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Some species of *Operculina* and *Heterostegina* from the Eocene of the Helvetic nappes of Switzerland and from Northern Italy

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ABSTRACT

Species of the Genera *Operculina* and *Heterostegina* have been investigated from a number of localities in the late Middle and early Late Eocene in the Helvetic nappes between the Lakes of Lucerne and Thun and south of them.

An evolutionary lineage of involute *Operculina* and *Heterostegina* is tentatively proposed, with *O. bericensis* at the base of the Hohgant Formation (Biarritzian), *O. gomezi* in the Biarritzian part of the Hohgant sandstone as well as in the uppermost Hohgant sandstone of early Priabonian age, grading into the involute *Heterostegina reticulata multifida* and *H. reticulata reticulata.*

Topotype material of *Heterostegina reticulata* RÜTIMEYER 1850 and *H. helvetica* KAUFMANN 1867 shows that *H. helvetica* is a junior synonym of *H. reticulata.* These species of *Heterostegina* from the Helvetic nappes were compared with forms found in the Priabonian sections of Possagno and Mossano (Northern Italy). There the *reticulata*-group is represented by a new subspecies, *H. reticulata italica.* In the uppermost Priabonian of Possagno (Calcare di S. Giustina) a second form of *Heterostegina*, *H. gracilis* n. sp. occurs, which is closely related to the Oligocene *H. praecursor.*

ZUSAMMENFASSUNG

Im Rahmen einer biostratigraphischen und mikropaläontologischen Bearbeitung des helvetischen Tertiärs wurden die Operculinen und Heterosteginen der eozänen Hohgant-Serie zwischen Vierwaldstättersee und Thunersee und südlich davon untersucht und mit Material aus dem Priabonien der Profile von Possagno und Mossano (Norditalien) verglichen. Die Gegenüberstellung von Topotypen der beiden aus dem Helvetikum bereits im letzten Jahrhundert beschriebenen Heterosteginen-Arten hat ergeben, dass *Heterostegina helvetica* KAUFMANN ein jüngeres Synonym von *H. reticulata* RÜTIMEYER ist. Davon können Formen abgetrennt werden, welche die Sekundärunterteilung der Septen erst in einem späteren Stadium der Spirale aufweisen. Sie lassen sich mit *H. multifida* (BIEDA) vergleichen, welche hier als Unterart von *H. reticulata* aufgeführt wird.

Bei den in der Discus-Schicht und an der Basis der Hohgant-Serie auftretenden Formen, die in der älteren Literatur als *H. helvetica* oder cf. *helvetica* zitiert wurden, handelt es sich um die involute *Operculina bericensis* OPPENHEIM. In diesen Horizonten kommen zudem *Nummulites biaritzensis* und die evolute *Operculina schwageri* vor, so dass die Basis der Hohgant-Serie nördlich des Thunersees noch ins Mitteleozän (Biarritzien) gestellt werden muss. In den östlichen Gebieten (z. B. Klimsenhorn) gehört die Hohgant-Serie in ihrer Gesamtheit ins Biarritzien, im Westen dagegen reicht sie ins untere Priabonien hinauf. *O. gomezi* wurde sowohl in mittel- als auch in obereozänen Anteilen gefunden.

Im obersten Priabonien von Possagno konnten neben *O. alpina* zwei Arten von Heterosteginen nachgewiesen werden. Die eine gehört der *reticulata*-Gruppe an und wird hier als neue Unterart, *H. reticulata italica*, definiert, wogegen die zweite, *H. gracilis* n. sp., Glied einer anderen Entwicklungsreihe ist, verwandt mit der oligozänen *H. praecursor.*

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1. Occurrences in the Helvetic nappes of the Swiss Alps

Introduction

Two species of Eocene *Heterostegina* were originally described from the Alpine border chain (Niederhorn nappe) between the Lake of Lucerne and the Lake of Thun. In 1850 RÜTIMEYER defined and figured *Heterostegina reticulata* from the "Ralligstöcke" near the Lake of Thun and in 1867 *H. helvetica* was described and illustrated by KAUFMANN from the locality "Gschwänt", west of the Pilatus area. Despite RÜTIMEYER's brief and summary description, the identification with the genus *Heterostegina* in the concept adopted here seems unequivocal. KAUFMANN's definition of *H. helvetica* is much more detailed with respect to external and internal features. The author gave a fine, although somewhat schematic figure of an equatorial section. Unfortunately, in his original publication of 1867 he did not refer to RÜTIMEYER's species established 18 years before. In his later monograph on the geology between the Lake of Lucerne and the Lake of Thun, however, KAUFMANN (1886) stated in a brief footnote on page 549 that *H. reticulata* differs from *H. helvetica* in showing definite ribs, which apparently are missing on the latter species. Transitional forms between the two he did not observe. In the same monograph he also listed the localities where the two species can be found.

From KAUFMANN's brief remark in 1886 about ribs on *H. reticulata* it is not quite clear to which morphologic feature he was referring. It is possible that he was considering the septal lines which may be visible on the surface. GÜMBEL (1868) compared the types of RÜTIMEYER's and KAUFMANN's species and stated that the two species are identical, thus giving priority to *H. reticulata.* HEIM (1908, p. 254) listed the two species and referred to KAUFMANN's remark. In other works on European Eocene both *H. helvetica* and *H. reticulata* have been used as names for Late Eocene forms, but with the exception of HOTTINGER (1977) no attempts have been made to differentiate the two species. In the literature on the Swiss Alps the name of *H. helvetica* has generally been adopted (SCHUMACHER 1948, GIGON 1950, and others). This may be explained by KAUFMANN's more detailed original description of the species when compared with RÜTIMEYER's *H. reticulata.*

For the present paper the author has collected samples with *Heterostegina* at the type localities of the two species in question, as well as at some other localities. Further samples from the area between the Lake of Lucerne and the Lake of Thun were provided by B. Bieri. As will be shown below, the internal features of the specimens investigated from the type localities are virtually identical and *H. helvetica* is therefore considered a junior synonym of *H. reticulata.*

Stratigraphy

In the Helvetic border chain between the Lake of Lucerne and the Lake of Thun transgressive sediments of the Eocene unconformably sit on Lower Cretaceous Schrattenkalk. In the southeastern areas the transgressive member is the Complanata limestone, which is characterized by abundant large Nummulites of the *N. mille-*

caput-group. In the section of the Klimsenhorn (Pilatus), it is under- and overlain by a glauconitic sandstone with *N. perforatus* (SCHUMACHER 1948). These sediments clearly belong to the upper part of the Middle Eocene. They are followed by the Hohgant Formation. This formation again is only complete in the southeastern and eastern areas considered here. During its deposition the transgression proceeded in a northwestern direction (Fig. 1). In the western and frontal areas of the Niederhorn nappe only the higher parts of the Hohgant Formation are found (see COLOMBI in HERB et al. 1978). In many areas where lower parts of the Hohgant Formation can be found the sequence begins with a sandy limestone with abundant *Discocyclina discus* (Discus bed or Discocyclina bed). It is often followed by a glauconite horizon (Glauconite beds of the Küblibad, see HERB et al. 1978, Fig. 9).

The Hohgant sandstone, the main member of the Hohgant Formation, shows a distinct cyclic sedimentation in the area north of the Lake of Thun (COLOMBI, unpublished, and BREITSCHMID 1978). In this area it is overlain by a sequence of algal limestones ("Lithothamnienkalk", "Rallig-Marmor"), while in the eastern and northeastern sections it is followed by sandy shales (Schimberg-Schiefer) and Globigerina shales.

The age of the Hohgant Formation has been the subject of long debates in the literature. The history of research was summarized by LEUPOLD & COLOMBI (1964), and the reader is also referred to this article for a more detailed account on the lithostratigraphy. SCHUMACHER (1948) found *"Heterostegina helvetica"* in the Discus bed and the lower part of the Hohgant sandstone and interpreted the formation as being Priabonian. HOTTINGER & SCHAUB (1960) proposed a correlation with their new Biarritzian stage, based on the occurrence of *Nummulites brongniarti*, *N. perforatus* and *N. striatus* in the Schimberg beds.

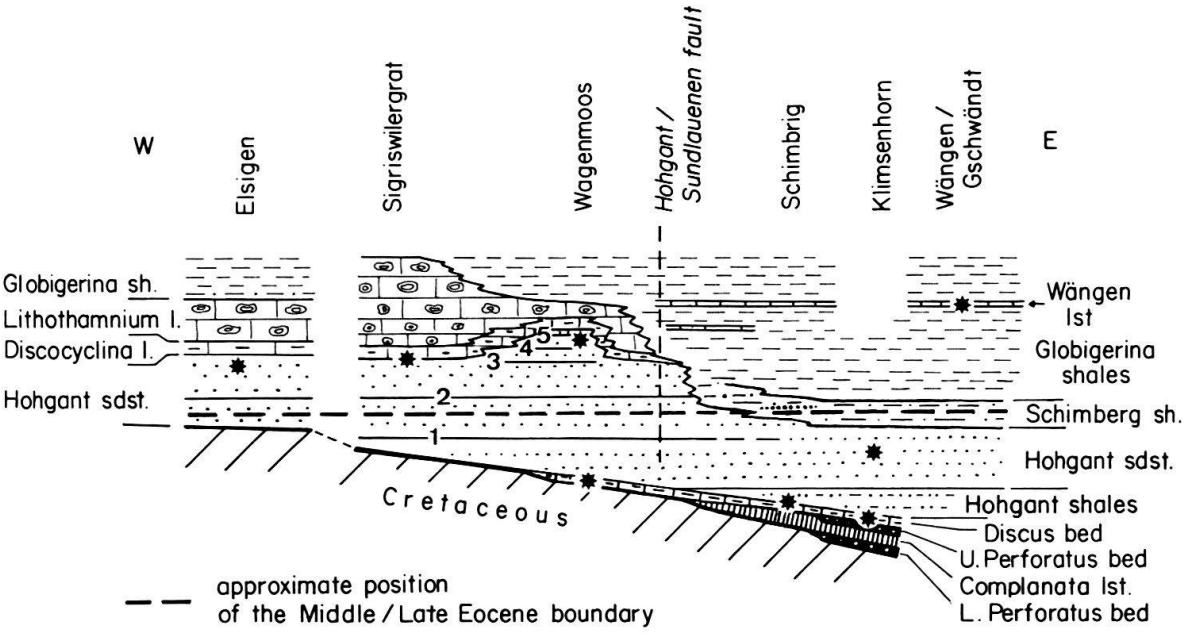


Fig. 1. Schematic stratigraphic cross-section of the Helvetic Eocene between the Lake of Lucerne, the Lake of Thun and south of it. The positions of the samples investigated for this paper are shown with asterisks. 1-5: boundaries of cyclothemes in the Hohgant sandstone (upper limits of Wagenmoos beds).

