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The Faunal Assemblages of Permian Terrestrial Vertebrates from Eastern Europe

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Abstract—The scheme of the faunal assemblages of Permian terrestrial vertebrates from Eastern Europe is considered. The following faunal superassemblages are distinguished: (1) Eryopoidean Superassemblage, consisting of the Inta Assemblage; (2) Dinocephalian Superassemblage, consisting of the Mezen, Ocher, and Isheevo assemblages; and (3) Theriodontian Superassemblage, consisting of the Sokolki and Vyazniki assemblages. Some assemblages are divided into subassemblages. Detailed descriptions of assemblages and subassemblages are given. The Proterosuchian Superassemblage from the Early Triassic of Eastern Europe is also considered.

INTRODUCTION

The first scheme of the faunal assemblages of Permian terrestrial vertebrates from Eastern Europe was proposed by Efremov (1937, 1939). He distinguished four assemblages consecutively replacing each other. Each reflected certain stage of Late Permian history of the tetrapod fauna. "Since these assemblages do not characterize strictly determined thin horizons, consistent with regard to bedding, lithologic characteristics, and stratigraphy," Efremov concluded that "it makes sense to follow the example of South African geologists and introduce the term stratigraphic zones corresponding to the changes of faunal assemblages by individual stages comprising a relatively wide range of deposits" (1939, p. 273). Thus, the zones considered by Efremov correspond to the currently used concept of complex biostratigraphic zones and, consequently, they describe stratigraphic rather than faunal aspects, as is generally believed.

The following zones were distinguished in the section of the Upper Permian strata of Eastern Europe, from the bottom upwards:

Zone I (*Rhopalodon*) consisting of the upper part of the Kungurian Stage (i.e., the strata currently referred to as the Ufimian Stage) and the lower part of the Lower Kazanian Substage;

Zone II (*Titanophoneus*) consisting of the upper part of the Lower Kazanian and the lower part of the Upper Kazanian Substages;

Zone III (pelycosaurian), including the upper part of the Upper Kazanian Substage;

Zone IV (pareiasaurian), including the Tatarian Stage.

This scheme was repeatedly refined and supplemented in subsequent studies, the faunal characteristics and stratigraphical positions of the zones were revised (Efremov, 1940, 1941, 1944). The latest variant of the scheme included the zones along with the faunal assemblages reflecting taphonomic differentiation of Permian tetrapod localities (Efremov, 1952; Efremov and Vyushkov, 1955). Efremov believed that the time intervals of existence of particular assemblages could overlap to a greater or lesser extent, as against those of zones. He distinguished five faunal assemblages in the Upper Permian of Eastern Europe. The Fore-Ural Dinocephalian Assemblage characterizes the Lower Kazanian Substage and the lower part of the Upper Kazanian Substage (zones I and II). The Isheevo Dinocephalian Assemblage existed later and was dated the upper part of the Upper Kazanian Substage (Zone II). The Mezen–Belebei Cotylosaurian Assemblage existed contemporarily with these assemblages. The Tatarian Stage (currently, only the Upper Tatarian Substage) is characterized by two assemblages of the same age (Zone IV), the Northern Dvina Pareiasaurian Assemblage and the Gorki City Batrachosaurian Assemblage. Currently, Zone III is distinguished only speculatively on the basis of great differences between the evolutionary levels of the faunas from zones II and IV. In actual fact, a transitive fauna has not been found; this is explained by the presence of a large gap in the Upper Permian deposits between zones II and IV. In addition to the listed zones, a new zone (Zone 0) characterizing the Lower Permian deposits was distinguished.

In general, the biostratigraphic scheme proposed by Efremov agrees with modern data on the occurrence of fossil tetrapods in the Upper Permian deposits; however, certain details need refinement.

To conclude this brief review of Efremov's studies, it should be emphasized that he was the first to distinguish the two main stages (Dinocephalian and Pareiasaurian phases) in the Permian faunas of terrestrial vertebrates from Eastern Europe.

Subsequently, the researchers involved in this field dismissed the zonal scheme proposed by Efremov and replaced it with by the scheme of faunal assemblages (Kalandadze *et al.*, 1968; Tchudinov, 1969, 1983, 1987; Ochev, 1976). The concept distinguishing the following three main faunal assemblages was developed by degree: (1) Ocher or *Estemmenosuchus* Assemblage from the Kazanian Stage; (2) Isheevo or *Moschops* Assemblage from the Early Tatarian; and (3) Northern Dvina or *Scutosaurus* Assemblage from the Late Tatarian. Ochev (1976) combined the first two faunas into the dinocephalian phase, assigned the *Scutosaurus* Fauna to the pareiasaurian–gorgonopian phase, and contrasted these with the proterosuchian and kannemeyeroid phases from the Triassic.

Later, the scheme of faunal assemblages was expanded and worked out in detail by Ivakhnenko (1990a, 1990b, 1990c, 1992, 1994, 1995a, 1995b, 1996). He distinguished six East European faunal assemblages of Permian tetrapods that sequentially replaced each other (from earliest to latest): Inta; Ocher (comprising Golyusherma, Ocher, and Mezen subassemblages); Isheevo (comprising Isheevo and Malaya Kinel subassemblages); Kotelnich; Sokolki (comprising Ilinskoe and Sokolki subassemblages); and Vyazniki. The latter three assemblages correspond to the Northern Dvina Assemblage distinguished by the workers cited above. Later, I propose to combine these assemblages into three superassemblages corresponding to large stages in the development of the tetrapod faunas from Eastern Europe: Eryopoidean, Dinocephalian, and Theriodontian superassemblages (Golubev, 1995a, 1995b, 1996, 1997, 1998a, 1999; Ivakhnenko *et al.*, 1997). The Eryopoidean Superassemblage includes the Inta Fauna only. The presence of this stage in the Permian history of terrestrial vertebrates of Eastern Europe was first indicated by A.S. Rautian. The Dinocephalian Superassemblage includes the Ocher and Isheevo faunas. It corresponds to the Dinocephalian Fauna distinguished by Efremov (1939, 1952) and the Dinocephalian phase after Ochev (1976). The Theriodontian Superassemblage comprises the Sokolki and Vyazniki faunas. It corresponds to the Pareiasaurian Fauna (after Efremov, 1939, 1952) and Pareiasaurian–Gorgonopian phase (after Ochev, 1976).

Recently, most of the material on Permian and Triassic tetrapods from Eastern Europe was revised (Ivakhnenko *et al.*, 1997); this allowed us to perform a thorough faunal analysis that resulted in the following observations. The Permian superassemblages are sharply distinguished from each other by the higher taxa (usually, higher than the family rank) of all blocks of the community of terrestrial vertebrates, i.e., dominant, subdominant, and aquatic blocks.[1] A relative number of common families in two successive superassemblages (coefficient of similarity) is, at most, 32%. Moreover, these families belong to the subdominant block and small members of the dominant block. The superassemblages separated from each other, do not include common families (Fig. 1). The transitions from one superassemblage to the other reflect large crisis stages in the development of tetrapod fauna (Golubev, 1995c).

The assemblages are distinguished from each other mainly by the composition of large members of the dominant block, i.e., the largest animals of different assemblages are represented by different large taxonomic groups (of order rank or higher). The composition of the subdominant block and small members of the dominant block change at the family level and lower-rank taxa. Only the pattern of the aquatic fauna remains invariable, i.e., the faunal changes involve the taxa of generic and specific rank. The coefficient of similarity between the assemblages of the same superassemblage is usually higher than 60%.

The subassemblages are distinguished from each other by general changes in the composition of the entire fauna at the taxonomic level of genera and species. They reflect a gradual course of community evolution. The coefficient of similarity between subassemblages of the same assemblage is usually higher than 75%.

The pattern revealed above allows one to revise the scheme of the faunal assemblages proposed by Ivakhnenko. I believe that the Mezen Fauna should be regarded as an assemblage, since it is distinguished from other Dinocephalian faunas by the composition of the dominant block. In particular, large phytophagous animals are represented by pelycosaurs, whereas in the Ocher and Isheevo assemblages, these are eotheriodonts and dinocephalians, respectively. In addition, the coefficients of similarity with other Dinocephalian

[1] The dominant block in the Paleozoic communities of terrestrial vertebrates is formed by large phytophagous animals and carnivores that preyed upon them (Olson, 1966; Sennikov, 1995; Kalandadze and Rautian, 1998); the subdominant block is formed by the forms feeding on invertebrates; the aquatic block comprises the forms consuming aquatic organisms (plants, invertebrates, fish, and tetrapods). Usually, members of the aquatic block can be easily identified in early tetrapod communities. In the terrestrial fauna, the identification is more difficult. In this case, the main distinctive feature is size; large animals (possessing skulls dozens of cm long) undoubtedly belong to the dominant block, and small animals (possessing skulls several centimeters long) belong to the subdominant block. However, the Paleozoic communities include many medium-sized tetrapod forms, such as *Microsyodon*, *Syodon*, most therocephalians, etc. On the one hand, they are too large to be obligatory feeders on invertebrates; consequently, they are assigned to the dominant block. On the other hand, they usually do not include effective phytophagous animals, and they are too small to consume large phytophagous tetrapods. Thus, a reconstruction of the trophic relationships of medium-sized terrestrial vertebrates is rather difficult. Below, I use the terms small and large members of the dominant block to distinguish these animal groups.

