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A New Oryctocenosis of the Aquatic Vertebrate Community from the Late Permian of Central Russia

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Abstract—In the Permian strata (Upper Tatarian Substage, Vyatkian Horizon, *Scutosaurus karpinskii* Tetrapod Zone, *Chroniosuchus paradoxus* Subzone) near the town of Gorokhovets (Vladimir Region), a locality of Late Permian vertebrates was discovered. As regards to the taxonomic composition and the abundance of specimens, this is one of the richest localities in Russia. The new oryctocenosis contains 12 tetrapod forms of the Sokolki Assemblage, including tempospondyls, anthracosaurians, seymouriamorphs, pareiasaurians, gorgonopians, therocephals, cynodonts, and dicynodonts, and at least eight fish forms. The oryctocenosis is dominated by fish and aquatic and semiaquatic tetrapods. The locality was formed in conditions with an extensive lowland with a strongly meandering system and branching channels of constant and temporary streams which alternate with vast sandy and silty banks.

INTRODUCTION

The East European fauna occupies a significant place among the Late Permian tetrapod faunas of the world. Regarding taxonomic diversity, it has no equal, since approximately 60 families have been described from the Upper Permian of European Russia (Ivakhnenko *et al.*, 1997). Moreover, both terrestrial and aquatic vertebrates are abundant in Eastern Europe, as opposed to other regions, including South Africa.

Aquatic vertebrates are widespread in the Ufimian–Lower Tatarian strata (Ivakhnenko *et al.*, 1997; Minikh, 1998). The aquatic oryctocenoses also prevail in the Severodvinian Horizon of the Upper Tatarian Substage; however, in the terminal Permian (Vyatkian Horizon), they occur much more rarely and all the thoroughly studied Vyatkian localities where aquatic vertebrates predominate are confined to the southern areas (Orenburg Region).

In the summer of 1999, A.G. Sennikov discovered a new locality dominated by aquatic vertebrates in the Vyatkian Horizon in the vicinity of the town of Gorokhovets (Vladimir Region) (Fig. 1). As a result of field work performed by the Paleontological Institute of the Russian Academy of Sciences (PIN) in 1999 and 2000 and a preliminary examination of specimens collected in the locality the following characteristics were obtained.

DESCRIPTION OF THE SECTION

The Gorokhovets locality is in a gully on the right bank of the Klyaz'ma River northwest of the town of Gorokhovets at the boundary of the village of Gorodishchi. This locality is 2 km east of the Zhukov gully where the reference section of the Upper Permian–Lower Triassic boundary strata has been described in detail and characterized by gastropods, conchostracans, and ostracodes and by paleomagnetic data (*Verkhnepermskie i nizhnetriasovye otlozheniya…*, 1984).

The Permian strata in the Gorokhovets gully are only weakly exposed. In the lower part of the gully, the debris of variegated, mainly red, rocks is observed. There is a bone-bearing sandy–clay member outcropping on either side of the gully 230–240 m above the gully mouth. Excavation on the right slope covered an area about 18 m long and 1.0 to 2.0 m wide and exposed a section about 7.0 m thick. The following beds were allocated up the sequence (Fig. 2):

(1) Indistinctly obliquely bedded and gently undulating laminated loose, fine-grained, polymictic, grayish yellow sandstone with thin cherry interlayers. The bed encloses rare lenticular interbeds (5–10 cm thick) composed of red clay gravel. Fish scales and two bones of tetrapods were found. The exposed thickness is 0.4–1.0 m.

The lower boundary of the bed is not observed; apparently, it is outlined by the traces of water seepage from the talus approximately 1 m below the exposed area. Bed 1 is a water-bearing layer; the aquifuge is likely formed by the red clay in the upper layers of the underlying member, down the channel as small sites in the thalweg of the gully. The roof of the lower clayey member forms a prominent ledge about 2 m high in the profile of the gully bottom.

(2) Indistinctly obliquely bedded or undulating, dense, course-grained, polymictic, yellowish brown to reddish and cherry brown sand with alternating lenticular yellowish brown, rusty, and cherry-red sandy

