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PERMIAN TRACE FOSSILS ATTRIBUTED TO TETRAPODS (TIERBERG FORMATION, KAROO BASIN, SOUTH AFRICA)

by

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ABSTRACT

The discovery of a paving slab with a number of prints suggestive of footprints of tetrapods led to a reinvestigation of a trace fossil, known from three localities, of which only two photographs had been published, each with only four prints. The slab was traced to a previously unrecorded site, De Puts, near Calvinia, located in the Tierberg Formation of the Ecca Group of the Karoo Supergroup. The prints from all the sites are referred to *Broomichnium permianum* Kuhn 1958, of which *Quadrispinichna parvia* of Anderson 1974 is a synonym.

KEYWORDS: Trace fossils; ichnology; Ecca; *Broomichnium; Quadrispinichna*

INTRODUCTION

Investigation in September 1996 of trace fossils on paving slabs used for the pathways at the Huguenot Memorial in the town of Franschhoek, near Cape Town, led to the discovery of a slab with a number of prints recognisable as similar to those illustrated from material in the South African Museum by Griffiths (1963), and attributed by him to Proanura (i.e. tetrapods of the group ancestral to the Anura). As the paving was under repair at the time, it was possible to obtain the slab for the palaeontological collection of the Department of Zoology, University of Stellenbosch. It was subsequently established that the paving stones had come from Downes, near Calvinia, Northern Cape, having been brought to Franschhoek by Mr Billy Clift of the Clift monument masonry firm of Paarl in 1942. Two other small slabs were subsequently observed at Franschhoek, at the entrance to the Huguenot Monument.

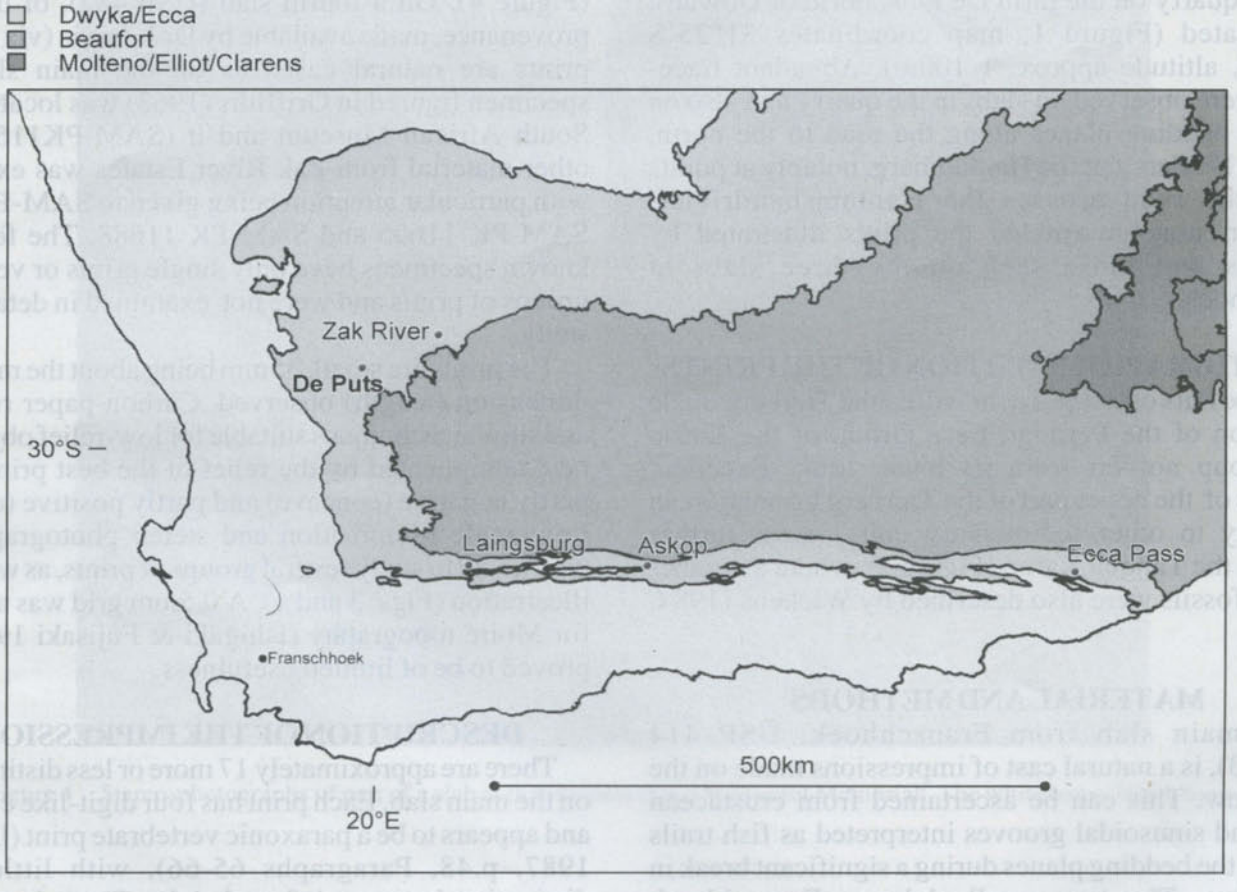


Figure 1. Map of southwestern and southern Karoo, showing *Broomichnium* localities.

