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Résumé de l'article

Dans les Basses Terres du St-Laurent de I'Est canadlen, les calcalres du Groupe de Trenton (Ordovicien moyen supeTieur) renferment, entre Montreal et Quebec, un assemblage d'ichnofossiles abondants et varies comprenant: Arenlcolltes sp., ?Calycraterion sp., Chondrites spp., Circullchnls montanus, Clema-tischnia sp., ?Conostlchnus sp., Cruzlana problematics, Cruzlana sp., cf. Dlpllchnltes sp., Furculosus carpathicus, Helminthopsis hieroglyphlca, Helminthopsis sp., Oichnus paraboloides, Palaeophycus tubularis, Palaeophycus sp., ?PIagiogmus sp., Planolltes beverleyensls, P. montanus, Planolltes sp., ?Rhizo-corallium cf. R. Irregulare, ?Rosselia sp., Scalarituba mlssourlensis, Scolicia sp., Skolithos linearis, Skolithos sp., Teichichnus rectus, Teichichnus sp., Trichichnus sp., Trypanites weisei, Vermlforichnus clarkel et Zoophycos sp. On y trouve egalement des galeries en boucle et fourchues, des terriers obliques ainsi que des perforations de bryozoaires, tous identifies de facon informelte. De toutes ces formes, seules les suivantes sont presentes en abondance: Chondrites spp., Palaeophycus tubularis, Palaeophycus sp., Planolltes spp., Teichichnus spp., et Trypanltes weisei; les autres sont rares ou peu communes. Nean-moins, nous decrlvons en detail toutes les traces fossiles et tentons par le fait mfime de resoudre plusfeurs problemes de nomenclature chez certains Ichnogenres qui font a l'heure actuelle t'objet de debats.

Le depOt des sediments du Croupe de Trenton s'est inltie dans un milieu de lagune puis de barre, de plate-forme de haut-fond et, flnalement, de plate-forme d'eau profonde. Les traces fossiles ne varient pas de facon significative d'un environnement de deposition a l'autre. On remarque plutot que chaque environnement se caracterlse par des assemblages typiques de I'lchnofacfes a Cruzlana tel qu'on I'observe dans les sequences detrltlques. Le substrat et ses caracterlstiques de base, qui refletent la disponibllite de la nourrlture et les conditions energetiques du milieu, constituent ('element majeur qui a, avant tout, limite la distribution spatiale et temporelte des traces fossiles.

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Systematic ichnology of the Middle Ordovician Trenton Group, St. Lawrence Lowland, eastern Canada

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Carbonate sediments of the upper Middle Ordovician Trenton Group between Montreal and Quebec City in the St. Lawrence Lowland, eastern Canada, contain a diverse and abundant trace fossil assemblage consisting of Arenicolites sp., ?Calycraterion sp., Chondrites spp., Circulichnis montanus, Clematischnia sp., ?Conostichnus sp., Cruziana problematica, Cruziana sp., cf. Diplichnites sp., Furculosus carpathicus, Helminthopsis hieroglyphica, Helminthopsis sp., Oichnus paraboloides, Palaeophycus tubularis, Palaeophycus sp., ?Plagiogmus sp., Planolites beverleyensis, P. montanus, Planolites sp., ?Rhizocorallium cf. R. irregulare, ?Rosselia sp., Scalarituba misouriensis, Scolicia sp., Skolithos linearis, Skolithos sp., Teichichnus rectus, Teichichnus sp., Trichichnus sp., Trypanites weisei, Vermiforichnus clarkei and Zoophycos sp. as well as informally diagnosed loop, oblique and pronged burrows and bryozoan borings. Of these forms, only Chondrites spp., Palaeophycus tubularis, Palaeophycus sp., Planolites spp., Teichichnus spp. and Trypanites weisei are abundant; the remainder are rare to only moderately common. Nevertheless, in this paper we describe all the trace fossils in detail and in doing so attempt to resolve several current and controversial problems of nomenclature regarding certain ichnogenera.

Sediments of the Trenton Group were deposited initially in lagoons followed in turn by offshore "bar", shallow and, finally, deeper offshore shelf environments. The trace fossils do not exhibit significant variation with respect to these broad depositional regimes and, instead, each environment is characterized by assemblages typical of the Cruziana ichnofacies as recognized in clastic sequences. The major factor primarily limiting the spatial and temporal trace fossil distribution was substrate and its primary characteristics, in turn a reflectance of food availability and environmental energy levels.

Dans les Basses Terres du St-Laurent de l'Est canadien, les calcaires du Groupe de Trenton (Ordovicien moyen supérieur) renferment, entre Montréal et Québec, un assemblage d'ichnofossiles abondants et variés comprenant: Arenicolites sp., ?Calycraterion sp., Chondrites spp., Circulichnis montanus, Clematischnia sp., ?Conostichnus sp., Cruziana problematica, Cruziana sp., cf. Diplichnites sp., Furculosus carpathicus, Helminthopsis hieroglyphica, Helminthopsis sp., Oichnus paraboloides, Palaeophycus tubularis, Palaeophycus sp., ?Plagiogmus sp., Planolites beverleyensis, P. montanus, Planolites sp., ?Rhizocorallium cf. R. irregulare, ?Rosselia sp., Scalarituba missouriensis, Scolicia sp., Skolithos linearis, Skolithos sp., Teichichnus rectus, Teichichnus sp., Trichichnus sp., Trypanites weisei, Vermiforichnus clarkei et Zoophycos sp. On y trouve également des galeries en boucle et fourchues, des terriers obliques ainsi que des perforations de bryozoaires, tous identifiés de façon informelle. De toutes ces formes, seules les suivantes sont présentes en abondance: Chondrites spp., Palaeophycus tubularis, Palaeophycus sp., Planolites spp., Teichichnus spp., et Trypanites weisei; les autres sont rares ou peu communes. Néanmoins, nous décrivons en détail toutes les traces fossiles et tentons par le fait même de résoudre plusieurs problèmes de nomenclature chez certains ichnogenres qui font à l'heure actuelle l'objet de débats.

Le dépôt des sédiments du Groupe de Trenton s'est initié dans un milieu de lagune puis de barre, de plate-forme de haut-fond et, finalement, de plate-forme d'eau profonde. Les traces fossiles ne varient pas de façon significative d'un environnement de déposition à l'autre. On remarque plutôt que chaque environnement se caractérise par des assemblages typiques de l'ichnofacies à Cruziana tel qu'on l'observe dans les séquences détritiques. Le substrat et ses caractéristiques de base, qui reflètent la disponibilité de la nourriture et les conditions énergétiques du milieu, constituent l'élément majeur qui a, avant tout, limité la distribution spatiale et temporelle des traces fossiles.

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INTRODUCTION

Detailed and systematic trace fossil studies of carbonate rocks, particularly of Lower Paleozoic age, are far outnumbered by comparable studies in their clastic counterparts. In part this is because paleontologists are generally attracted to carbonates by their normally abundant and well-preserved body fossils and are generally frustrated by the typically poor preservation, usually as a result of carbonate cementation and recrystallization, of their contained trace fossils. Yet many Lower Paleozoic carbonate sequences abound in trace fossils of various kinds and with careful and detailed analysis their systematics

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can be resolved at the ichnogeneric and even the ichnospecific level.

In this paper we describe the systematics of a suite of trace fossils contained in carbonates of the upper Middle Ordovician Trenton Group exposed between Montreal and Quebec City in the St. Lawrence Lowland, eastern Canada (Fig. 1). This study is one of the first of its kind in Lower Paleozoic carbonate sequences and highlights several controversial and taxonomical problems regarding certain ichnogenera. A companion paper (Fillion et al. 1984) has evaluated their spatial and temporal distributional patterns and primary controlling parameters within the sequence but, until now, the systematics remain unpublished despite the many recordings by previous authors of 'burrows', 'tracks' and 'trails' (eg. Flower 1945; Clark et al. 1972; Clark and Globensky 1975, 1976a).

As the content of this paper is decidedly taxonomic only a brief summary of the stratigraphic, sedimentologic and environmental setting of the Trenton Group is presented below. More detailed reviews can be found in the referenced papers.

STRATIGRAPHIC, SEDIMENTOLOGIC AND ENVIRONMENTAL SETTING

In the St. Lawrence Lowland between Montreal in the southwest and Quebec City in the northeast, a distance of approximately 250 km (Fig. 1), the upper Middle Ordovician Trenton Group has been subdivided into many lithostratigraphic units several of which, because of their overall similarity, are candidates for synonymy (Harland and Pickerill 1982). Because such stratigraphic revision has not been attempted to date, the previously established units are retained herein. Figure 2 summarizes the Trenton Group stratigraphy and places it in context with underlying and overlying formations. More detailed lithostratigraphic and biostratigraphic summaries are available in Clark (1972), Clark and Globensky (1975, 1976a,b,c) Riva (1968, 1969, 1972). Figure 3 summarizes the essential characteristics and interpreted environment of deposi-

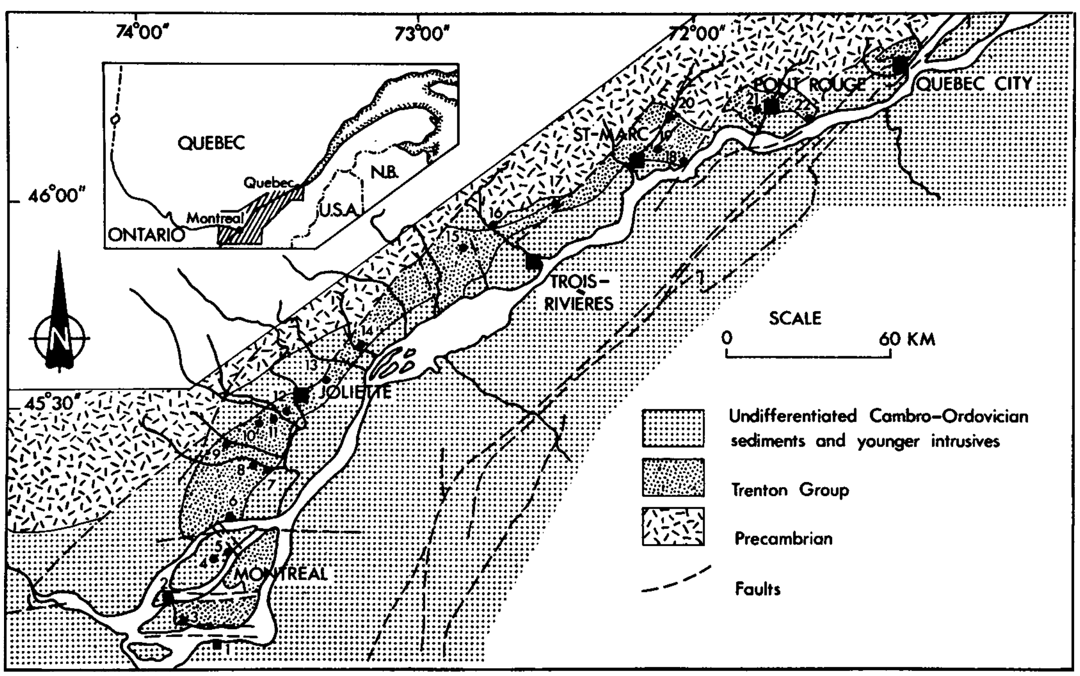

Fig. 1 - Simplified geological map of the St. Lawrence Lowland between Montreal and Quebec City. Numbered localities are: 1. Saint Constant, 2. Île Bizard, 3. Montreal, 4. Cap Saint Martin, 5. Saint Vincent de Paul, 6. Terrebonne, 7. L'Epiphanie, 8. Saint Roch, 9. Saint Esprit, 10. Saint Jacques, 11. Highway 158/Rivière Ouareau, 12. Highway 158/Rivière Rouge, 13. Pont Corriveau, 14. Barrage savoie, 15. Pont Bournival, 16. Saint Louis de France, 17. Radnor des Forges, 18. Grondines, 19. Saint Casimir, 20. Pont Saint Alban, 21. Pont Rouge, 22. Neuville.

