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# EXTINCTION OF RUGOSA AND TABULATA NEAR THE PERMIAN/TRIASSIC BOUNDARY

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The Permian stage of evolution within Rugosa and Tabulata took place in two distinct realms, isolated by the Palaeo-Pacific Ocean and the Pangea: the Palaeo-Tethys Realm and the Cordillera-Arctic-Uralian Realm. The corals discussed disappeared from the first Realm in the upper part of the Changxingian *Palaeofusulina sinensis* Subzone and from the second one in lower Djulfian. The fairly long time span between these events excluded acting of any rapid and common factor. The combined effect of global factors such as lowering of sea level and warming of climate and local factors such as tectonics, currents, absence of carbonate banks, etc. led to the successive disappearance of corals from individual areas of realms. The Chinese microcontinent was the last area colonized by corals.

Key words: Rugosa, Tabulata, Permian, extinction.

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## INTRODUCTION

The inadequate knowledge of some groups of Permian Coelenterata, such as Conulata and Hydrozoa, resulted in consideration of only Rugosa and Tabulata in the discussion that follows. The analysis is descriptive rather than statistical, because no objective and generally accepted taxonomic model exists within the taxa. Thus, any statistical approach is handicapped by subjectivity. Nevertheless some quantitative graphs of frequency have been introduced as helpful in understanding the description. The following restrictions of these graphs have to be taken into account, however: 1. Some, perhaps quite a few of the genera and species introduced during the last ten or so years, especially in China may well be synonyms. Thus, the differences in richness between two realms may not be so large as illustrated. 2. The large reduction in number of taxa in the Kungur-Kazan equivalents of the Cordillera-Arctic-Uralian

Realm is true mainly for the Uralian and Arctic parts of the Realm. Rich rugose and tabulate coral faunas which flourished during the Leonardian — Guadelupian time in the Glass Mts, the Guadelupe Mts, and in some adjacent areas, are currently being examined and have not been considered here. 3. The correlation of individual Permian stages and biozones remains controversial. The graphs introduced herein may thus vary slightly when different variants of the correlation are applied. This concerns first of all the time span of the *Pseudofusulina* to *Neoschwagerina* biozones in the Palaeo-Tethys Realm. Different stratigraphic interpretations may change the frequency differences between individual stages, but not the general re-interpretation of graphs.

To save space the purely taxonomic papers, which are the main source for the quantitative information, are only rarely recorded in the references, and the number of other references cited is restricted to the minimum.

I have not selected material by eliminating synonyms from the number of taxa mentioned in graphs, except for the most obvious ones.

All taxa occurring in a given stage or biozone are considered in graphs. Thus, long-ranging taxa may have been cited eight times. Numbers of taxa summarized in figs. 1—3 are thus much larger than the actual number of Permian taxa of rugose and tabulate corals, which in turn has been slightly reduced by putting some units in synonymy.

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## THE ROLE OF PANGEA DURING THE LAST PHASE OF RUGOSE AND TABULATE CORAL EVOLUTION

Collision of the continental cratons at the beginning of the Permian resulted in formation of a single, longitudinally disposed landmass, surrounded by a single super Ocean, the Palaeo-Pacific. This geography was the most important factor causing the parallel and independent evolution of Tabulata and especially of Rugosa along East and West margins of the Ocean.

Stevens (1984) discussed those two geographical barriers, and the role of the climate, especially during the Lower Permian. Even a substantial warming well before the end of Permian (Dickins 1984) did not result in opening of the polar migration routes between the two faunal realms.

Fedorowski (1986) strongly suggested a total segregation in the Lower Permian of the Cordillera-Arctic-Uralian Realm and the Palaeo-Tethys Realm of coral faunas. Stevens (1984) adapted different position. He accepted an independent status for the Gandian Province of Yancey (1975), but indicated the possibility of a connection between that Province and the Palaeo-Tethys Ocean at least two times: in the Asselian and Guadelupian. Spain and Southern France have been suggested as connecting areas. The occurrence of the rugose coral genera in the Asselian that are common for SW Texas and China is true (Fedorowski 1987) but only *Paraduplophyllum* appeared as early as *Uddenites*-bearing Member of Gaptank Formation. Also, there are no data known to me proving connection of the areas discussed through the south-eastern United States or northern Mexico towards the east. However, the occurrence of algae--bearing, marine intercalations have been documented in the lowermost Permian of the Cantabrian Mountains (C. Martinez Diaz (ed.) 1983). The possibility of the temporary marine connection up to that period should not be excluded. Also, Zonenshain *et al.* (1985) suggested the possibility of a connection of the eastern Palaeo-Pacific with the Palaeo-Tethys through the Uralian geosyncline up to the end of the Carboniferous. This is not generally accepted, however. The reconstruction by Dickins (1984, figs. 5, 6) of free communication between the western Palaeo-Tethys and the eastern Palaeo-Pacific both through the Uralian geosyncline and through the North Africa and southern Europe, is not supported by facts and is rejected.

The true waagenophyllids described recently by Nelson and Nelson (1985) from the accreted terranes of British Columbia (Canada) and by Stevens *et al.* (1987) from those of California (USA) confirm some connection between both margins of the Palaeo-Pacific. The problem is, however, how far had these terranes drifted before accretion occurred. Stevens *et al.* (1987) suggested that the distance between the McCloud terrane and the autochthonous Cordillera coral fauna had originally not been far. If this thesis is correct there must have been a chain of islands or carbonate banks through the whole Palaeo-Pacific to allow intermediate stops and metamorphosis of larvae. Given such a case, which is not proven, the distance between western and eastern margins of Palaeo-Pacific would have been much greater than that of the Recent Pacific, which itself is large enough for the appearance of distinct faunistic provinces within it. Moreover, the suspected palaeo-equatorial current would had gone rather to the West, thus making an additional barrier for the Palaeo-Tethys corals to emigrate eastwards. Despite the facts and hypotheses mentioned, the distinction and almost completely independent evolution of coral faunas along the western and eastern margins of the Palaeo-Pacific, the Palaeo-Tethys included, is well documented through the analysis of taxa occurring in both these areas (figs. 1—3). The distinction between genera occurring in individual Realms and restricted to the Permian is overwhelming. Only five of them can be considered as probably common. Those that form massive colonies are totally different in both Realms. The presence of the long-ranging genera common to both areas is explain-

