



Trace fossils from the Lower Cambrian Bastion Formation of North-East Greenland

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New trace fossil collections are described from Lower Cambrian siliciclastic shallow marine shelf deposits of the Bastion Formation of North-East Greenland, together with a taxonomic re-assessment of previously reported material. The entire assemblage comprises 19 ichnogenera, 25 ichnospecies, as well as two vernacular ichnotaxa. Although no new ichnotaxa are present the material reveals new information on the 3-dimensional structure of two of the contained ichnogenera, namely *Plagiognus* Roedel and *Psammichnites* Torell. The stratigraphic range of a single ichnospecies, *Rusophycus latus* Webby, is formally extended from the Lower Ordovician to the Lower Cambrian. The assemblage compares favourably with Lower Cambrian ichnocoenoses described from other continents, particularly at the ichnogenetic level. Comparison with similar sequences suggests that the sub-trilobitic Lower Bastion Formation is late Tommotian to early Atdabanian in age, possibly entirely Atdabanian.

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During the last two decades stratigraphic sections of late Precambrian to Early Cambrian age have been the subject of considerable international interest, principally in connection with attempts to define the Precambrian–Cambrian boundary (Cowie & Brasier, 1989). Trace fossils play an increasing role in these discussions on account of their wide distribution in siliciclastic boundary sequences often lacking in other fossil groups (Crimes, 1987, 1989; Narbonne & Myrow, 1988). In reviewing the global distribution of trace fossils in strata of this age, Crimes (1987) pointed to the Bastion Formation (Early Cambrian) of North-East Greenland (fig. 1) as one of several sequences which might repay further examination of its trace fossil assemblages.

Cowie & Adams (1957) first noted the occurrence of trace fossils in the Bastion Formation. They briefly described and figured long narrow grooves (Cowie & Adams, p. 52, fig. 14, here referred to *Plagiognus*) and ridges from the Lower Bastion Formation in the Albert Heim Bjerger area, northern Hudson Land, and recorded *Cruziana* (p. 176) on Ella Ø. Subsequently Cowie & Spencer (1970) briefly mentioned or described 'arthropod scratch marks' (here referred to *Monomorphichnus lineatus*), *Diplichnites*, *Scolicia* (here tenta-

tively referred to *Psammichnites*), *Planolites*, *Phycodes*, *Skolithos*, *Arenicolites* and 'feather stitch trails', the latter subsequently reported as *Treptichnus* by Fritz & Crimes (1985, p. 21), from Ella Ø. In this later paper Cowie & Spencer (1970) failed to mention the occurrence of *Cruziana* in the Bastion Formation although it was recorded from the overlying Ella Island Formation. Cowie & Spencer (1970, p. 97, pl. 2c) also figured an unidentified 'organic mark' which Crimes *et al.* (1977, p. 126) and, more recently, Crimes & Jiang (1986, p. 647) tentatively referred to as *Taphrhelminthopsis circularis* (but see systematic ichnology herein).

Fritz & Crimes (1985) cited Cowie & Spencer's (1970) ichnofaunal list but failed to include *Arenicolites*, *Diplichnites* and *Taphrhelminthopsis*. Crimes (1987) repeated the ichnofaunal list but omitted *Arenicolites*, *Taphrhelminthopsis* and *Treptichnus* and included *Diplichnites*. Crimes (1989) stated that the Lower Bastion Formation contained *Monomorphichnus*, *Phycodes*, *Planolites*, *Scolicia*, *Skolithos* and *Diplichnites* but again omitted *Arenicolites*, *Taphrhelminthopsis* and *Treptichnus*.

Despite the repeated, and somewhat confusing, literature citations noted above, it is apparent that the only primary contribution on the ichnology of the Bastion

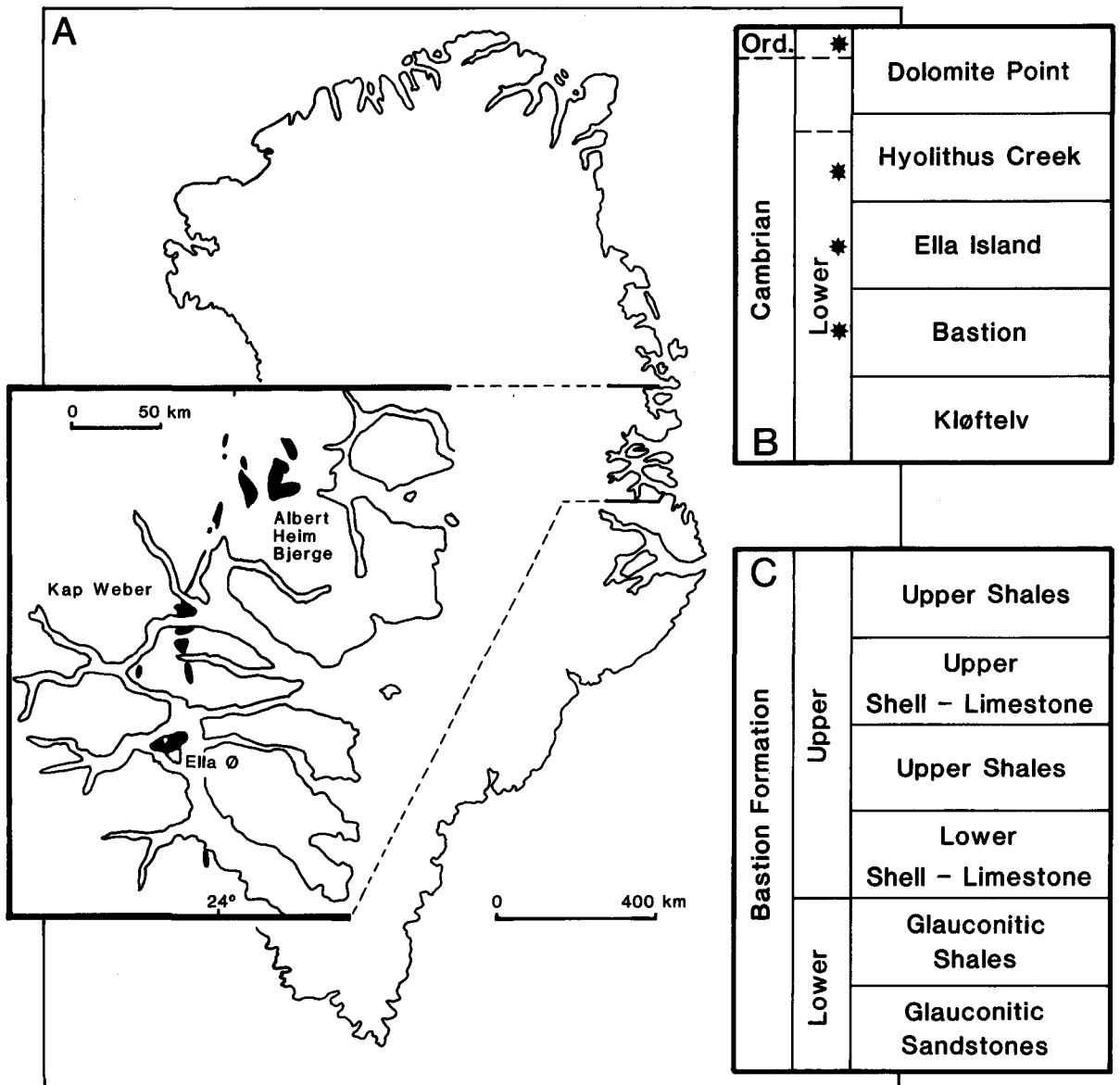


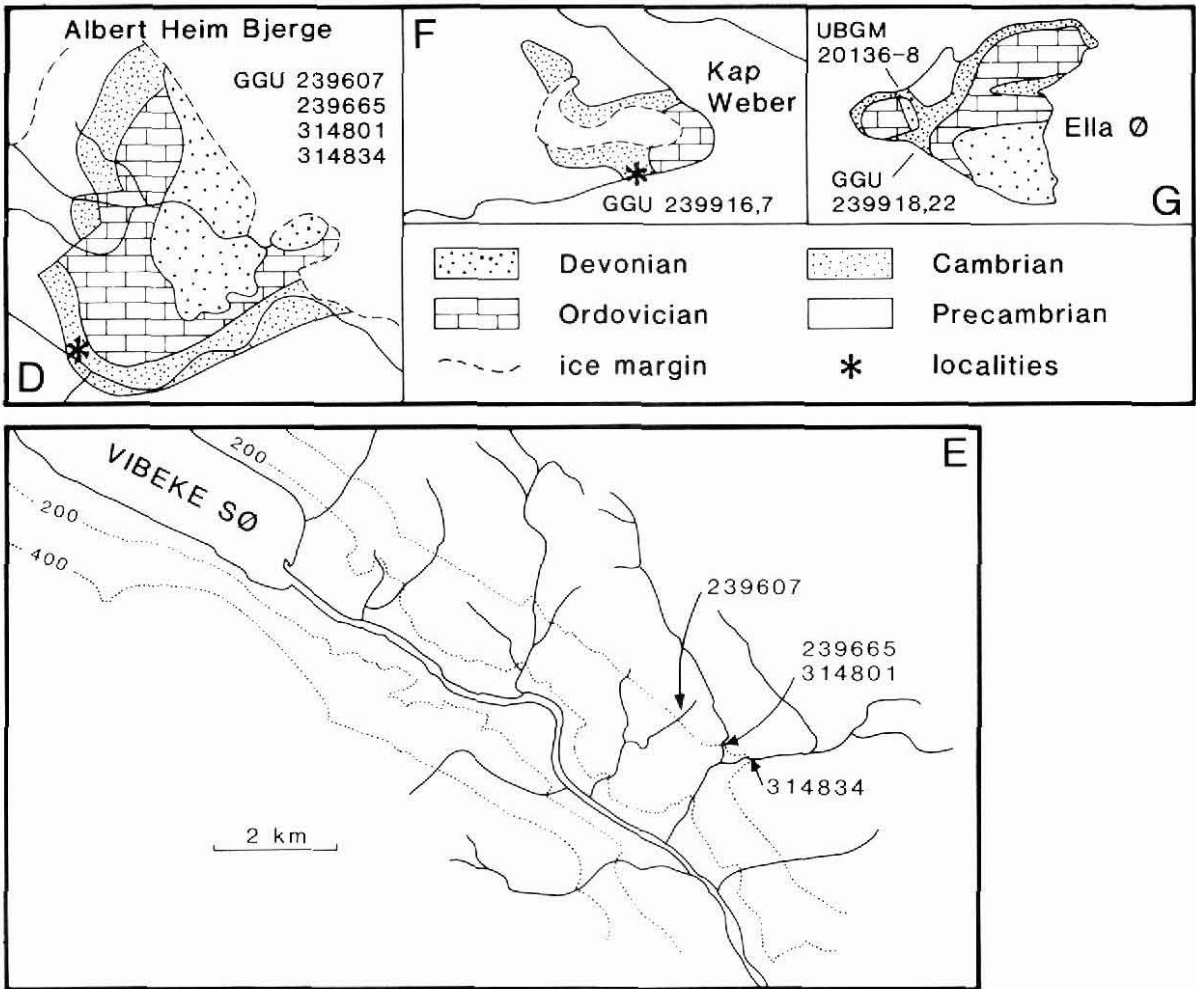
Fig. 1. Trace fossil localities in the Bastion Formation of North-East Greenland. A, general locality map showing the distribution of Cambrian and Ordovician sediments. B, Cambrian stratigraphy; those formations yielding age diagnostic body fossils are starred. C, sub-division of the Bastion Formation proposed by Cowie & Adams (1957). D-G, sample derivation from Albert Heim Bjerge (D,E), Kap Weber and Ella Ø; see text.

Formation is that by Cowie & Spencer (1970). However, trace fossil collections made in 1977 by P. Frykman and in 1988 by J. S. P., under the auspices of the Geological Survey of Greenland (GGU), have increased knowledge of the ichnofaunas within the formation. Interestingly, two of the slabs with trace fossils illustrated by Cowie & Adams (1957, fig. 14) were collected during 1988; part of one of these is described here (fig. 10b).

The main purpose of this paper is to systematically

describe these new collections. In so doing, material described by Cowie & Spencer (1970), housed in the Geological Museum of the University of Bristol, has been examined for a more detailed taxonomic re-evaluation. The ichnofauna as described is listed in fig. 2.

The study of Cambrian trace fossils from Greenland is still in its infancy, though the contributions of Cowie & Spencer (1970), Pickerill *et al.* (1982), Bergström & Peel (1988), Bergström & Ineson (1988) and Bryant & Pickerill (1990) are notable exceptions. This contribu-



tion therefore provides additional documentation and a more complete record of Cambrian trace fossils from Greenland. Although this article is decidedly taxonomic in nature, the described trace fossils provide additional information on the age of the Bastion Formation, a problem recently highlighted by Crimes (1987). No new ichnogenera or ichnospecies are recognised, but supplementary information is given on the 3-dimensional structure of two of the contained ichnogenera, namely *Plagiogmus* and *Psammichnites*. Finally, the stratigraphic range of one of the described ichnospecies, *Rusophycus latus* Webby, 1983, previously only formally recorded from the Lower Ordovician, is extended to the Lower Cambrian.

Stratigraphy and depositional environment

The Bastion Formation was named by Poulsen (1930) on the basis of outcrops forming the western promonto-

ry of Ella Ø (fig. 1). Cowie & Adams (1957) redefined the formation, referring a suite of quartzites and minor sandstones forming the lower part of Poulsen's formation to the Kløftelv Formation (70–80 m thick). Their restricted Bastion Formation, a sequence of siltstones, shales and subsidiary sandstones and carbonates varying in thickness from 137 m on Ella Ø to 151.5 m at Albert Heim Bjerge, has been adopted by subsequent workers (cf. Cowie, 1971; Henriksen & Higgins, 1976; Peel, 1982).

Cowie & Adams (1957, p. 25) recognised 6 units within the Bastion Formation. A basal unit of Glauconitic Sandstones (38–47 m) with siltstones and arenaceous shales is overlain by the Glauconitic Shales (6–12.5 m); these 2 units comprise the Lower Bastion Formation. The basal unit of the Upper Bastion Formation is the maroon to green or cream Lower Shell Limestone (0.5 m) which is composed almost entirely of comminuted shells, with some phosphatic pebbles. The over-

ICHNOTAXA	BASTION FORMATION									
	lower							upper		
<i>Arenicolites</i> isp.	•	•								
<i>Bergaueria</i> isp.	•									
<i>Cruziana</i> cf. <i>C. fasciculata</i>								•		
<i>Cruziana problematica</i>	•	•		•		•	•			
<i>Cruziana</i> isp. type A				•						
<i>Cruziana</i> isp. type B									•	
cf. <i>Curvolithus</i> isp.				•						
<i>Cylindrichnus</i> isp.	•									
<i>Dimorphichnus</i> isp.		•								
<i>Gyrolithes saxonicus</i>	•					•				
<i>Helminthopsis tenuis</i>				•						
<i>Monomorphichnus lineatus</i>					•					
<i>Neonereites biserialis</i>	•									
<i>Palaeophycus striatus</i>		•		•				•		
<i>Palaeophycus tubularis</i>	•	•	•	•	•	•	•			
<i>Phycodes palmatus</i>	•	•								
<i>Plagiogmus</i> isp.	•			•						
<i>Psammichnites gigas</i>	•		•		•					
<i>Rosselia socialis</i>	•					•				
<i>Rusophycus dispar</i>									•	
<i>Rusophycus latus</i>								•		
<i>Rusophycus</i> isp.						•				
<i>Skolithos linearis</i>	•			•	•	•	•			
<i>Taphrhelminthopsis</i> isp.					•					
<i>Teichichnus rectus</i>	•					•			•	
epichnial grooves	•	•		•		•				
pit and mound structures	•			•						
Samples	22	9	2	14	4	7	3	5	2	
GGU collection number	239665	314801	239607	314834	UBGM	239918	239916	239917	239922	
Location	A. H. B.			E. Ø.			K. W.		A	

Fig. 2. Summary diagram of ichnotaxa from the Bastion Formation; A. H. B., Albert Heim Bjerge; E. Ø., Ella Ø; K. W., Kap Weber; A, Antiklinalbugt, Ella Ø (see text for details). Solid circles indicate presence of an ichnotaxon within an individual collection.

lying Lower Shales (32–35.5 m) are glauconitic and micaceous and contain bands of limestone, arenaceous limestone or mudstone. The Upper Shell Limestone (2.5–10 m) consists of bands rich in fossil debris interbedded with shales and siltstones. The Upper Shales (48–56 m) are mainly arenaceous shales with massive mudstone beds which become more common towards the top of the formation.

Henrik Tirsgaard (Geological Survey of Greenland) briefly examined the Kløftelv and Bastion Formations at Albert Heim Bjerger and writes:

Kløftelv Formation

The quartzite units of the Kløftelv Formation are dominated by 0.2–1 m thick sets of large-scale planar cross-bedding, containing reactivation surfaces and sometimes showing herring-bone cross-stratification. Trough cross-stratification and ripple cross-lamination are subordinate structures. No distinct vertical sequences are apparent within the quartzite units. A tidally influenced nearshore marine origin is most likely but the poor preservation of sedimentary structures precludes a more detailed interpretation. The alternation of the 3 major quartzitic units with thin sandstone units is probably a result of minor transgressions, each commencing at the top of a quartzite unit.

Bastion Formation

The contact between the Kløftelv Formation and the overlying Bastion Formation represents a major transgression accompanied by the formation of a conglomerate containing glauconite and phosphate nodules. A similar conglomerate is found at about 20 m above the base of the Lower Bastion Formation which consists of heterolithic sandstone and siltstone layers (1–20 cm thick) interbedded with beds of sandstone (1–25 cm). The sandstone beds have sharp bases and internally contain parallel to hummocky cross-stratification. Ripple cross-lamination commonly occurs in the upper part of the sandstone beds. No vertical evolution is apparent within the lower 20 m of the Lower Bastion Formation.

Deposition of the Lower Bastion Formation occurred below fair weather wave base, in the marine offshore-transition zone (*sensu* Elliot, 1986). The alternation of sandstones and heterolites indicates sedimentation during alternating energy conditions, with the sandstones being deposited during storm events and the fine grained sediment during fair weather.

