Paleontological Journal, Vol. 32, No. 3, 1998, pp. 278–287. Translated from Paleontologicheskii Zhurnal, No. 3, 1998, pp. 64–73.

Narrow-armored Chroniosuchians (Amphibia, Anthracosauromorpha) from the Late Permian of Eastern Europe

V. K. Golubev

Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, Moscow, 117647 Russia
Received January 21, 1997

Abstract—The Permian and Triassic chroniosuchians are revised and the morphology of the dorsal armor scutes is discussed in detail. The first narrow-armored chroniosuchid *Uralerpeton tverdochlebovae* from the Late Permian Vyazniki faunistic assemblage of Eastern Europe is described and the age of the Vyazniki fauna discussed.

INTRODUCTION

The chroniosuchians (Chroniosuchia), an unusual group of Late Permian and Triassic reptiliomorph amphibians, dominated the aquatic tetrapod assemblages of Eastern Europe during the Late Tatarian age. Conventionally this group, consisting of two families: the Chroniosuchidae and the Bystrowianidae (Tatarinov, 1972; Ivakhnenko and Tverdokhlebova, 1980; Shishkin and Novikov, 1992) is included within the order Anthracosauromorpha as suborder. According to the latest revision of the Permian chroniosuchians (Ivakhnenko and Tverdokhlebova, 1980), the family Chroniosuchidae includes the genera *Chroniosaurus* and *Chroniosuchus*, and the family Bystrowianidae comprises the genera *Jugosuchus* and *Bystrowiana*. The Lower Triassic genus *Axitectum* was later referred to the bystrowianids (Shishkin and Novikov, 1992). These authors noted in passing, that according to M. F. Ivakhnenko and in their view, the genus *Jugosuchus* should be referred to the Chroniosuchidae (Shishkin and Novikov, 1992). Significant new material on the Permian and Triassic chroniosuchians enables a revision of this group.

DESCRIPTIONS

One of specific chroniosuchian features is the armor covering the body and the anterodorsal part of the animal's tail. The armor consists of separate scutes arranged in a row along the vertebral column. Their number strictly corresponds to the number of vertebrae in the region of the armour. In *Chroniosaurus dongusensis* the armor consists of 30 scutes, including those of the cervical, trunk and caudal regions (specimen PIN, no. 3713/54). The scutes were not fused to each other, but instead were effectively connected by ligaments. Completely preserved fossilized armor and isolated fragments indicate that the disintegration of the armor occurred late in the process of decomposition of the animal: the head, the brachial and pelvic girdles and even the vertebral column became disarticulated sooner.

In horizontal plane the chroniosuchian scutes are rectangular (Figs. 1a and 1b; 2b and 2c; 4a–4d), except for the anteriormost scute, which is shaped like a semicircle or semiellipsis (Fig. 1d). The scute consists of a massive axial part, or the scute body (*corpus scutulumi*) and two lateral horizontal plates, or the scute wings (*alae scutulumi*) (Fig. 1a). The wings may be wide (the width usually exceeds the length by no more than twice) or narrow (length exceeds width), while in some forms they may be absent.[1] The scute dorsal surface is sculptured with tubercles, crests or pits-and-ridges. The ventral surface of the wings of the scute is mainly smooth and bears numerous small foramina. These foramina give rise to poorly expressed and rapidly flattening grooves on the lateral surface, impressions of, blood vessels. The lock for the articulation of the neighboring scutes is a complicated structure located on the ventral side of the body of the scute. Two main types of scute are distinguished by the structure of the lock and articulation: the chroniosuchian and the bystrowianian.

The chroniosuchian type. This type includes the *Chroniosuchus*, *Jugosuchus* and *Chroniosaurus* scutes. The members of these genera stand out in the wide armor which covered practically the whole dorsal part of the trunk. The trunk scutes bear well expressed wide wings, the caudal scutes narrow greatly posteriorly, and the posteriormost lack wings. A long strip that is devoid of sculpture extends approximately a third of the whole wing length along the posterodorsal edge and represents the overlap area for the next wing of the scute. Thus, the wings of the neighboring scutes overlap each

[1] Here and further on the length is a measurement taken parallel to the median line, width and depth taken normal to the median line in the horizontal and vertical planes correspondingly.