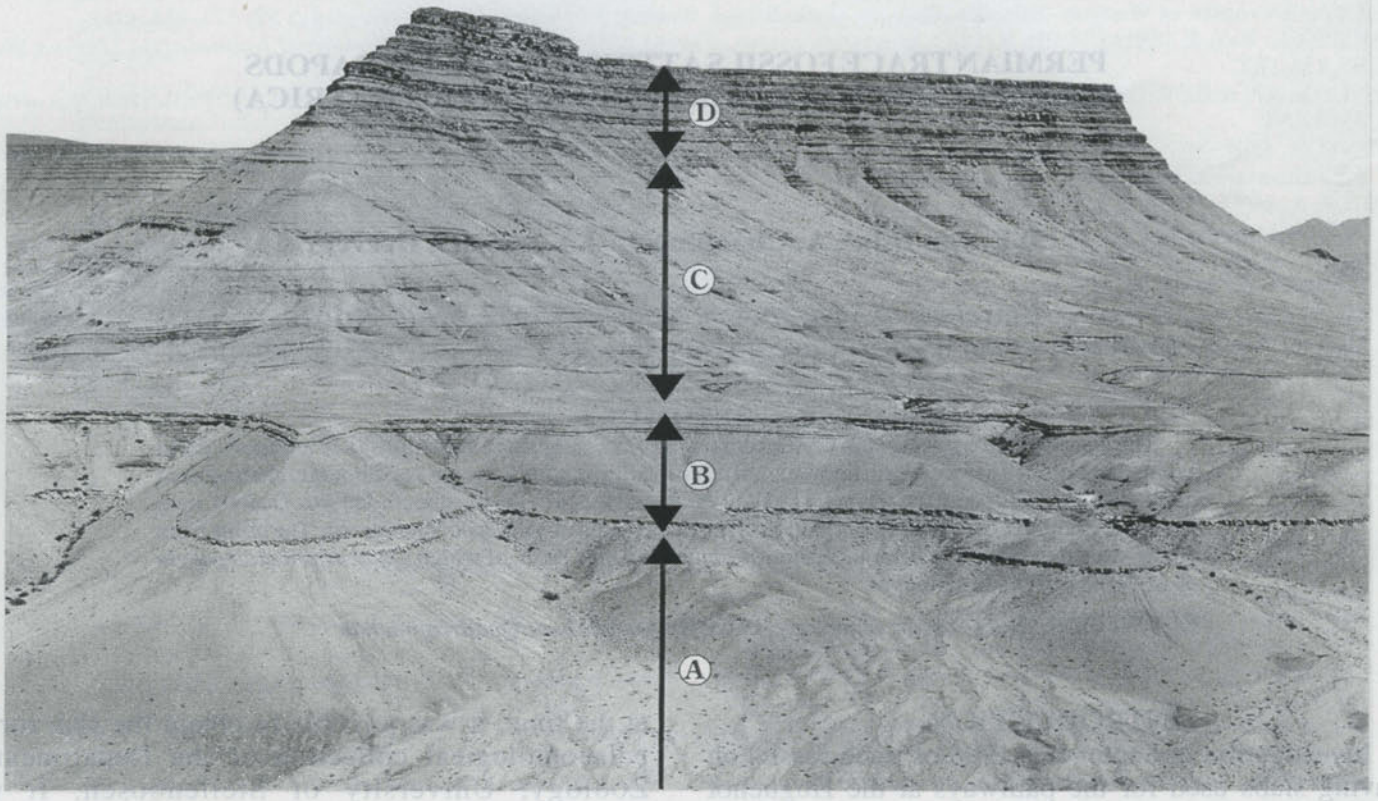


Figure 2. Photograph showing the Tierberg Formation in relation to other formations approximately 120km South of De Puts. Photograph and caption reproduced from Cole *et al.* (1990) with permission of H. deV. Wickens. Only the upper part of the Tierberg Formation is shown, while De Puts is not far from the lower limit of the Formation.

PROVENANCE

During a two-day visit to Calvinia (AC & EvD) the original quarry on the farm De Puts, north of Downes, was located (Figure 1, map coordinates 31°25'S 19°58'E, altitude approx. 1 100m). Abundant trace-fossils were observed on slabs in the quarry and also on exposed bedding planes along the road to the north, between De Puts and the Hantamberg, notably at points where the road crosses the Hantamshandrivier. However, none resembled the prints illustrated by Griffiths and those seen on the three slabs at Franschhoek.

STRATIGRAPHIC POSITION OF THE PRINTS

The De Puts outcrops occur within the Tierberg Shale Formation of the Permian Ecca Group of the Karoo Supergroup not far from its lower limit. Excellent outcrops of the upper part of the Tierberg Formation, in proximity to other sedimentary units, occur further south, in the Tanqua Karoo (Figure 2), where a number of trace fossils were also described by Wickens (1984, 1994).

