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# **Biogeography of the Northern Peri-Tethys from the Late Eocene to the Early Miocene**

## **Part 2. Early Oligocene**

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**Abstract**—This is the second part of the monograph “Biogeography of the Northern Peri-Tethys from the Late Eocene to the Early Miocene.” The main section, Biogeography of the Early Oligocene, considers the stratigraphy of the Lower Oligocene Paratethys, the biogeographic distribution of the planktonic and benthic marine biotas and the fresh-water and terrestrial fauna and flora in the Lower Oligocene, as well as the biogeographic zonation of water bodies and land areas. In the sections Latitudinal Climatic Zonation and Major Events in the Late Eocene–Early Oligocene, the climatic history of the Early Oligocene is discussed and the major Eocene–Early Oligocene tectonic, eustatic, hydrologic, and biotic events are considered.

## INTRODUCTION

This study is aimed at the most complete reconstruction of the pattern of the distribution of marine and terrestrial flora and fauna over Western Eurasia from the Terminal Eocene, through the Oligocene and to the Early Miocene against the background of major geological events and paleogeographic and climatic changes (the objectives of this study were discussed in greater detail in the first part of this monograph). The first part also covered the approaches and methods that are used in the biogeographic analysis of the Recent flora and fauna. The present section is devoted to the biogeographic distribution of planktonic and benthic marine biotas and freshwater and terrestrial fauna and flora in the Early Oligocene, as well as to the biogeographic zonation (integrated wherever possible) of water bodies and land areas. At the end of this section, the latitudinal-climatic zonation of the Early Oligocene is discussed and the major Eocene–Early Oligocene events are considered. The evolution of various floral and faunal groups and the dynamic aspects of the evolution of biostratigraphic subdivisions will be discussed in the final section of this study, after the biotas of the Late Oligocene and Early Miocene are considered.

The sections Lower Oligocene Stratigraphy of the Northern Peri-Tethys and Major Late Eocene–Early Oligocene Events were written by S.V. Popov; the section Paleogeography of the Paratethys, by S.V. Popov and I.G. Shcherba; and the section Latitudinal Climatic Zonation of the Early Oligocene, by M.A. Akhmetiev and S.V. Popov. Data on flora are presented by M.A. Akhmetiev; on dinocysts, by M.A. Akhmetiev, A.S. Andreyeva-Grigorovich, and N.I. Zaporozhets; on smaller benthic foraminifers, nummulitids, and disco-cyclinids, by E.M. Bugrova; on terrestrial vertebrates, by A.V. Lopatin; on nannoplankton, by A.S. Andreyeva-Grigorovich; on planktonic foraminifers, by V.A. Krashennikov; on ostracodes, by I.A. Nikolaeva; on mollusks, by O.V. Amitrov and S.V. Popov; on corals, by E.I. Kuzmicheva; on ichthyofauna, by E.K. Sytchevskaya; and on insects, by V.V. Zherikhin.

## BIOGEOGRAPHY OF THE EARLY OLIGOCENE

### Lower Oligocene Stratigraphy of the Northern Peri-Tethys

We consider the Lower Oligocene beds as equivalents to the Rupelian *sensu lato* (Cavelier and Pomerol,

1986; *Geologicheskies i bioticheskie...*, 1996); i.e., these beds are distinguished based on their correlation with Northwest European stratotypes rather than with the Mediterranean stratigraphic scale, which has been used for the Priabonian.

As a geochronological unit, the Rupelian was proposed by Dumont in 1849 based on outcrops in the Rupel cuesta (along the Rupel River), northern Belgium. There, the major lithostratigraphic unit is the Boom Clay. However, as a stage, the Rupelian *sensu lato* also includes the underlying Upper Tongrian beds, Berg Sands, and clay beds with *Nucula comta*. There are no outcrops with a complete sequence of these beds. The lowermost layers of the Rupelian Stage are exposed in eastern Belgium (Leuven Area), while the outcrop of the Boom Clay lies farther to the east (Boom Area). The Upper Tongrian clays yield dinocysts of the *Phthanoperidinium aomoenum* Zone, which are typical fossils of the Sannois Beds, Stampian (Cavelier and Pomerol, 1986), whereas the sands include nannoplankton of Zone NP22. Planktonic foraminiferal assemblages that contain no zonal species but include species typical of Zones P18–P21, nannoplankton of Zones NP23–NP24, and rich dinocyst assemblages of the *Wetzeliella gochtii* Zone, including the *W. symmetrica* assemblage (Stover and Hardenbol, 1993), have been found in the Boom Clay. Rich molluscan assemblages (Glibert and Heinzelin, 1954; Glibert, 1957) and assemblages of ostracodes, fishes, spores, and pollen were also recorded there.

In deep-sea cores from the warm-water area, two planktonic foraminiferal zones, P18 and P19 (Blow, 1971), or three zones and one subzone, P18–P21a (Berggren *et al.*, 1995), and three (or four) nannoplankton zones, the upper part of Zones NP21, NP22, and NP23 and the lower part of Zone NP24, are considered to be equivalents to the Rupelian. Three dinocyst zones, *Phthanoperidinium amoenum* (D13), *Wetzeliella symmetrica* (D14a), and *W. gochtii* (D14b) correspond to the Rupelian succession based on the sequential appearance of zonal species in the most complete Early Oligocene outcrops (table).

The stratotype of the Priabonian–Rupelian boundary has been established in the northeastern Apennines (the Massignano Section). There, in the homogenous sequence of pelagic marly beds, this boundary is defined based on the change in the planktonic foraminiferal zones (P17/P18) and the disappearance of Hanth-

Correlation of the Upper Eocene–Lower Miocene of the Paratethys and major events in the Eastern Paratethys (after Popov *et al.*, 2001, modified)

Age (Ma)	Epoch	Stage	PLANKTON ZONE correlation acc. to Berggren <i>et al.</i> , 1995		Carpathians	Central Paratethys (Hungary)	regional stage	Dinocysts Andr.-Grig., 1994 Zaporozhec, 1998	Foraminifera benthos plankton	Georgia	EASTERN PARATETHYS		Shallow salinity	Transgression/Regression	Main events in the Eastern Paratethys
35	EOCENE	Pliabon.	Foraminifera Blow, 1969, 1979	Nannoplankton Martini, 1971	Shesho- ra Marl	Buda Marl	BELOGLIANIAN	Charlesdowniella clathrata anquiosa Beds with Microdinium	Cibic. salensis Bol. antegressa G. tropicalis- Gl. corpulenta	Akhalsikhe Suite	Chegemian	Anom. munda B. antegressa	10 20 30‰ +	-	Regression, stagnation Lesser Caucasus orogenesis Eastern Paratethys separation
			Globigerina involuta P15	Ch. oamar. NP18											
30	OLIGOCENE	Rupelian	Globigerina sellii P19	Helicopontosphaera reticulata NP22	Lower Cherts	KISKELIAN	Weizeliella gochti	Troch. florifera	Sp. carinata oligocaenica	Corbula Beds	Tandy Suite	Chilikka- nian	10 20 30‰ +	-	Paratethys isolation, 1-st crisis of salinity
			Globigerina tapuensis P18	Coccolithus subdistans NP21											
25		Chattan	Globorotalia opima opima P21	Sphenolithus distentus NP24	Krosona Serie	KISCELLIAN	C. lipoldi Beds	Rhombodinium draco	Sphenolithus distentus NP24	Uplistskhe Suite	Upper	Aralian Suite	10 20 30‰ +	-	Short vast transgression
			Globigerina ciproensis P22	Sphenolithus ciproensis NP25											
20	MIOCENE	Burdigal.	Globigerina sicaris N8	Helicopontosphaera ampliapertura NN4	Mentilithic Serie	EGERIAN	D. spinulosa H. floripes	Cibicides omatus-	Globoquadrina dehiscens N5	Sakaraulian Suite	Upper	Aralian Suite	10 20 30‰ +	-	Full marine conditions 2-nd Paratethys isolation
			Globigerina sicaris N8	Helicopontosphaera ampliapertura NN4											

keninidae (*Hantkenina* and *Cribrhantkenina*), as well as *Turborotalia cunialensis* and *T. cocoaensis*. Outside the tropical zone, this boundary is difficult to determine because of the poor species composition of the Late Eocene Hantkeninidae assemblages and dominance of globigerinids (Rögl, 1996). No major events in the evolution of nannoplankton occurred at this boundary, which is drawn in the lower part of Zone NP21 (after Martini, 1971) or within Zone CP16a (after Okada and Burky, 1980). The volcanic biotite from the Massignano Section is dated by the K–Ar method approximately at  $34.3 \pm 0.3$  Ma (Premoli Silva *et al.*, 1988). Dating of deep-sea cores at the P17/P18 boundary indicates the age of 33.7 Ma (after Berggren *et al.*, 1995). Based on dinocysts, the boundary is drawn at the base of the local *Glaphyrocysta semitheca* Zone, thus virtually coinciding with the base of Zone P18, and through the middle part of Zone NP21. The Rupelian of the Mediterranean includes the local dinocyst interval-zones, *Areosphaeridium dictyoplokus*, *Reticulasphaera actinocoronata* (in the middle part of which *Wetzeliella gochtii* first appears), *Chiropteridium inornatum*, *Hystriochokolpoma pullillum*, and *Chiropteridium lobospinosum*, at the top of which the Rupelian–Chattian Boundary is drawn. This boundary runs through the middle part of Zone P21 according to planktonic foraminifer data (after Berggren) and through the upper part of the combined NP23–NP24 Zone according to nannoplankton data. Based on nummulites, the Oligocene of the Mediterranean (Rupelian and lowermost Chattian) corresponds to the *Nummulites intermedius* (= *N. fichtelli*)–*N. vascus* Zone with the following typical species: *Nummulites intermedius*, *N. vascus*, *N. fichtelli*, and *N. sublaevigatus* (Colloque..., 1968; Cavelier and Pomerol, 1985).

**Western Paratethys.** Within the Intra-Carpathian Region, in the Hungarian Paleogene Basin, the Eocene–Oligocene boundary is drawn in the upper part of the Buda Marl where the extinction of the group *Globorotalia cerroazulensis*, *Globigerina gortanii*, etc. and the appearance of species typical of the *Globigerina tapuriensis*–*Pseudohastigerina micra* (P18) assemblage are observed at the boundary between the carbonate and terrigenous facies (Tard Clay). Based on nannoplankton data, the base of the Tard Clay approximately corresponds to the NP20/NP21 boundary, whereas the upper part of these clay beds belongs to Zone NP23, includes brackish-water mollusks, and corresponds to the brackish-water period of the Paratethys. A thick horizon of the Kiscel Clay is distinguished higher in the succession. This horizon is characterized by planktonic foraminifers of the *Globorotalia opima opima* Zone and by nannoplankton of the *Sphenolithus distentus* (NP24) Zone (Nagymarosy and Báldi-Beke, 1988). The deposits that correlate with the Rupelian (the uppermost part of the Buda Marl and Tard Clay) and with the lowermost part of the Chattian in the Pannonian Region of the Paratethys were proposed as the Kiscellian Regional Stage (Báldi, 1969). The lower bound-

ary of the Kiscellian is drawn at the NP20/NP21 boundary, whereas its upper boundary is the lithological boundary between the Kiscel Clay and the finer-grained and shallower Egerian deposits.

In Transylvania, the Eocene–Oligocene boundary is based on planktonic data and passes through the upper part of the Brebi Marl (Bombita and Rusu, 1981; Rusu *et al.*, 1993). However, in the Early Oligocene, shallow-water carbonate sediments (Hoiia Limestone) still accumulated there. These sediments yield warm-water benthic assemblages, including typical Tethyan taxa. The overlying sandy–clay Mera Beds, which are followed by brackish-water interbeds higher in the succession, yield the same fauna. For these beds, the Merian Regional Stage (Moisescu, 1975) was proposed. The lower boundary of the Merian Stage is drawn at the NP21/NP22 boundary, whereas the upper boundary is defined by the appearance of brackish-water mollusks (“*Cardium*” *lipoldi* and *Janschinnella*). In the Getic Depression, the change from the Eocene planktonic assemblages (*Globigerina corpulenta* and *Coccolithus subdistihus*) to the assemblage with *Pseudohastigerina micra* is observed in sandy facies at the base of the conglomerate and sandstone beds (Cheia and Gorbi after Bombita and Rusu, 1981).

In the Flysch Carpathians, many researchers assign the upper part of the Sheshora Marl to the Lower Oligocene based on the appearance of planktonic foraminifers of Zone P18 and nannoplankton of Zone NP21 (Krhovsky *et al.*, 1995). This is overlain by the Subchert Member of the Menilithic Formation, dark non-calcareous or slightly carbonate clay beds (6–10 m thick) that were formed under low-oxygen conditions and are considered by certain paleontologists to be the basal Oligocene beds (Andreyeva-Grigorovich *et al.*, 1986). Carbonate components of the sediment are represented there by coccoliths of the *Helicopontosphaera reticulata* (NP22) assemblage or by smaller planktonic foraminifers of *Globigerina officinalis* in association with the species that allow the correlation of the base of the Menilithic Formation with Zone P18 and of the upper horizons with the transitional assemblage of the P18/P19 boundary. Dinocysts of the Subchert Member are represented by the assemblage of the *Wetzeliella symmetrica* Zone (Andreyeva-Grigorovich *et al.*, 1986). The Lower Oligocene *Phthanoperidinium amoenum* Zone is usually difficult to distinguish, because its zonal species is extremely rare in occurrence. In the middle and upper parts of the Subchert Member, interbeds with abundant *Limacina* (= *Spiratella*) are observed, as well as horizons showing a decrease in salinity indicated by the composition of nannoplankton (the proportion of *Braarudosphaera bigelowii* increased) and diatoms (the recrystallized cherts were predominantly composed of a single fresh- to brackish-water species *Melosira granulata*). Marl beds at the top of the chert member yield nannoplankton of Zone NP23 and correlate well with the lower part of the Solenovian

Horizon in the Eastern Paratethys by the presence of typical taxa (Krhovsky *et al.*, 1995).

This brackish-water level of the Paratethyan salinity, which is characteristic of the second half of the Rupelian and is well determined by the presence of brackish-water mollusks, monospecific rock-forming assemblages of nannoplankton, diatoms, and dinocysts of a typical composition, is a marker level for the Oligocene. This is traced everywhere (Voronina and Popov, 1984; Báldi, 1986; Rusu, 1988; Nagymarosy and Voronina, 1993) from Bavaria (Heller Mergelkalk) and Slovenia (Sotzca Beds) via Hungary (upper part of the Tard Clay), Transylvania (Bizusa, Ileanda, and Ciocmani), the Carpathians (Dynow Marl, Tylawa, and Tarcau), southern Ukraine (Molochnaya Beds), Ciscaucasia (Polbian Horizon), up to the northern Aral Sea coastal area and Central Asia ("ostracode layer" of the Solenovian Horizon).

In the Carpathians, the Upper Rupelian includes the overlying sediments of the Menilithic Formation (the Sitborice Member in Czech Republic, the Lower Menilithic Subformation in the Ukrainian Carpathians, and the Lower Dysodilic Shales in Romania). These beds include both brackish-water and polyhaline sediments, of which the latter are defined by the presence of nannoplankton (NP23/NP24), planktonic foraminifers of Zone P21a, and diatoms and dinocysts of the *Wetzeliella gochtii* Zone (Andreyeva-Grigorovich *et al.*, 1986; Rusu *et al.*, 1996; Krhovsky *et al.*, 1995).

In the Alpine Foreland Basin, the Upper Marine Molasse (UMM), represented by shallow-water facies and sands, is mainly dated as the Rupelian. The sediments are characterized by planktonic foraminifers of Zones P17–P20, nannoplankton (NP21–NP24), and dinocysts and mammals (MP-12 after Berger, 1992, 1996). These are traced in the Jura Mountains, as well as in the Rhine Graben System, where their upper part already belongs to the Chattian (NP25 after Berger, 1992).

Outside the Western Paratethys, within the study area, calcareous plankton assemblages that are representative enough for reliable recognition of zonal Rupelian subunits are only found south of the Lesser Caucasian land, in Armenia. In the reference section of the Biralu Borehole, the level of disappearance of the rosette-shaped discoasters (at the NP20/NP21 boundary) almost corresponds to the change of the *Turbototalia centralis*–*Globigerina gortanii* Zone to the *Globigerina tapuriensis* Zone (P17/P18) dominated by small-sized species of newly appeared globigerinids. The *Globigerina sellii* Zone is recognized higher in the succession, where closely similar species in association with rare specimens of the index species are found (*Geologicheskie i bioticheskie...*, 1998). This zone is overlain by sand beds with an impoverished assemblage of foraminifers, which probably belong to the *Globigerina ampliapertura* Zone.

**Eastern Paratethys.** In the Crimea, Ciscaucasia, Transcaucasia, Mangyshlak, and Turkmenistan, the

Eocene–Oligocene boundary that is considered as the *Turbototalia centralis*/*Globigerina tapuriensis* P17/P18 border passes in the vicinity of the abrupt lithological change from the biogenous-carbonate (Beloglinian Formation) to terrigenous sedimentation. The Lower Oligocene is represented almost everywhere by dark-colored noncarbonate or slightly carbonate clay of the Pshekhian Horizon (lower part of the Maykopian Formation). Zonal species of planktonic foraminifers usually are absent in the Maykopian Beds. In the dinocyst scale, the Eocene–Oligocene transition is correlated with the boundary between the *Wetzeliella clathrata angulosa* and *Phthanoperidinium amoerum* zones. The latter corresponds to the lower part of the Pshekhian Horizon, overlain the vast *Wetzeliella gochtii* sensu lato Zone, which includes beds of the Solenovian Horizon. Its lower half occasionally may be considered as the *W. symmetrica* Zone (Zaporozhets, 1993). Based on benthic foraminifers, the *Lenticulina herrmanni* regional Zone is distinguished in the lower part of the Pshekhian Horizon (*Reshenie...*, 1970). Higher, but not everywhere, the *Spiroplectamina oligocenica* (= *S. carinata oligocenica*) Zone is distinguished. This zone includes *Caucasina schischkinskayae*, *Cyclammina constrictimargo*, *Bolivina mississippiensis*, and a few sand-dwelling taxa. The boundary between them is not exactly synchronous, has a facial character, but is clearly traced in the majority of regions.

Opinions on the nannoplankton zonation differ. The difficulties in the recognition of Zone NP21 in this place were discussed above. In the upper half of the Pshekhian Horizon, all researchers distinguish the *Helicopontosphaera reticulata* (NP22) Zone, whereas, at the base of the Solenovian (Polbian) Horizon, an individual assemblage of endemic mollusks, nannoplankton, and dinocysts was discovered, thus indicating a change in salinity regimes. The Polbian Marl is usually dated at the *Sphenolithus praedistentus* NP23 Zone (Nagymarosy and Voronina, 1993) or at the NP22/NP23 transition (Muzylev and Tabachnikova, 1987). The lower boundary of the *Wetzeliella gochtii* sensu lato closely corresponds to the base of the *Spiroplectamina oligocenica* Zone. In the Eastern Paratethys, the composition of dinocyst assemblages markedly vary across the single *Wetzeliella gochtii* Zone because of the Solenovian drop in salinity. The lower assemblage is defined by mainly polyhaline taxa, whereas the upper assemblage is defined by euryhaline or brackish-water taxa. In the West European sections, the zones proposed correspond to Zones D13 and D14 (the latter zone consists of two subzones, D14a and D15a).

After the Solenovian drop in salinity, the salinity in the Eastern Paratethys began gradually to increase to restore the polyhaline groups of organisms. Usually, this event was dated based on mollusks and benthic foraminifers at the beginning of the Chattian (Ter-Grigoryants, 1964; Stolyarov, 1991; Popov *et al.*, 1993). However, recent data on phytoplankton indicate that this event should be assigned to the terminal Rupelian,

as in the Carpathians. Nannoplankton of the upper part of Zone NP23 was recorded by Khrovsky, whereas dinocysts of Zone D14a were identified by Zaporozhets from carbonate interbeds at the base of the Upper Subformation of the Morozkina Balka Formation in the Belaya River succession (Akhmetiev *et al.*, 1995).

In Transcaucasia, there are more complete assemblages of planktonic foraminifers with *Globigerina tapuriensis*, *G. ampliapertura*, and *Globorotalia permicra* (P18); nannoplankton of the *Coccolithus subdistichus* (NP21) Zone; mollusks of the typical Rupelian assemblage; and numerous remains of *Limacina* (= *Spiratella* and *Planorbella*). The Lower Oligocene beds in this zone are relatively thin, a few tens of meters thick (up to 100–150 m in the Kura–Iori interfluve).

In Transcaspia, the Lower Oligocene marine beds defined by nannoplankton of Zone NP22 and dinocysts are traced up to the Western Siberia and Tajik Depression (see the section Paleogeography of the Paratethys for more detail).

In shallower-water Lower Oligocene facies of southern Ukraine, Volga-Don Region, Mangyshlak, Ustyurt, northern Aral Sea coastal area, and Kopet-Dagh, fossil planktonic assemblages are either rare or represented by the transient species *Globigerina officinalis*. However, the Lower Rupelian marine beds are rather reliably recognized by the typical benthic taxa: mollusks, including species zonal for the Rupelian sensu stricto of the Stratotype Region (*Pecten stettenensis*), and foraminifers in common with the Rupelian fauna. The Solenovian Horizon may be also used as a marker level at the top of these beds. This horizon is easily distinguished by having a lighter color of rocks and the presence of carbonate clay imbedded in the dark-colored noncarbonate Maykopian Formation, benthic brackish-water molluscan and ostracode faunas (Popov *et al.*, 1985), and of a specific nannoplankton assemblage with *Reticulofenestra ornata* and *Transversopontis fibula*. The dinocyst assemblage becomes more impoverished. Two or three species predominate, comprising 95% of the total number of specimens. The zonal species *Wetzeliella gochtii* is extremely rare.

A break in the marine sedimentation that corresponds to the Oligocene base is usually observed in peripheral areas of the basin. Dinocyst assemblages from the Ergeni Highland, Mangyshlak, Ustyurt, and Turgay are abnormal in composition due to river water influxes and unstable facial environments. The Lower Oligocene *Phthanoperidinium amoenum* and *Wetzeliella gochtii* zones are easily recognized there, whereas the *W. simmetrica* Zone may be only preliminary distinguished because of the absence of the index species.

The available data on the stratigraphic position and age of the Sumsar Horizon in Ferghana and the Sanglak Horizon in the Tajik Depression are rather contradictory. On the one hand, the molluscan and ostracode assemblages are closely similar to the Chegan assemblages and were discussed in the first part of this study

(Popov *et al.*, 2001). Eocene nannoplankton and radiolarians were also reported (Muzylev *et al.*, 1996). Nannoplankton of the *I. recurvus* (NP19) Zone and Zones NP18–NP20 was recorded by Andreyeva-Grigorovich (see Starshinin, 1997) from the upper part of the Kushan Horizon; however, an impoverished Oligocene assemblage with *Reticulofenestra umbilicata*, *R. scussira*, *Cyclocargolithus floridanus*, *Cyclococcolithus formosus*, and *Sphenolithus prenistanianus* (NP22) was found in the upper part of the Sanglak Horizon in the Manzob Section.

A benthic foraminiferal assemblage from the Sanglak Horizon have quite dissimilar composition compared to the Late Eocene assemblages, including *Loithosomata macrura*, *Asianella subbotinae*, *Brotzenella munda*, *Cibicidoides khanabadensis*, and a few new species of the genus *Brotzenella*, which are unknown from the other regions of Central Asia prior to the Oligocene (Davidzon *et al.*, 1982). *Asianella subbotinae*, *Brotzenella munda*, *Cibicidoides khanabadensis* and sand-dwelling species of the genus *Trochammina* (Varzyk Section after Bugrova) described by Davidzon from the Sanglak Horizon were also recorded from the Sumsar red-colored beds in Ferghana. A closely similar assemblage was reported by Minakova (*Paleogenovaya*..., 1975, p. 275) from the crimson clay imbedded in a horizon with *Ostrea pygmaea* in Ferghana. This assemblage was compared with the fauna of the *Lenticulina hermanni* Zone. It is impossible to compare this fauna with the Beloglinian Assemblage, because it developed after the crisis at the Eocene–Oligocene boundary, according to Bugrova, and is discussed in this section of the present study.

### Paleogeography of the Paratethys

The Late Eocene Orogeny of the Alpine folded belt and the eustatic regression transformed the Early Oligocene Paratethys into a much more isolated sea basin compared to the Eocene marginal sea basins in this area. The uplift of the Alps, Dinarides, Anatolia, and the Lesser Caucasus–Kopet Dagh formed a continental barrier that separated the Paratethys from the Mediterranean area of the Tethys. In the Early Oligocene, the Paratethys still was connected with this area in the west via the Alpine Foreland Basin (Berger, 1996) and Slovenian Corridor, and probably in the east via the Vardar–Rhodope Area (Fig. 1). It also was connected with the North Sea Basin (based on faunal data, see below) via the Rhine Graben, as well as via the Dnieper–Don and Prypat depressions.

The Early Oligocene Paratethys markedly decreased in area along the entire periphery compared to the Late Eocene basin, whereas the deepwater part of the Paratethys inherited its major character of the paleobathymetric zonation. Its bathyal and shelf depressions became even deeper (Stolyarov, 1991; Shcherba, 1993).





**Fig. 1.** Paleogeographic map of the Tethys and Northern Peri-Tethys in the Rupelian. Explanations: (1) conglomerates; (2) sands; (3) clays; (4) marls; (5) limestones; (6) mountains; (7) highlands; (8) nondifferentiated land; (9) lowlands; (10) lake basins; (11) lagoons episodically covered by the sea; (12) shallow shelf; (13) deepwater shelf; (14) continental slope and bathyal; (15) terrigenous deposits; (16) flysh; (17) volcanoes; (18) normal faults; (19) thrusts; (20) shifts.

In the Rupelian, the depositional environments and the faunal living conditions in the Paratethys markedly changed due to the progressive isolation, overdeepening of the basin, water cooling, and the presence of a strong river influx. This resulted in the formation of the thermal and salinity water stratification, impairment of gas exchange regime, hydrogen-sulfide contamination, and accumulation of dark-colored clay sediments with high content of undecomposed biogenous material (Tard Clay, menilithic beds in the Carpathian Area and the Maykopian Facies in the Caucasus–Kopet Dagh Area of the Paratethys).

At the end of the Rupelian, this isolation resulted in a change in the hydrological regimes of the basin and in the accumulation of specific sediments containing endemic fauna characteristic of brackish-water environments. Marine environments were restored in these basins in different times. In the Carpathian Basin, marine fauna already appeared in the second half of the Rupelian (in the Early Menilithic Epoch), whereas, in the Eastern Paratethys, the appearance of polyhaline marine fauna is dated at the Terminal Rupelian–Early Chattian.

#### *Alpine–Carpathian Basin*

At the beginning of the Rupelian, the hydrological regimes of the central area of the residual marginal sea basin in the Carpathians remained relatively favorable for life. This area was inhabited by marine benthic fauna, although impoverished. These beds yield foraminifers, sponges, traces of echinoderms and mud-eaters (possibly worms), as well as fossil abyssal fishes with photophores, which indicate the sea depths of at least a few hundred meters. The increasing isolation of this basin subsequently resulted in salinity stratification, periodical anoxic environments, and the disappearance of the deepwater fauna. Growing hydrothermal activities that were accompanied by the supply of nutrients (nitrogen, phosphorus, and silica) resulted in the acme of diatoms in the Middle Rupelian (at the border between the nannoplankton zones NP23 and NP24). The diatoms were originally represented by marine taxa (Krhovsky *et al.*, 1993) and subsequently by brackish-water taxa, whereas their assemblage became monospecific (*Melosira granulata* and *Aulacosira*). Subsequently, the dominance of diatoms changed to the mass development of typical Paratethyan nannoplankton (*Reticulofenestra ornata* and *Transversopontis fibula*), while the sediments were carbonate everywhere (Nagymarosy and Voronina, 1993). At the end of the Rupelian, marine environments were restored and accumulation of dark-colored noncarbonate mud (Lower Menilithic, foliated, bituminiferous shale beds) started.

In the Early Oligocene, the Skole-Zdanice-Silesian (Tarcau) troughs and the Skibas-Pokut Trough were still the deepest-water depressions (Beer and Shcherba, 1984), in which condensed sediments accumulated below the level of carbonate compensation. These sed-

iments were represented by thin (a few ten meters thick) black-colored and dark-grayish noncarbonate mud layers. Strong fluxoturbidites arrived to these troughs from the East European Platform, as well as from the Silesian Cordillera and Inner Eastern Carpathians (Fusaru Sandstone and Otrit Sandstone). Two deep depressions, the Magura Trough and the Szolnok Trough, were still located southwest of the cordillera that bordered the axial trough. These depressions were compensated for by black-colored mud and diatomites. In the Rupelian, the Szolnok Trough decreased in area due to its shallowing and movement of the Bukk Volcanic Ridge in the southward direction (Nagymarosy and Báldi-Beke, 1993).

The southern shelf occurred within two large blocks, the Alcapa (Tatran Unit) and the Tisza-Dacia (Bihar Unit). The eastern area of the Alcapa was occupied by the central Carpathian Paleogene Basin and its continuation to Slovakia. This area increased in depth toward southeast, where the Tard Clay (60 to 100 m thick) accumulated in a basin of the euxine type with traces of hydrogen-sulfide contamination. This basin still continued into the North Italian Sea via the Slovenian Corridor (Báldi, 1986; Nagymarosy, 1990). This connection was interrupted in the second half of the Rupelian.

The eastern part of the Tisza-Dacia Block was occupied by the Transylvanian Shelf Sea with carbonate sedimentation (Hoja Limestone and sandy-clay Mera Beds). Shallow-water facies occurred in the western area of this basin and bordered the Apuseni Land, from which terrigenous and biogenous material arrived. In the southeast, the Transylvanian Basin joined the shelf area of the southern part of the deepwater Carpathian Depression. In the southwest, this basin rapidly became shallower and clay was replaced by sand and then by conglomerate of the Getic Depression, the products of erosion of the South Carpathian–Moesian Land.

The South Carpathian–Moesian Land and the Dinarides were probably separated by straits that connected the Carpathian Basin and the Rhodopian Foreland Basin, a gulf of the Ancient Mediterranean. This is indicated by the available biogeographic data, the composition of benthic fauna of Mediterranean origin that persisted in Transylvania up to the Solenovian drop in the Paratethys salinity, as well as by the common geological evolution of Transylvania and northeastern Greece, where the Lower Rupelian marine beds are also overlain by brackish-water sediments with *Corbula*. These straits are also traced in Serbia (Andelković *et al.*, 1991). In the Oligocene, they became probably even deeper compared to the Eocene. The same data indicate that the Inner (Eastern) Dinarides represented a slightly elevated land with depressions compensated for by freshwater, lagoonal, and volcanic sediments.

In the Oligocene, the Carpathian Foreland mainly represented a denudation area (Kul'chitskii and Sovchik, 1986). The northern shelf was probably very



narrow and joined the Sodomir Uplift, which was subject to erosion. The sediments of this shelf were only found in the Alpine Foreland Basin. These are represented by the lower marine molasse, i.e., by shallow-water clay beds. Farther to the northwest, the clay beds are replaced by sandy-carbonate lagoonal and lake beds (Berger, 1996). According to Berger, there was no marine connection between this shelf and the North Sea Basin in the Rupelian. However, the available faunal data (on mollusks) indicate that there existed at least episodic connections (see below). The existence of a certain connection between the Carpathian Shelf and the Greater Caucasian basin probably via the Gelati Strait is also indicated by the biota in common, especially by the endemic taxa of the Solenovian Epoch (mollusks, ostracodes, and nannoplankton).

#### *Greater Caucasus–Kopet Dag Basin*

The Greater Caucasus–Kopet Dag Basin (Eastern Paratethys) was connected in the first half of the Rupelian with the Carpathian Basin in the region of the Moesian Plate and was open to the North Sea Basin (Fig. 1). Concurrently, the uplift of the Lesser Caucasus–Iranian Land entirely separated this basin from the Mediterranean–Mesopotamian Basin already by the Late Eocene. The closure and shallowing of the Eastern Paratethys at the beginning of the Solenovian Epoch resulted in its short-term transgression, improvement of gas exchange regime, formation and wide distribution of endemic benthic fauna over the entire Paratethys, and the wide accumulation of biogenous (nannoplankton) carbonate mud. In the Late Solenovian, the basin again decreased in area. Nevertheless, its connection with the World Ocean became wider and euryhaline representatives of the marine fauna could reach the Paratethys, but its gas exchange regime was deteriorated and the sediments were saturated with organic material.

The deepwater zone still occurred within the Eastern and Western Black Sea depressions, Lazarevskoe–Kobystan Trough, and the South Caspian Depression (Shcherba, 1993; Kopp and Shcherba, 1998). The Oligocene–Early Miocene sediments of this part of the basin are represented by homogenous clay beds that are difficult to subdivide. At the beginning of the Oligocene, the Lazarevskoe–Kobystan Deep-water Trough was approximately 200 km wide, similarly to that in the Eocene (Shcherba, 1989). Farther south of the Schatsky Swell, the deepwater sediments accumulated in the Western and Eastern Black Sea depressions (Tugolesov *et al.*, 1985), where these are known only based on geophysical data as a component of the undivided Maykopian Formation. There, the Oligocene sediments are very shallower-water in character compared to the Eocene for the reason of the Lesser Caucasus Orogenesis and the decrease in the trough wide. The deepwater Talysk Foredeep is an equivalent to the Eastern Black Sea Depression in the east, however, separated from it by a shallower-water plateau (central and eastern Georgia).

In the Rupelian, the southern shelf was strongly affected by a newly formed land. The uplift and drying of the Lesser-Caucasus–Iranian Island Arc resulted in the accumulation of thick, coarse, clastic beds that border the modern-day Lesser Caucasian Arc and represent clay, sandstone, and conglomerate formations of the Akhaltsikhe Depression (up to 1000 m thick), Gyandja Region in Azerbaijan (400 m thick), and the Araks Depression (up to 700 m thick). These beds occasionally bear traces of sand streams, mudflow intrusions, and lagoonal environments (Akhaltsikhe).

The Lesser Caucasus–Iranian Land represented a low-mountain structure that was occasionally subjected to the early orogenic volcanism (of the acid or intermediate types) and was occupied by laurel-beech forests with a participation of palms. The plant fossils were preserved in tuff-sandstone beds of the Negram Plateau (Akhmetiev and Zaporozhets, 1989). At the beginning of the Oligocene, the deepwater gulf of the Central Iranian Basin reached this land in the south via the Yerevan–Ordubad Depression. The coastal zone with normal marine environments was inhabited by various colonial corals, numerous warm-water mollusks, small foraminifers, nummulitides, echinoids, ostracodes, and nannoplankton; and sandy-mud sediments (up to 1000 m thick) accumulated there. In the second half of the Rupelian, the sea left this region.

The northern shelf was very wide and included a complex system of deep and wide depressions that were not yet compensated for by the Oligocene sedimentation (Stolyarov, 1961, 1991). These depressions had their individual pseudo-oceanic structure, a shallow-water shelf, and fairly steep slopes. The Terek–Mangyshlak Depression was the deepest, where thin carbonate clay beds (40–20 m thick, or smaller) accumulated with remains of planktonic foraminifers and bathyal fishes with photophores. The second largest depression was the Indol–Kuban Depression separated from the Terek–Mangyshlak Depression by the Stavropol Uplift. This depression was situated much closer to the sources of terrigenous material; thus, the Lower Oligocene beds were there 300–400 m thick. Farther to the west, in the region of the Kerch Strait, the Indol–Kuban Depression was opened into the axial area of the basin.

Spore and pollen data and leaf flora from Ciscaucasian outcrops indicate an increase in the land area in the western part of the Greater Caucasus (Zaporozhets, 1993; Akhmetiev, 1995). This is also indicated by the occurrences of coastal molluscan assemblages at two stratigraphic levels, at the base of the Oligocene and in the lower part of the Solenovian Horizon (sections of the Belaya, Fars, and Kuban rivers). Similar uplifts probably existed in the vicinity of the southwest flank of the Terek–Mangyshlak Depression, where shallow-water sandy sediments with molluscan assemblages of the Solenovian Horizon were found (Northern Osetia, Fiagdon and Tsraudon rivers). These depressions were

also bordered in the north by fairly steep slopes, as indicated by the sharp changes in facies and thickness. This is the Mangyshlak Island, as well as the uplifts west of Astrakhan and the Rostov Uplift (Stolyarov, 1991).

In the western part of the Greater-Caucasus Basin, on the slope of the Moesian Platform, in the outer shelf environments, noncarbonate mud with pteropods, typical Paratethyan molluscan species ("assemblage with *Lucina batalpaschinica*") and fish fossils accumulated. In the south, the Moesian Shelf was bordered by the zone of Balkan thrusts. In their southern flank, in the Sredna Gora and Rhodopian Upland, the Lower Oligocene is represented by quite different facies: the coastal beds with a rich warm-water fauna represent sediments of Mediterranean gulfs (Karagyuleva, 1964). Available data on marine biota indicate that, starting from the Terminal Eocene, these basins were separated by a continental barrier rather than connected with each other. This land continued into the modern-day southwestern area of the Black Sea Basin and probably served as a continental bridge, via which Asian vertebrates could reach southeastern Europe (see below).

Farther east of the Moesian Land, the shelf sharply increased in width. In the northwestern area of the Black Sea Basin and the South Ukrainian Depression, typical coastal facies occur near the south slope of the Ukrainian Shield, which had transformed from an archipelago to the land area by the Oligocene. This land area separated the South Ukrainian Depression from a shallow-water epicontinental basin that occupied the Dnieper–Don and Pripet depressions, via which the Paratethys was connected with the North Sea Basin.

The entire vast area of marine sedimentation in Transcaspia, i.e., the Turanian Sea Basin, represented a shelf zone with depressions that were mainly compensated for by sedimentation. Only the axial area of the Southern Mangyshlak Depression, Buzachi Depression, and the Daryalyk–Daudan Depression may be assigned to the deep shelf zone. In the Daryalyk–Daudan Depression, fossil material is only represented by globigerinids and fish fossils, thus indicating the gas exchange regime unfavorable to the benthos and the sea depths of over 150–200 m. The southwestern part of the Krasnovodsk Peninsula and the Western Kopet Dagh also represented a relatively deep area of the Turkmenian Basin, where planktonic foraminifers accounted for up to 65% of the paleobiocoenoses (Nevmirich *et al.*, in *Geologicheskie i bioticheskie...*, 1996).

The rest of the area belonged to the shallow-water shelf with gas exchange regimes relatively favorable for benthic fauna. Its richest assemblages were found in the north, in the Northern Ustyurt and northern Aral Sea coastal area (Merklin, 1974; Amitrov, 1993). In the Terminal Eocene–Early Oligocene, the sea regression and lowering of the erosion basis resulted in deep erosion (up to 40–60 m in the northern Aral Sea coastal area). Subsequently, the depressions formed were compensated for by freshwater, terrigenous, and marine sandy

sediments. The maximal sea transgression was observed in the Middle Ascheairyk when the sea continued via Turgay into the Middle Trans-Uralian depressions and the Omsk Depression (marine Rupelian sediments were found along the southeast-facing slope of Trans-Urals, in the vicinity of the town of Kurgan and farther east, Akhmetiev *et al.*, in press). In the Terminal Ascheairyk (the lower part of the *Wetzelietta gochtii* D14a Zone), the sea retreated, and the sandy coastal facies of this epoch are known in the Northern Ustyurt.

At the Eocene–Oligocene boundary, the sea retreated from the territory of Kyzyl Kum and southeastern Kara Kum. In the Kyzyl Kum, the denudation cutoff reached 100–150 m (Pinkhasov *et al.*, in *Geologicheskie i bioticheskie...*, 1996). Subsequently, in the first half of the Early Oligocene, the Kara Kum–Kyzyl Kum Lowland was occupied by a shallow-water sea, whereas the red-colored and variegated silty-clay beds of the Sarybatyr and Murghab formations accumulated and were a few ten meters thick. At that period of time, the short-term sea transgression could probably reach the Ferghana and Tajik depressions, where Oligocene foraminifers were found, as well as nannoplankton of the *Helicosphaera reticulata* (NP22) Zone with a characteristic set of species (Manzob Section). This nannoplankton was determined by Andreyeva-Grigorovich from the southern area of the Hissar Upland. As in the Carpathians, the acme of the species *Cyclocargolithus floridanus* was found there. A narrow shallow-water marine strait markedly affected by a fresh-water influx probably continued farther east into the Tarim Depression. Here, red clay and fine-grained terrigenous beds of the Bashibulake Formation with the endemic mollusks *Platigena*, *Ferganea*, *Cubitostrea*, and *Donax* and with the cosmopolitan species *Chlamys*, *Anomia*, and *Crassatella* accumulated (Lan and Wei, 1991). The tree lower members of this formation are dated by these researchers at the Late Eocene, whereas the two upper members are assigned to the Early Oligocene.

Farther to the northeast, the coastal beds of this zone were gradually imbedded by terrigenous and alluvial sediments and then became entirely terrigenous. The presence of gypsum in some red-colored interbeds indicates a hyperhaline lagoonal paleoenvironment. The Mugodzhzar Hills Land, Kazakhstaniian Shield Land, and the Tien Shan, Altai, Hissar, and Kopet Dagh formed a zone of steady uplift in Transcaspia and represented a source of terrigenous material.

The tectonic rearrangement and the orogenesis also started farther east, in Central Asia, as indicated by the changes in the lithological structure of beds at the level of the Buranian Formation in the Zaisan Depression, as well as by the transformation of its freshwater ichthyofauna and molluscan fauna.

## Biogeography of Water Bodies

### *Planktonic Foraminifers*

The Oligocene planktonic foraminiferal fauna differs markedly from the Eocene assemblages in having a poorer composition. This fauna includes representatives of globigerinids and globorotaliids of mainly small and medium size. The taxonomic diversity seems to increase when we use the modern-day classification, which diminishes the volume of generic units. The assemblage of planktonic foraminifers includes ten genera: *Globigerina*, *Subbotina*, *Cassigerinella*, *Tenuitella*, *Tenuitellinata*, *Catapsydrax*, *Paragloborotalia*, *Globorotaloides*, *Pseudohastigerina*, and *Chiloguembelina*. The species composition of the Oligocene planktonic foraminifers is of limited diversity (about 40 species), but it should be emphasized that the species of *Globigerina*, *Subbotina*, and *Paragloborotalia* predominate, while the representatives of *Classigerinella*, *Globorotaloides*, *Tenuitellinata*, and *Chiloguembelina* are rare, and the species of *Pseudohastigerina* are entirely restricted to the Lower Oligocene.

