seem to confirm the mixing of the fauna since the form in his pl. 4: 2 is much more advanced than the other two as recognized already by Herb (1978). Bieda (1949) marked out the specimen in pl. 3: 1 as typical for the equatorial section of A-forms. In this specimen the parameter X counted by us is 8, therefore we apply the name "*multifida*" to populations with the above diagnosis. X_{mean} of the four specimens from the upper Hohgant sandstone of Elsigen (Switzerland) illustrated by Herb (1978) is 9.75, which is consistent with the above diagnosis although with some reservations because of the few numbers of specimens. The forms illustrated by Papazzoni and Sirotti (1993) and by Papazzoni (1994) are from the vicinity of our sample Mossano 2, therefore they are tentatively identified with "*multifida*". The specimens figured by Romero et al. (1999) from Puig Aguilera are re-evaluated in this paper and according to the parameters classified in synonymy with the present subspecies.

Geographic and stratigraphic distribution.—Latest Bartonian (SBZ 18 C) of Italy (samples Mossano 2 and Verona, Monte Cavro 4), Switzerland (Elsigen), NE Spain (Puig Aguilera) and Poland (Szaflary, Podhale Depression).

Heterostegina reticulata helvetica Kaufmann, 1867

Figs. 12N, R, S, 13A–L.

1867 *Heterostegina helvetica* sp. nov.; Kaufmann 1867: 153, pl. 9: 6–10.
part 1978 *Heterostegina reticulata reticulata* Rütimeyer, 1850; Herb 1978: 758–759, text-figs. 7–10, 12–13, 35.
1999 *Heterostegina reticulata reticulata* Rütimeyer, 1850; Stockar 1999: 6, 9, pl. 1: 4–5; pl. 3: 1–6.
2004 *Heterostegina reticulata urhidensis* ssp. nov.; Less and Gyalog 2004: pl. (black and white) 1: 5.

Diagnosis.—*Heterostegina reticulata* populations with X_{mean} ranging from 4.4 to 7.2.

The equatorial section of A-forms.—The shape of the quite regularly arranged chamberlets is hexagonal. For numerical features see Table 5.

Remarks.—The biometrical parameters of *Heterostegina reticulata* from sample Gschwänt, the type locality of Kaufmann's (1867) *H. helvetica*, designated by Herb (1978), indicate that populations with the above definition belong to this subspecies and clearly differ from those of *H. reticulata reticulata* with type locality in Oberbergli. Therefore, the name "*helvetica*" is valid in the subspecific level despite that Herb (1978) put Kaufmann's (1867) *H. helvetica* in synonymy with Rütimeyer's (1850) *H. reticulata* on both the specific and subspecific levels. *Spiroclypeus* could not be found in Gschwänt, therefore the early Priabonian age of this locality, attributed by Herb (1978), cannot be confirmed. The forms illustrated by Stockar (1999) are from our sample Prella 4. This population is re-evaluated and based on its parameters, it is

ranked in synonymy with the present subspecies. Less and Gyalog (2004) introduced the name "*urhidensis*" for *Heterostegina reticulata* populations from samples Úrhida 4 to 7 with no description. After the revision of *H. r. helvetica* from its type locality the new name turned out to be invalid.

Geographic and stratigraphic distribution.—Latest Bartonian (SBZ 18 C) of Hungary (Úrhida, samples 4 to 8), Switzerland (Gschwänt; sample Prella 4), and Armenia (Biralu, "*millecaput*" beds).

Heterostegina reticulata reticulata Rütimeyer, 1850

Figs. 13M–R, 14A–F.

1850 *Heterostegina reticulata* sp. nov.; Rütimeyer 1850: 109, pl. 4: 61.
part 1978 *Heterostegina reticulata reticulata* Rütimeyer, 1850; Herb 1978: 758–759, text-figs. 2–6 (non 7–10, 12–13, 35).
2004 *Heterostegina reticulata reticulata* Rütimeyer, 1850; Less and Gyalog 2004: pl. (black and white) 2: 2.

Diagnosis.—*Heterostegina reticulata* populations with X_{mean} ranging from 2.8 to 4.4.

The equatorial section of A-forms.—The shape of the regularly arranged chamberlets is distinctly to slightly hexagonal. For numerical features see Table 5.

Remarks.—The biometrical parameters of *Heterostegina reticulata* from sample Oberbergli, the type locality of Rütimeyer's (1850) *H. reticulata*, designated by Herb (1978), indicate that populations with the above definition belong to this subspecies. *Spiroclypeus* could not be found in Oberbergli, therefore the early Priabonian age of this locality, attributed by Herb (1978), cannot be confirmed. About the distinction of "*helvetica*" from "*reticulata*" put in synonymy by Herb (1978) see remarks on the former.

Geographic and stratigraphic distribution.—Latest Bartonian (SBZ 18 C) of Italy (Mossano, sample 3), Hungary (Úrhida, sample 9), Switzerland (Oberbergli) and Armenia (Vedi, "*millecaput*" beds).

Heterostegina reticulata mossanensis ssp. nov.

Figs. 14G–R, 15A–C.

1977 *Heterostegina helvetica* Kaufmann, 1867; Hottinger 1977: text-fig. 46B, E.
part 1978 *Heterostegina reticulata italica* ssp. nov.; Herb 1978: 759, 761, text-figs. 36, 38.
part 1993 *Heterostegina reticulata* Rütimeyer, 1850; Papazzoni and Sirotti 1993: 532, 535–536, pl. 1: 2; pl. 2: 3, 4, 5(?), 6(?).
2004 *Heterostegina reticulata mossanensis* ssp. nov.; Less and Gyalog 2004: pl. (black and white) 2: 3.
2007 *Heterostegina reticulata mossanensis* ssp. nov.; Özcan et al. 2007: pl. 1: 19.

Derivation of the name: Named after the type locality of the taxon.

Holotype: MÁFI E. 9555 (Fig. 14G), a megalospheric specimen split along the equatorial plane.

