Paleontological Journal, Vol. 32, No. 4, 1998, pp. 390–401. Translated from Paleontologicheskii Zhurnal, No. 4, 1998, pp. 68–77.

Revision of the Late Permian Chroniosuchians (Amphibia, Anthracosauromorpha) from Eastern Europe

V. K. Golubev

Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, Moscow, 117647 Russia

Received March 31, 1997

Abstract—The family Chroniosuchidae is revised. The systematic importance of various morphological features is evaluated. The family systematic structure is presented and the generic and specific diagnoses are reformulated. A new genus *Jarilinus* and a new species *Chroniosaurus levis* are established. Evolutionary peculiarities of chroniosuchids are discussed. A zonal biostratigraphic chart of the Upper Tatarian deposits of eastern Europe based on tetrapod data is suggested.

INTRODUCTION.

Chroniosuchians are one of the most characteristic elements of the Late Tatarian tetrapod faunas of European Russia. This group of relict anthracosaurs replaced the archegosauroid labyrinthodonts that dominated the aquatic tetrapod communities of the Kazanian and Early Tatarian in this territory. Chroniosuchians include two families: the Chroniosuchidae Vjuschkov, 1957 and the Bystrowianidae Vjuschkov, 1957 (Golubev, 1998). The bystrowianids were widely distributed mainly in the Triassic, only the earliest members of this family emerge at the end of the Permian (Shishkin and Novikov, 1992). The chroniosuchids, in contrast, are known only from the Permian.

The first known chroniosuchids: *Chroniosuchus paradoxus* and *C. mirabilis* were described by Vjuschkov (1957). A fragment of the vertebral column from Zavrazhye (Arkhangelsk Region) specimen PIN, no. 2353/6 was described as *Chroniosuchus* sp. in that paper.[1] At the end of the 1930s Riabinin in a manuscript described another chroniosuchid *Jugosuchus licharevi* from fragments of the lower jaws from Savvatii (Arkhangelsk Region). However, this description was published by Shishkin thirty years later (Riabinin and Shishkin, 1962). Tverdochlebova (1967) supplied the name *Chroniosuchus vjuschkovi* to a chroniosuchian from Zavrazhye described by Vjuschkov. Tverdochlebova (1968) pointed to a significant similarity of the present form to the genus *Chroniosuchus* and conditionally regarded it as *Chroniosuchus licharevi*, since *J. licharevi* is represented by poorly diagnostic remains. She also suggested, that *C. vjuschkovi* may turn out to be a junior synonym of *C. licharevi*. Tverdochlebova (1972) erected a new chroniosuchid genus and species *Chroniosaurus dongusensis*.

All published chroniosuchian data were revised and new material was described by Ivachnenko and Tverdochlebova (1980). These authors regarded the chroniosuchians as a suborder of the order Anthracosauromorpha. Two families: the Chroniosuchidae and the Bystrowianidae were recognized within the suborder. The family Chroniosuchidae includes the small-sized *Chroniosuchus paradoxus* and *Chroniosaurus dongusensis*, as well as the large *Chroniosuchus uralensis* Tverdochlebova originally described in that paper from the locality Blumental-3, (Orenburg Region). The name *Jugosuchus* is considered to be valid again. Apart from the type species *J. licharevi* (=*Chroniosuchus vjuschkovi*), *J. mirabilis* and two new species: *J. boreus* Ivachnenko (Mikulino, Vologda Region) and *J. hartmanni* Ivachnenko (Syomin Ovrag, Tatarstan), were referred to this genus. The genera *Jugosuchus* and *Bystrowiana* were united into the family Bystrowianidae. Later Ivachnenko and Shishkin (Shishkin and Novikov, 1992) suggested, that *Jugosuchus* should belong to the Chroniosuchidae. I did not accept this point of view (Golubev, 1998). The paper included a description of a chroniosuchid *Uralerpeton tverdochlebovae*, distinguished from other chroniosuchids by considerably narrowed scutes.

Thus, the Chroniosuchidae currently include four genera and eight species: *Chroniosuchus* (*C. paradoxus* and *C. uralensis*), *Jugosuchus* (*J. licharevi*, *J. mirabilis*, *J. boreus*, and *J. hartmanni*), *Chroniosaurus* (*C. dongusensis*) and *Uralerpeton* (*U. tverdochlebovae*).

The chroniosuchids are very uniform morphologically. The largest variability range is exemplified by the dermal ornament of the skull and dorsal armor scutes. Several scute types are distinguished in the chroniosuchids based upon sculpturing features that may be arranged in a single morphological row: pustular, pectinate, cristate and pitted.[2] The pustular sculpturing

[1] PIN—Paleontological Institute, Russian Academy of Sciences, SGU—Saratov State University, TsNIGR—Central Research Geological–Prospecting Museum (St. Petersburg). SGU collections used here are housed in PIN.

[2] The terms pectinate and cristate to denote the dermal ornamentation types are introduced here for the first time.

