Acta Geologica Polonica, Vol. 49 (1999), No. 2, pp. 159-173

Permian corals of the Cordilleran-Arctic-Uralian Realm

JERZY FEDOROWSKI[1], E. WAYNE BAMBER[2] & CALVIN H. STEVENS[3]

[1] *Institute of Geology, Adam Mickiewicz University, Makow Polnych 16, PL-61-606 Poznan, Poland*
E-mail: jerzy@main.amu.edu.pl
[2] *Geological Survey of Canada (Calgary), 3303-33rd Street N.W., Calgary, Alberta T2L 2A7, Canada*
E-mail: bamber@gsc.nrcan.gc.ca
[3] *Department of Geology, San Jose University, San Jose, California 95192, USA*
E-mail: stevens@geosun1.sjsu.edu

ABSTRACT:

FEDOROWSKI, J., BAMBER, E.W. & STEVENS, C.H. Permian corals of the Cordilleran-Arctic-Uralian Realm. *Acta Geologica Polonica*, **49** (2), 159-173. Warszawa.

Permian rugose corals of the Cordilleran-Arctic-Uralian Realm are abundant in shallow-water carbonates along the northwestern and western margin of Pangaea, from the Ural Mountains area in Russia, through the Svalbard Archipelago and arctic and western North America, to Bolivia and Peru. The colonial forms are of particular interest for the biostratigraphy and reconstruction of the paleogeography of this extensive region. A revision of the systematics of these corals has shown that, although important differences exist between the assemblages in the areas listed, the faunas are recognizable throughout the entire realm. Almost all of the faunas in the realm, on cratonal Pangaea, are Cisuralian (Asselian to Artinskian) in age although younger faunas occur in rocks of terranes subsequently accreted to North America. The cratonal faunas show a general trend from a predominance of relatively simple, fasciculate species with open axial areas or weakly developed axial structures in the lowest Permian, to younger, more complex fasciculate and massive species with a variety of morphological elements in their axial structures and dissepimentaria. Suppression of the walls occurs commonly in the youngest faunas. As a result of the northward movement of Pangaea into cooler waters, colonial rugose corals were exterminated from the more northerly areas by early to mid-Artinskian time, but persisted throughout the Artinskian and possibly into the Kungurian and early Guadalupian in the cratonic successions of the western U.S.A. Similarities between the coral faunas of cratonal North America and the western allochthonous terranes indicate that faunal interchange occurred between these various coral faunas during the Cisuralian. The only colonial corals recovered from Wordian to Lopingian rocks in this region are waagenophyllid corals of tethyan affinity from the Cache Creek and Quesnellia terranes of British Columbia and the Hayfork and Eastern Klamath terranes of California.

Key words: Permian, Rugosa, Western Pangea, Biogeography.

INTRODUCTION

Changes in world geography during Late Carboniferous time had profound effects on the distribution of marine faunas and affected their subsequent phylogeny. Prior to its closing in Gzhelian time, there surely was free communication through a Serpukhovian-Moscovian seaway

connecting the Prae-Tethys to the Uralian Ocean (FEDOROWSKI 1981, RODRIQUEZ & *al.* 1986, GOLONKA & *al.* 1994). The possibility that such a seaway leading to the southern Urals Ocean persisted through the Asselian or even into the Sakmarian has been postulated by some authors of palaeogeographic maps (*e.g.*, GOLONKA & *al.* 1994), but distribution of facies-sensitive rugose corals indicates a pre-Permian closure. Regardless of the exact timing of the closure, there is general acceptance that, beginning in Late Carboniferous time, Pangaea existed as a solid landmass with substantial differences in the marine faunas living on its eastern and western shelves. The differences between the rugose coral faunas in these regions are so striking that FEDOROWSKI (1986) introduced the idea of two independent realms: the Tethys Realm and the Cordilleran-Arctic-Uralian (CAU) Realm. (Text-fig. 1) Most of the latter realm was earlier referred to as the *Thysanophyllum* Belt by STEVENS (1982). The existence of two realms is accepted in the present paper because it has since been substantiated by new data and interpretations of both the palaeogeography and the systematics and distribution of rugose corals.

The unique geography of the world during the Cisuralian was a primary factor influencing relationships between invertebrate faunas of that age. The effect of this factor was proportional to the level of sensitivity of a given taxon to environmental conditions, its genetic potential for change, and its ability to disperse. Thus, the stenotypic, sessile benthic faunas were most strongly influenced, and these certainly include the rugose corals. The response of the latter to geographic and environmental changes was governed partly by differences between the sensitivity of individual morphotypes – a factor often omitted from palaeoenvironmental analyses. In general, the environmentally most resistant solitary, nondissepimental rugose corals may be distinguished from those with other growth forms. Normal salinity was the only general restricting factor for the former, whereas other factors governed the second group. Within the second group, dissepimental solitary corals and fasciculate colonial taxa apparently were less sensitive to their environment than were the massive colonial forms. In this paper, all of these morphological groups will be briefly analysed to provide a comprehensive historical overview of rugose corals in the CAU Realm.

In our analysis we use two Carboniferous subsystems and the three Permian Series (Cisuralian, Guadalupian, Lopingian) that have been recently recognized by the Subcommission on Permian Stratigraphy (*e.g.* JIN YUGAN 1996). We omit

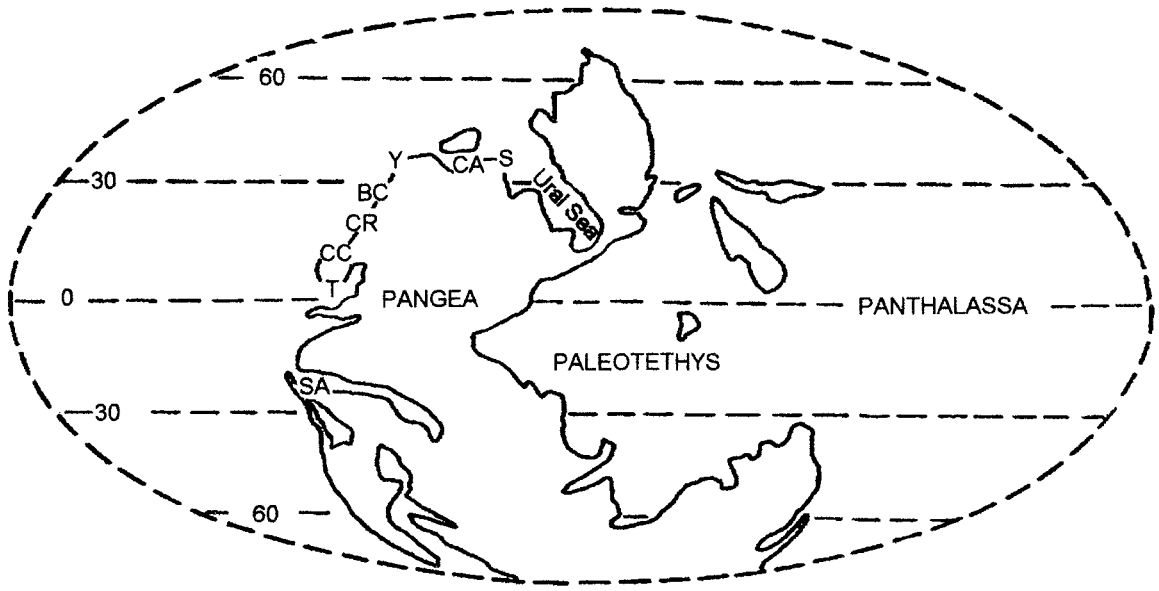

Fig. 1. Palaeogeographic map of Pangea based on ZIEGLER & *al.* 1996, Early Permian (Sakmarian). BC – British Columbia, CA – Canada, CC – Central Cordillera, CR – Canadian Rocky Mountains, S – Spitsbergen, SA – South America, T – SW Texas, Y – Yukon Territory

from our discussion all Lower Carboniferous and most of the Upper Carboniferous strata and coral faunas, except where the latter have a direct bearing on the history and distribution of Permian faunas. Unfortunately, there are difficulties in correlating upper Cisuralian (Leonardian/Kungurian) strata of southern North America with the internationally accepted standard in the Ural Mountains. For the remainder of the Cisuralian succession, however, the story of rugose coral development and extinction in the CAU Realm is reasonably clear.

