A New Narrow-Armored Chroniosuchian (Amphibia, Anthracosauromorpha) from the Upper Permian of Eastern Europe

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Abstract—A new narrow-armored chroniosuchid *Suchonica vladimiri* is described based on skeletal elements discovered in the lower part of the North-Dvinian Regional Stage of the Upper Tatarian Substage of the Sukhona River. The Late Tatarian faunal vertebrate assemblages are characterized. Assignment of the genus *Suchonica* to the Kotelnich assemblage is supported here. Correlation of the Tatarian of the Sukhona River and Kotelnich sections is discussed.

INTRODUCTION

In 1994 V.L. Mashin, a student of the Paleontology Department of the Geological faculty of Moscow State University, found the remains of a narrow-armored chroniosuchian, described below as *Suchonica vladimiri* gen. et sp. nov., on the left bank of the Sukhona River opposite the eastern edge of the village of Poldarsa and 0.5 km upstream from the village of Nikulino (Vologda Region, Velikii Ustyug District; Fig. 1). The skeletal fragments were recovered from light-green marls from the basal part of the Upper Tatarian Substage (the top of the Nyuksenitsa Member of the Sukhona Formation). The scutes and vertebrae of the present form are constructed typically for members of the family Chroniosuchidae (Golubev, 1998a), suggesting its assignment to this taxon.

SYSTEMATIC PALEONTOLOGY

CLASS AMPHIBIA Order Anthracosauromorpha Suborder Chroniosuchia Family Chroniosuchidae Vjuschkov, 1957 Genus Suchonica Golubev, gen. nov.

E t y m o l o g y. From the Sukhona River.

Type species: Suchonica vladimiri sp. nov.

D i a g n o s i s. Trunk scutes belong to narrow type (scute wings length exceeds their width). Ventral scute process does not fuse to neural spine. Scute dorsal surface ornamented by pectinate sculpturing. Longitudinal swollen cristae¹ absent from the dorsal scute surface.

Species composition. Type species.

C o m p a r i s o n. Differs from the genera *Jarilinus* Golubev, *Chroniosaurus* Tverdochlebova and *Chroniosuchus* Vjuschkov by narrow trunk scutes; from the genera *Chroniosuchus*, *Uralerpeton* Golubev and *Jarilinus* by a pectinate type of dermal sculpturing of the scutes; from the genera *Chroniosuchus* and *Jarilinus* by the absence of longitudinal swollen cristae from the scute dorsal surface; from the genus *Uralerpeton* in that the scutes do not fuse to the neural spines.

Suchonica vladimiri Golubev, sp. nov.

Etymology. In honor of paleoichthyologist Vladimir Mashin, who found the specimen.

H o l o t y p e. PIN, no. 4611/1, the anterior (? cervical) armor scute; Vologda Region, Velikii Ustyug District, village of Poldarsa; Upper Permian, Upper Tatarian Substage, North-Dvinian Regional Stage, the top of the Nyuksenitsa Member of the Sukhona Formation.



Fig. 1. Map of the Late Permian localities of the Kotelnich tetrapod assemblage in the territory of European Russia. (1) Ust'-Yelva, (2) Poldarsa, (3) Kotelnich and Port Kotelnich. Scale 1 : 10000000.

¹ For dermal ornamentation type terminology see Golubev (1998b).



Fig. 2. Suchonica vladimiri sp. nov., scutes of the dorsal armor from above: (a) holotype PIN, no. 4611/1; (b) specimen PIN, 4611/10; (c) specimen PIN, no. 4611/8; (d) specimen PIN, no. 4611/12.

Description (Fig. 2). Medium-sized chroniosuchid, estimated skull length no more than 25 cm. The armor scutes pertain to the narrow type. The armor probably overlapped only the axial part of the dorsal surface of the animal's body. The dermal scute sculpturing belongs to the pectinate type and is formed by short, 5–9 mm long, vermiform swollen ridges. Up to five variously expressed pustules, sometimes shaped as distinct tubercles, may be placed along the swollen ridges (pectens). The pectens are aligned predominantly transversely. The pectens become even shorter on the scute wings, frequently disintegrating into isolated tubercles. In these zones the dermal sculpture may become pectinate-pustular. A couple of well expressed longitudinal crests thicken the scute, extend along its upper surface along the boundary between the body of the scute and the wings. The dermal ornament pectens of these crests become aligned predominantly longitudinally and frequently form enclosed rings.

