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Pareiasaurian Tracks from the Upper Permian of Eastern Europe

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Abstract—The first footprints and tracks of large terrestrial reptiles were discovered in the Late Tatarian deposits in northern European Russia. The tracks were found in light gray thick-bedded limestone of the Upper Tatarian (*Proelginia permiana* Tetrapod Zone, Severodvinian Horizon, Upper Permian). The locality was formed on the shore of a large lake in the subhumid seasonal climate. Two tracks extending about two meters each are described in detail. These tracks belong to quadrupedal pentadactyl reptiles with a body length exceeding 1 m. The manus is elongated and turned medially, the first digit is positioned perpendicular to the axis of the animal's movement. The second digit of the forelimb is the longest. Pes imprints are subtriangular, the third digit is parallel to the movement axis, the longest pes digits are the second and third. We tentatively assign the tracks to large pareiasaurians of the family Bradysauridae with a glenoacetabular distance longer than 85 cm. A new ichnogenus and ichnospecies, *Sukhonopus primus*, is described.

Key words: Pareiasaurida, Parareptilia, Upper Permian, Northern Russia, tracks, ichnology, new taxa.

INTRODUCTION

Fossil tracks of quadrupeds are common in the Permian and Triassic continental deposits of central and western Europe. Thus, they are important not only for paleoenvironmental and paleoetological reconstructions but also for stratigraphy (Ceoloni *et al.*, 1986; Gand and Haubold, 1988; Gand, 1993). In eastern Europe, notwithstanding the abundant occurrences of Permian tetrapods (Ivakhnenko *et al.*, 1997), their tracks have been recorded only twice. The first record is a track of the small amphibian *Anthichnium* ichnosp. from deposits of the Severodvinian Horizon of the Upper Tatarian Substage, discovered near the village of Kul'chumovo in the Orenburg Region (Tverdokhlebov *et al.*, 1997). On the basis of imprints of tetradactyl manus, the authors interpreted them as tracks of a juvenile *Dvinosaurus*, the sole temnospondyl known in the Severodvinian Horizon.

The second record is represented at two points in the Lower Permian redbed deposits in the northern Caucasus (Lucas *et al.*, 1999). A group of footprints with four long and curved digits of the lacertoid type was determined as cf. *Dromopus* ichnosp. In addition, one isolated track with five straight and thin digits and a well-pronounced calcaneal area is referred to as cf. *Dimetropus* ichnosp. It most likely belongs to a sphenacodont pelycosaur (Lucas *et al.*, 1999). In the conclusion of the review, the earliest description of Paleozoic tracks from the former Soviet Union is worth noting. It is associated with the Middle–Upper Carboniferous sandstone of polymetallic mines of Dzheskazgan in Central Kazakhstan (Mladentsev and Narkelyun, 1958). Judging from the published photograph, some tracks may belong to an amphibian closely related to *Parabaropus* ichnosp. described by Haubold (1971).

The first locality of tracks of large Permian reptiles in European Russia was discovered by an employee of a field team of the Paleontological Institute of the Russian Academy of Sciences (PIN) S.V. Petuchov in the summer of 2000 during a prospecting trip (Fig. 1, exposure 0011). The site is located on the left bank of the Sukhona River 1 km downstream from the mouth of the

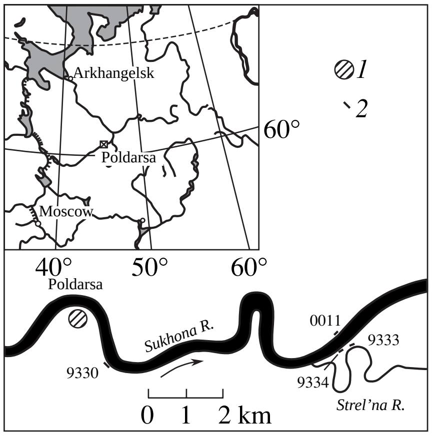

Fig. 1. Schematic map of studied sections in the basin of the lower flow of the Sukhona River: (*1*) settlement; (*2*) exposures: 0011. Esipovka, 9330. Nikulino, 9333. Mar'yushkina Sluda, 9334. Ust'e Strel'ny.

Fig. 2. Locality of tracks of Permian tetrapods on the left bank of the Sukhona River near nature park Esiptsevo (Vologda Region, Velikoustyugskii District).

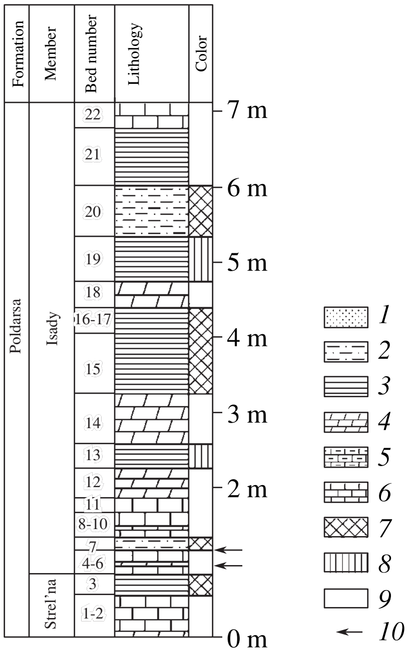

Fig. 3. Lower part of the section of Upper Permian deposits on the left bank of the Sukhona River at the nature park Esiptsevo (exposure no. 0011). Designations: (*1*) sand or sandstone; (*2*) siltstone; (*3*) clay; (*4*) marl; (*5*) clayey limestone; (*6*) limestone; (*7*) red beds; (*8*) variegated deposits; (*9*) gray beds; (*10*) localities of bone remains and tracks of tetrapods.

