THE FIRST OCCURRENCE OF FOOTPRINTS OF LARGE THERAPSIDS FROM THE UPPER PERMIAN OF EUROPEAN RUSSIA

by MIKHAIL V. SURKOV*, MICHAEL J. BENTON†, RICHARD J. TWITCHETT[a], VALENTIN P. TVERDOKHLEBOV* *and* ANDREW J. NEWELL[o]

*Institute of Nature Sciences of Saratov State University, Astrakhanskaya 83, 410075 Saratov, Russia; e-mail: SurkovMV@info.sgu.ru

†Department of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK; e-mail: mike.benton@bris.ac.uk

[a]School of Earth, Ocean and Environmental Sciences, University of Plymouth, Drake Circus, Plymouth, PL4 8AA, UK; e-mail: richard.twitchett@plymouth.ac.uk

[o]British Geological Survey, Maclean Building, Wallingford, OX10 8BB, UK; e-mail: a.newell@bgs.ac.uk

Abstract: Large footprints of terrestrial tetrapods have been found in the Cis-Urals region of European Russia. The footprint horizon is in deposits of the Vyatkian Gorizont (uppermost Tatarian) of Late Permian (Changhsingian) age, *ca*. 50m below the local Permian-Triassic boundary. Seventeen differently oriented footprints were excavated and are referred to the ichnospecies *Brontopus giganteus*. The footprints were emplaced in a reddish-brown mudstone that was deposited from suspension beneath shallow, ponded water in a floodplain environment. The footprints were subsequently cast on the base of the overlying fine-grained sandstone, which was deposited from a sheet flood event. The footprints were produced by a large therapsid, possibly a dinocephalian, but more probably a dicynodont, and represent the first ichnological record of the Therapsida from the Upper Permian of Russia.

Key words: Upper Permian, *Brontopus*, Dicynodontia, ichnofossils, tracks, Russia.

SEVERAL hundred localities from the Upper Permian and Triassic continental deposits of the European part of Russia have yielded skeletal remains of terrestrial tetrapods (Ivakhnenko *et al*. 1997; Tverdokhlebov *et al*. 2003, 2005). Even though these strata crop out over a vast area of European Russia, from the Barents Sea in the far north to the Pre-Caspian region in the south, only two finds of tetrapod footprints have been reported so far: amphibian tracks, *Anthichnium ichnops*, from the southern Cis-Uralian Trough (Tverdokhlebov *et al*. 1997), and pareiasaurian tracks assigned to *Sukhonopus primus* (Gubin *et al*. 2003) from the bank of the Sukhona River in the northern part of Russia. Both sets of tracks were found in the Severodvinskian Gorizont of late Tatarian age (latest Permian).

Here we report the third find of tetrapod tracks from the Russian Permo-Triassic; a set of tracks made by a very large quadrupedal tetrapod in a Vyatkian unit not far below the Permian-Triassic boundary. These are attributed to a third tetrapod group, the therapsids. The specimens were found during a field trip in summer 2004, jointly organised by the Universities of Bristol (UK) and Saratov (Russia) to the southern Cis-Uralian Trough.

GEOLOGICAL SETTING

The footprints were found by RJT at the 'Boyevaya Gora' locality (Tverdokhlebov *et al*. 2005, p. 66), situated 14 km NNW of Sol-Iletsk City, Orenburg region, in a narrow ravine flowing into the Elshanka river – a right tributary of the Ilek river (Text-fig. 1). The footprint site is located at 51.29965N, 54.90659E. The sedimentary rocks exposed in the ravine containing the footprint site range from the Vyatkian Gorizont of latest Tatarian age at the base, to the earliest Triassic (basal Scythian) Vokhmian Gorizont in the very uppermost part of the exposed section. The age has been determined by the fauna of ostracods (identifications by I. I. Molostovskaya) and tetrapods (Tverdokhlebov *et al*. 2005). The sediments containing the footprints belong to the Vyatkian Gorizont, which is equivalent in age to the *Dicynodon* Zone of South Africa, and equates with the Changhsingian stage of the Late Permian (Lopingian) (e.g. Benton *et al*. 2004).

Some 124 m of mudstones, siltstones, sandstones, and conglomerates are exposed in this section (Text-figs 2, 3). The local Permian-Triassic boundary is located approximately 94 m above the base of the measured section, at an abrupt facies change from red mudstones with well-developed caliche below to trough cross-bedded pebbly sandstones and conglomerates above. These latter beds have yielded Early Triassic *Tupilakosaurus* remains, a left angular of *Wetlugasaurus samarensis* (?) and limb and dermal bones of Temnospondyli. The mudstones a few metres beneath contain the Vyatkian ostracods *Volganella magna* (Spizharskyi), *V*. ex. gr. *laevigata* Schneider, *Wjatkellina fragilina* (Belousova), *Gerdalia* sp., *Suchonellina inornata* var. *macra* (Lunjak), *S. inornata* var. *magna* (Kotschetkova), *S. parallela* Spizharskyi, *S. parallela* var. *typica* (Lunjak), *S. futschiki* (Kashevarova), and *Suchonella typica* Spizharskyi. The youngest Permian vertebrate remains are found 22 m beneath the Permian-Triassic boundary, and comprise tetrapods (*Scutosaurus* sp., Karpinskiosauridae gen. indet., *Chroniosuchus paradoxus,* Theriodontia fam. indet.), and fishes (*Isadia aristoviensis* A. Minikh, *Toyemia blumentalis* Minikh, *Mutovinia stella* Minikh, *Saurichthys* sp., *Gnathoriza* sp.).

The footprint horizon is located 45 m above the base of the measured section (Text-fig. 3). Ostracods have been found 8 m and 1 m below this horizon and comprise the characteristic Vyatkian taxa *Suchonellina inornata* Spizharskyi, *S. inornata* var. *macra* (Lun.), *S. futschiki* (Kashevarova), *S. parallela* Spizharskyi, *S. parallela* var. *typica* (Lunjak), *S. inornata* var. *magna* (Kotschetkova), *S. undulata* (Mischina), *Gerdalia* sp. The footprints were emplaced in the upper part of a 0.34 m thick reddish-brown mudstone bed that has a blocky texture and lacks root traces. A grey, fine sandstone immediately overlies this mudstone and natural sandstone casts of the footprints are preserved in epirelief on the base of this bed. The sandstone is some 0.4 m thick, although thickness is variable, and the bed has a sharp base and a basal lag of mudstone rip-up clasts and occasional calcrete pebbles approximately 10-20 mm in diameter. The sandstone contains current ripple cross-laminae, with a uniform flow direction to the WSW (*ca*. 260°).

Approximately 3.4 m^2 of this sandstone bed was excavated and turned over to reveal 17 footprints. Fourteen natural footprint casts were mapped from the excavated layer (Text-fig. 4), but the positions of the remaining three were unclear because they were on detached blocks. Extensive documentation was made in the field, and several of the natural sandstone footprint casts were taken to Saratov State University, where they are now curated.

