A Gondwanan Coastal Arthropod Ichnofauna from the Muth Formation (Lower Devonian, Northern India): Paleoenvironment and Tracemaker Behavior

Author(s): Erich Draganits, Simon J. Braddy and Derek E. G. Briggs

A Gondwanan Coastal Arthropod Ichnofauna from the Muth Formation (Lower Devonian, Northern India): Paleoenvironment and Tracemaker Behavior

ERICH DRAGANITS

Institut für Geologie, Universität Wien, Althanstrasse 14, A-1090 Vienna, Austria

SIMON J. BRADDY and DEREK E. G. BRIGGS

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, United Kingdom

The recent discovery of abundant trace fossils in the Lower Devonian Muth Formation (Pin Valley, Spiti, northern India) contributes to our understanding of the diversity and distribution of Early Devonian arthropod activities in a marginal marine environment. The ichnoassemblage consists of abundant Palmichnium antarcticum *and* Diplichnites gouldi *with rarer* Diplopodichnus biformis, Taenidium barretti, Didymaulichnus cf. lyelli, Didymaulyponomos cf. rowei, Selenichnites isp., *and vertical burrows of unclear affinity. The abundance of trackways enables the documentation of size- and gait-variations among producers of single trackway ichnotaxa. The paleoenvironment of the Muth Formation is interpreted as a barrier island system. Four different facies associations are recognized; arthropod trackways occur only in beach to coastal dune environments (facies association 2). Most of the* Palmichnium *and* Diplichnites *trackways are interpreted as subaerial. The abundance and frequently sub-parallel orientation of the* Palmichnium antarcticum *trackways, predominantly perpendicular to the paleocoastline, suggest that stylonurid eurypterids, which are interpreted as their producer, were migrating across the shoreline and climbing up slip faces of barrier island dunes. The similarity of this ichnofauna to others in marginal marine environments of similar age in Antarctica and Australia allows the identification of a recurrent Lower Devonian ichnocoenosis around the margins of eastern Gondwana.*

INTRODUCTION

The arthropod invasion of the land, exploiting vast new ecospace, was one of the most significant events in the history of life (Buatois et al., 1998). The exact timing and environmental routes of this invasion are still relatively uncertain. Body fossils of early terrestrial arthropods (e.g., arachnids and myriapods) from the late Silurian and Devonian are rare, and mostly fragmentary (see Jeram et al., 1990; Shear et al., 1996, for review). Therefore, trace fossils provide important data that compliment the body fossil record, and allow the temporal and environmental distribution of early terrestrial arthropods to be constrained (e.g., Buatois et al., 1998). As trace fossils, such as track-ways, are preserved *in situ,* they reliably record the environmental distribution of arthropods and even provide evidence for their behavior (e.g., walking techniques, walking directions, etc.).

The discovery of more than eighty arthropod trackways in the Muth Formation in the Pin Valley, Spiti, northern India (Draganits et al., 1998), near the village of Mikkim (Fig. 1A, B), is an important record of Early Devonian arthropod activity in a coastal environment, and provides crucial data on the diversity and behavior of early terrestrial communities on the margins of Gondwana. The excellent preservation and abundance of trackways enables the analysis of trackway-size variations, which indicate that the traces have been produced by instars of single arthropod taxa and/or by different taxa creating similar traces; additionally, the documentation of gait variations within single ichnotaxa is facilitated.

The distribution of the ichnofauna is clearly facies controlled (Fig. 2); the combined study of trace fossils and associated sedimentary facies provides new insights in the paleoecology of Early Devonian barrier island coasts.

STRATIGRAPHY AND AGE OF THE MUTH FORMATION

The Muth Formation is a prominent unit within the Late Proterozoic to Eocene Tethyan sequences of the northwestern Himalayas. The Formation is fairly uniform in lithology throughout its entire outcrop and has been traced from Kashmir to western Nepal. It consists mainly of well-bedded, white to light gray, medium-grained, mature to supermature, quartz-cemented quartzarenites. At Spiti, these sediments were deformed during the Himalayan orogeny into large-scale, SW-vergent, inclined horizontal folds, with NW-SE trending axes and wavelengths of approximately 5 km (Wiesmayr et al., 1998).

The term "Muth Series" was first introduced by Stoliczka (1866) after the village of Muth in the Pin Valley and redefined as "Muth System" by Hayden (1908). Only the uppermost part of Hayden's (1908) fourfold Muth System, the white quartzarenites with some dolomitic intercalation at the top, is now regarded as Muth Formation *sensu stricto* (Fuchs, 1982; Bhargava and Bassi, 1998). Bhargava (1997) included only the pure, white quartzarenite within the Muth Formation and delineated the overlying Lipak Formation at the first appearance of carbonates.
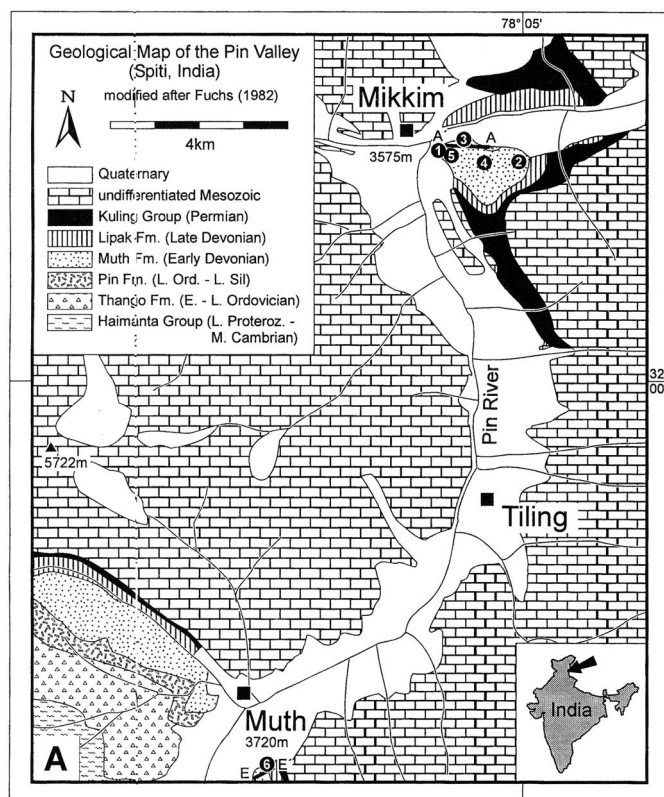
FIGURE 1—Geological and outcrop situation in the Pin Valley. (A) Locality map, Pin Valley, Spiti, Northern India. Filled circles indicate trackway localities mentioned in the text. Sections of the Muth Formation, A-A' near Mikkim and E-E' near Muth, are indicated. (B) General view from Mikkim towards the southeast to trackway locality 1, at the western termination of the anticline above the Pin River, where most of the trackways were found.

FIGURE 2—Generalized stratigraphic sections of the Muth Formation in the Pin Valley at the type locality and near Mikkim. Four facies associations are distinguished (see text). Note the nearly exclusive occurrence of the arthropod trackways in FA2 in the Mikkim section.

Here, the arenaceous dolomite incursion and the pure, white quartzarenite above it (Fig. 2) are included in the Muth Formation due to their intimate facies relation with the rest of the Formation (following Fuchs, 1982; Talent, 1982; Bassi, 1988; Bhargava and Bassi, 1998). The top of the Muth Formation herein is defined as the first appearance of dark, carbonaceous, argillaceous dolomites of the Lipak Formation.

At Spiti, the contact between the Muth Formation and the underlying Pin Formation (Goel and Nair, 1977), a shallow subtidal to nearshore dolomitic-calcareous, argillo-arenaceous succession with sporadic small reefal complexes (Bhargava and Bassi, 1986), is a sharp and well-defined lithostratigraphic boundary (Bhargava and Bassi, 1998). In the Mikkim section this contact represents a disconformity showing some small relief and a distinct orange-reddish oxidation of the uppermost Pin Formation bed, probably the result of subaerial exposure due to a relative sea-level fall. In the Baba La area, south of Muth, the contact forms an unconformity with erosional channels cutting up to 3 m into the Pin Formation. These observations indicate the presence of a major time gap below the Muth Formation (Fuchs, 1982; Bhargava and Bassi, 1998). The contact between the Muth Formation and the shallow subtidal sandstones, siltstones, and dark fossiliferous limestones of the Lipak Formation (Hayden, 1908), is conformable and gradational (Hayden, 1904). The thickness of the Muth Formation ranges from 258 m at Muth to c. 300 m at Mikkim. Throughout both sections, the whole Formation consists solely of pure quartz-cemented quartzarenites except an 11 m (at Muth) to c. 15 m (at Mikkim) thick dolomitic interval near the top (Fig. 2).

With only a few exceptions (Bassi, 1988), the Muth Formation, as now defined, is practically devoid of fossils and it has been dated mainly from the fauna of the strata above and below (Talent et al., 1988). The Pin Formation in its upper limestone interval, some 60 m below the base of the Muth Formation, contains numerous fossils and several reefal buildups of possible early to middle Silurian age (Bhargava and Bassi, 1986). The brachiopod *Pentamerus oblongus* occurs in several places (Hayden, 1904), indicating a late Early to earliest Late Silurian age (A. Boucot pers. comm., 1999). Talent et al. (1988) suggested a Wenlockian, possible Ludlovian age for the uppermost Pin Formation.

The gray limestones of the basal Lipak Formation contain typically late Middle Devonian to early Late Devonian brachiopods (Hayden, 1904; Reed, 1912; Fuchs, 1982). A late Fammenian age (middle *expansa* zone) is indicated by conodonts in alternating dolomitic sandstones and carbonates southeast of Muth in the Pin Valley (Garzanti et al., 1996). A well-preserved conodont fauna southeast of Muth, 30 m above the Muth Formation, indicates a well-constrained Givetian age (J. Talent pers. comm., 2000). Reports of Early Carboniferous fossils (Fuchs, 1982; Garzanti et al., 1996) originate from higher levels of the Lipak Formation.

Thus, the older age limit is given by the Late Silurian age of the uppermost part of the Pin Formation; the younger age limit is constrained by Givetian conodonts in the basal beds of the Lipak Formation SE of Muth. Assuming a time gap related to the disconformity at the top of the Pin Formation, the age of the Muth Formation in the Spiti area is probably Early Devonian in age, although latest Silurian cannot be ruled out.

DEPOSITIONAL ENVIRONMENT

The depositional environment of the Muth Formation is still controversial: inner- to mid shelf (Shanker et al., 1993), shallow littoral (Banerjee, 1974; Bhargava and Bassi, 1986; Gaetani and Garzanti, 1991), and eolian terrestrial settings (Dasgupta, 1971; Garzanti et al., 1996) have been suggested.

Detailed bed-by-bed profiles through the Muth Formation near Mikkim (section A-A') and at the Muth type locality (section E-E'; Fig. 1A, 2) show some differences in detail, but the sections can be correlated readily due to the laterally extensive architecture of the Formation. Both sections display a distinctive lower boundary with the Pin Formation and a gradual transition into the overlying Lipak Formation. With the exception of a thin horizon of sandy/silty dolomites in the uppermost third of the section, the Muth Formation in the Pin Valley comprises quartz arenites with high compositional and textural maturity. The high maturity in combination with the sedimentary structures described below indicates a high-energy depositional environment.

The Muth Formation is interpreted here as coastal sediments, deposited in a wave-dominated barrier-island system. These environments typically display a complexity of depositional structures due to the interaction of wind, waves, and tides. Four facies associations are distinguished (Fig. 2).

Facies Association 1: Horizontally Laminated and Minor Cross-bedded Quartzarenites

Facies association 1 (FA1) exclusively comprises pure quartz arenites, with a thickness of 205 m at Mikkim and 129 m at Muth. Bed thickness varies between 3 to 360 cm with an average of 50 and 39 cm at Mikkim and Muth, respectively. Due to the monotonous lithology, bed boundaries often have been difficult to recognize in horizontally laminated beds. Grain size is consistently in the upper fine sand to lower medium sand range. Root traces on top surfaces of beds are found in the lowest part of FA1. Low angle to horizontal lamination is dominant; cross-stratification is rare, although it increases in frequency upwards. Where cross-bedding occurs, it is usually high-angle tabular-planar, sometimes tangential, concave-up. Reactivation surfaces and herringbone cross-bedding are rare. Additional sedimentary structures include symmetrical and asymmetrical ripples. Paleocurrent directions, indicated by restored dip of foresets, are dominantly towards the SE in the Mikkim section, but towards the NW in the lower part and SE in the upper part of the Muth section.

FA1 is interpreted tentatively as transgressive beach sediments in the lowermost part and upper shoreface to upper foreshore deposits in the upper part on a coast with abundant sand supply. Sedimentation is influenced strongly by wave-generated longshore currents with minor tidal impact. The considerable thickness of pure quartzarenite indicates a favorable balance of depositional processes, sediment supply, sea level, and tectonics during its deposition.

Facies Association 2: Large-scale Cross-bedded Quartzarenites

At the Mikkim section, a local angular contact separates FA1 from FA2. FA2 consists of pure quartz arenites. The thickness is around 60 m at Mikkim (uppermost part not exposed) and reaches 87 m at Muth. Bed thickness is much higher than in the other facies associations, varying from 6 to 455 cm and averaging 70 and 81 cm at Mikkim and Muth, respectively. Grain size is similar to FA1. The arthropod dominated ichnofauna is restricted to FA2 in the Mikkim section (Fig. 2).

FA2 is characterized by large-scale tangential, concave-upward cross bedding with horizontally laminated interbeds. South-southwest of Muth, single, slightly curved foresets can be traced for more than 20 m in planview. Foresets of cross-bedded units display bimodal lamination of fine and coarse sand; some laminae display reverse grading similar to eolian pin-stripe lamination (Fryberger and Schenk, 1988). The angle between the foresets and bedding surfaces sometimes exceeds 30°. Bedding surfaces also display symmetrical, interference and adhesion ripples, spring pits (Quirke, 1930), tear-shaped ridges (McKee, 1957), desiccated bio-films (G. Gerdes pers. comm., 1999), and sandflows on foresets. Tear-shaped ridges are up to 4 cm long, 0.2 cm high, and 0.7 cm wide. They are a product of eolian deflation (McKee, 1957), indicating at least temporarily emergent conditions.

Domal build-ups occur on some level bedding surfaces forming widely to closely spaced laterally linked hemispheroids (Logan et al., 1964). Single domes are up to 1 m

in diameter and up to 40 cm high. The shape of the domal build-ups, and the wavy-undulose appearance and cohesive behavior of some laminae, make a microbial origin probable (Schieber, 1998, 1999).