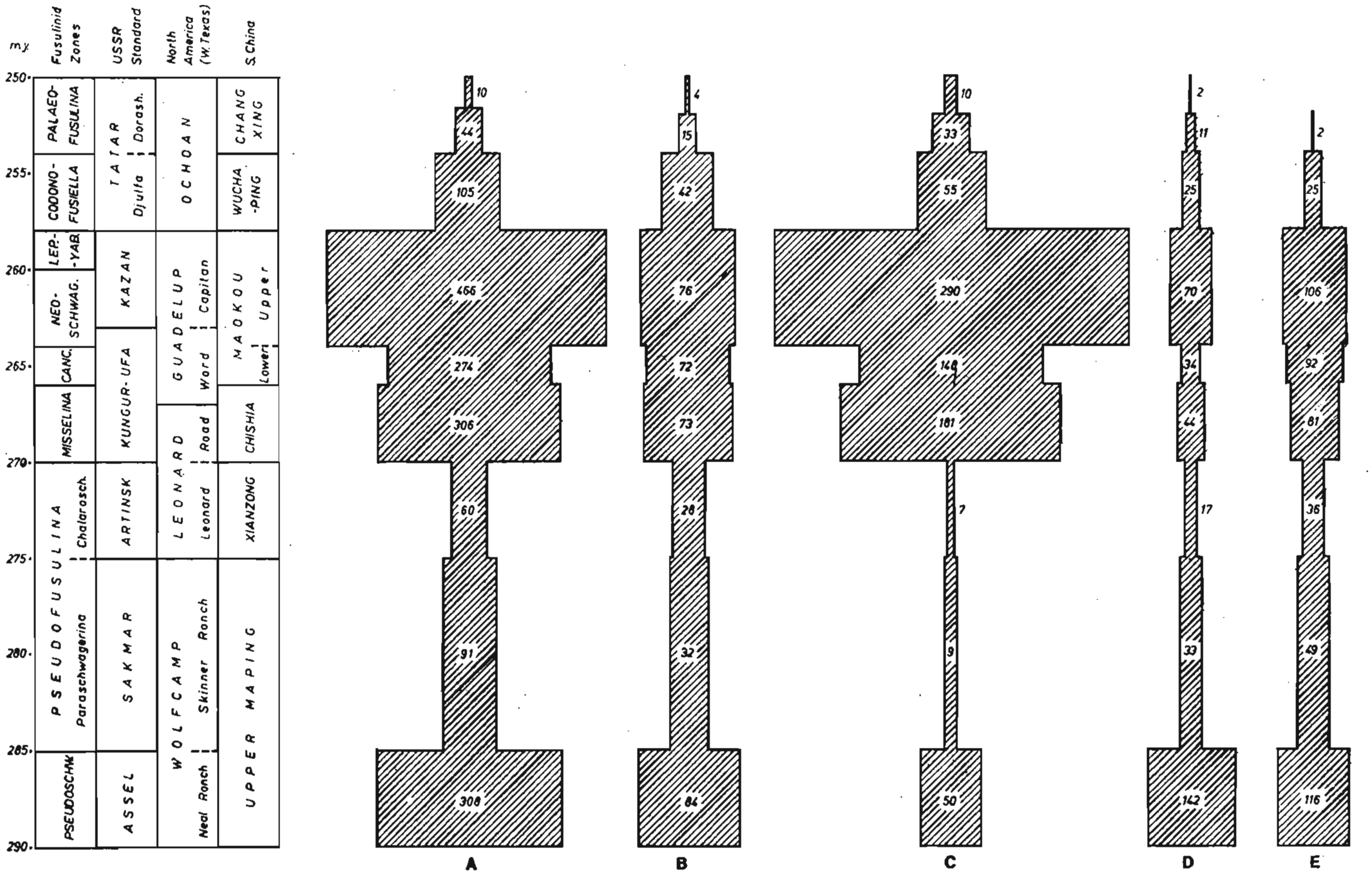

Fig. 1. Distribution pattern of Permian rugose corals. Tethys Realm. *A* distribution of species described from each stage or biozone. *B* distribution of genera identified from each stage or biozone. *C* "*Cyathaxonia* fauna". *D* "*Caninia-Clisiophyllum* fauna"+fasciculate colonies. *E* all massive colonial corals. Numbers indicate the number of taxa identified within each stage or biozone.

ed by the common roots and the independent, parallel evolution. The very few species considered common to both areas should be carefuly re--studied before accepting their real relationships.

## STRATIGRAPHIC SETTING

The stratigraphy of the Permian System, especially its lower and upper boundary included, remains a subject for discussion. For the purpose of this paper, the most commonly mentioned proposals are accepted and illustrated at the left margin of figures 1—3. These are: 1. The entry of the fusulinid genus *Pseudoschwagerina* and/or the beginning of the Asselian Stage is taken to mark the base of the System. 2. Its top is taken at the base of the conformably underlying ammonoid *Otoceras* Biozone. The following regions are most important stratigraphically: a) South China; b) Armenia (near Dorasham village); c) Central Iran (near Abadeh city). The concordant position of the Permian and Triassic strata does not exclude a possibility of hiatuses in the uppermost Permian, especially in the last two areas, where the topmost part of the *Palaeofusulina sinensis* Biozone is either missing or does not contain corals. 3. Stages and/or biozones accepted herein and their mutual relations are as proposed by the following and several unlisted authors: Furnish (1973), Stepanov (1973), Waterhouse (1976), Iranian-Japanese Research Group (1981), Sheng Jinzhang *et al.* (1984), Zhang Zuqui (1984), Lin Jiaxiang (1987), and the tables of J. M. Dickins and the Japanese Working Group ("Permophiles", 12, 1987). A more comprehensive stratigraphic discussion is omitted from this paper. It is only necessary to state that I consider the topmost beds of Changxingian in South China younger than the topmost part of the section in Armenia, and perhaps in Iran as well. In the latter case the non-coralliferous topmost part of the section may be equivalent to beds underlying the "beds with mixed fauna" in China.

## GENERAL REMARKS

Extinction of a taxon can be analysed in two main ways: 1) disappearance of representatives from a given area; in this case emigration of at least some individuals can be predicted, unless a total isolation of the area has been proven, 2) total extinction of a taxon. It seems possible that the total extinction of sessile organisms can well result from a series of a local or regional disappearances, listed as point 1. The second model of extiction may be especially common among the taxa that are either ecologically constant restricted in their response to the extrinsic factors, or depend for their migration and widespread geographical occurrence on

