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THE "TRILOBITE" TRACKWAYS IN THE TABLE MOUNTAIN GROUP (ORDOVICIAN) OF SOUTH AFRICA

by

Ann M. Anderson

ABSTRACT

A terminology for arthropod trackways is defined and the nomenclature of trace fossils is discussed briefly. Most of the trackways from the reddish sandstone Graafwater Formation are assigned to the ichnospecies *Petalichnus capensis* sp. nov. which includes bilaterally symmetrical walking trails consisting of a repetition of 9—12 pairs of unifid tracks sometimes accompanied by a median drag line. These trackways are associated with hemispherical burrows *Metaichna rustica* gen. et sp. nov. The same animals possibly made both the trackways and the burrows, but whether or not they were trilobites is not clear.

INTRODUCTION

In 1962 Taljaard recorded trilobite trackways from the Table Mountain Sandstone series on the farm Brandenburg 25 km west-south-west of Clanwilliam in the western Cape Province. He presented a sketch of a 7 m² slab, now mounted in an entrance hall of the Department of Geology at Stellenbosch University (Figure 2), and two photographs: one is of a specimen 1,5 m² housed at the South African Museum in Cape Town, the other is of a specimen retained on the farm (18° 38′ E, 32° 16′ S).

Rust (1967; 1969) elucidated the stratigraphic setting of trackways and discovered further occurrences (1967, p. 60):

> ". . . at Tierhoek and Waterval [farms], and in the vicinity of Stellenbosch and Hout Bay, Simonstown. In these localities the tracks occur in the Graafwater Formation [reddish sandstone and siltstone] but tracks have also been found [stratigraphically higher] in the Peninsula Formation [white quartz sandstone] at Matjiesgoedkloof, Urionskraal".

However, the material from Brandenburg remains the most useful because of its relatively good preservation and wide surface exposure; the other examples have been left in situ in the field. Rust (1967, Pl. 14, 18, 19, Figs. 70—78) provided photographs of the trackways and full-size carbon paper rubbings made directly from the rock.

Although both Taljaard (1958; 1962) and Rust (1967) described the morphology of the trackways and burrows, and discussed their possible origin, there has been no previous attempt at a formal systematic classification of these trace fossils.

TRACK TERMINOLOGY

To facilitate definition of the trackways it is necessary to define a few terms.

Tracks, Trails, Trackways

Pettijohn (1957, p. 220) defined "TRACKS . . . [as] impressions left in soft materials by the feet of birds

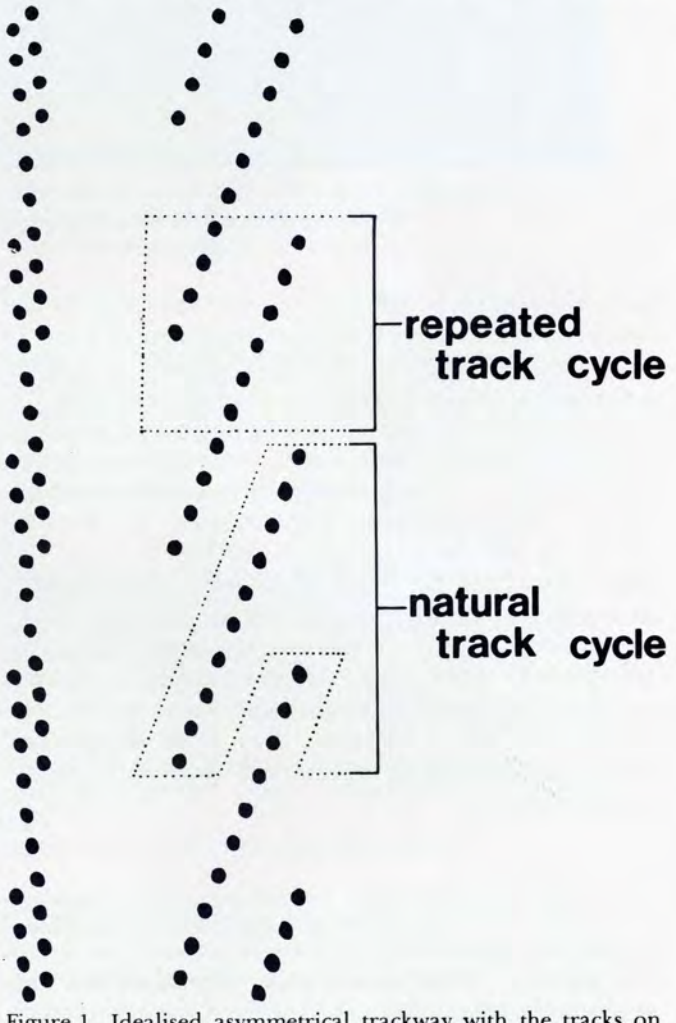


Figure 1. Idealised asymmetrical trackway with the tracks on one side separated into oblique lines of ten set *en echelon*. One such line is a natural track cycle, while the tracks between any two identical tracks in adjacent natural cycles form a repeated track cycle.