Super-assemblage	Assemblage	Sub-assemblage	Inta	Mezen	Golyusherma	Ocher	Isheevo	Malaya Kinel	Kotelnich	Ilinskoe	Sokolki	Vyazniki	Proterosuchian
Eryopoidean	Inta		6	0	3	2	2	1	0	0	0	0	0
Dinocephalian	Mezen			9	0	3	1	0	1	0	1	0	0
	Ocher	Golyusherma			12	10	3	3	1	2	2	1	0
		Ocher				15	4	4	2	2	2	0	0
	Isheevo	Isheevo					9	6	0	0	0	0	0
		Malaya Kinel						9	0	0	0	0	0
Theriodontian	Sokolki	Kotelnich							11	6	4	4	0
		Ilinskoe								13	8	4	1
		Sokolki									14	4	2
	Vyazniki											13	2
Proterosuchian													22

Fig. 1. The number of common families in Permian and Lower Triassic faunal assemblages of terrestrial vertebrates of Eastern Europe.

faunas is relatively low (33%). This is attributable to the fact that the Mezen Fauna probably has common genetic roots with other Dinocephalian faunas of Eastern Europe; however, it developed independently of the latter, since it was isolated, at least, from the terminal part of the Ufimian to the Early Tatarian (Golubev, 1995b). Theoretically, it should be most similar to the Golyusherma Subassemblage. However, an understanding of the latter leaves much to be desired.

On the contrary, the Kotelnich Fauna should be considered as a subassemblage of the Sokolki Assemblage. It differs from the Ilinskoe and Sokolki faunas by only the general primitive patterns of members of all groups. Large members of the dominant block of the Kotelnich Fauna belong to the same taxa, i.e., theriodonts, pareiasaurs, and dicynodonts.

Thus, the scheme of the faunal assemblages of Permian terrestrial vertebrates from Eastern Europe can be presented in the form shown in Fig. 2. Below, detailed descriptions of these assemblages are given. The names, ranks, and composition of the taxa follow those of Ivakhnenko *et al.* (1997), with rare exception reflecting the latest understanding of the Permian tetrapod faunas.

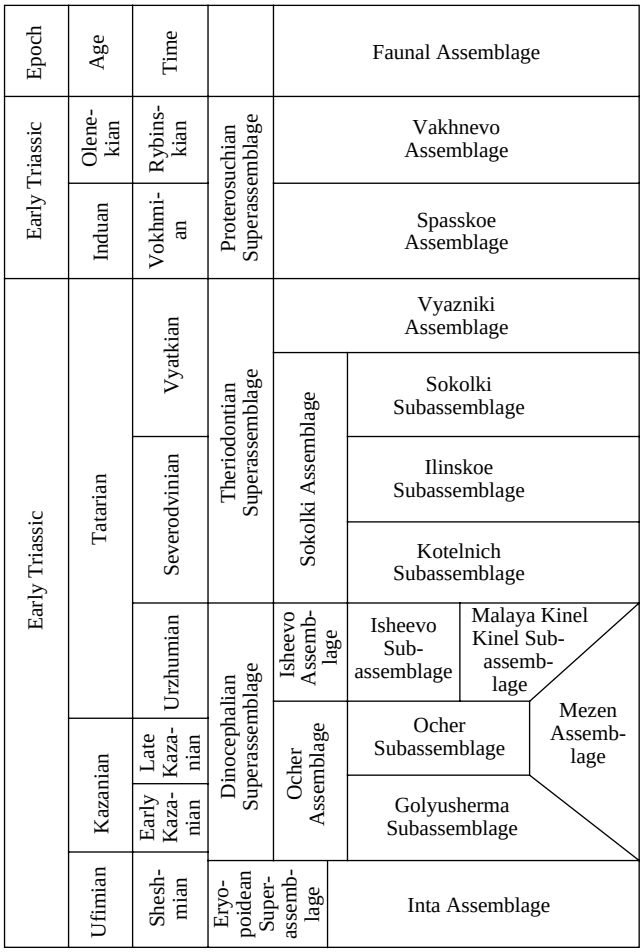

Fig. 2. The scheme of faunal assemblages of Late Permian terrestrial vertebrates from Eastern Europe.

PERMIAN

1. Eryopoidean Superassemblage

The Eryopoidean Fauna is characterized by widespread eryopoidean edopiform batrachomorphs, embolomere and gephirostegid anthracosauromorphs, and captorhinomorphs. The fauna is characterized by certain features inherited from the Carboniferous faunas of North America and Western Europe, being most similar

to the first (Kalandadze and Rautian, 1983; Gubin, 1985; Ivakhnenko, 1990c). This suggests that, in the Carboniferous, the Timano–Pechora Region contacted most closely with North America rather than with Western Europe. However, the absence of a number of dominant Early Permian members of both North American and Western European faunas indicates that, in the Permian, the Eryopoidean Tetrapod Fauna was isolated from the faunas of both Eurasia and North America.

Age. Early Permian, Ufimian Age.

1.1. Inta Assemblage

(*Clamorosaurus borealis* Fauna)

The Inta Assemblage is characterized mainly by the aquatic and subdominant blocks. Large members of the dominant block have not been found; they were probably represented by pelycosaurs. Small members of the dominant block include a number of phytophagous forms of the Bolosauridae, such as *Bolosaurus* and *Gnorhimosuchus* (Fig. 3). The subdominant block is formed by the Captorhinidae (*Riabininus*) and gephirostegid anthracosauromorphs of the endemic family, Enosuchidae (*Nyctiboetus*). General pattern of the aquatic block of the community is formed by eryopoidean batrachomorphs of the family Eryopidae (*Clamorosaurus*), most similar to North American forms (Gubin, 1983); endemic family Intasuchidae (*Intasuchus* and *Syndyodosuchus*); and less numerous eogyrinid embolomeres (*Aversor*) of North American appearance (Gubin, 1985).

Reference locality. Inta (155).[2]

Other localities (Fig. 4). Mylva (224), Pechora (156), Porog-1 (341), Porog-2 (342), Ters-Akkan, and Usva (159).

Age. Early Permian, Ufimian.

2. Dinocephalian Superassemblage

The Dinocephalian Fauna consists of widespread edopiform batrachomorphs (archegosauroideans and dissorophoideans), various small parareptiles (discosauriscins and nycteroleterins), gephirostegid anthracosauromorphs, captorhinomorphs, pelycosaurs, and primitive therapsids (eotheriodonts, dinocephalians, and primitive anomodonts, such as venyukoviid dromasaurs). In addition, the first less numerous theriodonts (pristerognathid therocephalians) appear.

The presence of certain groups known from the Carboniferous and Early Permian of Europe (archegosauroideans, discosauriscins, and ?pelycosaurs) and North America (dissorophoideans, captorhinomorphs, and pelycosaurs) is typical of the superassemblage. The presence of North American forms is probably explained by the Eryopoidean Superassemblage; however, dissorophids, rather common for the Early Dinocephalian Fauna and having a North American appearance (Gubin, 1980), have not been found in the latter superassemblage. This is attributable to a poor understanding of the Eryopoidean Fauna rather than to the presence of a direct contact between East European and North American tetrapod faunas early in the Late Permian.

The Dinocephalian Fauna includes caseids and varanopids, i.e., the most primitive groups of pelycosaurs. The territory they immigrated from is not clear, since both groups probably existed in the time interval of the Carboniferous when Western Europe and North America formed a united continent (Kalandadze and Rautian, 1980). Consequently, East European pelycosaurs could originate in either Western European or North America. This group of theromorph reptiles is known from the Mezen Fauna only. Other North American elements have not been found in this fauna. At the same time, the latter includes various parareptiles of undoubted Eurasian origin. This allows one to propose that pelycosaurs from the Mezen Fauna are also of European origin.

The occurrence of therapsids, similar to those from South Africa, in the Dinocephalian Fauna is evidence for certain faunal exchange with Gondwana (Golubev, 1995c, 1998d; Kalandadze and Rautian, 1998b). The dominant blocks of the Dinocephalian Fauna are formed mainly by the taxa of Gondwanan origin (except for the Mezen Assemblage including local elements, namely, pelycosaurs). Tetrapods of the aquatic blocks are of West European origin. The subdominant blocks are most diverse, they include both local, Gondwanan, and West European groups. The presence of West European and Gondwanan elements is a paramount feature distinguishing the Dinocephalian Fauna from the Eryopoidean Fauna.

Thus, by the end of the Ufimian Age, the territory of Eastern Europe adjoining the Ural Mountains and Timan had faunal contacts with both Western Europe and Gondwana. However, the time sequence of these events is not clear. In any case, from the Ufimian, Eastern Europe becomes a faunal province of Eurasia.

Age. The terminal part of the Ufimian to the Early Tatarian.

2.1. Mezen Assemblage

(*Ennatosaurus tecton* Fauna)

The dominant block of the community is formed (Fig. 3) by phytophagous caseosaurian pelycosaurs of the family Caseidae (*Ennatosaurus*) and by predatory eotheriodonts of the family Eotitanosuchidae (*Biarmosuchus*). The subdominant block of the Mezen Assemblage is most diverse and formed by (1) ophiacodont pelycosaurs of the family Varanopidae (*Mesenosaurus*); (2) various parareptiles, including the Nycteroleteridae (*Bashkyroleter* and *Nycteroleter*), Tokosauridae

[2] Hereinafter, the names of localities are followed by the numbers corresponding to those in the maps (Figs. 4–6).

