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 Spirolypeus and then by the disappearance of orthophragmines of middle Eocene acme. Based on the reduction of operculinid chambers, two chronospecies 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 Spirolypeus 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 Spirolypeus, 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.

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, Spirolypeus, 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
increasing size of their embryo (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 Spirolycpeus 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), Papazazeni and Siroti (1993), Less and Papazzi (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 thus successfully applied to several Oligocene and Neogene larger foraminifera (for details see Drooger 1993). However, the genus Spirolycpeus 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 Papazazeni and Siroti (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; MÂFI 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 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. rosselli, 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. italicca, 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 (Krasheninnikov 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. hyelli*) and shows some similarities with anastegnid *Opeculina gomezii*. 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 "mature-evolute" 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 basis, 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 oblolute, 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 *Spirocyclus*. 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 megalospheric (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
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).

### 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).
- **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:
  \[
  K = 100 \times \frac{(D - d)}{(D - P)}
  \]

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 formu-

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

(upper half-ellipse)

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

(lower half-ellipse),

where *x* and *y* are the studied parameters in the horizontal and vertical axes, whereas *x*<sub>mean</sub>, *x*<sub>s.e.</sub>, *y*<sub>mean</sub> and *y*<sub>s.e.</sub> 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 umbilicus (p) and of the granulation. Abbreviations: n, number of measured specimens; s, standard error.

<table>
<thead>
<tr>
<th>Proloculus diameter</th>
<th>Degree of opercular reduction</th>
<th>&quot;Heterostegina&quot;</th>
<th>First whorl diameter</th>
<th>Index of spiral opening</th>
</tr>
</thead>
<tbody>
<tr>
<td>P (µm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>H. tronensis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Locality</td>
<td>n</td>
<td>mean ± s.e.</td>
<td>range</td>
<td>n</td>
</tr>
<tr>
<td>Kielci (I)</td>
<td>12</td>
<td>13.00 ± 1.06</td>
<td>7−19</td>
<td>12</td>
</tr>
<tr>
<td>Kielci (II)</td>
<td>96</td>
<td>9.00 ± 1.12</td>
<td>7−19</td>
<td>96</td>
</tr>
<tr>
<td><strong>H. tigrisensis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Interlaken (CH)</td>
<td>12</td>
<td>12.96 ± 0.69</td>
<td>7−19</td>
<td>12</td>
</tr>
<tr>
<td><strong>H. mossanensis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Urhida 1</td>
<td>26</td>
<td>10.23 ± 0.77</td>
<td>7−19</td>
<td>26</td>
</tr>
<tr>
<td><strong>H. italica</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Verona, C.S. Felice (I)</td>
<td>27</td>
<td>12.91 ± 0.40</td>
<td>7−19</td>
<td>27</td>
</tr>
<tr>
<td>Verona, C.S. Felice (IV)</td>
<td>28</td>
<td>12.91 ± 0.28</td>
<td>7−19</td>
<td>28</td>
</tr>
</tbody>
</table>

Notes:
- X: number of un-divided chambers
- S: number of chamberlets in chamber 14
- K: (D-P)/(D−D-P)
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 gomezii* 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 gomezii*.

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 Schweighauser (1953) already from his “Oberes Lutétien” in bed 31, which corresponds to our sample Mossano 5.