Post-depositional deformation is shown by rare slumping structures. Vertical cylindrical dewatering structures, that resemble the structures described in eolian dunes by Deynoux (1990), occur in the uppermost beds, directly below FA3. Paleocurrent directions are consistently towards the NNE in the Mikkim section; the same is true for Muth, but some foresets dip towards the NW.

Based on the sedimentary structures, facies association 2 is considered to represent shallowest foreshore, backshore, and coastal dune sediments. Several of the above mentioned distinct sedimentary structures are thought to be indicative of shallow intertidal to supratidal conditions. Desiccated biofilms might be typical for this environment; the domal stromatolites may have grown in shallow intertidal areas with slightly reduced water energy.

Facies Association 3: Dolomite and Sandy Dolomite Horizon

FA3 is well exposed only in the Muth section, where it shows a sharp basal contact to FA2 and comprises dolomites, silty/sandy dolomites, and minor sandstones and quartzarenites. The proportion of quartzite increases upwards and the contact with FA4 is gradational. FA3 is 11 m thick in the Muth section. Bed thickness ranges from 1 to 98 cm with a mean of 31 cm. Grain size ranges from clay to medium sand; the average grainsize is distinctly lower than the grainsize in the other facies associations. Beds commonly are finely laminated; ripple lamination is rare and bioturbation is absent. Cylindrical dewatering structures occur at two horizons in the upper part of FA3. Three foresets were measured, indicating a westward paleocurrent direction.

FA3 is interpreted as low-energy, hypersaline lagoonal deposits, indicated by the fine grain size, thin lamination, and total lack of fossils and bioturbation. The minor quartzites may represent washover fans. The occurrence of lagoonal sediments above dune deposits indicates a rise in sea level in combination with progradation due to high sediment supply, a "depositional regression" (Curray, 1964).

Facies Association 4: Mixed Cross-bedded and Horizontally Laminated Quartzarenites

FA4 is well exposed only in the Muth section. Pure quartz arenites predominate, becoming less pure in the upper part. The upper contact to the Lipak Formation is gradational. FA4 is 33 m thick at Muth, with bed thickness ranging from 12 to 180 cm (mean = 55 cm). Both horizontal lamination and cross-stratification occur, and burrowed top surfaces of beds are more common in the upper part. Paleocurrent directions vary, although most are towards the NW.

The interpretation of FA4 is equivocal. It probably comprises foreshore to lower shoreface and displays a transgressive trend with a gradational contact with the inner shelf deposits of the overlying Lipak Formation.

ASSOCIATION AND DESCRIPTION OF TRACE FOSSILS

Trackways are described according to the terminology of Trewin (1994). All material remains *in situ* at the locality, because attempts to split off slabs bearing traces failed; four Formasil RTV© peels of very well preserved trackways were produced, which are stored in the collection of the Geology and Paleontology Department of the Museum of Natural History, Vienna (NHMW). The specimen numbers in this study refer to field numbers ascribed to each trace by ED and SJB during the fieldwork.

Trackway localities in the Pin Valley, Spiti district, Himachal Pradesh (Fig. 1A) are numbered as follows: (1) The western termination of the anticline of the Muth Formation (main trackway site), 0.4 km SE of Mikkim. GPS: N32°02'14"; E78°03'53"; EPE (estimated position error) 22 m. (2) The eastern termination of the anticline, 1.7 km ESE of Mikkim. GPS: N32°02'06"; E78°04'47"; EPE 23 m. (3) Directly at the edge of the prominent cliff (no GPS data). (4) Near the crestline of the anticline, a bedding surface directly below the stone cairn with a prayers flag (no GPS data). (5) Near the western termination of the anticline of the Muth Formation, 0.6 km southeast of Mikkim, c. 50 m SSE of the prominent chorten (Tibetan stupa). GPS: N32°02'01"; E78°04'38"; EPE 41 m. (6) 1.2 km SSE of Muth, at the top of the Formation in section E-E' (no GPS data).

The distribution of the ichnofauna in the Muth Formation, dominated by *Palmichnium* and *Diplichnites,* is facies controlled as indicated by its nearly exclusive restriction to FA2 (Fig. 2). Sedimentological evidence indicates a very shallow intertidal to barrier-island dune environment for FA2. Most of the trace fossils described herein were found at locality (1) at an altitude of about 3600 m at the western limb of this anticline (Fig. 1B) at the junction of the Pin River and Parahio River. Here, erosion by the Pin River has produced relatively fresh bedding and foreset surfaces in the quartzite. Poorly preserved trace fossils also occur rarely at other parts of the outcrop at a similar stratigraphic level. The abundance of trace fossils in FA2 in this western termination of the formation near Mikkim, their scarcity in other parts, and their near total absence in the Muth section, is probably a reflection of the nature of the outcrop and exposure of foresets and bedding surfaces of FA2.

Trace fossils have been reported from other parts of the Muth Formation, although never in the abundance recognized at the Mikkim locality. Bhargava and Bassi (1988, table 1) reported *Chondrites* and *Phoelus* at Kumaon, and *Palaeophycus, Planolites, Skolithos,* and "arthropod markings" in the Lipak valley (NW Kinnaur). They suggested chelicerates (xiphosurids) as the producer of these arthropod trackways. Srivastava and Kumar (1992) described *Arenicolites, Monocraterion, Planolites,* indeterminate burrows (cf. *Skolithos*), and trails (cf. *Didymaulichnus*) from the middle part of the Muth Formation at Malla Johar (Kumaon).

The trace fossils were generated on a quartz sand substrate, later lithified to quartzite. The surfaces on which the trace fossils are found are white when fresh, but become coated with an orange/dark brown/black shiny rock varnish, which often obscures both trace fossils and sedi-
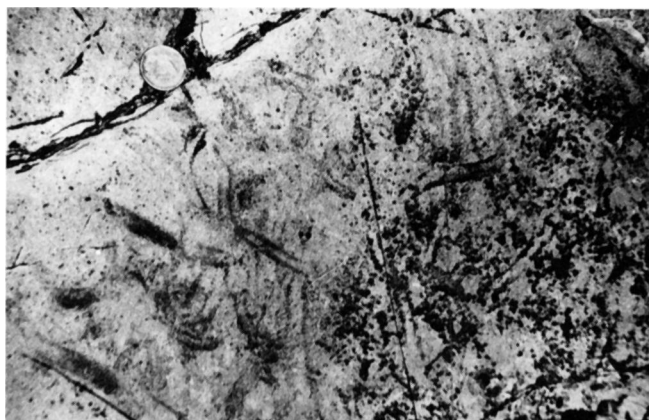
FIGURE 3—*Didymaulichnus* cf. *lyelli* (trace 85) on an abraded foreset surface without relief; traces are visible due to color differences. (Coin diameter 25 mm).

mentary structures. Surfaces exposed to the wind become abraded.

Most of the trackways are preserved on the surfaces upon which they were produced, as evidenced by undisturbed sand laminae directly above. Undertracks are rare. It seems that the homogenous sand-grain size of the Muth Formation did not facilitate the development of undertracks, which tend to be more widespread within laminations of finer grained, or lithologically varied, sediments (Goldring and Seilacher, 1971; Johnson et al., 1994).

Didymaulichnus cf. lyelli

One example is described herein (trace 85) from a lower part of a foreset at locality 1. This trace consists of narrow bilobed epichnial, straight to slightly curved, parallel grooves, commonly 9 mm wide and 45 mm long, shallowing out at both ends. They appear as dark grooves with a median ridge about 2 to 3 mm wide. Details of the trace have been abraded by the wind (Fig. 3).

This trace closely resembles *Didymaulichnus* described by Trewin and McNamara (1995, fig. 15), but the grooves of the latter are weathered out. Trewin and McNamara (1995) suggested an arthropod tracemaker and noted that *Didymaulichnus* possibly represents the bottom half of *Didymaulyponomos* burrows. The occurrence of very similar *Didymaulyponomos* traces in the Muth Formation supports this interpretation, although no direct association was observed.

Didymaulyponomos cf. rowei

One example is described herein (trace 76) from a bedding surface near locality 2. This trace comprises poorly preserved, straight to curved endichnial burrows, 12 mm wide and sometimes more than 100 mm long. Burrows are preserved as open tunnels with a 3-mm wide median ridge between the two grooves. Burrows commonly show cross-cutting relationships. No internal details are preserved.

Diplichnites gouldi

Nine trackways (traces 3–5, 11, 27, 28, 38, 48 and 86) are preserved on bedding surfaces and foresets at locality 1, and six trackways (traces 69–73, 77) have been found on a bedding surface at locality 3. One Formasil RTV© peel of trace 3 was made (Inv. NHMW2000z0098/0004). *Diplichnites* is rarer than *Palmichnium* and more common on bedding surfaces than foresets. *Diplichnites* and *Palmichnium* are associated on some surfaces, but there is no evidence of any interaction. *Diplichnites* tracks show hardly any pushback mounds, and the walking direction is difficult to determine; there is no evidence of any trend.

These trackways vary considerably in their external width, series arrangement, and the shape of single tracks. Following Trewin and McNamara (1995) and Buatois et al. (1998b), these trackways are not divided into different ichnospecies, to avoid a profusion of names. Within the variation of the trackways, two end-members have been recognized, which are described separately as Forms A and B, with no taxonomic significance. The size distribution of the traces is presented in Appendix 1.

Diplichnites gouldi Form A (traces 3–5, 11, 27, 28, 38, 48 and 86; Fig. 4A, B) consists of two parallel rows of closely spaced tracks. External width ranges from 18 to 140 mm, internal width from 15 to 75 mm. Some trackways are nearly 1 m long. Trackways are straight to gently curved, with straight parts commonly separated by relatively abrupt curves. In some trackways, a slightly raised ridge flanks one or both outer margins of the track rows (Fig. 4B). Well-preserved tracks vary from ellipsoidal to circular pits; when eroded to a deeper level, they coalesce into elongate track groups. Tracks are relatively large compared with the external width. They are arranged obliquely, typically inclined around 60° to the mid-line, and separated by distances from 8 to 27 mm. The symmetry of opposing tracks may change from opposite to staggered within a single trackway. Series are not discernible.

Diplichnites gouldi Form B (traces 69–73, 77; Fig. 4C) consists of two parallel rows of small conical to elongate tracks. External width ranges from 51 to 107 mm, internal width from 44 to 77 mm. Trackways are straight and can be traced for about 60 cm across the surface. Individual tracks commonly are superimposed; elongate tracks are arranged obliquely at around 60° to the mid-line, and separated by distances ranging from 12 to 32 mm. The symmetry of the opposing tracks is opposite to slightly staggered. Series are difficult to determine because of the straightness of the trackways but, in some cases, there is evidence for at least 8 tracks per series (trace 77) arranged at a low angle to the mid-line.

Diplichnites Forms A and B were found in different parts of the Muth Formation, but at a similar stratigraphic level. Only Form A occurs in combination with *Palmichnium* and the majority of all other traces at the western end of the outcrop, whereas Form B was found only at locality 3. Traces 69–73 appear on a single surface; trace 77 is just 5 m away. The appearance of the latter resembles closely *Diplichnites* Form B described by Trewin and McNamara (1995).

These trackways probably were produced by myriapod-like animals (see Johnson et al. [1994] and Buatois et al. [1998b] for a discussion of possible trailmakers). Differ-
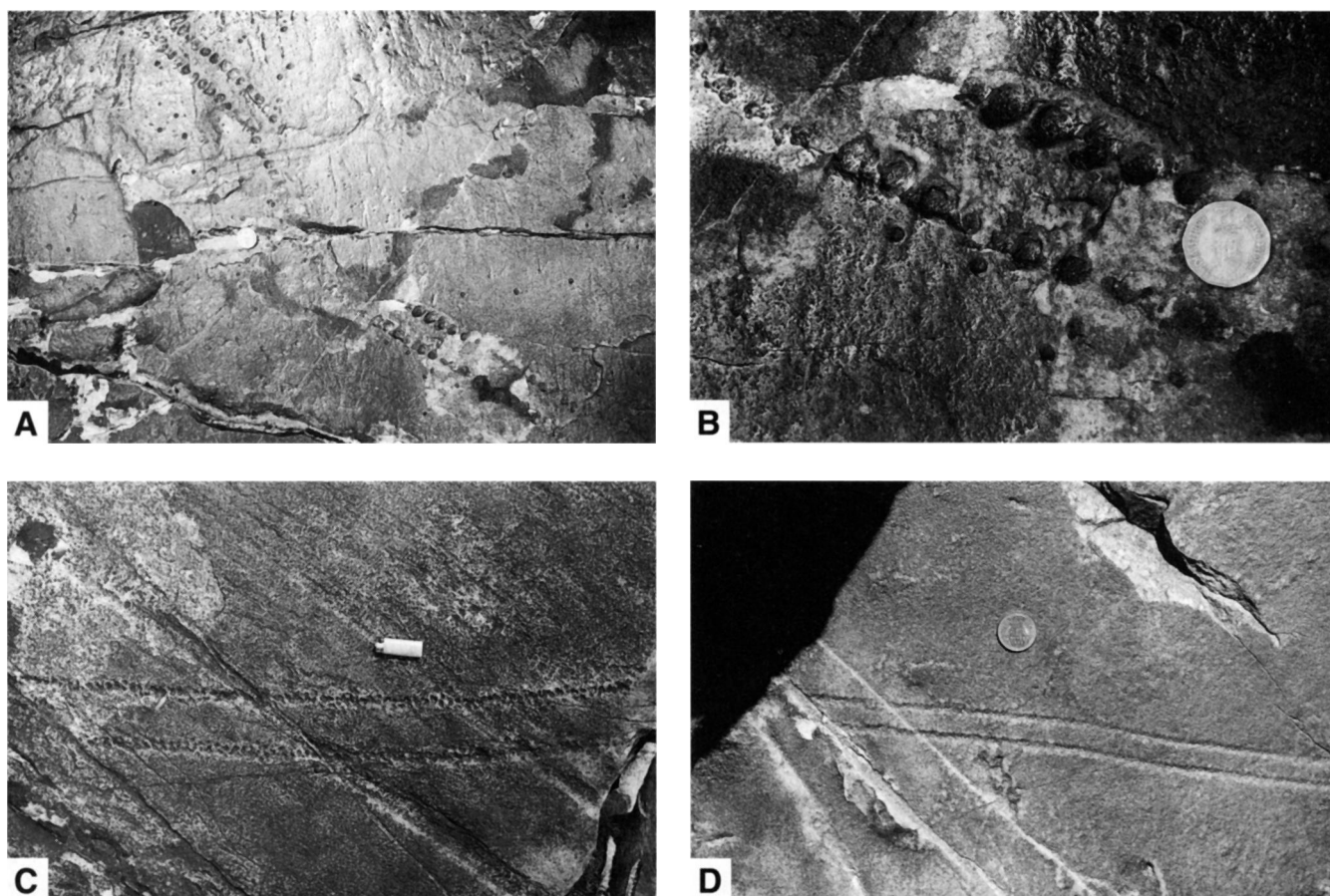
FIGURE 4—*Diplichnites gouldi* and *Diplopodichnus biformis* trackways. (A) *Diplichnites gouldi* Form A (trace 86) on a foreset surface. Note the relatively straight trackway segments separated by abrupt curves (Coin diameter 25 mm). (B) Detail of Fig. 4A (Coin diameter 26 mm). (C) *Diplichnites gouldi* Form B (trace 77) on a bedding surface (Lighter length 60 mm). (D) *Diplopodichnus biformis* (trace 19) on a foreset surface (Coin diameter 25 mm).

ences between the two forms of *Diplichnites gouldi* indicate that they probably were produced by different types of myriapods.