MATERIAL AND METHODS

The main slab from Franschhoek, USP 414 (Figure 3), is a natural cast of impressions made on the slab below. This can be ascertained from crustacean tracks and sinusoidal grooves interpreted as fish trails made on the bedding planes during a significant break in deposition. The two small slabs at Franschhoek represent the material on the surface of which the prints were made, i.e., the prints are on the upper surface (Figure 4). On a fourth slab (USP 482), of unknown provenance, made available by Dr J. Jarvis (via AC), the prints are natural casts, as on the main slab. The specimen figured in Griffiths (1963) was located in the South African Museum and it (SAM-PK11604) and other material from Zak River Estates was examined, with particular attention being given to SAM-PK 3457, SAM-PK 11605 and SAM-PK 11688. The few other known specimens have only single prints or very small groups of prints and were not examined in detail in this study.

The prints are small, 35mm being about the maximum dimension (length) observed. Carbon-paper rubbings, and similar techniques suitable for low-relief objects, are here complicated by the relief of the best prints being partly negative (concave) and partly positive (convex). Low-angle illumination and stereo photography was used as aid to study several groups of prints, as well as for illustration (Figs. 3 and 4). A 0,5mm grid was available for Moiré topography (Ishigaki & Fujisaki 1989), but proved to be of limited usefulness.

DESCRIPTION OF THE IMPRESSIONS

There are approximately 17 more or less distinct prints on the main slab. Each print has four digit-like elements, and appears to be a paraxonic vertebrate print (Leonardi 1987, p.48, Paragraphs 65-66), with little or no distinction between left and right. The prints tend to



Figure 3. Part of a flagstone from Franschhoek, ex De Puts, USP 414. Each bar of the scale is 10mm long). The relief has been reversed by lighting from the bottom right so that the natural cast will have the appearance of the surface on which the prints were made. Note the sigmoid grooves made by the fins of a fish (bottom right of figure) and the crustacean track (right of figure). The overlap of prints mentioned in the text is equidistant from the two dots, which also indicate the approximate line of orientation of the lighter prints.

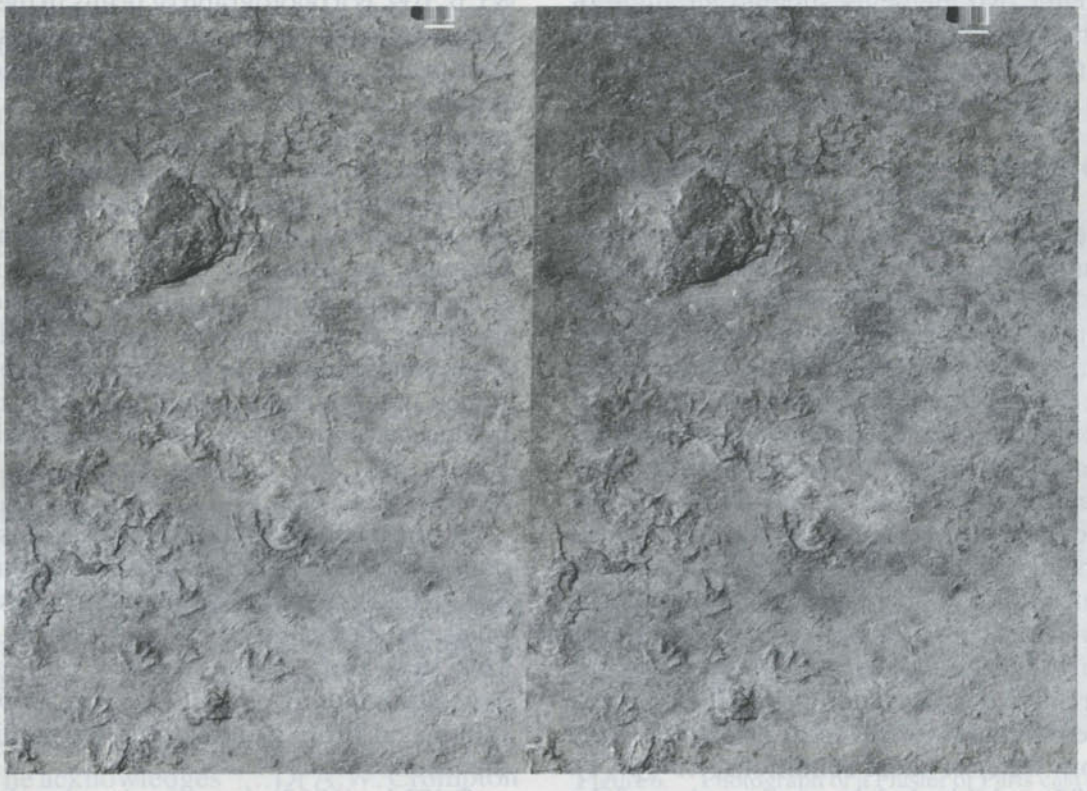


Figure 4 Stereo-photographs of part of a slab at the entrance to the Huguenot Memorial. The white bar is 10mm long.

