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Article abstract

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Systematic ichnology of the Mabou and Cumberland groups (Carboniferous) of western Cape Breton Island, eastern Canada, 2: surface markings

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Carboniferous (Namurian-Westphalian A) strata of the Mabou and Cumberland groups outcrop extensively in western Cape Breton Island. As well as a diverse collection of burrows, trails, pits, and coprolites described previously, numerous surface marks, mostly trackways, were encountered in these strata: *Diplichnites* cf. *logananus* (Marsh), *Diplichnites* isp. (types A and B), *Gluckstadtella cooperi* Savage, *Hexapodichnus horrens* Hitchcock, *Monomorphichnus* cf. *lineatus* Crimes *et al.*, *Protichnites* cf. *carbonarius* Dawson, *Protichnites* cf. *kennediea* (Smith), *Protichnites* cf. *scoticus* Salter, *Protichnites* cf. *variabilis* (Linck), *Protichnites* isp. (types A, B, C, and D), *Stiallia* cf. *pilosa* Smith, Appendage Marks (types A and B), an "Arthropod Resting" Trace, Horn-shaped Surface Traces, and Vertebrate Trackways (types A, B, C, D, E, and F).

Des strates du Carbonifère (Namurien-Westphalien A) des groupes de Mabou et de Cumberland affleurent sur une surface étendue dans l'ouest de l'île du Cap-Breton. On relève en outre dans ces strates une collection diversifiée de terriers, de pistes, de trous et de coprolites décrits antérieurement; un grand nombre de marques au sol, en majeure partie des pistes, comme celles du *Diplichnites* cf. *logananus* (Marsh), du *Diplichnites* isp. (types A et B), du *Gluckstadtella cooperi* Savage, de l'*Hexapodichnus horrens* Hitchcock, du *Monomorphichnus* cf. *lineatus* Crimes *et colll.*, du *Protichnites* cf. *carbonarius* Dawson, du *Protichnites* cf. *kennediea* (Smith), du *Protichnites* cf. *scoticus* Salter, du *Protichnites* cf. *variabilis* (Linck), du *Protichnites* isp. (types A, B, C et D) et de la *Stiallia* cf. *pilosa* Smith, des marques d'appendices (types A et B), une trace "d'arthropode au repos", des traces en surface en forme de corne et des pistes de vertébrés (types A, B, C, D, E, et F).

[Traduit par la rédaction]

INTRODUCTION

This paper describes and discusses several of the trace fossils encountered at various localities in western Cape Breton Island (Fig. 1). The numerous surface markings described (primarily tracks and trackways) occur in Carboniferous (Namurian-Westphalian A) Mabou and Cumberland Group strata that have been confidently inferred to be the products of fluvial, floodplain, and lacustrine sedimentation in half grabens maintained by a transtensional tectonic regime (Keighley and Pickerill, 1996a). The surface markings may occur exclusive of, or associated with, the trace fossils already described from these strata by Keighley and Pickerill (1997); Baird (personal communication, 1989, 1994) and his co-workers have collected additional material that remains undescribed. Future work will assess the palaeoenvironmental distribution of our specimens.

NOMENCLATURAL PROBLEMS AND TERMINOLOGY

Before presenting our taxonomic classification of the trace fossils from the study area, it is necessary to first comment on the chaotic taxonomic nomenclature that exists for both

vertebrate and invertebrate trackways and explain the principles behind our nomenclatural decisions. As stated in Keighley and Pickerill (1996b, 1997) and Pickerill and Keighley (1997), an ichnotaxon can only be formally named (and hence diagnosed) from distinguishing morphological features, following the guidelines of the International Code of Zoological Nomenclature (I.C.Z.N., 1985). Criteria such as (a) the phylogeny of the producer, (b) stratigraphic limitation of the trace fossil, or (c) the environment in which the trace fossil was produced, are not criteria that can be directly, or objectively, observed or proven in a type specimen. Therefore they remain hypothetical concepts and so cannot be used to provide a name based upon the 'Principle of the Name-bearing Type' (I.C.Z.N., 1985, p. xiii, Article 1b-1). Specifically, for a name now to be available, it must upon introduction include a description of characteristics that purport to make the (trace-) fossil unique (I.C.Z.N., Article 13a-i), which the above criteria cannot conclusively provide. Sarjeant and Kennedy (1973), Sarjeant (1975, 1990), and Magwood (1992), amongst others, have also provided excellent and compelling reasons for rejecting such criteria in favour of a morphologically based nomenclature. Sarjeant (1990) further noted that there is nothing to prevent use of parallel names based on systematic affinity where the investigation being undertaken requires such a

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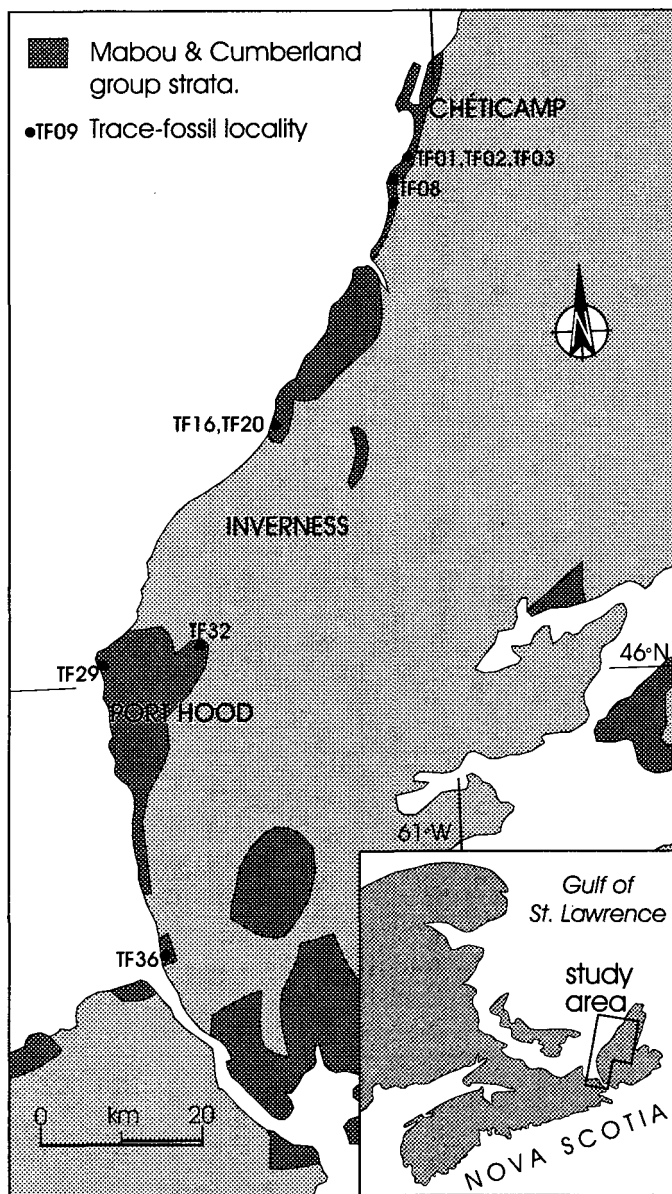
Fig. 1. Location map of trace-fossil localities within the Mabou and Cumberland groups in western Cape Breton Island.

classification. However, such names cannot compete with morphological nomenclature or be regulated by the I.C.Z.N. for reasons outlined above.

Unfortunately, many trace fossils were originally named prior to the existence of a nomenclatural code, and numerous others were published in the period 1961 to 1985 when the I.C.Z.N. inadvertently ruled that trace-fossil names first published after 1930 were not available (see Pickerill, 1994, for discussion). Accordingly, workers during these periods were not bound by formal regulations and so were free to utilize non-morphological criteria.

Another nomenclatural problem is the lack of uniformity as to which morphological features should be adopted as being diagnostic of an ichnotaxon. Fürsich (1974) suggested that ichnogenera be formulated, or revised, based upon morphological features resulting from what is interpreted to be

behaviour at a high level of significance (significant features), and ichnospecies from features considered to result from behaviour of less importance (secondary features). Such interpretations of significant behaviour are highly subjective and, futhermore, morphological terminology itself is not covered by the I.C.Z.N. or any other code. Accordingly such terms often have different definitions attached to them, resulting in nomenclatural confusion. For clarity, therefore, our use of certain morphological terms follows Keighley and Pickerill (1997) and the definitions below.

A 'trackway' is herein defined as a succession of individual marks that collectively form a ribbonlike structure at a sedimentary (or, potentially, an extrusive igneous) interface (in contrast, a trail represents a continuous mark left on the substrate: no separate marks are preserved—Trewin, 1994). A trackway should be characterized by two 'rows' of imprints, or two 'track rows' (or, interpretively, two rows of appendage marks, Fig. 2A). Typically the rows would represent records of both the left- and right-sided appendages of an animal that were produced while supporting itself above the substrate during locomotive activity, since almost all animals known to be capable of such locomotion have bilateral symmetry. If it cannot be determined whether two rows of imprints are present, then they can simply be described as a sequence of 'tracks' (Fig. 2). The shapes of individual prints also varies, and the terminology we use is given in Figure 2B. Within a row, a 'natural track cycle' (Anderson, 1975) contains a single imprint from each of the producing appendages (but that may include imprints of separate digits extending from one appendage) from one side of the body (Fig. 2C—this term is preferred to Trewin's 'imprint series').

Essentially, only two phylogenetic groups, the vertebrates and arthropods, produce trackways (but vagile Echinodermata are a potential exception, and need not have bilateral symmetry either, e.g., Sutcliffe, 1997). Trackways formed by vertebrates can usually be distinguished from those produced by invertebrates, primarily by their form and geometry. Thus, when the qualifiers 'vertebrate' or 'invertebrate' are applied to a trackway, they are used more in a descriptive rather than interpretive sense. However, use of such qualifiers has had its pitfalls. As detailed below, several trackways previously interpreted as vertebrate in affinity are now considered to be invertebrate in origin.

Terminology for vertebrate trackways mostly follows Leonardi (1987). The front print of repeated, longitudinally in-line couplets of prints is typically regarded as the manus (forefoot), as is the inner print of diagonally or transversely in-line couplets, or the smaller print of the couplet. However, in some cases where similar sized, longitudinally in-line prints are present (e.g., Sarjeant, 1975, p. 290, fig. 14.6), or where preservation is poor, decisions regarding which prints reflect the manus, and which reflect the pes (backfoot) have been relegated to comments within the remarks, since in the studied examples they are invariably interpretive decisions. Accordingly, we number prints within a trackway simply, on the left-hand side ('left side') of the trackway, L1, L2, L3, etc., and on the right-hand side ('right side') R1, R2, R3, etc.

A

TRACKWAY

○ ○ ○ ○ ○ ○ ○ } track row
○ ○ ○ ○ ○ ○ ○

——————————— median groove or ridge
(depending on preservation
on top or bottom surface)
- may be excentric and, or,
intermittent or absent

○ ○ ○ ○ ○ ○ ○
○ ○ ○ ○ ○ ○ ○

B

trackway ⟵→ axis

0 0 0 0 } symmetrical tracks (similar rows)
0 0 0 0

transversely oriented imprints

○ ○ ○ ○ } asymmetrical tracks (dissimilar rows)

oblique imprints   longitudinal imprints

C TYPES OF IMPRINTS (TRACKMARKS)

(Invertebrates)

○ Punctate mark, prod mark

striation (pl. striae), scratch mark

—— (straight)

⌣ (crescentic/lunate)

⌒ (apostrophe-form)

(Vertebrates)

Plantigrade

Semi-digitigrade

Digitigrade

(Type of Digitation)

Unifid (or monodactyl if vertebrate mark)

Bifid (or didactyl if vertebrate mark)

Trifid (or tridactyl if vertebrate mark)

Quadrifid, 'bird-foot-like' (or tetradactyl if vertebrate mark)

Pentadactyl

D

Imprint series or 'natural track cycle' from one set of limbs (left or right side) of a dodecapod

transverse series   oblique series

○¹ ○² ○³ ○⁴ ○⁵ ○⁶ } row

E

Decreasing distinction of individual imprints due to taphonomic factors, hence punctate sets are preserved as striae though the method of production is the same.

F

Decreasing distinction of individual imprints due to taphonomic factors, hence a trackway is preserved as a trail though the method of production is the same.
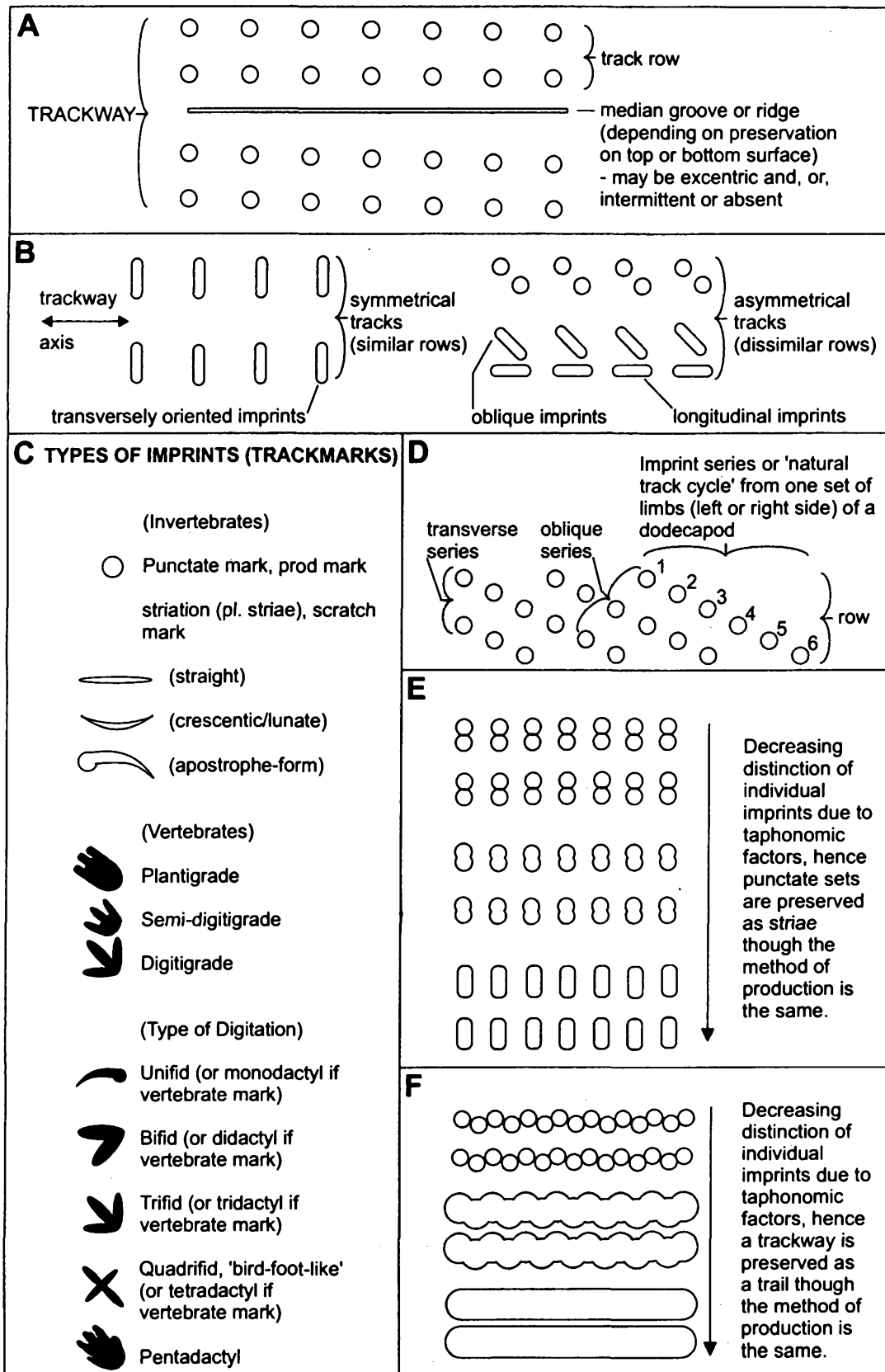
Fig. 2. General terminology and preservation of tracks and trackways (adapted from Anderson, 1975; Trewin, 1994). A, B = General terminology of a trackway. The series noted would be termed a transverse series. Other series are possible (as shown in D). Repeated series occur longitudinally along the trackway and form a row. C = Types of track marks. Note that Trewin's (1994) 'trifid' mark we would consider to be 'quadrifid'. D = Series and natural track cycles. Only the natural track cycle, a special type of series, includes one imprint of each appendage on one side of the producer. E = Preservational variation may result in individual marks not being preserved. The appearance may be of one striate mark, whereas it was actually produced by two, merged, punctate marks. F = Preservational variation may result in individual marks not being preserved. What was originally produced as a trackway may be preserved as a trail.