Diplopodichnus biformis

One example (trace 19) is described herein from a foreset close to the waterline of the Pin River at locality 1. The trackway consists of two epichnial parallel grooves, each 2.5 mm wide, with an external width of 20 mm and an internal width of 15 mm (Fig. 4D). The trail runs straight on a foreset surface. The small size relative to the grain size of the sediment renders most details invisible but, in some parts, faint tracks, 3.6 mm apart, are detectable within the track rows.

Diplichnites gouldi and *Diplopodichnus biformis* were considered by Buatois et al. (1998b) to represent compound ichnotaxa that could be produced by the same animal, probably a small myriapod. Buatois et al. (1998b, fig. 2A, B, 3A) documented examples of specimens that grade from one ichnogenus into the other. Their differing morphology is explained by variations related to substrate consistency: *Diplopodichnus* produced under moistened to wet surface conditions whereas *Diplichnites* under drier conditions (Johnson et al., 1994).

Palmichnium antarcticum

Palmichnium antarcticum traces are very abundant; fifty-six specimens have been noted (traces 1, 2, 8, 9, 12–18, 20–22, 24–26, 29–37, 39–47, 49–68 and 87) from bedding surfaces and foresets at locality 1. Formasil RTV© peels of trace 33 (Inv. NHMW2000z0098/0001), trace 36 (Inv. NHMW2000z0098/0002), and traces 2 and 37 (Inv. NHMW2000z0098/0003) were made.

Palmichnium appears in FA2 and occurs throughout its exposure in the Mikkim section, where just the lower part of the facies association is exposed (Fig. 2). It occurs on bedding surfaces but is more widespread on foresets, often displaying deep tracks with pronounced pushback mounds (Fig. 5A, B). *Palmichnium* shows a large size range (see below). The trackway attributes are presented in Appendix 1 according to the terminology of Trewin (1994). Although these trackways vary considerably in their width, series arrangement, number of tracks per series, and the shape of single tracks, they have not been divided into different ichnotaxa, to avoid a profusion of names. However, the variations within the numerous trackways allowed the recognition of two end-members, described separately as Forms A and B, which are not intended to have taxonomic significance. Both forms consist
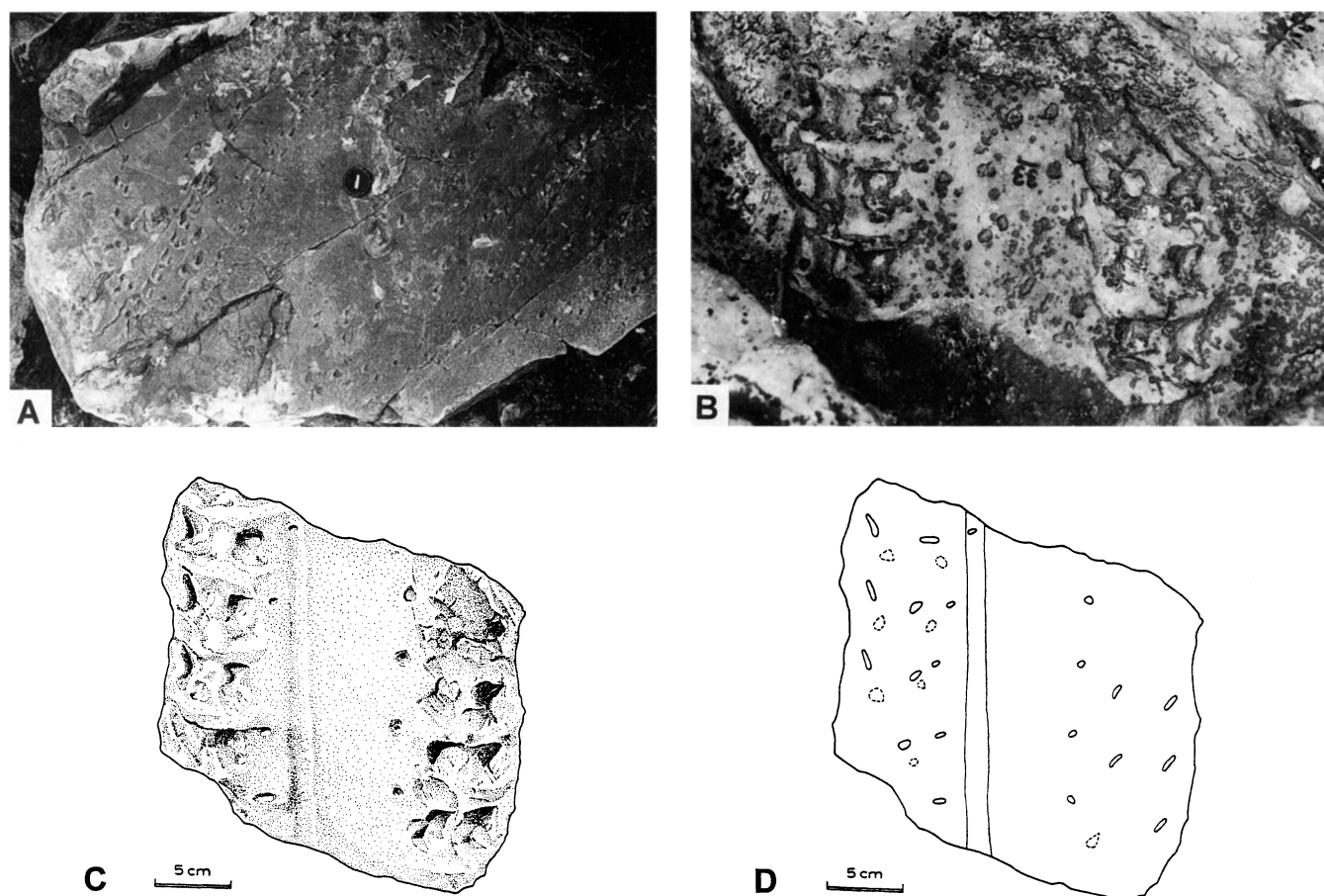
FIGURE 5—*Palmichnium antarcticum* Form A traces. (A) Several trackways (traces 1, 2, and 37) on a single bedding surface (Lens cap diameter 53 mm). (B) Typical *Palmichnium* Form A (trace 33) on a foreset with uphill walking direction (towards the top). Note the similar middle and outer tracks and the smaller inner track. (C) Drawing from a mould of trace 33. (D) Interpreted drawing of trace 33 with accentuated tracks. Dotted curves show position of unclear additional tracks in the pushback mounds, possibly from the recovery stroke.

of straight or more rarely slightly curved trackways consisting of two parallel rows of track series. Series are mainly straight but may be slightly curved, concave in the direction of movement (Fig. 5A-C).

Palmichnium antarcticum Form A (traces 1, 2, 12–18, 20–22, 24–26, 30–35, 37, 39–47, 49–68 and 87) ranges from 63 to 498 mm in external width, with internal width from 25 to 245 mm. Series generally show opposite or staggered symmetry (rarely alternate) and consist of three tracks or two where the shallower inner track is not preserved. The angle between series and the mid-line ranges from 23 to 90°, with most examples between 40 to 75°.

The outer and middle tracks are very similar, but differ from the inner track. The outer tracks are relatively large, deep, and mainly elongate (Fig. 5C, D) to teardrop-shaped (Fig. 5A), arranged sub-parallel to oblique to the mid-line. In places where they are eroded to a deeper level, it is evident that they were made by a limb with two movable spines. Well preserved trackways display pushback mounds behind the outer and middle track, some often more than 6 mm high (Fig. 5B, C). The inner tracks, where preserved, are smaller and shallower circular to elliptical imprints (Fig. 5B-D).

Medial impressions rarely occur and are sometimes displaced to one side of the mid-line (Fig. 5B-D). They vary in width from 0.2 to 1.5 cm, with a depth of 0.1 to 0.4 cm, and are semi-circular in cross-section. Some medial impressions show weak regular variations in depth (e.g., trace 12).

Palmichnium antarcticum Form B (traces 8, 9, 29 and 36) show external widths ranging from 74 to 170 mm; internal width is from 28 to 46 mm. Series comprise four circular conical tracks of equal size with an opposite to staggered (occasionally alternate) symmetry (Fig. 6A, B), and a stride of 49 to 82 mm. The angle between series and the mid-line ranges from 29 to 74°. No medial impressions were found associated with this form.

The *Palmichnium* trackways at Muth generally are relatively uniform, with similar strides and series angles. However, several trackways show modification of the gait, apparently influenced by the slope of the surface. Trackways walking uphill on dune slip faces generally show smaller stride values and higher series angles (Fig. 5B-D). Trace 29 (*Palmichnium antarcticum* Form B), which crosses a foreset surface along strike, clearly shows the influence of the slope on the producer; the series of the
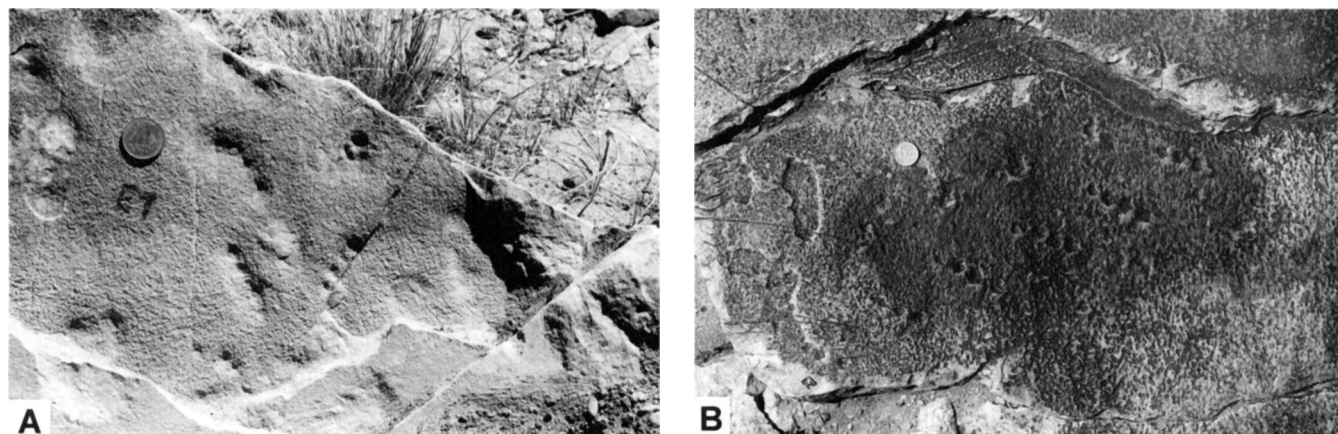
FIGURE 6—*Palmichnium antarcticum* Form B traces. (A) Trace 36 on a bedding surface, walking direction from bottom to top. Note the overlapping of tracks in the upper right series (Coin diameter 25 mm). (B) Trace 29 oriented along strike of a foreset with gait adjusted to the slope. Walking direction from left to right (Coin diameter 25 mm).

downhill side show four tracks with downhill-directed sediment mounds on one side, whereas on the uphill side the tracks are all overprinted (Fig. 6B). A part of trace 36 (*Palmichnium antarcticum* Form B) shows a similar gait variation (Fig. 6A).
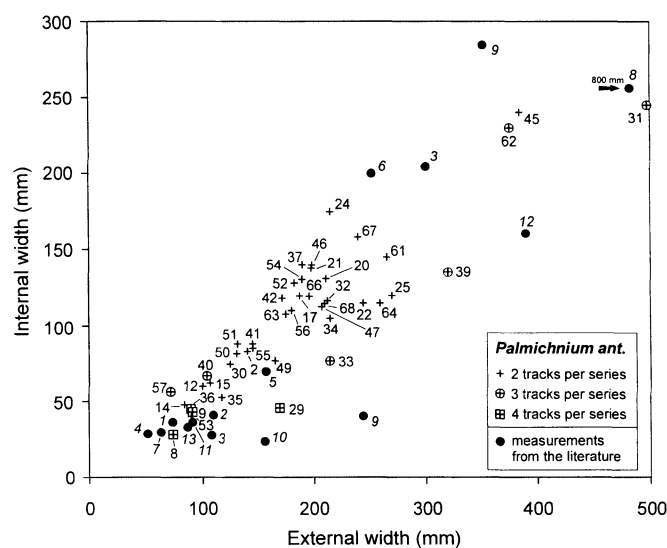
Both forms of *Palmichnium antarcticum* fall within the emended diagnosis of Braddy and Milner (1998). Most examples of *Palmichnium antarcticum*, in general, show an opposing or staggered symmetry. Several examples from this ichnofauna, however, show opposite series gradually

FIGURE 7—Diagram of external width *versus* internal width of *Palmichnium* trackways. Sizes of *Palmichnium* from the Muth Formation (crosses) cluster in 3 size groups. Trackways with 4 tracks per series (Form B) appear only in the smallest cluster. Filled circles with italicized numbers indicate *Palmichnium* attributes from the literature for comparison. Key: 1: Sharpe (1932), 2: Richter (1954), 3: Gevers et al. (1971), 4: Greiner (1972), 5: Hanken and Størmer (1975), 6: Friend et al. (1976), 7: Bradshaw (1981), 8: Briggs and Rolfe (1983), 9: Rogers (1990), 10: Trewin and McNamara (1995), 11: Braddy and Anderson (1996), 12: Braddy and Milner (1998), 13: J. Waddington (pers. comm., 1998).

grading into staggered or rarely alternating series within a single trackway, apparently reflecting differences in slope angle, surface conditions, and walking speed. Symmetry alone, therefore, is not a significant ichnotaxobase to discriminate ichnotaxa such as *Paleohelcura* and *Palmichnium*, although it may be useful in conjunction with external width and track size (Braddy and Milner, 1998).