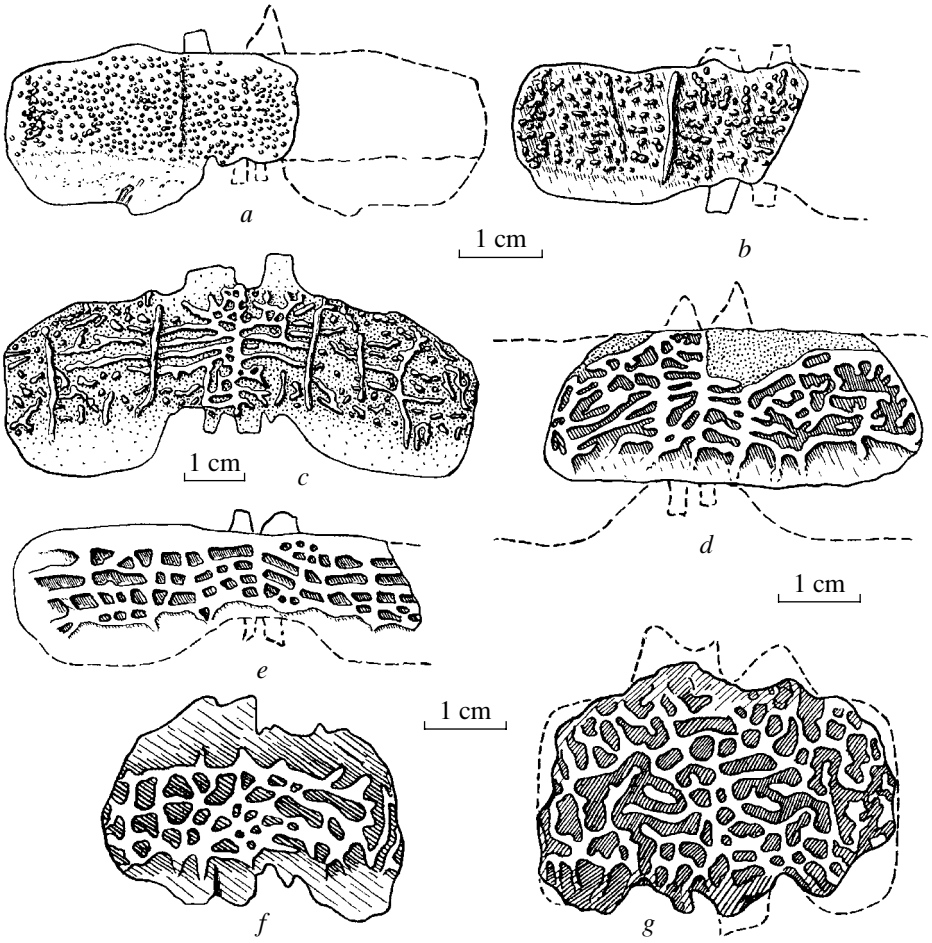


Fig. 1. Scute dermal sculpture types in the family Chroniosuchidae: (*a*) pustular, *Chroniosaurus dongusensis*, topotype PIN, no. 3585/119; (*b*) pectinate, *Chroniosaurus levis* sp. nov., holotype SGU, no. 104B/1102; (*c*) cristate, *Jarilinus mirabilis* gen. nov., topotype PIN, no. 523/20; (*d*) pitted, *Chroniosuchus licharevi*, specimen PIN, no. 2005/2578; (*e*) pitted, *Chroniosuchus paradoxus*, topotype PIN, no. 521/3; (*f*) and (*g*) pitted, *Uralerpeton tverdochlebovae*, paratype PIN, no. 1100/94 and holotype PIN, no. 1100/8 correspondingly.

type formed of isolated tubercles evenly distributed over the surface is the initial form (Fig. 1a; Pl. 4, figs. 1 and 2). This term was suggested by Shishkin (1987). The pectinate type is characterized by fusion of the neighboring tubercle bases that results in the formation of short low vermiform crests bearing several prominent knobs (pectens). The pectens are disposed mainly transversely. The other characteristic feature of this scute type is the presence of two–five distinctly exhibited longitudinal swollen crests (cristae). The cristae may occupy the area on the scute body along the medial line, along the scute body and borders of the wings (the most frequently occurring position) and directly on the wing surface (Fig. 1*b*; Pl. 4, figs. 3–5). The cristate type is distinguished by further fusion of tubercles resulting in the formation of several distinct transverse crests of the second order (Fig. 1*c*; Pl. 5, fig. 1) between the longitudinal crests of the first order. Occurrence of numerous anastomoses between the transverse cristae results in the formation of pitted sculpturing. The pits may be of regular isometric (Figs. 1*e*–1*f*), or irregular shape (Figs. 1*d* and 1*g*; Pl. 5, figs. 2–6). The distinct longitudinal cristae, characteristic of the pectinate and cristate types are less expressed in this case and sometimes are absent. Numerous intermediate ornamentation types are observable between the main ones.

A certain scute ornamentation type, independent of its size, is characteristic for the scutes from particular localities. The observable individual variation range does not exceed the extent of distinctions between the main types considered above, and includes intermediate sculpture forms from those typical for the given locality and the neighboring ones. For example, the pustular sculpture is characteristic of the "*Jugosuchus boreus*" scutes from Poteryakha-2 locality (Vologda Region). Nevertheless, some samples demonstrate sculpturing transitive towards the pectinate type. The extreme deviation type is displayed in the specimen PIN, no. 3713/57. The tubercle bases of the dorsal surface of the scute body fuse in this specimen forming short

Upper Tatarian correlation chart from the terrestrial vertebrate fauna

System	Division	Stage	Substage	Regional Stage	Provincial zones by tetrapods		Zonal assemblage	Faunistics	
					Zone	Subzone		Assemblage	Subassemblage
Permian	Upper	Tatarian	Upper	Vyatkian	*Archosaurus rossicus*		Archosaurus, Uralerpeton, Bystrowiana, *Dvinosaurus egregius, D. purlensis*, Whaitsiidae, Dicynodon, Karpinskiosauridae	Vyazniki	
					Scutosaurus karpinskii	*Chroniosuchus paradoxus*	Scutosaurus, Inostrancevia, Annatherapsidus, Chroniosuchus, Jarilinus, Karpinskiosauridae, Dicynodon, *Dvinosaurus primus*, Cynodontia	Sokolki	Sokolki
						Jarilinus mirabilis			
				Severodvinian	*Proelginia permiana*	*Chroniosaurus levis*	Proelginia, Chroniosaurus, Oudenodon, Sauroctonus, *Dvinosaurus primus*, Leptorophidae, Galeopidae		Ilyinskoye
						Chroniosaurus dongusensis			
					Deltavjatia vjatkensis		Deltavjatia, Tropidostoma, Galeopidae, Ictidosuchidae, Nycteroleteridae, Leptorophidae, *Chroniosuchidae* gen. et sp. nov.	Kotel'nich	

transverse vermiform tuberculated crests characteristic of the pectinate type scutes. Longitudinal crests are always present. However, in this case they are essentially pectens and do not look like swollen ridges typical for pectinate scutes. On the other hand, the "*J. boreus*" scutes from Mutovino (Vologda Region) belong to the pectinate type. However, there are also the forms varying towards the pustular (specimen SGU no. 104B/1109) or cristate (specimen SGU no. 104B/1100) types. Nonetheless, specimen SGU no. 104B/1109 is indistinguishable from specimen PIN, no. 3713/57 considered above. Nevertheless, typically pustular or cristate type scutes are absent from Mutovino.

The variation principle of the scute dermal ornament in the chroniosuchids described above is characteristic of all localities: the scutes of the typical pustular, pectinate, cristate or pitted type were never found together. Theoretically such a joint occurrence is possible, but only for the types next in the morphological row. However, in the particular sites, the scutes of the types representing extreme variation examples should be very seldom found. The bulk of scutes in the sample in this case would be those of intermediate type.

Thus, the character of the dorsal armor scutes dermal ornamentation is a character specific for various chroniosuchid groups. These groups are similarly geographically distributed, but separated from each other stratigraphically. The chroniosuchids possessing pustular and pectinate type scutes make a part of the Ilyinskoye faunistic subassemblage structure, and those with pitted type scutes occupy the place in the younger, Sokolki subassemblage structure (table). The chroniosuchid scute distribution pattern in the Tatarian section of the Sukhona River is even more distinctly represented (Fig. 2). The scutes of the pustular type are found in the Ustye Strelny locality (Poldarsa Formation, the upper part of the Strel'na unit). The pustular-pectinate type scutes are found in the stratigraphically higher Mikulino locality (the lower part of the Purtovino unit). The pectinate type scutes are found even higher in the Mutovino and Maryushkina Sluda-C localities (the Kichuga unit). The Salaryovo locality (Salaryovo Formation, the upper part of the Rovdino unit) yielded a scute fragment of the cristate-pitted type. Finally, in the uppermost part of the Sukhona River section (Aristovo locality, the Salaryovo unit) only the scutes of the pitted sculpturing type occur. Thus, the available data suggest, that the morphological row of dermal ornament scute types in the chroniosuchids (pustular–pectinate–cristate–pitted) described above reflects an evolutionary trend of this skeleton part in this group. Obviously, this feature can be used for systematic purposes.[3]

[3] Conclusion on the changing of the scute sculpturing type ontogenetically (Ivachnenko and Tverdochlebova, 1980, p. 7) is based upon the "*Jugosuchus boreus*" and "*J. hartmanni*" material. Both forms were described at the base of various chroniosuchid species remains (for synonymy see below) from the localities differing in their stratigraphical position: "*J. boreus*" from the Mikulino, Mutovino, Poteryakha and Kochevala-1; and "*J. hartmanni*" from the Syomin Ovrag and Klyuchevoi Ovrag.