Strel'na River (Velikoustyugskii District, Vologda Region). The track site was named Esipovka after the nearby park area Esiptsevo. Footprints are confined to two rather narrow outcrops of the platy limestone positioned one above the other. These outcrops armor the Sukhona River bank in less than one meter above the low-water level (Fig. 2). Obviously, the tracks are submerged during most of the warm season.

Tracks are traced for almost 500 m along the river bank.[1] The exposed part of the lower bed is 0.5 to 1.5 m wide and displays a total of 186 footprints detected on the surface not covered with talus. The track distribution is nonuniform, with zones of increased concentration alternating with places bearing individual or no footprints. The preservation of tracks and their orientation range widely. Many footprints are encircled by marginal mud walls with distinctly preserved imprints of digits and claws. The largest footprints are more than 35 cm in diameter and up to 5.5 cm deep. The upper limestone bed displays only isolated tracks. They are strongly obliterated and lack clearly expressed digits.

We cleared and examined two tracks in the lower bed. They are a distance of 95.5 m from each other and belong to animals of different size. The large track (TW-1) is composed of 12 footprints (6 right and 6 left), the smaller track (TW-2) has 11 footprints (5 right and 6 left). The position of distal digital phalanges are distinct in the majority of manus and pes imprints. The movement axis is straight in both cases; TW-1 is directed to the east-south-east, while TW-2 is directed to the west. The absence of other tracks crossing the studied tracks confidently rules out an opportunity of mixing up imprints of different individuals.

The pes and manus imprints in the two tracks are notably different in shape and size; nevertheless, their orientation, shape, and the length of digits in relation to the size of a footprint are identical within either track. This allows us to assign them to animals of the same species. The study of these tracks resulted in the description of a new ichnogenus and ichnospecies, *Sukhonopus primus*.

STRATIGRAPHY

In the area studied, the banks of the Sukhona River and its tributaries are built with exposed deposits of the Poldarsa Formation of the Upper Tatarian Substage. At the location of the tracks on the left bank of the Sukhona River upsection from the shoreline (August, 2000), the following sequence is described (Fig. 3):

The Strel'na Member

(1) Dark gray, horisontally bedded, and silty marl, with a bituminous smell; the exposed thickness is 0.1 m;

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[1] An inspection undertaken in 2001 showed the presence of footprints in limestone outcrops on either bank of the Sukhona River over at least several kilometers; the same is true for the river's tributaries.

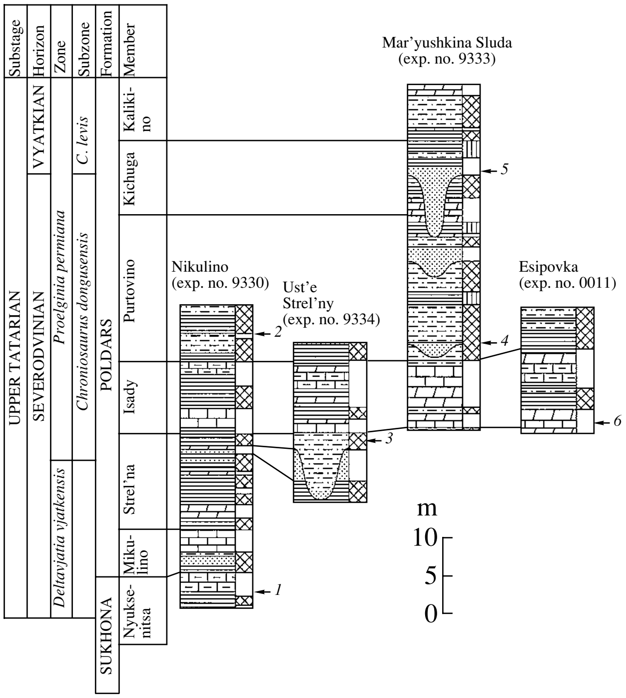

Fig. 4. Scheme of correlation of the Upper Permian sections in the lower flow of the Sukhona River. For designations, see Fig. 3. Tetrapod localities: (*1*) Poldarsa, (*2*) Mikulino, (*3*) Ust'e Strel'ny, (*4*) Mar'yuskhkina Sluda-A, (*5*) Mar'yuskhkina Sluda-S, (*6*) Esipovka.

(2) Bright greenish gray, indistinctly thick horizontally-bedded pelitomorph limestone, with narrow (fractions of millimeter) canals of plant roots, with interlayers of dark green clay; 0.47 m thick;

(3) Brown clay with rare large bluish gray spots, massive, nonplastic, poorly soaking, strongly silty, and isotropic; 0.28 m thick.

Isady Member

(4) Creamy gray, greenish gray, and light gray limestone (color varieties irregularly transient; weathered surfaces are light gray), massive, heterogeneous (alternation of crystalline and earthy texture zones), with numerous pores; in the middle part of the layer, with thin vertical and poorly twisting channels (cracks of plant roots), frequently filled with large crystals of calcite. Freshly split blocks stain the hands, without any bituminous smell, monolithic (not platy), strong, broken by vertical cracks into large blocks several decimeters in size. The upper surface of the layer is rough, wavy, with dissication cracks and footprints of large tetrapods; the thickness is 0.11 m.

(5) Gray marl, with a very indistinct thin horizontal bedding (bedding is weakly traced by color tints), homogeneous, averagely strong, not platy, and lacking a bituminous smell; 0.05–0.07 m thick.

(6) Creamy gray limestone, with spots of a greenish tint, massive, pelitomorph, very strong (hardly split by a hammer), similar to a crystalline limestone variety of layer 4. The rock is broken by vertical cracks into blocks ranging in size from several decimeters to several meters. The upper surface of the layer is rough, with dissication cracks and very indistinct tracks of large tetrapods; 0.15 m thick.

