

Molecular versus Taxonomic Rates of Evolution in Planktonic Foraminifera

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Neogene planktonic foraminifera are among the most widely used microfossils in the study of tempo and mode of evolution. Comparisons of taxonomic rates between the two major clades in this group have shown that the nonspinose globorotaliids have undergone a significantly more rapid evolutionary turnover than the spinose globigerinids (S. M. Stanley *et al.*, 1988, *Paleobiology* 14, 235–249). In order to test if similar fluctuations are observed in molecular data, we have used different methods to calculate absolute and relative rates of substitutions based on 16 partial SSU rDNA sequences from representatives of both groups. According to our data, rates of substitution are relatively constant within the globigerinids with a mean value of 4.3 subst./site/10⁹ years, but vary in the globorotaliid clade with three species having a rate of about 1 subst./site/10⁹ years and two species evolving much faster with rates of more than 7 subst./site/10⁹ years. Assuming that the fast rates result from recent accelerations, the globorotaliids have basically much slower molecular evolutionary rates than the globigerinids, in opposition to the fossil data. © 1998 Academic Press

INTRODUCTION

Planktonic foraminifera are among the most thoroughly studied groups of microfossils. Their world-wide abundance and diversity in marine sediments as well as their relatively complete and continuous stratigraphic record offer a unique opportunity to study evolution and the dynamics of evolutionary change. The fossil record of planktonic foraminifera has been largely used to investigate morphological and taxonomic rates of evolution. The most complete phylogenetic framework to date was established for foraminifera from the Neogene, i.e., 24 myr to the recent (Kennett and Srinivasan, 1983). Detailed analysis of morphological changes in some foraminiferal lineages demonstrated the presence of two different modes of speciation, phyletic gradualism (Wei and Kennett, 1988;

Malmgren and Kennett, 1981), and punctuated anagenesis (Malmgren *et al.*, 1984). Taxonomic frequency rates have been utilized to study evolutionary changes in planktonic foraminifera and their relations with major paleoceanographic events (Wei and Kennett, 1986; Malmgren and Berggren, 1987).

Taxonomic rates were also used to analyze the tempo of evolution of several planktonic foraminiferal lineages (Berggren, 1969; Stanley *et al.*, 1988). Important differences in species duration were observed between the two major clades of Neogene planktonic foraminifera: the nonspinose globorotaliids were found to undergo much more rapid evolutionary turnover than the spinose globigerinids (Stanley *et al.*, 1988). Based on fossil data, the authors have shown that rates of extinction and speciation are significantly correlated with size and repartition of the populations: globorotaliids are generally less abundant and have more restricted distribution than globigerinids. A relationship between high evolutionary turnover and relatively small populations in particular water masses was also found within both groups (Stanley *et al.*, 1988).

Recent data on molecular evolution of foraminifera have shown extreme differences in rates of substitutions within and between different lineages (Pawlowski *et al.*, 1997). Most of the factors that are generally considered as responsible for substitution rate variation (reviewed in Hillis *et al.*, 1996) seem to be unrelated to the process of speciation. However, an acceleration of the molecular rates during adaptive species radiation was proposed on the basis of protein sequence data (Goodman, 1981). In order to test if the heterogeneity of molecular rates corresponds to the variation of evolutionary turnover observed in the fossil record, we have analyzed the rates of substitution of the globigerinid and the globorotaliid clades using 16 partial SSU rDNA sequences of extant representatives of the two groups.

MATERIALS AND METHODS

Sequence Data

Partial SSU rDNA sequences of about 1100 bp were obtained from 10 globigerinids and 6 globorotaliids

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collected offshore in the Caribbean, Mediterranean, and Sargasso seas. The localities and methods of collection as well as the conditions of DNA extraction, PCR amplification, cloning, and sequencing have been described elsewhere (de Vargas *et al.*, 1997). Sequences reported in this paper are deposited in the EMBL/GenBank database, Accession Numbers Z69610 and Z83957–Z83973.