Fig. 12. Late Bartonian *Heterostegina* from different Western Tethyan localities (II). **A**, **B**. *Heterostegina reticulata tronensis* ssp. nov., Úrhida 1 (Hungary), middle late Bartonian, SBZ 18 B, A-form, equatorial sections, MÁFI E. 9514 (**A**), MÁFI E. 9515 (**B**). **C–I**. *Heterostegina reticulata hungarica* ssp. nov., middle late Bartonian, SBZ 18 B. **C–F**. Siest (SW France), equatorial sections, MÁFI E. 9516, A-form (**C**), MÁFI E. 9517, A-form (**D**), MÁFI E. 9518, B-form (**E**), MÁFI E. 9519, A-form (**F**). **G–I**. Úrhida 2 (Hungary), A-form, equatorial sections, paratype, MÁFI E. 9520 (**G**), holotype, MÁFI E. 9521 (**H**), paratype, →
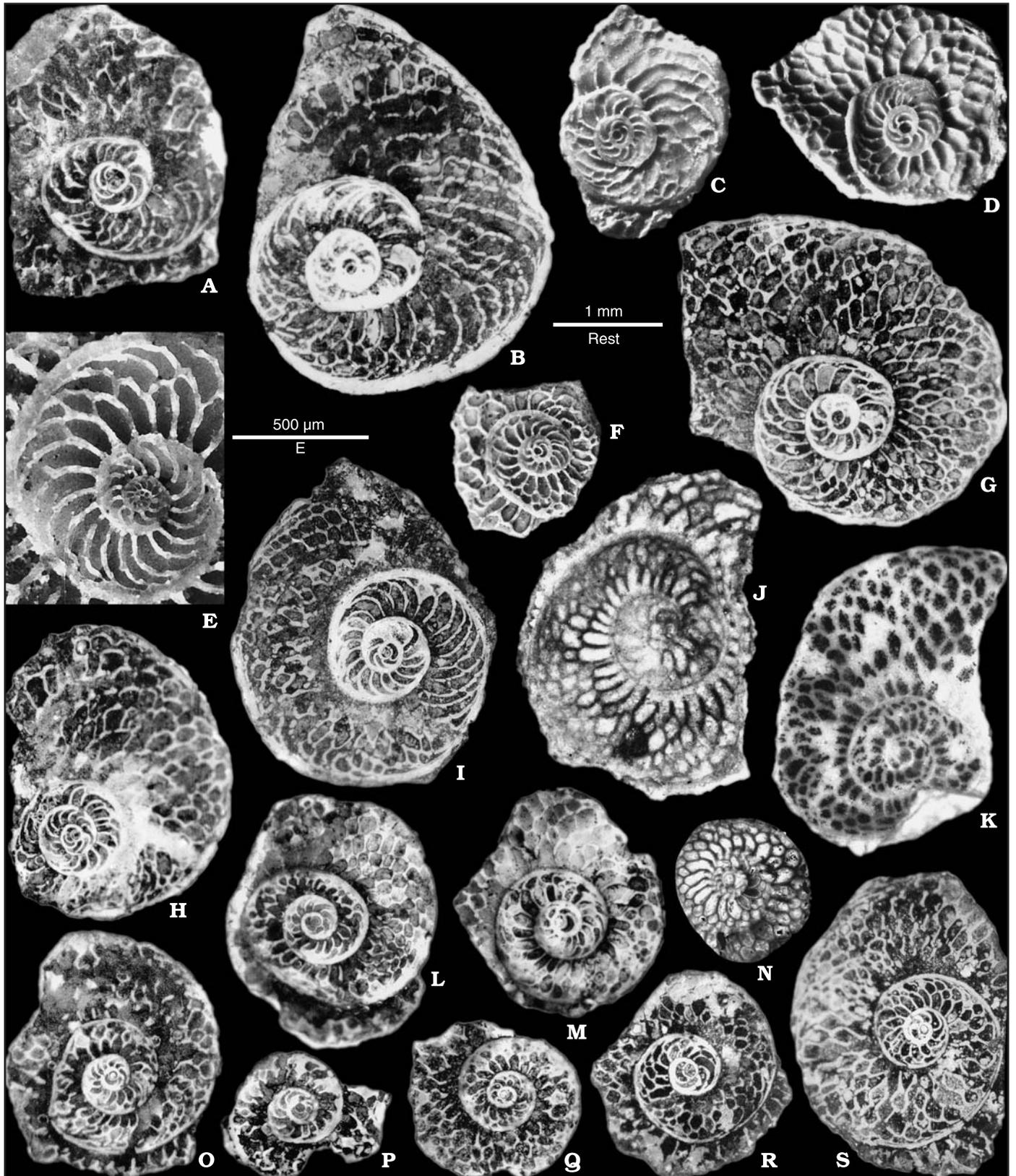
MÁFI E. 9522 (**I**). **J–M, O–Q**. *Heterostegina reticulata multifida* (Bieda, 1949), latest Bartonian, SBZ 18 C. **J, K**. Puig Aguilera (NE Spain), A-form, equatorial sections, MÁFI E. 9523 (**J**), MÁFI E. 9524 (**K**). **L, M, O**. Verona (N Italy), Monte Cavro 4, A-form, equatorial sections, MÁFI E. 9525 (**L**), MÁFI E. 9526 (**M**), MÁFI E. 9527 (**O**). **P, Q**. Mossano 2 (N Italy), A-form, equatorial sections, MÁFI E. 9528 (**P**), MÁFI E. 9529 (**Q**). **N, R, S**. *Heterostegina reticulata helvetica* Kaufmann, 1867, latest Bartonian, SBZ 18 C. **N**. Prella 4 (Switzerland), MCSNL P4/O2-6, A-form, equatorial section. **R, S**. Úrhida 4 (Hungary), A-form, equatorial sections, MÁFI E. 9530 (**R**), MÁFI E. 9531 (**S**).

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

Type level: Basal Priabonian, SBZ 19 A.

Material.—35 well-preserved megalospheric specimens split along the equatorial plane.

Diagnosis.—*Heterostegina reticulata* populations with X_{mean} ranging from 1.7 to 2.8.

The equatorial section of A-forms.—The shape of the regularly arranged chamberlets is slightly hexagonal to almost rectangular. For numerical features see Table 5.

Remarks.—This taxon has been preliminary 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, however with no description, so the taxon is defined formally here. The figures of Hottinger (1977), Herb (1978) and Papazzoni and Sirotti (1993) cited in the above synonymy list illustrate specimens from the very close vicinity of samples Mossano 5 to 7. These populations are re-evaluated in this paper and based on their parameters, they are classified in synonymy with the present subspecies (although only tentatively in the case of specimens from sample Mossano 16 of Papazzoni and Sirotti 1993 whose position could not be unambiguously correlated with our samples— see also at the description of the Mossano section).

Geographic and stratigraphic distribution.—Earliest Priabonian (SBZ 19 A) of Italy (Mossano, samples 5 to 7; Verona, Castel San Felice: Villa Le Are, Villa Devoto and the outcrop of the hairpin bend), Hungary (Úrhida, sample 10, and Turkey (Şarköy, samples 2, 4, and A).

Heterostegina reticulata italica Herb, 1978

Fig. 15D–K.

part 1978 *Heterostegina reticulata italica* ssp. nov.; Herb 1978: 759, 761, text-figs. 27–30 (non 36, 38).

2005 *Heterostegina reticulata italica* Herb, 1978; Less et al. 2005: 98, photo 101/7.

Diagnosis.—*Heterostegina reticulata* populations with X_{mean} less than 1.7.

The equatorial section of A-forms.—The shape of the nicely arranged secondary chamberlets is nearly rectangular. For numerical features see Table 5.

Remarks.—The biometrical parameters of *Heterostegina reticulata* from sample Possagno 2, very close to the type locality of Herb's (1978) *H. reticulata italica*, indicate that populations with the above definition belong to this subspecies. The figure of Less et al. (2005) cited in the above synonymy list illustrates a specimen from sample Noszvaj, Attila-kút.

Geographic and stratigraphic distribution.—Late early Priabonian (SBZ 19B) of N Italy (Mossano, sample 8), "middle" Priabonian (SBZ 19/20) of Hungary (Noszvaj, Attila-kút) to the very end of the Eocene (SBZ 19 B-20) and late Priabonian

(SBZ 20) of N Italy (Calcare di Santa Giustina, samples Possagno 1 and 2).

Heterostegina gracilis Herb, 1978

Fig. 15L–V.

1957 *Spiroclypeus granulosus* Boussac, 1906; Bieda 1957: 207–208, 223–224, pl. 12: 1, 2, 4, 7, 8.

1963 *Spiroclypeus granulosus* Boussac, 1906; Bieda 1963: 106–108, pl. 17: 9–11.

1964 *Heterostegina* cf. *praecursor* Tan, 1932; Hottinger 1964: pl. 7: 3 a–c.

1977 *Heterostegina reticulata* Rütimeyer, 1850; Hottinger 1977: text-fig. 44A–D.

1978 *Heterostegina gracilis* sp. nov.; Herb 1978: 761–762, text-figs. 31–34, 37.

part 1986 *Spiroclypeus granulosus* Boussac, 1906; Grigoryan 1986: 122, pl. 38: 7–11 (non 6).

Diagnosis.—Involute, slightly biconvex test with oval contour, rarely with a central pile but always with granules on the surface except at the periphery of the test where a rectangular sutural network is visible. The proloculus is relatively large, the spiral is very loose. The number of pre-heterosteginid post-embryonic chambers (parameter X) is usually 1 and the number of chamberlets in chamber 14 (parameter S) generally exceeds 9–10. The chamberlets are characteristically delicate, regularly arranged and almost rectangular.

Description

External features (Fig. 15O, P, S).—The test is involute, biconvex, rather flat and medium-sized (3–6 mm) with slightly oval contour. The central part of the surface of the test is covered by granules that are formed at the intersections of primary and secondary septal sutures (see also Herb 1978: fig. 37). The central pile could be found only in some specimens from sample Possagno 1. The septal sutures of the alar prolongations are indistinct but a regular rectangular network of primary and secondary septal sutures may be seen in the peripheral part of the test.

Internal features.—The equatorial section of A-forms: The relatively large proloculus is followed by the second chamber of similar size and then by a very loosely coiled spiral. The chambers are very high, very densely spaced and almost evenly arched. The number of post-embryonic undivided chambers (parameter X) is usually 1, rarely 2; the number of chamberlets in chamber 14 (parameter S) generally exceeds 9–10. The secondary septa are always complete; operculinid chambers do not re-appear after the first heterosteginid chamber. The chamberlets are characteristically delicate, regularly arranged and almost rectangular. Numerical features are tabulated Table 5.

Microspheric specimens have not been found yet.

