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Biogeography of the Northern Peri-Tethys from the Late Eocene to the Early Miocene: Part 1. Late Eocene

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Abstract—This monograph consists of three parts. The first part discusses principles and techniques of modern biogeography that are applicable to paleontological material. Data on zonation of the modern-day water area based on planktonic and benthic organisms are given, and the phytogeography of Western Eurasia and its main divisions are characterized. The main part *Biogeography of the Late Eocene* briefly considers the stratigraphy of the Upper Eocene, including data on the Priabonian of the stratotype region of Northern Italy and on the stratigraphy of the Alpine–Carpathian and Greater Caucasian basins. The paleogeography of these basins is described and illustrated by a paleogeographic map (Popov and Shcherba). Subsequently, the biogeography of the Ancient Mediterranean and Paleo-Paratethys is considered in detail on the basis of plankton, including planktonic foraminifers (Krasheninnikov), nannoplankton (Andreeva-Grigorovich), dinocysts (Akhmetiev, Andreeva-Grigorovich, and Zaporozhets), marine ichthyofauna (Sytchevskaya), and benthos, i.e., small benthic foraminifers and nummulitids (Bugrova), ostracodes (Nikolaeva), mollusks (Amitrov and Popov), and corals (Kuzmicheva). The biogeography of the surrounding landmasses is considered based on the terrestrial flora (Akhmetiev and Zaporozhets); insects (Zherikhin), terrestrial vertebrates (Lopatin), and freshwater ichthyofauna (Sytchevskaya). In the section *Latitudinal–Climatic Zonation*, the climate is reconstructed based on various groups of plankton, benthos, and flora. The time of the onset of the fall in temperature at the end of the Eocene, and the accompanying reduction of biodiversity, are considered. In the conclusion, the tectonic, paleogeographic, and climatic events that resulted in the fundamental reorganization of the biota of the Northern Peri-Tethys, extinction of the extremely rich fauna that existed in the early half of the Paleogene, and the replacement of the Paleocenophytic flora with the Neocenophytic, are considered.

INTRODUCTION

A major event of the Cenozoic history of the Earth was a massive collision of the African–Arabian and Indian plates with Eurasia. It resulted in the raising of a collision belt at the continental margin along the Tethyan Cretaceous Suture (Alpine Fold Belt consisting of northern and southern branches) and in the closure of the residual Tethyan basins. At that time, the role of the African–Arabian Suture was transferred to the Peri-Adriatic and Peri-Arabian sutures. In parallel to the closure of the Tethyan basins, new deep-water basins (Paratethys and Mediterranean domains) were formed at the continental margins of the Peri-Tethys. Only the Eastern Mediterranean Depression was a relict of the oceanic basin of the Tethys (that appeared in the Early Cretaceous) and was similar to the depression of the Indian Ocean.

These tectonic changes combined with the emergence of the Drake Passage between South America and Antarctica and the development of the Circum-Antarctic Current essentially changed the entire circulation of the oceans and climate of Earth. In the terminal Eocene to the beginning of the Oligocene, the thermal gradient from the pole to the equator sharply increased; and the glacial climate began to develop on Earth. As a result, the thermal stratification of the ocean, in particular, the psychosphere appeared, and the contrast in eustatic fluctuation became more pronounced. These Cenozoic events resulted in great biotic changes including changes in both the taxonomic composition of all planktonic and benthic groups and changes in the general biogeographic pattern of distribution of the marine and continental biotas (Krasheninnikov and Akhmetiev, 1996, 1998).

The paleogeographic, climatic, and biotic events in the Cenozoic were very apparent in the northernmost part of the Tethys. The region under consideration includes the largest part of the Alpine Fold Belt and the zone where it contacts the East European Platform and the Turanian Plate. At the beginning of the Paleogene, this region was occupied by the peripheral seas of the Tethys, i.e., the Alpine–Carpathian and Caucasian–Kopet Dagh basins, persisting from the Mesozoic. From the beginning of the Oligocene, they became the intracontinental seas named the Western (or Central) and Eastern Paratethys, characterized by unstable salinity and oxygen regime. These basins gradually lost their connections with the world oceans, their paleogeographic and biogeographic relationships changed. In the Paleogene to the Neogene, the boundaries between the regions of subtropical and temperate climates and between the arid and humid zones and the ecotonal zone (that separated the arid and humid zones) occurred and moved within this area.

These events had a profound effect on the evolution of the fauna and flora of the epicontinental basins of the northern Tethyan margin recently designated the Northern Peri-Tethys. Foraminifers, ostracodes, diatoms, nannoplankton, corals, mollusks, and fish inhabited these basins; and were preserved as fossils. As the climate, hydrological and oxygen modes, and stagnation conditions changed, they, depending on eurytopicity and evolutionary potential, either sharply decreased in number and became extinct or gave rise to numerous endemic species, genera, and families. Abiotic events developing on land were also clearly recorded in the history of terrestrial flora and fauna of mammals, freshwater fish, and insects. Study of biogeography through-

out a long time interval (about 20 Ma) allows estimation of the dynamics of biozonation.

The major aspect of biogeography reconstructed on the basis of various groups is the clarification of the individual responses of each group to abiotic events. The study of the development of faunal and floral provinces from their formation to their destruction enables one to interpret the factors causing integration and differentiation of fauna and flora and to reconstruct the stages in, and means of, migration of aquatic and terrestrial organisms. Detailed dating of geological and paleoclimatic events and reconstruction of the development of relict basins of the Tethys, straits, and continental bridges necessitate the study of extinct faunal and floral groups and their distribution in space and time, i.e., the use of the historical biogeographic approach. Thus, historical biogeography is not only the purpose of this study, but the main method for testing the paleogeographic, climatic, and other hypotheses. This method is especially appropriate in the study of events of the later half of the Cenozoic when actualistic approaches and models become almost completely applicable.

The most difficult task in the region considered is the reconstruction of tectonic events and paleogeography of the Alpine Fold Belt where the primary conditions of bedding and distribution of sediments have been strongly disturbed by subsequent processes. This is the area where it is most important to use biogeographical methods to test the hypotheses based on the material comprising various groups of fossil fauna and flora.

This study aims to reconstruct as completely as possible the pattern of geographic and climatic changes and development of marine and terrestrial flora and fauna of Western Eurasia from the terminal Eocene, through the Oligocene, and to the Early Miocene, and to outline major biogeographic divisions of the land and sea and their evolution up to the formation of the basins, relief, and distribution of biota indicating even more contrasting conditions of the Middle Miocene. The history of the biota and major abiotic events are considered for the entire Mediterranean Domain and northerly basins; although we concentrate primarily on the less well-studied northern and eastern margins of the Tethyan Realm. Within the framework of this study, we also try to resolve the reverse problem, i.e., reconstruction of climatic, biotic, and abiotic effects and of the events determining the changes of the biota based on the taxonomic composition of the fossil fauna and flora and their spatial distribution.

The present study is initially concerned with approaches and methods used in the biogeographic analysis of the Recent biota. Modern stratigraphic and paleogeographic reconstructions of the Paratethys are discussed based on new material. The main part of the study is devoted to the data on the biogeographic zonation, i.e., biogeographic distribution of fossil groups (based on different groups wherever possible). At the end of the first part, the latitudinal-climatic zonation of the Late Eocene is proposed, whereas the major events of the Late Eocene and the Early Oligocene are discussed at the end of the second part. The evolution of various floral and faunal groups and dynamic aspects of evolution of the biogeographic subdivisions will be discussed in the final part of the study, after the biotas of the Late Oligocene and Early Miocene are considered.

The general sections were written by S.V. Popov and M.A. Akhmetiev and the sections on the paleogeography, by S.V. Popov and I.G. Shcherba; they were later augmented by their coauthors. Data on flora are presented by M.A. Akhmetiev; on dinocysts, by M.A. Akhmetiev, A.S. Andreeva-Grigorovich, and N.I. Zaporozhets; on planktonic foraminifers by V.A. Krasheninnikov; on small and large benthic foraminifers by E.M. Bugrova; on nannoplankton by A.S. Andreeva-Grigorovich; on ostracodes by I.A. Nikolaeva; on mollusks by O.V. Amitrov and S.V. Popov; on corals by E.I. Kuzmicheva; on terrestrial vertebrates by A.V. Lopatin; on ichthyofauna by E.K. Sytchevskaya; and on insects by V.V. Zherikhin.

PRESENT-DAY BIOGEOGRAPHIC ZONATION OF WATER BASINS AND LAND AREAS

Concepts and Methods for Analysis of Fossil Biota

Biogeography is generally defined as "The study of patterns in distribution of life on the Earth's surface" (Starobogatov in *Morskaya biogeografiya*, 1982, p. 12). One fundamental result of this investigation is biogeographic zonation, i.e., "the subdivision of the Earth's surface, or of some its territories, based on the analysis of spatial (biogeographic) differentiation of living organisms, including the analysis of composition of fauna, flora, and biota, patterns of the geographical ranges of taxa of different ranks, and the distribution of assemblages and ecosystems" (Kafanov, 1991, p. 23).

A great diversity of approaches to such biogeographic zonation is used, depending upon the objectives, aims, and procedures applied. Among the approaches most often used are the following:

1. The zonal–biogeographic approach, when attention focuses on zonal peculiarities in the distribution of biota, for instance, on latitudinal or altitudinal zonation. Starobogatov in *Morskaya biogeografiya* (1982) states that such zonation should be based on communities of living organisms rather than on the abiotic factors restricting it, otherwise this zonation will not be biogeographic.

2. The biotic (faunistic or floristic) approach that is based on complete account of the taxonomic compositions of biotas without regard for frequency of occurrence of these taxa. The basis for this approach is usually the comparison of the lists of species or supraspecific taxa.

3. The chorologic approach that is based on investigation of geographical ranges of taxa and groups of coinciding ranges of species.

4. The faunogenetic approach, when not only present-day faunistic composition but also its evolution and the presence of centers of origin of taxa is considered.

5. The biocoenotic approach that takes into account dominant species and taxa first. If one or several species are overdominant, as observed, for instance, in plant assemblages, rare accompanying species can be casual and their consideration in the analysis will complicate the interpretation.

These approaches are not necessary alternative. Thus, Nesis (*Morskaya biogeografiya*, 1982) uses lists of taxa and recognizes the centers of speciation when comparing pelagic zonation and shelf provinces distinguished based on cephalopods. Kafanov (1991) subdivides the shelf areas of the North Pacific based on bivalve mollusks and uses both areas of densely spaced boundaries of ranges resulting from the comparisons of lists of species. Although the multiple approach that is based on different groups of organisms is rarely used in modern biogeography, because the investigators are usually monotechnic, it may, undoubtedly, be effective for studying ecologically similar groups. Each of the groups has its own specific limiting factors, ability for dissemination, evolutionary potency, etc., however, such specifics are also observed inside taxonomic groups. Therefore, complex biogeography will reflect more general principles of distribution. Zonation that is based on markedly ecologically different biotas will probably not coincide, when their environments are fundamentally different. Thus, benthos and phyto- and zooplankton demonstrate different principles of their distribution throughout the ocean, while the marine nekton is closely related to particular bodies of water, similar to the haliplankton (*Biologiya okeana*, 1977).

Distribution of vegetation, tetrapods, fresh-water fish, and insects throughout the land-area is affected by very different limiting factors; therefore, zonation based on these groups will differ markedly.

All the approaches and procedures enumerated are also applicable to fossil material, but with substantial restrictions imposed. It must be accepted that analysis of a certain point in geological time as if it was in the present is impossible because of the incomplete fossil record, and inexact correlation. It is possible to collect fossil assemblages that are representative for rather long geological timespans, during which the situation most likely changed. However, we often have to form a general view of the original biota on unrepresentative samples of various sizes from different habitats. Therefore, only rough estimates are possible. So, it is of great methodical importance to test and compare hypotheses based on different taxonomic groups.

Nevertheless, paleontological material provides a unique opportunity to study the evolution of taxa and the time of migration, formation, and disintegration of biogeographic units, as well as providing a new opportunity to reconstruct the dynamics of historical biogeography. It is practicable to form a view of the causes of differentiation or integration of floras and faunas and to show the synchronism and the heterochronism of such processes in ecologically and taxonomically different groups of biota based on fossil material alone.

Marine Biota

Plankton

Whatever taxonomic group one deals with (phytoplankton, zooplankton or planktonic fish), the geographical distribution of the present-day plankton in the ocean is determined by its suspension in the water and inability to migrate horizontally. Therefore, its distribution is closely connected with water circulation. The habitat of the pelagic organisms, the water body, is subdivided into particular volumes, water bodies that differ in temperature regimes, salinity, density, etc. The circulation in open inland water basins is associated with one or several water bodies of the World Ocean. Therefore, to realize the possibilities for plankton dissemination in such water basins it is necessary to allow for mechanisms of circulation of water bodies in the ocean, including the following (*Biologiya okeana*, 1977; *Morskaya biogeografiya*, 1982; Fig. 1):

1. Permanent currents in oceanic basins are related to permanent atmospheric circulation and form large-scale circles (circulating water bodies) that extend from coast to coast. Climatic factors act rather uniformly inside these circles. At present, there are six such circles in the Atlantic Ocean, six circles in the Pacific Ocean, and three–four circles, depending on season, in the Indian Ocean. These circles (two tropical, two subtropical, and two subpolar) form homologous pairs relative to the equator.

2. Boundaries between these circles occur sublatitudinally. In the vicinity of coasts the zonal current, common for two neighboring circles, bifurcate, resulting in formation of triangles between the circles and the coasts (neutral regions) with local water circulation (circles).

3. Within each of the large-scale circles there exists an individual vertical water stratification. Tropical structures have a subsurface isothermal layer up to a depth of 50–100 m with a uniformly high temperature (20–30°C). The temperature decreases evenly in the depth range from 100 m to 500–1000 m (the main thermocline), while the so-called internal homogeneous waters occur deeper. The subpolar water bodies include: (a) the subsurface isothermal layer (0–50 m) that is warmed up to +10°C, or higher, in summer and cooled up to 0–5°C in winter; (b) the summer intermediate cold layer (up to a depth of 300 m), where the tem-
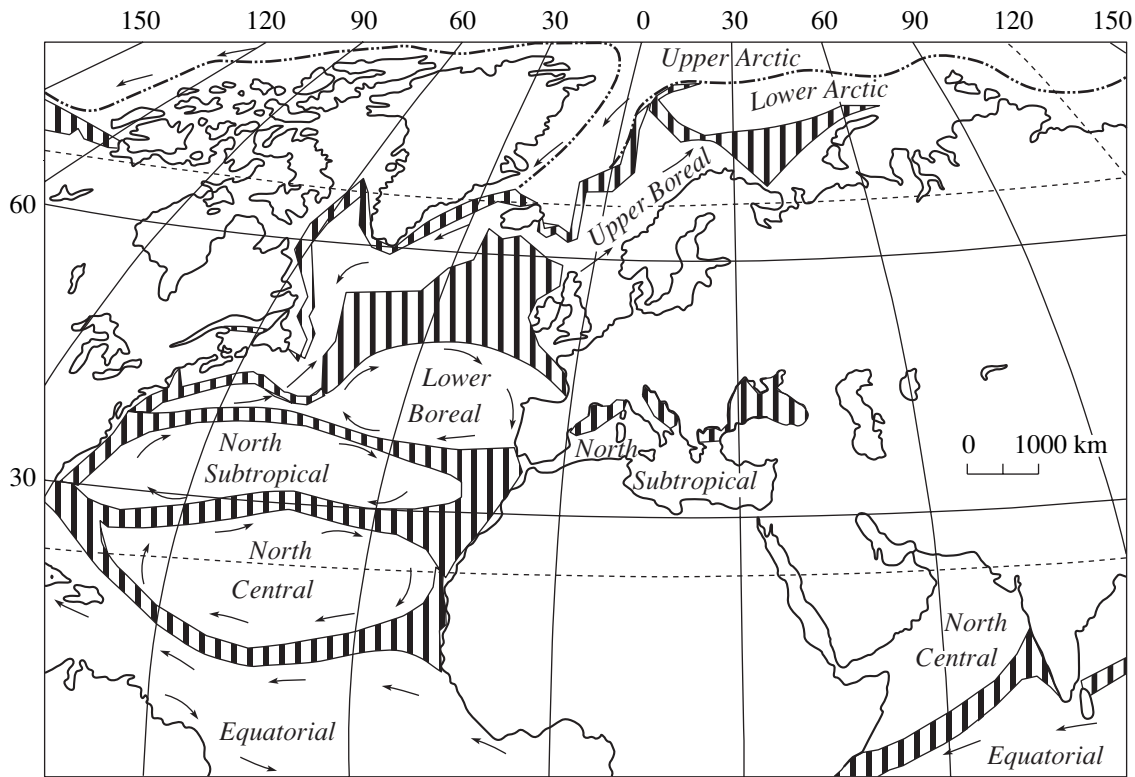
Fig. 1. Latitudinal zones of the pelagial of the North Atlantic Region and adjacent area (after K.N. Nesis in *Morskaya biogeografiya*, 1982, modified) and superficial water circulation. Vertical hatching shows transitional zones.

perature is always near its minimal winter value, while the salinity is higher than normal; (c) the intermediate warm layer; and (d) the internal homogeneous waters.

Since the entire World Ocean may be considered as an articulated system of biotopes (Fig. 1), a set system of biocoenoses and species that are their constituents correspond to it. Both the large-scale circles and local circles in neutral regions (for neritic species) may form a basis for taxon ranges. The ranges of widespread organisms may cover several circles. These ranges, as a rule, extend latitudinally and occur within one climatic zone. Therefore, the largest units of the oceanic pelagic zone correspond to the climatic zonation. These are the Arctic–Boreal, the Tropical, and the Antarctic regions, with the boundaries between them representing intermediate zones that contain very few endemic species. The Arctic–Boreal and the Tropical regions within each of the oceans are subdivided into subregions, i.e., there exist the Atlantic Boreal and the Atlantic Tropical subregions, the Pacific Boreal and the Pacific Tropical subregions, the Indian Tropical Subregion, and the single Antarctic Region. One Equatorial Province and two central provinces or zones with fairly low endemism, and with a predominance of widespread tropical species may be recognized within each of the Tropical Subregions (*Biologiya okeana*, 1977, p. 247; Nesis in *Morskaya biogeografiya*, 1982). Nesis (1982) also recognizes the northern and the southern subtropical

zones, the lower boreal, the higher boreal, the notal, the Arctic and the Antarctic zones based on the distribution of pelagic cephalopods in the Atlantic and Pacific oceans (Fig. 1).

Benthos

Development of the main concepts in the marine biogeography started based on shelf benthos fauna in the middle of last century. The earliest works (Dana, 1853; Forbes, 1856, cited after Kafanov, 1991) contained both faunistic and the zonal–biogeographic principles of zonation. Thus, Dana (1853) used the isocrims, isolines that connected habitats with the water temperature higher than a particular value during the coldest month, to recognize the latitudinal belts. He substantiated the zoogeographic significance of these isocrims by the distribution of crustaceans, scleractinians, and coral reefs. Thus, he bounded the coral reef zone by an isocrim of 68°F (=20°C). The intersection of isocrims with continental coasts indicates boundaries of 64 zoogeographic provinces. Forbes (1856) also recognized sublatitudinal climatic belts (homoiozoic belts) and 26 provinces at the intersection with the oceanic coasts. It should be mentioned that these two authors used different zonal and biogeographic nomenclature. Many provinces recognized by them are accepted in the modern zoogeography of the shelf

areas. In some cases, the very precise drawing the most significant boundaries (for example, along the Tatar Strait, Terpeniya Gulf and the Southern Kuril Isles in the Pacific Ocean) is surprising.

Since the majority of the present-day oceanic coasts are extended submeridionally, both the climatic zonation, and the biogeographic zonation of the shelf areas is based on the variation of the taxonomic composition of benthos with latitude. Since such variation is uneven, the areas of densely spaced boundaries of geographical ranges are considered as boundary regions between biogeographic subdivisions of different rank (Semenov in *Morskaya biogeografiya*, 1982). Hall (1964) studied the pattern of the northernmost points of mollusk ranges in the vicinity of the coasts of each of the oceans in the Northern Hemisphere and the pattern of annual dynamics of water temperature and superimposed these two patterns on one another. It appeared that the main limiting factor for mollusks and probably for many groups of benthic organisms is the duration of the warm summer season necessary for their reproduction and early development, rather than low winter temperatures (as was supposed by his predecessors):

—species inhabiting the *tropical zone* require a water temperature of about 20°C for more than six months of the year and above 18°C for the remaining months;

—*subtropical species* require the temperature of 20°C during four months, higher than 18°C for six months, and above 10°C during the winter months;

—*warm-water species* need a temperature of 15–18°C for four months and above 10°C during the winter months.

—the distribution of the *species of the moderately warm* zone require a temperature of about 15°C for three–four months, and these species are tolerant to temperatures below 10°C for six months;

—*moderately cold-water species* can reproduce providing temperatures higher than 10°C persist for three–four months.

Hall (1964) followed the distribution of such mollusk groups in the northern regions of the Atlantic and Pacific oceans, recognized six climatic zones and showed the boundaries of the mollusk provinces at the intersection with the oceanic coasts.

Semenov (*Morskaya biogeografiya*, 1982) constructs a chart of the biogeographic zonation of South America based mainly on the areas of densely spaced boundaries of bottom-dwelling invertebrate ranges. He insists that a strict line of demarcation should be established between the determination of the latitudinal zonation of fauna and of its faunistic structure. The latitudinal–zonal chart should be constructed based on the faunistic one, rather than the reverse. Therefore, the preliminary latitudinal–zonal characteristics of species should not be considered as arguments in drawing boundaries of faunistic zones. Semenov refines the rank and the boundaries of already recognized subdivisions

using estimates of the faunistic similarity–dissimilarity (Preston's and Jaccard's) coefficients. In the opinion of Kafanov (1991), who constructed a chart of zonation of the Northern Pacific Ocean based on bivalve mollusks, the main method is the analysis of species diversity, disappearance of thermophilic taxa, and correlation of the faunistic lists from several preliminarily recognized regions. He uses oriented columns of incorporation that show the overlap of species lists and the dendrograms of similarity of specific, generic, and family compositions. Such dendrograms at the specific and generic levels adequately illustrate the notion of the biogeographic structure of the region. The similarity of the family composition is determined mainly by the latitudinal–climatic zonation: regions from the similar climatic zones that occur on different sides of oceans are grouped together (Kafanov, 1991, text-fig. 28).

When considering the problem of bathyal zonation Kafanov first shows an increase and then a decrease in species abundance with depth, and suggests that the eurybathic species increase in number with distance from the equator. He considers the specific zonation of the bathyal zone to be unnecessary and points to the coincidence of boundaries of large zoogeographic subdivisions recognized based on littoral, sublittoral, and bathyal fauna. However, many authors pointed to a marked simplification of the structure of faunistic distribution and to some leveling in the latitudinal zonation with increase in depth (*Biologiya okeana*, 1977). The taxonomic composition of benthos that changes with depth is also very specific. Therefore, it is incorrect, in our opinion, to extend the zonation based on shelf fauna on the bathyal regions. The evolution of fauna in different bathyal zones may also be markedly distinct: the paleontological data indicate far greater stability of bathyal faunas both with space and with time (see below). Following is mainly the discussion of the shelf fauna.

The main biogeographic subdivisions of the shelf areas are regions and provinces, as well as subregions and superprovinces intermediate between them. The definition of the regions by different researchers is unambiguous. Thus, four regions are recognized within the tropical zone: the Indo–West Pacific Region, the East Pacific Region, the West Atlantic Region, and the East Atlantic Region. The boreal zone includes only two regions: the North Pacific and the North Atlantic.

The boundary between the regions within the oceanic shelf is usually drawn along the Northern Subtropical Front. However, such a boundary is not always present, and the biogeographic categories are not always in strict hierarchic order. Nesis (*Morskaya biogeografiya*, 1982) studied this problem for the eastern areas of the Atlantic Ocean. If the Lusitanian Province and the "Mauritanian" (Canary) Province are considered separately, the Lusitanian Province should undoubtedly be assigned to the North Atlantic Region by the predominance of boreal taxa, while the "Mauritanian" Province should be assigned to the East Atlantic
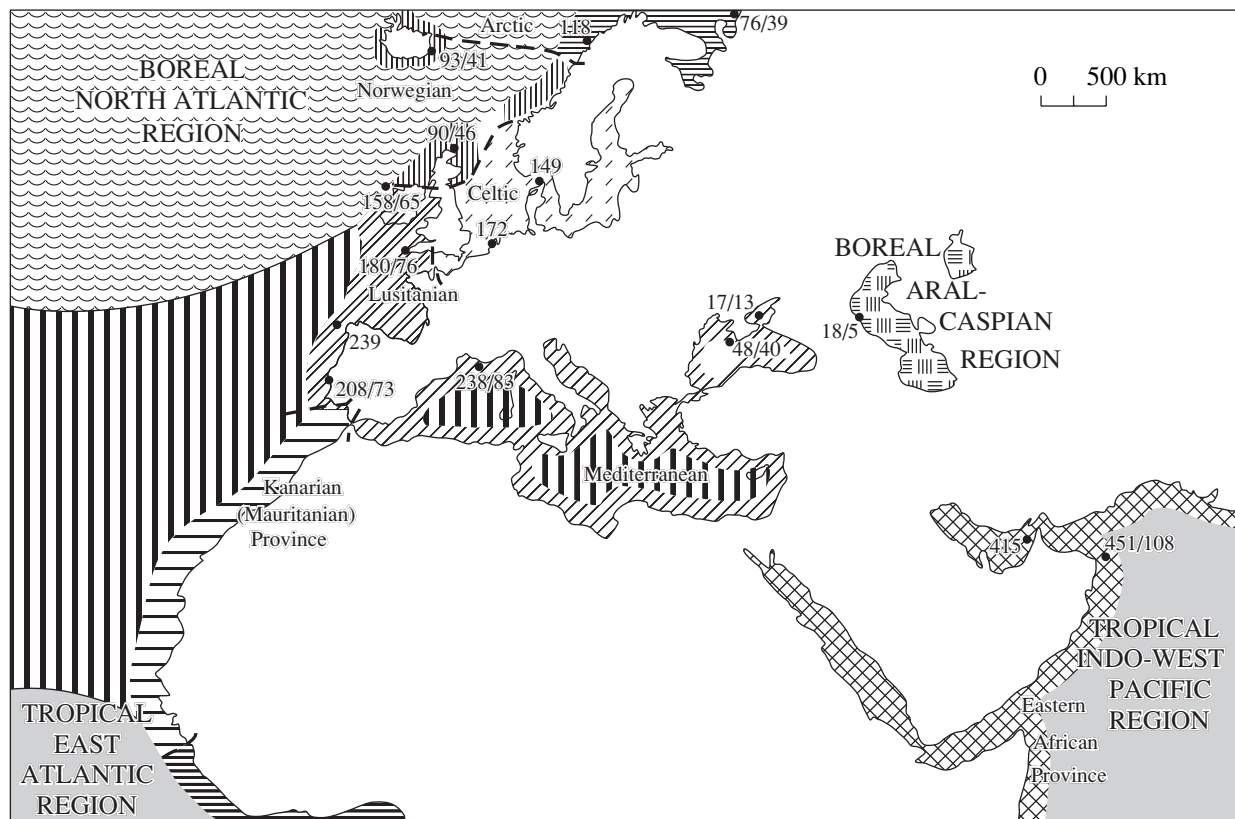
Fig. 2. Scheme of the zoogeographic zonation of the shelf of Western Eurasia and North Africa based on the Recent benthic fauna. The numbers designate species diversity of bivalves (denominator shows the number of genera).

Region. At the same time, faunas of these two provinces are rather closely similar. Along with the Mediterranean Province, these two provinces have a common center of formation of endemic subtropical–lower boreal species and constitute, therefore, a single superprovince. Furthermore Hall (1964) draws a boundary between the subtropical and lower boreal faunas inside the Mediterranean Sea. Nesis agrees with this, but points to the undoubted provincial unity of the Mediterranean fauna.

Thus, based on the benthic fauna (Fig. 2), the present-day Atlantic shelf areas of Western Eurasia mainly belong to the Boreal North Atlantic Region and include the Arctic, the Norwegian, the Celtic and the Lusitanian provinces. The Lusitanian Province, along with the Mediterranean and the Canary (Mauritanian) provinces that occur further to the south, may be considered as a wide transition zone to the Tropical East Atlantic Region. There are few endemic taxa, usually species, in these provinces. The taxonomic diversity is insignificant because of the leveling effects of the Gulf Stream and increases from north to south (see the numbers of species and genera in Fig. 2).

The southern and eastern coasts of the Arabian Peninsula are inhabited by fauna of quite another origin. These coasts are assigned to the Tropical Indo–West Pacific Region, to its Eastern African and Red Sea

provinces (Nesis in *Morskaya biogeografiya*, 1982) or subprovinces. The mutual effects of these faunas and the Mediterranean fauna are now only seen in the penetration of some species across the Suez Canal.

The distribution of the present-day shelf biota is affected by several factors in addition to climate, oceanic depths and geographical barriers. Among them are peculiar characters of hydrology, river run-off, currents, etc. These factors are of secondary importance for the oceanic fauna, but often of prime importance in continental marine basins, as exemplified by the Black Sea and the Caspian Sea. The isolation and brackishing of the Black Sea only results in a marked decrease in the biota of Mediterranean origin. On the other hand, the endemism of the Caspian Sea fauna is so great that higher biogeographic categories (regions) are recognized here (after Starobogatov in *Morskaya biogeografiya*, 1982).

Discussing the applicability of methods used in modern biology to the analysis of fossil Peri-Tethyan biotas, we can say that there are no present-day analogues to the vast, latitudinally extended, partially intracontinental marine basins. Only the Mediterranean Sea may be considered in some measure as such an analogue. A very wide ranges of benthic faunas in the absence of abrupt climatic barriers may be observed in the Indo–West Pacific Region that was considered as a

Table 1. Comparisons of boundary values of indices in the analysis of pairwise differences between the faunal assemblages of (1, 2) Recent benthic fauna (after Semenov, in *Morskaya biogeografiya*, 1982) and (3, 4) fossil molluskan fauna (after Popov, 1993, 1994), describing biogeographic boundaries of various rank. (K_{PS}) Preston index in comparisons at species level; (K_{PG}) Preston index in comparisons at generic and subgeneric level; and (K_{JS}) Jaccard index in comparisons at species level

	Subprovinces	Provinces	Subregions	Regions
1. K_{PS}, Recent		0.34–0.43	0.52–0.62	0.78–0.84
2. K_{JS}, Recent		0.45–0.57	0.59–0.75	0.82–0.86
3. K_{PS}, Paleogene	0.60–0.69	0.70–0.86	>0.86	
4. K_{PG}, Paleogene	0.40–0.49	0.50–0.69	>0.69	

single province by many authors (Forbes, 1856, cited after *Morskaya biogeografiya*, 1982).

As mentioned above, paleobiogeographic reconstructions are usually based on limited information. Thus, we have to use the chorologic approach as secondary, because only rough geographical ranges can be reconstructed for some genera and for the most widespread species. The basic method here is the correlation of lists of taxa from the few richest occurrences and groups of occurrences in paleobasins or their regions that should be considered in advance as more or less homogeneous in faunistic composition. In many cases, the specific compositions will be so incomplete or require revision, so it is better to use superspecific taxa, i.e., genera, subgenera, and even families, to correlate the information. The correctness of using the superspecific taxa for zoogeographic purposes was illustrated by the example of the analysis of recent mollusk faunas that indicates provincial distinctions at the generic level, and often also at the family level (Campbell and Valentine, 1977). If we have incomplete lists of taxa and try to make quantitative estimates of pairwise similarity–dissimilarity (Preston's and Jaccard's coefficients), we obtain far greater dissimilarities that are not comparable to data on recent fauna. Therefore, we have to introduce our own boundary values during the interpretation of results that will correlate better with the preliminary information (Table 1).

Two principle aspects of studying the regularities of biota distribution may be recognized, similar to that in the present-day biogeography. These are the analysis of dependence of composition and taxonomic diversity of biotas on the latitudinal–climatic zonation and the analysis of faunistic similarity–dissimilarity that was determined by hydrology, presence of barriers, currents, biotic relationships, etc., along with the temperature regimes.

It is possible to reconstruct the climatic zonation of past ages by direct transfer of data on the present-day occurrence of species, genera, subgenera, and families to the past (principle of actualism) or by indirect methods, for example, by analyzing the taxonomic diversity and temperature regimes of water habitats of the accompanying fauna and flora. Data on such zonation in latitudinally extended water basins may not form a basis for faunistic zonation, as illustrated by the exam-

ple of the present-day Mediterranean Sea and ancient marine basins, for example, of Oligocene age (Popov, 1995). Charts of biogeographic zonation of the past epochs should be constructed based on the similarity–dissimilarity of the faunistic and floristic assemblages, similar to those based on recent biota. The overlaps of lists, the dendrograms of similarity, the Preston's and Jaccard's coefficients, etc., show the extent of such similarity. However, if the similarity of lists indicates the similarity of the assemblages, the dissimilarity of the fossil assemblages may be caused by secondary factors (for example, by their occurrence in different facies, transportation before burial, or taphonomy), and requires further analysis.

Terrestrial Biota

Flora

The present-day floristic system of the Earth represents a hierarchical classification of coordinated phytochores, ranging from kingdom and subkingdom to district and subdistrict. If taxa of the highest category of endemism, families, correspond to the highest chorologic category, kingdoms, with the maximal distinctness of flora as a whole, regions are characterized by high generic endemism, while the provinces are distinguished by species endemism. Since borders between floras are indefinite, the boundaries between the phytochores of different rank are most often conventional and represent a certain transition zone. Nevertheless, these borders are nearly always marked by belts of densely spaced boundaries of geographical ranges. These densely spaced boundaries often coincide with orographic barriers, for example, with axes of large mountain systems, and usually have a historic nature.

The presently accepted principles of subdivision into phytochores with their coordination determine a more or less adequate number of the phytochorologic units of the same rank proposed by different phytogeographers. Thus, the subdivision of the Earth's terrestrial flora into six kingdoms is commonly accepted now: the Holarctic Kingdom, the Paleotropical Kingdom, the Neotropical Kingdom, the Cape Kingdom, the Australian Kingdom, and the Holantarctic Kingdom (Takhtadzhyan, 1978), although for many years previously only four kingdoms, the Boreal (or the Holarctic)
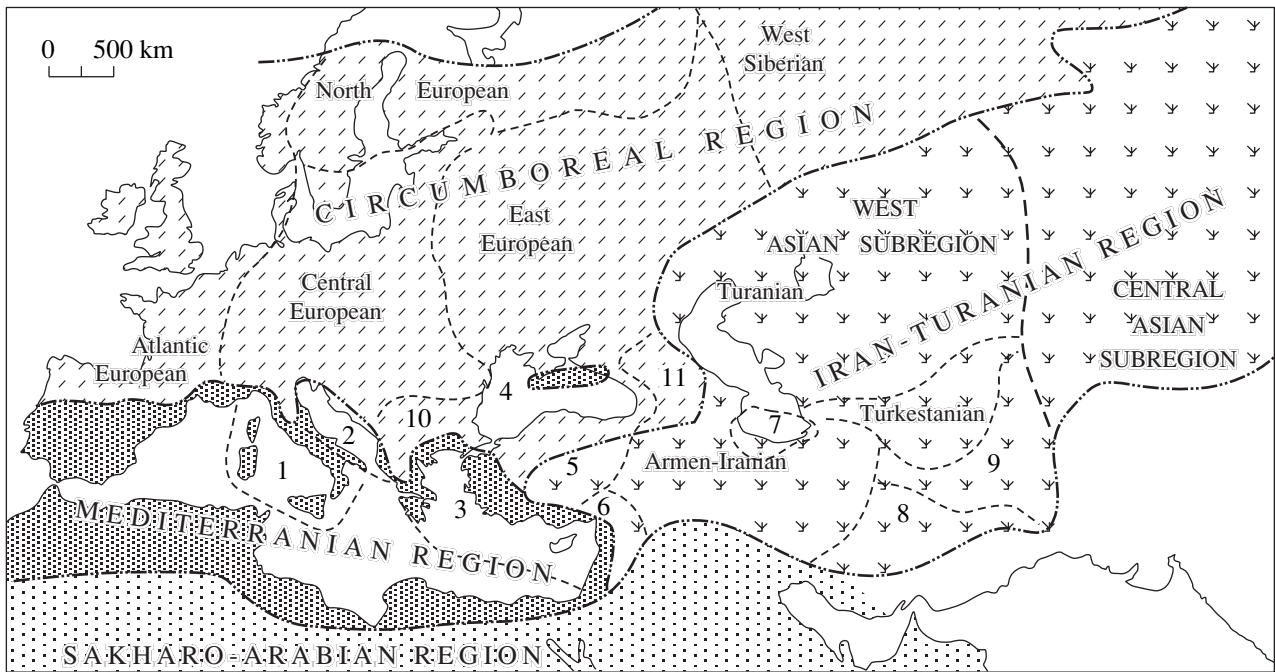
Fig. 3. Scheme of Recent phytogeographic zonation of Western and Central Eurasia (after Takhtadzhan, 1978). The numbers are the provinces of the Mediterranean Region: (1) Ligurian–Tyrrhenian, (2) Adriatic, (3) Eastern Mediterranean, and (4) Crimean–Novorossiisk; Iran–Turanian Region: (5) Central Anatolian, (6) Mesopotamian, (7) Hyrcanian, (8) North Beluchistanian, and (9) West Himalayan; and Circumboreal Region: (10) Illirian and (11) Caucasian.

