CHAPTER 15

TRACKS, TRAILS AND RESTING-TRACES

15.1.   GENERAL   INTRODUCTION

In the study area traces attributable to these catego-
ries are relatively few in terms of different ichnotaxa and are
also relatively rare in terms of abundance. They include two new
vertebrate ichnotaxa (i.e., tetrapod trackways, 'type A' and
'type B', probably referable respectively to a large labyrintho-
dont and a small reptile) and three invertebrate ichnotaxa,
including two resting-traces (Pelecypodichnus and ?Rusophycus)
and one grazing-trace (Agrichnium) (cf. Text-Fig. 15.1A). The
vertebrate and invertebrate trackways are treated below in sepa-
rate sections, the invertebrate ichnotaxa being classified ac-
cording to the scheme of Sarjeant & Kennedy (1973) and the verte-
brate ichnotaxa being classified in terms of a scheme newly
proposed here but based in part on that of Sarjeant (1975).

15.2.   GRAZING TRAILS

15.2.1.   Ichnotaxonomy

<div align="center">

Agrichnium Pfeiffer 1968

</div>

Palaeophycus fimbriatus Ludwig 1869.
Schaderthalis bruhmii Hundt 1931.

<div align="center">

Plate 63, Fig. b

</div>

Generic assignment: A group of narrow-diameter subparallel
branching furrows which have a variously smooth to transversely
and irregularly corrugated wall. The furrows are moderately long
but are typically of unequal length and probably manifest graz-
ing trails of an unknown producer.

Remarks (diagnostic features): Subparallel small furrow, branched

TEXT-FIG. 15.1. A. Schematic representation of the dendritic branching grazing trail _Agrichnium_ Pfeiffer (1968) (thin lines) overprinted by V-shaped didactyl tracks defining a running gait. Diagram is based on a portion of the bedding-plane surface shown in Plate 63 Fig. b. Loc.: Mona Vale Head; Strat. unit: Lower Newport Member.; T.F. Subint.: ID5/6.

B. Schematic representation of unbranched, loosely packed, scribbling/grazing traces. Diagram is based on a portion of the bedding-plane surface shown in Plate 76 Fig. a. Loc.: Bangalley Head; Strat. unit: Lower Newport Member. T.F. Subint.: IE1.

A

5 cm

B

5 cm
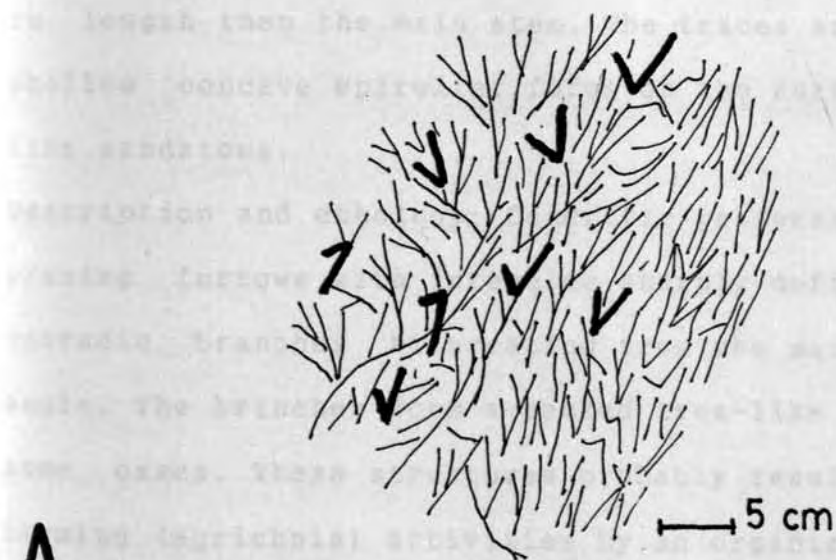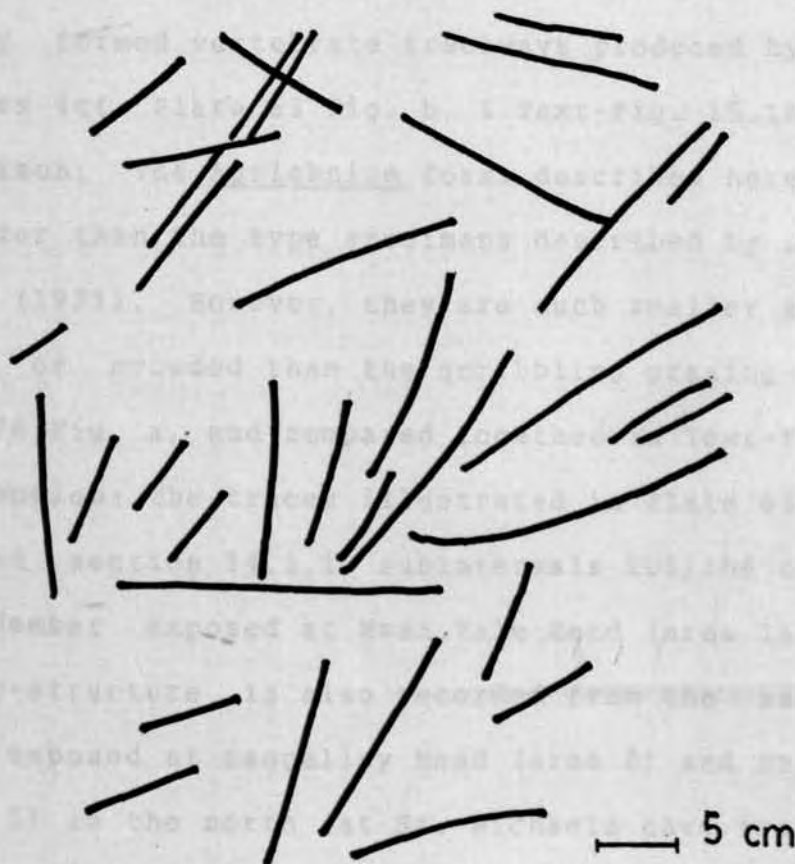
TEXT-FIG. 15.1.

in the case of dendritic forms, with well defined but very thin irregular wall-lining. The first-order branches join the main steam at an acute angle and are much smaller in size and shorter in length then the main stem. The traces are preserved as very shallow concave epirelief forms on the surface of a bed of very fine sandstone.

Description and ethology: Dendritic patterns of small subparallel grazing furrows with irregular sharply-defined edges, and with sporadic branches bifurcating from the main stem at an acute angle. The branches form a packed tree-like branching pattern in some cases. These structures probably resulted from grazing or farming (agrichnia) activities by an organism of unknown biological affinity. The width of the individual furrows is 0.1 cm to 0.3 cm and the length as much as 10 cm. At one locality these structures are associated with and are partly disrupted by subsequently formed vertebrate trackways produced by small running reptiles (cf. Plate 63 Fig. b, & Text-Fig. 15.1A).

Comparison: The Agrichnium forms described here are much longer and wider than the type specimens described by Ludwig (1869) and Hundt (1931). However, they are much smaller and more closely packed or crowded than the scribbling grazing-traces shown in Plate 76 Fig. a, and compared together in Text-Fig. 15.1)

Distribution: The traces illustrated in Plate 63 Fig. b are from measured section 14.1.1, subintervals ID5/ID6 of the Lower Newport Member exposed at Mona Vale Head (area 14). This type of grazing-structure is also recorded from the same stratigraphic level exposed at Bangalley Head (area 8) and St. Michaels Cave (area 5) in the north (at St. Michaels cave trace fossil subin-

tervals ID5 and ID6 occur as separate stratigraphic intervals but at Mona Vale Head and Bangalley Head they occur together as a coalesced, non-differentiable interval).

Studied material: Agrichnium occurs within trace fossil subintervals ID5 and ID6 at St. Michaels cave and within a coalesced interval (i.e. ID5/ID6) correlative with these two subintervals to the south at Mona Vale Head and to the north at Bangalley Head. The traces illustrated in Plate 63 Fig. b occur in trace fossil subinterval ID5 at Mona Valley Head. Photographs of the Agrichnium traces have been taken at the other two localities but are not documented here. No rock samples containing Agrichnium have been collected from any of these three localities.

Preservation and association: The specimens are preserved as concave-epirelief forms on the surface of beds of very fine sandstone, overprinted at the Mona Vale Head locality by running trackways produced by small reptiles (cf. Text-Fig. 15.1A). At St. Michaels cave and Bangalley Head Agrichnium occurs unassociated with any other trace fossils.

Ichnofacies and palaeoenvironmental affinities: These grazing-traces can occur both in marine deeper-water environments (typical of the Nereites ichnofacies) or in shallow-water brackish-marine environments but in either case the environment must typically be quite and calm (i.e., low-energy conditions).

Where the vertebrate trackways overprint the grazing-trails at Mona Vale Head the environment must either have been inundated by very shallow water (i.e., a few centimetres depth) or else subject to periodic and perhaps brief (?diurnal) exposure. Where

444

Agrichnium occurs unassociated with other trace fossils at St. Michaels Cave and Bangalley Head its ichnofacies affinities are unclear on this basis. However, its occurrence at these two localities in a sandstone lithofacies containing sporadically rippled cross-laminated phases gives no reason to doubt that the environment of deposition was a shallow, probably brackish-marine one. The affinities of _Agrichnium_ in the study area would there-fore seem to relate either to the _Cruziana_ or the _Skolithos_ ichnofacies.

Scribbling grazing- and feeding-traces
Plate 76, Fig. a

Remarks (diagnostic features): Long straight or slightly-curved concave-expirelief thin furrows, probably resulting from grazing or feeding activities or both.

Description: Long straight or gently-curved concave-expirelief thin furrows, probably due to grazing, feeding, or both by an unknown producer. Most of the structures are preserved as epichnial grooves infilled by sediment essentially the same as in the host rocks except that the boundary of the traces is well defined by concentrations of darker and probably finer sediment. The infilling sediment looks to have formed passively from the surrounding host rather than actively by faecal stuff produced by the organism itself. The width of individual traces is 0.5 cm and the length as much as 20 cm.

Distribution: The traces illustrated in Plate 76 Fig. a are from measured section 8.1.1, and trace fossil subinterval IE1 of the Lower Newport Member at Bangalley Head (area 8). These structures

also occur at the same horizon south of St. Michaels Cave (area 5).

Studied material: No specimens of these traces have been retrieved from the field. They have been photographed at both the abovementioned localities but are documented in Plate 76 Fig. a only from the Bangalley Head area.

