

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

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Abstract: Large footprints of terrestrial tetrapods have been found in the Cis-Urals region of European Russia. The footprint horizon is in Late Permian (Changhsingian) deposits of the Vyatkian Gorizont (uppermost Tatarian) approximately 50 m below the local Permian/Triassic boundary. Seventeen randomly orientated 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. They were subsequently cast by 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 in 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 discoveries of tetrapod footprints have been reported so far: amphibian tracks assigned to *Anthichnium ichnops* from the southern Cis-Uralian Trough (Tverdokhlebov *et al.* 1997), and pareiasaurian tracks assigned to *Sukhonopus primus* from the bank of the Sukhona River in the northern part of Russia (Gubin *et al.* 2003). Both sets of tracks were found in the Severodvinskian Gorizont of late Tatarian (latest Permian) age.

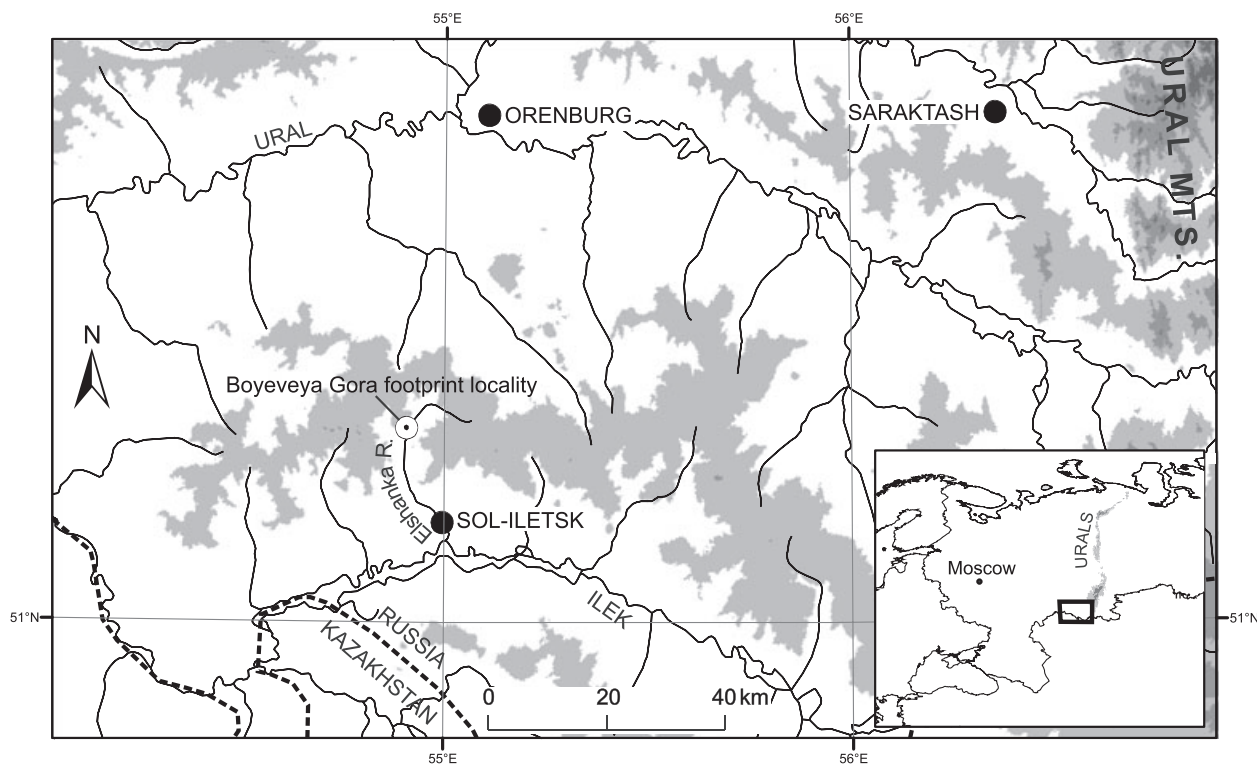
Here we report a third tetrapod track locality from the Russian Permo-Triassic; a set of tracks made by a very large quadrupedal tetrapod in Vyatkian Gorizont strata not far below the Permian/Triassic boundary. These are attributed to a third tetrapod group, the therapsids. The specimens were found during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

GEOLOGICAL SETTING

Sedimentary setting and age

The footprints were found by RJT at the 'Boyevaya Gora' locality (Tverdokhlebov *et al.* 2005, p. 66), situated 14 km north-north-west of Sol-Iletsk City, Orenburg region, in a narrow ravine flowing into the Elshanka River, a northern tributary of the Ilek River (Text-fig. 1). The footprint site is located at 51°29'65"N, 54°06'59"E. An area of 3·4 m² of the footprint-bearing sandstone bed was turned over, revealing 14 footprints in association. The spatial relationships of three more were unclear because they were on detached blocks. The 17 prints were extensively documented in the field, and a representative collection taken back to Saratov State University, where they are curated.