Kingdom, the Paleotropical Kingdom, The Neotropical Kingdom, and the Australian (Southern) Kingdom, were recognized after Engler (1912, 1924). The number of the regions recognized is also relatively constant, although it increased since Engler, who proposed 29 regions. Takhtadzhyan (1978) proposed the recognition of 34 regions. The number of provinces also did not increase greatly. Engler recognized 102 provinces in the first quarter of the 20th century, and now Takhtadzhyan proposes 147 provinces.

The approaches and the principles of recognizing units in floristic geography repeatedly changed with its development. The basic principle, the estimate of the flora endemism, put forward by Skow as early as the first quarter of the nineteen century, has been retained. It is also conventional to use the terms of the floristic geography proposed by him, "the kingdoms" and "the provinces." All the attempts to use an approach to creation of an articulate system of phytochores different from the historic–floristic approach, for example ecological, climatic, etc., failed. The character of the vegetative cover, which is determined by vegetative types, cannot be used as a basis in floristic zonation because these types may occur in many regions and provinces. It should be remembered, however, that many plant assemblages are good indicators for one or another phytochore, for example, maquis-scrub is an indicator of the Mediterranean Region, while chaparral is an indicator of the Californian Region.

Present-day Floristic Zonation of Western Eurasia

At present, the entire territory of Western Eurasia is included in the Holarctic Kingdom that is subdivided into two: the Boreal and the Ancient Mediterranean subkingdoms. The isolation of these neighboring subkingdoms is closely related to the antecedent geological and floristic history. The Ancient Mediterranean Subkingdom is an inheritor of the ancient Tethys. In the Neogene, this region transformed into two independent regions that exist now, the Mediterranean Region and the Iran–Turanian Region (Takhtadzhyan, 1978). The distinctions between the recent floristic compositions of these regions are related to differing climatic aridities that determined the presence of a large number of xerophytic endemic species in the Iran–Turanian Region. The Boreal Subkingdom with the vast Circumboreal Region that occurs further to the north of the Ancient Mediterranean Subkingdom inherits entirely the Tertiary Boreal Region that occurred in the temperate climatic belt throughout the Cenozoic. The line of demarcation between these floras coincides with boundaries between two main subkingdoms, the Boreal and the Ancient Mediterranean subkingdoms (Fig. 3). The phytochorologic boundary of the Mediterranean Region generally coincides with boundaries of the Mediterranean forests of *Quercus ilex* and with the primary ranges of the olive (*Olea*). The Sahara–Arabian Region occurs further to the south of the Ancient Mediterranean Region, on each side of the Tropic of Cancer, and is included in the Holarctic Kingdom, in its Ancient

Mediterranean Subkingdom, although many investigators assigned this region to the Paleotropical Kingdom (Engler, 1924; Good, 1947; Schmithcüsen, 1961; and Tolmachev, 1974). Flora of the Iran–Turanian Region that occurs further to the east of the Mediterranean Region and has the boundaries drawn by Boissier (1967) is characterized by high generic and specific endemism. This region occupies Central and Eastern Anatolia, larger area of Syria, including the Syrian Desert, the Armenian Highlands, arid regions of Southern and Eastern Transcaucasia, the Talysh Mountains, the Plateau of Iran (except for the tropical deserts that occupy its southern areas) and the foothills of the Hindu Kush and Western Himalayas. In the north the Iran–Turanian Region occupies the entire steppe and semidesert areas of Kazakhstan, from the lower reaches of the Volga River to the Zaisan Basin.

Below is a brief description of the present-day basic floristic regions and provinces that occur in the territory of the Neogene Paratethys and its surroundings.

ANCIENT MEDITERRANEAN SUBKINGDOM

Mediterranean Region

The peculiar floristic character of the Mediterranean Region is determined by the presence of plants that are adapted to unusual climatic environments, humid winters and dry summers season. Human activities markedly affected the original vegetation, especially forests, of this region. Forests of cork oak, Aleppo pine and cedar of Lebanon that previously occupied large areas now occur only as relicts. Representatives of the lower storey in the forests, juniper, green pistachio, and thyme, rarely occur as a single woodlands. Oak forests were replaced by brushwood of dwarf oak woodlands, myrtle, and *Arbutus* covered by thorny vines. This secondary formation, maquis, continues to degrade as it is affected by human activities and transforms into the so-called garrigue, when the thorn-brush disappears, while *Cistus*, thyme, and rosemary, and only dwarf palms and oaks are found.

Five families are characteristic of (or near-endemic to) the Mediterranean Region, with only one family, Aphyllanthaceae, restricted entirely to this region. There are over 150 endemic genera. In addition to the original ranges of *Aleaster* and continuous forests of Holm Oak (*Quercus ilex*), the boundary of this region is also marked by the range boundaries of the following trees and shrubs: *Pinus halepensis, P. brutia, P. punea, Aristolochia sempervirens, Quercus coccifera, Arbutus andrachne, A. unedo, Erica multiflora, Styrax officinalis, Cercis siliquastrum, Hamaerops humilis*, and by many other herbaceous plants, especially umbellifers and crucifers.

Unlike the Makaronesian Region (with its Canary endemics) that occurs further to the west, the Mediterranean Region contains a smaller number of Tertiary relics and larger number of neoendemics formed in the Late Cenozoic. Both the flora, and the character of the vegetation, change generally from north to south and from west to east with an increase in climatic aridity. The effects of neighboring floras as early as the Quaternary were seen in the invasion of some representatives of the Circumboreal Flora to mountain areas of this region in glacial phases. The effects of the African Flora on the Mediterranean Flora are most marked in its south-westernmost areas, such as Morocco. Flora in the Mediterranean Region differs markedly, especially in the east and the west, and therefore is subdivided into nine provinces (Takhtadzhyan, 1978), four of which are somewhat closer to the ancient Northern Paratethys:

The Ligurian–Tyrrhenian Province includes coastal areas of France and Italy and the islands of Corsica, Sicily, and Malta. Flora of this province contains four endemic genera and more than one hundred endemic species, the majority of which inhabits the islands.

The Adriatic Province covers coastal regions of Eastern Italy and Yugoslavia. There are only two endemic genera and 15 endemic species in the floristic composition.

The East Mediterranean Province occupies the greater part of Greece, islands in the Aegean Sea, Cyprus, Crete, etc., and coastal areas of Asia Minor. The eastern boundary of this province is marked by the boundaries of the geographical ranges of the representative Mediterranean tree taxa *Quercus coccifera, Arbutus unedo, Styrax officinalis*, and *Pistacia lentiscus*. The flora in this province includes more than 20 endemic genera and several hundred endemic species, the majority of which inhabit Greece and islands in the Aegean Sea.

The Crimean–Novorossiisk Province is a Mediterranean enclave within the Circumboreal Region. This province includes the southern coastal areas of the Crimea and the Black Sea coast from the town of Anapa to the town of Tuapse. This flora represents the impoverished Mediterranean Flora with numerous endemic taxa, especially in the Crimea. Representative Mediterranean tree taxa occurring here include *Pinus brutia, Cistus incanus, Lonicera etrusca, Arbutus andrachne, Ruscus hypoglossum*, etc.

Iran–Turanian Region

There are more than 350 endemic genera and a large number of endemic species in this province that comprise more than 25% of the entire flora. This region is subdivided into two subregions, the West Asian Subregion with its richer flora and the Central Asian Subregion. Only the West Asian Subregion is related to the eastern surrounds of the ancient basins. Geographically, it covers the greater part of Turkish Anatolia, Syria, some areas of Palestine and Sinai, the larger area of the Armenian Highland and of the adjacent ancient Mesopotamia, arid and semiarid areas of Eastern and

Southern Transcaucasia, the Talysh Mountains and the adjacent regions in Hyrcania, the Plateau of Iran, except for its southern tropical deserts, the Western Himalayas, as well as the vast steppe and semidesert areas from the lower reaches of the Volga River to the coastal areas of the Balkhash Lake (see Fig. 2). The maximum number of the endemic genera in the western subregion, as in the entire Iran–Turanian Region, are herbaceous and brush xerophytes of the families Brassicaceae, Apiaceae, Lamiaceae, and Asteraceae.

The West Asian Subregion occupies some areas of arid Asia with a mean annual precipitation of less than 200 mm in some places, nevertheless it is generally more humid, although not evenly. Ancient relict forests as well as xerophilous oak forests and light forests with the maximum number of the surviving ancient Mediterranean elements are found in various areas of the West Asian Subregion, such as Hyrcania, the Zagros Mountains, the Western Tien Shan, and the Western Himalayas. The Plateau of Iran is a basic center of formation of the Iran–Turanian Flora and the center of origin of numerous neoendemic taxa, especially species, which formed after the closure of the Tethys.

The West Asian Subregion includes several provinces: the Mesopotamian Province, the Central Anatolian Province, the Armenian–Iranian Province, the Hyrcanian Province, the Turanian Province (or the Aral–Caspian Province), the Turkestanian Province, the North Beluchistanian Province, and the West Himalayan Province (Takhtadzhyan, 1978).

The Central Anatolian Province shows a high degree of endemism at the species level (over 30% endemic species). Most of them belonged to halophilic associations and were closely connected with representatives of both the Mediterranean and Iran–Turanian floras.

The Armenian–Iranian Province is one of the largest provinces. This is characterized not only by high specific endemism, but also by high generic endemism. The plant assemblages in this province are fairly diversified and represent typical desert, semidesert, and mountain steppe assemblages with abundant cushion thorn-bushes, as well as assemblages composed of associations of xerophilous sclerophyllous shrubs, light juniper and larch forests, xerophilous oak forests, and open oak woodlands. The precipitation is unevenly distributed throughout the province. The province is subdivided into several subprovinces that are characterized by different endemism and floristic elements. The Central Iranian Subprovince has the dominant role for the province. This subprovince occupies inland plateaus in Iran and Western Afghanistan, where the majority of endemic taxa inhabit the most arid areas occupied by wormwood assemblages. Broken masses of tree vegetation (light almond–pistachio forests) indicate the connections between the basic core of the Iran–Turanian Flora and the Mediterranean Flora.

The Hyrcanian Province has the most distinct boundaries in the floristic terms and includes the areas occupied by relict forests in the Talysh Mountains and in the north-facing slopes of the Elborus and the South Caspian Lowland. The main forest-forming trees are the following paleoendemic taxa: nettle tree, *Parrotia persica, Quercus castanaefolia, Zelkova carpinifolia*, and *Carpinus betulus*, descendants of the ancient Tertiary Flora.

The Turanian (or the Aral–Caspian) Province covers desert areas of Eastern Transcaucasia and of the Caspian Sea and all Lowland areas from the Urals and Transcaspia to the Balkhash Lake coastal regions, including mountain systems of Mugodzhary, Ustyurt, desert areas of Western Kazakhstan and of the northern regions of Central Asia.

The vegetation of this province is represented mainly by steppe and desert assemblages that have much in common with the vegetation of the Armenian–Iranian Province. This is also similar to the vegetation of the Central Asian Province in having numerous species of Chenopodiaceae in its composition.

The West Himalayan Province occurs in the easternmost areas of the West Asian Subregion and differs from all the other provinces in having a monsoon climate. The analysis of flora from this province is of special interest because many paleoendemic taxa (mostly trees) are found within it. These taxa, for example the monotypic genus *Parrotiopsis*, are the descendants of the ancient Tethyan flora. This province is the eastern boundary for the ranges of some trees not only from the Iran–Turanian Region, but also from the Mediterranean Region, for example, for the ranges of myrtle, pomegranate, and olive. The endemic cedar *Cedrus deodara*, and many other coniferous trees, *Abies spectabilis, A. pindrow, Picea smithiana, Pinus griffithii, P. gerardiana, Taxus walliachiana, Cupressus torulosa*, and species of *Juniperus* are the descendants of ancient conifers that occurred much more widely in the ancient Mediterranean (when the Alpine Ranges started to rise, the climate was humid and there was no barrier between the East Asian and the West Mediterranean floras).

The lower belt of the subtropical forests is composed of evergreen oaks *Quercus incana, Q. dilatata*, and *Q. semecarpifolia*. Persian walnut and some species of azalea, including the endemic species *Rhododendron afghanicum* and *R. colletianum*, are also found. Laurel plants are diversified and include *Litsea, Neolitsea*, and *Machilus*. The range of endemic tree species of another genera is very wide: *Alnus nitida, Ulmus wallichiana, Skimmia laureola, Sorbus cashmiriana, S. lanata, Staphylea emodi, Aesculus indica, Syringa emodi*, etc. Plants from the East Himalayan Province of the East Asian Region that are strange to the Iran–Turanian Region, for example, the Paleotropical species *Mallotus philippinensis* and *Terminalia tomentosa* had migrated here from the south and east.

BOREAL SUBKINGDOM

Circumboreal Region

This region of the temperate flora occurrence occupies middle latitudes of the Northern Hemisphere and is subdivided by many researchers into two independent regions that occur in the Western Hemisphere and in the Eastern Hemisphere. This region is the largest on Earth, nevertheless it does not contain any endemic families and includes only a few (less than 50) endemic genera and species, the majority of which occupy the mountain systems of the Pyrenees, Alps, and the Caucasus. The basic forest-forming group of plants in this region is composed of widely known *Pinus, Picea, Abies, Larix, Quercus, Fagus, Betula, Alnus, Acer, Carpinus, Populus, Salix, Fraxinus, Ulmus, Tilia, Juglans, Celtis, Ostrya*, and *Cornus*.

The southern plain areas of the Circumboreal Region are occupied today by forest–steppe and steppe assemblages. Several belts of forest vegetation are recognized in mountain regions. The upper belts are occupied by coniferous forests and subalpine vegetation.

The Northern Peri-Tethys and its surrounds occupied southern areas of the West European Sector of this region. At present five of its fifteen provinces occur here. These are the Central European Province, the Illirian (or the Balkan) Province, the Euxine Province, the Caucasian Province, and the East European Province.

The Central European Province overlaps the territory of the Northern Peri-Tethys (the Carpathians, the Dniestr Region, and the Middle Danubian and the Lower Danubian lowlands) in its southeastern areas only. Its eastern boundary is determined by a closure of ranges of many Central European trees (e.g., *Taxus baccata, Abies alba, Fagus silvatica, Quercus petraea*) and other plants (e.g., *Hedera helix*). Apart from the Alps, the Carpathians are characterized by high endemism (12%).

The Illirian (or the Balkan) Province occupies the larger territory of the Balkan Peninsular. It contains four endemic genera and several dozens endemic species that occur in mountain systems (the Dinaric Alps and the Rhodope). Many endemic taxa are ancient relicts (the Balkan Refugium) with Himalayan and East Asian connections. Thus, *Pinus pluce* is close to the Himalayan *P. griffithii. Ostrya carpinifolia, Juglans regia*, species of *Quercus, Diospyros lotus, Buxus sempervirens, Vitis vinifera, Ilex aquifolium, Syringa vulgaris*, etc., are undoubtedly relict taxa.

The Euxine Province occupies the Western Caucasus (Abkhazia and Adzharia), the Black Sea Coast of the Krasnodar Territory, Bulgaria, and Turkey. Flora of this province includes three endemic genera and more than 200 endemic species. Many of the endemic taxa, especially in Colchis, are Tertiary relicts. Among the endemic trees are *Abies nordmanniana, Picea orientalis, Quercus pontica, Q. hartwissiana, Corylus colchica, C. pontica, Rhododendron smirnovii, Staphylea colchica, Rhuscus colchicus*, etc. Tree assem-

blages are dominant in the Euxine Province. Oak, beech, and beech–chestnut forests are widespread in the lower altitudinal belt, while conifer forests occur widely at higher altitudes. There are many Tertiary relicts, shrubs and vines *Rhododendron ponticeum, Laurocerasus officinalis, Hedera colchica*, and *H. helix* in the understorey.

The Caucasian Province covers the majority of mountain systems of the Caucasus, Stavropol Upland, Terek–Sunzha Upland, Dagestan, and Central and Western Transcaucasia. Flora in the western regions of this province includes many species in common with the Euxine Flora but with local endemic taxa (two genera and several tens of species). Central regions of the Greater Caucasus are characterized by the highest endemism. Mountain larch forests with beech and durmast oak *Quercus petraea* are typical of the Caucasian Province. Beech forests are replaced higher by a belt of subalpine parklands with *Acer trautvetteri* and *Quercus macranthera*.

The East European Province includes the southern piedmont Carpathian plains, some areas of the Lower Danubian Lowland, the Black Sea coastal lowland, Azov Sea coastal territories, and southeastern areas of the East European Platform, from the city of Volgograd to the Urals. The eastern boundary of this province coincides with the eastern boundaries of the oak forest ranges. Flora in this province includes only one endemic genus *Cymbochasma*, nevertheless several tens of endemic species are known in this province, especially in steppe assemblages.

The northern margins of this province are occupied now by oak forests with a participation of ash, maple, small-leaved lime, etc. There are oak–hornbeam forests in the Dniestr Region. A forest–steppe belt occurs further to the south, then being replaced by a steppe belt. *Quercus robur* is the main tree species in the forest–steppe assemblage. Grasses form the basis of the steppe assemblages.

BIOGEOGRAPHY OF THE LATE EOCENE

Upper Eocene Stratigraphy of Northern Peri-Tethys

The Upper Eocene is now considered as the Priabonian (Cavelier and Pomerol, 1986; *Geologicheskie i bioticheskie…*, 1996) and includes three planktonic foraminiferal zones, *Globigerapsis semiinvoluta, Turborotalia cocoaensis*, and *T. centralis* (P15–17), three or four *Chiasmolithus oamaruensis–Sphenolithus pseudoradians* (NP18–20) nannoplankton zones, and possibly the lower part of the *Coccolithus subdistihus* (NP21) zone (Berrgren *et al.*, 1995, pl. 2). In the stratotype region, the Vicenza Province, Northern Italy, the Upper Eocene is represented by a formation composed of shallow-water biogenous limestone, clays, and siltstones 80 m thick in outcrops near the village of Priabona and in the geochronologically younger Granelle Section. Here, the Upper Eocene is characterized by a complete sequence of the planktonic foraminiferal and

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nannoplankton zones (Cita, 1975). The *Charlesdown-iella clathrata angulosa* dinocyst zone that is recognized both in these sequences, and in the Massignano Section, which is proposed as a stratotype of the Eocene–Oligocene Boundary, corresponds with the Priabonian. The latter section occurs in the Northeastern Apennines and is characterized by a continuous sequence of pelagic marly beds. The boundary is defined by the boundary between the planktonic foraminiferal zones (P17/18). The extinction of the Hantkeninidae is considered to be the most important event at this boundary. The boundary is drawn inside the NP21 zone, or the CP16a zone after Okada and Bukry, 1980 (Coccioni *et al.*, 1988) and in the thirteen zone of magnetic polarity, in the vicinity of change of mainly reversed polarity to normal polarity (C13r/C13n). Four datings in these sections indicate the age of the Priabonian Boundary at between 37–38 to 33–34 Ma (Odin and Montanari, 1989) or between 36.8 to 33.7 Ma (Berrgren *et al.*, 1995).

Two nummulite zones, *N. fabianii* and *N. retiatus*, are recognized in the Priabonian of the Mediterranean Region (Cavellier and Pomerol, 1986). The development of *Nummulites fabianii, N. garnieri, N. bouillei, N. incrassatus, N. budensis, N. variolarius, N. stellatus*, and occasionally *N. millecaput* is typical of the first half of the Priabonian. In the second half, nummulites with large tests, real granulated taxa, disappear, while *N. retiatus* appears.

The assemblages of the major planktonic groups that are found in geological successions in the northern marginal basins are somewhat impoverished compared to the Mediterranean assemblages because of the latitudinal climatic zonation of biota and its biogeographic differences.

Alpine–Carpathian Basin. The nummulite assemblages are still rather representative in the Carpathians and in the intermontane Carpathian depressions. In the Hungarian Paleogene Basin the nummulite limestone beds (from the Szepvolgy Formation) are assigned to the Priabonian because of the presence of abundant nummulites, planktonic foraminifers of the *Globigerapsis semiinvoluta* Zone, and nannoplankton of the NP18 and 19 zones. The Bryozoan Marl and the Buda Marl that contain planktonic foraminifers of the P17 zone and nannoplankton of the combined NP19–20 zone are also assigned to the Priabonian. The Eocene–Oligocene Boundary is drawn in the upper part of the Buda Marl at the base of the *Globigerina tapuriensis* Zone by changes in the nannoplankton and planktonic foraminiferal assemblages (P17/18) (Báldi *et al.*, 1984; Nagymarosy and Báldi-Beke, 1988).

In Transylvania the Cluj Limestone Beds and the larger part of the Breby Marl are assigned to the Priabonian. The upper boundary is drawn by a change of the planktonic foraminifers of the *Turborotalia cerroazulensis* (P16–17) zone to the *Globigerina ampliapertira–Pseudohastigerina micra* Zone that occurs several

meters lower, the last appearance of the *Cyclococcolithus formosus* (NP21/22) Zone (Bombita and Rusu, 1981). Later on, this boundary was drawn lower in the succession, in the NP21 zone, based on the acme of the species *Coccolithus orbita*.

In the Flysch Carpathians the Upper Eocene is represented by a finely rhythmic, greenish–gray flysch formation 150–300 m in thickness with rare carbonate beds and with a marly Sheshora Horizon in the upper part. Beds with *Globigerapsis tropicalis* and *Cyclammina rotundidorsata* are recognized within the flysch part of the section (Vyalov *et al.* in *Geologicheskie i bioticheskie…*, 1996). These beds correlate with the combined *Discoaster barbadiensis* (NP18–20) nannoplankton zone. The lower beds of the Sheshora Marl Horizon contain large globigerinids of the *G. corpulenta* Zone and nannoplankton of the NP21 zone. Small globigerinids, *Globigerina officinalis, G. praebulloides, G. ampliapertura*, and *G. tapuriensis*, that are more typical of the Oligocene, as well as nannoplankton from the upper part of the NP21 zone, and then of the NP22 zone appear higher in the succession (Bombita and Rusu, 1981; Olszewska, 1984, and Krhovsky *et al.*, 1993). Thus, the boundary should be drawn inside the Sheshora Horizon based on plankton, but it is often placed at a marked lithological boundary in the top of this reference horizon that is supported by data on dinocyst occurrence (Andreeva-Grigorovich in *Geologicheskie i bioticheskie…*, 1996).

Transcaucasia. The Priabonian foraminiferal, nannoplankton and dinocyst zones, like those in the Mediterranean may be traced further east only in the territory of Armenia, which was occupied by a gulf of the Central Iranian Basin in the Late Eocene–Early Oligocene. All the three plankton foraminiferal zones, *Globigerapsis semiinvoluta, Turborotalia cocoaensis*, and *T. centralis* (P15–17) Zone (Krasheninnikov, Muzylev, and Ptukhyan, 1985), all the Upper Eocene nannoplankton (NP18–21) zones, and the *Charlesdowniella clathrata angulosa* dinocyst zone (Andreeva-Grigorovich, 1981; Zaporozhets, 1989) are recognized here within the Upper Eocene *Nummulites fabianii fabianii* and *N. fabianii retiatus* zones.

The principal zonal Priabonian subdivisions based on plankton data may also be traced further north of the Lesser Caucasus System, where facies typical of the Beloglinian Horizon (Regional Stage) of the Greater Caucasus–Kopet Dagh Basin occur. Thus, in the Rioni–Kura Facial Zone with a carbonate character of sedimentation regional zones were usually recognized based on the *Globigerapsis tropicalis* and *Globigerina officinalis* in association with small globigerinids. The *Globigerina officinalis* Zone correlates with the *Bolivina antegressa* Zone in shallower basins. However, recent studies indicate the presence of zonal species from the Blow Scale here and the correlation between the *Globigerapsis tropicalis* Zone and the *Globigerapsis semiinvoluta* and *Turborotalia cocoaensis* (P15–16) zones (Sulukvadze *et al.* in *Geologicheskie i biot-*

Table 2. Correlation of the Upper Eocene–Lower Miocene of the Paratethys and Major Events in the Eastern Paratethys

Age (Ma)	Epoch	Stage	PLANKTON ZONE correlation acc. to Berggren et al., 1995 — Foraminifera Blow, 1969, 1979	Nannoplankton Martini, 1971	Carpathians	Central Paratethys (Hungary)	regio-stages	dinocysts Andr.-Grig., 1994 Zaporozhec, 1998	EASTERN PARATETHYS — Foraminifera benthos plankton	Georgia	N. Ustyurt/pre-Aralian	Shallow salinity 10 20 30‰	Transgression/Regression − +	Main events in the Eastern Paratethys
	MIOCENE	Langh.	N9 Globigerinoides sicanis N8	Sph. hetero-morphus NN5		BADENIAN	CHOKRAKIAN		Florilus parvus	CHOKRAKIAN	CHOKRAKIAN			◁ Full marine conditions
20		Burdigal.	G. trilobus N7 Globogerinita dissimilis N6	Helicopontosphaera ampliaperta NN4 S. belemnos NN3		TARKHANIAN KARPATIAN	TARKHANIAN KOZAHURIAN		Globigerina tarchanensis Saccammina zuramakensis	TARKHANIAN KOZAHURIAN	TARKHANIAN Bishtyubjanian Suite			⇓ 2-nd Paratethys isolation
		Aquitan.	Globoquadrina dehiscens N5 Gl. kugleri N4	Discoaster druggi NN2 T. carinatus NN1		OTTNANGIAN EGGENBURGIAN	SAKARAULIAN KARADIAL-GANIAN	D. spinulosa H. floripes Rhombodi-nium draco	Neobulimina elongata Cibicides ornatus-Elphidium onerosum	SAKARAULIAN Upper Lower Uplisiskhe Suite	Kintykchenian Suite Aralian Suite Baigubekian Suite			◁ Short vast transgression
25	OLIGOCENE	Chattian	Globigerina ciperoensis P22	Sphenolithus ciperoensis NP25	Krosno Serie	EGERIAN	KALMYKIAN	C. partispinatum	Sp. terekensis Virgulinella		Karato-makian Chagraian			◀ Peak of anoxy ◁ Turbiditic activity
		Rupelian	Globorotalia opima opima P21 Globiger. am-pliapertura P20	Sphenolithus distentus NP24 Sph. praed. NP23	Menilithic Serie Lower Cherts	KISCELLIAN — Kiscellian Upper Tard C. lipoldi Beds Lower Tard Clay	SOLENOVIAN	Wetzeliella gochtii W. symmetrica	Troch. florifera Sp. carinata oligocaenica	Corbula Beds Otskhe Beds Abastumanian Suite	Tamdy Suite Asche-airyk Kutan-bulak			⇓ Paratethys isolation, 1-st crisis of salinity
30			Globigerina sellii P19 Globigerina tapuriensis P18	Helicopontosphaera reticulata NP22 Coccolithus subdistihus NP21	Shesho-ra Marl Bryozoan Marl	PSCHEKHIAN BELOGLINIAN Buda Marl	PSCHEKHIAN BELOGLINIAN	Ph. amoenum Charlesdowniella clathrata angulosa Beds Microdinium	Lentic. herrmanni Cibic. salensis Bol. antegressa G. tropicalis- Gl. corpulenta	Akhaltsikhe Suite	Chilikta-nian Anom. munda B. antegressa			⇓ Boreal immigrants ◁ Regression, stagnation Lesser Caucasus orogenesis Eastern Paratethys separation
35	EOCENE	Priabon.	T. cen.-G.g.P17 T. cocoa. P16 Globig. semi-involuta P15	Sp. ps.-1st. rec. NP19–20 Ch. oamar. NP18	Nummulitic marl		KUMIAN	Rh. perforatum	P. costata Gl. turcmenica		Chegan			

Fig. 4. Paleogeographic map of the Peri-Tethys Region in the Priabonian. Explanations: (*1*) conglomerates; (*2*) sands; (*3*) clays; (*4*) marls; (*5*) limestones; (*6*) evaporites; (*7*) mountains; (*8*) highlands; (*9*) nondifferentiated land; (*10*) lowlands; (*11*) lake basins; (*12*) lagoons episodically covered by the sea; (*13*) shallow shelf; (*14*) deepwater shelf; (*15*) continental slope and bathyal; (*16*) terrigenous deposits; (*17*) flysch; (*18*) volcanoes; (*19*) normal faults; (*20*) thrusts; (*21*) shifts; (A) Andrusov Uplift; (ALB) Alboran Land; (CAL) Calabria; (DH) Donets Uplift; (EBD) East Black Sea Depression; (KAB) Kabylia; (LC) Lesser Caucasus; (MC) Massif Central; (Sh) Shatsky Uplift; (PEL) Peloritanian Land; and (WBD) West Black Sea Depression.

icheskie…, 1996), while the assemblage with smaller foraminifers that occur higher in the succession contains representative species of the *Turborotalia centralis* (P17) Zone. The lower boundary of the *Bolivina antegressa* Zone occurs somewhat below the boundary of the *T. centralis* Zone, i.e., approximately at the level, where a sharp increase in the number of bolivins of the *B. antegressa* Group is observed in Northern Italy (Coccioni *et al.*, 1988). Both in Georgia and in Azerbaijan nummulites from the *Nummilites fabianii* Zone are present and all the four nannoplankton zones are recognized.

South Ukraine, Ciscaucasia, and Transcaspia. In the Beloglinian successions that are composed of carbonates the most thermophilic species, including the zonal ones, disappeared from the assemblages, while the other species had incomplete stratigraphic ranges. The plankton fossils are often absent in terrigenous facies of the marginal areas of basins. Therefore, it is rather difficult to recognize Priabonian equivalents in the successions of the Northern Peri-Tethys, especially in its far northern and eastern areas. Thus, the calcareous plankton assemblages in Ciscaucasia are more impoverished than those from the same carbonate sediments of Transcaucasia (Krasheninnikov and Muzylev, 1975). Of the planktonic foraminifers, *Globigerapsis semiinvoluta*, a group of species similar to *Turborotalia cerro-azulensis*, is absent here. Therefore, only local zones may be recognized here, the *Globigerapsis tropicalis–Globigerina corpulenta* Zone in the lower part of the section and the *Turborotalia centralis* and *Globigerina gortanii* zones in the upper part of the succession (Krasheninnikov and Muzylev, 1975; Bugrova *et al.*, 1988). Based on benthic foraminifers, the entire Beloglinian Formation correlates with the *Planulina costata* Zone with two subzones, the *Brotzenella taurica* and the *Bolivina antegressa* subzones (Bugrova, 1988). The first subzone is correlated with lower horizons of the Beloglinian Formation composed of pelagic nannoplankton foraminiferal marls that are widespread from Bulgaria and South Ukraine, across Ciscaucasia, the Fore-Caspian Region, and Transcaucasia, up to the South Aral area. Although the zonal species are absent here, this assemblage correlates with the standard *Globigerapsis semiinvoluta* and *Turborotalia cocoaensis* (P15, 16; Table 2) zones. The combined impoverished *Discoaster barbadiensis* (NP18–20) Zone is recognized here based on nannoplankton data (Krasheninnikov and Muzylev, 1975). Benthic foraminifers predominate, while plankton assemblages become progressively more impoverished in the beds with *Bolivina antegressa* that occur higher in the succession. Species
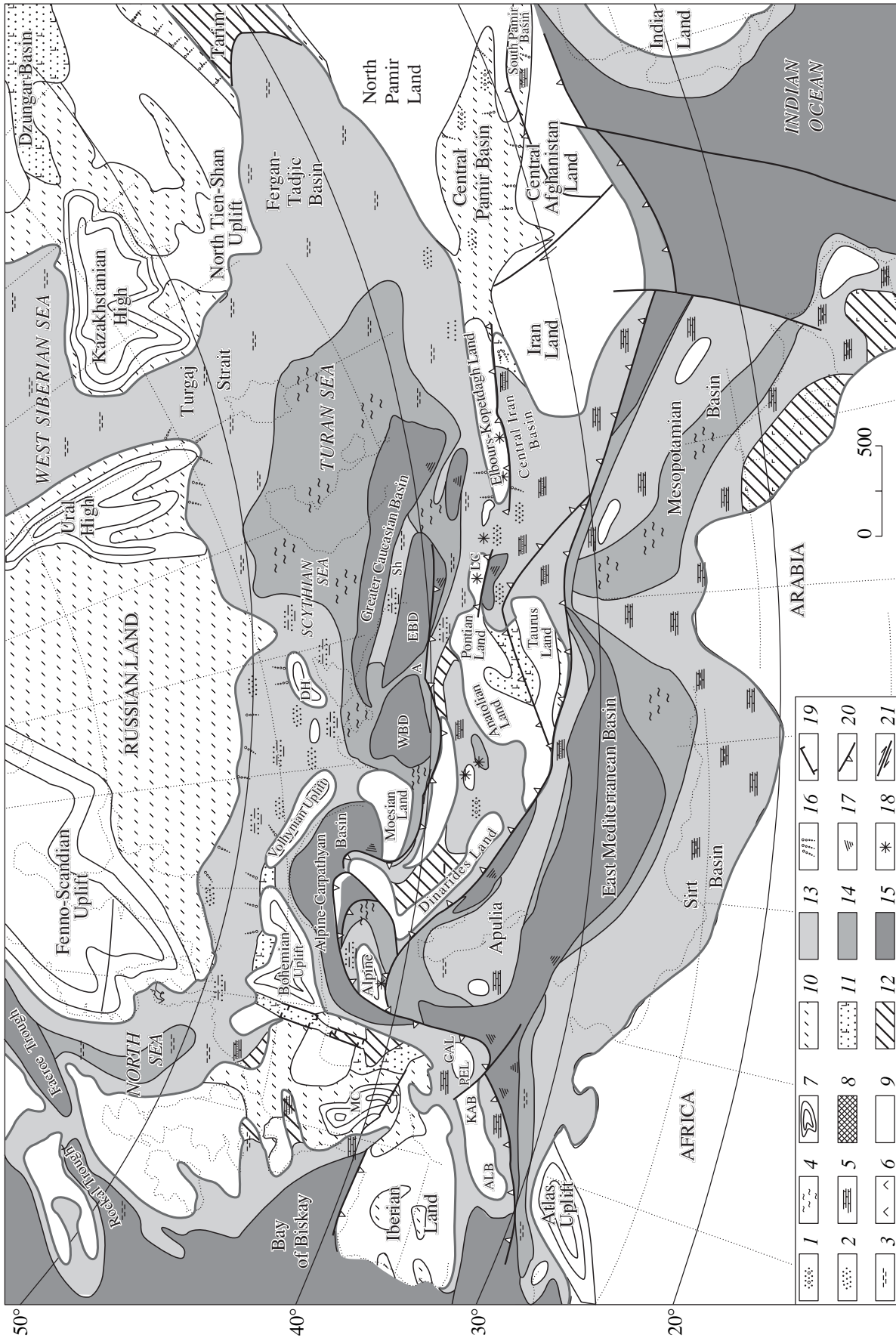
more typical of the Oligocene, *Globigerina ampliapertura, G. officinalis*, and *Turborotalia permicra*, are found here. This assemblage correlates with that from the standard P17 zone. Nannoplankton in this part of the succession correlates with the lower part of the NP21 zone according to Andreeva-Grigorovich. The planktonic foraminiferal assemblages become progressively more impoverished in pyritized marls that occur near the top of the Beloglinian Formation and in clays at the base of the Maykop Formation. Krasheninnikov correlates these assemblages with the *Globigerina tapuriensis* (P18) Zone. The nannoplankton indicates the NP21 zone (Krasheninnikov and Muzylev, 1975) or the NP22 zone (Nagymarosy and Voronina, 1993).

In the upper part of beds with *Bolivina antegressa* from the northern and eastern areas of the basin with terrigenous sedimentation "beds with *Asterigerina lucida* and *Cibicides salensis*" from the Volga–Don Region and Ergeni Highland (= "beds with *Anomalina munda*" from the Chegan Formation of Ustyurt and Aral Sea coastal areas) and their equivalents were identified. These beds contain few planktonic foraminifers and are assigned to the Oligocene based on benthic foraminifers (Nikitina, 1963; 1972). Nannoplankton from these beds in the Volga–Don Region, including "the beds with *C. salensis*" was found by Andreeva-Grigorovich and assigned to the *Discoaster barbadiensis* (NP18–20) and *Coccolithus subdistichus* (NP21) zones. Thus, these beds can be correlated with the Beloglinian Horizon. Beds with closely similar faunistic composition are also found in South Ukraine (Konenkova and Bogdanovich, 1986).

In the Eastern regions, in the Fergana and Tajik depressions, the Isfara + Hanabad (= Kushan) and the Sumsar (= Sanglak) horizons may correlate with the Priabonian. The Late Eocene age of these horizons and their correlation with the Cheganian of the North Pre-Aral area and Ustyurt was determined based on mollusk data (Amitrov, 1986; Popov *et al.*, 1993). This is supported now by occurrences of radiolarians of the *Thyrsocypris bromia* Zone (Standard Upper Eocene Scale) in the Isfara beds in Fergana and by occurrences of nannoplankton assemblages with *Isthmolithus recurvus*, NP19–20 zone (Muzylev *et al.*, 1996) in the Kushan and Sanglak horizons of the Tajik Depression and in the Sumsar Horizon of Fergana.