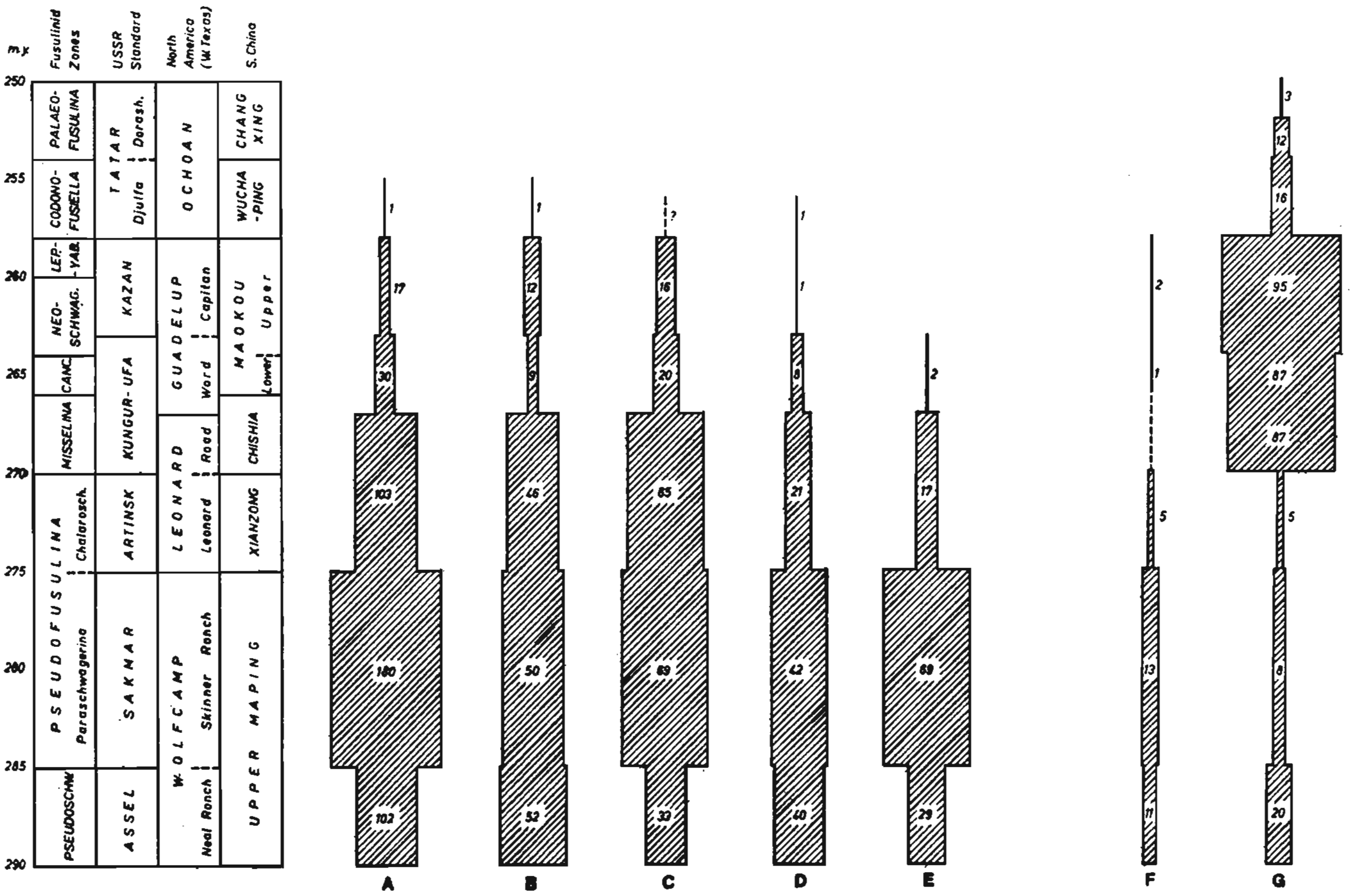

Fig. 2. Distribution pattern of Permian corals. *A—E* rugose corals of the Cordillera-Arctic-Uralian Realm. Sequence as explained above. *F—G* tabulate coral genera identified from each stage or biozene. *F* Cordillera-Arctic-Uralian Realm, *G* Tethys Realm.

a passive or weakly swimming, short living, planctic larvae that require shallow waters for their metamorphosis. Even comparatively minor ecological and geographical barriers may in such instances prevent any migration of a taxon, resulting in the division of the area of its occurrence into small, isolated regions. This problem has been to some extent discussed by Boecklen and Simberloff (1986). In the case of corals cold or strong currents, large areas of open and deep waters may be listed among such factors. The disappearance of a taxon from the isolated area, caused by a purely local factor, may sometimes appear permanent in the case of re-establishment of conditions suitable for corals. The re-colonization of such area may easily be prevented by one of the simple barriers mentioned. Several possibilities of that process have been discussed by Boecklen and Simberloff (1986), Jablonsky (1986) and Valentin (1986). A series of such local disappearances or extinctions, which can be explained as links dropping out of a chain, may eventually lead to the total extinction of a taxon, although conditions in many areas remain ecologically suitable for its development. The stage of evolution of the Permian rugose and tabulate corals illustrates this thesis well. The duplication of evolution that had begun with the formation of Pangea and Palaeo-Pacific Ocean was followed in both regions by further partition of the coral faunas into smaller, more or less isolated areas that could easily have been, and really were, eliminated by the combination of the local and global factors.

Permian was not the first time of strong impoverishment in the history of the Rugosa and Tabulata. Both had been close to total extinction at least twice: in the latest Famennian and in the Carboniferous *Homoceras* times. The isolation and poverty of coral faunas of these times did not lead to extinction and when the Tournaisian and Upper Carboniferous transgressions spread, the corals flourished again. This, however, was not the case at the end of the Permian.

Climate as an independent factor in the development or decline of faunas has been rejected by many authors (for detailed analysis see Schopf 1974 to 1984), and has been shown to have no effect on the extinction of large taxonomic units. The influence of climate on the migration of the fauna and flora is, however, unquestionable and it may cause local impoverishment or improvement of a fauna. The first reaction of a taxon to a climatic change is migration and not morphological or evolutionary change. Only a lack of migration routes and restriction of settlement areas made changes of climate a factor. The slow nature of climatic change (Schopf, *l.c.*), would allow taxon to adapt through evolutionary change but only to certain limits of tolerance. Any further extrinsic stress must lead either to extinction or to the appearance of genetic and morphological differences so large that evolution gives rise to a new taxon. In conclusion, climate is here considered to be an important additional factor in changes of faunas, but only in isolated and territorially restricted areas. Jablonsky (1986) indicated the lack of direct relationships between mass extinction and such major climate changes as glaciation, and discussed the causes of these events.

The reduction of habitable areas below a minimum sufficient for a given population to develop and reproduce has been considered by Schopf (1974) as the most important cause of extinction. Newell (1967) maintained a similar position, considering regressions and the reduction in the area of the continental shelves to be the most important factors of faunal changes in the Upper Palaeozoic. Simplification of such an approach and the role of the oceanic islands have been discussed by Jablonsky (1986). I would agree that as with the case of climate, the effect of reduction of habitable areas can be considerable, but not on a global scale. The same is true for such factors as increase of competition, overcrowding, lack of food, lack of ability to reproduce because of the reduction of the population below minimum levels, etc. Global reduction of shallow seas during the Permian is calculated by several authors (e.g. Forley 1975), but there must had been oceanic islands and shallow carbonate banks that have since been destroyed by subduction (Jablonsky 1986). Remnants of the continental shelves must also have existed and this is supported by the presence elsewhere of carbonate deposits as either accreted remnants of the former sea floors, or remnants of the circum--Pangea and circum-microcontinental shelves. Thus, the decrease in the area suitable for settlement should rather be considered a factor of the partition of the whole area into smaller regions exposed to adverse conditions. The habitats theoretically available to coral taxa in the uppermost Permian were not reduced below the limit considered damaging. The total area of the epicratonic shallow seas, estimated for that period by Forley (1975) as approximately $23\times10^6$ km$^2$ should be only $5\times10^6$ km$^2$ smaller than the Recent seas of this kind, in which the coral fauna develops widely.