Such a decrease in the taxonomic diversity of the planktonic foraminifers is usually associated with the climatic changes (climatic cooling) at the Eocene–Oligocene boundary. Actually, a number of typical Eocene genera and groups of species, (*Cribratkenina*, *Hantkenina*, *Globigerapsis*, *Globigerinatheca*, and the group “*Globorotalia*” *cerro-azulensis*), disappear (or decrease in number) at the lower boundary of the *Paragloborotalia centralis*–*Subbotina gortanii* Zone, which corresponds to the transitional Eocene–Oligocene beds. At this boundary, the terrestrial flora (spore and pollen assemblages) indicates a climatic change toward cooling. At the upper boundary of the *Paragloborotalia centralis*–*Subbotina gortanii* Zone (i.e., Eocene–Oligocene boundary), the last elements of the Eocene fauna of planktonic foraminifers disappear, and the Eocene assemblages are replaced by a typical Oligocene foraminiferal assemblage of the *Subbotina tapuriensis* Zone. At this level, a further temperature decrease occurred, as indicated by the terrestrial flora.

It is not improbable, however, that such a transformation of the planktonic foraminiferal fauna at the Eocene–Oligocene boundary was associated with the individual evolution of this group of microfauna. In subsequent Neogene epochs, the climatic conditions were very unstable and the temperature regime was often more severe compared to that in the Oligocene, but the taxonomic composition of the Neogene planktonic foraminifers was much richer compared to the Oligocene assemblages of this group of microfauna.

The factor indicated (the impoverished taxonomic composition) makes very difficult the reconstruction of the Oligocene biogeographic zonation based on planktonic foraminifers. The biogeographic zoning at the generic taxonomic level is not efficient. It is certainly possible to reconstruct the paleobiogeographic zonation with due consideration of specific proportions in

the foraminiferal assemblages and facial environments, but investigations of this type have not yet been performed.

The second factor that makes difficult the analysis of the biogeographic distribution of planktonic foraminifers in the Oligocene is associated with geological evolution in this epoch. The development of eustatic and tectonic processes resulted in a wide accumulation of regressive terrigenous (clayey and sandy-clay) sediments over continents and in the formation of the Paratethys and anoxic hydrochemical regimes. As a result, it is very difficult to differentiate which factor affects the composition of foraminiferal assemblages, the primary general factor (climatic zonation), the local factor (biochemical environments for the sedimentation), or the secondary taphonomic factor (selective dissolution of the fossils in non-carbonate or slightly carbonate sediments).

The available data on the distribution of the Oligocene planktonic foraminifers only allow an estimate of the general biogeographic pattern of this group of microfauna but not always the factors that form the individual taxonomic composition.

In the study area, we can distinguish two provinces, the Southern (Mediterranean) and the Northern (Crimean–Caucasian Region, Carpathians Foreland, and northwest Europe).

In the Southern (Mediterranean) Province, rich assemblages of planktonic foraminifers occurred in facies of true white chalk (northeastern Syria) or in carbonate clay facies (Cyprus and Italy). The Oligocene sections include the entire set of the foraminiferal zones, *Subbotina tapuriensis*, *Subbotina sellii*, *Globigerina ampliapertura*, *Paragloborotalia opima*, *Globigerina ciperoensis*, and *Paragloborotalia kugleri*. A distinctive character of the foraminiferal assemblages is the constant presence of these index species in combination with *Subbotina gortanii* (Bors.), *S. galavisi* (Berm.), *S. pseudovenezuelana* (Blow et Bann.), *S. prasaepis* (Blow), *S. tripartita* (Koch), *Globigerina anguliofficialis* Blow, *G. officinalis* Subb., *G. angulisuturalis* Bolli, *G. euapertura* Jenk., and *Tenuitellinata angustiumbilicata* (Bolli). The total taxonomic composition of these assemblage is closely similar to that from the Oligocene of the classic tropical Caribbean Region and the adjacent regions in the Atlantic Ocean. Possible distinctions between the assemblages may be only found based on the proportion of species, as mentioned above.

In the territory of the former Soviet Union, southern Armenia (Yerevan Basin) may be probably assigned to the northern periphery of the Mediterranean Basin. There, the Lower Oligocene beds (the *Subbotina tapuriensis* and *Subbotina sellii* zones) usually include *S. tapuriensis* (Blow et Bann.), *S. tripartita* (Koch), *S. prasaepis* (Blow), and *Globigerina ampliapertura* Bolli, as well as few specimens of *Subbotina sellii*, but globigerinids of small size start to predominate in quan-

tity. Unfortunately, more recent Oligocene beds are represented there by continental facies.

In the Oligocene of the Northern Province (Paratethys), noncarbonate and slightly carbonate clayey sediments (Maykopian and Menilithic formations) with very impoverished assemblages of planktonic foraminifers predominate. More precisely, these assemblages occur in the basal part of the Oligocene, whereas, in the overlying beds, the foraminifers are very rare or entirely absent. A similar pattern is observed in the Oligocene of the Northern Caucasus (Russia), northern Aral Sea coastal area (Kazakhstan), Turkmenistan, Azerbaijan, Georgia, the Crimea, and the Fore-Carpathians (Ukraine). Clearly, it is impossible to use this group of microfauna in the zonal division of the Oligocene beds. The planktonic foraminiferal assemblage is composed of small *Globigerina officinalis* Subb., *G. ouachitaensis* Howe et Wall., *G. praebulloides* Blow, *G. postcretacea* Myatl., *Tenuitella danvillensis* (Howe et Wall.), *T. liverovskae* (Bykova), *T. evoluta* (Subb.), *T. brevispira* (Subb.), *Paragloborotalia permicra* Blow et Bann., *Pseudohastigerina micra* Howe, *P. barbadoensis* Blow, and *Chiloguembelina cubensis* (Palm.). The presence of separate representatives of *Globigerina ampliapertura* Bolli, *Subbotina prasaepis* (Blow), and a few other species does not change the general pattern.

Similar assemblages of planktonic foraminifers were also found in the Oligocene clayey sediments in northwestern Europe (Germany, Belgium, and the Netherlands). According to some studies on the Oligocene of Europe, the assemblages of small globigerinids and globorotaliids should be considered as a general characteristic of the Oligocene fauna of planktonic foraminifers, but this is contrary to facts.

Supposedly, the major factor for such essential differences between the planktonic foraminiferal assemblages from the Oligocene of the Southern and the Northern provinces is the climatic zonation; however, the unfavorable chemical regimes in the Northern Province and the subsequent secondary dissolution of calcareous foraminiferal tests represent eliminating factors that further increased the differences between these Oligocene assemblages.

#### *Nannoplankton*

The climatic and paleogeographic changes in the Terminal Eocene—at the beginning of the Early Oligocene—resulted in a marked change in the coccolithophorid assemblages. In the southern basins, where the carbonate sedimentation continued, these changes were gradual. The extinction of typical tropical Eocene species of discoasters started in the Late Eocene, when their subtropical assemblages appeared. Representatives of the genus *Chiasmolithus* (except for *Ch. oamaruensis*) almost entirely became extinct. The species

composition of the genera *Sphenolithus*, *Helicosphaera*, *Reticulofenestra*, etc. changed.

**Northern Mediterranean.** In the Mediterranean, the Early Oligocene nannofloral assemblage mainly consisted of species of the genera *Discoaster*, *Sphenolithus*, *Helicosphaera*, *Reticulofenestra*, and *Cyclicargolithus*. The Early Oligocene nannoplanktonic assemblages from central and northern Italy include 38 species (Roth *et al.*, 1971). Their distinctive character is the presence of warm-water discoasters, *D. rufus*, *D. woodringi*, *D. adamanteus*, *D. cubensis*, and *D. dinquarensis*, as well as *Sphenolithus*, including *S. pseudoradians*, *S. distentus*, *S. predistentus*, *S. ciperoensis*, etc. This assemblage indicates southern subtropical environments.

At the beginning of the Early Oligocene, in the Armenian Gulf of the Turkish–Iranian Basin, the nannoplankton assemblage included 24 species (Andreyeva-Grigorovich, 1981; Krasheninnikov *et al.*, 1985). Almost all of the species were in common with the Italian species, with the exception of the species of the genus *Discoaster*. The latter are represented by isolated specimens in the Armenian assemblages. One more tropical genus, *Sphenolithus*, was abundant in the Armenian Basin, except for the species *S. ciperoensis*, which appeared in the Late Rupelian and was absent in Armenia.

**Eastern Mediterranean.** The Late Rupelian Mesopotamian Basin (Tavda Section, Syria) was dominated by the species *Sphenolithus distentus* and *S. ciperoensis*, as well as *Helicosphaera recta* and *Cyclicargolithus abisectus* (Müller, 1971). The nannofloral assemblage was almost entirely similar to the Early Oligocene flora from Trinidad Island (Bramlette and Wilcoxon, 1967); i.e., it was of the circumtropical type.

**North Sea Basin.** The development of the coccolithophorid flora in the basins of western and northern Europe was strongly affected by Atlantic cold waters. There, thermophilic discoasters were almost absent, representatives of *Sphenolithus* were rather rare, while boreal species and species of the genera *Reticulofenestra*, *Cyclicargolithus*, *Coccolithus*, and some other species tolerant with respect to temperature predominated. The assemblages from stratotype Rupelian sections (Berg Sand, clay beds with *Nucula*, Boom Clay, Herdorf and Framnvald septarian clay beds, and the Northern Germany cores Schach Profile Rossenray I and Hoersten) include 27 species, 13 of which are in common with the Latdorfian and Tongrian assemblages. A distinctive character is the wide development of the warm-water *Sphenolithus* species, *S. predistentus* and *S. distentus*, and the species *Braarudosphaera bigelowi*, which forms large accumulations at shallow shelf areas and is rather tolerant with respect to salinity. The same assemblage is typical of the Early Rupelian basins of southern Germany (Rhine Graben, Mainz Basin, and Sessische Senke). In the Late Rupelian basins of northern Germany, the species *Cyclicargolithus abisectus* and *Helicosphaera recta* were abundant (Müller,

1971). Twenty-eight species were reported from the Rupelian of the northwestern basins of Germany (Gar-tow–Kothe cores, 1986). Species of the genera *Reticulofenestra*, *Coccolithus*, and *Cyclicargolithus* were very numerous. Species of *Sphenolithus* were absent with an exception of the sole *S. moriformis*. This assemblage indicates the relatively deepwater boreal environments.

By the end of the Rupelian, the warm-water and relatively shallow-water assemblage had been replaced by a deeper water and colder water assemblage. *Sphenolithus* were entirely absent, *Braarudosphaera bigelowi* and *Cyclicargolithus abisectus* were rare, whereas the species *Helicosphaera bramlettei* was abundant.

**Paratethys.** The Early Oligocene Paratethyan nanofloral assemblages were closely similar and are characterized by cold-water species 15 to 25 in quantity. Among the most typical species were *Isthmolithus recurvus*, *Reticulofenestra umbilica*, *Cyclicargolithus floridanus*, *Zyrrhablithus biyugatus*, *Discoaster tani nodifer*, *Corannulus germanicus*, etc. The assemblages are closely similar to those from the Early Oligocene basins of Germany. The qualitative and quantitative compositions were controlled by the basin depths, proportion of terrigenous material, temperature regimes, and by a few other factors. Thus, in relatively shallow-water shelf areas, the assemblages with *Isthmolithus recurvus*, *Lanternithus minuthus*, and *Zyrrhablithus bifugatus* (from the base of the Kyzylzhar Beds in the Crimea) formed. The deeper-water areas were characterized by abundant *Cyclicargolithus floridanus* (acme-zone at the base of the Lower Menilithic Formation in the Carpathians).

A marked deterioration of the qualitative composition of nanoplankton assemblages and an acme of endemic floras is observed in the Oligocene basins of the entire Paratethys from the upper part of Zone NP22. The species *Reticulofenestra ornata* and *Transversopontis fibula* were of rock-forming importance, whereas *Braarudosphaera bigelowi*, *Orthozugys aureus*, and a few other species tolerant with respect to salinity were present in small quantities (Nagymarosy, 1983; Andreyeva-Grigorovich and Gruzman, 1994). The normal marine species, including the zonal species *Sphenolithus distentus* (NP23), were extremely rare (Báldi-Beke, 1977; Nagymarosy and Báldi-Beke, 1988; Andreyeva-Grigorovich, 1994).

This level with endemic nanoplankton is traced throughout the Paratethys, from the Bavarian Piedmont of the Alps and basins of the central Paratethys (base of Tard Clay after Nagymarosy, 1983; upper part of Brebi Marl, Romania, after Rusu *et al.*, 1993; Lower Menilithic Formation of the Carpathians) to the Aral Sea (Nagymarosy and Voronina, 1993). In the eastern Paratethys, the acme of the endemic flora was assigned to the Early Solenovian (Polbian and Molochnaya horizons), but the changes had started earlier, in the Pshek-hian (Veselov and Lyulieva, 1980; Andreyeva-Grigor-

ovich, 1986; Muzylev and Tabachnikova, 1987; Ananiashvili and Minashvili, 1990; Nagymarosy and Voronina, 1993).

The normal marine nanoplanktonic flora again appeared and dominated the central Paratethys only from the end of the Early Oligocene (at the base of Zone NP24). In the eastern Paratethys, it also appeared in the Middle Maykopian and was recorded from geological sections in the Northern Caucasus and Georgia (Andreyeva-Grigorovich, 1980; Ananiashvili and Minashvili, 1990; Minashvili, 1992; Nagymarosy and Voronina, 1993).

Thus, the major factors that controlled the distribution and the productivity of nanoflora in the Oligocene basins of the Paratethys were the proportion of terrigenous material and the salinity regimes. A partial isolation of the Paratethys in the middle part of the Early Oligocene resulted in a decrease in salinity and in the appearance of endemic flora.

#### *Organic-Walled Phytoplankton*

At the beginning of the Oligocene, the organic-walled phytoplankton was half-new compared to the Late Eocene assemblage. In the Terminal Eocene, as well as at the beginning of the Early Oligocene, in more northerly regions, *Rottnestia borussica*, *Areosphaeridium diktyoplokum*, *A. arcuatum*, *Tyrrhodiscus beloglinensis* and the Eocene species of the genera *Phthanoperidinium*, *Spiniferites*, *Hystrichokolpoma*, *Deflandrea*, *Thalassiphora*, *Wetzeliiella*, etc., disappeared. New taxa, *Phthanoperidinium amoenum*, *Areosphaeridium pectiniforme*, *Membranophoridium aspinatum*, etc., appeared and were widespread in the Early Oligocene.

**Northern Mediterranean.** Over 100 species of alga Dinophyta were found in the Oligocene of the Mediterranean Basin. The most typical genus, *Chiropteridium*, was almost globally distributed. The species of the genera *Spiniferites*, *Operculodinium*, *Systematophora*, and *Deflandrea* increased in quantity. In the Early Oligocene, species of the genera *Homotryblum* and *Wetzeliiella*, as well as the species *Hystrichokolpoma pussillum*, *Areosphaeridium pectiniforme*, *Chiropteridium lobospinosum*, and *Corrudinium incompositum* were very abundant.

A high biodiversity (over 100 species) was still observed in Armenian assemblages tolerant with respect to high salinity that was associated with hydrologic and climatic factors. Within the Yerevan–Ordubad Depression, the organic-walled phytoplanktonic assemblage mainly included stenohaline taxa, with many of them (especially chorate taxa) being descended from the Eocene.

**North Sea Basin.** The dinocyst assemblage included 75–80 species. A mixture of various ecological groups was typical similarly to that in the Late Eocene, but the qualitative and quantitative compositions markedly changed. The assemblage was domi-



nated by the neritic, normal marine genus *Impleto-sphaeridium*, especially in the Late Rupelian. The relatively deepwater and cold-water species *Cribopteridium* spp. was abundant (up to 35% in the upper part of Zone NP23), as well as the group *Spiniferites/Achomospaera*. The groups of species *Glaphyrocysta*, *Areoligera*, *Cordosphaeridium*, *Homotryblum*, as well as *Thalassiphora* spp. had almost equal proportion. The quantity of representatives of the latter genus markedly increased in the Early Rupelian Basin and in the Terminal Rupelian (in the vicinity of the Rupelian–Chattian boundary). The deflandrians and *Wetzeliella* spp. had small proportions.

The algal composition indicates an increase in the basin depths, especially in the Middle Rupelian, and a marked increase in the proportion of cold-water taxa and cosmopolites with respect to temperature.

**Carpathian Basin.** In the Flysch Carpathian Basin, the proportion of alga Prasinophyta increased, which was also typical of the terminal Eocene. However, their acme was observed at the beginning of the Early Oligocene. The West Carpathian assemblages were closely similar to those from northern Germany. In the terminal Rupelian, the acme of the species *Wetzeliella symmetrica*, *W.* spp., and *Thalassiphora pelagica* was observed, as well as the acme of *Rhombodinium draco* in the Eastern Carpathians. In the southern shelf (Transylvanian Basin), the acme of the cosmopolitan species *Deflandrea phosphoritica* is reported.

**Eastern Paratethys.** At the beginning of the Oligocene, the composition of the organic-walled phytoplanktonic assemblage was usually impoverished because of a general decrease in the subsurface water temperature (possibly by over 5–6°C) and a slight decrease in salinity, especially in the peripheral areas of the basin. In shallow-water sediments of the peripheral areas (Voronezh Anteclyse and Ustyurt), numerous fossil organisms redeposited from underlying Eocene beds were found, which disguise the Oligocene age of the assemblage.

The taxonomic diversity of the organic-walled phytoplankton in the assemblages tolerant with respect to high salinity reached 60–80 species, which is less than that in the Late Oligocene (120 species, or more). Anoxic environments that occasionally formed in the basin markedly affected the composition of the Maykopian assemblages and possibly the biota of the euphotic zone. These epochs were characterized by lower biodiversity, less quantity of taxa in the assemblage and facial changes (accumulation of black-colored noncarbonate clay beds with concretions and dispersed sulfides). The biodiversity also markedly decreased in brackish-water facies (up to 40–60 species) with a predominance of 2–3 species (up to 90–95% of the assemblage).

Climatic and local factors also markedly affected the biodiversity. The assemblages of open areas of the Scythian Basin (Northern Ciscaucasia) with high water

salinity are better represented than the corresponding assemblages from its northern areas (Voronezh Anteclyse and Ustyurt). In the peripheral eastern area of the basin, in conditions of periodical brackishing, the euryhaline taxa developed that today inhabit estuaries and lagoons. In the peripheral northeastern area of the basin, as well as within Ergeni Region, the composition of the dinocyst assemblages was abnormal and much closer associated with changes in facial environments, probably because of continuous inflow of fresh water from the land. This allows the definition of a sequence of dinofacies here with the alternating predominance of *Wetzeliella*, *Deflandrea*, *Hystrichokolpoma*, *Phthanoperidinium*, and of the group *Cyclonephelium–Adnatosphaeridium* or *Micrhystridium*. In the entire eastern peripheral area of the Paratethys, especially in regressive phases, green algae and acritarches markedly increased in importance. Their quantitative distribution corresponds well to the sedimentation cycles. The diversity and the number of taxa in the assemblage increased during the sea transgression in the Ascheiryk Epoch. Species of *Deflandrea*, *Wetzeliella*, *Phthanoperidinium*, and the group *Glaphyrocysta–Cyclonephelium–Adnatosphaeridium* were still the leading in combination with *Areosphaeridium pectiniforme*, *Membranophoridium aspinatum*, species of *Lejeunecysta*, *Hystrichokolpoma*, *Spineferites*, *Dapsilidinium*, *Dinopteridium*, etc. Other Paratethyan assemblages (from the Mangyshlak, Northern Ciscaucasia, southern area of the East European Platform, and the Carpathian Region) are characterized by the closely similar taxa but the higher diversity.

The compositions of the dinocyst assemblages within the single Zone *Wetzeliella gochtii* markedly differ due to the basin brackishing in the Solenovian Epoch; the more ancient assemblage is characterized by the presence of mainly stenohaline taxa, whereas the more recent assemblage includes brackish-water taxa. The latter assemblage is almost monospecific, includes two to three species, which make up 95% of the total quantity of specimens. The zonal species *Wetzeliella gochtii* is extremely rare. Thin-walled *Hystrichokolpoma* (up to 7 morphotypes) and species of *Batiacasphaera* (*B. sphaerica*, *B. baculata*, and *B. micropapillata*) are common. The accompanying taxa were *Gerdicocysta*, *Parallecaniella*, *Selenopemphix*, *Palaeocystodinium golzowense*, *Horologinella*, *Leberidocysta*, and *Chiropteridium*. A few assemblages, for instance the Kuban Assemblage, were dominated by cysts of the group *Cyclonephelium–Glaphyrocysta–Adnatosphaeridium*. Generally, the composition of dinocysts from the Solenovian Horizon (sensu lato) indicates the periodic fluctuations of the subsurface water salinity in the basin and the absence of entire separation from the open ocean, because the polyhaline taxa, although in small quantities, were constantly found in mixture with the euryhaline species and the species tolerant with respect to low salinity.

In the Early–Late Oligocene boundary beds, the composition and biodiversity of the organic-walled phytoplankton markedly increased again. However, this part of the Maykopian Formation should be probably assigned to the Upper Oligocene, because the species of *Chiropteridium* and *Rhombodinium draco* are very numerous.

#### *Plankton-based Biogeographic Zonation*

In the Early Oligocene, the distribution and the diversity of planktonic foraminifers, dinoflagellates, and nannoflora of the Mediterranean–Mesopotamian and Paratethyan basins also depended upon the latitudinal climatic zonation and water circulation. Two regions are still distinguished: the Ancient Mediterranean Region and the North European Region. The first region is characterized by a presence of a full set of zonal species of planktonic foraminifers and nannoplankton. Its distinctive character compared to the North European Region is the wide development of warm-water discoasters as well as *Sphenolithus*. This region may be considered as the southern subtropical subzone of the tropical zone.

In the North European Region, the planktonic foraminiferal assemblages and warm-water discoaster assemblages were very impoverished or even absent, the representatives of *Sphenolithus* were rare, whereas the boreal species and the species of the genera *Reticulofenestra*, *Cyclicargolithus*, and *Coccolithus*, as well as some other taxa tolerant with respect to temperature predominated. Thus, this region may be considered as the boreal by its temperature regime. The border between these regions went along uplands of the Alps, Dinarides, and Rhodope (Fig. 2) and then along the Pontides, Lesser Caucasus, and the Elburs, that separated the Tethyan Region (including the Armenian Gulf) from the North European basins and the Paratethys. The subsurface water circulation in Paratethys was probably closed and affected mainly by North Atlantic waters (Atlas..., 1997; Fig. 2). Only southern areas of the Carpathian Basin were slightly affected by the Tethys.

#### *Marine Ichthyofauna*

With the onset of the Oligocene, the run of development of the marine ichthyofauna in the Paratethys underwent fundamental changes. In Europe, a number of more or less isolated basins of various depth and salinity arose at that time. The composition of the fish assemblages that lived here during the Early Oligocene reflected the changes in the degree of isolation of particular basins, the dynamics of their shallowing or deepening, as well as climatic changes. Most local communities were dominated by both the autochthonous genera inherited from the Middle to Late Eocene and the groups of boreal origin, which came at that time from the Atlantic. The bulk of the latter was formed by

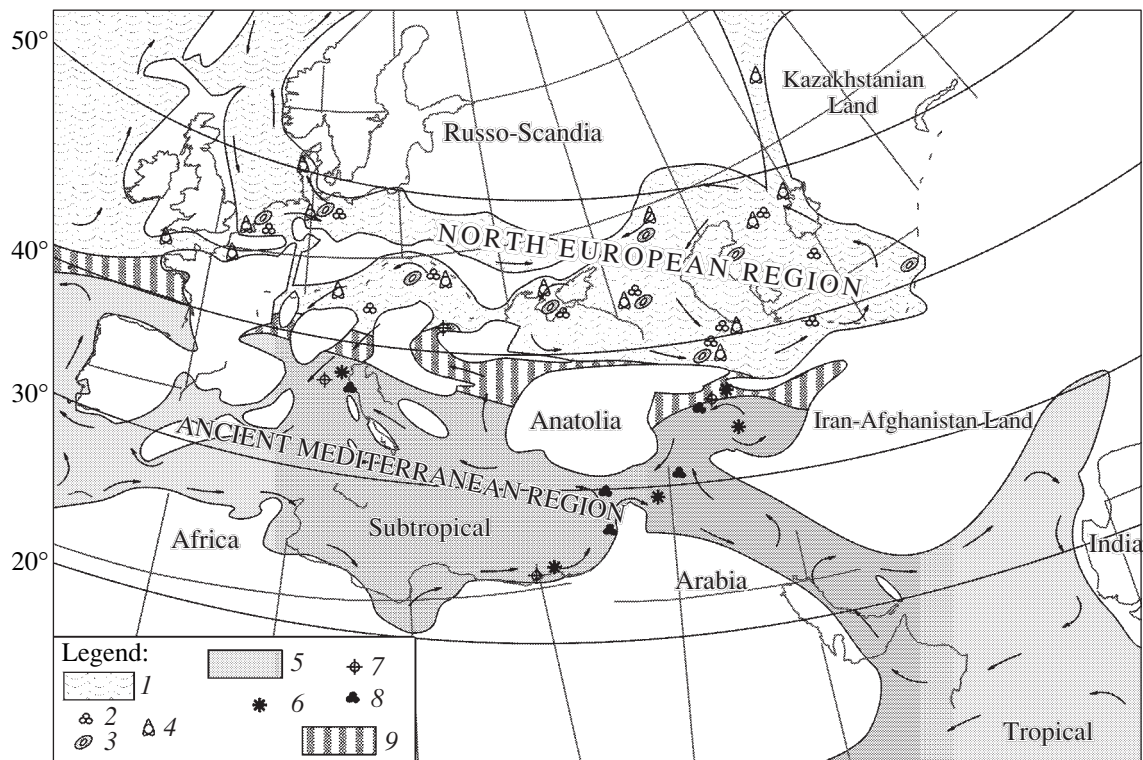
members of the gadiform genus *Palaeogadus*, distinctive for their broad dispersal and ecological diversity,<sup>1</sup> and osmerids. The first appearance of boreal elements and decline of tropical and subtropical forms are recorded in a number of the earliest Early Oligocene faunas of the Paratethys known from the Belgian and Caucasian basins.

In general, the faunal events of the Early Oligocene are most fully documented in the Caucasus and Transcaucasia (Bogachev, 1933, 1938, 1964; Danil'chenko, 1950, 1960; Menner and Ryabinin, 1949; Rozhdestvenskii, 1950; Aslanova, 1960; Novitskaya, 1961; Fedotov, 1976; Switchenska, 1979; Danil'chenko *et al.*, 1980; Fedotov and Bannikov, 1984; Bannikov, 1985, 1986, 1988, 1990, 1991, 1993; Bannikov and Danil'chenko, 1985; Dzhafarova, 1988; Bannikov and Tyler, 1992; Tyler and Bannikov, 1994; Sytchevskaya, 1998; Prokofiev, 2002), in the Lower Menilite Formation of the Carpathians (Kalabis, 1948, 1957, 1981; Jerzmańska, 1960, 1968, 1974; Gorbach, 1961a, 1961b; Jerzmańska and Kotlarczyk, 1968, 1976, 1978, 1979, 1981, 1983; Kotlarczyk and Jerzmańska, 1976, 1980, 1988; Gregorová, 1988), and in the Brown Marles and Disodylic Schists of Romania (Cosmovici, 1889, 1913, 1922, 1966; Paucă, 1934; Cosmovici and Paucă, 1943; Jonet, 1958; Ciobanu, 1970, 1975, 1977, 1978). Of further importance are also the data on the Early Oligocene fish faunas of Iran (Arambourg, 1967), Belgium (Leriche, 1910), and the basins of Balkans, and Western and Central Europe (Wettstein, 1887; Weiler, 1922, 1928, 1931, 1932, 1938, 1953, 1963, 1966; Böhm, 1941; Frohlicher and Weiler, 1952; Anđelković, 1970, 1989; Pharisat, 1991; Micklich and Parin, 1996; Pharisat and Micklich, 1998).

A general analysis of the history of the Early Oligocene ichthyofauna of the Paratethys is complicated for many reasons, which primarily include the controversial dating of some local assemblages; the low resolution of their discrimination (which results in that the one and the same assemblage may be reported to contain the taxa of different age) and, finally, the doubtful taxonomic attribution of a large number of forms described from the Early Oligocene.

**Central Iranian Basin.** A rich Rupelian ichthyofauna of Iran is known to include 31 genera (Arambourg, 1967), showing predominance of tropical and subtropical forms. The abundance of mesopelagic elements, such as *Praewoodsia mesogaeae* Aramb., *Scopeloides glarisianus* (Ag.), *Mauroliscus morgani* Aramb.,

<sup>1</sup> According to Danil'chenko (1950), the *Palaeogadus* species of the subgenus *Rupelianus* (*P. intergerinus* Dan. and *P. arambourgi*) found together with the deepwater fishes obviously dwelled at the great depths, whereas other members of the same genus could have populated more shallow zones, which is evidenced by their finds in association with clupeids, syngnathiforms, and scombrids. Finally, the members of the subgenus *Lotimorpha* (*P. simionescui* Dan. and *P. athanasiui* Paucă), known to be accompanied by *Ammodytes* and *Capros*, most likely populated the lower part of the sublittoral and were the bottom-dwellers.



**Fig. 2.** Superficial circulation of water in the Rupelian basins (after *Paleogeographic...*, 1997, modified) and the pelagial latitudinal zones. Explanations: (1) **Temperate and Boreal zones** with impoverished planktonic associations and the presence of specialized cold-water genera and species; (2) extremely impoverished assemblages of planktonic foraminifers with the predominance of small globigerinids (*Globigerina officinalis*) and globorotaliids; (3) nannoplanktonic assemblages with the absence of discoasters and the predominance of tolerant species of the genera *Reticulofenestra*, *Cyclicargolithus*, and *Coccolithus*; (4) boreal dinocyst assemblages, including *Wetzelliella simmetrica*, *Deflandrea phosphoritica*, *Enneadocysta pectiniforme*, etc.; (5) **Subtropical and Tropical zones** with complete zonal warm-water planktonic assemblages; (6) nannoplanktonic assemblages with abundant *Discoaster*, *Sphenolithus*, and *Helicosphaera*; (7) dinocyst assemblages of the southern type with the predominance of chorate cysts of the genera *Spiniferites*, *Cordosphaeridium*, etc.; (8) complete assemblages of planktonic foraminifers with *Subbotina*, *Globigerina*, and *Paragloborotalia*; and (9) **Transitional Zone**.

*Astronesthes simus* Aramb., *Proserriromer mecqueni* (Priem.), *Bregmaceros filamentosus* (Priem.), and *Myroconger roustami* Aramb., gives evidence of rich mesopelagic life and suggests considerable depth of the basin. The genera survived from the Eocene include *Astronesthes*, *Urosphen*, *Bregmaceros*, *Sphyraena*, *Pristigenys*, *Palaeorhynchus*, *Scomberomorus*, etc. The Iranian Ichthyofauna contained a number of genera and species shared with the coeval fish communities of the Caucasian, Carpathian, and Alpine basins. The indications of exchange with these basins are traceable for both the Early Rupelian (as evidenced by the presence of *Bregmaceros filamentosus* (Priem.), *Scopeloides glarisianus* (Ag.), *Palaeorhynchus*, *Isurichthys*, *Scomberomorus*, etc.) and the Late Rupelian, as seen, for instance, from the occurrence of *Thyrstitoides zaratus-trae* (Aramb.) known elsewhere from the ichthyozones IPM3–IPM4 of the Carpathian basin (Kotlarczyk and Jerzmańska, 1988).

**Greater Caucasian Basin.** In the Paratethys, as a whole, the main stages of development of the Early Oligocene ichthyofauna are most clearly distinguished in

the Caucasian Basin (Danil'chenko, 1960; Danil'chenko *et al.*, 1980; Bannikov, 1985, 1990; Sytchevskaya, 1998). These are documented in ascending order by the finds from the Pshekhian Horizon (which contain the sub-*Planorbella*, *Planorbella* and *Aeoliscus*, or "Amphisile" Beds), Polbian Horizon, and the basal part of the Morozkina Balka Horizon (and its equivalents), with the total range extending from the NP21 Zone to the lower part of NP24 in terms of the nannoplankton zonation. In this succession, four to five fish assemblages of different ages are detected (Sytchevskaya, 1998).

The earliest assemblage comes from the sub-*Planorbella* and *Planorbella* beds of the Pshekhian Horizon (*Ericsonia subdisticha* NP21 Zone) and includes in turn a number of successive assemblages whose differences reflect the change in the characteristics of the basin and the climatic conditions. The latest assemblage is ecologically closely linked to the next following assemblage of the *Aeoliscus* Beds (see below).

The assemblage of the sub-*Planorbella* level was impoverished and included *Lyrolepis* sp. (Elopidae) and *Thunnus* sp., (Thunnidae), i.e., the relicts of some

Late Eocene dominant genera (Sytchevskaya's data). The assemblage is traceable in Ciscaucasia and Transcaucasia (Dzhafarova and Aslanova, 1974) and bears resemblance to the basal fauna of the Early Rupelian (Upper Tongrian) of Belgium. The latter also shows the decrease in diversity accounted for by extinction of preceding (Early Tongrian) tropical and subtropical forms, and the survival of only a limited part of the Late Eocene components (Leriche, 1910).

The subsequent stage in the history of the fish fauna of the Caucasian Basin refers to the *Planorbella* Beds. It is represented by two essentially different assemblages. The earlier of them was dominated by the clupeids of the subfamilies Clupeinae (*Sardinella rata* Dan.) and Alosinae (*Pomolobus curtus* Dan.), the gadiforms of the genus *Palaeogadus* showing a great species diversity [*P. crassus* (Ag.), *P. intergerinus* Dan., *P. rarus* Novit., *P. eximius* Novit., and *P. germanus* Fed.],<sup>2</sup> the Trichiuridae (*Anachelum angustum* (Dan.) and *A. glarisianum* Blainv.), and the Zeidae (*Zenopsis clarus* Dan.). Detected is also the presence of osmerids (unpublished author's data), and the development of argentinids (*Proargentina inclinata* Dan. and *Glossanodon* sp.), paralepidids [*Holosteus mariae* (Menner)], brotulids (*Protobrotula sobijevi* Dan.), and euzaphlegids (*Palimphytes chadumicus* Dan.)<sup>3</sup> (Danil'chenko, 1960; Fedotov, 1976; Sytchevskaya, 1998; Prokofiev, 2002).

The presence of the four listed families testifies to the abundant mesopelagic life and the considerable depth of the basin. The fish assemblages of its neritic zone were dominated by trichiurids and zeids, while the gadids populated both the mesopelagic and sublittoral zones. Some characters, primarily the occurrence of osmerids and the abundance of gadids, point to a more moderate temperature of the basin in comparison with both the Late Eocene and the subsequent Late Pshekhian Time.

By the end of the Early Pshekhian (marked by upper levels of the *Planorbella* Beds), the composition of the fish community shows marked changes, which indicate

<sup>2</sup> The occurrence in this assemblage of *P. latebrosus* Dan. (Fedotov, 1976) seems doubtful. This species is known only by the type specimen from the lower part of the Miatlin Horizon of the Gumista River (Danil'chenko, 1960).

<sup>3</sup> The fish assemblage of the *Planorbella* Beds was traditionally considered as a single faunal unit (Danil'chenko, 1960; Fedotov, 1976; Bannikov, 1985, 1990; Bannikov and Parin, 1997; Sytchevskaya, 1998). However, with the increase in knowledge of its composition, it became clear that the upper part of the beds contains a considerable number of the deepwater and warm-requiring forms, which is unusual for the typical community of these beds. This justifies distinguishing the older and younger *Planorbella* Beds fish subassemblages, the latter bearing resemblance with the Later *Aeoliscus* Beds Assemblage with respect to the ecology of the predominant components. It should be noted that even Danil'chenko (1960) detected scarce finds of some tropical and deepwater species, such as *Archaeolicus* (*Palaeotroctes*) *strictus* Dan. (Sternoptychidae) and *Doryrhamphus* (*Acanthognathus*) *squalidus* (Dan.) (Syngnathidae), in the upper part of the *Planorbella* Beds.

considerable warming. Here is recorded the rise and coming to predominance of tropical and subtropical forms, such as trachyichthyids [*Gephyroberyx robustus* (Bog.)], turkmenids (*Analectis pala* Dan.), digoriids (*Digoria ambigua* Dan.), syngnathids [*Doryrhamphus squalidus* (Dan.)], serranids (*Serranus comparabilis* Dan.), priacanthids (*Pristigenys spinosus* Dan.), carangids (*Caranx daniltshenkoi* Ban.), acanthurids (*Caprovesposus parvus* Dan.), stromateids (*Pinichthys pulcher* Ban.), nomeids (*Rybapina caucasica* Ban. and *Psenicubiceps alatus* Dan.), scombrids (*Scombrosarda cernegurae* (Ciob.) and *Sarda rara* Ban.), thunnids (*Thunnus* sp.), and balistids (*Oligobalistes robustus* Dan.), along with the development of clupeids (appearance of *Paretrumeus avitus* Dan.), congrid eels (*Pavelichthys daniltschenkoi* Ban. et Fed.), and paleorhynchids (Danil'chenko, 1960; Fedotov, 1976; Danil'chenko *et al.*, 1980; Fedotov and Bannikov, 1984; Bannikov and Tyler, 1992; Tyler and Bannikov, 1994; Sytchevskaya, 1998; Prokofiev, 2001, 2002), while the gadiforms decrease in their role. By the predominant adaptation patterns and composition, the Upper *Planorbella* Beds Subassemblage is close to the immediately succeeding *Aeoliscus* (= "*Amphisile*") Beds Assemblage, which allows one to consider the both communities as a single faunal stage. This, in terms of the development of the marine fish fauna, the biochronological demarcation between the Early and Late Pshekhian Time evidently lies within the *Planorbella* Beds time span rather than between it and the *Aeoliscus* interval (as was generally accepted).

The next succeeding assemblage comes from the *Aeoliscus* Beds and corresponds to the *Helicopontosphaera reticulata* NP22 Zone. It was a subtropical community dominated by the nearshore, neritic-pelagic, and mesopelagic fishes. A wide distribution of the latter, especially of the distribution of photophore-bearing fish, shows that, at that time, the bottom of the Paratethys in the Caucasian area descended to a depth of about 1000 m. In the community discussed, a great role was played by the species inherited from the Late *Planorbella* Beds Association. In contrast to their scarcity there, in the *Aeoliscus* Beds Assemblage, some of them grew in numbers, which occurred in parallel to the increase in the generic and species diversity of tropical and subtropical groups. At the same time, the role of the moderately thermophilic groups was reduced. In particular, the *Palaeogadus* species were much reduced in abundance and diversity while the osmerids vanished.

In all, at the Late Pshekhian Time, the Great Caucasian Basin was a subtropical sea with normal salinity, open for exchange with the marine faunas of the Mediterranean, Carpathian, and West European basins. It contained a fish community displaying a wide diversity of syngnathiforms, including the Centriscidae [*Aeoliscus heinrichi* (Heckel)], Urosphenidae (*Oligosphenopsis gracilis* Par.), Fistulariidae (*Fistularia contermina* Dan.), and the Syngnathidae (*Syngnathus incertus* Dan., *Doryrhamphus squalidus* (Dan.), *D. incolumnis*

Par., and *Maroubrichthys serratus* Par.). These taxa formed a rich fauna of the nearshore zone along with the littoral and sublittoral dwellers, such as trachinids (*Trachinus rusticus* Ban.), leiognathids [*Leiognathus altapinnus* (Weiler)], turkmenids [*Analectis pala* (Dan.)], sparids (*Sparus priscus* Swich.), champsodontids [*Champsodon* (= *Myersiscus*, = *Pseudoscopelus grossheimi* (Dan.)], platacids (*Paraplatex absyrtus* Bog.), ammodytids (*Ammodytes antipai* Paucá), balistids (*Oligobalistes robustus* Dan.), tetraodontids (*Archaeotetraodon winterbottomi* Tyler et Ban.), lophotids (*Oligolophotes fragosus* Ban.), and caproids [*Capros radobojanus* (Kramb.)]. The stromateids (*Pinichthys pulcher* Ban.) and nomeids (*Rybapina caucasica* Ban. and *Psenicubiceps alatus* Dan.) continued to develop.

The pelagic zone was abundantly populated by members of the clupeid subfamilies Clupeinae (*Sardinella sardinites* Dan.) and Alosinae (*Pomolobus facilis* Dan.), along with scombrids (*Scombro-sarda cerne-guræ* (Ciob.) and *Sarda rara* Ban.) and palaeorhynchids [*Palaeorhynchus zitteli* (Kramb.) and *Homorhynchus colei* (Ag.)]. For the mesopelagic zone detectable is the further development of euzaphlegids (*Palimphyes chadumicus* Dan. and *P. longirostratus* Dan.) and a great role played by the photophore-bearing forms: phosichthyids [*Eovinciguerria* (*Vinciguerria*) *obscura* Dan. and *E. talgiensis* Dan.], gonostomatids [*Scopeloides glarisianus* (Ag.)], sternoptychids (*Argyropelecus cosmovicii* Cosm. et Pauca),<sup>4</sup> and myctophids (*Eomyctophum menneri* Dan., *E. koraense* Dan., and *E. limicola* Dan.). The bregmacerotids (*Bregmaceros filamentosus*), first recorded in the Middle Eocene of Georgia and known to predominate in the Middle and Late Eocene fish assemblages of the Eastern Paratethys, appeared again (Bogachev, 1933, 1938, 1964; Menner and Ryabinin, 1949; Rozhdestvenskii, 1950; Danil'chenko, 1960; Fedotov, 1976; Switchenska, 1979; Danil'chenko *et al.*, 1980; Bannikov, 1985, 1986, 1988, 1993; Dzhafarova, 1988; Sytchevskaya, 1998; Prokofiev, 2001, 2002, in press). In a whole, characteristic of the Pshekhian Ichthyofauna is a great role played by the members of the autochthonous Tethyan genera retained from the Middle–Late Eocene: *Lyrolepis*, *Sardinella*, *Glossanodon*, *Archaeolicus*, *Eovinciguerria*, *Eomyctophum*, *Bregmaceros*, *Analectis*, *Pristigenys*, *Caprovesposus*, *Palimphyes*, *Scombro-sarda*, *Sarda*, *Rybapina*, *Anenichelum*, *Thunnus*, *Palaeorhynchus*, *Homorhynchus*, and *Oligobalistes*.

To summarize the pattern of faunal events of the Pshekhian Time, the following points are to be noted. The temperature conditions that existed in the Caucasian Basin at the beginning of the Early Oligocene obviously restricted the dispersal of tropical and subtropical forms, so that the fish community of the basin was built up in many respects at the cost of survived

autochthonous forms, along with a contribution from the more boreal taxa of Atlantic origin, such as the gadiforms and osmerids. Only later, with the warming of both the superficial and deepwater masses at the end of the Early Pshekhian, the basin was populated by the tropical and subtropical ichthyofauna, which most likely came from the southern refuges of the Tethys. This run of events obviously accounts for the enormous amount of those genera in the Pshekhian Fish Fauna that were inherited from the Tethyan Eocene Ichthyofauna. In the course of development of the Pshekhian Basin, it shows the change in the dominants of the mesopelagic communities. In the Early Pshekhian Time, this part was played by euzaphlegids, paralepidids, brotulids, trachyctyids, and mesopelagic gadids of the genus *Palaeogadus*, while the Late Pshekhian (*Aeoliscus* Beds) Assemblage was dominated by the photophore-bearing forms: phosichthyids, gonostomatids, sternoptychids, myctophids, and bregmacerotids. The development of the rich mesopelagic fish fauna enables one to assume that both the Early and Late Pshekhian basins could attain the depths about 1000 m. A significant part of the deepwater genera of the *Aeoliscus* Beds Fish Fauna of the Caucasus was also represented in the Carpathian Basin.

