Diversifications of corals and coral reef associations in Mesozoic palaeogeographic units of northwestern Yugoslavia

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In the development of corals and coral reefs in northwestern Yugoslavia several phases can be distinguished. They are limited to different palaeogeographic units and contain different fossil associations: 1, Upper Triassic coral patch reefs and mud mounds are restricted to the Julian carbonate platform and Slovenian trough. The dominant reef builders, besides corals, are calcisponges; solenopores and microproblematica are rarer. They occur in the lower Carnian, upper Carnian and Norian-Rhaetian. 2, Upper Jurassic reefs are limited to the Dinaric carbonate platform and are of Oxfordian-Kimmeridgian age. The main reef builders, next to corals, are stromatoporoids and chaetetids. 3, Lower Cretaceous (Baremian-Aptian) coral reefs are rare and restricted to the Dinaric platform. More than 50% of coral genera continue from the Upper Jurassic. 4, Upper Cretaceous (Santonian-Campanian) corals are limited to the Inner Dinarides (?Supradinaricum) which represents a deeper marine environment. The corals here are resedimented within breccias, solitary non-builders, or colonies in patch reefs along island arcs.

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MESOZOIC corals and coral reefs in the Alpine-Dinaric contact in northwestern Yugoslavia, which includes Slovenia and northern Croatia have for the most part been investigated by myself, the Stromatoporoidea from coastal Croatia were studied by Milan (1969), and sponges from Hudajužna by Senowbari-Daryan (1981). The area had relatively stable carbonate platforms permanently or temporarily in the Mesozoic; numerous coral reefs may be observed in original position. Triassic reefs were resticted to northwestern, northern and central Slovenia; Jurassic reefs to southern Slovenia and to coastal Croatia; Lower Cretaceous ones to southern Slovenia only; and Upper Cretaceous reefs to northwestern and central Slovenia and to northern Croatia. (Fig.1).

Stratigraphy and fossil associations

Triassic

Triassic coral reefs can be divided into two main horizons: the lower Carnian and Norian-Rhaetian. The precise beginning and end of growth of lower Carnian reefs has not yet been determined. In some places they may have started growing in the Ladinian. These reefs are first built up by sponges and corals. Sphinctozoan sponges (Senowbari-Daryan,1981) predominated in lower parts of the reefs. Eighteen species have been determined, the most frequent genera being *Follicatena, Uvanella, Vesicocaulis, Cryptocoelia, Cystothalamia, Girtocoelia*, and *Colospongia*. Corals are more numerous in the upper parts of the reefs. Twenty-one species have been determined, the most frequent genera being *Margarosmilia, Margarophyllia, Volzeia, Tropidendron* and *Protoheterastraea*. The fossil assemblage also consists of rare stromatoporoids, chaetetids, microproblematica (*Bacinella, Ladinella, Tubiphytes*), and algae of the *Solenopora* type.

In the Norian-Rhaetian complex an entirely different assemblage appears dominated by the corals *Retiophyllia, Paradistichophyllum, Cuifia*, and *Distichophyllia*, and the sponges *Annacoelia, Cheilosporites, Paradeningeria*, and *Battaglia*. Characteristic are the microproblematica with *Microtubus* and *Pycnoporidium*. From the Norian-Rhaetian, 32 species of corals, 6 sponges, 4 chaetetids and stromatoporoids have been recognized.

