

PERMIAN AND TRIASSIC CHRONOSUCHIANS AND BIOSTRATIGRAPHY OF THE UPPER TATARIAN DEPOSITS OF EASTERN EUROPE BY TETRAPODS

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Chapter 5

THE STRATIGRAPHIC DISTRIBUTION OF REMAINS OF LATE TATARIAN TETRAPODS

The scheme of faunal assemblages of Late Permian terrestrial vertebrates, considered in the previous chapter, and the sequence of changes are mainly based on general ideas about the evolution of different levels of Late Permian tetrapod faunas. Since the majority of ranges of [stratigraphic] complexes overlap, the evolutionary levels of complexes may indicate their relative ages: more primitive complexes are more ancient. However, this assertion certainly requires further, more rigorous studies.

The phylogenetically reconstructed sequence of Permian tetrapod faunas is as follows (see Fig. 20): Inta [Intinskiy] Complex -> Golyusherma [Golyushermkiy] Subcomplex -> Ocher [Ocherskiy] Subcomplex -> Isheevo [Isheevskiy] Complex -> Kotel'nich [Kotel'nichskiy] Subcomplex -> Il'inskoye [Il'inskiy] Subkomplex -> Sokolki [Sokolkovskiy] Subcomplex -> Vyazniki [Vyaznikovskiy] Complex. The truth of this reconstruction can be confirmed by the coincidence of the phylogenetic sequence of complexes with the stratigraphic sequence characterizing their deposits. For the Eryopid and Dinocephalian Supercomplexes, the general form is shown in several studies: Golubev, 1992a, b, 1995b, d, 1996a; Gomankov et al, 1993; Shelekhov & Golubev, 1993a, b, 1995. In this chapter we detail the stratigraphic evidence that confirms the reconstructed phylogenetic sequence of complexes of the Theriodont Supercomplex.

To determine the relative stratigraphic position of localities of the Eryopid and Dinocephalian faunas, we used different stratigraphic (litho-, bio-, cyclostratigraphic) methods. This is a result of the sporadic distribution of remains of tetrapods in Permian sediments, and we are not currently aware of any section that produces fossils of terrestrial vertebrates at different stratigraphic levels, that are characteristic of different faunal complexes of the Eryopid and Dinocephalian faunas. The Theriodont Supercomplex in this regard is an exception, because such sections are known. Such sections of the Upper Tatarian Substage occur on the Vyatka River near the town of Kotel'nich and in the basins of the Sukhona, Malaya Severnaya Dvina River, and the North Dvina.

UPPER TATARIAN DEPOSITS AT KOTEL'NICH (VYATKA RIVER)

On the right bank of the Vyatka River, over 24 km downstream from the town of Kotel'nich, there is a chain of exposures up to 35 m high, showing sediments of the middle part of the Tatarian Stage. These deposits are known in the first place as a locality that uniquely

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preserves the fossils of terrestrial vertebrates, the bulk of which are bradysaurid pareiasaurs. In sections of the Tatarian Stage, the area shows the following layers, from the bottom upwards (see Fig. 35) (description according to V. M. Ivakhnenko).

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1. Siltstones reddish-brown, cream and red with spots, bands and lenses of light-blue and greenish-blue varieties, whose role increases up the section.

In the lower, mostly reddish parts of the packet, the thickness does not exceed 2-2.5 m, marked by numerous small calcareous concretions. In the middle parts (2-3 m thick) lenses of sandy clay-marl rocks are observed, in which are the remains of terrestrial vertebrates. Remains of tetrapods are largely intact skeletons. There are clusters and complexes of well preserved bones. The bone is red-brown in colour.

At the level of the bone-bearing layer at the south-western extremity of the locality, low-thickness (0.6-0.8 m), asymmetrical lenses of grey-coloured clay are observed, with a sharp right, south-western edge, and a maximum density of bones at a site located away from the centre on the left of the flat edge. The fossil remains are chocolate-black in colour, excellently preserved, and with an internal calcite filling.

In the upper parts of the variegated bundles are rare inclusions of small crystals of authigenic calcite.

The apparent thickness of the layer ranges from 3 m in the south-west to 7.4 m in the central location.

2. Sands of blue, light blue, fine-grained, quartz. Nature of contact with the underlying layer concordant. Thickness up to 0.7 m.

3. Sands of red, medium-grained, quartz-feldspar (quartz content of up to 60%, feldspars up to 35%, a small admixture of clay and clay-carbonate aggregates). The shape of the grains is rounded, at least subrounded, quartz grain surface is smooth, but uneven, with a shiny thin film of iron hydroxide. In the interior of the sandstone, there are from two to six bands of clay forming impermeable surfaces, that can be traced over considerable distances as dark moist subparallel bands, sometimes approaching or merging. For a typical medium-sized sandstone, multidirectional cross bedding and bedding in the form of lenticular bodies extend for up to 1.4 km (400 m above the village Mukha and 940 m below the village Zemstvo) and with a maximum thickness of up to 16 m.

4. Sands of blue, light blue, fine-grained sand, similar to sands of layer 2. Thickness up to 0.4 m.

5. Sands of light brown, polymictic, micaceous, with a smooth transition from fine-grained character in the lower part to medium in the upper section. Thickness up to 4.5 m. Sands form the base of the lens, which is a [channel] fill from an ancient river downcutting (Khutor [one-house village] Chizhi). The upper part of the lens is composed of grey clay, platy, comminuted, with an abundance of plant remains and dispersed organic matter, representing an origin as an oxbow. In this part of the lens are found the remains of the fishes *Platysomus biarmicus* Eichwald, *Toyemia tverdochlebovae* Minich, *Amblypterina* sp., *Watsonichthys* sp. Crossopterygii fam. indet. (Esin 1995; Esin, Mashin, 1996), miospores and plant remains of *Algites* sp. AVG-1, *Phyllothea* aff. *turnaensis*, *Paracalamites* sp., *Pecopteris* sp. AVG-1, *Peltaspermopsis* (?) sp., *Permothea sardykenense* Zalessky, *Alicospermum* sp., *Tatarina conspicua* Meyen, *Pursongia belousovae* (Radczenko) Gomankov et Meyen, *Phylladoderma (Aequistomia)* sp. indet., *Geinitzia* sp. (Gomankov, 1996, 1997). Thickness up to 4.5 m.

6. Interbedded marls, clays, silts of red, mottled colour, with an abundance of small calcareous concretions. Thickness ranges from 13.8 m in the north-east to 1.9 m at the southwestern end of the locality.

7. Canary-yellow, fine-grained sands at the bottom, and brownish-red, medium-grained in upper parts of the section, polymictic, micaceous. In the sands are observed lenses of conglomerate consisting of clay-carbonate pebbles, cemented by dense sandstone, and lenses of

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very dense brown polymictic fine-grained sandstone with calcite cement. Here are found the abraded fossil remains of tetrapods of light grey-yellowish colours in the form of scattered bones and articulated parts of skeletons. This layer consists of a series of deep lenses, of

which the most famous are the "Sokol'ya Gora" near the village Boroviki, and Agafonovo, near the village Agathon. The depth of downcutting of the lenses is up to 16 m.

8. Clay red-coloured, variegated, overlapping the sandstone layer 7 lenses "Agafonovo". The apparent thickness is 0.5 m.

Terrestrial vertebrate remains of the Kotel'nich Subcomplex, *Emeroleter levis*, *Deltavjatia vjatkensis*, *Karenites ornamentatus*, *Perplexisaurus foveatus*, *Suminia getmanovi*,

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Viatkosauchus sumini, *Viatkogorgon ivakhnenkoi*, Scylacosauridae gen. indet., Scaloposauridae gen. indet., are met here at the base of the section in the thickness of the red marl and siltstone of bed 1 (locality Kotel'nich).