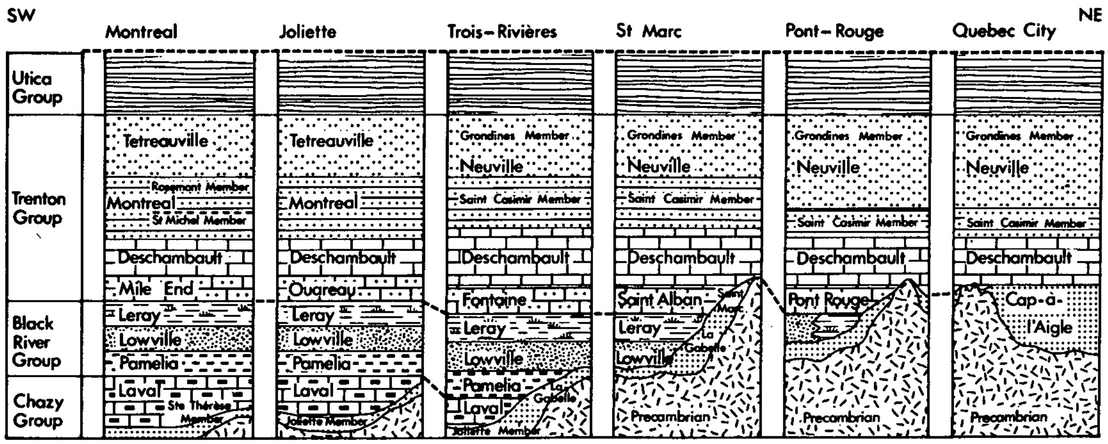

Fig. 2 - Stratigraphic profile of Middle Ordovician lithostratigraphic units between Montreal and Quebec City showing the relationship of the upper Middle Ordovician Trenton Group to underlying and overlying units. Modified after Harland and Pickerill (1982).

tion of each formation, generalized details of which are given below.

The basal Trenton Group formations comprise, from southwest to northeast, the Mile End, Ouareau, Fontaine, Saint Alban and Pont Rouge Formations. These are generally thin (2-6m) and consist of irregular beds of micritic and argillaceous calcisiltites which alternate with thin shales. The shales and most limestones are thoroughly bioturbated. Coquinas, lenses and layers of shell and skeletal hash and muddy skeletal intraclastic layers also occur. Each of these formations is similar to the underlying Lowville and Leray Formations of the Black River Group and are interpreted as having originated in broadly similar conditions, that is in a low to moderate energy outer lagoon or sheltered near-shore environment which became narrower and more confined from Montreal to Quebec City (Harland and Pickerill 1982). The common occurrence of shell layers indicates a fairly close proximity to fully marine environments.

The overlying Deschambault Formation, present throughout the St. Lawrence Lowland, is generally 24-28 m thick, but thins to about 5 m at Montreal, and is characterized by 20cm - 1m thick, fine- to coarse-grained, tabular and trough cross-stratified skeletal limestones with numerous coquinas and layers of shell hash and only minor shales. These represent high energy deposits which accumulated in a complex environment of migrating subtidal shoals, bars and large ripples (Harland and Pickerill 1982). Additionally, the formation contains more continuous parallel-laminated or low-angle cross-stratified beds which represent ephemeral beaches developed when shoals and bars were intermittently built up to sea level. Scouring appears to have been common and subtidal channels and runnels cut through the shoals and bars. From Montreal northeastwards, these skeletal limestones developed progressively closer to shore so that in the Quebec City area they accumulated along rocky shorelines and around islands (Harland and Pickerill 1984).

Overlying the Deschambault Formation is the Montreal Formation in the Montreal-Joliette area and the St. Casimir Member of the Neuville Formation from Trois Rivières to Quebec City (Fig. 2). The former is 110-140m thick and the latter 40-60m but generally thins northeastwards. Both consist of highly variable limestones interbedded with dark shales. The limestones are predominantly thinly and irregularly bedded, bioturbated argillaceous micrites but dark micritic rubbly beds or skeletal calcarenites and coquinas (generally 5-10cm but up to 25 cm thick) may also occur. Their high diversity marine faunas and predominantly fine-grained nature indicate a shallow subtidal, mainly low to moderate energy environment in which skeletal layers were produced by storm reworking of indigenous shelly faunas or periodically derived, perhaps during storm-ebbs or other unusually strong offshore currents, from shoreward shoaling environments (Harland and Pickerill 1982).

The uppermost units of the Trenton Group are the Tetreauville Formation (150m thick) in the Montreal-Joliette area and the Grondines Member of the Neuville Formation (100-120m thick) from Trois Rivières to Quebec City (Fig. 2). Both consist of 3-15cm thick argillaceous and dark micritic limestones interbedded with dark shales. Infrequent thin shelly or skeletal beds, which are commonly graded, are also present. Nodular or irregularly bedded limestones are common and typically progressively increase in frequency through the sequence. Fully marine faunas dominated by brachiopods and trilobites are sparse but diverse and widely distributed whereas bioturbation is high. The sediments were deposited essentially from suspension in a relatively deep, low energy subtidal environment. The infrequent thin skeletal layers are interpreted as distal storm deposits (Harland and Pickerill 1982).

SYSTEMATIC PALEONTOLOGY

As in Häntzschel (1962, 1975), the trace fossils are described below in alphabetical order. In adopting this scheme, subjective and often overlapping ethological groupings, as utilized by several previous studies (e.g. Osgood 1970, Chamberlain 1971, Fürsich 1974a), are avoided and the procedure enables ease of reference to a single ichnogenus. Informally named trace fossils are listed separately after the formally named ichnogenera. Preservational terminology follows that adopted by Seilacher (1964), Webby (1969) and Häntzschel (1975). For brevity, the geographic and stratigraphic distribution and environmental occurrence of each ichnogenus is omitted from the descriptions. Instead reference should be made to Figures 4, 5 and 6 which summarize this information. Representative examples of the majority of collected specimens are now housed in the Department of Geology, University of New Brunswick, as Collection S161 - D. Fillion.

Ichnogenus **Arenicolites** Salter, 1857.

<u>Type species</u> - **Arenicola carbonaria**

	FORMATION		LITHOLOGY	ENVIRONMENT
TRENTON GROUP	TETREAUVILLE NEUVILLE Grondines Member	150 m 100-120 m	Interbedded argillaceous and micritic limestones and shales. Occasional thin skeletal layers. Rubbly or nodular beds increase upwards.	Offshore, deep subtidal, low energy shelf subject to periodic storm influxes.
TRENTON GROUP	MONTREAL NEUVILLE Saint Casimir Member	110-140 m 40-60 m	Interbedded fine-coarse limestones with thin shales. Argillaceous micrites predominant but also thin skeletal limestones and coquinas.	Shallow subtidal, low to moderate energy environment. Periodic influxes of skeletal material from shoreward shoaling environments.
TRENTON GROUP	DESCHAMBAULT	5-28 m	Cross-stratified skeletal limestones coquinas and shell hash. Minor shales.	Shallow subtidal shoals, bars, large-scale migrating ripples and ephemeral beaches. High energy.
TRENTON GROUP	MILE END OUAREAU FONTAINE SAINT ALBAN PONT ROUGE	2-6 m	Micrites, argillaceous limestones and shale interbeds, with skeletal hash layers and lenses.	Low energy outer lagoon or sheltered nearshore environment with periodic influxes of storm and tidal overwashes from offshore shoals.
BLACK RIVER GROUP		—	Mixed tidal flat, lagoonal and nearshore siliciclastics and carbonate muds.	

Fig. 3 - Facies analysis and inferred depositional environments of the Trenton Group between Montreal and Quebec City (after Harland and Pickerill 1982).

Binney, 1852, by subsequent designation of Richter (1924, p. 137).

Diagnosis - Vertical U-tubes without spreite (after Fürsich 1974a).

Discussion - **Arenicolites** is generally considered to be both the dwelling and feeding burrow of suspension-feeding (particularly polychaete) annelids (Hakes 1976, Chamberlain 1978a) or possibly crustacean-like organisms (Goldring 1962). Though typically a shallow-water form it has also been reported from deep-water deposits (e.g. Crimes 1977, Pickerill and Keppie 1981, Hill 1981). It ranges in age from Cambrian-Recent (Chamberlain 1978b).

Arenicolites sp.
(Figure 7d)

Material - 8 specimens.

Description - Specimens are observed as either vertical U-plane sections or as paired circular openings on upper bedding plane surfaces of parallel laminated calcilutites. Burrow height is up to 18mm and width ranges from 5.6 - 28mm. The tubes are vertical, parallel and of identical diameter, range from 0.5 - 3mm and are typically lined. In U-plane sections they exhibit an evenly rounded base.

