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A DICYNODONT TRACKWAY FROM THE *CISTECEPHALUS* ASSEMBLAGE ZONE IN THE KAROO, EAST OF GRAAFF-REINET, SOUTH AFRICA.

by

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ABSTRACT

This paper reports a partially exposed late Permian palaeosurface with preserved vertebrate tracks at the "Asante Sana" private game reserve in the vicinity of Petersburg, 46km east of Graaff-Reinet. Excavation of the palaeosurface over an area of 34m^2 revealed clear footprints and trackways of six large tetrapods that walked in a westerly direction across a semi-consolidated muddy substrate in the distal floodplain area of a large fluvial system. Clear heteropodous impressions of the footpads and individual toes and claws are preserved as concave epirelief moulds. It is concluded that these fossil tracks were made by a group of therapsids, specifically a group of large dicynodonts, possibly *Aulacephalodon*. The tracks are here assigned to the ichnospecies *Dicynodontipus icelsi* sp. nov. A continuous trackway and numerous less distinct individual prints and markings made by smaller tetrapods are also preserved on the palaeosurface. It is probable that these tracks were left by *Diictodon*, a small common dicynodont of the time.

KEYWORDS: Karoo Basin, palaeoichnology; Late Permian; footprints; trackway; therapsid; dicynodont; *Dicynodontipus icelsi*; *Aulacephalodon*; *Diictodon*.

INTRODUCTION

In September 1998 Mr I.C. Els, a farmer and contract road builder, discovered fossil footprints on a palaeosurface on the farm Buffels Hoek (368) which forms part of the game farm "Asante Sana" in the Graaff-Reinet District of the Eastern Cape, South Africa. Further excavation, removing at least six tons of mudrock overburden, was undertaken during 1999 (Figure 1). During the early stages of excavation it was recognized that, once exposed, the palaeosurface was susceptible to rapid weathering and deterioration which effectively destroyed surface and trace fossil detail. Various binding and hardening compounds were used with varying degrees of success. Because of the susceptibility to rapid weathering, it was decided that only a sample area of the surface would be excavated for mapping and detailed investigation. Ultimately an area of 34m^2 was cleaned for this purpose. As an added conservation precaution, three run-off deflection barriers were constructed with a bulldozer up-slope of the palaeosurface to prevent further erosion during rainy periods.

Figure 1. Overview of the exposed Asante Sana palaeosurface looking west.

The palaeosurface extends beneath mudrock cover (between 10 and 150cm thick), to the south and east of the exposed surface. Conservatively, the unexposed palaeosurface is estimated to cover an area of c. 1200m². This estimate was obtained by noting the extent of small windows of exposed palaeosurface that are seen in shallow erosion gullies where the mudrock cover has been removed.

This palaeosurface and its associated trace fossils were first reported by De Klerk (2000) and De Klerk, Fourie & Bangay (2000). Detailed mapping of the palaeosurface (Figure 2) clearly shows the trackways of six large animals and that of a single small animal (Figure 3). In addition, numerous indistinct small tracks without any clearly recognizable continuity are evident on many parts of the palaeosurface.

Overview of trackways from the Beaufort Group: 1880 - 1993

Therapsid trackways of the Late Permian Beaufort Group in the South African Karoo are rare, which is surprising in view of the abundance of therapsid fossils that have been collected from these sediments over the past 160+ years (Smith 1993). The paucity of vertebrate trace fossils in these sediments is even more anomalous if one considers the abundant and diverse fauna that existed at the time and the nature of the fluvial sedimentary environment, that could well have regularly provided ideal conditions for their preservation

The first brief mention of tetrapod tracks in the Karoo was by Holub (1881) and they were later described by Seeley (1904). He reported footprints preserved on a

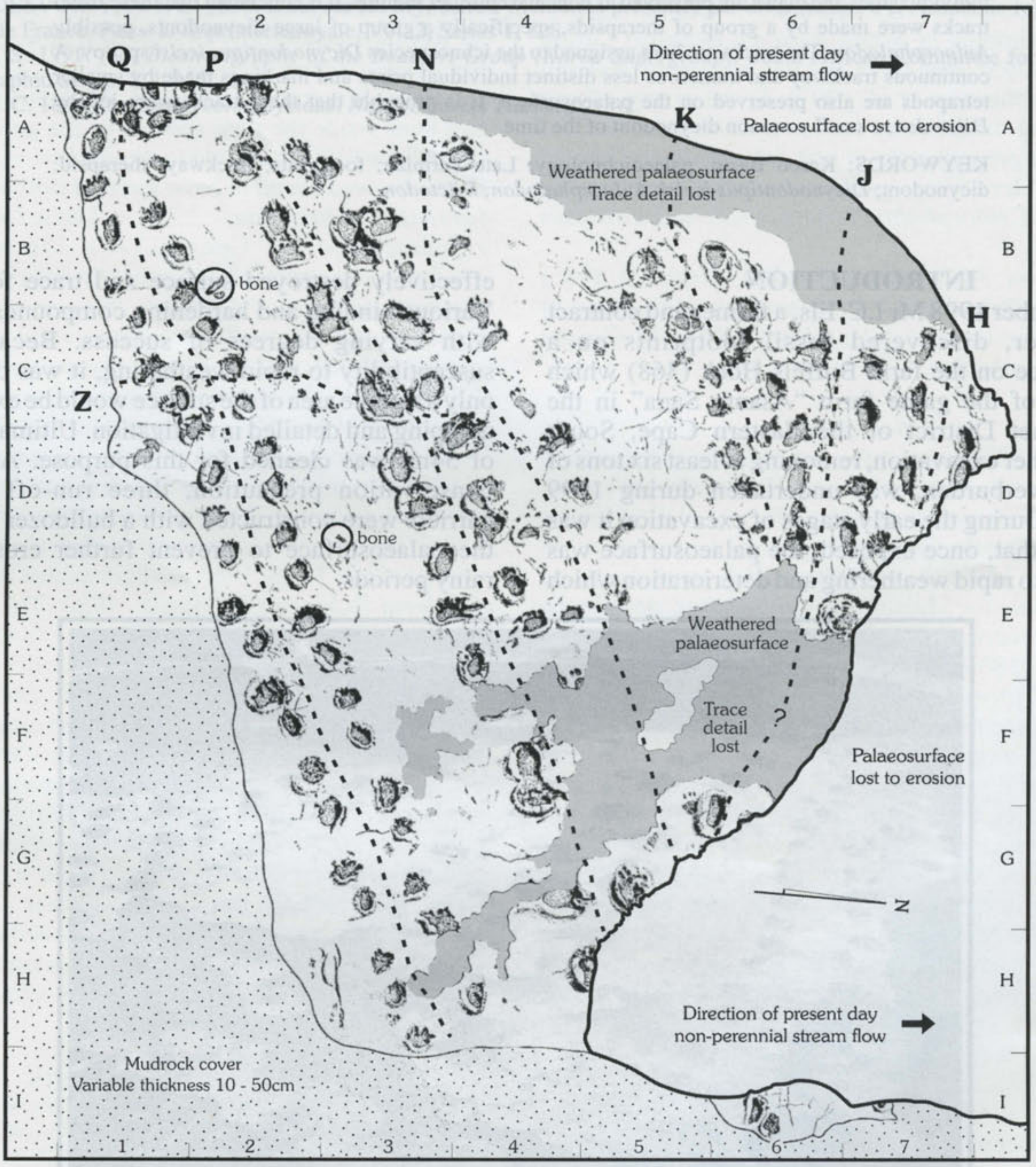

Figure 2 Detailed map of the Asante Sana palaeosurface showing distribution of all footprints and traces; position of the midline for each trackway; and positions of fossil bone (grid lines = 1m).

Figure 3 Part of trackway **Z** thought to have been produced by the small dicynodont *Diictodon*.

small slab of rock that had been accessioned by the palaeontological museum of the University of Munich in 1880. A cast of this trace fossil was prepared for study by Seeley and then stored in the Natural History Museum in London. Seeley (1904) was able to ascertain that the slab had been collected in the Middelburg district of the central Karoo, possibly from the *Dicynodon* or *Lystrosaurus* Assemblage Zone (Rubidge 1995). Seeley noted that footprints of at least three animals of varying size were evident on the slab, with the largest having feet about the size of those of the para-reptile, *Procolophon*, and it is to this genus he provisionally assigned the larger track-maker. He observed that the manual print is slightly smaller and less perfectly preserved than the pedal print, and in both manual and pedal prints "the moderately stout digits terminate bluntly without any indication of terminal claws" (Seeley 1904, p.288). He had no suggestion as to the identity of the trackmaker that produced the smaller footprints where the digits are parallel. Watson (1960) regarded these "*Procolophon*" tracks as having an appearance closer to those of a lizard-like reptile and not a dicynodont, as the fifth digit in both the manual and pedal prints is very long. Recently described dicynodont footprints from Australia (Retallack 1996) bear a remarkable similarity to these prints, however they are attributed to *Lystrosaurus* rather than *Procolophon*.

Watson (1960) reported an additional slab showing six associated prints which he had collected from the Middelburg area "from the summit of the *Cistecephalus* Zone, or the base of the *Lystrosaurus* Zone" (Watson 1960, p.180). These small prints, with an approximate diameter of 24mm, he attributed to being of dicynodont origin, and suggested that they had been made by *Dicynodon* itself. This trackway shows the impressions of right and left manual and pedal prints, all being "five-fingered and five-toed respectively and noticeably different in size, the fore feet being considerably larger than the hind. The animal was clearly plantigrade, the palm of the hand and the sole of the foot showing no continuation of the division into fingers or toes" (Watson 1960, p.180). Of particular note is the presence of a short, discontinuous, 3cm long groove interpreted as a "tail-drag" along the mid-line of the trackway. This feature is unusual, as dicynodonts have short stubby tails carried well above the ground surface and, as far as can be ascertained, no other tail drags have been reported previously.

Vertebrate tracks were reported by Smith (1980) in bank exposures of the Leeu River on the farm Brandewyns Gat (214), midway between Beaufort West and Fraserburg. Here the trackway occurs on a palaeosurface preserved within laminated mudstones and sandstones, representing distal flood-basin deposits. Based on the pace length, degree of overlap between manus and pes and the inward drag of the digits as the hind limb was raised, Smith (1980) initially regarded this "sinuous" gait as that of an amphibian rather than of a reptile. In addition he noted a matted appearance of the palaeosurface and suggested that this texture was of algal origin produced in shallow water conditions. After more detailed analysis and re-evaluation, Smith (1993) convincingly showed that the trackway had been made by the small dicynodont *Diictodon* on a distal crevasse splay surface.

A synapsid trackway on the farm Klipplaat (109), south of Richmond in the central Karoo, was reported by Fountain (1984) in the *Cistecephalus* Assemblage Zone of the Beaufort Group. He described the occurrence of sixty prints forming a continuous trackway 12.6m long in the bed of the Bakensklip River. Unfortunately most of the prints are poorly preserved because of recent water erosion, particularly on the downstream side of the prints, but in some cases the claw impressions were preserved. Fountain (1984) pointed out that the prints were, on average, 15 to 20cm in diameter, with the trackway being c.75cm wide. Fountain suggested that the most likely candidate that made these tracks was the dicynodont *Aulacephalodon baini*.

A trackway ascribed to an adult dinocephalian was reported by De Beer (1986) on the farm Droogvoots Fontein (356 - Gansfontein portion) some 8km north-west of Fraserburg. After further investigation, Smith (1993) reported on this trackway in some detail and pointed out that it occurs on a typical proximal crevasse splay surface which he termed Palaeosurface Type I. He showed that this homopodus animal was slender-toed, with pentadactyl manual and pedal prints of equal size and shape, each print being approximately 25 to 30cm in diameter. Smith (1993) drew attention to the similarity of footprint shapes and progression of the animal to that of the much smaller *Diictodon* trackway from the farm Brandewyns Gat (see above).

Two particularly long trackways extending over a distance of some 66m (39m and 28m respectively), made by relatively large dicynodonts, were discovered on the farm Van Tonders Kraal, east of Murraysburg in the central Karoo (MacRae 1990). These footprints are generally circular to oval in shape, and on average they vary between 25cm and 40cm in diameter. Unfortunately very little print detail, apart from the general impressions, has been preserved and the explanation for this is that the trackways were made sub-aqueously, as the animals walked across a submerged silty surface. As this locality occurs within the *Cistecephalus* Assemblage Zone, MacRae (1990) considered that the most likely track-makers were *Aulacephalodon* or possibly *Rhachiocephalus*.