Type localities and associated larger Foraminifera

Heterostegina reticulata RÜTIMEYER

RÜTIMEYER designated no type locality for the species, but he stated (1850, p. 109) that the material was found at the "Ralligstöcke". In the topographic map of Switzerland 1:25,000 (sheet No. 1208, Beatenberg) the name of Ralligstöcke is given to a series of cliffs north of Merligen, which consist of Lower Cretaceous Schrattenkalk. In the concept of RÜTIMEYER and other authors of the last century the name Ralligstöcke, however, often included at least the whole southwestern part of the Sigriswiler Grat.

I have investigated the area between the Ralligstöcke and the Sigriswiler Rothorn and have found rocks with frequent *H. reticulata* close to the chalet of Oberbergli. This locality is easily accessible and was also quoted by KAUFMANN (1886) as one of the localities where *H. reticulata* occurs. It is designated here as the type locality of the species. My samples were collected along the path, approximately 40 and 90 m northeast of the chalet (coord. 624860/174980). The stratigraphic position is at the limit between the Hohgant sandstone and the algal limestone (Rallig-Marmor) where a transitional zone between the two lithologic units is formed by a sandy limestone with abundant larger Foraminifera, mainly Discocyclinas and Nummulites and some Heterosteginas (Discocyclina limestone, Fig. 1). The larger Foraminifera, however, cannot be isolated from the rock, but in taking rock samples they frequently break in the equatorial plain. It is therefore possible to obtain a collection of more or less complete equatorial sections, but the surface features can only rarely been observed.

A preliminary inventory of the Nummulites at this locality shows the presence of *Nummulites incrassatus, N. chavannesi* and *N. stellatus*, an association which is typical for the Priabonian.

Heterostegina helvetica KAUFMANN

KAUFMANN (1867, p. 155), in his original description of the species did not designate a type locality either, but quoted two localities where he found the species. One of these, south-southwest of the Mittagsgüpfi, is particularly well described on page 36 of his monograph and may serve as type locality. It is located on the path which leads from the locality Gschwänt (1,575 m) to Wängen (1,571 m), in a small torrent 250 m northwest of Gschwänt (coord. 655800/200550, see topographic map of Switzerland 1:25,000, sheet No. 1170, Alpnach). Up to 2 m of a marly, nodular to brecciated limestone with abundant algal nodules and larger Foraminifera is intercalated in a thick sequence of sandy Globigerina shales. Such intercalations of limestones in the Globigerina shales are called Wängen limestones (Fig. 1). They are formed to a great extent by redeposited shallow water debris, mainly coralline algae and Foraminifera. This locality is one of the few in the area where the larger Foraminifera can be isolated.

Associated with *Heterostegina* is a similar assemblage of Nummulites as at Oberbergli, with *Nummulites incrassatus, N. chavannesi, N. stellatus* and *N. pulchellus.*

Comparison of topotypes

As indicated above, isolated specimens of *Heterostegina* are only available at the type locality of *H. helvetica*. Their surface morphology will be described in the systematic part. Equatorial sections of 20 specimens and drawings of most of them were made. From Oberbergli about 20 equatorial planes of *H. reticulata* were found on the cut rock surfaces. Although most of them are incomplete, they still allow observation of the main morphological features. Drawings were made of 10 specimens. Microspheric forms are rare; only one specimen was found at Oberbergli.

A selection of equatorial sections from both localities is given on Figures 2–13. They clearly show that *H. helvetica* is virtually identical with *H. reticulata*. The diameter of the initial chamber in megalospheric specimens is between 0.10 and 0.12 mm in most cases. The subdivision of chambers occurs within the first whorl, except for one specimen, where it occurs within the second whorl and another specimen where no or incomplete subdivisions were observed. In the taxonomic concepts explained below the first of these exceptions falls within *H. reticulata multifida* and the second within *Operculina gomezi*.

In the greater part of the spiral the chamberlets are polygonal or irregularly rounded and arranged in a more or less irregular network. The basal chamberlets are usually much higher than wide. In external parts of the whorl a transition from this irregular network to a more regular arrangement of chamberlets in arched rows of subrectangular or subhexagonal chamberlets is visible in more or less complete specimens.

The spiral is in the average somewhat more loosely coiled in specimens from Oberbergli than in those from Gschwänt. A great range of variation with a strong overlap is visible with respect to the coiling pattern at the two localities and this criterion is not significant enough for separating specifically the material from the two localities. *H. helvetica* is therefore regarded as being a junior synonym of *H. reticulata*. The differences in the surface structures noted by KAUFMANN, are due to preservation and weathering of specimens at the particular localities.

Heterostegina and Operculina from some other localities in the Helvetic nappes

Samples with *Heterostegina* and *Operculina* were also collected at a number of other localities in the Helvetic border chain (Niederhorn nappe) and in the Wildhorn nappe:

1. Upper Hohgant sandstone east of Elsigenalp, south of Frutigen and northeast of Adelboden (see topographic map of Switzerland 1:25,000, sheet No. 1247, Adelboden, coord. 615 800/152 100). At this location the middle part of the Hohgant sandstone transgressively overlies the Cretaceous Schrattenkalk. It is followed by two intercalations of brackish limestones with gastropods, corresponding to the "Brackwasserschichten der Berglikehle" (Fig. 1). The overlying upper Hohgant sandstone contains some levels with *Nummulites striatus* in the lower part and a more diversified assemblage of larger Foraminifera, with *N. incrassatus*, *N. pulchellus*, *N. chavannesi*, *N. striatus* s.l., *N. stellatus*, *Heteroste-*

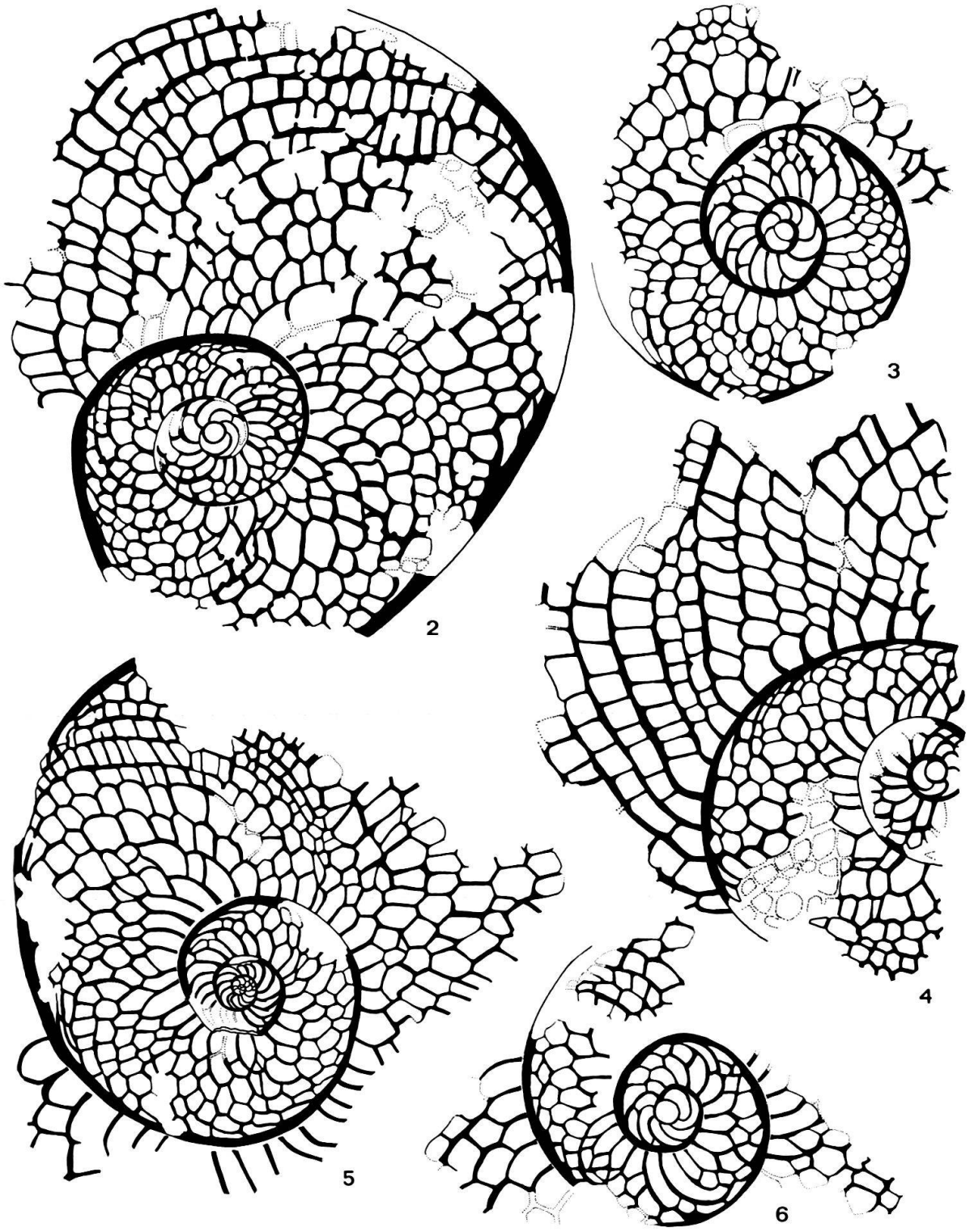


Fig. 2–6. *Heterostegina reticulata reticulata* RÜTIMEYER. Equatorial sections from Oberbergli (Sigriswiler Grat), the type locality designated herein. Upper limit of Hohgant sandstone, early Priabonian. 2, 3, 4, 6 = Megalospheric specimens; 5 = microspheric specimen. All ×20.

gina and *Operculina alpina* in the upper part. The upper Hohgant sandstone is again followed by algal limestones. Equatorial sections of the larger Foraminifera were collected in the upper part of the upper Hohgant sandstone. Their stratigraphic position is a little lower than the samples from Oberbergli, but the assemblage still belongs to the early Priabonian.