Paleogeography of Northern Peri-Tethys

The Late Eocene Basin of Northern Peri-Tethys was one of the largest marine basins in the territory of Western Eurasia in the Cenozoic. This basin occupied vast expanses in Northwestern and Central Europe, south-

Dzungar Basin

Tarim

North Pamir Land

South Pamir Basin

Indian Land

INDIAN OCEAN

North Tien-Shan Uplift

Fergan-Tadjic Basin

Central Pamir Basin

Central Afghanistan Land

Kazakhstanian High

Turgaj Strait

Iran Land

WEST SIBERIAN SEA

TURAN SEA

Elbours-Kopetdagh Land

Central Iran Basin

Ural High

Mesopotamian Basin

500

SCYTHIAN SEA

Greater Caucasian Basin

Sh

RUSSIAN LAND

0

EBD

L'C

Pontian Land

Taurus Land

ARABIA

DH

A

Anatolian Land

WBD

F

F

Fenno-Scandian Uplift

Volhynian Uplift

Moesian Land

Alpine-Carpathyan Basin

Dinarides Land

Apulia

East Mediterranean Basin

Bohemian Uplift

Alpine

Sirt Basin

NORTH SEA

MC

CAL

PEL

Faeroe Trough

KAB

AFRICA

Rockall Trough

ALB

Bay of Biskay

Iberian Land

Atlas Uplift

50°

40°

30°

20°

1   4
2   5
3   6
7
8
9
10   13   16   19
11   14   17   20
12   15   18   21

ern areas of the East European Platform, the Turan and the West Siberian plates, vast depressions in the territory subjected to the Cenozoic Orogeny in Central Asia and Northwestern China, as well as the territory of the present-day folded systems of the Alps, Carpathians, Crimea, Caucasus, and the Kopet Dagh (Fig. 4). Shelf areas and relicts of marginal sea basins of the Tethys Ocean can be distinguished in its structure. The deep-water part of the Paleo-Paratethys was composed of the Alpine–Carpathian Bathyal Basin, West and East Black Sea depressions, and the Greater Caucasian Bathyal Basin separated by the Moesian Land and the underwater Andrusov and Shatsky uplifts and was bordered by relatively narrow southern and by vast northern and eastern shelf areas. The Paleo-Paratethys was already separated from the Ancient Mediterranean Basin by islands of the Alpine Folded Zone: the Alps, the Dinarides, the Pontides, the Taurus Uplift, the Lesser Caucasus, the Elbours Uplift, and the Kopet Dagh Uplift. However, since the eustatic ocean level was rather high, the Paleo-Paratethys was connected with the Ancient Mediterranean Basin by the Fore-Alpine Trough, Trans-Tethyan Corridor–a strait between the Alps and Dinarides, and the Central Iranian Basin. The present-day sediment occurrence and the evolution of the Paleo-Paratethys indicate its subdivision into the western (Alpine–Carpathian) and the eastern (Greater Caucasus–Kopet Dagh) basins.

Alpine–Carpathian Basin

The axial areas of the Late Eocene Basin represented a system of deep troughs (the Silesian Trough, the Skibas–Pokut Trough, the Dukla Trough, and the Magura Trough) separated in the southern areas by uplifts (cordillera) that occasionally overhung the water (Beer and Shcherba, 1984). Thin flysch sediments accumulated in these troughs and were penetrated by thick sandy cones, mudstreams and stone streams, and turbidity currents from the cordillera and platform. The southern areas of this basin were bounded by islands of the Pieniny Klippen Belt and partially of the Silesian Zone that are recognized based on lithological and floristic data (see below).

The southern margin of these troughs originally occurred much further to the south of its present-day location. The flysch basin in the Carpathians was about 200 km wide in its central area (Báldi, 1986), but towards the end of the Late Eocene, sediments in the southern areas of the flysch basin started to fold as a result of drift of the East Alpine–Tatran Block in the northeastern direction along the system of transform faults (Balla, 1984; Nagymarosy, 1990). At present, the sediments of the southern areas of the flysch basin only partially survived. They occur mostly at great depths and are overlain by the Neogene beds of the Pannonian Depression, where these beds are penetrated by boreholes in the Szolnok Trough (Nagymarosy and Báldi-Beke, 1993).

Toward the second half of the Late Eocene, the contrast bottom topography in the axial area of the Alpine–Carpathian Basin was partly flatten by sediments, the sea depths increased above the level of carbonate compensation. The arrival of the terrigenous material decreased. This resulted in accumulation of biogenous mud (the Sheshora Globigerine Marl).

Shallow water areas of the East Alpine–Tatran Block (Pelso Unit after Nagymarosy, 1990) occurred in the rear part of the Podhale and Szolnok troughs. The central part of this block was submerged with deeper Paleogene Hungarian Basin with carbonate sedimentation. In the Eocene–Oligocene, the Hungarian Basin was opened to the South Alpine–Apulian Shelf of the Ligurian Segment of the Ancient Mediterranean Domain (Báldi, 1986). A similarity between the facies of the Northern Apennines and the Hungarian Basin, high percentage of species in common in the Eocene, and the coincidence of zonation of large foraminifers indicates the direct connection with the Ligurian Basin across Slovenia, between the Alps and Dinarides (Nagymarosy, 1990). The Slovenian Corridor became shallow or even occasionally dried.

Shelf areas of the Tisza (Bichor) Block was situated closer to the axial zone. The basin was originally about 120 km wide (Báldi, 1986). Evidently, the Bichor Block experienced substantial horizontal displacement in the northeast direction (Nagymarosy, 1990). Today, sediments of this part of the shelf areas are outcropped in the Transylvanian Basin. Despite the close location of the Transylvanian and Hungarian basins, their successions and their benthic faunas differ markedly. From the outer side, the Transylvanian geological history and fauna in the Eocene–Early Oligocene is similar to those of the basins of Serbia, Southern Bulgaria, and Macedonia. The Transylvanian shelf areas with the biogenous–carbonate sedimentation were probably connected with the shallow Fore-Rhodopian Basin by the Morava Zone in Serbia. In the Morava and Shumadian zones (further to the south of Belgrade) the sediments only survived in some depressions and are represented by volcanogenic rocks with nummulite assemblages closely similar to those from both Transylvania and Macedonia and Fore-Rhodope.

In the opinion of Yugoslav workers (Andjelković *et al.*, 1991), in the Eocene, the South Carpathian and Balkan areas of the Paleogene Basin experienced folding and thrusting for the first time (the Pyrenean Tectogenesis) and environments became mainly terrestrial. The Rtanj and Babusnica depressions that formed in the Late Eocene were filled by red-bed sediments up to 600 m thick with fossil flora and marine and brackish-water interbeds.

Judging from the benthic mollusk and nummulite fauna from the Fore-Rhodopian regions in Bulgaria (Karagyuleva, 1966) the shelf of these islands was inhabited by representatives of the Ancient Mediterranean tropical and subtropical fauna (large *Crassatella, Venericardia, Fimbria, Spondylus*, and *Corbula (Bicor-*

bula)). Such a fauna also inhabited the Burgas–Kazanlik regions in this basin, while colder-water mollusks occurred further to the north, in the Varna (Kamchia) Gulf, and the nummulite assemblage included *N. orbignyi*, a representative Eocene taxa of the northern type. These gulfs that occur side by side now probably belonged to different basins separated by a terrestrial barrier that extended from the Balkan Uplift along the Black Sea Coastal Region up to the Lesser Caucasus. Mammals of Central Asian origin (from the anthracothere assemblage) could migrate along this land up to Southern Bulgaria and Transylvania, where their fossils were found in the upper beds of the Cluj Limestone (the Middle Priabonian).

The external areas of the Fore-Carpathian Depression, where shallow-water sand-silty sediments accumulated, belonged to the northern shelf areas of the Alpine–Carpathian Basin. At present, these sediments are partially reworked by subsequent Neogene sea transgressions and are partially overlain by the Carpathian thrusts. In the central areas of the Carpathian Arc these thrusts have an amplitude of 60–90 km based on seismic data (Burov *et al.*, 1980; Oszczypko *et al.*, personal communication). This epicontinental area of the Carpathian Basin has not survived up to the present. It was surrounded by the uplift of the Bohemian Uplift and by the Swetokrzyskie–Sandomir Land that appeared here early in the Paleogene (Vyalov *et al.* in *Geologicheskie i bioticheskie…*, 1996). However, the distribution of benthic foraminifers (see below) indicates at least the episodical connections between the shelf areas of the Carpathian Basin and the epicontinental Poland–Germany Sea in the late Eocene (Pozaryska, 1977).

The Fore-Carpathian Shelf Sea opened in the east to the Greater Caucasus–Kopet Dagh (Beloglinian) Basin. The westernmost Beloglinian sediments (marly facies) are found in the southeastern areas of the Moesian Plate (Varna Region), while the coastal facies are known in Dobrudja (Gelati Region) and in the Tyrnov Region in Bulgaria.

Greater Caucasus–Kopet Dagh (Beloglinian) Basin

Similar to the Alpine–Carpathian Basin, the Greater Caucasus–Kopet Dagh Basin was still a marginal sea of the closing Tethys Ocean. This marine basin was separated from the ocean by the Lesser Caucasian–Pontic Island Arc System in the Early Cenozoic (Kopp and Shcherba, 1985; Shcherba, 1993). In the opinion of Kopp and Shcherba, toward the second half of the Eocene the deepest areas of this sea were composed of several depressions: West and East Black Sea depressions, the Greater Caucasian Basin with the Lazorevskoe–Kobystan Trough in its central areas that occurred along the south-facing slopes of the Greater Caucasus and continued into the South Caspian Depression (Fig. 4). The East Black Sea Depression

continued to the Adzhar–Trialet Trough, then to the Talysh Depression and was closed at a longitude of the western coast of the present-day South Caspian Depression. These deepest structures were separated by submarine terraces, the Shatsky Uplift (in the Black Sea), the Dzirulskii Swell and the Kyurdamir Uplift.

By straightening the folded structure of the south-facing slope of the Greater Caucasus that decreased the area that was covered by abyssal silty and flysch sediments in the Upper Eocene we could estimate the original width of the Greater Caucasian Basin at approximately 200 km or more. A correlation of the Adzhar–Trialet and Talysh depressions with the East Black Sea Depression that did not experienced any lateral compression shows that their original width may be of 100–120 km (Shcherba, 1993).

The abyssal Upper Eocene sediments in the West Black Sea Depression and East Black Sea Depression have not yet received a detailed study. It is only known that these sediments are represented by calcareous mud that leaned against the steep (originally free of sediments) slope of the Shatsky Uplift (*Tektonika…*, 1985). These mud sediments contained numerous bodies of sandy turbidites, or more rarely of volcanoclastic turbidites that are observed now in Guriya and in the Fore-Tbilisi Region of the Adzhar–Trialet Zone (the Tbilisi Flysch up to 1000 m) and in the Talysh Depression (more than 1000 m flysch bed that contains large bodies of volcanogenic material).

The occurrence of the wedge flysch bodies on the southern slopes of deep-water depressions shows that these depressions trapped the terrigenous material that arrived from the south (Shcherba, 1993). The presence of abundant nummulites in the top of the Late Eocene beds indicates that these depressions were mainly compensated for by sediments toward the end of the Late Eocene. Biogenous calcareous mud accumulated on more shallow-water uplands that separated these depressions. Toward the end of the Late Eocene benthic foraminiferal assemblages (of the *Bolivina antegressa* Zone) and sandy limestone with nummulitids and discocyclinids became widespread due to general shallowing of the basin.

Scythian and Turan basins. Vast northern and eastern shelf areas of the Greater Caucasus–Kopet Dagh Basin occurred on the Scythian and Turan platforms. A sequence of facies, from pelagic organic carbonate mud typical of the outer shelf areas to thick terrigenous silty sediments of the inner shelf areas and shallow littoral facies, is observed here. The most deep-sea, thin (20–30 m in thickness) nanno-foraminiferal mud beds composed entirely of planktonic organisms deposited in the Terek–Mangyshlak Depression that remained the deep-water depression throughout the Paleogene and was not compensated for by the sedimentation (Stolyarov, 1991). The sea depths were probably of several hundred meters in this zone. Similar biogenous-carbonate mud that also contained silty material and benthic foraminifers (up to 50%) but had far greater (up to 150–

200 m) thickness deposited over a vast territory, from Northeastern Bulgaria, South Ukraine and Crimea to the southern Aral Sea areas. This zone of the carbonate sedimentation protruded much further to the north in the Volga Region and Caspian Sea Region and probably overlay the Karatau Uplift and Karabogaz–Erbent Uplift, where these sediments are not found now. In the first half of the Late Eocene, planktonic foraminifers dominated this facies. This indicates a depth of sedimentation of several hundred meters. Such facies were typical of the majority of regions in Ciscaucasia and reached the present-day Greater Caucasus. Later on, this basin became shallower, especially in the terminal Eocene, when shallower benthic fauna (benthic foraminifers *Almaena taurica*, nummulitids, and mollusks of the *Propeamussium fallax* Assemblage) appeared in this marine zone.

Further to the north, in the shelf zone, the carbonate sediments were gradually replaced by the silty–clays and clayey–siliceous–carbonate sediments. These sediments reached 200 m in local depression. The regions of mainly terrigenous sedimentation were typical of the greater areas of South Ukraine, northwestern (Ciscaucasian) areas of the Scythian Platform, and northern and eastern areas of the Turan Platform. Within the Scythian Platform these areas were separated by a semi-circle of underwater highs of the Timashevsk Step and Stavropol–Ergeni Zone that limited the dispersion of terrigenous material in the zone of the carbonate sedimentation. Most coarse-grained, sandy–silty sediments occur here in the Azov Uplift (Stolyarov, 1991).

A vast lowland that surrounded the shelf areas in the north extended from the northern margin of the Fore-Caspian Depression (Saratov Area of the Volga Region) and protruded as a wide cape into the sea in the zone of the Don–Medveditsa dislocations. A vast shallow-water epicontinental marine basin occurred further to the west, within the Dnieper–Donets and Prypiat depressions. This marine basin was connected in the north with the North Sea Basin via the Mazovets–Mazur Bar. In the south this marine basin was separated from the Beoglinian Sea by the Ukrainian Crystalline Rock Massif that represented a chain of low islands in that time period. The eroded island land existed only in the region of the Donbass structures (Stolyarov, 1991; Stolyarov in *Geologicheskie i bioticheskie…*, 1996).

On the Turan Plate terrigenous facies replaced the carbonates via intermediate facies that are observed as a strip, extending from the eastern areas of the Fore-Caspian Region to Western Ustyurt and southeastern areas of Aral Sea coastal regions. An increase in the importance of micro- and macrobenthos in these sediments in the northeastward direction indicates the inner shelf areas with a depth of 50–150 m. Around the periphery of the Turan Sea carbonate sediments were replaced by greenish-gray clay facies (Cheganian clays and their equivalents) that were carbonate only in the lower part of the formation. Such facies are widespread in the Northern Ustyurt, northern areas of the Aral Sea

coastal regions, and are observed far further to the north, in the Turgaj Plateau and West Siberian Basin, and further to the east, along the Syr-Darya River, where these facies are only found in boreholes. Plankton groups were practically absent here, except for dinoflagellates. Microbenthos and macrobenthos, which were found here, including shallow water taxa that are related to underwater vegetation and indicate depths of several tens of meters.

Coarser-grained clastic littoral facies occurred rarely in the northern shelf areas of the Beoglinian Basin. These facies are found in the northern Pre-Aral areas and in the Turgaj, where in the second part of the Late Eocene, clays with siltstone and sand interbeds (Turanglinian Beds of the Chegan Formation) accumulated. The sand material, several meters in thickness, is also found further to the west of the assumed Mugodzhary Land (in the headstream of the Emba River). This land represented the southern termination of the elevated Uralian Folded Zone and projected as a cape between the Fore-Caspian Gulf and the wide Turgaj Strait that extended to the West Siberian Basin. A shallow water basin with terrigenous sedimentation (Cheganian facies) and fauna closely similar to that from the Ustyurt areas of the Beoglinian Basin also existed in this strait and in the southern areas of the West Siberian Sea.

Lowlands surrounded the basin in the north and east, as indicated by the fine-grained clastic material, as well as by the composition of large plant remains in floral assemblages of the Voronezh Anteclise (Tim), the Fore-Uralian Region, Aktyubinsk, Mugodzhary, and Kazakh Massif, where laurels, myrtles, *Liquidambar* and other trees and shrubs, typical of coastal lowlands, deltas, and river valleys, dominated.

The marine basin was surrounded in the northeast by a lowland plain of accumulation (Central Kazakh Land), where lacustrine sediments accumulated in depressions. The North Tien Shan Highland occurred further to the south, where plains of denudation with valleys occupied by red-bed sedimentation dominated (Pinkhasov *et al.* in *Geologicheskie i bioticheskie…*, 1996). A small island land could exist within the Turkestan–Altai Region. The Fergana Bay and the Afghan–Tajik Gulf were connected in the west with the open Turan Sea and formed, generally, a single basin that extended further to the east, to the Kashgar Region, Tarim Basin (Davidzon *et al.*, 1982; Shcherba, 1993). At the beginning of the Late Eocene (the Isfara Time), fine-grained silty sediments with an admixture of sand and gravel accumulated in the Fergana–Tajik Basin. These sediments were delivered by rivers from the Tien Shan Land (Hecker *et al.*, 1962). In the southern regions argillaceous siliceous sediments with radiolarians precipitated. The argillaceous sediments with benthic fauna precipitated further to the west also, in shallow water Kyzyl Kum and Fore-Kopet Dagh areas of the Turan Sea. These sediments were replaced by carbonate facies of the outer shelf areas with a probable

depth of 200 m, or more, only in the southern Aral Sea regions and in the Daryalyk–Daudan Depression.

In the second half of the Late Eocene (in the Sumsar Time), the sea regressed to the central areas of the Turan Region. This sea was connected with the Fergana Basin in the east only via the Alai Valley and Tajik Depression. In the west the Sumsar sand–silty littoral beds were replaced by red bed facies (Pinkhasov *et al.* in *Geologicheskie i bioticheskie…*, 1996). The mollusk composition indicates that in the Sumsar–Sanglakian Time, wide zoogeographic connections with the Turan Basin still existed, while only rare elements of the warmer-water fauna migrated to the Fergana and Tajik depressions.

The regression of the marine basin from the territory of Western Siberia and the Turgaj Plateau started in the middle of the Late Eocene. Northern Pre-Aral emerged in the terminal Eocene. In the terminal Oligocene, the sea only occurred within the axial areas of the North Ustyurt Depression.

Southern surrounds of the Paleo-Paratethys. The Alpine Fold Belt represented in the first half of the Late Eocene an archipelago, included the Balkan, the Pontic, the Samkhet–Agdam, the Talysh and the Elburs–Kopet Dagh uplifts. All these systems occurred within the volcanic island arc that constrained a marginal sea in the northern margin of the Tethys already in the Early Paleogene. In the Priabonian, chains of volcanoes also occurred along this archipelago.

A relatively narrow strip of terrigenous shelf sediments with rich littoral faunistic assemblages is observed along the northern margin of the Samkhet–Agdam Island (future anticlinorium of the Lesser Caucasus). Among these sediments are sand–carbonate beds in the Southwestern Georgia and volcanogenic and terrigenous–carbonate sediments in the Adzhar–Trialeti Zone. These sediments contain nummulites, mollusks, and benthic foraminifers (the Akhaltsikhe Sandstone and conglomerates from the Bolnisi Massif). The Cis-Lesser Caucasian and the Araks depressions occupied by terrigenous and volcanogenic shelf sediments continued this littoral zone further to the east. The Araks Trough was entirely filled by sediments in the middle of the Late Eocene and probably occasionally became dried. The inclusions of fane material, as well as abundant conifer pollen in the spore-and-pollen assemblages indicates active uplift and the transformation of archipelago into mountain systems with a distinct altitudinal zonation of the vegetative cover in the second half of the Late Eocene.

The Central and the South Anatolian (Taurus) regions that occur further to the south of the suture of the Neotethys transformed into highs as a result of the Pyrenean Orogeny. The Erevan–Vedi Depression with flysch sedimentation (after Sadoyan in Shcherba, 1993) continued in the west into the Sivas Depression, in which continental sediments accumulated in the Priabonian (Poisson *et al.*, 1997). The Erevan–Vedi Basin was connected in the east and the southeast with the Central Iranian and the Mesopotamian basins that were opened to the Mediterranean Sea and to the Indopacific (Fig. 4). The Nakhichevan Shelf represented a transition zone between the Erevan–Vedi and the Central Iranian basins and accumulated shallow water tuff–sandy and silty sediments (up to 650 m in thickness) and algal, coral, and bryozoan bioherms (up to 80 m in thickness).

The vast Iranian and Afghan land masses that separated the Turan Sea from the Indopacific regions extended further to the east.

Biogeography of Water Areas

To date, the assemblages of planktonic organisms from the Paleogene are well studied because of their practical importance for zonal stratigraphy. A relatively complete biogeographic pattern can be reconstructed on the basis of three planktonic groups, i.e., planktonic foraminifers, nannoplankton, and organic-walled phytoplankton. Unfortunately, diatoms from this time interval are still extremely poorly understood because of the low frequency of siliceous facies in the Northern Peri-Tethys.

Planktonic Foraminifers

Planktonic foraminifers from the Upper Eocene (Priabonian) of the Tethyan Realm and adjacent regions are presented by the assemblage of diverse highly specialized species belonging to the genera *Turborotalia, Globigerina, Dentoglobigerina, Subbotina, Pseudohastigerina, Globigerinita, Hantkenina, Cribrohantkenina, Globigerapsis, Globigerinatheca*, and *Globorotaloides*. In the Late Eocene sediments of the World Ocean, they occur everywhere, i.e., they do not indicate distinct paleobiogeographic regions or provinces. As with Recent planktonic foraminifers, their geographic distribution depends on general latitudinal–climatic zonation combined with local bionomic factors (warm and cold currents, upwellings, physicochemical characteristics of water, and bathymetric parameters). Therefore, planktonic foraminifers are of great importance in paleoclimatic and bionomic studies for the reconstruction of paleoclimatic belts, temporal dynamics of their displacements, and the local features of water masses within the belts.

In the extensive region under study, the northern part of the Atlantic Ocean, the Ancient Mediterranean Sea, and the inland basins of Europe and Africa, during the Paleogene, the Atlantic Ocean expanded in a latitudinal direction, thus preserving the relative positions of the paleoclimatic belts. A contrasting situation occurred in the Pacific and Indian oceans where the early paleoclimatic belts were broken and displaced by later spreading movements. At the same time, by analogy with the distribution of Recent planktonic foraminifers in the Atlantic Ocean, in its Paleogene equivalent the bound-

aries of the paleoclimatic belts deviated from the latitudinal zonation in connection with the presence of warm and cold currents and upwellings along the western coast of Europe and Africa.

The following main criteria are applied in the reconstruction of Paleogene paleoclimatic features based on planktonic foraminifers: (1) the taxonomic composition of foraminifers; (2) the proportions of warm-water and cold-water species; (3) the analysis of the extent to which the biozones and teil-zones of species are completed; and (4) the general pattern of decrease in the number of species of planktonic foraminifers from south to north.

The distribution of the foraminiferal assemblages in the deposits of the Northern Atlantic and adjacent regions of the Mediterranean Sea and the Northern Peri-Tethys allows one to distinguish four belts: Tropical, South Subtropical, Northern Subtropical, and Temperate belts.

The Tropical Paleoclimatic Belt is characterized by the greatest species diversity of planktonic foraminifers (approximately 30 taxa); constant presence of thermophilic (tropical) species, the representatives of the genera *Cribrohantkenina* and *Hantkenina* as well as *Globigerapsis semiinvoluta, Turborotalia cerro-azulensis, T. cocoaensis*, and *T. cunialensis*, in the deposits; and the distribution of these forms in the beds in accordance with the biozones of the species. A complete set of three zones, i.e., *Globigerapsis semiinvoluta* (P15), *Turborotalia cocoaensis* (P16), and *Turborotalia centralis–Globigerina gortanii* (P17) zones, are distinguished here in the Priabonian. Complete assemblages of planktonic foraminifers are well developed in the sections of the Upper Eocene of many countries of the Caribbean Basin (Trinidad, Barbados, Cuba, and the Dominican Republic); the coast of the Gulf of Mexico (USA, Panama, and Mexico); and the African coast, in Senegal (Krasheninnikov, 1969). Within the Atlantic Ocean, the deposits containing the above-mentioned assemblages of planktonic foraminifers were exposed by a series of boreholes produced within the framework of the Project of Deep Sea Drilling from the equator to 25–30° N (Krasheninnikov, 1978, 1980). The Tropical Paleoclimatic Belt is outside the area considered in the present monograph.

Mediterranean Region. The entire band of the Ancient Mediterranean Region belongs to the South Subtropical Belt. In the northern peripheral part of the Mediterranean Region, the pelagic deposits of the Upper Eocene contain a planktonic foraminiferal assemblage of the same taxonomic composition as the above mentioned association from the deposits of the Tropical Belt, i.e., from Spain (Molina *et al.*, 1988), Italy (Coccioni, 1988; Dieni and Proto Decima, 1964), Dalmatian coast of Bosnia (Krasheninnikov, 1969), Syria (Krasheninnikov, 1965; Krasheninnikov *et al.*, 1996), and Israel (Benjamini, 1980, 1984). Similar assemblages of planktonic foraminifers, containing *Cribrohantkenina* and the group of *Turborotalia cerro-*

azulensis are also known from the Upper Eocene beds of the southern periphery of Mediterranean–Morocco Region (Aubert, 1962). In this area, the ranges of vertical distribution of warm-water species also correspond to the biozones of these taxa. The differences of the South Subtropical assemblage of planktonic foraminifers from that of the Tropical Belt are associated with a decrease in the number of warm-water tropical elements, discontinuous distribution of the latter in the sections, and an increase in the role of globigerinids (species of the genera *Globigerina, Subbotina*, and *Dentoglobigerina*).

Within the former Soviet Union, the northern boundary of the South Subtropical Belt was in the south of Armenia (40–41° N). The Upper Eocene beds of this region contain scarce specimens of species of the genera *Cribrohantkenina* and *Hantkenina, Globigerapsis semiinvoluta*, and the group of *Turborotalia cerro-azulensis* (Krasheninnikov *et al.*, 1985). The basis of the assemblage is formed by globigerinids, among which taxa of temperate latitudes (*Globigerina angiporoides*) and tolerant species of the genus *Globigerapsis* (*G. index* and *G. tropicalis*) appear. The teil-zones of *Cribrohantkenina* and *Hantkenina* are recognized here, and these genera disappear in the uppermost *Globorotalia cocoaensis* Zone. An earlier disappearance of these taxa in Armenia than in the Mediterranean Region is probably associated with the onset of fall in temperature at the Eocene–Oligocene transition. In the later part of the *Turborotalia cocoaensis* Zone, the composition of the palynological assemblages abruptly changes, i.e., the proportion of pollen of coniferous and deciduous species increases (Krasheninnikov *et al.*, 1989).

In the eastern peripheral part of the Atlantic Ocean, the northern boundary of the belt considered was approximately in the south of the Bay of Biscay. In the north of the bay, the Upper Eocene deposits penetrated by boreholes 401 and 402 (47° N) contain only isolated specimens of *Globigerapsis semiinvoluta, Turborotalia cerro-azulensis*, and *Cribrohantkenina inflata* (Krasheninnikov, 1979). A more northerly position of this boundary in comparison with that in Armenia is probably associated with a combined effect of local bionomic factors and the general paleoclimatic background (see above).

Northern Peri-Tethys. In the former Soviet Union, the North Subtropical Belt covers the Transcaspian and Aral regions, Northern Caucasus, Crimea, southern part of the Black Sea Region, and northern part of the Carpathian Basin (42–50° N). Rich assemblages of planktonic foraminifers are well known from classical studies of Subbotina (1953), Morozova (1959), Shutskaya (1970), and many other researchers. The taxonomic composition of planktonic foraminifers is impoverished in this belt because of the disappearance of the entire set of tropical warm-water indicators, i.e., *Cribrohantkenina, Hantkenina, Globigerinatheca, Globigerapsis semiinvoluta*, the group of *Turborotalia cerro-azulensis*, and certain large globigerinids. There-

fore, the usefulness of planktonic foraminifers for stratigraphic resolution decreases, and the pelagic sediments of the Beloglinian Formation (and its analogues) are divided into only two indivisible zones, the *Globigerapsis semiinvoluta–Turborotalia cocoaensis* Zone (local name is the *Globigerapsis tropicalis* and large globigerinid Zone) and the *Turborotalia centralis–Globigerina gortanii* Zone. The foraminiferal assemblage consists of the species of the genera *Globigerina, Dentoglobigerina, Subbotina, Globigerinita*, and *Pseudohastigerina* and two species of *Globigerapsis*.

The assemblages of planktonic foraminifers of the Temperate Belt were found only at the northern boundary of the region considered, i.e., in the Rockall Plateau, in the north of the Atlantic Ocean (borehole 406, 55° N), and, probably, in the northern part of the Caspian Depression. In the Rockall Plateau, the pelagic deposits (chalk) of the Upper Eocene contain abundant planktonic foraminifers; however, the species diversity is rather low, approximately 10–12 species of globigerinids (including cold-water *Globigerina angiporoides*) combined with scarce *Globigerapsis index* and *G. tropicalis* (Krasheninnikov, 1979). They occur together with Radiolaria.

In the former Soviet Union, the planktonic foraminiferal assemblages, transitional between those of the North Subtropical Belt and the microfauna of the Temperate Belt, are probably presented by the associations from the deposits of the Upper Eocene penetrated by Tukbai borehole P-24 in the central part of the Caspian Depression, 70 km to the west of Lake Inder (49° N) (Charygin *et al.*, 1968; Vasil'ev *et al.*, 1970). At this point, the assemblage consists of various globigerinids combined with infrequent *Globigerapsis index*.

Boreal assemblages of planktonic foraminifers are virtually unknown in the Late Eocene of the region considered. In the Atlantic Ocean, they were not discovered by boreholes; in the northern Europe, the Upper Eocene deposits either formed by shallow-water or continental beds. A general knowledge of the assemblages is given by the microfaunal associations of the Upper Eocene deposits of the Notal Belt of the Atlantic Ocean, the Falkland Plateau (borehole 511, 51° S). The assemblages of planktonic foraminifers consist of 10–14 species, among which *Globigerina angiporoides* and *G. binaperta* strongly prevail; the other species of *Globigerina, Globigerinita*, and *Globorotaloides* are smaller in number; and the specimens of *Globigerapsis index* are scarce. In this case, it is impossible to perform the zonal division of the Upper Eocene based on planktonic foraminifers; however, this can be achieved using siliceous plankton (Krasheninnikov and Basov, 1986).

Nannoplankton

The latitudinal–climatic zonation based on nannoplankton was not as clear as that based on planktonic foraminifers. In all basins of the northern edge of the Tethys, except for certain northern and eastern regions, almost the same tropical flora of yellow-green algae dominated. This flora also occupied the subtropical basins.

Northern Mediterranean Domain. In the Late Eocene basin of Italy, there was a mixed algal flora consisting of tropical and southern boreal species, among which widespread tropical species of *Sphenolithus, Discoaster, Helicosphaera, Bramletteius, Cyclococcolithus*, etc. strongly predominated. Such relationships remained throughout almost the entire Late Eocene. Among the Late Eocene basins examined in the former Soviet Union, the warmest waters occurred in the basin of Armenia. A complete nannofloral association containing tropical species occurred in this are throughout the entire Late Eocene and in the Lower Oligocene; boreal species were virtually absent and widespread tropical species were abundant.

Basin of the North Sea. The type assemblages of the Latdorfian contain 24 nannoplankton species, including abundant *Coccolithus pelagicus, Istmolithus recurvus, Lanternithus minutus, Rhabdosphaera spinula*, and *Zygrablithus bijugatus*, an association characteristic of relatively shallow, cold-water basins (Martini and Ritzkowski, 1968). In deeper-water facies, 25 species were found, almost all of which were the same as in the Latdorfian. *Dictyococcithes dictyodus* and *Reticulofenestra umbilica* were abundant (Martini, 1971). A shallow-water boreal association of nannoplankton was also found in the Lower Tongrian (sands of Glimmer) and consisted of 16 species, all of which occurred in the Latdorfian (Martini and Moorkens, 1969).

Alpine–Carpathian and Beloglinian domains. In the more northerly basins (Flysch Carpathians, Southern Ukraine, Crimean–Caucasian Region, Mangyshlak, Aral Region, etc.) the nannoflora was similar to that of the Tethys; however, southern boreal species predominated and became especially abundant in the terminal Eocene. In the northern and eastern extremities of the basin (Volga–Don, Caspian Region, and Turgaj) tropical zonal species such as *Sphenolithus pseudoradians* and *S. predistentus* were absent, the number of thermophilic species of the genera *Discoaster* and *Helicosphaera* substantially decreased, and the number of southern boreal species, i.e., *Isthmolithus recurvus, Corannulus germanicus, Cribrocentrum reticulatum, Chiasmolithus oamaruensis*, and *Transversopontis obliquipons*, abruptly increased. This was especially well-apparent in the later half of the Late Eocene.

In addition to the latitudinal–climatic zonation, the nannoflora distribution in the Late Eocene basin depended on the sea currents and short-term periodic climatic fluctuation; occasionally, the latter allowed the tropical species to enter the more northerly regions (Northern Caucasus, Ukraine, etc.—the beds containing *Sphenolithus pseudoradians*). In addition, one should take into account the changes in taxonomic

composition associated with the deltas of large rivers, where unique impoverished associations were formed (Volga–Don and Ergeni).

Organic-walled Phytoplankton

The distribution of organic-walled phytoplankton in the marine basin of the Late Eocene was determined by latitudinal–climatic zonation and water depth.

Northern Atlantic. The dinocyst composition of the Northern Atlantic in the Priabonian is significant, as a comparative oceanic model closely associated with the Mediterranean Domain and the Paleo-Paratethys in the Eocene. Available data comprise 23 boreholes (Damassa and Williams, 1994) from the northwestern coast of Africa and southwestern part of North America (low latitudes); Newfoundland basin, Rockall Plateau, and Porcupine Trough (temperate latitudes); and Norwegian–Greenland basin (high latitudes). In this case, the dinoflagellate diversity depended on two factors, the paleolatitudes and the influence of marine currents. In general, it decreased from low to high latitudes but remained high in the north of the Atlantic Ocean because of the proto-North Atlantic Current, beyond which (for example, in the Newfoundland Bank) it substantially decreased.

Out of 104 dinocyst species known from the Priabonian, 25 only occurred in low latitudes; 18, in temperate latitudes; and only eight were specific to high latitudes. Altogether this is approximately half of all known species. A high proportion of cosmopolitans (25.9%) is evidence of the relatively weak latitudinal–climatic zonation of the Eocene compared to the present-day. A large proportion of common species (20%) found over the entire area influenced by the proto-North Atlantic Current is a result of its direct effect on the dispersion of phytoplankton. The differences in the composition of the assemblages of the Western and Eastern Atlantic are insignificant and substantially lower than in the Oligocene. The numbers of species limited in distribution to the European and American sectors are 25 (24%) and 18 (17.3%), respectively. The diversity ranges from 11 species on the Florida coast to 60 at New Jersey.

On the English coasts, *Homotryblium plectilum*, a euryhaline species, predominated (up to 70%). Occasionally, the groups of species *Spiniferites/Achomosphaera, Glaphyrocysta/Areoligera* spp., *Adnatosphaeridium* spp., and *Phthanoperidinium* spp. appeared in approximately the same quantities; the species of the genera *Thalassiphora, Deflandrea, Wetzeliella*, and *Impletosphaeridium*, which indicate the presence of a shallow, warm-water basin, occurred in somewhat smaller quantities.

North Mediterranean Domain. The species diversity of dinocysts in the North Mediterranean is higher than in the Atlantic, even in the low latitudes of the latter. In northern Italy (judging from the data on sections

of the Priabonian and certain others), the species of the assemblages *Operculodinium/Impletosphaeridium, Spiniferites/Achomosphaera*, and *Homotryblium* spp. were widespread. The species of the genera *Deflandrea* and *Wetzeliella* (widespread in the Oligocene) were scarce. In the later half of the Priabonian, the species *Thalassiphora pelagica* was occasionally numerous; this was attributable to short-term fall in temperature caused by impact events (Brinkhius, 1994). In the facies of deeper water (the sections Massignano and Contessa), species of the genera *Impagidinium* and *Cannosphaeropsis* prevailed.

Diverse algal assemblages were also widespread in the eastern part of the Priabonian basin, where dinoflagellates with chorate and proximate cysts predominated, and were represented by a wide range of genera and species (in Armenia, 120 species were recorded). In addition to the zonal species, local Late Eocene *Areosphaeridium diktyoplokus–A. arcuatum* Zone is characterized by the members of the genera *Cordosphaeridium, Spiniferites, Thalassiphora, Homotryblium, Impagidinium*, and *Impletosphaeridium*. Dinoflagellates with cavate cysts were less frequent and presented by the genera *Rhombodinium* and *Deflandrea* and by the genera of the *Wetzeliella* group. A characteristic feature is the presence of abundant green algae of the genera *"Lanjaria"* and *Tytthodiscus*. About 30 species of the Armenian Assemblage have not been recorded in more northerly localities (in Paleo-Paratethys).

Basin of the North Sea. The Dinocyst Association consisted of more than 80 species belonging to various ecological groups, including warm-water and relatively cold-water, neritic and coastal, normal marine and high-salinity tolerant forms. Such heterogeneity of assemblages is characteristic of peripheral seas, with mainly terrigenous sedimentation. The following groups of species prevailed: (1) *Spiniferites/Achomosphaera* spp., neritic and tolerant to a high salinity; (2) *Areosphaeridium* spp. neritic and tolerant to high salinity and temperature; and (3) abundant *Homotryblium plectilum*, a shallow-water, warm-water, and euryhaline species. The following groups occurred in approximately equal amounts: (1) *Wetzeliella sensu lato* and *Deflandrea/Cerodinium* spp., mainly shallow and warm-water forms, except for cosmopolitan *D. phosphoritica*; (2) *Glaphyrocysta/Areoligera* spp., warm-water species of the inner shelf; and (3) *Impletosphaeridium/Cordosphaeridium* spp., neritic and normal marine species.

