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# MOLECULAR DATA REVEAL PARALLEL EVOLUTION IN NUMMULITID FORAMINIFERA

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**ABSTRACT**

**Nummulitidae are the largest extant calcareous Foraminifera, and are widely distributed in tropical and subtropical shallow-water seas. Classical morphology-based taxonomy divides the Nummulitidae in two subfamilies, the Nummulitinae and Heterostegininae, according to the presence or absence of secondary septa. To test the evolutionary importance of this morphological feature, phylogenetic relationships of five Recent nummulitid genera were investigated by sequencing fragments of the SSU and LSU rRNA gene. According to our results, species characterized by septate chambers (*Heterostegina depressa*, *Planostegina operculinoides*, and *Cycloclypeus carpenteri*) either group with species lacking septate chambers (*Operculina ammonoides*, *Nummulites venosus*) or branch separately. This suggests that chamber subdivisions developed several times independently in the evolutionary history of the Nummulitidae, providing an example of parallel evolution in Foraminifera.**

## INTRODUCTION

The family Nummulitidae includes large calcareous Foraminifera, which are common in tropical and subtropical reef-environments. Recent nummulitid Foraminifera are restricted to the Indo-Pacific region with the exception of *Heterostegina*, which shows a circumtropical distribution (Brooks, 1973; Hottinger, 1977; Murray, 1991). Nummulitidae are considered as important biostratigraphic markers for Paleogene and Neogene neritic sediments; they serve as index fossils for biozonations (Serra-Kiel and others; 1998) and are also used for paleoenvironmental analyses (Arni, 1965; Hottinger, 1977; Herb, 1978; Schaub, 1981).

The biology and ecology of Recent nummulitid Foraminifera have been studied in detail for several decades (Röttger, 1972, 1974; Fermont and others, 1983; Reiss and Hottinger, 1984; Röttger and others, 1990; Hohenegger, 1994; Pecheux, 1995; Hohenegger and others, 1998, 1999; 2000; Hohenegger and Yordanova, 2001a, b). Nummulitids are characterized by planispiral tests with involute or evolute coiling and chambers that can be subdivided into chamberlets. All nummulitids possess a complex canal system and develop an internal skeleton (Barnett, 1974; Hottinger, 1977; Loeblich and Tappan, 1988; Hohenegger and others, 2000). Living nummulitids house diatoms as endosymbiotic algae with each species harbouring a different mixture of microalgae (Schmaljohann and Röttger, 1978; Lee and McEnery, 1983; Lee and others, 1989; Lee, 1994).

The systematics of Nummulitidae is based on morphological characters of their tests; e. g., growth form and presence and degree of development of endoskeletal and exoskeletal features (Tan Sin Hok, 1932; Loeblich and Tappan, 1964, 1988; Hottinger, 1977; Haynes, 1981; Banner and Hodgkinson, 1991, Hohenegger and others, 2000). Since the establishment of the taxon Nummulitidae by de Blainville (1827), they are regarded as a separate taxon of family or superfamily rank (Carpenter and others, 1862; Reuss, 1862; Rhumbler, 1895; Eimer and Fickert, 1899; Galloway, 1933; Cushman, 1940; Glaessner, 1945; Haynes, 1981; Loeblich and Tappan, 1988; Banner and Hodgkinson, 1991, Hottinger and others, 1993). The unanimity about the taxonomic status of nummulitids ends at this higher level systematics, as there is no agreement about the number of subfamilies, genera, and species included in this family. Traditionally, Recent nummulitids are divided in two subfamilies, Nummulitinae and Heterostegininae, the latter ones being distinguished by the possession of chamberlets (Galloway, 1933; Glaessner, 1945; Cushman, 1940; Papp and Küpper, 1954; Pokorny, 1958; Banner and Hodgkinson, 1991). The annular cyclo-clypeids are usually included into the Heterostegininae, but are regarded by some as a separate subfamily (Brady, 1884; Delage and Hérouard, 1896; Loeblich and Tappan, 1964) or even family (Haynes, 1981). Hottinger (1977) and Hottinger and others (1993) base nummulitid taxonomy on internal features of the canal system rather than on the classical morphological characters of test coiling and presence or absence of chamberlets and do not distinguish subfamilies within Nummulitidae. Hohenegger and others (2000) assemble Recent nummulitid genera in the family Nummulitidae, without further systematic subdivision. Cole (1953, 1958, 1959, 1960) takes an exceptional position in reducing nummulitid genera by lumping most previously described taxa with *Nummulites*. In the present work, eight Recent nummulitid genera are recognized according to Hottinger (1977) and Hohenegger and others (2000).

