The importance of Mesozoic floras and faunas from intraoceanic carbonate platforms for interpretation of palaeogeographic and geodynamic events in the Tethys

N. Pantič

A. Grubič

M. Sladič-Trifunovič

Faculty of Geology and Mining Beograd, Jugoslavija

(manuscript received June 8, 1982 accepted December 2, 1982)

« Anyone who has circled the Earth in a satelite equipped for time travel need read no further; he will already have seen whole continents migrate and collide, ... sea levels rise and fall, floras evolve and become extinct.»

J. Flenley, 1979

KEY WORDS — Mesozoic, Floras, Faunas, Carbonate platforms, Palaeogeography, Tethys.

ABSTRACT — The analysis of palaeophytogeographic situations and the analysis of the distribution and migration of shallow water faunas during the Jurassic and the Cretaceous are given based on considerations of Mesozoic continental flora and oceanic fauna from shallow water deposits of West Tethyan intraoceanic carbonate platforms. A tropical Tethyan phytogeographic realm is separated; its characteristics, and particularly the tracing of changes in it, compared to the situations in Gondwana and Laurasian phytogeographic realms, give much new information for understanding geodynamic processes in the Tethys (horizontal movements, troughs as some kind of barriers, etc.). Similar analysis is given for shallow water faunas, whose occasional expansion is associated with changes in climate (contraction or expansion of tropical and subtropical climatic belt). Using all the available data, Mesozoic Tethys can be reconstructed as a very complex basin bounded by continental shelfs (African and Euro-Asian), and with carbonate platforms, islands and other archipelagos between them, separated sometimes by very deep troughs which seldom had the oceanic crust.

RIASSUNTO — [Importanza delle flore e delle faune mesozoiche nelle piattaforme carbonatiche intraoceaniche per l'interpretazione degli eventi paleogeografici e geodinamici della Tetide] — L'analisi delle situazioni paleofitogeografiche e quella della distribuzione e migrazione delle faune di mar sottile nel Giurassico e nel Cretaceo vengono presentate in rapporto alle flore continentali ed alle faune delle piattaforme carbonatiche intraoceaniche della Tetide occidentale. È distinto un dominio fitogeografico tropicale tetisiano. Confrontando le sue caratteristiche e le sue variazioni con quelle dei domini della Gondwania e della Laurasia, si ottengono molte informazioni nuove utili per l'interpretazione dei processi geodinamici nella Tetide. Viene svolta un'analisi simile per le faune di acque poco profonde, la cui diffusione è condizionata da cambiamenti climatici e dalle conseguenti contrazioni ed espansioni delle fasce tropicali e subtropicali. Sulla base di tutti i dati disponibili si può ricostruire una Tetide mesozoica come un bacino molto complesso, collegato alle piattaforme continentali africana ed euroasiatica, con piattaforme carbonatiche, isole e arcipelaghi interni, talora separati da fosse profonde, raramente con crosta oceanica.

INTRODUCTION

Many research works published in the last several decades have revealed a lot of new informations about the complex dynamic Earth system, and about palaeogeographic, palaeoclimatological, palaeomagnetic and geodynamic events in the past geological times. The history of the Tethys, which for the greatest part is reconstructed from the study of the new continental regions formed after its disappearance, provides the basis of a great number of such informations. In this respect, formations of shallow water Palaeo- and Meso-

Tethys, distinguished by the abundance of fossil plants and animals, are particularly important.

Reconstructing palaeogeographic (phyto- and zoo-) changes, including the results of other methods (palaeomagnetism, palaeoclimatology, etc.), opens new opportunities for an advanced knowledge of horizontal movements, particularly of regions of the continental crust, and of geotectonic events, and contributes to a significant extent to an improvement of stratigraphic correlations.

The importance of palaeobiogeographic research for an improvement of stratigraphic correlations was

indicated long time ago (concerning fossil plants: Pantić, 1956-1980; Dörhöfer, 1977; for instance, or concerning foraminiferal and other faunas: Scheibnerova, 1971; Bolli and Krasheninnikov, 1977; Sladič-Trifunovič, 1976, for example).

Such or similar palaeontological researches are very important also for contemporary tectonic reconstructions (Krassilov, 1972; Pantič, 1980; Isler and Pantič, 1980; Beer and Jasamanov, 1982; for instance).

This approach to the problems includes also the question of how to consider specific features of palaeofaunas and floras of the same age, from different living and sedimentation environments, i.e. the different facial complexes. The present authors have indicated in many occasions the importance of comparative study of coeval faunas and floras from different facies (e.g. Sladič-Trifunovič & Campobasso, 1979/80, etc.). Here, however, the problem is considered more comprehensively, with the purpose to contribute more to an elucidation of the palaeogeographic distribution of continental floras and marine faunas and floras and their changes through the geological history and in relation to geodynamic events, changing climate, etc.

CONTINENTAL FLORAS FROM THE WEST TETHYAN INTRAOCEANIC CARBONATE PLATFORMS OF THE MESOZOIC TETHYS (1)

The remains of fossil macro-flora and continental plant palynomorphs from the Mesozoic West Tethyan intraoceanic carbonate platforms are scattered and so far (palynomorphs) inadequately studied. However, as has been shown by the investigation results, they can be very useful in reconstructing the geodinamics of Tethyan regions and even more in understanding the more recent tectonic events.

