

# Paleoclimatic significance of Phanerozoic reefs

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## ABSTRACT

**A database of pre-Quaternary Phanerozoic reefs is used to test the significance of ancient reefs as paleoclimatic tracers. The compilation of reef paleolatitudes through time and comparison with published paleoclimate curves shows that neither the width of the tropical reef zone nor the total latitudinal range of reefs is correlated with published estimates of paleotemperature. However, reefs trace paleoclimate indirectly: Algal reefs tend to prevail during icehouse climatic intervals, and distinct high-latitude reefs are only developed in cold intervals, whereas during greenhouse episodes, the reef zone usually ended abruptly at a particular latitudinal boundary in the subtropics. Additionally, different biotic reef types tended to be concentrated in different latitudes. The lowest latitudes have usually been occupied by coralline sponge or microbial reefs, coral reefs tended to grow in intermediate latitudes, and bryozoan reefs constantly occupied the highest latitudinal position.**

**Keywords:** paleoclimate, paleolatitude, reef builders, reefs, secular variations.

## INTRODUCTION

Reefs and other shallow-shelf carbonates are commonly considered as good tracers of the ancient tropics and subtropics (Ziegler et al., 1984), and the latitudinal range of reefs is commonly thought to indicate paleoclimate, especially the temperature component of climate (e.g., Frakes et al., 1992; Johnson et al., 1996). This concept refers to the observation that modern zooxanthellate coral reefs have a distinct latitudinal boundary that agrees well with minimum sea-surface temperatures. The latitudinal boundary of modern coral reefs is therefore largely dependent on the distribution of warm currents and today reaches 34°N and 32°S at the western margins of oceans.

However, although modern reefs appear to be vulnerable to cool water as well as excess warmth (Pockley, 2000), the paleoclimatic potential of Phanerozoic reefs still must be rigorously tested. In this paper, a database on pre-Quaternary Phanerozoic reefs (Kiessling et al., 1999) is used to test the paleoclimatic control of reef distribution and reef composition.

## DATABASE AND METHODS

The relational PaleoReefs database (Kiessling et al., 1999) currently contains 3030 entries from the earliest Cambrian to the Pliocene. Each entry contains information on age, reef type, environmental setting, and biotic and petrographic composition of a reef site (confined by a 20 km distance criterion). A reef is broadly defined herein as a laterally confined structure built by sessile benthic organisms.

Paleolatitudes were determined as described by Kiessling et al. (1999). The paleopositions were calculated for 32 time slices equivalent to supersequences. Because Paleozoic reconstructions and terrane paleopositions are still problematic, some manual corrections had to be made. All reefs from evidently allochthonous terranes were omitted from the data set if no independent constraints were available on paleolatitude. The reduced data set contains 2910 reef sites with fairly reliable paleolatitudes, where "fairly" refers to uncertainties of more than 10° in the Paleozoic and 5° in the Mesozoic.

The tropical reef zone is defined as the latitudinal range of reefs with an inferred warm-water preference, that is, reefs that occur close to the equator in shallow-marine settings and extend up to a specific latitudinal limit. Today the tropical reef zone contrasts with a high-latitude reef zone largely built by azooxanthellate corals or coralline