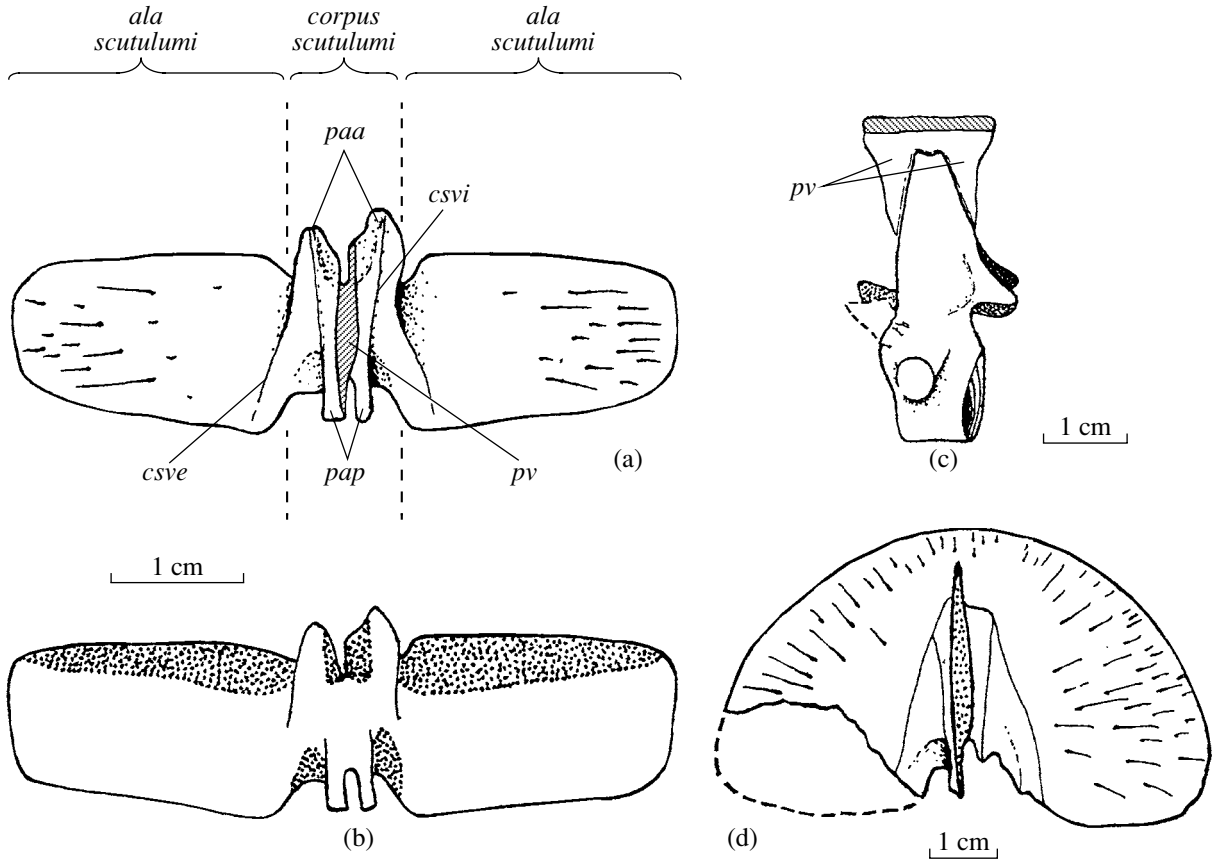

Fig. 1. *Chroniosaurus*: (a) *C. dongusensis* trunk scute ventrally, a reconstruction based upon the specimen PIN, no. 3713/1; (b) the trunk scute: dotted zones indicate overlap areas; (c) *C. boreus* trunk vertebra in left lateral view, specimen SGU, no. 104V/1145; (d) the first cervical scute of *C. dongusensis* ventrally, specimen PIN, no. 3713/39. Designations: *csve*—crista scutulumi ventralis externa, *csvi*—crista scutulumi ventralis interna, *paa*—processus articularis anterior, *pap*—processus articularis posterior, *pv*—processus ventralis.

other posteroanteriorly (specimens PIN, nos. 2005/2579; 3585/104; 3713/54, 55).

The descending ventral process (*processus ventralis*) forms the medial part of the lock; the former participates in the articulation of the scute with the neural spine (Figs. 1a and 1c). It is a vertical plate strongly flattened laterally and its length exceeds its width 8–10 times. In the horizontal section it is lens-shaped with pointed anterior and posterior corners. The process length notably exceeds the length of the body of the scute, hence the anterior and posterior parts of the process significantly stick out anteriorly and posteriorly in relation to the corresponding edges of the body of the scute. As a result, the ventral processes of the neighboring scutes contact each other laterally in articulation. The length of the overlapping surface constitutes from one fourth to one third of the process length. The lateral areas of the ventral process anteriorly and posteriorly bear a well expressed depression (*impressio processus ventralis*). The *Impressio processus ventralis* is a point of contact for the ventral process of the neighboring scute. The depression position in relation to the median line is not explicit for a species. All four possible combinations are known in *Chroniosaurus dongusensis* (specimens PIN nos. 3713/1 and 3713/37), with different variations of the contact of the ventral processes even within the same individual armor (specimen PIN, no. 3713/37). The ventral process in the anteriormost scute does not reach its anterior edge and its anterior *impressio processus ventralis* is not expressed (Fig. 1d).

The ventral process attains its maximum depth anteriorly and posteriorly, thus becoming arch-shaped in the sagittal plane (Fig. 1c). The neural spine enters a deep notch formed in the center. The anterior and posterior edges of the neural spine bear deep furrows, which housed correspondingly the anterior and posterior parts of the ventral process. The scutes do not usually fuse with the vertebrae. As a result, the neural spine is characteristically triangle-shaped when seen laterally.

The anterior and posterior articulation processes (*processus articulares anteriores* and *processus articulares posteriores*) are situated lateral to the ventral process (Fig. 1a). The articulation process is always separated anteriorly by a notch from the ventral process

from the *impressio processus ventralis* side. In contrast, from the opposite side of the *impressio processus ventralis* in relation to the median line both processes usually fuse dorsally at a right angle. A clearly expressed crest, the *crista scutulumi ventralis interna*, runs posteromedially from the anterior edge at the ventral surface of the anterior articulation process, which turns caudally into the lateral edge of the posterior articulation process. A deep furrow gradually becoming more shallow posteriorly, which housed the posterior articulation processes of the preceding scute, is placed medial to this crest. Laterally the *processus articularis anterior* is separated from the scute wing by a cleft, which deepens medially, closes and becomes shallow posteriorly. This cleft housed the posteromedial edge of the preceding scute wing. In the anteriormost scute the anterior articulation processes and related morphological structures are absent (Fig. 1d).

The posteromedial part of the scute wing ventral surface frequently bears a low crest, the *crista scutulumi ventralis externa*. It usually starts from the posteriormost edge of the wing and runs anteromedially, describing an arc, slightly convex externally. In front this crest transforms into the lateral edge of the anterior articulation process or flattens without reaching the ventral process in the anterior scute.

The posterior articulation processes are separated laterally from the wings of the scute by deep notches, the anterior edge of which is placed opposite or somewhat posterior to the boundary between the sculptured and non-ornamented areas of the dorsal wing surface. Wide grooves housing the anterior articulation processes of the posterior scute are found in front of the notches on the ventral surface.

Thus, the scute articulation in the chroniosuchian armor is rather complicated (Fig. 1b). This strongly limits the scute displacement in relation to each other. Nevertheless, possible small displacements of two neighboring scutes enable a possible bend of the whole armor in the horizontal plane almost at a right angle close to the right (specimen PIN, no. 3713/55). The overlap length of the articulation processes of two neighboring scutes makes half of the wing length. This completely excludes bending of the body of any significance in the vertical plane. The ability of some chroniosuchians to coil in order to protect themselves from predators (Ivakhnenko and Tverdochlebova, 1980) is not likely. It would be necessary to disconnect the scutes completely in order to curl, and this would require a strong extension of the body to twice its length, which is practically impossible.

The bystrowianian type. The *Bystrowiana* and *Axitectum* scutes belong to this type. The scutes are narrow, the wing length exceeds its width (*Bystrowiana*: Fig. 2b), or the wings are completely absent (in *Axitectum*). Thus, the armor protected only the axial part of the animal's back. The bystrowianian type scute structure somewhat differs from that described above. However, similar morphological elements (Fig. 2b and 2c) may be allocated here.