Nummulitid taxonomy is blurred because of a limited number of non-homologous morphological features throughout the family that can be used for distinction, as well as the great number of transitional forms and parallel evolution in several genera. An additional taxonomic problem is posed by iterative evolution in *Heterostegina* and *Cycloclypeus*. This has led to a polyphyletic origin, with both genera arising several times in different geographic locations during the Neogene (Tan Sin Hok, 1932; Papp and Küpper, 1954, Papp, 1963, Barnett, 1974). Papp and Küpper (1954) and Papp (1963) distinguish several lineages among European Neogene *Heterostegina*, each of them restricted to distinct epochs or geographic localities. Freudenthal (1969), however, claims that European Neogene *Heterostegina* arose only once, attributing morphological differences to paleoenvironmental changes.

Molecular methods allow us to distinguish between dif-

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TABLE 1. Collection localities and accession numbers for sequenced regions of the SSU rRNA gene and the LSU rRNA gene.

| Species | Locality | Collection date | Remarks | Accession numbers | |
|---|---|---|---|---|---|
| | | | | SSU rDNA | LSUrDNA |
| *Heterostegina depressa*_282 | USA, Florida Keys | Aug–96 | Shizont, F2, culture | AJ488892 | AJ488902 |
| *Heterostegina depressa*_308 | West Australia | Oct-96 | Agamont, F1, culture | AJ488891 | AJ488901 |
| *Heterostegina depressa*_642 | Maldives, Helengeli | Oct-97 | 3–5 m depth | AJ488890 | AJ488900 |
| *Heterostegina depressa*_377 | Israel, Elat, MBL Institute | Feb-97 | 3–5 m depth | AJ488893 | AJ488902 |
| *Operculina ammonoides*_232 | Japan, Sesoko, Okinawa | Aug-96 | 18 m depth | AJ488888 | AJ488898 |
| *Operculina ammonoides*_253 | Japan, Sesoko, Okinawa | Aug-96 | 18 m depth, keeled | AJ488889 | AJ488898 |
| *Operculina ammonoides*_494 | Australia, Lizard Island | Aug-97 | 6–10 m depth | AJ488887 | AJ488997 |
| *Cycloclypeus carpenteri*_659 | Japan, Minna Jima, Okinawa | Nov-97 | Gamont, 80–90 m depth | AJ488885 | AJ488894 |
| *Planostegina operculinoides*_662 | Japan, Minnu, Okinawa | Nov-97 | 80–90 m depth | AJ488886 | AJ488895 |
| *Nummulites venosus*_301 | Japan, Minnu, Okinawa | Oct-96 | 50 m depth | AJ311212 | AJ488896 |
| *Pararotalia nipponica*_862 | Japan, Cape Omaezaki, Shizuoka | Jul-98 | Tidal pool | AJ488884 | AJ240136 |

ferent taxonomic views as genetic data are independent of morphological characters. We investigated phylogenetic relationships of five Recent nummulitid genera by analysing partial SSU and LSU rDNA sequences. Molecular and morphological data sets are compared and discussed, both confirming the monophyly of the family, but showing different results at lower taxonomic levels.