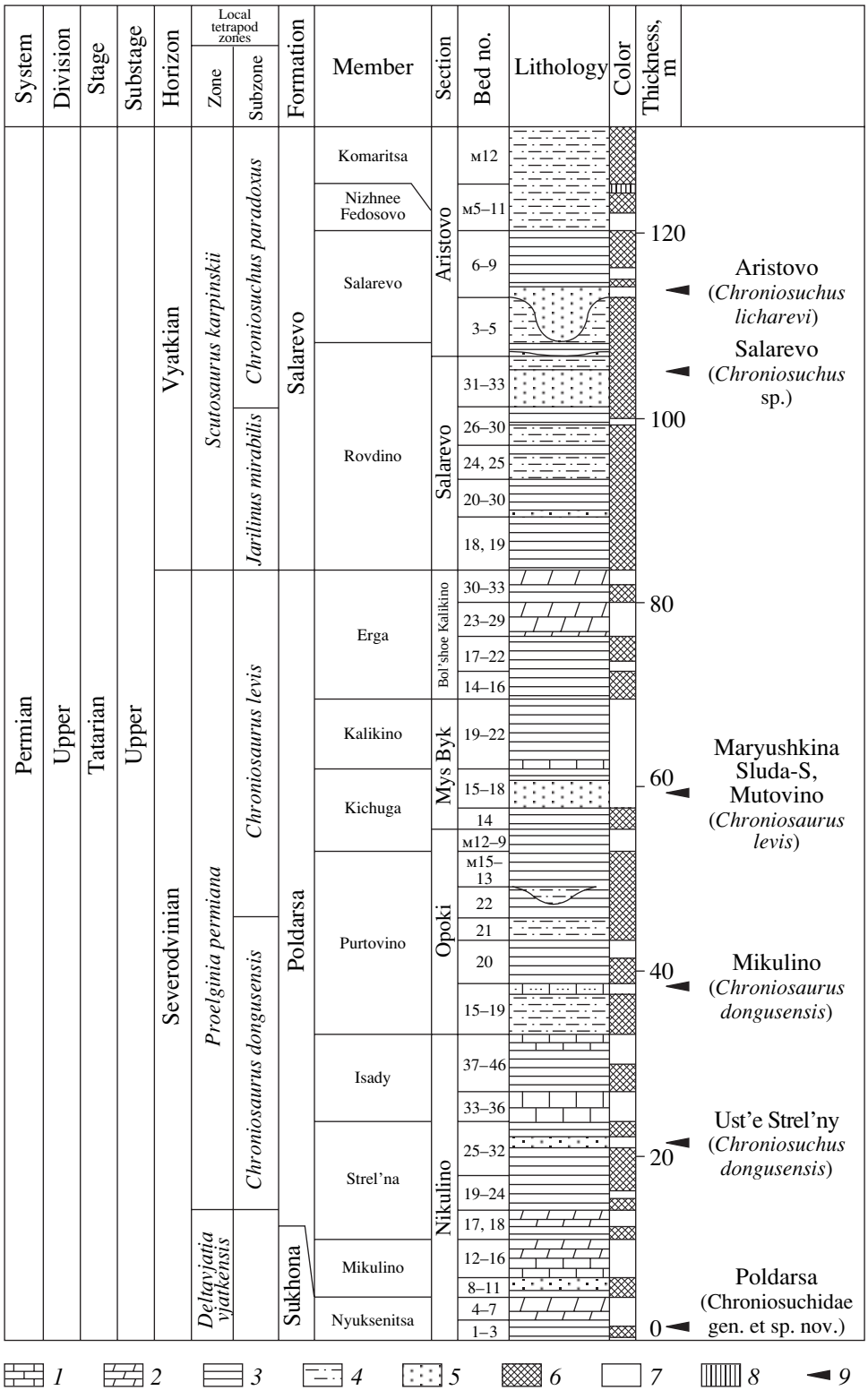
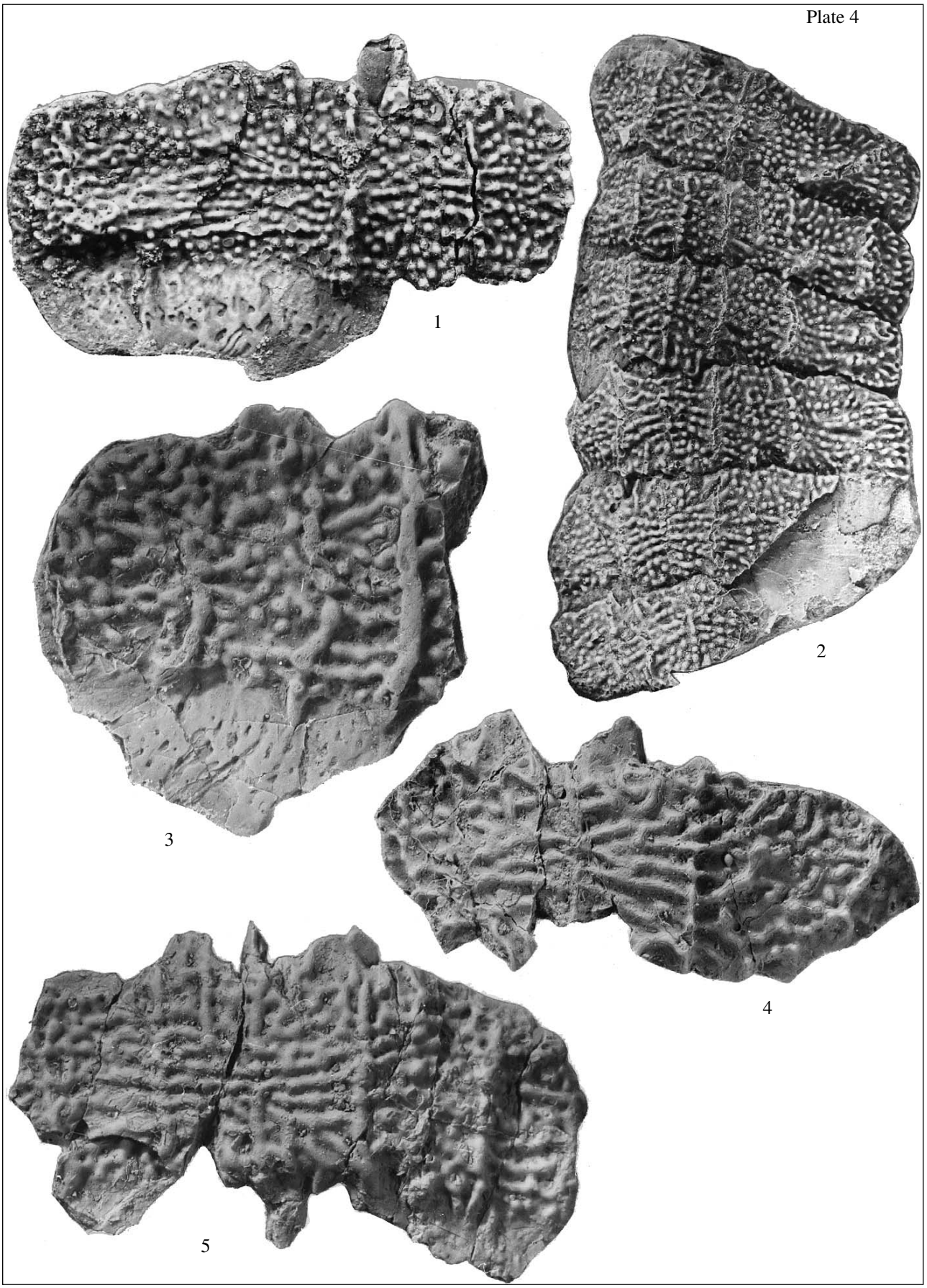


