

VICTOR N. DUBATOLOV and NINA P. VASSILJUK

## CORAL PALEOZOOGEOGRAPHY IN THE DEVONIAN AND CARBONIFEROUS OF EURASIA

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Eight provinces of coral distribution were established in the Early Devonian of Eurasia and Australia: Mediterranean, Maghrebian, Uralo-Tien-Shan, Altai-Sayan, Dzhungar-Balkhash, Indo-Sinian, East-Australian, Mongolo-Okhotsk and Indigiro-Kolyman. In the Middle Devonian large transgression caused enlargement of the provinces. As a result there appear such provinces as: Mediterranean, Uralo-North Asiatic, Mongolo-Okhotsk, Sino-Australian. Each province includes several zoogeographic areas. There are 4 regions (European, South Asian, Australian and North American) with 15 provinces in paleozoogeographical zonation of the Lower Carboniferous (Viséan) paleobasins and 3 regions (Ural-Arctic, Mediterranean, North American) with 7 provinces in the Late Carboniferous (Moscovian) paleobasins.

**Key words:** corals, Tabulata, Rugosa, Devonian, Carboniferous, coral paleo-provinces, Eurasia.

*Victor N. Dubatolov, Institute of Geology and Geophysics, USSR Academy of Sciences, Universitetsky prosp. 3, 630090 Novosibirsk, USSR. N. P. Vassiljuk, Faculty of Geology, Polytechnic Institute, Artema 8, 340066 Donetsk, USSR. Received: September 1979.*

### CORALS AS INDICATORS OF BIOCHORES

In Devonian and Carboniferous marine basins the corals were most common benthic organisms. Their dispersion took place at larval stage. During that stage which could last for several weeks off-shore currents transported corals far away from their initial habitats. Land (continents, islands and peninsulas) and marine barriers (abyssal depressions, areas with abiotic and biotic conditions unfavourable for corals) were obstacles to their migration. Coral expanded mainly during the periods of extensive transgressions due to the disappearance of land barriers or appearance of new basins, and during regressions due both to shallowing of water upon extensive areas and to the biological factors.

Migration of corals was accounted for by the geotectonic conditions of water basins. The geosynclinal coral assemblages are usually more diverse in their taxo-

onomic composition than those of the epiplatform seas where only few groups could develop intensively; thus the Altai-Sayan Devonian geosyncline and the Urals Carboniferous geosyncline were inhabited with more diverse corals than the epicontinental paleobasins of the Platform. Migration in the geosynclinal basins took place in different directions, but there existed usually one channel of migrations on the platforms, for instance, in the Middle and Late Carboniferous of the Urals there existed connections with the Arctic areas, the Donets basin and Central Asia, while on the Russian platform migrations were principally directed from the south.

Recognition of ecologic types of fauna is of great importance for zoogeographic subdivision since the differences or similarities of biochores could be reasonably established only for such faunas as occur in fairly similar environments. Many authors indicate that the Rugosa, whether caninoid-clisiophylloid solitary corals or colonial forms, together with tabulate corals and chaetetids occur in one and the same facies. It is noteworthy that fasciculate colonies and, rarely, massive ones, occupied an intermediate ecological position between the *Cyathaxonia* and *Caninia-Clisiophyllum* faunas.

All the above-mentioned characteristics of corals as well as their ability to produce endemic forms make them less suitable for interregional correlation but very important for paleozoogeographical reconstructions.

Endemism in corals is one of the most important criteria for zoogeographical zonation. The fauna of Devonian paleobasins featured a growing endemism from the end of the Silurian to the Eifelian that was replaced by a sharp decrease continuing well into the Frasnian time associated with an almost complete disappearance of endemic forms (Dubatolov 1972; Oliver 1976; Spassky 1977). The coefficient of coral endemism also varied throughout the Carboniferous. Endemic forms constituted almost 100 per cent of the Famennian coral fauna, their share being reduced during the Etroeungt and through the Tournaisian, with a minimum recorded in the Viséan time. There were several periods of increase and decrease of coral endemism in the Tournaisian—Late Carboniferous, the peak of endemism being reached in the Early Bashkirian and at the end of the Late Carboniferous. Each phase is usually synchronous to the rhythms of a transgression-regression cycle.