In northwest Yugoslavia reefs also exist in upper Carnian beds. They partly consist of characteristic upper Carnian corals *Pamiroseris zitteli* and *Retiophyllia tolminensis* and partly of a mixture of lower

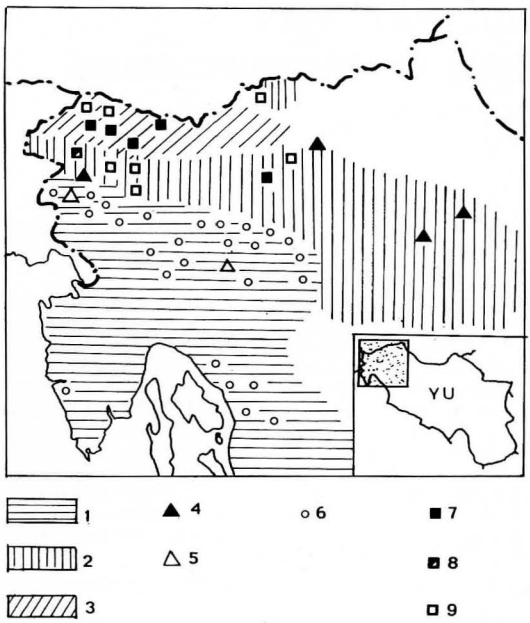

Fig.1. Geographical distribution of Mesozoic coral reefs in NW Yugoslavia. 1, Dinaric carbonate platform. 2, Slovenian trench. 3, Julian carbonate platform that existed until the end of Triassic. 4-9, Coral reef localities: 4, Upper Cretaceous (Santonian-Campanian). 5, Lower Cretaceous (Barremian-Aptian). 6, Upper Jurassic (Oxfordian-Kimmeridgian). 7, Triassic (Norian-Rhaetian). 8, Triassic (Upper Carnian). 9, Triassic (Lower Carnian).

Carnian and Norian species. The same mixed fossil association also occurs in the lowermost parts of some Norian reefs.

More detailed systematic descriptions of the Triassic reef fossils are presented in numerous papers in which they are compared with similar formations in the Dolomites, in the northern calcareous Alps, in the Carpathians, in Sicily, Greece, and the Pamirs (Buser *et al.*,1982; Ramovš & Turnšek,1984; Senowbari-Daryan,1981; Turnšek *et al.*,1982,1987; Turnšek & Ramovš,1987).

Jurassic

Rare Liassic corals have not yet been studied.

Numerous coral reefs flourished in the Lower Malm (Oxfordian-Kimmeridgian). Seventy-seven coral species were identified, belonging to 43 genera (Fig.2). Among them, the most characteristic are *Montlivaltia, Thecosmilia, Complexastraeopsis, Pseudocoenia, Heliocoenia, Stylosmilia, Mitrodendron, Microsolena, Comoseris, Ovalastraea*, and *Dermosmilia*. Fifty stromatoporoid species are also determined, belonging to 21 genera. Especially important are *Cladocoropsis, Parastromatopora, Dehornella, Hudsonella, Ellipsactinia, Sphaeractinia, Adriatella, Astrostylopsis, Actinostromina, Coenostella*, and *Tubuliella*. In some places the Upper Jurassic reef association also contains dasycladaceans, foraminifers, bivalves, and gastropods.

These reefs were described and compared with similar localities in France, the Carpathians, the Middle East, the Crimea, and Japan (Turnšek,1966, 1972, 1975; Milan,1969; Tišljar & Velić,1987). Their geographical distribution has been complemented by the latest findings in Portugal (Rosendahl,1985), Spain (Errenst,1987), and in Uzbekistan (Husanov,1984).

Discovery of structural features of stromatoporoids has suggested their affinity with the Porifera (Termier & Termier,1975; Wendt,1978; Stearn,1980; Wood,1986) rather than the Hydrozoa. Some stromatoporoids, however, show similarity to the microsolenid and actinacid corals and to milleporid hydrozoans (Mori,1984) and may be nearer to the Cnidaria than to Porifera.

Cretaceous

In the Cretaceous, coral reefs appear at two horizons. The first of these is of Barremian-Aptian age, and is typified by *Eugyra, Cyathophora, Microsolena*, and *Clausastraea*. The total number of coral species is 31 (Fig.2). There are also 2 species of stromatoporoids (*Dehornella*) and 2 species of chaetetids (*Chaetetopsis*). More than half the genera are the same as in the Upper Jurassic. This Barremian-Aptian assemblage resembles that of the Urgonian facies in France, Romania, eastern Serbia, the Crimea, and elsewhere (Turnšek & Buser,1974; Turnšek & Mihajlovic,1981).