Preservation and association: These scribbling/grazing traces are impressed as half- or full-epirelief forms on the surface of a bed of very fine sandstone. In the bed in which they occur they are not associated with any other trace fossils, only with plant remains. However, numerous other kinds of trace fossils indicative of the _Skolithos_ ichnofacies occur in the immediately overlying beds of this same trace fossil subinterval (Enclosure III.4). Hence, on this basis, the scribbling/grazing-traces can also be referred to the _Skolithos_ ichnofacies.

Ichnofacies and palaeoenvironmental affinities: This type of scribbling/grazing-trace belongs to ichnofacies of deeper environments but can also be developed in tranquil shallow-water environments. As argued in the foregoing section, these scribbling/grazing-traces in the study area belong to the _Skolithos_ ichnofacies.

15.3. RESTING TRACES

15.3.1 Ichnotaxonomy

<u>Rusophycus ?</u>

Plate 68, Figs. a - d

Specific assignment: Specimens of short bilobate-shaped buckle-like (rusophycid), and some irregularly-shaped (or weakly bilo-

bate) resting-traces (cubichnia) probably produced by an arthropod, preserved on the sole surface of sandstone beds.

Remarks (diagnostic features): Specimens are short bilobate or bean-shaped and irregularly-shaped (weakly bilobate) with highly irregular scratch marks impressed only on the edges. The median furrow or depression between the two lobes are well defined in the best preserved forms (Plate 68, Figs. b & c), but are not very clear in weakly bilobed examples (Plate 68, Fig. d). The anterior part of the burrow is wide, and subspherical or rounded and the V-shaped median furrow is also wider at this (gaping-) end (Plate 68 Figs. b & c). The posterior part of the burrow is more narrow and the angle of the V-shaped furrow is more acute (tapering-end).

Description and ethology: Specimens are preserved as casts on the sole surfaces of beds of fine sandstone. These bilobed- to irregularly-shaped structures are 2 to 3 cm wide, up to 5 cm long, and as much as 1.5 cm deep. Scratch marks are not very prominent on the surface of the lobes, but occur only on the edges of the burrows (probably because of poor preservation in the fine sand and possibly because they have been destroyed by bottom currents). The anterior part of the traces is subspherical with central V-shaped furrow/depression 0.5 cm wide and a few millimetres deep. The posterior portion is weakly bilobate, irregular or subrounded with narrower V- or without the V-shaped furrow structure. Measurements are only possible in the best-preserved examples. These bean-shaped bilobed resting-structures are not associated with or connected to generically related

crawling-traces (Cruziana) which are absent from the rocks of the study area (cf. Text-Fig. 15.2). These structures are undoubtedly produced by resting excavation made by an arthropod digging into the sediment to rest there temporarily for shelter, or for repose, or for incubation (cf. Dawson, 1864).

The parallel alignment of resting-traces to the bottom current (observed especially in the case of trilobite traces) has been documented many times in the literature (e.g. Birkenmajor & Bruton 1971). The most common orientation recognized in resting-traces produced by arthropods and other organisms relative to the direction of the bottom currents is one which places the anterior (more circular and wider V-shaped gaping-end) in the up-current position and the posterior (narrow V with tapering-end) in the down-current position. In the study area the Rusophycus-like traces show this kind of preferred arrangement in the case of the examples illustrated in Plate 68 Fig. a and other clusters of the same kind of traces elsewhere in the same bed. These are aligned in the direction 005°/185° and with their gaping-ends pointing to the south. However, no traction-produced sedimentary structures which can be used as independent current indices occur in the same bed so that no independent check can be made on the south-to-north bottom current that is implied by these resting-traces. The documentation in the literature (e.g. Birkenmajor & Bruton, 1971) of the preferred orientation of `smooth-lobed trilobite' resting traces (Rusophycus) parallel to the water current, helps to explain possible modes of formation of these smooth-lobes. In explaining the formation of the smooth-lobes we can assume that the anterior part of the arthro-

448

TEXT-FIG. 15.2. Reconstruction of the best preserved example
bilobed rusophycid-like resting trace (cf. Plate 68 Fig. b)
characterized by smooth lobes and appendages marks preserved as
short grooves on the edges. Also shown (though not present in
association with the resting traces in the study area) is a
schematically reconstructed crawling trace (repichnia) of the
producer organism and the suggested boundary between the resting
and crawling behavioral categories idealized in the frame at top.
The anterior/posterior orientation of the organism can be
reconstructed on the basic of the longitudinal asymmetry of the
resting trace because the lobes are deeper and wider at the
anterior and implying also (together with a common alignment of
associated similar resting traces) a bottom current (arrow B)
directed posteriorly with respect to the orientation of the
organism.
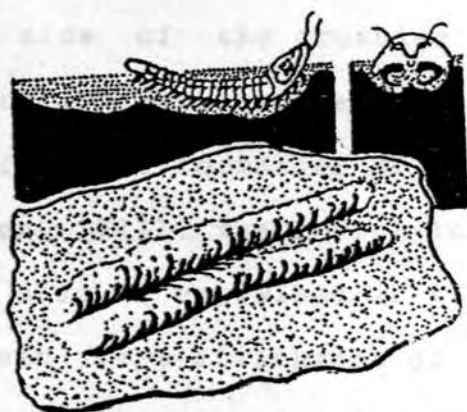
REPICHNIA | CUBICHNIA

BOUNDARY.

LENGTH
up to 5 cm

B CURRENT

ANTERIOR

WIDTH
2 to 3 cm

POSTERIOR

A

DIRECTION OF ANIMAL
MOVEMENT

ETHOLGICAL

DEPTH
0·1 to 0·5 cm

Cruziana

(CRAWLING BEHAVIOUR)
(Not indicated in the study
specimens)

Rusophycus

(RESTING BEHAVIOUR)

TEXT-FIG. 15.2.

pod was lifted slightly above the bottom (cf. Text-Fig. 15.2)
thus allowing the water current to sweep through under the ven-
tral side of the organism to oxygenate the gill areas. This
explanation assumes that the water current was largely responsi-
ble for the formation of some smooth rusophycids (Birkenmajor
&Bruton, 1971). The smooth-lobes with scratch marks on the edges
might also be explained if it is assumed that the animal tried to
maintain firm attachment of its body to the substrate while the
water current moved under its body. The organism will be taken
away by the current if its attachment is not secure. Only very
rarely is there likely to be preservation of the full body im-
pression of producer organism under such conditions of bottom
current activity.

Comparison: The presently described traces are not sufficiently
well preserved to show detailed imprints of segments, pygidia,
spines or other anatomical parts of the arthropod or arthropod-
like producing organism. But, these rusophycid traces can never-
theless be allied with the short bilobate buckle-like resting-
traces produced by trilobites or trilobite-like organisms. With
regard to forms intermediate between _Cruziana_ and _Rusophycus_,
these rusophycid structures are often regarded as synonymous
with _Cruziana_ (Seilacher, 1970). Seilacher proposed combining all
presumable `resting-traces', `resting-nests', and `resting-bur-
rows' of trilobites or trilobite-like organisms in the one genus
`Cruziana'. But, _Rusophycus_ (i.e. resting-traces of trilobites)
can stand alone for distinctive ethological resting behavior,
whether the rusophycid traces are or are not associated with or

connected to the genetically related crawling-traces (Cruziana). The boundary between these two ichnogenera can be readily drawn on the basis of ethological criteria (see Text-Fig. 15.2). These crawling- and resting-traces must be considered separately and regarded as different ichnogenera on account of their different ethological origin. Discrimination between these two ichnogenera is also recommended by Lessertisseur (1955), Seilacher (1955), and Osgood, (1970), Birkenmajor & Bruton (1971), and Crimes (1975). The presently described resting-traces are similar to but are larger than the resting-trace known as Sagittichnus Seilacher (1953), which also occur in rheotactically arranged clusters.

Distribution: These resting-traces occur only in subinterval ID4 of the lower Newport Member at Bilgola Head (area 10a) and in subinterval IE1 of the Middle Newport Member at Bungan Head (area 13).

Studied material: The specimens described here (Plate 68, Figs. a - c) are from measured section 13.1.1, subinterval IE1 of the Middle Newport Member exposed at Bungan Head (area 13); the specimen illustrated in Plate 68 Fig. d is from measured section 10a.2.1, subinterval ID4 of the Lower Newport Member exposed at Bilgola Head (area 10a). None of the specimens have been re-trieved from the field.

Preservation and association: All of these traces are preserved as bean-shaped or weakly-bilobed irregularly-shaped convex-hy-porelief casts on the sole of sandstone beds. They are not asso-ciated with any other trace fossils or the hard-part remains of their producers. These structures imply a preferred current-parallel orientation in the case of the best preserved examples.

No body impressions, lift-off structures, or associated crawling-traces (_Cruziana_) are indicated.

Ichnofacies and palaeoenvironmental affinities: These resting-traces belong to the _Skolithos_ ichnofacies, probably developed in tidal-channels, mixed-flat, sand-flat, or tidal facies in a river-dominated estuary or lagoon.

Pelecypodichnus Seilacher, 1953

Lockeia James, 1879.
Umbonichnus czarnockii Karaszewski, 1974.

Plate 76, Figs. d - f

Generic assignment: Symmetrical bilobed almond-shaped, elongated traces, preserved in convex-hyporelief, produced by resting behavior of bivalve molluscs. The trace lacks any underlying escape-root when seen in bedding-normal section.

Specific assignment: _Pelecypodichnus_ sp?

Remarks (diagnostic features): Hypichnial, bilaterally-symmetrical bilobed almond-shaped resting-traces with variable strong to weak biconvexity of the tear- or drop-shaped plan-view outline produced by the articulated valves of a pelecypod. The almond-shaped asymmetry manifests the identical anterior-posterior asymmetry of the producer bivalve. On the wider (less angular) end of the trace, additional disturbance of the host sediment may occur and may manifest motion of the animal's foot.

Description and ethology: Many workers have described these almond- or tear- or drop-shaped traces as bivalve resting-traces with or without the presence of an underlying escape-root (Seilacher, 1953; Hallam, 1970; Osgood, 1970; and Hakes, 1977)

(see also Text-Fig. 14.2). In the present study, the escape behavior of bivalves as manifested by the presence of escape burrows (fugichnia, Simpson, 1975) (commonly terminated upwards by overlying resting impressions) is described separately from the resting-traces (cubichnia). These escape-burrows are described in the Chapter 14 of this report. Many of the bivalve resting-traces are accessible for study in vertical sections in the field and almost all of them lack downturnings of the sedimentary laminae in the central portion (which, if present would generate a V-shaped pattern of layering indicative of orderly escape).