Local fluctuations of the sea level and global regression that took place through the whole of the Permian (e.g. Forley 1975) may have been important factors in the development of isolated basins (Fisher 1964). In the context of this paper these events were probably one of the major factors in the temporary disappearance of sessile faunas, and show some similarity to the equillibrium theory of island geography, discussed by Boeklen and Simberloff (1986). The greatest difference between the model here proposed and both the equillibrium theory of island geography and the species-area effect (Schopf 1974), is that the postulated extinction from a given area does not depend chiefly on its size and the diversity of the taxa but mainly on the factors that made it inhabitable. In contrast to the Schopf's (1974) model, the present proposal does not discuss local or global habitable areas, but draws attention to the effect of local factors that caused emigration or extinction from individual isolated areas. As a result taxa may became extinct, although the global area to be habitable may remain large. The combination of global regression, the local tectonics, and slow spread of coral faunas resulting from the passive, short lived larval stages were probably the most important factors in the isolation of particular areas, leading to changes of habitats and barriers for the re-colonization of many areas.

Changes in salinity (Stevens 1977) may had been a factor in the mass extinction of the stenohaline organisms, if the large volume of Permian salt deposits is considered (Stevens 1977). The Permian was a time of warm climate and the erosion of large land areas. The volume of salt precipitated therefore was largely balanced by the erosion products transported into the sea. Some reduction of salinity of the world's oceanic waters may have slowly taken place during the Permian, but its scale could not have been an important factor in the mass extinction at the end of the Permian.

The catastrophic extraterrestrial causes recently postulated for the late Permian and other mass extinctions are not discussed here because they are not supported by the data derived from the coral faunas. The slow reduction of both Rugosa and Tabulata and number of areas inhabited by corals during milions of years (figs. 1—3) makes the model of catastrophic extinction inapplicable. Also, the hypothesis of periodic extinction (Sepkoski and Raup 1986) is not discussed here because it does not appear to be applicable to the Permian data or to the longer history of Rugosa and Tabulata. The difficulties in applying this model to the Palaeozoic faunas has already been discussed by Sepkoski and Raup (1986, pp. 22, 23) who also suggested that approximately 36 rather than 26 m.y. may be an interval of extinction during that time. Why the periodicity changed rapidly by more than one third of the length of the cycle just at the Palaeozoic/Mesozoic boundary has not been explained.

The great value of the terms "*Cyathaxonia fauna*", "*Caninia* — *Clisiophyllum* fauna" and "Reef coral fauna" (Hill 1938—1941) as the palaeoecological indicators has been widely accepted, but the automatic acceptance to their palaeoecological value may lead to serious mistakes. For example the interpretation of relation of the "*Cyathaxonia* fauna" to both other "faunas" in the Tethys Realm (figs. 1, 3) may lead to the conclusion that the Chishia-Maokou interval was the coolest in the Permian, but this suggestion would be to opposite to that offered by the so called "*Eurydesma* fauna" (Dickins 1984 and earlier papers) and with other indications of Palaeontology, Sedimentology, Palaeoclimatology, and Palaeogeograhy. The available data suggest that the major part of the coral faunas in Palaeo-Tethys were restricted to the equatorial area. However, the faunas occupied different ecological habitates: geosynclinal, perhaps comparatively deep water areas (Tibet, Inner Mongolia), microcontinental shelves (South China, Indochina), and bathymetrically variable

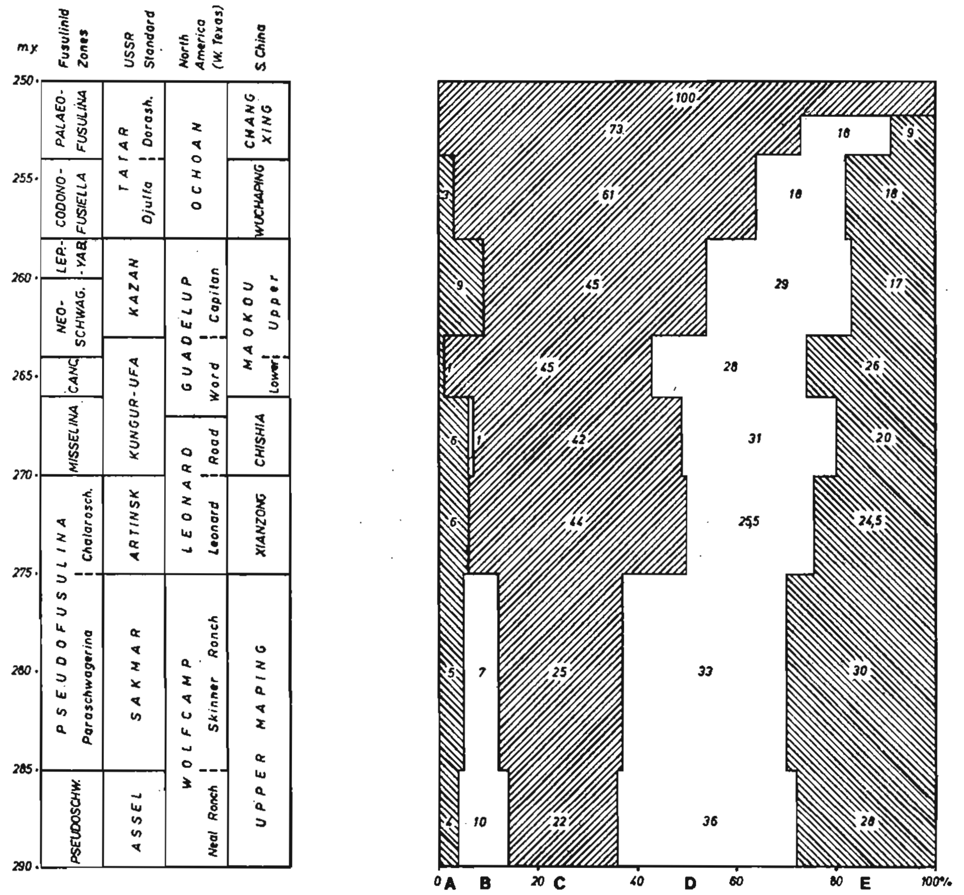

Fig. 3. Percentage distribution pattern of Permian rugose corals. *A*, *B* Cordillera-Arctic-Uralian Realm. *A* "*Cyathaxonia* fauna", *B* colonial corals. *C*—*E* Tethys Realm. *C* "*Cyathaxonia* fauna", *D* "*Caninia-Clisiophyllum* fauna"+fasciculate colonies, *E* all massive colonial corals. Numbers indicate the percent of genera identified within each stage or biozone.

areas on or near the shelves of Pangea (Yugoslavia, Grece, Carnic Alps, Armenia, Iran, Salt Range, Kashmir). Moreover, numerous species of the "*Cyathaxonia* fauna" commonly occur in association with representatives of two other "faunas" and, the morphology of these and the lithology of the strata clearly indicate shallow, warm water habitates. Many species of "*Cyathaxonia* fauna", for example those of the Timor Island, show the characters of the shallow, warm water faunas, precluding reconstruction of their habitates as deep or cold water. Also, the "*Cyathaxonia* fauna" is the only group of the rugose corals found so far in the carbonate build-ups of the Glass Mountains and Guadelupe Mountains (USA) and in the similar structures in the Zechstein seas of Central Europe and Greenland. In conclusion the exclusive occurrence of the "*Cyathaxonia* fauna" in the latest Permian does not indicate that deep and/or cold waters was the last refuge or rugose corals. They remained in shallow, warm water habitates up to their extinction. It should not be forgotten that the concentration of brine deeper in the oceans may closed these areas to corals and other sessile faunas (Fisher 1964).