SYSTEMATIC ICHNOLOGY

Ichnogenus BRONTOPUS Heyler and Lessertisseur, 1963

Brontopus giganteus Heyler and Lessertisseur, 1963

Text-figures 4, 5

1963 *Brontopus giganteus* Heyler and Lessertisseur, pp. 175-176, Pl. 8, fig. 1.

1973 *Ichniotherium giganteus* (Heyler and Lessertisseur); Haubold, p. 35.

1971 *Ichniotherium (Cyclopus) aequalis* Heyler and Lessertisseur; Haubold, p. 36.

1973 *Ichniotherium giganteus* (Heyler and Lessertisseur, 1963); Haubold, p. 25.

1983 *Brontopus giganteus* Heyler and Lessertisseur; Ellenberger, p. 553.

1987 *Brontopus giganteus* Heyler and Lessertisseur; Gand, p. 193.

1988 *Brontopus giganteus* Heyler and Lessertisseur; Gand and Haubold, p. 888.

1993 *Brontopus giganteus* Heyler and Lessertisseur; Gand, pp. 52-53.

1997 *Brontopus giganteus* Heyler and Lessertisseur; Gand, p. 303.

2000 *Brontopus giganteus* Heyler and Lessertisseur; Gand *et al*., p. 43, fig. 17-19.

2000 *Brontopus circagiganteus* Gand *et al*., pp. 43-52, fig. 17-19.

2000 *Brontopus giganteus* Heyler and Lessertisseur; Haubold, pp. 11, 13, 14.

Type material. Cast of pes print in the collection of the Museum National d'Histoire Naturelle, Paris ('plastotype') LOD 70, Heyler and Lessertisseur collection).

Diagnosis. Large prints of a semi-plantigrade to plantigrade quadruped, measuring several decimetres and rounded, a little longer than wide, and with well marked claws. The foot is pentadactyl with digits II to V of decreasing length, II being the largest, or subequal to I. The print extends back with a sole, more or less oval and shaped like a basin. The traces are surrounded by a pad of expelled sediment, seen in different states. Postulated pes prints 300-350 mm in diameter; postulated manus prints about 200 mm in diameter; stride length about 1.2 m; distance between midline of left and right prints 0.8-0.9 m. Based on Gand *et al*. (2000, p. 43), with measurements from Heyler and Lessertisseur (1963, pp. 175-176), who did not give a diagnosis.

Referred material. Saratov State University, Geology Collection, SGU N 161/240-245.

Description. The prints are preserved in different styles, from being nearly indistinct to very well impressed and with clear scratch marks (Text-fig. 5A-B). The orientations of the footprints are variable, and only part of one trackway, which comprises prints 1, 3, 7 and possibly 9, has been distinguished. Footprints 1 and 7, as well as 3 and 9, are apparently from the left side, based on asymmetry of the digits in *Brontopus* (Gand *et al*. 2000), representing respectively imprints of the fore- and hind-limbs. Footprint 3 is placed medially to prints 1 and 7. The direction of the trackway is 263^0 (corrected to true north). The stride length, estimated as the length between prints 1 and 7 of the same forelimb (top of second digit), is 1.25 m. All footmarks are semiplantigrade.

There are two footprint morphologies, but it is difficult to identify the manus and pes prints unequivocally because there is no extensive single trackway. For initial description, these will be termed print morphotypes A and B. Print A is best exemplified by number 3 (Text-fig. 4), which is 230 mm long and 467 mm wide. This print bears five digits, of which digit V is poorly recognisable. All digits are pointed and placed apart from each other, but only the ungual portion is separate, which might suggest the presence of a muscular palm or a web between them. The digits all point inward, and they increase in length from V to II, with I roughly equal to III. The best example of print morphotype B is number 7 (Text-fig. 4), which is 217 mm long and 428 mm wide. There are also five short digits, roughly similar in size, placed close to each other, especially digits IV and V. The digit impressions are separated by deep V-shaped depressions, but each digit does not extend much beyond the anterior margin of the print. All digits end in blunt terminations and, judging from preserved scratch marks (Text-fig. 5B), were hoofed. Digits I-III point forwards, while IV and V diverge slightly to the side. Both print types show similar relief/ depth (Text-figs 4, 5), which indicates that the autopodia of both limbs were broad and roughly similar in size, although the hand or foot producing print morphotype A was wider.

In their reproduction of the type specimen of *Brontopus giganteus*, Gand *et al.* (2000, fig. 24B) show both our print morphotypes A and B, and they assume that the broad print with clear digit impressions (morphotype A) is the manus, and the narrower and longer print (morphotype B) is the pes. We will argue for the opposite interpretation, based on relative position of the prints with respect to the midline of the track, and the locomotor movements implied by each. Prints of morphotype A (numbers 3 and 9) are placed closer to the midline than prints of morphotype B (numbers 1 and 7), assuming that these four were made by the left-hand limbs and are parts of a single trackway. Many Permo-Triassic tetrapods showed a 'dual gait' in which the hindlimbs were held in an erect or semi-erect position, and the forelimbs sprawled somewhat, expressed memorably by Kemp (1980) who described the locomotion as akin to a man pushing a wheelbarrow – the hindlimbs striding in erect, parasagittal posture, and the sprawling forelimbs scrabbling along in front. Such a dual gait has been reported for many Late Permian therapsids, based on their skeletal remains (Boonstra 1966; King 1981; Kemp 1980, 2005, Surkov 1998) and has also been reported in tracks of *Chelichnus* (McKeever 1994). Therefore, the more medially-placed prints (3, 9) would be pes prints, and the more lateral ones (1, 7) would be manus prints.

This is supported by details of apparent hand movements preserved in some prints. Print 7 (morphotype A; Text-fig. 5A, B) shows an extended back-push, with scratches directed outwards, which reflects a pronounced lateral component during limb retraction. Print 3 (morphotype B), on the other hand, does not have traces of backward pushing and scratching, even though it is deeper then print 7 (Table 1) and was made in the same type of substrate, as is seen from the quality of preservation. Posterolateral retraction, as seen in morphotype A, but not B, suggests a sprawling gait for the former, and a parasagittal gait for the latter. This implies that morphotype A (prints 1, 7) represents the manus, and morphotype B (3, 9) the pes. Our determinations of the other prints are indicated in Table 1.