In *Bystrowiana* the scute wings overlap each other anteroposteriorly, hence the overlap area lacking sculpture is situated along the anterior edge of the dorsal surface of the scute wing (specimen PIN, no. 1100/1, 1100/18) (Fig. 2b). The ventral process occupies the posteromedial part of the ventral surface of the body of the scute. Its length along the median line is over twice less than the total length of the scute. In the front section the process is elliptic, the long medial axis of which is 1.5–3 times shorter than the short scute. The anterior and posterior edges of the process are rounded and never extend behind the corresponding scute edges. The ventral processes of the neighboring scutes never meet each other in articulation. Accordingly, the lateral depressions on the ventral processes characteristic of the chroniosuchian type scutes, or the *impressio processus ventralis*, are absent in *Bystrowiana* and *Axitectum*. The ventral scute process always fuses to the neural spine forming an interdigitating suture and the ventral process appears as if mounted on the neural spine from above (Fig. 2d). The anterior and posterior edges of the neural spine are parallel to each other or slightly deviate dorsally.

Two massive posterior articulation processes, the analogues of the anterior articulation processes of the chroniosuchian scute type, are placed posteriorly from the ventral process. Usually these processes fuse, forming a single horizontal articulation plate. This plate lies slightly ventral to the plane of the wings of the scute. Three high crests run along its dorsal surface anteroposteriorly: the central crest is the most massive, and the two lateral ones are placed exactly along the axial line of the articulation processes. If the articulation plate is insufficiently developed, the central crest may look like an additional third central articulation process (specimen PIN, no. 1100/18). Two deep and wide furrows formed by the crests house narrower and shorter anterior articulation processes of the neighboring scute. The anterior articulation processes are more poorly expressed, than the posterior ones. They never meet the ventral process and are placed in the same plane with the wings of the scute, far anterior to the former.

The differences in the articulation of the scutes and related peculiarities of scute structure of the two chroniosuchian groups considered suggests that the dorsal armor in these groups originated independently.

Apart from the differences in the armor structure described above the two considered groups of chroniosuchians also differ from each other by the structure of other skeletal elements. In *Bystrowiana* and *Axitectum* the deep conical pits are located on the topmost surfaces of the neural arches, which frequently become canals directed anteroposteriorly (Fig. 2e). The origin of these structures is presumably related to the development of significant epaxial muscles (Tatarinov, 1972; Ivakhnenko and Tverdokhlebova, 1980). In *Chroniosu-*

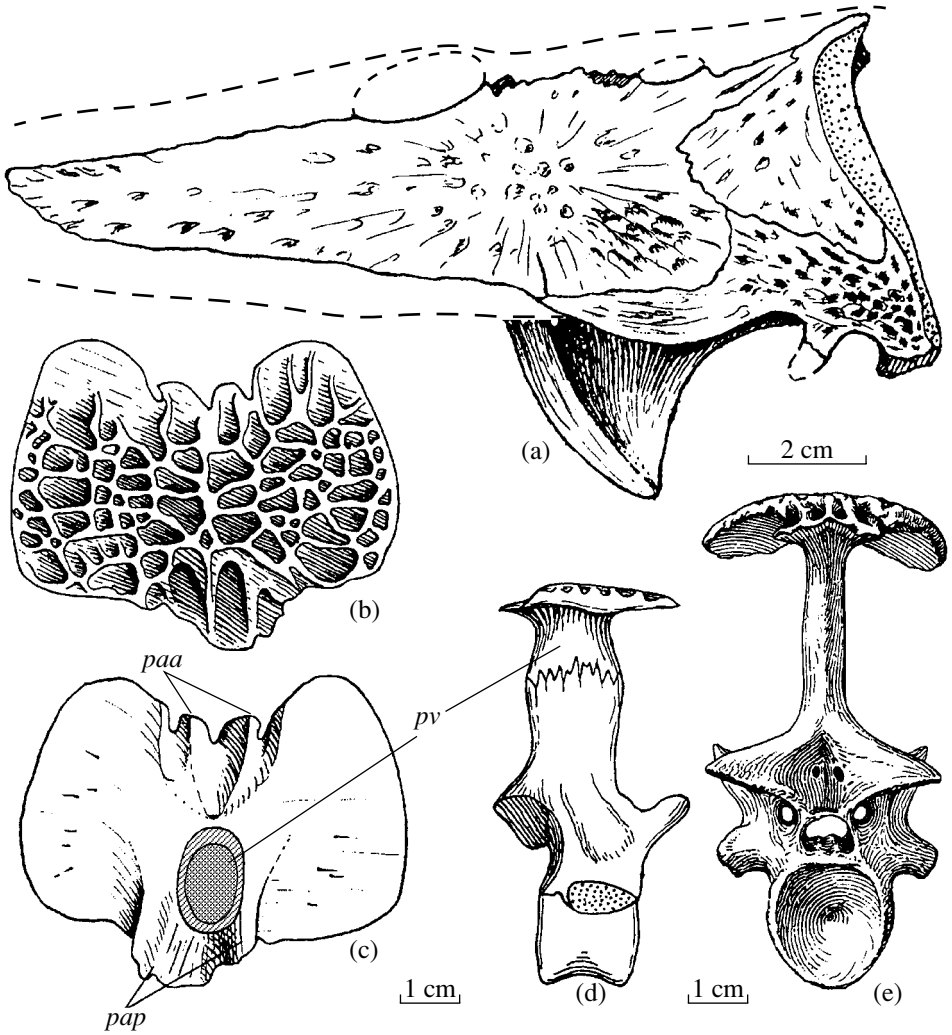

Fig. 2. *Bystrowiana permira* Vjuschkov; Upper Permian, Upper Tatarian Substage, Vyatkian Regional Stage: (a) the skull laterally, specimen PIN, no. 1100/88; (b) and (c) the trunk scute dorsally and ventrally, specimen PIN, no. 1100/9; (d) the trunk vertebra with a fused scute from the right laterally, specimen PIN, no. 1100/18; (e) the trunk vertebra with a fused scute posteriorly, holotype PIN, no. 1100/1 (Vjuschkov, 1957b, fig. 11 a). For designations see Fig. 1.

chus, *Jugosuchus* and *Chroniosaurus* these pits and canals are absent. Strong ossification of intersegmentary cartilage is characteristic of these forms and results in the spherical-shaped intercentra in the adult forms and formation of characteristic bony calli on the articulation surfaces of the centra (Tverdokhlebova, 1967; Borkhvardt, 1969; Ivakhnenko and Tverdokhlebova, 1980). Similar bony calli on the centra are sometimes also seen in *Bystrowiana* (specimen PIN, no. 1100/2), but they are much more poorly expressed. Probably, in the chroniosuchians possessing the bystrowianian type scutes the ossification of the intersegmentary cartilage was not as strong, in so far as the spherical intercentra in these forms are unknown.