TAXONOMIC DISCUSSION

We have been unable to access much of the relevant type material and so a thorough discussion, and formal revision, of taxonomic problems is not attempted herein. The following comments only provide an explanation of our choice of names for the western Cape Breton material, based upon the adoption of I.C.Z.N. procedures regarding synonymous ichnotaxa—primarily the 'Principle of Priority' (I.C.Z.N., 1985, Article 23; and see discussion in Keighley and Pickerill, 1996c) and the 'Stability of Usage' (I.C.Z.N., 1985, Article 23b). However, as advocated by Goldring *et al.* (1997), synonymy is not extended to include potential taphonomic and toponomic variants of specific ichnotaxa.

In many cases, the taxonomical problems of invertebrate and vertebrate trackways have stemmed from a worker's desire to either provide a new name for every slight morphological variation in trackway form (e.g., Holub and Kozur, 1981, introduced sixteen new ichnogenera and nineteen new ichnospecies; Walter, 1983, introduced sixteen new ichnogenera and thirty-four new ichnospecies), or allocate a trace or suite of traces to a particular zoological grouping such as a phylum, class, or family (e.g., Fischer, 1978, provided a complete classification of invertebrate trackways based on the biological nature of the producer). Following from our earlier comments, the latter procedure can now be seen as invalid, but the former procedure is valid though of debatable utility because the morphological variations encountered in trackways are enormous. For example, the invertebrate trackway diagrammatically illustrated in Figure 2A could, alternatively, have contained (a) sets of one, two, three, or more, striate, and, or, punctate imprints that may be (b) unifid (apostrophe-form), bifid, trifid, and, or, quadrifid, and (c) transversely, obliquely, and, or, longitudinally oriented. Morphology will also vary when (d) rows differ, thus forming an asymmetrical trackway (*sensu* Trewin, 1994), and (e) if the trackway has or has not a continuous or discontinous, singular or multiple groove.

The factors that can influence the observed morphology of a trackway are also varied and include: (i) the actual morphology of the producer (e.g., number of appendages), (ii) very slight variations in the behaviour of a trackway maker, such as whether the producer made a straight or curved path (e.g., Walker, in Briggs *et al.*, 1984) and whether the producer moved quickly or slowly (e.g., Crimes, 1970; Sarjeant, 1990), (iii) whether the producer moved along flat ground or up, across, or down a slope (e.g., Brand, 1979), together with the firmness or consistency of the substrate that was crossed (e.g., Brady, 1947; Brand, 1979, 1996), (iv) toponomy, and (v) preservation. In factor (iv), undertracks may be distinctly different in morphology from their surface expression, influenced by different depths of penetration by individual appendages, and the surface area each appendage covered when it was in contact with the substrate (Goldring and Seilacher, 1971).

It could be argued that factors (ii) and, more indirectly, (iii) and (iv) lead to morphological features based on ethology (e.g., moving on dry sand slowly uphill, or wet sand quickly downhill) and all such features are worthy of being either primary or secondary ichnotaxobases. If all these fea-

tures are used, the result is a multitude of potential ichnotaxobase combinations and a plethora of potentially valid ichnotaxa, with very tight constraints as to each of their diagnoses. This can then lead to an ichnotaxonomically multicompound specimen; for example, where an individual tracemaker, over one short journey, encounters variation in slope and substrate consistency and changes speed and direction irregularly. In a thinly laminated rock, on which the trackway may be preserved, a further profusion of ichnogenera may accompany various levels of undertracking, and differential weathering of the preserving stratum may produce even further variation (whereby taphonomic factors act to alter a trace fossil's morphology and make it resemble a different ichnotaxon—a taphoseries variant—see MacNaughton and Pickerill, 1995).

As previously noted, there have never been formal guidelines as to what morphological ichnotaxobases should be adopted. In order to keep the number of ichnotaxa within reasonable bounds, we believe the choice of primary ichnotaxobases should, therefore, be based on finite criteria and, where possible, avoid the placement of diagnostic boundaries in characteristics that are gradational.

We concur with McKeever and Haubold (1996) that the optimal state of preservation should be used for principal diagnoses. Specimens with suboptimal preservation can then be named as toponomic and taphonomic variants, following the suggestions of Sarjeant (1990), Goldring *et al.* (1997) and Keighley and Pickerill (1997). For 'vertebrate' trackways, criteria such as the maximum number of digits present on the manus and pes, relative sizes of manus and pes (cf. McKeever and Haubold, 1996), and most fundamentally, the presence or absence of a manus (i.e., biped or tetrapod) are probably the best primary ichnotaxobases. In avoiding gradational criteria, trackway width and pace angulation pattern would be considered less suitable criteria (McKeever and Haubold, 1996).

Some of the procedures already adopted for 'invertebrate' trackways by Seilacher (1955), and since followed by numerous authors (e.g., Glaessner, 1957; Bergström, 1976; Bromley and Asgaard, 1979), also have considerable merit with respect to I.C.Z.N. guidelines. Seilacher's (1955) suggestion was that, for 'invertebrate' trackways, the presence or absence of a median groove (or ridge, depending on epichnial or hypichnial preservation) was the primary ichnogeneric criterion in distinguishing invertebrate-trackway ichnotaxa. Though it has little ethological importance, it is a distinctive feature, and a finite statement can be made as to whether it is present, sporadically or continuously, or absent. Accordingly, Seilacher (1955) provisionally 'lumped' trackways containing a median groove(s) into *Protichnites* Owen, and all trackways lacking a median groove into *Diplichnites* Dawson.

The suggestion to assign such material to *Protichnites* is compatible with the Principle of Priority. *Protichnites* appears to have been the first ichnogeneric name used in the literature for indisputably invertebrate trackways (*Ichnites* having been a general term introduced for all track marks and trackways by Hitchcock, 1837). Owen (1852) did not provide an ichnogeneric diagnosis, but all his material was similar in having rows of more-or-less punctate imprints about a central, linear mark (groove or ridge, depending on top or bottom

surface preservation). His six ichnospecies were differentiated partly on the number of prod marks per repeated natural track cycle, and the angle that they subtended with the central linear mark (e.g., not fewer than seven marks, arranged in transverse to slightly oblique series of three, two, and two, in *P. septemnotatus* Owen, the type ichnospecies). Individual imprints varied in size but remained generally punctate in shape. Owen (1852) was conscious of the fact that the number of imprints did not necessarily indicate the number of appendages on each side of the vagile producer; some of the imprints could have been made by the same, bifid or trifid, limb. He made several suggestions as to the nature of the producing organism, but favoured a limulid. Subsequently, *P. scoticus* Salter was introduced for much smaller trackways that contained two or three imprints per transverse series on each side of the median ridge in repeated natural track cycles of up to six imprints. It was emphasized that '...the imposition of this generic name does not in any way imply that the creature which made the track was generically identical with those which produced the tracks in the Potsdam sandstone [described by Owen]...' (Salter, *in* Harkness, 1856, p. 243).

No additional trackway ichnotaxa were apparently described in the literature until Hitchcock (1858) introduced several new ichnogenera for morphologically quite diverse trackways, all of which lacked a median groove. Accordingly, *Protichnites* was a name used at the ichnogeneric level, prior to the introduction of any other formal name, for trackways (a) containing a median groove, (b) having repeating track cycles of variable number (but essentially of five or more) and that occured en echelon, resulting in transverse series of as few as two, (c) containing individual tracks that were typically punctate (variably circular, ellipsoidal, elongate, or tapered in the terminology of Trewin, 1994), and from unifid, bifid, trifid, or quadrifid appendages, (d) of variable size, and (e) not definitively assigned to any one producer—vertebrate or invertebrate. Note, however, that following Hitchcock's (1858) work, *P. logananus* Marsh was introduced for trackways that lacked a median groove, and thus (following the nomenclatural acts of Hitchcock, 1858, noted above) was inconsistent with an ichnospecies of *Protichnites*.

One of Owen's (1852) secondary ichnotaxobases was the number of imprints in a natural track cycle, a criterion also used by Salter (in Harkness, 1856). Accordingly, the natural track cycle in *P. octonotatus* Owen was apparently eight, in *P. septemnotatus*, seven, and in *P. scoticus*, six (this is *contra* Walker, 1985, who stated that the number of imprints in *Protichnites* and *Paleohelcura* Gilmore was three—three is the common number in oblique series rather than in a natural track cycle, although in *P. lineatus* Owen, the number in oblique series may be greater). Though of little ethological value, but of potential use in providing a phylogenetic interpretation, the criterion has merit: the maximum number of imprints in a natural track cycle can never exceed the total number of 'walking' appendages (or digits on these appendages) present on one side of the producer, and a finite statement can be made with regards to the maximum number of imprints in a natural track cycle. Thus a trackway may be infinitely variable in morphology along its length, but in treating the differ-

ent morphologies as part of a taphoseries (*sensu* MacNaughton and Pickerill, 1995), the trackway can be named after the morphology from 'highest' (i.e., with maximum number of imprints in a natural track cycle) within the taphoseries.

Subsequent to these earliest works, a multitude of new trackway ichnotaxa have been formulated, including new ichnogenera for trackways exhibiting a median groove. However, the distinction of several of these ichnotaxa relied on proposed ichnotaxobases that can be considered invalid by our earlier comments. For example, and *contra* Salter's (*in* Harkness, 1856) statement quoted earlier, the phylogeny of the *Protichnites* producer was suggested as a primary ichnotaxobase. Dawson (1862) noted that trackways similar to *Protichnites* were produced by the king crab, *Limulus*. Accordingly, Packard (1900a) introduced *Ostrakichnites* as a replacement name for *Protichnites carbonarius* Dawson, because he considered that *P. carbonarius* could not have been made by a fully grown limulid (*P. carbonarius* had been introduced in 1873 for small trackways whose imprints were grouped in rhomboidal sets either side of a median groove). Dawson's ichnospecies, by way of the arrangement of the individual marks in a rhomboidal manner, was certainly a novelty with respect to other *Protichnites* ichnospecies, but the morphology was still within the existing boundaries of the ichnogenus.

Protichnites carbonarius is similar in form to another problematic ichnotaxon, *Ichnites lithographicus* Oppel, which earlier had been introduced for trackways containing quadrifid imprints and unifid punctate imprints on both sides of a median groove. There is no indication that Oppel (1862) knew of Owen's earlier work and hence whether any subdivision of trackways with median grooves into different ichnogenera was intended, or whether *I. lithographicus* was introduced merely as a new type of trackway under the general heading of *Ichnites*, *sensu* Hitchcock (1837). *Kouphichnium* Nopsca was subsequently introduced for the trackways of Coelurid reptiles, with *K. lithographicum* (Oppel) included as the type. Following Caster (1939) and Nielsen (1949), these trackways were reinterpreted as the work of Xiphosurids, and numerous other ichnogenera were noted as synonymous. However, subsequent workers again overemphasized the connection of trackway and potential producer. After interpreting their trails to be the result of Xiphosurids, such workers named their tracks *Kouphichnium* (e.g., Hardy, 1970). *Kouphichnium* was thus noted to be distinctly polymorphic by Häntzschel (1975). For example, in contrast to *K. lithographicum*, *K. gracilis* Linck contains bifid and quadrifid tracks and lacks a central groove, and *K. rossendalensis* Hardy is a classic example of a compound specimen, the bilobate to ungulate part of the trace now being included by Romano and Whyte (1987) in *Selenichnites* Romano and Whyte as *S. rossendalensis* (Hardy).

Accordingly, *Kouphichnium* was introduced solely on the grounds of an interpretation that the trackways were of a particular (dinosaur) producer (Nopsca, 1923), which as previously stated, is an invalid nomenclatural procedure. Subsequently the name has been used based on material distinguished exclusively on an interpretation of a particular (Xiphosurid) producer, and for polymorphous material. Such material would be better included in ichnotaxa introduced with

morphological ichnotaxobases. Particularly, the material containing a median groove (e.g., *K. lithographicus*) could be incorporated within *Protichnites*, alongside *P. carbonarius*. It should also be pointed out to workers who advocate use of an interpreted producer or geological age in the naming of trace fossils that, if such considerations were utilized, *Kouphichnium* would again be synonymous with *Protichnites*, since Owen's (1852) preferred interpretation for a producer was a limulid, whose ancestors are now known to extend back to the Cambrian (Clarkson, 1993)!

Trackways with either an intermittent median groove or more than one median groove were originally described as *Protichnites octonotatus* or *P. alternans* Owen and subsequently as such, for example, by Birkenmajer and Bruton (1971). Both traits have also been considered as primary ichnotaxobases of *Siskemia* Smith; *Danstairia* Smith, *partim*; *Tarsichnus* Walter, *partim*; *Euproopichnus* Walter; and *Mitchellichnus* Walker. Although these latter ichnogenera may have been established on morphological grounds, they have to be considered junior synonyms because their primary ichnotaxobases are already incorporated within the previously established diagnosis of *Protichnites* and, specifically, the two aforementioned *Protichnites* ichnospecies. If intermittent or multiple grooves are to be considered (primary) criteria warranting separate ichnogenera, rather than (secondary criteria defining) separate ichnospecies (the latter being the treatment we advocate), then a systematic review of such trackways is necessary that shows how a change in what is permissible for assignment to *Protichnites* affects the synonymy of other material previously assigned to *Protichnites* (i.e., into which ichnotaxon should be placed other specimens previously described as *Protichnites* that preserve intermittent or multiple grooves).

Other ichnogenera have also been introduced or retained on morphological grounds. In the case of *Paleohelcura*, the number of imprints in a natural track cycle has been fairly conclusively observed to number only three. In *Stiaria* Smith, the number of imprints was stated to number between two and four (Walker, 1985), and *Paleohelcura* was thus considered its junior synonym by Pollard and Walker (1984). Since *Stiaria* would have a natural track cycle of four, *Paleohelcura* is not synonymous, but whether either or both should be considered acceptable at the ichnogenus level is debatable. Since trackways with natural track cycles of six, seven, and eight are included within *Protichnites*, it is inconsistent to have separate ichnogenera for trackways with natural track cycles of three and four. The latter morphologies would be better included as separate ichnospecies of *Protichnites* (and in the case where the maximum number of tracks is not clearly evident, assignment can simply be to '*Protichnites*' isp. rather than questionably and subjectively to one of *Paleohelcura*, *Protichnites*, or *Stiaria*). Walter's (1983) introduction of *Euproopichnus* for trackways with natural track cycles of six punctate imprints arranged obliquely, does not adequately distinguish it morphologically from its suspected senior synonym, *P. scoticus*.

In contrast to Seilacher's (1955) recommendation to 'lump' all 'invertebrate' trackways with median grooves into *Protichnites*, which, as shown, has considerable historical

merit, the case for using *Diplichnites* as a name for all 'invertebrate' trackways that lack a central groove is highly problematical. As already noted, the most senior names for trackways lacking median grooves were suggested by Hitchcock (1858, 1865) and so the use of *Diplichnites* for all trackways lacking a median groove does not follow the I.C.Z.N.'s Principle of Priority. Many of Hitchcock's (1858) ichnotaxa might have been considered 'forgotten names' but for the redescription of his collections by Lull (1915, 1953)—only synonymous ichnotaxa first described between the years 1908 and 1915 could strictly overturn use of Hitchcock's names (I.C.Z.N., Article 79c). Alternatively, a case might exist for applying I.C.Z.N., Article 23b, that allows stability of usage to overturn priority (e.g., Osgood and Drennen, 1975). In a non-exhaustive literature review, *Diplichnites* was encountered in over sixty articles, in contrast to the next most commonly used name, *Merostomichnites*, that has been used in less than twenty—Hitchcock's (1858, 1865) ichnogenera have been used in less than ten. Unfortunately, stability of usage is not demonstratable.