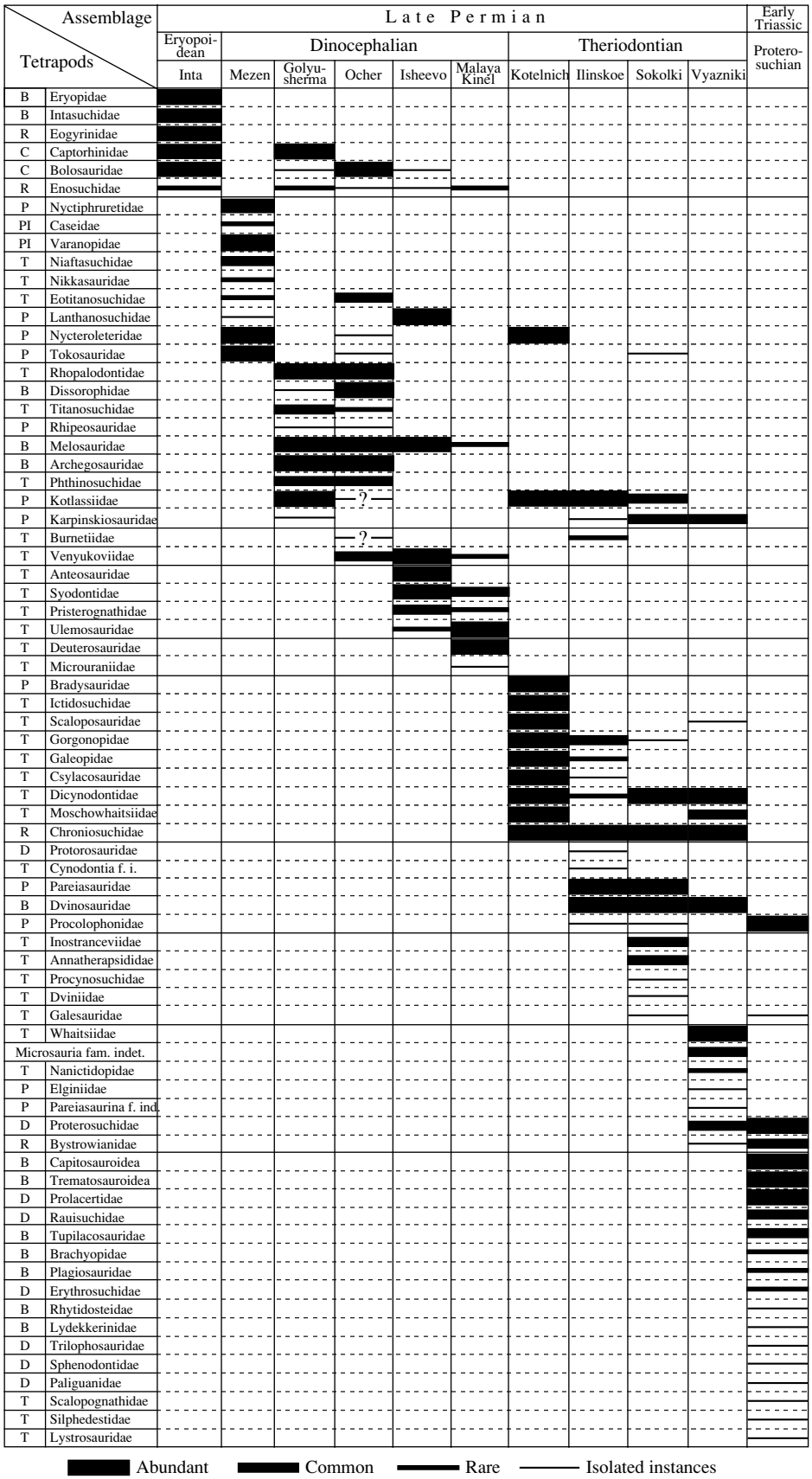

Fig. 3. Occurrence of vertebrate families in Late Permian and Early Triassic faunal assemblage of Eastern Europe. Designations: (B) Batrachomorpha, (C) Captorhinomorpha, (D) Diapsida, (P) Parareptilia, (Pl) Pelycosauria, (R) Reptiliomorpha, and (T) Therapsida.

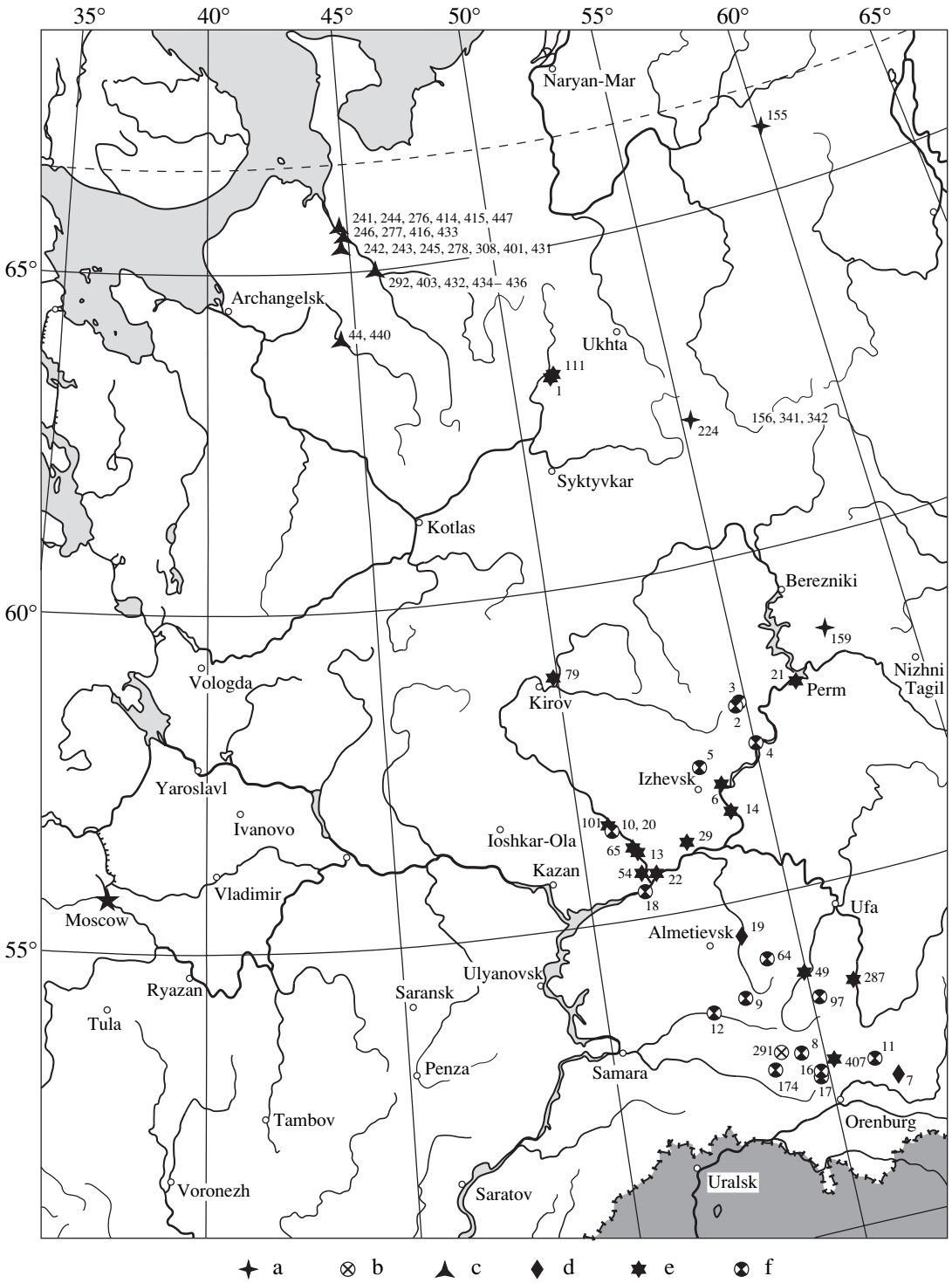

Fig. 4. Geographical position of the Upper Permian localities of terrestrial vertebrates: (a) Inta Assemblage, (b) Dinocephalian Superassemblage, (c) Mezen Assemblage, (d) Ocher Assemblage, (e) Golyusherma Subassemblage, and (f) Ocher Subassemblage. Localities: (1) Bozhyudor, (2) Ezhovo, (3) Luzhkovo, (4) Erzovka, (5) Sokol, (6) Sidorovy Gory, (7) Staroseika, (8) Krymskii, (9) Sarai-Gir, (10) Bolshoi Kityak, (11) Yaman-Yushatyr, (12) Borisov, (13) Berezovye Polyanki, (14) Mezhevaya, (16) Kuzminovskii Mine, (17) Rozhdestvenskii Mine, (18) Kamskie Polyany, (19) Biik-Tau, (20) Akbatyrovskii Mine, (21) Vyshka, (22) Kotlovka-1, (29) Golyusherma, (44) Moroznitsa, (49) Santagulovskii Mine, (54) Mamadysh-2, (64) Belebei, (65) Charli, (79) Shikhovo-Chirki, (97) Klyuchevskoi Mine, (101) Village of Gorki, (111) Ust-Koin, (155) Inta, (156) Pechora, (159) Usva, (174) Dubovka-1, (224) Mylva, (241) Peza-1, (242) Shchelya Osipova, (243) Krestovaya Shchelya, (244) Belokure, (245) Petrova Shchelya, (246) Blizhnyaya Shchelya, (276) Dorogaya Gora, (277) Glyadnaya Shchelya, (278) Kiselikha, (287) Sterlitamak, (291) Starobogdanovka, (292) Nisogora, (308) Shalomchataya, (341) Porog-1, (342) Porog-2, (401) Izba Rassolova, (403) Ust-Vashka, (407) Suroshnyi Ovrag, (414) Ust-Peza, (415) Ust-Nyafta, (416) Kozmogorodskoe, (431) Izba Usoltseva, (432) Bereznik, (433) Kimzha, (434) Leshukonskoe, (435) Karashchele, (436) Smolenets, (440) Soga-2, and (447) Belyi Nos.