(7) Gray predominantly wine-colored or grayish brown, brownish gray, and greenish gray siltstone; very indistinctly horizontally bedded, with strongly sandy greenish gray interlayers, clayey in the basal part and, in the upper part of the layer, with fine (several millimeters) greenish gray spots. Siltstone is not very strong, difficult to split by hand, with numerous ostracode shells; 0.17 m thick.

(8–11) Gray limestone, massive or with thick wavy bedding, very poorly bituminous, with narrow (up to 2 mm thick) channels of plant roots commonly filled with crystals of calcite, with clayey interbeds, platy; 0.55 m thick.

(12–14) Greenish gray marl, monochrome and massive (in the lower part) or with brown veins and spots and horizontally bedded (in the upper part), silty, with interbeds of greenish light gray and grayish pink, horizontally bedded, nonplastic, carbonate clay; 1.4 m thick.

(15–19) Brown clay, red brown in the lower part and light brown in the upper part, with interbeds of numerous red veins and, occasionally, distinct green round spots. Clay massive or very indistinctly thick, horizontally platy, with varying silt content, with an interbed (35 cm thick) of greenish gray massive marl; 2.1 m thick.

(20) Brown and massive siltstone; 0.7 m thick.

(21) Bluish and greenish gray massive clay. Homogeneous, carbonate, silty, nonplastic; 0.75 m thick.

(22–33) Gray, horizontally bedded, clayey limestone, with narrow channels of plant roots (in the roof of the bed, the channels of plant roots are up to 10 mm in diameter), with interlayers of gray and greenish, horizontal and wavy bedded, weakly bituminous clays and marls; 2.45 m thick.

(34) Gray, massive, and loose marl; 1.35 m thick.

(35) Dark green clay with thin beige wormlike veins, thin horizontally bedded, fragile, nonplastic, silty, with the carbonized rests of plants on bedding planes; 0.5 m thick.

Purtovino Member

(36–37) Dark brown clay, with individual or numerous (interlayer-like) beige and white rootlike veins (zones of gleization around plant roots, paleosols), horizontally bedded, nonplastic, fragile, with interbeds of siderite concretions; in the lowermost part of the layer, with numerous imprints of stalks and leaves of plants (horsetails, ferns), and also molds of bivalve mollusks; 2.45 m thick.

(38–43) Red siltstone with gray veins and spots (ancient zones of gleization around organic remains, including roots of plants), very indistinctly thick horizontally bedded, intermediately strong; 2.65 m thick.

(44) Brickred siltstone with fine (several millimeters in diameter) distinct, almost perfectly-round green spots (gleization around organic detritus), massive, homogeneous, and strong; 0.4 m thick.

Above it is a 5–6-m-thick bed of red-colored thickly striped siltstones.

The deposits described correspond to the middle part of the Tetrapod Subzone *Chroniosaurus dongusensis* of the Zone *Proelginia permiana* (comparison of the investigated sections to nearby sections, where vertebrates were found, is given in Fig. 4) and the upper part of the Severodvinian Horizon (Golubev, 2000).

GENESIS OF THE LOCALITY

The structure of the Esipovka section is typical of the Poldarsa Formation, which commonly shows a frequent alternation of clayey carbonate rocks with a subordinate role of fine clastic rocks (Golubev, 2000). Elementary layers of this formation usually have a low thickness (averagely 0.4 m) and stretch for many kilometers. This structure is typical for deposits of large basins with an unstable mode of sedimentation. In our case, this was a coastal zone of a large lake and adjacent extensive alluvial lowland with poorly dissected relief. Lake deposits are represented by gray clayey carbonate rocks; alluvial deposits are composed of red-colored silty clayey flood plain alluvium and, less often, sandy channel alluvium.

The presence in the Poldarsa Formation of numerous levels with plant roots, dissication cracks, and traces of tetrapods indicate that the deposits periodically emerged above water level. The aeration periods (i.e., oxidation conditions) might have been rather prolonged, which is evident from the redish color of individual layers and members. The absence in these deposits of easily soluble salts (sulfates and chlorides) points to the wash-out mode of surface deposits with the predominantly descending stream of water. The latter is possible only with a significant amount of atmospheric precipitation, which prevails over evaporation in the annual cycle (Ollier, 1984; Lobova and Khabarov, 1983; Dobrovol'skii *et al.*, 1998). However, judging from the montmorillonite content of clays and carbonate degree of deposits (Reference section.., 1981; Verzilin, 1993), this prevalence was insignificant. In the warm climate existing in Eastern Europe in the Late Permian (Zharkov and Chumakov, 2001), this phenomenon may indicate that atmospheric precipitation was nonuniformly distributed around the year, that is, humid and relatively dry seasons alternated. Numerous levels of gleization in the alluvial deposits, confined mainly to root bearing levels, indicate seasonal and rather prolonged excessive dumping of deposits by atmospheric and (or) flood waters. In part, the excessive dumping could be accounted for by the periodically high level of ground water (Dobrovol'skii *et al.*, 1998).

Thus, the climate of the considered area in Poldarsa Time was warm, subhumid, and seasonally wet. In humid seasons, the rivers flowing from the eastern slopes of the Baltic Schield delivered enormous amounts of fresh water together with silty material. The excess of water resulted in rivers flooding huge territories and in the formation of an extensive floodplain deposit. In the shorter dry seasons, the river drainage and associated transfer of clay material considerably reduced. On the contrary, the supply of carbonates increased, the area of reservoirs reduced, and, on their periphery, huge areas of gradually drying clayey-carbonate lake ooze formed. These areas were rich in peculiar vegetation tolerant to the overabundance of carbonates in the ground. The root systems of these plants, known as *Radicites sukhonensis*, are widespread in the Upper Permian carbonate deposits of European Russia (Aref'ev and Naugol'nykh, 1998).