The next following stage of the history of the Ciscaucasian Marine Ichthyofauna is poorly known. It is represented by the Polbian Horizon Assemblage (NP23 Zone) showing a severe reduction in systematic diversity which indicates the shallowing and brackishening of the basin. The only taxa recorded from here are the clupeid *Sardinella* sp. and the scarce nearshore syngnathid *Syngnathus* sp. (Danil'chenko, 1960). Since both these forms were inherited from the *Aeoliscus* Beds Assemblage, they can be regarded as its eurybiontic component, which survived after the drop of salinity.

The youngest Early Oligocene assemblage is that from the basal level of the Morozkina Balka Horizon and its equivalents (lower part of the NP24 Zone). It corresponds to the end of the Rupelian and indicates the reestablishing of normal salinity in the basin. The sections of this stratigraphic level exposed in western Ciscaucasia (Belaya River) yield the following taxa: the Clupeidae [*Sardinella sardinites* (Heckel)], Argentinidae (*Glossanodon* sp.), Syngnathidae (*Hyposyngnathus*), Merlucciidae (*Palaeogadus simionescui* Dan. and *P. latebrosus* Dan.), Serranidae (*Serranus* sp. nov.), Percichthyidae (*Repropca* sp. nov.), Priacanthidae (*Priacanthus* sp. nov.), Caproidae [*Capros radobojanus* (Kramb.)], and Scombridae (*Sarda remota* Dan.). This nerito-pelagic community existed in the water space with considerable depths under moderately warm climatic conditions (Sytchevskaya, Bannikov, and Prokofiev, in press).

**Carpathian Basin.** The Early Oligocene marine fish fauna of the Carpathians is known from the localities of Romania, Czech, Poland, and Ukrainian Cis-Carpathians (Cosmovici, 1889, 1913, 1922, 1966; Paucá, 1934; Cosmovici and Paucá, 1943; Rozh-

<sup>4</sup> The presence here of *Argyropelecus cosmovicii* is in question (Jerzmańska and Kotlarczyk, 1983).



destvenskii, 1950; Jonet, 1958; Jerzmańska, 1960, 1968, 1974; Gorbach, 1961a, 1961b; Ciobanu, 1970, 1977, 1978). The composition of this fauna and the stratigraphic position of many its constituent elements need revision.<sup>5</sup> A correlation of the Carpathian assemblages is also hampered by controversial assessments of data on the accompanying nannoplankton microfossils.<sup>6</sup>

An important piece of data on the Rupelian history of the regional marine ichthyofauna is provided by the Menilithic–Krosno Series of the Polish Carpathians. In this unit, there were distinguished the six ichthyozones, which span a sequence of stratigraphic levels from the Oligocene to Early Miocene, (Jerzmańska and Kotlarczyk, 1980, 1981, 1983; Kotlarczyk and Jerzmańska, 1988). The lowermost of them, Ichthyozone IPM1, or the lower bathypelagic assemblage is characterized by the following index taxa: *Scopeloides glarisianus* (Ag.) (Gonostomatidae), *Eomyctophum limicola* Dan. (Myctophidae), *Aeoliscus heinrichi* (Heckel), *A. teleajensis*, and *A. longispinus* (Centriscidae). According to the latest interpretation by Kotlarczyk and Jerzmańska (1988), this faunal unit is correlated with the interval ranging from the upper part of Zone NP21 to the lower half of NP23.

In the younger Ichthyozone IPM2, attributed to the upper part of NP23, the typical forms are the gadid species *Paleogadus simonescui* and the argentinoid *Glossanodon musceli*. The assemblage is estimated as the neritic-sublittoral community devoid of deepwater components, which is believed to evidence the shallowing of the basin in comparison to the preceding epoch. The next following two ichthyozones, IPM3 [with the index species *Bregmaceros filamentosus* (Priem), *Kotlarczykia bathybia* Jerzm., and *Polyipnus brevis* Gorb.] and IPM4 (with *Polyipnus sobniovensis* Jerzm.), tentatively equated to the lower and upper parts of the NP24 Zone respectively (Kotlarczyk and Jerzmańska, 1988), are designated as the upper bathypelagic assemblage (Jerzmańska and Kotlarczyk, 1983), whose further evo-

lution is represented by the ichthyozones IPM5 and IPM6 (Late Oligocene–Early Miocene).

Correlation of these events revealed in the Carpathian Rupelian with the evolution of the Early Oligocene ichthyofauna of the Caucasus and Ciscaucasia remains somewhat unclear. According to Jerzmańska and Kotlarczyk (1980, 1983), the Carpathian Ichthyozone IPM1 (the lower bathypelagic assemblage) can correspond to the both of main faunal levels of the Pshekhian Horizon in Caucasia, i.e., the *Planorbella* and *Aeoliscus* Beds assemblages. Judging from current datings of these faunas in terms of the nannoplankton zonation (NP21–NP22 for Ciscaucasia, and NP21 to the base of NP23 for Polish Carpathians), such a correlation looks plausible. However, it is not immediately corroborated by the comparison of these regional faunas.

In fact, the above viewpoint would imply that the time range of the lower bathypelagic fish assemblage of the Carpathian Basin should correspond to three different events in the history of the Caucasian Basin (see above): (1) the existence of the impoverished relict post-Eocene community (just before the “*Planorbella*” Time); (2) the formation of community with admixture of moderately thermophilic forms and the boreal forms of Atlantic origin (Early “*Planorbella*” Time); only after that (3), the appearance of subtropical communities with the mesopelagic component dominated by phosichthyids, gonostomatids, myctophids, and sternopychids (Late Pshekhian Time, spanning the Late “*Planorbella*” and “*Aeoliscus*” intervals).

In this sequence, the main faunal replacement, first noted by Danil’chenko (1960), is expressed as a difference between the Early Pshekhian Fish Assemblage, yielded by the *Planorbella* Beds (Early “*Planorbella*” Subassemblage in our interpretation), and the mesopelagic assemblage of the *Aeoliscus* Beds. It is only the latter that is directly comparable with Ichthyozone IPM1 of the Carpathians. Correspondingly, all the parallels between this zone and the Pshekhian Ichthyofauna stressed by Kotlarczyk and Jerzmańska (1988) to ground their concept of correlation, such as the presence of *Scopeloides glarisianus* (Ag.), *Eomyctophum limicola* Dan., *Aeoliscus heinrichi* (Heck.), etc., refer only to the “*Aeoliscus*” Assemblage.

To account for the difference between the Early and Late Pshekhian ichthyofaunas, the above-cited authors referred to the strictly ecological factors, on presumption that in the “*Planorbella*” Time the Caucasian Basin was still too shallow to enable the wide distribution of the deepwater forms typical of the “lower bathypelagic assemblage” (Jerzmańska and Kotlarczyk, 1983). However, this hypothesis does not explain the contrast between the abundance of the boreal taxa in the Early Pshekhian Assemblage (six species of *Palaegadus*, along with the presence of osmerids) and their scarcity in both the Late Pshekhian Fauna and Carpathian Ichthyozone IPM1. The same concerns the contrast between subordinate role of the tropical elements

<sup>5</sup> This refers, in particular, to the richest assemblage of Peatra Neamț in Romania which is reported to include (along with Early Oligocene forms) some taxa common for the Miocene. For example, the set of the local deepwater taxa is said to include *Vinciguerrria merclini* Dan., which is known from the Tarkhan deposits of the Caucasus and Crimea (Ciobanu, 1977).

<sup>6</sup> For instance, this is the case for the ichthyozones distinguished in the Polish Carpathians by Kotlarczyk and Jerzmańska (1980, 1988; Jerzmańska and Kotlarczyk, 1981). At different times, they equated the lower ichthyozones IPM1 and IPM2 with either the nannoplankton NP22 Zone, based on the data by Martini and Lebzom (1971), or the end of NP21 plus NP22, or, finally, concluded that most of the IPM1 Ichthyozone corresponds to the end of NP21 plus NP22, while its upper part belongs to the lower half of NP23 (cf. Kotlarczyk, Jerzmańska, 1988). In addition, it remains unclear which particular Ichthyozone within the sequence established for the Polish Carpathians actually conforms to the end of the Early Oligocene. Formerly, this age was implied for Ichthyozone IPM4, but later, this zone was supposedly assigned to the upper part of NP24 which should mean that it belongs to the Late Oligocene (cf. Jerzmańska and Kotlarczyk, 1981; Kotlarczyk and Jerzmańska, 1988, p. 348).

in the Early Pshekhian Assemblage and abundance of them (both in diversity and numbers), especially the syngnathiforms and deepwater photophore-bearing taxa, in both the “*Aeoliscus*” Assemblage and the basal Ichthyozone IPM1 of the Carpathian Oligocene. In two latter communities the above-named groups include a number of shared species, such as *Aeoliscus heinrichi* (Heckel), *Eovinciguerrria* (*Vinciguerrria*) *obscura*, *Eomyctophum menneri*, *E. koraense* Dan., and *E. limicola* Dan. (Danil’chenko, 1960; Jerzmańska, 1968; Jerzmańska and Kotlarczyk, 1983).

In the light of these facts, it seems very likely that, in reality, Carpathian Ichthyozone IPM1 conforms only to the *Aeoliscus* Beds Assemblage (NP22 Zone) as was formerly assumed by Polish authors (Kotlarczyk and Jerzmańska, 1976). The equivalents of the earlier Caucasian ichthyofaunas, reflecting the invasion of the boreal taxa and gradual increase in the role of tropical forms, could also occur there, but they have not been found. This view is in accord with the fact that, in Ichthyozone IPM1, the mass finds of the genus *Aeoliscus* fall on the middle part of the zone but are lacking in its basal part (Kotlarczyk and Jerzmańska, 1976; Jerzmańska and Kotlarczyk, 1983, pp. 4–5).

The next point to be discussed with respect to the Early Oligocene fish faunas of the Caucasus and Polish Carpathians is a comparison of their terminal assemblages. If one follows the dating of the Carpathian ichthyozonal succession (in terms of NP zones) accepted by Kotlarczyk and Jerzmańska (1988), the Caucasian fish assemblages of the Polbian Horizon and of the lower part of the Morozkina Balka Horizon should be equated to the Carpathian ichthyozones IPM2 and IPM3, and, possibly to a part of IPM4. If this is the case, the episode of shallowing and brackishing distinguished in the Caucasian Basin as the Polbian Horizon can probably be correlated with the nerito-pelagic assemblage IPM2 containing the index species *Palaeogadus simionescui* Dan. and *Glossanodon musceli* (Pauca). Likewise, the younger community of the basal part of the Morozkina Balka Horizon may correspond to a more deepwater Carpathian assemblage of Ichthyozone IPM3 with *Bregmaceros filamentosus* (Priem.), *Kotlarczykia bathybia* Jerzm., and *Polyipnus brevis* Gorb. Hence, on the strength of evidence provided by the fish fauna, at the end of the Early Oligocene, the Carpathian Basin was deeper and did not suffer freshening, which was so markedly expressed in the Caucasian Basin during the Polbian Time. The data on the Early Oligocene fauna of Moravia (Gregorová, 1988), showing the presence there of at least two lower ichthyozones that were recognized for the Polish Carpathians, corroborate these conclusions.

In the Romanian Carpathians, the Early Oligocene ichthyofauna is known from the Brown Marls and the overlying Lower Disodylic Schists, which are assigned together to zones NP21–NP23 and the base of NP24 (Melinte, 1995; Rusu *et al.*, 1996). In these units, the

stratigraphic distribution of fish fossils has not been studied in detail. The fauna is known from a number of localities (Homoriču, Suslanești, Peatra Neamț, etc.) and comprises a rich set of the littoral–sublittoral, pelagic, neritic, and mesopelagic fishes (Cosmovici, 1889, 1913, 1922, 1966; Pauca, 1934; Cosmovici and Pauca, 1943; Jonet, 1950, 1958, 1971; Ciobanu, 1970, 1973, 1975, 1977). In the Early Rupelian (Brown Marls of the Peatra Neamț locality), there were abundantly represented the various pelagic clupeids: *Sardinella rata* Dan., *S. denticulata* Ciob.\*,<sup>7</sup> *Alosa sculptata* Weiler, *Pellonula gracionescui* Ciob.\*, and *Pomolobus facilis* Dan.; neritic argentinoids [*Glossanodon musceli* (Pauca)], trichiurids (*Anachelum glarisianum* Blainv.); caproids [*Capros radobojanus* (Kramb.)\*]; priacanthids [*Pristigenys spinosus* (Blainv.)], leiognathids [*Leiognathus altapinnus* (Weiler)]; and a number of mesopelagic groups such as brotulids (*Propteridium profundae* Ciob.\*), merlucciids (*Palaeogadus intergerinus* Dan.), gonostomatids [*Scopeloides glarisianus* (Ag.)], sternoptychids [*Archaeolicus?* (*Vinciguerrria*) *macarovicii* (Ciob.)],<sup>8</sup> and various myctophids of the genera *Myctophum*\* (*M. weileri* Ciob., *M. praeptertum* Ciob., *M. robustus* Ciob., and *M. antelatarnatum* Ciob.), *Lampanictus* (*L. longaevus* Ciob.), and *Diaphus* (*D. duosensitivus* Ciob.) (Ciobanu, 1977). This assemblage was largely formed by inhabitants of a deep warm marine basin with oceanic salinity. It displays certain relationships to the Caucasian *Planorbella* Beds Ichthyofauna by the presence of *Sardinella rata* Dan., *Pomolobus*, *Glossanodon*, *Palaeogadus intergerinus* Dan., *Anachelum glarisianum* Blainv., and *Pristigenys spinosus* (Blainv.) but differs by the abundance of deep-water photophore-bearing taxa (which in the Caucasus first appear in the younger *Aeoliscus* Beds) and by a lower diversity of the gadid genus *Palaeogadus*, which is represented here by a single species, *P. intergerinus* Dan. These features may point to a mixed origin of the assemblage, which appears to combine some typical mesopelagic components of the “*Aeoliscus*” community with those of the earlier assemblage from the basal Oligocene.

The second half of the Rupelian (the Lower Disodylic Schists) in the Romanian Carpathians is documented by a mixed fish assemblage, which embraces the late Early Oligocene communities of different age. Here is recognized the presence of the index taxa of Ichthyozone IPM1 of the Polish Carpathians (*Aeoliscus heinrichi*, *Scopeloides glarisianus*, and *Eomyctophum limicola*), which are associated with a number of typical species of the mesopelagic, pelagic, and nearshore communities known in the *Aeoliscus* Beds Assemblage

<sup>7</sup> The taxa marked with the asterisk need to be revised.

<sup>8</sup> According to the data by Prokofiev (2002), the attribution of *Vinciguerrria macarovicii* to the Phosichthyidae is doubtful. This form appears to be close to the genus *Maurolicus* (Oligocene–Recent) or *Archaeolicus* (Oligocene) and belongs to the Sternoptychidae. *V. praeattenuata* is possibly a synonym to *Eovinciguerrria obscura*.

of the Caucasus: *Eovinciguerrria* (*Vinciguerrria*) *obscura* (Dan.)\*, *E. talgiensis* (Dan.), *Eomyctophum koraense* Dan., *E. limicola* Dan., *E. menneri* Dan., *Pomolobus facilis* Dan., *Scombrosarda cernegurae* (Ciob.), *Aeolisiscus heinrichi* (Heckel), and *Syngnathus incertus* Dan.

**Balkan Basin.** In this basin, the Early Oligocene ichthyofauna is known from several localities of Slovenia and Serbia (Gorjanović-Kramberger, 1882a; Anđelković, 1989). In Slovenia, the Rupelian contains an impoverished marine fish assemblage, which is recorded in the Sava River basin (Inner Dinarids) and stratigraphically positioned above the beds with *Anthracotherium*. It includes *Clupea alta* Steind., *C. mucronata* Kramb., *Sardinella* (*Clupea*) *sardinites* (Heckel), *Alosa sagorensis* (Steind.) (Clupeidae), *Morone lata* (Kramb.), *M. elongata* (Kramb.), *M. mojsisovicsi* (Kramb.), *M. stiriaca* (Rolle), *M. sagorensis* (Kramb.) (Moronidae), *Anenchelum?* (*Lepidopus*) *caudatum* (Trichiuridae), *Scomberomorus* sp. (Scombridae), *Thunnus planovatus* (Kramb.) (Thunnidae), *Palaeorhynchus riedly* Kramb., *P. deschmani* (Palaeorhynchidae), *Serranus validus* Kramb., *S. stiriacus* Kramb. (Serranidae), *Caranx gracilis* Kramb., *Lichia alta* Kramb. (Carangidae), *Sparus hertlei* (Kramb.), *Sparnodus inflatus* Kramb. ?*Pargus* sp. (Sparidae), *Chaetodon hoeferi* Kramb. (Chaetodontidae), *Zeus robustus* (Zeidae), *Rhinoptera* aff. *studeri* (Myliobatidae), *Gadus?* sp. (Gadidae), *Saurodon* cf. *phlebotomus* (Cope) (Saurocephalidae), and *Isurus* sp. (Isuridae) (Gorjanović-Kramberger, 1882, 1884, 1895; Anđelković, 1989).<sup>9</sup> The assemblage populated relatively shallow warm sea with some zones of reduced salinity, as indicated by abundance of moronids (preferring the fresh- and brackishwater settings) and by a possible admixture of cyprinids (*Barbus crenatus*). Most forms were the nearshore and pelagic inhabitants. Some of the genera are also known from the Rupelian of Western and Central Europe and (or) the Caucasus (*Clupea*, *Alosa*, *Sardinella*, *Serranus*, *Caranx*, *Morone*, *Sparus*, *Lepidopus*, *Thunnus*, *Scomberomorus*, and *Palaeorhynchus*). Some degree of freshening evidenced by the Slovenian Ichthyofauna enables one to suggest its proximity to the poorly known assemblage of the Polbian Horizon of the Eastern Paratethys.

**Belgian Basin.** In this area, the fish community of the Upper Tongrian (the basal Oligocene) demonstrates the loss of most of the Late Eocene tropical forms. On the other hand, it comprises *Odontaspis acutissima* and *Myliobatis* sp., which survived from the Lower Tongrian (Eocene). The increase in taxonomic diversity is demonstrated by the younger assemblage of the Berg Sands comprising *Squatina angeloides*, *Odontaspis acutissima*, *O. cuspidata*, *Notidanus primigenius*, *Lamna rupeliensis*, *Oxyrhina desori*, *O. benedeni*, *Galeus latus*, *Chimaera gosseleti*, *Myliobatis aguila*, and *Cybium dumonti*. The tropical and temperate forms

predominate; the presence of *Chimaera* testifies to some cooling (Leriche, 1910).

The later assemblage of the Boom Shales shows further diversification and, in particular, the appearance of the abyssal forms (*Macrurus*), which indicates the deepening of the basin. At that time, a great variety of the subtropical genera existed in the pelagic and littoral zones, such as *Sarda*, *Cybium*, *Neocybium*, *Xiphias*, *Sphyraenodus*, *Scombramphodon*, *Glyptorhynchus*, *Sparus*, *Eutrichiurides*, and *Trigla*. Their presence provides evidence of warming. However, distinct from the Carpathian and Caucasian basins, the development of the rich deepwater mesopelagic fauna is not observed and the photophore-bearing taxa are absent. Likewise, there is no tropical syngnathiforms that constituted one of leading components in the Caucasian and Carpathian communities of the same age. In general, the Belgian Rupelian Ichthyofauna differed from other coeval European assemblages in showing a more important role of the boreal and Arctic forms, which undoubtedly reflected a greater influence of the Atlantic Ichthyofauna. On the other hand, the relationships of the Belgian Fauna with other Rupelian fish communities of Europe are proved by the presence in them of the shared genera of sharks and scombrids. The present data are not enough to substantiate the establishment of the Belgian Rupelian Fauna as a separate biogeographic unit, but such a possibility is not ruled out with the increase in knowledge of its composition.

**Basins of Central and Western Europe.** The Rupelian fish faunas of Central and Western Europe need revision. The bulk of pertinent data come from the fish schists of the Bavarian-Switzerland Molasse, Rhine Valley, and northeastern France. These beds are of a different age and stratigraphic position (Rath, 1859; Weiler, 1922, 1928, 1931, 1932, 1953, 1963, 1966; Leriche, 1927, 1927-1928, 1941; Theobald, 1934; Frohlicher and Weiler, 1952; Hess and Weiler, 1955; Micklich and Parin, 1996; Pharissat and Micklich, 1998). Of the assemblages yielded by them, the earliest one apparently comes from the Glarus Canton in Switzerland and is distinguished in that it contains deepwater elements. For most other faunal assemblages (usually assigned to the Middle Rupelian), typical is the presence of the beds with *Aeolisiscus* (“*Amphisile*”) and clupeid beds with “*Meletta*”, attributed to zones NP23 and NP24, respectively (Martini and Müller, 1971).

In Switzerland, the Rupelian fish assemblage includes the mesopelagic gonostomatids [*Scopeloides glarisanus* (Ag.)], euzaphlegids (*Palimphytes chadumicus* Dan.), and merlucids [*Palaeogadus crassus* (Ag.)], along with trichiurids (*Anenchelum glarisanum* Blainv.), fistulariids (*Fistularia koenigi* Ag.), gempylids (*Thyrsocephalus*), scombrids, palaeorhynchids [*Palaeorhynchus*, *Homorhynchus colei* (Ag.)], ariommids [*Isurichthys macrurus* (Ag.)], balistids (*Acanthoderma*), etc. (Rath, 1859; Wettstein, 1886). This community is indicative of the warm deep basin

<sup>9</sup> Most taxa of this ichthyofauna need revision.

and may be compared to Ichthyozone IPM1 of the Polish Carpathians as well as to the entire Pshekhian Fauna of the Caucasus, since it contains a number of forms common for both the Early *Planorbella* Beds Subassemblage and the *Aeoliscus* Beds Assemblage.

The one more Early Rupelian assemblage might be represented by that of Aschwil in Central Europe (Weiler, 1955). It is close to the *Aeoliscus* Beds Assemblage of the Pshekhian Horizon of the Caucasus and to Ichthyozone IPM1 of the Carpathians by the presence of the genera *Pristigenys*, *Leiognathus*, *Palimphyes*, *Sarda*, and *Palaeorhynchus* (apart from common syngnathiforms). However, the absence here of the deepwater elements, in contrast to the Carpathian–Caucasian Early Rupelian fish faunas, precludes their unequivocal correlation.

Of the apparently younger Rupelian ichthyofaunas of Western Europe, the most comprehensively studied are those from the northeastern France (Froidefontaine, the Belfort area) and Germany (Frauenweiler, south of Heidelberg) (Weiler, 1931, 1966; Theobald, 1934; Pharissat, 1991, 1992; Micklich and Parin, 1996; Pharissat and Micklich, 1998). Both are thought to correspond to zones NP23–NP24 (Müller, 1970).

In France, the Froidefontaine Assemblage includes 36 species of sharks and teleosts which dwelled in a shallow and warm sea of normal salinity (Pharissat, 1991). Two successive assemblages are distinguished here, both having the same species composition, with the younger one (that of “*Meletta*” Beds) being distinct in smaller body size of the forms recovered. In addition, the earlier assemblage was dominated by the syngnathiform *Aeoliscus heinrichi*, while the later assemblage was dominated, by the clupeid *Sardinella sardinites* (Heckel). The shallow nearshore zone was populated by the Aulostomidae and Syngnathidae, along with the acanthopterygians *Capros*, *Serranus*, *Properca*, *Caranx*, *Sparus*, *Pristigenys*, *Leiognathus*, *Trachinus*, etc.; the epipelagic component included *Anachelum glarisianum* Blainv., *Palaeorhynchus glarisianus* (Blainv.), and the Scombridae (*Sarda*, *Cybium*, *Sphyraenodus*, and *Glyptorhynchus*) (Pharissat, 1991). On the whole, by the set of the dominants contained, this assemblage is most close to that of Frauenweiler (see below) and, along with the latter, characterizes the seas of the epoch of the Early Oligocene transgression.

In Germany, the Rupelian assemblage of Frauenweiler (Micklich and Parin, 1996; Pharissat and Micklich, 1998) similarly displays a broad scope of taxa, including over 40 genera that pertain to 32 families and 13 orders. The sharks and rays include *Physogaleus* (*Eugaleus*) *latus* (Storms), *Galeocerdo* sp., *?Rhizoprionodon* sp., *Synodontaspis acutissima*, *S. cuspidata*, *Alopias* (*Alopecias*, *Vulpecula*) *exigua*, *A. latidens*, *Cetorhinus parvus*, *Isurus desori*, *Lamna rupeliensis*, *Charcharocles* (*Charcharodon*) *angustidens*, *Notorhynchus primigenius*, *Squalus alsaticus?*, *Squatina angeloides?*, *Myliobatis oligocaena*, and *M. serratus*.

The teleosts comprise elopids (cf. *Elops* sp.), congrid (cf. *Conger* sp.), clupeids (*Sardinella sardinites* and *Alosa sculptata?*), phycids (*Eophycis* sp.), merlucciids (*Palaeogadus emarginatus* and *P. cf. intergerinus*), hemiramphids (*Hemiramphus jerzyi*), caproids (*Capros longispinatus* and *C. radobojanus*), aulostomids (*Aulostomus medius* and *Frauenweilerstomus synarcualis*), urosphaenids (*Oligosphenopsis* cf. *O. gracilis*), centriscids (*Aeoliscus heinrichi* and *A. distinctus*), syngnathids (*Doryrhamphus* sp., *?Microphis* sp., and *Syngnathus incompletus*), moronids (*Dicentrarchus* sp.), serranids (*Properca sabbai* and *Serranus budensis*), priacanthids (*Pristigenis spinosus*), eheneids (cf. *Eheneis*), carangids (*Caranx* cf. *glarisianus*), bramids (*Pterycombus* sp.), sparids (*Sparus* cf. *S. schopii*), trachinids (*?Trachinus minutus*), ehipids (*?Archaephippus* sp.), sphyraenids (*Sphyraena* sp.), gempylids (cf. *Gempylus* sp. and cf. *Epinnula* sp.), trichiurids [*Anachelum* (*Lepidopus*) *glarisianum* and *Eutrichiurides* (*Trichiurides*) *delbeidi*], scomprids [*Scomber* sp., *Scomberomorus* (*Cybium*) *lingulatus*, *Sarda brachycephala*, *Scombrsarda* sp., *Scombramphodon* sp., and *Sphyraenodus* sp.], palaeorhynchids (*Palaeorhynchus glarisianus*), xiphiids (*Xiphias rupeliensis?*), nomeids (*?Psenicibiceps* sp.), stromateids (*Pinichthys* cf. *P. pulcher*), Psettidoidei indet., and Pleuronectoidei indet.

The core of this assemblage was formed by the taxa of southern origin, which appear to have come from the southeastern Paratethys (Pharissat and Micklich, 1998). Along with that, there was a limited group of immigrants from the Atlantic indicating links with that region. The occurrence of a few mesopelagic forms points to a moderate depth; on the other hand, the abundance of syngnathiforms and littoral forms characterizes the rich nearshore communities. The presence of the taxa shared with the faunas of the Carpathians and Caucasus (Danil'chenko, 1960; Jerzmańska, 1968; Danil'chenko *et al.*, 1980; Pharissat, 1992; Micklich and Parin, 1996; Pharissat and Micklich, 1998) reflects the interconnections with these basins. It worth noting that the above-surveyed principal West European assemblages of the Middle Rupelian (Froidefontaine and Frauenweiler) were devoid of the bathypelagic photophore-bearing forms, which differs them from the Carpathian and Caucasian *Aeoliscus* (= “*Amphisile*”) faunas synchronized with Zone NP22. Judging by their datings in terms of the nannoplankton zonation (NP23–NP24), these assemblages should correspond in age to the poorly known terminal Rupelian faunas of the Eastern Paratethys, i.e., to those of the Polbian Horizon and the basal part of the Morozkina Balka Horizon. In a broad sense, all these faunas inhabited relatively shallow seas. By contrast, the coeval faunas of the Carpathians (ichthyozones IPM2–IPM4?) belong to the basins of considerable depth.

**Discussion.** Heterogeneity and marked differentiation of the marine fish communities observable in the Carpathian and Caucasian realms during the Early Oligocene make one very cautious when comparing the faunas of that age known from various regions of the Paratethys, since the distinctive features of particular basins reflected by them may be related to the different time intervals. Hence, the analysis of spatial differentiation of the Paratethyan Rupelian fish faunas heavily depends not only on the knowledge of their composition but also on the dating accuracy for the assemblages under comparison. At present, the data on the distribution patterns of the regional fish faunas are not enough to elaborate a clear picture of the overall biogeographic structure of the Paratethys in the Early Oligocene. Only a few more or less common events of different scale, characterizing the history of the fish fauna of the realm under discussion may be currently outlined. They are as follows:

(1) The development of the Rupelian marine fish faunas of Europe started on the basis of the autochthonous Tethyan Ichthyofauna whose local communities were abundantly represented by the assemblages of the Caucasus, Carpathians, and the Mediterranean. During the Rupelian, the faunal evolution was mostly controlled by the changes in salinity and depth of the local basins along with changes in climatic conditions. The faunal exchange detectable for the Rupelian Time demonstrates that the particular Paratethyan basins were open for interconnection to a considerable extent.

(2) The earliest faunal event of the Rupelian Time, most readily detected in the Belgian Basin (Upper Turgian) and Caucasian Basin (sub-*Planorbella* level), was the appearance of the impoverished fish assemblages formed mostly by the survivors of the preceding Late Eocene fauna. Subsequently, they were enriched by the boreal (Atlantic) newcomers and the further evolution of autochthonous elements.

(3) As early as the first half of the Rupelian (at the end of the Early Pshekhian Time), with the increase in temperature in both surface and deep waters of the Caucasian Basin, there was started a wide expansion of the tropical and subtropical elements that most likely came from the Tethyan refuges, judging by the presence in the Pshekhian Fauna of a great amount of the genera inherited from the Tethyan Eocene Ichthyofauna. These trends were accompanied by the deepening of most basins, which resulted in the appearance in some cases of a great variety of photophore-bearing forms and the overall development of the rich mesopelagic fish biota. This condition persisted into the Mid-Rupelian (*Aeolis-cus* Beds time span) and is best typified by the fish communities of the Caucasian and Carpathian basins and, to some extent, by that of the Alpine Basin.

(4) The succeeding event, recorded to various degrees in some parts of the Paratethys, was the shallowing and (or) brackishing of the basins. This was most markedly expressed in the Eastern Paratethys

(Polbian Horizon) and not so much in the Carpathian Basin. Some evidence of brackishing is recorded for the Balkan Basin. The coeval West European basins were of moderate depth, with the fish fauna including a great variety of the nearshore dwellers.

(5) By the end of the Rupelian, a full salinity of the Paratethys was restored. This was accompanied by the deepening of some basins, which was moderately expressed in the Eastern Paratethys and much more strongly in the Carpathian Basin (which resulted in reappearance here of the mesopelagic fauna).

In summary, it may be concluded that, based on the present evidence, the Paratethyan marine fish faunas of the Early Oligocene appear to have developed within a single biogeographic province. It is not ruled out that with further increase in data it will be possible to ground the biogeographic discrimination of the West European, Carpathian, and Caucasian fish faunas of the terminal Rupelian. One more possibility is the distinguishing in the future of a separate Iranian Province.

#### *Smaller Benthic Foraminifers*

Abrupt paleogeographic, climatic, and faunal changes in the terminal Eocene—at the beginning of the Oligocene resulted in similar abrupt changes in the composition of small benthic foraminiferal assemblages throughout the Northern Peri-Tethys. The taxonomic diversity and the faunal abundance markedly decreased, whereas the tests became small and medium in size. However, such changes did not mean substantial evolutionary changes in this group, because, in warm seas, where carbonate sedimentation continued (Mediterranean Sea and Armenian Gulf), numerous species—descendants from the Eocene were found in the Oligocene assemblages (up to 46%, after Krashennikov, in *Geologicheskije i bioticheskie...*, 1998). It was established that the evolutionary changes of benthic foraminifers in oceanic basins were very gradual, without catastrophic extinction (*Geologicheskije i bioticheskie...*, 1998). Certain groups of organisms were simply replaced by others. Such changes are observed at different levels, in the terminal Eocene and at the Eocene–Oligocene Boundary.

**Northern Mediterranean Region.** Tropical and subtropical fauna of the Mediterranean Region is known from northern Italy, and Armenia, where, apart from small foraminifers, nummulitid assemblages were distributed and reef facies developed. The composition of the foraminiferal assemblages indicates the shelf environments closely similar to those in the terminal Eocene. Thus, in northeastern Italy, a coral reef biofacies was found (Frost, 1981), in which the foraminiferal assemblages markedly differed from the North European and Chadumian assemblages in generic composition, including *Halkyardia*, *Chapmanina*, *Asterigerina*, and the Gypsinidae. Northern Italy and northern Spain were also inhabited by thermophilic genera. *Halk-*



*yardia*, *Chapmanina*, *Borelis*, *Haddonina*, *Gyroidinella*, *Asterigerina*, and *Sphaerogypsina* are known from the northern Adriatic coasts, where reef facies are present (Pavlovec *et al.*, 1986).

The Oligocene foraminiferal assemblage from Armenia is very rich and diverse and includes over 70 species of 53 genera. This assemblage differs in both specific and generic composition from the Paratethyan Assemblage, because it includes many Tethyan species (Bugrova, 2001). These are species of the genera *Almaena*, *Queraltina*, *Herondenia*, *Pseudoplanulinella*, *Sphaerogypsina*, *Asterigerina*, *Rotalia*, and *Pararotalia*. In addition, this assemblage includes a few species that are known from West European basins (*Valvulineria petrolei*, *Cibicidina amphisyliensis*, *Svratkina perlata*, *Rotaliatina mamillata*, *Turrilina alsatica*, *Angulogerina gracilis*, *Bitubulogerina kasselensis*, *Bolivina melettica*, and *Spiroloculina canaliculata*). Some of these species, as well as *Melonis dosularenensis*, *Heterolepa almaensis*, *Vsegeina nana*, and *Falsoplanulina*, sp. nov., were also found in the assemblages from the Crimean–Caucasian area of the Pshokhian (Chadumian) Basin. In addition, this area is inhabited by endemic species and species that were only found in Azerbaijan (species of the genera *Bolivia*, *Chilostomella*, and *Pararotalia*). Such a mixed composition of fauna indicates the presence of contacts of the Yerevan Basin with the open Mediterranean Basin and with the neighboring Azerbaijan Basin. There was probably no direct connection with the Greater Caucasus Basin.

**Eastern Mediterranean.** Benthic foraminifera dominate the Oligocene assemblages from Syria. Three zones were distinguished based on the differences in the temporal compositions of the benthic foraminiferal assemblages (Krasheninnikov, 1969). The fauna from the lower zone, the *Almaena taurica* Zone, included typical Late Eocene species and certain species that appeared in the Oligocene of the Crimea and Caucasus. The majority of species of the middle zone, the *Cibicidoides pseudoungerianus* Zone, including the zonal species *Cibicidoides oligocenicus*, *Cibidina amphisyliensis*, *Melonis dosularenensis*, *Angulogerina gracilis*, etc., are typical of the assemblage of the *Lenticulina herrmanni* Local Zone from the Caucasus–Kopet Dagh Basin (*Reshenie kollokviuma...*, 1970). The thermophilic species that were only found in the Tethyan part of the basin are absent from the two upper zones.

**Eastern Atlantic.** In the Oligocene, the Aquitaine Basin was still characterized by very warm water, as indicated by the presence of the Tethyan genera *Bullalveolina*, *Sphaerogypsina*, *Amphistegina*, *Halkyardia*, *Queraltina*, *Victoriella*, *Falsocibicides*, *Carpenteria*, *Eorupertia*, etc. (Boulinger and Poignant, 1971; Boulinger *et al.*, 1970), which are often associated with reef beds. This fauna has no equivalents among the assemblages from the northeastern marginal areas of the Paratethys.

Numerous miliolids (*Quinqueloculina*, *Articulina*, and *Spiroloculina*), Polymorphinidae (*Globulina* and *Guttulina*), and the genera *Discorbis*, *Nonion*, *Cibicidoides*, and *Planorbulina* widespread in the Lower Stampian of the Paris Basin (see *Syntese geologique...*, 1980) indicate facial individuality of the assemblage, which do not include the species characteristic of the North Sea and Paratethyan faunas. One hundred and ten species of benthic foraminifera were recorded there (after LeCalvez).

**North Sea Basin.** In the basin of northwestern Europe (Alsace, Belgium, Holland, and Germany), the *Rotaliatina bulimoides*–*Cibicidoides ungerianus* assemblages were distributed (Doppert and Neele, 1983; Andreae, 1884). Many species from these assemblages, including *Lenticulina herrmanni*, were described from the Alsace Basin (Andreae, 1884). *Rotaliatina bulimoides*, *Svratkina perlata*, and *Turrilina alsatica* are present only in these assemblages, whereas *Cibicidoides ungerianus*, *C. sulzensis*, *Ceratobulimina contraria*, and *Hoeglundina elegans* appeared there and were widespread in the Eastern Paratethys. The North Sea Basin was inhabited by some of these species, *Svratkina perlata*, *Rotaliatina bulimoides*, and *Turrilina alsatica*, as well as *Ceratobulimina contraria* (Gramann and Hiltermann in *Colloque...*, 1964).

In the region of the English Channel (Isle of Wight in the southern area of England), the fauna is similar to that from the Belgian Basin. Sixty-two species of 33 genera are known from this region (Bhatia, 1958). The foraminiferal assemblages are facially changeable, but usually dominated by secreting (Miliolidae and the genera *Nonion*, *Rotalia*, *Valvulineria*, *Bulimina*, and *Buliminella*).

In the Norwegian–Greenland Basin (Knipovich Ridge), the foraminiferal assemblages were similar to those from the North Sea basins but slightly impoverished. This basin was inhabited by *Pullenia quinqueloba*, *Nonionella* aff. *odiliae*, *Alabamina tongentialis*, *Pseudoparrella oveyi*, *Cibicidoides sulzensis*, *Globocassidulina* aff. *oblonga*, *G. subglobosa*, *Bulimina* cf. *elongata*, *Buliminella elegantissima*, *Fursenkoina schreibersiana*, *Bolivina melettica*, and *B. variabilis* (the total of 17 species after Bugrova *et al.*, 2001). Foraminifera were small in size and thin-walled, which indicates environments unfavorable for the secreting forms. Representatives of the orders Nodosariida and Polymorphinida, which, in association with miliolids and nonionids, predominated in the assemblages from Belgium, Germany and England, were absent from this basin.

The foraminiferal assemblage that inhabited the western area of Belgium includes 49 species of 27 genera (Willems, 1972). Among foraminifera, nodosariids (five *Dentalina* species and five *Lagen* species), polymorphinids (seven species of three genera), and nonionids (five species) were numerous. *Heterolepa dutemplei*, *Cibicidoides tenellus*, and *Cribronion subno-*

*dosum* were most frequently found. This assemblage differs from those in other areas of the North Sea Basin in the species and generic composition, which may be considered as facial dissimilarities. The association also markedly differs from the Paratethyan assemblages. The only species in common are *Cibicidoides sulzensis* and *Grammostomum teretum*. In other areas of the Belgian Basin, the assemblages typical of the Rupelian, including *Svratkina perlata*, *Rotaliatina bulimoides*, *Turrilina alsatica*, *Angulogerina gracilis*, and *Bolivina melettica*, were found (Batjes, 1958; Drooger, see Colloque..., 1964).

In the North German Basin, the Early Rupelian fauna was impoverished and still similar to the Late Eocene fauna in composition (Spiegler, 1966). This included arenaceous foraminifers of the genera *Rhabdammina*, *Rhizammina*, *Ammodiscus*, *Uzbekistania*, *Haplophragmoides*, *Cyclammina*, *Spiroplectammina*, and *Karreriella* (Rupel 1). Calcareous forms were represented by 21 species of 14 genera and by a group of polymorphinids. Species in common with the fauna from the northeastern area of the Paratethys were *Triloculina enoplostoma*, *Spiroloculina canaliculata*, *Cibicidoides pseudoungerianus*, *C. sulzensis*, *Ceratobulimina contraria* (= ? *C. intrusa*), *Rotaliatina bulimoides*, *Alabamina tongentialis*, *Svratkina perlata*, *Vsegeina* sp., *Epistomina elegans*, *Turrilina alsatica*, *Bulimina alsatica*, and *Angulogerina oligocenica*. In other areas of this basin, the assemblages were less representative and included 35 species of 21 genera (Jung and Langer, 1990). A total of 167 Rupelian species was reported (Spiegler, 1966).

In Poland in the Late Rupelian (NP24 Zone), an assemblage that was similar to the West European assemblages rather than to the Chadumian assemblage was widespread. This assemblage included *Lenticulina herrmanni*, *Ceratobulimina contraria*, *Rotaliatina bulimoides*, *Svratkina perlata*, *Pararotalia canui*, *Turrilina alsatica*, *Robertina germanica*, etc. (Odrzywolska-Bienkowska and Pozaryska, 1981; Odrzywolska-Bienkowska, 1983). Forty-one species were in common with the East German assemblages. This similarity decreased further west to 30 species. Twenty-one species were in common with the Belgian Assemblage, and only nine species (including *Rotaliatina bulimoides*) were in common with the Ukrainian Assemblage. The mediterranean genera were absent from the Polish area of the basin.

**Alpine-Carpathian Basin.** In the Rupelian, the fauna from the deepwater (Skibas) zone of the Eastern Carpathians was mainly represented by endemic species that were unknown further east (Mjatluk, 1970). This assemblage markedly differed from those from other Paratethyan areas, even in generic composition. The comparison between the Oligocene East Carpathian Assemblage and the North Caucasian assemblages made by Dabagyan needs a revision; nevertheless, it may be said that these assemblages were domi-

nated by local species of the genera *Cibicidoides* and *Elphidium*.

The southern shelf of the Carpathian Basin (Kiscell Clays, northern Hungary) was inhabited by littoral and lagoonal assemblages. Of 160 forms registered there (Hantken, 1875; Koreczne-Laky and Nagy-Gellai, 1985), 69 species of 27 genera belong to the arenaceous group; less than half of these genera are of a primitive morphotype. The lagoonal inhabitants, miliolids, are rather diverse (six genera and 16 species); the Polymorphinidae are represented by 18 species of five genera. Some species are also present in the Chadumian and North European assemblages, including *Pararotalia canui*, *Epistomina elegans*, *Ceratobulimina contraria*, *Svratkina perlata*, *Alabamina tongentialis*, *Grammostomum teretum*, *Quinqueloculina seminula*, and *Spiroloculina canaliculata* (Nagy-Gellai, 1968). The generic composition of other secreting foraminifers (47 genera) markedly differs from that of the assemblages that inhabited the Caucasus-Kopet Dagh Basin in the presence of the Tethyan genera *Amphicoryna*, *Lankesterina*, *Bolivinella*, *Sagrina*, *Escornebovina*, *Patellina*, etc.