Axial section: Relying on Herb's (1978: fig. 32) drawing, the test is biconvex and involute with elongated last whorl and with distinct piles. They are decreasing in size from the centre towards the periphery of the shell where finally they are miss-

Fig. 13. Late Bartonian *Heterostegina* from different Western Tethyan localities (III). **A–L**. *Heterostegina reticulata helvetica* Kaufmann, 1867, latest Bartonian, SBZ 18 C. **A–E**. Gschwänt (Switzerland), topotypes. **A**. MÁFI E. 9532, A-form, axial section. **B**. MÁFI E. 9534, external view. **C–E**. A-form, equatorial sections, MÁFI E. 9533 (**C**), NHMB 75/116/11 (**D**), MÁFI E. 9535 (**E**). **F, G**. Úrhida 6 (Hungary), A-form, equatorial sections, MÁFI E. 9536 →

MÁFI E. 9536 (**F**), MÁFI E. 9537 (**G**). **H, I**. Úrhida 7 (Hungary), A-form, equatorial sections, MÁFI E. 9538 (**H**), MÁFI E. 9539 (**I**). **J**. Biralu (Armenia), MÁFI E. 9540, A-form, equatorial section. **K, L**. Úrhida 8 (Hungary), A-form, equatorial section, MÁFI E. 9541 (**K**), MÁFI E. 9542 (**L**). **M–R**. *Heterostegina reticulata reticulata* Rütimeyer, 1850, latest Bartonian, SBZ 18 C. **M–O**. Úrhida 9 (Hungary), equatorial sections, MÁFI E. 9543, A-form (**M**), MÁFI E. 9544, A-form (**N**), MÁFI E. 9545, B-form (**O**). **P–R**. Oberbergli (Switzerland), topotypes. **P**. MÁFI E. 9546, naturally broken surface. **Q, R**. A-form, equatorial sections, MÁFI E. 9547 (**Q**), MÁFI E. 9548 (**R**).
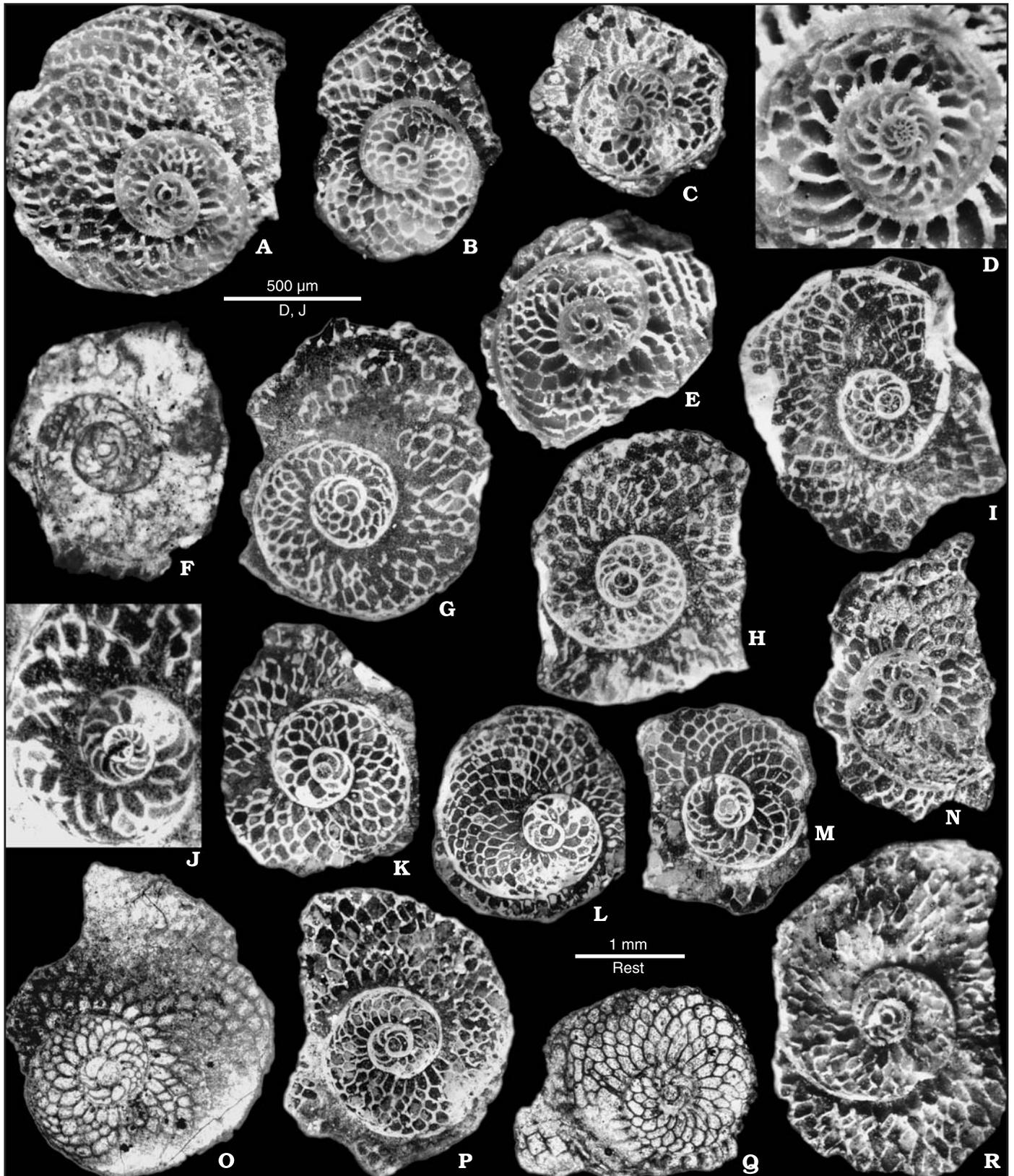
Fig. 14. Latest Bartonian and early Priabonian *Heterostegina* from different Western Tethyan localities. **A–F**. *Heterostegina reticulata reticulata* Rütimeyer, 1850, latest Bartonian, SBZ 18 C. **A–E**. Mossano 3 (N Italy), equatorial sections, MÁFI E. 9549, A-form (**A**), MÁFI E. 9550, A-form (**B**), MÁFI E. 9551, A-form (**C**), MÁFI E. 9552, B-form (**D**), MÁFI E. 9553, A-form (**E**). **F**. Vedi (Armenia), MÁFI E. 9554, A-form, equatorial section. **G–R**. *Heterostegina reticulata mossanensis* ssp. nov., earliest Priabonian, SBZ 19 A. **G–J**. Mossano 6, equatorial sections, holotype, MÁFI E. 9555, A-form (**G**), paratype, MÁFI E. 9556, A-form (**H**), paratype, MÁFI E. 9557, A-form (**I**), paratype, MÁFI E. 9558 (**J**), B-form. **K–M**. Úrhida 10 (Hungary), →

ing. The subdivision of the chambers into secondary chamberlets is well recognizable in all the whorls.

Remarks.—The forms described above can be undoubtedly identified with Herb's (1978) "*gracilis*" since we could investigate the material from sample Possagno 2 closely corresponding to sample 728b in Herb and Hekel (1975), which is the type level of this species. Its validity is confirmed, since *Heterostegina gracilis* differs from *H. reticulata* by the presence of granulations, by its looser spiral, by the significantly smaller (more delicate) secondary chamberlets whose number in chamber 14 (parameter S) is significantly higher (see also Fig. 9). The proloculus is also somewhat larger than that of *H. reticulata* (see Fig. 10).

In samples Possagno 1 and 2 *Heterostegina gracilis* occurs together with *H. reticulata italica*. In these samples they can be separated not only by their qualitative features (see above) but also biometrically (see Fig. 7). Herb's (1978) specimens from Possagno are self-evidently put into the synonymy list while Hottinger's (1964, 1977) forms from Benidorm are coming from the same sample which we have studied.

As it can be seen from the synonymy list *Heterostegina gracilis* can be confused with *Spiroclypeus* because of their similar surface with granules. The difference between the two forms is manifested not only in the absence or presence of lateral chamberlets (the latter are diagnostic for *Spiroclypeus*) but also in the tightness of their spirals. The confusion is partly because Boussac (1906) failed to provide an adequate figure of the equatorial section of his *S. granulosus* and until Roveda (1961), the character of the spiral of these forms from Priabona was not well-known. We could not find any real *Heterostegina* in Priabona, but *Spiroclypeus* with much tighter spiral (than that of *Heterostegina gracilis*) has been abundantly found. The Priabona material is described and figured in Less and Özcan (2008) and the two forms under discussion can be compared and clearly distinguished. This is the reason why Bieda's (1957, 1963) and Grigoryan's (1986) forms can be identified as *H. gracilis*.

Heterostegina gracilis has derived most probably from *H. reticulata italica* since they occur together and almost overlap in their internal morphology in samples Possagno 1 and 2 (see Fig. 7). Moreover, on the surface of *H. gracilis* from sample Possagno 1, the central pile (characteristic for *H. reticulata*) can also be observed (in the case of some specimens from sample Possagno 2 an indistinct umbo can also be recognized). Some kind of intraspecific evolution can be recognized between the population of sample Possagno 1 and the other three ones (see Table 1) in the increase in the size of the proloculus (P) and consequently of the diameter of the first whorl (d) and, less significantly, in the increase of parameter S. Since the size of the proloculus can be controlled not only stratigraphically but also ecologically we do not attempt to

subdivide *H. gracilis* into chronosubspecies yet. According to our recent knowledge *H. gracilis* became extinct with no successors at the very end of the Eocene.