The comparison of the skull structure in the members of these two chroniosuchian groups present some difficulties. *Bystrowiana permira* is described from trunk vertebra, with a fused scute from the Vyazniki-2 locality (Vladimir Region) (Vjuschkov, 1957a). However, a revision of all chroniosuchian material from this locality revealed the presence of the bystrowianian and chroniosuchian type scutes and vertebrae. The chroniosuchian type materials are described here as *Uralerpeton tverdochlebovae* gen. et sp. nov. The remains of *Uralerpeton* are also found in the localities of Purly (Nizhnii Novgorod Region) and Sambullak (Orenburg Region). Its scutes are somewhat similar to those of *Bystrowiana*: the wings are narrow (the dorsal surface of the animal's trunk was not completely armored), and the ventral process fuses to the neural spine. However, the lock structure, and the condition of articulation of the scutes to each other and to the neural spines, are typically chroniosuchian (Fig. 4).

The cranial chroniosuchian remains from the Vyazniki-2 locality also belong to two forms. The following features distinguish this form (specimen PIN,

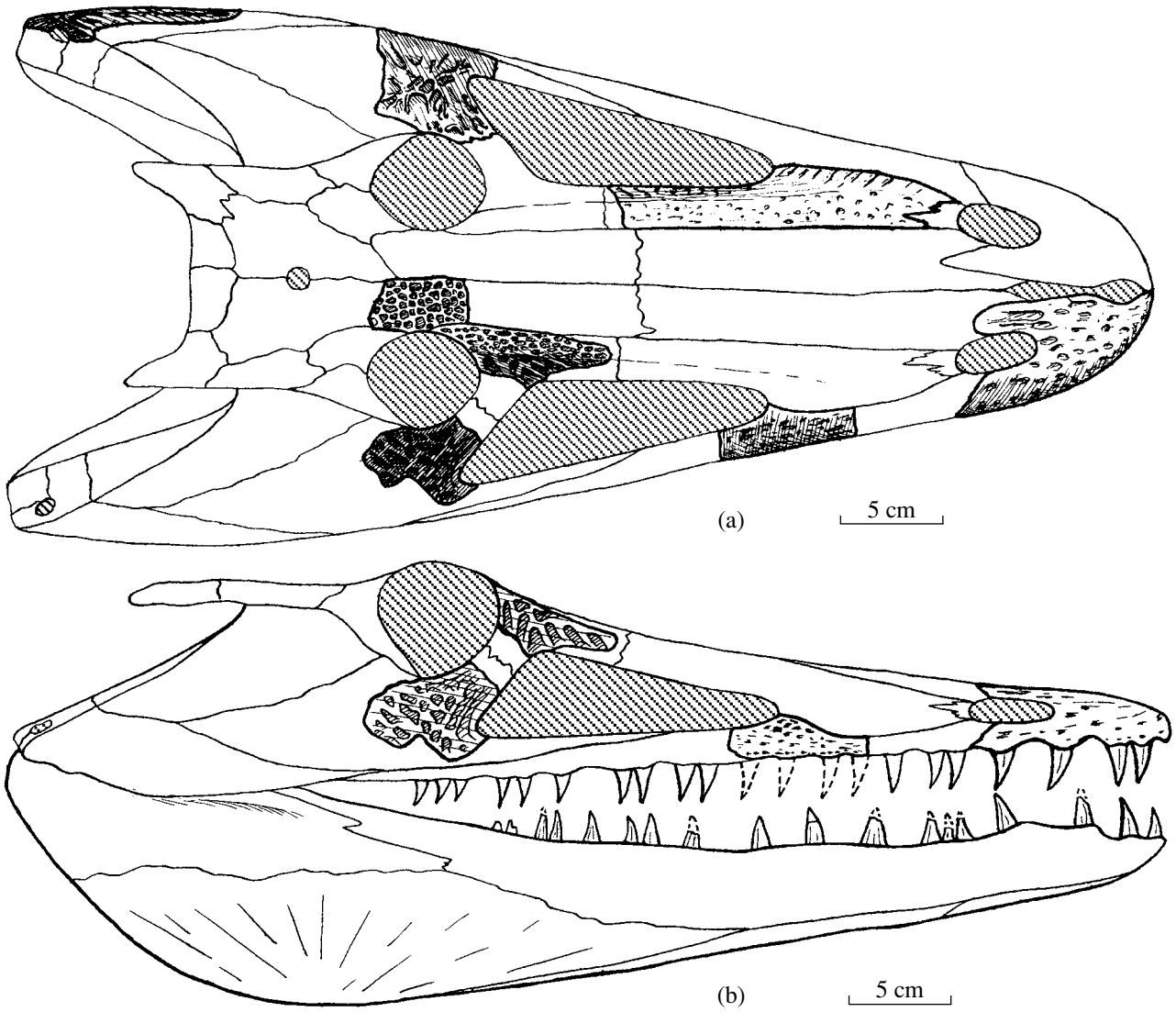

Fig. 3. *Uralerpeton tverdochlebovae* Golubev gen. et sp. nov.; Upper Permian, Upper Tatarian Substage, Vyatkian Regional Stage: (a) and (b) the skull dorsally and laterally, reconstructed from the specimens PIN, nos. 1100/89, 90, 144, 1538/45 and 46, SGU, nos. 104B/166–168, 191.

no. 1100/88, the left cheek bone complex with a fragment of palate; Fig. 2a) from *Chroniosuchus*, *Jugosuchus* and *Chroniosaurus*: the absence of the praeorbital fenestra situated in these three genera between the praefrontal, lacrymal, jugal and maxillary; the presence of the postorbital fenestra at the contact of the skull roof with the cheek; significant overlap of the posterodorsal edge of the jugal upon the squamosal at the contact of the latter with the cheek (the postorbital and squamosal probably had no direct contact); the steep rise of the posterodorsal edge of the cheek, the angle between which and the ventral edge of the upper jaw is 62° (in *Chroniosuchus*, *Jugosuchus* and *Chroniosaurus* this angle is 30°–35°, as a result, the jaw condyles are shifted backwards and situated caudally in relation to the posterior edge of the skull roof); the pterygoid flange is strongly depressed (in *Chroniosuchus*, *Jugosuchus* and *Chroniosaurus* it is situated almost in the plane of the palate); the ventral edge of the quadratojugal is slightly concave and forms a well expressed process directed downwards and slightly anteriorly in the posterior part; the jugal is deep, the shallow orbit notch is placed slightly ventrally from the upper cheek edge (probably, the orbits largely faced dorsally).