In contrast to the approach of Owen (1852), who permitted considerable morphological variation within *Protichnites*, Hitchcock (1858, 1865) introduced numerous ichnogenera, some of which were differentiated on very minor variations in form. Although most of his ichnogenera must be considered validly introduced names based upon their initial morphological descriptions, he later clouded their distinction (Hitchcock, 1865) by including specimens exhibiting characteristics of one ichnogenus within another. For example, *Acanthichnus* Hitchcock was characterized by having oblique to longitudinally oriented striae with no indication of a natural track cycle. However, new specimens that locally indicated a natural track cycle of three were later included (Hitchcock, 1865, unpaginated, pl. 6.1) within the type ichnospecies, *A. cursorius* Hitchcock. These new tracks were actually excellent specimens for demonstrating the potential variation in trackway form over a short distance. Hitchcock's (1865) later material was noted to make *Acanthichnus* similar to *Lithographus* Hitchcock, *Hexapodichnus* Hitchcock, *Grammepus* Hitchcock, and *Copezia* Hitchcock (these other ichnotaxa had been differentiated on the basis of the varying orientations, mostly oblique to longitudinal, of the three imprints relative to one another). Furthermore, one ichnospecies of *Acanthichnus*, *A. tardigradus* Hitchcock, was subsequently transferred to a new ichnogenus, *Pterichnus* Hitchcock, solely because the trackway more closely resembled that produced by a myriapod than an insect (all of the above named ichnotaxa of Hitchcock, 1858, were considered the work of insects). Re-examination of the type material might confirm that all the forms can be accommodated within, perhaps, two ichnogenera (e.g., *Acathichnus* or *Hexapodichnus* for symmetrical, striate trackways, and *Ptilichnus* for trackways with dissimilar rows) depending upon what primary ichnotaxobases were to be retained. Regardless of how many ichnogenera are retained, ultimately, they would have to be considered potential senior synonyms to all other trackways having primarily striate imprints and lacking a median groove.

Subsequent ichnogenera have been introduced for trackways with distinct natural track cycles comprising three imprints, but lacking a median groove. Numerous ichnospecies

of *Heterotripodichnus* Walter display a variety of arrangements of the three imprints (see Walter, 1983, p. 186, figs. V.10, V.13; p. 187, figs. VI.2, VI.3, VI.7; p. 188, fig. VII.1). However, other ichnospecies of *Heterotripodichnus* have four imprints (e.g., *H. medioimpressus* Walter, 1983, figs. VI.6, VII.13) or possibly more (e.g., *H. marginodigitatis* Walter, 1983, figs. VI.4, VII.3). These morphological inconsistencies were further compounded by Walter's (1983) other nomenclatural decisions. *Tarsichnus* contained both *T. kommatus* Walter with three or possibly four (generally punctate) imprints in a variably arranged natural track cycle without a median groove, and *T. tripedalis* Walter with the same number of imprints, variably arranged, and a median groove. In contrast, *Etterwindichnus* Walter is illustrated as having a natural track cycle of three punctate marks arranged in oblique series. Furthermore, he also included within *Permichnium* Guthörl (which has a natural track cycle of two) the more senior ichnotaxa *Hamipes* Hitchcock and *Bifurculipes* Hitchcock (that also have natural track cycles numbering two), and *Hexapodichnus* (natural track cycle of three), yet *Lithographus* (natural track cycle of three) was retained as a distinct ichnotaxon.

It might be wise to consider the number of imprints as a primary ichnotaxobase, with their arrangement as a secondary ichnotaxobase, as Walter (1983) appears to have accepted, in part, for *Heterotripodichnus*. However, if this were to be done for morphological classification of his trackways, all the material should be included in the most senior name given in Walter's (1983) synonymy, namely *Lithographus*—which, incidentally, Hitchcock (1865) considered a synonym of *Copezia*. On morphological grounds, Walter (1983) should not have introduced new ichnotaxa (I.C.Z.N., Articles 17, 23d). Similarly, the inclusion of 'four footed' ichnogenera within *Permichnium* disregards the Principle of Priority which would have either *Hamipes* or *Bifurculipes* as the senior synonym.

Diplichnites was not introduced until Dawson's (1873) work, and problems exist in that the holotype was not particularly well illustrated or described, and the type cannot now be located. It is therefore uncertain whether the type consists of rows of parallel, transverse striae, which Dawson's (1873) description and illustration certainly imply, or of rows of merging punctate imprints arranged in transverse series (e.g., as illustrated in Fig. 2D). Accordingly, the name could be a candidate for synonymy with, for example, *Lunula* Hitchcock that comprises transversely oriented, slightly lunate, parallel striae.

Diplichnites has subsequently been adopted for both morphologies described above, as well as for rows containing en echelon series of punctate imprints, namely *D. gouldi* (Gevers *et al.*) and *D. cuithensis* Briggs *et al.* This latter morphology has also been described as *Trachomatichnus* Miller, although Osgood and Drennen (1975), following Seilacher (1955), considered the name synonymous with *Diplichnites*. More sparsely distributed subcircular to apostrophe-form imprints, exhibiting variably en echelon series (natural track cycles?), have been named, for example, as *Merostomichnites narragansettensis* Packard, *Acripes leavitti* Matthew, and *Maculichna* Anderson, as well as *Protichnites logananus*. Transverse, tapering to near striate imprints have also been included within *Merostomichnites strandi* Størmer by Størmer (1934) and by Häntzschel (1975), and within *Maculichna* by

Aceñolaza and Buatois (1993—an intermittent median groove also being recorded).

The use of *Merostomichnites* for trackways is contentious. Packard (1900a) initially described trackways that comprised rows of distinct oval to crescentic imprints in single (or rare oblique double) series as a new ichnospecies of *Protichnites*, namely *P. narragansettensis*, comparing it to *P. octonotatus* and *P. logananus*. Subsequently, Packard (1900b) introduced *Merostomichnites*, including within the ichnogenus *M. narragansettensis* (*nom. transl.*), and a previously undescribed form, *M. beecheri* Packard. However, *M. beecheri* consists of what appear to be stacked, bow-shaped marks (Packard, 1900b, p. 69, fig. 5), and was selected as the type ichnospecies by Häntzschel (1962). Since polymorphous material cannot be included within the same ichnotaxon (otherwise the name provided would not then convey a unique, precise meaning—I.C.Z.N. Introduction, p. xiii), *Merostomichnites* should be restricted to trails similar in form to *M. beecheri* (e.g., as illustrated by Fischer, 1978; and as stated by Walter, 1986). All other ichnospecies previously included in *Merostomichnites* are true trackways and must therefore be included in another ichnotaxon. For example, *M. triassicus* has already been included within *Diplichnites* by Bromley and Asgaard (1979)—a decision followed by Pickerill (1992). Indeed, the only difference between *Protichnites logananus* (which, as previously argued herein, is better included as '*Diplichnites*' *logananus*) and *M. narragansettensis* noted by Packard (1900b) was that the latter ichnotaxon was probably the work of a limulid whereas the former ichnotaxon was thought to be the work of a trilobite. As stated previously, such phylogenetic distinctions are not considered to be viable ichnotaxobases or valid nomenclatural acts.

Although Seilacher (1955) and Häntzschel (1962), amongst others, had previously included *Acripes* within *Diplichnites*, Pollard (1985) followed Walter (1983) in retaining *Acripes*, and placed *M. triassicus* within *Acripes* as *A. triassicus*. The reasoning was that *Acripes* could not have been formed by a merostome (itself an action that from our earlier comments cannot now be considered an acceptable ichnotaxonomical procedure). Walter (1986) and Demathieu *et al.* (1992) also chose to retain *Acripes*.

A further problem exists because of Seilacher's (1955) introduction of *Dimorphichnus* for trackways with dissimilar rows that lacked a median groove. This was done in the same publication as the recommendation that *Diplichnites* be used for all trackways lacking a median groove. Consequently, Fillion and Pickerill (1990) suggested restricting *Diplichnites* to trackways consisting of similar rows of punctate to striate (striae being transversely oriented), regularly spaced imprints.

On this basis, *Acripes*, by way of the type ichnospecies *A. incertipes* (actually by original designation in Matthew, 1910, p. 124, and not by Häntzschel, 1962—I.C.Z.N., Article 68b.i) that exhibits considerable heterogeneity between rows, should not be included within *Diplichnites*. However, this heterogeneity feature had been adopted earlier in the diagnosis of *Petalichnus* Miller and initially in *Ptilichnus*, making *Dimorphichnus*, *Acripes*, and *Petalichnus* potential synonyms of *Ptilichnus*. The dissimilarity of track rows does not extend to all other ichnospecies of *Acripes* that are candi-

dates for synonymy within 'Diplichnites'. For instance, A. leavitti is essentially identical to Diplichnites logananus for most of its length.

The outcome of Fillion and Pickerill's (1990) modification to the use of Diplichnites is that most of Hitchcock's (1858, 1865) trackway ichnotaxa are not synonymous with it, either because they do not contain similar rows, such as Ptilichnus, or that they do not contain regularly spaced punctate to transversely oriented striate imprints, such as Hexapodichnus. However, the question remains open, pending review of the type material, as to which of Hitchcock's (1858, 1865) ichnotaxa should be considered synonymous with one another.

Accordingly, in the description of 'invertebrate' trackways that follows, historical precedence is followed with respect to nomenclature. We have included all punctate trackways with a median groove in Protichnites, and used the oldest ichnospecies name available for a specimen with a particular number and orientation of punctate imprints. Diplichnites is of uncertain morphology, lacks priority over several other 'grooveless' ichnotaxa, and has inconsistent historical usage. Although the name is entrenched in the literature, it would be difficult to provide a case for 'stability' as an all-encompassing name for 'grooveless' ichnotaxa. We choose to retain Diplichnites, but utilize the diagnostic restrictions advocated by Fillion and Pickerill (1990), which do not produce conflict with Hitchcock's (1858, 1865) more senior ichnotaxa. This permits numerous subsequently introduced ichnotaxa that have obscure or inconsistently adopted morphologies to be included within either Diplichnites or a Hitchcock ichnotaxon. Though the resulting stock of trackway names is considerable, it should not be found unwieldy to future workers.

SYSTEMATIC ICHNOLOGY

Trace fossils were encountered at various localities, designated TF00 to TF36, in western Cape Breton Island. Every separate toponomic occurrence of trace fossils has been given an 'assemblage' number. Hence, each different trace-fossil assemblage at a particular locality is given the same locality number but distinguished with a separate letter. Complete assemblage numbers, for example, would be 'TF03a' and 'TF03b' from locality 3. Assemblages from localities containing tracks and trackways are shown in Figure 1. Other localities preserve only burrows, trails, pits, or coprolites (see Keighley and Pickerill, 1997). Specimens, where collected, are currently housed in the collections of the Geology Department at the University of New Brunswick (U.N.B. S-255). In total, six trackway ichnogenera were identified that comprise a total of two named ichnospecies, seven ichnospecies retained in open nomenclature, and six unnamed ichnospecies. A further ten track

and trackway morphologies were retained in the vernacular since they are not attributable to particular ichnotaxa. Systematic listings follow the format of Keighley and Pickerill (1997).

Ichnogenus Diplichnites Dawson, 1873

Diagnosis: Trackway consisting, in epirelief, of two similar rows of simple, striate to punctate marks oriented transverse to slightly oblique to the axis of the trackway, and lacking an intersecting longitudinal furrow. Preservation is reversed in hyporelief (modified from Fillion and Pickerill, 1990).

**Type ichnospecies**: Diplichnites aenigma Dawson, by original monotypy.

Nomenclatural discussion: At least four ichnospecies of Diplichnites have been named, with several other ichnospecies having, at various times, been transferred to this ichnogenus, for example: D. aenigma Dawson, D. incertipes (Matthew), D. minor (Matthew), D. triassicus (Linck), D. gouldi (Gevers et al.), D. govenderi Savage, D. cuithensis Briggs, Rolfe, and Brannan, and D. binatus Webby. However, several are likely junior synonyms either of each other, or of other ichnospecies currently contained within alternative ichnogenera that, following Seilacher's scheme (sensu Fillion and Pickerill, 1990), could be included within Diplichnites. Others are probably best excluded from such synonymy because they do not comply with Fillion and Pickerill's (1990) restriction.

Numerous different trackway morphologies assignable to Diplichnites (or one of its many potential junior synonyms) have been identified in the present study, but because of the problems in determining viable ichnospecific taxobases, the material described herein is left in open ichnospecific nomenclature. Affinities to particular ichnospecies are given where material is of sufficient quality and distinctiveness, though it is recognized that more senior synonyms for such ichnospecies may ultimately be found to exist. The remaining material is grouped together as 'types' of Diplichnites isp.

Diplichnites cf. logananus (Marsh, 1869) [nov. comb.— isp. previously in Protichnites]
Figure 3A

Description: Three trackways are preserved as TF02d in positive hyporelief on the sole of a low angle, cross-stratified, fine-grained sandstone. The trackways lack a median groove and comprise individual marks, transversely oval or crescentic in outline, and up to 2 mm in width. The individual marks are well spaced, and arranged either in single series or, rarely, in

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Fig. 3. 3A = Diplichnites cf. logananus: three specimens (arrowed) from TF02d preserved in positive hyporelief (mag. x 0.7). 3B = Diplichnites isp. type A, Protichnites cf. variabilis and cf. Protichnites carbonarius, preserved as undertracks in convex hyporelief, from TF01a (mag. x 0.5). Diplichnites runs from centre to right (arrows). ?Protichnites carbonarius is shown bottom right (black arrow), and Protichnites cf. variabilis is shown top left (white arrow)—detailed in 3C (mag. x 1.7) and 3D (mag. x 1.7), respectively. 3E = Protichnites isp. type C and Gluckstadtella cooperi, preserved in concave epirelief, from TF02a (mag. x 0.5). Where G. cooperi passes into Protichnites isp. type C (white arrow) is detailed in 3F (mag. x 3.0), and where the trackways cross (black arrow), is detailed in 3G (mag. x 1.7). Ethologically, the organism most likely alighted on the substrate with its posterior end facing the right of the page and then moved off towards the left. Illumination of all specimens is from the top left.
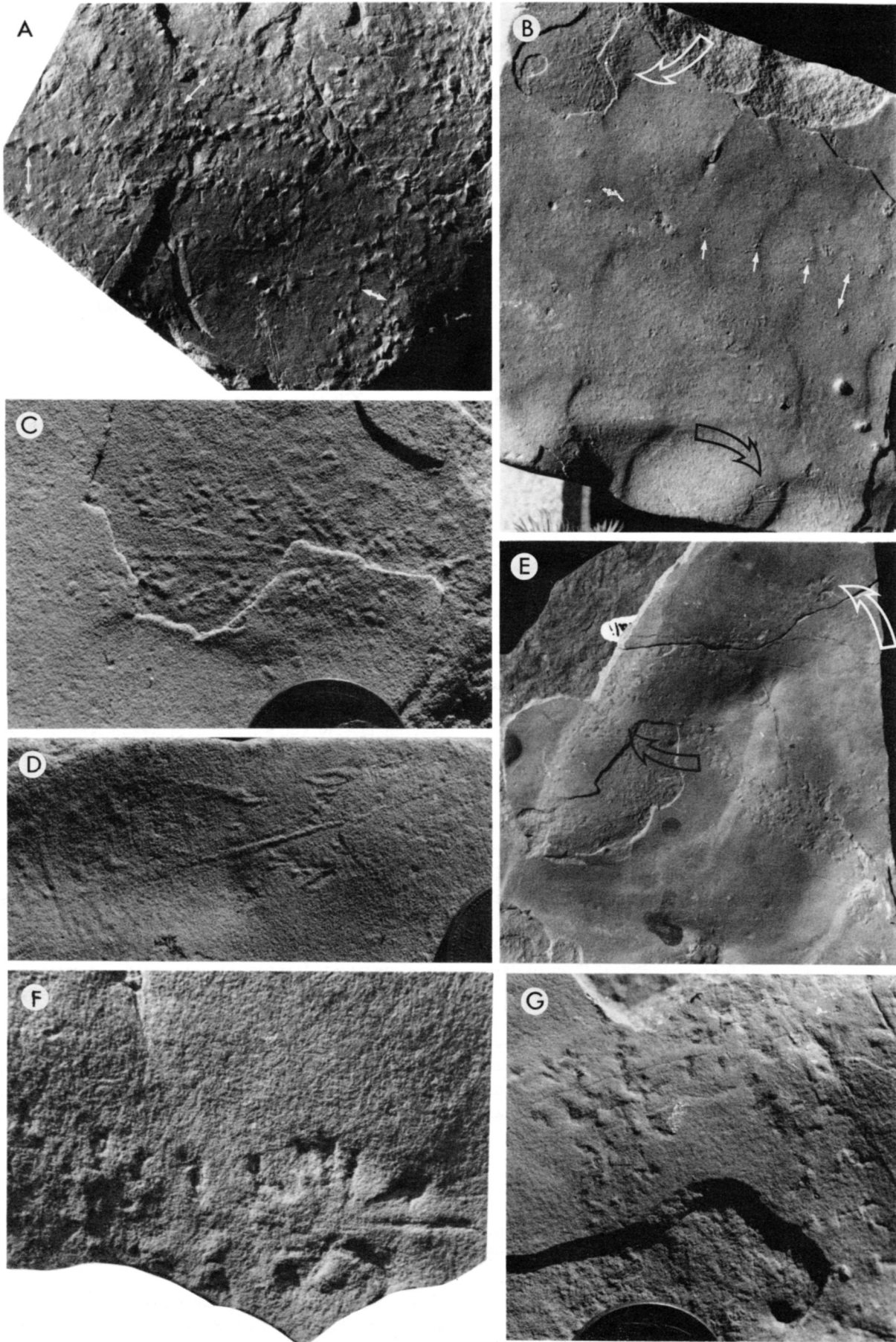
paired oblique series where natural track cycles develop en echelon. Due to poor preservation, there is no clear indication of how many imprints form a natural track cycle. Two of the trackways, one 15 mm wide, the other 18 mm wide, converge but do not cross. The other trackway is of similar width but less distinct.