Form A was produced by large heteropodous, hexapodous animals, whereas Form B was produced by smaller, octopodous animals. Trackways with series of four tracks (Form B) are less than 200 mm in external width and 100 mm in internal width, whereas those of Form A occur across the whole size range (Fig. 7).

Only a few Devonian arthropods were big enough to have produced these trackways. Eurypterids or scorpions are prime candidates. Besides their size, there are several arguments in favor of eurypterids (see Briggs and Rolfe, 1983 for discussion). Gevers et al. (1971, p. 90) preferred an eurypterid to a trilobite as the producer of the Antarctic trackways, but remarked that "the regular pattern of footprints here indicates an animal capable of an extremely well balanced gait, in no way encumbered with an unduly long abdominal section such as characterized by most eurypterids." Briggs et al. (1979), Rolfe (1980), and Trewin and McNamara (1995) suggested that large amphibious scorpions produced these trackways. Bradshaw (1981) considered that these trackways were produced subaqueously by stylonurid eurypterids.

The morphology of the trackways, and the large size and absence of any paddle-shaped outer tracks, suggest that the Indian *Palmichnium* traces were produced by stylonurid eurypterids. Many Devonian forms attained sufficient size to have produced these trackways (cf. Waterston, 1979). The bifid tracks indicate that the distal podomere of the leg had two movable spines or claws. The differences between *Palmichnium* Forms A and B most probably indicate that they were produced by different types of eurypterid, although behavioral and environmental differences (Sadler, 1993) and/or different instars of one species may account for the variation in trackway morphology (e.g., number of tracks per series).

FIGURE 8—*Selenichnites* isp. (trace 89) on a bedding surface in the uppermost part of the Muth Formation near Muth (Coin diameter 25 mm).

FIGURE 9—*Taenidium barretti* traces. (A) Axial section of *Taenidium* (trace 79) on a bedding surface. Note the meniscate back-fill packets and the lack of any special wall structures (Coin diameter 25 mm). (B) Section of a *Taenidium* burrow in a loose block in the Muth section starting oblique to the bedding surface curving to a vertical direction with distinct meniscate back-fill packets (Watch width 40mm).
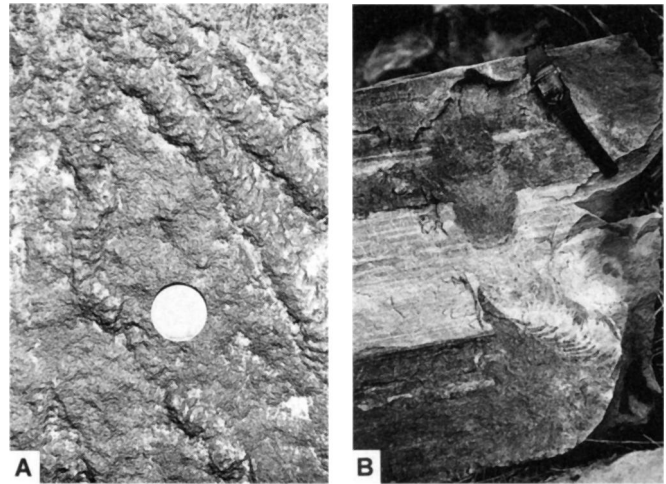
The Indian *Palmichnium* trackways generally show opposing series diverging in the direction of movement, the walking direction determined by pushback mounds behind the tracks. This is in clear contrast to the general assumption that eurypterid trackways display opposing series converging in the direction of movement, as in the xiphosuran trackway *Kouphichnium*.

Selenichnites isp.

Several traces (trace 89) have been found on a single bedding surface in the uppermost part of the type section of the Muth Formation at locality 6. The trace comprises horseshoe-shaped epichnial hollows on bedding surfaces, the lateral margins of the trace parallel or diverging at about 30°; width ranges from 25 to 90 mm, mostly from 40 to 60 mm (Fig. 8). The trace is deepest at the anterior, but in some cases also deep laterally, up to some 5 mm. Traces are aligned consistently with the apices pointing towards the southwest.

In contrast to all other traces described herein, *Selenichnites* occurs within FA4, interpreted as a shallow marine environment (see above), and is not part of the trackway dominated ichnoassemblage of FA2. Although paleocurrent directions vary in FA4, the preferred southwestern alignment of *Selenichnites* may indicate an orientation of the apices against depositional currents.

Five ichnospecies of *Selenichnites* are known (see Romano and Whyte, 1987 for review): *S. rossendalensis* Hardy, 1970 (Carboniferous, U.K.); *S. cordoformis* Fischer, 1978 (Ordovician, Colorado); *S. bradfordensis* Chisholm, 1985 (in part; Carboniferous, U.K.); *S. hundalensis* Romano and White, 1987 (Jurassic, U.K.); and *S. langridgei* Trewin and McNamara, 1995 (Siluro-Devonian, Western Australia). Additionally, *Selenichnites* isp. occurs in the ?Lower Ordovician of western Antarctica (Thomson and Weber, 1999, fig. 3a). Comparing the size and overall shape, the Indian material is most similar to *S. langridgei*, although the lack of a medial trefoil-shaped feature (a characteristic of this ichnospecies), and the poor preservation, prevents ichnospecific assignment. *Selenichnites*

generally is regarded as representing digging traces of a xiphosurid, although other arthropods (?eurypterids, crustaceans) could produce similar traces by employing similar behavior.

Taenidium barretti

Three well-preserved near axial sections (traces 6, 7 and 23) on bedding and foresets surfaces, and four transverse sections (traces 80, 81, 83 and 84) on bedding surfaces have been found at locality 1. One near axial section (trace 79) occurs on a bedding surface at locality 2, one transverse section (trace 75) on a bedding surface at locality 4, and one near axial section (trace 88) near locality 6.

This trace comprises gently curved endichnial burrows several tens of centimeters in extent, with a horizontal to slightly oblique orientation to the bedding surface, commonly shallowing out across the bedding plane. Traces are usually crowded, and cross-cutting relationships are common. Burrows are circular in cross-section, usually some 4 to 30 mm wide. The sand fill of the burrows is massive or shows poorly defined meniscate back-fill packets. Neither special wall structure nor contrast between burrow fill and host sediment is evident (Fig. 9). A loose block from the Muth section shows a partial, 65-mm-wide, burrow both oblique and vertical to the bedding (Fig. 9B), crossing two differently colored, well laminated, quartzite layers.

The traces appear in two different forms in transverse section: vertical tube-like and hemispherical (elliptical in plan view) morphologies. Vertical tube-like structures (e.g., trace 75) are circular in plan view with a diameter of about 70 mm. Margins are irregular. Pits are up to 40 mm deep, most of them shallower, with a relatively sharp contact at the bottom, implying that the bottom is not the end of the trace but just the level of downward erosion. Vertical tubes are spaced at least 20 cm apart. Abundant near-

horizontal orientated traces occur close by, some of them crosscutting vertical tubes.

Hemispherical burrows (e.g., traces 80, 81, 83 and 84) consist of elliptical to elongate shallow hollows; length ranges between 101 to 203 mm, width from 39 to 142 mm. They have a concave shape with a smooth, structureless downward tapering margin. Apart from some vertical burrows, no other traces were found on the same surfaces.

Taenidium is not as abundant as *Palmichnium* and *Diplichnites*, but it is relatively common, particularly on bedding surfaces of horizontally laminated beds. In rare occurrences on foresets, *Taenidium* appears in the lowest part of the tangential foresets. On a bedding surface near the stone cairn, vertical *Taenidium* with diameters around 50 mm are found together with horizontal *Taenidium* with diameters around 25 mm. At the western termination of the anticline, transverse sections through *Taenidium* forming elongated shallow hollows occur on the bedding surface of the horizontally laminated bed Ma567. This bed is directly above the large-scale cross-bedded bed of Ma566, which contains abundant *Palmichnium* and *Diplichnites* and very rare *Didymaulichnus*.

There is still no consensus regarding the distinction between *Taenidium* and *Beaconites*. Ichnotaxonomic problems associated with meniscate filled burrows were discussed by Goldring and Pollard (1995) and Keighley and Pickerill (1994). In this paper the definition of Keighley and Pickerill (1994) is followed: *Beaconites* possesses a wall structure and *Taenidium* lacks one. The burrows in the Muth Formation are attributed to *Taenidium*. The near-axial meniscate backfilled burrows and the transverse sections are associated closely in one place. Indeed, reports of similar burrows (e.g., O'Sullivan et al., 1986; Allen and Williams, 1981) show these traces in various orientations. Although most of the horizontal burrows are smaller than the transverse sections, the larger detailed trace (Fig. 9B) supports this relationship. However, the transverse sections also closely resemble *Metaichna* (Anderson, 1975), but their association with axial sections probably indicates that they are the same trace.

Trewin and McNamara (1995) noted two types of *Beaconites* (= *Taenidium*; Keighley and Pickerill, 1994) from the Tumblagooda ichnofauna. Smaller ones (*B*. cf. *antarcticus*) were attributed to the *Heimdallia* animal, whereas larger ones were attributed to the animal responsible for the larger *Diplichnites* trackways. Indeed, Gevers et al. (1971) recorded *B*. *antarcticus* on the same bedding planes (and predating) small *Diplichnites* trackways, which occasionally ended in small rounded terminations. Rounded terminations to Lower Permian myriapod trails from New Mexico were interpreted as the point where the animal began burrowing beneath the substrate (Braddy, 1995). *Beaconites* has been attributed variously to polychaete worms (Gevers et al., 1971), a worm-like animal (e.g., an amphisbaenid [worm lizard] or a blind snake; Ridgeway, 1974), limbed reptiles or amphibians (Pollard, 1976), ostracoderms (Allen and Williams, 1981), lungfish (O'Sullivan et al., 1986), "desert dwelling arthropods" (Rolfe, 1980), "myriapod-like arthropods" (Bradshaw, 1981), and arthropleurids (Pearson, 1992).

In the Muth ichnofauna, the narrow width of the near-axial *Taenidium* sections is similar to that of the narrower
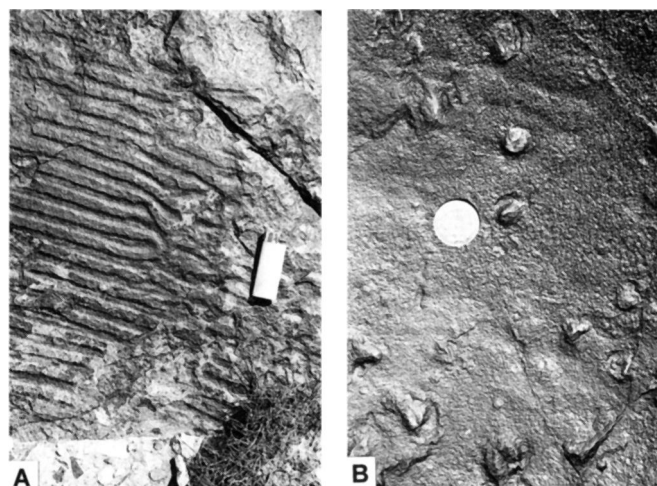

FIGURE 10—Traces of unknown taxonomic position. (A) Regular meandering trace (trace 74) with narrow median cord-like ridge on a bedding surface (Lighter length 60 mm). (B) Vertical burrows in plan view on an upper bedding surface (Coin diameter 25 mm).

Diplichnites and *Diplopodichnus* trackways (here attributed to myriapods). Larger examples (e.g., trace 88) also have a similar width to larger *Diplichnites*. Therefore, it is possible, that these *Taenidium* burrows were produced by myriapods or arthropleurids, but other animals may have formed the different ichnospecies of *Taenidium*.

Meandering Grazing Trail

One example (trace 74) has been found on a bedding surface at locality 5. The trace shows very regular, parallel, closely spaced, meandering grooves extending for more than 20 cm. Grooves are some 10 mm wide and show a narrow median cord-like ridge, which is lower than the bedding surface (Fig. 10A). The preserved relief is less than 3 mm. The regularity and arrangement of the trail implies a grazing behavior, and the traces are interpreted as surface feeding traces. The affinities of this trace remain unclear; according to Uchman (1995), guided meandering traces are referred to *Helminthorhaphe* Seilacher.

Vertical Burrows

These traces are quite abundant, but only two groups of specimens have been recorded (traces 10 and 82) on bedding surfaces and foresets at locality 1. They consist of vertical or near vertical burrows, commonly in dense concentrations, sometimes paired or in rows, circular to oval in cross-section, diameter 6 to 22 mm. No difference between the burrow fill and host sediment is evident. Some examples show slight raised rims around the entrance of the burrow (Fig. 10B), implying an excavation mound, or binding agent for stabilization around the burrow entrance.

These traces are very common in the Muth Formation as small depressions in bedding and foreset surfaces. In some cases they seem to be crowded on the asymptotic bases of eolian dunes, becoming gradually less abundant upwards. No vertical section was found. The sandfill is

slightly weathered below the surface level. They may represent Skolithos, Diplocraterion, or Tigillites, which occur in the Australian (Trewin and McNamara, 1995) and Antarctic ichnofaunas (Bradshaw, 1981).

TRACKWAY PRESERVATION

The lithology in which the Muth trackways are preserved is an unusual setting. Most fossil trackways occur in fine grained, finely laminated sediments. Sand, especially dry sand, is unsuitable for their preservation unless a suitable binding agent is present, such as water (from dew, a light rain fall, or saline surf-spray), infiltrating clay minerals (McKeever, 1991), or algal slime (Gevers and Twomey, 1982).

Brady (1939, 1947) and Sadler (1993) conducted neo-ichnological investigations with arthropods, but did not consider trackways produced subaqueously. Brand (1979, 1996) carried out extensive studies on trackways produced by modern amphibians and reptiles with different substrates, slope angles, and moisture contents, under both subaqueous and subaerial conditions. Different substrate conditions caused considerable variation in the appearance of trackways produced by one species. The trackways produced by uphill-walking salamanders on sloping dry sand in Brand's (1979, fig. 6a, 6b) study are similar in their track depth and shape of pushback mounds to some uphill Palmichnium trackways found on foresets in the Muth Formation (Fig. 5B). Although the producers were different, these neoichnological studies provide an analogue for the mechanism of production of some of the Muth Palmichnium trackways.

Saline surf-spray and/or microbial mats are suggested as probable candidates for the stabilization of trackways in the Muth Formation (Gevers and Twomey, 1982). Even during slight wind these would have stabilized the surface, allowing trackway preservation. The existence of microbial mats in peritidal siliciclastic sediments has been mentioned increasingly in recent years (Gerdes et al., 2000; Schieber, 1998, 1999). The existence of microbial mats in the pure quartzite of the Muth Formation is indicated by domal stromatolites at the eastern limb of the anticline SE of Mikkim, and smaller sedimentary structures such as polygonal fractures resembling desiccated biofilms on surfaces at the outcrop where the trackways occur.