The second form in contrast is characterized by the characters that distinguish it from the first form and align it closer to *Chroniosuchus*, *Jugosuchus* and *Chroniosaurus* (Fig. 3): the presence of the praeorbital fenestra (the lacrymal: specimen PIN, no. 1100/89; the prefrontal: specimens PIN, nos. 1100/90 and 1100/110 bear characteristic notches along the lateral margin) and well expressed pterygoid flange situated in the pal-

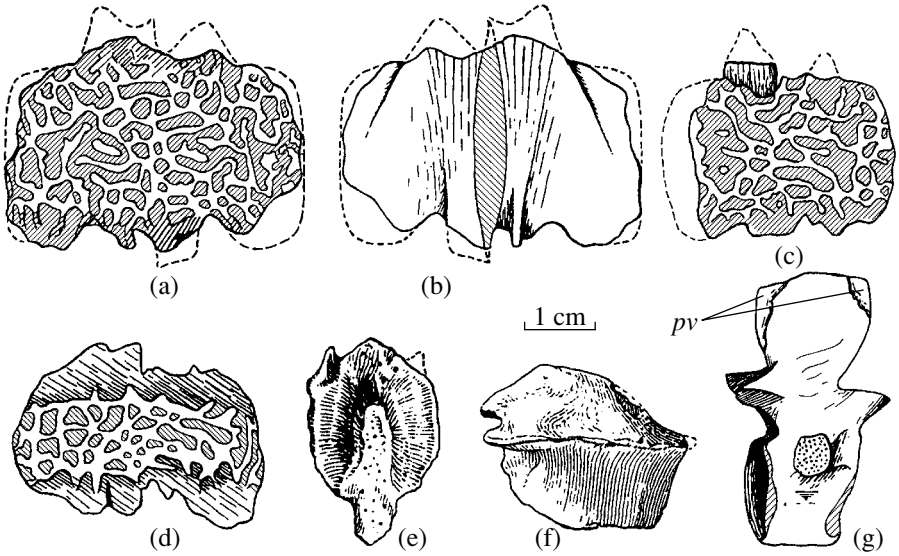

Fig. 4. *Uralerpeton tverdochlebovae* Golubev gen. et sp. nov.; Vladimir Region, Vyazniki-2; Upper Permian, Upper Tatarian Substage, Vyatkian Regional Stage: (a) and (b) the trunk scute dorsally and ventally, holotype PIN, no. 1100/8; (c) the trunk scute dorsally, specimen PIN, no. 1100/11; (d) the trunk scute dorsally, specimen PIN, no. 1100/91; (e) and (f) the caudal scute dorsally (Ivakhnenko and Tverdokhlebova, 1980, text-fig. 14 j) and laterally (Vjuschkov, 1957b, text-fig. 12); (g) the vertebra from the right laterally, specimen PIN, no. 1100/109.

ate plane (specimen PIN, no. 1100/428). These facts make possible a confident assignment of the cranial remains of the second form to *Uralerpeton tverdochlebovae*, and the first one to *Bystrowiana permira*. This conclusion is confirmed by the material on the Triassic chroniosuchians presented only by scutes and vertebrae of the exceptional bystrowianian type (Shishkin and Novikov, 1992; Novikov and Shishkin, 1995), as well as by the squamosal (specimen PIN, no. 4584/28; Orenburg Region, Perevozinka; the Lower Triassic) similar to that of the first form (the vertical posterior margin, short contact zone with the skull roof).

Thus, two groups are present within the chroniosuchians, that are regarded here as families: the Chroniosuchidae Vjuschkov, 1957 (*Chroniosuchus* Vjuschkov, 1957; *Jugosuchus* Riabinin, 1962; *Chroniosaurus* Tverdochlebova, 1972 and *Uralerpeton* Golubev gen. nov.) and the Bystrowianidae Vjuschkov, 1957 (*Bystrowiana* Vjuschkov, 1957 and *Axitectum* Shishkin et Novikov, 1992).

SYSTEMATIC PALEONTOLOGY

Class Amphibia

Order Anthracosauromorpha

Suborder Chroniosuchia

D i a g n o s i s. Late Permian and Triassic anthracosauromorphs with skull length attaining 50–55 cm. Skull elongated. Lateral line canals absent. Trunk short, no more than 25 praecaudal vertebrae. Neural arch in adults always fuses with centrum. Variously expressed intersegmentary cartilage ossification is characteristic. Dorsal armor consists of kinetically articulated scutes. Scutes arranged in row along median line of trunk. Scute numbers correspond to number of vertebrae of protected body part. Scutes connected to neural spines by means of ligaments or fuse to them.

S u b o r d e r c o m p o s i t i o n. Two families: Chroniosuchidae Vjuschkov, 1957 and Bystrowianidae Vjuschkov, 1957.

O c c u r r e n c e. The Upper Permian and Triassic of Eurasia.

Family Bystrowianidae Vjuschkov, 1957

T y p e g e n u s. *Bystrowiana* Vjuschkov, 1957; Russia, Vladimir Region; Upper Permian, the upper part of the Vyatkian Regional Stage.

D i a g n o s i s. Late Permian and Triassic amphibiotic chroniosuchians with skull length attaining 20 cm. Orbits face dorsally. Narrow postorbital fenestra situated between skull roof and cheek. Posterodorsal cheek margin steep (angle formed between it and upper jaw is 60°–65°). Squamosal short. Jugal forms larger part of cheek dorsal margin. Squamosal does not contact postorbital. Ventral edge of quadratojugal slightly bent dorsally, process in posterior part directed anteroventrally. Pterygoid flanges well expressed and strongly depressed. Trunk scute lock of bystrowianian type. Scute wings, if present, overlap each other anteroposteriorly. Ventral scute process always fuses with neural spine dorsally from all directions. Neural arch bears numerous deep pits dorsally, which sometimes turn into canals directed anteroposteriorly. Intercentra are ring-shaped or disk-shaped.

Composition. Two genera: *Bystrowiana* Vjuschkov, 1957 and *Axitectum* Shishkin et Novikov, 1992.

Occurrence. The Upper Permian (Upper Tatarian Substage) of European Russia and Northern China; the Lower and Middle Triassic of European Russia.

Family Chroniosuchidae Vjuschkov, 1957

Type genus. *Chroniosuchus* Vjuschkov, 1957; Russia, Orenburg Region; Upper Permian, Upper Tatarian Substage, the Vyatkian Regional Stage.

