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# A marginal marine ichnofauna from the Blaiklock Glacier Group (?Lower Ordovician) of the Shackleton Range, Antarctica

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ABSTRACT: A diverse arthropod-dominated ichnofauna, associated with a poorly preserved crustacean fauna and soft-bodied ?medusoid impressions, is described from the Blaiklock Glacier Group of the north-western Shackleton Range (Coats Land), Antarctica. The ichnofauna consists of *Asaphoidichnus*, *Beaconites*, *Didymaulichnus*, *Diplichnites*, *Gordia*, ?*Laevicyclus*, *Merostomichnites*, *Monomorphichnus*, *Palaeophycus*, *Planolites*, *Rusophycus*, *Selenichnites*, and *Taphrhelminthoides* (ichnogen nov.). Three new ichnotaxa are recognised: *Taphrhelminthoides antarcticus* n. ichnogen. et ichnosp. is a bilobate trail, composed of two parallel flat lobes, separated by a median ridge with a characteristic figure-of-eight pattern. *Merostomichnites gracilis* n. ichnosp. is characterised by its proportions (external:internal width ratio >3) and series of 10 to 12, thin, linear tracks. *Selenichnites antarcticus* n. ichnosp. is characterised by small elongate horseshoe-shaped marks, the medial portion showing three to five transverse scratch-marks.

The palaeoenvironment is interpreted as extremely shallow marine water, possibly a tide-dominated estuary, based on sedimentological evidence and the composition of the ichnofauna. Radiometric and palaeomagnetic data indicate that this assemblage is Lower Ordovician in age, representing the first autochthonous Ordovician fossiliferous succession to be described from Antarctica. The succession shows several sedimentological and palaeontological similarities with the basal units of the Ordovician Table Mountain Group in South Africa, supporting palaeogeographic models placing the Palaeozoic Blaiklock basin close to the Ordovician Table Mountain basin.

KEY WORDS: Arthropods, crustaceans, Gondwana, tidal, trace fossils.

The Shackleton Range (Coats Land) of W Antarctica was discovered during the British Transantarctic Expedition of 1955–1958 (Stephenson 1966). A detailed account of the regional geography and geology was published by Clarkson (1972) and Clarkson & Wyeth (1983), who renamed the "Blaiklock Beds" of Stephenson (1966), which outcrop in the NW of the Shackleton Range, as the Blaiklock Glacier Group (BGG hereafter), after the neighbouring Blaiklock Glacier. Accessible outcrops of this siliciclastic succession are restricted to more-or-less permanent ice-free tops of nunataks and ridges, in an area between about 29° to 30°W and 80°20′ to 80°30′S (Fig. 1), in the Haskard Highlands (S of Mount Provender), Mount Gass, Honnywill Peak, Wedge Ridge, Dragons Back (S of Mount Skidmore, SW of the La Grange Nunataks), and at Macquarrie Edge (N Otter Highlands) on the western flank of the Blaiklock Glacier.

These outcrops may be covered by a thin snow layer, making the fossil sites undetectable, sometimes during the whole southern summer season. It appears that the first British workers met this situation, as no hint of the relatively obvious and frequently occurring trace fossils of the BGG were reported by Stephenson (1966), Clarkson (1972) or Clarkson & Wyeth (1983). It was not until the German GEISHA Expedition to the Shackleton Range in 1987/88, that trace fossils were first discovered (Buggisch *et al.* 1994). An initial, brief, report on the fossils was provided by Thomson & Weber (1999).

The constant weathering and wind-blasting of the BGG sediments on the ice-free ridges and tops of the nunataks produce flaggy decimetre- to metre-sized debris which covers the outcropping sediments and accumulates downslope. Only in a few cases, of more weathering-resistant sandstone layers, could trace fossil horizons be observed *in situ*. Trace fossils occurring in such horizons were mostly uncollectable, and remain at the outcrop. The material described herein was collected mainly from the weathered flaggy rock debris on the slopes. The scattered distribution of BGG outcrops, as well as the lack of large accessible bedding planes, prevented any quantitative analysis of the stratigraphic distribution of the trace fossils. Only semi-quantitative estimates were possible, based on the traces preserved on the loose slabs of debris, correlated to locally-occurring (up-slope) sections.

## 1. Stratigraphy and age of the Blaiklock Glacier Group

Fossiliferous sediments are known from several localities in the Shackleton Range. Late Proterozoic to early Palaeozoic siliciclastic sediments yielding biostratigraphically useful micro- and/or macrofossils occur along the S and NW margin of the Shackleton Range (e.g. Thomson 1972; Soloviev & Grikurov 1978; Clarkson & Wyeth 1983; Buggisch *et al.* 1990; Weber 1991, 1995; Buggisch *et al.* 1995a, 1995b). In the NW of the Shackleton Range, the lower BGG rests unconformably on (Precambrian to ?early Palaeozoic) metamorphic basement rocks of the Pioneers and Stratton Group (Tessensohn & Thomson 1990; Buggisch *et al.* 1994).

Clarkson & Wyeth (1983) distinguished two different lithological units within the BGG: the (?older) Mount Provender Formation (MPF hereafter) in the east, and the (?younger) Otter Highland Formation (OHF hereafter) in the west. Although Clarkson & Wyeth (1983) assigned the sediments of the Dragons Back area to the OHF, Buggisch *et al.* (1994) assigned this succession to the uppermost MPF, but also noted

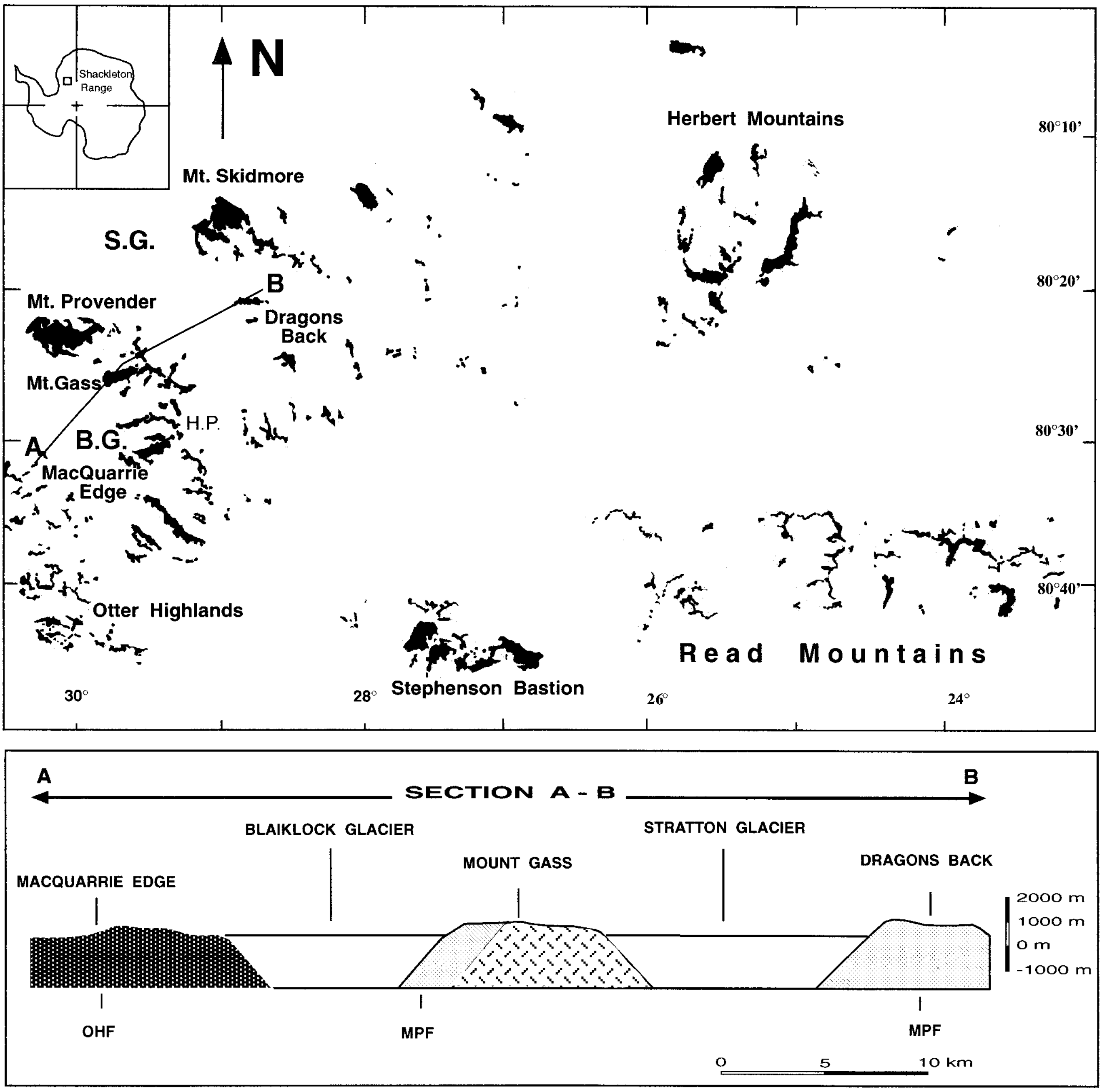


**Figure 1** Locality map and sketch section of the Shackleton Range (Coats Land, Western Antarctica) showing the main outcrops of the Blaiklock Glacier Group at Mount Gass (locality 1), Dragons Back (locality 2), and Honnywill Peak (H.P.; locality 3). Abbreviations: Stratton Glacier (S.G.); Blaiklock Glacier (B.G.). The section (A–B), modified from Stephenson (1966), shows the distribution of the Otter Highland Formation (OHF) and the Mount Provender Formation (MPF).

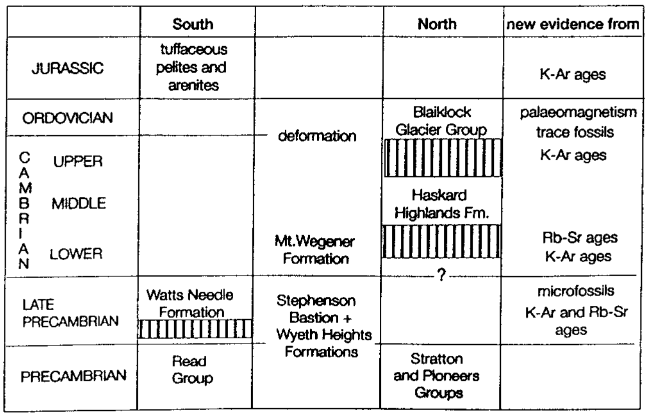
that it was unclear whether the MPF and OHF were true stratigraphically separated units or whether they simply represent two different (proximal and distal) facies of the same stratigraphic level.

According to radiometric and palaeomagnetic data, the BGG is dated as (?Lower) Ordovician in age. Radiometric dates for the underlying schists constrain the oldest age for the overlying BGG. Pankhurst *et al.* (1983) obtained a Rb/Sr-isochron with an age of 500 ± 5 Ma (Tremadoc) for the underlying schist, an age of 475 ± 40 Ma from samples of red shale at Mount Provender, and an age of 482 ± 1 Ma (Arenig) from three BBG samples. More recent K/Ar dating of BGG samples (data from the EUROSHACK expedition: Buggisch *et al.* 1999) indicate that the BGG is somewhat younger than earliest Ordovician. Palaeomagnetic data (Buggisch *et al.* 1994, 1999) also support a (probably Lower) Ordovician age for the BGG succession, on the basis of low palaeomagnetic inclination values. A revised stratigraphy of the Shackleton Range (Fig. 2), based on these new data, was published by Tessensohn & Thomson (1990).

The sediments of the BGG hitherto yielded no additional biostratigraphic data (Thomson & Weber 1995; Weber 1995). Although trace fossils are less suitable than body fossils for biostratigraphic purposes, the BGG ichnofauna described here shows some similarities with other typically Lower Palaeozoic (Cambro-Ordovician) trace fossil assemblages (see below), supporting the radiometric data for the age of the BGG.

## 2. Sedimentary facies and palaeoenvironment

The BGG consists mainly of a succession of red sandstones intercalated with minor conglomerates (therefore not indicated



| | South | | North | new evidence from |
|---|---|---|---|---|
| JURASSIC | tuffaceous pelites and arenites | | | K-Ar ages |
| ORDOVICIAN | | deformation | Blaiklock Glacier Group | palaeomagnetism<br>trace fossils<br>K-Ar ages |
| CAMBRIAN UPPER | | | | |
| CAMBRIAN MIDDLE | | | Haskard Highlands Fm. | |
| CAMBRIAN LOWER | | Mt.Wegener Formation | ? | Rb-Sr ages<br>K-Ar ages |
| LATE PRECAMBRIAN | Watts Needle Formation | Stephenson Bastion + Wyeth Heights Formations | | microfossils<br>K-Ar and Rb-Sr ages |
| PRECAMBRIAN | Read Group | | Stratton and Pioneers Groups | |

**Figure 2** Revised stratigraphy of the Shackleton Range, after Tessensohn and Thomson (1990), but updated based on new data from the 1994/95 EUROSHACK expedition.

in Fig.3), siltstone and mudstone layers. Based on sedimentological data (e.g. Buggisch *et al.* 1994), an idealised and simplified section of the Mount Gass outcrop of the lower BGG (MPF) is presented (Fig. 3).

