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Phanerozoic Reef Evolution: Basic Questions and Data Base

Erik **Flügel** and Erentraud **Flügel-Kahler**, Erlangen

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CONTENT

SUMMARY

An up-dated data base is a matter of importance and urgency in order for encouraging a process-oriented approach to the study of reef evolution.

The evolution of reefs is a major section of a Priority Program of the Deutsche Forschungsgemeinschaft devoted to 'Global and regional controls of biogenic sedimentation'. Biological, paleontological and geological approaches in the study of ancient and modern reefs are needed for providing a better understanding of the following basic questions:

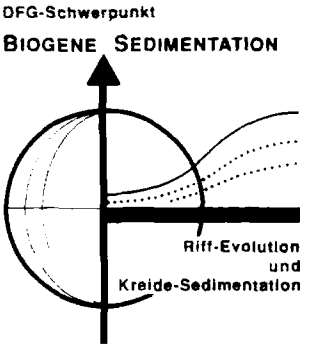
— Biological and non-biological processes responsible for the construction and destruction of recent reefs. Studies should be focused on those processes which might also be regarded as important controls in the history of fossil reefs.

— Paleontological data describing the changes in the biological controls of reef development over time. Studies should aim for a better understanding of major crises in the reef ecosystem during the earth's history.

— Geological factors governing the short-term and long-term development of reefs. Studies should be concentrated on the controls of reef accretion by sea-level fluctuations, climatic changes and possible changes in early diagenetic factors.

The Reef Bibliography presented includes more than 4000 references dealing with Cambrian to Pleistocene reefs and more than 750 references referring to processes relevant to the interpretation of ancient reefs.

The constraints of reef evolution will become clearer through intensivying comparative studies of reefs of different ages. The new data base should encourage this comparative research approach.



1 CURRENT INTEREST IN REEF RESEARCH

Modern and ancient reefs have been studied for more than 150 years starting with the classic work by Charles DARWIN (1842). Among the first fossil reefs recognized as such were the Silurian reefs surrounding the Michigan Basin, the Devonian reefs of England and Germany, and the spectacular Triassic reefs of the Dolomites.

The discovery and production of oil and gas from reef carbonates in the 50s triggered the interest of geologists and paleontologists in ancient reefs. The recognition of recent reefs as a unique and highly sensitive biotope recording short- and long-term environmental changes led to a rapid expansion

Address: Prof. Dr. E. Flügel, Dr. E. Flügel-Kahler, Institut für Paläontologie, Universität Erlangen-Nürnberg, Loewenichstr. 28, D-8520 Erlangen

of biological investigations during the last thirty years. Reefs are the world's largest 'carbonate factories'. The growth and demise of reefs during the earth's history should, therefore, reflect overall changes in global calcium dioxide dynamics. Man-made environmental perturbations of modern reefs is rapidly becoming a large problem (KÜHLMANN, 1988) demanding a global monitoring of recent reef ecosystems (WELLS, 1988).

Diversification of reef research

The broad interest in reefs has been reflected by the establishment of an International Society for Reef Studies (which publishes CORAL REEFS) and an increasing number of international symposia (seven CORAL REEF SYMPOSIA since 1969), national meetings and workshops resulting in proceedings (OLIVER et al., 1984; ZENG et al., 1984; SOKOLOV, 1986; JELL & PICKETT, 1989) and books (SCHUHMACHER, 1976; HARRIS, 1983; SCHROEDER & PURSER, 1986; SOKOLOV & IVANOVSKY, 1987; FAGERSTROM, 1987; GELDSETZER et al., 1988) as well as in special issues of journals (e.g., PALAIOS, vol. 3/2, 1988; FACIES, vol. 25, 1991). These activities have accelerated the rapid diversification of reef research and explain the predominance of specialists over generalists. Generalizations, however, are necessary for understanding reef development throughout the geological column.

The Priority Program 'Global and regional controls of biogenic sedimentation': 'Evolution of Reefs'

In 1990 the Deutsche Forschungsgemeinschaft instituted a Priority Program directed to the study of biological and geological factors controlling the processes of biogenic sedimentation.

A major part of this program is devoted to the 'Evolution of reefs in time'. The specific goals are to provide a better understanding of the processes controlling reef evolution, global changes in reef ecosystems, and reef sedimentation. Today more than thirty projects spanning a time range from the Devonian to the Holocene are being studied by groups from about twenty German research institutions.

Investigations of recent tropical reefs (Red Sea and Indian Ocean, Pacific Ocean, Carribean Sea) and modern temperate and cold- water bioconstructions (Atlantic, Mediterranean) are focused on the processes controlling the growth rates of reef-building organisms, the carbonate production of phototrophic and heterotrophic scleractinian corals, the long-term dynamics of reef communities, biota and sedimentation on deeper fore-reef slopes, modern relicts of ancient reef communities, bryozoan ecology in reefs, the destruction of reefs by microborers and by hurricanes, as well as the role of sea-level fluctuations in Holocene reef development.

Studies of ancient reefs have concentrated on non-actualistic reef types and on global changes in reef biota and reef types:

Examples of fossil reef types having no recent counterparts are Devonian and early Carboniferous mud mounds and Permian stromatolite reefs, Upper Jurassic 'sponge-algal reefs' as well as Cretaceous rudistid reefs.

Studies of the changes of reef types and biota concern Devonian reef-builders, reef extinction during the Frasnian/Famennian crisis as well as the turnover of reef types during the Permian and Triassic, and during the Cretaceous and early Tertiary.

2 REEF EVOLUTION: BASIC QUESTIONS

To be successful in better understanding reef evolution, it is necessary to concentrate on basic questions. A combination of biological and paleontological as well as geological approaches is needed to answer these questions.

2.1 Different approaches in reef research

2.1.1 Biological aspects

'The 'reef phenomenon' is chiefly a 'biological phenomenon' (FAGERSTROM, 1987).

Modern reefs offer the possibility of studying basic biological processes responsible for the formation of reef structures and for recognizing the biological and non-biological constraints controlling the construction and destruction of reefs.

It should be kept in mind, however, that recent reefs in many repects are inadequate models for pre-Cenozoic reefs, owing to the evolutionary changes in the taxonomic composition of reef communities, differences in dominating guilds and ecological patterns, in the degrees in calcification of reef organisms and because of the very special situation following the post-Pleistocene rise of the sea-level.

Keeping in mind this better understanding of 'reef evolution', we must concentrate on the study of those biological factors which might also be regarded as controls in the history of ancient reefs. Some of those biological factors important for ancient reefs are listed without further comment:

— the growth and calcification of reef-building organisms (zooxanthellate and non-zooxanthellate organisms, light-saving mechanisms, shallow- und deeper-water reef organisms)

— functional morphology, biomechanics and the mechanical resistance of reef organisms (ability of organisms to act as constructors, bafflers or binders)

— the dynamic aspects of reef development (zonation patterns, ecologic successions, competitive interactions of reef organisms)

— nutrients as controls of reef growth and reef demise (HALLOCK & SCHLAGER, 1986)

— microbial activities (including the role of microbes during early stages of reef diagenesis)

— quantitative aspects of carbonate production (reef growth, biological and non-biological reef destruction, export of sediment).

2.1.2 Paleontological aspects

Paleontological studies of ancient reef communities could contribute to a better understanding of the timing and the impact of significant changes in biological factors and processes during the earth's history.

Major questions are:

'Reef development: just episodes of extinctions and symbiosis ?'

TALENT (1988) has argued that the episodicity of reef building during the earth's history may, in part, reflect changing patterns of symbiosis and extinction through time. Symbiotic algae and light-enhanced calcification are regarded as the major factors in the development of framework reefs.

This has been emphasized especially for the evolution of coral reefs during the early Mesozoic (STANLEY, 1981). Evidence of algal symbiosis in the fossil record, however, is difficult to find (COATES & JACKSON, 1987), but some criteria offer the possibility for testing reef builders and reef dwellers with regard to the existence of photosynthesis (COWEN, 1983; 1988). Stable isotopes of oxygen and carbon may assist in recognizing calcification of reef builders triggered by symbiosis, but isotopic data must be handled very carefully because of vital effects and diagenetic processes (WEFER & BERGER, 1991).

Role of reef organisms as constructors, bafflers or binders

Sessile organisms found in ancient 'reefs' should not be designed as 'reefbuilders' without interpreting their potential functional role in the development of reef structures. A critical use of the 'reef guild concept' (FAGERSTROM, 1987, 1991) provides a very promising approach to defining the role of reef organisms in spatial resource exploitation regardless of their geological age. Steps in reef evolution are reflected by changing patterns in the composition of guild structures over time. Becuse these changes might be controlled by extrinsic factors (sea-level fluctuations) studies of guilds in ancient reefs offer the possibility to recognize cyclic processes within reef environments as well (GRÖTSCH & BUSER, 1991).