PRODUCERS AND PALEOECOLOGICAL IMPLICATIONS

The Muth Formation ichnofauna represents a low-diversity community in a coastal paleoenvironment. The most abundant trackways are Palmichnium antarcticum, some of which are very large and show large tracks relative to the external width of the trackway (Appendix 1). Their large size (e.g., trace 31) and morphology favor a eurypterid producer (see below). The absence of any paddle-shaped outer tracks suggests that they were produced by stylonurid eurypterids. During the Devonian, many stylonurids were large enough to have produced these trackways (cf. Waterston, 1979). Diplichnites gouldi, Diplopodichnus biformis, and possibly Taenidium barretti can be

assigned to the activity of myriapod-like arthropods (?eoarthropleurids; see below). The vertical burrows were not exposed in vertical section; hence, so their precise ichnotaxonomy is unclear and producers cannot be assigned.

The trace fossil diversity of the Muth Formation is low compared with that of contemporaneous body fossil assemblages, such as, for example, the Lower Devonian coastal Nellenköpfchen Schichten of Alken (Germany) that is interpreted as an elongate lagoon bordered by a sandy bar (Størmer, 1976). Thus, is similar to the environment of the Muth Formation, but is located within the Euramerican province. This discrepancy might support the widely held belief that, in general, trace fossil diversity under-represents zoological diversity (Farlow and Pianka, 2000).

Some eurypterids are considered to have had an amphibious habit; short excursions out of water were made possible by protected accessory aerial respiratory tissues (Kiemenplatten: Manning and Dunlop, 1995; Braddy et al., 1999). Ichnological evidence, such as trackways (e.g., Sharpe, 1932) formed under at least temporarily dry conditions, supports their amphibious habit.

The Palmichnium trackways on the Muth foresets show very deeply impressed tracks with pronounced pushback mounds (Fig. 5B, C). Formation of very deep tracks under water is unlikely, as buoyancy would have reduced the weight of the producers considerably, resulting in much shallower tracks (although it is possible that they may have been "paddling" in very shallow water, their bodies effectively exposed). This supports the sedimentological evidence (see above) for subaerial production of most of the Muth Palmichnium trackways.

Why were these arthropods "invading" the land? Størmer (1976) suggested that arthropods terrestrialized for three possible reasons: (1) obtaining new areas for food, (2) escaping enemies, and (3) protecting the next generation from marine predators. Gevers et al. (1971) stressed the importance of an abundant terrestrial food supply. However, eurypterids would not have been able to feed subaerially as they did not possess a pre-oral cavity (as in arachnids, myriapods, and insects), which is regarded as an important adaptation to terrestrial life (Størmer, 1976). Trewin and McNamara (1995) argued that the driving force behind short subaerial excursions was the drying up of pools that the arthropods inhabited, causing high population densities and predatory pressure, forcing the animals to seek safer places.

Briggs and Rolfe (1983) proposed that eurypterids may have undertaken seasonal nuptial walks. This may not necessarily have involved only large individuals. There is paleobiological evidence that eurypterids acquired sexual maturity before their final molt stage (Braddy and Dunlop, 1997). A "mass-molt-mate" hypothesis was proposed by Braddy (1996), analogous with the behavior of extant xiphosurans and some semi-terrestrial crabs, whereby these animals migrated en-masse into nearer shore waters or quiet lagoons, molted, and mated before returning to their usual (marginal marine) habitats. This hypothesis might explain the abundant accumulations of exuviae (e.g., in the Bertie Formation [New York State] and Viita Formation [Saarema, Estonia]), which were previously
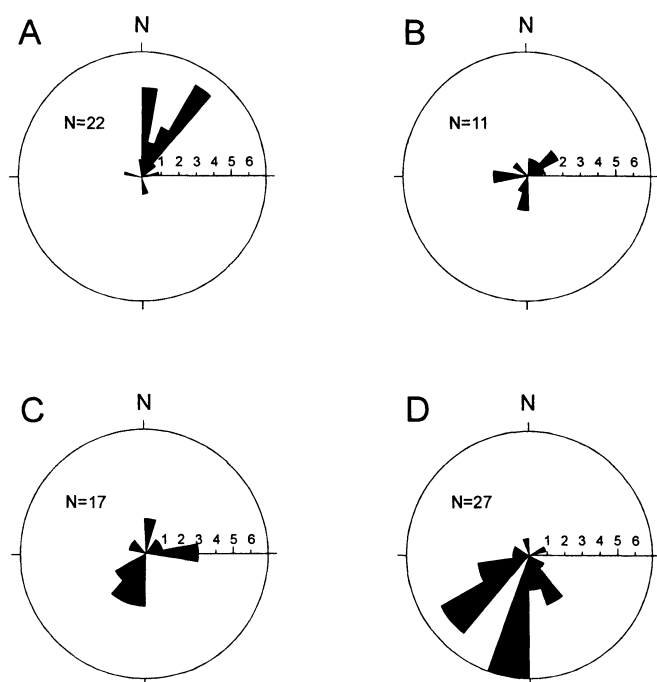
FIGURE 11—Rose diagrams (linear scale) of slip face directions and trackway walking directions in the Muth Formation near Mikkim. (A) Dip directions of restored foresets in facies association 2. (B) Orientation of *Diplichnites* traces without walking direction. (C) *Palmichnium* walking directions on bedding surfaces. (D) *Palmichnium* walking directions on foresets. Note that most of the *Palmichnium* traces are directed opposite to the dip of the foresets indicating uphill walking directions.

considered mass death assemblages (Andrews et al., 1974).

The size range of the Muth trackways varies considerably (Appendix 1). Although various instars of one eurypterid species could have produced these trackways, it is more likely that several eurypterid species were involved in these subaerial excursions, bearing in mind the diverse eurypterid faunas at this time (e.g., Alken assemblage in Germany; Størmer, 1976).

The abundance, straightness, and sub-parallel orientation of most of the Muth *Palmichnium* trackways suggests that the eurypterids responsible were migrating across the beach/dune environment of FA2 to a specific destination, suggesting that the beach/dune environment does not represent their normal habitat. The main walking direction of the eurypterids, indicated predominantly by push-back mounds behind the tracks, was towards the southwest. This trend is clearly visible on bedding surfaces and even stronger on dune foresets (Fig. 11C, D).

Most of the *Palmichnium* run up the slip faces of the dunes (Fig. 11A), close to the dip line of the foresets, suggesting that eurypterids were migrating across the shoreline, possibly to sites behind the dunes. The orientation of most *Palmichnium* trackways close to the dip line (Appendix 1) might be explained by comparisons with modern arthropods attempting to walk uphill on the slip faces of eolian dunes; if they depart too far from the direction of maximum dip line they lose balance and roll down the slope (B.

Grasemann pers. observ., 1997). The so-called "beaten track" (Draganits et al., 1998, fig. 6) apparently consists of several sub-parallel *Palmichnium* trackways occurring on the same bedding surface, c. 30 cm wide and more than 1.5 m long. Although the superimposition of the trackways and some erosion of this surface complicate the distribution of tracks, it is suggested that this is more evidence that the eurypterids were migrating in the same direction. In contrast, the orientation of *Diplichnites* does not show any preferred alignment (Fig. 11B). They commonly are curved, indicating that the producer of these trackways moved around in this environment.

COMPARISON WITH OTHER ICHNOFAUNAS

Devonian terrestrial trace fossils are rare. About twenty non-marine invertebrate ichnogenera currently are known from the Devonian (Buatois et al., 1998a), but only a small number has been assigned to arthropods. Most of them occur in marginal marine and lacustrine settings, although traces in subaerial environments are also known (Rolfe, 1980; Pollard, 1985). According to Buatois et al. (1998a), marine coastal to alluvial plain settings were colonized by the Silurian, and similar ichnofaunal trends continued throughout the Devonian. Deep, infaunal, suspension-feeding organisms (the *Skolithos* ichnoguild) were established in higher-energy fluvial settings. A moderately diverse, mobile, predaceous and detritus-feeding, arthropod epifauna (*Diplichnites* ichnoguild) occurred in transitional alluvial-lacustrine environments. Buatois et al. (1998a) suggested that Devonian trace fossils occur in two contrasting environments: (1) alluvial deposits, particularly fluvial channel and overbank facies with low diversity ichnofaunas comprised of bivalve and branchiopod burrows, rare arthropod trackways, vertical burrows and *Taenidium* (the only form present in fluvial settings), and (2) transitional alluvial-lacustrine deposits dominated by arthropod trackways, which are restricted to marginal lacustrine and subaerial settings.

Only two occurrences with a comparable ichnofauna, facies, and age to that of the Muth Formation are mentioned in the literature: (1) the Beacon Supergroup of Antarctica (Gevers et al., 1971), and (2) the Tumblagooda Sandstone of western Australia (Trewin and McNamara, 1995). All three ichnofaunas are late Silurian to Middle Devonian in age, and are preserved in marine-terrestrial or marine-fluvial transition depositional environments dominated by sand. Paleogeographical reconstructions for the Early Devonian (Young, 1990) show the Australian and Indian ichnofaunas at around 30° S latitude, and the Antarctic ichnofauna at 45° S, all three along the margin of Gondwana (Fig. 12).

The Muth Formation ichnofauna is similar to that of the diverse Early Devonian ichnofauna described from several outcrops of the Taylor Group at the base of the Beacon Supergroup in the Darwin Glacier area of Antarctica (Gevers et al., 1971; Bradshaw, 1981; Gevers and Twomey, 1982; Bradshaw et al., 1990; Woolfe, 1990: see Trewin and McNamara, 1995, for a summary). Fish, molluscs, and plants indicate an Early to early Late Devonian age of the Taylor Group (Trewin and McNamara, 1995 and references
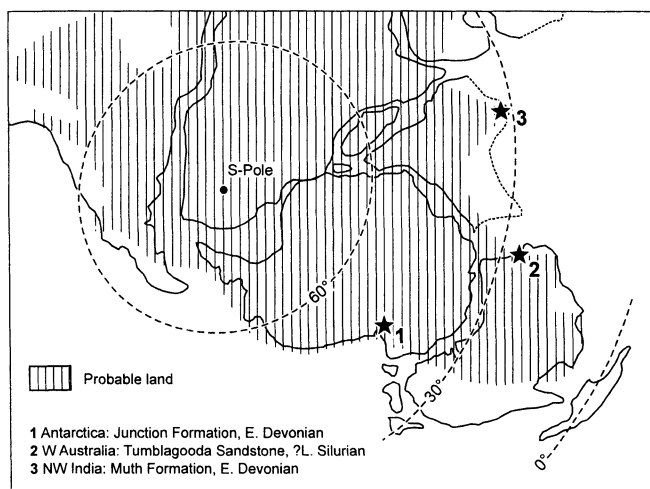
FIGURE 12—Distribution of comparable Late Silurian to Early Devonian ichnofaunas in similar coastal sedimentary environments. Paleogeographic map modified after Young (1990).

therein). Trace fossils occur in fine- to medium-grained, mature sandstones and orthoquartzites, which display thick cross-bedding with interbedded thin horizontally laminated beds (Gevers et al., 1971), that are very similar to FA2 in the Muth Formation. Gevers et al. (1971), Bradshaw (1981), and Bradshaw et al. (1990) interpreted these formations as marine based mainly on the hypothesis that the large *Beaconites* (= *Taenidium* Keighley and Pickerill, 1994) was made by polychaete annelids. In contrast, Gunn and Warren (1962), Plume (1982), and Woolfe (1990, 1993) suggested a non-marine environment including fluvial, estuarine, littoral, and eolian facies, on the evidence of sedimentary structures and a reinterpretation of some trace fossils. This ichnofauna includes large *Palmichnium,* up to 37 cm wide (Bradshaw et al., 1990), smaller *Diplichnites* and *Diplopodichnus, Taenidium, Skolithos,* as well as some *Aulichnites* and *Heimdallia.* In contrast to the abundant trackways on foreset surfaces in the Muth Formation, the Antarctic *Palmichnium, Diplichnites,* and *Diplopodichnus* have been found only on the upper surface of horizontally laminated beds (Gevers et al., 1971). One slab, described by Gevers et al. (1971, plate 20, fig. 3) as a "veritable stamping ground" shows several *Palmichnium* on the same surface. Similar surfaces with several *Palmichnium* also have been found in the Muth Formation (Fig. 5A). Gevers et al. (1971) described various *Taenidium,* narrow sinuous forms and larger relatively straight ones, up to 130 mm wide. *Taenidium* in the Muth Formation is mainly narrow, rarely exceeding 30 mm wide. *Diplopodichnus* is less abundant in the Muth Formation than in the Taylor Group, which probably reflects differences in the water content of the sediment during formation (Buatois et al., 1998b; Johnson et al., 1994).

The Muth Formation ichnofauna is also similar to an ichnofauna from the Tumblagooda Sandstone of the Kalbarri Group of Western Australia. Like the Muth Formation, it comprises mainly sand-sized sediments with virtually no mud. The unit tentatively was dated as late Silurian on the basis of regional correlation, but an Early

Devonian age was not dismissed (Trewin and McNamara, 1995 and references therein). It is divided into four facies associations, the uppermost three containing trace fossils (Trewin and McNamara, 1995). In common with the Indian ichnofauna, the highly diverse ichnoassemblage includes an arthropod-dominated *Heimdallia-Diplichnites* ichnofauna, concentrated in mixed waterlain and eolian sediments in a coastal fluvial outwash facies, especially in eolian sandsheet/pond subfacies (Trewin and McNamara, 1995). In contrast to the Indian and Antarctic ichnofaunas, there is also a *Skolithos-Diplocraterion* ichnofauna attributed mainly to filter feeders.

The Tumblagooda ichnofauna displays a much greater ichnodiversity, especially in the infaunal component; *Heimdallia* is abundant. This may reflect a lack of quiet, shallow interdune ponds in the Muth Formation, the dominant environment in which *Heimdallia* occurs in the Tumblagooda Sandstone (Trewin and McNamara, 1995). Alternatively, Hocking (1991) interpreted the Tumblagooda Sandstone as an intertidal marine environment fringing a braided fluvial plain and, therefore, the differences between the two ichnofaunas might be explained by the brackish influence of the Tumblagooda Sandstone. *Diplichnites* is common in the Australian ichnofauna. It varies in morphology and can be found on horizontal and low angle cross-bedded units. *Palmichnium* is scarce and relatively small. These differences might be explained in, that the barrier island setting of the Muth Formation provided an environment much closer to the shoreline than the coastal fluvial outwash area of the Tumblagooda Sandstone, which was perhaps more suited to the habit of eurypterids.

