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The phanerozoic diversity of agglutinated foraminifera: Origination and extinction rates

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New diversity curves for agglutinated foraminiferal genera are presented based on the stratigraphic ranges of 764 genera distributed over the 91 Phanerozoic chronostratigraphic subdivisions given in the ICS timescale. The data set for this analysis is based on the stratigraphic ranges of agglutinated genera published in *Foraminiferal Genera and their Classification*, 218 of which have been modified based upon subsequently published studies and new observations. Additionally, a total of 136 genera have been newly described or reinstated subsequent to the publication of *Foraminiferal Genera and their Classification*. The revision of stratigraphic ranges is part of the effort by the Grzybowski Foundation's International Working Group on Foraminiferal Classification to compile a new *Catalogue of Agglutinated Foraminiferal Genera*. The mean standing diversity of agglutinated foraminiferal genera was compiled by counting the number of boundary crossers rather than the number of genera in each stage. This diversity curve displays a general upward trend throughout the Phanerozoic, punctuated by peaks and troughs of variable magnitude. The curve shows a period of initial radiation from the Early Cambrian to the Early Silurian, followed by a plateau to the Late Permian. The Permian/Triassic and the Triassic/Jurassic boundaries are characterised by small dips in the diversity record. The Jurassic begins with an exponential rise in mean standing diversity that continues to the Cenomanian. The Cenomanian to Holocene record of mean standing diversity is characterised by four peaks and troughs that are roughly in line with the cycles of global climate, with reductions in diversity in the end-Cenomanian, end-Cretaceous, and end-Miocene. Excluding modern values, the Phanerozoic maximum in the number of genera with a fossil record is observed in the Cenomanian, whereas the maximum Phanerozoic mean standing diversity is observed in the Langhian stage of the Miocene. The highest per-capita origination rates are observed in the Hettangian, Dapingian, Pleistocene, and Sheinwoodian (mid-Silurian). Linear regression analysis of the origination rates reveals a decrease towards the Holocene, in agreement with findings of Raup and Sepkoski. The highest per-capita extinction rates are observed in the Messinian, late Silurian (Gorstian), Hirnantian (latest Ordovician), and Maastrichtian. The background extinction rate shows an increasing trend towards the Recent, which is in disagreement with the findings of Raup and Sepkoski. We attribute this apparent discrepancy to the Late Cretaceous to Palaeogene extinctions of shallower-water larger agglutinates and the pull of the end-Miocene extinction event.

Key words: Agglutinated foraminifera, phanerozoic, biodiversity, extinction, origination.

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Introduction

The agglutinated foraminifera represent a large group of marine protozoans (over 750 genera), possessing the longest and most complete fossil record of any foraminiferal group, extending back to the latest Pre-Cambrian (over 570 million years). Because these organisms build shells made of agglutinated mineral grains cemented by organic or calcareous cement, their fossils are readily preserved and can be found in nearly all marine environments, from the high marshes to the deepest ocean trenches, and even in isolated salty springs in Transylvania, Romania. By virtue of their abundance, vari-

ety, long fossil record, good preservation potential, and relative ease of recovery, they are a good choice to study macro-evolutionary patterns among marine protozoans.

Agglutinated foraminifera as a group are regarded to be “conservative” in terms of their evolution, and indeed some genera that first evolved in the Cambrian are still present in the modern ocean. Because the modern agglutinated foraminifera are largely deep-marine organisms, they are to some extent insulated from global climate changes that affect shallow marine organisms. However, many Mesozoic genera were shallow marine organisms, occupying a niche that was previously inhabited by fusulinids and subsequently by larger rotaliids.

Nevertheless, it is instructive to quantify just what is understood by “conservative”, in terms of evolution. The main purpose of this study, therefore, is to analyse the diversity record of agglutinated foraminifera in terms of origination and extinction rates. Although the work on the revision of the agglutinated foraminiferal genera is still in progress, even at this early stage in the project we now have a much more complete diversity record of the agglutinated foraminiferal genera than has been published previously (e.g., Tappan and Loeblich 1988).

Other abbreviations.—DSDP, Deep Sea Drilling Project; LPIA, Late Palaeozoic Ice Age; ODP, Ocean Drilling Program.

Previous studies

The latest study to chart the Phanerozoic diversity of foraminiferal groups (suborders) was carried out by Tappan and Loeblich (1988). The stratigraphic ranges of the foraminifera genera from their book *Foraminiferal Genera and their Classification* (Loeblich and Tappan 1987) were plotted by suborder in the belief that records of the diversity of smaller taxonomic groups would be more meaningful than the group as a whole, because of variable life habits and habitats. However, one of the initial criticisms of the Loeblich and Tappan volume was the fact that in many cases, stratigraphic ranges of the genera were inaccurately reported, with many genera reported only from the Holocene (Decrouez 1989). Since 1987, a wealth of stratigraphical studies on agglutinated foraminifera has been published thanks in no small part to the efforts of the Grzybowski Foundation and the International Workshops on Agglutinated Foraminifera.

For the past several years, two of us (MAK and CGC) have been compiling a catalogue of all valid genera of the agglutinated foraminifera. The database now consists of over 750 genera, and represents an update of Loeblich and Tappan's (1987) book, which listed 624 agglutinated genera. As part of the work on our *Catalogue of Agglutinated Foraminiferal Genera*, we have been correcting and updating the stratigraphic ranges of the agglutinated foraminiferal genera based upon our new findings and on 20 years of literature published subsequently to the Loeblich and Tappan volume. Additionally we have established an “International Working Group on Foraminiferal Classification” with the aim of revising the tax-

onomy and classification of the foraminiferal genera, and producing a new database that will eventually replace the Loeblich and Tappan volume. An updated classification of the agglutinated foraminifera (comprising 747 genera) was presented by Kaminski (2004), and a summary of the newly revised stratigraphical ranges of the agglutinated foraminiferal genera compiled from the existing literature and new observations was published by Kaminski et al. (2008a).

Methods

We used Microsoft Excel to construct a spreadsheet containing all the validly recognised agglutinated genera (764 genera) with their stratigraphic ranges over 91 chronostratigraphic subdivisions in the ICS Timescale (Ogg et al. 2008). The data matrix contains the stratigraphic ranges of agglutinated foraminiferal genera published by Loeblich and Tappan (1987), supplemented by a search of over 1,000 publications published over the last 20 years, 177 of which contained more detailed information on stratigraphic ranges, as well as new observations carried out by the senior author. Our literature search resulted in 218 modifications to the stratigraphic ranges reported by Loeblich and Tappan (Kaminski et al. 2008a). The matrix also includes 136 genera that have been newly described or reinstated subsequent to the publication of *Foraminiferal Genera and their Classification*. We assumed that the stratigraphic range of each genus is continuous between its first and last occurrence, thereby eliminating Lazarus taxa that occur as a result of pseudoextinctions often following mass extinction. Curves of total diversity, mean standing diversity, originations, and extinctions were plotted using our data matrix.