Temporal changes in destructive processes

The destruction of reefs is caused by physical processes (waves, currents; storms and hurricanes) as well as by bioerosion. Physical and biological destruction have undergone changes during the earth's history – hurricanes because of major differences in the climatic situation, and bioerosion because of the evolutionary changes of destructive organisms.

The activities of the destroyer guild have a major impact on the carbonate budget of reefs (HUTCHINGS, 1986). Changes in the type of boring, rasping, crushing and burrowing organisms would have controlled the time needed in the formation of reef structures and for the production of 'reef debris' and other carbonate sediment. Important changes include differences in the diversity and freqency of rasping organisms (e.g. fishes) as well as of microborers and macroborers overtime (KOBLUK et al., 1978; CAMPBELL, 1983) and differences in the strategies used by boring organisms to search for food or protection. The style of bioerosion seen in modern reefs is believed to have occurred as early as the Tertiary (PLEYDELL & JONES, 1988) but the 'evolution of bioerosion' is far from being understood (KLEEMANN, 1980). In addition, distributional patterns of microborings in ancient reefs are of high value in the reconstruction of paleoenvironmental parameters (GLAUB, 1988).

Changes in organisms living in cryptic reef habitats

In many modern reefs, growth cavities, shaded undersides of ledges and growing corals as well as spaces under and between reef boulders and the interior of vacated boreholes provide a larger surface area for colonization than the surface area of the outer reef surface. The life of these cavity-dwelling organisms is strongly controlled by the reduced photosynthetic capacity caused by lower light levels, reduced access to food resources, and specific kinds of water movement and sedimentation. Holocene cryptic communities may be highly diverse and are dominated by bryozoans, sponges, corals as well as coralline algae, encrusting foraminifera, serpulids, vermetids, bivalves, brachiopods, barnacles crinoids and colonial ascidians.

Some of these groups are also represented in the coelobite community of ancient reefs. In addition, many microfossils of uncertain systematic affinities are parts of fossil cryptic associations. A detailed study of these communities is necessary because of their probable major impact on the formation and early diagenesis of Paleozoic and Mesozoic mud mounds and reef mounds.

Current information indicates an increasing trend towards a polarization of exposed surface-dwelling and cavity-dwelling organisms from the Paleozoic to the Mesozoic (KOBLUK, 1988).

'Ecological successions in ancient reef ecosystems: Are they real ?'

COPPER (1988) has emphasized the importance of differentiating between 'ecological successions' characterized by a gradual change from pioneer to climax phases, which leads to an increasing biological control of reef environments, and 'community replacement' in time, forced by changes of external factors.

The model postulated by WALKER & ALBERSTADT (1975) strongly emphasizes the development of successions during reef growth. Because ecological successions provide a valuable tool in the recognition of intrinsic biological controls of reef growth, this model should, however, only be used if fossil reefs provide enough information on population sizes, species diversity, tiering, competitive interactions, number of niches available, area occupied and community structure.

To answer these questions we need sound systematic and taxonomic data as well as statistically processed field observations describing the frequency, distribution, taphonomy and preservation of reef fossils.

Evolutionary and environmentally controlled changes in the composition of crust-building associations acting as binders and encrusters of reef frameworks are of major importance in the discussion of the influence of short-term extinction events on reef evolution (MOUSSAVIAN, 1992).

Surviving reef-builders

Some of the organisms, e.g. coralline sponges, which were important reefbuilders during the Paleozoic and Mesozoic seem to have survived at least on higher taxonomic levels.

A comparison of the modern relicts with ancient communities is an important approach in the recognition of

changes in controlling ecological parameters, habitats and the role as reefbuilders (REITNER, 1989).

2.1.3 Geological aspects

'Reefs are unique sedimentary systems' (TUCKER & WRIGHT, 1990)

Reef dynamics are characterized by an interplay of biological, physical and chemical factors, governing constructive and destructive processes mentioned above as well as cementation and sedimentation (SCHROEDER & ZANKL, 1974). Geological processes such as sea-level fluctuations, antecedent topography and climatic changes are reflected in the long-term and short-term history of reefs.

Reef accretion and sea-level: keep-up, catch-up or give-up?

Skeletal growth rates of recent coral reefs may be higher than the time involved for sea-level fluctuations. Reefs and reef organisms, therefore, should theoretically have the potential to compensate for sea-level rises (KÜHLMANN, 1989), but in the earth's history they often did not, as shown by the 'paradox of drowned reefs and platforms' (SCHLAGER, 1981). Losses of carbonate sediment from the reef framework and the export of reef-derived material (HUBBARD et al., 1990) as well as reduction of reef growth by deterioration or particularly rapid sea-level rises connected with 'giving-up' of reef growth could be responsible for this discrepancy.

Drowning is the most spectacular factor in the demise of Paleozoic and Mesozoic reefs, e.g. during the mid-Cretaceous (MATTHEWS et al., 1974; SCHLAGER & PHILIP, 1990)but depending on differences in relative growth rates and relative sea-level rises various responses of reef development to a rising sea-level are possible (BUDDEMEIER & SMITH, 1988). These include the formation of retreating or backstepping reefs (if the rate of sea-level rise is not rapid relative to reef growth), continued upward accretion of reefs (if the rate of sea-level rise is approximately equal to the growth rate of the reef, 'keep-up reefs'; or 'catch-up reefs' with lag periods, (JAMES & MACINTYRE, 1985, NEUMANN & MACINTYRE 1985) and prograding reefs (if the rate of sea-level rise is less than the growth rate) responsible in the accretion of carbonate platforms.

Falling sea-levels will result in the exposure of shallow-water reefs (as exhibited by Pleistocene and Holocene reefs, e.g., TRACEY & LADD, 1974, BRASIER & DONAHUE, 1985) or in seawards prograding and downstepping of reefs as exemplified by the Messinian reefs of southeastern Spain (DABRIO et al., 1981).

Temperature control: Warm- and cold-water reefs

Recent reef-building hermatypic corals occur in 'warm waters', ranging between 16° and 36° with an optimum of 25°-29°. These temperature limits (as well as water depths) could certainly not be postulated for the wide spectrum of organisms responsible for the formation of all ancient skeletal reefs or reef mounds (NELSON, 1988). This is impressively illustrated by recent high-boreal to subarctic red algal reefs off northern Norway (FREIWALD et al., 1991) and by the sponge/bryozoan build-ups described from the Vesterisbanken of the Central Greenland Sea (HENRICH et al., 1992). Studies of ancient 'cold-water reefs' are just beginning and should be intensified.

Reef cements

Early diagenetic cementation is the major process responsible for the initiation of reef growth by consolidation of the pre-existing substrate and for the formation of a rigid reef structure with a defined geometry and in places steep slopes.

Of particular interest in understanding reef evolution are 'cement reefs', common during the Permian and Middle Triassic (FLÜGEL, 1989), and characterized by immense volumes of carbonate cements occurring together with 'algal' or 'microbial' crusts and by the rarity or absence of an organic framework.

Despite the large number of cement types in recent and ancient reefs (SCHROEDER & PURSER, 1986), the ultimate controls of cementation are still poorly understood.

2.2 'Reefs — just a problem of semantics ?'

'Reefs have been defined and redefined , classified and codified, inspected, dissected, investigated and reinvestigated....' (LONGMAN, 1981) Most authors have an idea of what reefs are and what they are not, the latter depending on a more biological or a more geological research approach. BRAITHWAITE (1973) has argued that the definition of reefs might sometimes be predominantly a problem of semantics.

To follow reef development over geological time, 'reefs' have to be defined in a very broad and rather simple way. In order to recognize changes during reef evolution, we have to compare 'reefs' of different ages. A restriction of the comparison to 'ecologic reefs' (DUNHAM, 1970)would mask the genetic relationships between frame-built and non-frame-built build-ups, e.g. reef mounds and mud mounds.

For ancient reefs it therefore seems reasonable to designate all those structures as 'reefs' which are characterized by at least the following features: Biological control during the formation of the structure (especially by sessile organisms), rigidity of the structure and a laterally restricted topographic relief.

Consequently, the data base presented in the reef bibliography includes references dealing with all kinds of 'reefs': Ecologic and stratigraphic reefs, skeletal (frame-built) reefs and non-skeletal reef mounds, mud mounds and microbial build-ups, bioconstructions, bioherms and biostromes, marine and non-marine 'reefs', large and very small 'reefs', 'reefs' with high- or low-diverse biota, with rapid or low growth rates, with a high or low amount of sediment and reef cement.

