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BRYOZOAN GENERIC EXTINCTIONS AND ORIGINATIONS DURING THE LAST ONE HUNDRED MILLION YEARS

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ABSTRACT

Stage-level analysis of extinctions and originations of bryozoan genera of the orders Cyclostomata and Cheilostomata for the Upper Cretaceous and Cenozoic yields some predictable and some unexpected results. Extinction rates in cyclostomes and cheilostomes track one another except for some lower Upper Cretaceous stages in which apparently random extinctions among the small numbers of cheilostome genera generated 'noise'. Both orders experienced high rates of extinction during or at the end of the Maastrichtian (our data cannot resolve position of extinctions within a stage) but, surprisingly, Danian extinction rates were essentially equal to Maastrichtian rates. High extinction rates for the Danian are attributed to loss of the 'chalk' sea of northern Europe, which was a centre of bryozoan diversity from early in the Late Cretaceous until its disappearance at the end of the Danian. Origination rates of cyclostomes and cheilostomes were similar and relatively high during the Late Cretaceous, but following the K-T extinction event, cyclostome origination rates dropped and remained at low levels through the Cenozoic, while cheilostome origination rates rebounded by the Eocene and then declined through the Pleistocene. The different Cenozoic diversity trajectories of cyclostomes and cheilostomes appear to derive primarily from differences in origination rather than extinction rates.

KEY WORDS: extinctions, originations, Cretaceous-Tertiary, K-T, benthic invertebrates

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INTRODUCTION

Much attention has been focused on the K-T extinction since the now famous hypothesis of bolide impact was first mooted in 1980. Substantial information has been amassed and used to address issues relating to the causal mechanism(s) of the extinction (e.g., Alvarez et al. 1980, Bohor et al. 1984, Venkatesan and Dahl

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1989, Hildebrand and Boynton 1990, Izett et al. 1991), as well as to patterns of extinction and recovery experienced by particular groups of organisms (e.g., Jablonski and Raup 1995, Marshall and Ward 1996, Sheehan et al. 1996, MacLeod et al. 1997, d'Hondt et al. 1998, Jablonski 1998, Smith and Jeffrey 1998). With regard to the latter, biological groups with more utilitarian fossil records (e.g., planktonic foraminifera) or broad scientific and public appeal (e.g., dinosaurs) have received the most attention, whereas relatively little is currently known about extinction patterns in many other groups, including bryozoans.

Bryozoans are a phylum of colonial metazoans with a rich marine fossil record due to the readily fossilisable calcareous skeletons possessed by most species. Two clades of calcareous bryozoans are represented in the Cretaceous and Cenozoic, cyclostomes (Class Stenolaemata) and cheilostomes (Class Gymnolaemata). Both clades were diverse during the Late Cretaceous; however, knowledge of their systematics is woefully inadequate—many species have yet to be formally described and others remain unrevised and are virtually unrecognisable using the original descriptions published in the 19th Century. This lack of knowledge is compounded for the cyclostomes which, in contrast with the skeletally more complex cheilostomes where a close correspondence has been demonstrated between genetically and skeletally determined species (Jackson and Cheetham 1990), have relatively simple and easily confounded morphologies (McKinney and Jackson 1989; Håkansson and Thomsen 1999). Ranges of species in time and space at all scales of resolution, from single stratigraphical sections to globally, are poorly documented, and almost nothing is known about phylogenetic relationships that might aid the interpretation of extinction patterns (e.g., Smith and Jeffery 1998, for echinoids). Despite these problems in documentation, the completeness of the fossil record apparently is rather high for bryozoan genera, with an approximately 70 percent probability of the preservation of a genus in each stratigraphic stage throughout its range (Foote and Sepkoski 1999). With regard to global patterns, the finest level of analysis that can reasonably be attempted at present for bryozoan genera is at the level of the stratigraphical stage/age, as done, for example, by Viskova (1980, 1997).

Alternative approaches to understanding the historical record of bryozoans have looked at changes in species assemblage diversity and in relative skeletal biomass around and across the K-T boundary (Lidgard et al. 1993; McKinney et al. 1998, in press). The only bed-by-bed study of bryozoan species distributions across the K-T boundary is that of Håkansson and Thomsen (1999) at Nye Kløv in Denmark. In this paper, we track the history of originations and extinctions of Late Cretaceous through Cenozoic bryozoans at the genus level. Therefore, we utilise primarily the global record of temporal distribution of the genera rather than local species assemblage diversities or skeletal biomass.

The existence of two distinct clades of bryozoans crossing the K-T boundary provides a replicate data-set of extinction and origination patterns, thereby lessening potential problems caused by factors specific to one clade. Cyclostomes date back in the fossil record to the Lower Ordovician, cheilostomes to the Upper Jurassic (Taylor 1993). Each group is thought to have acquired its mineralised skeleton independently from a bryozoan of ctenostome-grade and to share a common ancestor no younger than Early Ordovician (Todd 2000). They show important differences in zooidal baupläne, which apparently are linked with the greater rate of suspension feeding, growth rate, and – in tropical and temperate waters – ability to compete for substrate space in cheilostomes (McKinney 1993, 1995; but see Barnes and Dick 2000 for reversal of competitive interactions in high latitude waters). Species belonging to the two clades commonly co-exist and compete with one another in the same habitats, and a comparable range of colony forms is developed in the two clades. Cyclostomes and cheilostomes, therefore, occupy broadly similar 'ecospace'; however, some cheilostomes have invaded brackish waters and a few others have evolved free-living colonies, while cyclostomes have done neither. Other than these two categories of exceptions, the two clades might be expected to show parallel responses to the majority of environmental changes.

To put our consideration of extinction at the K-T boundary into a broader evolutionary context for the phylum and to identify other times of enhanced generic turnover during the past 100 million years—whether resulting from changes in extinction or origination rates - we analysed a new database of uppermost Lower Cretaceous to Recent (Albian-Recent) bryozoans containing genus ranges at stage/age-level precision. The three principal questions we set out to address initially were

1. Did generic extinction of Albian-Recent bryozoans peak in the Maastrichtian, corresponding with the K-T event?

2. Are temporal patterns of generic extinction and origination intensities the same for cheilostomes and cyclostomes?

3. Do generic origination rates support Voigt's (1981) notion of the Danian as a stage of low 'creativity'?

DATA AND METHODS

Stage-level ranges for Albian-Recent cheilostome and cyclostome bryozoan genera were provided by J. J. Sepkoski, Jr. from his unpublished global genus database. Accuracy of the database was checked by us, resulting in various alterations to about 20 percent of the records, largely changes in ranges but also including elimination of some synonyms, addition of some genera, and reassignment of a few genera from cyclostomes to cheilostomes or vice versa. This proportion of errors is consistent with the findings of Adrain and Westrop (2000) for trilobites in Sepkoski's database, and like they, we found that the error was randomly distributed, so that results of analyses based on the database did not differ greatly between the original and corrected versions.

The analysed data comprised 808 genera (545 cheilostomes; 263 cyclostomes), of which 24 percent are confined to one stage. Origination and extinction metrics were calculated both with and without such stage-only genera. Error bars for the origination and extinction metrics were calculated using the 'Percentage Error Bars' program, freeware available from Steve Holland at http://www.uga.edu/~strata/Software.html. The program is based on a calculation procedure given in Raup (1991).

The Gradstein and Ogg (1996) timescale was used for stage boundary dates. Numbers of appearances and disappearances, hereby referred to as originations and extinctions respectively, per stratigraphic interval constitute the raw data and must be calibrated in order to be of most use. The method of calibration, however, has not been standardised, with extinctions and originations variously being presented as (1) number per million years (N/myr); (2) proportion of standing diversity (i.e., per capita rate; N/D); and (3) number per million years as a proportion of standing diversity (N/D/myr). In addition, one may include or exclude taxa that are confined to the stratigraphic interval being studied (e.g., stage, series). Foote (1994) used Monte Carlo simulations to examine the validity of extinction and origination metrics. He concluded that normalising per-taxon extinction rate by introducing uniform time intervals (e.g., per million years) potentially introduces bias, especially for extinction metrics. Apparently, the problem cannot be entirely avoided, but 'For comparing extinction intensity over a small number of intervals, it may still be safest to check for concordance among several metrics' (Foote 1994, p. 442). In this paper, we present the three types of metrics listed above, both with and without taxa confined to a single stage, and examine degree of concordance among them.

Recently, Foote (2000b) discussed problems of bias in origination and extinction rates due to incomplete knowledge of temporal distribution of taxa, the effects of variable interval length (e.g., in the analysis here, stages vary over almost an order of magnitude, from 1.6 to 13.3 myr), and possible secular trends in probability of preservation. He reviewed the various measures used to estimate origination and extinction rates and advocated use of measures in which interval-only taxa ('singletons') become irrelevant, because both their inclusion or exclusion can introduce error. Such measures, therefore, are based only on taxa that cross range boundaries. We have nonetheless used the more straightforward calculations of origination and extinction rates as described above. We have done so for three reasons. First, we find no systematic effect of increased stage duration on rates of origination and extinction in our data (Figure 1). Secondly, exclusion and inclusion of stage-only genera produces only minimal differences in the rates plotted, and in some instances is of interest in itself. Thirdly, the major points of interest in the study (i.e., the anomalously high Maastrichtian and Danian extinction rates) are so far above background rates that they should stand out in virtually any method of calculation of rates.

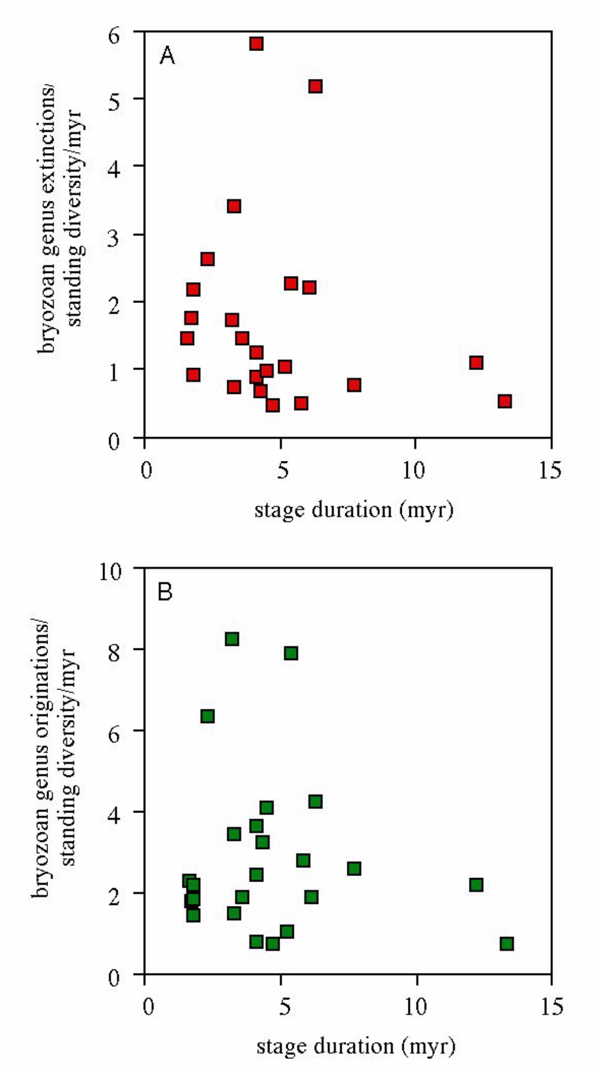

Figure 1. Relationship between stage duration and rates of origination and extinction. A. Origination rate (originations/standing diversity/myr) plotted against stage duration; r = 0.145. B. Extinction rate (originations/standing diversity/myr) plotted against stage duration; r = 0.173.

RESULTS

Table 1 summarises the data on cheilostome and cyclostome generic diversity changes.