The second transgression, initiated some 20 m above the base of the Lower Bastion Formation, resulted in a decrease in the sandstone content and a marked de-

crease in the abundance of biogenic structures. Sandstone content subsequently increases slightly upwards towards the top of the Lower Bastion Formation, indicating gradual shoaling. Sedimentation, however, remained within the offshore-transition zone.

A third transgression, manifested by the Lower Shell Limestone, marks the contact between the Lower Bastion Formation and the Upper Bastion Formation. The latter consists mainly of shales with thin beds of limestones and mudstones. Deposition within the Upper Bastion Formation occurred mainly from suspension, well below wave base in an offshore shelf environment.

Repository and material

Collection numbers for all material collected by the Geological Survey of Greenland are prefixed by GGU. Individual specimens or slabs within single collections are consecutively numbered according to the order in which they were examined in the laboratory (e.g. GGU 239665–1, GGU 239665–2). Figured specimens also bear a number prefixed by MGUH and are housed in the Geological Museum, University of Copenhagen. Material described by Cowie & Spencer (1970) is housed in the Geological Museum, University of Bristol, and is prefixed by UBGU. This latter material was collected from Bastionbugt on the northern side of Ella Ø (fig. 1A,F; see Cowie & Spencer, 1970, p. 92). The material from 1977 and 1988 comprises 64 samples (single specimens or slabs of varying dimensions) from 8 collections made from Albert Heim Bjerger, Kap Weber and Ella Ø, as located in fig. 1 and discussed below.

GGU collections 239665 and 314801. Talus material adjacent to the lowermost few metres of the Lower Bastion Formation at Albert Heim Bjerger (fig. 1D,E). Collection GGU 239665 by P. Frykman, 1977; 22 samples; collection GGU 314801 by J. S. Peel and M. P. Smith, 1988; 9 samples.

GGU collection 239607. Talus material from the Lower Bastion Formation at Albert Heim Bjerger collected by P. Frykman, 1977; 2 samples (fig. 1D,E).

GGU collection 314834. Talus material adjacent to the lowermost few metres of the Lower Bastion Formation at Albert Heim Bjerger collected by J. S. Peel and M. P. Smith, 1988; 14 samples (fig. 1D,E).

GGU collection 239916. *In situ* material from the Lower Bastion Formation at Kap Weber, collected by P. Frykman, 1977; 3 samples (fig. 1E,F).

GGU collection 239918. Talus material from the Lower Bastion Formation at Antiklinalbugt, west side of anticline, Ella Ø, collected by P. Frykman, 1977; 7 samples (fig. 1F,G).

GGU collection 239917. *In situ* material from the Upper Bastion Formation adjacent to the contact with the overlying Ella Island Formation at Kap Weber, collected by P. Frykman, 1977; 5 samples (fig. 1F).

GGU collection 239922. *In situ* material from the Upper Bastion Formation at Antiklinalbugt, east side of anticline, Ella Ø, collected by P. Frykman, 1977; 2 samples (fig. 1F,G).

Systematic ichnology

Following conventional practise in palichnology the ichnotaxa are described alphabetically for ease of reference; vernacular ichnotaxa are briefly described for completeness following the formally documented forms. Preservational terminology follows that adopted by Seilacher (1964), Webby (1969), Martinsson (1970) and Simpson (1975), as summarised in Häntzschel (1975) and Ekdale *et al.* (1984). The material listed for each ichnotaxon represents those specimens or slabs from a collection where confident or reasonably confident identification was made. Some slabs contain only non-descript or poorly preserved material insufficient for identification even at the ichnogenic level and therefore this material is excluded from the following descriptions. Most specimens are preserved in fine-grained to medium-grained sandstones; this grain size inhibits both preservation and the observation of fine details; figured specimens (apart from those housed in the Geological Museum, University of Bristol) were coated with sublimate of ammonium chloride.

Ichnogenus *Arenicolites* Salter, 1857

Arenicolites isp.
Figs 3a,b, 4b, 5a

Material. Twenty-four specimens from GGU collections 239665–20, 239665–21, 239916–1, 314834–18, 314801–1.

Description. Specimens occur as either rare vertical U-plane (*sensu* Osgood, 1970) sections (figs 3a,b) or more typically as paired circular openings usually preserved in

concave epirelief (fig. 4b) but also in convex hyporelief (fig. 5a). In bedding surface sections, the tubes are 8 to 21 mm apart, typically 2 to 4 mm in diameter; diameter is constant for a single pair, and the sediment between the tubes is undisturbed. In vertical U-plane section the tubes are vertical to sub-vertical, thinly lined or unlined. The fill is finer-grained (muddy sandstone) than the enclosing sandstone matrix. The restricted thickness of the slabs containing the traces normally precludes observation of the basal U-bend (e.g. fig. 3b) and hence the depth of penetration of the material, although the undisturbed nature of the material between the tubes can clearly be ascertained.

Remarks. Cowie & Spencer (1970) briefly noted the occurrence of *Arenicolites*, with individual tubes 10 to 15 mm apart, from the Bastion Formation of Ella Ø, but no additional information was given. *Arenicolites* is a commonly occurring ichnotaxon in the Lower Bastion Formation of Albert Heim Bjerge (J. S. P., field observations). The limited material described here is therefore no reflection on its actual abundance within the Lower Bastion Formation.

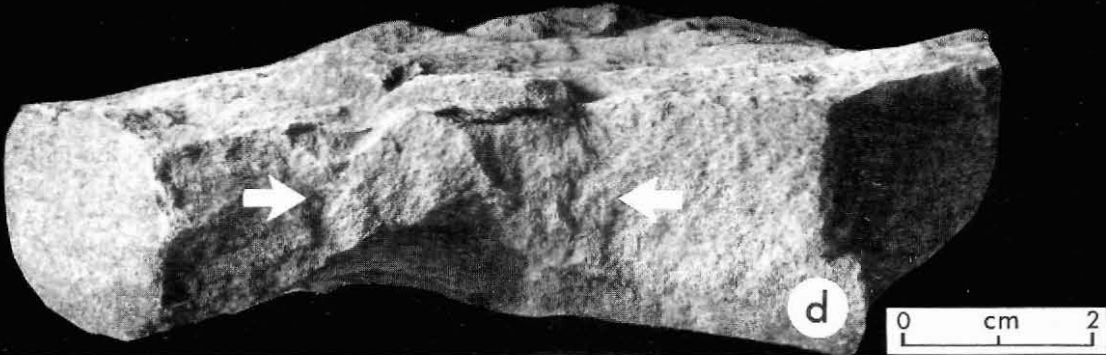
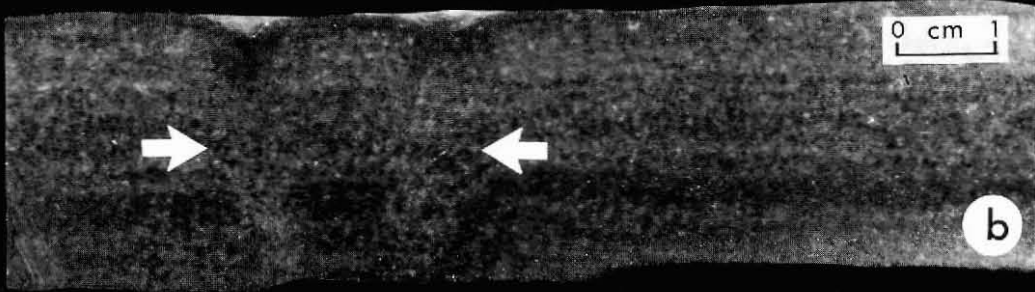
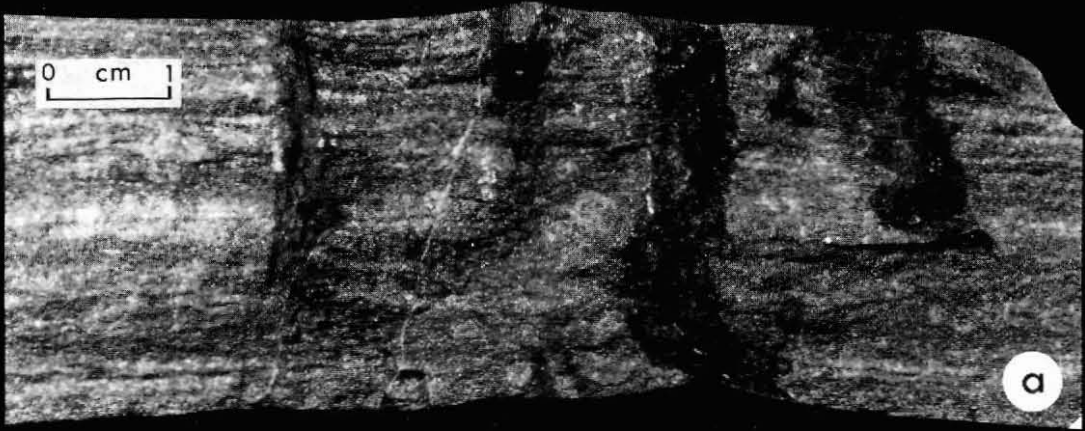
Ichnospecific identification of *Arenicolites* requires knowledge of both bedding surface and U-plane expressions and, therefore, the material described here is only identified at the ichnogenic level. Bedding plane expressions are assigned to *Arenicolites* because of the paired tube association and lack of sediment disturbance between the tubes. Several vertical U-plane sections resemble *A. statheri* Bather, 1925 in that this ichnospecies possesses lined vertical to sub-vertical tubes, but this ichnospecies is considerably larger and may possess funnel-shaped openings (Fürsich, 1974). Incomplete 3-dimensional knowledge of the majority of additional ichnospecies of *Arenicolites*, such as *A. compressus* (Sowerby, 1829), *A. subcompressus* (Eichwald, 1860), *A. carbonaria* (Binney, 1852), *A. curvatus* Goldring, 1962, and *A. naraensis* Badve & Ghare, 1978 suggests that taxonomic re-evaluation of the ichnotaxon is necessary, particularly at the ichnospecific level.

Ichnogenus *Bergaueria* Prantl, 1945

Bergaueria isp.
Figs 3c,d

Material. One specimen from GGU collection 239665–15.

Fig. 3. a, b, U-plane cross-sectional views of *Arenicolites* isp.; a is MGUH 19.654 from GGU collection 239916–1 and b is MGUH 19.655 from GGU collection 239665–21. c, d, basal (c) and lateral (inverse) view (d) of *Bergaueria* isp.; MGUH 19.656 from GGU collection 239665–15. Note the relatively steep walls (arrowed) in d.



Description. The specimen consists of an irregular, somewhat compactionally flattened and erosionally truncated, thinly walled hemispherical structure preserved in convex hyporelief and endorelief, 1.6 to 1.9 cm in diameter and extending vertically for at least 2.3 cm. The external walls are sharp, steeply inclined and unornamented. The basal surface is irregular and possesses rudimentary concentric ornamentation. Burrow fill is structureless and of similar grain size to the host rock.

Remarks. Based on the criteria recently comprehensively reviewed by Pemberton *et al.* (1988) for distinguishing single-entrance, plug-shaped ichnogenera, the specimen can best be regarded as a truncated and irregularly eroded *Bergaueria*. The incomplete and poor preservation of the single specimen negates ichnospecific assignment, as the four ichnospecies recognised by Pemberton *et al.* (1988) are primarily based on detailed analysis of the nature of the distal terminations and the wall characteristics (here unobserved). *B. perata* Prantl, 1945 and *B. hemispherica* Crimes, Legg, Marcos & Arbolea, 1977 would be favourable candidates for comparison, however, should additional material become available. These ichnospecies are both thinly walled and commonly possess concentric ornamentation (Pemberton *et al.*, 1988; Pickerill, 1989), particularly *B. perata*.

Ichnogenus *Cruziana* d'Orbigny, 1842

Remarks. Seilacher (1970) united under *Cruziana* both cruzianaeform and rusophyciform arthropod burrows and, although some authors have subsequently adopted this scheme, most have preferred to retain *Cruziana* d'Orbigny, 1842 and *Rusophycus* Hall, 1852 as distinctive and separate ichnogenera (for references see Crimes *et al.*, 1977; Bromley & Asgaard, 1979). This is more in accordance with CTFN, Article 40 (*Code for Trace Fossil Nomenclature*, Sarjeant, 1979) and ICZN, Article 231 (*International Code of Zoological Nomenclature*, 3rd Edition, 1985), and therefore we adopt this latter scheme and describe the ichnotaxa separately.

Cruziana cf. *C. fasciculata* Seilacher, 1970
Figs 4d, 12c,d

Material. One specimen from GGU collection 239917–3.

Description. The specimen consists of a short segment of a generally poorly but variably preserved cruzianid, preserved in convex hyporelief on a sandstone sole, which essentially exhibits, and obviously formed subsequent to, *Rusophycus dispar* Linnarsson, 1869 (see fig. 12c). The trace is relatively shallowly impressed and bilobed, with each lobe possessing fine and relatively narrow scratches; where preservation is clear, these are arranged in bundles of four to six and are oriented at angles of 35 to 60 degrees with respect to the poorly developed median furrow. Scratches within individual bundles do not intersect, are straight to slightly sinuous and are subequal in length. Specimen width is 2.7 cm and maximum exposed length is 2.8 cm.

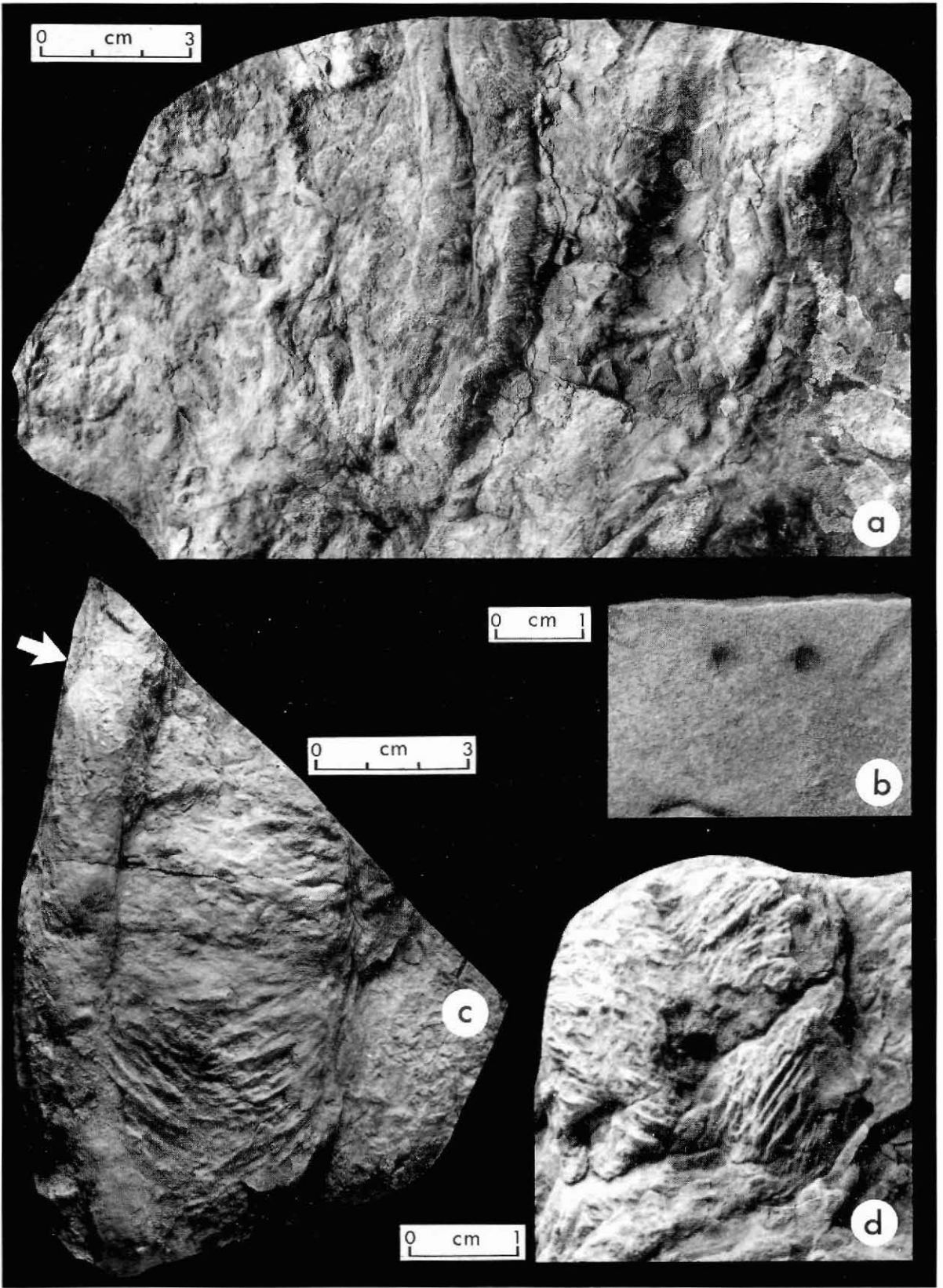
Remarks. In view of the fact that just a single and generally poorly preserved specimen is present, the identification as *Cruziana* cf. *C. fasciculata* is only tentative. This ichnospecies is an important member of the 'fasciculata group' of Seilacher (1970), members of which are all of Early Cambrian age, and are characterised by cruzianids possessing bundles of four to six subequal scratches that are relatively finely impressed and form obtuse angles to the median furrow. Crimes *et al.* (1977, p. 99, pl. 1a) figured a similar but much wider example than that described here from the Lower Cambrian of Spain and Crimes & Anderson (1985, p. 317) described a 2.5 cm wide specimen from the Lower Cambrian of south-eastern Newfoundland.

Cruziana problematica (Schindewolf, 1921)
Figs 5a,b

Material. Eighteen specimens from GGU collections 314801–1, 314801–2, 314801–3, 239665–3, 239665–7, 239916–3, 239918–7, ?314834–12.