These resting-traces of bivalves occur in groups or cluster in which the long axes of each individual trace lacks a preferred orientation. The average length of the individual traces is about 0.7 cm to 1 cm and their width is about 0.5 cm. These almond-shaped bilaterally symmetrical resting traces of bivalves normally are more angular at one end (Plate 76, Figs. d & f) but this degree of lengthwise asymmetry may be weaker and more irregular in some cases (Plate 76, Fig. e).

Comparison: In the material of the present study the traces referred to the ichnogenus Pelecypodichnus are of smaller size (in respect to both length and width) than those of P. amygdaloides described by Seilacher (1953), and those of Umbonichnus czarnockii described by Karaszewski (1974).

Distribution: The traces illustrated in Plate 76 Fig. e are from trace fossil subinterval IE1 of the Middle Newport Member at Mona Vale Head (area 14), and those in Plate 76 Figs. d and f are from trace fossil subinterval ID5/6 of the Lower Newport Member

at Bilgola Head (area 10b).

Studied material: The traces shown in Plate 76 Fig. d are the only ones that have been retrieved from the field (sample 1007/MU.44429), from trace fossil subinterval ID5/6 of the Lower Newport Member at Bilgola Head. Other traces illustrated in the plates have not been retrieved from the field.

Preservation and association: All of the traces studied here are preserved as convex hyporelief forms in very fine sandstone units. They are not associated with any other trace fossils.

Ichnofacies and palaeoenvironmental affinities: In the study area the resting-traces of bivalves occur in the Skolithos ichnofacies of shallow brackish-marine estuarine or lagoonal palaeoenvironments.

Addendum: The above treatment of this ichnotaxon follows mainly Seilacher (1953) in regard to taxonomic nomenclature. Since completing this section I have become aware of the recent paper by Maples & West (1989) in which they claim that the name Lockeia James, 1879, is not invalid as suggested by Seilacher (1952, 1953), and that for this and other reasons the name Lockeia should replace Pelecypodichnus. Although I am in agreement with the argument of Maples & West (1989) time constraints have prevented revision of this section as well as that dealing with escape-structures (Chapter 14) in accordance with their arguments.

15.4. VERTEBRATE TRACKWAYS

15.4.1. Summary review of existing classifications

The classification of vertebrate trackways (footprints)

occupies a separate problematical area in the classification of trace fossils and has been reviewed most recently by Sarjeant (1975). Sarjeant's review forms the basis of the present summary. The earliest application of a formal taxonomic name to vertebrate tracks was by Kaup (1835) on some hand-like imprints in a German Triassic sandstone. The earliest series of classifications of vertebrate trackways were advanced by Hitchcock (beginning in 1836), initially under the discipline of `Ornithoichnology'. The culmination of his classifications was based on the inferred animal that produced the trackways and not on the animal's ethology or behavior that led to the trackway being formed. Possibly because of the numerous revisions that were involved in the evolution of Hitchcock's classification it ultimately failed to secure widespread acceptance (Sarjeant, 1975).

The renowned German palaeontologist W. Pabst modified Hitchcock's classification in 1900 and attributed all tracks encountered to the single genus 'Ichnium'. However, this classification was also mainly based on the inferred palaeontology of the producer animal rather then on palaeoichnological criteria. A similar type of classification was used by Lull (1915ᵗ, 1953) for fossils tracks from the Connecticut Valley (USA). The Hungarian palaeontologist Ferenc Nopcsa (1923) also attempted a comprehensive review of all amphibian and reptile tracks. Nopcsa's classification has no formal hierarchal order and his six categories are named according to the inferred producing taxa.

Kuhn (1958) reviewed fossil reptilian and amphibian tracks, placing post-Permian reptile tracks into osteologically

based suborders but listing all Carboniferous and Permian tracks alphabetically by trace generic names; he made no attempt to assign amphibian trackways to systematic categories. Not all palaeoichnologists have adopted his approach but an alternative scheme of approach was proposed by Vialov (1966). In his proposal the hierarchal order is comparable in many ways with Hitchcock's classifications (1841, 1843, 1844). He collected together all tracks and trails into the Zooichnia (Vivichnia), divided into vertebrate and invertebrate traces. His approach to the classification of tracks and trails is more logical, and stands alongside the classification of body fossils and living animals and is described by Sarjeant (1975, p. 299) as "conceptually excellent". In 1972 Vialov proposed a very comprehensive modified classification of both vertebrate and invertebrate tracks and traces (and other signs of animals' physiological functions) based on animal function. However, this classification has not been used by palaeoichnologists and appears unlikely to prove helpful in the organization of data because it is difficult to apply in practice. The latest views concerning a proposed code of nomenclature for all trace fossils, including vertebrate trackways, was given by Sarjeant & Kennedy (1973), but at the present stage no single system for the classification of vertebrate footprints has secured general acceptance by ichnologists.

15.4.2. A proposed new classification of vertebrate trackways

The proposed classification of vertebrate trackways (cf. Text-Fig. 15.3) deals only with vertebrate trackways (including tail and body drag-marks) and incorporates ideas based mainly on ethological background reviewed by Sarjeant (1975).

TEXT-FIG. 15.3. Proposed classification of vertebrate trackways and associated drag-marks produced by vertebrates (in part after Sarjeant, 1975). Asterisks indicate track types that are present in the study area.

VERTEBRATE TRACKWAY

PRODUCED BY FINS AND BODY

PRODUCED BY LIMB(S)

PRODUCED BY TAIL AND BODY.

FISH RESTING SWIMMING AND PARTLY BURROWING

REPTILE OR AMPHIBIAN GAIT (INDIVIDUAL PRINT) AND BIRD TRACKS.

MAMMALIAN GAIT (COMPLETE STEP)

*Tail drag-mark & body drag-marks.

WALKING GAIT *

WALKING & RUNNING GAIT TYPE A

RUNNING GAIT * TYPE B

PLANTIGRADE

SEMIDIGITIGRADE

DIGITGRADE

CLEAR PALM PRINT (PES & RAMUS)

(with tridactyl or tetradactyl)

ONLY FRONT OF THE PALM IS IMPRESSED (PES & RAMUS)

ONLY TOE PRINT WITHOUT PALM (PES ONLY)

Run slow

Run fast

* III II

* III II (case 1)

TYPE A2   SOFT PART   TYPE A1

IV
TRIDACTYL
Moodieichnus tridactylus

IV (case 2)
III
DIDACTYL

WEBBED FOOT | NORMAL FOOT

Moodieichnus didactylus (Sarjeant,1971)

ROTARY GALLOP GAIT

SPRINGING GAIT

BOUNDING GAIT (hop, jump)

The morphology of soft parts, size and shape of palm and digit, number of digits, interdigital angle, step angle, measurement of stride (s), pace (p) and print position from midline are used as criteria in the lower levels (species and variety) of the classification.
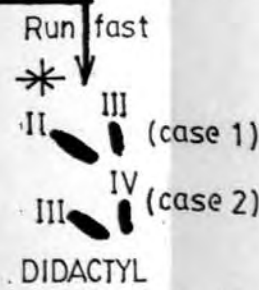
var.1 (running cursorial) imprints aligned M.didactylus var. permiansis

var.2 * (running saltatorial) imprints random M.didactylus var. triassicus

Forelimbs (1&2) used only for stabilisation

STRONG FORELIMBS

WEAK FORELIMBS

Movements of four limbs synchronised

EXPLANATION OF MAMMALIAN GAIT

LM ● 1. Print of left manus (left forelimb).
RM ● 2. Print of right manus (right forelimb).
RP ● 3. Print of right pes (right hindlimb).
LP ● 4. Print of left pes (left hindlimb).

↑ Direction of animal movement.

② Step two.

① Step one.

Four imprints (1-4) in wider grouping.

Four imprints (1-4) in closer grouping

L.M2
LP2
R.M2
RP2
LM1
LP1.
RM1
RP1

TEXT-FIG. 15.3.

457

TABLE 15.1. Morphological criteria and ethological inferences used in the proposed classification of vertebrate trackways (including body and tail drag-marks) made on essentially horizontal or near horizontal ground (cf. Text-Fig. 15.3).

(I) Significant features (supra-generic level).

- (1) Taxonomic or biological affinity of the producer (i.e., reptile, amphibian, or mammal).
- (2) Anatomical parts preserved as impressions (e.g., limb impression, or tail drag-marks etc.).

(II) Major accessory features (generic level).

Mode of locomotion (behavior or ethology of the animal: e.g., hunting for prey or fleeing from predator).

- (1) Walking gait.
- (2) Running gait.
- (3) Galloping gait.
- (4) Springing gait.
- (5) Bounding gait.

(III) Minor accessory features (specific and varietal levels).

- (1) Size and shape of palm and digits.
- (2) Number of digits (didactyl, or tridactyl etc.).
- (3) Running cursorial or saltatorial.
- (4) Interdigital angle.
- (5) Distance of stride (s) and pace (p); step angle (pace angulation), and print position from midline.
- (6) Presence/absence of imprint soft parts (webbing) and their/its morphology.
- (7) Relative strongness and weakness of the limb imprints.
- (8) Other features.

The morphological criteria and ethological inferences on which the classification is based are detailed in Table 15.1. This classification separates trace fossil ichnotaxa from the inferred producer animal taxa and in this respect departs from the approach embodied in several previous classifications (Hitchcock, 1841 & 1844; Vialov, 1966 & 1982). The classification deals primarily with trackways that were made on essentially horizontal or near-horizontal surfaces (which is commonly the case in fossil trackways) and does not attempt to address or incorporate the mechanical/dynamical complications that arise in the case of trackways that were made on inclined surfaces (cf. Sherwin, 1969; Matsukawa & Obata, 1985; & Allen, 1989).

In the proposed classification there are two major groups of trackways classified according to the type of producer organism: namely (1) reptiles or amphibians; and (2) mammals. Reptile and amphibian trackways are quite similar, commonly difficult to distinguish, and hence are best grouped into a single category.

The classification of the latter group is based on the individual shape of the limb impression (this can be right or left, or manus or pes). The shape of imprint of the palm is the most important feature in the classification because it reflects the natural behavior of the animal during the making of the imprints. The plantigrade gait manifests normal walking (normal locomotion) and results in a track with a clear full-sized palm imprint. The semidigitigrade gait results from a mode of locomotion that is intermediate between walking and running (referred

to here as active locomotion) and produces a track in which only the frontal part (frontal mounds) the palm is impressed. The digitigrade gait manifests a running mode (swift locomotion) which results in a track showing only the toe (digit) imprints, either tridactyl or didactyl (cf. Text-Fig. 15.3). However, departures from these simple patterns and relationships characterize vertebrate trackways made on inclined surfaces (e.g., Sherwin, 1969; that Matsukawa & Obata, 1985; Allen, 1989) and such cases must be examined specially and in the context of their own particular palaeotopographic situation.

