Extinction patterns and biogeography of scleractinian corals across the Cretaceous/Tertiary boundary

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We examine coral diversity, palaeoecology, palaeobiogeographical and extinction patterns across the Cretaceous/Tertiary boundary. Our analyses indicate that zooxanthellate-like corals were more susceptible to extinction than non-zooxanthellates, especially in the Late Cretaceous. Zooxanthellate-like corals were confined to northern mid-palaeolatitudes during much of the Cretaceous, but in the Paleocene, faunas became more cosmopolitan with non-zooxanthellate-like corals dominating. It is therefore difficult to say whether palaeolatitudinal and palaeogeographical factors were more important influences on extinctions than major global events that could have caused the breakdown of the symbiosis between corals and zooxanthellae. Our sampling is also too broadly based stratigraphically to say exactly when and how rapidly late Cretaceous coral extinctions happened. Our results are more or less compatible with several extinction models, including palaeogeographical changes associated with marine regression, substantial reduction in illumination, or global warming.

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PRELIMINARY ANALYSIS is made of scleractinian coral distributions across the Cretaceous/Tertiary (K/T) boundary, particularly with respect to finding patterns in standing diversity, in extinctions, and in palaeoecology, based on inferred symbiotic and non-symbiotic categories of genera.

The literature on extinctions and diversity about the K/T boundary is extensive, but the nature of coral data prevents rigorous testing of many of the more important theories about extinctions, so we concentrate on presenting methods and results. Nevertheless, patterns in our results relate to questions of palaeogeographical change, eustasy, climate, volcanicity, and illumination levels.

This study is mostly based on 1, an extensive species-level compilation (D.T.), including revisions, from the primary taxonomic literature of Maastrichtian and Paleocene corals (Table 1) and 2, a generic extraction (B.R.R.) from Wells (1956). The senior author is largely responsible for the analyses and interpretation of results.

Data

General limitations

There are three general problems in using corals to investigate K/T extinction patterns:

1, insufficient systematic revision of late Cretaceous and Paleocene corals and likelihood of numerous specific and generic synonyms in the literature. There are no modern phylogenetic analyses of Cretaceous corals, and numerous taxa in our compilation are probably not monophyletic. Patterson & Smith (1987) pointed out that in cladistic terms non-monophyletic taxa cannot become extinct and many extinction studies are based on data sets in which non-monophyletic and wrongly-dated taxa may be as high as 75%. In their case (fishes and echinoderms), taxa left after removal of non-monophyletic forms showed very different extinction patterns from those recorded by other authors.

2, the need for greater stratigraphical precision in dating Late Cretaceous to Paleocene coral-bearing formations.

3, rarity of localities with continuous, stratigraphical sequences of coral-bearing strata. This is a familiar K/T problem and is usually attributed to global regression. Regression would have had a marked effect on many of the reef and shallow water facies associated with corals.

In time, it should be possible to remedy the first two problems; we have tried to offset these by using partly complementary data sets. The *Treatise* compilation (Wells, 1956) has less stratigraphical resolution than our species compilation because of the broad time intervals it uses. On the other hand, this allowed us to compare the pattern we found for the Late Cretaceous, with those for the early and middle Cretaceous. Wells's (1956) use of genera, rather than species, might at first seem another disadvantage, but in practice, scleractinian workers identify genera far more consistently than they do species. For palaeobiogeographical analysis of extinction, we used our species compilation.

Our species compilation was intended to provide finer taxonomic, stratigraphical and geographical detail than the generic data set. For reasons of available time however, we restricted it to a selection of regions (Table 1) chosen to maximize records for a given sample region, and to obtain a reasonable spread of sample regions across palaeolatitudes.

Generic data base

Wells's (1956) work remains one of the few comprehensive compilations of scleractinian genera based on explicit formal taxonomic procedure, that also gives synonymies and full stratigraphical ranges. More recent compilations do not appear to have been assembled so rigorously. Alternative classifications have since been published, and many new taxa erected but this may not be a major problem in extinction analysis because the general tendency to name new taxa, or to continue using established names for a particular region or horizon, without making complete checks for possible senior synonyms elsewhere [the 'chauvinotypy' factor (Rosen,1988)] tends to exaggerate figures for endemicity, diversity, extinction numbers, and % extinctions. This tendency can only be dampened by integration of the newer literature. Four particular problems arose when assembling the generic database.

Cretaceous classification. Wells (1956) used a three-part division of the Cretaceous, but we are unable to establish international stratigraphical stage name equivalents for these divisions. Cretaceous divisions are usually in 2 series, the only exception known to us being the tripartite division in North America of Coahuilian, Comanchean and Gulfian. It seems unlikely that Wells used these as a basis because the North American divisions do not correlate neatly with stage names applied elsewhere. Wells's divisions might correspond to those of Felix (1914a,b,c,) being Neocomian-Albian, Cenomanian, and Turonian-Danian. If so, then its disadvantage would be inclusion of Danian records in the Cretaceous rather than in the Paleocene. We use Wells's (1956) divisions *verbatim*, only when referring to results from that database; otherwise we use current stratigraphical terminology.

Whole system records (WSR). Wells (1956) usually gave ranges as Lower, Middle or Upper Cretaceous but gave some in terms of whole systems (e.g., 'Jurassic to L. Cretaceous', 'Cretaceous to Eocene'). It is not clear whether WSRs are by default of better resolution of ranges, or whether they are shorthand for 'Lower to Upper inclusive'. We therefore made two sets of analyses. For one, we used the first assumption and omitted all WSRs ('WSRO compilations'). For WSRI compilations we included WSRs using the second assumption.

Paleocene records. Wells (1956) listed no ranges that started or ended in the Paleocene; many spanned from older to younger horizons. This is probably an artefact of older literature pre-dating international adoption of Paleocene epoch, or subsequent changes in its correlation (e.g., placing of the Danian in the Paleocene).

Hermatypic and ahermatypic categories. For palaeoenvironmental analysis, we made use of Wells's (1956) 'hermatypic' and 'ahermatypic' categories despite their ambiguity (Rosen,1977,1981; Schuhmacher & Zibrowius,1985). There is as yet no concensus approach to inference of Schuhmacher & Zibrowsius's (1985) terms for fossil corals (but see Coates & Jackson, 1987).

