Biogeography of the Northern Peri-Tethys from the Late Eocene to the Early Miocene. Part 3. Late Oligocene–Early Miocene. Marine Basins

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Abstract—This contribution, the third part of a monographic series, deals with the biogeography of the Tethys and Paratethys sea basins in the Late Oligocene and Early Miocene and includes reviews of the stratigraphy and paleogeography of the Paratethys, descriptions of the biogeographic distribution of planktonic foraminifers, nanno- and organic-walled phytoplankton, benthos (benthic foraminifers, ostracodes, and mollusks), and the ich-thyofauna, and provides biogeographic zonation based on these groups. The final section deals with the evolution of the main biochores in the western Eurasian basins during the second half of the Paleogene and Miocene.

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INTRODUCTION

The goals and objectives of the present study, i.e., the reconstruction of the composition and distribution of the basic groups of marine and terrestrial fauna and flora of western Eurasia from the latest Eocene, Oligocene, and Early Miocene, against the background of the main geological events and the paleogeographic and climatic changes, as well as the concepts and methods of biogeographical analysis of modern flora and fauna that can be used in studies of fossil material, were discussed in the first part of the monograph. The present part discusses data on the biogeographic distribution of the planktonic and benthic organisms of the Late Oligocene-Early Miocene and the biogeographic zonation (integrated where possible) of water bodies. In conclusion, some aspects of the evolution of biogeographical units of the Late Eocene-Early Miocene are considered.

The body of data on the marine fossil faunas, and on the microplankton of the Late Oligocene–Early Miocene of the Eastern Paratethys, is considerably smaller than that for the Priabonian or Early Oligocene. The major facies of the Middle–Upper Maikopian, i.e., non-calcareous pyritized clays indicative of anoxic sedimentary environments, lack many groups of fossils. Thus, planktonic foraminifers are not preserved, and occurrences of nannoplankton are extremely rare. Only the shallowest marginal facies occasionally yield benthic foraminifers, ostracodes, and mollusks. Since these groups are small in number and are represented by small amounts of material, it is possible to publish their discussion in a single volume. The next volume will be devoted to the terrestrial biogeography of the same time interval, and will contain final chapters addressing climatic changes, major events of the Late Oligocene–Early Miocene, and the evolution of basic land biochores.

The sectional Stratigraphy of the Upper Oligocene– Lower Miocene has been written by S.V. Popov; the section Paleogeography of the Paratethys, by S.V. Popov and I.G. Shcherba. Data on dinocysts are presented by M.A. Akhmetiev, A.S. Andreyeva-Grigorovich, and N.I. Zaporozhets; on foraminifers, by E.M. Bugrova; on nannoplankton, by A.S. Andreyeva-Grigorovich; on ostracodes, by I.A. Nikolaeva; on mollusks, by O.V. Amitrov and S.V. Popov; and on ichthyofauna, by E.K. Sychevskaya.

CHAPTER 1. MARINE BIOGEOGRAPHY OF THE LATE OLIGOCENE

Stratigraphy of the Upper Oligocene

The stage was suggested by Fuchs and precisely fits the Upper Oligocene in the sense of Beyrich.

Northwestern Europe. The stratotype sections of the Chattian are located in northwestern Germany. Since the historical stratotype, sands at Kassel, corresponds only to the lower Chattian, Görges (1957) proposed the sections at Doberg as a hypostratotype. In Kassel the boundary between the Rupelian clays and the Chattian sands coincides with the boundary between the NP23 and NP24 nannoplankton zones, but in more complete Doberg sections and near Berlin, the base of the Chattian, as well as the upper Rupelian clays, are characterized by nannoplankton of the *Sphenolithus distentus* Zone (NP24). The *S. ciperoensis* Zone (NP25) has only been recorded in the middle of the Doberg section (Gramann and Spiegler, 1986).

Foraminifers are scarce in these sections: they are represented by the microfauna of the upper *Globigerina ciperoensis* Zone (P22: Pomerol, 1981) and, in the middle Chattian, by larger benthic foraminifers *Lepidocyclina morgani* and *Miogypsina septentrionalis*. The latter species is the earliest representative of the genus, descendants of which are common in the Early Miocene. There are two phytoplankton zones: D14b and D15. These sections are rich in ostracodes and mollusks. Anderson and R. Janssen (Pomerol, 1981) divide the Chattian into three parts (A, B, and C) based on pectinids. Because these sections do not contain a continuous succession of strata, the Chattian–Vierlandian transition is known from deeper water sections in northwestern Germany. A continuous section of Oligocene sediments was revealed by the Gartow Borehole in northern Saxony, where the Chattian comprises the horizon with *Asterigerina*, the Eochattian, and the Neochattian, which is represented by the uppermost D14b Zone and the entire D15 Zone (Kothe, 1990).

In the Vierlandian, nannoplankton is represented by *Triquetrorhabdulus carinatus* Zone (NN1). A Lower Miocene dinocyst assemblage with *Tuberculodinium vancampoae* was recognized in northwestern Germany in Borehole Böhme 6 (Benedek, 1986). In addition, Borehole Wursterheide (at a depth of 340–333 m) yielded an assemblage with *Hystrichokolpoma poculum* and *Hystrichosphaeropsis obscura* from zones D16 and D17 (Heilmann-Clausen and Costa, 1989). Judging from the pectinid fauna, the upper Chattian more closely resembles the Miocene; however, the Chattian–Vierlandian boundary in boreholes of northern Germany also shows considerable changes in the taxonomic composition of mollusks (Hinsch, 1993).

In complete sequences of deep-sea cores, the Chattian is represented by planktonic foraminifers of the *Globigerina angulisuturalis–Globorotalia opima opima* (P21b) and *Globigerina ciperoensis* (P22) zones (Berggren *et al.*, 1995), nannoplankton of the upper NP24 Zone and Zone NP25, and dinocysts of the upper D14b Subzone and Zone D15 (the upper *Chiropteridium partispinatum* Zone).

Western Paratethys. In the Hungarian Paleogene Basin, which is considered as the type area for the Western (or Central) Paratethys, the Chattian corresponds to the Upper Kiscellian (the Kiscell Clays Formation and its equivalents) and the lower, larger part of the Egerian. The Kiscell Clays are characterized by the nannoplankton of Zone NP24 and planktonic foraminifers of the *Globorotalia opima opima* Zone (Nagymarosy and Báldi-Beke, 1988) and rich assemblages of ostracodes and mollusks (Báldi, 1986). The calcareous clays of the Eger Formation conformably overlie the Kiscellian and contain nannoplankton in the upper NP24 Zone and in Zone NP25 and foraminifers of the *G. opima opima–Miogypsina septentrionalis* Zone (Nagymarosy and Báldi-Beke, 1988).

In the Alpine Foreland the Chattian corresponds to the upper Lower Marine Molasse (Berger, 1992). The Upper Kiscellian is correlated here with relatively deep-water carbonate clays, the Tonmergelstufe (Báldi, 1986), and the Lower Egerian is correlated with coarser sandy clays of schlieric facies up to 1000 m thick (the Puchkirchen Beds). These sediments show a facies transition into continental deposits of the Lower Freshwater Molasse, represented by lacustrine sediments and sands and conglomerates of alluvial fans (Berger, 1996).

In Northern Transylvania (Preluca) the Chattian corresponds to the larger part of the Vima Formation, the upper portion of which is dated Lower Miocene (Rusu **BIOGEOGRAPHY OF THE NORTHERN PERI-TETHYS**

et al., 1996). The nannoplankton includes species of zones NP24 and NP25 (up to NN2), and the planktonic foraminifers include Globigerina ciperoensis (P22) in the middle part of the formation, and the Lower Miocene species *Globigerinoides triloba* in the upper part. Further west and southwest the lower Vima Clays give way to the Buzas sandstones and still further (the Meses and Gilau areas) to coarse terrigenous lagoonal, brakish-water estuarine facies with Corbula shells (the Cetate Beds, Zimbor).

Carpathian Basin. In the Flysch Carpathians the Chattian is correlated with the Middle Menilite Subgroup (100 to 200 m thick): Lopyanka Formation with the bed of the Golovetskian Limestone at the base. These deposits contain planktonic foraminifers with Globigerina ampliapertura; nannoplankton characteristic of the Sphenolithus distentus Zone (NP24) in the lower part and nannoplankton with Turborotalia opima opima, Globigerina ciperoensis (P22), and Sphenolithus ciperoensis (NP25) in the upper part; and dinocysts of the Chiropteridium partispinatum Zone (Andreyeva-Grigorovich and Gruzman, 1994; Andreyeva-Grigorovich et al., 1995). This predominantly claystone-siltstone sequence is overlain by the Upper Menilite Subgroup of the Lower Miocene with marker levels of the upper silicious bed at the base. In the Krosno-type section the Chattian corresponds to the lower part of the Krosno sandstones (the Lower Krosno Subformation), and the uppermost flysch beds of the lower Krosno are correlated with the Lower Miocene (Andreyeva-Grigorovich and Gruzman, 1994; Andreyeva-Grigorovich et al., 1995). In the Western Carpathians, based on the presence of nannoplankton of zones NP24 and NP25 to NN1, the Egerian is correlated with the Zdánice-Hustopeče Formation, which is up to 1300 m thick. These are transitional facies from flysch to molasse (Krhovsky et al., 1995).

Further to the east, in the Romanian Carpathians, within the inner zone of the Flysch Carpathians, the Krosno facies pass into the Pucioasa Formation with sandstones and interbeds of Jaslo-type striated coccolith limestones, which contain nannoplankton assemblages characteristic of zones NP24-NP25 (Rusu et al., 1996). In the outer zone the formation is an age equivalent of the lower Kliwa sandstones with interbeds of the same limestones containing a similar nannoplankton assemblage.

Eastern Paratethys. The boundary of the Rupelian and Chattian was drawn here in the roof of the Solenovian Horizon, based on the occurrence of marine benthic fauna with the foraminiferal assemblage of the "Virgulinella Beds," (Virgulinella ex gr. pertusa, V. karagiensis, Globigerina parva, and G. officinalis see Mikhailova, 1968; Semenov and Stolyarov, 1970), ostracodes, and mollusks, including the Chattian A index species, Chlamys bifida (Merklin, 1974; Popov et al., 1993). Detailed study of nannoplankton (data from J. Krhovsky) and dinocysts in western Ciscaucasia (the section of the Belaya River) shows a somewhat higher position of the plankton-based boundary, possibly inside the upper, calcareous subformation of the Morozkina Balka Formation (Akhmetiev et al., 1995). Thus, the Upper Oligocene in western and central Ciscaucasia should include the uppermost Morozkina Balka Formation (indicated by the nannoplankton of the upper NP24 Zone and dinocysts of Zone D14b), the Batalpashinsk Formation (D14b–D15), and the Septarian Formation (NP25; D15, including the epibole of Deflandria spinulosa). The overlying Karadzhalga Formation belongs to the Miocene on the basis of the presence of Triquetrorhabdulus carinatus (NN1) and dinocysts of Zone D16 on the Belaya River. However, the Caucasian geologists (Dmitrieva et al., 1959) traditionally accept the same level as the base of the Alkun Formations.

In the North Black Sea Region and Crimea, the Lower–Upper Oligocene boundary is usually drawn at the top of the Serogozy Formation. The Chattian includes the Askanian and Gornostaevka formations and their age equivalents in the Crimea, the Kerleut beds. Planktonic foraminifers have only been found in the deepest water parts of the Askanian Formation in association with *Globigerina ciperoensis*. Dinocysts are abundant throughout the sequence and belong to the Chiropteridium partispinatum Zone. Frequent discrepancies between lithological and biostratigraphical boundaries are noteworthy, presenting further evidence of diachronism among formations of Maikopian deposits (Andreyeva-Grigorovich and Gruzman, Konenkova, 1993; Andreyeva-Grigorovich and Gruzman, 1994).

In the more northern regions of the Volga–Don Interfluve and the Ergeni Upland, Semenov and Stolyarov (1988) established the Kalmykian Formation for the Chattian age deposits of the Maikop Group. The formation was later raised to become the Kalmykian Regional Stage of the Eastern Paratethys (Popov et al., 1993). In the deeper water zone, the lower parts of this unit contain Virgulinella layers; and in the shallow-water zone, they yield mollusks with Chlamys bifida and benthic foraminifers of the Spiroplectammina terekensis and Haplophragmoides kjurendagensis zones.

The assemblage of organic-walled phytoplankton of the Kalmykian Regional Stage allows recognition of two dinocyst zones, which are widely observed beyond the Paratethys. These are the Chiropteridium partispinatum-Rhombodinium draco Zone (lower) and the Deflandrea spinulosa-Homotriblium tenuispinosum Zone (upper) (data from N.I. Zaporozhets and M.A. Akhmetiev in Popov et al., 1993). The rich assemblage of foraminifers, ostracodes, and dinocysts of Zone D14b, and marine mollusks with Chlamys *bifida* allows continuation of the lower Kalmykian Regional Stage, which is defined in the North Black Sea Region (lower Askanian), as far as the Aral Sea Region (the Karatomak Formation). The upper beds of the regional stage are characterized by the impoverished assemblages of mollusks with *Cerastoderma* prigorovskii and *Corbula helmerseni*, and benthic foraminifers with *Cibicides ornatus* and *Elphidium onero*sum, which are traceable along the entire northern and eastern margins of the Eastern Paratethys (the Upper Kalmykian Subformation of the Ergeni Upland, the Upper Karagie Subformation in Mangyshlak, the Baigubek Formation of the Ustyurt Plateau, and the Upper Sarbatyr of the Kyzylkum Desert).

In eastern Ciscaucasia the Batalpashinsk Formation is correlated with the Mutsudakal-Miatly Formation, which includes considerable sandstone members, and the Argun Formation; the correlation is mostly based on their stratigraphic position of the formations between the somewhat more carbonaceous equivalents of the Solenovian Horizon and the Alkun Horizon. The lower beds of the overlying Assa Formation contain an impoverished microfauna with *Bolivina goudkoffi* in the western part of the region (Kabardino-Balkaria and Northern Ossetia) and septarian nodules in the eastern part, and are correlated with the lower beds of the "Caucasian," i.e., with the Zelenchuk or Septarian Formations.

In Transcaucasia the Chattian corresponds to the lower Uplistsikhe Formation of Georgia based on its stratigraphic position above the *Corbula* Beds (the Solenovian Horizon) and on the microfaunal and nannoplankton content. In the lower beds of the formation, A.P. Pechenkina recorded benthic foraminifers characteristic of the "*Virgulinella* Horizon" (Voronina *et al.*, 1991), and A. Nagymarosy determined here species characteristic of the *Sphenolithus distentus* Zone, NP24 (Nagymarosy and Voronina, 1993).

Paleogeography of the Paratethys

The Late Oligocene Basin was the most regressive of all the Late Paleogene basins of the Paratethys (Fig. 1). It was reduced in size, losing areas that were the northern and southern margins of the preceding Rupelian Basin. To the south the Savian Orogeny created a continuous land massive, which completely isolated the Eastern Paratethys from the Tethys. At the same time the axial part of both the Carpathian and Euxino-Caspian basins inherited the principle paleobathymetric pattern of the Rupelian and was subjected to a new phase of deepening, which had a stronger effect within the deep shelf depressions (Beer and Shcherba, 1984; Shcherba, 1987, 1993). Sedimentary and facies environments experienced only slight changes over time, water stratification and hydrogensulfide contamination affected the outer shelf zone and persisted throughout the greater part of the Paratethys (the Menilite and Maikopian facies).

The Carpathian Basin was connected to the Mediterranean predominantly in the west, through the Slovenian Corridor which, judging by sedimentary features, was relatively wide and deep in the Chattian (Nagymarosy, 1990). It is likely that at the beginning of the Chattian the Western Paratethys was connected with the North Sea via the system of Rhine grabens (Berger, 1996). Zoogeographic evidence suggests that the Eastern Paratethys may have had connections, even if intermittent, with the North Sea. These connections ran either through the axial zone of the Dnieper–Donets and Pripayt' depressions (as in the Rupelian, see below) or, less likely, may have passed through the Carpathian Basin via a presumed connection with its northern shelf through the Byrlad Corridor. The latter connections are inconsistent with the appearance of the Carpathian faunas, which suggest warmer waters than those of the Eastern Paratethys.

Carpathian Basin

In the Chattian this basin retained nearly the same bathymetric pattern as in the Rupelian, but experienced a slight reduction of its southern shelf. Contrary to the Lower Oligocene, the Upper Oligocene sediments have a generally regressive character and represent gradual infillings of sedimentary basins, in which the contribution of terrigenous (coming both from coastal zones and inter-basin uplifted areas) sandy material increased upsection. The overall composition of sediments became considerably more carbonaceous.

The axial part of the Carpathian flysch basin west of the Silesian Cordillera and its equivalents in the Romanian Carpathians underwent folding and uplifting in the Middle Oligocene (Beer and Shcherba, 1984; Sandulescu, 1987). This development led to drying up of the Ceahlau Zone and, during the Egerian, of the Dukla and, partly, Magura zones. This reduced the width of the deep-water part of the basin and resulted in increased differentiation of the bathymetric and hydrodynamic conditions of sedimentation and, thus, in the formation of zones that varied considerably in their sedimentary pattern along the axis of the trough.

The deepest water portions were located in the eastern Silesian, Krosno, and Tarcau zones and in the Verkhovina Depression of the southwestern Skibas Zone. These regions were characterized by carbonaceous and bituminous mud with small quantities of sands and occasional influxes of sandy turbidites of the upper distal Lower Krosno flysch and the lower Middle Krosno medium-rhythmic flysch, and the upper Romanian Pucoasa Beds. The thickness of deep-water sediments amounts to 700 m. In the western direction, towards the newly formed uplift, these sediments show increasing proportions of sandy turbidites and fluxoturbidites (30-40 cm thick in the Otritian sandstones of Poland and their equivalents in the Ukrainian Carpathians; see Kul'chitskii and Sovchik, 1986). The Marmaroš Massif was a source of micaceous sand and large wood fragments. Olistostromes of these deposits were produced by nappes of the Burkut-Dukla and Magura zones, their frontal parts reached the western

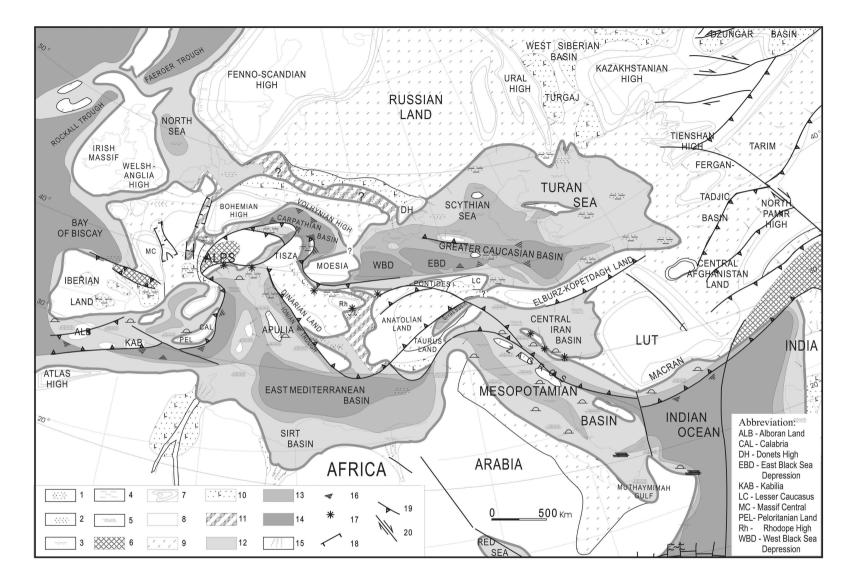


Fig. 1. Paleogeographic map of the Tethys and the northern Peri-Tethys in the Chattian. Designations: (1) conglomerates, (2) sands, (3) clays, (4) marls, (5) limestones, (6) mountains, (7) highlands, (8) undifferentiated land, (9) lowlands, (10) lake basins, (11) lagoons occasionally invaded by sea, (12) shallow shelf, (13) deep shelf, (14) continental slope and bathyal, (15) terrigenous material, (16) flysch, (17) volcanoes, (18) faults, (19) nappes, and (20) shifts.

margins of the Ždánice–Silesian Depression (Beer and Shcherba, 1984; Shcherba, 1993).

In the Romanian Flysch Carpathians the uplifting and folding affected the Audia Zone, the eastern extension of the Silesian Zone. Here coarse sandy material (the Fusaru sandstones) and olistostrome occurred almost throughout the front of the deep-water sequence of the Tarcau Zone (Stefanesen *et al.*, in Shcherba, 1993). Simultaneously with the nappe formation, shallow-water depressions of the Magura, Burkut-Dukla, and Audia zones were infilled by sandy fans (the Malyi Vizhen' Formation, Jawornik Beds of Poland).

In the Skibas-Pokut Zone, which was situated at the base of the continental slope, the sedimentation was dominated by bituminous muds with interbeds of sandy-micaceous fluxoturbidites (though less frequent than in the Verkhovina Depression) and 1–3 m thick members of oligomictic Kliwa sands coming from the Sandomierz Range (the Lower Menilite Subgroup with the Kliwa sand and the Lopyanka formations). All these deposits were subjected to consedimentary sliding, which became stronger towards the continental slope (the Pokut Zone) (Beer and Shcherba, 1984). The presence of beds with shells of shallow-water mollusks, which were transported here by turbidite flows, indicates the close proximity of sedimentary sources.

In the eastern (Romanian) part of the Carpathian Basin, the continental slope margin was situated further into the Carpathian Foredeep, which accumulated thick (500–600 m) sandy-muddy deposits. The sandy material originated both from the foreland (white quartz Kliwa sandstones) and from the Marmaroš and Getic Mesozoic crystalline massifs of the Inner Carpathians (micaceous gray carbonaceous Fusaru Sandstones). The fact that the contribution of the latter sources increases upsection indicates that these structures rose during the Chattian. The presence of olistostrome members, coarse gravelly material, and gravitational sliding point to the steepness of the continental slope, which increased at the beginning of the Late Oligocene.

Southern shelf. At the beginning of the Late Oligocene, the Alcapa Block experienced a considerably eastward shift resulting in the closure of the peripheral Podhale Depression, where the flysch sedimentation was terminated as early as the Rupelian. The shelf was further enlarged by the addition of the Magura Depression. Flysch continued to accumulate only in the considerably reduced Szolnok Trough. The inner part of the block differentiated into two parts: the Tatran Highland rose and the Hungarian Paleogene Basin and its extensions in Slovenia and Northern Croatia subsided. The Kiscell-type clays with their characteristic assemblage of benthic foraminifers and nannoplankton continued to accumulate in this region (Zone NP24). The connection between the Western (Central) Paratethys and the Mediterranean, interrupted in the second half of the Rupelian (Nagymarosy, 1990), was reestablished along the Slovenian Corridor. Thus, the Tethyan migrants, like mollusks and large foraminifers (*Miogypsina*, *Lepidocyclina*), reappeared here. In the northwest, at the boundary with the Tatran Uplift, this basin became shallower, and clays changed into sandstones and conglomerates (Harshegy, northern part of Buda).

Regressive features increase upsection of the sediments of the Hungarian Basin, with shallow-water and even brackish-water lagoonal facies emerging during the Egerian. The tectonically active Peri-Adriatic Suture was a source of sporadic andesite volcanism from the latest Kiscellian to the earliest Egerian.

The Tisza Block was not subjected to such significant horizontal movements as the Alcapa Block, but it was involved in a general uplifting. Clear indications of the Apuseny Land rising are observed in the deposits of the Transylvanian Basin. In its coastal part the conditions of brackish-water lagoons and river deltas (the Cetate Formation) prevailed. The Gilau area is characterized by coastal marine sandy deposits of the Buzas Formation with a rich benthic fauna. Along the strike and in the sections, these deposits gave way to more pelagic clayey sediments (the Vima Formation), which were fairly thoroughly characterized by plankton assemblages. Further east, nearer the axis of the Carpathian Basin, the Transylvanian Shelf Depression is still deeper. Here, the sediments bear indications of hydrogen-sulfide contamination of the water, such as bituminousity of clay and a lack of benthos. At the same time, these clays are interlayered with sandy fans that originated from the Marmaros Upland and contributed considerably to the build-up of the total thickness (up to 700 m) of these deposits.

The connection between the Carpathian Basin and the Thracian or Pre-Rhodopian Basin was interrupted in the Late Oligocene. This basin was nearly completely sealed by deposits. In Turkish Thrace, East Macedonia, and Southern Bulgaria, the marine facies changed into lagoonal, coal-bearing, and lacustrine sediments. The depressions in the Morava-Sumadian Zone of Serbia were also filled with lagoonal, lacustrine, coal-bearing, and red-colored deposits. In the Egerian, active volcanism was manifested in Serbian Moravia, Shumadia, and East Dinarids (Andjelkovic *et al.*, 1991)

Northern shelf, most probably remained very narrow, and its deposits in the Precarpathian area are known only in the Moravian Depression. Here they are represented by shallow-water dark sandy clays with *Miogypsina complanata*. Drilling data show that a wide open sea had existed in the area that was later to be the Vienna Basin, and in the Waschberg area. The shelf deposits are much more widespread in the Alpine Foreland in Bavaria, where they are represented by the upper part of the Lower Marine Molasse. These are relatively deep-water clays with foraminifers of the late Kiscellian and sandy schlieric clays (up to 1 km thick), indicating a progressive shallowing of the basin in the Egerian. Sandy deposits located south of the Bohemian Massif represent off-shore facies, and further south, sands of the Alpine Foreland were deposited by turbidite flows. Further west, the marine facies of the basin are replaced by fresh-water and terrestrial fan sands and conglomerates of the Lower Freshwater Molasse (Berger, 1996). In the Chattian the rate of uplifting of the Alpine–Western Carpathians Land increased, thus resulting in mountain structures that provided an abundant supply of clastic materials, which filled the Alpine Foreland and prevented marine sedimentation in its western part.

Biogeographic data show that during the Egerian the Tethyan influence increased in the eastern part of the Alpine Foreland and in the Inner Carpathian basins. Thus, warm-water molluskan taxa and *Miogypsina formosensis* appeared in the equivalents of the Early Egerian (Báldi, 1986). There are reconstructions that mean direct communication with the Mediterranean at the Eastern–Central Alps boundary (Steininger and Wessely, 2000, text-fig. 9).

It seems likely that in the southeast the northern shelf was constantly connected with the Euxino-Caspian Basin of the Eastern Paratethys through the Pre-Dobragean passage located north of the Moesian Plate (Fig. 1). Although no deposits from this time are yet known in this area, this link is fairly clearly indicated by the similarity of the geological history and fauna.

Greater Caucasus-Kopet Dagh Basin

In the Late Oligocene, an uplifted dry land appeared at the southern margin of the Eastern Paratethys for the first time, and the molasse accumulation started in the areas surrounding the Lesser Caucasus. During the same tectogenetic cycle, the bottom differentiation of the shelf area increased. An increase in the slope processes and an accumulation of breccias and large sandstone members occurred on the slopes of the deepening depressions.

The appearance of species shared with the North Sea Basin, including the zonal Chattian A species (*Chlamys bifida*), which are unknown from the Carpathian Basin, in the Eastern Paratethys after the Solenovian brackishing event, suggests that direct communication through the Dnieper–Donets and Pripayt' Depressions occurred intermittently (Amitrov, 1993). However, there is still insufficient evidence, in our opinion, of the Chattian age of the sandy sediments of Ukraine. Marine deposits of the Chattian are also unknown in Belarus and northern Poland.

The intake of marine water temporarily improved the gas exchange regime in comparison with Late Solenovian times. This is supported by the appearance of both planktonic and benthic faunas of the *Virgulinella* Beds and their equivalents (NP24). Subsequently, however, the most prolonged and dramatic anoxic period took place in the Maikopian Sea. It was reflected in the deposition of slaty clays with pyrite and without fauna.

The axial zone slightly changed its configuration due to the initiation of the closure of the residual marginal basin of the Greater Caucasus, specifically, in its western part (Kopp and Shcherba, 1998). In the Oligocene the profile of the continental slope became gentler but more dissected. An underwater uplift in the upper part of the slope along the southern flank of the Indol–Kuban Depression of the western Caucasus intercepted sandy flows and led to a significant increase in sand content and sliding of the Oligocene sediments in the zone of the Akhtyrsk Fault.

The peripheral Kerch–Taman and Tuapse depressions and the Sorokin Trough were subjected to rapid subsidence and were filled by muddy sediments several kilometers thick, containing sandy material. It was probably the time of the onset of numerous clay diapirs.

Deposits of the Lazarevskoe–Kobystan deep-water trough represented by a thin (300 m) member of pyrobituminous clay shales are only preserved in the east (the North Kobystan Zone of the southeastern Caucasus). Further north and south, these sediments become higher in sand content and increase in thickness up to 350–400 m. The southern slope of the depression was an accumulation zone for thick lenses of flyschoid sediments, which were rich in sandy turbidites, fluxoturbidites, and olistostromes (the Kinta Formation of Kakhetia), an indication of the increasing steepness of the trough valley at the beginning of the Chattian.

The axial parts of the Schatsky and Kyurdamir swells were generally shallower than in the Rupelian. A considerable transverse uplift took place in the area of the modern Dzirul Massif, which became an area of erosion from which sandy material was transported into the Kartli Depression (Uplistsikhe Formation). The increase in the sand content of Oligocene sediments is also observable off the axial zone of the Middle Kura Depression towards the eastern extension of the Dzirul Massif.

The volcanic activity in the Adzhar-Trialet and Talysh Depressions almost ceased. It was an accumulation area of non-calcareous bituminous oozes disturbed to varying degrees by the rhythmic supply of sandy turbidites. The latter are dominated by graywacke varieties with ligulate hieroglyphs, pointing to the local source of erosion. Unlike previous stages, there are lenses of quartz sand, which most likely originated from more remote erosional sources in the south. In the Adzhar-Trialet region the southern slope of the depression became steeper and experienced a large-scale sliding of non-lithified deposits. Here, as well as in the Talysh, the overall northward progradation of flysch clinoforms is observed. In the Adzhar-Trialet region continental sediments appear on the uplifted wing of the Paleocene-Early Oligocene clinoforms (Shcherba, 1993).

The southern shelf in the Chattian was reduced as a result of the retreat of the sea and establishment of continental conditions (Akhaltsikhe). In the Late Oligocene the Yerevan-Ordubad Depression became an area of accumulation of continental molasse. Along the southern scarp of the Somkhet-Agdam Uplift ran a narrow strip of lacustrine coal-bearing basins, relicts of earlier lagoons. The shallow coastal zone with widespread sandy contourites is clearly traced along the Adzhar-Trialet, Lesser Caucasian, Talysh, and Elburs zones of uplift. The deposits of this zone are represented by poorly sorted, mainly sandy rocks with shallow-water benthic fauna (sand with gravelly interbeds in the Gori and Gyandzha districts). But even this shallowest zone shows indications of long periods of standing water with hydrogen-sulfide anoxia and insertion of pyrite-containing deposits.

In the deeper zone of the Transcaucasian shelf, an accumulation of mainly clay deposits continued. These are predominantly calcareous sediments with benthic foraminifers *Uvigerinella californica*, *Bolivina goud-koffi caucasica*, *Virgulinella* ex gr. *caucasica*, and *Caucasina schischkinskayae* (data from A.P. Pechenkina in Voronina *et al.*, 1991) and nannoplankton of the *Sphenolithus distentus* Zone (NP24) (Nagymarosy and Voronina, 1993). The overlying clays with insertions of sandy members contain no faunal remains and accumulated under anoxic conditions (sections of the Hashuri District, and the Zemo-Avchaly Hydroelectric Station, the Tbilisi area).

Northern shelf. After the Late Solenovian regression in the Early Kalmykian time (Early Askanian, Late Morozkina Balka, and Karatomak), the basin showed a small expansion and a short-term improvement in the gas exchange regime, which resulted in the accumulation of calcareous facies with the nannoplankton of Zone NP24 and wide dispersion of benthic foraminifers (*Virgulinella* Beds) along the Eurasian shelf. The shallower water zone was populated by mollusk assemblages with *Chlamys bifida*, traceable along the entire northern and eastern margins of the Eastern Paratethys from the North Black Sea Region to the Aral Sea Region and the Kyzylkum Desert (Merklin, 1974; Popov *et al.*, 1993), as well as an assemblage of ostracodes (Askanian and Karatomak Beds).

During the subsequent period of maximum (Batalpashinsk) hydrogen-sulfide anoxia, the benthic fauna could only survive in the shallowest coastal zone. Judging from the composition of the ichthyofauna and planktonic flora and by the increased role of prasenophytes in dinocyst assemblages, the rise of the anoxic zone can be reconstructed up to a few tens of meters below sea level (Danil'chenko *et al.*, 1980) and affected even the photic zone (data from M.A. Akhmetiev and N.I. Zaporozhets).

The western and central parts of the shelf (the North Black Sea Region, the Steppe region of the Crimea, the Indol-Kuban Depression, and central Ciscaucasia) are dominated by muddy sediments without benthic fauna. Throughout nearly the entire territory of Ciscaucasia, however, the background clay sediments were interpolated by sandy lenses supplied by undercurrents (Zelenchuk sands, Mutsudakal-Miatly sands, and sands of the Neftegorsk District). The most abundant sandy material came to eastern Ciscaucasia from the Russian Platform. In the Kuma Depression numerous seismic survey profiles show a thick (up to 900 m) prograding detrital cone (Kunin et al., 1989), which by the end of the Oligocene completely filled the early Oligocene deep-water depression. Condensed sedimentation with an abundant fish material was a characteristic feature of the northern edge of this depression, which was steadily eroded. The fish detritus absorbed uranium and rare earth elements from the seawater and provided economic concentrations of these elements (Stolyarov et al., 1991).

Thick (up to 400 m) clays with sand beds accumulated along the northern scarp of the Indol-Kuban Depression. The depths around 800 m are reconstructed here for mid-Oligocene based on the magnitude of sandy clinoforms detected in the Sea of Azov (Tugolesov *et al.*, 1985). Sand was also transported from the southeastern flank, from the island of the western Caucasian Uplift (sands of Neftegorsk District, sandy fans of Gubs and Fars rivers, deltaic sands of the Bolshaya Laba River) (Kalinenko, 1990).

The northern steep slopes of the depressions considerably deepened in the Middle Oligocene and, thus, became an area of thick underwater gravitational sliding affecting both the bedrock of the slope and sands of fore-deltas that accumulated on the slope. Particularly intensive sliding occurred on the slope of the Terek Depression: the seismic profiles in this area show chaotic patterns instead of reflecting surfaces. The southeastern slope of the Indol–Kuban Depression, faulted in the zone of the Akhtyrsk Dislocations, was also steep. The Akhtyrsk Cordillera was subjected to gravitational sliding supplying large blocks of Cretaceous and Paleogene bedrocks into the depressions. These breccias are exposed in sections along the Pshish and Pshekha rivers and are also well traceable in the seismic profiles.

In Transcaspia, the clayey sedimentation under hydrogen-sulfide anoxic conditions occurred only in the relatively deep-water western parts of the South Mangyshlak and cis-Kopet Dagh shelf depressions. The rest of the extensive eastern shelf, occupied by the Turanian Sea, was fairly shallow and shows no evidence of anoxic conditions. Even in the deepest Daryalyk–Daudan Depression, all levels of the Oligocene are characterized by the fauna of benthic foraminifers (Ivanova, 1971) and mollusks (data from N.A. Fokina and R.L. Merklin from the boreholes drilled by the Soyuzburgaz in the 1960s).