Description. Specimens are variably preserved in convex hyporelief on sandstone soles and consist of short (2.5 cm) to long (20 cm), 4 to 7 mm wide, essentially

Fig. 4. a, *Cruziana* isp. type A preserved in convex hyporelief on sandstone sole; MGUH 19.657 from GGU collection 314834–13. b, *Arenicolites* isp. on upper bedding surface preserved as paired circular openings; MGUH 19.658 from GGU collection 239665–20. c, *Cruziana* isp. type B preserved in convex hyporelief on sandstone sole; MGUH 19.659 from GGU collection 239922–1. Note also the basal portion of *Teichichnus rectus* (arrowed) which is shown in cross-section in fig. 14a. d, *Cruziana* cf. *C. fasciculata* preserved in convex hyporelief on sandstone sole; MGUH 19.660 from GGU collection 239917–3.



bilobed, horizontal and symmetrical burrows that may follow a straight, curved or flexuous course. Individual burrows may or may not intersect. Specimens possess different characteristics depending on depth of impression. Fig. 5b, for example, exhibits two specimens. The more deeply impressed example is relatively wide with individual lobes possessing transverse or highly obtuse, irregularly spaced (0.5 to 2 mm) sediment pods that extend from the very narrow axial furrow to the margins of the lobes. The associated narrower and less deeply impressed example possesses lobes that are narrower with respect to the wider axial furrow and transverse ornament that is only feebly developed. Fig. 5a (upper left to central right) exhibits a third variation where a single specimen is relatively deeply impressed at one end and therefore exhibits the typical bilobed appearance, each lobe possessing very delicate, transverse and unevenly spaced scratches. For the majority of its course, however, this specimen is very shallowly impressed and assumes the appearance of a simple and smooth, unilobed, horizontal burrow. Some specimens extend upward as endichnial burrows into the overlying sandstone at their terminations. Rare examples exhibit slightly enlarged and more deeply impressed bilobed expansions along their length.

Remarks. These morphologically variable traces, a result of preservational conditions, burrowing level, interface relationships etc., clearly represent preservational variants of a single ichnotaxon, but this is not unusual in ichnology (for example, see Seilacher, 1970). We refer the material to *Cruziana* rather than *Isopodichnus* Bornemann, 1889 following the reasoning of Bromley & Asgaard (1979) and more recently Romano & Whyte (1987). As noted by Trewin (1976), distinction between different ichnospecies of small and narrow *Cruziana* (= *Isopodichnus* of many previous authors) is difficult without large numbers of well-preserved specimens that illustrate the whole range of burrow morphology. However, although the material described here is limited to eighteen specimens we regard it as conspecific with *C. problematica*, an ichnospecies characterised by transverse and unevenly spaced scratches and typically less than 7mm in width. Bromley & Asgaard (1979) have described and illustrated *C. problematica* exhibiting a similar range in morphological variation to that described herein.

Cruziana isp. type A

Fig. 4a

Material. Two specimens from GGU collection 314834–13.

Description. Both specimens occur as convex hyporeliefs on a silty sandstone sole and are variably and poorly preserved. The figured specimen is a curved, 12.5 cm long, 2.9 to 3.9 cm wide bilobed trace. It exhibits moderately developed endopodal lobes and an axial furrow at the deeper impressed (1.2 cm) extremity, and poorly developed equivalents where it merges with the more typical stratification level of the sandstone sole. Portions of the endopodal lobes, particularly towards their outer margins, possess faint and relatively dense (one per mm), typically transverse scratches that may be oriented, however, up to 70 to 80 degrees with respect to the axial furrows. The scratches are unidirectional and only finely impressed. The second specimen is less well preserved, 18 cm in length and 2.3 cm in width, with similarly developed but poorly preserved scratches.

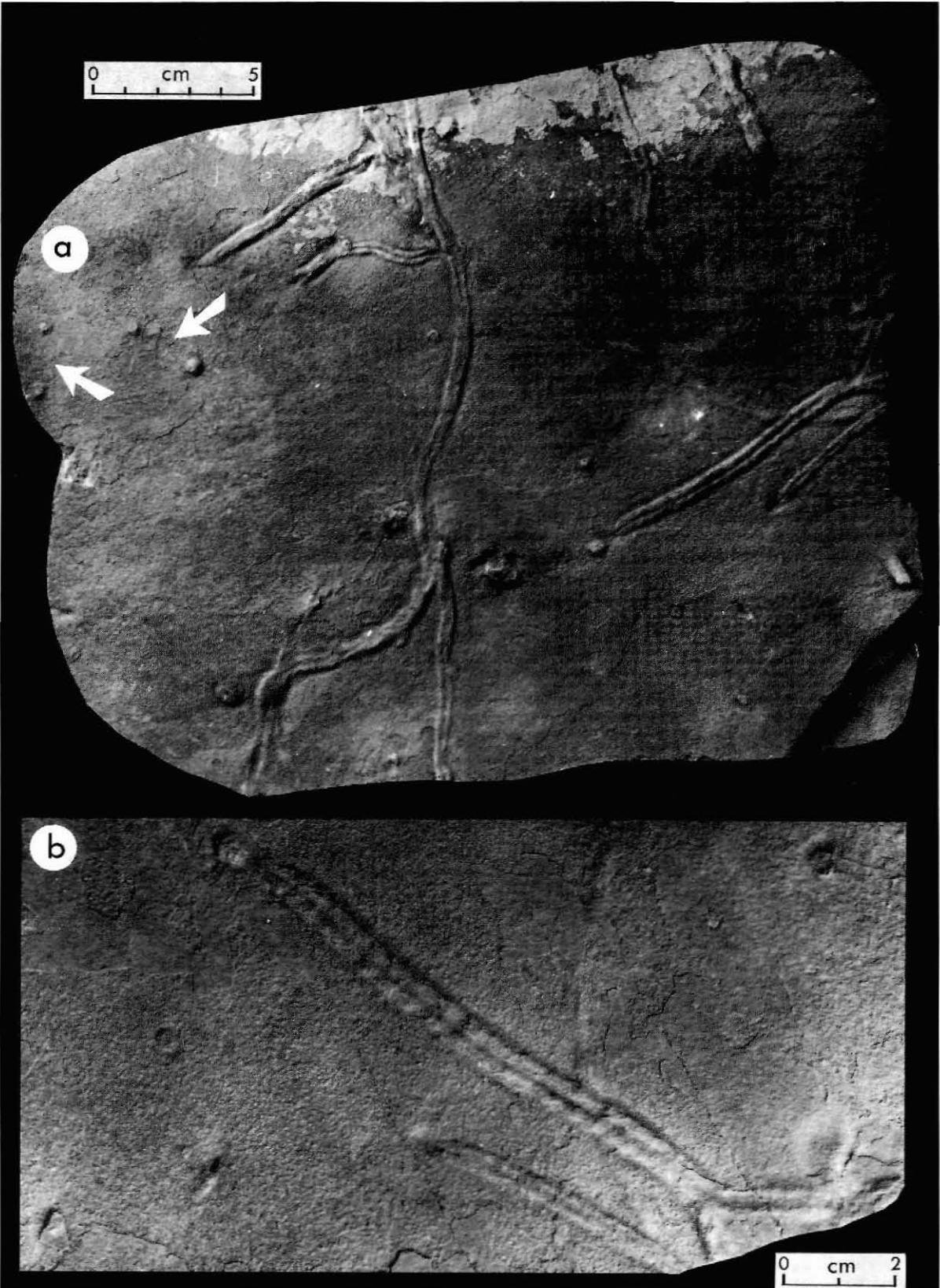
Cruziana isp. type B

Fig. 4c

Material. One specimen from GGU collection 239922–1.

Description. Preserved in convex hyporelief on a sandstone sole also containing *Teichichnus rectus* Seilacher, 1955 (fig. 4c), the single specimen is at least 11.4 cm long, 4.8 cm wide and 1.2 cm deep. Preservation is generally poor but variable; endopodal lobes are only weakly developed towards the posterior end of the specimen where they possess relatively deeply impressed scratches. The remainder of the specimen is virtually unilobate with no axial furrow development and sporadically and irregularly distributed scratches (fig. 4c). The scratches, where preserved, are generally coarse, sharp and clearly defined, bifid, or at least associated in pairs, and only rarely intersect. They are oriented at an average angle of 60 to 70 degrees to the mid-line of the trace; they curve to assume a more acute angle towards the mid-line and a less acute angle near the external margins.

Fig. 5. a, b, *Cruziana problematica* preserved in convex hyporelief on sandstone sole; larger specimen in b is MGUH 19.661 from GGU collection 314801–1. Note the variable morphology depending on depth of impression; b is an enlarged view of the specimens exhibited at mid-right in a; note also several examples of *Arenicolites* isp. (two of which are arrowed) in a, which represent MGUH 19.662 and MGUH 19.663 from GGU collection 314801–1.



Remarks. Crimes (1987, p. 105) noted that the majority of Lower Cambrian *Cruziana* have only been previously identified at the ichnogeneric level because of the difficulty in deciphering the claw patterns in what is commonly poorly preserved material. This is certainly true for the material described here, where preservation is typically poor and the limited number of specimens does not permit observation of the complete range of morphological variation necessary for valid ichnospecific assignment. Nevertheless, it is still clear that two additional and different ichnospecies, herein referred to as *Cruziana* isp. types A and B, are present in the Bastion Formation collections. We are unfamiliar with any comparable analogues to *Cruziana* isp. A. *Cruziana* isp. B, at its posterior extremity, somewhat resembles *Cruziana dispar* (Linnarsson, 1869), a distinctive Lower Cambrian ichnospecies more recently discussed and described by Seilacher (1970) and, particularly, Bergström & Peel (1988). However, most of the specimen is essentially unilobate, similar to *C. barrosi* Baldwin, 1977, and *C. dispar* is decidedly bilobate; this, however, may simply be a reflection of preservational variability.

Ichnogenus *Curvolithus* Fritsch, 1908

cf. *Curvolithus* isp.
Fig. 6

Material. One specimen from GGU collection 314834–21.

Description. The specimen is poorly preserved on a pale green sandstone bedding surface and consists of an incomplete, curved, 10 cm long, 1.6 cm wide trilobed trace. Each lobe, two marginal and one axial, is gently convex, smooth and unornamented, approximately but uniformly 3 mm wide and raised slightly less than 1 mm. The lobes separate 3.5 mm wide, smooth and unornamented, flat surfaces which are at the same level as the plane of stratification.

Remarks. Fritsch (1908) introduced *Curvolithus* for trilobed burrows from the Ordovician of Czechoslovakia. Heinberg (1970, 1973) demonstrated the considerable morphological variation exhibited by the ichnogenus, which prompted Fillion & Pickerill (1990) to regard it as a candidate for taxonomic revision. Heinberg (1973) and Heinberg & Birkelund (1984) suggested the most likely producers to have been molluscs burrowing within the sediment, though more recently Lockley *et al.* (1987) suggested polychaetes, nermerteans and holothurians as possible candidates.

It is unknown whether the specimen is preserved on

an upper or lower bedding plane surface but we tentatively identify it as *Curvolithus* based on its trilobed morphology. Other potential alternatives include *Scolicia* de Quatrefages, 1849 and *Subphyllochorda* Gotzinger & Becker, 1932, both of which also exhibit a wide range of morphology depending upon style and level of preservation.

Ichnogenus *Cylindrichnus* Toots in Howard, 1966

Cylindrichnus isp.
Fig. 7a

Material. Two specimens from GGU collection 239665–14.

Description. Specimens occur as concentrically lined cylindrical structures preserved in concave epirelief on the upper surface of a sandstone bed. The concentric linings consist of alternating light and dark, less than 1 mm thick, sandstone and muddy sandstone layers. Burrow diameters are 5.1 mm and 4.2 mm; length unobserved, course presumably vertical. Burrow walls are sharp and clearly defined; fill is darker in colour but generally of similar grain size to the enclosing sandstone.

Remarks. As the specimens were not observed longitudinally it is unknown whether they represent *C. concentricus* Toots in Howard, 1966, *C. pustulosus* Frey & Bromley, 1985 or *C. errans* D'Alessandro & Bromley, 1986. *C. concentricus* is smooth-walled, whereas *C. pustulosus* possesses inconsistently spaced ridges and irregular large knobs on the outer wall. *C. errans* possesses lateral, randomly orientated, limited displacements of the causative shaft, producing vertical spreiten. Preservation in concave epirelief demonstrates that the structures do not taper downwards into a funnel-shape, such as in the ichnogenera *Rosselia* Dahmer, 1937 or *Monocraterion* Torell, 1870, thus enabling recognition at least at the ichnogeneric level. More complete descriptions and discussions of the ichnogenus are available in Fürsich (1974), Howard & Frey (1984), Frey & Bromley (1985), Frey & Howard (1985) and D'Alessandro & Bromley (1986).

Ichnogenus *Dimorphichnus* Seilacher, 1955

Dimorphichnus isp.
Fig. 7b

Material. One specimen from GGU collection 314801–4.

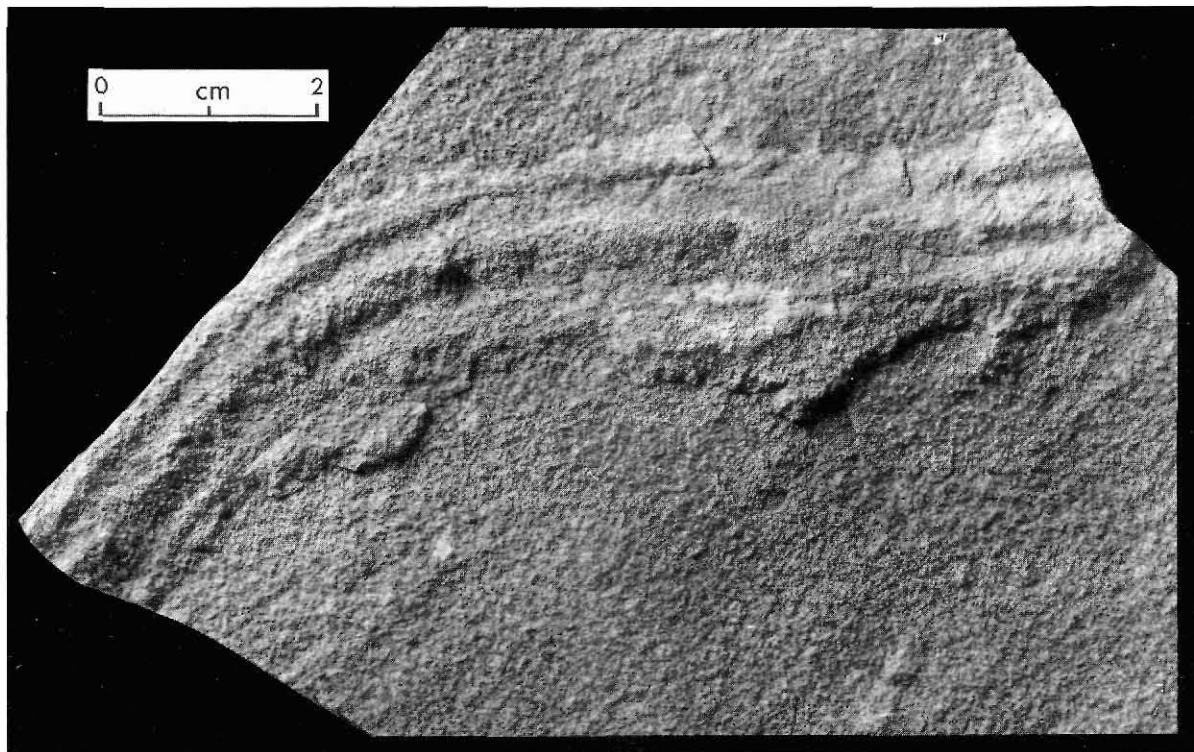


Fig. 6. Bedding plane view of cf. *Curvolithus* isp., MGUH 19.664 from GGU collection 314834–21.

Description. The specimen consists of a paired and parallel series of imprints preserved in convex hyporelief on a sandstone sole. One series of imprints is composed of three, possibly four, impressions, each 4 to 5 mm in length and 1 mm wide. These imprints are straight to slightly arcuate and are separated from the second series by 6 mm of undisturbed sediment. The second series comprises four, possibly five, straight imprints, each 2 to 3 mm in length and 1 mm in width. Individual imprints are featureless and are oriented normal to the track axis.

Remarks. Seilacher (1955) erected the ichnogenus *Dimorphichnus* for arthropod-produced dimorphic imprints of this configuration, erecting *D. obliquus* Seilacher, 1955 as the type. Although the ichnogenus still remains monospecific, the majority of authors have preferred to recognise *Dimorphichnus* at the ichnogeneric level (e.g. Crimes, 1970; Baldwin, 1977; Legg, 1985), presumably a reflection of its inherent morphological variability. The single and generally poorly preserved specimen from the Bastion Formation does not resemble *D. obliquus*. This ichnospecies is characterised by imprints of dot and sigmoidal shape but, following Legg (1985), the asymmetry of the imprints is the diagnostic feature allowing identification at the ichnogeneric level.

Fillion & Pickerill (1990) have recently discussed in detail the distinction of *Dimorphichnus* from the morphologically similar tracks *Diplichnites* Dawson, 1873 and *Petalichnus* Miller, 1880.

Ichnogenus *Gyrolithes* de Saporta, 1884

Gyrolithes saxonicus (Häntzschel, 1934)
Fig. 7c

Material. Three specimens from GGU collections 239665–6, 239665–17, 239918–4.

Description. The specimens, preserved in endorelief within fine-grained sandstones, are poorly preserved, incomplete and much compacted. Each consists of incomplete portions of dextrally coiled vertical burrows, with upward spirals decreasing in diameter. Coiling is regular and successive whorls are in contact but do not intersect. Burrows possess smooth surfaces, are oval in cross-section (probably a result of compaction) and have a maximum and apparently uniform diameter of approximately 5 mm. Maximum interpolated whorl diameter is approximately 5 cm.