The equatorial sections of *Heterostegina* differ from those of the type of *H. reticulata* as described above in showing no subdivision of chambers into

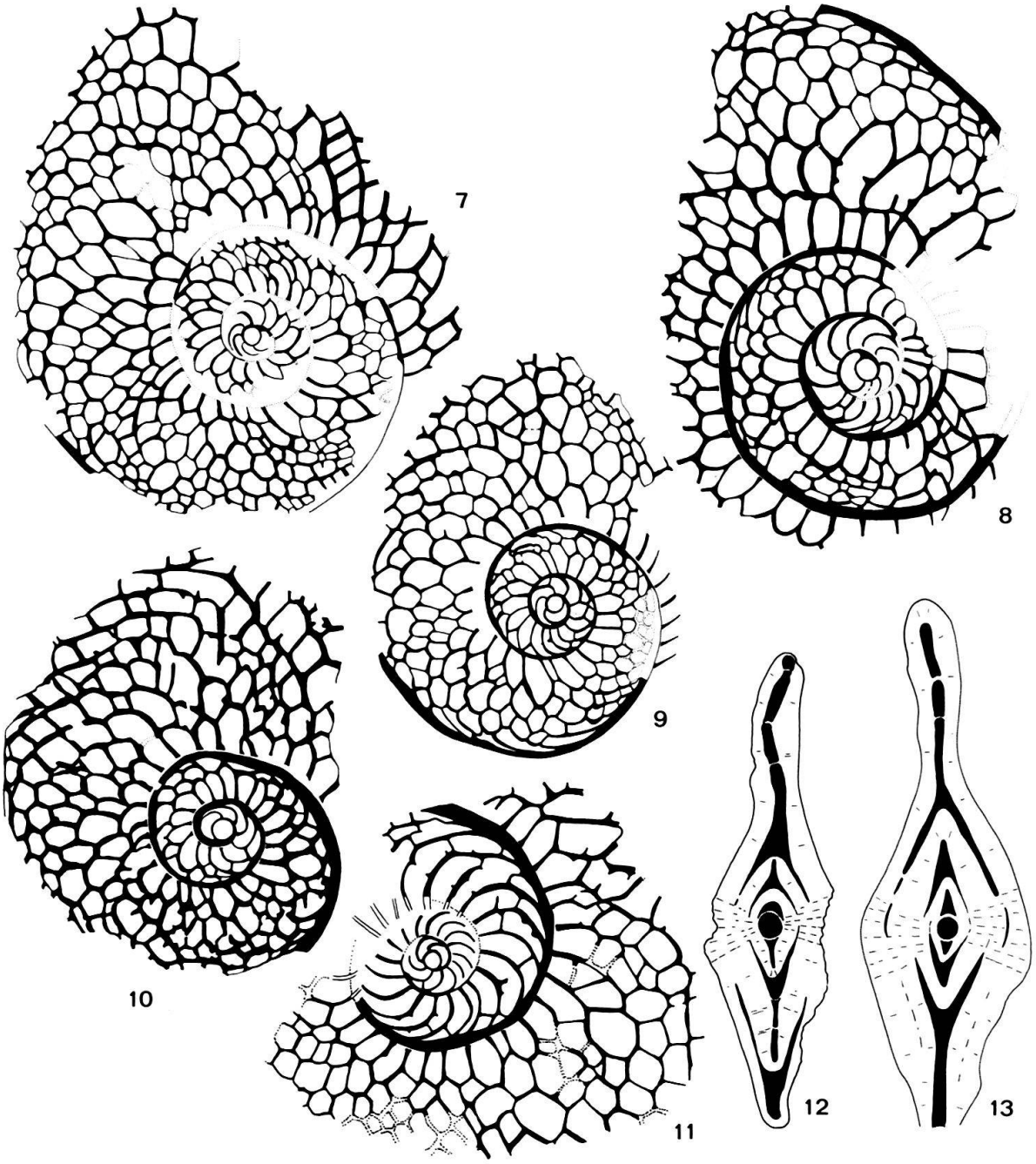


Fig. 7-13. Assemblage of *Heterostegina* form the type locality of *H. helvetica* KAUFMANN near Gschwänt (Pilatus area). Wängen limestone, Priabonian. 7-10 = *Heterostegina reticulata reticulata* RÜTIMEYER; 11 = *Heterostegina reticulata multifida* BIEDA; 12, 13 = *Heterostegina reticulata* ssp., axial sections. All ×20.

chamberlets before the second whorl. Scattered subdivisions frequently occur ¼ to ½ of a whorl before the main subdivided part of the spiral begins (Fig. 14–17). The arrangement of the chamberlets is even more irregular than in the type of *H. reticulata*, but again becomes more regular in outer portions of the spiral if preserved. The relationship with the type of *H. reticulata* is very close, however. The form from Elsigenalp can be regarded as an earlier evolutionary stage or an ecological variant. It was described by BIEDA (1950, 1963) as a separate species, *H. multifida*. Due to the close relationship and the possibility that it is merely an ecological variant, it is here defined as a subspecies of *H. reticulata*, *H. reticulata multifida*.

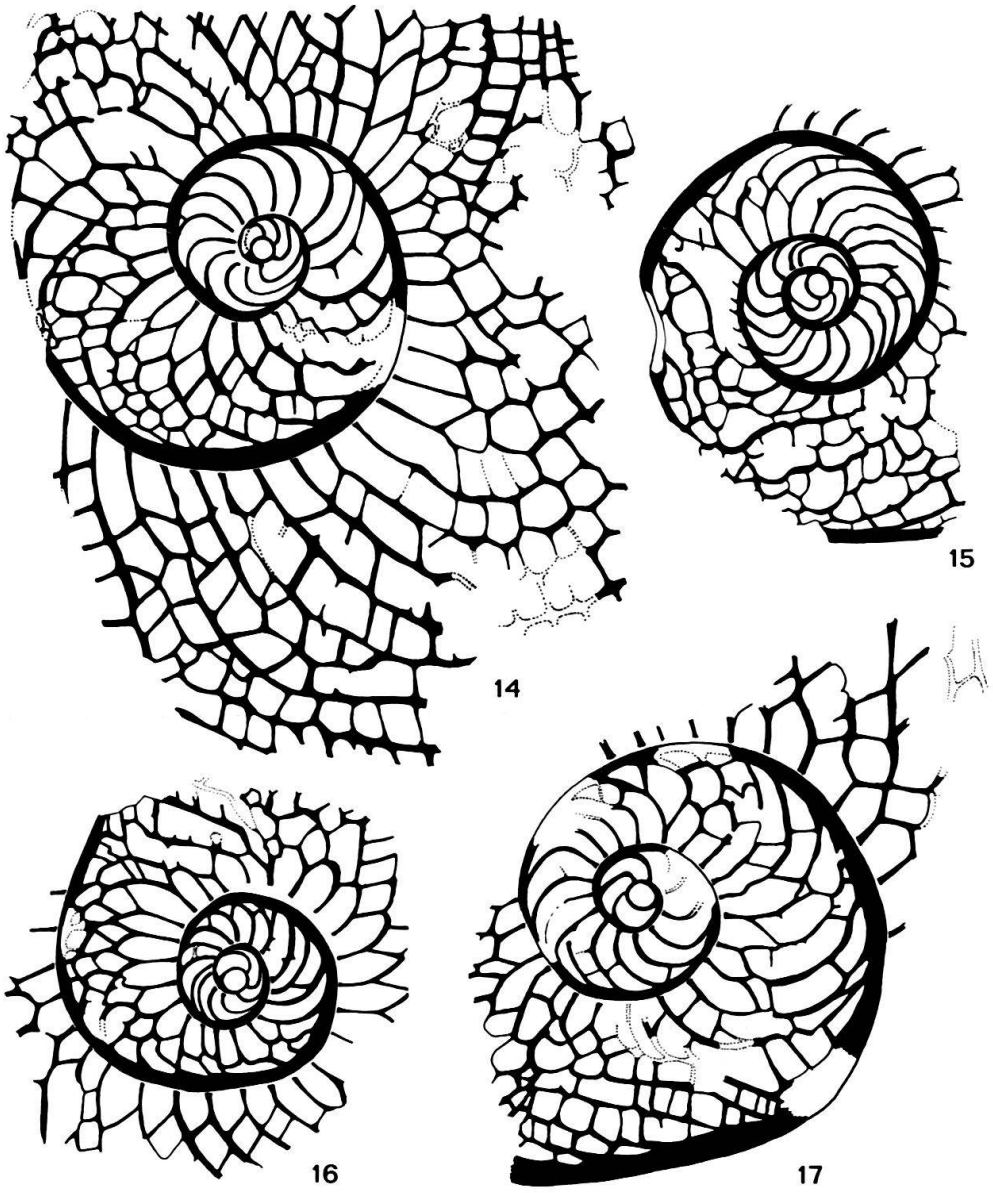


Fig. 14–17. *Heterostegina reticulata multifida* BIEDA, equatorial sections of megalospheric specimens, upper Hohgant sandstone (early Priabonian) of Elsigen. Figure 15 is a transitional form to *Operculina gomezi* COLOM & BAUZÀ. 14 = Sample Hb 75/112; 15–17 = sample Hb 75/108. All ×20.

Associated are large specimens of *Operculina alpina* (Fig. 40) and an assemblage of Nummulites with *N. pulchellus*, *N. incrassatus* and *N. striatus* s.l. which indicates an early Priabonian age.

2. At the locality Wagenmoos, 4 km northwest of Habkern, B. Bieri has collected a rich assemblage of Nummulites and Operculinas in the uppermost Hohgant sandstone. In this material a few equatorial sections were found which show subdivisions of chambers even in later portions of the spiral than in *Heterostegina reticulata multifida* from Elsigen (Fig. 18, 19) and with many of these subdivisions incomplete; this form can be compared with one of the specimens figured by HOTTINGER (1977, Fig. 38D) as *Operculina gomezi*. At Wagenmoos *Nummulites striatus*, *N. stellatus*, *N. pulchellus* and *Operculina alpina* are associated with this form. This again indicates an early Priabonian age.