Comparison. The Russian footprints may be compared to three previously described ichnogenera: *Brontopus* (Heyler and Lessertisseur 1963; Gand *et al*. 2000), *Pachypes*

(Leonardi *et al.* 1975), and *Chelichnus* (Huxley 1877; Benton and Walker 1985; McKeever and Haubold 1996), which have all been reported from the Upper Permian. The closest resemblance is to *Brontopus giganteus*, which is similar in morphology and size, with a combination of shortened hoofed digits on the manus prints and elongated pointed digits on the pes prints. *Pachypes dolomiticus* (Leonardi *et al.* 1975) differs from the Russian specimens by the longer manus digits and the broader, less pointed pes digits. The various ichnospecies of *Chelichnus* differ in having imprints of elongate claws on the pes prints, and they are generally much smaller, ranging in length from 10-125 mm (McKeever and Haubold 1996). The ichnospecies *C. gigas* (including *C. megacheirus* from the Late Permian of Scotland; Huxley 1877) is smaller than the current tracks, with a pes length of 75-125 mm, and the posture is generally plantigrade. The largest *Chelichnus, C. titan* has prints up to 200 mm wide, half the width of the present material, but the posture is exclusively plantigrade (McKeever and Haubold 1996). Gand *et al.* (2000, pp. 47-50) also noted the similarities between *Chelichnus* and *Brontopus*, but kept them distinct based on morphological differences.

The type material of *Brontopus giganteus* from the La Lieude Formation (mid Tatarian) of southern France (Heyler and Lessertisseur 1963, pp. 175-176, Pl. 8, fig. 1) was rather poorly preserved and indistinct. Only a plaster cast of a pes print was illustrated in the original paper, which shows a roughly circular outline, and a number of short digit impressions. Despite the poor preservation, the overall morphology and measurements correspond well to the Russian material. The later illustration of the type specimen in Gand *et al.* (1964, fig. 24B) allows some comparisons. The digits in the Russian material are pointed and more sharply defined in the pes print, while the digit impressions are rounded and perhaps more hoof-like in the manus. In the Russian material, the pes digit impressions bend markedly towards the midline of the track, while this is not seen in the manus print. All these features are seen in *B. giganteus* from France.

Gand *et al.* (2000, pp. 43-52) erected the new ichnospecies *Brontopus circagiganteus* for a slightly larger track from the latest Permian of France. The pes print measures 295 x 280 mm, and the manus 355 x 300 mm. The prints are oval, rounded, and each bears five digit impressions. In the manus print, the digits increase in size from V to II, with I roughly equal to III. In all details, and details are hard to determine in these large prints, *B. circagiganteus* appears to be the same as *B. giganteus*, and the first author, Georges Gand, indicates (Gand *et al.* 2000, p. 47) that he would prefer to use the original name, while his co-author, Paul Ellenberger, argued that the new name was required as Heyler and

Lessertisseur's (1963) decription was imprecise and incomplete and their material fragmentary. There is apparently no diagnostic difference between the two ichnospecies. We prefer to follow Gand's view and synonymise *B. circagiganteus* with *B. giganteus* since the two taxa are essentially the same morphologically, and Ellenberger's objections are not sufficient to reject the original name.

Variation in dimensions

The footprints from the excavated area are morphologically similar, and they appear to form one or more trackways, so they almost certainly all belong to the same ichnotaxon. This assumption was checked by estimation of the coefficient of variance (CV) for the main print dimensions (Table 1). Since the shapes of the manus and pes are very different, we calculated the CV separately for each. Values of the CV for print width reach as much as 14.76%. The length showed more variability – up to 29%. Pronounced variation in print length may be explained by the quality of preservation, where the backwards push may be preserved (print 7) or not (print 2). According to Demathieu (1987b), CV values above 25% may reflect a population of prints that was left by different species, by animals of different size, or in a wide range of preservation modes. Thus, the small CV values for print width support the suggestion that one species made all the prints. Whereas the high CV values for print depth almost certainly reflect highly variable preservation in a variable substrate, and/or variations in body mass between different animals.

DISCUSSION

Depositional environment

The Vyatkian succession at the trackway locality (Text-figs 2, 3) is dominated by red mudstones and sandstones. The mudstones are generally massive and often contain root traces and weakly-developed palaeosols with calcrete nodules. The associated sandstones are generally less than 0.5 m thick, have sharp erosive bases and are cross-bedded or ripple cross-laminated with bioturbated tops. The red coloration of the mudstone and the presence of rootlets and palaeosol horizons with calcrete indicates a continental setting with a semi-arid to subhumid climate. The mudstones were probably deposited from suspension in shallow ephemeral lakes (Tverdokhlebov *et al.*, 2005) and on floodplains adjacent to broad, shallow river channels, which are represented by the thin, erosively-based sandstones. Cross bedding indicates that the flow direction was generally towards the west. Recession of the flood water allowed plant colonisation of the muds and the bioturbation of channel sandstone tops. Longer subaerial exposure led to the development of palaeosol horizons with calcrete nodules. Overall, the range of facies is similar to that described by Newell *et al.* (1999) from Vyatkian deposits 75 km to the northeast, and they suggested that the overall depositional system was a fluvial ‘terminal fan’ characterised by a network of shallow channels ending in a muddy floodbasin.

The environment may also have sustained some perennial water bodies. In sections in, and close to, the Korolki Ravine, these lakes are reflected by thin (up to 1.5 m) and wide (up to 100 m) lenses of grey-coloured mudstone, siltstone, and sandstone with abundant plant remains. The plant remains from similar levels in Vyatkian deposits nearby are typical shrubs of the Tatarian flora (Gomankov and Meyen 1986): *Peltaspermopsis buevichiae* (Gomankov et Meyen)?, *P.* sp., *Lopadiangium* sp., *Tatarina olferievii* S. Meyen, *T.conspicua* S. Meyen, *T. pinnata* S. Meyen et Gomankov, *Stiphorus biseriatus* S. Meyen, *Glossophyllum* cf. *permiense* S. Meyen, *Lepidopteris* sp., *Salpingocarpus* cf. *variabilis* S. Meyen, *Phylladoderma (Aequistomia) tatarica* S. Meyen, *Rhaphidopteris* cf. *kiuntzeliae* S. Meyen, and *Dvinostrobus* (?) *sagittalis* Gomankov et S. Meyen, all of which grew by the lakeside.

The mudstone bed containing the footprints overlies a pink-grey, cemented palaeosol containing abundant root traces (the terminal plug of a heterolithic channel fill). However, the mudstone itself contains no root traces, indicating insufficient time for significant plant colonisation prior to deposition of the overlying bed, and was likely deposited subaqueously beneath ponded floodwaters. The absence of mudcracks may indicate that the substrate did not dry out completely prior to the deposition of the overlying sandstone bed, and it is plausible that a thin layer of water was present during the formation of at least some of the footprints. However, the lack of a preserved raised displacement rim (cf. Manning 2004, p. 94) around the footprints implies that the flooding event that brought in the overlying sand was initially erosive, which is supported by the presence of rip-up clasts in the base of the sandstone, and thus evidence of emergence such as shallow mudcracks or superficial mudcurls may also have been removed. Certainly, the well-preserved footprint casts with detailed hoof scratches would have required a firm, but not waterlogged, substrate and were probably emplaced on an emergent, but not desiccated, surface. Given the consistent palaeocurrent directions above and below the footprint level, it is likely that the animals were moving in a shallow, ENE-WSW-oriented depression that had recently been flooded. They may have been foraging for new shoots.