#### PRINCIPLES AND METHODS OF CORAL PALEOZOOGEOGRAPHY

No uniform system of biochores exists as yet. Most frequently used categories are as follows: belt, region, province and district.

A paleozoogeographical subdivision of Carboniferous paleobasins by corals was carried out by a number of authors. Hill (1948) determined provinces by dominating genera drawing attention to the fact that discrimination of provinces changed during the Carboniferous. Vassiljuk, Kachanov and Pyzhjanov (1970) characterized provinces by assemblages of genera and their main trends of evolution. Fedorowski (1977) focused his attention upon the centres of speciation and the most important routes of migration. Minato and Kato (1970, 1975, 1977) applied the faunal method preceded by a thorough work on the morphology and taxonomy of the same families. Their

works on Durhaminidae, Waagenophyllidae and Geyerophyllidae contributed a lot to paleozoogeography. Rowett (1975) considered the analysis of genera assemblages to be the main criterion of provinces division and explained the similarity of some provinces by the position of the continental plates. Sando, Bamber and Armstrong (1977) elaborated the most direct systematic basis for the paleozoogeographic division introducing new concepts of "total diversity", "diversity", "endemism index", "similarity index".

A paleozoogeographical zonation in Devonian paleobasins on the basis of corals had been carried out many times (Dubatolov and Spassky 1964; Dubatolov 1972; Spassky 1977; Oliver 1973, 1978, and others).

### CORAL ZOOGEOGRAPHY IN THE DEVONIAN AND CARBONIFEROUS

Coral studies allowed to recognize such large paleozoogeographic subdivisions as belts in Devonian basins (Dubatolov 1972; Spassky 1977, and others). However, the discrimination of climatic belts in the Carboniferous on the same basis is doubtful.

Given below is a chart of Devonian and Carboniferous zoogeographic subdivision as results from a thorough consideration of the data obtained by the present authors and by other coral-workers (table 1).

### RELATIONSHIP BETWEEN PALEOZOOGEOGRAPHICAL RECONSTRUCTION AND STAGES OF CORAL EVOLUTION

We recognize one stage in the evolution of corals in the Devonian and two main stages in the Carboniferous, i.e. the Early Carboniferous and the Middle-Late Carboniferous.

Six distinct stages in coral development may be recognized in the Devonian: (1) Lochkovian (Gedinnian-Early Siegenian); (2) Pragian (Upper Siegenian-Early Emsian); (3) Zlichovian (Late Emsian); (4) Eifelian; (5) Frasnian and (6) Famennian.

The Early Carboniferous stage consists of four phases: (1) Famennian-Entoëungt phase of appearance and formation of type faunas; (2) Tournaisian phase of diversion and prosperity; (3) Viséan-Early Serpukhovian phase of diversion and prosperity; (4) Late Serpukhovian phase of extinction.

The following four phases can be distinguished in the Middle-Late Carboniferous: (1) *Homoceras-Reticuloceras* time; initial phase of formation of coral fauna; (2) Middle-Late Bashkirian-Early Moscovian phase of adaptation and steady development; (3) Late Moscovian phase of diversion and prosperity and (4) Late Carboniferous phase of extinction.

At the initial phase of faunal development the subdivision into provinces is sometimes impossible. What one can differentiate are speciation centres. Later provinces evolve as suggested by the general character of the fauna. At the phase of steady faunal development, regions can be recognized according to the general character of the fauna, and provinces — according to dominant genera.