Figure 2. Part of the "Brandenburg slab" which is mounted in a wall in the Stellenbosch University Geology Department. It is the type specimen for both the *Petalichnus capensis* trackways and the *Metaichna rustica* burrows. (x0,1)

and other animals. TRAILS . . . [as] the more or less continuous markings left by an organism as it moves . . .". With reference to the markings left by walking arthropods, Bandel (1967, p. 5) explained that "In . . . current American usage the individual imprints of organs of locomotion are . . . referred to as tracks, while a series of tracks made by one individual is a trail." This usage was implemented by Packard (1900, p. 63) and Osgood (1970, p. 351). To emphasise that an arthropod trail consists of a succession of discrete tracks (unlike the trails of the recent amphipod *Corophium volutator* shown by Häntzschel, 1939, Figures 1, 2), it could be termed an arthropod walking trail. Alternatively, it may be termed a TRACKWAY (Frey, 1971, p. 94; Bergström, 1973, p. 53). The latter is preferred because of its comparative brevity.

Track Cycles

A track cycle is a unit sequence of tracks which is repeatedly reproduced to form a continuous length of trackway. Track cycles can be distinguished only where individual tracks are sufficiently characteristic to allow their differentiation. A REPEATED TRACK CYCLE is the sequence between two successive identical tracks; a NATURAL TRACK CYCLE is the consecutive sequence of tracks left by the walking appendages when each, starting with the fore- or hind-most, has pivotted on the substrate once. The natural track cycles usually overlap, i.e. they tend to be longer than the repeated track cycles (see Figure 1). Of course, in one trackway both natural and repeated cycles involve the same number of tracks.

TRACE FOSSIL NOMENCLATURE

A binomial nomenclature usually is employed for the classification of trace fossils (see Häntzschel, 1962; Sarjeant and Kennedy, 1973). This is a "form" nomenclature based on the morphologies of the traces themselves, and the connotation of "ichno-genera" and "ichno-species" is necessarily different from that of phylogenetic genera and species.

Seilacher (1953; 1967; 1974) has demonstrated that behaviour is a significant factor in trace formation. In general, the more meagre the anatomical information in a trace, the more prominent the behavioural aspect. Trackways potentially reveal more about the anatomy of the creature responsible than do most trails. Indeed, the ichno-generic and ichno-specific names of trackways can be almost phylogenetic if the diagnoses are based on a sufficiently extensive collection from one locality. The behavioural change implicit in a change in morphology along the length of a single trail then

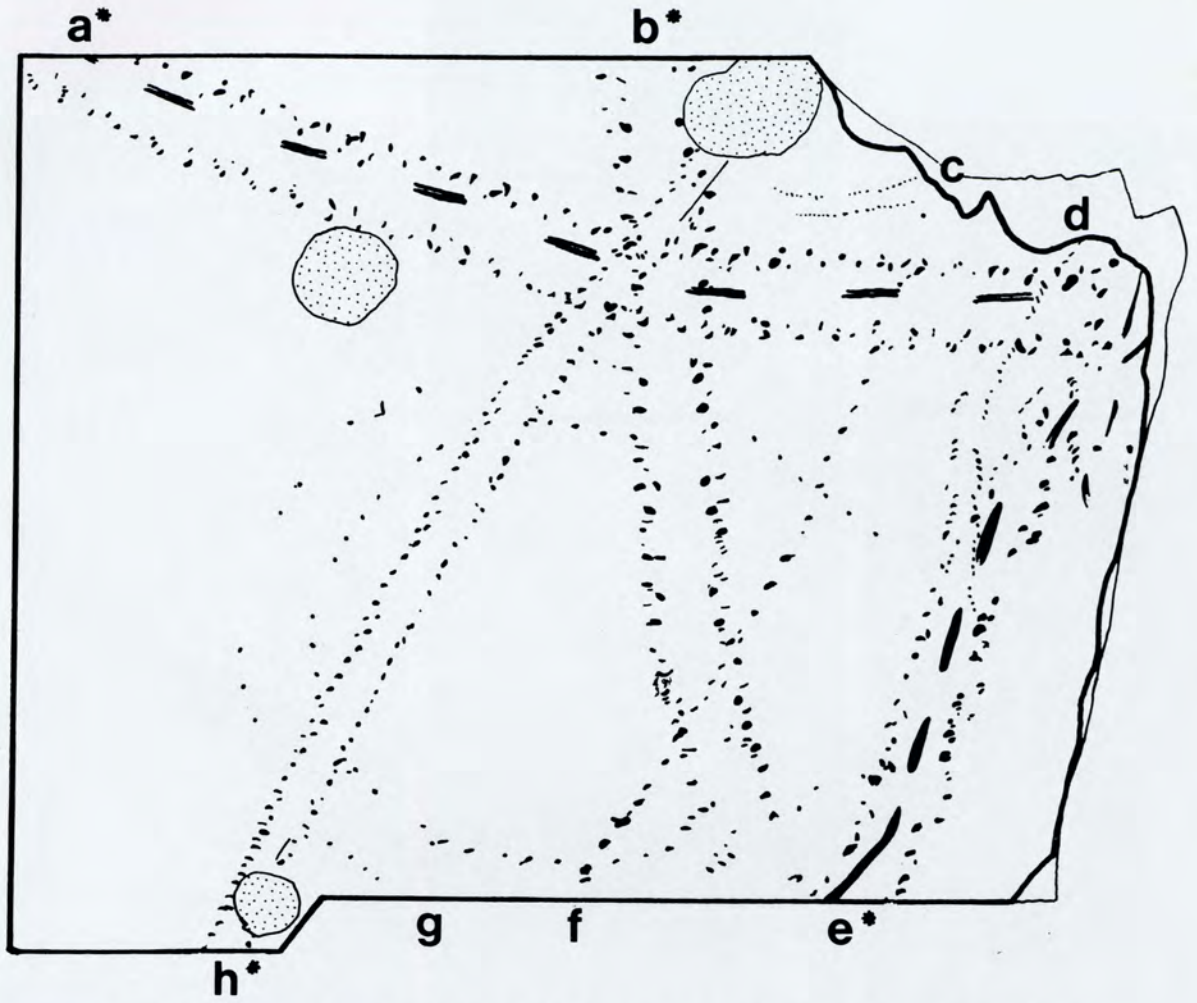


Figure 3. Diagram of the Brandenburg slab (cf. Figure 2). To facilitate reference to particular trackways each is arbitrarily assigned an identifying letter, placed where one end of the trackway intersects the outline of the photographed slab surface. These letters do not correspond with Rust's (1967) individuals A to E described from the slab. The definite *Petalichnus capensis* trackways are marked with an asterisk.