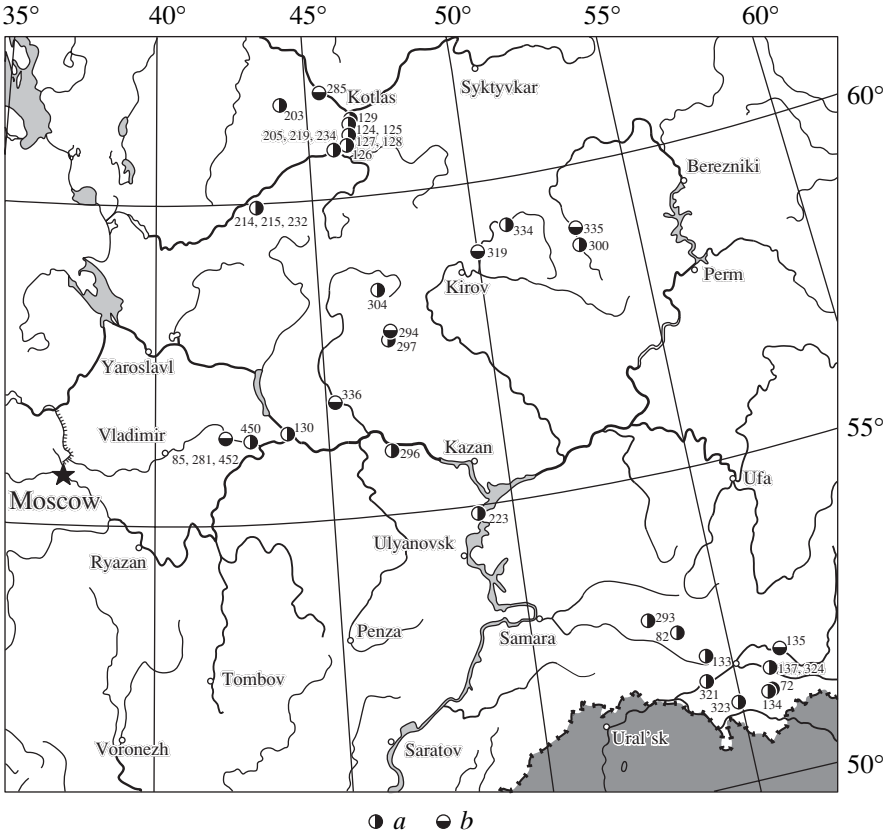

Fig. 1. Geographical position of the tetrapod localities containing the (*a*) Sokolki Subassemblage and (*b*) the Vyazniki Assemblage in European Russia. Localities: (*72*) Klyuchevka, (*82*) Pron'kino, (*85*) Vyazniki-1, (*124*) Sokolki, (*125*) Zavrazh'e, (*126*) Aristovo, (*127*) Krasavino, (*128*) Savvatii, (*129*) Boltinskaya, (*130*) Gorki-1, (*133*) Adamovka, (*134*) Blumental-3, (*135*) Sambullak, (*137*) Vyazovka-1, (*203*) Kadyevskaya, (*205*) Klimovo-1, (*214*) Strizhenskaya Gora, (*215*) Titova Gora, (*219*) Salarevo, (*223*) Klyuchevoi Gully, (*232*) Obirkovo, (*234*) Popolzukha, (*281*) Vyazniki-2, (*285*) Rasha, (*293*) Pokrovka, (*294*) Purly, (*296*) Vomba-Kassy, (*297*) Tonshaevo, (*300*) Averinskoe, (*304*) Bolshoe Linovo, (*319*) Berezhane, (*321*) Zubochistenka-2, (*323*) Boevoi, (*324*) Vyazovka-2, (*334*) Orletsy, (*335*) Shabarshata, (*336*) Voskresenskoe-2, (*450*) Gorokhovets, and (*452*) Bykovka.

interbeds. The slanting series are long and relatively thin (ca. 20 cm thick), with gently inclined layers (up to 30°). Small sandy lenses the bases of which are mainly composed of poorly or moderately rounded pebble and gravel and, less often, grus and debris of red clays occur over the entire bed.

Bed 2 is a 1.2-m-thick lens located in the central part of the excavation (in the middle and upper part of the excavation with reference to the gully side) and thinning out upsection in the left (lower) part of the excavation. The base of the central area of the lens is a lenticular interbed of an argilloferruginous conglomerate up to 30 cm thick and 3.5–4 m in strike length with especially coarse and poorly rounded red clay pebbles (in places, the largest rock fragments have a rough surface and are barely rounded); in the marginal areas of this interbed, the pebble decreases in size and is replaced by gravel. The lower boundary of Bed 2 under the basal conglomerates is rather rough and has ledges and depressions up to 10 cm deep filled by thin (up to 1 cm thick) reddish blue argillaceous aleurite with clear desiccation cracks. Another lens 0.1×0.3 m in dimensions at the base is located in the left (lower) part of the bed. In the roof of Bed 2, in the left part of the section immediately under the argillaceous layer of Bed 3, there is a lens 30 cm thick and 3 m in strike length,

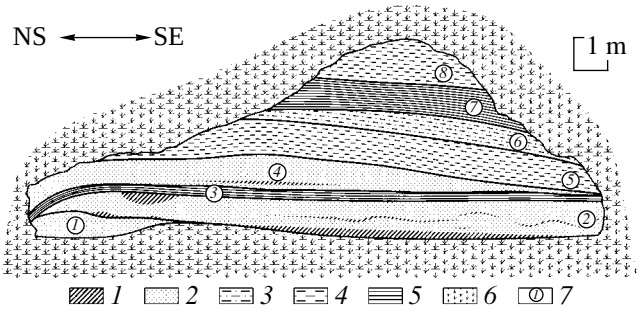

Fig. 2. A section of the Upper Permian continental strata in the gully investigated northwest of the town of Gorokhovets (Vladimir Region). Designations: (*1*) interbeds containing argillaceous gravel and pebble with vertebrate fossils; (*2*) sand; (*3*) siltstone; (*4*) interbedding clay and siltstone; (*5*) clay; (*6*) grass-covered area of the section; and (*7*) the number of a bed.