In addition to the footprints and trackways reported from the Beaufort Group above, purported therapsid tracks with a phalangeal formula of 2-3-3-3-3 have been mentioned by Ellenberger (1970) from the late Triassic Elliot Formation in the Karoo Basin. Some of these prints bear a superficial resemblance to dicynodont prints and are in all cases rather small, having a diameter less than 5cm.

More recently, therapsid footprints of early Triassic age have been reported by Retallack (1996) from the Sydney Basin, Australia. These tracks have been referred to the ichnospecies *Dicynodontipus bellambiensis* and are reported to be very similar to the kinds of tracks thought to be produced by *Lystrosaurus*, a common dicynodont species of the Triassic of South Africa and possibly Australia. "Given the abundance of these species in Early Triassic faunas of low diversity and the occurrence of members of *Lystrosaurus* fauna in Queensland and Antarctica, chances are good that this is indeed a trackway of *Lystrosaurus*" (Retallack, 1996). The approximate width of the manus is 82mm and that of the pes is 65mm, and Retallack (1996) estimates that the track-maker would have had a body length, from forehead to tailtip, of 84cm and would have been some 22cm high. Illustrations of this ichnofossil indicate that the animal was heteropodous with the outer digit (V) of the manus angled outward and the whole manus more divaricate than the pes. These Australian footprint impressions are remarkably similar to those described by Seeley (1904) from South Africa.

From the above overview, it can be seen that the ichnofossil record for large Permian dicynodonts is particularly poor and those tracks that have been ascribed to large dicynodonts (Fountain 1984; MacRae 1990) show a low degree of print detail. The well-preserved palaeosurface with its associated trackways at Asante Sana presents, for the first time, an opportunity to study the subtleties of detail of large dicynodont footprints. The probable track-makers of the three sets of well-preserved trackways have, with a reasonably high degree of confidence, been identified as the dicynodont *Aulacephalodon* (Seeley 1898) and are here referred to a new ichnospecies, *Dicynodontipus icelsi* sp. nov. Based on the detailed work of Smith (1993) on *Diictodon* tracks, it is evident that the smaller trackway and isolated prints on the Asante Sana palaeosurface were made by this small dicynodont. In this account of the Asante Sana palaeosurface and its associated trace fossils, the tetrapod palaeoichnological terminology proposed by Leonardi (1987) has been adhered to throughout.

LOCALITY

The palaeosurface and associated trace fossils occur on the farm Buffels Hoek (368) which now forms part of Asante Sana - a large private game farm development 45 km east of Graaff-Reinet in the Petersburg valley. The fossil site (S32°19.970'; E25°00.745') is located on the south eastern valley floor of the reserve, where the topography is, for the most part, a flat-lying plain with a gentle drainage slope to the north at the foot of the Bouwershoekberge to the south (Figure 4).

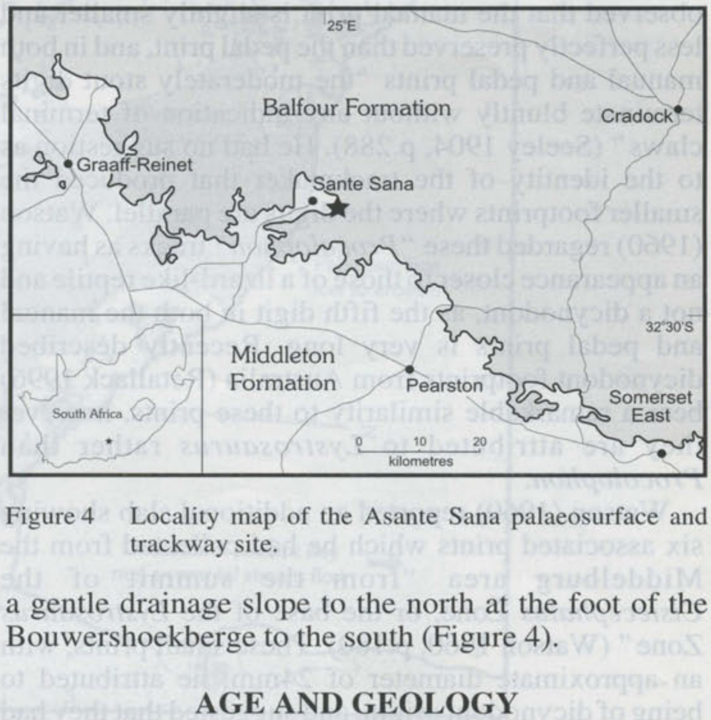

Figure 4 Locality map of the Asante Sana palaeosurface and trackway site.

AGE AND GEOLOGY

The fluvial sediments in which the trace fossils are preserved are of Late Permian age (c. 253Ma) and stratigraphically the palaeosurface is situated in the

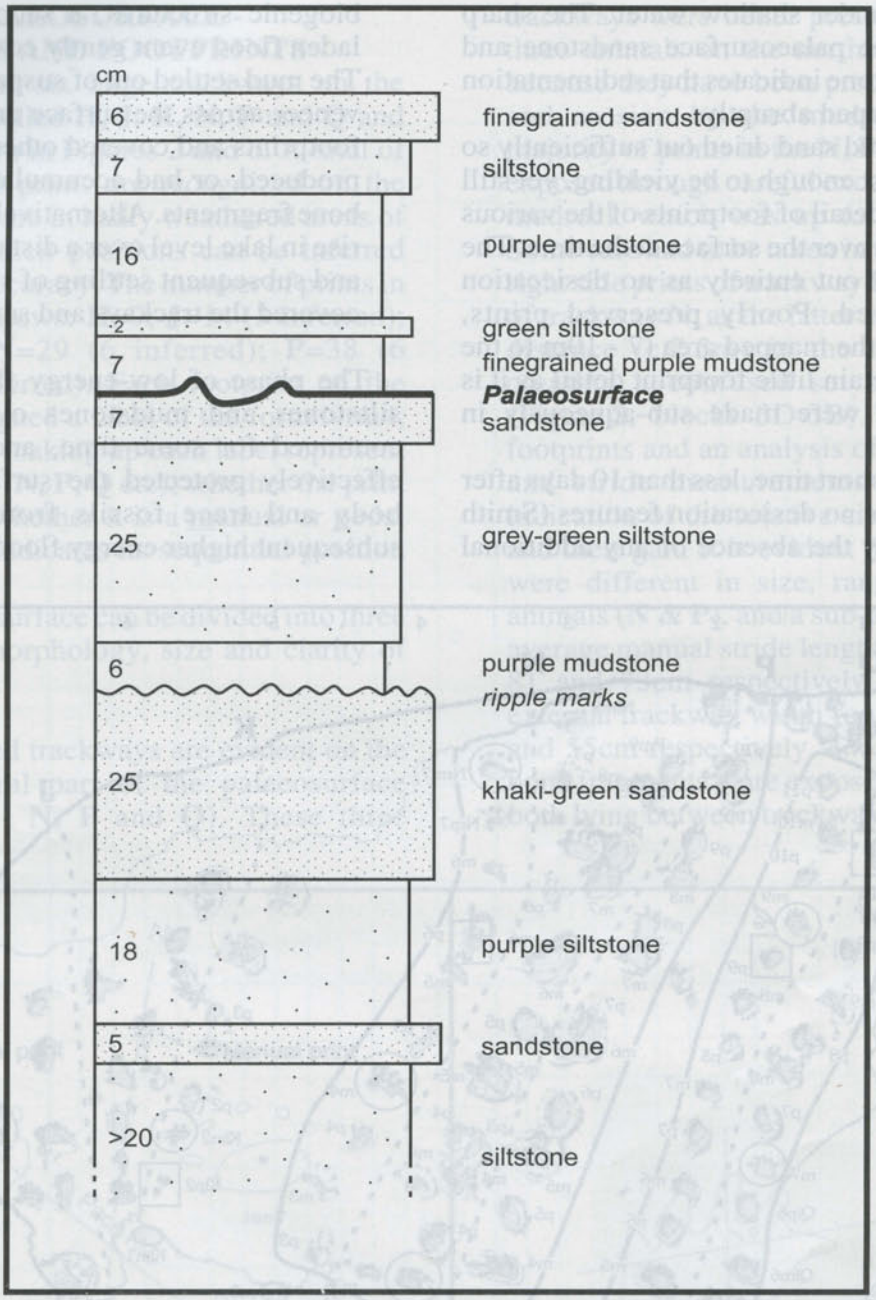

Figure 5 Localized geological log of the sedimentary succession above and below the palaeosurface.

Cistecephalus Assemblage Zone of the Beaufort Group, Karoo Supergroup (Rubidge 1995). These sediments form part of the lower Balfour Formation (Oudeberg Member) of the upper Adelaide Subgroup. Because of the flat-lying nature of the terrain in the general vicinity of the palaeosurface, only limited vertical stratigraphic exposures are available to ascertain the nature of the sediments and the type of environment they represent. The palaeosurface is composed of grey fine-grained sandstone (7cm thick) structured with horizontal lamination, overlain by fine-grained purple mudstone (7cm thick), the lower 5mm of which, and the print infill, have a dark-green colour. These thinly bedded sediments are interpreted as representing overbank flood deposits adjacent to a larger fluvial system (Figure 5). The sedimentary sequence represents a distal floodplain facies which Smith (1993) termed Palaeosurface Type 2 - distal crevasse splay. A small ripple-marked surface of limited extent, five meters to the north of the palaeosurface, is evident at the top of a fine sandstone layer 10cm below the palaeosurface.

Sedimentary Environment and the Preservation of the Palaeosurface.

The sequence of sedimentary events leading to the formation and preservation of the Asante Sana palaeosurface are as follows:

1. During a flood event of a large river system the flood waters breached the levee and fanned out over the floodplain depositing the fine-grained sand as a distal crevasse splay deposit.
2. The flood water subsided, exposing the newly deposited planar-bedded fine grained sand in places. At this stage the sediment would have been

fully-saturated or under shallow water. The sharp contact between the palaeosurface sandstone and the overlying mudstone indicates that sedimentation of the sand had stopped abruptly.

3. In places, the exposed sand dried out sufficiently so that it was still moist enough to be yielding, yet still able to retain good detail of footprints of the various animals that moved over the surface at the time. The surface did not dry out entirely as no desiccation cracks are observed. Poorly preserved prints, exposed outside of the mapped area (7 - 10m to the west of Figure 6) retain little footprint detail as it is apparent that they were made sub-aqueously in shallow water.
4. Within a relatively short time, less than 10 days after exposure if there are no desiccation features (Smith 1993), supported by the absence of any additional biogenic structures, a second, low-energy, mud-laden flood event gently covered the surface again. The mud settled out of suspension, producing a thin veneer across the surface and effectively filled the footprints and covered other features that had been produced, or had accumulated on the surface, e.g. bone fragments. Alternatively there may have been a rise in lake level over a distal crevasse splay surface and subsequent settling of suspended sediment that covered the trackays and surface.

The phase of low-energy flood events, depositing siltstones and mudstones over the palaeosurface, continued for some time, and this series of events effectively protected the surface with its preserved body and trace fossils from being destroyed by subsequent higher energy flood events.