Alpine–Carpathian Basin. The Late Eocene Algal Flora of the Alpine–Carpathian Basin was impoverished and consisted of slightly more than 50 species. The groups of species *Spiniferites/Achomosphaera* spp. and *Operculodinium/Impletosphaeridium* predominated; *Cordosphaeridium* spp., *Cribroperidinium giuseppei*, and *Thalassiphora pelagica* were abundant; and *Deflandrea* spp., *Rhombodinium* spp., *Wetzeliella*

spp. *sensu lato*, and *Homotryblium* spp. characteristic of inland waters were common. *Areosphaeridium diktyoplokus, Glaphyrocysta* spp., *Batiacasphaera* spp. were less frequent. In the deepwater part, the role of *Impagidinium* spp. substantially increased. The dinoflagellate composition of the southern shelf (Transylvanian and Hungarian Paleogene basins) was somewhat more diverse. In general, it essentially differed from the dinocyst composition in the Mediterranean basin and was similar to that in the Crimean–Caucasian associations.

At the end of the Late Eocene, the role of green algae substantially increased; occasionally, they, along with *Cribroperidinium giuseppei* and *Thalassiphora pelagica*, abruptly increased in number (at the NP21 zone).

Caucasus–Kopet Dagh Basin. In the Beloglinian Time, the Dinocyst Association of the Caucasus–Kopet Dagh Basin retained a high biodiversity but was distinguished by a substantial decrease in the species diversity of chorate cysts at the expense of cavate cysts; this was associated primarily with a decrease in water temperature. In more deepwater shelf facies of the Beloglinian basin of Ciscaucasia (the data on the sections at the Belaya and Kuban rivers), a total of 90–100 species occurred; *Achomosphaera, Impagidinium, Spiniferites*, and *Systematophora* predominated. Out of the taxa characteristic of the Late Eocene there were *Areosphaeridium arcuatum, Cordosphaeridium funiculatum, Rottnestia borussica, Tytthodiscus beloglinensis*, and *Pterodinium*. The zonal species *Charlesdowniella clathrata angulosa* was common.

The taxonomic diversity of dinocysts decreased at the northern and eastern edges of the marine basin. In the Ustyurt part of the basin, the maximum diversity of species was characteristic of the onset of the Late Eocene (101 species); at the end of the Late Eocene, the number of species decreased to 80, a great role was played by green algae and acritarchs. Subsequently, the proportion of chorate cysts decreased, and the proportion of cavate cysts (*Rhombodinium, Wetzeliella*, and *Deflandrea*) increased. The numbers of species common with Ciscaucasia and Armenia were approximately 60 and 40%, respectively. Finally, in the extreme east, in Turgaj, the species diversity widely varied in time; occasionally, it reduced to 10–15 species; however, the total number of species (in all samples) was at least 100. This part of the basin was characterized by the constant presence of *Horologinella* and green algae. The cavate cysts comprised the widest range of species.

The paleoalgal ecosystems from the Central Asiatic part of the basin (Tajik Depression and Hissar Mountains) were characterized by a high diversity of species belonging to the genera *Deflandrea, Rhombodinium, Areosphaeridium, Thalassiphora, Pentadinium*, and *Impagidinium*. In the Late Priabonian, green algae also played an important role in this area.

The lowest diversity of the dinocyst associations was in the peripheral shelf zones of the Baltic Region, Belarus, and the Ukrainian Platform where the dinocyst assemblages included single or, at least, a small number of dominants and a major role was played by deflandrians, green algae, and acritarches. In the deeper water facies, the proximate cysts of the genus *Impagidinium* prevailed in the paleoalgal assemblages of these basins.

Biogeographic Zonation Based on Plankton

The distribution of planktonic groups in the Priabonian of the region considered allows one to distinguish two belts, the South and North Subtropical belts. The first was characterized by complete assemblages of tropical species; however, it differed from the Tropical Belt by a decrease in the number of warm-water tropical elements and discontinuous temporal distribution of the latter. The North Subtropical Belt was characterized by substantially impoverished associations, including peculiar relatively cold-water species and genera of nannoplankton and dinoflagellates, and a large role was played by globigerinids. The boundary between the belts extended on the elevation of the Alpine Fold System separating the Tethyan Realm from the Northern Peri-Tethys, i.e., on the Alps, Dinarides, Pontids, Lesser Caucasus, and Kopet Dagh (Fig. 5). The circulation of water is given after *Paleogeographic Atlas...* (1997). All water bodies of the Paleo-Paratethys were characterized by more or less impoverished planktonic assemblages and belonged to the North Subtropical Subzone. There are no well-grounded data on the northern boundary of the latter, the Temperate Zone is only weakly distinguished by the composition of planktonic foraminifers at the northern boundary of the region considered.

The composition of planktonic foraminifers most clearly reflects paleoclimatic zonation and its changes in time. Based on these data, the northern part of the Tethyan Realm (Armenian Gulf) belonged to the North Subtropical Belt beginning at the later half of the Priabonian (Krasheninnikov in *Geologicheskie i bioticheskie...*, 1996).

Small Benthic Foraminifers

Eastern and Southern Mediterranean. Thirty-seven species of 27 genera inhabiting soft carbonate muddy grounds are recorded from the Syrian Basin (Krasheninnikov, 1964, 1969). With the exception of a single species *Discorbis* is only recognized from Azerbaijan, all others are known in the Crimean–Caucasian (Beloglinian) Basin and along the northern coast of the Mediterranean–Mesopotamian Basin, in the area where, apart from the above, the genus *Queraltina* was found (also known from Syria).

The data on the fauna of Egypt is scarcer. Only 11 species of 10 genera common for the Syrian and
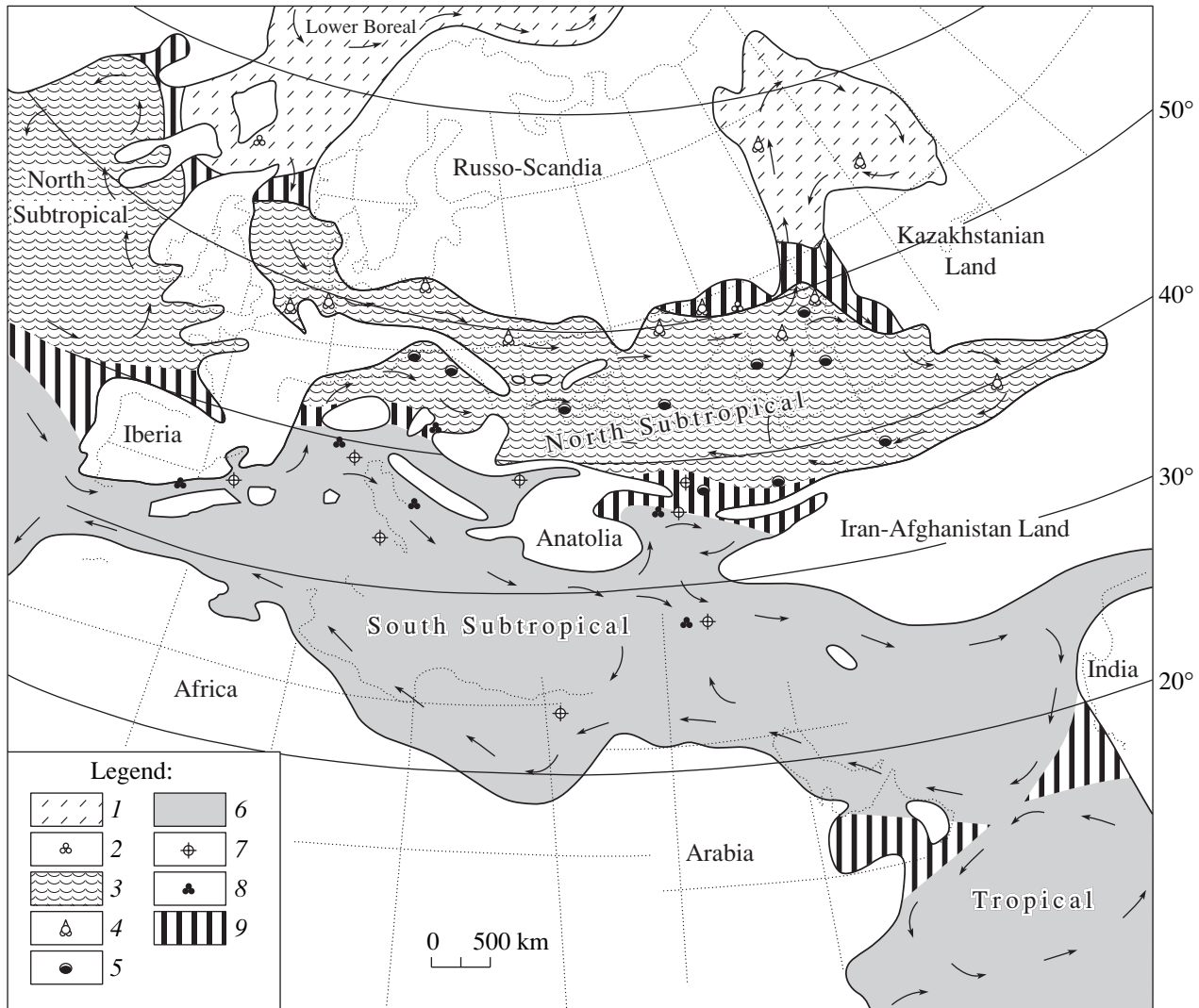
Fig. 5. Superficial circulation of water in the basins of the Priabonian (after *Paleogeographic Atlas…*, 1997, modified) and the pelagial latitudinal zones. Designations: (*1*) Temperate and Boreal zones with impoverished planktonic associations and the presence of specialized cold-water genera and species: (*2*) impoverished assemblages of planktonic foraminifers with the prevalence of globigerinids (*Globigerina angiporoides* and *G. linaperta*); (*3*) North Subtropical Zone lacking the most thermophilic (tropical) aquatic species and containing certain relatively cold-water taxa: (*4*) dinocyst assemblages of the northern type, including abundant green algae and such characteristic genera as *Rhombodinium, Deflandrea, Wetzelliella*, and *Phthanoperidinium*; (*5*) assemblages of planktonic foraminifers, including *Globigerapsis tropicalis* but lacking tropical genera; (*6*) South Subtropical Zone with the planktonic assemblages, similar to the tropical assemblages but including a decreased number of the most thermophilic tropical taxa: (*7*) dinocyst assemblages of the southern type, including the genera *Cordosphaeridium, Spiniferites, Heteraulacacysta, Systematophora*, and *Areosphaeridium*; (*8*) complete assemblages of planktonic foraminifers, including *Cribrohantkenina* and the group of species *Turborotalia cerro-azulensis*; and (*9*) Transitional Zone.

Crimean–Caucasian Regions are indicated from this region (Krasheninnikov and Ponikarov, 1964).

Northern Mediterranean. The biogenic carbonate grounds on the north coast of the Mediterranean (Italy, Coastal Alps, Eastern Spain) were inhabited by small foraminifers that formed similar associations (localities Trento, Mossano, Brendola). At least 90 species of 57 genera are known from the stratotype region of the Priabonian (Braga *et al.*, 1975). Of these the majority of genera and at least 20 species also occurred in the Crimean–Caucasian Basin.

Many associations show the presence of shallow-water, thermophilic species of the *Quinqueloculina, Triloculina, Pyrgo, Asterigerina, Amphistegina, Rotalia, Queraltina, Schlosserina, Chapmanina*. Besides, the zone of the shallow-water (ca. 50 m) carbonate sedimentation (including reef facies) contained a peculiar group of genera, *Biarritzina, Victoriella, Carpenteria, Nubeculina, Korobkovella*, that were unknown in the Crimean–Caucasian Basin.

Near the coast of Coastal Alps (Mortola Cape) the association of the shallow-water foraminifers contains

58 species of 43 genera including the thermophilic genera *Fabiania, Queraltina, Chapmanina, Gyroidinella, Nubeculina* (Bodelle *et al.*, 1968). About 20 species also occur in the Crimean–Caucasian Basin.

On the Iberian Coast (Spain: Provinces of Navarre and Catalonia) the littoral carbonate beds with nummulitids contain a diverse assemblage of small foraminifers (Ruiz de Gaona, Colom, 1950). It comprises 55 species of 38 genera, 7 of which belong to the Nodosariida. The generic composition is the same as that of the foraminiferal assemblage of the Crimean–Caucasian Basin and contains at least 16 common species. In Aragon the reef facies contain the genus *Chapmanina* and some characteristic Tethyan taxa. This assemblage is similar to that of the Aquitainian Basin. Molima, Monako, *et al.*, in *Terminal events…*, 1986 indicate 11 genera from the carbonate sediments with large foraminifers and red algae from southern Spain. This assemblage includes the thermophilic *Chapmanina, Astergerina*, and Gypsinidae. The assemblage is similar to that distributed in the central part of the Apenninian Peninsula (Nocchi *et al.*, in *Terminal events…*, 1986).

The reef facies of the Dynarides contain the most important Tethyan genera *Borelis, Haddonia, Chapmanina, Gyroidinella*, and also *Halkyardia, Asterigerina, Sphaerogyspina* (Pavlovec *et al.*, in *Terminal events…*, 1986). The genus *Chapmania* is also known in more southerly regions (in Albania [Cavelier, 1979]). Both the entire faunal composition and facial features of these beds indicate that sedimentation occurred in the coastal and shallow-water zones of the tropical sea.

Further to the east, in the Erevan–Vedino Bay (Armenia) 134 species of 76 genera are recognized (Bugrova, in press). About 25 species of eight genera are not found in the more northerly regions, although they are present in the Mediterranean (genera *Pseudoplanulina, Queraltina, Halkyardia, Schlosserina, Chapmanina*, and *Pyrgo*).

Eastern Atlantic. The shallow-water shelf of the Aquitainian Basin was inhabited by nummulitids and the thermophilic genera *Chapmanina* and *Baculogypsina*. The presence of these genera indicates connections with the Mediterranean Basin.

The foraminiferal association of the Paris Basin (Ludes Marne) is impoverished and is represented by a specific ecological group. The assemblage contains miliolids (five species belonging to two genera) and two species of *Elphidium*. Such a fauna is usually typical of shallow-water zones, perhaps lagoons with abnormal salinity. Judging from the presence even in the pre-Priabonian associations of the abundant nonionids, miliolods, polymorphinids this was a semi-isolated brackish-water basin with a fauna that was more similar to the northern rather than to the southern type.

Alpine–Carpathian Basin. In the westernmost, Fore-Alpine part of the basin, the *Lithotamnia* detritic carbonate grounds of the Bavarian Alps were inhabited by the diverse foraminiferal assemblage containing 34 genera. 19 of these genera also occur in the Beloglinian fauna.

On the southern shelf of the Carpathian Basin (Hungary) the shallow-water (up to 50 m) biogenic carbonate facies infrequently contain small benthic foraminifers (Báldi, 1984). The carbonate mud (lower part of the Buda Marl) of the deep-water facies contain a much more diverse assemblage, approximately 176 species belonging to 67 genera (Hantken, 1875 and others). Many of these species occur in both the shelf zone of the northern Mediterranean and in the Beloglinian Basin.

Marly and clayey facies of the Priabonian in Slovakia contain about 100 species belonging to 43 genera (Samuel, 1975), with nodosariids being particularly diverse (27 species). The characteristic feature of this association is the presence thermophilic genera (e.g., *Pyrgo* and *Glabratella*) that indicate close connection with the Mediterranean. However, the same association contains *Bolivinella* and *Tubulogerina* of the Latdorfian assemblage, two species of *Almaena* including *A. taurica* also recognized from the Ukrainian part of the Carpathian Basin, in the Crimea, and in the Northern Caucasus. Some species known in the Beloglinian Basin were also observed here. Samuel (1975) suggested that this assemblage is intermediate between the South European and North Germany faunal types.

The non-carbonate facies of the deep-water zones of the Carpathian Basin (Ukrainian Flysch Carpathians) contain an assemblage of arenaceous (mainly primitive) foraminifers (Kraeva and Maslun, 1984) that do not occur in other regions. The more carbonate-rich facies (Popelskaya Formation) were also inhabited by calcareous foraminifers including species in common with the Crimean–Caucasian fauna.

North Sea Basin. The most representative association of the southern shelf of the North Sea Basin (the Latdorfian of Germany) contains 66 species of 30 genera of small foraminifers, and some nummulites. This assemblage is referred to as the "Kalaus-type fauna." It is distinct in the presence of the genus *Lacazina* (abundant), which also probably occurs in the western part of the Beloglinian Basin (Mandrikovka, Ukraine). Such genera as *Bolivinella, Planorbulina, Tubulogerina, Articulina, Asterigerina, Rotalia*, etc. are also known from the Mediterranean. Species of the latter two genera have also been recognized from the shelf zone of the Ukrainian Basin. The presence of this fauna, and the test morphology of *Rotalia* and *Asterigerina* species indicate a shallow-water and warm environment. Benthic foraminifers are different from the Mediterranean Priabonian assemblages in their species and partly generic composition (genera *Biapertorbis, Conorbina, Tubulogerina, Diocibicides*, etc.). The presence of abundant tests of *Lepidocyclina*, the genus that was widespread in the Oligocene, is noteworthy.

The plains of Poland had a wide shallow-water strait that probably entered the Carpathian Basin and the Beloglinian Basin (through the Pripyat–Dnieper System of depressions). As a result its fauna is very similar to that of the Beloglinian assemblages (Pozaryska, 1978). The presence of many taxa in common with those assemblages, including *Tergrigorjanzaella sectile*, is noteworthy.

The fauna of the Fore-Sudetian part of the basin (Odrzywolska and Pozaryska, 1984) belongs to a different type. It contains 87 species belonging to 48 genera among which there are species of the Beloglinian assemblage. In contrast to the Beloglinian assemblage, the fauna under consideration contains the thermophilic Tethyan genera *Articulina, Glabratella, Planorbulina*, that indicate an interconnection with the Mediterranean fauna. At the same time the assemblage contains eight genera unknown in other regions, but also occurring in the Latdorfian, which indicates a similarity between these faunas. The high diversity of miliolids (17 species of six genera) suggests a shallow basin.

Greater Caucasus–Kopet Dagh (Beloglinian) Basin. Carbonate mud in the major part of the basin contains remains of planktonic foraminifers and nannoplankton and rich associations of benthic foraminifers. The most representative are the assemblages of the Crimean–Caucasian part of the basin. In the Crimea, the foraminifers are represented by 77 genera and over 140 species (*Planulina costata* Zone (Bugrova, 1988a)), most of which are widespread outside this region. Calcareous taxa were dominant (64 genera and 120 species, i.e., up to 90%). The assemblage generally contains one–two species of each genus, except for the more diverse *Robulus, Marginulina, Cibicidoides, Bulimina, Uvigerina, Bolivina*, and some others. The taxonomic composition and morphology of the majority of species indicate favorable conditions (a shelf of a subtropical sea with an open connection with both the Mediterranean and the North Sea basins (via Poland)).

The deeper parts (Northern Caucasus, localities on the rivers Kuban and Kheu) show the presence of the same assemblage as in the Crimea. This assemblage includes up to 149 species belonging to 79 genera. The association is also dominated by calcareous foraminifers, although the proportion of agglutinated taxa was somewhat higher (up to 14.7%) than in the Crimean one.

Further to the north, in the more clay-rich facies of the Ciscaucasia, the increase in the number of species and a higher proportion of agglutinated taxa. At the same time the associations from the more carbonate-rich grounds are more similar to the North Caucasian ones. In total the assemblage contains 52 species of 29 genera (Ter-Grigorjantz, 1965). Further to the north, the assemblage becomes even more impoverished and contains 34 species of 24 genera (Ipatovo Region (Ter-Grigorjantz *et al.*, 1968)).

The fauna of the shallow-water zones of the East European Platform is somewhat more impoverished than that of the Crimean–Caucasian (71 species of 51 genera from the calcareous clays of the Volga–Don Watershed). While the majority of these species occur in both assemblages, the East European Platform assemblage also includes other species and genera (e.g., *Plectofrondicularia, Sporobulimina, Asterigerina?, Astrononion*, etc.) and some endemic taxa. *Robulus, Bulimina*, and *Uvigerina* dominate in the number of individuals. The most shallow-water beds (lower reaches of the Don River, Karpinsky Arch, etc. [Nikitina, 1963, 1972]) and the sediments of the coastal zone contain large quantities of agglutinated foraminifers, including *Cyclammina pseudocancellata*. The shallow-water beds of the Dnieper–Donets Depression (Obukhovo assemblage) contain an impoverished association of the Beloglinian species (Konenkova and Bogdanovich, 1986). Some of these species (*Planulita costata* Zone) occur in the southwest of the basin (Odessa Region and Moldova).

In the southern Transcaucasian shelf, the Adzhar–Trialeti facial zone where the environment was influenced by the influx of the terrigenous material (Kacharava, 1977) the foraminiferal assemblages are impoverished (the assemblages in the Akhaltsikhe Basin contains up to 24 species of 21 genera). They contain all the characteristic genera that occur in the Crimean–Caucasian part of the basin. The species of the genera *Robulus, Heterolepa*, and *Bulimina* predominate. Endemic taxa are rare; many species originally determined from this region have been shown to occur outside it, up to the western areas of Central Asia. This suggests close connections between this part of the basin and the northern regions.

The composition of the assemblages of the North-Eastern Caucasus and Transcaucasia greatly depended on the facies (Khalilov, 1962). Generally, this fauna is similar to the Beloglinian assemblage, although it contains numerous and diverse *Nonion, Bolivina*, Anomalinidae, and *Chilostomella*, mostly endemic species.

The foraminiferal assemblage from the carbonate clays included 29 species of 17 genera (mostly calcareous foraminifers) (northeastern Azerbaijan). The fauna from the northeastern and eastern coasts of the Lesser Caucasus shows a distinct generic (41 genera) and species (83) composition. The assemblage includes a small quantity of agglutinated, mainly primitive species, and also *Bolivina* (17 species), *Nonion* (6 species), *Chilostomelloides* (5 species), *Chilostomella* (3 species), *Rotalia* (2 species). The majority of the representatives, including anomalinids, are endemic. The Kobystan association contains 41 genera and 84 species and includes some taxa typical of the Mediterranean fauna (genera *Articulina, Halkyardia, Planorbulina, Rotalia*, that indicates a good connection of this inland shallow-water basin of Transcaucasia with the Mediterranean. Further to the south, in the Ciscaspian region of Azerbaijan, the fauna was quite diverse (ca. 40 species;

20 genera) and included the genus *Pyrgo* (normally Mediterranean associations).

Clayey sediments of the northern outer shelf of the Turanian Sea (northwestern Ustyurt Plateau [Nikolaeva and Prussova, 1979]) also contained a Beloglinian assemblage with a typical large quantity of *Nonion curviseptum* and *Bolivina antegressa*. The assemblages of Mangyshlak Peninsula, western chinks (border scarps) of the Ustyurt Plateau, and the South Embe Depression contain up to 57 species of 37 genera. Further to the northeast, the clay sediments of the shallower and apparently cold-water part of the basin were reported to contain an impoverished assemblage (36 species of 23 genera from the Chegan Formation [Bronevoi *et al.*, 1967, collections of N.N. Bryzzheva]). Their composition is close to that of the associations of the Crimean–Caucasus Region: of 30 species 76.6% are in common, including the species *Tergrigorjanzaella sectile* that is known from the Northern Caucasus, East European Platforms, and in Poland. This fauna was distinct in that it contained miliolids (Serova, 1962) and the appearance of nonionids at the end of the Late Eocene.

Further to the north, in the shallow-water zones of the Turgaj Strait, the fauna was very impoverished (11 species of 11 genera) and contained only a few species of the Beoglinian assemblage including numerous tests of *Cyclammins pseudocancellata.*

All 88 species of 45 genera known from the southern part of the Turanian Sea (Krasnovodsk Peninsula) also occurred in the Crimean–Caucasian Basin. The non-carbonate and aleurite muddy grounds near Kopet Dagh were inhabited by impoverished assemblages. Thirty-five species of 26 genera are recognized from Malyi Balkhan, of them two-thirds of species and 85% of genera belong to the Beoglinian Association, although the genera *Rotalia, Astrononion, Florilus, Baggatella*, and the species *Textularia hockleyensis* occur only within this region (Bugrova, 1988b). The genera *Bulimina* and *Uvigerina* dominated in number of individuals. Further to the east, in the shallower water zone (Gyaursdag) half of the assemblage of about 20 species was represented by the species also occurring in the Beoglinian Basin, while the other half was endemic or in common with the fauna of the Tajik Basin (*Paleogen Turkmenii…*, 1975 and others).

In the southeastern part of the basin the fauna was less diverse. The major part of the fauna was Beoglinian taxa, although a characteristic Tajik species *Brotzenella vakhshica* occurred in the Maryi Region of Turkmenia.

The foraminiferal assemblage of the Tajik Bay is quite representative, in total it includes 73 species of 31 genera. Associations of its opened western part (Gaurdak Region [Bugrova, 1985]) are the most similar to those of the Crimean–Caucasian region: of 40 species belonging to 24 genera, only two species were endemic. Further to the east (Davidzon *et al.*, 1982) the fauna was impoverished and was often dominated by

the agglutinated taxa (*Trochammina, Textularia, Haplophragmoides*). This assemblage included over 17% endemic species.

The assemblage from the Fergana Bay contained rare miliolods (these species could survive unstable salinity regimes).

Biogeographic Zonation

The pattern of the distribution of small benthic foraminifers in the Priabonian was considerably different from that of other benthic groups that are considered separately. Similar to other fossil groups, two major types of assemblages may be recognized in the territory. These assemblages indicated two paleobiogeographic regions: Ancient Mediterranean (or Mediterranean) and North European. However, the boundary between these regions and subdivisions of the second are different.

Ancient Mediterranean Region. This fauna contains thermophilic taxa including many species with a large, thick-walled, ornamented test (*Gyroidinella, Asterigerina, Queraltina, Rotalia*, etc.) and highly specialized genera (*Gypsina, Halkyardia, Stomatorbina, Schlosserina*). The most deep-water part of the Carpathian Basin with a flysch accumulation the fauna is represented by a unique association of primitive agglutinated foraminifers.

The incompleteness of the fossil record prevents recognition of the area of characteristic genera, although the approximate pattern of their distribution, the endemic character of the fauna, and the degree of separation of the Ancient Mediterranean from the North European regions are shown in Fig. 6.

Northern and northeastern borders of the Mediterranean region were inhabited by impoverished, but generally similar assemblages. Hence, the Euxian–Caspian (Beoglinian) Basin is considered as a northern province of the Ancient Mediterranean Paleobiogeographic Region.

Beoglinian Province. This province is recognized over the entire Greater Caucasus–Kopet Dagh Basin. The fauna from different parts of this basin is similar in its generic and species composition. The basin was inhabited by an association of benthic foraminifers that included up to 150 species of 80 genera and almost all orders. The representatives of the orders Nodosariida, Rotaliida, Buliminida usually dominated these associations. The majority of these species possess a large, often ornamented shell. In the shallow-water regions (Volga River Region, Scythian Plate) the fauna was impoverished, the assemblages were dominated by anomalinids, including local species and subspecies.

The inner shallow-water seas of Western Georgia (Adzharo-Trialetia, Akhaltsikhe) also showed the presence of foraminiferal associations with species characteristic of the Beoglinian Basin. However, in the fauna

Fig. 6. Scheme of zoogeographic zonation of the shelf of the Priabonian basins based on benthic foraminifers. Designations: (*1–3*) **North European Region** characterized by the presence of abundant members of the genus *Lacasina* and the genera *Reussella, Tabulogerina, Conorbulina*, etc., which absent or scarce in easterner and southerner basins; the presence of the genera (*2*) *Bolivinella* and (*3*) *Tubulogerina* characteristic of the North European Region and Transitional Zone; (*4–12*) **Ancient Mediterranean Region** characterized by the presence of thermophilic forms with large, thick-walled, and sculptured shells (*Gyroidinella, Asterigerina, Queraltina*, and *Rotalia*) and high-specialized genera; (*4*) Beoglinian Province, with the prevalence of the orders Nodosariida, Rotaliida, and Buliminida; distribution of (*5*) *Nonion curviseptum*, (*6*) *Tergrigorjanzaella sectile*, (*7*) *Brotzenella vakhshica*, and (*8*) *B. taurica*; (*9*) North Mediterranean Province: (*10*) *Queraltina*, (*11*) *Amphistegina*, and (*12*) associations of reef facies; and (*13*) boundary regions. Major localities: (1) Aquitaine, (2) southeastern Spain, (3) coastal (Nummulit) Alps, (4) northern Italy, (5) Armenia, (6) Syria, (7) Iran, (8) Crimea, (9) Ciscaucasia, (10) western Georgia, (11) southern Georgia, (12) Azerbaijan, (13) Middle Volga Region, (14) northern part of the Ustyurt Plateau, (15) Mangyshlak, (16) southern part of the Aral Region, (17) western Kopet Dagh, (18) southern Turkmenistan, (19) Tajikistan, (20) Slovakia, (21) southern Poland, and (22) northern Germany.

of the shallow-water bays of southwest Azerbaijan the degree of endemism was high. Local species of *Bolivina, Anomalinoides, Heterolepa*, and *Nonion* are unrecorded outside this area. In addition, the presence of the genera *Chilostomella* and *Chilostomelloides*, barely known in other regions, is typical.

The basin of Eastern Transcaucasia (Kobystan) was also characterized by a distinct foraminiferal association. The assemblage was dominated by species from the Crimean–Caucasian region, although it also contained the Mediterranean genera *Articulina, Planorbulina*, and *Halkyardia*. Evidently, this part of the basin was connected with the Tethyan by a system of straits and through the Armenian Bay.

The northeastern and eastern borders of the Beoglinian Basin showed a particularly high degree of endemism. They are recognized as the Turanian and Tajik subprovinces, whereas the central part of the basin may be designated the Crimean–Caucasian Subprovince.

North European Region. The data of the taxonomic composition and distribution of fauna come mostly from the Latdorfian association of North Germany. This association contains the abundant genus *Lacazina* previously known from the Paris Basin, the genera *Reusseella* (five species), *Tubulogerina* (3 species), *Conorbina, Biapertorbis, Sphaerogypsina, Bolivinella* (two species), *Planorbulina, Ceratobulimina*, and *Asterigerina*. Some of these genera were absent in the Mediterranean and Crimean–Caucasian Region, and some appeared here only in the Oligocene. The Latdorfian fauna contains species known in the basins of the platform part of Ukraine (Mandrikovka), some in the Crimea, but generally the fauna of the North European Basin showed high levels of endemism.

Associations of the mixed type that included elements of both the northern (*Planorbella, Bolivinella, Tubulogerina*) and southern (*Almaena, Pyrgo, Glabratella, Pararotalia, Rotalia*) fauna are known in the Fore-Sudetian Trough and Slovakia. This western

region of Fore-Carpathian Region was a connecting ring between the North European and Ancient Mediterranean regions.

Nummulitids and Discocyclinids

Southern and Eastern Mediterranean. Nummulites are recognized from the southern border of the Mediterranean Basin (Morocco, Algeria, Tunisia, Libya, Turkey, and Egypt) (Roveda, 1961, Schaub, 1981, etc.); occasionally the same assemblages contain *Operculina*. Further to the east (Syria), large foraminifers are widely represented in the shallow-water carbonate facies. These assemblages contain *Nummilites* (at least 12 species), *Operculina* (two species), *Operculinella*, *Heterostegina* (two species), *Spiroclypeus* (two species), *Grzybowskia, Discocyclina, Asterocyclina, Aktinocyclina* (Krasheninnikov and Nemkov, 1975; Krasheninnikov and Ptukhyan, 1973, 1986; Abdulrakhim and Nemkov, 1972). Nummulitids and discocyclinids are recorded from the eastern part of the Tethyan Basin (from India to Indonesia), although their Late Eocene age is uncertain. The southernmost record from this nummulitid province is *N. fabiani* (and two other species of this genus) and *Spiroclypeus* in the territory of Somalia (Cabdulqadir and Carush, 1982).

Northern Mediterranean. In northern Italy (stratotype and parastratotype Priabonian region) large foraminifers are very diverse and abundant. These assemblages contain *Nummulites* (17 species and subspecies), *Operculina* (2 species), *Heterostegina* (2 species), *Grzybowskia, Spiroclypeus, Pellatispira, Discocyclina* (3 species), *Asterocyclina* (3 species), *Aktinocyclina, Alveolina* (Roveda, 1961; publications in *Colloque sur l'Eocene*, 1964, 1968, 1969; Cita, 1975, Herb and Hekel, 1975; Cavelier, 1979; Schaub, 1981; Barbin and Bignot in *Terminal… Events*, 1986).

In other parts of the basin the fauna is less diverse but its major composition was virtually the same. For instance, the shallow-water facies of Apulia (Central Italy) contain rare nummulitids, discocyclinids, and *Pellatispira* (Molina *et al.* in *Terminal… Events*, 1986). Further to the west (Maritime Alps, southern France), the assemblages contain *Nummulites* (eight species), *Operculina, Spiroclypeus, Discocyclina, Asterocyclina* (Bilgutay *et al.*, 1969, Bodel *et al.*, 1968, Cavelier, 1979). The Priabonian of Sicily contains *Nummulites* and *Grzybowskia* (Montanari, 1968). Rare nummulitids, *Pellatispira*, and numerous discocyclinids are recorded from the shallow-water facies of southern Iberia (Spain, near the town of Malaga) (Molina *et al.* in *Terminal… Events*, 1986). Quite abundant *Nummulites* and species of *Operculina* are recorded from northeastern Iberia (Aragon and Catalonia), although other genera of large foraminifers are not recorded (Ruizd de Gaona and Colom, 1950; *Colloque…*, 1969, *Terminal… Events*, 1986).

The assemblages from the Dynarides coastal area (southwest Albania) contain *Discocyclina, Asterocyclina, Pellatispira, Nummulites*, and *Alveolina* (Roveda, 1961; *Colloque sur l'Eocene*, 1968; Cavelier, 1979) further to the northwest (Dalmatian Maritime Area and Herzegovina)—*Nummulites* (three species), *Operculina, Pellatispira, Discocyclina* (Pavlovec *et al.*, in *Terminal… Events*, 1986). The Rhodopian Basin contained *Nummulites* (12 species and subspecies), *Operculina* (five species), *Pellatispira* (two species), *Spiroclypeus, Discocyclina* (10 species), *Asterocyclina* (five species) and two species of *Aktinocyclina* (Belmustakov, 1959). Two species of *Nummulites* are recorded from northern Anatolia, including *N. fabianii* (*Terminal… Events*, 1986).

In the east, near the southern coast of Lesser Caucasus, associations of large foraminifers are as diverse as those of North Italy. The inner zones of the shelf in the Armenian Bay were inhabited by the genera *Nummulites* (12 species and subspecies), *Operculina* (five species), *Pellatispira* (two species), *Spiroclypeus* (two species), *Grzybowskia* (two species), *Discocyclina* (nine species), *Asterocyclina* (five species), *Aktinocyclina* (two species) (Grigoryan, 1986).

Further to the southeast (Nakhichevan Basin) the fauna contains *Nummulites* (five species, including *N. fabiani*), *Operculina*, and *Discocyclina* (Mamedov, 1965). The Talysh Basin, connected with the Nakhichevan basin by a shallow-water strait contained only nummulitids (Khalilov, 1962).

Alpine–Carpathian Basin. The Alpine part of the basin (Swiss and Austrian Alps) contain only sparse nummulitids and discocyclinids (Roveda, 1961, 1970; Báldi, 1984). The western part of the Carpathian Basin (Moravia, Slovakia) the assemblages contain *Nummulites* (ca. seven species and subspecies), *Operculina, Grzybowskia* (two species), *Spiroclypeus* (two species), *Discocyclina* (five species), *Asterocyclina, Aktinocyclina* (Bieda, 1959, 1960, 1963; Samuel, 1975; Vanova, 1962). Further to the east (Flysch Ukrainian Carpathians) the assemblages contain *Nummulites* (seven species), *Operculina* and *Grzybowskia* (Zernetskii, 1980).

The assemblage of large foraminifers was more diverse on the southern shelf of the Carpathian Basin. The Hungarian Paleogene Basin (Buda Mountains, Bakoni), in addition to nummulitids contained *Operculina, Heterostegina, Pellatispira, Discocyclina* (four species), *Asterocyclina* (two species), *Aktinocyclina* (three species) (Hantken, 1875; Kopek and Kecskemeti, 1961; Cavelier, 1979). *Nummulites* (eight species), *Operculina, Spiroclypeus, Discocyclina, Neoalveolina* are recorded from Transylvania (Dudich and Meszaros in *Colloque…*, 1964; Bombita and Moisescu, 1968, etc.). Nummulitid facies are traced in the Transcarpathian Trough, in the Marmarosh Zone where they contain *Nummulites* (including *N. fabianii*), *Discocyclina* (three species), *Asterocyclina* (two species) (Nemkov, 1967).

Eastern Atlantic. Four *Nummulites* species inhabit the area along the Atlantic Pyrenees (Schaub, 1981). The shallow-water Early and Middle Priabonian Basin of Aquitaine contained *Nummulites* (seven species), *Operculina, Spiroclypeus, Grzybowskia, Discocyclina* (two species) and also *Alveolina* (three species), and *Neoalveolina* (Boulanger in *Colloque…*, 1969; Cavelier, 1979, etc.).

Two species (*Nummulites fabiani* and *N. prestwichianus*) are recorded from the Breton Peninsula, the latter species is characteristic of the northern nummulitid province. *N. fabiani*, *N. prestwichianus* and *N. rectus* are recorded from the region of the English Channel (both are species from the northern province) (Curry *et al.*, 1970).