Remarks: *Protichnites logananus* was the first name used to describe quite widely spaced punctate marks that formed single series (or rare dual series where the natural track cycle became en echelon) of imprints. The ichnogeneric assignment, as discussed earlier, is without merit but, because the morphology is distinct, the ichnospecific epithet '*logananus*' remains available for that morphotype when in combination with a different ichnogeneric name (I.C.Z.N., Article 48). Following Fillion and Pickerill's (1990) use of *Diplichnites*, and the inapplicability of *Merostomichnites* and *Acripes* as names for such trackways, it is included as *Diplichnites* cf. *logananus*.

Diplichnites isp., type A
Figure 3B

Description: Vague series of punctate impressions and inner bifid impressions preserved in convex hyporelief, likely as undertracks, on the base of a current rippled, fine-grained sandstone (TF01a). The marks are dispersed, with a 10 to 20 mm gap between series, and they are quite wide (25 mm). No median groove is preserved.

Remarks: No ichnospecific affinities could be attempted due to the poor preservation of the trackways.

Diplichnites isp., type B
Figure 5E

Description: Two vague trackways preserved in convex hyporelief, crossing or crossed by one or two specimens of *Protichnites* cf. *scoticus* on the base of a fine-grained sandstone (TF20b). The better-preserved trackway (11 mm wide) crosses within a bend of (?one of) the *Protichnites* specimens. It preserves, in one row, three series, and in the second row two sets of small punctate prints numbering three or four and oriented nearly normal to the trackway axis.

Remarks: The transversely in-line, triple-punctate nature of the individual marks invites comparison with *Etterwindichnus* (=*Diplichnites*) *regularis* Walter. However, an insufficient length of trackway is preserved even for this provisional ichnospecific assignment.

Ichnogenus *Gluckstadtella* Savage, 1971

Modified diagnosis: Surface impression consisting of up to six pairs of radiating striae. One or two pairs are oriented parallel to the long axis of the trace at one end. Other pairs are shorter and directed away from the other pairs (modified from Savage, 1971).

Type ichnospecies: *Gluckstadtella cooperi* Savage, by original monotypy.

Nomenclatural discussion: Savage's (1971) original diagnosis has been modified herein to make it less interpretative. In the original diagnosis, the longer striae were considered to be the anterior appendage marks, though without explanation or evidence to the contrary (i.e., that the longer striae could be the posterior appendage marks). Though the distinctiveness of the overall shape makes recognition of the producer as an arthropod virtually without doubt, such commentary has also been removed from the diagnosis. *Rotterodichnium longinum* Walter also has six pairs of appendages and could be incorporated within the ichnogenus, though the considerable length of many of the striae may warrant retention of the ichnospecies name.

Gluckstadtella cooperi Savage, 1971
Figure 3E, G

Diagnosis: As for the modifed ichnogenus.

Description: The specimen is preserved in concave epirelief on a current rippled, very-fine-grained sandstone (TF02a). A median groove terminates at one end of the trace fossil, where it is more deeply impressed, but at the opposite end it is continuous into the trackway *Protichnites* isp., type C. Six striae radiate out on each side of the median groove. Those arranged anticlockwise from the terminal end of the median groove are the best preserved. They consist of a pair of almost longitudinally oriented striae, a group of three striae arranged more or less transversely, and a single stria arranged obliquely to longitudinally at the transition of the trace into the adjacent trackway. The same pattern is less well distinguished in a clockwise direction on the other side of the median groove.

Remarks: Apart from the original diagnostic work and a comparison of material with this ichnospecies by Dias-Fabrício and Guerra-Sommer (1989), no other specimens have been assigned to this ichnotaxon. In our material the trace fossil forms, with the trackway of *Protichnites* isp. type C, a compound specimen. It is considered to mark the commencement of the trackway, the organism having settled on the substrate at this location before moving away. This interpretation is supported by the presence of the deeply impressed median groove, likely a telson drag mark, that continues through the length of the trace and was likely produced as the organism moved away (Fig. 3E). The termination of the median groove was where the organism first rested its telson on the substrate and must be considered posterior (Fig. 3G). Accordingly, the most obliquely oriented and paired striae probably represent the hindmost appendages, *contra* Savage (1971).

Ichnogenus *Hexapodichnus* Hitchcock, 1858

Diagnosis: Trackway comprising two similar rows of marks lacking a median groove (or ridge in hyporelief). Natural track

cycle of three striate imprints, inner imprints oriented longitudinally, outer imprints parallel to each other or outwardly divergent and oriented obliquely to the axis of the trackway (after Hitchcock, 1858).

Type ichnospecies: *Hexapodichnus magnus* Hitchcock, by subsequent designation (Lull, 1953).

Nomenclatural discussion: By following Fillion and Pickerill's (1990) criteria for assignment of material within *Diplichnites*, this ichnotaxon must be excluded from such synonymy. This is because, as with several other 'six-footed' ichnogenera introduced by Hitchcock (1858), at least one of the imprints in the natural track cycle is oriented longitudinally. Herein, we have followed Hitchcock (1858, 1865) and not considered *Hexapodichnus* as synonymous with the other 'six-footed' ichnogenera, *Copezia* or *Grammepus*; however, a final decision should be left to a more complete review of trackway ichnotaxa. Two ichnospecies of *Hexapodichnus* were originally described, *H. magnus* Hitchcock, and *H. horrens* Hitchcock. Whereas in Hitchcock's (1858) ichnogeneric diagnosis the track series was stated to have alternate symmetry, herein such a comment has been excluded because, whereas such symmetry is true for most of the type trackway of *H. horrens*, locally there is staggered or opposite symmetry (*sensu* Trewin, 1994).

Hexapodichnus horrens Hitchcock, 1858
Figure 4A-C

Description: As many as eight trackways are present, forming suites TF36a and TF36b. Almost all are preserved in concave epirelief on a 15 mm thick, parallel (subhorizontal) laminated, very-fine-grained sandstone. The one (or two) trackway forming TF36b is preserved in convex hyporelief and counterpoint concave epirelief.

Although it can be determined that a maximum of three imprints occur in a natural track cycle, preservation is highly variable even within one trackway. The imprints range from three distinct and offset tapering marks, to three intergrading marks that could be mistaken for separate oblique striae (Fig. 4C), to a mixture of striate to punctate marks per natural track cycle (Fig. 4B). Individual prints are best observed at turns in the trackways; straighter sections usually result in individual prints being overprinted and a near-continuous but highly irregular tramline is present. It is at some of the turns that the trackway most resembles *H. horrens*. Here, the natural track cycle consists of a distinct grouping of one inner, longitudinally oriented stria and two outer, transversely to obliquely oriented striae, subparallel to each other (Fig. 4C). All the specimens, however, are of comparable width (10-18 mm) and the trackways may cross each other at any angle. Indeed, the apparent number of six trackways may, in reality, have been part of one long, self-crossing trackway, the connecting parts not having been preserved.

Remarks: The trackways that comprise TF36a illustrate, more than any other in the collection, the difficulties in assigning names to invertebrate trackways. The amount of variation in the detail of the imprints in any single trackway is shown to be considerable and particularly notable between straight and curved parts of the trackways (Fig. 4B, C). Herein, we have named the trackways after the best preserved morphology, namely *H. horrens*, as shown in Figure 4C. However, it should be noted that a straighter trackway (Fig. 4A) is comparable to *Diplichnites gouldi*. Other relatively straight sections have not been quite so much worn down to a tramline form and are more comparable to *Trachomatichnus numerosus* Miller. Where transverse sets of three are more visible, the material is comparable to several of the ichnospecies still included in '*Heterotripodichnus*' and awaiting revision. Taking the trackways as a whole, in the sense that they become slightly wider, and individual punctate imprints become more distinct at specific turns, the material is also comparable in part to *Diplichnites cuithensis* described by Briggs *et al.* (1984). However, the trackways from TF36 are much smaller than *D. cuithensis*, considerably fewer sets of appendages were involved in producing them and, accordingly, there is usually greater spacing between individual prints at the turns. These multiple forms, each with a potentially different ichnogeneric name, emphasize the need for future rationalization of trackways or the more extensive use of compound ichnotaxa (*sensu* Pickerill, 1994).

Ichnogenus *Monomorphichnus* Crimes, 1970

Diagnosis: In concave epirelief or convex hyporelief, a series of straight to slightly wavy, parallel to intersecting striae. Groups or sets of striae may be repeated in series, or obliquely, or parallel to each other (after Fillion and Pickerill, 1990).

Type ichnospecies: *Monomorphichnus bilinearis* Crimes, by original monotypy.

Nomenclatural discussion: *Monomorphichnus* was originally established to encompass traces '...produced by a number of clawed limbs...' that were interpreted as having raked the sediment surface while the animal was being carried by a current (Crimes, 1970, p. 57). A total of eight ichnospecies have now been proposed. As well as the type, that is distinguished as having paired, parallel striae within a set, *M. multilineatus* Alpert has unpaired striae, the more central of the five or six striae being deeper and thicker than the marginal forms; *M. lineatus* Crimes *et al.* has diagnostic striae that are in unpaired sets; *M. cretacea* Badve and Ghare has only been recognized based on its geological range; *M. gaopoensis* Yang and Yin and *M. fusiforemis* Shah and Sudan are of unknown form; *M. pectenensis* Legg has two scales of striae in the form of two thicker ridges and intervening fine striae of variable number; and *M. intersectus* Fillion and Pickerill has intersecting marks. *M. cretacea* has
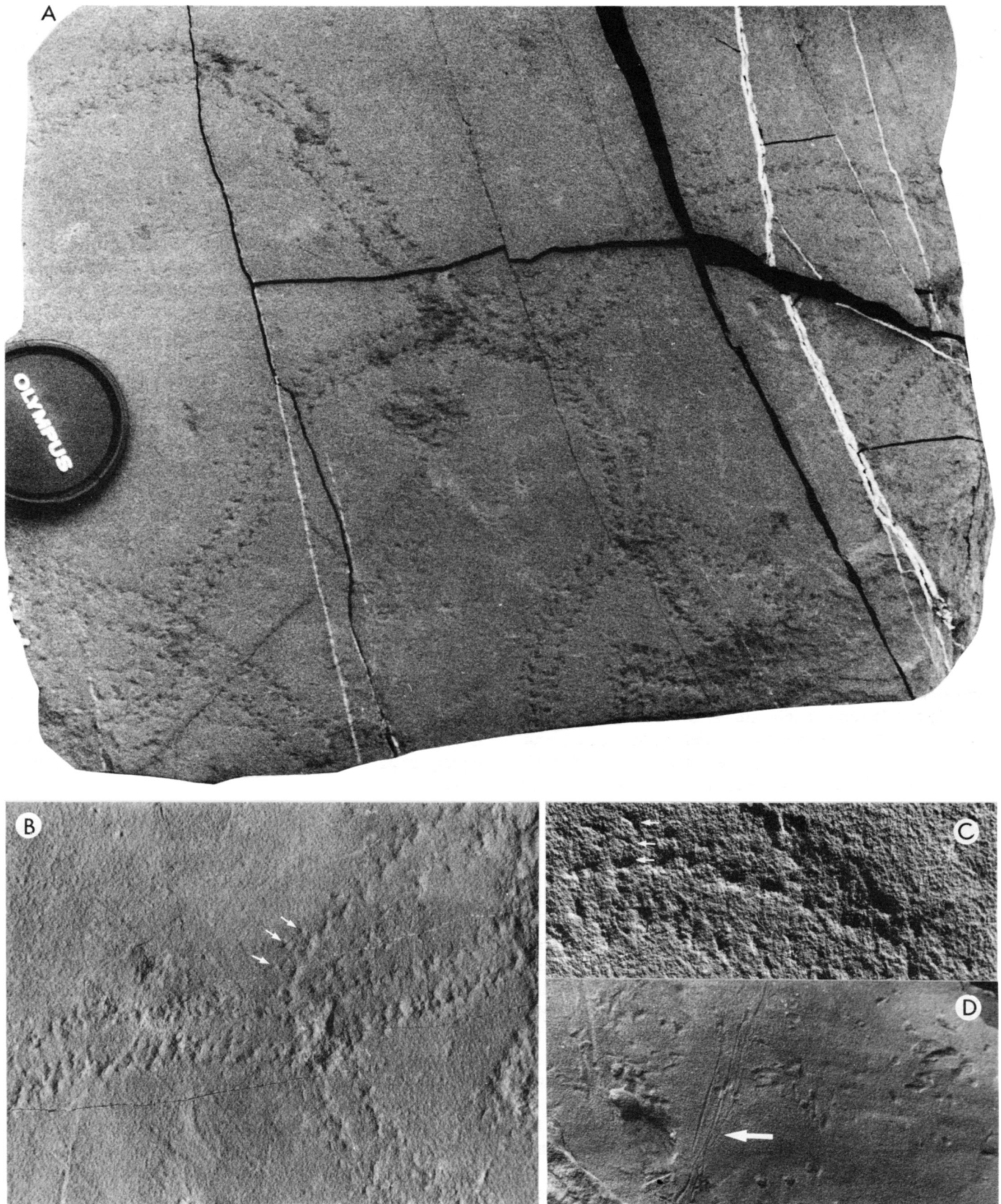
Fig. 4. 4A = *Hexapodichnus horrens*: several specimens preserved in concave epirelief from TF36a (mag. x 0.6). 4B = Detail of 4A. On the outside of the curving trackway the outer set of punctate tracks (arrows) becomes more distinct and separated from the other imprints (mag. x 1.1). 4C = This detail of 4A is where the trackway imprints are most distinct (arrowed) and where the characteristic morphology of *H. horrens* is best developed (mag. x 1.9). 4D = *Monomorphichnus* cf. *lineatus* (arrowed) and Appendage Marks, type B, preserved as concave epichnia, from TF16b/i (mag. x 0.9). Some of the appendage marks show convex-up puckering. Illumination of all specimens is from the top left.

no valid morphological criteria for its distinction and is best considered a junior synonym of *M. lineatus* (Stanley and Pickerill, 1998).

Monomorphichnus cf. *lineatus* Crimes *et al.*, 1977
Figure 4D

Description: On the top surface of a wedge-shaped, fine-grained sandstone (TF16b), is found a group of three, mostly parallel but slightly wavy, grooves. Where parallel, the individual grooves are 30 mm long, <1 mm wide, and up to 3 mm apart. Toward one end of the structure, one of the outer grooves converges and then diverges from the central groove. At the equivalent position on the other side of the median groove, the third groove disappears.

Remarks: Without recurrent sets running parallel or oblique to this one, doubt remains as to whether this is a true trace fossil or simply a small, current-induced drag mark of some sort. The individual striae are unusually long, but the lack of other current indicators (e.g., tool marks) and the presence of other trace fossils on this surface suggest that the marks are biogenic in origin. Ichnospecific assignment is conditional because only one set of striae, which are not demonstrably characteristic even of *M. lineatus*, is present.

Crimes (1970) noted that a trilobite arthropod using one set of its appendages could be the producer of *Monomorphichnus*. Although a trilobite is unlikely to have formed this trace fossil, the strata being nonmarine, an arthropod is definitely favoured: the other trace fossils on this surface are appendage marks, presumably of invertebrate, arthropod origin, and an arthropod 'resting' trace. However, the possibility that a swimming vertebrate produced the trace cannot be entirely excluded.

Ichnogenus *Protichnites* Owen, 1852

Diagnosis: Trackways that, in epirelief, consist of any number of simple, punctate or short striate imprints in similar series on either side of a central, intermittent or permanent, groove or grooves (modified from Owen, 1852; Seilacher, 1955).