Footprint depth

Footprint depth is controlled by substrate rheology, especially the water content of the sediment, as well as by possible erosion prior to deposition of the overlying bed, and by the size of the animal (Manning 2004). In the Russian specimens, footprint depth varies enormously. A plot of all values of length, width and depth against 3D coordinates (Text-fig. 6A) shows two clusters of seven shallow and ten deep footprints. There is a reasonable positive correlation between width of footprints and their depth ($r = 0.76$), which suggests that the size of the animals was a key factor that controlled variations in depth.

Most prints are about 100 mm deep, which suggests that substrate rheology did not vary much. However, prints 4, 5, 6, and 13 seem to be shallower than expected, and they all lie towards one side of the excavated slabs, suggesting that the sediment might have been firmer there, or that more erosion occurred after footprint production. The surfaces of some prints show different conditions of the substrate. The surface of print 1 is covered with imprints of multiple elongated stripes (Text-fig. 5C) which may represent imprints of mud cracks that were formed when the leg stepped on to mud that had a thin hardened crust, or these could be multiple digital transmission features (Manning 2004) that appeared on the clay surface in the area behind/around the heel if the leg stepped on to clay covered with sand. The next time this leg stepped on the mud (print 7), it was not so dry, or there was no sand cover, as shown by the well-preserved imprint surface with hoof scratches (Text-fig. 5B). The well-preserved surface of a pes print (no. 3) that is placed between footmarks 1 and 7 also shows no traces of mudcracks, so this leg also stepped on to unhardened mud. Therefore it is possible to argue that the spatial transition between hardened, or partly sand-covered, and soft mud was rather sharp, but hardening of the substrate obviously was not enough to reduce footprint depth over a distance of at least 0.5 m. The similarly-sized prints 6 and 10 are very close together (Text-fig. 4), but print 6 is twice as shallow. This suggests that the spatial distribution of substrate softness was not a significant factor in producing variations in footprint depth.

The third factor that controlled imprint preservation was the time when footprints were left and the relative position of the waterline. There are few obvious generations of footprints in the reconstructed area. The well preserved fine scratches of hooves on prints 3 and 7 (Text-fig. 5A, B), and the slightly cracked surface of print 1 (Text-fig. 5C), suggest that the prints were made in firm mud that was not covered with water at the time, but also had not dried out and become mudcracked. These prints, as well as the similarly preserved prints 11 and 14, were presumably the last generation of footprints to be made before the whole surface was rapidly covered with fine sand. Prints 2, 8, and 12 were made earlier, because later prints cut across them (Text-fig. 4D). The older prints are as deep as those in the trackway, except for print 8 which was probably left even earlier. The similar depth of older prints 2 and 12, and the younger ones in the trackway, suggests that the substrate was equally soft throughout. However, the superimposed prints do not show any traces of scratches or mudcracks, so they may have lost such detail from being submerged for a short time. Similar preservation and orientation of print 10 suggests that it was left at the same time as prints 2 and 12. The remaining prints, numbers 4, 5, 6, 8, 13, 15, and 16, are the shallowest, and their surfaces do not bear any traces of hoof scratches or mudcracks, as seen in print 1. The smooth surface of these prints suggests that they were made in mud that was covered with water for a longer time, or details were partly obliterated by water movement.

The two generations of prints are oriented differently (Text-fig. 6B). Seven of the 11 individual prints are oriented NW- SE, while the last footprint generation, including the mini trackway 1, 3, 7, 9, has a different orientation, SW- NE.

Identity of the trackmaker

There are a number of potential trackmakers for *Brontopus*– pareiasaurs or synapsids (basal ‘pelycosaurs’ or therapsids). Other Permian reptiles were much smaller and had long, slender digits, and amphibians had typically four digits in the hand, and in any case were also much smaller.

Pareiasaurs were contemporaries of the footprint horizons, and they were large enough, up to 3 m in total body length. Their hands and feet each had five short digits terminating in hoof-like, somewhat pointed unguals. Heyler and Lessertisseur (1963, p. 176) ascribed their *Brontopus* tracks to a therapsid or a pareiasaur, and they preferred the latter interpretation, but did not offer morphological evidence.

Haubold (1971) assigned *Brontopus* (as a synonym of *Ichniotherium*) to the Edaphosauria, prints made by a ‘pelycosaur’ therapsid. Most basal therapsids were too small, but some had large enough hands and feet, and they had five digits in each. However, the digits of ‘pelycosaurs’ are longer than indicated in the *Brontopus* prints, and they were essentially Late Carboniferous and Early Permian in age, rather than latest Permian.

Gand *et al.* (2000) and Haubold (2000), on the other hand, interpreted *Brontopus* as the tracks of a therapsid. Gand *et al.* (2000, pp. 50-52) argued tentatively that the *Brontopus* prints were not made by a pareiasaur or a caseid pelycosaur, but probably by a dinocephalian, based on the morphology and size of the prints, the calculated long body and short limbs, the inferred 'long coupled' gait type, and centrally located centre of mass. These authors did not consider dicynodonts as possible track makers.

The largest Russian herbivorous dinocephalians that could have produced *Brontopus*-sized footprints were *Ulemosaurus* and *Deuterosaurus*, which were waterside forms. Known fossil remains are too old, however, being known only from the upper part of the Urzhumian, which is older than the Vyatkian Gorizont, the source of the *Brontopus* prints (Tverdokhlebov *et al*. 2005). This is true worldwide, that dinocephalians had largely disappeared by the Tatarian, and especially by the mid to late Tatarian (Kemp 2005).

So the printmaker might have been a large dicynodont. Dicynodonts are known from the Vyatkian of Russia, such as *Vivaxosaurus* (Kalandadze and Kurkin 2000) with a 0.4 m skull. Truly giant dicynodonts have not been reported from Russia, although such forms, with 0.5 m skulls (*Rachiocephalus*, *Aulacephalodon*) are known from the uppermost beds of the Upper Permian in South Africa (Rubidge 1995).

The inferred posture confirms the identity of the track maker, and allows pareiasaurs to be rejected. Pareiasaurs were sprawlers fore and aft, their digits were asymmetrical with pes digital formula 23343 (Boonstra 1932) and they left plantigrade footprints such as *Suchonopus* (Gubin *et al*. 2003) or *Pachypes* (Leonardi *et al*. 1975; Haubold 2000). *Brontopus* footprints, on the other hand, were semiplantigrade, and some of the present specimens even indicate semisprawling locomotion, as has been inferred from skeletal remains for various groups of Late Permian therapsids.