The second major group of trackways is produced by the mammals. The classification of the mammalian trackways is also based on ethology, and the trackways are differentiated according to whether they reflect galloping, springing, or bounding gaits (Text-Fig. 15.3). Mammalian trackways are not discussed here further because they are not present in rocks of the study area. A third group of tracks produced by fishes (Text-Fig.15.3) is also excluded here for the same reason. The fourth group of tail and/or body drag-marks produced by reptiles or amphibians is included in the classification. These latter types of structures are associated with labyrinthodont trackways in the Turimetta Head area in subinterval IC5.2 (Text-Fig. 15.3, and Plate 69 Figs. i & j).
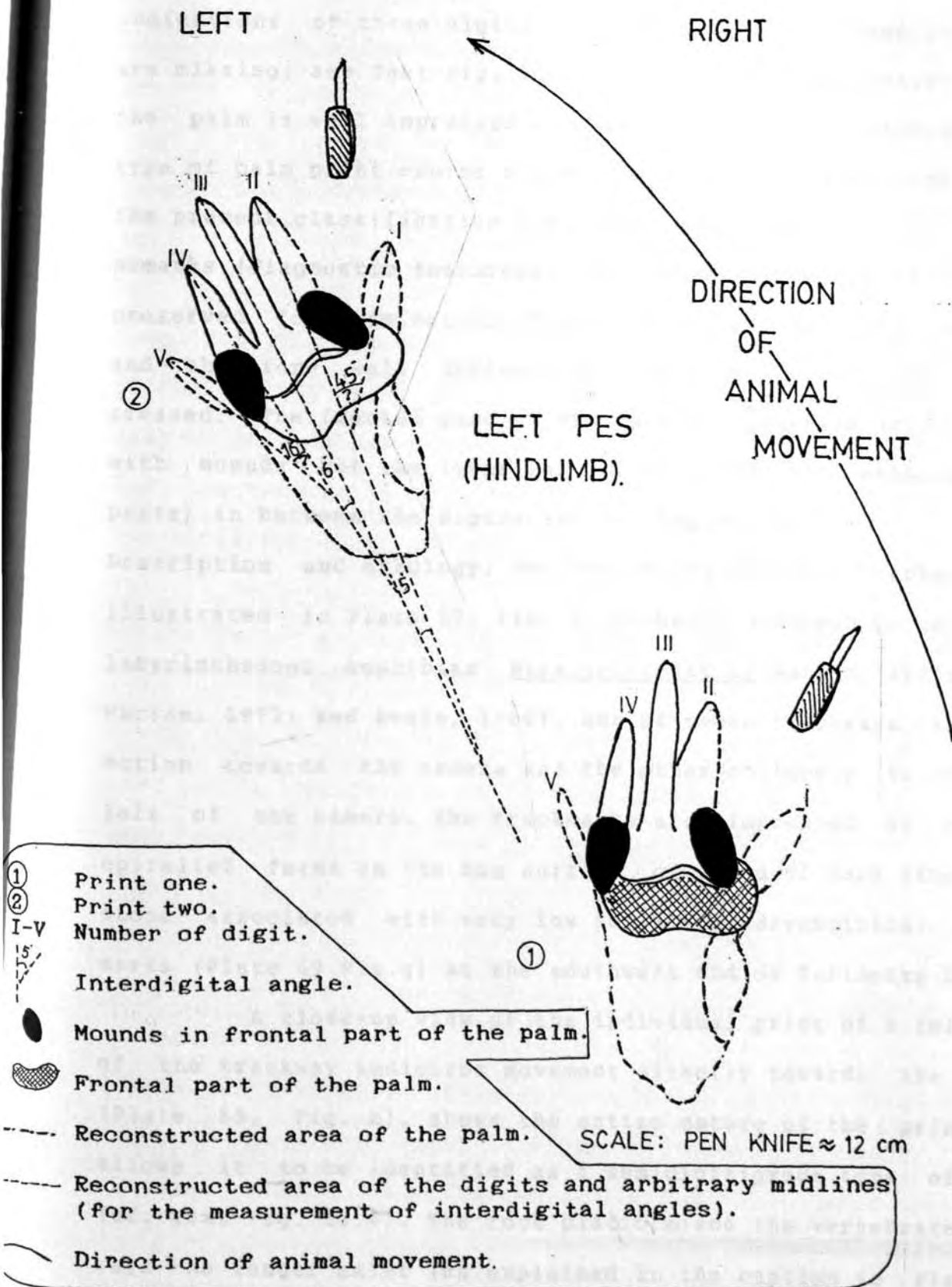
15.4.3. Ichnotaxonomy

Trackway type A1

(Large tetrapod trackways without indications of webbing)

Plate 69, Figs. a & b

TEXT-FIG. 15.4. Reconstruction of imprint and gait of the left pes of the large tetrapod trackway (Type A1) illustrated in Plate 69 Figs. a & b. Measurement of the interdigital angles of the hindlimb are made by arbitrary choice of midlines for digits (in print two). This type of measurement defined the nature and orientation of the digits diagrammatically and allows comparison with the other prints. In this illustration two left hindlimbs are put together in series (but not to scale and not in a straight line) to dramatize the semidigitigrade behavior of the animal. Digits III and IV are well preserved in the trackway but digits I and V and part of II are reconstructed. The frontal mounds of the palm are well preserved.

TEXT-FIG. 15.4.

Legend within figure:

LEFT

RIGHT

DIRECTION
OF
ANIMAL
MOVEMENT

LEFT PES
(HINDLIMB).

① Print one.
② Print two.
I-V Number of digit.
15° Interdigital angle.
● Mounds in frontal part of the palm.
▨ Frontal part of the palm.
---- Reconstructed area of the palm.
----- Reconstructed area of the digits and arbitrary midlines
(for the measurement of interdigital angles).
⌐ Direction of animal movement.

SCALE: PEN KNIFE ≈ 12 cm

Type assignment: Large tetrapod trackways in with there are indications of three digits (i.e., digits II, III and IV; I, V are missing; see Text-Fig. 15.4) and in which the frontal part of the palm is well impressed without indications of webbing. This type of palm print can be classified as a semidigitigrade form in the present classification (cf. Text-Fig. 15.3).

Remarks (diagnostic features): Only three digits out of five are preserved for examination. Digits II and III are well impressed and therefore well defined, but digit IV is only partly impressed. The frontal part of the palm is impressed very clearly with mounds but the lower part of the palm and webbing (soft parts) in between the digits are not impressed.

Description and ethology: Two vertebrate tetrapod trackways are illustrated in Plate 69, Fig. a, probably produced by the large labyrinthodont amphibian Paracyclotosaurus Watson (1958) (cf. Warren, 1972; and Beale, 1986). One of these trackways indicates motion towards the camera and the other obliquely towards the left of the camera. The trackmarks are impressed as concave-epirelief forms on the top surface of a bed of very fine sandstone associated with very low amplitude asymmetrical ripple-marks (Plate 69 Fig.g) at the southwest end of Turimetta Head.

A close-up view of the individual print of a left pes of the trackway indicates movement directly towards the camera (Plate 69, Fig. b), shows the entire nature of the print, and allows it to be identified as a semidigitigrade type of print (cf. Text-Fig. 15.4). The rock platform and the vertebrate trackways no longer exist (as explained in the caption to Plate 69) and I do not have close-up photographs of the second trackway.

However, it appears from what can be seen of it in Plate 69 Fig.a that it is similar in gait to the first trackway. Hence the behavior of the amphibians that produced these prints at the time must have involved active locomotion and this was approximately towards the southwest, possibly chasing or searching for prey. No body or tail drag-marks occur in association with these particular trackways at Turimetta Head consistent with the observation that amphibian animals normally perform this mode of active locomotive behavior (in semidigitigrade gait) by raising up their body as well as their tail above the ground. Another explanation for the absence of tail and body drag-marks associated with the two trackways shown in Plate 69 Fig.a could be that the producer animals were walking in shallow water with their bodies and tails buoyed-up by the water clear of the substrate.

In the left pes impression shown in Plate 69 Fig.b digits II, III, and IV are preserved together with the frontal part of the palm with clearly impressed mounds in what must have been soft very fine sand at the time the imprints were made. Digits I and V and the lower part of the palm are not preserved and hence must be reconstructed (cf. Text-Fig. 15.4); the probable interdigital angles for digits II, III, and IV are also reconstructed.

Comparison: Trackways of large vertebrates in the Permo-Triassic rocks of the Sydney Basin have been documented by Harper (1907), Fletcher (1948), and Sherwin (1969) but the first systematic study was carried out by Pepperell & Grigg (1973) in the roof of a sewerage tunnel in the Middle Triassic Ashfield Shale at the

base of the Wianamatta Group. Fossil bones of <u>Paracyclotosaurus</u> have been discovered in recent years by an amateur fossil hunter in the Bald Hill Claystone at Long Reef (Beale, 1986) a few kilometres south of Turimetta Head. Because of the large size of the palm in the pes illustrated in Plate 69 Fig. b, and the interdigital angles, and because the only fossil tetrapod presently known from this formation is an amphibian, it is conceivable that the trackway maker was likewise the same large labyrinthodont amphibian <u>Paracyclotosaurus</u>. This adult amphibian is thought to have been an a fearsome 3-m-long animal with large teeth, webbed feet, and eyes located on the top of the head (Watson, 1958; and Warren, 1972). It has been suggested (Chernin & Cruikshank, 1978) that it hunted as modern crocodiles do, lurking near the shore until it could lunge up to grab its prey and drag it into deeper water. Absence of evidence indicating body or tail drag-marks suggests either that the animal may have been wading in shallow water so that the body was buoyant and hence above the substrate or that the animal was capable of moving with its body clear of the ground (a characteristic behavior in the semidigitigrade and digitigrade gaits). In the literature of vertebrate trackways body and tail drag-marks have been documented in some tetrapod trackways, especially when the animal became more plantigrade in its locomotion and the body and tail were in touch with the ground during movement (e.g., Sarjeant, 1975, fig. 14.4). But such body and tail drag-marks are not associated with the presently described semidigitigrade type A1 trackways. Webbing between the digits is not indicated in either pes or manus. This is also true in the case of the labyrintho-

dont trackway from the Middle-Triassic Ashfield Shale described Pepperell & Grigg (1973). The webbing between the digits is not normally impressed in the case of tracks made by modern animals because it is a soft membrane.