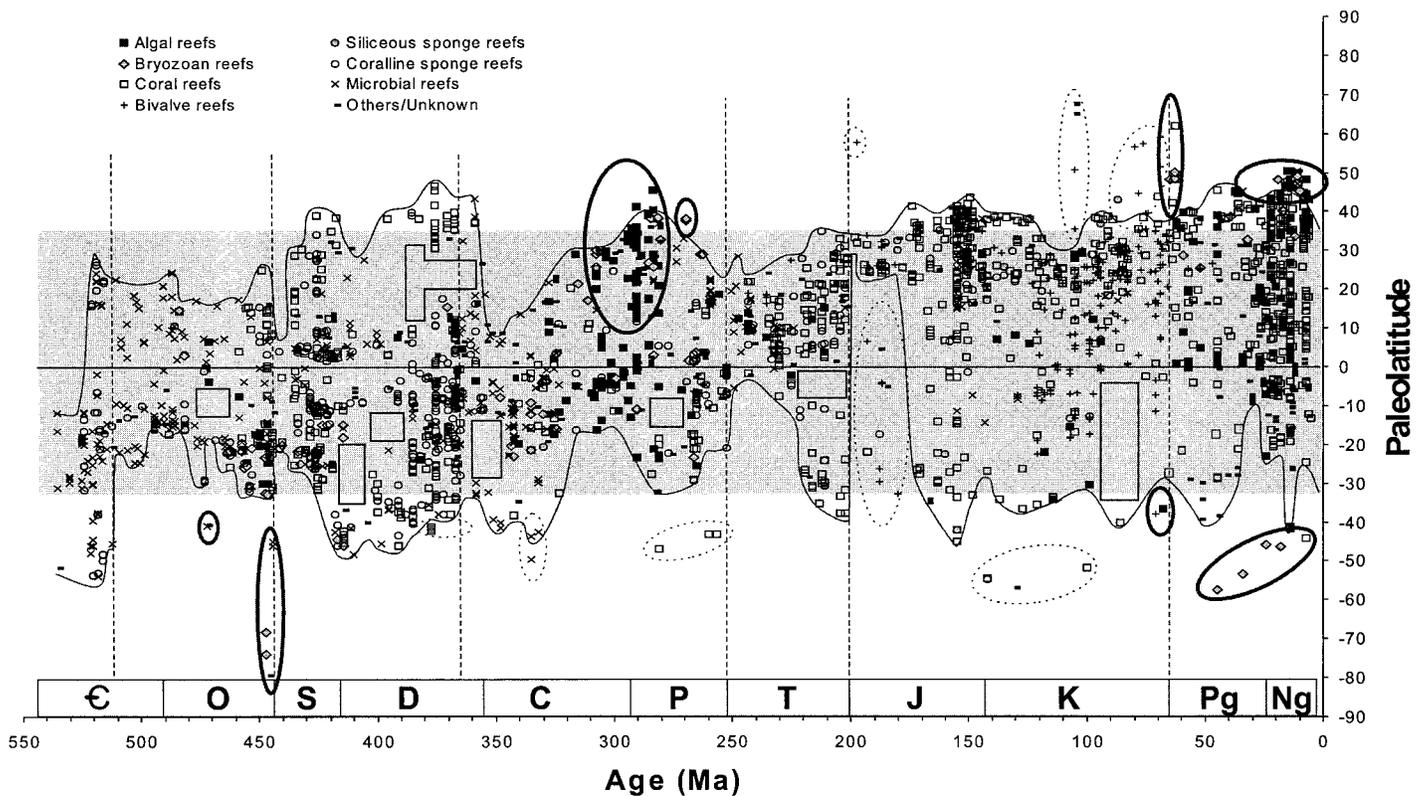
algae (Freiwald, 1993; Freiwald et al., 1997). Distributional, compositional, and geometrical differences permit a clear separation between both reef zones. Applying uniformitarian principles, the recognition of distinct ancient high-latitude reef zones was thus guided by geographic isolation and compositional differences between reefs in high and low latitudes.

## SECLAR VARIATIONS OF THE TROPICAL REEF ZONE

The fluctuations in the width of the tropical reef zone are pronounced (Fig. 1), considerably more than admitted by Parrish (1998). Apart from the problematic Early Cambrian with poorly determined paleogeography, the Cambrian and Ordovician reef zone was significantly narrower than today. The reef zone widened profoundly during the Silurian and Devonian, many of the reefs extending well beyond the limits of modern tropical reef growth. A major constriction occurred after the Devonian-Carboniferous boundary, mostly owing to a loss of Northern Hemisphere reefs. Apart from a short-lived southern high-latitude expansion in the Viséan-Serpukhovian, there was no significant change in the width of the tropical reef zone for most of the Carboniferous. However, the tropical reef zone shifted considerably northward. The Early Permian saw a major expansion of the reef zone and a more symmetrical reef distribution on both hemispheres. A strong restriction is evident in the Lopingian (Late Permian).

The reef zone remained confined during the Early and Middle Triassic, but expanded profoundly in the Late Triassic. The Early Jurassic reef zone was extremely limited around 30°N. Although several reefs are reported from the Southern Hemisphere and at high northern latitudes, most of them are bivalve banks, small coral biostromes, and sponge-coral banks, which are statistically identified as outliers. The reef zone expanded substantially during the Jurassic. Coral reefs to near 40° paleolatitude are known until the Neocomian. Rare high-latitude reefs are statistically treated as outliers, and little is known about their composition (e.g., Ramos, 1978; Ludwig, 1983).