Trackway **a*** is the paratype figured in Figure 4c. (It is Rust's individual A.)

Trackway **b*** is the holotype figured in Figure 4b.

Trackway **c** is Rust's (1967) individual E.

Trackway **d** has the tracks on both sides divided into series set *en echelon*. There are only four or five tracks per series and the series do not overlap. This is probably a deep "undertrack" version of a symmetrical *P. capensis* trackway in which the more superficial tracks are not recorded (see Goldring and Seilacher, 1971).

Trackway **e*** is the one reported by both Taljaard (1962) and Rust (1967, individual B) as having a median drag line for only part of its length. The portion without the drag line is now elsewhere (cf. Taljaard, 1962, Figure 1).

Trackway **f** is represented by a single straight row of tracks; those in the other row have not been recorded probably as a result of "undertrack fallout" in an initially asymmetrical trackway similar to trackway g.

Trackway **g** consists of two curving rows of identical tracks. This is apparently Rust's individual D.

Trackway **h*** is the paratype illustrated in Figure 4a. (Apparently Rust's individual C.) The animal moved from the top to the bottom of the slab as figured (cf. Seilacher, 1959, Figure 2a, b).

There are three *Metaichna rustica* burrows: one on each end of trackway h* and another alongside trackway a*.

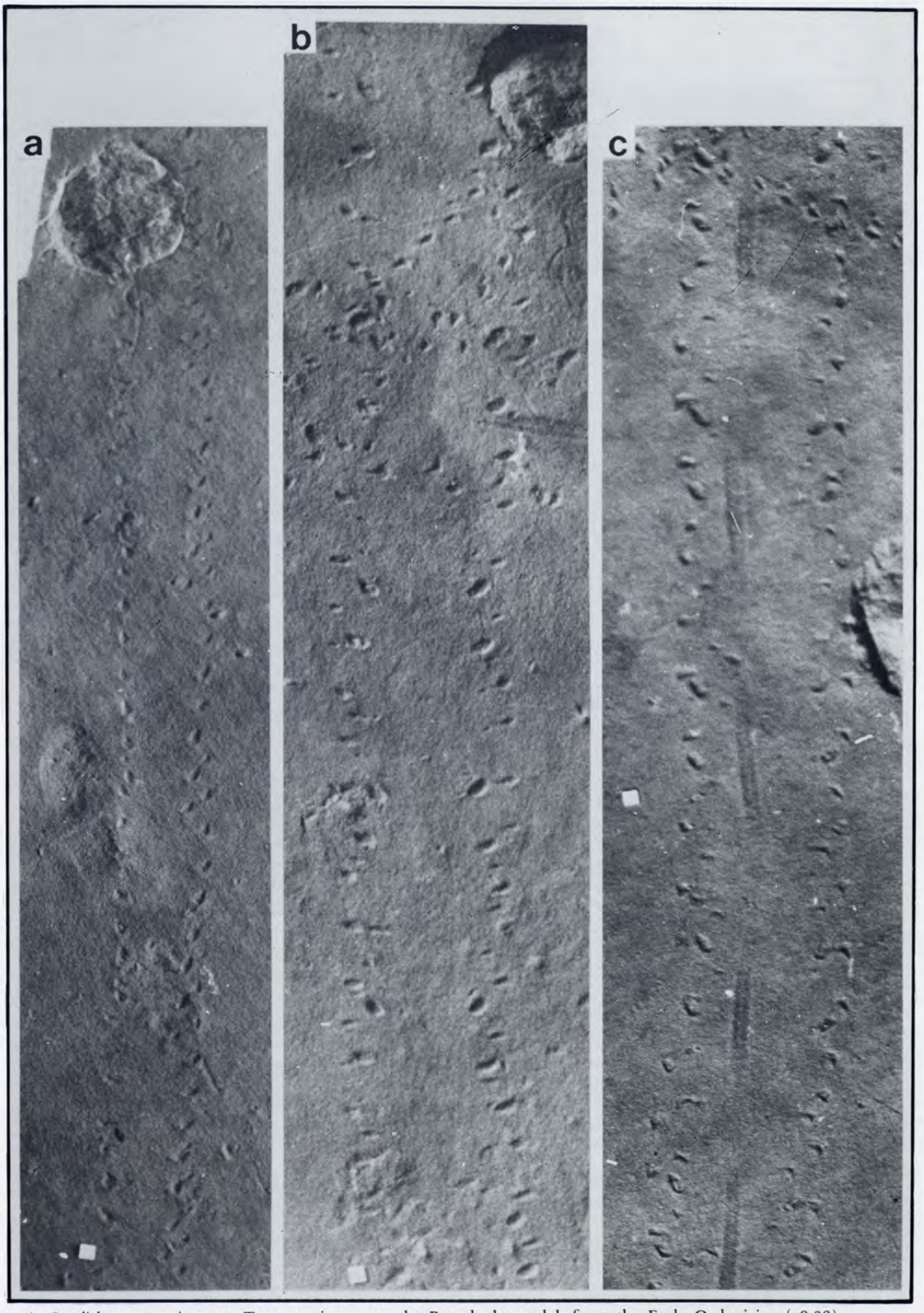


Figure 4. *Petalichnus capensis* n. sp. Type specimens on the Brandenburg slab from the Early Ordovician (x0,33).