Table 1

Coral zoogeography in the Devonian and Carboniferous

Stage	Region	Province	Area
Lochkovian ( Cadimian-Lower Siegenian)	Atlantic	Mediterranean (= Old World)	Ardenno-Rhinish, Barrandian, South European, Caucasus-Pamirian
	Australo- Asiatic	Maghrebian, Uralo-Tien-Shan	Maghrebian, Urals, Novaya Zemlya Tien-Shan, Sin'dzjanian(?)
		Altai-Sayan	Salair, Horny Altai, Rudny Altai Southern Altai
		Dzhungar-Balkhash	Dzhungar, Balkhash
		Indo-Sinian	Bacbo, Laos-Viet, Southern Viet-Nam
		East Australian	East Australian, Tasmanian
	North Pacific	Mongolo-Okhotsk	Trans-Baikalian, near Amur River area, Khinganian, East Mongolian
		Indigiro-Kolymian	Tas-Khajaktakh, Omulev-Kolymian Sette-Dabanian, Taimyrian
		California-Canadian	Californian, Canadian
	Appalachian	Appalachian	Appalachian
Pragian ( Upper Siegenian-Lower Emsian)	Atlantic	Mediterranean ( = Old World )	Ardenno-Rhinish, Barrandian, South European, Caucasus-Pamirian
		Maghrebian	Maghrebian
	Australo- Asiatic	Uralo-Tien-Shan	Urals, Novaya Zemlya, Tien-Shan, Sin'dzjanian
		Altai-Sayan	Salair, Horny Altai, Rudny Altai Southern Altai
		Dzhungar-Balkhash	Dzhungar, Balkhash
		Indo-Sinian	Bacbo, Laos-Viet, Southern Vietnam
		East Australian	East Australian, Tasmanian
	North Pacific	Mongolo-Okhotsk	Trans-Baikalian, near Amur River area, Khinganian, East Mongolian
		Indigiro-Kolymian	Tas-Khajaktakh, Omulev-Kolymian Sette-Dabanian, Taimyrian
		California-Canadian	Californian, Canadian
Appalachian	Appalachian	Appalachian	
Zlichovian	Atlantic	Mediterranean (= Old World)	Ardenno-Rhinish
		Maghrebian	Maghrebian

continued

Stage	Region	Province	Area
Zlichovian (Upper Emsian)	Australo-Asiatic	Uralo-Tien-Shan	Urals, Novaya Zemlya, Tien-Shan Sin'dzjanian
		Altai-Sayan	Salair, Horny Altai, Rudny Altai Southern Altai
		Dzhungar-Balkhash	Dzhungar, Balkhash
		Indo-Sinian	Bacbo, Laos-Viet, Southern Viet-Nam
		East Australian	East Australian, Tasmanian
	North Pacific	Mongolo-Okhotsk	Trans-Baikalian, near Amur River area, Khinganian, East Mongolian
		Indigi-ro-Kolyman	Tas-Khajakhtakh, Omulev-Kolyman Sette-Dabanian, Taimyrian
	Appalachian	California-Canadian	Californian, Canadian
Appalachian		Appalachian	
Eifelian	Not distinguished (apparently a single region)	Medirerranean	Maghrebian, South European Ardenno-Rhinish, Caucasus-Pamirian
		Uralo-North Asiatic	East European, Urals, Tien-Shan Dzhungar-Balkhash, Altai-Sayan Indigi-ro-Kolyman
		Mongolo-Okhotsk	Mongolo-Okhotsk
		Sino-Australian	Indo-Sinian, East Australian
		Appalachian	Appalachian
Givetian		Mediterranean	Maghrebian, South European, Ardenno-Rhinish, Caucasus-Pamirian
		Uralo-North Asiatic	East European, Urals, Tien-Shan Dzhungar-Balkhash, Altai-Sayan Indigi-ro-Kolyman
		Mongolo-Okhotsk	Mongolo-Okhotsk
		Sino-Australian	Indo-Sinian, East-Australian
		Appalachian	Appalachian
Frasnian		Australo-Euro-Asiatic	European, Uralo-North European Sino-Australian
		North American	Appalachian, Californian, Canadian
Famen-nian	Geographic differentiation of coral fauna is sharp, but poorly studied for the present		

continued

Stage	Region	Province	Area
Etroeungt		West European	Polish, French, Belgian, German, English
		Novaya Zemlya Donets basin	Novaya Zemlya, Urals, Donets basin, North Caucasus
		Mediterranean subprovince	Transcaucasian, Chinese
		Kazakhstan-Altai	Central Kazakhstan, Altai
		Japanese-North American	Japanese, North American (Utah, South Dakota, Missouri, New Mexico)
Tournaisian	European	West European	English, French, Belgian, German, Spanish, North African, Polish, Lvov basin
		East European	Dnieper-Donets basin, Moscow basin, Central Asiatic
	Asiatic	Uralian	Uralian, Novaya Zemlya, Siberian
		North-East Siberian	Omolon, Chukotsk, Verkhoyanian Alaskan
		Kuznetsk	Kuznetsk
		Kazakhstanian	East Kazakhstanian, Altai
		Chinese	Chinese, Japanese
	Transcaucasian	Transcaucasian	
	Australian	East Australian	East Australian
	North American	Western Interior	Northern, Central, Southern
		South-Eastern	Mississippian, Appalachian
Viséan	European	West European	West European, Central European
		North African	North African
		East European	north-western part of Moscow basin, southern part of Moscow basin, Voronezh anticline, West Uralian
		Donets-Central Asiatic	Donets basin, Central Asiatic
	North Asiatic subregion	East Siberian	Taimyrian, Kuznetsk, North-East Siberian, Alaskan
	Uralian	East Uralian, Novaya Zemlya	