Type ichnospecies: *Protichnites septemnotatus* Owen, by subsequent designation (Häntzschel, 1962).

Nomenclatural discussion: Herein, use of *Protichnites* follows the proposal by Seilacher (1955). Because of the problems in determining viable ichnospecific taxobases for trackways, the material described herein is left in open ichnospecific nomenclature. Affinities to likely ichnospecies are given where material is of sufficient quality and distinctiveness, though it is recognized that more senior synonyms for such ichnospecies may ultimately be found to exist, depending upon what ichnospecific taxobases are employed in future detailed systematic study. Remaining material, though of disparate form, is grouped simply as '*Protichnites* isp.' of various types.

The six ichnospecies introduced by Owen (1852) were based on slight variations in the maximum number of prod marks ('feet') per sublinear 'series', and the angle that each

series subtended with the central ridge(s) and, or, groove(s). However, the type ichnospecies, *P. septemnotatus*, did not have the same number of prod marks in each repetitive 'natural track series', rarely totalling, for instance, eight (characteristic of *P. octonotatus*) instead of seven. In the terminology used herein, the number of imprints per oblique series repeat in a three, two, and two (or three) sequence. Accordingly, Owen's (1852) ichnospecific diagnosis of the type should be more liberally interpreted and possibly include *P. alternans* and *P. octonotatus*, though the latter typically has an intermittent central line. In contrast, *P. multinotatus* Owen is characterized by more densely packed imprints, and in *P. lineatus* the imprints are so dense that they commonly merge to form up to four ridges or grooves on one side of the median ridge or groove (on the other side up to five imprints form distinct punctate sets).

No ichnogeneric diagnosis was provided by Owen (1852), but a perusal of his illustrations certainly indicates that he did not restrict the number of marks per natural set in the ichnogenus, and transverse sets could have between two and five imprints. In *P. scoticus*, the pattern of imprints is similar to *P. septemnotatus*, but in the former a natural track cycle of six imprints is recognizable along with repetitive transverse sets of three imprints. *P. carbonarius* can be considered a distinct ichnospecies in that it contains alternating quadripunctate sets, arranged in a rhomboidal pattern, about a central groove. *P. logananus* is considered to be synonymous with *Diplichnites*. *P. gallowayi* Sharpe, has well spaced, inline, and obliquely oriented pits about a central groove.

Protichnites cf. *carbonarius* Dawson, 1873
Figures 3C, 5A-C

Description: The five specimens form part of TF16a, and are preserved in convex epirelief on a wafer-thin, micaceous, very-fine-grained sandstone (Fig. 5A). Tracks vary between 12 and 15 mm in width. The 'median' groove, which is most frequently displaced toward, or overprints, one set of the imprints, is essentially continuous and <1 mm diameter. The imprints are typically of shallow ovate shape (or rarely of short, blunt striae), arranged in rhomboidal sets repeated every 7 to 9 mm along the trackway. One specimen, illuminated oblique to the trackway direction (Fig. 5B) shows this arrangement. However, if this trackway is illuminated from the opposite direction, some prints merge to form a single impression, 4 mm long by 2 mm wide, that resembles a bird's foot (Fig. 5C). The specimen from TF01a is poorly preserved in cleavage hyporelief on a current rippled, fine-grained sandstone (Fig. 3C). Two series, comprising sets of rhomboidally clustered, semipunctate marks, are parallel about an off-centre ridge. Maximum track width is 13.5 mm.

Remarks: The figured drawing of the original specimen (Dawson, 1873, p. 23, fig. 1) illustrates the imprints surrounding the central groove as separate punctate to striate marks. The holotype has not been examined, but with different illumination the same 'bird's foot' impression noted in TF16a might be revealed. Miller and Knox (1985, p. 78, pl. 1G) have illustrated similar material, but, noting that the rhomboidal arrangement
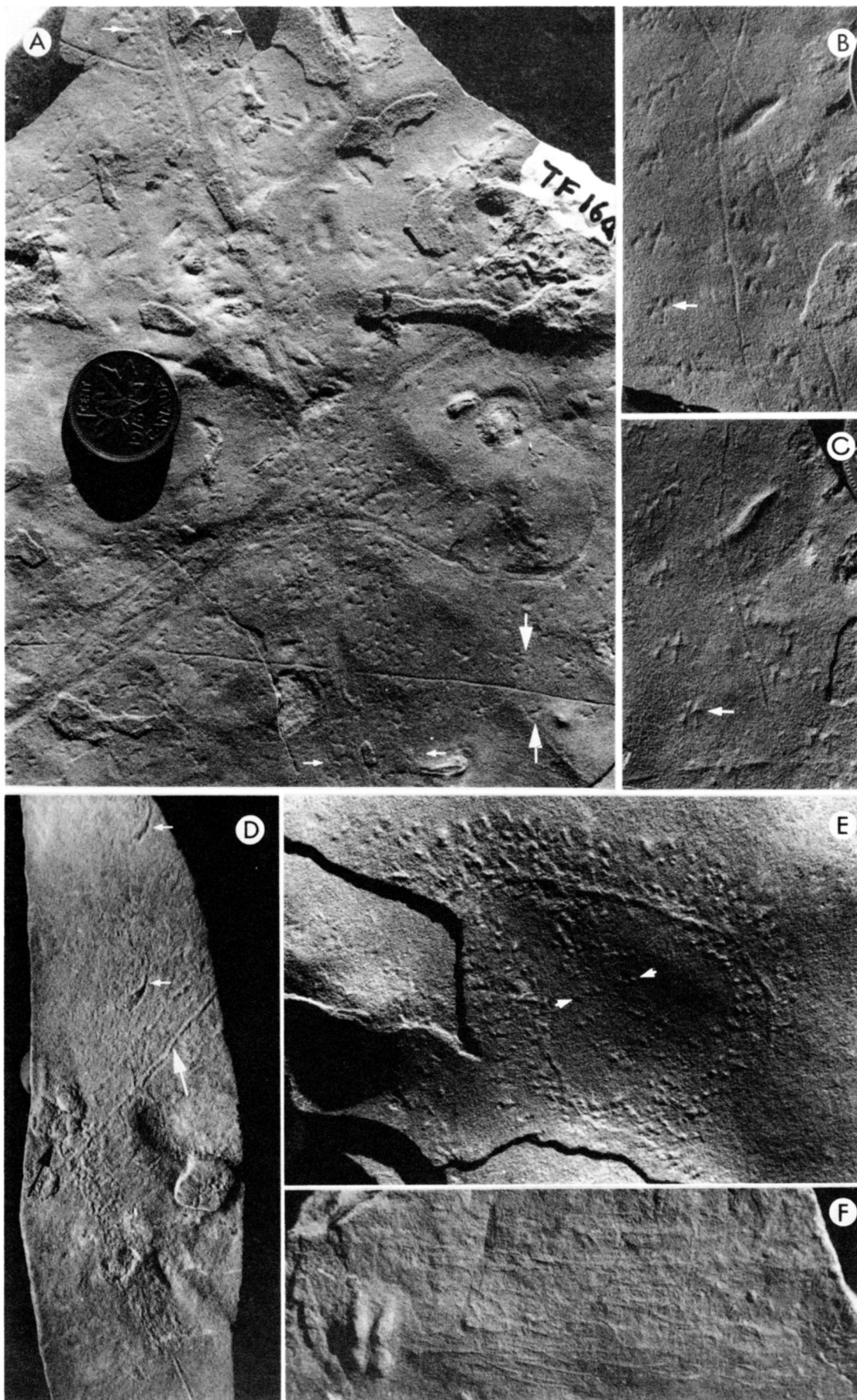
of pits enclosed an occasional bifid impression, assigned the specimen to *Kouphichnium*. Part of one series in the trackway assigned to *Stiaria quadripedia* Smith similarly displays four punctate imprints arranged in a rhomboidal manner. However, the sets in *S. quadripedia* grade into a form where the four imprints per set are arranged in a straight line (Walker, 1985, p. 291, fig. 5) and could not have been formed by a single, quadrifid appendage. Like Walker's material, the apparent single quadrifid appendage of the present specimens seems to be merely a taphonomic merging of four separate imprints.

Protichnites cf. *kennediea* (Smith, 1909) [*nov. comb.*— isp. previously in *Danstairia*]
Figure 5D

Description: This specimen forms part of a compound trace fossil with *Selenichnites* (TF01a). The compound trace is preserved in convex hyporelief on a thin, rippled, fine-grained sandstone. At one end, the 50 mm long trackway extends for a further 10 mm exclusively as a central ridge. At this end of the trackway the diffuse punctate marks gradually widen toward the middle of the trackway as the central ridge disappears. The maximum width of 9 mm is achieved 10 mm from this end of the trackway and a similar width is then maintained to the termination of the trackway where it abruptly becomes *Selenichnites*.

Remarks: This material closely resembles some specimens of *Danstairia kennediea* Smith, although the ichnogenus was introduced for dissimilar material (Walker, 1985). Pollard and Walker (1984) and Walker (1985) therefore included *D. intermedia* Smith, *D. unispina* Smith, and *D. kennediea* within *Stiaria intermedia*. As previously noted, *Stiaria* itself can be included within *Protichnites*, and from the illustrations by Smith (1909) and Walker (1985), *D. intermedia* can probably be included within *P. scoticus*. *D. kennediea* has very densely packed imprints on either side of the central groove, and is also synonymous with *Protichnites*. Accordingly, we have provisionally included the material as *P. kennediea*, though the orthography of this ichnospecies has never been elucidated: it may be a feminized surname in the genitive, in which case it should be given the termination *-ae*, not *-ea* (I.C.Z.N., Article 31a). Irrespective, for most of the length of the trackway, the central ridge is not present; the material also resembles *Trachomatichnus numerosus* that, in lacking a central groove, can be considered synonymous with *Diplichnites*.

As well as the specimen figured by Smith (1909) and Walker (1985), similar trackways were described and illustrated by Brady (1947) under the name *Isopodichnus filiciformis* Brady (= *Oniscoidichnus filiciformis* by Brady, 1949) and by Hardy (1970, unpaginated, pl. 40) as *Kouphichnium rossendalensis* who attributed his compound specimens to a Xiphosurid producer.

A confident ethological interpretation can be presented because of the compound nature of our specimen, although two possible scenarios can be advanced. In the first, the groove and gradually widening series of imprints indicate the initial 'landing' of an arthropod. The organism then moved along the substrate for a distance before stopping, possibly concealing itself for a period of time and then returning to the water column. The 'launch' is thus marked by the anteriorly divergent lobes of *Selenichnites*. A similar interpretation was placed on some compound *Protichnites*—*Rusophycus* trace fossils by Birkenmajer and Bruton (1971). The alternative scenario reverses the direction of progress: the *Selenichnites* trace marks an initial settlement and possible concealment trace. The animal then moved off, and gradually became waterborne, the telson groove being the last part of the producer in contact with the substrate.

Protichnites cf. *scoticus* Salter [in Harkness], 1856
Figure 5E

Description: The specimen(s) is (are) preserved in convex hyporelief on the undulating base of a ?wave rippled, micaceous, fine-grained sandstone (TF20B). Where the 15 mm wide trackway, consisting of punctate imprints and a distinct 'median' ridge, starts to turn, the outside imprints and ridge disappear. Though the imprints on the inside of the turn continue, it is difficult to determine whether the outer imprints are still preserved or not. A poorly preserved trackway at the edge of the preserving sandstone surface contains an intermittent and ex-centric ridge, but it is uncertain whether this is a continuation of the same trackway at the completion of the turn. It appears that three punctate marks form a set that is usually linear in shape, in some cases coalescing into a simple striate mark. Such marks are oriented obliquely or perpendicular to the median ridge.

Remarks: Although a detailed description of *P. scoticus* was provided by Salter (in Harkness, 1856), only passing reference was made to Owen's (1852) work. The only clearly differ-

Fig. 5. 5A = *Protichnites* cf. *carbonarius* (thick arrows), and *Protichnites* isp. type D (thin arrows), from TF16a (mag. x 1.0). A trackway of *Protichnites* isp. type D (centre) forms a loop. All trackways are preserved in concave epirelief. 5B = Detail of two other specimens of *Protichnites* cf. *carbonarius* preserved in concave epirelief, also from TF16a (mag. x 1.5). 5C = Same trackway as 5B (mag. x 1.5), but with reversed illumination (from bottom right) providing a different morphological appearance to the imprints; in particular two striate imprints in B (arrowed) are shown to be one quadrifid imprint in C (arrowed). 5D = *Protichnites* cf. *kennediea*, *Protichnites* isp. type A, *Selenichnites* isp. and horn-shaped trace, preserved as convex hypichnia, from TF01a (mag. x 1.0). *P.* cf. *kennediea* is the most distinct of the traces present, extending from the bottom of the photo to the centre left where it is transitional into (i.e., a compound specimen with) *Selenichnites* isp. (black arrow). The median groove of a poorly preserved specimen of *Protichnites* isp. type A (thick white arrow) crosses just below *Selenichnites*. Horn-shaped traces marked with a thin white arrow. 5E = *Diplichnites* isp. type B (arrowed), is present crossing within the loop of *Protichnites* cf. *scoticus*. Preservation is in convex hyporelief, from TF20a (mag. x 1.0). 5F = *Stiallia* cf. *pilosa* preserved as convex hypichnia, from TF02b (mag. x 1.5). The trace fossil *Rusophycus* cf. *carbonarius* is present far left. Illumination of all specimens, except 5F, is from the top left.

ing feature of this ichnospecies from *P. septemnotatus* therefore appears to be its much smaller size in relation to the type ichnospecies, and the recognition of a natural track cycle involving six, as opposed to seven or eight appendage marks. Though in the original illustration (Harkness, 1856, p. 243, fig. 2) a natural track cycle of six imprints can be discerned, the most clearly recognizable grouping of imprints are in the form of oblique sets of three, as is the case in TF20b. No definitive natural track cycle is recognized. Since Walker (1985) did not definitively state how many appendage marks per natural set were present in her review of similar material assigned to *P. (Stiaria) intermedia*, this ichnotaxon is potentially a junior synonym of *P. scoticus*.

Protichnites cf. *variabilis* (Linck, 1949) [*nov. comb.*—isp. previously in *Kouphichnium*]
Figure 3D

Description: Poorly preserved specimen, 12 mm wide, in cleavage hyporelief, toward the base of a current rippled, fine-grained sandstone (TF01a). Only one set of indistinct, bifurcating bifid imprints is preserved on either side of a central ridge.

Remarks: Due to the poor quality of preservation in this specimen, it cannot be confidently stated that the trackway is invertebrate in origin rather than a small digitigrade vertebrate trackway. The specimen does, however, bear some resemblance to the material figured by Jarzembowski (1989, p. 224, fig. 6) as *Kouphichnium* aff. *variabilis*, that is more definitively invertebrate in origin. As previously noted, *Kouphichnium* is an invalid name used for polymorphous material—though typically for material containing bifid, trifid, or quadrifid imprints—hence our provisional assignment within *Protichnites*. Assignment is provisional also because it cannot be ascertained whether the producer of the TF01a trace truly had bifid appendages, since the pattern may be due to the fortuitous overprinting of striae from different appendages that were not bifid at all.

Protichnites isp., type A
Figure 5D

Description: The specimens cross-cut and seemingly predate *Protichnites* cf. *kennediea* and *Selenichnites* isp. on a low angle cross-laminated, very-fine-grained sandstone (TF01a). A distinct median ridge (the specimen is preserved in convex hyporelief) seems to be central to nearly continuous marginal imprints that virtually coalesce to form tramlines. The overall width of the two specimens is 15 and 16 mm respectively. Individual ridges are 1 mm wide.

Remarks: These specimens cannot be assigned to any ichnospecies because of their poor preservation.

Protichnites isp., type B
(not figured)

Description: The extensively crossing trackways of TF01b are very poorly preserved on a rippled, very-fine-grained sand-

stone and were not suitable for photography. No apparent preferred path direction is noted. Preserved in concave epirelief, the central furrow in each case is the best preserved part of the trackway, the marginal punctate imprints occurring only intermittently. The width of the best preserved trackway is 13 mm.

Remarks: The multiple cross-cutting nature of these poorly preserved trackways negates any accurate observation of trackway form beyond recognition of a median groove, hence no ichnospecies assignment is possible.