The sedimentary rocks exposed in the Boyevaya Gora ravine 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 from the fauna of ostracods and tetrapods (Tverdokhlebov *et al.* 2005). The Vyatkian Gorizont is equivalent in age to the *Dicynodon* Assemblage Zone of South Africa, and equates



TEXT-FIG. 1. Map of the Orenburg region, South Urals, Russia, close to the border with Kazakhstan. The Elshanka River, and the footprint site, Boyevaya Gora, are marked.

with the Changhsingian Stage of the Late Permian (Lopingian) (Benton *et al.* 2004).

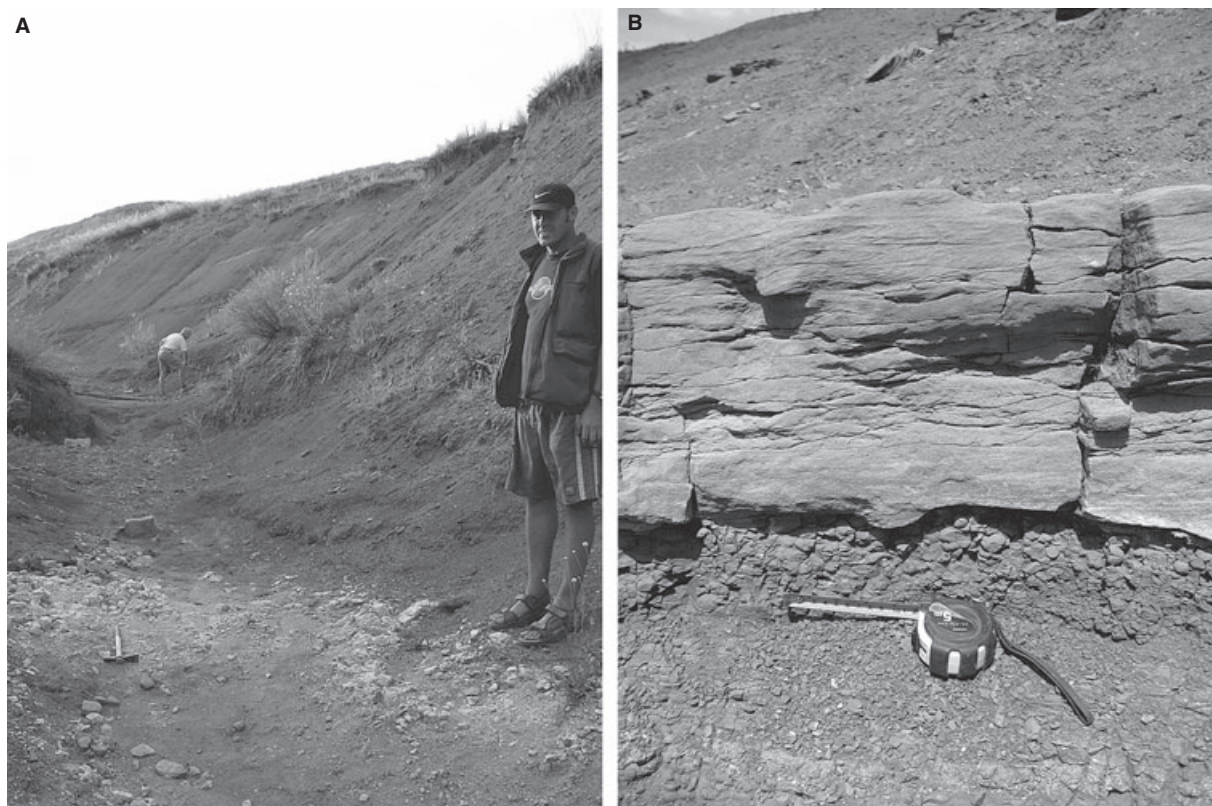
Approximately 124 m of mudstones, siltstones, sandstones and conglomerates are exposed in this section (Text-figs 2A, 3). The local Permian/Triassic boundary is located 94 m above the base of the measured section, at an abrupt facies change from red mudstones with well-developed caliche to trough cross-bedded pebbly sandstones and conglomerates. These latter beds have yielded Early Triassic *Tupilakosaurus* remains, a left angular of *Wetlugasaurus samarensis* (?), and limb and dermal bones of indeterminate Temnospondyli. The mudstones a few metres beneath the boundary contain the Vyatkian ostracods *Volganella magna*, *V. ex. gr. laevigata*, *Wjatkellina fragilina*, *Gerdalia* sp., *Suchonellina inornata* var. *macra*, *S. inornata* var. *magna*, *S. parallela*, *S. parallela* var. *typica*, *S. futschiki* and *Suchonella typica*. 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*, *Toyemia blumentalis*, *Mutovinia stella*, *Saurichthys* sp., *Gnathoriza* sp.).