3 A DATA BASE OF PHANEROZOIC REEFS

We believe that an up-dated data base in the form of a reef bibliography is a matter of importance and urgency for encouraging a process-oriented approach to reef evolution research.

3.1 Previous bibliographies

No comprehensive bibliographies of ancient reefs have been published up to now.

More or less extended reference lists can be found in publications summarizing the knowledge of reef communities and reef ecology (WELLS, 1957a, 1957b; FAGERSTROM, 1987) development of reefs over time (HECKEL, 1974; LAPORTE, 1974; JAMES, 1979; TOOMEY, 1981; TALENT, 1988) reef diagenesis (SCHROEDER & PURSER, 1986) and reservoir rock properties (KUZNETSOV, 1978; HARRIS, 1983; ROEHL & CHOQUETTE, 1985).

3.2 Organization of the new data base

The bibliography consists of two parts.

The first part (Chapter 4.1 with sub-Chapters 4.1.1 to 4.1.11) is devoted to 'reefs over time', the second part (Chapter 4.2) to 'processes in reefs and reef models'. Part 1 is subdivided according to geological systems (distinguishing between the Mississippian and the Pennsylvanian).

This first part contains papers dealing with
— palecology, facies, sedimentology and the development of reefs
— the distribution of reefs (hence papers focused on regional geology have also been included in the bibliography)
— the timing of reef building and of reef crises.

Papers dealing with the following are rarely included or not at all:
— detailed and specialized paleontological data, e.g. systematic descriptions of reef-building and reef-dwelling organisms. Some important paleontological papers (monographs), however, have been cited in order to facilitate a first taxonomic assignment of reef biota.
— references concerning reef diagenesis and the importance of reef rocks as potential reservoirs

Part 2 (Chapter 4.2) contains references dealing with those biological and non-biological processes in recent reefs which might also have been relevant for ancient reefs:

Chapter 4.2.1 deals with general aspects of modern and ancient reefs, Chapter 4.2.2 with biological and ecological aspects and with environmental controls. Chapter 4.2.3 collates references on the calcification, diagenetic modifications and growth of reef-building organisms (including papers on algal symbiosis), and growth rates of reefs. Chapter 4.2.4 includes references describing the destruction of reefs by physical processes, e.g., hurricanes, and bioerosion. The last part, Chapter 4.2.5, contains papers related to the development of reef types over time, the evolution of reef communities and to general 'reef models' describing the major theoretical controls of reef growth.

The major number of references was collected using an Apple Macintosh IIsi and Bookends Mac (Version 2) software.

Citation

The citations of most of the references are as complete as possible including author, year of publication, title, journal, pages, plates, textfigures, tables and location of the paper. A few references are incomplete but have been nevertheless included because they often contain the only information available on reefs in remote areas.

3.3 Sources

References on ancient (and modern) reefs have been compiled by the authors for years. These references comprise books, symposia and papers published in journals but also information included only in short abstracts or guide books. Diploma theses and Ph.D. theses have been also considered if the results have not been extensively published.

3.4 Cui bono ?

When a very first draft of the 'reef bibliography' was distributed in the Paleontological Institute in Erlangen, an unknown colleague or student expressed his frustation by writing 'cui bono ?' on the first page.

The recognition of general trends in the overall processes influencing reef evolution requires comparative research.

Comparisons of ancient reefs of various ages were common up to the 70s. Later on, most authors seem to have capitulated because of the immense, diffuse and specialized

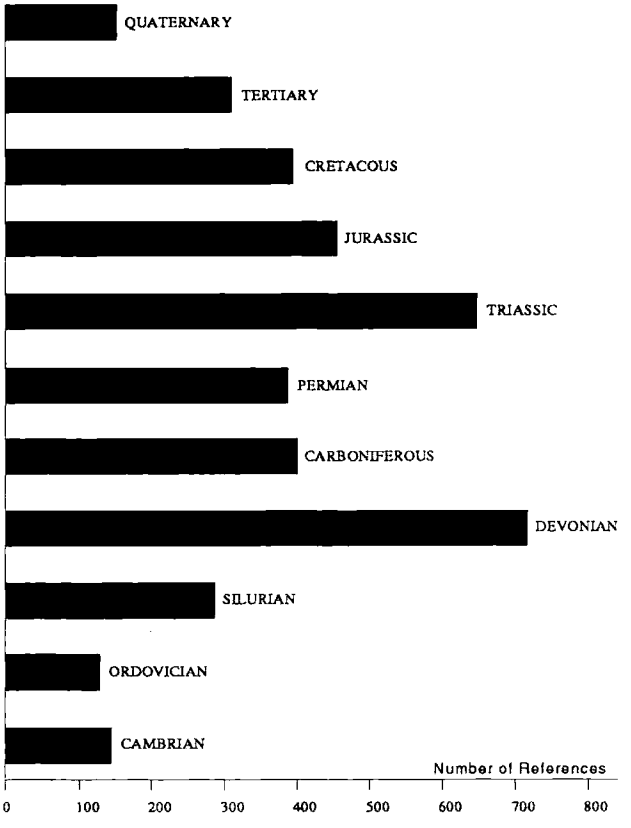


Fig. 1. Number of references dealing with Phanerozoic reefs. Most of the information available concerns Devonian and Triassic reefs, followed by Late Paleozoic and Cretaceous reefs.
Note: The Triassic file includes more paleontological references than the other files. Subtraction of paleontological references results in a number of about 600 publications for Triassic reefs.

literature. The increasing bulk of information on ancient and modern reefs makes an evaluation of the current state of art difficult, but there is no reason to persist in being frustrated and to retreat from comparative research:

The reef bibliography, consisting of more than 4800 references (not including recent reefs), provides a sufficient base for the search and retrieval of relevant information.

Perhaps surprising to some users of the bibliography, no farther-reaching data processing has been done. This would counteract the aim of a more comprehensive critical comparison of ancient reef data because computer-derived lists of references summarizing, e.g., only reefs of a particular Cretaceous time interval or only Cretaceous reefs in Europe, would easily lead the reader down a one-way road.

The bibliography, though comprehensive, is certainly not complete and probably biased with regard to the authors' own experience but we believe that about 80 % of the pertinent papers have been included.

Each data base is susceptible to becoming a victim of critical, sometimes censorious comments complaining of larger or smaller gaps in the documentation. We suggest the reef bibliography be assessed by looking at the information provided rather than by pointing out missing references.

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4 REEF BIBLIOGRAPHY

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English alphabetization has been used, i.e. German vowels ä, ö, ü are found at the end of the alphabet.

4.1 Reefs in time

Each section is introduced by short remarks concerning the state of the art followed by indications of important papers.

The distribution of reefs is shown on paleogeographical maps. For the sake of homogeneity the base maps published by SMITH, HURLEY & BRIDEN (1981) have been used despite the difficulties arising particularly from continent configurations during the Paleozoic (cf. SCOTESE & MCKERROW, 1990). In interpreting the distributional patterns of reefs in terms of speculations on paleoequatorial belts or paleoclimatic situations, one should consider the sometimes only very approximate location of the 'reefs' and the problem of time averaging.

Most of the information about ancient reefs available concerns Devonian and Triassic reefs followed by Jurassic reefs (Fig. 1). Carboniferous, Permian and Cretaceous reefs are represented by comparable numbers of references. Silurian and Tertiary reefs are represented by approximately the same numbers of references. Documentation of Cambrian, Ordovician and Pleistocene reefs is moderate in comparison to other Phanerozoic reefs.

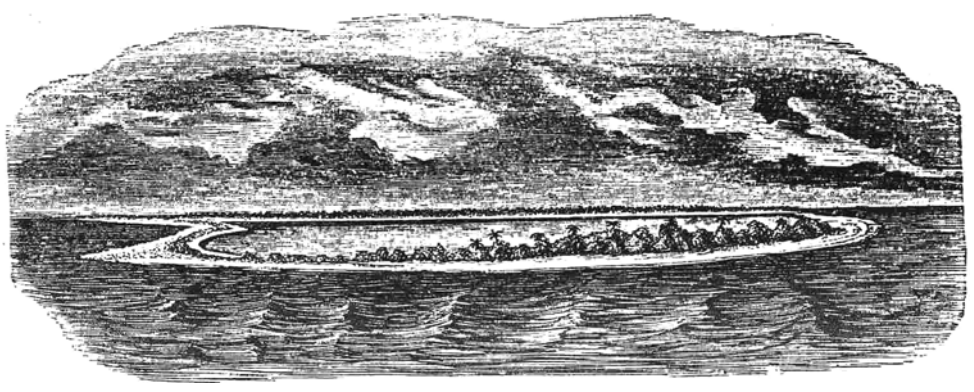

Fig. 2. View of a 'genuine' atoll (after DANA 1851).