The approximate position of the centre of gravity of the body helps identify the trackmaker further. This may be estimated (Demathieu 1987a) from the equation:

$$\frac{a_1 r_1}{a_2 r_2} = \frac{O_2G}{O_1G},$$

where a_1, and a_2 are the surface areas of the manus and pes imprints, r_1 and r_2 are the maximum thicknesses of relief, O_1G and O_2G are the distances between the glenoid and centre of gravity and acetabulum and centre of gravity. Estimation of the surface area was made from topographic reconstruction of the imprint relief (Text-fig. 4) with Mapinfo 7.0 software. The surface area for the manus is 0.872 m^2, and for the pes, 0.934 m^2. The ratio O_2G/O_1G is 47/53, which indicates a posterior position of the centre of gravity, closer to the acetabulum than the shoulder girdle. This, and the presence of hooves on the manus, indicate that *Brontopus* was made by a herbivore.

Comparison with the Karoo

Trace fossils, including tetrapod tracks, have been reported from many horizons in the Upper Permian of the Karoo Basin in South Africa (e.g. Smith 1993; de Klerk 2003). Smith (1993), for example, identified five types of tetrapod tracks on crevasse splay palaeosurfaces, ascribed tentatively to pareiasaurs, dinocephalians, and dicynodonts. None of the prints he illustrated bears a resemblance to our Russian tracks. Smith (1993, fig. 14) ascribed one print morphotype to the small, 0.5 m long dicynodont *Diictodon*, but these are much smaller than our tracks, consisting of sets of three or four distinct subcircular digital pad prints with forward claw scrapes, and no palm print.

Larer tetrapod tracks ascribed to dicynodonts were described in detail by de Klerk (2003). He reported six subparallel tracks from sediments ascribed to the *Cistecephalus* Assemblage Zone, and named them *Dicynodontipus icelsi*. The individual prints are smaller than those reported here (manus 130-220 mm long; pes 115-150 mm long), they are spaced more widely in the trackway, and the five digits fore and aft are generally well defined and quite long, rather than being little more than claw or hoof prints, as here. The assignment of these South African tracks to *Dicynodontipus*, an ichnogenus erected by Rühle von Lilientstern (1944) for a range of ichnospecies from the Lower and Middle Triassic of England and Germany, seems reasonable. The Russian material though is quite different morphologically and in terms of size.

The new tracks from Russia then confirm the presence of dicynodonts in the latest Permian of Russia, as indicated also by skeletal fossils. An enduring mystery is, however, the relative rarity of track sites in the Russian Upper Permian, when compared to the seeming abundance of skeletal fossils, and to the much commoner occurrence of track sites in the Karoo Basin.

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TABLE 1. Main measurements of the footprints.

Number of print	Manus/ pes	Length (mm)	Width (mm)	Max. depth (mm)	Length/Width
1	manus	375	432	98	0.87
2	manus	198	372	104	0.53
3	pes	230	467	105	0.49
4	manus	175	323	37	0.54
5	pes	150	340	47	0.44
6	pes	195	370	52	0.53
7	manus	217	428	101	0.51
8	pes	110	340	60	0.32
9	pes	215	435	108	0.49
10	manus	205	365	88	0.56
11	uncertain	192	430	115	0.45
12	pes	165	345	95	0.48
13	manus	215	295	40	0.73
14	manus	214	320	78	0.67
15	uncertain	175	208	54	0.84
16	uncertain	180	255	54	0.71
17	uncertain	190	465	103	0.41
Mean pes		177.50	382.83	77.83	0.46
Mean manus		228.43	362.14	78.00	0.63
CV of manus		29.00	14.76	36.38	21.16
CV of pes		27.06	13.76	33.80	18.57

TEXT-FIG. 1. Map of tetrapod localities in the Orenburg region, Vyatkian Gorizont, Upper Permian. Numbers of localities correspond to those in Tverdokhlebiov *et al.* (2005).

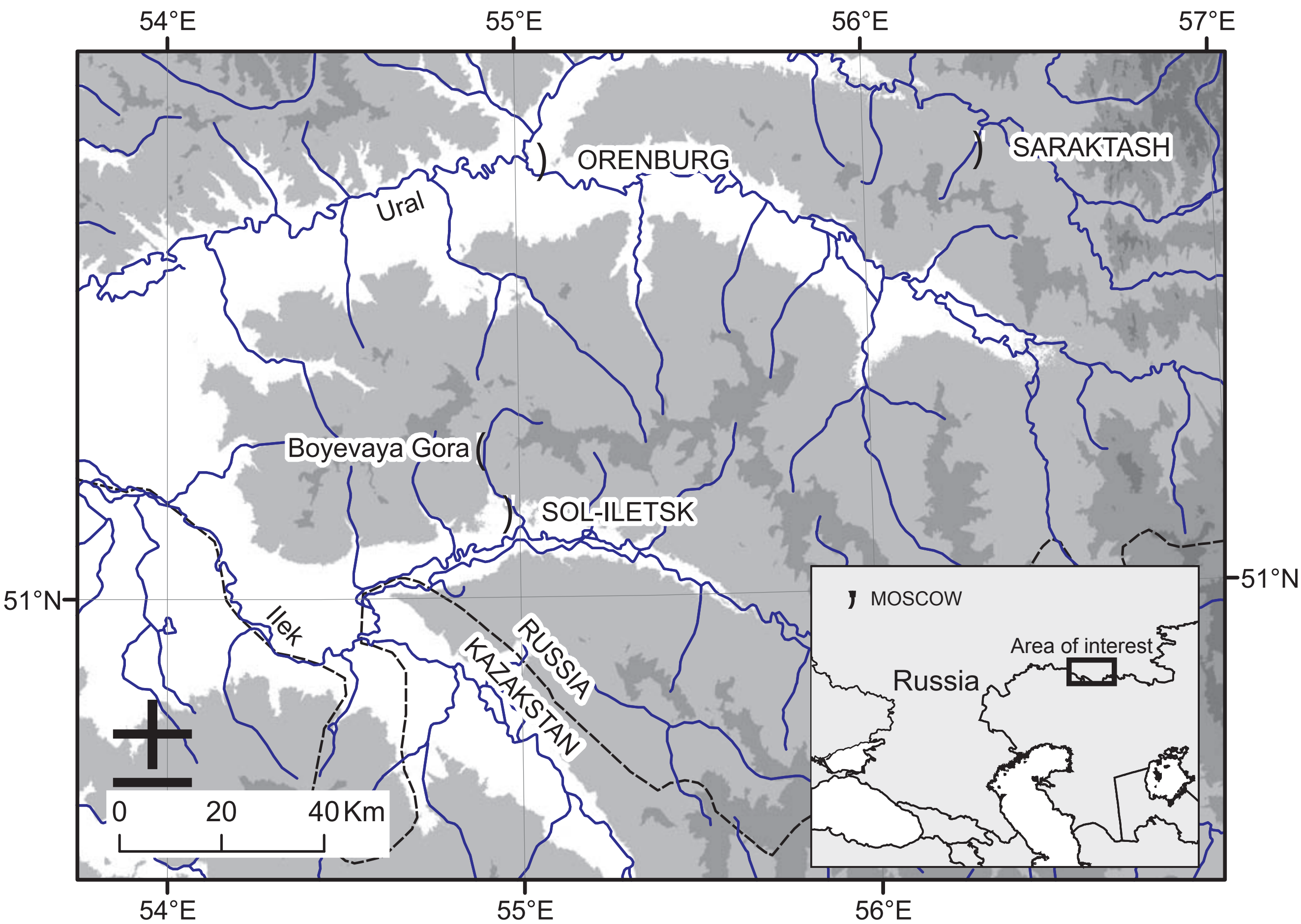
TEXT-FIG. 2. The footprint site and footprints in the Korolki Ravine, near Boyevaya Gora. A, View up the ravine from the footprint site, with MJB in the background, and AJN standing beside a weathered palaeosol in the floor of the ravine. B, Close-up of a profile view of the footprint-bearing sandstone bed, showing a curved negative hyporelief above the tape measure, the impression of a digit of *Brontopus*. The footprint bed lacks other sedimentary structures in the lower 60-70 mm, but shows small-scale ripple cross lamination above.