Geographic and stratigraphic distribution.—Late Priabonian (SBZ 20) of Italy (Calcare di Santa Giustina, samples Possagno 1 and 2), Spain (Benidorm), and Armenia (Urtsadzor), and of the Polish (Andrychów, etc.) and Slovakian (Raslavice, etc.) Carpathians.

Discussion

Correlation with other fossil groups.—In order to calibrate chronostratigraphically the heterosteginid succession described above we have to correlate them with different fossil groups. In Table 7 we summarize the co-existence data discussed in detail at the description of particular localities. The *Assilina schwageri–alpina* and *Operculina roselli–gomezi* groups are not considered here because their successive taxa (said to be age-dependant) are still separated on a highly subjective typological basis.

According to Table 7 the boundary between the P 14 and 15 Planktic Foraminiferal Zones can be placed into the interval between the ranges of *Heterostegina armenica armenica* and *H. reticulata multifida*. Data from Azatek can be taken into account only with great uncertainty because the redeposition of the larger foraminiferal assemblage cannot be excluded in this case. The boundary between zones P 15 and 16 seems to be close to the boundary of *H. reticulata mossanensis* and *H. r. italica*.

The lower boundary of the NP 18 Calcareous Nannoplankton Zone is highly uncertain in the shallow benthic scale because the data from Azatek are again problematic. Therefore, based on the data from Biralu and Vedi (Krashenninikov et al. 1985), we can only say that the stratigraphical range of *H. reticulata helvetica* and *H. r. reticulata* belong to NP 18. The NP 18/19 boundary is somewhat lower than the limit between *H. r. mossanensis* and *H. r. italica* whereas the lower boundary of NP 20 (if this zone can be separated from NP 19 at all) nearly coincides with the appearance of *H. gracilis*.

The OZ 14 Orthophragminid Zone corresponds to the whole range of *Heterostegina armenica* and to almost the whole duration of *H. reticulata* except of *H. r. italica*. Its lower boundary nearly coincides with the appearance of *H. armenica* as shown by Özcan et al. (2007) while the upper limit (characterized by the disappearance of orthophragmines of middle Eocene acme such as *Discocyclina pratti*, *Nemkovella strophiolata*, *Asterocyclina alticostata*, and *A. kecskemetii*) corresponds approximately to the boundary between *H. reticulata mossanensis* and *H. r. italica*. The highest occurrence of *Discocyclina discus* (thought to have become extinct just before the Bartonian/Priabonian boundary) has been found in sample Úrhida 7 together with *H. r. helvetica*. The correlation of the OZ 15 and 16 zones with the heterosteginid succession is to be studied further.

The first occurrence of *Spiroclypeus* (represented by the less advanced *S. sirottii* sp. nov. described by Less and Özcan 2008) coincides with the first appearance of *H. reticulata*

A-form, equatorial sections, MÁFI E. 9559 (**K**), MÁFI E. 9560 (**L**), MÁFI E. 9561 (**M**). **N**, **R**. Verona (N Italy), Castel San Felice, Villa Le Are, A-form, equatorial sections, MÁFI E. 9562 (**N**), MÁFI E. 9563 (**R**). **O**. Şarköy 2 (NW Turkey), ITU O/ŞAR.2-2, A-form, equatorial section. **P**. Şarköy A (NW Turkey), MÁFI E. 9564, A-form, equatorial section. **Q**. Şarköy 4 (NW Turkey), ITU O/ŞAR.4-83, A-form, equatorial section.
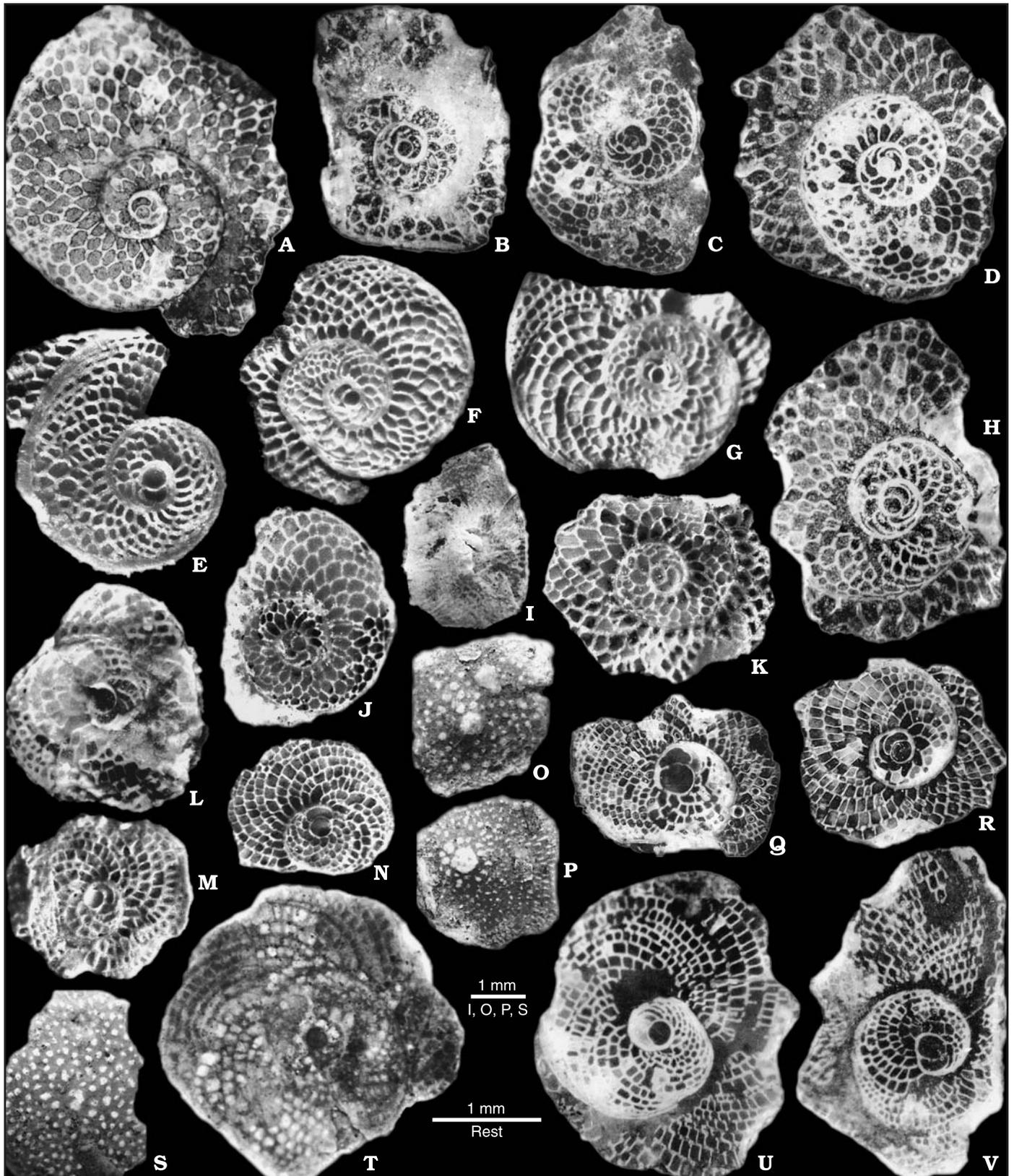
Fig. 15. Priabonian *Heterostegina* from different Western Tethyan localities. **A–C**. *Heterostegina reticulata mossanensis* ssp. nov., earliest Priabonian, SBZ 19 A. **A**. Verona (N Italy), Castel San Felice, hairpin bend: MÁFI E. 9565, A-form, equatorial section. **B**, **C**: Mossano 7 (N Italy), A-form, equatorial sections, MÁFI E. 9566 (**B**), MÁFI E. 9567 (**C**). **D–K**. *Heterostegina reticulata italica* Herb, 1978. **D**, **H**. Mossano 8 (N Italy), late early Priabonian, SBZ 19 B, A-form, equatorial sections, MÁFI E. 9568 (**D**), MÁFI E. 9569 (**H**). **E–G**, **I**. Noszvaj (Hungary), "middle" Priabonian, SBZ 19/20. **E–G**. A-form, equatorial sections, MÁFI E. 9570 (**E**), MÁFI E. 9571 (**F**), MÁFI E. 9494 (**G**). **I**. MÁFI E. 9572, external view. **J**, **K**. Possagno 1 (NE Italy), late Priabonian, →

mossanensis in four localities (Mossano, Verona, Úrhida, and Şarköy) that suggests the simultaneity of this event on the geological time scale. *Spiroclypeus sirottii* is replaced by the more developed *S. carpaticus* (in Biarritz, Lou Cachaou by *S.* aff. *carpaticus*) nearly simultaneously with the first appearance of *Heterostegina gracilis*.