As a first step, we used a straightforward taxic approach to produce a curve showing the number of genera in each geological stage, extending from the Early Cambrian to the Holocene (Fig. 1). Secondly, the mean standing diversity of agglutinated foraminiferal genera was plotted using the methods described by Foote (2000), counting the number of boundary crossers rather than the number of genera in each stage (Fig. 2). Consequently, the occurrences of genera reported from only a single stage are omitted, as these could derive from Lagerstätten (examples of exceptional fossil preservation) and may contribute artificial peaks to the diversity curve. A total of 155 genera that are only reported from the Holocene were also omitted from this curve in order to re-

Table 1. Definition of estimated mean standing diversity and taxonomic rate metrics.

Estimated mean standing diversity	$(X_b + X_t) / 2$ (Foote 2000)
Estimated per-capita rate, \hat{p} and \hat{q}	$\hat{p}: -\ln(X_{bt} / X_t) / \Delta t$ (Foote 2000)
	$\hat{q}: -\ln(X_{bt} / X_b) / \Delta t$ (Foote 2000)
Percent origination, p	$p: X_{Ft} / (X_{bL} + X_{Ft} + X_{bt})$ (Raup and Sepkoski 1982)
Percent extinction, q	$q: X_{bL} / (X_{bL} + X_{Ft} + X_{bt})$ (Raup and Sepkoski 1982)

N_{Ft} , the number of taxa crossing the top boundary only; X_{bL} , the number of taxa crossing the bottom boundary only; X_{bt} , the number of taxa crossing the both boundaries; $X_b (= X_{bL} + X_{bt})$, the total number of taxa crossing the bottom boundary; $X_t (= X_{Ft} + X_{bt})$, the total number of taxa crossing the top boundary (after Foote 2000).

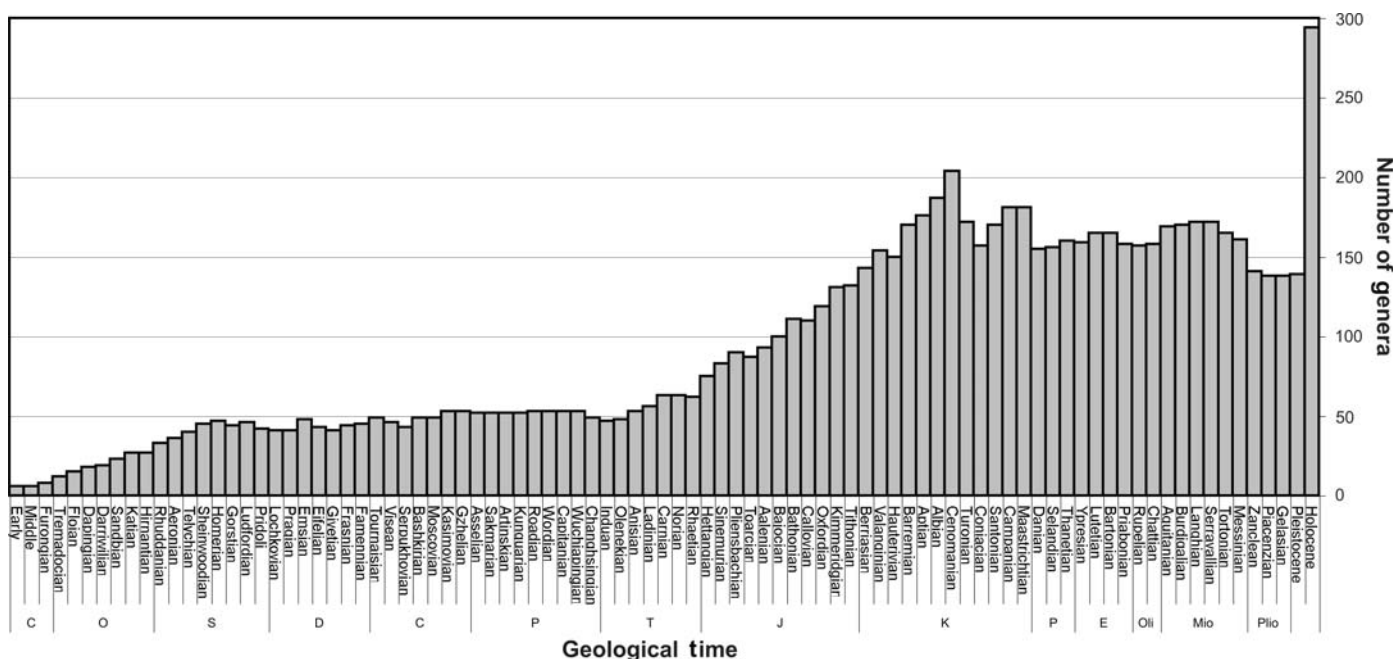


Fig. 1. Number of agglutinated foraminiferal genera in each geological stage based on updated ranges of 764 genera (including genera reported only from a single stage).

duce the “Pull of the Recent”. This method of plotting diversity is independent of stage duration and is less sensitive to preservational effects (Lagerstätten and genera reported only from the Holocene). To further examine the history of the agglutinated foraminiferal groups that contribute to the total diversity, we plotted the stratigraphic occurrence of individual suborders, using the taxic approach (Fig. 3).

Estimates of per-capita origination and extinction intensities were calculated using the methods of Foote (2000), which allow for differences in stage duration. The per-capita extinction and origination metrics were re-arranged in rank order to identify any discontinuities in their magnitude, and to identify above-background rates (Figs. 4, 5). The formulae used to construct these curves are given in Table 1.

Results

The Phanerozoic diversity of the agglutinated foraminifera

The oldest known fossil representative of the agglutinated foraminifera is the genus *Titanotheka*, which was found in sedimentary rocks of the latest Pre-Cambrian age (the Vendian or Ediacarian stage) in Argentina (Gaucher and Sprechmann 1999). This supposed ancestral form was a single-chambered sac-shaped genus, with later two-chambered and multichambered morphologies derived from this primitive ancestor. Early Cambrian forms such as *Platysolenites* from the lower Cambrian of Estonia have been discovered to possess a primitive proloculus (McIlroy et al. 2001) and were transferred to the Hippocrepinacea. This adds to the evidence

that the agglutinated foraminifera are derived from a simple sac-shaped ancestor.