Triassic phytogeography and palaeoclimatology of the « circum-mediterranean realm » have been thorougly studied during the last few years under I.G.C. Project. These studies have made it clear that during the Ladinian and Carnian, the « Mediterranean » realm formed a separate Mediterranean phytogeographic region: with mixed northern (Laurasia) and southern (Gondwana) types of flora. This zone was populated by a specific arid tropical (!) flora, with more arid conditions towards the west.

The occurrence of coals and hydrophilic palynomorphs in the northern regions of the present-day Europe is explained by a more abundant water inflow in an extensive system of rivers over large continental surfaces. In the regions of the carbonate platform, marine environmental conditions dominated with archipelagos: small continental regions in which extensive river systems could not have been developed, except in extreme situations, therefore specific arid tropical vegetation dominated.

This general picture of the Triassic palaeophytogeographic, palaeoecological and palaeoclimatological situation is very important, because from the palaeofloral aspect it marks the initial stage, which was to be considerably changed under the effect of complex and intensive geodynamic events during Jurassic and Cretaceous. The events that had an effect on these transformations were: considerable expansion of the Meso-Tethys, formation of deep trough zones - some kind of « barriers » for dissemination of continental plants, which were displaced more and more apart and separated from the continental regions of the Euro-Asian continents and African-Asia Minor continent. Continental floras on archipelagos in the realm of the west Tethyan intraoceanic carbonate platforms, at the time were much closer to the African continent; through the Jurassic and even more during the Lower Cretaceous they were under a strong influence of African continental floras. From the Euro-Asian continent, to the north, the groups of intraoceanic carbonate platforms were seperated by a number of deepsea troughs of Piedmontian-Bosnian and Adula-Walis type (Isler & Pantič, 1980).

JURASSIC CONTINENTAL FLORAS OF THE WEST TETHYAN INTRAOCEANIC CARBONATE PLATFORMS

From the realm of the west Tethyan intraoceanic carbonate platforms relatively little information is available on Jurassic continental climate, but what exists is very specific and important. Most of the data refer to the terminating division of the Liassic (from Italy - Veneto: De Zigno, 1856-85; Wesley, 1966; van Erve, 1977; etc. and from the Dinarides - Budoš, Montenegro, Pantič, 1952, 1981). Fossil remains of continental flora from the Middle and Upper Jurassic are rare.

The younger Jurassic continental floras from Italy and Montenegro are very similar: in both cases it is a typical continental flora of island archipelagos from tropical regions of the Tethys.

Younger Liassic flora from the intraoceanic carbonate platform (Italy, Montenegro) can be reconstructed as follows:

(a) Wet coastal regions of islands and low marshy

⁽¹⁾ The «Italo-Dinaric» segment of Earth's crust consisted of a number of carbonate platforms (Dinaric, Dalmatian, Adriatic, Apulian, Abruzzi-Campanian, South-Alpine, etc.) separated by troughs (Budva-Cukali, etc.). The group of all «Italo-Dinaric» carbonate platforms is presently referred to as west tethyan intraoceanic carbonate platforms. The term is conditionally used, because, if accepted that the Tethys covered in the Mesozoic also the Caribbean, the presently considered regions would be a part of the central Tethys.

regions on islands were overgrown with vegetation of dominating ferns (*Klukisporites*, *Deltoidospora*) and seed ferns (*Pachypteris*), with some specimens of cycadophytes. Whether much of this vegetation was in the tidal zone cannot be definitely clarified, but it seems (Harris, 1964) quite acceptable that « mangrove » type of swamps prevailed. Such an opinion can ben confirmed by the fact that all localities on the carbonate platform do not contain significant coal occurrences. It is explained by the known fact that in the generally dense « mangrove » swamps the organic substance could not be preserved, due to continuous fluctuation of water level (and tropical heat); fast oxidation processes made it impossible accumulation and preservation of the abundant organic matter.

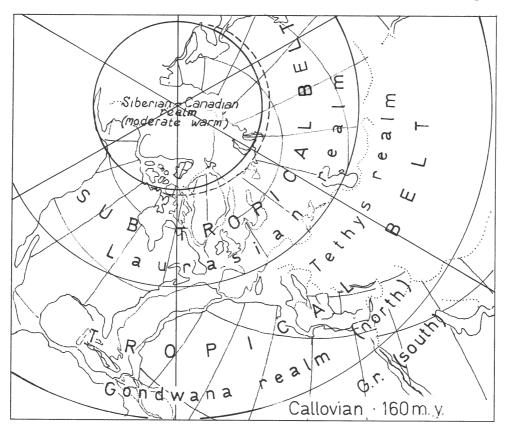
(b) Prominent areas on islands had xerophile flora. It is evinced by the abundance of conifers (Araucariacea, especially pollen from the group of Cheirolepidacea type - *Classopollis*, and respective macroremains of the genera *Brachyphyllum* and *Pagiophyllum*) in all the localities so far known on the west tethyan intraoceanic carbonate platforms.