Remains of primitive toothed dicynodonts close to *Tropidostoma* and the pareiasaur *Deltavjatia* cf. *vjatkensis*, were found at the southern outskirts of the town of Kotel'nich (locality Port Kotel'nich) and, based on unconfirmed reports from different researchers, were confined to the bottom parts of bed 6. The primitive appearance of this fauna suggests this locality should be included in the Kotel'nich Subcomplex.

At the top of the section, in sand lenses at Sokol'ya Gora and Agafonovo (bed 7), are met fossils of the tetrapods of the Il'inskoye Subcomplex, *Chroniosaurus levis*, *Proelginia* cf. *permiana*, *Proburnetia viatkensis*, *Dvinosaurus primus*.

Thus, the distribution of tetrapod remains in the section of the Upper Tatarian

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Substage in the Kotel'nich region indicates that the Kotel'nich Subcomplex is more ancient than the Il'inskoye, as suggested above.

The question of the stratigraphic position of the bone-rich layers so far described remains unresolved. Study of the Kotel'nich pareiasaurs led A.P. Hartmann-Weinberg (Hartmann-Weinberg, 1937, 1938) to conclude that these forms are more primitive in comparison with the Middle Volga (Semin ravine, Klyuchevoy ravine) and Severodvinian (Sokolki, Zavrazh'e) pareiasaurs. On this basis, he considered the Permian deposits in the Kotel'nich region as the lowest layers of sediment with a pareiasaur fauna (i.e. the lowest part of the Upper Tatarian in the modern sense). I.A. Efremov (1939, 1941, 1944) was of the same opinion. Subsequently, when the deposits with pareiasaur faunas of Eastern Europe have been allocated to the upper Tatarian Substage in the Severodvinina (lower) and Vyatkian (upper) horizons, the Kotel'nich locality is usually attributed to the Severodvinian Horizont, but at different levels (V'yushkov, 1950, 1953; Ignat'ev, 1962; Tchudinov, 1965; Ochev, 1966a; Chudinov, 1969, 1983, Strok, 1987; Tverdokhlebova et al., 1989; Ivakhnenko, 1992; Minikh, 1992; Esin, 1995; Shelekhova & Golubev, 1995; Golubev, 1996a; Goman'kov, 1996). Correlation of the Kotel'nich section with strata of the Severodvinian Horizont of the Sukhona River will be considered below.

UPPER TATARIAN SUBSTAGE OF THE RIVERS SUKHONA, MALAYA SEVERNAYA DVINA AND SEVERNAYA DVINA

Among the sections of the terminal Permian of the Russian Platform, for exposure and richness in fossils, a detailed study of the combination of Tatarian sections on the rivers Sukhona, Malaya Severnaya [Little North] Dvina and the Severnaya [=North] Dvina is unique (Fig. 27). A high (up to 55 m) outcrop stretches along the banks of these rivers for many miles, and monocline bedding layers make it possible to see the entire Upper Tatarian

Substage almost in a continuous form, as well as the underlying and overlying sediments (Fig. 30-34). Here, throughout the section are met fossils of algae, higher plants, ostracods, conchostracans, insects, dvustvorok, gastropods and fishes (Fig. 28, 29).

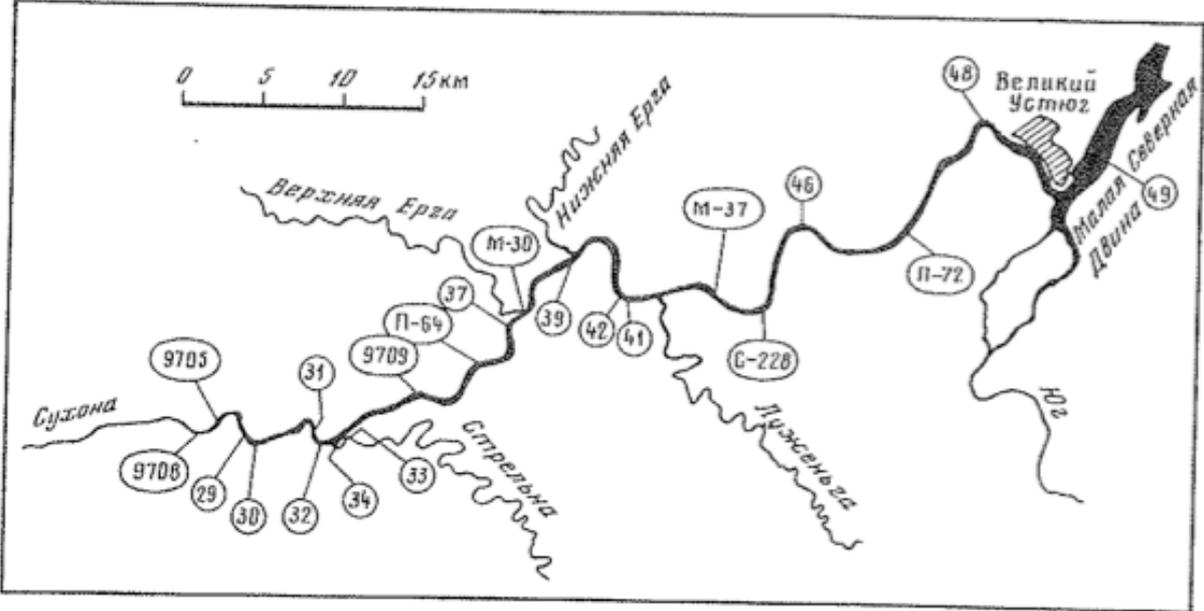


Fig. 27. Arrangement of the studied fossiliferous localities of the Tatarian Stage in the lower reaches of the Sukhona River. [Labels are, from the left: Sukhona, Verkhnyaya Erga, Strel'na, Nizhnyaya Erga, Luzhen'ga, Velikiy Ustyug, Malaya Severnaya Dvina. Transl.]

(Gusev, 1996, p. 154, fig. 2. 3. 3.3). It should be noted that some of the points previously indicated a much greater age. Thus, the Vyazniki and Sambullak localities belong to the Severodvinian Gorizont (Ivakhnenko, & Tverdokhlebova, 1980; Molostovsky, 1983, Upper Permian and Lower Triassic ..., 1984). The close location of the same lower boundary of the Triassic, in such cases is usually attributed to strong erosion of the Upper Permian deposits (or a break in sedimentation) in pre-Triassic time.

Thus, data on the stratigraphic distribution of the remains of terrestrial vertebrates in the Upper Tatarian sections of the rivers Vyatka and Sukhona suggests that the revised phylogenetic sequence of faunal assemblages of the Theriodont fauna (Kotel'nich Subcomplex -> Il'inskoye Subcomplex -> Sokolki Subcomplex -> Vyazniki Complex) coincides with the fossil sequence.

CORRELATION OF UPPER DEPOSITS OF THE KOTEL'NICH AND SUKHONA SECTIONS

The stratigraphic position of layers with the Kotel'nich fauna in the context of the Upper Permian of the Russian Plate are still not precisely defined. The locality Kotel'nich is usually referred to the top of the Severodvinian Gorizont. Consequently, in the Sukhona sectional stratotype of the Severodvinian Gorizont, the layers with the Kotel'nich fauna correspond to the upper part of the Poldarsskaya Svita (see Fig. 28). Currently, palaeontological and palaeomagnetic data for the Kotel'nich and Sukhona sections allow for a more reliable correlation between them (see Fig. 35).