(*Macroleter*), first procolophonids of the family Nyctiphruretidae (*Nyctiphruretus*), and isolated Lanthanosuchidae (*Lanthaniscus*); and (3) small eotheriodonts, including the Niaftasuchidae (*Niaftasuchus*) and Nikkasauridae (*Nikkasaurus* and *Reiszia*). The composition of the aquatic block is not known.

The Mezen Fauna is the most primitive fauna of all East European dinocephalian faunas; this is evidenced by the presence of pelycosaurs, a wide variety of parareptiles, and the absence of dinocephalians. However, it existed at the same time as the Ocher and Isheevo assemblages. The localities containing the Mezen Fauna are isolated geographically from the localities of other dinocephalian faunas and concentrated in the regions adjoining the Baltic Shield from the southeast (Fig. 4). Paleogeographically, this corresponds to the western[3] coast of the Kazanian and Early Tatarian lake-marine basin. All known localities containing the Mezen Fauna are of the same taphonomic pattern; therefore, they only slightly differ from each other in the composition of the oryctocenoses; the forms belonging to the subdominant block are numerous and relatively diverse, members of the dominant block are extremely scarce, and the aquatic block is not represented at all. A peculiar pattern of the Mezen Fauna indicates it was isolated from the Kazanian and Early Tatarian tetrapod faunas inhabiting the regions adjoining the Ural Mountains (Golubev, 1995b).

A g e. Late Kazanian and Early Tatarian.

R e f e r e n c e l o c a l i t y. Glyadnaya Shchelya (277).

O t h e r l o c a l i t i e s (Fig. 4). Belokure (244), Belyi Nos (447), Bereznik (432), Blizhnyaya Shchelya (246), Dorogaya Gora (276), Izba Rassolova (401), Izba Usoltseva (431), Karashchele (435), Kimzha (433), Kiselikha (278), Kozmogorodskoe (416), Krestovaya Shchelya (243), Leshukonskoe (434), Moroznitsa (44), Nisogora (292), Petrova Shchelya (245), Peza-1 (241), Shalomchataya (308), Shchelya Osipova (242), Smolenets (436), Soga-2 (440), Ust-Nyafta (415), Ust-Peza (414), and Ust-Vashka (403).

2.2. Ocher Assemblage

The dominant block is formed by eotheriodonts, including large phytophagous forms of the family Rhopalodontidae, large predatory forms of the superfamily Phthinosuchoidea (Eotitanosuchidae and Phthinosuchidae), and relatively infrequent primitive predatory dinocephalians (Titanosuchidae). Small members of the dominant block comprise numerous phytophagous captorhinomorphs (Bolosauridae), relatively infrequent phytophagous dromasaurs of the family Venyukoviidae (subfamily Venyukoviinae), and primitive predatory dinocephalians (Titanosuchidae). Members of the subdominant block are rather diverse and include widespread captorhinomorphs (Captorhinidae) and dissorophoidean batrachomorphs (Dissorophidae) and relatively infrequent nycteroleterin parareptiles (Rhipaeosauridae, Tokosauridae, and Nycteroleteridae), gephirostegids (Enosuchidae), eotheriodonts (?Burnetiidae), and discosauriscin parareptiles (Karpinskiosauridae). In the aquatic community, archegosauroideans (Archegosauridae and Melosauridae) predominate and discosauriscin parareptiles (Kotlassiidae) are relatively infrequent.

A g e. The terminal part of the Ufimian Stage to the Early Tatarian.

The assemblage is divided into two parts, the Golyusherma and Ocher subassemblages.

2.2.1. Golyusherma Subassemblage

(*Parabradysaurus silantjevi* Fauna)

Large members of the dominant block (Fig. 3) include primitive phytophagous rhopalodontids (*Parabradysaurus*) and predatory phthinosuchids (*Kamagorgon*). Small members of the dominant block are not numerous and belong to bolosaurids (*Timanosaurus*) and titanosuchids (*Microsyodon*). The subdominant block consists of captorhinids (*Gekatogomphius* and *Riabininus*) and isolated finds of enosuchids (*Nyctiboetus*), dissorophids (*?Alegeinosaurus*), rhipaeosaurids, and karpinskiosaurids. The aquatic block consists of widespread archegosaurids, including medium-sized platyoposaurins (*Platyoposaurus watsoni*), various melosaurids of the subfamily Melosaurinae (*Melosaurus* and *Koinia*), and kotlassiids of the subfamily Leptorophinae (*Biarmica*, *Leptoropha*, and *Phreatophasma*).[4]

A g e. The terminal part of the Ufimian to the early part of the Late Kazanian.

R e f e r e n c e l o c a l i t y. Golyusherma (29).

O t h e r l o c a l i t i e s (Fig. 4): Berezovye Polyanki (13), Bozhyudor (1), Charli (65), Village of Gorki (101), Kotlovka-1 (22), Mamadysh-2 (54), Mezhevaya (14), Santagulovskii Mine (49), Shikhovo-Chirki (79), Sidorovy Gory (6), Sterlitamak (287), Suroshnyi Ovrag (407), Ust-Koin (111), and Vyshka (21).

[3] Hereinafter, the modern directions of the cardinal points are used.

[4] The holotype of *Phreatophasma aenigmatum* (PIN, no. 294/24) is a femur from the Santagulovskii Mine. In the original description Efremov (1954) assigned this form to uncertain synapsids (theromorphs). However, this femur is most similar morphologically to the femurs of Late Tatarian kotlassiin parareptiles (*Kotlassia*), the closest relatives of leptorophins (Ivakhnenko *et al.*, 1997; Bulanov, 1999). The latter were widespread in the Golyusherma Fauna and were usually found in lagoon or delta deposits. In the Santagulovskii Mine locality, bone beds were discovered in Lower Kazanian copper brachiopod–bryozoan limestone (Efremov and Vyushkov, 1955). Thus, morphological, stratigraphical, and taphonomic data indicate that *Phreatophasma* should be assigned to leptorophin parareptiles.

2.2.2. Ocher Subassemblage

(*Estemmenosuchus uralensis* Fauna)

The dominant block (Fig. 3) is formed by large phytophagous rhopalodontids (*Estemmenosuchus*) and bolosaurids (*Davletkulia*) and predatory eotitanosuchids (*Biarmosuchus*). Small members of the dominant block are rather diverse and include bolosaurids (*Belebey*), rhopalodontids (*Rhopalodon* and *Phthinosaurus*), venyukoviins (*Otscheria* and *Venyukovia*), phthinosuchids (*Dinosaurus*), and titanosuchids (*Archaeosyodon*). The subdominant block of the community consists of dissorophids (*Iratusaurus*, *Kamacops*, and *Zygosaurus*), nycteroleterids (*Bashkyroleter*), rhipaeosaurids (*Rhipaeosaurus*), tokosaurids (*Tokosaurus*), enosuchids, and problematic burnetiids (*Biarmosuchoides*). The aquatic block includes numerous archegosaurids (*Collidosuchus*, *Bashkirosaurus*, and large platyoposaurins, such as *Platyoposaurus stuckenbergi*) and melosaurids (*Konzhukovia*, a member of the subfamily Tryphosuchinae). Reliable finds of leptorophins have not been registered. Possibly, skeletons of small parareptiles from the Klyuchevskoi Mine, usually referred to as *"Discosauriscus" netschajevi* (Ivakhnenko *et al.*, 1997) should be assigned to this group. However, these fossils could belong to larvae of other primitive parareptiles, rather diverse in the Ocher Fauna.

Age. The terminal part of the Late Kazanian to the early part of the Early Tatarian.

Reference locality. Ezhovo (2).

Other localities (Fig. 4). Akbatyrovskii Mine (20), Belebei (64), Bolshoi Kityak (10), Borisov (12), Dubovka-1 (174), Erzovka (4), Kamskie Polyany (18), Klyuchevskoi Mine-1 (97), Krymskii (8), Kuzminovskii Mine (16), Luzhkovo (3), Rozhdestvenskii Mine (17), Sarai-Gir (9), Sokol (5), and Yaman-Yushatyr (11).

2.3. Isheevo Assemblage

The dominant block consists of large dinocephalians, including phytophagous tapinocephalians of the family Ulemosauridae and predatory titanosuchians of the families Deuterosauridae and Anteosauridae. Small members of the dominant block include numerous predatory titanosuchian dinocephalians (Syodontidae), phytophagous dromasaurs of the family Venyukoviidae (subfamily Ulemicinae), the first predatory therocephalians (Pristerognathidae), and scarce phytophagous captorhinomorphs (Bolosauridae). The subdominant block is substantially reduced in comparison with the Ocher Fauna. It is formed by widespread gephirostegids (Enosuchidae) and extremely scarce rhopalodontoidean eotheriodonts (Microuraniidae). In the aquatic block, nycteroleterin parareptiles (Lanthanosuchidae) emerge; melosaurid archegosauroideans (Tryphosuchinae) still predominate, whereas leptorophin kotlassiids and archegosaurids disappear.

The Isheevo Assemblage is characterized by a substantial decrease in taxonomic diversity (at the family level and higher ranks) in comparison with the Ocher Assemblage. The diversity of edopiform batrachomorphs and parareptiles is abruptly reduced. The first group consists of melosaurids; the second, by widespread forms of the Lanthanosuchidae only. Eotheriodonts (represented by only one specimen of *Microurania*, family Microuraniidae) and captorhinomorphs (one specimen of bolosaurids) almost completely disappear, whereas dinocephalians reach the highest diversity.