The evolution of the *Nummulites fabianii*-lineage can also be followed in the heterosteginid evolutionary scale. As mentioned in the description of the Keçili section, *N. garganicus* (with a mean proloculus diameter below 140 μm) is found together with *Operculina* ex. gr. *roselli–gomezi* below the first appearance of *Heterostegina armenica*. The latter is associated with *N. hormoensis* (= *N.* "*ptukhiani*" by Papazzoni 1998; mean proloculus diameter between 140 and 200 μm) that can be followed until the first appearance of *H. reticulata mossanensis*, when it is replaced by *N. fabianii* (with a mean proloculus diameter between 200 and 300 μm). According to our current studies (Less et al. 2006; and unpublished data), this latter species can be followed into the lower Oligocene without involute *Heterostegina*. Meanwhile the flatter *N. fabianii* (formerly *N. retiatus*), having adapted to somewhat deeper outer shelf environments, can only be found in the upper part of the Priabonian together with *Spiroclypeus carpaticus*.

The extinction of large-sized *Nummulites* as correlated with the heterosteginid evolution is the most complicated and therefore most interesting story because it seems to be geographically controlled. In SW Europe the extinction level corresponds approximately to the boundary between *Heterostegina reticulata hungarica* and *H. r. multifida* because *N.* ex. gr. *perforatus* has been found in Siest (SW Aquitaine) with the first of them while the Puig Aguilera sample (NE Spain) containing *H. r. multifida* lacks large-sized *Nummulites*.

In N Italy the extinction level can be placed at about the boundary of *H. reticulata multifida* and *H. r. helvetica* since according to Papazzoni and Sirotti (1995) the highest occurrence of *N. biedai* corresponds approximately to the level of samples Mossano 2 and Verona, Monte Cavro 4.

In Úrhida (Hungary) the last representatives of *N.* ex. gr. *millecaput–maximus* can be rarely found in sample Úrhida 8 with *H. reticulata helvetica*. In all the lower samples (Úrhida 1–3 and 4–7 with *H. r. hungarica* and *H. r. helvetica*, respectively) these *Nummulites* are abundant whereas in the higher samples (in Úrhida 9 and 10 with *H. r. reticulata* and *H. r. mossanensis*, respectively) they are completely missing. Thus, the extinction level in Úrhida nearly coincides with the boundary between *H. reticulata helvetica* and *H. r. reticulata*.

In Armenia a recognizable horizon, 2–10 m in thickness, with abundant *Nummulites* ex. gr. *millecaput–maximus* can be

followed in several profiles (Vedi, Shagap, and Biralu). Above this bed large-sized *Nummulites* occur rarely. Based on the critical evaluation of the description of these profiles by Krashenninikov et al. (1985) and also on our experience from Keçili (eastern Anatolia) we suppose that above the "*millecaput*" level of Armenia, all the large-sized *Nummulites* are redeposited. According to our studies the "*millecaput*" level contains *Heterostegina reticulata helvetica* in the Biralu and *H. r. reticulata* in the Vedi profile; thus, the extinction level of large-sized *Nummulites* in Armenia may correspond to the boundary between *H. r. reticulata* and *H. r. mossanensis*. It is worth noting that *Nummulites fabianii* reported by Krashenninikov et al. (1985) and by Grigoryan (1986) from the "*millecaput*" beds of Vedi (according to our new, unpublished results) turned out to be *N. hormoensis* (defined as explained above).

The eastward migration of the extinction level of large-sized *Nummulites* described above is based on data from only four geographical regions. Therefore we may consider this as a working hypothesis.

The middle/late Eocene boundary on the heterosteginid evolutionary scale.—There is no general agreement on the exact location of the middle/late Eocene boundary in the different geological time scales), although everybody (Krashenninikov and Ptukhian 1986; Strougo 1992; Berggren et al. 1995; Papazzoni and Sirotti 1995; Serra-Kiel et al. 1998; Sztrákos and Castelltort 2001; Gradstein et al. 2004) agrees that it corresponds to the limit of the Bartonian and Priabonian stages.

To ensure world-wide correlation, experts on planktic fossils are inclined to put the boundary either onto the base of the P 15 (*Globigerinatheka semiinvoluta*) Planktic Foraminiferal Zone (Toumarkine and Bolli 1975; Krashenninikov and Ptukhian 1986; Strougo 1992; Sztrákos et al. 1998; Sztrákos and Castelltort 2001) or at the base of the NP 18 (*Chiasmolithus oamaruensis*) Calcareous Nannoplankton Zone (Berggren et al. 1995). However, there is no agreement in the succession of these two events (Sztrákos and Castelltort 2001). According to Cita (1975), Krashenninikov and Ptukhian (1986), Strougo (1992), Mathelin and Sztrákos (1993) and Sztrákos et al. (1998,) the base of the NP 18 Zone is older than that of the P 15 Zone, while Cañudo et al. (1988) and Berggren et al. (1995) indicate a reverse order between them. Sztrákos and Castelltort (2001) suggest that the first appearance of *Chiasmolithus oamaruensis* is more heterochronous than that of the *Globigerinatheka semiinvoluta*, and therefore the latter has to be preferred in marking the middle/late Eocene boundary.

If we accept this opinion, the Bartonian/Priabonian boundary will nearly coincide with the first appearance of *Heterostegina reticulata*, thus several sites—containing large-sized *Nummulites* and traditionally assigned to the middle Eocene (Siest, Mossano 2, Úrhida 1–8)—have to be put into the Priabonian. The other disadvantage of this solution is that the lower limit of the Priabonian is not linked to the stratotype or to a nearby section that can be correlated with it.

These two disadvantages are eliminated by the experts on larger foraminifera (Papazzoni and Sirotti 1995; Serra-Kiel et al. 1998; Bassi et al. 2000), who define the lower limit of the Priabonian as the lower boundary of the SBZ 19 Zone. It is de-

Table 7. Assemblages of different fossil groups co-occurring with *Heterostegina* from particular localities that are ranged among shallow benthic subdivisions. Abbreviations: ↑, above; ?, dubious occurrence.

Taxa	Zone	Samples	P 14	P 15	P 16	NP 18	NP 19	NP 20	N. hormoensis	N. fabianii	lyelli-group	perforatus-group	millecaput-group	S. sirottii	S. carpaticus	OZ 14	OZ 15	SBZ 18	SBZ 19	SBZ 20
H. gracilis		Benidorm													•					•
H. gracilis		Biarritz, Cachaou			•			•							aff.					•
Heterostegina reticulata	italica	Possagno 2			•			•		•					•					•
Heterostegina reticulata	italica	Possagno 1			•			•		•					•					•
Heterostegina reticulata	italica	Noszvaj								•				•					•	
Heterostegina reticulata	italica	Mossano 8			•		•							•			•		B	
Heterostegina reticulata	mossanensis (Verona)	Mossano 7		•			•							•		•			A	
Heterostegina reticulata	mossanensis (Verona)	hairpin bend								•				•		•			A	
Heterostegina reticulata	mossanensis (Verona)	C.S. Felice												•		•			A	
Heterostegina reticulata	mossanensis (Verona)	Úrhida 10												•		•			A	
Heterostegina reticulata	mossanensis (Verona)	Şarköy												•		•			A	
Heterostegina reticulata	mossanensis (Verona)	Mossano 5+6		•		•				?				•		•			A	
Heterostegina reticulata	reticulata	Vedi		•		•			•				•					C		
Heterostegina reticulata	reticulata	Mossano 3							•									C		
Heterostegina reticulata	reticulata	Oberbergli				↑												C		
Heterostegina reticulata	reticulata	Úrhida 9														•		C		
Heterostegina reticulata	helvetica	Úrhida 8											•			•		C		
Heterostegina reticulata	helvetica	Biralu		•		•							•					C		
Heterostegina reticulata	helvetica	Úrhida 7											•			•		C		
Heterostegina reticulata	helvetica	Úrhida 6											•			•		C		
Heterostegina reticulata	helvetica	Gschwänt																C		
Heterostegina reticulata	helvetica	Úrhida 4+5											•			•		C		
Heterostegina reticulata	helvetica	Prella 4		?												•		C		
Heterostegina reticulata	multifida	Mossano 2										•						C		
Heterostegina reticulata	multifida	M. Cavro							•									C		
Heterostegina reticulata	multifida	P. Aguilera		•														C		
Heterostegina reticulata	hungarica	Úrhida 2+3											•			•		B		
Heterostegina reticulata	hungarica	Siest	?	?								•				•		B		
Heterostegina reticulata	tronensis	Úrhida 1											•			•		B		
Heterostegina reticulata	tronensis	Vic, La Trona		?					•			↑						B		
Heterostegina reticulata	tronensis	Prella 5		?												•		B		
H. armenica	tigrisensis	Keçili 11							•		•					•		B		
H. armenica	armenica	Azatek		?		?					•							A		
H. armenica	armenica	Keçili 3	•						•		•		•			•		A		

fined by the first appearance of *Nummulites fabianii* and of the genus *Spiroclypeus* as the most important markers. The most suitable profile to locate this boundary is the Mossano section where below the above mentioned first appearances (corresponding to the base of the Marne di Priabona), the disappearance of large-sized *Nummulites* and that of *N. hormoensis* (marking the top of SBZ 18) can also be studied. Moreover, the lower boundary of the SBZ 19 coincides with the base of the Marne di Priabona that allows correlating with the stratotype in Priabona and marks a regional transgression. The main disadvantage of locating the middle/upper Eocene boundary in the Mossano section is that larger foraminifera are chosen as the main tool in the correlation of this boundary. According to Luciani et al. (2002), the base of the Marne di Priabona corresponds very probably to the upper part of both the P 15 and NP 18 zones, which makes the world-wide correlation rather difficult.