Remarks. Though superficially resembling the ichnogenus *Fuersichnus* Bromley & Asgaard, 1979, which ex-

hibits horizontal, retrusive, curved burrow systems, the material described here is decidedly vertical and is therefore included within *Gyrolithes* de Saporta, 1884. *G. saxonicus* (Häntzschel, 1934) differs from the type ichnospecies *G. davreuxi* de Saporta, 1884, as described by Bromley & Frey (1974), by its smaller diameter, smooth external surface and regularity of coiling. *G. marylandicus* (Mansfield, 1927) and *G. bularti* Macsotay, 1967 are considerably larger and exhibit more open coiling. *G. polonicus* Fedonkin, 1980 is characterised by an incomplete circular whorl inferred to represent one turn of a coil about a vertical axis (Crimes & Anderson, 1985) and clearly differs from the material described here. Additional ichnospecies of *Gyrolithes*, as erected by de Saporta (1884), together with the junior synonym *Xenohelix* Mansfield, 1927 and its various ichnospecies (see Häntzschel, 1934, 1975; Macsotay, 1967) are no longer in general use. *Daemonhelix* Barbour, 1892 and *Dinocochlea* Woodward, 1922 are also probably junior synonyms of *Gyrolithes*, but re-examination of types will be necessary to confirm this. In view of the considerable degree of morphological variability of even the type material (Bromley & Frey, 1974), *Gyrolithes* and its synonyms are serious candidates for taxonomic re-evaluation. Until then, however, the material described here is assigned to *G. saxonicus*. More complete discussions on the nature and affinities of *Gyrolithes* are given in Gernant (1972), Bromley & Frey (1974) and Powell (1977).

Ichnogenus *Helminthopsis* Heer, 1877

Helminthopsis tenuis Książkiewicz, 1968
Fig. 7d

Material. Several specimens from GGU collections 314834–5 and 314834–6. Note that these two numbered collections are part of the same but broken slab.

Description. Thin, slender burrows preserved in convex hyporelief on a sandstone sole, uniformly 0.8 to 1 mm in diameter and up to a maximum length of 5 cm. Individual burrows loop or meander irregularly, some meanders high and narrow, others low and broad. Single burrows never display self level-crossing but may be intersected by alternate systems. Burrow surfaces are

smooth; burrow fill is similar in grain size to enclosing sediment.

Remarks. The specimens somewhat resemble *Helminthoidichnites* Fitch, 1850, placed into synonymy with *Gordia* Emmons, 1844 by Häntzschel (1975, p. W64) but recently resurrected by Hofmann & Patel (1989). They differ from this ichnotaxon by the presence of common meandering, a feature absent in the types displayed by Fitch (1850). They also resemble *Gordia*, but this ichnogenus is characterised by strings that wind but do not meander, with a marked tendency to intersection within single systems (Fillion & Pickerill, 1990). An exception to this is *G. meandria* Jiang in Jiang *et al.*, 1982, as also figured by Crimes & Jiang (1986, p. 646, fig. 4h), but this ichnotaxon exhibits large guided meandering strings that do not cross-cut; the ichnotaxon should best be assigned to an alternative ichnogenus. As such, we consider the material here conspecific with *H. tenuis* and do not concur with Häntzschel (1975, p. W70) to include this ichnospecies as a junior synonym of *Gordia*. More complete discussions and descriptions of *H. tenuis* are given in Książkiewicz (1968, 1977).

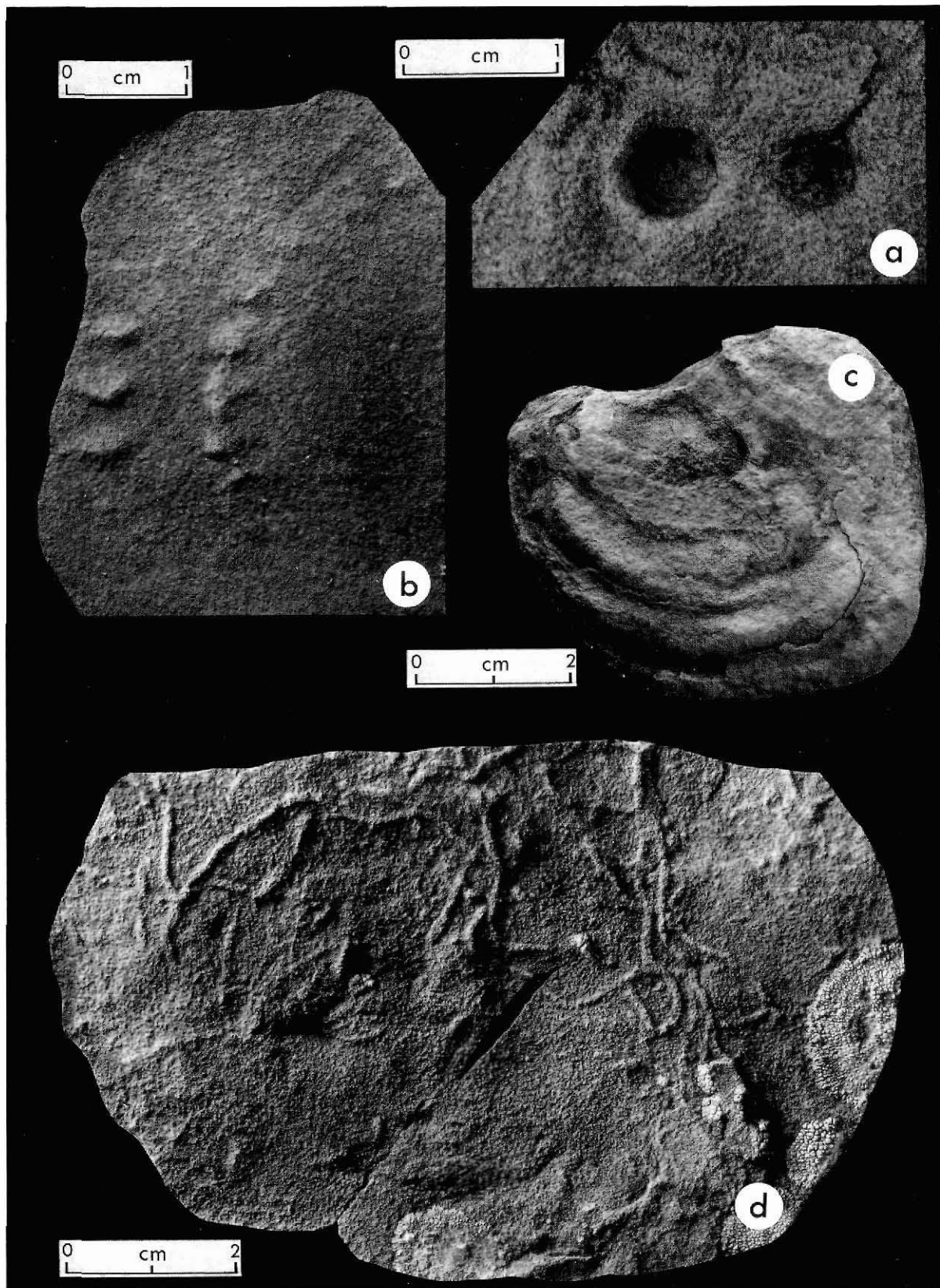
Ichnogenus *Monomorphichnus* Crimes, 1970

Monomorphichnus lineatus Crimes, Legg, Marcos & Arboleya, 1977
Figs 8a,b

Material. Two specimens from the collections made by Cowie & Spencer (1970); UBG M 20136 and UBG M 20137; both figured.

Description. Specimen UBG M 20136 comprises a set of seven slightly arcuate ridges preserved in convex hyporelief on a sandstone sole. The ridges are of unequal length (4 to 14 mm), approximately 1 mm in width (average) and are separated by 1 to 2 mm of undisturbed sediment. The central ridges are longer and slightly more deeply impressed. All ridges taper consistently in one direction (fig. 8a, to the left) and thicken in the other. Specimen UBG M 20137 (fig. 8b) comprises two sets of slightly smaller, narrower, less deeply impressed ridges preserved in convex hyporelief. Each set consists of four, possibly five, ridges of unequal length

Fig. 7. a, Two examples of *Cylindrichnus* isp. preserved in concave epirelief on upper sandstone surface; MGUH 19.665 and MGUH 19.666 from GGU collection 239665–14. b, *Dimorphichnus* isp. preserved in convex hyporelief on a sandstone sole; MGUH 19.667 from GGU collection 314801–4. c, *Gyrolithes saxonicus* preserved in endorelief; MGUH 19.668 from GGU collection 239665–6. d, *Helminthopsis tenuis* preserved in convex hyporelief on sandstone sole; MGUH 19.669 from GGU collection 314834–5 and 314834–6, two parts of the same slab which are rejoined in the illustration.



and impression similar to UBG 20136 as described above.

Remarks. Cowie & Spencer (1970, p. 97, pl. 2a, 2b) figured the material described here but only referred it to as 'arthropod scratch marks'. However, we concur with Fritz & Crimes (1985) and Crimes (1987) that the material can be assigned to *Monomorphichnus*. We regard it as conspecific with *M. lineatus*, originally defined by Crimes *et al.* (1977), which is characterised by sets of isolated, straight to sigmoidal ridges (or corresponding grooves). *M. bilineatus* Crimes, 1970 possesses ridges associated in pairs. *M. pectenensis* Legg, 1985 also has paired straight ridges but possesses intervening fine, comb-like striations.

Ichnogenus *Neonereites* Seilacher, 1960

Neonereites biserialis Seilacher, 1960

Fig. 8c

Material. One specimen from GGU collection 239665–18.

Description. The small and incomplete specimen is poorly preserved in convex hyporelief on a sandstone sole and consists of two rows of subcircular sediment pods. One row (upper row in fig. 8c) comprises four pods arranged slightly arcuately, individual pods being separated by a very small gap (0.3 to 0.5 mm). The second row comprises four more irregularly sized and disposed pods which may or may not be juxtaposed. Individual pods vary in size from 0.2 by 0.3 mm to 0.4 by 0.5 mm; total length of the trace is 1.7 cm.

Remarks. The ichnogenus *Neonereites* has been the topic of much nomenclatural controversy since Seilacher & Meischner (1965) first considered it to be a behavioural variant, but not synonymous with the related ichnogenus *Nereites* Macleay, 1839 and *Scalarituba* Weller, 1899. Chamberlain (1971) actually synonymised it with *Scalarituba*, the definition of which he expanded to include a '*Nereites* view' in convex hyporelief and a '*Phyllocytes* view' in concave epirelief. However, as more fully discussed by Fillion & Pickerill (1990), most subsequent authors, as we do herein, have preferred to retain *Neonereites* as a distinctive ichnogenus (see also Crimes, 1987).

Three ichnospecies are currently recognised, *N. uniserialis* Seilacher, 1960, *N. biserialis* Seilacher, 1960 and *N. multiserialis* Pickerill & Harland, 1988, being composed, respectively, of uniserial, biserial and multiserial rows of sediment pustules or pods. The single specimen described here, although poorly preserved, can be assigned to *N. biserialis*.

Ichnogenus *Palaeophycus* Hall, 1847

Palaeophycus striatus Hall, 1852

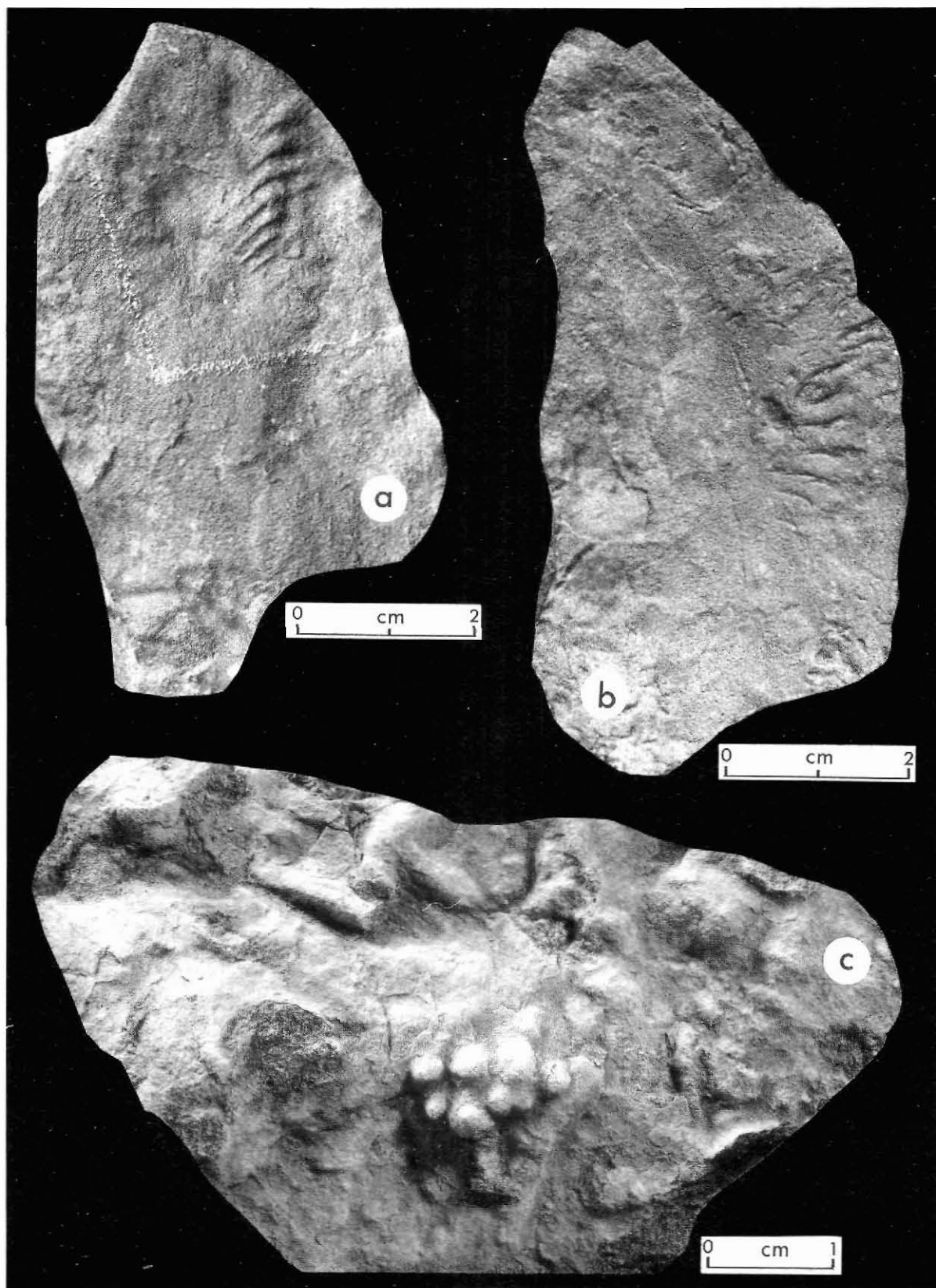
Figs 9a,b

Material. Four specimens from GGU collections 314801–9, 314834–10, 314834–11, 239917–5.

Description. Simple, unbranched, horizontal to sub-horizontal burrows preserved on upper sandstone surfaces, with each burrow combining preservation in concave and convex epirelief through its exposed length. Each possesses poorly preserved fine, parallel, longitudinal striations which, however, are not preserved through the entire burrow length, probably as a result of relatively coarse grain size. Burrows are straight to curved, approximately 4 mm in diameter, up to 9 cm in length, possess a fill of similar grain size to the host rock and an extremely thin lining of finer-grained material.

Remarks. Differentiation of the morphologically similar ichnogenus *Palaeophycus* Hall, 1852 and *Planolites* Nicholson, 1873 was addressed by Pemberton & Frey (1982) and more recently Fillion (1989). Fillion & Pickerill (1990) emended the diagnoses of these two ichnogenus, and also discussed their relationship to the morphologically similar burrow *Macaronichnus* Clifton & Thompson, 1978. Material from the Bastion Formation possesses a burrow fill of similar grain size to the host rock and burrow walls that are lined and possess parallel and longitudinal striations, thus permitting assignment to *P. striatus*.

Collections containing *P. striatus* also contain additional examples of epichnial grooves (as described later) and *P. tubularis* (as described below) and therefore the distinction between these three ichnotaxa, at least in these collections, would appear to be dependent on the variable and differential preservation exhibited between individual specimens.



Palaeophycus tubularis Hall, 1847

Figs 9c, 10a,b

Material. More than 60 specimens from GGU collections 314834-12, 314834-15, 314834-17, 314834-18, 314801-7, 314801-8, 314801-9, 314801-10, 239665-4, 239665-10, 239665-19, 239607-2, 239916-2, 239916-3, 239918-3; UBG 20135.

Description. Most specimens comprise simple, unbranched, horizontal to sub-horizontal burrows, preserved essentially in convex hyporelief and convex epirelief. Burrows are straight to curved to slightly tortuous, smooth and unornamented, thinly lined and possess a fill of similar grain size to the enclosing sediment. Dimensions are variable, up to a maximum 8 mm in diameter and 15 cm in length. Rare examples (e.g. fig. 10a) possess a 'beaded' lower surface along portions of their length; other examples exhibit evidence of burrow collapse, particularly those specimens preserved essentially in convex epirelief, along small segments of their course.

Remarks. Following Pemberton & Frey (1982) and Fillion (1989), these morphologically simple smooth burrows can best be assigned to *P. tubularis*. Notably, the rare 'beaded' examples strongly resemble *P. tortuosus* Hall, 1852, questionably synonymised with *P. tubularis* by Pemberton & Frey (1982). Although we were unable to section or observe burrow linings in all specimens, we suspect, on the basis of their smooth external surfaces and fill of similar grain size to the enclosing sediment, that these are conspecific and also include them within *P. tubularis*. The thin wall-lining of *P. tubularis* is easily removed by weathering, commonly resulting in apparently unlined burrows which, nevertheless, belong to this ichnospecies (Howard & Frey, 1984).

The above listed material represents only those collections in which the ichnospecies is clearly defined or occurs commonly. Other collections typically contain the ichnotaxon, as it is the most abundant trace fossil within the Bastion Formation; they are omitted from the description because of poor preservation.

Ichnogenus *Phycodes* Richter, 1850*Phycodes palmatus* (Hall, 1852)

Fig. 9d

Material. Two specimens one each from GGU collection 314801-7, and GGU collection 239665-10.