ROOTS OF PERMIAN RUGOSE CORALS OF THE CORDILLERAN-ARCTIC-URALIAN REALM

Almost all main stocks of Permian rugose corals contain three categories of taxa: long-lasting taxa that are rooted in Carboniferous or older strata and are common to both Permian realms; taxa clearly restricted to one of the realms, although not necessarily restricted to Permian strata; and taxa morphologically similar in both realms, but probably homeomorphic. The latter category includes mostly species and genera, whereas the former two groups are at the family or suborder level. This division often crosses general taxonomic boundaries and corresponds only partly to growth forms and/or ecotypes (i.e., the so called "Faunas" of HILL 1938-1941).

Perhaps all of the "horn corals", or "*Cyathaxonia* Fauna" of HILL (1938-1941) – i.e., nondissepimental taxa at the genus and higher taxonomic level – are rooted in strata older than Permian. Also, "horn corals" constitute the most widely distributed and longest lasting morphotype because of their great environmental opportunism and, perhaps, largest genetic plasticity. As a result, "horn corals", as a group, are of little use for palaeogeographical and palaeoecological analysis unless considered individually as low level taxa. Many of them belong to deep, cold water faunas and are important environmental indicators. However, we will not consider this group further, except in our discussion of the mid-Permian faunas.

Almost all of the dissepimental solitary Rugosa – i.e., the "*Caninia-Clisiophyllum* Fauna" of HILL (1938-1941) – are rooted in the Carboniferous. This is especially true for the most widely distributed and the most frequently represented family Bothrophyllidae FOMICHEV, 1953. Representatives of this family dominate in the CAU Realm, but some are present in the Tethys Realm as well, where they persisted longer than in the CAU Realm. For instance *Arctophyllum* is known to occur in Vietnam into the Guadalupian Roadian and Wordian Stages. In the CAU Realm, Permian representatives of this family were most abundant in the Asselian. *Arctophyllum, Bothrophyllum, Siedleckia, Timania*, and *Caninophyllum*?, which originated in the Carboniferous, continued to occur throughout most of the realm and *Fedorowskiphyllum* appeared and spread from the Northern Urals to California. Some of these genera continued through the Sakmarian, but none survived beyond the earliest Artinskian Burtsevsky Horizon (= *Pseudofusulina concavuta* Biozone). They never created their own communities in the Cisuralian and did not dominate over colonial morphotypes – a character clearly distinguishing Asselian coral faunas from those of the Gzhelian.

Iranophyllum, which is a dissepimental, solitary representative of the Wentzelellinae, is one of the most diversified, widespread and abundant genera in the Tethys Realm. It has never been found on the western shelves of Pangaea and therefore provides a reliable marker for distinguishing between the two realms.

Permian remnants of the families Petalaxidae FOMICHEV, 1953 and Geyerophyllidae MINATO, 1955 include solitary dissepimental and colonial corals – both fasciculate and massive. Following tradition, we distinguish between those two families in this paper, but they are most probably synonyms. The very few representatives that occur in the Asselian of the CAU Realm are obvious holdovers from the Carboniferous Period. The only genus that may be considered typical for the Asselian-Sakmarian, rather than Gzhelian, is *Lytvophyllum*, although it possibly appeared very late in the Carboniferous. Representatives of these families were much more abundant and also lived longer in the Tethys Realm than in the CAU Realm.

Among the colonial forms rooted in the Carboniferous, the family Lithostrotionidae is represented by the single, but geographically widespread genus *Tschussovskenia*. Its taxonomic relationships are discussed by us elsewhere (FEDOROWSKI & *al., in prep.*). Our analysis shows, however, that it can be linked through intermediate genera to the Viséan genus *Diphyphyllum*.

Representatives of *Tschussovskenia* are known to occur in Asselian-Sakmarian strata from the Ural Mountains through Svalbard and the Canadian Arctic Archipelago to California and Nevada. We cannot exclude their presence in South China and Indochina, although those tethyan corals assigned to *Tschussovskenia* may be distinct at the genus level (FONTAINE 1961, WU 1962).

The stratigraphically and geographically most important families – the Durhaminidae and "Heritschioididae" of the CAU Realm and the Waagenophyllidae and Yatsengiinae of the Tethys Realm – are rooted in the Late Carboniferous as well. However, unlike the lineages discussed above, those four families were separated geographically from the beginning of their development, thus creating the main basis for the distinction between realms. The solitary, dissepimental *Amandophyllum* may perhaps be the only genus present in both realms. It is rooted low in the Carboniferous if its identification by FEDOROWSKI (1971) in the Upper Viséan of Poland is accepted. The development and relationships of Durhaminidae and "Heritschioididae" will be discussed later. Further discussion of the Waagenophyllidae and Yatsengiinae is omitted because this paper deals only with the rugose corals of the CAU Realm. Throughout this paper, the name *Heritschioides* and its derivatives appear in inverted commas, because our recent re-investigation (FEDOROWSKI & *al.*, *in prep.*) of *H. columbicum* SMITH, 1935, the type species of the genus, has shown it to differ in morphology and age from all described Permian species currently assigned to that genus in the literature.

Except for the Diffingiina FEDOROWSKI, 1986 new taxa at the family or higher level have not been recognized from Permian strata of the CAU Realm, but some exclusively Permian genera such as *Allotropiochisma, Assimulia, Euryphyllum, Leonardophylum, Lophbillidium* (subgenus), *Lytvolasma, Fedorowskiphyllum, Hornsundia, Langenheimia, Kleopatrina, Permastraea, Protolonsdaleiastraea, Stikinastraea*, and *Stylastraea*, as well as many species have already been described. In addition, several new genera will be introduced by FEDOROWSKI & *al. (in prep.)*. Most of the colonial genera and all of those to be introduced by us belong to the Durhaminidae and "Heritschioididae", the most abundant and diversified Cisuralian rugose coral families in the CAU realm. The first six genera listed above are solitary, non-dissepimental corals, the next two are solitary, dissepimental corals, and the remaining genera are massive colonial forms. The relative proportion of these different growth forms reflects the composition of the entire fauna, briefly discussed later.

Although it is possible, as mentioned above, that homeomorphic genera may be present in both realms, this cannot be definitely proven, because current data are incomplete. It is probable, that Japanese species such as *Durhamina kitakamiensis* MINATO & KATO, 1965 are not durhaminids because they possess clinotabellae (FEDOROWSKI 1997, p. 101), and the North American *Yabeiphyllum rossi* MINATO & KATO, 1965 is included by us (FEDOROWSKI & *al.*, in prep.) in the Durhaminidae. Also, some tethyan bothrophyllids and caniniids do not necessarily belong to the same genus as those in the CAU Realm. The same may be true for the genus *Paracaninia*. Abundant Gzhelian and Kazanian horn corals from the East European Platform were included in that Chinese genus by WEYER (1982) and WEYER & ILINA (1979), but our knowledge of the type material for *Paracaninia* is only fragmentary, so we may well be dealing with homeomorphs.

COMPARISON OF RUGOSE CORAL FAUNAS FROM AUTOCHTHONOUS DEPOSITS WITH THOSE OF ALLOCHTHONOUS TERRANES

Permian rugose coral faunas of western North America occupied the western cratonic margin of Pangaea and the margins of more westerly island chains and platforms accreted to North America as allochthonous terranes during the Mesozoic. The reader is referred to MONGER & NOKLEBERG (1996) for a summary of the interrelationships and tectonic history of these terranes. Cisuralian colonial rugose coral faunas occur along the margin of cratonic Pangaea and in the following allochthonous terranes: Northern Sierra, Eastern Klamath, Grindstone, Quesnellia, Stikinia, and Wrangellia. Guadalupian colonial corals are known from the Eastern Klamath, Hayfork, Quesnellia and Cache Creek terranes, but are unknown from the Pangaean margin of North America, except for new genera of possible Roadian age, recently discovered in Nevada. Lopingian corals are known only from the Hayfork Terrane, where rare, early Wuchiapingian colonial waagenophyllids occur.

The Permian positions of the allochthonous terranes relative to North America are uncertain.