Protichnites isp., type C
Figure 3E-G

Description: Three trackways are preserved in epirelief on a (linguoid) current rippled, very-fine-grained sandstone (TF02a). All specimens are approximately the same width (~10 mm). One trackway is transitional with the trace fossil *Gluckstadtella cooperi* at one end (the other 'end' corresponds to the edge of the slab). Individual appendage marks are usually transversely oriented, striate or apostrophe-form, but occasionally triangular or punctate, with one or two marks forming oblique series on each side of an intermittent, thin, median groove. This groove becomes excentric in places where the 0.15 m long trackway follows a slightly curving course. The two other trackways run perpendicular to the crests of the ripples, at one point converging to follow the same path for 30 mm before diverging and crossing the other trackway at right angles. Both have only a sporadic, short, thin median groove present, but imprint morphologies are similar to those of the other trackway. The material is therefore all considered conichnospecific.

Remarks: Though this trackway is well preserved in relation to the other '*Protichnites* isp.' material, no provisional ichnospecific assignment is made because, to our knowledge, no named ichnospecies or ichnogenus with similar morphology has been defined. The only comparable material previously illustrated are the 'Type E Tracks Fp. 8a' of Nielsen (1949, p. 28, fig. 19). If better quality material were to be recovered, formal introduction of a new ichnospecies would be warranted.

Protichnites isp., type D
Figure 3E

Description: In comparison with the previously described specimens of *Protichnites* (including *P.* cf. *carbonarius* present on the same thin sandstone), the four variably preserved, crossing, epichnial specimens in TF16a have a much thicker, slightly sinuous, shallow central furrow that itself typically contains two grooves, 1.5 to 2 mm apart. The total track widths are between 16 to 23 mm, though in two specimens only one row of tracks is distinct. Imprints are punctate, with an inner set of two to four prints arranged in an oblique line, and an outer set clustered in groups of two to four (in two cases possibly indicating a bifid mark).

Remarks: If better quality material were to be recovered, introduction of a new ichnospecies would again be warranted, since we are unaware of any similar named trackways.

Ichnogenus *Stiallia* Smith, 1909

Diagnosis: Trackway consisting of rows of very elongate, wispy striae oriented parallel or subparallel to each other and longitudinally to the axis of the trackway (modified from Smith, 1909; Walker, 1985).

Type ichnospecies: *Stiallia pilosa* Smith, by subsequent designation (Walker, 1985).

Nomenclatural discussion: Following Fillion and Pickerill (1990), we do not consider this ichnotaxon for synonymy within *Diplichnites* because, in the first four of the five originally introduced ichnospecies of *Stiallia*, the individual striate imprints are not transversely oriented.

The ichnogenus was never adequately described, and no type ichnospecies was originally indicated. The five ichnospecies introduced by Smith (1909) were all similar to each other in having long, wispy striae. In order of introduction, these striae were directed longitudinally (*S. aca* Smith; *S. pilosa* Smith), obliquely (*S. coma* Smith), obliquely with crossing longitudinal striae (*S. gigantea* Smith), and with overlapping, transverse striae (*S. scalaris* Smith). Walker (1985) subsequently included *S. (Carrickia) berriana* Smith as another ichnospecies and listed *S. pilosa* as the type. The remaining ichnospecies were considered synonymous with the type because the forms can grade into each other.

In contrast, *S. scalaris*, having transverse striae, can be considered for inclusion within *Diplichnites*. Of the remaining ichnospecies, *S. coma* and *S. gigantea* are similar to *Acanthichnus tardigradus (non Pterichnus)*, though in *S. coma* the natural track cycle of three imprints is more easily distinguished. *S. aca* and *S. pilosa* distinctively have longitudinally oriented striae and more than three imprints in a natural track cycle. These features distinguish these ichnospecies, and accordingly the ichnogenus, from the current definition of *Acanthichnus* (Hitchcock, 1858, 1865).

Stiallia cf. *pilosa* Smith, 1909
Figure 5F

Description: Preserved in positive relief on the sole of a fine-grained sandstone (TF02b), this 19 mm wide trackway comprises numerous striae (likely more than six per natural track cycle) that are parallel, longitudinally oriented, discontinuous, and not clearly distinguishable into any series or separate track rows (a 'left' or 'right'). Sporadic, marginal, paired striae are present that are slightly oblique from longitudinal, and gently curving. The striae are all superimposed on a broad, rounded, very shallow ridge.

Remarks: The only information originally given about *S. pilosa* is: '...a marking probably made by an animal in swimming and touching the mud in a pretty regular manner with two whisks

of hairs which it drew along pretty much in the direction it was moving...' (Smith, 1909, p. 15). In fact, up to six longitudinal striae were illustrated (Smith, 1909, p. 15, fig. 23; Walker, 1985, p. 294, fig. 9a) as forming a natural track cycle, and successive series were easily distinguishable, as were the two rows. The material in TF02b does not show how many striae are present, nor are successive series distinguishable from one another. Accordingly, ichnospecific assignment is only provisional.

Appendage Marks

Discussion: The term 'Appendage Marks' is used descriptively for small punctate pits or more elongate striae. Such marks are considered to have only one possible way of having being formed, that is, by the impression of one or more of an animal's skeletal appendages, hence the open nomenclatural term adopted. Two distinct forms are recognized.

Appendage Marks, type A
Figures 5A, 6A, B

Description: The specimens from TF03d (Fig. 6A) are present as concave epireliefs on a wave rippled surface of silty, very-fine-grained sandstone that has a thin coating (almost a sheen) of muddy siltstone. These appendage marks form small, subrounded pits, each less than 1 mm in diameter, or rarely as pits at the end of thin, apostrophe-like marks. The individual imprints typically form a semicircular pattern in groups of three, four, five, or six marks per semicircle. The widest parts of the semicircular groupings are 8 to 10 mm apart. Specimens forming part of TF03e (Fig. 6B) and TF16a (Fig. 5A) occur on a coarser, micaceous, fine-grained sandstone. The similarly sized, subrounded pits are here much more densely packed and may form diffuse or distinct, rounded or elongate groupings. In TF16a, the appendage marks locally become sufficiently organized to suggest the presence of biserial trackways (that could possibly be assigned to *Diplichnites sensu lato*).

Remarks: Where the marks are more densely packed (TF03e and TF16a), the immediate subsurface may have been repeatedly 'massaged' by the arthropod limbs in order to disturb micro-organisms for food. In contrast, on TF03d, the producers appear to have been stationary, possibly indicating a resting or concealment behaviour, or a less suitable substrate for foraging.

Appendage Marks, type B
Figure 6B, C

Description: In contrast to the marks described above, these appendage marks are typically much larger (up to 12 mm long by 2 mm wide), blade-like or scimitar-like in plan view, and V-shaped in cross-section. They occur widely on a fine-grained sandstone (TF16b). No major, geometrically organized patterns can be identified from the collection of marks (i.e., they do not form regular trackways). However, occasionally paired, parallel marks are noted, and possibly a series of three longi-
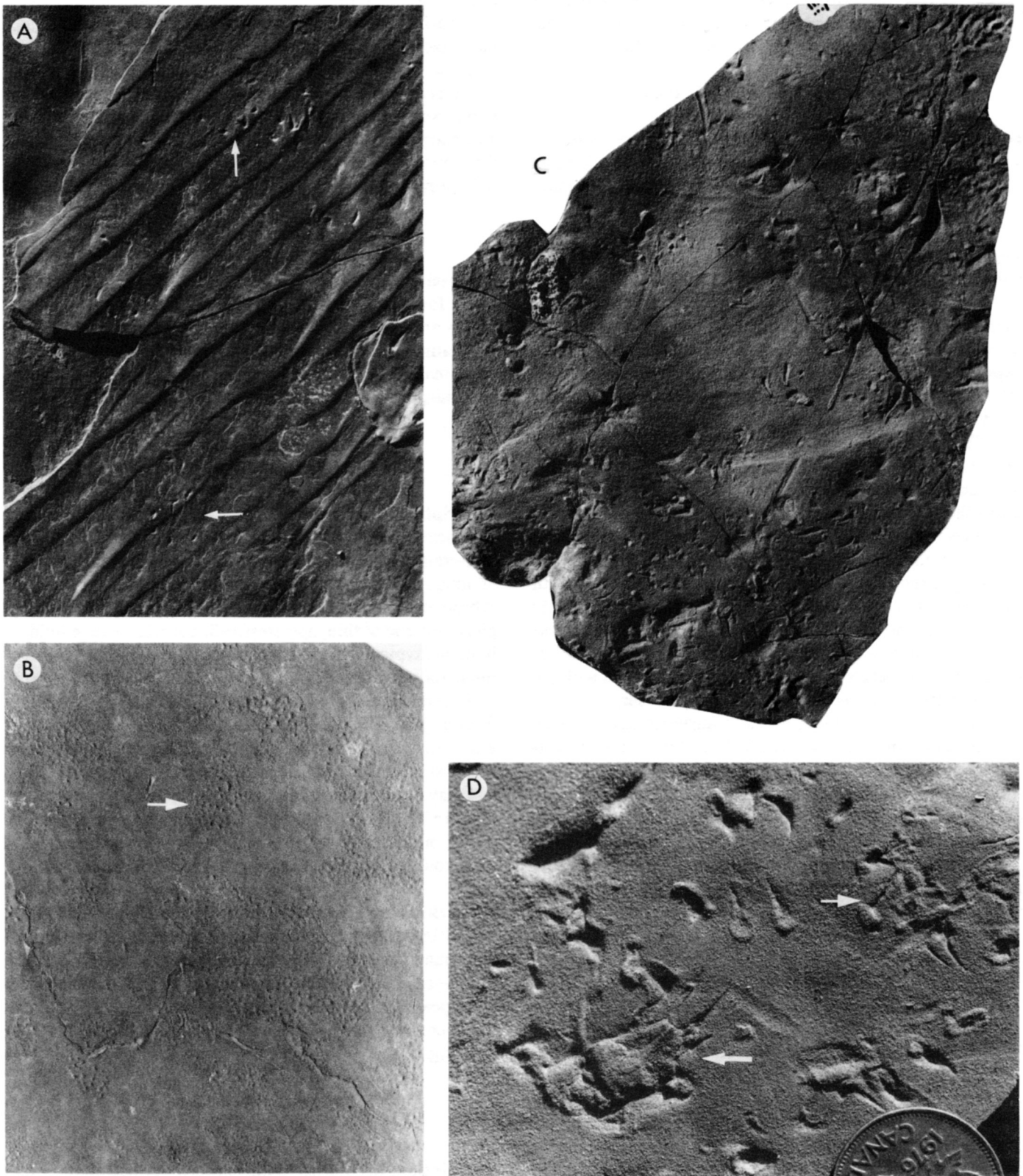
Fig. 6. 6A = Appendage Marks, type A (large arrows), preserved as concave epichnia, from TF03d (mag. x 1.0). 6B = Appendage Marks, type A, as concave epichnia, from TF03e (mag. x 0.7). In contrast to 6A, the concave epichnial markings are more densely clustered and semicircular patterns are not as distinct (example arrowed). 6C = Appendage Marks, type B, preserved in concave epirelief, from TF16b (mag. x 0.5). Some markings may be part of a poorly defined trackway of which a median groove (lower left of centre to bottom right) is partly preserved. 6D = 'Arthropod Resting' Traces (arrowed) and Appendage Marks, type B, in concave epirelief, from TF16b (mag. x 1.7, penny coin for scale). Illumination of all specimens is from the top left.

tudinally oriented striae form sets that recur on each side of a central groove (Fig. 6C) that might indicate a poorly preserved trackway.

Remarks: The paired, parallel marks match in size what appear to be the rearmost pair of appendage marks of the specimen described as an 'arthropod resting' trace in TF16b. The striae that occur in triplets are more problematical. They may be arthropod limb prints or, alternatively, digitigrade vertebrate prints. The very angular nature of the marks, that rarely have rucked-up margins, indicates that they are not undertracks and were likely formed on the sediment surface when it was quite firm (subaerially exposed?).

'Arthropod Resting' Trace
Figure 6D

Description: The specimen occurs in concave epirelief on a vaguely current rippled, very-fine- to fine-grained sandstone (TF16b). The generally lobate mark, 13 mm long by 7 mm wide, is round at one end (interpreted as anterior) and tapers to two terminal striae at the other (posterior). External to the lobate mark and emanating striae, the preserving sandstone is slightly raised to form a rim. The lobate mark is bisected by a transverse ridge 3.5 mm from the anteriormost part of the trace, and a vague central ridge extends longitudinally toward the posteriormost part. Two further striae emerge from the lobate mark slightly to the anterior of the two terminal striae.

Remarks: Considerable phylogenetic interpretation encompasses the informal naming of this trace-fossil form. However, the highly distinctive shape described above means that only an arthropod could logically have produced it, since this is the only animal group that has bilateral symmetry, is segmented, and contains jointed appendages. The trace is readily interpreted as a resting or concealment imprint. In the present specimen, the transverse ridge likely marks the division of a cephalo-thorax and abdomen, the emanating striae, pairs of appendages. The abdomen of arthropods is usually larger than the cephalo-thoracic region, and since the longer striae emerge from the end of what is therefore considered to be the abdomen, the striae probably represent the hindmost appendages. The lack of adjoining trackways on the preserving medium suggests that the producer must have flown, hopped, or swam to its resting place—numerous insect groups (e.g., grasshoppers) hop using their hindmost appendages. The sharpness of the outlines to all the marks on TF16b indicates that the sediment was likely firm and subaerially exposed, favouring a hopping or flying producer.

Horn-shaped Surface Traces
Figure 5D

Description: The two horn-shaped impressions are 7 and 9 mm long with a maximum width of 3 mm. Both are oriented in the same direction and are approximately 35 mm apart adjacent to the other trace fossils forming TF01a.

Remarks: The orientation of the two horn-shaped tracks suggests that they might represent the repetition of a large appendage that produced successive imprints on one side of a large, wide trackway—the rest of the trackway not being preserved.

Vertebrate Trackways

Discussion: In light of nomenclatural confusion due to the frequent assignment of a particular 'vertebrate trace' to a particular producer (and to a particular age), and the generally poor quality of the specimens encountered in the present study, the trackways are retained in open nomenclature. However, the dimensional information that was obtained from them is summarized in Table 1.

Vertebrate Trackway, type A
Figure 7A, B

Description: The specimens in TF03h are present as positive hyporeliefs on a vaguely wave rippled, fine-grained sandstone. Two of the trackways cross, and are divergent from each other at an angle of ~70°. One of these trackways is 65 mm wide, but poorly preserved: there is only scant preservation of both right- and left-sided footprints. The best preserved print may indeed be part of the other trackway that crosses at this point. This other trackway is 0.2 m long and up to 57 mm wide. It contains seven right-sided footprints, of which prints R3 to R6 are best preserved, and seven left-sided footprints, though L1 to L4 and L7 are particularly poorly preserved (L1-L2 have been partly destroyed by the opening of a large desiccation crack, subsequently infilled by the sand that now moulds and preserves the remaining prints). Both series are in-line (i.e., they do not sprawl), and successive serial prints are approximately equidistant. Accordingly, determination of manus and pes is subjective. Stride length of all the footprints appears to be between 55 and 72 mm, and the better-preserved footprints give pace lengths of 45 to 64 mm, and a step angle of 76° to 84° (Table 1). Most of the distinctive prints are semidigitigrade, between 21 and 26 mm in length and 17 to 22 mm in width. R4, R6, and L5 have the 'toes' of the first three digits in-line and forming a somewhat oblique angle to the trackway axis. R5 and L6 have the first three digits offset and slightly in-turned. The fourth digits are longest and point down the trackway axis, the fifth digits being short, offset, and out-turned.

Remarks: Though two trackways are poorly preserved, all three footprint trackways have similar dimensions and morphology. Two different types of prints are present in the better-preserved trackway, indicating a quadripedal producer, although determining which prints are the manus, and which are the pes, is difficult. Both the manus and pes are likely five toed. The producer of the trackways did not sprawl, as shown by the in-line nature of each series of footprints, and was not moving efficiently, as illustrated by the low step angles. Of previously described Carboniferous vertebrate prints, those ascribed to *Hylopus minor* Dawson or *Pseudobradypus* (*non*

Table 1. Vertebrate Trackway, type A

Trackway breadth: 57 mm (max)

Trackway length: 200 mm

Print:	L1	L3	L4	L5	L6	L7	R1	R2	R3	R4	R5	R6	R7
(impression)	-	-	-	sd	sd	-	-	-	sd	sd	sd	d(?sd)	?pl
(length)	-	-	-	26 mm	-	-	-	-	-	23 mm	21 mm	-	-
(width)	-	-	-	21 mm	-	-	-	-	-	22 mm	17 mm	-	-
(number of digits)	3+	?3	?4	5	?3	?3	-	-	3+	3+	5	3+	-

Stride:	R2--R4	R3--R5	R4--R6	R5--R7
(length)	73 mm	72 mm	65 mm	70 mm

Pace:	R4--L5		L5--R6		R5--L6		L6--R7	
(length)	64 mm		55 mm		59 mm		45 mm	
(angulation-degrees)	\	68 deg.	/		\	84 deg.	/	

Hylopus, non Asperipes) caudifer (Dawson) bear the closest resemblance, both being five toed with manus and pes of 20 mm diameter, the former having a gait of 60 mm and stride of 80 mm, the latter a gait of 80 mm and stride of 75 mm (Sarjeant and Mossman, 1978).

they may be the undertracks of an agile (?running) vertebrate. Most similar are *Attenosaurus jonesii* Aldrich and *Hylopus logani* (Dawson) although the latter ichnotaxon displays up to five straight, sausage-shaped marks per set (Sternberg, 1933; *non* Matthew, 1904, 1905).