**Eastern Paratethys.** In the Paratethys, at the Eocene-Oligocene boundary, the foraminiferal group experienced profound changes, which resulted in the disappearance of highly specialized taxa, general impoverishment of the composition, and the appearance of new groups with a simpler morphotype.

In the Priabonian, the foraminifers were represented by over 150 species of 80 genera of all orders; this generally indicates the biological progress of their evolutionary development. In the terminal Priabonian, the changes were primarily associated with shallowing; the quantity of plankton decreased, whereas the proportion of arenaceous foraminifers increased and they included a great number of primitive forms. Nevertheless, the evolutionary changes, in particular, the appearance of new genera and species, were also observed. Some new taxa appeared shortly before the crisis, originally occupied subordinate positions in communities, but became more representative and widespread after the crisis; others existed only during the short-term crisis phase, in which new elements also appeared.

In the Early Maikopian (Pshekhian) Basin, before its brackishing in the Solenovian Time, the species of two assemblages, i.e., the earlier assemblage with *Lenticulina herrmanni* and the later assemblage with *Spiroplectammina oligocenica*, were widespread. These assemblages are well traced throughout the Early Maikopian Basin and are designated together as the Chadumian Assemblage. In the basal Rupelian, the composition of assemblages abruptly changed and a marked decrease in the diversity occurred. However, in particular sections, assemblages of a mixed type were often found. In addition, the tests were redeposited through the bottom erosion; as a result, the assemblages include the Eocene-Oligocene species. The composi-

tion, structure, and ecological type of these assemblages considerably depended upon the facies; nevertheless, benthic forms started to predominate everywhere. The impoverished composition and the morphology of the foraminifers indicate more unfavorable environments compared to those of the Late Eocene.

The typical species of the earlier assemblage (*Lenticulina herrmanni* Local Zone) are *Lenticulina herrmanni*, *Plectofrondicularia volgensis*, *Heterolepa almaensis*, *Cibicidoides* aff. *pseudoungerianus*, *C. sulzensis*, *C. extremus*, *C. oligocenicus*, *Cibicidina amphisyliensis*, *Melonis dosularensis*, *Bolivina mississippiensis* (Maikopskie otlozheniya..., 1964; Reshenie kolokviuma..., 1970), *Haplophragmoides deformabilis*, *Gaudryinopsis gracilis*, etc. In the lower part of this zone, transitional species and the species that appeared at the end of the Eocene and occurred in the boundary beds (*Robulus diaphanus*, *Almaena taurica*, *Svratkina perlata*, *Vsegeina nana*, *Tergrigorjanzaella sectile*, *Angulogerina gracilis*, etc.) were found.

Foraminifers from the Solenovian Basin are either unknown or represented by rare alien forms.

**Scythian Shelf.** In the western area of Moldova (Pechenkina in Maikopskie otlozheniya..., 1964), the assemblage from the Lower Oligocene noncarbonate beds is composed mainly of the agglutinating forms and dominated by the primitive genera *Rhabdammina*, *Saccammina*, *Reophax*, *Ammobaculites*, and *Haplophragmoides*. An assemblage of the primitive arenaceous foraminifers was also distributed in the Azov area of the Early Oligocene Basin. These assemblages of arenaceous foraminifers represented a facies variety of the fauna from the *Lenticulina herrmanni* Zone of the Early Chadumian Basin.

At the beginning of the Oligocene, the northern area of the Black Sea Depression was inhabited by arenaceous foraminifers ("the zone of arenaceous foraminifers," after Kraeva, 1960, 1961; Kraeva and Pechenkina, 1965; Maikopskie otlozheniya..., 1964), mainly of the primitive genera *Rhabdammina*, *Protonella*, *Saccammina*, *Hyperammina*, *Reophax*, *Ammodiscus*, *Ammomarginulina*, *Ammobaculites*, *Haplophragmoides* (*H. deformabilis* and *H. stavropolensis*), *Spiroplectammina* (*S. azovensis*), and *Gaudryinopsis gracilis*. However, rare calcareous forms (about ten genera), including *Lenticulina herrmanni*, *Cibicidoides pseudoungerianus*, and *C. oligocenicus*, were also found. The above species were typical of the Early Oligocene (*Lenticulina herrmanni* Zone) of the northern Caucasus.

The later assemblage (*Spiroplectammina oligocenica* = *S. carinata* Zone) includes *Cyclammina constrictimargo*, *Verneuilina rasilis*, *Caucasina schischkinskayae*, and *C. oligocaenica* (Kraeva and Pechenkina, 1965); these species also occur in the Caucasus and in Transcaucasia.

On the southeastern slope of the Dnieper–Donets Depression, an assemblage of the *L. herrmanni* Zone is

widespread. This assemblage includes the species from the North German and Chadumian basins, *Lenticulina herrmanni*, *Cibicidoides oligocenicus*, *Cibicidina amphisyliensis*, *Caucasina schischkinskayae*, *Angulogerina oligocenica*, lagenids, miliolids, and nonionids (Yartseva, 1959). The impoverished foraminiferal assemblage from other areas of the Dnieper–Donets Depression includes *Cibicidoides oligocenicus*, *Melonis dosularensis*, and several species with the calcareous test. In the Rostov Region (Belyaeva, 1964), the foraminiferal assemblage includes species of the *Lenticulina herrmanni* Zone: the zonal species *Cibicidoides oligocenicus*, *C. aff. pseudoungerianus*, *Cibicidina amphisyliensis*, etc. Further to the north (Belarus and Lithuanian Depression), the Oligocene foraminifers are absent.

The Early Oligocene assemblage from the Crimea (from the carbonate siltstones of the Kyzylzhar Horizon) is rather diverse compared to the fauna from other regions and includes 35 species of 24 genera. Of the arenaceous taxa, only *Spiroplectammina azovensis* was found; nodozariids were absent, except for the zonal species *Lenticulina herrmanni*. Each genus is usually represented by a single species, except for *Cibicidoides*, which is represented by six species, including *C. oligocenicus*, *C. extremus*, *C. crimensis*, *C. pseudoungerianus*, and *C. tahtaensis*. *Heterolepa almaensis* and *Bolivina mississippiensis*, which also occur beyond the Crimea, are present there. In the beds adjacent to the Priabonian, *Almaena taurica* and *Vsegeina nana* are known. Higher in the succession, the assemblage of the *Spiroplectammina oligocenica* Zone occurs; it includes *Caucasina schischkinskayae* and *Melonis dosularensis*. Silty calcareous sediments in the plain territory of the Crimea were inhabited by agglutinating forms of the genera *Ammodiscus* (*A. tenuiculus*) and *Haplophragmoides* (Pechenkina, 1971).

In Ciscaucasia, in the deepwater western, central (Kuban River), and eastern areas of the Pshekhian (Early Chadumian) Basin, rare impoverished fauna occurs. There are about 20 genera there; each is usually represented by one species. In addition to the widespread species (such as *Heterolepa almaensis*, *Cibicidoides* aff. *pseudoungerianus*, *C. oligocenicus*, *Cibicidina amphisyliensis*, *Melonis dosularensis*, and *Bolivina mississippiensis*), rare findings of *Pararotalia canui* and *Cassidulina* sp. have been registered (Kuban River). The foraminifers are usually small-sized and thin-walled, indicating unfavorable environments. Noncarbonate sediments were inhabited by the arenaceous species of the genera *Saccammina*, *Rhizammina*, *Trochamminoides*, *Ammodiscus*, *Haplophragmoides*, and *Cyclammina*.

Further to the north, in shallower-water facies of the Stavropol Region, Kuban Lowland, and the Trans-Terek Lowland, an increase in the content of arenaceous foraminifers is observed, whereas the calcareous forms decrease in number. *Haplophragmoides fidelis*

and *H. deformabilis* zones, which correspond to the *Lenticulina herrmanni* Zone, were established there (Ter-Grigorjants, 1965; *Reshenie kollokviuma...*, 1970). In association with the species typical of this zone and widespread in the Crimea and northern Caucasus, two new index species and *Haplophragmoides stavropolensis*, *Ammomarginulina foliacea*, *Trochamminoides* sp., *Ammobaculites grossecameratus*, *Trochammina parva*, *T. caucasica*, *Verneuilina* aff. *risilis*, *Gaudryinopsis gracilis*, *Pseudogaudryina trigona*, *Plectofrondicularia volgensis*, *Heterolepa almaensis*, *Pararotalia canui*, *Asterigerina gurichi*, *Caucasina* aff. *schischkinskayae*, *Tergrigorjanzaella sectile*, *Uvigerina* sp., etc. (a total of 16 genera, mostly of the agglutinating group) are also present. Occasionally, species of *Planorbella* were found in association with foraminifers. In Western Ciscaucasia and in the Indol–Kuban Depression, the assemblages including *Haplophragmoides deformabilis*, *H. stavropolensis*, *Ammobaculites grossecameratus*, *Melonis dosularensis*, and *Lenticulina herrmanni* occur; they are also typical of the Stavropol Region. The foraminiferal assemblages from the Sal–Manych and Don–Sal interfluvies are transitional. These assemblages include species known from the Stavropol Region (from the *Haplophragmoides fidelis* and *H. deformabilis* zones) and from more widely distributed fauna of the *Lenticulina herrmanni* Zone, i.e., the zonal species, *Heterolepa almaensis*, *H. pileola* (abundant), *Melonis dosularensis*, *Plectofrondicularia volgensis*, *Bolivina mississippiensis*, etc. (*Maikopskie otlozheniya...*, 1964; Nikitina, 1972).

In the northwestern area of the Fore-Caspian Depression, the foraminifers that characterize the Chadumian Assemblage, *Cibicidoides oligocenicus* and *Cibicidina amphisyliensis*, are present (Maslun *et al.*, 1984). A rather impoverished assemblage, which included both arenaceous (six genera) and calcareous (seven genera) forms, is known from the central area of this depression. The northeastern assemblages of a mixed type include species of the *Lenticulina herrmanni* and *H. deformabilis* zones (Grachev *et al.*, 1971; *Paleogenovaya sistema...*, 1975). *Melonis dosularensis* is abundant in this region. In addition, the first miliolids (*Quinqueloculina errmanni*) typical of the Oligocene of Western Europe and of the more easterly areas of the Pshekhian Basin, but unknown further west, appear there. In the North Ergeni Upland, *Haplophragmoides fidelis* and *Cibicidoides oligocenicus* were found (*Geologicheskie i bioticheskie...*, 1996). The proportion of foraminifers gradually decreases from north to south down to their disappearance.

**Transcaucasia.** In the western area of Georgia (Abkhazia), dark-colored silty sediments were inhabited by a very impoverished foraminiferal assemblage with *Melonis dosularensis* and *Bolivina mississippiensis*; it was also distributed in the Ciscaucasian area of this basin (Archvadze and Kacharava in *Maikopskie otlozheniya...*, 1964). The Akhaltsikhe Depression was

inhabited by a more representative fauna (18 genera of calcareous foraminifers) having much in common with the Rupelian fauna of Western Europe (Kacharava in *Maikopskie otlozheniya...*, 1964). At the same time, it includes the species of the Chadumian Assemblage; this suggests the presence of connections between these basins.

The foraminiferal assemblage discovered in the Early Oligocene of Azerbaijan is extremely impoverished in both composition and abundance. This region was inhabited by the fauna with a large proportion of endemic forms. This fauna markedly differed in generic composition from the assemblages of the Pshekhian and Mediterranean basins; the species composition depended upon the facial characteristics of sediments. Thirteen genera were recorded there, including *Elphidium* (three species), *Nonion* (three species), and *Nonionella*, which presence indicates the existence of lagoonal, possibly brackish-water areas (Khalilov, 1962; Khalilov and Mamedova, 1984). In addition, local species of the genera *Cibicidoides*, *Pararotalia* (five species), *Caucasina*, *Bolivina* (four forms), *Chilostomella*, and *Ammosphaeroidina* were distributed. Only the species *Melonis dosularensis*, *Rotalia canui*, and *Cibicidina amphisyliensis* were in common with those from the Chadumian Assemblage.

**Turanian Sea.** In the northeastern area of the Fore-Caspian Lowland, species with calcareous tests (*Heterolepa almaensis*, *Cibicidoides* ex gr. *oligocenicus*, *Cibidina amphisyliensis*, *Melonis dosularensis*, and *Bolivina mississippiensis*) typical of the *Lenticulina herrmanni* Zone were found. The index species of the *Brotzenella munda* Zone that was distinguished in the Aral–Turgai Region appeared. In the Southern Emba Region, an assemblage of a mixed type was also found: miliolids (of the genus *Quinqueloculina*) and *Brotzenella munda* were present in association with the species of the *Lenticulina herrmanni* Zone, including the index species, *Spiroplectammina azovensis*, *Cibicidoides expertus*, *C. kugultaensis*, *C. aff. pseudoungerianus*, and *Bolivina mississippiensis* (*Paleogenovaya sistema...*, 1975; Tengiz, collected by S.K. Nikolaeva).

In the Buzachi area of the Turanian Sea (Bykova and Azbel', 1962), at the beginning of the Oligocene (Burlin or Uzunbas Formation), a rather abundant benthos of the *Heterolepa almaensis* Zone (26 genera) with the presence of Eocene species was found. Arenaceous forms (three genera) were rare and only reported from the base of this formation. The major part of the assemblage was composed of calcareous foraminifers. Of them, *Heterolepa almaensis*, *H. pileola*, and *Lenticulina herrmanni* were of particular importance. In the Oligocene of Mangyshlak, a series of foraminiferal assemblages were recorded (*Paleogenovaya sistema...*, 1975) that included polymorphinids and miliolids, *Lenticulina herrmanni*, *Heterolepa almaensis*, *Melonis dosularensis*, *Bolivina mississippiensis*, *Pararotalia canui*, and *Pseudoparrella caucasica*, typical of the

*Lenticulina herrmanni* Zone, as well as *Cassidiella mustoni*, known from the Rupelian of Northwestern Europe. In the northern area of Fore-Kara Bagaz Gol, an assemblage of the *Lenticulina herrmanni* Zone was found, which included this species, *Spiroplectamina oligocenica*, *Quinqueloculina errmanni*, *Spiroloculina canaliculata*, *Melonis dosularensis*, *Cibicidoides pseudoungerianus*, *C. oligocenicus*, *Loithostomata macrura*, *Planorbulina hadlei*, etc. (Bugrova, 1986). These species were widespread in the Aral Region of the basin. In the northwestern area of the Ustyurt Plateau, foraminifers were represented by species in common with those of the Kyzylzhar Assemblage from the Crimea (Nikolaeva and Prusova, 1978).

The problem of changes in the foraminiferal assemblages at the Eocene–Oligocene boundary in the Aral–Turgai Region deserves special consideration (Bugrova, 2001). Bondareva established the “*Anomalia*” (= *Brotzenella*) *munda* Zone there and placed the Eocene–Oligocene boundary at the base of this zone. *Melonis dosularensis*, *Ceratobulimina intrusa* (= ?*C. contraria*), and *Tergrigorjanzaella sectile* appeared in the lower part of this zone (in the beds with *Cibicidoides salensis*, which probably belonged to the Eocene), although, in other regions, these species occur at the Eocene–Oligocene boundary.

The current territory of the North Ustyurt and Chagrai plateaus was inhabited by an impoverished assemblage that was similar to the Caucasian assemblages in composition (Bronevoi *et al.*, 1967). This assemblage included arenaceous forms, *Brotzenella munda*, *Ceratobulimina intrusa* (= ?*C. contraria*), and *Lenticulina herrmanni*. This is similar to the European North Sea assemblages in composition but has not been found in other areas of the Paratethys; therefore, it is difficult to trace its migration.

The fauna from the North Aral Region of this basin markedly differs from the typical Chadumian Assemblage and includes representatives of the order Miliolida, 16 species and subspecies of the genera *Quinqueloculina*, *Triloculina*, and *Spiroloculina* (Serova, 1962). Besides the endemic taxa, of 13 taxa that first appeared in the Oligocene, eight were in common with those of the West European assemblages, including *Quinqueloculina akneriana* (three subspecies), *Q. selene*, *Q. gracilis*, *Tritoculina enoplastoma*, and *T. austriaca*. Outside the Aral–Turgai Region, only individual species of this assemblage were found. In addition to miliolids, species of 13 genera from the *Brotzenella munda* Zone occurred there, including species that had wide geographical ranges (*Melonis dosularensis* and *Turrilina alsatica*).

Foraminifers from the southern part of the Turanian Basin–South Aral Region, southeastern Ustyurt, and northeastern area of the Zaunguzskie Kara Kum have already been studied in detail (Ivanova, 1971; *Paleogen Turkmenii*, 1975). Foraminifers of the *Lenticulina herrmanni* Zone (with the zonal species) represented by

34 species of 29 genera were found there (data from boreholes in the vicinity of the towns of Nukus and Tashauz). Among the arenaceous forms (seven genera), *Haplophragmoides deformabilis*, *Gaudryinopsis gracilis*, and *Pseudogaudryina trigonia* (typical of the Oligocene of the Stavropol Region) were found there. *Lenticulina* aff. *herrmanni* (in the lower part), *L. herrmanni*, *Cibicidoides pseudoungerianus*, *C. oligocenicus*, *Cibicidina amphisyliensis*, *Melonis dosularensis*, and *Bolivina mississippiensis*, known from the deeper-water area of the Caucasus–Kopet Dag Basin, also occurred. Planorbells were recorded.

In addition, this region was inhabited by *Brontzenella munda* ssp. *assakensis*, miliolids (*Triloculina enoplastoma*, *Quinqueloculina errmanni*, *Spiroloculina canaliculata*, etc.), *Ceratobulimina* cf. *intrusa*, *Loithostomata macrura*, and polymorphinids typical of the Aral–Turgai Region of this basin. Thus, the foraminiferal assemblage from the South Aral Region was a fauna of the transitional (mixed) type. In the southwestern Aral Region, an assemblage comprising 26 species of 21 genera (borehole 495, Torangly) was found, almost half of which was represented by typical Rupelian species of northwestern Europe, including *Cibicidoides pseudoungerianus*, *C. sulzensis*, *C. kiliani*, *Ceratobulimina contraria*, *Rotaliatina bulimoides*, *Valvulinera petrolei*, *Alabama tongentialis*, *Svratkina perlata*, *Hoeglundina elegans*, *Angulogerina oligocenica*, *Grammostomum teretum*, and, in the upper part of the zone, *Robertina* sp. In addition, the taxa in common with those from the Ciscaucasian area of the basin were found, including *Cibicidoides oligocenicus*, *C. extremus*, and *Melonis dosularensis*, and the subspecies *Brotzenella munda assakensis*, which was restricted to the eastern marginal area of the basin (to some area of Kazakhstan and Central Asia).

Central and northern Turkmenistan, the western area of the Dariyalyk–Daudan Depression, and the Zaunguzskie Kara Kum were inhabited by an assemblage of the *Lenticulina herrmanni* Zone that was mixed in composition. This assemblage included species of the Chadumian Basin and miliolids typical of the Aral Region: *Lenticulina herrmanni*, *Haplophragmoides deformabilis*, *Cibicidoides* aff. *pseudoungerianus*, *C. oligocenicus*, *Heterolepa almaensis*, *Cibicidina amphisyliensis*, *Caucasina schischkinskayae*, *Quinqueloculina errmanni*, *Q. akneriana*, and *Spiroloculina canaliculata*. In the Zaunguzskie Kara Kum, *Brotzenella munda assakensis* appeared (*Paleogen Turkmenii*, 1975).

In the Western Kopet Dag area of the basin, over 35 species of at least 25 foraminiferal genera were found. The *Lenticulina herrmanni* Zone was distinguished based on these taxa. Among the arenaceous forms (eight genera), the following are of special interest: *Haplophragmoides fidelis*, *H. deformabilis*, *H. stavropolensis*, and *Gaudryinopsis gracilis*, the species that also inhabited shallow-water areas of the

Ciscaucasian Basin (Stavropol Region, etc.). Among other typical species of the Chadumian Assemblage, there were *Lenticulina herrmanni*, *Heterolepa almaensis*, *Cibicoides expertus*, *C. oligocenicus*, *Planorbulina ammonoida*, *Cibicidina amphisyliensis*, *Melonis dosularensis*, *Caucasina schischkinskayae*, *Angulogerina gracilis*, *Uvigerinella californica*, and *Bolivina mississippiensis*. This region was also inhabited by *Brontzenella munda assakensis* reported from the Aral Region of the basin and by the species in common with the Tajik–Ferghana Region (*Asianella subbotinae*, *Brontzenella postacanicus*, *B. multa*, and *B. schurabica*). In addition, the genera *Nonion*, *Astrononion*, and *Nonionella*, which were absent or rare in other regions, were found there. Shallower-water assemblages from the far southwestern area of the Kopet Dag included species from the Tajik–Ferghana Region and miliolids (*Quinqueloculina errmanni* and *Triloculina enoplasotoma*) typical of the Pre-Aral–Turgai Region (*Geologicheskie i bioticheskie...*, 1996). In another area of this basin (Gyaurlı), a unique assemblage was found; it was dominated by miliolids but had different composition compared to the Pre-Aral–Turgai assemblages. In particular, the genus *Pyrgo*, unknown in other regions, was found there.

Further to the east, in the Central Kopet Dag and Gyaurs Dag areas of this basin, the fauna was impoverished and included endemic forms and *Brontzenella munda assakensis* (*Paleogen Turkmenii*, 1975), although species recorded from Ciscaucasia (*Haplophragmoides* aff. *fidelis*, *Gaudryinopsis gracilis*, *Plectofrondicularia volgensis*, and *Uvigerinella californica*) were also recorded there. Further east, (in the piedmont area of the Eastern Kopet Dag), an assemblage with *Uvigerinella californica*, *Cibicoides oligocenicus*, and nonionids occurred.

The Middle Amu Darya and Mary regions were inhabited by a mixed fauna (*Paleogen Turkmenii*, 1975; Bugrova, 1987, data by L.E. Nevmirich). This fauna included the species of the Chadumian Assemblage (*Lenticulina herrmanni*, *Melonis dosularensis*, *Cibicoides pseudoungerianus*, *C. expertus*, *C. oligocenicus*, *Heterolepa almaensis*, *Cibicidina amphisyliensis*, *Angulogerina gracilis*, and *Bolivina mississippiensis*) and miliolids typical of the Pre-Aral regions (*Quinqueloculina errmanni*, *Q. akneriana*, *Q. subungeriana*, *Q. rotunda*, *Q. romboidea*, and *Spiroloculina canaliculata*). In addition, both these regions were inhabited by the species usual for the Tajik–Ferghana Region (*Brontzenella postacanicus*, *B. multa*, *B. schurabica*, *Biapertorbis asiaticus*, and *Caucasina* sp. nov.). The assemblages include at least 15 genera.

In the western Kyzyl Kum, foraminifers are represented by species having wide ranges (*Lenticulina herrmanni*, *Spiroplectamina oligocenicus*, *Cibicoides* aff. *pseudoungerianus*, *Loithostomata macrura*, and *Uvigerinella californica*) and by a small number of endemic species (Makarova and Tsatsir, 1964).

**Tajik-Ferghana Basin** was an isolated peripheral area of an Early Oligocene basin that was inhabited by endemic fauna. The majority of species found there are unknown outside the Tajik–Ferghana Region (Davidzon *et al.*, 1982). The assemblage includes many arenaceous forms, local species of the genera *Haplophragmoides* and *Trochammina*, *Spiroplectamina tuaevi*, and species of the genera *Nonion* and *Cribrononion*. *Brontzenella munda*, *B. postacanicus*, *B. multa*, *B. schurabica*, *Asianella subbotinae*, and *Cibicoides khana-badensis* had wider ranges (including Turkmenistan). According to Tsatsir, *Loithostomata macrura* occurred in the area of the basin that today belongs to the southwestern offshoots of the Hissar Mountains. Some of the above species were recorded from Ferghana (*Reshenie kollokviuma...*, 1970, data by Bugrova) and from northern Afghanistan.

#### *Nummulites and Discocyclinids*

In the Oligocene, the geographical range of large foraminifers sharply decreased. In the Northern Nummulite Province, these organisms became entirely extinct, and only at the end of the Oligocene (in the Chattian), sole species of the genera *Lepidocyclina*, *Miogypsina*, and *Miogypsinoides* entered this region. In the southern province, large foraminifers still existed, but the diversity of the assemblages substantially decreased. The basin cooling affected nummulites; their tests became smaller and nongranulated; and, in the terminal Oligocene, this genus became extinct.

At the Eocene–Oligocene boundary, marked changes in the taxonomic composition of this foraminiferal group occurred. Only a small number of species of the genus *Nummulites* (subfamily Nummulitinae) survived this boundary and coexisted with rare operculins for a short time in transitional layers. In the other subfamily, Heterostegininae, the genus *Grzybowskiia* disappeared, species of the genera *Spiroclypeus* and *Heterostegina* became rare, and a new family, Miogypsinidae (two genera), appeared. In the Early Oligocene, among orbitoidids, one or two residual discocyclinid species still existed; in the upper part of the P18 or the lower part of the P19 zones, the family Discocyclinidae was replaced by the Lepidocyclinidae, including the typical Oligocene genus *Lepidocyclina* was represented by a series of subgenera (or, possibly by separate genera).

**Eastern and Southern Mediterranean.** Syria may be considered to be a typical region where the Oligocene fauna of the Mediterranean–Mesopotamian Basin developed (Krasheninnikov and Ptukhyan, 1973; Krasheninnikov and Nemkov, 1975). Here, sandy sediments and bioherms were inhabited by abundant nummulites (five species) and lepidocyclines that were also found in Iraq and Iran (Adams *et al.*, 1983). Lepidocy-



clinids were abundant in the southern coastal areas of Turkey (Krasheninnikov and Ptukhyan, 1973).

In a narrow belt in North Africa, nummulites were reported from Morocco (Ennouchi, in Colloque..., 1964) and Tunis (two species). In the shallow-water zone of Libya (in carbonate silt), five nummulites species, two species of *Eulepidina*, and *Miogypsinoides* were found in association with sea urchins, oysters, and other mollusks (Schaub, 1981; *Terminal Eocene Events*, 1986). Nummulites reached Somali and Madagascar.

**Eastern Atlantic.** Shallow-water carbonate muds in the southwestern area of the Aquitaine Basin were inhabited by small nummulites (four species), operculines, large lepidocyclines, and the genus *Miogypsinoides*, which appeared later (Schaub, 1981; Veillon, cited by Cavelier, 1979). *Lepidocyclina*, *Miogypsina*, and *Miogypsinoides* (one species in each genus) probably reached the North European Basin in the terminal Oligocene (in the Chattian) and inhabited northwestern Germany (Van-der-Flerk, 1966; Drooger, in Colloque..., 1964).

**Northern Mediterranean.** Northern provinces of Italy were inhabited by large foraminifers. Their assemblages were more diverse compared to fauna from other areas. In the northwestern area (Piedmont), nummulites (three species) occurred; *Eulepidina* and *Nephrolepidina* (two species) appeared later and were followed by *Miogypsina* and *Miogypsinoides* (Lorenz, cited by Cavelier, 1979). Northwest of Verona (Monto Baldo), nummulites (four species, including *N. intermedius* and *N. vascus*) and *Operculina* were found (Cita and Scipolo, 1961). In some areas where water was probably deeper (Possagno and Brendola), nummulites were absent (Herb and Hekel, 1975; Broglio, cited by Cavelier, 1979). The occurrence of *N. vascus* was reported from the Oligocene of southeastern France (French Alps).

Shallow-water areas of southern Spain (Malaga) were inhabited at the beginning of the Oligocene by Priabonian discocyclinids and *Pellatispira*, and, subsequently, by *Lepidocyclina* (Molina *et al.*, cited after Cavelier, 1979).

The eastern area of the Northern Mediterranean and the northeastern areas of the Adriatic coasts were inhabited by *Nummulites* (four species), including *N. fichtelli*, *N. vascus vascus*, and the Late Eocene species *N. germanicus* from the northern province (*Terminal Eocene Events*, 1986). In the coastal area of the Dinarides (Albania), nummulites, as well as lepidocyclines and *Miogypsinoides* that appeared later (in the P19 and P20 planktonic zones, respectively) were found (Cavelier, 1979). *Nummulites intermedius* and *N. vascus* were recorded from the northern coastal area of Turkey (*Terminal Eocene Events*, 1986). According to data by Belmustakov (1959), the Bulgarian Shelf was inhabited by seven species of Oligocene nummulites and operculines.

At the beginning of the Oligocene, the Armenian Basin was still inhabited by Priabonian nummulites (three species), operculines, and discocyclines, as well as by four new species of the genus *Nummulites* (Grigoryan, 1986; *Geologicheskie sobytiya...*, 1988). In the basins of Georgia, scarce nummulites were also found (Mrevlishvili, 1978). Local species of this genus inhabited the Rupelian basins in both Transcaucasian regions, while representatives of other foraminiferal groups were absent.

**Carpathian Basin.** At the beginning of the Oligocene, large foraminifers inhabited the southern shelf area of this basin: *Nummulites intermedius*, *N. vascus*, and three other species of this genus were recorded from Hungary (Sztrakos, 1971, in Cavelier, 1979). Transitional forms between *N. fabiani* and *N. intermedius* occurred in Transylvania, and *Lepidocyclina* (*Nephrolepidina*) and miogypsinides were in Zagorje, Slovenia (Papp, 1954, 1955).

Five species of Late Eocene nummulites were recorded from the shallow-water area of the Central Carpathian Cordillera (Slovakia), as well as a form transitional to *N. intermedius* (Samuel and Salaj, 1968). The northern shelf area of the Carpathians (Galizia) was inhabited by six nummulite species, including *N. intermedius*, *N. vascus*, and *N. fichteli* (Bieda, 1963; Uhlig, 1886).

It is worth mentioning that the Intra-Carpathian basins and the northern regions of the Mediterranean (Hungary, Romania, Bulgaria, northern Turkey, and Armenia) were only inhabited by nummulites and rare, disappearing operculines and discocyclines. Such impoverishment is most probably associated with the effects of boreal basins. The presence of species with narrow geographical ranges (for instance, in Georgia) cannot serve as a guide for recognizing a specific paleobiogeographic unit. However, nummulitids could occur there only at the beginning of the Oligocene, before the appearance and expansion of lepidocyclinids and miogypsinids.

### Ostracodes

Terminal Eocene–Early Oligocene events consisted in great paleogeographic and climatic changes, rearrangement of the oceanic circulation, and the formation of the psychrosphere; consequently, they evidently affected the evolution and distribution of ostracodes. In the Oligocene, the ostracode biota was represented by all its types: continental, fresh-water, brackish-water, lagoonal, marine shelf, and deepwater, as well as deep-water fauna of psychrosphere.

**Northern Mediterranean.** At the beginning of the Oligocene, shelf areas of the north Italian basins (the sections of Priabona, Brendola, and Bressana) were still inhabited by numerous Eocene ostracode species; however, the taxonomic diversity and abundance of the assemblages decreased compared to the Eocene

(Barbin and Guernet, 1988). The quantity of ostracode species in the Oligocene was halved (20 compared to 40 in the Late Eocene). The generic composition also became less diverse. In the terminal Eocene, 14 genera, including *Eopaijenborchella*, *Protoargilloecia*, and *Phacorhabdotus*, which are indicators of depths of the outer shelf, as well as *Triebelina* and *Callistocythere*, which are indicators of warm water regimes, disappeared from the shelf area of northern Italy. The Oligocene basin was probably of colder water and less deep-water. The appearance of any new species has not been reported.

In the Armenian Gulf in the Oligocene, there was no marked change in the ostracode assemblages. Against the background of still existing deep-water, totally blind fauna, the genus *Trachyleberidea* disappeared and the new genus *Buntonia* from the family Buntoniidae, the typical inhabitants of the Mediterranean Region, appeared. The first appearance of sighted ostracodes (genus *Costa*, also of Mediterranean origin) is assigned to the formation of the *Globigerina selii* Zone; this likely indicates shoaling of the basin in the Oligocene.

**Eastern Atlantic.** The terminal Eocene–Early Oligocene events are traced differently in different bathymetric zones. In the lower bathyal and abyssal zones in the northern area of the Bay of Biscay, representatives of deep-water, so-called psychrospheric cold-water ostracode fauna (genera *Poseidonamicus*, *Bradleya*, and *Agrenocythere*) appeared in the eurythermal ostracode assemblages since the terminal Eocene. Such composition of assemblages was mainly associated with oceanic currents and the formation of a two-layered structure of water masses, with the lower layer being formed by cold Arctic waters and the upper layer being formed by Mediterranean waters. North of the Bay of Biscay (Rockall Plateau), ostracodes were represented in the Early Oligocene by the genera *Cytherella*, *Bairdia*, *Bythoceratina*, *Argilloecia*, *Atlanticythere*, *Trachyleberidea*, and *Cardobairdia* in association with the newly appearing psychrospheric genera *Poseidonamicus* and *Bradleya*. In the lower bathyal zone, in the southeastern area of the Bay of Biscay, the majority of the ostracode fauna was composed in the terminal Eocene and, beginning with the Oligocene of the genera *Cytherella* and *Argilloecia*, the numbers of slowly evolving groups. The assemblage was generally uniform.

In the littoral zone that occupied a large part of Aquitaine, the evolution of the ostracode fauna tolerant with respect to salinity was normal. The Oligocene ostracode assemblage in the Aquitaine Basin included 58 ostracode species of 36 genera, with 44 species and 32 genera descending from the Late Eocene. Four genera did not continue into the Oligocene. Seven genera, *Neocyprideis*, *Bythoceratina*, *Triebelina*, *Costa*, *Callistocythere*, *Hemicyprideis*, and *Eucythere* newly appeared (Deltel, 1962; Ducasse, 1969, 1974, 1975, 1981, 1983;

Ducasse and Peypoquet, 1978, 1979, 1986; Ducasse and Roussele, 1978, 1979a, 1979b; Peypoquet, 1979; Peypoquet *et al.*, 1981). The changes included a partial change in the species composition and structural rearrangement of the populations of certain species of the genera *Quadracythere*, *Schuleridea*, *Cytheretta*, *Pokornyella*, and *Hammatocythere*. Lagoonal and marine environments, which first appeared in northern Aquitaine in the terminal Eocene, were dominated in the Oligocene by *Hemicyprideis helvetica* and *Cyamocytheridea infanta*.

**North Sea Basin.** Shallow-water shelf areas that were situated south of the central part of the North Sea (Central Graben) and occupied the entire northern area of Western Europe contained especially abundant ostracode fauna (Gramann, 1988; Keen, 1989; Uffenorde, 1989). The ostracode assemblages were extremely diverse there. Ostracodes typical of the water salinity of 17–32‰ inhabited the Isle of Wight in the Late Hemstead during the accumulation of Sannois Limestones in the Paris Basin and beds with *Nucula comta* in the Belgian area of the shelf zone, as well as the Rhine Graben in the first half of the Rupelian (Keij, 1957; Goerlich, 1958).

The Rupelian ostracode assemblages are characterized by a mixture of brackish-water and polyhaline groups. The first group includes the genera *Neocyprideis*, *Hemicyprideis*, *Cytheromorpha*, *Cytheridea*, *Cyamocytheridea*, and *Loxoconeha*. The second group comprises the genera *Cytherella*, *Cytherelloidea*, *Cytheretta*, *Cytherura*, *Echinocythereis*, *Konarocythere*, *Leguminocythereis*, and *Pontocythere*. In the Paris Basin, the proportion of marine groups was much higher. The genera *Hammatocythere*, *Pokornyella*, *Trachyleberidea*, and *Pterygocythereis* predominated the shelf zone of the Armorica Massif and the north German shelf area. The generic composition indicates moderately warm water temperature regimes. The Rupelian ostracode assemblage was generally characterized by a low proportion of endemic forms. Many species, such as *Paracyprideis rarefistulosa*, *Leguminocythereis scrobiculata*, *Echinocythereis hispida*, *Cuneocythere marginata*, *Cyamocytheridea punctatella*, and *Hemicyprideis helvetica*, that first appeared in the Oligocene, had very wide geographical ranges.

Ostracodes tolerant of high water salinity appeared in the Belgian shelf area during the formation of Boom Clays. This assemblage is characterized by a small proportion of early transitional species and by the first appearance of *Henryhowella*. In the deeper-water areas of the north German and Danish shelf zones, shallow-water groups are absent. The ostracode assemblage is composed of the genera *Argilloecia*, *Krithe*, *Cytheropteron*, and *Henryhowella*; however, no psychrospheric groups have been registered.

As a result of the Rupelian sea transgression in the North Sea Basin, marine waters reached lagoons and intracontinental water basins; ostracodes penetrated the

neighboring zones, and a large number of mixed ostracode faunas appeared. At the beginning of the Rupelian, fresh-water and brackish-water ostracodes of the lake and lagoonal types inhabited Isle of Wight, the Paris Basin, and Rhine Graben (Middle Hemstead, Middle Sannois, and Middle Pechelbronner assemblages). These assemblages included species of the transitional genera *Cypris*, *Ilyocypris*, *Eucypris*, and *Cypridopsis*; representatives of *Moenocypris* and *Virgatocypris*, the genera that first appeared in the Late Eocene; and one species of the Oligocene genus *Lineocypris*.

**Alpine–Carpathian Basin.** The Oligocene evolution of ostracodes in the Bavarian and Swiss molassa depressions displaced certain unique features. The Rupelian assemblage included 43 species in the Swiss Depression and at most 10 species in the Bavarian Depression (Oertli, 1956; Witt, 1967). Polyhaline assemblages of the infralittoral zone (20–80 m) had rather narrow geographical ranges and inhabited clayey-marly facies, where the occasionally formed mass accumulations. The shallow-water species *Hemicyprideis helvetica*, *Cyamocytheridea punctatella*, and *Cytheridea pernota* were widespread, whereas inhabitants of the deep shelf zone, the genera *Henryhowella*, *Argilloecta*, etc., were absent.

In the Western Carpathians (Moravia), in the Early Oligocene that corresponds to the initial stage of the formation of the Menilitic Beds, deepwater ostracode fauna still occurred, the genus *Krithe* predominated, whereas the genera *Abyssocypris* and *Agrenocythere* were rare. The morphology of the representatives of the genus *Krithe* indicates rather good aeration of bottom waters, whereas the increase in the size of species that came from the Eocene indicates cooling (Pokorný, 1980). However, the temperature of water in the Western Carpathians in the Oligocene was still much higher than that of the oceanic water of the psychrosphere.

The Rupelian ostracode fauna of the Hungarian Basin was clearly associated with the structure of the basin, the increase in sea depths from west to east and the marked fluctuations of the sea level. At the beginning of the Oligocene, the structure of the basin was almost the same as in the Eocene (Monostori, 1985, 1986). The final stage of the Buda Marls formation and the initial stage of the Tard Clays formation coincided with the major deepening of the eastern area of this basin. The ostracode assemblages included the deepwater genera *Henryhowella*, *Agrenocythere*, *Argilloecia*, *Cytherella*, *Cardobairdia*, and *Parakrithe* in association with epinerithic groups (*Cuneocythere marginata*) and the fresh-water genera *Candona*, *Cypridopsis*, and *Moenocypris*, which were brought there by the turbid flows. A decrease in the oxygen content dissolved in water that was observed since the terminal Eocene and continued in the Rupelian affected the ostracode assemblages and resulted in a marked decrease in abundance and taxonomic diversity of ostracodes, and in subsequent

disappearance of this group by the final stage of the formation of the lower beds of the Tard Clays.

Ostracodes that appeared during the accumulation of beds enclosing *Cardium lipoldi* composed an entirely new polyhaline assemblage of shallow-water and deepwater forms (Monostori, 1985), accompanied by ecologically tolerant fresh-water and brackish-water groups. This assemblage included the genera *Cytheretta*, *Schuleridea*, *Pterygocythereis*, *Megahemicythere*, *Leguminocythereis*, *Echinocythereis*, and *Cytheridea*. The taxonomic composition of the assemblage indicates a shallow basin with wide paleogeographical connections. This basin could periodically experience marine invasions. The formation of the upper beds of Tard Clays and the Lower Kiscell Clays in the Rupelian occurred in the environments unfavorable for ostracodes, possibly also in anoxic environments.

In the Transylvanian sShelf, the change from the Late Eocene to the Oligocene assemblages was gradual (Olteanu, 1980). The generic composition experienced only slight changes (above the horizon containing *Pycnodonte gigantea*); the genus *Argilloecta* disappeared; however, the species composition was nearly halved (67 and 35 species in the terminal part of the Breb Marls). At the same time, certain species, mainly from the family Cytherideidae, increased in number. Subsequently (during the formation of the Hoja Marls), no marked changes in the quantity and quality of the ostracode composition were registered (27 species of closely similar taxonomic composition). The assemblage became more diverse in the Middle Rupelian (Mera Beds); the number of species increased to 47. Mediterranean groups appeared, including the genera *Triebelina*, *Costa*, and *Callistocythere*. The assemblage also included the forms that were widespread in the Rupelian of northern Europe, i.e., *Schuleridea perforata*, *Cytheropteron gulincki*, *Echinocythereis* ex gr. *scabra*, and *Leguminocythereis scrobiculata*.

In the Late Eocene–Early Oligocene, the composition of the ostracode assemblages only slightly changed in the percentage of eurybathic and shallow-water shelf polyhaline groups (approximately 25–20% and 75–80%, respectively). Along with the marine assemblages, species of the brackish-water groups *Hemicyprideis helvetica* and *Cytheridea pernota* (Curtuius Formation) were abundant in some brackish-water areas of the Early Rupelian basin; this indicates the effects of river inflows.

A sharp impoverishment of the polyhaline ostracode assemblages was associated with the basin brackishing in the Middle Rupelian (during accumulation of the Bizusa Marls, and especially of Ileanda Clays). The number of species in the assemblage decreased to 7–10, including euryhaline *Cytheridea ventricosa*, *Bosquetin* sp., *Cyamocytheridea bouendensis*, and “*Thracella apostolescui*”, as well as the fresh-water species *Candona* sp. and *Ilyocypris* sp.

**Greater Caucasus–Kopet Dagh Basin.** Ostracodes inhabited the shallow shelf area of this basin and have not been found in its deepwater area, in typical Maikopian facies. Ostracodes from the shelf zone of Eastern Paratethys markedly differ from the Rupelian ostracode fauna of Western Paratethys.

(1) The assemblage was uniform throughout the area of its distribution (the Rubanovka, Kyzylzhar, Ascheiryk, Uzunbas, Kujulus), and Lower Sarybatyr assemblages, as well as the assemblages of Lower Rupelian ostracodes from the South Aral Region and Central Turkmenistan only slightly differed from each other (Gramm, 1963; Sheremeta, 1969; Nikolaeva, 1985).

(2) In these assemblages, over 30 euryhaline genera (including *Bairdia*, *Argilloecia*, *Xestolebers*, *Eopaijenborchella*, etc.) that inhabited the Western Paratethyan Region from the Eocene to the beginning of the Rupelian, and later, were absent.