TEXT-FIG. 3. Sedimentary succession exposed at the Boyevaya Gora [gora = mountain] locality, in a tributary on the right-hand side of the Ilek River. Base of section at 51.29805N, 54.90949E.

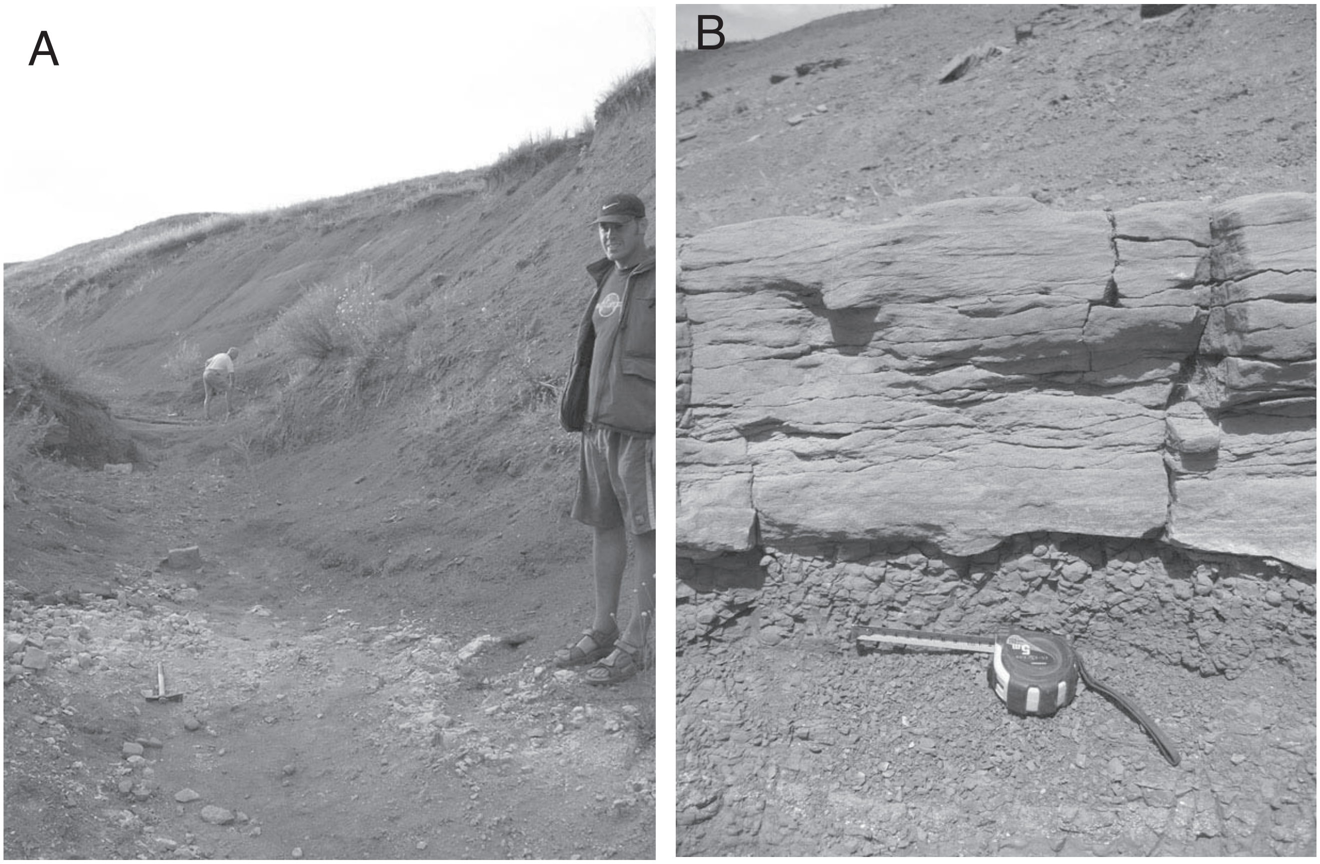
TEXT-FIG. 4. Part of the *Brontopus* trackway, showing 14 individual prints, and (in box) relief of anterior and posterior footmarks, marked in contours of 20 mm. Scale bar is 200 mm.

TEXT-FIG. 4. Cast of *Brontopus giganteus* prints. A-B, footprint no. 7, in dorsal (A) and antero-lateral (B) views, with footprint outline indicated by dashed lines, and scratch marks indicated by arrows. C, footprint no. 1 in dorsal view, with the print outlined by a dashed line, and thin mud laminae ahsering to the sandstone, perhaps remnants of large mudcracks, indicated by the arrows. D, footprints no. 11 and 12 in dorsal view, with the distorted posterior boundary of footprint no. 12 indicated by an arrow. Scale bar is 40 mm.