The Kotel'nich tetrapod fauna is the phylogenetic precursor of the Il'inskoye fauna. Consequently, beds with the Kotel'nich fauna should be located stratigraphically below strata with Il'inskoye fauna. Indeed, at the top of the Kotel'nich section, are beds assigned to the Kotel'nich Subcomplex, thick sandy lenses (localities Agafonovo and Sokol'ya Gora) with remains of tetrapods of the Il'inskoye Subcomplex: the pareiasaurid *Proelginia cf. permiana*, the chroniosuchid *Chroniosaurus levis*, the batrachomorph *Dvinosaurus primus* and the burnetiid *Proburnetia viatkensis*. However, these locations are characterized not by the ancient Il'inskoye fauna. The latter is characterized by a more primitive chroniosaurid, *Chr. dongusensis*. In association with *Chr. dongusensis* at various localities of the East European Platform (Semin ravine, Babintseva, Donguz-6, Navoloki, Poteryakha, Kochevala, Ust'ye Strelny, Mikulino) we meet the pareiasaurid *Proelginia permiana*, the gorgonopid *Sauroctonus progressus* and *Suchogorgon golubevi*, the burnetiid *Niuksenitia sukhonensis*, the batrachomorph *Dvinosaurus primus*, the diapsid *Eorasaurus olsoni*, the leptorophid *Raphanodon tverdokhlebovae*, the galeopid *Suminia cf. getmanovi*, the dicynodont *Oudenodon* sp., and the procolophonid *Microphon exiguus*. This complex has a common genus with the Kotel'nich fauna, *Suminia*. However, the presence of the large gorgonopids *Sauroctonus* and *Suchogorgon*, the pareiasaurid *Proelginia* and the toothless dicynodont *Oudenodon* certainly makes it evolutionarily more advanced. In addition, in the faunas of the localities Agafonovo and Sokol'ya Gora we also find the burnetiid *Niuksenitia* and the pareiasaurid *Proelginia*. Thus, the fauna of the *Chr. dongusensis* is intermediate between the Kotel'nich Subcomplex (*Deltavjatia vjatkensis* fauna) and the faunas of the localities Agafonovo and Sokol'ya Gora (*Chr. levis* fauna). Consequently, the Kotel'nich fauna is more ancient than the *Chr. Dongusensis* fauna.

In the Sukhona sections, the most ancient locality with the *Chr. dongusensis* fauna is Ust'ye Strel'na (Upper Strelenskoj packet of the Poldarsskaya Svita, see Fig. 35). Consequently, the layers with the Kotel'nich fauna here correspond to deposits located

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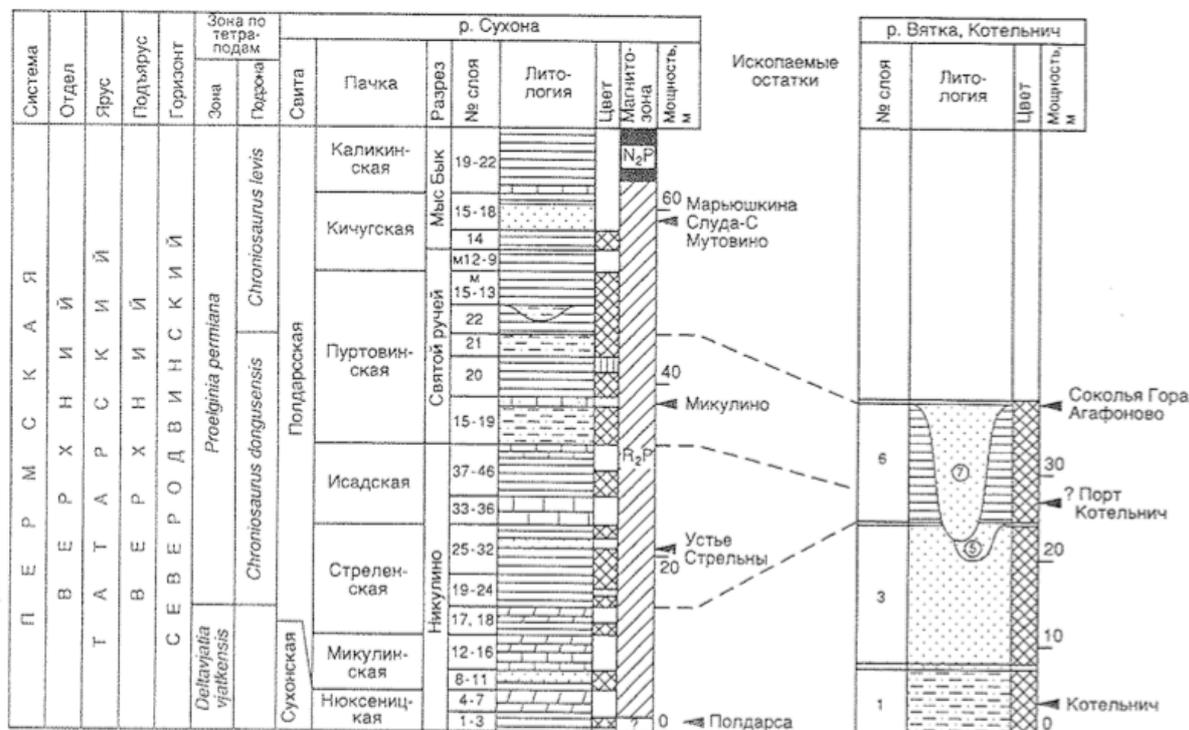


Fig. 35. Correlation of the sections of the Upper Tatarian Substage of the rivers Sukhona (the part from the settlement Poldarsa to the mouth of the Upper Erga River) and Vyatka (city Kotel'nich). Abbreviations as in Fig. 28. [Labels, from left to right: Permская Система, Верхний Отдел (part), Северодвинский Горизонт, Zones from tetrapods: zone, subzone); River Sukhona – Sukhonskaya/ Poldarsskaya Svita, Niuksenitskaya/ Mikulinskaya/ Strelenskaya, Isadskata/ Putovinskaya/ Kichugskaya/ Kalikinskata Packet, Nikulino/ Svyatoy ruchey/ Mys byk Section, Bed number, Lithology, Colour, Magnetozone, Thickness (m); Poldarsa/ Ustye Strel'na/ Mikulino/ Mutovino/ Cluda-C/ Mar'yushkina Measured sections; River Vyatka/ Kotel'nich - Bed number, Lithology, Colour, Thickness (m); Kotel'nich/ ?Port Kotel'nich/ Arfonovo/ Sokolya Gora. Transl.].

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stratigraphically lower: the lower part of the Strelenskoj, Mikulinskaya and Nuksenitskii packets, i.e. the lowest part of the Severodvinskian Gorizont.

The Port Kotel'nich locality is characterized by numerous remains of various dicynodonts, among which is a toothed form close to *Tropidostoma*. Such primitive dicynodonts are not known anywhere else in Eastern Europe. Together with the dicynodonts in this locality was also found an incomplete, poorly preserved skeleton of a pareiasaur probably similar to *Deltavjatia vjatkensis* and a gorgonopsian *Viatogorgon* (?) sp. Morphologically close to the Kotel'nich *Tropidostoma*, but the more progressive (toothless) dicynodont *Oudenodon* sp. is known from the Semin Ravine locality. *Proelginia*, the

phylogenetic descendant of *Deltavjatia*, first appears in the Semin Ravine, Mikulino, and Babintseva localities. All of these three localities are characterized by the presence of remains of the progressive *Chroniosaurus dongusensis*. Thus, at present we do not know what forms of dicynodonts and pareiasaurs occur with typical *Chr. dongusensis* (location Donguz-6, Poteryakha-1 and -2, Kochevala-1, Ust'ye Strel'na). Therefore, we can assert quite confidently only that the stratigraphic layers of counterparts of the Port Kotel'nich locality on the Sukhona are located below the Mikulino locality, i.e. not higher than the Isadskoy packet (see Fig. 35). Unfortunately, current data are not enough to answer the question: is the Port Kotel'nich locality older or younger than the Ust'ye Strel'na locality?