(3) The oceanic genus *Henryhowella* and the Mediterranean genera *Costa*, *Callistocythere*, and *Triebelina*, which are rather typical for Western Paratethys, were absent from the Pshekhian Basin. The Pshekhian Assemblage included 20–25 species of 16 mainly polyhaline genera, with a predominance of cythereidids and trachyleberidids of the subfamily Echinocythereidinae. *Cuneocythere marginata*, *Cytheropteron steinmanni* and species of the genus *Leguminocythereis* ex gr. *striatopunctata* were found everywhere. The decrease in the proportion of stenohaline groups from west to east (the absence of the genus *Krithe* in the Ascheiryk Assemblage) was registered.

**Solenovian Basin.** In the Solenovian Time, a unique ostracode assemblage was formed. It comprised elements of inherited marine fauna and the fauna that appeared in shallow brackish-water basin. Among Solenovian marine ostracodes, there were *Cytheridea*, *Cuneocythere*, *Cyamocytheridea*, *Eucytheridea*, *Haplocytheridea*, *Schuleridea*, *Pterygocythereis*, *Echinocythereis*, *Bosquetina*, and *Cytheropteron*. The species of these genera (that had wide geographical ranges in the majority of cases) composed over 75% of taxa of the Solenovian Assemblage. However, regarding the abundance, certain brackish-water species of the genera *Disopontocypris*, *Cyprinotus*, and *Haplocytheridea* predominated. The type species *Disopontocypris oligocaenica* of the genus *Disopontocypris* was widespread in the lower part of the Solenovian Horizon and in the upper part of the Rupelian in the North Sea Basin and in the Western Paratethys (Veselov and Sheremeta, 1966; Popov *et al.*, 1985; Jiricek and Riha, 1991). Other brackish-water species of ostracodes were similar in distribution. Thus, *Moenocypris olmensis* found in the Polbian Assemblage was common in the Middle Pechelbronner of the Mainz Basin. Along with marine and brackish-water genera, the species of the widely eurybiont genera *Loxoconcha* and *Cytheromorpha* were found in the Solenovian Basin; however, they were not numerous. At the initial stage of the Solenovian Basin

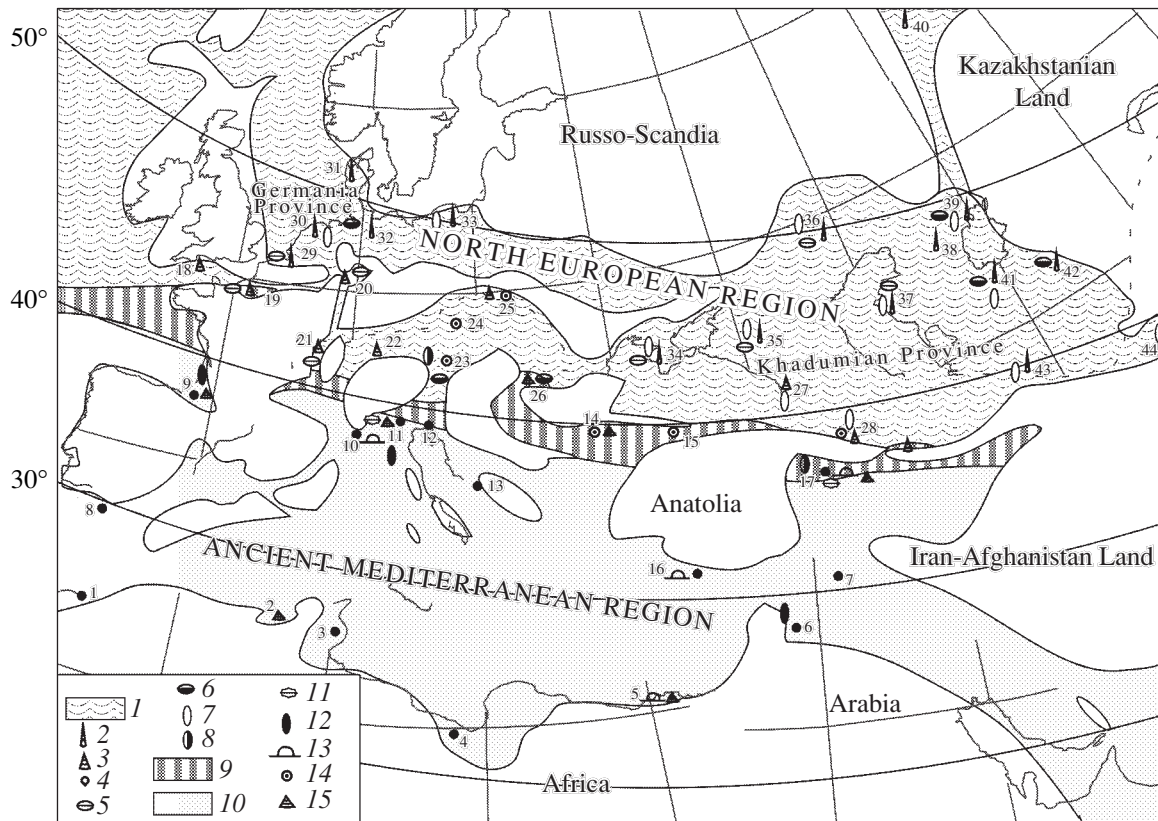
formation, ostracode assemblages were especially abundant and represented by a large number of brackish-water taxa (the Polbian, Molochanian, Solenovian, and the Middle Daryalyk assemblages of shallow areas of the basin). *Disopontocypris oligocaenica*, *D. majkopiensis*, *Cyprinotus medianus*, and *Haplocytheridea solenica* occurred throughout the basin. The absence of ostracodes in deepwater areas of the basin (the section of the Kheu River in Ciscaucasia and the Caspian Region) is typical. The ranges of the Solenovian ostracode biota became indistinct in the eastern area of the basin. The South Aral Region was the eastern boundary of the genus *Disopontocypris* and *Cyprinotus medianus* and *Haplocytheridea solenica*. At the final stage, the Solenovian Basin was filled by noncarbonate Maikopian-type clayey beds that formed unfavorable conditions for ostracodes. The North Ustyurt Plateau was the sole region where a relatively numerous ostracode assemblage was found. The species diversity was rather low, and the assemblage was formed by transitional marine species. Of the brackish-water ostracodes, only *Disopontocypris kasachstanica* was present. The first representative of *Paracyprideis*, *P. punctata*, appeared that differs this assemblage from the Early Solenovian Assemblage. The Solenovian Basin was inhabited by over 30 species of 17 ostracode genera.

#### Mollusks

**North Africa.** Available data on the Early Oligocene molluscan fauna from North Africa are very scarce, unlike those on the Priabonian mollusks. The impoverished assemblages recorded in Algeria (Cuvillier, 1930; Flandrin, 1938) indicate that the African coast had lost its peculiarity by the onset of the Oligocene. All the 13 bivalve genera reported were widespread in Europe, almost a half of the species being known from southern Europe. The assemblage included typical Mediterranean taxa (*Chlamys biarritzensis*, *Pecten arcuatus*, and *Pycnodonte brongniarti*) that were abundant in Europe from the Eocene, but were absent in the Eocene of Egypt.

**Northern Mediterranean.** Representative assemblages of the Rupelian molluscan fauna of the southern type were recorded from the French Alps, northern Italy, Transylvania, southern Bulgaria, and Armenia (Popov, 1995; Amitrov, 1996; Fig. 3).

These data indicate that molluscan fauna from the coastal area of the Mediterranean–Mesopotamian Basin was mainly inherited from the Eocene and included numerous warm-water tropical–subtropical elements (*Trisidos*, *Crassatella* sensu stricto, *Cardium* sensu stricto, *Vepricardium*, *Corculum*, strombids, and diastomas), as well as many typical Bartonian and Priabonian genera and species that retained their ranges unchanged and were widespread in the Rupelian. The proportion of the newly appearing species is less than 30%.



**Fig. 3.** Complex benthos-based zoogeographic zonation of the shelf of the Rupelian basins. Explanations: (1) **North European Region** with the presence of moderately warm-water benthic fauna of the Rupelian type; (2) molluscan assemblages, including *Arcitica*, *Cyrtodaria*, *Scalaricardita*, and lacking the most warm-water taxa; (3) richer transitive molluscan assemblages, including the warm-water taxa, but lacking the typical Tethyan species; (4) impoverished assemblages of large foraminifers with *Nummulites*, *Operculina*, and *Discocyclus*; (5–6) ostracode assemblages: (5) assemblages of smooth-walled groups descended from the Priabonian, including new “psychrospheric” genera *Poseidonamicus*, *Brodleya*, and *Agrenocythere*; (6) assemblages with high proportion of euryhaline and brackish-water groups; (7–8) assemblages of small foraminifers: (7) of the northern type; (8) of the transitional (mixed) type; (9) boundary zones; (10) **Ancient Mediterranean Region** with the benthic fauna including various assemblages of colonial corals, nummulitids, and benthic foraminifers with large sculptured tests: (11) assemblages of the Mediterranean ostracode genera with typical sculptured forms and with the presence of Buntoniidae of the Mediterranean origin; (12) assemblages of small foraminifers with *Pararotalia*, *Herondenia*, and *Queralina*; (13) reef-building corals; (14) assemblages of large foraminifers with nummulitids, lepidocyclines, and miogypsinids; (15) molluscan assemblages of the southern type with tropical taxa. The main localities of the benthic fauna from the Rupelian: (1) Morocco; (2) Algeria; (3) Tunisia; (4) Libya; (5) Egypt; (6) Syria; (7) Iraq; (8) southern Spain; (9) Aquitaine; (10) Coastal (Nummulite) Alps; (11) northern Italy; (12) Slovenia; (13) Albania; (14) southern Bulgaria; (15) northwestern Turkey; (16) southern Turkey; (17) Armenia; (18) southern England; (19) central France; (20) Mainz Basin; (21) Switzerland; (22) Austria; (23) Hungary; (24) Slovakia; (25) Ukrainian Carpathians; (26) Transylvania; (27) western Georgia; (28) southern Georgia (Akhaltzykhe); (29) Belgium; (30) the Netherlands; (31) Denmark; (32) northern Germany; (33) Poland; (34) Crimea; (35) Northern Caucasus (Kuban River); (36) Ergeni; (37) Mangyshlak; (38) northern Ustyurt; (39) Pre-Aral Coastal Area; (40) southern part of Western Siberia (Kurgan Beds); (41) Southern Aral Coastal Area; (42) Kysyl Kum; (43) Kopet Dag; (44) Tajikistan, Ferghana.

Nevertheless, the available data on bivalves indicate substantial changes as compared to the Late Eocene.

(1) Both the generic and species compositions of molluscan faunas were impoverished (41 genera were found in northern Italy as opposed to 59 Priabonian genera, and 24 genera were recorded in Bulgaria as opposed to 63 Priabonian genera).

(2) The similarity between the assemblages decreased, and the fauna lost its integrity; the comparison of the generic compositions of bivalves indicates that the Preston’s coefficients of dissimilarity increased from 0.40–0.69 for the Priabonian to 0.64–0.91 for the Rupelian

(Popov 1994, 1995). This was probably caused by differential extinction in different areas of the basin. However, it is not inconceivable that the compared assemblages are unrepresentative.

(3) The species of north European origin, such as *Barbatia nysti*, *Anadara sulcicosta*, *Glycymeris lunulata*, *G. obovata*, *Astarte kickxi*, *Nemocardium tenuisulcatum*, *Glossus subtransversus*, and *Pelecypora westendorpi*, appeared in all south European assemblages.

The gastropod composition also indicates very warm-water environments in the Northern Mediterra-

nean. Judging from the gastropod faunas, it was not colder in this region in the Rupelian than in the Priabonian. Much more species (580 versus 190) and families (63 versus 51) were found in the Rupelian of northern Italy compared to the Priabonian. The quantity of the most warm-water families also increased; strombids, diastomatids, etc., were accompanied by tonnids, vasids, and harpids. The Early Oligocene molluscan assemblage from the Yerevan Gulf (Shorakbyur Formation in Armenia) is also more diverse than the Late Eocene assemblage (from the Rind Horizon, Late Eocene). Only assemblages from Bulgaria and the French Alps decreased in diversity. The number of new gastropod species is substantially greater than those of bivalves; the proportion of gastropod species that are unknown in the Eocene is 70% (mainly at the expense of the large North Italian Assemblage). Of 180 species in common with the Eocene, 36 were recorded from the Middle Eocene and were not registered in the Priabonian. The similarity of the Rupelian and Priabonian gastropod assemblages did not decrease, unlike that of the bivalve assemblages.

Similar to bivalves (although not so clearly), the ranges of certain gastropod species decreased, and some species possibly migrated from the north to the south. Of species known from both the Priabonian and the Rupelian, 98 species were only found in southern areas, 55 species were only recorded in northern assemblages, nine species occurred everywhere in the Priabonian and only in southern areas in the Rupelian, and 16 species were found in northern assemblages in the Priabonian and only in southern assemblages in the Rupelian.

**Eastern Atlantic.** Molluscan assemblages from the Aquitaine shelf of Atlantic were very rich and diverse and included 140 bivalve species and 200 gastropod species (Stampian of Aquitaine after Cossmann, 1921; Saubade, 1970). Although this fauna included warm-water genera and species in common with the Mediterranean, this assemblage is rather unique; the Stampian molluscan assemblages were dominated by the species that were first discovered there.

Similar to the situation in bivalves, the Rupelian gastropod assemblage from Aquitaine was more diverse compared to that from the Priabonian (about 200 species versus 60 and 62 families versus 30). Strombids were absent in the Priabonian of Aquitaine. The Rupelian assemblage in this region was of the southern type and included two strombide species and representatives of other warm-water families. The absolute quantity of the species in common (34) and the dissimilarity estimated by the Preston's coefficient indicate that the Rupelian assemblage from Aquitaine is most similar to that from Italy.

In the Paris Basin, normal marine environments were restored after a brackishing in the Ludian Time (Late Eocene) and in the Sannois Time (beginning of the Rupelian). The composition of the Stampian mol-

luscan assemblage (from the Etampes Sands) supports this fact. Mediterranean species and genera were absent in this fauna. Endemic species constituted a large part of the assemblage; the other species were widespread and the same as in the Rupelian of northern basins. The bivalve assemblages were almost as diverse as in the Aquitaine and included 112 species (Cossmann and Lambert, 1884; Furon and Soyer, 1947); however, the warm-water groups decreased in diversity. They included 33 species in common with those from the Mainz Basin and only 10 species in common with Belgium; this indicated the direct faunal connections with the Rhine Basin via Alsace (Saubade, 1970).

Strombids, Velates, and some other warm-water gastropod groups (neritopsids and harpids) were absent from the Stampian of the Paris Basin, although diastomatids were present. For the Oligocene, this assemblage may be considered to be a standard transitional assemblage. This assemblage is clearly more cold water than the transitional Eocene assemblages (for example, the Mandrikovka Assemblage and the Bartonian assemblage from the Paris Basin); in the family and generic compositions, it is similar to the Eocene assemblages of the northern type (Latdorfian Assemblage, etc.). The quantity of species in common with the Eocene assemblages is rather small, 44 of 206 (21.3%).

The molluscan composition indicates that there existed a faunal exchange between the Aquitaine and the Paris basins via the Atlantic; however, it was complicated by a climatic barrier. This is indicated by the small number of species in common and by the transitional pattern of the fauna found in Brittany (Renn).

As distinct from the Paris Basin in the southern area of England, the molluscan habitats became unfavorable in the Early Oligocene compared to the Late Eocene. Only 24 bivalve species were found in the Hemstead Beds of the Hampshire Basin. This is mainly endemic fauna with fresh-water taxa. Some marine species are in common with those from the Paris Basin. The Hemstead Gastropod Assemblage includes 56 species of 19 marine families in addition to fresh-water species. In the family and species compositions, this assemblage is similar to the northern Oligocene type. It virtually lacks moderately psychrotolerant groups (ampullinids are the most warm-water forms of Hemstead gastropods). Of 56 gastropod species from the Hemstead Beds, only 18 were reported from other Rupelian assemblages; 18 species are in common with those from the Eocene, with 8 of them being found only in the Headon Beds in the Eocene of England.

**North Sea Basin.** Of molluscan assemblages from this region, the assemblage from sandy facies of the Mainz Basin is the most abundant (Sandberger, 1856–1863; Neuffer, 1973; Kuster-Wendenburg, 1973, 1982; Gürs, 1995; Fig. 3, locality 20). It includes 128 bivalve species and 212 gastropod species (hereinafter, continental groups that are occasionally described in associ-



ation with marine taxa are not considered). A recent revision by Gürs has markedly extended the list of mollusks from this assemblage, especially of gastropods. In addition to new species, this list today includes the genera and families previously unknown there. Naturally, this revision somewhat changed the values of the Preston's coefficients; nevertheless, this supported rather than changed previous conclusions (Amitrov, 1993, 1996).

The Mainz Basin had the maximum species in common with the Paris Basin (93, the Preston's coefficient is 0.64; Fig. 3, locality 19). The family and generic compositions indicate that these two basins had similar temperature regimes. As distinct from the Paris Basin, in the Mainz Basin diastomas were absent, but there were many groups that were absent in both the Eocene assemblages and the Oligocene northern assemblages (cocculinids, littorinids, omalogyrids, vasids, philinids, atyids, umbraculids, siphonariids, and juliids), as well as the groups that are known from northern Eocene assemblages, but are absent or very rare in northern Oligocene assemblages (pleurotomariids, patellids, turbinids, lacunids, cypraeids, etc.).

In more northern regions, certain distinctions in the patterns of bivalve and gastropod assemblages are observed. The bivalve assemblage from the Rupelian of Belgium (Berg Sands, clay with *Nucula compta* and Boom Clays) is rather unique. About 60 bivalve species were recorded there (Gilbert and Heinzelin, 1954). Warm-water elements of this fauna are much more diverse than those of other molluskan assemblages from the Lower Oligocene of the North Sea Basin. *Glycymeris (Tucetilla)*, *Claidornites*, *Arcopagia*, *Isognomon*, and *Spondylus* showing certain similarity between this fauna and the faunas from the Mainz Basin and Switzerland were found only there. This diversity may be determined by the shallow-water facies that were only known in Belgium or by the proximity of a strait that flew through the Rhine Graben, Mainz Basin, and Alsace (Saubade, 1970, fig. 3).

In more northern area of the basin (in the Netherlands, Denmark, northern Germany, and Poland), a uniform fauna (about 40 bivalve species) typical of the Rupelian clay facies was found. This assemblage was dominated by paleotaxodonts, thyasirids, astartes, and pectinids. However, any true comparison is impossible, because these features were primarily determined by facial conditions in which the sediments accumulated and bivalves occurred.

All the gastropod assemblages in northern areas, from Belgium and the Netherlands to Denmark, northern Germany and Poland, are closely similar to each other, assigned to the northern type, and have similar distinctions from the Mainz Assemblage. The above-listed relatively warm-water families that are known from the Mainz Basin are absent there. At the same time, their species composition is closely similar to that of the Mainz Assemblage. The Preston's dissimilarity

coefficient for the Mainz Basin and Belgium—the Netherlands (0.65) is almost as low as that for the Mainz and Paris basins. The assemblages of the northern areas under consideration differ more markedly from those of the Paris Basin than from those of the Mainz Basin; however, several common species absent from the Mainz Basin, were registered in the Paris Basin and the northern areas (Amitrov, 1996). This indicates the probable existence of an occasional direct connection between the Paris Basin and the North Sea Basin (in a narrow sense), not via the Mainz Basin.

The Alsace Region generally may be assigned to the North Sea Basin. Only 14 gastropod species were determined there with certainty. Alsace is situated south of the Mainz Basin; however, its assemblage is closer to the northern assemblages based on both the family (only psychrotolerant groups) and the species composition (12 species in common with Belgium and the Netherlands, the Preston's coefficient is 0.57).

The proportion of gastropods that were inherited from the Eocene fauna is about 30% in the Mainz Basin; 55% in Belgium and the Netherlands; 37% in Denmark, northern Germany, and Poland; and about 57% in Alsace.

A representative molluskan assemblage is known from the Fore-Alpine Depression, namely, from Switzerland, Bern Jurassic (Kissling, 1896). In the Early Oligocene, this depression was a strait, which connected Western Mediterranean and the Carpathian Basin. Although the assemblage was composed of rather warm-water groups, it almost lacked typical Mediterranean genera and species. It was similar to the fauna from the Mainz Basin (of 55 bivalve and 29 gastropod species, 41 and 23 are in common, the Preston's coefficient is 0.65); this indicates direct connections between these basins, probably via a system of Rhine grabens. This is a transitional assemblage, like the Mainz Assemblage. As concerns of gastropods, it includes ampullinids, patellids, and vermetids. Only three species are in common with those from the neighboring region of the French Alps. It was mentioned above that the assemblage from the French Alps is assigned to the southern type and we consider this region as a component of the Northern Mediterranean Region.

In the Rupelian of Bavaria, turritellids are the most warm-water gastropod group, and this assemblage may be only conventionally considered to be transitional. Its species composition is most similar to those of the Mainz Assemblage (16 species in common, the Preston's coefficient is 0.68) and the Belgian–Netherlands Assemblage (17 species in common, the Preston's coefficient is 0.53).

The assemblage from the Swiss Alps includes 15 species in common with the Priabonian Assemblage (52%).

**Carpathian Basin.** In the Czech and Polish Carpathians, the Lower Rupelian deepwater facies do not yield mollusks or include very impoverished assem-

blages that are very difficult to compare. The shallow-water assemblage from the Pokut (Ukrainian) Carpathians was transported to deepwater facies by turbid flows and still requires a revision. However, preliminary data indicate that this assemblage clearly belongs to the North European Faunal type (Studencka *et al.*, 1999) based on its generic composition (the presence of *Astarte* and *Scalaricardita* and the absence of specific Mediterranean taxa). At the same time, the presence of such gastropod families as the Turritellidae, Volutidae, Conidae, and Marginellidae indicates more warm-water regimes in the North Carpathian shelf than in the northern shelf of the Eastern Paratethys.

In the southern shelf of the Carpathian Basin, an abundant molluscan fauna was only found in Transylvania (Lower Rupelian Hoja and Mera beds). The bivalve assemblage is not very rich but rather representative. Although the content of the warm-water elements is relatively low, this assemblage is characterized by the presence of genera and species specific for the Mediterranean Region (*Chlamys biarritzensis*, *Spondylus cisalpinus*, *Macrosolen hollowaysi*, etc.). The gastropod assemblage is rather large, including 117 species of 41 families. This is assigned to the transitional type; the warm-water groups include only diastomas. Recall that the Priabonian assemblage from Transylvania included both strombids and *Velates* and was assigned to standard southern assemblages. Despite this transition from the southern to the intermediate type, in the Rupelian, southern assemblages (northern Italy, southern Bulgaria, and Armenia) were still most similar to the Transylvanian assemblage in species composition. This indicates the persistence of direct connections between the Transylvanian shelf and the Mediterranean Region at the beginning of the Oligocene. Nevertheless, the Preston's coefficients increased from 0.71–0.75 to 0.83–0.86. Eighty-six gastropod species in common are reported for the Rupelian and Eocene of Transylvania (in the Priabonian, 11 of them were absent), i.e., 63% species in the assemblage were in common and 37% were not known in the Eocene. The proportion of bivalve species that first appeared in the Oligocene is only 14%.

At the end of the Rupelian, the Carpathian Basin, as the entire Paratethys, was of a closed or semiclosed type, inhabited by endemic brackish-water fauna (Baldi, 1986; Rusu, 1988). This molluscan assemblage is the richest in Transylvania, where *Janschinella garetzkii*, *Ergenica* sp., *Urbnisia lata*, *Merklinicardium apostolovense*, *Korobkoviella* sp., *Cerastoderma serogosicum*, and *C. lipoldi* (determination by Popov from the material collected by Rusu) were found (Popov, 1995). In Hungary, *Janschinella* sp., *Urbnisia* sp., and *Cerastoderma lipoldi* were found (Baldi, 1986).

**Caucasus–Kopet Dagh (Pshekhian) Basin.** In the first half of the Early Oligocene, normal marine regimes existed in the basin. The molluscan assemblages in the southern shelf area (recorded from Georgia and Azerbaijan) markedly differed from those in

northern and eastern shelf areas (from southern Ukraine, Crimea, northern Caucasus, Ergeni Highland, and the entire Transcaspien) in water temperature regimes. Among the southern shelf assemblages, the assemblage from southern Georgia is most diverse (Akhalsikhe, about 100 bivalve species). The species of Tethyan origin are very rare there (*Modiolus rutimyeri*, *Pecten arcuatus*, and *Chlamys meissonieri*), with all of them probably from the Eocene. Only eight species are in common with the Armenian Assemblage. Their presence does not support the existence of any direct connections between Transcaucasia and Tethys. The marked impoverishment of fauna indicates that these connections could disappear as early as the Middle Priabonian. Approximately a half of the bivalve species was in common with those from more northern assemblages of southern Ukraine, Mangyshlak, and Ustyurt.

Of gastropods from relatively warm-water groups that were absent in northern Oligocene assemblages, diastomas, melongenids, and large ampullinids were found in Georgia. To characterize the species composition, it is of interest to compare the dissimilarities of the assemblages from Georgia and other regions of western Eurasia in the Rupelian and Priabonian. The similarity of the Georgian and southern assemblages (from Italy, Bulgaria, and Armenia) evidently decreased with time, i.e., the Preston's coefficients increased from 0.77–0.84 in the Priabonian to 0.82–0.93 in the Rupelian. At the same time, the similarity between the Georgian and northern assemblages (from Belgium–Netherlands, northern Germany, and Transcaspien) increased; the Preston's coefficients decreased from 0.91–0.93 to 0.82–0.84 (Amitrov, 1996). However, in gastropods, this tendency is not as clear as in bivalves; in particular, in the Rupelian, the similarity to the Armenian Assemblage remained high. Unlike bivalves, there were gastropod species there unknown in the Eocene and found only in the Rupelian of Armenia, Georgia, and Azerbaijan (*Benoistia korobkovi* Zotova), or in Armenia and Azerbaijan (*Melongena azerbaijanica* Alizade et Bagmanov). A small assemblage from Azerbaijan (village of Mirlyar, Kubatly District) resembles the Georgian Assemblage. Gastropod fauna, as benthic foraminiferal assemblages, indicates that at the beginning of the Oligocene, an indirect connection could exist in Transcaucasia between the Pshekhian and the Mediterranean basins, possibly, via the Armenian Gulf. In the Rupelian of Georgia, 41% of species in common with the Eocene species were found.

Pshekhian mollusks from the northern shelf area (southern Ukraine, Crimea, Ciscaucasia, Volga–Don Region, Mangyshlak, and Ustyurt) are rather diverse (about 130 bivalve species of 80 genera and 60 gastropod species) and similar to each other, despite an impoverishment of some assemblages. The molluscan assemblages from these regions (even if considered to be an integral fauna) are more markedly impoverished than the more northern Eocene assemblages (for exam-

ple, the Chegan Assemblage) and the Oligocene assemblages from the northern areas of Western Europe. Concerning gastropods, not only tibiids, melongenids, marginellids, and turritellids, but also trochids, xenophorids, olivids, volutids, conids, etc., which were found in some Rupelian assemblages of northern Europe are absent. A good preservation of fauna (for example, in the Uzunbas Formation in Mangyshlak) indicates that these assemblages are complete; i.e., the impoverishment is characteristic of the assemblage rather than a result of secondary changes. Despite the low proportion of warm-water elements (the proportion of subtropical taxa was at most 15–20%), this fauna was similar to that from the Transcaucasian shelf in the species composition (about 40% of species and 70% of genera in common). Outside the Eastern Paratethys, this fauna was most similar to the assemblages from the North Sea Basin. The ranges of many species were restricted to the Eastern Paratethys (about 20% of this fauna) a large part of these species were dominants and contributed to the general pattern of the assemblage (*Pterolucina batalpaschinica*, *Yoldiella chadumica*, etc.).

Of 60 gastropod species, 34 (57%) are in common with the Eocene fauna, although in some regions, the proportion is higher, i.e., ten species of 13 in the northern Caucasus and 20 species of 25 in the Crimea.

The composition of molluscan assemblages from the platform part of Ukraine deserves special consideration. More warm-water Eocene taxa were probably included into the list of assemblages from the Nikopol Formation of the South Ukrainian Depression. The situation is even more complicated in the Zhukovtsy and Bishki Beds of the Dnieper–Donets Depression. Some researchers deny their Oligocene age. The poor preservation of mollusk fossils does not allow any justified assumption. However, even if the presently known assemblages do not belong to the Rupelian, the analysis of the molluscan distribution in adjacent regions indirectly but strongly supports the connection between the sea basins in the southern areas of the former USSR and the North Sea Basin in the Rupelian via a strait in northern Ukraine and Belarus, rather than via the Carpathian Basin. In the Crimean–Transcaspiian and Polish–Belgian assemblages, species in common are present that were absent from both the Eocene and Rupelian of Central Europe, as well as from the Mainz and Paris basins. Compare the gastropod assemblages from the Crimea–Transcaspiian and northern Europe.

	Number of species in common	Preston's coef.
With the eastern area of the North Sea Basin (Pol- land, northern Germany, Denmark)	27	0.76
With the western area of the North Sea Basin (Netherlands–Belgium)	21	0.79
With the Mainz Basin	22	0.82
With the Paris Basin	17	0.87

An increase in the dissimilarity is very natural, nearly all the species in common with a more distant assemblage are also present in a closer located assemblage.

A molluscan assemblage of the same (northern) type inhabited the Fore-Kopet Dagh Gulf of the Turanian Sea; 33 bivalve species and 15 gastropod species were recorded in the upper part of the Torymbeur Formation (Lower Oligocene), Western Kopet Dagh (data by Amitrov; Popov *et al.*, 1993).

Thus, the comparison of molluscan distribution in the Early Oligocene and Late Eocene clearly indicates the impoverishment of assemblages and the appearance of new species; this is especially well pronounced in the northern regions. An increase in the temperature gradient is especially well traced in the gastropod distribution.

**Caucasus–Kopet Dagh (Solenovian) Basin.** In the second half of the Early Oligocene, numerous bivalve species and genera endemic to the Paratethys appeared in Paratethyan lagoons in the Late Pshekhian after the closure and brackishing. Among these forms, there were *Ergenica*, *Urbnisia*, *Janschinella*, *Corbula* (*Lenticorbula*), and some species of *Cerastoderma*. At the same time, gastropods of this basin were mainly the lagoonal forms that had wide geographic and stratigraphic ranges (Popov *et al.*, 1985).

The integrity of the molluscan fauna of the entire Paratethys, as well as the distinctions in the composition of the western, northern, and southern shelf areas, are more prominent in the taxonomic composition of the impoverished brackish-water–lagoonal Early Solenovian Molluscan Fauna (18 bivalve species and 22 gastropod species) than in that of the marine fauna. The majority of molluscan genera were in common, but the species composition was much more diverse in Transcaucasia. The species composition of mollusks from the Alpine–Carpathian Basin has not yet received a detailed study. At present, nearly all the taxa identified there are in common with those from Eastern Paratethys. Only ten bivalve species were found in the northern shelf area (from southern Ukraine to the Ustyurt Plateau), including the most characteristic *Ergenica* and *Janschinella garetzkii*, which are unknown further south. A more diverse assemblage (20 species) was typical of the southern (Transcaucasian) area of the basin; it was dominated by the forms that were rare or unknown in the northern regions, including *Urbnisia lata*, *Janschinella vinogradskii*, *Merklinocardium*, *Korobkoviella*, and *Corbula* (*Lenticorbula*) *mefferti*. The northern shelf of Caucasian Island (sections of the rivers of Fars, Tsraudon, and Fiagdon) was probably inhabited by impoverished fauna of a southerner type.

#### *Scleractinian Corals*

**Transcaucasia.** Environments favorable for the development of coral reefs were retained in the Early Oligocene only in the Yerevan Gulf that continued into

the Central Iranian Basin. The coral assemblage was closely similar in taxonomic composition to the Late Eocene and Oligocene assemblages from the southern regions of Europe. It included representatives of the suborders Archeocoeniina, Faviina, Meandriina, and Fungiina. Representatives of the families Acroporidae, Stylophoridae, Faviidae, Heliastreaeidae, Astrangiidae, Agariciidae, Agathiphyllidae, and Poritidae are most frequent. About 35 species of 20 genera of the Armenian Assemblage are assigned to the colonial taxa.

#### *Complex Benthos-based Zoogeographic Zonation*

At the onset of the Oligocene, the faunal distinctions between the North African and Eurasian coastal areas of the Mediterranean–Mesopotamian Basin probably decreased because of an exchange between benthic shallow-water faunas; the Ancient Mediterranean Region became integral, since it was not divided into subregions.

Distinctions between the Ancient Mediterranean and the North Sea regions still existed. The tropical and subtropical fauna of the former included the reef facies inhabited by nummulites of the Southern Nummulitid Zone. Among small benthic foraminifers, there were the specialized genera typical of only the Mediterranean assemblages, such as *Pararotalia*, *Herondenia*, *Queraltina*, *Pseudoplanulinella*, and *Sphaerogypsina*, which usually had large, thick-walled, and sculptured tests. Although the faunal differentiation within the Ancient Mediterranean Region is rather high, the differences appear to be occasional and do not allow for the subdivision into provinces.

In the Atlantic coastal area of Europe, the boundary was between the Aquitaine and the Paris basins (Fig. 3), similarly to that in the Priabonian. The northern coastal area of the Carpathian Basin was included in the North European Region. In the south, in the region of the Transylvanian shelf, the basin was still opened in the first half of the Rupelian and inhabited by a fauna of the Mediterranean type. The fauna of the Hungarian Paleogene Basins was mixed, which indicates the climatic nature of this boundary in the Carpathian Basin. This area was inhabited by both the Tethyan species and genera, and the characteristic taxa of the North European basins. This border (that was probably determined by a continental barrier) further continued to the Balkanides and isolated the Varna Gulf of the Eastern Paratethys from the Fore-Rhodope Basin, in which the Mediterranean Gulf entered. Similarly obvious faunal distinctions were observed in Transcaucasia; Armenia was still inhabited by the Tethyan fauna with reef-building corals, whereas the southern area of Georgia (Akhaltzikhe) was a component of the Eastern Paratethys assigned to the North European Region. The boundary between the Balkanides and the Lesser Caucasus probably extended across the Black Sea Basin, since the northern coastal area of the Anatolian Land belonged to the Ancient Mediterranean Region (based

on scanty data on nummulitids). Nummulitids and, to certain extent, gastropods indicate that the Mediterranean influence was also rather marked in the Georgian area of the Paratethys, which should certainly be included in the North European Region.

The North European Region is distinctly divided into smaller units: however, the patterns of differentiation varies depending on the groups involved in the analysis. This region includes (1) the southerner zone inhabited by impoverished assemblages of large foraminifers, *Nummulites*, *Operculina*, and *Discocyclina* and by diverse subtropical-boreal molluskan assemblages; and (2) the colder-water impoverished zone with mainly boreal biota inhabiting the northern and eastern shelf areas. This division by the water temperature regimes is supported by the data on nummulites and gastropods; in the case of mollusks, the Oligocene assemblages are divided into transitional and northern (Amitrov, 1996, fig. 3). However, other groups indicate that this zonation is complicated by the paleogeographic peculiarities of particular basins. Thus, a clear integrity of the Eastern Paratethyan Fauna is indicated by the compositions of bivalves (Popov, 1995), benthic foraminifers, and ostracodes; this allows one to consider these assemblages to be components of an integrated province. These assemblages commonly designated as the Chadumian assemblages are similar to the North Sea assemblages in species and generic compositions. Benthic foraminifers of these assemblages included the same species of the genus *Cibicidoides* (*C. pseudoungerianus* and *C. sulzensis*) and *Cibicidina amphisyliensis*, *Ceratobulimina contraria*, *Rotaliatina bulimoides*, *Svratkina perlata*, *Turrilina alsatica*, etc. In the shallow-water areas, an important role in the faunal composition was played by several species of arenaceous foraminifers (*Haplophragmoides fidelis*, *H. deformabilis*, *Gaudryinopsis gracilis*, etc.) that were widespread in only the Pshekhian Basin and local taxa that mainly had primitive tests. Similar relationships of the molluskan and ostracode faunas from the Eastern Paratethys and northern Europe combined with clear differences between them allow one to designate the Eastern Paratethys as the Eastern Chadumian Province of the North European Paleobiogeographic Region. Based on this assumption, the distinctions between the faunas of the northern and southern (Transcaucasian) coastal areas that are also very marked should be regarded as minor (subprovincial) differences.

The biogeographical position of the Azerbaijan shelf of the Caucasus–Kopet Dagh Basin, with its endemic fauna of benthic foraminifers, remains uncertain. It may only be mentioned that, judging by the generic composition, this assemblage belonged to the North European Region and included certain rare species of the Chadumian Province. The faunal distinctions of the benthic foraminifer assemblages from the Turanian Subprovince were probably inherited from the Eocene and gradually disappeared in the Rupelian. The complicated stratigraphy of the Tajik–Ferghana

Region does not allow for the discussion of biogeographic importance of distinctions of the unique faunas from this region.

A puzzle is the biogeographic similarity of the Syrian area of the Mediterranean–Mesopotamian Basin to the Eastern Paratethys, which was inhabited by the foraminiferal assemblages closely similar to the Crimean–Caucasian assemblages, as in the Priabonian (Krashennikov, 1965). The routes of exchange between these faunas remain uncertain.

The faunas of the Paris Basin also appear to be unique; this, along with the distinctions of the more warm-water Aquitaine Fauna, probably displayed the peculiarity of the Atlantic biota. Although the microfauna and the macrofauna of the Aquitaine Basin included warm-water genera and species in common with the Mediterranean, this assemblage is rather unique and dominated by the species that were originally described there.

Shallow-water areas of the Paris Basin were inhabited by numerous endemic miliolids (among benthic foraminifers) and mainly endemic mollusks. The species in common with the North European and Mediterranean faunas were mainly the cosmopolitans. However, we assign this region to the North European Region based on the absence of characteristic Mediterranean warm-water genera and species and the transitional pattern of the Mainz and Alsace assemblages.

Biota of the North Sea Basin (assemblages of the North Sea, Belgium, Netherlands, Denmark, northern Germany, and Poland) is the type of the Rupelian. The composition of this fauna was mainly descended from the Latdorfian (Late Eocene). Of the highest category of endemism is the assemblage of benthic foraminifers, in which species of the genus *Cibicidoides* were numerous; *Lenticulina herrmanni*, *Ceratobulimina contraria*, *Rotaliatina bulimoides*, *Cibicidina amphisyliensis*, *Svatkina perlata*, *Turrilina alsatica*, *Angulogerina oligocenica*, and the genera of the order Miliolida (*Quinqueloculina*, *Triloculina*, and *Spiroloculina*) were common. Tropical elements and nummulites were absent from these assemblages.

The faunas of the North Alpine and Mainz basins are similar to each other and substantially differ from the assemblages of the North Sea. However, the transitional pattern of the Belgian Fauna indicates that these distinctions are possibly facial, and, therefore, these faunas may be components of the integral German Province with two subprovinces, the northern subprovince with the typical Rupelian fauna and the southern subprovince enriched by warm-water elements.

The distribution of biota over the Paratethys changed in the Solenovian time. However, available data on the faunal peculiarity of this area with reference to different taxonomic groups are rather contradictory. Bivalves show an extremely high peculiarity; of ten genera and 18 species that inhabited Paratethys in the first half of the Solenovian Time, six genera and 11 spe-

cies were found only there. In the category of endemism, this fauna is comparable to the modern-day Caspian Assemblage; the zoogeographic status is very high, at a level of a separate region (Starobogatov, 1970). However, among gastropods, only one species was endemic; 75% of ostracodes were marine species and endemic species were rare (Popov *et al.*, 1985). The Solenovian endemic genera and species of mollusks, ostracodes, and nannoplankton occurred from the Western Carpathians to Kysyl Kum and Kopet Dag. For this reason, we consider the entire Paratethys of the second half of the Rupelian as the separate Solenovian Province (= Proto-Paratethyan Province after Rusu, 1988). The Solenovian endemic species and genera of fauna and microflora probably appeared in lagoons of the Eastern Paratethys; subsequently, they occupied the entire Paratethys. Thus, the Carpathian Basin, which at the beginning of the Oligocene was partially included in the German Province, whereas its southern (Transylvanian) area was included in the Ancient Mediterranean Region, was involved in the Solenovian Province of the Paratethys from the second part of the Rupelian, as indicated by biogeographical data. It is evident that the Solenovian Province is a component of the North European Region and subdivided into two subprovinces, the northern (Scythian–Turanian) subprovince and the southern (Caucasus) subprovince. The latter probably included the entire shelf of Greater Caucasian Island. It remains uncertain whether the Carpathian Basin fauna belongs to the southern or northern subprovince.

## Terrestrial Biogeography

### *Phytogeography*

In the Early Oligocene, the transition from the Paleocenophytic to the Neocenophytic was accomplished and resulted in a drastic change in the terrestrial flora and vegetation. Plants of the ancient Cenozoic flora represented by form-genera were entirely lost from the vegetative cover and replaced by the Recent genera, which formed the major core of the new flora. At the beginning of the Early Oligocene, the floras of all regions were characterized by approximately equal proportions of the Paleocenophytic and Neocenophytic forms. By the end of the Early Oligocene, the transformation had been completed almost everywhere. This transformation was especially prominent in the midlatitudes of western Eurasia and extended from the Tethyan Region to the Boreal Region or to the ecotone zone at the end of the Early Oligocene.

As the northern boundary of the subtropical zone and the entire ecotone zone, which divided the major phytochores was displaced southward, plants also migrated submeridionally from north to south so that the ranges of moderately thermophilic deciduous plants, forming the core of the Boreal Region Flora, increased. This process resulted in the formation of a

moderately thermophilic, deciduous, mesophilic Oligocene flora designated by A.N. Krishtofovich the Turgai Flora.

**North Africa and Arabia.** The North African Tropical Flora was widespread in the southern coastal area of the Mediterranean Basin, similarly to that in the Eocene, although the southern ecotone zone, in which the exchange of floras occurred, occupied this area. The modern-day Eastern Mediterranean, Asia Minor, and Iran were components of the Tethyan Region inhabited by relatively hydrophilic flora in the first half of the Early Oligocene and by a subarid flora in its second part.

**Southern Europe–Lesser Caucasus.** In the northern coastal area of the Mediterranean Region, humid climate changed to arid type at the onset of the Oligocene. These new environments and the corresponding type of xerophytic floras covered southern areas of France, Italy, and Balkan Peninsular and expanded to Anatolia and the Lesser Caucasus. The earliest floras of this South European Oligocene Province were recorded from the Marseille and Manosque depressions in the southern area of France, Liguria, and Serbia. Their age is supported by the occurrences of assemblages from the MP21 and MP22 vertebrate zones. In the Marseille Depression, Mai (1995) assumes the Saint-Jean-de-Garquier Flora from the vicinity of Semeno in marly limestones and gypsum beds at the base of the Estak Limestones to be the stratigraphic type of this level (names of the main floras shown in Fig. 4 are underlined). This is a typical subxerophytic laurel-leaved flora, in which laurels were accompanied by pines, legumes, and *Tetraclinuis*. The Taxodiaceae are represented by *Glyptostrobus europaeus* and *Sequoia abietina*. This flora and floras of similar age are dominated by *Laurophyllum primigenium*, *Daphnogene lanceolata*, *Persea princeps*, *Myrica longifolia*, *Comptonia schrankii*, *Zizyphus zizyphoides*, and *Pinus paleostrobus*. *Dolios-trobus taxiformis* is common. Palms and ferns are frequent. The deciduous plants *Carpinus cuspidens*, *C. grandis*, *Acer primaevum*, *Betula oblongata*, *Platanus leucophylla*, *Pterocarya parasidiaca*, *Craigia europaea*, and *Cedrelospermum leptospermum* are relatively rare. Semievergreen sclerophyllous low-growing forests and brushes are the major components of the zonal vegetation.