In the middle of the Tethys ocean, during the younger Liassic, within the extent of west Tethyan intraoceanic carbonate platforms, there were many islands, archipelagos with dense vegetation on island

rims and drier coniferous vegetation inland. Wesley (1966) actually compared such environments with modern vegetation (from the ecological aspect) on the Bahama Islands (latitude 20°-30° north).

One more note should be added to the above consideration concerning the palaeoclimate (Pantič, 1982, to be published): tropical and subtropical belts during Jurassic were wider than nowdays. The important information is that most of « palaeocontinental » maps (Smith & Briden, 1977) or global « palaeocontinental » maps (Barron et al., 1981) show the west Tethyan intraoceanic carbonate platforms placed between latitudes 20° and 25° north. In view of the extent of the modern equatorial zone to only 10° north and south of the equator (J. Flenley, 1979), and its possible extent to 25° or more north in the Jurassic, it can be assumed that the realm of the west Tethyan intraoceanic carbonate platforms was situated in the Jurassic on the margin of the equatorial climate belt.

The older Jurassic continental flora from west Tethyan intraoceanic carbonate platforms differs from the floras of the same age in central and northern Europe (East Serbia, Rumania, Caucasus, Poland, etc.). Differences between Liassic floras of Italy and other localities have been noted before (see Vakhrameev et al., 1978). The older Jurassic « Euro-Asian » floras, that existed on the northern margin of the Tethys



Text-fig. 1 - Distribution of phytogeographic realms and climatic belts in Middle Jurassic.

(near-shore islands on the margin of epicontinental seas) were as a rule associated with coal-bearing series - paralic series. They often contain very rich deposits of fossil flora with dominating leaf prints, spores and pollen of Filicales (particularly many representatives of the genus *Cladophlebis*), Ginkgoales, Czekanovskiales, and the genus *Nilssonia* in particular.

Other species of pteridosperms (frequent species of the genus Pachypteris) and cycadophyte (very many species of the genus Otozamites), and conifers (Brachyphyllum and Pagiophyllum types) were dominating in localities of west Tethyan intraoceanic carbonate platforms. As a rule, these localities did not contain coal beds, and carbonates prevail among sedimentary members. This difference was clear even before, but it was not given the adequate importance. Specific characteristics of these older Jurassic continental floras (Veneto, Italy; Budoš, Montenegro) can be used to separate the realm of the west Tethyan intraoceanic carbonate platforms from the European floral province (the area of « Indo-European realm » after Vakhrameev, 1975) and to classify it as a separate Tethyan phytogeographic realm.

It is important to note, especially referring to data by Soviet botanists, that climatic belts and therefore phytogeographic realms had a polyphase variation in width during the Jurassic. These variations, which reflected the climatic fluctuations within now clear general climatic characteristics of the Jurassic period, should receive more attention in future investigations.

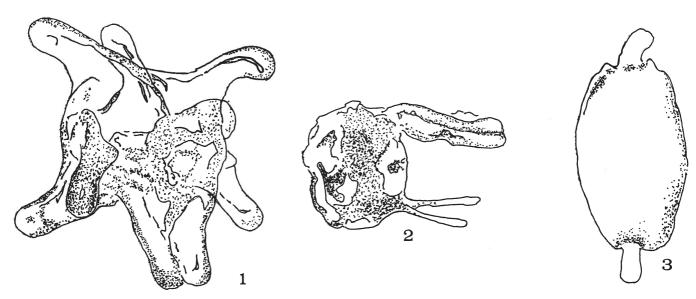
Middle Jurassic (Bajocian) flora from the klippen zone in the Swiss Alps (Pantič & Felber, to be printed) is known to have some features similar to the Jurassic floras of the Tethys province; it can be an important information for the interpretation of subsequent dynamics, especially if associated with palaeofloral data of the Cretaceous.

LOWER CRETACEOUS CONTINENTAL FLORAS OF THE TETHYAN INTRAOCEANIC CARBONATE PLATFORMS

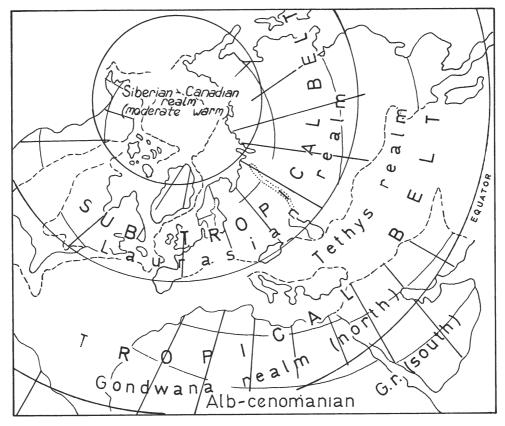
Lower Cretaceous fossil floras from the region of the west Tethyan intraoceanic carbonate platforms, though inadequately studied, are very important for the reconstruction of a more complete general picture of the Lower Cretaceous floral development. The flora from this region (Tethyan phytogeographic realm) helps to explain the relationships between Lower Cretaceous « Laurasian » floras and Lower Cretaceous floras from African continent (Gondwana realm). A number of works has been written about the specific development of continental floras of the Tethyan phytogeographic realm during the Cretaceous, viz.: Trevisan, 1971; Jardiné, Kieser & Reyre, 1974; Hochuli & Kelts, 1980; Hochuli, 1981; Pantić, 1978, 1980; Vakhrameev et al., 1978; etc.