The curves showing the number of genera in each stage and mean standing diversity are given in Figs. 1 and 2. These curves suggest the evolutionary history of the agglutinated foraminifera can be divided into five main stages:

(1) The early evolution was rapid until the mid-Silurian, with several new morphologies appearing during the Cambrian and Ordovician. Culver (1991) described simple ammodiscids and enigmatic two-chambered forms from the Lower Cambrian of West Africa. The earliest pseudo-multichambered genus *Ammolagena* first appeared in the early Middle Ordovician (Kaminski et al. 2008b).

(2) The mean standing diversity curve then shows a diminished rate of increase over the mid-Silurian to mid-Carboniferous interval, while the curve of the number of genera shows a variable plateau. This plateau is evident even though the ranges of quite a few Palaeozoic genera have been recently modified, owing largely to the laudable efforts of Ken Bell and co-workers in Australia (e.g., Bell 1996; Bell et al. 2000).

(3) Stasis is recorded in both curves from the mid-Carboniferous to the end of the Permian. Only a very minor reduction in diversity is seen at the Permian/Triassic boundary, and over the whole interval the origination and extinction rates are roughly balanced.

(4) An interval of renewed diversification begins in the Early Triassic, with diversification rates increasing dramatically in the Hettangian stage of the Early Jurassic. This phase of diversification lasts until the Cenomanian stage of the Late Cretaceous, when the maximum number of genera is recorded (Fig. 1).

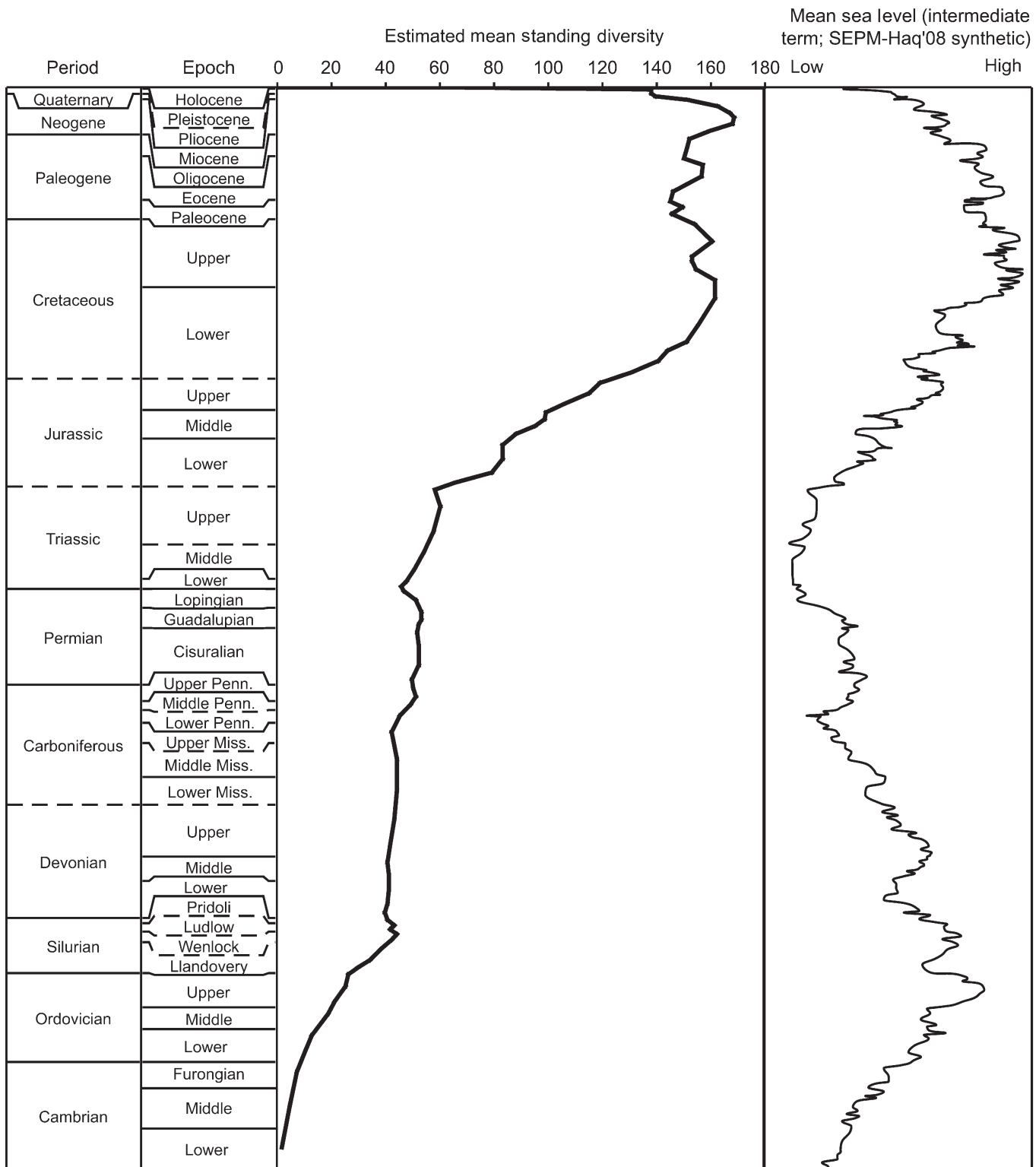


Fig. 2. Phanerozoic mean standing diversity of agglutinated foraminifera and mean sea level. The mean sea level curve was generated using Time Scale Creator, version 4.0.2 [<http://www.tscreator.com>]

(5) From the mid-Cretaceous to the Holocene, the diversity curve shows three broad maxima that compare well to the cycles of global sea levels and warming/cooling that took place over the Late Cretaceous to Cenozoic interval (Miller et al. 2005). Three critical intervals of extinction are ob-

served over this interval: the Cenomanian/Turonian, Cretaceous/Palaeogene, and Miocene/Pliocene boundaries.