Remarks - No single specimen provided both vertical U-plane and bedding surface expression thus negating ichnospecific identification. In bedding plane expression the Trenton material differs from **A. curvatus** Goldring, 1962, **A.** (?) **compressus** (Sowerby 1829) and **A. subcompressus** (Eichwald 1860) in having burrows with a circular cross-section. Additionally, they are too small and too regular to be included within **A. variabalis** Fürsich 1974a. U-Plane sections compare favourably with **A. carbonaria** (Binney 1852) whereas bedding plane ex-

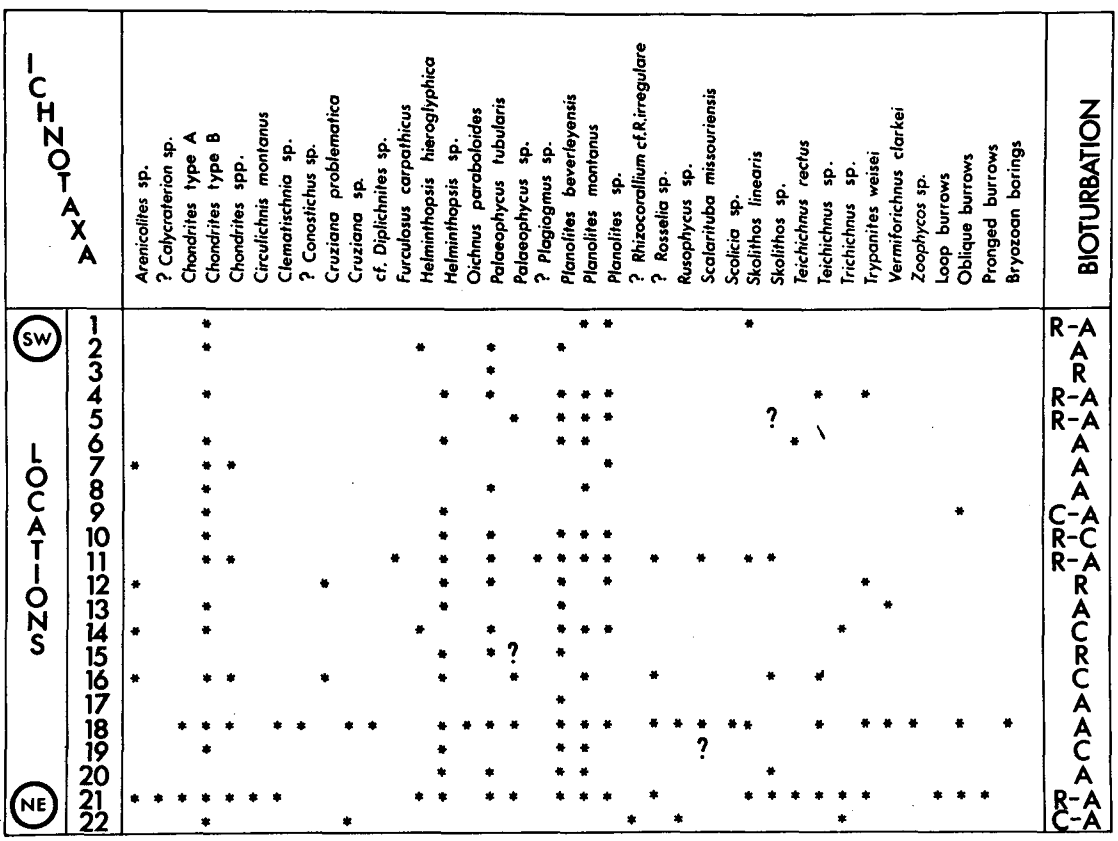

Fig. 4 - Spatial distribution of trace fossils in the Trenton Group between Montreal and Quebec City from locality 1 in the southwest to 22 in the northeast. Localities 1-22 as indicated in Figure 1. Asterisks indicate the presence of a particular ichnogenus/ichnospecies and questionable occurences refer to uncertain identifications. The relative degree of associated bioturbation at individual locations is indicated by R=Rare, C=Common and A=Abundant.

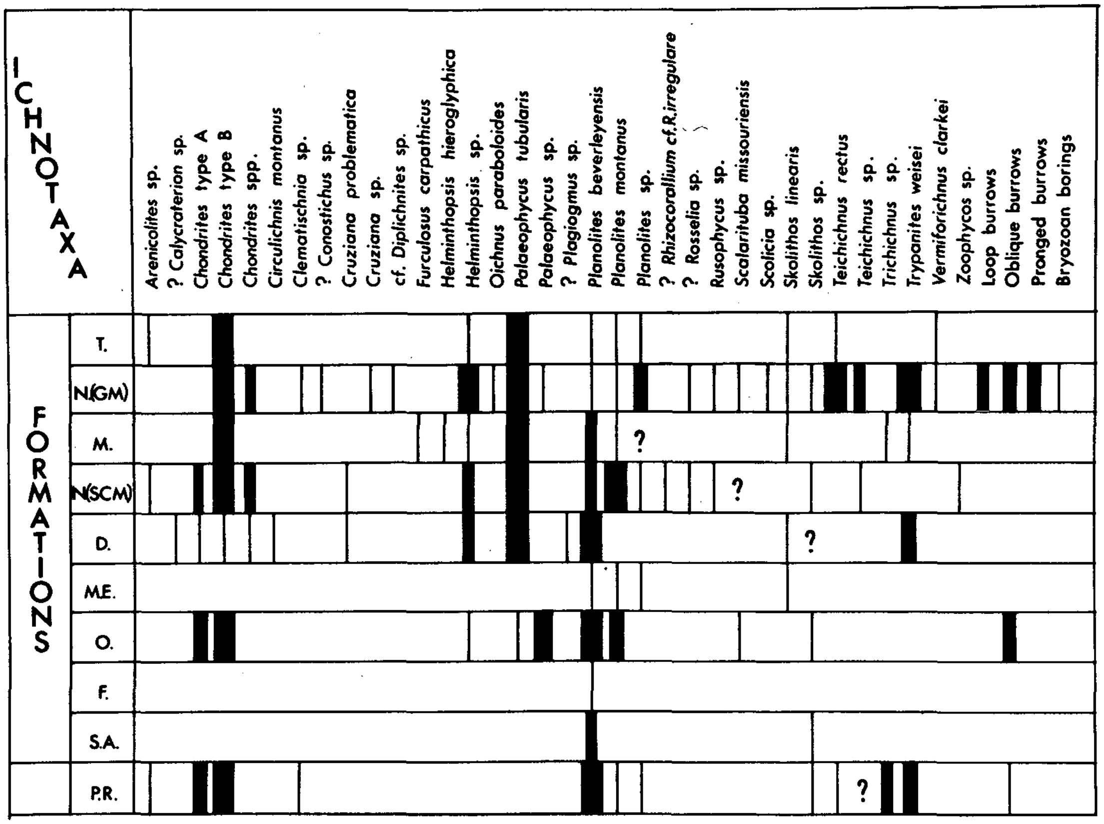

Fig. 5 - Stratigraphic distribution and abundance of trace fossils in the Trenton Group between Montreal and Quebec City. The relative bar widths represent respectively from thinnest to thickest 1<10 specimens, 10<50 specimens, 50<100 specimens and >100 specimens. Questionable occurrences refer to uncertain identifications. Formational nomenclature is P.R. = Pont Rouge, S.A. = Saint Alban, F = Fontaine, O = Ouareau, M.E. = Mile End, D = Deschambault, N(SCM) = Saint Casimir Member (Neuville), M = Montreal, N(GM) = Grondines Member (Neuville), and T = Tetreauville Formations.

pressions compare with **A. sparsus** Salter 1857) and **A. statheri** Bather 1925, particularly with respect to the presence in some specimens of a distinct wall lining. Thus, more than a single ichnospecies may be present but the paucity of material and the nature of its preservation precludes more detailed analysis.

Ichnogenus **Calycraterion** Karaszewski, 1971

Type species - **Calycraterion samsonowiczi** Karaszewski 1971, by monotypy.

Diagnosis - Regular and smooth calyx-shaped depressions (on upper bedding surfaces) or knobs (on both upper and lower bedding surfaces) possessing up to three smaller depressions or knobs (after Karaszewski 1971).

Discussion - Karaszewski (1971) considered the structures to have been produced by annelids, the smaller depressions or knobs representing burrow outlets. The ichnogenus has, to date, only been recorded in nearshore (Karaszewski 1971), deltaic (Chaplin 1980) and intertidal environments (Fillion and Pickerill, in prep.) from, respectively, Jurassic, Carboniferous and Lower Ordovician strata. The asymmetry of the burrow and the smaller knobs or depressions differentiate **Calycraterion** from the closely related ichnogenera **Bergaueria** Prantl 1945 and **Mammillichnis** Chamberlain 1971.

?**Calycraterion** sp. (Figure 7e)

Material - 1 specimen.

Description - The trace occurs as a slightly elongated and ovoid mound preserved in convex epirelief on the upper

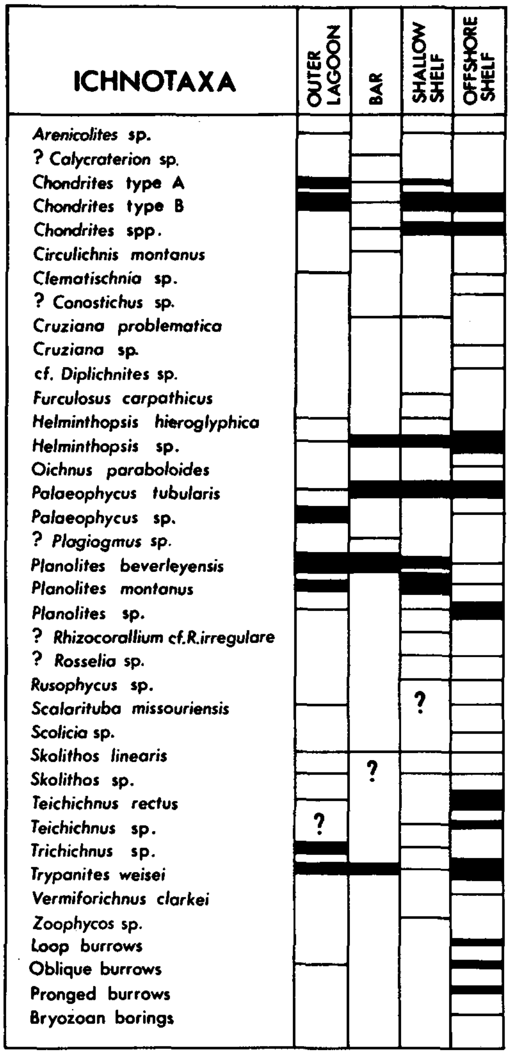

Fig. 6 - Environmental distribution of trace fossils in the Trenton Group between Montreal and Quebec City. Relative bar widths and questionable occurrences are as indicated in Figure 5.

surface of a 25mm thick calcilutite which immediately overlies a 10cm thick skeletal calcarenite. The 'mound' is filled with this bioclastic material, is 7mm in height and has a diameter of 9 - 11mm. A poorly preserved knob is present on the upper extremity of the structure.

Remarks - Since knowledge of the vertical aspect of the structure is unknown, even its ichnogeneric assignment is uncertain. However, the asymmetry and the presence of the problematical knob are closely comparable to Ordovician examples of **Calycraterion** we have observed on Bell Island, eastern Newfoundland and we therefore tentatively diagnose the Trenton specimen as such. In the Newfoundland examples it is evident that **Calycraterion** can be repeated vertically and its preservation as convex epirelief structures is related to subsequent infilling of calyx-shaped burrow outlets. This style of preservation is similar to that of **Margaritichnus** Bandel 1973 but the Trenton specimen can be differentiated from this ichnogenus because **Margaritichnus** is usually remarkably symmetrical and flattened.

Ichnogenus **Chondrites**
von Sternberg, 1833

Type species - **Fucoides antiquus** Brongniart 1828, by subsequent designation of Miller (1889, p. 114).