(a) Example in which the tracks on the right side are in series of 9, possibly 10, set *en echelon* (see Figure 5a). The circular structure at the top is a *Metaichna rustica* n. gen. et sp. burrow in plan view. The contact between the two is coincidental: the tracks on one side of the trackway continue unaffected past the burrow.

(b) Holotype of the trackway ichnogenus *Petalichnus capensis*. Unlike the specimen in Figure 4a, direction of movement was straight ahead and it is difficult to distinguish the natural track cycles. There are nine or ten tracks in each repeated cycle (see Figure 5b).

(c) Example with a discontinuous median drag line, which does not maintain a strictly median position. The drag line has a distinct median ridge along its length, suggesting that the inscribing organ, probably the tail of the animal, was bifurcate. Each section of the drag line is accompanied by one of the repeated cycles of nine or ten tracks.

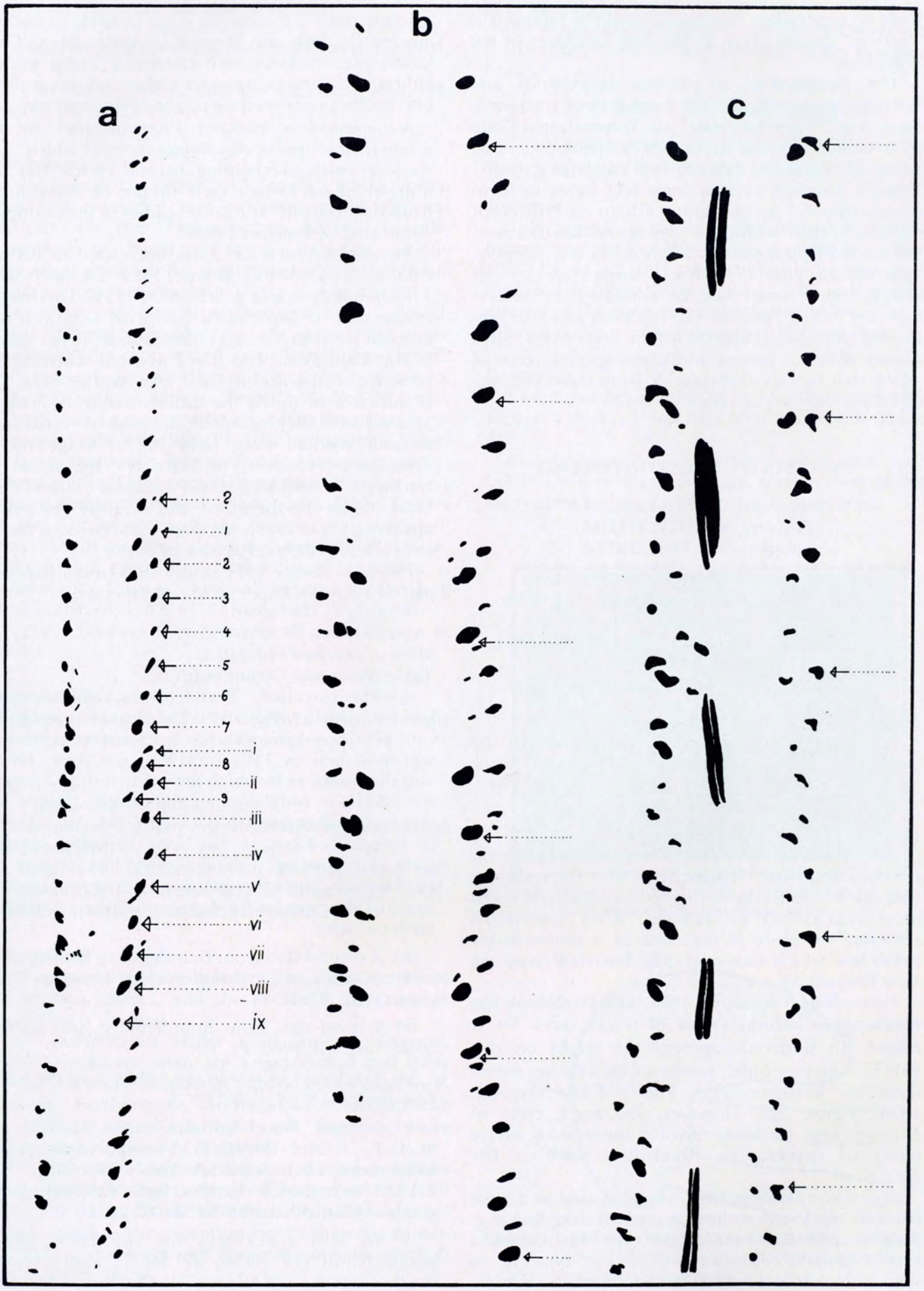


Figure 5. Tracings of the *Petalichnus capensis* trackways shown in Figure 4. In (a) the individual tracks in two natural cycles are numbered, one with Arabic symbols, the other with Roman symbols. In (b) and (c) repeated cycles are marked. In the latter, one portion of the intermittent median drag line is accompanied by one repeated cycle of tracks.

finds no expression. (Perhaps it could be reflected in "variety" names given to the end members of the gradation.)

