Evolution of the Triassic reef communities

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(with 10 figures)

The Triassic reef ecosystem underwent a three-step development. The process started with microbial reefs in the Scythian, and was followed by metazoan reefs. In the Anisian–Carnian the Wetterstein reefs and then by the Dachstein reefs in the Norian–Rhaetian. Wetterstein reefs are characterised by the dominance of the segmented calcisponges (sphinctozoans). In the Norian Dachstein reefs the sphinctozoans play a leading role, but the corals have already become serious rivals for them. The Rhaetian Dachstein reefs are characterised by the dominance of corals. The faunal turnover took place during the Carnian–early Norian interval.

The diversity of the segmented calcareous sponges (sphinctozoans) increases from the Anisian until the end of the Norian, but the number of species decreases in the Rhaetian. The diversity of the corals increases gradually in the middle–late Triassic to reach its peak in the Norian. Crises can be observed in the evolution of both main reef-building fossil groups at the end of the Carnian–beginning of the Norian, when a large proportion of the species became extinct. The sphinctozoan-dominated Wetterstein reefs were formed at 40–60 m depth, whereas the coral-dominated Dachstein reefs existed in the shallower (4–20 m) region.

Both the development of the coral colony and the coral-zooxanthella symbiosis can be traced during the Triassic.

During the Triassic the paleo-latitudinal distributional pattern of reefs changed considerably. Generally, an increasing expansion of reefs from the northern to the southern hemisphere can be observed. Anisian microbial-sponge reefs occur between 5º N and 20º N, Wetterstein reefs between 10º N and 30º N and Dachstein reefs between latitudes of about 30º N and 30º S.

Introduction

For many people the word "reef" means coral reef – and for a good reason: nowadays the main reef builders are corals and coralline algae. Sponges, serpulids, oysters and vermetid gastropods are of limited importance. In the past, practically all invertebrate groups have at one time or another contributed to reef growth (TUCKER 1985). In the Precambrian and Cambrian it was the blue-green algae (stromatolites) then the archaeocyathids, in the Ordovician to Devonian the stromatoporoids, in the Silurian to Carboniferous the rugose corals, from the Triassic onwards the scleractinian corals, in the Carboniferous–Permian the phylloid algae, in the Triassic–Jurassic the sponges, and in the Cretaceous the rudist bivalves (Fig. 1). There were four short periods in the history of Earth, when there were no reefs at all. (In this article the term "reef" is used in a broad sense for any biologically influenced build-up).