Many colonial corals labelled 'hermatypic' by Wells (1956) have morphologies that in living corals are restricted to corals which are symbiotic with zooxanthellae (i.e. 'z-corals'). These forms are principally meandroid, thamnasterioid, circumoral, ramose, columnar, and foliose. Cerioid, plocoid and other coenosteoid forms are ambivalent in this respect, unless they are also ramose; while phaceloid (simple branching) corals can be either symbiotic or not. Most solitaries labelled 'hermatypic' by Wells (1956) resemble modern zooxanthellate

Table 1. Localities for Maastrichtian-Paleocene scleractinian records. Each record known only by genus scores as one towards species totals. Palaeolatitudes given as ranges to account for size of region and different reconstructions (Adams,1981; Howarth,1981). Maa = Maastrichtian; Pal = Paleocene. SW Sind locality said by Felix (1914c) to be in south India, evidently in error. *Palaeolatitude of SW Sind assumes its palaeoposition on southern margin of Eurasian plate west of Indus suture.

REGION	AGE	PALAEO-LATITUDE (approx)	NUMBER OF SPECIES	NUMBER OF GENERA	SOURCE LITERATURE
Sjaelland (mainly) (Eastern Denmark)	Maa	55-58°N	6	6	Floris, 1979
St. Pietersberg, Maastricht (Southern Netherlands)	Maa	47-56°N	22	12	Felix, 1914c (after various authors)
Slovakia (Eastern Czechoslovakia)	Maa	43-50°N	2	2	Scheibner, 1960
Dordogne (SW France)	Maa	42-50°N	11	3	Alloiteau, 1953; 1954; 1960b
Catalonia (NE Spain)	Maa	40-45°N	102	51	Alloiteau, 1960a; Bataller, 1937a; b; Reig, 1987
Fruška Gora (NE Yugoslavia)	Maa	38-43°N	5	4	Pasić, 1951
Eastern Serbia (SE Yugoslavia)	Maa	35-40°N	34	15	Milovanović, 1939; Pasić, 1953
Breznik (Western Bulgaria)	Maa	35-40°N	67	31	Cheshmezhieva, 1969; 1970; 1971; 1972a; b; 1974; 1975; 1986
SW Sind (Southern Pakistan)*	Maa	c.30°N	7	4	Felix, 1914c (after Duncan, 1880)
Dakar (W. Senegal)	Maa	12-17°N	6	6	Alloiteau, 1952
Western Madagascar	Maa	13-30°S	16	13	Alloiteau, 1958
Seymour Id. & Snow Hill Id. (James Ross Gp., Antarctic Peninsula)	Maa	60-65°S	1	1	Felix, 1909
W. Greenland (c. 70°N)	Pal	c.65°N	18	17	Floris, 1972
Sjaelland (Eastern Denmark) & S. Sweden	Pal	55-57°N	17	14	Felix, 1914c (after various authors); Floris 1979; 1980
Western Belgium	Pal	c.51°N	2	1	Felix, 1914c (after various authors)
Southern Ukraine (USSR)	Pal	c.50°N	14	11	Kuz'micheva, 1975
Salzburg, (Austria)	Pal	c.45°N	7	5	Kühn & Traub, 1967
N. Croatia (N. Yugoslavia)	Pal	c.40°N	7	6	Polsak, 1985
Libya & Egypt	Pal	28-30°N	11	9	Felix, 1914c (after various authors)
Abidjan area (S. Ivory Co.)	Pal	c.2°N	9	7	Barta-Calmus, 1969; 1970
Northern Somalia	Pal	c.5°N	33	20	Russo 1988 (unpublished, and after various authors)

solitaries in being large in diameter and often also discoid, patellate or cupolate in form. Wells's (1956) usage of hermatypic/ahermatypic can reasonably be used here as a working approximation for 'zooxanthellate -like' and 'non-zooxanthellate-like' categories, respectively (shortened to 'z-like' and 'non-z-like'). This is not something we advocate generally, however, as we otherwise agree with Schuhmacher & Zibrowius's (1985) distinctions. Wells's (1956) hermatypic/ahermatypic categories are useful because the implied distinction is between corals restricted to warm, shallow, well-lit waters and those that were not so restricted.

In a few genera, Wells (1956) did not indicate hermatypic or ahermatypic status, and in a few cases, extant genera are known to include some species that are zooxanthellate and some that are not (e.g., *Oculina*). We omitted these 'borderline' genera from analyses with the hermatypic/ahermatypic distinction.

The alternative usage of 'hermatypic/ahermatypic' to mean reefal/nonreefal should be mentioned because others may prefer to interpret our results accordingly. Many modern zooxanthellate corals occur on tropical coral-algal reefs, though this is not universally true, either today or in the geological past (Coates & Jackson,1987). Many fossil reefs were different in structure, biotic composition and distribution from modern tropical coral-algal reefs, and may not even have been restricted to warm, shallow, well-lit waters in tropical latitudes (Rosen, 1989). If 'hermatypic' is taken to mean reefal, rather than symbiotic, our analyses would represent a search for a sedimentological pattern to extinctions, without connotations of temperature, climate, absolute water depth, latitude, or illumination (Rosen,1989).

Species data

Since many of our sources (Table 1) postdate Wells (1956), generic names in our compilation are not always compatible with his. However, all the generic names are listed as valid by Wells (1986).

There is apparently very little species overlap between our localities in either the Maastrichtian (7%) or the Paleocene (2%). This implies a higher degree of endemism even within southern Europe than seems likely, and is possibly an artefact of the chauvinotypy factor and of taxonomic splitting (e.g. in *Cunnolites)*. We therefore use generic data from this data base.

We denote the *Treatise*-derived (Wells,1956) data set with 'T' and the species compilation and generic derivations from it, with 'S'. We also make occasional reference to a separate compilation of species made by D.T.(full details not given here) from only European localities. Its localities and time intervals only partly correspond to the S-data; we refer to it as the 'Europe-only' compilation. Where no distinction is made in referring to data or conclusions from analyses (and where the distinction is otherwise not self-evident), as in broader discussion of patterns, a generalized view based on all analyses of the various data sets is implied.