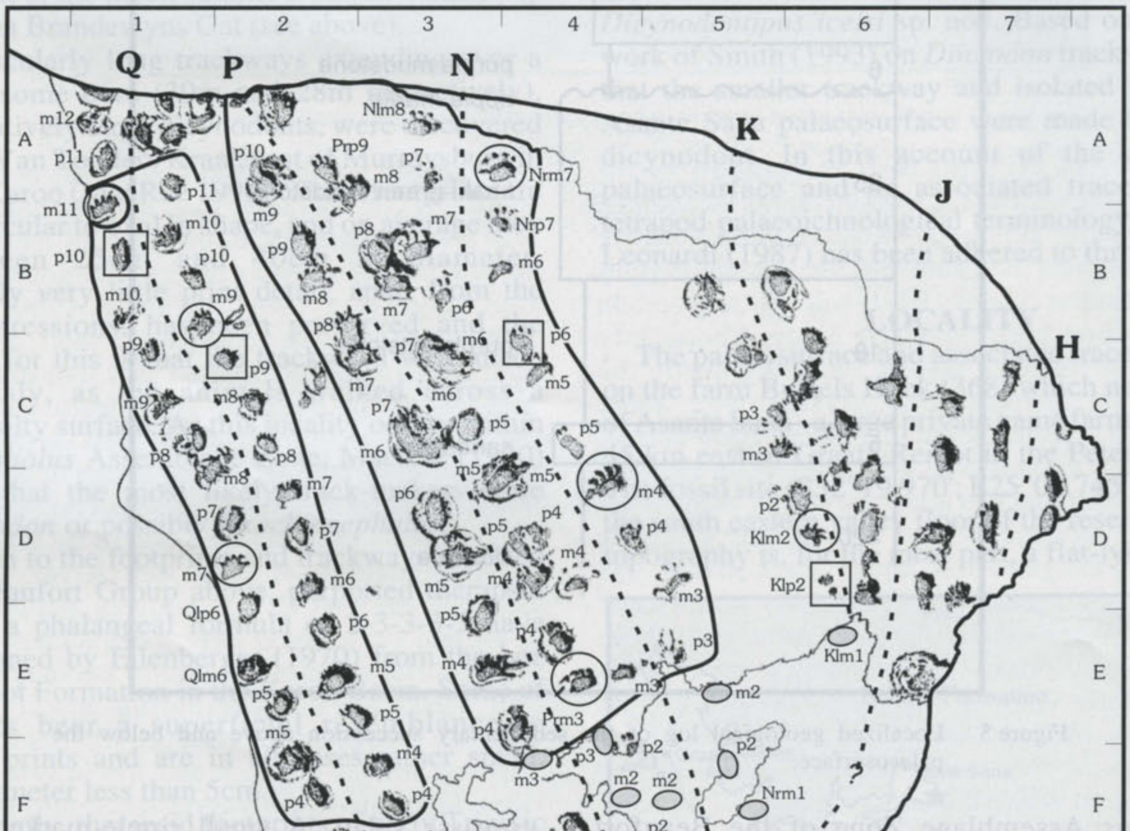

Figure 6 Stylized and annotated map of the palaeosurface showing (a) footprint numbering convention; (b) Position of manual (circles) and pedal prints (squares) used for detailed 3D analysis and ; (c) two large areas, outlined in bold, showing the position of the areas covered by the surface fibreglass casts (grid lines = 1m).

THE PALAEOSURFACE - TRACKWAYS AND FOOTPRINTS

For convenience, the six large trackways on the palaeosurface were labelled **H, J, K, N, P** and **Q** and their midlines are shown in Figures 2 and 6. A total of 158 manual and pedal prints are recognized on the surface and of these 17 are in badly weathered areas of the palaeosurface but their positions can be inferred with a good degree of accuracy. The number of prints in each trackway is as follows: **H**=9; **J**=14 (3 inferred); **K**=21 (1 inferred); **N**=29 (6 inferred); **P**=38 (6 inferred); **Q**=47 (1 inferred). Each footprint on the palaeosurface was assigned a label of the form Nrm4, Qlp9, etc; the elements making up each label represent the particular trackway (**N, P, Q** etc); whether the print is of the left or right; whether it is a manual or pedal print; and the number indicates its sequential position from east to west.

Tracks on the palaeosurface can be divided into three types based on their morphology, size and clarity of print detail, as follows:

1. Three well-preserved trackways are evident on the southern and central part of the palaeosurface (Figures 2 and 6 - **N, P** and **Q**). These three trackways were better preserved than those of the three animals on the northern edge (**H, J** and **K**) because they have been protected from weathering and erosion by the mudrock overburden. The majority of prints in the **N, P** and **Q** trackways were exposed through careful excavation of the overlying mudrock which was up to 50cm thick in places. Some care had to be taken in the interpretation of the right side prints of trackway **P** and the left side prints of trackway **N**, as the latter animal walked for some distance (c.2.5m) in the right footprints of **P**, creating a confused set of interference prints (Figure 2, blocks 3D-3B). Size variation of the footprints and an analysis of pace, pace-angulation and stride measurements (Figure 7) gives an indication of the relative sizes of the track-makers and their gait. It is evident that these three animals were different in size, ranging from large adult animals (**N & P**), and a sub-adult/juvenile (**Q**), with average manual stride lengths for **N, P** and **Q** of 88, 81 and 73cm respectively (Table 1). The mean external trackway width for these animals is 71, 68 and 55cm respectively. Two well-preserved fossil bone fragments were exposed on the palaeosurface, both lying between trackways **P** and **Q** (Figures 2, 5

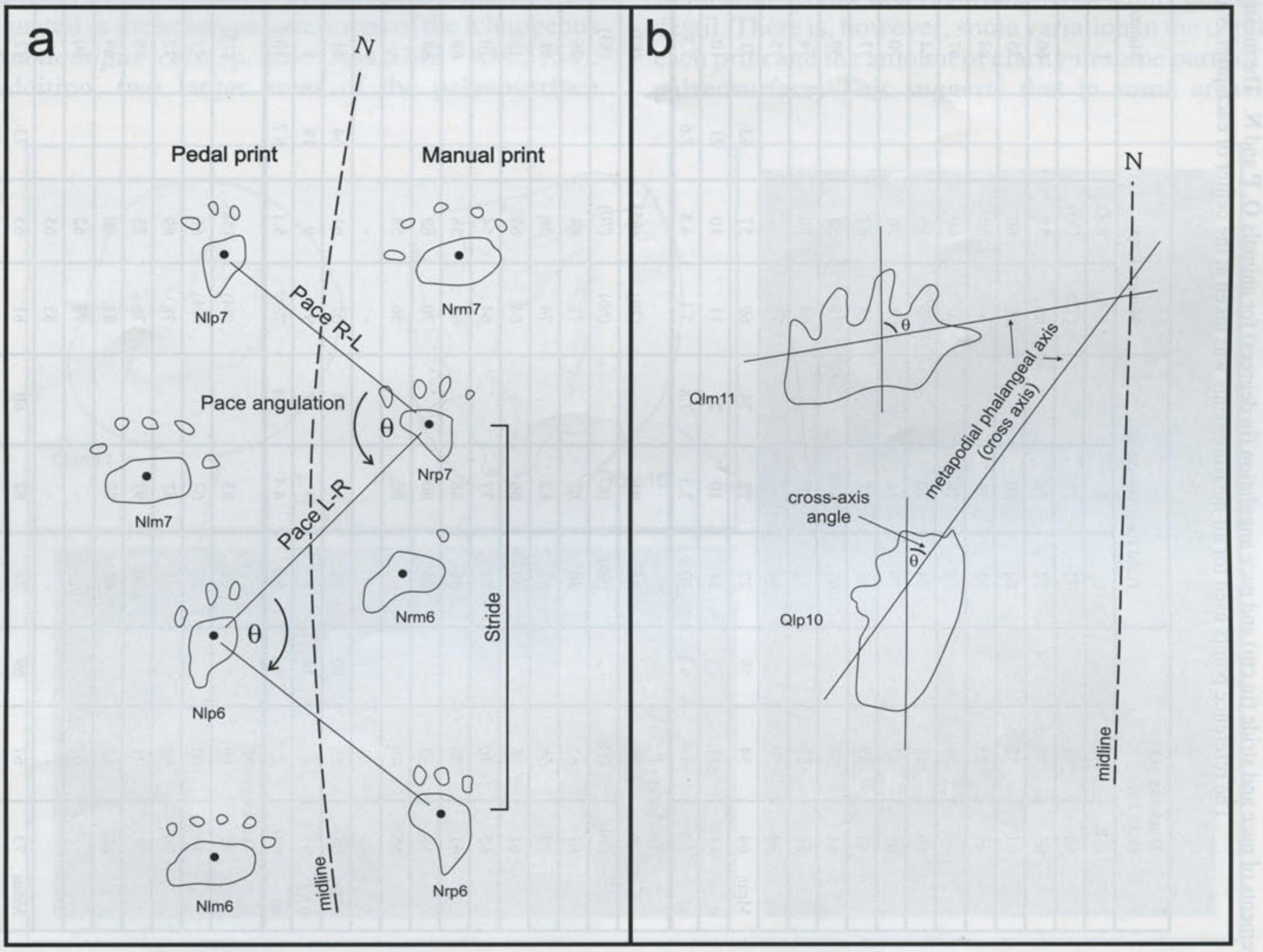

Figure 7 a) Sketch describing pace, pace angulation and stride (Nos. 18, 24 and 16 in Leonardi, 1987).
b) Sketch showing the Metapodial-phalangeal axis (Cross axis) and the Cross-axis angle (Nos. 35 and 57 in Leonardi, 1987).

TABLE 1.

Measurements of pace and stride (in cm) and pace angulation (in degrees) for animals **Q**, **P** and **N**. The mean and sample standard deviation are also given for each set of trackway measurements. The reference points used for all measurements was taken at the center of each print. Values in parentheses indicate the use of estimated print positions.

	Pedal Pace			Pedal Pace Angulation			Manual Pace			Manual Pace Angulation			Pedal Stride			Manual Stride		
	L-R	R-L		L	R		L-R	R-L		L	R		L	R		L	R	
Trackway - Q																		
	66	62		62	77		(72)	(55)		-	(67)		77	65		71	(66)	
	65	58		52	78		66	55		66	79		77	80		77	77	
	67	58		84	80		70	60		75	80		78	83		84	84	
	65	53		73	75		66	60		84	70		73	70		72	71	
	64	54		74	79		67	60		67	65		76	71		73	72	
	66	55		74	70		75	56		64	72		66	73		79	73	
	61	47		79	73		68	56		70	73		66	69		75	70	
	63	49		86	77		58	67		77	54		72	70		56	69	
	61	53		67	81		73	52		59	73		76	64		76	70	
	64	55		75	76		64	50		74	91		72	73		82	78	
	59	50		64	-		75	-		75	75		-	58		63	-	
Mean	64	54	59	72	77	74	69	57	63	71	73	72	73	71	72	73	73	73
n	11	11	22	11	10	21	11	10	21	10	11	21	10	11	21	11	10	21
sd	2.5	4.4	6.1	10.0	3.3	7.8	5.1	4.8	7.6	7.3	9.9	8.5	4.4	7.0	16.6	8.1	5.3	6.7
Trackway - P																		
	69	56		94	91		(79)	(65)		(82)	(79)		88	(90)		84	(88)	
	(70)	(58)		(90)	(87)		(66)	(70)		(83)	(74)		88	(85)		83	(94)	
	61	65		80	87		71	64		76	74		88	89		81	83	
	73	56		82	82		74	56		81	83		84	76		88	76	
	61	66		90	86		64	63		101	87		85	92		88	96	
	65	46		73	77		64	54		70	81		66	79		78	68	
	61	58		86	88		61	58		68	67		84	79		65	73	
	58	55		83	80		70	63		84	73		73	74		78	79	
	55	40		-	86		56	58		-	76		65	83		70	-	
	-	-		-	-		-	-		-	-		69	-		-	-	
Mean	64	56	60	85	85	85	67	61	64	81	77	79	79	83	81	79	82	81
n	9	9	18	8	9	17	9	9	18	8	9	17	10	9	19	9	8	17
sd	6.0	8.2	8.1	6.7	4.4	5.4	7.0	5.1	6.7	10.2	6.0	8.2	9.6	6.4	8.3	7.8	10.0	8.5
Trackway - N																		
	77	69		78	83		(84)	(58)		(73)	(68)		94	89		(83)	(88)	
	74	63		84	67		(84)	66		77	82		78	91		(100)	(89)	
	76	68		71	82		78	69		72	61		95	91		75	86	
	71	71		70	92		76	75		78	79		99	83		96	99	
	66	66		84	87		81	60		69	77		89	81		90	80	
	-	63		-	-		79	62		60	63		-	89		91	74	
	-	-		-	-		83	65		-	75		-	-		90	-	
Mean	73	67	69	77	82	80	81	65	73	72	72	72	91	87	89	89	86	88
n	5	6	11	5	5	10	7	7	14	6	7	13	5	6	11	7	6	13
sd	4.4	3.3	4.8	6.8	9.4	8.1	3.1	5.8	9.3	6.5	8.2	7.2	8.1	4.3	6.2	8.2	8.5	8.2

and 9). The larger bone fragment adjacent to Qrm9 (Figure 9) was identified as a partial dicynodont lower jaw.