However, periods without reefs are rare in the Earth's history. One of the four follows the greatest extinction event, which took place at the Permian/Triassic boundary.
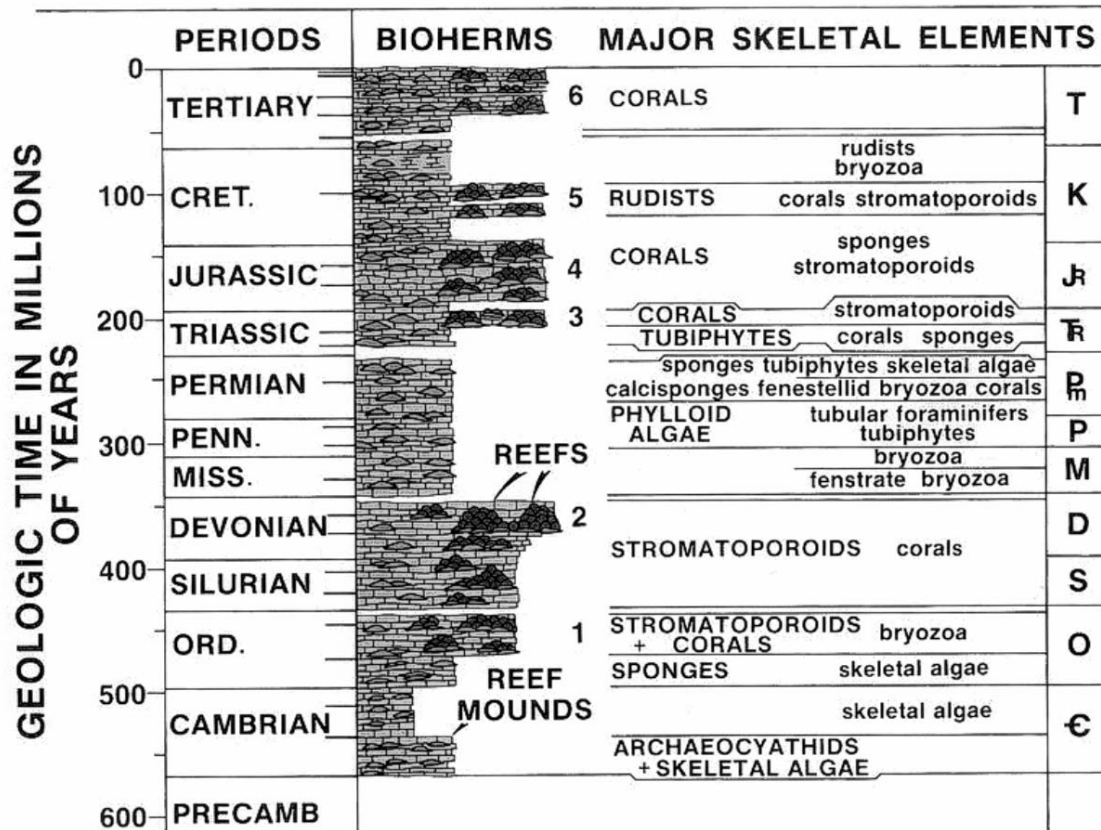
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Fig. 1 Reef-building fossils in certain periods of geohistory, after JAMES (1983). Note that there are four periods when there appear to be no reefs at all (gaps), times when there were only reef mounds, and times when reefs and reef mounds existed concurrently.

Preliminaries: Late Permian reefs

Before the Permian/Triassic boundary (Changhsingian) sponge-microbial and dendroid coral reefs flourished until the end-Permian (Fig. 2), when they disappeared in the end-Permian extinction. Rugose corals, tabulate corals and richthofeniid brachiopods all became extinct. Sponges were strongly affected, and only started to recover after a considerable time gap.

Triassic reefs

The Triassic reef ecosystem underwent a three-step development (FLÜGEL 2002). The process started with microbial reefs in the Scythian, followed by Anisian–Carnian Wetterstein reefs, which were then succeeded by the Norian–Rhaethian Dachstein reefs (Fig. 3). The latter two are metazoan reefs. The second and third intervals are distinguished by the biotic composition, the dominant reef builders, the size and abundance of reef structures, their depositional setting and their latitudinal distribution pattern. The middle Triassic–Carnian reefs were dominated by segmented calcisponges (sphinctozoans) and the late Triassic reefs by corals. The change and turnover between the second and third phases took place during the Carnian–early Norian interval over a time span of about 13 Myr. During this time interval major extinctions, climatic disturbances and significant paleo-oceanographic changes occurred. The high late-Carnian–early Norian extinction rates of reef biota were compensated by synchronous high origination rates (FLÜGEL 2002).

Microbial build-ups

After the reef collapse at the Permian/Triassic boundary, probably during the late Griesbachian, the first true microbial build-ups grew in an area comparable to the latest Permian reef domain (KERSHAW et al. 1999).

In the next step, microbial communities occupied an extended equatorial belt and later invaded deeper marine environments (WEIDLICH et al. 2003).

II. Metazoan reefs

With the end-Permian extinction metazoan reefs also disappeared and their recovery started only after a considerable time gap. FLÜGEL (2002) estimated a gap of about >8 million years.