Landscapes of this type were favorable pasture areas of herbivorous reptiles. Unfortunately, solid ground does not preserve any traces of tetrapods. However, softer wetted grounds might keep imprints of their paws, which in the following damp season were washed out by fresh water or, on the contrary, were buried under a layer of the clayey sediment brought down and deposited by these waters. Moreover, more viscous and swampy grounds (of lacustriane or floodplain origin) might present actual traps for terrestrial animals. It is likely that the Kotelnich and Port Kotelnich localities found on the bank of the Vyatka River in the Kirov Region in the deposits chronologically close to footprint-bearing beds of the Poldarsa Formation were formed under such conditions (Golubev, 1999).

As concerns the Esipovka locality, the sequence of its formation might be the following: (1) retreat of the lake (regress) and formation of an extensive field of slowly drying ooze, with rich vegetation; (2) the occurrence of large herbivorous reptiles and the formation of tracks; (3) complete drying of carbonate oozes with the formation of dissication cracks; (4) a burial of traces under a layer of clayey deposits during the following flood period; (5) lake transgression, the beginning of accumulation of limnic oozes, the end of a cycle and the beginning of a new one.

Obviously, the situation frequently reoccurred.[2] However, along with the formation of track-bearing carbonate deposits, the burial of tracks was also accompanied by washing out of the deposited sediments and destruction of the already formed localities. It is indi-

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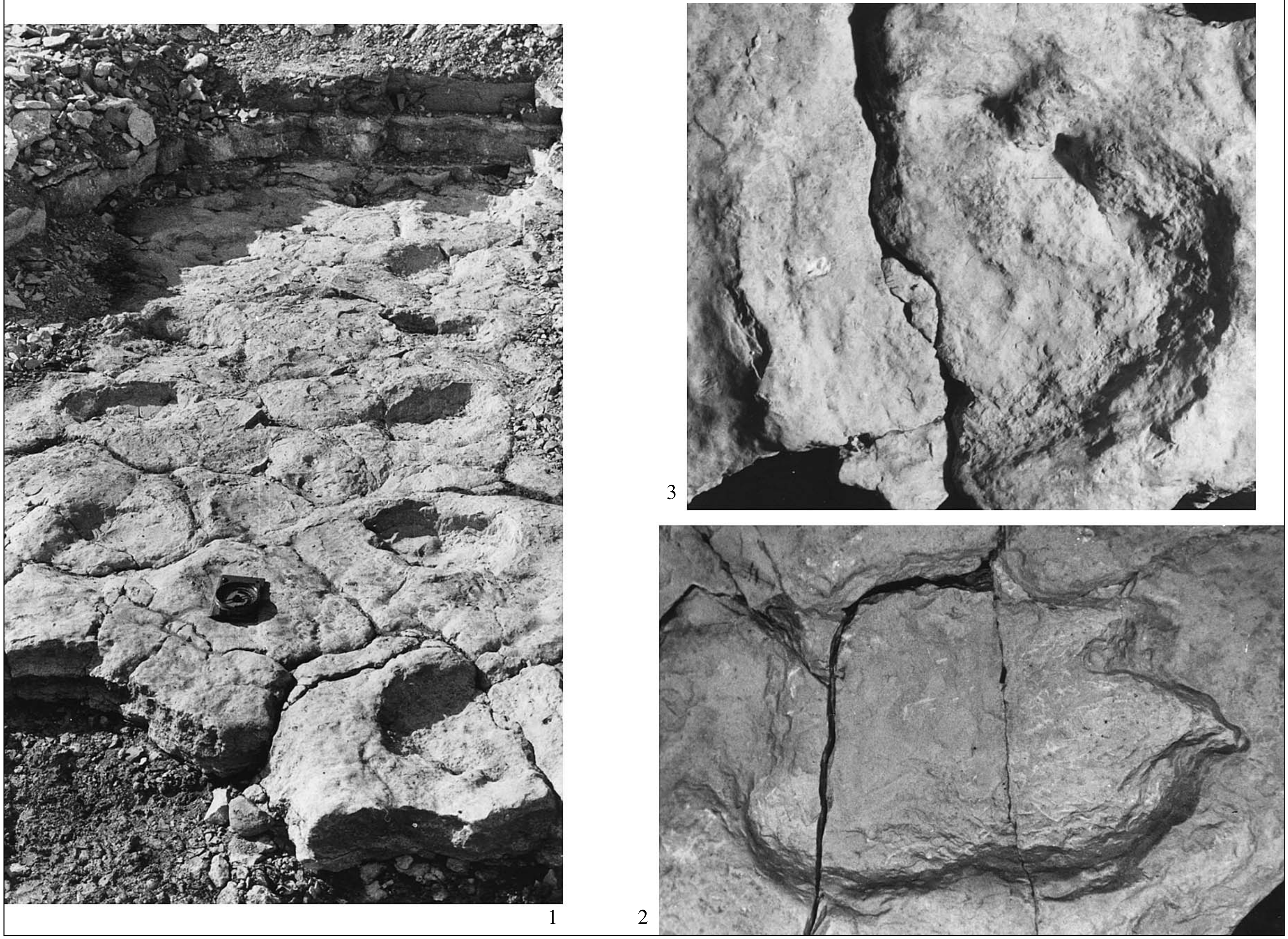
[2] In 2001, among other footprints on the track-bearing limestone, an individual imprint of the hind foot of a tetrapod was discovered. During its formation, the pressure of the foot affected not only the limestone, but also the underlying marl. The marl surface, however, bears only a small cone encircled by mud ridges. Obviously, in this case, the carbonate ooze deposited at stage 5 covered the clayey sediment that was freshly formed and still not completely lithified.