3. A few equatorial sections of involute *Operculina* (Fig. 20, 21) were found in the upper part of the Hohgant sandstone of the Klimsenhorn section (Pilatus mountains). One of them shows some subdivisions of chambers in the first and second whorl. In the main part of the spiral, however, chambers are not subdivided, but instead show a number of "septal flaps" (HOTTINGER 1977). Another does not show any subdivision before the third whorl. These forms may again be attributed to *O. gomezi* in the concept of HOTTINGER. Larger Foraminifera are not frequent in most of the Hohgant sandstone in this section. Nummulites

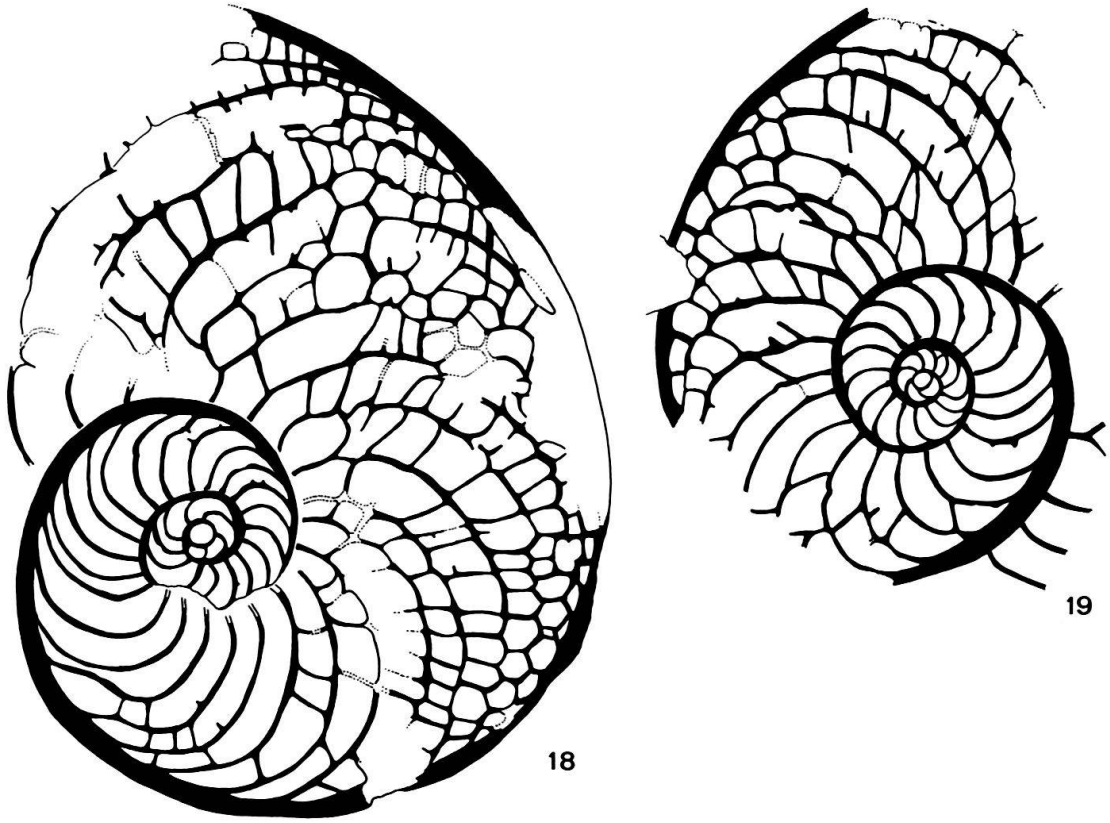


Fig. 18, 19. *Operculina gomezi* COLOM & BAUZÀ, equatorial sections. Uppermost Hohgant sandstone (early Priabonian), Wagenmoos (Habkern). Sample B. Bieri Wa 37. ×20.

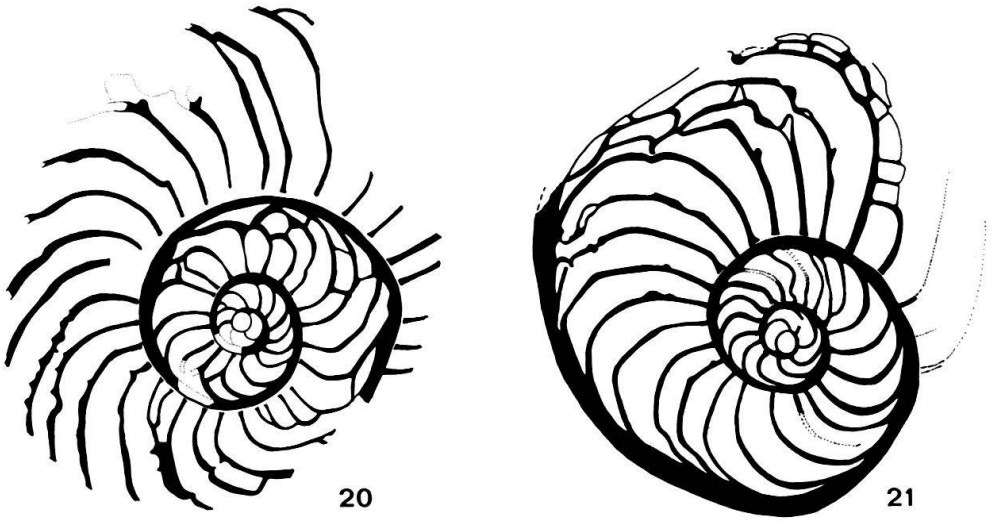


Fig. 20, 21. *Operculina gomezi* COLOM & BAUZÀ, equatorial sections. Hohgant sandstone (Biarritzian), Klimsenhorn (Pilatus area). 20 = Coll. R. Herb 75/121; 21 = Coll. B. Bieri. ×20.

predominantly belong to *N. striatus* s.l. In the sandy shales above the Hohgant sandstone, which are equivalents of the Schimberg beds, B. Bieri has collected an assemblage of *N. striatus* and *N. incrassatus* with a few megalospheric specimens of *N. puschi.* This last form indicates a latest Middle Eocene (Biarritzian) age. The entire Hohgant sandstone of the Klimsenhorn section therefore belongs to the Middle Eocene. The formation is heterochronous as indicated in Figure 1.

4. Discus bed and Glauconite beds of the Küblibad. Samples from these basal members of the Hohgant formation were collected by the author in the Waldegg anticline (HERB et al. 1978, Fig. 9), at Wagenmoos and at the base of the Klimsenhorn section (see also SCHUMACHER 1948). Further samples were provided by B. Bieri from the Schimbrig section. Equatorial sections occur less frequent on cut rock surfaces and preparation procedures are more difficult in this material than in the Hohgant sandstone.
Small involute Operculinas with only occasional subdivision of chambers can be found in these beds (Fig. 22-26). They may well be compared with *Operculina*

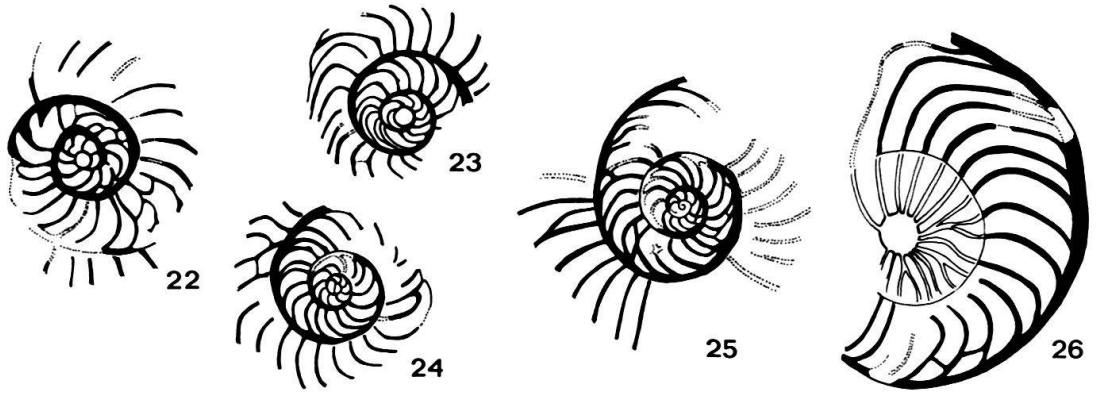


Fig. 22-26. *Operculina bericensis* OPPENHEIM, equatorial sections. 22-24 = Glauconitic base of Hohgant sandstone, Schimberg, Coll. B. Bieri; 25, 26 = Discus bed, Wagenmoos (Habkern), Coll. R. Herb 78/37. ×20.

bericensis OPPENHEIM as redefined by HOTTINGER (1977). SCHUMACHER (1948) has identified their axial sections erroneously as *Heterostegina helvetica*. Based on this misidentification these beds were placed by him and most subsequent workers in the Priabonian.

Associated with these involute Operculinas are *Nummulites biaritzensis* D'ARCHIAC and related forms as well as rare evolute Operculinas (*O.* cf. *schwageri* SILVESTRI, see HOTTINGER 1977). These assemblages are typical for latest Middle Eocene (Biarritzian).

2. Occurrences in the Late Eocene of Northern Italy

In his monograph on operculiniform Foraminifera HOTTINGER (1977) mentioned the existence of two species of *Heterostegina* in the Late Eocene. One, which he named *H. reticulata*, has a relatively flat test and an open spiral. The other is more inflated and shows a closer spiral; it was named *H. helvetica*. Based on specimens from the sections of Possagno and Mossano in the Priabonian of Northern Italy HOTTINGER's statement can be confirmed except for the nomenclature.

In the Late Eocene of Possagno the genus *Heterostegina* has been found in many samples from the Calcare di S. Giustina (latest Priabonian). For location of samples and associated Larger Foraminifera, mainly Nummulites, see HERB & HEKEL (1973, 1975). Most of the specimens clearly belong to the group of *H. reticulata* as defined in the present paper. They correspond to what has been named *H. helvetica* by HOTTINGER (1977, Fig. 46B–E). They differ, however, from the type of *H. reticulata* in being larger, in having a slightly larger protoconch with diameters between 0.14 and 0.20 mm, and in showing a more regular pattern in the arrangement of the chamberlets. In megalospheric specimens the subdivision of chambers almost invariably occurs already in the third or fourth chamber, in exceptional cases even in the second chamber. A reoccurrence of undivided chambers, as noted in the type of *H. reticulata* or in *H. reticulata multifida*, can usually not be observed. These differences are, however, not considered enough of a distinction for a separation from *H. reticulata* on a specific level. The form is here defined as a new subspecies, *H. reticulata italica*. It has also been found in the lower and middle part of the Priabonian of Mossano (Colli Berici). A specimen from the lower part of the section, corresponding approximately to sample 4 in HERB & HEKEL (1973, Fig. 4), was also figured by HOTTINGER (1977, Fig. 46E).