According to our present knowledge the oldest Triassic reef is known from south China, in the Nanpanjiang Basin (PAYNE et al. 2006a, b), its age is late Olenekian–Anisian–?early Ladinian.

One can best understand the Triassic evolution of the metazoan reefs by following the evolution of the two main reef building organisms: the sphinctozoans and the corals.
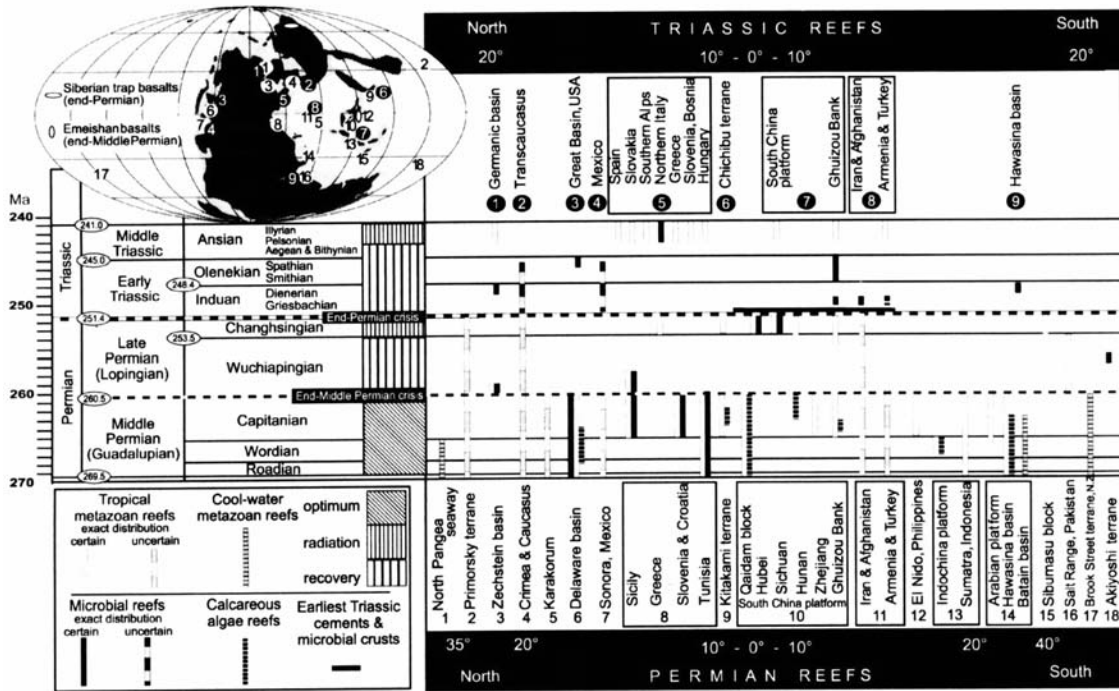

Fig. 2. Middle Permian – Middle Triassic chronostratigraphy and stratigraphic ranges of reefs plotted against paleolatitude (WEIDLICH et al. 2003). Inset map is late Permian paleogeographic reconstruction. Black numbers: Permian reefs, white numbers: Triassic reefs.
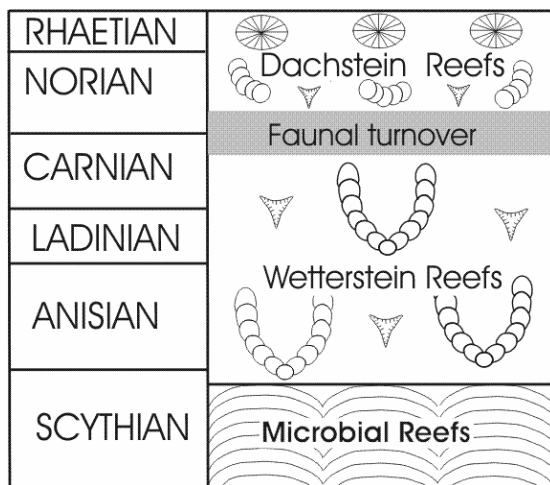

Fig. 3. The three different reef ecosystems during the Triassic. The faunal-floral turnover between the Wetterstein and Dachstein reefs took place during Carnian–early Norian over a longer period.