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 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) from the type level of Herb’s (1978) two new taxa (*Heterostegina reticulata italica* and *H. reticulata italica*).
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>
<thead>
<tr>
<th>Locality</th>
<th>Locality information</th>
<th>Rock</th>
<th>Comment in the text</th>
<th>Information on planktic foraminifera</th>
<th>Information on calcareous nannoplankton</th>
<th>Planktic foraminiferal zone (P)</th>
<th>Calcareous nannoplankton zone (NP)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oberbergli</td>
<td>Herb (1978); Fig. 4</td>
<td>+ sandy limestone</td>
<td>not known</td>
<td>Breitschmid (1978)</td>
<td>unknown</td>
<td>18 just above</td>
<td></td>
</tr>
<tr>
<td>Gischnändt</td>
<td>Herb (1978)</td>
<td>+ allodapic limestone</td>
<td>Eckert (1963)</td>
<td>Eckert (1965)</td>
<td>15, not relevant</td>
<td>19, not relevant</td>
<td></td>
</tr>
<tr>
<td>Prella 4</td>
<td>Stockar (1999)</td>
<td>+ bioclastic limestone</td>
<td>Herb (1976); Mancin et al. (2001)</td>
<td>not known</td>
<td>15 from matrix</td>
<td>unknown</td>
<td></td>
</tr>
<tr>
<td>Prella 5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mossano 2</td>
<td>Bassi (2005) with references; Figs. 3B, 5, 6</td>
<td>+ nummulitic limestone</td>
<td>not known</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mossano 3</td>
<td></td>
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<td>Montecavro 4</td>
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<td>Fabiani (1915, 1919); Fig. 3C</td>
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<td>Tournaminekine and Bolli (1975)</td>
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<td>20 (below and above)</td>
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<td>not known; magneto-stratigraphy: Burbank et al. (1992): C17.2n</td>
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<td>- 17 (upper part)</td>
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<td>Ferrer (1971)</td>
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<td>15</td>
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<td>Bendendorf</td>
<td>Hottinger (1964)</td>
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<td>Sztrákos et al. (1998)</td>
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<td>14 or 15</td>
<td>unknown</td>
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<td>Krashennikov et al. (1985): bed 9</td>
<td>+ tuffitic sandstone</td>
<td>Krashennikov et al. (1985)</td>
<td>basal 15, indirect data</td>
<td>18 just below</td>
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<td>Vedi</td>
<td>Krashennikov et al. (1985): bed 8</td>
<td>- marly limestone</td>
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<td>15</td>
<td>18</td>
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<td>Özcan et al. (2007)</td>
<td>+ allodapic sandy limestone</td>
<td>Özcan et al. (2007)</td>
<td>14</td>
<td>16, 'reworked'</td>
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<td>Keçili 11</td>
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<tr>
<td>Şarköy</td>
<td>Özcan et al. (2007); Fig. 3E</td>
<td>+ marly limestone</td>
<td>Özcan et al. (2007)</td>
<td>16–21</td>
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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.


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<td>Oberbergli</td>
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<td>Gischwänt</td>
<td>Herb (1978); own data</td>
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<td>absent</td>
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<td>absent</td>
<td>absent</td>
<td><em>sirrotii</em></td>
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<td></td>
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<td><em>multifida</em></td>
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<td>Papazzoni and Sirotti</td>
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<td><em>N. ex. gr. fabianii</em></td>
<td>very rare</td>
<td><em>sirrotii</em></td>
<td><em>mossanensis</em></td>
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<td></td>
<td><em>N. biedai</em> just below</td>
<td><em>N. hornoensis</em></td>
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<td><em>sirrotii</em></td>
<td><em>mossanensis</em></td>
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<td>Villa Devoto &amp; Le Are</td>
<td>own data</td>
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<td>absent</td>
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<td><em>N. hornoensis</em></td>
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<td>Vic, La Trona</td>
<td>Papazzoni and Sirotti</td>
<td><em>N. biedai</em> above</td>
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<td>absent</td>
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<td>Romero et al. (1999)</td>
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<td>Less (1987)</td>
<td><em>N. ex. gr. perforatus</em></td>
<td>rare 'N. hornoensis'</td>
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<td><em>N. hornoensis</em></td>
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<td>Vedi</td>
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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 multiforma. 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.

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<td>Úrhida 1</td>
<td>Kossuth Str. 60., lower</td>
<td>Kossuth Str. 60., lower</td>
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<td>Úrhida 2</td>
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<td>Kossuth Str. 50.</td>
<td>Other outcrop with N. “millecaput”</td>
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<td>Kossuth Str. 60., upper</td>
<td>Kossuth Str. 60., upper</td>
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<td>Petőfi Str. 42–44., lower</td>
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<td>Borehole Úrhida 1, 284–285 m</td>
<td>Úrhida U–1, 284.0–285.0 m</td>
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<tr>
<td>Úrhida 6</td>
<td>Petőfi Str. 120., lower</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Úrhida 7</td>
<td>Petőfi Str. 106.</td>
<td>Petőfi Str. 42–44., middle</td>
<td>–</td>
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<tr>
<td>Úrhida 8</td>
<td>Petőfi Str. 120., upper</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Úrhida 9</td>
<td>Petőfi Str. 108.</td>
<td>Petőfi Str. 42–44., upper</td>
<td>–</td>
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<td>Úrhida 10</td>
<td>Jókai Str. 7.</td>
<td>Jókai Str. 7.</td>
<td>Stop 2B</td>
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</table>