show an orientation in one direction, although obliquely (Figure 3), but no trackway could be observed, nor could fore and hind prints be distinguished. A similar lack of distinct differentiation between individual prints, but the presence of an orientation in one general direction, was observed on other slabs, both from De Puts (e.g. Figure 4) and from Zak River Estates (Figure 5). There are indications on the main slab from De Puts that the prints were made in two phases, since there is overlap of a deeper print and a lighter, more slender print, which appears to be one of a series angling towards the right of the photograph and the main orientation direction. Since the prints are natural casts, the more slender print which appears as overlapped would in fact have been made subsequent to the other (Figure 3). There is considerable variation in divarication between the two outermost elements and also in the spacing and angle between the inner two elements. The angle between the distal ends of the outer two elements varies from about 125° to 35°. The slab of unknown provenance has three slender prints, well-spaced from one another and on a slightly curved line, and a fourth (Figure 6) to the side of the third print. In many prints, on several slabs, the two middle elements distally show a reversal from convexity downwards, to convexity upwards. There are indications of webbing between elements, and also beside one or both outer elements, as may be seen in Figure 4 and on the right-hand side of the print on the left in Figure 3. The apparent webbing to the sides could be folds of the web, as it has not been seen in prints where the elements ("toes") are spread out ("divaricated" at a large angle). In Figure 4 the outer two elements subtend an angle of about 50°. If the apparent folds in this print were to be eliminated by moving the outer elements outwards, the angle between them would still be only about 85°.

REVIEW OF EARLIER DESCRIPTIONS AND INTERPRETATIONS

As some references are difficult to obtain, for instance outside of South Africa unpublished theses, in South Africa some books, relevant passages are quoted verbatim. In a review of the reptilian fauna of the Karoo Basin of South Africa, Haughton (1919) under "Ecca Series" referred to two reptile skeletons and to slabs of flagstone from the Zak River Estates containing tracks of invertebrates and vertebrates as being the only other indications of animal life in the Ecca Beds of the west. He writes: "The vertebrate tracks are those of a small animal with semi-webbed feet and but four functional toes, the two median ones lying almost parallel to one another, while the laterals diverge at a strong angle. No bones have yet been found to indicate the affinities of the form." Further down the page he writes: "Considerable interest attaches to the footprints from Zak River. They indicate shallow-water or shoal conditions, ..." (p.11). Haughton (1925) exhibited slabs at a meeting of the Royal Society of South Africa on May 20, 1925 and reported briefly on them: "The specimens are from two localities in the Ecca Beds, one in the Zak River area, Calvinia, and the other from the cutting (Ecca Pass) on the road from Grahamstown to Fort Beaufort, localities separated by a distance of 350 miles. The tracks are very well defined, and there are several forms common to the two localities." He also refers to both invertebrate and vertebrate tracks and writes of the latter: 'The vertebrate tracks consist in part of small groups of four-toed so-called "amphibian" prints, which lack a heel-pad, and which suggest that the feet were used for progression over very short distances of a few steps; in part, doubtfully of oval impressions with a finely corrugated surface, as if due to the impress of a skin-covered "hoof-like" foot; and in part of a series of peculiar parallel sinuous lines. No similar occurrence to the last has been found in the literature; and the suggestion is made that they are markings made by ventral spines of a fish armed after the fashion of the Carboniferous and Permian *Acanthodes.*' (Haughton 1925, p. xxviii).

"Tracks" in the region of the Ecca Pass are again referred to in Haughton (1928, p. 15), where observations of von Huene and Rogers are also mentioned. There is a reference to amphibian "tracks" near Calvinia in Haughton (1929, p. 131).

Abel (1935), in a seminal book on trace fossils, interprets footprints in the Permian Red Beds of the Grand Canyon and Texas as involving concentration of tetrapods in shrinking water-bodies in deserts, and states that the same was the case in the Permian of South Africa, where similar prints occur at Zak River: "Das gleiche ist auch im Perm von Südafrika der Fall gewesen, wo wir am Zak River ähnliche Fährten in Tonschiefern der Ekkaschichten antreffen (Fig. 85)" (p. 107). His Fig. 85, p. 109, is a photograph of prints in the South African Museum, in the caption of which he states that only hind-foot prints appear to be represented and that they are reminiscent of *Artiodactylus sinclairi* insofar that the middle two toes are equally long, as are the longer outer toes, and that the systematic position of the animal that left the prints is uncertain: "Fährten aus den permischen Ekkaschiefern am Zak River, Calvinia, Südafrika. Original im Museum zu Kapstadt. Die Fährten (es scheinen nur Hinterfussfährten vorzuliegen) erinnern insoferne an *Artiodactylus sinclairi* Abel aus der oberen Trias von Princeton, New Jersey, als die beiden mittleren Zehen untereinander gleich lang sind, ebenso wie die beiden äusseren Zehen. Die systematische Stellung des Tieres, das die Fährten hinterliess, ist unsicher. (Natürliche Grösse.)".

On the basis of Abel (1935), the traces were formally named *Broomichnium permianum* (Kuhn 1958, p. 13 & Taf. III/22). A subsequent publication (Kuhn 1963) gives the taxon on p. 14 and Taf. 9, Fig.30 on pp. 160-161, and, unlike Kuhn's earlier publication, consultation of *Zoological Record Amphibia* for 1963 (published 1965) would lead to the publication, but not the taxon.