## Vertebrate Trackway, type B
Figure 7C

Description: These marks are preserved on the base of a rootlet-bearing red sandstone (TF08a), and form sets of two, three, or four, essentially straight (10-13 mm long by 2-3.5 mm wide), sausage-shaped marks in positive relief. Components in each set are parallel and oriented longitudinally to the trackway direction. Separate sets within a series appear to be widely spaced and out-of-phase with what probably is the other series.

Remarks: The trackways, being oriented longitudinally, may represent the swimming activity of a vertebrate. Similar, but much larger, sausage-shaped marks that occur in pairs as opposed to threes, have likewise been interpreted by Boyd and Loope (1984) as vertebrate swimming tracks. Alternatively,

Vertebrate Trackway, type C
Figure 7D

Description: Only two left-sided and three right-sided prints are preserved hypichnially on the undulating, ?wave rippled base of a very-fine-grained sandstone (TF20a). Accordingly, the ~0.09 m long by ~0.11 m wide trackway is not well defined (Table 2). The R1 print has four prominent, parallel digits of approximately equal length (8-11 mm) extending forward from what appears to be an elliptical sole print 20 mm long by 15 mm wide. The 5th digit is outwardly (abaxially) offset from this sole but is of similar length to the other digits. The more axial R2 print is less distinct and only three parallel, forward pointing, and rather thick digits, 15 mm in total width, are present. R3 preserves only three elongated digits extending from a 15 mm wide sole. L1 and L2 are slightly smaller and only preserve three digits. Both are considered incomplete.

Fig. 7. 7A = General distribution and preservation of Vertebrate Trackways, type A, from TF03h (mag. x 0.3). Two trackways, preserved in convex hyporelief, are figured extending (in the directions of movement of the producers) from top centre to lower left, and from top centre to bottom right. The latter trackway is detailed, in part, in 7B, and shows footprints L4 to L6 and R4 (arrowed in 7A) to R6. 7C = General morphology of Vertebrate Trackway, type B, from TF08a (mag. x 0.4). Trackway, comprising widely spaced sets (arrowed) of two or three, parallel, sausage-shaped markings, is preserved as convex hypichnia. 7D = Vertebrate Trackway, type C, from TF20a (mag. x 0.5). The five prints making up this trackway are present as convex hypichnia on a rippled surface. Lighter coloured parts of the surface represented the upslope for the tracemaker. 7E = Vertebrate Trackway, type E, from TF29d (mag. x 0.1). Oblique-angle field photograph of large vertebrate trackways preserved, uncertainly, as hypichnia. For the better preserved trackway, the producer moved from top left of centre to bottom right, and the producer's right-sided imprints are best preserved. The left-sided imprints of another, less distinctively preserved trackway, are present on the right of the photo—the producer having been moving in the opposite direction (from bottom to top). Specimen uncollectible. 7F = Vertebrate Trackway, type F, from TF32a (mag. x 1.7, penny coin for scale). Trackway (likely swimming tracks) is preserved in convex hyporelief. Illumination of all specimens is from the top left.
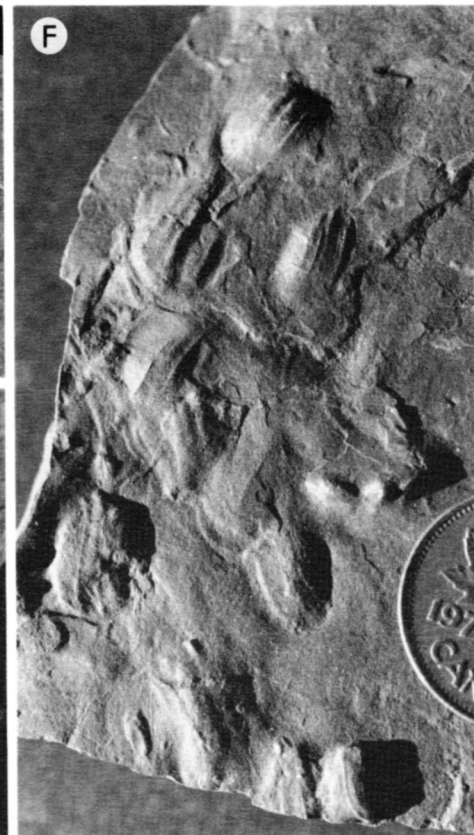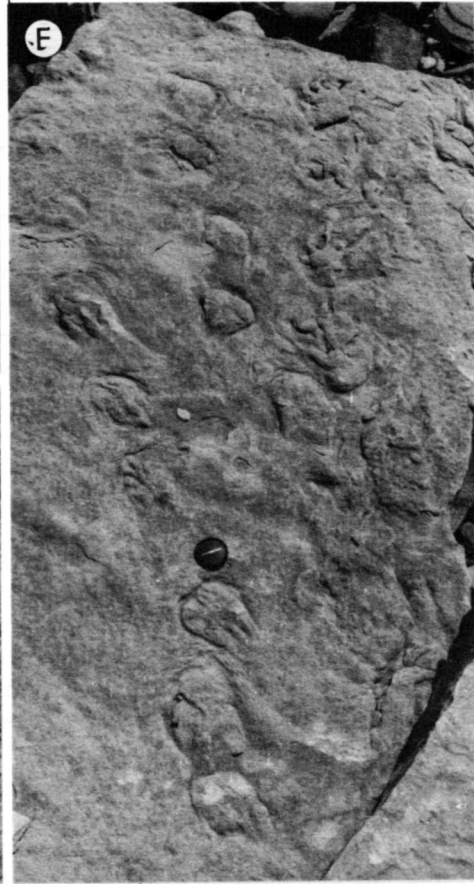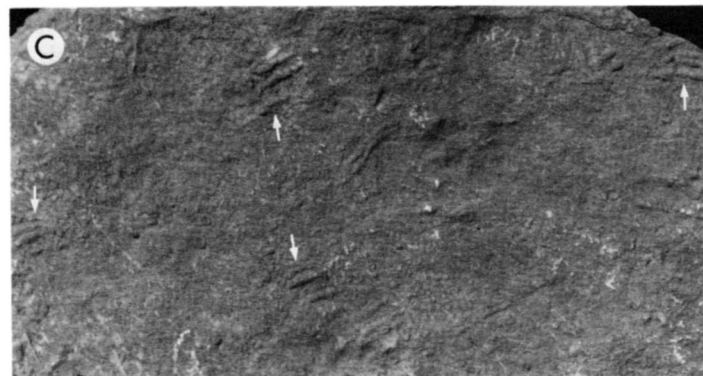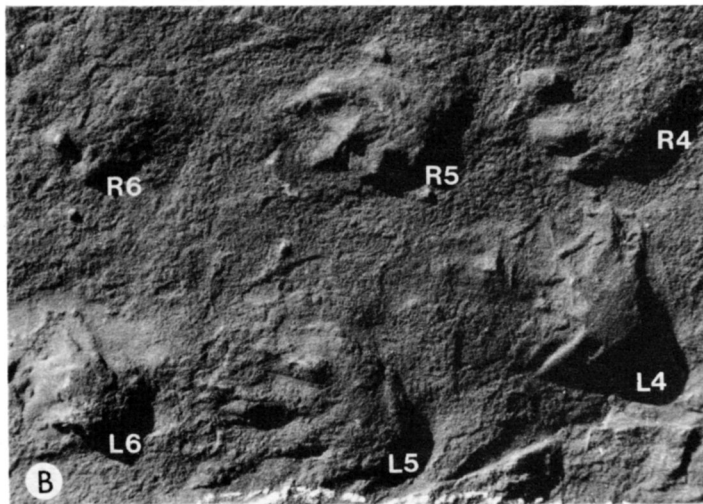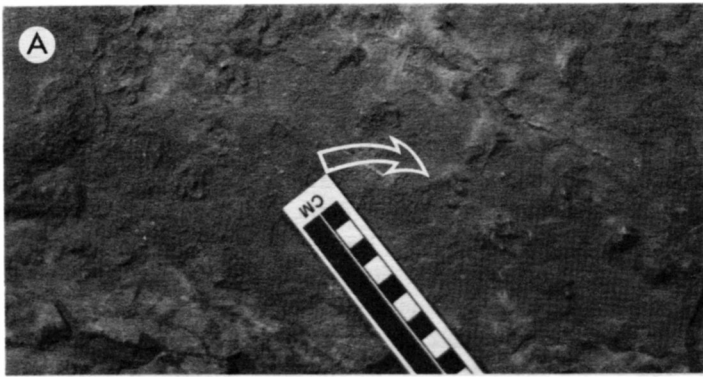
Remarks: Prints R1, L2, and R3 are considered to be the pes prints because of their larger size. On the basis of size, overall shape of the sole, and number and arrangement of digits, R1 is readily comparable to the pentadactyl hindfoot mark of *Asperipes avipes* Matthew. L2 and R3, however, are insufficiently well preserved to provide supporting evidence. L1 and R2, as preserved, are both tridactyl, which also corresponds to the diagnosis of *A. avipes*, though the supposedly long sole of an *A. avipes* manus was not noted. Consequently, the few complete prints in this trackway makes conclusive assignment to this ichnotaxon unwarranted.

Part of the problem for the incompleteness of each mark appears to be the undulating nature of the substrate upon which the trackmaker walked. In particular, R3 appears to indicate some slippage of the producer's foot back down the side of a ripple.

Vertebrate Trackway, type D
Figures 8A-C, 9A-C

Description: A considerable variety of individual prints can again be observed as hypichnia on the bases of massive or vaguely horizontally laminated, fine- to medium-grained sandstone boulders (TF29b and TF29c—measured specimens C and D of Table 3 respectively, and TF29e—measured specimens A and B of Table 3). However, two general types of print are present. The semidigitigrade prints are five toed: the innermost digit is rarely recorded but when present is usually opposed and laterally directed; the fourth digit is usually the longest; the fifth digit is narrow and pointed. The distinctly plantigrade prints are long soled, tridactyl, and usually less well preserved. Data on stride lengths for two of the more distinct trackways (C and D respectively, Table 3) give an average stride length of 103.5 mm, pace lengths for the pentadactyl prints averaging 77.5 mm and 93.5 mm, and tridactyl

pace lengths averaging 84 mm and 98 mm. These more distinct trackways (92 mm broad and 100 mm broad respectively) also preserve a repeatedly imprinted, axial tail mark. In Specimen B there is the rare indication that L1 and L3 were manus prints, since L2 seems to partly overprint, and hence postdate L3.

Remarks: The plantigrade marks resemble several previously defined ichnogenera. *Megapezia pineoi* Matthew has three relatively short blunt digits, similar to the specimens described herein, but also a fourth, offset, divergent digit (this may simply not be preserved in the Port Hood Formation material). *M. pineoi* has pentadactyl forefeet but, as illustrated in the holotype, these are divergent in a semiradial pattern, with the digits all being of similar length. Interestingly, Dawson had compared this holotype with *Hylopus logani* several years prior to Matthew providing the specimen with its formal name (Sarjeant and Mossman, 1978). Like *Palaeosauropus* Hay, *Hylopus* contains a longer second-last digit (i.e., digit 4 on the pes). All three ichnogenera were grouped within the ichnofamily Batrachichnidae by Haubold (1970). The specimens may alternatively be compared to *Matthewichnus caudifer* Kohl and Bryan, or to *Ichnotherium* Pohlig, that Haubold and Katzung (1978) considered to be primarily Permian footprints from pelycosaurian communities that had their evolutionary roots in the faunas of the Upper Carboniferous.

The generally low step angle, typically between 70° and 85°, indicates a slow moving producer. This is also indicated by the low stride length with respect to trackway breadth, though the trackmaker did not sprawl. Assuming that the pentadactyl prints represent the mani, then the glenoacetabular distance (body length) of the trackmaker was in the range of 80 to 90 mm. Digits are generally rounded at their periphery, rarely with an indication of claws, as shown by the two pentadactyl prints from TF29e (Fig. 8C). Claws would suggest a

Table 2. Vertebrate Trackway, type C

Trackway breadth: 111 mm (max)

Trackway length: 95 mm

Print:	L1	L2	R1	R2	R3	Stride:	n/a
(impression)	sd	pl	sd	sd	sd	(length)	
(length)	-	-	-	-	-		
(width)	-	-	-	-	-	Pace:	n/a
(number of digits)	3+	3+	5	3+	3+	(length)	
						(angulation-degrees)	

Fig. 8. 8A = Vertebrate Trackway, type D, from TF29e (mag. x 0.3). The trackway (measured specimen A) is preserved in convex hyporelief. The producer moved from bottom to top. 8B = Detail of area arrowed in 8A (mag. x 0.7). Prints L2 and L3 (top left) are the best preserved, the sharply pointed digits possibly indicating that the producer was clawed (reptilian). 8C = Detail of another trackway from an unfigured portion of the same slab shown in 8A (mag. x 0.7). L3 (middle left) seems to be partly overprinted by L2, suggesting that L3 (and L1, lower left) was a manus print. The drag marks of the producer's tail are well preserved to the right of L2 and L3. All are field photographs with illumination from the top left. Specimens uncollectible.
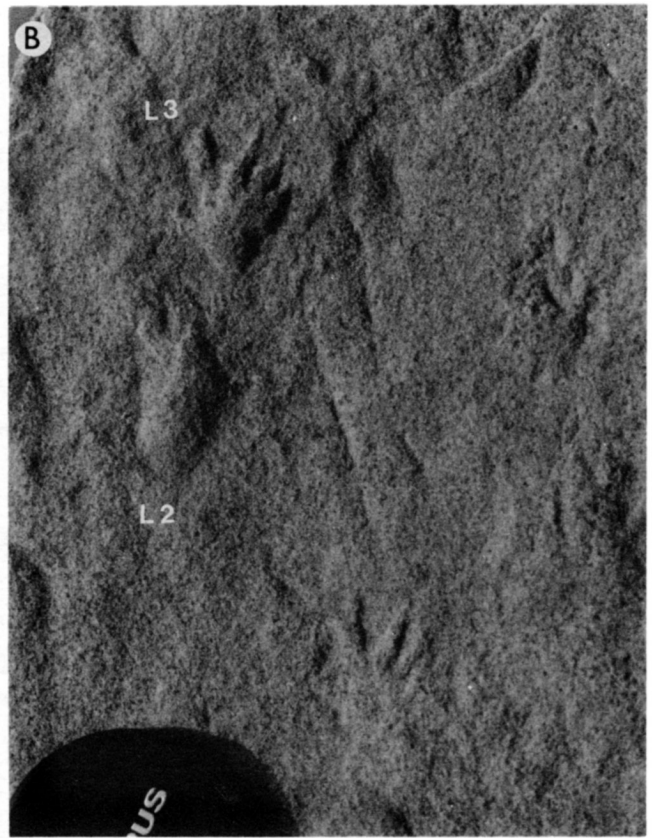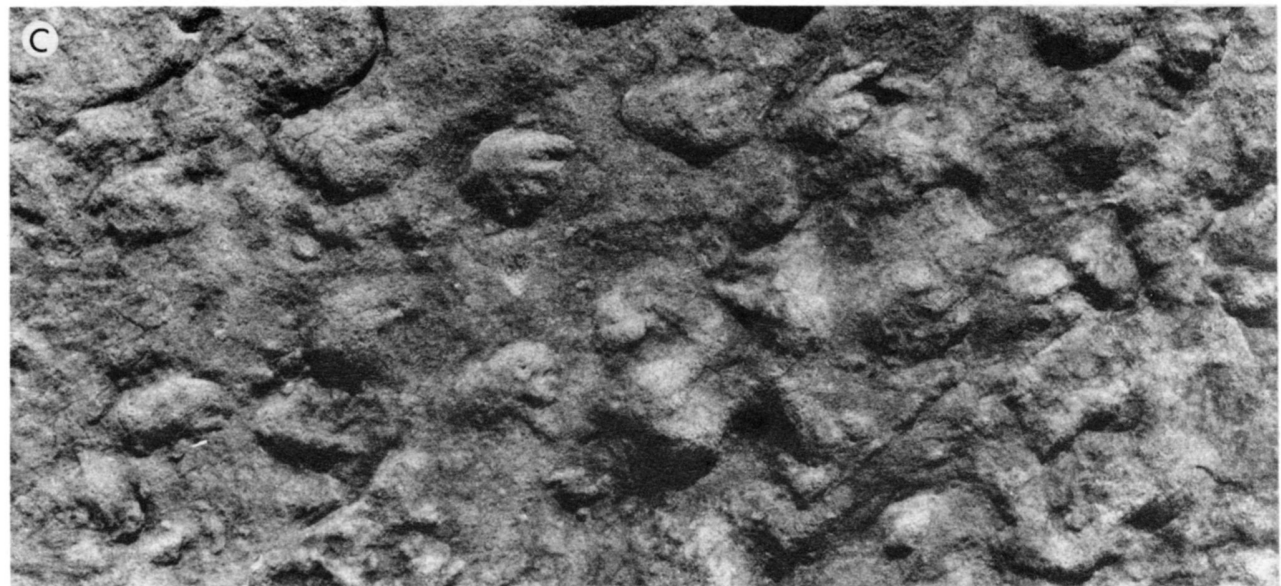
reptilian producer and, circumstantially, Baird and Carroll (1967) recovered the oldest remains of the reptile *Romeriscus* from beds lower within the same sequence that includes locality TF29.