Methods

Data expressed in numbers of taxa are based on all the relevant records of taxa within a given time interval. Thus extinctions are the taxa in one time interval that are not recorded from any subsequent time interval. Percent extinctions are the proportion of extinctions, derived in this way, to standing diversity within the same stratigraphical interval. Results from out S-data and Europe-only compilations are therefore not global, as they relate only to their own locality sets.

Patterns

Standing diversity: corals in general

Results. WSRO and WSRI T-generic patterns (Fig.1A,B) show a statistically significant rise in diversity through the Cretaceous and a marked fall in the Paleocene. Species patterns from our Europe-only data show an apparent decline from c.400 in the Santonian-Campanian, to c.160 in the Maastrichtian. Our S-data indicate a continuing decline into the Paleocene from 255 species in 105 genera in the Maastrichtian, to 114 species in 70 genera in the Paleocene.

Remarks. The rise in generic diversity through the Cretaceous and subsequent fall in the Paleocene may reflect a variety of sampling biases as discussed by Signor (1985). Moreover, if the Europe-only species numbers are time-averaged the apparent decline becomes statistically insignificant (27.59 species per million years in the Santonian-Campanian, and 20.00 in the Maastrichtian; chi-square test gives $0.1<p<0.5$, where p is the probability of these observed time-averaged diversities diverging from their mean (i.e. their 'expected') value of 23.8). On the other hand, the S-data show that the fall in time-averaged diversity across the Maastrichtian/Paleocene boundary from 31.88 to 11.29 is highly significant ($p<0.005$, calculated in the same way), though the corresponding fall in generic diversity from 13.13 to 6.93 genera per million years is not significant ($0.1<p<0.5$).

Unfortunately, we cannot time-average our T-data, though the upper Cretaceous of this compilation could be as long as 46.5 my which would be much longer than the Paleocene (10.1 my), and on these figures, time-averaging would reduce the apparent differences in T-data diversity between these two intervals. Beauvais & Beauvais (1974) recorded a fall in species-level diversity of their reef-building corals within the late Cretaceous, though they did not analyze their data statistically. It therefore seems that evidence for such a decline is weak, but a more convincing fall occurred globally, at or about the K/T boundary. These conclusions take account only of the problems of sampling different lengths of geological time, but not of any other sampling problems.

Extinctions: corals in general

Results. Both the WSRO and WSRI extinction patterns (Fig.1A-D) are statistically significant, with an Upper Cretaceous peak. Within the late Cretaceous (Europe-only data), 310 extinctions occurred out of 400 Santonian-Campanian species, but only 5 species survived from the Maastrichtian into the Paleocene (155 extinctions out of 160 species). This fall in the number of extinctions is highly significant (chi-square test; $p<0.005$). Note however that when these extinctions are converted to percent extinctions, they actually represent a rise from 77.5% in the Santonian-Maastrichtian to 97% in the Maastrichtian. For our S-data, 6 species and 18 genera survived from Maastrichtian to Paleocene, giving 98% and 83% estimations respectively.

Remarks. These results provide tentative support for the idea that coral extinctions increased during the Cretaceous as a whole, and towards the end of the Cretaceous in particular.

The much higher percent extinctions of the Europe-only species compilation, the S-data species and the S-data genera than of the T-data genera is possibly due to these former compilations being restricted in time and space. With wider geographical and stratigraphical sampling, one might expect more post-Cretaceous survivors. A conservative estimate suggests that at least 9 Maastrichtian S-genera that apparently became 'extinct' (i.e. they are not in our Paleocene compilation) are actually known

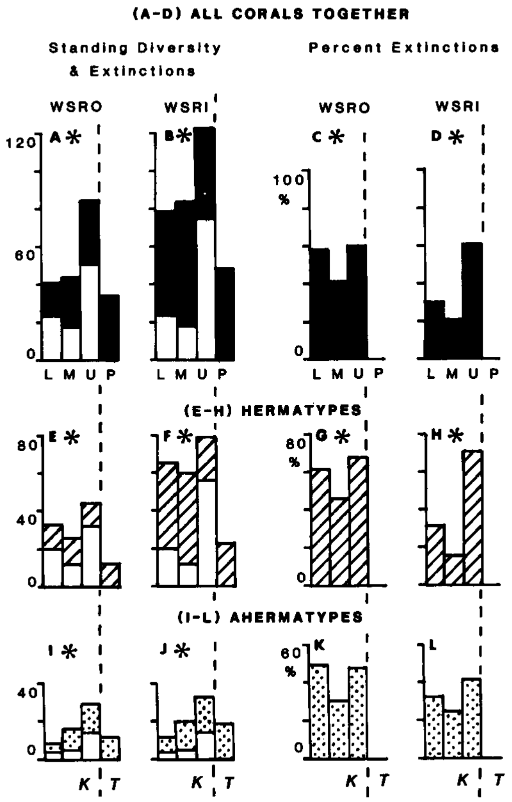

Fig.1. Standing diversity, number of extinctions and % extinctions of Cretaceous-Paleocene scleractinian genera (data from Wells, 1956). L,M,U, = lower, middle, and upper Cretaceous respectively, P = Paleocene, K = Cretaceous, T = Tertiary. A,B,E,F,I,J, standing diversity = column height; number of extinctions = unshaded column segments. Change in standing diversity statistically significant (*) in all plots ($0.01<p<0.025$ in J; $p<0.005$ in A,B,E,F,I). Significance (chi-squared) based on null hypothesis that for a given plot, standing diversities for each time interval should be the same and = average standing diversity for whole time span of plot. C,D,G,H,K,L, change in number of extinctions statistically significant (*) for all corals together ($0.01<p<0.025$ in C; $p<0.005$ in D) and for hermatypes ($0.025<p<0.05$ in G; $p<0.005$ in H), but not for ahermatypes. Significance of change in extinction numbers based on null hypothesis that ratio of extinction to diversity for each interval and for whole time span should be the same. Significance tests based on Cretaceous only.

from other localities or younger Cainozoic horizons (or both). They reduce percent extinctions of Maastrichtian S-genera to about 75%. These additional genera may therefore be 'Lazarus' taxa (Jablonski,1986). Such a selective pattern of regional extinction is plausible, since our species compilation is dominated numerically by European records.