continued

Stage	Region	Province	Area
Viséan	South Asiatic	Central Kazakhstan	Central Kazakhstan
		Asia Minor	Transcaucasian, Turkish
		Japan-Chinese	Chinese, Japanese
		West Australian	West Australian
	Australian	East Australian	East Australian
	North American	Pacific coast	Northern, Southern
		Western Interior	Northern, Central, Southern
		South-Eastern	South-Eastern
		Maritime	Nova Scotia
	Serpukhovian	Euroasiatic	West European
East European			north-west of Moscow basin, south of Moscow basin, Voronezh anticline, Volga district
Uralian			Uralian, Novaya Zemlya
North-East Siberian			North-East Siberian, Taimyrian, Alaskan
Mediterranean subregion		West Mediterranean	North African, Donets basin, Caucasian, Asia Minor
		East Mediterranean	Central Asiatic, Central Kazakhstanian, Japanese
North American		Pacific coast	Northern, Southern
		Western Interior	Northern, Central, Southern
		South-Eastern	South-Eastern
		Maritime	Nova Scotia
Bashkirian	Mediterranean	West Mediterranean	North African, Spanish, Donets basin, Asia Minor
		Kazakhstan-Balkhash	East Kazakhstanian
		Chinese	North Chinese, South Chinese
		Japanese	Japanese
	Euroasiatic	Uralo-Tien-Shan	Uralian, Novaya Zemlya, Tien-Shan, Pamirian
		East European	Voronezh anticline, Volga district, Yugoslavian

continued

Stage	Region	Province	Area
Bashkirian	North American	Mississippian	Central midcontinent, north-west of South America
		Cordilleran(?)	Cordilleran
		Alaskan (?)	Alaskan
Moscovian	Uralo-Arctic	Uralo-Arctic	Uralian, Novaya Zemlya, Arctic Canadian, Moscow basin (?)
	Mediterranean	West Mediterranean	Spanish, Carnian Alps, Yugoslavian, North African
		Central Mediterranean	Donets basin, Pamirian, Balkhash
		Chinese	South Chinese, North Chinese Viet-Nam, outer zone of Japan
		Japanese	Japanese
	North American	Mississippian	Midcontinental, north of South America
		Cordilleran (?)	Cordilleran
Late Carboniferous	Uralo-Arctic	Uralian	Uralian, Moscow basin
		Arctic	Spitsbergen, Bear Island, Boreal Urals
		Canadian	Canadian
	Mediterranean	West Mediterranean	Carnian Alps, Yugoslavian
		Central Mediterranean	Donets basin, Pamirian
		Chinese	Chinese, Viet-Nam
	North American	Mississippian Cordilleran (?)	

At the time of faunal flourishing, the areas inhabited by dominant genera may serve as the criterion for regional subdivision while prevailing groups of species together with the stratigraphic distribution of both genera and species account for distinguishing provinces. Wide intermediate zones appear. At the final phase, regions are recognized on the basis of family and generic domination, the provincial differences being eliminated.



SIGNIFICANCE OF PALEOZOOGEOGRAPHICAL RECONSTRUCTIONS FOR  
BIOSTRATIGRAPHY

The West-European scale of Devonian and Carboniferous deposits subdivision which has been in use for 150 years does not fully account either for the evolution of the most significant groups of fossil organisms or for the stages of geological development of global importance. At present, an attempt is being made at developing a comprehensive scale of Devonian and Carboniferous stratigraphy which would consider the evolutionary advance of organic world. Making up such a scale is impossible without an interregional and intercontinental correlation, which, in turn, involves assessment of the relationship between the development of organisms and the physico-geographic conditions of particular basins, that is, the dependence of such development on the paleogeographic structure of the past. As can be seen from numerous detailed studies, the appearance of new groups of fauna, their distribution and duration are accounted for by the climatic conditions and topographic setting; this deprives such processes of a global aspect making the elaboration of a global scale particularly difficult. It seems reasonable to apply stratigraphic units of the stage level for correlation within one region, sometimes, province, while finer subdivisions should be confined to one province or area. Therefore, correlation is associated with solving some basic paleozoogeographic problems, namely: establishing speciation centres, ways of migration, relations between paleozoogeographic units and structural-facies zones of the earth crust.