The ventral scute process is not preserved. Taking into account the imprint at the ventral surface of the scute (specimen PIN, no. 4611/1), it was thin and long, with pointed anterior and posterior edges and had completely occupied the median part of the scute. A similar construction of the ventral process is typical of members of the family Chroniosuchidae and distinguishes them from members of the family Bystrowianidae Vjuschkov (Golubev, 1998a). The neural arch of the vertebra fuses to the centrum without any sutural marking. The neural spine is shaped as a triangle, elongated dorsally in lateral view. Its anterior and posterior edges bear distinct shallow notches that correspondingly housed the anterior and posterior projections of the ventral scute process. The ventral process and the neural spine did not fuse and probably made contact by the connective tissue only. The neural spine structure described above and the character of its articulation to the ventral process is also a distinctive feature of members of the family Chroniosuchidae.

The intercentra, as in the other chroniosuchids, are amphicoelous and rounded in cross section.

Occurrence. Lower part of the North-Dvinian Regional Stage of the Upper Tatarian Substage, Vologda Region.

R e m a r k s. The absence of longitudinal swollen crests on the scutes and presence of replacement crests that thicken the scutes are shared by *Suchonica vladimiri* and the most primitive wide-armored chroniosuchid, *Chroniosaurus dongusensis* Tverdochlebova. Presence of narrow scute wings suggests that *Suchonica* is the morphological predecessor of this chroniosaur. This conclusion coincides with the data on the stratigraphic distribution of these two taxa. The



Fig. 3. Correlation of the Upper Tatarian deposits of the Sukhona River area (from the village of Poldarsa to the mouth of the Nizhnyaya Yerga River) and the Vyatka River (Kotelnich). Designations: (1) limestones, (2) marls, (3) clays, (4) aleurolites, (5) sandstones, (6) redbeds, (7) graywacks, (8) redbeds and graywacks intercalation, (9) direct polarity magnetozone, (10) reverse polarity magnetozone, (11) tetrapod localities.

bones of *Suchonica vladimiri* from the Sukhona River originate from the top of the Nyuksenitsa Member of the Sukhona Formation (Fig. 3), and *Chroniosaurus* remains occur here in the section for the first time 18 m above it, in the upper part of the Strel'na Member of the Poldarsa Formation (Ust'ye Strel'ny locality). However, *Suchonica* is characterized by a more progressive pectinate dermal ornament of the armor scutes. This makes it impossible to consider this form as a direct ancestor of *Chroniosaurus dongusensis*, which contrasts with it in the primitive pustular sculpture.

M a t e r i a l. Apart from the holotype from the type locality, specimens PIN nos. 4611/2–5, vertebrae; 4611/6, intercentrum; 4611/7, sacral rib; 4611/8–14, scutes and scute fragments.

DISCUSSION

Chroniosuchids are characteristic of the aquatic branch of the theriodont superassemblage (Late Tatarian) of the Permian terrestrial vertebrates in Eastern Europe. Three faunal assemblages are currently known within the structure of this superassemblage (Fig. 4): the Kotelnich, the Sokolki (including the Il'inskoye and the Sokolki subassemblages) and the Vyazniki (Ivachnenko, 1990, 1992; Golubev, 1996, 1998b).

The most primitive members of all the main groups of the theriodont fauna are known from the Kotelnich assemblage (the *Deltavjatia vjatkensis* fauna). This suggests, that the Kotelnich fauna is the earliest among all theriodont faunas. The Kotelnich assemblage is well known mainly from a single base (type), the Kotelnich locality situated on the right bank of the Vyatka River downstream from the town of Kotelnich (Kirov Region). Rich material became available from this site during the past several years as a result of annual excavations previously conducted by D.L. Sumin and presently by A.Yu. Khlyupin.