Vertebrate Trackway, type E
Figure 7E

Description: By far the largest vertebrate tracks belong to this type of trackway, with individual prints being up to 0.1 m wide by up to 0.12 m long. They are preserved as subdued ?hyporelief moulds on a thick (dm-scale) slab of fine- to medium-grained sandstone (TF29d). Unfortunately, preservation is not good anywhere along the 1.25 m length of the trackway. The right-sided prints are slightly deformed and the generally smaller, left-sided prints are virtually indistinguishable, but an approximate trackway breadth of 0.35 m has been measured. The other (very indistinct) tracks occur to the left of the first trackway (on the right of Fig. 7E). They appear to form the left row of a second trackway, made by a vertebrate travelling in the opposite direction.

Obtaining significant measurements from even the main trackway is difficult. It is not certain that all the prints are preserved, even on the right side (eight prints are delimited on the right side, four on the left side). If all prints are present, then the stride length is quite variable (Table 4), ranging from 0.25 m (L1-L3) to 0.35 m (R5-R7). Pace lengths, and hence step angle, cannot be ascertained with certainty, since the left-sided prints preserve too little detail to correlate a forefoot—backfoot sequence with the right-sided prints.

What little detail that can be gleaned from individual prints indicates a tridactyl plantigrade form for both manus and pes prints (though which prints are the manus or pes cannot be determined). The best preserved prints (R3 and R6) contain three virtually parallel (little divarication) and rather stumpy digits, the widest part of the foot (on R6 and R8) being midway along the sole. Most of the right-sided prints are somewhat turned inward, and R7 and R8 are displaced slightly to the right of the line formed by the preceding tracks.

Remarks: The poorly preserved nature of these prints precludes any nomenclature of the trackway, though in print size, trackway width, and gait, some resemblance to *Pseudobradypus ungifer* (Dawson) should be noted. Similar criteria also define *Chelichnus gigas* Jardine (cf. McKeever and Haubold, 1996, p. 1017, fig. 4) that could be the senior synonym of *Pseudobradypus* and thus extend the occurrence of the ichnotaxon from the Permian back into the Carboniferous. This suggestion is contrary to McKeever and Haubold's (1996) assertion that the former name should not be expanded to include trackways from older or younger strata, because

we do not consider stratigraphy as relevant in the diagnosis of an ichnotaxon (see earlier comments).

The diffuse nature of some of the margins and the grooved margins of other prints suggest that the substrate (likely a grey mudstone forming in an overbank or floodplain environment) was not firm, and likely wet, when the vertebrate trackmaker traversed this area. Wet sediment would promote collapse at the margins of prints, leading to the diffuse margins and lack of distinction between digits, together with an aureole of deformed sediment surrounding them (the ?mould of the surface of this deformed sediment is visible particularly on R3 and R4). The poor definition and slightly inward turn of the footprints suggest that the underlying sediment was submerged, with a cross-current (from right to left as viewed on Fig. 7E), though the preserving strata provide no evidence to support or refute this suggestion, being diffusely horizontally laminated sandstone.

The vertebrate itself was likely an inefficient walker, as it produced a trackway that is as broad as the animal's stride length. This would suggest an amphibian producer although, conceivably, environmental conditions (e.g., the cross-current) may have precluded large strides even if the trackmaker were reptilian.

Vertebrate Trackway, type F
Figure 7F

Description: The specimens occurring as TF32a are present as a cluster of mounds (positive hyporeliefs) on the base of a silty, very-fine-grained sandstone. Up to four, narrow, approximately parallel, positive relief striae cross each of a group of four elliptical mounds, the striae being oriented more-or-less parallel to the long axes of the mounds. The striae and the long axes of the mounds themselves have similar orientations and form a loose biserial trackway of four prints (left of centre, Fig. 7F). Several other low elliptical mounds, of similar dimensions but with less distinct ridges or lacking ridges (bottom left, Fig. 7F), are oriented at a slight angle to the others.

Remarks: The trace fossil is interpreted to be the trackway produced by a vertebrate swimming just above the sediment surface. The ethological interpretation of a swimmer, as opposed to a walker, is preferred because the termination (or commencement—direction of travel is not certain) of the trackway is in the middle of the preserved slab and the striae traverse the length of the mound. The narrow parallel striae are likely evidence of protruding claws that scoured slightly deeper into the underlying sediment as the animal 'doggy paddled' over the surface. It is the observation of two rows of marks that leads to the suggestion of a vertebrate producer, one row reflecting left-sided paddling limbs, the other row right-sided

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Fig. 9. 9A = Vertebrate Trackway, type D, from TF29b (mag. x 0.2). A multitude of similar trackways are present in convex hyporelief crossing this slab. Measured specimen C is present from upper centre to upper left (the direction of movement of the producer). 9B = Vertebrate Trackway, type D, from the same slab illustrated in 9A (mag. x 0.5). Producer moved from right to left. 9C = Vertebrate Trackway, type D, from TF29c (mag. x 0.4). Detail of measured specimen D, that is preserved in convex hyporelief. Producer moved from left to right. All are field photographs with illumination from the top left. Specimens uncollectible.

Table 3. Vertebrate Trackway type D

Specimen A

Trackway breadth: 84 mm (max)

Trackway length: 200 mm

Print:	L1	L2	L3	R1	Stride: L1–L3
(impression)	sd	pl	sd	pl	(length) 88 mm
(length)	22 mm	-	25 mm	-	
(width)	20 mm	-	18 mm	-	
(number of digits)	?4	?3	5	?4	

Specimen B

Trackway breadth: 100 mm (max)

Trackway length: 230 mm

Print:	L1	L2	L3	R1	R2	R3	R4	R6
(impression)	sd	-	sd	sd	?pl	?pl	sd	sd
(length)	22 mm	-	25 mm	-	-	-	-	-
(width)	20 mm	-	18 mm	-	-	-	-	-
(number of digits)	?4	2	4	4	?	?	3	?3

Stride:	L1–L3	R1–R3	R2–R4	R4–R6					mean
(length)	95 mm	100 mm	95 mm	90 mm					95 mm

Pace:	R2–L1		L1–R4		R4–L3		L3–R6		mean
(length)	63 mm		75 mm		62 mm		70 mm		67.5 mm
(angulation-degrees)	\	88 deg.	/\	86 deg.	/\	86 deg.	/		~87 deg.

Specimen C

Trackway breadth: 92 mm (max)

Trackway length: 365 mm

Print:	L1	L2	L3	L4	L5	L6	L7	L8	R2	R3	R4	R6
(impression)	pl	sd	pl	sd	pl	sd	pl	sd	sd	pl	sd	sd
(length)	-	-	-	-	-	-	-	-	-	-	-	-
(width)	-	-	-	-	-	-	-	-	-	-	-	-
(number of digits)	3+	2+	3	2+	3+	3	?4	?5	?5	2+	?5	4

Stride:	L1–L3	L2–L4	L3–L5	L4–L6	L5–L7	L6–L8	R2–R4	R4–R6	mean
(length)	107 mm	105 mm	100 mm	112 mm	100 mm	100 mm	102 mm	102 mm	103.5 mm

Pace:	L2–R2		R2–L4		L4–R4		R4–L6		L6–R6		R6–L8		mean
(length)	82 mm		70 mm		82 mm		75 mm		84 mm		72 mm		77.5 mm
(angulation-degrees)	\	82 deg.	/\	80 deg.	/\	86 deg.	/\	80 deg.	/\	80 deg.	/		82 deg.

Pace:	L3–R3		R3–L5			mean
(length)	88 mm		80 mm			84 mm
(angulation-degrees)	\	73 deg.	/			

Glenoacetabular	Midpoint of L3–R3 to midpoint of R4–L6	Midpoint of R3–L5 to midpoint of L6–R6	mean
distance:	91 mm	91 mm	91 mm

Specimen D

Trackway breadth:100 mm (max)

Trackway length: 265 mm

Print:	L1	L2	L3	L4	L5	R1	R2	R3	R6	R7
(impression)	pl	pl	pl	sd	pl/sd	pl	pl	pl	-	-
(length)	38 mm	45 mm	37 mm	42 mm	38 mm	42 mm	33 mm	38 mm	-	-
(width)	22 mm	28 mm	32 mm	22 mm	22 mm	25 mm	-	22 mm	-	-
(number of digits)	?3	3	?5	3	?5	3	?3	?4	3	3

Stride:	L1–L3	L2–L4	L3–L5	R1–R3	mean
(length)	102 mm	110 mm	115 mm	112 mm	103.5 mm

Pace:	L1–R2		R2–L3		mean
(length)	85 mm		102 mm		93.5 mm
(angulation-degrees)	\	78 deg.	/		

Pace:	R1–L2		L2–R3		R3–L4		mean
(length)	100 mm		92 mm		103 mm		98.3 mm
(angulation-degrees)	\	70 deg.	/\	68 deg.	/		69 deg.

Table 4. Vertebrate Trackway type E

Trackway breadth: 355 mm (max)

Trackway length: 1.35 m

Print:	L1	L2	L3	L4	R3	R4	R6	R7	R8
(impression)	pl	pl	pl	pl	pl	pl	pl	pl	pl
(length)	-	-	-	-	110 mm	100 mm	110 mm	112 mm	110 mm
(width)	-	-	-	-	85 mm	-	95 mm	-	88 mm
(number of digits)	-	-	-	-	3	-	3	-	?3

Stride:	R4--R6	R6--R8		mean
(length)	345 mm	280 mm		312.5 mm

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paddling limbs. If two series had not been observed, then assignment would have been with *Monomorphichnus*, which is essentially identical except for the lack of a second series of marks. Except for the presence of striae on mounds, comparison with *Acanthichnus* would also be warranted.

CONCLUSIONS

The trace fossils described herein are from fluvial, lacustrine, and floodplain strata comprising the Mabou and Cumberland groups. Coupled with the burrows, pits, trails, and coprolites described from the same strata by Keighley and Pickerill (1997), they represent a relatively diverse Carboniferous nonmarine ichnofauna, the surface markings alone probably having been produced by insects, reptiles, and amphibians. They also add to the diversity of trackway ichnotaxa collected from Carboniferous strata elsewhere in the Maritimes (Table 5). Collectively, the Mabou and Cumberland Group trace fossils are indicative of components of the *Scoyenia* ichnofacies of Seilacher (1967) and *Mermia* ichnofacies of Buatois and Mángano (1993), both of which, because of definitions inconsistent with the original ichnofacies concept (Seilacher, 1963, 1964), await revision—which we shall present in a future contribution.

ACKNOWLEDGEMENTS

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Table 5. Trackways recorded from Carboniferous nonmarine strata of the Maritimes.

FORMATIONS & AUTHORS (& ASSEMBLAGE):	TRACE FOSSILS:	FORMATIONS & AUTHORS (& ASSEMBLAGE):	TRACE FOSSILS:
HORTON GP, Horton Bluff, Windsor area, Sarjeant and Mossman, 1978	*Anticheiropus bishopi*, *Baropezia* isp., *Hylopus logani*.	CUMBERLAND GP, Joggins, Sarjeant and Mossman, 1978*	*Anthichnium obtusum*, *Anthichnium quadratum*, *Asperipes avipes*, *Asperipes flexilis*, *Barillopus arctus*, *Barillopus confusus*, *Barillopus unguifer*, *Baropezia abscissa*, *Cursipes dawsoni*, *Dromillopus celer*, *Dromillopus quadrifidus*, *Hylopus minor*, *Limnopus? mcnaughtoni*, *Matthewichnus velox*, *Ornithoides trifidus*, *Quadropedia levis*, *Pseudobradypus caudifer*, *Salichnium adamsi*.
HORTON GP, Parrsboro area, Sarjeant and Mossman, 1978	*Hylopus hardingi*, *Megapezia pineoi*, *Palaeosauropus antiquior*.		
AINSLIE FM, HORTON GP, Western Cape Breton Island, Hamblin, 1989	Trackways (unnamed, ?invertebrate), (+ pits and trails).		
STRATHLORNE FM, HORTON GP, Western Cape Breton Island, Hamblin, 1989	Trackways (unnamed, ?invertebrate), (+ burrows, pits, and trails).		
ALBERT FM, HORTON GP, Moncton area, Pickerill, 1992	*Diplichnites* cf. *incertipes*, *Diplichnites triassicus* *Monomorphichnus_bilinearis*, (+ burrows, pits, and trails).	JOGGINS FM, CUMBERLAND GP, Joggins, Archer *et al.*, 1995	*Diplichnites aenigma*, *Kouphichnium* isp., *Protichnites* isp., Tetrapod trackways, (+ burrows, trails).
POMQUET FM, MABOU GP, this work (TF01a, TF01b, TF02a, TF02b, TF02d, TF03d, TF03e, TF03h, TF08a, TF32a, TF36a, TF36b)	*Diplichnites* cf. *logananus*, *Diplichnites* isp., type A, *Gluckstadtella cooperi*, *Hexapodichnus horrens*, *Protichnites* cf. *carbonarius*, *Protichnites* cf. *kennediea*, *Protichnites* cf. *variabilis*, *Protichnites* isp., type A, *Protichnites* isp., type B, *Protichnites* isp., type C, *Stiallia pilosa*, Appendage Marks, type A, Horn-shaped Surface Trace, Vertebrate Trackway, type A, Vertebrate Trackway, type B, Vertebrate Trackway, type F, (+ burrows, pits, and trails).	CUMBERLAND GP, Joggins, Miller, 1996*	*Myriapodites* isp.
		CUMBERLAND GP, Pictou area, Briggs *et al.*, 1984	*Diplichnites cuithensis*.
		LOWER PORT HOOD FM, CUMBERLAND GP, this work (TF16a, TF16b, TF20a, TF20b)	*Diplichnites* isp., type B, *Monomorphichnus* cf. *lineatus*, *Protichnites* cf. *carbonarius*, *Protichnites* cf. *scoticus*, *Protichnites* isp., type D, Appendage Marks, type A, Appendage Marks, type B, Arthropod Resting Trace, Vertebrate Trackway, type C, (+ burrows, pits, trails).
CUMBERLAND GP, River Philip area, Sarjeant and Mossman, 1978*	*Asperipes longidigitatus*, *Laoporus canadensis*, *Ornithoidipus pergracilis*, *Pseudobradypus unguifer*.		
LANCASTER FM, CUMBERLAND GP, Saint John area, Miller, 1996*	*Acripes incertipes*, *Acripes leavitti*, *Acripes minor*.	UPPER PORT HOOD FM, CUMBERLAND GP, this work (TF29b, TF29c, TF29d, TF29e)	Vertebrate Trackways, type D, Vertebrate Trackways, type E, (+ burrows, coprolites, pits, trails).
		PICTOU GP, Pictou area, Ryan, 1986	*Diplichnites cuithensis*.
		PICTOU GP, Sydney area, Sarjeant and Mossman, 1978*	*Baropezia sydnensis*.

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