Paleomagnetic data suggest that many of these terranes have been displaced northward (MONGER & NOKLEBERG 1996), but the longitudinal placement is more difficult. STEVENS & *al.* (1990) and BELASKY (1994) used data on modern corals and Permian colonial corals in different manners to postulate that some of the terranes bearing Cisuralian corals originated a considerable distance west of the Pangaean margin, but still well within the eastern part of the Panthalassan Ocean. Their conclusions are based on differences between the allochthonous faunas and those of cratonal North America, and the complete lack of similarity between western North American Cisuralian corals and coeval tethyan faunas of Asia. The new, comprehensive review of North American Permian colonial faunas, by FEDOROWSKI & *al.* (in prep.), has shown that the cratonic faunas are closely related to each other and are similar to the faunas of the arc terranes to the west.

The Guadalupian colonial coral faunas found in the Cache Creek, Eastern Klamath and Quesnellia allochthonous terranes are entirely tethyan in aspect. All other colonial rugose corals of the CAU Realm had become extinct near the end of the Cisuralian, with the possible exception of locally occurring Roadian? species on the cratonal margin of western-central U.S.A. In the Eastern Klamath Terrane (STEVENS & *al.* 1987) these Tethyan corals occur stratigraphically above faunas of CAU aspect, whereas in the Quesnellia terrane (NELSON & NELSON 1985) the tethyan corals occur in structurally complex successions and are associated with fault blocks containing older, non-tethyan faunas. The reason for the presence of tethyan corals and other tethyan fossils in North America is not known. They could have arrived by migration across Panthalassa using mid-ocean islands as dispersal points, by transport on moving ocean plates, or by a combination of these two methods.

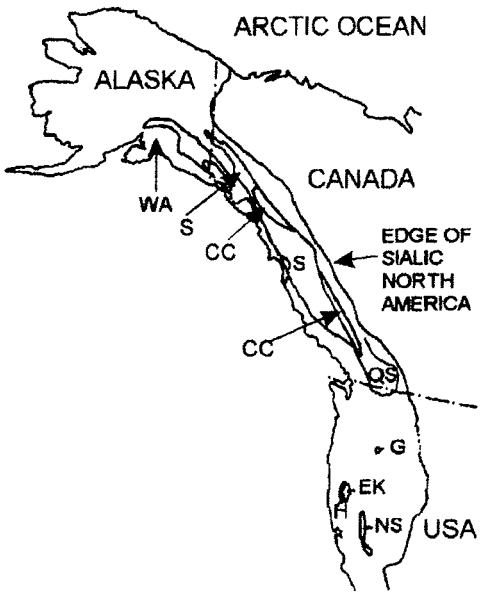

Fig. 2. Terrane map of northwestern North America showing terranes containing Permian rugose corals. Terranes: CC – Cache Creek, EK – Eastern Klamath, G – Grindstone, H – Hayfork, NS – Northern Sierra, QS – southern Quesnellia, including Harper Ranch subterrane, S – Stikinia, Wa – Wrangellia

COMPOSITION OF THE RUGOSE CORAL FAUNAS

Cisuralian

Our knowledge of the composition of a fossil fauna depends, in many instances, on the state of its preservation, the intensity with which it has been collected and investigated, and the approach to the taxonomy, as demonstrated by the following three examples:

1. In almost two hundred years of investigation of the central European Permian, no more than two, and perhaps only a single coral species belonging to *Calophyllum* have been discovered. Thus, there is practically no chance of collecting an abundant Zechstein coral fauna.

2. The mainly solitary, nondissepimental coral fauna from the Cisuralian and Guadalupian of southwestern Texas, which is the richest in the realm, was unknown until it was described in papers by ROSS & ROSS (1962, 1963) and FEDOROWSKI (1986, 1987). Thus, in earlier analyses that area would have been considered almost barren of corals. However, the richest, Roadian part of the fauna remains undescribed, making our analysis incomplete because we cannot include taxa from that part of the collection, although one of us (JF) has several thousand specimens at his disposal.

3. The morphology of colonial taxa of the families Durhaminidae and "Heritschioididae" is extremely variable, and the type material of some of the more common species has been inadequately studied. This has resulted in the introduction of many species, which we consider to be synonyms. Our conclusion is based on a review of

many of the type specimens and our analysis of the variability shown by all described colonial species from Permian strata of the CAU Realm (FEDOROWSKI & *al.*, in prep.). Thus, the actual number of species recognized by us is drastically reduced, compared to the number of species names that have been introduced into the literature. For instance, re-investigation of the holotype of *Stylastraea inconferta* LONSDALE, 1845 showed that species to be synonymous with 13 subsequently named species. A quantitative analysis based on such names taken uncritically from the literature would have been considerably different from the analysis we propose.

Although our analysis is strongly handicapped by factors such as those listed above, we have compensated for this to some extent by the use of unpublished data from undescribed faunas in western U.S.A. and western and northern Canada.

Eastern European Platform, Ural Mountains and northern Timan

KOSSOVAYA (1996) summarized the distribution data for uppermost Carboniferous and Cisuralian rugose corals from the eastern part of the Eastern European Platform, the Urals and northern Timan and proposed a coral zonation calibrated with the existing fusulinacean zonal scheme for the area. Also, she presented correlations within the CAU Realm, based on coral faunas (KOSSOVAYA 1996, fig. 11). Our distribution data do not confirm her conclusions concerning Vestspitsbergen, Eastern Nevada, the Klamath Mountains in California, and southwestern Texas, but we have adopted her biostratigraphic analysis for the Russian faunas. It confirms the succession of rugose coral faunules through the Carboniferous/Permian transition, previously outlined by FEDOROWSKI (1981, 1986) – i.e., the absence of colonial corals except for some Petalaxidae high in the Carboniferous; domination by Bothrophyllidae in Gzhelian strata; rapid disappearance of that family (except for the genus *Timania*) early in the Permian and their replacement by colonial taxa. KOSSOVAYA (1996) supplemented the data on Permian faunules of the Russian part of the CAU Realm with information on nondissepimental solitary corals, almost unknown from earlier studies. Following FEDOROWSKI (1997) we are not certain of the assignments of most of these nondissepimental corals to taxa of southwestern Texas, but the documentation of their occurrence by KOSSOVAYA (1996) is a welcome addition to our knowledge of the Russian coral fauna.

The succession of colonial taxa in the Russian sections, as reconstructed by KOSSOVAYA (1996, fig. 10) follows a very regular pattern, leading from domination by fasciculate morphotypes in the lower Asselian *Sphaeroschwagerina vulgaris-S. fusiformis* Biozone to domination by massive cerioid forms higher in the Asselian and into the Sakmarian. These are followed by the youngest fauna in the area, consisting mainly of cerioid-aphroid colonies, from the middle Sakmarian *Pseudofusulina verneuilli-P. uralica* Biozone to the Lower Artinskian *Pseudofusulina concavuta* Biozone. Our analysis (FEDOROWSKI & *al.*, *in prep.*) shows that several species and genera distinguished within those faunas by earlier Russian authors (*e.g.* STUCKENBERG 1895; DOBROLYUBOVA 1936a, b; SOSHKINA & *al.* 1941) and subsequently repeated by SIMAKOVA (1986) and KOSSOVAYA (1996, 1997) are synonyms. Without further discussion in this paper, we agree with WILSON (1998) that "*Heritschioides*" is absent from the Russian part of the CAU Realm. Also, we restrict the occurrence of *Thysanophyllum* to Lower Carboniferous strata and consider *Borealephyllum* KOSSOVAYA, 1997 and *Protowentzelella* PORFIRIEV, 1941 to be junior synonyms of *Stylastraea* LONSDALE, 1845. Thus, the massive colonial corals from the Urals and northern Timan are in fact restricted to *Kleopatrina, Stylastraea, Pseudocystophora, Protolonsdaleiastraea*, *Permastraea* and at least two new genera presently being described by us (FEDOROWSKI & *al.*, *in prep.*). The fasciculate genus *Heintzella* is also present. Other fasciculate colonies assigned by Russian authors to either *Corwenia* or "*Heritschioides*" and to *Ferganophyllum* require further study to be fully understood. Thus, we do not recognize them in this paper, but we confirm the occurrence of *Lytvophyllum* and *Tschussovskenia*.