Griffiths (1963), in reviewing the phylogeny of the Salientia (Anura), interpreted the prints as having been made by fore-feet of Proanura with head-down, caudally driven, swimming movements, - his type (b), during which movement "...the body axis would slope



Figure 5. Stereo-photographs of part of SAM 11605. (Each bar of the scale is 10mm long). Note the difference between the relief of the depressed more proximal parts and the elevated more distal ones of the middle two elements ("toes").

obliquely upwards and the extended hind limbs would not normally touch the substrate. The fore limbs, on the other hand, were probably used for manoeuvring and bottom probing." He concludes: "This is the only feasible explanation of recently discovered footprints from the Ecce (*sic*) Formation of South Africa (Pl. I, fig. I). All these prints are four-toed and therefore were made by fore-limbs. The middle pair of toes, in particular, terminate in mounds suggesting that the foot entered the substrate at an acute angle, precisely as would be expected in type (*b*) swimming movements. This view is strengthened by the significant lack of palmar impressions and the consistent absence of hind-limb imprints. If this interpretation is valid it not only supports the above analysis of proanuran-salientian locomotion, but also protracts the history of the Proanura into the basal Permian." (Griffiths 1963: p. 278). In point four of his summary (Griffiths 1963, p. 286) he has: "It is concluded ... that the so-called 'saltatory' trends of modern Salientia evolved primarily for swimming. Fossil footprints from the Ecce (*sic*) formation of South Africa may indicate that the Proanura were already established by the Permian." On the same page he acknowledges "...Dr A.W. Crompton for photographs of the fossil footprints ...", which thus indicates that the specimen is from the South African Museum (i.e. specimen SAM-PK11604). In his Plate 1, Fig. 1. ("Fossil footprints from the Ecce *(sic)* Formation (basal Permian) of South Africa.") there are four

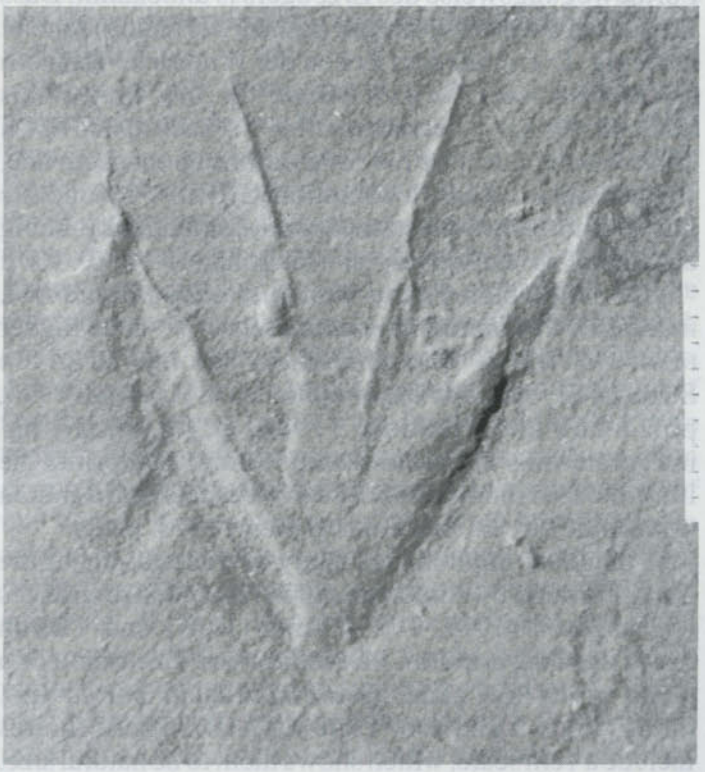


Figure 6. Photograph of a Plaster of Paris cast of the last print on USP 482. Scale is 10mm. The substrate has the appearance of having been squeezed inwards from the two sides, and so being raised in the middle and particularly in front beneath the middle two elements. The curved lines at the sides suggest a web, which possibly also made the impression on the left beyond the print.

imprints, close together, two on the left, and two on the right slightly behind those on the left. All the prints are rather similar with greater differences between sides than between back and front on either side.

Theron (1967), investigating an area near Laingsburg, illustrated in Plate 12: "Epireliefs from the Fish Track Range Zone (Laingsburg Formation)", including "Vertebrate tracks". These "vertebrate tracks" consist of two clear prints with an L-shaped mark to the right and in advance of each. He notes: "Four toed vertebrate tracks 1 cm. wide and occurring in pairs 1.5 cm. apart and with an apparent stride length of 1.5 cm. occur in the Fish Track Range Zone." (p.14). A reference to mention of "small vertebrate tracks" near Grahamstown, i.e. Ecca Pass, by Haughton (1928) follows. A search of the collections of the Department of Geology, University of Stellenbosch, for material collected by Theron was unsuccessful.