In Lower Cretaceous, in the still large Tethys, continental flora of the Tethyan phytogeographic realm existed on the many archipelagos (intraoceanic west Tethyan carbonate platforms included) situated between the south « Laurasian phytogeographic realm » in the north and the north « Gondwana realm » in the south (terms used by Brenner, 1976).

The « South Laurasian realm » is characterized by the abundance of various pterophytes (Gleicheniaceae, Schizaceae: especially the genera *Cicatricosisporites* and *Appendicisporites*), various bisaccate pollens of pinaceans and podocarpaceans origin, less abundant



Text-fig. 2 - Floral elements of the Gondwana realm in the Tethyan realm: 1 and 2. Elaterocolpites sp. (Hochuli, 1981), 3 Sofrepites sp. (Pantić, 1980).



Text-fig. 3 - Distribution of phytostratigraphic realms and climatic betls in Middle Cretaceous.

pollen of *Classopollis* group (the incidence decreasing to the north), more inferior representatives of *Ephedripites* genus, etc.

The Tethyan phytogeographic realm is much poorer in pteridophytes and bisaccate pollens, but much richer in pollens of *Classopollis* group and *Ephedripites* genus; it also had several floristic types from the Gondwana phytogeographic realm: *Dicheiropollis etruscus* (from Berriasian to Barremian), *Elaterosporites* (*Galeocornea*) in Albian and Cenomanian and much more pollens of angiosperms (*Reticulatasporites jardinus* group). This flora from Spain is being studied (Hochuli *et al.*, in preparation) and new and interesting information is expected.

The incidence of floral forms from the Gondwana realm in the phytogeographic regions of the Tethys during the Cretaceous changed in phases, which can be associated with the climatic variations in Lower Cretaceous (expansion and contraction of tropical and subtropical climate belts), as noted also from the studied Cretaceous faunas (see Text-fig. 6).

The whole development of Mesozoic continental floras from the Triassic to the Middle Cretaceous in the Tethyan realm and on its northern and southern margins shows that the difference («individualization» Jardiné *et al.*, 1974) of continental floras between Laurasia and Gondwana increased from the Lower Jurassic. The expansion of the Tethyan ocean which, as noted by Florin (1963), was some kind of «barrier» between the continental floras of Laurasia and Gondwana (2), certainly contributed to this differentiation.

Since Cenomanian, in the « dramatic » period (beginning of frequent climatic changes of yet inadequately explained origin, intense volcanic activity, etc.), the Earth entered an era of very complex events (the Alpine-Himalayan orogeny, possible asteroid impact in the Cretaceous/Tertiary transition, etc.), which surely had an effect on the development of organic world, gradually resulting in a transformation of Mesozoic world into the living world of the Cainozoic.

The specific development of continental floras on the Tethyan intraoceanic archipelagos, within these events, is very important.

Often isolated, insular floras had surely a specific and fast development; therefore these regions could

⁽²⁾ From the aspect of tracing the integral development of Mesozoic continental floras, uniform names should be given for phytogeographic realms: Siberian-Canadian (moderate warm) realm with provinces, Laurasian (subtropical) realm with provinces, Tethyan (tropical-transitional) realm with possible provinces, Gondwana (tropical) realm with the northern province north of equator and the southern province south of equator.

have been the sources of new genera and species. For instance, the genus *Cicatricosisporites* is known to have developed in this region in middle Jurassic, to be spread to the north far into the Laurasian realm only in the transition from the Jurassic into the Cretaceous (Dörhöfer, 1977; Pantić & Fölber, to be printed). There are many similar examples.

The elucidation of actual palaeobiogeographic relations for each division of the geologic time will certainly improve the stratigraphic correlations (global or regional) in the future.

The study of Mesozoic continental floras (particularly different in Lower Cretaceous) from the Tethyan phytogeographic realm, has a great importance for the reconstruction of tectonic events. Such research has only been started, but the example of elements of « African » types of flora in the klippen zone of Swiss Alps (Schlieren Flysch, Pantič, 1980; Bayer, to be printed) indicates wide possibilities of similar research for reconstruction of horizontal movements of Earth's crust segments. Scheibnerova (1971) was obviously right in placing the tropical and the « boreal » biogeographic provinces one over the other in the Alpine region.