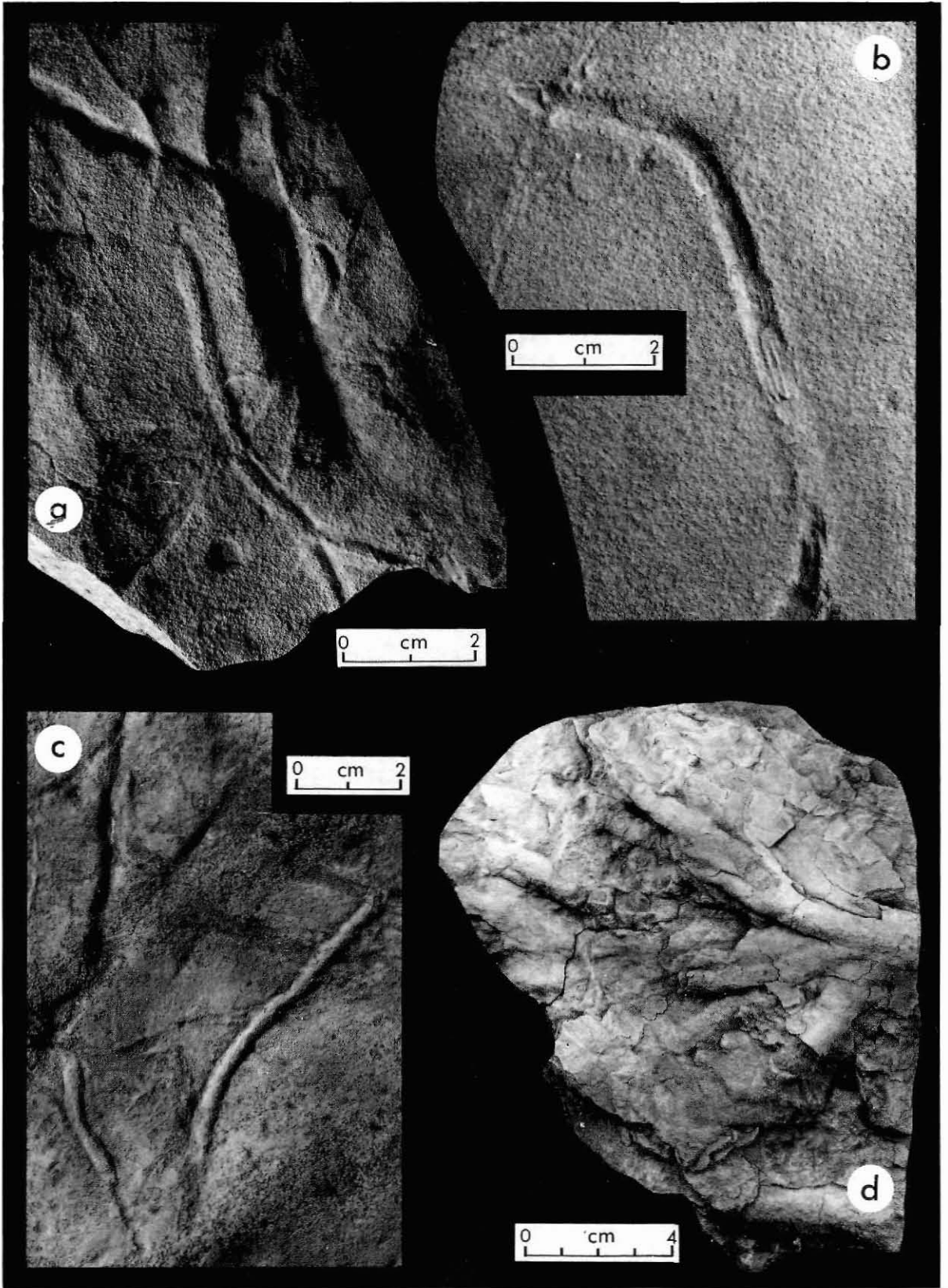
Description. The figured specimen is preserved essentially in convex hyporelief on a sandstone sole (fig. 9d); it consists of a 9 to 13 mm wide, smooth, horizontal and incomplete master burrow from which ramify six, possibly seven, other horizontal, slightly curved, burrows that radiate outwards from one side of the master burrow so that the entire system assumes a palmate or digitate form. Diameter of the unbranched secondary burrows varies from 8 to 11 mm and length is at least 13 cm in a single example. Their distal extremities are typically preserved in concave hyporelief. The secondary burrows originate at slightly different levels from the master burrow; thus the presence of a spreite can be inferred, even though the proximal portion was not vertically sectioned. Burrow fill is similar in grain size to the enclosing sediment; burrow surfaces are smooth and unornamented.

The second specimen is less well preserved and smaller; six 4 mm diameter, smooth, unbranched burrows ramify from a short initial master shaft in a fashion to that described above. The presence of a spreite can again be inferred as the secondary burrows are at slightly different levels within the enclosing sandstone.

Remarks. Since *Buthotrephis palmata* Hall, 1852 was first regarded as an ichnospecies of *Phycodes* by Seilacher (1955) the ichnotaxon has been referred to as *P. palmatum* in ichnological literature. However, as pointed out by Fillion & Pickerill (1990), *Phycodes* is a substantiated adjective and is masculine and the ichnotaxon should therefore be referred to as *P. palmatus*. *P. palmatus* is distinguished from other ichnospecies of *Phycodes* by its simple horizontal palmate form (for review see Fillion & Pickerill, 1990). The most similar ichnospecies, *P. curvipalmatus* Pollard, 1981, has shorter and more curved branches compared to *P. palmatus*.

The interpretation and detailed taxonomy of *Phycodes* have been extensively treated by Mägdefrau (1934), Seilacher (1955), Osgood (1970) and Fillion & Pickerill (1990).

Fig. 9. a, b, *Palaeophycus striatus* preserved on upper sandstone surfaces in positive epirelief; a is MGUH 19.671 from GGU collection 314834-11, b is MGUH 19.672 from GGU collection 314801-9. c, *Palaeophycus tubularis* preserved in positive epirelief on upper ripple-marked sandstone surface, MGUH 19.673 from GGU collection 314834-18. The same specimen is also shown in fig. 10b. d, *Phycodes palmatus* preserved in positive hyporelief on a sandstone sole, MGUH 19.674 from GGU collection 239665-10.



Ichnogenus *Plagiogmus* Roedel, 1929*Plagiogmus* isp.

Figs 10b-e

Material. Seven, possibly eight, specimens from GGU collections 314834-17, 314834-18, 314834-19, 314834-20, 239665-1, 239665-12, ?239916-2.

Description. Specimens are preserved on upper sandstone surfaces and consist of straight, curved to sinuous, isolated or rarely intersecting horizontal epirelief structures comprising a central flattened portion, preserved in concave epirelief, that possesses straight to slightly arcuate transverse ribs, preserved in convex epirelief. The central flattened portion is flanked by variably preserved external ridges, preserved in convex epirelief, that are typically straight but rarely exhibit slight convexity between individual transverse ribbed sections. The transverse ribs are 1 to 2 mm thick and extend to, or closely approach, the marginal ridges but never extend beyond them; they are variably developed but commonly are irregularly spaced within individual specimens. Though of variable dimensions, each specimen is typically 1.7 to 2.5 cm wide; the maximum observed length is 40 cm.

The specimen illustrated as fig. 10e is also preserved on an upper sandstone surface but at two stratification levels, and preserves the lower (similar to the above description) and the upper surfaces of the trace. The lower surface is a short, 2.5 cm long, and narrow, 0.8 cm wide, flattened section with pronounced marginal ridges preserved in convex epirelief and each approximately 1 mm wide. The upper surface consists of a variably preserved, 13.5 cm long, bilobed section of variable width (1.7 to 2.5 cm) preserved in convex epirelief. The lobes exhibit only moderate and slightly variable relief and are separated by a 2 to 3 mm wide axial furrow of variable but typically small depth. A portion of one of the lobes exhibits imbricated sediment pads.

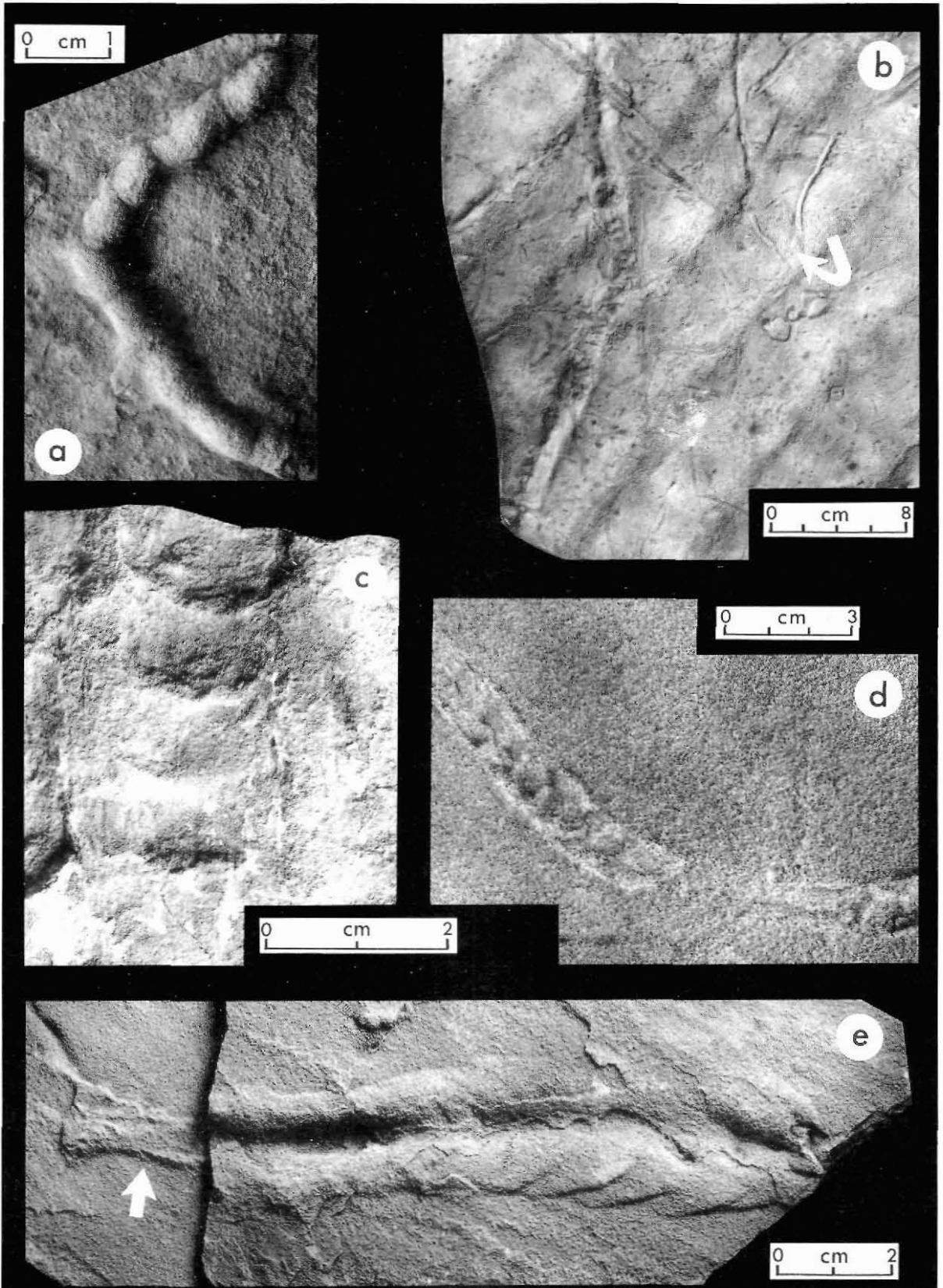
Remarks. Specimens illustrating the lower portions of the traces closely resemble *P. arcuatus* Roedel, 1929, subsequently designated by Häntzschel (1962, p. W210) as the type ichnospecies, from the Lower Cambrian of Sweden, but are not as well preserved. Jaeger & Mar-

tinsson (1980) restudied Roedel's types and, with the addition of topotype material, they demonstrated that *P. simplex* Roedel, 1929 was a synonym of *P. arcuatus*, though earlier Häntzschel (1964) and Glaessner (1969) reported them as distinct ichnospecies. Jaeger & Martinsson (1980) also demonstrated that *P. arcuatus* possessed a smooth unilobate upper surface which obviously differs from the bilobate and partially imbricated upper surface of the material described here. For this reason we only identify the material at the ichnogenetic level, but note that the ichnogenus remains monospecific, to our knowledge, providing Jaeger & Martinsson's (1980) conclusions are correct with respect to *P. simplex*. Indeed, most authors (e.g. Glaessner, 1969; Banks, 1970; Cloud & Bever, 1973; Peterson & Clark, 1974; Crimes *et al.*, 1977; Fritz & Crimes, 1985) have preferred to identify the trace only at the ichnogenetic level, despite the material, in some cases, being extremely well preserved.

In view of the morphological and preservational variability exhibited by the ichnogenus (see above cited references) it is an obvious candidate for taxonomic re-assessment at the ichnospecific level. We disagree with Fritz & Crimes (1985, p. 15) that the type material needs redescription as we feel that Jaeger & Martinsson's (1980) analysis of the types is perfectly adequate for comparative purposes.

The specimen illustrated in fig. 10e is of particular interest as it preserves both lower and upper surfaces of *Plagiogmus*; upper views are extremely rare in comparison to well-documented epirelief and hyporelief lower counterparts. As noted above, Jaeger & Martinsson (1980) figured and described a unilobate upper surface of a single specimen of *P. arcuatus*. Peterson & Clark (1974, p. 766, pl. 1, fig. 2) also figured upper surfaces preserved in both convex and concave epirelief and although apparently unilobate their exact nature cannot be determined from the plate. Singh & Rai (1983) described *Plagiogmus* possessing indistinct, smooth and rather flattened upper surfaces from the Lower Cambrian Tal Formation of the Lesser Himalaya. Kruse & West (1980) figured a specimen of *Plagiogmus* preserving both lower and upper surfaces. It possessed a better-preserved and more obviously transversely ribbed lower surface than the specimen described here, and a bilobed

Fig. 10. a, *Palaeophycus tubularis* preserved in convex hyporelief on a sandstone sole, MGUH 19.675 from GGU collection 314801-8. b, upper surface of ripple-marked sandstone slab representing GGU collection 314834-18 and illustrating *Palaeophycus tubularis* (arrowed), as illustrated in more detail in fig. 9c, and *Plagiogmus* isp., as illustrated in more detail in fig. 10c. c, detailed view of central portion of *Plagiogmus* isp. as shown in fig. 10b, MGUH 19.676 from GGU collection 314834-18. d, *Plagiogmus* isp. preserved in epirelief on upper sandstone surface, MGUH 19.677 from GGU collection 314834-17. e, *Plagiogmus* isp. illustrating the bilobed upper surface which possesses imbricated sediment pads and a short section of the corresponding lower surface (arrowed); MGUH 19.678 from GGU collection 239665-12.



upper surface with a well-developed median longitudinal groove. These authors noted that the 'molluscan trails' previously figured by Glaessner (1969, p. 388, figs 9B-D) strongly resembled the upper view of their *Plagiogmus*, and, indeed, referred these to the ichnogenus. The figured specimen of Kruse & West (1980, p. 168, fig. 4) did not exhibit the backfilled imbricated sediment pads, described herein and predicted by Glaessner (1969) in his 3-dimensional reconstruction of the trace which he correctly interpreted as an endichnial burrow (see also Jaeger & Martinsson, 1980). To our knowledge this is the first record of backfilled imbricated sediment pads within the ichnogenus.

These backfilled sediment pads are reminiscent of those observed in a portion of the ichnogenus *Psammichnites* Torell, 1870 described by Bryant & Pickerill (1990) from the Lower Cambrian Buen Formation of central North Greenland. Indeed, as first noted by Glaessner (1969, p. 387), both *Plagiogmus* and *Psammichnites* are currently considered to represent endichnial burrows produced by primitive molluscs and the complex and variable behaviour of the producers could potentially result in intergradational forms making assignment to one or the other extremely difficult, particularly if only poorly preserved or incomplete material was available.

Glaessner (1969) and more recently Crimes (1987, 1989) suggested that *Plagiogmus* was stratigraphically restricted to pre-trilobite late Tommotian to early Atabanian strata. This is clearly an oversimplification, however, as undoubted examples of the ichnogenus have been recorded from the Middle Cambrian of Utah (Peterson & Clark, 1974) and Montana and possibly Wyoming (Cloud & Bever 1973). Possible preservational variants have also been reported by Pickerill *et al.* (1984) from the Middle Ordovician of eastern Canada and Whitaker (1979) from the Upper Silurian to Lower Devonian of southern Norway (as *Steinsfjordichnus brutoni* Whitaker, 1979). Thus, while most commonly reported from strata of Early Cambrian age (see Crimes, 1987), its stratigraphic range is considerably more extensive.

Ichnogenus *Psammichnites* Torell, 1870

Psammichnites *gigas* (Torell, 1868)

Figs 11a-c

Material. Five, possibly six, specimens from GGU collections 239665–11, 239665–13, 239607–1, 239607–3 and a possible example in UBGM 20135.