## MATERIAL AND METHODS

### CELL COLLECTION

Living nummulitid specimens used in the present study were collected from the Indo-Pacific, the Red Sea, and the Caribbean (Table 1). Representatives of most Recent nummulitid genera were investigated in the present work, with the exception of three taxa (*Heterocyclina, Planoperculina, Operculinella*), for which no living specimens were available. A taxonomic appendix of the investigated species is given in Table 2.

Nummulitids were collected by dredging, SCUBA diving, or snorkling (Hohenegger and Yordanova, 2001a). Living individuals were identified by protoplasmic coloration due to endosymbiotic diatoms and isolated for subsequent studies. Photographs were prepared from specimens of each investigated species.

### DNA EXTRACTION, AMPLIFICATION, CLONING AND SEQUENCING

Before extracting DNA, each specimen was transferred into an individual receptacle containing filtered seawater and cleaned by brushing. A total of 11 DNA extractions were used in the present study. DNA was extracted by grinding each specimen separately in 1.5 ml microfuge tubes containing DOC extraction buffer, following incubation for 1h at 60°C and short centrifugation to remove insoluble material. (Holzmann and Pawlowski, 1996).

Ribosomal DNA was amplified by PCR in a total volume of 50 μl. The thermal cycle parameters consisted of 40 cycles of 30 s at 94° C, 30 s at 50° C and 120 s at 72° C, followed by 5 min at 72° C for final extension. The amplified PCR products were purified using High Pure PCR Purification Kit (Roche Diagnostics), then ligated into pGEM-T Vector system (Promega) and cloned in XL-2 Ultracompetent Cells (Stratagene). Sequencing reactions were prepared by using ABI-PRISM Big Dye Terminator Cycle Sequencing Kit and analyzed with an ABI-377 DNA sequencer (Perkin-Elmer), all according to the manufacturer's instructions.

SSU rDNA was amplified by using the primer pair s14F3-sBf (Holzmann and others, 2001). LSU rDNA was amplified by using the primer pair Rib 2TA- Rib7 (Holzmann and Pawlowski, 1996). The new sequences reported in this paper have been deposited in the EMBL/Genbank database under accession numbers AJ488884-AJ488903 (Table 1) and AJ504678-AJ504690. The following sequences have been published previously: *Trochammina* sp. (X86095), (Pawlowski and others, 1996), *Textularia* sp. (Z69613), (Pawlowski and others, 1997), *Nummulites venosus* (AJ311212) and *Bolivina spathulata* (AJ318227), (Pawlowski and others, 1999), *Haplophragmoides wilberti* (AJ312436), *Trochammina hadai* (AJ317979) and *Bolivina* sp. (Z69613), (Pawlowski, 2000), *Pararotalia nipponica* (AJ240136) and *Arenoparrella mexicana* (AJ307742), (Pawlowski and Holzmann, 2002).

### SEQUENCE ANALYSIS

Sequences were aligned manually by using GDE 2.2 software (Larsen and others, 1993). Selected sites in homologous regions without gaps were retained for phylogenetic analyses. Analyses were based on three methods: the neighbour joining (NJ) method, using various models such as Kimura's two-parameter (K2P) model (Kimura, 1980), the Tamura and Nei (TN) model, (Tamura and Nei, 1993), and the Hasegawa, Kishino and Yano 6 parameter (HKY85) model (Hasegawa and others, 1985) for distance correction as implemented in the PHYLO_WIN program (Galtier and others, 1996); the maximum likelihood (ML) method, using the fast DNAm1 program (Olsen and others, 1994), includ-

TABLE 2. Taxonomic Appendix.