Diagnosis - Regularly branching tunnel systems consisting of a small number of mastershafts open to the surface which ramify at depth to form a dendritic network (after Osgood 1970, Fürsich 1974a).

Discussion - Although the trace is easily recognizable at ichnogeneric level, distinction between the more than 170 supposed ichnospecies (Chamberlain 1977), many of which are candidates for synonymy, is at present impossible without a thorough and detailed taxonomic study. Many of the ichnospecies proposed in the literature are based on variation in size, preservation and angle of braching and our review of this literature has indicated that the majority of these can probably be placed into synonymy with the 11 chondritid ichnospecies (from a total of 36 **Fucoides** species - see Osgood 1970) originally designated by Brongniart (1823, 1828). Chamberlain (1971, 1977) has in part resolved some of the ichnospecific nomenclatural problems but the taxonomic status is still unsatisfactory. Because of these difficulties we do not attempt to identify our material beyond the ichnogeneric level but recognize various form types (cf. Osgood 1970).

Chondrites has been interpreted as a plant (Brongniart 1823), the burrow of a sipunculoid (Simpson 1957), or polychaete annelid (Osgood 1975), or the burrow of unknown tentacle-bearing organisms (Taylor 1967), anthoptiloid sea-pens (Bradley 1981) and even small arthropods (Ekdale 1977). Simpson (1957) and Osgood (1970) have discussed the manner of production and preservation at some length. It is a marine but eurybathic form, having been reported from marginal marine (e.g. Hakes 1976, 1977; Fisher 1978), shallow subtidal (e.g. Hofmann 1979, Marintsch and Finks 1982), deep sea fan (e.g. Crimes et al. 1981, Hill 1981) and abyssal (e.g. Ekdale 1977, 1978; Larson 1982) environments. It ranges in age from Cambrian-Recent (Häntzschel 1975).

Finally, it is noteworthy that the nomenclatural type of **Chondrites** was designated by Miller (1889, p. 130) as **Fucoides antiquus** and subsequent designations (e.g. Bassler 1915, p. 217; Andrews 1955, p. 130) of **Fucoides targionii** are invalid by rule of priority. Additionally, **Fucoides lycopodioides** as listed in the Treatise by Häntzshel (1975) and adopted by some subsequent authors (e.g. Marintsch and Finks 1982) is in fact an error. This species is the nomenclatural type of **Caulerpites** von Sternberg, 1833.

Chondrites sp. type A
(Figures 8a, b)

Diagnosis - As for ichnogenus.

Material - 64 specimens.

Description - Dense, horizontal networks preserved in convex epirelief or hyporelief, composed of straight cylindrical burrows which exhibit regular symmetrical dichotomous branching at angles between 20 - 65°. Burrow diameter varies from 1.5 - 7mm but is constant within a single specimen. Branches are up to 150mm long and a maximum of 5 orders have been observed although there can be long segments without bifurcations. Burrow cross-sections are ellipsoidal and their contact with host material is sharp and well-defined. Burrow fill is variable but is typically finer than the host rock, is usually structureless but occasionally exhibits concentric or meniscate structures (cf. Taylor 1967). The largest observed network covers an area of 120 x 150mm .

Remarks - The burrow systems frequently run in close proximity without interpenetration, thus suggesting phobotactic behaviour of the producer. The internal meniscate structures present in some of the specimens suggests, at least for these, an origin as stuffed burrows rather than open burrow systems (for a review on the genesis of **Chondrites** see Osgood 1970, Ekdale 1977). Although **Chondrites** type A has not been formally speciated it bears strong resemblance to **Buthotrephis succulens** Hall (1847, pl. 22, fig. 2a).

Chondrites sp. type B
(Figures 8a, c)

Diagnosis - As for ichnogenus.

Material - Several hundreds of specimens.

Description - Oblique networks preserved in endorelief with burrow diameters varying from 0.6 - 2mm and burrow cross-sections circular or elliptical. Burrow fill is of the same or coarser grain size as the host rock and is ubiquitously calcilutite or calcisiltite. The fill is typically of a different colour than the enclosing sediment and is derived from immediately overlying strata. The tubes, which are up to 25mm long, are often lined with micrite. Individual networks may possess 3 orders of branching and have been observed to penetrate at least 36mm of host sediment.

Remarks - These smaller networks of **Chondrites** sp. type B also exhibit good evidence of phobotactic behaviour. They are frequently observed between **Chondrites** type A networks but never penetrate them or, indeed, each other. Type B networks, although always initially oblique to stratification, may turn to become parallel at their distal extremities. The producer(s) of the trace is responsible for much of the bioturbation observed in the Trenton Group.

Chondrites spp.
(Figures 8a, d, e, f)

Specimens included here exhibit poor and variable preservation or are too irregular to permit assignment to types A and B as described above. Three variants can be recognized:- (i) Elaborate, moderately dense and now flattened networks preserved at shale-calcilutite interfaces of the Grondines Member of the Neuville Formation (Figs. 8a, d). Individual networks are composed of sinuous tunnels which vary in diameter along their length from 2 - 8.5mm. Up to 5 orders of branching are present and the branching is very irregular. Branching angles are equally irregular varying from 20 - 90°. Burrow fill is of the same grain size as the enclosing material (micrite), is typically structureless but occasionally exhibits a crudely developed meniscate appearance. (ii) A loose horizontal network preserved at a calcisiltite - calcarenite bed in the Deschambault Formation (Figs. 8a, f). Tunnels vary in diameter from 2 - 4mm but the diameter of a single tunnel remains constant along its length. The branching is curved, asymmetrically dichotomous but never crossing, occurs at angles of 35 - 60° and up to 5 orders can be observed. Burrow fill is micrite. In many respects, this network is very similar to **C. furcatus** as figured by Marintsch and Finks (1982, pl. 2, fig. 4) and **C. antiquatus** as figured by Hofmann (1979, pl. 15, fig. F). (iii) A widely spaced regularly branching network of asymmetrically dichotomous tunnels (Figs. 8a, e). Individual tunnels are straight and retain a constant diameter of 1 - 3 mm. Branching angles vary from 30 - 40° and up to 2 orders were observed. Burrow fill is calcilutite but a dark shale lining can be observed in some specimens. This variety resembles **C. targionii sensu** Marintsch and Finks (1982).

Ichnogenus **Circulichnis** Vialov, 1971

Type species - **Circulichnis montanus**, Vialov, 1971, by original designation.

Diagnosis - "Annular trace, almost circular (or oval) formed by some cylindrical object" (Vialov 1971, p. 91, **trans. litt.**).

Discussion - The original diagnosis by Vialov (1971) is somewhat confusing in that it is clear in the remainder of his text that the circular (or oval) trace is in fact a burrow of 0.7 - 1.5mm in diameter. Since the original designation it has only been formally recorded from the Tremadoc of Nova Scotia (Pickerill and Keppie 1981). Similar structures have been reported and, or, figured but not described by various authors (Ulrich 1904, pl. 22, fig. 3; Häntzschel 1975, fig. 44, 2a; Książkiewicz 1977, fig. 32; Nicholson 1978, pl. 3, fig. 2; Crimes et al. 1981, p. 975). Preferably such structures should be included within the ichnogenus **Circulichnis** with which they best conform. Accordingly, **Circulichnis** would range from Tremadoc-Palaeocene age. Although its producer and environmental range are uncertain Pickerill and Keppie (1981) suggested a worm-like originator and a preference for deeper-water regimes. Crimes (pers. comm., 1983) has also recorded it from deep-water turbidites of Carboniferous age in Spain and England.

Circulichnis montanus Vialov, 1971
(Figure 7g)

Diagnosis - As for ichnogenus.

Material - 1 specimen.

Description - Slightly elliptical trace preserved in convex epirelief on the upper surface of a 7cm calcarenite. The trace measures 115 x 90mm and the burrow forming it is 4mm in diameter and consistent in width throughout the ellipse. Evidence of burrow collapse is present locally (Fig. 7g). Burrow fill is identical to the host rock.

Remarks - Since Vialov (1971) only gave size measurements of his holotype, the full variation in ellipse size and burrow diameter of the original material is unknown. In view of the incomplete description and the unavailability of type material for restudy, the Trenton specimen can best be regarded as conspecific. Its occurrence in the Trenton Group, although rare, suggests that it is possibly more a eurybathic form.

Ichnogenus **Clematischnia** Wilson, 1948

Type species - **Buthotrephis succulens** Hall, 1847, by original designation of Wilson (1948, p. 10).

Diagnosis - Irregularly branched or unbranched cylindrical burrows with prominent external ornament of transverse ribs which completely or partially cross the burrow; in the latter case the burrow assumes a distinctive mammilated appearance (modified after Wilson 1948).

Discussion - Wilson (1948) designated **Buthotrephis succulens** Hall as her type ichnospecies of **Clematischnia** but it is apparent that Hall's (1847) two figured specimens are morphologically separate; his figure 2a, plate XXI is more akin to a chondritid (**Chondrites** type A as described herein) and his figure 2b, plate XXI falls within **Clematischnia** as defined by Wilson (1948). Furthermore, even Wilson's (1948) material is taxonomically variable; her plesiotype G.S.C. 9283 (plate 1, fig. 4) is likewise more akin to **Palaeophycus** sp. or **Chondrites** sp. whereas her plesiotype G.S.C. 13442 (plate 1, fig. 5) falls within **Clematischnia** and is very similar to Hall's (1847) figure 2b. Clearly a detailed systematic review of the ichnogenus is warranted but until this is undertaken we regard it as a useful form to describe these distinctive mammilated burrows. Because of the rarity of actual recordings of **Clematischnia** (for example the ichnogenus was only listed as an unrecognized form in Häntzschel (1975) and briefly discussed by Osgood (1970) in his redescription of **Buthotrephis succulens**) it is difficult to comment on its producer and stratigraphic range. Its similarity to chondritids and **Palaeophycus** suggest, however, that it is the feeding and dwelling burrow of an unknown annelid. Similarly, although to date it has only been reported from Ordovician strata, its stratigraphic range is likely to be considerably more extensive.

Clematischnia sp.
(Figure 7i)

Material - 12 specimens.

Description - Unbranched cylindrical burrows up to 7mm in diameter and 10cm in length preserved on upper surfaces and all parallel to stratification. In all of the observed specimens the burrows occur in groups of four to seven, apparently radiating from some common centre which is not preserved. Burrow surfaces are mammilated, this being produced by an alternating series of transversely oriented interlocking pear or cylindrical shaped protruberances, each separated by a narrow depression. Burrow fill (siltstone) is coarser than the surrounding matrix and is structureless.

Remarks - Congeneric material from the Trenton Group immediately around Quebec City was previously identified by Pickerill and Forbes (1979) as cf. **Biformites.** However, both their material and that described herein lacks the initial short and longitudinally furrowed section more typical of **Biformites** and the material is therefore best included within **Clematischnia.** In view of its unresolved taxonomic status it is herein only identified at ichnogeneric level.