The footprint horizon is located 45 m above the base of the measured section (Text-fig. 3). The footprints occur 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-grained sandstone immediately overlies this mudstone, and natural sandstone casts of the footprints are preserved in epirelief on the base of this bed (Text-fig. 2B). The tabular sandstone body is some 0.4 m thick, although the thickness varies, with a sharp base and a basal lag of mudstone rip-up clasts and isolated calcrete pebbles 10–20 mm in diameter. The sandstone contains current ripple cross-laminae, with a uniform flow direction to the west-south-west (260°). Ostracods have been found 8 m and 1 m below this horizon and comprise the characteristic Vyatkian taxa *Suchonellina inornata*, *S. inornata* var. *macra*, *S. futschiki*, *S. parallela*, *S. parallela* var. *typica*, *S. inornata* var. *magna*, *S. undulata* and *Gerdalia* sp.

Depositional environment

The sedimentary succession at the track 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,

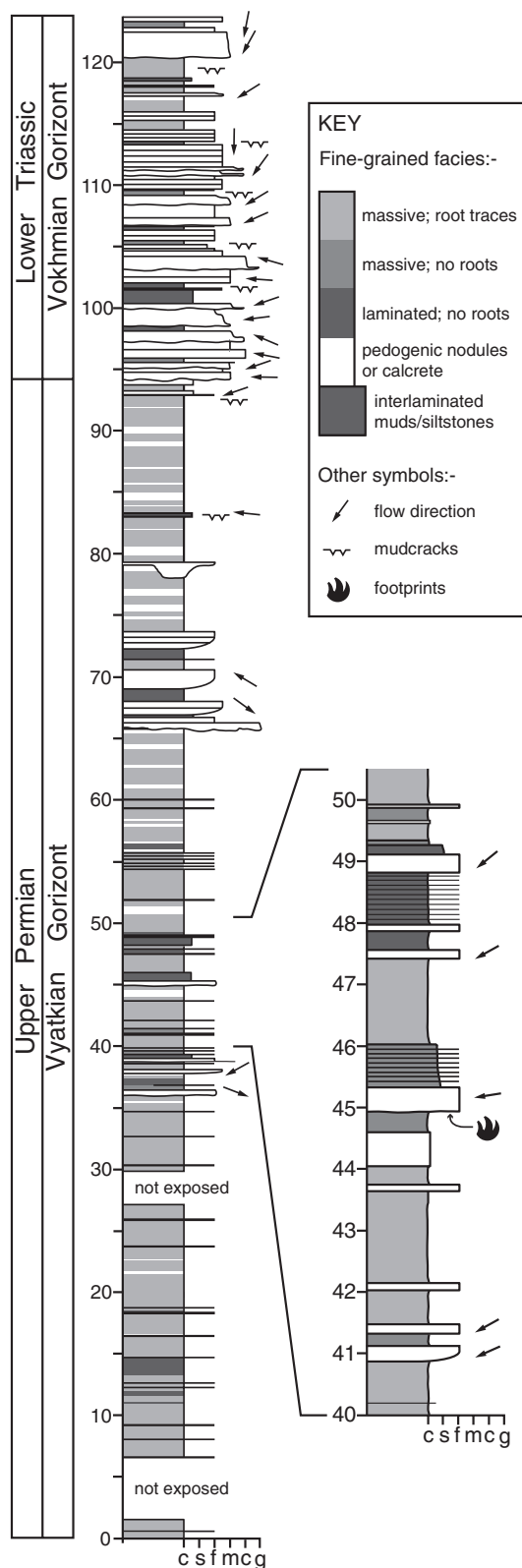


TEXT-FIG. 2. The footprint site and footprints in the Korolki Ravine, near Boyevaya Gora. A, view up the ravine from the footprint site, with MJB in the background, and AJN standing beside a weathered palaeosol in the floor of the ravine. B, close-up of a profile view of the footprint-bearing sandstone bed, showing a curved negative hyporelief above the tape measure of 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.

and are cross-bedded or ripple cross-laminated with bioturbated tops. The red colouration of the mudstone and the presence of rootlets and palaeosol horizons with calcrete are taken to indicate a continental setting with a semi-arid to subhumid climate (Sheldon 2005). 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 thin, erosive-based sandstones. Cross-bedding indicates that the flow direction was generally towards the west. Recession of the flood water allowed plant colonization of the muds and 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 north-east, and they suggested that the overall depositional system was a fluvial 'terminal fan' characterized by a network of shallow channels ending in a mud-dominated flood basin.