II.A. Evolution of the segmented calcisponges (sphinctozoans)

No sphinctozoa is known from the Scythian (Fig. 4). Anisian sphinctozoans are generally smaller than those from the Upper Permian. According to our present data we do not know any Permian sphinctozoan in the Triassic reefs at species level (SENOWBARI-DARYAN et al. 1993, VELLEDITS et al. in prep.).

Only some morphologically similar or identical Permian genera (e.g. *Colospongia*, *Solemolmia*) survived the Perm/Triassic boundary. The number of genera grew continuously during the Anisian–Carnian interval. Sphinctozoans reach the first peak of their diversity in the Carnian, when 50 species and 24 genera are known (RIEDEL 1990). One-third of the genera and two-thirds of the species are new. The interval between late Tuvalian and Lacian represents a significant crisis in the evolution of the sphinctozoans.

Only 4 species survived this period. Thus, 92% of the species disappeared forever. Extinction is not as significant at genus level. Only 45.8% of the genera died out. But the sphinctozoans recovered rapidly from the crisis, and in the Norian flourished to their greatest extent
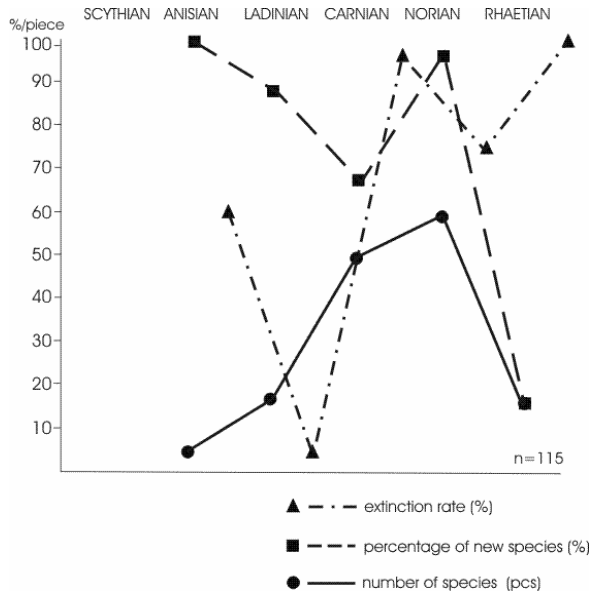

Fig. 4. Number and extinction rate of the sphinctozoan (segmented calcareous sponge) species, and number of new species during the Triassic (RIEDEL 1990).

Norian–Rhaetian reefs are characterised by a new sponge association. 29 genera and 60 species are known from this period, and 96.6% of the species, and 55.2% of the genera are new. In the Norian reefs the sponges dominate (mainly the non-segmented calcareous sponges, the inozoans), but already the corals are seriously rivalling them.

In the Rhaetian the decline of sponges is apparent. The number of species fell to 18 and the number of genera to 10. No new genera originate in the Rhaetian, ands only 3 species are new. In the Rhaetian the sponges lose their dominance in the reef, which is taken over by the corals (Fig. 4).

During the Triassic sphinctozoans follow a similar evolutionary trend to churches in the Middle Ages (Fig. 5). The churches of the early Middle Ages were built in the Romanesque style, characterised by thick walls, small windows, and a robust, fortress-like appearance. In the Wetterstein reefs the majority of the sphinctozoans belong to the aporate suborder, which is also characterised by thick walls, a fortress-like appearance, and only some bigger pores: the osculum, break through the wall.

Churches built in Gothic style are characterised by thinner walls, because the static role of the walls were partly taken over by pillars. The windows are much larger than those of churches in Romansque style.