Palaeoenvironmental patterns of standing diversity and extinction

Results. T-data hermatypes and ahermatypes each follow the same pattern of increasing generic diversity through the Cretaceous, followed by decline in the Paleocene (Fig.1E,F,I,J), as shown by T-data corals generally (Fig.1A,B). This pattern is statistically significant in all cases. Ahermatypes however show a steeper diversity rise than that shown by hermatypes, or total corals, roughly trebling in generic standing diversity from 8-12 in the L. Cretaceous to 29-33 in the U. Cretaceous (WSRO-WSRI, respectively). T-data hermatypes were generically more diverse than ahermatypes throughout the Cretaceous (Fig.2A,B; statistically significant in all cases), but this difference disappeared in the Paleocene when there is no statistical difference between them.

Extinction patterns of the two T-data coral categories are complementary to the diversity patterns. Hermatypes (Fig.1E-H) follow the all-coral pattern (Fig.1A-D) with a rise in extinctions in the U.Cretaceous (WSRO and WSRI both statistically significant). The apparent rise in extinctions in the ahermatypes (Fig.1I-L) is not statistically significant. When the two categories are directly compared with each other for each Cretaceous subdivision (Fig.2), the only significant pattern shown is in the U. Cretaceous (WSRO & WSRI) when hermatypic extinctions exceeded ahermatypic extinctions.

Of 18 S-data genera that survived from Maastrichtian to Paleocene, 5 are still living today and are non-z-like (*Caryophyllia, Dendrophyllia, Dungulia* (?Recent), *Parasmilia, Trochocyathus*); 3 are extinct but have typical non-z-like forms (*Coelosmilia, Palaeopsammia, Paratrochocyathus*); 2 are extant and consist of some species that are zooxanthellate and some that are not (*Cladocora, Oculina*). This amounts to a more or less equal number of non-z-like and z-like coral genera surviving from the Cretaceous, a pattern similar to that of Paleocene hermatypic T-genera (Fig.2A,C).

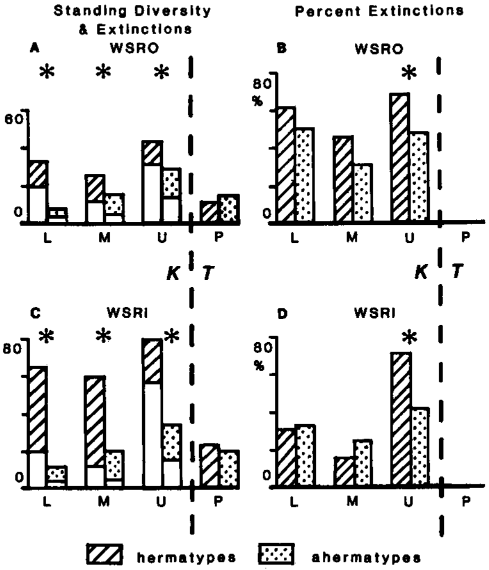

Fig.2. A,C, standing diversity and numbers of extinctions. Hermatypes are significantly (*) more numerous (binomial test) than ahermatypes through Cretaceous (A, $p = 0.001$ in L,M,U, Cret.; B, $p < 0.00001$ for L. Cret., and $p < 0.01$ for M & U Cret.). Significance based on null hypothesis that for each pair of hermatype-ahermatype comparisons, diversity for each ecological category should be the same and equal to half the total diversity for the two coral categories together. B,D, % extinctions derived from A,B significant in U. Cret. where extinctions of hermatypes exceeded those of ahermatypes (A, B $0.005 < p < 0.01$; C,D, $p < 0.005$). Significance based on null hypothesis that for each pair of hermatype-ahermatype comparisons, extinctions should number the same and each be in the same ratio to the diversity of the two categories together.

Z-like corals predominate in the Maastrichtian S-compilation, in the same way that hermatypes dominate the T-data analysis (Fig.2A,C). However, since the Paleocene S-genera survivors were approximately equally divided between z-like and non-z-like corals it seems that z-like corals must have experienced higher extinctions than non-z-like corals.

Remarks. The analyses show that z-corals differed from non-z-corals in their diversity and extinction patterns, suggesting divergent responses to extinction factors, especially in the late Cretaceous. Z-corals appear to have been more susceptible to extinctions than non-z-corals, while non-z-corals appear to have shown greater relative increases in diversity. This may also imply differences in origination patterns. It seems that while net global conditions through the Cretaceous favoured z-corals, this pattern changed at or about the K/T boundary and subsequent approximate equality of standing diversity between z- and non-z-corals lasted for some or all of the Paleocene. [Approximate equality also applies to modern Scleractinia (Rosen,1981)].

Patterns of diversity and extinction in relation to stratigraphical longevity of genera and their palaeoenvironment

Methods. We took the T-data corals that were extant in each of the four Cretaceous to Paleocene time intervals and partitioned them each into classes based on age of origin. We further partitioned the data into the palaeoenvironmental categories, giving us 24 sets of diversity data in all, according to stratigraphical interval (L/M/U Cretaceous/Paleocene), ecological category (corals generally/hermatypes/ahermatypes), and compilation set (WSRO/WSRI).

We also determined the number of T-data genera that became extinct within each age class using the same breakdown headings and the same data. No genera are actually stated to have ranges that ended during the Paleocene in the *Treatise* (Wells, 1956), so there were only 18 sets of extinction data.

Results. All results are based on T-data only. Just one basic pattern emerged from the diversity/longevity analyses, and only one pattern for the extinction/longevity analyses.

The youngest age class generally shows the highest values of standing diversity, regardless of the geological interval sampled, the ecological category of the corals concerned, or the particular data set. Diversity diminishes with increasing age class though in only one of the Lower Cretaceous sets (ahermatypes, WSRI) was this pattern statistically significant. Middle and Upper Cretaceous patterns were stronger, being all statistically significant. Although no genera appear to have originated during the Paleocene the same pattern of decreasing diversity from oldest to youngest age class shown by the other analyses applies to all age classes of Paleocene corals up to and including the U. Cretaceous age class. In all but one Paleocene case (ahermatypes, WSRI), this pattern was statistically significant. The p value for all analyses that were statistically significant was <0.005, using the null hypothesis that the standing diversity should be the same in all age classes and equal to the average number of genera in each age class. As the very oldest classes were represented by fewer than 5 taxa, these were omitted from the significance tests.