The dominant part of the Kotelnich assemblage of terrestrial vertebrates (Fig. 4) is composed of relatively small and primitive herbivorous bradysaurid pareia-saurs *Deltavjatia vjatkensis* (Hartmann–Weinberg) and the dicynodonts *Tropidostoma* sp. The predators include the therocephalians (the moschowhaitsiid *Viatkosuchus sumini* Tatarinov) and medium sized gorgonopids. The characteristic members of the subdomi-

Superassemblage		Theriodont			
Assemblage		Kotel- nich-	Sokolki		Vyaz-
Subassemblage			Il'in- skoye	Sokolki	niki
Amphibia	Microsauria f.i.				
	Dvinosauridae				
	Chroniosuchidae				
	Bystrowianidae				
Parareptilia	Nycteroleteridae				
	Leptorophidae				
	Kaspinskiosauridae				
	Rhipeosauridae				
	Elginiidae				
	Bradysauridae				
	Pareiasauridae				
	Procolophonidae				
Theromorpha	Burnetiidae				
	Galeopidae				
	Dicynodontidae				
	Gorgonopidae				
	Ictidosuchidae				
	Inostranceviidae				
	Whaitsiidae				
	Moschowhaitsiidae				
	Scylacosauridae				
	Annatherapsididae				
	Nanictidopidae				
	Cynodontia f.i.				
	Dviniidae				
	Galesauridae				
	Procynosuchidae				
Diap-	Protorosauridae				
sida	Proterosuchidae				
		a b		■ c ■ d	

Fig. 4. Terrestrial tetrapod families occurring within the Late Tatarian faunal assemblages of Eastern Europe: (*a*) abundant, (*b*) frequent, (*c*) rare, (*d*) unique.

nant block are numerous small-sized therocephalians (the ictidosuchids, *Karenites ornamentatus* Tatarinov and *Perplexisaurus foveatus* Tatarinov), the galeopids *Suminia getmanovi* Ivachnenko and the relic nycteroleterids *Emeroleter levis* Ivachnenko. The remains of the aquatic tetrapods were not found in Kotelnich. Probably, as in the other theriodont assemblages, the aquatic block of the Kotelnich fauna was formed by the chroniosuchids, primitive leptorophid parareptiles and the colosteiform labyrinthodonts, dvinosaurids.

The Kotelnich assemblage is preceded by the Isheyevo dinocephalian assemblage (Ivachnenko, 1990, 1992, 1995, 1996). However, these faunas do not share a single common family. Such a sharp faunal contrast probably resulted from the alteration of the Isheyevo assemblage by the Kotelnich during the local ecological crisis that was one of the largest in the his-

tory of the Permian assemblages of terrestrial vertebrates in Eastern Europe (Golubev, 1995).

The Kotelnich assemblage of terrestrial vertebrates is replaced by the Sokolki assemblage (Fig. 4). The latter is the best known among all theriodont assemblages. It is currently known from more than 50 localities.

The early Sokolki fauna is specified as the Il'inskoye subassemblage (*Proelginia permiana* fauna). The base locality is Syomin Ovrag (village of Il'inskoye, Tatarstan). The dominant block of the Il'inskoye community (Fig. 4) is formed of the herbivorous pareiasaurids, *Proelginia permiana* (Hartmann-Weinberg), probably the descendants of the Kotelnich bradysaurids, and the dicynodonts, *Oudenodon* sp. The predators are exemplified by abundant gorgonopids *Sauroctonus progressus* (Hartmann-Weinberg) and burnetiids (*Proburnetia vjatkensis* Tatarinov and *Niuk*-

senitia sukhonensis Tatarinov). The subdominant block includes a variety of forms: the galeopsids Suminia cf. S. getmanovi characteristic only of the early II'inskoye fauna (Chroniosaurus dongusensis fauna), as well as much less abundant procolophonids Microphon exiguus Ivachnenko, the therocephalians (scylacosaurids Scylacosuchus orenburgensis Tatarinov), protorosaurid diapsids (the protorosaurid Eorasaurus olsoni Sennikov) and problematic cynodonts. The aquatic block includes the wide-armored chroniosuchids Chroniosaurus dongusensis and C. levis Golubev; primitive parareptiles (the leptorophids Raphanodon tverdochlebovae Ivachnenko) and the colosteiform labyrinthodonts (the dvinosaurid, Dvinosaurus primus Amalitzky).