Artinskian strata of the Eastern European Platform, northern Timan, and especially the Ural Mountains yield fairly abundant nondissepimental rugose coral faunas. Three cerioid-aphroid species, included by KOSSOVAYA (1996) in the genus *Protolonsdaleiastraea* are present in the Lower Artinskian *Pseudofusulina concavuta* Biozone of the Timan Mountains. SOSHKINA & *al.* (1941) summarized earlier descriptions and described some new Artinskian taxa. Many identi-

fications of genera included in that paper do not conform to modern taxonomic practices and need careful revision. Also, the precise stratigraphic positions of most species are unknown. The positions of only a few species have been documented by SIMAKOVA (1986). These include two species of *Amplexocarinia*, two species of *Ufimia*, and a single species of *Cyathocarinia, Hexalasma* and *Soshkineophyllum*, assigned to the Lower Artinskian *Pseudofusulina concavuta-Ps. pedissequa* Biozone, and one species of *Amplexocarinia*, assigned to the Upper Artinskian *Ps. juresanensis-Parafusulina lutugini* Biozone. Among the Artinskian taxa described by SOSHKINA & *al.* (1941) and not recognized by SIMAKOVA (1986) or KOSSOVAYA (1996), we were able to confirm the occurrence of *Calophyllum, Lophophyllidium (Lophbillidium)* (and perhaps the nominative subgenus *Lophophyllidium*), *Lophocarinophyllum, Paralleynia, Plerophyllum* and *Pseudowannerophyllum*. The exact stratigraphic position of those genera is unknown. Thus, following the original descriptions, we consider them to be Artinskian. Following FEDOROWSKI (1974, 1986) we do not accept the reported occurrence in the Ural Mountains of the genera *Timorphyllum* and *Verbeekiella*, both of which are restricted to the Tethys Realm.

Svalbard Archipelago

Cisuralian rugose corals are abundant in the Svalbard Archipelago, but their ages are uncertain. They are present on several islands of the Archipelago, but are best known from the Hornsund area of Vestspitsbergen (FEDOROWSKI 1997). Unfortunately, lack of associated index fossils has prevented a reliable age determination for that abundant fauna. FEDOROWSKI (1997) considered its age to be Sakmarian by comparison with other coral faunas of the realm. It consists mostly of cerioid colonial corals of the genera *Stylastraea, Kleopatrina* and a new, undescribed genus. Cerioid-aphroid colonies are not abundant and, in contrast to the succession of the Urals and northern Timan, they occur stratigraphically below the cerioid genera listed above. The cerioid-aphroid colonies are accompanied by abundant representatives of the Bothrophyllidae and a few species of the fasciculate genera *Heintzella* and *Tschussovskenia*, which are less common in higher strata (FEDOROWSKI 1965, 1967, 1986). Solitary nondissepimental taxa have not yet been found. Also, the genus "*Heritschioides*", which is common in North America, is absent from this part of Vestspitsbergen, as it is from the Urals and northern Timan. The occurrence of this fauna reflects a short transgressive episode in the history of the area, and its rapid disappearance coincides with a fairly abrupt regression.

The most complete Carboniferous-Permian succession occurs in Central Vestspitsbergen. An abundant coral fauna was described from that area by HERITSCH (1939), but unfortunately, the type material for that monograph appears to have been lost, thus making taxonomic revision impractical. Also, the stratigraphic occurrence of the fauna is mostly unknown. Some introductory identifications by FORBES & *al.* (1958) added little to our understanding of the Central Vestspitsbergen fauna. More recently, however, SOMERVILLE (1997) began a restudy of the stratigraphic distribution and taxonomy of the rugose corals from this area. He recognized fairly abundant solitary dissepimental corals low in the Asselian-Sakmarian succession, accompanied by fasciculate colonies of *Heintzella* and *Tschussovskenia* and, higher in the section (probably in Sakmarian strata), by massive colonies of *Kleopatrina* and *Stylastraea*. He did not mention cerioid- aphroid taxa. *Cystophora svalbardica* HERITSCH, 1939 is the only cerioid-aphroid coral described from this area. Unfortunately, the only location given for this specimen is "east side of Green Harbour". Two species assigned by HERITSCH (1939) to *Orionastraea* were collected from the Hornsund area and belong to *Stylastraea*. Thus, it appears that cerioid-aphroid corals are extremely rare in Central Vestspitsbergen.

On Bear Island, the Carboniferous-Permian succession resembles that of Central Vestspitsbergen. Unfortunately, the abundant Bear Island fauna, collected in the late seventies by one of us (JF) and housed in Paleontologisk Museum in Oslo, has never been described. Introductory field identifications by J. FEDOROWSKI indicate that cerioid colonies of *Kleopatrina* and *Stylastraea* greatly outnumber other rugosan growth forms, but bothrophyllids and *Heintzella* are present as well.

Canadian Arctic Archipelago

Cisuralian rugose corals are abundant in the Sverdrup Basin, but most of them remain unde-

scribed. From papers by SALTER (1855), TSCHERNYSCHEV & STEPANOV (1916), MINATO (1960), HARKER (1960) and introductory identifications by two of us (E.W.B and J.F.) it is obvious that the rugose coral fauna comprises all growth forms, with fasciculate colonial corals prevailing slightly over massive corals and solitary nondissepimental taxa remaining in the minority. The latter group occurs mainly in the middle to upper Sakmarian part of the succession. The succession of growth forms appears to be similar to that described by KOSSOVAYA (1996), but this cannot be verified at present. Colonial rugose corals are very rare in the lowest part of the Asselian succession, where only a single occurrence of "Heritschioides" is known. This level contains fairly abundant solitary, dissepimental *Siedleckia*, *Timania*, and *Fedorowskiphyllum*. These and related genera also occur in varying abundance throughout younger Cisuralian strata. Younger, upper Asselian to lower Sakmarian strata are dominated by fasciculate genera, including *Paraheritschioides* and *Heintzella*, accompanied by *Durhamina,* and *Tschussovskenia*. Also at this level there are a few cerioid durhaminid corals belonging to *Pararachnastraea* and a new, undescribed genus. *Kleopatrina*, *Stylastraea* and *Pararachnastraea* are the most abundant genera in the overlying, mid-Sakmarian ? part of the succession. *Protolonsdaleiastraea* and other cerioid-aphroid forms dominate the upper part of the succession, ranging through the upper half of the Sakmarian and into strata of possible early Artinskian age. These are accompanied by *Permastraea* and the new cerioid durhaminid genus referred to above.

East-central Alaska

A small Asselian/Sakmarian fauna, described by ROWETT (1969) from the Wrangellia Terrane in east-central Alaska, contains taxa in common with both autochthonous and allochthonous faunas elsewhere in the CAU Realm. These include colonial species of "*Heritschioides*" and *Durhamina*, also found in allochthonous strata of east-central British Columbia and arctic mainland Canada. In addition, undescribed collections available to one of us (CHS) contain the genera ?*Lytvophyllum*, ?*Stylastraea*, *Kleopatrina, Stikineastraea* and ?*Protolonsdaleiastraea*. Also present are dissepimental solitary corals with complex axial structures, at least some of which belong to *Fedorowskiphyllum*. Such solitary corals also occur in allochthonous terranes in northwestern British Columbia (undescribed) and California (WILSON 1982). The non-dissepimental coral taxa identified by ROWETT (1975), and briefly re-interpreted by FEDOROWSKI (1997) as *Allotropiochisma, Calophyllum, Euryphyllum* and *Soshkineophyllum*, are typical for the youngest coral-bearing strata of Vestspitsbergen, Greenland and the Sverdrup Basin. Thus, it may be suggested that rugose coral faunas persisted in Alaska as long as in the other arctic areas listed and became extinct when extrinsic conditions became unacceptable for coral growth.

British Columbia

The Cisuralian rugose corals of British Columbia have been only partly described (WU & *al.* 1985; STEVENS & RYCERSKI 1983, 1989) or preliminarily identified by one of us (EWB). They occur in the thin, cratonic succession of east-central British Columbia and in the accreted Stikinia and Quesnellia terranes of northwestern and south-central British Columbia.