Haubold (1971) placed *Broomichnium* Kuhn 1958 in the Family Dissorophidae of the Superfamily Eryopoidea of the amphibian Order Temnospondyli. Of *Broomichnium* he notes that print sequence and locomotory mode of their maker are unknown, he questions that Proanuran prints are represented, and remarks that the slender toes of the prints are reminiscent of *Cursipes* or *Gracilichnium*: "Digitigrade, tetradactyle Eindrücke, mit schlanken spitzen Zehen, die beiden mittleren jedes Eindruckes sind am längsten, zwei weitere Zehen liegen seitlich etwas zurück. Die Fährtenanordnung und damit auch die Fortbewegungsweise des Erzeugers is unbekannt. Dass Proanuren-Fährten vorliegen (GRIFFITH 1963) scheint abwegig. Die schlanken Zehen der Eindrücke erinnern an *Cursipes* oder *Gracilichnium.*" (p. 19). On p.18 his Abb. 13 (9) has a reconstruction "... nach GRIFFITH 1963.", which despite his reservations about sequence, suggests quadrupedal locomotion. Griffiths' taxonomic interpretations are questioned more emphatically, being described as erroneous, in Haubold (1974, p. 100): "...die Amphibien-Fährte *Broomichnium permianum*, irrtümlich Proanuren zugeschrieben, ...". The higher taxon to which *Broomichnium* belongs is given Superfamily status as Dissorophoidea in Haubold (1974, pp.24-26) and Haubold (1984, p.37). Griffiths' interpretations of relationship of the footprints he illustrated to Anura have not been well received in anuran systematic circles (see Estes & Reig, 1973, p.42).

A detailed, unpublished study of trace fossils of the Early Permian by Anderson (1974) included references to Haughton (1919, 1925), Abel (1935) and Theron (1967) and description, illustration and discussion of a taxon given the name *Quadrispinichna parvia* (pp. 78-81, Figs. 5 and 6 of Plate LXXIII). These figures include a 1cm scale, which shows them to be natural size. The caption for Fig. 6 is as follows: "Holotype of *Quadrispinichna parvia.* As usual, the impressions in a group have a similar orientation. In this group, the outer two 'toes' are not joined; instead, each is connected to the adjacent inner 'toe' by a straight line from the distal tip of the former to the proximal tip of the latter. Orientation uncertain. (S.A.M., 3547, x1)". SAM-PK 3547 is the same specimen as used for Abel's Fig. 85, and the scale in Anderson's Fig. 6 shows Abel's and Kuhn's figures to be smaller than 1/1, their stated size. Listed as type material (all except SAM 3547 paratypes), are SAM 3535-3551; 3584-3591; 11598-11617; 11680-11688. Anderson notes the absence of a definite trackway and considers the possibility of irregular touch-down of a swimming animal, vertebrate or invertebrate: "The isolated position of each imprint and the sharp incision do indicate that they were impressed on the free sediment surface, and their sporadic distribution does support the concept of a descent by swimming animals onto the substrate (see above). The direction of movement along the line of symmetry is not clear. Perhaps these were the imprints of the feet, not of vertebrates, but of invertebrates." (pp. 79-80). No further reference to possible invertebrate origin is made. Mention of an isolated print from Askop is noteworthy because the site is described as just above the Whitehill Formation.

Braddy & Briggs (2002), published while this article was at the final editing stage, give a thorough, illustrated, account of Anderson's *Quadrispinichna parvia*, quoting from her thesis at some length. The traces are regarded as resting impressions of a crustacean.

Viljoen (1989), studying the lithostratigraphy of the Laingsburg Formation, under Palaeontology notes: "Anderson (1974) described the trace fossils in the vicinity of Laingsburg." He gives a list of trace fossils, then states: "They usually occur in the thin argillaceous partings between more arenaceous beds (Fig.4)." His Figure 4 (p. 3), has the caption: "*Quadrispinichna parvia* impressions (right) and *Umfolozia longula* trackway (left) in the Laingsburg Formation. Road cutting 2,5 km west of Laingsburg. Lens cap diameter 50 mm." The figure shows four prints, orientated in the same direction, but not constituting a trackway. The photograph was taken *in situ* (Viljoen, pers. comm.) and has excessive contrast. His fold-out Fig. 9, "Composite lectostratotype (Laingsburg) of the Laingsburg Formation", shows the symbol for "Tracks, trails" at only one level, indicated as upward-fining siltstone.

DISCUSSION

Classification and Nomenclature

Implicit in publications such as Kuhn (1958) is the assumption that the rules of zoological nomenclature apply to trace-fossils. Complications were recognized, and a code for the nomenclature of trace-fossils was made quite recently (Sarjeant & Kennedy, 1973; Simpson, 1975). There is general consensus that rules concerning publication of names, and questions of synonymy, should be applied to trace-fossils in the same way as to animals and plants. *Broomichnium permianum* Kuhn 1958, although based on a photograph and without identification of a type specimen, has been regarded as a valid name: It was made known in a publication available for sale to the public, before any other published name for the taxon. *Quadrispinichna*

parvia of Anderson is therefore a junior synonym of *B. permianum*. Anderson's holotype is the same specimen as illustrated by Abel 1935, which formed the basis of Kuhn's taxon. This specimen can now conveniently be regarded as the type specimen of *B. permianum*. Neither *Broomichnium* nor *Quadrispinichna* have been noted in Neave's *Nomenclator Zoologicus* for the appropriate periods.