The Late Sokolki fauna is specified as the Sokolki subassemblage (Scutosaurus karpinskii fauna). The base locality of this subassemblage is the Sokolki site well known from the V.P. Amalitsky excavations at the Malaya Severnaya Dvina River (Arkhangelsk Region). The dominant block of the Sokolki subassemblage (Fig. 4) includes the large phytophagous pareiasaurs Scutosaurus karpinskii (Amalitzky), S. tuberculatus (Amalitzky) and S. itilensis Ivachnenko et Lebedev, the dicynodonts Dicynodon trautscholdi Amalitzky and the predators: the inostranceviid gorgonopians Inostrancevia alexandri Amalitzky, I. latifrons Pravoslavlev, I. uralensis Tatarinov and Pravoslavlevia parva (Pravoslavlev); the annatherapsidids Annatherapsidus petri (Amalitzky) and *Chthonosaurus velocidens* Vjuschkov. Diverse cynodonts (the dviniid Dvinia prima Amalitzky, the galesaurid Nanocynodon seductus Tatarinov and the procynosuchid Uralocynodon tverdokhlebovae Tatarinov), rare procolophons (Suchonosaurus minimus Tverdochlebova et Ivachnenko) and problematic rhipaeosaurids are characteristic of the subdominant block. The aquatic block, as well as the Il'inskoye fauna, includes the wide-armored chroniosuchids, Jarilinus mirabilis (Vjuschkov), Chroniosuchus paradoxus Vjuschkov and C. licharevi (Riabinin), primitive parareptiles (the leptorophids Raphanodon cf. R. tverdochlebovae and R. ultimus (Tchudinov et Vjuschkov), the karpinskiosaurids Karpinskiosaurus secundus (Amalitzky) and Kotlassia prima Amalitzky, and the colosteiform labyrinthodonts (the dvinosaurid Dvinosaurus primus).

The Vyazniki assemblage, or the Archosaurus rossicus fauna (base locality Vyazniki-2, Vladimir Region), typifies the closing stage of the evolution of the theriodont assemblage of the terrestrial tetrapods (Ivachnenko, 1990; Golubev, 1998a, 1998c). The pareiasaurs and the gorgonopians disappear from the dominant block (Fig. 4). The herbivorous dicynodonts, *Dicynodon* sp. become widespread. The predators are represented by the therocephalians (a large moschowhaitsiid *Moschowhaitsia vjuschkovi* Tatarinov, a nanictidopid *Hexacynodon purlinensis* Tatarinov, and large problematic whaitsiids) and the first large thecodonts (the proterosuchid *Archosaurus rossicus* Tatarinov). The bystrowianid chroniosuchians *Bystrowiana permira* Vjuschkov, mainly characteristic of the Triassic, appear in the subdominant block. Microsaurs become abundant. The relic subdominants Nycteroleterinae *Elginia* sp., are more rare. The significant changes which occur in the dominant and subdominant blocks do not touch the aquatic block. The narrow-armored chroniosuchids *Uralerpeton tverdochlebovae* Golubev, the leptorophids, the karpinskiosaurids *Kotlassia grandis* Tverdochlebova et Ivachnenko and the dvinosaurids *Dvinosaurus egregius* Shishkin and *D. purlensis* Shishkin, still dominate here.

The faunal assemblages discussed above characterize certain evolutionary stages of the terrestrial tetrapod community of the Late Permian of Eastern Europe. They replaced each other during the Late Tatarian in the same sequence that was described above: the Kotelnich assemblage—the Il'inskoye subassemblage-the Sokolki subassemblage-the Vyazniki assemblage. This assumption is based upon the evolutionary levels of the faunas considered and is also supported by stratigraphic data. Thus, the layers around the town of Kotelnich containing the tetrapod remains of the Kotelnich assemblage (Kotelnich locality), are situated about 30–35 m below the beds containing the Il'inskoye fauna (Proelginia cf. P. permiana, Chroniosaurus levis, Dvinosaurus primus, and Proburnetia viatkensis in the Agafonovo and Sokolya Gora localities). The localities of the Il'inskove subassemblage in the basin of the Sukhona River, the Malaya Severnaya Dvina River and the Severnaya Dvina River are restricted to the Poldarsa Formation and those of the Sokolki subassemblage to the above Salaryovo Formation (Golubev, 1998b), and the Vyazniki assemblage to the uppermost part of the Salaryovo Formation, which underlies the Triassic (Rasha locality). All known sites of the Vyazniki fauna are situated on the boundary of the Vyatkian Regional Stage (Upper Permian) and Vokhmian Regional Stage (Lower Triassic) (Golubev, 1998a).