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 Keckseméti 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 level between “hungarica” and “multiforma” 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 chronospecies. 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

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 foraminifers 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. mossaenensis) as in the basal Priabonian of Mossano (samples 5 and 6), Verona (Castel San Felice and hairpin bend) and in sample Üritch 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 Gschwànt. 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 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.

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.

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.
(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 *Spiroclpeus* in the centre; those with *Spiroclpeus 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 *Spiroclpeus*, are very consistent within populations. The *Heterostegina* populations occurring with *Spiroclpeus 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 Kecili 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 protolocus (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-
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*.
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 Kečili 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 Kečili 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).

<table>
<thead>
<tr>
<th>Sample</th>
<th>Subspecies</th>
<th>Illustration</th>
<th>X</th>
</tr>
</thead>
<tbody>
<tr>
<td>Siest</td>
<td>hungarica</td>
<td>Fig. 12E</td>
<td>37</td>
</tr>
<tr>
<td>Úrhida</td>
<td>reticulata</td>
<td>Fig. 13O</td>
<td>29</td>
</tr>
<tr>
<td>Mossano 3</td>
<td>reticulata</td>
<td>Fig. 14D</td>
<td>25</td>
</tr>
<tr>
<td>Mossano 6</td>
<td>mossanensis</td>
<td>Fig. 14J</td>
<td>20</td>
</tr>
<tr>
<td>Şarköy 4</td>
<td>mossanensis</td>
<td>not figured</td>
<td>21</td>
</tr>
<tr>
<td>Şarköy 4</td>
<td>mossanensis</td>
<td>not figured</td>
<td>18–20</td>
</tr>
</tbody>
</table>

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 tigrisenis ssp. nov. X mean < 8

Description
External features (Fig. 11A–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 ontogenetic 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. Pmean, Xmean, etc. indicate the mean values of the given parameter for particular populations.

<table>
<thead>
<tr>
<th>Taxa / parameters</th>
<th>Diameter of proloculus</th>
<th>Number of undivided post-embryonic chambers</th>
<th>Number of chamberlets in 14 chambers</th>
<th>Diameter of the first one whorl</th>
<th>Diameter of 1.5 whorls</th>
<th>Index of spiral opening K=100×(D−dy/(D−P))</th>
</tr>
</thead>
<tbody>
<tr>
<td>H. armenica armenica</td>
<td>90–205 130–175</td>
<td>2–23</td>
<td>8–16</td>
<td>1–4 1–2.8</td>
<td>490–1400 750–1140</td>
<td>38–53</td>
</tr>
<tr>
<td>H. armenica tigrisensis</td>
<td>115–225 155–175</td>
<td>3–20</td>
<td>5.5–8</td>
<td>1–5 2.6–3.4</td>
<td>630–1300 830–950</td>
<td>33–56</td>
</tr>
<tr>
<td>reticulata hangarica</td>
<td>55–140 75–105</td>
<td>6–25</td>
<td>11–17</td>
<td>1–3 1.05–1.6</td>
<td>415–880 520–655</td>
<td>29–51</td>
</tr>
<tr>
<td>reticulata multipliata</td>
<td>60–170 80–135</td>
<td>3–17</td>
<td>7.2–11</td>
<td>1–4 1.6–2.4</td>
<td>440–935 515–780</td>
<td>32–50</td>
</tr>
<tr>
<td>reticulata helvetica</td>
<td>55–165 90–125</td>
<td>1–14</td>
<td>4.4–7.2</td>
<td>1–7 2–3.5</td>
<td>345–1030 540–800</td>
<td>25–56</td>
</tr>
<tr>
<td>reticulata recticulata</td>
<td>85–190 95–140</td>
<td>1–8</td>
<td>2.8–4.4</td>
<td>2–6 2.6–3.9</td>
<td>505–1350 630–860</td>
<td>33–58</td>
</tr>
<tr>
<td>reticulata mossanensis</td>
<td>70–240 120–140</td>
<td>1–5</td>
<td>1.7–2.8</td>
<td>3–7 3.9–5.1</td>
<td>420–1320 720–925</td>
<td>31–60</td>
</tr>
<tr>
<td>reticulata italica</td>
<td>90–250 130–190</td>
<td>1–4</td>
<td>1.1–1.7</td>
<td>3–9 4.7–7.2</td>
<td>580–1340 800–1060</td>
<td>31–58</td>
</tr>
<tr>
<td>gracilis</td>
<td>130–300 155–225</td>
<td>1–2</td>
<td>1–1.4</td>
<td>7–24 10–16</td>
<td>750–2300 1020–1480</td>
<td>38–68</td>
</tr>
</tbody>
</table>