The landscape may also have sustained some perennial water bodies. In sections in, and close to, the Boyevaya Gora Ravine, these lakes are reflected by thin (up to 1.5 m) and wide (up to 100 m) lenses of dark grey mudstone, siltstone and sandstone with abundant plant remains. Plant remains from the same interval in nearby outcrops are of typical shrubs of the Tatarian flora (Gomankov and Meyen 1986): *Peltaspermopsis buevichiae*?, *P. sp.*, *Lopadiangium sp.*, *Tatarina olferievii*, *T. conspicua*, *T. pinnata*, *Stiphorus biseriatus*, *Glossophyllum cf. permienne*, *Lepidopteris sp.*, *Salpingocarpus cf. variabilis*, *Phylladoderma (Aequistomia) tatarica*, *Rhaphidopteris cf. kiuntzeliae* and *Dvinostrobus (?) sagittalis*, all of which are interpreted as having grown along the lake margins.

The mudstone bed containing the impressed footprints overlies a pinkish-grey, cemented palaeosol containing abundant root traces, and is interpreted as the uppermost unit of a heterolithic channel fill. However, the impressed mudstone itself was most likely deposited beneath ponded floodwaters, and contains no root traces, indicating that



TEXT-FIG. 3. Sedimentary succession exposed at the Boyevaya Gora locality, in a tributary on the northern flank of the Ileik River. Base of section at 51°29805'N, 54°90949'E.

there was insufficient time for significant plant colonization prior to deposition of the overlying bed. The absence of mud cracks 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 preserved raised displacement rims (cf. Manning 2004, p. 94) around the footprints implies that the flooding event that brought in the overlying sand was initially erosive; this is supported by the presence of rip-up clasts in the base of the sandstone, and thus evidence of emergence such as shallow mud cracks or superficial mud-curls 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-orientated depression that had recently been flooded.

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.
- 1971 *Ichniotherium* (*Cyclopus*) *aequalis* Heyler and Lessertisseur; Haubold, p. 36.
- 1973 *Ichniotherium giganteus* (Heyler and Lessertisseur); Haubold, p. 35.
- 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 *et al.*, p. 303.
- 2000 *Brontopus giganteus* Heyler and Lessertisseur; Gand *et al.*, p. 43, figs 17–19.
- 2000 *Brontopus circagiganteus* Gand *et al.*, pp. 43–52, figs 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.



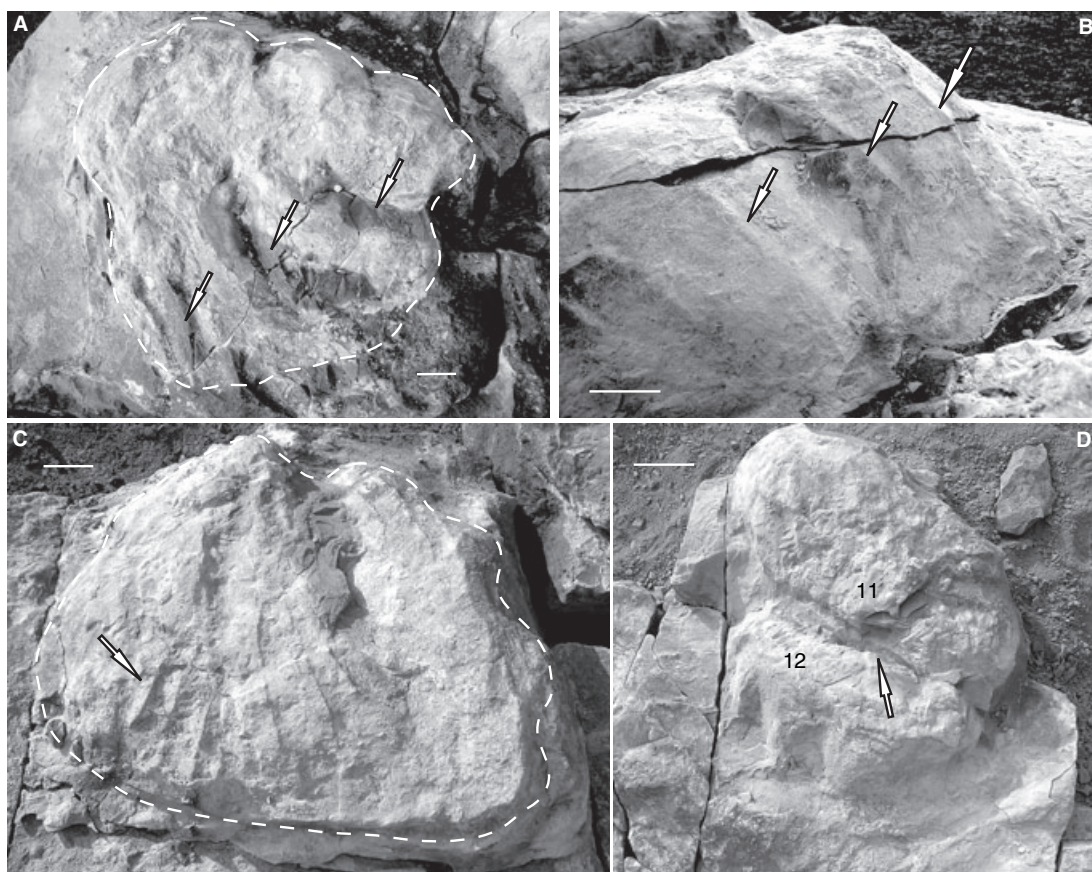
TEXT-FIG. 4. Outline plan of the footprint site and model of print emplacement and modification. A, part of the *Brontopus* trackway showing 14 individual prints, and (in box) relief of anterior (7) and posterior (3) footmarks, marked in contours of 20 mm. B, mode of formation and preservation of the prints: (1) impression of the foot in soft sediment; (2) backward push during retraction; (3) temporal/partial drying of impression, and possible mud cracking of the surface; (4) covering of imprints with fine sand and erosion of raised displacement rims; (5) final stage of preservation. Scale bar represents 200 mm (A).