which contains mainly clayey gravel and small pebbles. A stout lens of obliquely bedded sand 0.5 × 1.5 m is located in the right (upper) marginal area of the excavation; its base is composed of gravel and red clay pebbles; above the lens, an interbed of clay gravel and pebble is observed. In the right (with reference to the gully, upper) part of the excavation, Bed 2 is underlain by an argillaceous aleuritic 5-cm-thick interbed composed of finely interbedded thin bluish and red layers; the lower boundary of Bed 2 is gently undulating. In the left (with reference to the gully, lower) area of the excavation, sands of Bed 2 overlie with unconformity Bed 1.

In the upper layers of the bed, especially in the peripheral area, thin extended red clay and bluish aleuritic layers 1–3 cm thick and 2–3 m in strike length are observed.

The sand layer of Bed 2 yielded large conchostracan shells (up to 1 cm in diameter) and stem fragments of sphenopsids filled by clay. Several fragments are 1 cm thick and up to 10 cm long and one is 8 cm thick and 50 cm long. Isolated fossils of vertebrates, including fish scale and bones, teeth, cranial and postcranial tetrapod bones disarticulated and rounded to a greater or lesser extent, and coprolites 1 to 5 cm long occur throughout the bed, being especially abundant in small rusty course-grained sand lenses with argillaceous gravel and pebble. The maximum accumulation of bones is in the basal interbed of an argilloferruginous conglomerate where complete and fragmentary bones are comparable in number to clay pebble and gravel.

The lower boundary of the bed is distinct, gently undulating, and in places, including the central area of the lens, very rough. The upper boundary of the lens is also rough. The bed is 0.2–1.2 m thick.

(3) Variegated, aleuritic, dense, fragmented clay, with alternating interbeds of red clays (prevailing in the middle of the bed) and bluish gray argillaceous silts (prevailing at the upper and lower boundaries). The lower boundary is distinct and gently undulating. Bed 3 overlies Bed 2; in the left (lower) marginal area of the excavation, it overlies Bed 1. The bed is 0.4 m thick.

(4) Brownish yellow, undulating or vaguely obliquely bedded (predominantly), fine- and medium-grained, dense, polymictic sand with thin (about 1 cm thick) red clay interbeds alternating with light-blue aleurites and interbeds of red clay gravel. Bed 4 contains scarce isolated fish scales and tetrapod bones, increasing in abundance in its lower layers. The upper 10–15-cm-thick layer of the bed is bluish gray. The maximum thickness is in the central area of the excavation, since the upper boundary of Bed 4 curves upward. In the right (with reference to the gully wall, upper) part, the bed becomes 0.2 m thick and, in places, decreases to 0.1 m in thickness; the sand becomes fine-grained, aleuritic, bluish in color, and is broken in places by thin red clay interbeds up to 5 cm thick. Thus, in this area of the excavation, clays of Beds 3 and 5 form an almost integral unit. The lower boundary of the bed is distinct and gently undulating. The bed is 0.1–0.8 m thick.

(5) Interbedding rose-red, variegated, cloddy clay and light-blue silt; the boundaries between the interbeds are obscure, a mottled pattern is observed. At the bottom, bluish laminated silt (10 cm thick) alternates in places with bright red fragmented aleuritic clay. In the middle and upper layers of the bed, the clay is pale rose with bluish gray and greenish gray spots and interbeds, aleuritic, and strongly carbonaceous. Bluish spots form pockets, which enter the central part of the bed. The lower boundary of the bed is distinct and gently undulating. The bed is 0.8–1.0 m thick.

(6) Bluish gray stout, marly, and dense siltstone with light rosy spots at the bottom of the bed. The transition between Beds 5 and 6 is gradual and uneven, it appears as bluish spots, ledges, and pockets of marly silt in the underlying rosy aleuritic clay. The bed is 0.3–0.6 m thick; in the central and right areas of the excavation, clear bulges are observed.

(7) Red aleuritic clay; in the middle of the bed, reddish cream-colored and light fulvous red interbeds and spots occur. The lower boundary is distinct and undulating. The bed is up to 1 m thick.

(8) Interbedding variegated clay and silt; in the upper layers, two 10-cm-thick greenish gray fine-grained interbeds of aleuritic sand. The exposed thickness is up to 1.5 m.

Up the gully channel, there is a cliff; in its central area, a red dense fragmented clay outcrop about 1 m in exposed thickness is observed.

The grass-covered top of the cliff is a 10–15-m-long area formed by an extremely dense layer most likely composed of limestone. The talus near the excavation contains isolated dark gray limestone blocks, including white and rosy dense argillaceous spots with narrow branching canals formed by roots of the plant *Radicites* cf. *sukhonensis.* The blocks are up to 40 cm thick. This limestone is likely a strongly carbonated soil horizon crowning the sandy-argillaceous cyclite described above.