The undescribed, upper Asselian to mid-Sakmarian corals of the autochthonous succession in east-central British Columbia consist almost entirely of colonial forms belonging to taxa that are widespread in correlative strata of the CAU Realm. Precise age ranges are not yet firmly established but there appears to be an older, upper Asselian to lower Sakmarian fauna containing the fasciculate genera "*Heritschioides*", *Paraheritschioides*, *Heintzella*, and *Durhamina*, as well a notable occurrence of the cerioid-aphroid genus *Protolonsdaleiastraea*. Cerioid-aphroid forms also occur this low in the succession in the Svalbard Archipelago and in the Stikinia Terrane of northwestern British Columbia, as noted elsewhere. This fauna is overlain by a younger, lower to middle Sakmarian fauna dominated by cerioid colonies of *Stylastraea* and *Kleopatrina*, associated with fasciculate *Durhamina*.

A rich fauna of Asselian to lower ? Sakmarian colonial and solitary, dissepimented corals (WU & *al.* 1985; STEVENS & RYCERSKI 1989) occurs in the lower part of the Permian succession of the allochthonous Stikinia Terrane of northwestern British Columbia (GUNNING & *al.* 1994). The vertical succession of taxa within this terrane is not

well established, but the age range of the fauna appears to be restricted to Asselian and early Sakmarian, based on associated fusulinacean faunas. Genera present include: Petalaxidae – *Cystolonsdaleia*, *?Lytvophyllum*, *Petalaxis*; "Heritschioididae" – *Heintzella*, "*Heritschioides*", *Paraheritschoides*, *?Protolonsdaleiastraea*, *Stikineastraea*; Durhaminidae – *Durhamina*, *Pararachnastraea*, and two new cerioid-aphroid genera. The latter constitute a third occurrence of cerioid-aphroid forms at a relatively low stratigraphic level. The presence of *Petalaxis* and *Cystolonsdaleia*, which are absent from more northerly successions of North America, the Svalbard Archipelago and Russia (BAMBER & FEDOROWSKI 1998), is a feature in common with more southerly faunas of the western U.S.A. and Bolivia. Such complex colonial genera as *Langenheimia* and new, unnamed genera with extra septal lamellae, found in more southerly successions, are absent from northwestern British Columbia. Solitary corals occurring in the Stikinia Terrane fauna have not yet been studied in detail, but appear to comprise mainly Bothrophyllidae similar to those elsewhere in CAU Realm, and also include forms with complex axial structures known from east-central Alaska (ROWETT 1969) and Eastern Klamath Terrane in California (WILSON 1982).

In south-central British Columbia, the Quesnellia Terrane contains a small, undescribed Asselian colonial coral fauna, which includes the genera *Petalaxis*, *Cystolonsdaleia* and *?Lytvophyllum*, in common with the Stikinia Terrane and other, more southerly allochthonous terranes of the CAU Realm. Also occurring in this structurally complex succession, however, is a lower Guadalupian species of *Parawentzelella*, a genus with tethyan affinities, as noted below.

West-central U.S.A.

In west-central U.S.A., Cisuralian colonial rugose corals are present in both the allochthonous terranes and the autochthonous rocks of the Pangaean margin. The best succession of allochthonous corals, associated with fusulinacean zones (SKINNER & WILDE 1965), occurs in the Eastern Klamath terrane. This fauna was described by WILSON (1982, 1985) and is apparently the richest of all those represented in the allochthonous terranes of North America. Similarly, the autochthon to the east has yielded the richest fauna known from the Pangaean cratonal margin. Several workers, including EASTON (1960), STEVENS (1967), WILSON (1991, 1994), and WILSON & LANGENHEIM (1962, 1993) have studied this fauna, with many additional undescribed forms collected by one of us (CHS) and identified by us in 1996.

In the Eastern Klamath terrane, relatively simple fasciculate corals probably belonging to *Paraheritschioides* first appear in the Upper Carboniferous along with solitary dissepimental rugose corals. The cerioid genus *Petalaxis* appears in the lowermost Permian strata, followed by a cerioid durhaminid and several species of "*Heritschioides*". Younger, middle Asselian corals of fusulinacean Zone D include cerioid-aphroid genera and fasciculate "heritschioidids" with septal lamellae outnumbering major septa. *Kleopatrina* with extensive development of lonsdaleoid dissepiments occurs in fusulinacean Zone F (lower Sakmarian). In the youngest beds some of the corallites are very large, reaching diameters of 27 mm and 16 mm in fasciculate and cerioid-aphroid corals, respectively. Thus, the sequence of appearance of different coral morphotypes in this area is similar to that in other parts of the CAU Realm. In the faunas of the Eastern Klamath terrane we recognize the following colonial coral genera: *Petalaxis*, *Cystolonsdaleiastraea*, *?Lytvophyllum*, *Durhamina*, two new genera of cerioid durhaminids, *Paraheritschioides*, a new "heritschioidid" genus with extra septal lamellae, *Stylastraea*, *Kleopatrina*, *Langenheimia*, *Pseudocystophora*, and a new cerioid-aphroid genus.

In the autochthon of west-central U.S.A. the sequence of appearance of coral morphotypes is similar to that in the Eastern Klamath terrane, but some taxa appeared later if the correlations used here are correct. Fasciculate corals, including *Paraheritschioides*, appear in the Upper Carboniferous. In the lowermost Permian strata cerioid corals belonging to the simple genus *Stylastraea* and simple durhaminid fasciculate corals are present. These are succeeded by the more complicated cerioid genus *Kleopatrina*. Higher in the section (in the Artinskian) there are fasciculate durhaminids with extra septal lamellae and cerioid-aphroid genera. Interestingly, whereas "*Heritschioides*" is abundant in Asselian rocks of the allochthonous terranes, the genus may not occur in the autochthon below the Artinskian.

Finally, cerioid forms with extra septal lamellae occur in the youngest beds containing colonial corals. These colonial corals also appear to be the youngest colonial corals to originate in the CAU Realm, probably having lasted through the Artinskian and possibly into the early Guadalupian (Roadian).

Genera recognized in the autochthonous part of west-central U.S.A. include *Tschussovskenia*, *Petalaxis*, *Durhamina*, a new durhaminid genus with a continuous axial column, 3 new cerioid durhaminid genera, *Heintzella*, *Paraheritschioides*, a new durhaminid genus with extra septal lamellae, *Stylastraea*, *Kleopatrina*, *Permastraea*, ?*Protolonsdaleiastraea*, and "*Heritschioides*".

Rare colonial rugose corals similar to those in the autochthon of west-central U.S.A. are present in northwestern Mexico, Guatemala, Bolivia, and Peru (*e.g.* ROWETT & WALPER 1972, WILSON 1990, STEVENS 1995), but our present knowledge of those faunas is insufficient for a meaningful discussion.

Southwestern Texas and southeastern New Mexico

The rugose coral fauna of southwestern Texas and adjacent part of New Mexico (Glass Mountains and Guadalupe Mountains) can best be characterized as follows: paucity of massive colonial taxa; impoverishment of fasciculate colonial and solitary dissepimental taxa and restriction of these groups mainly to the Upper Carboniferous and lower Cisuralian; abundance of solitary nondissepimental taxa, continuing into the Guadalupian, when coral faunas were generally impoverished or absent from other areas of the CAU Realm. Those characteristics, combined with the presence of the endemic suborder Diffingiina, led FEDOROWSKI (1997) to propose the name Diffingiina Province for this area.

In addition to the Diffingiina, represented by two families, three genera and several species, fourteen nondissepimental rugose coral species have been described from this area. The most abundant and diversified genera are *Assimulia*, *Lophophyllidium* and *Paraduplophyllum*, each represented by two subgenera and several species. For some of these species, very large numbers of specimens were investigated (FEDOROWSKI 1987). *Allotropiochisma*, *Bradyphyllum*, *Euryphyllum*, *Falsiamplexus*, *Lophotichium* and *Lytvolasma* should be mentioned as being very common and abundant. *Bradyphyllum* and *Lophotichium* are genera rooted in the Carboniferous and present in both the Tethys and CAU realms. The greatest number of species and specimens in the Cisuralian fauna of the Diffingiina Province occur in the upper Wolfcampian part of this succession. In undescribed collections, the richest faunas are those from the Cisuralian and the Roadian. The youngest corals of the Diffingiina Province are found in Capitanian strata. A drastic change in environmental conditions ended the history of this coral province.