The Late Tatarian faunal assemblages of the terrestrial tetrapos described may be successfully used for stratigraphic purposes. Four complex provincial biostratigraphical zones are currently recognized at their base in the composition of the Upper Tatarian Substage (Golubev, 1998b, Table 1): the *Deltavjatia vjatkensis* Zone (the lower part of the North-Dvinian Regional Stage), the *Proelginia permiana* Zone (the upper part of the North-Dvinian Regional Stage), the *Scutosaurus karpinskii* Zone (the lower part of the Vyatkian Regional Stage) and the *Archosaurus rossicus* Zone (the upper part of the Vyatkian Regional Stage).

The incorporation of *Suchonica vladimiri* in the composition of one of the faunal assemblages described above creates serious problems. This new narrow-armored chroniosuchid is unfortunately known only from the type Poldarsa locality, that contains no other terrestrial tetrapod skeletal parts. The localities of

the Il'inskove subassemblage: Ustve Strel'ny, Mikulino, Mutovino and Maryushkina Sluda-C are situated in the Tatarian section of the Sukhona River stratigraphically higher than the Poldarsa locality (Fig. 3). Hence, Suchonica may be included either in the composition of the Il'inskoye subassemblage of the Sokolki assemblage, or in the earlier Kotelnich assemblage. In so far as the typical Il'inskove fauna is characterized everywhere by wide-armored chroniosaurs, it is possible to assume, that Suchonica is a member of the aquatic block of the Kotelnich community of the terrestrial tetrapods. It seems to be impossible to confirm this suggestion more accurately since it is based principally upon the information obtained from the terrestrial tetrapods. Nevertheless, this problem may be regarded from another point of view. The question on the faunal position of Suchonica is conceptually analogous to the following one: does the Poldarsa locality belong to the Deltavjatia vjatkensis Zone or to the Proelginia permiana Zone? Thus, the solution to the problem becomes dependent on detailed comparison of the Sukhona River and the Kotelnich sections.

The summary section of the Upper Tatarian outcropping on the right bank of the Vyatka River downstream from the town of Kotelnich is presented in Fig. 3 (the section description is kindly provided by V.M. Ivachnenko). The skeletal parts of the Kotelnich assemblage terrestrial tetrapods, Deltavjatia vjatkensis, Emeroleter levis, Viatkosuchus sumini, Karenites ornamentatus, Perplexisaurus foveatus, Suminia getmanovi, and Gorgonopidae gen. indet., are found here at the base of the section in the red marls and aleurolites of layer 1 (Kotelnich locality). According to unverified information from various researchers, numerous remains of the primitive denticulated dicynodonts, similar to Tropidostoma, and an incomplete skeleton of Deltaviatia viatkensis were found at the base of Bed 6 (town of Kotelnich, southern edge, Port Kotelnich locality). The sandy lenses of Sokolya Gora and Agafonovo higher up the section (Bed 7) yielded the remains of the Il'inskoye tetrapod subassemblage, Chroniosaurus levis, Proelginia cf. P. permiana, Proburnetia viatkensis and Dvinosaurus primus.