The second coral reef horizon of the Cretaceous is of Santonian-Campanian age. Besides reef-building colonial corals *Columastraea, Columactinastraea, Elasmophyllia, Procladocora*, and *Neocoenia*, the

Fig.2. List of fossil genera from Mesozoic coral reefs in NW Yugoslavia. A mark before the name means that the genus is known from the older beds too. A mark after the name means that the genus continues into the younger beds.

	Triassic			Jurassic	Cretaceous	
	Lower Carnian	Upper Carnian	Norian - Rhaetian	Oxfordian-Kimmeridgian	Barremian-Aptian	Santonian-Campanian
Anthozoa	Andrazella Cassianastraea Coryphyllia Gumbelastraea Koilocoenia Margarophyllia * Margarosmilia * Myriophyllum Omphalophyllia Protoheterastraea Tropidendron * Volzeia *	Astraeomorpha * * Margarophyllia * Margarosmilia Pamiroseris Retiophyllia * Thamnotropis * Volzeia	* Astraeomorpha Craspedophyllia Cuifia Cyathocoenia Elysastraea Distichophyllia Gillastraea * Margarosmilia Pachydendron Phacelostylophyllum Paradistichophyllum Parathecosmilia Procyclolites * Retiophyllia Toechastraea * Tropidendron	Acanthogyra Actinaraea Actinastraea * Amphiastraea Aplosmilia Axosmilia * Calamophylliopsis * Ceratothecia Clausastraea Comoseris Complexastraea Convexastraea Dermoseris Dermosmilia * Diplaraea Donacosmilia * Epistreptophyllum Ettalonia Fungiastraea * Goniopora Heliocoenia Isastraea Kobyastraea Latomeandra Meandrophyllia Microphyllia * Microsolena * Mitrodendron Montlivaltia Myriophyllia Ovalastraea * Placophyllia * Proaplophyllia Pseudocoenia Pseudocoeniopsis Schizosmilia Stylina * Stylosmilia Synastraea * Thamnasteria Thecosmilia Amphiaulastraea Pseudopistophyllum	* Axosmilia * Clausastraea Cyathophora * Dermosmilia * Donacosmilia Eohydnophora Eugyra Felixigyra Glenaraea Latusastraea * Microphyllia * Microsolena * * Ovalastraea Phyllocoenia * Placophyllia Pseudopolytremacis Siderastraea * Stylina * Calamophylliopsis Diplogyra * Fungiastraea	Acrosmilia Actinacis * Actinastraea Astraraea Aulosmilia Columactinastraea Columastraea Cunnolites Dasmiopsis Dermosmiliopsis Diploctenium Conicosmilotrochus Elasmophyllia Ellipsosmilia Hydnophoraraea Mycetophylliopsis Neocoenia Phragmosmilia Phyllocoeniopsis Phyllosmilia Pleurocora Procladocora Rennensismilia Stephanosmilia * Synastraea Thamnoseris Columellogyra Heterocoenia Meandroria * Microsolena Pseudofavia
Stromato poroidea	Balatonia Disjectopora *	* Disjectopora Stromatomorpha	Cylicopsis * Pamirostroma Spongiomorpha	Actinostromaria Actinostromarianina Actostroma Adriatella Astrostylopsis Burgundia Cladocoropsis Coenostella * Cylicopsis Dehornella * Desmopora Disparistromaria Ellipsactinia Hudsonella Milleporella Milleporidium * Parastromatopora Reticullina Sphaeractinia Sporadoporidium Tubuliella	* Dehornella * Milleporidium	Sporadoporidium
Chaetetida	Atrochaetetes *	* Atrochaetetes Blastochaetetes Pamirochaetetes	Pseudoseptifer	Bauneia Chaetetopsis * Pseudochaetetes Ptychochaetetes	Chaetetopsis	Acanthochaetetes Blastochaetetes
Spongia	Ceotinella Colospongia Cystothalamia Dictyocoelia Follicatena Girtycoelia Hartmanina Paravesicocaulis Sestrostomella Stylothalamia Uvanella Vesicocaulis Walteria * Zardinia	Corynella Precorynella Paradeningeria * * Walteria	Annacoelia Battaglia Cheilosporites Cryptocoelia * Paradeningeria Vesicocaulis			
Micro proble matica	Baccanella Bacinella Barbafera Ladinella Macrotubus Tubiphytes		Microtubus Pycnoporidium Radiomura			
Algae	Cayeuxia * Solenopora * Marinella		* Cayeuxia * Solenopora			