Although 10 out of 18 analyses appear to show an extinction trend in which progressively younger classes show progressively higher percent extinctions, this was not statistically significant in any instance. Although the remaining 8 analyses show a slightly different pattern of extinction in relation to age (e.g. bimodality), none of these was statistically significant either. (We used the null hypothesis that the proportion of extinctions in each age class should be the same as for all the corals in that particular data set.) We conclude that extinctions did not significantly affect corals of different age classes any differently.

Palaeolatitudinal patterns

Methods. We derived palaeolatitudinal patterns from our S-data compilation only, by comparing diversities and extinctions in the different sample localities according to their respective palaeolatitudes (Table 1). 'Survivors' are genera that occurred within both data sets, though not necessarily in the same region. The data are not sufficient for rigorous analysis.

Results. Diversity values for each sample locality (Table 1) show highest species and generic diversity at palaeolatitudes of c. 35-45°N in the Maastrichtian, being more than double the value found in localities in either the lower or higher palaeolatitudes. Z-like corals dominate these intermediate palaeolatitudes. Unfortunately, fewer regions were sampled in high and low palaeolatitudes.

The Paleocene pattern is a weak reverse of the Maastrichtian one, with highest diversities in boreal and tropical localities. Whether this Paleocene pattern is real, or whether it should be read simply as palaeolatitudinal uniformity with random, insignificant regional variations, it does appear that the pre-Paleocene pattern of a strong diversity peak in intermediate palaeolatitudes was lost some time around the K/T boundary.

So few species survived the K/T boundary that no useful species-level extinction pattern can be inferred with respect to palaeolatitude. Two of the 6 survivors are z-like forms of southern Europe (intermediate palaeolatitudes); 4 are non-z-like corals from low southern palaeolatitudes of western

Madagascar. They apparently survived in the intermediate northern palaeolatitude of Libya/Egypt. If this sample were not so small, one might conclude that species survivorship was greater in the high coral diversity belt in intermediate palaeolatitudes.

Percent extinctions of S-genera were highest in the high diversity coral belt: Netherlands (85%), Catalonia (92%), Eastern Serbia (93%) and Bulgaria (97%). Percent extinctions in other palaeolatitudes were much lower: Madagascar (69%), Senegal (57%) and Denmark (0%). (We omit mention of remaining regions with standing diversities in the Maastrichtian of four or fewer genera.)

The above regions with lower percent generic extinctions are those whose records are predominatly of non-z-like corals. Conversely, high percent extinctions occurred in regions whose records are predominantly of z-like corals.

Remarks. Our conclusions should be viewed with great caution as our sampling is so uneven and mostly rather small. It may be fortuitous that our intermediate palaeolatitude localities are predominantly zooxanthellate but Beauvais & Beauvais (1974) found a complementary pattern in their analysis of U. Cretaceous distributions of reef-building corals.

Palaeobiogeographical (faunistic) patterns

Method. We used only genera from our S-compilation to analyze palaeobiogeographical distributions, because at species level we have too little geographical overlap between sample localities to derive any pattern. The method used here is Parsimony Analysis of Endemicity (PAE) (Rosen & Smith,1988; Rosen,1988). Note that in this method certain taxa and areas are omitted as uninformative.

Results. Both Maastrichtian (Fig.3A) and Paleocene (Fig.3B,C) results (S-genera throughout) lacked good resolution (note their basal polychotomies) and gave regional groupings that are difficult to interpret biogeographically. The polychotomies make it impossible to suggest any detailed faunal histories.

The clearest grouping is found in the southern and central Europe set of the Maastrichtian analysis (Fig.3A). These are dominated by z-like corals. They were also located in relatively close geographical proximity according to most late Cretaceous palaeogeographical reconstructions, and lay within the Tethyan Realm (Kauffmann, 1973; Beauvais & Beauvais,1974). Within this set, diversity, and hence possibly a palaeoecological gradient, seem to be the most likely influence on area relationships (Rosen & Smith,1988).

Apart from the Netherlands-Pakistan pairing, each of the two remaining sister pairs in the Maastrichtian analysis contains a high and a low palaeolatitude locality in which both have low diversity. All four localities are non-z-dominated and lay on either side of the 'Tethyan' belt of z-like corals in intermediate palaeolatitudes. Thus, although the Maastrichtian area cladogram is only weakly resolved it suggests 1, a mutual affinity of mid-latitude-restricted (or 'Tethyan') localities, these being also those dominated by z-like corals, as distinct from 2, affinities betwen a broader geographical range of localities outside this mid-palaeolatitude set, apparently dominated by more cosmopolitan non-z-like corals.

In the Paleocene analysis, the Ukraine-Yugoslavia grouping (without Somalia) and the Denmark-Greenland pairing seem the most reasonable, being palaeogeographically close, but otherwise there is very little to remark upon, positively. Apart from Denmark-Greenland, diversity is low throughout, and the resulting patterns may only represent fortuitous arrangement within a poor sample set of relatively widespread taxa. Non-z-like corals dominate all Paleocene localities, and removal of the only three z-like genera from the data set, results in even less resolution (Fig.3B).

Remarks. Perhaps the PAE cladograms reflect sampling bias and taxonomic problems. If not, their clearest indication is that in contrast to the late Cretaceous, coral faunas became more cosmopolitan in the Paleocene. This may have been due to distributional reorganization (e.g. 'dispersal') of those genera that survived the K/T boundary, but survivors were so few that this was more likely to be the result of an extinction bias towards genera that were restricted to intermediate palaeolatitudes (mainly z-like corals). This pattern might then have been further enhanced by a speciation bias towards more cosmopolitan, non-z-like taxa during the Paleocene (not tested here).