4.1.1 Cambrian

Cambrian reefs are characterized by rather small reef mounds dominanted by the binder guild consisting of often poorly skeletonized algae and many microproblematica, as well as by archaeocyathids.

Distribution (Fig. 3): Nearly all Cambrian reefs have been found within a narrow belt between 30° S and 30° N of the Cambrian paleoequator. An exception is the location of reefs in Morocco.

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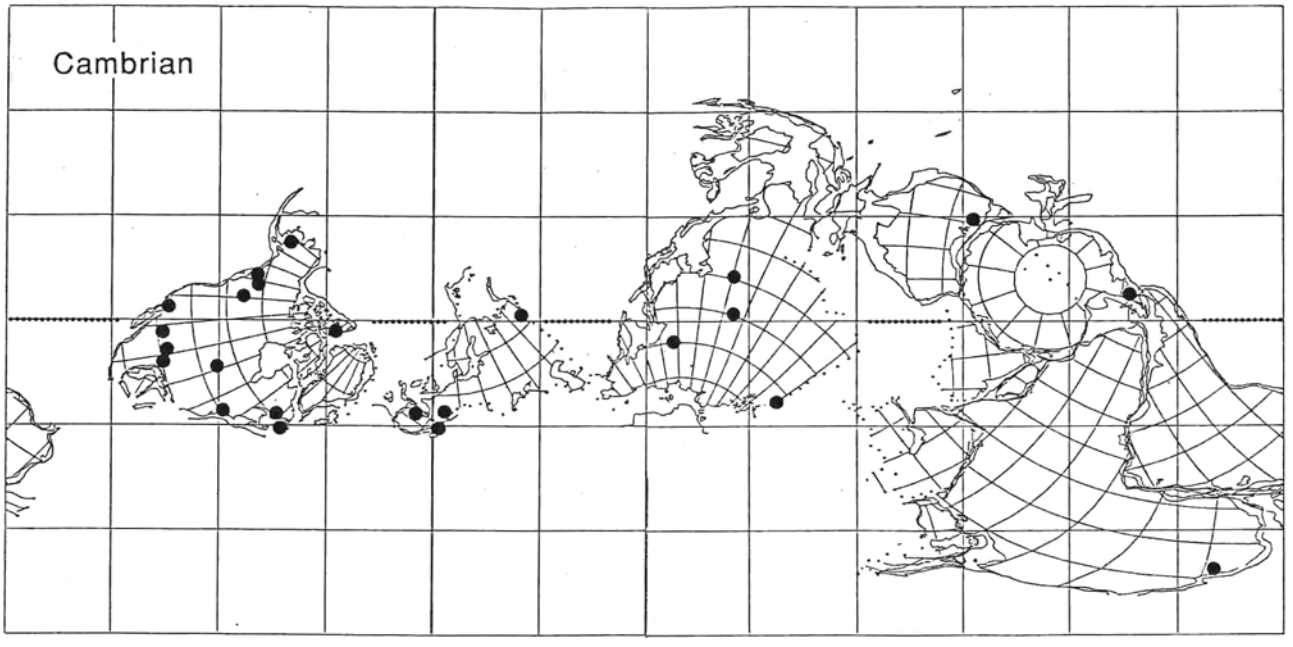

Fig. 3. Cambrian reef distribution. Base map: Middle Cambrian (SMITH et al., 1981).

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4.1.2 Ordovician

During the early Ordovician, reef communities were reorganized, algal diversity increased and lithistid demosponges became important reefbuilders. A profound change took place during the early Middle Ordovician, characterized by the displacement of the algae by a variety of better-skeletonized metazoa (bryozoans, tabulate corals, sponges) and by an increase in reef borers.

Distribution (Fig. 5): Most of the Ordovician reefs have been described from Northern America. Many reefs occur south of the paleoequator, but Fig. 5 should be contrasted with the results of WEBBY (1984).

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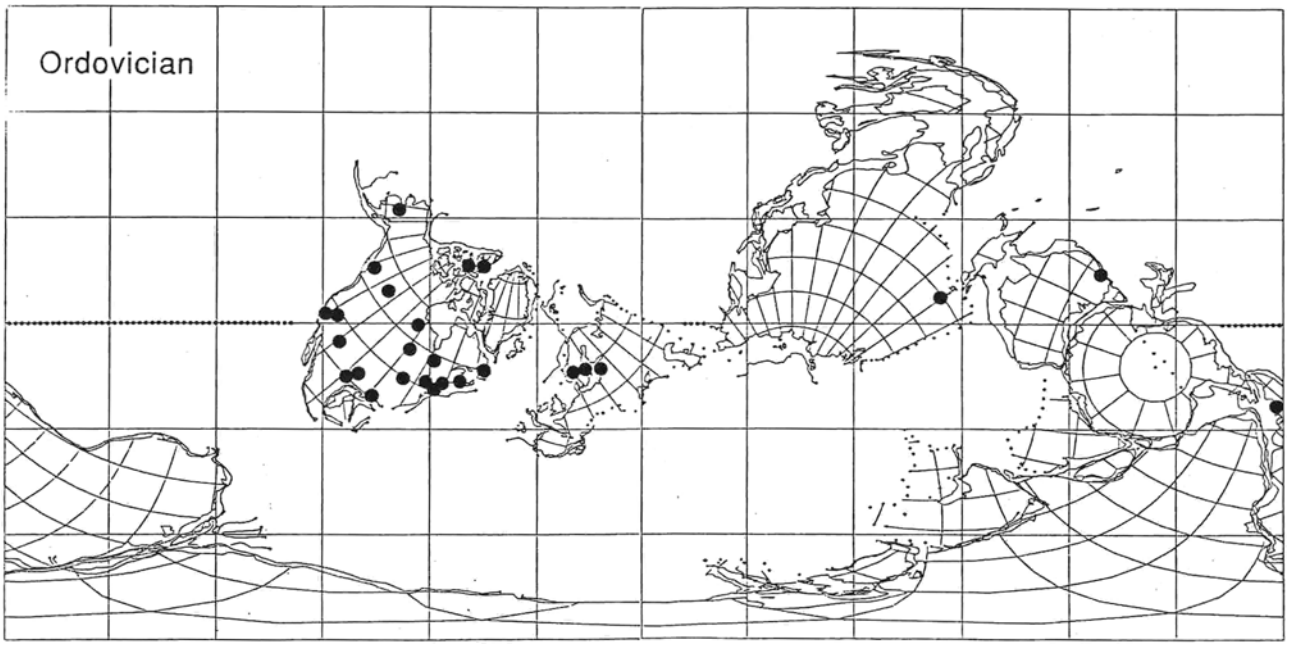

Fig. 5. Ordovician reef distribution. Base map: Ashgillian (SMITH et al., 1981).

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4.1.3 Silurian

Silurian reefs include a variety of reef types of different sizes composed predominantly of stromatoporoids as well as tabulate and rugose corals.

Distribution (Fig. 6): In comparison with the Ordovician the distributional pattern of Silurian reefs seems to be characterized by concentrations in Northern America (and Australia) near and south of the paleoequator and by occurrences in central and northern Asia.

Reviews: Bourque (1989), Copper & Brunton (1991), Riding (1981).

Important papers: Abbott (1976), Archer et al. (1980), Archer & Feldman (1986), Bourque (1987), Bourque & Gignac (1983), Cumings & Shrock (1928), Frykman (1984, 1989), Hadding (1950), Heckel & O'Brien (1975), Hurst (1980), Ingels (1963), Jux (1957), Kano (1990), Laufeld & Bassett (1981), Lowenstam (1950), Manten (1971), Narbonne & Dixon (1984), Pray (1976), Ruhrmann (1971), Rutten (1958), Scoffin (1971, 1972), Shaver & Sunderman (1984), Smosna & Warshauer (1983), Watts (1981), Wedekind & Tripp (1930).

Paleontological data: Brood (1976), Fagerstrom (1983), Kershaw (1981, 1984, 1990), Kershaw & Riding (1978), Mori (1968, 1970), Nestor (1966, 1990), Nicol (1962), Rigby & Dixon (1979), St.Jean (1979), Stel (1978).