Further efforts (magnetostratigraphical studies, investigation of stable isotopes or other methods to be introduced in the future) will likely solve the worldwide correlation of the

Bartonian/Priabonian boundary. In the meantime, the exceptionally rapid evolution of heterosteginids in the vicinity of this limit already ensures its regional correlation in the Western Tethys. Therefore, in this paper we correlate the middle/late Eocene boundary with the base of the SBZ 19 Shallow Benthic Zone marked by the first appearance of the genus *Spiroclypeus* and by the substitution of *Heterostegina reticulata reticulata* by *H. r. mossanensis* and of *Nummulites hormoensis* by *N. fabianii*. All three events can be detected easily because the genus *Spiroclypeus* can be distinguished typologically from all the other genera without any difficulties and the changes within both evolutionary lineages are biometrically defined. In the case of the *Nummulites fabianii* lineage, the two crucial taxa are separated by the 220 μm limit of the mean outer diameter of the proloculus along the main axis (Papazzoni 1998) or by the 200 μm limit of its inner cross-diameter (Less et al. 2006; and unpublished data).

Our investigations confirmed the very close synchronicity of the first appearance of the genus *Spiroclypeus* by demonstrating the co-occurrence of its less advanced evolutionary stage (*Spiroclypeus sirottii* sp. nov. described by Less and Özcan 2008) with *Heterostegina reticulata mossanensis* in four different localities from three quite remote areas (North Italy: Mossano and Verona; Hungary: Úrhida; NW Turkey: Şarköy). *Nummulites hormoensis* is associated with *H. reticulata reticulata* in sample Mossano 3 (and is found also in Mossano 4, still below the Marne di Priabona) and Vedi (Armenia), meanwhile *N. fabianii* co-occurs with *H. reticulata mossanensis* in sample Verona, hairpin bend.

Our studies on *Heterostegina* demonstrated also the favorable conditions of the Mossano section to mark here the Bartonian/Priabonian boundary at the base of the Marne di Priabona since two successive evolutionary stages, *H. reticulata reticulata* (from sample Mossano 3) and *H. r. mossanensis* (in samples Mossano 5 and 6) have been found on opposite sides of the boundary, stratigraphically separated by about 10 m. This means that no serious hiatus can be expected between the top of the Calcari nummulitici (terminating the SBZ 18) and the base of the Marne di Priabona marking the base of the SBZ 19, thus the profile is nearly continuous through this boundary. This, together with the very good accessibility and outcropping conditions and with the extensive literature dealing with it, makes the Mossano section almost ideal for fixing the middle/upper Eocene boundary at the base of the Marne di Priabona in this profile.

Refinement of the shallow benthic zonation.—It is clear from the above discussion and can be read from Table 7, too, that there are no serious contradictions between the heterosteginid evolutionary succession and those of the other fossil groups. Moreover, the biostratigraphic resolution power of the *Heterostegina* lineages seems to be the highest of all in the vicinity of the middle/late Eocene boundary. Therefore, the SBZ 18 and 19 zones can be refined and subdivided into subzones. Since the tight connection of the evolution of the *H. reticulata*-lineage with time has not yet been shown, for the time being we define these subzones with caution, and propose only three ones for SBZ 18 (A to C) and two for SBZ 19 (A and B),

Table 8. Updated range-chart for some late Lutetian to early Rupelian larger benthic foraminiferal taxa of the Western Tethys. The subdivision of the stratigraphic scale is not time-proportional.

		Eocene								Oligocene
		middle					late			early
		Lutetian	Bartonian				Priabonian			Rupelian
Shallow benthic zones (SBZ)		16	17	18 A	18 B	18 C	19 A	19 B	20	21
	Alveolina	←		---	?					
Giant Nummulites	*N. brongniarti-puschi* -group	←	◆							
	N. gizehensis-lyelli -group	←		—						
	N. millecaput-maximus -group	←		---	---	---	---			
	N. perforatus-biedai -group	←		—						
Reticulate Nummulites	*N. lorioli-ptukhiani* -group	←	◆							
	N. bullatus	—	—							
	N. garganicus		◆							
	N. hormoensis		◆	—	—	◆				
	N. fabianii						◆	—	—	◆
	N. fichteli								—	→
Radiate Nummulites	*N. discorbinus-beaumonti* -group	←								
	N. striatus	←---				?				
	N. incrassatus			---					◆	
	N. chavannesi			---					◆	
	N. pulchellus						---		◆	
	N. stellatus					?			◆	
	N. vascus								◆	→
	Nummulites garnieri -group	?							◆	
Giant Assilina	*A. spira* -group	←	◆							
	A. exponens -group	←	—	◆						
Small Assilina	*A. schwageri*	---	---	---	---	---	---	?		
	A. alpina						?	—	◆	
Operculina	*O. gomezi* -group	◆	—	◆						
	O. complanata								?	---→
Heterostegina	*H. armenica armenica*		◆	—						
	H. armenica tigrisensis			◆◆						
	H. reticulata tronensis			◆	—					
	H. reticulata hungarica				◆◆					
	H. reticulata multifida				◆	—				
	H. reticulata helvetica					◆◆				
	H. reticulata reticulata					◆	—			
	H. reticulata mossanensis						◆	—		
	H. reticulata italica							◆	?	
	H. gracilis							◆	—	
Spiro-clypeus	*S. sirottii*						◆	—		
	S. carpaticus							◆	—	
	Pellatispira					?				
	Discocyclina discus	←							---	
Orthophragmines of Lutetian acme (*D. pulcra, Orbitoclypeus douvillei*)		←	◆							
Orthophragmines of middle Eocene acme (*D. pratti, Nemkovella strophiolata, Asterocyclina alticostata, A. kecskemetii*)		←								
Orthophragmines of Priabonian acme (*D. euaensis, D. nandori, D. aspera, D. ruppi, A. ferrandezi, A. priabonensis*)								---	---	◆
Other orthophragmines (*D. dispansa, D. augustae, D. radians, D. trabayensis, O. varians, O. furcatus, A. stella, A. stellata*)		←								◆

respectively. The three subzones of the late Bartonian SBZ 18 are defined as follows.