non reef-building solitary corals *Aulosmilia, Rennensismilia, Diploctenium*, and *Cunnolites* occur in many places. Some of the corals were also found in breccias. The reef-building corals are accompanied by rare chaetetids (*Acanthochaetetes, Blastochaetetes*), the solitary ones by gastropods.

From the Santonian-Campanian interval, 54 species of corals have been described. Only 3 genera continued through from the older horizons. It was possible to compare them with the Santonian-Campanian Gosau localities in Austria and other places (Turnšek & Buser,1976; Turnšek,1978; Turnšek & Polsak,1978). Maastrichtian corals from Bulgaria (Tchechmedjieva,1986) are also similar or even identical.

Palaeoecological remarks

In the Mesozoic of NW Yugoslavia 3 principal palaeoecologic units (Fig.3) can be distinguished. 1, the Julian carbonate platform to the north of Slovenia, which existed until the end of Triassic, 2, the Slovenian trough in central Slovenia, and 3, the Dinaric carbonate platform to the south of Slovenia, in coastal Croatia, and extending throughout the Dinarides (Buser, in press; Herak,1986).

The Triassic reefs are limited to the Julian carbonate platform and Slovenian trough. On the Julian platform, a primary site for patch reefs of various sizes, reef organisms prospered. The reefs differ from each other according to their fossil associations partly because of differences of age, and partly owing to their different microhabitats. On the platform, various types of irregularly intermixed shallow marine sediments can be distinguished. Classic reef zonation has not been found here (Ramovš & Turnšek,1984; Turnšek & Ramovš,1987).

In the Slovenian trough the reefs occur in the form of lenses in clastic strata. Some researchers consider these reefs to be primary mud mounds. It is also possible that they slipped as olistostromes from the margin of the carbonate platform (Turnšek *et al.*,1982,1987).

In northern Slovenia, from the Lower Jurassic onwards, a deeper marine sedimentation predominated. This indicates that the Julian platform had sunk and joined with the Slovenian trough into a uniform deeper marine sedimentary environment. The Dinaric platform remained stable and continued to provide conditions for shallow marine sedimentation.

During the Oxfordian-Kimmeridgian reef development on the Dinaric platform, back-reef, reef and fore-reef sediments can be distinguished, and traced laterally towards the north and northeast into basin sediments. In the back-reef, *Cladocoropsis* prevails. The central reef consists almost entirely of the skeletons of reef organisms. Besides corals there are numerous stromatoporoids which divide the reef into 2 contemporaneous concentric belts, extending from the lagoon towards the basin. In the inner belt parastromatoporids predominate. In the outer reef belt Sphaeractiniidae associated with actinostromariids constantly occur. They always grow on the margin of the platform and never in the basin nor in the back-reef area. For that reason the Sphaeractiniidae seem to be the most important palaeoecological indicator of the exterior margins of the platforms. The Upper Jurassic reef on the Dinaric platform is the most completely developed barrier reef complex in Europe (Turnšek *et al.*,1981).