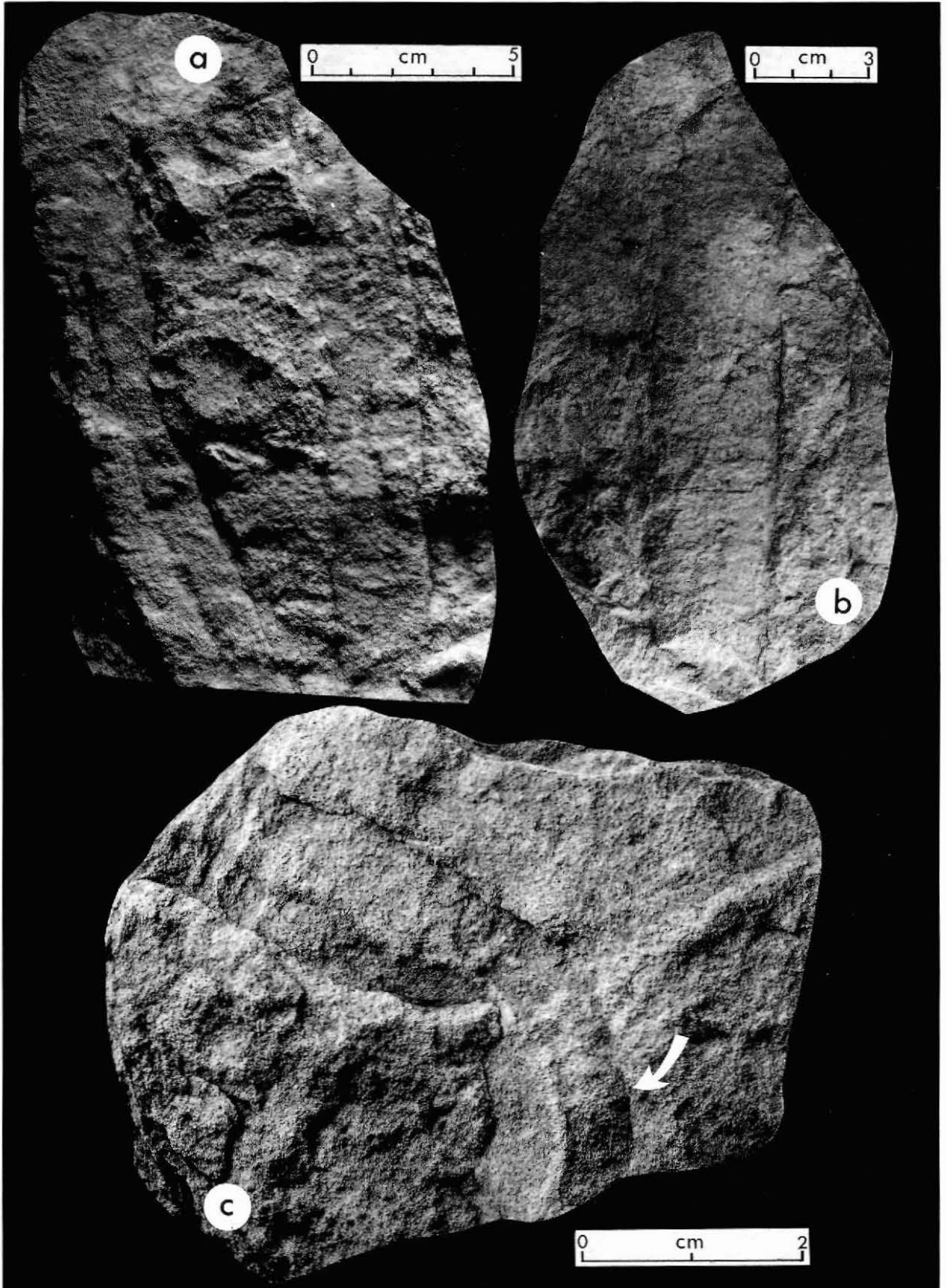
Description. Specimens exhibit variable morphology depending on style of preservation and level of view. The specimen illustrated at the extreme left in fig. 11a is preserved on a top surface and consists of a slightly raised, smooth, bilobed, straight to gently curved band, up to 17 cm in length and 2.4 cm in width. An axial furrow separates the two lobes but this feature is variably developed along the length of the specimen, so that in places the band appears almost unilobed. Individual lobes are flattened or very gently convex; they possess steep, almost vertical, outer margins so that where the axial furrow is developed the specimens displays an m-shaped cross-sectional profile. The specimen to the right in fig. 11a is morphologically similar, being preserved on the same bedding surface, but is less well preserved.

An additional specimen (fig. 11b) is preserved on a lower surface and comprises a straight, unilobed band (16 cm long, 3.3 cm wide) preserved in convex hyporelief. The trace is gently convex and possesses sharp and clearly defined straight external margins. Delicately preserved, evenly spaced, transverse arcuate striations are present on the external surface of the specimen but these proved almost impossible to reproduce photographically.

We suspect that a third preservational variant (fig. 11c) is also preserved on a lower surface. The specimen consists of a small and incomplete segment of a curved band, 7 cm in length along the median axis, and 1.2 cm in width. As with the specimen described above (fig. 11b), the trace is unilobed and gently convex with clearly defined outer margins. However, a narrow (1.5 mm) and slightly raised (1 mm) median ridge extends down the length of specimen. Crudely developed, transverse ornamentation is present on some segments of the trace.

Remarks. The taxonomy of *Psammichnites* and morphologically similar ichnogenera, such as *Olivellites* Fen-

Fig. 11. a, *Psammichnites* *gigas* preserved in epirelief on an upper sandstone surface, MGUH 19.679 (extreme left) and MGUH 19.680 (to the right) from GGU collection 239607–1. b, *Psammichnites* *gigas* preserved on a lower sandstone surface in positive hyporelief, MGUH 19.681 from GGU collection 239665–11. c, *Psammichnites* *gigas* preserved on an unknown upper or lower sandstone surface but illustrating a well-developed median ridge and crude transverse ornamentation (arrowed); MGUH 19.682 from GGU collection 239665–13.



ton & Fenton, 1937a, *Aulichnites* Fenton & Fenton, 1937b and *Laminites* Ghent & Henderson, 1966, is still in a state of confusion. In part, this is because it is still not clear as to whether or not Torell's (1868, pl. 1, fig. 2) original illustration represents its upper or lower surface (Fillion & Pickerill, 1990). Seilacher (1955) grouped *Psammichnites* with *Scolicia* de Quatrefages, 1849, as did Häntzschel (1962) who did not regard it, however, as a synonym. Fisher & Paulus (1969) selected the largest of Torell's four species, *Arenicolites* (*Psammichnites*) *gigas*, as the type ichnospecies and Häntzschel (1975) subsequently regarded it as a distinctive ichnotaxon. Chamberlain (1971) considered *Olivellites* to be a junior synonym of *Psammichnites* and D'Alessandro & Bromley (1987) placed *Olivellites* and *Aulichnites* as junior synonyms of *Psammichnites*, regarding *Laminites* as an additional possible synonym. However, Hofmann & Patel (1989) and Fillion & Pickerill (1990) argued that *Aulichnites* should be retained pending re-description and vertical sectioning of at least topotype material of *Psammichnites*. Additionally, if Torell's material proves to be preserved in convex hyporelief, as we suspect from comparison of material described here, then *Psammichnites* clearly differs from *Olivellites*. The latter is preserved in convex or concave epirelief (see Yochelson & Schindel, 1978; Eager *et al.*, 1985) and therefore possesses a totally different 3-dimensional configuration. More recent authors (e.g. Plaziat & Mahmoodi, 1988) have also retained *Olivellites* as a distinct ichnotaxon.

Complete knowledge of *Laminites*, its morphological range and preservational variants, is also lacking, though Plaziat & Mahmoodi's (1988, p. 222, fig. 13) reconstruction does favour incorporation within *Psammichnites* as tentatively proposed by D'Alessandro & Bromley (1987). Although it is clear that there is still much confusion regarding these varied ichnogenera, we follow current usage and utilise *Psammichnites* for relatively large burrows or trails with bilobed upper surfaces and steep outer margins (cf. Hofmann & Patel, 1989; Fillion & Pickerill, 1990).

Classification at the ichnospecific level is equally as unsatisfactory and re-study of Torell's (1870) material and other ichnospecies of *Psammichnites* is considered necessary. Indeed, most recent authors have only identified it at the ichnogenic level (e.g. Fisher & Paulus, 1969; Brasier *et al.*, 1978; McCarthy, 1979; Brasier &

Hewitt, 1979; Chaplin, 1980) and several such identifications, even at the ichnogenic level, are tenuous at best.

Hofmann & Patel (1989) provided a comprehensive description and analysis of *P. gigas* from the Lower Cambrian of New Brunswick, eastern Canada. Material from the Bastion Formation falls well within the morphological range of the New Brunswick samples (R. K. P., personal observation) and, pending re-assessment of types, we regard the material as conspecific. Hofmann & Patel's (1989, p. 145, fig. 5) schematic reconstruction of the ichnospecies clearly demonstrates that it represents an endichnial burrow (see also Fillion & Pickerill, 1990); their material is preserved as dorsal and ventral views which correspond to the first two preservational variants described here. Interestingly, the third preservational variant is not present in their material but is almost identical to Torell's (1868, pl. 1, fig. 2) type as figured, for example, by Häntzschel (1975, p. W100, fig. 62.2c). Clearly, *P. gigas* is a most complex ichnotaxon which exhibits a wide range of internal and external morphologies, presenting different morphologic aspects depending on level of view.

Finally, *Scolicia* figured by Cowie & Spencer (1970, p. 94, pl. 1a) is tentatively referred to *P. gigas*, a conclusion also made by Hofmann & Patel (1989). This specimen exhibits the ventral surface view of the burrow and, although somewhat flattened, possesses densely spaced (6 to 8 per cm) transverse to slightly arcuate striations, with clearly defined, 1 to 2 mm wide, marginal grooves. This latter feature has not been observed in other specimens from the Bastion Formation and so this comparison is only tentative. Hofmann & Patel (1989) also questionably included *Scolicia* figured by Crimes *et al.* (1977, p. 123, pl. 7d) from the Lower Cambrian of Spain within *Psammichnites*. However, this is preserved on an upper sandstone surface and does not conform to the reconstruction of *Psammichnites* by Hofmann & Patel (1989); it is best still regarded as *Scolicia*.

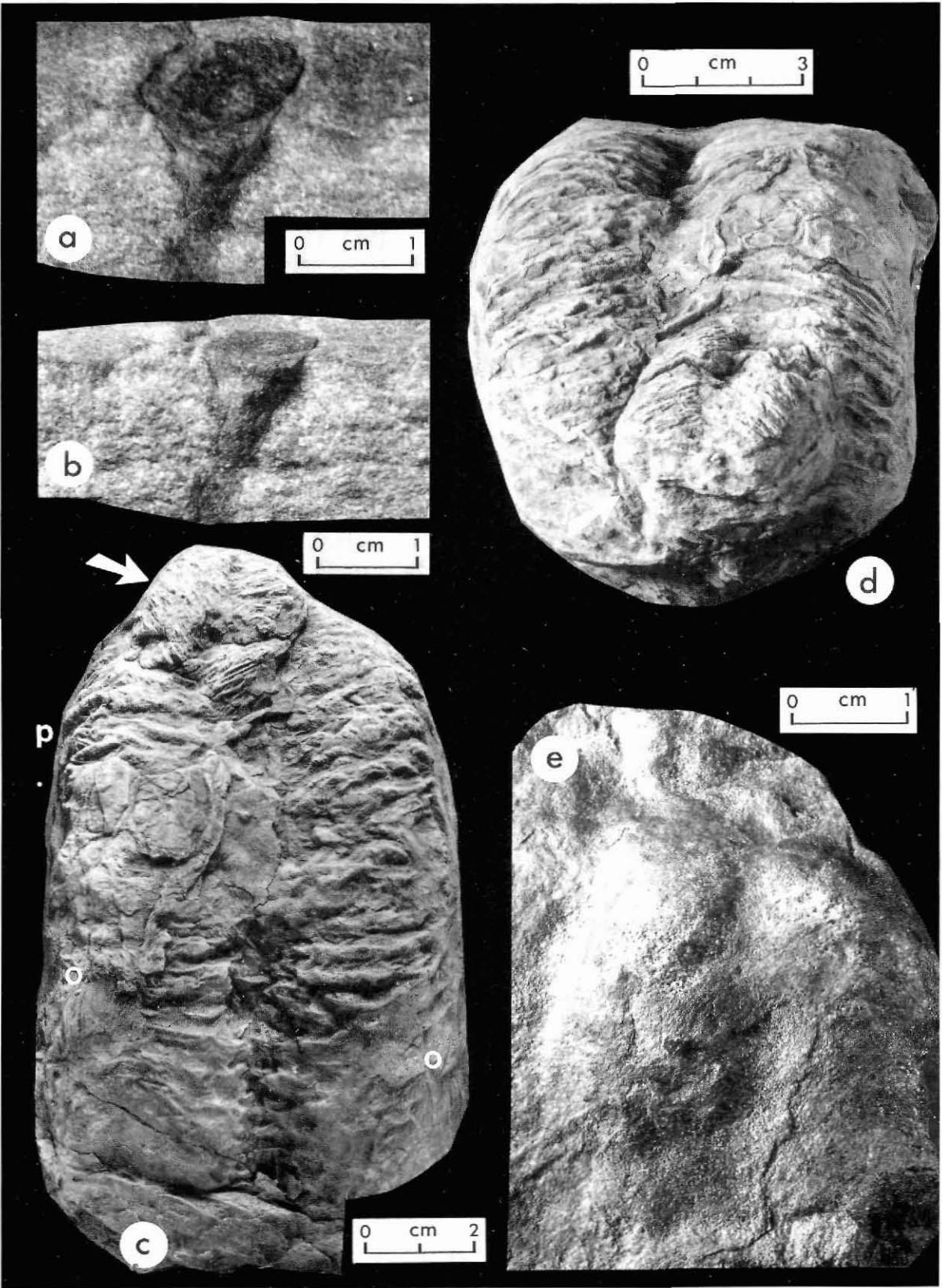
Ichnogenus *Rosselia* Dahmer, 1937

Rosselia socialis Dahmer, 1937

Figs 12a,b

Material. Three specimens from GGU collections 239665–21, 239918–2, 239918–5.

Fig. 12. a, b, oblique and lateral views of *Rosselia socialis* preserved in full relief in a laminated sandstone, MGUH 19.683 from GGU collection 239665–21. c, d, lower and oblique views of *Rusophycus dispar*, MGUH 19.684 from GGU collection 239917–3, in association with *Cruziana* cf. *C. fasciculata* (arrowed), as shown in more detail in fig. 4d. In c, p represents location of second-order scratches and o represents third-order scratches (for details see text). e, *Rusophycus* isp. preserved in convex hyporelief on a sandstone sole, MGUH 19.685 from GGU collection 239918–6.



Description. The figured specimen is a funnel-shaped, steeply inclined, sharp-walled, incomplete burrow preserved in full relief within a parallel-laminated sandstone (fig. 12a,b). The upper flared portion is 1.15 cm in diameter and this tapers downwards through the 2 cm thick slab to become 0.4 mm in diameter at its exposed base. The burrow possesses a concentrically laminated fill throughout; burrow fill is darker in colour and slightly finer-grained than the host material. Laminae adjacent to the burrow are not deflected.

The additional two specimens are less well preserved and generally incomplete, but clearly possess similar characteristics. The specimen from GGU collection 239918–5 has an upper funnel width of 0.9 cm and tapers downwards for at least 1.2 cm. The specimen from GGU collection 239118–2 has a 1.4 cm wide top which tapers down to a 0.6 mm wide tube. Both are concentrically lined.

Remarks. Although Seilacher (in Häntzschel, 1975, p. W101) considered the ichnogenus *Rosselia* to be a junior synonym of *Asterosoma* von Otto, 1854, most subsequent authors (e.g. Howard & Frey, 1984; Frey & Bromley, 1985; Frey & Howard, 1985; Miller & Knox, 1985; D'Alessandro & Bromley, 1986) retain it as a distinctive ichnogenus, as we do herein. Fillion & Pickerill (1984) and Frey & Howard (1985) have outlined the differences between these two ichnogenera together with the morphologically similar ichnogenus *Cylindrichnus* Toots in Howard, 1966. Indeed, basal stems of *Rosselia* are identical in construction to *Cylindrichnus*. Although the overlap in morphology presents a potential problem in their differentiation, the presence of a laminated fill helps distinguish both *Rosselia* and *Cylindrichnus* from the morphologically similar ichnogenus *Monocraterion* Torell, 1870, the base of which is a simple shaft (Frey & Howard, 1985). *Rosselia* is easily identifiable if the funnel-shaped upper portion of the burrow, with its distinctive concentrically lined fill, is preserved. Nevertheless, a range of preservational variants can exist where assignment to one or the other of these ichnogenera is difficult (see Howard & Frey, 1984; Frey & Bromley, 1985).

The specimens are rather small compared to most previously described examples of *R. socialis*, though Frey & Howard (1985) and Fillion & Pickerill (1990) do describe material of comparable size and Chamberlain (1971) has described even smaller examples. However, they clearly fall within the diagnosis of *R. socialis*, as defined by Dahmer (1937), and are regarded as conspecific. They differ from the two other currently commonly recognised ichnospecies, *R. rotatus* McCarthy, 1979 and *R. chonoides* Howard & Frey, 1984, in having

concentric laminae and lacking helicoidal swirls or crescentic backfill structures formed by rotary movements of the tube within the funnel.

Ichnogenus *Rusophycus* Hall, 1852

Rusophycus dispar Linnarsson, 1869
Figs 12c,d

Material. One specimen from GGU collection 239917–3.

Description. The specimen consists of an almost complete, moderately well preserved, deeply impressed bilobed trace preserved in convex hyporelief on a sandstone sole. Estimated length is 12.5 cm and maximum width is 8.2 cm to give a shape factor (length divided by width, see Crimes, 1970) of approximately 1.5. Maximum depth, developed towards the anterior portion of the specimen, is 3.2 cm. The trace is essentially straight-sided but broadens slightly anteriorly. Each lobe is separated by a moderately deep (fig. 12d) but variably preserved axial furrow which ranges in width from 2 to 5 mm and generally widens anteriorly. The anterior extremity is cut by a small segment of *Cruziana* cf. *C. fasciculata* (figs 12c,d).

Each lobe possesses three types of variably developed and preserved scratches. The most obvious of these are sharp, wide (up to 2 mm), deeply impressed, essentially transverse scratches, that are typically unid, more rarely bifid or trifid, particularly towards the outer margins of the lobes. Herein, these are termed first-order scratches. These scratches extend from the axial furrow across the entire lobes; they vary in depth and width and tend to become slightly proverse towards the anterior end of the specimen. Second-order scratches (fig. 12c-p) are thinner, less deeply impressed and isolated, or occur in bundles of up to at least three. These scratches are located between the first-order scratches and only towards the outer margins of the lobes at the anterior end of the specimen. Third-order scratches (fig. 12c-o), conversely, are only located at the posterior end of the specimen but again towards the external margins of the lobes. They consist of very finely impressed, densely spaced and essentially parallel scratches which run parallel to the external margins of the lobes; where they are present, first and second-order scratches are conspicuously absent.