Standing diversities

Following the end-Palaeozoic extinction, cyclostome bryozoans reappear in the fossil record by the Carnian Stage of the Upper Triassic (Bizzarini and Braga 1981). They diversified slowly through the Late Triassic and Early Jurassic but more rapidly during the Mid Jurassic and Early Cretaceous. Sixty-three genera are known from the latest Early Cretaceous (Albian), the oldest stage included in this study. During the Late Cretaceous, cyclostomes steadily increased in diversity to the 170 genera known in Maastrichtian rocks (Figure 2). They declined drastically from the

Table 1. Summary of data on cheilostome and cyclostome generic first and last records, genera confined to a single stage, and standing diversity.

			Cheilostome genera				Cyclostome genera			
stage	Midpoint (myr)	duration (myr)	cheilo lasts	cheilo firsts	stage only	standing	cyclo lasts	cyclo firsts	stage only	standing
Albian	105.6	13.3	3	4	1	10	2	3	0	63
Cenomanian	96.2	5.4	8	31	7	44	9	28	6	95
Turonian	91.3	4.5	4	14	2	45	2	11	0	91
Coniacian	87.4	3.2	8	30	5	74	2	18	1	108
Santonian	84.7	2.3	11	23	4	88	1	6	0	111
Campanian	77.4	12.2	21	47	6	126	14	22	3	135
Maastrichtian	68.2	6.3	55	60	26	185	61	34	18	170
Danian	63	4.1	33	31	13	148	26	6	3	100
Thanetian (& Seelandian)	57.9	6.1	20	19	4	125	7	4	0	75
Ypresian	51.9	5.8	5	29	3	133	1	5	0	73
Lutetian	45.2	7.7	12	49	8	182	3	2	0	74
Bartonian	39.2	4.3	6	36	3	201	2	2	1	74
Priabonian	35.4	3.3	24	29	4	225	10	5	3	79
Rupelian	31.1	5.2	13	10	1	208	2	5	0	71
Chattian	26.2	4.7	5	8	1	203	1	1	0	70
Aquitanian	22.2	3.3	6	14	5	216	1	0	0	69
Burdigalian	18.5	4.1	13	28	7	240	3	3	1	72
Langhian	15.6	1.6	6	9	5	234	1	2	0	70
Serravalian	13	3.6	13	18	9	250	4	4	2	75
Tortonian	9.2	4.1	6	10	2	240	5	0	0	69
Messinian	6.2	1.8	9	8	5	245	3	0	0	64
Zanclean	4.4	1.7	5	7	0	238	4	2	2	65
Piacenzian	2.7	1.8	6	9	3	245	6	3	2	64
Pleistocene	0.9	1.8	4	8	1	245	1	2	0	58

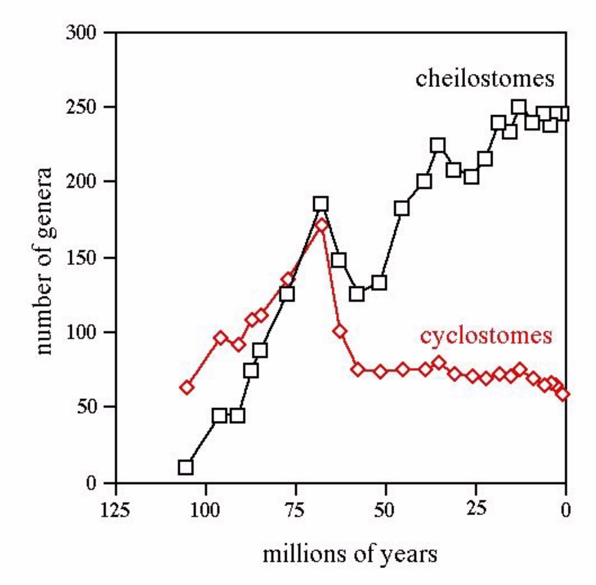

Figure 2. Standing diversity of cyclostome and cheilostome bryozoans during the Late Cretaceous and Cenozoic. For this and other graphs displaying data through time, data are grouped by stage, and each point is plotted at mid-Stage.

Maastrichtian to the Thanetian and then remained at an approximately constant diversity level through the Cenozoic. (Note that Figure 2 plots only fossil diversity; Holocene data are not plotted.)

Cheilostomes first appeared in the Late Jurassic (Taylor 1994) but diversified very slowly during the Early Cretaceous, with only 10 genera known from the Albian. During the Late Cretaceous, cheilostomes diversified rapidly to reach a level of 185 known genera in the Maastrichtian (Figure 2). Subsequently, they declined through the Palaeocene to a Thanetian diversity of 125 genera. After the Thanetian, they again diversified through much of the remaining Cenozoic, interrupted by a modest Oligocene reversal, apparently reaching a plateau of 240 to 250 genera during the Neogene.

Extinctions

The absolute number of extinctions for both clades is highest for the Maastrichtian (Figure 3). Sixty-one cyclostome genera that ranged through two or more stages have their last record in the Maastrichtian, and 18 are known only from the Maastrichtian, making a total of 79 Maastrichtian cyclostome genera that did not survive beyond the K-T boundary. Fifty-five long-ranged cheilostome genera have their last record in the Maastrichtian, and 26 are known only from that stage, totalling 81 Maastrichtian cheilostomes that did

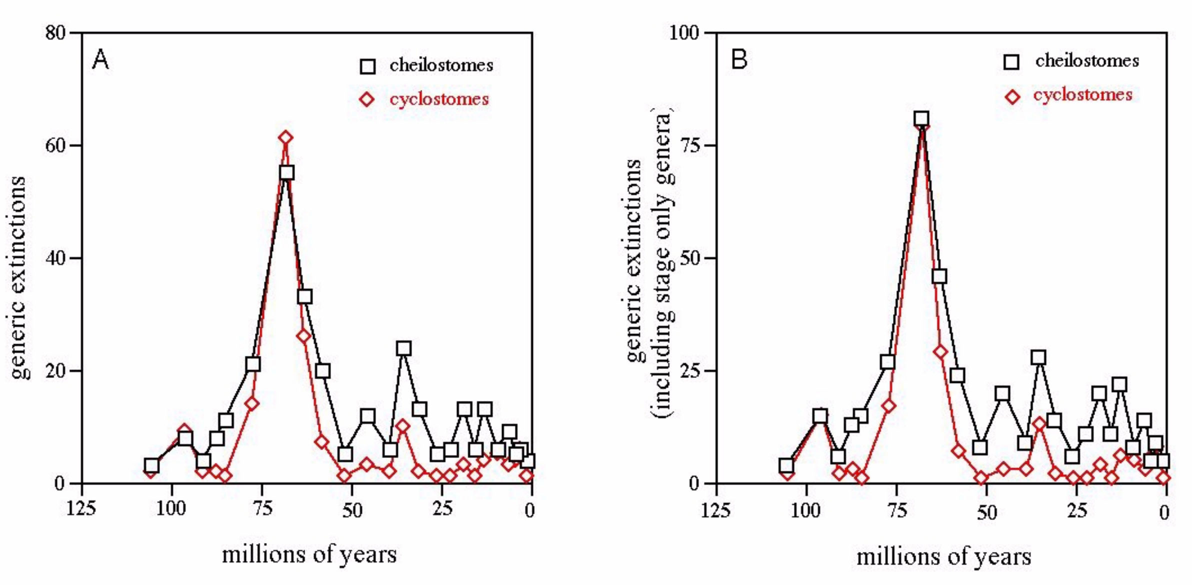

Figure 3. Number of generic extinctions per stage. A. Including only genera known to range through two or more stages. B. All generic extinctions, including stage-only.

not cross the K-T boundary. The second-highest number of extinctions occurred during the Danian for both clades: 26 long-ranged plus 3 stage-only cyclostomes, and 33 long-ranged plus 13 stage-only cheilostomes became extinct in the Danian. These Maastrichtian and Danian extinctions are much higher than extinctions in any other Late Cretaceous or Cenozoic stage. The next highest number of extinctions for cyclostome genera occurred during the Campanian (14 long-ranged plus 3 stage-only), and for cheilostomes during the Priabonian (24 long-ranged plus 4 stage-only).

Extinctions per million years (E/myr) were also high during the Maastrichtian and Danian both when the two clades are considered together (Figure 4A, B) and individually (Figures 5A, B, 6A, B). Based on genera not confined to a single stage, for cyclostomes Maastrichtian extinction rate was 9.7 genera/myr and Danian rate 6.3 genera/myr; for cheilostomes Maastrichtian extinction rate was 8.7 genera/myr and Danian rate 8.0 genera/myr. Including stage-only genera, cyclostome extinction rates were 12.5 genera/myr and 7.1 genera/myr and cheilostome rates were 9 genera/myr and 11.2 genera/myr, respectively. As with absolute numbers of extinctions, these rate values are well above background levels (Figure 7A, B). The next highest rates for cyclostomes are 3.3 genera/myr and 4.4 genera/myr (including stage-only genera) in the Piacenzian, and for cheilostomes 7.3 genera/myr and 8.5 genera/myr (including stage-only genera) in the Priabonian.

Number of extinctions per standing diversity (E/D) also peaked during the Maastrichtian and Danian (Figures 4C, D, 5C, D, 6C, D). Cyclostome extinctions were 0.38 genera/D (0.46 genera/D including stage-only) for the Maastrichtian, and 0.26 genera/D (0.36 genera/D including stage-only) for the Danian. Values for cheilostomes are 0.30 genera/D (0.44 genera/D including stage-only) for the Maastrichtian, and 0.22 genera/D (0.33 genera/D including stage-only) for the Danian. Again, these are well above background levels (Figure 7C, D). Next highest values for cyclostomes are 0.13 genera/D (0.16 genera/D including stage-only) for the Priabonian, and for cheilostomes 0.17 genera/D (0.21 genera/D including stage-only) for the Campanian.

Finally, calibrating extinctions by both standing diversity and time (E/D/myr), Maastrichtian and Danian extinctions still stand above background levels (Figures 4E, F, 5E, F, 6E, F). Cyclostome extinctions were 0.06 genera/D/myr (0.07 genera/D/myr including stage-only) for the Maastrichtian, with the same values for the Danian. Values for cheilostomes are 0.05 genera/D/myr (0.07 genera/D/myr including stage-only) for the Maastrichtian, and 0.05 genera/D/myr (0.08 genera/D/myr including stage-only) for the Danian. While Maastrichtian and Danian extinctions per standing diversity per million years stand well above background level (Figure 7E, F), they are essentially matched in the Piacenzian for cyclostomes (0.05 genera/D/myr, and 0.07 genera/D/myr including stage-only), and in the Santonian for cheilostomes (0.05 genera/D/myr and 0.07 genera/D/myr including stage-only).