The timing and magnitude of diversification and decline vary widely among the different suborders of agglutinated foraminifera (Fig. 3). All four suborders that have representa-

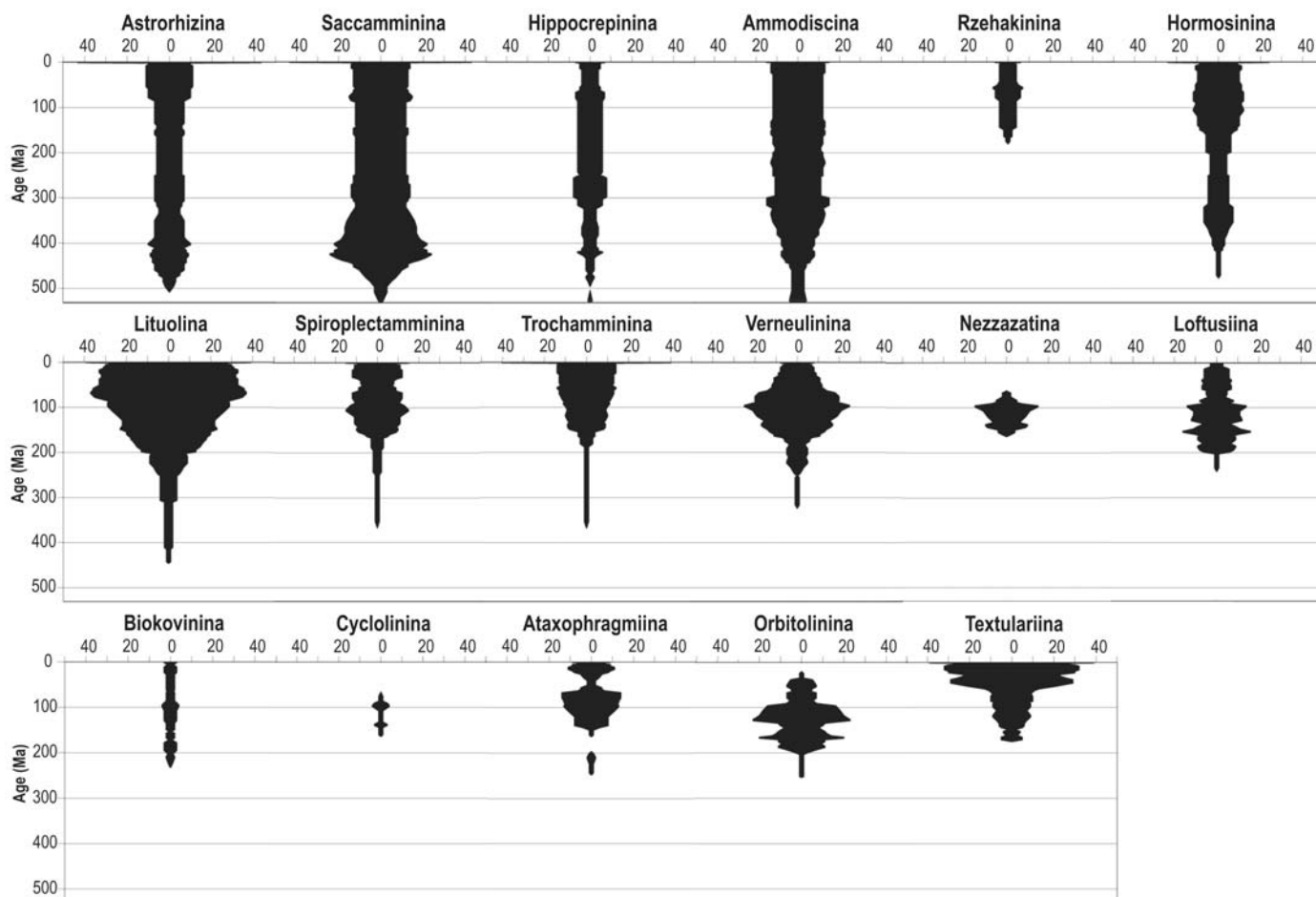


Fig. 3. Stratigraphic ranges of agglutinated foraminiferal suborders (Kaminski 2004) over the Phanerozoic.

tives in the Cambrian (Astrorhizina, Saccamminina, Hippocrepinina, and Ammodiscina) are still extant today. The Ammodiscina is the dominant group in the Cambrian, while the Saccamminina show a rapid radiation until the Late Silurian, and become the dominant group among the four suborders at that time. The Hormosinina first appear in the Ordovician and diversify during the Devonian. The rest of suborders appear by the Oxfordian. The Lituolina, Spiroplectamminina, Trochamminina, Verneulinina, Loftusiina, and Ataxophragmiina increase in diversity very rapidly during the Mesozoic, and most of these groups show a decline at the end-Cretaceous. Another peculiarity in the diversity patterns of the suborders is that the Hippocrepinina, Verneulinina, Biokovinina, and Ataxophragmiina appear to be Lazarus taxa. The Ataxophragmiina, for example, are absent from the Hettangian to Callovian, an interval of about 35 Myr. The Cainozoic is characterised by the rapid radiation of the Textulariina. The stratigraphic records of the Astrorhizina, Hormosinina, and Trochamminina need to be further resolved, as these groups possess many genera that are only recorded from the Holocene.

For the diversity falls identified in the estimated mean standing diversity at the Changhsingian/Induan, Norian/Rhaetian, Cenomanian/Turonian, Campanian/Maastrichtian, Maastrichtian/Danian, Bartonian/Priabonian and Messinian/

Zanclean boundaries, simultaneous decreases in the diversity of several suborders are recognised. The Spiroplectamminina, Ataxophragmiina, and the suborders of larger agglutinated foraminifera (Loftusiina and Orbitolinina) in particular show prominent evolutionary bottlenecks. Three groups that first appeared in the Mesozoic (Cyclolinina, Nezzazatina, and Orbitolinina) suffered extinction in the Campanian, Maastrichtian, and Chattian, respectively.

Extinction and origination rates

Taxonomic metrics performed on the curve include percent originations and extinctions in a given geological stage, and these rates were normalised to differing stage durations, providing origination and extinction rates per million years (Figs. 4, 5). The origination and extinction rates were then ranked to graphically illustrate the events of highest amplitude, and to determine whether their distribution is continuous (Fig. 6).

The extinction record shows that these marine protozoans were adversely affected by the five major Phanerozoic mass extinction events recognised by Sepkoski and co-workers. In Sepkoski's data (Sepkoski 2002), the highest extinction rate is observed at the end-Permian, with other major peaks in extinction observed at the end-Ordovician, end-Devonian, end-