Plate 4



Explanation of Plate 4

Figs. 1–3. *Sukhonopus primus* ichnosp. nov.: (1) track of a large animal, TW-1; (2) fragment of the holotype, PIN, no. 4850/2b, footprint of the left forelimb, ×0.27; and (3) fragment of the holotype, PIN, no. 4850/2a, footprint of the left hind limb, ×0.27; Vologda Region, Velikoustyudskii District, Sukhona River; Upper Permian, Upper Tatarian Substage.

cated by the lenticular structure of the trace-bearing carbonate member, with its individual separate layers traced only for very small distances. Thus, the layers, observed in the Esipovka section, are not recognized in sections of Ust'e Strel'ny (0.6 km from Esipovka) and Mar'yushkina Sluda (1.5 km).

SYSTEMATIC PALEONTOLOGY

CLASS PARAREPTILIA

GROUP PAREIASAURIDA

Family ?Bradysauridae Huene, 1948

Ichnogenus *Sukhonopus* Gubin et Bulanov ichnogen. nov.

Etymology. From the Sukhona River and the Greek *pous* (foot).

Type ichnospecies. *Sukhonopus primus* ichnosp. nov.

Diagnosis. Tetrapod animal, footprints pentadactyl, fifth digit very poorly developed. Traces of tail drag absent. Pes imprints rounded subtriangular, their width about 40% of track; manus imprints elongated, with a length to width ratio of 0.65–0.7. Digits short, with pointed claw phalanges, first digit on both pes and manus not set aside. Third digit of pes directed parallel to animal's movement axis, second and third digits longest. Medial (internal) edge of manus showing position of first digit turned perpendicular to movement axis, with longest second digit.

Species composition. Type ichnospecies.

Comparison. In the shape of footprints and in short equidistant pes digits, the new ichnogenus is similar to the ichnogenera *Dicynodontipus, Gallegosichnus,* and *Calibarichnus* (Haubold, 1971; Conti *et al.*, 1977). It, however, appreciablly differs in the size of footprints, the shape and orientation of the manus, and the expression of its external digit. The shape of the pentadactyl manus of *Brontopus* (Ellenberger, 1983; Gand and Haubold, 1988) resembles the manus of the new ichnogenus. It, though, differs in its position in relation to the movement axis and in the longer first digit. Moreover, *Brontopus* differs in rounded pes (contrary to subtriangular in *Sukhonopus*) and in digits of different length. In addition, the new ichnogenus has smaller feet in relation to the width of the track. Tracks of the pareiasaurian *Pachypes dolomiticus* described from the Upper Tatarian of Italy (Conti *et al.*, 1977) resemble imprints of hind legs of *Sukhonopus* in size and shape. However, in *Pachypes*, the longest pes digit is fourth, pointed distal phalanges are only weakly developed, and pes and manus imprints are very similar. These characteristics are sharply different from the conditions of *Sukhonopus*.

Sukhonopus primus Gubin et Bulanov ichnosp. nov.

Plate 5; Figs. 1–3

Etymology. From the Latin *primus* (first).

Holotype. PIN, no. 4850/2; partial track with consecutive left imprints of front and hind feet; Vologda Region, Velikoustyugskii District, Sukhona River, Esipovka locality; Upper Permian, Upper Tatarian Substage, Severodvinian Horizon, *Proelginia permiana* Zone.

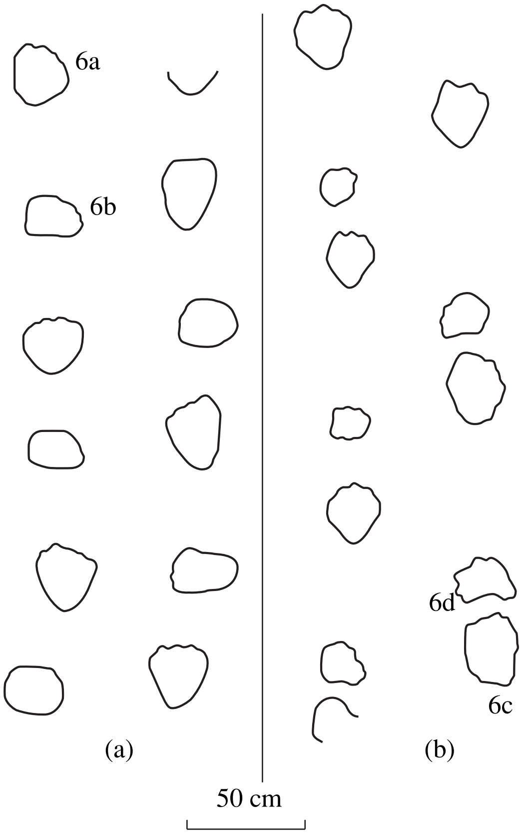


Fig. 5. *Sukhonopus primus* ichnogen. et ichnosp. nov.: tracks, (a) larger animal (TW-1), (b), smaller animal (TW-2). Designations of imprints within tracks (6a–6d) correspond to track images in Fig. 6.

Description (Figs. 5, 6a–6d). The track with larger imprints (TW-1; Pl. 5, fig. 1; Fig. 5a) consists of six pairs of footprints of fore and hind legs. It is nearly straight, 58–63 cm wide; the distance between the medial parts of pes imprints (interpes distance)[3] is 36–40 cm, and the length of the double step (stride) is 82–95 cm. The left overlap lag is 45 cm, the right one is 36–38 cm (footprints are "reciprocally opposed" sensu Haubold, 1971). The pace angulation varies from 70° to 79° in the hind foot and from 67° to 72° in the forefoot. The constant of the step (const) is 108–112 cm, the basic component of the constant of the step varies from 90 to 94 cm. The majority of footprints area deep, with well-pronounced terminal phalanges, and associated with ridges showing the position of the anterior and posterior drag of feet (after Rukovskii, 1988).