The morphology of resting impressions and burrows is entirely distinct from that of trackways. Each is an "imperfect state" (cf. International Code of Botanical Nomenclature, 1972, Article 59), none being the complete animal. It is customary to distinguish between various imperfect states in form nomenclature by assigning them to different "genera", each within its own form classification; the levels of phylogenetic implication are independent of one another. Thus, a single "species" of resting impression may be affiliated to several "species" (even "genera") of trackway and vice versa, and one animal species will be responsible for a variety of ichno-genera and ichno-species, some of which may be indistinguishable from those produced by another animal species.

SYSTEMATIC PALAEONTOLOGY

Kingdom INVERTEBRATA
Phylum ARTHROPODA
Subphylum TRILOBITA

Ichnogenus PETALICHNUS Miller 1880.

Type species: *Petalichnus multipartitum* Miller 1880, monotypic.

1863 undesignated trackways, Roberts, Figure 4.
1909 *Acripes* Matthew.
1955 *Diplichnites* Dawson 1873, sensu Seilacher.

Diagnosis (from Osgood, 1970, p. 362):

"Trilobite tracks showing straight-ahead or slightly oblique movement. Each series [track cycle] consists of 9—12 unifid or bifid imprints. Generic designation of producer unknown"

Comparison

Acripes Matthew 1909 has, at least in the species *A. incertipes* (lectotype, Häntzschel, 1965), the tracks on one side of the trackway divided into series of about nine tracks set *en echelon*. This Devonian trackway therefore is regarded as a synonym for *Petalichnus* which was originally described from the Late Ordovician.

Dimorphichnus Seilacher 1955, like *Petalichnus*, has overlapping natural cycles of tracks often set *en echelon*. In both ichnogenera the tracks on one side may be sigmoidal, produced by a raking movement (cf. Seilacher, 1955, Figure 2 and Osgood, 1970, Figure 22). However, the track cycle of *Dimorphichnus* seems to involve more than twelve pairs of tracks, the maximum number for *Petalichnus*.

Diplichnites Dawson 1873 has been used to denote trilobite trackways without a median drag line (e.g. Seilacher, 1955). Osgood (1970, p. 352) remarked that "Dawson's illustration of the type is so schematic that it is impossible to determine if it is a trilobite track". It certainly is not possible to discern any track cycle in Dawson's sketch of a Carboniferous trackway with transverse linear tracks, although the tracks are not a constant distance from one another or from the midline of the trackway.

Merostomichnites Packard 1900 includes in the original description *M. narragansettensis* which is a trackway with overlapping natural cycles, but the number of tracks in a cycle cannot be determined from the diagram. The same applies to the examples illustrated by Størmer (1934).

Protichnites Owen 1852 has been used to denote trilobite (and other cf. Sharpe, 1932) trackways with a median drag line (e.g. Seilacher, 1955). This usage, unlike that of *Diplichnites*, conforms well with the original descriptions and illustrations of the genus in the Cambrian. The moot point is whether the presence or absence, in itself, of a median drag line is sufficient to justify the differentiation of genera. Häntzschel (1962) included trackways both with and without median drag lines in his diagnosis of *Protichnites*. However, he restricted the name to trackways with trifid tracks; *Petalichnus* has unifid or bifid tracks. Furthermore, the original *Protichnites* apparently had no more than eight pairs of tracks per cycle; *Petalichnus* has nine to twelve.

Umfolozia Savage 1971 from the Permian has only half as many tracks per cycle as *Petalichnus*.

Material examined in this study

Table Mountain Group examples:

(a) The so-called "Brandenburg slab", Stellenbosch University (Figure 2). Unfortunately a significant portion of the slab has been removed since it was described by Taljaard (1962) and Rust (1967), and the trackway in which the median drag line was recorded for only part of the length (Rust's individual B illustrated in his Figures 71 and 72, and in Taljaard's Figure 1 has been truncated, leaving only the portion with the drag line (Figure 3, trackway e). The other portion is now mounted in front of the fireplace at 4 Anreith Street, Karindal, Stellenbosch.

(b) A second slab from Brandenburg locality now in the custody of the South African Museum (Taljaard, 1962, Pl. I).

(c) A third slab from Brandenburg, still on the farm (Taljaard, 1962, Pl. II).

(d) Trackways in situ in the hills east of the town Graafwater (18° 38′ E, 32° 09′ S).

(e) Bernard Price Institute casts Hb./C.T. 1, St./C.T. 1 and Th./C.T. 1 respectively from Helderberg near Somerset West (18° 53′ E, 34° 01′ S), Stellenbosch vicinity and Tierhoek farm south of Clanwilliam (18° 51′ E, 32° 24′ S).

(f) In situ trackways on the farm Matjiesgoedkloof (18° 59′ E, 31° 39′ S), about 35 km south-south-west of Nieuwoudtville (Figure 8c).

Petalichnus capensis sp. nov.
Figs. 2—5

1962 undesignated trilobite trackways, Taljaard, Pl. I, II.

1967 undesignated trilobite trackways, Rust, Pl. 14 -D, -F; 19 -C; Figures 70—72, 76, 78.