North Sea Basin. In the large territory of northwestern Europe large foraminifers are represented mainly by nummulitids with interrupted geographic areas. The territory of Belgium and the North Sea were inhabited by *N. germanicus* and *N. orbignyi* (Drooger *et al.*, 1971; Cavelier, 1979). The southern shelf (Germany–Latdorfian sands from the vicinity of Brandenburg and Magdeburg) was inhabited by *Nummulites* (eight species), *Discocyclina* (two species). Numerous *Lepidocyclina* appeared at the end of the Oligocene (Krutzsch and Lotsch, 1957; Jartseva *et al.*, 1968; Cavelier, 1979; Nemkov and Yartseva, 1991). The territory of western Poland contains only nummulitids (Pozaryska, 1978).

Beloglinian Basin. In the western part of the shallow-water northern shelf (Black Sea Basin, slopes of the Ukrainian Shield and the Dnieper–Donets Depression) the environment was favorable for large foraminifers. The clayish-sandy substrates were inhabited by nummulitids. Their associations included up to 16 species and subspecies; in addition to nummulitids the organogenic-detritic and sandy substrate was inhabited by rare *Operculina*, and *Discocyclina* (Yartseva, 1966; Zernetskii, 1980, etc.). The impoverished associations of nummulitids inhabited the territory of Lower reaches of the Volga River (localities in the vicinity of the city of Volgograd) and the Crimea (Bugrova, 1985).

In the North Caucasian part of the basin nummulitids were absent. Only at the end of the Eocene, declined species appeared in the shallow-water areas: *Nummulites* (two species) in the central part of the basin (Kuban River), *Asterocyclina* (2 species) and further to the north in addition to these species two species of *Discocyclina* are recorded (Nemkov, 1967; Bugrova, 1984).

In the first half of the Priabonian the southern Transcaucasian shelf (territory of Georgia) contained a nummulitid fauna of the southern type, although impoverished. The association with *Nummulites fabiani* was widespread over the entire territory (Abkhazia, Akhaltsikhe Depression, Kakhetia). However, the nummulitid assemblage of 11 species included only a single species with a granulated test and three with a reticulate test. From the second half of the Priabonian the assemblage included the species of the northern province. Of eight nummulitid species from the Kura Depression majority are the species of the northern province (*N. rectus, N. concinnus*, etc.). and only *N. budensis* and *N. incrassatus* are more typical of the southern province. The assemblage also contains *Operculina, Discocyclina* (4 species), *Asterocyclina, Aktinocyclina* (Mrevlishvili, 1978). The assemblage from the coastal areas of the northeastern piedmont of the Lesser Caucasus contains six nummulitid species of which *N. rectus* is a species of the northern nummulitid province (*Geologiya…*, 1982).

Ostracodes

The major factors that affect the composition of the marine ostracode fauna include the depth of the basin, currents, salinity fluctuations, and taxonomic features inherited from the ancient faunas. Ostracodes have been studied over a long period from the first classical Western European papers of the 19th century to the series of modern studies from the stratotype regions of stages and their boundaries. However, a general revision of the taxonomic composition of Paleogene ostracodes has never been made. Hence, in comparing synchronous faunas one has to utilize taxa of generic rank, and use such terms as "group of species" and widely accepted species.

North Africa. Priabonian ostracodes are recognized from Egypt from the upper part of the Mokkattam Formation. The dominant group of Trachyleberidaceae (Bassiouni, 1969, 1970; 1971) was represented by 25 species of 17 genera of which seven (*Trachyleberis, Acanthocythereis, Hornibrookella, Martinicythere, Leguminocythereis, Opimocythere, Pterygocythereis*) were ancient transitive genera of subglobal distribution, while three (*Cativella, Orionina, Reticulina*) in other areas appeared later. The assemblage was characterized by the family Buntoniidae usual in the southern Mediterranean and north African sector of the Atlantic as early as the Early Paleogene.

North Mediterranean. The shelf of North Italy in the Priabonian stratotype region was inhabited by 40 species of 30 genera (Ascoli, 1975; Barbin and Guernet, 1988). The taxonomic composition of this assemblage was similar to that of the Middle Eocene, although new genera and species emerged that became widespread in the Oligocene. The majority of genera were of subglobal distribution, but in such a complete composition this association has not been discovered further to the north, The genus *Triebelina* is regarded typical of the Cenozoic of the Tropical area; the genus *Verrucocythereis* was not found in the Priabonian in any of the more northern regions. The genus *Callistocythere* was apparently of Mediterranean origin, although later it occurred further to the north. The North Italian association differs in the quantitative

dominance of the species of the thermophilic genus *Cytherelloidea*.

In the Priabonian the Armenian Bay contained an association of ostracodes that showed a low taxonomic diversity and low number of individuals, features that are normally characteristic of the deep-water assemblages. This is supported by the predominance of cosmopolitan eurybathial ancient transitive genera that lacked eyes (*Cytherella, Argilloecia, Dumontina*, Trachyleberidea). In addition, the assemblage includes species of the specific deep-water genus *Agrenocythere*.

Eastern Atlantics. In the late Eocene the Aquitainian Basin contained an abundant taxonomically diverse ostracode assemblage (94 species of 44 genera [Ducasse *et al.*, 1986]). All the genera were transitive, appeared in this region in the Early and Middle Eocene and majority of them (except for seven) continued into the Oligocene. The assemblage did not contain endemic genera. The Trachyleberidacea, the major superfamily of Cenozoic ostracodes, was dominated by the Thaerocytheridae. The genus *Hazelina* (Trachyleberididae) is usual for the North Sea Basin and Euxino–Caspian Basin. The shallow-water groups: 64% of species belong to groups inhabiting the photic zone, 28% were eurybathyal groups, 5% relatively deep-water, while not more than 3% were specifically deep-water taxa (genera *Agrenocythere, Henryhowella, Abyssocypris*). The species composition was quite specific. According to Ducasse *et al.* (1986) there are only a few species in common with the Paris Basin (11 in the Marinesian and two for the Ludian).

In the Anglo–Paris Basin the ostracodes in the Priabonian were affected by the changes in the marine and continental regimes that were followed by the impoverishment of the marine fauna. The greatest similarity of the Hampshire and Paris basins were revealed during the marine transgression in the Middle Headonian and during the accumulation of marls with *Pholadomya ludensis* when the fauna of Latdorf type appeared there. In the Paris basin the ostracode association is more numerous and diverse (30 species, 22 genera), in England—14 species of 12 genera (Keen, 1968). Most of these species, or their close relatives, occur in both basins, with the exception of *Hazelina indigena* characteristic of the North Sea assemblages and not found in the Paris Basin. Compared to the ostracodes of the Aquitainian basin, the Ludian assemblage is more uniform and contains fewer individuals. Of 22 genera, 15 are also widespread in Aquitaine, two species occur in both localities, but the assemblages differ considerably in the absence of deep-water genera and in the low number of eurybathyal genera that were replaced by taxa inhabiting shallow-water shelves and euryhaline groups.

North Sea Basin. The Latdorfian ostracode assemblage is noteworthy in its high diversity and abundance (Moos, 1969, 1973). The assemblage contains ca. 80 species mainly belonging to transitive Eocene genera and is dominated by the Thaerocytheridae, while the Cytheridae and Trachyleberididae also played a significant part. The assemblage contained the Hemicytheridae, the group dominant in the Oligocene and Neogene. The presence of shallow-water groups (with eyes), eurybathyal groups (*Cytherella, Bairdia*, etc.) and groups highly tolerant with respect to salinity (Cytherideidae), is typical. The presence of the "*Hazelina indigena*" group is also typical.

Ostracodes have not been found in the Lower Priabonian of the Belgian part of the shelf. Two transitive species of the genus *Leguminocytheris* appeared at the beginning of the Tongrian. In the Rein and Mainz basins ostracodes of the Latdorfian type have not been recorded. In the Middle Pechelbronner time some representatives of the family Thaerocytheridae occurred together with foraminifers of the Latdorfian type.

Priabonian ostracode associations of the more easterly basins (northern Germany, Poland, Ukraine [Mandrikovka assemblage]) were quite close to the Latdorfian type (Pietrzeniuk, 1969, Szczechura, 1977, Sheremeta, 1969), although these faunas showed the predominance of earlier transitive species.

Alpian–Carpathian Basin. Ostracodes have not been discovered in the central part of the basin. In the southern shelf in the Hungarian Paleogene basin the Priabonian nummulitid limestones contains scanty ostracode material (Monostori, 1985). The Upper Priabonian sediments (lower part of the Buda marls) were deposited in an environment with varying depths and the assemblage contains a deep-water genus *Abyssocypris*, eurybathyal genera *Bairdia, Cytherella, Argilloecia, Krithe*, Trachyleberidea, and the shallow-water shelf genera *Uroleberis, Eucytherura, Schizocythere*, and *Hazelina*. The species composition was mainly endemic, with the exception of the widespread species *Hazelina indigena* and *Trachyleberidea pasteroacuta* (Monostori, 1985b, 1986).

The shelf in Transylvania in the Priabonian was inhabited by an ostracode assemblage represented by 74 species of 30 genera (Olteanu, 1973, 1977). Together with the shelf ostracodes a large role was played by the eurybiontic genera (up to 25%). The assemblage was dominated by species that occurred over the entire Peri-Tethys in the Early and Middle Eocene, while the endemic species represented not more than 14% of the total content. There were two periods when the quantity of individuals sharply increased corresponding to the time of formation of the Kluzh Limestones and to the terminal stage of the formation of the bryozoan marls.

Beloglinian Basin. This basin contained two types of ostracode assemblages that included ostracodes inhabiting different range of depth: (1) of the deep-water shelf of Ciscaucasia and (2) more shallow-water, of the Chegan type. The former assemblage is taxonomically uniform, with a low density of populations.

It was an inherited assemblage of the Early–Middle Eocene deep-water association. It lacked deep-water taxa (inhabiting depths over 600 m), although it contained eurybathyal groups (*Cytherella, Bardoppilata, Bairdia, Argilloecia, Trachyleberidea, Hazelina*, and *Krithe*) without eyes, and very few forms with eyes. Hence, this assemblage is considered to be relatively deep-water.

The northeastern part of the basin, where the clayish Chegan Beds were accumulated in a relatively shallow-water environment, ostracodes were numerous and taxonomically diverse, there were over 60 species of 29 genera. Together with the dominating shelf fauna, the assemblage contained representatives of more deep-water eurybathyal groups: *Pontocypris, Argilloecia*, and *Krithe*. Generally, the assemblage was dominated by Eocene elements, although some (not more than nine) continued into the Oligocene. In its generic composition the Chegan assemblage is close to the Latdorfian; the differences resulted from the features inherited from the ancestral associations: in the Chegan assemblage the Trachyleberidaceae were dominated by the subfamily Echinicytherideinae (Trachyleberidae), and by the subfamily Thaerocytherideinae (Thaerocytheridae) in the Latdorfian.

The Chegan association has the largest number species in common with the Sanglak (Khanabad–Sumsarian) assemblage of Central Asia. In its generic composition the Sanglak assemblage was close to the Chegan, although it differed in the absence of the eurybathyal stenohaline marine fauna (genera *Argilloecia, Xestoleberis, Krithe*) that apparently indicated a more shallow-water basin. An assemblage similar to the Sanglak association is recorded from eastern Turkmenia. Despite the Chegan assemblage belonging to the northern type, it contained a few species the same or similar to the Priabonian species of Northern Mediterranean.

The region of Western Turkmenia and eastern Ustyurt showed a relatively deep-water "Ciscaucasian" type ostracode fauna.

Mollusks

The biogeography of the Priabonian marcrobenthic communities is still poorly studied. Despite a long history of studies of the fossil mollusk faunas, revisionary work is still required, the true diversity of the Eocene fauna is only partly known. Analysis of similarity and distinctions is not possible since the assemblages even from the closely located occurrences are often incomparable. Popov (1994) proposed comparison of generic and subgeneric compositions of bivalves. Using a similar approach for gastropods is difficult since their generic taxonomy is poorly developed. Often it is easier to identify the species than to assign it generically. Amitrov (1999) analyzed the degree of similarity of the familial and species composition for the major gastropod assemblages. For mollusks it is difficult to show

truly cold-loving and not just cold-tolerant genera and more so families. Hence, the warm-water assemblages should embrace the colder-water ones. However, this rule is not always observed and northern assemblages appear even more abundant than southern: some factors except for temperatures (including taphonomic and other secondary factors) also affect the distribution of taxa.

North Africa. The representative data based on the updated revision of bivalves were presented by Srtougo (1977) for the Priabonian of Egypt. The fauna from this region included about 100 species, mainly endemic. Twenty species were in common with the faunas of Somalia and India. Of 70 genera and subgenera, 27 are unknown in the Priabonian of Europe. The generic composition is similar to that of the fauna of the Indo–Pacific region (the tropical genera *Havaiarca, Trisidos, Vasticardium, Notocorbula, Carolia* are unknown in the Late Eocene of Europe). Only eight species were in common with the fauna of southern Europe.

Abbass (1967) proposed a revision of gastropods from the same beds. In its familial composition the assemblage is not different from the Mediterranean, the generic determinations are uncertain, but the species composition is very distinct: of 76 species, 75 are unknown outside North Africa, and only the one remaining species is in common with the Eocene assemblages of Eurasia.

North Mediterranean. In the north coast of the ancient Mediterranean the most representative molluscan assemblages are recorded from North Italy, French and Swiss Nummulite Alps, South Bulgaria, and Armenia. Each of them contains about 100 species of bivalves. The number of gastropod species varies more considerably: the assemblages from Alps (Boussac, 1911b) and Bulgaria (Karagyuleva, 1964) each contains about 100 species. About 200 species are described from Italy (Oppenheim, 1900–1901) and only 37 from Armenia (Aslanyan, 1970), although the latter assemblage contained many forms that could only be identified to generic and familial level. In their taxonomic composition the assemblages are similar to one another, and differ from typical northern assemblages. Northern Mediterranean assemblages contain representatives of tropical genera and species, *Pinna* s.s., *Lima* s.s., *Vasconella, Trachycardium, Corbula (Bicorbula), Glycymeris (Tucetilla) jacquoti, Macrosolen hollawaysii, Trapezium alpinum*, etc., the most thermophilic gastropod groups the family Strombidae s.s. (genera *Strombus* and *Canarium*), genus *Velatus* (Neritidae), etc. The assemblage lacked, or had very few representatives of, over 20 genera and subgenera characteristic of northern assemblages. It is noteworthy that the Bulgarian assemblage, although similar to the others in its generic and species composition, judging from Preston's coefficients, differs from the northern assemblages as much as the others, but contains some species typical of the northern assemblages: *Charonia multigrana, Genota pseudocolon*, etc.

Alpine–Carpathian Basin. The most complete data are on the fauna of the southern shelf. The bivalve assemblages occurring in the territory of Hungary (70 species of 46 genera and subgenera [Szöts, 1956]) and Romania (Transylvania [Meszaros, 1957]) contained *Spondylus*, large *Crassatella* and other warm-water groups including characteristic Mediterranean species *Glycymeris jacquuoti, Spondylus cisalpinus*, and *Vulsella dubia*. At the same time the assemblages contained many geographically widespread species. Similar conclusions may be made based on the relatively poor fauna of Austria and more diverse (51 species [Schlosser, 1925]) assemblage of bivalve mollusks from the Bavarian Alps.

The gastropod assemblages of these regions each contain 45–65 positively identified species. Assemblages of Hungary, Romania, and Austria contain strombids, Romania and Bavaria *Velates*. In their species composition these assemblages were close to the Mediterranean and differed from the northern ones; compared to the Bulgarian assemblage they contained fewer species characteristic of the northern assemblages.

The Austrian assemblage differs from other southern assemblages slightly more than they differ between themselves. However by its Preston's coefficient it is more similar to the Hungarian than to any of the northern assemblages. All four assemblages are apparently secondarily impoverished, some taxa were not preserved. Perhaps the absence of strombids in Bavaria and difference of the Austrian assemblage may have resulted from that.

The data on mollusks from the northern shelf of the Outer Carpathians are too scanty to positively determine their biogeography. The most representative assemblage, from the village of Konyushi in the vicinity of Pšemysl (Poland) contained both Tethyan and North European species. According to a recent revision by Krach (1985) the assemblage was dominated by southern species, and the greatest similarity was to Italian assemblage. However, the true warm-water groups are absent, and in its generic and familial composition the assemblage is similar to the North European ones.

Eastern Atlantic. The Atlantic assemblages differ greatly from the typically southern and northern assemblages and from each other.

Sixteen bivalve species are described from the Priabonian of the Aquitainian Basin (France [Cossmann, 1921]), of these seven are known only from Aquitaine, seven are in common with the Mediterranean, and two are widespread. Of 61 gastropod species (Boussac, 1911a), 18 are in common with Northern Italy, 10 with Nummulite Alps, and only two species are recorded in the northern assemblages and were absent in the Mediterranean. Only two species were in common with the Headon Beds of England, and no species were shared with the Ludian assemblage of the Paris basin. Some assemblages described below, and slightly similar to the Ludian and Headonian assemblages, show similar features to the more ancient Bartonian of the Paris Basin and England, but the Priabonian assemblage from Aquitaine is not similar to these. The Aquitainian assemblages contained no strombids in the entire Eocene, for which reason Amitrov (1993) assigned the Aquitainian Basin to the North European Zoogeographic Region. Cossmann (1921) was the first to note the similarity of the Eocene assemblages of Aquitaine to the North European ones. However, the species composition of the Priabonian assemblage does not support this: both in the absolute number of common species and in coefficients it is more similar to the Mediterranean.

The assemblages of the Headon Beds of England (Newton, 1891) and especially from the Ludian of the Paris Basin (Furon and Soyer, 1947) showed an impoverished composition of marine mollusks, predominance of euryhaline and eurythermal groups. This indicates lower and unstable salinity in the basins, and lower temperatures than in the Bartonian.

The Headonian bivalve assemblage contains 100 species of 52 genera and subgenera. The species typical of the Mediterranean assemblages are absent, and only a few widespread species are in common with these assemblages. About a half of the species are known from the Bartonian of England, although the Headonian assemblage lacks representatives of the warmest water Bartonian genera. A similar pattern is observed among gastropods: of 122 Headonian species, 47 are present in the Bartonian, and only 25 species are in common with other Priabonian assemblages. The similarity with the northern assemblages is slightly greater than with the southern. Genera and families that were characteristic in the Eocene of the southern assemblage were absent in England.

The Ludian bivalve assemblage of the Paris Basin contains only 44 species of 33 genera. In its generic composition and the number of thermophilic taxa the assemblage is similar to that of England, although there are only a few species in common. The Ludian gastropod assemblage contains 46 species, of which 27 occur in the Middle Eocene of the Paris Basin and only nine in other Priabonian assemblages, including four species in the Headonian assemblage. The assemblage contains no distinctively thermophilic species.

North Sea Basin. This basin was certainly colder than the Mediterranean, however the diversity and taxonomic composition of the molluscan assemblages suggest that it may be only tentatively regarded as cold-water. The Latdorfian assemblage of northern Germany contains 175 bivalve and 538 gastropod species (Koenen, 1889–1894). Among bivalves, the presence of numerous arcids, the genera *Spondylus, Crassatella, Discors*, indicates that the basin was close to the subtropical type. Among gastropods, strombids, *Velates*, hypponicids, *Diastoma*, and others of the most warm-water taxa are absent but there are terebellids, cypreids

and melongenids, taxa that indicate rather high temperatures in present-day seas.

The assemblages of the more western parts of the basin (Tongrian of the Netherlands [Albrecht and Valk, 1943], Lower Tongrian–Grimmertingen of Belgium) were more impoverished than the North German: the Belgian assemblage contains 96 bivalve species and 142 gastropod species (Glibert and Heinzelin, 1954) and the Netherland assemblage even fewer. The degree of similarity with the Latdorfian associations is quite high. In their species composition (especially regarding gastropods) the Tongrian assemblage is almost entirely embraced by the Latdorfian assemblage. There is a single family in The Netherlands that in unknown in northern Germany–euryhaline potamiids indicating that in the Netherlandish part of the basin the influx of the fresh water was increased. The relative impoverishment of these two assemblages is apparently partly due to taphonomic reasons (fossil preservation in the Tongrian is poorer than in the Latdorfian). However, the analysis of the generic and familial composition of bivalves and gastropods show that the most thermophilic groups are absent.

Two Priabonian assemblages are known from the more eastern part of the North Sea Basin (from the Zamland Peninsula–Kaliningrad Region–Noetling, 1888 and from the village of Siemien near Lublin–northeastern Poland–Woźny, 1968, 1977). Both these assemblages are more impoverished and not representative, but it is noteworthy that both these assemblages, although geographically close, are strikingly different taxonomically. The assemblage of the Prussian Formation of the Zamland Peninsula is apparently completely composed of Latdorfian species. In the assemblage from Poland of 19 bivalve species only seven are in common with the Latdorfian assemblage, and 13 are in common with the Mandrikovka Beds of Ukraine; of six gastropod species only one (widespread) is recorded in the Latdorfian and all six were recorded from the Mandrikovka Beds.

Greater Caucasus–Kopet Dagh (Beloglinian) Basin. Vast areas in the southern Russia and adjacent countries were occupied by a single basin, although the molluscan assemblages from different parts of the basin were quite different.

The shallow-water shelf of the Ukrainian Shield was inhabited by a rich Mandrikovka assemblage (Klyushnikov, 1958; Popov, 1994; Amitrov, 1999). It contained at least 130 species of 81 genera and subgenera of bivalves including tropical and subtropical genera *Spondylus, Fimbria, Fragum*, etc. Although the generic composition of bivalve mollusks is close to that of the Mediterranean assemblages, there are no characteristic Tethyan species in this fauna. Gastropods in the Mandrikovka assemblage are represented by at least 435 species (the majority undescribed) from 70 families (only 62 families are recorded in the Latdorfian). The assemblage contains major thermophilic groups

that are absent in the North Sea assemblages: *Neritopsis, Diastoma*, Hipponicidae, genus *Cepacea* from the naticids, large ampullinids and even strombids (only *Velates* is absent). Some of these and other groups are represented by the species that are in common with the Mediterranean and Alpine–Carpathian Priabonian assemblages, and also with the Paris Basin, but with the more ancient Bartonian assemblage and not with the coeval impoverished eurybiontic Ludian one. Nevertheless, the similarity of the species composition of the Mandrikovka gastropod assemblage with one of the North Sea Basin is high, whereas the degree of similarity with southern assemblages is slightly higher than of the assemblages of the North Sea Basin.

Among other regions of the Euxino–Caspian basin, the Adzharo–Trialeti zone of the southern shelf (Georgia–Akhaltsikhe) was warm-water judging from the molluscan fauna. The Lower Priabonian Marda and Ivlita beds contain 76 bivalve species. Judging from the presence of *Glycymeris (Tucetilla) jacquoti, Spondylus cisalpinus, Trapezium alpinum*, etc., this fauna belonged to the north Mediterranean type. At the same time despite the similarity of the facies (coastal sandstones), the similarity with the Rindian fauna of Armenia is low (15 species in common, which is 13% of the total number of species). The Georgian fauna lacked the most thermophilic genera recorded from Armenia, the proportion of the widespread species was higher (37%).

As to gastropods, the Early Priabonian (Marda Beds) contained such taxa as *Diastoma* and *Velates*, although strombids were absent. The assemblage contains at least five species characteristic mainly of the northern assemblages (Amitrov, 1999). However, the Akhaltsikhe gastropod assemblage (90 species [Isaeva, 1933]), in contrast to the Mandrikovka assemblage, is much closer to the southern that to the northern type. It is particularly similar to the assemblages of Romania and Armenia. However, all species common between Georgia and Armenia are present in other southern assemblages, hence gastropods do not indicate direct connections between these two basins. A small gastropod assemblage from Racha–Lechkhumi is close to the Akhaltsikhe assemblage in its species composition, although *Diastoma* and *Velates* were absent. In the Late Priabonian (Borbalo Beds) the Akhaltsikhe part of the basin was inhabited by a considerably poorer assemblage that lacked thermophilic groups.

The large areas (the Crimea, Northern Caucasus, Transcaucasia, Mangyshlak, Fore-Kopet Dagh Trough) in the Priabonian were occupied by pelagic carbonate (Beloglinian) sedimentation that was not favorable for mollusks. Further to the east, the terrigenous grounds were inhabited by the molluscan assemblages of the "Chegan type." The assemblage from the northern part of the Turan Sea (from the Chegan Formation of the North Ustyurt, Aral Regions and Turgaj Trough) was the richest. The assemblages of the basin of Western

Siberia (Tavda Formation), the southeastern regions of Kazakhstan, Kopet Dagh (Torymbeur Formation excluding it upper (Oligocene) part), Fergana–Tajik Depression (Rishtan–Sumsarian Beds) (for review see Amitrov, 1993, 1999; Popov et al., 1993; Popov, 1994) were more or less impoverished but contained mostly Chegan species.

The Chegan assemblage is quite similar to the North Sea ones, although considerably more impoverished. For instance, gastropods (Amitrov, 1993) are represented by only 160 species (538 in the Latdorfian) of 33 families (62 in the Latdorfian). Certainly, this may be partly explained by taphonomy, but partly by less favorable environment, including lower temperature: compared to the Latdorfian, the Chegan assemblage lacks thermophilic groups, the same as that from the Tongrian of Belgium and from The Netherlands. The Transcaspian assemblage contains fewer arcids, lucinids, venerids, and crassatellids. More southern assemblages (Kopet Dagh, Fergana–Tajik Depression) differed from the Kazakhstan assemblages only in the presence of several more warm-water bivalve genera; no such differences were observed among gastropods.

At the species level, approximately the half of the bivalve assemblage and 40% of gastropods were Transcaspian endemics, although this assemblages contained quite a few species closely related to those from the Latdorfian. There are very few peculiar species with uncertain origin (e.g., major species of Transcaspian turritellids). Preston's and Zhakkar's coefficients support a large similarity of the Chegan assemblage with the Latdorfian and also with the assemblages of the Tongrian of Belgium and The Netherlands (Amitrov, 1993; 1999; Popov, 1994). The similarity with the Mandrikovka assemblage is high but still lower than with the above assemblages. It is noteworthy that in addition to 53 gastropod species that are in common with the Mandrikovka, Latdorfian and Chegan assemblages, 38 species are present only in the Latdorfian and Chegan, 81 in the Latdorfian and Mandrikovka and only three rare species are present in the Mandrikovka and Chegan assemblages! Besides, the Transcaspian assemblage contains several gastropod species that are absent in Ukraine and northern Germany but are in common with the assemblages from England (with the Bartonian rather than the Headonian assemblage). At the same time the Transcaspian assemblage does not contain at least one certainly southern species. Despite the geographical similarity of the Central Iranian Basin near the Kopet Dagh there is no evidence of the connections of these two basins.

Scleractinian Corals

Climate, depth, and sedimentation were the most important factors in distribution of corals. Temperature determined the latitude zonation in the distribution of coral assemblages, especially reef-building corals.

North Mediterranean. Corals were widespread in the photic zone of the shallow shelf along the north coast of the Ancient Mediterranean. They are known from northern Spain (near Barcelona), southern France, northern Italy, southern Bulgaria, etc. In these regions a warm marine basin with normal salinity contained reefs with diverse scleractinians. In total, about 80 scleractinian genera (mainly of the suborders Archaeocoeniina, Faviina, Fungiina, Meandriina, and Dendrophylliina) were reef-builders in this basin.

In the more northern subtropical basin of Western and Central Europe coral facies were absent despite the presence of the potential reef-building coral genera that formed "coral meadows" in the shallow parts of the sublittoral. Along with the colonial corals these areas were inhabited by solitary corals, mainly from the suborders Caryophylliina and Dendrophylliina.

Beloglinian Basin. A large coral assemblage similar to that from Northern Europe was described by Kuzmicheva (1987) from southern Ukraine (Dnepropetrovsk Region, Mandrikovka Beds). This assemblage, unique in its taxonomic diversity and preservation, includes 24 species belonging to 22 genera, nine families, and five suborders: Archaeocoeniina, Faviina, Fungiina, Caryophylliina, and Dendrophylliina. This assemblage contains 16 colonial and six solitary genera. Some colonial genera described from the Mandrikovka Beds were reef-builders in the more southern basins of Europe (Spain [Barcelona], Bosnia). These are *Astraeopora, Montipora, Siderofungia, Cyathoseris, Lithophyllon*. In the basin where the Mandrikovka Beds were formed, these representatives, together with other taxa were formed "coral meadows." The colonies (massive and branches) were usually small-sized. Apparently, temperature and other factors (substrate, influx of terrigenous material) restricted their distribution.

An assemblage close to that from the Mandrikovka Beds was recorded from northern Turkey (Kartun-dere Section, Samsun Mountain; collection of A.P. Chepalyga). These are *Astraeopora spharoidalis, Cyathoseris infundibuliformis, Trochoseris heliathoides*, and *Throchosmilia corniculum.*

Complex Benthos-based Zoogeographic Zonation

Summarizing the above analysis, the geographic distribution of the majority of benthic groups in the Priabonian, had the similar pattern, although had some specific features. This allows a scheme of a complex zoogeographic zonation of the Western Eurasian basins based on all studied benthic faunal groups (Fig. 7), except benthic foraminifers that showed a considerably different pattern (see above).

The most considerable biogeographic differences between faunas in the territory under consideration that were revealed in all benthic groups were those between the faunas of the Latdorfian type and Ancient Mediterranean faunas. The differences between these faunas
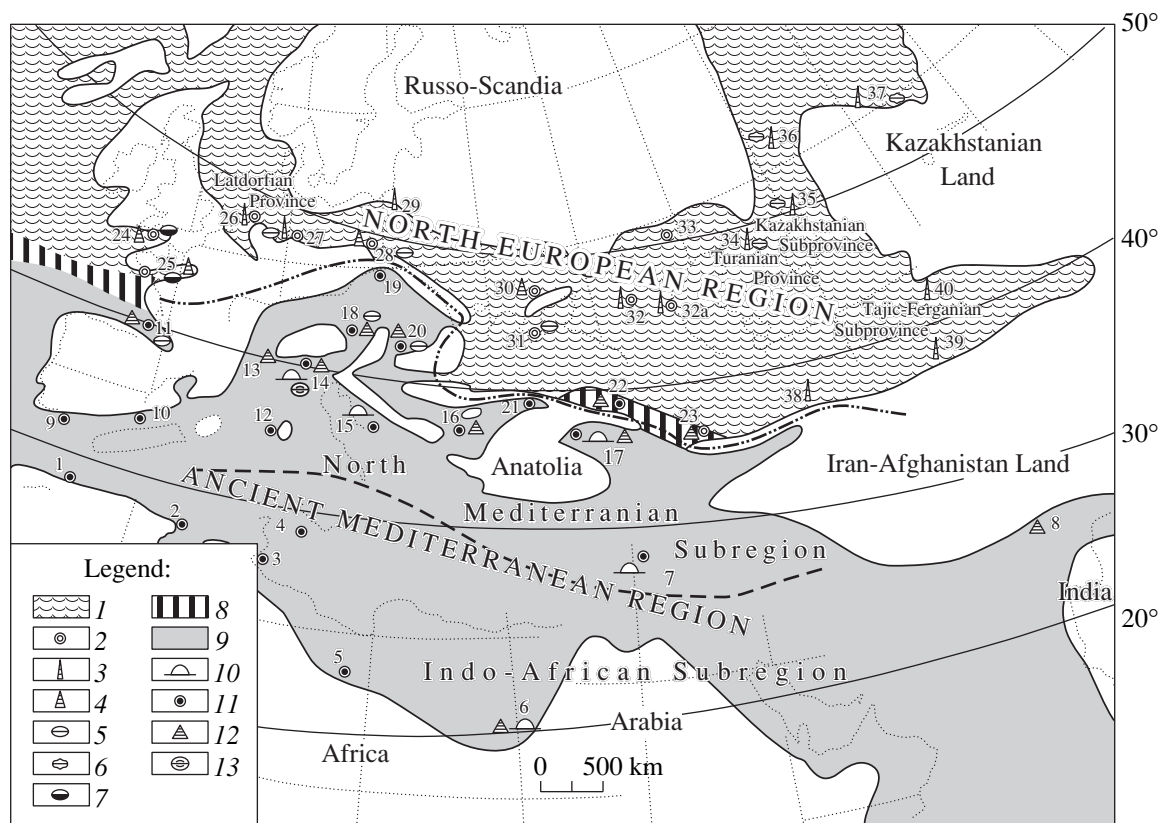
Fig. 7. Scheme of complex zoogeographic zonation of the Priabonian shelf based on benthos. Designations: (*1*) **North European Region** with moderately thermophilic benthic fauna of the Latdorfian type: (*2*) impoverished nummulite assemblages of the northern type, consisting of a small number of species of the genus *Nummulites*; (*3*) rich molluskan assemblages lacking the most thermophilic taxa; (*4*) intermediate molluskan assemblages with not numerous thermophilic (tropical) taxa, but lacking the species characteristic of the Tethys; (*5–7*) ostracode assemblages: (*5*) assemblages of uniform taxonomic composition, with the prevalence of relatively cold-resistant ancient transitional bathyal smooth-walled groups; (*6*) thermophilic assemblage of diverse taxonomic composition, with the prevalence of sculptured groups; and (*7*) assemblages including a large proportion of euryhaline groups; (*8*) transitional zones; (*9*) **Ancient Mediterranean Region** with tropical benthic fauna, including various assemblages of colonial corals and other taxa inhabiting only the warmest basins: (*10*) reef-building corals; (*11*) rich nummulite assemblages, including up to ten genera; (*12*) molluskan assemblages of the southern type, including tropical taxa; (*13*) assemblages of diverse taxonomic composition, including such thermophilic genera as *Tricbelina, Callistocythere*, and sculptured forms. The main localities of the benthic fauna from the Priabonian: (1) Morocco, (2) Algeria, (3) Tunis, (4) Sicily, (5) Libya, (6) Egypt, (7) Syria, (8) Western Pakistan, (9) southern Spain, (10) southeastern Spain, (11) Aquitaine, (12) Central Italy, (13) coastal (Nummulite) Alps, (14) northern Italy, (15) eastern Adriatic Sea, (16) southern Bulgaria, (17) Armenia, (18) Hungary, (19) Ukrainian and Polish Carpathians, (20) Transylvania, (21) northwestern Turkey, (22) Georgia, (23) southern Azerbaijan (Nakhichevan), (24) southern England, (25) central France, (26) Belgium, (27) northern Germany, (28) Poland, (29) Kaliningrad Region, (30) Dnieper–Donets Depression, (31) Crimea, (32) Northern Caucasus (Kuban River), (32a) Northeastern Caucasus (Dagestan), (33) Middle Volga Region, (34) northern part of the Ustyurt Plateau, (35) northern part of the Aral Region, (36) Turgaj, (37) southern part of Western Siberia, (38) Kopet Dagh, (39) Tajikistan, and (40) Fergana.

were primarily determined by climatic factors that existed even before, at least since the Mesozoic. The Mediterranean–Mesopotamian Priabonian Basin contains a fauna that was similar to tropical faunas, with numerous reef-building corals, diverse nummulitids and discocyclids, large ornamented foraminifers and mollusks including families and genera that presently occur only in quite warm basins. The Priabonian faunas of the North Peri-Tethys were also quite warm-water, although they differed from the Mediterranean faunas in the impoverished benthic assemblages. The same genera occurring in the warm-water areas of the shelf did not produce large reef buildups and formed "coral

meadows." Nummulitids were represented only by a few *Nummulites* species. The taxonomic composition of all benthic groups was distinctly different at the level of genera, and sometimes even families, and included only a few cosmopolitan species.

In the Priabonian the boundary between these two major biogeographic provinces was quite distinct and can be traced identically in most fossil groups as the northern borders of the Priabonian "nummulitid seas." In Western Europe this border separated the Anglo–Paris and Aquitainian basins. The Fore-Alpian and Carpathian basins are more similar in their faunas to the Ancient Mediterranean. The boundary can be traced

along the Balkans, Pontids, and Elburs. The Atlantic coast of middle France (Brittany) and the Fore-Sudetian Basin of Poland may be regarded as a relatively narrow intermediate zone. At the beginning of the Priabonian this border in the central part of the Beloglinian Basin ran along the deep-water zone of the Greater Caucasus. The fauna of the Transcaucasian Shelf remained Tethyan. However, the molluscan fauna and nummulitids of the second half of the Priabonian in the same region were more northern. Apparently, at the end of the Priabonian the entire territory of the future Paratethys was part of the North European Region.

Considering the high rank of taxonomic differences and stability of this border in time we propose to consider it a border between the regions that are usually named **North European** and Mediterranean (often as provinces). However, we believe that the name should indicate a faunal type, rather than a region. Therefore, the latter name is not suitable since it is naturally associated with the recent Mediterranean fauna that was formed later, in the Chattian. Hence, we use **Ancient Mediterranean Region** to name it.

The faunal assemblages of the North European Region with the Latdorfian type of faunas were distinctly differentiated and their composition had been changing considerably throughout the Priabonian. The most striking differences are observed between the shelf benthic assemblages of Transcaspia, the territory that Salibaev (1983) suggested to designate as the **Turanian Province**. In contrast to his views, we subdivide this regions into two, rather than three subprovinces: northern, **Kazakhstanian** that contains the Chegan faunas of Ustyurt, Cisaralian and Turgaj and the southern, **Tajik–Fergana** that also included Kopet Dagh.

Further to the north occurred the **Latdorfian Province** that contained the faunas of the North Sea basins. So far it remains uncertain whether or not the differences of the fauna of the Ukrainian shallow-water basin were really geographical, or the distinct character of the Mandrikovka assemblage, the presence of some southern taxa, including colonial corals were in fact geochronological, typical of the first half of the Priabonian only.