Distribution: In the study area these type A1 tetrapod trackways are presently known only from trace fossil subinterval IC5.2 in the topmost part of the Bald Hill Claystone at Turimetta Head (area 2; Enclosures III.4 & III.8).

Studied material: The rock platform featuring the two trackways described here from Turimetta Head no longer exists, having been destroyed by the (Sydney) Metropolitan Water, Sewerage and Drainage Board in the early 1970's during engineering work associated with the construction of a sewage outlet. Figures a and b of Plate 69 were made from colour transparencies taken by Dr. P.J. Conaghan, Earth Sciences, Macquarie University, in 1970 or 1971. The present reconstructions have been based exclusively on these photographs. The recent discovery of fossil bones (Beale, 1986) of the amphibian Paracyclotosaurus from the same formation at Long Reef (5 km south of Turimetta Head) provides circumstantial evidence that the trackways at Turimetta Head were produced by the same amphibian.

Preservation and association: These trackway occurred as concave-epirelief forms in very fine sandstone. This sandstone bed also contains plant remains and Planolites but no other trace fossils. Very low amplitude ripple-marks and plant remains occur in the immediately underlying and overlying beds but no Planolites. Vertebrate body and tail drag-marks also occur in the

immediately overlying bed together with <u>webbed</u> tetrapod foot-
prints (i.e., type A2 footprints) and the same body and tail
drag-marks occur in the immediately underlying bed but without
associated footprints.

Ichnofacies and palaeoenvironmental affinities: The inferred
producer labyrinthodont amphibian is related to modern
amphibians, and these animals live on beaches or shores of
shallow brackish-water lagoons and estuaries. Association of the
trackways at Turimetta Head with asymmetrical ripple-marks im-
plies shallow parts of such water bodies. The environment is
thought to have been a fluvially-dominated muddy and silty brack-
ish coastal lake or lagoon or estuary confined by sandbars. This
association of trace fossils can be attributed to the <u>Skolithos</u>
ichnofacies.

<div align="center">

Trackway Type A2

(large tetrapod trackway with indication of webbing)

Plate 69, Figs. g & h

</div>

Type assignment: Large tetrapod trackway with well impressed
digits (II, III, and IV) and webbing. The impression of digit I?
is also well preserved behind the other three digits. The entire
shape of palm print is well preserved and can be classified as a
plantigrade form in the present classification (cf. Text-Fig.
15.3).

Remarks (diagnostic features): Digits II, III, and IV with im-
print of the entire palm are well preserved. The nature of the
left pes is shown in Text-Fig. 15.5 and in Plate 69, Figs. g and
h. The impression of the webbing can be observed between digits
II and III, and III and IV.

TEXT-FIG. 15.5. Reconstruction of imprint of plantigrade (walking) gait of the left pes of the large tetrapod trackway Type A2 illustrated in plate 69, Figs. g and h. Digits I?, II, III, IV, and the entire outline of the palm is well preserved. The impression in webbed and clawed. The animal walked slowly towards the south on a substrate of very fine sand fashioned into a train of very-low-amplitude asymmetrical ripples (linear features in diagram). The presence of inferred tail and body drag-marks (cf. Plate69 Figs. i & j) suggest the animal's body was not supported by water at the time it moved across this ground and hence suggests that the immediate area was part of a strandline that was not inundated by water at the time trackway was formed. This could mean that the trackway was formed during a period of low tide.

Direction of movement
(approximately to south)
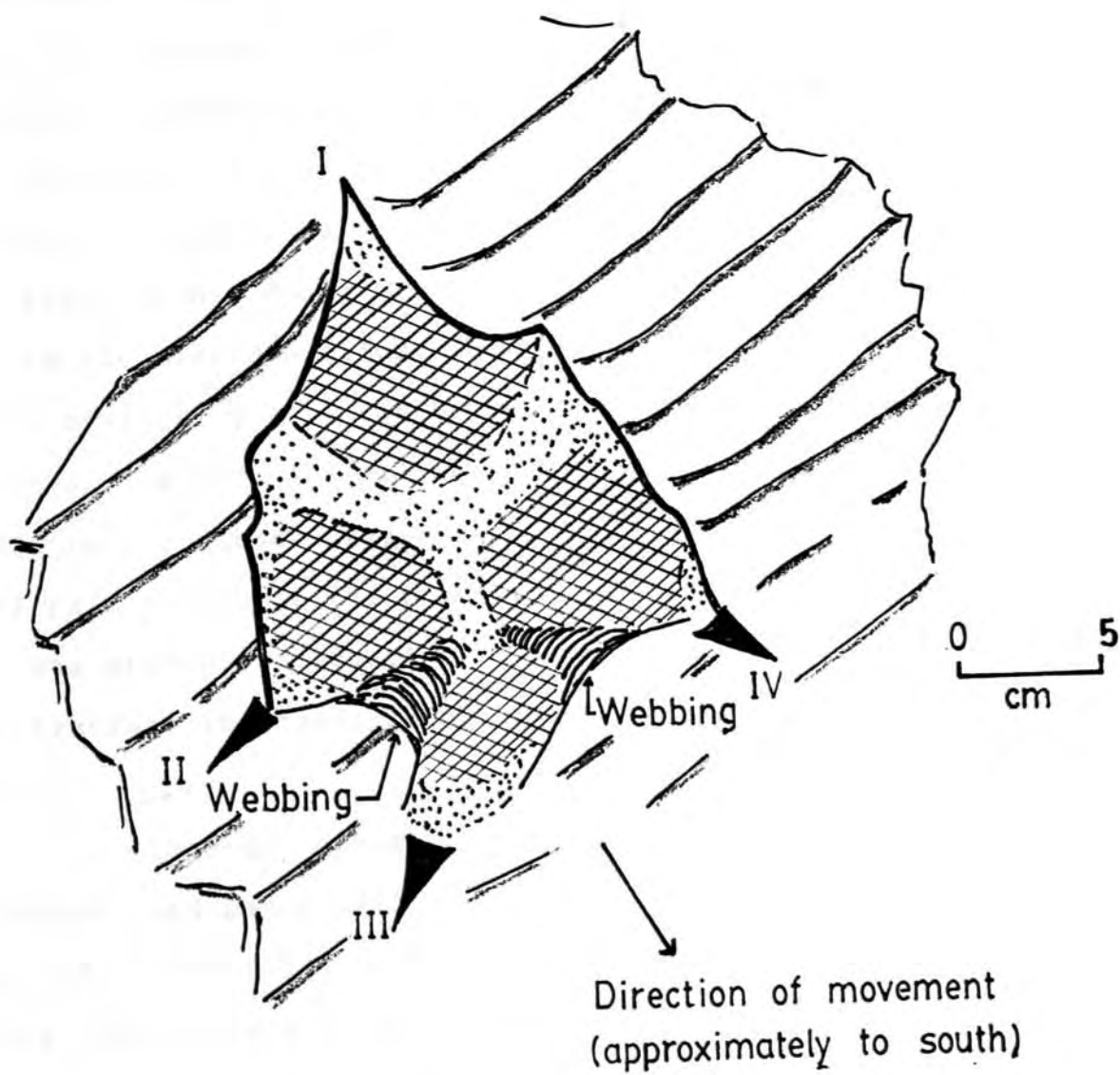
TEXT-FIG. 15.5.

Description and ethology: The track marks are preserved as concave-epirelief forms on the top surface of a bed of very fine sandstone associated linear markings (Plate 69 Figs. i & j) that appear to manifest body and/or tail drag-marks and with low amplitude asymmetrical ripple-marks (Plate 69, Figs. g & h) at the southwest end of Turimetta Head. However, the trackway is imcomplete insofar as only one of the print is well preserved, the other either being missing entirely or less well preserved due to the modern erosion. The palm print is the best preserved (Plate 69 Figs. g & h) can be reconstructed as a left pes on the basic of its left lateral relationship with respect to the inferred tail and body drag-marks and its noticeably larger size to other palm prints in the trackway. The type A2 vertebrate trackway was probably produced by a large labyrinthodont amphibian. The trackway indicates locomotion towards the south (Text-Fig. 15.5).

Close-up views of the individual print of the well impressed and hence well preserved left pes are shown in Text-Fig. 15.5 and Plate 69, Figs. g and h. The well preserved imprints of the palm allows the trackway to be identified as the plantigrade type. Hence the behavior of the producer amphibian must have involved slow locomotion towards the south. Possibly the amphibian walked slowly, intermittently touching its body and tail on the ground, which would explain the inferred well preserved body and tail drag-marks along the locomotion tracks (Plate 69, Figs. i & j).

The length of the entire palm of the left pes is about

15 cm and the width is about 10 cm on average. Approximate inter-digital angles between digits I?, II, III, and IV can be recon-structed. The interdigital angle between digits I? and II is 120°, between digits II and III is 35°, and between digits III and IV is 80°. The pointed shape of the digits can be interpreted to manifest the presence of claws. The presence of webbing denotes that the amphibian can swim fairly well like modern crocodiles. The additional presence of inferred body and tail drag-marks (Plate 69 Figs. i & j) indicates that the animal walked along the strandline of an estuary or lagoon during low tide as did the other amphibian that produced the type A1 trackways.

Comparison: Differs from the type A1 trackway in having webbing and clawed digits and also because of preservation of the entire shape of the palm and the smaller size of the latter relative to that in Type A1. The approximate interdigital angles are also different to those in the type A1 imprints.

Distribution: In the study area the type A2 tetrapod trackway is presently known only from trace fossil subinterval IC5.2 (just above the sandstone bed in which the type A1 trackway occured) in the topmost part of the Bald Hill Claystone at Turimetta Head (area 2; Enclosures III.4 & III.8).

Studied material: The studied trackways has not been retrieved from the field.

Preservation and association: The imprints of the trackway occur as concave-epirelief forms in very fine sandstone with asymmetrical very low amplitude ripple-marks. The trackway is also associated with concave-epirelief forms of body and tail drag-marks but with no other kinds of trace fossils.

Ichnofacies and palaeoenvironmental affinities: The inferred producer labyrinthodont amphibian, web-footed Paracyclotosaurus lived on beaches or shores of shallow brackish-water lagoons and estuaries as well as in fresh-water lakes as do modern crocodiles. Association of the low amplitude asymmetrical ripple-marks implies shallow parts of such water bodies. The environment is thought to have been a fluvially-dominated muddy and silty brackish coastal lake or lagoon or estuary confined by sand bars. This environment can be attributed to the Skolithos ichnofacies.