Originations

The absolute number of originations for both clades is highest for the Maastrichtian (Figure 8). Thirty-four cyclostome genera that ranged through two or more stages have their first record in the Maastrichtian. Adding the 18 that are known only from the Maastrichtian brings the total to 52 Maastrichtian cyclostome originations. Sixty long-ranged cheilostome genera have their first record in the Maastrichtian. Adding the 26 that are

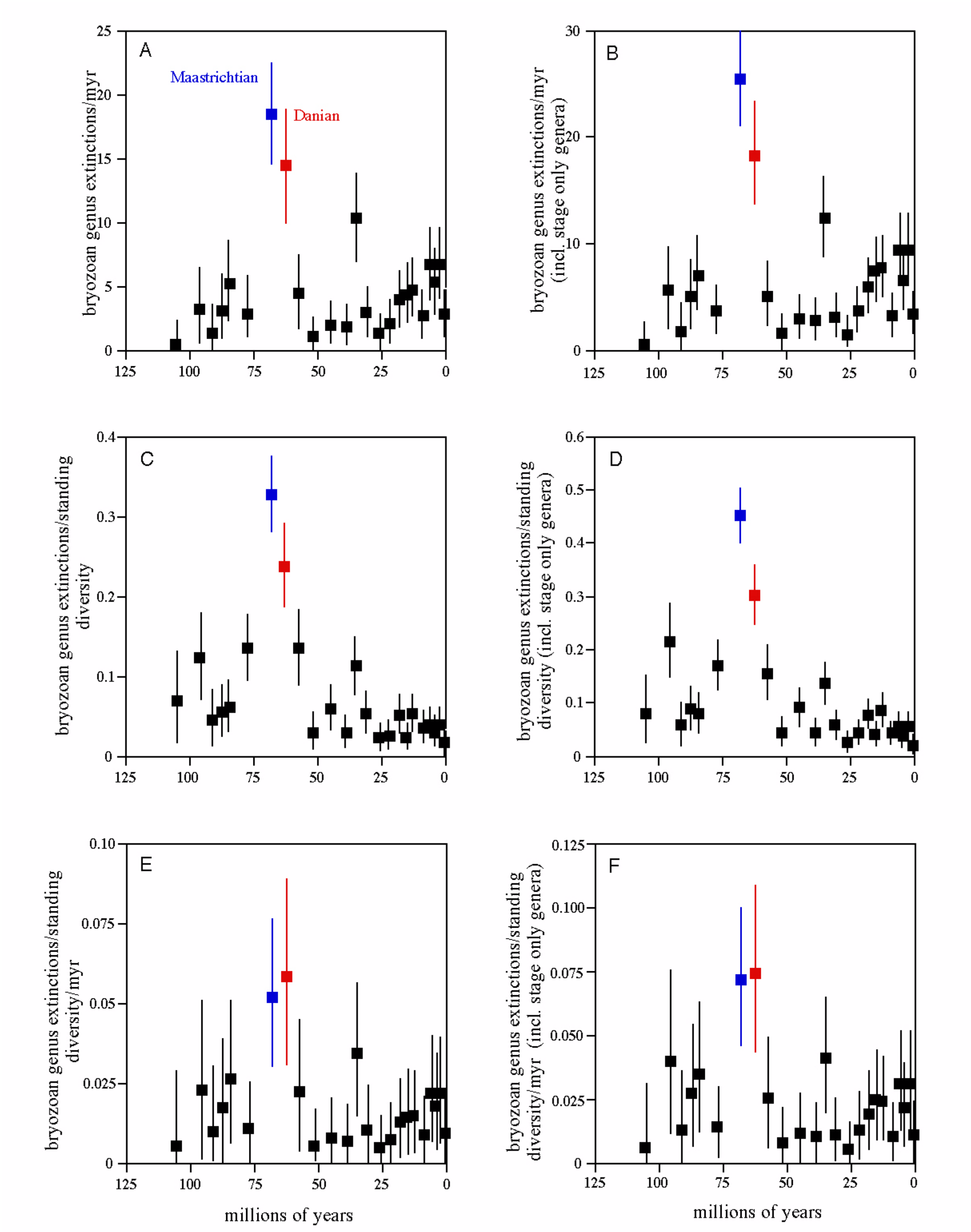

Figure 4. Total bryozoan (cyclostome plus cheilostome) generic extinctions by stage. A, B. Extinctions per million years. C, D. Extinctions per standing diversity. E, F. Extinctions per standing diversities per million years. Graphs on the left do not include genera known only from a single stage, and those on the right do include stage-only genera. Error bars represent 95% confidence intervals.

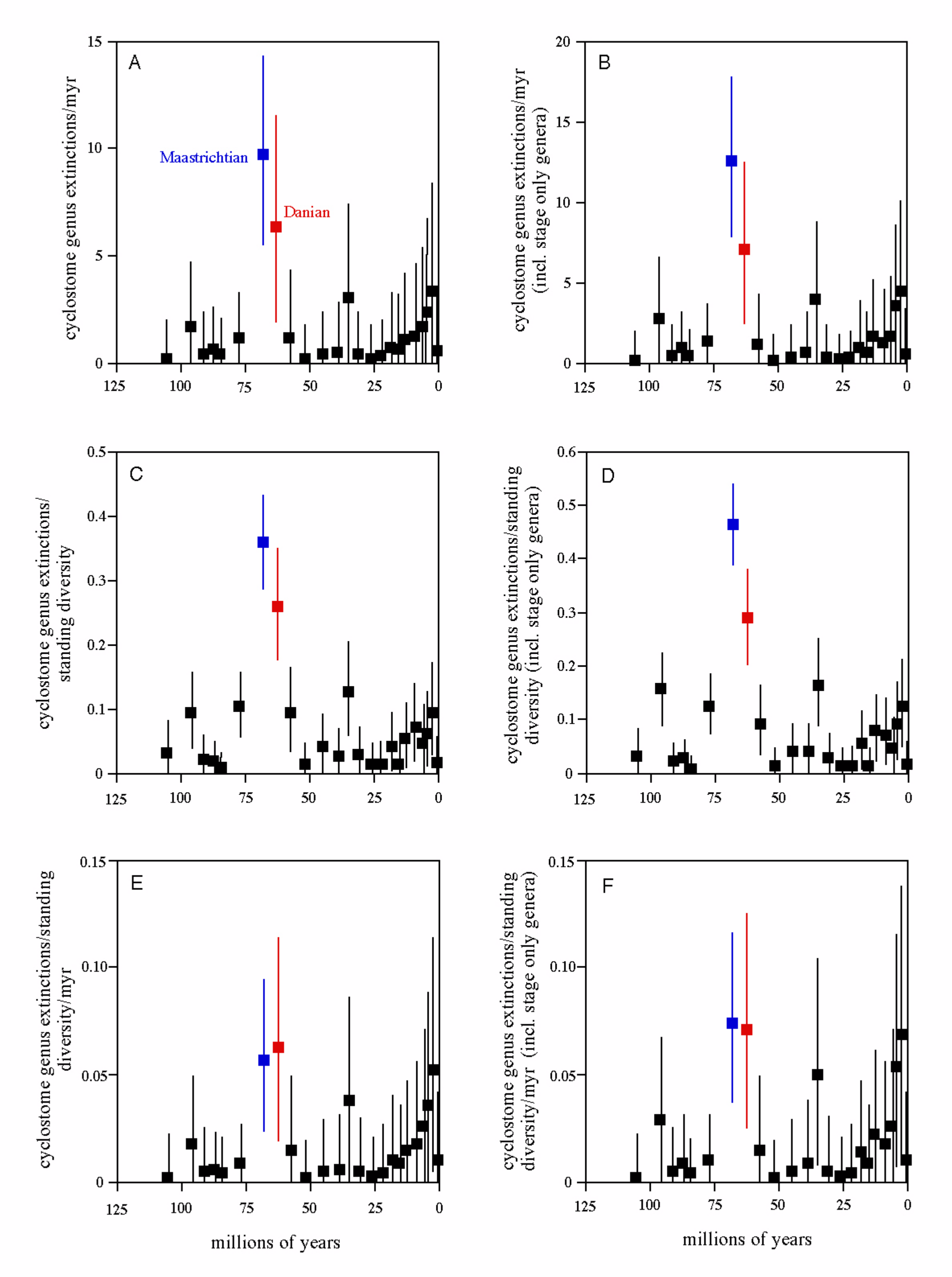

Figure 5. Cyclostome generic extinctions by stage. See Figure 4 for explanation of layout.

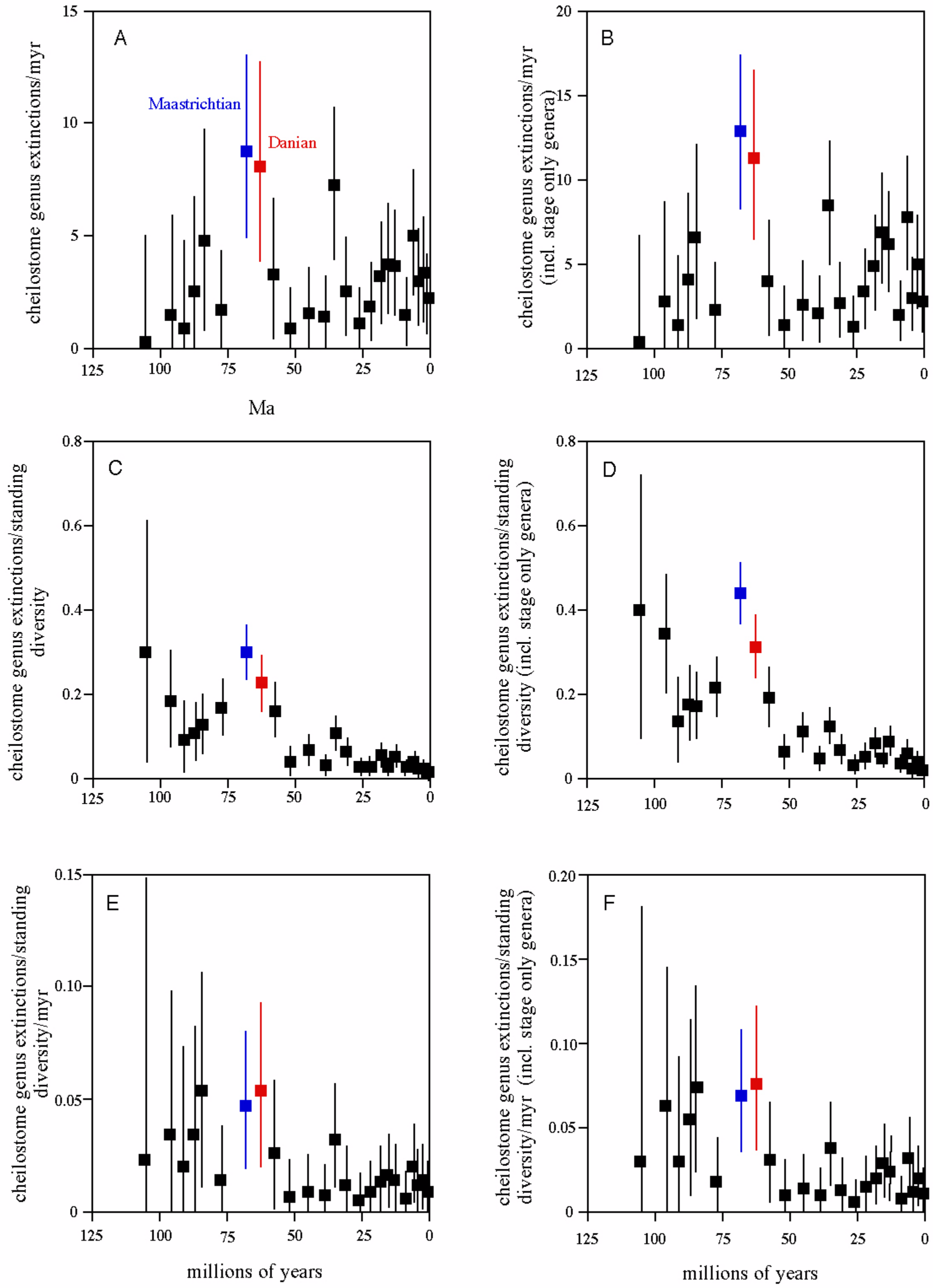

Figure 6. Cheilostome generic extinctions by stage. See Figure 4 for explanation of layout.