Sequence Analysis

The sequences were aligned, using the Genetic Data Environment 2.2 software (Larsen *et al.*, 1993). The resulting alignment followed the universal SSU rRNA secondary structure model (Van de Peer *et al.*, 1996) and was improved in reference to the abundant compensatory mutations found in planktonic foraminifera. All analyses were performed using 546 unambiguously aligned sites. Foraminiferal phylogenetic trees were reconstructed with the maximum likelihood method (ML) with a transitions/transversions ratio of 2, as implemented in the fastDNaml program (Olsen *et al.*, 1994), and with the maximum parsimony method (MP), using Branch and Bound search option included in PAUP 3.1.1 (Swofford, 1993). Distance computations were achieved with the Phylo_win program (Galtier and Gouy, 1996). When used in tree reconstruction, constrained topologies were compared to the best hypothesis, respectively, by a likelihood ratio test (Kishino and Hasegawa, 1989) using the DNAML program taken from the PHYLogeny Inference Package (Felsenstein, 1981) and by the number of extra steps for ML and MP trees.

Rates of Substitution Calculation

Three different approaches were used for estimating the rates of substitution between and within the globigerinid and globorotaliid clades: (1) the relative rate test (RRT) using Kimura-2 distances between each species, according to Wu and Li (1985); (2) pairwise divergence rates (PDR) calculated for couples of closely related species, using pairwise Kimura-2 distances divided by divergence times inferred from fossil record; and (3) individual lineage rates (ILR) calculated directly on tree reconstructions by attributing divergence times to either terminal or terminal and internal branch lengths (as proposed by Hillis *et al.*, 1996). The topology of the ML tree rooted on the benthic foraminifer *Peneroplis* sp. was used for estimation of independent absolute rates. All other calibrated trees, obtained by different reconstruction methods, were constrained to this topology, if necessary. When internal segments were considered, branch lengths values were plotted against time for estimating the molecular clock of each group by simple weighted linear regression constrained through the origin. Additionally, all analyses were

carried out separately for the globigerinids and the globorotaliids.

Taxonomic Rates

We referred to a study of Stanley *et al.* (1988) for the general comparison of taxonomic turnover and lineage duration between the globigerinid and globorotaliid clades. Taxonomic rates of evolution for each lineage leading to the modern species were estimated by dividing the number of species by the duration of each lineage. The time of lineage origination, the most subjective aspect of this kind of calculation was based on first apparition of the lineage in a fossil assemblage, usually followed by gradual changes in planktonic foraminifera (Malmgren *et al.*, 1984). Lineage divergence times, number of species, and mean extinct-species durations were essentially based on the phylogenetic atlas of Neogene planktonic foraminifera (Kennett and Srinivasan, 1983). The longevities of the modern species are confirmed by a more recent analysis, based on DSDP/ODP data (H. Hilbrecht, personal communication).

RESULTS

Phylogenetic Framework

Phylogenetic relationships of planktonic foraminifera, inferred from partial SSU rDNA sequences, using the ML method are presented in Fig. 1. The taxa cluster in two monophyletic groups corresponding to the clades of spinose globigerinids and nonspinose globorotaliids in agreement with existing systematic relationships of foraminifera. The phylogenetic relationships within both clades agree with the accepted paleontological interpretations of the fossil record but are weakly supported by branch support measures. The MP tree that has the same topology is two steps longer than the shortest MP tree because the parsimony analysis invariably unites the two long branches leading to *Globorotalia truncatulinoides* and *Globorotalia menardii*. This branching, occurring also in NJ reconstruction, was proposed to result from long branch attraction phenomenon (de Vargas *et al.*, 1997).