Fig. 2. Distribution of chroniosuchid remains in the Upper Tatarian section of the east wing of the Sukhona Rampart (Sukhona River from the village of Poldarsa to the river mouth). Legend: (*1*) limestones, (*2*) marls, (*3*) silts, (*4*) packstones, (*5*) sandstones, (*6*) redbed rocks, (*7*) greybed rocks, (*8*) redbed and greybed rocks intercalation, (*9*) tetrapod sites.

Plate 4



Explanation of Plate 4

Figs. 1 and 2. *Chroniosaurus dongusensis* Tverd.; Upper Permian, Upper Tatarian, Severodvinian Regional Stage, *Chroniosaurus dongusensis* provincial subzone: (1) topotype PIN, no. 3585/119, the body and left dorsal armor trunk scute wing from above, ×2.9, Orenburg Region, Orenburg District, Donguz-6; (2) specimen PIN, no. 3713/55, dorsal armor fragment from above, ×1.7, Vologda Region, Nyuksenitsa District, Poteryakha-2.

Figs. 3–5. *Chroniosaurus levis* sp. nov.; Upper Permian, Upper Tatarian, Severodvinian Regional Stage, *Chroniosaurus levis* provincial subzone: (3) paratype PIN, no. 4645/5, trunk scute left wing from above, ×2.9, Orenburg Region, Buzuluk District, Preobrazhenka; (4) paratype SGU, no. 104B/1100, ×2.1, trunk scute from above, Vologda Region, Velikii Ustyug District, Mutovino; (5) paratype SGU, no. 104B/1097 ×2.0, trunk scute from above, Vologda Region, Velikii Ustyug District, Mutovino.

Various skeletal parts are selected as holotypes of available chroniosuchid species, that are frequently hardly suitable for species diagnostics. However, extensive additional material including armor scutes is known in the majority of taxa from the type localities.

The pustular type scutes are known in *Chroniosaurus dongusensis* (Pl. 4, fig. 1) and "*Jugosuchus hartmanni*". The scutes of "*Jugosuchus boreus*" from the type locality belong to the intermediate pustular–pectinate type (specimen PIN, no. 3712/6–8). However, all chroniosuchids occurring in the Severodvinian Regional Stage of the Sukhona River (Ivachnenko, Tverdochlebova, 1980) were assigned to this species. Typically pustular (Poteryakha-1 and Poteryakha-2, Navoloki, Ustye Strelny; Fig. 1*b*; Pl. 1, fig. 2) as well as pectinate (Mutovino, Maryushkina Sluda-C; Pl. 4, figs. 4 and 5) type scutes are currently known from these deposits.

The chroniosuchids possessing the pustular and pectinate scutes are characterized by common distinctive features of the cranial morphology. The skull surface is ornamented by pustules, pectens or intermediate sculpture. Two pairs of well expressed sculpturing crests are characteristic. The first pair of crests evolves in the ossification centers of the postparietals and runs forwards along the parietals, postfrontals, frontals and prefrontals becoming gradually shallower. In a number of cases the crests may start immediately on the parietals. The crests of the second pair run anteromedially from the postero-lateral corner of the skull roof along the tabulars and parietals and sharply terminate behind the pineal foramen slightly posteriorly from the crests of the first pair.

There are some distinctions between the members of different localities within the chroniosuchid group under consideration. However, these distinctions are size-dependent and are displayed only because in the particular sites the skeletal parts of certain dimensional class forms prevail. Thus, *Chroniosaurus dongusensis* in the type locality is exemplified generally by very small individuals whose medial skull length does not exceed 7 cm. In these specimens the neural arches do not fuse to the centra and the intercentra are ring-shaped.[4] Nevertheless, four comparatively large spherical intercentra usual for chroniosuchids are present in the collection (specimen PIN, no. 3585/115–118). Slightly larger chroniosaurs (medial skull length of about 10 cm) from the Babintsevo locality (Orenburg Region) are also characterized by unfused neural arches to the vertebral centra. However, their intercentra are already mainly disk-shaped (specimen PIN, no. 4617/108). *Chroniosuchus paradoxus* (Pron'kino) is similar in size and its vertebral column elements are similarly built. Probably, these morphological features of small chroniosuchids are only juvenile.

The other variable character is the relative size of interorbital distance. Data describing interorbital width (Iow) and skull roof width (Iiow) in various chroniosuchids are listed below.

Locality and specimen number	Iow, mm	Iiow, mm	Iiow/Iow
Chroniosaurus dongusensis			
Donguz-6 (PIN, no. 3585/96)	6.0	18.0	3.0
Donguz-6 (PIN, no. 3585/94)	7.0	21.0	3.0
Donguz-6 (PIN, no. 3585/95)	7.5	21.5	2.9
Donguz-6 (PIN, no. 3585/100)	6.7	22.5	3.4
Donguz-6 (PIN, no. 3585/97)	7.0	22.5	3.2
Donguz-6 (PIN, no. 3585/99)	8.0	24.0	3.0
Babintsevo (PIN, no. 4617/20)	9.0	27.0	2.5
Babintsevo (PIN, no. 4617/1)	10.0	28.0	2.3
Poteryakha-2 (PIN, no. 3713/13)	14.0	34.0	2.4
Poteryakha-2 (PIN, no. 3713/38)	21.0	43.0	2.1
Poteryakha-2 (PIN, no. 3713/58)	24.0	50.0	2.1
Syomin Ovrag (PIN, no. 156/250)	31.0	59.0	1.9
Chroniosuchus licharevi			
Zavrazhye (SGU, no. 104B/1630)	16.0	44.0	2.8
Aristovo (PIN, no. 2357/2)	22.0	56.0	2.6
Sokolki (PIN, no. 2005/2579)	29.0	62.0	2.1
Chroniosuchus paradoxus			
Pron'kino (PIN, no. 521/5)	9.0	31.0	3.4
Blyumental-3 (PIN, no. 2896/6)	12.5	39.0	3.1
Blyumental-3 (SGU, no. 104B/1014)	20.0	52.0	2.6
Jarilinus mirabilis			
Gorkii-1 (PIN, no. 523/1)	25.0	52.0	2.1

In the Donguz forms the maximum width of the postorbital parts of the skull roof is 2.9–3.4 times larger than the width of the interorbital space; in the Babintsevo ones it is 2.3–2.5 times larger and in the Poteryakha taxa it is 2.1–2.4 times larger; in the Syomin Ovrag species it is 1.9 times larger. The amounts of these