In the second half of the Chattian, during the Late Kalmykian (Baigubek) time, the water body of the entire northern shelf was considerably freshened, as indicated by the benthic mollusk and foraminifer faunas. The impoverished assemblages with Cerastoderma prigorovskii–Corbula helmerseni and Cibicides ornatus-Elphidium onerosum were distributed universally from the North Black Sea Region to the Aral Sea Region. On the eastern shelf it was the time of the maximum Oligocene transgression. The composition of phytoplankton shows the presence of this phase of considerable freshening of the Paratethys in the deep-water facies of Ciscaucasia as well (Septarian Formation in the section of the Belava River) (Zaporozhets, 1998). This was probably caused by intensification of river drainage during the humid Late Oligocene. Data from benthic foraminifers indicate that this freshening affected the southern shelf too (see below).

Biogeography of Water Bodies

Planktonic Foraminifers

The presence, abundance, and diversity of plankton, as well as its genus-level structure, depended not only on the climatic zonality but mostly on the degree of communication of a given area with the oceanic basin and also on the local facies environments (Fig. 2). Moreover, similarities and distinctions between faunas of different regions that are based on data from the literature can be misleading, since some species may be absent and others may be attributed to different genera. Therefore, the evaluation of the regional diversity of a group depends on the level of knowledge, and on the taxonomic system followed by a paleontologist. This review follows the genus-level taxonomy used by the authors; the number of genera would increase if the latest taxonomic system, of A. Loeblich and H. Tappan, were used.

The planktonic foraminifers of Syria are among the most thoroughly studied (Krasheninnikov, 1969a, 1971, and other publications). In this region the group is abundant, taxonomically diverse, and contains many ubiquitous species. The composition and facies confinement of the plankton in this region can be considered as typical for the Mediterranean Basin. No less than seven species of so-called "smaller globigerines," which were widely distributed in Oligocene basins and were close to the fauna of the Chattian stratotype (Globigerina ouachitaensis, G. praebulloides, G. angustiumbilicata, G. angustisuturalis, G. brevispira, etc.) are known here. The presence of Globigerina ciperoensis, a characteristic species not only in the Mediterranean fauna, but also of the northern European fauna, including that of the Paratethys, is very important. In addition to Globigerina species, there are species of the genera Turborotalia (two species), Globorotalia, Glo*bigerinita* (two species), relatively abundant *Cassiger*inella chipolensis, and Chiloguembelina gracillima; the latter has not been recorded from other Mediterranean regions. The end of the Oligocene is marked by the appearance of *Globigerinoides trilobus* and *Globigerinita dissimilis*, forms characteristic of the Miocene. The listed genera and species are known from assemblages of the southern shelf of the Mediterranean from Morocco to the Gulf of Suez (Fig. 2.8), "smaller globigerines," including *Globigerina ciperoensis*, penetrated even into the southwestern part of the Mesopotamian Basin (Krasheninnikov, 1969a).

In the western and northern Mediterranean, the plankton had basically the same taxonomic composition, with its abundance being controlled by the depth of the corresponding part of the basin. The shallow Aquitanian Basin is rather poor in plankton, which is represented by the genera *Globigerina*, *Globorotalia*, and *Globigerinoides*; the latter appeared at the very end of the Oligocene. The plankton of northern Italy is more abundant and diverse and includes *Globigerina* species (including *G. ciperoensis*), *Globorotalia* opima (two subspecies), *Globigerinita unicava*, and *Globorotalia* opima (two subspecies). In addition to these forms, the fauna of Sicily includes *Cassigerinella chipolensis* (Krashenin-nikov, 1971).

In some parts of the Carpathian Basin, planktonic foraminifers are relatively abundant and belong to zones P21 (Globorotalia opima opima) and P22 (Globigerina ciperoensis). The southern shelf (northern Hungary) contains Globigerina species (including Globigerina ciperoensis and G. globularis), the minute shells of which sometimes formed accumulations. The plankton of the Carpathian Foredeep is the most diverse and contains the genera Cassigerinella, Globigerina (three species), Globorotalia (two species), Chiloguembelina (three species), Globigerinella? (two species), and Beella (Subbotina and Pishvanova, 1960; Pishvanova in *Maikopian Beds...*, 1964; Krasheninnikov, 1969a, 1975; Paleogene System..., 1975; Cicha et al., 1998). Other parts of this basin (for example, Bavaria) contain rare Globigerina species, including Globigerina ciperoensis.

The basin of northern Germany yielded *Globigerina ciperoensis*, *G. angustiumbilicata*, *G. angustisuturalis*, *G. praebulloides*, *G. venezuelana*, *Globorotalia opima* (two subspecies), *Globigerinita munda*, *G. humilis*, *Globoquadrina globularis*, *G. praedehiscens*, *Neogloboquadrina siakensis*, *Cassigerinella chipolensis*, *Sphaeroidina bulloides*, and *S. variabilis* (forms are cited according to the original taxonomy). This assemblage gives an idea of the plankton of the North European Basin (Fig. 2.2). It differs from the Mediterranean plankton in the absence of the most thermophilic genera and in the presence of some species unknown in the south.

In the Eastern Paratethys planktonic foraminifers are not constantly present, not along the entire sequence. They are poor in taxonomic composition because of the latitudinal-climatic biotic zonality and due to its facies

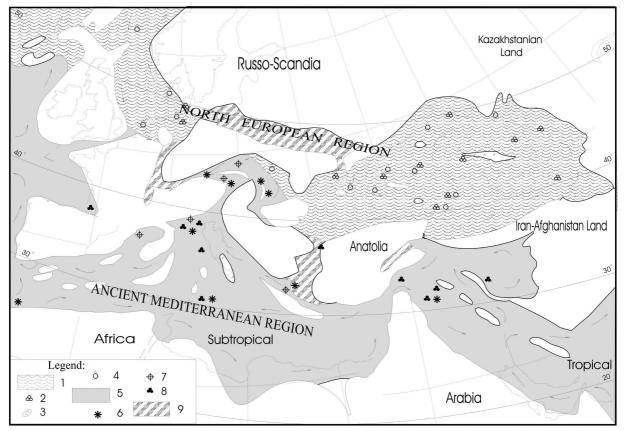


Fig. 2. Circulation of surface waters in the Chattian basins (after *Paleogeographic Atlas...*, 1997, modified) and latitudinal zones of the pelagic region. Designations: (1) Moderate or boreal zone with the impoverished associations of plankton and presence of specialized cold-water genera and species; (2) impoverished assemblages of planktonic foraminifers with prevalence of smaller globigerinids (including *Globigerina ciperoensis*) and *Spheroidina*; (3) assemblages of nannoplankton lacking discoasters and sphenolithes and dominated by tolerant species of the genera *Coccolithus, Reticulofenestra*, and *Cyclicargolithus*; (4) boreal dinccyst assemblages with predominance of *Wetzelliella, Deflandrea*, and *Thalassiphora*; (5) subtropical and tropical zones with warm-water complete zonal assemblages of plankton; (6) nannoplankton assemblages with numerous *Discoaster, Sphenolithus*, and *Helicosphaera*; (7) dinocyst assemblages of southern type, with domination of chorate cysts of the genera *Spiniferites, Chiropteridium, Lingulodinium*, etc.; (8) complete assemblages of planktonic foraminifers with *Turborotalia, Globorotalia, Globigerina*, and *Cassigerinella*; and (9) land occasionally inundated by the sea.

features. *Globigerina* species, including *Globigerina ciperoensis*, and the genus *Sphaeroidina* dominated here.

In places, the North Black Sea Region yields numerous *Globigerina ciperoensis*, *G. praebulloides*, *G. leroyi*, *G. ouachitaensis*, *G. parva*, and other species. Partly, these forms survived from the lower Oligocene (*Stratigraphic Scheme...*, 1987). The Azov–Kuban Depression, depressions of the Karpinsky Swell, and the Volga–Ural interfluve have an assemblage with *Globigerina ciperoensis*. According to T.E. Ulanovskaya, associations of the Azov–Kuban Depression contains, in addition, *Sphaeroidina variabilis*. Faunal lists of the Transcaucasian basins occasionally refer to undetermined *Globigerina*. Forms such as *Globigerina* ex gr. *bulloides*, *Globigerinoides trilobus*, and *Globigerinella* sp. have only been reported from the Pambak Formation of the northern Talysh (*Regional Stratigraphic...*, 1989).

The Turanian Basin was poor in plankton because it was located away from the open sea and existed under relatively shallow-water conditions. In southern

Mangyshlak, the facies of the outer shelf zone contain remains of *Globigerina*, which become rarer further to the north (Mikhailova, 1968; Stolyarov 2001; Paleogene System..., 1975). Associations of the northern Turkmenistan, Trans-Unguz Karakum, the southern Aral Sea Region, the central part of the Kopet Dagh Depression, and the depression of the Mary District contain the species Sphaeroidina variabilis. The same species is also known from the Buzachi Peninsula, the shallow-water shelf zone of the Ustyurt and Aral Sea regions (Paleogene System..., 1975), and the Northern Ustyurt Depression. The eastern shelf (Central Kyzylkum, the Upper Sarbatyr Formation) contains Sphaeroidina bulloides (Tsatsir, 1969), and the territory of the Kara Kalpak ASSR (now Qoragalpoghiston) contains Sphaeroidina aff. austriaca.

Nannoplankton

Northern Mediterranean. The Late Oligocene warm-water marine nannoplankton assemblage of the

Northern Mediterranean amounts to more than 25 species. The most typical were the representatives of the genera Discoaster, Sphenolithus, Helicosphaera, Retic*ulofenestra*, and *Cyclicargolithus* (Fig. 2.6). By the end of the Late Oligocene, the number of warm-water species of the genus Sphenolithus reduced considerably, and species such as S. distentus and S. ciperoensis completely disappeared. The species diversity of discoasters was reduced to two species (Roth et al., 1971; Fornaciari and Rio, 1996). Cyclicargolithus abisectus, Reticulofenestra bisecta, R. scrippsae, R. daviesii, and Helicosphaera euphratis remained dominant up to the end of the Late Oligocene. Another remarkable feature is the appearance (24 Ma) and rapid extinction (23.6 Ma) of the species S. delfix, a result of the shortterm warming at the Oligocene–Miocene boundary. The abundance of other warm-water species remained unchanged (Fornaciari and Rio, 1996).

North Sea Basin. In contrast to the Mediterranean, this region completely lacked warm-water normal marine species of the genera *Discoaster* and *Sphenolithus* and yielded only rare isolated specimens of *Helicosphaera* species. The nannoplankton assemblage was impoverished, characteristic of relatively cold-water, and included about 15 species. Species of the genera *Coccolithus, Cyclicargolithus,* and *Reticulofenestra* were most typical. During the existence of the basin, the composition of nannoplankton changed: the middle Late Eochattian is characterized by species of the genera *Braarudosphaera* and *Pontosphaera*, which were relatively tolerant to changes in the salinity and depth of the basin (Kothe, 1986).

Carpathian Basin. The nannoplankton assemblage of the Late Oligocene basin of the Carpathians was close in composition to that of the Mediterranean but differed from the latter in the presence at the beginning of the Late Oligocene of the species *Reticulofenestra* ornata, an endemic of the Paratethys, and in the almost total absence of species of the genus Discoaster. At the end of the Late Oligocene, species of the genera Sphenolithus, Cyclicargolithus, Reticulofenestra, and Helicosphaera became widespread, and the relatively shallow-water portions of the basin were dominated by Zygrhablithus bijugatus, Pontosphaera spp., and Braarudosphaera bigelowii (Andreyeva-Grigorovich and Gruzman, 1994; Starek et al., 2000).

Caucasian Basin. The nannoplankton association of the Late Oligocene Basin of the Eastern Paratethys in its Caucasian part is only known from scattered sites with carbonaceous sedimentation (in the Black Sea Region, western Ciscaucasia, and Georgia). It contains an assemblage of species that is close in composition to that of the Carpathians but differs from the latter in the almost complete absence of representatives of the genus *Sphenolithus* and rarer occurrence of species of the genus *Helicosphaera* (*H. recta*, *H. bramlettei*, *H. compacta*, and *H. intermedia*). Cyclicargolithus abisectus, C. floridanus, Reticulofenestra bisecta, R. lockeri, and Zygrhablithus bijugatus were abundantly represented (Andreyeva-Grigorovich et al., 1993; Krhovsky et al., 1995; Minashvili, 1992).

Organic-Walled Phytoplankton

The organic-walled phytoplankton in the Late Oligocene basins of western Eurasia is reasonably well studied. Especially extensive data were collected in the North Sea Basin, northern Mediterranean (Italy and France), the marine basin of the East European Platform, Scythian and Turanian plates, and the Caucasian region. In the territory of the former USSR, the organicwalled phytoplankton was investigated in sections of the Carpathians, the Black Sea Region, eastern Crimea, the Greater and Lesser Caucasus, Azerbaijan, Volga– Don area, and western Kazakhstan, where a change in the composition of assemblages from that of the littoral to that of the deep-water shelf was revealed.

The species diversity of phytoplankton in the northern areas (150 taxa at most) is markedly different from that of the southern areas (230–250 species). However, taxonomic revision of algal assemblages may change these proportions. In many instances the first and last occurrences of some taxa, including index species of regional dinocyst zones, were recorded in different stratigraphic levels in different parts of the Peri-Tethys. It is quite possible, however, that future studies will reconcile the discrepancies; nonetheless, the climatic control of the dispersions and migrations should be reflected in the composition of phytoplankton assemblages.

The regional time scale of the Late Oligocene usually considers this subdivision in the framework of the uniform Chiropteridium s. l. Zone, which is subdivided into three subzones: the lower Chiropteridium partispinatum-Rhombodinium draco Subzone, the middle Ch. partispinatum-Lingulodinium xanthium Subzone, and the upper Chiropteridium spp.-Deflandrea spinu*losa* (non *typica*) Subzone. Each of these subzones is characterized by a set of taxa, which includes up to 60– 80 species, most of which survived into the next subzone. In Eastern Europe the Early-Late Oligocene boundary is marked by the mass appearance of *Chirop*teridium species accompanied by Rhombodinium draco. The type species of the former has been described from Eochattian deposits of northwestern Europe. Slightly earlier, but also near this boundary, Enneadocysta pectiniformis disappeared and Hystrichosphaeropsis obscura appeared both in the North Sea and Mediterranean regions. As to representatives of the family Wetzelielaceae, the reduction of the last species, including Wetzeliella gochtii and W. articulata, occurred as early as the Chattian.

Studies of dinocysts at the Oligocene–Miocene boundary in the Lemme section (Piedmont, Italy), a standard reference section for this boundary, and in other sections of the type area, show that *Chiropteridium* species disappeared slightly below this boundary. In the middle latitudes cysts of the Deflandrea phoshor*itica* group disappeared at this boundary. In low latitudes the group became extinct in the Early Aquitanian. Those *Deflandrea* species that were united into the group D. spinulosa, without its type species, formed an epibole in the Italian and North Caucasian sections at the beginning of the Aquitanian and then completely disappeared during this stage, earlier than *Globorotalia* kugleri, an index species of the Lower Aquitanian planktonic foraminifer zone. The most significant 'phytoplanktonic events" of the Late Oligocene are the appearance and extinction of *Distatodinium biffii*, the universal distribution of Tuberculodinium vancampoae, the extinction of *Homotryblium tenuispinosum* in the southern climatic zone at the end of the Late Oligocene, and the extinction of *Rhombodinium draco* in the east of the middle latitudes.

Northern Mediterranean. The Mediterranean shows a high diversity of dinocysts owing to the presence of warm-water forms and species that inhabit the open sea (species of Operculodinium, Impagidinium, etc.). The dinocyst assemblage included more than 60 species. The assemblage was dominated by Spiniferites complex and species groups of the genera Chiropteridium and Lingulodinium. The species of the genera Deflandrea, Wetzeliella, Systematophora, Impagidinium, Nematosphaeropsis, and others were less abundant. The majority of the genera listed were characteristic of the neritic zone, which was widely connected with the ocean. This is apparent from the presence of species of the genera Impagidinium and Nematosphaeropsis. The abundance of the cold-water Wetzelielaceae was much lower; Rhombodinium draco, which was widespread at the beginning of the Late Oligocene in waters of the northern province, has not been recorded. It is necessary to emphasize that the composition of the Upper Oligocene assemblages of the southern province is closer to that of the assemblages of coeval sediments of the eastern Atlantic; the latter, however, include many North Sea taxa.

Paleotemperature analysis of these assemblages shows that the waters of the Mediterranean Basin that were warm at the beginning of the Late Oligocene became subsequently colder and then experienced an abrupt short-term warming at the Oligocene–Miocene boundary (Zevenboom, 1995).

Carpathian basin. The dinocyst assemblage of the central part of the Late Oligocene Carpathian Basin (the Polish portion of the Podhale Flysch) was dominated by chorate cysts (Gonyaulacoids) such as *Polysphaeridium* spp., *Homotryblium* spp., and *Spiniferites* spp. The dominance of the first two dinocyst genera possibly indicates that the salinity increased in the marginal areas of the Podhale part of the basin in the Late Oligocene. Representatives of peridinoid cysts (Peridinioids) such as Wetzelielloideae and *Deflandrea* (which dominated) were less abundant. Rare occurrence of open-ocean species of the genera *Nem*-

atosphaeropsis and Impagidinium provides evidence that this basin was relatively shallow and underwent partial isolation. The presence of Impagidinium velorum and larger representatives of the Wetzelielloideae (>200 μ m) indicates that the climate was relatively cold (Gedl, 2000).

The dinocyst assemblage of the eastern part of the Late Oligocene Carpathian Basin had nearly equal proportions of the chorate gonyaulacoid cysts of the genera *Spiniferites* spp., *Polysphaeridium*, *Hystrichokolpoma*, and *Homotryblium* and that of peridinoids. Just as in the Podhale part of the basin, the peridinoids were dominated by forms of *Deflandrea*. The species of the genera *Impagidinium*, *Chiropteridium*, and *Cribroperidinium* were more abundant, and larger representatives of *Wetzeliella* were absent. These observations show that this portion of the basin was relatively deeper and warmer than the its marginal Podhale part (Andreyeva-Grigorovich, 1991; Andeyeva-Grygorovich and Gruzman, 1994).

Basins of Northern Europe. The assemblage of Dinophyta of the Norwegian–Greenland Sea included more than 50 species. The most abundant of them were species of the genera *Hystrichokolpoma, Impagidinium, Nematosphaeropsis, Lingulodinium, Systematophora, Operculodinium,* and *Spiniferites.* This assemblage indicates that the basin was under relatively warm-water conditions (apparently, at the boundary between the subtropical and moderate zones), deep, and broadly connected with the ocean. The predominance of warm-water species is attributable to warm sea currents (Dmitrienko, 1993). Some cold-water species (*Impagidinium velorum*, etc.) have been recorded from the latest Oligocene (Manum *et al.*, 1989).

The association of the North Sea Basin had more than 50 dinocyst species. Among the most abundant were Systematophora placacantha, Cordosphaeridium cantharellum, Chiropteridium partispinatum, Homotryblium plectilum, Melitasphaeridium sp., etc. At the beginning of the Late Oligocene, the dinocyst assemblage of the basin was markedly dominated by forms tolerant to changes in salinity and oxygen regime, like Wetzeliella, Deflandrea, and Thalassiphora. In general, the Late Oligocene assemblage was a mixture of forms adapted to normal salinity and shallow-water conditions (Impletosphaeridium + Cordosphaeridium), deep and warm water (Systematophora), and to deep and cold water (Cribroperidinium) (Köthe, 1990). The most shallow portions of the basin (the region of the modern Elbe River) were inhabited by species of the genera Homotryblium, Wetzeliella, and Polysphaeridium. The presence of *Homotryblium plectilum* possibly indicates an insignificant increase in salinity in the marginal part of the basin (unpublished data from A.S. Andreyeva-Grigorovich).

Eastern Paratethys. In the Late Oligocene Paratethys, the composition of the assemblages of organic-walled phytoplankton was under fairly strict ecological controls. As the sea level rose during the Chattian trans-

gression after the Solenovian freshening event, the assemblages showed a higher species diversity and composition that was closer to that of normal marine environments.

The phytoplankton assemblages of the Transcaucasian part of the basin show a high diversity of organicwalled phytoplankton, which amounts to more than a hundred species. The assemblages of the lower zone of the Late Oligocene were dominated by *Deflandrea* spp. and *Rhombodinium draco*. These were accompanied by several tens of taxa which were also common in other regions of the Eastern Paratethys (Palaeocystodinium golzovense, and species of the genera Impagidinium, Lingulodinium, Chiropteridium, Selenopemphix, Membranophoridium, Dapsilidinium, Thalassiphora, Caligodinium, etc.). As in Ciscaucasia, the Late Oligocene assemblages of the Azerbaijan part of the sea basin (Sumqayit District, the surroundings of Baku, the northern slope of the Lesser Caucasus) contain organic matter of algal origin. The sections contain numerous intervals rich in prasinophytes and acritarchs, indicating anoxic environments in the sedimentary basin.

In the central Ciscaucasian and Crimean parts of the basin, the assemblages of dinocysts were markedly different from those of the shallower northern areas. In the Belaya River section the Upper Oligocene interval, which according to A.S. Stolyarov is represented by the Batalpashinsk Formation and most of the Septarian Formation, is distinctly subdivided into two parts corresponding to the two dinocysts subzones of the uniform Chiropteridium s. l. Zone: the Ch. partispinatum-Rhombodinium draco Subzone (lower) and the Chiropteridium-Deflandrea spinulosa (nontype) Subzone (upper) (Zaporozhets, 1999). As the abundance of Deflandrea increases upsection, the abundance and species diversity of Chiropteridium decreases. The diversity of organic-walled phytoplankton in the section along the Belaya River is perhaps lower than that known from the Crimean sections. However, the section also reveals levels rich in prasinophytes and acritarchs, specifically leiosphaeridias, thus indicating limited oxygen exchange in the basin.

The southern, deeper water portion of the Crimean shelf was inhabited by dinocysts different from those in the shallower water portion. Thus, peridinoids were much less frequent, and the species diversity of the genera Phthanoperidinium, Gerdiocysta, Glaphyrocysta, Impagidinium, Distatodinium, and Operculodinium increased. The highest taxonomic diversity was recorded in the deposits of the deep shelf of the eastern Crimea. The composition of these samples indicates conditions of normal oceanic salinity, and a slightly higher abundance of *Hystrichokolpoma*, *Deflandrea* spinulosa, Operculodinium sp., Spiniferites spp., Membranophoridium aspinatum, Chiropteridium spp., and Selenopemphix spp. characterizes the Early Chattian. The taxa represented by isolated specimens amount to more than 30 species. In addition to the taxa typical of the coastal shelf zone, there are more abundant forms that are closer to those of the open sea (Impagidinium sp., Cordosphaeridium gracile, and species of Distatodinium and Dapsilidinium). A number of thin-walled morphotypes of the genera Selenopemphix and Hystrichokolpoma are characteristic of these deposits. In the second half of the Late Oligocene, the abundance of Deflandrea spinulosa and species of the genera Selenopemphix, Spiniferites, and Hystrichokolpoma began to increase, the abundance of Chiropteridium, Operculodinium, and Membranophoridium aspinatum decreased, and Melitasphaeridium sp. and Gerlachodinium sp. appeared. A very distinctive phytoplankton assemblage has been recorded at the Chattian-Miocene boundary in the section located west of the Cape Chauda (eastern Crimea). The abundance of larger Leiosphaeridia in combination with Cymatiosphaera and Tytthodiscus and the almost complete absence of dinocysts suggest the onset of a stagnation phase.

The northern shelf of the Late Oligocene basin to the north of the western North Black Sea Depression was characterized by the presence of abundant peridinoid cysts. *Deflandrea* species were most diverse and abundant. Species of the genera *Wetzeliella* and *Rhombodinium* were slightly less abundant, and members of the genera *Homotryblium*, *Spiniferites*, and *Chiropteridium* were represented by isolated specimens. This assemblage is characteristic of the marginal shallowwater part of the Maikopian Basin, which was rich in nutrients.

In addition to species of Wetzeliella amounting to 50% of the overall composition of assemblages, early Late Oligocene associations of organic-walled phytoplankton of shallow shelf zones in the south of the East European Platform and northern marginal parts of the Scythian Plate were dominated by Hystrichokolрота salacia. *Membranophoridium* aspinatum, Homotryblium tenuispinosum, and species of Chiropteridium and Spiniferites. They were associated with species of Deflandrea, including D. phosphoritica, and common Glaphyrocysta undulata, G. pastielsii, Tectatodinium sp., Distatodinium sp., Cribroperidimum sp., Impletosphaeridium sp., Turbiosphaera sp., Batiacasphaera micropapillata, etc. Further east (Northern Ergeni Upland), the abundance of *Chiropteridium*, Rhombodinium draco, Wetzeliella articulata increased in the lower Upper Oligocene, and the abundance of Deflandrea spinulosa (nontype) increased in the upper Upper Oligocene, which is considered here as the Chiropteridium partispinatum-Homotryblium tenuispinosum Subzone (Zaporozhets, 1998). In addition, Palaeocystodinium golzowense, Apteodinium maculatum, Systematophora placacantha, Selenopemphix nephroides, Impagidinium sp., Pentadinium laticinctum, Leje*unecvsta hvalina*, *Phelodinium* sp. have been recorded. In a number of sections that characterize the outer shelf zone (slopes of the Rostov Uplift, Southern Ergeni, and Ustyurt), the lower part of the Chiropteridium par*tispinatum–Rhombodinium draco* Zone is marked by the appearance of abundant *Wetzeliella* cysts (especially *W. articulata*). During the periods when the water was low in oxygen, the assemblages in the inner parts of the basin showed a peculiar composition. They were markedly impoverished and often showed a mono- or oligotypic character, i.e., one or two taxa dominated. The presence of reducing conditions in a sedimentary basin is usually indicated by prasinophytes and acritarchs (especially *Cymatiosphaera* and *Leiosphaeridia*). As the basin became shallower in the upper part of the section, the role of prasinophytes and acritarchs increased (*Mic-rhystridium* sp., *Schizocysta* sp., etc.).

The dinophyte algae of the marginal basins of the Late Oligocene that were confined to negative structures of the Ukrainian Shield were characterized by a very poor species diversity. Prasinophytes and acritarchs are almost equal to dinophytes in abundance. The most widespread genera were Homotryblium, Achomosphaera, Spiniferites, Adnatosphaeridium, and Operculodinium. Paleoecological analysis of this assemblage indicates that these basins were shallow and partly isolated, of lower salinity, and lower surfacewater temperature than the Early Oligocene Basin of the same part of the shelf (Shevchenko, 2003). The assemblages of the marginal parts of the marine basin within the East European Platform and the Turanian Plate show a considerably increased abundance of prasinophytes and acritarchs, especially Micrhystridium. The impoverished assemblages of this type corresponding to the lower subzone of the Chiropteridium partispinatum-Rhombodinium draco Zone are traceable further east, up to the northwestern Aral Sea Region.

At the end of the Oligocene the diversity and abundance of dinophyte algae decreased markedly. The genera *Chiropteridium, Rhombodinium,* and *Wetzeliella* became extinct, while the others, including *Deflandrea*, were represented by one or, more rarely, two or three species (Grigorovich, 1972; Andreyeva-Grigorovich, 1994).

Plankton-Based Biogeographic Zonation

As in the previous time interval, the abundance and composition of the Late Oligocene planktonic assemblages were controlled by latitudinal climatic zonation, water circulation, and connections of the inland basins with the ocean. In the south, the Ancient Mediterranean Region (Fig. 2) is distinguished. This is characterized by complete plankton assemblages, including zonal species, characteristic of the tropical and subtropical zones. In addition to Globigerina species, the assemblages of planktonic foraminifers of the Mediterranean contained members of the genera Turborotalia, Globorotalia, Globigerinita, and Cassigerinella. The nannoplankton assemblages included numerous Discoaster, Sphenolithus, and Helicosphaera; however, the number of warm-water species of Sphenolithus and Discoaster sharply decreased by the end of the Oligocene. The dinocyst assemblages of this area were of the southern type with dominant chorate cysts of the

genera *Spiniferites, Chiropteridium, Lingulodinium*, etc. More cold-adapted forms of *Wetzeliella* were rare, and *Rhombodinium draco*, common in northern assemblages of the early Chattian, was absent.

The temperate or boreal zone (North European Region) included the basins of northwestern Europe and the Paratethys, and differed considerably in more impoverished plankton assemblages and in the presence of specialized cold-adapted genera and species. The Norway-Greenland and North Sea basins were inhabited by relatively diverse assemblages of planktonic foraminifers, nannoplankton, and dinocysts indicating warm currents, although the most thermophilic genera and species were absent. The most significant nannoplankton assemblages are those in which Discoaster and Sphenolithus were totally absent and the tolerant species of the genera Coccolithus, Reticulofenestra, and Cyclicargolithus dominated. The boreal assemblages of dinocysts were characterized by the predominance of tolerant species of Wetzelliella, Deflandrea, Thalassiphora, etc. In the Eastern Paratethys planktonic foraminifers were rare and represented mainly by *Globigerina* species (including *Glo*bigerina ciperoensis) and the genus Sphaeroidina. The nannoplankton assemblage is only known from individual sites and intervals with carbonaceous sedimentation (early Chattian) and resembles the Carpathian assemblages in species composition but differs from them in the absence of the genus Sphenolithus and the lower abundance of species of the genus Helicosphaera. The composition of the assemblages of organic-walled phytoplankton is controlled by environmental rather than biogeographic conditions: for example assemblages rich in prasinophytes and acritarchs provide evidence of anoxic conditions in the sedimentary basin.

The larger part of the Carpathian Basin, in which planktonic assemblages resemble those of the Mediterranean in composition but differ from them in having lower diversity, constitutes a transitional zone. A characteristic feature of the nannoplankton assemblage of the Late Oligocene Carpathian Basin was the presence of *Reticulofenestra ornata*, a Paratethyan endemic, at the beginning of Late Oligocene and the nearly complete absence of *Discoaster* sp. The fact that the assemblage contains the dinocyst species *Impagidinium velorum* and larger representatives of the Wetzelielloideae (>200 µm) indicates that the climate was colder than in the Mediterranean.

Marine Ichthyofauna

Carpathian basin. During this time interval the Central Paratethys was, probably, deeper than the Eastern Paratethys. Its water mass was not stratified to the extent known in the Maikopian Basin. According to Jerzmańska (1960; Kotlarczyk and Jerzmańska, 1988), the materials from the Jasło Shales, Middle Krosno Beds, and Ichthyozone IPM 4 through the upper NP24–NP25 indicate that at the beginning of the Late Oli-

gocene the Polish part of the Central Paratethys was populated by *Clupea sardinites* (Heck) (Clupeidae), *Idrissia carpathica* Jerzm. (Gonostomatidae), *Polyipnus sobnioviensis* Jerzm. (Sternoptychidae), *Eomyctophum koraense* Dan. (Myctophidae), *Equula*? sp. (Carangidae), *Sarda* sp. (Cybiidae), and Cottidae gen. indet.

Judging from the predominant meso-bathypelagic forms (gonostomatids, sternoptychids, and myctophids), the Polish part of the Late Oligocene Carpathian Basin was relatively deep (up to 700–1000 m). Although such transitional deep-water forms as *E. koraense* survived into the latest Oligocene (Zone NP25, Ichthyozones IPM 5?–IPM6), the composition of the deep-water assemblage markedly changed: the appearance of *Carpatichthys polonicus* and *Argyropelecus priscus* were recorded in IPM5 and IPM6, respectively (Jerzmańska, 1974; Kotlarczyk and Jerzmańska, 1988; Gregorova, 1989).

In the Late Oligocene the Hungarian Basin was a warm subtropical sea, which was inhabited by a rich ichthyofauna including (according to otolith data) about 52 species (Nolf and Brzobohaty, 1994). The earlier assemblage of this fauna from the Kiscell Clays (with nannoplankton characteristic of the lower and upper parts of Zone NP24) included altogether about 30 species that formed a deep-water association in which mesopelagic forms dominated. In the Eastern Paratethys it can be partly correlated with the fish assemblage of the terminal Lower Oligocene (the lower Subformation of the Morozkina Balka Formation and its equivalents) and with the lower Upper Oligocene (the upper Subformation of the Morozkina Balka Formation and part of the Batalpashinsk Formation and its equivalents).

The later Egerian assemblage (upper parts of zones NP24 and NP25, about 25 species) apparently inhabited the continental shelf in a shallower sea, as indicated by the presence of sparids, centrarchids, sciaenids, and abundant gobiids, inhabitants of coastal habitats. Three successive assemblages that were recorded in the Egerian reflect a gradual shallowing of the basin by the end of the Late Oligocene. Moreover, the abundance of euryhaline ambassids, which inhabit coastal waters with considerable fresh water inflow, in the *Cerithium* Horizon (terminal beds of the Egerian) indicates a freshening of the Hungarian Basin in the terminal Late Oligocene.

During the entire Late Oligocene, the Central Paratethys and its Carpathian part retained characteristic deep sea conditions with normal salinity. The Hungarian part of the Central Paratethys was favorable to mesopelagic fishes in the Kiscellian (late Early–early Late Oligocene). However, the predominance of coastal and epipelagic forms in the Egerian assemblage indicates a possible shallowing of this part of the Central Paratethys during this time.

The study of otoliths (Nolf and Brzobohaty, 1994) shows a homogenous character of the Late Oligocene

ichthyofauna from the Paratethys to the western Atlantic (Aquitania), and the presence of Indo-Pacific families among the neritic components of these faunas (Ambassidae, Silaginidae, and Leiognathidae) points to a connection of these faunas with the Indo-Pacific. The Late Oligocene association of the Aquitanian Basin (northwest France, the locality of Saint-Étienne d'Orte, Zone NP 25) contained deep-water neritic and nearshore marine elements, including about 60% of species in common with the Late Oligocene Hungarian Basin. It is worth noting, however, that specified Indo-Pacific groups are recorded only at the end of the Egerian (levels 4 and 5), i.e., they occur in the Hungarian and Aquitanian Basins at the very end of the Late Oligocene.

Caucasian Basin. The taxonomic composition of the Late Oligocene ichthyofauna of the Eastern Paratethys is highly problematic, since there are different views on the range of the Upper Oligocene in Ciscaucasia, Crimea, and the Caucasus (see Danil'chenko, 1960; Grossgeim and Korobkov, 1975; Danil'chenko et al., 1980; Bannikov, 1985; Bannikov and Parin, 1997, and the Stratigraphy of the Upper Oligocene section). Moreover, the majority of fish fossils are usually assigned to regional horizons rather than to specific levels or formations (Fedotov, 1976; Danil'chenko et al., 1980; Bannikov, 1985, 1990; Bannikov and Parin, 1997). It is therefore difficult to recognize new refined assemblages from earlier established fish associations. As a result, lists of Late Oligocene communities may frequently contain forms from the late Early Oligocene (Danil'chenko et al., 1980; Bannikov and Parin, 1997), for example, species from the lower Subformation of the Morozkina Balka Formation and its equivalents, i.e., from a time interval after which some groups experienced considerable changes in taxonomic composition. Likewise, differing views on the position of the Oligocene-Miocene boundary frequently led to the placement of some Late Oligocene taxa in the Early Miocene and some Aquitanian faunas (Chernaya Rechka in northern Ossetia, and the Assa Formation) in the Ol'ginskian Formation (Sakaraulian) (Menner, 1948; Bannikov and Parin, 1997). Some Early Miocene groups were included among the Late Oligocene assemblages or assemblages of the Oligocene-Miocene boundary (Danil'chenko et al., 1980; Prokof'ev, 2001, 2002). Unfortunately, data on the composition of the Oligocene ichthyofauna of Azerbaijan (Prokof'ev, 2001, 2002) are based on mixed material, the greater part of which belongs to the Miocene and, therefore, requires stratigraphic revision.