GUADALUPIAN

As mentioned above, the richest Guadalupian coral fauna occurs in the Diffingiina Province. According to the description of rugose corals from Greenland by FLÜGEL (1973), the Guadalupian fauna from the northeastern part of this Island should be considered as the second richest. However, re-description and revision of part of that fauna by FEDOROWSKI (1982) and by FEDOROWSKI & BAMBER (*in prep.*) show that an excessive number of taxa has been recognized (for instance, FLUGEL's five new species of *Calophyllum* all belong to one previously described species) and that some important taxa have not been recognized. In our opinion the Greenland Guadalupian fauna is represented by the following: *Calophyllum columnare* (SCHLOTHEIM, 1813), which is common for the entire northern part of the realm, including Alaska; *Paracaninia variabilis* (SOSHKINA, 1941), which is almost as widespread as *C. columnare*; three species of *Allotropiochisma* (one in common with the Sverdrup Basin fauna); and single species of *Tachylasma, Ufimia* (new species in common with Sverdrup Basin), probably *Leonardophyllum* and *Soshkineophyllum*. Most of these genera have long stratigraphic ranges and are cosmopolitan. Only *Leonardophyllum*, if truly present in Greenland, is a surprising newcomer from the south.

A fauna very similar to that of northeastern Greenland, and equally diverse, has been described by FEDOROWSKI & BAMBER (*in prep.*) from the Sverdrup Basin in the Canadian Arctic Archipelago. It contains two species of *Allotropiochisma* (one unnamed), two species of *Euryphyllum*, and single species of *Calophyllum*

(*C. columnare*), *Lytvolasma*, *Soshkineophyllum* (also found in correlative strata of Svalbard) and *Ufimia*. Although represented by relatively few specimens, this fauna is surprisingly diverse.

Some rugosan taxa from the Kapp Starostin Formation of Central Vestspitsbergen are identical with those of Greenland and the Sverdrup Basin, but further analysis of the content of the Kapp Starostin fauna is not possible because no modern, detailed investigation of these corals has been completed. Preliminary lists and illustrations of the Kapp Starostin corals were published by EZAKI & KAWAMURA (1992) and EZAKI (1997).

The rugose coral fauna of the Central European Basin and Eastern European Platform is taxonomically monotonous, although commonly rich in specimens. Revisions by WEYER (1979, 1997), WEYER & ILINA (1979) and FEDOROWSKI & BAMBER (*in prep.*) indicate that no more than two species of *Calophyllum (C. columnare* and *C. quadrifidum*) and *Paracaninia variabilis* occur in this large area. *Ufimia* and *Allotropiochisma* could each be represented by one species as well, but such occurrences are doubtful.

Precise stratigraphic relationships and ages are difficult to establish for the Guadalupian occurrences discussed above. They have all been assigned to the Kazanian or correlated with that stage, but the term Kazanian may, in some instances, equate to the entire Guadalupian. The age of the Sverdrup Basin fauna has been fairly well established as Wordian (Middle Guadalupian) and early Kazanian on its association with rare ammonoids (NASSICHUK 1995, p. 218), brachiopods (THORSTEINSSON 1974, p. 72) and palynomorphs. In eastern Greenland, the youngest beds of the Permian succession contain early Wuchiapingian (=earliest Lopingian) ammonoids of the genus *Cyclolobus* (NASSICHUK, 1955, p. 229). Older strata in the area, from above the coral-bearing limestone, have yielded conodonts of late Wordian or Capitanian age (NASSICHUK 1995, p. 230), thus indicating a probable upper limit of Wordian for the age of the Greenland coral fauna. The brachiopod fauna of the coral-bearing Kapp Storostin Formation of Vestspitsbergen (see above), was equated by NAKAMURA & *al.* (1992, p. 83) with that of the Trold Fiord Formation (Wordian), which contains part of the solitary coral fauna of the Sverdrup Basin, and also with the brachiopod fauna associated with the Greenland corals. They also noted a correlation between the brachiopod faunas of Greenland and Vestspitsbergen and those of the Zechstein in the Central European Basin. Thus, from several lines of evidence, it would appear that a Wordian (=early? Kazanian) age may be assigned to all occurrences of this widespread solitary coral fauna, which includes some of the youngest corals in the CAU Realm.

THE NEWCOMERS

As discussed earlier in the paper, with the possible exception of the youngest autochthonous faunas of the west-central U.S.A., all Cisuralian colonial rugose coral faunas of the CAU Realm, along the margins of Pangaea and in adjacent allochthonous arc terranes (Text-fig. 2), became extinct prior to the beginning of the Guadalupian. During mid- Guadalupian (Wordian) to early Lopingian (early Wuchiapingian) time, however, an impoverished colonial coral fauna of obvious tethyan affinities developed on the Palaeopacific carbonate buildups presently preserved in allochthonous terranes of western North America (NELSON & NELSON 1985; STEVENS & *al.* 1987; BAMBER, Geological Survey of Canada collections). Waagenophyllids identified to date include *Waagenophyllum*, *Parawentzelella*, and possibly *Pseudohuangia* (newly discovered, not yet described), one or more of which occurs in the following terranes: the Quesnellia and Eastern Klamath terranes, which also contain Cisuralian corals of the CAU Realm; the Cache Creek terrane, in which fossils as old as mid-Carboniferous have strong tethyan or mixed tethyan-North American affinities; and in limestone blocks of the Hayfork terrane. As previously noted, such waagenophyllid corals are typical of the tethyan Realm and the means by which they arrived in North America has not been established.

Unlike the colonial waagenophyllids, the Guadalupian solitary, nondissepimental corals known from Texas, arctic Canada, Greenland and Svalbard (see above) do not appear to be newcomers to the CAU Realm for the following reasons: 1) There was a permanently developing fauna in the Diffingiina Province to serve as a potential source for the fauna of other areas. 2) Most, if not all of the solitary, nondissepimental genera occurring in the Guadalupian are known to occur in the Cisuralian as well, thus providing the possibility for a natural lineage to develop. 3) All species present are endemic to the realm,

although the wide geographic distribution suggests that they had long-living larvae, and therefore the potential ability to cross Panthalassa. Most of them, except for *Lytvolasma*, belong to cosmopolitan genera.

CONCLUSIONS

Two distinct rugose coral faunal realms (Cordilleran-Arctic-Uralian and Tethys) developed on the eastern and western margins of Pangaea during the Early Permian (Cisuralian), although several families or suborders occurring in both realms have common Carboniferous and/or older ancestors.

A clear distinction between the rugose corals of the CAU Realm and those of the Tethys Realm can be made only in Cisuralian strata. Differentiation between the realms is more difficult in Guadalupian and Lopingian strata, because of the extinction of CAU colonial corals in late Cisuralian or earliest Guadalupian time, followed by the Guadalupian development of cosmopolitan, non-dissepimental taxa, and the appearance in the western allochthonous terranes of colonial corals with tethyan affinities.

Corals of the CAU Realm occur in autochthonous, cratonic and pericratonic successions deposited on the northwestern and western margins of Pangaea, from the Urals and Svalbard Archipelago through arctic and western North America and into South America. They also are found in a number of allochthonous arc and accretionary complex terranes in western North America. The lack of tethyan Cisuralian corals in the arc terranes shows that these terranes lay on the eastern side of the Panthalassan Ocean during Cisuralian time. Comparison of the taxonomic composition of the Cisuralian autochthonous faunas with that of coeval faunas in the arc terranes suggests that the arc terranes were close enough to allow regular faunal exchange with near-shore areas to the east. During the Guadalupian a small fauna of tethyan colonial corals appeared in several of the arc and accretionary complex terranes, but did not appear on the margins of cratonal Pangaea, where a coeval fauna of solitary corals belonging to cosmopolitan genera developed locally.

The abundance of ecologically restricted, colonial rugose coral faunas in the Asselian to lower Artinskian of the northern parts of the CAU Realm (northern Urals, northern Timan, Svalbard Archipelago, arctic North America and British Columbia) is consistent with a low latitude position for those areas during much of Cisuralian time. As a result of northward movement of Pangaea into cooler waters by early to mid-Artinskian time, these corals were exterminated from the northern areas, but persisted throughout much of the Artinskian and possibly in the early Guadalupian (Roadian) in the more southerly autochthonous successions of the western U.S.A.