[4] The semilunar intercentra noted by earlier authors (Tverdochlebova, 1972; Ivachnenko and Tverdochlebova, 1980), belong to a leptorophid parareptile *Raphanodon tverdochlebovae* instead of *Chroniosaurus.*

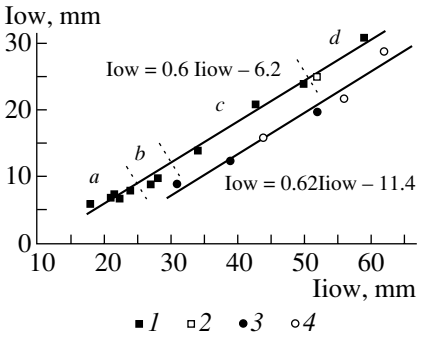


Fig. 3. Dependence of interorbital space width (Iow) from the skull roof width (Iiow) in various Chroniosuchidae members: (*1*) *Chroniosaurus dongusensis* (localities (*a*) Donguz-6, (*b*) Babintsevo, (*c*) Poteryakha-2, (*d*) Syomin Ovrag); (*2*) *Jarilinus mirabilis*; (*3*) *Chroniosuchus paradoxus*; (*4*) *Chroniosuchus licharevi*. For digital information see the Table in the text.

parameters are characterized by linear dependence (Fig. 3), linear regression described by an equation:

$$\text{Iow} = 0.61 \times \text{Iiow} - 6.2.$$

The revealed distinctions in the proportions of this skull part in various forms are the consequences of allometric growth.

Pitted scutes are characteristic of *Chroniosuchus paradoxus* (Pl. 5, figs. 2–4), "*C. uralensis*" and *Uralerpeton tverdochlebovae*. Pits may vary in shape significantly, but remain more or less regular. The chroniosuchids from the Aristovo and Sokolki localities (Arkhangelsk and Vologda Regions) contrast in the irregular shape of the scute pits. Skull fragments were found here together with the postcranial material. The chroniosuchids possessing pitted scutes also share some cranial morphological features. Their skull surface is pitted, more seldom pitted and cristate. The sculptural crests on the skull roof in large individuals are lacking, but in comparatively small specimens (*C. paradoxus*) two short anterolaterally directed crests on the parietal behind the pineal foramen may be present (specimen PIN, no. 521/5). As well as in the *Chroniosaurus dongusensis* group, the skull proportions in the interorbital part in the discussed forms also change with the increase in size. At the same time, the dependence of the interorbital space width (Iow) from the skull roof width (Iiow) is also linear (Fig. 3), but is described by an equation of linear function with other factors:

$$\text{Iow} = 0.62 \times \text{Iiow} - 11.4.$$

Comparison of this equation with a similar equation for the *Chroniosaurus dongusensis* group shows, that they are authentically distinguished only by factors "–6.2" and "–11.4". That means that at the same Iiow sizes the distance between the medial orbit edges in the *Chroniosuchus paradoxus* group would be 5 mm less on average, than in the *Chroniosaurus dongusensis* group, i.e., the chroniosuchids of *Chroniosuchus paradoxus* group are characterized by more closely spaced orbits. The skull fragment of a chroniosuchid from Zavrazhye ("*Chroniosuchus vjuschkovi*" topotype, specimen SGU, no. 104B/1630) is also characterized by rather close position of the orbits (Fig. 3). The crests on the parietals are similar to those of *Chroniosuchus paradoxus* topographically and morphologically.

"*Jugosuchus mirabilis*" occupies an intermediate position between the chroniosuchid groups considered. This form is characterized by an intermediate, cristate type of scute sculpture (Pl. 5, fig. 1). The skull roof surface is covered by a pitted sculpture and does not bear sculptural crests, as in the *Chroniosuchus paradoxus* group members. However, the distance between the orbits is comparatively large, as in the *Chroniosaurus dongusensis* group members (Fig. 3).

RESULTS

As was already mentioned, the chroniosuchids are very uniform morphologically. All characters making possible classification of chroniosuchids, and useful for systematic purposes were, discussed above: (1) scute width; (2) scute sculpturing type; (3) skull surface sculpturing type; (4) presence and traits of the sculptural crests on the skull roof; (5) relative size of interorbital space. These features being displayed in a complex characterize certain chroniosuchid morphotypes. All other distinctions, as suggested by abundant material, are a consequence of individual or ontogenetic variability.

Minor morphological variability in the chroniosuchids, smooth transitions from one morphotype to another, stratigraphical separation of chroniosuchid remains of various morphotypes, conformity of the morphological types sequence with the stratigraphical distribution sequence of their remains and common distribution territory, suggest that all known chroniosuchids belong to a single phylogenetic lineage. The general chroniosuchid evolutionary direction was displayed by adult size increase, change of the dermal skull and scute armor ornament from pustular to pitted type, reduction of interorbital space, and beginning of the dorsal armor reduction in the late phylogenetic stages. The particular stages of chroniosuchid evolution match certain morphotypes. The chroniosuchids, characterized by particular morphotypes, evidently inhabited the basins in the territory of the whole of eastern Europe at precise times of the Late Tatarian. The earlier morphotypes that existed here had been their ancestors, and those which lived here later were the descendants. Thus, known chroniosuchid interrelations are defined only as ancestor–descendant relationships.

Obviously, certain chroniosuchid morphotypes may be considered as separate species. These species are connected to each other by gradual evolutionary transitions and characterize only certain parts of a single phy-

logenetic lineage. As the chroniosuchids were a rapidly and smoothly evolving group, the amount of particular sections constituting this phylogenetic lineage, that is the amount of species, may be rather large. However, the more fractional the chroniosuchid system, the more difficult would it be to diagnose the species. The evolution of this group looks continuous, and the borders between species appear rather conditional. Great difficulties arise in the definition of the specific position of intermediate forms. Individual variability, which influences the result of diagnostics, is inversely proportional to the amount and quality of the available material and complicates the task as well. In my opinion, the species in this case should be erected on the basis of morphotypes that strictly differ from the neighboring ones within the morphological row. Thus, the distinctions between morphotypes should exceed the range of individual variability.

The dermal scute armor ornament is characterized by the fastest evolutionary rate among the features defining the particular chroniosuchid morphotypes. It is this character that is considered here to be of the specific rank. Chroniosuchid members possessing the scutes belonging to one of the sculptural types described above are regarded here as separate species. All other characters change much slower and are regarded here as generic. Four genera and six species of the family Chroniosuchidae, forming a single phylogenetic lineage: *Chroniosaurus dongusensis–Chroniosaurus levis* sp. nov.*–Jarilinus mirabilis* gen. nov.*–Chroniosuchus paradoxus* and *Chroniosuchus licharevi–Uralerpeton tverdochlebovae* could be currently recognized.

SYSTEMATIC PALEONTOLOGY

Family Chroniosuchidae Vjuschkov, 1957

Genus *Chroniosaurus* Tverdochlebova, 1972

Chroniosaurus: Tverdochlebova, 1972, p. 95; Ivachnenko and Tverdochlebova, 1980, p. 7.

Jugosuchus: Ivachnenko and Tverdochlebova, 1980, p. 10 (partim).