Refined data show that in the Late Oligocene (upper Zone NP24–Zone NP25) the Eastern Paratethys was characterized by an impoverished community that included clupeids *Suchumia caucasica* Menner; gadiforms *Merluccius inferus* Dan. and *M. lednevi* Bog. (Merlucciidae); syngnathiforms *Aeoliscus apsheronicus* (Centriscidae); *Hipposyngnathus convexus* Dan. (Syngnathidae); acanthopterygians *Chaetodon penniger* Bog. (Chaetodontidae); *Capros longispinatus* Dan. (Caproidae); Caprovesposus (Acanthuridae), sp. Abadzekhia marinae Ban. (Gempylidae); Scomber cubanicus Dan., Sarda remota Dan. (Scombridae); Thunnus sp. (Thunnidae) Pseudotetrapturus luteus Dan. (Palaeorhynchidae); Propercarina sp. (Propercarinidae); and pleuronectiforms Soleidae? gen. et sp. 1960; Fedotov, 1976: indet. (Danil'chenko, Danil'chenko et al., 1980; Bannikov and Parin, 1997; Prokof'ev, 2002).

Sardinella sardinites (Haeckel), Palaeogadus latebrosus Dan., P. simionescui Dan., Serranus budensis (Haeckel) (Serranidae), and Repropca sumgaitica Ban. (Repropcidae), which were assigned to the Late Oligocene (Bannikov and Parin, 1997), apparently originated from the terminal Lower Oligocene (lower Subformation of the Morozkina Balka Formation), and Nerophis gracilis Serg. (Sergienko, 1971), which was described from the Upper Riki Formation, most likely belongs to the Aquitanian.

In the first half of the Late Oligocene, eastern Ciscaucasia (Mutsudakal-Miatly Horizon and its equivalents, except for the basal layers apparently correlatable with the Lower Subformation of the Morozkina Balka, which crowns the terminal part of the Lower Oligocene) was inhabited by an ichthyofauna that was impoverished both in its taxonomic diversity and in abundance. The assemblage was dominated by clupeids, fossils of which are encountered throughout the Upper Oligocene, the other forms (merlucciids, cyprinids, and scombrids) are represented by rare isolated specimens. The end of the Batalpashinsk time was marked by the abundance of *Merluccius inferus* Dan.

The end of the Late Oligocene (the Riki Regional Horizon, except for its upper part, which is assigned to the Miocene; i.e., the Argun and Alkun formations and the basal part of the Assa Formation and their equivalents) is characterized by the appearance of abundant Sardinella brevicauda (Menner) and Capros longispinatus and the disappearance of Merluccius inferus, which was replaced by *M. lednevi*. The latter species outnumbered the other fish of the terminal Late Oligocene (Fedotov, 1976). Less abundant members of the Late Oligocene assemblages were Holosteus sp., Scomber cubanicus Dan., Thunnus sp., Aulostomus fractus, and Pseudotetrapturus luteus, only isolated specimens of which were encountered in sediments (Danil'chenko, 1960; Danil'chenko et al., 1980; Bannikov, 1985, 1990; Prokof'ev, 2001).

In general, the Late Oligocene ichthyofauna of the Eastern Paratethys constituted an impoverished community in which endemic forms dominated. The most important among the latter were clupeids and gadiforms. The latter group was represented by the genus *Merluccius*, the species composition and abundance of which varied during the Late Oligocene. Thus, the rare *M. inferus* Dan. occurred at the beginning of this time (the Batalpashinsk Formation, middle and upper parts of the Mutsudakal-Miatly Horizon, and their equivalents), and M. lednevi Dan. (Fedotov, 1976), in the middle and at the end of the Late Oligocene. The latter species probably survived into the beginning of the Aquitanian (the Voskovaya Gora Formation of western Ciscaucasia). The ichthyofauna of the Late Oligocene Caucasian Basin included both pelagic and coastal forms characteristic of a marine basin with normal salinity. Some of them, for example the bentho-pelagic Capros longispinatus Dan., could have lived as deep as 600 m, thus suggesting that the basin may have reached significant depths. However, the complete absence of deep-water meso-bathypelagic elements in the Late Oligocene ichthyofauna of the Eastern Paratethys is indicative of unfavorable conditions in the deep water, which was presumably affected by hydrogen sulfide anoxia (Danil'chenko, 1960; Danil'chenko et al., 1980; Fedotov, 1976; Bannikov, 1985, 1990).

Comparative analysis of the ichthyofaunas of the Central and Eastern Paratethys and Aquitanian Basin indicates that the Eastern Paratethyan Basin was either shallower, or its depths were anoxic, stagnant, and unfavorable for life (Danil'chenko, 1960; Danil'chenko *et al.*, 1980; Fedotov, 1976; Bannikov, 1985, 1993). The Carpathian Basin provided suitable habitats for deep-water fishes during the entire Late Oligocene (ichthyozones IPM4–IPM6, second half of Zone NP24 to Zone NP25), with its bottom layers involved into the general system of the basin circulation. The Hungarian Basin probably became somewhat shallower in the Egerian (Zone NP25) and showed the presence of Indo-Pacific elements at the end of the Late Oligocene.

Similarity between the Late Oligocene otolith ichthyofaunas of the Aquitanian and Hungarian Basins shows that they belong to the same biogeographic province, and the presence of Indo-Pacific groups in these faunas reflects ties with the Indo-West Pacific. In the Late Oligocene the ichthyofauna of the Eastern Paratethys had little communication with that of the Central Paratethys and was characterized by low taxonomic diversity and by endemism. The bottom water layers of the Eastern Paratethys were stratified, affected by the hydrogen sulfide anoxia, and unsuitable for life.

Benthic Foraminifers

Mediterranean. The knowledge of the foraminifers of the Southern Mediterranean is very fragmentary. Sections of the Moroccan Reef are known to contain *Nummulites, Lepidocyclina, Heterostegina,* and numerous rotaliids (Marine and Blumenthal, 1930). The Oligocene sediments of Algeria have yielded nummulites and lepidocyclines; larger foraminifers have been also recorded in Libya (Fig. 3).

In the East Mediterranean (Syria) shallow-water organoclastic limestones are packed with shells of *Lepidocyclina*, with occasional occurrences of *Numnulites* (four species) and *Operculina*; and *Miogypsinoides* and

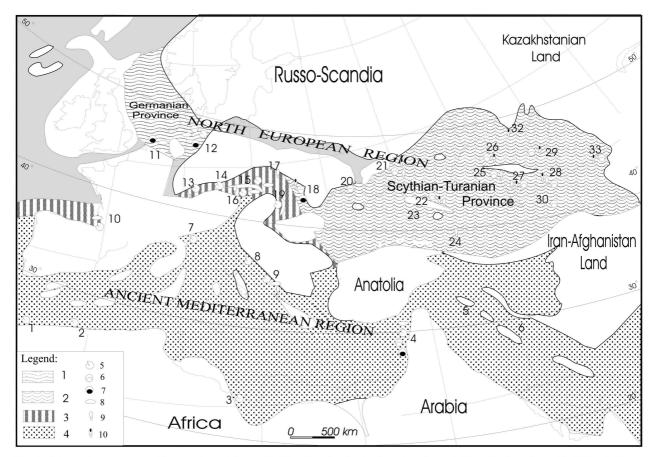


Fig. 3. Schematic zoogeographic zonation of the shelf of the Chattian basins based on foraminifers. Designations: (1–2) North European Region with a moderately warm-water foraminiferal fauna and absence of the most warm-water taxa: (1) Germanian Province, (2) Scythian–Turanian Province, (3) areas with abundant intermediate assemblages, (4) Ancient Mediterranean Region with fauna that included diverse warm-water foraminiferal assemblages, (5) larger foraminifers (*Miogypsina, Miogypsinoides, Lepidocyclina*, etc.), (6–10) Characteristic genera with wide geographic range: (6) *Cassigerinella*, (7) *Sphaeroidinella*, (8) *Almaena*, (9) *Virguinella*, and (10) *Caucasina*. Localities of Late Oligocene foraminiferal associations considered in the present study: (1) Morocco, (2) Algeria, (3) Libya, (4) Syria, (5) Iraq, (6) Iran, (7) northern Italy, (8) Croatia and Slovenia, (9) Albania, (10) Aquitanian Basin, (11) Belgium, (12) northern Germany, (13) Bavaria, (14) Austria, (15) southern Slovakia, (16) northern Hungary, (17) Polish Carpathians, (18) Carpathian Foredeep, (19) Transylvania, (20) North Black Sea Depression, (21) Lower reaches of the Don River and Manych Region, (22) northern Caucasus and Ciscaucasia, (23) western Georgia, (24) Lesser Caucasus and Middle Kura Depression, (25) Mangyshlak, (26) Buzachi Peninsula, (27) Kara Bogaz Gol Region, (28) northern Turkmenistan (Kara Kum), (29) southern Aral Region, (30) Fore-Kopet Dagh Depression, (31) Maryiskii District, (32) Ustyurt Depression, and (33) central Kyzyl Kum.

Miogypsina had appeared in the latest Oligocene. In addition, miliolids (Quinqueloculina, Alveolina, etc.) and peneroplids (Peneroplis, Archaias, Dendritina, Meandropsina, and Spirolina) were widely distributed in the shallow-water facies (Krasheninnikov, 1969a, 1971). Peneroplids also occur in other regions of the Mediterranean and in the Mesopotamian Basin, including Iraq and Iran, but these genera are unknown in the northwest of Europe and in the Paratethys. Sediments formed in deeper waters contain smaller benthic forms. According to data by Krasheninnikov (1969a), this region was inhabited by at least 32 species. The assemblage shares some forms with both the Chattian Basin of the North Sea (marked by N) and with some basins of the Eastern Paratethys (marked by P). These are Almaena osnabrugensis (N), Cibicidoides tennelus (N, P), C. sigmoidalis (P), C. pseudoungerianus (P),

Nonion postgraniferus (P), Elphidium minutum (N), E. subnodosum (N, P), Asterigerina guerichi (N, P), A. falcilocularis (P), Bitubulogerina kasselensis (N, P), Bolivina fastigia (N, P), Robertina declivis (N, P), and other species of genera that are in common with the fauna of northern Eurasia. Krasheninnikov's (1971) opinion that Syrian sections serve as "a certain intermediate link" in correlations between the assemblages of the Paratethys and northwestern Europe is noteworthy.

The thermophilic genera Nummulites and Lepidocyclina are known from the Northern Mediterranean; Miogypsina is known from northern Italy, the genera Nummulites and Lepidocyclina have been recorded from the undivided Oligocene–Neogene flysch sequence of Albania (Cizancourt, 1930). The larger foraminifers Lepidocyclina and Miogypsina (each genus represented by two species) are known from Croatia and Slovenia along with forms that are also widespread in more northern basins, i.e., *Virgulinella pertusa* and *Almaena osnabrugensis*, (Cicha *et al.*, 1998).

Eastern Atlantic. The fauna of the Aquitanian Basin was close to that of the Mediterranean but contained many northern European elements. According to the data of Krasheninnikov (1971), the assemblage was dominated by lepidocyclines and included smaller numbers of Miogypsina, Miogypsinoides, Heterostegina, Spiroclypeus, and Nummulites. The smaller benthos (35 species of 22 genera) included Almaena osnaburgensis, A. hieroglyphica, and two other species of this thermophilic genus; *Alabamina tongentialis; *Cibicidoides tennelus; *Pararotalia canui; Lamarckina halkyardi; *Bolivina fastigia; *B. melletica; Bitubulogerina vicksburgensis; and other forms. Some widespread species (asterisked) were shared by the fauna of the North Sea Basin and Paratethys. Such genera as Pseudoplanulinella, Mississippina, Escornebovina, Rotalia, and Pararotalia are characteristic of the Mediterranean.

Basin of the North Sea. The foraminiferal assemblage of the type area for the Chattian Stage (Germany) is the most representative among the basins of northwestern Europe. It includes 55 genera and no less than 80 species with secreting forms prevailing (Batjes, 1958; Kummerle, 1963; The Northwestern ..., 1988). The Chattian fauna is characterized by Asterigerina guerichi, Almaena osnabrugensis, Elphidium subnodosum, Rotalia propingua, Bitubulogerina kasselensis, Fursenkoina schreibersiana, and Bolivina fastigata and species of the genera Cibicidoides, Robertina, Planorbulina, etc. This assemblage differs from that of the Mediterranean at the family, generic, and species level, although both assemblages have some genera and species in common. Such genera as Asterigerina, Almaena, Patellina, and Gypsina are thermophilic, and the presence of Lepidocyclina, Miogypsina, Miogypsinoides, and Sphaerogypsina (Van der Flerk, 1966; Drooger in Colloque..., 1964) unambiguously indicates the influence of the Mediterranean fauna. The presence of numerous lagenids (20 species), miliolids and polymorphinids (10 species each), discorbids, cibicidids, etc. indicates that the basin was shallow and its waters were of moderate temperature. In the lists of the Mediterranean fauna, these groups occur only rarely, if at all; however, this may be because of the incompleteness of available data. The end of the Chattian (Neochattian) was marked by decreased diversity and by the appearance of some forms tolerant of changes in normal salinity; the new genus Ammonia, Florilus boueanus, and other nonionids (Nonion, Elphidium, and Cribrononion).

In the Netherlands and Belgium, there is an assemblage that is similar in composition to the German assemblage. However, it is quite impoverished, and its characteristic forms are restricted to *Asterigerina guerichi* and *Sphaeroidina bulloides* (*The Northwestern* ..., 1988). These assemblages include widespread genera and species known in the basins of the Paratethys and the Mediterranean (particularly, Syria), together with lagenids and some genera from the order Rotaliida that are absent in the fauna of the Eastern Paratethys.

Carpathian Basin. In the Central Paratethys the structure of the foraminiferal communities of the Egerian Stage was relatively diverse (Cicha et al., 1998) but strongly depended on local conditions. The shallow Bavarian part of the molasse basin was inhabited by *Miogypsinoides*; the assemblage of smaller benthic forms is close in composition to that of northern Europe (Almaena osnabrugensis, Elphidium subnodosum, Asterigerina guerichi, and Cassidulinoides bodeni and species of the genera Sigmoilopsis, Nonionella, Uvigerina, and Bolivina) but differs in the presence of two thermophilic genera, Biapertorbis and Pavonitina. Arenaceous forms, large foraminifers (two species of the genus *Miogypsinoides* and *Lepidocyclina*), and the Tethyan genera Sphaerogypsina and Amphistegina inhabited the Austrian part of molasse basin. The Danube Lowlands and the southern Slovak Basin were characterized by a fauna of mixed composition, which includes genera and some species known in the German Basin (Almaena osnabrugensis, Heterolepa dutemplei, Nonion granosum, etc.) in combination with the Mediterranean *Miogypsinoides* and *Miogypsina*.

Lepidocyclina (two species), Miogypsina, and Miogypsinoides were reported for the southern shelf (northern Hungary, Eger Region) by Krasheninnikov (1971). Among smaller foraminifers there are genera and species typical of the northern basin of Germany (Nonion, Heterolepa, Bolivina, polymorphinines, Rotalia propingua, Quinqueloculina seminula, Fursenkoina schreibersiana, Almaena osnabrugensis, and Bitubulogerina kasselensis) (Nagy-Gellai, 1968; Koreczne-Laky, Nagyne-Gellai, 1985; Cicha et al., 1998). The endemic species of the Central Paratethys, Virgulinella chalkophila, also known from Bavaria and the Polish Carpathians, has been recorded. The latter region contains fossils of the thermophilic genera Biapertorbis and Stomatorbina (Cicha et al., 1998). At the end of the Oligocene (in the second half of the Egerian), the general shallowing of the southern shelf took place. It was accompanied by the appearance of lagoonal sediments with coal interbeds and with a brackish-water fauna represented by the genera Cribrononion (two species), Protelphidium, and Ammonia beccarii (Horvath-Kollany and Nagy-Gellai, 1988). The shallow areas in Transylvania (Cicha et al., 1998) were inhabited by rare arenaceous foraminifers, Almaena osnabrugensis, and the warm-water genera Miogypsinoides and Amphycoryna, the last is unknown in other regions.

In the Carpathian Foredeep (Ukraine), the benthic group is represented by arenaceous foraminifers (*Rhabdammina*, *Ammodiscus*, *Haplophragmoides*, *Spiroplectammina*, *Verneuilina*, etc.); secreting forms such as lagenids (4 genera), discorbids (7 species of 3 genera), and nonionids (4 genera); and no less than 25 genera of other families (*Alabamina, Heterolepa, Cibicidoides, Asterigerina, Caucasina, Reussella, Angulogerina, Bulimina, Uvigerinella, Fursenkoina, Bolivina, Cassidulina, Virgulinella*, etc.). These genera were also distributed in the basins of northwestern Europe and in the Eastern Paratethys, while the genera *Baggatella, Turillina, Buliminella, Pleurostomella*, and *Bolivinita* have not been reported from outside this region.

Eastern Paratethys. In the central parts of the basin under outer-shelf conditions in the latest Rupelian-earliest Chattian, a distinctive foraminiferal community with a predominance of representatives of the genus Virgulinella was widely distributed. Shells of these forms even form thick accumulations known as "microcoquinas." Deposits of this time in Ciscaucasia, Ergeni Upland, and eastern Transcaspia are sometimes called "Virgulinella Beds." Stolyarov (2001) noted the presence of Virgulinella pertusa, V. karagiensis, and V. ex gr. aequalis together with Uvigerinella californica, Bolivina spp., and plankton (genus Globigerina) in clayey-marly facies and even in anoxic "fish facies." Foraminifers with morphology characteristic of the genera Virgulinella, Uvigerinella, and Bolivina, which possess thin-walled non-ornamented subcylindrical shells frequently serve as indicators of muddy sediments with anoxic conditions in the bottom layer (Kaiho, 1991). There is reason to believe that smaller, thinwalled shells of *Virgulinella*, as well as numerous apertures along the sutures, evolved under these conditions.

Muddy substrates on the shelf of the Caucasian Basin were mostly inhabited by arenaceous foraminifers (genera with a primitive morphotype such as *Saccammina*, *Proteonella*, *Rhabdammina*, *Hyperammina*, *Reophax*, *Ammodiscus*, *Haplophragmoides*, etc.). In the cis-Kubanian area the calcareous benthic foraminifers *Pseudoparrella caucasica*, *Virgulinella* ex gr. *pertusa*, *Uvigerinella* ex gr. *californica*, and *Bolivina plicatella* were distributed (Pechenkina, 1971; *Paleogene System...*, 1975).

Foraminifers of the shallow zone of the Stavropol Uplift are relatively diverse and well studied. Since many species were shared by other regions, this assemblage is representative of the distinctive fauna of the entire Eastern Paratethys. The most widely distributed forms in this facies are arenaceous foraminifers Hyperammina djanaica, H. caucasica, Ammodiscus tenuiculus, Cyclam-Haplophragmoides kjurendagensis mina torosa, kjurendagensis, H. kjurendagensis karadjalgensis, Trochammina florifera, Spiroplectammina terekensis, Rotaliammina depressa, Trochammina caucasica, Verneuilina rasilis, and V. tripartita; secreting benthic foraminifers are represented by the species Melonis dosularensis (= Nonion praevius), Pseudoparrella caucasica, Caucasina schischkinskayae, C. oligocenica, C. buliminoides, C. magna, Uvigerinella californica, Fursenkoina schreibersiana, Bolivina spp., etc. (Bogdanovich in Paleogene Deposits..., 1960; Bogdanovich and Bugrova, 1987; Ter-Grigorjantz in *Maikopian Beds...*, 1964, Ter-Grigorjantz, 1969, etc.). Most of them are restricted to the Eastern Paratethys.

In the North Black Sea Region, the terrigenous non-calcareous or poorly carbonaceous muds (the Askanian Formation) are characterized by typical species of the North Caucasian assemblage: Spiroplectam*mina terekensis* (= *S. carinata follies* sensu Kraeva; see Kraeva in Maikopian Beds..., 1964); Haplophragmoides kjurendagensis, Cibicidoides oligocenicus, and at least two other species of this genus; Caucasina C. buliminoides, schischkinskavae, Fursenkoina schreibersiana, and Uvigerinella majkopica; and the genera Quinqueloculina (three species), Miliolina (three species), *Globulina* (two species), *Nodosaria*, Nonion, Nonionella, and Pullenia (two species) (Kraeva, 1960, Kraeva in Maikopian Beds..., 1964; Resolutions ..., 1965, etc.). Later, in the Gornostaevka Formation, the assemblage became impoverished, and *Cibicidoides ornatus* and *Rotalia* ex gr. *propingua* and forms tolerant of changes in salinity such as Elphidium onerosum, Porosononion dendridicus (= Nonion polymorphus), Nonion granosum, etc. appeared. According to recent data (Zernetskii et al., 2001), this is the level of zones NP25 and D16. On the southern flank of the Depression (East Crimea, the Kerleut Formation), the assemblage of Haplophragmoides kjurendagensis Zone has been recognized. It contains Spiroplectammina terekensis, Uvigerinella californica, and Fursenkoina schreibersiana (Paleogene System..., 1975).

In the Azov–Kuban Depression, depressions of the Karpinsky Swell, and in the Volga–Ural interfluve, the benthic group is represented by North Caucasian species, including Spiroplectammina terekensis (abundant), Uvigerinella ex gr. californica (sometimes very abundant), Fursenkoina schreibersiana, Caucasina buliminoides, Virgulinella aff. pertusa, and the genera Melonis and Porosononion. Further to the south, in the Manych region, Haplophragmoides kjurendagensis is added to this assemblage, and somewhat later, Cibicidoides ornatus, Pseudoparrella caucasica, and abundant Cibicidoides pseudoungerianus entered the assemblage (Nikitina, 1972). At the Oligocene-Miocene boundary, the assemblage included nonionids, a possible indication that the basin became shallower, and its water became somewhat fresher.

Transcaucasia. In the eastern part (Azerbaijan), the assemblage was impoverished and included only endemic species; the sole exception is the genus *Chilostomella*, which has been recorded in Syria (Krasheninnikov and Nemkov, 1975). At the beginning of the Late Oligocene, associations of the Middle Kura Depression contained *Spiroplectammina caucasica, Bolivina floridana, Bolivina* ex gr. *plicatella*, and other taxa, which were replaced somewhat later by *Virgulinella poiliensis, V. aequale, V. pertusa*, and *Bulimina ovula*. However, the latter assemblage may have been of at least partly Miocene age. Similar assemblages are

known from the piedmonts of the Lesser Caucasus, which in addition contain Uvigerinella californica, *Porosononion dendridicum*, and *Elphidium onerosum*; local species of the genera Rotalia (two species), Cibicides, Chilostomella, and Virgulinella, and radiolarians (Khalilov, 1962; Khalilov and Kuznetsova in Maikopian Beds..., 1964; Khalilov and Mamedova, 1984). In the northern Talysh (the Pambakian Formation), Rotalia audouini and R. affinis were recorded (Regional..., 1989). Further to the west (in Georgia), widespread species of the genera Nonion (two species), Elphidium, Discorbis, Cibicidoides, Uvigerina (three species), Fursenkoina, Bolivina (two species), and the thermophilic genus Halkyardia were present (Archvadze in Maikopian Beds..., 1964). The low diversity of this fauna, the presence of the euryhaline genera Nonion and Elphidium, and the appearance of the genus Ammonia indicate that the basin became shallower, and its water became fresher by the end of the Oligocene.

Turanian Basin. The Mangyshlak assemblages of foraminifers are similar to those of the Ciscaucasian part of the basin. Deposits of the southern part of the shelf (the Karagie Formation) contain numerous shells of the endemic species *Virgulinella* sp. and *V. karagiensis*. Further northwards, the remains of the latter species account for 80–100% of the assemblage (Mikhailova, 1968; Stolyarov 2001; *Paleogene System...*, 1975).

The western part of the Turanian Basin (the Kara Bogaz Region) is characterized by the presence of the North Caucasian species *Spiroplectammina terekensis*, *Haplophragmoides kjurendagensis*, *Melonis dosularensis*, *Elphidium onerosum*, *Uvigerinella californica*, *Caucasina schischkinskayae*, C. *buliminoides*, *Virgulinella* ex gr. *aequalis*, etc. (Shutskaya *et al.*, 1963; Rozyeva and Lapteva, 1975; data from G.M. Korovina; collections from V.T. Balakhmatova). An assemblage with a similar taxonomic composition has been recorded in northern Turkmenistan and in the Trans-Unguz Karakum.

The northern part of the shelf (the Buzachi Peninsula, lower Zhikimshik Formation) was inhabited by a fauna that closely resembles that of the North Caucasus (Spiroplectammina ex gr. terekensis, Neogyroidina memoranda, Caucasina schischkinskayae, and Sphaeroidina variabilis) but contains genera unknown in the latter (Pyrulinoides, Marginulina, Frondicularia, etc.) (Bykova and Azbel', 1962). The species Caucasina schischkinskayae, Uvigerinella californica, and Cibicidoides ornatus are known in the South Emba Region (Averburg and Kurgalimova, 1990) and Haplophragmoides ex gr. kjurendagensis, Cibicidoides pseudoungerianus, and C. ornatus are known in the central part of the Caspian Depression (Paleogene System..., 1975).

The shelf zones of the Ustyurt and the Aral Sea Region were inhabited by characteristic species in common with the North Caucasian assemblages (Spiroplectammina terekensis, Pseudoparrella caucasica, Melonis dosularensis, Nonion granosum, Elphid*ium onerosum, Uvigerinella californica, Caucasina schischkinskayae*, etc.) (*Paleogene System...*, 1975). Associations of the North Ustyurt Depression (the Baigubek Horizon) are represented along with the genera *Robertina, Rotalia*, and numerous miliolids (six species of the genera *Triloculina* and *Quinqueloculina*) (Prusova in *Maikopian Beds...*, 1964; *Paleogene System...*, 1975) known from the Oligocene of northwestern Europe. The end of the Oligocene was marked by the appearance of polymorphinids, *Porosononion dendridicum* and *Elphidium onerosum*, showing a possible brack-ishing of the basin. Further to the east and north, closer to the coastal line, the fauna became strongly impoverished and disappeared.

The most diverse fauna is that of the southern Aral Sea Region (Ivanova, 1966, 1971; Ivanova et al., 1961; Averburg, 1970; Paleogene of Turkmenistan, 1975; collections by V.T. Balakhmatova). Judging from its composition, it was closely connected with the fauna of western Europe and the Mediterranean. The fauna of the middle part of the Daryalyk Formation contains numerous polymorphinids, Quinqueloculina ermanni, Q. enaplostoma, Q. ungeriana, *Melonis dosularensis, *Cibicidoides pseudoungerianus, *C. ornatus, *Neogyroidina memoranda, *Pseudoparrella caucasica, *Uvigerinella californica uruchensis, *Caucasina schischkinskayae, Fursenkoina schreibersiana and species of 22 genera, including Spiroplectammina, Cornuspira, Spiroloculina, Sigmoilina, Bolivina, etc. Some of these species (asterisked) are also known in the fauna of the Stavropol Region, and Quinqueloculina species and the genera Planorbulina and Robertina occur outside the Eastern Paratethys. Later, a brackish-water assemblage with nonionids and *Elphidium* emerged (areas located west of Khiva and Urgench and northwest of Tashauz).

The western part of the Fore-Kopet-Dagh Depression is characterized by species of the two zones established in Ciscaucasia. The lower zone contains Verneulina tripartita, V. rasilis, Trochammina florifera, T. chadumica, Saccammina (two species), and Ammodiscus granatus. In addition to these forms, the upper zone includes Haplophragmoides kjurendagensis, Ammodiscus tenuiculus, Cyclammina torosa, and Pseudocyclammina? insignedentata and, in the uppermost part, Haplophragmoides kjurendagensis karadjalgensis, Cyclammina kubanica, and Trochammina rotaeformis (Paleogene of Turkmenistan, 1975).

In the Central Kopet Dagh part of the Depression, L.E. Nevmirich recorded numerous agglutinating forms; nonionids (Astrononion, Melonis, and Florilus), Quinqueloculina cf. selene, Discorbis globularis, Asterigerina aff. guerichi, Cibicidoides sigmoidalis, Heterolepa dutemplei, Rotalia aff. propinqua, Bitubulogerina aff. kasselensis, Bulimina tumidula, and Sphaeroidina variabilis; and diverse polymorphinids. This is a mixed assemblage that has some species in common with both the North Caucasian Region and the Chattian of Germany. This assemblage was replaced by a fauna with *Porosononion dendridicum* and *Cibicidoides ornatus* (Paleogene of Turkmenistan, 1975; Rozyeva and Lapteva, 1975) characteristic of the entire Eastern Paratethys in the latest Oligocene–earliest Miocene.

The particular assemblage characteristic of the Gyaursdag contains numerous nonionids such as *Florilus*, *Porosononion* (four species), and *Elphidium*; polymorphinids; miliolids such as *Quinqueloculina* and *Miliammina*; and rare *Rotalia* aff. *propinqua*, *Discorbis* sp., *Uvigerinella californica parva*, etc. Further to the east (eastern Kopet Dagh), species that are known in Ciscaucasia (*Spiroplectammina terekensis*, *Uvigerinella californica*, etc.) have been recorded. They are also present in the depression of the Mary District together with *Cibicidoides pseudoungerianus*, *C. oligocenicus*, *Melonis dosularensis*, and *Caucasina schischkinskayae*.

The eastern shelf (the central Kyzylkum, the Upper Sarbatyr Subformation) contains Cyclammina placenta, Verneuilinoides compressa, and Ammomargin*ulina* cf. *lobsanensis*, which are known in northwestern Europe. Later, a mixed assemblage combining North Caucasian and some West European species appeared: Spiroplectammina terekensis, Pseudopolymorphina obscura, Nonion granosum (and two more species), Melonis dosularensis, Porosononion dendridicum, Elphidium onerosum, Asterigerina guerichi, Cibicidina amphisyliensis, Caucasina schischkinskavae, Uvigerinella californica, Cibicidoides ornatus, etc. (Tsatsir, 1969; Kakhanova and Korobkov, 1969; Paleogene Sys*tem...*, 1975). Further to the south, the Bukhara Depression was inhabited by many of these species along with Rotalia propingua, Caucasina buliminoides, and abundant nonionids (Averburg, 1970 etc.). The Kara-Kalpak Gulf, connected with the Northern Ustyurt Depression and the basin of northern Turkmenistan, was inhabited by the North Caucasian assemblage of calcareous forms, together with Spiroloculina canaliculata and polymorphinids (Polyakov et al., 1971). The presence of miliolids and nonionids indicates that the basin showed a gradual trend towards shallower and fresher water.

Ostracodes

North Sea Basin. Fluctuations of the sea level of the North Sea and migration of the shoreline in the Late Oligocene strongly influenced the ostracode fauna of the shelf, which inhabited various bathymetric zones from 5 to 120 m (Goereich, 1958; Keen, 1989; Uffenorde, 1981, 1986).

The Rupelian–Chattian boundary is not characterized by ostracodes in the larger part of the outer shelf in northern Germany. The exception is the Wursterheide area, which in the latest Rupelian–earliest Chattian lay in the upper bathyal zone under conditions that were favorable only to representatives of the genera *Henryhowella, Krithe, Phacorhabdotus, Cytherella*, and

Cytheropteron, and excluded of shallow-water groups. In Lower Saxony the succession from a relatively deep water ostracode community with Henryhowella asperrima to that of the middle infralittoral zone with Cytheridea pernota and then to that of the shallowwater zone with Eucytheidea fissodentata shows that the waters of the basin became progressively shallower. The assemblage included up to 40 species of genera belonging to the euryhaline spectrum: Henryhowella, Cytherelloidea, Echinocythereis, Cytheridea, Cuneocythere, Flexus, Falunia, Muelleria, Bairdia, Cytheretta, Cushmanidea, Callistocythere, Eucytheridea, etc. The boundary with the Vierlandian is emphasized by the sharp impoverishment of the assemblage. In evolutionary terms, the time interval between the end of the Rupelian and the very beginning of the Vierlandian corresponds to a single evolutionary stage, the biozone occupied by Cytheretta semipunctata.

The Late Oligocene ostracodes of the Kassel Sands, which were deposited in the shallow-water zone on the southern margin of the North Sea, were extremely abundant and diverse (Faupel, 1975). Their genus-level composition was close to that of the assemblage of Chattian ostracodes from Lower Saxony but surpassed the latter in diversity (more than 75 species) and abundance. The Chattian ostracode assemblages of the Rhine graben system were also close in taxonomic composition to those of northern Germany; the Rupelian-Chattian boundary was marked by an increase in biodiversity (Goerlich, 1958). In the Mainz Basin, a short-term sea invasion at the beginning of the Middle Pechelbronner time introduced Henryhowella asperrima and Paracypris sp., but the predominant forms of the Middle Pechelbronner were the freshwater genera Candona, Eucypris, Moenocypris, and numerous representatives of the brackish-water genus Hemicyprideis (H. gilletae, and other species) (Triebel, 1963, Malz and Triebel, 1970).

Alpine Carpathian Basin. During the Chattian, in the Swiss Depression, the limnic ostracode communities became widespread, while the euryhaline assemblages reduced their diversity by more than 50%. In Bavaria, the composition of assemblages changed only slightly; however, the Mediterranean species *Costa hermi* was recorded from the Chattian of Bavaria.

In the late Kiscellian (Chattian), the Hungarian Paleogene Basin returned to normal marine conditions. The ostracode fauna of this time was diverse: the genera *Krithe, Henryhowella, Argenocythere, Cardobairdia,* and *Argilloecia* accounted for about 40% of the species, and the genus *Cytherella accounted* for 45%. In addition, representatives of the genus *Buntonia* and *Costa hermi*, probable Mediterranean migrants, appeared. The taxonomic pattern indicates conditions characteristic of the outer shelf (upper bathyal zone). Many groups survived into the Egerian and the abundant species *Hemicyprideis gilletae* and *Myocyprideis rara* appeared (Jiriek and Riha, 1990). In addition, forms

similar to *Disopontocypris oligocaenica* appeared (Monostori, 1985).

In Transylvania, the marine transgression at the beginning of the Chattian only slightly enriched the ostracode community. The Vima Formation is characterized by some representatives of the stenohaline genera *Cytherella, Bairdia, Krithe*, and *Occultocythereis*. The relatively deep-water species *Henryhowella asperrima* appeared for the first time in the Transylvanian Basin. Simultaneously, in some parts of Transylvania, the lagoonal-lacustrine basins (Cetate Beds) continued to sustain fresh-water genera, i.e., *Candona, Ilyocypris*, and *Darwinula*.