The second species which was found in the Calcare di S. Giustina of Possagno is less frequent than *H. reticulata italica*. It is distinguished from the *reticulata*-group by a different surface structure. Instead of a distinct central pillar the test has a slightly elevated central portion with a fine surface granulation. Compared with the *reticulata*-group the chamberlets are mostly rectangular or hexagonal and arranged in a much more regular pattern, a difference which is particularly significant in the early portion of the spiral. The spiral wall of the protoconch and the deuteroconch is not as thick as in *H. reticulata italica*. The spiral is generally more open than in the *reticulata*-group.

HOTTINGER (1977) has called this form *H. reticulata*. For the reasons stated above it must be separated from the *reticulata*-group and is here defined as a new

species, *H. gracilis*. It seems to be closely related to *H. praecursor* TAN SIN HOK, of which it may be an ancestral form.

3. Problems of generic and specific assignments

The evaluation of the taxonomic problems which are raised by the material from the Helvetic nappes, is made difficult by the fact that in many cases only equatorial sections are available. Important features of the test, such as pillars, septal lines or ornamentation, for which isolated specimens are needed, can only occasionally be observed. The restricted number of specimens per assemblage in randomly cut rock surfaces limits a full estimation of the variability within the species.

Despite these shortcomings the present material demonstrates the presence of a gradational sequence of morphotypes between involute *Operculina* with virtually undivided chambers on the one hand and involute *Heterostegina* with a full development of secondary chamber partitions on the other. Within this sequence a number of morphotypes can be characterized and assigned to names of species or subspecies already available in the literature. Their biostratigraphic or ecologic significance, however, remains open in most cases.

HOTTINGER (1977) separated the involute species of *Heterostegina* from the *Operculina gomezi* group in which he distinguished between the more primitive forms of the Biarritzian with virtually no chamber partitions, such as *O. bericensis* and *O. roselli*, and the larger *O. gomezi*. The latter species is found in the Biarritzian as well as in the Priabonian and, according to HOTTINGER, even in the Oligocene. It occurs in a number of morphotypes, for some of which VITALIS-ZILAHY (1966) introduced new names. Most of the specimens of this group which have so far been found in the Helvetic nappes, do not fall within the species defined by VITALIS-ZILAHY, however. The concept of a highly variable *O. gomezi*, as used by HOTTINGER (1977) is therefore adopted here, although, in contrast to HOTTINGER's grouping of species, the present material rather indicates a transition from *O. gomezi* to the involute *Heterostegina reticulata* group.

Despite the great range of morphotypes, the intraspecific variation of *O. gomezi* within a single assemblage is usually quite limited, as investigations of samples with abundant specimens from the Eocene of the Varesotto (HERB 1976), Priabona (see also ROVEDA 1961) and Biarritz (Villa Marbella beds) have shown. As no evolution with a specific trend has so far been recognized, the occurrence of a particular morphotype of *O. gomezi* seems to be mainly ecologically controlled. It cannot be excluded that a similar pattern in the occurrence of morphotypes exists for *Heterostegina reticulata multifida* and *H. reticulata reticulata*, although the stratigraphic record so far available rather indicates a time evolutionary sequence. Unfortunately the stratigraphic position of BIEDA's type of *H. multifida* is not known with sufficient accuracy.

The taxonomic nomenclature adopted in this paper for the group of *Operculina gomezi–Heterostegina reticulata* mainly serves to characterize a number of morphotypes within a gradational sequence of still insufficiently known significance; names already used in the literature are retained. It has no ambition to be a "natural" classification.

There are other problems concerning the generic nomenclature. BIEDA (1950) designated the species *multifida* as genotype for his new genus *Grzybowskia*, which has subsequently been widely used as genus name for Eocene Heterosteginids. However, HOTTINGER (1977) has shown that the definition of the genus *Grzybowskia* falls within the range of variation of *Heterostegina depressa*, the genotype of *Heterostegina*. We therefore follow HOTTINGER in not using *Grzybowskia* as a genus name for the Eocene involute *Heterostegina*.

The distinction of the genera *Operculina* and *Heterostegina* within the group of Eocene involute species seems problematic also. HOTTINGER's main argument for separating the *gomezi*-group from the involute species of *Heterostegina* was the observation of a large amount of variability within the species *O. gomezi*, whereas the genus *Heterostegina* always shows chambers subdivided in a specific manner. HOTTINGER regards the type of chamber divisions in *O. gomezi* as a first attempt towards construction of secondary chambers, independent, however, from the *Heterostegina* lineage.

If a gradational sequence as explained above is accepted for this group, a separation on a generic level seems not justified, but it is admitted that the preservation of the specimens from the Helvetic nappes did not allow a sufficiently detailed study of the test morphology, particularly with respect to the wall structure. The generic concept of HOTTINGER is therefore adopted here in order to respect the stability of nomenclature as far as possible.

4. Description of species

Operculina bericensis OPPENHEIM

Fig. 22-26

1896 *Operculina bericensis* OPPENHEIM, p. 37, Pl. 5, Fig. 14.

1977 *Operculina bericensis* OPPENHEIM, HOTTINGER, p. 95, Fig. 37D-N. For further synonymy and definition of species see this publication.

The small involute *Operculina* which is found in the Discus bed and the glauconitic beds at the base of the Hohgant Formation belongs to this species. Its equatorial section is characterized by a small proloculus (0.08 mm or less) of the megalospheric form, and a relatively slowly growing spiral. Few secondary septa may occur occasionally at various intervals in the spiral, but are often absent. The surface structure of the test could not be observed in the available material from the Helvetic nappes except of one specimen (Fig. 26) where the surface of the last but one coil is visible. It shows a distinct central pillar and radial to slightly sigmoidal septal lines which bifurcate sometimes.

In the literature on the Helvetic Eocene this species has usually been named as *Heterostegina helvetica* (e.g. SCHUMACHER 1948) or cf. *helvetica* (e.g. GIGON 1952).

Operculina gomezi COLOM & BAUZÀ

Fig. 18-21

1950 *Operculina canalifera gomezi* COLOM & BAUZÀ, p. 219, Pl. 17, Fig. 1-3, Textfig. 1 and 2.

1977 *Operculina gomezi* COLOM & BAUZÀ, HOTTINGER, p. 98, Fig. 38A-F. For further synonymy and definition of species see this publication.

Relatively few equatorial sections of this species have so far been found in the Helvetic zone, most of them from the Hohgant sandstone of the Klimsenhorn and of Wagenmoos. They show an open spiral with usually no subdivisions of chambers before the second whorl. Septal flaps, however, may occur in earlier portions of the spiral. Form and size of the chamberlets are highly variable and the secondary septa often incomplete. Diameter of the megalosphere 0.10–0.13 mm, which is slightly less than the values given in the emended diagnosis of HOTTINGER (1977). The specimens from the Klimsenhorn are incomplete. They are of Biarritzian age; those from the Wagenmoos occur in the early Priabonian.

Heterostegina reticulata RÜTIMEYER

Based upon differences in the internal structure, as shown in the equatorial section, three forms can be distinguished which are here defined as subspecies of *H. reticulata.* All are distinctly involute. They show a similar surface structure of the test with a well-pronounced central pillar, from which straight or slightly sigmoidal septal lines radiate. These pass into a more or less regular pattern of chamberlets which is visible on the surface of the external, depressed portion of the test.

Heterostegina reticulata multifida (BIEDA)

Fig. 11, 14–16

1950 *Grzybowskia multifida* BIEDA, p. 151, 167, Pl. 3, Fig. 1–9, Pl. 4, Fig. 1, 3 (non Fig. 2).
1963 *Grzybowskia multifida* BIEDA, BIEDA, p. 108, 198, Pl. 17, Fig. 1, 2.

The equatorial section shows an open spiral, similar to *Operculina gomezi* or *Heterostegina reticulata reticulata.* A subdivision of chambers occurs only sporadically in the first whorl. It begins to be continuous within the second whorl. The form and often also the arrangement of chamberlets is variable, a feature in which *H. reticulata multifida* differs from *H. reticulata reticulata,* but is similar to *O. gomezi,* although the irregularities are usually less pronounced. Diameter of the protoconch 0.10–0.14 mm.

Most specimens have been found in the section of Elsigen and very few at Oberbergli and Gschwänt. Their equatorial sections are identical with the well-illustrated types of BIEDA. This subspecies of *H. reticulata* seems to occupy an intermediate position between *O. gomezi* and the type of *H. reticulata* as defined below.

Heterostegina reticulata reticulata RÜTIMEYER

Fig. 2–10, 12, 13, 35

1850 *Heterostegina reticulata* RÜTIMEYER, p. 109, Table 4, Fig. 61.
1867 *Heterostegina helvetica* KAUFMANN, p. 153, Pl. 9, Fig. 6–10.
1963 *Grzybowskia reticulata* (RÜTIMEYER), BIEDA, p. 109, 199, Pl. 17, Fig. 3–6.

Holotype. – The specimen figured by RÜTIMEYER (1850, Table 4, Fig. 61) is housed in the Museum of Natural History in Bern. It is an equatorial section included in a small piece of calcareous sandstone which also contains one specimen of *Nummulites incrassatus.* Form and arrangement of chamberlets are only visible in the external portions of the spiral, as shown in the figure of RÜTIMEYER.

Type locality. - Designated as "Ralligstöcke" by the author. This name has been used by earlier authors to designate the southwestern portion of the Sigriswiler Grat. The specimens from the locality Oberbergli on Figures 2-6 are considered as topotypes, as explained on page 748.

Type level. - Not clearly indicated by RÜTIMEYER. The lithology of the rock containing the holotype, and the associated *N. incrassatus*, as well as my field investigations indicate uppermost Hohgant sandstone or transitional beds to the Lithothamnium limestone of early Priabonian age.