The Anglo–Paris Basin also contained a very distinct fauna. However these differences were mostly ecological, hence their zoogeographic rank is unclear.

The second large zoogeographic boundary in the Priabonian occurred in the deep-water area of the Mediterranean–Mesopotamian Basin and separated the faunas of its northern and southern shelves. The differences of these faunas are not traced in all groups. They are very distinct in the molluscan faunas, especially among species, and in ostracodes. Based on echinoids the separation of the African shelf is dated the Middle Eocene (Strougo, 1977), earlier North Africa and Arabia were parts of the "Mediterranean Province." In the Priabonian the generic composition and presence of species in common made this fauna similar to that of

North India and East Africa. All this supports Douvillé's (1920, see Strougo, 1977) proposal to separate the Indo–African zoogeographic subdivision of a high rank. However, the data on nummulitids and other benthic foraminifers show the similarity in the taxonomic composition of the Priabonian assemblages of Southern Europe, North and East Africa, Syria, and India (Strougo, 1977; Cabdulgadir and Carush, 1982). Hence, based on the entire faunal assemblage we consider this boundary a boundary of the second order, i.e., between subregions, and recognize the **Indo–African Subregion** of the Ancient Mediterranean Region in addition to the **North Mediterranean Subregion**. The data on the geographical distribution of faunas in the former subregion is very scanty. The assemblages of the latter subregion known from Southern and Central Europe and Transcaucasia are very similar, hence we do not propose a further subdivision.

Marine Ichthyofauna

The bulk of data on marine fish of the Eocene of Northern Eurasia refers to the Middle Eocene or earlier. A number of faunas previously considered Late Eocene (for example, the assemblage from the Kumskian Horizon of the Caucasus) are now assigned to the Middle Eocene. Marine fish undoubtedly assigned to the Late Eocene are poorly studied. A comparatively small number of impoverished local communities of this age are known; they can only provide a general outline of the nature of Late Eocene ichthyofauna of the Paleo-Paratethys, and its zoogeographic relationships. The preceding Middle Eocene assemblages of the Eastern Paleo-Paratethys in Transcaucasia (Dabakhanka River near Tbilisi, Georgia, the Dabakhan Formation) and the Northern Caucasus (Pshekha and Belaya rivers, Kumskian Horizon), were represented by a set of genera that provided a basis for the development of the majority of terminal Eocene and Early Oligocene communities of this region.

In the Dabakhan ichthyofauna, the dominant position was occupied by deepwater fishes, such as the generalized new genus recently proposed for *?Vincigueria distincta*, considered to be the sister group of the remaining Photichthyidae (Prokofiev, in press), *Polyipnoides levis* (Sternoptychidae), and *Astronesthes praevius* (Astronesthidae, Stomiiformes). The bathypelagic component of the community included *Proargentina nebulosa* (Argentinidae, Salmoniformes), *Eomyctophum gracilis* (Myctophidae, Myctophiformes), *Bregmaceros filamentosus?* (Bregmacerotidae, Gadiformes), and *Palimphies pinnatus* (Euzaphlegidae?, Perciformes); the epipelagic forms comprised *Scombrosarda devia* (Scombridae) and *Palaeorhynchus senectus* (Palaeorhynchidae) (Danilchenko, 1962; Danilchenko *et al.*, 1980).

The ichthyofauna from the Kumskian Horizon (Pshekha and Belaya rivers, Ciscaucasia) was more

diverse. Apart from the genera in common with the Dabakhan ichthyofauna, i.e., *Bregmaceros, Palimphyes, Lepidopus, Scombrosarda*, and *Palaeorhynchus*, it contained a new genus of the order Stomiiformes (Prokofiev and Bannikov, in press); epipelagic *Lyrolepis caucasica* (Elopidae, Elopiformes), *?Sardinella* sp. (Clupeidae, Clupeiformes), *Palaeorhynchus* sp. nov. (Palaeorhynchidae, Perciformes), *Eomola bimaxillaria* (Molidae, Tetradontiformes); and a coastal–marine assemblage, including the syngnathiforms *Paraeoliscus* sp. nov. (Paraeoliscidae), Syngnatidae gen. et sp. nov.?, and various acanthopterygians, such as ?Epigonidae gen. et sp. indet., *Pristigenis* sp. (Priacanthidae), gen. et sp. nov. (Siganidae), and *Caprovesposus* cf. *parvus* (Acanthuridae) (Bannikov, 1993). Both faunas give evidence of a warm-water (tropical–subtropical) basin of considerable depth, with a densely populated shelf zone. Almost the entire set of genera of the Middle Eocene ichthyofauna of Eastern Paleo-Paratethys persisted into the Early Oligocene, whereas the Late Eocene communities retained only a small part of the Middle Eocene epipelagic association.

Beloglinskii Basin. The Late Eocene ichthyofauna of the Beloglinskii Basin is represented by an impoverished assemblage of teleostean fishes that remains almost uniform throughout the entire southern part of the basin. The associations from the Beloglinian Horizon of Abkhazia, Southern Georgia, and Ciscaucasia included *Lyrolepis caucasica* (Elopidae), *Thunnus abchasicus* (Thunnidae), and *Bregmaceros filamentosus* (Bregmacerotidae), i.e., a set of taxa inherited from the Middle Eocene autochthonous ichthyofauna. All of them passed into the Early Oligocene, forming a transitional Eocene association in the basal Early Khadumian ichthyofauna. Among the above forms, the first two are typical pelagic inhabitants, whereas *Bregmaceros filamentous* was a bathypelagic form that could have dwelled at great depth. This species occurred in a wide stratigraphic range from the Middle Eocene (the Dabakhan Formation of Georgia and the Kumskian Horizon of Ciscaucasia) to the Chokrak level (Danilchenko *et al.*, 1980). This taxon seems to actually comprise a complex of closely related species, and requires thorough revision. In a shallow southern part of the basin (Georgia, Akhaltsikhe Depression), the assemblage was supplemented by unsatisfactorily identified members of the Clupeidae. As mentioned above, all the components of the Late Eocene assemblage have their roots in the Middle Eocene fauna of the Kumskian Horizon. However, compared to the latter, the Beloglinian ichthyofauna was much less diverse.

In the Late Eocene (Priabonian), the shark fauna of the shallow basins of the Turanian Platform was impoverished and comprised the assemblages formed by the genera with a low species diversity (*Jaeckelotodus, Borealotodus*, and *Striatolamia*) inherited from the Bartonian fauna. In addition, the Priabonian fauna developed a number of widespread forms rich in species, such as *Synodontaspis, Araloselachus, Clerolamna, Lamiostoma*, and *"Odontaspis"* ex gr. *dubia*. The Late Eocene shark fauna shows climatic zonation of the Eastern Peri-Tethys by the occurrence of the assemblages of the southern type in the southwest of the Turanian Plate and mixed southern–boreal assemblages in the northeast of the plate (Zhelezko and Kozlov, 1999). The genera *Jaeckelotodus, Synodontaspis, Striatolamia, Otodus, Lamiostoma, Macrorhizodus*, and *Isurolamna* prevailed in the southern basins; in the transitional basins, there were diverse and numerous *Borealotodus, Araloselachus, Clerolamna, Tobolamna, Striatolamia*, and *Jaeckelotodus*. The dominants included local genera as well as those also distributed in the Priabonian of Ukraine (Mandrikovskie beds) and in the Lower Tongrian of Belgium (Glikman, 1964; Lerische, 1910, 1951).

Terrestrial Biogeography

Phytogeography

North America and Arabia. Areas that occurred further to the south of the Peri-Tethyan marine basins are occupied by North African flora from the Paleotropical regions (Fig. 8). In the Middle Eocene the majority of North Africa was covered by moist tropical forests. By the Late Eocene, a distinct seasonal climate belt had formed in northern areas of the North African Region, while the moist tropical forests were replaced by light forests of the savannah type with the wide range of legumes typical of the African flora, as well as representatives of Annonaceae, Combretaceae, Ebenaceae, Eophorbiaceae, Fabaceae, and Sterculiaceae. Forest vegetation of this type extended from Senegal and Mauritania to the Great Horn of Africa. These forests were replaced by laurel forests further to the north, closer to the coastline. Nevertheless, legumes, palms, some other trees adapted to the hot seasonal climate were still very diverse. These laurel forests entered into a so-called ecotone zone between the African and the Tethyan regions, where plants of tropical affinities were still dominant. The present-day forests of the Canary Islands typified by *Laurus canariensis, Dracaena, Sideroxylon, Apollonias*, etc., are a relict of the ancient North African laurel forests that existed up to the second half of the Paleogene.

On the Abyssinian Plateau, moist forests that were climatically more temperate than those in other areas of Africa, occurring further north of the equator, survived to the end of the Paleogene.

Southern Europe. Some islands of intrazonal tropical vegetation extended along the coast of the Ancient Mediterranean Basin and penetrated further north into the Holarctic subtropical regions. Floras of this coast are known from the southern areas of the Iberian Peninsula, Southern France, Italy, Southern Greece and further east, in Transcaucasia. These forests are broadleaved and do not have xeromorphic characters. There
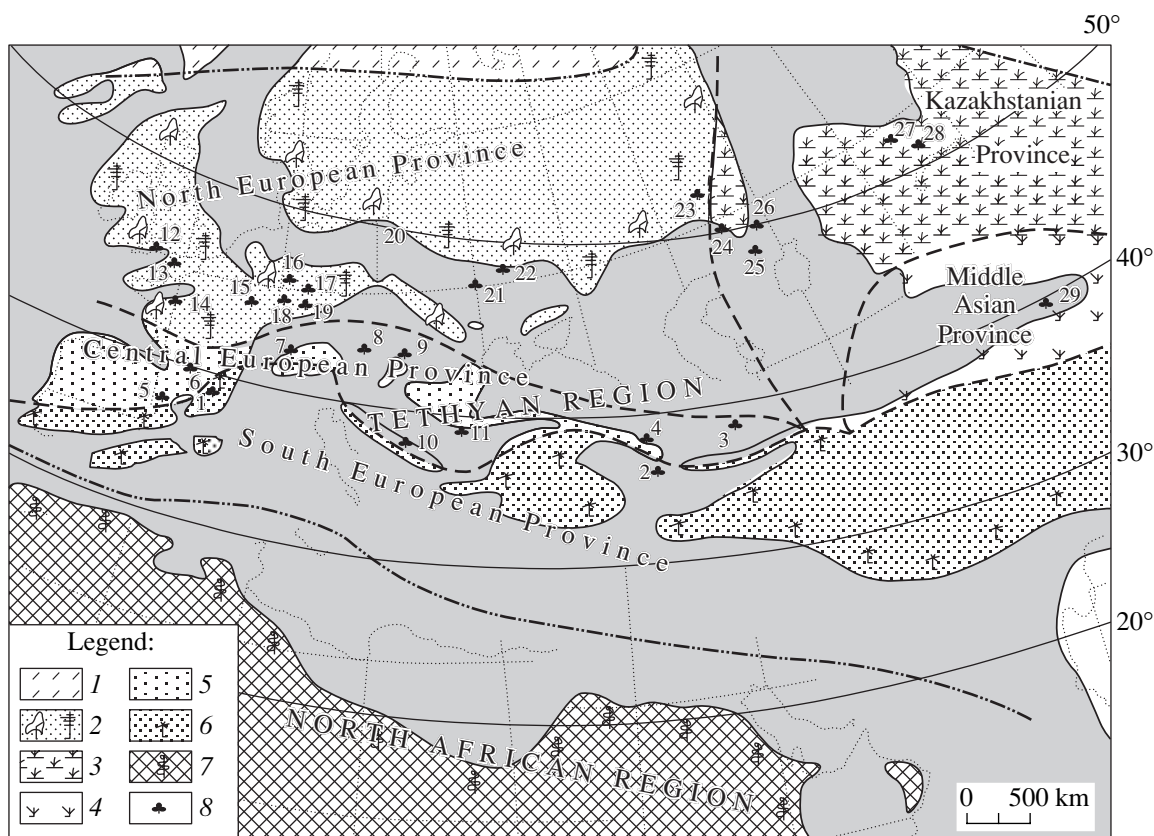
Fig. 8. Phytogeographic zonation of Western Eurasia–Northern Africa in the Priabonian. Designations: (*1*) Boreal Region: summergreen taxodiacean–broad-leaved mesophilic forests; (*2–6*) Tethyan Region: (*2*) evergreen and summergreen coniferous–broad-leaved, mainly oak–laurel forests; (*3*) oak–laurel hard-leaved forests, bushes formed by anacardiaceans, ericaceans, legumes, and myricaceans; in the coastal zone, fruticose associations formed by ericaceans, legumes, and halophytes; (*4*) bush–grassy formations, including halophytes (*Ephedra* and chenopodiaceans); (*5*) hard-leaved xerophilous forests, including cupressaceans, lauraceans, fagaceans, and legumes; (*6*) evergreen mesophilic subtropical and tropical forests, including lauraceans, fagaceans, and magnoliaceans; at the marine coasts, coniferous–palmaceous forests with luxuriant fern underwood, occasionally, with mangroves; (*7*) North African Region: tropical forests formed by lauraceans, legumes, and fagaceans; deep into the continent, they are replaced by savanna; and (*8*) the main floral localities. The numbers show the Upper Eocene floral localities considered in the text: (1) Selas, (2) Darry-Dag, (3) Talysh, (4) Akhaltsikhe, (5) Ebro, (6) Briv, (7) Hering, (8) Brezno, (9) Girbou, (10) Ovtse Polie, (11) Hvoina, (12) Hampshire, (13) Isle of Wight, (14) Sarche, (15) Mulhaus, (16) Zeitz, (17) Mosel, (18) Stare Sedlo, (19) Kučlin, (20) Svetlogorsk, (21) Kochetyn, (22) Tim, (23) Or River, (24) Baky, (25) Shanda Trough, (26) Romanovsk, (27) Zhamantuz, (28) Takyrsor, and (29) Hissar.

are more tropical elements in their composition compared to floras that occur further to the north, therefore these forests may be considered climatically as transitional between the subtropical to tropical. The **Selas** Flora in Languedoc on the left bank of the Rhone River is the most representative in the western areas of this province (names of the main flora occurrences shown in Fig. 8 are underlined). Palms, conifers *Tetraclinis* and *Doliostrobus*, as well as *Dryophyllum* and *Eotrigonobalanus*, Pandanales, tropical ferns, and Lauraceae are included in this flora. In Transcaucasia, the **Darry-Dag** Flora (Akhmetiev and Zaporozhets, 1989) is of this type. Palms *Sabal* and *Trachycarpus*, pines, ferns *Blechnum* and *Acrostichum*, *Daphnogene*, Myrtaceae, and Ericaceae. Traces of mangrove vegetation and of related coastal assemblages with a participation of palms *Sabal* and *Trachycarpus*, Myrtaceae, evergreen

Fagaceae, Lauraceae, and ferns *Blechnum* and *Acrostichum* are found in the **Talysh**, on the south-facing slopes of the Lesser Caucasus, in the northern surrounds of the Erevan–Ordubad Trough, and in the **Akhaltsikhe Depression**. The pollen assemblage includes Taxodiaceae, *Nyssa*, and Fagaceae. The floristic composition indicates the vegetation of a coastal plain occupied by pine–palm forests with ferns in the understorey and shrubs composed of Leguminosae, Ericaceae, and Lauraceae. Modern vegetative cover forests of this type occur in the Florida Peninsula and in coastal areas of the Gulf of Mexico, in the vicinity of the mouth of the Mississippi River. This region is characterized by heavy precipitation and by a mean annual temperature around 25°C.

Central Europe. Floras of the northern coast of the archipelago that separated the Mediterranean Region

from the Paleo-Paratethys differed markedly from those described above. A belt of subtropical, evergreen and semi-evergreen, small-leaved, subxerophilous, laurel-leaved forests existed here. This belt formed under a drier seasonal climate. The floristic composition of these forests was comparatively stable and included a group of representative conifers, *Doliostrobus, Athrotaxus, Tetraclinis, Glyptostrobus, Chamaecyparis*, and *Pinus* (with five leaves in a cluster). Among the flowering plants were Rhamnaceae (*Berchemia* and *Zizyphus*), Sapotaceae (*Bumelia*), Rutaceae (*Zanthoxylum*), Myrsinaceae and Theaceae, as well as sclerophyllous Fagaceae, small-leaved Leguminosae and Myricaceae and the palms *Sabal* and *Trachycarpus*. The zone of floras of this type extended from the Pyrenees to Transcaucasia. This zone included floras from the Northern Alps (**Höring**), inner areas of the Carpathians, including the raised region of the Tatra (Hruby Regel and Olshesky Potok near Zakopane and Poronino), coastal zones in Slovakia, near Banska Bystrica (Brezno) and Košice (Radatice), the Transylvanian Depression, near Cluj (**Girbou**, Legia, Suseg), Vardar Volcanic Zone, near Skopje (**Ovce Polie**, Pčeinja), the Rhodope Mountains (Devin, **Hvoina**, surroundings of Smolian), and the Burgas Depression (Rudnic). The representative Early Paleogene *Platanus, Dewalquea, Persea, Populus kanei*, etc., as well as the most thermophilic ferns, some of them from the tropical alliance, such as *Acrostichum, Blechnum, Cyathea, Lygodium*, etc., were still in the composition of these refugial floras. Deciduous taxa (*Acer, Carya, Fraxinus, Juglans, Populus, Zelkova*, etc.) were occasionally present in the paleophytocenoses. The percentage of taxa with entire leaves ranged from 55 to 65%. The Priabonian age of the majority of floras is precisely determined. Thus, the floras from the surroundings of Cluj (Gibrou, etc.) were found in nodules enclosed in calcareous marls with *Cryphaea* that is assigned to the NP18–19 nannoplankton zones.

The semiarid climatic zone is also observed from Tirol further to the west, up to the central areas of the Iberian Peninsula in the Atlantic regions. This can be judged from the distribution of xerophilous sclerophyllous floras in the basin of the Upper Loire (**Briv**, Le Puy) and in the basin of the **Ebro**, between Barcelona and Saragossa. In the last-named region all the plants of the humid subtropics disappeared toward the Late Eocene. The advance of the arid seasonal climate is supported here by the dominance of *Ephedra*, Chenopodiaceae, *Combretum, Lunum*, Plumbaginaceae, Bignoniaceae (*Spathoidea* and *Tecomaria*), Cesalpiniaceae (*Crudia*), Boraginaceae (*Tournifortia*), Nyctaginaceae (*Myrabilis*), some genera of Ericaceae, Polygalaceae and Rhamnaceae from the tropical and subtropical alliances (Cavagneto and Anadon, 1996). This pollen assemblage occurs in the red clay bed, which contains vertebrate fossils of the MP19 zone. *Lirum*, as an element of the African Eocene palm savannahs, migrated further to the north with an increase in the climatic aridity in Western Europe. The growing diversity of Leguminosae and Cesalpiniaceae also indicates African effects. The appearance of *Baringtonia*, a representative inhabitant of sea-coasts in regions occupied by tropical and subtropical savannah, also indicates seasonal precipitation, as well as the effects exerted by the Paleotropical Flora on the Tethyan Flora.

Numerous data on climatic parameters are given for the subxerophilous floras of Central Europe. Mean annual temperatures of 22–25°C and a mean annual precipitation of 1200–2000 mm is given for the **Devin** Flora, in the Rhodope Mountains (Palamarev and Petkova, 1966) and a mean annual temperature of 22.5–27.5°C is given for the **Höring** Flora (Ettingshausen, 1859). The flora of **Hvoina** in the Rhodope Mountains is characterized by mean annual temperatures of 18–20°C, the temperature of the coldest month being 6°C, and of the warmest month of 25°C, and by a mean annual precipitation of 1300–2000 mm (Chernjavska *et al.*, 1988). It is suggested that precipitation was seasonal everywhere in this zone.

This zone continues further to the east on the north-facing slope of the Lesser Caucasus. In Georgia floras from the **Akhaltsikhe Depression** may be assigned to this zone. These floras should be considered as floras of the second half of the Eocene. *Dryophyllum*, Lauraceae, *Magnolia, Engelhardtia*, and Sapindaceae enter into their composition. The deciduous taxa, *Betula, Populus, Salix*, and *Juglans* also usually occur. This flora is small-leaved, sclerophyllous, subxeromorphous, and differs little from the Balkan Late Eocene floras.

Northern Europe. Floras that extended from the British Isles and Northern France across the northern areas of the Bohemian Massif and further to the east, into the East European Platform also had an individual character. These floras are also found further to the east, in South Urals (basin of the **river of Or'**) and even within the Kazakh Massif (**Zhamantuz** and **Takyrsor** floras, etc.) by representative indicator plants in the floristic assemblages of this belt, *Eotrigonobalanus* and *Quercus pseudoneriifolia*, however some of them may be of Middle Eocene age.

Subtropical floras from coastal areas that occur further to the north of the Paleo-Paratethys may be subdivided into Late Eocene floras and Eocene–Oligocene floras. Lauraceae, Fagaceae, Ericaceae and Taxodiaceae dominated the composition of the main core of the more ancient Late Eocene floras. The predominant forest assemblages were composed of *Eotrigonobalanus* and *Daphnogene* in various combinations with *Pinus*, Taxodiaceae, Ericaceae, *Macclintockia*, and *Steinhaurea*. These taxa were accompanied by a wide range of evergreen plants (*Actinodaphne, Eomastixia, Ficus, Nyssa oviformis, Sterculia, Ternstroemia*, etc., including ancient *Dryophyllum*). Palms and ferns from the tropical alliance are found in the composition of some floras. Deciduous also genera numbered in tens,

including *Ampelopsis, Platanus, Populus, Sambucus*, etc. However, these taxa were generally of secondary importance in the composition of the Late Eocene forests, as compared to the evergreen taxa. In Western and Central Europe the basic floras of this type occur mainly in the **Hampshire Basin**, on the north-facing slope of the Massif Central (France) in the Loire Basin, in coal-bearing basins in the northern areas of the Bohemian Massif, in the Weis–Elster lignite-bearing basin in Southern Saxony (**Zeitz**) and in Thuringia. In the Volhynia Heights among these floras are the Karpikha Flora, the Tochil'nitsa Flora and the **Kochetyn** Flora. The Late Eocene age of many of these floras is controlled by occurrences of marine fauna. Plant fossils from concretions in the Nizhnii Novgorod Formation are included into beds with an assemblage of nannoplankton of the NP19–NP20 zones. In the Weis–Elster Basin beds that contain flora overlay marine beds with the nannoplankton of the NP17 zone and with the assemblages of vertebrates of the MP16 zone.

Floras from the Eocene–Oligocene boundary beds are also of the subtropical type, with the presence of Fagaceae, Lauraceae, Moraceae, Sapindaceae, palm plants, and legume shrub plants. Among the main forest-forming taxa were *Daphnogene, Laurophyllum, Neolitsea, Ilex, Myrica, Engelhardtia*, and *Sterculia*. However, the participation of the deciduous taxa in the composition of these floras was far more active. In pollen assemblages pollen of gymnospermous plants (up to 90–95% of the total pollen spectrum) dominated over the pollen of flowering plants. Among the conifers are *Pinus, Doliostrobus, Athrotaxis, Glyptostrobus*, and *Sequoia*). The deciduous plants are represented by *Alnus, Betula, Carpinus, Populus, Salix*, etc. Floras of this type are known from the Bembridge Beds in the **Isle of Wight**, Pshelbronn salt-bearing beds in Alsace, in the vicinity of **Mulhouse**, as well as from **Kuclin**, in the vicinity of Bilina, the north-facing slope of the Bohemian Massif. Fossils of vertebrates from the paleothere assemblage (MP19–MP20 zone) are found here in numerous occurrences along with plant fossils. In the Voronezh Massif the **Tim** and the Molotychi floras, in which *Quercus pseudoneriifolia* and *Steinhauera subglobosa* were found, are assigned to the Oligocene–Eocene Boundary floras.

The Late Eocene spore-and-pollen assemblages are assigned to the *Quercus gracilis–Q. graciliformis* Pollen Zone. The pollen content of the gymnospermnous plants (*Pinus* and Taxodiaceae) increased markedly at the Eocene–Oligocene Boundary, while the content of the pollen of the evergreen flowering plants and of the families Hamamelidaceae, Anacardiaceae, etc. reduced.

This indicates a growing climatic cooling. The indication of this climatic cooling is seen from the second half of the Late Eocene.

Mai and Walter (1983) reported the following climatic parameters for the Late Eocene floras in the Weis–Elster Basin (the Zeitz Flora): the mean annual temperature is 15–20°C, the temperature of the coldest month is 6–13°C, the temperature of the warmest month is 15–23°C, and the mean annual precipitation is 2000 mm, while the precipitation is seasonal.

The flora from the amber in the Baltic coastal areas (fossil flowers, fruits and single fragments of conifers) occupies separate positions in the composition of the Late Eocene floras. In the Late Eocene, these regions were occupied by conifer–oak–palm forests with a participation of *Eotrigonobalanus, Pinus, Thuja* and various flowering plants, representatives of the families that inhabit subtropical and tropical areas today. It is not improbable that these regions belonged to an independent province that occupied the northern areas of the Polish Lowlands, the East-country, some areas in Belarus, southern areas of the Scandinavian Peninsula and northwestern areas of the European part of Russia.

Data on the northernmost floras are obtained in Spitsbergen, where in the Late Eocene, deciduous broad-leaved and mixed coniferous–broad-leaved forests were widespread under temperate climatic conditions. These forests were composed of Taxodiaceae (*Metasequoia occidentalis, Taxodium*, and *Taiwania*) in combination with a mixed assemblage of flowering plants that still included the archaic Early Paleogene elements (*Nordenskioldia borealis, Trochodendroides richardsonii*, and *Nyssidium eckmanii*) along with the new, present-day genera *Acer, Aesculus, Tilia*, etc.

Northwest Asia. Floras of the North European type may be observed further to the east in Kazakhstan. Although the main above-described plants that are indicators of the floras of the East European Platform survived here, the local flora differs in the more active participation of Myricaceae, Ericaceae and Leguminosae often accompanied by Myrtaceae and Proteaceae. The age of the majority of floras is not proved and is based on the participation of indicator plants that have narrow stratigraphic ranges. Nevertheless, these plants could be of both Late Eocene and Mid-Eocene (Bartonian) age.

The western boundary of these more xerophytic floras crossed the Ustyurt from the north southward and separated the Mangyshlak, because the pollen assemblages of the Adaevo Formation in the Mangyshlak did not differ significantly from the Beloglinian Formation in Ciscaucasia. The position of the northern boundary of this zone is not clear enough because this boundary is not supported by occurrences of flora. Nevertheless, the South Urals, the Turgaj Plateau, and the southern areas of Western Siberia definitely belonged to this zone. The majority of occurrences of the Late Eocene floras in Kazakhstan occurs around the periphery of the Mugodzhary mountains or in the Pavlodar Area of the Irtysh Region. A narrow-leaved vacciniaceous plant *Leucothoe protogaea* dominated the **Baky** Flora that was the richest of the Fore-Mugodzhary floras, however this flora could be of Middle Eocene age. This plant was accompanied by sclerophyllous oaks, *Dryophyllum*, the palm *Sabal*, Lauraceae, Rhamnaceae,

Myrtaceae and Leguminosae. In another flora from this region that was found in the vicinity of **Romanovsk** and is assigned more safely to the Late Eocene the evergreen taxa (*Laurus, Quercus elaena, Q. pseudoneriifolia, Myrica banksiaefolia*, and *Leucothoe protogaea*) are found in combination with deciduous taxa (*Alnus, Liquidambar, Ulmus, Juglans* and *Acer*). Conifers are represented by *Sequoia* and *Glyptostrobus*. Flora from the **Shanda Trough** that was found in the vicinity of the town of Aktyubinsk is similar to the above-described flora. This flora is larger-leaved and mesophilous in character. *Taxodium* and *Liquidambar* are present in its composition along with Fagaceae and Lauraceae.

Floras from the Pavlodar Area of the Irtysh Region, some of which were found along the Irtysh–Karaganda Channel (Makulbekov, 1972), are xeromorphic and small-leaved (**Takyrsor**, Olenty, Selety, Alekseevka, Kuboldy and **Zhamantuz**). Sclerophyllous oaks (*Quercus takyrsorianus* and *Q. pseudoneriifolia*), *Laurus, Leucothoe protogaea, Lomatia*, the palm of *Trachycarpus* and the conifers *Sequoia* and *Pinus* enter into their compositions. These floras are probably also Middle Eocene (Bartonian), or belong to the Middle Eocene–Late Eocene transition beds.

The final stage in the development of the subtropical floras in this region is seen in the Shiderta, Kik and Akzhar floras. These floras occur in the continental analogues of the Tavda Formation. Floating fern *Azolla vera* is found in abundance in the marine beds. The list of evergreen taxa, *Laurus, Leucothoe protogaea, Quercus pseudoneriifolia, Myrica lignitum, M. banksiaefolia, Dryophyllum curticellense*, and *Sequoia*, in these floras is usual for the Late Eocene floras of the Kazakhstan Province. Nevertheless, single deciduous taxa, *Sassafras ferretianum, Liquidambar europaea, Comptonia acutibola*, and the dentate *Quercus*, are also found alongside the evergreen taxa.

Makulbekov (1972) reports the following climatic parameters for the floras of Zhamantuz and Takyrsor: the mean annual temperature is 15–20°C, the mean annual precipitation is 800–1500 mm, and the precipitation is seasonal.

The pollen of Fagaceae, especially of the evergreen oaks *Quercus gracilis* and *Quercus graciliformis* that are the zonal species of the regional Late Eocene *Quercus gracilis–Q. graciliformis* Pollen Zone, dominated the Late Eocene pollen assemblages. This pollen corresponds easily to remains of leaves of the evergreen oaks. Among the flower pollen, *Nyssa, Rhus*, Moraceae, Hamamelidaceae, *Ilex* and Araliaceae were present. The proportion of conifer pollen, especially pine, increases in the Eocene–Oligocene boundary beds. The proportion of pollen of herbaceous and low-growing shrub plants, indicators of growing climatic aridity, increases markedly from the north southwards.

Central Asia. The Central Asian floras that occurred further to the south of the **Hissar Range** indi-

cated more contrasting climates. Within the coastal plain around the Tajik–Afghan Depression the climate was of the arid type as indicated by the presence of pollen of Chenopodiaceae, Compositae and *Ephedra* in the pollen assemblages. There are more than ten species of *Ephedra* in the Sumsar beds (Pen'kova, 1973). Uplands that surrounded this depression were occupied by coniferous and coniferous–broad-leaved forests and more humid. The climatic aridity within the Tajik Depression increased markedly from the east westwards.

Phytogeographic Zonation

Starting in the mid-19th century, many botanists and paleobotanists proposed their versions of the paleophytogeographic or paleophytochorologic zonation of Western Eurasia after the first attempts to construct the chart of the climatic and phytogeographic zonation were made by Saporta and Heer. Such attempts were also later made by Engler (1879; 1882), Krishtofovich (1928; 1955), Szafer (1961), etc. The paleofloristic zonation of this territory was proposed by specialists in palynology (Boitsova and Panova, 1973).

Taking into consideration all the data obtained by the previous investigators and the spatial arrangement of the Early Tertiary (Paleocene–Eocene) floras, two principle paleofloristic regions of the Holarctic Kingdom, the Boreal Region and the Tethyan Region, may be recognized (Akhmetiev in Meyen, 1987). Migration of the subtropical floras further to the north in the Eocene, up to the territory of England and the Baltic Coast, allows the inclusion of the whole of Western Eurasia into the Tethyan Region.

As for the subdivision into provinces, the most convincing, in our opinion, is the version proposed by Mai (1995). His version takes into consideration the climatic–latitudinal zonation and the participation of tropical and subtropical deciduous elements, on the one hand, and of temperate deciduous elements, on the other hand, in the floras. The phytochores recognized by Mai correspond rather well to the criteria of dissimilarity of the floristic compositions that are used by botanists for the recognition of present-day phytogeographic provinces. Nevertheless, Mai's version needs some correction because the names of the main phytochores that he proposed for Europe are the same for the whole of the Paleogene and Neogene. In this connection, the author has to "average" the areas occupied by temperate and tropical–subtropical floras. As a result, many subtropical floras are included into the Atlantic Boreal Province in the Eocene.

We propose using a particular chart of zonation for each of the time periods, between which a marked rearrangement in the distribution of floras is observed. Thus, Mai's chart for the Priabonian is interpreted in another way. We propose that two subprovinces, the European Arctic Subprovince that occurs in the temper-

ate climatic zone and the West–Central European Subprovince that occurs in the subtropical climatic zone, should obtain the status of provinces, while the West–Central European Province should be included into the Tethyan Region. Two of Mai's other provinces, the East European Province (or the East Paratethyan Province) and the Caucasian Province, should not be recognized for the Eocene. The East European Province is included into the North European Province. The territory of the Caucasian Province is included into three sublatitudinal provinces. The north-facing slope of the Greater Caucasus is also included into the North European Province, the larger areas of Transcaucasia is included into the Central European Province (the Central-European–Transcaucasian Province), while the south-facing slopes of the Lesser Caucasus and the Talysh are included into the South European–Iranian Province. For the eastern areas of the Beloglinian Basin we propose the recognition of the West Asian Subregion composed of two provinces, the Kazakhstanian Province that occurs in the eastern extension of the North European Province and the Central Asian Province that occurs further to the south of the North European Province in the arid zone and is characterized by a widespread herbaceous and low shrub xerophytes.

Thus, we propose the following phytochore subdivisions for the Late Eocene:

Holarctic Kingdom
Boreal Region
Arctic–Atlantic Province
Tethyan Region
European Subregion
North European Province

(= *West European + Central European subprovinces* after Mai)

Central European–Transcaucasian Province

(= *Transeuropean Paratethyan Province* after Mai)

The South European–Iranian Province

(= *the Mediterranean Tethyan Province* after Mai)

West Asian Subregion
Kazakhstanian Province

Central Asian Province

Ultimately, the whole of the territory occupied by Paleo-Paratethys and its direct surrounding entered into the Tethyan Subtropical Region of the Holarctic Kingdom in the Late Eocene. The zonal type of vegetation was represented by oak–laurel forests formed from evergreen narrow-leaved *Quercus*, *Castanopsis*, *Eotrigonobalanus*, Lauraceae (*Daphnogene* and the *Cinnamomum*) and Myrtaceae (*Rodomyrtophyllum*). Mountain ranges and ranges of hills were occupied by pine forests and forests including Taxodiaceae and Cupressaceae of the southern type (*Doliostrobus, Tetraclinis*, etc.). These forest assemblages of the North European Province were replaced further to the east by more open forests including Leguminosae, such as the Kazakhstanian Province of the West Asian Region. In

the Central Asian areas of the Paleo-Paratethyan coastal regions that entered into the independent Central Asian Province forest vegetation in plains was replaced by unforested vegetation dominated by the xerophilous assemblages, as indicated by the high proportion of pollen of *Ephedra* and low-growing shrub taxa of Chenopodiaceae in the pollen spectra. Slopes of hills were occupied by coniferous and coniferous–broad-leaved forests.

In the southern areas of the Paleo-Paratethys the plant assemblages that occurred in the northern and southern coastal areas of large archipelagos of the Rhodopian, Pontic, and Lesser Caucasian type and of some small islands differed markedly. A boundary between the tropical and subtropical, and the mesophilous and xerophilous vegetation went along the axial zone of these uplifts. In our opinion, this boundary should be considered as the boundary between the Central European and South European–Transcaucasian provinces.

The main means of migration in these provinces ran along the marine coasts: along the northern and southern coastal areas of archipelagos in the ophiolite zone of the ancient Tethys (the Alps, the Dinaric Alps, the Vardar Zone, the Rhodope Mountains, the Pontic Uplift and the Lesser Caucasus) and along the northern coasts of the Paleo-Paratethys.

Insects

The study of the Eocene insect faunas of Western Eurasia, including Late Eocene taxa, has been very inconsistent. On the one hand, the very rich faunistic assemblages of the Baltic amber (among others) have long been known and studied. On the other hand, such faunas are few, and they differ in their taphonomy and age. In fact, we know individual assemblages rather than the composition of regional faunas. Nevertheless, we can obtain additional valuable information on paleoclimates, landscapes and types of communities using insects that can be reliably assigned to extant genera. Late in the Eocene, the percentage of the extant insect genera increased markedly (up to 50% in the Baltic amber), so the reliable comparisons with present-day conditions are possible.

Representative assemblages of the Late Eocene insects are discovered in Southern, Western and Northern Europe (France, England, and the Baltic countries). In Eastern Europe the insect assemblages from the Late Eocene amber of Polesye and the Dnieper Region have not yet received detailed study. Data on fossil insects from single occurrences in Transcaucasia (Akhaltsikhe), Central Asia (Er-Oilan-Duz in Turkmenistan) and in Eastern Kazakhstan (the Aksyir Formation in the Zaisan Depression) have not yet been processed, while their preliminary identification does not allow any paleobiogeographic reconstruction. Therefore, these regions are not considered in this work. There is also no data on the

Eocene insects from the North Africa except for some ichnofossils.

Southern Europe. In Southern Europe in the Late Eocene, insect fossils are known from France, where several rather rich but poorly studied occurrences were found. Among these occurrences is the assemblage from Célas and from several other localities in the Department of Gard in Languedoc (Theobald, 1937). There are small collections from Sezanne-sur-Marne (Nel and Blot, 1990), and some occurrences from the phosphorites of Quercy may be assigned to the Late Eocene (Handschin, 1947). The majority of species described (about 50) are from Languedoc, however most these need some revision. The great majority of species are assigned to widespread genera and families that do not indicate particular environmental conditions.