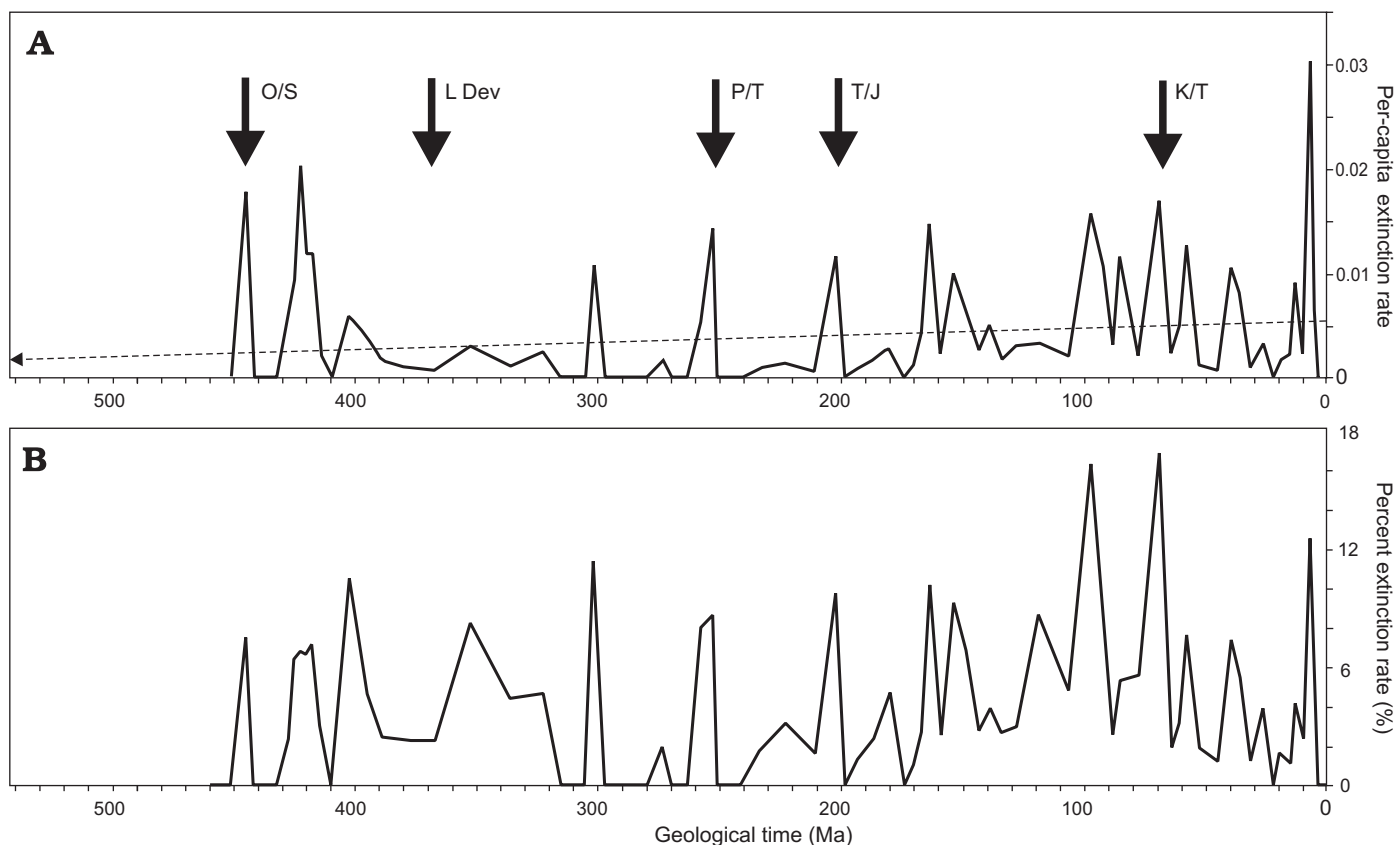


Fig. 4. Per-capita (A) and percent (B) extinction rates of agglutinated foraminiferal genera over the Phanerozoic, compared with the “Big-5” mass extinctions of Sepkoski (1984).

Triassic, and end-Cretaceous. In comparison to Sepkoski's (2002) record of marine macrofaunal biodiversity, the diversity decrease in agglutinated foraminifera that we observe associated with these mass extinction events is much lower, which highlights the resilience of these more primitive marine protozoans to environmental change. However, unlike Sepkoski's (2002) biodiversity curve, we also observe extinction rates that are significantly above background levels in the Gorstian, Callovian, end-Cenomanian and end-Miocene. In our record, the end-Cenomanian extinction event rivals the Cretaceous/Palaeogene event in terms of magnitude, with extinction of about 16% of genera. The end-Miocene extinction appears to be an especially significant one, when about 12% of the genera went extinct, while Sepkoski's (2002) data show an extinction rate of less than 10%. The time-corrected extinction rate (per-capita rate), however, suggests it is the most rapid extinction event in the Phanerozoic record for agglutinated foraminifera. The background extinction rate shows an increasing trend towards the Recent, which is in disagreement with the findings of Raup and Sepkoski (1982). This increasing trend is likely due in part to the two devastating extinction events observed mostly among larger agglutinated genera at the end-Cenomanian and end-Cretaceous, as well as the pull of the end-Miocene extinction event, which may be caused in part by a sample/observer bias (see discussion below).

The origination rate appears to vary greatly through geological time (Fig. 5), and the ranked dataset of origination rates (Fig. 6) shows a discontinuous distribution. The per-capita origination rate (diversification) is particularly high in the Early Ordovician, early Silurian, late Carboniferous, Early Jurassic, mid-Cretaceous, early Eocene, and early Miocene. Curiously, the background extinction rates are higher for the Jurassic to Holocene part of the record than for the pre-Jurassic.

In the Palaeozoic record of per-capita origination rate the peaks are generally higher from the Early Cambrian to the late Silurian (Gorstian) than those in the remainder of the Palaeozoic, and the maximum is reached in the Dapingian. The “universal depression” of origination and extinction rates displayed by marine invertebrates during the Late Carboniferous to Early Permian ice ages (Stanley and Powell 2003) is not apparent in our record. If anything, origination rates during the period between 275–325 Ma are characterised by their high variability. As is the case with the fusulinid taxa (Groves and Lee 2008), average per-capita origination rates within the Late Palaeozoic Ice Age (LPIA) period are higher than in the intervals immediately before or after the LPIA. Instead of displaying elevated rates in the late Permian as is the case with marine invertebrates, with the exception of the basal Permian Asselian stage, the origination rate of agglutinated foraminifera remains at zero for the rest of the Permian. After the Permian period of no origination, there is