BENTHONIC FAUNA ON JURASSIC AND CRETA-CEOUS INTRAOCEANIC CARBONATE PLATFORMS AND SHELFS OF THE TETHYS

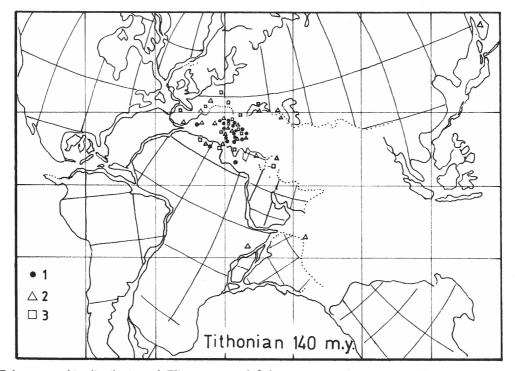
During the Jurassic and the Cretaceous, for this analysis three important groups of benthonic orga-

nisms existed on shelfs of the Mediterranean region of the Tethys, viz.:

- (1) which lived only on Mediterranean carbonate platforms and on the southern Tethyan shelf;
- (2) which, in addition to the above mentioned regions, lived also on the northern Tethyan shelf, and;
- (3) which populated both carbonate platforms and the southern and northern shelf of the Tethys, but also many regions outside the Mediterranean.

Such a distribution of fossil remains of Jurassic and Cretaceous animal groups does not readily reveal the factors that influenced it; for, if open oceanic regions of the Tethys were a barrier to dissemination of a group of animals to the north, they were not for another. If the extent and the superpositional incidence of each of the groups, however, were analysed, the paleogeography would become much clearer.

1 — On the west Tethyan intraoceanic carbonate platforms, sedimentation of carbonates continued during the Jurassic and the Cretaceous, with short breaks. The organic world, which populated many environments, was very rich and differentiated. Among various groups, the most notable is the presence of: (1) lithyotids, megalodontids and orbitopsellas in the Liassic; (2) cladocoropsis in the Malm; (3) ellipsactinias and sphaeractinias, diceratids, nerineids, and hermatypic corals in the Tithonian; (4) pachyodonts and orbitolinas in the Barremian and Aptian; (5) rudists, orbitoids and loftusias in the Senonian; and many others which are here not mentioned. All the recalled



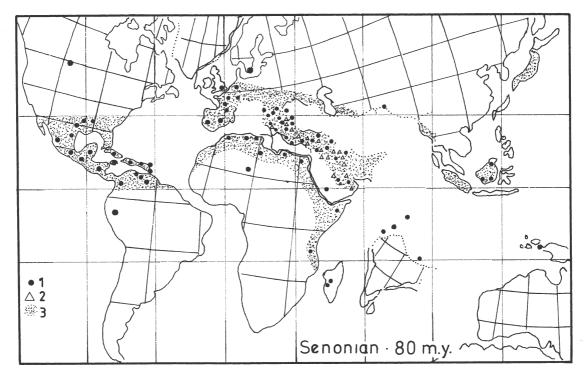
Text-fig. 4 - Palaeogeographic distribution of *Ellipsactinia* and *Sphaeractinia* (1), hermatypic madrepore corals (2), and diceratids (3) in Tithonian. Base map after Smith & Briden, 1979.

groups of fossils of the minor recurrences are continuously present in intraoceanic carbonate platforms; they were there from the beginning to the end of the existence, in larger or smaller communities.

2 — The situation was quite different on the northern Tethyan shelf and in epicontinental seas behind the shelf. None of the mentioned groups existed in any place through the geological age, nor even during any longer continuous interval. Therefore, hermatypic corals, diceratids, caprinids, rudists s. str., nerineids, and other fossil remains found in the regions of the northern Tethyan shelf are confined in bioherms, sometimes few meters thick or even thinner. Most frequently, they lie in the form of a number of sets or single beds in marls with ammonites or in clastics with shells, brachiopods, echinoids and other Euro-Asian shelf fauna, or, sometimes, in marly and sandy limestones with the preserved sublittoral population. This mode of occurrence have: (1) diceratids and nerineids of Oxfordian limestones of Swientokrzyskie Mountains in Poland and on Crimea and (2) in Upper Tithonian limestones on Crimea, (3) pachyodonts and orbitolinas in Urgonian sediments of Orgon (France), and in north Bulgaria (Lovčanske and Vračanske Mts.); (4) caprinids in Middle and Upper Cenomanian limestones of Provence; (5) hippuritids and radiolitids in Angoumian, Coniacian and Santonian limestones of Provence: and (6) rudists and orbitoids in Maastrichtian of Holland.

- 3 An analysis of palaeogeographic and stratigraphic extent of many Jurassic and Cretaceous groups of animals, which populated the sublittoral Tethys, has shown that Liassic megalodontids, and younger diceratids, nerineids, hippuritids, radiolitids, caprinids orbitolinas and orbitoids were always present on intraoceanic carbonate platforms and therefore were their patrial organisms. Unlike these, the same groups on the Euro-Asian shelf had not a continuous existence but populated it only from time to time as allophilic organisms. (The two underlined terms were used by N.S. Šatskii in 1960 referring to members of geological formations).
- 4 The questions are: What caused some of the mentioned Jurassic and Cretaceous groups to have only endemites remained on carbonate platforms throughout their history of evolution, and what made it possible for others occasionally as allophilic groups, to infiltrate on the northern Tethyan shelf and, in few cases, reach far north (e.g. Urgonian community to Japan, hermatypic corals in the Jurassic to Sahalin, and Senonian rudists to Scania)?