The sediments of the BGG are essentially undeformed and show a large variety of sedimentary structures. Herringbone cross-bedding is common in the sandstones, which are interpreted as indicating a high-energy intertidal to supratidal environment. The sedimentological data, as well as the ichnological characteristics of the red beds, indicate a shallow marine (locally extremely shallow marine water, possibly a tide-dominated, freshwater-influenced estuary) palaeoenvironment. The trace fossil-rich lower BGG shows a shallow marine influence, according to the ichnotaxa present and the sedimentological characteristics. The sandstones frequently contain oscillation and interference ripples (Figs 4a, b) and convolute bedding structures. In several examples, the parallel oscillation ripples show characteristic crests (Fig. 4b), described by Seilacher (1982) as ‘spill-over oscillation ripples’, and interpreted as formed in the tidal zone on the top of (inactive) oscillation ripples covered by a thin layer of mud in very shallow receding water. These crests therefore indicate very shallow, relatively quiet water conditions (e.g. tidal ponds). The widespread occurrence of strong primary current lineations on some bedding planes also points to locally-intensive current activity (probably local channel activity). Other small-scale sedimentary structures (Fig. 4d), preserved on mud-covered surfaces, resemble ‘Kinneya’ (so-called ‘elephant skin structures’), which were interpreted by Seilacher (1982) as representing very shallow water conditions. ‘Kinneya’ are known from Precambrian to Recent marginal marine settings and are related to biogenically stabilised sediment surfaces (microbial mats), which became wrinkled by low energy currents in tidal ponds. Similar rill-like structures can be observed on modern flat sandy to muddy shores during the outgoing tide.

Furthermore, the marked reddish colouration of the sediments, particularly of the lower beds of the BGG, generally suggests deposition in an oxidising (partly subaerial) environment. Mudcracks frequently occur on the pelitic interbeds (Fig. 4c), indicating subaerial conditions with periodic desiccation phases. Rare, possible rain-drop impressions (Fig. 4e), support subaerial exposure, although the origin of these structures remains uncertain; similar knob-like structures were generated experimentally by Karcz *et al.* (1974) by fluid stressing of freshly deposited clay surfaces. On the other hand, these structures are generally preserved on surfaces that show no signs of any current activity. The variety of sedimentary structures, and the intercalated minor conglomerates, indicate that the BBG sedimentation occurred in a typical molasse facies related to the Ross orogeny, as described by Buggisch *et al.* (1994). Locally-occurring fresh water influence or brackish environments cannot be excluded.

Casts of crustacean body fossils and most of the trace fossils occur mainly on bedding sole surfaces of fine-grained red-coloured sandstones and pelitic interbeds. Mass occurrences of *Planolites*-type burrows are restricted to relatively thin (mica-rich) layers of siltstone, showing no other types of bioturbation. In no case are any of the trace fossils directly associated with sedimentary structures (i.e. mud cracks or rain-drop impressions) characteristic of sub-aerial deposition. The BGG ichnofauna contains palaeobathymetrically significant ichnotaxa (see below) that indicate, in accordance with the sedimentological data, a range of settings from extremely shallow water coastal (sub-littoral) to well-ventilated shallow marine shelf conditions.

## 3. Fauna and ichnofauna of the Blaiklock Glacier Group

The BGG assemblage contains the following fossils: (1) Circular to subcircular resting traces or impressions of unknown (probably soft-bodied, ?medusoid) organisms (some are probably pseudofossils); (2) *Planolites*-type bioturbation layers; horizontal and partly meandering burrows and trails of non-arthropod producers (e.g. *Gordia*, *Taphrhelminthoides* n. ichnogen., *Didymaulichnus*, *Palaeophycus*, and ?*Laevicyclus*), (3) Trackways, resting traces and scratch-marks of arthropods (e.g. *Asaphoidichnus*, *Monomorphichnus*, *Merostomichnites*, *Diplichnites*, and *Rusophycus*), (4) Horseshoe-shaped casts or impressions of empty bivalved arthropod carapace valves or arthropod-produced digging traces (e.g. *Selenichnites*), (5) Casts and convex hyporeliefs of bilobate ‘coffee-bean’-shaped carapaces of bivalved arthropods, some with vein-like impressions (i.e. body fossils), and (6) Impressions and casts of complete crustaceans showing two (partly ornamented) carapace valves separated by a dorsal hinge line, with partly preserved impressions of body segmentation and appendages, c. 5 to 12 cm long, here provisionally referred to (?leptostracan) crustaceans.

The bivalved arthropod body fossils (i.e. 5 and 6 above), which represent a hitherto-unknown arthropod assemblage, are not described in detail here. Their preservation (natural casts and moulds) shows various transitions to *Rusophycus*-like trace fossils (cubichnia), but many forms are so detailed that they cannot be regarded as trace fossils. They are therefore described here in open nomenclature, but will be the subject of a future study by the authors.

### 3.1. Biostratigraphic implications

Although trace fossils are less suitable than body fossils for biostratigraphic purposes, various studies have shown that ichnoassemblages can show characteristic large-scale patterns of composition throughout geological time (e.g. Seilacher 1970, 1992, 1994), which simply reflect the evolution of certain groups of trace makers with particular behavioural patterns. In this way, the fossil record of various infaunal and epifaunal invertebrates is quasi-parallel with the ichnological record. In a few cases, ichnotaxa (e.g. *Cruziana*) with characteristic morphologies have been used successfully as index fossils (e.g. Crimes 1968; Baldwin 1977b; Seilacher 1960, 1970, 1992, 1994; Fortey & Seilacher 1997) or have been related to a certain biostratigraphically important (trilobite) producers (e.g. Baldwin 1977a; Fortey & Seilacher 1997).

Apart from the crustacean fauna, the BGG ichnoassemblage shows similarities with some other Lower Palaeozoic ichnofaunas, for example from the Ordovician of Cincinnati (Osgood 1970), and the Lower Cambrian of southern Sweden (Jensen 1997). *Asaphoidichnus* is known from the Upper Ordovician of Cincinnati (Osgood 1970) and the Upper Cambrian Salt Range of Pakistan (Seilacher 1955). *Didymaulichnus* is known from the Upper Precambrian to the Lower Devonian, and is a typical member of Lower Palaeozoic marine ichnoassemblages. The BGG ichnoassemblage contains several ichnogenera that are exclusively Palaeozoic: *Monomorphichnus* and *Asaphoidichnus* are only known from Lower Cambrian to Devonian strata. *Beaconites* is a typical trace fossil of the Devonian; this occurrence in the BGG is therefore significant in that it is the earliest occurrence of this ichnotaxon. Therefore, the BGG ichnoassemblage resembles other typically Lower Palaeozoic shallow marine ichnofaunas (*Cruziana* ichnofacies), supporting the radiometric and palaeomagnetic age data (see above).

### 3.2. Palaeoenvironmental implications and producers

The composition of the BGG ichnoassemblage resembles other Lower Palaeozoic examples of the *Cruziana* ichnofacies (Mángano *et al.* 1996). According to Frey *et al.* (1990), the *Cruziana* ichnofacies is characteristic of a nearshore shelf environment (ca. 0 to 200 m water depth), although some elements (e.g. *Rusophycus*, *Cruziana*) can also occur in the very shallow (marginal marine) *Scoyenia* ichnofacies (Woolfe 1990). In tide-dominated settings the energy and ichnofacies gradient is opposite to that seen in wave-dominated shallow marine environments; the *Skolithos* ichnofacies tends to occur seaward of the *Cruziana* ichnofacies (Mángano *et al.* 1996, 2002). The absence of *Skolithos*-type trace fossils in the BGG ichnofauna therefore probably relates to an estuarine, tide-dominated environment. The abundant *Merostomichnites* trackways in the BGG further indicate an environmental range from the shallow marine *Cruziana* ichnofacies (e.g. Cooper & Romano 1982) to the limno-terrestrial *Scoyenia* ichnofacies (e.g. Frey *et al.* 1990; Woolfe 1990). In conclusion, the BGG ichnofauna represents a shallow, restricted environment intermediate between the *Cruziana* and *Scoyenia* ichnofacies.

The BGG ichnofauna is dominated by epifaunal trace fossils produced by mobile arthropods. Apart from the *Planolites* bioturbation horizons and rare ?*Laevicyclus* burrows, the BGG contains no other infaunal trace fossils. Although the BGG ichnofauna shows similarities to the *Cruziana* ichnofacies (see above), this does not imply that these trace fossils were produced by trilobites. Neither trilobites nor any true trilobite trace fossils (e.g. *Cruziana* ispp.) are known from the BGG. Indeed, the frequently occurring body fossils of crustaceans (see below), sometimes with body segmentation and appendages preserved, indicate that suitable taphonomic conditions prevailed for the preservation of arthropod body impressions. The BGG crustaceans may be regarded as suitable candidates for the producers of all of the arthropod trace fossils; they were relatively large arthropods with a vagrant benthic mode of life and variety of behaviours (i.e. crawling around on the substrate and digging into it), as evident by the variety of trace fossils.

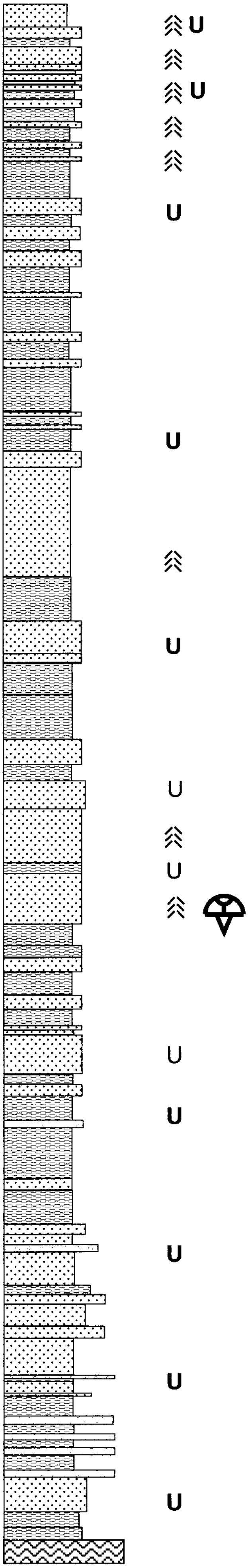


**Figure 3** Stratigraphy of the lower Blaiklock Glacier Group (Mount Provender Formation) at Mount Gass (locality 1) (approximately 800 m thick) showing the vertical distribution of non-arthropod trace fossils (U-icon), arthropod trace fossils (mostly trackways) (trackway-icon) and the lowermost position of arthropod body fossils (arthropod-icon). Modified from Buggisch *et al.* (1994).

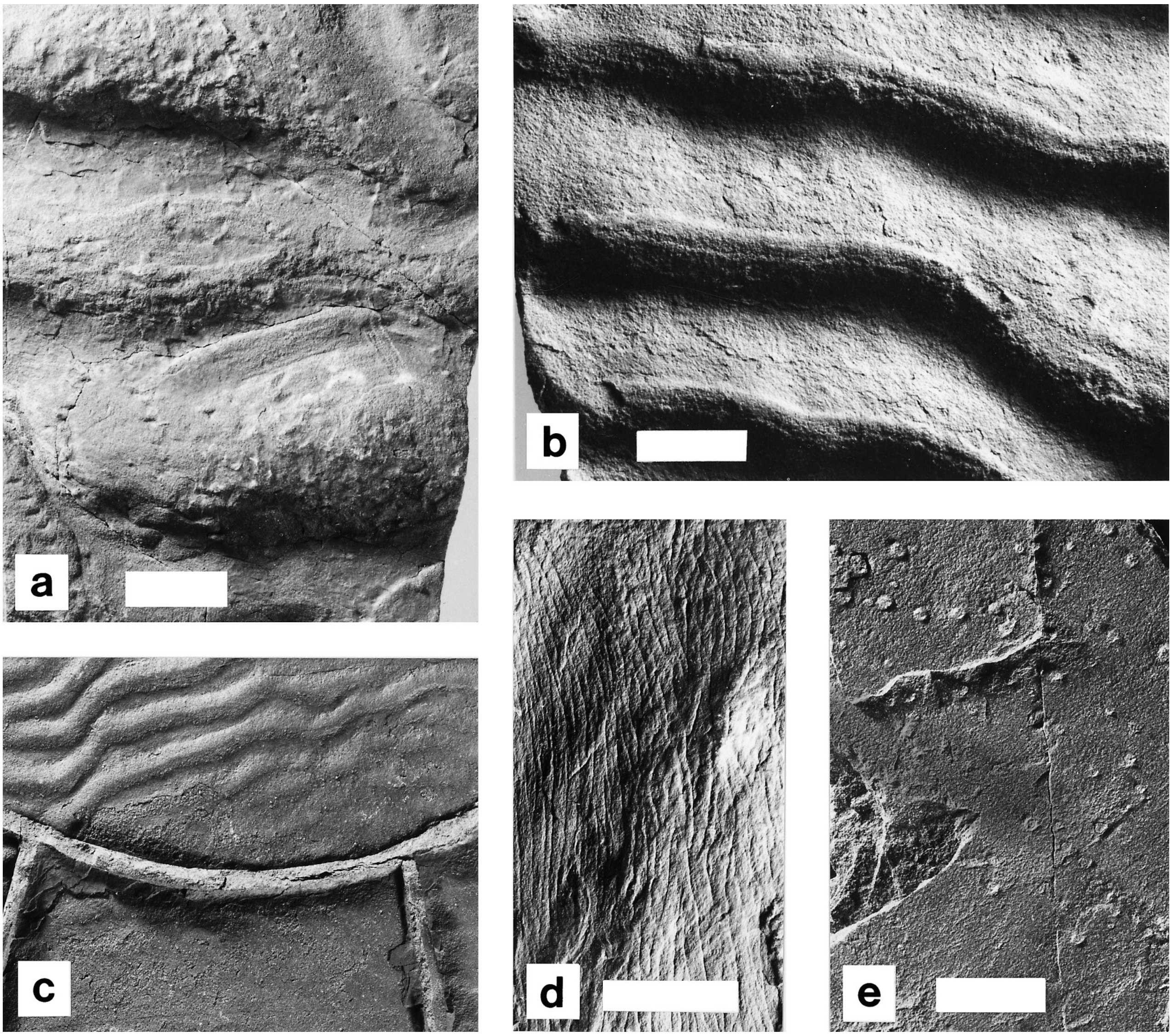


**Figure 4** Sedimentary structures: (a) Reticulate interference ripples; locality 1; (b) Parallel oscillation ripples showing "spill-over" ripple crests; locality 2; (c) Subsurface of sandstone slab showing parallel oscillation ripples and sand-filled mudcracks; locality 2; (d) 'Kinneya'-like rill marks; locality 1; (e) Subsurface of a siltstone slab showing probable rain-drop impressions; locality 1. Scale bars = 2 cm.