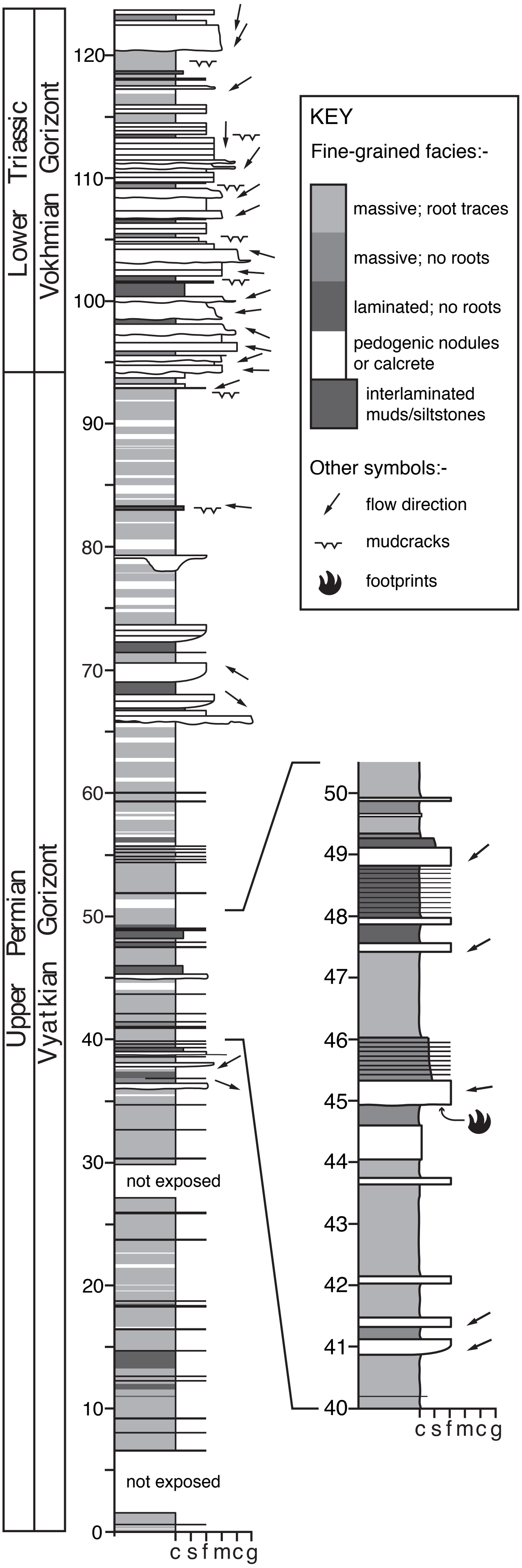
TEXT-FIG. 6. Diagrams of footprint measurements and orientation. A, 3-D diagram of length and width against depth; B, vector diagram of footprint orientation (corrected to true north). Black unit of sector corresponds to one footprint; footmarks of trackway have been referred to one unit.