Diagnosis. Late Permian aquatic chroniosuchians with skull length attaining 50–55 cm. Orbits face dorsolaterally. One pair of praeorbital fenestrae between jugal, praefrontal, lacrymal and maxillary present. Contact between lacrymal and maxillary, kinetic. Posterodorsal edge of cheek gentle (angle formed between it and upper jaw, 30°–35°). Intertemporal absent. Squamosal contacts postorbital. Ventral edge of quadratojugal straight or slightly concave. Pterygoid flanges situated within plane of palate. Trunk scutes' lock of chroniosuchian type. Scute wings overlap each other posteroanteriorly. Ventral scute process loosely connected to neural spine or fuses to it. Intercentra vary from ring-shaped in young individuals to spherical in adults.

Composition. *Chroniosuchus* Vjuschkov, 1957, *Jugosuchus* Riabinin, 1962, *Chroniosaurus* Tverdochlebova, 1972 and *Uralerpeton* Golubev gen. nov.

Comparison. Differs from the family Bystrowianidae by the orientation of the orbits, presence of the praeorbital and absence of the postorbital fenestrae, presence of squamosal and postorbital contact, the position of the pterygoid flanges, the structure of the armor scutes, the character of scute articulation to each other and to the neural spines, the absence of pits on the anterior and posterior surfaces of the neural arches and spherical intercentra.

Occurrence. The Upper Tatarian Substage of European Russia.

Uralerpeton Golubev gen. nov.

Bystrowiana: Vjuschkov, 1957a, p. 103 (part.); Ivakhnenko and Tverdokhlebova, 1980, p. 13 (part.)

Etymology. From the Ural mountains and the Greek *herpeton* (a reptile).

Type species. *Uralerpeton tverdochlebovae* Golubev sp. nov.; Upper Tatarian Substage, European Russia.

Diagnosis. Large chroniosuchid, reconstructed skull length attains 50–55 cm. Trunk scutes of narrow type (scute wings length exceeds width). Ventral scute process fuses to neural spine. Dorsal surface scutes ornamented by pits and ridges.

Species composition. The type species.

Comparison. Differs from the genera *Chroniosuchus*, *Jugosuchus*, and *Chroniosaurus* by large size, narrow trunk scute wings, scute fusion to the neural spines; from *Chroniosaurus* also by pits-and-ridges scute dermal sculpture.

Uralerpeton tverdochlebovae Golubev sp. nov.

Bystrowiana permira: Vjuschkov, 1957a, p. 103 (*part.*), fig. 12 (*non* fig. 11); Ivakhnenko and Tverdokhlebova, 1980, p. 13 (*part.*), fig. 8 b (*part.*), 14 g and j (*non* fig. 8a, *nec* figs. 14h and 14i).

Chroniosuchus cf. *mirabilis*: Tverdokhlebova, 1967, p. 31, figs. 1–6.

Chroniosuchus mirabilis: Tverdokhlebova, 1976, p. 81 (*sine descr.*).

Chroniosuchus uralensis: Ivakhnenko and Tverdokhlebova, 1980, pp. 9 and 37 (*part.*).

Jugosuchus cf. hartmanni: Tverdochlebova and Ivakhnenko, 1994, p. 122 (*sine descr.*).

Etymology. After the paleontologist G.I. Tverdokhlebova.

Holotype. PIN, no. 1100/8, trunk scute; Vladimir Region, Viazniki District, Viazniki town, locality Viazniki-2; Upper Permian, Upper Tatarian Substage, the Vyatkian Regional Stage.

Description (Figs. 3 and 4). A large form with the skull length attaining 50–55 cm from the tip of the snout to the level of the jaw condyles. The dorsal skull surface is ornamented by pits and ridges. The nostrils are oval-shaped and elongated anteroposteriorly. The praeorbital fenestra is strongly elongated, no shorter than 10 cm in the large individuals (specimen PIN, no. 1100/89). Its posterior edge is situated behind the level of the anterior orbital edges. There is a small rounded through opening followed posteriorly by a long, slit-like fontanella between the praemaxillaries on the dorsal side immediately behind the symphysis. The lacrymal overlaps the maxillary anteriorly from the praeorbital fenestra. The anterodorsal surface of the maxillary overlapped by the lacrymal is a wide and long area sculptured by small crests parallel to each other and to the lateral edge of this surface. These crests mark the attachment of ligaments, which connect the lacrymal to the maxillary and provided some mobility of these bones in relation to each other. The area on the maxillary described above is present in all chroniosuchids and served as the base for the reconstruction of the anterior pairs of praeorbital fenestrae in the chroniosuchian skull in earlier papers (Ivakhnenko and Tverdokhlebova, 1980). In fact, these fenestrae are absent in the chroniosuchians.

The praefrontal is sharply bent ventrolaterally. The curvature starts from the medial edge of the orbit and runs anteriorly along the entire bone parallel to the median line, passing further to the lacrymal. Anteriorly the curvature becomes less noticeable and disappears completely in the area between the praeorbital fenestra and the nostril. The dorsal surface of the frontal bears a well marked longitudinal depression. The posterior edge of the frontal does not reach the level of the posterior orbital edges. The pterygoid does not form an interdigitating suture with the parasphenoid. The artic-

ulation facet is a deep smooth-walled, large pit, which suggests a kinetic basipterygoid articulation. The ventral surface of the posterior part of the preserved pterygoid palatal plate is shagreen-like.

The scute wings are narrow, their width is at least twice smaller than the length. Almost the whole dorsal surface is sculptured. The area without sculpture along the posterior edge of the wing of the scute, overlapped by the neighboring wing of the scute, is short. This, as well as the narrow wings may suggest that the armor of *Uralerpeton* was more kinetic than in the other chroniosuchids. The dermal ornamentation consists of variously sized, irregularly shaped pits surrounded by crests. In some specimens three well expressed longitudinal swellings are present: along the median line and on the boundaries of the body of the scute and its wings (specimen SGU, no. 104B/51). In several specimens the ornamentation is intermediate between the vermiform and pits-and-ridges type (specimen PIN, no. 1100/11; SGU, nos. 104B/76 and 81) (the terminology of the dermal sculpture types by Shishkin, 1987, p. 89). This is especially characteristic of the lateral zones of the dorsal surface of the scute. The isolated ornamentation tubercles may also appear in these areas. The ventral scute process is deep, almost reaches the level of the zygapophyses. The neural spine fusing with the ventral scute process covers it only laterally, and the anterior and posterior edges of the ventral process are seen completely. Thus, the ventral process appears to be wedged between the neural spine, and the latter becomes shaped like a trapezium resting upon its smaller side. This type of fusion of the ventral process and the neural spine is completely different to that observed in the bystrowianids (see above). The caudal wings of the scute are absent. The shape of the tail scutes considerably differs from that of the trunk (Fig. 4e and 4f). In the tail scutes the anterior articulation processes are shaped as short thorns. The posterior articulation processes are absent. The dorsal surface in the central part is a high boss elongated along the median line. The dermal sculpture is practically absent and its pits-and-ridges shape may be only surmized in some areas.