Several other broadly contemporaneous (Upper Silurian to Devonian) marginal to terrestrial ichnoassemblages (see Table 1 for ichnodiversity) are known from: (1) The Upper Silurian Ringerike Group (fluvial to marginal marine settings [Dam and Andreasen, 1990]) of Norway (Hanken and Størmer, 1975; Pollard and Walker, 1984, fig. 3); (2) The Upper Silurian Cape Storm and Leopold Formations (only intertidal ichnofauna considered) of Somerset, Cornwallis, and Devon Islands in the Canadian Arctic (Narbonne, 1984); (3) The Lower Devonian Old Red Sandstone (continental ephemeral to shallow lacustrine settings) of the Midland Valley of Scotland (Pollard and Walker, 1984; Walker, 1985); (4) The Lower Devonian Esopus Formation (only *Skolithos-Planolites* ichnofacies [very shallow subtidal] considered) of Highland Mills, New York State (Marintsch and Finks, 1982); (5) The Middle Devonian Hornelen Basin (fluvial to shallow lacustrine settings) of Norway (Pollard et al., 1982); (6) The Middle Devonian Middle Old Red Sandstone Orcadian Basin ichnofauna (fluvial to shallow lacustrine setting) of Scotland (Trewin, 1976; Pollard and Walker, 1984; Rogers, 1990); and (7) The Upper Devonian Catskill Group (only fluvial and tidal ichnofaunas considered) of New York State (Miller, 1979).

To test the similarity of these ten ichnofaunas (i.e., Muth Formation, Taylor Group, Tumblagooda Sandstone and seven others above) data on the composition (trace fossils present) of each ichnofauna were compiled (Table 1). In each case, the presence or absence of ichnotaxa (or

Table 1—Ichnoassemblage composition ("1" presence, "0" absence) of Upper Silurian-Devonian ichnoassemblages. Ichnotaxa 1–9 epifaunal traces. Ichnotaxa 10–21 infaunal traces. Key: 1 *Palmichnium* (cf. *Paleohelcura*), 2 *Diplichnites* and *Diplopodichnus*, 3 Bilobed trails (i.e., *Cruziana*, *Isopodichnus* and *Tumblagoodichnus*), 4 *Petalichnus*, 5 Small horizontal meandering (looping) trails (e.g., *Mermia*, *Gordia*), 6 Arthropod resting traces (i.e., *Selenichnites* and *Rusophycus*), 7 *Merostomichnites*, 8 *Siskemia*, 9 Grazing trails (i.e., "epichnial ridge" of Bradshaw [1981], *Helminthoidia*, *Helminthopsis*, 10 *Heimdallia*, 11 *Didymaulichnus*, *Didymauloponomous* and *Focusopsis*, 12 Simple vertical burrows (e.g., *Skolithos*), 13 *Diplocraterion*, 14 *Tigillites* (cf. *Beaconites*), 16 *Thalassinoides*, 17 Paired burrows (e.g., *Arenicolites*), 18 *Planolites* and *Agrichnium*, 19 *Polarichnus*, 20 *Chondrites*.

Ichnoassemblage	Ichnotaxa/trace type present																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Taylor Group, Antarctica	1	1	1	1	0	1	0	0	1	1	1	1	1	1	1	1	0	1	0	0
Tumblagooda Sandstone, Australia	1	1	1	0	1	1	0	1	0	1	1	1	1	1	1	0	1	1	0	0
Muth Formation, India	1	1	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0
Orcadian Basin, Scotland	1	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0
Midland Valley, Scotland	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Hornelen Basin, Norway	0	0	1	0	1	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0
Ringerike, Norway	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Arctic Canada	0	0	1	1	1	1	0	0	0	0	0	1	1	0	1	0	1	0	1	1
Catskill, New York State	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1
Highland Mills, New York State	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1

trace fossil types, i.e. morphologically similar ichnotaxa) was recorded. These data were then analysed via a cluster analysis, using SYSTAT 5.2.1 (single linkage method, distance metric equals Euclidean distance between 0–1). For details of the methodology the reader is referred to Digby and Kempton (1987).

The Muth Formation ichnofauna consistently clusters with the Antarctic ichnofauna (Fig. 13). According to an analysis based only on epifaunal traces, the Muth ichnofauna clusters closest to the Taylor Group ichnofauna of Antarctica (Fig. 13B). If the entire (epifaunal and infaunal) ichnofauna is considered, however, the Australian ichnofauna clusters closest to that of Antarctica (Fig. 13A). This difference might reflect the brackish water influence on the infaunal components of the Tumblagooda Sandstone, while the Muth assemblage represents essentially the product of an epifaunal, terrestrial ichnoguild.

The similarity between these three ichnofaunas (Antarctica, Australia, India), and their occurrence on the margin of Gondwana, identifies a recurrent Gondwanan ichnocoenosis. There is also considerable paleobiogeographic similarity between the other ichnofaunas (i.e., Scandinavian-Scottish and North American clusters), particularly if overall trace composition is considered (Fig. 13A). Although provincialism is supported by this analysis, the similarity of these ichnofaunas also may be due, in part, to their palaeoenvironmental setting (e.g., a lacustrine cluster unites the Midland Valley, Orcadian and Hornelen basin ichnofaunas, yet this cluster also includes the Ringerike ichnofauna, which represents marginal marine-fluvial facies, which should cluster closer to the Taylor and Tumblagooda ichnofaunas if environment were the most significant control). Another consideration is that the diversity of ichnotaxa described from these settings probably also reflects the amount of fieldwork done in each area, the available outcrop, and the accessibility of the localities.

CONCLUSIONS

The trace fossils of the Muth Formation represent an important record of Early Devonian arthropod activity in a marginal marine to terrestrial environment. The ichnoassemblage consists of abundant *Palmichnium antarcticum* and *Diplichnites gouldi* with rarer *Diplopodichnus biformis, Taenidium barretti, Didymaulichnus* cf. *lyelli, Didymaulyponomos* cf. *rowei, Selenichnites* isp., and vertical burrows of unclear affinity.

The paleoenvironment of the Muth Formation is interpreted as a barrier island system. Four different facies associations are recognized. The distribution of the ichnofauna is clearly facies controlled; arthropod trackways occur only in beach to coastal dune environments (facies association 2). Most of the *Palmichnium* and *Diplichnites* trackways are interpreted as subaerial.

Trackways are preserved on the surfaces upon which they were produced, as evidenced by undisturbed sand laminae directly above. It is suggested that saline surf-spray and/or microbial mats are the probable candidates responsible for stabilization of trackways in the quartz arenite of the Muth Formation.

The excellent preservation and abundance of trackways enable analysis of trackway-size variations, which indicates that the traces were produced by instars of single arthropod taxa and/or by different taxa creating similar traces. Trackway variations facilitate the separation of two forms of *Palmichnium* and *Diplichnites*. Additionally, gait variations within single ichnotaxa, in some cases within single trackways, have been documented; they are interpreted as a response to differences in the substrate and slope angle.

The abundance and frequently sub-parallel orientation of *Palmichnium antarcticum*, predominantly perpendicular to the paleo-coastline, suggest that stylonurid eurypterids, which are interpreted as their producer, were migrating across the shoreline and climbing up slip faces of
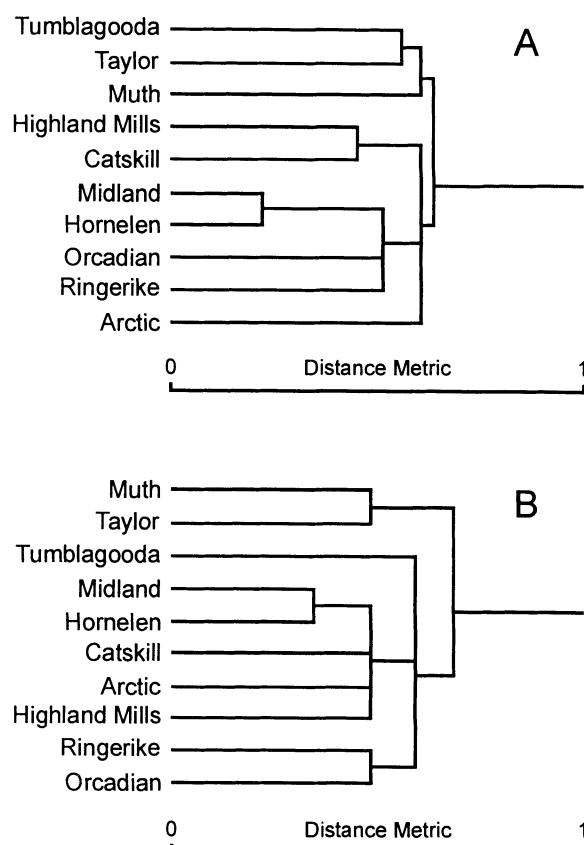
FIGURE 13—Cluster analyses of ichnoassemblage composition for ten Late Silurian and Devonian ichnoassemblages. See text and Table 1 for details. Distance metric is Euclidean distance (0–1). (A) Epifaunal and Infaunal traces. (B) Epifaunal traces only. Key: Arctic (Arctic Canada), Catskill (Catskill, New York State), Highland Mills (Highland Mills, New York State), Hornelen (Hornelen Basin, Norway), Midland (Midland Valley, Scotland), Muth (Muth Formation, India), Orcadian (Orcadian Basin, Scotland), Ringerike (Ringerike, Norway), Taylor (Taylor Group, Antarctica), Tumblagooda (Tumblagooda Sandstone, Australia).

barrier island dunes, perhaps en route to back barrier settings.

The similarity of this ichnofauna to others in marginal marine environments of similar age in Antarctica and Australia, supported by cluster analysis of contemporaneous ichnofaunas, allows the identification of a recurrent Lower Devonian ichnocoenosis around the margins of eastern Gondwana.

ACKNOWLEDGMENTS

REFERENCES

ALLEN, J.R.L., and WILLIAMS, B.P.J., 1981, Beaconites antarcticus: A giant channel-associated trace fossil from the Lower Old Red Sandstone of South Wales and the Welsh Borders: Geological Journal, v. 16, p. 255–269.

ANDERSON, A.M., 1975, The "trilobite" trackways in the Table Mountain Group (Ordovician) of South Africa: Palaeontologia Africana, v. 18, p. 35–45.

ANDREWS, H.E., BROWER, J.C., GOULD, S.J., and REYMENT, R.A., 1974, Growth and variation in Eurypterus remipes Dekay: Bulletin of the Geological Institute of the University of Upsala, v. 4, p. 81–114.

BANERJEE, D.M., 1974, Stratigraphy and depositional characteristics of Tethyan sediments in Kuti-Kalapani area, Kumaun, India: Himalayan Geology, v. 4, p. 296–322.

BASSI, U.K., 1988, Orthis aff. rustica from the Devonian quartz-arenite of the Muth Formation, Khimokul La (Kinnaur), Himachal Himalaya: Current Science, v. 57, p. 329–331.

BHARGAVA, O.N., 1997, Tethyan Sequences in the Spiti Valley, Himachal Himalaya: in BANERJEE, D.M., ed., Response of the ocean/atmosphere system to the past global changes, IGCP-386: 1st International field workshop in Spiti Valley, Himachal Himalaya, India, Field guide book and abstracts, p. 6–34.

BHARGAVA, O.N., and BASSI, U.K., 1986, Silurian reefal buildups: Spiti-Kinnaur, Himachal Himalaya, India: Facies, v. 15, p. 35–52.

BHARGAVA, O.N., and BASSI, U.K., 1988, Trace fossils from the Palaeozoic-Mesozoic sequence of Spiti-Kinnaur (Himachal Himalaya) with comments on palaeoenvironmental control on their frequency: Journal of the Geological Society of India, v. 32, p. 227–238.

BHARGAVA, O.N., and BASSI, U.K., 1998, Geology of Spiti-Kinnaur Himachal Himalaya: Memoirs of the Geological Survey of India, v. 124, p. 1–210.

BRADDY, S.J., 1995, A new arthropod trackway and associated invertebrate ichnofauna from the Lower Permian Hueco Formation of the Robledo Mountains, southern New Mexico: in LUCAS, S.G., and HECKERT, A.B., eds., Early Permian Footprints and Facies: New Mexico Museum of Natural History and Science Bulletin, v. 6, p. 101–105.

BRADDY, S.J., 1996, The palaeobiology of the Eurypterida: Unpublished Ph.D. Thesis, University of Manchester, 505 p.

BRADDY, S.J., and ANDERSON, L.I., 1996, An Upper Carboniferous eurypterid trackway from Mostyn, Wales: Proceedings of the Geologists' Association, v. 107, p. 51–56.

BRADDY, S.J., and DUNLOP, J.A., 1997, The functional morphology of mating in the Silurian eurypterid, Baltoeurypterus tetragonophthalmus (Fischer, 1839): The Zoological Journal of the Linnean Society, v. 121, p. 435–461.

BRADDY, S.J., and MILNER, A.R.C., 1998, A large arthropod trackway from the Gaspé Sandstone Group (Middle Devonian) of eastern Canada: Canadian Journal of Earth Sciences, v. 35, p. 1116–1122.

BRADDY, S.J., ALDRIDGE, R.J., GABBOTT, S.E., and THERON, J.N., 1999, Lamellate book-gills in a late Ordovician eurypterid from the Soom Shale Lagerstätte, South Africa: Support for a eurypterid-scorpion clade: Lethaia, v. 32, p. 72–74.

BRADSHAW, M.A., 1981, Paleoenvironmental interpretations and sys-

tematics of Devonian trace fossils from the Taylor Group (Lower Beacon Supergroup), Antarctica: New Zealand Journal of Geology and Geophysics, v. 24, p. 615–652.

BRADSHAW, M.A., HARMSEN, F.J., and KIRKBRIDE, M.P., 1990, Preliminary results of the 1988–1989 expedition to the Darwin Glacier area: New Zealand Antarctic Record, v. 10, p. 28–48.

BRADY, L.F., 1939, Tracks in the Coconino Sandstone compared with those of small living arthropods: Plateau, v. 12, p. 32–34.

BRADY, L.F., 1947, Invertebrate tracks from the Coconino Sandstone of Northern Arizona: Journal of Paleontology, v. 21, p. 466–472.

BRAND, L., 1979, Field and laboratory studies on the Coconino Sandstone (Permian) vertebrate footprints and their paleoecological implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 28, p. 25–38.

BRAND, L., 1996, Variations in Salamander trackways resulting from substrate differences: Journal of Paleontology, v. 70, p. 1004–1010.

BRIGGS, D.E.G., and ROLFE, W.D., 1983, A giant arthropod trackway from the Lower Mississippian of Pennsylvania: Journal of Paleontology, v. 57, p. 377–390.