Apart from minor fluctuations, the Cretaceous and early Paleogene reef zone remained fairly wide, although the southern boundary is not well defined. An exceptionally wide tropical reef zone is evident in the late Paleocene and Eocene. In the Northern Hemisphere, reefs as far north as 46° have a tropical affinity. Reefs in the Southern Hemisphere are poorly known, but seismic exploration suggests substantial coral-



**Figure 1.** Paleolatitudinal distribution of 2910 reef sites through pre-Quaternary Phanerozoic time. Shaded area indicates modern reef zone, and enveloping pair of lines demarcates inferred width of ancient tropical reef zone. Thick-line ellipses indicate distinct high-latitude reef provinces, dashed-line ellipses refer to isolated reefs of problematic affinity, and angular blocks indicate significant reef gaps in low latitudes. Straight dashed lines demarcate major mass-extinction events. Note that, compared to today, the ancient reef zone was often more confined.

reef growth down to 35°S (Salman and Abdula, 1995). After a slight constriction in the late Eocene–early Oligocene, the tropical reef zone widened in the late Oligocene and Neogene.

#### TEMPORAL DISTRIBUTION OF HIGH-LATITUDE REEF ZONES

A distinct high-latitude reef province is first recognized in the Ordovician (Fig. 1). First in Baltica and then, by the latest Ordovician, geographically isolated high-latitude reefs formed in the extreme high-latitude sites of Gondwana (Bergström and Massa, 1992; Vennin et al., 1998). Reefs in high latitudes did not differ substantially in composition from their tropical counterparts during the Silurian, the Devonian, and most of the Carboniferous. By the Middle Pennsylvanian until the Sakmarian–Artinskian (Early Permian), higher latitude reefs in the Northern Hemisphere were characterized by common *Palaeoaplysina*, an enigmatic alga (Watkins and Wilson, 1989). Although lower-latitude reefs were also dominated by algae, they lacked *Palaeoaplysina*, and commonly contained substantial amounts of *Shamovella* (= *Tubiphytes*) and encrusting red algae. The lowermost occurrences of *Palaeoaplysina*-bearing reefs are found along the western margin of North America, presumably affected by cool eastern boundary currents (Kiessling et al., 1999). Later in the Permian, isolated reefs are known from the high-latitude Southern Hemisphere. Their detailed composition is poorly known, and it cannot be determined whether the reefs represent excursions of the tropical reef zone or formed an isolated high-latitude reef province.

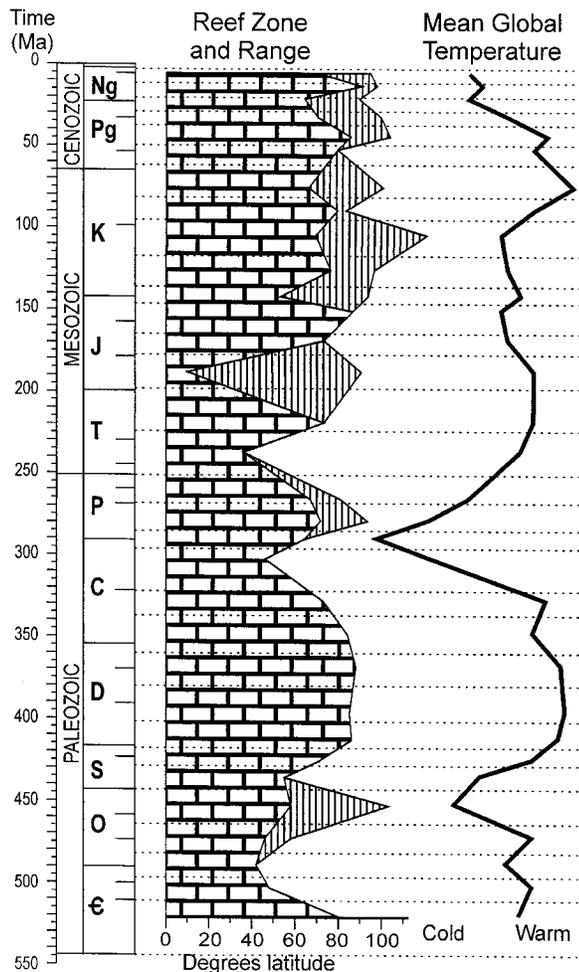
Distinct high-latitude reefs are again evident in the Maastrichtian–Danian. Bryozoan mounds and azooxanthellate coral reefs proliferated in the Boreal Realm (Bernecker and Weidlich, 1990; Surlyk, 1997), and though high southern-latitude reefs are again poorly known, they

appear to be sufficiently different to be excluded from the tropical reef zone. The Cenozoic saw a pronounced increase in the abundance of high-latitude reefs. The transition in the Northern Hemisphere was fairly continuous from coral-algal reefs to reefs with a distinct high-latitude aspect composed of, among others, bryozoan-algal mounds and algal-vermetid reefs (Pisera, 1996). The azooxanthellate coral and bryozoan-dominated high-latitude reef sites in the Southern Hemisphere, in contrast (Feary and James, 1995), are geographically isolated.