Surkov et al. Figure 1

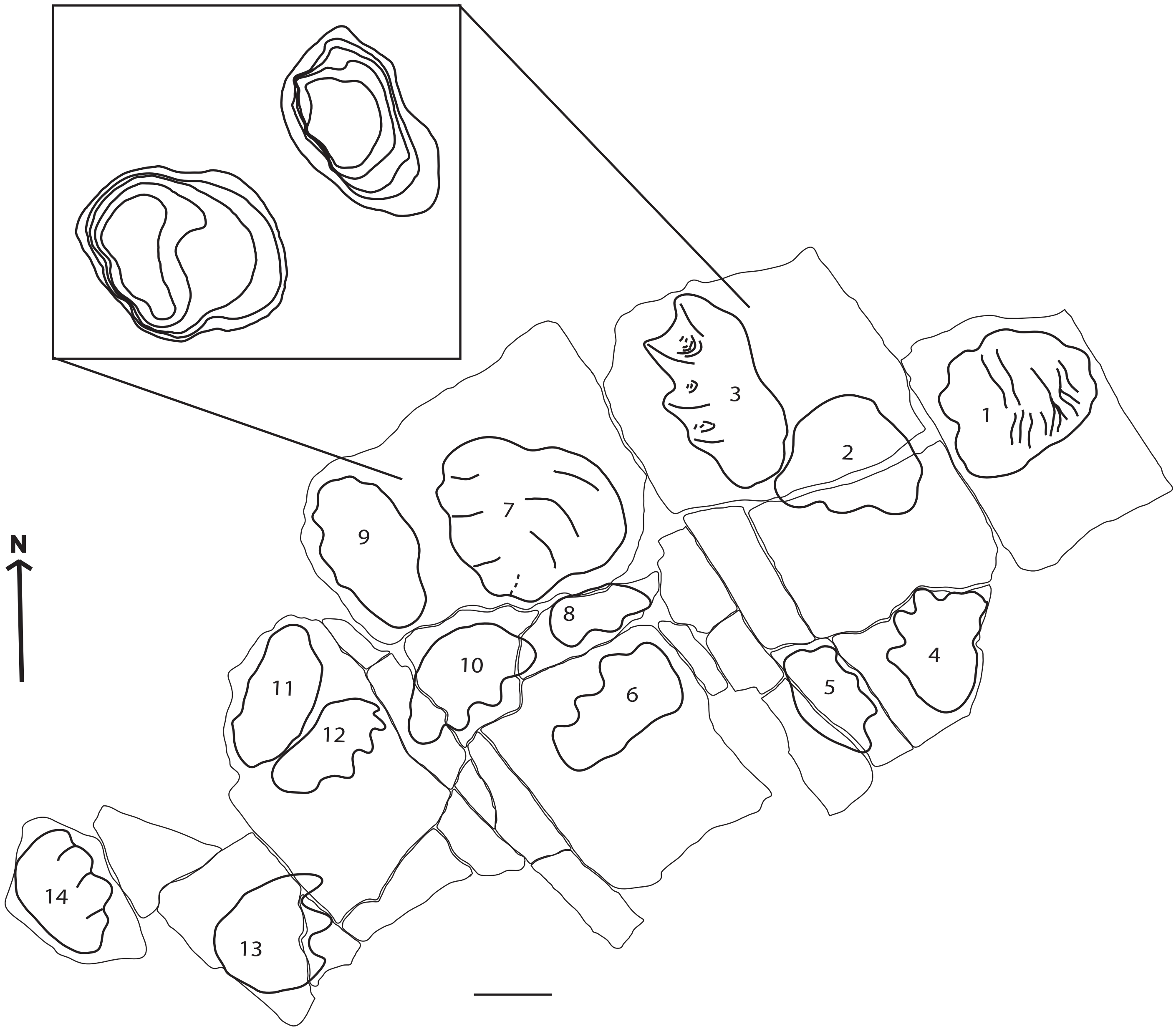


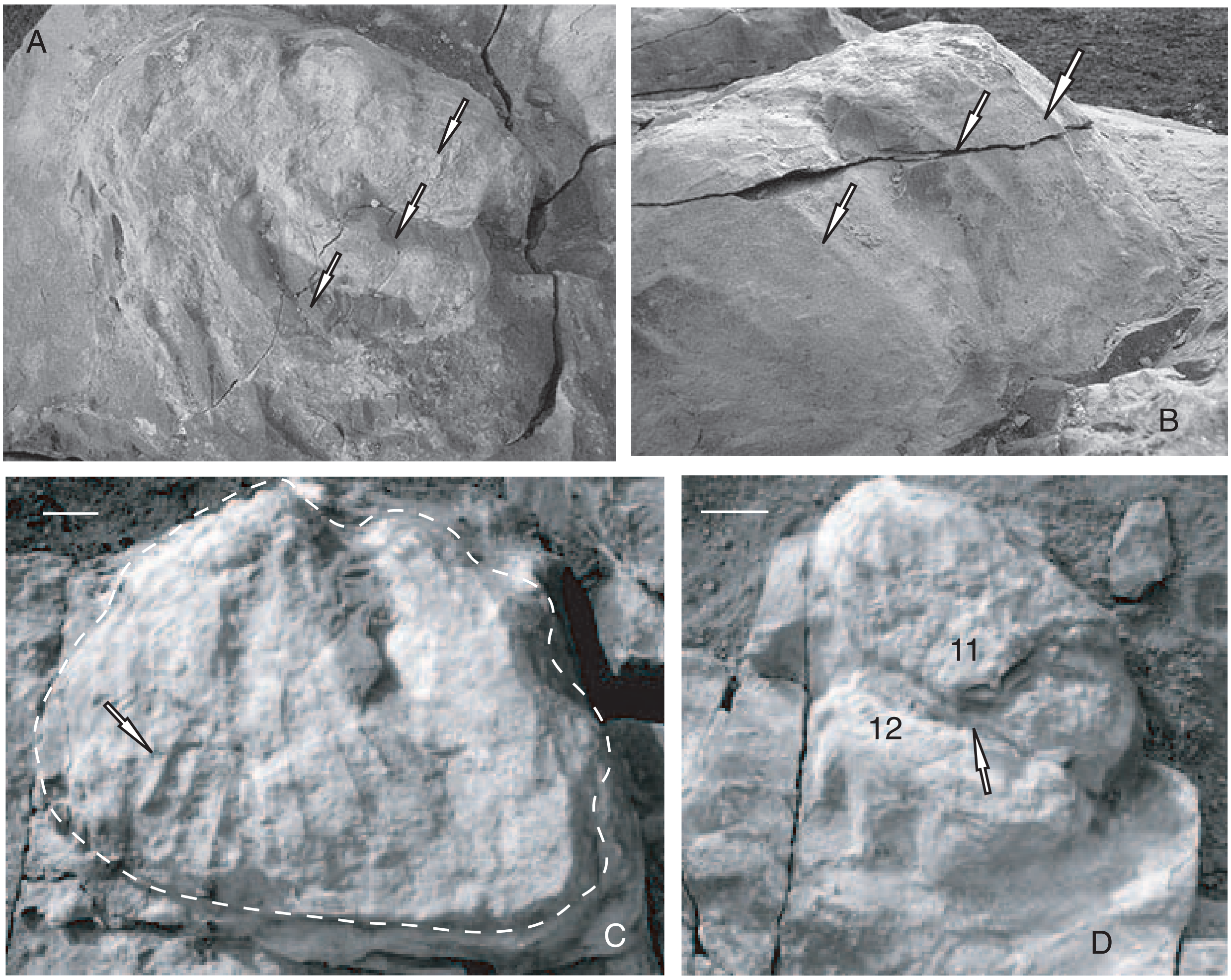
Surkov et al. Figure 2



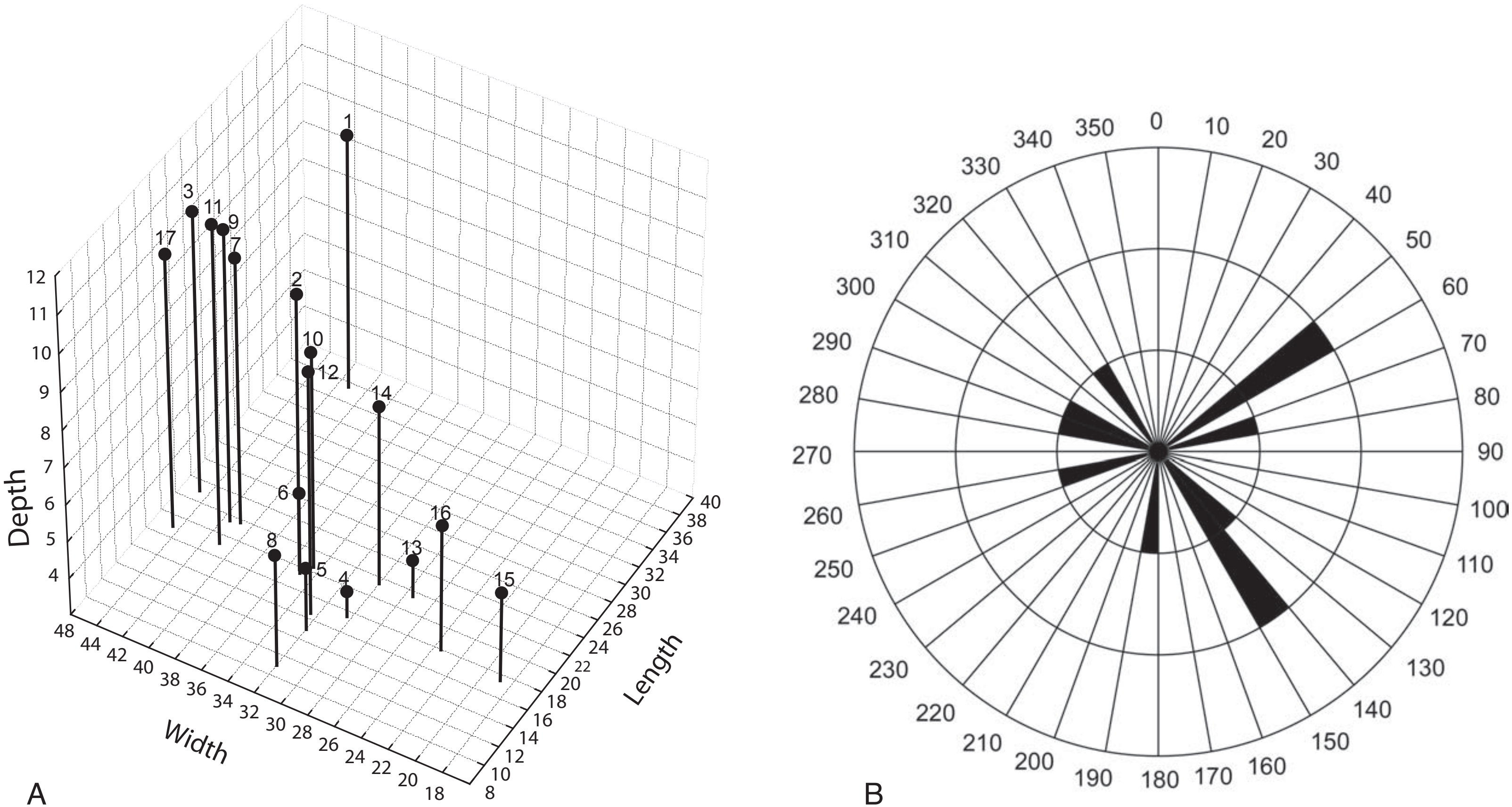
Surkov et al. Figure 3

Surkov et al. Fig. 4





Surkov et al. Figure 5



Surkov et al. Figure 6