The sphinctozoans belonging to the porate suborder are characterised by an inner skeleton, thin wall and many small pores breaking though the wall. The structural role of the wall was taken over by the internal skeleton (Fig. 6), so the walls of the porate sphinctozoans are thinner. As in the architecture of the Middle Ages, when Romanesque churches were succeeded by churches built in the Gothic style, in the reef community the simple robust aporate forms were phased out and the graceful porate form became dominant (Figs 5 and 6).

Another trend of the evolution of the sphinctozoan calcispongies is their increase in size. The size of the Anisian sponges is small (2–3 cm), whereas the Norian–Rhaetian sponges can be up to 13 cm.

II.B. Evolution of the corals

The modern Hexacorals or Scleractinians appeared as early as the Anisian, but they became dominant only in the Rhaetian after the decline of the sponges.

From the Anisian only some species and genera are known (Fig. 7), and some of them did not survive the Anisian/Ladinian boundary (Riedel 1990).

In the Ladinian the number of species doubled although the number of genera did not increase as rapidly, and moreover during the Ladinian 18.5% of the genera and 44.6% of the species died out. This did not restrict their evolution, because in the Carnian the number of species almost doubled (from 46 in the Ladinian to 84), although only 5 new genera appeared. 70.2% of the species and 31.25% of the genera were new. Around the Carnian/Norian boundary a crisis appears in the evolution of the corals.

Despite this crisis, the corals reached their highest diversity in the Norian from which we know 159 species and 61 genera. It means that the number of the Carnian taxa doubled.

In the Rhaetian the evolution of the corals slowed down, and 46.5% of the species and 41.4% of the genera died out: "only" 128 species and 48 genera are known.

The evolution of the corals is as follows: the diversity grew from the Anisian until the Carnian. At the end of the Carnian many species died out, but nevertheless, they reached their greatest diversity in the Norian. Their diversity decreased in the Raethian, and at the end of the Triassic all the Triassic species and genera died out.

Another very important feature of the evolution of the corals is that the number of solitary species decreases while the number of colonial species increases. Individuals integrated more and more within the colonies, at thamnasteroid corals the wall between the individuals disappeared (Fig. 8).

Fig. 5. Similarities in the structures of the aporate sphinctozoans and churches built in Romanesque style. Both are characterised by thick walls, small windows/some oscula and a robust, fortress-like appearance. **A.** *Enopocoelia armata* (KLIPSTEIN) Hór Valley, Bükk Mts., Hungary, Triassic, Ladinian. **B.** St. Krsevan church built in the 10th century and rebuilt in 1175, Zadar, Croatia.

Fig. 6. Similarities in the structures of the porate schinctozoans and Gothic churches. Both have a graceful appearance. The static role of the walls were partly taken over by the internal skeleton/pillars respectively, which in both cases allows thinner walls. Many small pores break though the wall of the porate shinctozoans, and similarly, the windows of Gothic churches are bigger. **A.** *Solemolmia manon manon* (MÜNSTER) Hór Valley, Bükk Mts., Hungary, Triassic, Ladinian. **B.** Notre Dame of Paris, the masterpiece of Gothic architecture. Its construction was started in 1163 and completed in 1345.
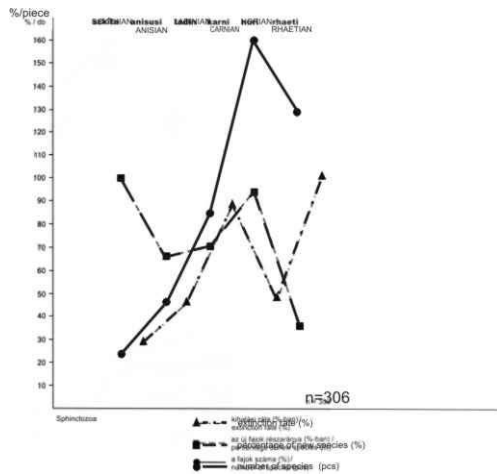
Fig. 7 Number of coral species, extinct species and new species during the Triassic (RIEDEL 1990)
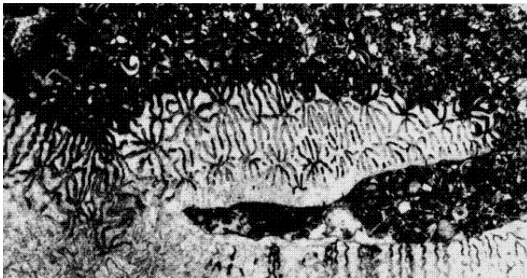