Remarks. Following the interpretations of many previous authors (e.g. Seilacher, 1970; Bergström, 1973; Bergström & Peel, 1988), the coarse and transverse scratches (first-order) were probably made by the telopodites or walking legs of the producing arthropod. The

other scratches are more difficult to interpret, though we suspect that the intermediate, second-order scratches, located between the dominantly transverse scratches, are also a product of the telopodites. This is perhaps supported by the observation that, where present, they are located between first-order scratches that are essentially unid; they are not present between first-order bifid or trifid scratches. The producing arthropod was obviously multi-digitated, as revealed by the nature of the first-order scratches, which seems to support our explanation. The third-order scratches are herein interpreted as exite 'brushings' as not only do they resemble previously described exite-produced impressions on cruzianaeform and rusophyciform traces, but also they are located lateral to the telopodite-produced scratches. This latter observation is consistent with scratches interpreted as exite 'brushings' by previous authors (e.g. Seilacher, 1970; Bergström, 1973).

Our identification as *R. dispar*, based on only a single and incomplete specimen, clearly requires additional material for confirmation. Ideally, this ichnospecies, an integral component of the '*dispar* group' of Seilacher (1970), should exhibit proverse and obverse scratches on, respectively, the anterior and posterior portions of the trace. Although the first-order scratches are slightly proverse towards the anterior end, no obverse scratches are observed. Nevertheless, the coarse and deep first-order scratches, its relative depth and similarity with other examples of *R. dispar* (e.g. Linnarsson, 1869; Bergström, 1973; Alpert, 1976; Fillion & Pickerill, 1990) suggest that the specimen is correctly identified. Additionally, as pointed out by Bergström & Peel (1988), Seilacher's (1970) representations of the ichnospecies are highly schematic and do not represent the more typical preservation of the ichnospecies.

To date, *R. dispar* and its possible synonym *Cruziana rusiformis* Orłowski, Radwanski & Roniewicz, 1970, are known only from Lower Cambrian to Tremadoc strata (Fillion & Pickerill, 1990). The recording of *Cruziana* cf. *dispar* by Bandel (1973) from the Upper Devonian of Germany is best disregarded as this trace should clearly be assigned to a different ichnospecies.

Rusophycus latus Webby, 1983

Figs 13a,b

Material. Two specimens, one each from GGU Collection 239917-1 and GGU collection 239917-2.

Description. Both specimens are moderately well preserved in convex hyporelief on sandstone soles, each consisting of two moderately, but unequally impressed, well-defined lobes separated by a relatively shallow and

imperfectly and variably preserved axial furrow. General outlines are essentially heart shaped. The first specimen (fig. 13a) is 12 cm wide, 11 cm long and is widest and deepest (2.8 cm) in its anterior portion. The second specimen (fig. 13b) is 7.7 cm wide, 7.5 cm long and 2.8 cm in maximum depth. Shape factors (Crimes, 1970) of both specimens are therefore approximately 0.9.

Lobes possess sharp or rounded, unequally but clearly impressed, scratch marks that are 0.5 to 2 mm wide and 2.5 to 4 mm apart. The scratches are predominantly transverse but rarely may be deflected slightly forward immediately adjacent to the axial furrow. Though typically extending from the axial furrows across the convex lobes to their external margins, some scratches actually extend across the furrows. The scratches are typically unid, rarely bifid and possibly trifid; bunching into discrete sets is not apparent.

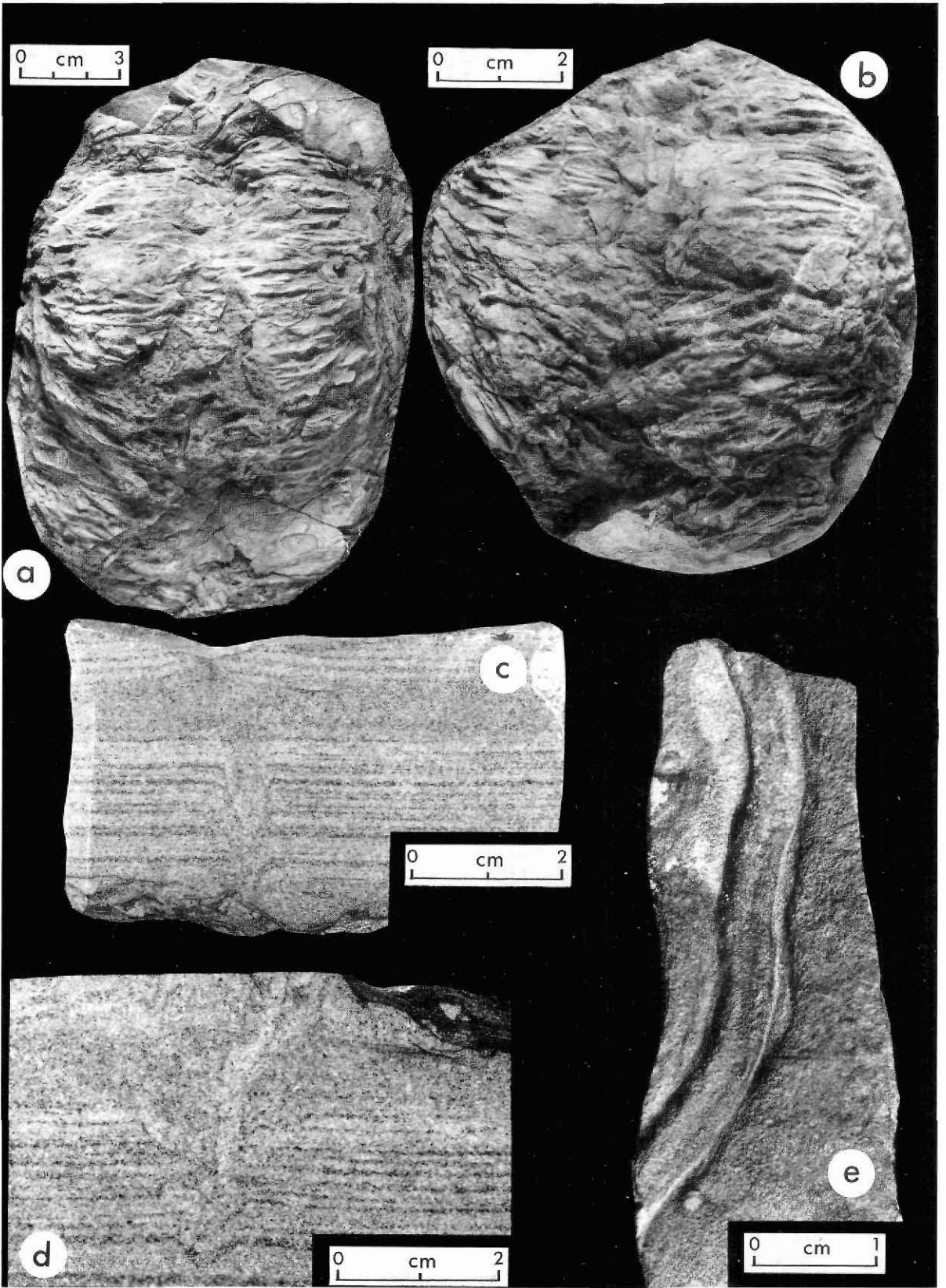
Remarks. *R. latus* is characterised by a transversely elliptical, through subquadrate to heart-shaped outline, a shape factor of less than one, transverse scratches that are not grouped into sets and may cross the relatively shallow axial furrow, with lobes widest and deepest in the anterior half (Webby, 1983; Fillion & Pickerill, 1990). The ichnospecies was first described from the Lower Ordovician of western New South Wales, Australia, by Webby (1983). Until now, only Fillion & Pickerill (1990) have subsequently formally recorded it from elsewhere, though these authors did note that several of Bergström's (1976) specimens of *Rusophycus* cf. *R. jenningsi* (Fenton & Fenton, 1937c) and *Rusophycus* isp. from the same Lower Ordovician sequence in eastern Newfoundland should more appropriately be regarded as *R. latus*. Webby (1983) did not provide a diagnosis, but the ichnospecies was validly erected; Fillion & Pickerill (1990) have since provided a diagnosis and have discussed differences between morphologically similar ichnospecies. Although the records of *R. latus* herein apparently extend its range to the Early Cambrian, Alpert (1976) has figured similar, albeit smaller, traces from the Lower Cambrian of California (e.g. Alpert, 1976, p. 232, fig. 4).

Rusophycus isp.

Fig. 12e

Material. One specimen from GGU collection 239918-6.

Description. The specimen is poorly preserved in convex hyporelief on a sandstone sole and consists of two smooth lobes separated by a poorly developed smooth median furrow which widens quite markedly post-



eriorly. The lobes are more deeply impressed, up to 0.4 cm, anteriorly and then slope gently posteriorly until they merge with the sandstone sole. Maximum width is 4 cm and incomplete length 3.8 cm to give a shape factor (Crimes, 1970) of approximately one.

Remarks. The single specimen is so poorly preserved that ichnospecific assignment is impossible. We know of no comparable ichnotaxon, though it does vaguely resemble *R. bonnarensis* Crimes, Legg, Marcos & Arboleya, 1977, as figured by Crimes *et al.* (1977, p. 107, pl. 3) from the Lower Cambrian of Spain. In overall shape it also resembles, particularly the anterior portion, *Rusophycus* cf. *R. dispar* as figured by Alpert (1976, p. 232, pl. 2, fig. 1) but differs from this by the absence of scratches; nevertheless, this difference may be preservational.

Ichnogenus *Skolithos* Haldeman, 1840

Skolithos linearis Haldeman, 1840

Figs 13c,d

Material. At least fifteen specimens in GGU collections 239665–21, 239665–22, 239918–3, 314834–15 and UBG M 20135.

Description. The material is typically observed on upper surfaces as generally isolated, circular to oval structures preserved in both convex and concave epirelief and on lower surfaces in convex hyporelief. Vertical sectioning (figs 13c,d) reveals these to be planar expressions of vertical to sub-vertical, straight to slightly sinuous, unbranched, cylindrical to sub-cylindrical tubes. Diameter of the tubes varies from 3 to 8 mm and is relatively constant throughout the length. Maximum observed length is dependent on thickness of the collected slabs but is at least 4 cm. Walls are typically distinct, more rarely indistinct, rarely thinly lined with mudstone and apparently smooth; burrow fill is of similar grain size to the enclosing host rock.

Remarks. As with several other commonly occurring ichnogenera, *Skolithos* has received considerable discussion and taxonomic evaluation. Although a thorough systematic review is undoubtedly necessary the nomenclatural scheme proposed by Alpert (1974) is regarded as still the most satisfactory for distinction at the ichnospecific level. Adopting this scheme, specimens from

the Bastion Formation can be regarded as *S. linearis*. We note, however, that complete knowledge of the 3-dimensional form of *Skolithos* is necessary for ichnospecific assignment, and that those specimens not sectioned longitudinally could possibly belong to additional ichnospecies.

Ichnogenus *Taphrhelminthopsis* Sacco, 1888

Taphrhelminthopsis isp.

Fig. 13c

Material. One specimen from the collections made by Cowie & Spencer (1970); UBG M 20138.

Description. The incomplete specimen is preserved in convex hyporelief on a sandstone sole and consists of a gently sinuous bilobed structure, 6.5 cm in total length and a constant width of 6 mm. The lobes are smooth and somewhat flattened and are separated by a variably developed, approximately 1 to 2 mm wide, 1 mm deep, narrow axial furrow which is itself rather flattened. The external margins of the lobes are relatively steep and pass into 1 to 2 mm deep and wide marginal grooves which extend down the whole length of the specimen and are slightly more deeply impressed than the stratification plane preserving the specimen.

Remarks. This specimen was first figured by Cowie & Spencer (1970, p. 97, pl. 2c) as an unidentified 'organic mark'. More recently Crimes *et al.* (1977, p. 126) and Crimes & Jiang (1986, p. 647) tentatively referred the specimen to *Taphrhelminthopsis circularis* Crimes, Legg, Marcos & Arboleya, 1977. Later, however, Crimes (1987, 1989) omitted the ichnogenus from his list of trace fossils occurring in the Bastion Formation of Greenland.

While we are in complete agreement with Crimes *et al.* (1977) and Crimes & Jiang (1986) that this specimen can be assigned to *Taphrhelminthopsis*, we disagree with their tentative ichnospecific assignment. *T. circularis* is characterised, in part, by an irregularly circling habit (see Crimes *et al.*, 1977; Crimes & Anderson, 1985; Fritz & Crimes, 1985; Crimes & Jiang, 1986; Narbonne *et al.*, 1987; Hofmann & Patel, 1989) which clearly cannot be ascertained from the short and incomplete section of the specimen described here. Accordingly, the specimen is best identified only at the ichnogeneric

Fig. 13. a, b, *Rusophycus latus* preserved in convex hyporelief on sandstone soles. a is MGUH 19.686 from GGU collection 239917–1 and b is MGUH 19.687 from GGU collection 239917–2. c, d, *Skolithos linearis* in vertical section cutting laminated sandstone layer. c is MGUH 19.688 and d is MGUH 19.689, both from GGU collection 314834–15. e, *Taphrhelminthopsis* isp. preserved in positive hyporelief on a sandstone sole, UBG M 20138.

level until additional material from the Bastion Formation becomes available for comparative purposes.

Ichnogenus *Teichichnus* Seilacher, 1955

Teichichnus rectus Seilacher, 1955

Figs 4c, 14a-c

Material. Seven, possibly eight, specimens from GGU collections 239922-1, 239922-2, 239918-1, ?239665-4.

Description. Specimens are preserved in full relief and consist of straight to slightly curved, typically smooth, unbranched burrows, parallel or slightly oblique to stratification and possessing a vertical retrusive spreite. Burrow length is variable, up to 13 cm; depth cannot always be ascertained but is at least up to 3 cm, and width, consistently less than depth, is up to 2 cm. Burrow fill is of similar grain size to host rock.

Remarks. *T. rectus*, the most commonly reported ichnospecies of the ichnogenus *Teichichnus*, is characterised by its vertical or near vertical, relatively straight unbranched retrusive spreite without evidence of back-fill. One specimen (fig. 14a) is slightly curved and therefore somewhat resembles *T. flexuosus* Schneider, 1962; this latter ichnospecies, however, tends to be more sinuous in plan view.

Epichnial grooves

Fig. 14d

Material. At least twenty specimens from GGU collections 239665-14, 239665-21, 239665-22, 314834-14, 314834-15, 314834-18, 314834-19, 239916-2, 239918-3, 239607-2.

Description. All specimens are preserved in negative epirelief and consist of simple, straight, curved or tortuous, unbranched, grooves, impressed 1 to 2 mm below stratification planes. The grooves are flat-bottomed, smooth and structureless and of variable dimensions, up to 1 cm in width and 20 cm in length. Width is relatively constant throughout individual specimens. Gently convex marginal ridges, 1 mm in width and height above the stratification planes, are commonly present but may be absent.

Remarks. It is impossible to determine from the preservational style whether these structures represent the basal sections of eroded and, or, collapsed burrows, or whether they represent former surficial trails. Specimens with marginal ridges strongly resemble collapsed portions of *Palaeophycus tubularis* as described herein. However, the absence of definitive morphological criteria precludes assignment even at the ichnogenetic level.

Pit and mound structures

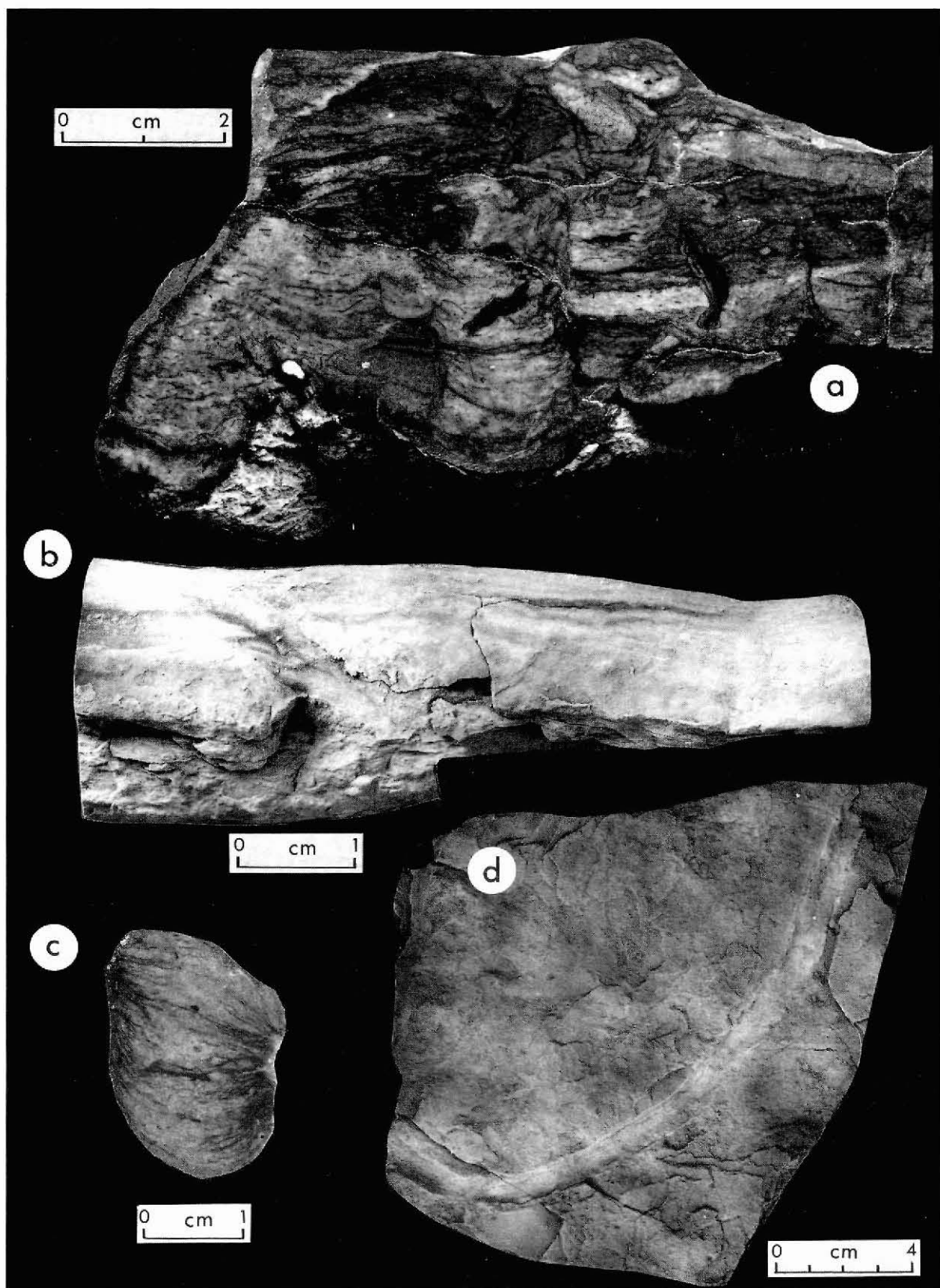
Fig. 15a

Material. Nine specimens from GGU collections 314834-14, 314834-15, 239665-20.