British Isles. There are several occurrences of Eocene insects in England. However, only the entomofauna from the Bembridge Beds in the Isle of Wight may be assigned to the Late Eocene (Jarzembowski, 1980). Fossil insects, including representatives of 16 orders, are numerous in the layer of alternating limestone and mudstone that were formed in brackish paleoenvironments. Over 150 species are described (the majority needing revision), comprising less than one third of the total number of species represented in the collections. The Bembridge Entomofauna differs markedly from the Baltic amber fauna. This may be partly due to taphonomy and partly due to its more recent age; nevertheless a number of differences are clearly of a biogeographic nature.

The Bembridge Fauna, in particular, is more markedly thermophilic in character. The abundance of termites, dominated by *Mastotermes anglicus* von Rosen (Mastotermitidae), and with one fossil fragment probably belonging to a representative of Termitidae (Jarzembowski, 1980), indicates a warmer climate than that of the Baltic amber origin. Both families are absent in the Baltic amber, and are now more thermophilic than Termopsidae, Kalotermitidae, and Rhinotermitidae that occur there. Kalotermitidae and Rhinotermitidae are also present in the Bembridge Faunistic Assemblage, but Termopsidae, the least thermophilic and the only present-day family restricted to extratropical regions, are absent there. The ant fauna is numerically dominated by several species assigned to the present-day tropical genus *Oecophylla* (Cockerell, 1915; Donisthorpe, 1920). It is not improbable that these species should be assigned to a separate, closely related genus. The same is probably true of the social wasps that are placed to the present-day tropical genus *Polybia* (Cockerell, 1921). There are probably a number of thermophilic taxa among the Bembridge dragonflies, orthopterans, cicads and moths. Nevertheless, the Bembridge Insect Assemblage should not be considered as true tropical. In contrast, there is also high diversity of parasitic wasps of the family Ichneumonidae, as well as

aphids of the extinct family *Elektraphididae* (close to the present-day Holarctic Adelgidae) represented here by the genus *Schizoneurites*, also known from the Baltic amber and from the Eocene–Oligocene of Russian Far East (Cockerell, 1921). The abundance of fossil grasshoppers of the subfamily Catantopinae, represented by the single species *Proschistocerca oligocaenica* (Zeuner, 1941), is noteworthy, and indicates the presence of open areas.

Central Europe. It should be emphasized that entomofaunas similar to the most thermophilic Middle Eocene assemblages from Geiseltal and Messel (Germany) have not yet been found anywhere in the Late Eocene of Central Europe. Rich entomofauna from the salt-bearing beds of Alsace (Brunstatt, Wittenheim, Rouffach and Zimmersheim: more than 250 named species) and from adjacent regions in Germany (Kleinkembs) may be of Late Eocene age, however this entomofauna is often assigned to the Lower Oligocene (Forster, 1891; Quivreux, 1934; Theobald, 1937). Some of the species recorded from Alsace were originally described from the Baltic amber, from the Eocene of Languedoc, from the Oligocene of the Marseilles Basin and even from the Miocene of Baden; however, all these records are doubtful. The entomofaunas from Alsace and Languedoc are rather similar in composition, unlike the corresponding floras, and there are no obvious differences between them that could indicate different climates in these territories. Some relatively hydrophilous groups (for example, the fungus gnats of the superfamily Mycetophiloidea), are probably better represented in Alsace.

In addition to the occurrences in the westernmost areas of Germany adjacent to Alsace, the insect-bearing lacustrine dolomite beds in Kučlin, the Bohemian Massif, are assigned to the Late Eocene. A dozen insect species, mainly beetles, are only known from Kučlin; the data available do not allow estimation of the biogeographic peculiarities of this fauna.

Northern Europe. Baltic amber occurs over a vast territory, from Denmark to Sweden, Poland, Kaliningrad Region and Lithuania. The richest Palmniken Locality was found in the Kaliningrad Region (the village of Yantarnyi). The amber here occurs mainly in the glauconitic sands ("blue earth") of the Prussian Formation (Savkevich, 1970). The Late Eocene age of this formation was determined based on microfaunistic data (Grigyalis *et al.*, 1971; Zatula, 1973) and supported by the results of absolute age determination (Chedzhemov and Babikov, 1971). The amber was supposedly transported by rivers to the deltaic beds of the Prussian Formation from the Scandinavian Shield, most probably from a vast but not very homogeneous territory (Larsson, 1978; Bachofen-Echt, 1996). In the majority of other regions the Baltic amber was redeposited in younger deposits, mainly into the Quaternary (Larsson, 1978), so its Late Eocene age is the conjectural. The faunas of dipterans from the amber of Denmark and

from the Eastern Baltic Region differ markedly (Hennig, 1967; Larsson, 1978). These distinctions are probably related to somewhat different climates because the thermophilic groups, termites and ants of the genus *Iridomyrmex*, in particular, seem to be less common in the material from Denmark.

The origin of so-called Saxonian amber from the Miocene of Bitterfeld in the vicinity of Leipzig, where a rather representative collection of inclusions was made, is widely debated (Barthel and Hetzer, 1982; Schumann and Wendt, 1989). Many species of insects and spiders found in the Saxonian amber are closely similar to the Baltic species. Therefore, in the opinion of some authors, the Saxonian amber is redeposited Baltic amber (Wunderlich, 1983; Weitschat, 1997; Wichard and Weitschat, 1996). However, the Saxonian Faunistic Assemblage also has some distinctions that shed doubt on the common origin as well as the common age of the two assemblages. In particular, several psyllomorph homopterans were found in the Saxonian amber. This group occurs very rarely in the Cretaceous and Early Paleogene and becomes more and more frequent, starting from the end of the Eocene (the Bembridge Formation of England). It is not improbable, therefore, that the Saxonian amber is slightly younger that the Baltic amber.

Thus, the materials available characterize the fauna of rather vast, and most probably, geographically heterogeneous territory over a rather long period. Nevertheless, at the present state of knowledge we are forced to consider the amber fauna of the Baltic Region as a single data point.

At present, about 3500 insect species belonging to over 150 families and almost all insect orders known from the Cenozoic are described from the Baltic amber (Larsson, 1978; Poinar, 1992; Bachofen-Echt, 1996; Wichard and Weitschat, 1996). The taxonomy of many groups, including those rich in species, have not yet received detailed study, so the number of species mentioned is unlikely to exceed a quarter of their real number. Nearly all insect families and, as mentioned above, about 50% of the genera found in the Baltic amber are extant. However, many of them now occur in other regions, mainly in warm temperate and subtropical climatic zones, and truly tropical groups are practically absent. The extant relatives of the thermophilic taxa represented in the amber typically occur in East Asia and in the southern areas of North and Central America, with some of them restricted to the southern hemisphere only (see Eskov, 1992, for a review). Thermophilic orders known from the amber, but which are poorly represented in modern temperate, include termites (eight species from 6 genera of 3 families in the amber, including two extant genera). Mantids, which have not yet received detailed study, also occur; some Baltic mantids are considered to be relatives of the extant South American taxa (Bachofen-Echt, 1996). Other thermophilic orders include stick insects (three

species from 2 extinct genera of 2 families); and Embioptera (one monotypic extinct genus). A number of thermophilic elements is also found among representatives of the orders Orthoptera, Psocoptera, Hemiptera, Neuroptera, Coleoptera, Diptera and Hymenoptera. At the same time, a large number of species found in the amber are assigned to the species presently widespread in the Palaearctic or Holarctic. Of special note is the presence of Raphidioptera, and of the extant families Raphidiidae and Inocelliidae that today do not occur in regions with frost-free climates. Trichoceridae, as well as the great diversity of aphids, including those with a marked seasonal polymorphism (Heie, 1967; Steffan, 1968; Kulicka and Wegierek, 1996), also occur. In the opinion of some researchers, this mixture of relatively cold-tolerant and thermophilic groups may be due to the fact that material transported from different altitudinal zones in mountain territories was buried together. However, as early as 1915, Wheeler noted that taxa with different climatic preferences may occur in the same amber piece. The climatic conditions of Scandinavia in the Eocene were most probably similar to the present-day climatic conditions in medium-altitude regions of Southern China or Mexico, where episodic winter frosts and heavy precipitation is observed.

According to the majority of authors, the composition of the amber fauna suggests the prevalence of dense moist forests. However, Rüffle and Helms (1970) suggested that light forests resembling the present-day pine savannah in Cuba dominated the landscapes. The extreme rarity of solitary bees indicates a shortage of open areas (Zherikhin, 1978). Insects that develop in water are of great paleogeographical interest. A number of groups with aquatic larvae are very abundant in the Baltic amber (Wichard and Weitschat, 1996). Inhabitants of small, fast flowing streams occupy a very important place among them. Groups associated with small stagnant pools and swamps are also abundant. Thus, the territory was probably rich in water. At the same time, taxa that are associated with large lowland rivers are almost absent, indicating the mountainous topography of Eocene Fenno-Scandia. Besides, a great diversity of aquatic insects, including those that could hardly overcome marine barriers (mayflies and stoneflies), indicates the large area of the land mass.

Negative characters of the Baltic entomofauna are also of great interest. The absence of many groups may be due to taphonomic factors. Thus, the majority of odonatans, many Orthoptera, Lepidoptera as well as any inhabitants of herb layer are found very rarely in the present-day conifer resin (Zherikhin and Sukacheva, 1989, 1992). In other cases, we are dealing with evolutionary young taxa that probably did not exist in the Late Eocene. Among these taxa are, for example, the majority of families of higher brachyceran flies, aphids of the families Lachnidae and Aphididae, seed beetles and advanced bark beetles, etc. (Zherikhin, 1978). There are, however, several groups, the absence of

which is unassignable to taphonomic factors or to their age. Therefore, their absence may be related to the biogeographic conditions only. This is primarily true of a number of mainly tropical insects mentioned above. Some beetles of the superfamily Curculionoidea, such as Brentinae and Platypodinae, should be mentioned in this connection, in addition to mastotermitid and termitid termites. These taxa mainly occur today in tropical zones, and Platypodinae are very abundant in the Oligocene fossil resins in Italy, Dominican Republic and Mexico. Nevertheless, their reported presence in the Baltic amber (Burmeister, 1831) has not been supported by subsequent finds and is most certainly wrong.

It is much more difficult to interpret the absence of some present-day Holarctic taxa. An example of this is the sawfly family Xyelidae. This is a very ancient group well represented in the Mesozoic, is now a relict taxon, occurring solely in the Holarctic regions, where, nevertheless, it is widespread. Many members of this family are biologically associated with conifers, primarily pines, which are the most probable producers of the Baltic amber. The occurrence of Xyelidae in present-day conifer resins suggests that their absence in the amber cannot simply be explained by taphonomic biases. In the Paleogene, Xyelidae were already rather rare, but several species are known from the Oligocene of Germany and of the Maritime Territory. Taking into account that very large quantities of Baltic amber have been studied, we have to suppose that representatives of Xyelidae were absent in Scandinavia in the Eocene. The same is apparently true for beetles of the family Nemonychidae, with the only difference that this family today exhibits a bipolar distribution in temperate zones in both the northern and the southern hemispheres. The majority of representatives of Nemonychidae inhabit conifers (pines in the northern hemisphere). This family is abundant in the Mesozoic but is now a rather species-poor relict group. The occurrence of Nemonychidae in the Cretaceous Lebanese amber indicates the possibility of its burial in resins (Kuschel and Poinar, 1993). However, no Nemonychidae are found in the Baltic amber. Thus, some rather ancient components of the present-day fauna of coniferous forests in the Northern Hemisphere were possibly absent from the Scandinavian forests of the Eocene.

In Eastern Europe there are several amber occurrences that are closely similar mineralogically to the Baltic succinite. The amber is found both in the Eocene and in the Lower Oligocene of the Dnieper Region and Polesye (Kiev, Kharkov, and Polesye beds), as well as in the redeposited mode in the Quaternary beds in these regions. Little is known about the taxonomic composition of inclusions in amber of the Dnieper Region and Polesye. For the Ukrainian Polesye only a list by Makarenko (1988) is available. This list mainly contains determinations to family, or even of order. As far as could be judged, the total set of the most common groups is rather similar to the Baltic amber fauna. Of particular importance is the presence of a megalyrid

wasp of the genus *Prodinapsis* described from the Baltic amber. Only two species of Diptera and one species of ant were described from the Belarus Polesye (Nazarau, Bagdasarau and Ur'eu, 1994).

Judging from the information above, it might be assumed that the available data on Late Eocene insects in Western Eurasia are rather scanty for a justified zoogeographic demarcation of this territory, or for drawing any conclusions on the climatic dynamics in the Latest Eocene. It is safe to say only that there are some faunistic distinctions between the warm temperate Scandinavia (with its eastern areas probably having a slightly warmer climate than its western areas) and the subtropical regions that occurred further to the south (at least from the Southern England). It can be also supposed that some climatic cooling occurred in Central Europe in the Late Eocene compared to the Middle Eocene.

Terrestrial Vertebrates

North Africa. In the Late Eocene, the territory of North Africa was dominated by endemic groups of mammals, while the majority of orders and families typical of the northern continents were absent. Among the Eocene African endemics were proboscideans (Numidotheriidae, Moeritheriidae, and Barytheriidae), hyracoids (Pliohyracidae) and elephant shrews (Macroscelidea), rodent families Zegdoumyidae, Phiomyidae and Anomaluridae, anthropoid primates Propliopithecidae and omomyids (Azibiinae), creodonts of the subfamily Koholiinae (Hyaenodontidae), as well as birds of the family Balaenicipitidae (Ciconiformes), mesosuchian ziphodont crocodiles of the family Dyrosauridae and side-necked turtles of the family Eusarkiidae (Sudre, 1979; Mahboubi *et al.*, 1984; Jaeger *et al.*, 1985; Hartenberger, 1986; Carrol, 1988; Crochet, 1988; Simons, 1995b; Vianey-Liaud *et al.*, 1994). The majority of the autochthonous groups of mammals had a rather long history of their endemic development. Thus, the most ancient proboscideans are found in the Upper Paleocene of Morocco (Gheerbrant *et al.*, 1996), creodonts, hyracoids and elephant shrews are found in the Lower Eocene of Algeria and Central Tunisia (Hartenberger *et al.*, 1985, 1997; Hartenberger, 1986; Crochet, 1988).

On the other hand, mammals of Holarctic (European) origin, including the insectivores *Afrodon* similar to *Adapisoriculus* and to the mixodectids *Remiculus* (Cappetta *et al.*, 1978; Gheerbrant, 1988), were already known from the Late Paleocene (Morocco and Adrar Mgorn). Marsupials Peradectidae (Didelphoidea) and nyctitheriid insectivores close to the European taxa (Mahboubi *et al.*, 1983, 1984; Crochet, 1984, 1986; Hartenberger *et al.*, 1985, 1997) were found in the Lower Eocene of Algeria (El Kohol) and Tunis (Chambi). Occurrences from the Qasr el Sagha Formation of the Fayum Depression (Egypt) indicate that artiodactyls, palaeodonts *Achaenodon* and anthracotheres *Bothriogenys*, as well as creodonts from the

hyaenodontine subfamily, *Apterodon, Hyaenodon*, and *Propterodon*, penetrated North Africa for the first time in the Late Eocene (Holroyd *et al.*, 1996). All these facts indicate evidently the overland connections that appeared occasionally in the Paleocene and Eocene between North Africa and Europe (in the vicinity of Gibraltar and (or) in Sicily). The main invasions occurred probably at the Paleocene–Eocene and Eocene–Oligocene boundaries (Bonis *et al.*, 1985; Crochet *et al.*, 1992; Mahboubi *et al.*, 1997).

The endemic Late Eocene hystricomorph rodents, anomalurids *Nementchamys lavocati* and phiomyids *Protophiomys algeriensis* (Coiffait *et al.*, 1984; Jaeger *et al.*, 1985), are known from Eastern Algeria (Nementcha). Representatives of Anomaluridae are observed in the present-day African fauna. These taxa were probably descended from the Early Eocene Zegdoumyidae (Vianey-Liaud and Jaeger, 1996), which was in turn descended from Paleocene ischyromyoid rodents that migrated to Africa from the Holarctic regions (Vianey-Liaud *et al.*, 1994). Phiomyidae are relatives of the extant African cane rats (Thryonomyidae), also endemic African taxa. They probably shared a common ancestor with the Asian Chapattimyidae (or were even descended from them) and the European Theridomyidae. The ancestors of Phiomyidae supposedly immigrated from Southwest Asia to Africa across Europe late in the Middle Eocene—early in the Late Eocene (Wood, 1983; Jaeger *et al.*, 1985; Vianey-Liaud *et al.*, 1994). The possibility of direct faunistic connections between Africa and the Indian Subcontinent in the post-Paleocene time is not presently accepted (Sahni *et al.*, 1981; Hartenberger, 1982b; Briggs, 1989). The similarity of the Middle Eocene Indo–Pakistani Antracobunidae and the Late Eocene North African Moeritheriidae (West, 1983, 1984) should be probably interpreted as a result of parallel evolution of different forms of tethytheres in some isolated areas (Carroll, 1988). However, in the opinion of Ducrocq (1997), who studied the Paleogene African and Asian anthracotheriids, short-term faunistic connections could have existed between the Arabo–African Land Mass and South Asia late in the Eocene.

Western Europe. In the Late Eocene the West European mammalian fauna (of the MP17–20 zone) included many endemic families. Among these families were Pseudorhynchocyonidae (Leptictida), Amphilemuridae (Insectivora), Microchoeridae (Primates), Pseudosciuridae, Theridomyidae (Rodentia), Choeropotamidae, Cebochoeridae, Mixtotheriidae, Cainotheriidae, Anoplotheriidae, Xiphodontidae, Haplobunodontidae, Amphimerycidae (Artiodactyla), Palaeotheriidae and Lophiodontidae (Perissodactyla). The marsupials Didelphidae, apatotheres Apatemyidae, cimolestes Pantolestidae and Paroxyclaenidae, insectivores Nyctitheriidae and Talpidae, creodonts Hyaenodontidae and Oxyaenidae, carnivores Miacidae, Viverravidae, Amphicyonidae and Canidae, perissodactyls Dacrytheriidae, Anthracotheriidae and Gelocidae, primates Adapidae,

rodents Paramyidae, Ischyromyidae, and Gliridae were also present in this fauna (Sigé, 1977; Carroll, 1988). The majority of genera of the above-listed families only occurred in Western Europe.

In the Late Eocene, the endemic Theridomyodea dominated the European rodents. The recent data show that they had a common ancestor with the Indo–Pakistani Chapattimyidae (Ctenodactyloidea). The occurrence of fossil *Zamoramys* in the Middle Eocene of Spain, the taxon that is between Theridomyoidea and Ctenodactyloidea, indicates that the ancestors of theridomyids migrated to Europe in this very time period (Peláez-Campomanes and López-Martínez, 1996). In the Late Eocene, the evolutionally advanced hypsodont taxa appeared among Theridomyoidea for the first time (Hartenberger, 1973a; Vianey-Liaud and Ringeade, 1993).

Individualization of biogeographic provinces is typical of the Priabonian fauna of the European mammals. This is probably related to a fragmentation of land of the European Archipelago (Russell *et al.*, 1982). This fact is supported by blurred distinctions in the faunistic composition (usually at the specific and generic levels), of occurrences of the same age from various European territories: Spain, Southern France, Southern Germany, and England.

The Late Eocene faunas of terrestrial vertebrates of the northern areas of the Mediterranean coast are known from Southern France and Spain.

In Southern France the Ludian, or the Headonian, faunas from Quersy and Languedoc included tailed and tailless amphibians, turtles Testudinidae and Emydidae, crocodiles Alligatoridae, lizards Anguidae, Necrosauridae, Gekkonidae, Scincomorpha, and Amphisbaenia, snakes Boidae and Scolecophidia and birds Galliformis, Charadrii, and Apodiformes. Among mammals marsupials *Amphiperatherium* and *Peratherium* are numerous. The archaic "insectivores" (leptictidae, apathotheres, amphilemurids, and pantolestids) are rather rare in occurrence. Conversely, nyctitheriids (*Saturninia*) are widespread. Numerous chiropterans, creodonts–hyaenodontids *Paracynohyaenodon, Quercytherium, Hyaenodon, Prototomus, Cynohyaenodon*, and *Paroxyaena*, true carnivores *Miacis, Quercygale, Cynodictis*, and *Simamphicyon*, primates Adapidae and Microchoeridae, rodents *Blainvillimys, Patriotheridomys, Paradelomys, Suevosciurus, Sciuroides, Estellomys, Remys, Elfomys, Pseudoltinomys, Theridomys* (Theridomyoidea), *Plesiarctomys* (Ischyromyidae), and *Gliravus* (Gliridae), artiodactyls Dichobunidae, Cebochoeridae, Mixtotheriidae, Choeropotamidae, Dacrytheriidae, Anoplotheriidae, Xiphodontidae, and Amphimerycidae, perissodactyls *Propalaeotherium, Pachynolophus, Lophiotherium, Anchilophus, Palaeotherium, Plagiolophus, Leptolophus* (Palaeotheriidae) and *Lophiodon* (Lophiodontidae) are found (Sigé, 1977; Geze *et al.*, 1978; Remy *et al.*, 1987; Crochet, 1991).

The Early Headonian (MP17) mammalian fauna of Spain (Llamaquique) has marked provincial characters that indicate the isolated position of the territory of the Iberian Peninsular. Some representatives of the perissodactyls (palaeotheriids *Cantabrotherium* and the archaic *Anchilophus*) and of the artiodactyls are examples of local endemism (Casanovas-Cladellas and Santafe-Llopis, 1987). The endemism is also observed at earlier stages of development of the Eocene mammalian fauna in this territory (the Middle Lutetian autochthonous condylarths Phenacodontidae). The Late Headonian (MP19) fauna of Spain included marsupials *Peratherium* sp., insectivores *Saturninia*, rodents *Gliravus, Theridomys, Blainvillimys, Pseudoltinomys, Pairomys* and *Elfomys*, primates *Microchoerus, Pseudoloris, Necrolemur*, and *Moiachoerus*, and artiodactyls *Dichodon*. The representative species of Spanish theridomyids of this age, *Theridomys golpeae* and *Pairomys crusafonti*, are only found in the Ebro Basin (Agustí *et al.*, 1987; Cuenca *et al.*, 1992). The rodent fauna from the terminal Eocene of Spain is known from the occurrence of Fuenferrada 3 (Freudenthal, 1997). This fauna includes theridomyids *Theridomys* sp., *Pseudoltinomys* aff. *cuvieri*, glirids *Glamys olallensis, Gliravus* aff. *fordi*, and *Bransatoglis priscus*.

The Early Ludian fauna from Majorca (Balearic Islands) included the endemic theridomyid species *Pseudoltinomys gliriformis*, as well as marsupials, nyctitheriids, rodents ?*Plesiarctomys* sp., *Elfomys* cf. *tobieni*, *Suevosciurus minimus*, and *Gliravus* priscus, and paleotheres *Lophiotherium cervulum.* The Late Ludian fauna represented a rather impoverished set of representative European taxa (two species of paleotheres, two species of anoplotheres, and two species of rodents). This fact indicates the existence of an ecological barrier, the present territory being an island (Bruijn *et al.*, 1979). Late in the Eocene, Majorca as an extension of the Betica Cordillera, probably joined the land mass that was composed of the Alboran Block, Kabilia (North Algeria), Corsica–Sardinia (Pelaritan) Block, and Calabria (Italy) and became a component of the Iberian Subprovince (Hugueney and Adrover, 1982). However, the existence of local forms of genera and species shows that the isolation of some populations was still rather high.

Some endemic elements were also found in the Headonian mammalian faunas of the northern areas of Western Europe (Isle of Wight, Hampshire Basin, Southern England) that indicate the temporary isolation of this territory. These elements were represented by endemic species (artiodactyls *Pseudamphimeryx hantonensis* and *Amphirhagatherium* sp., primates *Microhoerus erinaceus*, and apatotheres *Heterohyus* sp.) and by one endemic genus (insectivores *Scraeva*). The supposed distinctions at a higher level (the endemic character of all the genera of insectivores of the family Nyctitheriidae and the persistence of artiodactyls (*Catodontherium*) have not been confirmed (Hooker, 1987). Closed forest habitats changed gradually to more open habitats here, as in the other European territories. This process was slightly delayed in the northern areas compared to Southern Europe but progressed more rapidly than in what is now Southern Germany (Hooker, 1987; Legendre, 1987).

The provincial character of the Late Eocene mammalian fauna in Southern Germany is seen in the predominance of brachyoselenodont taxa (pseudosciurids *Suevosciurus* and *Pseudosciurus*) among the theridomyoid rodents (Hartenberger, 1973), as well as in the longer existence of some species. Thus, the species *Palaeotherium duvali* survived into the MP20 zone in Southern Germany and only into the MP19 zone in France. Late in the Eocene (MP20), the first Asian immigrants (for example, suiformes *Entelodon*) existed for some time in South Germany along with the more ancient autochthonous fauna but did not migrate further to the west. It is probable that some physical or ecological barrier existed in the Late Eocene between South Germany and the other European territories and disappeared early in the Oligocene (Legendre, 1987). Such a barrier may have been a marine strait that occurred in the position of the modern Rhine Graben and connected the Alpine and North seas (Schmidt-Kittler and Vianey-Liaud, 1975). However, geological data show that such a strait only appeared in the Early Oligocene (Herb *et al.*, 1984), so the ecological conditions of this territory were probably the main limiting factor.

Thus, in spite of small provincial distinctions related to disintegration of the European Region, in the Late Eocene, the mammalian fauna of Western Europe belonged undoubtedly to a single zoochore that was isolated from the other Palaearctic regions and was not markedly affected by the North African Fauna.

The so-called "anoplothere immigration" is assigned to the second half of the Priabonian (Sigé, 1977). Artiodactyls of five families, anoplotheriids, cainotheriids, anthracotheriids, gelocids, and amphimerycids, as well as the evolutionarily advanced nyctirtheriids–amphidozotheriins, appeared in Western Europe in the Late Ludian (Sigé, 1977; Russell and Tobien, 1986). It is assumed that this immigration occurred due to formation of a continental bridge between Western Europe and a geographically close region, the fauna of which developed independently for some time but had common roots with the West European Fauna (Sigé, 1977). It is rather difficult to indicate the exact position of this region. It is usually placed in Asia (Hartenberger, 1973). However, anoplotheres and cainotheres are known only from Europe, and their origin is a puzzle, similar to that of the majority of Middle Eocene endemic European families. Since the cainotheres appeared in Southern Germany later than in France (Legendre, 1987), they supposedly did not migrate from the east. The anoplotheroids probably have a European origin. New occurrences indicate their presence in the Early Ludian faunas from Quercy (Remy *et al.*, 1987). More ancient anthracotheres and primi-

tive ruminants were most probably immigrants from Asia. Their migration to Europe late in the Eocene (MP19–20) probably marked the onset of the unprecedented rearrangement of the European mammalian fauna at the Eocene–Oligocene Boundary that was termed the "Grande Coupure" (the "Great Cutting").

Southeastern Europe, Lesser Caucasus. Fossils of the Late Eocene mammals of Central Asian origin (the Anthracothere Assemblage) were found in Southeastern Europe (Transylvania, Slovenia, and Southern Bulgaria). A hyracodont *Prohyracodon orientale* (Perissodactyla, Ceratomorpha), that is probably conspecific with the Chinese *P. meridionale* and *P. progressa* (Codrea, 1993) is known from the basal Priabonian (NP18–19, MP17–18) of Transylvania (Radaja). *P.* aff. *meridionale* was found in Bulgaria (Bobov Dol), and other hyracodonts were found in Slovenia (Motnik). *Prominatherium dalmatinum* was described from Dalmatia. This taxon represents the first occurrence of anthracotheres in Europe (Russell *et al.*, 1982). The anthracothere *Elomeryx* was found in the Bulgarian lignite locality of Tsherno More. Anthracotheres, e.g., *Prominatherium dalmatinum*, brontotheres, e.g., *Brachydiastematherium transilvanicum*, and embrithopods, e.g., *Crivadiotherium iliescui* are known from the Upper Eocene of Romania (Râdulesko and Sudre, 1985; Codrea, 1993). The presence of hyracodonts, anthracotheres, and brontotheres indicate close zoogeographic connections between this territory and Asia. The embrithopods *Crivadiotherium* (Palaeoamasiidae) are closer to the Early–Middle Eocene West Asian *Palaeoamasia* and *Hypsamasia* (Turkey) then to the Early Oligocene North African *Arsinoitherium* (Carroll, 1988; Maas *et al.*, 1998).

In the Lesser Caucasus (Akhaltsikhe, Georgia), fossils of the Late Eocene Chalicotheriidae occur (a group that was absent in Europe at that time) (Gabounia, 1957). Erinaceidae are observed in the Late Eocene of Turkey in the Çorum Province (Russell *et al.*, 1982).

The Late Eocene mammalian fauna of Southeastern Europe, Lesser Caucasus, and Asia Minor is probably more closely related to the Central Asian fauna and may be considered as a single zoochore within the Eastern Palaearctic regions. The main marine barrier that excluded any faunistic exchange between the West European Archipelago and the continental Palaearctic regions in the Late Eocene apparently occurred further to the west (the North Alpine Trough).

Northwest and Central Asia. The Late Eocene in Asia corresponds to the Sharamurunian Land Mammal Age (Russell and Zhai, 1987). Currently the succeeding Ergilian Age has been included into the Late Eocene by some researchers (Lucas and Emry, 1996; Emry *et al.*, 1997). However, the opinion (Dashzeveg, 1993) that only the Zangut, Sevkhul, and, the Shavag beds of the Ergilin–Dzo Formation and their analogues that contain fossils of representative Eocene genera of brontotheres, amynodonts, forstercooperiids, entelodontids, mesonychids, and creodonts may be assigned to the ter-

minal Eocene is probably more substantiated. The mammalian fauna from this stratigraphic level may be assigned to the Sharamurunian Age, while the mammals of the Ergilian Age (from the upper beds of this Formation, or from the Ergilin Beds) and from the Kaetsu-Tsav beds should be dated at the onset of the Early Oligocene (MP21 zone of the European Stratigraphic Chart) and assigned to the Ergilian Age.

The Late Eocene mammals from the Sharamurunian of Northwest Asia were represented by a large number of families in common with the North American fauna or endemic. Erinaceids, pantolestids, omomyid primates, tillodonts Tillotheriidae, lagomorphs Leporidae and Palaeolagidae, rodents Sciuravidae and Cylindrodontidae, creodonts Hyaenodontidae, carnivores Miacidae, mesonychians Mesonychidae, brontotheres Brontotheriidae, chalicotheres Eomoropidae, tapiroids Isectolophidae and Helaletidae, rhinocerotoids Hyracodontidae, Amynodontidae, and Forstercooperidae, palaeodonts Dichobunidae, suiformes Entelodontidae, and ruminants Leptomerycidae from North Asia were common with those from Nearctic regions in the Late Eocene. Genera in common with those from Nearctic regions are also found, including *Telmatherium* and *Manteoceras* (brontotheres), *Prohyracodon, Forstercooperia, Amynodon*, and *Metamynodon* (Rhinocerotoidea), *Hyaenodon* and *Pterodon* (creodonts), *Miacis* (carnivores), and *Ardynomys* (rodents–cylindrodontidae). Among the Late Eocene endemic families in Northwest Asia were Didymoconidae, insectivores Soricidae, pantodonts Coryphodontidae, mixodonts Eurymilidae, rodents Chapattimyidae (=Yuomyidae), Cricetidae, and Zapodidae, chalicotheres Chalicotheriidae, tapiroids Deperetellidae and Lophialetidae, giant rhinoceroses Indricotheriidae, as well as gruiformes Eogruidae. Here, as in South Asia, palaeodonts Helohyidae, Tayassuidae, and various anthracotheres occurred (Li and Ting, 1983; Russell and Zhai, 1987; Tong, 1989; Wang and Li, 1990; Dashzeveg, 1993, 1996; Dashzeveg and Hooker, 1997; Wang and Dawson, 1994; Lindsay, 1994; Reshetov, 1994).

Perissodactyls were the most important large mammals in this fauna, as those in the Middle Eocene. Among perissodactyls, Rhinocerotoidea (amynodonts, hyracodonts, and giant rhinoceroses) were especially numerous and diverse, while tapiroids, especially Lophioletidae, had decreased in importance. The role of artiodactyls increased. Ruminants appeared, while pantodonts, condylarths, and mesonychians only survived in some Central Asian regions (Tong, 1989).

This fauna is best studied in the Central Asian localities of Northern China (Changxindian, Ula Usu, Yuanqui, etc.) and in Mongolia (Alag Tsav and Ergilin Dzo). In Eastern Kazakhstan Late Eocene mammals are found in the Lower Aksyir Subformation in the Zaisan Depression (localities of Mogila Sultana and Kiinkerish). These mammals include insectivores *Tupaiodon* sp., *Ictopidium* cf. *lechei* and Galericinae (Erinaceidae), rodents *Ardynomys* cf. *glambus* (Cylindrodon-

tidae), Ischyromyoidea indet., Cylindrodontidae indet., Cricetidae indet., Zapodidae indet., pantolestid *Kiinkerishella zaisanica*, the swamp rhinoceros *Zaisanamynodon borisovi*, palaeodonts *Gobiohyus* sp. (Helohyidae), suiformes *Eoentelodon* sp. (Entelodontidae), cf. *Anthracokeryx* sp. (Anthracotheriidae), and ruminants *Archaeomeryx* sp., Leptomerycidae (Shevyreva, 1972; Gabunia, 1984; Gabunia, L.K. and Gabunia, V.J., 1987; Russell and Zhai, 1987; Dashzeveg and Russell, 1992; Gabunia and Chkhikvadze, 1997). According to the unpublished data by N.S. Shevyreva, the occurrence of Baldys from the Lower Aksyir Subformation contains and unidentified taxon of Pantolestidae that differs from *Oboia argillaceus* from the Kusto Formation of the Early Oligocene age.

The Middle Aksyir Subformation should probably also be dated at the terminal Eocene because fossils of *Ardynomus* cf. *glambus* and Pantolestidae indet. were found here that are conspecific with the Early Aksyir taxa (Shevyreva and Lopatin, pers. comm.). The Middle Aksyir Subformation also contains Brontotheriidae indet., ancient Asian moles Talpinae gen. (close to the Late Eocene European *Eotalpa*), shrew moles Uropsilinae gen., erinaceids–tupaiodontines *Tupaiodon* sp. and *Ictopidium* sp., gymnures Galericinae gen., erinaceomorphs, cf. Dormaalidae, shrews Heterosoricidae gen., rodents *Eucricetodon* and *Eomys*, and the first Asian marsupial, opossums *Asiadidelphis zaisanensis* (Russell and Zhai, 1987; Gabunia, 1987; Gabunia, L.K. and Gabunia, V.J., 1987; Gabunia *et al.*, 1990; Gabunia and Chkhikvadze, 1997).

Among the other tetrapods, gigantic salamanders *Zaissanurus beliajevae*, various turtles (Gabunia and Chkhikvadze, 1997) and false gavials *Tomistoma borisovi*, that is considered the littoral ichthyophagous taxa, were found in the Aksyir Formation (Efimov, 1984, 1988). The appearance of gavialis may be closely related to the maximum ingression of the Late Eocene Zaisan Basin during a flood of the so-called Dzungarian Lake-Sea (Efimov, 1988).

The marked distinctions between this assemblage and the Central Asian assemblages (the presence of gymnures and moles, the peculiar genus of swamp rhinoceros *Zaisanamynodon*, and the endemic rodent species *Ardynomys*) indicate that the territory of Kazakhstan should be assigned to a separate zoochore.

In the Northeastern Kirgizia (Toruaigyr), fossils of the Eocene dinocerates, brontotheres, tapiroids, hyracodonts, and amynodonts are known. The supposed Late Eocene age of this locality was overturned. It is now agreed that this locality is of Middle Eocene age (Russell and Zhai, 1987). Thus, data on the occurrences of Late Eocene mammals in this territory is absent. It is interesting paleogeographically to note that this territory was of great importance in the formation of the Middle and Late Eocene mammalian fauna in Central Asia. Thus, it is assumed that synchronous evolution of different branches of the Early Eocene Glires in humid habitats of coastal plains in South Asia, including the territory of Kirgizia, resulted in the appearance of progressive groups, such as the tamquammyid and ctenodactylid rodents, lagomorphs, and highly specialized mimotonids that were subsequently distributed among the terrestrial faunas of Central Asia (Hartenberger, 1982a; Averianov, 1996a). The diversity of Late Eocene artiodactyls in South and Central Asia may indicate that this territory was also the center of the early radiation of the Artiodactyla, including all of the main families of this order (Averianov, 1996b). In the Middle Eocene, the mammalian fauna in Central Asia was actually uniform.

The Late Eocene mammalian fauna of the Central Asian type migrated further to the east up to the Pacific Ocean. Thus, in Far East (Artem, Uglovoe Formation) perissodactyls of genera that are the same as those of Central Asia, brontotheres *Rhinotitan* and rhinocerotoids *Juxia* and *Paracadurcodon*, were found (Yanovskaya, 1957; Reshetov, 1994).

Zoogeographic Zonation

The high levels of endemism and the individual character of Late Eocene African, European, and Asian faunas of mammals and of some other terrestrial vertebrates substantiate the subdivision of these faunas into several paleogeographic regions (Fig. 9), the African Region, the European Region, and the Asian Region (*Zoogeografiya…*, 1974). The faunistic connections that existed in that time period between West Asia and Eastern Europe; Northern Europe and North America; and between East Asia and North America did not change the general pattern.