Eastern Paratethys. Ostracodes are known only during the initial stages of the transgression and their distribution was far from universal. In the North Black Sea Region and the northern Ustyurt, the Askanian and Karatomak time is characterized by scarce assemblages of ostracodes (14 species of 12 genera) represented by transient species of euryhaline groups, inherited from the Pshekha and Solenovskoe basins, along with newly appearing stenohaline forms, species of the genera Krithe and Cytherella. It is worth noting that members of the dominant brackish-water genera of the Solenovian time, Disopontocypris and Cyprinotus, were absent. Paracypris rarefistulosa and Flexus concinnus, widespread in the Western Paratethys since the beginning of the Rupelian, appeared in the Eastern Paratethys for the first time.

Mollusks

It seems that no assemblages of Chattian mollusks have been recorded from North Africa.

Northern Mediterranean. The single known representative assemblage of mollusks was described from the eastern part of northern Italy (Venzo, 1937; Accordi, 1955; Fig. 4; see also Amitrov, 1993 for a revision of some gastropod families). The bivalve mollusks of this fauna amount to more than 100 species of 64 genera and subgenera. They include tropical and subtropical forms such as Trisidos, Spondylus, Florimetis, Crassatella sensu stricto, Cardium sensu stricto, Vepricardium, Trachycardium, and Venus sensu stricto. Ten genera and about 60% of the species known in this area (most of them belong to the above-mentioned warmwater taxa) do not occur outside southern Europe (Popov, 1996). However, a significant part of this assemblage was represented by species of wide geographical distribution (22%). Species in common with the basins of Central Europe were numerous. About 40% of the species were inherited from the Rupelian fauna. The proportion of species of northern European origin continued to increase. Among the new migrants from the seas of the northeastern Atlantic were Astarte concentrica, Nemocardium cingulatum, Arctica rotundata, Callista reussi, and Gari angusta.

The list of gastropods from this area contains only 80 species of 27 families. The assemblage lacks (probably owing to some secondary taphonomic factors) strombids, Diastoma, and the other most characteristic warm-water groups; the only indicators of high water temperatures are tonnids and magilids. There are at least 50 species in common with the Rupelian (most of them from Italy) and only 7 species shared with the Neogene fauna, some of which are represented by different subspecies. This assemblage has little similarity with other Chattian assemblages of Eurasia. Preston's dissimilarity coefficient (C_P) is 0.95–0.98 for assemblages of the North Sea and Transcaspia and 0.87–0.90 for those of Central Europe. A total of 23 species shared with the Hungarian assemblage was reported (see below for details); however, these values, as well as the list of Kiscellian gastropods, seem unreliable and require revision.

Eastern Atlantic. In Aquitania, the Chattian part of the section is distinguished from the sedimentary strata (Peyrière Beds), which was previously entirely attributed to the Miocene (Czepreghy-Meznericz, 1964, Báldi, 1973). Among the mollusks that have been described from this Chattian part, only very few species of bivalves, and 178 gastropods species of 50 families (Peyrot, 1934), appear to have originated from the Peyrière Beds. This assemblage includes members of very warm-water families and genera (strombids, Diastoma, vasids, pyrenids, etc.). The majority of species in Aquitania are known only from these beds; however, 11 species have survived from the Rupelian, and 59 species are shared with the Miocene fauna. This assemblage is highly endemic: comparison with other Chattian assemblages of Eurasia shows that Preston's coefficient exceeds 0.93, and its values for the North Sea Basin and Transcaspia are close or equal to 1.0; 14 species (according to Báldi, 17) are shared with the Egerian Beds of Hungary, and only 5 species are shared with the Chattian of northern Germany.

North Sea Basin. Marine assemblages of Chattian mollusks are known from Belgium, the Netherlands, Germany, and Denmark. It is convenient to start the review with the richest and most studied assemblage of the North German Lowland, the type area of the Chattian. The assemblage of bivalve mollusks here amounts to more than 160 species of 111 genera and subgenera (Popov, 1996, Table 2 based on the data of Görges, 1957; Hinsch, 1972; R. Janssen, 1979) and was revised for the Lower Chattian interval by Janssen (1979). The considerable diversity and the presence of many subtropical genera and species (Arca, Atrina, Pinctada, Pteria, Spondylus, Arcopagia, and Venus sensu stricto) show that this assemblage cannot be referred to as boreal. Up to 35 subtropical forms can be counted in the assemblage of the Kassel Sands of the Lower Chattian (Janssen, 1979). According to Janssen (1978a, 1978b), the North German gastropod assemblage contains 282 species of 60 families. The family and genus composition of the assemblage is very indicative; it lacks

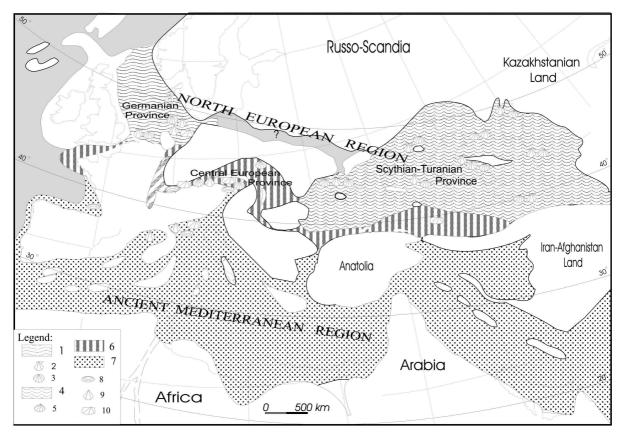


Fig. 4. Schematic zoogeographic zonation of the Chattian Basin based on mollusks. Designations: (1–5) North European Region with moderately warm-water benthic fauna of the Chattian type, (1) Germanian Province with presence of taxa characteristic of the North European Region: (2) *Chlamys bifida* and (3) *Scalaricardita*, (4) Scythian–Turanian Province with characteristic taxa of the North European Region and endemic species: (5) *Cerastoderma prigorovskii, C. karaschokense, Plagiocardium abundans;* (6) areas with transitional faunal composition, (7) Ancient Mediterranean Region with benthic fauna, including diverse assemblages of subtropical mollusks with characteristic genera: (8) *Crassatella* sensu stricto, (9) *Spondylus*, and (10) *Arca* sensu stricto.

many warm-water groups characteristic of southern assemblages (angariids, strombids, tibiids, *Diastoma*, ampullinids, melongenids, pyrenids, vasids, harpids, etc.) but contains 20 families, most of which are unknown in other Rupelian faunas of the North Sea Basin but are characteristic of the Rupelian of the more southern Mainz and Paris basins (turbinids, lacunids, architectonicids, turritellids, vermetids, cypraeids, sinids, marginellids, terebrids, etc.). Therefore, it can be inferred that in the Chattian the shallow shelf sea became warmer than in the Rupelian.

At the same time, the other assemblages of Germany, Denmark (Harder, 1913), and Belgium (Glibert, 1957), which probably inhabited slightly deeper waters, were strongly dominated by boreal genera and species widely distributed in the Oligocene (*Nucula comta, Chlamys bifida*, several *Astarte* sp., and others), did not contain gastropod species of the families that indicate relatively cold conditions, and retained the same northern appearance, as in the Rupelian. Janssen's analysis of the continuity of the Early Chattian assemblage shows that 35% of the bivalve species survived from the Rupelian and that the majority of them (56%) first appeared in the Chattian. Only 17% of the Early Chattian mollusks persisted into the Miocene, with bivalves being more numerous than gastropods. The bivalve assemblages of Belgium, the Netherlands (Albrecht and Valk, 1943), and Denmark are much poorer than that of northern Germany but have many species in common (58) and, thus, are similar to them. The differences between them are apparently due to facies variability. The suggestion that the assemblages of Belgium, the Netherlands, and Denmark have a lower diversity because of differences in facies rather than in climate was supported by the description of the Chattian mollusks from the Mogenstrup area in Denmark (Schnetler and Beyer, 1990), which is located well north of those in northern Germany and even those that have been previously recorded in Denmark at Aarhus. For the first time in Denmark, this fauna yielded 20 families of gastropods, including 12 families that are absent in the northern Rupelian assemblages. Thus, these records eliminated the "principle" difference between the fauna of Denmark and that of northern Germany and made it clear that the Aarhus assemblage is impoverished because of local conditions rather than the general climatic zonality (perhaps, this area had greater water depth). This may be also true for the assemblages of Belgium and the Netherlands. Preston's coefficient for the assemblages of northern Germany and Denmark is 0.47.

Despite differences in the completeness of the assemblages, the similarity between the molluscan lists of northwestern Europe, and between these lists and lists from the basin of southern Bavaria is very strong (C_P is 0.49–0.56, and up to 0.66 for gastropods). The molluscan faunas of the North Sea Basin and Eastern Paratethys also show a large number of species in common, which is reflected in the values of Preston's coefficient (C_P is 0.68–0.80). This similarity was especially high at the beginning of the Chattian.

If the North Sea Basin became warmer during the Chattian, it seems reasonable that the similarity between the Chattian molluscan faunas and the Rupelian fauna of the more southern Mainz Basin increased. This similarity is evident at the family, genus, and species level: of more than 100 gastropod species from the Chattian of the North Sea that existed in the Rupelian, approximately 25 are known from the Mainz Basin and have not been recorded from the Rupelian of the North Sea Basin. This raises the question of where and when the warm-water elements penetrated into the North Sea Basin. It is known that the Mainz Basin was freshened at the end of the Rupelian and then dried up. These observations allowed the investigators to conclude that warm-water elements penetrated from the Mainz Basin into the southern part of the North Sea Basin as early as the Rupelian (Anderson, I960; Kadolsky, 1973) or that the Mainz Basin persisted until the beginning of the Chattian, was occasionally invaded by marine faunas, and was connected with the North Sea Basin (Janssen, 1978a). Janssen also believed that the northern basin was connected with the Aquitanian Basin by a passage that existed in the area of the English Channel.

Carpathian Basin. The bivalve assemblage of the Alpine Foreland Basin from the molasse of southern Bavaria (Hölzl, 1962) is similar to the assemblages of the Carpathian Basin discussed below (C_P is 0.61–0.72) and to the faunas of the North Sea Basin (C_P is 0.56 for mollusks and 0.78 for gastropods). The assemblage lacked characteristic Mediterranean species but contained abundant widespread taxa, and species typical of northern associations. The percentage of the species of subtropical genera was low (14%), endemic species amounted to 18% (13 species among bivalves), other species were mostly those in common with the Chattian of northern Germany and Belgium.

Although the Bavarian gastropod assemblage is not poor (113 species from 36 families), it seems to be impoverished and, thus, insufficiently representative. The assemblage could not have inhabited waters warmer than those of the North German assemblage, because it lacks some families (probably due to secondary factors), which are also absent in the typical northern Oligocene assemblages of Transcaspia and the Rupelian of the North Sea Basin, but occur in the Chattian of northern Germany. The Bavarian fauna, however, includes some true warm-water groups characteristic of the Central European and Mediterranean assemblages and absent in northern Germany. These are the genus Diastoma, ampullinids, tibiids, and melongenids. At the species level, the assemblage shows only minor distinctions from other assemblages, C_P varies widely (most probably because some of the associations compared are low in species). The Bavarian assemblage shares nearly equal numbers of species with the large assemblages of northern Germany and the Egerian Beds of Hungary (46 and 44, respectively). In general, the Bavarian assemblage contains, along with numerous widespread species and a few endemics, about 30 species in common with the Hungarian and more southern assemblages, which are absent in the northern basins. Furthermore, it contains only about 20 species that are characteristic of northern assemblages but are absent in the southern ones (half of them belong to the family Turridae).

Thus, the Bavarian assemblage is intermediate in composition but is slightly closer to the Carpathian faunas. There is also evidence for direct zoogeographic connections between the Chattian seas of the North Sea Basin and the Alpine Foreland Basin. The passage apparently passed along the Rhine graben system, which was in direct contact with the Mainz Basin. In contrast to the North German assemblage, however, none of the 47 species (42%) of Bavarian gastropods that are known since the Rupelian came from the Mainz Basin. More than 25 species of the Bavarian gastropods survived into the Neogene, but none of them were predominantly Neogene forms.

On the southern shelf of the Carpathian Basin, the composition of mollusks shows a sharp distinction between the Kiscellian and Egerian associations. The composition of Kiscellian mollusks, which inhabited soft substrates, indicates the evolutionary stability of associations of this type. Báldi (1986) noted their taxonomic similarity to the assemblages of the upper Belaya Glina Formation in Ciscaucasia (Korobkov, 1939). Taking into account that these assemblages are separated by the Rupelian, which included the Solenovian brackishing, it is necessary to assume that the muddy sediments of the Paratethys were repeatedly colonized from open oceanic basins by the same or similar species. Noszky (1940) described numerous Kiscellian forms and identified them as Neogene, Rupelian, and Eocene species of different regions. Báldi (1973, 1986) critically treated the results of his predecessor but without a complete revision. However, he supported the view that the Kiscell Clays contain a mixture of Mediterranean (northern Italian) and boreal species of mollusks.

The differences between the Egerian and Kiscellian assemblages are not due to the difference in water temperature (because both faunas contain southern genera, *Strombus* and *Diastoma*) but due to the general regression, the increased supply of coarse material, and the decreased or unstable salinity in the marginal parts of the Egerian Sea. It is further supported by the appearance here of shallower water and euryhaline groups, including large thick-walled bivalves, *Polymesoda*, neritids, thiarids, and nassariids. Preston's coefficient for the comparison of species from the Kiscellian and Egerian associations is about 0.90; however, as previously mentioned, these species (especially Kiscellian) needs a revision.

The Egerian assemblage of Hungary was closely revised by Báldi; therefore, its numerical values seem to be more reliable. Its species composition sharply differs both from the extensive Chattian assemblages of the North Sea Basin and from the northern Italian and Aquitanian associations (C_P is about 0.90) but is close to other Egerian assemblages of the Carpathian Basin (those of Austria, Slovakia, Romania, and Croatia, for which C_P varies from 0.60 to 0.72) and includes numerous warm-water, subtropical, and even tropical genera (Pinctada, Crassatella, Cardium sensu stricto, and Vepricardium). Among warm-water bivalve mollusks, 19 species (15%) are in common with the Mediterranean and are unknown in more northern assemblages. They include such typical species descending from Eocene and Tethyan faunas as Pecten arcuatus, Pycnodonte brongniarti, and Crassatella carcarensis and new species of possibly Mediterranean origin: Pecten (Flabellipecten) burdigalensis, Megacardita arduini, Venus multilamella, etc. During the Miocene, many of them widely expanded into the northern assemblages. At the same time, the number of species in common with northern faunas is not so high. These forms include some very characteristic species such as Chlamys picta, Scalaricardita orbicularis, Astarte gracilis, Callista beyrichi, etc. The assemblages of Austria, Romania, Slovakia, and Croatia consist predominantly of species known in Hungary. But these four assemblages are much poorer than those of Hungary. None of them contain Strombus, the best indicator of the tropical climate, but there are other warm-water groups (large Crassatella and cypraeids in Austria; melongenids in Croatia; and Diastoma, tibiids, melongenids, terebrids, and others in Slovakia).

According to Báldi (1973), 75 species of the Egerian assemblage are known since the Rupelian or earlier; 60 species, from the beginning of the Chattian, and about 120 species first appear during this time. Ninety species pass into the Neogene, i.e., more than the number of species inherited from the Rupelian. The Lower Egerian assemblage, as well as the Kiscellian one, was dominated by north European species, whereas the second half of the Egerian was marked by a decrease in the influence of boreal assemblages and stronger connection with the Mediterranean. In the lower Egerian, the number of species in common with the Oligocene was 7.3 times the number of "Miocene" species, while in the upper Egerian, it was only 2.3 times as high.

The Chattian assemblages of the northern coast of the Carpathian Basin, as well as the Rupelian ones, are taxonomically poor and insufficiently studied. They are known from the base of the Lopyanka Formation of the Menilite Group in the Ukrainian Carpathians (Maksimov, 1963) and from the Krosno facies of the Polish Carpathians. Although these faunas clearly require additional studies and revision, the materials collected in the Ukrainian Carpathians indicate that they (particularly lucinids and venerids) were relatively diverse from the outset. The presence of *Cardita* sensu stricto, *Chama*, and gastropods of the families Lacunidae, Ampullinidae, and Marginellidae indicates the relatively warm water conditions of the basin. This fauna sharply differs from the known molluscan assemblages of the Eastern Paratethys even at family and genus level, and from the Kiscellian-Egerian faunas; however, the intermediate character of the assemblage of the Alpine Foreland Basin in Austria (Harzhauser and Mandic, 2001) shows that these differences may be attributed to the differences in facies and environmental conditions rather than to the difference in water temperature alone.

Euxino-Caspian (Kalmykian) Basin. The known assemblage of the Chattian bivalves of the southern shelf is not so representative. It contains 33 species (in Georgia) and is distinct from more northern assemblages in the presence of such warm-water subtropical forms as *Arca, Obliquarca, Isognomon, Arcopagia*, and *Caryocorbula* (Popov *et al.*, 1993). Although these genera and subgenera are represented by widely distributed species, they do not include characteristic Tethyan forms.

The gastropod assemblages of Transcaucasia are also very poor: the Uplistsikhe Beds of Georgia and the Indzhachoi Horizon of Azerbaijan yielded only 18 species each (Kurtskhalia, 1982; Amitrov, 1995); it is worth noting that the latter deposits may correspond to the Rupelian rather than the Chattian, while the Uplistsikhe Beds can extend into the lower Miocene. Not all species have been identified reliably. The family composition points to a relatively warm-water appearance of both assemblages. In contrast to the associations of the northern and eastern shelf, they include turritellids, vermetids, and (in the Indzhachai fauna) melongenids.

The assemblages of the northern shelf (the Askanian Formation of the North Black Sea Region and the Kalmyk Formation of the Volga–Don Region) are also rather poor and mostly contain bivalve mollusks, about 20 species each (Popov *et al.*, 1993). Representatives of warm water subtropical genera and species are almost absent, whereas the prevailing group was shared with the North Sea Basin (20 of 28 forms identified without use of the open nomenclature). Nevertheless, the fauna was dominated by endemic species of the Eastern Paratethys. Some of them, like *Plagiocardium abundans, Cerastoderma prigorovskii*, and *Corbula helm-* *erseni*, formed the pattern of this fauna, particularly starting from the second half of the Chattian when a certain freshening of the Eastern Paratethys led to the extinction of many sea immigrants and increased the endemicity of the fauna.

The molluscan assemblages of the northeast shelf (the Karagie Formation of Mangyshlak, Karatomak, and Baigubek Formations of the northern Ustyurt) are considerably more abundant (Merklin, 1974; Popov et al., 1993; Amitrov, 1971, 1995). They were also dominated by species in common with the seas of northwestern Europe. The proportion of endemic species among the bivalve mollusks was one-third in the Karatomak assemblage and reached nearly one-half in the subsequent Baigubek fauna (Table 2 in Popov, 1996). Of the 30 bivalve species shared by the northeastern part of the Eastern Paratethys and the North Sea Basin, 5 locally widespread forms were absent in the basins of Central Europe (Nuculana gracilis, Yoldiella pygmea, Chlamys bifida, Ch. hoeninghausi, and Palliolum simile). The most typical among these is *Chlamys bifida*, the zonal species of the Chattian A. This species was an abundant, widely distributed form that reached as far as the Kyzylkum and Kopet Dagh.

Judging from the gastropod composition, the associations of the Karagie Formation of Mangyshlak and the Karatomak layers of the northern Ustyurt and northern Aral Sea Region can be considered as the same assemblage. About 30 species of gastropods of 15 families have been fairly reliably determined in Transcaspia. The material is rather poorly preserved, which may be the reason for the absence of some groups with fragile shells. However, the impoverishment of the assemblage is mainly actual rather than an artifact and, along with its composition, indicates that it is from cold-water conditions. It lacks not only rather warm-water groups that occurred in the Chattian of the North Sea and groups known in the Rupelian of the North Sea but absent in the colder waters of the Rupelian of Transcaspia (trochids, olivids, volutids, etc.) but also some families that were present in the Rupelian of Transcaspia (rissoids, mitrids, acteonids, etc.). No new families appeared compared to the "pre-Solenovian" assemblages. Probably, in contrast to the North Sea Basin, the water temperature in the Late Oligocene of Transcaspia decreased.

Despite the differences in both family composition and number of species, the species of the assemblage under consideration show a close similarity to those of the Chattian faunas of the North Sea, with Preston's dissimilarity coefficient being no more than 0.60. Almost all Transcaspian species (except for two endemics and one doubtful form) were widespread in the Oligocene and are known both in the Chattian and Rupelian of northern Germany. On the other hand, no less than six species of this assemblage were absent in the Chattian of Central Europe (C_P for the assemblages of Hungary, Slovakia, Romania, and Austria is 0.76– 0.90) and no less than eleven species were absent in the Rupelian of Transcaspia. Some species that were broadly distributed in Europe during the entire Oligocene (*Cochlespira volgeri* (Philippi), *Acamptogenotia morreni* (Koninck), etc.) first entered the Transcaspian Basin only in the post-Solenovian time, although an equally close connection with the European seas was already present in the Rupelian (Popov *et al.*, 2002). This indicates that, notwithstanding the similarity of these assemblages, the Chattian Basin did not inherit the Rupelian fauna of the same region but was repopulated from the outside after the Solenovian brackishing.

The Chattian molluscan associations of the eastern shelf, known from the sections of the Kyzylkum and Kopet Dagh, are much poorer. They are represented mostly by the same species known in the sections of Mangyshlak and Ustyurt, with the endemics of the Eastern Paratethys being the most typical.

Benthos-Based Biogeographic Zonation

The data presented show that in the Chattian the distinctions between the northern (North Sea Basin, Eastern Paratethys) and the Mediterranean assemblages of foraminifers, ostracodes, and mollusks remained significant. Preston's dissimilarity coefficient for species of gastropods ranges between 0.95 and 1.00, values for bivalves are 0.87–0.90. Thus, the Mediterranean and North European zoogeographic regions persisted, but their delimitation became more vague because of the existence of intermediate associations. The composition of the faunas (especially of bivalve mollusks) shows a gradual convergence due to the reduction of climatic barriers and increasing faunal mixing, which resulted in a wider distribution of most genera and some species.

Mediterranean Paleobiogeographic Region. The tropical and subtropical fauna of this area is known in the Aquitanian Basin, the southern coast of the Mediterranean, northern Italy, Croatia and Slovenia, Syria, and the Iranian and Mesopotamian basins. Shallow water facies of different regions were inhabited by larger foraminifers Lepidocyclina, Miogypsina, Miogypsinoides, Spiroclypeus, Heterostegina, rare Nummulites, and Operculina. The genera listed are unknown in more northern areas. Regional associations of smaller foraminifers were represented by miliolids (including the specialized genus Alveolina), evolutionarily advanced rotaliids (the genera Lamarckina, Mississippina, Escornebovina, and Pseudoplanulinella), and the family Peneroplidae with the genera Peneroplis, Archaias, Dendritina, Meandropsina, and Spirolina (the latter in the territory of the Mediterranean, Iranian, and Mesopotamian basins). The genera listed do not occur in northwestern Europe or in the Paratethys. Another widespread group is represented by ubiquitous taxa. Thus, the species Almaena osnabrugensis, Bitubulogerina kasselensis, and Alabamina tangentialis, along with the genera Pararotalia, Rotalia, Robertina, Bolivina, and others, occur in the North European Region and in the Paratethys, being frequently represented by the same species.

The assemblage of northern Italy is reported to consist of more than 100 species of 64 genera and subgenera of bivalve mollusks and 80 species of 27 gastropod families, including tropical and subtropical genera such as Trisidos, Spondylus, Florimetis, Crassatella sensu stricto, Cardium sensu stricto, Vepricardium, Trachycardium, and Venus sensu stricto. Among gastropods, the indicators of high water temperatures are tonnids and magilids. Ten genera and about 60% of bivalve species (mainly among the most warm-water taxa) of this area are unknown outside Mediterranean. However, species with a wide geographical distribution form a considerable portion of this assemblage (22%). Species in common with basins of the Central Europe were numerous.

The fauna of the Carpathian Basin differs from that of the Mediterranean both at species and, partly, at genus level. Thus, it can be considered to be intermediate between the faunas of the Mediterranean and North European regions. The composition of foraminiferal associations is, perhaps, closer to the former, as indicated by the occurrence, even in small numbers, of shallow water Lepidocyclina, Miogypsina, Miogypsi*noides*, which were widespread in the Mediterranean. Different parts of the basin hosted the thermophilic genera Biapertorbis, Pavonitina, Stomatorbina, Amphycoryna, and Patellina, and the characteristic Tethyan genera Sphaerogypsina and Amphistegina. This basin, except for its northeastern margin (western Ukraine), is characterized by the presence of the endemic species Virgulinella chalkophila. In the Carpathian Foredeep, a distinctive assemblage of foraminifers that was closer to the fauna of the Eastern Paratethys in genus and species composition occurred.

The gastropods of the Carpathian Basin were also closer to those of the Mediterranean Region (Amitrov, 2000); however, the resemblance was in the presence of the most thermophilic families rather than in the general composition. In this area Harzhauser, Piller, and Steininger (Harzhauser *et al.*, 2002) distinguished the independent Danubian Province and noted its intermediate character. On the basis of bivalves, this area was earlier considered as the Central Paratethys Province (Báldi, 1986) because it cannot be confidently attributed to any region. Moreover, the composition of the fauna varied considerably over time. Therefore, we accept the opinion of Báldi that at the beginning of the Egerian the Central Paratethys Province was part of the North European Region and belonged to the Mediterranean Region during the second half of the Egerian.

The molluscan assemblages of the Alpine Foreland Basin are close to those of the Central Paratethys Province, and the bivalves are closer to those of the Germanian Province (Popov, 1996). The biogeographic position of the fauna of the eastern part of the Carpathian Foredeep is also problematic. Its molluscan assemblages are rather poor and poorly preserved, sharply differing from those of the Eastern Paratethys, and resemble those of the Alpine Foreland Basin. However, the genus and species composition of benthic foraminifers was close to the fauna of the Eastern Paratethys, although genera widespread in the Carpathian Basin and in northwestern Europe were also present. The distinctive pattern of the foraminiferal associations of this transitional zone is due to the presence of *Cassiger*inella chipolensis, Caucasina tenebricosa, and C. schischkinskayae; the genera Baggatella, Turillina, Buliminella, Uvigerinella, Bolivinita, Fursenkoina, and Virgulinella; and the occurrence of the thermophilic genus Biopertorbis.

North European Paleobiogeographic Region. The Germanian Province. Judging from the composition of benthic foraminifers and both groups of mollusks, it is clear that the North Sea fauna had a rather warm-water (subtropical-boreal) character, whereas the boreal fauna of the Eastern Paratethys inhabited the coldest waters of this region. The most thermophilic in the group of smaller foraminifers of the Germanian Province were the genera Asterigerina, Almaena, Patellina, and Gypsina; and the presence of large foraminifers of the genera Lepidocyclina, Miogypsina, *Miogypsinoides*, and *Sphaerogypsina* indicates the clear influence of the Mediterranean fauna.

Further evidence of warm water conditions is provided by the diversity of mollusks and the presence of many subtropical families and genera (Arca, Atrina, Pinctada, Pteria, Spondylus, Arcopagia, Venus sensu stricto in bivalves and turbinids, lacunids, architectonicids, turritellids, vermetids, cypraeids, sinids, marginellids, and terebrids in gastropods). In the Chattian, the coastal part of the sea in this area became warmer than in the Rupelian, probably owing to the stronger activity of the North Atlantic Current. At the same time, groups characteristic of the Mediterranean associations (angariids, strombids, tibiids, *Diastoma*, ampullinids, melongenids, pyrenids, vasids, harpids, etc.) were absent.

Scythian–Turanian Province. The benthic fauna of the northern and eastern shelves of the Eastern Paratethys is characterized by impoverished composition and the presence of characteristic endemic species. The fauna of this part of the Paratethys certainly belonged to the North European Region because of evident similarities in the overall taxonomic structure. However, it was poor and lacked warm water elements because of both climatic zonality and the complicated connection with southern basins.

This part of the basin was inhabited by at least 32 genera of benthic foraminifers, 22 of which were secreting species, and 10 were agglutinating forms. The latter group is more representative and diverse in this region than in the North European Basin. The genus and species composition of the communities of secreting foraminifers was close to that known in Northern Europe. The following forms in common with the north European assemblages occurred here: Cibicidina amphisyliensis, Asterigerina guerichi, Bitubulogerina kasselensis, and Fursenkoina schreibersiana and forms of the genera Elphidium, Robertina, Bolivina, and Cibicidoides. However, C. oligocenicus, C. nefastus, C. majcopicus, C. ornatus, and Elphidium onerosum are known only in the Eastern Paratethys. Other endemic species of the Middle Maikopian Basin were represented by Virgulinella, which occasionally form mass accumulation (with local species in Mangyshlak and in Azerbaijan); species of the genus Caucasina (C. schischkinskayae, C. oligocenica, C. buliminoides); and Uvigerinella ex gr. californica (several forms), Pseudoparrella caucasica, Neogyroidina memoranda, Porosononion dendridicum, Melonis dosularensis, and the genus Sphaeroidina.

Arenaceous foraminifers played a significant role in shallow-water assemblages. In addition to the species with a simple shell structure (the genera Saccammina, Proteonella, Rhabdammina, two species of Hyperammina, Reophax, and three species of Ammodiscus), they included widespread forms Spiroplectammina terekensis (and two more species), Haplophragmoides kjurendagensis (with two subspecies), Trochammina (with three local species), the endemic species of the genus Cyclammina, Rotaliammina depressa and Verneuilina rasilis. The composition of the associations was relatively uniform throughout the area from the North Black Sea Depression to the Kyzylkum and Bukhara depressions with some distinctions, which were apparently due to differences in facies.

At the beginning of the Chattian, mollusks were dominated by species shared with the seas of northwestern Europe. The proportion of endemic species reached a quarter for the Early Chattian Karatomak assemblage, and about half in the younger, Baigubek assemblage, where the endemic species of the Eastern Paratethys became dominant. Some of them, like Plagiocardium abundans, Cerastoderma prigorovskii, and Corbula helmerseni, were widespread and formed the pattern of this fauna. Of the 30 bivalve species shared by the assemblages of the northeast part of the Eastern Paratethys and North Sea Basin, 5 are unknown in basins of Central Europe. One of them, Chlamys bifida, is the zonal species of the Chattian A. This form was a widespread abundant species that reached as far as the Kyzylkum and Kopet Dagh.

Although the North Sea origin of the ancestors of this fauna is evident, the route of this invasion is not quite clear. The presence of many species that are shared by these basins and are unknown in the Chattian of Central Europe suggests that these basins have direct connections (probably, as well as in the Rupelian) through the Dnieper–Donets and Pripayt' depressions (Amitrov, 1993, 2000, etc.), or, less likely, through the northern shelf of the Carpathian Basin. However, the former route is not documented by the deposits: the Chattian age of the Bereka Beds of the Dnieper–Donets Depression remains disputable, while no marine sediments of Chattian age are known in Poland or Belarus. In the Transcaucasian part of the Eastern Paratethys, endemic forms of the Scythian–Turanian Province are rare and unsuitable for characterization; therefore, the former area cannot be included in this province. Its molluscan fauna known from Georgia and benthic foraminifers found in Azerbaijan show specific features in the general composition and in the presence of subtropical genera. These data allow the conclusion to be drawn that, on the basis of its genus composition, this part of basin also belonged to the North European Region, and some of its species were widespread throughout the Eastern Paratethys.

CHAPTER 2. MARINE BIOGEOGRAPHY OF THE EARLY MIOCENE

Lower Miocene Stratigraphy of the Paratethys

The stages of the Lower Miocene, Aquitanian and Burdigalian, were proposed by K. Mayer-Eymar in 1858 and Ch. Deperet in 1892 with the type sections in shallow water sandy sequences of Aquitania (southwestern France). The Early Miocene Aquitanian Basin, as well as in the Oligocene, was close to the Mediterranean in fauna and climate. The Lower Miocene and subsequent stages of the Neogene were defined in the Mediterranean. This is why it is difficult to establish biostratigraphic correlations of the Paratethys with the stratotypes because of the climatically induced biotic zonality.

East Atlantic. Aquitania. The stratotypes of the Aquitanian and Burdigalian were established by G. Dollfus in the vicinity of Bordeaux. The stratotype of the Aquitanian is located near the small town of Saucats (Carloni et al., 1971; Alvinerie, 1980) and is built by shallow marine sandy-calcareous sediments characterized by an extremely rich assemblages of mollusks (Cossmann and Peyrot, 1909–1914). The microfauna is rather poor, the sections neighboring the stratotype yielded planktonic foraminifers of the Globorotalia kugleri Zone (N4) and the lower part of the Catapsydrax dissimilis Zone (N5). Miogypsina species are represented by *M. tani* and *M. guntari*. Nannoplankton of the type areas contains species of the zone Triquetrorhabdulus carinatus (NN1) (Müller and Pujol, 1979). These deposits are underlain and overlain by lagoonal sediments.

The stratotype of the Burdigalian is located near the small town of Léognan. It is represented by yellow sands with rich assemblages of mollusks and diverse microfauna. Rare planktonic foraminifers allow attribution of these deposits to the *Catapsydrax dissimilis* Zone (N5) and to the lower parts of the *Catapsydrax stainforthi* Zone (N6). *Miogypsina* species are represented by *M. globulina* and *M. intermedia*. According to Droger, these species are members of the same evolutionary line with the Aquitanian species *M. tani*. The nannoplankton of the type area contains species of the zones of *Discoaster druggii* (NN2, after Alvinerie,

1980), Sphenolithus belemnos (NN3), and Helicopontosphaera ampliaperta (NN4) (Müller and Pujol, 1979). The underlying deposits are represented by lagoonal facies. The known hiatus between the Aquitanian and Burdigalian and the absence of marine facies at the upper and lower boundaries indicates an incompleteness of sections of the both stages in the type area.

Mediterranean. The more complete Aquitanian section, Carry-le-Rouet at the Mediterranean coast of France to the west of Marseilles in the mouth of the Rhône River, is better characterized by the fauna, and was suggested as the parastratotype of this stage (Aglada and Catzigras, 1974 cited after Steininger and Nevesskaya, 1975). It is also represented by shallowwater biogenic-calcareous sediments with a thickness of about 80 m. The base of the section is built by continental conglomerates succeeded by marine deposits with planktonic foraminifers Globigerinoides primordius, G. quadrilobatus, etc. (zones N4, in the middle part, and N5, in the upper parts of the section), Miogypsina gunteri, M. cf. socini, nannoplankton, ostracodes, and mollusks, including Flabellipecten carryensis, a species common in the Upper Egerian sediments (Báldi and Seneš, 1975). The more complete parastratotype of the Burdigalian (Burdigalian sensu lato) is also located in the Rhône Valley. The section is represented by sands (76 m) overlain by clayey biogenic limestones (41 m). These deposits erosionally overlie Lower Eocene rocks and contain remains of mollusks and benthic and planktonic foraminifers of zones Catapsydrax dissimilis (N5), Catapsydrax stainforthi (N6), and Globigerinella insueta-Globigerinoides trilobus (N7) and basal beds of the *Globigerinoides* bisphaericus Zone (N8) (Demarcq, 1980).