In addition to the type flora, the group of the earliest Early Oligocene floras of the Marseille Depression includes the Fenestrelle and Montespina floras, as well as the Cereste Flora in the Manosque Depression, the Gargas and Sult floras in Vaucluse, and the Santa Giustina Flora in Liguria. In Serbia, the Ljiljanska Reka Flora from the Pćeinja Depression is similar in general pattern.

The flora of the second half of the Early Oligocene is represented by the Vicenza Flora found in the homonymous province of Italy in the vicinity of Farra. Mai (1995) considered this to be the type flora. This flora was found in the littoral marl beds with *Nummulites*

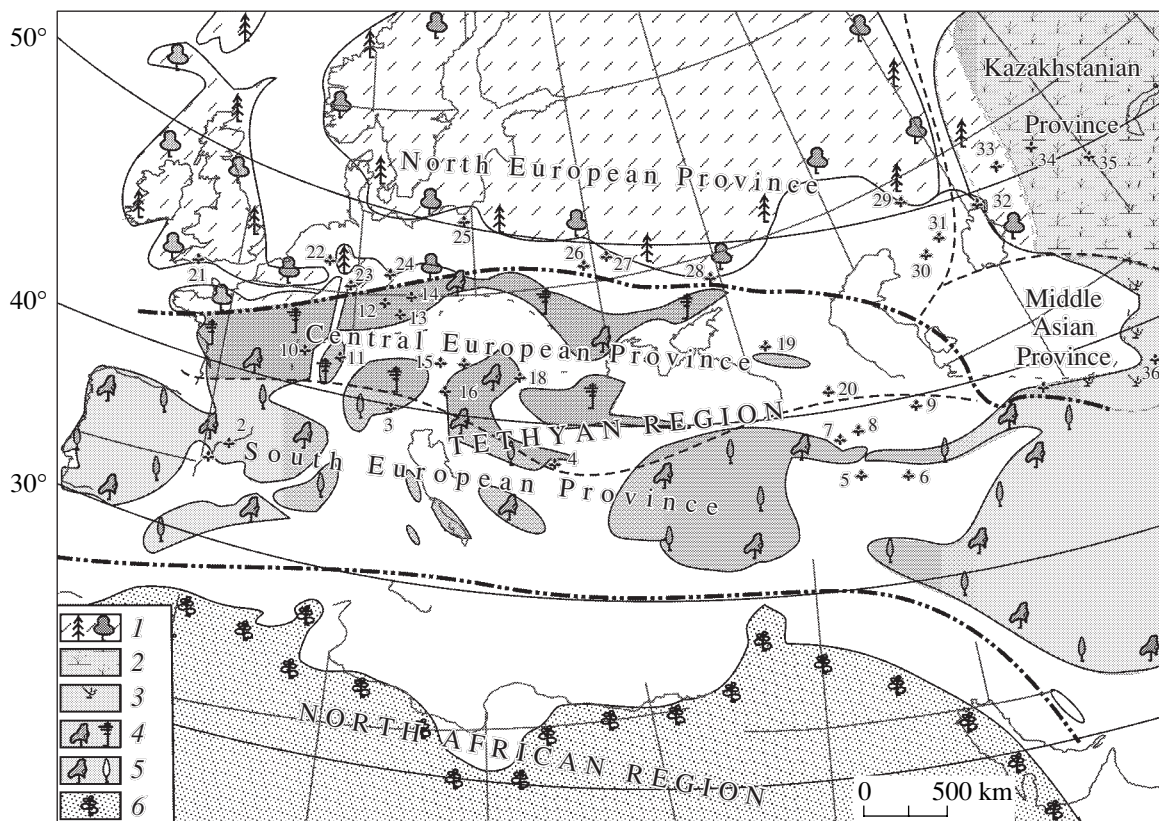
*vascus* and a nannoplankton assemblage of the NP23 Zone. The Vicenza Assemblage was dominated by sclerophyllous laurels, Myricaceae, Quercus accompanied by Myrsinaceae, Sapotaceae, Ericaceae, Araliaceae, Sapindaceae, Anacardiaceae, Myrtaceae, Rhamnaceae, Rutaceae, and Leguminosae; the latter family composed at least 10% of the entire flora. *Zizyphus zizyphoides*, *Myrica lignitum*, and *Tetraclinuis brongniartii* were common. Certain early conifers, such as *Dolios-trobus taxiformis* and *Athrotaxis couttsiae*, remained. Exotic tropical plants, dragon-tree and even *Zamites* (Bonnieux Flora), were recorded. The deciduous taxa include *Alnus*, *Ailanthus*, *Acer*, *Aralia*, *Betula*, *Carpinus*, *Carya*, *Corylus*, *Cornus*, *Crataegus*, *Fagus*, *Gleditschia*, *Juglans*, *Nyssa*, *Ostrya*, *Platycarya*, *Populus*, *Platanus*, *Pterocarya*, *Sassafras*, *Ulmus*, and *Zelkova*. *Quercus* sect., *Ilex*, *Pistacea*, *Arbutus*, *Ceratonia*, and *Smilax* first appeared in the floras of this level (floras of Aix, Bonnieux, and Chiavon). The major occurrences of the floras of the second half of the Oligocene in the arid province are the Aix en Provence, Camoins-Bains, Saint-Zacharie, and Bonnieux in the Provence Province; Chiavon, Salcedo, and Novale in the Vicenza Province; and one occurrence in Pavia. The floras of the southern province are similar to those of the northern province in the presence of Arcto-Tertiary elements, differing by the presence of xerophilous and microphyllous evergreen elements.

In the second half of the Early Oligocene, this flora was in direct contact with the belt of subarid floras in Transcaucasia (Akhaltzikhe, Lesser Caucasus). Rich Lower Oligocene subtropical floras were studied by Kasumova on the northern slope of the Lesser Caucasus (Zeyva and Nizhnii Adzhakend in the Gyandzha District, Azerbaijan). A small collection from these outcrops were subsequently treated by Akhmetiev. The Lauraceae and Fagaceae (*Eotrigonobalanus*, *Lithocarpus*, *Cinnamomum*, and *Daphnogene*) were the major forest-forming taxa; they were accompanied by the Taxodiaceae, Myricaceae, and Ericaceae (*Myrica agdjakendica* and *Leucothoe protogaea*).

Palibin described a subtropical flora from the basal sandy member of the Shorakbyur Formation of the Yerevan–Ordubad Zone (Shorakbyur) underlain by the marly clayey Zovashen Formation with *Nummulites fabiani* and the Later Eocene planktonic foraminiferal assemblage of the P17 Zone. In addition to herbaceous monocotyledons, the Shorakbyur Assemblage includes *Litsea primigenia*, *Sapindus graecus*, *Ilex ambigua*, *Myrica hakaefolia*, etc. Based on planktonic foraminifers (analyzed by Krashennikov), this part of the section belongs to the *Globigerina tapuriensis* (P18) Zone.

The spore and pollen assemblages from the basal Oligocene of Armenia were characterized by a high proportion of pollen of the Pinaceae and an increased range of subtropical xerophytes (*Nypa*, Elaeagnaceae, Malvaceae, Bombacaceae, etc.). Frequent fluctuations of the temperature and the climatic humidity were





**Fig. 4.** Phytogeographic zonation of the Boreal and Tethyan regions in the Rupelian. Explanations: (1–3) **Boreal Region:** (1) deciduous mesophilic conifer–broad-leaved forests, including pinaceous, taxodiaceans, juglandaceans, betulaceans, and fagaceans; (2) xerophytic oak–laurel forests and sclerophyllous shrubs formed by legumes and ericaceans; tugai forests with poplar, alder, and ulmus in valleys; (3) shrub–herb formations, including halophytes (*Ephedra*, *Artemisia*, and *Salsola*); (4–5) **Tethyan Region:** (4) subtropical mesophilic forests formed by taxodiaceans, cupressaceans, fagaceans, and lauraceans; (5) subxerophilous and xerophilous forests formed by lauraceans, legumes, fagaceans, and ericaceans; (6) **North African Region:** tropical forests formed by lauraceans, legumes, and, occasionally, by fagaceans; farther inland, these are replaced by open savannah woodlands with legumes and eophobous plants. The main Rupelian floral localities: (1) Aix en Provence; (2) Saint Jean de Garquier; (3) Vicenza; (4) Edirne; (5) Shorakbyur; (6) Darry-Dagh; (7) Akhaltsikhe; (8) Tori; (9) Zeyva; (10) Lobstann; (11) Vivey; (12) Nerhau; (13) Valec; (14) Haselbach; (15) Csillaghegy (NP22); (16) Sotzca (NP23); (17) Kiscell; (18) Mera; (19) Belaya River; (20) Mayakovski; (21) Devonshire; (22) Sieblos; (23) Dormach; (24) Haselbach; (25) Svetlogorsk; (26) Volhynia; (27) Starodubka; (28) Pasekovo; (29) Kyzyltobe; (30) Ashcheiryk; (31) Zhabyske; (32) Kumbulak; (33) Altyn Chokysy; (34) Chelkar Nura; (35) Tortmolla; (36) Tajik Depression.

favorable for rapid disintegration of the Eocene flora. The frequent humidity fluctuations in the spore and pollen assemblages of Armenia are supported by the opposite phase distribution of cryptogams as indicators of humid regimes and pollen of grasses, *Ephedra*, the Cupressaceae, and certain other plants that characterize the arid regime. Zaporozhets indicated that the frequent alternation of humid and arid climatic phases in the second half of the Late Eocene in the southwestern regions of the former USSR was also typical of the Early Oligocene. The first humid phase in Armenia corresponds to the epoch of accumulation of beds of the lower (but for the basal beds) part of the *Globigerina tapuriensis* (P18) Zone, whereas the arid phase corresponds to the lowermost part of this zone. The second part of the *G. tapuriensis* Zone was characterized by a more humid climate, followed by an arid phase that corresponds to the transition area of the P18 and P19 zones.

The floras of the second half of the Early Oligocene of Transcaucasia were more xerophilous; this indicates a new increase in aridity. Among these floras, there is the well dated Tori Flora from the Corbulla Beds, Borzhomi District, of the Solenovian age, although, in addition to the xeromorphic sclerophyllous plants this flora includes large-leaved taxa. This flora is polytopic, dominated by *Dryophyllum curticillense* and *Myrica lignitum*. Avakov found fruits of legumes in Tori. The floras from the Solenovian level of the north-facing slope of the Lesser Caucasus are far more xenomorphic after Kasumova.

**Central Europe and Northern Caucasus.** The earliest Early Oligocene floras in the midlatitudes of western Eurasia correlates with the NP21–NP22 nannoplankton zones, the *Globigerina tapuriensis* Planktonic Foraminiferal Zone, the *Phthanoperidinium amoemum* Dinocyst Zone, Grande Caupure, and the MP21 Mam-

malian Zone. These floras differed little from the flora from Bembridge Beds of the terminal Eocene; therefore, some paleobotanists assigned them to the Early Oligocene. Mai (1995) considers the western Bohemian Valeč Flora from the beds containing mammals of the MP21 Zone to be the type flora of this level. This flora and the floras of similar age from the northern coastal area of the Paratethys display the vegetation of the mesophilic forests formed by the Lauraceae (including *Daphnogene*), oaks with the entire leaves, magnolias, etc. Among thermophytes, an important role was played by the Eocene *Doliosobus certus*, *Zizyphus zizyphoides*, *Myrica banksiaefolia*, and *Lygodium kaulfusii*. However, the Valeč Flora also includes many deciduous plants, such as *Alnus*, *Carpinus*, *Ulmus*, *Zelkova*, *Celtis*, *Carya*, *Cercidiphyllum*, etc.

The subsequent subtropical floras of Central Europe are the following. The Nagybatony Ujlak Flora (Hungary) and Mera Flora (Romania) come from the beds with the NP22 nannoplanktonic assemblage. The floras of Csillaghegy, Budapest, Kiseged (found in the vicinity of Eger), and many Romanian floras [in the vicinity of Cluj; Aghires, Muereasca des Sus, and Sulanesti (in the vicinity of Pitești), and Clit, Jac, and Ileanda (in the vicinity of Calau)] come from the NP23 zone. In Slovenia, the Sotzca Flora (from the beds of the NP23 Zone and the MP23 Vertebrate Zone) and the floras from Savine, Trbovlje, and Zagorje are of the same age. The same type of flora was found in the Zenica-Sarajevo Basin in Bosnia and in Reit, Horw (near Bern), and Vevey (Lake of Geneva). In the southeastern area of the Balkan Peninsula, the floras from the Rhodope Massif (Momčiloviči) and Edirne are assigned to the same type. In addition to the Kiscell Flora, the latest flora of this type is the Bystriče Flora from Bohemia; it comes from the NP24 Zone.

According to Andreansky and Givulescu (1980), the majority of the Early Eocene floras from Central Europe indicate the luxuriant mesophilic forests. The major forest-forming plants were *Eotrigonobalanus* (*Castanopsis*), evergreen oaks, and laurels accompanied by the conifers *Doliosobus* and *Athrotaxis*. The Arcto-Tertiary forms are usually scarce; their proportion in the taphocenoses only rarely increases to 5–10%; only in the Sulanesti Flora (Romania) it is 18%.

Mai considers the Kiscell Clays Flora (Budapest, Obuda) from beds transitional from the Lower to the Upper Oligocene (NP24 Zone) as the type Early Oligocene flora of Central Europe. This flora is large-leaved and dominated by *Eritrobalanus*, *Daphnogene*, *Laurophyllum*, *Zizyphus zizyphoides*, and species of *Myrica*. The Fagaceae are represented by *Trigonobalanus*, *Lithocarpus*, and *Quercus*; the Lauraceae include *Litsea*, *Ocotea*, *Persea*, *Laurus*, and *Sassafras*. *Platanus neptunei*, *Comptonia shrankii*, *Palaeocarya macroptera*, *Cedrelospermum leptospermum*, and *Sterculia labrusca* are common. Mai considers this assemblage to be a typical mastixial association, because *Mastixia*

*meyeri* was found in the adjacent Brežani Flora of approximately the same age. The taxodiaceae are represented by the early *Doliosobus* and *Athrotaxis*, as well as by *Sequoia abietina*. The Leguminosae are rare because of the humid type of flora; however, all of them belong to evergreen plants. Legumes dominate only the more xerophytic Sotzca Flora in Slovenia from the beds with *Rzhehaka*. The proportions of laurels, legumes, and conifers in this flora are 25 : 51 : 23.8. Palms occur in the floras from the Red Molassa in Switzerland and are even more usual in the Balkan floras. Deciduous elements mainly inhabited river valley facies, as in Turgai.

Further to the east, the floras of this type are traced in the Crimean–Caucasian Region. The Belaya River Flora from the Planorbella Beds (transitional interval between the NP21 and NP22 zones) with the presence of evergreen *Myrica*, Fagaceae, Lauraceae, and Taxodiaceae (Akhmetiev, 1995) is similar to the subtropical floras of Western Europe. Uznadze earlier reported the presence of palm fossils in western Ciscaucasia. She also recorded a similar but more taxonomically impoverished assemblage from the Lower Oligocene beds in the vicinity of the town of Mayakovski (western Georgia).

**Western and Northern Europe.** Evergreen and deciduous plants were jointly found in the majority of taphocenoses from the northern margin of the epeiric sea; this allows for their inclusion in the ecotone zone. Subtropical plants dominated the coastal zone in western regions, whereas plants of moderately warm climates inhabited the eastern regions.

The West European floras from the Rhine Graben (Sieblos Flora) and Mainz Basin (Dormach Flora) include numerous plants with the entire leaves typical of the Leguminosae. The abundance of *Nyssa* and *Glyptostrobos* in the Sieblos Flora indicates the development of swampy forests at that time. The type spore and pollen assemblage of this level is recorded from a section in the vicinity of the town of Marburg (Heskembild, PG19 Pollen Zone); it includes abundant and diverse pollen of deciduous plants exceeding coeval megafossil assemblages in diversity. This is associated with a high pollen productivity of conifers and the Amentiflorae and a low pollen productivity of laurels and other evergreen plants pollinated mainly by insects. The Heskembild Assemblage is dominated by the Gymnospermae and includes abundant pollen of *Carpinus*. Pollen of *Tsuga*, *Juglans*, *Carya*, *Pterocarya*, *Fagus*, and *Betula* play a significant part. *Boehlersipollis* absent in the Eocene is very typical, as well as *Milfordia* and pollen allied to the Chenopodiaceae. In addition to the above-enumerated floras, this group also includes the floras of Hagenau and Habsheim located in the vicinity of Mulhouse in the Rhine Graben.

In the eastern continuation of the ecotone zone, Portnyagina considers the transition Eocene–Oligocene Sheshora Beds in the Carpathians (beds with *Globigerina vialovi*) to be the *Tricolporopollenites villensis*–*Tricolporopollenites cingulum* Pollen Zone with a high

proportion of pollen of the Taxodiaceae and the Pinaceae and a lower pollen diversity of thermophytes compared to that in the underlying Upper Eocene beds. The spore and pollen assemblage from the lower beds of the Mezhygorian Formation of the Dnieper–Don Depression is characterized by the miospores assemblage including *Sciadopitys vertillaciformis* and *Retitri-colpites foraminatus* (Stotland, 1984).

The next level of the Early Oligocene floras from the ecotone zone of Europe was designated by Mai the Haselbach Flora after the type locality Haselbach found in the vicinity of Altenburg south of Leipzig. Although this flora has not been aged with certainty based on other fossil groups, its assignment to the Early Rupelian is beyond question. The Haselbach Assemblage displays a mixed mesophilic forest vegetation with a high proportion of hydrophilic holophytes. This assemblage includes deciduous Arcto-Tertiary elements, as well as laurel-leaved subtropical plants composing at least 50% of the assemblage. The latter include relatively early taxa, in particular, *Aquilaria*, *Caricoidea*, *Litsea phoenica*, *Myrica longifolia*, *Phoebe*, etc. At the same time, representatives of the so-called young mastixian flora, i.e., *Aralia haselbachensis*, *Ampelopsis hibschi*, *Manglietia zinkeisenii*, *Mastixia meyeri*, *Myrica*, *Nyssa*, *Meliosma*, *Ilex*, etc., play a significant part in this group. However, this flora also includes numerous typical deciduous plants. Some of them occurred to the Early Miocene (*Acer haselbachense*, *Carpinus mediomontana*, *Carya quadrangula*, *Comptonia goniocarpa*, *Populus hermanica*, *Taxodium balticum*, *Rosa lignitum*, etc.); however, the species known from the earlier beds, such as *Alnus kefersteinii*, *Carpinus cordataeformis*, *Ceratophyllum lusaticum*, *Disanthus bavaricus*, *Liquidambar europaea*, etc., were also reported. The flora-bearing beds include pollen of *Boehlersipollis* and other taxa that allow for the assignment of the Haselbach Assemblage to the PG20 Pollen Zone.

The Haselbach Flora from the ecotone zone of Western and Central Europe may be correlated with the Devonshire Flora (Boney Tracey, Heathfield), Altenrath Flora in Siebengebirge along Rhine, and with the floras from the Baltic coastal areas (Svetlogorsk and Otradnoe), Voronezh Anteclyse (Pasekovo), Ustyurt (Ashcheairyk), and the Aral Region (Kumbulak). In the Svetlogorsk Flora, the deciduous *Populus zaddachii*, *Alnus heerii*, *A. pseudogracilis*, and *Pinus thomasiana*; the evergreen *Athrotaxis couttsiae* and *Sequoia abietina*; the palm *Calamus daemonorops*, etc. are common as well as the above-enumerated taxa (after Budantsev and Sveshnikova).

The Pasekovo Flora, occurring in the ecotone zone, is more similar to those of the Tethyan Region, while the others are similar to the Boreal Flora. According to Vikulin (1991), the Pasekovo associations (compared to the Eocene groups including laurels, castanopses, and the other primitive Fagaceae) belong to a unique type that developed in the course of regression of sea.

This resulted in the formation of cypress–nyssa bogs within the dried areas with the presence of abundant evergreens, ericaceous *Epacridicarpum rossicum* and deciduous *Acer tricuspdatum*, *Nyssa zhilini*, *Populus populina*, and *Sorbus praealnifolia*. The appearance of new migration tracts after the sea regression resulted in the formation of wide connections of the Pasekovo Flora with the Svetlogorsk Flora that occurred further north, as well as with the western (Haselbach) and eastern (Kazakh) floras. This is supported by both the similarity in age and the commencement of active floristic exchange. *Taxodium balticum* is a typical species of the Pasekovo, Svetlogorsk, and Haselbach floras. *Nyssa zhilini* with the dentate leaves was described from Pasekovo and Kazakhstan, whereas its vicarious species was found in the Altenburg Flora coeval with the Haselbach Flora. The entire leaves of *N. punctata*, as well as *Apocynophyllum* unite the Pasekovo and Svetlogorsk floras; the large-leaved *A. helveticum* is known from these floras and the Haselbach and Aral floras. The Pasekovo flora is similar to the Kazakh floras in the presence of lobe-leaved red oak *Quercus pseudoalexeevii*. The absence of *Quercus pseudoneriifolia*, which was wide spread in all floras of the northern subtropical province of the Tethyan Region in the Late Eocene, is noteworthy. This species remained in the Early Oligocene floras, but only in typical subtropical floras.

The floristic assemblages of Flörsheim and Nerchau belong to the NP23 Nannoplankton Zone and the lower part of the *Wetzelia gochti* Dinocyst Zone (after Mai, 1995). Flörsheim is the type locality found in fish-bearing shales of the Mainz Graben; Nerchau is in clayey beds of the Weissenster Depression, in the vicinity of Grimma, southwest of Leipzig. Both these assemblages are dated to the beginning of the Late Rupelian (NP23 Zone). The Nerchau Flora is a typical laurel-leaved flora with Arcto-Tertiary accessories; therefore, among the ecotone floras, it is closer to subtropical floras. Its major components are *Eotrigonobalanus furcinervis*, *Zizyphus zizyphoides*, *Myrica longifolia*, *Comptonia schrankii*, *Trigonobalanus rhamnoides*, and *Sterculia labrusca*. Based on available carpological data, Mai considers this flora among young mastixian floras, which include *Tetrocarya nerchauensis*, *Mastixia boveyana*, *Symplocus anglica*, etc. The Nerchau Flora includes the following Arcto-Tertiary deciduous taxa: *Acer angustilobum*, *A. intergerrimum*, *Betula brondniartii*, *B. prisca*, *Cercidiphyllum crenatum*, *Craigia europaeum*, *Fagus deucalions*, *Pterocarya paradisiaca*, etc. An extensive group of floras of this age with various proportions of paleotropical and Arcto-Tertiary elements is known in Europe. The floras from the volcanic-detrital beds of the Bohemian Sredna Gora are distinguished by the abundance of the entire-leaved laurophilous plants combined with a smaller proportion of deciduous Arcto-Tertiary forms (60 : 40 in the Berand and Markvartice floras and 30 : 70 in the Suleitice Flora). In the spore and pollen assemblages, the typical taxa are *Boehlersipollis hohlii*, *Slovakipollis*

*hypophaeoides*, *Tricolpopollenites henrici*, and pollen of the Chenopodiaceae. After the type sections, this spore and pollen assemblage is designated the Bergisch–Gladbach or the Calau Assemblage (PG20a–b Pollen Zone) from the type sections. This group also includes certain other floras from the Mainz Depression and the Weissenstein lignite-bearing basin, Dittelsheim–Kloppberg (east of Else), and Niederwalluf (in the vicinity of Eltville). The deciduous taxa are more numerous and diverse in the Bechlejovice and Hrazeny floras. However, they existed later and were aged to the transition between the NP23 and NP24 nannoplankton zones.

**Northwestern Asia.** Further to the east, in the ecotone zone, the Rupelian floras are well known based on spore and pollen data and, to a lesser extent, on megafossils. The floral composition at the beginning of the Oligocene is mainly judged based on the analysis of pollen assemblages from the beds that are assigned to the *Phthanoperidium amoenum* Dinocyst Zone. Of the megafossil assemblages, only the Kyzyltope Flora from Mugodzhary, which was studied by Rayushkina (1979), is conventionally assigned to the floras of this level. This flora includes derivatives of both the subtropical flora (*Torreya* and *Sequoia* with the typical unguiform leaves, *Myrica*, *Magnolia*, and an unidentified genus of the Lauraceae) and the temperate deciduous flora. The spore and pollen assemblages from the East European Platform and the northern area of the Turgai Platform (Northern Ustyurt, Aral Region, and Turgai) differ in the predominance of the Taxodiaceae and the Pinaceae, a rather high proportion of the Juglandaceae and Betulaceae pollen that dominate over the Fagaceae pollen, and in the presence of the Hamamelidaceae, Myricaceae, Ulmaceae, etc. The proportion of pollen of evergreen plants is low. Judging from the above facts, this is associated, on the one hand, with a high pollen productivity of the anemophilous Amentiflorae, and, on the other hand, with a better representativeness of pollen of plants that inhabit riparian areas, where deciduous forms appear earlier than on low and relatively dry flat interfluvium.

The earliest Early Oligocene flora is the Kumbulak Flora (Kutanbulak Formation, North Aral Region); it is dominated by moderately thermophilic forms with reference to the number of specimens, whereas the evergreen microphyllous forms with marked xeromorphic characteristics are more diverse taxonomically (*Sequoia*, *Cinnamomum*, *Myrica*, *Apocynophyllum*, etc.). *Myrica lignitum* and *Apocynophyllum* are solitary in the Kutanbulak Formation of the Altyn-Chokysy outlier and in the Urkimbai Formation of Turgai (Chelkar-Nura).

A high proportion of pollen of pine and the Taxodiaceae in the floral assemblages is typical of the basal beds of the Ashcheairyk Formation of the Northern Ustyurt Plateau (*Phthanoperidium amoenum* Dinocyst Zone). Panova designated these beds as the beds with the Pinaceae, *Quercus graciliformis*, and *Juglans poly-*

*porata*. In the southern part of Western Siberia and in Northern Turgai, a typical transitional assemblage with abundant gymnospermous pollen and a high proportion of thermophilic pollen of the Fagaceae (*Quercus gracilis*–*Q. graciliformis* group) was recorded from the Kurgan Beds; Zaporozhets identified *Phthanoperidium amoenum* in the same locality.

The spore and pollen assemblages from the Pasekovo–Kumbulak level of the ecotone zone (correlated with the NP22 Nannoplankton Zone and the *Wetzeliella symmetrica* Dinocyst Zone of marine beds) are dominated by conifer pollen (pine or the Taxodiaceae) and contain a high proportion of the Amentiflorae, especially the Juglandaceae. According to Panova and Zaporozhets, in Kazakhstan, the pollen floras of this type are combined into the *Carya spackmania*–*Tilia grandireticulata*–*Juglans sieboldianiformis* Pollen Zone. This zone corresponds to the peak of the Ashcheairyk Transgression (beds with *Cypris*) and to the accumulation of the upper beds of the Kutanbulak and Urkimbai formations. According to Stotland, in the Ukrainian Shield, the upper beds of the Mezhygorian Formation with *Pinus silvestris*, *Carya spackmania*, etc., correspond to this zone.

The spore and pollen assemblages from the Solenovian Horizon of the East European Platform and Turan Plate were assigned by Boitsova (1973) to an integral *Juglans sieboldianiformis*–*Betula gracilis* Pollen Zone. This zone was recorded in the Northern Ustyurt beds, the lower beds of the Chilikty Formation in the North Aral Region, and the lower beds of the Betpak-Dala Formation of the Chu-Sarysu Depression. For this level, Zaporozhets (Akhmetiev and Zaporozhets, 1992) reported a decrease in the proportion of gymnospermous pollen and an acme of the *Quercus* pollen (including the fine pollen of the *Quercus gracilis*–*Q. graciliformis* group); the researcher treated this as a result of climatic warming in the Solenovian Time, increased seasonality, and aridity of climate, especially in Turgai.

The floras with *Ergenica cimlanica* from the Solenovian Horizon of Northern Ustyurt were mainly composed of deciduous species, although *Myrica longifolia* was still found. In the Chagrai Plateau, in the Zhabyske locality, the flora was also formed by deciduous taxa but also included *Myrica longifolia*. The Kenkous Flora recorded by Budantsev (1959) from this plateau included certain evergreen plants (*M. longifolia* and *Apocynophyllum*), along with the broad-leaved genera *Juglans*, *Fagus*, *Ulmus*, *Liquidambar*, etc.

The distribution of mesophytic and xerophytic plants in the Late Rupelian floras of the Aral Region and Turgai (correspond to the Solenovian Horizon *sensu lato*) is of great interest. The floras from the flat interfluvium (assigned to this group based on the phytocenoses of temporal streams) were dominated by the derivatives of the Eocene evergreen xerophytic flora, *Palibinia* and *Rhus turcomanica*, microphyllous sclerophyllous laurels, etc. (Tortmolla, Zhaman-Kaindy, Mynyske-Suiek,

etc). At the same time, coeval riparian floral assemblages that characterize taphocenoses of the oxbow facies were dominated by macrophyllous deciduous poplars, elms, alders, and ashes. In the Late Oligocene, these trees formed the core of the Turgai vegetation. Hypoautochthonous burials include both the fossils of xenomorphic leaves and the larger dentate leaves of deciduous species. According to Kornilova (1963), such a mixed type of taphocenoses allows for the recognition of floras of a transition type between the subtropical and the temperate (so-called Shintuzsai) floras in the Lower Oligocene of Kazakhstan. However, the xeromorphic pattern of the Turgai floras may indicate not only the arid habitats but also physical adaptation to halophytic and littoral facies, taking into account the occupation by flora of coastal lowlands formed as a result of recent sea regression. In the Solenovian, the Turgai flat interfluves were mainly bald, being gradually occupied by shibliak, low grasses and dwarfshrubs. This inference follows from the presence of abundant pollen of the Chenopodiaceae, including *Artemisia*, and the Compositae in the spore and pollen assemblages from the Chelkar Nura beds with indricotheres (after Zaporozhets).

**Central Asia.** At the beginning of the Oligocene, the climate in Central Asia became more humid because of a climatic cooling; however, arid regimes returned in the second half of the Oligocene. The commencement of tectonic destruction of the Epihercynian Platform resulted in the development of heterogeneous vegetative cover in different areas of the province, as indicated by spore and pollen data obtained in the Tajik Depression (data obtained by M.Z. Pulatova and A.M. Pen'kova). In the Baisun District, desert-steppe formations with the participation of the Gramineae, *Artemisia*, *Ephedra*, the Compositae, and the Chenopodiaceae were widespread. Southern slopes of the Hissar Mountains were occupied by conifer-broad-leaved forests with laurels. The forests alternated with open areas. This zone was most humid within the depression. In the Vakhsh District, steppe grassy formations of flat interfluves alternated with the bush formations. In valleys, the intrazonal forest communities were formed by *Populus*, the Juglandaceae, and the Fagaceae. In the eastern area (Pyandzh River Basin), the steppe and meadow formations were dominated by the Chenopodiaceae, Compositae, *Artemisia*, Gramineae, Leguminosae, and low-growing *Ephedra*. The main changes in the floral assemblages from the Tajik Depression occurred in the Late Sumsar Time, when the majority of the Eocene forms disappeared and the spore and pollen assemblages were dominated by the Taxodiaceae, Juglandaceae, and Oleaceae.

#### *Phytogeographic Zonation*

The study of the Early Oligocene floras and vegetation and their comparison with the Late Eocene pattern allow the following conclusions (Fig. 4):

(1) In the Early Oligocene, as in the Late Eocene, western Eurasia was included in two regions of the Holarctic Kingdom, the Boreal Region occupied by a moderately thermophilic deciduous flora and the Tethyan Region with subtropical flora. The regions are isolated from each other by a wide ecotone zone. The latter replaced the Late Eocene North European Province of the Tethyan Region because of the development of hydrophilous subtropical flora and included the entire territory of central and northwestern Europe.

(2) Climatic cooling in the terminal Eocene and the beginning of the Oligocene resulted in the displacement of the boundary between the Boreal and Tethyan regions by at least 10°–15° to the north. The southern boundary of the ecotone zone, which should be assigned to the Boreal Region, extended across Western Europe, the Carpathian Basin, the Dnieper–Don Depression, and continued across the Eastern Paratethys. A decrease by 4–6°C in the average annual temperatures (the average winter temperatures decreased, while the average summer temperatures remained constant) in the Early Oligocene compared to those in the Late Eocene was the major factor of the changes in vegetation.

(3) In the Early Oligocene, the Tethyan Region (*sensu stricto*) significantly decreased in area down to only two former Late Eocene provinces, the Central European Province and the South European Province. It retained the division into two provinces; however, their characteristics substantially changed. The Central European Province was inhabited by hydrophilous flora, whereas the South European Province was occupied by subarid assemblages. The boundary between these provinces differed from that in the Eocene (Fig. 4). Despite marked climatic and humidity changes, the entire northern coastal area of the Mediterranean Basin retained the provincial status in the Early Oligocene Tethyan Region; in the Late Eocene, it was included in the South European Province with flora of the transition type between subtropical and humid tropical floras. At the onset of the Oligocene, this province experienced aridification. Further expansion of the arid zone occurred in the Solenovian Time, as indicated by a wide development of xerophilic forms in certain Balkan assemblages. This flora occupied the Iberian Peninsula, southern France, the major area of Italy, and partially the Balkan Mountains and extend to Transcaucasia.

To the contrary, the climate in the northern area of the Tethyan Region became more humid with cooling. The Late Eocene xeromorphic flora of Central Europe was replaced by the humid type, as indicated by the macrophyllous character of the majority of floras. The Early Oligocene floral assemblages were rather homogeneous in composition in both western and eastern areas, where this flora occupied the entire northern part of the Crimean–Caucasian Region and the Scythian Platform.



(4) The ecotone zone extended from Western Europe to the Aral Region and covered the entire northern coastal area of the Paratethys. This zone was inhabited by the broad-leaved mesophilic forests with laurels; the Eocene relicts played a significant part. The flora of this zone markedly changed during the Rupelian.

(5) The predominance of deciduous forms in the taphocenoses of Ustyurt and the Aral Region, and a low proportion of evergreens allow for the exclusion of these regions from the ecotone zone, beginning from the second half of the Early Oligocene, and their reliable assignment to the Boreal Region. In the Aral Region and Turgai, the floras from riparial facies are represented by deciduous plants, whereas the floras from the sediments accumulated by temporal streams of the flat interfluves are composed of evergreens. Only at the end of the Solenovian, the flora of northern and central Kazakhstan took on the Turgai characteristics; this allows one to assign with certainty this flora to the Boreal Region.

(6) In contrast to the floras of the Northern Ustyurt and North Aral Region, which insignificantly differed from the floras of westerner regions of the ecotone zone in the Early Oligocene, the Turgai floras were more unique. We have good grounds to consider this territory as a descendant of the Late Eocene Kazakh Province.

(7) In the Early Oligocene, the Central Asian Province of the Tethyan Region retained the same boundaries; however, its characteristics changed. The differentiation of floras in this territory probably indicates the reactivation of the Alpine Orogeny in Central Asia.

(8) Two stages may be distinguished in the development of the Late Oligocene floras. They may be conventionally designated as the earlier (Presolenovian) stage and the later (Solenovian) stage. At the first stage, the floral rearrangement was especially well pronounced due to a commencement of active expansion of the Arcto-Tertiary deciduous elements into the subtropical flora and the elimination of Eocene elements from the vegetative cover. At the second stage, the arid zone expanded, especially in the eastern area of the Tethyan Region; this resulted in complete formation of the southern subarid province, which included the southern province of the Tethyan Region in the west (this was earlier involved in a more humid zone) and the southern area of the Kazakh and Central Asian provinces in the east. This wide zone of subarid floras became more distinct from the Late Rupelian (Solenovian) Time (NP23). This zone extended from southern France via Italy, the Balkan Uplift, and Transcaucasia to Kazakhstan and Central Asia. In Turgai, it expanded northward, where the arid flora of the Tethyan Region and flora of the Boreal Region met.

(9) A climatic warming that occurred in the Eastern Paratethys in the Solenovian time (Akhmetiev and Zaporozhets, 1992) was also observed in Central Europe. This became evident when we compared the

climatic parameters of the Late Rupelian floras with those of earlier floras from the Northern Province of the Tethyan Region and from the ecotone zone. The increase in yearly average temperatures in the west was associated with the increase in average winter temperatures combined with unchanged average summer temperatures. Conversely, in the east (Turgai), this was associated with an increase in average summer temperatures combined with increased seasonality of climate and the development of continental climate.

### *Insects*

The Early Eocene entomofaunas of Western Eurasia have not yet been studied in detail. Several large localities that have been long considered to be of the Lower Oligocene age most likely belong to the terminal Eocene; therefore, they were discussed in the first part of this work (Zherikhin in Popov *et al.*, 2001). It should be emphasized that the entomofaunas (at least those of North America and Africa) had probably taken the Oligocene pattern before the commencement of marked cooling at the Eocene–Oligocene boundary. For this reason, it is very difficult to distinguish between the Eocene and Oligocene insect assemblages at the present state of study. This task necessitates consideration of other stratigraphically more important groups of organisms from the same beds, especially plant fossils, which usually accompany insects in the burials. The major features of the terminal Eocene assemblages, such as the Brembridge Marls Fauna in England and the Célas Fauna and fauna from the salt-bearing beds of Alsace in France, may probably be extrapolated to the Early Oligocene entomofaunas of Western Europe.

The most important Early Oligocene entomofaunas are known from Italy (amber from Sicily and the northern Apennines), southern France (Camoins-les-Bains in the Bouches du Rhone Department), and Germany (Sieblos in Bavaria). Other regions of Western Europe (from Spain, central France, and Menilithic Formation in the Carpathians, in particular) yield only isolated findings. These specimens insufficiently characterize entomofaunas of this age. The occurrences of termitaria in Fayum (Egypt) are also noteworthy.

In North Africa, the Early Oligocene insects are only known by ichnolites. In Egypt, soil termitaria of rather diverse types (five ichnospecies of four ichnogenera) were found in the Jebel Quatrani Formation of the Lower Oligocene. They include large and complex termitaria indicating families of large size (Genise and Brown, 1994). The taxonomy of termites that built these nests remain uncertain. It is not improbable that some of them belong to the tropical Termitidae. It should be emphasized that two ichnospecies are in common with those from the underlying Upper Eocene Qasr el Sagha Formation, in which termitaria are relatively rare and less diverse.



Of particular interest is a fauna from the Italian amber that was generally described by Kohring and Schlüter (1989) and by Skalski and Veggiani (1990). Until recently, the Sicilian amber (known only in re-deposited state) was aged as the Miocene. However, it is now established that this amber is closely similar to that from the Arenarie di Ranzano (Lower Oligocene; Ranzano Sandstone, northern Apennines) in both chemical properties and in faunal composition (Skalski and Veggiani, 1990). The fauna from the Italian amber is of particular interest, because it has no equivalents among Cenozoic insect assemblages of western Eurasia and closely resembles the faunas from the Lower Miocene amber from the Dominican Republic and southern Mexico (Chiapas). This naturally does not indicate any direct faunal connections. The similarity is evidently associated with similar landscapes and climates. The most distinctive feature in all three cases is the abundance of timber beetles of the subfamily Platypodinae. This indicates the production of these resins by angiosperms rather than by conifers; moreover, in the American amber, the resins were produced by the Caesalpinaceae. The other distinctive feature is abundant stingless bees of the subfamily Meliponinae. Both these groups are common in subfossil copals in South America and Africa. Their abundance is a reliable indicator of a very warm climate. Dlussky (1981) reported that the ant fauna from the Sicilian amber closely resembles the extant forest faunas of southern Asia. The absence of wasps of the family Ichneumonidae is also noteworthy. The presence of such a thermophilic assemblage in the Early Oligocene of Europe is somewhat unexpected. However, certain facts indicate that the Italian faunas were not of the true tropical type, in contrast to the Dominican and Mexican faunas. This inference follows from the presence of a few aphids, which are very rare in tropics, in a small sample, and the absence of termites of the family Termitidae, which are typical of tropical regions and abundant in the Dominican and Mexican amber (some other termites are rather usual in the Italian amber; this supports the supposition of a warm climate). The islands that were located in the Early Oligocene in the territory of the modern-day Italy were supposedly faunally connected with Africa rather than with the residual Europe. The climate in these regions was a very warm (and supposedly humid) version of the subtropical type that was possibly comparable only to the modern-day climate of humid low mountains of Mexico and Yunnan, rather than with that of tropical coastal areas.

The Camoins-les-Bains Insect Fauna is quite different in general pattern and resembles the well-studied Late Oligocene faunas from southern France (Aix-en-Provence, Cereste, and some other localities). A general characteristic of this fauna was presented by Théobald (1937) and Timon-David (1943). Unfortunately, this was only partially described, and some taxa need revision. The significant role of taxa that inhabit well-insolated landscapes (probably open woodlands

and bushes) is typical. These taxa include, in particular, the Pompilidae and large Sphecidae (of the Hymenoptera) and the Asilidae and Bombyliidae (of the Diptera). These features differ the Camoins-les-Bains Fauna from all the Late Eocene faunas of the more northern regions of France (Languedoc and Alsace), the Early Eocene entomofaunas of which have received only fragmentary study. The generic composition of ants (which have not been described) was determined (if correctly) by Timon-David (1943) and is also consistent with the assumption of the landscapes of open woodlands. A preliminary study of material on the Coleoptera (without a description) from the National Museum of Natural History (Paris) supports the similarity to the Late Eocene faunas from Provence. In our opinion, the Camoins-les-Bains Fauna occurred in warm and seasonally arid (possibly summer-dry) climates and was most likely an ancestor of the extant Mediterranean entomofaunas. Autochthonous aquatic entomofauna is absent (insects were probably buried in a brackish-water lagoon), and the finds of imagoes of allochthonous insects that develop in aquatic environment are rare. The presence of the Sieblosiidae represented by the genus *Stenolestes*, which was also found in Sieblos (Nel, 1986), is noteworthy.