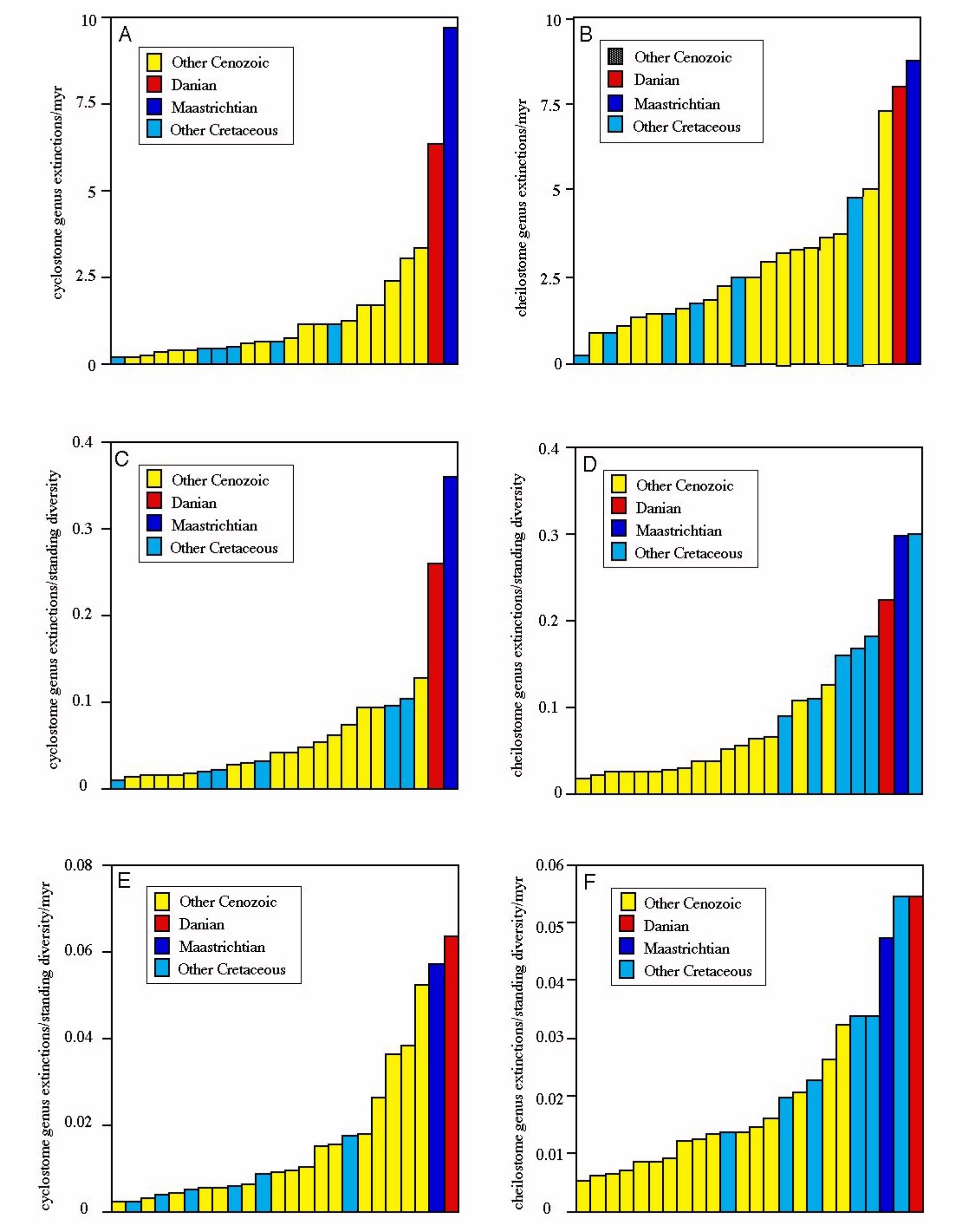

Figure 7. Stage-level extinction intensities (without stage-only genera) arranged in ascending order. Extinctions per million years; A, cyclostomes, B, cheilostomes. C, D. Extinctions per standing diversity; C, cyclostomes, D, cheilostomes. Extinctions per standing diversities per million years; E, cyclostomes, F, cheilostomes.

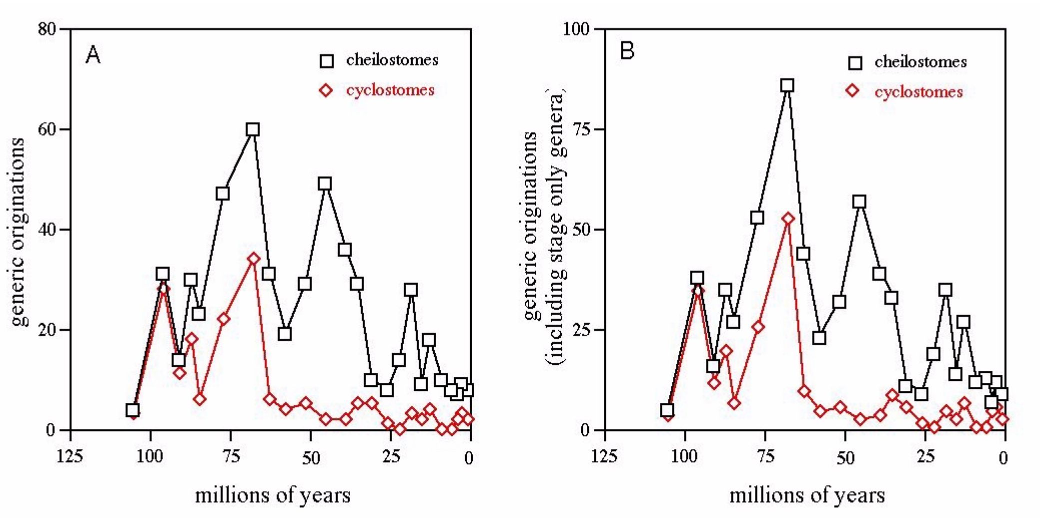

Figure 8. Number of generic originations per stage. A. Including only genera known to range through two or more stages. B. All generic extinctions, including stage-only.

known only from that stage brings total Maastrichtian cheilostome originations to 86. The second-highest number of cyclostome originations was during the Cenomanian when 28 long-ranged and six stage-only (making 34 in total) cyclostome genera appeared. The second-highest number of cheilostome originations is found in the Lutetian, which has the earliest records of 49 long-ranged and 8 stage-only genera (57 total).

Originations per million years (O/Ma) were also high near the transition from Cretaceous to Cenozoic (Figures 9A, B, 10A, B, 11A, B). Maastrichtian cyclostome originations were 5.4 genera/myr for long-ranged genera and 8.3 genera/myr including stage-only genera. However, cyclostome originations/myr were not above background levels during the Danian (Figure 12A). Instead, the Cenomanian had originations/myr almost equal to the Maastrichtian (5.2 genera/myr without and 6.3 genera/myr with stage-only genera). Cheilostome originations/myr were high during both stages: 9.5 genera/myr without and 13.7 genera/myr including stage-only genera for the Maastrichtian, and 7.6 genera/myr and 10.7 genera/myr, respectively, for the Danian. However, these Maastrichtian and Danian values for cheilostome originations/myr scarcely differ from those for the Coniacian, Santonian, Bartonian, and Priabonian (Figures 11A, B, 12B).

Number of genera originating per standing diversity (O/D) was high for cyclostomes during the Maastrichtian (0.20 genera/D for long-ranged and 0.33 genera/D including stage-only genera), but these values are exceeded by those for the Cenomanian (Figures 10C, D, 12C) and are not much above those for the Coniacian and Campanian. The value of O/D for the Danian is not above background levels. Cheilostome O/D for the Maastrichtian (0.32 genera/D for long-ranged and 0.46 genera/D including stage-only genera) are exceeded by or approximately equal all other Late Cretaceous stages and were almost equalled by Lutetian O/D values. Danian cheilostome generic O/D values are only slightly above the median value for all stages (Figures 11C, D, 12D).

Originations calibrated by both standing diversity and time (O/D/myr) for the Maastrichtian and Danian are even closer

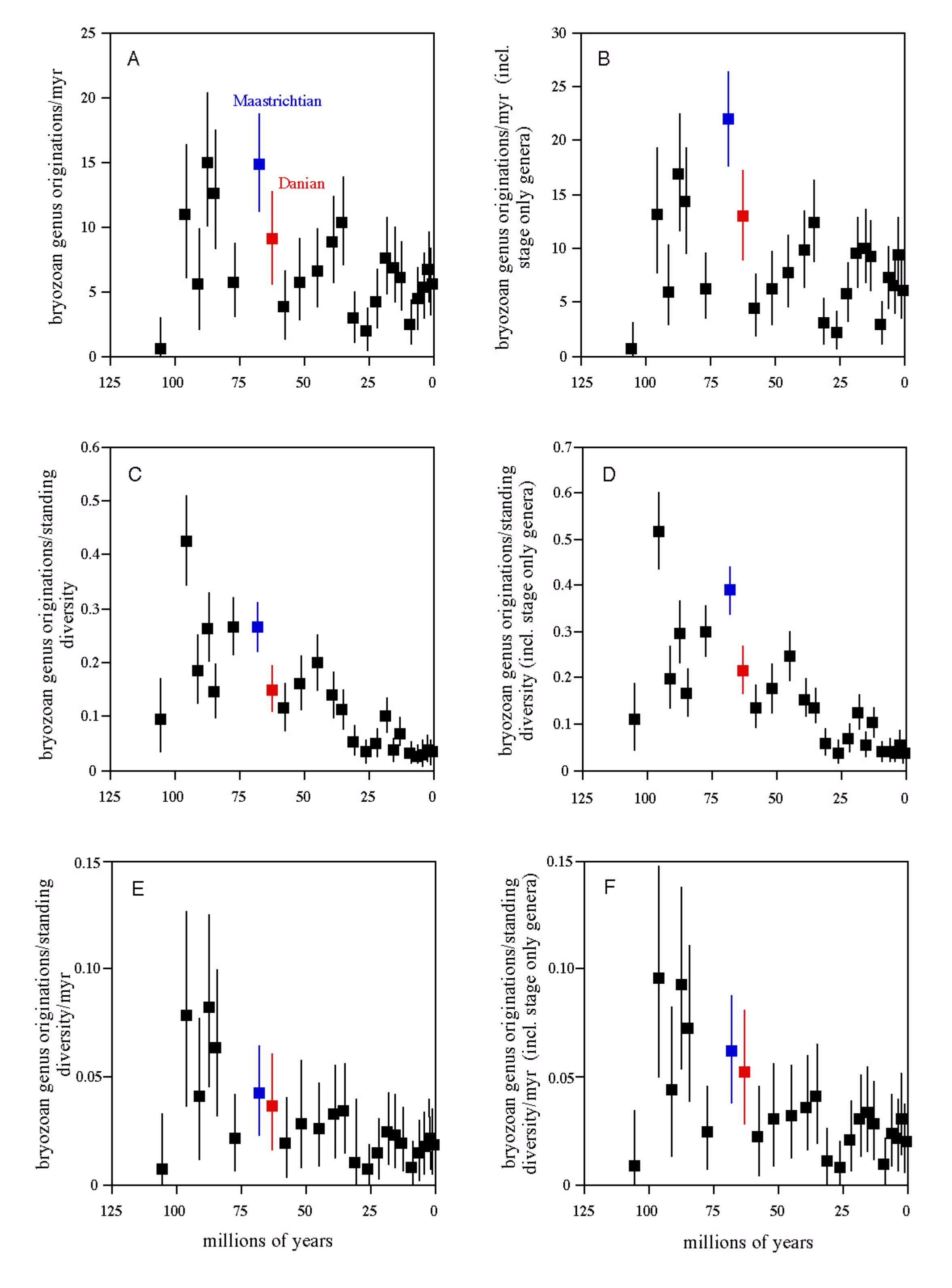

Figure 9. Total bryozoan (cyclostome plus cheilostome) generic originations by stage. A, B. Originations per million years. C, D. Originations per standing diversity. E, F. Originations per standing diversities per million years. Graphs on the left do not include genera known only from a single stage, and those on the right do include stage-only genera. Error bars represent 95% confidence intervals.