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

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 manus is pentadactyl, with digits separated by grooves, but not independent. The pes is pentadactyl with digits II–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 variously shaped push-up ridges. Manus prints are 175–275 mm long (mean 230 mm) and 295–425 mm wide (mean 360 mm); pes prints are 110–230 mm long (mean 175 mm) and 340–470 mm wide (mean 380 mm); stride

length about 1.2 m; distance between midline of left and right prints 0.8–0.9 m. Diagnosis and measurements are based on Gand *et al.* (2000, p. 43), with measurements from Heyler and Lessertisseur (1963, pp. 175–176) and from the present Russian material.

Description. The prints are preserved in different styles, from vague shallow impressions to sharp-edged, deeply impressed digitiform prints with clear striations (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



TEXT-FIG. 5. Natural casts of *Brontopus giganteus* footprints. A, dorsal view of print 7 with outline indicated by dashed line; arrows indicate mudstone ridges preserved between the grooves (now cast in sandstone) formed during the 'back-push'. B, anterolateral view of print 7; arrows indicate scratch marks, presumably made by the claws. C, view of print 1 in dorsal view, with outline indicated by a dashed line; arrow indicates an elongate groove (now cast in sandstone) interpreted as representing deformation of a hardened surface crust. D, prints 11 and 12 in dorsal view, with the distorted posterior boundary of print 12 indicated by an arrow. Scale bars are 40 mm.

medially to prints 1 and 7. The direction of the trackway is 263 degrees (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 foot impressions are semi-plantigrade.

Identification and comparison. The Russian footprints may be compared to four 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 Upper Permian strata, and *Therapsipus* from the Mid Triassic (Hunt *et al.* 1993). The closest resemblance is to *Brontopus giganteus*, which is similar in morphology and size, with a combination of short hoofed digits on the manus prints and elongated pointed digits on the pes prints. *Pachypes dolomiticus* (Leonardi *et al.* 1975) differs from the new tracks described here 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 to 125 mm (McKeever and Haubold 1996). The ichnospecies *C. gigas* (including *C. megacheirus* from the Upper 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. *Therapsipus*, although Middle Triassic in age, is a similar-sized track ascribed to dicynodonts. The manus prints measure 193–253 mm wide and 159–247 mm long, and the pes prints measure 174–256 mm wide and 226–257 mm long; both are pentadactyl. Although of similar size to our prints, *Therapsipus* differs in having manus and pes prints that are more similar to each other in size, and the manus is shorter than the pes. The digit impres-

sions are also more distinct from each other, and the pes digits do not show such a clear lateral twist. The other Triassic track assigned to dicynodonts, *Dicynodontipus*, is much smaller, with a pes length of about 50 mm and long narrow digit impressions (Haubold 1971, p. 41).

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 new Russian tracks. A later illustration of the type specimen in Gand *et al.* (2000, 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. Thus, in both shape and curvature of the digit impressions, the Russian tracks compare closely with those of *B. giganteus* from France.