Although a number of the BGG arthropod ichnotaxa (e.g. *Beaconites* and *Diplichnites*) have been attributed to myriapod-like producers elsewhere (see below), their similar size to the BGG crustaceans (and other traces produced by them) could equally indicate a crustacean producer for these ichnotaxa. It is possible, however, that the body fossil assemblage is biased and some of these trace fossils were produced by other arthropods (e.g. myriapods). The BGG crustaceans are therefore assumed to be the producers of the bulk of the traces (especially the predominant *Merostomichnites*). Apart from the crustaceans the other ichnotaxa in the BGG indicates the presence of worms (e.g. *Gordia*, *Didymaulichnus*, *Planolites*, *Palaeophycus*, and ?*Laevicyclus*) and molluscs (e.g. *Taphrhelminthoides* n. ichnogen.).

Therefore, the lack of trilobites and other typically marine groups in the BGG indicates that a relatively low diversity fauna was responsible for producing the trace fossils. Other early marginal- to non-marine ichnoassemblages are interpreted as representing a low diversity of producers, for example the Paseky Shale (Early Cambrian) of the Czech Republic, interpreted as a restricted brackish lagoon setting (Mikuláš 1995). During the Cambrian, and ?Lower Ordovician, it appears that relatively few specialised invertebrate groups (e.g. arthropods and some molluscs) had developed the special adaptations and life styles required to inhabit euryhaline, tidal and freshwater influenced (brackish) coastal habitats, with oscillating water depth and episodic emergence. By the Middle Ordovician some animals developed amphibious life strategies to permanently occupy subaerial estuarine flats and freshwater ponds (Buatois *et al.* 1998).

### 3.3. Palaeobiogeographic implications

The BGG succession is stratigraphically equivalent to the Peninsula and Graafwater Formations (Ordovician) of the lower Table Mountain Group (TMG hereafter) of the Western Cape Province in South Africa. The BGG and TMG show similarities in their sedimentology (Buggisch *et al.* 1994, 1999) and components of their trace fossil assemblages. Although the Graafwater Formation was previously interpreted as an estuarine/tidal flat and shallow subtidal setting, particularly in the northern outcrop area (Rust 1977), the southern outcrop area has been reinterpreted as fluvial in origin, based on the sedimentary structures (Flemming 1988; Broquet 1992). Trace fossils from the southern part of the TMG include worm traces, meniscate horizontal burrows, '*Isopodichnus*'-like resting traces (cf. *Rusophycus*), *Monomorphichnus* scratch arrays

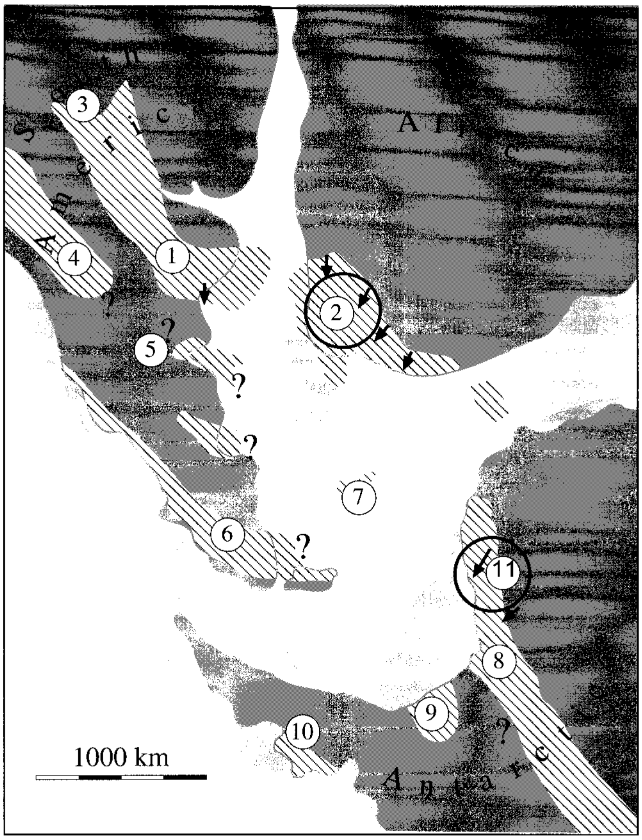


**Figure 5** Palaeogeographic reconstruction of western Gondwana during the Ordovician, showing the distribution of probable (1–11) and questionable (?) sedimentary basins: Dark shading, continent; Light shading, shelf; Diagonal shading, sedimentary basins. Arrows indicate main direction of sediment transport. Circles indicate similar sedimentology and ichnofauna. Key: 1, Ventana Basin; 2, Cape Basin; 3, Chaco-Pampeana Basin; 4, Pre- and W-Cordillera; 5, Valdes; 6, S Patagonia; 7, Falkland Islands; 8, Central W-Antarctica; 9, Ellsworth Mountains; 10, Thurston-Bear Islands; 11, Shackleton Range (BGG). Modified from Cobbold *et al.* 1986.

and small *Merostomichnites* trackways (Braddy & Almond 1999, fig. 5). In particular, the predominance of *Merostomichnites*-type traces in the BGG correlates with the TMG, indicating similar sedimentary and ecological conditions.

The similarities between the BGG and TMG successions is consistent with current palaeogeographic models which suggest a Lower Palaeozoic position of the TMG sedimentary basin close to the BGG shelf (e.g. Williams 1995). The TMG and BGG basins were both probably part of a larger Lower Palaeozoic west Gondwanan system of (intracratonic) sedimentary basins (Fig. 5). They became filled (locally at high rates) during the Palaeozoic with (late- to post-orogenic) molasse sediments from the surrounding highlands of the pan-African/Ross- orogenies of southern Africa and west Antarctica (Buggisch *et al.* 1994, 1999). Large braided river systems produced widespread fluvial sedimentation that locally intercalated with coastal and marine shelf deposits.

## 4. Systematic ichnology

The material described herein (in alphabetical order) represents the best preserved specimens, which were collected by BW, mainly from the lower MPF of the lower BGG, during the EUROSHACK expedition to the Shackleton Range in 1994/95. These specimens are held at the Museum für Naturkunde, Humboldt University, Berlin, Germany (MB-W- and MB-A- numbers), and the British Antarctic Survey, Cambridge, UK (BASC numbers). Additional material (not figured) is held in the collection of the Bundesanstalt für Geologie und Rohstoffe, Hannover (ES-BW- numbers). The total number of collected specimens available for the present study is given in square brackets under "Material and locality". Considerably more material remains *in situ* at the localities, which are here numbered as follows: (1) Mount Gass; (2) Dragons Back; and (3) Honnywill Peak. Precise locality details (Fig. 1) may be obtained from Buggisch *et al.* (1995a, 1995b). Trackways are described according to the terminology of Braddy (2001).

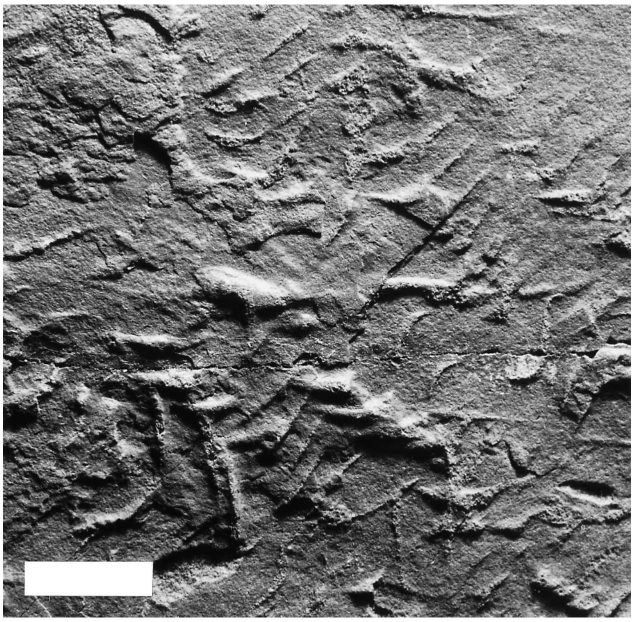


**Figure 6** *Asaphoidichnus* isp.; locality 2: Hyporelief, showing numerous overprinted trackways. In places bifid termination of tracks are evident. MB-W-845. Scale bar = 2 cm.

Ichnogenus *Asaphoidichnus* Miller, 1880
*Asaphoidichnus* isp.
(Fig. 6)

**Material and locality**. [2]. MB-W-845 (Fig. 6); locality 2.

**Description**. MB-W-845, preserved in positive hyporelief, consists of relatively wide (c. 7–9 cm) asymmetrical, relatively straight trackways composed of parallel rows of bifid or trifid, curved or angular tracks, each about 2 cm long, orientated transverse to the mid-line (Fig. 6). These are overprinted by many short scratch marks, each about 1–2 cm long, also orientated transverse to the trackway axis.

**Discussion**. *Asaphoidichnus* is rare in the BGG. Some specimens show *Asaphoidichnus*, *Monomorphichnus*, and *Dimorphichnus*-like morphologies grading into each other. We refer this material to *Asaphoidichnus*, however, due to the bifid and trifid form of the tracks.

Ichnogenus *Beaconites* Vialov, 1962 (emended by Keighley & Pickerill 1994)
*Beaconites* cf. *antarcticus* Vialov, 1962
(Fig. 7)

**Material and locality**. [1]. MB-W-776 (Fig. 7); locality 2.

**Description**. Poorly preserved as positive hyporelief, in a coarse sandstone. Large, horizontal, septate endichnial burrow, consisting of meniscate back-filled packets, concave relative to presumed movement direction. Trace gradually fades out across the bedding plane. Length 9 cm, maximum width

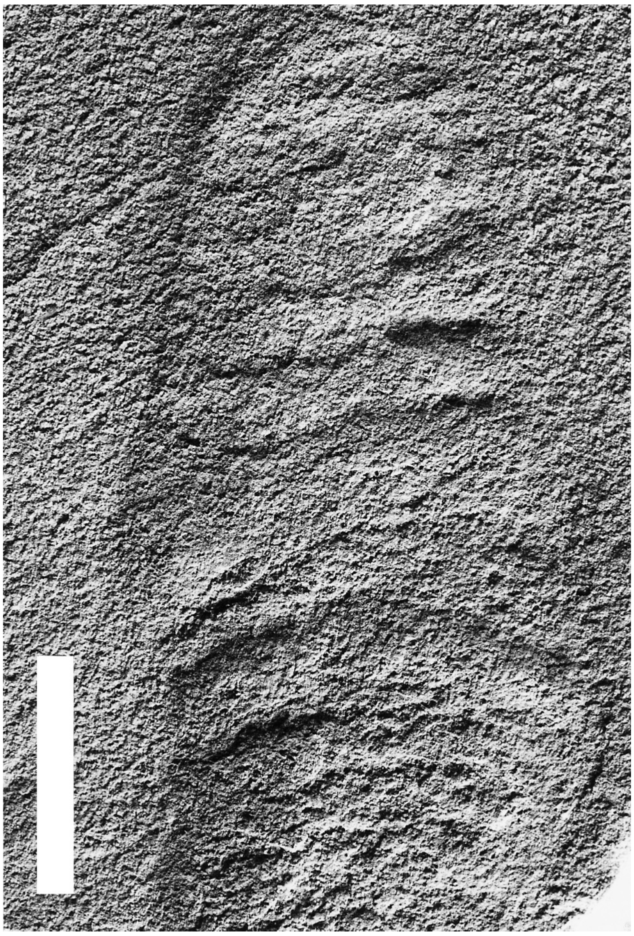


**Figure 7** *Beaconites* cf. *antarcticus*; locality 2: Poorly preserved positive hyporelief in coarse sandstone. MB-W-776. Scale bar = 2 cm.

3 cm, distance between back-filled packets 5–6 mm. In places a lateral wall, 2–3 mm wide, is evident as a depression at the edge of the burrow.

**Remarks**. *Beaconites* was first described by Vialov (1962) from the Devonian of Victoria Land, Antarctica, where it occurs in heavily bioturbated horizons. Keighley & Pickerill (1994) discussed the relationships of backfilled burrows, with particular reference to *Beaconites*, *Taenidium* and *Anchorichnus* (see also Goldring & Pollard (1995) for opposing view). Based on Keighley & Pickerill's review, the BGG material is here assigned to *Beaconites* cf. *antarcticus*, due to the presence of a (faint) marginal wall and the form of the infill. The BGG material is at the smaller end of the size range recorded for *Beaconites*, and generally differs in the larger thickness of meniscate packets.