Subzone SBZ 18 A (early late Bartonian) is characterized by the interval between the first occurrence (FO) of *Nummulites biedai*, *N. cyrenaicus*, *N. vicaryi*, *N. boulangeri*, and *Heterostegina armenica* and the FO of *H. reticulata*. Subzone SBZ 18 B (middle late Bartonian) is defined by the joint biostratigraphic range of *H. reticulata tronensis* and *H. r. hungarica* in succession while SBZ 18 C (latest Bartonian) is characterized by the
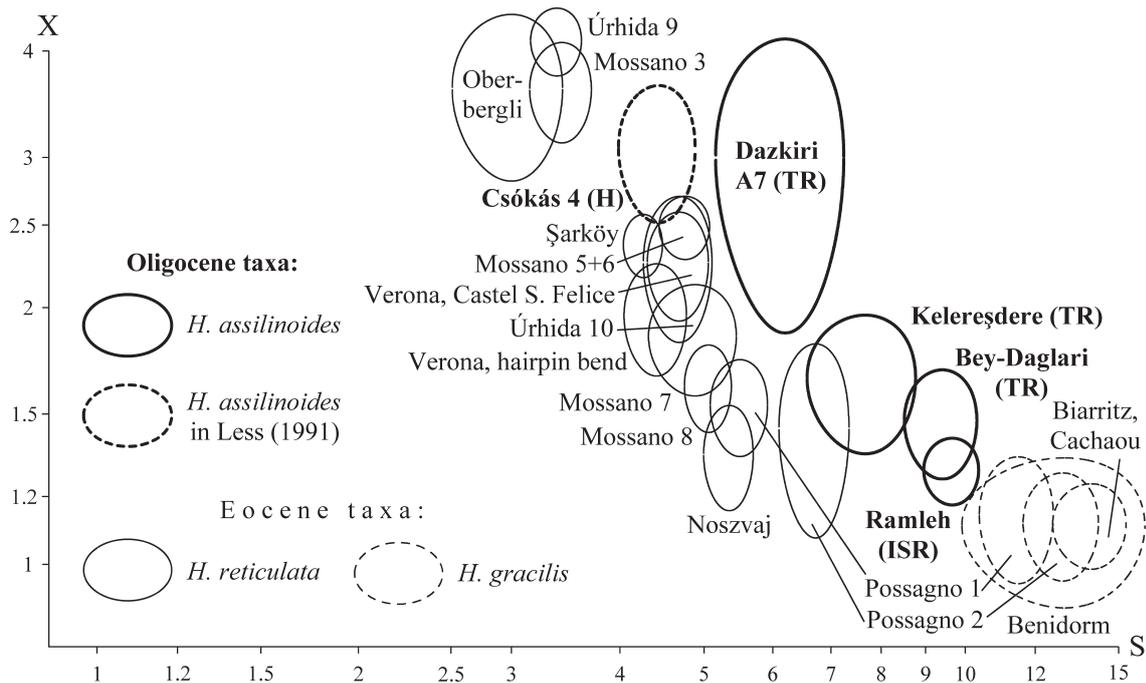
Fig. 16. Distribution of the latest Bartonian, Priabonian and Oligocene heterosteginid populations (mean values at the 95.44% confidence level) on the S–X (density of chamberlets in chamber 14 versus number of undivided post-embryonic chambers) bivariate plot (both scales are logarithmic).
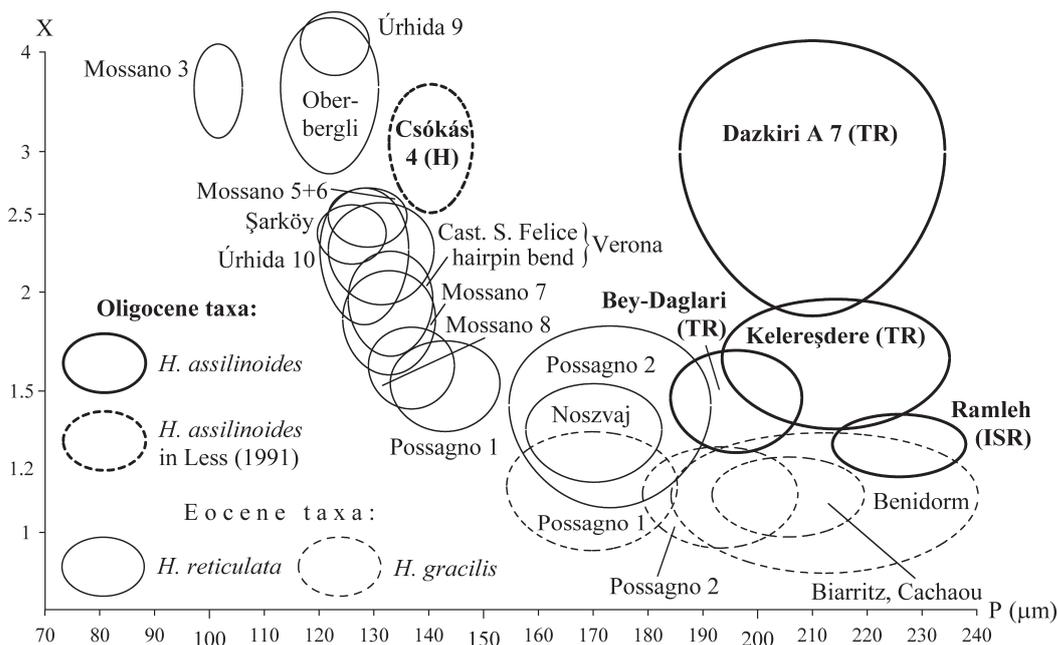

Fig. 17. Distribution of latest Bartonian, Priabonian and Oligocene heterosteginid populations (mean values at the 95.44% confidence level) on the P–X (proloculus diameter versus number of undivided post-embryonic chambers) bivariate plot (X is on logarithmic scale).

joint biostratigraphic range of subsequent *Heterostegina reticulata multifida*, *H. r. helvetica*, and *H. r. reticulata*.

Subzone SBZ 19 A (earliest Priabonian) corresponds to the biostratigraphic range of *H. reticulata mossanensis* while SBZ 19 B (late early Priabonian) is defined by the joint occurrence of *H. reticulata italica* and *Spiroclypeus sirottii* Less and and Özcan, 2008 (described and defined as X_{mean}>2.7 in Less and Özcan (2008); with the same parameter X as in this paper).

The definition of SBZ 20 (late Priabonian) by Serra-Kiel et al. (1998) is completed by adding the biostratigraphic range of *Spiroclypeus carpaticus* (with X_{mean}<2.7 as defined in Less and Özcan 2008). *H. reticulata italica* also occurs in this zone.

The ranges of most important Bartonian–Priabonian larger foraminiferal taxa in the modified shallow benthic scale are shown in Table 8.
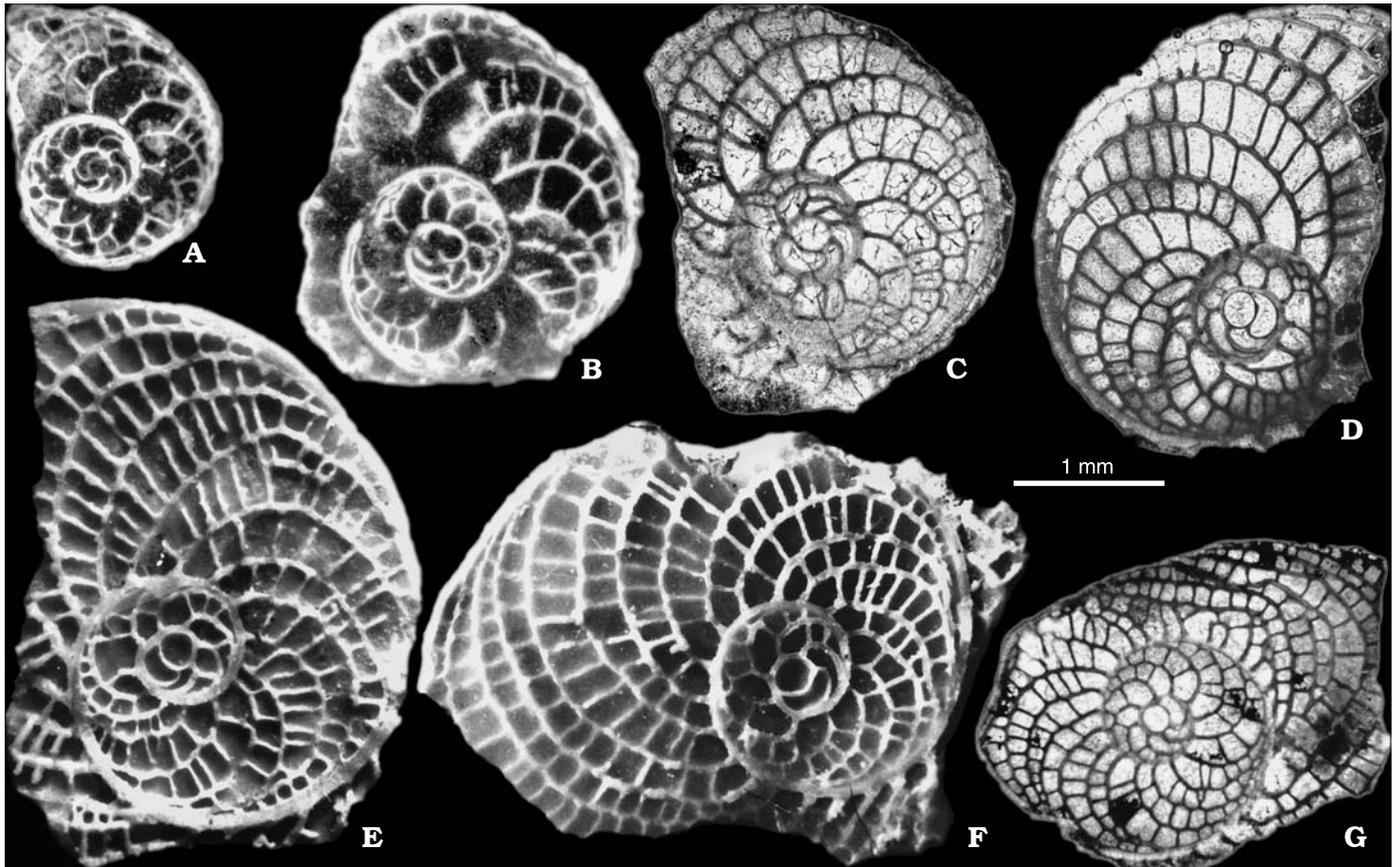
Fig. 18. Oligocene *Heterostegina* from different Western Tethyan localities. **A**, **B**. *Heterostegina* sp. (*Heterostegina assilinoides* Blanckenhorn, 1890 emend. Henson, 1937 in Less 1991), middle Chattian, SBZ 22B/23, Csókás 4 (NE Hungary), A-form, equatorial sections, (**A**) MÁFI O. 413, (**B**) MÁFI O. 416. **C**. *Heterostegina* aff. 1 *assilinoides* Blanckenhorn, 1890. Henson, 1937, Rupelian/Chattian boundary, SBZ 22A/B, A-form, equatorial section, Dazkırı A 7 (SW Turkey), ITU O/DAZ.A7-9. **D–G**. *Heterostegina assilinoides* Blanckenhorn, 1890 emend. Henson, 1937, early Chattian, SBZ 22B, A-form, equatorial sections. **D**. Kızılcaağaç (Bey Dağları, SW Turkey), ITU O/KIZ.4-23. **E**, **F**. Ramleh (Israel), (**E**) MÁFI O. 08.1, (**F**) MÁFI O. 08.2. **G**. Kelereşdere (E Turkey), ITU O/KEL.19-31.