The composite tetrapod assemblage from the vicinities of the town of Kotelnich is most similar to that of the lower part of the Poldarsa Formation of the Sukhona River section that includes *Chroniosaurus* dongusensis, Raphanodon tverdochlebovae, Dvinosaurus sp., Suminia cf. S. getmanovi, Niuksenitia sukhonensis, Sauroctonus cf. S. progressus, Proelginia cf. P. permiana (Poteryakha-1 and Poteryakha-2, Kochevala-1 and Kochevala-2, Navoloki, Ust'ye Strel'ny and Mikulino localities). Chroniosaurus levis from Sokolya Gora is more primitive, than the type *C*. *levis* from the Mutovino and occupies an intermediate position between the latter and C. dongusensis from the Mikulino locality (Fig. 3). The scutes of Chroniosaurus from the Sokolya Gora are ornamented by pectinatepustular sculpturing that is more characteristic of *C. dongusensis.* Only the presence of distinct swollen longitudinal crests on the dorsal surface makes possible the identification of this fragment with *C. levis.* Assuming the gradual evolution of chroniosuchid scutes and a constant sedimentation rate in the Sukhona River area during the Poldarsa period, it is possible to suggest, that Sokolya Gora and Agafonovo are stratigraphic analogues of the upper part of the Purtovino Member of the Sukhona River section.

Thus, based on the terrestrial tetrapod data, the layers of the Kotelnich can be confidently correlated with the lower part of the Poldarsa Formation (Mikulino, Strel'na, Isady and Purtovino Members). This conclusion is also supported by paleomagnetic information. The interval of the Sukhona River section considered refers to the paleomagnetic zone of reversed polarity R_2P (*Opornyi razrez ..., 1981*). The upper boundary of this magnetozone is situated within the Kalikino Member and the lower one within the middle of the Nyuksenitsa Member (Fig. 3). The Kotelnich section is also characterized by rocks of reversed polarity (Burov *et al., 1996*).

Apart from the terrestrial tetrapods the plant remains of Algites sp., Phyllotheca cf. P. turnaensis Gorelova, Paracalamites sp., Pecopteris sp., Peltaspermopsis (?) sp., Permotheca sardykense Zalessky, Alicospermum sp., Tatarina conspica Meyen, Pursongia beloussovae (Radczenko) Gomankov et Meyen, Phylladoderma (Aquistomia) ex gr. P. annulata and Geinitzia sp. were found in the Kotelnich section (determinations by A.V. Gomankov). These fossils originate from the lens of light-brown, polymictic, loose sandstones and gray clays (Bed 5) situated on the Chizhi farm. In Gomankov's opinion (1996), this assemblage is the closest to the plant assemblage from the Sukhona River locality, Ust'ye Strel'ny (the uppermost part of the Strel'na Member).

The Chizhi lens (Bed 5) also yielded the scales of fishes, *Platysomus biarmicus* Eichwald, *Toyemia tver-dochlebovae* Minich, *Amblypterina* sp., *Watsonichthys* sp. and Crossopterigii fam. indet. (Esin, 1995; Esin and Mashin, 1996). The genus *Platysomus* is an index of the *Platysomus* assemblage, characterizing the Ufimian and Kazanian Stages and the Lower Tatarian Substage (Esin, 1995; Esin and Mashin, 1996). Four subassemblages are recognized within the structure of this assemblage, the latest of which, the *Amblypterina costata* subassemblage, characterizes mainly the Lower Tatarian deposits, being associated until recently exclusively with the Isheyevo terrestrial tetrapod assemblage.

The genus *Toyemia* is an index of the *Toyemia* assemblage characterizing the Upper Tatarian Substage (Esin, 1995; Esin and Mashin, 1996). Three subassemblages are recognized within the structure of this assemblage, the earliest of which, the *Amblypterina pectinata* subassemblage, correlates only with the II'inskoye tetrapod subassemblage. The Kotelnich ich-

thyoassemblage is probably transitional between the *Amblypterina costata* and *Amblypterina pectinata* ich-thyoassemblages (Esin, 1995; Esin and Mashin, 1998).