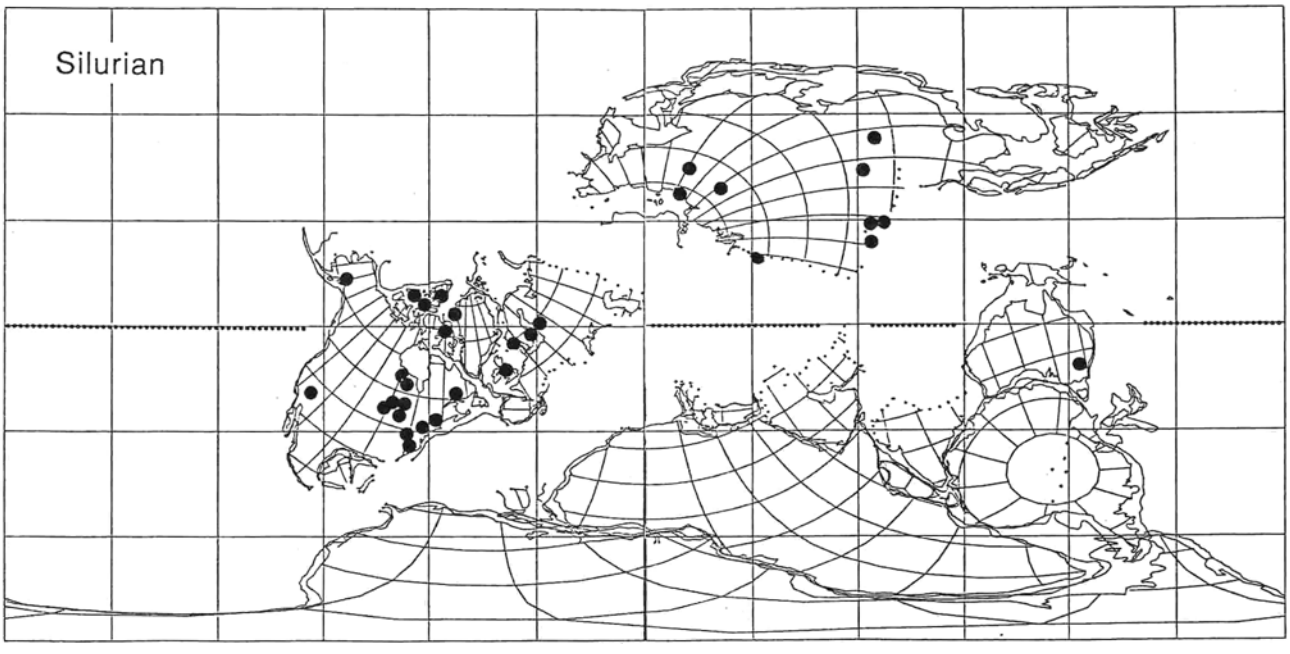

Fig. 6. Silurian reef distribution. Base map: Ludlowian (Smith et al., 1981).

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4.1.4 Devonian

The rareness of Lower Devonian reefs is in sharp contrast to the frequency of Middle and early Upper Devonian reefs which were common and widespread during these intervals. Stromatoporoids, tabulate and rugose corals are the most important reefbuilders and often highly diverse. Reef types are highly diversified, including immensely large reef complexes (e.g., Canning Basin, Western Australia; Frasnian reefs of Western Canada) but also small reef mounds and mud mounds

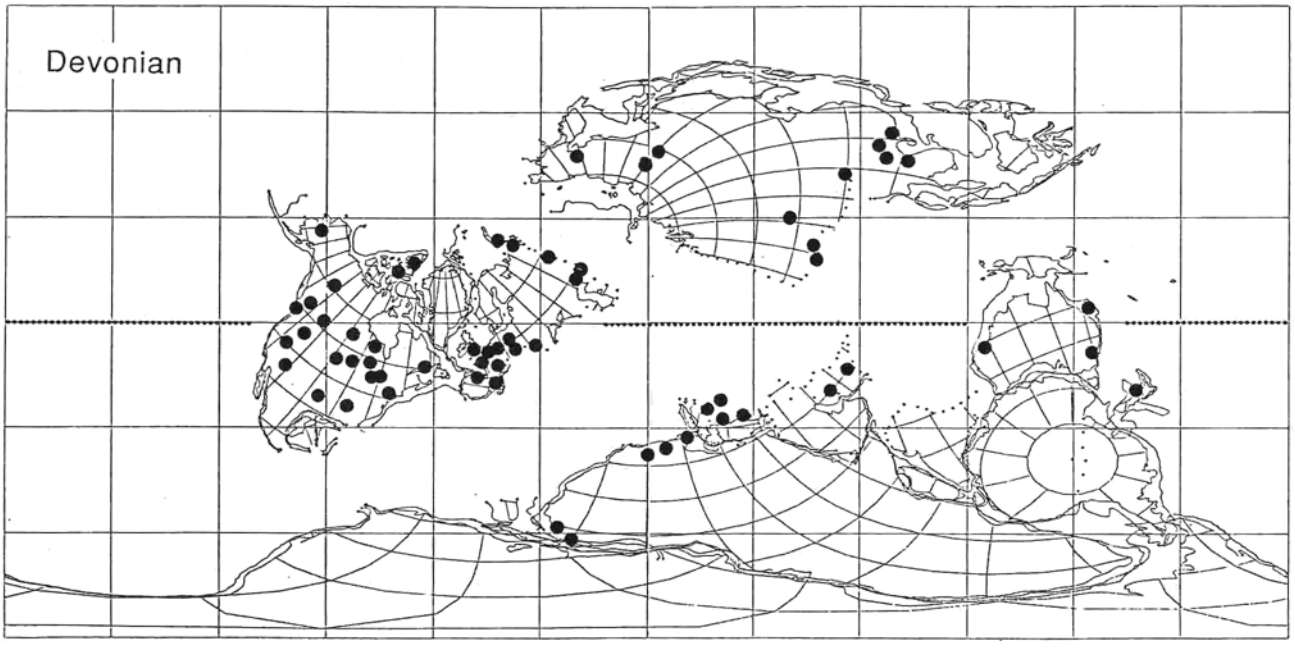

Fig. 7. Devonian reef distribution. Base map: Frasnian (SMITH et al., 1981).

(e.g., Frasnian of Belgium). A major extinction of reef biota and reefs took place during the Frasnian mass extinction (BUGGISCH, 1991). The fate of Famennian reefs is not well known.

Distribution (Fig. 7): Devonian reefs are widely distributed, exhibiting a broad paleolatitudinal pattern which is not consistent with other paleobiogeographical maps (e.g., WITZKE & HECKEL, 1988).

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Fig. 8. 'Flower-pot', last part of a coral island destroyed by the sea. Stewart Atolls (after F. v. HOCHSTETTER, 1866, k. u. k. Austrian-Hungarian Novara Expedition).

4.1.5 Carboniferous

Distribution: (Fig. 9): The map shows only a very rough distributional pattern, because occurrences of Mississippian and Pennsylvanian reefs are not separated and because the Namurian paleogeography has been used. The distribution of Mississippian ('Waulsortian') reefs fits well into a paleoequatorial pattern: Pennsylvanian reefs, however seem to have been also formed in higher latitudes.

Early Carboniferous (Mississippian)

Subsequent to the Frasnian extinction event, algae became the main reefbuilder during the Famennian and early Mississippian, contributing to the formation of mud mounds. 'Waulsortian' reef mounds, characterized by high amounts of bioclastic sediment and (microbially induced ?) lime mud were widespread in Europe and southwestern North America during the late Mississippian.

Reviews: BOLTON et al. (1982), DAVIES et al. (1988), WEST (1988).

Important papers: AHR (1989), BANCROFT et al. (1988)), BATHURST (1959, 1982), BRIDGES & CHAPMAN (1988), BROWN & DODD (1990), CUTCHEON (1988), DAVIES (1975), DELEPINE (1926), DIX & JAMES (1987), DUPONT (1969), GEORGE & AHR (1988), HAIKAWA & OTA (1978), KING (1986), KUZNETSOV (1969), LANE (1982), LANE & ORMISTON (1982), LEES (1964, 1982, 1988), LEES et al. (1985), LEES & HENNEBERT (1982), LEES & MILLER (1985), LEES, NOEL & BOUW (1977), MACQUOWN (1982), MCKINNEY et al. (1987), MEYERS et al. (1982), MILLER (1986), MILLER & GRAYSON (1982), PARKINSON (1967), PHILCOX (1967), PRAY (1961, 1969, 1982), PRAY et al. (1977), SCHWARZACHER (1969), VAN LAER & MONTY (1984), WALKDEN et al. (1987), WALLACE (1987), WEBB (1987).

Paleontological data: BROADHURST & SIMPSON (1973), HUDSON et al. (1966), MONTY (1964), MORGAN (1980), TAYLOR (1972), WOLFENDEN (1958), WHRIGHT & WRIGHT (1981).