In search for the answers to these questions, it should be proceeded from the realistic view point that most of the mentioned groups consist of fossil remains of organisms from the Jurassic and Cretaceous tropical belt. Also the fact should be remembered, that these animals by their way of life were strictly connected to sublittoral belt, unable to leave it. Or rather, it must



Text-fig. 5 - Palaeogeographic distribution of radiolitids, hippuritids and caprinids (1), Loftusia (2), and orbitoids (3) in Senonian. Base map after Smith & Briden, 1979.

be assumed that rudists, hermatypical corals, nerineids and other organisms under study were able to extend their area only during the larval stage, especially if it occurred in the pelagic waters, where individual groups or even individual species of one genus became differentiated. Berrger (1973) wrote that in the gastropod genus *Littorina* there were species which had pelagic larval stage and species which had not.

In view of all the statements of the previous paragraph, the following is directly inferred. The species of shallow water benthonic organisms, which had none or had larvae which spent their short life in neriticum, could spread only over the shallow bottom and, doing so, either colonize the endemically limited area (e.g. ellipsactinias, sphaeractinias, and loftusias) or, moving slowly, spread over the approachable for them system of shelfs (as, according to Hallam, 1973, a shell of the genus Weyla colonized the Mediterranean in the Liassic moving from eastern Pacific shelfs of North and South America, around South America and east Africa and, in our opinion, at the same time lithyotids migrated in the opposite direction). The deep troughs of the Tethys and the expanse of its surface were an unsurmountable barrier for dissemination of all such organisms.

Other organisms (as probably many species of hermatypic corals, rudists and nerineids) had pelagic

Animal world of subtropical

Animal world

of tropical of the northern Tethys carbonate platforms K³Maastrichtian K³ Campanian K³ Santonian K3 Coniacian K, Turonian K¹ Cenomanian K₄ Albian K. Aptian K³ Barremian K² Hauterivian K¦ Valanģinian Tithonian J^a Kimeridgian J, Oxfordian

Text-fig. 6 - The invasion of allophilic tropical faunal elements onto the North Tethyan shelf.

larvae of sufficiently long life. Until recently almost nothing was known of the length of the development period for larvae of marine invertebrates, but it was lately discovered that pelagic larvae of many tropical gastropods in the tropical and warm regions of the North Atlantic have the development period longer than three months, and some even longer than ten months (Scheltema, 1971). This information allows the assumption that among sublittoral organisms of the tropical Tethys, should have been some the larvae of which could cover considerable distances, i.e. which, by the life span of larvae, could colonize the whole of the Tethys. This, however, was not easy to accomplish for the presently considered groups, because of the current systems in the Tethys and also because their fragile larvae could survive only in strictly determined (tropical) living conditions. As the boundary between the tropical belt and subtropical belt during the Jurassic, for instance, passed between Italo-Dinaridic carbonate platforms and Alpine-Carpathian-Balkanic regions, the northern shelf of the Tethys laid deep into subtropicum, and this was sufficiently big climatic obstacle even for long-lived larvae of tropical organisms populating the remote carbonate platforms to reach the shelf at any time. Only a changed climate (i.e. the movement of tropical/subtropical boundary to the north) offerred an opportunity to such larvae to use their long life for dissemination also to the north.

Besides the climatic changes, the intensive allophilic dissemination of animals from carbonate platforms onto the north Tethyan shelf had a strong effect by the approach of these microcontinents to Eurasian continent and the beginning of their collision in the Upper Cretaceous/Palaeogene. Hence, a greater number of levels with allophilic immigrants (foremostly rudists) in the southern European margin of the Upper Cretaceous, i.e. the same number of allophilic invasions was registered as through the Jurassic and Lower Cretaceous.

It should be mentioned, however, that allophilic species on the Euro-Asian southern shelf had a safe existence only during the changed climatic conditions which provided for their settlement. As soon as the tropical/subtropical boundary moved again to the south, the colonized allophilic members expired.

The most realistic answer to the raised question seems to be in the present data, assumptions and interpretations. Besides, the described relations contain the answer to the question: How the three groups of animals mentioned at the beginning could exist in the Tethys in complex relations one beside the others during Jurassic and Cretaceous? It should be mentioned, however, that, for instance, some rudist genera and species are present only in individual restricted

realms of the old Tethys. Further work on palaeogeographic regionalization of the old archipelagos and Tethyan carbonate platforms may be expected to give results for a detailed division of this realm into provinces.