**Discussion**. *Beaconites* has been ascribed to many possible producers, including arthropods or holothurians (Häntzschel 1975), polychaete worms (Gevers *et al*. 1971), unknown "desert dwelling arthropods" (Rolfe 1980) and "myriapod-like arthropods" (Bradshaw 1981). Other authors have suggested vertebrates (e.g. lungfish, reptiles or amphibians) as producers of younger examples of *Beaconites*. Trewin & McNamara (1995) noted two types of *Beaconites* from the Tumblagooda ichnofauna of Australia: 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 (i.e. arthropleurids). Indeed, Gevers *et al*. (1971) recorded trackways that occasionally ended in small rounded terminations. Similar rounded terminations to myriapod trackways were reported by Braddy (1995) from the Robledo Mountains ichnofauna (Lower Permian) of southern New Mexico, and interpreted as representing the point where the animal (myriapod) began burrowing beneath the substrate. It is possible that many different producers are responsible for *Beaconites*-type traces in the geological record. In the BGG, the association of this rare trace fossil with other crustacean-produced traces fossils and body fossils (see below) may imply a crustacean producer, although there is little correlation between their morphology.

Numerous occurrences of *Beaconites* ispp. have been reported from the ?Late Ordovician (Trewin & McNamara 1995) to the Carboniferous (Graham & Pollard 1982), although it is particularly frequent in the Old Red Sandstone (Devonian), for example from Wales (e.g. Allen & Williams 1981) and Ireland (e.g. Brück 1987). Allen & Williams (1981) described large *Beaconites antarcticus* from a sandstone succession in South Wales, representing a fluviatile-lacustrine Devonian coastal palaeoenvironment. The sedimentology of this occurrence led them to the assumption that the *Beaconites* animal lived in or near active river channels, in a permanently moist and sandy environment. The BGG specimens occur in a coarse sandstone layer, without any other bioturbation, in contrast with Vialov's (1962) observation that *Beaconites* occurs in highly bioturbated horizons. The palaeoenvironment of the Welsh (Devonian) *Beaconites antarcticus*, described by Allen & Williams (1981) as a 'coastal mudflat, with mixed tidal and river influence' agrees with the depositional environment interpreted for the BGG.

It is possible that the BGG specimen represents an early (Ordovician) ancestral form of the subsequently emerging Devonian forms of *Beaconites antarcticus*, which had a slightly different morphology. The BGG occurrence is the earliest example of *Beaconites* in the fossil record. As it is a unique specimen, we only refer this material questionably to *Beaconites* cf. *antarcticus*.

### Ichnogenus *Didymaulichnus* Young, 1972
### *Didymaulichnus* isp.
### (Fig. 8)

**Material and locality**. [3]. ?MB-W-828; locality 1. ES-BW 43/34a, b, MB-W-777 (Fig. 8); locality 2.

**Description**. Bilobed trails (with a slightly curved course), poorly preserved in positive hyporelief, width 15–25 mm, consisting of two flat lobes, each ca. 2 mm high and 5–10 mm wide, sloping distally, separated by a steep medial groove, width 2–3 mm.

**Discussion**. *Didymaulichnus*, first described by Young (1972) from the Lower Cambrian of SW Canada, consists of simple, horizontal, non-ornamented, slightly meandering bilobed trails, with typically flat lobes separated by a steep median furrow, as in the BGG examples. Häntzschel (1975) discussed the possible synonymy of this form with "Rouaultia" (nomen invalidum *sensu* Häntzschel, 1965), and the "molluscan trails" described by Glaessner (1969) from the Precambrian of Australia. *Didymaulichnus* ranges from 3 to 30 mm wide (Crimes & Anderson 1985; Fritz & Crimes 1985); "Rouaultia" is 25–30 mm wide and Glaessner's "molluscan trails" are 15–20 mm wide. Trewin & McNamara (1995) noted small (3–9 mm wide) *Didymaulichnus* from the Tumblagooda Sandstone of W Australia. This ichnogenus is also known from the Cretaceous of James Ross Island, northeast of the Antarctic Peninsula (Buatois & Lopez Angriman 1992). The ichnospecific assignment of the BGG material is uncertain due to its poor preservation, although this represents the first occurrence of *Didymaulichnus* from the Palaeozoic of Antarctica. Glaessner (1969) and Häntzschel (1975) suggested a molluscan producer for these traces, whereas Trewin & McNamara (1995) favoured an arthropod producer.

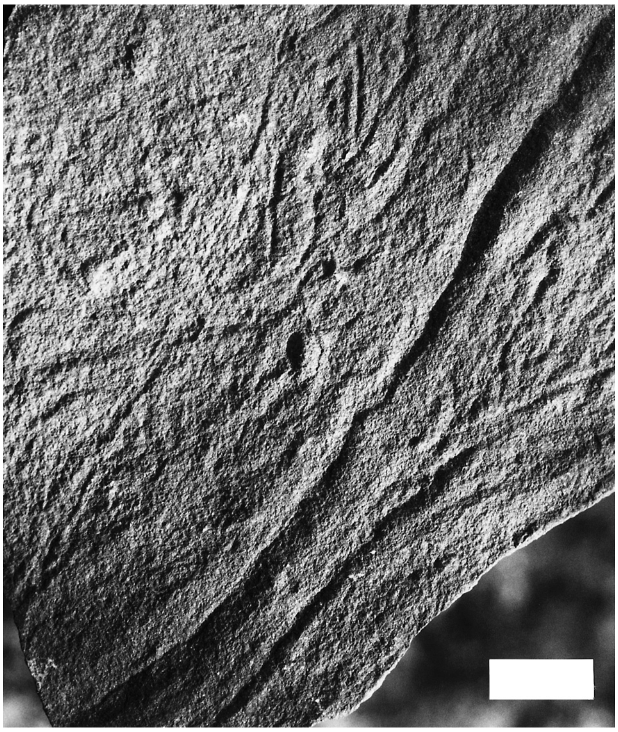


**Figure 8** *Didymaulichnus* isp.; locality 2: MB-W-777. Scale bar = 2 cm.

### Ichnogenus *Diplichnites* Dawson, 1873
### *Diplichnites* isp.
### (Fig. 9)

**Material and localities**. [4]. MB-W-779 (Fig. 9a), MB-W-782 (Fig. 9b); locality 1. MB-W-780 (Fig. 9c), MB-W-781 (Fig. 9d); locality 3.

**Description**. Trackways, preserved in hypo- and epirelief, c. 1–2 cm wide, consisting of two parallel rows of straight or slightly curved, smooth oval ridges or slightly elongated tracks, 0·5–2 mm wide, orientated transverse or oblique to the mid-line, distributed in an opposite or staggered arrangement. In some specimens series of nine tracks are apparent (Figs 9a, c).

**Discussion**. *Diplichnites* is a relative common Palaeozoic trace fossil, which has been described from many localities representing marine settings, and is generally attributed to trilobites, for example the Precambrian/Cambrian transition of East Greenland (Cowie & Spencer 1970), the Cambrian/Ordovician transition of NW Spain (Baldwin 1977b) and of Wales (Crimes 1970); the latter is attributed to olenid trilobites, showing transitional forms between *Diplichnites* and *Cruziana*. Although Dawson's (1873) original description was based on Westphalian material from alluvial channel/floodplain deposits, *Diplichnites* has been widely used for trilobite trackways (e.g. Seilacher 1955). It could be argued, however, that this trace type should be restricted to non-trilobite traces (e.g. Briggs *et al*. 1979, 1984), although this distinction is sometimes difficult to make (and producer-related inferences for ichnotaxonomy should be avoided).

*Diplichnites* is generally ascribed to myriapod- or arthropleurid-produced trackways, for example from subaerial-lacustrine units within the Borrowdale Volcanic Group (Upper Ordovician; Caradoc) of the English Lake District (together with *Diplopodichnus*), representing one of the earliest occurrences of non-marine arthropod trails (Johnson *et al*. 1994), and the Clam Bank Formation (Upper Silurian) of Newfoundland (Wright *et al*. 1995).

The BGG *Diplichnites* shows no transitional forms to *Cruziana*-type trace fossils. Indeed, *Cruziana* is absent from the whole BGG section. There is no indication of trilobites in the BGG fauna (see above). Also, the BGG *Diplichnites* trackways are not composed of a dense array of tracks, as in *Diplichnites gouldi* (see Gevers *et al*. 1971; Gevers 1973; Gevers & Twomey 1982; Smith *et al*. 2003), attributed to myriapodous producers. The BGG *Diplichnites* may therefore be attributed to another producer. Given the abundance of crustacean-produced ichnotaxa in the BGG ichnofauna, and the fact that series of about nine tracks are evident in some of these specimens (i.e. series of up to twelve tracks occur in the *Merostomichnites* trackways), it is possible that small crustaceans were the producers. Although myriapodous forms may have been present, they are not preserved in the BGG as body fossils.

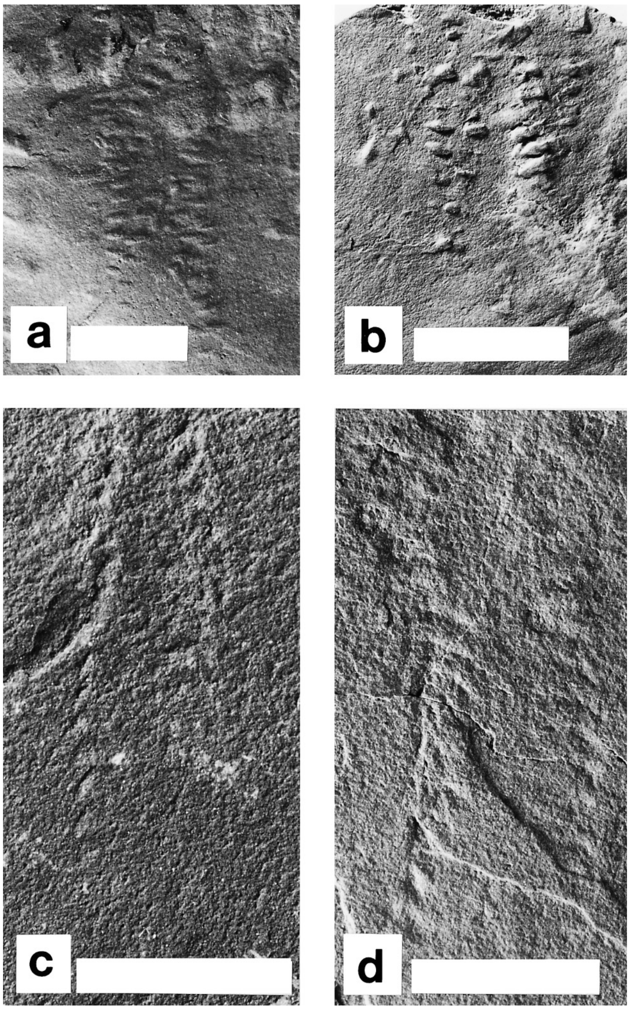


**Figure 9** *Diplichnites* isp. (a) MB-W-779 (hyporelief); locality 1; (b) MB-W-782 (hyporelief); locality 1; (c) MB-W-780 (epirelief); locality 3; (d) MB-W-781 (epirelief); locality 3. Scale bars = 2 cm.

### Ichnogenus *Gordia* Emmons, 1844
### *Gordia* cf. *arcuata* Książkiewicz, 1977
### (Fig. 10)

**Material and localities**. [2]. MB-W-783 (Fig. 10); locality 2. ES-BW 41/80; locality 1. More material remains *in situ* at localities 1 and 2.

**Description**. Several self cross-cutting burrows, preserved in positive hyporelief, composed of thin, 2–3 mm wide, unbranched, non-ornamented, worm-like horizontal burrows, which cross each other in wide loops, 3–8 cm in diameter. One burrow is about 20 cm long. A second, slightly smaller burrow (ES-BW 41/80) displays more tightly-crossing loops.

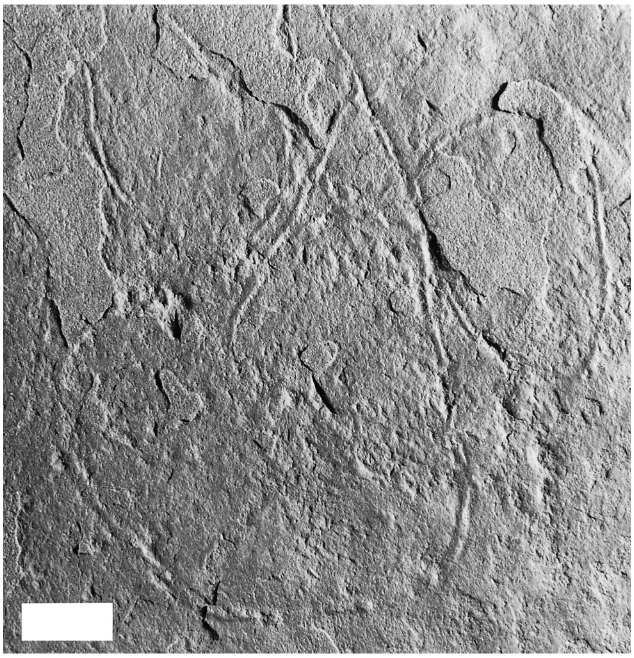


**Figure 10** *Gordia* cf. *arcuata*: Hyporelief, siltstone slab with several self cross-cutting looping burrows; locality 2. MB-W-783. Scale bar = 2 cm.