2. The three sets of less distinct tracks, **H, J** and **K** on the northern edge of the palaeosurface, appear to have been made by the same types of animals, but a high percentage of the surface detail has been lost to weathering and erosion. Only the left side prints of trackway **K** are sufficiently well-preserved for detailed analysis. Nevertheless it was possible to extrapolate a mean external trackway width of 44, 56 and 47cm for trackways **H, J** and **K** respectively.
3. In addition to the footprints of the larger animals, there are numerous smaller prints on parts of the palaeosurface. These are preserved as a discontinuous trackway (**Z**) and as isolated footprints and other traces found predominantly between trackways **N** and **K** (Figure 3).

From the 158 exposed footprints of the large animals, a sample of the best-preserved and representative prints was selected for detailed study, including eight manual and five pedal prints. In each case, plaster casts of the prints and immediate surrounding palaeosurface were prepared and reproduced in fibreglass. The positions of these selected prints are shown in Figure 6 and are here designated as the holotype specimens of the ichnogenus *Dicynodontipus icelsi* sp. nov. (AM.5742 - AM.5754). In addition, two larger areas of the palaeosurface (Figure 6) were reproduced in fibreglass (using robust burlap/hessian and latex-rubber peels). These casts are on permanent display in the Rhodes University Geology Department and the Albany Museum, Grahamstown (AM.5755 and AM.5756).

The 13 fibreglass models were laser scanned at Fort Hare University Computer Science Department using a Minolta Vl-700 Non-Contact 3D Digitizer to produce three-dimensional meshes. The raw data for the 13 prints were cleaned up using 3D Studio Max (R3) software and these were then visualized as contour maps and as artificially lit, shaded 3D surfaces. The MAX images were manipulated and orientated to obtain the best light and view-point orientation such that good 3D effects were obtained for the images. The following types of images were produced for each of the 13 prints: raw digitized data (.vvd files); 3-D wire mesh images (.wrl files); 3-D images showing "best view-point and light orientation" (.jpg files - see Figures 10 - 12); monochrome contour maps, at both 1mm and 2mm contour intervals (.gif files - illustrated in Figures 8 - 13).

Substrate

For the most part the substrate, at the time that the prints were made, was of an even consistency and all sequential prints are recorded with some degree of detail. There is, however, some variation in the depth of each print and the amount of clarity in some parts of the palaeosurface. This suggests that in some areas the

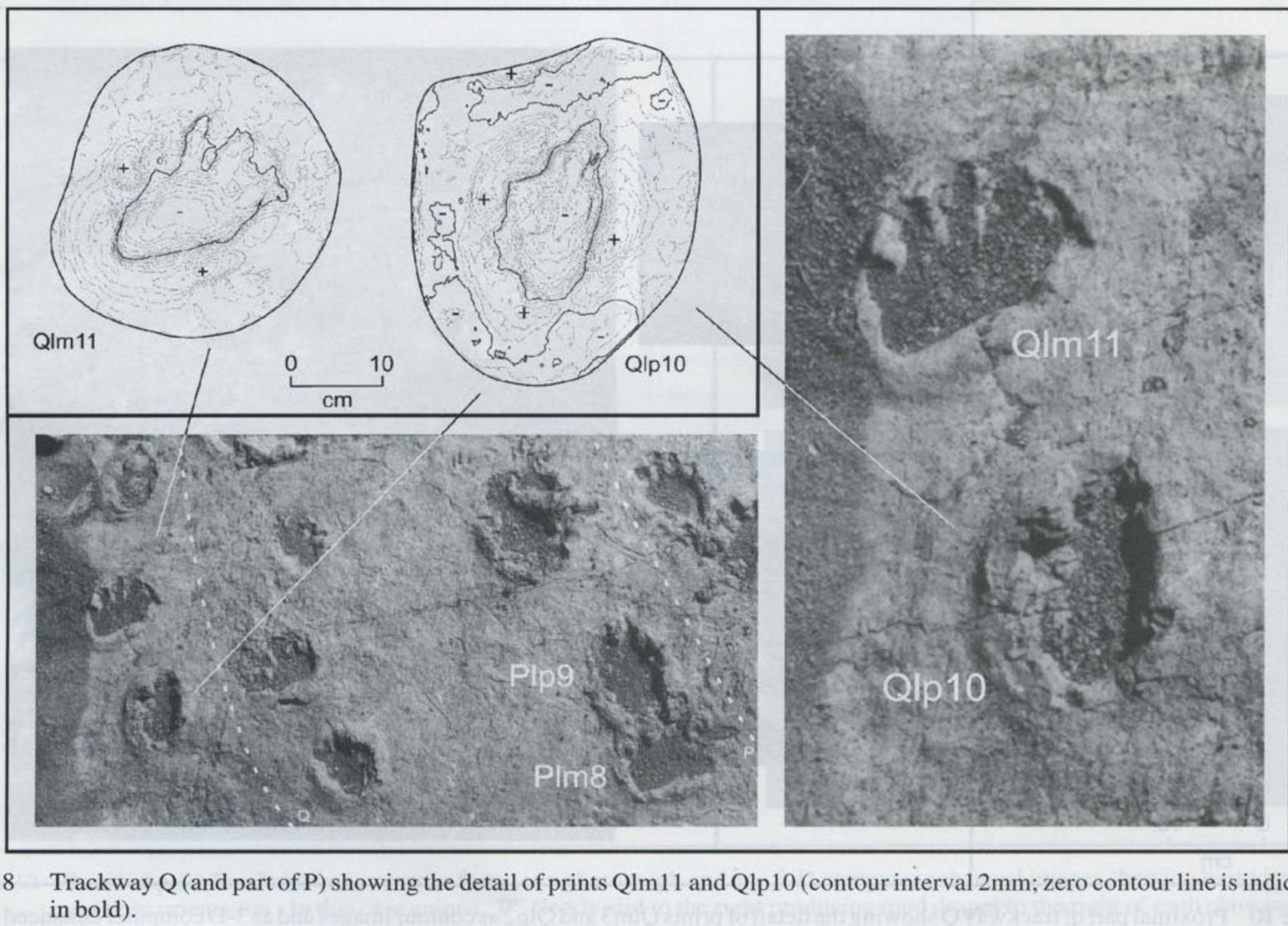

Figure 8 Trackway Q (and part of P) showing the detail of prints Qlm11 and Qlp10 (contour interval 2mm; zero contour line is indicated in bold).

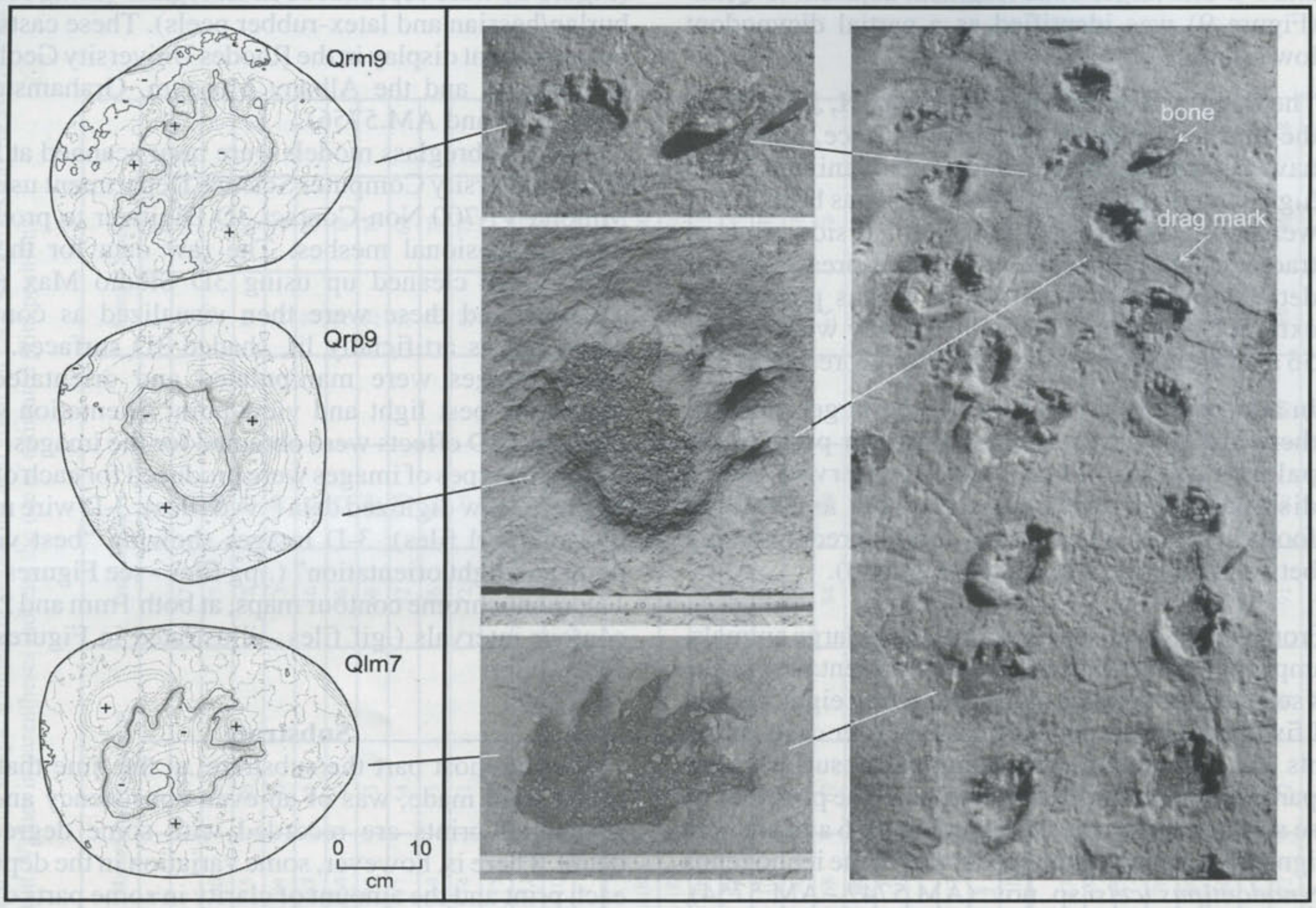

Figure 9 Trackway Q showing the detail of prints Qrm9, Qrp9 and Qlm7. Note the partial dicynodont lower jaw adjacent to print Qrm9 (contour interval 2mm; zero contour line is indicated in bold).