Fig. 8 *Astraeomorpha crassisepta* REUSS. A thamnasteroid coral from the Rhaetian. The wall between the individuals disappeared. Adnet. Photo: BERNECKER et al. 1999: Plate 37/5.

What are the evolutionary advantages and disadvantages of solitary and colonial organisms? Every organism strives to conquer an area, retain it and then expand after a while. A solitary organism has the advantage of rapid settlement, but can only control the area it occupies during the life of the individual, and it is much more visible to predators. By contrast, a colony lives longer, although the individuals die, the colony itself survives, because not all the individuals die at the same time. Furthermore, it is easier for a colony to expand.

Despite the above factors, the most significant change in the evolution of corals in the Triassic is the symbiosis with the zooxanthellae.

The Triassic coral colonies became more and more integrated, a process taking place concurrently with increasing symbiosis of the corals and zooxanthellae. Although the scleractinians had already appeared in the Anisian, they played a subordinate role in the reef community for more than 30 Mys, and only took over the leading role in the Rhaetian after the decline of the sponges in the Norian.

Sponges build up low-growing communities in the 'deeper-water' or protected habitats (e.g. lower slopes). Corals were common in shallow reef crest, reef flat and upper slope environments (FLÜGEL 2002).

II.C. Change of reef depth during the Triassic

When the corals took over the leading role in the reef community, the depth of the reefs changed as well. The sponge-dominated Wetterstein reefs existed at 40–60 m deep, whereas the coral-dominated Rhaethian Dachstein reefs were formed in the peritidal zones. The change in the depth can be easily explained by the different ecologic requirements of the two reef-building groups.

In many shallow-water reef-building corals, small single-celled plants (dinoflagellate algae – zooxanthellae) live in the body of tissues. In this symbiotic relationship the zooxanthellae appear to help dispose of coral waste products and the corals use the carbohydrates and oxygen produced by the zooxanthellae to aid their own metabolism and promote calcification. Most reef-building corals are zooxanthellate (SCOFFIN 1987). The photosynthetic activity of the symbiotic zooxanthellae decreases with the light. At 20 m depth there is not enough light for the zooxanthellae, that is why coral reefs dominated by scleractinians are concentrated in the upper 20 m.

Contrary to this, sponges live alone and thus they are not restricted to the upper 20 m. Their skeletons are full of pores, enabling them to create a vacuum inside their bodies causing the water to circulate through them, and thus they filter the nutrients from the water. Consequently, the sponges do not rely either on light or on wave movements, and accordingly sponge reefs were formed at 40–60 m depth.