Table 6. p[t(X)]−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.

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 100μm) 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.
Derivation of the name

Type horizon: Grzybowskia armenica (Grigoryan, 1986) Fig. 11A–F.

Diagnosis.—Heterostegina armenica—populations with $X_{\text{mean}}$ 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 and 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 populations.

Diagnosis.—Heterostegina armenica populations with $X_{\text{mean}}$ 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. $X_{\text{mean}} > 17$
- H. reticulata hungarica ssp. nov. $X_{\text{mean}} = 11–17$
- H. reticulata multifida $X_{\text{mean}} = 7.2–11$
- H. reticulata helvetica $X_{\text{mean}} = 4.4–7.2$
- H. reticulata reticulata $X_{\text{mean}} = 2.8–4.4$
- H. reticulata mossanensis ssp. nov. $X_{\text{mean}} = 1.7–2.8$
- H. reticulata italicca $X_{\text{mean}} < 1.7$

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 megalospheric 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 “italicca” 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-
Heterostegina 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 Kečili and also in Missano 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 Spiroclupeus from Heterostegina reticulata cannot be excluded since the former have a similar heterosteginid spiral but bear lateral chamberlets. Thus the Spiroclupeus 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, Swizerland (sample Prella 5). This population is re-evaluated in this paper here. Stockar’s (1999) figures illustrate the specimens from 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.
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 Úrhida 11, however, with no description, so the taxon is introduced formally here.
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 Kečili, sample Kečili 11), and Switzerland (sample Prella 5).

Heterostegina reticulata hungarica ssp. nov.
Fig. 12C-I.
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 Grzybowska 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 Sirioti 1993: 532, 535–536, pl. 1: 1; pl. 2: 1, 2.
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 Grzybowska multifida is a pebbly sandstone (“grès conglomeratique”) intercalation in the Podhale flysch in Szaflary, in the northern slope of the Polish Tatars. It is associated with characteristic middle Eocene forms like large-sized Nummulites of the “perforatus”, “millecaput”, and “brongniarti” groups and Assilina exponens and Assilina sphinctica 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). Biada (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. $X_{\text{mean}}$ 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 (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.


1999 *Heterostegina reticulata reticulata* Rütimeyer, 1850; Stockar 1999: 6, 9, pl. 1: 4–5; pl. 3: 1–6.


**Diagnosis.**—*Heterostegina reticulata* populations with $X_{\text{mean}}$ 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 Pliobanian 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–C.

1850 *Heterostegina reticulata* sp. nov.; Rütimeyer 1850: 109, pl. 4: 61.


**Diagnosis.**—*Heterostegina reticulata* populations with $X_{\text{mean}}$ 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 Pliobonian 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 3, sample 9), 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 1993 *Heterostegina reticulata* Rütimeyer, 1850; Papazzoni and Sirotti 1993: 532, 535–536, pl. 1: 2; pl. 2: 3, 4, 5(?), 6(?).


**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, →
**Heterostegina reticulata italica** Herb, 1978

Diagnosis.—Heterostegina reticulata populations with $X_{\text{mean}}$ 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 Šarköy 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 (Šarköy, samples 2, 4, and A).