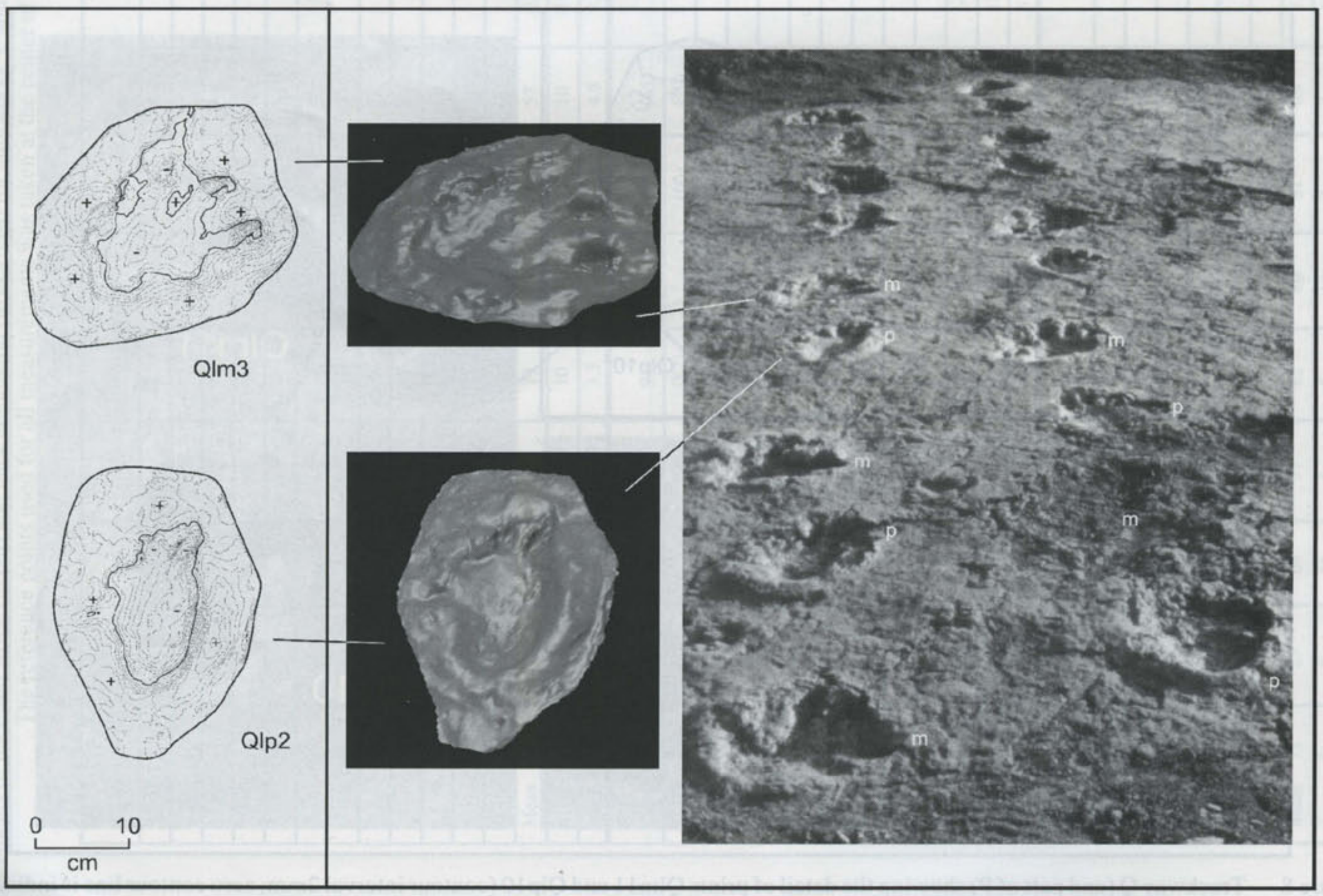

Figure 10 Proximal part of trackway Q showing the detail of prints Qlm3 and Qlp2 as contour images and as 3-D computer enhanced images showing best view-point and light orientation (contour interval 2mm; zero contour line is indicated in bold).

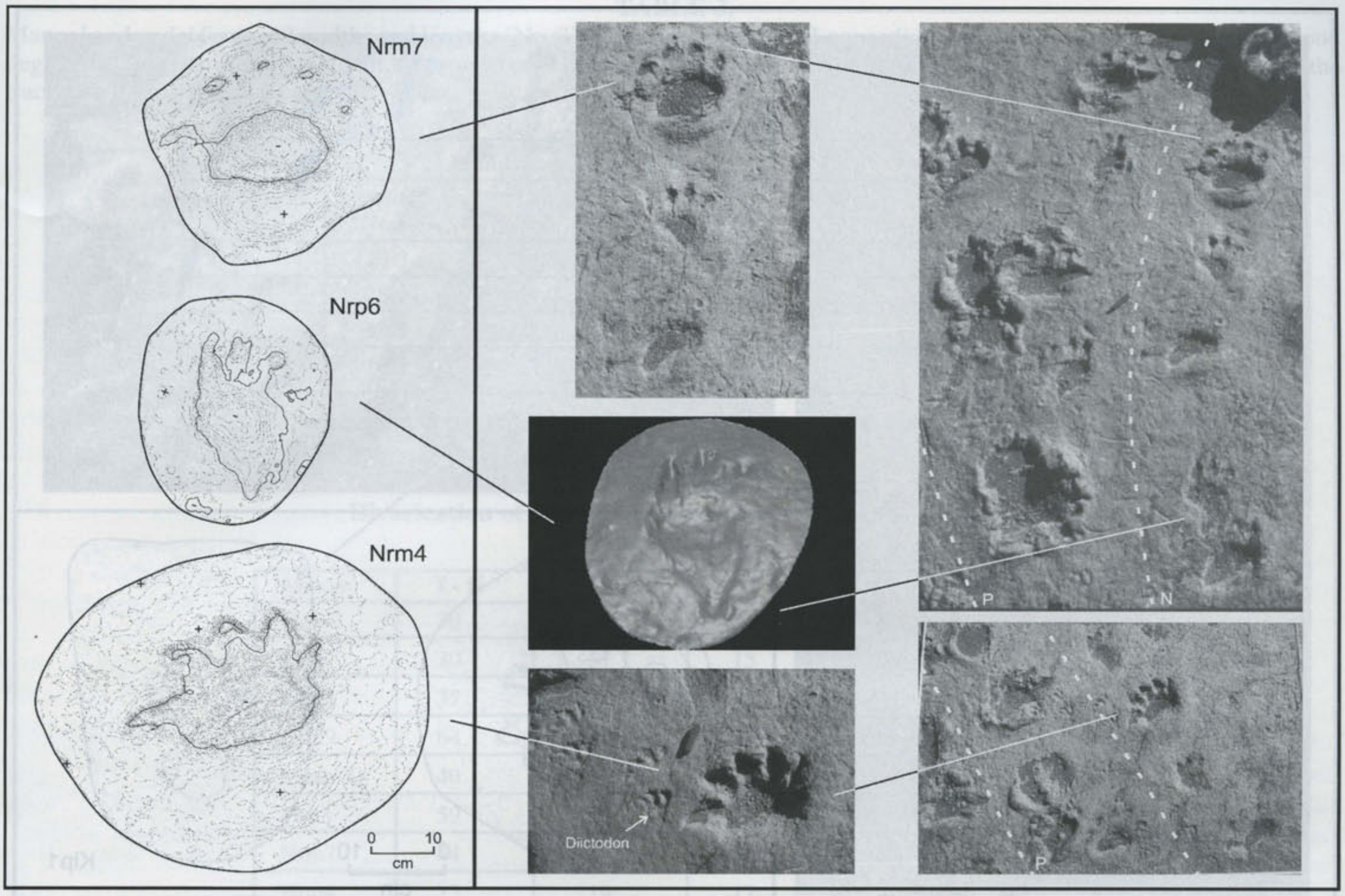

Figure 11 Distal part of trackway "N" showing the detail of prints Nrm7, Nrp6 and Nrm4. A 3-D computer enhanced image of Nrp6 shows best view-point and light orientation (contour interval 2mm; zero contour line is indicated in bold).

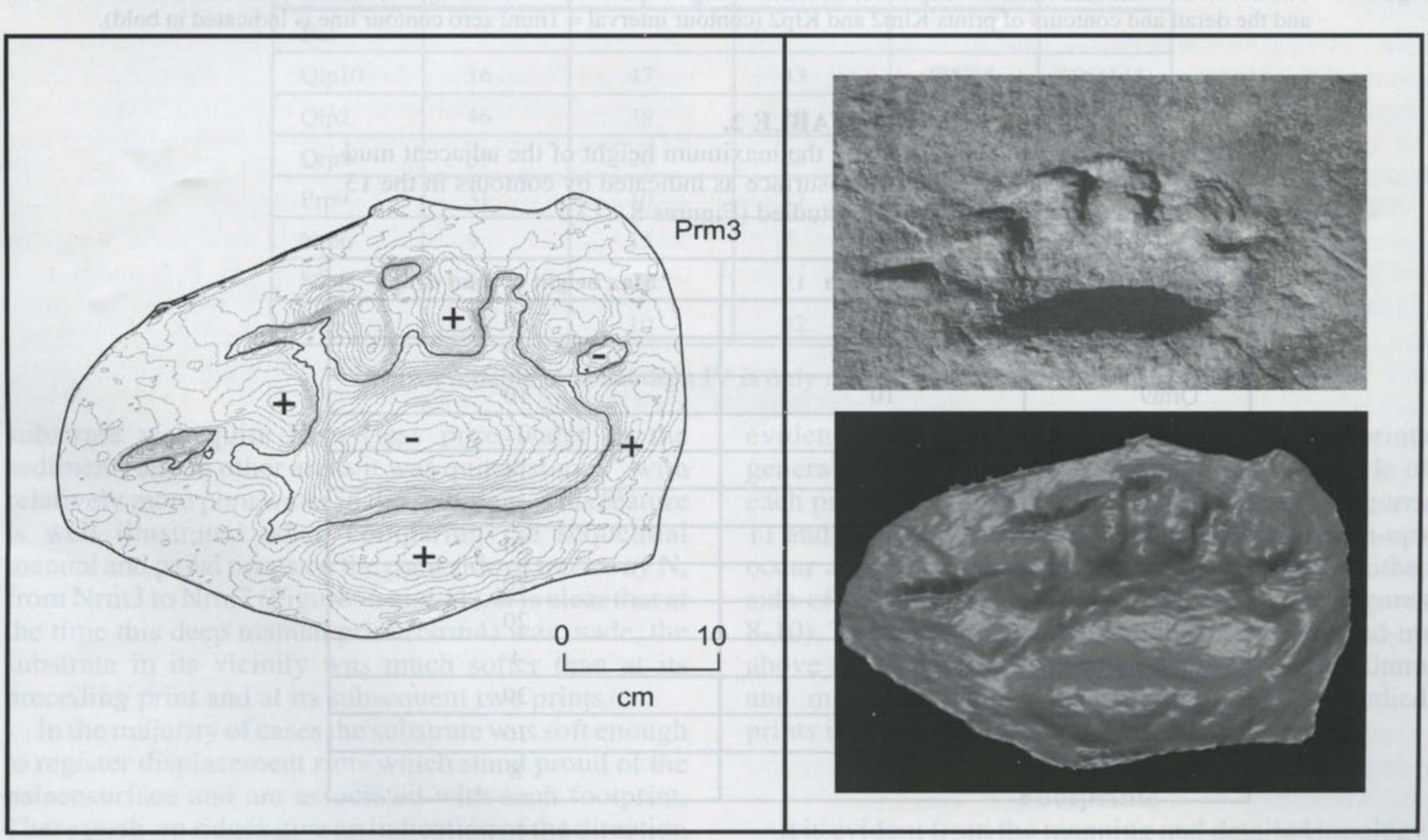

Figure 12 Detail of print Prm3 shown in contour form, as a photograph and as a 3-D computer enhanced images showing best view-point and light orientation . In this case animal "P" clearly slid to the right producing mud drapes to the right of each claw and to the rear and right of the foot pad (contour interval 2mm; zero contour line is indicated in bold).