## CHARACTERISTICS OF REALMS

### The Palaeo-Tethys Realm

Systematic descriptions of rugose and tabulate corals of some parts of this area require revision and their stratigraphic positions are difficult to compare with the current standards. Flügel (1970) made analysis of those early descriptions.

A summary of the occurrence of the genera and species (figs. 1, 3) indicates two periods of prosperity, and two periods of impoverishment of the coral faunas, the second of which ended with their extinction. First period of prosperity, restricted to the *Pseudoschwagerina* Biozone, was in several areas a continuation of the Upper Carboniferous development. The second period was the peak in the evolution of Permian corals in the Palaeo-Tethys Realm. It started with the *Misselina* Biozone (Chishian), reached its maximum in the *Lepidolina-Yabeina* Biozone (Upper Maokouan) and passed rapidly into the impoverishment period at the beginning of the *Codonofusiella* Biozone.

In the search for common global factors causing the increase and decrease of the coral faunas discussed I eliminated climate for the reasons discussed above, and also because of the following facts: (a) Asselian was one of the coolest periods during the Upper Carboniferous and Permian, whereas warming of the climate was already well advanced during the Chishia-Maokou equivalents (Dickins 1984). This makes the same influence of climate in both periods unacceptable. (b) Vast majority of the corals inhabited equatorial waters, where the climatic fluctuations are always the smallest. The lesser resistance of the equatorial faunas to temperature changes may decrease a value of this argument. Some changes of climate in particular areas, generated by the rotation of Pangea and drift of micro-continents (Zonenshain *et al.* 1985) may have influenced the composition of the coral faunas, but mainly effected migrations.

The reduction in salinity also did not have a major effect on faunas (see above). Considerable changes in proportion of the components of sea water that took place near the end of the Permian (Gruszczyński *et al.* 1989) may had been one of the adverse factors, but its simultaneous, world-wide occurrence must first be proven.

Two factors are here considered to have caused the faunal changes that may eventually have led to the extinction of rugose and tabulate corals.

These are: the global fall of the sea level combined with the local tectonic events that caused uplifting and/or subsidence of given parts of the oceanic floor and of land. The fall more than 170 m of the sea level, perhaps generated by the reduction of ocean floor spreading when the Pangea was formed, caused reduction of the shallow, epicratonic seas from $72\times10^6$ at the beginning to $23\times10^6$ km$^2$ at the end of Permian (Forley 1975). Local tectonics was responsible for most of the changes in the local coast lines and bathymetry, in accumulation of flysh and molasse sediments, and also of carbonate deposits during the quieter periods. The combination of global and local factors mentioned above lead to the creation and disappearance of settlement areas, and permanent or temporary opening and closing of migration routes. The succession of the coral faunas in Japan illustrates this well. The lithostratigraphic sequence (Minato *et al.* (eds.) 1979: fig. 2k-2) shows the relationships between the character of the sediment and the local tectonics. Carbonates accumulated when subsidence of the sea floor and uplift of the adjacent land or islands was slow. This in turn lead to smoothing of relief, reduced erosion and transport of the terrigenous fabric to the sea. The lowering of sea level may in some instances have resulted in slower subsidence of the sea floor, allowing accumulation of carbonate sediments, in most cases containing corals. The close similarity of these corals to the coral faunas of China and Indochina up to the *Lepidolina-Yabeina* Biozone indicates that the local environmental changes did not cause isolation of the Japanese area, which became re-colonized by corals each time the ecological conditions acceptable by them were re-established. These processes took place up to and including the *Lepidolina-Yabeina* Biozone. However, factors leading accumulation of the Toyama Series stopped the development of almost any fauna. The rugose corals did not return even to the areas where the carbonate build-ups were being developed, although fusulinids and rare Tabulata penetrated these isolated areas. Thus, in Japan the development of rugose corals ceased before the *Codonofusiella* Biozone and the tabulate corals somewhere within that biozone.

The detailed analysis in particular areas of the palaeoecology, development of carbonates, and biostratigraphy on one hand, and the development of corals on the other, is not possible in this paper. I have restricted discussion to the general conclusion that periods of coral prosperity especially in Asselian and Chishia-Maokou equivalents coincided with periods of widespread carbonate deposition within the Palaeo-Tethys. The variety of taxa (fig. 1) and the large number of individuals to a large extent resulted from favourable conditions. A second dependence can also be observed, however, and this is the location of a given area within the Realm. The richest and most diversified coral faunas of the Asiatic microcontinents were those located at the Palaeo-Tethys Palaeo-Pacific border (fig. 4). In the Chishia-Maokou time very rich faunas appeared in the geosynclinal waters of Inner Mongolia and Tibet, and these occurred where carbonate deposits were widespread. The coral faunas that occurred on the Pangea shelves, and especially those on the present territories of Grece, Yugoslavia, Austria and Hungary were very poor when compared with the former regions. The morphologically more complex genera are unknown in the Western Palaeo-Tethys area and the number of species recorded from there is limited. Climate was not a factor in this faunal poverty, because the territories in question were located near the equator. It is more likely that this poverty resulted from the shape of the Palaeo--Tethys and its largely open areas. The equatorial palaeo-current probably

Fig. 4. Permian palaeogeography. The equatorial palaeocurrent is reconstructed here as flowing between the Chinese and Indochinese microcontinents that were anchoraged at the border between Palaeo-Pacific and Palaeo-Tethys Oceans (the basic map from Zonenshain *et al.* 1985, slightly modified). *Af* Afghanistan, *Am* Amuria, *Ap* Apulia, *Ar* Arctica *Ch* Chinese Microcontinent, *Ich* Indochinese Microcontinent, *Ir* Iran, *Ko* Kolymia, *Ta* Tarim.

flowed directly into the westernmost part of Palaeo-Tethys where it divided into two return currents that run north-east and south-west along the Pangea coast line (fig. 4). The pattern of these main currents reconstructed herein almost exactly fits the theoretical model of Schopf (1979). This equatorial current would certainly have been able to carry larvae from the faunule-creative regions of the Palaeo-Tethys/Palaeo--Pacific border. However, most of larvae would probably not have survived such a long passage through open waters where they would not been able to pause for metamorphosis to take place. Thus, only larvae of the most resistant taxa probably reached the western Palaeo-Tethys, where endemic species dominated. Some taxa that originated in the western area may had migrated with the currents returning to the east.