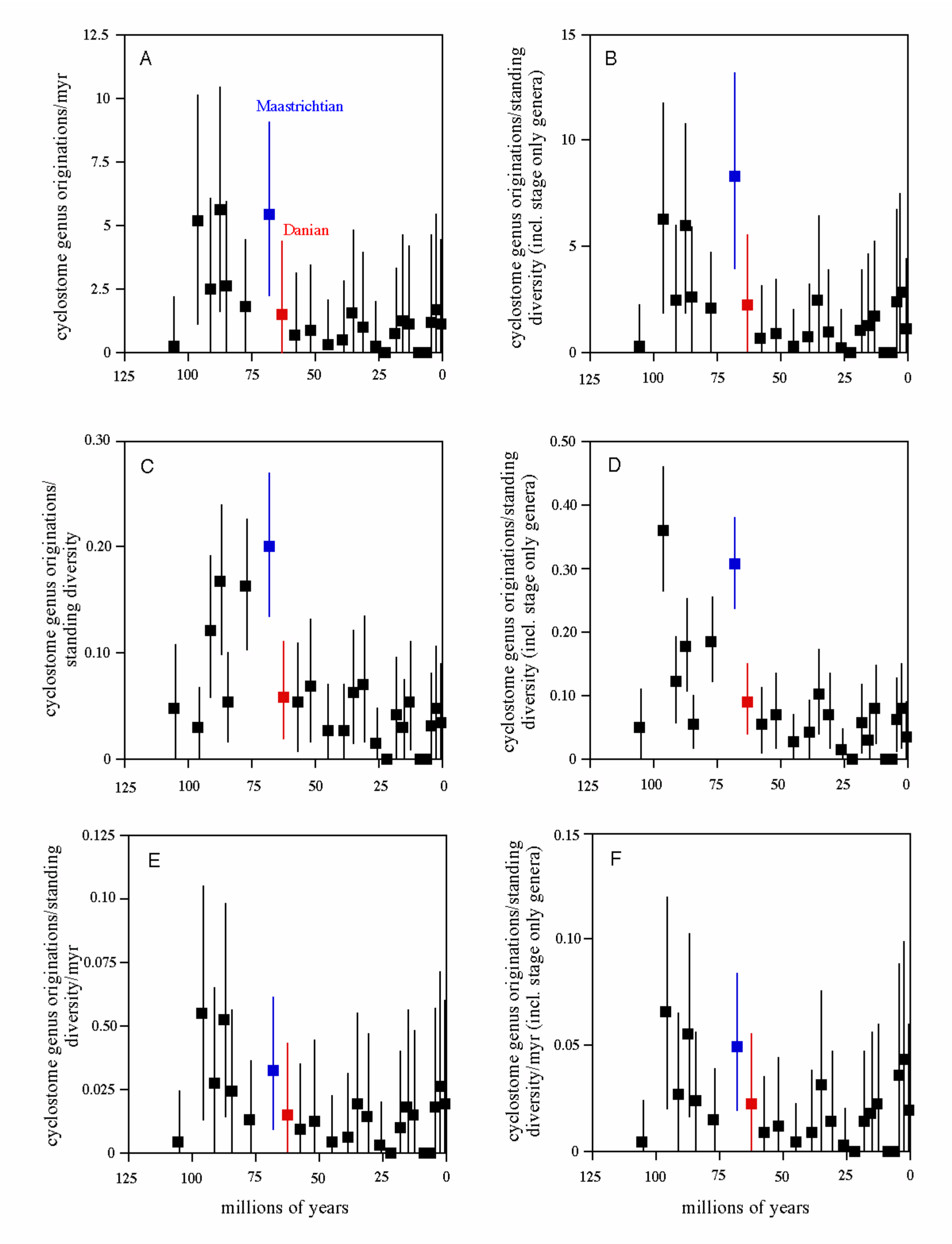

Figure 10. Cyclostome generic originations by stage. See Figure 9 for explanation of layout.

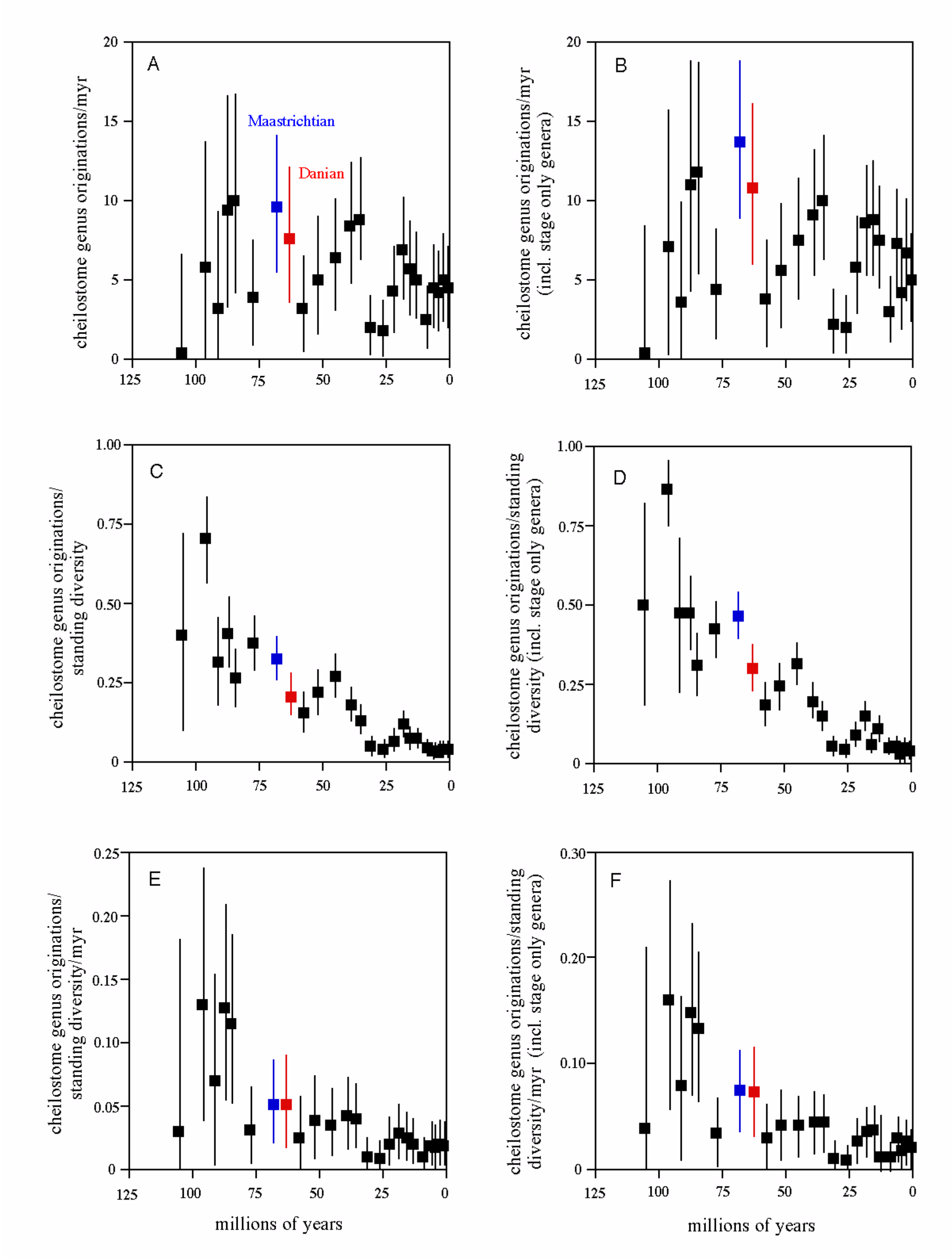

Figure 11. Cheilostome generic originations by stage. See Figure 9 for explanation of layout.

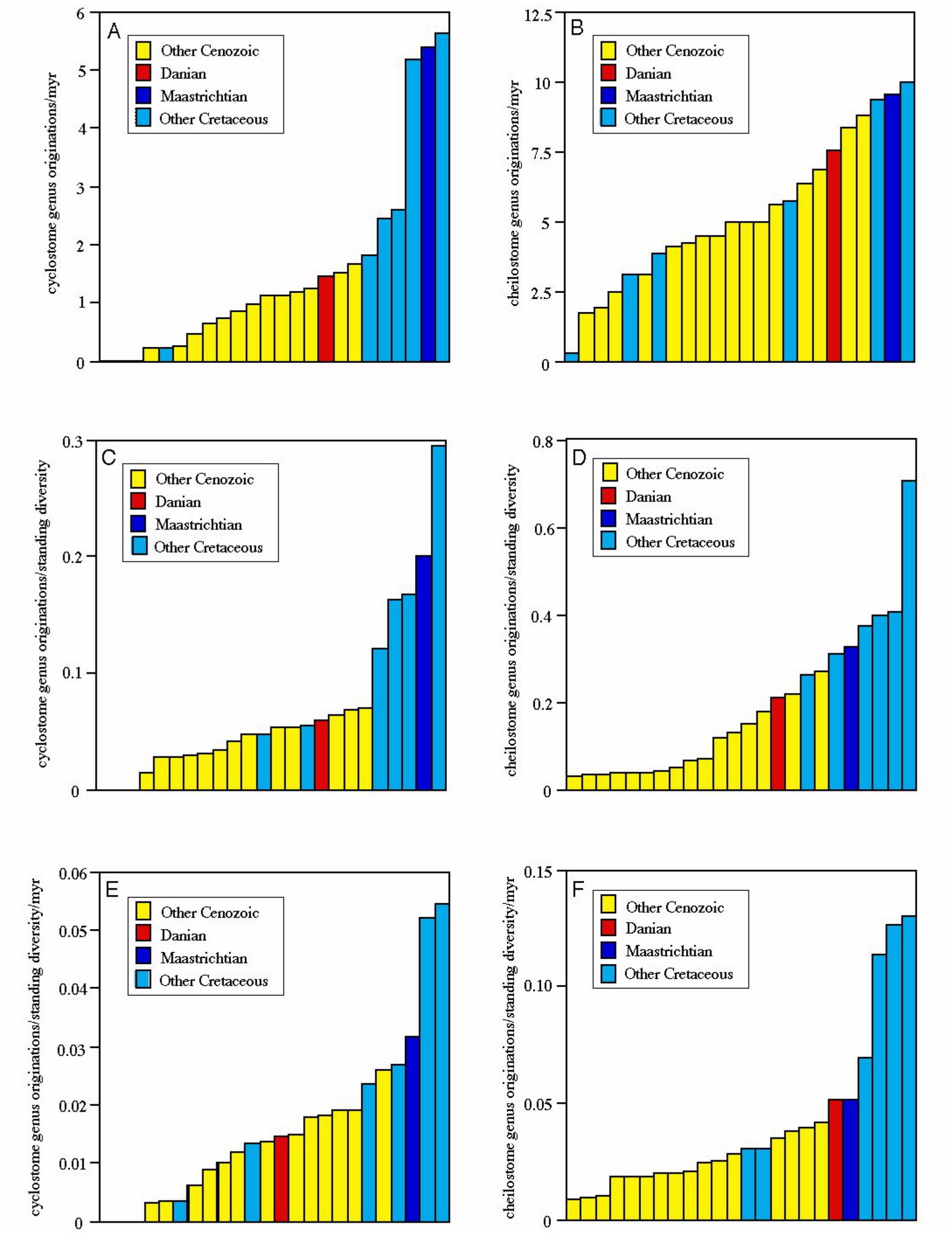

Figure 12. Stage-level originations (without stage-only genera) arranged in ascending order. Originations per million years; A, cyclostomes, B, cheilostomes. C, D. Originations per standing diversity; C, cyclostomes, D, cheilostomes. Originations per standing diversities per million years; E, cyclostomes, F, cheilostomes.

to the norm for Late Cretaceous and Cenozoic stages (Figures 9E, F – 12E, F). Maastrichtian cyclostome values (0.03 genera/D/myr for long-ranged genera and 0.05 genera/D/myr including stage-only) are far exceeded by Cenomanian and Coniacian values, and the Danian values are near the median for all stages. Cheilostome generic originations/D/myr for both Maastrichtian and Danian are only slightly above typical values for the Cenozoic and are exceeded minimally by Turonian and substantially by Cenomanian, Coniacian, and Santonian values; i.e., Maastrichtian and Danian cheilostome O/D/myr are below the norm of Late Cretaceous stages but high relative to Cenozoic stages.

DISCUSSION

Potential error

Potential error (represented by bars in Figures 4-6, 9-11) in determining extinction and origination intensities is higher for small sample sizes than for larger samples. Standing diversity of cyclostomes was relatively low in the Albian and in all post-Danian Cenozoic stages, and standing diversity of cheilostomes was very low in the Albian, Cenomanian and Turonian (Figure 2). Consequently, error bars for these are longer than for any other stages.