Fossil data used for calculation of taxonomic rates are given in Table 1. Mean species duration and number of species per million years are about 2.5 times higher in the globorotaliids than in the globigerinids. This confirms the difference in mean evolutionary turnover derived by Stanley *et al.* (1988). A similar difference is observed in the extant species and lineage durations, which is partly due to the fact that both clades radiated at different epochs, the globigerinids during the late Oligocene, about 27 myr ago, and the globorotaliids at the end of the early Miocene, about 18 myr ago. It seems, however, that evolutionary rates are not seriously affected by extant species duration. The

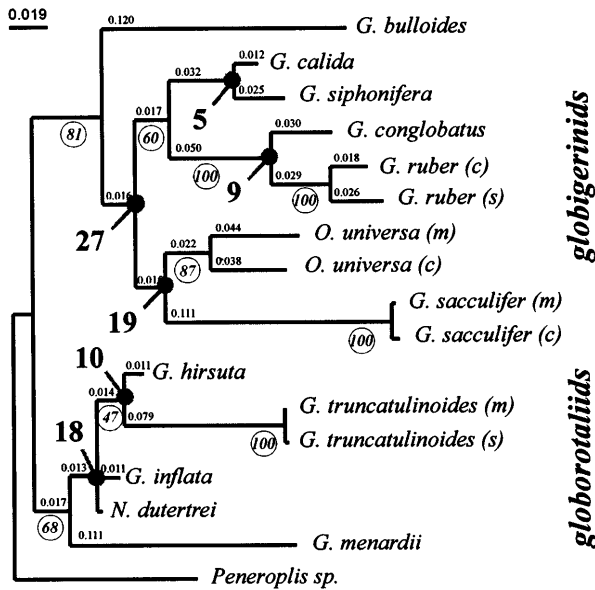


FIG. 1. SSU rDNA phylogenetic relationships (ML) between 12 species of planktonic foraminifera, using the benthic foraminifera *Peneroplis* sp. as outgroup. Fossil divergence times between lineages are given at the nodes of the tree in million years. Branch lengths and scale are in substitutions/site. Bootstrap proportions greater than 50% are given next to each internal branch. Abbreviations: *c*, *m*, *s* are used for species collected in Caribbean, Mediterranean, and Sargasso seas.

same results were obtained when modern species were excluded from the calculations (Stanley *et al.*, 1988).

Rates of Nucleotide Substitution

Results obtained with different methods for estimating the rates of molecular evolution are presented in Tables 2 and 3. Comparison of these methods allows the detection of biases due to mistakes in interpretations of the fossil record (RRT), errors in tree reconstruction (PDR), and interspecies rate variations (ILR).

Globigerinid clade. There is general good agreement between all methods used concerning the mean evolutionary rate of the globigerinids. It averages 4.3 subst./site/10⁹ years, with values ranging from 4.0 to 4.6 subst./site/10⁹ years. However, examination of the individual lineages reveals a striking difference between the rates calculated on individual lineages (ILR) and pairwise divergences (PDR). The latter are very similar (4.2 to 4.6 subst./site/10⁹ years) and suggest an extremely precise clock-like behavior during globigerinid evolution. In fact, this is an artifact due to the nonindependence of pairwise comparisons: the number of substitutions that occurred since the divergence of the two species is shared between those species, even if they have evolved at different rates (e.g., *Orbulina universa*–*Globigerinoides sacculifer*). The ILR (3.2 to 6.1 subst./site/10⁹ years) seems to be a more significant measure of the variation between individual lineages. They are dependent, however, on the method of tree reconstruction and on the number of sequences used in the

TABLE 1

Fossil Data on the DNA Analyzed Species

Lineage	Extant sp. duration	Lineage duration	Nb of sp. per lineage	Mean sp. duration	Nb of sp. per Myr	Mean ^a turnover
Globigerinids						
<i>G. bulloides</i>	20.9	34	6	12.7	0.18	
<i>G. siphonifera</i> / <i>G. calida</i>	14.2/3.8	25	5	11.8	0.20	
<i>G. conglobatus</i> / <i>G. ruber</i>	5.6/5.2	20	7	7	0.28	
<i>G. sacculifer</i>	20.9	22	6	14.1	0.26	
<i>O. universa</i>	15.4	17	4	12.2	0.24	
Mean	12.3	23.6	5.6	11.6	0.20	
Stanley <i>et al.</i> (1988) ^b				10.5–13.3		0.031
Globorotaliids						
<i>G. inflata</i>	4.4	18	6	5.8	0.33	
<i>N. dutertrei</i>	5.1	11	7	3.3	0.64	
<i>G. hirsuta</i>	6.5	11	3	4.8	0.27	
<i>G. truncatulinoides</i>	2.8	7	5	2.6	0.71	
<i>G. menardii</i>	13.5	17	8	4.4	0.47	
Mean	6.5	12.8	5.8	4.2	0.50	
Stanley <i>et al.</i> (1988) ^b				6.3–6.9		0.089

Note. All time durations are given in million years.