*Nummulites venosus* (Fichtel and Moll) = *Nautilus venosus* Fichtel and Moll, 1798
*Operculina ammonoides* (Gronovius) = *Nautilus ammonoides* Gronovius, 1781
*Heterostegina depressa* d'Orbigny, 1826
*Planostegina operculinoides* (Hofker) = *Heterostegina operculinoides* Hofker, 1927
*Cycloclypeus carpenteri* Bradyi, 1881

ing the F84 model (Felsenstein 1984), and the maximum parsimony (MP) method, using PAUP* 4.0b version (Swofford, 2000). Parsimony analysis consisted of heuristic searches with 100 random-addition replicates using tree bisection-reconnection (TBR) branchswapping and stepwise addition of taxa. The reliability of internal branches was assessed using the bootstrap method (Felsenstein, 1988) with 100, 1000 and 1000 replicates for ML, NJ and MP analyses respectively. The PHYLO_WIN program (Galtier and others, 1996) was used for distance computations, NJ and ML tree-building and bootstrapping.

## RESULTS

### Sequence Data

#### *SSU rDNA Fragment*

A fragment of the SSU rDNA, ranging in length from 1000 to 1030 bp (basepairs) was obtained for all investigated nummulitids and compared to 21 other rotaliids and textulariids. The fragment corresponds to the 3' terminal region of *Rattus norvegicus* (K01593) starting at position 1181 and ending at position 1871. It includes six variable regions; among them, region I corresponds to the universal variable region V6 of the prokaryotic secondary structure model (Neefs and others, 1993). Within nummulitids, the G+C content ranges from 43.9% (*Operculina ammonoides*_232,_253) to 44.5% (*Cycloclypeus carpenteri* and *Heterostegina depressa_282*).

#### *LSU rDNA Fragment*

Partial LSU rDNA was amplified and sequenced for all nummulitids and *Pararotalia nipponica*. The fragment is situated at the 5′ terminal end of the LSU rRNA gene and includes the divergent domain D1, as well as flanking regions of the conserved domains C1 and C2 (Hassouna and others, 1984). The length of the sequences ranges from 448 to 495 bp, which is about one and a half as much than in other known eukaryotes. This is due to insertions in the divergent domain D1 that are unique to Foraminifera (Holzmann and others, 1996). They correspond to the 5' terminal region of *Rattus norvegicus* (X01069), extending from position 1 to 324. The G+C content ranges from 38.4% (*Pararotalia nipponica*) to 44% (*Operculina ammonoides*_494).

#### *Combined Analysis of the LSU and SSU rDNA Fragment*

The corresponding sequences of the LSU rDNA were joined to the SSU rDNA data set and analysed as one fragment. The length of the fragment ranges from 1434 to 1530 bp, the G+C content reaches from 42.8% (*Pararotalia nipponica*) to 44% (*Heterostegina depressa*_642, *Operculina ammonoides*_494).

### Phylogenetic Analysis

The phylogenetic position of the Nummulitidae was analysed using partial SSU rDNA sequences (826 homologous sites) of 7 nummulitids, 13 other rotaliids, and 8 textulariids. Our results show that the Nummulitidae form a monophyletic group supported by high bootstrap values (87%, 100%, and 97% for ML, NJ, and MP analyses respectively). The Nummulitidae branch as a sister group to the Calcarinidae and Rotaliidae (Fig. 1). The three families cluster together in all types of analyses, although their grouping is not always equally well supported. They form a sister group to other rotaliids examined in this study, i.e., Rosalinidae, Planorbulinidae, Cassidulinidae, Bolivinidae, and Planulinidae. Textulariids branch at the base of the tree in two well supported clades, one containing *Trochammina*, *Textularia*, *Bigenerina*, *Siphoniferoides* and *Spiroplectammina*, the other including *Haplophragmoides* and *Arenoparrella*. The same topology was found in all types of analyses (ML, NJ, MP), including different evolutionary models applied in distance methods.