The section Lemme-Carrosio, which was proposed as the Oligocene-Miocene boundary stratotype, is situated in northern Italy, in the Piedmont area (Steininger, 1994). The Lemme Section is formed by a series of homogeneous Rigoroso marls. The boundary between the Oligocene and Miocene in this section is drawn through the first occurrence of Paragloborotalia *kugleri*, coincident with the disappearance of species of the genus Chiropteridium. In this continuous sequence, the proposed position of this boundary is close to the base of the nannoplankton zones NN1 (after Martini) or CN1A (after Bakri). In terms of planktonic foraminifers, it corresponds to the base of Zone N4 and the base of zones M1 and Mt-1 (Berggren et al., 1995) and coincides with the change of magnetic polarity at the boundary of chrons C6Cn2r and C6Cn2n, dated to 23.8 Ma (Steininger, 1994; Berggren et al., 1995). In contrast to northern Europe, and similar to the sections of the Caucasus, the lower parts of the Aquitanian section contain the epibole of *Deflandrea spinulosa*. It has a short stratigraphic range and the genus itself completely disappears within the Paragloborotalia kugleri Zone. Powell (1986) noted the occurrence of Hystrichosphoeropsis obscura just a few meters below the Oligocene-Miocene boundary, while *Melitasphaerid*-

ium choanophorum and *Tunerculodiraum vancanpoae* appear slightly above it.

In oceanic deep-sea cores, the Aquitanian comprises the range from nannoplankton zones NN1 to the lower parts of NN2, and from the planktonic foraminifer Zone N4 to the lower parts of Zone N5, and has an absolute age of 23.8 to 20.5 Ma; the Burdigalian corresponds to zones NN2-NN4, the upper parts of zones N5–N7, and is dated to 20.5–16.4 Ma (Berggren et al., 1995). A differing opinion states that the Aquitanian corresponds to zones Globigerinoides primordius-Paragloborotalia kugleri (N4), Catapsydrax dissimilis (N5), and lower parts of the Catapsydrax stainforthi Zone (N6), whereas the Burdigalian is understood as the interval of the zones *Globigerinatella insueta–Glo*bigerinoides trilobus, and Praeorbulina glomerosa (Krasheninnikov et al., 1999, p. 20). In the Mediterranean this interval (without the latter zone) corresponds to the planktonic foraminifer zones Globigerinoides altiapertus, and Catapsydrax dissimilis up to Zone G. trilobus (Rögl, 1996).

Although very substantial, the restructuring of the fauna at the Oligocene–Miocene boundary occurred gradually and recognition of this boundary is very problematic everywhere. These difficulties even increase within inland basins.

Western Paratethys. In this region, the Aquitanian is believed to correlate to the upper Egerian Regional Stage, and the Burdigalian, to the Eggenburgian, Ottnangian, and to the complete range or the lower part of the Karpatian (Báldi and Seneš, 1975; Rögl, 1996).

The upper Egerian in the type area (northern Hungary, southern Slovakia) are represented by regressive, schlieric facies. The occurrence of Miocene index species of different groups was recorded at markedly different levels. The index-species of the Aquitanian, Paragloborotalia kugleri, is absent in the entire Paratethys (Rögl, 1996). When divided into four members, a-d (Báldi and Seneš, 1975), the Egerian interval shows the occurrence of the Miocene species Globigerinoides quadrilobatus and G. primordius within member "b," whereas the change of nannoplankton zones NP25 and NN1 and the appearance of the Aquitanian larger foraminifers Miogypsina gunteri and M. tani takes place in the upper parts of member "c," in littoral facies of the Bretka-Nagymarosy limestones (Müller, 1988; Rögl, 1996). In the type area, the Egerian deposits are unconformably overlain by rhyolite tuffs (presumably of the Ottnangian age), and outside the area, by transgressive deposits of the Eggenburgian. In the axial part of the Carpathian Basin, the upper, Miocene part of the Egerian is correlated to the Upper Menilite and Middle Krosno Subformation. In northern Transylvania, an early Miocene age is suggested for the upper part of the Vima Formation based on the records of the nannoplankton assemblage with Helicosphaera scissura, Zone NN1 (Rusu et al., 1996).

The Eggenburgian marine transgression affected more extensive areas and was characterized by a warmwater subtropical molluscan fauna (Schaffer, 1910). The stratotype of this clearly expressed unit of the inner Carpathian area was selected in the section of Loibersdorf Formation near the city of Eggenburg in Lower Austria (Steininger and Senes, 1971). The deposits are represented by sandy and sandy-calcareous facies with rich assemblages of mollusks, ostracodes, and benthic foraminifers with *Miogypsina intermedia*. The base of the section contains remains of vertebrates, including Mastodon angustidens. The sections correlated to the stratotype yielded planktonic foraminifers of the upper parts of zones N4 and N5 and the lower parts of Zone N6, nannoplankton from the ?uppermost of NN1, NN2, and the lower parts of NN3 zones (Steininger and Nevesskaya, 1975; Nagymarosy and Müller, 1988). In Transylvania the Eggenburgian is correlated with the Corus and Chechis beds in the Gilau and Meses districts, and, based on the records of planktonic foraminifers, with the uppermost part of the Vima Formation in Preluca (Rusu, 1989). In the Transcarpathian Foredeep it is correlated with the Burkalo Formation. In the Western Carpathians, the Eggenburgian is thought to be equivalent to the Boudky Formation of Moravia by the presence of rich foraminifer assemblages (Krhovsky et al., 1995), and in the Ukrainian and Polish Carpathians, of the lower parts of the Upper Krosno and Polanica Formation based on foraminifers and nannoplankton of zones NN2–NN3 (Andreyeva-Grigorovich et al., 1997).

Deposits of the following Ottnangian Regional Stage are less widely distributed and are characterized by a poorer, moderately warm-water fauna. The stratotype section is located near the village of Ottnang in Upper Austria. This site provides the outcrop of the Ottnangian schlieric deposits, only 10 m of which are exposed in the quarry, and the rest of the total thickness of 60–80 m is known from the borehole. These deposits are conformably underlain by equivalents of the Eggenburgian. The stratotype yielded the nannoplankton of zones NN3–NN4 (Nagymarosy and Müller, 1988). It allows correlation between the Ottnangian and the upper Burdigalian. In the type area the upper Ottnangian sediments are represented by coal-bearing and lagoonal facies (Upper Freshwater Molasse). Sands with interbeds of siltstones, clays, and marls of considerable thickness (up to 120 m) represent alternating members of fresh- and brackish-water origin. The latter contain remains of Rzhehakia, Cerastoderma, and Limnopappia. Members of the same molluscan genera, but often represented by other species, are known both from the Alpine Foreland Basin (Kirchberg Beds of Upper Bavaria and Switzerland; see Seneš, 1973) and from the Central Paratethys: southern Moravia (described by A. Rzehak), and South Slovak-North Hungarian Basin). The presence of endemic species of mollusks in common with the Eastern Paratethys, like

Rzehakia dubiosa, Cerastoderma ivericum, Eoprosodacna kartlica, and *Limnopappia* (Popov and Voronina, 1983), enables a confident correlation of the Upper Ottnangian sediments with the Kotsakhurian.

The deposits of the Karpatian Regional Stage are again characterized by marine assemblages. However, benthic groups are closer to those of the Middle Miocene. Nannoplankton is the same as in Zone NN4 (at the base of the stage) and Zone NN5 (up the sequence), where *Globigerinoides bisphericus* appears (Nagymarosy and Müller, 1988; Rögl, 1996). Thus, the Upper Karpatian may correlate with the lower Middle Miocene and at least with the Lower Tarkhanian of the Eastern Paratethys. Therefore, both these units, separated from the underlying deposits by regressive and brackish-water sediments, are more closely related to the overlying sedimentary series.

In the Alpine Foreland Basin, the Aquitanian corresponds to the deposits of the Lower Freshwater Molasse, while the Burdigalian, to the Upper Marine Molasse (OMM). The deposits of the latter have been dated by planktonic foraminifers (zones N5–N6), nannoplankton (NN3), mollusks (pectinid zone PN3), and mammals (MN2b, MN3). The upper part of the Upper Marine Molasse belongs to the middle or upper Burdigalian (Berger, 1992, *et al.*), whereas its uppermost parts in the distal zone (Jura Mountains) probably corresponds to the Langhian.

In the Flysch Carpathians, in the Krosno type of the sequence in the Skole-Silesian Zone, the Lower Miocene corresponds to the larger part of the medium rhythmic flysch of the Middle Krosno based on records of nannoplankton and foraminifers (Andreyeva-Grigorovich *et al.*, 1997) and to thinner deposits of the Upper Krosno. In the Menilite type of the section, the boundary of the Oligocene and Miocene is drawn between the Middle and Upper Menilite Subgroup based on the upper cherts marker horizon. The boundary is characterized by the occurrence of *Globigerinoides trilobus* and the nannoplankton of the Triquetrorhabdulus carinatus Zone (NN1) in clays, overlapping the siliceous horizon (Andreyeva-Grigorovich et al., 1997). The Menilite Group is unconformably overlain by deposits of the Polanica Formation and gypsiferous and saltbearing sediments of the Vorotyshcha Formation with the poor fauna of Miocene planktonic foraminifers and nannoplankton of zones NN2-NN3. Still higher, in the Borislav-Pokut and Sambor zones and their extension in Poland, there are the Stebnik and Balitch formations with marine microfauna with Globigerina bolli and Globigerinoides bisphericus. The nannoplankton of Zone NN4 found in the latter formation indicates their Karpatian age. The Balitch Formation of the Carpathians possibly corresponds to the Nagorjany Beds (with marine fauna and species of Rzehakia) of the Carpathian Foredeep on the margin of the East European Platform (Andreyeva-Grigorovich et al., 1997).

In the East (Romanian) Carpathians, a Lower Miocene age is assigned to the deep-water deposits (Vinetisu Formation) by the presence of nannoplankton of zones NN1–NN2. The Oligocene–Miocene boundary is placed in the lower parts of this formation, above the Pucioasa Formation with the Fusaru Sandstone (Rusu *et al.*, 1996). The Burdigalian in this region is also correlated with the upper *Dosinia* shales (NN3) and the overlying gypsiferous sequence (Sarata and Cornu formations).

Eastern Paratethys. In the Eastern Paratethys, the Lower Miocene should most likely be represented by the Karadzhalginian (or Upper Caucasian), Sakaraulian, Kotsakhurian, and lower Tarkhanian regional stages. Three former stages are comprised by the Maikopian Group, the subdivision of which presents difficulties.

The location of the Oligocene–Miocene boundary in the sections of the Maikopian Group is very problematic because of the extremely poor fossil content of these sediments. Different researchers give different positions of the boundary, from the Upper to the Middle Maikopian (Neogene System..., 1986). The elaboration of the dinocyst scale and records of nannoplankton in the Belaya River Section in Ciscaucasia (data by N.I. Zaporozhets and J. Krhovsky) led to a more definite position of the boundary. It is drawn at a level where the nannoplankton of Zone NP25 changes into an assemblage with Triquetrorhabdulus carinatus (NN1), and the dinocysts of the *Chiropteridium par*tispinatum Zone (D15) is succeeded by the assemblage of Zone D16 with the reduction of cavate cysts. However, correlation of these data with the local stratigraphic scale of Ciscaucasia remains controversial. We follow A.S. Stolyarov and G.I. Semenov, who described the section in detail, in placing the boundary in the interval from the upper Septarian to the lower Karadzhalga Formation (Akhmetiev et al., 1995). The Caucasian geologists (Dmitrieva et al., 1959, E.I. Kovalenko and E.V. Beluzhenko) recognize this level at the base of the Alkun Formation; hence, different approaches to the Caucasian Stage accepted in the scheme of Neogene recent unified deposits (Nevesskaya et al., 2004). We believe that the Caucasian Regional Stage as it was defined by its authors, Bogdanovich, Muratov, Nosovskii, and Ter-Grigorjantz (see Nevesskaya, 1975) does not correspond to any distinct stage in the development of the Eastern Paratethys, and its equivalents are extremely difficult to recognize and trace even within the type area of Ciscaucasia. Moreover, the stage was established as an equivalent of the Aquitanian, whereas at least its lower part is of Oligocene age (see Nevesskaya et al., 2004, p. 67: "Dissenting opinions").

In the Eastern Paratethys, we accept the Lower Miocene age for the entire Upper Maikopian, including the Karadzhalga, Olginskaya, and Ritsa formations, and, possibly, the lower parts of the Tarkhanian (Popov *et al.*, 1993). The range of the Karadzhalginian Regional Stage corresponds to the Karadzhalga Formation. Outside the type area, the equivalents of the Karadzhalginian Regional Stage are recognized in the deep-water part of the basin mostly from lithological evidence (Semenov and Stolyarov, 1970). In marginal parts of the Eastern Paratethys, this level is correlated to sharply transgressive deposits of predominantly sandy beds with a distinctive molluscan assemblage (Kintykche Beds of the northern Aral Sea Region, Aktepe Beds of Kopet Dagh, Gissarak Beds of Tajikistan (Voronina *et al.*, 1993); upper Uplistsikhe Beds of Georgia (Kurtskhaliaya, 1982; Voronina *et al.*, 1991); Sivashi Beds of Ukraine): however, this correlation needs further proof.

The Kartli Depression of Georgia, located in the middle reaches of the Kura River, is the type area for the younger Lower Miocene regional stages of the Eastern Paratethys, the Sakaraulian and Kotsakhurian (Steininger and Nevesskaya, 1975). Their sections are characterized mostly by mollusks, the warm-water subtropical assemblage of the Sakaraulian, and endemic, brackish-water Kotsakhurian assemblage. The Sakaraulian deposits are underlain by Maikopian clays without fauna or by coarsely-terrigenous, mostly sandy deposits of the Uplistsikhe Formation. The latter unit, in its complete initial volume, was correlated to the Chattian, the Lower Uplistsikhe Subformation, and to the lower Miocene, the Upper Uplistsikhe Subformation (Voronina *et al.*, 1991).

Likewise, the faunal characterization of these units provides few chances for both in- and out-basin correlations. Thus, microfauna and nannoplankton are absent in the Lower Miocene of Kartli, while the rich molluscan assemblages remain nearly unmatched throughout the Eastern Paratethys and are well compared only to the sections of western Georgia and poorer assemblages of the middle and upper parts of the Aktepe Sands of the Kopet Dagh (Voronina et al., 1993). Outside the Eastern Paratethys, the Sakaraulian molluscan association is most similar to that of the Eggenburgian (one-third of species in common); and that of the Kotsakhurian, to the Late Ottnangian. In western Ciscaucasia they are correlated to the Olginskaya Formation, which is characterized by euryhaline assemblages of mollusks, benthic foraminifers, and fishes, and to the Ritsa Formation (or the Zuramakent Formation in more eastern areas), with impoverished, endemic mollusks (with *Rzehakia*) and foraminifers (Saccammina zuramakensis). However, their reliable correlation with the Sakaraulian and Kotsakhurian of Georgia remains problematic. The equivalents of the Sakaraulian in the Ciscaucasian part of the Maikopian Basin are often tentatively defined on the basis of the occurrence of coarser facies (silty clays in the Olginskaya Formation) and the appearance of the new assemblage of benthic foraminifers with Caucasinella elongata. In eastern Ciscaucasia, the Karadzhalga and Olginskaya formations are correlated with the Sulak Formation based on their position in the sequence below the Zuramakent Formation.

The equivalents of the Kotsakhurian in the Ritsa and Zuramakent formations and their correlates in the Ustyurt and Kopet Dagh are recognized by indications of salinity fluctuations: the foraminiferal assemblage with *Saccammina zuramakensis*, which was frequently monospecific, and mollusks *Rzehakia dubiosa*. In the marginal parts of the basin, the overlying deposits of the Tarkhanian or Chokrakian occur with sharp unconformity and stratigraphic hiatus.

Paleogeography of the Paratethys

The Early Miocene Paratethys retained the same sedimentation regime and bathymetric zonality as was known for the Oligocene. Only by the end of this time, the anoxic environments that prevailed in the deepwater parts of the Maikopian and Menilite basins changed into more favorable conditions for benthos. The Western and Eastern Paratethys probably communicated with each other and with the Mediterranean in the south. Connections with the Atlantic and the North Sea were completely lost (Fig. 5).

Carpathian Basin

The Oligocene sedimentary pattern was retained at the beginning of the Early Miocene. The Krosno-Menilite Group continued to accumulate in the deepwater part, while the southern shelf was still the zone of mainly clayey-carbonaceous sedimentation of the Egerian. At the same time, the beginning of the Miocene was marked by a new, non-uniform deepening of the entire Carpathian Basin. It led to the initiation of new depressions (the Vienna Depression) and to the reduction of the extreme deep-water area (Beer and Shcherba, 1984; Sandulescu, 1987). After that the basins were filled with sediments deposited mainly above the carbonate compensation depth, and since the second half of the Early Miocene, in conditions of residual depressions and shallow lagoonal salt-bearing basins.

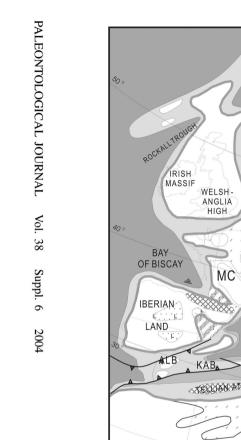
At the beginning of the Early Miocene, the connection of this inland sea with the ocean was relatively well established, indicated by marine euryhaline biota and sedimentological evidence for strong tidal currents (Sztano, 1994). During this time, the connection proceeded through the southwestern Slovenian Corridor. This link was interrupted or became very limited since the second half of Early Miocene, i.e., the late Eggenburgian. The passage through the Alpine Foreland Basin remained closed at the beginning of the Miocene, the accumulation of the Lower Freshwater Molasse continued, but the marine conditions were resumed in the Burdigalian–Eggenburgian.

Axial zone. The beginning of the Early Miocene, the renewed burst of biological productivity and accumulation of diatomites occurred in the axial zone of the basin. Later, they were diagenetically changed into black siliciliths of the second Chert Bed. This Bed, as well as the first Lower Oligocene Chert Bed, in its most complete occurrence (10–20 m of striated silicilytes– phthanites and silicified marls) was deposited on the continental slope and was subjected to strong consedimentary sliding. The strongest sliding occurred in the upper part of the slope because of the fast subsidence of the basin. This subsidence shifted the deepest area closer to the base of the continental slope, into the Skibas–Pokut Trough. During the first half of the Early Miocene (Aquitanian?) this was the accumulation zone of black bituminous muds of the Upper Menilite Subgroup (400 m thick) below the carbonate compensation depth.

On the contrary, the Silesian Depression experienced the prevailing sedimentation of essentially carbonate composition. The sequence of the Middle Krosno Flysch (600 m) is represented by medium rhythmic alternation of carbonaceous claystones and micaceous sandstones (up to 30–40 cm thick). The material was brought here by grain flows of different genesis from the source areas of the internal uplifts in the Silesian, Burkut-Dukla, Marmaroš, and Pieniny zones subjected to folding at the end of the Oligocene. Lower Miocene sandy–clayey sediments accumulated in the inner zones of these uplifts within the southern shelf and represented the lower marine molasses.

The deposits that filled the axial zone of the Carpathian Basin gradually gained shallower water character. The Eggenburgian (Polanica time synchronous with sediments of the Boudky Formation in Moravia) is characterized by the universal start of carbonate sedimentation, probably, in connection with a climatic warming and the emergence of an anti-estuarine (Mediterranean) type of water circulation (Krhovsky et al., 1995). Rich assemblages of benthic foraminifers are evidence for a favorable gas regime at this time, whereas the occurrence of deep-water sharks indicates the retention of depths not less than a few hundred meters. The flysch sedimentation in the upper bathyal zone continued as well. Thus, the flysch clinoform of the Silesian and Krosno zones is crowned by the carbonate Upper Krosno Flysch. Only in the Ottnangian, in the course of the clinoform's accumulation it lost the flysch features and was replaced by gypsiferous clays. In the early Ottnangian, the flysch sedimentation also resumed in the Western Carpathians (the Krepice Formation, up to 300-400 m thick).

The beginning of accumulation of regressive series in the basin coincided with the manifestation of the folded nappe deformations in the Pokut-Skibas deepwater trough. In the western flank of the trough, it resulted in the formation of olistostromes that, in the center of the trough, merged with the distal parts of collapse and sliding structures of the continental slope, the Vorotyshcha Formation (Beer and Shcherba, 1985; Shcherba, 1993). The base of the continental slope became the accumulation zone of grain flows and olis-



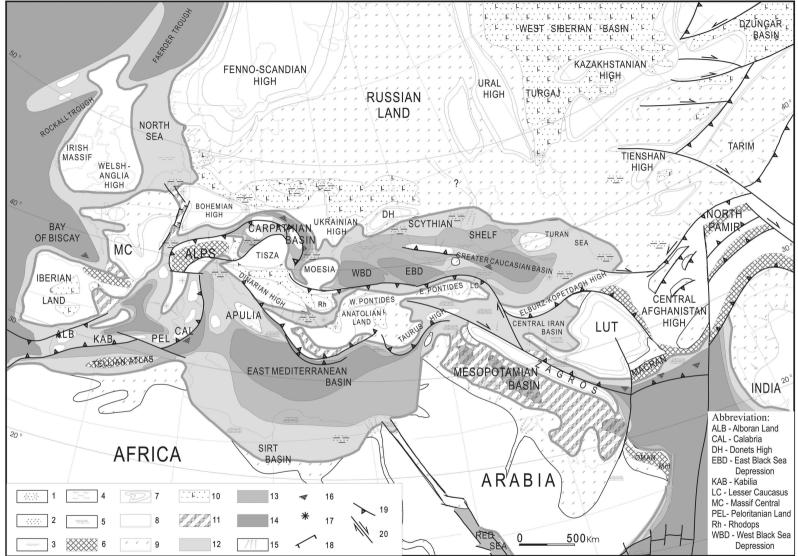


Fig. 5. Paleogeographic map of the Tethys and the northern Peri-Tethys in the Early Miocene. Designations: (1) conglomerates, (2) sands, (3) clays, (4) marls, (5) limestones, (6) mountains, (7) highlands, (8) undifferentiated land, (9) lowlands, (10) lake basins, (11) lagoons occasionally invaded by the sea. (12) shallow shelf. (13) deep shelf. (14) continental slope and bathyal, (15) terrigenous material, (16) flysch, (17) volcanoes, (18) faults, (19) nappes, and (20) shifts.

tostromes composed of carbonaceous fragments and blocks of diatomites, which were deposited in the central parts of the basin and transported from the southwest. By the end of the deposition of the Polanica and Vorotyshcha formations (in the Ottnangian), two prograding lenses of deposits have filled in the residual depression, and the entire axial zone of the Carpathian Basin turned into a saliferous lagoon. From the north it was supplied by coarse clastic materials, conglomerates from highlands along the Carpathians (Oszczipco et al., 1999). Starting from the late Ottnangian, the subsidence of the Carpathian Foredeep occurred along the edge of the former continental slope. The inner zone of the growing depression up to the end of the Burdigalian accumulated red- and gray-colored saliferous shallow water and continental molasses of the Stebnik and Balitch Formations (up to 1500 m). Their clastic material was mainly transported from the Carpathians.

In the Karpatian time, the paleogeography remained similar to that of the Ottnangian, but evaporites were replaced by marine deposits of the Balitch Formation represented by calcareous oozes with sandy interlayers.

Southern shelf. By the end of the Egerian, the inner Carpathian regions experienced a general regression and frequent transition to lagoonal facies with brackishwater mollusks *Polymesoda* and foraminifers *Ammonia*. Nevertheless, in the axial zone of the North Hungarian–South Slovak Gulf, the marine conditions were preserved, but deposits were represented by coarsely terrigenous sediments (Terekbalint and Kovacov Sandstones). Their molluscan fauna indicates a growing Tethyan influence (Báldi, 1973, 1986). In northeastern Transylvania, the sea basin persisted too. In the Egerian and Eggenburgian, the more southern deeply incised Petrosani Gulf is characterized by alternating marine and lagoonal conditions with coal formation.

The Eggenburgian was marked by the extensive marine transgression. Filling up and shallowing of the Carpathian Basin, warming and a favorable oxygen exchange regime led to the universal unification of facies, environments, and fauna (Báldi, 1986). In the west, the accumulation of sediments started in the newly formed depression of the Vienna Basin and in the intermontane depressions along the valleys of the Vah and Nitra rivers. Deposition of coarse-grained sands with gravel, with sedimentary features indicating strong tidal influence (Sztano, 1994) and diverse fauna (Budafok, Pétervására Sandstones, Lučenec) occurred along the western and eastern flanks of the Hungarian Basin. In the internal parts of the North Hungarian-South Slovak Gulf of the Carpathian Basin, deeper water schlieric deposits accumulated. Depths, inferred from the fauna, are estimated around 100-150 m. By the end of the Eggenburgian the sea regressed, the deposits changed into sandy lagoonal and continental facies (the Ipolytarnóc Beds with trunks of trees, imprints of leaves, and trackways of mammals).

In the Ottnangian, the sea left the North Hungarian part of the basin with limited sedimentation continued in lagoonal conditions favorable for coal accumulation (the Salgotarian Formation). The Trans-Danube Gulf of the Tethys continued to exist in more southern area. It connected the shelf of northern Italy with the Slovenian and South Hungarian basins (Seneš, 1973; Rögl and Steininger, 1983). This depression dried up at the end of the Eggenburgian and was refilled by the sea in the Ottnangian, when the marine passage reached up to the Budapest District (Bentapusztaer Schichten Gruppe).

The second passage connected the Carpathian Basin with the Tethyan Rhône Basin through the Alpine Foreland Basin. It was open from the second half of the Eggenburgian and in the early Ottnangian. Then the marine facies of the Upper Marine Molasse (the Ottnangian "a" and "b") were replaced by lagoonal sediments, with species of *Rzehakia* and fresh-water deposits (M₂cd, according to Seneš, 1973). The marine deposits of the early Ottnangian are well dated only in the Western Carpathians. Seneš (1973, p. 121) suggests that at this time the eastern basin of the Carpathians could lose the connection with the western basin and establish closer connections with the Eastern Paratethys. We consider this assumption improbable, but it is relatively difficult to get biogeographic evidence for or against due to the poor faunal content of both the East Carpathian sediments of the upper Lower Miocene (Stebnik and Balitch Formations) and the upper parts of the Maikopian Group of the Eastern Paratethys.

As a result of the regression in the late Ottnangian, the Carpathian Basin broke into several brackish-water basins (Seneš, 1973). At least four of these basins are recognized: in Upper Bavaria and Switzerland, in Lower Bavaria and Upper Austria, in Moravia and Lower Austria, and in southern Slovakia and northern Hungary. All of them were characterized by brackishwater conditions and had similar faunas of mollusks with *Rzehakia*, brackish-water cardiids, *Congeria* and *Melanopsis* (Popov and Voronina, 1983). The presence of species in common between these faunas and the fauna of the Kotsakhurian in the Eastern Paratethys points to an approximate synchroneity and occasional connections between these basins.

Northern shelf. In the west, in the Alpine Foreland Basin, the continental sedimentation continued at the beginning of the Miocene. The sea came back to this region in the Burdigalian (Upper Marine Molasse, OMM) and covered only the external, platform part of the depression, with facies and fauna similar to those of the inner Carpathian Basin. The East Bavarian Sea was a shallow basin with the sandy sedimentation and rich benthic fauna, whereas deeper water deposits with abundant turbidites occurred closer to the modern edge of the Alps (Steininger and Wessely, 2000).

There are almost no data on lower Miocene shallow water deposits and the fauna of the northern shelf of the Carpathian Basin. It was likely a very narrow zone overlain by subsequent nappes. At the same time, biogeographic data suggest that in the Eggenburgian–Karpatian and Sakaraulian–Tarkhanian this shelf provided a connection between the Eastern and Western Paratethys. According to Barg (1993), this connection is documented by thin deposits of the Komrat Beds (6 m) in the pre-Dobrogea Depression (Lower Ottnangian after L.S. Pishvanova) and the presence of the Eggenburgian in the Romanian part of the Depression (near Piatra Neamţ), where they are dated using nannoplankton of zones NN2–NN3.

This shelf broadened by the end of the Early Miocene, when the subsidence of the Carpathian Foredeep formed to result in a considerable expansion of the shallow water Nagorjany Bay (Early Karpatian). Shallow water coarsely-terrigenous deposits of this basin with rich benthic fauna are traced from Moravia and southwestern Poland up to Volhynia-Podolia (Nagorjany Beds). The uniformity of this fauna points to its connections with the Early Tarkhanian Basin.

Greater Caucasus-Kopet Dagh Basin

In the Early Miocene, the Maikopian Basin continued its development. Any essential paleogeographic heterogeneity of its Miocene history can be recognized only in the marginal parts of the basin. The occurrence of warm-water Tethyan elements in the benthic fauna of the Eastern Paratethys indicates a resumed direct communication with the Tethys through eastern Turkey and Iran, which in the Burdigalian were covered by an extensive sea basin (Erunal-Erentoz, 1950; Luttig and Steffens, 1975). Faunal data indicate that these connection emerged already at the beginning of the Early Miocene but became easier and wider in the Burdigalian (Sakaraulian), probably, stimulated by the peak of the Styrian tectonic phase.

After the intense but short transgression into the marginal parts of the basin (probably in the Karadzhalginian-Aquitanian time), which, in our view, reached northern Ukraine (Sivashi Beds of the Dnieper-Donets Depression) and Tajikistan, the Gissarak Beds (Voronina et al., 1993; the same beds were dated to the Oligocene by V. Zosimovich and G.H. Salibaev), the basin considerably regressed in the Sakaraulian time. The regression was especially extensive in the North Black Sea Region, in the Volga–Don Region (down to the Manych), and in the eastern margin of the basin. The lowering of the base level of erosion caused the first post-Chattian inflow of sandy material from both the European and the Turkish-Lesser Caucasus land masses. The sandy material formed thick clinoforms on the renewed bottom scarps and was subjected to consedimentary sliding.

Axial zone. The bathymetric zonality of the Sakaraulian Basin was retained during the entire Maikopian time. The Lower Miocene deposits of this zone have poor paleontological control and cannot be

recognized within the Maikopian sequence. Obviously, the axial zone of the Eastern Paratethys in the Early Miocene comprised the two North Black Sea depressions, Lazarevskoe–Kobystan Trough, and the Southern Caspian Depression. The pre-Miocene contraction resulted in the closing of the northwestern part of the Lazarevskoe–Kobystan Trough and its reduction in the southeast (Kopp and Shcherba, 1985; Shcherba, 1989). These deepest water depressions were surrounded by an extensive shelf with its deeper parts affected by hydrogen-sulfide contamination. Deposits of this zone do not contain remains or traces of benthic fauna but are enriched with organic matter and pyrite.

The southern shelf of the Sakaraulian Basin is clearly traced from western Georgia, along the Adzhar– Trialet highlands and the Lesser Caucasus. Deposits of deeper parts of this shelf are known in the Tuapse Depression, where they are represented by chocolatecolored non-calcareous clays with fish remains (Adler Formation, 800 m) and in the Kura Depression. The latter basin had the predominantly clayey sedimentation with anoxic features, but with abundant supply of sandy material from the south and southwest, from the Turkish–Lesser Caucasus land. Sandy and gravelly–sandy shallow zones occurred closer to the coast (typical Sakaraulian facies of Kartli) and were populated by the rich warm-water benthic fauna. The Sakaraulian molluscan fauna of Georgia includes about 100 species of bivalves. All assemblages contain marine euryhaline forms suggesting nearly normal salinity. Strong similarity of the fauna with that of the Western Paratethys (one-third of the shared species) indicates active zoogeographic connections of these basins. However, the Sakaraulian fauna contains some marine allochthonous forms of different origin and suggests some Indo-Pacific influence. These are mollusks *Fragum* and *Pla*giocardium (Popov et al., 1993) and the genus Alepes in the ichthyofauna of the Bathysiphon Formation of the eastern Crimea (after A.F. Bannikov).

Thus, the composition and abundance of the Sakaraulian fauna indicated the presence of a sea passage connected with the Central Iran Basin that had the fauna influenced by the Indo-Pacific biota up to the Burdigalian (Adams *et al.*, 1983).

The wide distribution of sandy facies with remains of warm-water shallow mollusks can be traced into more eastern areas as well, for example, in the pre-Kopet Dagh part of the basin (Voronina *et al.*, 1993). This time corresponds here to the middle part of the Aktepe Sand.

The northern shelf in the Sakaraulian was considerably reduced in comparison with the Oligocene. It, retained, however, a relatively strong bathymetric differentiation. Its deepest part remained in the Indol-Kuban Depression with the continued accumulation of very thick clay deposits (up to 1000 m). The Terek– Mangyshlak Depression in the Late Oligocene to the beginning of Miocene was markedly leveled by in-filling deposits. By the middle of the Early Miocene (the Olginskaya time), the coarsening and shallower water character of the deposits is manifested almost throughout the basin shelves. Sites of former anoxic deposition became populated by benthic fauna. However, the coastal facies of the Early Miocene are absent along the periphery of the Greater Caucasus. In the Western Caucasus, the only elevated island is represented by the Lagonaki Highland. Its northern slope served a source of fluvial transportation of abundant sandy materials accompanied by the formation of manganese concretions (Laba and Fars rivers: Kalinenko, 1990; data of E.I. Kovalenko).

The coastal facies are also absent (or not preserved) along the low northern coast of the Maikopian Sea. They occur only along the Ukrainian and Donets Highlands (Chernobaevka Formation in the North Black Sea Region, terrigenous deposits of the Rostov Swell). In Transcaspia, shallow sandy facies with remains of large warm-water mollusks are known only in the southern Aral Sea Region, Kyzylkum, and foothills of the Kopet Dagh. The sandy material was transported here from areas of the newest orogeny of Central Asia, where the accumulation of synorogenic sequences started in the Baldzhuanian time.

Starting from the Early Miocene, the geological history of the Turanian Plate entered the "Great Lake Stage" (terminology of V.V. Lavrov). As early as in the Aquitanian, four large landscape regions were formed here (Lavrov *et al.*, 1979). These are the seaside lacustrine-lagoonal plain in the northern Aral Sea Region; inland lake plain of the Irtysh Region and Turgai; lake plains of the Kazakh Shield upon an ancient Paleozoic base, and the fore-mountain zone of the modern Northern Tien Shan with large depressions. In Kazakhstan, the lake stage continued up to the Middle Miocene.

Biogeography of Water Bodies

Planktonic Foraminifers

This review is based on data from Krasheninnikov (1969b, 1971), who analyzed the composition and stratigraphic distribution of fauna in both the Mediterranean and Central Paratethys and open oceanic basins. These data are combined with data from later publications of other researchers.

Mediterranean. At the Oligocene–Miocene boundary in the Mediterranean, plankton became more diverse (at least 12 genera), and many new genera and species appeared. This boundary is typically marked by the appearance of the genera *Globigerinoides* and *Globoquadrina*. Changes in plankton at the boundary of the Aquitanian and Burdigalian were mostly apparent in species associations and were characterized by the appearance of the genus *Globigerinatella* and, at the end of the Early Miocene, *Orbulina* and *Candorbulina*.

Abundant and diverse foraminifers occur in the Mediterranean and Paratethys in the basins most closely connected with oceanic waters. Their characteristic species are widespread in sea basins of the tropical and subtropical zones. They occur, for example, in the Atlantic Region, Trinidad Island, and Venezuela (Krasheninnikov, 1969b).