^a Defined as the percentage of species that are replaced numerically within any one million-year interval.

^b Stanley *et al.* results are based on all Neogene globigerinid (45) and globorotaliid (50) species. Mean species durations have been calculated with a variety of metrics considering or not extant and/or extinct species.

TABLE 2
Rates of Substitution per Site per 10⁹ Years of the Planktonic Foraminifera

Lineage	Individual lineage rates (ILR) ^a						
	ML tree		MP tree		Pairwise divergence rates (PDR) ^b		
	Total	Ingroup	Total	Ingroup	All sites	Stem/2	Tv only
Globigerinids							
<i>G. bulloides</i>	5.6	5.6	5	5	4.4	4.52	1.78
<i>G. siphonifera</i> / <i>G. calida</i>	4.8/2.2	5.4/2.2	4.8/3.3	4.8/3.3	4.2	4.30	2.10
<i>G. conglobatus</i> / <i>G. ruber</i>	3.3/5.7	4/5.9	3.3/6.1	3.3/6.1	4.6	4.61	1.11
<i>G. sacculifer</i>	5.8	6.1	4.9	4.8	4.5	4.95	1.76
<i>O. universa</i>	3.3	3.2	3.6	3.8	4.5	4.95	1.76
Mean ^c	4.4 (1.44)	4.6 (1.5)	4.4 (1.05)	4.4 (1.02)	4.4 (0.16)	4.6 (0.27)	1.7 (0.41)
Linear regression ^d	4.1 (0.67)	4.2 (0.66)	4.0 (0.68)	4.0 (0.71)			
Globorotaliids							
<i>G. inflata</i>	0.6	1.0	1	1	1.0	0.92	0.25
<i>N. dutertrei</i> ^e	(0.1–0.2)	(0.4–0.9)	(0.3–0.7)	(0.5–1)	(0.3–0.7)	(0.2–0.45)	(0.08–0.18)
<i>G. hirsuta</i>	0.9	1.0	1.1	0.9	1.0	0.92	0.25
Linear regression ^d	7.1 (0.92)	7.5 (0.89)	6.7 (0.83)	6.8 (0.81)			
<i>G. truncatulinoides</i>	7.9	8.4	7.7	7.8	4.8	4.95	1.50
<i>G. menardii</i>	6.9	7.2	6.4	6.5	3.9	4.25	1.53
Linear regression ^d	0.8 (–4.5)	1.0 (0.99)	1.1 (0.98)	1.0 (0.98)			

Note. Time intervals used for calculating the different substitution rates are shown in Fig. 1.

^a See Material and Methods section for more detail on ILR calculation.

^b PDR = $K/2T$, where K is the Kimura-2 distance between two closely related species, and T is the divergence time of these two species. *G. bulloides*, *G. sacculifer*, *O. universa*, *G. inflata*, *N. dutertrei*, *G. hirsuta*, *G. truncatulinoides*, and *G. menardii* were, respectively, compared to *G. sacculifer*; *O. universa*, *G. sacculifer*, *G. hirsuta*, *G. inflata*, *G. inflata*, *G. hirsuta*, and *G. inflata*.

^c Mean value are given with their standard deviation.

^d Calculated as presented in Fig. 2. In brackets are indicated the coefficient of regression R^2 . For the globorotaliids, linear regression have been performed separately for the slow and fast evolving species (see Results).