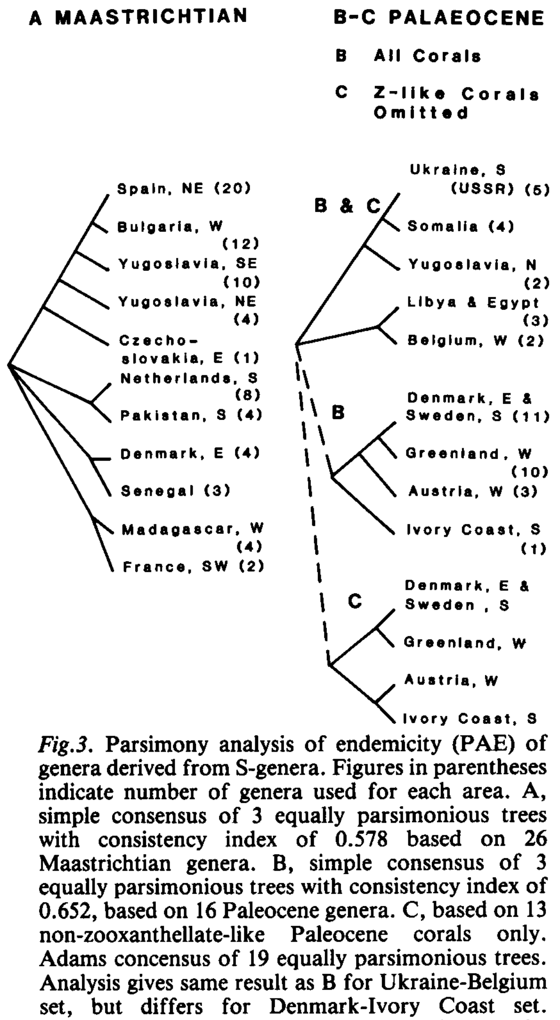

Fig.3. Parsimony analysis of endemicity (PAE) of genera derived from S-genera. Figures in parentheses indicate number of genera used for each area. A, simple consensus of 3 equally parsimonious trees with consistency index of 0.578 based on 26 Maastrichtian genera. B, simple consensus of 3 equally parsimonious trees with consistency index of 0.652, based on 16 Paleocene genera. C, based on 13 non-zooxanthellate-like Paleocene corals only. Adams concensus of 19 equally parsimonious trees. Analysis gives same result as B for Ukraine-Belgium set, but differs for Denmark-Ivory Coast set. Numbers of genera for this analysis not given on the diagram but same as in B except Ukraine (2), Somalia (2), Yugoslavia (1).

Our Maastrichtian analysis can also be compared with Rosen & Smith's (1988) PAE results for Campanian-Maastrichtian sea urchins to establish possible congruence. Unfortunately nearly all the sampled sea urchin localities lie within intermediate palaeolatitudes, so they do not provide an adequate test of the coral results.

What of the patterns within intermediate palaeolatitudes? The sea urchin locality set includes four localities that we also used for our present coral analysis (i.e. if N. Germany is taken to be part of the same area as Netherlands, S.W. France the same area as Dordogne, and Baluchistan the same area as S. Pakistan; Madagascar is common to both studies), so it is equally difficult to compare results of the two studies even for mid-palaeolatitude localities alone. The only common element between the two sets of results is that in which S.W. France-Dordogne is more closely related to Madagascar than either area is to Baluchistan-S.Pakistan. (Netherlands differs in its relationship in each of the two studies, being sister either to France or to Baluchistan-S.Pakistan.) Historically, one might conclude from this that France and Madagascar faunally diverged from Baluchistan-S.Pakistan before they diverged from each other.

Discussion

K/T extinctions have received more attention than extinctions at any other time in the geological column. Causes have been summarized by Hallam (1987). Our data do not allow us to test properly most current hypotheses, nor even to comment on how rapidly coral extinctions took place. We first compare our patterns with those of other authors, especially for marine organisms, and then discuss the most immediately relevant hypotheses.

Comparison of diversity patterns

Highest taxonomic diversity of living corals is found in the tropics and is strongly related to climate and to temperatures in particular (Rosen,1981,1984). The same pattern is also found in numerous other marine organisms. The present day high diversity belt of corals is also dominated numerically by z-forms. In the Late Cretaceous, the pattern was apparently similar to this in all but one respect: the palaeolatitudinal position of the corals' highest diversity zone lay at 35-45°N palaeolatitude. Few quantitative analyses of other Late Cretaceous organisms allow comparison with this coral pattern, but Taylor *et al.* (1980), found that Campanian-Maastrichtian diversity of predatory gastropods was also higher in intermediate (and high) palaeolatitudes, than in low palaeolatitudes.

Generally, diversity was highest for most marine organisms in the 'Tethyan' belt (Sylvester-Bradley,1967). This belt appears to have occupied a palaeolatitudinal zone similar to that of present-day warm water faunas: 30° N-S throughout the Mesozoic, according to Hallam (1984). In other words, high diversity of corals and predatory gastropods was apparently unusual in being outside, or perhaps only partly within 'Tethys' and the palaeo-tropics.

Diversity decline of corals during the late Cretaceous is statistically insignificant when time-averaged but in the Paleocene, our results suggest that the Late Cretaceous palaeolatitudinal coral pattern was lost, diversity overall declined, the marked diversity gradient disappeared, and non-z-like corals became dominant. Flattening of the diversity gradient can again be compared with the predatory gastropod pattern, though the closest horizon analyzed by Taylor *et al.* (1980) to our Paleocene one is Eocene. This shows virtually no palaeolatitudinal gradient at all. Note that the strongly equatorial latitudinal gradient found in living corals is also similar to the predatory gastropods (and numerous other organisms), and this is usually taken as evidence that latitudinal high diversity patterns in the past were similarly associated with warmer climatic conditions.

Another pattern that bears on ours is that (Coates & Jackson,1985) in which the percentage of colonial corals with 'high integration' noticeably declined from the Campanian-Maastrichtian to the Paleocene, in contrast to a slight rise in those showing 'low integration' (Coates & Jackson,1985, fig.3.23). The relevance of this is provided by a more recent paper (Coates & Jackson,1987) in which they showed a good correlation between living corals showing well-developed morphological integration and zooxanthellate symbiosis. Thus, taking their two papers together, their findings are consistent with our observed changes in diversity across the K/T boundary (but see remarks below on morphological complexity).