Pes (Pl. 5, fig. 3; Fig. 6a). Imprints have the shape of an almost equilateral triangle with rounded corners;

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[3] We use terminology of V.B. Sukhanov (1968) and Haubold (1971).

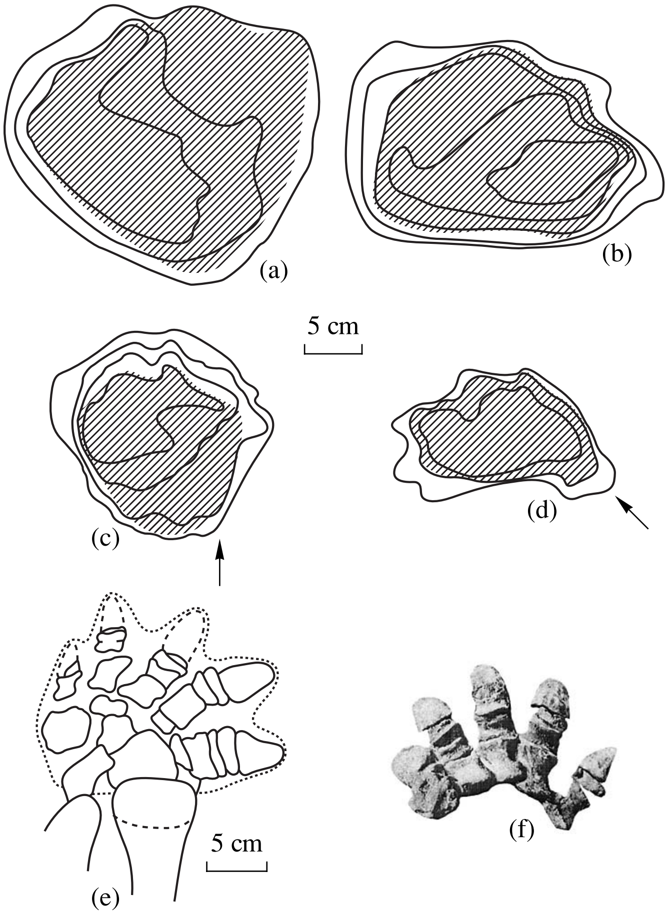

Fig. 6. (a–d) *Sukhonopus primus* ichnosp. nov.: (a, b) holotype PIN, no. 4850/2a and b (TW-1): sketches of imprints of the left feet: (a) hind foot and (b) fore foot; (c, d) specimen PIN, no. 4850/4 (TW-2): sketches of imprints of right feet: (c) hind foot and (d) fore foot. The shaded area marks the presumed shape of the autopodium. Arrow points the direction of the appendage movement during its application. Increment of isolines is 1 cm. (e) *Deltavjatia vjatkensis* (Hartmann-Weinberg, 1937): specimen MS, no. 5324: left forefoot, view from above; the dotted line shows the lost phalanges; the contour deliniates presumed imprint of this foot; (f) *Scutosaurus karpinskii* (Amalitzky, 1922), holotype PIN, no. 2005/1532, metacarpals and digits of a forefoot.

their length along the third digit is 21–23 cm (in the holotype, 21 cm), the width at the digital bases is 23–27 cm (in the holotype, 24 cm). The length of other digits is approximately the same as in the third digit. The pes is pentadactyl, the external digit is usually weakly expressed. In five of six imprints, the third digit is positioned in parallel to the movement axis of an animal, and only one footprint is weakly inclined medially. The footrints have the greatest depth along the medial edge, particularly, in its middle region and in the imprints of claw phalanges of the second and third digits. Judging from the position of the anterior and posterior drag traces, a foot moved first falling, then rising forward at lowering and rise. The number of pes digits can be determined only from the anteriorly projecting distal phalanges. This is probably is a result of the development of a thick skin membrane between the digits and thick skin on the pes sole.

Manus (Pl. 5, fig. 2; Fig. 6b). In all imprints of TW-1, the orientation of the medial sides places the first digit perpendicular to the movement axis. In the holotype, the imprint axis of the longest digit (probably, the second one) is at an angle of 80°, the following digit is at 70°, and the fourth external digit (last clearly imprinted) is at an angle of 50°. The imprint measured parallel to the movement axis is 16 cm long, 24 cm wide, and the ratio of length to width is 0.67. The manus measured along the fourth digit is 18.5 cm long. The medial edge of the manus has a weak anterior curvature in the middle, probably showing the position of the carpus. The maximal depth (about 5 cm) is at the medial side of the footprint and in midpoints of digits I and II, similar to those of the hindfoot. Impressions of digits II to IV clearly imply pointed claw phalanges, the claw-tip of the second digit being bent rearward. Anteriorly posteriorly, the print is accompanied by ridges, the anterior ridge is shifted forward. The absence of ridges on the carpal side probably indicates that the manus was lowered into the mud in a lateral-medial direction and, retrieved frontwards.

Track no. 2 (PIN, no. 4850/4; Fig. 5b). The track is 49 cm wide; the distance between the medial pes sides is 25–28 cm; the stride is 79–85 cm long. The overlap lag is 22–24 cm, the pace angulation varies from 82° to 87°, the pace constant is 83 cm, and the basic component of the pace constant is 66 cm.

Pes (posteriormost right foot, Fig. 6c) is rounded triangular is shape. As in TW-1, the maximal deepening is in the area of digits I and II. Digits II to IV are nearly equal in length, digits I and V are noticeably shorter. The width of feet equals its length along digit III and makes 17 cm. Claws are well pronounced on digits II–IV.