THE TAXONOMIC COMPOSITION OF THE ORYCTOCENOSIS

Fish. D.N. Esin indicated the presence of scales of the following fish forms in the Gorokhovets locality: *Toyemia tverdochlebovi* Minich, *Boreolepis tataricus* Esin, *Mutovinia stella* Minich, *Amblypterina grandicostata* Esin, *Amblypterina* sp., *Plegmolepis* sp., *Isadia* sp., and *Watsonichthys* sp. A.V. Minich and M.G. Minich determined the following fish species in Gorokhovets: *Isadia aristoviensis* A. Minich (teeth and scales), *Toyemia blumentalis* A. Minich (scales, premaxilla, and other membrane cranial bones), *?Geryonichthys longus* A. Minich (fin spines and skin plates), *Mutovinia stella* Minich (a bone of the skull roof and scales), and *Saurichthys* sp. (teeth).

Tetrapods. Batrachomorph amphibians from the Gorokhovets oryctocenosis include the neotenic genus *Dvinosaurus* (specimen PIN, no. 4818/465). In the Late Tatarian, these representatives of the family Dvinosauridae occurred almost everywhere in Eastern Europe (Ivakhnenko *et al.*, 1997). The overwhelming majority of dvinosaurs were found in the basal layers of Bed 2: more than ten lower jaw fragments of at least six or seven animals, including two morphologically complete rami; skull roof fragments and isolated cranial bones; numerous bones of pelvic and pectoral girdles; limbs; an axial skeleton; and fragmentary ribs. Dvinosaurs from Gorokhovets substantially differ morphologically from *D. egregius* of the Vyazniki Assemblage and are similar to *D. primus* from the Sokolki Assemblage. In particular, the lower jaw of the form from Gorokhovets is distinguished from that of *D. egregius* (Shishkin, 1973) by the presence of a tooth row on the coronoids, a different position of pits for the palatal canines, and a shorter sulcus dentalis. At the same time, this form differs from *D. primus* by the larger size, the position of the posterior Meckel's foramen, a shorter prearticular, etc. Apparently, dvinosaurs from Gorokhovets belong to a new species of the genus *Dvinosaurus*; this form likely belongs to the species group *D. primus* but shows a separate developmental stage of the group.

Seymouriamorphs are represented mainly by isolated vertebrae of the characteristic shape with deeply amphicoelus centra and broad and stout zygapophyses. The examination of cranial bones (isolated jaws and bones of the skull roof) shows that at least two forms are present in the locality. The first is *Kotlassia prima* Amalitzky; to date, this species has been represented by only two poorly preserved specimens from the type locality Sokolki. Determinable specimens include a dentary (PIN, no. 4818/615) containing several teeth; an ectopterygoid with a well-developed postchoanal row of palatal teeth (specimen PIN, no. 4818/614); a squamosal with a small semicircular concavity on the occipital flank, which corresponds to the otic notch; and the marginal teeth of characteristic shape the crown of which lacks supplementary denticles, in contrast to those of other kotlassiids.

The second form (specimen PIN, no. 4818/1) is new and also belongs to kotlassiids; it is similar to *Raphaniscus* (Kotlassiinae) in the structure of crowns of marginal teeth; however, the specific fusion between the labial wall of the teeth and the external jaw plate and a strong longitudinal compression of the tooth bases which is characteristic of this form has previously been marked only in *Leptoropha* (Leptorophinae). The combination of these characters suggests that the new form belongs to a new genus which is impossible to assign to a certain kotlassiid subfamily because of the poor preservation of the specimens (an incomplete dentary and isolated teeth).

Some vertebrae from the collection under study have rugose expansions at the ends of the spinous processes (specimen PIN, no. 4818/612) and probably belong to *Karpinskiosaurus* (Karpinskiosauridae); however, there are no other specimens giving evidence of the presence of this genus in the locality.

Nycteroleterids determined as Tokosauridae gen. indet. are represented by a fragmentary membrane bone of the skull roof the external surface of which has a large round flattened tubercle surrounded by small pits (specimen PIN, no. 4818/613).

The pareiasaurians Pareiasauridae gen. indet. are scarce and represented by three cheek teeth (specimen PIN, no. 4818/616) and ten thoracic osteoderms similar to those of *Scutosaurus*, both high conical (specimen PIN, no. 4818/617) and broad and relatively low osteoderms with a tubercle in the center (specimen PIN, no. 4818/610) are present.

The chroniosuchid *Chroniosuchus licharevi* (Riabinin) is the most abundant form of the Gorokhovets oryctocenosis. It is mainly represented by vertebrae, predominantly vertebral centra; complete and fragmentary plates of the dorsal armor occur less often, and cranial bones are extremely scarce. The plates found in the locality are distinguished by wide wings the ventral surface of which is covered by the characteristic irregular cells (specimen PIN, no. 4818/618). The collection includes two pelvic vertebrae fused with the plates (specimen PIN, no. 4818/619). This phenomenon was previously marked only in *Uralerpeton tverdochlebovi* from the terminal Permian of Eastern Europe (Golubev, 1998). Apparently, the same occurs in chroniosuchians as an aberration.