Comparison of extinction patterns

A feature of our results is the greater effect of extinctions on z-like corals than on non-z-like corals in the late Cretaceous, shown through comparison of their extinction patterns using T-data, and indirectly through our palaeolatitudinal and palaeogeographical analyses of S-data. These two approaches may not be totally independent. Southern Europe, with its rich fauna of z-like corals, dominates our S-data, but taxonomic works based on the same region presumably also provided a numerically important source of Cretaceous taxa in our T-data, even if one allows for a higher proportion of taxa from the Americas in the T-data. This is generally true for most late Cretaceous compilations (e.g. Beauvais & Beauvais, 1974, fig.1).

Extinction patterns of corals, Cretaceous or otherwise, have previously been little studied. Kauffman's (1984) discussion is one of the few exceptions, though he mostly treated corals incidentally to a much wider study of numerous organisms and without detailed or statistical analysis. He pointed out 1, extinctions were progressive through the Maastrichtian — there was not a simple and sudden catastrophe at the end of the Maastrichtian, and 2, 'Tethyan' faunas were more affected by extinctions than were non-Tethyan faunas. Our pattern of 77.5% extinctions in the Santonian-Campanian, which then rose to 97% in the Maastrichtian, seems compatible. Our results show that corals were apparently most susceptible to extinctions in lower palaeolatitudes. In his case, these extinctions are Tethyan/palaeotropical, whereas we found that they largely occurred at, or close to, the northern margins of 'Tethys'. As with diversity patterns, the apparent difference here may relate to use of 'Tethys'.

It is difficult to be more precise about marine extinction biases in the late Cretaceous other than a loose consensus that extinctions were greatest amongst marine organisms in one or more of the following overlapping categories: 1, symbiotic with zooxanthellae, 2, reefal, 3, palaeotropical, 4, warm shallow water or 5, 'Tethyan' (in any of its possible meanings). In strong contrast to this selective view of extinctions, Raup & Boyajian (1988) found that in their statistical analysis of nearly 20,000 Phanerozoic genera, there was little evidence for such differential extinctions. Their 'reef faunas' (i.e. 476 Phanerozoic reef genera, including 'frame-building corals' and numerous other genera that are 'strongly representative of a single environment limited to shallow marine areas of the tropics and subtropics') showed patterns of percent extinctions through time that differed very little from those of all other organisms taken together. At the K/T boundary in particular, there was no difference at all.

One clue to selective or uniform extinctions in the late Cretaceous is implicit in Fagerstrom's (1987) review of extinctions. He stated (Fagerstrom,1987, p.439) that 'Tethyan (tropical) taxa suffered higher extinction rates than non-Tethyan (temperate)' taxa (cf. Kauffman), but then observed (Fagerstrom,1987, p.460) that 'first order' extinction events at the end of the Cretaceous 'were indiscriminant as far as their impact on marine biotas was concerned', and that 'Reef communities were affected at least as powerfully as level-bottom and other communities' (cf. Raup & Boyajian). However, the examples he gives in his discussion of Paleocene reefs include none that was dominated (or even occupied?) by z-like corals (Fagerstrom,1987, p.448; and note that the corals in his coral-algal example at Vigny are not z-like (personal observation of Vigny corals by B.R.R.)]. This suggests that the question of uniformity versus selectivity of K/T (or any other) extinctions amongst reef corals may well turn on the use and interpretation of the word 'reef'. In preference to these generalized reefal attributes of corals, a morphological approach is probably a more satisfactory way of partitioning coral data for palaeoenvironmental analysis. Until reefal attributes are treated more rigorously, and problems of distinguishing between corals that were 'Tethyan', reefal, tropical, and symbiotic are resolved, we can only concentrate discussion on our own pattern of greater susceptibility of z-like corals to extinctions at the end of the Cretaceous.

Schopf *et al.* (1975) found that morphological complexity gives a positive bias to patterns of evolutionary rates amongst different groups of organisms, possibly accounting for the observation that 'only complicated animals evolve.' By extension, complex organisms are presumably more likely to show higher extinction rates. Morphological features of many z-corals are probably more complex than non-z-corals (Rosen,1986), so complexity alone could be invoked to explain our results. This should be tested in future studies. In the meantime, we can attempt to explain our results according to one of two assumptions: results are either 1, an artefact of a strongly European sampling bias, or 2, the results are part of a global pattern.

Sampling bias and marine regression

If our results reflect sampling bias, then our extinctions were presumably caused by regional factors in the area of our high-extinction localities (i.e. what is now southern Europe). A relevant explanation that has been invoked frequently in the K/T literature (e.g. Hallam,1987) is the well-documented, sharp, global regression at the very end of the Cretaceous. Though global in itself, it seems that its effects would have been geographically patchy. Organisms inhabiting carbonate environments of epicontinental seas and continental shelves, such as those of the late Cretaceous of southern Europe, would have lost their habitats through marine withdrawal, and those slightly lower in the water column would have experienced major habitat disruption. Even if marine organisms were able to keep pace with marine withdrawal by migrating down slope, many would also have been adversely affected by increased amounts of freshwater run-off and terrigenous sedimentation. Consequences of reduced total area and its implications in terms of equilibrium theory might also have applied (but see Jablonski (1985) for criticisms). In contrast, regression would have had 1, less effect on deeper water benthic organisms like non-z-corals, and 2, less effect on offshore carbonate platforms and oceanic carbonates (Jablonski,1985). The Cretaceous equivalent of the latter are notably absent from our sampling, but we know that they existed as possible survival areas. Many modern Pacific atolls, and the Bahamas, for example, have carbonate accumulations that date back to the Cretaceous (Schlanger,1981). It follows that our results may be giving a false impression of a z-bias to global extinctions, when it may have been only the carbonate environments of southern Europe that were affected. Our sampling does not allow us to test this. After all, z-coral genera were not wiped out completely at the end of the Cretaceous. Assuming that the survivors and their descendants did not redevelop the symbiosis after the extinction period, they may simply have continued to exist and evolve in offshore and oceanic carbonate environments during K/T boundary times, but remained 'hidden' from our analyses.

Some indication of the regionally selective effects of regression (together with transgression) of z-corals can be gained from the Quaternary of the Caribbean. Z-corals in this region were more severely affected by extinctions (Frost,1977) than those in other parts of the global z-coral zone. Indeed the coral literature usually emphasizes the relative stability of z-corals during this time (e.g. Newell,1971). ['Stability' does not refer only to lack of large scale extinctions. Some authors have invoked eustasy as an agent of other kinds of evolutionary change in z-corals (Potts,1983,1984; Rosen,1984)]. Caribbean extinctions however might be attributable to temperature falls.