Ichnogeneus **Conostichus** Lesquereux, 1876

Type species - **Conostichus ornatus** Lesquereux, 1876, by original monotypy.

Opposite page

Fig. 7 - a. **Cruziana** sp. on lower bedding surface in convex hyporelief, Grondines Member, locality 22. b. **Cruziana problematica** on lower bedding surface in convex hyporelief, Deschambault Formation, locality 12. c. **Scolicia** sp. and **Diplichnites** sp. (arrowed) preserved on upper bedding surface of thin chert, Grondines Member, locality 18 (see text for details). d. **Areniçolites** sp. tubes (arrowed) on upper bedding surface, Saint Casimir Member, locality 16. e. ?**Calycraterion** sp. on upper bedding surface in convex epirelief with arrow indicating possible location of burrow outlet, Deschambault Formation, locality 21. Coin diameter 2 cm. f. ?**Conostichus** sp. actually preserved on lower bedding surface in convex hyporelief but here reversed to exhibit faint longitudinal fluting, Grondines Member, locality 18. g. **Circulichnis montanus** on upper bedding surface in convex epirelief, arrow indicating burrow collapse, Deschambault Formation, locality 21. h. **Rusophycus** sp. on lower bedding surface in convex hyporelief, Grondines Member, locality 22. i. **Clematischnia** sp. on upper bedding surface in convex epirelief, Pont Rouge Formation, locality 21.


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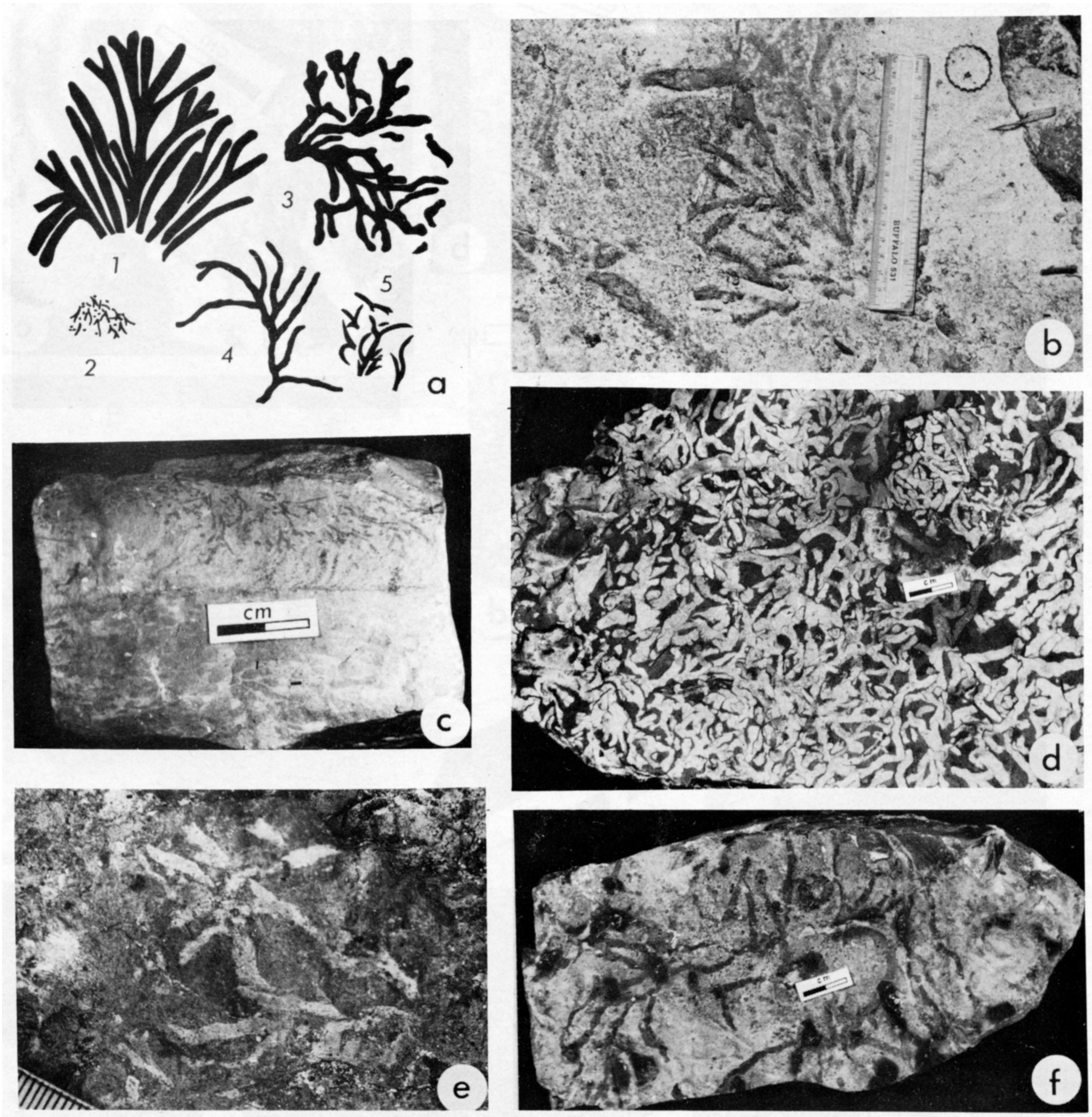


Fig. 8 - a. Variation in chondritids in the Trenton Group. 1 = Chondrites sp. type A, 2 = **Chondrites** sp. type B, 3 = **Chondrites** sp. dense and elaborate networks, 4 = **Chondrites** sp. loose horizontal networks, and 5 = **Chondrites** sp. widely spaced horizontal regularly branching networks (see text for details). All redrawn from actual specimens and all x 0.5. b. **Chondrites** sp. type A on upper bedding surface, Pont Rouge Formation, locality 21. c. **Chondrites** sp. type B in vertical cross-section, Tetreauville Formation, locality 8. d. Dense horizontal network of **Chondrites** sp. on lower bedding surface, Grondines Member, locality 18 (cf. Fig. 8a [3]). e. Loose horizontal network of **Chondrites** sp. on upper bedding surface, Deschambault Formation, locality 21 (cf. Fig. 8a [5]). f. **Chondrites** sp. on upper bedding surface, Deschambault Formation, locality 16 (cf. Fig. 8a [4]).

Diagnosis - Variable but mostly small conical to subconical structures preserved in full relief. Bodies commonly fluted by transverse constrictions and longitudinal furrows and ridges originating from the apical end. Concentric laminae may be present internally (after Häntzschel 1975, Hakes 1976).

Discussion - Following its original interpretation as an alga (Lesquereux 1876) the structure has been interpreted as a sponge, a scyphomedusoid, a burrow of a filter-feeding organism, a funnel-shaped opening of **Arenicola**-like burrows and a trace produced by upward migration of actinian-like organisms (see Pfefferkorn 1971, Chamberlain 1971, Barthel and Barth 1972, Hakes 1976). Its origin still remains enigmatic and, indeed, its producers may be polyphyletic. Many of its numerous species are probably synonymous and it is a prime candidate for serious taxonomic revision (see Branson 1960). It ranges in age from Arenig (pers. observ. - Wabana Group of eastern Newfoundland) to ?Lower Cretaceous (Imlay 1961) and, although exceptions do occur (e.g. Chamberlain 1971), is typically associated with near-shore environments subject to rapid sedimentation.

?**Conostichus** sp.
(Figure 7f)

Material - 1 specimen.

Description - A truncated conical structure 15mm in diameter and 13mm in height preserved in convex hyporelief below a 25mm-thick bioclastic calcilutite. Poorly preserved longitudinal ribs (ca. 6-7) are present.

Remarks - The specimen, although not well enough preserved for definite identification, may be distinguished from the allied ichnogenus **Conichnus** Myannil, 1966 by the presence of longitudinal fluting. Additionally, **Bergaueria** Prantl, 1945 is more flattened and less conical. A more important difficulty is demonstrating that the structure is in fact organic and not inorganic in origin. The former, however, is suggested by the regularity of the structure, its association on the same bedding surface with abundant trace fossils, particularly **Chondrites** sp. type B and **Planolites beverleyensis,** and a complete absence on that bedding surface of additional physicaly produced inorganic structures.

Ichnogenus **Cruziana** d'Orbigny, 1842

Type species - **Cruziana rugosa** d'Orbigny 1842, by subsequent designation of Miller (1889, p. 115).

Diagnosis - Elongate band-like furows covered by herringbone-shaped ridges, with or without two outer sooth or finely longitudinally striated zones outside the V-markings, occasionally with lateral ridges and, or, wisp-like markings when preserved on bedding soles (after Häntzschel 1975).

Discussion - Although Seilacher (1970) united under **Cruziana** both long furrows and short coffee bean-like excavations (=**Rusophycus**) most subsequent authors have, as we do, preferred to retain the two as distinctive ichnogenera (see Crimes **et al.** 1977). Furthermore, we herein accept the reasoning by Bromley and Asgaard (1979) to include **Isopodichnus** Bornemann, 1899 within **Cruziana** as the only essential differences between the two previously separated ichnogenera are in accessory features (**sensu** Fürsich 1974b) which should be employed only for classification at the ichnospecific level. It is, nevertheless, clear that Bromley and Asgaard (1979) 'lumped' heterogeneous material into a single ichnospecies (**C. problematica**) and revision of their and other material is still necessary.

Undoubtedly, the majority of **Cruziana** furrows were produced by trilobites (Seilacher 1970), although the small Triassic forms described by Bromley and Asgaard (1970) may have been produced by trilobite-like arthropods or notostracan branchiopods and the large Middle Ordovician and Triassic forms described by, respectively, Fisher (1978) and Shone (1978, 1979) may be the result of aglaspids or even vertebrates. Many ichnospecies of **Cruziana** now exist and it is perhaps the most useful of all trace fossils in stratigraphic studies (Seilacher 1970, Crimes 1975). The ichnogenus ranges in age from Cambrian - Triassic and is a typically shallow-water marine form constituting the type ichnogenus of Seilacher's (1967) **Cruziana** ichnofacies, though it has also allegedly been observed in freshwater deposits (e.g. Helwig 1972).

Cruziana problematica (Schindewolf, 1921)
(Figure 7b)

Diagnosis - Straight or curved, often self-crossing, **Cruziana** up to 5mm wide possessing faint, unevenly spaced transverse striations which may reach the margins of the trace in low relief specimens or terminate before reaching the margins in high relief specimens (adapted from Schindewolf 1928, Häntzschel 1975, Trewin 1976, Bromley and Asgaard 1979).

Material - 2 specimens.