The Dinaric platform was also a shallow-water sedimentary environment in the Lower Cretaceous. Suitable conditions for reefs prevailed during the Barremian-Aptian. During that time few localities show *in situ* reef development. The extent of reefs was probably much greater because Lower Cretaceous corals have been discovered north of the platform, transported into the Senonian breccia.

The paleoecologic position of Upper Cretaceous corals in NW Yugoslavia has not been elucidated yet. On the Dinaric carbonate platform, which still existed, no coral reefs have been found. All the Upper Cretaceous corals were discovered in the area of northern Slovenia and Croatia, which belongs to deeper marine sedimentary environments (Inner Dinarides). Corals have been found in breccias, in small reefs, or as solitary non-reef-building forms. Solitary corals found in marls are considered to be in their primary position, because they are characteristic of a deeper environment. Small reefs are composed of colonial corals and rudists. At very small distances they are surrounded by clastic sediments on one side, and by pelagic sediments with globotruncanid foraminifers on the other side. 'These environments may have developed in the island arc region, in the subduction zone'

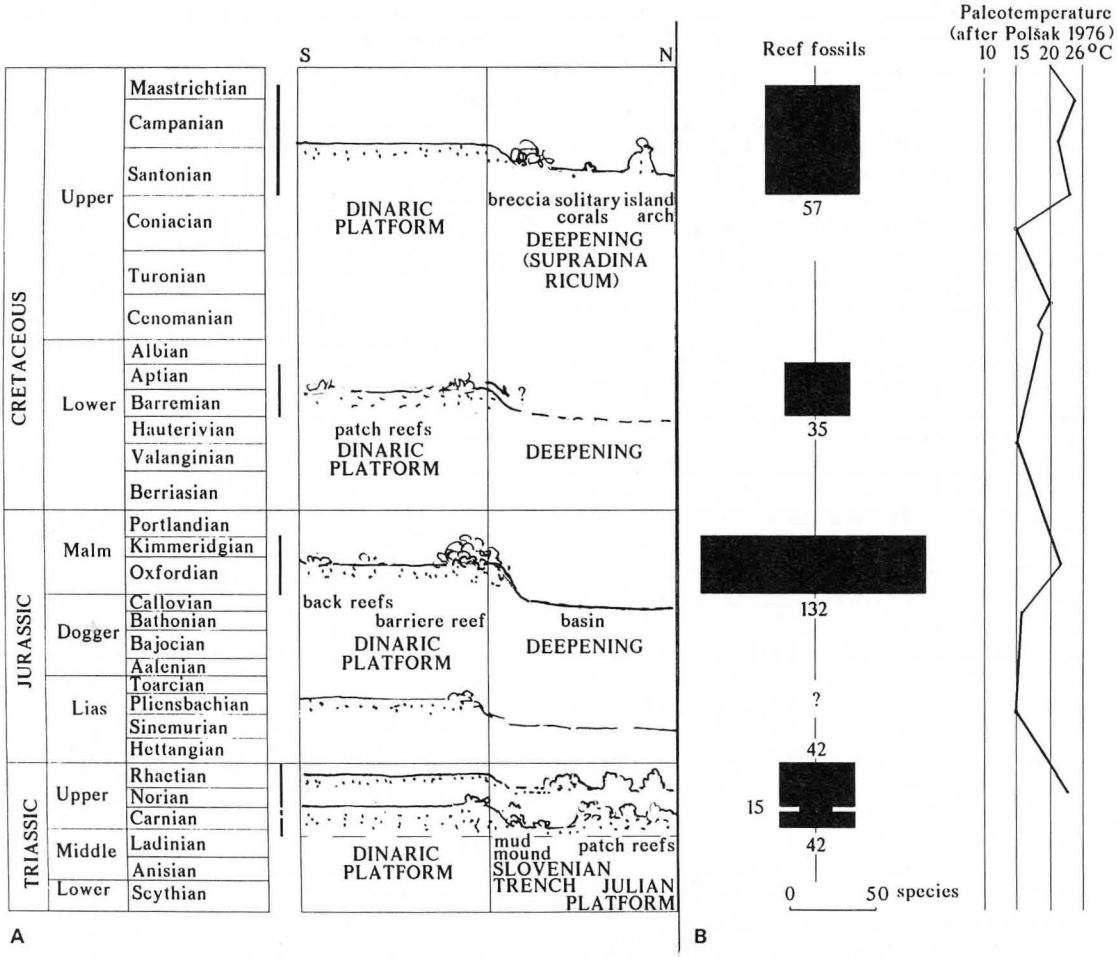

Fig.3. Palaeogeographical and stratigraphical situation of Mesozoic coral reefs in NW Yugoslavia. A, Schematized palaeogeographic conditions in the periods of reef growth. The Dinaric platform was stable throughout the Mesozoic. The Slovenian trough and Julian platform were joined after the Triassic into the labile deepening (Inner Dinarides, Supradinaricum) with pelagic and mixed sedimentation. B, Parallel to palaeogeographic units the stratigraphic development of reefs is shown with total number of determined species, and their coincidence with the palaeotemperature values from the Jurassic and Cretaceous Periods.

(Polsak,1979). These reefs had steep slopes, so sedimentation from reef to basin changed rapidly.

The third type of Upper Cretaceous corals are redeposited, at least in part, into breccias. The corals in these breccias represent several horizons. Jurassic and Lower Cretaceous corals must have slipped from nearby primary localities on the Dinaric platform. The Upper Cretaceous corals which also appear in these breccias could be of different origin. Possibilities are: 1, they were growing on the margin of a nearby platform in Santonian-Campanian time and were penecontemporaneously resedimented into the breccia and mixed with the other older fossils; 2, they had been