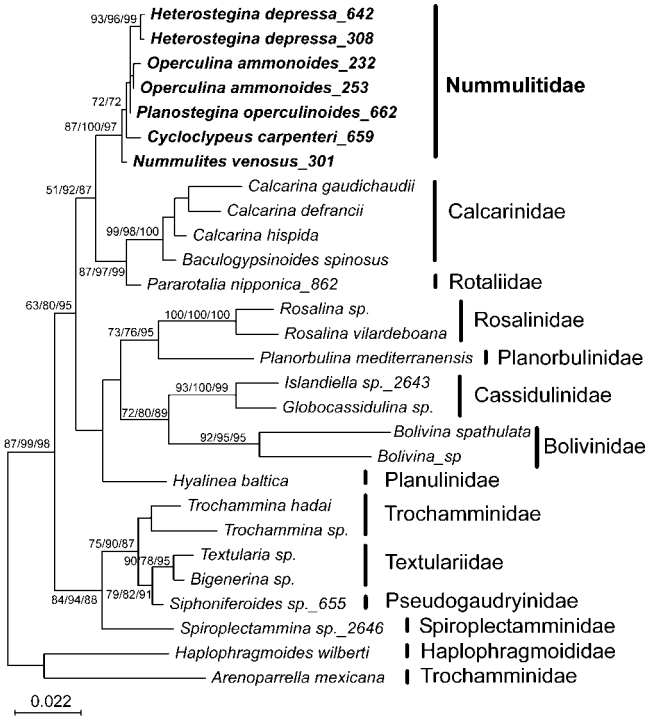


FIGURE 1. Phylogenetic position of Nummulitidae inferred using maximum likelihood method, based on 826 homologous sites of the SSU rDNA. The tree length is ln(L) = −4334.859. Bootstrap values are based on 100 resamplings for ML analyses and 1000 resamplings for NJ and MP analyses (first, second, and third numbers, respectively). Note: Numbers following the name of species refer to DNA isolates.

Intrageneric relationships in Nummulitidae were analysed by using partial SSU and LSU rDNA sequences (1367 homologous sites). We have excluded more distantly related groups from the SSU rDNA gene analysis, keeping only the sequence of *Pararotalia nipponica* as an outgroup. This allowed us to increase the total number of analysed sites. Analysis of combined SSU and LSU rDNA data for 10 nummulitid specimens and *P. nipponica* was performed using ML, NJ, and MP methods (Fig. 2). In ML and MP trees, *Nummulites venosus* and *Planostegina operculinoides* branch together at the base of the tree, followed by *Cycloclypeus carpenteri* and the clade grouping 4 sequences of *Heterostegina depressa* and 3 sequences of *Operculina ammonoides* from different localities. In the NJ tree, *C. carpenteri* branches as a sister group to the clade containing