The relationship of Eocene and Oligocene involute *Heterostegina*.—Involute *Heterostegina* are unknown so far from the Rupelian (SBZ 21–22A) of the Western Tethys (Cahuzac and Poignant 1997). The Chattian (SBZ 22B–23) representatives (Turkey: Henson 1937, our unpublished data; Israel: Hottinger 1977; SW Aquitaine: Butt 1966, Cahuzac and Poignant 1997; N Spain: Ferrández-Cañadell et al. 1999; and NE Hungary: Less 1991), are described usually under the name of "*assilinoides*" and supposed to be the descendants of the Eocene forms (Hottinger 1977).

In Figs. 16 and 17 we exhibit our data on Oligocene involute *Heterostegina* in the P–X and S–X bivariate plots. The figures correspond to the lower halves of Figs. 9 and 10 in plotting on them for comparison all the Priabonian and the latest Bartonian *H. reticulata reticulata* populations as well. The Oligocene population of Csókás 4 (SBZ 22B/23) corresponds to that of Less (1991), the Kelereşdere population (SBZ 22B according to our unpublished data) corresponds to samples 108–117 of that section in Sancay et al. (2006). Based on our unpublished data from the Western Taurides, the population of Bey-Daglari corresponds to the SBZ 22B zone, whereas Dazkiri A 7 to the basal part of the same zone. Finally, the locality of Ramleh (SBZ 22B) is described in Drooger (1986). In Fig. 18 we illustrate representative specimens from all the discussed Oligocene sites.

From Figs. 16–18 it is clear that the population of Csókás 4 is different from all the other Oligocene populations, and therefore, represents a taxon, different from *H. assilinoides* whose type locality (Gaziantep region, southern Turkey) is much closer to the location of the other populations. According to Figs. 16 and 17 the Csókás 4 population does not fall into the continuation of the late Bartonian–Priabonian *H. reticulata*-chain and it is also quite remote from the populations of *H. gracilis*. Thus, for these Hungarian forms (together with those from N Spain, see Ferrández-Cañadell et al. 1999 and from SW Aquitaine, see Butt 1966 and Cahuzac and Poignant 1997) a new taxon should be introduced in the near future. As concerns the other four Oligocene populations identifiable with *H. assilinoides*, they seem to fall into the same cluster, which, however, cannot be considered as the continuation of either the *H. reticulata*-chain or *H. gracilis*. This is also clear from the photos in Fig. 18.

Thus, the Chattian *Heterostegina* do not appear to be the successors of the Eocene forms, moreover no *Heterostegina*

are recorded from the (at least) Western Tethyan Rupelian. Therefore, we conclude that the Eocene branch of involute *Heterostegina* became extinct and their development is restricted to the late Bartonian to Priabonian time-span.

Paleoecology

Middle–late Eocene involute *Heterostegina* are characteristic usually for the outer shelf where they can be found together with flat forms like orthophragmines, *Spiroclypeus* (in the Priabonian), some radiate *Nummulites*, the *N. millecaput*- (in the late Bartonian) and *Assilina alpina*-groups. Such an association is characteristic for samples Mossano 5 to 8, Castel San Felice and hairpin bend in Verona, Úrhida 1 to 10, Puig Aguilera, Benidorm, Lou Cachaou in Biarritz, Oberbergli, Gschwänt, Prella, and Şarköy. The absence or subordinate quantity of the above-listed larger foraminifera and the presence of the *Nummulites fabianii*-group observed in some samples like Mossano 2, 3, Monte Cavro 4, and Noszvaj may indicate inner shelf conditions. In other samples like Possagno 1, 2, Vic (La Trona), Biralu, Vedi, Siest, Azatek, Keçili 3 and 11, the faunal assemblage is rather mixed. Moreover in the last six samples, large-sized, more or less inflated *Nummulites* of the *perforatus*- and *gizehensis–lyelli*-groups can also be found, indicating high-energy, shallow-water conditions.

Thus, Eocene *Heterostegina* could be adapted to relatively different conditions within the photic zone of tropical, oligotrophic shelves. This allowed their rapid dispersal at least from Spain to Armenia. Their relatively wide paleoecological niche is useful in correlating the subdivision based on different fossil groups. These two factors, added to their extremely rapid evolution, highly increase their biostratigraphic potential.

Conclusions

Based on the morphometrical study (especially on the statistical evaluation of the equatorial section of A-forms) of *Heterostegina* from thirty-four European localities (marking different ecological conditions, extending from Spain to Armenia and covering the whole late Bartonian to latest Priabonian interval) and also on the critical evaluation of bibliographic data we conclude that:

(i) Populations can be ranked into three species, *Heterostegina armenica* (Grigoryan, 1986), *H. reticulata* Rütimeyer, 1850 and *H. gracilis* Herb, 1978 based on the presence/absence of granulation, on the arrangement, shape and density of secondary chamberlets and on the relative size of the proloculus. The three species follow each other with overlap in time.

(ii) The three species form evolutionary lineages within which (especially within *Heterostegina reticulata*) a very rapid evolution can be observed with the reduction of the number of operculinid chambers (parameter X), the increase of the number of chamberlets (parameter S, counted at chamber 14) and in the increase of the size of the proloculus (parameter P), although the last turned out also to be ecologically controlled.

(iii) The evolution within the lineages is proven by the stratigraphical succession of populations in the Mossano section (Italy) and also by superpositions from other localities. The evolutionary changes are also accompanied by the change of co-occurring fossils starting with the disappearance of large-sized *Nummulites*, then followed by the appearance of the genus *Spiroclypeus* and then by the disappearance of the orthophragmines of middle Eocene acme.

(iv) Based on the reduction of undivided, operculinid chambers as the most reliable parameter (X), two chronosubspecies of *Heterostegina armenica* (one of them is newly erected) and seven ones of *H. reticulata* (with three new subspecies) are defined biometrically.

(v) The rapid heterosteginid evolution allows us to subdivide the Shallow Benthic Zone (SBZ) 18 very cautiously into three (SBZ 18 A–C) and SBZ 19 into two subzones (SBZ 19 A, B). *Heterostegina gracilis* (the only species with granulation) characterizes the SBZ 20 Zone.

(vi) The middle/upper Eocene (= Bartonian/Priabonian) boundary is suggested to be placed at the base of the "Priabona marls" in the Mossano section corresponding to the SBZ 18/19 limit, to the first appearance of genus *Spiroclypeus*, to that of *Nummulites fabianii* and *Heterostegina reticulata mossanensis*. It falls into the upper part of both the P 15 planktic foraminiferal and NP 18 calcareous nannoplankton zones.

(vii) The extremely rapid evolution of *Heterostegina reticulata* combined with a relatively large geographic distribution and a wide ecological niche allows to calibrate the timing of events concerning larger foraminifera around the proposed Bartonian/Priabonian boundary. As a working hypothesis, the extinction of large-sized *Nummulites* seems to be heterochronous in the late Bartonian in having migrated eastward. Relying on data from Italy, Hungary and Turkey, the first appearance of *Spiroclypeus* (with the same evolutionary degree) is proven to be synchronous at the very base of the Priabonian.

(viii) It is highly probable that the Western Tethyan Eocene involute *Heterostegina* became extinct at the very end of the Priabonian and had no successors.

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