Planktonic foraminifers are known from the south coast (in Morocco, Algeria, Tunis, and Egypt), but their composition is insufficiently known. In northwestern Algeria, nannoplankton of zones N6–N7 are reported to be accompanied by numerous foraminifers (Jenny *et al.*, 1986). However, only *Globigerinoides* (four species, among them *G. trilobus*), *Globigerina* (three species), *Globorotalia* (two species), *Turborotalia*, and rare *Catapsidrax* (two species) are listed.

Foraminifers of the eastern Mediterranean are among the best studied. In Syria, there are occasional mass occurrences of plankton forms represented by at least 30 species. Some of these forms survived since the Late Oligocene and occurred at the beginning of Miocene, some rarer species persisted throughout the Miocene, while new genera and species appeared at the Aquitanian–Burdigalian boundary. The Aquitanian record includes the genera *Globigerina* (seven species), Globigerinita (five species), Globoquadrina (two species), Globorotalia, Turborotalia (two species), Globigerinoides, Cassigerinella (C. chipolensis, known since the Late Oligocene), Sphaeroidina (two species). The Burdigalian is marked by the appearance of members of the genus *Globigerinatella* (in small numbers), new species of *Globorotalia* and *Turborotalia*, *Globi*gerinoides and Globoquadrina (two new species each), and, at the very end, rare forms of Praeorbulina, Condorbulina, and Biorbulina.

Relatively diverse planktonic foraminifers are also known in the zone of the Gulf of Suez. The same genera are represented here with a slightly different species composition. As in Syria, there are frequent occurrences of *Cassigerinella chipolensis*, also known in the Paratethys. Plankton of similar but impoverished composition are present in Israel and Cyprus.

The Aquitanian Basin in southern France was open to the Atlantic. The shallow-water sediments of this area contained infrequent but rather diverse planktontic foraminifers of the genera *Globigerina* (nine species), *Globigerinoides* (two species), *Globorotalia* (four species), *Globoquadrina* (three species), *Globigerinita*, *Porticulasphaera* (two species), and *Cassigerinella chipolensis*). In the western Mediterranean (Balearic Islands), the deeper water marls of the Burdigalian are dominated by plankton of the same generic composition and similar species composition.

In northern Italy (sections in the vicinity of the city of Torton), the foraminiferal association includes more than 100 species of plankton and benthos, with the planktonic forms sometimes constituting up to 70% of an assemblage, and in central and southern Italy, up to 85% (Krasheninnikov, 1971). As in Syria, the species of the genera *Globigerina*, *Globorotalia*, *Globigerin*- *ita, Globoquadrina, Globigerinoides, Catapsidrax,* and *Globigerinatella* are also present. Typical Early Miocene plankton is known from deposits of Sicily and Sardinia, the western coast of the Adriatic Sea (Albania), and the coasts of the Ionian (northwestern Greece) and Aegean seas (northeastern Greece). Planktonic for-aminifers from Greece include the widespread species *Cassigerinella chipolensis*.

North Sea Basin. At the beginning of the Miocene, the North Sea Basin was still inhabited by relatively numerous genera of planktonic foraminifers *Globigerina*, *Globigerinoides*, *Globorotalia*, *Neogloboquadrina*, and *Globoturborotalia*, usually represented by one or two species. Certain genus-level differences from the fauna of the Mediterranean are the result of different taxonomies used by researchers (*The Northwestern...*, 1988). The presence of species widespread in the Mediterranean area, such as *Globigerinoides trilobus* and *Cassigerinella chipolensis*, is remarkable. The Middle Miocene is marked here by the disappearance of the genus *Cassigerinella* and the appearance of *Orbulina*. *Cassigerinella* is known in the Polish Carpathians (Cicha et al., 1998).

Paratethys. In the Transcarpathian Deep, the planktonic association of the Burdigalian includes *Sphaeroidina austriaca* and *S. bulloides* (Venglinskii, 1975). The Carpathian Foredeep of Ukraine (bottom of the Vorotyshcha Formation, Zone NN1) yielded only the genera *Globigerina* (several species), *Cassigerinella*, and the genus *Chiloguembelina*, which is endemic to this region. They are accompanied by abundant radiolarians. In the Krosno sediments of the Skibas Zone, the planktonic assemblage includes representatives of the genera *Globigerinoides* (*G. trilobus* and *G. sacculifer*), *Globorotalia* (*G. opima*), and *Globigerina* (the group of "smaller globigerines" after Gruzman, 1983).

In the Upper Maikopian sediments of the Eastern Paratethys, planktonic foraminifers are nearly absent. According to the data of T.E. Ulanovskaya, planktonic forms are known from the shelf of the Sea of Azov, and in the Danube area of the Scythian Platform (*Neogene System...*, 1986). At the end of the Early Miocene (Tarkhanian), the connection between the basin and oceanic waters increased, and the anoxic regime yielded to more favorable conditions. In different areas, this led to the appearance of very abundant accumulations (sometimes of rock-forming significance) consisting of shells of *Globigerina tarchanensis*.

Nannoplankton

Northern Mediterranean. The nannoplankton association of the Late Oligocene-Early Miocene Basin included more than 35 species and rapidly changed over time. By the end of the Aquitanian, among the most typical species, some, like *Reticulofenestra bisecta, Helicosphaera recta, H. perch*- nielseniae, Claucicoccus fenestratus, Cyclicargolithus abisectus (larger than 10 µm), and Zygrhablithus bijugatus became extinct, and others (Helicosphaera euphratis) sharply reduced their productivity. Only two Aquitanian species, Sphenolithus delfix and S. capricornutus, are not known in either the Oligocene or the Burdigalian. Another emerging species, *Helicosphaera* carteri, increased its productivity as early as the end of the Aquitanian. The end of the Aquitanian to the beginning of the Burdigalian is marked by the appearance of Discoaster druggii and Sphenolithus disbelemnos, and the beginning of the Burdigalian, by Helicosphaera ampliaperta and H. mediterranea. The appearance and rapid extinction of the species Sphenolithus belemnos is characteristic of the Middle Burdigalian Basin; S. heteromorphus, Discoaster variabilis, and D. exilis appeared in the Late Burdigalian. Along with the above listed species, the Mediterranean Basin was inhabited by Reticulofenestra pseudoumbilica, Pontosphaera spp., Orthorhabdus serratus, Cyclicargolithus floridanus, Discoaster deflandrei, Triquetrorhabdulus carinatus, T. milowii, Braarudosphaera bigelowii, etc. (Fornacciari and Rio, 1996).

The nannoplankton association of the Dinarid Basin was similar to the Mediterranean association, but it was much poorer and included 22 species. It is a mixture of Oligocene species passing into the Miocene (Cyclicargolitus abisectus, Discoaster deflandrei, D. adamanteus, Triquetrorhabdulus carinatus, Helicosphaera euphratis, Sphenolithus delfix, and S. conicus,); Miocene forms, like Helicosphaera carteri, H. gertae, Triquetrorhabdulus milowii; and transitional forms, such as Sphenolithus moriformis, Reticulofenestra perplexa, Pontosphaera spp., Coronocyclus nitescens, Cyclicargolithus floridanus, etc. The Burdigalian Basin yielded Discoaster druggii, Helicosphaera mediterranea, H. obliqua, Sphenolithus cf. belemnos, and S. dissimilis (de Caroa et al., 1995). The analysis of nannoplankton associations indicates the incompleteness of the Lower Miocene sequence, particularly in its Burdigalian part. This is a possible consequence of sea level fluctuations in the Mediterranean and the migration of the coastline in the marginal Dinarid Basin during the Early Burdigalian.

North European Basin. The inherited Early Miocene basins of northern Europe were involved in mostly noncalcareous sedimentation. The recorded associations of nannoflora are very poor. The basin of northwestern Germany was dominated by *Coccolithus pelagicus*, along with occurrences of individual specimens of *Helicosphaera* sp. (cf. *ampliaperta*), *Reticulofenestra* sp., and redeposited Cretaceous–Paleogene species (Kothe, 1986).

Carpathian Basin. The productivity and distribution of nannoflora in the region were influenced by the instability of paleogeographic conditions, caused by the impulses of the Late Alpine folding. This resulted in the formation of numerous small basins with restricted connections and a significant role of terrigenous sedimentation, accumulation of flysch and molasse deposits. These conditions were unfavorable for the productivity of haptophyte algae.

During the earliest Miocene (Late Egerian), the inherited Late Oligocene basins of the eastern Alps, western, northern, eastern and southern Carpathians were characterized by a nannoflora that was taxonomically similar but significantly less abundant than that of the Mediterranean. The nannoplankton frequently included up to 90–95% of allochthonous elements and only 5-10% of autochthonous forms. The Late Egerian association consisted of rare representatives of the genus Sphenolithus (S. delfix, S. capricornutus, S. conicus, S. dissimilis, S. moliformis, and S. compactus). The Oligocene-Miocene boundary interval is often marked by the monospecific assemblage with Syclicargolithus abisectus (eastern Carpathians) (Andreyeva-Grigorovich and Gruzman, 1994). The occurrence of the typical Miocene species Discoaster druggii, Sphenolithus disbelemnos, Orthorhabdulus serratus, Helicosphaera carteri, and Reticulofenestra pseudoumbilica is characteristic for the terminal Late Egerian Basin (Oszczypko et al., 1999; Oszczypko and Oszczypko-Glowes, 2002). These associations are also characteristic of small residual basins in the Early Miocene of Transylvania and Pannonia (Nagymarosy and Müller, 1988; Meszaros, 1992; Marunteanu, 1992). Other areas of the inner Carpathians were predominantly occupied by dry land (Kováč et al., 2001).

After the Early Eggenburgian transgression, the newly formed inner Carpathian basins were inhabited by shallow-water associations with abundant carbonate dinocysts, such as *Thoracosphaera* spp., and an insignificant role of *Coccolithus pelagicus, Triquetrorhabdulus* spp., *Orthorhabdus serratus, Helicosphaera carteri, H. granulata, H. ampliaperta, Sphenolithus* spp., and others (Vienna Basin) (Andreyeva-Grigorovich and Halasova, 2000). In the eastern Alps and Carpathians, the inherited basins demonstrate a nannoplankton association similar to that of the Late Egerian. It differs in the increased number of earlier Miocene species, and in the emergence of *Helicosphaera vederi, H. scissura, H. mediterranea, Calcidiscus leptoporus*, and *Umbilicosphaera rotula*.

The Middle-Late Eggenburgian Basin (the maximum transgression) is characterized by the appearance of Sphenolitus belemnos (the range equal to its zone, NN3). Apart from the zonal species, other species of the genus Sphenolitus are widely represented by S. disbelemnos, S. dissimilis, S. moriformis, together with Helicosphaera ampliaperta, H. scissura, H. mediterranea, H. vederi, Calcidiscus leptoporus, Umbilicosphaera rotula, Discoaster deflandrei, D. druggii, Triquetrorhabdulus spp., Cyclicargolithus floridanus, Orhtorhabdulus serratus, Braarudosphaera bigelowii, and others (altogether up to 45 species). The given association is characteristic of the Burkalo time of the Transcarpathian Deep (Andreeva *et al.*, 2002), Vienna, the South Slovakian–North Hungarian, Danubian, and Transylvanian basins of the Carpathian Foredeep (the Czech, Polish, Ukrainian, and Romanian parts), and the basins in the western, northern, eastern, and southern Carpathians of the Menilite and Krosno types (Garecka and Olszewska, 1998; etc.). The differences in nannoplankton associations were basically associated with the basin type. The flysch and molasse basins of the Carpathian Foredeep usually yielded poorer associations (Andreyeva-Grigorovich and Stupnitskii, 1976), while the inner Carpathian basins (Transcarpathian, Vienna, Pannonian, and Transylvanian) are characterized by rich assemblages.

The Late Eggenburgian Basin corresponded to the time of accumulation of the uppermost strata of the NN3 Zone, and to the NN4 Zone, except for its uppermost part. *Sphenolithus heteromorphus* appeared in the marine basin, but the association was generally similar to the Middle Eggenburgian one.

In the Early Ottnangian (lower part of Zone NN4) of the Carpathian region, marine conditions were mainly retained in the flysch basins of the Krosno type and in molasse basins in the Carpathian Foredeep of Poland, Ukraine, and Romania. The Late Ottnangian-Early Karpatian transgression affected only the northwestern and western areas of the Alpine–Carpathian Region. Marine basins were inhabited by associations very similar to those of the Mediterranean. These assemblages include about 60 species, such as *Calcidiscus tropicus*, C. premacintyrei, Coccolithus miopelagicus, D. variabilis, and widely represented species of Helicosphaera (H. ampliaperta, H. carteri, H. mediterranea, H. obliqua, H. intermedia, H. vederi, H. euphratis, H. perch-nielseniae, and H. scissura,). The diversity of sphenolithes is notably reduced, the typical species are Sphenolithus heteromorphus and S. moriformis (Andreyeva-Grigorovich and Halasova. 2000; Andreyeva-Grigorovich et al., 2001). In the western and southwest regions (Styrian Basin, Zala, Sava, Drava basins, etc.), in addition to the above mentioned forms, the diversity of discoasters is increased by Discoaster adamanteus, D. rufus, D. deflandrei, and D. exilis (Rögl et al., 2002; Coric in Svabenicka et al., 2004). The marine basin, and a series of brackish-water basins (the latter were characteristic of some zones of the Carpathian Foredeep), with impoverished associations of nannoflora and numerous redeposited species, continued to exist in the flysch and molasse sedimentary zones of the outer Carpathians.

In general, the Early Miocene nannoplankton association indicates warm-water sea basins with unstable hydrodynamic and salinity regimes.

Eastern Paratethys. In the Eastern Paratethys, the Late Oligocene–Early Miocene nannoplankton association is characteristic of the Late Septarian Basin of the northern Caucasus. It is characterized by the impoverished composition of Oligocene–Miocene species

(Coccolithus pelagicus, Cyclicargolithus floridanus, C. abisectus, Helicosphaera recta, H. intermedia, Helicosphaera sp., Zygrhablithus bijugatus, Triquetrorhabdulus carinatus, and Braarudosphaera bigelowii). The nannoflora of the Karadzhalginian basin included mainly transitional species (Krhovsky et al., 1995).

Organic-Walled Phytoplankton

Neogene dinocysts have been studied, mainly for stratigraphic purposes, for only two decades. A number of regional zonal scales have been elaborated. They vary in numbers of constituent biostrata and corresponding index species. These scales were constructed for the Western European water bodies that were connected to the Norwegian and North seas, for the Mediterranean (Italy), and for the Crimean-Caucasian Region. To date, dinocysts have been investigated from many reference sections of the above mentioned regions, including the stratotypes of the Miocene of the Mediterranean area: the Lemme section, accepted as the limitotype of the Oligocene-Miocene boundary; sections of the eastern Mediterranean (Svria, Egypt). the Crimean-Caucasian Region (Belava River, the eastern Crimea, the Black Sea coast of Abkhazia, Apsheron Peninsula, Sumgait River), Carpathians, the southern East European Platform (including the North Black Sea Depression), and the Scythian and Turanian Plates.

Throughout the Peri-Tethys, the Oligocene-Miocene boundary is marked by the change in the composition of pyrrophyte algae. The extinction of Paleogene taxa is most conspicuous, while the appearance of new taxa is stretched in time throughout, at least, the first half of the Miocene. The extinction primarily affected the dominants of the Paleogene flora, the cavate dinocysts of the genus Deflandrea (except smaller dinocysts of the *Deflandrea spinulosa* group), Wetzeliella, Kisselevia, etc. The species that did not, or only just, pass into the Neogene include Areoligera, Chiropteridium, Enneadocysta, Phthanoperidinium, Thalassiphora, etc. At the same time, some forms that played a secondary role in the Paleogene flora flourished from the beginning of the Miocene. This group includes Selenopemphix, Distatodinium, Impagidinium, Operculodinium, Lingulodinium, Dinopterygium, etc. The role of Spiniferites and Cordosphaeridium markedly increased.

In the Early Miocene, it is very difficult to recognize biogeographic zonality or clear differences between the associations of Aquitanian and Burdigalian. Distinctions in the composition of zonal assemblages of the Lower Miocene are associated with gradual displacement of Paleogene taxa by those of the Miocene, spatial isolation of the Peri-Tethyan basins, and regional features of hydrological conditions, and are undoubtedly of climatic nature. This is evident from the taxonomic comparison of the northern (Norwegian Sea) and southern (Mediterranean) associations. Therefore, it is not incidental that even the same index species appear in different regions at different stratigraphic levels. However, a common feature of all the organic-walled algal flora of the Northern Hemisphere is the more or less synchronous renewal of its composition at the Paleogene-Neogene boundary. Cavate dinocysts of genera that had a wide distribution in the Paleogene (Wetze*liella*. *Deflandrea*) were almost universally reduced. and new taxa appeared. Some of them are used as index species of zonal units of the Lower and early Middle Miocene scales (Labyrinthodinium truncatum, Hystrichosphaeropsis obscura, Tuberculodinium vancampoae, and species of Sumatradinium and Bitectatodin*ium*). Between latitudes 30° and 60° North, the species diversity of dinocysts remained at a stable level of about 40-60 species in normal salinity marine sediments, although the actual taxonomic diversity was significantly higher. Anoxic conditions in the basins are indicated by a notable increase in the content of leiosphaeridias, especially in eastern Transcaucasia. The evidence of freshening is provided by mono- or oligodominant phytoplankton assemblages with the occurrence of species belonging to the genera Batiacasphaera and Hystrichokolpoma (thin-walled morphotypes). Forms that characterized Paleogene open sea basins with normal salinity (Spiniferites, Operculodinium, Impagidinium, etc.), by the end of the Early Miocene (in particular, Spiniferites), tend to occur in deposits with slightly lowered salinity, and from the middle of the Miocene appear in brackish-water environments.

Mediterranean. Dinocysts from the Lower Miocene of Italy are known in the sections of Piedmont. These are the Lemme section, limitotype of the Oligocene-Miocene boundary, and a group of sections 40 km to the east, the stratotype area of the Langhian. the lower stage of the Middle Miocene). In contrast to northern Europe and similar to the sections of the Caucasus, the lower beds of the Aquitanian section are marked by the epibole of *Deflandrea spinulosa* and the disappearance of *Chiropteridium* sp. The genus *Deflan*drea also completely disappears within the Paragloborotalia kugleri Zone. Powell (1992) notes the occurrence of Hystrichosphaeropsis obscura several meters below the Oligocene-Miocene boundary and Melitasphaeridium choanophorum and Tuberculodinium vancampoae slightly above this level. Powell's lower dinocyst zone (LAN1) partly belongs to the Upper Oligocene. The type species of this zone is Tuberculodinium vancampoae. Of the taxa known in this zone, Lejeunecysta diversiforma, Melitasphaeridium choanophorum, Thalassiphora pelagica, and Homotryblium floripes do not pass into the overlying deposits. The middle zone of the Lower Miocene, Nematosphaeropsis "A" (LAN2), completely belongs to the Aquitanian. As inferred from planktonic foraminifers, it partly corresponds to Zone P4. The last appearances of Cordosphaeridium cantharellum, Distatodinium paradoxa, and Hystrichokolpoma sp. "B" are recorded within this zone. Comparison of this zone with other dinocyst zones of the European Lower Miocene should be done in coordination with data on the co-occurrence of *D. paradoxa* and *Labyrinthodinium* in the section of the Hodde Formation (Denmark). There, in contrast to other West European sections, the latter species appears in the Aquitanian (Piasecki, 1980). Zone LAN3 belongs to the Burdigalian. Its lower boundary is drawn by the occurrence of the zonal species *Spiniferites robusta*. In addition, the first records of *Tectatodinium psilatum*, *Pyxidiella simplex*, and *Impagidinium patulum*, and others are confined to this zone.

In the Zenie section of the Latakia Depression in Syria, the composition of the dinocyst assemblage is close to those of Italy and includes *Hystrichosphaerop*sis obscura (dominates), *Tectatodinium pellitum* (dominates), *Hystrichokolpoma* cf. salacia, *Impagidinium* strialatum, and Spiniferites cornutus. In the section of the Abu Madi Formation in the Nile Delta (Egypt), the assemblage of the Lower Miocene includes forms that do not cross its upper boundary. These are Achomosphaera sagena, Homotryblium pallidum, Achilleodinium biformoides, Dinopterygium cladoides, Cordosphaeridium cantharellum, and Distatodinium paradoxum.

Northern Atlantic. North Atlantic assemblages (Vöring and Rockall plateaus) differ in composition from their chronological equivalents of the neritic assemblages of Peri-Tethys in the somewhat higher species diversity and the absence of Oligocene taxa that persisted in the Mediterranean up to the Middle Aquitanian (for example, Deflandrea ex gr. spinulosa). In the section of the borehole 406 DSDP (Rockall Plateau), the Lower Miocene corresponds to the range of the uniform Tuberculodinium vancampoae Zone. Its boundaries are controlled by the data on nannoplankton and planktonic foraminifers. The upper boundary of this zone is recognized by the occurrence of Labyrinthodinium truncatum and, as on the Vöring Plateau, it coincides with the boundary between the Lower and Middle Miocene. Several forms appear within this zone at a number of levels: Ectosphaeropsis burdigalensis [first described from the Burdigalian stratotype in the vicinity of Bordeaux (Jan du Chen and Masure, 1986)], Hystrichosphaeropsis obscura, Impagidinium patulum, Betectadinium tipikiense, Operculodinium crassum, Apteodinium tectatum, etc. At the same time, the zone includes the last occurrences of Membranophoridium aspinatim, Hystrichokolpoma cinctum, Thalassiphora pelagica, Apteodinium spirioides, Ectosphaeropsis burdigalensis etc. Cordosphaeridium cantharellum, Distatodinium craterum, and Nematosphaeropsis downiei disappear very close to the upper boundary of this zone.

A number of Lower Miocene taxa of the Atlantic are common in the middle latitudes, for example, in the deposits of the Norwegian Sea. The sequence of four zones was established in the borehole 643 section of deepsea drilling at the northern margin of the Vöring Plateau (Manum et al., 1989). These zones are differentiated in the continuous section from the zones of the Upper Oligocene and Middle Miocene and are named after taxa that appear at their boundaries. The lower zone, Ascostomocystis granosa, is established based on the appearance of zonal species with simultaneous disappearance from the section of the Upper Oligocene forms Cordosphaeridium mespilanum and C. partispinatum. The base or the lower part of the zone is marked by the first occurrences of Invertocysta tabulata, Cribroperidinium tenuitabulatum, Hystrichosphaeropdis obscura, and Tuberculodinium vancampoae. Some newly appearing taxa are also recorded in the basal Miocene beds of the sections of Piedmont and the Rockall Plateau (T. vancampoae) as well as in the east of the United States (Batiacasphaera sphaerica and T. vancampoae). The upper boundary of the zone is controlled by the occurrence of index species of the next following zone, Evittosphaerula paratabulata. This second zone also belongs to the Aquitanian. In addition to the zonal species, which also has an Aquitanian range too, the first records of Pentadinium laticinctum, P. imaginatum, Impagidinium paradoxum, Lophocysta sulcolimbata, and Tectatodinium psilatum are reported there. The presence of Sumatrodinium sp. is also noted there for the first time. The third Lower Miocene zone of the Vöring Plateau, the Impagidinium patulum Zone, is characterized by the appearance at its lower boundary of the zonal species along with Batiacasphaera baculata and Dinopterygium cladoides. In the Bay of Biscay, this taxon appears in nannoplankton Zone NN2 in co-occurrence with Distatodinium paradoxum, Apteodinium spiridoides, and Hystrichosphaeropsis obscura. However, on the Rockall Plateau, Impagidinium patulum is recorded only in the Middle Miocene. The upper boundary of the zone is defined by the first record of Cordosphaeridium cantharellum, which is an index species of the fourth Lower Miocene unit, the Apteodinium spiridoides Zone. The boundary between the Lower and Middle Miocene is drawn by the occurrence of Labyrinthodinium truncatum at the top of this zone, although in the North Caucasian sections, this species appears earlier, at the boundary of the Oligocene and Lower Miocene. C. cantharellum, D. cladoides, and A. spiridoides do not cross the upper boundary of the fourth zone of the Vöring Plateau.

Carpathian Basin. Fossil dinoflagellates from Neogene deposits of this region are insufficiently known. There are almost no data from the Ukrainian and Polish Carpathians, except for the lowermost Aquitanian. In the earliest Miocene, the Krosno and Menilite basins of the Ukrainian Carpathians were dominated by *Tuberculodinium vankampoae, Distatodinium* spp., *Spiniferites* spp., *Militasphaeridium choanophorum, Apteodinium* sp., *Tasmanites* spp., and *Thalassiphora pelagica* (the last form prevails in the Menilite Basin). According to the unpublished data of N. Hudackova, the dinocyst associations from the Late Egerian–Early Eggenburgian of the Moravian part of the Carpathian Foredeep (materials of V. Bubik) and the Vienna Basin are similar to those of the Mediterranean. They are, however, distinct in their lower diversity and in much worse preservation, and are characterized by the appearance of *Membranilarnacia picena*, Distatodinium cavatum, D. apenninicum, and Stoveracysta conerae. The epibole of Heteraulacacysta companula and two species Selenopemphix spp. (the level of Zone NN3) is also recorded. In the Lower Miocene, the association of organic-walled phytoplankton from the Burkalo Formation (Zone NN3) of the Transcarpathian Deep of Ukraine is much poorer in both abundance and diversity. The dominant species belong to the genera Selenopemphix, Tectatodinium, the group Spiniferites, Batiacasphaera, and Lingulodinium. Isolated specimens of Stoveracysta cf. conerae, Membranilarnacia sp., Distatodinium sp., etc., are also known by sporadic records (unpublished data of A.S. Andreyeva-Grigorovich).

Eastern Paratethys. The composition of the Lower Miocene associations of the majority of sections in the Crimean-Caucasian Region is closer to those of the Mediterranean sections of Italy, Syria, and Egypt than to the North Sea and Atlantic. There are, however, some distinctions as well. In the North Caucasian sections, the assemblage of the Labyrinthodinium truncatum Zone (D16) succeeds the Upper Oligocene assemblage with Chiropteridium partispinatum–Deflandrea spinulosa (D15a) at the Oligocene-Miocene boundary. In the Belaya River Basin, it occurs in the upper beds of the Septarian Formation (undivided nannoplankton zones NP25–NN1). In sections of the Mediterranean, as in northwestern Europe (except for Denmark), Labyrinthodinium truncatum occurs only from the Middle Miocene. Therefore, in the regional schemes of southern regions, the first zone of the Lower Miocene is indexed by different species. This zonal assemblage also embraces the Burdigalian part of the section, which is still very poorly understood. At the same time, the lower part of the Miocene sequence, including the basal part of the Karadzhalginian Formation in the section of the Belaya River, contains the epibole of *Deflan*drea spinulosa. A similar situation is established in the Carpathian Region, sections of the Black Sea, coastal zones of Adzharia and Abkhazia, and in the lectostratotype of the Caucasian Regional Stage, the Pokrovskaya-4 borehole near Tikhoretsk. In the Mediterranean, this taxon is only recorded in noticeable quantities in the Lemme section. In the majority of the Caucasian sections, the core of the Aquitanian assemblage is formed by species of Cordosphaeridium, Cleistosphaeridium, Cribroperidinium, Dapsilidinium, Spiniferifes, Batiacasphaera, Selenopemphix, and Lingulodinium. Along with Labyrinthodinium truncatum, the appearance of Tuberculodinium vancampoae, Hystrichosphaeropsis obscura, and Sumatradinium spp. are noted at different levels of the Lower Miocene sections.

An assemblage of the Late Aquitanian and Burdigalian is described from the upper beds of the Maikopian section in the eastern Crimea (the Bulganak Bay). Along with a large number of taxa characteristic of Aquitanian deposits, there are a number of species which became widespread in the Middle and even Late Miocene (*Spiniferites bentorii, Hystrichosphaeropsis minimum, Operculodinium israelianum,* etc.).

In the Sumgait River Basin and in the Apsheron Peninsula, Lower Miocene assemblages are impoverished because of anoxic conditions in the basin. Over 50% of the assemblage is *Leiosphaeridia*. Dinocysts are scarce and represented by *Selenopemphix*, *Batiacasphaera*, and *Lingulodinium*.

Plankton-Based Biogeographical Zonation

Warm-water plankton assemblages, indicators of subtropical conditions, inhabited the southern shelf of the Mediterranean Basin (known from Morocco up to the Gulf of Suez), the eastern Mediterranean, the Aquitanian Basin, southeastern Spain, the Balearic Islands, the whole of Italy, the islands of Sicily and Sardinia, and the coasts of the Adriatic, Ionian, and Aegean seas. The fauna of this area includes abundant planktonic foraminifers. They occasionally occur in vast quantities, and their shells frequently prevail in associations. The species composition of the plankton is diverse (for example, no fewer than 30 species in Syria). This group is known to include the genera Globigerina, Globoquadrina, Globorotalia, Turborotalia, Globigerinita, Globigerinoides, Globigerinatella, Catapsidrax, Porticulasphaera, and Cassigerinella. At the end of the Early Miocene, rare Praeorbulina, Candorbulina, and Biorbulina, which are typical for the Middle Miocene, appeared in various areas of the basin. An important role in nannoplankton associations is played by warm-water discoasters and sphenolites. Many of these genera also occur in present-day tropical and subtropical basins. Nevertheless, in the majority of the studied dinocyst associations of the Early Miocene, in both the Mediterranean and the Crimean-Caucasian Region, the index of marine conditions (the ratio of the total organic-walled phytoplankton to the total palynomorph content in macerates) is relatively low (ranging from 3 to 12%).

Planktonic foraminifers from northwestern Europe considerably differed in the generic and species composition from the fauna of the Mediterranean. The plankton, being sometimes relatively numerous, was not diverse. Species of the genera *Globigerina* and *Globorotalia* occurred together with *Globigerinoides trilobus* and *Cassigerinella chipolensis*, which are widespread in the Mediterranean Region. The currently known associations of nannoflora are very poor, which was caused by facies features of the basin. Assemblages of organic-walled phytoplankton of the northern Atlantic differ from the contemporaneous neritic assemblages from the Peri-Tethys in the somewhat higher species diversity and the absence of Oligocene taxa, which survived in the Mediterranean until the Middle Aquitanian.

The productivity and distribution of planktonic assemblages in the Carpathian Region were affected by the instability of paleogeographic conditions and biogeographic connections. The planktonic assemblages were similar to the Mediterranean ones in taxonomic composition, but were markedly inferior in terms of species abundance and occasionally degraded into sharply impoverished and monospecific associations. The analysis of distribution of dinocyst taxa in the Lower Miocene indicates a relatively similar composition of associations within the whole of the neritic zone of the Mediterranean, Carpathian basins, and the Crimean-Caucasian Region. Some taxa are recorded at lower stratigraphic levels in southern sections (Labirinthodinium trancatum), whereas in the high-latitude sections, they appear only in the Middle Miocene. The late culmination of smaller dinocysts of Deflandrea *spinulosa* in the lower beds of the Miocene sequence is observed in the sections of the Carpathians, the Crimean-Caucasian Region, and in some sections of the Mediterranean. As regards the high-latitude zone, the disappearance of *Deflandrea* and *Chiropteridium* is recorded there at an earlier level, at the Oligocene-Miocene boundary.

The record of the Eastern Paratethys contains only the poorest assemblages of calcareous plankton. In conditions of low oxygen exchange and stagnant benthic waters, large organic-walled *Leiosphaeridia* became widespread in the Early Miocene Maikopian Basin. It is accompanied in preparations by masses of amorphous organic remains, probably of cyanobacterial origin (as exemplified by the materials from the Apsheron and Sumgait sections). As for dinocysts, they are nearly absent or represented by isolated specimens of species of the genera *Batiacasphaera, Selenopemphix,* and *Hystrichokolpoma*.

Marine Ichthyofauna

The ichthyofauna of the Aquitanian¹ is known from two localities in the northern Caucasus and Ciscaucasia. The first is in the Assa Formation of the Chernaya Rechka, suburbs of Vladikavkaz, Northern Ossetia; and the second is in the Voskovaya Gora Formation of the Pshekha River, near the village of Shirvanskaya, Apsheronskii District, Krasnodar Region. The richest is the assemblage from the Assa Formations, which surpasses in diversity all known Early Miocene ichthyofaunas with complete skeletons preserved. It includes pelagic

clupeids Sardinella brevicauda (Men.), Pomolobus antiquus (Smirn.), and Alosa genuina Dan.; gadiforms of the families Merlucciidae: *Merluccius lednevi* Bog. and M. errans (Smirn.); and Gadidae: Palaeomolva smirnovi (Dan.), P. monstrata Fed., Bregmacerina antiqua (Smirn.), Onobrosmius sagus (Fed.), O. parcus (Dan.), and O. oligocaenicus (Bog).; beloniforms of the family Belonidae: Belone crior Smirn.; beryciforms of the family Holocentridae gen. indet.; syngnathyforms of the families Centriscidae: Aeoliscus apscheronicus (Led.), Aulostomidae: Aulostomus fractus Dan., Syngnatidae: Syngnathus altus Dan., Nerophis gracilis Serg.; diverse acanthopterygians: Priacanthus longispinus (Led.) (Priacanthidae); Lednevia oligocenica (Smirn.) (Pomatomidae); Echeneis urupensis Dan. (Echeneidae); Seriola smithvanizi Ban., Seriola sp., Scomberoides spinosus (Smirn.), Selar fedotovi Ban., Alepes pin Ban., Caranx quietus Ban., Decapterus praegracilis Ban., D. fusiformis Ban., Trachurus sp. (Carangidae), Leiognathoides minutus (Dan.) (Leiognathidae); Sparus sp. (Sparidae); Larimus ignotus (Smirn). (Sciaenidae); Chaetodon heptodon Smirn. (Chaetodontidae); Mugil latus Switch. (Mugilidae); Blennius sp. (Blenniidae); Gobiidae gen. indet.; Caprovesposus sp. (Acanthuridae); Hemithyrsites maicopicus Dan. (Gempylidae) Anenchelum lednevi (Men.) (Trichiuridae); Scomber gnarus Ban., Sarda memorabilis Dan. (Scombridae); Pinichthys fractus Ban. (Stromateidae); pleuronectiforms of the families Bothidae: Arnoglossus macropterus (Smirn.), A. bogatshovi (Dzhaf.), A distinctus Switch.; Pleuronectidae: Platichthys pavulus (Smirn.), P. daniltshenkoi (Dzhaf.); Soleidae gen. indet. (Danil'chenko, 1960; Fedotov, 1976; Danil'chenko et al., 1980; Bannikov, 1985, 1990; Bannikov and Parin, 1997).