The general characteristic of the Sieblos Fauna was made by Martini (1971a) and Willmann (1988). Unfortunately, a number of taxa described from this locality need revision. The terrestrial insect assemblages are dominated by the taxa that inhabit forest landscapes. The high proportion of beetles of the family Buprestidae and the presence of termites indicate a mild (possibly warm temperate) climate. It is very difficult to make clear the forest patterns because neither insects nor floras have received a detail study. The leaf floral assemblages from Sieblos include certain evergreen elements (Martini, 1967). The composition of terrestrial entomofauna does not directly indicate a markedly warmer climate than that in the terminal Eocene of southern England and northern France (Alsace). However, a direct comparison of these faunas is impossible because they do not include common taxa of a lower rank than families. The seasonal climatic aridity proposed by some researchers (Lutz, 1997) was not corroborated. The aquatic entomofauna includes certain obviously taphonomically autochthonous lake elements; however, the imagoes of aquatic insects apparently include the species that developed beyond the lake, in which the sedimentation occurred. In particular, the dragonfly "*Petalura*" *acutipennis* Hagen probably belongs to the family Gomphidae mainly associated with flowing water bodies, rather than to the Petaluridae (Nel *et al.*, 1998). The autochthonous assemblage is unusual, because of the abundance of aquatic weevils "*Pissodes*" *effossus* Heyden [actually belonging to Bagoini or to Tanysphyrini rather than to Pissodini (Willmann, 1988)], probably inhabiting floating plants (possibly, the Nymphaeaceae), and the presence of nymphs of dragonflies of the family Lestidae. These

two groups have not been found in comparable quantity in other localities. However, it is unclear whether or not this peculiarity of the aquatic entomofauna from Sieblos is mainly determined by the biogeographic individuality of the region, or by the local features of the lake basin. According to Lutz (1997), Sieblos Lake experienced marked fluctuations of the water level and occasional increases in water salinity. The presence of dragonflies of the family Sieblosiidae, the only extinct insect family known from the Oligocene, is noteworthy. This family existed to the end of the Neogene, and its range was probably always restricted to western Eurasia (the easternmost finds of the Sieblosiidae were in the Miocene of northern Caucasus).

The Sieblos Fauna does not markedly differ in general pattern from the terminal Eocene Bembridge Marl Fauna from England and possibly inhabited similar landscapes.

Data on the Early Oligocene insects of Eastern Europe, Caucasus, and the western area of Asia are almost absent.

Thus, the three major Early Oligocene entomofaunas in Europe are markedly distinct. The Bavarian Fauna indicates a warm temperate and probably a rather humid climate and forest landscapes. The southern French fauna demonstrates a warm temperate or a subtropical summer-dry climate of the Mediterranean type and landscapes of the open woodlands and bushes, whereas the Italian Fauna indicates a humid subtropical climate and forest landscapes.

#### *Terrestrial Vertebrates*

**North Africa and Arabia.** The Early Oligocene mammal fauna of North Africa generally inherited the Late Eocene composition. This is especially well illustrated by the example of the Qasr el Sagha and Jebel Quatrani formations in Egypt (Fayum), where the proboscidean *Moeritherium* and the creodonts *Hyaenodon* and *Apterodon* from the Eocene to the Oligocene and were represented by closely related species (Holroyd *et al.*, 1996). Rapid development of local faunal elements was still observed. In addition to *Moeritherium* and *Barytherium*, the primitive mastodonts *Palaeomastodon* and *Phiomia* (Palaeomastodontidae) appeared among proboscideans. Hyracoids of the family Pliohyracidae represented by a large quantity of genera and species were at the acme in the Early Oligocene. Some of them probably occupied the ecological niches of large Holarctic ungulates; even highly specialized cursorial forms were present. A marked adaptive radiation of endemic rodents of the family Phiomyidae (*Phiomys* and *Metaphiomys*) occurred, and they became widely distributed in North Africa and Arabia (Fejfar, 1987b; Thomas *et al.*, 1989). Thryonomyids represented by the genus *Gaudeamus* deviated from this family. The creodont *Masrasetor* (Proviverrinae) and numerous anthropoid primates, the Parapithecidae, Propithecidae,

and Oligopithecinae, composed the autochthonous evolutionary lineages. The Macroscelidea (*Metoldobotes*) and the unique family Ptolemaiidae (Pantolestia) also represented the Early Oligocene endemic groups of North Africa (Simons, 1995a; Savage and Russel, 1983).

A marsupial that was described as *Peratherium africanum* from the Jebel Quatrani Formation actually belongs to the endemic genus *Quatranitherium* and is assigned to an individual group of the African Peradectidae that independently developed at least from the beginning of the Eocene (Crochet *et al.*, 1992). The assignment of this form to the genus *Peratherium* has been rejected; therefore, the presence of this animal should not be considered as an argument (Bonis *et al.*, 1985) in favor of the invasion of North Africa by European mammals. However, available data on other groups indicate the presence of the Early Oligocene immigrants of European origin in North Africa. In particular, the artiodactyls *Botriogenys*, *Brachyodus* (Anthracotheriidae), *Rhagatherium* (Haplobunodontidae), and *Mixtotherium* (Mixtotheriidae); creodont *Metasinopa*; and turtles of the family Testudinidae were recorded in the Early Oligocene of Egypt (Simons and Wood, 1968; Savage and Russell, 1983; Bonis *et al.*, 1985). At the Eocene–Oligocene boundary, the Embrithopoda from western Asia or southeastern Europe probably penetrated Africa via the Sicilian Corridor (Bonis *et al.*, 1985) and gave rise to the highly specialized giant *Arsinoitherium*.

On the Arabian Peninsula, the Early Oligocene mammals were found in the Ashwaq Formation of Dofar Province (Sultanate of Oman). They included the marsupials *Quatranitherium* aff. *africanum*, primates (adapids, tarsioids, propithecoid anthropoids *Moeripithecus markgrafi*, and *Oligopithecus rogeri*), the proboscidean *Barytherium*, embriothopods, hyracoids, the creodont *Masrasetor ligabuei*, and rodents of the family Phiomyidae (Thomas *et al.*, 1988, 1989, 1991; Crochet *et al.*, 1990, 1992; Gheerbrant *et al.*, 1993, 1995). No immigrants of European origin have been found in Arabia. In the Early Oligocene, North Africa and the Arabian Peninsula probably belonged to the same zoogeographic region: the European elements could penetrate North Africa from Western Europe.

**Western Europe.** The beginning of the Oligocene in Europe was associated with the so-called Grande Coupure (Great Cutting), the greatest rearrangement of the West European Fauna. By that time in Europe, four artiodactyl families (Choeropotamidae, Mixtotheriidae, Xiphodontidae, and Haplobunodontidae) had become extinct; the other five families continued to the Oligocene with a sharp decrease in taxonomic diversity (Dichobunidae, Cebochoeridae, Dacrytheriidae, Anoplotheriidae, and Cainotheriidae). The number of genera and species of palaeotheres (Perissodactyla), which dominated the ungulate associations in the Late Eocene, decreased; the Lophiodontidae disappeared.

The diversity of creodonts decreased; miacids, *Cynodictis*, and almost all primates disappeared. In the terminal Eocene, ischyromyoid rodents became extinct; the generic composition of the theridomyoid rodents changed; in particular, the brachyselenodont taxa (pseudosciurids) disappeared (Russell and Tobien, 1986).

At least 20 mammalian families migrated to Europe from Asia at the beginning of the Oligocene, including the Erinaceidae, Plesiosoricidae, Heterosoricidae, Soricidae, Lagomorpha, Cricetidae, Aplodontidae, Sciuridae, Eomyidae, Castoridae, Felidae, Viverridae, Mustelidae, Procyonidae, Ursidae, Entelodontidae, Tayassuidae, Suidae, Leptomerycidae, Tragulidae, and the Rhinoceroidea, as well as a new assemblage of anthracotheriid genera, the so-called neoanthracotheres (Sigé, 1977; Sigé and Vianey-Liaud, 1979). Apparently, this migration was gradual and included several successive stages occurring in the Rupelian (MP21–MP25 zones); however, the majority of the groups mentioned above appeared at the onset of the Oligocene (MP21 Zone). Among the factors for these events were new continental connections that formed between Europe and Asia at the Eocene–Oligocene boundary, the absence of climatic barriers, and the higher level of evolutionary dynamism of the immigrants as compared to the local taxa and, hence, their higher competitive ability (Brunet, 1979).

The mammalian composition indicates that, in the Early Oligocene, the periods of European land consolidation alternated with the periods of isolation of individual regions; this is seen in the zoogeographic zonation of Western Europe.

In southern France (Quercy), some Late Eocene lineages of marsupials persisted after the Grande Coupure (Remy *et al.*, 1987). At the beginning of the Early Oligocene, insectivores were dominated by the Nyctitheriidae in association with the gymnura *Tetracus nanus*. The Carnivora also markedly changed, *Cynodictis* disappeared, whereas *Eusmilus* (Felidae), *Amphicyonodon* (Ursidae), and *Mustelictis* (Mustelidae) appeared. The number of creodont genera decreased down to two (*Hyaenodon* and *Thereutherium*), with *Hyaenodon* being represented by a large number of species; however, this was associated with successive immigrations rather than with cladogenesis. Primates became extinct. Primitive lagomorphs (Desmatolaginae) appeared at the MP21 Zone; however, they were rather rare and soon disappeared from Western Europe (MP22–MP23).

On the extinction of the Ischyromyidae and the majority of the Pseudosciuridae and Sciuroidea in the terminal Eocene, theridomyids differentiated widely and rapidly. Representatives of this family dominated the rodent associations of Western Europe, whereas the groups that appeared in the Oligocene (Aplodontidae, Cricetidae, and Eomyidae) were minorities. After the Grande Coupure, three phases in the evolution of Early Oligocene European rodents are recognized. The first phase (MP23) is characterized by the cladogenesis of

theridomyids of the *Blainvillimys*–*Taeniodus* lineage, the extinction of the genus *Pseudoltinomys*, and the appearance of *Issiodoromys*. The second phase (MP24) is associated with immigration of the cricetids *Melissiodon* and *Paracricetodon*, and the third phase (MP25) is associated with a new diversification of the Theridomyinae (*Archaeomys*) and immigration and (or) adaptive radiation of new cricetids and eomyids.

Artiodactyls were represented by descendants of certain archaic lineages (*Dichobune*, *Tapirus*, and *Diplobune*) in association with new cainotheriids (*Plesiomeryx* and *Caenomeryx*) and rare Asian immigrants (Entelodontidae, Suidae, Anthracotheriidae, and Ruminantia). Among perissodactyls, autochthonous palaeotheriids still existed (the last *Plagiolophus* disappeared in MP23); rhinoceroses and chalicotheres appeared (in MP23 and MP25, respectively).

The earliest Oligocene mammals of Spain were recorded from the localities of Saintpedor (Ebro) and Ciruelos (Betic Cordillera). The Saintpedor Fauna includes the rodents *Theridomys* aff. *aquatilis*, *Pseudoltinomys gaillardi*, *Atavocricetodon atavus*, and *Gliravus* aff. *priscus*; the Palaeotheriidae; and the Anoplotheriidae (Agustí *et al.*, 1987). In Ciruelos, the rodents *Blainvillimys* cf. *langei*, *Atavocricetodon* ex. gr. *atavus*, *Eomys* sp., and *Gliravus* sp. were found (Ferriz *et al.*, 1993). *Glamys olallensis* was a typical species of the Gliridae of this level (Freudenthal, 1996). In Spain, there are 20 more localities of the Early Oligocene mammals (especially rich in rodents); they correspond to the MP22, MP23, and MP25 zones (Agustí *et al.*, 1987; Cuenca *et al.*, 1992). In the first half of the Oligocene, the fauna of the Iberian Peninsula was not only affected by Asian elements but also occasionally experienced autochthonous development due to temporal geographical isolation. This is indicated by an impoverishment of the Iberian fauna, as compared to other European faunas, and by a large number of endemic species among rodents, including the Theridomyidae, Gliridae, Cricetidae, and Eomyidae (Alvarez Sierra *et al.*, 1987a; Daams *et al.*, 1989; Pelaez-Campomanes, 1995; Freudenthal, 1996).

The presence of mammalian taxa typical of continental Europe in the Early Oligocene of Majorca (Cainotheriidae, Anthracotheriidae, Tayassuidae, Tragulidae, Theridomyidae, Pteromyidae, and Cricetidae) indicates the periodical faunal contacts of this territory with other European regions (and primarily with the Iberian Land). Judging from the findings of anthracotheriids, the Balearic Massif was also connected to the Corsica–Sardinia Block, Kabilia, and Calabria. The mammalian assemblage was substantially impoverished in taxonomic composition compared to the continental faunas, similar to that in the Late Eocene (Bruijn *et al.*, 1979; Hugueney and Adrover, 1982). The isolation of the Balearic Land resulted in the appearance of individual endemic rodents. Thus, *Moissenetia paguerensis* (MP23–MP24) has no equivalents among the Oli-

gocene–Miocene Gliridae in the structure of the grinding surface of teeth and is an example of the diachronic parallelism with the extant genus *Eliomys* (Hugueney and Adrover, 1995). Of great interest is the presence of pseudosciurids of the genus *Suevosciurus* in the Majorca Fauna that became extinct in the terminal Eocene everywhere in Europe, except for southern Germany. Thus, we should assume the existence of direct faunal connections between the Balearic and German zochores via the Alpine Land or consider these regions as parts (refugia) of an integral Eocene range of *Suevosciurus*, which became isolated in the Oligocene. In our opinion, the second assumption is preferential (Hugueney and Adrover, 1982), although the similarity of the Balearic taxon and the southern German species *S. ehingensis* is also beyond question. Approximately in the middle of the Oligocene, rodents of the family Thryonomyidae, immigrants from North Africa, appeared in Majorca; they are represented in the Paguera Fauna (MP23–MP24) by the endemic genus and species *Sacaresia moyaepsoni* (Hugueney and Adrover, 1991). This species dominates the Rodentia in abundance. For the first time, these occurrences reliably indicate the existence of trans-Tethyan migrations from Africa to Europe in the Early Oligocene. In the latest Oligocene fauna of Majorca (Sineu, MP25), no descendants of the Thryonomyidae were found. These probably yielded to new European immigrants, *Pseudocricetodon* and *Paracricetodon* (Cricetidae) and the advanced Theridomyidae of the *Blainvillimys–Archaeomys* lineage (Hugueney and Adrover, 1990).

The Asian elements in the Early Oligocene of England (Hampshire Basin; MP21) were represented by the anthracotheres *Anthracotherium alsaticum*, *Elomeryx porcinus*, and *Bothriodon* spp.; rhinoceros *Ronzotherium* sp.; entelodont *Entelodon magnum*; erinaceid *Tetracus* sp.; castorid *Steneofiber* sp.; cricetid *Atavocricetodon atavus*; and the eomyid *Eomys* sp. The marsupial *Amphiperatherium*; anoplotheriid *Tapirulus*; and the rodents *Pseudoltinomys*, *Isoptychus*, *BranSAToglis*, and *Gliravus* were inherited from the Late Eocene. The Early Oligocene endemic taxa of England were represented by the primate *Leptadapis stintoni* (one of the last in Europe) and the pantolestid *Dyspeterna woodi* (Hooker, 1987). The Early Rupelian mammalian fauna of Belgium (Hoogbutsel) was closely similar to the English Fauna.

The Early Oligocene rodent fauna of southern Germany markedly differed from those of the western localities. Only there, brachyselenodont theridomyids of the genus *Pseudosciurus* remained (Hartenberger, 1973b). Among other distinctions of the southern German fauna is the persistence of the pseudosciurid *Suevosciurus*, the endemic theridomyid lineage *Theridomys brachydens–T. ludensis* (from MP21 to MP24, migrated to France in MP25), early appearance of the eomyid *Pseudotheridomys*, and the extreme rarity of cainotheres, which were widespread in western and southern provinces (Hartenberger, 1973b; Heissig,

1987; Gad, 1987). These facts may be explained by the existence of a physical barrier (marine strait) in place of the Rhine Graben. In the German Province, immigrants gradually replaced the autochthonous elements. The large palaeotheres *Palaeotherium* and anoplotheres became extinct at the very beginning of MP21; the majority of primitive pseudosciurids and the last palaeotheres, dichobunids, and anoplotheres disappeared in MP23; and the last *Suevosciurus* disappeared in MP25 (Heissig, 1987). Certainly, many species and genera of immigrants also became extinct; however, almost all their families persisted to the Late Oligocene (Aplodontidae, Pteromyidae, Castoridae, Eomyidae, Rhinocerotidae, Suidae, etc.). The exception is provided by lagomorphs (*Shamolagus franconicus*) and entelodontids, which disappeared at the end of MP22 or at the beginning of MP23.

The easternmost Early Rupelian mammalian fauna of the West European type was recorded in northwestern Bohemia, Czechia (Fejfar, 1987a). This fauna includes the marsupial *Amphiperatherium* sp.; erinaceids cf. *Neurogymnurus* sp.; talpid cf. *Paratalpa* sp.; heterosoricid *Qurcysorex* sp.; pseudosciurid *Suevosciurus ehingensis*; sciurid *Palaeosciurus* sp.; cricetids *Paracricetodon* cf. *dehmi*, *Atavocricetodon* cf. *murius*, and *Pseudocricetodon montalbanensis*; eomyid *Eomys* cf. *zitteli*; zapodid cf. *Parasminthus* sp.; glirid *Gliravus* sp.; aplodontid *Plesispermophilus angustidens*; ruminants *Pseudogelocus laubei*, *Bachitherium* cf. *curtum*, and *Lophiomeryx* cf. *pomeli*; cainotheres *Paroxacron* sp.; entelodontid *Entelodon* cf. *antiquus*; anthracotheres *Anthracotherium* sp. and *Elomeryx* cf. *woodi*; suid *Propalaeochoerus* cf. *paronae*; carnivores *Cephalogale* and *Pseudocynopsis* cf. *antiquus*; creodont *Hyaenodon* sp.; and rhinocerotoid *Ronzotherium* cf. *filholi*. This assemblage is generally typical of the MP21 Zone and rather similar to the southern German Fauna. On the other hand, it clearly differs from the westerner faunas by the absence of the Theridomyidae; a very early appearance of *Paracricetodon*, *Pseudocricetodon*, and the Zapodidae; and by unusually large sizes of representatives of the genera *Palaeosciurus*, *Suevosciurus*, *Paracricetodon*, *Atavocricetodon*, *Gelocus*, and *Lophiomeryx*. These distinctions are possibly accounted for by paleogeographical and paleoecological factors (Fejfar, 1987a). This region was most probably a continuation of the German Province and played the role of an ecotone zone, i.e., the same role that the German Province played with reference to the entire Western Europe.

The South German mammalian faunas is similar to the Rupelian faunas of Austria and Hungary. *Anthracotherium magnum*, *Protaceratherium albigense*, *Diplobune*, and the endemic rodents *Meteomys noskyi* and *Pseudotheridomys (Anomegodus) baconicus* (Eomyidae), and *Heterocricetodon (Alsocricetodon) telonii* (Cricetidae) were recorded from Hungary (Russell *et al.*, 1982).

Thus, in the Early Oligocene, the faunal distinctions between Western Europe and Asia markedly decreased. Of 15 endemic European families of the Late Eocene mammals, only eight existed up to the onset of the Oligocene (with the Mixtotheriidae and Haplobunodontidae migrating at the Eocene–Oligocene boundary to Africa and persisting there up to the Early Oligocene). By the end of the Early Oligocene, only two endemic families (Theridomyidae and Cainotheriidae) still existed. By that time, the number of families in common with the Asian families had increased almost threefold. Migrations occurred throughout the Early Oligocene. After MP20/MP21, the expansion of the Asian elements was more gradual and well traced in each Suevoian (Rupelian) mammalian zone.

**Southeastern Europe and Lesser Caucasus.** In the Early Oligocene, the giant rhinoceroses Indricotheriidae first reached southeastern Europe. The earliest member of the group, *?Urtinotherium* sp. was found at the base of the Mera Beds (Lower Rupelian) in the vicinity of Cluj, Transylvania (Codrea, 1993; Codrea and Suraru, 1995). *Benaratherium gabunia* was described from the later beds (Upper Stampian, MP24 Zone); it was more primitive than *B. callistrati* from the Oligocene of Georgia. In addition, the rhinoceros “*Ronzotherium*” *kochi*, anthracothere *Anthracotherium magnum*, entelodontids *Entelodon* aff. *deguilhemii* and *E. magnum*, embrithopod *Crivadiatherium mackennai*, and the pantolestid *Kochictis centenii* were found in Romania (Rădulesko *et al.*, 1976; Russell *et al.*, 1882; Codrea, 1993). In Bulgaria (Dragovica), a typical representative of the North Asian (Kazakh) giant rhinoceroses, *Indricotherium transouralicum*, was found (Russell *et al.*, 1982).

The widely known Benara Fauna from Georgia is usually dated to the Late Oligocene (Gabunia, 1964; Russell and Zhai, 1987). However, this supposition lacks support from the other taxonomic groups and the position in the geological sections support this fact; moreover, the presence of Brontotheriidae indet., *Ardynia* (Hyracodontidae), and *Hyaenodon dubius* (Creodonta), found in Europe in zones MP21–MP23, and *Bothriodon* cf. *velanus* (Anthracotheriidae), recorded from the MP21 Zone, allows for the assignment of this fauna to the Early Oligocene (Codrea, 1993). The generic composition of the fauna is generally consistent with this dating. The Benara Fauna is characterized by a large proportion of endemic genera and species and includes elements of different origin: the true European taxa (rhinoceros *Eggsyodon* and anthracothere *Elomeryx*); native Asian taxa (chalicothere *Borissiakia*; hyracodontid *Ardynia*; rhinoceros *Meschotherium*; suiforms *Paraentelodon*, *Hyoboops*, and *Telmatodon*; ruminant *Iberomeryx*; and the giant rhinoceroses Indricotheriidae); Asian-American taxa (Brontotheriidae, tapirid *Colodon*, and rodents Cylindrodontidae); Pan-Paleoartic taxa (chalicothere *Schizotherium*, anthracotheres *Bothriodon* and *Anthracotherium*, and ruminants *Lophimeryx* and *Pro-*

*dremotherium*); and Pan-Holarctic taxa (carnivores *Nimravus*, *Amphicyon*, *Cephalogale*, and *Plesictics* and creodont *Hyaenodon*). The Asian taxa also include the rodents *Parasminthus* sp. (Zapodidae) and *Yindiremys* sp. (Ctenodactylidae), which were identified by Lopatin based on Benara material from the collection of the Paleontological Institute of the Russian Academy of Sciences.

At the beginning of the Oligocene, Greece and the European area of Turkey (Thrace) was widely inhabited by the anthracotheres *Anthracotherium prealsaticum*, *A. magnum*, *A. cf. mosvialense*, *Eomeryx woodi*, and *E. cf. porcinius*. The Early Oligocene rodents from the Turkish Thrace, and especially the Cricetidae, are very diverse. The Kavakdere locality (MP23–MP24) includes the pseudosciurid *Suevosciurus fraasi*; cricetids *Paracricetodon kavakderensis*, *Trakamys saratji*, *Pseudocricetodon* cf. *moguntiacus orientalis*, *P. philippi*, and *Kerosinia variabilis*; eomyid *Eomys* sp.; flying squirrels *Oligopetes* cf. *lophulus* and *O. aff. obtusus*; glirids *Glis* aff. *guerbuezi* and *Bransatoglis sjeni*; castorid *Steneofiber* sp.; and Ctenodactyloidea indet. The Kocayarma Fauna (MP25) includes *Suevosciurus ehingensis*, *Paracricetodon kodjayarmensis*, *Pseudocricetodon orientalis*, *P. philippi*, *Lignitella sue-mengeni*, *Edirnella sinani*, *Eucrietodon* aff. *dubius*, *Heterocricetodon* cf. *schlosseri*, *Eomys fahlbuschi*, *Eomys* sp., *Glis guerbuezi*, and *Bransatoglis sjeni* (Ünay and Bruijn, 1987; Ünay-Bayraktar, 1989; Freudental *et al.*, 1994). Unlike the West European faunas, this assemblage lacked theridomyids and was dominated by the Muroidea. The above facts allow one to assign the East Mediterranean Region and Transcaucasia to the Balkan–Caucasian Zoogeographic Province, which was probably isolated from the typical European faunas. One can conclude that in the Early Oligocene, as in the Late Eocene, the southeastern Europe, Anatolia, and Transcaucasia were components of the North Asian Subregion of the Asian Zoogeographic Region.

**Northwestern and Central Asia.** The Early Oligocene evolution of Asian mammals is usually divided into two ages, the Ergilian and the Shandgolian (Russell and Zhai, 1987). The Ergilian is correlated with the European MP21 Mammalian Zone. The Shandgolian is usually correlated with the MP22–MP27 mammalian zones (Vislobokova, 1996) and, consequently, includes a part of the Late Oligocene (the uppermost horizons of the Shand-Gol Formation correspond to the Upper Oligocene, but this epoch is usually designated the Tabenbulukian Age). Dashzeveg (1996b) has recently proposed the division of the Shand Gol Formation (= Hsanda-Gol Formation) into two members, the Tatal Beds (below the basalt bed that is dated as 31–32 Ma) and the Shand Beds (above this bed), with the Shandgolian Fauna being generally correlated with the MP22 Zone.

In Central Asia, faunas from a number of localities in Mongolia (Ergilin-Dzo, Khoer-Dzan, Dzamyn-Ude,

the upper part of the Ergilin-Dzo Formation, or Ergilin Beds; Shand-Gol, Tatal-Gol, Menkhen-Teg, Ikhe-Argaluntu-Nuru, the lower part of the Shand Gol Formation below the basalt bed dated at 31–32 Ma, or the Tatal Beds) and in northern China (Urtyn Obo, Tsaganbulag formations, etc.) are assigned to the Ergilian Age. This epoch is generally characterized by the persistence of certain archaic Eocene mammalian genera, including the swamp rhinoceros *Gigantamynodon*, hyracodontids *Ardynia* and *Prohyracodon*, deperetellid *Teleolophus*, chalicotheres *Eomoropus*, brontothere *Embolotherium*, didymoconid *Ardynictis*, lagomorph *Gobiolagus*, and carnivore *Stenoplesictis*, as well as by the appearance of a number of new taxa, including the carnivore *Nimravus*; perissodactyls *Cadurcodon*, *Hypsamynodon*, *Symphysorrhachis*, *Ronzotherium*, *Allocerops*, and *Indricotherium*; suiforms *Entelodon* and *Bothriodon*; ruminants *Miomeryx*, *Eumeryx*, and *Palaeohypsodontus*; and rodents *Pseudocylindrodon*, *Eucricetodon*, *Allosminthus*, *Sinosminthus*, and *Heosminthus* (Wang, 1985; Wang and Meng, 1986; Dashzeveg, 1993, 1996a, 1996b; Vislobokova, 1997). Ruminants were represented by the most primitive (for the Oligocene) taxa, including *Lophiomeryx angarae*, *L. gobiae*, *Miomeryx* cf. *altaicus*, *Gobiomeryx dubius*, and *Eumeryx culminis* (Vislobokova, 1996; Vislobokova *et al.*, 1996). Fossils of true Asian leptictids (*Ongghonia dashzevegi*) has been recently discovered in the lower part of the Shand-Gol Formation in the locality of Tatal-Gol (Kellner and McKenna, 1996). However, the primitive tooth structure of *Ongghonia* indicates that the terminal Paleocene—the beginning of the Eocene rather than the Early Oligocene should be considered to be the time of the leptictid dispersion in Asia. The pantolestid *Gobiopthecus khan* found in the Khoer-Dzan locality (Dashzeveg and Russell, 1992) indicate the possibility of migration of certain European (in origin) mammals (Dyspterninae in this case) to Asia in the terminal Eocene.

The Central Asian faunas of the Shandgolian Age are rather abundant in Mongolia and northern China. The first stage of the development of the true Shandgolian faunas is considered to occur 32 to 29.5 Ma BP and comprises Shand-Gol, Tatal-Gol, and Shunkht in Mongolia and Ulantatal, Sanshenggon (Saint Jacques), Shuidonggong and Chanlishan in China; these ages correspond to the European MP22–MP23 zones (Vislobokova, 1996). This period is characterized by the extinction of the majority of the Late Eocene Ergilian relicts and many true Ergilian taxa, as well as by the appearance of many new taxa (erinaceids *Amphechinus*, *Tupaiodon*, and *Exallerix*; heterosoricid *Gobisorex*; rodents *Tsaganomys*, *Cyclomylyus*, *Anomoemys*, *Prosciurus*, *Selenomys*, *Tataromys*, *Karakoromys*, *Cricetops*, *Parasminthus*, *Shamosminthus*, and *Gobiosminthus*; carnivores *Amphicticeps*, *Palaeogale*, *Plesictis*, *Palaeoprionodon*, *Proailurus*, *Amphicyonodon*, *Asiavorator*, and *Stenogale*; gelocid *Pseudomeryx*; bovids *Palaeohypsodontus* and *Hanhaicerus*; and the didymoconid

*Didymoconus* (= *Tshelkaria*, and *Archaeomangus*) (Huang, 1992; Dashzeveg, 1993; 1996b; Spassov and Lange-Badré, 1995; Vislobokova, 1996; Lopatin, 1997a). The giant rhinoceros *Indricotherium parvum* was replaced by *I. transouralicum* and the lagomorph *Desmatolagus ardynensis* was replaced by *D. gobiensis* and *D. robustus*. Ruminants were represented by more advanced taxa than in the Ergilian and included *Eumeryx imbellis*, *Lophiomeryx* cf. *mouchelini*, and *Pseudomeryx gobiensis* (Vislobokova *et al.*, 1996). The commencement of the later stage of the Shandgolian fauna development (MP24–MP27), which continued to the Late Oligocene, was characterized by the appearance of large progressive *Lophiomeryx* of the *L. chalangia* type; lagomorph *Sinolagomys*; and the rodents *Tachyryctoides*, *Eomys*, *Pseudotheridomys*, and *Eomyodon* (Wand and Ermy, 1991; Vislobokova, 1996). Almost all the Early Shandgolian mammalian genera and species still persisted.

In Kazakhstan, the Ergilian includes the Upper Aksyir Subformation and the Kusto and Tuzkabak formations of the Zaisan Depression (eastern Kazakhstan).

The Upper Aksyir Formation includes the hedgehogs *Amphechinus* sp., *Tupaiodon* sp., *Ictopidium* sp., *Galerix* sp., and Galericinae gen.; moles Talpidae gen.; lagomorphs *Gobiolagus*, *Zaissanolagus*, and *Desmatolagus*; didymoconid *Ardynictis* sp.; ruminant *Archaeomeryx* sp.; anthracotheres *Brachyodus* and *Bothriodon*; brontotheres Brontotheriidae indet.; aymynodontids; and the rodents *Symplokeomys zaysanicus* (Eomyidae); *Sinosminthus* sp., *Allosminthus* cf. *ernos*, *Allosminthus* sp., and *Heosminthus primiveris* (Zapodidae); *Eucricetodon* sp. (Cricetidae); *Ardynomys glambus* and *Ardynomys* sp. (Cylindrodontidae), and cf. *Karakoromys* sp. (Ctenodactylidae). Amphibians, turtles, lizards, and snakes are abundant; crocodiles and birds were also found (Shevyreva, 1972; Gabunia, 1977; Gabunia and Gabunia, 1987; Emry *et al.*, 1997; Erbajeva and Tyutkova, 1997; Gabounia and Chkhikvadze, 1997).

The Kusto Formation yields the pantolestid *Oboia argillaceus* (Gabunia, 1989); swamp rhinoceros *Cadurcodon ardynensis* (= *C. tuskabakensis*); entelodontid *Entelodon gobiensis* (Ermy *et al.*, 1997); hedgehogs *Tupaiodon* sp. and Galericinae gen.; moles Talpinae gen.; rodents Cylindrodontidae indet., Cricetidae indet., Ctenodactylidae indet., Zapodidae indet., and Eomyidae indet.; anthracotheres *Bothriodon* sp., cf. *Brachyodus*; leptomerycids *Archaeomeryx* sp., cf. *Miomeryx* sp., and *Gobiomeryx dubius*; and the cervid cf. *Eumeryx* sp. (Gabunia, 1977; Russell and Zhai, 1987).

The assemblages from the Chiliky (= Chelkarnura; = Indricothere) and the Betpak-Dala formations in western and central Kazakhstan, as well as the Buran and Aktau formations in eastern Kazakhstan, are assigned to the Shandgolian Asian Land Mammal Age.

The Chelkarnura (Indricothere) Fauna of terrestrial vertebrates in central Kazakhstan (Turgai Depression, a



number of localities in the vicinity of Chelkar-Teniz Lake) includes the amphibian Pelobatidae gen., turtles *Planiplastron tatarinovi*, *Ocadia turgaica*, *Chrysemys lavrovi*, “*Trionyx*” *turgaicus*, and “*T.*” *ninae*; and various birds and mammals. Rodents are represented by the castorid *Steneofiber kazachstanicus*; cylindrodontids *Ardynomys kazachstanicus*, *Cyclomylus turgaicus*, and *Polinaomys shintuzsaensis*; aplodontids *Prosciurus arboraptus* and *Plesispermophilus* sp.; eomyid *Eomys* sp.; zapodid *Parasminthus quartus*; cricetids *Cricetops aeniensis*, *C. dormitor*, *C. elephantus*, *Eucricetodon caducus*, and *E. asiaticus*; and the ctenodactiloid *Karakoromys decessus* (= *Woodomys chelkaris* = *Terarboraeus arcanus*: Wang, 1994). Among other small mammals, there are the lagomorphs *Desmatolagus gobiensis* and *Desmatolagus* sp. and insectivore *Ictopidium* sp. In addition, Lopatin (1999) described a new galericine species, *Neurogymnurus indricotherii*, and a new talpid genus and species, *Pseudoparatalpa shevyreva* (Urotrichini), from the Donguztau locality. Large mammals include the creodont *Hyaenodon dubius*; carnivore *Cynodictis minor*; didymoconids *Didymoconus rostratus* (= *Tshelkaria rostrata*) and *D. gromovae*; tapiroid ?*Colodon* sp.; chalicothere *Schizotherium turgaicum*; hyracodontid *Ardynia kazachstanensis*; amynodontid *Cadurcodon kazakademius*; giant rhinoceroses *Indricotherium transouralicum* and *I. minor*; rhinoceroses ?*Allacerops turgaica*, ?*Allacerops* sp., *Aceratherium aralense*, and *Aceratherium* sp.; entelodontids *Entelodon diconodon*, *E. major*, and *Entelodon* sp.; anthracotheres *Brachyodus* sp., *Hemimeryx turgaicus*, *Hyoboops* sp., and Anthracotheriidae gen.; suid *Propalaeochoerus* sp.; and ruminants *Lophimeryx turgaicus*, *Gobiomeryx dubius*, *Prodremotherium flerovi*, *P. longipes*, and *Eumeryx culminis* (Flerov and Yanovskaya, 1971; Russell and Zhai, 1987; Bendukidze, 1994, 1997; Kordikova, 1994; Lopatin, 1997a; Tyutkova, 1997). In the opinion of Kordikova (1994), this fauna belongs to at least two stratigraphic levels of the Lower Oligocene. In the opinion of Shevyreva (1995), this fauna existed later than the Buranian Fauna but slightly earlier than the Shandgolian Fauna.

The Aktau Formation (Aktau Mountains, Dzhungar Alatau) includes *Ardynia kazachstanensis* (Russell and Zhai, 1987; Kordikova and Mavrin, 1996), Ceratomorpha indet., Suiformes indet., Creodonta indet.; the turtles *Paraplastromenus* cf. *mlynarskii* and Emydidae indet.; and crocodiles Crocodylidae indet. (Kordikova and Mavrin, 1996).

The Buranian Fauna (numerous localities in the Zaisan Depression) is generally dated as the end of the first half and the beginning of the second half of the Oligocene (Shevyreva, 1995) and corresponds to the European MP22–MP23 zones. This fauna includes various vertebrates: fishes, amphibians Pelobatidae gen. indet., turtles (*Zaisanemys*, *Chelidropsis*, *Rafetus*, *Ergilemys*, *Chrisemys*, *Plastomenus*, *Trionyx*, *Planiplastron*, and *Ocadia*), lizards, snakes, and numerous mammals. The

latter are represented by the marsupial *Asiadidelphis tjutkova*; chiropterans cf. *Myotis* sp.; Tupaiidae gen.?; erinaceids *Tupaiaodon* cf. *morrisi*, *Ictopidium* cf. *tatalgolensis*, *Ictopidium* sp., *Galerix* sp., *Pseudoneurogymnurus shevyreva*, *P. zchickvadzei*, Galericinae gen., *Amphelinus* cf. *rectus*, and *Amphelinus* sp.; talpids Uropsilinae gen., Desmaninae? indet., *Desmanella* sp., Urotrichini indet., Talpinae gen., and Talpidae indet.; heterosoricids *Gobisorex* cf. *kingae* and Heterosoricidae gen.; lagomorphs *Gobiolagus* cf. *major*, *Gobiolagus* sp., *Procaprolagus* sp., *Desmatolagus* cf. *gobiensis*, *D.* aff. *robustus*, and *Desmatolagus* sp.; carnivore cf. *Cynodictis* sp.; creodont cf. *Hyaenodon* sp.; didymoconid *Didymoconus* (= *Tshelkaria*); swamp rhinoceros *Cadurcodon ardynensis* (= *C. zaisanensis*); and the tragulid *Miomeryx* sp. (Shevyreva, 1995; Emry *et al.*, 1995; Lucas and Emry, 1996; Gabounia and Chkhikvadze, 1997). Rodents (Shevyreva, 1995) include castorids *Agnotocastor devius*, *Steneofiber kazachstanicus*, *S. zaisanensis*, *S. shevyreva*, and *S.* aff. *shevyreva*; cylindrodontids *Cyclomylus mashkova* and *Beatomys gloriadei*; cricetids *Cricetops collator* and *Leidymys asybaevi*; and ctenodactyls *Karakoromys dimetron*, *Muratkhanomys velivolus*, *M. kulgayniae*, *M. djanarae*, *Roborovskia collega*, *Tataromys raeda*, and *T. boreas*.

In the southern area of Eastern Siberia (Olkhon Island, Lake Baikal; Ular' Formation), the Oligocene lagomorphs *Desmatolagus* cf. *gobiensis* and Leporidae indet. and rodents *Cricetops* cf. *dormitor*, which are closely similar to the Mongolian species, are known (Pokatilov and Nikolaev, 1986).

Thus, the Early Oligocene fauna of large mammals in North Asia was rather homogenous. Territories from western Kazakhstan to Ordos in China and even to Japan were inhabited by the species of perissodactyls and artiodactyls that were the same, or closely similar, to those from Mongolia (Tomida, 1986; Russell and Zhai, 1987; Vislobokova, 1996; Lucas and Emry, 1996). The most important distinction of the Early Oligocene Kazakhstan Fauna as compared to that from Central Asia is the presence of certain groups of small mammals clearly associated with closed and rather humid biotopes and marsupials, gymnures, moles, and beavers, which are unknown in Mongolia and northern China. The available shared genera of the majority of small and medium-sized mammals are represented by different species. In particular, among didymoconids, the genus *Didymoconus* is represented by *D. colgatei* (= *Tshelkaria robusta*) and *D. berkeyi* in Mongolia and *D. rostratus* and *D. gromovae* in Kazakhstan (Lopatin, 1997a). Rodents of the genus *Ardynomys* are represented by *A. olsenii* and *A. vinogradovi* in Mongolia, *A. kazachstanicus* in Central Kazakhstan, and by *A. glambus* in eastern Kazakhstan; the same is typical of the genera *Cynodictis*, *Cyclomylus*, *Beatomys*, *Karakoromys*, *Cricetops*, and *Tataromys* (Yanovskaya, 1970; Shevyreva, 1995).

These faunal distinctions are most probably associated with ecological and geographical factors, the lower climatic aridity compared to that in Central Asia and the localization of the Kazakhstan faunas in the coastal areas of two water basins (the lagoonal-lake system of Turgai and the Aral Sea, in the coastal lowlands of the Eastern Paratethys, on the one side, and large Zaisan Lake, on the other side), which were separated by a higher and more arid area.

### *Zoogeographic Zonation*

The disappearance of the Turgai Strait and the consolidation of the major part of European Land at the Eocene–Oligocene boundary resulted in a marked decrease in the faunal distinctions between the European and Asian zoogeographic regions. Nevertheless, they remained separate regions.

After the mass immigration of Asian mammals at the beginning of the Oligocene, the European fauna and the individual island and peninsular zoochores again became isolated. In the Later Rupelian, the provincial distinctions of the European theriofauna still persisted and became even more pronounced. There existed at least four provinces, the English–French–Belgian Province in the northeast; the French–Swiss Province and the Iberian Province, which differentiated the latter, in the southwest; and the German Province in Central Europe. Continental bridges were occasionally formed between the neighboring provinces; however, the proportions of endemic taxa indicates their independence.

The Balkan–Caucasian Province was a component of the North Asian Subregion of the Asian Zoogeographic Region (like that in the Late Eocene). Within this subregion, there are two more provinces, the Central Asian Province and the Kazakhstan Province, or in a wider sense, the Central Asian Biochore may be considered to be an equivalent to the entire Northern Asian Subregion (Shevyreva, 1995), with the exclusion of the Balkan–Caucasian Province.

Since mammals of the Shandgolian Age of western and eastern Kazakhstan markedly differ from those of Central Asia and from each other by the taxa of species rank, these territories may be distinguished as separate zoochores, namely, the subprovinces of the Kazakhstan Province.

Thus, in the vicinity of the Tethys in the Early Oligocene, the following zoochores are distinguished (Fig. 5).

### **Holarctic Kingdom**

#### *European Region*

- English–French–Belgian Province
- French–Swiss Province
- Iberian Province
- German Province

#### *Asian Region*

#### *North Asian Subregion*

- Balkan–Caucasian Province
- Kazakhstan Province
  - West Kazakhstan Subprovince
  - East Kazakhstan Subprovince
- Central Asian Province

### **Afrotropical Kingdom**

#### *African Region*

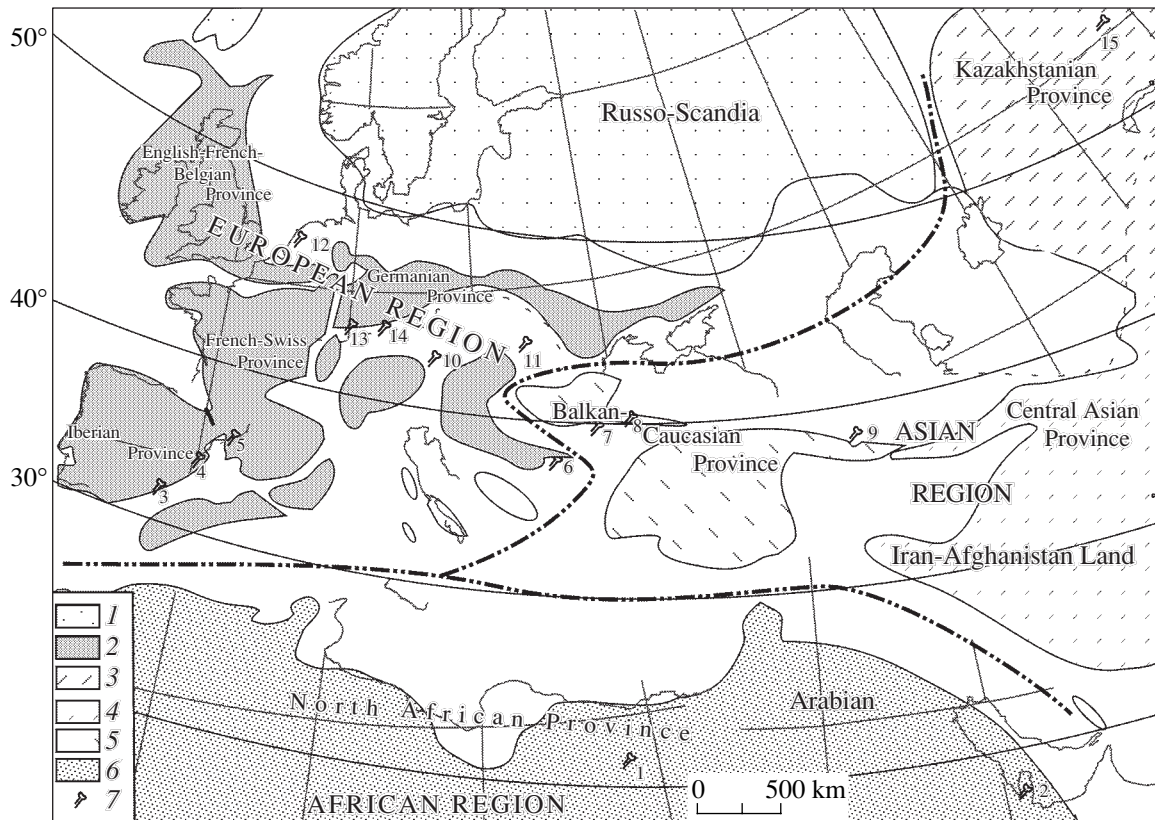
- North African–Arabian Province

At the beginning of the Oligocene, three routes of migration between Asia and Europe were possible: (1) from northwestern Asia via the Turgai Depression and farther along the northern coastal area of the Paratethys; (2) from northwestern and central Asia via Asia Minor and farther along the old tract of an island system that had existed as early as the Late Eocene and separated Paratethys from Tethys; and (3) from western Asia via the continental bridges of the East Mediterranean Region. The most important area of emigration probably was the North Asian Biochore. The faunal exchange between the Iberian Land and North Africa could occur in the region of Gibraltar at the beginning of the Early Oligocene and via Kabilia and the Balearic continental block at the end of the Early Oligocene.