Remains of *Chroniosaurus levis* on the Sukhona come from the top of the Kichugskoy Packet (Mutovina and Mar'yushkina Sluda-C localities). Some 20 m lower in the section (lower part of the Purtovinskoy Packet, Mikulino locality), remains of the progressive *Chr. dongusensis* are met with. Scutes of *Chr. levis* from Sokol'ya Gora are covered with pectinate-pustular sculpture, which is more typical for *Chr. dongusensis*. However, the presence of distinct bolster-like, longitudinal cristae on the dorsal surface can determine that the remains belong to *Chr. levis*. At an evolutionary level of the dermal ornament, this form takes an intermediate position between the Mikulinskaya and Mutovina chroniosaurs and probably its stratigraphic distribution is intermediate between that of these forms. Remains of chroniosaurs like those from Sokol'ya Gora can be found on the Sukhona at the top of the Purtovinskaya or at the bottom of the Kichugskaya packets, and these facts allow us to compare this interval of the Sukhona section with bed 7 of the Kotel'nich section.

Thus, based on data from terrestrial vertebrates, beds of the Kotel'nich section can be reliably compared with the lower part of the Poldarsskaya Svita (Mikulinskaya, Strelenskaya, Isadskaya, and Purtovinskaya packets). This conclusion is also confirmed by palaeomagnetic data. The studied interval of the Sukhona section refers to the palaeomagnetic zone of reversed polarity R₂P (see Fig. 28, data from Khramov et al., 1981). The upper boundary of the magnetozone falls within the Kalikinskaya Packet, and the lower boundary is not higher than the middle of the Nyuksenitskaya Packet. The Kotel'nich section is also characterized by reverse magnetization of the rocks (Burov et al., 1996).

Besides the remains of terrestrial vertebrates in the Kotel'nich section, in the Chizhevsky sand lens (bed 5, see Fig. 35) are found the remains of plants *Algites* sp. AVG-1, *Phyllothea* aff. *turnaensis*, *Paracalamites* sp., *Pecopteris* sp. AVG} -1, *Peltaspermopsis* (?) sp. *Permothea sardykense* Zalessky, *Alicospermum* sp., *Tatarina conspicua* Meyen, *Pursongia belousovae* (Radczenko) Gomankov et Meyen, *Phylladoderma (Aequistomia)* sp. indet., *Geinitzia* sp. (Gomankov, 1996, 1997). According to A.V. Goman'kov (1996, 1997), this complex is the closest to a range of plants from the Ust'ye Strel'na location on the Sukhona (upper Strelenskaya Packet).

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In the Chizhevsky lens are also found the fish scales *Platysomus biarmicus* Eichwald, *Toyemia tverdochlebovae* Minich, *Amblypterina* sp., *Watsonichthys* sp., *Crossopterygii* fam. indet. (Esin 1995; Esin, Mashin, 1996). *Platysomus* is the index genus of the *Platysomus* Complex, characterizing the Ufimian and Kazanian Stages and the Lower Tatarian Substage (Esin 1995; Esin & Mashin, 1996). As part of this complex includes four subcomplexes, the most recent of which – the *Amblypterina costata* Subcomplex –characterizes primarily lower Tatarian deposits, associated, until recently, exclusively with the Ishevo Complex of terrestrial vertebrates.

Toyemia was originally the index of the *Toyemia* Complex, characterizing the upper Tatarian (Esin 1995; Esin & Mashin, 1996). As part of this complex are three subcomplexes,

the earliest of which – the *Amblypterina pectinata* Subcomplex – is only associated with Il'inskoye Subcomplex tetrapods. Obviously, the Kotel'nich ichthyocomplex is transitional between the *Amblypterina costata* and *Amblypterina pectinata* ichthyocomplexes (Esin, 1995, Esin & Mashin, 1996).

In the context of the Sukhona section, *Platysomus biarmicus* is met together with the typical *Amblypterina costata* ichthyocomplex: *Amblypterina costata* (Eichwald), *Lapkozubia barbalepis* Minich, *Paramblypterus* sp., *Varialepis* sp., *Acropholis* sp., *Xenosynechodus* cf. *egloni* in sandstones of the Mikulinskaya Packet (bed 10 of the Nikulino section, Nikulino-1 locality), as well as in the underlying deposits (at the Poldarsa locality, found together with the remains of scales and teeth of the fishes *Platysomus biarmicus* Eichwald, *Kargalichthys efremovi* Minich, *Reticulepis insolita* Mashin et Esin, *Amblypterina costata* (Eichwald), *Xenosynechodus* cf. *egloni*). The first appearance of *Toyemia* (*T. tverdochlebovi* Minich) is noted in conjunction with other typical representatives of the *Amblypterina pectinata* Subcomplex: *Amblypterina pectinata* Esin, *Varialepis minichorum* Mashin, *Varialepis* cf. *orientalis*, *Elonichthys* sp., *Acropholis* sp. at the top of Strelenskaya Packet (Ust'ye Strel'na). Given all of the above, it can be said with certainty that the layers with Kotel'nich ichthyocomplex in the Sukhona section are located within a limited 15-metre interval, with bone-bearing layers at the Nikulino-1 and Ust'ye Strel'na localities (upper part of the Mikulinskaya and lower part of the Strelenskaya packet). Consequently, the beds with the tetrapod fauna of the Kotel'nich Complex, which are more ancient than the layers with the Kotel'nich ichthyocomplex, cannot be located in the Sukhona section above the top of the Strelenskaya Packet. Add to this that the Il'inskoye tetrapod fauna throughout the East European platform is found in association only with the *Amblypterina pectinata* fish subcomplex. Therefore, on the Sukhona the Il'inskoye fauna cannot characterize the sediments that are located below the middle of the Mikulinskaya Packet (base of bed 11 in the Nikulino section, see Fig. 30), because the underlying sediments, as noted above, are characterized by the *Amblypterina costata* Subcomplex.

The data just considered on terrestrial vertebrates, fishes, plants, and palaeomagnetism [all] suggest that the beds at the Kotel'nich locality match the lower parts of the Strelenskaya Packet and the immediately underlying deposits on the Sukhona.

Thus, the Kotel'nich and Sukhona sections can be correlated as follows (Fig. 35): beds 1-5 of the Kotel'nich section correspond to the Nyuksenitskaya, Mikulinskaya, and lower Strelenskaya packets, the lower part of bed 6 to the upper Strelenskaya and Isadskaya packets, the upper part of bed 6 to the Purtovinskaya Packet, and beds 7-8 to the upper Purtovinskaya and lower Kichugskaya packets.

Chapter 6

ZONAL BIOSTRATIGRAPHIC SCALE OF THE UPPER TATARIAN DEPOSITS OF THE EAST EUROPEAN PLATFORM ON TERRESTRIAL VERTEBRATES

The first scheme to divide up the upper Tatarian sediments using the tetrapod fauna was developed by A.P. Hartmann-Weinberg (1937, 1938). On the basis of his personal views on the evolution of the Eastern European pareiasurs in the context of the upper Tatarian, he gave two zones (phylozones in the modern sense). The lower zone, the *Pareiasuchus-Anthodon* Zone, covered deposits with the Kotel'nich pareiasaur fauna. The upper zone, the *Scutosaurus – Proelginia* Zone, characterizes the layers with Middle Volgian (Semin Ravine, Klyuchevo Ravine) and Severodvinian (Sokolki, Zavrazh'e) pareiasaurs.