Theromorph reptiles are rather scarce in the locality. Anomodonts are represented by two vertebral fragments (specimens PIN, nos. 4818/32, 33) and three canines of dicynodonts (specimens PIN, nos. 4818/30, 31, 34). Only vertebral centra and disarticulated neural arches are preserved; this is characteristic of dicynodonts, since even if the neural arches are fused with the vertebral centra, a distinct suture is usually retained. A relatively large tubby and deeply amphicoelus (most likely, thoracic) vertebra may belong to a medium-sized dicynodont at most 1 m long. A smaller vertebra is compressed somewhat laterally and its lower surface has two facets. A similar structure is characteristic of the caudal vertebrae; thus, this vertebra could belong to an animal of the same size. One canine could also belong to the same dicynodont. The lingual surface of this canine has an extensive wear facet, occupying the entire extent of the crown. Such a facet could be formed by scraping the tooth on the horny cover of the lower jaw. The other two canines are substantially smaller. Only one has wear signs and the posteromedial surface of its crown is damaged. The canines are referred to as Dicynodontidae gen. indet. Isolated foot bones (specimens PIN, nos. 4818/620, 621), very large ribs (specimen PIN, no. 4818/630), and vertebral fragments

(specimen PIN, no. 4818/628) belong to large and stout reptiles, such as dicynodonts or pareiasaurians.

Gorgonopians are represented by *Inostrancevia* sp. (specimen PIN, no. 4818/631, incisor) and Gorgonopidae gen. indet. (two small canines). The crowns of gorgonopian canines are 1.6–1.8 cm high, flattened tear-shaped in section, and slightly posteriorly curved. One canine has a serrated cutting crest on the internal edge (i.e., comes from an upper jaw); in the second canine, both internal and external edges are serrated (lower jaw). In addition, the collection includes an articular bone of the lower jaw (specimen PIN, no. 4818/632) identical in structure to that of *Sauroctonus*. The postcranial bones include the proximal region of the right humerus (specimen PIN, no. 4818/383) and the left femur (specimen PIN, no. 4818/385) of a small gorgonopian (? Gorgonopidae gen. indet.). An isolated narrow neural arch with a high spinous process (specimen PIN, no. 4818/384) probably belongs to a large gorgonopian (*Inostrancevia*? sp.).

Three isolated cranial bones and several postcranial bones most likely belong to therocephals of the family Annatherapsididae. The left palatine (specimen PIN, no. 4818/634) has a row of nine pits (imprints of the lower teeth) along the lateral margin; medial to this row, there is a poorly pronounced flat and rugose crest with rudimentary palatine teeth. In addition, the collection contains two incomplete maxillae, specimens PIN, nos. 4818/633 and 28, right and left maxillae, respectively. Possibly, the left ulna (specimen PIN, no. 4818/386) and the following amphicoelus vertebrae also belong to annatherapsidids: (a) a lumbar vertebra (specimen PIN, no. 4818/635), including a partially preserved neural arch isolated from the vertebral centrum by a clear suture with an anteroposteriorly short spinous process; (b) a sacral vertebra (specimen PIN, no. 4818/636); and (c) a caudal vertebra (specimen PIN, no. 4818/637).

In the Gorokhovets locality, a cynodont resembling *Procynosuchus* sp. was discovered for the first time in Russia. It is represented by a fragment of the middle region of the left maxilla (specimen PIN, no. 4818/35) with the alveoli of six postcanines and the third and fourth anterior teeth. The tooth crowns are expanded bulbous and have a high lingual cusp and a cingulum surrounded by six cuspules.

THE ECOBIOMORPH COMPOSITION OF THE ORYCTOCENOSIS

The tetrapod oryctocenosis from the Gorokhovets locality is dominated by aquatic and amphibiotic forms, such as chroniosuchians, seymouriamorphs, and dvinosaurs (Fig. 3); moreover, they are represented by the most complete and well-preserved bones. Chroniosuchians are most abundant, their vertebrae compose the greater part of the collection; the second most numerous are seymouriamorphs also represented mainly by vertebrae; and the third place is occupied by dvinosaurs (cranial and postcranial bones). On the contrary, the large amphibiotic parareptiles pareiasaurians (represented by teeth and scales) are very scarce. Terrestrial theromorph reptiles, including theriodonts and dicynodonts, are also scarce and fragmentary in the locality. These features clearly distinguish the Gorokhovets oryctocenosis from that of the Sokolki locality. The two oryctocenoses are almost identical in the list of taxa of family and generic ranks. However, the proportions of taxa in these localities are opposite (Fig. 3). In particular, chroniosuchians and seymouriamorphs composing the main component of the Gorokhovets oryctocenosis are rather scarce in Sokolki, whereas pareiasaurians and therapsids are numerous in Sokolki and rarely occur in Gorokhovets. Only the proportions of dvinosaurs, cynodonts, and gorgonopids are similar in the two oryctocenoses.