Type species: *Chroniosaurus dongusensis* Tverdochlebova, 1972.

Diagnosis. Skull length along median line up to 25 cm. Skull dermal ornamentation pustular or pectinate. Two pairs of well expressed sculptural crests on skull roof present. Orbits widely separated. Tubercles are basic elements of dorsal armor scute dermal ornament.

Species composition. Two species: *C. dongusensis* Tverdochlebova, 1972 and *C. levis* sp. nov.

Chroniosaurus dongusensis Tverdochlebova, 1972

Plate 4, figs. 1 and 2

Chroniosaurus dongusensis: Ivachnenko and Tverdochlebova, 1980, p. 7, text-figs. 1, 9b, 11a, 12, 13a, 14a; Tverdochlebova, 1972, p. 96 (partim), text-figs. 1 and 2.

Jugosuchus boreus: Ivachnenko in Ivachnenko and Tverdochlebova, 1980, p. 12 (partim), text-fig. 6 (partim).

Jugosuchus hartmanni: Ivachnenko in Ivachnenko and Tverdochlebova, 1980, p. 12 (partim), text-fig. 7 (non text-fig. 14f).

Holotype. SGU, no. 104B/198, skull; Orenburg Region, Orenburg District, Donguz-6; Upper Permian, Upper Tatarian, middle part of the Severodvinian Regional Stage.

Diagnosis (Fig. 1*a*; Pl. 4, figs. 1 and 2). Scute sculpture of pustular type.

Remarks. "*Jugosuchus hartmanni*" was described from the material from the Syomin Ovrag and Klyuchevoy Ovrag, which was combined in one collection (PIN, no. 156). This material includes the scutes of the pustular (*Chroniosaurus dongusensis*, specimens nos. 254, 256–260) and pitted types (*Chroniosuchus* cf. *paradoxus* specimens nos. 252, 253, 255). It should be stated, that the former comes from the Syomin Ovrag locality, and the latter from the Klyuchevoy Ovrag judging from the specimen's preservation type, as well as faunistic considerations.

Occurrence. Upper Permian, Upper Tatarian, middle part of the Severodvinian Regional Stage; Eastern Europe.

Material. Apart from holotype, numerous skeletal parts from the type locality specimens PIN, nos. 3585/93–97, 100, 115–120, 124 and SGU, nos. 104B/238; Poteryakha-2 (Vologda Region) specimens PIN, nos. 3713/1, 2, 11, 13, 19, 38, 39, 54–58; Babintsevo (Orenburg Region) specimens PIN, nos. 4617/1, 2, 108; Mikulino (Vologda Region) specimens PIN, nos. 3712/1, 6–8; Ustye Strelny (Vologda Region) specimens PIN, nos. 4548/11–15; Navoloki (Vologda Region) specimen PIN, no. 3709/5; Syomin Ovrag (Tatarstan), specimens PIN, nos. 156/250, 251, 254, 256–260.

Chroniosaurus levis Golubev sp. nov.

Plate 4, figs. 3–5

Jugosuchus boreus: Ivachnenko in Ivachnenko and Tverdochlebova, 1980, p. 12 (partim), text-fig. 6 (partim), 10a and 10d.

Etymology: From Latin *levis* (swift).

Holotype. SGU, no. 104B/1102, trunk scute; Vologda Region, Velikii Ustyug District, Mutovino; Upper Permian, Upper Tatarian, upper part of the Severodvinian Regional Stage.

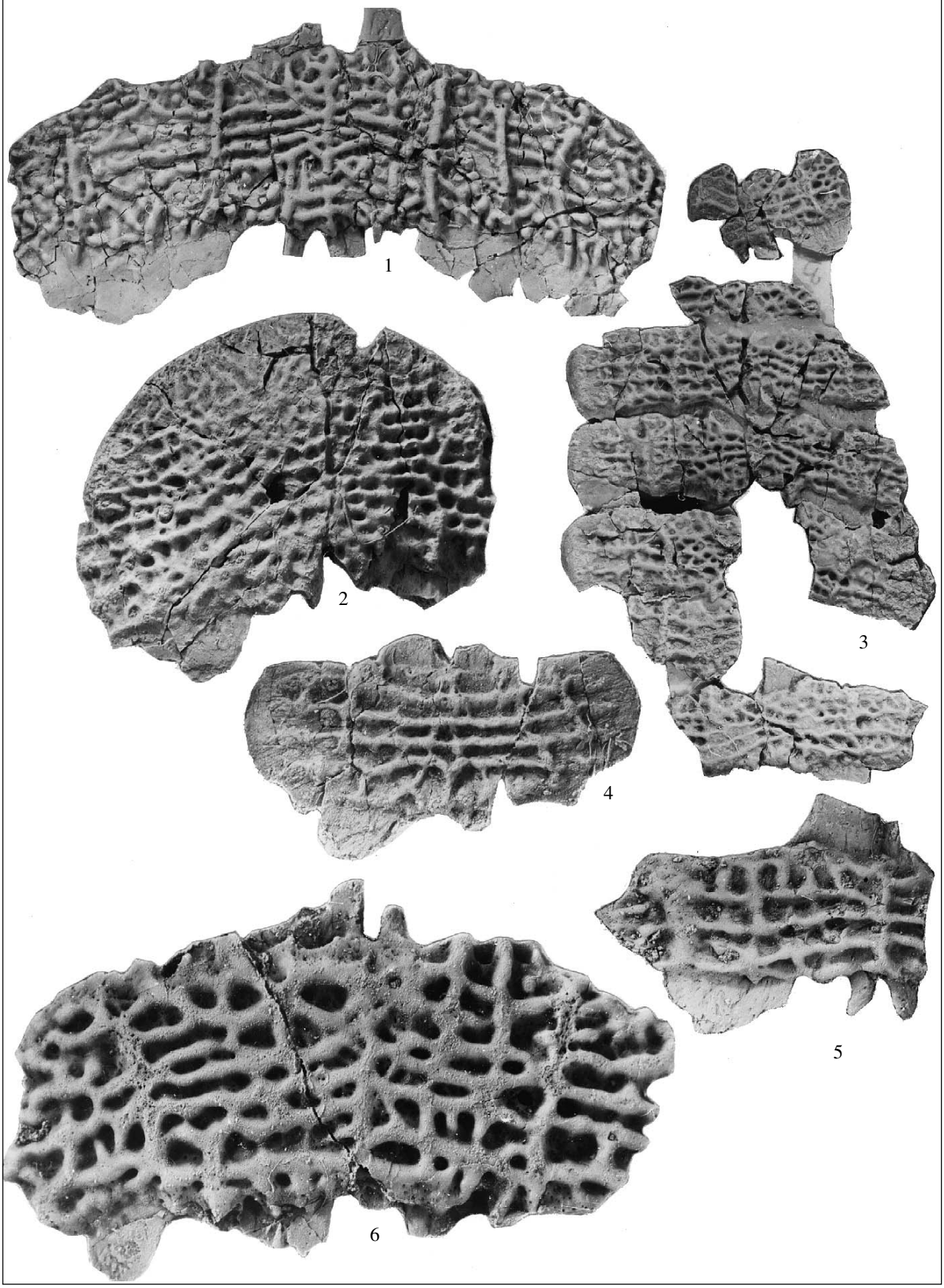
Diagnosis (Fig. 1*b*; Pl. 4, figs. 1–3). Scute ornament of the pectinate type.