**Remarks**. Since the type ichnospecies (*Gordia marina* Emmons, 1844) was described, other ichnospecies have been established (e.g. *G. molassica* Heer, 1865 (although probably synonymous with *G. marina* (Fillion & Pickerill 1990), and *G. arcuata* Książkiewicz, 1977). Other *Gordia*-type traces have been left in open nomenclature (e.g. *Gordia* isp. A Geyer & Uchman, 1995; *Gordia* isp. Crimes & Anderson, 1985). Important contributions to the ichnotaxonomy of *Gordia* were published by Książkiewicz (1977), Fillion & Pickerill (1990) and Pickerill & Peel (1991). The closely related ichnogenus *Helminthopsis* Heer, 1877 was considered distinct from *Gordia* by Crimes & Anderson (1985), in that *Helminthopsis* is usually less than 1 mm wide, and the burrows do not cross (i.e. no loops). *G. arcuata*, from the Oligocene flysch of Poland, was considered distinct from *G. molassica* by Książkiewicz (1977) because of the more regular form of the loops in *G. arcuata*. The BGG material is most similar to *G. arcuata* but shows some similarities to *Gordia* isp. A (Geyer & Uchman 1995), from the Late Proterozoic Nama Group of SW Africa. The restricted amount of material available from the BGG precludes a reliable ichnospecific assignment.

**Discussion**. The producers of *Gordia* have been variously interpreted as a small polychaete worm (Książkiewicz 1977), or other mobile sediment feeder which fed on nutrient-rich layers within the substrate (Geyer & Uchman 1995). The environmental range of *Gordia* is relatively broad; it is recorded from deep to very shallow water settings (e.g. Orr 1996; Crimes & Anderson 1985). *Gordia* has been characterised by Geyer & Uchmann (1995) as a facies-crossing form with a wide stratigraphic range, from the Upper Vendian through to the Holocene.

### Ichnogenus ?*Laevicyclus* Quenstedt, 1879 (emended by Seilacher, 1955)

?*Laevicyclus* isp.
(Fig. 11)

**Material and locality**. [6]. MB-W-846 (Fig. 11), MB-W-847; locality 1. Several additional specimens occur *in situ* in abundant silty layers at locality 1.

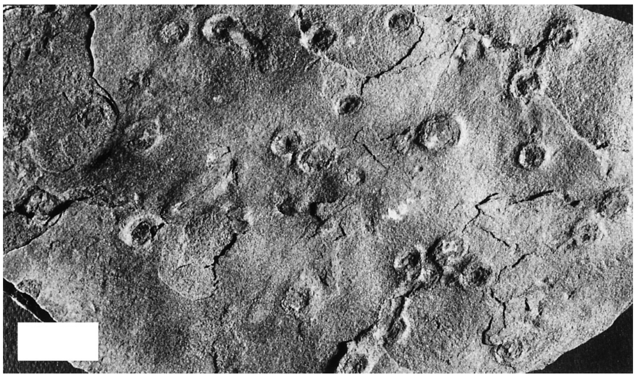


**Figure 11** ?*Laevicyclus* isp.: (a) MB-W-846; locality 1. Shows circular walls and central "canal" preserved as a small pit in positive hyporelief. Scale bar = 2 cm.

**Description**. Faintly preserved short (c. 5–10 mm long) vertical cylindrical burrows, about 5–15 mm in diameter. Cross-sections through the burrows (on the bedding planes) show concentric circles (i.e. circular walls) and a central 'canal' generally preserved as a small central pit in positive hyporelief.

**Discussion**. These burrows may be distinguished from similar (sedimentary) structures in the BGG succession (e.g. rain-drop impressions, which show no vertical extension) and the short, smaller cross-sections of flat *Planolites*-type burrows (which show a constant thickness in cross-section) as they show varying burrow diameters. Similarly, other vertical burrow-type ichnotaxa, such as *Monocraterion*, *Skolithos*, or *Cylindrichnus* show much longer vertical burrows, or are gently curved. Seilacher (1955) suggested that *Laevicyclus* probably represents a feeding burrow comparable to dwelling shafts and scraping circles of recent annelids (e.g. *Scolecolepis*). Because of the limited material, the ichnospecific assignment of the BGG specimens remains questionable.

### Ichnogenus *Merostomichnites* Packard, 1900

**Remarks**. *Merostomichnites* is an arthropod trackway, consisting of two parallel rows of subcircular to spindle-shaped tracks, each with between three and seven scratch marks, which are orientated parallel to the mid-line. *Merostomichnites* is known from Cambrian to Triassic, marine (coastal) to limnic shallow water environments. *Merostomichnites* is a misnomer as it was assumed by early workers to have been produced by merostomes, although its morphology is unlike typical eurypterid (e.g. *Palmichnium*) or xiphosuran (e.g. *Kouphichnium*) trackways. Størmer (1934) also considered that Palaeozoic *Merostomichnites* were produced by eurypterids (see also Hanken & Størmer 1975), although suggested that Triassic occurrences were probably produced by phyllopod crustaceans (see Häntzschel 1975).

The BGG material supports a crustacean producer in that no eurypterids, nor traces of their activity, are known from the BGG, whereas body fossils and resting traces of (?leptostracan) crustaceans are relatively abundant and of an appropriate size. *Merostomichnites* constitutes the majority of the arthropod traces from the BGG ichnofauna. Two different ichnospecies are recognised from the BGG: most are assigned to *M*. cf. *strandi* Størmer, 1934, but another type with thinner tracks, more tracks per series (c. 10 to 12) and a larger external:internal width ratio (>3) is assigned to a new form, *Merostomichnites gracilis* n. ichnosp.

**Figure 12** *Merostomichnites* cf. *strandi*: Well-preserved specimen, showing series of six spindle-shaped, striated tracks. MB-W-784; locality 2. Scale bar = 2 cm.

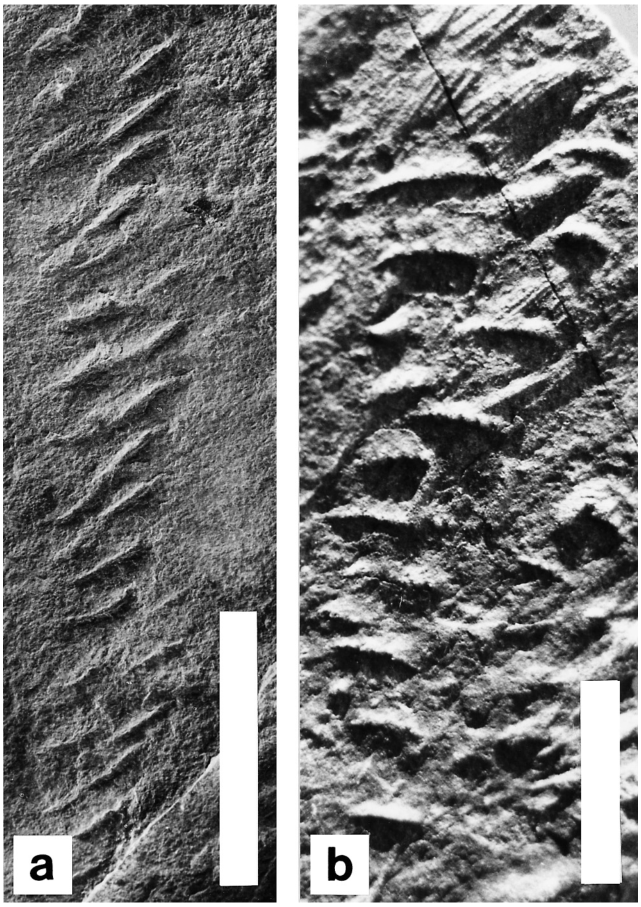


**Figure 13** *Merostomichnites gracilis*: (a) Holotype, MB-W-793; locality 1. Showing thin, linear, elongate tracks; (b) Paratype, MB-W-785; locality 2. Showing striations on tracks grading into scratch-bundles. Scale bar = 2 cm.

### *Merostomichnites* cf. *strandi* Størmer, 1934
(Fig. 12)

**Material and localities**. [11]. MB-W-784 (Fig. 12), MB-W-792, MB-W-834, ES-BW 43/45, ES-BW 43/47; locality 2. MB-W-782, ES-BW 41/89, ES-BW 41/91, ES-BW 41/92, ES-BW 41/22; locality 1.

**Description**. Trackways, mainly preserved as positive hyporeliefs, with opposing oval-curvilinear tracks generally transverse (in some cases inclined) to the mid-line, external width 20–58 mm (average 34 mm), internal width 10–28 mm (average 17 mm). Most of these trackways consist of two parallel rows of thick, spindle-shaped tracks, which show scratch marks orientated parallel to the trackway axis. Series are rarely clearly evident (because the rows are parallel), but some specimens (e.g. MB-W-784; Fig. 12) show series of about six tracks.

**Discussion**. We attribute these trackways to *M.* cf. *strandi*, because of their similarity to Størmer's (1934) material. They show relatively broad, club-shaped or oval tracks and a relatively low external width:internal width ratio (<3).

### *Merostomichnites gracilis* n. ichnosp.
(Fig. 13)

**Etymology**. Name denotes the thin track shape, consisting of thin, linear tracks.

**Material and localities**. [5]. Holotype, MB-W-793 (Fig. 13a); locality 1. Paratypes, MB-W-785 (Fig. 13b), ES-BW 43/21; locality 2. ES-BW 41/97; locality 1. ES-BW H4; locality 3.

**Diagnosis**. *Merostomichnites* consisting of long, thin, linear tracks, with several scratch-marks along each track. Tracks generally inclined to the trackway axis, distributed opposite. External:internal width ratio greater than 3. Series of 10–12 tracks may be evident.

**Description**. Trackways, mainly preserved as positive hyporeliefs, with opposing long, thin, linear tracks generally inclined to the mid-line. External width 20–65 mm (average 36 mm). Internal width 6–21 mm (average 10 mm). Most of these trackways consist of two parallel rows of thin linear tracks, therefore series are rarely evident. MB-W-793 (holotype) is one-sided, although shows inclined series of 10–12 tracks (Fig. 13a). Individual tracks show several short scratch-marks, although they may grade into scratch-bundles composed of about five linear marks, orientated oblique to the mid-line (Fig. 13b).

**Remarks**. *Merostomichnites* is widely used to denote arthropod trackways, although most ichnospecies should be assigned to other ichnogenera; only *M. beecheri* and *M. strandi* are considered valid ichnospecies (see Keighley & Pickerill 1998, for review). *Merostomichnites gracilis* is distinguished from these ichnospecies by the trackway proportions (i.e. external:internal width ratio >3), the greater number (10–12) of tracks per series, and the thinner, linear form of the tracks.

### Ichnogenus *Monomorphichnus* Crimes, 1970
### *Monomorphichnus lineatus* Crimes *et al.*, 1977
(Fig. 14)

**Material and localities**. [5]. BASC Z.1363.5 (Fig. 14a), ES-BW 43/36; locality 2. ES-BW 41/3, BS-BW 41/1, MB-W-805 (Fig. 14b); locality 1.

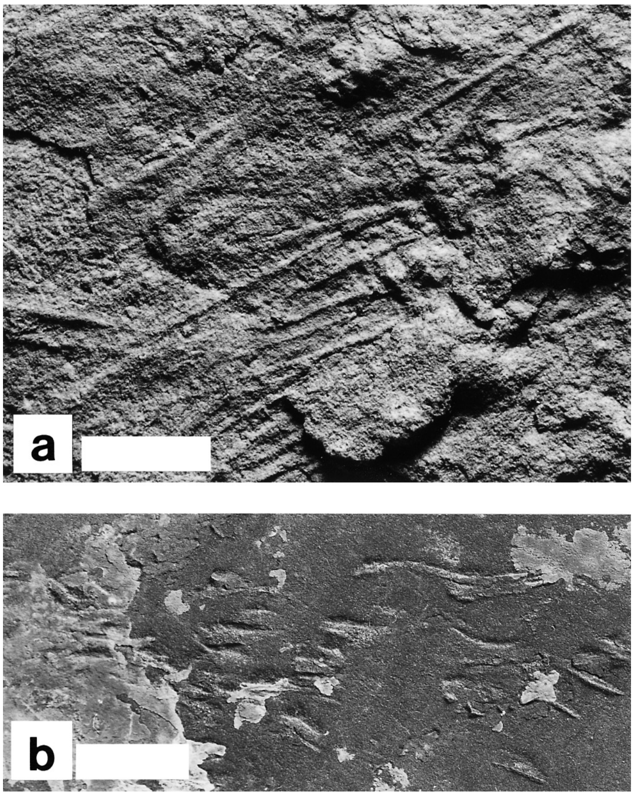


**Figure 14** *Monomorphichnus lineatus*: (a) BASC Z.1363.5; locality 2. Parallel rows of straight thin scratch marks, in positive hyporelief; (b) MB-W-805; locality 1. *Monomorphichnus* cf. *semilineatus*. Irregularly-distributed semi-parallel, slightly undulatory scratch marks. Scale bars = 2 cm.

**Description**. Parallel rows of decimetre-long, generally straight, thin scratch marks, mainly preserved in positive hyporelief. The number of the scratch marks per 'bundle' (c. 10) probably relates to the number of walking legs the arthropod producer possessed. MB-W-805 (Fig. 14b) is a transitional form with *M*. cf. *semilineatus* Mikuláš 1995 (i.e. irregularly distributed rows of semi-parallel, in places slightly undulatory scratch marks; faintly preserved bifid imprints on some of the scratch marks resemble those in *Asaphoidichnus*). One other (very faint) specimen (ES-BW 41/3) shows possible bifid scratch marks (cf. *M. bilineatus* Crimes, 1970).