Diagnosis. - Involute test, biconvex with a thin marginal portion. The surface shows the typical structural elements of the *reticulata*-group: a central pillar, radial or slightly sigmoidal septal lines passing into the reticulate structure of chamberlets in the marginal portion. Diameter: mostly 3-4, up to 5 mm, thickness: 0.8-1.2 mm.

Equatorial section of the megalospheric form: Diameter of the proloculus 0.10-0.12 mm. The number of nondivided chambers in the initial portion of the spiral varies between 4 and 11 before the first chamberlets are formed. Both divided and nondivided chambers may occur in the first whorl. In the inner portion of the spiral the chamberlets are polygonal or subtrapezoidal and mostly irregular in their arrangement. They become rather subhexagonal or subrectangular in the external portions.

Equatorial section of microspheric form: only one incomplete specimen was found at Oberbergli (Fig. 5). It shows mostly nondivided chambers in the first three whorls, with only few chambers having a secondary septum in the upper part of the chamber. Continuous formation of chamberlets occurs at the end of the third whorl. Form and arrangement of the chamberlets are similar to that known in the megalospheric form.

Remarks. - Megalospheric specimens of *H. reticulata reticulata* differ from *H. reticulata multifida* in showing continuous subdivision of chambers in earlier portions of the spiral, i.e. not later than at the beginning of the second whorl, and from *H. reticulata italica* by the discontinuous occurrence of secondary septa in the first whorl. The size of the initial chamber is slightly smaller than in *H. reticulata italica.*

Heterostegina reticulata italica n. ssp.

Fig. 27-30, 36, 38

1977 *Heterostegina helvetica* KAUFMANN, HOTTINGER, p. 109, Fig. 46B-E.

Holotype. - Megalospheric specimen of Figure 26, deposited in the Museum of Natural History in Bern.

Type locality. - Val Organa, 1.3 km south of Possagno (Treviso, Italy).

Type level. - Calcare di S. Giustina, late Priabonian, sample 728b of HERB & HEKEL (1975, Fig. 2, 4).

Diagnosis. - Involute, slightly biconvex test with a surface structure characteristic of the *reticulata*-group: a distinct central pillar, radial or slightly sigmoidal septal lines in the central, convex portion, passing to the rectangular or hexagonal network

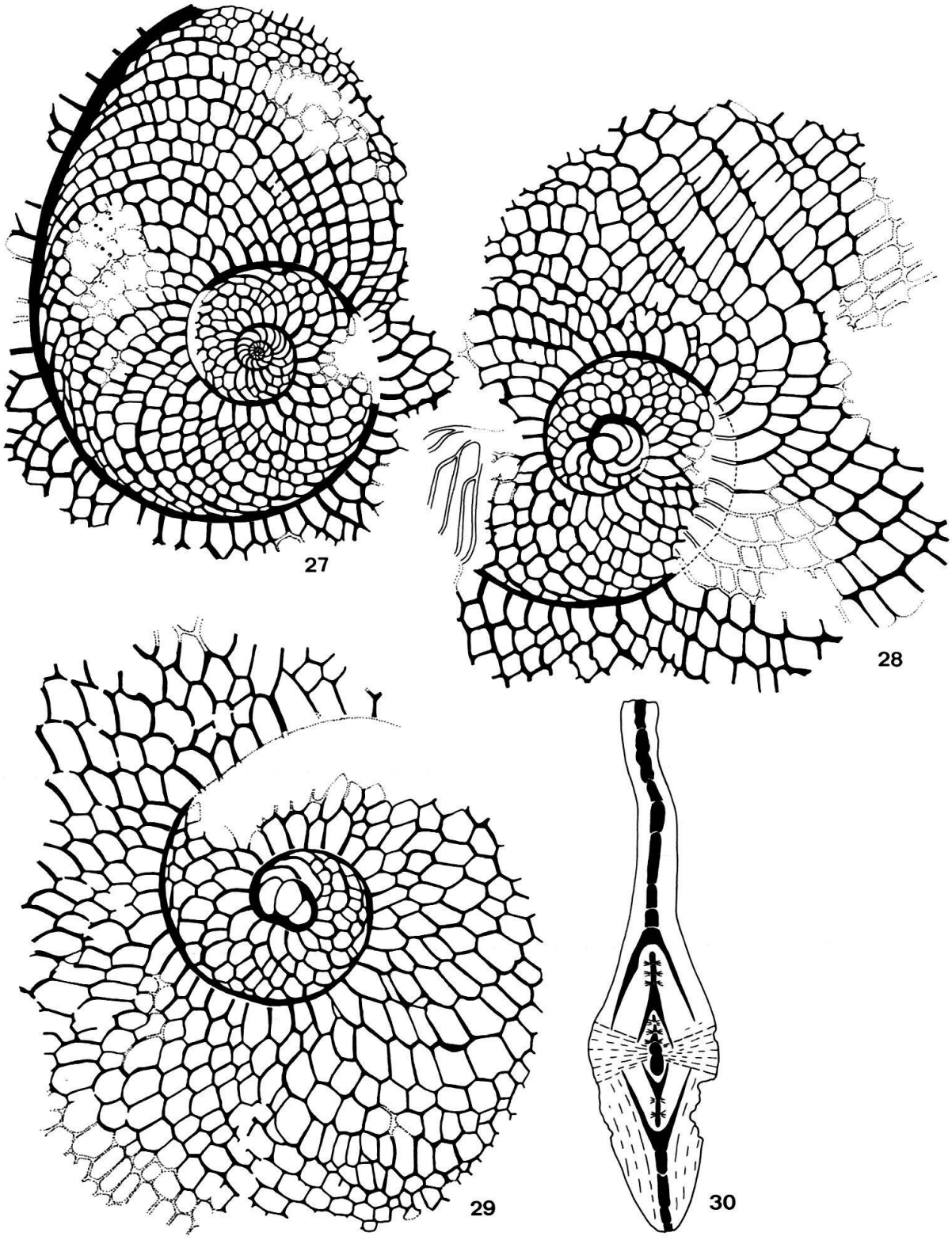


Fig. 27–30. *Heterostegina reticulata italica* n.ssp. 27 = Equatorial section of microspheric specimen. Calcare di S. Giustina, latest Priabonian, Val Organa, Possagno, sample 728c, in HERB & HEKEL (1975). 28 = Equatorial section of megalospheric specimen (Holotype), same locality as Figure 27, sample 728b. 29 = Equatorial section of megalospheric specimen with double protoconch, Priabonian of Mossano (Colli Berici), sample Mo 4 in HERB & HEKEL (1973). 30 = Axial section of megalospheric specimen. Calcare di S. Giustina, latest Priabonian, Cunial/Col dell'Asse, Possagno, sample 689 in HERB & HEKEL (1975). All ×20.

of primary and secondary septa which is usually visible on the depressed external portion of the test. Diameter of the test mostly 4–6 mm, thickness 0.9–1.2 mm.

Equatorial section of the megalospheric form: diameter of the proloculus 0.14–0.20 mm. A relatively thick spiral wall occurs around ⅓ of the proloculus and over the first few chambers. A doubled initial chamber was observed in one specimen (Fig. 29). Second, third and in most cases also the fourth chamber are nondivided. Subsequent chambers are divided into a relatively regular network of chamberlets in the first 1–1½ whorls. This portion is followed by subrectangular or subhexagonal chamberlets which usually are higher than large.

Equatorial section of the microspheric form: one incomplete specimen has so far been found (Fig. 27). It shows 2¾ whorls of nondivided chambers, followed by some chambers which are divided only in their upper part. In the following section of about ⅓ of a whorl the chamberlets are polygonal and arranged in form of a network, but in the main portion of the spiral they are subrectangular or subhexagonal and arranged in arched rows. In most of the preserved part of the test they are smaller than in the megalospheric form, but apparently become larger in external parts of the spiral.

Remarks. – This subspecies differs from the type of *H. reticulata* in showing a larger initial chamber in the megalospheric form, with a thicker spiral wall above the first few chambers, and a continuous formation of chamberlets already after the third or fourth chamber, the arrangement of chamberlets being more regular than in *H. reticulata reticulata*. *H. reticulata italica* is clearly distinguished from *H. gracilis* by its different surface structure as well as by its equatorial section (see definition of *H. gracilis*).

Heterostegina gracilis n. sp.

Fig. 31–34, 37

1977 *Heterostegina reticulata*, HOTTINGER, p. 109, Fig. 44A, B, ?C, ?D.

Holotype. – Megalospheric specimen of Figure 29, deposited in the Museum of Natural History in Bern.

Type locality. – Val Organa, 1.3 km south of Possagno (Treviso, Italy).

Type level. – Calcare di S. Giustina, latest Priabonian, sample 728b of HERB & HEKEL (1975, Fig. 2 and 4).

Diagnosis. – Thin, but involute test, slightly biconvex over the central portion of the spiral. Diameter of specimens from Possagno up to 8 mm, thickness 0.8–1.0 mm. On the depressed external portion of the test surface a regular pattern of strongly curved chambers, regularly subdivided into rectangular small chamberlets is visible. Pillars are formed towards the centre at intersections of primary and secondary septa, and over the central portion of the spiral a granular structure of pillars is visible which is quite regular in some specimens, but may be more irregular in others. No distinct central pillar is formed. The axial section (Fig. 32) demonstrates, that *H. gracilis* is a truly involute form only in its inner whorls. In the last whorl the test itself is involute, but the chambers have no lateral extension. They are therefore evolute, and, as a consequence of this, no septal lines are therefore visible on the

surface of the test. Equatorial section of the megalospheric form: diameter of the proloculus 0.18-0.24 mm; large, kidney shaped second chamber; both proloculus and second chamber with a thin wall. Subdivision of chambers into regularly arranged, rectangular, subrectangular or hexagonal chamberlets beginning with the third or fourth chamber. Spiral wall and primary and secondary septa are relatively thin; the equatorial section therefore shows a quite delicate structure.

Remarks. - This form was briefly described by HOTTINGER (1977) under the name of *Heterostegina reticulata.* It differs, however, from the type of this species, as defined herein, in being larger (although complete specimens are rare), in having a thinner test, and in showing a more delicate wall structure in the equatorial section. The arrangement of chamberlets is more regular from their first appearance, with smaller chamberlets than the *reticulata*-group. *H. gracilis* has a granular surface structure of pillars over the central portion of the spiral, whereas the *reticulata*-group shows a distinct, relatively large central pillar.