The ecological conditions were the second factor leading to reduction of faunas in the western Palaeo-Tethys. In contrast to carbonates of the Asiatic microcontinents, terrigenous deposits were common there, and areas of coral-bearing strata were restricted, and occurred in fairly isolated enclavas, precluding the development of rich and diversified faunas. It is very poor even in the carbonate build-ups, where rare horn corals occur in the lower *Palaeofusulina sinensis* Biozone on some Grece islands (prof. E. Flügel, oral communication, 1988).

The fairly rapid reduction of the coral faunas in the Palaeo-Tethys at the beginning of the *Codonofusiella* Biozone (figs. 1, 3) may to some extent be artificial, resulting from the unprecise or incorrect correlation accepted in this paper. For instance, the Amarassi fauna from Timor, here included in the Upper Maokou, may belong to lower part of *Codonofusiella* Biozone. Such adjustments of stratigraphic correlations, however, will change the graphs only slightly, because the biozone discussed was a period of substantial deterioration of habitats suitable for corals in many areas within the Palaeo-Tethys. There may had been temporary emergence above the sea level in some areas, and in most of them terrigenous sediments were deposited and the habitat was unsuitable for corals as has happened in Japan (see above) and in several areas of western European countries and the northern (Salt Range, Kashmir) parts of the Palaeo-Tethys shelves of Pangea. It is not clear whether reduction of coral diversity in geosynclinal areas, where there was a reduction of carbonate deposits, was connected to their faster subsidence.

The reduction in the richness of coral faunas begun the last stage of their history, which was different for Rugosa and Tabulata. The tabulate fauna was poor, monotonous and little changed through the last two stages (fig. 2) and was dominated by michelinids. Some species of this genus continued to develop up to the topmost coral-bearing strata in many areas, and the last two Permian stages formed a single period of development of this fauna in the Palaeo-Tethys Realm.

In contrast to Tabulata, the rugose coral fauna exhibits substantial differences between the *Codonofusiella* and *Palaeofusulina* biozones. In spite of the large reduction in number of genera, the rugose coral fauna of the *Codonofusiella* Biozone remained comparatively rich, with numerous genera, which disappeared before its end. Ten new genera have been established from this biozone, and even considering most of them to be younger synonyms, such corals do not occur in younger strata.

The areas abandoned by coral faunas within the *Codonofusiella* Biozone were not re-colonized by them in the following biozone even in the case where the habitats were suitable for corals. The abandoned areas form a fairly regular pattern within the Palaeo-Tethys. The New Zealand and Australia far south of the Pangea shelves were areas abandoned first and were followed by the far-western Palaeo-Tethys except for very rare occurrences on some Greece islands, and northern shelves of Pangea (Kashmir, Salt Range). The Indochina microcontinent may had been the next area, but data are uncertain. The only Pangea shelves inhabited by corals in *Palaeofusulina* Biozone were those of Armenia, Iran, and some Grece islands, and even there corals were declining before the end of the biozone. The southern Chinese microcontinent, anchoraged somewhere near the Palaeo-Pacific limit of Palaeo-Tethys (fig. 4) was the last refuge of the rugose and tabulate coral faunas.

The rugose genera of the *Palaeofusulina* Biozone form two unequal groups. The exclusively Permian, Palaeo-Tethyan genera with complex morphology, such as *Huayunophyllum*, *Ipciphyllum*, *Liangshanophyllum* and *Waagenophyllum* belong to the first group. They first occur in the *Pseudofusulina* or *Misselina* biozones and disappear in the lower or middle part of the *Palaeofusulina* Biozone. Thus, although they range was reasonably long, they were restricted to the Permian. Long-ranging, morphologically simple, cosmopolitan genera form the second group. All of them are solitary, non-dissepimentate genera, some of which appeared as early as in the Devonian. The taxonomic status of most of Permian members of this group of corals is uncertain. Some of them are probably synonyms and/or morphotypes, not true genera. Thus, the list that follows is only provisional. The following taxa(?), all belonging to the suborder Plerophyllina, have been recorded: *Calophyllum*+possible synonym *Tetralasma*, *Lophophyllidium* (+*Sinophyllum* as a synonym), *Lophocarinophyllum*, some representatives of which may belong either to *Lophophyllidium* or to *Asserculinia*, the group of genera(?) and/or morphotypes such as *Plerophyllum*, *Pleramplexus*, *Paracaninia*, *Tachylasma*, *Pentaphyllum*, *Pentamplexus*, *Ufimia*. The suborder Stereolasmatina is represented by rare example of morphotypes similar to *Hapsiphyllum* or *Zaphrentites*. The records of Metriophyllina near the top of the Permian are doubtful. Both "*Amplexus*" and "*Amplexocarinia*" of that age may belong to Plerophyllina, but the ontogeny, the only certain taxonomic character of higher rank, has not been reported from these late Permian taxa.

Assuming current correlations to be correct the last representatives of rugose and tabulate corals were restricted to the single region of the world, the southern Chinese microcontinental shelves. It is striking that the better known species that range near to the top Permian demonstrate large intraspecific variability, allowing the persistant occurrence of the genetic plasticity to be suggested (Fedorowski, in press).

Another character of the Permian Palaeo-Tethyan corals, observed also among the Cordillera-Arctic-Uralian corals, is the sequence of migration and/or extinction of rugose corals, first discussed by Flügel (1970). The most complex, massive colonial corals disappeared from a given area first, and were followed by fasciculate colonies and solitary corals with dissepiments ("*Caninia-Clisiophyllum* fauna"), and finally by the "*Cyathaxonia* fauna". The diachronous nature of this sequence can be established from records of other fossils, but has not been noted previously. For instance, the last representatives of massive and fasciculate corals in Armenia occur only up to the Djulfian, and in the Dorashamian only plerophyllids accompanied by Tabulata are reported. In South China the fasciculate colonies, and even massive *Ipciphyllum*, are present up to the lower and/or middle part of the Changxingian, i.e. up to the probable limit of Dorashamian. "*Cyathaxonia* fauna" corals and Tabulata were the sole representatives in southern China from the strata that are probably higher than Dorashamian. The situation is even more striking when the Kazanian or lowermost Djulfian coral fauna from Greenland is taken for comparison. Being very similar on the generic level to those from Armenia and South China, it represents much older strata.

From some areas, such as Japan, the extinction of the coral faunas was rapid and the sequence discussed above is not seen. Faunas composed sometimes of morphologically complex taxa disappear and the habitats changed so rapidly that the more resistant corals were not able to inhabite them.

Similarities of diachronous change at the generic level in different areas invariably concerns the long-ranging, morphologically simple genera, recorded from various habitats. These taxa are therefore likely to be the most resistant to the external factors. It may also be concluded that changes in the conditions effecting coral growth also occurred diachronously. It seems probable therefore that local factors plus some global ones were responsible for the deterioration and extinction of the coral fauna from the Palaeo-Tethys Realm rather than solely global factors. One can only speculate on why the return of the coral faunas did not take place with the Triassic transgression, and why the Palaeo-Pacific Ocean did not become a refuge for corals. No corals have so far been found in the so called "beds with mixed fauna" in China. Thus, it is possible that the Triassic transgression came too late for corals to survive because they had became extinct in their last refuges due to factors that may had been so local that they have not yet been established. The accumulation of brine, for example the application of Fisher's (1964) or similar model, may have formed barriers to stop corals migrating into deeper waters. The last populations of rugose and tabulate corals were probably so small and the open waters of Palaeo-Tethys so wide, that even the equatorial palaeo-current did not allow the re--colonization of Pangea shelves, although carbonate deposits are recorded suggesting that the habitat was suitable for corals in some areas.