^e Some confusion concerns the position of *N. dutertrei* in the fossil record; we used a large interval for its time of separation from the other globorotaliids (11–24 myr) for accommodating the discrepancies between authors.

analysis. We found important discrepancies between ML and MP analyses that change the rank of the most rapidly evolving species. We also tested the influence of outgroup sequences on rate computations by performing ingroup analyses with unrooted trees (compare columns 1 and 2, 3, and 4 in Table 2). The changes observed in MP analysis are minor compared to those found in ML. Regardless of the method, the linear regression analyses show that the observed values of substitutions/time can be fitted by straight lines with relatively high R^2 values. Residual analyses indicate that the points are distributed normally around the line, except one outlier, which is the branch leading to the cluster *Globigerinella calida*–*Globigerinella siphonifera* (22 myr). This confirms a relatively good molecular clock for the globigerinids.

Globorotaliid clade. Two groups of species having extremely different rates are observed within the globorotaliids: (1) the slowly evolving *Globorotalia inflata*, *Globorotalia hirsuta*, and *Neogloboquadrina dutertrei* that have relatively constant substitution rates of about 1 subst./site/10⁹ years and (2) the rapidly evol-

ing *G. truncatulinoides* and *G. menardii* whose rates average 7 subst./site/10⁹ years (Table 2). Because of such heterogeneity, the pairwise divergence rates are strongly biased and depend on the compared species. For instance, *G. hirsuta* rate equals either 4.8 subst./site/10⁹ years if it is compared with its sister species *G. truncatulinoides* or 1 subst./site/10⁹ years when compared with *G. inflata*. The rates of *G. truncatulinoides* and *G. menardii* are underestimated because they are artificially balanced by the slowly evolving species. In such a case, the ILR seem to be much more appropriate and give similar results for all methods (Table 2).

Globigerinids versus globorotaliids. Comparison of globigerinid and globorotaliid rates reveals important differences between the clades (Fig. 2). All analyses show that globigerinids have rates of substitution at least four times higher than those of more slowly evolving globorotaliids. They evolve, however, slower than the two fast clock globorotaliids. We tested the difference between globigerinids and slowly evolving globorotaliids by performing regression analyses with different constrained evolutionary scenarios concern-

TABLE 3

Relative Rate Test (RRT) of Wu and Li (1985), Applied to All Pairwise Combinations of 7 Globigerinid and 5 Globorotaliid Planktonic Foraminiferal Species and with the Benthic Foraminifera *Peneroplis* sp. as Reference Taxon

1	2	<i>bull.</i>	<i>sipho.</i>	<i>calida</i>	<i>conгло.</i>	<i>ruber</i>	<i>univer.</i>	<i>sacc.</i>	<i>menar.</i>	<i>inflata</i>	<i>hirsut.</i>	<i>trunc.</i>	<i>duter.</i>
Globigerinids													
<i>G. bulloides</i>		0.066	0.074	0.046	0.042	0.065	0.041	0.039	0.112	0.115	0.064	0.130	
<i>G. siphonifera</i>	0.024		0.007	-0.020	-0.025	-0.001	-0.026	-0.028	0.045	0.048	-0.002	0.064	
<i>G. calida</i>	0.024	0.011		-0.028	-0.032	-0.009	-0.033	-0.035	0.038	0.041	-0.010	0.056	
<i>G. conglobatus</i>	0.027	0.018	0.018		-0.005	0.019	-0.006	-0.008	0.066	0.068	0.018	0.084	
<i>G. ruber</i>	0.026	0.020	0.020	0.016		0.023	-0.001	-0.003	0.070	0.073	0.023	0.089	
<i>O. universa</i>	0.024	0.019	0.018	0.021	0.021		-0.024	-0.026	0.047	0.050	-0.001	0.065	
<i>G. sacculifer</i>	0.026	0.022	0.022	0.024	0.024	0.021		-0.002	0.071	0.074	0.023	0.090	
Globorotaliids													
<i>G. menardii</i>	0.026	0.023	0.023	0.025	0.025	0.024	0.027		0.073	0.076	0.026	0.092	
<i>G. inflata</i>	0.023	0.018	0.017	0.020	0.020	0.020	0.022	0.020		0.003	-0.048	0.017	
<i>G. hirsuta</i>	0.023	0.019	0.017	0.020	0.021	0.019	0.022	0.019	0.010		-0.050	0.015	
<i>G. truncatulinoides</i>	0.025	0.020	0.020	0.023	0.023	0.022	0.025	0.021	0.017	0.016		0.065	
<i>N. dutertrei</i>	0.023	0.018	0.017	0.020	0.020	0.019	0.022	0.019	0.006	0.009	0.016		