Comparison. Differs from *C. dongusensis* by the pectinate type of armor scute dermal sculpturing.

Occurrence. Upper Permian, Upper Tatarian, upper part of the Severodvinian Regional Stage; East Europe.

Material. Beside holotype, skull and armor fragments from the type locality specimens PIN, nos. 3711/2, 21 and specimens SGU, nos. 104B/1086,

Plate 5



1097, 1100, 1101, 1106, 1107, 1109, 1112, 1114, 1117, 1118, 1180; Maryushkina Sluda-C (Vologda Region) specimens PIN, nos. 4412/12–14; Gorkovskii Gidrouzel (Nizhnii Novgorod Region) specimens PIN, nos. 3710/1–5; Preobrazhenka (Orenburg Region) specimens PIN, nos. 4645/5, 7–10; Sokolya Gora (Kirov Region) specimen PIN, no. 4679/1.

Genus *Jarilinus* Golubev gen. nov.

Chroniosuchus: Vjuschkov, 1957, p. 184 (partim).

Jugosuchus: Ivachnenko and Tverdochlebova, 1980, p. 10 (partim).

Etymology. From the Yarilskii Ovrag, the type locality.

Type species. *Chroniosuchus mirabilis* Vjuschkov, 1957.

Diagnosis. Skull length along median line up to 25 cm. Skull dermal sculpture of pitted type. Orbits widely spaced. Cristae are basic elements of armor scute dermal ornament.

Species composition. Type species.

Comparison. Differs from the genus *Chroniosaurus* by pitted dermal sculpture of the skull and absence of sculptural crests on the skull and pectinate type armor scute dermal sculpture.

Jarilinus mirabilis (Vjuschkov, 1957)

Plate 5, fig. 1

Chroniosuchus mirabilis: Vjuschkov, 1957, p. 184, text-fig. 3.

Jugosuchus mirabilis: Ivachnenko and Tverdochlebova, 1980, p. 11, text-figs. 5, 10c, and 14d.

Holotype. PIN, no. 523/1, skull fragment; Nizhnii Novgorod Region, Nizhnii Novgorod District, Gorkii-1; Upper Permian, Upper Tatarian, lower part of the Vyatkian Regional Stage.

Diagnosis (Fig. 1*c*, Pl. 5, fig. 1). As for the genus.

Occurrence. Upper Permian, Upper Tatarian, lower part of the Vyatkian Regional Stage; Eastern Europe.

Material. Beside the holotype, trunk scutes from the type locality specimens PIN, nos. 523/13, 20, 24–26, 35; Zubochistenka-2 (Orenburg Region), specimens SGU, nos. 104B/688 and 689.

Genus *Chroniosuchus* Vjuschkov, 1957

Chroniosuchus: Vjuschkov, 1957, p. 184 (partim); Ivachnenko and Tverdochlebova, 1980, p. 8.

Jugosuchus: Ivachnenko and Tverdochlebova, 1980, p. 10 (partim); Riabinin and Shishkin, 1962, p. 141.

Type species. *Chroniosuchus paradoxus* Vjuschkov, 1957.

Diagnosis. Skull length along median line up to 30 cm. Skull dermal sculpture of pitted or pitted-cristate type. One pair of sculptural crests on skull roof on parietals postero-laterally from pineal foramen present only in juveniles, if any. Orbits rather closely spaced. Armor scute sculpture pitted.

Species composition. Two species: *C. paradoxus* Vjuschkov, 1957 and *C. licharevi* (Riabinin and Shishkin, 1962).

Comparison. Differs from *Chroniosaurus* and *Jarilinus* by larger size, comparatively narrower interorbital space and pitted type of the armor scute dermal sculpture. Besides that, differs from *Chroniosaurus* by pitted or pitted-cristate dermal sculpture of the skull, absence or presence of a single pair of short sculptural crests on the parietals.

Remarks. The phylogenetic relations between *C. paradoxus* and *C. licharevi* remain unclear. Each of those may be regarded as transitional from *Jarilinus mirabilis* to *Uralerpeton tverdochlebovae*. On the other hand, their remains are similarly distributed stratigraphically, but their geographical domains are different. This may indicate, that these forms are the subspecies of a single species. Nevertheless, until this conclusion becomes more satisfactorily supported, it should be more correct to consider them as distinct species.

Occurrence. Upper Permian, Upper Tatarian, middle part of the Vyatkian Regional Stage; Eastern Europe.

Chroniosuchus paradoxus Vjuschkov, 1957

Plate 5, figs. 2–6

Chroniosuchus mirabilis: Tverdochlebova, 1968, p. 11 (partim), text-figs. 1–4.

Chroniosuchus paradoxus: Vjuschkov, 1957, p. 184, text-figs. 1 and 2; Ivachnenko and Tverdochlebova, 1980, p. 8, text-figs. 2, 9a, 13b, 14b.

Chroniosuchus uralensis: Tverdochlebova in Ivachnenko and Tverdochlebova, 1980, p. 9 (partim), text-figs. 3 and 14c.

Jugosuchus hartmanni: Ivachnenko in Ivachnenko and Tverdochlebova, 1980, p. 12 (partim), text-fig. 14f (non text-fig. 7).

Explanation of Plate 5

Fig. 1. *Jarilinus mirabilis* Vjuschkov, topotype PIN, no. 523/20, trunk scute from above, ×1.5, Nizhnii Novgorod Region, Gorkii-1; Upper Permian, Upper Tatarian, Vyatkian Regional Stage, *Jarilinus mirabilis* provincial subzone.

Figs. 2–6. *Chroniosuchus paradoxus* Vjuschkov; Upper Permian, Upper Tatarian, Vyatkian Regional Stage, *Chroniosuchus paradoxus* provincial subzone: (2)–(4) topotypes, PIN, no. 521/4, first cervical scute, ×2.0, no. 521/3, dorsal armor fragment, ×1.2, no. 521/77, anterior caudal scute, ×2.8, all from above; Orenburg Region, Sorochinsk District, Pron'kino; (5) specimen SGU, no. 104B/810, trunk scute from above, ×3.1, Orenburg Region, Perevoloki District, Adamovka; (6) specimen SGU, no. 104B/528, trunk scute from above, ×2.8, Orenburg Region, Orenburg District, Vyazovka-1.

Holotype. PIN, no. 521/6, vertebral column fragment; Orenburg Region, Sorochinsk District, Pron'kino; Upper Permian, Upper Tatarian, middle part of the Vyatkian Regional Stage.

Diagnosis (Fig. 1*e*, Pl. 5, figs. 2–6). Scute dermal sculpturing consists of regular, often isometric pits.

Occurrence. Upper Permian, Upper Tatarian, middle part of the Vyatkian Regional Stage; East Europe.

Material. Beside holotype, skull and armor fragments from the type locality specimens PIN, nos. 521/3–5, 77; Blumental-3 (Orenburg Region) specimens SGU, nos. 104B/431, 432, 1014, 1015 and specimen PIN, no. 2896/6; Klyuchevka (Orenburg Region), specimen PIN, no. 4415/2; Vyazovka-1 (Orenburg Region), specimens SGU, nos. 104B/528, 529; Adamovka (Orenburg Region), specimens SGU, nos. 104B/804, 808, 810, 812, 814, 816.