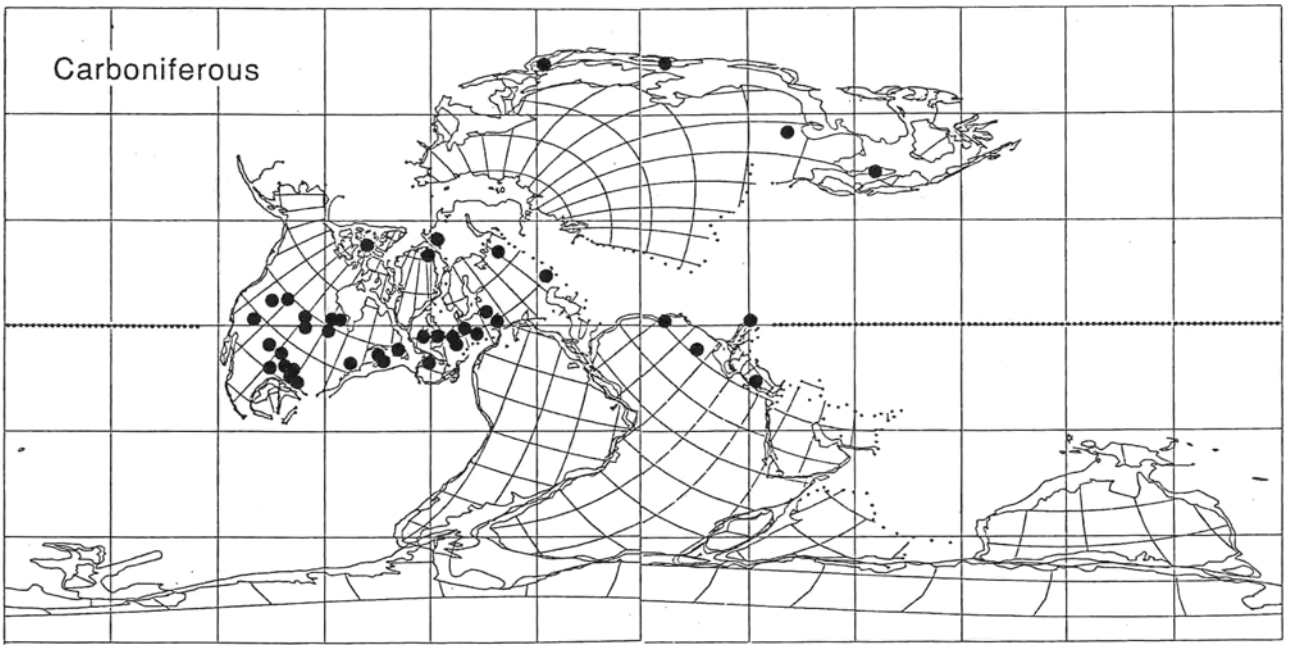

Fig. 9. Carboniferous reef distribution. Base map: Namurian, early Pennsylvanian (SMITH et al., 1981). Note: Mississippian and Pennsylvanian reef configuration differs significantly. This is not shown in this map, which combines the distribution of Lower and Upper Carboniferous reefs.

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Late Carboniferous (Pennsylvanian)

Upper Carboniferous reefs vary strongly in their dominating biotic elements. Early Upper Carboniferous reefs are characterized by a framework composed of chaetetids, late Pennsylvanian (and Lower Permian) reefs, banks and mounds are dominated by phylloid algae, which have probably acted as bafflers, binders or as a source for the accumulation of bioclastic sediment build-ups. Other reef mounds are formed by *Palaeoaplysina*, an enigmatic fossil, or by calcareous algae (*Donezella*).

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4.1.6 Permian

Lower Permian reefs can be compared with late Upper Carboniferous reefs with regard to biotic composition and reef geometry. Often large-dimensioned Middle and Upper Permian reefs are developed as calcisponge-dominated reefs and 'cement reefs' characterized by high amounts of synsedimentary carbonate cements and 'algal crusts' as well as *Tubiphytes*. Other reefs have been formed by stromatolites and by bryozoans. Major changes in the evolution of Permian reefs occurred near the Lower/Middle Permian boundary. Uppermost Permian reefs are highly diverse.

Distribution (Fig. 10): The Permian base map used in Fig. 10 does not clearly exhibit the Paleotethyan region and the transition from the Paleotethys to the Tethys during the Permian. In comparison to the Carboniferous, most reef locations would be north of the paleoequator, which is probably wrong.

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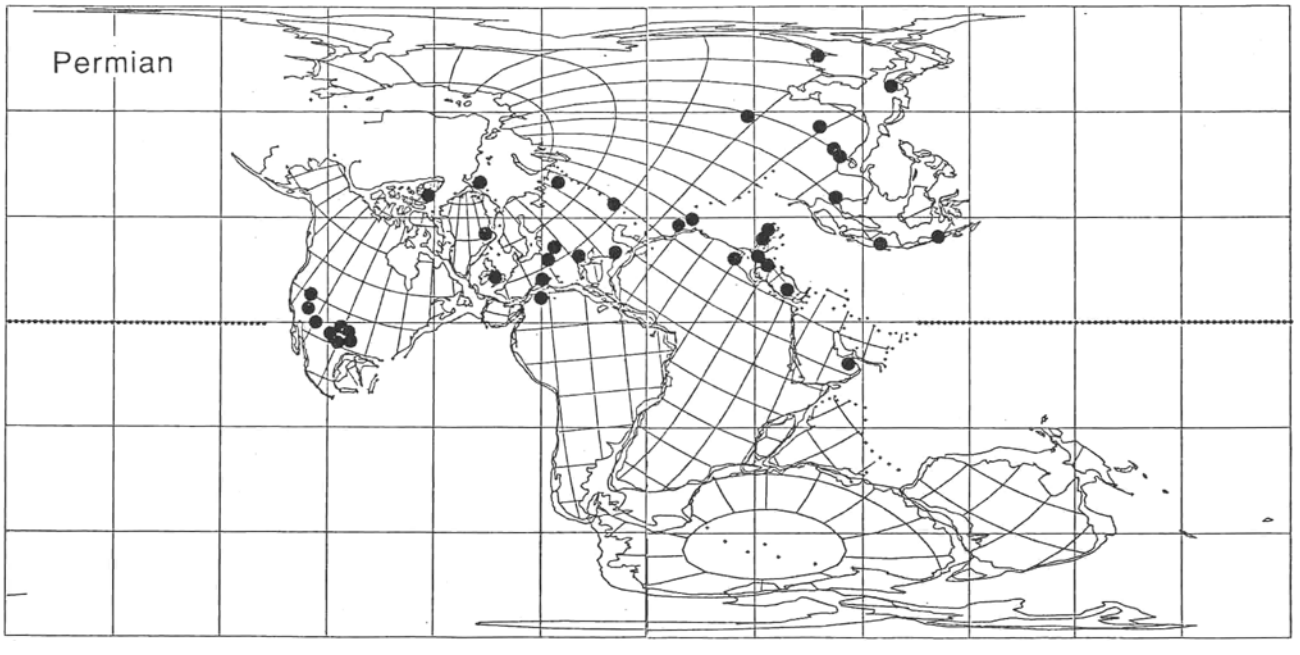

Fig. 10. Permian reef distribution. Base map: Tatarian, Upper Permian (SMITH et al., 1981). Note: The configuration of the continents differs strongly from more recent reconstructions (cf. SCOTESE et al., 1990).

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4.1.7 Triassic

No reefs are known from the Lower Triassic. The first reefs subsequent to the Permian/Triassic crisis are known from the Anisian. Middle Triassic reefs and Carnian reefs are characterized by a specific association of 'calcisponges', algae as well as various microproblematica belonging to cryptic communities and acting as binders and dwellers. There was a major turnover in the composition of reef biota and reef geometry during the early Norian. Norian reefs form large and widespread complexes, Rhaetian reefs also occur as platform and intraplatform reefs. The reefs became extinct near the end of the Triassic.

Distribution (Fig. 11): Most Triassic reefs are concentrated at the western and northern border of the Tethys in a paleolatitude near 30° N. Reefs described from the Australasian region, Japan and the Wladiwostok area differ distinctly from this pattern, perhaps because they are located within 'terranes' similar to the 'reefs' known from western North America and from southern Peru and northern Chile.