Gand *et al.* (2000, pp. 43–52) erected the new ichnospecies *Brontopus circagiganteus* for a track slightly larger than *B. giganteus* from the uppermost Permian of France. The pes print measures 295 × 280 mm, and the manus 355 × 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 are hard to determine in these large prints, *B. circagiganteus* appears to be the same as *B. giganteus*, and in Gand *et al.* (2000, p. 47) Georges Gand indicated a preference for the original name, while his co-author, Paul Ellenberger, argued that the new name was required because Heyler and Lessertisseur's (1963) description 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 synonymize *B. circagiganteus* with *B. giganteus* because the two taxa are essentially the same morphologically, and Ellenberger's objections are not sufficient to reject the original name.

DISCUSSION

Identifying the manus and pes

There are two footprint morphologies, but it is difficult to identify the manus and pes prints unequivocally because there is no continuous single trackway. For initial description, these will be termed print morphotypes A

and B. Print A is best exemplified by footprint cast 3 (Text-fig. 4), which is 230 mm long and 467 mm wide. This print bears five digits, of which digit V is poorly recognizable. 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 skin stretched between them. The digits all point towards the midline, and they increase in length from V to II, with I roughly equal to III. The best example of print morphotype B is cast 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. On the cast, the digits 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 covered in horny material similar to the keratin of modern hooves. Digits I–III point forwards in the interpreted direction of movement, while IV and V diverge slightly to the side. Both print types show similar relief/depth (Text-figs 4–5), which indicates that the animal was a quadruped with feet that were broad and roughly similar in size, although the foot that made print morphotype A was wider.

In their reproduction of the type specimen of *Brontopus giganteus*, Gand *et al.* (2000, fig. 24B) showed both print morphotypes, and they assumed 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 argue for the opposite interpretation, based on the position of the prints relative to the midline of the track, and the limb movements implied by each. Assuming that prints 3, 9, 1 and 7 were made by the left limbs of a single quadruped, then prints of morphotype A (3 and 9) are placed closer to the midline than those of morphotype B (1 and 7). Many Permo-Triassic tetrapods apparently moved with 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 an erect, parasagittal posture, and the sprawling forelimbs scrabbling along in front. Dual gait has been reported for many Late Permian therapsids from studies of their skeletal remains (Boonstra 1966; Kemp 1980, 2005; King 1981; Surkov 1998) as well as the morphology of *Chelichnus* trackways (McKeever 1994). Based on these findings, the more medially placed prints (3, 9) would be pes prints, and the more lateral ones (1, 7) would be manus prints.

This interpretation is supported by details of movements of digits in the substrate that are preserved in some prints. Print 7 (morphotype A; Text-fig. 5A–B) shows a 'back-push', with scratches that are directed outwards

TABLE 1. Main measurements of the footprints.

No. 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

from the midline, 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 than print 7 (Table 1) and was made in the same substrate. 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) was made by the manus, and morphotype B (3, 9) the pes. Our determinations for the other prints are indicated in Table 1.

Variation in print dimensions

All the excavated tracks are morphologically similar, and even though they appear to form more than one trackway, they almost certainly all belong to the same ichnotaxon. This assumption was tested by calculating the coefficient of variance (CV) for the main print dimensions (Table 1). Because 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 14.8 per cent. The length showed up to 29 per cent more variability. Pronounced variation in print length may be explained by the substrate consistency and whether the push-up ridge is preserved (print 7) or not (print 2).