Description - Two poorly preserved specimens, one in convex hyporelief at the base of a 30mm thick calcisiltite, the second in concave epirelief on an 80mm thick calcilutite. The former is a short 8mm long straight band-like trace, 4mm wide with lobes 1.5mm deep and the latter a 120mm long slightly sinuous trace, 2mm in width, composed of two furrows each 0.7mm wide separated by a median ridge. Both specimens possess transverse but poorly preserved and faint scratch markings irregularly developed along their exposed length.

Remarks - Although poorly preserved the material lacks the '**Isopodichnus**' - type bilobed expanded terminations (sensu Trewin 1976) typical of **C. stromnessa** and the well-defined scratches, often arranged in a V-pattern, of **C. eutendorfensa.** Conspecific material was described by Pickerill and Forbes (1979) from the Trenton Group northeast of Quebec City.

Cruziana sp.
(Figure 7a)

Material - 8 specimens.

Description - The specimens consist of variably preserved, straight or slightly sinuous bilobate furrows preserved in convex hyporelief. Mean width is 20mm and length is variable, up to a maximum observed of 100mm. Endopodal lobes are poorly to moderately well-preserved giving the trace a depth of 1-8mm. V-markings, when preserved, are moderately deep, closely spaced and V at 160 - 180°. Genal spine markings are absent.

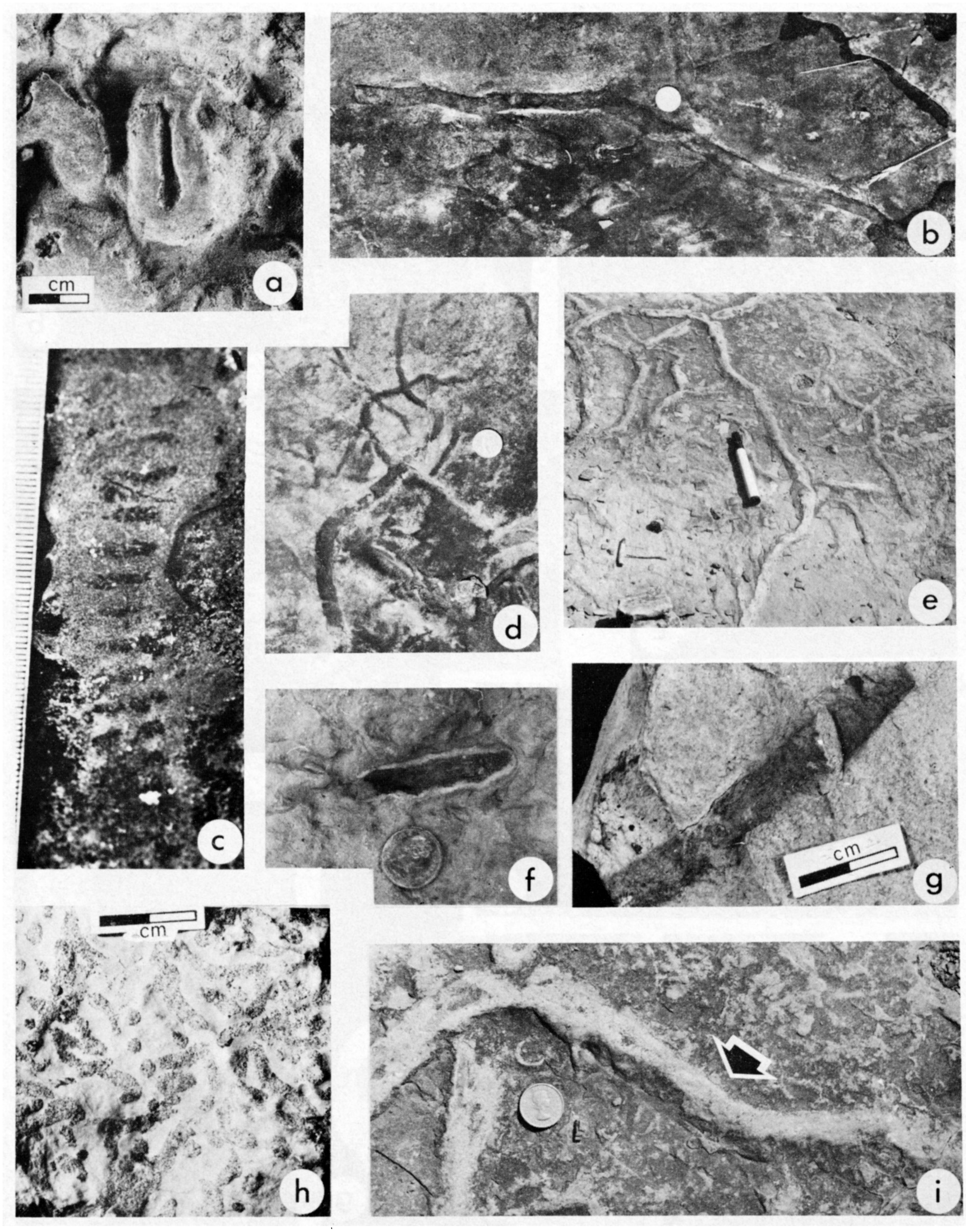
Remarks - Though not well enough preserved for ichnospecific identification the furrows can be clearly diagnosed as **Cruziana.** They are reminiscent of specimens described as **Cruziana** sp. by Alpert (1976, pl. 1, fig. 4) from the Cambrian of California and also resemble **C. pudica** described from Middle Ordovician to Middle Silurian strata of the United States, southern Jordan and Wales by, respectively, Osgood (1970), Seilacher (1970) and Pickerill (1977). Congeneric material has also been figured by Pickerill and Forbes (1979) from the Trenton Group northeast of Quebec City.

Ichnogenus **Diplichnites** Dawson, 1873

Type species - **Diplichnites aenigma** Dawson, 1873, by original montypy.

Opposite page

Fig. 9 - a. **Furculosus carpathicus** on lower bedding surface in convex hyporelief, Montreal Formation, locality 11. b. Unbranched **Palaeophycus tubularis** on upper bedding surface in convex epirelief, Deschambault Formation, locality 21. Coin diameter 2 cm. c. ?**Plagiogmus** sp. on upper bedding surface in convex epirelief, Deschambault Formation, locality 11. d. **Helminthopsis** sp. on upper bedding surface in convex epirelief, Deschambault Formation, locality 21. Coin diameter 2 cm. e. **Helminthopsis hieroglyphica** on upper bedding surface in convex epirelief, Pont Rouge Formation, locality 21. Pen length 10 cm. f. Lined **Planolites** sp. on upper bedding surface in concave epirelief, Grondines Member, locality 18. Coin diameter 2 cm. g. **Planolites beverleyensis** on upper bedding surface in convex epirelief, Pont Rouge Formation, locality 21. h. **Planolites montanus** on upper bedding surface, Grondines Member, locality 18. i. **Helminthopsis** sp. (arrowed) and **Palaeophycus** sp. (to left of coin) on upper bedding surface in convex epirelief, Deschambault Formation, locality 21. Coin diameter 2 cm.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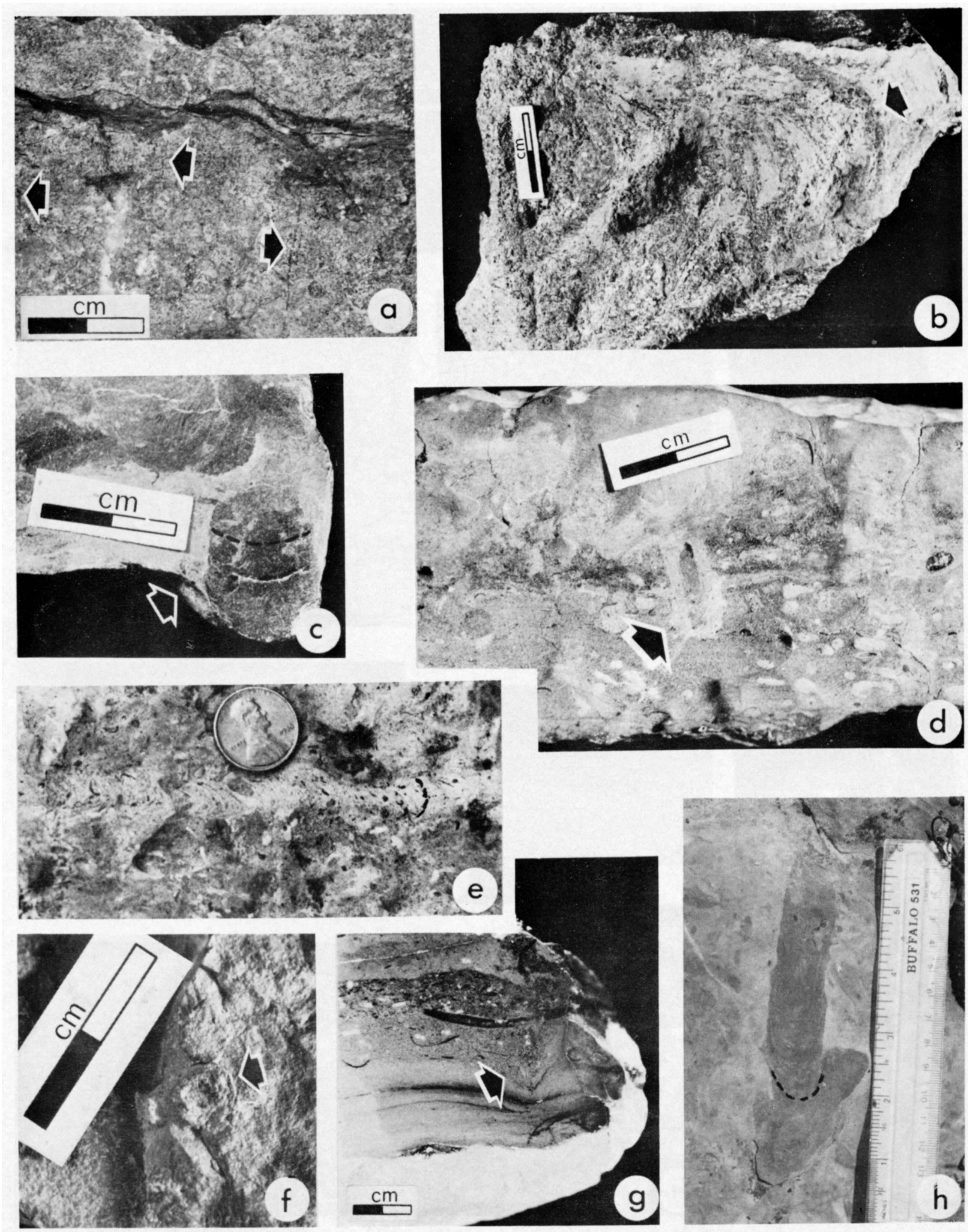
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Diagnosis - Morphologically simple trails up to 36cm wide and consisting of two parallel series of tracks (each up to 9cm wide); individual tracks elongate, closely and regularly spaced up to one per centimeter and roughly normal to trace axis (**emend.** Briggs et al. 1979).