**Discussion**. *Monomorphichnus* is a very common Palaeozoic arthropod trace fossil-type, with a wide stratigraphic and geographic range. Seilacher (1985) has suggested that it may be synonymous with *Dimorphichnus*. Crimes (1970) suggested that *Monomorphichnus* is related to a swimming-foraging behaviour in trilobites. A slightly sinuous *Monomorphichnus* was described from the Lower Cambrian Paseky Shale by Mikuláš (1995), and attributed to the enigmatic arachnomorph arthropod *Kodymirus*, from the same succession. A relationship to benthic arachnomorphs is indeed convincing, but by no means exclusive. Similar swimming-foraging and anchoring behaviour likely occurred in other benthic arthropods (e.g. crustaceans). Given the lack of any evidence for trilobites in the BGG, these *Monomorphichnus* are attributed to similar behaviour in the BGG crustaceans. It is also not clear whether these trace fossil types represent purely behavioural variations; passive movements of an arthropod by waves, especially when swimming in very shallow water, could easily transform straight scratch marks (e.g. *M. lineatus*) into the sinuous undulatory scratch marks (e.g. *M. semilineatus*).

**Figure 15** *Palaeophycus tubularis*. MB-W-832; locality 1. Positive hyporelief of straight, long, mostly collapsed burrows preserved on a sandstone-mudstone interface. Scale bar = 2 cm.

### Ichnogenus: *Palaeophycus* Hall, 1847
### *Palaeophycus tubularis* Hall, 1847
(Fig. 15)

**Material and localities**. [4]. MB-W-811, MB-W-832 (Fig. 15); locality 1. Additional (uncollectable) material remains *in situ* at localities 1 and 2.

**Description**. Relatively long, straight to slightly curved, essentially horizontal, cylindrical to subcylindrical-shaped burrows cross-cutting each other and covering bedding planes in high abundance. Traces are 1–5 mm wide; partly collapsed burrows also occur. Mainly preserved in positive hyporelief on sandstones overlying thin mudstones. The material of the burrow fill is the same as the surrounding matrix. The walls of the burrows are smooth.

**Discussion**. see *Planolites*.

### Ichnogenus: *Planolites* Nicholson, 1873
### *Planolites montanus* Richter, 1937
(Fig. 16)

**Material and localities**. [9]. MB-W-825 (Fig. 16), MB-W-823, ES-BW 41/63, ES-BW 41/25–27, ES-BW 43/9; locality 1. ES-BW 43/44; locality 2. Additional material (uncollectable big slabs) remain *in situ* at localities 1 and 2 (one of the most common traces in the BGG ichnofauna).

**Description**. Small (c. 1–3 mm wide) straight or gently curved, unbranched, unornamented, inclined (low angle to horizontal or slightly curved) back-filled burrows (Fig. 16). Cross-section of the burrows is circular, subcircular or flattened (collapsed). Burrows preserved in positive hyporelief or rarely furrow-shaped negative epirelief (collapsed and eroded burrows). Sediment filling the burrows differs from the surrounding matrix. Very abundant occurrence in relatively thin

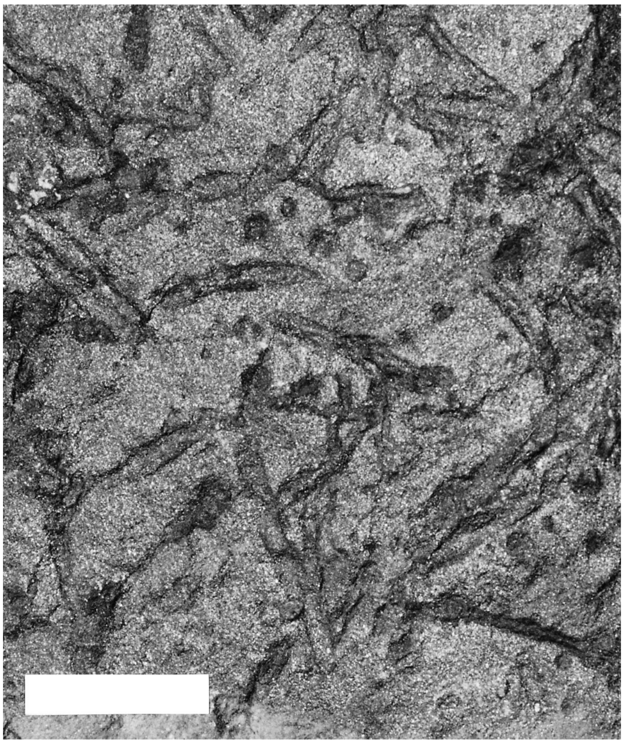


**Figure 16** *Planolites montanus*. MB-W-825; locality 1. Mica-rich siltstone layer showing slightly U-shaped short and collapsed burrows. Burrow fill differs from surrounding rock matrix. Scale bar = 2 cm.

(5–15 mm thick) mica-rich, sometimes intensely bioturbated (*Planolites*) beds. Never associated with any other trace fossil types.

**Remarks**. *Planolites* and *Palaeophycus* are very common trace fossils known from many ichnoassemblages ranging from the Precambrian to the Holocene. Due to its simple morphology, *Planolites* has been easily confused with other simple burrows, especially *Palaeophycus*. The criteria for distinguishing *Planolites* and *Palaeophycus* have been discussed by several workers (e.g. Osgood 1970; Pemberton & Frey 1982; Fillion 1989; Fillion & Pickerill 1990; Keighley & Pickerill 1995; Jensen 1997). As mentioned by Osgood (1970), and later discussed by Pemberton & Frey (1982), these ichnotaxa may be distinguished by the nature of their burrow fill. We follow the criteria given by Pemberton & Frey (1982) to distinguish *Planolites* from *Palaeophycus*: *Planolites* is a back-filled structure produced by an infaunal and sediment-feeding worm-like animal. Richter (1937) showed that in Carboniferous examples of *Planolites montanus*, the sediment-feeding animal selectively digested the substrate and back-filled the burrow with the non-digestible remains. The selective digestion of the substrate, together with syn- and post-sedimentary effects, result in the typical *Planolites*-type trace in which the trace fill is clearly different from the surrounding sediment (Fig. 16). Pemberton & Frey (1982) provided an ichnotaxonomic review of *Planolites*, which recognised only three valid ichnospecies: *P. montanus* Richter, 1937, *P. annularis* Walcott, 1890 and *P. beverleyensis* Billings, 1862, each characterised by their shape and size.

In contrast, in *Palaeophycus* the material within the burrow fill is the same as that outside, indicating secondary passive filling of a simple furrow-shaped burrow from overlying sediment. *Palaeophycus* therefore represents simple, probably slightly stabilised, open tunnel-shaped dwelling burrows of an epibenthic producer, preserved simply by the passive infilling of sediment into the burrows. Jensen (1997), however, was critical of this simple taxonomic approach as no Recent example is known which compares with any representative of one of the huge amount of fossil *Palaeophycus*-*Planolites*-type traces which occur in the geological past. The simple morphology and extremely wide stratigraphic range of these trace types indicates different producers of *Palaeophycus*-*Planolites*-type traces through geological time, as many different small worm-like animals (probably very different taxa) could produce such simple burrows.

**Discussion**. In the BGG, these intensive bioturbation horizons ('*Planolites*-*Palaeophycus* Complex' *sensu* Pemberton & Frey, 1982) are especially common at localities 1 and 2. Based on the criteria of Pemberton & Frey (1982), the bulk of these trace fossils may be assigned to *Planolites montanus*. *Palaeophycus*-type traces are relatively rare. Both trace fossil types differ in their shape and size, and never occur together in the same sedimentary environment. This may indicate that two different (taxonomic) producers, with different life styles, were responsible for these two trace fossil types. The mass occurrence of *Planolites montanus* in irregularly distributed thin, laterally extensive layers (bioturbation horizons) may be explained by local and occasional (storm-related) flood events which resulted in locally increased sedimentation rates. Rapid deposition of larger amounts of fine sediment is usually fatal to small benthic organisms. Such nutrient-rich layers of decomposing remains of organisms are very attractive to opportunistic infaunal scavengers, which would have dominated these habitats for a relatively short period.

### Ichnogenus: *Rusophycus* Hall, 1852

**Remarks**. This characteristic arthropod resting trace fossil (cubichnia) is a typical element of the *Cruziana* ichnofacies, and has been shown to intergrade, on occasion, with *Cruziana* (repichnia), representing different behavioural patterns (digging and resting versus active crawling) of their arthropod producer. *Rusophycus* was assumed to be the resting trace of benthic trilobites, but Birkenmajer & Bruton (1971) demonstrated that certain *Rusophycus* ispp. could also be produced by representatives of Gastropoda, Polychaeta and other (non-trilobite) arthropods (e.g. Phyllopoda). Following this interpretation, several smaller and heart-shaped *Rusophycus* ispp. are presumably not trilobite-produced.

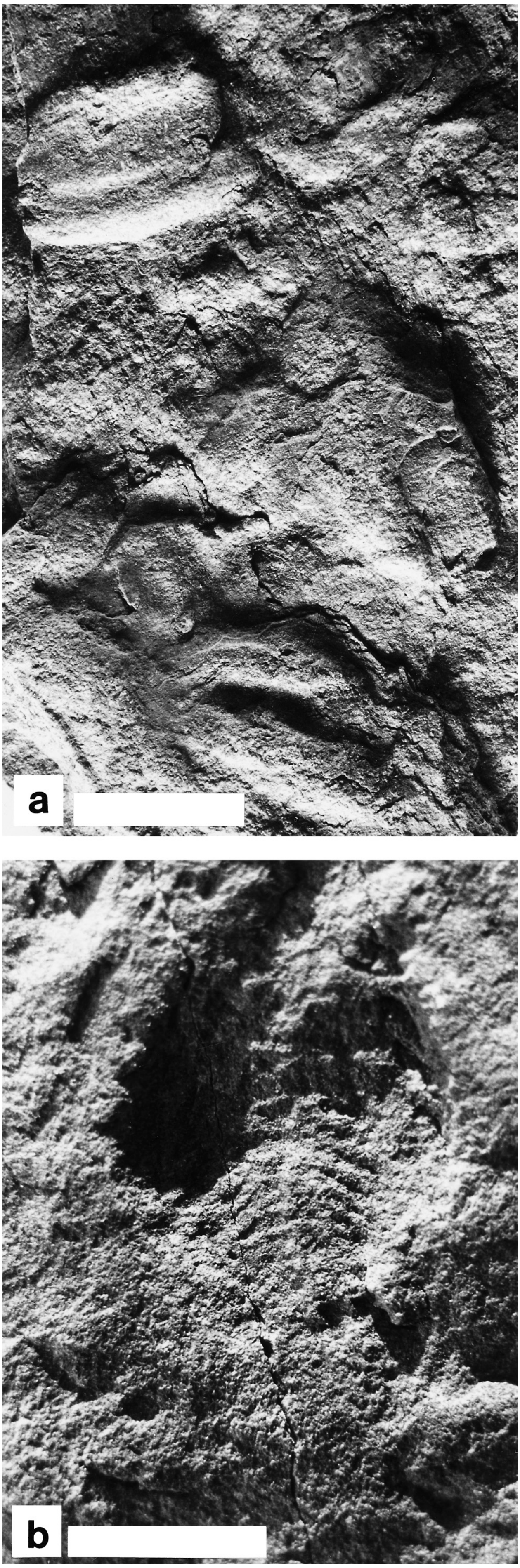
The BGG ichnofauna contains various different *Rusophycus*-like trace fossils, implying various different producers. Pending a review of the whole ichnogenus (and related resting traces) we designate these different types as 'Forms'. No 'trilobitoid' *Rusophycus*-type trace fossils, nor any other trilobite-produced trace fossils, are known from the BGG. In contrast, several transitional forms between *Rusophycus*-like trace fossils and natural casts of empty carapaces of several unknown crustaceans are known (see below). Furthermore, transitional forms between *Rusophycus* and *Selenichnites* are known (see below). We therefore regard the BGG crustaceans as producers of these *Rusophycus*-like resting traces.

### *Rusophycus* isp. Form A
(Fig. 17a)

**Material and locality**. [1]. ES-BW 43/9 (Fig. 17a); locality 2.

**Description**. Preserved as positive hyporelief. Bilobate trace fossils with a flat and broad median furrow, but without or with only very faint scratch marks.

**Remarks**. Similar structures were published by Rindsberg (1994) as *Rusophycus hartselleanus* from the Upper Mississippian (Carboniferous) of the Hartselle Formation of Alabama.



### *Rusophycus* isp. Form B
(Fig. 17b)

**Material and locality**. [4]. MB-W-833 (Fig. 17b); locality 1.

**Description**. A *Rusophycus*-type trace fossil, about 3 cm long, having regularly obliquely orientated and chevron-shaped scratch marks.

**Remarks**. The scratch marks may indicate the activity of digging appendages, although the faint forked tail impression in ES-BW-41/51 may imply that this trace fossil is transitional with a body imprint (e.g. Fig. 21a), probably preserved as a relatively faint and flat undertrace.