SUMMARY

- 1 The study of Mesozoic continental floras and shallow water faunas in the Tethyan regions is of a great importance for interpretations of palaeogeographic transformations and geodynamic events, which transformed the regions of Mesozoic Tethys into new segments of the Euro-Asian continent (Alpine-Himalayan mountain belt) and mountains in the northern rim of Africa.
- 2 The facts considered in the present paper indicate that limitations were clearly marked in the distribution of many groups of continental plants and shelf benthonic animals in the Tethys, particularly during Jurassic and Lower Cretaceous. Besides, endemic phenomena are also conspicuous. All this suggests that during Jurassic and Lower Cretaceous the Tethys was a large and very complex basin, which included wide and deep troughs, in addition to shallow features. In addition to climatic changes and accompanying systems of sea currents, the former constituted unsurmountable barriers for dissemination of many continental floras and a serious obstacle for dissemination af shallow water faunal groups.
- 3 The study of Mesozoic shelf facies and fossilassociations in the Mediterranean has a long tradition, because they are distributed over a large area, are relatively little tectonized and primarily contain notably more macrofossil elements than the deep water formations. This is why they were discovered early and were quite easily and thoroughly studied. These are « shallow parts of the Tethys ». In addition to these, however, there are remains of the « deep parts of the Tethys », preserved in the form of formations very poor in fossils (the so-called « mute series »). more or less metamorphosed, highly tectonized, and mostly brought in abnormal tectonic relation to the surrounding formations. Very little was known of these formations until recently, and one of the most important goals in geology was to document the deepsea origin of a formation. Only in the last decade, mediterranean geologists have found the right and efficient methods for a more successful and complete study also of the formations developed on the deep oceanic bottom (i.e. schistes lustres, deep marine flysches, silicite from ophiolitic series, olistostrome and serpentinite melange). The long selective study of shallow segments of the old Tethys by many authors created an illusion that only sublittoral to possibly bathyal

- sea formations developed in it. However, it does not imply that deep sea sediments were not really formed in the Tethys. Moreover, many early searchers indicated the possibility of abyssalid formation in the Tethys (Bertrand, 1894; Steinmann, 1925; Kober, 1929; to Kelt, 1981). This has become known by now.
- 4 The answer to the principal question of this symposium: What was the nature of the Tethys: wedge shaped deep ocean with bordering shelfs or relatively shallow intercontinental sea? it could be said that the Tethys (between Europe and Africa) was neither of these. From what is presently known, this realm of the Tethys could not be compared to the large oceans of the present time, but it certainly was neither a shallow intercontinental sea, because its preserved parts indicate it as a very complex basin, bounded by shelfs and internally composed of archipelagos and carbonate platforms, separated sometimes each other by deep troughs with oceanic bottom. With such characteristics Tethys is resembling most the Caribbean-Mexican sinus of the Atlantic.
- 5 The driftings away and colliding of microcontinental blocks in the Mesozoic Tethys and its Euro-Asian and African margins, and opening and closing of its troughs and forming of composite Alpinetype structures, were in the opinion of present authors the main consequences of geodynamic processes in the Tethys itself. They emphasize, however, that much time will certainly elapse before the riddle of the sequence of climatic changes will be solved for each period of the geologic time (from Triassic to Anthropogen); all changes in phytogeographic situation, all specific features of the faunal development in relevant realms and, in this connection - the whole complexity of geodynamic processes. But now already may be said that palaeogeography, combined with other studies (palaeomagnetics, palaeoclimatology, palaeovulcanology, etc.) gives the opportunity of new knowledge about the evolution of the Earth's crust in the realm of the present-day Mediterranean, Balkan Peninsula, Central Europe, Iran and further East, and also about the development of the organic world in the geologic times.

REFERENCES

Barron, E., et al., 1981, Paleogeography, 180 million years ago to the present: Eclogae Geol. Helv. v. 74 (2), pp. 443-470.

Beer, M. A. & Jasamanov, N. A., 1982, Tektoničeskaja evoljucija Mezo-Tetisa i migracija faunističeskih provincii: Bjultenj Moskov. Obšć. Ispit. Prirody, Geol., v. 57, (1), Moskva.

Berrger, E. M., 1973, Gene-enzyme variation in three sympatric species of *Littorina*: Biol. Bullet., v. 145, pp. 83-90. Bertrand, M., 1894, Structure des Alpes francaises et récurrence de certains facies sédimentaires: Congr. Géol. In-

tern. Sess. 6, pp. 163-177.

BOLLI, H. & KRASHENINNIKOV, V., 1977, Problems in Paleogene and Neogene correlations based on planctonic foraminifera: Micropaleontology, v. 23 (4), pp. 436-452.

Brenner, G., 1976, Middle Cretaceous floral provinces and early migration of Angiosperms. In C.B. Beck (Ed.). Origin and Early Evolution of Angiosperms, pp. 23-44, Columbia Univers. Press, New York.

DÖRHÖFER, G., 1977, Discrimination and correlation of highest Jurassic and lowest Cretaceous terrestrial palynofloras in North-west Europe: Palynology, v. 1, pp. 79-93.

ERVE, VAN, A. W., 1977, Palynological investigation in the Lower Jurassic of Vicentinian Alps (N. Italy): Rev. Paleob. Palynol., v. 23, pp. 1-177, Amsterdam.

FLENLEY, J., 1979, The Equatorial Rain Forest: a geological history: Butterworths, pp. 1-162, Sydney.

FLORIN, R., 1963, The distribution of conifer and taxad genera in time and space: Acta Horti Bergiani, v. 20 (4), pp. 1-278.