The intercentra are spherical in shape, their diameters ranges from 9 mm (specimen SGU, no. 104B/44') to 19–20 mm (specimen SGU, no. 104B/30', PIN, no. 1538/30).

O c c u r r e n c e. The upper part of the Vyatkian Regional Stage, Upper Tatarian Substage, European Russia.

M a t e r i a l. Besides the holotype from the type locality, specimens PIN, nos. 1100/11, 15, 79, 81, 82 and 91, trunk scutes and their fragments; PIN, no. 1100/12, the caudal scute; PIN, no. 1100/89, the left lacrymal; PIN, nos. 1100/90 and 110, the praefrontals; PIN, nos. 1100/99, 105, 106 and 109, the trunk vertebrae; PIN, no. 1100/144, the right frontal; PIN, no. 1100/428, the pterygoid. From the Purly locality (Nizhnii Novgorod Region): specimen PIN nos. 1538/16 and 17, vertebrae; PIN, no. 1538/30, the intercentrum; PIN, no. 1538/32, the right frontal; PIN nos. 1538/36–38, the trunk scutes fragments; PIN, no. 1538/45, the anterior part of the maxillary; PIN nos. 1538/46, the right lower jaw ramus. From the Sambullak locality (Orenburg Region): specimen SGU, nos. 104B/1'–3', 5'–7', 17', 27', 30', 33', 37', 40', 44', the intercentra; SGU, nos. 104B/3a and 23a, the vertebrae; SGU, nos. 104B/24a and 26a, the trunk vertebrae with the fused scutes; SGU, nos. 104B/50–52, 74–77, 80 and 81, the scutes and their fragments; SGU, no. 104B/166, the quadratojugal; SGU, nos. 104B/167 and 168, the jugal SGU, no. 104B/91, the praemaxillary.

DISCUSSION

The chroniosuchids are one of the most characteristic forms of the Permian tetrapod fauna of the theriodontian (Late Tatarian) stage, which is currently subdivided into three faunistic assemblages: the Kotel'nich, the Sokolki and the Vyazniki (Ivakhnenko, 1990, 1992; Golubev, 1995, 1996). The Sokolki assemblage is the best studied (more than 50 sites). Exceptionally wide-armored chroniosuchids are known from here, the narrow-armored forms are not known.

In contrast to the Sokolki assemblage, the wide-armored chroniosuchids are unknown from the Vyazniki assemblage, but the narrow-armored chroniosuchians are a common form of this fauna. The type localities of the Vyazniki assemblage are the Vyazniki-1 and Vyazniki-2 (*Uralerpeton tverdochlebovae, Bystrowiana permira, Dvinosaurus egregius, Dicynodon* sp., *Moschowhaitsia vjuschkovi, Whaitsiidae* (?) gen. ind., *Archosaurus rossicus*, *Elginia* sp., *Karpinskiosauridae* gen. ind.[2] The remaining localities of the assemblage are: (1) Purly (*Uralerpeton tverdochlebovae, Dvinosaurus purlensis, Hexacynodon purlinensis, Archosaurus rossicus, Dicynodon* sp., *Whaitsiidae* (?) gen. ind.), (2) Sambullak (*Uralerpeton tverdochlebovae, Kotlassia grandis*) and (3) Shabarshata (Kirov Region) (*Whaitsiidae* (?) gen. ind.). The faunas of the following localities may possibly also be included within this assemblage: (4) Rasha (Arkhangelsk Region) (*Uralerpeton* (?) sp., Pareiasaurina (?) gen. ind.), (5) Voskresenskoye-2 (Nizhnii Novgorod Region) (*Uralerpeton* (?) sp., *Dvinosaurus* sp., *Dicynodon* sp. nov.) and (6) Berezhane (Kirov Region) (*Dicynodon* sp. nov., the form, identical to that from the Voskresenskoye-2-V locality). The fauna of the Vomba-Kassy locality (Chuvashiya) (*Dvinosaurus primus, Raphanodon* cf. *tverdochlebovae*, *Chroniosuchus* sp., *Dicynodontidae* gen. ind.) can not be referred to the Vyazniki assemblage (Sennikov, 1995), as it is charac-

[2] The tetrapod fauna from the localities under consideration was determined by M.F. Ivakhnenko (parareptiles and theriodonts), V.K. Golubev (chroniosuchians and parareptiles), A.A. Kurkin (dicynodonts), and A.G. Sennikov (thecodonts).

terized by *Dvinosaurus primus* and *Chroniosuchus* sp., typical of the Sokolki assemblage.

The Vyazniki assemblage is characterized by the dominance of herbivorous dicynodonts (*Dicynodon* sp.), large predatory thecodonts (proterosuchids *Archosaurus rossicus*) and diverse carnivorous therocephalians (*Hexacynodon purlinensis*, *Moschowhaitsia vjuschkovi*, Whaitsiidae (?) gen. ind.) in the terrestrial community. The aquatic community composition is typical of the Theriodontian Stage: the colosteiform labyrinthodonts (dvinosaurids *Dvinosaurus egregius, D. purlensis*), primitive parareptiles (the karpinskiosaurid *Kotlassia grandis*) and chroniosuchids (*Uralerpeton tverdochlebovae*). The bystrowianids (*Bystrowiana permira*) and relic Nycteroleterinae (*Elginia* sp.) appear as subdominants. The Vyazniki assemblage is without doubt transitional from the late Tatarian theriodontian to the early Triassic proterosuchid assemblages. The pareiasaurs and gorgonopsids, the dominants of the Sokolki assemblage, are missing from it, but the proterosuchids and bystrowianids, common in the Triassic, appear. The Vyazniki assemblage characterizes the final stage of the late Permian tetrapod community developmental history in Eastern Europe and is the youngest among the late Tatarian faunistic assemblages. It should characterize the younger deposits of the Upper Tatarian Substage rather than the Sokolki assemblage. Unfortunately, no sections are currently known to include the localities of both assemblages. However, the relative arrangement of layers containing the fauna of the Sokolki and Vyazniki assemblages within the general chart of the Upper Tatarian Substage of the Russian Plate may be resolved in an indirect manner.