I.A. Efremov (1939, 1941, 1944) regarded all beds with pareiasaur faunas as the Pareiasaur Zone IV. He notes that the Kotel'nich pareiasaurs are more primitive than the Severodvinian, and the beds that contain their remains are located stratigraphically below the Severodvinian strata, but their selection as an independent stratigraphic unit is premature. In later works, I.A. Efremov (Efremov, 1952; Efremov & Vyushkov, 1955) in the pareiasaur fauna identified two coeval, taphonomically disparate complexes: the Severodvinian pareiasaur and Gorky batrachosaur¹.

In his study of the Tatarian deposits of the Volga-Vyatka and Sukhona areas, V.I. Ignat'ev (1962) concluded that the taphonomic complexes of Efremov characterize different stratigraphic units: the pareiasaur complex the Severodvinian Gorizont, the batrachosaur complex the Vyatkian Gorizont. Later, it was shown that remains of pareiasaurs are also known from Vyatkian deposits and batrachosaurs from Severodvinian beds (Olfer'ev, 1974; Tverdokhlebova, 1975).

G.I. Tverdokhlebova (Tverdokhlebova, 1975; Ivakhnenko & Tverdokhlebova, 1980) identified two groups in the batrachosaur complex, which characterize, respectively, Severodvinian (*Chroniosaurus dongusensis*, *Chroniosuchus licharevi*, *Chroniosuchus mirabilis*, *Kotlassia prima*, *Bystrowiana permira*) and Vyatkian (*Chroniosuchus paradoxus*, *Chroniosuchus mirabilis*, *Kotlassia* sp., *Nycteroleter* cf. *ultimus*, *Bystrowiana* sp.) gorizonts. In our opinion, the first group characterizes the entire Upper Tatarian, the second only the Vyatkian Gorizont.

Thus, a detailed biostratigraphic scale for deposits of the upper Tatarian based on tetrapods has not yet been developed. In our opinion, this is due to the technique of faunal assemblages that is being applied. Traditionally, complexes of Permian and Triassic vertebrates are formed on stratigraphic principles. Faunal localities, confined to a single stratigraphic unit (e.g. Severodvinian and Vyatkian Gorizonts) are combined into one complex. However, in respect of land vertebrates, this technique has significant drawbacks. Remains of terrestrial vertebrates

¹ The batrachosaur pareiasaur faunas – discosauriscids, parareptiles, and chroniosuchids, previously combined into one group.

differ the rarity of their distribution. Usually, they come from localities that do not cover large sections, and most of which are characterized by low stratigraphic precision. As a result, the stratigraphic position of many localities is unclear or incorrectly defined (the classic example is the pareiasaur fauna locality on the Malaya Severnaya Dvina River, which for a long time was referred to the Severodvinian Gorizont (Ignat'ev, 1962)). And this concerns almost all of the richest localities of Permian tetrapods (Isheev, Ezhovo, Semin Ravine, Vyazniki, Malaya Kinel, etc.). Stratigraphic and reference sections usually or entirely do not contain the remains of terrestrial vertebrates, or characterize poor locations. Therefore, there is nothing surprising in the fact that the complexes distinguished on stratigraphic principles are constantly mixed and little different from each other.

In our opinion, a more productive approach would be the reverse: first form a complex, reflecting the different levels of community evolution of terrestrial vertebrates, then use them to distinguish stratigraphic subdivisions. Because terrestrial vertebrates are characterized by high rates of evolution of individual groups and the community as a whole, the detail of the scheme faunistic systems will be determined only by the amount of material used and the degree of scrutiny.

A detailed scheme of faunal assemblages of Permian tetrapods of Eastern Europe has already been developed (see Chap. 4). The main phylogenetic sequence of these complexes has been identified, which, as has been demonstrated by us (see Chap. 5), coincides with their stratigraphic sequence. These data allow us to proceed directly to the creation of a detailed zonal scale for the Upper Permian of the East European platform, [based] on tetrapods. In this chapter, we will focus only on the upper Tatarian sediments, since chroniosuchians are common in these deposits.

The above late Tatarian faunistic complexes (Kotel'nich, Il'inskoye, Sokolki, and Vyazniki) characterize certain stages of development and successive communities of tetrapods. Based on these faunas in the upper Tatarian sediments, four biostratigraphic zones can be distinguished. By analogy with phylozone-beds "in which a common taxon (taxa), which represents a segment-specific phylogenetic lines or tendency (trend) of this line" (*Stratigraphic Code*, 1992, p. 45), allocated biostratigraphic zones can be identified as phylozones - layers in which fossils of common representatives of taxa occur that were part of a community, is a segment-specific phylogenetic line. Since these areas are allocated on the basis of the complexes, they are complex. Characterizing them are localities known from most areas of European Russia, where the Upper Permian extended. Consequently, the allocated zones are provincial [in scale].

In the composition of the upper Tatarian Substage of Eastern Europe [based] on tetrapods are four complex provincial zones (from the bottom up): the *Deltavjatia vjatkensis* Zone, *Proleginia permiana* Zone, *Scutosaurus karpinskii* Zone, and *Archosaurus rossicus* Zone (Fig.3b). The bases of the zonal complexes are mostly taxa of generic rank. This is because the remains of tetrapods are characterized by wide morphological diversity, and their exact species affiliation is often difficult to determine. On the other hand, Permian terrestrial vertebrates are characterized by a high rate of evolution, so they are mostly short-lived genera and families. Nevertheless, many taxa have relatively extended stratigraphic distribution, and they may occur in different zones. However, their maximum frequency of occurrence is usually achieved only in certain areas. These taxa, we also

Система	Отдел	Ярус	Подъярус	Горизонт	Лона	Провинциальные зоны по тетраподам		Комплексы хронизухий	Провинциальные зоны по рыбам		Палино-комплексы
						Зона	Подзона		Надзона	Зона	
П Е Р М С К А Я	В Е Р Х Н И Й	Т А Т А Р С К И Й	В Е Р Х Н И Й	Вятский	<i>Suchonellina fragilibides</i>	<i>Archosaurus rossicus</i>		<i>Uralerpeton tverdochlebovae</i> , <i>Bystrowiana permira</i>	<i>Toyemia</i>	<i>Mutovina stella</i>	ПК 8–10
						<i>Scutosaurus karpinskii</i>	<i>Chroniosuchus paradoxus</i>	<i>Chroniosuchus paradoxus</i> , <i>Chr. licharevi</i>			
							<i>Jarilinus mirabilis</i>	<i>Jarilinus mirabilis</i>			ПК 6
						<i>Proelginia permiana</i>	<i>Chroniosaurus levis</i>	<i>Chroniosaurus levis</i>			ПК 5
							<i>Chroniosaurus dongusensis</i>	<i>Chroniosaurus dongusensis</i>			
					<i>Deltavjatia vjatkensis</i>		<i>Suchonica vladimiri</i>	<i>Platysomus</i>	<i>Amblypteria costata</i>		

Fig. 36. Zonal biostratigraphic scheme for the upper Tatarian deposits of Eastern European platform, based on terrestrial vertebrates, and their comparison and correlation with stratigraphic scales based on fishes (Esin, 1995; Esin & Mashin, 1996) and miospores (Shelekhova, 1995). [Labels, from left to right: Permskaya Sistema, Verkhniy (Upper) Part, Tatarian Stage, Upper Substate; Severodvinian/ Vyatkian Gorizont, Provincial zones based on tetrapods – Zone, Subzone; Chroniosaurid complex, Provincial zones based on fishes – Superzone, Zone; Palynocomplexes – PK 8-10, PK 7, PK 6, PK 5. Transl.]

include in zoned complexes (in the lists of taxa of zonal complexes below, these are highlighted in bold).

Each established zone was named after one of the most characteristic species of this zone of the dominant family unit (we have tried, whenever possible, to choose species of herbivorous groups).