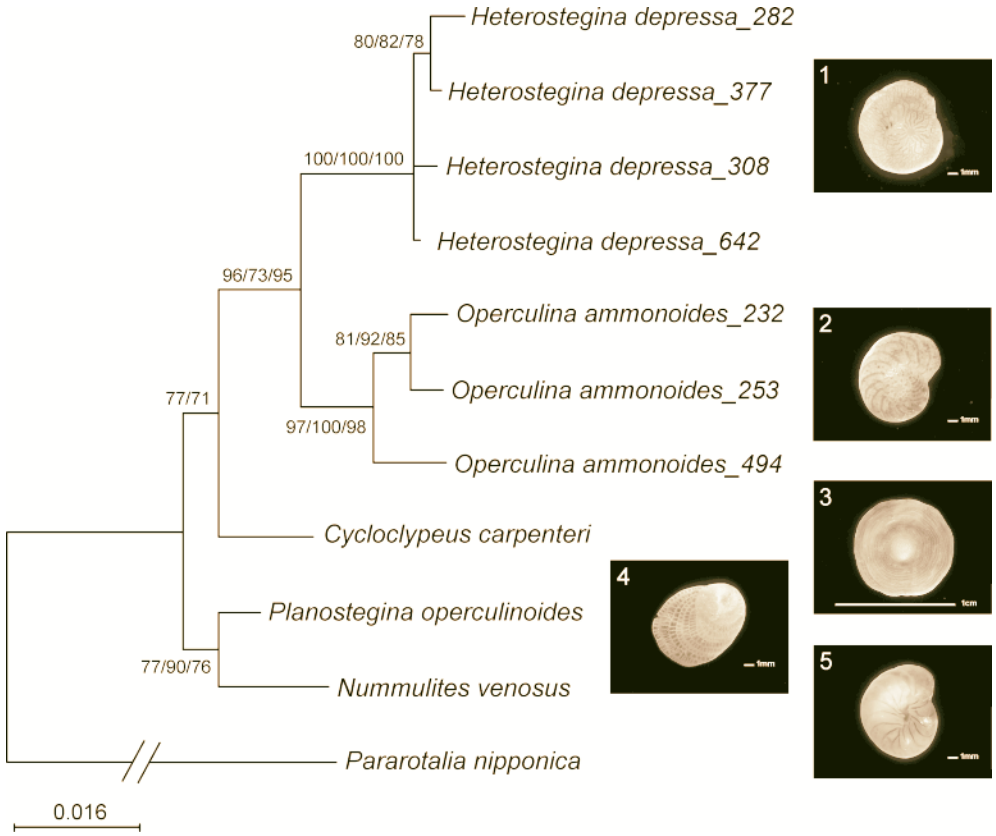


FIGURE 2. Phylogenetic relationships within Nummulitidae inferred using maximum likelihood method, based on 1367 homologous sites of combined SSU and LSU rDNA. The tree length is ln(L) = − 3438.570. Bootstrap values are based on 100 resamplings for ML analyses and 1000 resamplings for NJ and MP analyses (first, second, and third numbers respectively). Using maximum parsimony analyis, the total length of the most parsimonous tree is 405. 104 out of 1627 sites are parsimony informative. Ci and ri indices are 0.8691 and 0.7675 respectively. Note: Numbers of the investigated specimens refer to DNA isolates.

*N. venosus* and *P. operculinoides*. In all trees, the *Heterostegina* + *Operculina* clade is supported by relatively high bootstrap values (96%, 73%, 95% for ML, NJ, and MP analyses, respectively). Relationships between other Nummulitidae (*Cycloclypeus*, *Planostegina*, *Nummulites*) are moderately well supported, and can change slightly, depending on whether the two ribosomal gene fragments are analysed separately or combined. In particular, the trees obtained by separate analysis of the SSU fragment only differ in the branching order within the *Heterostegina depressa* cluster, while in the LSU trees, *N. venosus* and *P. operculinoides* either form independent branches (ML) or cluster together with *C. carpenteri* (NJ, MP) (data not shown).

## DISCUSSION

One hundred and seventy-five years after nummulitid Foraminifera were given family status, their taxonomy and phylogenetic relationships are still a source of controversy among micropaleontologists. The traditional taxonomy of nummulitids is based on involute or evolute test coiling and the presence or absence of chamberlets. The Nummulitidae are usually divided in two subfamilies: Nummulitinae, containing forms without secondary septa (*Nummulites, Operculina*) and Heterostegininae, including forms with subdivided chambers (*Heterostegina, Planostegina, Cycloclypeus*) (Galloway, 1933; Glaessner, 1945; Sigal, 1952, Banner and Hodgkinson, 1991).

Because of the many problems related to the morphology-based taxonomy in nummulitids, some authors have abandoned classification at the subfamily level (Hottinger and others, 1993, Hohenegger and others, 2000). Hohenegger and others (2000) classify the Nummulitidae in 4 different morphogroups, according to involute/semiinvolute/evolute/annular test coiling and presence or absence of chamberlets, but without assigning taxonomic rank.

Our results confirm the monophyly of the family Nummulitidae. Analyses of the molecular data show a close relationship of nummulitids to Rotaliidae and Calcarinidae. This is in agreement with the evolutionary scenario as proposed by Glaessner (1945), Pokorny (1958), Haynes (1981), and Tappan and Loeblich (1988), all of whom claim that calcarinids and nummulitids are close relatives, both descending from a common rotaliid ancestor, and that their separation from each other and from early Rotaliidae took place in the Upper Cretaceous. It contradicts the view of Cushman (1940), who concluded that the Calcarinidae diverged from a rotaliid ancestor whereas the Nummulitidae developed from the Nonionidae.