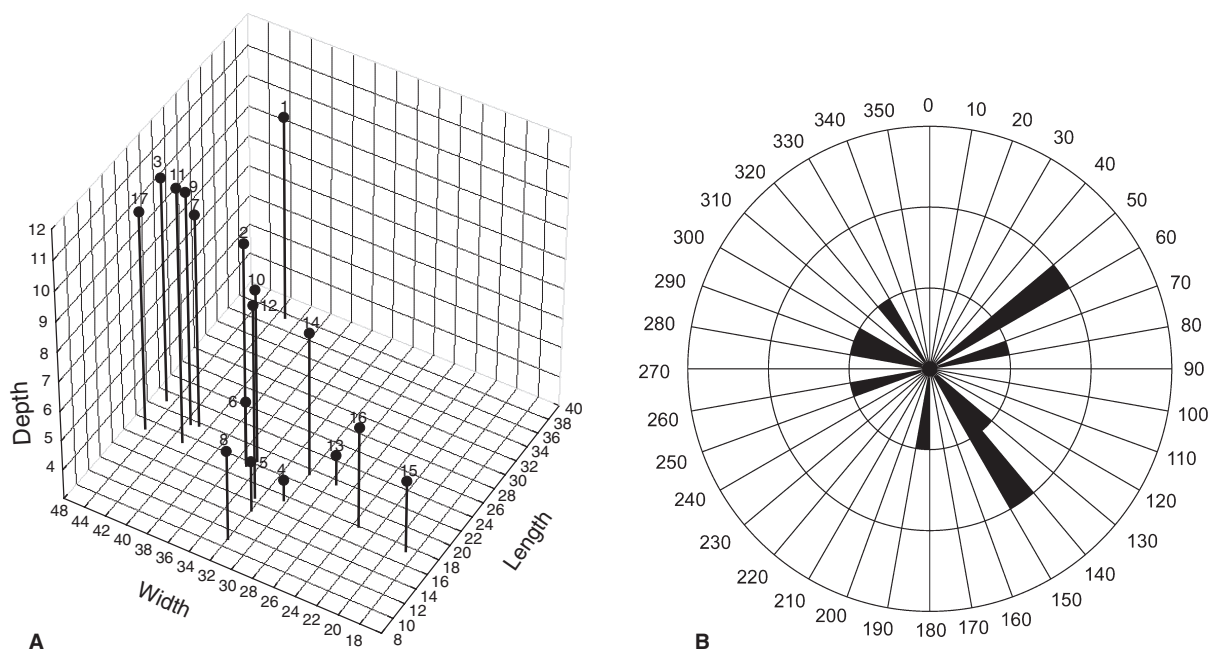
According to Demathieu (1987b), CV values above 25 per cent may reflect a population of prints that was left by different species, by animals of different size or in a wide range of preservation modes. Thus, the small CV values for print width of the Russian tracks support the suggestion that one species made all the prints, whereas the high CV values for print depth and length almost certainly reflect differing preservation in a variable substrate, and/or variations in body mass between different animals.

Depth of the preserved tracks

The preserved footprint depth is initially controlled by the pedal mechanics and mass of the animal, modified by substrate rheology, especially the water content of the sediment, then later by possible erosion prior to deposition of the overlying bed (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 mass of the animals was the 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 4–6 and 13 are shallower than predicted from their dimensions, 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 grooves (Text-fig. 5C) that may have formed when the leg stepped onto mud that had a thin hardened crust. The next time this leg stepped on the mud (print 7), it was not so dry, or there was no hardened crust, 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 footprints 1 and 7 also shows no traces of mud cracks, so this leg also stepped onto unhardened mud. Therefore, it is possible to argue that the spatial transition between hardened and soft mud was rather sharp, but hardening of the substrate was obviously not enough to reduce footprint depth over a distance of at least 0.5 m. The similar-sized prints 6 and 10 are very close together (Text-fig. 4), but print 6 is half as deep. These two prints are heading in different directions, and so may have been formed at different times and with different water content in the sediment.

Another factor that controlled imprint preservation was whether the footprints were impressed before or



TEXT-FIG. 6. Diagrams of footprint measurements and orientation. A, 3D 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.

after emergence of the surface above the waterline. 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 to form a crust or shrunk to form mud cracks. 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 buried beneath 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 4–6, 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 orientated differently (Text-fig. 6B). Seven of the 11 individual prints are orientated north-west–south-east, while the last footprint generation, including the mini trackway 1, 3, 7 and 9, has a different orientation, south-west–north-east. None of the trackways appears to be influenced by the topography of the depression or the depth of the water.

Identity of the trackmaker

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

Haubold (1971) assigned *Brontopus* (as a synonym of *Ichniotherium*) to the Edaphosauria, prints made by a ‘pelycosaurian’ synapsid. Most basal synapsids were too small, but some such as *Cotylorhynchus* and *Ennatosaurus* 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. Furthermore, most were Late Carboniferous and Early Permian in age, rather than latest Permian, although *Ennatosaurus* from the Mezen’ Basin of the Archangel’sk region is late Permian (late Kazanian/early Tatarian) in age (Modesto and

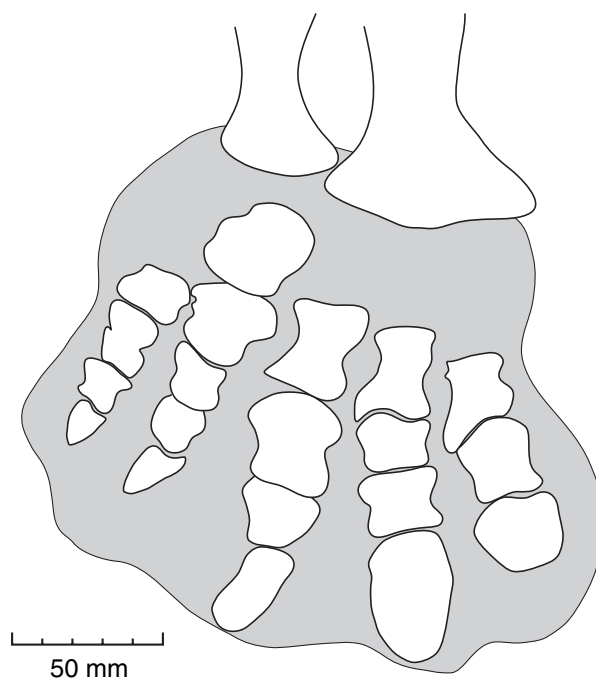
Rybczynski 2000). The feet of *Ennatosaurus* are unknown, but they may have been like its relative, the caseid *Cotylorhynchus*, although the hands and feet were probably half the size of the current tracks.