Age. The later part of the Early Tatarian.

The assemblage is divided into two parts, Isheevo and Malaya Kinel subassemblages.

2.3.1. Isheevo Subassemblage

(*Titanophoneus potens* Fauna)

Large members of the dominant block (Fig. 3) include phytophagous ulemosaurids (*Ulemosaurus svijagensis*) and predatory anteosaurids (*Titanophoneus*). Small members of the dominant block include widespread syodontids (*Syodon efremovi*) and ulemicins (*Ulemica*), somewhat less numerous primitive pristerognathid therocephalians (*Porosteognathus*), and scarce bolosaurids (*Permotriturus*). The subdominant block consists of scarce enosuchids (*Enosuchus*). The aquatic block is formed by various tryphosuchins (*Tryphosuchus*, *Konzhukovia*, and *Uralosuchus*) and lanthanosuchids (*Lanthanosuchus* and *Chalcosaurus*).

Age. The later part of the Early Tatarian.

Reference locality. Isheevo (88).

Other localities (Fig. 5). Butlerovka (264), Dolinovka (142), Donguz-4 (74), Maiorskoe-1 (325), Malyi Uran (98), Novo-Nikolskoe-3 (93), Podgorodnyaya Pokrovka-1 (34), and Podgorodnyaya Pokrovka-2 (145).

2.3.2. Malaya Kinel Subassemblage

(*Deuterosaurus biarmicus* Fauna)

Large members of the dominant block (Fig. 3) include phytophagous ulemosaurids (*Ulemosaurus gigas*) and predatory deuterosaurids (Deuterosaurus). Small members of the dominant block are relatively diverse and include widespread syodontids (*Syodon gusevi*) and somewhat less numerous pristerognathids (*Porosteognathus*) and ulemicins (*Ulemica*). The subdominant block is formed by enosuchids (*Enosuchus*), isolated finds of microuraniid eotheriodonts (*Microurania*), and problematic anthracosauromorphs. The aquatic community consists of tryphosuchins only (*Tryphosuchus*).

Age. The later part of the Early Tatarian.

Reference locality Malaya Kinel (90).

Other localities (Fig. 5). Ibryaevo (288), Ivanovka-2 (87), Kichkass (89), Klyuchevskoi Mine-2

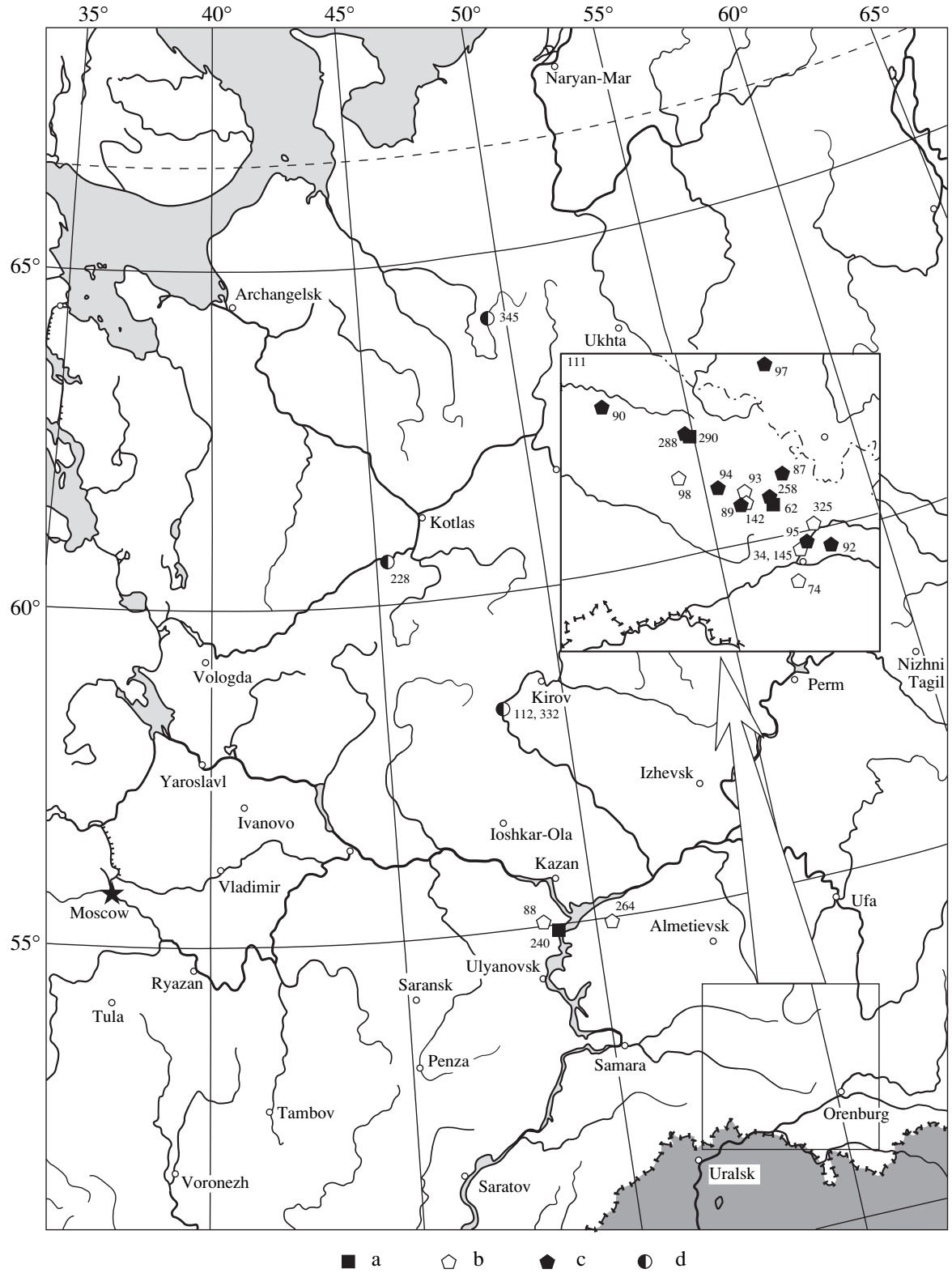

Fig. 5. Geographical position of the Upper Permian localities of terrestrial vertebrates: (a) Isheevo Assemblage, (b) Isheevo Subassemblage, (c) Malaya Kinel Subassemblage, and (d) Kotelnich Subassemblage. Localities: (34) Podgorodnyaya Pokrovka-1, (62) Dudki, (74) Donguz-4, (87) Ivanovka-2, (88) Isheevo, (89) Kichkass, (90) Malaya Kinel, (92) Nezhinka, (93) Novo-Nikolskoe-3, (94) Ozerki, (95) Tevkelev, (97) Klyuchevskoi Mine, (98) Malyi Uran, (112) Kotelnich, (142) Dolinovka, (145) Podgorodnyaya Pokrovka-2, (228) Poldarsa, (240) Monastyrskii Ovrag, (258) Staro-Myasnikovskii Mine, (264) Butlerovka, (288) Ibryaevo, (290) Uteevo, (325) Maiorskoe-1, (332) Port Kotelnich, and (345) Ust-Elva.

(97), Nezhinka (92), Ozerki (94), Staro-Myasnikovskii Mine (258), Tevkelev (95), and Zhaksy-Kargala.

The Isheevo and Malaya Kinel subassemblages are characterized by diametrically opposite faunal composition, i.e., the forms widespread in one subassemblage are rare or completely absent in the other (Fig. 3). This feature is possibly attributable to the fact that the subassemblages are taphonomically different parts of the same fauna and do not reflect the stages of evolution of the Permian tetrapod community. The hypothesis of a contemporary existence of the Isheevo and Malaya Kinel subassemblages offers a suitable explanation for numerous difficulties and contradictions concerned with the determination of the relative age of these subassemblages.

3. Theriodontian Superassemblage

The Theriodontian Superassemblage is characterized by widespread colosteiform batrachomorphs, large (pareiasaurins) and relatively small (discosauriscins) parareptiles, chroniosuchian anthracosauromorphs, various anomodonts (galeopid dromasaurs and dicynodonts), and theriodonts (gorgonopians, therocephalians, and cynodonts). The groups characteristic of the Early Permian are completely absent; however, the following taxa surviving till the Triassic appear: bystrowianid chroniosuchians, prolacertid and thecodont diapsids, dicynodonts, cynodonts, and procolophonid parareptiles.

The superassemblage is divided into two parts, the Sokolki and Vyazniki assemblages.

A g e. Late Tatarian.

The taxonomic composition of the Theriodontian Fauna is distinguished from that of the Dinocephalian Fauna by the high-rank taxa (higher than family rank). Only five common families have been revealed: Burnetiidae, Kotlassiidae, Nycteroleteridae, Tokosauridae, and Karpinskiosauridae. However, each (except for the Kotlassiidae) is widespread in one superassemblage and scarce in the other; the family Kotlassiidae is represented in the Theriodontian Fauna by the other subfamily (Kotlassiinae). In addition, in the Dinocephalian Fauna, these families are observed in the Ocher Assemblage only, whereas in the Isheevo Assemblage, they have not been found. As a result, the latter contrasts even more with the Kotelnich Fauna. Perhaps this is an artifact, i.e., these families may have existed but have not been discovered in the Isheevo Assemblage or it is real. In the latter case, all common families are immigrants from other regions of Eurasia, in particular, from the Baltic Region, i.e., the area which adjoined other regions of Eastern Europe only from the onset of the Late Tatarian when the isolation by the Kazanian–Early Tatarian lake-marine basin had disappeared (Golubev, 1995b).