Manus (posteriormost right and left imprints, Fig. 6d). Impressions of the right and left manus distinctly indicate four digits, the external fifth digit is faintly seen. The footprint is 16 cm wide and 10 cm long. The longest is the second digit, the other ones arranged in decreasing order are digits I, III, IV, and V. The maximal depth is observed in the posterior third to the center of footprints. The first three digits of the left manus clearly display terminal phalanges. Compared to TW-1, the manus digits are more distinctly expressed. It is likely an indication of a thinner or as yet underdeveloped interdigital membranes in this individual compared to the larger animal. Judging from the location of mud ridges in TW-2, it is clear that the foot was applied from the postero-external direction (Fig. 6d).

Material. Holotype and the additional specimen PIN, no. 4850/4, track with six left and six right footprints (TW-2).

DISCUSSION

Features of Anatomy and Locomotion of Sukhonopus

Sukhanov (1968) proposed a method for size determination in quadrupedal animals, in which the glenoacetabular distance was defined as a half sum of a stride and overlap lag. When applied, this gives the trunk length of the tetrapod, which produced TW-1, ranging from 85–90 cm (TW-2: 62–66 cm). The estimate fits well with results of distance measurement between consecutive prints of front and hind limbs (method of Lilienstern and Beird, after Sukhanov, 1968). Furthermore, the length is 3.5–3.75 times (TW-2: 3.1–3.15) longer than the pes of the animal and 4.85–5.15 (TW-2: 6.2–6.6) times longer than the manus. The length of a body without a tail (which length strongly varies in different groups) in large Permian tetrapods ranges from one and a half of the glenoacetabular distances (pareiasaurians) to an almost doubled distance in predatory therapsids. Therefore, the length of the larger *Sukhonopus* (TW-1) should be about 140–170 cm, and in the smaller individual (TW-2), 90–110 cm.

In summary, the evidence allows us to conclude that animals, which walked on carbonate substrate in Severodvinian Time, had a rather large body. The tail was either short or kept in the raised position thus leaving no trace on the substrate. Both tracks lack any depressions between the right and left feet. This indicates that the body was at least 5–6 cm above the ground level. Large short-toed hind feet had five digits and, possibly, interdigital membranes and moved from the rear to the front. The manus, also five-digited and with membranes, were elongated. In the course of movement, they were applied from the lateral direction and taken out in the frontal direction. TW-1 clearly shows a nonuniformity in the movement of the animal: the measured stride differs on the left and right sides of the track, being 84 and 88–90 cm in forelimbs, and 82–84 and 86 cm in hind limbs, respectively. Apparently, this is a manifestation of a certain individual feature, or this path represents a partial arch in the left turn of the animal.

Noteworthy are the proportionally smaller size of forelimbs in TW-2. Being identical in shape, the length ratio of hind to fore feet in TW-1 is close to 1, whereas this index exceeds 1.2 in TW-2. In addition, the size of footprints in relation to the glenoacetabular distance is clearly different. The tracks may belong to individuals of different sexes.

Sukhanov (1968) analyzed the movement of modern lizards and the tracks they left. He concluded that it is impossible to deduce the animal's movement (slow pace, trot, or run) based solely on tracks.[4] The data on mammals show that, at an increase in the speed, the overlap lag and distinctness of tracks decrease. If this is the case with reference to the track-makers under study, both tracks represent slow movements, apparently, with a symmetric diagonal sequence of feet application. This type is characteristic of primitive tetrapods and provides the maximal stability. Nevertheless, the animal TW-2 moved a little faster, which is reflected in the extent of the overlap lag and in the position of the deepest parts of pes impressions in their middle area rather than in the digital portion.

Taxonomic Position of Sukhonopus

Continental deposits of the Upper Tatarian Substage in the north of European Russia have been studied for more than a hundred years. It is thus possible to assume a fairly complete knowledge of the tetrapod fauna composition. Animals of a relatively large size-class include dvinosaurian labyrinthodonts, anthracosaurian chroniosuchids, pareiasaurian parareptiles, burnetid eotheriodonts, gorgonopian and scylacosaurid theriodonts, and dicynodontid anomodonts (Ivakhnenko *et al.*, 1997). Most likely, it is this array that includes our track-makers. Let us consider them according to the degree of probability.

Amphibians. Obviously, this group should be excluded from the analysis because, in amphibians, the position of the autopodia is usually parallel to the movement axis (in addition, labyrinthodonts have tetradactyl forelimbs). Indirectly, this is evident from the asymmetrically distributed weight pressure in the track (a typical feature of reptiles) and the absence of tail drags.

Eotheriodonts and theriodonts. In general, TW-1 and TW-2 could be referred to the theromorphoid type (Sukhanov, 1968) with short imprints of closely spaced digits, pentadactyl appendages, and a median position of the pressure axis. However, many theromorphs (theriodonts and eotheriodonts) do not fall under this definition. These forms had long, distinctly nonuniform in length, and well-expressed narrow digits. Moreover, footprints of the theromorphoid type could be produced by pareiasaurian parareptilies.

Dicynodonts. In Eastern Europe, these animals are known from the entire range of the Upper Tatarian deposits. The genus *Australobarbarus* occurs in the *Deltavjatia vjatkensis* Zone; *Oudenodon* is known in the *Proelginia permiana* Zone; *Dicynodon* and *Elph* appears in the *Scutosaurus karpinskii* Zone; *Vivaxosaurus*, *Interpresosaurus*, and *Delectosaurus* are found in the *Archosaurus rossicus* Zone. Unfortunately, records of articulated limbs of dicynodonts are so far unknown. Watson (1960) exemplified footprints of Permian dicynodonts on the basis of a South African record. Typical features of these tracks are likely the elongated and pointed third digit, commonly large fore- and smaller hind limbs, and broadly spaced manus digits. This description does not fit the characters observed in TW-1 and TW-2. In Triassic *Lystrosaurus* (PIN, no. 3447/1;

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[4] The formulas used for the determination of the movement type of an animal with the parasagittal position of appendages (see, for example, Thulborn, 1984) is difficult to apply in our case, and this question is beyond the scope of the present paper.