Definition

Petalichnus trackways with unifid tracks, often laterally elongated and not necessarily identical (Figure 4). The trackways are rarely bilaterally asymmetrical. When they are, the tracks on one side are set *en echelon* and a slight taper is revealed in the distance between opposite tracks in one natural cycle (Figure 4a; see also photograph in Taljaard, 1958). There generally are not more than three natural cycles represented in the longitudinal length of trackway occupied by one such cycle of tracks. There mostly are nine tracks per cycle (see Figure 5). There may or may not be a median drag line, continuous (Taljaard, 1962, Pl. I) or intermittent. When it is discontinuous, one section accompanies one cycle of tracks (Figure 4c). The median drag line does not maintain a strictly median position (see Figures 2 and 3). On occasion, the median drag line itself has a slight median ridge (on the epichnial surface) (Figure 4c). Sometimes the adjacent sediment is puckered to form a "chevron" pattern over the drag line (Taljaard, 1962, Pl. I; Rust, 1967, Figure 76).

The trackways vary between 50 and 125 mm in width.

Derivation of name

Capensis (Latin adjective) derived from the Cape in Cape Province and Cape Supergroup.

Types

Type Locality: Brandenburg.

Holotype: Trackway on Brandenburg slab shown in Figure 4b.

Paratypes: Trackways on Brandenburg slab shown in Figures 4a and 4c, plus those on the South African Museum specimen (Taljaard, 1962, Pl. I).

Comparison

P. capensis is generally larger than other described *Petalichnus* species, and the presence of a median drag line is unusual.

P. multipartitum Miller 1880 (amend. Osgood, 1970) trackways often are asymmetrical and there usually is more overlap of natural cycles than in *P. capensis*. Furthermore, the tracks of *P. multipartitum* sometimes are clearly bifid and they are more elongate than those of *P. capensis*.

P. incertipes Matthew 1909 and the other species originally described under the ichnogenus *Acripes* all have the tracks on one side set *en echelon*, an arrangement which is the exception rather than the rule in *P. capensis* (however, see Figure 4a and photograph in Taljaard, 1958).

Museum specimens

(a) Brandenburg slab at Stellenbosch University.

(b) South African Museum slab from Brandenburg.

Phylum — ARTHROPODA?

Ichnogenus METAICHNA nov.
Type species: *Metaichna rustica* sp. nov.

Definition

This regular conical or hemispherical burrow transgresses the bedding planes (Figures 6, 7; Rust, 1967, Pl. 14 -C). It is orientated with the apex pointing stratigraphically downwards. The wall and the interior of the cone usually are structureless. The infill material is always coarser than the host rock.

Comparison

Conostichus Lesquereux 1876 (cf. Häntzschel, 1962, Figures 116 -2, -3) has structured outer wall and infill.

Kulindrichnus Hallam 1960 is also a conical body, but it is oriented subvertically, is composed of shell aggregates and the matrix may be phosphatic.



Figure 6. *Metaichna rustica* burrow viewed laterally in situ at Tierhoek, south of Clanwilliam (x0,33).

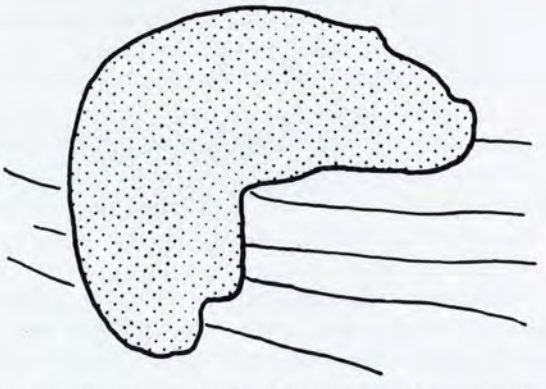


Figure 7. Explanatory sketch of the burrow shown in Figure 6 above. The burrow infill is stippled. It cuts across the bedding of the host strata.

Rusophycus Hall 1852 (cf. Häntzschel, 1962), the typical resting impression made by trilobites (Seilacher, 1955, 1959; Crimes, 1970, 1975; Bergström, 1973), has a bilobed outline reminiscent of a coffee bean. Each lobe is transversely scratched. *Metaichna* therefore is not a typical trilobite excavation.

Material examined in this study

Besides the material mentioned under *Petalichnus*, burrows were observed in situ on the farm Tierhoek south of Clanwilllam.

Metaichna rustica nov.
Figures 2, 4a, 6, 7, 8c.

1962 undesignated trilobite "nests", Taljaard, Pl. I.

1967 undesignated trilobite burrows, Rust, Pl. 14.

Definition

As for genus.

The diameter of the mouth of the burrow (see Figures 4a, 8c) seldom exceeds 15 cm.

Derivation of name

Metaichna = meta-ae f.(L): cone + ichna;
rusticus -a -um (L.): homely, simple.

Types

Type locality: Brandenburg.
Holotype: Brandenburg slab.

Museum specimens

As for *Petalichnus capensis* trackways.

THE ARTHROPOD TRACKWAYS AND ASSOCIATED BURROWS IN THE TABLE MOUNTAIN GROUP

Cocks *et al.* (1970) described marine invertebrate body fossils from the Table Mountain Group. They concluded that the horizon is uppermost Ordovician in age and they estimated that the stratigraphically lower Graafwater Formation, which has yielded most of the "trilobite" tracks, is Early Ordovician.