The rapid pace of evolution of chroniosuchids and the wide distribution of their fossils in the sediments of the upper Tatarian deposits allow customizing of this zonal scale and to provide for this group of tetrapods four subzones representing phylozones: in the *Proelginia permiana* Zone, the *Chroniosaurus dongusensis* Subzone and the *Chroniosaurus levis* Subzone, and in the *Scutosaurus karpinskii* Zone, the *Jarilinus mirabilis* Subzone and *Chroniosuchus paradoxus* Subzone.

The elaborated biostratigraphic scale using tetrapods currently can only be reliably compared with similar scales based on fishes and miospores. The reliability of these comparisons is possible because of the presence of a large number of common localities. Unfortunately, a similar correlation with the ostracods scale is not possible because a modern revision is necessary for this group, as old data are contradictory. Based on the biostratigraphic scheme (see Fig. 36), a comparison of zones allocated specifically for ostracods, is mediated through a section of the upper Tatarian on the Sukhona River. Here the

Suchonellina futschiki Zone characterizes the Sukhonskaya and Poldarsskaya svitas, and the *Suchonellina fragiloides* Zone the Salarevskaya Svita. This allows us to compare conditionally the *Deltavjatia vjatkensis* and *Proelginia permiana* zones with the *Suchonellina futschiki* Zone, the *Scutosaurus karpinskii* and *Archosaurus rossicus* zones with the *Suchonellina fragiloides* Zone.

Remains of terrestrial vertebrates are found in sediments of the upper Tatarian relatively rarely compared with other groups. As a result, stratotypes

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of many local and regional strata are not characterized. The same available information about the restriction of tetrapod localities to specific local strata is generally not credible. The facelessness of many local strata, strong facies variability of upper Tatarian sediments, and weak exposure – all this greatly complicates the diagnosis of stratonomic sediments exposed in specific sections. Therefore, in many localities with fossils of terrestrial vertebrates, there is no information about restriction to local stratigraphic units. In those cases where this information is given, they are often wrong. Also wrong are the current views on spatial-temporal relationships of local strata. As an example might be given the Samara-Orenburg region of the Trans-Volga.

It is usually assumed that all local strata of the area of East Europe follow in succession vertically. At least that is how they are represented in the regional scheme (*Decision Interagency ...*, 1990). In the Samara-Orenburg Trans-Volga region, upper Tatarian sediments are represented below by the Malokinelaya Svita (Severodvinian Gorizont), and higher by the Kutulukskaya Svita (Vyatkian Gorizont). From both svitas tetrapod remains are known. But if the Kutulukskaya Svita (Adamovka, Blyumenthal'-3, Boevoy, Pron'kino: Ivakhnenko & Tverdokhlebova, 1980; Ochev et al., 1979; Tverdokhlebova, 1976; Forsh, 1966) actually contains only remains of Vyatkian terrestrial vertebrates, the Svita is confined to the Malokinelskaya as the location of almost all currently known theriodont complexes: Donguz-6 - Il'inskoye Subcomplex, Severodvinian Gorizont; Zubochistenka-2, Vyazovka-1 - Sokolki Subcomplex, Vyatkian Gorizont; Sambullak - Vyazniki Complex, upper Vyatkian Gorizont). Consequently, the localities Zubochistenka-2, Vyazovka-1 and Sambullak were mistakenly attributed to the Malokinelskaya Svita, or the Malokinelskaya Svita is partly an age-analogue of the Kutulukskaya Svita. Since the latter conclusion is not supported by any researcher, we have to admit the truth of the first assumption.

The above example is typical for the Permian of the East European platform. This is what prevents the presentation of a chart of the correlation of upper Tatarian sediments of the Russian Plate based on tetrapods. Below and in the description of zones, we consider only the local stratigraphic units, in which, in our opinion, there are undoubtedly remains of terrestrial vertebrates, which characterize this area.

In sum, we have to admit that, despite the fact that the zonal biostratigraphic scale of terrestrial vertebrates from the upper Tatarian deposits of the East European platform is at present the most detailed among similar scales for other groups, remains of tetrapods cannot be used in actual geological survey works for a detailed dissection of specific sections. Currently, terrestrial vertebrates may be used only as an auxiliary in correlation, which allows a high degree of accuracy in determining the relative position of only a few layers in the context of upper Tatarian sediments of the Russian Plate, which are associated with the location of their remains.

DELTAJATIA VJATKENSIS PROVINCIAL ZONE

Characterizes the Kotel'nich Subcomplex.

Zonal complex - *Deltavjatia vjatkensis*, *Suchonica vladimiri*, Ictidosuchidae, Scaloposauridae, **Suminia**, **Gorgonopsidae**, **Leptorophidae**, **Nycteroleteridae**.

Remains of terrestrial vertebrates, constituting the zonal complex, are stored in the Paleontological Institute, Russian Academy of Sciences (PIN RAS), coll.

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№ 2212 (Kotel'nich locality). Representatives of the zonal complex are described in the following papers (Ivakhnenko, 1987, 1992, 1994; Ivakhnenko et al., 1997; Tatarinov, 1995, 1997; Tatarinov, 1995).

Stratotype (see Fig. 35) is located on the right bank of the Vyatka River, below the town Kotel'nich at the village Boroviki (Kirov region, Kotel'nich district). Description of stratotype (bed 1) is given in Chapter 5.

The lower boundary of the zone is established by the appearance of remains of the terrestrial vertebrate families Bradysauridae, Galeopidae, Ictidosuchidae, Moschowaitsiidae, Gorgonopidae, and Dicynodontidae. This boundary reflects the most important event in the history of the Tatarian tetrapod fauna of Eastern Europe - the invasion of Gondwanan taxa into Eastern Europe. The upper boundary of the zone is marked by the base of the *Proelginia permiana* Zone.

The zone is characteristic of the lower half of the Severodvinian Gorizont of the upper Tatarian Substage. In the Tatarian section on the Sukhona River, it answers to the Niuksenitsia Packet of the Sukhonskaya Svita and the Mikulinskaya and the lower part of the Strelenskaya packets of the Poldarskaya Svita.

The zone corresponds to the top of the biostratigraphic fish zone *Amblypterina costata* Zone of the *Platysomus* Superzone (Esin 1995; Esin & Mashin, 1996). Representatives of the zonal ichthyocomplex meet representatives of the Kotel'nich fauna in sections of the Severodvinian Gorizont near Kotel'nich town (see Chap. 5), as well as at the localities Poldarsa (Vologda region) and Ust'-Elva (Komi).

In the Kotel'nich section, the lens of light-brown sandstones, at the village Chizhi (bed 5), bears isolated spore-pollen (PK) 5 *Vesicaspora-Vitreisporites* (Shelekhova, 1995). This PK also characterizes the overlying sediments, which allows one to compare the conditional zone *Deltavjatia vjatkensis* only with the lower parts of beds in PK 5.

PROELGINIA PERMIANA PROVINCIAL ZONE

Characterizes Il'inskoye Subcomplex.

Zonal complex - *Proelginia* (*Pr. permiana*), *Chroniosaurus*, *Raphanodon tverdochlebovae*, Burnetiidae, *Oudenodon*, **Gorgonopidae**, **Suminia**, **Dvinosaurus primus**.

Remains of terrestrial vertebrates constituting the zonal complex are stored at PIN, coll. № 156 (Semin Ravine locality) and coll. № 4548 (Ust'ye-Strel'na locality).

Representatives of the zonal complex are described in the following papers (Ivakhnenko, 1987; Ivakhnenko & Tverdokhlebova, 1980; Ivakhnenko et al., 1997; Tatarinov, 1974; Shishkin, 1973).