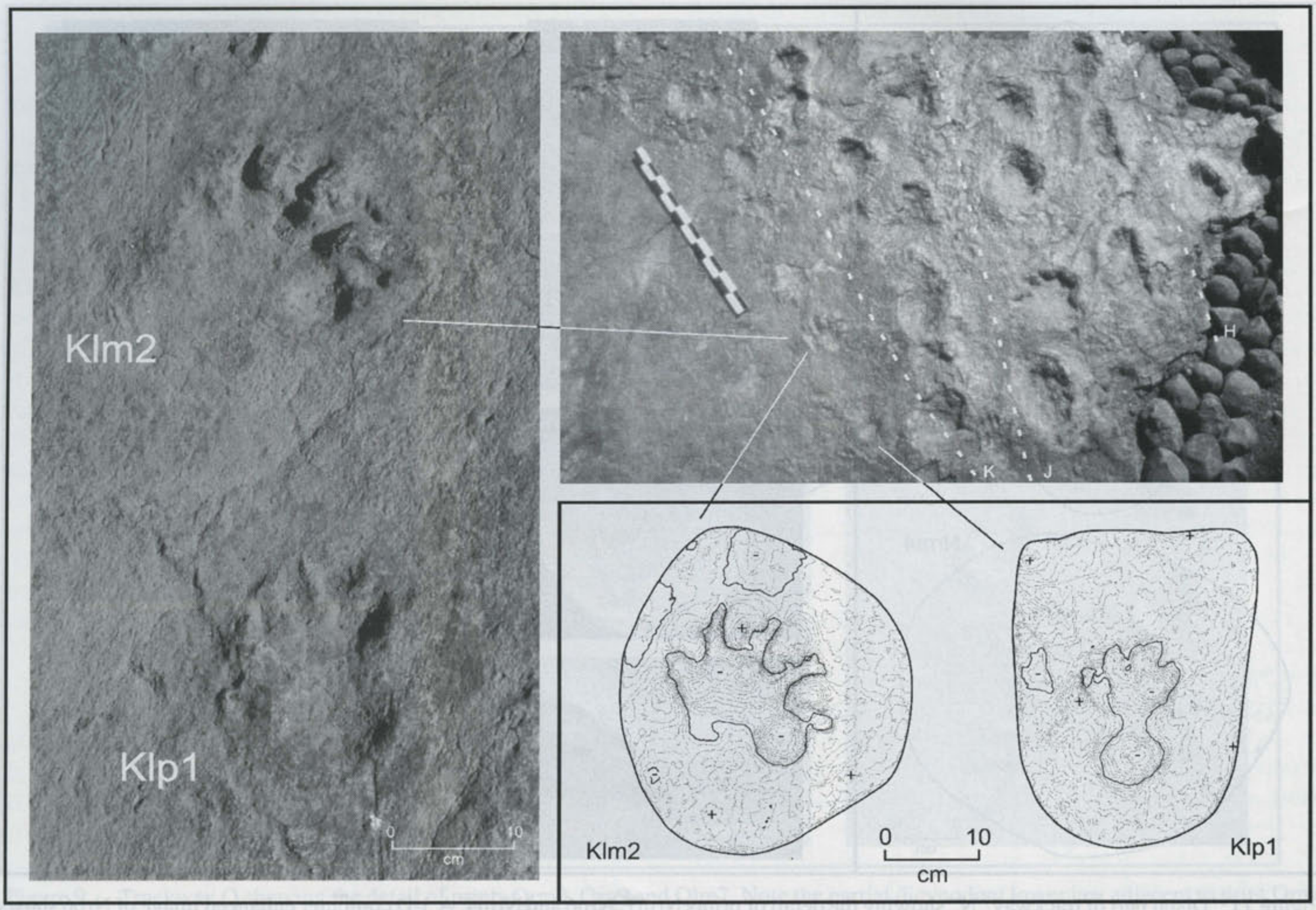

Figure 13 The northern weathered flank of the palaeosurface showing the positions of trackways K, J and H (checkered scale bar = 1m) and the detail and contours of prints Klm2 and Klp2 (contour interval = 1mm; zero contour line is indicated in bold).

TABLE 2.

Maximum depth of each print and the maximum height of the adjacent mud drapes (mm) relative to the palaeosurface as indicated by contours in the 13 detailed prints studied (Figures 8 - 13).

Footprint	Max depth	Max height of mud drape
Qlm11	14	16
Qlp10	24	20
Qrm9	10	10
Qrp9	16	22
Qlm7	10	14
Qlm3	10	16
Qlp2	16	20
Prm3	26	20
Nrm7	22	20
Nrp6	14	4
Nrm4	42	30
Klm2	12	10
Klp1	8	8

TABLE 3.

Manual and pedal footprint widths and lengths (No. 37 and 36 as defined by Leonardi, 1987) for those animals in which a good degree of preservation was evident. Measurements (in cm) were obtained from the 13 fiberglass casts and directly from the tracks on the palaeosurface.

	Manus			Pes		
	Width	Length	Ratio (w:l)	Width	Length	Ratio (w:l)
Q	20.0	14.5	1.38	12.0	19.0	0.63
P	28.0	19.0	1.47	13.5	26.0	0.52
N	30.5	22.0	1.37	15.0	27.0*	0.56
K	16.5	13.0	1.27	11.5	18.0	0.64

* - Not quite the true length of the pedal print as the animal appears not to have placed its "heel".

TABLE 4.

Divarication of digits in degrees (Leonardi, 1987, No.56).

* Not well defined.

Manus	**I - II**	**II - III**	**III - IV**	**IV - V**	**Total**
Qlm11	30	28	20	25	103
Qlm7	30	37	15	12	94
Qlm3	37	25	25	13	100
Qrm9	64	27	27	23	141
Mean **Q**	40	29	22	18	110
Prm3	59	15	18	50	142
Nrm7	44	27	30	22	123
Nrm4	72	19	17	34	142
Mean **N**	58	23	24	28	133
Klm2	33	29	27	34	123
Pes					
Qlp10	16	47	43	(35?)*	106(141)
Qlp2	46	38	29	- *	113
Qrp9	39	26	42	17	124
Prp9	31	10	37		78
Nrp6	9	15	7	- *	31
Nlp6	17	22	21	- *	60
Klp1	29	10	42	-	81

* - Not reliable as pedal digit IV is only recorded once for **N**.

substrate was quite firm (less pore water in the sediment) and in other areas it was quite "sloppy" with relatively more pore water in the sediment. This feature is well illustrated when comparing the sequential manual and pedal prints on the right side of trackway **N**, from Nrm3 to Nrm7 (Figures 6 and 11). It is clear that at the time this deep manual print (Nrm4) was made, the substrate in its vicinity was much softer than at its preceding print and at its subsequent two prints.

In the majority of cases the substrate was soft enough to register displacement rims which stand proud of the palaeosurface and are associated with each footprint. These push-up ridges give an indication of the direction in which the displaced sediment moved, relative to the force that was exerted by the placing of the feet. A general impression of the character of the mud rims is evident in trackway **Q** (Figure 9). Manual prints generally show push-ups to the rear and outer side of each print, best illustrated in Nrm7 and Prm3 (Figures 11 and 12). In the case of the pedal prints the push-ups occur as arcuate bulges of the palaeosurface on either side of the prints (e.g. Qlp10, Qrp9, Qlp2 in Figures 8-10). The extent to which the mud has been pushed-up above the palaeosurface varies between 4 and 30mm and maximum values measured for the 13 studied prints is presented in Table 2.

Footprints

It is evident from the mapping and detailed topology of the 13 selected prints that there is a marked morphological difference between the manual and pedal prints of the animals that made them. They were

TABLE 5.
Digit lengths (mm) and proportions (Leonardi, 1987, No. 47).
Average measurements taken on the palaeosurface and from the fibreglass casts.

Manus	I	II	III	IV	V
Q Proportions	60 1	65 1.08	60 1.00	48 0.80	35 0.58
P Proportions	80 1	60 0.75	70 0.88	65 0.81	50 0.65
N Proportions	85 1	83 0.98	85 1.00	80 0.94	63 0.74
K Proportions	45 1	50 1.11	55 1.22	55 1.22	30 0.67
Pes					
Q Proportions	40 1	30 0.75	30 0.75	26 0.65	none -
P Proportions	69 1	76 1.10	68 0.99	44 0.64	none -
N Proportions	81 1	82 1.01	70 0.86	70* 0.86	none -
K Proportions	65 1	85 1.31	85 1.31	65 1.00	none -

heteropodous quadrupeds and the morphological detail and depth of the eight manual and five pedal prints are illustrated in Figures 8 - 13 and Table 2. An estimate of the sizes of both manual and pedal prints was obtained for animals K, N, P and Q (Table 3). Size estimates for prints in H and J were regarded as unreliable because of the extent of the weathering.

It is evident from Table 3 that the width of the manus is in all case greater than the length by a ratio of 1.27, 1.37, 1.47, 1.38 for K, N, P and Q respectively. In contrast, the pedal width is in all cases less than the length in ratios of 0.64, 0.56, 0.52 and 0.63.

Manual Prints.

These are pentadactyl and plantigrade. In all cases the manus is somewhat divaricate (Q=110°; P=142°; N=133°; K=123° (Table 4) with a width to length ratio greater than 1.25 (Table 3). The digits are relatively elongate (Q, 35 - 65mm; P, 50-80mm; N, 63-85mm; and K, 30-55mm) (Table 5). It is evident that the manual print metapodial-phalangeal axis (or cross axis; No. 35 of Leonardi, 1987; Figure 7b) in most cases is at right angles to the midline of each trackway with the cross-axis angle close to 90° (Leonardi, 1987, No.57; Figure 7b). In the larger animals (**N** and **P**) the sole pad of the manus has produced the bulk of the print, while the distal unguals of each digit produced individual impressions separated from the sole pad by a raised portion, where each digit was curved upward. This feature is well illustrated in Figure 11 (Nrm7 and Nml8 - the last two manual prints in the **N** progression). Some prints show impressions of all digits where the substrate was soft enough to register all digits, e.g. Nrm4.

The interdigital divarication angle between I-II for **N**, **P** and **Q** is evidently larger than that for the other digits (Table 4) with Digit I being extended medially approaching right angles to the midline. At first glance it appears that Digit I is longer than the other four digits (Figure 2). This is misleading because in those cases where no lateral movement of the manus is evident, Digit I is similar in size to the other four digits - e.g. Nrm7 (Figure 12). The interpretation of this phenomenon is that in the majority of cases, as the animal put its front foot down, it did so with the manus partially rotated such that Digit I was pointing slightly downward. Consequently, it came into contact with the substrate before the other digits and then slid a short distance outward before the rest of the foot was planted. Examples of this movement can be seen in Plm4, 5 and in particular in Prm3 (Figure 12), where the manus slid 45mm to the right before it commenced with the next step. A limited degree of rotational movement is seen in only the manual prints of trackways **Q, P, N** and **K**, and is best illustrated in Figure 13 where the digit impressions of Klm2 have a pronounced, arcuate, inward curve in contrast to the straight-forward pedal print behind it (Klp1).

In the case of trackway Z, both the manual and pedal prints have a pronounced inward curve (see Figures 3 and 11). These tracks closely match those described by Smith (1980, 1993), which he attributed to *Diictodon* and it is likely that this small dicynodont was the small trackmaker at Asante Sana.

Pedal Prints

Generally the pedal prints are elongate in form and some degree of morphological variability is apparent between the pedal prints in the larger and smaller trackways. Only one pedal print on the surface (Qrp9) clearly shows that these animals had five digits. The animals were functionally tetradactyl, meaning that although these animals had pentadactyl feet, impressions of only four digits (in some cases three) were made on the substrate.

In trackway **Q** the prints are entirely plantigrade and the long-axis of the print is either parallel to the midline or slightly inward-pointing (Figures 8 - 10), resulting in an average cross-axis angle (Leonardi 1987, No. 57) varying between 10° and 35°(Figure 7b). The metapodial-phalangeal axis (or cross axis; No. 35 of Leonardi 1987; Figure 7b) is at an angle to the trackway midline, contributing to the inward pointing aspect of the pedal prints in Q. In addition it is difficult to identify individual digits as they appear to have been stubby and rather short, effectively being incorporated into the general footprint depression. It is only in Qrp9 (Figure 9) that five digits are apparent while in Qlp10 and Qlp2 only four digits (at best) are recognized.

The larger animals, **P** and **N**, are semiplantigrade and the elongated form of the print is retained, but here distinct, distal ungual impressions are separated from the main sole pad of the pes, e.g. in Nrm4 (Figure 11). The metapodial-phalangeal axis of these larger pedal prints is, in most cases, at right angles to the midline. It appears as if the weight distribution on the feet of the larger animals was shifted forward resulting in only slight impressions being made by the "heel" on the substrate (Figure 11). In contrast however, the pedal prints of the small animal **Q** display an even weight distribution (Figures 8 - 10).

SYSTEMATIC ICHNOLOGY

Dicynodontipus Rühle von Lilienstern, 1944.

Dicynodontipus icelsi sp. nov.

Holotype: The preserved *in situ* palaeosurface with concave epirelief moulds at Asante Sana (Figures 1 and 2). In addition, the 13 fibreglass print casts (AM.5742 - AM.5754) and the two large fibreglass surfaces on display in the Albany Museum, Grahamstown (AM.5755 and AM.5756) (Figure 6).

Locality: S32°19.970': E25°00.745' - Buffelshoek (368) which is part of Asante Sana game farm, 45km east of Graaff-Reinet district, Eastern Cape, South Africa (Figure 4). Late Permian fluvial sediments in the Karoo Basin, Beaufort Group, upper *Cistecephalus* Assemblage Zone.

Etymology: *D. icelsi* (eye-sells-i), named after Mr I.C. Els, who discovered the fossil site.