The prints in the photographs in Abel (1935) and Anderson (1974) are smaller than those in the photographs in Griffiths (1963). Nevertheless the orientation of the inner two elements are similar, and thin distal extensions of these elements are visible in Abel and Anderson and very clear in Griffiths. Groups of larger and smaller prints occur in material from De Puts, Calvinia (Figures 3 and 4 respectively), and in the South African Museum material. Smaller prints often do not show the extensions of the middle two elements, e.g. most of the prints in Figure 4. Large and small prints have not been found together on the same slab. Nevertheless specific distinction is unwarranted at this stage, as the differences in print size may be attributed to sexual dimorphism.

Stratigraphic Implications of the Prints

Ichnologists recognize that the same trace-fossil may be made by different animals, since it represents an activity of an animal, in a specific environment (Sarjeant & Kennedy, 1973; Simpson, 1975). Classification within the zoological framework, if it is possible, is therefore a bonus. Where the trace-fossil is very characteristic, it may represent a single genus or species, in which case it may be of biostratigraphic significance. The presence of this ichnogenus in both the Tierberg Shale Formation and the Laingsburg Formation confirms their chronostratigraphic relationship (depending on the stratigraphic range of *Broomichnium*) and the similarity in environment of deposition. The Laingsburg Formation represents a deep-water fan complex deposited in a basin floor to slope environment of a subsiding foreland basin.



Figure 7. Polished surface of a section of USP 482, imaged by computer scanning. Distance from the top to the print-bearing light layer near the bottom is 25mm.

The Tierberg Formation and its stratigraphic equivalent, the Fort Brown Formation (Southern Karoo), both represent predominantly suspension deposition which "host" the deep-water fan complexes of the southwestern Karoo Basin (Wickens, 1984, 1994).

Palaeoenvironment and Palaeoecology of *Broomichnium*

The main slab from Franschhoek (USP 414) has a hard, coherent lower surface, which contrasts somewhat with a flaky upper surface. The only slab which had some adherent material on both upper and lower surfaces, the slab of unknown provenance (USP 482), was found to have a sharp change to a more arenaceous composition at the point which marked the undersurface on which the prints, and crustacean traces, were found (Figure 7). A section of USP 414 showed its undersurface to be similar to this layer. This suggests that prints made in a muddy substrate were rapidly covered with material which, after lithification, provided a surface which survived erosion better than the material below, producing a hyporelief (natural cast). This is somewhat similar to the situation seen in a varvite (e.g. Savage 1970, 1971), as was evident from sections of adherent varves in the region of tracks (invertebrates and fish). Prints from both the Tierberg Shale Formation and the varvites of the Mbizane Formation were made subaqueously, and hence with little gravitational pressure. A relatively quiet, deep water setting dominated by suspension deposition of clay and silt, is visualized. Sarjeant & Leonardi (1987) discuss the relationships between substrate and footprints (p.53), but there are no prints appropriate to the Tierberg indicated.

Trace-fossils from the Tierberg Formation are common on the slabs at Franschhoek, at the quarry at De Puts and on paving slabs in the town of Calvinia. However *Broomichnium* is relatively rare. This supports the idea that it was a swimming animal, rarely touching the bottom, a suggestion already made by Anderson. If *Broomichnium* is a tetrapod, as is suggested by the resemblance of the prints to footprints of an animal with diverging toes, it would almost certainly have had lungs. An excursion of an air-breathing amphibian or reptile of small size to a level below wave base would appear to be remarkable, but lungs in small aquatic tetrapods are often as much used as hydrostatic organs as for oxygenation of the blood. *Broomichnium* could well have been an animal of more or less neutral buoyancy at the levels at which the prints were made, making rare contact with the substrate. It must also be borne in mind that with increasing depth lung volume would decrease, which might cause unintended sinking to the bottom. A current may cause animals near the bottom to drift to one side as they moved, which may account for orientation of prints in a common general direction. There is also a tendency of many aquatic animals to sense currents, and often to orientate against them.

SUMMARY AND CONCLUSIONS

Trace fossils, attributed to tetrapods, are here recorded from De Puts, which is, like the first recorded site, Zak River, in the Tierberg Shale Formation. Some similar trace fossils are known from Laingsburg and, seemingly site records only, from Ecca Pass, in the Eastern Cape. At both these localities the traces are reported from deep-water fan deposits, namely the Laingsburg and Ripon Formations.

The valid name for the taxon, based on publication priority, is *Broomichnium permianum*. The specimen slab on which the taxon is based is identified as SAM-PK 3547 in the South African Museum, which is here designated the lectotype.

The prints appear to fall into two size classes, *Broomichnium permianum* being based on specimens in the smaller size class. The two size classes have not been found together on a slab, but occur at both Tierberg sites, and may indicate sexual dimorphism.

The trace fossils are consistent with the interpretation that they were made on a firm muddy to silty subaqueous surface by tetrapods in water depths below the level of wave action, i.e., below storm wave base. The animals made contact with the substrate without producing trackways, leaving prints which were preserved when covered by a layer of less fine sediments.

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REFERENCES

ABEL, O. 1935. *Vorzeitliche Lebensspuren.* Jena, Gustav Fischer Verlag.

ANDERSON, A. M. 1974. *Arthropod Trackways and Other Trace Fossils From the Early Permian Lower Karroo Beds of South Africa.* Unpublished Ph.D. Thesis, University of Witwatersrand, Johannesburg.