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Important papers: ABATE et al. (1977), BECHSTÄDT & BRANDNER (1970), BHARGAVA & BASSI (1985), BIDDLE (1980), BOSELLINI & ROSSI (1974), BRANDNER et al. (1991), BRANDNER & RESCH (1981), CAR et al. (1981), DISTEFANO et al. (1990), DRONOV et al. (1982), DULLO & LEIN (1982), FABRICIUS (1966), FAN (1980), FLÜGEL & FLÜGEL-KAHLER (1963), FOIS & GAETANI (1980, 1984), GAETANI et al. (1981), GOLDHAMMER & HARRIS (1989), HALLAM & GOODFELLOW (1990), HENRICH (1982, 1983), HENRICH & ZANKL (1986), KOTLJAR et al. (1987), KRISTAN-TOLLMANN (1986, 1988, 1990, 1991), KRISTAN-TOLLMANN & TOLLMANN (1982, 1983), KUSS (1983), LEIN (1987), LEONARDI (1961, 1979), LOBITZER (1973), MARTIN & BRAGA (1987), MATZNER (1986), MICHALIK (1982), MIRSAL & ZANKL (1979), NICOL (1987), OHLEN (1959), OTT (1967a, 1967b), PFEIFFER (1988), PILLER (1981), PRINZ (1991), RAMOVS & TURNSEK (1984), REID (1985, 187, 1988), REID & GINSBURG (1986), REIJMER & EVERAARS (1991), RIEDEL (1988), RIEDEL & SENOWBARI-DARYAN (1991), RUSSO et al. (1991), RÖHL et al. (1991), SADATI (1981), SCHLAGER & SCHÖLLNBERGER (1973), SCHNEIDER (1964), SCHOLZ (1972), SCHOTT (1983, 1984), SCHÄFER (1979, 1984), SCHÄFER & SENOWBARI-DARYAN (1978, 1981, 1982), SENOWBARI-DARYAN (1980, 1981, 1990, 1991), SENOWBARI-DARYAN & SCHÄFER (1979), SENOWBARI-DARYAN et al. (1982), SENOWBARI-DARYAN & STANLEY (1988), SIEBER (1937), STANLEY (1979, 1980, 1981, 1982, 1988), STANLEY & SENOWBARI-DARYAN (1986), STANTON & FLÜGEL (1987, 1989), TURNSEK & BUSER (1989), TURNSEK et al. (1982, 1984, 1987), TURNSEK & RAMOVS (1987), VORTISCH (1926, 1927), WENDT (1980, 1982, 1986), WENDT et al. (1989), WU (1989), WURM (1982), ZANKL (1969, 1971), ZAPFE (1959, 1967), ZORN (1972).

Paleontological data: The biota and paleoecology of Triassic reefs have been studied in much greater detail than those

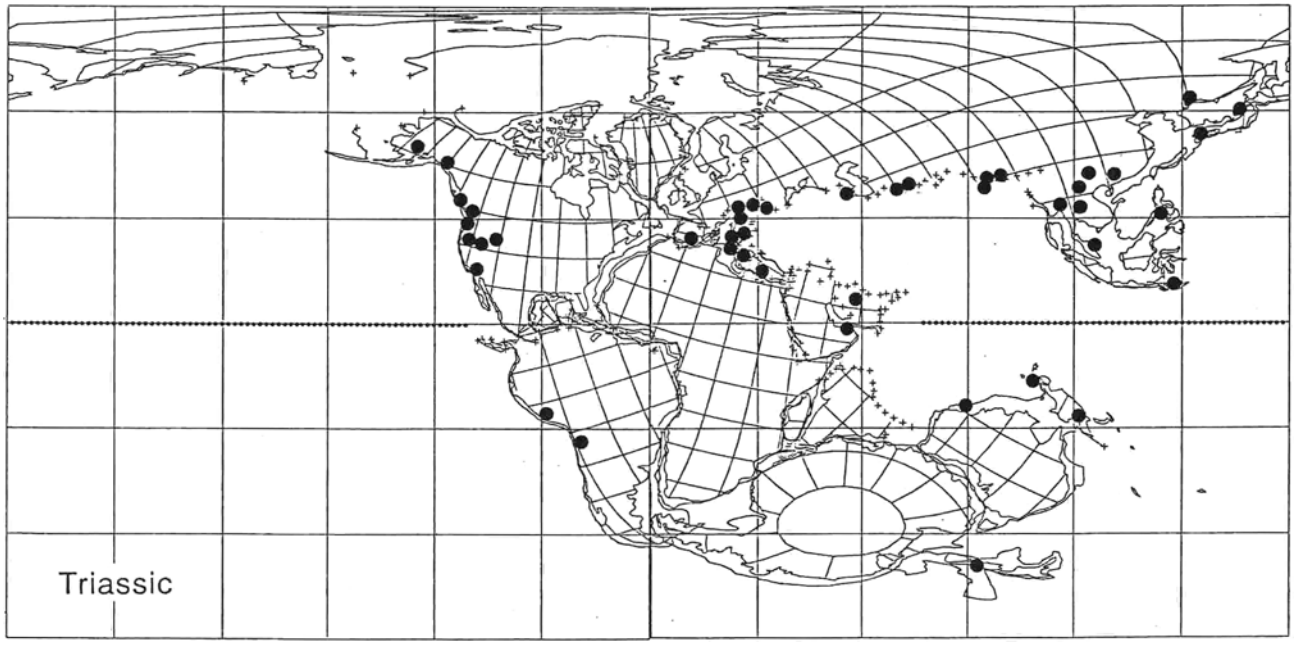

Fig. 11. Triassic reef distribution. Base map: Rhaetian, Upper Triassic (SMITH et al., 1981).

of reefs from other time intervals. Therefore, most of the paleontologically oriented papers dealing with Triassic reefs have been included in the bibliography. Calcareous algae have been predominantly studied by FLÜGEL and SCHÄFER & SENOWBARI-DARYAN; foraminifera by BRÖNNIMANN et al., GAZDZICKI, HOHENEGGER & PILLER, KRISTAN-TOLLMANN, PILLER, SCHÄFER, SENOWBARI-DARYAN and ZANINETTI; 'calcisponges' and 'hydrozoans' by BOIKO, DIECI et al., FLÜGEL & SY, JABLONSKY, KOVACS, OTT, REITNER, SENOWBARI-DARYAN and WU; corals by CUIF, MELNIKOVA, MONTANARO-GALLITELLI, RONIEWICZ, STANLEY and TURNSEK; bryozoans by SCHÄFER & FOIS; and microproblematica by BORZA, FLÜGEL, PANTIC and SENOWBARI-DARYAN.

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4.1.8 Jurassic

Following a reduction during the Lower Jurassic in abundance, geographic distribution and size of the reefs, a turnover of the biotic composition took place during the Middle Jurassic, changing the coral/'calcisponge' reefs of the Upper Triassic and Liassic to demosponge/coral-dominated reefs, widespread during the Upper Jurassic. Upper Jurassic 'sponge/algal reefs' are unique in reef history because of the importance of significant microbial contribution and the siliceous sponge-dominated guild structures. A turnover to coral-dominated reefs seems to have taken place during the late Upper Jurassic, continuing in the Lower Cretaceous.

Distribution (Fig. 12): Jurassic reefs seem to have been concentrated near 30° N, especially in Europe and at the eastern margin of northern America, but there are several deviations from this pattern which might be explained by 'terrane' situations.

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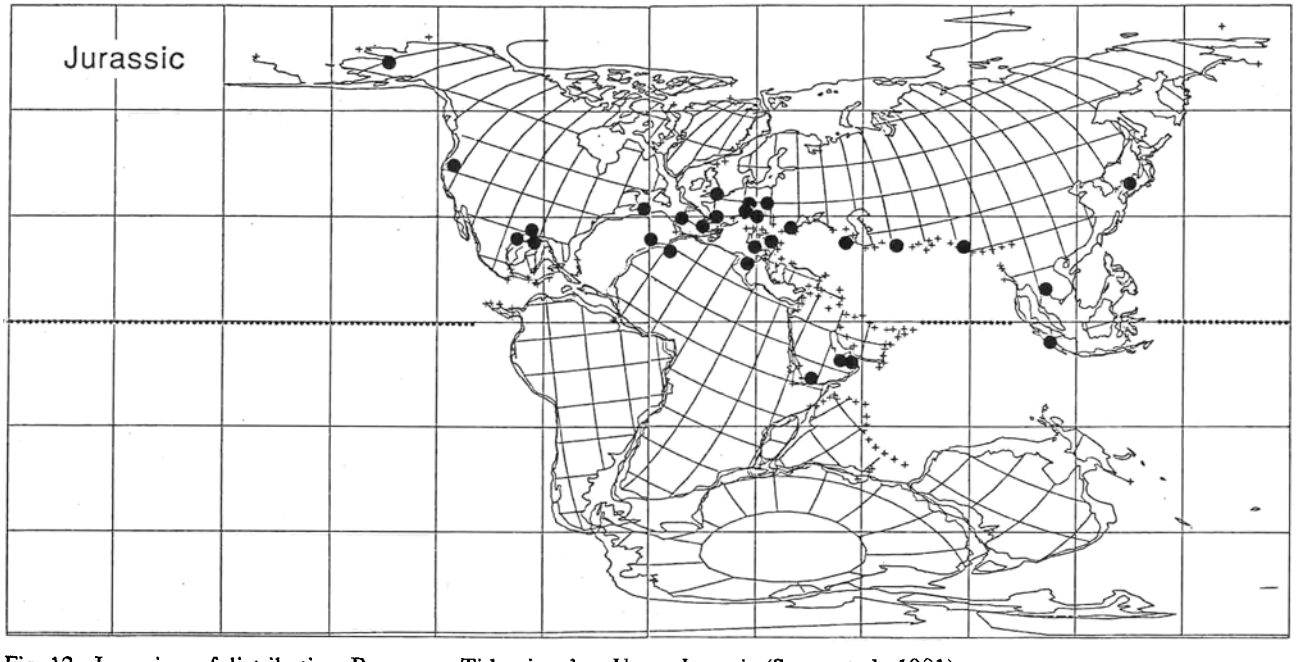

Fig. 12. Jurassic reef distribution. Base map: Tithonian, late Upper Jurassic (SMITH et al., 1981).