The stratotype (see Fig. 31) is located in the Semin Ravine, which flows into the Ulemka River at the south end of Il'inskoye village (Tatarstan, Tetyushsky district). The parastratotype is located on the right bank of the Sukhona River, 900 m below the mouth of the Strel'na River, locality Ust'ye-Strel'na (Vologda Region, Velikiy district). For description

of stratotype see Efremov & V'yushkov, 1955, p. 95; parastratotype see Appendix, exposure № 34 (Ust'ye-Strel'na), beds 2-5.

The lower boundary of the zone is established by the appearance of remains of *Proelginia permiana* and *Chroniosaurus dongusensis*. The upper boundary of the zone is marked by the base of the *Scutosaurus karpinskii* Zone.

The zone occupies the upper part of the Severodvinian Gorizont of the upper Tatarian Substage. The components of the zone include: Sukhona - Poldarsskaya Svita (upper part of Strelenskaya Packet, Isadskaya, Purtovinskaya, Kichugskaya, Kalikinskaya and Erogodskaya packets² (Igmas, Kochevala-1, Mar'yushkina, Sluda-C, Mikulino, Mutovina, Navoloki, Poteryakha-1,

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Poteryakha-2, Ust'ye-Strel'na); Kazan' in the Volga region - the lower part of the Svita V (Semin Ravine), Samara-Orenburg Trans-Volga - Malokinelskaya Svita (Vyazovka-5, Donguz-6). In addition to the points are localities not tied to local strata: Nizhny Novgorod region - Gorkovskny waterworks, Kirov region. - Agafonovo, Sokol'ya Gora, Orenburg region. – Babintsevo, Preobrazhenka.

The zone corresponds to the *Amblypterina pectinata* fish biostratigraphic zone (included localities: Ust'ye-Strel'na, Kochevala-1, Donguz-6, Navoloki, Mikulino, Poteryakha-2) and lower parts of the *Amblypterina grandicostata* biostratigraphic zone (included localities: Mutovino, Mar'yushkina Sluda-C (= Strel'na)) of the *Toyemia* Superzone (Esin 1995; Esin & Mashin, 1996).

From rocks of the Mutovina locality, representatives of the palynospectrum PK 5 occur: *Vesicaspora - Vitreisporites* (Shelekhova, 1995). This complex also characterizes the underlying *Deltavjatia vjatkensis* Zone, which allows us to compare the *Proelginia permiana* Zone only to upper parts of the beds of PK 5.

The *Proelginia permiana* Zone is divided into two subzones (phylozones) based on chroniosuchids: the lower *Chroniosaurus dongusensis* Subzone and the upper *Chroniosaurus levis* Subzone. The boundary between these subzones in the Sukhona section is at the top of the Purtovinskaya Svita (rationale, see Chap. 5, Sec. 5.3). The *Scutosaurus karpinskii* Zone consists of the *Amblypterrina pectinata* biostratigraphic zone of the *Toyemia* Superzone (included localities: Ust'ye-Strel'na, Kochevala-1, Donguz-6, Navoloki, Nikulino-3, Poteryakha-2); *Chroniosaurus levis* Subzone – lower parts of the *Amblypterina grandicostata* Zone of the *Toyemia* Superzone (included localities: Mutovino, Mar'yushkina Sluda-C (= Strel'na)) (Esin, 1995; Esin & Mashin, 1996).

SCUTOSAURUS KARPINSKII PROVINCIAL ZONE

The zone characterizes the Sokolki Subcomplex.

Zonal complex - *Scutosaurus* (*Sc. karpinskii*, *Sc. tuberculatus*), *Jarilinus*, *Chroniosuchus*, *Inostrancevia*, Annatherapsiidae, Karpinskiosauridae, **Cynodontia**, **Dicynodon**, **Dvinosaurus primus**.

Remains of terrestrial vertebrates constituting the zonal complex are stored in PIN, coll. № 2005 and 2245 (Sokolki locality) and coll. № 2357 and 3582 (Aristovo locality). Representatives of the zonal complex are described in: Amalitsky, 1921a, b, 1927;

² The lower boundary of the zone is located here between beds 10 and 30 in the Nikulino section (see Fig. 35). We conditionally hold this as the base of bed 19.

V'yushkov, 1955; Golubev, 1998b; Ivakhnenko, 1987; Ivakhnenko et al., 1997; Tatarinov, 1974; Shishkin, 1973; Amalitzky, 1922; Bystrow, 1944.

The stratotype (see Fig. 34) is located on the right bank of the Malaya Severnaya Dvina River at the Aristovo pier, opposite Velikiy Ustyug (Vologda Region, Velikiy Ustyug District). Description of the section, see Appendix, exposure № 49 (Aristovo), bed 6.

The lower boundary of the zone is established by the appearance of remains of *Scutosaurus karpinskii* and *Jarilinus mirabilis*. The upper boundary of the zone is marked by the base of the *Archosaurus rossicus* Zone.

The zone characterizes the middle parts of the Vyatkian Gorizont of the upper Tatarian Substage. Its lower boundary on the Sukhona section is conventionally held at the base of the Salarevskaya Svita. In the Samara-Orenburg Trans-Volga region it matches the Kutulukskaya Svita (Adamivka, Blyumental-3, Boevoy, Pron'kino), and in the Kazan' Volga region, the upper part of the Svita V (Klyuchevoy Ravine).

The zone corresponds to the upper parts of the *Amblypterina grandicostata* fish biostratigraphic zone (joint location of the remains of fishes and tetrapods, Gor'kiy-1) and the lower parts of the *Mutovinia stella* Zone (included localities: Aristovo, Obirkovo, Salaryevo, Pron'kino) of the *Toyemia* Superzone (Esin, 1995; Esin & Mashin, 1996). The zone corresponds to beds of PK 6 *Vittatina subsaccata* f. *connectivalis* - *Protohaploxypinus amplus* and PK 7 *Cedripites priscus* - *Lueckisporites* (Shelekhova, 1995).

The zone is divided into two distinct subzones (phylozones) based on chroniosuchids: the *Jarilinus mirabilis* Subzone and *Chroniosuchus paradoxus* Subzone. The *Chroniosuchus paradoxus* Subzone includes deposits with the remains of all members of the genus *Chroniosuchus*: *Chr. paradoxus* and *Chr. licharevi*. In the basin of the Sukhona River, the boundary between the subzones is likely to match upper parts of the Rovdinskaya Packet: *Jarilinus mirabilis* remains are not detected in sediments of the upper ~Tatarian of the Sukhona River.

The *Jarilinus mirabilis* Subzone corresponds to the upper parts of the *Amblypterina grandicostata* Ichthyozone (Gor'kiy-1 locality) and probably lower parts of the *Mutovinia stella* Zone (Klimovo-1 locality). This part of the upper Tatarian Substage corresponds to the PK 6 *Vittatina subsaccata* f. *connectivalis* - *Protohaploxypinus amplus*. This PK is known for the palynospectrum, selected from the upper parts of the Rodvinskaya Packet at the village Bol'shoe Kalikino (beds 48 and 49 in the Markovo section, exposure № 42, see Fig. 33).

The *Chroniosuchus paradoxus* Subzone corresponds to middle parts of the *Mutovinia stella* ichthyozone (localities: Salaryevo, Aristovo, Obirkovo, Strizhenskaya Gora, Pron'kino) and is characteristic of PK 7 *Cedripites priscus* - *Lueckisporites* (Shelekhova, 1995), the palynospectrum of which was isolated from rocks at the Aristovo locality.

ARCHOSAURUS ROSSICUS PROVINCIAL ZONE

The zone is characterizes the Vyazniki Complex.

Zonal complex - *Archosaurus* (*Arch. rossicus*), *Uralerpeton*, *Dvinosaurus egregius*, Bystrowianidae, Nanictidopidae, **Whaitsiidae**, **Moschowaitsiidae**, **Dicynodon**, **Karpinskiosauridae**.