Diagnosis: Heteropodous trackways **N**, **P** and **Q** displaying primitive alternate gait with the manual prints being pentadactyl plantigrade and somewhat divaricate, varying between 110° and 142°. The manual prints are broader than they are long, having a width/ length ratio between 1.37 - 1.47 and the pedal prints are more elongate with a width/length ratio between 0.52 - 0.64. Although the animals had pentadactyl feet, they generally show impressions of only 3 - 4 digits, suggesting that the animals were functionally tetradactyl. Average dimensions of the manual and pedal prints are given in Table 3.

Comparison: A quadrupedal vertebrate ichnofossil that displays similar characteristics to those recorded at Asante Sana is the narrow trackway of *Dicynodontipus geinitzi* (Hornstein 1876; as reported and well illustrated in Haubold, 1984, 140-141; and Leonardi, 1987, Plate IXd & Plate XIIIb) from the Triassic of Germany and Britain (Haubold 1971). This ichnofossil is regarded as the best known species of this genus. Manual and pedal prints are plantigrade and regularly spaced with a relatively long stride along a narrow trackway. Some features of *Dicynodontipus* clearly show that both the pes and the manus have five toes and that the manus is larger than the pes. In addition, the gait of *Dicynodontipus* indicates that this animal was an efficient walker with a much increased pace angulation of 130° compared to the maximum average of 79° seen in **N**.

An illustration of *Dicynodontipus hildburghausensis* (Rühle von Lilienstern 1944) in Kuhn (1958, p.140) indicates a pentadactyl manual print quite similar in appearance to the deeper impressions of trackway **N** (e.g. Nrm4, Figure 11) but unfortunately no scale is given with the illustration. The *Dicynodontipus bellambiensis* (*Lystrosaurus*?) prints reported by Retallack (1996) from the Sydney Basin, Australia, show well defined divaricate, and more elongate, digits that are morphologically quite different from those at Asante Sana. These supposed *Lystrosaurus* footprints from Australia are remarkably similar to the unnamed trackway that was reported by Watson (1960) from the Middelburg area of the Karoo.

A similar trackway to that of **Q**, which has been attributed to *Laoporus* (Caseidae)(Lull, 1918), a herbivorous pelycosaur of similar size to the Asante Sana trackmakers, is illustrated in Leonardi (1987, Plate XIIIc). The general pattern of manual and pedal prints here is notably similar to those of **Q**, except that the impressions are angled inward as opposed to the outward splay of the pedal prints in Q.

Other tetrapod ichnofossils that have been attributed to therapsids include *Deuteroterapous* (Nopsca 1923; as illustrated in Haubold, 1971 showing four blunt toes and little else), *Cynodontipus* (Ellenberger 1976) and *Therapsipus* (Hunt, *et al* 1993), which all have relatively large tracks with relatively short, stumpy digits.

DISCUSSION

A degree of primary overlap (Leonardi 1987, No.27) occurs in the second half of trackway **P**, where the placing of the pes upon part of the manual impressions is evident. This condition is better illustrated on the left hand side of **P**, where no interference from **N** has obscured print detail. It is best illustrated in Figure 8 (Plp9 and Plm8) and is also evident in the following **P** pairs: Plm5&Plp6, Plm6&Plpy7, etc., continuing to the western edge of the palaeosurface (Figure 6). The same

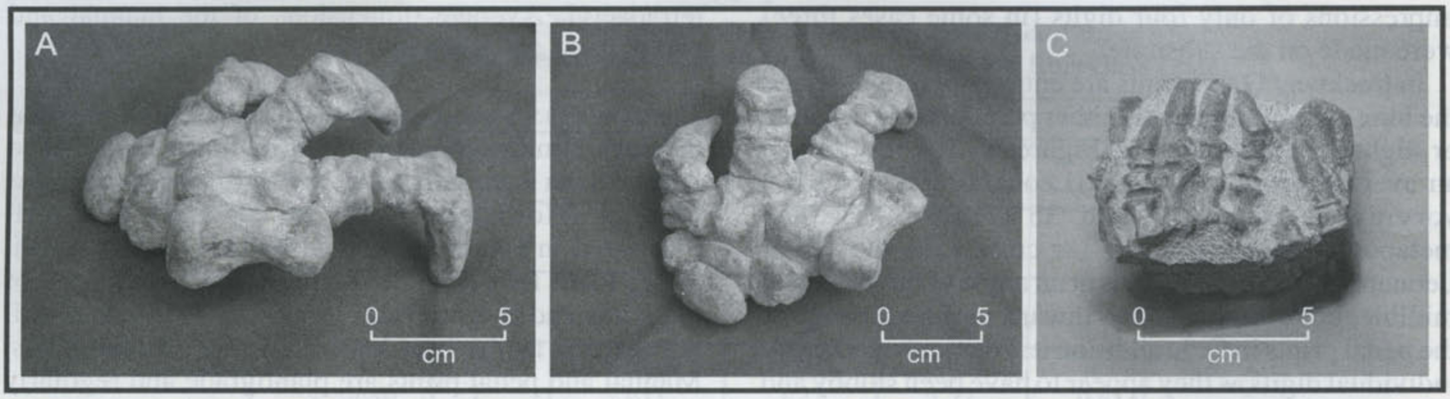

Figure 14 Fossils of the left manus of the dicynodont *Aulacephalodon* collected in the *Cistecephalus* Assemblage Zone of the Beaufort Group, Karoo. A & B shows an incomplete adult form from the Wellwood Basin, Graaff-Reinet (RC.825, Wellwood Collection) in left lateral and dorsal views. Here Digit I has been lost and the distal part of Digit II is missing; C. represents a juvenile form (in dorsal view) collected at Asante Sana (AM.5730, Albany Museum collection).

condition is seen in the right hand prints from Prm4&Prp5, Prm5&Prp6, etc. (Figure 6). This observation indicates that the animal had increased its speed of movement relative to its preceding tracks.

Tail-drag marks are rare on the palaeosurface and this is not unexpected, as the most abundant tetrapods at that time were the therapsids (mainly dicynodonts). Most of these animals had short, stubby tails which did not extend to the ground (King 1988). Some drag marks do occur on the palaeosurface at H3 and C2 (Figure 2). Those at H3 are almost parallel to trackway **Q** but have no association to the **Q** trackmaker. No clear footprints are associated with these drag marks and their origin is unclear. The distinctive arcuate drag mark at C2 (Figure 9, below the "bone") is an extension of the manual print Qrm8. It would appear that this drag mark was made as the manus was lifted and dragged a digit in an inward arc over a distance of 30cm.

Close examination of footprints which are in close proximity to prints from another animal, and study of the nature of the mud push-ups associated with each print, has led to an idea of the order in which the animals walked across the surface. It is evident that trackmaker **P** walked ahead of **N**, and similarly **K** walked ahead of **J.** Prints for animal **Q** do not interfere with any of the other tracks and could therefore have been made before or after the rest of the group. Too few tracks of **H** are preserved to establish its position in the group. In the case of the small trackway **Z**, it is evident that it was made before the larger animals had moved across the surface, as the trackway is discontinuous and broken by the larger tracks.

The regular progression of manual and pedal footprints in all trackways show that these animals had a primitive alternate gait with support on the diagonal limbs changing periodically - a progression which is well illustrated by MacRae (1990). In addition the manus is more deeply impressed than the pes and this is particularly well-illustrated in the right side prints of trackway **N** (Figure 11). This feature is typical of walking quadrupedal animals in which, as Retallack (1996) puts it, "*... the forelimbs were habitually load-bearing.*" It is evident in the large animal trackways **N** and **P** that the manus impressions lie outside the lane formed by the pedal prints but this is not as obvious in trackway **Q**. On inspection, the difference of the mean average pace angulation between manual and pedal prints for animals **N, P** and **Q** is 7°, 6° and 2° degrees respectively (Table 1 and Figure 7a). In all cases the manual pace angulation is smaller than that for the pes, indicating that these animals had front limbs that were more widely splayed than those at the back. This feature was more pronounced in the larger animals, **N** and **P**. The small difference in pace angulation of animal **Q** (2E), compared to the larger animals **N** and **P** (7° and 6°), can possibly be explained by the ontogentic development of these animals during their life span.

Possible Trackmakers

The pattern of the trackways and the presence (or absence) of certain trace markings on the palaeosurface give some clues as to the identity of the various trackmakers. The identity can be narrowed down by considering digit numbers and relative length. Animals that produced the distinctive large footprints were clearly heteropodous quadrupeds that had front feet that were pentadactyl, with digit proportions and joints compatible with a phalangeal formula of 2:3:3:3:3. Although the pedal prints in many cases do not show clear digit impressions, it is concluded that they were morphologically pentadactyl but functionally tetradactyl. MacRae (1990), in his work on the Van Tonders Kraal palaeosurface, concluded that the trackway prints were made by homopodous animals and suggested that they had been made by the large dicynodont *Aulacephalodon* Seeley 1898. This observation was based on the deduction that the sediment substrate (now sandstone) at Van Tonders Kraal, at the time the tracks were made, was fully saturated and was therefore too soft to produce and preserve sufficient print detail. At Asante Sana the substrate was clearly drier and capable of better preservation, particularly that seen in trackways **Q**, **P** and **N**. The vertebrate fossil record for the *Cistecephalus* Assemblage Zone of the Beaufort Group (Kitching 1977; Rubidge, 1995) indicates that there are four possible candidates that were capable of producing the larger trackways. They are the dicynodonts *Aulacephalodon*, *Rhachiocephalus* and *Dicynodon* and possibly the para-reptile *Pareiasaurus*. As far as can be ascertained, *Pareiasaurus* or *Rhachiocephalus* fossil remains have not been recovered from the Asante Sana area, but several skulls and some post-cranial material of *Aulacephalodon* and *Dicynodon* have been collected in the area recently.

It is noteworthy that very few feet of large dicynodonts have been collected from the *Cistecephalus* Assemblage Zone. A partial right manus of *Rachiocephalus* (Olsen & Byrne 1938) and only two left manus specimens of *Aulacephalodon* are known (Figure 14). The larger specimen (Figure 14A and B) was collected from *Cistecephalus* Assemblage Zone rocks on the farm Wellwood to the north of Graaff-Reinet. Although this specimen lacks Digit I and the distal part of Digit II, it nevertheless makes a good fit with manual print impressions of the larger trackways, **N** and **P**. The smaller (juvenile) left manus of *Aulacephalodon* (Figure 14C) was collected in association with a well-preserved skull and other post cranial elements 1.7km to the north of the trackway site at Asante Sana. Again the morphology of this left manus, although smaller, is consistent with the shape of the manual prints on the trackway. In the mounted skeleton of *"Aulacephalodon peavoti"* (Olsen & Byrne 1938) in the Field Museum of Natural History, Chicago (UC.1532), only part of the right manus is preserved and both the front and back feet on display are plaster approximations. Nevertheless the reconstructed right manus is also in agreement with the print impressions.

To-date, very few back feet of large dicynodonts are known and, based on the illustration of the right pes of Dicynodon by King (1988, p.143), it is apparent that the foot was quite elongate and the digits possibly quite close to each other. This may well have been more pronounced in the younger (smaller) animals like **Q**, accounting for the more elongate pedal prints in this trackway.

Based on the available evidence, it is suggested that the larger trackmakers were very likely to have been the dicynodont *Aulacephalodon* Seeley, 1898.

The trackway, and isolated prints, produced by the smaller animals (trackway **Z**) show a remarkable similarity to those that were reported by Smith (1980, 1993) and are similarly interpreted as having been made by a small dicynodont, the most likely candidate being *Diictodon,* or less likely, *Pristerodon.* It is unlikely that *Cistecephalus* was the track-maker as they were more adapted to a fossorial way of life (King, 1990). Several skulls and some post-cranial material of *Diictodon* have been collected from the Asante Sana valley (J.W. Kitching, pers. comm.).

The subtle difference in the morphology of the manual and pedal prints between the smaller (**Q**) and larger animals (**N** and **P**) coupled with the difference in magnitude of the pace angulation between these animals (see Gait above) may well be a function of ontogentic development of these animals. This suggestion is supported by the work done on the ontogeny of *Aulacephalodon* by Tollman, Grine & Hahn (1980).