REFERENCES

BAMBER, E.W. & FEDOROWSKI, J. 1988. Biostratigraphy and systematics of Upper Carboniferous cerioid rugose corals, Ellesmere Island, arctic Canada. *Geological Survey of Canada Bulletin*, **511**, 1-126. Ottawa.

BELASKY, P. 1994, Biogeography of Permian corals and the determination of longitude in tectonic reconstructions of the Paleopacific region. *In*: A.F. EMBRY, B. BEAUCHAMP & D.J. GLASS (*Eds*), Pangea: Global environments and resources. *Canadian Society of Petroleum Geologists, Memoir* **17**, 621-646. Calgary.

DOBROLYUBOVA, T.A. 1936a. Upper Carboniferous corals of the western slope of the central Urals and their stratigraphic significance. *Trudi Vsesoyuznogo Nauchno-issledovatelskogo Instituta, Mineralnogo Seriya*, **81**, 1-68. Moskva. [*In Russian*].

— 1936b. Rugose corals of the Upper Carboniferous and Lower Permian of the northern Urals. *Trudy polyarnoi komissii, Akademiya Nauk SSSR*, **28**, 158 p. Moskva. [*In Russian*].

EASTON, W.H. 1960. Permian corals from Nevada and California. *Journal of Paleontology*, **34**, 570-583. Tulsa.

EZAKI, Y. 1997. Cold-water Permian Rugosa and their extinction in Spitsbergen. *Boletin de la Real Sociedad Epanola de Historia Natural (Sec. Geol.)*, **92**, 381-388. Madrid.

EZAKI, Y. & KAWAMURA, T. 1992. Carboniferous-Permian corals from Skansen and Festningen, central Spitsbergen: their faunal characteristics. *In*: K. NAKAMURA (*Ed.*), Investigations on the Upper Carboniferous-Upper Permian succession of West Spitsbergen 1989-1991, pp. 59-75. *Hokkaido University Press*; Sapporo.

FEDOROWSKI, J. 1965. Lower Permian Tetracoralla of Hornsund, Vestspitsbergen. *In*: K. BIRKENMAJER (*Ed.*), Geological Results of the Polish 1957-1958, 1959, 1960 Spitsbergen Expeditions. Part 4. *Studia Geologica Polonica*, **17**, 7-173. Warszawa.

— 1967. The Lower Permian Tetracoralla and Tabulata from Treskelodden, Vestspitsbergen. *Norsk Polarinstitutt Skrifter*, **142**, 5-44. Oslo.
— 1971. Aulophyllidae (Tetracoralla) from the Upper Viséan of Sudetes and Holy Cross Mountains. *Palaeontologia Polonica*, **24**, 1-137. Warszawa.
— 1974. The Upper Palaeozoic tetracoral genera *Lophophyllidium* and *Timorphyllum*. *Palaeontology*, **17**, 441-473. London.
— 1981. Carboniferous corals: distribution and sequence. *Acta Palaeontologica Polonica*, **26** (2), 87-160. Warszawa.
— 1982. Some rugose corals from the Upper Permian of East Greenland. *Grønlands Geologiske Undersøgelse, Rapport* **108**, 71-91. Copenhagen.
— 1986. The rugose coral faunas of the Carboniferous/Permian boundary interval. *Acta Palaeontologica Polonica*, **31** (3-4), 253-275. Warszawa.
— 1987. Upper Palaeozoic rugose corals from southwestern Texas and adjacent areas: Gaptank Formation and Wolfcampian corals. Part 1. *Palaeontologia Polonica*, **48**, 1-271. Warszawa.
— 1997. Diachronism in the development and extinction of Permian Rugosa. *Geologos*, **2**, 59-164. Wrocław.

FLÜGEL, H.W. 1973. Rugose Korallen aus dem oberen Perm Ost-Grönlands. *Verhandlungen der Geologischen Bundesanstalt, Jhrg. 1973*, **1**, 1-57. Wien.

FONTAINE, H. 1961. Les Madréporaires Paleozoiques du Viet-nam, du Laos et du Cambodge. *Archives Geologiques du Viet-Nam*, **5**, 1-276. Saigon.

FORBES, C.L., HARLAND, W.B. & HUGHES, N.F. 1958. Palaeontological evidence for the age of the Carboniferous and Permian rocks of Central Vestspitsbergen. *Geological Magazine*, **95** (6), 465-490. Hertford.

GOLONKA, J., ROSS, M.I. & SCOTESE, C.R. 1994. Phanerozoic paleogeographic and paleoclimatic modeling maps. *In*: A.F. EMBRY, B. BEAUCHAMP & D.J. GLASS (*Eds*), Pangea: global environments and resources. *Canadian Society of Petroleum Geologists, Memoir*, **17**, 1-47. Calgary.

GUNNING, M.H., BAMBER, E.W., BROWN, D.A., RUI, L., MAMET, B.L. & ORCHARD, M.J. 1994. The Permian Ambition Formation of northwestern Stikinia, British Columbia. *In*: A.F. EMBRY, B. BEAUCHAMP & D.J. GLASS (*Eds*), Pangea: global environments and resources. *Canadian Society of Petroleum Geologists, Memoir*, **17**, 589-619. Calgary.

HARKER, P. 1960. Corals, brachiopods, and molluscs of Grinnell Peninsula, part 3, p. 39-79. *In*: P. HARKER & R. THORSTEINSSON, Permian rocks and faunas of Grinnell Peninsula, Arctic Archipelago. *Geological Survey of Canada Bulletin*, **309**, 1-89. Ottawa.

HERITSCH, F. 1939. Die Korallen des Jungpalaozoikums von Spitzbergen. *Arkiv for Zoologi*, **31A** (16), 1-138. Stockholm.

HILL, D. 1938-41. A monograph of the Carboniferous rugose corals of Scotland. *Palaeontographical Society*, 1-213. London.

JIN, YUGAN 1996. A global chronostratigraphic scheme for the Permian System: Two decades of the Permian Subcommission. *Permophiles, Newsletter of the Subcommission on Permian Stratigraphy*, **28**, 4-9. Calgary.

KOSSOVAYA, O.L. 1996. Correlation of uppermost Carboniferous and Lower Permian rugose coral zones from the Urals to western North America. *Palaios*, **11**, 71-82. Tulsa.
— 1997. Rugosa of the typical sections of the Gzhelian-Artinskian stages of northern Timan and the western slope of the Urals. *In*: G.A. STUKALINA (*Ed.*), Atlas of standard complexes of Palaeozoic benthonic fauna of northeastern European Russia. *P. Karpniskyi All-Russian Scientific-Research Geological Institute (VSEGEI)*, 53-96. St. Petersburg. [*In Russian*].

MINATO, M. 1960. Eine permische Koralle von König Oscarland im nordwestlischen Ellesmereland. *Stockholm Contributions in Geology*, **6**, 25-36. Stockholm.

MONGER, J.W.H. & NOKLEBERG, W.J. 1996. Evolution of the northern North American Cordillera: generation, fragmentation, displacement and accretion of successive North American plate-margin arcs. *In*: A.R. COYNER & P.L. FAHEY (*Eds*), Geology and ore deposits of the American Corillera. *Geological Society of Nevada Symposium Proceedings*, 1133-1152. Reno – Sparks.

NAKAMURA, K., TAZAWA, J., & KUMAN, F. 1992. Permian brachiopods of the Kapp Starostin Formation, west Spitsbergen. *In*: K. NAKAMURA (*Ed.*), Investigations on the Upper Carboniferous-Upper Permian succession of West Spitsbergen, 1989-1991. pp. 77-85. *Hokkaido University Press*; Sapporo.

NASSICHUK, W.W. 1995. Permian ammonoids in the arctic regions of the world. *In*: P.A. SCHOLLE, T.M. PERYT & D.S. ULMER-SCHOLLE (*Eds.*), The Permian of northern Pangea, **1**, 210-235. Berlin – Heidelberg.

NELSON, S.J. & NELSON, E.R. 1985. Allochthonous Permian micro- and macrofauna, Kamloops area, British Columbia. *Canadian Journal of Earth Sciences*, **22** (3), 442-451. Ottawa.

RODRIGUEZ, S., SANDO, W.J. & KULLMAN, J. 1986. Utility of corals for biostratigraphic and zoogeographic analyses of the Carboniferous in the Cantabrian Mountains, northern Spain. *Trabajos de geologia Universidad de Oviedo*, **16**, 37-60. Oviedo.