Trackway type B (running gait of small reptiles)

Ichnogenus Moodieichnus Sarjeant, 1971
Ichnospecies M. didactylus Sarjeant, 1971

Variety (1): (type species) M. didactylus var. permiansis Sarjeant, 1971)

Variety (2): M. didactylus var. triassicus

Plate 69, Figs. c, f, k & e

Specific assignment: Trackways produced by small reptile(s) manifesting running behavior, characterized by pes imprints only with two digits (probably digits II and III, and hence without impression of the palm (i.e., digitigrade didactyl gait; cf. Text-Fig. 15.3).

Remarks (diagnostic features): Running trackways of small reptiles, famous and interesting because of the extreme reduction of the impressed digits (only two present, probably digits IV and III; Moodie, 1930, and Sarjeant, 1971) and because they manifest an early history of running behavior in the reptiles before the development of flying reptiles. The trackway imprints of the pes show only two digits; one is probably of digit III which is much
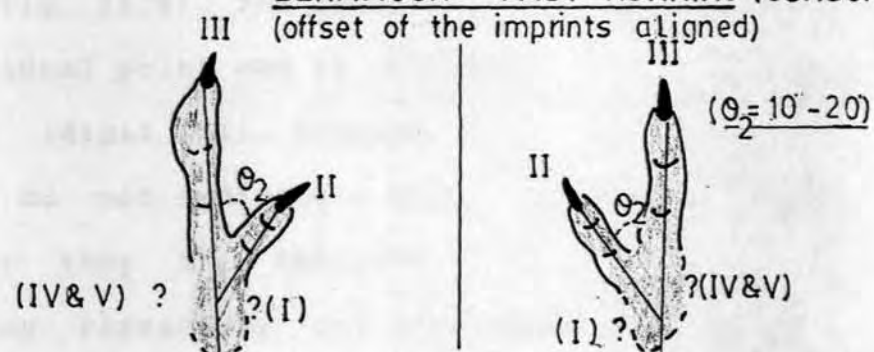
TEXT-FIG. 15.6. A – C: Ethological interpretation of didactyl and tridactyl running reptilian trackways. **D:** Orientation of the digits and related interdigital angles. **E:** Hypothetical reptiles in saltatorial running gait.
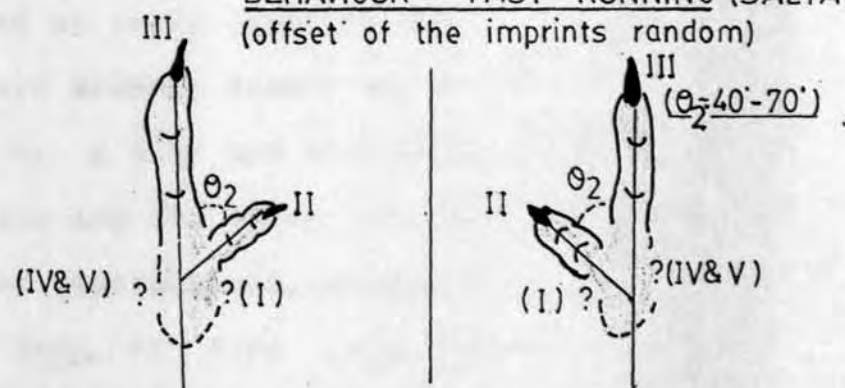
LEFT PES (LP) | RIGHT PES (RP)

A

BEHAVIOUR - FAST RUNNING (CURSORIAL)
(offset of the imprints aligned)

$(\theta_2 = 10° - 20°)$

Moodieichnus didactylus var. permiansis (Sarjeant, 1971)

B

BEHAVIOUR - FAST RUNNING (SALTATORIAL)
(offset of the imprints random)

$(\theta_2 = 40° - 70°)$

Moodieichnus didactylus var. triassicus (new variety)

C

BEHAVIOUR - SLOW RUNNING (SALTATORIAL)
(offset of the imprints random) $(\theta_2 = 40° - 70°)$
$(\theta_3 = 40° - 50°)$
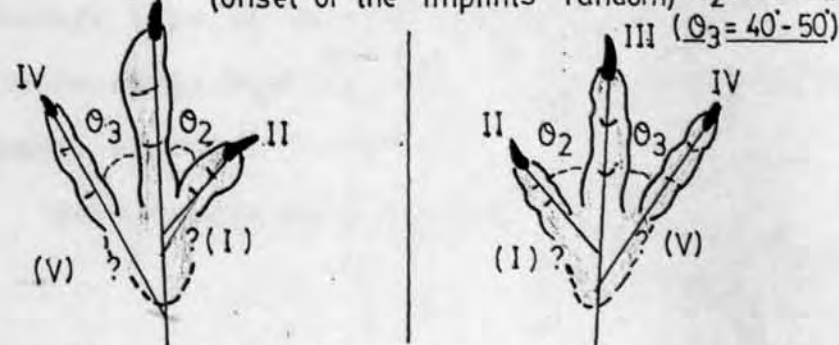
Moodieichnus tridactylus (new species)

D
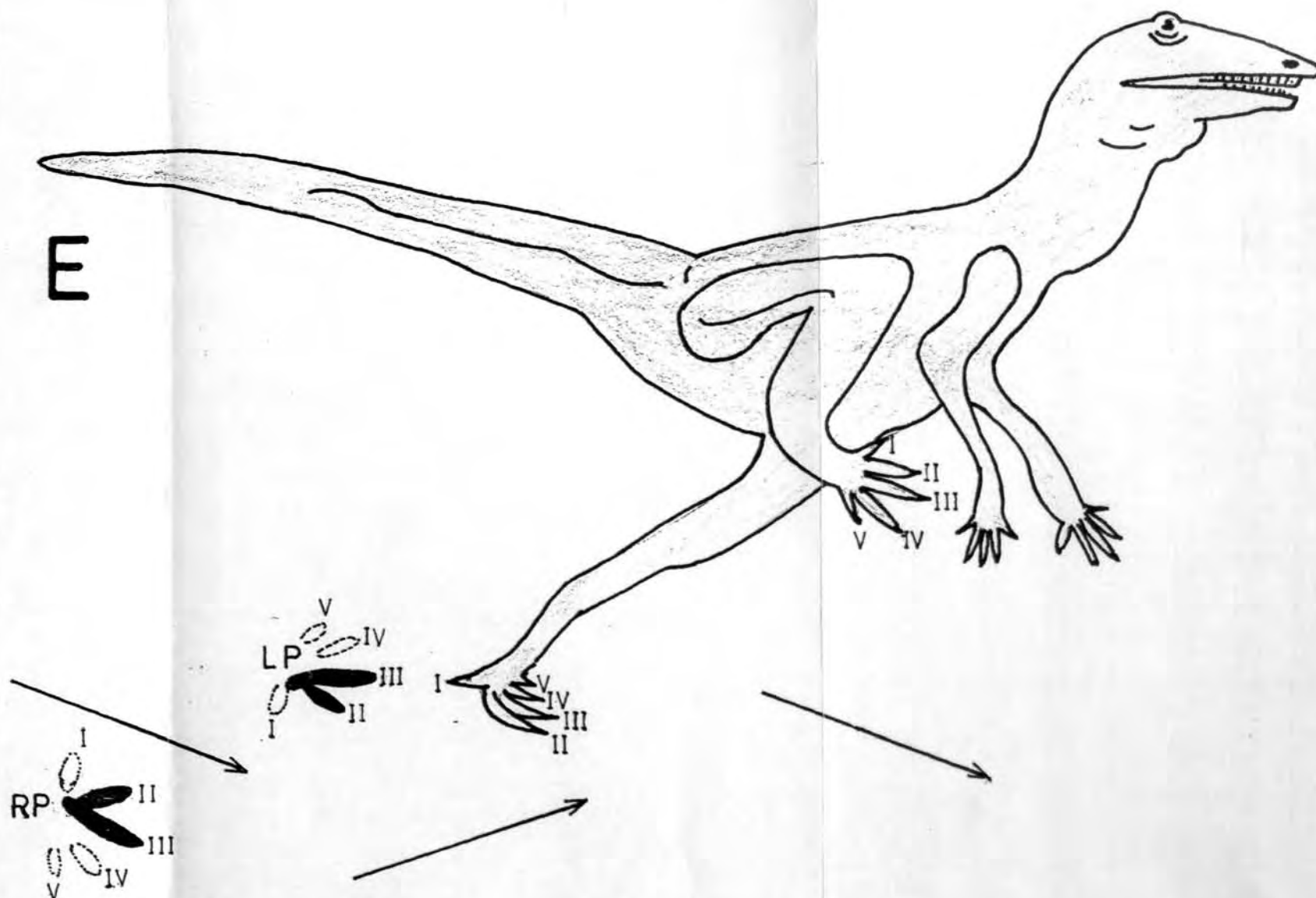
INTERDIGITAL ANGLES

LEFT PES (LP) | RIGHT PES (RP)

θ_1 - Digits I & II
θ_2 - Digits II & III
θ_3 - Digits III & IV
θ_4 - Digits IV & V

E

TEXT - FIG. 15.6.

471

larger, longer and more deeply impressed than the other smaller and less impressed digit II. The interdigital angle between these two digits ranges between 40° and 70° (Tables 15.2 & 15.3, and Text-Fig. 15.6). The immediate movement direction indicated by an individual print can be determined by the direction of the longer digit (d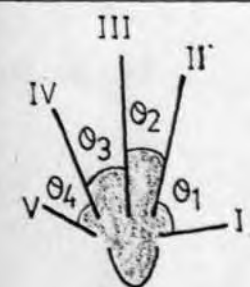igit III). However, most of the trackways in the study area do not indicate a single steady direction of locomotion: rather they are believed to be foot impressions of reptiles running repeatedly and saltatorially in different directions along a shoreline (Plate 69, Figs. g & h; Text-Fig. 15.7 and Table 15.2). The trackways are preserved as concave-epirelief forms on beds of fine sandstone.

Description: The running digitigrade forms of didactyl trackways produced by small reptiles occur on a horizontal rock platform of the Lower Newport Member exposed at St. Michael's Cave (Plate 69, Figs. c, g & h) and constitute the first examples known from Australia and the first for the Triassic of the world. The small producer reptiles ran repeatedly in different directions over the same area of fine sand resulting in the overlapping or cris-cross-like trackway pattern. Close-up views of the impressions (Plate 69, Figs. d - f, k & l) show that they are didactyl, and some are even tridactyl, neither of which forms have been previously recorded in Triassic rocks (Sargeant, 1975, p.307). This didactyl type of imprint is an unexpected feature in tracks of certain early bipedal reptiles which show an extremely reduced number of digit functions to enhence running.