#### PHANEROZOIC PALEOCLIMATE AND THE REEF ZONE

One-dimensional paleotemperature curves for the Phanerozoic probably give an insufficient depiction of ancient paleoclimates. However, for the purpose of testing whether a relationship between Phanerozoic paleoclimate and reef distribution exists at all, a simple comparison between reef distribution and published paleotemperature curves is appropriate (Fig. 2). I used the estimates of Frakes et al. (1992) and applied a supersequence subdivision of the Phanerozoic as defined by Kiessling et al. (1999). Other paleoclimatic curves (Berner, 1994; Veizer et al., 2000) were also tested for correlations and provide the same basic results.

Neither the total latitudinal range of reefs nor the width of the tropical reef zone shows a highly significant correlation with inferred paleoclimate. The absence of correlation between paleotemperature and the width of the tropical reef zone implies that the paleolatitudinal position of a reef does not allow any conclusions on paleoclimate, even if the reef’s composition suggests a “tropical” affinity. A significant inverse correlation between age and the total latitudinal range of reefs ( $r = -0.53$ ,  $p = 0.002$ ), however, suggests that reefs became progressively better adapted to higher paleolatitudes. This widening of the



**Figure 2.** Latitudinal range of tropical reef zone (brick pattern) and total latitudinal range of reefs as compared to inferred global paleotemperature (Frakes et al., 1992) on a supersequence stratigraphic resolution (indicated by dotted lines). There is no significant correlation between paleoclimate and width of reef zone, but overall latitudinal range of reefs increased through time, suggesting that reefs became progressively better adapted to high-latitude settings.

latitudinal range applies only to the total reef range. There is no significant widening of the tropical reef zone through time. Thus, the latitudinal widening is due largely to the more widespread reefs outside the tropical reef zone, whereas the fluctuations in the tropical reef zone cannot be explained by long-term evolutionary trends or climatic var-

iations, except perhaps for the Cenozoic, when changes in paleoclimate are in phase with changes of the central tropical zone (Fig. 2).

## ROLE OF MASS EXTINCTIONS

Many but not all mass-extinction events appear to have a profound and long-lasting impact on the width of the tropical reef zone. Although the paleogeographic reconstruction of the Early Cambrian is problematic and the whole reef zone appears artificially shifted southward in Figure 1, the overall latitudinal range of Early Cambrian reefs is likely to exceed the range of Middle Cambrian–Early Ordovician reefs by some 20° latitude. The Permian-Triassic mass extinction appears to have had a profound impact on the reef zone as well, but the major drop was actually associated with the Guadalupian-Lopingian (Middle–Late Permian) crisis (Stanley and Yang, 1994). The Triassic-Jurassic mass extinction resulted in a strong concentration of reefs around 30°N, whereas only few and isolated reefs are known from lower latitudes and the Southern Hemisphere. The constriction of the tropical reef zone lasted until the Aalenian. Other major mass extinctions had only a minor or short-lasting impact on the reef zone. Paradoxically, these events are commonly thought to coincide with significant climatic changes (Copper, 1994).

## DISCUSSION

Although there is obviously no straightforward way in which reefs can be used either for paleoclimatic or paleogeographic studies, a closer look at the biotic composition of reefs and the timing of development of distinct high-latitude reef provinces underlines the paleoclimatic potential of ancient reefs. The tropical reef zone was narrower in times when microbial reefs were dominant and wider when coral reefs or coral-sponge reefs were dominant. Indeed, the biotic reef types show a strong correlation with paleolatitude (Table 1).

Microbial and coralline sponge reefs consistently grew in significantly lower latitudes than did any other reef type. The tropical preference of microbial reefs is puzzling considering the great range of paleoenvironments in which microbes are able to thrive. However, the great majority of Phanerozoic microbial reefs certainly originated from the growth or metabolic activity of cyanobacteria, whose temporal distribution pattern suggests that temperature constitutes a strong control (Riding, 1992).