For the times of lowest diversity enumerated above, any source of error – such as how completely the fossil record is known and random events in ‘background’ extinctions and originations – has a proportionally greater influence on calculated extinction and origination rates than during times of higher diversity. Consequently, in the discussion and interpretations that follow, we de-emphasise the earliest (Albian-Turonian) record of cheilostomes.

Extinctions

Maastrichtian/Danian. By virtually all measures, generic extinction in the Maastrichtian was greater for both cyclostomes and cheilostomes than in any other stage during the past 100 million years. However, it is almost equalled or even exceeded (Figures 4E, F – 6E, F, excepting 5F) by bryozoan generic extinction in the Danian. Error bars for all Maastrichtian and Danian extinction measures overlap, apart from measures of total bryozoan and cyclostome generic extinctions per standing diversity when stage-only genera are included (Figures 4D, 5D). The proportion of stage-only genera for both cyclostomes (11 percent) and cheilostomes (14 percent) was much higher for the Maastrichtian than for any other stage; in the Danian, the 3 percent cyclostome stage-only genera is at ‘background’ level, but the 9 percent cheilostome stage-only genera is much higher than the norm of 2 to 3 percent. The greater difference in stage-only genera between Maastrichtian and Danian for cyclostomes apparently resulted in the higher Maastrichtian than Danian extinction per standing diversity per million years when stage-only genera were included. It also contributed to lack of overlap of error bars for this measure for Maastrichtian and Danian cyclostomes (Figure 5D), as well as for bryozoans as a whole (Figure 4D).

Bryozoans experienced essentially identical generic extinction intensities in the Maastrichtian and Danian, except that the Maastrichtian extinction appears to have been somewhat more intense than the Danian extinction for cyclostomes. Including stage-only genera, extinctions per standing diversity were slightly higher for cyclostomes than for cheilostomes in the Maastrichtian, resulting in a smaller absolute diversity of cyclostomes relative to cheilostomes during the Danian. There was only a slight decline in within-fauna cyclostome species richness from the Maastrichtian into the Danian, part of a longer-term trend (Lidgard et al. 1993). Conversely, there was an abrupt transition across the Maastrichtian-Danian boundary from cheilostome to cyclostome dominance of assemblage biomass as measured by relative skeletal mass (Håkansson and Thomsen 1979, 1999; McKinney et al. 1998). Therefore, the generic extinction pattern stands in sharp contrast with the abundance patterns.

High generic extinction rates of bryozoans at the end of the Cretaceous have been noted previously by Viskova (1980, 1997), McKinney et al. (1998), and Sepkoski et al. (2000). This concentration of bryozoan extinctions is consistent with a K-T mass extinction, now generally attributed to impact of an extraterrestrial bolide (Alvarez et al. 1980, and many papers since). However, our data lack the precision necessary to determine whether bryozoan extinctions occurred at the end of the Maastrichtian rather than being distributed more widely through that stage.

The equally high bryozoan extinction rates for the Danian must be explained by other cause(s). They apparently correlate with the loss of carbonate shelf environments across northern Europe, which hosted a high proportion of bryozoan taxa known in the Danian fossil record (Håkansson and Thomsen 1999). The widespread 'chalk'-depositing environments were established during the Cenomanian Stage of the mid-Cretaceous (e.g., Rawson 1992; Gale 2000; Gale et al. 2000) and lasted through to the end of the Danian (e.g., Smith and Jeffery 2000). Although local bryozoan diversity and abundance were reduced essentially to zero immediately above the K-T boundary in the few complete sections studied in detail, both abundance and diversity rebuilt within a few decimetres of the base of the Danian section in northern Europe (Håkansson and Thomsen 1979, 1999). The subsequent disappearance of the chalk environments by the end of the Danian and correlated bryozoan extinction may possibly be explained by (1) long-term fall in sea-level (Haq et al. 1987) to a level that shut off oceanic circulation onto the shelf (e.g., Gale et al. 2000); and/or (2) development or increase of cyclonic circulation across the opening Atlantic (Parrish and Curtis 1982).

Background extinctions

Background intensities of cheilostome extinctions, calculated as extinctions per million years (Figure 6A, B), are similar for the Upper Cretaceous and Cenozoic, whereas Maastrichtian and Danian extinction rates are substantially greater (although their error bars overlap appreciably with those of several other stages). However, Maastrichtian and notably Danian extinction rates group with the highly variable earlier Cretaceous extinctions in plots of extinctions per standing diversity (Figure 6C, D) and also with extinctions per standing diversity per million years (Figure 6E, F). In contrast, for cyclostomes the measures of extinction rate are much lower for virtually all other stages than for the Maastrichtian and Danian, especially extinctions per standing diversity (Figure 5C, D). The low pre-Maastrichtian and post-Danian extinction rates likely are a good reflection of background extinction, which are more constant over time than are origination rates (e.g. Van Valen 1985; Gilinsky and Bambach 1987).

Extinction rates of cheilostomes and cyclostomes during the past 100 myr have been remarkably similar, with a median ('background') E/D/myr of 0.009 for cyclostomes and 0.013 for cheilostomes. An arithmetic plot of cyclostome versus cheilostome extinction rates (Figure 13A)

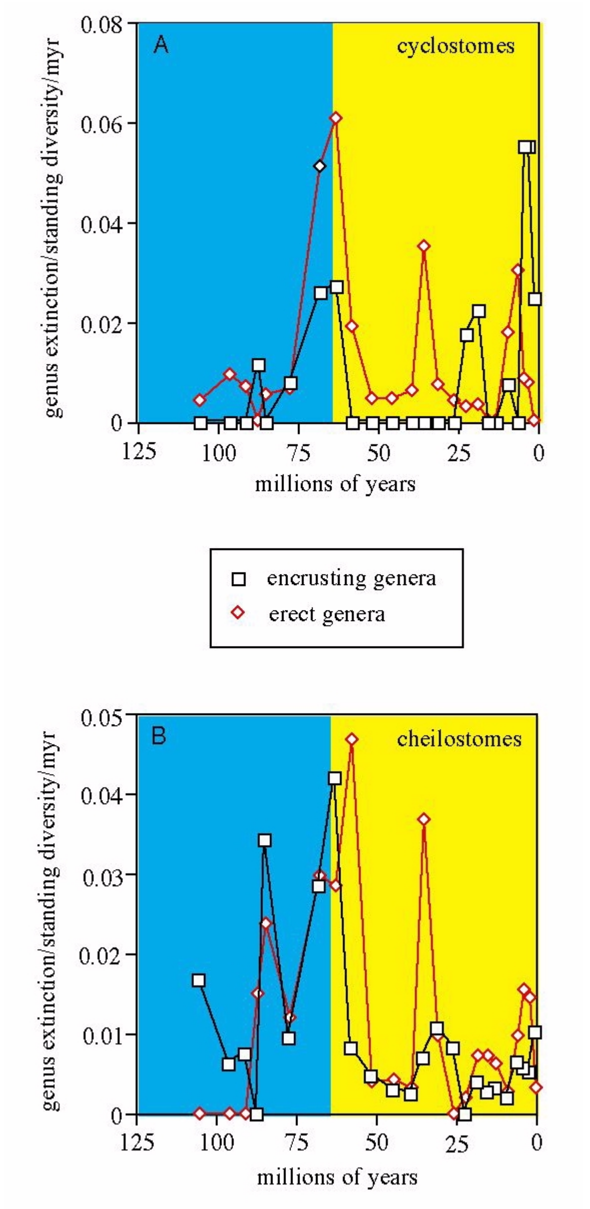

Figure 13. Cheilostome versus cyclostome extinctions (A) and originations(B) per stage, plotted as rates per standing diversity per million years. Blue fields represent Mesozoic, yellow Cenozoic.

shows low correlation (r = 0.487) if all Upper Cretaceous and Cenozoic stages are considered together. However, if stages are separated into the two major time intervals, low correlation (r = 0.429) is seen for paired Upper Cretaceous extinction rates, but Cenozoic extinction rates correlate well with one another (r = 0.742). The poor correlation in the Upper Cretaceous is due largely to high variation in extinction rate of low-diversity, pre-Campanian cheilostomes, but not of cyclostomes.

Sepkoski et al. (2000) determined background extinction rates for cyclostomes and cheilostomes by counting frequency of longevity of genera, grouping them into ‘bins’ of 5-million-year multiples, and taking the slope of log-linear regression for bins other than the shortest (0 to 5 million years). Their estimates were 0.31 genus/genus-million years for cyclostomes and 0.48 genus/genus-million years for cheilostomes. Background extinction rate of cyclostomes by their calculations is, therefore, 65 percent that of cheilostomes. Our results (previous paragraph) for background extinction rate calculated in a very different way—extinctions per standing diversity per million years—is remarkably similar: cyclostome extinction rate is 69 percent that of cheilostomes.

Priabonian

Among post-Danian cheilostome and cyclostome extinction rates, the Priabonian (latest Eocene) stands anomalously high in all measures except for cheilostome extinctions per standing diversity inclusive of stage-only genera. This is probably part of the widely recognised Eocene/Oligocene extinction associated with the world change from greenhouse to icehouse conditions (Prothero 1994). We cannot resolve extinction rates in bryozoans to zone as has been done for some other taxa affected during the mid- to late Eocene extinction. However, the extinction of bryozoans appears different from the detailed extinction patterns documented for coccolithophores (Aubrey 1992) and foraminiferans (Boersma et al. 1987). While extinction patterns for these groups are collectively complex, their respective times and places of most profound extinction and displacement occurred either early or late in the middle Eocene and can be related to successive stages in the long-term cooling. Eocene extinction of echinoids also occurred in multiple phases, with the maximum diversity in the Lutetian, followed by moderate extinction at the Lutetian/Bartonian boundary and maximum extinction during the Priabonian (M. L. McKinney et al. 1992). However, extinction rates of bryozoans in the early to middle Eocene (Ypresian – Bartonian) were not above background levels but instead were intense during the Priabonian at a time when extinction rates of other taxa were declining. A possible reason for this delayed extinction of bryozoans during an extended period of global cooling is that their peak abundance occurs in shelf-depth temperate rather than tropical waters (Taylor and Allison 1998). The organisms that had been affected in the earlier phase of the extended Eocene extinction were predominantly tropical and deep-water.

Neogene

Cyclostome extinction rates seem to increase through the Miocene and Pliocene, culminating in a late Pliocene peak. This apparent increase in cyclostome extinctions through the Neogene, if real, finds a parallel in coral and mollusc extinctions documented in the western Atlantic and Caribbean (Stanley and Campbell 1981; Petuch 1995; Allmon et al. 1996; Jackson et al. 1993; Budd et al. 1996; Jackson and Johnson 2000). These extinctions have been attributed to a variety of environmental causes related to the closure of the Isthmus of Panama and long-distance effects of intensified glaciation.

Growth habits

A broad range of colony growth habits has developed in both cyclostomes and cheilostomes (Lagaaij and Gautier 1965; McKinney and Jackson 1989; Hageman et al. 1998), most of which can be categorised as either encrusting or erect (a minority are free-living or have morphologies that are difficult to place, and these are not considered here). As a first step towards analysis of the ecological history of bryozoan extinctions, we examined the extinction rate of encrusting and erect genera over the past 100 million years. Some genera include both encrusting and erect colonies, and we assigned a value of 0.5 for each such genus to the tally for encrusters and also for erect forms.

The most notable patterns for cyclostomes (Figure 14A) are that (1) erect forms went extinct at twice the rate of encrusters during both the Maastrichtian and Danian; and (2) the Priabonian extinction eliminated only erect genera. Indeed the Priabonian cyclostome extinction can be viewed as an intensification of the pattern seen for the Thanetian through Chattian (i.e., almost the entire Palaeogene) during which no encrusting cyclostomes are known to have gone extinct. The absence of encrusting cyclostome extinctions during the post-Danian Palaeogene and its concentration in the Neogene may, however, be a taxonomic artefact given that encrusting cyclostome genera are poorly defined.