When compared to the Late Oligocene, the beginning of the Aquitanian (the Assa (roof?) and Voskovaya Gora formations) is characterized by changes in the species composition of clupeids, scombrids, priacanthids, and gadiforms. Sardinella sardinites was replaced by S. brevicauda.; new forms appeared in the clupeid subfamily Alosinae; in scombrids, Scomber cubanicus and Sarda remota were replaced by S. gnarus and S. memorabilis. New syngnathiform species include the Aulostomidae Aulostomus fractus Dan. and the Syngnatidae Syngnathus altus Dan. and Nerophis gracilis Serg., which were absent from the Late Oligocene. M. errans Dan., which persisted to the Sakaraulian (Olginskian and Arabat formations of Ciscaucasia and the Crimea), appeared and became abundant. At the end of the Late Oligocene to the Aquitanian (most likely, in the Aquitanian–Upper Riki), the genera *Pseudoraniceps* (*P. sagus* Fed.) and Palaeomolva (P. monstrata Fed.) appeared. They survived in the Eastern Paratethys in the Sakaraulian (Fedotov, 1976). At the same time, only some gadiforms (Merluccius lednevi), priacanthids (Priacanthus longispinus), and syngnathyforms of the family

¹ All known assemblages from the Early Miocene are analyzed separately. Earlier, some of them were considered either within the ichthyofauna of the Abadzekh–Voskovaya Gora Horizon as an integral Late Oligocene assemblage (Danil'chenko *et al.*, 1980, p. 180) or as an undivided Early Miocene ichthyofauna correlated to the Sakaraulian (Bannikov and Parin, 1997).

Centriscidae (*Aeoliscus apscheronicus*) crossed the boundary of the Late Oligocene and Early Miocene.²

The ichthyofauna from the Arabat (Kerch Peninsula, Crimea) and Olginskian (Ciscaucasia) formations, dated Sakaraulian, is an assemblage basically inherited from the Aquitanian. However, there are a number of specific features that distinguish it from the Aquitanian fauna. It has a more warm-water subtropical appearance and a different composition of Indo-Pacific elements. It also lacks many acanthopterygians that are abundant in the coastal ichthyofauna of the Aquitanian of the Eastern Paratethys.

The Kotsakhurian ichthyofauna of the Eastern Paratethys is strongly impoverished. It contains clupeids and syngnathyforms. The composition of the ichthyofauna points to a shallowing and a decrease in salinity of the basin, that is, an obvious consequence of the isolated position of the Eastern Paratethys at that time.

In conclusion, it should be noted that the Early Miocene (the Aquitanian and the Early Burdigalian) history of the ichthyofauna of the Eastern Paratethys can be subdivided into three stages, each characterized by a specific assemblage:

(1) The Aquitanian stage. The intensified biogeographic connections with the Central Paratethys and prochoreses of fishes from the Indo-Pacific Basin;

(2) The Early Burdigalian stage. The increased warm-water appearance of the ichthyofauna, new prochoreses from the Indo-Pacific Basin;

(3) The Late Burdigalian (Kotsakhurian) Stage. The isolation of the Eastern Paratethys, a decrease in salinity of its waters and the impoverishment of the ichthyofauna.

Benthic Foraminifers

Mediterranean. Foraminifers are known from the Early Miocene beds of the North African shelf, southern Turkey, Cyprus, Syria, Lebanon, and Israel (Krasheninnikov, 1971). Among the larger foraminifers, the nummulites became extinct, the operculines almost

completely disappeared, and the role of lepidocyclines substantially decreased at the Oligocene-Miocene boundary. However, such typical Tethyan genera as *Lepidocyclina, Miogypsina, Miogypsinoides, Heterostegina, Spiroclypeus, Amphistegina*, and *Sphaerogypsina* persisted in shallow-water areas; and the genus *Grzybowskia* (known from the Oligocene of the Alpine Basin) appeared (Fig. 6).

The composition of smaller foraminifers was associated with facial conditions in their habitats. However, the generic composition of the benthos seems to remain essentially the same as in the Oligocene. The genera Archaias, Dendritina, Meandropsina, Peneroplis, Quinqueloculina, Triloculina, Spiroloculina, Pyrgo, Rotalia, Stomatorbina, and Almaena, which had inhabited this region in the Oligocene, still occurred in the shallow-water areas. Deeper water areas of the shelf were inhabited by diverse genera characterized by wide (or even global) geographical ranges and known as early as the Eocene and Oligocene: Textularia, Discorbis, Valvulineria, Baggina, Asterigerina, Cibicidoides, Heterolepa, Cribrononion, Nonion, Elphidium, Florilus, Eponides, Almaena, Rotalia, Caucasina, Virgulinella, Hopkinsina, Bolivinella, Bolivina, and many others. At the end of the Early Miocene, Almaena, Cassigerinella, and larger foraminifers Lepidocyclina, Miogypsina, and Miogypsinoides disappeared (Krasheninnikov, 1971). Unfortunately, the data on smaller benthic foraminifers provided by Krasheninnikov (1969b, 1971, etc.; Krasheninnikov et al., 1999) and other researchers are rather poor.

In Morocco, the genera *Miogypsina*, *Miogypsi*noides, Lepidocyclina, Grzybowskia, and Spiroclypeus were recorded. Among the smaller foraminifers (about 20 genera), it is difficult to indicate any characteristic taxa; Elphidium and Ammonia, which probably inhabited shallow-water areas, should be mentioned (Jenny et al., 1986). They come from terrigenous rocks of the South Reef Strait, which connected the Atlantic Ocean to the Mediterranean Sea, where lithothamnioid limestones of the reef type are spread. Krasheninnikov (1971) has shown that almost all species of planktonic and benthic foraminifers are also characteristic of Syria. At the beginning of the Miocene, northeastern Algeria was covered by shallow waters where limestones with lithothamnions, operculines, and heterostegines accumulated, while *Miogypsinoides* and *Lepi*docyclina occurred in isolated interbeds. The generic composition of small benthic faunas was the same as in Morocco. Tunis was inhabited by diverse smaller benthic foraminifers, including certain taxa in common with the Eastern Paratethys, such as Virgulinella pertusa (Reuss), and abundant Caucasina sp., a small quantity of which occurred in Syria but was not recorded in other regions. Miogypsina and Lepidocy*clina* occurred in bioclastic deposits of Libya. In Egypt, faunal assemblages clearly display facies-related distribution. In the western areas, shallow-water carbonate silts were inhabited by *Miogypsina* and *Spiroclypeus*,

² Material described by Prokofiev (2001, 2002) from the Miocene or Oligocene of the Apsheron Peninsula (Azerbaijan) is a mixture of Late Oligocene and Early Miocene taxa. The Late Oligocene admixture is present in both associations studied. For example, in the coastal pelagic assemblage of Apscheronichthys-Leiognathus-Scomber (Prokofiev, 2001), composed of Clupeidae indet., Palaeomolva monstrata, Pseudoraniceps sp., Pseudoraniceps parcus, Apscheonichthys bogatshovi, Pelates islamdagicus, Priacanthus artus, Leiognathoides minutus, Selar cf. quassus, Scomber cubanicus, and Bestiolablennius eugeniae, such species as Apscheonichthys bogatshovi, Selar cf. quassus, Scomber cubanicus, and Priacanthus artus come from the Late Oligocene. The later assemblage of Hemithyrsites-Lednevia-Pinichthys, including Clupeidae indet., Palaeomolva, Pseudoraniceps, Priacanthus artus and containing also Merluccius lednevi, Nerophis gracilis, Percoidei indet., Lednevia oligocenica, Hemithyrsites maicopicus, Lepidopus sp., cf. Abadzekhia sp., Pleuronectoidei indet. and the mesopelagic Pinichthys fractus (Stromateoidei, Perciformes) and Glossanodon sp. nov. (Argentiniformes), has a Late Oligocene admixture of Abadzekhia sp.

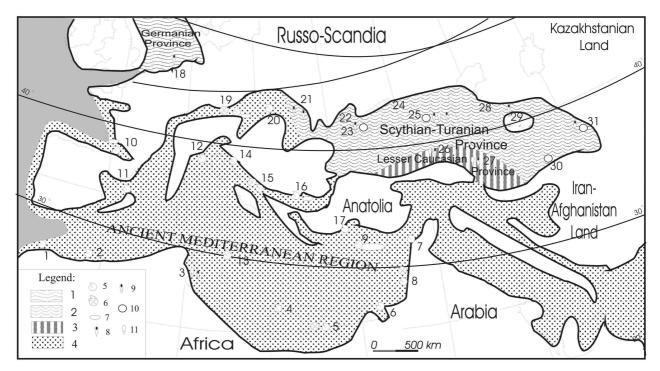


Fig. 6. Schematic zoogeographic zonation of the Early Miocene shelf areas based on foraminifers. Designations: (1–2) North European Region with moderately warm-water fauna of foraminifers with the lack of the most warm-water taxa: (1) Germanian Province and (2) Scythian-Turanian Province; (3) Lesser Caucasian Province, lacking larger foraminifers, containing species shared with the Mediterranean, and having up to 40% of endemic species; (4) Ancient Mediterranean Region, including diverse warm-water assemblages of foraminifers: (5) larger foraminifers (*Miogypsina, Miogypsinoides, Heterostegina, Lepidocyclina*, etc.); (6–11) characteristic genera with wide geographic range: (6) Amphistegina, (7) Almaena, (8) Caucasinella elongata, (9) Caucasina, (10) Saccammina, and (11) Virgulinella. Localities of the Early Miocene foraminiferal associations considered in the present study: (1) Morocco, (2) Algeria, (3) Tunis, (4) Libya, (5) western Egypt, (6) eastern Egypt, (7) Syria, (8) Israel and Lebanon, (9) Cyprus, (10) Aquitanian Basin, (11) Balearic Islands, (12) northern Italy, (13) Malta Island, (14) Croatia and Slovenia, (15) Albania, (16) Greece, (17) Turkey, (18) Germany, (19) Austria, (20) Slovakia, (21) Carpathians, (22) North Black Sea Depression, (23) Crimea, (24) eastern Sea of Azov Region and Manych Region, (25) northern Caucasus and Ciscaucasia, (26) Georgia, (27) Lesser Caucasus, (28) Mangy-shlak, (29) Kara Bogaz Gol Region, (30) western Kopet Dagh, and (31) southern Aral Region.

and reef communities with *Miogypsina* and *Amphistegina* were recorded, while in the coastal zone of the southern areas, *Elphidium* and rotaliids probably appeared for the first time (Krasheninnikov, 1971, textfig. 48). In the Suez Canal and adjacent regions, *Miogypsina* and *Miogypsinoides* were recorded, and the small benthos was represented by at least 15 widespread genera.

Krasheninnikov (1971; Krasheninnikov *et al.*, 1999) thoroughly studied foraminifers from Syria. Relatively deepwater shelf areas were occupied by a particularly diverse fauna. Benthic forms composed a small proportion of assemblages, which comprised more than 300 species. Among the species mentioned in that study, 23 belong to 13 agglutinating genera and 95 belong to 57 secreting genera, most of which occur in other regions of the Mediterranean. Areas that had only limited contacts with the oceans (Mesopotamian type of facies) were inhabited by earlier known thermophilic genera *Dendritina, Borelis, Peneroplis*, and *Meandrospira*, which commonly occurred in beds on carbonate platforms. *Elphidium, Florilus*, and *Ammonia*, which are tolerant of lower salinity, probably expanded

in coastal areas. The larger foraminifers are represented by small lepidocyclines, *Miogypsina*, and *Miogypsinoides*. Israel and Lebanon were also inhabited by *Lepidocyclina*, *Operculina*, and *Amphistegina*, while *Miogypsina* and *Miogypsinoides* occurred in Cyprus.

In southern France (Aquitanian Basin), benthic assemblages included numerous *Miogypsina*. The smaller foraminifers are represented by 33 genera (Krasheninnikov, 1971), as in the Mediterranean; some of these taxa are also present in the Eastern Paratethys. *Lepidocyclina* expanded its range in southeastern Iberia. In the Burdigalian of neritic facies of the Balearic Islands, *Miogypsina, Miogypsinoides, Operculina*, and *Heterostegina* were recorded. In both shallow-water and relatively deepwater areas, the small benthos was represented by diverse assemblages, some species of which were in common with Syria.

In northern Italy, the larger foraminifers *Lepidocyclina, Operculina, Miogypsina*, and *Miogypsinoides* were recorded. The small benthic group from both northern and central Italy includes genera in common with the eastern Mediterranean. Coralline limestones with *Miogypsina* and *Miogypsinoides* were found in

Malta. *Miogypsina* and *Lepidocyclina* are also known from Croatia and Slovenia. The flysch beds in Albania are rich in arenaceous foraminifers from the same genera as in the same deposits in the Carpathian Foredeep. At the same time, Heterostegina, Miogypsina, and Amphistegina and diverse small benthic forms occurred in shallow-water areas. Bioclastic limestones with Lepidocyclina, Miogypsina, Miogypsinoides, Operculina, Heterostegina, and small benthos, including Almaena escornebovensis, were widespread in Greece. In the northwest, the roof of flysch deposits yielded Lepidocyclina and Miogypsinoides, while Miogypsina and Almaena escornebovensis were recorded in Physsalia. Deposits formed under deeper water conditions in Turkey contain plankton; in addition, limestones composed of algae and corals, which contain *Heterostegina* (three species), occur in places.

Northwestern Europe. No larger foraminifers have been recorded in northwestern Europe. The small benthos from Zone B7 was of low diversity, since it had lost the genera Robertina, Patellina, Rotalia, Svratkina, Palmula, and some other genera. Bitubulogerina kasselensis, Virgulinella pertusa, Fursenkoina schreibersiana, and the genera Steinforthia and Stilostomella persisted for some time. The newly emerging forms included Asterigerina staeschi, Uvigerina tenuipustulata, Elphidium inflatum, which were absent from the Eastern Paratethys and the Mediterranean Region, and Caucasinella elongata (a zonal species of the Eastern Paratethys), which was cosmopolitan. The fauna from this region differed considerably in generic and species composition from the fauna of the Paratethys and Mediterranean, and these differences may not be reduced to facial conditions or climatic zonation.

Carpathian Basin. The Carpathian Basin was connected to the Mediterranean and remained very warm, which is evident from the presence of the larger foraminifers Heterostegina, Amphistegina, and Almaena osnabrugensis in its western part (Austria) (Anleitung zur biostratigraphischen..., 1970; Cicha et al., 1998) and the genera Miogypsina and Miogypsinoides in the eastern part (Slovakia) (Papp, 1960). To the east of these regions, the faunal composition was different. In the Polish Carpathians, the small benthos is represented by Bolivina fastigia (Cicha et al., 1998). In the Transcarpathian Deep, in the molassed strata dated as basal Miocene (Negrovskaya Formation) foraminifers are virtually absent (*Neogene System...*, 1986; Venglinskii, 1975). Diverse assemblages (65 species of 37 genera) appeared only in the Burdigalian and were dominated by calcareous taxa, while arenaceous foraminifers were represented by only eight genera. The widespread Caucasinella elongata and a few species known beyond the Carpathian Basin first appeared.

At the end of the Burdigalian, noncarbonate clayey deposits with salt lenticles and interbeds of coarsegrained rocks (Verkhnie Vorotyshchi Formation) were formed. They contain radiolarians, spicules of sponges,

isolated shells of arenaceous foraminifers, small globigerines, and cassigerinellas. Such changes in faunal composition and lithological structure are evidence of chemical alterations in the water. According to L.S. Pishvanova (in Maikopian Beds..., 1964), these changes occurred because the basin in the Carpathian Foredeep became closed. In the Carpathian Foredeep, 32 genera were recorded. Many species that emerged at that time persisted subsequently and composed a typical Middle Miocene fauna (Pishvanova, in Maikopian Beds..., 1964). Out of 40 species composing this fauna, 40% were endemic. They belong to the genera Spiroplectammina, *Siphonodosaria, Porosononion, Cibicidoides (two species), Elphidium, *Baggatella (three species), *Buliminella, Uvigerinella, Caucasina, *Reussella, Fursenkoina, and Bolivina (two species); the genera marked by asterisks have not been recorded in the Eastern Paratethys. Larger foraminifers are represented only by *Lepidocyclina* (in the Stebnik Formation).

Eastern Paratethys. The foraminifer composition in the Eastern Paratethys differed from that of the Mediterranean and Carpathian faunas. The fauna from the central Ciscaucasian area of the basin was especially thoroughly studied (materials and publications of A.K. Bogdanovich, L.S. Ter-Grigorjantz, and others; *Neogene System...*, 1986). In the Karadzhalginian and Olginskaya time, this region was inhabited by an impoverished assemblage with *Caucasinella elongata*, which included both transitional and newly emerging (*) species: the arenaceous *Hyperammina caucasica, Haplophragmoides spp., and *Trochammina vera and the secreting *Caucasinella elongata, *Cibicidoides stavropolensis, *Astrononion ergenicus, Porosononion dendridicus, Elphidium onerosum, Bulimina tumidula, Uvigerinella californica, and Bolivina floridana. Many species occurred over the whole of the basin. In the Kotsakhurian, foraminifer assemblages were sharply impoverished and contained Saccammina (S. zuramakensis, S. suzini, and S. ovalis) and Ammodiscus tenuiculus (beds with Saccammina zuramakensis, Ritsa Formation).

The Tarkhanian Fauna (Kuvinskie, Terek, and Argun beds) was much more diverse due to immigrant genera and species from the Carpathian Basin and, to a lesser extent, from the Mediterranean (along with plankton) and local taxa. The benthic assemblage includes at least 18 genera, a third of which have not been recorded in other regions of the Eastern Paratethys. In general, this fauna is composed of stenohaline species and taxa that are tolerant of various deviations from normal marine salinity (diverse miliolids, nonionids, and *Ammonia*).

The data on foraminifers from other regions are rather scarce (*Neogene System...*, 1986). *Bolivina goudkoffi caucasica, Caucasina buliminoides* (Bogdanovich and Bugrova, 1987), and local representatives of the genera Virgulinella and Uvigerinella appeared in western Ciscaucasia (Alkun Formation). Later (Voskovaya Gora Formation), assemblages with *Caucasinella elongata* and, then, the arenaceous foraminifer assemblage with *Saccammina zuramakensis* and *S. ovalis*, containing the same species as in central Ciscaucasia, became widespread. The eastern Ciscaucasian part of the basin has yielded *Saccammina variabilis*, *Hyperammina caucasica*, *Porosononion dendridicus*, and *Uvigerinella californica* (the presence of which does not exclude the assignment of some strata of the section to the terminal Oligocene). At that time, the adjacent areas of the Caspian Sea were inhabited by *Caucasinella elongata*, *Bulimina tumidula*, *Cibicidoides stavropolensis*, and *Porosononion dendridicus* (recorded in the Upper Maikopian beds).

The foraminifer assemblage from the North Black Sea Depression is rather scanty and consists of widespread species, including forms known in the northern Caucasus, such as *Elphidium onerosum*, *Nonion granulosum*, *Porosononion dendridicum*, and others (Veselov, 1968; *Neogene System...*, 1986). The presence of *Quinqueloculina*, *Ammonia*, and nonionids suggests a relatively low salinity in this part of the basin. The Crimean part was inhabited by *Caucasinella elongata*, *Elphidium onerosum*, *Porosononion dendridicum*, *Bulimina tumidula*, *Fursenkoina schreibersiana*, and *Cibicidoides stavropolensis*. Later, isolated *Saccammina* also appeared (Korolevo Formation, see *Neogene System...*, 1986, Nosovskii, 1993).

At the onset of the Miocene, the Sea of Azov and Manych regions were occupied by a shallow basin. In the eastern part the Azov Region, the scanty foraminifer assemblage included *Caucasinella elongata* (Konenkova, 1984). *Caucasinella elongata, Cibicidoides stavropolensis, Uvigerinella californica,* and *Bolivina plicatella,* which occurred in the northern Caucasian part of the Paratethys, and the endemic *Astrononion ergenicum* appeared on the Ergeni Highland and Sal–Manych interfluve (in Tsagankhak Formation) (Nikitina, 1971).

Transcaucasia. The Sakaraul Basin of western Georgia yielded a diverse foraminifer assemblage composed of 37 species of 17 genera: Spiroplectammina, Quinqueloculina, Lagena, and Entosolenia (three species in each), Discorbis (three species), Nonion, Porosononion, Melonis, Elphidium (five species), Virgulinella, Caucasina (two species), Bolivina (six species), etc. (Kacharava et al., in Paleogene Beds..., 1960; Dzhanelidze, in Maikopian Beds..., 1964). Only a few species are in common with the faunas from the northern Caucasus and other regions (Spiroplectammina caucasica, Porosononion dendridicum, Elphidium onerosum, Bulimina tumidula, and Virgulinella pertusa), and 40% of the assemblage are endemic forms. Similar faunal compositions were observed in the foraminifer assemblages from Abkhazia (26 species of 13 genera) and eastern Georgia (ten genera) (Archvadze, in Maikopian Beds..., 1964). Nonion depressu*lum* and *Uvigerina auberiana*, recorded in the Central Paratethys, were also present in the vicinity of Tbilisi. In the Kotsakhurian beds of Georgia, a microfauna has not been discovered. The Tarkhanian beds and other areas yielded a new marine fauna with plankton.

To the east, in the Azerbaijan part of the basin, a poor foraminifer assemblage was observed (Khalilov, 1962; Khalilov and Kuznetsova, in *Maikopian Beds...*, 1964; Khalilov and Mamedova, 1984). It includes *Caucasinella elongata* (a local subspecies), *Bulimina tumidula, Virgulinella, Bolivina*, etc. Its generic and partially species composition was the same as in the Ciscaucasian fauna and some species were also recorded in Georgia. The piedmont areas of the Lesser Caucasus (where the Oligocene and Miocene beds are difficult to differentiate) yielded *Quinqueloculina gracilis* and *Q. akneriana*, which also occurred in the Central Paratethys.

Turanian Basin. At the onset of the Early Miocene, the maximum transgression was observed in the Transcaspian Region, so that the sea basin entirely occupied the Fore-Kopet Dagh Depression and entered the Zaunguz Kara Kum, the southern Aral Region, and the central Kyzyl Kum (Voronina *et al.*, 1993, text-fig. 2). The areas newly covered by shallow water and coastal sites characterized by terrigenous sedimentation were unfavorable environments for foraminifers, in particular, those with lowered salinity. Subsequently, beds with foraminifers underwent considerable erosion and were only preserved in isolated sites; therefore, their faunal composition and ranges of particular genera and species were judged based on rather fragmentary data.

The foraminifer assemblage from the southern Mangyshlak Peninsula (Kashkarata Formation) is somewhat more diverse than those of other regions. In addition to the species known from earlier strata (genera Uvigerinella, Porosononion, Elphidium, etc.), this fauna includes shallow-water miliolids (Quinqueloculina and Triloculina). In the northwestern part, the proportion of marine taxa becomes higher (Dentalina, Cibicidoides, Pseudoparrella, and polymorphinids) (Mikhailova, 1968; Neogene System..., 1986).

In western Turkmenistan, small numbers of foraminifers are known from the northern part of the Karabogaz Region and the Krasnovodsk Peninsula. This assemblage includes the widespread species *Cibi*cidoides stavropolensis, Porosononion dendridicum, Florilus boueanus, Caucasinella elongata, and Bolivina tarchanensis (Rozyeva and Lapteva, 1975; Neogene System..., 1986; unpublished data by E.K. Shutskaya; etc.). The impoverished assemblage from the basal Miocene of the western Kopet Dagh is composed of Quinqueloculina, Porosononion, Elphidium, and Rota*lia* (*Neogene System...*, 1986), which are characteristic of basins with lowered salinity. Subsequently, a marine fauna, including *Cibicidoides stavropolensis*, appeared in this region (Rozyeva and Lapteva, 1975); later, Saccammina zuramakensis was present in analogues of the Kotsakhurian in the southwestern Kopet Dagh; at the

end of the Early Miocene, rare *Globigerina* ex gr. *tarch-anensis* occurred in this area and in the West Turkmenian Lowland.

In the southern Aral Region (upper beds of the Daryalyk Formation), the foraminifer assemblage contained Oligocene relicts along with species characteristic of the Early Miocene: *Porosononion dendridicum, Caucasinella elongata*, and *Saccammina zuramakensis* (Averburg, 1970; Voronina *et al.*, 1993). In the Kyzyl Kum, E.F. Tsatsir discovered the Tethyan genus *Discorbinella*, which suggests that the basin had southern contacts in the Early Miocene. However, this genus has not been recorded in other regions of the Paratethys.

In the North Ustyurt Depression, the Miocene assemblage from the Aral Formation (Prusova, in *Maikopian Beds...*, 1964) contains *Cibicidoides ornatus, Elphidium onerosum, Porosononion dendridicum* (also known from the Oligocene), and rather numerous miliolids (*Quinqueloculina*, including a local species, and *Triloculina*).

Biogeographic Zonation Based on Benthic Foraminifers

The data on the composition and distribution of foraminifers suggest that, in the Early Miocene, the Ancient Mediterranean and North European paleobiogeographic regions still remained. The boundary between them corresponded to the northern boundary of the range of larger foraminifers, as in the Oligocene (Fig. 6).

Ancient Mediterranean Paleobiogeographic Region. The thermophilic aquatic subtropical fauna was spread on the southern shelf (from Morocco to the Suez Gulf), in the eastern Mediterranean, and the Aquitanian Basin; it was recorded in southeastern Spain, the Balearic Islands, the whole of Italy, Sicily and Sardinia, and coasts of the Adriatic, Ionian, and Aegean seas.

Larger foraminifers were the most typical group of the Mediterranean Region. As compared to the situation in the Oligocene, the role and species diversity of *Lepidocyclina* decreased, *Operculina* almost completely disappeared, while the genera *Miogypsina*, *Miogypsinoides*, *Heterostegina*, *Spiroclypeus*, and *Grzybowskia* persisted everywhere (as was noted above, their shells were abundant in some localities).

The shallow-water areas were inhabited by thermophilic stenohaline genera of smaller benthic foraminifers: *Peneroplis, Archaias, Dendritina, Meandropsina, Spiroloculina, Pyrgo, Rotalia, Stomatorbina, Almaena, Amphistegina,* and *Sphaerogypsina.* Nonionids (*Cribrononion, Nonion, Elphidium, Florilus,* and *Ammonia*) and miliolids (*Quinqueloculina* and *Triloculina*) were tolerant of fluctuations of salinity in nearshore areas. Relatively deeper areas of the shelf were inhabited by agglutinating and secreting taxa of all foraminifer orders. The genera of the order Rotaliida, which had wide geographic ranges (*Discorbis*, Valvulineria, Baggina, Asterigerina, Cibicidoides, Heterolepa, Eponides, and many others), buliminids, and bolivinids (Hopkinsina, Caucasina, Virgulinella, Bolivinella, Bolivina, etc.) were particularly numerous. Nodosariids were rather diverse, whereas they were scarce in the Central Paratethys and almost completely absent from the Eastern Paratethys.

The data on benthic foraminifers are insufficient to judge the provincial differences in their distribution in this region.

The fact that the Carpathian Basin was entirely occupied by larger foraminifers suggests that this area should be assigned to a transitional province of the Mediterranean Region. Its western and central parts were inhabited by four larger foraminifer genera, the genus *Almaena*, and some other thermophilic forms, whereas the Carpathian Foredeep yielded only *Lepidocyclina*, and almost half of its assemblage was composed of endemic forms. Apparently, the Carpathian Foredeep part of the basin should be regarded as a subprovince.

North European Paleobiogeographic Region. Foraminifers from northwestern Europe substantially differed in generic and species composition from the Mediterranean fauna. These differences were associated with the terrigenous pattern of sedimentation in this more cold-water climatic zone. The water temperature was too low for larger foraminifers. The diversity of benthos was also low. Some genera known from the Oligocene disappeared, while the remaining genera gave rise to species that were not present in the Eastern Paratethys and the Mediterranean Region (for example, the genera Asterigerina, Uvigerina, and Elphidium). The widespread species include *Caucasinella elongata*, which was present in both territories. Based on the list of foraminifers, the basin of northwestern Europe should be referred to as the Germanian Province of the North European Region.

Another province is composed of the basins in the area of the Eastern Paratethys, which at times had limited contacts with open seas. Benthic foraminifers were rather diverse in the basins with normal salinity (Caucasinella elongata Zone), in the areas where a local decrease in salinity was not observed. In addition to the species inhabiting almost the whole of the Eastern Paratethys, foraminifer associations included species with small (probably incompletely known) ranges, such as Bulimina tumidula, Cibicidoides stavropolensis, Porosononion dendridicum, Elphidium onerosum, Sac*cammina* spp. etc., which were absent from both the Mediterranean and North European regions. In some areas, endemic forms were recorded (for example, Astrononion ergenicum, which occurred in the Kuban Lowland, the Ergeni Highland, and Sal–Manych interfluve).

The similarity in generic (and partially species) composition of smaller benthic foraminifers with the fauna from the North European Basin, and the absence of larger foraminifers in these regions suggest that the Eastern Paratethys be assigned to the North European Paleobiogeographic Region. The differences in species and, partially, generic composition correspond to the provincial levels (i.e., the **Scythian–Turanian** Province is recognized).

Lesser Caucasian Province. This province of the North European Region includes Georgia and Azerbaijan. A few species were in common with the north Caucasian part of the basin, while about 40% of the assemblage were endemic forms. As in the whole of the Eastern Paratethys, larger foraminifers and other thermophilic genera characteristic of the Mediterranean were absent from the area under consideration. Smaller benthic foraminifers include the euryhaline genera *Nonion, Porosononion, Melonis,* and *Elphidium.* In addition, *Spiroplectammina, Lagena, Discorbis, Cibicidoides, Bolivina, Bulimina,* etc., i.e., genera characteristic mainly of northern Europe and deepwater (that is, more cold-water) areas of the Mediterranean have been recorded.

The fauna from the eastern (Azerbaijan) part of the Transcaucasian Basin displayed the same generic composition as the Ciscaucasian fauna; however, some species also occurred in more westerly areas (known from Georgia). At the same time, this region was inhabited by a series of endemic taxa (a local subspecies of *Caucasinella elongata*, and members of *Virgulinella* and *Bolivina*). *Quinqueloculina gracilis* and *Q. akneriana*, known from the Central Paratethys, were also recorded.

Mollusks

The changes initiated by global warming resulted in a substantial increase in the diversity of mollusk assemblages and a reorganization of their composition in the basins of the Mediterranean Region, western and central Europe, and the Eastern Paratethys, which manifested themselves in full measure in the Burdigalian. The composition and dominant taxa substantially changed in both bivalves and gastropods. From the onset of the Miocene, a large number of species emerged, that persisted up to the present day; taxa characteristic of the Miocene such as venerids, pectinids, mitilids, lucinids, and cardiids (bivalves) and the trochids, neritids, cerithiids, and nassariids (gastropods) became widespread. The species that were limited in the Chattian to the southern (i.e., warmest water) assemblages became widespread. The composition of Aquitanian mollusk assemblages was everywhere transitional between the Oligocene and Burdigalian ones. Because it is difficult to date some assemblages from this stratigraphic interval, they are sometimes referred to as Aquitanian–Burdigalian. Nevertheless, the results obtained reflect mainly the distribution of mollusks characteristic of the Burdigalian, since assemblages of this age are substantially more diverse and more widespread, in particular, in southern Europe.

North Africa. Lower Miocene mollusks are known from Algeria (Freneix et al., 1974). This is a relatively poor bivalve assemblage, comprising 30 species of 24 genera and subgenera; however, it is rather representative. It is undoubtedly a warm-water assemblage; however, members of tropical genera are almost absent (except for *Trisidos*). Only a few endemic species are present, while a dominant role is played by the Miocene and Oligocene species of Tethyan origin, which expanded widely over the area considered at the beginning of the Miocene. Species that first appeared in the Lower Miocene but became widespread in the Middle Miocene (Anadara turonica, Clausinella basteroti, Dosinia lupinus, etc.) were described. All species from this assemblage, except for several forms, are also found in the extremely diverse mollusk assemblage of Aquitania, many common taxa are also recorded in the mollusk fauna from Portugal (Fig. 7).

Northern Mediterranean. The data on northern Italy are based mostly on early studies (Sacco, 1887–1904; Accordi, 1955; Piccoli *et al.*, 1977), where dating is not always reliable, and on data on occurrences of particular species in other regions. The list of bivalves consists of about 70 species, but it needs improvement. Judging from these data, mollusks recorded in Italy and Spain mostly belonged to species and genera characterized by wide geographical ranges. The similarity with the basins of central Europe is rather high (C_P = 0.67–0.78).

Eastern Atlantic. The mollusk assemblage from the Aquitanian Basin, which contains stratotypes of the Aquitanian and Burdigalian (Cossmann and Peyrot, 1909–1914), resembles the above considered faunas; however, it is much more diverse, including a total of 360 bivalve species of 184 genera and subgenera. The extremely high faunal diversity, the presence of many large taxa, giant pectinids, the tropical genera *Trisidos, Cardium* sensu stricto, *Bucardium*, and *Discors*, various lucinids and venerids suggest a very thermophilic pattern of this fauna. Naturally, many species from this rich fauna have not been recorded in any other regions or in earlier deposits (65%); however, many became widespread as early as the second half of the Early Miocene.

The Burdigalian mollusk assemblage from Portugal is relatively poor, containing about 50 species (Dollfuss *et al.*, 1903–1904). It includes a high proportion of widespread species, but it mostly agrees with the much more diverse fauna from Aquitania.

North Sea Basin. Representative assemblages of Lower Miocene mollusks are known from northern Germany (Kautsky, 1925; Anderson, 1959; Hinsch, 1972) and the Netherlands (Janssen, 1984). Bivalves from the Hemmorian, corresponding to the Burdigalian, are particularly diverse. The Vierlandian fauna was transitional. As in other regions, many thermophilic groups characteristic of the Miocene appeared in this fauna. Anadara diluvii, Venus multilamella, Pitar rudis, Acanthocardia, Dosinia, etc., which distinguish this

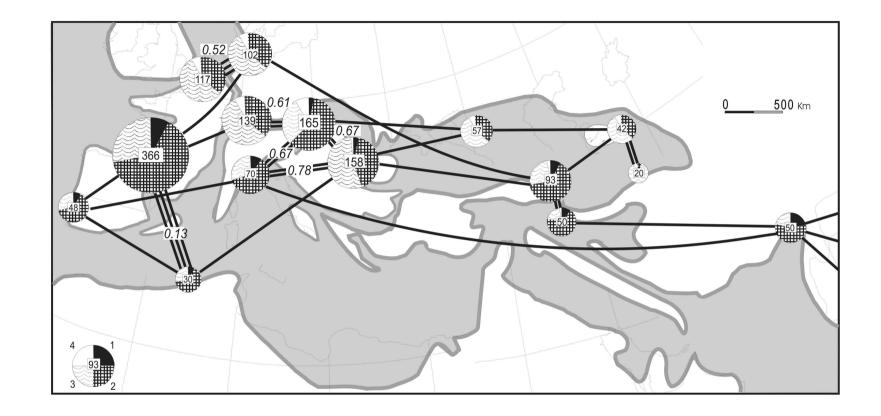


Fig. 7. Circular diagrams of diversity and degree of thermophilic adaptations of the main bivalve assemblages in the Early Miocene. The area of circles is proportional to the number of species in an assemblage (shown as a figure in the center of a circle); the area of sectors reflects relative proportion of species of certain biogeographic zone: (1) genera with exclusively tropical distribution of extant species, (2) tropical–subtropical genera, (3) genera of wide distribution, and (4) genera of boreal distribution. Connecting lines show a degree of similarity between assemblages according to the threshold values of the Preston's index (Popov, 1994; Popov *et al.*, 2001). The gray line stands for the land–sea boundary.

assemblage from those of the Oligocene, occurred as early as the Vierlandian. However, the proportion of species inherited from the Oligocene was relatively high in the Vierlandian [in the boreholes in northern Germany, more than 70% (Hinsch, 1972)]. In the Hemmorian, mollusk assemblages were even more enriched by thermophilic taxa, and the proportion of species belonging to the subtropical genera composed about 30%. Atrina, limids, diverse lucinids, Cardium sensu stricto, and others were recorded in this region. The proportion of species known from the Oligocene decreased to 40%. Along with widespread Miocene species and genera, these assemblages include many endemic forms, which have not been found beyond northwestern Europe. The Netherlands assemblage is unique, which is attributable not only to the primary composition of this fauna but also to preparation techniques, preservation, and the extent of understanding: many small, thin-walled forms, which usually escape examination in the fossil state, have been described from this area.