growing on the carbonate platform in the Albian-Cenomanian or Turonian, and were resedimented in the Senonian. Thus, determination of their Santonian-Campanian age is wrong. The same might have happened in some of the classic localities of Gosau facies; or 3, it might be that, prior to breccia formation, a shoal existed in the same area, on which older fossils and sediments accumulated. From time to time, Senonian corals also found favourable conditions for growth on these accumulations.

Reason for success and extinction of the reefs

For active reef growth, favourable

temperature, convenient shallow water foundation with a constantly subsiding platform, and enough nutrition and oxygen are necessary.

The question as to whether, in the Mesozoic, all the Northern Hemisphere was warmer or whether our reef areas were situated more to the south, remains unresolved. Peaks on the palaeotemperature curve for northern Yugoslavia in the Jurassic and Cretaceous, (Polsak,1976), correspond to times of reef growth (Fig.3). Prolific reef growth also followed immediately the acme of local tectonic movements, which in some places increased sea water upwelling and supply of nutrients. The Julian carbonate platform offered favourable conditions for Upper Triassic reefs but its subsidence at the end of the Rhaetian caused the end of reef growth there. Before the flourishing of Upper Jurassic reefs, tectonic movements had caused the 'Supradinaricum' to subside, and the Dinaric platform became an ideal environment for reefs. On the other hand, Upper Jurassic reefs ceased growing at the end of the Kimmeridgian, when, the Dinaric platform stopped subsiding and became too shallow for coral growth. In the late Upper Jurassic, coral reefs were overgrown and choked by the alga *Clypeina jurassica*, one of the most abundant dasycladacean algae in the whole Dinaric region.

A small expansion of reefs in the lowermost Cretaceous (Berriasian to Hauterivian) and complete absence of them in the Albian, Cenomanian and Turonian can probably be explained by subsequent erosion. In the Senonian, sedimentary deeper marine environments of the Inner Dinarides became progressively infilled, relatively too stable and insufficiently oxygenated, so reef growth gradually ceased. The coral species of this region are numerous but many of them are solitary and non reef-building.

Conclusion

The pattern of Mesozoic coral reef development in northwestern Yugoslavia shows that local palaeoecological conditions were important for favourable growth at different times.

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