III. The spatial distribution of Triassic reefs

There are conspicuous differences in the paleo-latitudinal distributional patterns of reefs in the Triassic (FLÜGEL 2002). During the Triassic the reefs can be seen expanding from the Northern to the Southern Hemisphere. Different reef types exhibit differences with respect to their latitudinal ranges: Microbial-sponge reefs of the Anisian occur between 5º N and 20º N, late Anisian–Ladinian–Carnian sponge-dominated reefs occur predominantly between 10º N and 30º N (Fig. 9), and Norian–Rhaetian sponge-coral reefs and coral-dominated reefs between latitudes of about 30º N and 30º S (Fig. 10).
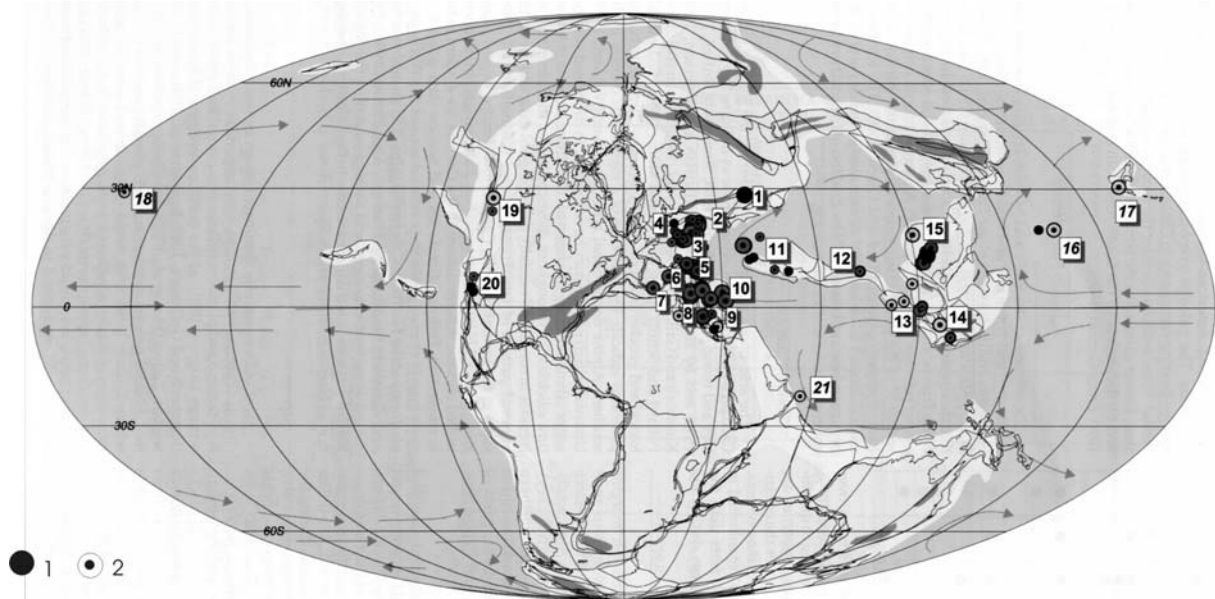
Fig. 9 PaleoReef map showing the distribution of Scythian to Carnian reefs. Note the asymmetrical distribution in the middle Triassic and early Carnian, changing to a more symmetrical pattern during the middle and late Carnian and in the Norian (see Fig. 10). 1, Scythian microbial reefs 2, Anisian, Ladinian and early middle Carnian reefs. The size of symbols reflects reef thickness. Reef domains (square boxes): 1, Caucasus; 2, Western Carpathians, Slovakia and northern Hungary; 3, Northern Calcareous Alps, Austria and Bavaria; 4, Southern Germany; 5, Southern Alps and Slovenia; 6, northern Spain and southern France; 7, southern Spain; 8, southern Italy and former Yugoslavia; 9, Greece and southern Turkey; 10; Romania; 11, Iran; 12; Pamir Mountains, Tadzhikistan; 13, Myanmar (Burma) and Thailand; 14, Thailand and Sumatra; 15, southern China; 16, southern Japan; 17, Hokkaido region, Japan; 18, Primor'ye region; Far East Russia; 19, British Columbia, Canada; 20, New Pass, Nevada, USA; 21, Oman (after FLÜGEL 2002).
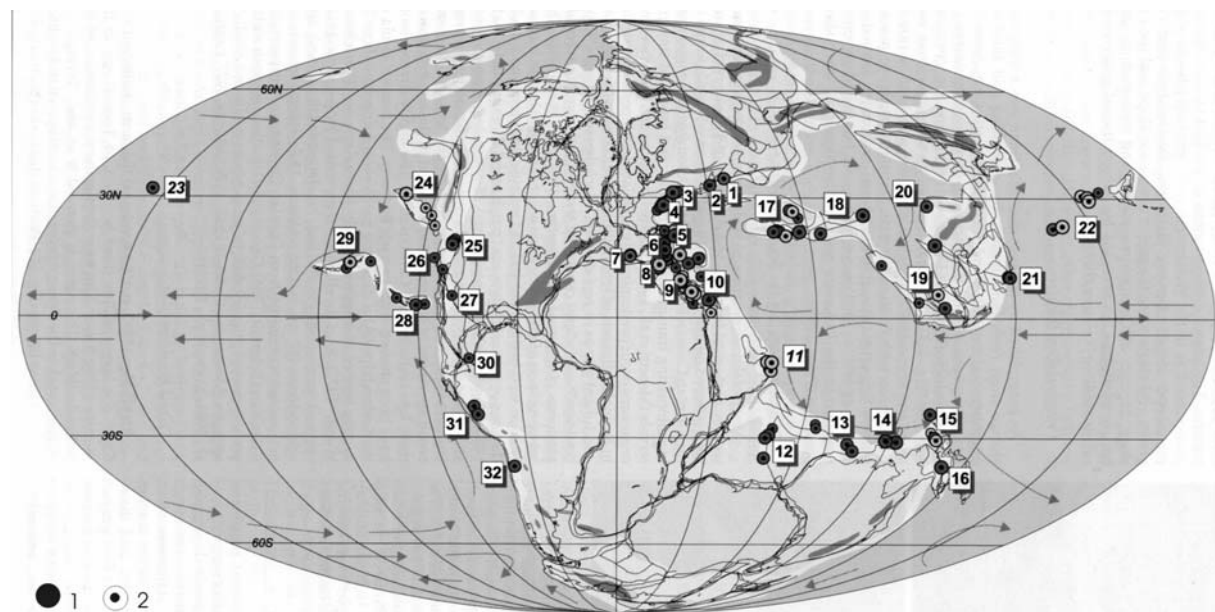