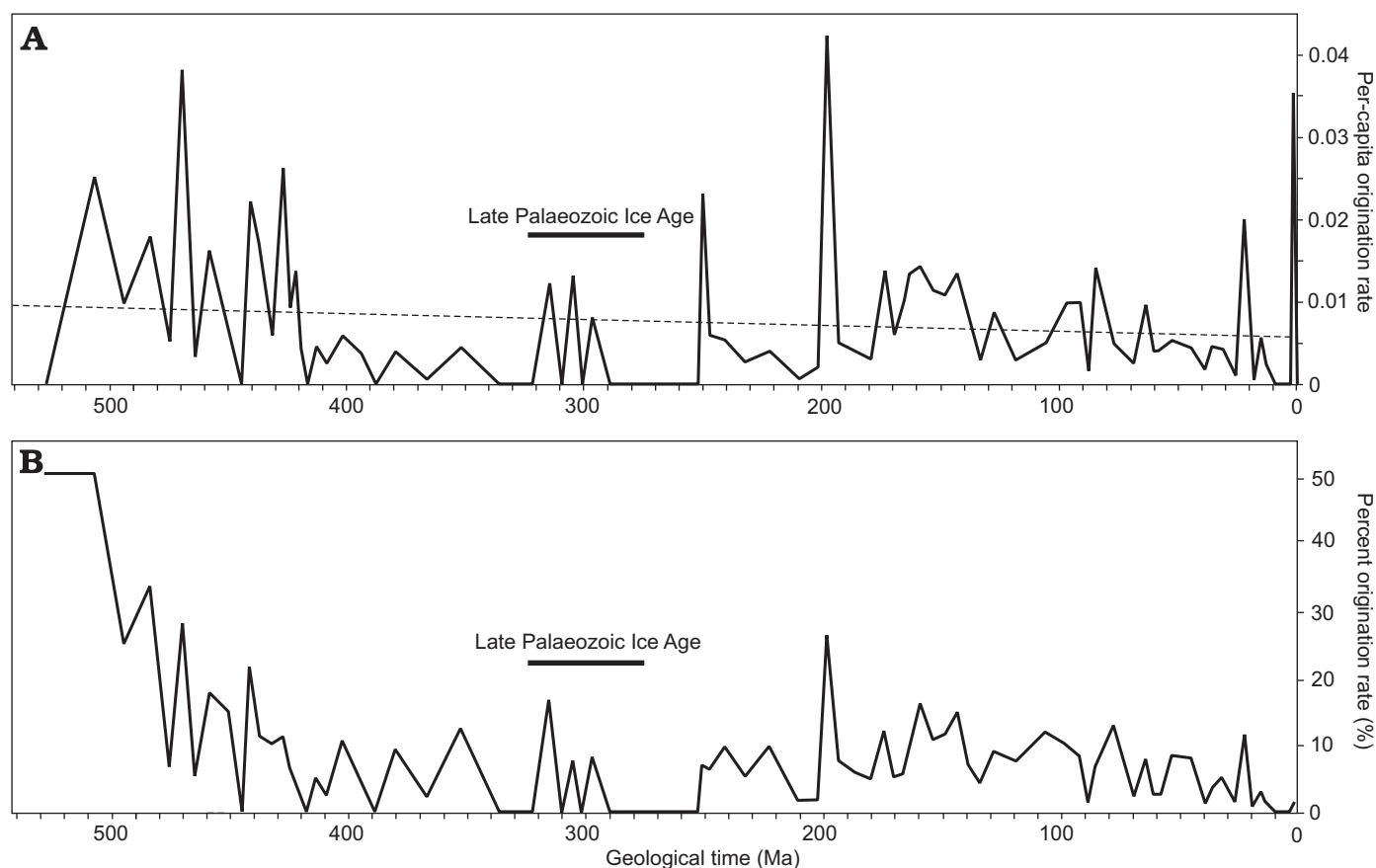


Fig. 5. Per-capita (A) and percent (B) origination rates of agglutinated foraminiferal genera over the Phanerozoic.

a massive radiation in the beginning of the Triassic, the Induan, followed by an interval of relatively low rates. The origination rate reaches its Phanerozoic maximum in the Hettangian and then drops rapidly in the next stage. During the Middle and Late Jurassic, the rate remains relatively high in comparison with rates in the rest of the Mesozoic and the Cenozoic. There is a fluctuation of the origination rate during the Cretaceous, and the rate reaches its highest value in the Santonian. The Cenozoic appears to be a period of low origination, except for the peaks in the Aquitanian (Early Miocene), and the Pleistocene. The rate remains at zero in the Late Miocene, and the Pliocene. The background origination rate indicated by a linear regression line decreases towards the Holocene (Fig. 5). This is in agreement with the findings of Raup and Sepkoski (1982) and Gilinski and Bambach (1987).

Discussion

Origination and extinction events

Global climate (and associated species-area effects) undoubtedly played a role in the diversification of agglutinated foraminifera. For example, nearly all the peaks in origination rate correspond to well-known marine transgressions or long-term sea level rises, which are linked to global climatic trends

(Miller et al. 2005). Twenty years of subsequent work on the stratigraphic records of the agglutinated foraminifera after the publication of the Loeblich and Tappan (1987) volume (especially some recent key studies on the Palaeozoic and Mesozoic) now give us much improved resolution of the early diversification of the group, bringing the early diversification rates more in line with general trends in the Sepkoski (2002) curve. Several origination and extinction events stand out above the background rate. Extinction events, such as ones at the Cenomanian/Turonian and Cretaceous/Palaeogene boundaries, are relatively well studied, but the record of agglutinated foraminifera points to some lesser-known extinction and origination events:

The Late Palaeozoic Ice Age period.—The “universal depression” of origination and extinction rates displayed by marine invertebrates during the Late Carboniferous to Early Permian ice ages between 275–325 Ma (Stanley and Powell 2003) is not apparent in our record. Stanley and Powell (2003) claimed that non-fusulinid foraminifera conform to the general pattern of suppressed origination and extinction rates during the LPIA, but this is clearly not the case with agglutinated foraminifera. As is the case with the fusulinid taxa (Groves and Lee 2008), average per-capita origination rates within the LPIA are variable, but are distinctly higher than in the intervals immediately before or after the LPIA. The three