Estimated size of animals

The general post-cranial morphology of large Late Permian dicynodonts like *Aulacephalodon*, *Rachiocephalus* and *Dicynodon* appear to be quite similar (King 1988) and they would therefore have had similar body shape and posture. The mounted skeleton of *"Aulacephalodon peavoti"* (Olsen & Byrne 1938) in

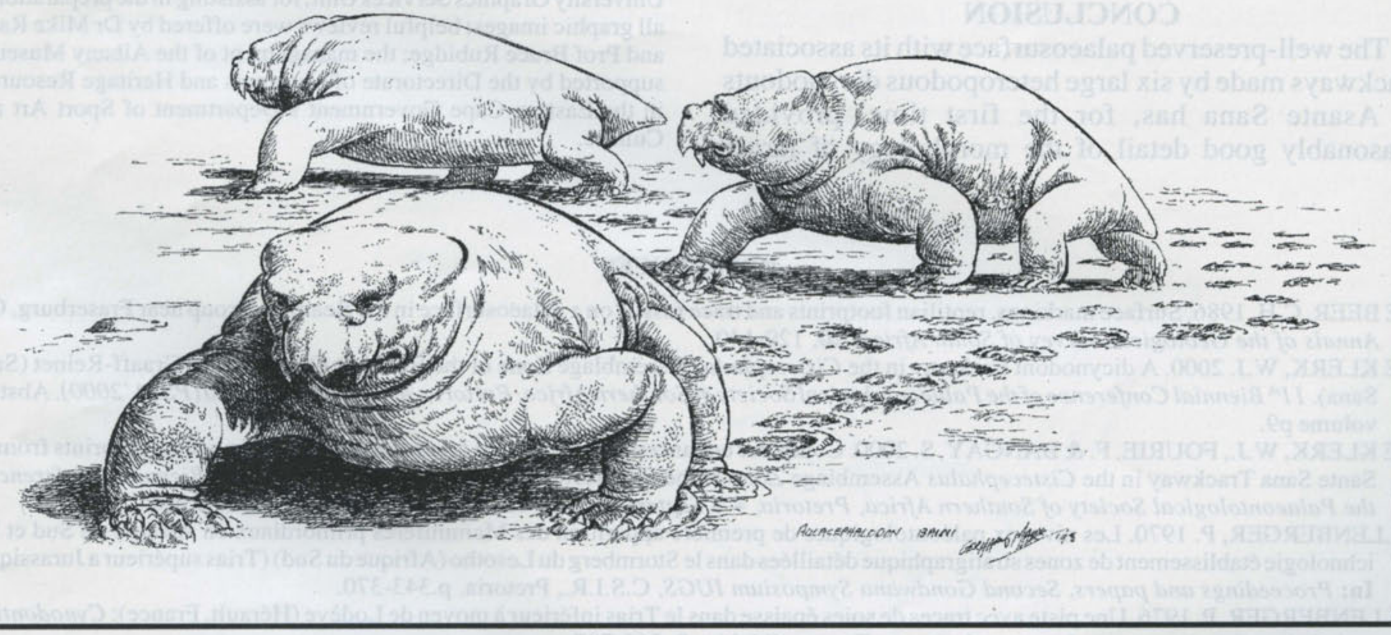

Figure 15 Reconstruction of three *Aulacephalodon* dicynodonts walking across a Karoo mudflat during late Permian times (artist - Gerhard Marx).

the Field Museum, Chicago, now regarded as *Rhachiocephalus,* has been used as a model to estimate the sizes of the trackmakers at Asante Sana.

Estimates of body length (BL) from nose to tailtip were made by two independent techniques, one related to assumptions regarding locomotor postures of *A.peavoti*, whose reconstructed skeleton is known to be short-limbed and extremely robust. If a stereotyped slow, lumbering gait is assumed for *A.peavoti*, with a close ipsilateral pes-to-manus distance of 0.3 BL and a distant ipsilateral pes-to-manus distance of 0.9 BL, then, from measures of *in situ* distances on the palaeosurface, estimates of the trackmakers' BL can be made. Using this technique BL was estimated to be 1.14, 1.65, 1.50 and 1.13m for **Q**, **P**, **N** and **K** respectively. The second technique was to bisect manual and pedal oblique pace measures and to determine the distance between these bisected axes in the line of progression (midline) to give an estimated trunk length. Given that trunk length of *A.peavoti* is 0.573 BL, it was possible (assuming isomorphy in the trackmakers) to estimate BLs of 1.18m for **Q** (96% congruent with estimate from technique 1); 1.64m for **P** (99% congruent); 1.58m for **N** (95% congruent); 1.20m for **K** (94% congruent).

The estimated sizes of animals **P** and **N** appear to be at variance with the suggested sizes as indicated by their average stride measurements of 81 and 88 cm respectively (Table 1). It must however be emphasized that because of print interference between the right prints of **P** and the left prints of **N**, the exact position of these prints were estimated and this may have affected the results of the size estimates obtained for the two methods outlined above. Relative to *A.peavoti*, the Asante Sana trackmakers are all smaller (**Q** = 55%; **P** = 78%; **N** = 73%; **K** = 55%) and it may be that **P** and **N** were similarly-sized adults and **Q** and **K** equally-sized sub-adults.

CONCLUSION

The well-preserved palaeosurface with its associated trackways made by six large heteropodous dicynodonts at Asante Sana has, for the first time, provided reasonably good detail of the morphology of larger dicynodont tracks. The track-makers of these larger prints are believed to have been a family group of *Aulacephalodon* dicynodonts of varying sizes as they walked across a wet, yet pliable and yielding fine sandstone layer that had been deposited by overbank flooding of a nearby meandering river system. In addition to the larger tracks, traces and discontinuous trackways of smaller dicynodonts are preserved on the palaeosurface and are attributed to the small dicynodont *Diictodon*. These vertebrate trace fossils were fortuitously preserved by a second, mud laden, flood event that deposited a fine layer of mud which settled out of suspension across the surface and effectively filled the footprints, preserving them for c.253 million years. Size variation of the larger prints and the inferred gait of each animal indicates that there were two large adult animals and four smaller animals as they all moved in a westerly direction across the newly deposited sediments. The detail of prints preserved in trackways **N, P** and **Q** are here referred to the new ichnospecies *Dicynodontipus icelsi* sp. nov.

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REFERENCES

DE BEER, C.H. 1986. Surface markings, reptilian footprints and trace fossils on a palaeosurface in the Beaufort Group near Fraserburg, C.P. *Annals of the Geological Survey of South Africa*, **20**, 129-140.

DE KLERK, W.J. 2000. A dicynodont trackway in the *Cistecephalus* Assemblage Zone of the Beaufort Group east of Graaff-Reinet (Sante Sana). *11th Biennial Conference of the Palaeontological Society of Southern Africa, Pretoria, 4-8 September 2000 (PSSA'2000)*. Abstract volume p9.

DE KLERK, W.J., FOURIE, F. & BANGAY, S. 2000. Computer enhancement of selected manual and pedal dicynodont footprints from the Sante Sana Trackway in the *Cistecephalus* Assemblage Zone of the Beaufort Group east of Graaff-Reinet. *11th Biennial Conference of the Palaeontological Society of Southern Africa, Pretoria, 4-8 September 2000 (PSSA'2000)*. Abstract volume p65

ELLENBERGER, P. 1970. Les niveaux paléontologiques de première apparition des Mammifères primordiaux en Afrique du Sud et leur ichnologie établissement de zones stratigraphique détaillées dans le Stormberg du Lesotho (Afrique du Sud) (Trias supérieur a Jurassique). **In:** *Proceedings and papers, Second Gondwana Symposium IUGS,* C.S.I.R., Pretoria, p.343-370.

ELLENBERGER, P. 1976. Une piste avec traces de soies épaisse dans le Trias inférieur à moyen de Lodève (Hérault, France): *Cynodontipus polythrix* nov. gen. nov. sp. Les cynodontes en France. *Géobios* **9**, 769-787.

FOUNTAIN, A.J. 1984. Notes on the occurrence of synapsid footprints in the Adelaide Subgroup of the lower Beaufort Group in the Richmond area, Cape Province. *Annals of the Geological Survey of South Africa*, **18**, 67-68.

HAUBOLD, H. 1971. *Handbuch der Paläoherpetologie, Teil 18: Ichnia Amphibiorum et Reptilorum fossilium*. Stuttgart, Gustav Fischer. p.124.

HAUBOLD, H. 1984. *Saurierfärhten*.Wittenberg, Lutherstadt, Germany, A. Ziemsen, p.231.

HOLUB, E, 1881. *Sieben Jahre in Südafrika. Ergebnisse, Forschungen und Jagden auf meinen Reisen von den Diamantenfeldern zum Zambesi* (1872-1879).Wien, Alfred Hölder, p532.

KING, G.M. 1988. *Anomodontia: Encyclopedia of Paleoherpetology*, Stuttgart, Gustav Fischer Verlag, Part 17C, p.174.

KING, G. 1990. *The Dicynodonts: A study in palaeobiology*. London, Chapman and Hall, p.233.

KITCHING, J.W. 1977. *The Distribution of the Karroo Vertebrate Fauna*. Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg. Memoir No.1, p.131.

KUHN, O. 1958. *Die Fährten der vorzeitlichen Amphibien und Reptilien*. Bamberg, Meisenbach KG, p.64.

KUHN, O. 1963. *Ichnia tetrapodorum*. Fossilium Catalogus I. Animalia pars *101*. s'Gravenhage: Uitgeverij Dr W. Junk, p.176.

LEONARDI, G. (ed.) 1987. *Glossary and Manual of Tetrapod Footprint Palaeoichnology*. Brazilia, Brazilian Department of Mines and Energy (Departmento Nacional da Producao Mineral, Brasilia), p.117

LULL, R.S. 1918. Fossil footprints from the Grand Canyon of the Colorado. *American Journal of Science* **4**, 337-346.

MACRAE, C.S., 1990. Fossil vertebrate tracks near Murraysburg, Cape Province. *Palaeontologia africana* **27**, 83-88.

OLSON, E.C. & BYRNE, F. 1938. The osteology of *Aulacocephalodon peavoti* Broom. *Journal of Geology* **46**, 177-190

RETALLACK, G. J. 1996. Early Triassic therapsid footprints from the Sydney Basin, Australia. *Alcheringa*, **20**, 301-314.

RUBIDGE, B.S. (ed) 1995. Biostratigraphy of the Beaufort Group (Karoo Supergroup). *Council for Geosciences, S.A. Committee for Stratigraphy, Biostratigraphic Series* No.1, p46.

RÜHLE VON LILIENSTERN, H., 1944. Eine Dicynodontierfährten aus dem Chirotheriumsandstein von Heßberg. *Paläontologische Zeitschrift* **23**, 368-385.

SEELEY, H.G. 1898. On *Oudenodon* (*Aulacocephalus*) *pithecops* from the *Dicynodon* beds of East London, Cape Colony. *Geological Magazine* (new series decade IV), **5**, 107-110.

SEELEY, H.G. 1904. Footprints of a small fossil reptile from the Karoo rocks of Cape Colony. *Annals and Magazine of Natural History (Series 7)* **14**, 287-289.

SERJEANT, W.A.S. 1989. "Ten paleoichnological commandments": A standard procedure for the description of fossil vertebrate footprints. **In:** Gillette, D.D. & Lockley, M.G. (eds), *Dinosaur Tracks and Traces*. 369-371. Cambridge University Press.

SMITH, R.M.H. 1980. The lithology, sedimentology and taphonomy of flood-plain deposits of the Lower Beaufort (Adelaide Subgroup) strata near Beaufort West. *Transactions of the Geological Society of South Africa* **83**(3):399-414.

SMITH, R.M.H. 1993. Sedimentary and ichnology of palaeosurfaces in the Beaufort Group (Late Permian), Karoo Sequence, South Africa. *Palaios*, **8,** 339-357.

TOLLMAN, S.M., GRINE, F.E. & HAHN, B.D. 1980. Ontogeny and sexual diomorphism in *Aulacephalodon* (Reptilia, Anomodontia). *Annals of the South African Museum*. **81**(4),159-186.

WATSON, D.M.S. 1960. The anomodont skeleton. *Transactions of the Zoological Society, London*. **29**(3), 131-208.