The endemism at specific and generic levels typical of the European mammalian faunas allows the subdivision of the European Region into three paleozoogeographic provinces (Schmidt-Kittler and Vianey-Liaud, 1975). These are the French–Swiss Province (that was occasionally connected to the Iberian Subprovince), the English–French–Belgian Province (including the Paris Basin and the territory further to the west of the Rhine Graben), and the German Province (further to the east of the Rhine Graben).

Southeastern Europe, along with Asia Minor and Transcaucasia, may be considered as a peculiar zoochore (province), a component of the Asian Zoogeographic Region. This zoochore may be termed the Balkan–Caucasian Province. This term was proposed earlier for the Late Oligocene zoochore of this territory (*Zoogeografiya…*, 1974).

The zoogeographic zonation of Late Eocene Asia presents difficulties because the paleotheriology and biostratigraphy of the major part of this territory has not yet been studied in any detail. Accumulation of data on the regional character of Eocene Asian terrestrial vertebrate faunas allows the extension of the division of this zoogeographic region into North Asian and South Asian subregions, as was suggested for the Oligocene–Eocene (*Zoogeografiya…*, 1974). The North Asian
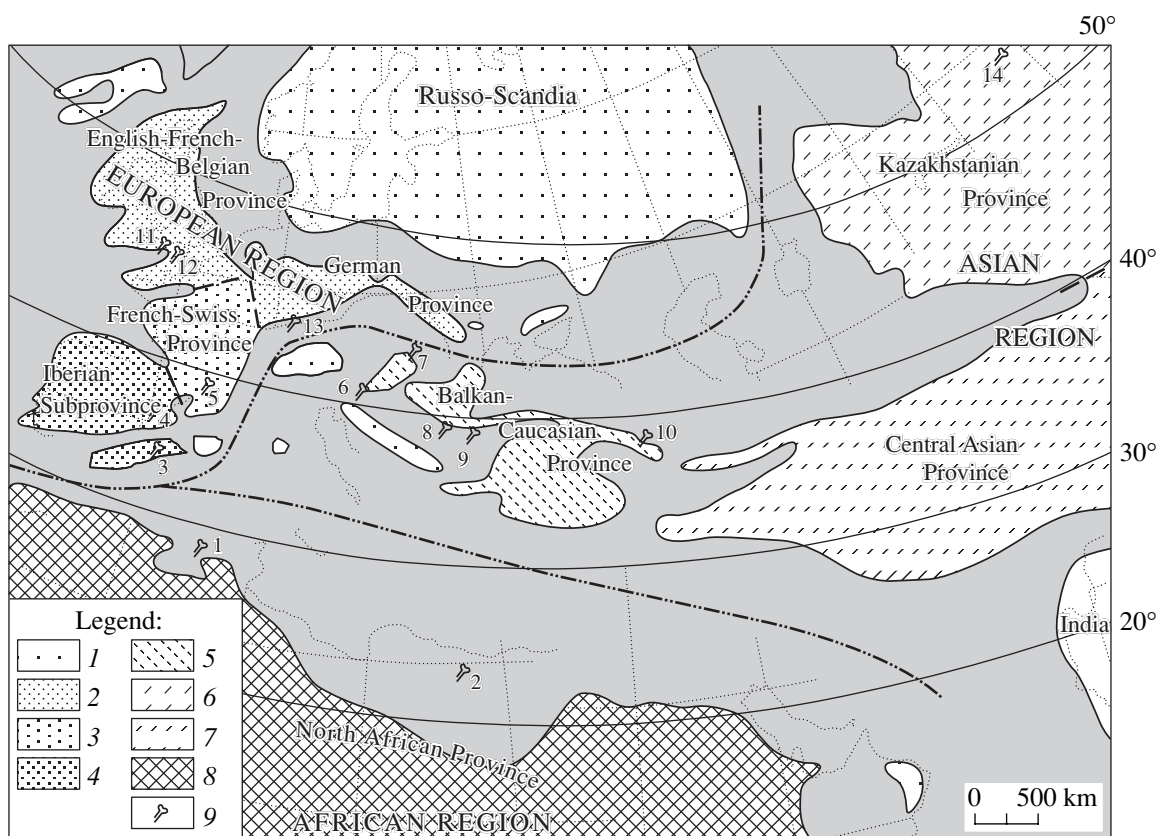
Fig. 9. Zoogeographic zonation of Western Eurasia in the Priabonian based on terrestrial vertebrates. Designations: (*1*) land lacking vertebrate finds, (*2–4*) **European Region** isolated from other parts of Palearctic and free of strong influence of the North African Fauna: (*2*) English–French–Belgian Province distinguished by endemic forms of specific rank and one endemic genus (insectivore *Scraeva*), (*2a*) German Province characterized by the prevalence of brachyoselenodont forms (pseudosciurids *Suevosciurus* and *Pseudosciurus*) among theridomyoid rodents, (*3*) French–Swiss Subprovince, and (*4*) Iberian Subprovince characterized by well-pronounced provincialism of perissodactyls (palaeotheriids *Cantabrotherium* and archaic *Anchilophus*) and artiodactyls; (*5–7*) **Asiatic Region**: (*5*) Balkan–Caucasian Province; (*6*) Kazakhstanian Province characterized by the presence of gymnures, moles, swamp rhinoceroses *Zaisanamynodon*, and endemic species of the genus *Ardynomys*; and (*7*) Central Asian Province; (*8*) **African Region**, North African Province; and (*9*) the main vertebrate localities. The localities and groups of localities considered in the text: (1) Nemetcha; (2) Faiyum Depression; (3) Majorca; (4) Ebro; (5) Quercy, Languedoc; (6) Motnik, Slovenia; (7) Radaya, Transylvania; (8) Bobov Dol; (9) Cherno-More; (10) Akhaltsikhe; (11) Hampshire; (12) Isle of Wight; (13) Southern Germany; and (14) Zaisan.

Subregion includes Kazakhstan, Mongolia, Middle Asia, Northern China, and the Far East. The South Asian Subregion includes Southern China, the Indo–Pakistani Region, and Southeast Asia. The faunas of these territories were probably separated from one another by a physical (and ecological) barrier in the region of the present-day Himalayas.

It is impossible to reliably divide the North Asian territory into zoochores without updating the age of the available localities, which is required for true interpretation of specific and generic distinctions in the composition of the assemblages. At present, the separation of three zoochores, the Kazakhstanian, the Central Asian (Mongolia and Northern China) and the Far Eastern zoochores, may be suggested. The Balkan–Caucasian Province should also be included in the North Asian Subregion.

Thus, in the Late Eocene, in the coastal territories of the Mediterranean–Mesopotamian basin and Paleo-Paratethys, there existed faunas of the following paleozoogeographic subdivisions:

Holarctic Kingdom
 European Region
   English–French–Belgian Province
   French–Iberian Province
    French–Swiss Subprovince
    Iberian Subprovince
   German Province
 Asian Region
  North Asian Subregion
   Balkan–Caucasian Province
   Kazakhstanian Province
   Central Asian Province
Afrotropical Kingdom
 African Region
   North African Province

The main routes of migration between Asia and Europe (up to the North Alpine Strait) run along archipelagos in the ophiolite zone of the ancient Tethys (the Lesser Caucasus, the Pontic System, the Rhodope Mountains, the Dinaric Alps, and the Alps). The Gibraltar Bridge that appeared occasionally formed temporary connections between Southern Europe and North Africa. The North Asian Zoogeographic Subregion was faunistically connected with North America (in its northern areas) by the Bering Bridge, which appeared periodically. Thus, the helaletid tapiroid *Plesiocolopirus kushiroensis* that was found in the Late Eocene of Japan (Hokkaido Island) is allied with the North American *P. hancocki* (Tomida, 1994). The most ancient and primitive representative of Tayassuidae, the Late Eocene *Egatochoerus jaegeri* that was found in Southern Thailand, is the ancestor of the Oligocene North American *Perchoerus* (Ducrocq, 1994). This probably indicates migrations of the Late Eocene mammals from Southeast Asia across the Northeast Asia to North America. Recent data (occurrences on the Ellesmere Island) show that there was a faunistic exchange between Europe and North America over the North Atlantic Bridge (McKenna, 1980; Storch, 1990) in the Early and Middle Eocene, up to the Late Eocene, when it terminated. Terrestrial vertebrates probably migrated to Europe from North Africa. This is only explanation for the presence in the Eocene of Europe of exotic "South American" (West Gondvanan) elements, such as ceratophryin frogs, mesosuchian ziphodont crocodiles, birds Phorusrhacidae, and edentate mammals, e.g., an anteater (Storch, 1990).

Freshwater Ichthyofauna

At present, nearly all the available data on the Paleogene freshwater ichthyofauna of Europe are from the Paleocene and Eocene of Western and Central Europe. Only two localities outside this region are known, Boltyshka (Late Paleocene–Early Eocene of the Ukraine) and western Spitsbergen (Ferkanten Formation, Paleocene). In the Paleocene and Eocene, the European freshwater ichthyofauna consisted of a limited number of authochtonous, primarily freshwater taxa which was periodically supplemented by marine migrants or taxa coming from Northern Europe, the Nearctic, or neighboring areas of Gondwanaland. Biogeographically, the Early Paleogene freshwater fauna of Europe belonged to the Amphiatlantic Subregion (Sytchevskaya, 1986).

Western and Central Europe. The Eocene freshwater ichthyofauna of Europe is known from several localities in France, England, Belgium, Germany, the Czech Republic, and Ukraine (Priem, 1900, 1908, 1911; White, 1931; Voigt, 1936; Obrhelova, 1975, 1976; Danilchenko and Sytchevskaya, 1975; Wiley, 1976; Gaudant, 1979, 1981a, 1981b, 1984, 1987; 1993; Micklich, 1985, 1988; Sytchevskaya, 1986). In general, it was represented by a limited number of primarily freshwater groups of a low taxonomic diversity. These

include the Amiidae (with the genus *Cyclurus* which was also widespread in the Eocene of Asia and North America), Lepisosteidae (Lepisosteus), and the endemic Thaumaturidae and Palaeoesocidae (the genera *Thaumaturus* and *Palaeoesox*, respectively). In the Early and Middle Eocene, this set of taxa was occasionally enriched by the Characidae. An important role was played by eurybiontic Gonorhynchidae (*Notogoneus*). In the Middle and Late Eocene, the European fresh waters were repeatedly colonized by marine immigrants. The major invasion occurred in the Middle Eocene, where a large number of primarily marine groups is documented in the European freshwater assemblages; these include the Chandidae (genus *Dapalis* Gistel, which later became widespread in the fresh waters of the Oligocene of Europe), Percichthyidae (*Amphiperca* Weitzel; *Vixperca* Pena), Percoidei inc. sed. (genus *Anthracoperca* Voigt, *Rhenanoperca* Micklich et Gaudant, and *Pararhenanoperca* Micklich et Wuttke), ?Moronidae (*Palaeoperca proxima* Micklich), Anguillidae (*Anguilla* Shaw), and Beloniformes (Jimenez, 1977; Gaudant, 1984, 1993; Micklich, 1985, 1988; Micklich and Wuttke, 1988; Micklich and Gaudant, 1989; Gaudant and Micklich, 1990; Peña, 1991).

The Late Eocene invasion of marine taxa was less extensive and involved Percoidei inc. sed. (*Sargus* Cuvieri), Gobiidae (*Pomatoschistus* Sauvage), Atherinidae (*Palaeoatherina* Gaudant), and Clupeidae (*Alosa*). It is noteworthy that the double-armored clupeid subfamily, Pellonulinae (*Vectichthys* Newton) (Gaudant and Quayle, 1988), first recorded in fresh waters of Western Europe (British Isles) in the Late Eocene, was already widespread by that time in the freshwater basins of Asia (Zhang *et al.*, 1985; Chang and Chow, 1986; Chang and Zhou, 1993) and the Western Nearctic (Grande, 1982, 1984). The presence of this group in the Late Eocene of the British Isles is most probably attributable to its immigration from the Nearctic and Russo-Scandia. In the Late Eocene of Europe, the genera of the following dominant Early Paleogene European groups, descended from the Middle Eocene, continued to evolve: the Amiidae, Lepisosteidae, Gonorhynchidae, the endemic Thaumaturidae and Paleoesocidae, as well as the Percichthyidae, Chandidae, and Acipenseridae (Newton, 1899; Priem, 1900, 1911; Obrhelova, 1971, 1975, 1889; Wiley, 1976; Gaudant, 1987, 1993; Micklich, 1990). This time was also marked by the first appearance of advanced umbrids (*Proumbra* and *Umbra*) and the invasion of the Alosinae, Atherinidae and Gobiidae (Stinton, 1975–1984; Gaudant, 1993).

The Late Eocene freshwater ichthyofauna of Europe was the immediate successor to the Early–Middle Eocene fauna and is best represented by the assemblages of the Paris basin (Priem, 1900, 1911; Gaudant, 1979a, b, 1981a), southern France (Ferrandini *et al.*, 1976; Chedhomme and Gaudant, 1984), the Hampshire basin of the British Isles (Gaudant and Quayle, 1988), Isle of Wight (Newton, 1899), and Central Europe (Gaudant, 1987; Obrhelova, 1971, 1975; Micklich, 1990).

These assemblages provide records of almost all the families known to dominate the European Early Paleogene: the Amiidae, Lepisosteidae, Acipenseridae, Clupeidae, Thaumaturidae, Palaeoesocidae, Umbridae, Percichthyidae, Gonorhynchidae, Serranidae, Gobiidae, and Atherinidae.

As a whole, throughout the Eocene, the freshwater ichthyofauna of Europe was an insular community consisting of a few primarily freshwater elements and a great number of marine newcomers that adapted to freshwater. A percentage of primarily freshwater taxa was probably inherited from the Late Cretaceous fauna and reflected the Late Cretaceous Holarctic faunal links; however, this does not exclude the possibility of penetration of these forms to Western Europe from the Eastern Nearctic in the Paleocene and Eocene. The discovery of the Eocene Lepisosteidae, Amiidae, and Esocidae in Ellesmere Island in the eastern part of the Canadian Arctic Archipelago (Estes and Hutchinson, 1980) along with the presence of the genus *Cyclurus* in the Eocene of Spitsbergen (Gaudant, 1993) indicate the route of the European–Nearctic migrations. In the Eocene, the Gondwanan elements entered Europe several times. This primarily concerns the Early and Middle Eocene invasions of characins which most likely came from North Africa (Cappetta *et al.*, 1972; Cappetta and Thaler, 1974; Jimenez, 1977; Gaudant, 1993). In the Eocene, the European freshwater ichthyofauna remained isolated from the Asiatic fauna by the Peri-Tethys and West Siberian Sea.

According to Gaudant (1993), the Eocene ichthyofauna of Europe, including that of the Late Eocene, existed under the conditions of subtropical climate. This conclusion appears to be only correct with reference to Western and Central Europe, from where nearly all evidence on Eocene ichthyofauna was obtained and where the climatic zonation was certainly absent. However, in terms of Europe as a whole (including Russo-Scandia with its high latitude ichthyofauna), climatic differentiation probably existed. This is indirectly corroborated by the invasion of boreal elements (Osmeridae and Esocidae) to the South European basins during the Early Oligocene cooling (Gaudant, 1978, 1985), most probably, from Russo-Scandia. In addition, the data on Oligocene insects and plants (see accounts by Zherikhin and Akhmetiev in this volume) clearly point to climatic zonation in the Late Eocene.

Compared with the Amphipacific freshwater ichthyofauna, the fishes from the Early Paleogene of Europe demonstrate a lower taxonomic diversity. The only shared elements of both faunas were the Amiidae, Lepisosteidae, Clupeidae (Pellonulinae), Acipenseridae, and Gonorhynchidae, the latter represented by the genus *Notogoneus*. The most important feature of the European ichthyofauna is the complete absence of such primarily freshwater groups as Cyprinidae and Catostomidae (predominating in coeval Asiatic faunas). Herbivorous fishes are absent. As a whole, this was a community of stagnant or slow flowing water bodies.

Northern Asia. The data on the composition and nature of the Late Eocene freshwater ichthyofauna of Northern Asia were obtained from the study of assemblages of the Aksyir Formation of the Zaisan Depression (Eastern Kazakhstan), Eocene–Oligocene Uglovskaya Formation of the Primorye Region, Middle Eocene Kamchikskaya Formation of Kamchatka, Mongolia (Sytchevskaya, 1976, 1986), and from the analysis of published data on the Eocene faunas of China (Cheng, 1962; Wang *et al.*, 1981; Chang *et al.*, 1985; Zhou and Sun, 1985; Chang and Chow, 1986; Chang and Zhou, 1993) and Turkey (Rückert-Ulkümen, 1963). Since relationships with North America are of great importance, these faunas should be considered against the wider background of the entire Northern Hemisphere.

In the Late Eocene, the following forms predominated in the North Asiatic freshwater assemblages (based on the data from the Primorye and Kamchatka regions of Russia, Mongolia, China, and Eastern Kazakhstan): the Amiidae (*Cyclurus efremovi* and a number of problematic taxa); Hiodontidae (*Eohiodon* sp.); Salmonidae (*Eosalmo*); and numerous and diverse Catostomidae, widespread from the Zaisan Depression to the Primorye Region (*Vasnetzovia artemica, Amyzon zaissanicus, A. gosiutensis, Cycleptus robustus, Carpiodes brevidens, Erimyzon luxus, Minytrema shevyrevae, Xyrauchen rotundus, Xyrauchen sp., Moxostoma fungidens, Moxostoma cf. carinatum, Catostomus columnaris,* and *Catostomus* sp.). A wide distribution of the Catostomidae in Asia at that time is accentuated by the presence of this group in Eastern Kazakhstan, Primorye Region, and South China (Sytchevskaya, 1986; Chang and Chow, 1986; Lei, 1990). The Cyprinidae were scarce in Northern Asia, in contrast to the assemblages from the Eocene of South China, which contain a larger set of genera. In the Late Eocene of Eastern Kazakhstan, the presence of Barbinae is recorded and in Northern China (Zhang *et al.*, 1985) of problematic unidentified Cyprinidae. A noteworthy element was the catfishes of the family Bagridae.

To date, a large number of localities yielding Eocene fishes are known from China where they occur in 12 provinces (Chang and Zhou, 1993). The first data on fish from China (Hussakof, 1932) already contained information on the presence of the Amiidae (*"Pappichthys" mongoliensis*) and Catostomidae (*Catostomus* sp.) which were collected from the Ulan Shire Formation, Inner Mongolia (Shara Murun locality). The discovery of a large number of Eocene localities in Southern China and at the coast of Bohai Gulf (Liu 1957; Tang, 1959; Cheng, 1962; Liu *et al.*, 1962; Zhang *et al.*, 1985; Chang and Chow, 1986; Wang *et al.*, 1981; Shen, 1989) much improved our concept of the composition of the Chinese Eocene freshwater ichthyofauna. In the south of China, the presence of Cyprinidae, Bagridae, and Serranidae was detected in the Buxin Formation

(Wang *et al.*, 1981). Subsequently, this list was extended to include the Catostomidae and Osteoglossidae recorded in South China (Lei, 1990). In northeastern China, close to the Bohai Gulf, the Eocene beds were shown to contain the Dasyatidae, Paraclupeidae (*Diplomystus shengliensis*), Clupeidae (*Knightia bohaiensis*), Percichthyidae (*Tungtingichthys eocaena*), and pharyngeal teeth of the Cyprinidae (Zhang *et al.*, 1985). In the Eocene of the Jilin Province of North China, the Amiidae, Clupeiformes, Catostomidae, and Acanthopterygii were reported (Zhou and Sun, 1985). In Shandong, the fish assemblage includes Catostomidae, Amiidae, Hiodontidae, and uncertain teleosts; and in the Jiangsu Province, *Eohiodon shuyangensis* (Shen, 1989), *Liuheus gracilis* (Clupeidae), and *Tungtingichthys*. The Eocene freshwater fish of China show the split into two separate faunas. The first occurs on the coast of the Bohai Gulf and adjacent areas, and contains members of the families Dasyatidae, Amiidae, Hiodontidae, Clupeidae, Paraclupeidae, Catostomidae, Cyprinidae, and Percichthyidae. In most components, it is close to the fauna of Eastern Kazakhstan. The second Chinese fauna occurs in the southern provinces of China (Chang and Chow, 1986). In contrast to the northern community, it is dominated by cyprinids (with the genera *Barbodes, Varicorhinus, Zacco, Aphiocypris, Rasbora*, and Leuciscinae inc. sed.), bagrids (*Mystus* and *Aoria*); and acanthopterygians of the family Percichthyidae (*Tungtingichthys*). The southern fauna also includes the catostomid genus *Jianghanichthys* (Lei, 1990), previously identified as the cyprinid *Osteochilus*, and the osteoglossoid *Phareodus.*

As a whole, in the Eocene, North Asia (Eastern Kazakhstan, Primorye and Kamchatka regions of Russia, North China) was populated by a fish fauna which closely resembled that of the Western Nearctic, in the presence of freshwater sharks Dasyatidae, osteoglossomorphs Hiodontidae (*Eohiodon*) and Osteoglossidae (*Phareodus*), freshwater herrings Paraclupeidae (*Diplomystus shengliensis*) and Clupeidae (*Knightia*), salmonids (*Eosalmo*), and catostomids (*Amyzon*). This fauna thereby included the typical Eocene Amphipacific genera spread throughout both Asiatic and Nearctic realms of the Amphipacific Subregion. It should be noted that certain Eocene North Asiatic species of the Amphipacific fauna are extremely similar or even identical to their North American equivalents, as in the case of *Amyzon gosiutensis* (Sytchevskaya, 1986).

Zoogeographic Zonation

Until recently, the zoogeographic structure of Holarctic terrestrial regions in the Paleogene remained unknown because of the almost complete absence of reliable data on the ichthyofaunas existing at that time in Northern Asia and Eastern Europe. For this reason, the concepts of the distribution of Paleogene fish in the above area were either based on the data referring to the Neogene, and therefore implying a strong severance of

the Nearctic and Palearctic faunas (Yakovlev, 1961, 1964), or on even more indirect way of reasoning (Jerzmańska, 1979).

This situation has recently changed with the discovery of numerous North Asiatic Paleogene fish assemblages in the former Soviet Union and Mongolia (Sytchevskaya, 1976, 1986, 1989) and new data on fish assemblages that has been obtained from Europe, China, and North America (Liu 1957; Tang, 1959; Cheng, 1962; Liu *et al.*, 1962; Wilson, 1977, 1978, 1980; Gaudant, 1979a, 1979b, 1980, 1981a, 1981b, 1984; 1987, 1993; Micklich, 1985, 1988; Grande, 1980, 1982, 1984, 1999; Wang *et al.*, 1981; Zhang *et al.*, 1985; Zhou and Sun, 1985; Chang and Chow, 1986; Gaudant and Quayle, 1988; Shen, 1989; Lei, 1990; Gaudant and Micklich, 1990; Chang and Zhou, 1993; Grande and Bemis, 1998). The most valuable data, which overturned previously existing concepts of the biogeography of the Holarctic Paleogene fish came from Northern Asia. As noted above, in the Early Paleogene, this area together with the western part of North America formed a single zoogeographic unit, the Amphipacific Subregion, that persisted from the Late Cretaceous (Sytchevskaya, 1986). The rest of Holarctic apparently formed the Amphiatlantic Subregion that included the eastern part of North America and Europe. In the Eocene, these subregions were isolated in Eurasia by the Paleo-Paratethys and the West Siberian Sea and, in most parts of Nearctic, by a meridional marine gulf in the south of the continent and by a waterless area in the central North American continent (Strakhov, 1948).

The revision of the freshwater ichthyofauna of Central and Western Europe (Gaudant, 1979a, 1981a, 1981b, 1987, 1993, 1997; Micklich, 1985, 1988; Gaudant and Quayle, 1988; Gaudant and Micklich, 1990) along with the data on freshwater fish from the Paleogene of Eastern Europe (Danilchenko and Sytchevskaya, 1975; Sytchevskaya, 1976, 1986) and China (Zhang *et al.*, 1985; Zhou and Sun, 1985; Chang and Chow, 1986; Shen, 1989; Lei, 1990; Chang and Zhou, 1993) corroborated these conclusions. According to recent data on the fishes of Asia (China, Mongolia, Russia, Kazakhstan and Turkey) and North America (Rückert-Ulkümen, 1963; Chang and Chow, 1986; Sytchevskaya, 1986; Chang and Zhou, 1993), in the Eocene, the Nearctic and Asiatic realms of dispersal of the Amphipacific ichthyofaunas showed some distinctions in taxonomic composition, which warrants distinguishing them as two provinces of the Early Paleogene Amphipacific Zoogeographic Subregion.

Overall, the typical elements of the Amphipacific Eocene ichthyofauna were the families Amiidae, Dasyatidae, Hiodontidae (*Eohiodon*), Osteoglossidae (*Phareodus*), and Catostomidae. Freshwater clupeiforms of the family Paraclupeidae (*Diplomystus*) and subfamily Pellonulinae (*Knightia*), indicative of the Lower–Middle Eocene of North America (Grande,

1982, 1984; Chang and Chow, 1986), are recorded in Asia from the Early Cretaceous of Japan (Uyeno, 1979), the Late Cretaceous of Central Kazakhstan (Khisarova, 1971), and the Cretaceous and Eocene of China (Zhang *et al.*, 1985; Chang and Chow, 1986; Grande and Chang, 1999). Other common elements are closely related species of *Cyclurus* (Amiidae), long-bodied pikes of the subgenus *Esox* (Wilson, 1977, 1980; Sytchevskaya, 1986; Grande, 1999), and the early salmonoid *Eosalmo* recorded in the Eocene of British Colombia and Kamchatka (Wilson, 1977; Sytchevskaya, 1986; Wilson and Li, 1999). The above-mentioned similarity between the freshwater ichthyofaunas of Asia and the Western Nearctic was undoubtedly passed down from the Late Cretaceous. At that time both areas were connected by the Bering Land Bridge, while the western part of North America was separated from the eastern part by an epicontinental sea (Strakhov, 1948, Schuchert, 1957). For a number of families, their presence in the Cretaceous of both continents provides evidence for their Cretaceous origin (Amiidae, Hiodontidae, Paraclupeidae, and Clupeidae). This is also corroborated by the biogeographic links within other components of the terrestrial Cretaceous biota. Likewise, the Paleogene mammalian faunas give evidence that the Bering Land Bridge repeatedly appeared during several episodes from the Late Eocene to Early Oligocene (Kurten, 1966; Flerov *et al.*, 1974). Slower evolution of aquatic groups in comparison with terrestrial ones appears to account for the fact that the composition of the Amphipacific freshwater ichthyofauna retained the evidence of these old intrinsic interconnections for a relatively long time after the separation of Eurasia and North America. It is particularly remarkable that, in the latter, the main elements of the Amphipacific ichthyofauna, i.e., Amiidae, Hiodontidae, and Catostomidae, have survived up to the present day.

The evidence for the unity of the Amphiatlantic Subregion is more indirect, since the Paleogene ichthyofauna of the eastern regions of North America remains unknown. The main argument in this case relies on the parallels between the Recent ichthyofauna of this area and the extinct Paleogene communities of Europe. Each includes the families Cyprinodontidae, Umbridae and, apparently, a common lineage of deep-bodied pikes with a reduced vertebral count (judging by the morphological similarity of Paleogene European pikes to the recent Nearctic subgenus *Kenoza*). The faunas of the Amphiatlantic and Amphipacific subregions were isolated in Eurasia by an extensive epicontinental West Siberian Sea and, in the Nearctic, largely by a submeridional marine gulf. Nevertheless, occasional exchange between the faunas could have occurred through both the northern parts of Nearctic and a short-term land bridge in the Turgaj Region (Grossgeim, 1975). The evidence for such an exchange is the presence of the Gonorhynchidae in both zoogeographic subregions (in Europe and in the west of North America) starting from

the Eocene, and the Asiatic record of the Palaeoesocidae (*Palaeoesox asiaticus*) (Sytchevskaya, 1986), a group otherwise known in Europe since the Paleocene and there forming a characteristic element of the local Early Paleogene ichthyofauna. The penetration of the Palaeoesocidae into Asia is also indirectly corroborated by the occurrence of its descendants, the Dalliidae, in the Western Nearctic.[1] The other similar elements of both subregions include the percoids of the family Percichthyidae (*Tretoperca, Amphiperca*, and *Bilinia* in Europe and *Kiinkerishia* and *Tungtingichthys* in Asia). However, it is not ruled out that these forms or their ancestors could have spread via marine routes.

Against the background of the above general pattern of Paleogene fish distribution, some specific features of two Amphipacific realms are distinguishable. The Percopsidae, Aphredoderidae, and early Percidae and Esocidae are characteristic of the Eocene of North America and have not been found in Asia. However, this may be caused by extreme scarcity of finds of complete fish skeletons in Asia, which complicates the identification of the groups mentioned. A more reliable distinction is the presence in the Western Amphipacific of the Cyprinidae, which originated in Southern Asia and are unknown from the Paleogene of North America.

In the Late Eocene, the freshwater ichthyofaunas of Europe and North Asia still belonged to different zoogeographic subregions, a condition retained from the Paleocene and Eocene or even the Late Cretaceous. Over the entire Early Paleogene, these faunas were isolated by epicontinental seas. Rare faunal exchanges could occur through short-term insular contacts, most probably, in the region of the southern boundary of the Paleo-Paratethys. Certain euryhaline forms could have spread over desalinated coastal–marine belts.

The Late Eocene ichthyofauna of Europe was typically insular, and included a number of vicariant forms. It shared some dominants with the fauna of the eastern part of the Nearctic, i.e., the Amiidae (*Cyclurus*), Gonorynchidae (*Notogoneus*), Clupeidae (*Vectichthys*), and Umbridae (*Proumbra?* and *Umbra*). At the same time, some peculiar features of the European fauna suggest that it be referred to the specific European Province of the Amphiatlantic Zoogeographic Subregion. It seems likely that a certain degree of spatial differentiation could have existed for the ichthyofaunas of Northern (Russo-Scandia), Central, and Southern Europe.

The Late Eocene ichthyofauna of Northern Asia retained a similarity to that of the Western Nearctic in the presence of such dominant groups as the Dasyatidae, Amiidae (*Cyclurus*), Osteoglossidae (*Phareodus?*), Hiodontidae (*Eohiodon*), Catostomidae, Salmonidae

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[1] It is noteworthy that the areas of historical radiation of two lineages of the advanced umbroids (Amphiatlantic Umbridae and Amphipacific Dalliidae) have proven to be completely isolated, which emphasizes the severance of the two zoogeographic subregions under discussion.

(*Eosalmo*), freshwater clupeiforms of the family Clupeidae (genus *Knightia*), and Paraclupeidae (*Diplomystus*). At that time, as previously (in the Paleocene and Early–Middle Eocene), the range of the Asiatic fauna continued to be a part of the Amphipacific Zoogeographic Subregion and so formed a distinct Asiatic Province. The latter was characterized by abundance of catostomids (including almost all recent genera of this family) and by the appearance of rare of cyprinids, which remained absent in the Western Nearctic throughout the entire Paleogene and most of Neogene. It should be emphasized that, with the progress of the study on freshwater fish of Asia and the discovery of new localities, the list of common Amphipacific taxa tends to increase.

To conclude, in the Late Eocene, the freshwater ichthyofauna of Eurasia retained the basic zoogeographic structure characteristic of the Early Paleogene, primarily including a strong severance of the Asiatic and European communities. In summary this structure can be presented as follows:

> ### Holarctic Region
>> *Amphipacific Subregion*
>>> Western Nearctic Province
>>> Asiatic Province
>>>> North Asiatic Subprovince
>>>> South Asiatic Subprovince
>> *Amphiatlantic Subregion*
>>> European Province
>>> (?)Eastern Nearctic Province

LATITUDINAL CLIMATIC ZONATION OF THE LATE EOCENE

Based on the distributions of planktonic organisms, in particular, planktonic foraminifers, it should be concluded that, in the Priabonian, the Tropical Paleoclimatic Belt was located to the south of the region considered in this monograph. It included the region of the Caribbean basin and coasts of Central Africa. The planktonic assemblages on both southern and northern coasts of the Mediterranean did not differ in taxonomic composition from tropical assemblages; however, a decrease in the number of warm-water elements, discontinuous distribution of the latter, and an increase in the role of globigerinids indicate the climate most likely characteristic of the South Subtropical Zone. At the same time, judging from the presence of colonial reef-building corals and tropical genera of mollusks at both southern and northern coasts of the Mediterranean in the Late Eocene, the environment in shallow waters resembled tropical conditions. Proceeding from the ecological requirements of Recent shallow tropical genera of benthos, this implies the shallow waters retained temperatures of approximately 20°C for six months, and the temperature did not fall below 16–18°C. The faunas and floras of the southern coast were characterized by a higher diversity and a larger number of tropical taxa than those of the northern coast. In the Late Eocene, tropical forests of the northern coast of the Mediterranean included broad-leaved flora lacking any trace of xeromorphic features. In the Recent vegetation, forests of this type are evidence of abundant precipitation, distinct seasonal fluctuation of rainfall, and an average annual temperature of approximately 25°C. The rather rich taxonomic composition of shallow-water benthos and flora was probably determined by a climate in the Priabonian that was not only warm, but relatively consistent. Thus, it can be referred to as a paratropical climate. Similar paratropical faunas were also found at the American coast of the Atlantic in the Neogene (Petuch, 1988).

The fauna and flora of the Armenian Basin (which in the eastern part, opened into the Central Iranian Basin) were also rich and diverse. Up to the middle of the Early Oligocene, this area was inhabited by reef-building corals; however, they did not form large reef bodies. Complete assemblages of tropical plankton and benthos were found there, being distinguished by the fact that the most thermophilic species of planktonic foraminifers were not numerous or disappeared from the assemblages prior to complete evolutionary extinction (*Geologicheskie i bioticheskie…*, 1998). In this zone of a transitional climate between semi-tropical and subtropical, there was the boundary between the Humid and Arid belts, and abrupt climatic changes of humidity occurred over time. A large phase of increased aridity occurred at the interval of zones P15/P16. The greatest fluctuation of humidity occurred at the Eocene–Oligocene boundary.

The fauna of the northern coasts of the archipelago separating the Tethyan Realm from the Paleo-Paratethys was distinguished by the absence of the most thermophilic species of plankton and benthos and colonial reef-building corals, although is was characterized by an almost complete set of genera of warm-water mollusks and nummulites. These faunas can be regarded as subtropical, the development of which in coastal conditions required a temperature of approximately 20°C for four months and, at least, 18°C for 6 months. At the beginning of the Late Eocene, a slight fall in temperature probably occurred in the surface waters. Judging from the data on isotope analysis, at the latitude of Crimea, the water temperature in the warm season decreased from 22–23°C to 21°C (Marzuk, 1992).

The floras of these coasts consisted of small-leaved subxerophilous evergreen laurel-leaved forests (semiarid subtropics); this is evidence of dry seasonal climate, with the average annual temperature of 18–25°C and a temperature during the coldest month of, at least, 6°C.

The shallow-water faunas and floras of the northern coast of the Paleo-Paratethys also indicate subtropical conditions. The taxonomic composition of benthos was rich, numerous subtropical genera occurred; however, it substantially differed from that of the southern coast.

A diverse assemblage of colonial corals included many taxa, as in the Tethys; however, they did not form reef bodies in this area. The nummulite composition was especially distinct.

The flora of this coast was also undoubtedly subtropical, evergreen forms predominated; however, it was more mesophilic (semihumid subtropics). Judging from the flora, the average annual temperature was 15–20°C and the temperatures of the coldest and warmest months were 6–13 and 15–23°C, respectively. The average annual precipitation was 2000 mm in the west of the zone and 1000–1500 down to 800 mm in the eastern area; the fluctuation of rainfall was seasonal.

In this zone, the fall in temperature in the Late Eocene had a particularly strong effect; thus, the diversity of the marine fauna decreased in the later half of the Priabonian. The role of deciduous and coniferous elements of the floras, and general aridity, substantially increased towards the end of the Eocene.

The assemblages of planktonic foraminifers from this area were substantially impoverished. Short-term climatic fluctuations were pronounced (Marzuk, 1992). In the northernmost assemblages, the prevalence of globigerines provides evidence of transitional assemblages to those of the Temperate Belt.

The isolation of the Tethyan Realm from the Arctic Basin in the Late Eocene when the strait across Western Siberia was closed probably promoted the development of the Arid Belt along the boundary of the Ancient Mediterranean and the Paleo-Paratethys. Since a marine gulf of the Tethys extended deep into the continent through the Turgaj Depression and closed only in the high latitudes of Western Siberia, the newly formed climate resembled that of the Recent Mediterranean Region and was characterized by the same mode of seasonal precipitation. Against this background, the Transcaspian faunas and floras especially strongly differed from the others, this was determined by the highest aridity of climate and reflected historical isolation of their development.

Judging from the floral data, the subtropical conditions extended to the north of the coast of the Paleo-Paratethys, and the boundary between the subtropics and the Temperate Zone extended at the latitudes 60–65° N or further north. This is indicated by the presence of subtropical plants and insects in amber from the Baltic Region, and deciduous moderate floras in Spitsbergen and the Faeroe Isles. To the east of this region, the Temperate Zone is traced by palynological data in the Pechora Depression and at the boundary between the Northern and Middle Ural Mountains (Akhmetiev in *Geologicheskie i bioticheskie…*, 1998). In the Transural area this boundary deviated to the north and the entire West Siberian basin was in the Subtropical Zone because of the influence of warm waters entering there through the Turgaj Strait. Within Middle Siberia, the southern boundary of the Temperate Zone abruptly deviated to the south and was traced by floral data near the Zaisan Depression.

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