**Discussion**. *Rusophycus* ispp. are very variable in shape and size (e.g. Häntzschel 1975; Osgood 1970), and certain *Rusophycus* ispp. which intergrade with *Cruziana* ispp., are the work of the same producer. *Rusophycus* shows a general similarity to some *Selenichnites* (see below). Seilacher (1970) suggested that related resting and digging traces, together with crawling traces (*Cruziana*), should be synonymised in one ichnogenus (*Cruziana*). However, a recent International Working Group (International Workshop on Ichnotaxonomy, Bornholm (Denmark), 1998) suggested that these transitional forms between obviously related trace fossil types should be referred to as *Cruziana* isp. X *Rusophycus* isp.

Generally, the morphology of *Rusophycus* reflects that of its arthropod producer. *Rusophycus* has been generally assumed to represent resting and digging activity of benthic trilobites (e.g. Seilacher 1955; Osgood 1970). Osgood (1970) showed the obvious similarity in shape and size between *Rusophycus pudicum* Hall, 1852 and *Flexicalymene meeki*, interpreted as the producer, from the Upper Ordovician Corryville Beds of the Cincinnati area. However, in many examples of Palaeozoic *Cruziana* and *Rusophycus*, one or more different trilobite producers are possible (Baldwin 1977a; Fortey & Seilacher 1997), and other arthropod taxa cannot be completely excluded (see also discussion of *Selenichnites*, below). A trilobite origin of *Rusophycus* X *Cruziana*-type trace fossils is generally suggested for earliest Cambrian to Carboniferous forms, especially from marine settings, whereas the similar but generally smaller ichnogenus *Isopodichnus* is generally used to denote younger marine (and non-marine) forms, which occur in the Carboniferous (e.g. Glaessner 1957), Permian (e.g. Gand 1994) and Triassic (e.g. Müller 1955), and are attributed to a non-trilobite (sometimes non-arthropod) producer (e.g. an infaunal polychaete was proposed as the producer of *Isopodichnus*-type trace fossils from the German Triassic by Müller (1955)). While *Isopodichnus* resembles the *Cruziana* X *Rusophycus* complex in many respects, workers are divided over whether these trace fossils should be referred to separate ichnotaxa. The general trend, however, has been to abandon *Isopodichnus*, in favour of *Cruziana* and *Rusophycus*, due to the lack of clear morphological ichnotaxobases separating them.

The BGG succession contains numerous natural casts of empty carapaces and completely preserved impressions of archaeostracan crustacean body fossils (see below), which are similar to these *Rusophycus* in their shape and size range. The BGG *Rusophycus*-type trace fossils differ from most other *Rusophycus* ispp.. Hannibal & Feldmann (1983) reported the *Rusophycus*-like *Chagrinichnites osgoodi*, from the late Devonian

**Figure 17** *Rusophycus* isp. Forms A and B: (a) *Rusophycus* isp. Form A. ES-BW 43/9; locality 2. Bilobed structure with smooth surface, without scratch marks; (b) *Rusophycus* isp. Form B. MB-W-833; locality 1. Showing faint opposing chevron-shaped marks along the body axis. Scale bars = 2 cm.

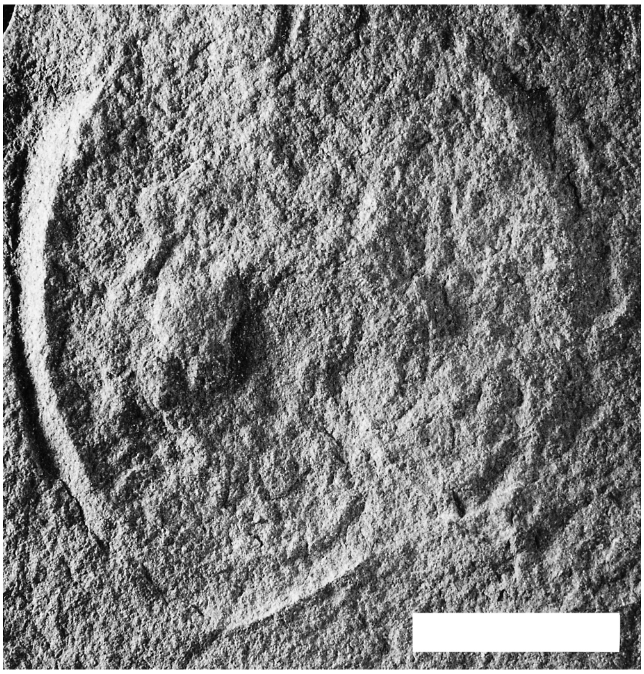


**Figure 18** Body fossil (natural cast) of bivalved arthropod (crustacean) carapace. MB-A-1017; locality 3. Bilobed structure showing thickened marginal rim of carapace. Scale bar = 2 cm.

of Ohio, and interpreted them as possible escaping burrows of ?leptostracan (echinocarid) crustaceans; these are similar in many respects to the BGG arthropods and their trace fossils.

The BGG sediments contain numerous (?*Rusophycus*-like) bilobate structures without any scratch marks or any indication of activity of a living producer (e.g. MB-A-1013 (locality 2), MB-A-1017 (Fig. 18; locality 3), MB-A-1012 (locality 2), MB-A-1016 (locality 2), MB-A-1015 (Fig. 19; locality 2), and BASC Z.1360.8 (Fig. 20; locality 2). These body fossils are presumably related to the producers of *Rusophycus* ispp., and consist of impressions (natural casts) of bivalved arthropod carapaces. They are variously preserved. Some show impressions of a thickened marginal rim (Fig. 18). Most show smooth surfaces (Fig. 19), although a few examples show paired impressions of adductorial muscles or a vein-shaped vascular system preserved on the surface (Fig. 20); this fidelity indicates that these specimens, at least, are body fossils, as opposed to detailed resting traces. They are interpreted as natural casts or impressions of empty carapaces (exuviae) or degraded carcasses of bivalved arthropods (crustaceans), not *Rusophycus*-type trace fossils. The association of numerous bivalved casts (Fig. 19) supports this taphonomic interpretation; this specimen probably represents an accumulation of degraded and empty crustacean carapace valves, washed together in a muddy tidal pond. Although the precise affinities of these crustaceans remain unclear, some specimens (e.g. Fig. 18) resemble the (Middle Cambrian) Burgess-type arthropod *Carnarvonia* Walcott, 1912 (order and family uncertain; Rolfe 1969).

Other specimens are well-preserved, and reveal their affinities more clearly. They consist of completely-preserved impressions and natural casts of bilobed crustaceans (e.g. BASC Z.1360.9 (Fig. 21a; locality 2), BASC Z.1360.11 (Fig. 21b; locality 2)). They show the outer margin of a bivalved carapace forming a horseshoe-shaped anterior margin, impressions of paired body appendages and a slender (?segmented), abdomen. One specimen (ES-BW-41/51) also shows the faint impression of a forked tail. These fossils show no signs of any active movement (e.g. scratch marks). The taxonomic position of these crustaceans remains uncertain (Thomson & Weber 1995, 1999), but it seems that at least two different taxa are present. They will be the subject of a future paper.

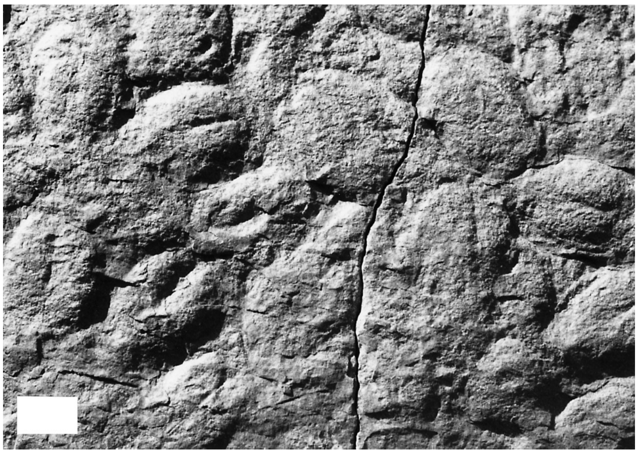


**Figure 19** Body fossils (natural casts) of bivalved arthropod (crustacean) carapaces. MB-A-1015; locality 2. Numerous, similarly-sized (sorted) bivalved arthropod carapaces washed together in a muddy tidal pond. Scale bar = 2 cm.

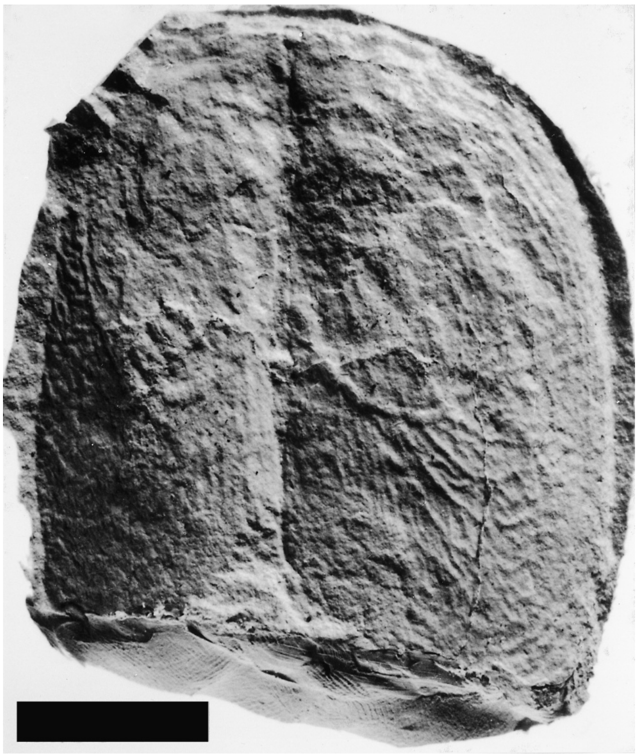
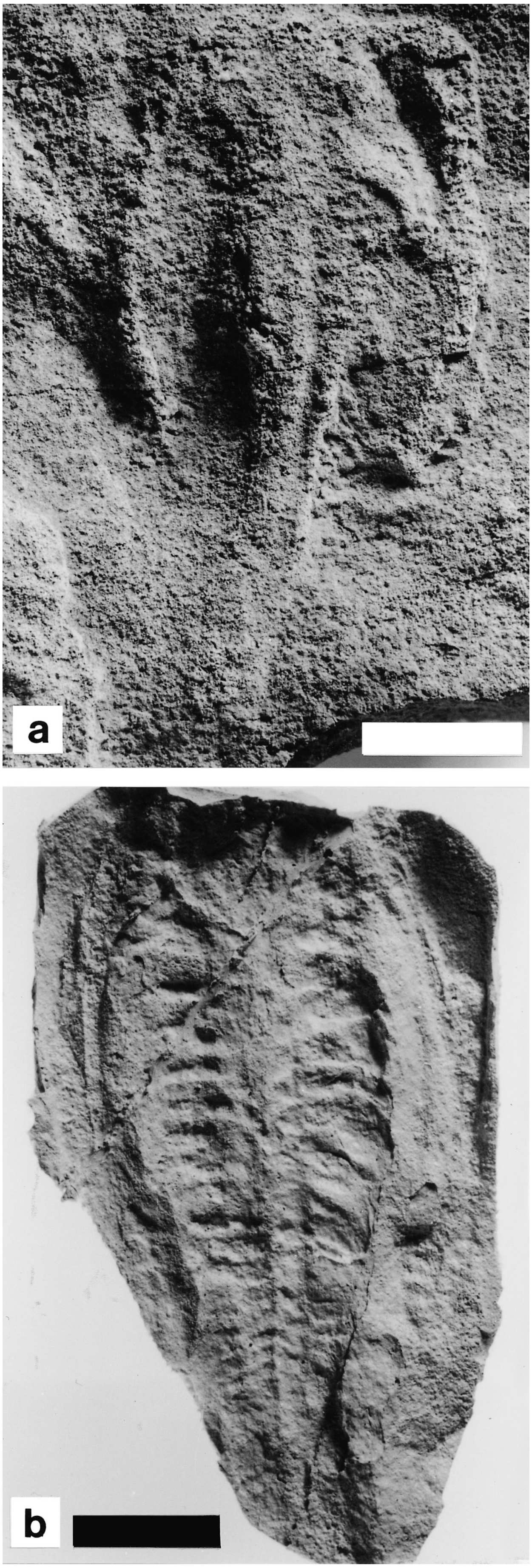


**Figure 20** Latex cast of a bivalved arthropod carapace. BASC Z.1360.8; locality 2. Showing median hinge line, adductorial muscle scars, and veinose pattern (vascular system) on the inner surface of the right valve. Scale bar = 2 cm.

### Ichnogenus *Selenichnites* (Romano & Whyte, 1987)
### *Selenichnites antarcticus* n. ichnosp.
(Fig. 22)

**Etymology**. Named after the provenance of this form, from Antarctica.

**Material and localities**. [8]. Holotype, MB-W-839 (Fig. 22a); locality 2. Paratypes, MB-W-842 (Fig. 22b), MB-W-837, BASC Z.1360.17 (Fig. 22e); locality 1. MB-W-843, MB-W-835 (Fig. 22c), MB-W-840 (Fig. 22d); locality 2. Further material remains *in situ* at localities 1 and 2.



**Diagnosis**. Small, elongated horseshoe-shaped imprints, 1·5–5 cm wide (average 2·5 cm). Greatest depth at anterior, tapering and shallowing posteriorly. Medial portion bears 3–5 transverse lineations.

**Description**. Preserved as positive hyporelief (Figs 22b–e) or negative epirelief (Fig. 20a), these elongated horseshoe-shaped imprints consist of a thickened (deep) anterior region and two (shallowing posteriorly) lateral margins which terminate in faint pointed structures. In their anterior portion, the structures sometimes show small, mostly poorly preserved V-shaped medial marks (Fig. 22a). In well-preserved material, faint transverse lineations (scratch-marks) are preserved in the medial region. Size generally 1·5–3 cm wide at maximum (n>100, based on field observations), but rare large forms may be up to 5 cm wide.