Extinction rates of encrusting and erect cheilostomes were similar during the Maastrichtian and Danian (Figure 14B), followed by disproportionally higher periods of extinctions of erect cheilostomes during the Thanetian and the Priabonian; at other times, encrusting and erect cheilostomes exhibited similar patterns of extinction rate. The substantial Palaeogene to Neogene decline in erect species from approximately 50 percent to approximately 25 percent of the bryozoan fauna (McKinney and Jackson 1989) may be due, at least in part, to the Priabonian extinction.

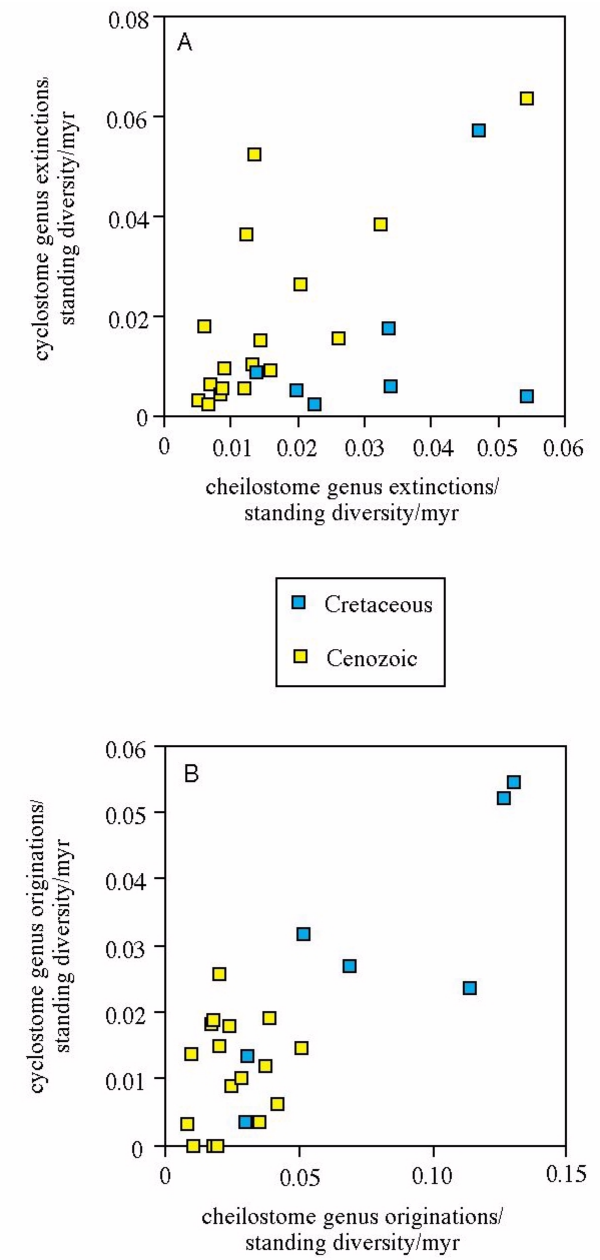

Figure 14. Extinctions per standing diversity per million years for encrusting and erect (A) cyclostomes and (B) cheilostomes. Standing diversities of erect cyclostomes and of encrusting cheilostomes were relatively large throughout, but standing diversities of encrusting cyclostomes and of erect cheilostomes were relatively low.

Our data suggest contrasting extinction patterns of erect and encrusting cheilostome genera in the Pliocene and Pleistocene (Figure 14B), with high extinction rates of erect cheilostomes in the Pliocene followed by low extinction rate in the Pleistocene, and the opposite pattern in encrusting genera. These patterns for genera parallel the strong Neogene decline of erect cheilostome species in the Caribbean described by Cheetham and Jackson (1996). They noted that the decline in proportion of erect cheilostomes is in part due to more vigorous speciation of encrusting species but is largely due to preferential extinction of species in erect genera.

Originations

Origination rates for bryozoan genera (Figure 9) do not show the Maastrichtian and Danian anomalies that characterise extinction rates. In general, origination rates were higher and more variable during the Late Cretaceous than during the Cenozoic and were the cause of the steep rise in overall bryozoan diversity through the Late Cretaceous (Figure 2).

Cyclostomes

Cyclostome originations were high throughout the Late Cretaceous (Figures 8, 10). Maastrichtian originations are the highest among these only in three of the six measures (Figure 10B-D), suggesting that Maastrichtian originations are part of the continuum of high originations during the most active period of cyclostome diversification. Following the K-T extinction, however, cyclostome originations remained very low throughout the Cenozoic by most measures, although there may have been a slight increase in originations during the Neogene (Figure 10E, F). This possible Neogene increase did not result in an increase in cyclostome diversity (Figure 2) because it was matched by a slight increase in extinctions (Figure 5E, F).

Cheilostomes

Cheilostome generic originations show an overall pattern of decrease through the Late Cretaceous and Cenozoic (Figures 8, 11). The decline in cheilostome generic origination rate may reflect the general temporal decline in origination rates of higher taxa as a progressively greater proportion of new species are established within previously established higher level clades (cf. Flessa and Jablonski 1985), or it may mark near-saturation of the ecosystem as suggested by Sepkoski et al. (2000).

Cheilostome originations during the Maastrichtian and Danian are remarkable only for the fidelity with which they fit within the long-term trend. There are three stages for which originations fall substantially below the long-term trend-line (e.g. Figure 11E, F): Upper Palaeocene (Thanetian) and both stages of the Oligocene (Rupelian, Chattian). Generic origination rates do not support Voigt's (1981) notion of the Danian as a stage of low 'creativity'. For the Cenozoic, the Danian was characterised by high origination rates, even though many of the bryozoan genera thought of as typical of the Cenozoic (e.g., *Sertella*, *Schizoporella*, *Microporella*) did not appear until later in the Palaeogene. The general taxonomic composition of Danian cheilostome faunas has greater similarity to Late Cretaceous faunas than to later Cenozoic faunas. This is because numerous genera that originated in the Cretaceous survived into the Danian before becoming extinct, not because of anomalously few generic originations.

Cenozoic contrasts in origination rates

In contrast with the similarity in median extinction rates of cyclostomes and cheilostomes, median origination rates (O/D/myr) for cyclostomes are 0.013 and for cheilostomes are 0.028. Overall Late Cretaceous through Cenozoic origination rates of the two clades (Figure 13B) correlate better (r = 0.786) than do overall extinction rates. However, the correlation is almost entirely due to correspondence of rates during the Cretaceous (r = 0.838) when both clades were vigorously diversifying, whereas the rates are almost independent of one another (r = 0.101) during the Cenozoic. The low correlation in the Cenozoic is due to the Eocene rebound in origination rates of cheilostomes, while the cyclostomes had no corresponding rebound.

Our analysis of extinction and origination of post-Palaeozoic bryozoans corroborates the inference by Sepkoski et al. (2000) that the essentially flat diversity of cyclostomes following the K-T extinction was due to sustained low origination rates rather than an increase in extinction rates. Sepkoski et al. (2000) were comparing mid-Mesozoic through Cenozoic diversities of cyclostome and cheilosotme bryozoans with coupled-logistic curves in which standing diversity of each clade suppresses origination rate (but has no effect on extinction rate) of the other. (Parameterization of variables in the calculation of the model was based on estimates of background extinction rates, equilibrium diversity, and the *initial* diversification rates only of the bryozoan clades.) The model, perturbed by a sudden diversity reduction simulating the K-T extinction, closely matched the actual diversity histories of cyclostomes and cheilostomes. Sepkoski et al. (2000), therefore, concluded that actual diversity history of cyclostomes and cheilostomes is consistent with competitive interference between them, which suppresses origination rates. Our analysis of origination and extinction of cyclostomes and cheilostomes broadly supports the assumptions of the Sepkoski et al. model, although, like Sepkoski et al., we note that while the history of post-Palaeozoic bryozoan diversity is consistent with a model based on competitive interference, other biological – or physical – factors may have been influential.

CONCLUSIONS

The diversity histories of cyclostome and cheilostome bryozoans have followed different trajectories during the past 100 million years, although both clades have experienced (apparently) simultaneous periods of anomalously high extinction when data are resolved to stage-level occurrences. (At present, they cannot be differentiated into finer-scale stratigraphic units.) The highest, essentially equivalent extinction rates occurred during or at the ends of the latest Cretaceous (Maastrichtian) and earliest Palaeogene (Danian); the latest Eocene (Priabonian) also was a time of high extinction rates for the two clades.

The Maastrichtian and Priabonian extinctions appear to be parts of well-documented global extinctions that affected both terrestrial and marine ecosystems. The Maastrichtian extinction was one of the four or five major extinctions of the Phanerozoic (Raup and Sepkoski 1982), whereas the mid- to Late Eocene extinction was in the second tier (Raup and Sepkoski 1984, 1986). The relative scale of bryozoan extinctions at these two times is proportional to the intensity of the two extinctions for the biosphere as a whole. Of the bryozoan genera alive at the beginning of the Maastrichtian, approximately 46 percent were extinct by its end, whereas only 13 percent went extinct during the Priabonian.

The scale of the Danian extinction of bryozoans has previously been underappreciated, but it was almost as intense as the Maastrichtian extinction, with 30 percent of genera alive at the beginning of the Danian going extinct. The Danian is not recognised as a time of major global, pan-ecosystem extinction. The demise of so many bryozoan genera appears to be the result of the end-Danian disappearance of the broad carbonate (‘chalk’) sea that had covered northern Europe and parts of Asia since the Cenomanian. The majority of Danian bryozoan genera are known from northern Europe, and those that went extinct likely were endemic to chalk sea environments. The combined Maastrichtian and Danian extinction pattern for bryozoans is generally similar to that for echinoids, which showed 36 percent and 26 percent extinction of genus-level clades in the Maastrichtian and Danian, respectively (Smith and Jeffery 1998). Ending of widespread shallow-water carbonates was suggested by Smith and Jeffery as the probable cause of the high rate of Danian extinctions.

The earlier suggestion (Voigt 1981) that the Danian was a time of low ‘creativity’ for cheilostomes is not supported by our data on originations. The Danian had the highest Cenozoic rate of O/D/myr for cheilostomes. The Cretaceous affinity of its faunas is due to the large proportion of genera that originated during the Cretaceous and ranged into the Danian before going extinct; it is not due to anomalously low origination rate of new genera.

There is some indication of increasing extinction rate of cyclostomes during the Neogene, although extensive overlap of the 95 percent error bars makes the trend equivocal. A simultaneous, similarly equivocal increase in origination rates almost cancels the possible increase in extinction rate, so that total cyclostome diversity declines only slightly during the Neogene.

Cheilostome and cyclostome origination rates correlate in both the Late Cretaceous and Cenozoic, but origination rates correlate only in the Late Cretaceous. During the Cenozoic, cyclostomes maintained low rates of origination while cheilostome rates were much more variable. This pronounced difference in Cenozoic origination rates appears to be the basic cause for the contrasts in diversity histories of the two clades and is consistent with the prediction of the coupled-logistic curves of Sepkoski et al. (2000) that simulated bryozoan diversity based on competitive interaction between members of the two clades. This difference in origination rates during the Cenozoic also bears on Foote's (2000a) findings that the post-Palaeozoic diversity history of gymnolaemates (mostly cheilostomes) is weakly driven more by originations than by extinctions, while the post-Palaeozoic history of stenolaemates (mostly cyclostomes) is driven more by extinctions than by originations. Indeed, stenolaemates have the most strongly extinction-driven diversity history of all post-Palaeozoic clades.

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REFERENCES

Adrain, J. M. and Westrop, S. R. 2000. An empirical assessment of taxic paleobiology. Science, 289:110-112.

Allmon, W. D., Rosenberg, G., Portell, R. W. and Schindler, K. S. 1996. Diversity of Pliocene-Recent mollusks in the western Atlantic: extinction, origination, and environmental change, p. 271-302. In Jackson, J. B. C., Budd, A. F. and Coates, A. G. (eds), Evolution and environment in tropical America. University of Chicago Press, Chicago.