H. gracilis seems to be closely related to the Oligocene *H. praecursor* TAN SIN HOK, of which it may be an ancestral form (HOTTINGER 1977). *H. praecursor* has a granular surface structure and the pillars are also formed at intersections of primary and secondary septa. The pillars are, however, more numerous, smaller and extend over a greater surface of the test than in *H. gracilis.* In the equatorial section *H. praecursor* shows a more open spiral than *H. gracilis.* Some of the sections figured by HOTTINGER (1977) under the name of *H. praecursor* are closer to *H. gracilis* than to the type of *praecursor.* A more detailed investigation, comparing surface structures as well as equatorial sections is needed for this group of Late Eocene to Oligocene Heterosteginas.

Operculina alpina DOUVILLÉ

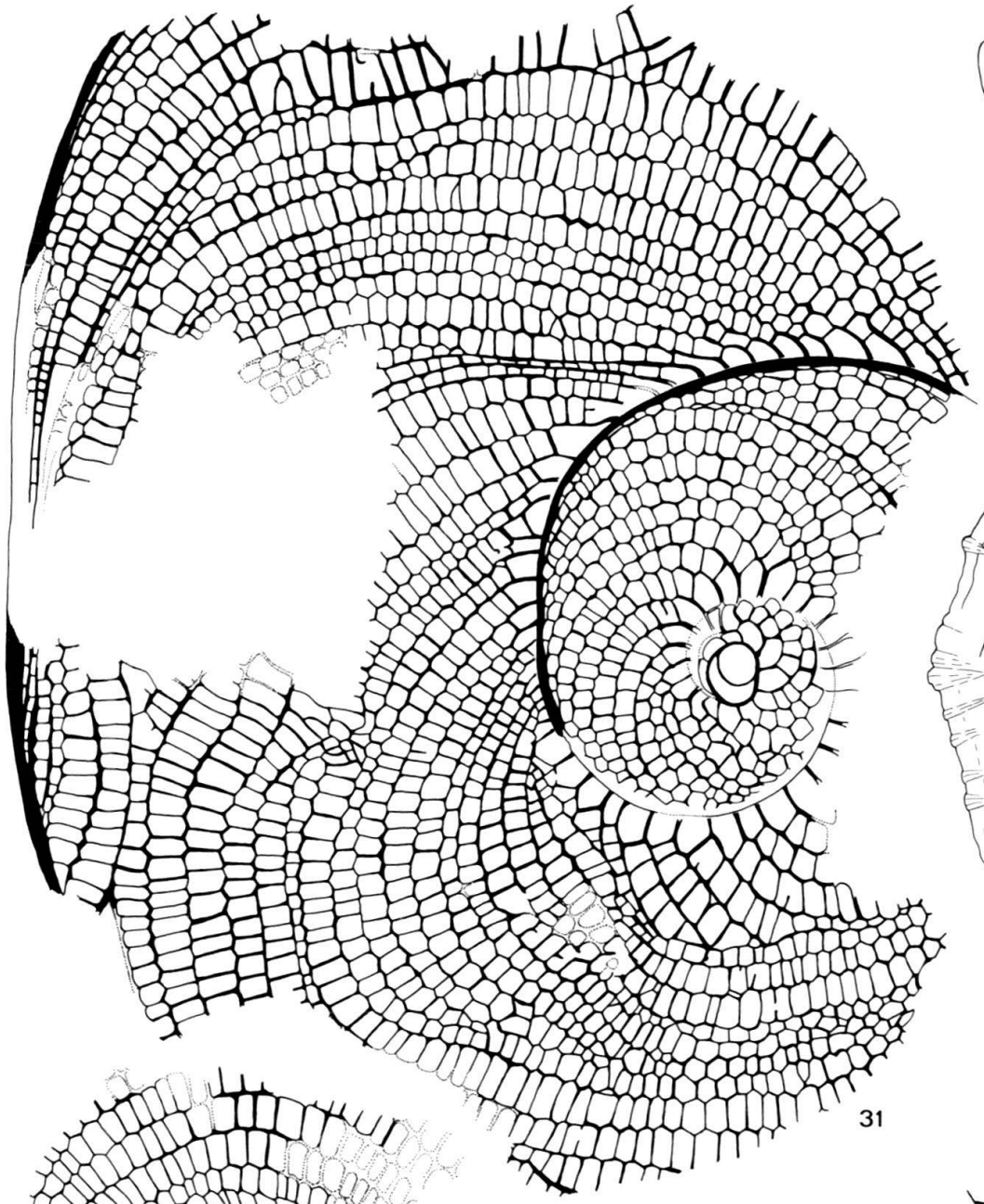
Fig. 40, 41

1916 *Operculina alpina* DOUVILLÉ, p. 329, Fig. 1.
1977 *Operculina alpina* DOUVILLÉ, HOTTINGER, p. 85, Pl. 38, Fig. 4-6, Textfig. 33, 34.

For a detailed description of this evolute *Operculina,* as well as for the discussion of synonyms we refer to HOTTINGER (1977). At some localities in the Helvetic nappes, such as Elsigen or Wagenmoos, *O. alpina* is a common species in the uppermost Hohgant sandstone. *O. schwageri,* its precursor, has been found in the glauconitic beds at the base of the Hohgant Formation.

Operculina alpina also occurs abundantly in the upper part of the Marna di Possagno and in some levels of the Calcare di S. Giustina of the Possagno section (HERB & HEKEL 1975). The size of the specimens as well as of the megalosphere, however, is much smaller in the Possagno clay than in the overlying limestone (GRÜNIG & HERB, in press).

Fig. 31-34. *Heterostegina gracilis* n.sp. Calcare di S. Giustina, latest Priabonian, Possagno. 31 = Equatorial section of megalospheric specimen (Holotype), Val Organa, sample 728b in HERB & HEKEL (1975). 32 = Axial section of megalospheric specimen, Cunial/Col dell'Asse, sample 694. 33 = Equatorial section of megalospheric specimen, same sample as Figure 31. 34 = Centre of megalospheric specimen, same sample as Figure 31. All ×20.



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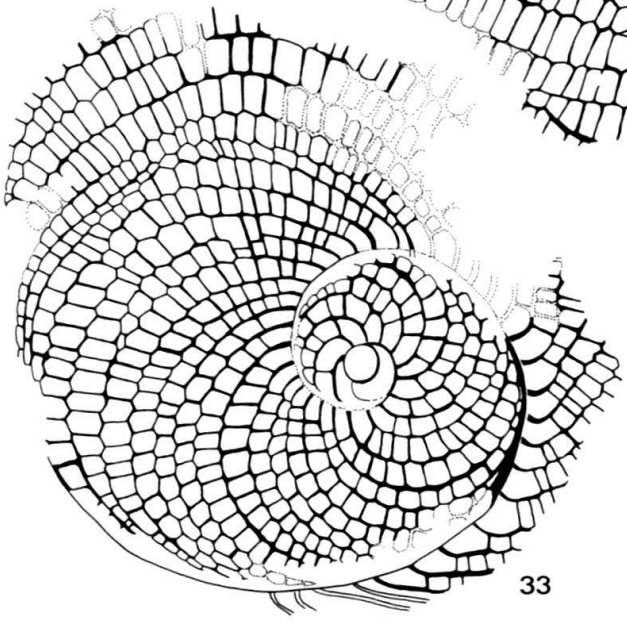

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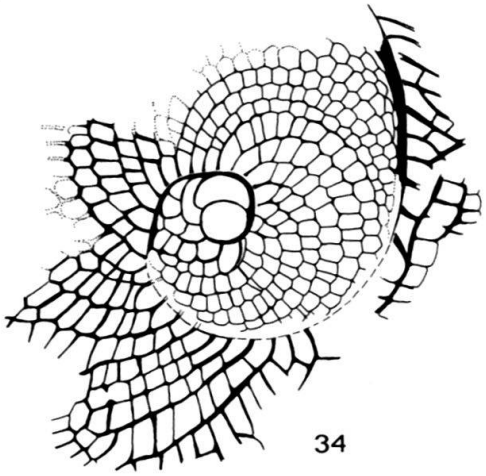

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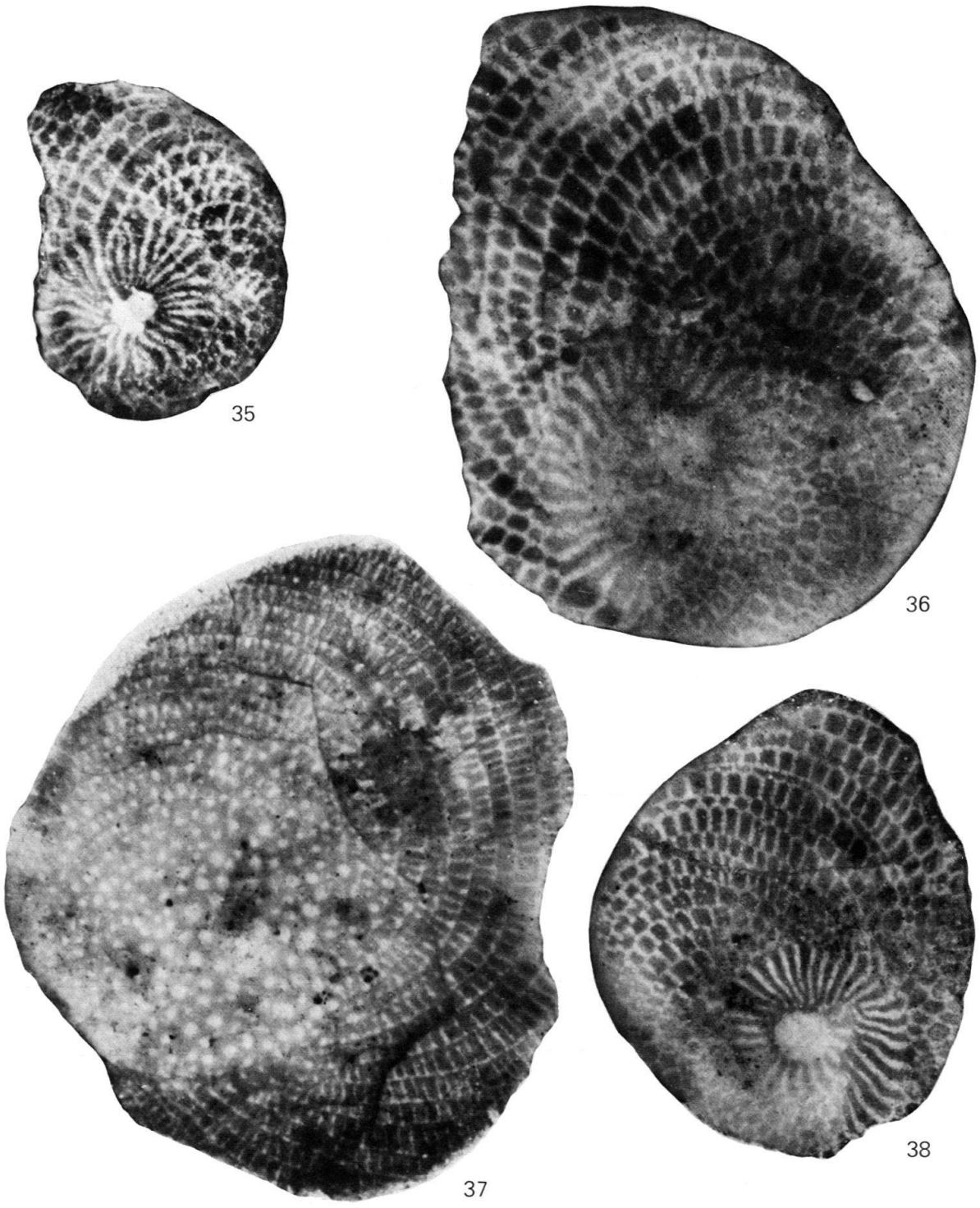