BRIGGS, D.E.G., ROLFE, W.D.I., and BRANNAN, J., 1979, A giant myriapod trail from the Namurian of Arran, Scotland: Palaeontology, v. 22, p. 273–291.

BUATOIS, L.A., MÁNGANO, M.G., GENISE, J.F., and TAYLOR, T.N., 1998a, The ichnologic record of the continental invertebrateinvasion: Evolutionary trends in environmental expansion, ecospace utilization, and behavioral complexity: PALAIOS, v. 13, p. 217–240.

BUATOIS, L.A., MÁNGANO, M.G., MAPLES, C.G., and LANIER, W.P., 1998b, Taxonomic reassessment of the ichnogenus *Beaconichnus* and additional examples from the Carboniferous of Kansas, U.S.A.: Ichnos, v. 5, p. 287–302.

CHISHOLM, J.I., 1985, Xiphosurid burrows from the Lower Coal Measures (Westphalian A) of West Yorkshire: Palaeontology, v. 28, p. 619–628.

CURRAY, J.R., 1964, Transgressions and regressions: *in* MILLER, R.L., ed., Papers in Marine Geology: Macmillan, New York, p. 175–203.

DAM, G., and ANDREASEN, F., 1990, High-energy ephemeral stream deltas; an example from the Upper Silurian Holmestrand Formation of the Oslo Region, Norway: Sedimentary Geology, v. 66, p. 197–225.

DASGUPTA, P.K., 1971, On textural characteristics of the Muth Quartzite of Spiti and Kuti regions, central Himalayas: Journal of the Geological Society of India, v. 12, p. 152–158.

DAWSON, J.W., 1873, Impressions and footprints of aquatic animals and imitative markings on Carboniferous rocks: American Journal of Science, v. 5, p. 16–24.

DEYNOUX, M., 1990, Water-transfer cylindrical structures in the Late Proterozoic eolian sandstones in the Taoudeni Basin, West Africa: Sedimentary Geology, v. 66, p. 227–242.

DIGBY, P.G., and KEMPTON, R.A., 1987, Multivariate analysis of ecological communities: Chapman and Hall, London, 206 p.

DRAGANITS, E., GRASEMANN, B., and BRADDY, S.J., 1998, Discovery of giant arthropod trackways in the Devonian Muth Quartzite (Spiti, India): Implications for the depositional environment: Journal of Asian Earth Sciences, v. 16, p. 109–118.

FARLOW, J.O., and PIANKA, E.R., 2000, Body Form and Trackway Pattern in Australian Desert Monitors (Squamata: Varanidae): Comparing Zoological and Ichnological Diversity: PALAIOS, v. 15, p. 235–247.

FISCHER, W.A., 1978, The habitat of the early vertebrates: Trace and body fossilevidence from the Harding Formation (Middle Ordovician), Colorado: The Mountain Geologist, v. 15, p. 1–26.

FRIEND, P.F., ALEXANDER-MARRICK, P.D., NICHOLSON, J., and YEATS, A.K., 1976, Devonian sediments of East Greenland II: Sedimentary structures and fossils: Meddelelser om Grønland, v. 206, p. 1–91.

FRYBERGER, S.G., and SCHENK, C.J., 1988, Pin stripe-lamination: A distinctive feature of modern and ancient eolian sediments: Sedimentary Geology, v. 55, p. 1–15.

FUCHS, G., 1982, The geology of the Pin valley in Spiti, H.P., India: Jahrbuch der Geologischen Bundesanstalt, v. 124, p. 325–359.

GAETANI, M., and GARZANTI, E., 1991, Multi cyclic history of the northern India continental margin (northwestern Himalaya): American Association of Petroleum Geologists Bulletin, v. 75, p. 1427–1446.

GARZANTI, E., ANGIOLINI, L., and SCIUNNACH, D., 1996, The Mid-Carboniferous to lowermost Permian succession of Spiti (Po Group and Ganmachidam Formation; Tethys Himalaya, Northern India): Gondwana glaciation and rifting of Neo-Tethys: Geodinamica Acta, v. 9, p. 78–100.

GERDES, G., KLENKE, T., and NOFFKE, N., 2000, Microbial signatures in peritidal siliciclstic sediments: A catalogue: Sedimentology, v. 47, p. 279–308.

GEVERS, T.W., and TWOMEY, A., 1982, Trace fossils and their environment in Devonian (Silurian?) Lower Beacon strata in the Asgard Range, Victoria Land Antarctica: *in* CRADDOCK, C., ed., Antarctic Geoscience: University of Wisconsin Press, Madison, p. 639–648.

GEVERS, T.W., FRAKES, L.A., EDWARDS, L.N., and MARZOLF, J.E., 1971, Trace fossils in the lower Beacon sediments (Devonian), Darwin Mountains, southern Victoria Land, Antartica: Journal of Paleontology, v. 45, p. 81–94.

GOEL, R.K., and NAIR, N.G.K., 1977, The Spiti Ordovician-Silurian succession: Journal of the Geological Society of India, v. 18, p. 47–48.

GOLDRING, R., and SEILACHER, A., 1971, Limulid undertracks and their sedimentological implications: Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 137, p. 422–442.

GOLDRING, R., and POLLARD, J.E., 1995, A re-evaluation of *Ophiomorpha* burrows in the Wealden Group (Lower Cretaceous) of southern England: Cretaceous Research, v. 16, p. 665–680.

GREINER, H., 1972, Arthropod trace fossils in the Lower Devonian Jaquet River Formation of New Brunswick: Canadian Journal of Earth Sciences, v. 9, p. 1172–1177.

GUNN, B.M., and WARREN, G., 1962, Geology of Victoria Land between the Mawson and Mulock Glaciers, Ross Dependency, Antarctica: New Zealand Geological Survey Bulletin, v. 71, p. 1–157.

HANKEN, N.-M., and STØRMER, L., 1975, The trail of a large Silurian eurypterid: Fossils and Strata, v. 4, p. 255–270.

HARDY, P.G., 1970, New xiphosurid trails from the Upper Carboniferous of Northern England: Palaeontology, v. 13, p. 188–190.

HAYDEN, H.H., 1904, The geology of Spiti with parts of Bashahr and Rupshu: Memoirs of the Geological Survey of India, v. 36, p. 1–129.

HAYDEN, H.H., 1908, A sketch of the geography and geology of the Himalaya Mountains and Tibet: The Geology of the Himalaya, Part 4: Government of India Press, Calcutta, 236 p.

HEER, O., 1877, Flora Fossilis Helvetiae: J. Wüster & Co., Zürich, 182 p.

HOCKING, R.M., 1991, The Silurian Tumblagooda Sandstone, Western Australia: Geological Survey of Western Australia Report, v. 27, p. 1–124.

JERAM, A.J., SELDEN, P.A., and EDWARDS, D., 1990, Land animals in the Silurian: Arachnids and myriapods from Shropshire, England: Science, v. 250, p. 658–661.

JOHNSON, E.W., BRIGGS, D.E.G., SUTHREN, R.J., WRIGHT, J.L., and TUNNICLIFF, S.P., 1994, Non-marine arthropod traces from the subaerial Ordovician Borrowdale Volcanic Group, English Lake District: Geological Magazine, v. 131, p. 395–406.

KEIGHLEY, D.G., and PICKERILL, R.K., 1994, The ichnogenus *Beaconites* and its distinction from *Ancorichnus* and *Taenidium*: Palaeontology, v. 37, p. 305–337.

LOGAN, B.W., REZAK, R., and GINSBURG, R.N., 1964, Classification and environmental significance of algal stromatolites: Journal of Geology, v. 72, p. 68–83.

McKEE, E.D., 1957, Primary structures in some recent sediments: American Association of Petroleum Geologists Bulletin, v. 41, p. 1707–1747.

MCKEEVER, P.J., 1991, Trackway preservation in aeolian sandstones from the Permian of Scotland: Geology, v. 19, p. 726–729.

MANNING, P.L., and DUNLOP, J.A., 1995, Respiratory organs of eurypterids: Palaeontology, v. 38, p. 287–297.

MARINTSCH, E.J., and FINKS, R.M., 1982, Lower Devonian ichnofabrics at Highland Mills, New York and their gradual replacement across environmental gradients: Journal of Paleontology, v. 56, p. 1050–1078.

MILLER, M.F., 1979, Paleoenvironmental distribution of trace fossils in the Castskill deltaic complex, New York State: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 28, p. 117–141.

NARBONNE, G.M., 1984, Trace fossils in Upper Silurian tidal flat to basin slope carbonates of Arctic Canada: Journal of Paleontology, v. 58, p. 398–415.

O'SULLIVAN, M.J., COOPER, M.A., MACCARTHY, A.J., and FORBES, W.H., 1986, The palaeoenvironment of *Beaconites*-like burrows in the Old Red Sandstone at Gortnabinna, SW Ireland: Journal of the Geological Society of London, v. 143, p. 897–906.

PEARSON, P.N., 1992, Walking traces of the giant myriapod *Arthropleura* from the Strathclyde Group (Lower Carboniferous) of Fife: Scottish Journal of Geology, v. 28, p. 127–133.

PLUME, R.W., 1982, Sedimentology and palaeocurrent analysis of the basal part of the Beacon Supergroup (Devonian (and older?) to Triassic) in south Victoria Land, Antarctica: *in* CRADDOCK, C., ed., Antarctic Geoscience: University of Wisconsin Press, Madison, p. 571–580.

POLLARD, J.E., 1976, A problematical trace fossil from the Tor Bay Breccias of south Devon: Proceedings of the Geologists' Association, v. 87, p. 105.

POLLARD, J.E., 1985, Evidence from trace fossils: *in* CHALLONER, W.G., and LAWSON, J.D., eds., Evolution and environment in the late Silurian and early Devonian: Philosophical Transactions Royal Society London, series B, v. 309, p. 241–242.

POLLARD, J.E., and WALKER, E.F., 1984, Reassessment of sediments and trace fossils from the Old Red Sandstone (Lower Devonian) of Dunure, Scotland, described by John Smith (1909): Geobios, v. 17, p. 567–576.

POLLARD, J.E., STEEL, R.J., and UNDERSRUD, E., 1982, Facies sequences and trace fossils in lacustrine/fan delta deposits, Hornelen Basin (M. Devonian), western Norway: Sedimentary Geology, v. 32, p. 63–87.

QUIRKE, T.T., 1930, Spring pits; Sedimentation phenomena: Journal of Geology, v. 38, p. 88–91.

REED, F.R.C., 1912, Devonian fossils from Chitral, Persia, Afganisthan and the Himalayas: Records of the Geological Survey of India, v. 41, p. 86–114.

RICHTER, R., 1954, Fährte eines Riesenkrebses im Rheinischen Schiefergebirge: Natur und Volk, v. 84, p. 261–269.

RIDGEWAY, J.M., 1974, A problematical trace fossil from the New Red Sandstone of south Devon: Proceedings of the Geologists' Association, v. 85, p. 511.

ROGERS, D.A., 1990, Probable tetrapod tracks rediscovered in the Devonian of N Scotland: Journal of the Geological Society, London, v. 147, p. 746–748.

ROLFE, W.D.I., 1980, Early invertebrate terrestrial faunas: *in* PANCHEN, A.L., ed., The Terrestrial Environment and the Origin of Land Vertebrates: Academic Press, London, p. 117–157.

ROMANO, M., and WHYTE, M.A., 1987, A limulid trace fossil from the Scarborough Formation (Jurassic) of Yorkshire: Its occurrence, taxonomy and interpretation: Proceedings of the Yorkshire Geological Society, v. 46, p. 85–95.

ROMANO, M., and WHYTE, M.A., 1990, *Selenichnites,* a new name for the ichnogenus *Selenichnus* Romano & Whyte, 1987: Proceedings of the Yorkshire Geological Society, v. 48, p. 221.

ROUAULT, M., 1850, Note preliminaire sur une nouvelle formation decouverte dans le terrain Silurian inferieur de la Bretagne: Société Geologique de France Bulletin, series 2, v. 7, p. 724–744.

SADLER, C.J., 1993, Arthropod trace fossils from the Permian De

Chelly Sandstone, North-eastern Arizona: Journal of Paleontology, v. 67, p. 240–249.

SCHIEBER, J., 1998, Possible indicators of microbial mat deposits in shales and sandstones: Examples from the Mid-Proterozoic Belt Supergroup, Montana, U.S.A: Sedimentary Geology, v. 120, p. 105–124.

SCHIEBER, J., 1999, Microbial Mats in Terrigenous Clastics: The Challenge of Identification in the Rock Record: PALAIOS, v. 14, p. 3–12.

SHANKER, R., BHARGAVA, O.N., BASSI, U.K., MISRA, R.S., CHOPRA, S., SINGH, I.B., and SINGH, T., 1993, Biostratigraphic controversy in the Himalaya: An evaluation in Lahaul-Spiti, Himachal Pradesh: Indian Minerals, v. 47, p. 263–286.

SHARPE, C.F.S., 1932, Eurypterid trail from the Ordovician: American Journal of Sciences, v. 24, p. 355–361.

SHEAR, W.A., GENSEL, P.G., and JERAM, A.J., 1996, Fossils of large terrestrial arthropods from the Lower Devonian of Canada: Nature, v. 384, p. 555–557.

SRIVASTAVA, A.K., and KUMAR, S., 1992, Trace fossils from the Muth Quartzite of Malla Johar Area, Tethys Kumaon Himalaya, India: Journal of the Geological Society of India, v. 40, p. 43–47.

STOLICZKA, F., 1866, Geological section across the Himalayan Mountains, from Wangtu bridge on the River Sutlej to Sungdo on the Indus: With an account of the formations of Spiti, accompanied by a revision of all known fossils from that district: Memoirs of the Geological Survey of India, v. 5, p. 1–173.

STØRMER, L., 1976, Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 5: Myriapoda and additional forms, with general remarks on fauna and problems regarding invasion of land by arthropods: Senckenbergiana Lethaea, v. 57, p. 87–183.

TALENT, J.A., 1982, comment on: BHATIA, S.B., JAIN, S.P., and GUPTA, V.J., Lower Devonian ostracode fauna from Spiti and its palaeobiogeographical significance: Geological Survey of India Miscellaneous Publications, v. 41, p. 292–293.

TALENT, J.A., GOEL, R.K., JAIN, A.K., and PICKETT, J.W., 1988, Silurian and Devonian of India, Nepal and Bhutan: Biostratigraphic and Palaeobiogeographic Anomalies: Courier Forschungsinstitut Senckenberg, v. 106, p. 1–57.

THOMSON, M.R.A., and WEBER, B., 1999, Discovery of an Ordovician invertebrate fauna in the Blaiklock Glacier Group, Shackleton Range, Antarctica: Terra Antarctica, v. 6, p. 241–248.