Fig. 10 PaleoReef map showing the distribution of Norian to Rhaetian reefs. Reefs occur within a wide latitudinal and longitudinal range. 1, microbes 2, reefs built up by calcareous algae, corals, coralline sponges, siliceous sponges, serpulid worms, etc. The size of symbols reflects reef thickness. Reef domains (square boxes): 1, Caucasus; 2, Crimea, Ukraine; 3, Western Carpathians, Slovakia and Hungary; 4, Northern Calcareous Alps, Austria and Bavaria; 5, Southern Alps and Slovenia; 6, Apennines, Italy; 7, southern Spain; 8, Sicily, Italy; 9, Greece; 10, southern Turkey and northern Israel; 11, Oman; 12, Spiti, Himalaya region, India; 13, off north-western Australia and southern Tibet; 14, Timor; 15, Buru, Ceram, and Sulawesi, Indonesia; 16, Papua New Guinea; 17, Iran, 18, Pamir Mountains, Tadzhikistan; 19, Thailand, Malaysia, and Singapore; 20, southern China; 21, Palawan, Philippines; 22, Japan and Sikhote-Alin, Far East Russia (paleoposition hypothetical); 23 Koryak, Far East Russia (paleoposition hypothetical); 24, British Columbia, Canada; 25, Oregon and Idaho, U.S.A.; 26, California and Nevada, U.S.A.; 27, Sonora, Mexico; 28, Vancouver Island and Alaska, U.S.A.; 29, Alaska (Peninsular Terrain), 30, Colombia; 31, central Peru; 32, northern Chile (after FLÜGEL 2002).

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