Note. The test statistic is the distance from the reference taxon 3 to taxon 1 minus the distance from taxon 3 to taxon 2, divided by the square root of the variance along these distances. Entries above the diagonal are the results of the test ($d_{13}-d_{23}$). Entries below the diagonal are the standard deviations associated with $d_{13}-d_{23}$ values. Both values define a standard normal distribution; differences of evolutionary rates between two taxa are significant (bold values in the table) if the absolute values of $d_{13}-d_{23}$ are two times higher than their standard deviation. A positive $d_{13}-d_{23}$ value indicates that taxon 1 evolves faster than taxon 2, and inversely for a negative value.

ing the order of branching and times of divergence of the globigerinid clusters (data not shown). In all cases, globigerinid rates of substitution were 3.2 to 4.9 times higher. We also examined the effect of compensatory mutations (Dixon and Hillis, 1993) that occur principally (80%) in globigerinids. The elimination of one strand of each stem does not decrease the globigerinids/globorotaliids difference. When only transversions are analyzed, the difference between both clades is higher (6.8 times) than when all sites are investigated. However, this is certainly due to the reduction of the number of compared sites. A Tv-only MP regression

analysis confirmed a fourfold difference between the globigerinids and the globorotaliids.

Relative Rate Test

The RRT largely corroborates the results obtained for absolute rates of evolution (Table 3). The majority of significant differences of evolutionary tempo (69%) are found between the globorotaliid and globigerinid taxa, confirming that the latter evolve faster. Moreover, the RRT presents the spinose globigerinids as a relatively stable group, except for *Globigerina bulloides* that evolves significantly faster than *G. siphonifera*, *O. universa*, and *G. calida*. Concerning the globorotaliids, the RRT corroborates the absolute rates about the acceleration of *G. truncatulinoides* and *G. menardii*. But both fast evolving globorotaliids do not evolve significantly faster than globigerinid species, which is in agreement with the PDR, but not the ILR values. This bias may be due to the sensitivity of the RRT to the stem-distance differences of each clade to the outgroup (Sorhannus, 1994).

DISCUSSION

Comparative studies of the rates of evolution in the two major clades of Neogene planktonic foraminifera, the globigerinids and the globorotaliids, reveal important differences between molecular rates based on SSU rDNA sequences and taxonomic rates inferred from the fossil record. Micropaleontological data suggest about three times higher origination-extinction rates for the globorotaliids than for the globigerinids. Our results

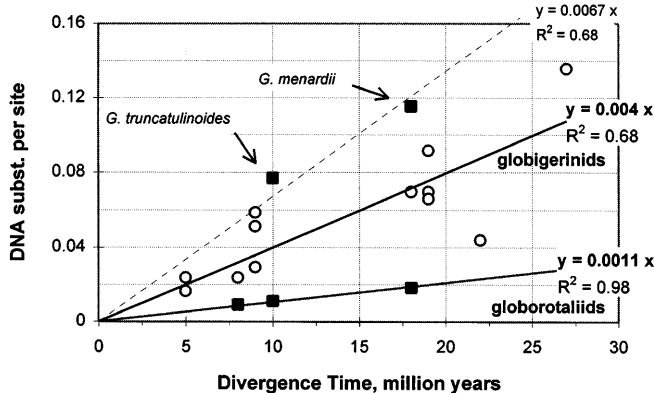


FIG. 2. SSU rDNA molecular clock calibration for the globigerinid and globorotaliid clades. Seventeen independent branch lengths (inferred from a MP total analysis in this plot) are regressed against time intervals given by the fossil record. Simple weighted linear regressions are constrained through the origin.

indicate that the rates of rDNA substitution in globigerinids are about four times higher than in globorotaliids, except for the globorotaliid species *G. truncatulinoides* and *G. menardii*.