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4.1.9 Cretaceous

Cretaceous reef-building guilds were dominated during the early Cretaceous by scleractinian corals and algae, sometimes also by stromatoporoids and chaetetids, and during the latest Early and Late Cretaceous by rudistid bivalves. Encrusting and binding organisms were of specific importance. Compared with pre-Cretaceous and Cenozoic reefs, wave/current resistance and rigidity is poorly developed in many Cretaceous reefs, the original topographic relief was low resulting in 'banks' and 'biostromes' rather than in bioherms or reefs. The effect of the global Maastrichtian extinction to reef communities is not clearly understood. Most rudists were probably not extinct at the Maastrichtian/Paleocene boundary but rather two million years before. The major algal groups involved in reefbuilding survived the extinction.

Distribution (Fig. 13): Cretaceous reefs were widespread in the tropical and subtropical Tethys. Paleolatitudes with reefs were much broader than during the Jurassic or Triassic. Reefs were common at the margins of the Gulf of Mexico and in the Carribean region as well as around the Mediterranean region and continuing through the Middle East.

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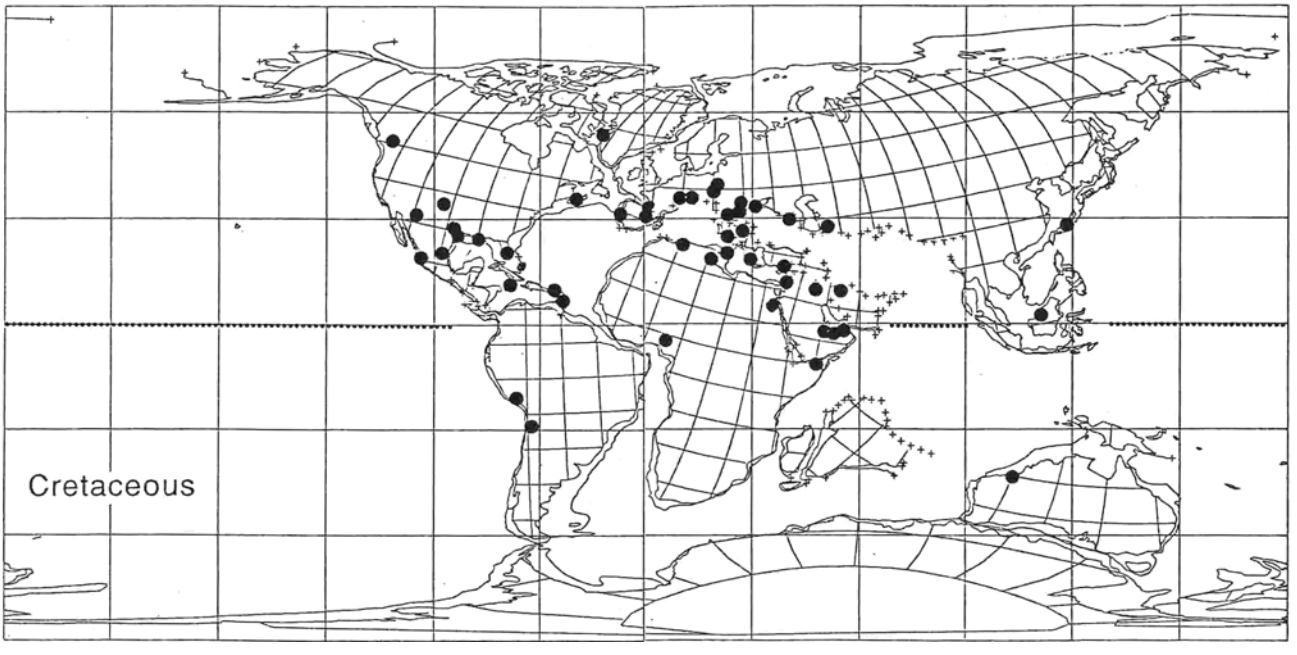

Fig. 13. Cretaceous reef distribution. Base map: Lower Cenomanian, Middle Cretaceous (SMITH et al., 1981).

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4.1.10 Tertiary

Paleocene and early Eocene reefs are rare. Reef abundance, geographic distribution and coral diversity increased during the Middle to Late Eocene; many modern reef-building coral genera appeared during that time interval. The Oligocene was marked by a decrease in taxonomic coral diversity but an abundance of coral reefs. Paleogene red algae exhibit a distinctly modern aspect. During the Miocene the differentiation between the Indo-Pacific reef province and the Atlantic reef province took place.

Aphotic coral reefs are known from the lowermost Paleocene as well as from the Miocene and Pliocene.

Distribution (Fig. 14): Most Tertiary reefs are concentrated in a rather narrow belt north of the paleoequator.

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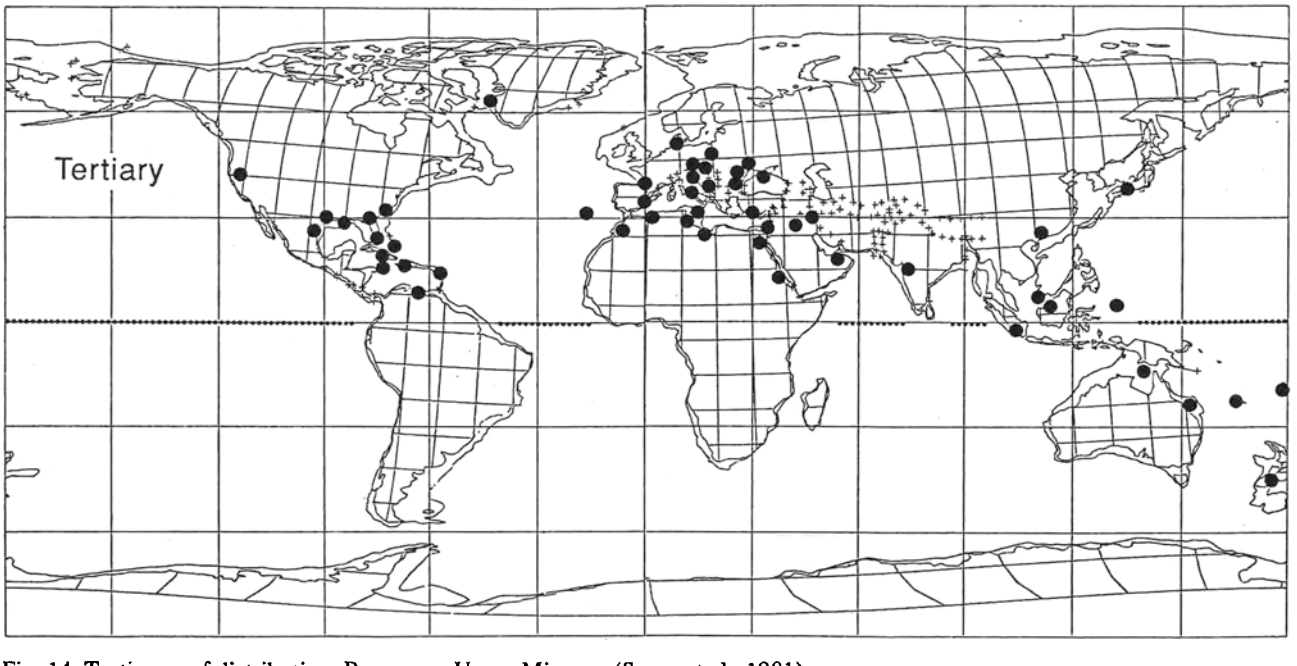

Fig. 14. Tertiary reef distribution. Base map: Upper Miocene (SMITH et al., 1981).

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4.1.11 Pleistocene

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4.2.3 Reef growth, calcification, algal symbiosis, carbonate production

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