### The Cordillera-Arctic-Uralian Realm

The knowledge of the rugose and tabulate coral faunas of this Realm varies both with respect to the stratigraphical and geographical distribution. Complex palaeotectonics, and especially the accretion of many different areas, makes the reconstruction of the history of coral faunas of this area difficult. Therefore, despite the generally simple summary, showing the step by step impoverishment of the coral faunas within the Realm, leading to their extinction not later than in the lower part of the *Codonofusiella* Biozone (fig. 2), some better known areas have to be discussed separately.

The Uralian geosyncline and the eastern margin of the Eastern European Platform that bordered it on the south, together formed a region in which the carbonate coral-bearing deposits are known to occur up to the Kazanian. However, the rich and varied faunas flourished only in the Asselian to Artinskian stages. In the Asselien the coral faunas and habitats were similar to those in Gshelian. Only the re-appearance of massive colonial rugose corals, absent from this area since the Middle Carboniferous, is important. These forms reached a dominant position in the Sakmarian, but declined during the Artinskian both in number of specimens and in the taxonomic variety, and the "*Cyathaxonia* fauna" became dominant. Tabulate coral faunas in the area discussed are comparatively poor both on the genera and species level. The colonial rugose corals have not been found in the deposits younger than Artinskian. The "*Cyathaxonia* fauna" occurred up to the Kazanian, but it is poor and restricted mainly to plerophyllids.

The Uralian rugose and tabulate corals show a striking similarity, sometimes on the species level, to the comparable faunas of the Svalbard Archipelago and the Sverdrup Basin in the Canadian Arctic Archipelago. The peak development of coral faunas in the latter two areas occurred in the Sakmarian, a situation which is again closely comparable to that in the Uralian geosyncline. The coral faunas of these northern regions, although intensively collected, have only in small part been described in detail.

After a period when coral faunas flourished during the Asselian, Sakmarian and partly Artinskian, they decline fairly quickly because the habitats were destroyed over a large area between the Uralian geosyncline and the Sverdrup Basin. Only in the Kazanian and/or probably in the Lower Djulfian there were some areas in the remnants of the Uralian geosyncline and in the Zechstein seas of Western and Central Europe and Central East Greenland where carbonates were deposited. The rugose coral faunas from the Kazanian (Surlyk *et al.* 1986) or Lower Djulfian (Nakamura *et al.* 1987) carbonate build ups of the Wegener Halvø Formation were probably the youngest and certainly the richest faunules of the whole northern region of the Realm. Dr. K. Małkowski (oral communication, 1988) has recorded very rare, small, solitary rugose corals near the top of the Kapp Starostin Formation (Central Vestspitsbergen), which may be even younger, although Nakamura *et al.* (1987) correlated the uppermost brachiopod-bearing beds of the Kapp Starostin Formation with the so called Fossil II Zone in Central East Greenland.

The terrestrial Tatarian deposits in Ural Mountains, and the regressive, sandy Schuchert Dal Formation in Greenland, ended with the pre--Triassic disconformity. Also, the sandy Assistance Formation and the late Permian emergence in the Sverdrup Basin were clearly environmental factors that caused the extinction of corals from those areas.

Corals of the autochtonous areas within the Cordillera, especially those younger than Wolfcampian, are not well known. Most of the records are from Nevada and Oregon where species of the fasciculate *Heritschioides* are among the most common and this genus ranged up to the equivalents of Kungurian. Massive colonial rugose corals, and some solitary Rugosa with dissepiments confirm the similarity of this fauna to that from the Canadian Arctic Archipelago. No records of the Upper Permian coral faunas are available from these areas.

The richest coral faunas have been described from the McCloud area in California and from SW Texas. Although allochthonous, the McCloud fauna shows close similarity to the autochthonous Nevada and Oregon faunas and there is no doubt that they both had access to the same Realm. The richest assemblages, mostly representing "*Caninia-Clisiophyllum*" and "Reef coral" faunas have been described from the Wolfcampian. Corals younger than Wolfcampian are very rare or not recorded in California, although carbonate rocks are present.

The most abundant and taxonomically diverse coral faunas in SW Texas are those of the Wolfcampian. This abundance was not entirely dependent on the size of the favourable habitat, because similar ones, variable in details, but with well developed areas of carbonate rocks persisted into the Upper Guadelupian. Also, the carbonate build-ups were continuously being formed, with the largest occurring in the Guadelupian, at a time when the coral fauna had already been greatly impoverished. I cannot at present offer any explanation for this sequence of events, for the abundance of Bryozoa and calcareous algae in all these build-ups (Newell *et al.* 1953). These facts suggest that there were no drastic changes in the chemistry of the sea waters. Among the tens of thousands of Rugosa collected from that area by Dr. G. A. Cooper, Smithsonian Institution, Washington, and being studied by me, only about 100 were from the topmost coral-bearing Lamar Member. The drastic changes at the beginning of the Ochoan stopped the further development of corals, but only this final stage of their extinction can undoubtedly be attributed to ecological control.

The data relating to rugose and tabulate coral faunas from the regions south of SW Texas are so incomplete and uncertain that they were omitted from this paper. There are no indications, however that any of those southern coral faunas is younger than Guadelupian.

The waagenophyllids described by Stevens *et al.* (1987) from the *Codonofusiella* Biozone are stratigraphically the youngest corals described from North America, but this is a Palaeo-Tethys fauna. Stevens *et al.* (1987) considering this fact suggested that the development of this allochthonous fauna may had been close to the autochthonous Cordillera occurrences, and that intermediate faunas may occur. If this is correct, such faunas would be intermediate in time, space and taxonomy between these allochthonous and the autochthonous Cordillera faunas, because the latest autochthonous Cordillera fauna disappeared well before the *Codonofusiella* Biozone and had nothing in common with Waagenophyllidae.

## CONCLUSIONS

1. Permian rugose and tabulate corals evolved along parallel lines in two separated Realms: the Palaeo-Tethys Realm and the Cordillera-Arctic-Uralian Realm. Less than 19% of genera are common to both Realms and this percentage is less than 3% for the taxa restricted to the Permian. Very few species are considered common to both Realms and all of them require revision.
2. Taxa common to both Realms mainly belong to the "*Cyathaxonia* fauna" with some belonging to the "*Caninia-Clisiophyllum* fauna". Simple fasciculate colonies were included in this fauna for the present analysis. Several of these common "genera", such as "*Caninia*" or "*Amplexus*" are morphotypes, and most of the common taxa are long and/or very long-ranging. Their parallel evolution from common ancestors must therefore have been taken place when free communication between areas was possible.
3. Massive rugose coral genera are totally different in both Realms and therefore are the most important group for distinguishing between Realms.