The Early Theriodontian Fauna includes many elements widespread in the Gondwanan Fauna but not registered in the Dinocephalian Fauna of Eurasia: pareiasaurs, most theriodonts, galeopids, and dicynodonts. Throughout the entire Late Tatarian, the degree of provincialism of the Theriodontian Fauna increased until the onset of the Triassic when the faunal composition changed abruptly. This probably indicates the presence of a short-term contact between the tetrapod faunas of Gondwana and Eurasia just before the time of the Kotelnich Fauna (Ivakhnenko, 1994; Golubev, 1995a, 1998c; Kalandadze and Rautian, 1998b). In the Theriodontian Fauna, the Gondwanian elements form the dominant block (pareiasaurs, anomodonts, gorgonopians, and therocephalians) and a large part of the subdominant block (therocephalians and cynodonts). The forms of the aquatic fauna are probably local, i.e., originate from Eurasia (colosteiform batrachomorphs, chroniosuchians, and discosauriscins).

3.1. Sokolki Assemblage

Large members of the dominant block are phytophagous pareiasaurins (Bradysauridae and Pareiasauridae) and dicynodonts (Dicynodontidae), predatory theriodonts, including gorgonopians (Gorgonopidae and Inostranceviidae) and therocephalians (Annatherapsididae and Moschowhaitsiidae), and scarce relict eotheriodonts (Burnetiidae). Small members of the dominant block include phytophagous dromasaurs (Galeopidae) and dicynodonts (Dicynodontidae) and predatory therocephalians (Scylacosauridae and Scaloposauridae). The subdominant block consists of various parareptiles, including discosauriscins (Karpinskiosauridae), nycteroleterins (Nycteroleteridae and Tokosauridae), and procolophonids (Procolophonidae); scaloposaurian therocephalians (Ictidosuchidae); cynodonts (Dviniidae, Procynosuchidae, and Galesauridae); and prolacertid diapsids (Protorosauridae). The aquatic community is characterized by widespread brachyopoidean bathrachomorphs (Dvinosauridae), chroniosuchian anthracosauromorphs (Chroniosuchidae), and kotlassiid discosauriscins (Kotlassiinae).

A g e. The first, larger part of the Late Tatarian (Severodvinian and the first, larger part of the Vyatkian).

The assemblage is divided into three parts, Kotelnich, Ilinskoe, and Sokolki subassemblages.

3.1.1. Kotelnich Subassemblag

(*Deltavjatia vjatkensis* Fauna)

The subassemblage is characterized by a relatively primitive faunal composition in comparison with the other subassemblages of the Sokolki Assemblage (Fig. 3). Primitive phytophagous bradysaurid pareiasaurins (*Deltavjatia*) and dicynodontids (*Tropidostoma*) are numerous and relatively small in size. Large predators of the dominant block, gorgonopids (*Viatkogorgon*) and moschowhaitsiids (*Viatkosuchus*), are also relatively small and comparable in sizes to small predators

of the dominant block represented by scaloposaurids (*Scalopodon* and *Scalopodontes*) and scylacosaurids (*Kotelcephalon*). Small phytophagous members of the dominant block include numerous galeopids (*Suminia*). In the subdominant block, ictidosuchids (*Karenites*, *Perplexisaurus*, and *Chlynovia*), relict nycteroleterids (*Emeroleter*), and problematic diapsids are widespread. The aquatic block is formed by primitive chroniosuchids (*Suchonica*) and kotlassiins (*Raphaniscus*). Batrachomorphs have not been found; they were probably represented by dvinosaurid brachyopoideans, as in the other Theriodontian Faunas.

The subassemblage strongly differs from the Isheevo Subassemblage in the faunal composition; common families are absent. Out of ten families of the subassemblage, only two (Nycteroleteridae and Kotlassiidae) occur in earlier assemblages (Ocher and Mezen).

Age. The early part of the Late Tatarian (Early Severodvinian).

Reference locality Kotelnich (112).

Other localities (Fig. 5). Poldarsa (228), Port Kotelnich (332), and Ust-Elva (345).

3.1.2. Ilinskoe Subassemblage

(*Proelginia permiana* Fauna)

Large members of the dominant block (Fig. 3) include widespread phytophagous pareiasaurids, *Proelginia* (probably, relatively more aquatic descendants of bradysaurids of the Kotelnich Fauna), and less numerous (because of taphonomic conditions, since only a few localities containing members of the terrestrial fauna of the Ilinskoe Subassemblage have been found) dicynodonts (*Oudenodon*), as well as predatory burnetiids (*Proburnetia* and *Niuksenitia*) and gorgonopids (*Sauroctonus* and *Suchogorgon*). Small members of the dominant block include phytophagous galeopids (*Suminia*) and scarce predatory scylacosaurids (*Scylacosuchus*). Members of the subdominant block are not numerous and consist of cynodonts (first emerging in the Late Ilinskoe Fauna), scarce procolophons (*Microphon*), karpinskiosaurids (*Karpinskiosaurus ultimus*), and protorosaurid diapsids (*Eorasaurus*). In the aquatic block, chroniosuchids (*Chroniosaurus*), kotlassiins (*Raphaniscus* and *Isasaurus*), and dvinosaurids (*Dvinosaurus primus*) predominate.

Age. The middle part of the Late Tatarian (the later part of the Severodvinian).

Reference locality Semin Ovrag (Ilinskoe) (114).

Other localities (Fig. 6). Agafonovo (333), Babintsevo (139), Donguz-6 (117), Gorkovskii Gidrouzel (312), Igmas (231), Kochevala-1 (154), Kochevala-2 (230), Maryushkina Sluda-C (206), Mikulino (202), Mutovino (109), Navoloki (199), Poteryakha-1 (220), Poteryakha-2 (233), Preobrazhenka (337), Sokolya Gora (302), Uste Strelny (113), and Vyazovka-5 (81).

3.1.3. Sokolki Subassemblage

(*Scutosaurus karpinskii* Fauna)

In the dominant block (Fig. 3), the composition of large predators changes, i.e., annatherapsidid therocephalians (*Annatherapsidus*) and specialized inostranceviid gorgonopians (*Inostrancevia*) appear; the number and diversity of gorgonopids is strongly reduced (*Pravoslavlevia*, only one specimen). Large phytophagous animals are still represented by pareiasaurids (*Scutosaurus*) and dicynodontids (*Dicynodon*). The dominant block lacks undoubted small members; only small phytophagous dicynodontids (*Elph*) and small predatory annatherapsidids (*Chthonosaurus*) can be tentatively assigned to this group. The subdominant block consists of widespread cynodonts, including dviniids (*Dvinia*), procynosuchids (*Uralocynodon*), and galesaurids (*Nanocynodon*); karpinskiosaurids (*Karpinskiosaurus ultimus* and *K. secundus*); relict tokosaurids; and substantially less numerous procolophons (*Suchonosaurus*). In the aquatic community, chroniosuchids (*Jarilinus* and *Chroniosuchus*), dvinosaurids (*Dvinosaurus primus*), and kotlassiins (*Raphaniscus* and *Kotlassia*) are still widespread.

Age. The later part of the Late Tatarian (the first larger part of the Vyatkian).

Reference locality Sokolki (124).

Other localities (Fig. 6). Averinskoe (300), Adamovka (133), Aristovo (126), Blumental-3 (134), Boevoi (323), Boltinskaya (129), Bolshoe Linovo (304), Gorki City-1 (130), Gorokhovets (450), Kadyevskaya (203), Klimovo-1 (205), Klyuchevka (72), Klyuchevoi Ovrag (223), Krasavino (127), Obirkovo (232), Orletsy (334), Pokrovka (293), Popolzukha (234), Pronkino (82), Salarevo (219), Savvatii (128), Strizhenskaya Gora (214), Titova Gora (215), Tonshaevo (297), Vomba-Kassy (296), Vyazovka-1 (137), Vyazovka-2 (324), Zavrazhe (125), and Zubochistenka-2 (321).

3.2. Vyazniki Assemblage

(*Archosaurus rossicus* Fauna)

The assemblage shows the onset of the destruction of the Paleozoic type of terrestrial vertebrate community (Fig. 3). In the dominant block, large predatory gorgonopians and annatherapsidids disappear and thecodonts of the family Proterosuchidae (*Archosaurus*) arise. Large predators also consist of various therocephalians, including the Whaitsiidae and Moschowhaitsiidae (*Moschowhaitsia*). Phytophagous dicynodonts (*Dicynodon*) are rather numerous, but pareiasaurs are absent. Small members of the dominant block are more diverse than in the Sokolki Fauna and include scarce phytophagous nycteroleterid parareptiles of the family Elginiidae (*Elginia*), predatory chroniosuchians of the family Bystrowianidae (*Bystrowiana*), and therocephalians of the family Nanictidopidae (*Hexacynodon*). The subdominant block consists of microsaurs, discosauriscin parareptiles of the family