Not all the trackways in the Table Mountain Group can be referred to *Petalichnus capensis*. Most of the walking trails in which the tracks are a variable distance from one another and from the midline of the trackway probably belong in the ichnospecies (e.g. Figure 8a): the youngest trackways occurring in the Peninsula Formation at Matjiesgoedkloof (Figure 8c; Rust, 1967, Pl. 14 -D) fall into that category. However, even with the expanded definition, there are some trackways that are obviously different, notably Rust's (op. cit.) individuals D, E, H and I. There is no illustration of H, but in the other three the tracks are evenly spaced in straight rows. In trackway D the two rows and the component tracks in them are far apart, while in trackway E the rows and tracks are both relatively close together. These two trackways (c and g in Figure 3) are on the Brandenburg slab; trackway I is from Tierhoek. It has two continuous parallel median drag lines (Figure 8b).

The sediment in which the Table Mountain trackways are recorded is usually too coarse to allow the preservation of fine detail. Nonetheless, at Helderberg near Somerset West and in the vicinity of Stellenbosch there are some tracks that show striations along their long axes. These are each preserved as moulds on the sole of a sandstone which overlay a shale horizon, while the other examples are all impressions on the upper surfaces of sandstone beds. This difference could account for the finer detail, the original impressions having been made in finer sediment. Although no track cycles can be discerned in the museum specimens (B.P.I.P.R. casts Hb./C.T. 1 and St./C.T. 1) it is likely that these striated tracks were left by the animals responsible for the *Petalichnus capensis* trackways.

The *Metaichna rustica* burrows are more widely preserved than the associated trackways, largely because they are more robust structures. The coarse material filling the cones includes ". . . shale gritty sand with pebbles 5—6 mm in diameter at Gansekraal, Worcester" (Rust, 1967, p. 65). The structures stand proud or weather out to form hollows depending on the relative cohesion of the infill. Rust (ibid.) observed that "On the Brandenburg bedding plane the filling of the burrows projects above the bedding surface, thereby indicating that the burrows were dug from a higher level than the surface on which the tracks occur." This is not necessarily so as trackways frequently are preserved as "undertracks" made by the walking appendages penetrating the substrate and intersecting buried laminae just below the free surface (Goldring and Seilacher, 1971). As a result, the burrows could have commenced from the surface on which the arthropods walked.

THE POSSIBLE ORIGIN OF THE *PETALICHNUS CAPENSIS* TRACKWAYS AND THE *METAICHNA RUSTICA* BURROWS

There are four arthropod subphyla in which as many as nine pairs of limbs are employed in walking: the Onychophora, the Trilobita, the Myriapoda and the crustacean Malacostraca.

Taljaard (1958, p. 60; 1962, p. 27) decided that the Table Mountain Group arthropods most probably were trilobites. Rust (1967, p. 67) reached the same conclusion, and Seilacher confirmed that opinion in a private communication. The association of the trackways with burrows apparently atypical of trilobite activity and the absence of the characteristic