The relationships within Nummulitidae as inferred from molecular data contrast with classical morphological taxonomy. In particular, the distinction between the Nummu-

litinae and Heterostegininae cannot be substantiated according to our molecular data. The genera possessing septate chambers, *Planostegina* and *Heterostegina,* cluster in each analysis next to taxa without secondary septa (*Operculina* and *Nummulites,* respectively), whereas *Cycloclypeus* occupies a position intermediate between both clades. Furthermore, our data do not show a separation of nummulitids into evolute and involute forms, as evolute forms (*Planostegina, Operculina*) branch with involute ones (*Nummulites* and *Heterostegina,* respectively). Our results are in agreement with the classification used by Hottinger and others (1993) and Hohenegger and others (2000), as the two commonly recognized subfamilies do not seem to correspond to natural units.

It is generally believed that taxa with secondary septa evolved from simple forms having undivided chambers. According to this principle, most authors have concluded that *Operculina* gave rise to *Heterostegina* and that annular cycloclypeids evolved from the latter group (Galloway, 1933; Cushman, 1940; Glaessner, 1945; Papp and Küpper, 1954; Barnett, 1974, Hottinger, 1977). Our molecular data corroborate the close connection between *Operculina* and *Heterostegina,* as both groups build a well supported clade in each type of analysis (bootstrap $>$90%). Our results, however, do not confirm a close relationship between *Heterostegina* and *Cycloclypeus,* as the latter one branches independently in each type of analysis.

Early representatives of *Heterostegina* and *Operculina* display very similar if not identical morphological features, except for secondary septa, whose gradual development can be retraced by intermediate forms. Morphologic resemblances between early *Heterostegina* and *Operculina* concern the canal system in the spiral cord and differences between micro- and macrospheric generations, which are restricted in both to the central part of the test (Papp and Küpper, 1954). Recent *Heterostegina* first develop undivided, operculinoid chambers before the onset of secondary septa. In early heterosteginids, a gradual development of secondary septa can also be seen within individuals, where the first chambers following the deuteroconch are operculinoid, the next ones bear one short secondary septa each, and the remaining chambers each develop several, long secondary septa (Papp and Küpper, 1954). *Cycloclypeus* is characterized by a juvenile *Heterostegina*-stage which is followed by the development of annular chambers (Tan Sin Hok, 1932; Papp and Küpper, 1954; Hottinger, 1977; Hohenegger and others, 2000). The three genera share the possession of vertical sutural canals, which are forked in *Operculina* and undivided in *Heterostegina* and *Cycloclypeus.* The latter two genera are further characterized by Y-shaped intercameral stolons, which can also be crossed in *Cycloclypeus* (Hottinger, 1977).

Our molecular data further confirm the basal position of *Nummulites,* as proposed by Galloway (1933) and Cushman (1940). The basal position of *Operculina,* however, cannot be substantiated by our results. *Operculina* branches in the crown of our tree, which would indicate that its Recent representatives are not direct descendants of basal nummulitids, as proposed by Galloway (1933), Glaessner (1945), Cushman (1940), Barnett (1974), and Banner and Hodgkinson (1991).

*Nummulites* and *Operculina* share both undivided chambers and radial intercameral stolons which are distributed irregularly, but the sutural canals are ramified and oblique in *Nummulites.* Nummulitid tests are involute, smooth, possess high chamber numbers and chamber cavities that extend over previous whorls (alar prolongations), whereas operculinids are charcterized by evolute to semi-involute tests and septal elevations visible as various surface ornamentation (Hottinger, 1977; Hohenegger and others, 2000). Some authors have assumed that *Operculina* developed from *Nummulites* by changing to evolute coiling, reducing the number of coils and losing the alar prolongations (Galloway, 1933; Cushman, 1940), whereas others presumed that both evolved separately from a common, yet unknown ancestor (Glaessner, 1945; Barnett, 1974, Hottinger, 1977; Haynes, 1981).