### **Freshwater Ichthyofauna**

Most data on the composition of the Early Oligocene freshwater fish faunas of Europe and Asia were obtained from the revision of fossil assemblages of France, Germany, and Czech (Obrhelová, 1975; Gaudant, 1978a, 1978b, 1978c, 1979a, 1979b, 1979c, 1981a, 1981b, 1982, 1984, 1985a, 1985b, 1987, 1988, 1993) and the material from eastern and central Kazakhstan, Far East, Mongolia (Lebedev, 1959; Sytchevskaya, 1968, 1973a, 1973b, 1974, 1976, 1981, 1984, 1986, 1989a, 1989b, 1998; Khisarova, 1971, 1974), Turkey (Rückert-Ülkümen, 1963), and China (Tang, 1959; Cheng, 1962; Wang *et al.*, 1981; Zhang *et al.*, 1985; Chang and Chow, 1986; Chang and Zhou, 1993; Chang and Chen, 2000; Chang *et al.*, 2001).

**Europe.** In Europe, the Early Oligocene freshwater faunas display further development of the genera inherited from the Eocene. These were primarily forms of marine origin, such as the gonorhynchids, chandids, atherinids, percichtiids, gobiids, and members of some Early Paleogene relict families: the Amiidae, Thaumaturidae, Umbridae, and the Lepisosteidae. By the onset of the Oligocene, only a moderate part of the Early Paleogene forms went extinct. This includes the esociform *Palaeoesox* and the double-armored herrings unknown from the succeeding faunal record. The reports on the extinction of the Thaumaturidae by that time (Gaudant, 1993) are invalidated by the finds of the *Thaumaturus* otoliths in the Early Oligocene of the Hessen Depression (Weiler, 1961, 1973). The persistence into the European Early Oligocene Freshwater



**Fig. 5.** Zoogeographic zonation of the Tethyan Region in the Rupelian based on terrestrial vertebrates. Explanations: (1) Land lacking vertebrate finds; (2) **European Region** penetrated by over 20 mammalian families from Asia throughout the Rupelian, but keeping its independence and provincial subdivisions: of 15 endemic families, 12 still existed; (3–5) **Asian Region**, extending up to China and Japan, characterized by homogenous fauna with the same species of Rhinocerotidae and Entelodontidae; (3) Kazakhstanian Province, differing from the Central Asian Province (4) in the presence of small mammals associated with forest, humid biotopes; (5) Balkan–Caucasian Province, experiencing migration from Asia but being still separated from the European faunas; (6) **African Region**, North African–Arabian Province, retaining distinctions of the Late Eocene faunas in the composition of proboscideans, hyracoids, subhuman primates, and endemic rodents; (7) the main vertebrate localities. The localities and group of localities considered in the text (1) Fayum Depression; (2) Dofar, Sultanate of Oman; (3) Ciruelos; (4) Ebro; (5) Quercy; (6) Chantras (Greek Thrace); (7) Dragovica, South Bulgaria; (8) Turkish Thrace; (9) Benara, Akhaltsikhe; (10) Szapar and Pustavam, Hungary; (11) Cluj, Transylvania; (12) Hoogbutsel, Belgium; (13) Bohemia; (14) Austria; (15) Chelkar-Teniz, Northern Kazakhstan.

Fauna of the gonorrhynchids, amiids, and lepisosteids (Gaudant, 1978c, 1981a, 1987b; Martini, 1988; Weiler, 1973), along with further evolution here of umbrids, chandids, and gobiids (Gaudant, 1979a, 1979b, 1981a, 1987a, 1993; Martini, 1965, 1988), point to a considerable degree of continuity of this fauna with reference to the Late Eocene fauna.

Throughout the Early Oligocene, the European fish fauna showed only gradual changes, which did not essentially affect its structure. At that time, some Characidae emerged (Gaudant, 1979c). Since they are represented by forms other than those known from the Eocene, this fact testifies to a short-term link of the European fauna with the African fauna. Another coeval event is the continuing inhabitation of fresh waters by new marine invaders such as the osmerid *Enoplophthalmus* (Gaudant, 1985a, 1993). The spreading of this form to the southern regions of Europe suggests the cooling. At the same time, there is recorded the rise of

the cyprinodontid *Prolebias*, which became widespread in the European basins by the Middle Stampian (Gaudant, 1981b, 1982, 1988). The distribution of the short-bodied Amphiatlantic pikes of the subgenus *Kenoza* also occurs in the Middle Stampian, as documented by the finds of *Esox primaevus* and *E. sp.* in France and Switzerland, respectively (Gaudant, 1978a, 1979b); this subgenus is now known to widely populate the east of North America.

In the Rupelian lacustrine basins of Europe, the various Chandidae, first recorded in the Middle Eocene (Gaudant, 1993), continued to develop (Anđelković, 1989; Gaudant, 1985b, 1987a, 1989). At that time, their range covered Spain, France, Serbia, Germany, and Romania. In particular, the Rupelian of Serbia (Anđelković, 1989) is characterized by a wide species diversification of the chandid genus *Dapalis* (“*Smerdis*”), which included *D. macrurus*, *D. minutus*, *D. sieblosensis*, and *D. microcanthus*, in association with the cyp-

rinid ?*Palaeoleuciscus (Leuciscus) papyraceus* and cyprinodontids (*Prolebias goretii*).

The invasion of cyprinids into European fresh waters started as late as the Early Oligocene. This event is evidenced by the occurrence of "*Chondrostoma elongata* Kramb. in the Lower Oligocene beds of Bohemia (Gaudant, 1993), along with the first appearance of unquestionable Asiatic immigrants, *Palaeoleuciscus* and *Varhostichthys* (*V. cf. brevis*), in the European freshwater assemblages of the Lower–Middle Stampian (Gaudant, 1977, 1979b, 1984), and also by the reports on the problematic Barbinae (?*Barbus* sp.: Anđelković, 1989) in the Rupelian of Slovenia.

Former reports on the earliest cyprinid finds from the Paleocene–Eocene of Europe proved to be erroneous. In particular, the genus *Chela* known from isolated pharyngeal teeth is not a cyprinid (Patterson, 1975); the same was demonstrated for "*Blicca croydonensis* White from the Lower Eocene of England on the strength of its scale structure (Gaudant, 1993). Likewise, isolated teeth from the Priabonian (Late Eocene) of Isle of Wight, once attributed to the cyprinids *Phyllocladens* and *Diplodens* (Rutte and van de Weerd, 1980), as well as teeth from the Eocene of Turkey designated as the cyprinid *Caryophyllocladens* (Rutte and Becker-Platen, 1980), in fact, belong in fact to rodents.

Cyprinids gradually progressed in their role through the Oligocene–Miocene faunal succession of Europe, in parallel with spreading of the long-bodied north Asiatic pikes. At the same time, most of former autochthonous Paleogene dominants came to decline and disappeared. Among them, the last amiids, lepisosteids, and thaumaturids are still traceable by the scales and otoliths (Weiler, 1973), and the gonorhynchids by the skeletal remains (Schraft, 1979), until the Early Miocene. By contrast, the umbrids attained the peak of their abundance by that time (Gaudant, 1979b; Martini, 1988; Weiler, 1973) and survived into the present European Fish Fauna. In general, the Early Oligocene European Freshwater Fish Fauna remained rather poor in terms of diversity. Most of its localities yield impoverished assemblages comprising a few forms dominated as a rule by the derivatives of marine families, such as the Gobiidae, Chandidae, Cyprinodontidae, Moronidae, and Osmeridae that penetrated freshwater bodies (Gaudant, 1977, 1981a, 1985a). These were accompanied by a small admixture of the autochthonous relicts and of immigrants from adjacent land areas.

The primarily freshwater forms belonging to the Umbridae, Esocidae, Characidae, Cyprinidae, Thaumaturidae, Amiidae, and Lepisosteidae were scarce and few in number. Substantially, the freshwater ichthyofauna of the European Early Oligocene remained formed by the insular dwellers and had very restricted links to other land regions from where some new elements might occasionally have come. Such faunal contacts were quite episodic and resulted in the invasion of a few natively freshwater newcomers. For instance, the

short-bodied pikes of the subgenus *Kenoza*, known from the Middle Stampian, obviously reached there from Rosso-Scandia. Similarly, the rare Leuciscinae belonging to the genera *Palaeoleuciscus* and *Varhostichthys* (with the earliest finds from the Stampian of France: Gaudant, 1977, 1984) and problematic Barbinae (Rupelian of Slovenia: Anđelković, 1989) came from Asia; and the characids came from Africa. As noted above, previous reports on the appearance of cyprinids in the Paleocene–Eocene of Europe have been recently disproved. The earliest known cyprinid records fall on the Eocene of China (Wang *et al.*, 1981), eastern Kazakhstan (Sychevskaya, 1984, 1986), and Turkey (Rückert-Ülkümen, 1963).

**Northern Asia.** The bulk of data on the composition and pattern of the freshwater fish fauna of the Early Oligocene of northern Asia was obtained from Kazakhstan. For the Late Eocene to the Early Oligocene, the most informative fossil-bearing levels (with respect to both the fauna and flora) have been detected in eastern Kazakhstan. On the evidence from the plant fossils and mammals, it is usually believed that the Early Oligocene is covered here by the upper part of the Aksyirskaya Formation, and the Kustovskaya and Buranskaya formations. According to an alternative viewpoint (Tolstikova, 1976, 1980), the Eocene–Oligocene boundary in this section occupies a higher position.

When accepting the predominant dating of the above units, followed in the present volume, one should conclude that in northern Asia the earliest Oligocene (judging by data from the Upper Aksyirskaya and Kustovskaya formations) was characterized by the further evolution of the Late Eocene dominants. Specifically, these were represented by amiids (genus *Cyclurus* with a number of species), hiodontids (subgenus *Gobihiodon*), and a great variety of catostomids inherited from the Late Eocene: *Amyzon*, *Cycleptus*, *Carpiodes*, *Erimyzon*, *Minytrema*, *Xyrauchen*, *Moxostoma*, and *Catostomus*.<sup>10</sup> The percichthids were represented by the endemic genus *Kiinkerishia (K. kazakhstanica)*. The cyprinids, with the earliest local record in the Early

<sup>10</sup>It is surprising that, in spite of unquestionable evidence of wide occurrence of catostomids in the Eocene–Oligocene fish communities of northern Asia (Hussakof, 1932; Sychevskaya, 1986), repeated attempts were made to disprove this fact in a quite arbitrary way, without any reexamination of the fossils in question (Nelson, 1949; Smith, 1992; Yakovlev, 1961). In reality, the abundance of catostomids in the continental Eocene–Oligocene of eastern Kazakhstan is proved beyond any doubt by the mass finds of their most diagnosable remains, i.e., the pharyngeal teeth, which in turn are accompanied by numerous fragments of typical skull bones, vertebrae, and scales. To this end, it is worth noting that, in the samples obtained from washing of the bone-bearing rocks of the Aksyirskaya and Kustovskaya formations, the catostomid pharyngeal teeth by far outnumber all other remains (in contrast to the samples from the succeeding Buranskaya Formation, in which the material is dominated by the cyprinid pharyngeal teeth). The reality of a broad dispersal of catostomid fishes in the Paleogene of northern Asia is further corroborated by the finds of their articulated skeletons in the Eocene–Oligocene of the Maritime Province (Sychevskaya, 1986) and in the Eocene of China (Chang *et al.*, 2001).

Eocene (Obailinskaya Formation), contained *Parabarbus* sp. and still retained their status of a scarce and poorly diversified group (Sytchevskaya, 1986).

Additional data are provided by the Oligocene ichthyofauna of Mongolia (yielded by the Ergiliin-Dzo Formation, Ergiliin Member, Zone MP21). This fauna was impoverished and included scarce amiids (*Cyclurus* sp.), cyprinids (*Rutilus* sp.), catostomids (Catostomidae gen. indet.), and bagrids (*Gobibagrus hoerdzanicus* Sytch.). The fish fauna of the Maritime Province, similar in age, included catostomids (*Vasnetzovia artemica* Sytch.) and cyprinids of the subfamily Gobioninae (Sytchevskaya, 1986).

Compared to these features, the younger fauna of the Buranskaya Formation of eastern Kazakhstan (dated on mammals as the end of the first half, or beginning of the second half of the Early Oligocene, zones MP22–MP23?), displays a quite different pattern. It is almost devoid of amiids and catostomids, which had dominated the preceding Paleogene communities (Sytchevskaya 1986, 1998). Specifically, the diversity of catostomids was reduced to a single genus, with their finds (as well as these of amiids) becoming exceedingly scarce, whereas the hiodontids disappear at all. On the other hand, the cyprinid fishes for the first time attained the role of dominating group and showed a marked increase in both diversity and abundance. These comprise the Leuciscinae (*Rutilus* sp., *Tribolodon* sp., and *Zissanotınca cristidens*), Barbinae (*Parabarbus* sp.), and Schizothoracinae (*Eodiptychus longidens* and *Schizothorax* sp.). Another new dominants include the Esocidae (*Esox* sp.), Siluridae, and Percidae. Similar assemblages occur in Central Kazakhstan and Fore-Aral Region (in Kenderlykskaya and Chelkarnurinskaya formations respectively); they also yield the Esocidae (*Esox aralensis* Sytch.) and Cyprinidae (*Rutilus* sp., *Tribolodon* sp., *Palaeotınca turgaica*, *Zaissanotınca cristidens*, and *Parabarbus mynsayensis*) (Sytchevskaya, 1986, 1998).

This dramatic faunal turnover observed in the transition from the Kustovskian to Buranskian time evidently reflects the large-scale changes in the geological history, climate, and paleogeography of northern Eurasia during the Early Oligocene. The approach of early phase of the Alpine orogeny obviously affected and destabilized the regular hydrological regime that had been established in the north Asiatic freshwater basins during the Eocene. The new unstable conditions in aquatic environment, perhaps devoid of clearly expressed cyclicality, gave the advantage to more eurybiontic fish groups, primarily the cyprinids, allowing them to oust and replace the Early Paleogene dominants, such as the Catostomidae, Hiodontidae, and Amiidae. These changes in the pattern of the fish fauna, along with changes in the accompanying freshwater mollusk fauna, also indicate the relative cooling during the Buranskian Time (Tolstikova, 1976, 1980; Sytchevskaya, 1986).

In China, the paucity of data on the Oligocene fish fauna complicates very much the analysis of faunal events of that time. The cyprinids, known from there since the Eocene (Wang *et al.*, 1981) continued to develop in this area during the Early or Middle Oligocene. In eastern China, these were dominated by the subfamily Leuciscinae (Zhang *et al.*, 1985). The Chinese catostomids, also showing the earliest record in the Eocene (*Amyzon hunanensis*), so far remain unknown in the Oligocene (Chang *et al.*, 2001).

In sum, compared with the run of events in the Early Oligocene of Europe, the contemporaneous history of the freshwater fish fauna of northern Asia reveals a much more marked transformation. In the most spectacular way, it is expressed in the faunal turnover (involving both fishes and accompanying organisms) seen in the transition from the Kustovskian to Buranskian time in eastern Kazakhstan. In contrast to the Late Aksyirskian and Kustovskian assemblages (associated with the Ergilian Mammalian Fauna of Zone MP21), which retained a rich set of the catostomid taxa typical of the Paleogene Amphipacific Ichthyofauna, the Buranskian community demonstrates a sharp switch toward the domination of cyprinid fishes that later ultimately conquered the fresh waters of northern Eurasia.

**Analysis of Biogeographic Structure.** Of the studies that most closely touched upon the history of dispersal of freshwater fishes in Eurasia, one should mention at first the works by Yakovlev (1961, 1964) who analyzed the Neogene history of the Holarctic ichthyofauna. Demonstrating the lack of zoogeographic integrity of Holarctic in the Neogene, he believed this condition to be inherited from the preceding epoch and stated on these grounds that the exchange between the Eurasian and North American freshwater fishes was much complicated during the whole Cenozoic. Based on comparison of the Neogene families recorded from these two continents, Yakovlev concluded that in the Cenozoic the faunal exchange between them took place only twice: in the Paleogene, via the North Atlantic land, and in the Pleistocene, across the Bering Bridge. However, the extensive studies of the Paleogene ichthyofauna of northern Asia (Chang and Chow, 1986; Chang and Chen, 2000; Sytchevskaya, 1986) actually revealed its close similarity to the coeval fish communities of North America. With further progress of such studies, the unity of both discussed Paleogene biotas becomes more and more evident, which led us to distinguish them as a single biogeographic unit, the Amphipacific Province (Sytchevskaya, 1986, 1998, 2001).

However, the arguments used by various authors to explain the reasons for the similarity of the Amphipacific ichthyofaunas much differ. The most common is the assumption that the Amphipacific fish groups known in Asia had immigrated to there via different routes from Western Nearctic. Chang and Chow (1986), Chang and Zhou (1993), and Chang and Chen (2000) suggest the spreading of some of these groups during

the Eocene across a broad land connection between Asia and North America provided by the Bering Bridge.

Grande (1994) proposed another way of transpacific migration, based on the so-called Pacifica hypothesis, which implies the existence in South Pacific of an early continent, whose disintegrated fragments later drifted to, and finally collided with, the Pacific rims.

In contrast to these hypotheses based on the idea of transpacific migrations, Sytchevskaya (1986, 1998, 2001) put forward the above-mentioned concept of the integral Amphipacific Province, according to which western Nearctic and northern Asia had a common biota and developed as a single biogeographic unit from the Late Cretaceous to Early Paleogene. During the Early Paleogene, the Amphipacific Province remained isolated from Europe by the West Siberian Sea and from the Eastern Nearctic Realm by the epicontinental submeridional Nearctic Gulf, which is fully consistent with the available paleogeographic data.

Disintegration of the Amphipacific Province, as well as the Amphiatlantic Province (which is presumed to have embraced Europe and Eastern Nearctic: Sytchevskaya, 1986, 1998, 2001), proceeded during the Oligocene and was largely caused by the paleogeographic rearrangement of the northern landmasses. This resulted in a gradual transition to a new, Neogene pattern of biogeographic differentiation of the freshwater ichthyofauna. The decisive paleogeographic changes involved in this process may be summarized as follows:

- (1) Integration of Europe and northern Asia (via Turgai Bridge);
- (2) Isolation of Asia from North America;
- (3) Broad unification of the western and eastern parts of Nearctic (North America);
- (4) Break of the land connection between North America and Europe.

Of these four events, the first two most directly underlay the disintegration of the Amphipacific Province and then vanishing of its western (Asiatic) part, with the spreading there of the newly arisen fauna of the Palearctic type. The first event, i.e., the integration of Europe and Asia, is thought to fall on the Eocene–Oligocene boundary (or on the Early Oligocene, following some alternative datings), taking into account both the geological data and the most probable time of replacement of the dominants within the north Asiatic cypriniforms.

The reasons for which the Asiatic catostomid fishes became ousted by cyprinids in the Late Paleogene are of a special interest. The cyprinids evidently originated in Asia, where they were first recorded in the Eocene. Ecologically, they are rather extensively diversified and so pertain to the eurybiontic groups. By contrast, the catostomids, judging by the biology of their Recent North American members, were mainly the stenobiontic benthophages that populated the lakes and streams with hard, usually stony, bottom and clean, well-oxygenated water. This mode of life makes them very sen-

sitive to the mudding and pollution of the aquatic environment (Scott and Crossman, 1973).

In northern Asia, the onset of tectonic activity during Eocene–Oligocene transition resulted in the breakdown of the Kazakh Plain and adjacent areas (Grossheim, 1957). This in turn caused the break of the stable hydrologic regime in the local basins, so that they became less suitable for the existence of catostomids. The intensification of irregular fluvial erosion led to an increase in the transport of the terrigenous material and, in consequence, to occasional mudding of water and the appearance of swamps and ephemeral shallow pools. All of these changes gave the advantage to eurybiontic cyprinids and stimulated their rapid ecological expansion, including the rise of forms adjusted to life in shallow, muddy, and poorly oxygenated water setting with dense vegetation. It seems most likely that the replacement of the Asiatic catostomid dominants by cyprinids that occurred in the Oligocene basically proceeded under such conditions. As indirect evidence of this scenario of faunal events, it may be pointed out that the only Recent survivor of Asiatic catostomids, the Chinese genus *Myxocyprinus*, which is most likely of the autochthonous origin, dwells in exceedingly muddy waters of the Yangtze River basin.

In spite of the removal of marine barrier in the Turgai area (western Kazakhstan), which had prevented free dispersal of the natively freshwater fishes in Eurasia during the Early Paleogene, the integration of the freshwater ichthyofaunas of Europe and northern Asia still remained much hampered during the Oligocene and partially Miocene. As is seen from the paleontological data, the exchange between the fish faunas of both continents progressed rather slowly, so that the high degree of consistency in their systematic composition was most likely attained as late as the end of the Neogene.

In northern Asia, the breakdown of the previous biogeographic realm known as the Amphipacific Province was accompanied by the rise of the new dominants: the Esocidae, Cyprinidae, Siluridae, and Percidae. This event fell on the Eocene–Oligocene transition or, following other datings, on the Early Oligocene. At the same epoch, these new dominants made the first steps in their spreading into Europe across the Turgai Bridge and along the southern coast of the Paratethys. This latter route might have been followed by some Leuciscinae, judging by their fragmentary finds in the Eocene and Oligocene of Turkey. (The same way could equally have been used by some European groups, such as the Cyprinodontidae and Gobiidae, for counter migration to Asia.) The earliest cyprinids (Leuciscinae) in Europe are recorded immediately after that time, in the Middle Stampian (Gaudant, 1977, 1979b, 1984).

To summarize, it may be stressed again that Early Oligocene rearrangement of the freshwater fish fauna in Asia was much more clearly expressed than in Europe. In Asia, this resulted in the decline of amiids and nearly entire extinction of catostomids and hiodontids as early as the Middle Oligocene. By contrast, in Europe, the



extinction of the local Early Paleogene dominants, such as amiids, thaumaturids, and gonorhynchids, was more gradual, and it was completed only in the Miocene. It seems very likely that these events were preceded by the break of the Bering Land connection between Asia and North America, because the Oligocene expansion of cyprinids in Asia did not result in their broad penetration to Nearctic.

The Early Oligocene faunal turnover, which closed the existence of the former Amphipacific Province and the succeeding expansion of the new North Asiatic Fish Fauna to Europe (with the integration of both Palearctic continents on the close of the marine Turgai Strait), led to a rise of a new biogeographic unit, the Palearctic Subregion. The core of the Palearctic Freshwater Fish Fauna, dominated by esocids, cyprinids, silurids, and percids, began to form in northern Asia during the Early Oligocene; its composition was later extended to incorporate some European elements.

It should be noted that, by their ancestry, the above-listed principal dominants of the new North Asiatic Fauna, which appeared in the course of the "Oligocene Revolution," are autochthonous to the Amphipacific area. In particular, cyprinids and silurids are known from this area since the Eocene (China); esocids, since the Cretaceous (northern Nearctic); and the percids, since the Eocene. As mentioned above (with respect to cyprinids), the discussed faunal changes did not affect the eastern part of the Amphipacific Province, North America, which seems to suggest that by the end of the Eocene its land connection with Asia had already been lost. In connection with this, no broad invasion of Asiatic cyprinids ever took place to America, such that until now this group plays only a subordinate role in the North American Fish Fauna. On the other hand, some Amphipacific dominants, such as the amiids, hiodontids and catostomids, have survived into the North American Fish Fauna until present, due to which this fauna still retains its relict Amphipacific (Paleogene) pattern in many respects.

As a whole, on the evidence from freshwater fishes, the Early Oligocene biogeographic structure of Holarctic is outlined as follows:

- Holarctic Region
  - Palearctic Subregion
    - European Province
    - Asiatic Province
  - Nearctic Subregion

#### LATITUDINAL CLIMATIC ZONATION OF THE EARLY OLIGOCENE

Even those numerous determinations of the early Oligocene climatic parameters that are based on similar initial data (predominantly on the floras of western and central Europe) show a wide scatter, because they use different methods for reconstructing the paleoclimatic

regimes. Nevertheless, a comparison of these determinations with those made for the Late Eocene reliably indicates that at the Eocene–Oligocene boundary the average annual temperatures dropped by over 4–6°C in midlatitudes, mainly due to a decrease in the average winter temperatures.

Less marked changes occurred in the *Tethyan Realm*, where environments that are closely similar to those in the late Eocene still persisted in the shelf area. Even the north European shelf area was inhabited by reef-building corals, numerous tropical and subtropical benthic genera and species inherited from the Eocene, as well as by fairly complete planktonic assemblages. These changes resulted in the poorer taxonomic composition of the majority of groups and in the appearance of individual species, which, in the Priabonian, were restricted to the northern regions of Europe. In the early Oligocene, the European coast of the Mediterranean probably was a part of a tropical–subtropical transition zone, where the water was constantly heated to a temperature of 18–20°C, which is required for a normal development of reef-building corals.

The terrestrial vegetation of this coastal area changed its character. The microphyllous evergreen plants indicate an advance of arid environments, and the appearance of certain Arcto-Tertiary forms indicates a slight climatic cooling. Floristic data indicate that the climate of the southern slopes of the Lesser Caucasus was of a subtropical type without any tropical indications.

**South–Central European–Lesser Caucasian Coastal Area of the Paratethys** was characterized by a marked impoverishment of the benthic and planktonic assemblages in the early Oligocene and by the disappearance of the most thermophilic taxa before their evolutionary extinction. The colonial corals did not build any reefs. As during the Eocene, this coastal area belonged to a subtropical zone. The plant fossils indicate the existence of luxuriant mesophilic forests along the central European coastline. For the Kiscel Flora, the average annual temperatures were 21–23°C, the average winter temperatures were 15°C, and the average summer temperatures were 23°C. The average annual temperatures for the Brežani Flora were estimated at 20–23°C (Palamarev, 1967); those for the Sotzka Flora, at 17.6°C (Unger, 1861); and the mean annual precipitation for the Brežani and Kudratice floras, at 1200–1800 and 700–1300 mm, respectively. The majority of heavy rainfalls occurred in summer (Andreansky, 1964).

**North Sea Basin and the northern coastal area of the Paratethys** were most significantly affected by the global Eocene–Oligocene climatic cooling, as well as by regional rearrangements of the paleogeographic connections and currents. The character of the distribution and migration of benthos reliably indicate that the Eastern Paratethys was most strongly affected at the beginning of the Oligocene by the water exchange with the North Sea Basin. The taxonomic diversity of

benthic fauna sharply decreased, corals and nummulitids were almost absent, and the molluscan assemblages were dominated by boreal taxa. In planktonic assemblages, the majority of warm-water zonal species of planktonic foraminifers and nannoplankton were also absent. Thus, the composition of marine biota indicates that in the early Oligocene this area was assignable to the boreal low-latitude zone. Its temperature parameters may be estimated as follows: the water remained heated to 15–18°C for three or four months, whereas in winter, it could experience long-term cooling to temperatures below 10°C.

The floral composition, i.e., the joint occurrence of evergreen and deciduous taxa, allows the inclusion of the coastal area of northwestern and eastern Europe into the ecotone Subtropical–Boreal Zone. Its more westerly regions were dominated by subtropical floras, whereas farther to the east, these were replaced by floras of a moderately warm climate. The climatic parameters of this zone are estimated as follows: the Haselbach Flora existed at average annual temperatures of 10–15.5°C, average winter temperatures of 2–4°C, average summer temperatures of 20–22°C, and the average annual precipitation ranged from 1000 to 3000 mm (Mai and Walter, 1978). For comparison, the climatic parameters for the late Eocene Zéitz Flora located in the same Weisse-Elster Depression were as follows: the average annual temperatures were 15–20°C, the average winter temperatures were 6–13°C, the average summer temperatures were 15–23°C, and the average annual precipitation was over 2000 mm (Mai and Walter, 1983). The Nerhau Flora was characterized by the average annual temperatures of 13–16.5°C, average winter temperatures of 6°C, average summer temperatures of 25°C, and the average annual precipitation over 2000 mm. The subarid climatic zone became more humid compared to that in the Eocene and was displaced farther south, to the Crimean–Caucasian Region.

The temperate climatic zone became markedly wider. Its southern border was displaced farther south. This zone covered the entire East European Platform, most of the Turan Plate, and the territory of northern and central Kazakhstan and Western Siberia. This zone occupied the northern, most humid area of the late Eocene subtropical zone. The Kyzyltobe Flora, the most ancient of the early Oligocene Kazakhstan floras, developed in climatic conditions closely similar to those in the modern-day Colchis Refugium with average January temperatures of 2°C, average July temperatures of 20°C, and average annual precipitation of 1500–2000 mm (Rayushkina, 1979).

#### MAJOR EVENTS IN THE LATE EOCENE–EARLY OLIGOCENE

The studied region, extending from northern Africa and the Atlantic coastal area of Europe to Central Asia, covers a considerable part of the Earth's Northern Hemisphere. The events that occurred there reflected

and determined, to a large extent, the character of the global changes at the Eocene–Oligocene boundary. The trigger mechanism for large-scale paleogeographic, climatic, and biotic events during the late Eocene–early Oligocene was a tectonic rearrangement that resulted in changes in the patterns of oceanic and climatic circulations, which conspicuously affected the composition and geographic distribution of biota.

**Tectonics.** A collision of the African and Arabian plates with the European Plate was the determining factor for changes in the Tethyan Realm. The approach of these plates to each other resulted in a progressive closure and separation of Tethyan relics, reduced connection between the Atlantic and Indian oceans, higher relief, and in the formation of the land bridge that separated the Paratethyan basins.

The results of the collision are also traceable at a regional level throughout the Alpine Zone. In the Alpine–Carpathian Region, the collision resulted in a large-scale horizontal displacement, decrease in the basin area, and rearrangement of paleogeographical connections: shallowing and closure of the Slovenian Corridor, a strait between the Alps and the Dinarides. The Pyrenean Orogeny resulted in drying and folding of the South Carpathian–Balkan area of the Paleogene basin and in the formation of depressions that were compensated for by land sediments.

At the beginning of the late Eocene, the system of the Balkanids, Pontides, Lesser Caucasus, Elburz, and Kopet Dagh still represented an archipelago. Subsequently, this system occasionally formed a continuous land mass, which already in the late Eocene served as a land bridge to southeastern Europe for large Asian vertebrates and separated the Eastern Paratethys from the Tethyan Realm. In the Oligocene Paratethys, the sea bottom became much more differentiated to form deep depressions not compensated for by sedimentation.

Large land massifs also formed in that epoch farther south (Eastern Taurus and the Ararat Massif). This resulted in the closure of water circulation in the Mediterranean, and in the cessation of biogeographic isolation of benthic fauna that inhabited the North African coastal area.

The activation of the Tian Shan zone first resulted in the loss of connections and drying of the Tarim Basin and subsequently in the closure of the Ferghana and Tajik basins and accumulation of continental deposits there. Previously, at the end of the middle Eocene, the continental environments had already formed in the Central Pamir Basin.

**Eustatic motions.** Three transgressive phases of the Late Eocene (Beloglinian) Basin have been recorded in the sections of the northern passive margin of the Paleo-Paratethys where marine facies are wedged in land sediments (*Geologicheskije i bioticheskie...*, 1998, p. 197). The first transgressive phase has been dated as nannoplanktonic zone NP18; the second phase, as zones NP19 and NP20. At the boundary between these

phases, a short-term decrease in the sea level (by 50 m, or more) occurred. This was accompanied by climatic cooling and anoxic events, which are indicated by the sharp increase in the abundance of *Uvigerina* (Marzuk, 1992). The sea level was even higher during the second transgression, the transgressive sediments of which overlie more ancient beds (the Mandrikovka Beds in Ukraine, the Balyklei Beds in the Volga Region, and the Sumsar Beds in Tajikistan) (Muzylev *et al.*, 1996).

A marked sea advance and a coarser-grained composition of the sediments is indicated in the northern shelf area, starting from the second half of the Priabonian (*Bolivina antegressa* Zone). The peak of sea regression is observable in the Eocene–Oligocene boundary beds, where shallow-water benthic fossils and leaf flora were even recorded from deepwater marly facies. These fossils indicate the appearance of islands in the western area of the Greater Caucasus (Akhmetiev, 1995). In the northern Aral Sea coastal area and Turgay, the sea level decreased by over 60–80 m, as indicated by the depths of ravines that eroded the underlying Chegan Formation. The denudation in the Kyzyl Kum Desert is estimated at 100–150 m in depth (*Geologicheskije i bioticheskie...*, 1996, 1998). Even in the central areas of the Caucasus–Kopet Dag Basin still occupied by sea, breaks in sedimentation and erosive forms are observable in the Eocene–Oligocene boundary beds. These are often indicated in argillaceous facies only by the active redeposition of fossils of the Eocene microfauna and flora.

Although the scale of the subsequent sea transgression in the first half of the early Oligocene of the Paratethyan region fell short of the scale of the late Eocene transgression, this transgression involved fairly large areas, including the Dnieper–Donets Depression, central areas of the Volga Region, the northern area of the Turan Plate, the Turgay Strait, as well as the major area of the West Siberian Basin, the Kyzyl Kum area of the Turanian Basin (Fig. 1), and possibly the Ferghana–Tajik and even the Tarim basins.

The subsequent Solenovian Closure was determined by tectonic rather than eustatic factors. It was sometimes accompanied by sea regressions and basin shallowing (in the Dnieper–Donets Depression, Volga Region, and Ciscaucasia) sometimes by deposition of transgressive sediments and erosion of underlying beds. The Late Solenovian was undoubtedly an epoch of sea regressions.

**Hydrology and sedimentology.** The normal marine conditions and the warm current that went from the southeast (Indian Ocean) and was inherited from the Middle Eocene still persisted in the Priabonian in the Tethyan Realm. The distribution of biota in the second half of the Priabonian–Early Rupelian indicates an increased separation of this region and the formation of the Circum-Mediterranean Current (Fig. 2). Since the supply of terrigenous material was limited, biogenic

(coral and nummulitid) carbonates were widespread on the shelf.

In the Northern Peri-Tethys of the first half of the Priabonian, the eustatic sea level was high and the water salinity was still closely similar to that of the ocean. The entire Alpine-Carpathian Basin and the southern Transcaucasian shelf area of the Caucasian Basin experienced strong effects of warm Tethyan water, whereas no such effects are known in the more easterly regions, the Fore-Carpathian shelf area of the basin inhabited by endemic fauna. In basin facies, fine biogenous-carbonate silt dominated to be replaced by terrigenous sediments only in the shallow shelf zone. The water exchange via the Turgay Strait and the cyclonic current in the West Siberian Basin served as a radiator that heated the adjacent coastal areas (*Geologicheskije i bioticheskie...*, 1998).

As a result of the separation of the Paleo-Paratethys in the second half of the Priabonian, the entire Paratethys came under progressively stronger influence of the North Sea. The only exception was the southern (Transylvanian) area of the Carpathian shelf and the southern (Turkish) coastal area of the Euxine Basin, where the benthic fauna indicates that the Tethyan effects persisted into the early Oligocene. Marked deepening of basins, the appearance of isolated deep-water basins, partially blocked connections with the world ocean, an increase of the temperature gradient with latitude, and an active inflow of fresh water all resulted in the formation of a distinct temperature and salinity stratification. The appearance of stagnation conditions and the accumulation of undecomposed biogenous material in bottom sediments resulted in the formation of anoxic facies very typical of the Carpathian (Menilithic) Basin, as well as of the Caucasus–Kopet Dag (Maykopian) Basin. The productivity of calcareous nannoplankton and planktonic foraminifers, which in the Eocene were rock-forming organisms, sharply decreased.

The subsequent Solenovian closure of the basin resulted in the first brackishing of the Paratethys, changes in the character of sediments, extinction of marine fauna, and development of the individual endemic brackish-water fauna and microflora to restore for a short period of time the favorable gas exchange regimes and the biogenous-carbonate character of sediments (Polbian Beds).

**Climate.** Despite the very warm climate of the Middle Cenozoic, the latitudinal-climatic zonation was even in the Late Eocene defined sufficiently well to determine its biogeographic subdivision into provinces (Popov *et al.*, 2001).

A marked, although gradual, climatic cooling started in the second half of the late Eocene, with the peak of the temperature drop recorded at the Eocene–Oligocene boundary. In the northern Peri-Tethys, this global cooling became even more marked because of the eustatic sea regression and paleogeographic rear-

rangements that partially blocked Tethyan connections to increase the boreal effects of the Northern Atlantic. This cooling is well traced by the change of the subtropical biota to the boreal type and by the abundance of conifer pollen in the spore and pollen assemblages from the beds with *Propeamussium fallax* from Ciscaucasia and the South Ukrainian Depression, as well as from the basal Oligocene beds of these regions, southern areas of the East European Platform, and western Kazakhstan. The major factors of the changes in the vegetative cover were a decrease in the average annual temperatures in the early Oligocene by 4–6°C compared to those in the late Eocene (the average winter temperatures decreased, while the average summer temperatures were the same). The shelf water temperature similarly decreased (by 3–5°C after Marzuk, 1992), as indicated by isotopic data.

Although the southern cooling was not so important, some floristic data show that it was accompanied by wide fluctuations in atmospheric humidity (for more detail see the previous section).

**Biotic events.** The very marked abiotic environmental changes considered above also determined the character of the geographical distribution of biota and its changes at the Eocene–Oligocene boundary. The climatic cooling and the eustatic regression in the terminal Eocene and at the beginning of the Oligocene resulted in the most important of the Cenozoic rearrangements of biota, which persisted throughout the Rupelian. The direct result of this cooling was an extinction of biotas of the early Paleogene type and formation of communities with a quite different taxonomic composition. The evolutionary changes in biota were accompanied by local northward displacements of geographical ranges and of the majority of biogeographical borders following the paleogeographic, climatic, or facial changes, which are often difficult to trace in available data.

The response of different groups of biota to this crisis was much the same and amounted to the partial extinction of richer and taxonomically more diverse Eocene association of species and formation of a new typical Oligocene assemblage that was based on the remaining opportunist species. Northern taxa penetrated assemblages of the southern type during the climatic cooling, but not in large quantity. For this reason, the main biogeographic subdivisions were generally closely similar to those in the Eocene, although their borders and taxonomy markedly changed.

In different groups of biota, the evolutionary transformation occurred at basically different times and was not catastrophic in character. Thus, the most marked changes in the composition of planktonic foraminiferal and nummulitid assemblages occurred as early as the terminal Priabonian (inside the *Turborotalia centralis*–*Globigerina gortanii* (P17) and *Nummulites fabianii reitatus* zones). At the bases of these zones, highly specialized groups *Globigerapsis* and *Gribohantkenina*, a family of discocyclides, and three genera of nummulit-

ids became extinct, whereas *Hantkenina* became rare. At the same time, the development of typical Oligocene species started later, at the Eocene–Oligocene boundary, which is considered as a base of the *Globigerina tapuriensis* (P17/P18) Zone.

The appearance of the modern species of marine mollusks and the formation of benthic assemblages typical of the Miocene–Pleistocene was gradual and not contemporary in different climatic zones. In the late Eocene–early Oligocene, a gradual impoverishment of typical Eocene assemblages was widespread in the warm-water zone. Starting from the second half of the Oligocene, the composition of benthic assemblages was closely similar to that in the Miocene. At the same time, the boreal communities were very closely similar to each other and distinctive in the taxonomic composition throughout the Oligocene. The abrupt changes in the composition of boreal assemblages followed the paleogeographic and climatic changes and occurred at the Eocene–Oligocene boundary.

The change in the dinoflagellate assemblages, which was accompanied by the extinction of more than a half of the Eocene taxa (at the base of the *Phthanoperidinium amoenum* Zone), approximately corresponds to the Eocene–Oligocene boundary. Major changes in the composition of nannoplanktonic assemblages occurred much later, in the middle of the Rupelian at the base of the *Sphenolithus praedistentus* (NP23) Zone, when the impoverishment of assemblages was over, and a new thermophilic group, *Sphenolithus*, appeared.

The most substantial change in flora, the transition from the Paleocenophytic to the Neocenophytic, which was characterized by the predominance of modern-day assemblages and modern taxa, was gradual (*Geologicheskie i bioticheskie...*, 1998; Akhmetiev, 1999). This started in the middle of the late Eocene. The level of the most marked elimination of thermophilic taxa approximately corresponds to the Eocene–Oligocene boundary. Frequent fluctuations in temperature and atmospheric humidity contributed to more rapid disintegration of the Paleocenophytic flora. The presence of such fluctuations in the spore and pollen assemblages of Armenia is supported by mutually exclusive ranges of cryptogams as indicators of humid regimes and pollen of grasses, *Ephedra*, Cupressaceae, and other taxa characteristic of arid regimes. The change in flora occurred in both major phytochores of the Holarctic Land, the Boreal and the Tethyan regions, as well as in the ecotone zone that separated them. At the beginning of the early Oligocene, the floras of each of these regions were characterized by more or less equal proportions of the Paleocenophytic and Neocenophytic representatives. This process was over in the second half of the Rupelian and resulted in the formation of the moderately thermophilic, deciduous, mesophilic Oligocene flora, which was designated by A.N. Krishtofovich as the Turgay Flora.

The evolutionary transformation of terrestrial vertebrates was also gradual. For the vertebrates, the Early–Late Oligocene boundary, when the Indricotheriidae fauna formed, and the active radiation of rodents and insectivores started (Reshetov in *Geologicheskie i bioticheskie...*, 1998), was of greater importance.

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