Broom, 1932 after Vjuschkov, 1964) and *Parakannemeyeria* (PIN, no. 2421/1), the shape of the autopodia strongly differs from each other and from the assumed shape of *Sukhonopus* feet.

Pareiasaurians in the Tatarian deposits of European Russia are represented by the bradysaurid *Deltavjatia* and the pareiasaurids *Proelginia* and *Scutosaurus*. The structure of appendages is best known for *Deltavjatia* from a number of localities near the town of Kotelnich in the Kirov Region (Khlyupin *et al.*, 2000). Pareiasaurians are buried in peculiar conditions here. Animals died after becoming stuck in sticky clayey silt and preserved as undistorted, nearly complete skeletons. Trying to free themselves, they put their hind limbs upon solid ground, while the forelimbs made raking movements. As a result, the manus of these animals is stretched out and preserved in different positions. They can be extended forward, turned under the forearms, or turned laterally; the carpal elements are not preserved in most cases. Nevertheless, in one skeleton [MS (Federal State Enterprise Samotsvety Museum, Moscow), no. 5324; glenoacetabular distance is 95 cm] bones of the left forelimb (Fig. 6d) are preserved in the living position. This specimen gives us the chance to reconstruct the shape and the position of the manus. The ulna and radius join the manus in its posterolateral region, and the manus is oriented in a manner so that digit I is perpendicular to the axis of the zeugopodium. At the same time, digit V does not extend beyond the projection of the external side of the ulna. Digit II is the longest, digits III and IV gradually decrease in size. Phalanges of the fifth digit are not preserved; however, inferring from available figures of other skeletons (Khlyupin *et al.*, 2000), this digit was much smaller than digit IV. The length to width ratio of the manus measured along the long body axis is 0.75 (12.5 : 16 cm). In sketches of hind and forefeet footprints of TW-1 and TW-2 (Figs. 6a–6d), we attempted to reconstruct the shape of the autopodia of these animals based on the pattern of transitions of steep regions of footprints into more gentle ones. It is obvious that the shape of the forefoot imprint of *Deltavjatia* is similar to that of TW-1 and TW-2. The difference is observed in proportions (the ratio of the glenoacetabular distance to the manus length in specimen MS, no. 5324 is 9.0, whereas in the similarly sized TW-1, it is 4.8–5.2) and the longer first forefoot digit of Kotelnich specimen. This may be evidence that the animal from Sukhona belongs to a different but closely related genus of bradysaurids. Moreover, the structure of the autopodia in South African *Bradysaurus* (see Gregory, 1946), the type genus of the family Bradysauridae, notably differs from that of *Deltavjatia* (and *Sukhonopus*). In *Bradysaurus*, the fourth digit of the manus is of approximately the same length as digit II, whereas the first digit is considerably enlarged in comparison with other digits; on the contrary, in hind limbs, the digits gradually increase in size from digit I to the longest digit IV, and the fifth digit is shorter than the fourth but longer than digit I.

Among Eastern European forms, the postcranial skeleton of *Proelginia* is not known. As to scutosaurs, the collection of PIN contains a single incomplete manus without carpal elements (Fig. 6f). Its digits are nearly equal in length and short. Imprints of its foot are similar to *Sukhonopus* in short digits; however, it is closer to Italian records of *Pachypes* (Conti *et al.*, 1977). Ivahnenko's (2001) believes that details of the skeleton structure of *Scutosaurus* point to its aquatic mode of life and its poor terrestrial locomotion. Hence, it is hardly probable that representatives of this genus were associated with the tracks under study.

Tetrapod oryctocoenoses from the Poldarsa Formation are comprised exclusively aquatic and amphibiotic forms. Large reptiles are represented by only herbivorous pareiasaurians (Kochevala-1, Mikulino, and Mar'yushkina Slyuda-S localities) and predatory burnetiids (Navoloki locality) and gorgonopids (Navoloki, Poteryakha-2, Ust'e Strel'ny, Mar'yushkina Slyuda-S, and Mutovino localities). Dicynodonts have not been found in the Poldarsa Formation. For the first time, they appeared in the lower part of the Rovdino Member of the Salarevo Formation deposited in more terrestrial conditions. Throughout the territory of European Russia, Permian dicynodonts are associated with the most elevated ecotopes. Obviously, excessively watered swampy lowlands, like that in the basin of the Sukhona River in the Poldarsa Time, hardly constituted a favorable environment for these animals. This reasoning indirectly indicates that the studied tracks belong to pareiasaurians rather than to dicynodonts.

As was noted above, in northern Italy, the Upper Permian sandstones Val Gardena yielded short-digited tracks *Pachypes dolomiticus*, described as pareiasaurians (Conti *et al.*, 1977). Unfortunately, the sandstones completely lack any tetrapod bones. The Italian authors arrived at their conclusion by consecutive exclusion of probable fits among large forms of the world tetrapod fauna of the Upper Permian. In the course of analysis of the tracks from Esipovka, we used the same approach. In addition, we used data on the tetrapod association from the entire Poldarsa Formation in the basin of the Sukhona River. As shown in Fig. 4, localities with a tetrapod association (including pareiasaurians) typical for the Poldarsa Formation are in the same stratigraphic neighborhood, only several meters above or below the track-bearing limestone of Esipovka. This may serve as an additional argument in favor of our conclusions.

Summarizing the review above and based on our knowledge of the structure of the autopodia in large land tetrapods of the Late Permian, it is possible to conclude that tracks TW-1 and TW-2 were produced by pareiasaurians. The closest fits among the forms with the described appendages are *Deltavjatia* (family Bradysauridae) rather than *Scutosaurus* (family Pareiasauridae).

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