ROSS, J.P. & ROSS, C.A. 1962. Pennsylvanian, Permian rugose corals, Glass Mountains, Texas. *Journal of Paleontology*, **36**, 1163-1188. Tulsa.

— 1963. Late Paleozoic rugose corals, Glass Mountains, Texas. *Journal of Paleontology*, **37**, 409-420. Tulsa.

ROWETT, C.L. 1969. Upper Paleozoic stratigraphy and corals from the east-central Alaska Range, Alaska. *Arctic Institute of North America, Technical Paper*, **23**, 120 p. Montreal.

— 1975. Stratigraphic distribution of Permian corals in Alaska. *In*: M. CHURKIN, Jr. (*Ed.*), Geologic and paleogeographic setting of Paleozoic corals in Alaska. Part D. *United States Geological Survey Professional Paper*, **823-A-D**, 59-75. Washington.

ROWETT, C.L. & WALPER, J.L. 1972. Permian corals from near Huehuetenango, Guatemala. *Pacific Geology*, **5**, 71-80. Tokyo.

SALTER, J.W. 1855. Account of the Arctic Carboniferous fossils. In: Last of the Arctic Voyages; being a narrative of the expedition in H.M.S. Assistance, under the command of Captain Sir Edward Belcher, **2**, 377-389. London.

SIMAKOVA, M.A. 1986. Tetracorals – Rugosa. *In*: B.P. GORSKII & M.A. KALMIKOVA (*Eds*), Atlas of characteristic complexes of Permian fauna and flora of the Urals and Russian Platform. *Vsesoyuznii Ordena Lenina Nauchno-issledovatelskii Geologicheskii Institut im. A. P. Karpinskogo*, **331**, 327 p. *Nedra*; Leningrad. [*In Russian*].

SKINNER, J.W. & WILDE, G.L. 1965. Permian biostratigraphy and fusulinid faunas of the Shasta Lake area, northern California. *University of Kansas Paleontological Contributions, Protozoa*, **6**, 1-98. Topeka.

SOMERVILLE, I.D. 1997. Biostratigraphy and biofacies of Upper Carboniferous – Lower Permian rugose coral assemblages from the Isfjorden area, central Spitsbergen. *Boletin de la Real Sociedad Española de Historia Natural (Sección Geológica)*, **92**, 365-380. Madrid.

SOSHKINA, E.D., DOBROLYUBOVA, T.A. & PORFIRIEV, G.S. 1941. Permian Rugosa of the European part of the USSR. *Akademiya Nauk SSSR, Paleontologicheskii Institut*, **5**(3)(1), 1-304. Moskva. [*In Russian*].

STEVENS, C.H. 1967. Leonardian (Permian) compound corals of Nevada. *Journal of Paleontology*, **41**, 423-427. Tulsa.

— 1982. The Early Permian *Thysanophyllum* coral belt: another clue to Permian plate-tectonic reconstructions. *Geological Society of America Bulletin*, **93**, 798-802. Boulder.

— 1995. New species of the Early Permian cerioid coral *Kleopatrina* from northwest Chihuahua, Mexico. *Journal of Paleontology*, **69**, 1176-1179. Tulsa.

STEVENS, C.H. & RYCERSKI, B. 1983. Permian colonial corals in the western Americas – aids in positioning of suspect terranes. *In*: C.H. STEVENS (*Ed.*), Pre-Jurassic rocks in western North American suspect terranes. *Society of Economic Paleontologists and Mineralogists*, 23-36. Los Angeles.

— & 1989. Early Permian colonial rugose corals from Stikine River Area, British Columbia, Canada. *Journal of Paleontology*, **63**, 158-181. Tulsa.

STEVENS, C.H., MILLER, M.M. & NESTELL, M. 1987. A new Permian waagenophyllid coral from the Klamath Mountains, California. *Journal of Paleontology*, **16** (4), 690-699. Tulsa.

STEVENS, C.H., YANCEY, T.E. & HANGER, R.A. 1990. Significance of the provincial signature of Early Permian faunas of the eastern Klamath Terrane. *In*: D.S. HARWOOD & M.M. MILLER (*Eds*), Paleozoic and Early Mesozoic paleogeographic relations; Sierra Nevada, Klamath Mountains and related terranes. *Geological Society of America, Special Paper*, **255**, 201-218. Boulder.

STUCKENBERG, A. 1895. Corals and bryozoans of the Carboniferous deposits of the Urals and Timan. *Trudy Geologicheskogo Komiteta*, **10** (3), 1-244. Sankt Petersburg. [*In Russian*]

THORNSTEINSSON, R. 1974. Carboniferous and Permian stratigraphy of Axel Heiberg Island and western Ellesmere Island, Canadian Arctic Archipelago. *Geological Survey of Canada Bulletin*, **224**, 1-115. Ottawa.

TSCHERNYSCHEV, T. & STEPANOV, P. 1916. Oberkarbonfauna von König Oskars und Heibergs Land. *The Society of Arts and Sciences of Kristiania*, **4** (34), 9-14. Kristiania.

WEYER, D. 1979. Korallen-Funde im europäischen Zechstein-Meer. *Zeitschrift für Geologische Wissenschaften*, **7** (8), 981-1021. Berlin.

— 1982. *Paracaninia variabilis* (SOSHKINA, 1941) aus dem Kazanian der Russischen Platform (Anthozoa, Rugosa; Mittelperm). *Abhandlungen und Berichte für Naturkunde und Vorgeschichte*, **12** (4), 65-78. Magdeburg.

— 1997. Korallen im oberpermischen Kazan-Meer von

Russland. *Freiberger Forschungshefte*, **C466**, 85-107. Freiberg.

WEYER, D. & ILINA, T.G. 1979. Die permischen Rugosa-Genera *Pleramplexus* und *Pentamplexus*. *Zeitschrift für Geologische Wissenschaften*, **7** (11), 1315-1341. Berlin.

WILSON, E.C. 1982. Wolfcampian rugose and tabulate corals (Coelenterata; Anthozoa) from the Lower Permian McCloud Limestone of northern California. *Los Angeles County Natural History Museum Contributions in Science*, **337**, 1-90. Los Angeles.

— 1985. Rugose corals (Coelenterata, Anthozoa) from the Lower Permian McCloud Limestone at Tombstone Mountain, northern California. *Los Angeles County Natural History Museum Contributions in Science*, **366**, 1-11. Los Angeles.

— 1990. Permian corals of Bolivia. *Journal of Paleontology*, **64**, 60-78. Tulsa.

— 1991. Permian corals from the Spring Mountains, Nevada. *Journal of Paleontology*, **65**, 727-741. Tulsa.

— 1994. Early Permian corals from the Providence Mountains, San Bernardino County, California. *Journal of Paleontology*, **68**, 938-951. Tulsa.

— 1998. Not *Heritschioides* in Europe yet. *Permophiles, Newsletter of Subcommission on Permian Stratigraphy*, **31**, 15. Boise.

WILSON, E.C. & LANGENHEIM, R.L., Jr. 1962. Rugose and tabulate corals from Permian rocks in the Ely Quadrangle, White Pine County, Nevada. *Journal of Paleontology*, **36**, 495-520. Tulsa.

— & 1993. Early Permian corals from Arrow Canyon, Clark County, Nevada. *Journal of Paleontology*, **67**, 935-945. Tulsa.

WU, W.S. 1962. Upper Carboniferous corals from Yishan, Kwangsi. *Acta Palaontologica Sinica*, **10** (3), 335-350. Nanjing.

WU, W.S., STEVENS, C.H. & BAMBER, E.W. 1985. New Carboniferous and Permian Tethyan and Boreal corals from northwestern British Columbia, Canada. *Journal of Paleontology*, **59**, 1489-1504. Tulsa.

ZIEGLER, A.M., HULVER, M.L. & ROWLEY, D.B. 1996. Permian World topography and climate. *In*: I.P. MARTINI (*Ed.*), Late glacial and postglacial environmental changes – Quaternary, Carboniferous-Permian and Proterozoic. *Oxford University Press*; New York.

Manuscript submitted: 15th October 1998
Revised version accepted: 5th December 1998