**Heterostegina reticulata italica** Herb, 1978

Fig. 15D–K.


Diagnosis.—Heterostegina reticulata populations with $X_{\text{mean}}$ 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.—Earliest 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 (Calcari de Santa Giustina, samples Possagno 1 and 2).

**Heterostegina gracilis** Herb, 1978

Fig. 15L–V.


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.


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 →
ing. The subdivision of the chambers into secondary chambers 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 chambers 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 italic a. 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 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.

Correlation with other fossil groups.—In order to calibrate chronostratigraphically the heterostegnid 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–gomezii groups are not considered here because their successive taxa (said to be age-dependant) are still separated on a highly subjective typological basis.

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. reticulata multifida. Data from Azatek can be taken into account only with great uncertainty because the reposition 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. italic a.

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

The evolution of the Nummulites fabiani−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. “ptukhian” 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. fabiani (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. fabiani (formerly N. retiatus), having adapted to somewhat deeper outer shelf environments, can only be found in the upper part of the Priabonian together with Spirolypeus 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 Sist (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 Ūrhida (Hungary) the last representatives of N. ex. gr. millecaput−maximus can be rarely found in sample Ūrhida 8 with H. reticulata helvetica. In all the lower samples (Ūrhida 1−3 and 4−7 with H. r. hungarica and H. r. helvetica, respectively) these Nummulites are abundant whereas in the higher samples (in Ūrhida 9 and 10 with H. r. reticulata and H. r. mossanensis, respectively) they are completely missing. Thus, the extinction level in Ūrhida 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 Krashennikov 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 fabiani reported by Krashennikov 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 (Krashennikov and Ptuikhian 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 foraminifers are inclining to put the boundary either onto the base of the P 15 (Globigerinatheka seminovoluta) Planktic Foraminiferal Zone (Toumarkine and Bolli 1975; Krashennikov and Ptuikhian 1986; Strougo 1992; Sztrákos et al. 1998; Sztrákos and Castelltort 2001) or at the base of the NP 18 (Chiasmolithus oamarusensis) 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), Krashennikov and Ptuikhian (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 Cañedo 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 oamarusensis is more heterochronous than that of the Globigerinatheka seminovoluta, 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, Ūrhida 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−
fined by the first appearance of *Nummulites fabianii* and of the genus *Spiroclupeus* 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

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<table>
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<th>Table 7. Assemblages of different fossil groups co-occurring with <em>Heterostegina</em> from particular localities that are ranged among shallow benthic subdivisions. Abbreviations: †, above; ?, dubious occurrence.</th>
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<td><strong>Taxa</strong></td>
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<td>Samples</td>
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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 lines 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 protolocus 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 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 Calcare 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 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. Our investigations confirmed that 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 heterostegid 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), 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

<table>
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<tr>
<th>Subzone</th>
<th>Early Late Bartonian</th>
<th>Middle Late Bartonian</th>
<th>Late Bartonian</th>
<th>Priabonian</th>
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<td>SBZ 18 A</td>
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<td>H. r. hungarica</td>
<td>H. armenica</td>
<td>H. hormoensis</td>
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<td>H. reticulata helvetica</td>
<td>H. reticulata mosaensis</td>
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<td>H. reticulata italica</td>
<td>H. reticulata helvetica</td>
<td>H. reticulata hungarica</td>
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**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.**

**Table 7. List of larger benthic foraminiferal taxa in the Western Tethys.**

**Figure 1. Simplified biozonation for the middle–late Eocene.**

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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 italicca* and *Spiroclypeus sirottii* Less and and Özcan, 2008 (described and defined as $X_{\text{mean}}>2.7$ 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 $X_{\text{mean}}<2.7$ as defined in Less and Özcan 2008). *H. reticulata italicca* 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.
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 orthospharamines, *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, Urhida 1 to 10, Puig Aguilera, Benidorm, Lou Cachau in Biarritz, Oberbergli, Gschwänt, Prella, and Šarköy. The absence or subordinate 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* groups. These two factors, added to their extremely rapid evolutionary changes, 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* Rüttimeyer, 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 orthospharamines 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 “Pliabona 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 nanoplancton 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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