The Sokolki assemblage characterizes both the North Dvinian and the Vyatkian Regional Stages. Hence, the layers containing the Vyazniki fauna should correlate with the upper part of the Vyatkian Regional Stages. This conclusion is supported by the position of all the Vyazniki localities immediately adjacent to the Permian and Triassic boundary (the upper boundary of the Vyatkian Regional Stages coincides with the Permian and Triassic systems boundary): Vyazniki, about 15 m below the boundary (Tikhomirov, 1984, p. 34, fig. 11), Purly (Efremov and Vjuschkov, 1955, p. 131; Blom, 1968, p. 255); Sambullak (Ivakhnenko and Tverdokhlebova, 1980, p. 39, Appendix 2); Shabarshata (Blom, 1968, p. 212); Rasha, 3–4 m below the boundary (Pakhtusova, 1962, p. 8); Voskresenskoye-2 (Blom, 1968, p. 186); Berezhane, 17-18 m below the boundary (Gusev, 1996, p. 154, text-figs. 2.3.3-3). It is noteworthy that the earlier age was indicated previously for some of the localities investigated. Thus, the Vyazniki and Sambullak localities were referred to the North Dvinian Regional Stage (Tikhomirov, 1984; Ivakhnenko and Tverdokhlebova, 1980; Molostovskii, 1983). A close location of the lower Triassic boundary in cases like this is explained by the strong erosion of the Upper Permian deposits (sedimentation hiatus) during the pre-Triassic time. The concept of a large break at the Permian and Triassic boundary in the territory of Eastern Europe is now popular (Lozovsky, 1992). However, it is not supported by the terrestrial vertebrate data. In contrast, within the limits of this entire area from the Orenburg Region in the south to the Arkhangelsk Region in the north the Triassic rests upon deposits characterized by the youngest assemblage of Permian tetrapods.

ACKNOWLEDGMENTS

The paper is supported by Russian Foundation for Basic Research, project no. 96-15-98069.

REFERENCES

Blom, G.I., *Katalog mestonakhozhdenii faunisticheskikh ostatkov v nizhnetriasovykh otlozheniyakh Srednego Povolzh'ya i Prikam'ya* (The Catalogue of the Faunistic Remains and Localities in the Lower Triassic Deposits of the Middle Volga and Kama Region), Kazan: Kazan Univ., 1968.

Borkhvardt, V.G., On the Peculiarities of the Chroniosuchid Vertebrae Structure, *Paleontol. Zh.*, 1969, no. 3, pp. 146–148.

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

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

Gusev, A.K., The Reference Section of the Tatarian Stage on the Vyatka River, in *Stratotipy i opornye razrezy verkhnei permi Povolzh'ya i Prikam'ya* (The Stratotypes and Reference Sections of the Upper Permian in the Middle Volga and Kama Region), Kazan: Ekotsentr, 1996, pp. 141–186.

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

Ivakhnenko, M.F., The Faunistic Tetrapod Assemblages of the Late Permian of Eastern Europe, *Byull. Mosk. O-va Ispyt. Prir., Otd. Geol.*, 1990, no. 6, pp. 55–60.

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

Ivakhnenko, M.F. and Tverdokhlebova, G.I., *Sistematika, morfologiya i stratigraficheskoe znachenie verkhnepermskikh khroniozukhov vostoka Evropeiskoi chasti SSSR* (Systematics, Morphology and Stratigraphic importance of the Upper Permian Chroniosuchians of the East of the European Part of the USSR), Saratov: Saratov Univ., 1980.

Lozovsky, V.R., The Early Triassic Development Stage of Western Laurasia, *Doctoral (Geol.-Min.) Dissertation Thesis*, Moscow: Paleontol. Inst., Ross. Akad. Nauk, 1992.

Molostovskii, E.A., *Paleomagnitnaya stratigrafiya verkhnei permi i triasa vostoka Evropeiskoi chasti SSSR* (The Paleomagnetic Stratigraphy of the Upper Permian and Triassic of the East of the European Part of the USSR), Saratov: Saratov Univ., 1983.

Novikov I.V. and Shishkin M.A. Palaeozoic Relict in Triassic Tetrapod Communities: the Last Anthracosaurian Amphibians, *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*, Beijing: China Ocean Press, 1995, pp. 29–32.

Pakhtusova, N.A., On the Permian and Triassic Boundary in the North Dvina Basin, in *Materialy po geologii i poleznym iskopaemym severo-zapada RSFSR* (Material on the Geology and Mineral Resources in the Northwest of RSFSR), vol. 3, Leningrad: Gostoptekhizdat, 1962, pp. 3–18.

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

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., Relic Anthracosaurs in the Early Mezozoic of Eastern Europe, *Dokl. Ross. Akad. Nauk*, 1992, vol. 325, no. 4, pp. 829–832.

Tatarinov, L.P., *Seymouriamorphen aus der Fauna der UdSSR*, vol. 5, *Batrachosauria (Anthracosauria), Teil B, Gephyrostegida-Chroniosuchida of Handbuch der Paläoherpetologie*, Stuttgart: Gustav Fischer Verlag, 1972, pp. 70–80.

Verkhnepermskie i nizhnetriasovye otlozheniya Moskovskoi sineklizy (The Upper Permian and Lower Triassic Deposits of the Moscow Syneclise), Tikhomirov, S.V., Ed., Moscow: Nedra, 1984.

Tverdokhlebova, G.I., On the Remains of the Genus *Chroniosuchus* from the Permian of the Orenburg Cisurals, *Izv. Vyssh. Uch. Zav., Geologiya i Razvedka*, 1967, no. 9, pp. 31–35.

Tverdokhlebova, G.I., *Katalog mestonakhozhdenii tetrapod verkhnei permi Yuzhnogo Priural'ya i yugo-vostoka Russkoi platformy* (The Tetrapod Localities Catalogue of the Upper Permian of the South Cisurals and the South-East of the Russian Plate), Saratov: Saratov Univ., 1976.

Tverdokhlebova, G.I. and Ivakhnenko, M.F., New Tetrapods from the Tatarian of Eastern Europe, *Paleontol. Zh.*, 1994, no. 2, pp. 122–126.

Vjuschkov, B.P., New Kotlassiomorphs from the Tatarian Deposits of the European part of USSR, in *Kotilozavry i batrakhozavry verkhnei permi SSSR* (The Cotylosaurs and Bathrachosaurs of the USSR Upper Permian), in *Tr. Paleontol. Inst., Akad. Nauk SSSR* (Moscow), 1957a, vol. 68, pp. 89–107.

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