In the Sukhona section, Platysomus biarmicus is found in association with the typical Amblypterina costata ichthyoassemblage: Amblypterina costata (Eichwald), Xenosynechodus egloni Glückman, Lapkosubia barbolepis Minich, Paramblypterus sp., Varialepis sp. and Acropholis sp. in the Mikulino Member sandstones of Bed 10 of the Nikulino section (Nikulino-1 locality), as well as in the stratigraphically lower deposits. Apart from the Suchonica remains, the Poldarsa locality produced the scales and teeth of fishes, Platysomus biarmicus, Kargalichthys efremovi Minich, Reticulolepis insolita Mashin et Esin, Amblypterina costata, and *Xenosynechodus egloni.*² The first occurrence of the genus Toyemia (T. tverdochlebovi Minich) is recorded simultaneously with other typical Amblypterina pectinata subassemblage members: Amblypterina pectinata Esin, Varialepis minichorum Mashin, Varialepis cf. V. orientalis (Eichwald.), Elonichthys sp. and Acropholis sp. in the upper part of the Strel'na Member (Ust'ye Strel'ny). Thus, it may be suggested, with a certain degree of confidence that the layers containing the Kotelnich ichthyoassemblage in the Sukhona River section are situated within the 15 meter interval limited by the fossiliferous layers of the sites Nikulino-1 and Ust'ye Strel'ny (the upper part of the Mikulino Member and the lower part of the Strel'na Member). Hence, the layers containing the tetrapod fauna of the Kotelnich assemblage, which are older than those of the Kotelnich ichthyoassemblage, may occur less frequently within the Sukhona River section above the upper part of the Strel'na Member. This may also be supported by the fact, that the Il'inskoye tetrapod fauna is always found in association only with the Amblypterina pectinata subassemblage fishes anywhere within the limits of the East-European platform. Therefore the lower boundary of the Proelginia permiana Zone at the Sukhona River cannot be situated below the middle part of the Mikulino Member (the base of layer 11 of the section Nikulino; Fig. 3), in so far as the underlying deposits, as was mentioned above, are characterized by the Amblypterina costata subassemblage.

Thus, the data on the terrestrial tetrapod, fishes, plants, and paleomagnetism suggest that the layers in the Kotelnich locality correlate with the lower part of the Strel'na Member and immediately underlying deposits of the Sukhona River. Moreover, the boundary of the *Deltavjatia vjatkensis* and the *Proelginia permiana* zones runs here between the layers 10 and 30 in the Nikulino section. It is here tentatively traced at the base of layer 19 (Fig. 3). Thus, the Poldarsa locality is dated by the *Deltavjatia vjatkensis* Zone. Hence, *Suchonica* may be included within the Kotelnich assemblage com-

prising its aquatic block, which is missing from the Kotelnich locality due to taphonomic reasons.

In conclusion it should be noted that the *Deltavjatia vjatkensis* Zone is an interval of the Tatarian section characterized by a mixed vertebrate assemblage: the typically "Late Tatarian" tetrapods of the theriodont superassemblage are associated with the "Early Tatarian" fishes of the *Platysomus* assemblage. This suggests, that the largest events in the Late Permian history of tetrapods and fishes in Eastern Europe were asynchronous and that a significant change in the terrestrial tetrapod community occurs earlier than in the ichthyofauna. Even the aquatic block of the terrestrial tetrapod community, most closely bound to the fish community trophically, is quite independent in relation to the latter.

Apart from the Kotelnich and Poldarsa localities, the Ust'-Yelva locality (the upper part of the Mezen River, Komi Republic; Fig. 1) is distinguished by a mixed vertebrate assemblage. In 1994 V.V. Bulanov discovered here the skull roof of *Raphanodon* cf. *R. tverdochlebovae* and scales and teeth of fishes, *Platysomus biarmicus, Kargalichthys efremovi, Reticulolepis insolata, Xenosynechodus egloni,* and *Paramblypterus kucenkoi* Esin. In D.N. Esin's opinion (pers. comm.), this ichthyoassemblage is the closest to that of the Poldarsa locality. Hence, the Ust'-Yelva tetrapod fauna may also be included in the Kotelnich assemblage.

Thus, the aquatic block of the Kotelnich terrestrial tetrapod community of Eastern Europe is formed of the groups typical of the theriodont superassemblage: the chroniosuchids and the leptorophids.

ACKNOWLEDGMENTS

The work was supported by the Russian Foundation for Basic Research, project no. 96-15-98069.

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² Here and further on the fish remains identifications were carried out by D.N. Esin and V.L. Mashin. Some identifications may be found in Esin and Mashin (1996).

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