Description. Specimens are preserved on upper sandstone surfaces as elliptic mounds (2 specimens) in positive epirelief or depressions (7 specimens) in negative epirelief. Individual ellipses range from 2.3 cm by 1.1 cm to 3.7 cm by 2.1 cm; the mean is 2.9 cm by 1.8 cm. Mounds are composed of sandstone of similar grain size to the enclosing host rock; pits possess a fill of muddy sandstone, commonly with a swirl-like concentric structure and slightly elevated marginal sandstone rims, elevated 1 to 3 mm above the stratification planes. Transverse sectioning reveals that the structures are surface expressions of massive or concentrically ornamented, v-shaped, vertical disturbance zones which extend downwards, typically eccentrically (fig. 15), for at least 1.4 cm. Specimens do not exhibit a consistent vertical morphology; several simply terminate at the base of the eccentric v-shaped disturbance zone, whereas others exhibit evidence of underlying, essentially vertically oriented, biogenic activity. Fig. 15 illustrates such a specimen in which this underlying basal portion of the burrow possesses an incipient spreite similar to that of *Teichichnus* and laminae of the enclosing host rock are clearly deflected downwards.

Remarks. These structures are regarded as biogenic in origin as they bear no morphological resemblance to inorganically-produced (e.g. dewatering) structures. Although internally complex and variable, we group them collectively as pit and mound structures which is their typical upper surface expression. Upper surface expressions as pits surrounded by slightly raised sand-

Fig. 14. a-c, *Teichichnus rectus* shown in vertical cross-section (a and c) and vertical longitudinal section (b). a is MGUH 19.690 from GGU collection 239922-1 and b and c represent MGUH 19.691 from GGU collection 239922-2. The basal surface of the polished face in a is illustrated in fig. 4c, d, epichnial groove with well developed convex marginal ridges, MGUH 19.692 from GGU collection 239601-2.



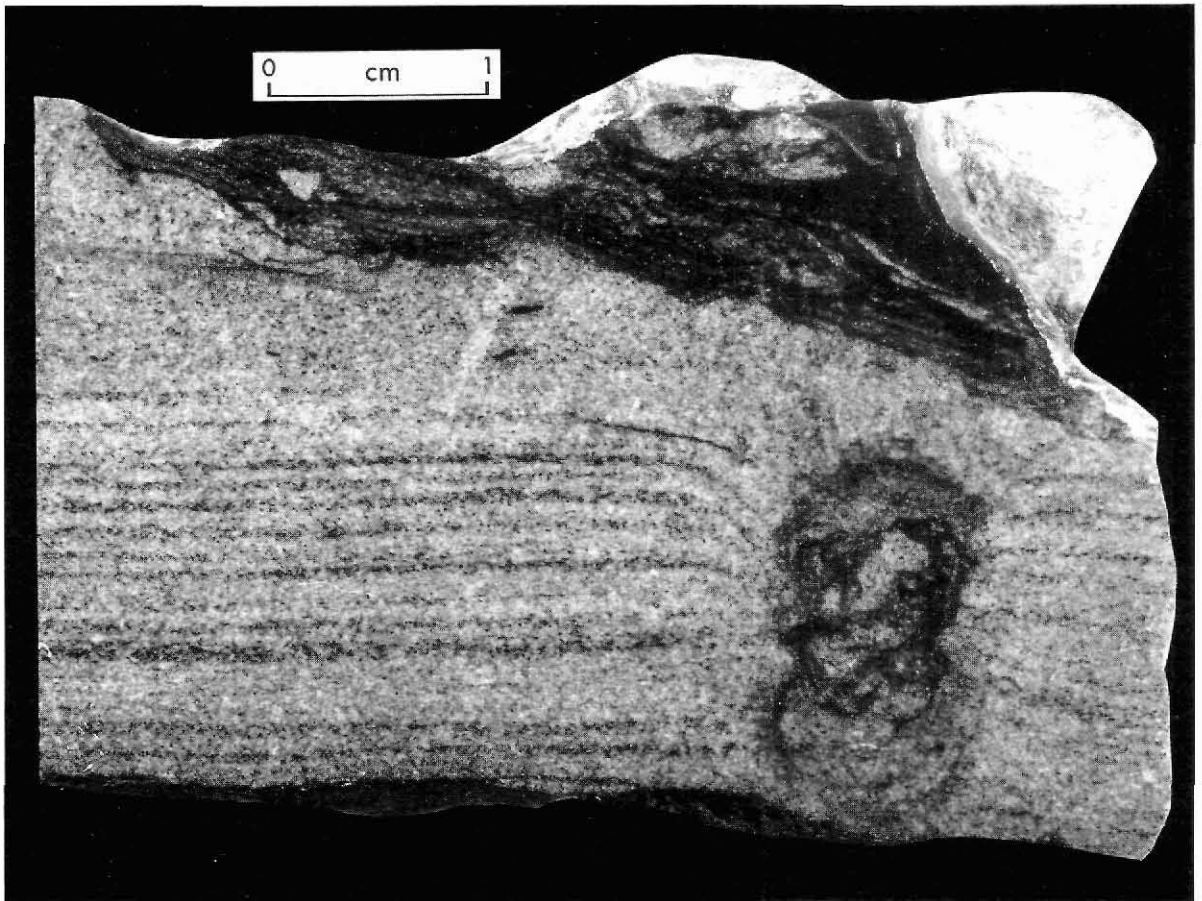


Fig. 15. Vertical cross-sectional view of a pit and mound structure underlain at the right by *Teichichnus*-like vertical spreite. Note the eccentric V-shaped disturbance zone with its concentric mudstone fill.

stone rims bear a vague resemblance to *Lingulichnus* Hakes, 1976, as figured by several previous authors (e.g. Durand, 1984; Fillion & Pickerill, 1990). However, the complex and morphologically variable transverse sections bear no resemblance to this ichnogenus which, incidentally, has only previously been recorded from a single example from Cambrian strata (Pember-ton & Kobluk, 1978). We know of no previously reported comparable analogues of these specimens and, in view of the relatively limited material which is itself not sufficiently morphologically distinct to warrant formal taxonomic treatment, we prefer to describe them informally.

Discussion and conclusions

This contribution is intended essentially as a more complete analysis and taxonomic treatment of trace fossils available from the Bastion Formation. Although representatives of 19 ichnogenera (25 ichnospecies) and

2 vernacular ichnotaxa are described, we believe that further sampling will reveal additional forms and will undoubtedly result in a more refined taxonomic evaluation. In part, this is because the collections were made randomly with no view to a thorough ichnological analysis. As the ichnospecies list (fig. 2) demonstrates, the more diverse and confidently identified material is present in the larger collections. Thus, the spatial and temporal variability of the ichnotaxa may not be realistic.

In our analysis we have usually avoided any discussion of potential producers of the described ichnotaxa because such information is available in many of the cited publications and in monographic studies (e.g. Frey, 1970; Osgood, 1970; Hakes, 1976; Książkiewicz, 1977; Durand, 1984; Fillion & Pickerill, 1990) or special symposia on trace fossils (e.g. Crimes & Harper, 1970, 1977; Miller *et al.*, 1984; Curran, 1985). It is clear from a review of these publications that although body fossils are not reported from the Lower Bastion Formation, a

variety of organisms inhabited the shallow marine substrates during its formation. These include arthropods, responsible for the production of *Cruziana*, *Dimorphichnus*, *Monomorphichnus* and *Rusophycus*, possible molluscs, responsible for *Plagiogmus* and *Psammichnites*, anthozoans, responsible for *Bergaueria*, and a variety of annelids that probably produced the remaining ichnotaxa described here. Such metazoans were obviously present in many Early Cambrian, pre-trilobite, shallow shelf areas as similarly suggested by their contained ichnofaunal assemblages.

Crimes (1987, 1989) recently reviewed the global occurrence of Lower Cambrian pre-trilobite shallow shelf successions and provided an extensive discussion of their contained trace fossils. The great majority of the ichnogenera recorded from the Bastion Formation have been reported from many Lower Cambrian successions (see Crimes, 1987, fig. 5). *Treptichnus*, reported by Fritz & Crimes (1985) and Crimes (1987; the 'feather stitch trails' of Cowie & Spencer (1970)), has not been recorded in the present collections, but also clearly falls within this category of well documented forms. Only *Cylindrichnus* and *Rosselia* were not considered by Crimes (1987) and are apparently rare forms in Lower Cambrian strata. *Rosselia* has been recorded, however, from the Lower Cambrian of the Salt Range of Pakistan by Seilacher (1955). The absence of *Cylindrichnus* is more enigmatic but may be due to the fact that although originally erected in 1966, it was only more clearly defined in 1985 by Frey & Howard, who were also the first to designate types. Most literature reviewed by Crimes (1987) pre-dates this publication and therefore the absence of *Cylindrichnus* may not be real; possible examples could have been previously identified as an alternative ichnotaxon, particularly *Skolithos*.

Considerable interest has been expressed during the last two decades in stratigraphic sections containing late Proterozoic and Early Cambrian transitional sequences, particularly for the purpose of defining the base of the Cambrian (Cowie & Brasier, 1989; Hofmann & Patel, 1989). Although a variety of fossil groups occur in the Precambrian–Cambrian transition most research has focused on small shelly fossils and trace fossils (e.g. Narbonne *et al.*, 1987; Landing *et al.* 1989). The stratigraphic succession of early skeletalised metazoans has been in primary focus (cf. Cowie & Brasier, 1989) but, despite substantial advances in the study of these small shelly fossils, major problems remain in the interpretation of their palaeobiology, palaeontology and evolutionary history (Brasier, 1986; Conway Morris, 1987; Narbonne *et al.*, 1987; Cowie & Brasier, 1989; see also Crimes, 1987, 1989).

Trace fossils have several significant advantages over

shelly fossils, particularly with respect to international correlation of the boundary interval. First, trace fossils are easily found and collected and most are easily identifiable at the ichnogenetic level (Crimes, 1989). Second, trace fossils are cosmopolitan in contrast to shelly faunas, many of which are decidedly provincial. Third, trace fossils always occur *in situ* and are not subject to secondary transportation. Fourth, several trace fossils have a restricted stratigraphical range and seem to have a regular order of first appearance at widespread locations (Crimes, 1989). Fifth, although essentially restricted to siliciclastic sequences spanning the boundary interval, trace fossils can also occur in carbonate facies (e.g. Jiang *et al.*, 1982; Crimes & Jiang, 1986; Fedonkin, 1987); therefore, unlike shelly fossils, trace fossils are facies-crossing (Narbonne & Myrow, 1988).

The importance of low-diversity assemblages of morphologically simple trace fossils in Precambrian strata, compared to the more diverse and complex assemblages within Early Cambrian strata, has long been recognised (for references, see Crimes, 1987, 1989; Narbonne *et al.*, 1987). Yet it is only relatively recently that zonal schemes for boundary-interval trace fossils have been proposed. The first such scheme, proposed by Jiang *et al.* (1982) from the boundary candidate at Meishucun in Yunnan province, China, has not generally received universal acceptance, as the lowermost two zones, in ascending order, the Precambrian *Sellaulichnus meishucunensis* and *Cavaulichnus viatorus* Zones, are based on non-diagnostic or poorly preserved material (Narbonne & Myrow, 1988). The uppermost two zones, in ascending order the *Didymaulichnus mietensis* and *Plagiogmus arcuatus* Zones, contain more typical Cambrian-type trace fossils but again are probably only locally significant; they were not even considered by Crimes & Jiang (1986) and Crimes (1987) in their more detailed discussion of the ichnology of the Meishucun section.

More recently Crimes (1987, 1989) proposed a truly global trace fossil zonation and recognised three zones of latest Precambrian and earliest Cambrian (sub-trilobite) trace fossils. These zones, based essentially on the first appearance and not the stratigraphic range of the trace fossils are:

Ichnofossil Zone I. Late Vendian. Composed of simple, horizontal or subhorizontal ichnogenera (e.g. *Cochlichnus*, *Didymaulichnus*, *Gordia*, *Neonereites*, *Scolicia*) with fewer vertical traces (e.g. *Arenicolites*, *Skolithos*). Several ichnogenera (e.g. *Bilinichnus*, *Harlaniella*, *Intrites*, *Nenoxites*, *Palaeopascichnus*, *Vendichnus*, *Vime-nites*) are apparently restricted to this zone.

Ichnofossil Zone II. Early Tommotian. Contains the first appearance of more complex and deeper burrowing ichnogenera (e.g. *Bergaueria*, *Diplocraterion*, *Phycodes*, *Teichichnus*, *Treptichnus*). All ichnogenera occur in younger strata.

Ichnofossil Zone III. Late Tommotian – early Atdabanian. Contains a considerably more diverse ichnofauna with the first appearance of arthropod traces (e.g. *Cruziana*, *Diplichnites*, *Dimorphichnus*, *Monomorphichnus*, *Rusophycus*) and spreiten-dwelling burrows (e.g. *Diplocraterion*). Ichnogenera such as *Astropolichnus* and *Plagiogmus* are considered to be restricted to this zone, though as previously noted, the latter has a more extensive stratigraphic range.

Narbonne *et al.* (1987) and Narbonne & Myrow (1988) also recognised three trace fossil zones for boundary-interval trace fossils. These three zones, in ascending order the *Harlaniella podolica*, *Phycodes pedum* and *Rusophycus avalonensis* Zones, were broadly equated with the Ichnofossil Zones I, II and III of Crimes (1987). Based on correlation with sequences containing published reports of small shelly fossils, Narbonne *et al.* (1987) regarded the *H. podolica* Zone as equivalent to only the upper half of Ichnofossil Zone I of Crimes (1987). The *P. pedum* Zone was equated with Ichnofossil Zone II which they suggested, based on published studies of the Rovno 'Horizon' of the East European Platform and in the Nemakit Daldyn of Siberia, together with their own work in eastern Newfoundland, possibly slightly predated the base of the Tommotian. Finally, the *R. avalonensis* Zone was correlated with Ichnofossil Zone III of Crimes (1987) but was regarded to range in age from possibly the early or middle Tommotian through the Atdabanian.

Based essentially on the report by Cowie & Spencer (1970), Crimes (1987, 1989) tentatively suggested a late Tommotian to Atdabanian age, equivalent to Ichnofossil Zone III, for the trace fossils of the Lower Bastion Formation. Narbonne & Myrow (1988, p. 75) regarded the sequence as attributable to the *P. pedum* Zone, that is, equivalent to Ichnofossil Zone II.

Disregarding the problem in relative ages proposed by these various authors, it is clear that the trace fossil assemblage described here and by Cowie & Spencer (1970) from the Bastion Formation can be correlated to Ichnofossil Zone III as proposed by Crimes (1987) or the *R. avalonensis* Zone as proposed by Narbonne *et al.* (1987) and Narbonne & Myrow (1988). Using data provided by these authors, *Arenicolites*, *Neonereites* and possibly *Monomorphichnus* (Crimes, 1987, p. 104) and *Skolithos* (but see Narbonne & Myrow, 1988, p. 74)

have been reported from strata as old as Ichnofossil Zone I or the *H. podolica* Zone. Ichnofossil Zone II, the *P. pedum* Zone, and younger strata have been reported to contain *Bergaueria*, *Gyrolithes*, *Helminthopsis*, *Monomorphichnus*, *Palaeophycus*, *Phycodes*, *Skolithos* and *Treptichnus*. The remaining ichnogenera make their first appearance in Ichnofossil Zone III or the *R. avalonensis* Zone. Clearly the entire assemblage from the Bastion Formation can be correlated to this latter zone, which is in accord with the conclusion of Crimes (1987, 1989).

The precise age of the Bastion Formation is difficult to assess. The Upper Bastion Formation has yielded olenellid and eodiscid trilobites, brachiopods, molluscs, hyoliths and bradoriids (Cowie & Adams, 1957; Cowie & Spencer, 1970) of Atdabanian or younger age. The underlying Lower Bastion Formation has not yielded body fossils but contains an extensive trace fossil assemblage (fig. 2) equivalent to Ichnofossil Zone III of Crimes (1987, 1989) or the *R. avalonensis* Zone of Narbonne *et al.* (1987) and Narbonne & Myrow (1988). As noted above, there is still some confusion regarding the exact age of the lower limit of these zones and considerably more research is required before general agreement can be reached. Nevertheless, we regard the Lower Bastion Formation to be late Tommotian to early Atdabanian, possibly entirely Atdabanian, based on a combination of the following observations:

1. The Lower Bastion Formation is overlain by Atdabanian or younger Lower Cambrian strata of the Upper Bastion Formation.
2. Crimes (1987, p. 105) noted that the general order of appearance of arthropod traces in Ichnofossil Zone III is, in ascending order, *Monomorphichnus*, *Diplichnites*, *Rusophycus* and *Cruziana*, and that *Rusophycus* and *Cruziana* are generally first encountered not far below the first trilobites. The occurrence of *Cruziana* in the lowermost few metres of the Lower Bastion Formation suggests, therefore, that the entire ichnoassemblage extends well into Ichnofossil Zone III.
3. The overall trace fossil assemblage is relatively diverse; comparison with other sequences of broadly comparable age (see Crimes, 1987, 1989) suggests that the range of behavioural activity represented in the Lower Bastion Formation is clearly reminiscent of other late Tommotian or, more specifically, Atdabanian sequences.

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