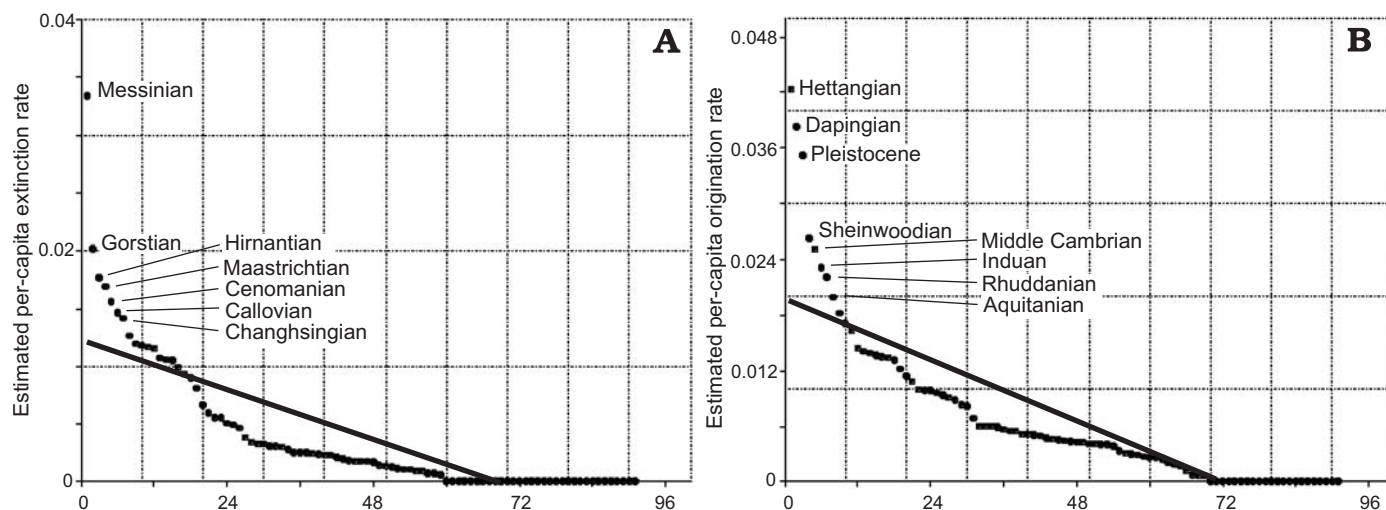


Fig. 6. Ranked per-capita extinction (A) and origination (B) rates, showing events of highest amplitude.

peaks in origination in our record correspond to the Serpukhovian, Kasimovian, and Asselian stages, the former and latter of which represent the cooler intervals (glacials II and III) of the LPIA. In the case of the fusulinids, the invention of algal symbiosis and fragmentation of their geographical ranges are widely regarded as key factors that promoted their diversification, but among the agglutinated foraminifera no evolutionary innovations or geographical provincialism are observed. The agglutinated genera appearing during the LPIA are mainly simple smaller ammodiscids, hippocrepinids, and astrorhizids, as well as some multichambered genera that today inhabit both shallow and deep environments taxa such as *Trochammina*, *Spiroplectammina*, and *Haplophragmoides*. Expansion and contraction of epicontinental habitat size would have had the same effect on foraminifera as on other shallow-marine invertebrate taxa, but does not explain why marine invertebrates had subdued evolution while some groups of foraminifera display enhanced evolution during the LPIA. However, one feature relating to the habitat of agglutinated foraminifera is clearly apparent in our data set: eight out of the 15 agglutinated genera that suffered extinction during the LPIA or were confined to the interval were sessile, whereas most of the genera that either survived the LPIA or originated during the period (45 out of 49 genera) were motile. Perhaps sessile forms were at a disadvantage during a period of rapidly fluctuating sea levels? In any case, the classic studies of late Palaeozoic agglutinated foraminifera were largely based on acid residues of shallow-water carbonates, mostly in the North American and European coal measures. Therefore a sampling bias is likely present in our data set. We need more studies on agglutinated foraminifera from a range of environments across the LPIA to resolve the question of elevated origination rates.

The Hettangian origination.—This event represents the largest peak in the per-capita origination rate, and is characterised by the first appearance of some “larger” agglutinated foraminiferal genera, derived from *Lituola*, such as *Cym-*

briaella, *Haurania*, *Orbitopsella*, *Everticyclammina*, *Litosepta*, *Biokovina*, etc. This origination event actually covers the interval from the Hettangian to Pliensbachian, and the background origination rate remains above the pre-Jurassic rate well into the Cretaceous. The appearance of larger foraminifera with complex inner structures is associated with the Hettangian transgression and the development of widespread carbonate platform environments in the Peri-Tethyan region, with the establishment of a stable, oligotrophic, shallow-water environment. These conditions led to the development of larger foraminifera with chamberlets that may have housed algal symbionts, and such forms become well established by the late Sinemurian (Septfontaine 1988; Fugagnoli 2004). At first glance, from our diversity record may appear unusual for a major origination event to appear without a precursor extinction event, as the two phenomena in the marine biodiversity record are causally linked (Stanley 2007). However, the larger agglutinated foraminifera of the early Jurassic have taken over the ecological niche vacated by the calcareous microporiferate fusulinids. This foraminiferal group suffered a double extinction event in the late Permian (Stanley and Yang 1994), with the last morphologically primitive survivors becoming extinct in the late Triassic. By the Pliensbachian, the Tethyan carbonate platforms had been colonised by new lineages of large, morphologically complex loftusiids and textulariids, including the pfenderinids, hauraniids, mesoendothyrids, biokovinids, and chrysalidinids (see review by BouDagher-Fadel 2008).

The Cenomanian turnover.—The Cenomanian stage represents the Phanerozoic maximum in the diversity of agglutinated foraminifera, with a total of 204 genera present (Fig. 1). It also contains the largest number of genera that possess stratigraphic ranges restricted to a single stage (16 genera). We note the first occurrences of 35 genera within the Cenomanian stage, most of which belonging to the loftusiids, including *Orbitolinella*, *Dohaia*, *Cyclolina*, *Littonella*, *Quataria*, *Spirocyclina*, *Coxites*, and others. In addition, some notable deep-

water forms such as *Praecystammina* and *Bolivinopsis* also make their appearance in the stratigraphic record. The Cenomanian witnessed the Phanerozoic peak in global sea levels (Miller et al. 2005), and most of Cenomanian larger agglutinated foraminifera had their origin in the subtropical lagoons and shallow carbonate shelf seas of the Tethyan region, with only one genus restricted in the Caribbean (BouDagher-Fadel 2008). The Cenomanian extinction rate (ca. 16%) ranks just below the Cretaceous/Paleogene boundary extinction event (Fig. 6). The extinction of many of the Cretaceous larger agglutinated foraminifera, as well as Jurassic survivors such as *Everticyclammina* and *Siphovalvulina* is causally linked to the drowning and collapse of the tropical reef ecosystems in the late Cenomanian (see review by Skelton 2002). A number of smaller agglutinated genera did not survive Oceanic Anoxic Event 2 at the Cenomanian/Turonian boundary (Schlanger and Jenkins 1976), including *Spiroplectinata*, *Quasispiroplectammina*, *Kaminskia*, *Aaptotoichus*, *Buccicrenata*, and *Pfenderina*. Carbon-rich sediments and associated taxonomic turnover in agglutinated foraminifera have been documented from numerous DSDP and ODP sites and onshore sections worldwide (e.g., Kuhnt 1992; Kaiho and Hasegawa 1994; Coccioni et al. 1995), and reflect a major perturbation of the global carbon cycle that lead to widespread oceanic anoxia.