BRADDY, S.J. & BRIGGS, D.E.G. 2002. New Lower Permian nonmarine arthropod trace fossils from New Mexico and South Africa. *Journal of Paleontology* **76:** 546-557.

COLE, D. I., SMITH, R. M. H. & WICKENS, H. deV. 1990. Basal-plain to fluvio-lacustrine deposits in the Permian Ecca and Lower Beaufort Groups of the Karoo Sequence. *Guidebook Geocongress '90 Geological Society of South Africa,* PO2: 1-83.

ESTES, R. & REIG, O. A. 1973. The Early Fossil Record of Frogs A review of the evidence. **In:** Vial, J. L. (ed.), *Evolutionary Biology of the Anurans*. Columbia, University of Missouri Press.

GRIFFITHS, I. 1963. The phylogeny of the Salientia. *Biological Reviews* **38,** 241-292.

HAUBOLD, H. 1971. Teil 18 Ichnia Amphibiorum et Reptilium fossilium. **In:** O. Kuhn (ed.), *Handbuch der Paläoherpetologie*, Stuttgart, Gustav Fischer Verlag.

HAUBOLD, H. 1974. *Die Fossilen Saurierfährten.* Wittenberg Lutherstadt, A. Ziemsen Verlag.

HAUBOLD, H. 1984. *Saurierfährten, 2., Erweiterte Auflage.* Wittenberg Lutherstadt, A Ziemsen Verlag.

HAUGHTON, S. H. 1919. A review of the reptilian fauna of the Karroo System of South Africa. *Transactions of the geological Society of South Africa* **22,** 1-25.

HAUGHTON, S.H. 1925. Exhibit: - Tracks of animals preserved in the Ecca Shales of the Cape Province. *Transactions of the royal Society of South Africa* **13,** xxviii-xxix.

HAUGHTON, S.H. 1928. *The geology of the country between Grahamstown and Port Elizabeth.* Explanatory Notes to Cape Sheet 9, Geological Survey, Dept. of Mining, South Africa.

HAUGHTON, S.H. 1929. Ecca Series, **In:** Rogers, A.W., Hall, A.L., Wagner, P.A. & Haughton, S.H. (eds), *Handbuch der Regionalen Geologie VII. Band. 7a Abteilung. The Union of South Africa*, 131-132 Heidelberg, Carl Winters Universitätsbuchhandlung.

ISHIGAKI, S. & FUJISAKI, T. 1989. Three dimensional representation of *Eubrontes* by the method of Moiré Topography, **In:** Gillette, D.D. & Lockley, M.G. (eds.), *Dinosaur Tracks and Traces*, 421-425 Cambridge, Cambridge University Press.

KUHN, O. 1958. *Die Fährten der Vorzeitlichen Amphibien und Reptilien.* Bamberg, Meisenbach KG.

KUHN, O. 1963. Pars 101 Ichnia tetrapodorum **In:** Westphal, F. (ed.), *Fossilium Catalogus 1: Animalia*. Gravenhage, W. Junk.

LEONARDI, G. (ed.) 1987. *Glossary and Manual of Tetrapod Footprint Palaeoichnology.* Brasília, República Federativa do Brasil, Ministério das Minas e Energia, Departmento Nacional da Produção Mineral.

SARJEANT, W.A.S. & KENNEDY, W.J. 1973. Proposal of a Code for the Nomenclature of Trace-Fossils. *Canadian Journal of Earth Sciences* **10:** 460-475.

SARJEANT, W.A.S. & LEONARDI, G. 1987. Substrate and footprints. **In:** Leonardi, G. (ed.), *Glossary and Manual of Tetrapod Footprint Palaeoichnology*, p. 53. Brasília, Repúblic Federativa do Brasil, Ministério das Minas e Energia, Departmento Nacional da Produção Mineral.

SAVAGE, N.M. 1970 A preliminary note on arthropod trace fossils from the Dwyka Series in Natal. **In:** Haughton, S.H. (ed.), *Proceedings and Papers, Second Gondwana Symposium South Africa, 1970 Proceedings and Papers*: 627-635. Pretoria, Council for Scientific and Industrial Research.

SAVAGE, N.M. 1971. A varvite ichnocoenosis from the Dwyka Series of Natal. *Lethaia* **4:** 217-233.

SIMPSON, S. 1975. Classification of trace fossils **In:** R.W.Frey (ed.), *The Study of Trace Fossils*, 39-54. Berlin, Springer-Verlag.

THERON, A.C. 1967. *The Sedimentology of the Koup Subgroup Near Laingsburg.* Unpublished M.Sc. Thesis, University of Stellenbosch.

VILJOEN, J. H. A. 1989. Lithostratigraphy of the Laingsburg Formation (Ecca Group). *South African Committee for Stratigraphy Lithostratigraphy Series* **No. 20:** 7pp + fold-out.

WICKENS, H. de V. 1984. *Die Stratigrafie en Sedimentologie van die Groep Ecca Wes van Sutherland.* Unpublished M.Sc. Thesis, University of Port Elizabeth.

WICKENS, H. de V. 1994. *Basin Floor Fan Building Turbidites of the Southwestern Karoo Basin, Permian Ecca Group, South Africa.* Unpublished Ph.D. Thesis, University of Port Elizabeth.