BIOSTRATIGRAPHY

The majority of tetrapod forms registered in Gorokhovets, i.e., *Chroniosuchus licharevi* (Riabinin), *Kotlassia prima* (Amalitzky), *Scutosaurus* sp., *Inostrancevia* sp., annatherapsidids, cynodonts, and tokosaurids, are characteristic of the Sokolki Subassemblage of the Sokolki Faunal Assemblage (Ivakhnenko *et al.*, 1997; Golubev, 2000a, 2000b); they are absent from both the earlier Ilinskoe Subassemblage and the later Vyazniki Assemblage. The proper Sokolki Fauna is characteristic of the Vyatkian Horizon of the Upper Tatarian Substage, i.e., the *Scutosaurus karpinskii* Zone. The presence of the genus *Chroniosuchus* in the Gorokhovets Fauna suggests that the bone beds of this locality belong to the upper part of the *Scutosaurus karpinskii* Zone, namely, the *Chroniosuchus paradoxus* Subzone (Golubev, 2000a). The faunas that are most similar in composition to the Gorokhovets Fauna are observed in the basin of the Malaya Northern Dvina River: Sokolki, Zavrazh'e, and Savvatii. They are characteristic of the middle of the Komaritsy Member of the Salarevo Formation.

The data on fish taxa do not contradict this conclusion about the age of the locality. The presence of *Amblypterina grandicostata* Esin, *Mutovinia stella* Minich, and *Isadia aristoviensis* A. Minich in the Gorokhovets Ichthyofauna and the absence of *Boreolepis tataricus* Esin suggest that it should be assigned to the Late Tatarian *Mutovinia stella* Ichthyofaunal Subassemblage (Esin and Mashin, 1996). This subassemblage is characteristic of the biostratigraphic zone of the same name, which covers the terminal Permian of Eastern Europe (most of the Vyatkian Horizon). The species composition of fishes from the Gorokhovets oryctocenosis is very similar to that of the Pron'kino locality and differs from the latter only in the absence of *Boreolepis tataricus* Esin, a typical form of the earlier *Amblypterina grandicostata* Zone. This species is also absent from Vyazniki (Klyaz'ma River, Vladimir

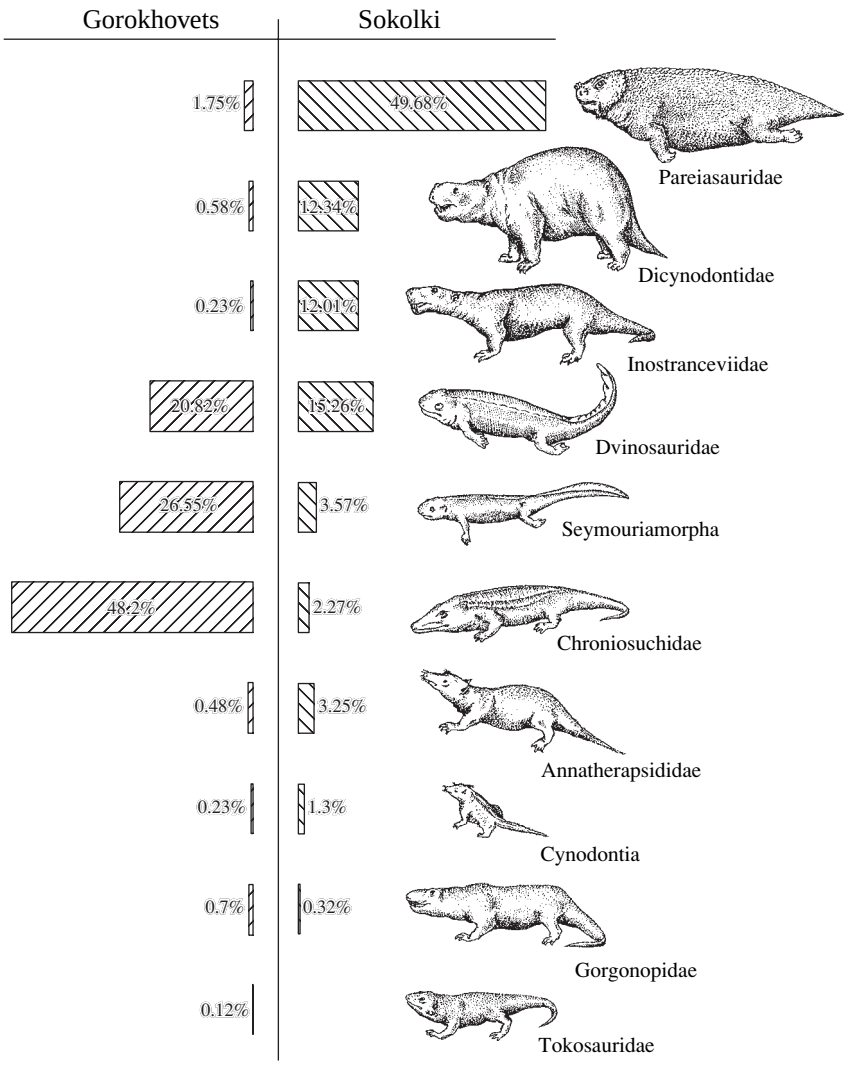

Fig. 3. Proportions of various tetrapod groups in the Gorokhovets and Sokolki localities.