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 are *Ulemosaurus* and *Deuterosaurus*, but their skeletal remains are too old, being known only from the upper part of the Urzhumian (Tverdokhlebov *et al.* 2005). Worldwide, dinocephalians had largely disappeared by the end of the Tatarian, and mostly by the mid–late Tatarian (Kemp 2005). Dinocephalians are thus rejected from consideration as potential trackmakers for the Russian material on stratigraphic grounds.

Pareiasaurs are possible candidates for the footprints as they were large enough, up to 3 m in total body length, and 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, favouring the latter interpretation but without offering any morphological evidence. The inferred posture of the trackmaker, however, allows pareiasaurs to be rejected as candidates. Pareiasaurs were sprawlers fore and aft, their digits were asymmetrical with the pes digital formula 2-3-3-4-3 (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 semi-plantigrade, and some of the present specimens even indicate semi-sprawling locomotion, as has been inferred from skeletal remains for various groups of Late Permian therapsids.

Another possible candidate for the footprints is a large dicynodont. Some of these therapsids with 0.5-m skulls (*Rhachiocephalus*, *Aulacephalodon*) are known from the uppermost beds of the Upper Permian in South Africa (Rubidge 1995). Although such truly giant dicynodonts have not been reported from Russia, the genus *Vivaxosaurus* (Kalandadze and Kurkin 2000) has nearly the same skull size (0.4 m) and is known from the Vyatkian of Russia. The digital formula for dicynodonts is 2-3-3-3-3. To assess whether the dicynodont autopodium fits *Brontopus* prints, we used digitized photographs of the manus of a large *Lystrosaurus* (SAM-PK-04458, *in situ*) with a



TEXT-FIG. 7. The right hand of *Lystrosaurus* drawn over the manus print of *Brontopus*, to scale. The manus print is traced from print 7 (left manus of *Brontopus*) and mirrored.

skull length of about 0.4 m to contour the manus bones. This stencil was cut out and a paper model of the manus was placed in the contour of *Brontopus* footprint 7 in a semi-plantigrade position (Text-fig. 7). This model showed that the topology of the dicynodont manus generally fits well in the imprint of the *Brontopus* manus, except for a slightly shorter digit 4 that may be explained by morphological variances among the dicynodonts themselves and the very simplified 2D model of the manus. The postcranial morphology of advanced dicynodonts shows features associated with possession of a dual gait during locomotion (King 1981; Surkov 1998) and these features are also clearly seen in the *Brontopus* trackway. Therefore, we consider large dicynodonts as the most likely trackmakers of *Brontopus* prints.

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:

$$\frac{a_1 r_1}{a_2 r_2} = \frac{O_2 G}{O_1 G}$$

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, and $O_1 G$ and $O_2 G$ 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 of tracks

7 (manus) and 3 (pes) (Text-fig. 4) with Mapinfo 7.0 software. The surface area for the manus is 0.934 m² and 0.872 m² for the pes. 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, indicates that *Brontopus* was made by a herbivore.

Comparison with the Karoo

Trace fossils, including tetrapod tracks, have been reported from many horizons in the Middle 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 the Russian tracks described here. Smith (1993, fig. 14) ascribed one print morphotype to the small, 0.5-m-long dicynodont *Diictodon*, but these are much smaller than the Russian tracks, consisting of sets of three or four distinct subcircular digital pad prints with forward claw scrapes and no palm print.

Later 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 appear to be more widely spaced 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 seen in the tracks described here. The assignment of these South African tracks to *Dicynodontipus*, an ichnogenus erected by Rühle von Lilienstern (1944) for a range of ichnospecies from the Lower and Middle Triassic of England and Germany, seems reasonable. The Russian material though is different morphologically and in terms of size, yet similar enough in overall geometry to have been made by dicynodonts.

The new tracks from Russia thus confirm the presence of large dicynodonts in the latest Permian of Russia, a new record because the skeletal fossils are from smaller dicynodonts, and they represent the first record of therapsid tracks from Russia. An enduring puzzle is, however, the relative rarity of track sites in the Russian and South African Upper Permian when compared with the seeming abundance of skeletal fossils.

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