Remains of terrestrial vertebrates, constituting the zonal complex, are stored at PIN, coll. № 1100 (Vyazniki locality). Representatives of the zonal complex are described in many papers (V'yushkov, 1957b, Golubev, 1998a, b; Ivakhnenko & Tverdokhlebova, 1980; Ivakhnenko et al., 1997; Sennikov, 1995; Tatarinov, 1960, 1963, 1974; Shishkin, 1973).

The stratotype is located on the right bank of the Klyaz'ma River, near the town of Vyazniki (Vladimir region, Vyazniki district). Descriptions of the section, see Efremov &

V'yushkov, 1955, p. 93; image - see *Upper Permian and Lower Triassic ...*, 1984, p. 4, fig. 11).

The lower boundary of the zone is established by the appearance of remains of *Archosaurus rossicus* and *Uralerpeton tverdochlebovae*. The upper boundary of the zone is marked by the base of the Vokhmian Gorizont of the Lower Triassic (*Tupilakosaurus* remains).

The zone characterizes the uppermost part of the Vyatkian Gorizont of the upper Tatarian Substage. The composition of the zone includes: basins of the rivers Sukhona, Malaya Severnaya Dvina and Severnaya Dvina – upper parts of the Komaritskaya Packet of the Salarevskaya Svita (Rasha River), Volga-Vyatka region - the upper parts of the Isfedovskiy beds (Berezhanye). Throughout, the zone directly underlies Lower Triassic sediments: Vyazniki - approximately 15 m below the boundary (*Upper Permian and Lower Triassic ...*, 1984, p. 34, fig. 11), Purly (Efremov & V'yushkov, 1955, p. 131; Blom, 1968., p. 255); Sambullak (Ivakhnenko & Tverdokhlebova, 1980, p. 39, Annex 2); Shabarshata (Blom, 1968, p. 212); Voskresenskoe-2 (Blom, 1968, p. 186); Berezhanye - 17-18 m below the boundary (Gusev, 1996, p. 154, figs. 2.3, 3.3).

The zone corresponds to the top of the *Mutovinia stella* fish biostratigraphic zone of the *Toyemia* Superzone (Esin 1995; Esin & Mashin, 1996). Joint location of remains of fish and tetrapods - Vyazniki-2.

The palynological characteristics of the zone are not accurately known. According to M.N. Shelekhova (Shelekhova & Golubev, 1995), a similar stratigraphic position with a given zone - the terminal portion of the Vyatkian Gorizont – is occupied by beds of PK 8 *Gnetaceapollenites* - *Brevitriletes*, PK 9 *Lueckisporites* – *Taeniasporites*, and PK 10 *Vittatina* - *Gutulapollenites* (Shelekhova, 1995).

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CONCLUSIONS

1. In the late Tatarian fauna of terrestrial vertebrates, chroniosuchids were widely distributed - a kind of armoured group anthracosauromorph amphibians.

2. Chroniosuchids divide into two families: Chroniosuchidae Vjuschkov and Bystrowianidae Vjuschkov - clearly differing in morphological features of the skull, axial skeleton and dorsal carapace. In the Permian, mainly aquatic chroniosuchids were widely distributed; only at the end of late Tatarian time is there the first representative of an amphibious bystrowianid - *Bystrowiana*. This family is typical of the Triassic.

3. Chroniosuchids were morphologically very uniform. Their observed variability is largely by age (size-dependent) or individual (size-independent). Taxonomic and practically important features are: 1) form of the dorsal scutes; 2) the type of sculpture of the scutes; 3) the type of dermal ornament of the skull roof; 4) the existence and nature of the ridges on the skull roof; 5) the relative magnitude of the interorbital distance; 6) the size of the adults.

4. The sculptural type of the scutes is the most rapidly evolving feature and is seen as a species indicator. The four main types of sculptural scutes, reflecting the direction of evolution of this part of the skeleton in chroniosuchids are: pustular (primitive), pectinate, crested, and cellular. Between these basic types there are many intermediates.

5. On the basis of selected characteristics, the family Chroniosuchidae is revised, and includes five genera and seven species: *Chroniosuchus paradoxus* and *Chr. licharevi*, *Chroniosaurus* (*Chr. dongusensis* and *Chr. levis*), *Jarilinus* (*J. mirabilis*), *Uralerpeton* (*Ur. tverdochlebovae*) and *Suchonica* (*S. valdimiri*).

6. Chroniosuchid taxa succeed each other in Eastern Europe in the late Tatarian. They form the following palaeontological sequence: *Suchonica vladimiri* - *Chroniosaurus dongusensis* - *Chroniosaurus levis* - *Jarilinus mirabilis* - *Chroniosuchus paradoxus* and *Chroniosuchus licharevi* - *Uralerpeton tverdochlebovae*. The *Chroniosaurus* - *Uralerpeton* series is phylogenetic.

7. Chroniosuchids are characterized by rapid evolution, which manifested itself in the direction of increasing size of adults, change in the dermal ornament of the skull and armour plates from pustular to cellular type, the disappearance of ridges on the postorbital part of the skull roof, reduced interorbital spacing, expansion of the dorsal armour in the early stages of the phylogeny and the beginning of its reduction in later stages.

8. Refinements are made in the scheme of faunal assemblages of Late Permian tetrapods of Eastern Europe. Isolated supercomplexes, which combine individual complexes and characterize major stages in the development of communities of terrestrial vertebrates: Eryopoid (Inta Complex), Dinocephalian (Mezen', Ocher and Isheevo complexes), and Theriodont (Sokolki and Vyazniki complexes). The transition from one supercomplex to the next signified major

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events in the history of communities, among which invasions from other regions (Gondwana, Western Europe) occupy an important place.

9. The major phylogenetic sequence of tetrapod faunas of Eastern Europe is identified, confirmed for theriodont faunas by stratigraphic data from sections on the rivers Vyatka Sukhona, Malaya Severnaya Dvina, and Severnaya Dvina: Inta Complex -> Gol'yusherma Subcomplex -> Ocher Subcomplex -> Isheevo Complex -> Kotel'nich Subcomplex -> Il'inskoye Subcomplex -> Sokolki Subcomplex -> Vyazniki Complex.

10. The section of the Tatarian Stage on the Sukhona River is studied in detail, the local stratigraphic scheme of Plotnikova-Pakhtusova revealed the distribution of fossils of chroniosuchids and other terrestrial vertebrates in the upper Tatarian deposits of those sections. Currently, the Sukhona section can be used as a reference for regional correlation of upper Tatarian deposits based on terrestrial vertebrates.

11. For the first time for the upper Tatarian sediments of the East-European platform, a detailed biostratigraphic scale based on terrestrial vertebrates has been developed, and it is correlated with the timescales based on other groups. The four integrated provincial zones are: the *Deltavjatia vjatkensis* Zone (lower part of the Severodvinian Gorizont), the *Proelginia permiana* Zone (upper Severodvinian Gorizont), the *Scutosaurus karpinskii* Zone (lower part of the Vyatkian Gorizont), and the *Archosaurus rossicus* Zone (upper part of the Vyatkian Gorizont).

12. The high rates of evolution of chroniosuchids and the wide distribution of their fossils in sediments of the upper Tatarian have made possible a detailed biostratigraphic scheme: four subzones, which are phylozones, are based on this group: *Chroniosaurus dongusensis* Subzone and *Chroniosaurus levis* Subzone in the *Proelginia permiana* Provincial Zone, and *Jarilinus mirabilis* Subzone and *Chroniosuchus paradoxus* Subzone in the *Scutosaurus karpinskii* Provincial Zone.

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