It will be useful to include data from oceanic localities in future studies of Cretaceous extinctions. If the present bias towards z-coral extinctions holds good, one could consider truly global factors with more confidence. For further discussion of these possibilities, however, we will assume that our results are globally representative.

Symbiosis and extinction: global causes?

Susceptibility of z-corals to extinctions might be most readily explained in terms of factors that might 1, cause failure of the symbiosis and/or 2, adversely effect z-corals more than non-z-corals because of their different ecological or physiological characteristics.

Breakdown in symbiosis. Breakdown in symbiosis could result from poor illumination, excessively low or high teperature levels, high levels of phosphorus and nitrogen in sea water and high primary productivity. Most of these are not mutually exclusive. Their effects on living z-corals can be almost immediate, causing mass mortalities or substantial community changes on a local or regional scale (e.g. Glynn,1984; Birkeland,1989). Such adverse conditions need not have persisted for long, provided they were sufficiently intense and widespread to have caused outright extinctions.

Knoll (1989) recorded a general reduction of free-living dinoflagellates through the Campanian-Maastrichtian. Whether the species symbiotic with corals would have been sheltered from the factors that affected the free-living ones cannot be gauged. Knoll noted that general phytoplanktonic collapse at the end of the Cretaceous is consistent with a major ecological disruption. Incidentally, this collapse would rule out a surge of high productivity killing off z-corals.

Without evidence for glaciation near the K/T boundary any cooling may not have been sufficient to have had more than a regional effect on z-corals. Even with polar ice caps today, they thrive and it seems that even more severe cold phases in the Quaternary caused very few z-coral extinctions. The notable exception is the relatively small, northerly situated, and continentally influenced Caribbean part of the coral reef belt (Frost, 1977), though as already mentioned it may be difficult here to separate effects of glacio-eustasy from those of temperature falls. There is the additional possibility of combined effects, perhaps in some kind of chain response, involving cooler seas, changes in marine circulation patterns, marine regression, and possibly also anoxia (Hallam,1989). It is difficult to see why anoxia should have affected z-corals more than non-z-corals, but otherwise it is difficult to test these combined hypotheses.

El Niño events, currently attributed by some to global warming and human intensification of the greenhouse effect, are now recognized as a cause of recent widespread expulsion of zooxanthellae and subsequent mass mortality of z-corals (Glynn, 1984). This raises the interesting unconventional possibility of climatic warming, perhaps in connection with a surge in carbon dioxide levels, as a cause of K/T extinctions.

Reduced illumination could have resulted from persistent high dust levels in the oceans and atmosphere. In this respect, land plants, phytoplankton and z-corals were all affected by extinctions. Although these organisms occupy different habitats, they share a dependence on photosynthesis. It is more difficult to understand how global marine regression could have adversely affected all three groups directly. Two possible causes of high dust levels are volcanicity or bolide impact but coral data do not indicate one or the other. Late Cretaceous volcanicity, being more widespread and prolonged than most impact scenarios, may have been more likely to have had a lasting effect on organisms. Although many authors have discussed Deccan Trap volcanism as a likely source of dust, there was also extensive Late Cretaceous volcanicity throughout the central Pacific, at or above sea level (Schlanger, 1981; Klaver & Smedley,1989). This volcanism is so extensive that it might have caused sea-level changes so the interrelationship of possible extinction factors (Kauffman,1984; Hallam,1987) makes it difficult to separate the direct effects of extensive oceanic volcanism from its resulting tectono-eustatic regression.

Adverse effects on the ecology and physiology of symbiotic corals. Loss of zooplanktonic food because of the plankton collapse, might have been important, but not enough is known of non-z-coral feeding habits to be sure that this would have affected z- and non-z-corals differently. Disruption of the primary productivity pattern as implied by phytoplankton collapse, would have had consequences throughout the oceanic food chain, and so have affected z-and non-z-corals alike.

Finally, one can invoke biological differences between z- and non-z-corals. For example, z-corals are numerically dominated by colonial forms that often attain great size, great age and that give rise to new colonies by cloning as well as sexual reproduction (Jackson & Coates, 1986; Rosen, 1986; Coates & Jackson,1987). Many z-corals in many parts of the world, moreover, reproduce sexually only once a year in mass spawning events (Harrison *et al.*, 1984). In contrast, non-z-corals are numerically dominated by solitary forms, some of which certainly clone too, but not as prolifically as z-corals. Nor do most of them attain great size (their life history patterns are not well known). Colonial z-corals have long generation times and may have a slower genetic response to the selection effects of a sudden environmental change (Potts,1983,1984). Thus, if the late Cretaceous was a time of sudden and more rapid environmental change, then z-corals were perhaps less well-equipped to respond to it and survive. Z-corals do not appear to have suffered major extinctions during Quaternary glacial cycles and Jackson *et al.* (1985) found no evidence for differences in speciation rates between clonal and non-clonal organisms through geological time.

Conclusions

Whatever symbiosis-related theories one might put forward, lack of adequate data hinders rigorous testing of them. The question of our symbiotic bias being an artefact of morphological complexity has also been mentioned. Leaving aside these problems, z-corals did not all become extinct at the K/T boundary which might reflect regionally related extinction factors or even differing degrees of autotrophy amongst z-corals (Porter,1976). But there may also be a low level of reliability on symbiosis in fossil corals. While comparison between symbiotic and non-symbiotic corals introduces a new dimension to the extinction debate, it will also be vital to carry out further work on recognition criteria if good use is to be made of the distinction.

Nevertheless, our results suggest that high productivity, anoxia and climatic cooling were unlikely factors (taken in isolation) in our particular pattern of K/T coral extinctions. While marine regression certainly seems to have occurred, and may well have been regionally important, it is difficult to test here because of sampling bias. Moreover, there is as yet no convincing model of how it might affect corals. Though currently unorthodox, the idea of climatic warming, perhaps in connection with carbon dioxide increase, is not contradicted by the coral evidence. So far however, prolonged and intense volcanicity seems to be the strongest candidate for explaining coral extinctions because of its effect on illumination. It could also underlie other explanations like marine regression.

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