There are several reasons to assume that the higher rates observed in *G. truncatulinoides* and *G. menardii* result from independent lineage accelerations rather than constitute basic rates of globorotaliids: (1) there is no direct phylogenetic relationship established between both species, *G. truncatulinoides*, diverged from the slow-clock *G. hirsuta* lineage only about 10 myr ago; (2) the lineages leading to the slowly evolving globorotaliids diverged independently during the radiation of the group; and (3) most of all, the slowly evolving globorotaliids possess rDNA variable segments that show high similarity with those of some benthic foraminifera that could be their ancestors (de Vargas *et al.*, 1997). It seems unlikely that these ancient sequences could have been recovered independently during the slow down of evolutionary rates.

A lack of correlation between the taxonomic and molecular rates in planktonic foraminifera confirms that both types of rates depend on different factors. Differences in taxonomic rates between globigerinids and globorotaliids have been proposed to be related to the size and structure of populations (Stanley *et al.*, 1988). The higher turnover of the globorotaliids was explained by smaller size of their populations and patchy, upwelling-dependent distribution, which stimulated more rapid speciation in response to changes in oceanic circulation and stratification (Stanley *et al.*, 1988). We can not exclude, however, that the taxonomic rates of the globorotaliids are biased due to the higher morphological complexity of this group, as suggested for other fossil taxa (Schopf *et al.*, 1975). Different lineages of globorotaliids develop similar morphological structures that could play a role in colonization of the deeper pelagic environments, by analogy with iterative evolution observed in Cretaceous planktonic foraminifera (Caron and Homewood, 1982). On the other hand, several cryptic speciations could have occurred in the globigerinids, characterized by more simple, globular tests. This has been demonstrated in *G. siphonifera* (Huber *et al.*, 1997) and it is suggested by the high genetic distance between the Mediterranean and Caribbean *O. universa* revealed by our study (Fig. 1).

Among the factors responsible for the heterogeneity of molecular rates in planktonic foraminifera, the generation time (Martin and Palumbi, 1993) could partly explain the difference observed between globigerinids and globorotaliids. The former exhibit lunar or semilunar reproduction cycles while the latter have generation times of up to 1 year (Hemleben *et al.*, 1989). Another factor to be considered will be the planktonic mode of life itself. It has been observed, at least in two groups of microorganisms, the foraminifera and the diatoms, that planktonic species have much higher

substitution rates than benthic ones (Kooistra and Medlin, 1996; Pawlowski *et al.*, 1997). The differences in the number of gametes and mode of reproduction linked to the planktonic condition were invoked to explain these higher rates of mutation. If we admit that the globigerinids adopted a planktonic mode of life independently and much earlier than the globorotaliids, as was suggested by de Vargas *et al.* (1997), that could explain their higher substitution rates.

The same factors, however, can hardly explain the differences observed between the fast and slowly evolving globorotaliids, in particular the eightfold acceleration of *G. truncatulinoides* in less than 10 million years. Such abrupt changes may be related to the peculiar character of foraminiferal rRNA genes (Holzmann *et al.*, 1996; Pawlowski *et al.*, 1996). In globorotaliids, we have found a positive correlation between the rates of substitution and the length of the rDNA expansion segments (about 100 bp have been added in different areas in *G. menardii* and *G. truncatulinoides*). We have also observed, using an ancestral benthic foraminiferal sequence as reference, that in 8 of the 14 sequenced rRNA helices (stem areas), substitutions are present only in globigerinids and/or fast-evolving globorotaliids. This evidence would suggest that differential structural constraints or biochemical mechanisms of foraminiferal rRNA are responsible for the variations of substitution rates. In order to test this hypothesis, an analysis of foraminiferal protein coding genes is in progress in our laboratory.

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