Alvarez, L. W., Alvarez, W., Asaro, F. and Michel, H. V. 1980. Extraterrestrial cause for the Cretaceous-Tertiary extinction. Science, 208:1095-1108.

Aubrey, M. P. 1992. Late Paleogene calcareous nannoplankton evolution: a tale of climatic deterioration, p. 272-309. In Prothero, D. R. and Berggren, W. A. (eds), Eocene-Oligocene climatic and biotic evolution. Princeton University Press, Princeton.

Barnes, D. K. A. and Dick, M. H. 2000. Overgrowth competition in encrusting bryozoan assemblages of the intertidal and infralittoral zones of Alaska. Marine Biology, 136:813-822.

Bizzarini, F. and Braga, G. 1981. Prima segnalazione del genere *Stomatopora* (Bryozoa Cyclostomata) nel Trias superiore delle Dolomiti orientali (Italia). Lavori Società Veneziana di Scienze Naturali, 6:135-144.

Boersma, A., Premoli-Silva, I., and Shackleton, N. J. 1987. Atlantic Eocene planktonic foraminiferal paleohydrographic indicators and stable isotope paleoceanography. Paleoceanography, 2:287-331.

Bohor, B. F., Foord, E. E., Modreski, P. J. and Triplehorn, D. M. 1984. Mineralogic evidence for an impact event at the Cretaceous-Tertiary boundary. Science, 224:867-869.

Budd, A. F., Johnson, K. G. and Stemann, T. A. 1996. Plio-Pleistocene turnover and extinctions in the Caribbean coral-reef fauna, p. 168-204. In Jackson, J. B. C., Budd, A. F. and Coates, A. G. (eds), Evolution and environment in tropical America. University of Chicago Press, Chicago.

Cheetham, A. H. and Jackson, J. B. C. 1996. Speciation, extinction, and the decline of arborescent growth in Neogene and Quaternary cheilostome Bryozoa of tropical America, p. 205-233. In Jackson, J. B. C., Budd, A. F. and Coates, A. G. (eds), Evolution and environment in tropical America. University of Chicago Press, Chicago.

Flessa, K. W. and Jablonski, D. 1985. Declining Phanerozoic background extinction rates: effect of taxonomic structure? Nature, 313:216-218.

Foote, M. 1994. Temporal variation in extinction risk and temporal scaling of extinction metrics. Paleobiology, 20:424-444.

Foote, M. 2000a. Origination and extinction components of taxonomic diversity: Paleozoic and post-Paleozoic dynamics. Paleobiology, 26:578-605.

Foote, M. 2000b. Origination and extinction components of taxonomic diversity: general problems. Paleobiology, 26 (4, Supplement):74-102.

Foote, M. and Sepkoski, J. J. Jr. 1999. Absolute measures of the completeness of the fossil record. Nature, 398:415-417.

Gale, A. S. 2000. The Cretaceous world, p. 4-19. In Culver, S. J. and Rawson, P. F. (eds), Biotic response to global change: the last 145 million years. Cambridge University Press, Cambridge.

Gale, A. S., Smith, A. B., Monk, N. E. A., Young, J. A., Howard, A., Wray, D. S. and Huggett, J. M. 2000. Marine biodiversity through the Late Cenomanian-Early Turonian: papaeoceanographic controls and sequence stratigraphic biases. Journal of the Geological Society, London, 157:745-757.

Gilinsky, N. L. and Bambach, R. K. 1987. Asymmetrical patterns of origination and extinction in higher taxa. Paleobiology, 13:427-445.

Gradstein, F. M. and Ogg, J. 1996. A Phanerozoic time scale. Episodes, 19:3-5, plus fold-out chart.

Hageman, S. J., Bock, P. E., Bone, Y. and McGowran, B. 1998. Bryozoan growth habits: classification and analysis. Journal of Paleontology, 72:418-436.

Håkansson, E. and Thomsen, E. 1979. Distribution and types of bryozoan communities at the boundary in Denmark, p. 78-91. In Birkelund, T. and Bromley, R. G. (eds), Cretaceous-Tertiary boundary events. I. The Maastrichtian and Danian of Denmark. University of Copenhagen.

Håkansson, E. and Thomsen, E. 1999. Benthic extinction and recovery patterns at the K/T boundary in shallow water carbonates, Denmark. Palaeogeography, Palaeoclimatology, Palaeoecology, 154:67-85.

Haq, B. U., Hardenbol, J. and Vail, R. R. 1987. Chronology and fluctuating sea levels since the Triassic. Science, 235:1156-1166.

Hildebrand, A. R. and Boynton, W. V. 1990. Proximal Cretaceous-Tertiary boundary impact deposits in the Caribbean. Science, 248:843-847.

d'Hondt, S., Donaghay, P., Zachos, J. C., Luttenberg, D. and Lindinger, M. 1998. Organic carbon fluxes and ecological recovery from the Cretaceous-Tertiary mass extinction. Science, 282:276-279.

Izett, G. A., Dalrymple, G. B. and Snee, L. W. 1991. ^{40}Ar/^{39}Ar age of the Cretaceous-Tertiary boundary tektites from Haiti. Science, 252:1539-1542.

Jablonski, D. 1998. Geographic variation in the molluscan recovery from the end-Cretaceous extinction. Science, 279:1327-1330.

Jablonski, D. and Raup, D. M. 1995. Selectivity of end-Cretaceous marine bivalve extinctions. Science, 268:389-391.

Jackson, J. B. C. and Cheetham, A. H. 1990. Evolutionary significance of morphospecies: A test with cheilostome Bryozoa. Science, 248:579-583.

Jackson, J. B. C. and Johnson, K. G. 2000. Life in the last few million years. Paleobiology, 26 (4, Supplement):221-235.

Jackson, J. B. C., Jung, P., Coates, A. G. and Collins, L. S. 1993. Diversity and extinction of tropical American mollusks and the emergence of the Isthmus of Panama. Science, 260:1624-1626.

Lagaaij, R. and Gautier, Y. V. 1965. Bryozoan assemblages from marine sediments of the Rhone delta, France. Micropaleontology, 11:39-58.

Lidgard, S., McKinney, F. K. and Taylor, P. D. 1993. Competition, clade replacement, and a history of cyclostome and cheilostome bryozoan diversity. Paleobiology, 19:352-371.

MacLeod, N., Rawson, P. F., Forey, P. L., Banner, F. T., Evans, S. E., Jeffery, C., Kaminski, M. A., Lord, A. R., Milner, A. C., Milner, A. R., Morris, N., Owen, E., Rosen, B. R., Smith, A. B., Taylor, P. D., Urquahrt, E. and Young, J. R. 1997. The Cretaceous-Tertiary biotic transition. Journal of the Geological Society, London 154:265-292.

Marshall, C. R. and Ward, P. D. 1996. Sudden and gradual molluscan extinctions in the latest Cretaceous of western European Tethys. Science, 274:1360-1363,

McKinney, F. K. 1993. A faster paced world?: contrasts in biovolume and life-process rates in cyclostome (Class Stenolaemata) and cheilostome (Class Gymnolaemata) bryozoans. Paleobiology, 19:335-351.

McKinney, F. K. 1995. One hundred million years of competitive interactions between bryozoan clades: asymmetrical but not escalating. Biological Journal of the Linnean Society, 56:465-481.

McKinney, F. K. and Jackson, J. B. C. 1989. Bryozoan evolution. Unwin Hyman, Boston.

McKinney, F. K., Lidgard, S., Sepkoski, J. J. Jr. and Taylor, P. D. 1998. Decoupled temporal patterns of evolution and ecology in two post-Paleozoic clades. Science 281:807-809.

McKinney, M. L., Carter, B. D., McNamara, K. J and Donovan, S. K. 1992. Evolution of Paleogene echinoids: a global and regional view, p. 348-367. In Prothero, D. R. and Berggren, W. A. (eds), Eocene-Oligocene climatic and biotic evolution. Princeton University Press, Princeton.

Parrish, J. T. and Curtis, R. L. 1982. Atmospheric circulation, upwelling, and organic-rich rocks in the Mesozoic and Cenozoic Eras. Palaeogeography, Palaeoclimatology, Palaeogeography, 40:31-66.

Petuch, E. J. 1995. Molluscan diversity in the late Neogene of Florida: evidence for a two-staged mass extinction. Science, 270:275-277.

Prothero, D. R. 1994. The Eocene-Oligocene transition. Columbia University Press, New York.

Raup, D. M. 1991. The future of analytical paleobiology, p. 207-216. In Gilinsky, N. L. and Signor, P. W. (eds), Analytical paleobiology. Paleontological Society Short Courses in Paleontology, 4.

Raup, D. M. and Sepkoski, J. J. Jr. 1982. Mass extinctions in the marine fossil record. Science, 215:1501-1503.

Raup, D. M. and Sepkoski, J. J. Jr. 1984. Periodicity of extinctions in the geologic past. Proceedings of the National Academy of Science, U.S.A., 81:801-805.

Raup, D. M. and Sepkoski, J. J. Jr. 1986. Periodic extinction of families and genera. Science, 231:833-836.

Rawson, P. F. 1992. Cretaceous, p. 355-388. In Duff, P. McL. D. and Smith, A. J. (eds), Geology of England and Wales. The Geological Society, London.

Sepkoski, J. J. Jr, McKinney, F. K. and Lidgard, S. 2000. Competitive displacement among post-Paleozoic cyclostome and cheilostome bryozoans. Paleobiology, 26:7-18.

Sheehan, P. M., Coorough, P. J. and Fastovsky, D. E. 1996. Biotic selectivity during the K/T and Late Ordovician extinction events, p. 477-489. In Ryder, G., Fastovsky, D. and Gartner, S. (eds), The Cretaceous-Tertiary event and other catastrophes in Earth history. Geological Society of America Special Paper, 307.

Smith, A. B. and Jeffery, C. H. 1998. Selectivity of extinction among sea urchins at the end of the Cretaceous period. Nature, 392:69-71.

Smith, A. B. and Jeffery, C. H. 2000. Changes in the diversity, taxic composition and life-history patterns of echinoids over the past 145 million years, p.181-194. In Culver, S. J. and Rawson, P. F. (eds), Biotic response to global change: the last 145 million years. Cambridge University Press, Cambridge.

Stanley, S. M. and Campbell, L. D. 1981. Neogene mass extinction of western Atlantic mollusks. Nature, 293:457-459.

Taylor, P. D. 1993. Bryozoa, p. 465-489. In Benton, M. J. (ed.), The Fossil Record 2. Chapman & Hall, London.

Taylor, P. D. 1994. An early cheilostome bryozoan from the Upper Jurassic of Yemen. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 191:331-344.

Taylor, P. D. and Allison, P. A. 1998. Bryozoan carbonates through time and space. Geology, 26:459-462.

Taylor, P. D. and McKinney, F. K. 1999. Mass extinction and habitat collapse: extinction patterns of post-Paleozoic Bryozoa. Geological Society of America Abstracts with Programs, 31(7):398.

Todd, J. A. 2000. The central role of ctenostomes in bryozoan phylogeny, p. 104-135. In Herrera Cubilla, A. and Jackson, J. B. C. (eds), Proceedings of the 11th International Bryozoology Association Conference. Smithsonian Tropical Research Institute, Balboa, Panama.

Van Valen, L. 1985. How constant is extinction? Evolutionary Theory, 7:93-106.

Venkatesan, M. I. and Dahl, J. 1989. Organic geochemical evidence for global fires at the Cretaceous/Tertiary boundary. Nature, 338:57-60.

Viskova, L. A. 1980. Phylum Bryozoa, p. 4-21. In Development and change of the Invertebrata at the boundary of the Mesozoic and Cenozoic. Nauka, Moscow.

Viskova, L. A. 1997. Changes of the generic diversity of marine bryozoans (Triassic – Recent). Records of the Queen Victoria Museum and Art Gallery Launceston, 104:31-34.

Voigt, E. 1981. Critical remarks on the discussion concerning the Cretaceous-Tertiary boundary. Newsletters on Stratigraphy, 10:92-114.