Such tracks were first discovered in Permian sandstones

TABLE 15.2. Measurements of the didactyl reptilian footprints (<u>Moodieichnus</u>) in trace fossil subinterval ID1.2 at St. Michaels Cave. Measurement of the digit length corresponds to the length of the digit impression only and not the length of the digit as defined by the distance from the forward tip of the impression to the point of convergence of the digit with the other digit(s) in the same footprint. The data comprise two samples of measurements each made within a 1-m-sq. area in which the location of each measured footprint was also mapped as shown in Text-Fig. 15.7. The numbered footprints in the left column of this table correspond with those in the latter text-figure.
Abbreviations: L/R - left/right. L/W - length/width. I/ANGLE - Interdigital angle. D/I - Direction of the individual print assumed to correspond with that of the longest digit impression (measured relative to true north). X/Y - mapped area cf. Text-Fig. 15.7.

Foot print No.	PES L/R	I	DIGITS II	III	IV	V	Length L (cm)	Width W (cm)	I/ANGLE (degrees)	D/I (deg.)	AREA BLOCK (Gr. loc.)
1	L	.	II	.	.	.	8.5	1.5	40	058	X(7.4-B5)
		.	.	III	.	.	11.0	1.5			
2	L	.	II	.	.	.	8.0	1.0	50	058	X(3.7-C1)
		.	.	III	.	.	15.0	1.5			
3	L	.	II	.	.	.	10.0	1.0	50	080	X(4.0-E8)
		.	.	III	.	.	13.0	2.0			
4	R	.	II	.	.	.	4.0	1.0	30	174	X(9.5-F5)
		.	.	III	.	.	9.0	1.3			
5	R	.	II	.	.	.	5.0	1.5	45	315	X(9.5-G3)
		.	.	III	.	.	13.0	1.5			
6	L	.	II	.	.	.	2.5	0.7	60	110	X(2.9-H8)
		.	.	III	.	.	6.0	0.7			
7	L	.	II	.	.	.	8.0	1.0	65	005	X(4.2-H5)
		.	.	III	.	.	11.0	1.0			
8	L	.	II	.	.	.	5.0	0.8	70	003	X(4.8-H2)
		.	.	III	.	.	13.0	1.2			
9	L	.	II	.	.	.	6.0	1.0	55	185	X(2.4-I8)
		.	.	III	.	.	8.0	2.0			
10	L	.	II	.	.	.	3.5	1.8	65	185	X(3.5-I5)
		.	.	III	.	.	7.0	1.0			

TABLE 15.2 (continued)

Foot print No.	PES L/R	DIGITS I	II	III	IV	V	Length L (cm)	Width W (cm)	I/ANGLE (degrees)	D/I (deg.)	AREA BLOCK (Gr. loc.)
1	R	.	II	.	.	.	4.5	0.5	70	190	Y(7.5-A9)
		.	.	III	.	.	7.5	1.0			
2	L	.	II	.	.	.	5.0	1.5	60	043	Y(2.5-C1)
		.	.	III	.	.	7.0	1.0			
3	L	.	II	.	.	.	4.5	0.8	65	115	Y(4.1-C2)
		.	.	III	.	.	6.0	1.5			
4	L	.	II	.	.	.	7.0	1.0	70	255	Y(5.8-C9)
		.	.	III	.	.	8.0	1.2			
5	L	.	II	.	.	.	5.5	0.5	50	200	Y(0.8-D9)
		.	.	III	.	.	9.0	1.0			
6	L	.	II	.	.	.	6.0	1.0	60	060	Y(2.5-D7)
		.	.	III	.	.	7.0	1.0			
7	L	.	II	.	.	.	3.0	1.5	60	095	Y(7.9-D1)
		.	.	III	.	.	6.0	1.2			
8	R	.	II	.	.	.	7.5	0.8	75	170	Y(1.0-E1)
		.	.	III	.	.	9.0	1.5			
9	R	.	II	.	.	.	3.0	1.3	70	040	Y(9.5-E2)
		.	.	III	.	.	7.0	1.0			
10	R	.	II	.	.	.	2.5	1.2	60	345	Y(2.9-F9)
		.	.	III	.	.	6.0	1.0			
11	L	.	II	.	.	.	2.5	2.0	70	115	Y(3.3-G1)
		.	.	III	.	.	4.0	1.0			

LENGTH (cm)

Digit II -
- n = 21
- $\bar{x}$ = 5.31
- σn = 2.14
- $\sigma(n-1)$ = 2.19
- Σx = 111. 5
- $\Sigma x2$ = 688.25

Digit III -
- n = 21
- $\bar{x}$ = 8.69
- σn = 2.86
- $\sigma(n-1)$ = 2.93
- Σx = 182.5
- $\Sigma x2$ = 1737.25

WIDTH (cm)

Digit II -
- n = 21
- $\bar{x}$ = 1.11
- σn = 0.391
- $\sigma(n-1)$ = 0.4
- Σx = 23.4
- $\Sigma x2$ = 29.28

Digit III -
- n = 21
- $\bar{x}$ = 1.24
- σn = 0.33
- $\sigma(n-1)$ = 0.34
- Σx = 26.1
- $\Sigma x2$ = 34.75

MEAN INTERDIGITAL ANGLE - 59°

of Texas, USA (Moodie, 1930), and later were named formally by Sarjeant (1971). The Permian tracks comprise imprints of two digits (as described by Moodie, they are of digit IV which is much larger and more impressed and digit III which is smaller and less impressed). The didactyl tracks in the present study area are the pes (hindlimb) imprints (only) of small reptiles which may well have had four (tetradactyl) or even five (pentadactyl) toes, all of which might have been impressed during the walking gait (i.e., plantigrade imprint; cf. Text-Fig. 15.3), and the reptiles may have been quadrupedal in which case the names will also have been impressed as well during the walking gait. However, in the running (digitigrade) gait, the animal became bipedal, resulting only in pes imprints (Text-Fig. 15.6. Additionally, since the animal's ability to run more swifly was functionally dependent on the relative size of the digits of the pes, such modification to these digits occurred as an evolutionary trend (cf. Simpson 1941; Sargeant 1975), in a similar way to such modifications in the horses. In this way these reptiles became more didactyl. The presently described imprints (Plate 69, Figs. d – f, Text-Fig. 15.6, and Table 15.2) show both left and right didactyl pes imprints with one larger digit (III) 1.2 cm in width, 8.7 cm in length, and more deeply impressed than the other. The other is a smaller digit (II), 1.1 cm in width, 5.3 cm in length, and less deeply impressed. The two digits join together at a certain angle called the interdigital angle (e.g., angle $\Theta 2$, the angle between digits II and III), which ranges between 40° and 70° (Table 15.2). While the reptile was running, it became bipedal and the principal stress of the whole body was

TEXT-FIG. 15.7. Didactyl footprints (<u>Moodieichnus</u>) of small running reptiles exposed in trace fossil interval ID1.2 at St. Michaels Cave (Lower Newport Member). Footprints shown are ones mapped within two 1-m-sq. areas (X and Y) of <u>in situ</u> pavement are selected for individual measurement of length of digits and interdigital angle (cf. Table 15.2). The footprints were mapped using a 1-m-sq. grid as shown in Plate 69 Figs. m and n .

AREA
BLOCK-X

AREA
BLOCK-Y

TEXT-FIG. 15.7.