Carpathian Basin. Upper Egerian mollusk associations were still similar to Late Oligocene assemblages, so that Báldi (1973) proposed that they were impossible to distinguish with confidence, although he indicated that they contained a considerably higher proportion of Mediterranean forms.

Eggenburgian assemblages from Romania, Hungary, Slovakia, Upper Bavaria, and Austria are diverse and similar to one another ($C_P = 0.54-0.67$). Almost half of the species recorded there are the same as in the assemblages from southern Europe, most of the species belong to thermophilic Tethyan genera. At the same time, they include specific forms, so that more than a third of bivalve species (36%) have not been recorded outside central Europe. Most species in common with the assemblages from the North Sea Basin were inherited from the Oligocene, while a few Miocene species were characterized by extremely wide ranges. Species in common with the mollusk assemblages from Transcaucasia and Ukraine also include many Oligocene forms; however, some species first appeared in the Miocene and were not recorded outside the Paratethys (Laevicardium spondyloides, Acanthocardia grandis, Fragum semirugosum, Glossus maior, Callista lilacinoides, etc.). The Eggenburgian fauna was mostly composed of species that appeared in the Miocene, while the proportion of Oligocene species was approximately 30%.

Greater Caucasian–Kopet Dagh Basin. Mollusk assemblages from the southern shelf are only known in Transcaucasia (Kartli, Georgia), as was in the Oligocene. At the beginning of the Early Miocene, they were similar in composition [known from the Upper Uplistsikhe Subformation: 26 bivalve species and seven gastropod species (Kurtskhaliya, 1982; Popov *et al.*, 1993)] to those from the Chattian (Lower Uplistsikhe Subformation) and differed in the presence of more thermophilic genera and species, i.e., *Arca, Barbatia*

(Obliquarca), Isognomon, Ctena, Arcopagia, Cardita calyculata, Cerithium, Nassarius, and Olivia flammulata.

The mollusk assemblage from the Burdigalian of Sakaraul (Georgia) is more representative, including 90 bivalve species and more than 50 gastropod species (Kharatishvili, 1952; Amitrov, 1973, Popov et al., 1993), although the currently known species do not reflect the actual diversity of this fauna. The large sizes and relatively high diversity of mollusks, the presence of subtropical and some tropical genera suggest that this is a thermophilic assemblage. The species characterized by wide geographical ranges included many forms common with the Eggenburgian of central Europe (more than 35%); however, only few species not known in the Eggenburgian were in common with the Burdigalian faunas from the Mediterranean Region and Aquitania. At the same time, the Sakaraulian Fauna contains many allochtonous species, which are tentatively considered to be endemic. The extent of continuity of this fauna with reference to the Oligocene fauna is approximately the same as in the Eggenburgian fauna (about 40%).

A mollusk assemblage from the northern shelf that probably existed in the Aquitanian is known from the Sivashi Subformation of Ukraine (Popov et al., 1993; Amitrov, 1995). Because of poor preservation (molds and imprints in loose sandstone), many forms from this assemblage are determined only approximately (with cf.) or to genus. Nevertheless, this assemblage undoubtedly includes many thermophilic genera and species (Atrina, Isognomon, Divalinga, Europicardium, Venus cf. multilamella, Callista lilacinoides, Glycymeris pilosa deshayesi, and Glossus maior), which displays its similarity to the Upper Egerian mollusk faunas of central Europe. Relatively high coefficients of dissimilarity between these faunas and the Sivashi Assemblage are attributable to the fact that, out of 57 bivalve forms, only 28 are determined to species and only about ten gastropod species have been identified. A large proportion of this fauna is composed of species that persisted from the Oligocene, including forms endemic to the Eastern Paratethys (Plagiocardium abundans, Cerastoderma prigorovskii, and Sphenia nana).

The mollusk assemblage from the Olginskaya Formation of Ciscaucasia comes from clayey facies. It is rather poor (25 bivalve species), almost without thermophilic taxa, and cannot be compared with the other faunas under consideration because of differences in facies and biotopes (deeper-water community). Thus, the shallow-water Burdigalian assemblages from sandy host rocks, which provide the main diversity of mollusks, have not been found in the sections on the northern shelf of the Eastern Paratethys.

Mollusk assemblages from the Kyzyl Kum, southeastern Turkmenistan, and Tajikistan have a rather poor taxonomic composition (altogether comprising 42 bivalve species) and are poorly preserved. They are similar to

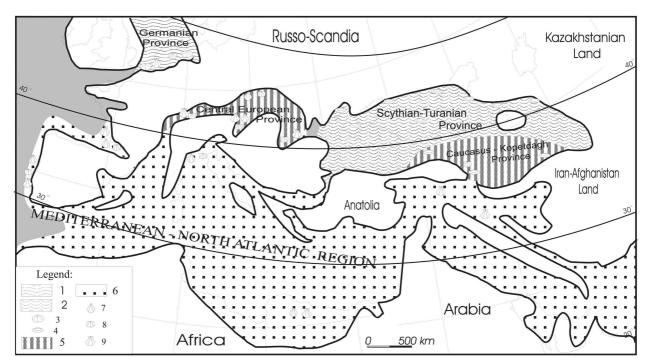


Fig. 8. Schematic zoogeographic zonation of the Early Miocene shelf areas based on mollusks. Designations: (1, 2) Area that still belonged to the North European Region in the Aquitanian, (1) Germanian Province with moderately warm-water molluskan fauna with the lack of most warm-water taxa and the presence of characteristic endemic species: (3) Astarte angulata and Laevicardium dingdense, (2) Scythian–Turanian Province with poor fauna, including characteristic endemic species: (4) Callista uretzkii and Plagiocardium abundans; (5) Central European and Caucasian–Kopet Dagh provinces of the Mediterranean–North Atlantic Region, with diverse assemblages of the Eggenburgian and Sakaraulian, including tropical taxa; (6) Mediterranean–North Atlantic Region not divided into provinces, with fauna including diverse warm-water mollusk assemblages with characteristic genera: (7) Lima and Spondylus; (8) Cardium sensu stricto, and (9) Pecten sensu stricto.

the Sivashi Assemblage from Ukraine in generic composition, zoogeographic characteristics, and, probably, age. The thermophilic genera and species, such as *Atrina, Isognomon, Megaxinus, Glycymeris pilosa deshayesi, Venus* sp., and *Callista lilacinoides* (absent from the Chattian associations of the Eastern Paratethys), are also present in these assemblages.

Zoogeographical Zonation Based on Mollusks

A trend toward leveling out of biogeographical differences was observed in the basins of western Eurasia as early as the Chattian and continued to develop in the Miocene. The similarity in malacofaunas is especially clearly pronounced between the basins of central Europe and between these and the faunas of the Mediterranean part of the Tethys, including the coasts of North Africa and the basins of Portugal and Aquitania, which were open in the Atlantic Basin. In the Burdigalian, assemblages from the North Sea Basin of northwestern Europe became rather similar to the Tethyan faunas. The Germanian Province gradually lost its distinctions in the Early Miocene, as the species inherited from the Oligocene were replaced by migrants from the eastern Atlantic and Mediterranean regions. Species having very wide, global distribution in the Early Miocene included both Oligocene and newly emerging Miocene taxa. A large proportion of Miocene species persist up to the present time.

Against this background, the differences of the faunas from the Eastern Paratethys are probably increased by the incompleteness of available data, erroneous identifications, and by the fact that they come from different facies and may differ somewhat in age. At the onset of the Burdigalian (Eggenburgian, Sakaraulian, Hemmorian), mollusk faunas in the entire area under study, including the whole of the Paratethys, became rather similar, so that they are assigned to a single Mediterranean–North Atlantic Zoogeographical Region (Fig. 8).

The North European Region, which was recognized beginning from the Mesozoic, probably ceased to exist in the Burdigalian. The faunal composition and zoogeographical relationships of the basins of northern and eastern Europe substantially changed, since the westto-east migrations, which were characteristic of the Paleogene, became impossible because of the loss of meridional paleogeographical links. Each basin received members of the more thermophilic Tethyan fauna. The South European–North African Province, including the coasts of the eastern Atlantic Basin up to Aquitania, was the largest province with a subtropical fauna. In the Late Egerian and Eggenburgian, the basins within the Carpathians and in the Alpine Foreland Basin had rather similar mollusk faunas dominated by Mediterranean taxa; therefore, they are assigned to the Central European Subtropical Province of the Mediterranean–North Atlantic Region. In the Eggenburgian, this fauna included individual tropical members.

The data on the fauna from the northern part of the Eastern Paratethys (which belonged to the Scythian– Turanian Province in the Oligocene) are extremely scarce. At the very beginning of the Miocene, this province probably remained independent and continued to belong to the North European Region. It was distinguished from central European faunas by endemic species inherited from the Oligocene.

There are no data on later (Sakaraulian) shallowwater mollusk faunas from the northern part of the Eastern Paratethys. A new province (Caucasian–Kopet Dagh) of the Mediterranean–North Atlantic Region was probably formed in the southern part of the basin. Along with western contacts with the ocean, it had additional links, which were probably located in the south and connected the basin to the eastern Turkish and Iranian basins. Currently available data on the fauna from the Kopet Dagh part of this province are extremely scarce.

CHAPTER 3. EVOLUTION OF THE BASIC MARINE BIOCHORES AT THE TRANSITION FROM THE PALEOGENE TO THE NEOGENE

In previous sections, we attempted to reconstruct the distribution of the main faunal and floral groups during long intervals of geologic time, lasting for millions of years, and paid only little attention to biotic changes at the boundaries, or within these intervals. Below, we schematically discuss the succession of the distribution of biotas from the Eocene to the beginning of the Miocene and evolution of the main biochores.

Prior to discussing dynamic aspects of biogeography, we should consider the use of biogeographic terminology in time, with special reference to the developing biochores. The term *Tethys* was introduced by E. Suess in 1893 to designate the Mesozoic latitudinally extended equatorial sea basin and was used mainly as the paleogeographic name of an ocean or a vast sea that existed from the Carboniferous to the Paleogene (for review, see Naidin, 1986). The biogeographic term Tethyan Region or Realm was used along with the names Mediterranean Region or Mesogaea and was also applied mainly to Mesozoic faunas. It is frequently thought that the term Tethys Realm was introduced by E.G. Kauffman (1973), who proposed it to designate the Mesozoic circumequatorial faunas established primarily based on bivalves, although the names Tethyan Fauna and Tethyan Region were undoubtedly used long before this study. With regard to the Cenozoic, the term Tethys Region was used by

M. Harzhauser *et al.* (2002) and applied up to the middle of the Burdigalian, when the collision of the Afro-Arabian continent with Eurasia gave rise to the continental bridge between Arabia and the system of the Zagros Mountains, which provided a bridge for vertebrate expansion, the *Gomphotherium* landbridge (after Rögl, 1999). However, such reasoning based on paleogeographical events seems to be in error, although it is often used in paleontological studies.

In our opinion, the biogeographic terms applied to both spatial and temporal events should be based on the data on distinctive features of particular biotas, which occupied the area under study, and the same criteria should be used in comparisons in time and space. In other words, we believe that, as biotas change in time, the biogeographic nomenclature should be changed as well. Therefore, even the terms of such a high rank as realm or region proposed for the Mesozoic biota may not be applied to the Eocene-Miocene faunas, since even their generic and familial compositions cannot be compared with those in the Mesozoic. According to the data provided by many researchers, up to 50% of genera and 75% of species existing at the end of the Cretaceous became extinct by the onset of the Paleogene, and the greatest changes occurred in the composition of marine faunas (for review, see Shimanskii and Solov'ev, 1982). The rates of appearance of new taxa were also high. In this context, the use of the name Mediterranean Region, which is associated with the Recent fauna and microflora from the Mediterranean Sea, for Mesozoic and Paleogene biotas seems to be an unfortunate choice. In our opinion, it is also undesirable to use in biogeographic zonation the terms boreal, tropical, etc., which agree with a latitudinal climatic zonation and may be based on essentially different data than analysis of similarities-dissimilarities of assemblages. However, these terms are in common use, in particular, in phytogeography; therefore, it seems impossible to reject them completely.

The Tethyan Basin and the circumtropical current, which provided the similarity between biotas from the Caribbean Region to southeastern Asia, continued to exist in the first half of the Cenozoic. The shelves of this basin were undoubtedly the major centers for the formation of shallow-water faunas. Therefore, taking into account the differences between the Paleogene and Mesozoic biotas, it is probably better to use the term Neotethyan Realm or Supraregion (or Neotethys Realm, Superregion), which includes the Ancient Mediterranean Region, to describe the situation in the Paleogene. Later, as this basin became closed, the sea currents of the World Ocean transformed, and the temperature decreased, the faunal composition substantially changed once again at the end of the Paleogenebeginning of the Neogene, although these changes were not as rapid as at the Cretaceous-Paleogene boundary. The center of the formation of Neogene benthic faunas in the area considered was displaced to the Mediterra-

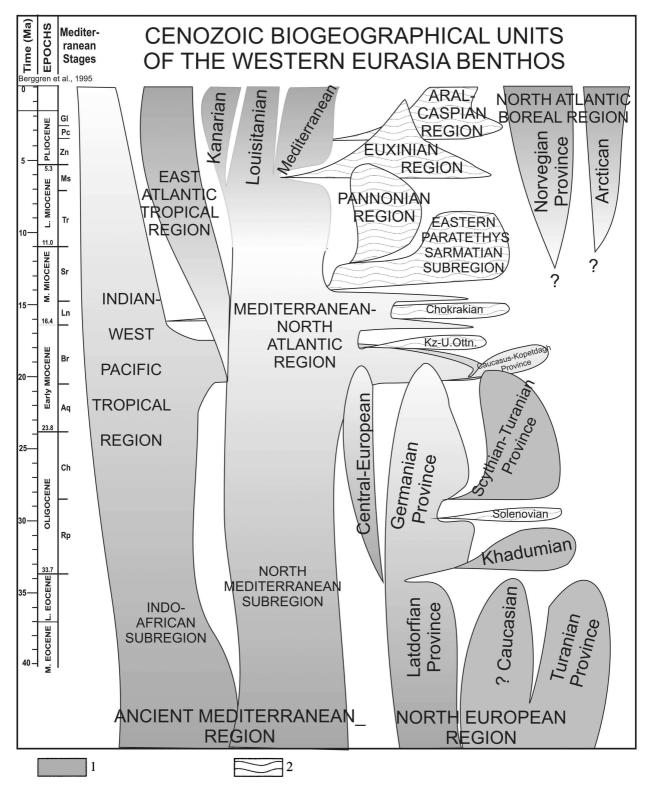


Fig. 9. Schematic diagram of succession of benthos-based biogeographic divisions in shelves of western Eurasia in the second half of the Cenozoic. Designations: (1) marine faunas and (2) hemimarine and brackish-water Paratethyan biotas.

nean and North Atlantic regions. Therefore, from the beginning of the Miocene, we use the term *Mediterra-nean–North Atlantic Region* (Figs. 8, 9).

This raises the question of the time limits in which these biogeographic terms are applicable; however, this question is related to the establishment of such boundaries in space. When comparing a pair of substantially different faunas, one should recognize the time when the most abrupt changes in biotas of large regions occurred and take such moments as the beginning and end of the existence of biochores.

Many researchers have shown that the most significant changes in many benthic groups, zoo- and phytoplankton, and vertebrates occurred at the Cretaceous– Paleogene boundary and coincided with the Maastrichtian–Danian boundary (Russel, 1977; Shimanskii and Solov'ev, 1982; etc.). This was a global transformation that occurred in all latitudinal belts, being particularly well-pronounced in the more diverse faunas of the Tethys. Therefore, these abrupt changes should be indicated as the lower boundary for the application of the terms Neotethys Superregion, Ancient Mediterranean Region, and North European Region.

It is much more difficult to recognize the final boundaries limiting the use of these names. Although it is evident that, from the Paleocene–Eocene to the Miocene, faunas significantly changed, these changes passed several stages and were not simultaneous in different faunal groups and different latitudes. Since these transformations fall within the time framework of the present study, they are considered below in more detail.

The Messinian crisis of salinity and repetitive, probably frequently repeated, colonization of the Mediterranean by the faunas of Atlantic origin show that, by the end of the Miocene, the Mediterranean Region had already lost its position as the center of the formation of marine faunas, and this role had passed to the eastern Atlantic. Therefore, the term North Atlantic Boreal Region, which is frequently used in modern biogeography, is probably correctly applicable beginning from the onset of the Pliocene, when up to 60% of benthic species and 30-40% of plankton species (Dmitrienko, 1993) were represented by Recent species, the generic composition was the same as at the present day, and the order of domination was similar to that in Recent communities. The next significant reorganization in the composition of marine biotas occurred at the end of the Pliocene-beginning of the Pleistocene, when the drop in temperature and the development of glaciation on the coastal shelf of the northeastern Atlantic and Mediterranean resulted in the extinction of 35-40% of bivalve species (Raffi et al., 1985). At the same time, at these boundaries, faunas changed mostly at species level and to a much lesser extent than at the transition from the Eocene to the Miocene, and the more so at the Cretaceous-Paleogene boundary.

Plankton

It was previously shown that the biogeographic distribution of plankton is determined by the climatic zone, paleogeographic relations, and sea currents. Therefore, the true biogeographic zonation is commonly not performed, while the spatial distribution of groups in open basins is discussed in terms of latitudinal climatic belts. At the level of biogeographic regions, we use here the names that are applied to the benthic faunas. Therefore, discussing the evolution of these biochores, one should take into account temporal changes in the taxonomic composition of planktonic groups.

The development of the plankton biota is closely associated with the water circulation in the ocean. In the Cenozoic, it was determined by the transition from the warm biosphere mode (*green house*) with a relatively weak haline type of circulation to the glacial biosphere (*ice house*) with thick cover glaciations, sharp climatic zonation, and the formation of the psychrosphere with a more intense, predominantly thermohaline circulation type.

Under the subtropical conditions of the Ancient Mediterranean Region, changes in complete phyto- and zooplankton assemblages in the Paleogene reflected the general global evolution of these groups. At the end of the Paleogene-beginning of the Neogene, their composition changed substantially but not simultaneously. In particular, an abrupt decrease in the diversity of the diatom flora occurred at the end of the Middle Eocene, when the extratropical zone of the Northern Hemisphere had lost 41 genera of the extremely rich Middle Eocene flora, and only one new genus appeared (Strel'nikova, 1992). The Late Eocene diatom flora from this region was similar in composition to the Middle Eocene flora, but was substantially impoverished. In the Oligocene flora, the role of pennaceous diatoms gradually increased, which reflects a significant reorganization in the floral structure. The Early Oligocene flora inherited from the Late Eocene only 11 transitional genera (31%) and 30 species (36% of the total number of Oligocene species), while six new genera appeared (Strel'nikova in Geological and Biotic..., 1998). In the Early Oligocene, a flora of the transitional type was formed; in the Late Oligocene-Neogene, an essentially new flora dominated by the order Thalassiosirales and the class Pennatophyceae developed. The formation of this flora was accomplished only at the end of the Early Miocene. Subsequently, no mass appearances or disappearances of taxa of generic or species rank were recorded (Gladenkov, 2003). Changes in taxonomic composition were accompanied by profound reorganization of regions of silica accumulation (as compared to the Oligocene), which was determined by changes in water circulation. This was the time when the equatorial, southern, and northern temperate belts of silica accumulation were formed. The last of them was at times situated in the Paratethys.

Nannoplankton assemblages also achieved their maximum diversity in the Middle Eocene, when 120 species were recorded. From the Late Eocene, typical Eocene species of *Discoaster* gradually became extinct; the genus *Chiasmolithus* almost completely disappeared (except for *Ch. oamaruensis*); the species

composition of the genera Sphenolithus, Helicosphaera, Reticulofenestra, and others changed. The zonal scale of the Lower Oligocene is only based on negative characters, i.e., the levels where particular species disappeared. In the Oligocene–Early Miocene, the diversity of nannoplankton remained low, and the appearance of any new genera was not recorded. Typical Neogene species of the genera Discoaster and Sphe*nolithus* first appeared at the beginning of the Miocene, when Oligocene species clearly dominated. They increased in number and diversity from the second half of the Early Miocene; in particular, 35 species were recorded in the northeastern Atlantic (data provided by L.A. Golovina, in Krasheninnikov et al., 1999). The diversity of the Middle Miocene nannoflora was determined by the flourishing of the genus *Discoaster*, which continued to increase in diversity in the Late Miocene.

At the beginning of the Oligocene, more than half of the species of the organic-walled phytoplankton were replaced (Zaporozhets and Andreyeva-Grigorovich in *Geological and Biotic...*, 1998). At the end of the Late Eocene or, in more southerly areas, at the beginning of the Oligocene, many characteristic Eocene species disappeared, while *Phthanoperidinium amoenum*, *Areospheridium pectiniforme*, and *Membranophoridium aspinatum* emerged and became widespread in the Early Oligocene. The most typical genus of the Oligocene of the Mediterranean Basin was *Chiropteridium*, which acquired an almost global range. The number of species in the genera *Spiniferites*, *Operculodinium*, *Systematophora*, and *Deflandrea* increased.

The main changes in this group occurred at the end of the Oligocene-beginning of the Miocene. At this boundary, extinction of Paleogene taxa was particularly clearly pronounced, while the appearance of new taxa was gradual and extended for a long time, throughout at least the first half of the Miocene. The extinction primarily involved the dominant Paleogene groups of covate dinocysts, i.e., Deflandrea (except for small dinocysts from the group Deflandrea spinulosa), Wetzeliella, Kisselevia, etc. The genera Areoligera, Chiropteridium, Enneadocysta, Phthanoperidinium, Thalassiphora, and others almost disappeared in the Neogene. At the same time, taxa that were not numerous in the Paleogene, such as Selenopemphix, Distatodinium, Impagidinium, Operculodinium, Lingulodinium, and Dinopterygium, became dominants from the onset of the Miocene. The role of *Spiniferites* and *Cordosphaerid*ium increased particularly markedly. Immediately at this boundary, dinocysts from the Deflandrea phospho*ritica* group disappeared in the middle latitudes; in the low latitudes, they became extinct in the Early Aguitanian. The group *Deflandrea spinulosa* had the epibole at the beginning of the Aquitanian and completely disappeared in the same age.

Planktonic foraminifers were also particularly numerous and diverse in the middle of the Eocene and

decreased in diversity in the Late Eocene, especially, at the Eocene–Oligocene boundary. The drop in temperature was followed by the disappearance of the highly specialized genera Globigerapsis, Globigerinatheca, Hantkenina, Cribrohantkenina, and groups of species from Turborotalia and Globigerina, i.e., the dominant taxa of the first half of the Paleogene. These changes developed in two stages, at the base and roof of the Turborotalia centralis-Globigerina gortanii Zone, in the uppermost strata of the Eocene (Krasheninnikov in Geological and Biotic..., 1998). Oligocene assemblages were impoverished and dominated by small and medium-sized globigerinids and globorotaliids. Early Miocene assemblages also displayed low species diversity. Extratropical assemblages from the northeastern Atlantic included 36 species, many of which passed from the Oligocene (Krasheninnikov et al., 1999). New species of the genera Globigerinoides, Globoquadrina, and Praeorbulina were rare in the Aquitanian and began to dominate only in the Burdigalian.

In the North European Region, planktonic assemblages underwent an even greater decrease in diversity at the Eocene–Oligocene boundary in connection with a sharper drop in temperature. In the Oligocene, this region yielded only extremely uniform assemblages of planktonic foraminifers dominated by small globigerinids (Globigerina officinalis) and globorotaliids; nannoplankton assemblages lacking Discoaster and dominated by tolerant species of the genera Reticulofenestra, Cyclicargolithus, and Coccolithus; and boreal dinocyst assemblages with Wetzelliella simmetrica, Deflandrea phosphoritica, and Enneadocysta pectini*formis.* The last algal group was particularly tolerant of fluctuations of temperature and salinity but, in the Paratethys, the taxonomic diversity of its associations decreased to 60-80 species in marine conditions (in contrast to 100-120 in the Late Eocene).

In the Miocene, in connection with general warming, the diversity of planktonic groups substantially increased in the ocean and seas adjacent to the Tethys and the northeastern Atlantic. The composition of this biota displayed general evolutionary features of groups from warm-water areas, but with the disappearance or isolated occurrence of the most stenothermal taxa (Krasheninnikov *et al.*, 1999).

Thus, during the time interval considered, the four main planktonic groups, which determined the rate of primary production in the ocean and were thoroughly examined in the Cenozoic sections, experienced a profound reorganization in their taxonomic composition. These changes in assemblages developed through similar stages of sharp depletion of diversity and extinction of taxa at the end of the Middle Eocene, in the Priabonian, and at the Eocene–Oligocene boundary; the presence of impoverished transitional assemblages in the Oligocene; and gradually increasing taxonomic diversity in the Neogene.

Benthos

Late Eocene. The characteristic features of the taxonomic composition of Priabonian benthic assemblages from the Ancient Mediterranean Region (reviewed in the first part of this study) were undoubtedly formed before the Late Eocene. The Priabonian faunas from the Mediterranean Region mostly inherited the composition of benthic foraminifers, ostracodes, and mollusks from the Lutetian and Bartonian. The majority of benthic genera and species were old migrants, which appeared in the region under study in the Early and Middle Eocene and persisted in the Early Oligocene, though with a noticeable decrease in species diversity in the Priabonian and, particularly, in the Rupelian. Therefore, as in the case of planktonic groups, the Middle Eocene biota should be taken as the type of the Ancient Mediterranean Region.

The Late Eocene fauna from the North European Region also had much in common with the Middle Eocene fauna. The rich Latdorfian ostracode assemblage was dominated by the transitional Eocene genera along with the newly emerging family Hemicytheridae: members of 50 transitional genera are known from this region, while only one (*Rabilimis*) appeared at the end of the Eocene (Nikolaeva in *Geological* and *Biotic...*, 1998). A similar domination of taxa and a large number of common species are observed in the Lutetian and Priabonian (Mandrikovka) faunas from Ukraine.

The taxonomic composition of the Beloglinian ostracode assemblages was inherited from the deepwater association of the Early-Middle Eocene. In the ostracode assemblages from Chegan, transitional Eocene taxa clearly prevailed, although some (no more than nine) also persisted in the Oligocene. The high similarity between the Latdorfian mollusk assemblage and earlier faunas is evident from the fact that some faunas described in the classic study by Koenen (1893) were dated to the Latdorfian, while currently they are referred to the Middle Eocene based on nannoplankton. In oceanic basins, the composition of benthic faunas underwent gradual evolutionary changes by the replacement of some species groups by others, which was not accompanied by catastrophic extinctions (Geological and Biotic..., 1998, p. 181).

Early Oligocene. An increase in the rate of changes in the taxonomic composition occurred at several levels: in the second half of the Late Eocene and, then, at the Eocene–Oligocene boundary. Nonetheless, in warm seas, where carbonate sedimentation continued, Oligocene assemblages contained many species of benthic foraminifers inherited from the Eocene (up to 46%: Krasheninnikov in *Geological and Biotic...*, 1998). In the southern province, Eocene taxa of larger foraminifers persisted; however, they substantially decreased in diversity. The drop in temperature was accompanied by changes in the appearance of nummulites: their shells became smaller, nongranular, and, at the end of the Oligocene, this genus became extinct. In the other subfamily (Heterostegininae), the genus Grzybowskia disappeared, species of the genera Spiroclypeus and Heterostegina became rare, and a new family, the Miogypsinidae with two genera, emerged. Within orbitoidids, one or two residual discocycline species still existed at the beginning of the Oligocene. In the upper part of Zone P18 or the lower part of Zone P19, the family Discocyclinidae was replaced by the Lepidocyclinidae, including the typical Oligocene genus Lepidocy*clina*, which was represented by a series of subgenera (or, possibly, by separate genera). The number of ostracode species in the Oligocene was halved (20 in comparison with 40 in the Late Eocene). Generic diversity also decreased. At the end of the Eocene, members of 14 genera, including Eopaijenborchella, Protoargilloecia, Phacorhabdotus, and Triebelina disappeared in the northern provinces. The appearance of any new groups has not been recorded.

In the substantially impoverished Rupelian mollusk assemblages from the Mediterranean Region, half of the species were in common with the Eocene (Piccoli *et al.*, 1977). In small faunas known from southern Bulgaria (Karagyuleva, 1964), Armenia, and Romania, such species composed two-thirds or an even greater proportion. The Preston's coefficients of dissimilarity in these faunas were 0.43–0.63, i.e., according to the threshold values accepted in the present study for comparisons in space, they would be qualified as intraprovincial differences (see Popov *et al.*, 2000).

The Rupelian benthic faunas from the northern Peri-Tethys substantially changed because of a considerable drop in temperature in this climatic belt at the Eocene-Oligocene boundary and universal changes in facies: the most thermophilic groups became extinct, while inhabitants of soft silty substrates expanded their ranges. In the "Northern Nummulitic Province," nummulitids and discocyclinids completely disappeared and, only at the end of the Oligocene (in the Chattian), isolated species of larger foraminifers of the genera Lepidocyclina, Miogypsina, and Miogypsinoides penetrated this area. Among ostracodes, 35 genera disappeared, while transitional species composed at most 15% (Nikolaeva in Geological and Biotic..., 1998). In the Rupelian mollusk faunas from Belgium, southern Ukraine, and the Transcaspian Region, the proportion of species inherited from the Eocene ranged from half to a third. The Preston's coefficients of dissimilarity between Rupelian and Priabonian assemblages from the same regions were substantially higher (0.73-0.81)than in the Ancient Mediterranean Region, which in spatial comparisons would correspond to provincial differences. However, these changes in mollusk composition are primarily accounted for by changes in facies and climate. In the evolutionary aspect, Rupelian faunas were directly related to the most cold-water members of the Latdorfian biota and continued its development. Therefore, we propose that, at the Eocene-Oligocene boundary, the biogeographical pattern underwent a fundamental change at the level of provinces; however, the North European Region still remained (Fig. 9).

At the Eocene–Oligocene boundary, all benthic faunas of the Paratethys fundamentally changed: taxonomic diversity decreased, many thermophilic genera and species were lost, and new more cold-water groups appeared. Among foraminifers, the proportion of arenaceous foraminifers increased, and many new taxa with relatively simple morphological structure appeared. Some new genera and species appeared shortly before the crisis event and initially occupied a subordinate position in communities; however, they became widespread after the crisis. Other species only existed during the short crisis phase, when new taxa characteristic of the Oligocene also appeared.

Late Oligocene. Changes in the Chattian benthic faunas from the Ancient Mediterranean Region are only documented by fragmentary records. In different groups, typical Paleogene faunas were probably noncontemporaneously replaced by Neogene faunas. The earliest extensive mollusk group of species that passed into the Neogene first appeared in the Chattian of the Mediterranean Region. Some of these species persist to the present time. In northern Italy, transitional species from the Rupelian composed less than half of the bivalve fauna. The familial composition changed substantially; arcids and carditids were still rather diverse, while the dominant position was occupied by venerids, cardiids, and pectinids, which replaced more primitive groups (Spondylidae, Crassatellidae) and achieved the maximum diversity in the Neogene.

Mollusk assemblages from the Egerian of central Europe also had transitional composition between those characteristic of the Paleogene and Neogene, which was intensified by the increasing effect of Mediterranean elements on their composition (Báldi, 1973, 1986). In the Chattian, assemblages from this area were composed of about 250 bivalve species, 75 species (30%) were known from the Rupelian and earlier, 60 appeared at the onset of the Chattian, 120 were recorded from the beginning of the Egerian, and 90 (35%) passed into the Miocene.

In the rich and unique Chattian mollusk assemblages from northwestern Europe, one-third of species were inherited from the Rupelian, 157 species out of 450 (based on the data by Janssen, 1979). A total of 252 species (56%) emerged in the Chattian. Thermophilic members of these assemblages have not been recorded in the Mediterranean. However, such a high originality seems to be an overestimation caused by taphonomy: these assemblages contain many small thin-walled forms, which are usually not preserved in the fossil record. Only 78 species (17%) passed into the Miocene.

On the contrary, in the poor assemblages from the Chattian of the Eastern Paratethys, almost two-thirds of species were inherited from the Rupelian, although these faunas were separated by the period of Solenovian decrease in salinity. Apparently, this similarity is attributable to repeated immigration from the North Sea Basin of the most cold-water transitional species, which are common for the Rupelian and Chattian faunas. In the second half of the Chattian, the fauna underwent an even greater decrease in diversity, while the proportion of endemic taxa increased, which probably resulted from a decrease in the salinity of the basin.

Early Miocene. From the Miocene, mollusk faunas that were dominated by such bivalves as venerids, pectinids, mytilids, lucinids, and cardiids and, among gastropods, trochids, neritids, cerithiids, and nassariids, and a large proportion of Recent species gradually increased their range. This concerns extremely diverse faunas from the Aquitanian and Burdigalian of Aquitania, comprising 365 species (Cossmann and Peyrot, 1909–1914), and Early Miocene faunas from northern Italy (Sacco, 1887–1904). In central Europe, typical Miocene faunas are represented by the Eggenburgian Fauna, which includes about 30% of species known from the Oligocene. In the Early Miocene of northern Europe, the Vierlandian Fauna contains 70% of Oligocene species, whereas in the Hemmorian, they decreased to 40%, and the dominant position was occupied by the species and genera common with the Mediterranean Region. The boundary of the Vierlandian is marked by an abrupt decrease in the diversity of the ostracode assemblage.

Mollusk faunas from the basal Miocene of the Eastern Paratethys display a relatively low diversity and are only known from isolated localities (Popov *et al.*, 1993). Their expansion was associated with an extensive short-term transgression, where the mollusk faunas were of Mediterranean origin.

In the middle of the Middle Miocene, the faunas characteristic of the Neogene reached the maximum development. The center of the formation of these faunas was the Mediterranean and eastern Atlantic regions. The pattern of communities fundamentally changed, i.e., the position of lucinids, crassatellids, arcids, spondylids, and carditids, which were very diverse in the Eocene, was occupied in the Miocene by new dominants: pectinids, venerids, and other cardiid genera. Many species playing a significant role in Recent communities emerged. Mollusk assemblages of very similar taxonomic composition were widespread from the eastern Atlantic throughout the whole of the Mediterranean Region to Iran (in the Burdigalian) or, in the Middle Miocene, up to the southern Aral Region and the Kopet Dagh (in Langhian-Serravalian, Badenian-Konkian) and persisted without significant change in the Mediterranean Region to the end of the Miocene. Apparently, the Middle Miocene fauna is what should be taken as the type fauna of the Mediterranean–North Atlantic Region. This biogeographical region is considered to have appeared at the onset of the Miocene, while the benthic faunas of the Miocene type became widespread from the Burdigalian.

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