Discussion - Although Dawson (1873, p. 7) originally interpreted **Diplichnites** as the result of 'a large crustacean or gigantic annelid or myriapod' subsequent workers, following Seilacher (1955), have frequently utilized the ichnogenus to describe morphologically similar but smaller scaled trilobite-produced traces (e.g. Crimes 1970, Osgood and Drennen 1975). Although Briggs **et al.** (1979) questioned the trilobite origins of originally described specimens and suggested a more restricted usage to exclude trilobite trails, suggesting that those specimens of **Diplichnites** previously interpreted as trilobite trails to be included in one of the junior synonyms listed by Osgood (1970), the taxonomic confusion has still not been resolved. Because of the limited material and its poor preservation and the unresolved taxonomic difficulties, we herein retain **Diplichnites** even though we assume it to have been produced by trilobites. The ichnogenus has been reported from Cambrian-Triassic strata and though typically a shallow marine form (e.g. Crimes 1977) has also been recorded from deep-water sediments (e.g. Pickerill 1980, 1981).

cf. **Diplichnites** sp.
(Figure 7c)

Material - 2 specimens collected and 5 recorded in the field.

Description - Paired(?) elongated dot-like impressions preserved in concave epirelief on the upper surface of a chert bed. Each impression is 2.5mm long, 1mm wide and 1mm deep and set width (**sensu** Osgood 1970, p. 354) is 7-11mm. Up to 13 sets have been observed in a single track, giving a maximum length of 45mm.

Remarks - The poor preservation precludes positive identification even at ichnogeneric level, although of all published 'trackways' they compare most favourably to **Diplichnites.**

Ichnogenus **Furculosus**
Roniewicz and Pieńkowski, 1977

Type species - **Furculosus carpathicus** Roniewicz and Pieńkowski, 1977, by original designation.

Diagnosis - Cylindrical burrows forming tight fork-line loops with endings parallel or diverging.

Discussion - Roniewicz and Pieńkowski (1977) hypothesized that the loops of **F. carpathicus** were formed by a deposit-feeding organism passing through an interface boundary. Although to date no other occurrence of the ichnogenus has formally been made, similar forms are known in the external Carpathians (Kaiążkiewicz, pers. comm. in Roniewicz and Pieńkowski 1977). The occurrence of **Furculosus** in the Trenton Group extends its known stratigraphic range from Middle Ordovician - Oligocene and its environmental range from shallow to deep-water regimes. **Gordia arcuata** Książkiewicz, 1977 is a morphologically similar form but can be distinguished from **Furculosus** by its more arcuate shape and smaller burrow diameter.

Furculosus carpathicus
Roniewicz and Pieńkowski, 1977
(Figure 9a)

Diagnosis - As for ichnogenus.

Material - 1 specimen.

Description - Tight-looped smooth and

Opposite page

Fig. 10 - a. **Trichichnus** sp. (arrowed) in vertical section, Montreal Formation, locality 14. b. Zoophycos sp. on upper bedding surface in convex epirelief, Grondines Member, locality 18. Note the peripheral tube (arrowed). c. Teichichnus rectus in transverse vertical section with the longitudinal burrow arrowed, Grondines Member, locality 21. d. Thickly lined Skolithos sp. burrow (arrowed) in transverse vertical section, Pont Rouge Formation, locality 21. e. Scalarituba missouriensis on upper bedding surface in convex epirelief, Ouareau Formation, locality 11. f. g. ?Rosselia sp., f. on upper bedding plane surface, and g. in transverse vertical section, Saint Casimir Member, locality 16. h. Teichichnus sp. on upper bedding surface, Grondines Member, locality 18.

cylindrical burrow preserved in convex hyporelief on the base of a parallel laminated calcarenite. Burrow diameter is 3.5 - 4mm and the loop is 35mm long and 11mm wide. The burrow terminates as a result of both distal extremities turning up into the overlying calcarenite. Burrow fill is calcarenite.

Remarks - Although Roniewicz and Pieńkowski (1977) discussed the 3-dimensional aspect of **F. carpathicus** they omitted to include it in their diagnosis, according to which, knowledge of the bedding plane expression of the burrow is sufficient for positive identification. The tight fork-like loop is therefore the most characteristic feature of the species and the Trenton material is therefore regarded as conspecific.

Ichnogenus **Helminthopsis** Heer, 1877

Type species - **Helminthopsis abeli,** by subsequent designation of Książkiewicz (1977, p. 116).

Diagnosis - "Unbranched, very long, very much snake-like winding tubes or cylinders of very different sizes. **Helminthopsis magna** was undoubtedly tubular but this is uncertain for the two other species .... The outer surface is smooth. It is similar to **Helminthoida** Schafh. in which, however, the meanders are closer and the string-like or cylindrical body touches itself" (Heer 1877, p. 116 - **trans. litt.**).

Discussion - Heer (1877) originally established three species of **Helminthopsis** but did not designate a type. Subsequently, Ulrich (1904, p. 144) designated **H. magna** a somewhat unfortunate choice as this trace is a bilobate structure (see Heer 1877, pl. XLVII, figs. 1,2) resembling **Taphrhelminthopsis** Sacco, 1888 or **Scolicia** de Quatrefages, 1849. In view of this problem Książkiewicz (1977) proposed to utilize a specimen originally figured by Abel (1935, p. 290, fig. 261B) and subsewuently illustrated by Häntzschel (1962, p. W197, fig. 4a; 1975, p. W71, fig. 2b) as the type ichnospecies under the name **Helminthopsis abeli.** Compared to **H. magna** this latter ichnospecies conforms best to Heer's (1877) original diagnosis and is retained herein as the type.

It must be noted that although most authors have utilized the ichnogenus for winding or loosely meandering, unbranched, generally unornamented 'burrows', the original diagnosis did not specify that the traces had necessarily to be of burrow origin. Thus, it seems logical that morphologically and geometrically similar 'trails' (e.g. Hall 1852, pl. 11, fig. 2b; Dörjes 1978, fig. 4 and Swinbanks and Murray 1981, fig. 10A) should also be included within the ichnogenus.

Many authors, too numerous to mention here, have reported the ichnogenus in strata of ?Late Precambrian (Webby 1970, fig. 17, **H. hieroglyphica**) to Oligocene (Książkiewicz 1977) or even Recent (Dörjes 1978, Swinbanks and Murray 1981) age. It is a eurybathic form, though more frequently reported from deep-water flysch successions (Pickerill 1981) and is generally regarded as having been produced by polychaete and possibly priapulid annelids.

Helminthopsis hieroglyphica
Heer in Maillard, 1887
(Figure 9c)

Diagnosis - **Helminthopsis** in which the windings are irregular, low and the course of the trace is often alternately winding and straight (after Książkiewicz 1977).

Material - 7 specimens.

Description - The traces are moderately well-preserved in convex epirelief on the upper surface of a massively bedded crinoidal calcarenite. They consist of burrows, up to 2cm in diameter and 50cm in length which are characterized by long straight segments up to 30cm long, but usually smaller, with a low turn between individual segments. Burrow diameter is constant along the length, burrow fill is identical to the enclosing calcarenite material and the burrows are smooth and unornamented.

Remarks - As noted by Książkiewicz (1977, p. 119), this ichnospecies is not well defined and the material originally figured in Maillard (1887, pl. 2, fig. 4;

pl. 1, fig. 2) resembles both a **Helminthoida** (pl. 1, fig. 2) and a loose irregularly winding trace (pl. 2, fig. 4) which Książkiewicz argued be adopted as the nomenclatural type of the species. To maintain stability this approach is adopted herein.

Helminthopsis sp.
(Figures 9d, i)

Material - 5 specimens and numerous occurrences recorded in the field.

Description - Variably preserved burrows preserved in convex and concave epirelief on upper surfaces of thinly bedded calcilutites or bioclastic calcisiltites. Burrows are smooth, slightly sinuous or meandering but meanders are always incomplete. Burrow fill is coarser or of the same grain size as underlying sediments. They are up to 150cm in length and range in diameter from 1.8 - 30mm (mean 7mm), the diameter remaining constant in a single specimen. Collapse in some specimens has resulted in their preservation as two epichnial ridges separated by a narrow furrow.

Remarks - The most workable scheme for ichnospecific identification of **Helminthopsis** is that proposed by Książkiewicz (1977), who utilized the nature and type of winding, the burrow diameter and the presence or absence of surface ornamentation. Because of their generally poor and incomplete preservation, particularly regarding the meander patterns, the Trenton specimens can therefore best only be identified at ichnogeneric level. Although **Helminthopsis** is generally regarded to be a deposit-feeding burrow (Książkiewicz 1977) the presence of collapsed tunnels in some of the Trenton specimens suggests, at least for these specimens, that they remained open after the passage of the producing organism(s).

Ichnogenus **Oichnus** Bromley, 1981

Type species - **Oichnus simplex** Bromley, 1981, by original designation.
Diagnosis - Circular to subcircular holes of biogenic origin bored into hard substrates. The hole may pass right through the substrate as a penetration, where the substrate is a thin shell; or end within the substrate as a shallow to deep depression or short, subcylindrical pit (Bromley 1981).

Remarks - The borings are considerably shorter than **Trypanites** Mägdefrau, 1932, range in age from possibly early Cambrian to Recent, and certainly Tertiary and younger examples are produced by predatory snails, as more fully discussed in Bromley (1981).

Oichnus paraboloides Bromley, 1981
(Figure 11a)

Diagnosis - **Oichnus** having a spherical paraboloid form, truncated in those cases where the boring penetrates right through the substrate. Where it does not so penetrate, the paraboloid may be deformed by a slightly raised central boss (Bromley 1981).

Material - 1 specimen.

Description - A round perforation within the pygidium of the trilobite **Isotelus gigas**, 1.2mm in diameter at the initial point of penetration of the dorsal surface narrowing to 1mm at its ventral exit. Walls of the truncated paraboloid are smooth.

Remarks - Although we observed no evidence of etching patterns on the boring it is identical to and diagnosed as **O. paraboloides** Bromley, 1981, as **O. simplex** Bromley, 1981 possesses a cylindrical to subcylindrical form. The producer of the Trenton specimen remains enigmatic.

Ichnogenus **Palaeophycus** Hall, 1847

Type species - **Palaeophycus tubularis** Hall, 1847, by subsequent designation of Miller (1889, p. 130).

Diagnosis **(emended)** - Branched or unbranched, straight to slightly curved to slightly undulose or flexuous, smooth or ornamented, lined essentially cylindrical, predominantly horizontal burrows of variable diameter; infillings typically structureless, of same lithology as host rock (after Pemberton and Frey 1982).