The time of existence of provinces and regions is subject to variation. Some of them, such as the Ural-Tien-Shan, Altai-Sayan and Indigiro-Kolyman subdivisions, persisted throughout the Early Carboniferous and lasted for a very long time. Other regions, e.g. the Asiatic region, can be clearly recognized in the Tournaisian only. As a rule, each stage is associated with one predominant region and some provinces within it; thus, the Bashkirian and Tournaisian stages would feature the Ural-Arctic region and the Asiatic region respectively.

The boundaries of sharp change in coral fauna development do not always coincide with the stage boundaries within different regions and large provinces. Thus, the corals allow a fairly distinct discrimination of the Tournaisian and Viséan stages in European regions whereas in Asia and North America changes in faunal assemblages occur not near the accepted stage boundaries but somewhat higher. Establishing the Bashkirian and Moscovian boundaries by corals is possible in Asia alone while in North America what one can probably do is merely to distinguish the assemblages corresponding to the Upper Bashkirian-Lower Moscovian deposits. It is difficult to correlate those areas which are closely located but attributed to different regions and provinces. To such areas belong the Ural-Tien-Shan and Dzhungar-Balkhash basins in the Early Devonian; the Donets basin and the Voronezh anticline at the end of the Early Carboniferous, and in the Bashkirian or the Moscovian syncline and the Urals in the Middle Carboniferous. At the same time, correlation of distant areas that are attributed to one and the same region or province is much more feasible, for example: Spain and Donets basins in the Mos-

covian stage, North Africa and the Donets basin in the Viséan and Serpukhovian, Transcaucasus and China in the Tournaisian, North-East of Siberia and the Urals in the Tournaisian, etc.

Intermediate zones are of particular importance for correlation of stratigraphic schemes. Referred to such zones in the Carboniferous may be the southern slope of the Voronezh anticline, the eastern part of the Russian platform and the Western Urals, the Northern Tien-Shan, the North-Western Balkash area and the Transcaucasus.

## PALEOZOOGEOGRAPHICAL RECONSTRUCTION AND GEOTECTONICS

At present the Carboniferous coral zoogeography is scarcely involved into paleogeotectonical reconstructions. Rowett (1975) explained the similarity of coral assemblages of the North-West of South America by the breaking of precontinent and the shifting of separate blocks. Hill (1971, 1973) analysed the proliferation of Late Paleozoic reefs and coral assemblages and came to the conclusion that the position of coral zoogeographic provinces proved the location of the continent of the Northern hemisphere in the Early Carboniferous close to the recent one.

A comparison between the zoogeographic provinces outlined on ordinary paleogeographic maps of the Carboniferous and those on the map made up with regard for continental drift shows very little difference. However, it is easier to explain a number of small facts in coral distribution in terms of continental drift.

Thus, the following facts could be evidences of platform spreading: (1) the presence of European corals in Meramecian and Chesterian of Nova Scotia (2), common forms of the Lower Pennsylvanian in the Midcontinent of North America, Spain and the Donets basin, (3) the presence of Chinese fauna in the North-Western Australia during the Tournaisian.

Subduction can explain: (1) the divergence of the coral assemblages in the Western and Eastern Urals, (2) the divergence of assemblages in the Donets basin and the southern slope of Voronezh anticline, (3) the appearance of Spanish species in the Moscovian in the western part of the Moscow syncline, (4) the divergence between internal and external provinces of Japan, (5) the absence of the greater part of the Japanese province — Pseudopavonidae district — on modern maps, (6) the absence of a geosyncline region where North America midcontinental Mississippian fauna originated and developed, (7) the absence of a coral province on the modern maps to the East from Australia. The main realm of Carboniferous fauna might have been developed eastward of the present Pacific coast.

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