TREWIN, N.H., 1976, *Isopodichnus* in a trace fossil assemblage from the Old Red Sandstone: Lethaia, v. 9, p. 29–38.

TREWIN, N.H., 1994, A draft system for the identification and description of arthropod trackways: Palaeontology, v. 37, p. 811–823.

TREWIN, N.H., and MCNAMARA, K.J., 1995, Arthropods invade the land: Trace fossils and palaeoenvironments of the Tumblagooda Sandstone (?late Silurian) of Kalbarri, Western Australia: Transactions of the Royal Society of Edinburgh: Earth Sciences, v. 85, p. 177–210.

UCHMAN, A., 1995, Taxonomy and paleoecology of flysch trace fossils: The Marnoso-arenacea Formation and associated facies (Miocene, Northern Apennines, Italy): Beringeria, v. 15, p. 1–115.

WALKER, E.F., 1985, Arthropod ichnofauna of the Old Red Sandstone at Dunure and Montrose, Scotland: Transactions of the Royal Society of Edinburgh: Earth Sciences, v. 76, p. 287–297.

WATERSTON, C.D., 1979, Problems of functional morphology and classification in stylonuroid eurypterids, (Chelicerata, Merostomata), with observations on the Scottish Silurian Stylonuroidea: Transactions of the Royal Society of Edinburgh: Earth Sciences, v. 70, p. 251–322.

WIESMAYR, G., GRASEMANN, B., DRAGANITS, E., FRANK, W., FRITZ, H., and MILLER, C., 1998, The main pre-Himalayan and Himalayan deformation phases in the Pin Valley (Spiti, Tethyan Himalaya, NW India): Geological Bulletin, University of Peshawar, v. 31, p. 212–213.

WOOLFE, K.J., 1990, Trace fossils as paleoenvironmental indicators in

the Taylor Group (Devonian) of Antarctica: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 80, p. 301–310.

WOOLFE, K.J., 1993, Devonian depositional environments in the Darwin Mountains: Marine or non-marine?: Antarctic Science, v. 5, p. 211–220.

YOUNG, F.G., 1972, Early Cambrian and older trace fossils from the Southern Cordillera of Canada: Canadian Journal of Earth Sciences, v. 9, p. 1–17.

YOUNG, G.C., 1990, Devonian vertebrate distribution patterns and cladistic analysis of palaeogeographic hypotheses: in McKERROW, W.S., and SCOTESE, C.R., eds., Palaeozoic Palaeogeography and Biogeography: Geological Society Memoir, no. 12, p. 243–255.

Appendix 1—Trackway attributes based on the nomenclature of Trewin (1994). Bed numbers refer to sections where trackways were found. Abbreviations: bedding surface (SS); foresets (Sfor); trackway alignment (L) with azimuth of dip direction and angle of dip (Orientation); probable walking direction (>); external width (Ext. width); internal width (Int. width); Stride: values with "*" are paces of *Diplichnites*; series angle to the midline based mainly on mid and outer tracks (Ser. ang.); orientation of tracks to the midline (Tr. orient.); number of tracks per series (Tr./Ser.); symmetry of opposing series (Sym.); opposite (O); staggered (S), alternate (A); medial impression (Med.).

Trace	Name	Bed	Surface	Orientation	Ext. width	Int. width	Stride	Ser. ang.
3	*Diplichnites* Form A	Ma543	SS263/40	L207/26 >?	31	16	11*	—
4	*Diplichnites* Form A	Ma543	SS263/40	—	33	15	12*	—
5	*Diplichnites* Form A	Ma543	SS263/40	L220/12 >?	48	28	15*	—
11	*Diplichnites* Form A	Ma548	SS250/50	L002/03 >?	90	57	11*	—
27	*Diplichnites* Form A	Ma566	Sfor282/25	L260/25 >080	140	75	27*	—
28	*Diplichnites* Form A	Ma566	Sfor282/25	L240/19 >?	31	21	10*	—
38	*Diplichnites* Form A	Ma544	Sfor299/27	L009/14 >?	38	15	15*	—
48	*Diplichnites* Form A	Ma543	SS263/40	L263/40 >?	18	15	8*	—
86	*Diplichnites* Form A	Ma585	Sfor290/44	L230/23 >230	51	22	15*	—
69	*Diplichnites* Form B	—	SS224/12	L228/12 >228	51	44–49	12*	—
70	*Diplichnites* Form B	—	SS224/12	L235/13 >235	68	51–66	13*	—
71	*Diplichnites* Form B	—	SS224/12	L235/14 >235	80	50–77	16*	—
72	*Diplichnites* Form B	—	SS224/12	L174/08 >?	77	36–70	17*	—
73	*Diplichnites* Form B	—	SS224/12	L191/12 >191	107	51	32*	—
77	*Diplichnites* Form B	—	SS246/09	L204/08 >204	90	50	102/12*	—
19	*Diplopodichnus*	Ma556b	Sfor281/21	L218/09 >?	20	15	3.6*	—
1	*Palmichnium* Form A	Ma543	SS263/40	L234/25 >234	177	100	70	53
2	*Palmichnium* Form A	Ma543	SS263/40	L214/11 >214	140	83	54	79
12	*Palmichnium* Form A	Ma543	—	—	100	60	38	64
13	*Palmichnium* Form A	Ma555	SS268/31	L310/22 >310	?	?	90	36
14	*Palmichnium* Form A	Ma556b	Sfor286/35	L192/01 >192	84	48	19	34
15	*Palmichnium* Form A	Ma556b	Sfor286/35	L354/14 >174	107	62	27	68
16	*Palmichnium* Form A	Ma556b	Sfor286/35	L174/01 >?	?	25	46	86
17	*Palmichnium* Form A	Ma555	SS283/35	L196/01 >16	188	120	30	81
18	*Palmichnium* Form A	Ma555	SS283/35	L310/32 >?	250	110	91	?
20	*Palmichnium* Form A	Ma558	Sfor270/26	L218/16 >218	211	131	44	88
21	*Palmichnium* Form A	Ma558	Sfor270/26	L301/20 >?	198	138	42	41
22	*Palmichnium* Form A	Ma558	Sfor270/26	L220/19 >?	245	115	58	?
24	*Palmichnium* Form A	Ma560	Sfor264/36	L234/28 >234	215	175	66	71
25	*Palmichnium* Form A	Ma566	Sfor274/30	L335/02 >335	270	120	70	68
26	*Palmichnium* Form A	Ma566	Sfor274/24	L004/02 >?	63	37	15	?
30	*Palmichnium* Form A	Ma565	SS262/47	L242/41 >062?	125	75	51	46
31	*Palmichnium* Form A	Ma565	SS262/47	L226/40 >046	498	245	255	62
32	*Palmichnium* Form A	Ma566	Sfor248/16	L226/15 >226	212	116	53	72
33	*Palmichnium* Form A	Ma566	Sfor247/16	L237/16 >237	215	78	45	71
34	*Palmichnium* Form A	Ma566	Sfor245/26	L335/26 >155	215	105	112	24
35	*Palmichnium* Form A	Ma566	Sfor274/29	L271/26 >?	118	53	40	?
37	*Palmichnium* Form A	Ma543	SS263/40	L004/05 >184	190	140	67	47
39	*Palmichnium* Form A	Ma544	Sfor299/27	L295/25 >295	320	135	214	29
40	*Palmichnium* Form A	Ma510	—	—	104	67	48	44
41	*Palmichnium* Form A	Ma554	Sfor282/20	L227/14 >227	145	88	54	74
42	*Palmichnium* Form A	Ma553	SS268/26	L268/26 >088	172	118	150	26
43	*Palmichnium* Form A	Ma559	SS284/30	L235/21 >?	?	?	54	30
44	*Palmichnium* Form A	Ma561	SS270/25	L213/10 >213	?	?	31	68
45	*Palmichnium* Form A	Ma561	SS270/25	L230/23 >230	385	240	125	90
46	*Palmichnium* Form A	Ma556b	Sfor280/35	L198/03 >198	198	140	47	79
47	*Palmichnium* Form A	Ma543	SS263/40	L288/32 >288	208	113	113	42
49	*Palmichnium* Form A	Ma555	SS283/35	L268/31 >088	165	77	118	40
50	*Palmichnium* Form A	Ma555	SS283/35	L196/04 >196	131	82	30	23
51	*Palmichnium* Form A	Ma555	SS283/35	L203/04 >203	132	88	36	63
52	*Palmichnium* Form A	Ma555	SS283/35	L013/02 >193	183	128	46	64
53	*Palmichnium* Form A	Ma556b	Sfor286/35	L204/14 >?	90	40	36	90
54	*Palmichnium* Form A	Ma556b	Sfor285/41	L308/39 >128	190	130	40	68
55	*Palmichnium* Form A	Ma556b	Sfor285/38	L014/06 >194	145	85	50	70
56	*Palmichnium* Form A	Ma556b	Sfor285/38	L012/06 >192	180	110	53	71
57	*Palmichnium* Form A	Ma556b	Sfor285/38	L194/01 >194	74	58	44	67
58	*Palmichnium* Form A	Ma566	Sfor176/25	L330/12 >150	—	—	35	67
59	*Palmichnium* Form A	Ma566	Sfor176/25	L333/13 >153	—	—	49	?
60	*Palmichnium* Form A	Ma566	Sfor268/29	L357/02 >?	400	—	—	—
61	*Palmichnium* Form A	Ma566	Sfor278/30	L228/21 >?	265	145	153	?
62	*Palmichnium* Form A	Ma566	Sfor280/29	L006/04 >186	375	230	50	55
63	*Palmichnium* Form A	Ma566	Sfor240/60	L255/12 >255	175	108	45	74
64	*Palmichnium* Form A	Ma566	Sfor250/21	L241/18 >061	260	115	60	84

Appendix 1—Extended.

Shape of Tracks	Tr. Orient.	Tr./Ser.	Sym.	Med.	Remarks
ellipsoidal	oblique	?	O-A	—	well preserved
?	?	?	?	—	curves, poorly preserved
elongate	oblique	?	?	—	curves, poorly preserved V-series
crescentic	?	?	?	—	ridges parallel to trackway
D-shaped	?	?	?	—	poorly preserved
ellipsoidal (6 × 4)	?	?	A	—	
ellipsoidal	oblique	?	?	—	poorly preserved
ellipsoidal	?	?	O-A	—	poorly preserved
ellipsoidal (14 × 11)	oblique	?	O-A	—	very well preserved
circular	?	?	?	—	
circular	oblique	?	?	—	poorly preserved-V
circular	?	?	?	—	
circular	?	?	?	—	
circular	?	?	?	—	poorly preserved-V
circular	oblique	?	?	—	
—	—	—			well preserved
tear-drop–ellipsoidal	parallel	2 (3)	A	yes	well preserved, back-push mounds
tear-drop	parallel	2 (3)	O	—	well preserved, back-push mounds
elongate–ellipsoidal	parallel	2	S	yes	loose block
circ/ellipsoidal	?	2	?	—	poorly preserved
comma	parallel–obl	2	O	?	
circular–ellipsoidal	?	2	O	—	
?	?	2	?	—	poorly preserved
tear-drop	oblique	2	O	—	
D-shaped (63 × 38)	perpendicular	?	—	—	fairly preserved
linear	?	2	?	—	poorly preserved
oval	?	2	?	—	poorly preserved
?	?	2	?	—	poorly preserved
ellipsoidal–elongate	oblique	2	O	?	
ellipsoidal–elongate	oblique	2	?	—	poorly preserved
?	?	?	—	—	curves, poorly preserved
ellipsoidal (20 × 14)	oblique	2	O	—	
ellipsoidal (35 × 20)	perpendicular	3 (2)	O	—	largest trackway
elongate	oblique	2 (3)	A	yes	very well preserved, backpush mounds
tear-drop/circular	oblique	3	A	yes	very well preserved, backpush mounds
crescentic	perpendicular	2	S	—	big stride
elongate	oblique	2	?	—	poorly preserved
ellipsoidal (20 × 10)	parallel	2 (3)	A	—	well preserved, backpush mounds
crescentic	perpendicular	3 (4)	?	—	backpush mounds
circular	—	3	?	—	loose block
?	?	2	?	—	poorly preserved
elongate	oblique	2	S	—	poorly preserved
?	?	2	?	—	poorly preserved
?	?	2	?	—	
?	?	2 (3)	O	—	poorly preserved
?	?	2 (3)	S	—	
crescentic	perpendicular	2	A	—	backpush mounds
D-shape (25 × 12)	perpendicular	2	S	—	
?	?	2	?	—	poorly preserved
tear-drop	parallel	2	A	—	
elongate?	parallel	2	?	—	poorly preserved
elongate	parallel	2	O	—	
tear-drop	oblique	2	S	—	backpush mounds
elongate	parallel	2	?	—	
elongate	parallel	2	A	—	backpush mounds
circular	—	3	?	yes	
?	?	?	?	—	poorly preserved
?	?	2	?	—	poorly preserved
D-shaped/elongated	perpendicular	—	—	—	abundant superimposed Palm.
circular?	—	2	S	—	
?	?	3	?	—	
elongate	parallel	2	?	yes	
elongate	?	2	?	—	

Appendix 1—Continued.

Trace	Name	Bed	Surface	Orientation	Ext. width	Int. width	Stride	Ser. ang.
65	*Palmichnium* Form A	Ma566	Sfor250/21	L248/17 >248	—	—	56	64
66	*Palmichnium* Form A	Ma566	Sfor250/21	L251/21 >251	196	120	43	?
67	*Palmichnium* Form A	Ma566	Sfor232/16	L265/14 >265	240	158	49	85
68	*Palmichnium* Form A	Ma568	Sfor250/18	L171/07 >171	210	115	?	?
87	*Palmichnium* Form A	Ma585	Sfor290/44	L224/21 >224	160	85	39	67
8	*Palmichnium* Form B	Ma515	—	—	74	28	52	74
9	*Palmichnium* Form B	Ma506	—	—	90	43	49	49
29	*Palmichnium* Form B	Ma566	Sfor290/26	L322/20 >322	170	46	82	59
36	*Palmichnium* Form B	Ma535	SS257/36	L268/35 >088	90	45	60	29

Appendix 1—Extended. Continued.

Shape of Tracks	Tr. Orient.	Tr./Ser.	Sym.	Med.	Remarks
elongate	?	2	?	—	
crescentic	?	?	?	—	backpush mounds
elongate	?	2	?	—	
?	?	?	?	—	
ellipsoidal	oblique	2	A	—	poorly preserved
circular	—	4	A	—	loose block, asymmetric gait, similar to trace 29
circular	—	3 (4)	O	—	loose block
circular	—	4 (1)	S	—	backpush mounds, asymmetric gait, similar to trace 8
circular	—	4	S-A	—	