4. The division into two Realms was the first step in the isolation of coral faunas and was caused by global palaeotectonic factors that formed two main geographical barriers: the Palaeo-Pacific Ocean and the Pangea.
5. Taxonomic diversity and advanced morphology of the coral faunas indicate that the Asiatic microcontinents were the centres for evolution within the Palaeo-Tethys Realm. The more scattered faunas of the Cordillera-Arctic-Uralian Realm do not allow any evolutionary centres to be identified for this Realm.
6. The size of the Palaeo-Tethys was the major factor causing isolation within this Realm. The suggested westward flowing equatorial palaeo-current and its north-east and south-east return currents helped with the spread of coral faunas, and the longliving larvae were able to survive such a long migration, but coral faunas in western Palaeo-Tethys were mostly endemic. The coral faunas described from the Cordillera-Arctic-Uralian Realm do not allow the direction of palaeo-currents to be plotted.
7. The combined effect of global factors such as the lowering of sea level, and local tectonics led to further separation, either permanent or temporary of areas where coral faunas occurred.
8. The emigration or extinction of a coral fauna from a given area may have led to its failure a re-colonization that area even with the return of favourable ecological conditions. This may have been caused by such simple ecological barriers as cold, strong or wrongly directed currents or the disappearance of shallow water banks allowing larvae to stop for metamorphosis. The fact that there are no corals in the late Permian shallow water carbonate deposits, a potentially favourable habitat, supports this thesis. This process is explained here as "links dropping out of a chain".
9. The process mentioned above led to the step by step reduction of number of taxa within rugose and tabulate corals. However, this process, although considered fundamental, was not the only reason for the impoverishment and extinction of coral faunas. The progressive disappearance of corals in such areas as the Gandian Province, where there were no obvious ecological changes is not yet understandable.
10. The disappearance of coral faunas from a given area may be either rapid and directly connected to the environmental change for instance the end of the *Lepidolina-Yabeina* Biozone in Japan, or slow and not connected in an obvious way to such changes. In all instances of the latter, there is a sequence in the disappearance of individual morphotypes. Massive colonial corals were the first to disappear, followed by the "*Caninia-Clisiophyllum* fauna" and then the "*Cyathaxonia* fauna", represented mainly by plerophyllids. This sequence is seen to be diachronous when different areas are compared. Sometimes differing by as much as two biozones, as is the case with the youngest coral faunas of Greenland and

South China. Although these differences were probably caused by common factors, I cannot detect them, except for the ambiguous explanation: "deterioration of habitats" that could have been responsible. The diachronism discussed is observed both between and within the Realms.

11. The long-ranging, cosmopolitan genera of the suborder Plerophyllina, known to occur in various habitats, are the last representatives of the Rugosa, and the cosmopolitan and long-ranging micheliniids are the last of the Tabulata. Thus, the conservative, morphologically simple forms were alligible to survive longer than more specialized genera. This may be an explanation for the sequence in the disappearance of coral faunas discussed above.

12. The pattern of disappearance of coral faunas from the Cordillera-Arctic-Uralian Realm is diachronous, but rather irregular, whereas in the Palaeo-Tethys Realm the situation is different. The pattern of disappearance of coral faunas shows a sequence, with those developing on the Chinese microcontinent being the last to disappear. In this context Zonenshain *et al.* 1985 placed this microcontinent too far north at the end of Permian, even allowing for the extremely warm climate reconstructed for that period of time. This has been slightly modified here in fig. 4.

13. Much of the Palaeo-Pacific oceanic floor was destroyed by subduction, but the remnants that were accreted to the Asiatic and American continents do not contain the youngest Permian rugose and tabulate corals. Changes of the composition of sea water with a decrease in salinity and accumulation of brine deeper in the Ocean are among the reasons suggested for oceanic waters becoming uninhabitable for stenohaline organisms. None of these factors has been satisfactorily shown to have reached levels that would have adversely effected corals. Thus, it remains uncertain why the Palaeo-Pacific Ocean was not a refuge for the rugose and tabulate coral faunas in latest Permian.

14. Restriction of those faunas to very small areas may had resulted in their extinction due to a local and generally unimportant factors.

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### JERZY FEDOROWSKI

# WYMIERANIE RUGOSA I TABULATA W POBLIŻU GRANICY PERMU I TRIASU

## *Streszczenie*

Permski okres ewolucji Rugosa i Tabulata przebiegał równolegle w dwóch królestwach izolowanych od siebie Paleo-Pacyfikiem i Pangeą. Były to: królestwo oceanu Tetyda, rozciągające się na wschód od wybrzeży Pangei i królestwo Kordyliersko-Arktyczno-Uralskie na zachód od tych wybrzeży. W żadnym z tych królestw przedstawiciele Rugosa i Tabulata nie dotrwali do końca permu: w królestwie oceanu Tetyda koralowce te występują do końca podzony *Palaeofusulina sinensis,* Changxingian, podczas gdy w królestwie Kordyliersko-Arktyczno-Uralskim wymarły one ostatecznie w zonie *Codonofusiella* (Midian lub dolny Djulfian). W obydwu królestwach proces wymierania był powolny. Jego ostatnie etapy trwały w ciągu około 8 milionów lat, nie może więc być mowy o wymieraniu nagłym lub katastroficznym. Przyczyn wymierania Rugosa i Tabulata upatruję głównie w nakładaniu się czynników lokalnych, jak diastrofizm, zmiany kierunków i temperatury prądów morskich i zmiany w występowaniu mielizn umożliwiających metamorfozę larw itp., na czynniki globalne, jak ciągłe obniżanie się poziomu oceanu światowego, wielka przestrzeń wód Paleo-Pacyfiku, ocieplanie się klimatu.

Analiza stratygraficzno-geograficzna wskazuje na wyraźny diachronizm w wycofywaniu się lub wymieraniu koralowców z poszczególnych obszarów siedliskowych. Proces ten został w niniejszej pracy nazwany wypadaniem ogniw łańcucha, ponieważ wiele obszarów opuszczonych przez koralowce, nie zostało przez nie ponownie zasiedlonych, pomimo zaistnienia tam warunków ekologicznych umożliwiających rozwój tych zwierząt. W rezultacie kolejnych redukcji obszarów siedliskowych w obydwu królestwach, koralowce pozostają tylko na szelfie mikrokontynentu chińskiego. Są tam reprezentowane przez michelinidy spośród Tabulata oraz przez prymitywne, osobnicze Rugosa, należące głównie do podrzędu Plerophyllina i reprezentowane przez rodzaje o stosunkowo dużej tolerancji ekologicznej, trwające od dolnego karbonu, a nawet od dewonu. Stawiam tezę, że ostateczne wymarcie Rugosa i Tabulata spowodował czynnik o charakterze tak ograniczonym i lokalnym, iż nie został on dotychczas ustalony. Jest faktem, że koralowce nie występują już w tzw. „beds with mixed fauna" z szelfu mikrokontynentu chińskiego, w których znaleziono permskie ramienionogi współwystępujące z triasowymi głowonogami i małżami.