Chroniosuchus licharevi (Riabinin, 1962)

Chroniosuchus sp.: Vjuschkov, 1957, p. 185, text-fig. 4.

Jugosuchus licharevi: Riabinin in: Riabinin and Shishkin, 1962, p. 142, text-figs. 1 and 2; Ivachnenko and Tverdochlebova, 1980, p. 10, text-figs. 4 and 10b.

Chroniosuchus vjuschkovi: Tverdochlebova, 1967, p. 34.

Chroniosuchus licharevi: Tverdochlebova, 1968, p. 12.

Holotype. TsNIGR, no. 5813/1, lower jaw imprint; Vologda Region, Velikii Ustyug District, Savvatii; Upper Permian, Upper Tatarian, middle part of the Vyatkian Regional Stage.

Diagnosis (Fig. 1d). Scute dermal ornament pits irregularly shaped.

Comparison. Differs from *C. paradoxus* by pit shape of the armor scutes dermal ornament.

Remarks. The material from the type locality Savvatii is hardly diagnostic. The chroniosuchid fragments from the Malaya Severnaya Dvina River are known also from the Sokolki, Zavrazhye and Aristovo localities. According to the geological information, kindly supplied by M.P. Arefyev, these sites belong to the same stratigraphic level, as Savvatii. The considered fragments are similarly built and probably belong to the same species. The valid name *Chroniosuchus licharevi* is retained for this group of remains.

Occurrence. Upper Permian, Upper Tatarian, middle part of the Vyatkian Regional Stage; Eastern Europe.

Material. Besides the holotype, skull and armor parts from: Sokolki (Arkhangelsk Region), specimens PIN, nos. 2005/2578, 2579; Aristovo (Vologda Region), specimens PIN, nos. 2357/2, 3, 5, and specimen SGU, no. 104B/1266; Zavrazhye (Arkhangelsk Region), specimen SGU, no. 104B/1630, specimen PIN, no. 2353/6.

Genus *Uralerpeton* Golubev, 1998

Uralerpeton: Golubev, 1998 (*cum syn.*).

Type species. *Uralerpeton tverdochlebovae* Golubev, 1998.

Diagnosis. Large chroniosuchid, reconstructed skull length up to 50–55 cm. Trunk scutes of narrow type (length of scute wings exceeds their width). Ventral scute process fuses with vertebral neural spine. Scute dorsal surface ornamented by pitted sculpture.

Species composition. Type species.

Comparison. Differs from *Chroniosuchus*, *Jarilinus*, and *Chroniosaurus* by large size, narrow trunk scute wings, scute fusion with the vertebral neural spine; from*Chroniosaurus* and *Jarilinus* by pitted dermal scute ornament.

Uralerpeton tverdochlebovae Golubev, 1998

Uralerpeton tverdochlebovae: Golubev, 1998 (*cum syn.*).

Holotype. PIN, no. 1100/8, trunk scute; Vladimir Region, Vyazniki District, Vyazniki-2; Upper Permian, Upper Tatarian, upper part of the Vyatkian Regional Stage.

Diagnosis (Figs. 1*f* and 1*g*). Same as for the genus.

Occurrence. Upper Permian, Upper Tatarian, upper part of the Vyatkian Regional Stage; Eastern Europe.

Material. The holotype and the type series (Golubev, 1998).

CONCLUSION

The fast rate of chroniosuchid evolution and wide distribution of their remains makes it possible to use this group for stratigraphic purposes. Four complex provincial zones may be currently established at the base of the tetrapod fauna in the Upper Tatarian deposits (from the bottom upwards, Pl. 1): *Deltavjatia vjatkensis* Zone (the lower part of the Severodvinian Regional Stage), *Proelginia permiana* Zone (upper part of the Severodvinian Regional Stage), *Scutosaurus karpinskii* Zone (the lower part of the Vyatkian Regional Stage), and *Archosaurus rossicus* zone (the upper part of the Vyatkian Regional Stage). These zones are characterized by the presence of the terrestrial vertebrate remains of the Kotel'nich, Ilyinskoye, Sokolki and Vyazniki assemblages respectively. Detailed faunistic characteristics of the assemblages was published by Golubev (1996). Specified assemblages put back the main developmental stages of the whole tetrapod fauna of Eastern Europe during the Late Tatarian. Chroniosuchid material makes possible a refinement of this zonal chart and institution of two subzones within the structure of the Proelginia permiana zone (*Chroniosaurus dongusensis* Subzone and *Chroniosaurus levis* Subzone) and Scutosaurus karpinskii zone (subzone *Jarilinus mirabilis* and subzone

Chroniosuchus paradoxus, including deposits containing the remains of all *Chroniosuchus members*: *C. paradoxus* and *C. licharevi*).

ACKNOWLEDGMENTS

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

REFERENCES

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

Golubev, V.K., Narrow-Armored Chroniosuchians (Amphibia, Anthracosauromorpha) from the Late Permian of Eastern Europe, *Paleontol. Zh.*, 1998, no. 3 (in press).

Ivachnenko, M.F. and Tverdochlebova, G.I., *Sistematika, morfologiya i stratigraficheskoe znachenie verkhnepermskikh khroniozukhov vostoka Evropeiskoi chasti SSSR* (Systematics, Morphology and Stratigraphical Importance of the Upper Permian Chroniosuchians of the East of the European part of the USSR), Saratov: Saratov Univ., 1980.

Riabinin, A.N. and Shishkin, M.A., On the Upper Permian Labyrinthodont *Jugosuchus*, *Paleontol. Zh.*, 1962, no. 1, pp. 140–145.

Shishkin, M. A., Evolution of the Early Amphibians, in *Tr. Paleontol. Inst., Akad. Nauk SSSR* (Moscow), 1987, vol. 225, pp. 1–143.

Shishkin, M. A. and Novikov, I. V., Relict Anthracosaurs in the Early Mezozoic of Eastern Europe, *Dokl. Ross. Akad. Nauk*, 1992, vol. 325, no. 4, pp. 829–832.

Tverdochlebova, G. I., On the Remains of the Genus *Chroniosuchus* from the Permian of the Orenburg Cisurals, *Izv. Vyssh. Uchebn. Zaved., Geol. Razved.*, 1967, no. 9, pp. 31–35.

Tverdochlebova, G.I., On the Genera *Chroniosuchus* and *Jugosuchus* from the Upper Tatarian deposits of the USSR, in *Verkhnepaleozoiskie i mezozoiskie zemnovodnye i presmykayushchiesya SSSR* (Upper Paleozoic and Mezozoic Amphibians and Reptiles of the USSR), Moscow: Nauka, 1968, pp. 11–15.

Tverdochlebova, G.I., A new Batrachosaur Genus from the Upper Permian of the South Urals, *Paleontol. Zh.*, 1972, no. 1, pp. 95–103.

Vjuschkov, B. P., New Unusual Animals from the Tatarian Deposits of the European part of the USSR, *Dokl. Akad. Nauk SSSR*, 1957, vol. 113, no. 1, pp. 183–186.