HALLAM, A., 1973, Distributional patterns in contemporary terrestrial and marine animals. Organisms and Continents through time: Spec. Papers Paleontology. n. 12, pp. 41-93, London.

HARRIS, T. M., 1961-1979, The Yorkshire Jurassic flora, I-V: British Mus. Nat. Hist. London.

HOCHULI, P. A., 1981, North Gondwanan Floral elements in Lower to Middle Cretaceous sediments of the southern Alps: Rev. Paleobot. Palynol., v. 35, pp. 337-358

HOCHULI, P. & KELTS, K., 1980, Palynology of Middle Cretaceous black clay facies from Deep Sea Drilling Project sites 417 and 418 of the western North Atlantic: Init. Rep. Deep. Sea Drill. Proj. 51-53, pp. 897-935.

ISLER, A. & PANTIĆ, N., 1980, Schistes lustres- Ablagerungen

der Tethys: Eclogae Geol. Helv., v. 73 (3), pp. 799-822. Jardiné, S., Kieser, G., & Reyre, Y., 1974, L'individualisation progressive du continent africain vue à travers les données palynologiques de l'ère secondaire: Sci. Géol. Bull., v. 27 (1-2), pp. 69-85.

Kelt, K., 1981, A comparison of some aspects of sedimentation and translative tectonics from the Gulf of California and the Mesozoic Tethys Northern Penninic Margin: Eclogae Geol. Helv., v. 74 (2), pp. 317-338.

KOBER, L., 1929, Die Grossgliederung der Dinariden: Centralb. Mineral., Abt. B, pp. 425-437.

Krassilov, V. A., 1972, Phytogeographical Classification of Mesozoic Floras and their Bearing of Continental Drift: Nature, v. 237, pp. 49-50.

Pantić, N., 1952, Liasische fossilen Pflanzenreste von Gebirge Budoš - Crna Gora: Glasnik Prirodnj. Muzeja Beograd, ser. A, v. 5, pp. 293-307.

-, 1956, Biostratigraphie des flores tertiaires de Serbie:

Geološki Anali Balkanskog Poluostrva, v. 24, pp. 199-317, Beograd.

-, 1978, Cenomanian palynoflora from upper Austria: Glas. Acad. Serbe Sc. Arts, Cl. Sc. Nat. Mat., v. 43, pp. 83-93, Beograd.

1980, Environments, paleobiogeography and tectonics: Comptes Rend. Soc. Serbe Géol., 1979, pp. 7-13, Beograd.

1981, Macroflora and palynomorphs from lower Jurassic of Budoš Mountain, Montenegro: Geološki Anali Balkanskog Poluostrva, v. 15, pp. 157-171, Beograd.

SCHEIBNEROVA, V., 1971, Implications of Deep Sea Drilling in Atlantic for Studies in Australia and New Zealand -Some new view on Cretaceous and Cenozoic Paleogeography and Biostratigraphy: Search, v. 2 (7), pp. 251-254.

SCHELTEMA, R. S., 1971, The dispersal of the larvae of shoolwater bentonic invertebrates over long distances by ocean currents: Proceed. 18th European Sympos. Marine Biology.

SLADIĆ-TRIFUNOVIĆ, M., 1976, Globotruncanas from the Maestrichtian sediments of the Tijanska reka River, Western Serbia and from Markov potok Brook, Eastern Serbia: Geološki Anali Balkanskog Poluostrva, v. 40, pp. 194-196,

& CAMPOBASSO, V., 1979-1980, Pseudopolyconites and Colveraia from Maestrichtian of Poggiardo (Lecce, Puglia), Italy: Ibid, v. 43-44, pp. 273-286, Beograd.

SMITH, A. G. & BRIDEN, 1977, Mesozoic and Cenozoic Paleocontinental Maps: pp. 1-66, Cambridge Univers. Press, Cambridge.

STEINMANN, G., 1925, Gibt es fossile Tiefseeablagerungen von erdgeschichtlicher Bedeutung: Geol. Rundschau, v. 16, pp. 435-465.

ŠATSKII, N. S., 1960, Paragenezy osadočnyh vulkanogennyh porod i formacii: Izabraniye Trudy, v. 3, pp. 153-174, Moskva.

TREVISAN, L., 1971, Dicheiropollis, a pollen type from Lower Cretaceous sediments of Southern Tuscany (Italy): Pollen Spores, v. 13 (4), pp. 561-596.

VAKHRAMEEV, V. A., 1975, Main features of global phytogeography in the Jurassic and Early Cretaceous: Paleontol. Journ. v. 2, pp. 247-255.

-, Dobruskina, I. A., Meyen, S. V. & Zaklinskaya, E. D., 1978, Paläozoische und mesozoische Floren Eurasien und die Phytogeograpie dieser Zeit: pp. 1-300, Fischer, Jena.

WESLEY, A., 1966, The Fossil Flora of the grey limestones of Veneto, Northern Italy, and its relationships to the other European Floras of similar age: Palaeobotanists, v. 14 (1-3), pp. 124-132.

ZIGNO DE, A., 1856-1885, Flora fossilis formationis oolithica: v. 1-2. Padova.