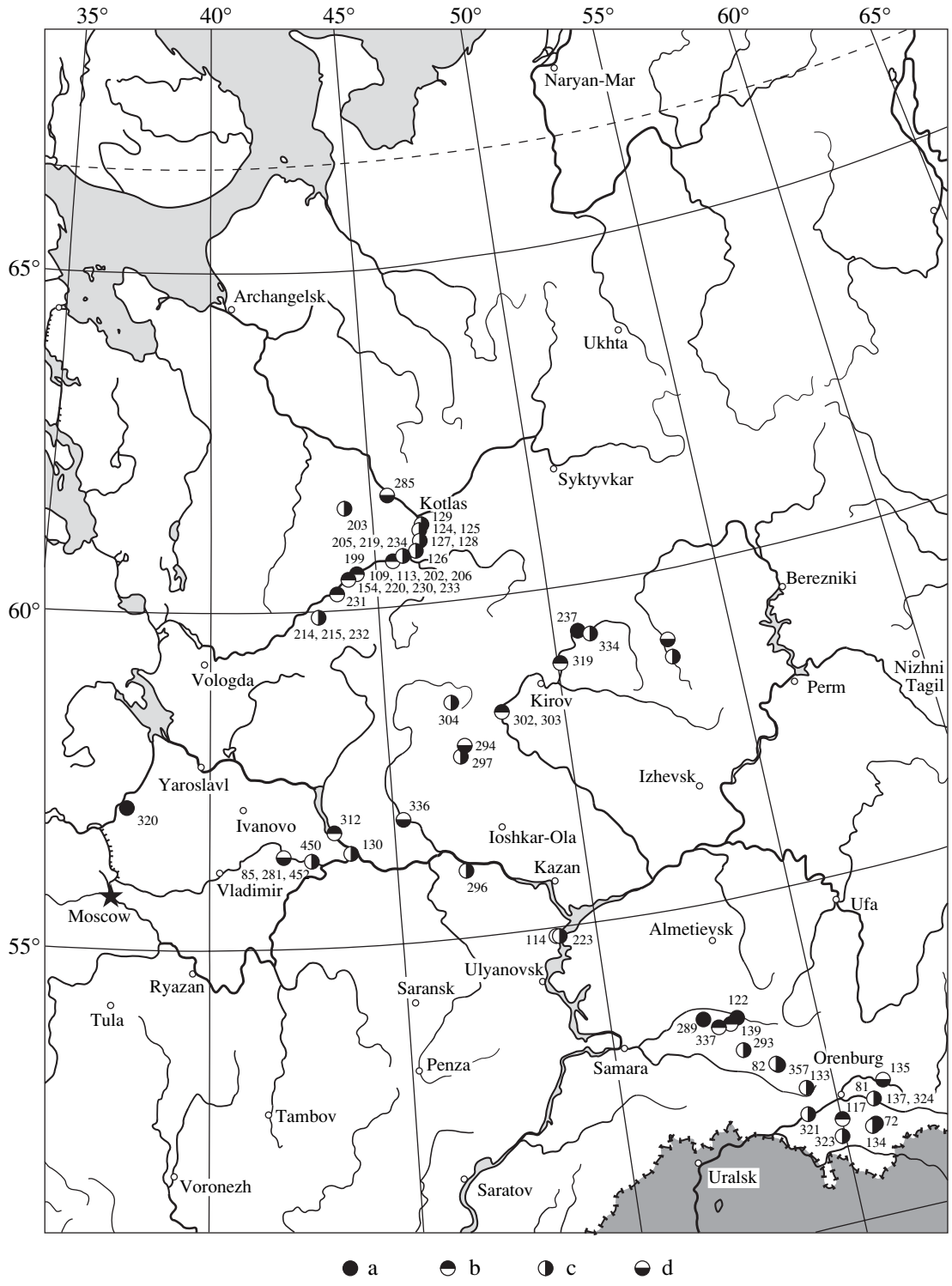

Fig. 6. Geographical position of the Upper Permian localities of terrestrial vertebrates: (a) Sokolki Assemblage, (b) Ilinskoe Subassemblage, (c) Sokolki Subassemblage, and (d) Vyazniki Assemblage. Localities: (72) Klyuchevka, (81) Vyazovka-5, (82) Pronkino, (85) Vyazniki-1, (109) Mutovino, (113) Uste Strelny, (114) Semin Ovrag, (117) Donguz-6, (122) Vozdvizhenka, (124) Sokolki, (125) Zavrazhe, (126) Aristovo, (127) Krasavino, (128) Savvatii, (129) Boltinskaya, (130) Gorki City-1, (133) Adamovka, (134) Blumental-3, (135) Sambullak, (137) Vyazovka-1, (139) Babintsevo, (154) Kochevala-1, (199) Navoloki, (202) Mikulino, (203) Kadyevskaya, (205) Klimovo-1, (206) Maryushkina Sluda-C, (214) Strizhenskaya Gora, (215) Titova Gora, (219) Salarevo, (220) Poteryakha-1, (223) Klyuchevoi Ovrag, (230) Kochevala-2, (231) Igmas, (232) Obirkovo, (233) Poteryakha-2, (234) Popolzukha, (237) Mulino, (281) Vyazniki-2, (285) Rasha, (289) Koptyazhevo, (293) Pokrovka, (294) Purly, (296) Vomba-Kassy, (297) Tonshaevo, (300) Averinskoe, (302) Sokolya Gora, (304) Bolshoe Linovo, (312) Gorkovskii Gidrouzel, (319) Berezhane, (320) Kalyazin, (321) Zubochistenka-2, (323) Boevoi, (324) Vyazovka-2, (333) Agafonovo, (334) Orletsy, (335) Shabarshata, (336) Voskresenskoe-2, (337) Preobrazhenka, (357) Roptanka, (450) Gorokhovets, and (452) Bykovka.

Karpinskiosauridae (*Karpinskiosaurus*), and relatively infrequent small therocephalians of the family Scaloposauridae (*Malasaurus*). In the aquatic block, chroniosuchian anthracosauromorphs of the family Chroniosuchidae (*Uralerpeton*) and brachyopoidean batrachomorphs of the family Dvinosauridae (*Dvinosaurus egregius* and *D. purlensis*) are still widespread; however, kotlassiid discosauriscins disappear.

Age. The terminal part of the Late Tatarian (terminal part of the Vyatkian).

Reference locality. Vyazniki-2 (281).

Other localities (Fig. 6). Berezhane (319), Bykovka (452), Purly (294), Rasha (285), Sambullak (135), Shabarshata (335), Voskresenskoe-2-A (336), Voskresenskoe-2-B (336), and Vyazniki-1 (85).

EARLY TRIASSIC

1. Proterosuchian Superassemblage

(*Benthosuchus-Wetlugasaurus* and *Parotosuchus* Fauna)

The Early Triassic Proterosuchian Fauna of Eastern Europe is characterized (Fig. 3) by widespread batrachomorphs, including colosteiforms, zatracheiforms, and trematosaurian edopiforms; procolophonid parareptiles; bystrowianid chroniosuchian anthracosauromorphs; and various diapsids, including eolacertids, rhynchocephalids, prolacertids, and thecodonts. Therapsids are extremely scarce; only isolated finds of lystrosaurid dicynodonts, scaloposaurian and scalopocynodont therocephalians, and galesaurid cynodonts occur.

The Proterosuchian Fauna usually lacks distinct dominant block (Sennikov, 1995; Golubev, 1998c). Only the Spasskoe Assemblage (*Tupilakosaurus* Fauna) probably includes small members of this block of evidently Eurasian origin, dicynodonts (Lystrosauridae) and thecodonts (Proterosuchidae). In other Proterosuchian assemblages, only large thecodonts (proterosuchids, rauisuchids, and erythrosuchids) can be tentatively referred to as the dominant block; they were probably the consumers of the higher orders in the terrestrial and aquatic blocks of the community.

Similar to the dominant block, the subdominant block of the Proterosuchian Fauna is formed by Eurasian groups, including bystrowianids, procolophonids, diapsids, therocephalians, and cynodonts. Only the aquatic community includes Gondwanan elements, i.e., trematosaurian (capitosauroideans, trematosauroideans, and lydekkerinids) and rhytidosteid batrachomorphs.

REFERENCES

Bulanov, V.V., Seymouriamorphs from the Late Permian of Eastern Europe, *Cand. Sci. (Biol.) Dissertation*, Moscow: Paleontol. Inst. Ross. Akad. Nauk, 1999.

Efremov, I.A., On the Stratigraphic Division of the Continental Permian and Triassic of the USSR Based on the Fauna of Terrestrial Vertebrates, *Dokl. Akad. Nauk SSSR, Ser. Geol.* (Moscow), 1937, vol. 16, no. 2, pp. 125–132.

Efremov, I.A., On the Development of the Permian Tetrapod Fauna of the USSR and Division of the Continental Permian into Stratigraphic Zones, *Izv. Akad. Nauk SSSR, Ser. Biol.* (Moscow), 1939, no. 2, pp. 272–289.

Efremov, I.A., Kurze Übersicht über die Formen der Perm- und Trias-Tetrapoden-Fauna der UdSSR, *Zbl. Mineral., Geol., Palaeontol. Abt. B.*, 1940, no. 12, pp. 372–383.

Efremov, I.A., A Brief Review of the Fauna of Permian and Triassic Tetrapoda from the USSR, *Sovet. Geol.*, 1941, no. 5, pp. 96–103.

Efremov, I.A., On the Questions of Stratigraphy of the Upper Permian Deposits in the USSR Based on Vertebrates, *Izv. Akad. Nauk USSR, Ser. Geol.* (Moscow), 1944, no. 6, pp. 52–60.

Efremov, I.A., On the Stratigraphy of Permian Red Beds of the USSR Based on Terrestrial Vertebrates, *Izv. Akad. Nauk USSR, Ser. Geol.* (Moscow), 1952, no. 6, pp. 49–75.

Efremov, I.A., The Fauna of Terrestrial Vertebrates in the Permian Copper Sandstones of the Western Fore-Urals, in *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1954, vol. 54, pp. 1–416.

Efremov, I.A. and Vyushkov, B.P., The Catalogue of the Localities of Permian and Triassic Terrestrial Vertebrates from the Territory of the USSR, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1955, vol. 46, pp. 1–185.