Region), Aristovo (Malaya Northern Dvina River, Vologda Region), Gorki-1 (Oka River, Nizhni Novgorod Region.), and rich collections from the Garibikha (Vetluga River, Nizhni Novgorod Region) and Obirkovo (Staraya Tot'ma River, Vologda Region) localities. These localities are confined to the Vyatkian Horizon.

Thus, the data on vertebrates enable one to date the Gorokhovets locality to the Vyatkian Time. In our opinion, the Gorokhovets bone beds correspond to the Komaritsy Member of the Salarevo Formation of the Sukhona–Northern Dvina section (Golubev, 2000a).

PRESERVATION OF FOSSILS

Vertebrates occur in each sandy bed of the locality. Bed 1 yielded scarce fish scales and two large rounded bones of tetrapods and Bed 4 contained isolated scales and a lower jaw of a chroniosuchian. The greatest number of specimens come from Bed 2 where the accumulation of bones was maximum.

Fishes are represented by numerous and usually very large (up to 3 cm long) and massive scales and isolated bones, including cranial bones.

Almost all vertebrate specimens are disarticulated cranial bones and limbs, vertebrae, ribs, and their fragments. The exception is provided by several relatively complete lower jaw rami of dvinosaurs and, less often, the lower jaws fragments of chroniosuchians and seymouriamorphs.

The size and the state of preservation of bones in the Gorokhovets locality largely agrees with the dimensions of the deposits. The following three main states of preservation are observed in the locality: (1) relatively complete, firm, dense, mainly dark, brown and fulvous brown bones, including lower jaws, only weakly rounded, if at all; fine morphological details are retained; the most complete, large, and well-preserved bones of this type come from the basal conglomerate of

Bed 2; (2) dense, firm, with a dense surface, mainly dark brown and fulvous brown fragmentary bones strongly rounded to pebble; and (3) complete and fragmentary bones widely ranging in the extent to which they are rounded from almost completely preserved to strongly rounded bony fossils, which are brittle, occasionally crumbling, relatively light cream-brown or dark fulvous, reddish, and, often, mottled, with a damaged, delaminated, or pitted surface; this type is registered with certainty in Bed 2 only. Intermediate states between these types also occur. The first type of preservation is likely a result of short-term disarticulation in semiaquatic conditions and subsequent rapid transportation and rapid burial. Apparently, the second type was also formed in semiaquatic conditions, but transportation was longer so that bones became rounded and burial was not so rapid. The third type is accounted for by a longer disarticulation, which most likely occurred in subaerial conditions followed by a short transportation and burial.

GENESIS OF THE LOCALITY

In general, the bone members are of alluvial origin. The sandy beds (1, 2, and 4) are shallow river channels, coastal, and bank deposits. These beds are distinguished by a nonuniform and rhythmic structure, the presence of numerous lenticular interbeds (which were apparently deposited in individual river branches and depressions formed by shallow meandering streams), and thin silty interlayers, especially in the marginal region of streams (lenses). The presence of deposits ranging granulometrically from clays to gravelstones and fine-pebbled conglomerates is evidence of constant changes in the intensity of water currents.

The argillo-aleuritic beds (3, 5, 6, and 7) are formed of floodplain deposits and silts accumulated in shoals and banks. The upper layers of Bed 5 and carbonaceous Bed 6 are probably of subaerial floodplain origin; this is a drainage level where the initial stage of the soil formation developed. An overlying limestone bed discovered in the talus creates this sedimentation rhythm and apparently represents a carbonaceous paleosol formed in semiaquatic floodplain conditions. Thus, it is valid to regard the entire strata described above as an integral cyclite, beginning with the sandy riverbed deposits and crowned by floodplain argillaceous beds with soil horizons.

The locality was formed as follows. The lower sandy layers (Bed 1) were formed in conditions of a relatively quiet, slow, and uniform stream; this is evidenced by the fine-grained sand with widely spaced interbeds of small gravel, mainly undulating lamination, and the extent of horizontal sandy interbeds. Under such conditions, scarce, small, and fragmentary remains of vertebrates (of the second type of preservation) transported by streams were buried in small depressions of the river bed where the current was relatively rapid and course-grained deposits, including gravel, accumulated.

Subsequently, the river rapidly dried and only isolated puddles remained in the middle where silt deposits accumulated. Before long, they also dried up, which is evident from the numerous desiccation cracks in the argillaceous interbed in the central part of the depression in the roof of Bed 1.