The Aquitanian origination.—In the latest Oligocene to earliest Miocene a number of trochospiral agglutinated genera with alveolar or canaliculate walls first appeared in the fossil record. Genera, such as *Alveovalvulina*, *Guppyella*, *Goesella*, and *Alveovalvulinella*, are typical of assemblages found in subtropical oxygen minimum zones, especially in West Africa and the Caribbean. It is likely that the global warming of the latest Oligocene to Early Miocene contributed to intensification of dysoxic conditions in upwelling regions, creating an expanded niche for these organisms that flourished in low-oxygen conditions. In a recent study of the lower bathyal Miocene foraminiferal assemblages of the Congo fan, offshore Angola, Kender et al. (2008) noted steadily increasing diversity and proportions of infaunal morphotypes over the lower Miocene interval. The proportion of infaunal types increased dramatically in the lower mid-Miocene, indicating expansion of the Oxygen Minimum Zone into deeper waters. In addition to the trochospiral alveolar genera, species of *Reticulophragmium* and *Cyclammina* display rapid diversification into numerous separate lineages that are at present not reflected in our generic diversity record owing to their poorly established taxonomy. It is likely that a more detailed phylogenetic approach to these genera would result in the description of new genera for individual lineages.

The Messinian extinction.—This event appears to be the largest extinction event in the diversity record of agglutinated foraminifera (Fig. 6), and it is arguably the most poorly understood event. The extinction is partly due to the disappearance of some of the alveolar or canaliculate genera that evolved in the Early Miocene. These include *Matanzia*, *Jarvisella*, *Pseudotriplasia*, *Alveovalvulinella*, and *Colominella*. The fact

that so many of these genera belong to the infaunal morpho-group suggests that the end-Miocene extinction may be a precursor of the “*Stilostomella* Extinction Event” noted among calcareous deep sea benthic foraminifera (Schönfeld 1996). However, the actual “Messinian extinction event” among agglutinated genera may be influenced by an observer bias (see below). The lack of published early Pliocene records means that the stratigraphic ranges of some genera are simply reported as “Miocene”. This interval in particular requires further study to improve stratigraphic resolution, in particular in offshore upwelling regions where the alveolar genera are found.

Possible bias in the diversity curve

We cannot exclude the possibility that at least some features of the diversity curve may be due to observer or stratigraphic bias or uneven sampling intensity. The Phanerozoic history of the group has probably been influenced by various biases, such as the rock-volume, sampling intensity, and taxonomical effort biases. The effects of possible biases on diversity records have been reviewed by Smith (2003) with reference to marine invertebrates. It is perhaps no coincidence that the large rise in our mean standing diversity observed in the Jurassic also corresponds to the largest increase in the curve of marine rock outcrop area in Western Europe compiled by Smith and McGowan (2007). The influence of these possible biases on the diversity record of agglutinated foraminifera needs to be evaluated.

In the case of agglutinated foraminifera we see additional biases. For example our oldest record of the deep-sea environment (the largest biotope on our planet) sampled by the Ocean Drilling Program hails from the Late Jurassic. Whole environments where agglutinated foraminifera are common (such as salt marshes, mangrove swamps, the Central Arctic, and the Antarctic seas) have very patchy stratigraphic records. Single studies of agglutinated assemblages from deep-sea cores can still produce numerous changes to the known ranges of agglutinated genera. The end-Miocene diversity fall in particular may be a precursor of the “*Stilostomella* Extinction Event” or may be partly due to the fact that we have so few good published records of agglutinated foraminifera from Pliocene and Pleistocene strata. We list a total of 293 living genera of agglutinated foraminifera, whereas our Pliocene record shows only 132 fossil genera. Part of this apparent discrepancy may be due to the fact that not all modern forms have shells that are readily preserved, as already noted by Tappan and Loeblich (1988), but part of the discrepancy is no doubt due to the “incompleteness of the sampled fossil record”. If we accept that all the genera listed as existing only in the modern ocean might some day be found preserved as fossils in Mesozoic to Cenozoic sediments, then the diversification rate of the group would appear to continue undiminished since the Early Jurassic. It is possible that in the future, a more phylogenetic approach (rather than a simple taxic approach) to compiling the diversity record may improve the robustness of our curve and give us higher diversification rates over the post-Triassic inter-

val. Nevertheless, the current shape of our diversity curve does indeed mimic the records of calcareous nannoplankton (Bown et al. 2004) and planktonic foraminifera (Tappan and Loeblich 1988)—groups of marine protists that have much more complete and well-established fossil records. The effect of global climate on the diversity record of these primitive single-celled organisms is undeniable, but to exactly what extent remains to be quantified.

Conclusions

New data on stratigraphic ranges of agglutinated foraminifera have been compiled as a result of a literature search of over thousand publications, and analysed to produce curves of diversity, and rates of origination and extinction. The ranges of 218 genera (29%) have been modified compared with the ranges reported by Loeblich and Tappan (1987), based on subsequently published literature and new personal observations (Kaminski et al. 2008a).

The diversity curve of agglutinated foraminifera increases rapidly during the interval between the Cambrian and mid-Silurian, and then remains stable for the rest of the Palaeozoic. The Mesozoic represents a period of rapid diversification up to the Phanerozoic maximum in the Albian–Cenomanian. The diversity decreases after the Cenomanian maximum, and drops again at the Cretaceous/Palaeogene boundary. The diversity recovers after the end-Cretaceous event and reaches the Cainozoic maximum in the Langhian of the middle Miocene. Agglutinated foraminifera appear to have undergone the most severe extinction in the late Miocene, although we question whether this is a real phenomenon or the consequence of sampling or preservational bias.

The background rate of origination shows a downward trend towards the Recent, while the background extinction rate increases slightly. However, the ultimate causes of these trends are still uncertain, and may be partially attributable to observer biases. A discontinuous distribution of origination and extinction intensities is identified by the analyses of ranked data of the taxonomic rates. Origination rate peaks that deviate from a continuous distribution are identified in the Hettangian, Pleistocene, Dapingian, Sheinwoodian, Middle Cambrian, Induan, and Rhuddanian. The highest peaks in extinction intensity occur in the Messinian, Gorstian, Hirnantian, Maastrichtian, Cenomanian, Callovian, and Changhsingian. All these marked extinction rates either coincide with or are followed by elevated origination rates within several million years of the extinction. This indicates that mass extinctions can be an important factor that drives evolution. Oceanic anoxic events often occur in the stage in which diversity drops and significantly elevated extinction rates are identified. However, some proposed anoxic events, for example those in the Toarcian and Aptian–Albian, do not coincide with diversity depletions or high extinction rates, which brings into question causal relationships between oceanic anoxic events and faunal turnovers among agglutinated foraminifera.

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