Golubev, V.K., The Main Stages of the Late Permian History of Development of the Terrestrial Vertebrate Fauna from Eastern Europe, *Paleontologiya i stratigrafiya kontinental'nykh otlozhenii permi i triasa Severnoi Evrazii. Tezisy Soveshchaniya* (Paleontology and Stratigraphy of Continental Deposits of the Permian and Triassic of Northern Eurasia: Abstr. Conf.), Moscow: Paleontol. Inst. Ross. Akad. Nauk, 1995a, pp. 6–7.

Golubev, V.K., The Mezen Fauna of Terrestrial Vertebrates from the Late Permian of Europe, *Paleontologiya i stratigrafiya kontinental'nykh otlozhenii permi i triasa Severnoi Evrazii. Tezisy Soveshchaniya* (Paleontology and Stratigraphy of Continental Deposits of the Permian and Triassic of Northern Eurasia: Thes. Conf.), Moscow: Paleontol. Inst. Ross. Akad. Nauk, 1995b, pp. 7–8.

Golubev, V.K., Crucial Events in the Evolution of the Tetrapod Community in the Permian of Eastern Europe, *Evolyutsiya ekosistem. Mezhdunarodnyi simpozium* (Ecosystem Evolution: Int. Conf.), Moscow: Paleontol. Inst. Ross. Akad. Nauk, 1995c, pp. 28–29.

Golubev, V.K., The Terrestrial Vertebrates, in *Stratotipy i opornye razrezy verkhnei permi Povolzh'ya i Prikam'ya* (The Stratotypes and Reference Sections of the Upper Permian of the Volga and Kama Regions), Kazan: Ekotsentr, 1996, pp. 381–389.

Golubev, V.K., Permian Chroniosuchians and Biostratigraphy of the Upper Tatarian Deposits of European Russia Based on Terrestrial Vertebrates, *Cand. Sci. (Geol.-Miner.) Dissertation*, Moscow: Paleontol. Inst. Ross. Akad. Nauk, 1997.

Golubev, V.K., Narrow-armored Chroniosuchians (Amphibian, Anthracosauromorpha) from the Late Permian of Eastern Europe, *Paleontol. Zh.*, 1998a, no. 3, pp. 64–73.

Golubev, V.K., A Revision of the Late Permian Chroniosuchians (Amphibia, Anthracosauromorpha) from Eastern Europe, *Paleontol. Zh.* (Moscow), 1998b, no. 4, pp. 68–77.

Golubev, V.K., The Spasskoe Assemblage of Tetrapods from the Permian–Triassic Boundary of Eastern Europe, *Geologiya i geoekologiya Urala i Povolzh'ya. Tezisy dokladov mezhvedomstvennoi nauchnoi konferentsii, posvyashchennoi semidesyatiletiyu so dnya rozhdeniya i pamyati V.A. Garyainova* (Geology and Geoecology of the Ural Mountains and the Volga Region: Abstr. Conf. Devoted to Seventieth Anniversary and Memory of V.A. Garyainova), Saratov: Kolledzh, 1998c, pp. 25–26.

Golubev, V.K., A Correlation between the Upper Permian Deposits of European Russia and the Tethys, *Verkhnepermskie stratotipy Povolzh'ya. Mezhdunarodnyi simpozium* (The Upper Permian Stratotypes of the Volga Region: Int. Conf.), Kazan: Master Lain, 1998d, pp. 56–57.

Golubev, V.K., A New Narrow-armored Chroniosuchian (Amphibia, Anthracosauromorpha) from the Upper Permian of Eastern Europe, *Paleontol. Zh.*, 1999, no. 2, pp. 43–50.

Gubin, Yu.M., New Permian Dissorophids from the Fore-Urals, *Paleontol. Zh.*, 1980, no. 2, pp. 82–90.

Gubin, Yu.M., The First Eryopids from the Permian of the East European Platform, *Paleontol. Zh.* (Moscow), 1983, no. 4, pp. 110–115.

Gubin, Yu.M., The First Member of the Anthracosaurs from the Permian of the East European Platform, *Paleontol. Zh.*, 1985, no. 3, pp. 118–122.

Ivakhnenko, M.F., Elements of the Early Permian Tetrapod Faunal Assemblages of Eastern Europe, *Paleontol. Zh.*, 1990a, no. 2, pp. 102–111.

Ivakhnenko, M.F., The Late Paleozoic Faunal Assemblage of Tetrapods from the Deposits of the Mezen Basin, *Paleontol. Zh.*, 1990b, no. 4, pp. 81–90.

Ivakhnenko, M.F., The Faunal Assemblages of Tetrapods from the Late Permian of Eastern Europe, *Byull. Mosk. O-va. Ispyt. Prir., Otd. Geol.*, 1990c, vol. 65, no. 6, pp. 55–66.

Ivakhnenko, M.F., The Late Permian Faunal Assemblages of Tetrapods from Eastern Europe and Their South Gondwanian Analogues, in *Paleontologiya i stratigrafiya kontinental'nykh otlozhenii permi i triasa Severnoi Evrazii* (Paleontology and Stratigraphy of the Continental Deposits of the Permian and Triassic of Northern Eurasia), Moscow: Paleontol. Inst. Ross. Akad. Nauk, 1992, pp. 6–7.

Ivakhnenko, M.F., A New Late Permian Dromasaurian (Anomodontia) from Eastern Europe, *Paleontol. Zh.*, 1994, no. 1, pp. 76–83.

Ivakhnenko, M.F., Primitive Dinocephalians, Titanosuchians, from the Late Permian of Eastern Europe, *Paleontol. Zh.* , 1995a, no. 3, pp. 98–105.

Ivakhnenko, M.F., New Primitive Therapsids from the Permian of Eastern Europe, *Paleontol. Zh.*, 1995b, no. 4, pp. 110–119.

Ivakhnenko, M.F., Primitive Anomodonts, Venyukovias, from the Late Permian of Eastern Europe, *Paleontol. Zh.*, 1996, no. 4, pp. 77–84.

Ivakhnenko, M.F., Golubev, V.K., Gubin, Yu.M., *et al.*, Permian and Triassic Tetrapods of Eastern Europe, *Tr. Paleontol. Inst. Ross. Akad. Nauk*, 1997, vol. 268, pp. 1–216.

Kalandadze, N.N., Ochev, V.G., Tatarinov, L.P., *et al.*, The catalogue of Permian and Triassic Tetrapods of the USSR, in *Verkhnepaleozoiskie i mezozoiskie zemnovodnye i presmykayushchiesya SSSR* (Upper Paleozoic and Mesozoic Amphibians and Reptiles of the USSR), Moscow: Nauka, 1968, pp. 72–91.

Kalandadze, N.N. and Rautian, A.S., On the Historical Zoogeography of Terrestrial Tetrapods of the Terminal Part of the Paleozoic and the Beginning of the Mesozoic, in *Paleontologiya. Stratigrafiya: Mezhdunarodnyi geologicheskii congress. XXVI sessiya. Doklady sovetskikh geologov* (XXVI Sess., Int. Geol. Congr.: Paleontol. and Stratigr.: Rep. Sov. Geologists), Moscow: Nauka, 1980, pp. 93–102.

Kalandadze, N.N. and Rautian, A.S., The Role of Central Asia in the Zoogeographical History of the Mesozoic, in *Tr. Sovm. Sovet.-Mongol. Paleontol. Eksped.* (Moscow), 1983, vol. 24, pp. 6–44.

Kalandadze, N.N. and Rautian, A.S., Commented Geochronological Schedule (Calendar) of the Major Events in the Community Phylogeny (Taxocene) of Terrestrial Vertebrates: Part III, in *Ekosistemnye perestroiki i evolyutsiya biosfery* (Ecosystem Reorganization and Biosphere Evolution), Moscow: Paleontol. Inst. Ross. Akad. Nauk, 1998a, vol. 3, pp. 38–41.

Kalandadze, N.N. and Rautian, A.S., Commented Geochronological Schedule (Calendar) of the Major Events in the Community Phylogeny (Taxocene) of Terrestrial Vertebrates: Part IV, in *Ekosistemnye perestroiki i evolyutsiya biosfery* (Ecosystem Reorganization and Biosphere Evolution), Moscow: Paleontol. Inst. Ross. Akad. Nauk, 1998b, vol. 3, pp. 42–46.

Ochev, V.G., The Landmarks in the History of Late Permian and Triassic Tetrapods of the European Part of the USSR, in *Voprosy stratigrafii i paleontologii* (Questions of Stratigraphy and Paleontology), Saratov: Saratov Gos. Univ., 1976, vol. 2, pp. 44–49.

Olson, E.C., Community Evolution and the Origin of Mammals, *Ecology*, 1966, vol. 47, no. 2, pp. 291–302.

Sennikov, A.G., Early Thecodonts of Eastern Europe, in *Tr. Paleontol. Inst. Ross. Akad. Nauk*, 1995, vol. 263, pp. 1–141.

Tchudinov, P.K., On the Stratigraphic Distribution of Permian Vertebrates in the East of the European Part of the USSR, in *Voprosy geologii Yuzhnogo Urala i Povolzh'ya* (Questions on the Geology of the Southern Ural and Volga Region), Saratov: Saratov Gos. Univ., 1969, vol. 6, part 1, pp. 96–105.

Tchudinov, P.K., Early Therapsids, in *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1983, vol. 202, pp. 1–230.

Tchudinov, P.K., Terrestrial Vertebrates and the Division of the Upper Permian into Stages, in *Materialy po geologii vostoka Russkoi platformy* (Material on the Geology of the Eastern Part of the Russian Platform), Kazan: Kazan Gos. Univ., 1987, pp. 54–73.