**Remarks**. The morphology of this trace is consistent with *Selenichnus* (Romano & Whyte 1987; later emended and redescribed by Romano & Whyte 1990 as *Selenichnites*). Five ichnospecies of *Selenichnites* are known: *S. rossendalensis* Hardy, 1970 (Carboniferous, England); *S. cordoformis* Fischer, 1978 (Ordovician, Colorado); *S. bradfordensis* Chisholm, 1985 (in part; Carboniferous, England); *S. hundalensis* Romano & Whyte, 1987 (Jurassic, England); and *S. langridgei* Trewin & McNamara, 1995 (Late Ordovician, W. Australia). *Selenichnites* isp. is also known from the Muth Formation (Lower Devonian) of Northern India (Draganits *et al.* 2001). *S. antarcticus* is longer and thinner than related ichnospecies and shows medial transverse lineations, a feature also lacking in the other ichnospecies.

**Discussion**. These trace fossils occur almost exclusively on palaeosurfaces with current lineations, indicating temporary and/or locally-prevailing intense current activity (e.g. tides in very shallow water). The traces are invariably orientated with their anterior part in-line with the palaeocurrent direction, probably reflecting the hydrodynamic stability of the animals in these currents. These trace fossils are very common and distributed throughout the entire BGG succession. They are not a sedimentary clast-shadow or flood cast (i.e. inorganic origin) as no obstacle (e.g. pebble or mud pellet) is ever associated with these structures; the mature BGG succession yielding these trace fossils does not contain any coarser fragments which could have provided such obstacles. The presence of appendage scratch marks confirms their organic origin.

*Selenichnites* has generally been attributed to xiphosurans (e.g. Hardy 1970; Romano & Whyte 1987, 1990; Wang 1993), although Trewin & McNamara (1995) suggested that *S. langridgei* may be related to the activity of a euthycarcinoid (e.g. *Kalbarria brimellae* McNamara & Trewin, 1993, known from the same succession). No body or trace fossil attributable to xiphosurans is known from the BGG. *Selenichnites antarcticus* is most likely to have been produced by the BGG crustaceans. Well-preserved resting traces, impressions of empty crustacean valves (exuviae), and completely preserved natural casts of bivalved crustaceans of comparable shape and size to these *Selenichnites*, were observed on adjacent finer units. *Selenichnites antarcticus* is therefore interpreted as produced by different growth stages of the BGG crustaceans, resting or digging into the substrate for food, which were subsequently current-eroded. They would have aligned themselves to the

**Figure 21** Phyllocarida indet.: (a) BASC Z.1360.9; locality 2. Faintly-preserved hyporelief of the impression of a complete bivalved arthropod, showing both carapace valves (with thickened marginal rim), slender segmented body axis (with proximal portions of the appendages); (b) BASC Z.1360.11; locality 2. Latex cast of a complete bivalved arthropod, showing the same morphology. Scale bar = 2 cm.

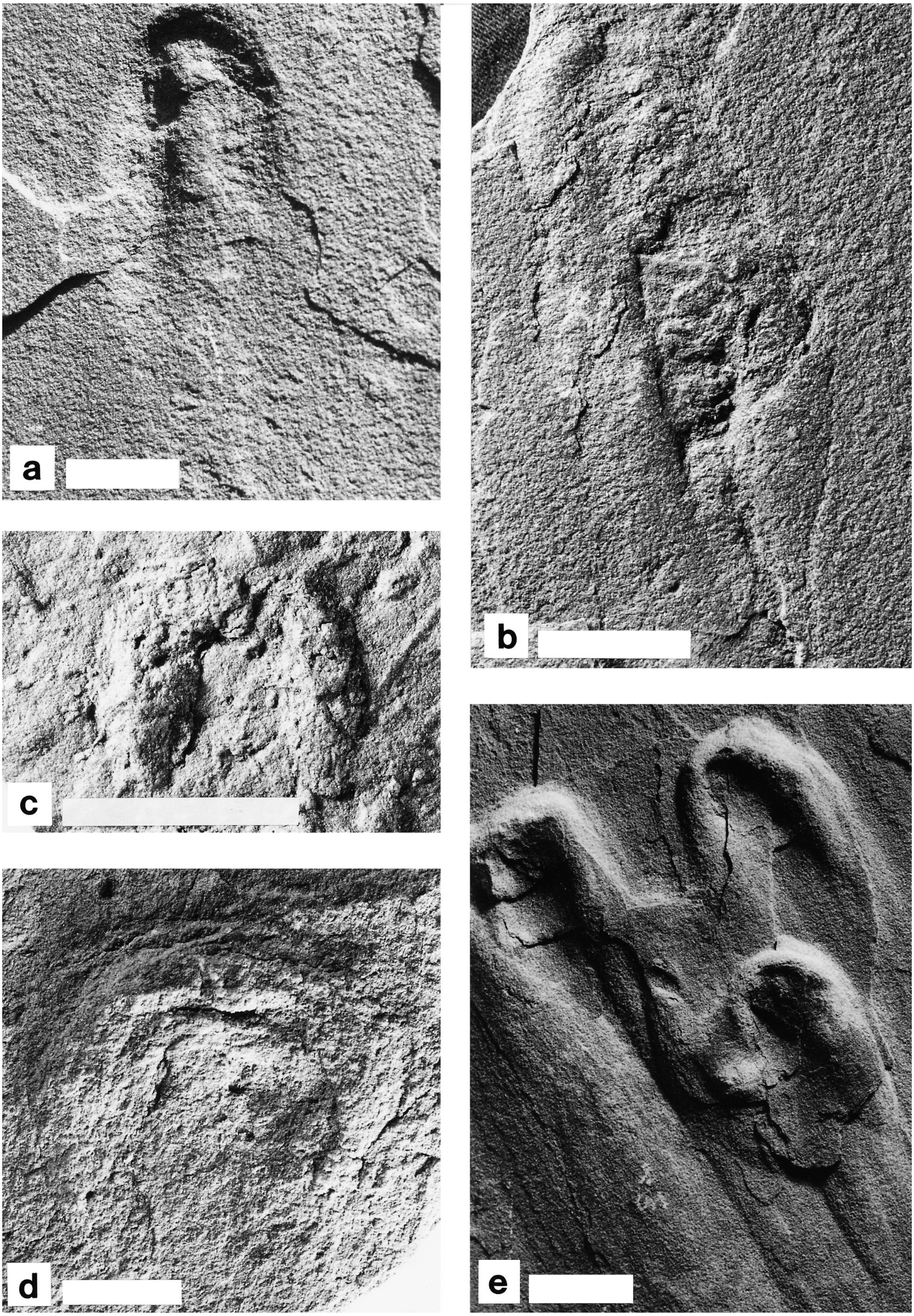


**Figure 22** *Selenichnites antarcticus*: (a) Holotype, MB-W-839 (epirelief); locality 2. Showing anterior V-shaped medial structure, and faintly-preserved appendage imprints; (b) MB-W-842 (hyporelief); locality 1. Showing faintly-preserved appendage imprints, and repeated digging behaviour (trace repeated forwards); (c) MB-W-835 (hyporelief); locality 2; (d) MB-W-840 (hyporelief); locality 2; (e) BASC Z.1360.17 (hyporelief); locality 1. Three traces, orientated parallel to the current direction. Scale bars = 2 cm.

current and burrowed into the substrate to avoid drifting away. The current-transported sediment would accumulate in front of the animal (i.e. thin marginal wall in Fig. 22a). The active digging of the animal would produce the anterior hollow of the trace (and the medial scratch marks). After the animals abandoned their resting places (possibly due to the decreasing water depth) these structures became partly eroded before being preserved. There is no evidence for subaerial exposure, or drying-up of the surfaces. According to this toponomic model, most of the detailed trace fossil morphology (e.g. body and leg imprints) would have been destroyed by the current; only in rare cases are faint imprints of the body or legs preserved (Figs 22a, b). In this context, *Selenichnites* could be interpreted as a taphoseries (i.e., heavily eroded) of a resting trace (e.g. *Rusophycus*).

It seems likely that the different types of *Selenichnites* (and transitional ichnotaxa), known from the Ordovician through to the Jurassic, were produced by different groups of arthropods (e.g. xiphosurans, ?trilobites, ?euthycarcinoids, phyllocarids and related archaeostracans) with generally similar life styles and behaviour (e.g. shovel-like carapace and strong appendages for digging into the substrate).

### Ichnogenus: *Taphrhelminthoides* n. ichnogen.

**Etymology**. Named after its general resemblance to *Taphrhelminthopsis* Sacco, 1888.

**Diagnosis**. Large, horizontal bilobate trail, generally 3 cm wide, composed of two parallel flat lobes showing transverse striations, separated by a median ridge with a figure-of-eight pattern.

### *Taphrhelminthoides antarcticus* n. ichnosp.
(Fig. 23)

1999 *Taphrhelminthopsis* sp.; Thomson & Weber, fig. 2e

**Etymology**. Named after the provenance of this form, from Antarctica.

**Material and locality**. [2]. Holotype, BASC Z.1360.13 (Fig. 23b). Paratype, MB-W-843 (Fig. 23a); locality 2.

**Description**. Preserved in positive hyporelief. Large, bilobate and slightly meandering trail (40 cm long in MB-W-843), about 3 cm wide, composed of two parallel flat lobes, each 1–1·5 cm wide, separated by a steep median ridge, which has a characteristic figure-of-eight pattern. Under low-angle illumination, the lobes show weakly developed transverse striations, at a low angle to mid-line (Fig. 23b). Two steep marginal ridges are also evident in BASC Z.1360.13 (Fig. 23b), although they are only faintly preserved in MB-W-843 (Fig. 23a).

**Discussion**. These traces share general similarities with *Taphrhelminthopsis circularis*, as described by Crimes *et al.* (1977), Crimes & Anderson (1985, figs 6, 7) and Fritz & Crimes (1985, fig. 4, pl. 5), from the Precambrian–Cambrian transition of North America and Canada. Häntzschel (1975) noted this ichnogenus from the Lower Tertiary (flysch) deposits of Europe, which differs from the Palaeozoic forms, and the BGG specimens, in that they show narrow curving meanders and a simple steep median furrow, with no figure-of-eight pattern. Indeed, it is questionable whether the Palaeozoic forms are really the same taxon as the Tertiary forms; they are more likely to represent poorly preserved *Scolicia* (Uchman 1995). Their distribution also differs; in the Mesozoic/Cenozoic flysch deposits, '*Taphrhelminthopsis*' is a member of the upper deep sea benthos (upper bathyal zone) whereas the Palaeozoic forms occur in shallow marine (coastal) environments.

**Figure 23** *Taphrhelminthoides antarcticus* n. ichnogen. et ichnosp.: (a) MB-W-843; locality 2. Large specimen in hyporelief, showing characteristic figure-of-eight-shaped median furrow; (b) BASC Z.1360.13; locality 2. Hyporelief, showing faintly-preserved figure-of-eight-shaped median ridge, transverse striation of lateral lobes, and prominent lateral ridges (i.e. furrows in original trace). Scale bars = 2 cm.

*Taphrhelminthoides* (and Palaeozoic *Taphrhelminthopsis*) represent large (probably grazing) trails that were probably produced by large Palaeozoic molluscs. The figure-of-eight pattern could have been produced infaunally by the movement of a rhythmically-ejected organ (snorkel-like siphon or sensory tentacle), and the fine lateral striations of the lobes could be related to a peristaltic movement of the muscular foot of the producer. On the other hand, the figure-of-eight pattern may be the result of the rhythmical activity of a radula-like organ rasping over the surface.

### Dubiofossils (?medusoid impressions)
(Fig. 24)

**Material and locality**. [3]. BASC Z.1366.4; locality 2. Further material remains *in situ* at locality 2.

**Description**. Some relatively frequently occurring ?dubiofossils were noted. They consist of circular to subcircular-shaped "medusoid"-like impressions, ranging from about 10 cm to 25 cm in diameter (Fig. 24). They show varying morphological characteristics, and therefore may represent different objects (or phenomena, respectively). The most common impressions display concentric circular or subcircular grooves and ridges. At least four concentric tiers are apparent. No structure is evident in the flat central portion. A traverse sand-filled mudcrack indicates subsequent drying up of the surface during episodic subaerial conditions.

**Figure 24** "Medusoid" dubiofossil, consisting of concentric circular structures, cut by a sand-filled mudcrack, indicating subaerial conditions. BASC Z.1366.4; locality 2.

**Discussion**. Several of these dubiofossils were observed *in situ* in the BGG. These structures are questionable in origin, and some may represent pseudofossils of (non-organic) sedimentary origin. The structures do, however, share strong similarities with several Precambrian/Cambrian problematic medusoid taxa such as *Cyclomedusa* Sprigg, 1947 (Glaessner & Wade, 1966, pl. 98, fig. 1) and *Ovatoscutum* Glaessner & Wade, 1966 (Glaessner & Wade, 1966, pl. 97, fig. 8). These impressions therefore probably represent medusoids which were stranded on the shoreline. A specimen referred to ?*Dickinsonia* sp. by Thomson & Weber (1999, fig. 2c) may represent a medusoid impression, or a sedimentary structure (cf. 'Kinneya', Fig. 4d) given the Ordovician age of the BGG.

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