The observation that coral reefs grew in significantly higher latitudes than coralline sponge and microbial reefs was not expected. PaleoReefs indicates their mean latitude throughout the Phanerozoic to be around 22°, close to the limit of the tropics. The fairly high mean paleolatitude of coral reefs is explained partly by the inclusion of presumably azooxanthellate coral mounds. However, coral mounds evidently dominated by azooxanthellate corals are rare in PaleoReefs, and the database suggests that the temperature tolerance of Phanerozoic coral reefs was probably greater than commonly assumed.

TABLE 1. MEAN PALEOLATITUDES OF BIOTIC REEF TYPES

Dominant reef builder	Mean paleolatitude (Phanerozoic)	No.	Latitudinal group*	Mean paleolatitude (Paleozoic)	No.	Latitudinal group*	Mean paleolatitude (post-Paleozoic)	No.	Latitudinal group*
Microbes	17.6	430	1	17.0	363	1–2	20.6	67	1–2
Algae	21.4	280	2	16.8	152	1–2	26.7	128	3
Coralline sponges†	16.0	456	1	15.7	366	1	17.3	90	1
Siliceous sponges	25.5	64	3	12.1	23	1	32.7	41	4
Corals	22.8	1060	2	20.0	278	2–3	23.9	782	2–3
Bivalves‡	21.1	234	2	N.A.‡	1	N.A.	21.2	233	1–2
Bryozoans	27.7	120	3	22.8	90	3	44.3	30	5
Others or unknown	17.4	267	N.A.	14.5	142	N.A.	20.6	125	N.A.
Total	20.5	2911	N.A.	17.2	1415	N.A.	23.6	1496	N.A.

\*Homogeneous subsets defined by analysis of variance and post-hoc Duncan test.

†Including stromatoporoids, archaeocyaths, chaetetids and pharetronids.

‡Rudists and other bivalves combined.

#N.A. = not applicable.

Bivalve and algal reefs fall into the same paleolatitudinal group as coral reefs, although their ecological requirements are presumably strongly different. The paleoclimatic potential of algal reefs lies in their temporal rather than their spatial distribution. Algal reefs become prominent during icehouse intervals—phyllloid algae in the Pennsylvanian–Early Permian and coralline algae in the Neogene. The algal reef expansion in icehouse intervals may be linked to nutrient levels enhanced by intensified oceanic cycling. Dust delivering the important nutrient iron was also suggested to explain the pattern (Soreghan and Soreghan, 2000).

Bryozoan-dominated reefs formed in the highest latitudes throughout the Phanerozoic, although there was a significant shift in absolute values from an average of 23° in the Paleozoic to a mean of 44° in the post-Paleozoic. The shift in absolute values agrees with the pattern observed for bryozoan carbonates (Taylor and Allison, 1998), but the fact that bryozoan reefs remained in high latitudes relative to other reef types does not call for explanations involving changing organism interactions. A real change from tropical preference in the Paleozoic to fairly high latitudes in the post-Paleozoic is observed only in siliceous-sponge reefs.

The temporal distribution of distinct high-latitude reef factories agrees well with the temporal distribution of cold intervals. The short-lived glaciation in the Late Ordovician and the Permian–Carboniferous and Neogene icehouse intervals are all characterized by high-latitude reefs that are compositionally different from tropical reefs, whereas intermediate or high-latitude reefs in greenhouse periods tend to be similar to their tropical counterparts. This correlation may be used as a tool to evaluate paleoclimate. The presence of distinct high-latitude mounds suggests that Maastrichtian–Danian paleoclimate was cool, perhaps even cooler than currently proposed (Barrera and Savin, 1999). More work is needed on other high-latitude reefs, particularly in the Permian and Cretaceous, to judge for or against cool-water reef factories.

## CONCLUSIONS

The distribution of Phanerozoic reefs has a great potential in paleoclimatic studies, but the use is less straightforward than previously postulated, for the following reasons. The tropical reef zone shows no correlation with inferred global paleotemperature and precipitation. The total latitudinal range of reefs increased significantly through time. The tropical reef zone has often been constricted after mass-extinction events, particularly after the late Early Cambrian, the latest Devonian, the Permian–Triassic, and the Triassic–Jurassic events. Microbial and coralline-sponge reefs occurred in significantly lower latitudes than coral reefs throughout the Phanerozoic, and bryozoan reefs were always more likely to grow in higher paleolatitudes. Algal reefs tended to become more abundant globally during icehouse intervals. Development of a pronounced high-latitude reef zone is closely linked to climatic cooling. The reason for many of the above observations is still unclear, but I speculate that many of the changes are linked to changing nutrient requirements of the prevailing reef builders and nutrient availability in the oceans, which is ultimately controlled by climatic change.

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