Fig. 35. *Heterostegina reticulata reticulata* RÜTIMEYER. Wängen limestone, Priabonian, Gschwänt (Pilatus area), sample 75/116.

Fig. 36. *Heterostegina reticulata italica* n.ssp. Priabonian of Mossano (Colli Berici), sample Mo 9 in HERB & HEKEL (1973).

Fig. 37. *Heterostegina gracilis* n.sp. Calcare di S.Giustina, latest Priabonian, Cunial/Col dell'Asse, Possagno, sample 689 in HERB & HEKEL (1975).

Fig. 38. *Heterostegina reticulata italica* n.ssp. Priabonian of Mossano, sample Mo 4 in HERB & HEKEL (1973).

All $\times 15$, slightly etched with hydrochloric acid.

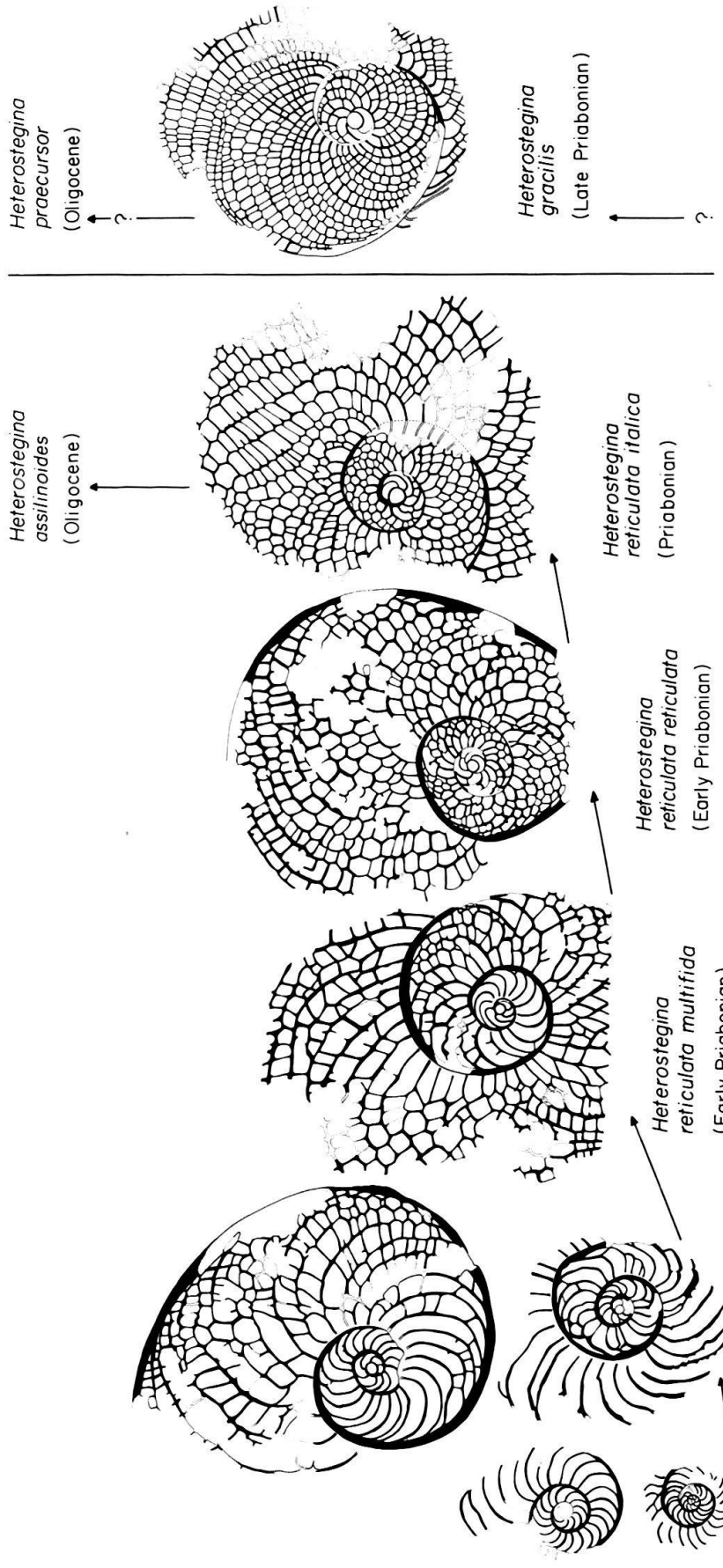

Fig. 39. Tentative interpretation of evolutionary trends of involute *Operculina* and *Heterostegina* between the late Middle Eocene and the Oligocene.

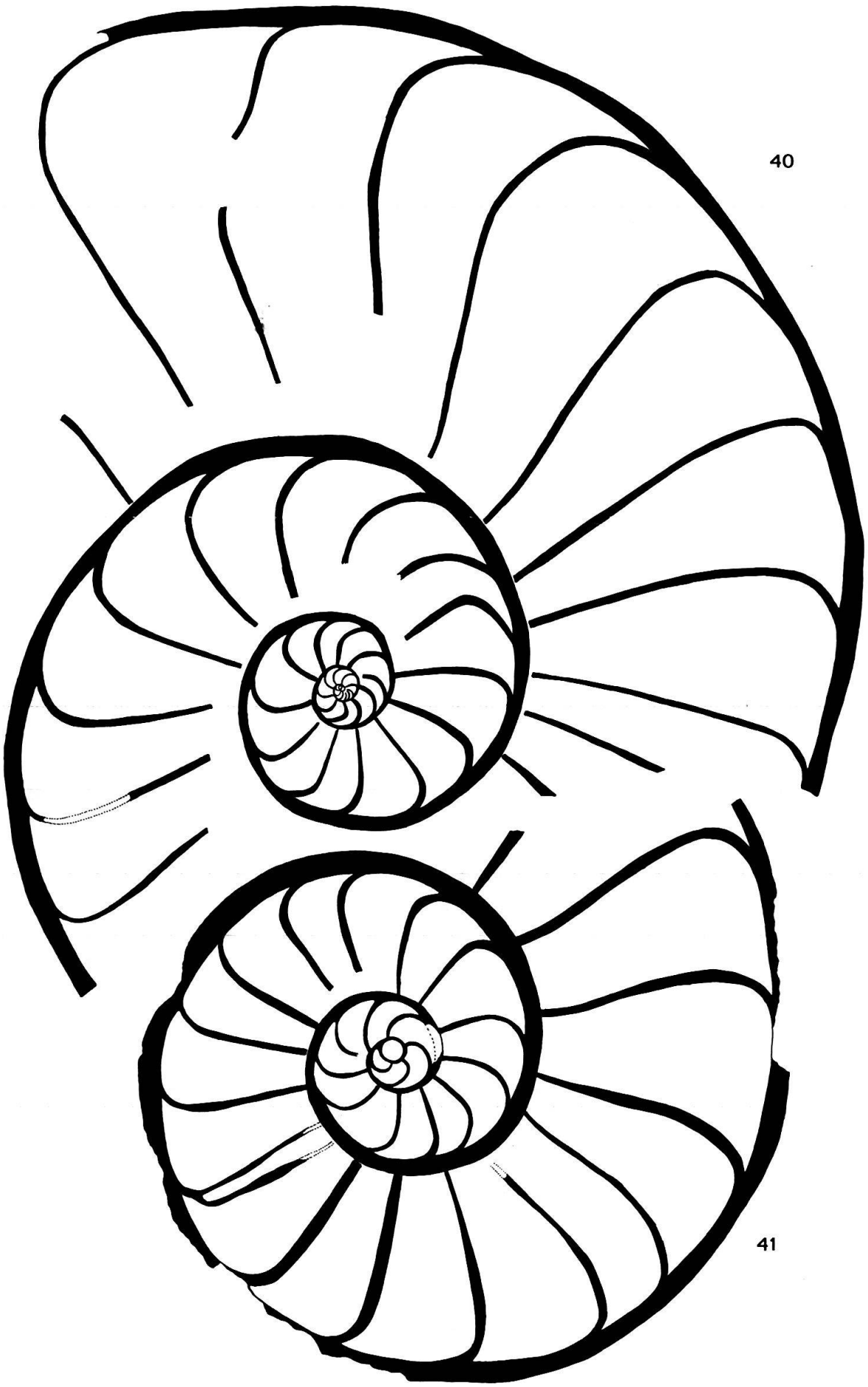

Fig. 40, 41. *Operculina alpina* Douvillé. Upper Hohgant sandstone, early Priabonian. 40 = Equatorial section of microspheric specimen from Elsigen, Coll. R. Herb 75/112. 41 = Equatorial section of microspheric specimen from Wagenmoos, Coll. B. Bieri Wa 37. × 20.

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