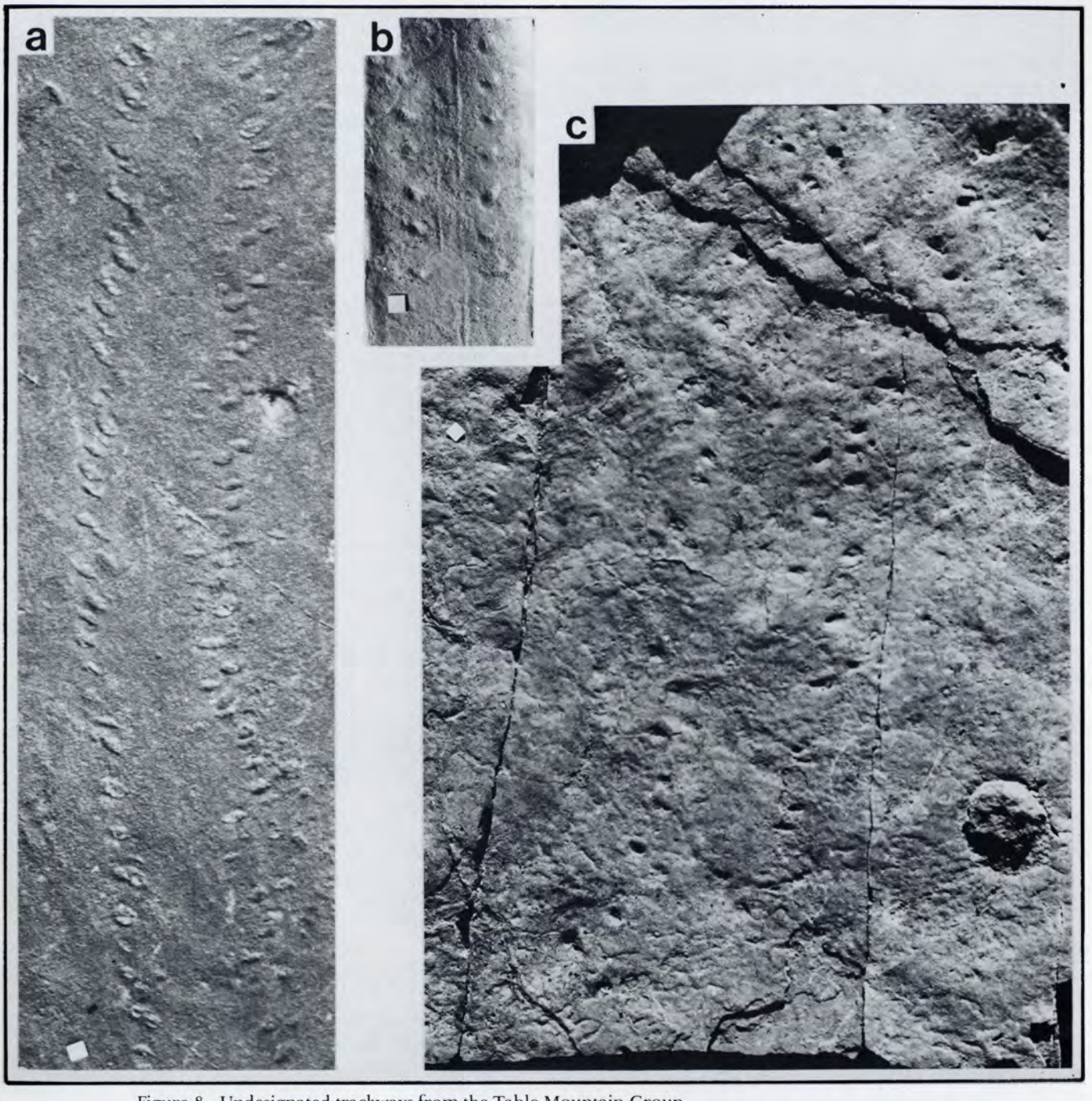


Figure 8. Undesignated trackways from the Table Mountain Group.
(a) Trackway on the Brandenburg slab (not included in Figure 2) with individual tracks a variable distance from one another and from the midline of the trail (x0,33).
(b) Trackway from Tierhoek with opposite paired tracks and a double median drag line (x0,33).
(c) This trackway from Matjiesgoedkloof is slightly younger than the others figured. It has its individual tracks a variable distance from one another and from the midline of the trail, but no cycle is discernible. Note the *Metaichna rustica* burrow on the right (x 0,25).

"raking" tracks cast some doubt on this identification.

The Myriapoda are not particularly promising candidates because they usually have identical legs which pivot on the substrate at a generally constant distance from the animal's axis of bilateral symmetry. In the Diplopoda the legs are very numerous and those on each side produce a continuous furrow rather than individual tracks; in the Chilopoda there are fewer legs, but the footprints on one side are often all superimposed, with the composite "tracks" on one side alternating with those

on the other, simulating the trackway of a bipedal animal (cf. Manton, 1952).

The more "primitive" Onychophora produce overlapping natural cycles similar to those in *Petalichus capensis*, but as their speed increases they superimpose their footprints to produce identical composite "tracks" which may be opposite or alternate (Manton, 1950). The undesignated trackways in the Table Mountain Group could bear the same relationship to *P. capensis*. However, until examples are found which exhibit both forms in one trackway, any relationship between the more common *P. capensis* trails and those with little differentiation between individual tracks must remain speculative.

The Malacostraca, like the Trilobita, have a posteriorly decreasing distance between the distal tips of opposite limbs; this is suitable for the production of a tapering natural cycle of tracks. Seilacher (1955; 1959) considered the direction of movement of creatures responsible for walking trails in which the tracks in one natural cycle are arranged in a "V". Where there are more than four pairs of tracks involved it does seem unlikely that there would be sufficient overstepping to form the long-armed acute-angled "V" developed in *Petalichnus* trails: he concluded that the trackway probably reflects the taper of the limb extremities directly and that the angle of the "V" points backwards. Osgood (1970, p. 351) did not altogether agree, stressing that while Seilacher's hypothesis is logical, it is nevertheless only a theory. Crimes (1970) and Bergström (1973) supported Seilacher's theory.

The *Metaichna rustica* burrows are as enigmatic as the associated trackways. Taljaard (1962) supposed that they were:

> ". . . nests, scooped out for 'egg repositing'. *Limulus*, a present-day distant relative of trilobites, still does that. The hollows could also be the hollows scooped out in search of food, but their small number militates against such a suggestion."

The structures are in fact numerous in some beds, so Rust (1967) favoured the interpretation as feeding burrows (pascichnia), but he noted that they

> ". . . differ from those ascribed by Seilacher (1959; 1960; 1967) to trilobites in that the burrows . . . are not elongated scooped out grooves, but are hemispherical hollows which show no digging marks or any internal structures."

The lack of digging marks and internal structures admittedly could be a preservational feature; the Table Mountain Group sediment is very coarse-grained and not generally suitable for the preservation of fine detail. Rust (pers. comm.) argues that the very coarse nature of the infill might have been the result of an active winnowing away of the finer sediment particles during feeding.

Another explanation is suggested by the extant isopod *Tylos granulatos* Krauss which gains temporary shelter by burying itself backwards in dry beach sand: it rotates around its firmly down-turned tail and a conical or hemispherical depression is produced. The Table Mountain Group conical burrows are also in coarse sediment, and they might have originated in the same way. The heavier particles in the subsequent influx of sediment would accumulate in the open hollows, thus accounting for the relatively coarser infill in the burrows. However, the substrate would need to be damp, at least, for the walls to be sufficiently cohesive to survive an overflow of water bearing coarse detritus.

This interpretation of the *Metaichna* burrows lends support to the Malacostraca as possible authors of the *Petalichnus capensis* trackways. Nevertheless, the evidence is far from conclusive, and it may well be that trilobites or other early arthropods were responsible. It is not even certain that burrows and trackways were made by the same animals; it is only the similar widths of the two traces that provokes the inference.

ACKNOWLEDGEMENTS

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