Our results validate the genus *Planostegina,* which is genetically distinct from *Heterostegina* and confirm its basal position as suggested by Banner and Hodgkinson (1991). The phylogenetic position of *Cycloclypeus,* as inferred from our molecular data, shows an intermediate placement between the *Planostegina/Nummulites* and *Heterostegina*/*Operculina* groups. This branching order is in agreement with the evolutionary scheme presented by Banner and Hodgkinson (1991), who assume that *Cycloclypeus* derived from *Planostegina.*

The genus *Planostegina* was erected by Banner and Hodgkinson (1991). Specimens of this genus have formerly been described as *Heterostegina* spp. by many authors (for a review see Banner and Hodgkinson, 1991). Both genera are characterized by secondary septa, subrectangular chamberlets, Y-shaped intercameral stolons, and undivided, vertical sutural canals (Hottinger, 1977, Banner and Hodgkinson, 1991), but they also show some morphological differences: *Planostegina* has an evolute, extremely flat test with strong ornamentation including granulation and knobs in the central part of the test, whereas *Heterostegina* possesses an involute, thick test with raised sutures as the only surface ornament. In *Planostegina,* the embryonic test of megalospheric individuals is followed by one undivided chamber, whereas all subsequent chambers are subdivided into chamberlets. In *Heterostegina,* several undivided chambers are developed before secondary septa are built. The number of secondary septa per chamber is also much higher in *Planostegina* than in *Heterostegina. Planostegina* neither develops lateral chamberlets nor alar prolongations, whereas *Heterostegina* is characterized by both (Hottinger, 1977; Banner and Hodgkinson, 1991; Hohenegger and others, 2000). According to Banner and Hodgkinson (1991), the evolute ancestors of *Planostegina* are found among *Planoperculina*-like *Operculina* species which gradually developed secondary septa. *Heterostegina* and *Cycloclypeus* evolved separately from *Planostegina,* the first descendant becoming initially involute, the second one retaining its evolute form, but losing its planispirality and developing an annular test.

The results of our study imply that parallel evolution has played an important part in the history of the Nummulitidae. Parallel evolution is regarded as the development of similar phenotypes in rather closely related organisms, which are likely to share similar genetic and developmental potentials,

while convergent evolution involves similarities in lineages that are unrelated far back in time (Simpson, 1961; Mayr, 1975; Futuyma, 1998). These concepts continue to be debated. Eldridge and Cracraft (1980) recognize the concept of convergent evolution, but state that parallelism requires information about genetic and developmental bases in ancestral forms and information about the selection forces acting on ancestral forms. They claim that this is impossible to evaluate and therefore claim that the concept of parallelism is unscientific. In the present work, we adhere to the definition of parallelism as presented by Simpson (1961), Mayr (1975), and Futuyma (1998), based on independently acquired, similar features in two or more lineages of common ancestry.

In Nummulitidae, a combination of external and internal features such as test form, ornamentation and growth rate, number and form of chambers, form of primary and secondary septa, and the fine structure of sutural canals and stolons allows taxonomic distinction. The phylogenetic significance of each single feature, however, is difficult to determine, as nummulitid Foraminifera seem to share a set of characters which is expressed differently in each group. Morphological features like secondary septa, which have been regarded as a generic or even suprageneric feature by most workers (Galloway, 1933; Glaessner, 1945; Cushman, 1940; Papp and Küpper, 1954; Pokorny, 1958, Haynes, 1981), apparently evolved independently several times within the Nummulitidae and are shared by three Recent genera: *Cycloclypeus, Planostegina,* and *Heterostegina.* In the latter two genera, the evolution of secondary septa corresponds to an example of parallel evolution in the Nummulitidae.

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