475
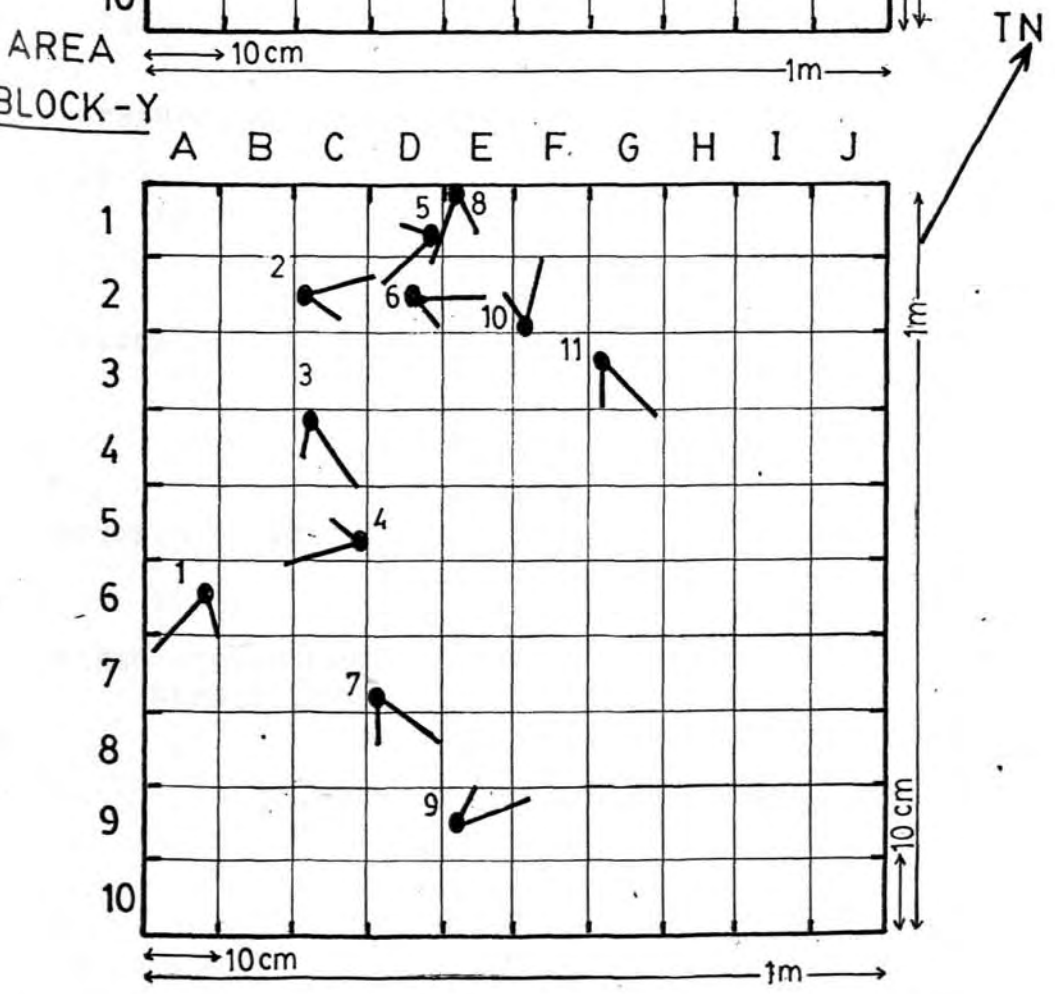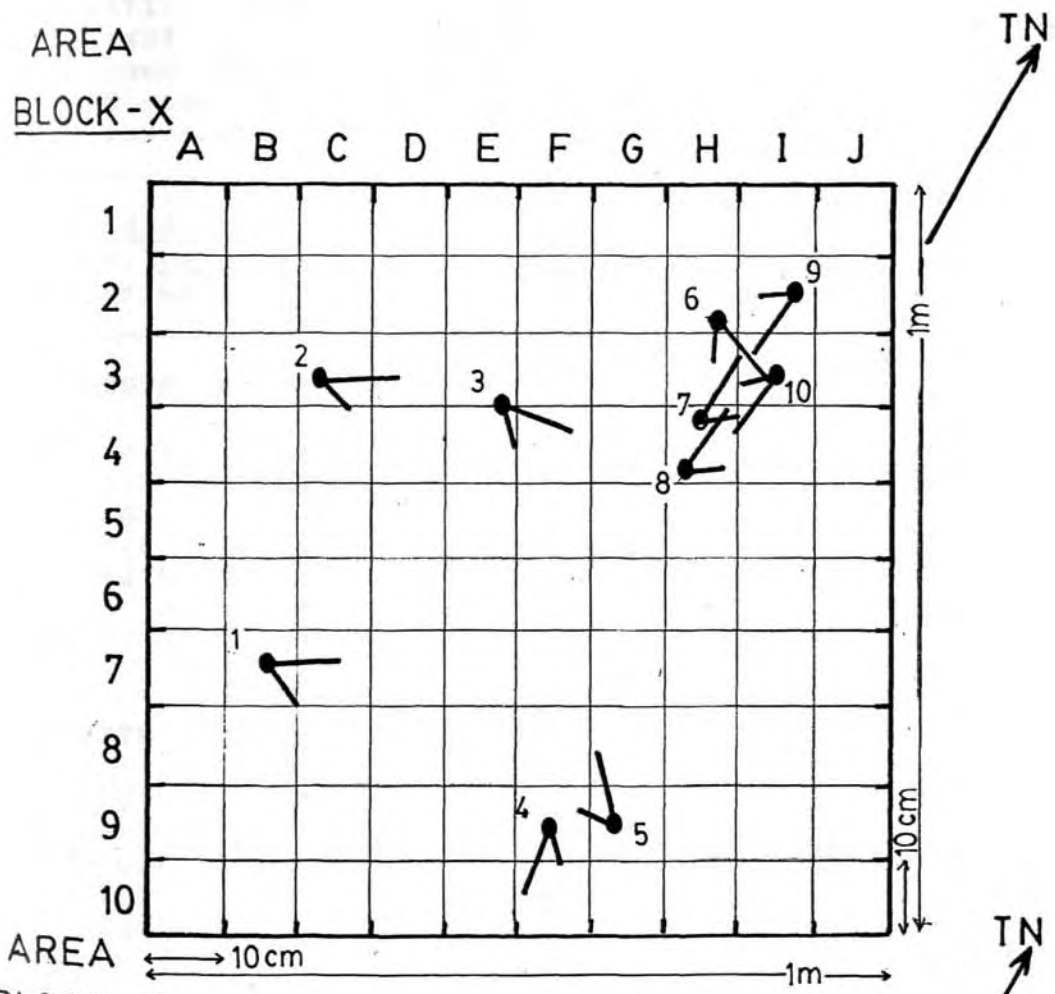
TABLE 15.3. Comparative dimensions of the digits and interdigital angles of _Moodieichnus_. Data in column one are from Sarjeant (1971); data in column two are summary data from Table 15.2 (based on 21 measurements). The data for digits II and III in column three are the same as in column two; the data for digit IV and the III – IV interdigital angle are based on just a few measurements.

M. didactylus var. _permiansis_ (Sarjeant, 1971)	_M. didactylus_ var. _triassicus_	_M. tridactylus_
LENGTH (cm)		
Digit III (IV?) 1.9 – 6.0	8.69	8.69
Digit II (III?) 0.8 – 2.0	5.3	5.3
Digit (IV) ?	?	Comparatively shorter than III and longer than II
WIDTH (cm)		
Digit III (IV?) 0.9	1.24	1.24
Digit II (III?) 0.7	1.11	1.11
Digit IV ?	?	1.2
INTERDIGITAL ANGLE (DEGREES)		
Θ2 (II & III) 10-20	Θ2 (II & III) 40-70	Θ2 (II & III) 40-70
		Θ2 (III & IV) 40-50
STRIDE (cm)		
9.0	(cannot be determined even by geometry because of the saltatorial gait and crowded pattern of overlapping prints)	
BREADTH OF TRACK) (cm)		
5.2		
GLENO-ACETABULAR **LENGTH** (cm)		
?		

focused on the middle digit (digit III), which is larger, long-er, and more impressed. The other digit (digit IV, on the other side of digit III) is less commonly (and less deeply) impressed, manifesting either a slower running gait or the use of this additional digit in the correction of balance. The additional impression of digit IV to the otherwise didactyl imprint is very important and this imprint is described below as a new ichnospe-cies, M. tridactylus (cf. Text-Fig. 15.6c). The relatively lateral spatial offset of the footprints indicates a more salta-torial (i.e. random) rather than cursorial (i.e., aligned in the type variety) line of movement (cf. Text-Fig. 15.7, and Plate 69, Figs. c, g, & h). in the present material the depth of the im-print of the long toe (digit III) is sufficiently well preserved to suggest a bounding type of locomotion. The random offset of the footprints strongly suggests that the trackways are all saltatorial forms. This evidence strongly suggests that the reptile was bipedal in running but was not as cursorial in its running behaviour as was the type species (i.e., M. dactylus var. permiansis) but rather was saltatorial (Text-Fig. 15.6e). In the present examples it is very difficult to measure the stride, pace, and breadth of the trackways, and the gleno-acetabular length (these cannot even be determined by geometry).

Distribution: The trackways are developed at two different stratigraphic levels (Enclosure III.4). The stratigraphically lowest of these is subinterval ID1.2 of the Lower Newport Member exposed at St. Michael's Cave (area 5). This trackway horizon extends to Bangalley Head (area 8) in the north to Hole in the

Wall (area 11) in the south; but with the exception of some large loose slabs which contain both didactyl and tridactyl footprints at Bangally Head (cf. Plate 69, Figs. k & l) the exposures at these localities are restricted to the clifflines. The second horizon (Plate 63 Fig. b) is in subinterval ID5/6 in the Lower Newport Member at Mona Vale Head (area 14).

Studied material: At St. Michaels Cave the trackways occur on a single bedding plane (in subinterval ID1.2) which is exposed in several large and small _in situ_ platforms as well as in numerous large loose slabs (Plate 69 Figs. g & h). This same bedding plane is also exposed at Bangalley Head in the cliffline as well as in several large loose slabs which feature the trackways (Plate 69 Figs. k & l). Although this same bedding plane also occurs at the Hole in the Wall locality it is exposed these only in the cliff-line. No rock samples containing the trackways have been re-trieved from the field from the stratigraphic horizon but numer-ous photographs of the trackways have been taken at St. Michaels Cave and Bangalley Head, some of which appear in the plates. The trackway maps of Text-Fig. 15.7 were also made on exposures at St. Michaels Cave. The second stratigraphic horizon containing the trackways (i.e., subinterval ID5/6) at Mona Vale Head is exposed both in the cliffline and in several small _in situ_ plat-forms. No rock samples containing the trackways have been col-lected from this locality but several photographs of the track-ways have been taken here, one of which appears in the Plates (Plate 63 Fig. b).

Preservation and association: These trackways are preserved as concave-epirelief forms on the surface of beds of fine sandstone.

Where the trackways occur in subinterval ID1.2 at St. Michaels Cave and Bangalley Head the sandstone bed also contains Plano-lites, Rhizocorallium jenense, and Chondrites type C. Where the trackways occur in subinterval ID5/6 at Mona Vale Head the sandstone bed also contains Agrichnium.

Ichnofacies and palaeoenvironmental affinities: These trackways occur within the Skolithos ichnofacies (in soft-ground), and are inferred to indicate extremely shallow-water conditions along a shoreline of an estuary or a coastal lagoon.

<center>Ichnospecies M. tridactylus ichnosp. nov.</center>

<center>Plate 69, Figs. d, k & l)</center>

Specific assignment: Trackways probably produced by the same small reptile(s) described above (for M. didactylus var. triassi-cus) in saltatorial running behavior, but are different from the latter in that three digits are impressed probably as a result of slow running. The impressed digits are probably II, III, and IV, from the pes limbs, and without the impression of the palm (i.e., the trackways define a digitigrade tridactyl gait; cf. Text-Figs. 15.3 & 15.6).

Remarks (diagnostic features): Tridactyl imprints probably pro-duced by same reptiles as in M. didactylus var. triassicus. The imprints of the pes trackways have a tridactyl form (three di-gits) rather than a didactyl form (2 digits). The third digit that occurs in this form (i.e., the digit that is additional to digits II and III in M. didactylus var. triassicus) is digit IV, but is not deeply impressed.

Description and ethology: The imprints are of three digits, the

largest (central) one probably being digit III; this is much longer, larger and more deeply impressed than the other two. The shorter and thinner digits (digits II and IV) are impressed on both sides of digit III in separate left- and right-limb imprints (see Text-Fig. 15.6c). The interdigital angle Θ2 (between digits II and III) is 40° to 70° and angle Θ3 (between digits III and IV) is 40° to 50° (Table 15.3). The lateral offset of the footprints is random so that the trackway is not straight or unidirectional. Ethologically it is probable that these imprints result from a slow-running gait involving a more balanced deportment of the same reptiles that produced M. didactylus var. triassicus (the impressed third digit IV on the other side of digit III indicates use for balancing purposes). These trackways are less common, and less deeply impressed than are those of M. didactylus var. triassicus but also the imprints are random and offset as in the latter. The third digit (probably digit IV) is invariably impressed more faintly than the other two, and is invariably impressed on the other side of digit III (see Text-Fig. 10.6c).

Comparison: Differs from the type species M. didactylus var. permiansis and from M. didactylus var. triassicus only in the presence of a third digit, i.e., digit IV. Differs from the former also in defining a saltatorial style of locomotion.

Distribution: As for M. didactylus var. triassicus.

Studied material: As for M. didactylus var. triassicus.

Preservation and association: These trackways are preserved as concave-epirelief forms and are associated with and have the same associated trace fossils as M. didactylus var. triassicus.

Body and tail drag-marks and webbed soft-parts are not indicated in the preservation. See M. didactylus var. triassicus for other details.

Ichnofacies and palaeoenvironmental affinities: As for M. didactylus var. triassicus.