Later, judging by the coarse-grained structure, oblique bedding, and lenticular inclusions in Bed 2, a rapid and unevenly flowing stream returned to this region. As a result, the sedimentation alternated with redeposition of previously formed layers. In the sites characterized by especially intense hydrodynamic processes, more obliquely bedded course-grained interbeds were formed. The flow became slower at the bank and at the late stage of the channel being filled by deposits, thin silty interbeds were formed.

Numerous vertebrate fossils collected in Bed 2 followed different methods of accumulation, so that the above three types of preservation occurred. The presence of strongly rounded bones of the second type (similar to those from Beds 1 and 4) in the basal part of the lens shows that animals died in the water or close to the stream but were not buried immediately. On the contrary, bone fragments referred to the third type of preservation were for some time in subaerial conditions and were subsequently washed down by a relatively slow stream.

The basal bone conglomerate of Bed 2 was formed differently, since vertebrate specimens from this bed are mainly of the first type of preservation. The skull fragments and jaws of dvinosaurs in which the brittle tooth apices are preserved are evidence that the taphocenosis discovered in the conglomerate was at least partly formed at the point where animals died or the transportation was insignificant. It is evident that ichthyophagous chroniosuchians inhabited the area near the water body. Apparently, a large number of mainly aquatic and amphibiotic vertebrates were accumulated in depressions in the river floor during a drought and, as the silt was dried out, they died. At the close of the drought season, their remains were washed down by streams, accumulated at the bottom of the old dry channel, and were rapidly buried together with the debris. Such a pattern of burial is evidenced by the fragmentary nature and the good preservation of many specimens, the weakly rounded argillaceous pebble of the conglomerate, and the presence of clayey debris and a thin noneroded clayey interbed with desiccation cracks at the base of the bed. The specimens that differ in preservation (types 2 and 3) probably had a longer postmortem history before they were buried.

Remarkable specimens come from the obliquely bedded gravel lens located in the left upper part of Bed 2 (Fig. 2). They include a large number of scales and bones of large fishes, whereas the tetrapod bones are scarce and fragile and underwent a long and, probably, subaerial disarticulation (the third type of preservation); these deposits were formed by a rapidly flowing stream where vertebrates were gradually accumu-

lated in the absence of disastrous effects, as opposed to the situation in the basal interbed.

When the channel was filling up with deposits, the clayey floodplain deposits in Bed 3 were formed. Subsequently, a short-term erosion was followed by the accumulation of sandy deposits formed by a new moderately rapid stream (Bed 4); this is evidenced by the smaller grains of sand, rare interbeds of small gravel, the undulating lamination of deposits, and the presence of silty interbeds. The scarce vertebrate remains are fragmentary (the most complete specimen is a fragmentary lower jaw of a chroniosuchian) and do not form a large accumulation.

Bed 4 gradually becomes Bed 5. This demonstrates that the deposits filling the channel gradually became more and more fine-grained and subsequently dried out.

The diverse biota, including various plants, numerous conchostracans, fishes, amphibians, and reptiles, some of which were rather large, is evidence for the presence of favorable habitats in this area during the formation of the locality. However, this biotope only allowed for the existence of a rich and diverse aquatic community; this inference follows from the quantitative prevalence of aquatic forms in the Gorokhovets oryctocenosis. There were no stable suitable conditions for the formation of a rich terrestrial biota. In our opinion, such a biotope could be an extensive lowland with a system of strongly branching and meandering channels of constant and temporary streams alternating with vast sandy and marshy silt banks and small elevations.

CONCLUSIONS

(1) The list of vertebrates from the Gorokhovets locality includes about ten fish species and at least twelve amphibian and reptile forms, including *Dvinosaurus* sp., *Kotlassia prima* Amalitzky, Kotlassiinae gen. nov. (cf. *Raphaniscus*), *Karpinskiosaurus* (?) sp., Tokosauridae gen. indet., *Scutosaurus* sp., *Chroniosuchus licharevi* (Riabinin), Dicynodontidae gen. indet., *Inostrancevia* sp., Gorgonopidae gen. indet., Annatherapsididae gen. indet., and *Procynosuchus* sp. As regards taxonomic diversity, this is the richest Permian locality in European Russia.

(2) The Gorokhovets Tetrapod Fauna belongs to the Sokolki Subassemblage of the Sokolki Assemblage; however, it includes certain new forms, the cynodont *Procynosuchus* sp. and, probably, a new brachyopoid of the genus *Dvinosaurus*.

(3) The bone beds of the locality belong to the middle of the Vyatkian Horizon, *Chroniosuchus paradoxus* Subzone of the *Scutosaurus karpinskii* Zone.

(4) The core of the Gorokhovets oryctocenosis is composed of hydrobionts, whereas representatives of terrestrial communities are rather scarce. This sharply differs the Gorokhovets Vertebrate Association from that of the Sokolki locality where forms from the aquatic and terrestrial communities are approximately equal in number.

(5) The locality was formed in an extensive marshy lowland in a channel of a small stream that became dry from time to time.

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