Discussion - There is still much confusion regarding the original designation of the type of the ichnogenus **Palaeophycus.** In their thorough and detailed review of **Palaeophycus** and **Planolites** Pemberton and Frey (1982) followed Häntzschel (1975) and suggested the type was **P. tubularis** Hall, 1847, subsequently designated by Bassler (1915, p. 939). At an earlier date, however, Miller (1889, p. 130), in a frequently overlooked and comprehensive text, had also designated **P. tubularis** Hall, 1847. Unfortunately, both Bassler (1915) and Miller (1889) did not design any type material, and indeed, the first to designate such material was Andrews (1955, p. 202). In the absence of any formal and universal code, however, at present we regard the subsequent designation of Miller (1889) and not Bassler (1915) as the most acceptable.

Minor emendation of the diagnosis of **Palaeophycus** by Pemberton and Frey (1982) is considered necessary to exclude systematic and non-systematic winding and, or, meandering burrows (e.g. **Gordia** Emmons, 1844, **Helminthopsis** Heer, 1877, **Cochlichnus** Hitchcock, 1858). Otherwise, the review of the taxonomy of **Palaeophycus** by Pemberton and Frey (1982), following several decades of inconsistent usage and confusion, is considered the most workable nomenclatural system and is adopted herein, even if problems may arise in the case of concealed bed-junction preservation (Hallam 1975), interface-crossing burrows (Hofmann 1979) or faintly meniscate burrows (Clifton and Thompson 1978).

Palaeophycus is a eurybathic form ranging in age from Proterozoic to Recent (Häntzschel 1975) and is usually attributed to represent the burrows of predaceous or suspension-feeding organisms, commonly but not universally polychaete annelids.

Palaeophycus tubularis Hall, 1847
(Figure 9b)

Diagnosis - Smooth, unornamented **Palaeophycus** of variable diameter, thinly but distinctly lined (Pemberton and Frey 1982).

Material - Several hundreds of specimens.

Description - Straight to slightly sinuous, generally smooth, horizontal to slightly inclined, frequently collapsed cylindrical burrows, 1-24mm in diameter and up to 57cm in length. Burrow diameter is constant along the length of a single burrow. True branching is rare, but when observed is irregular and occurs at 30-70°; cross-cutting is common. Burrow walls are thinly lined, burrow fill is identical to enclosing material and rare backfill structures are present. The burrows are preserved in convex hyporelief and convex and concave epirelief typically on thin beds of fine calcarenite, calcisiltite or calcilutite.

Remarks - Some of Hall's (1847) original material which he described as **P. rugosus** and **P. simplex,** but now both included in **P. tubularis,** was collected from the Trenton Group of New York and therefore the ichnospecies is apparently widespread and abundant throughout the Group. Although we have chosen to adopt the classification scheme of Pemberton and Frey (1982), some of the Trenton **P. tubularis** specimens illustrate some of the difficulties of its universal application. In particular, several specimens were observed to pass from calcilutites and calcisiltites into and even through patchily distributed lenses of calcarenite, though still retaining a calcisiltite or calcilutite fill throughout. Had only the portion of the burrows within the calcarenite been observed then they would have had to be referred to as **Planolites** which, of course, would necessitate, in such cases, erroneous ethological interpretations. Nevertheless, in most cases it was possible to observe the transition and such 'compound' specimens were named according to their dominant component (cf. Bromley and Frey 1974, Frey et al. 1978).

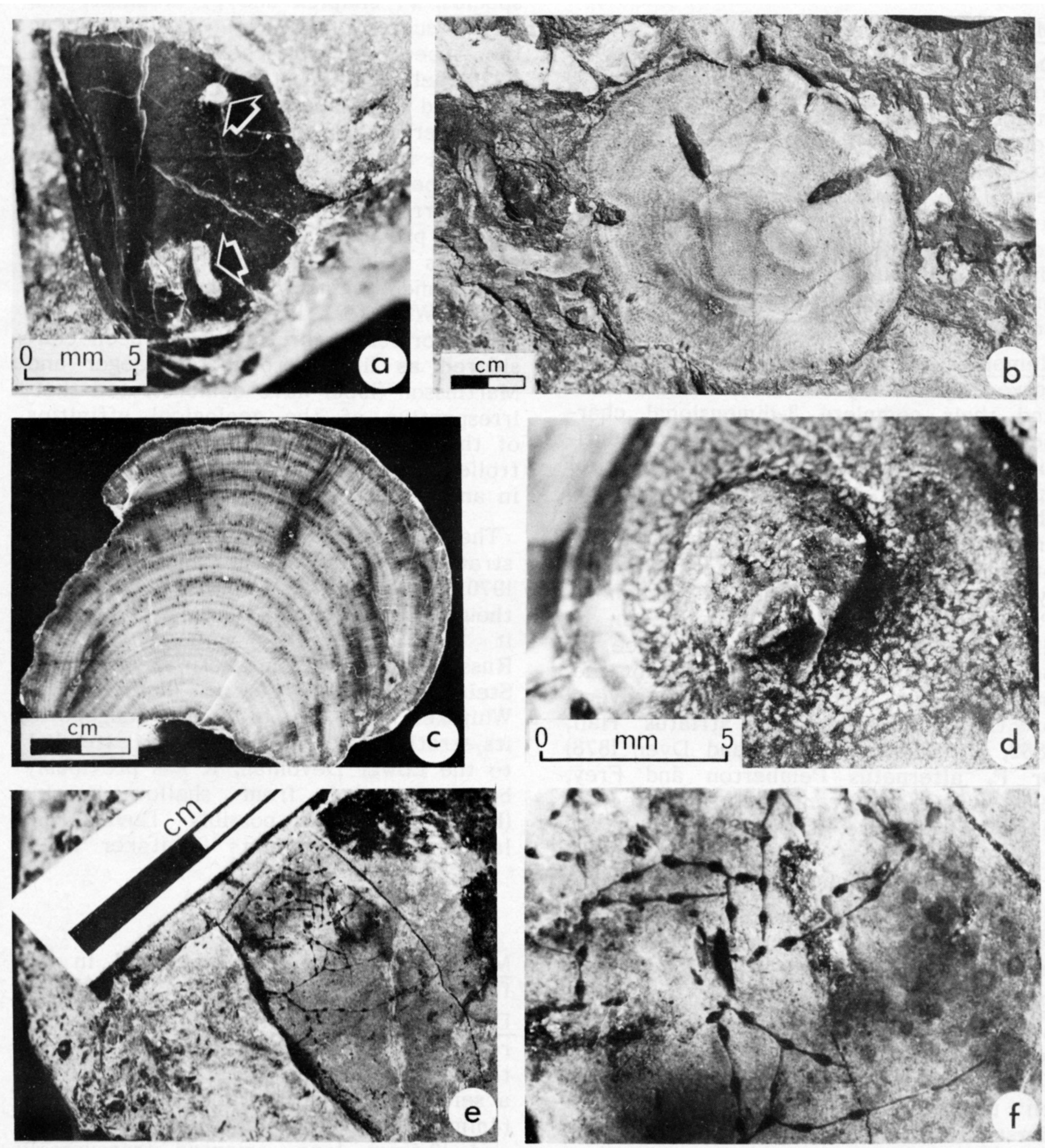

Fig. 11 - a. **Oichnus paraboloides** (upper arrow) and **Vermiforichnus clarkei** (lower arrow) in the pygidium of the isotelenid **Isotelus gigas**, Grondines Member, locality 18. b. Micrite filled borings of **Trypanites weisei** in a hemispherical colony of the bryozoan **Prasopora** sp., Pont Rouge Formation, locality 18. c. Longitudinal section through the bryozoan **Prasopora** sp. illustrating essentially vertical **Trypanites weisei** borings, Grondines Member, locality 18. d. Numerous small borings of **Vermiforichnus clarkei** in the cephalon of the isotelenid **Isotelus gigas**, Grondines Member, locality 18. e. f. Two views of reticulate bryozoan borings on a pygidium of the isotelenid **Isotelus gigas**, with f. an enlargement of the central area exhibited in e. Grondines Member, locality 18.

Palaeophycus sp.
(Figure 9i)

Material - 67 specimens.

Description - Ellipsoidal, thinly lined burrows, 3-7mm in diameter and observed mainly as full relief structures in transverse section. Burrow fill is identical to host rock and is apparently structureless. The few examples observed in semirelief are poorly preserved and incomplete, but essentially straight to slightly sinuous, horizontal to gently inclined, smooth, unbranched and rarely branched at up to 25°.

Remarks - Since the specimens are observed essentially in transverse section and their complete 3-dimensional character is unknown they are only identified at ichnogeneric level. Semirelief specimens are apparently smooth and therefore possibly **P. tubularis.** This smoothing, however, could be a result of weathering as the specimens are badly preserved and weathered throughout. **P. heberti** (de Saporta 1872-73) can be dismissed because of the presence of only thin linings, but whether or not the material also represents one or several of the ichnospecies **P. striatus** Hall, 1852, **P. sulcatus** (Miller and Dyer 1878) or **P. alternatus** Pemberton and Frey, 1982, whose differentiation is based on external sculpture, is unknown.

Ichnogeneus **Plagiogmus** Roedel, 1929

Type species - **Plagiogmus arcuatus** Roedel, 1929, by subsequent designation of Häntzschel (1962, p. W210).

Diagnosis - Horizontal endichnial burrow, straight or slightly curved 10 - 28mm wide, possessing sausage-shaped or fusiform transverse ventral ridges (as viewed on upper surfaces) and corresponding dorsal furrows (as viewed on lower surfaces), the spacing of which varies considerably. Narrow smooth zones separate the ends of the ridges from the margins of the trace (after Häntzschel 1975, Jaeger and Martinsson 1980).

Discussion - **Plagiogmus** was originally described from Sweden by Nathorst (1897) but not formally erected until 1929 by Roedel, who defined two species, **P. simplex** and **P. arcuatus,** the latter subsequently being designated as the type by Häntzschel (1962). Roedel (1929) believed the structures were trails produced by polychaetes, but later Glaessner (1969) and more recently Jaeger and Martinsson (1980), who restudied the type material, demonstrated their true burrow nature. Although the nature of the producing organism is enigmatic, molluscs (Glaessner 1969, Crimes **et al.** 1977) and segmented annelids (Roedel 1929, Whitaker 1979 - described as **Steinsfjordichnus brutoni**) have been considered as likely producers. Jaeger and Martinsson (1980) have demonstrated that irrespective of the geological affinities of the producer, the movement was controlled and locomotory and not peristalic in any sense.

The ichnogenus commonly occurs in strata of early Cambrian age (e.g. Banks 1970, Alpert 1977, Crimes **et al.** 1977) though Häntzschel (1975, p. W95) reports it from the Upper Precambrian of Russia. If, as we suspect, specimens of **Steinsfjordichnus brutoni** described by Whitaker (1979, p. 87) are congeneric, its stratigraphic range must be extended to the Lower Devonian. It has previously been recorded from shallow marine (Banks 1970) to possibly fluvial and lacustrine environments (Whitaker 1979).

?**Plagiogmus** sp.
(Figure 9c)

Material - 1 specimen recorded in the field.

Description - Preserved in convex epirelief on the upper surface of a 15cm thick massive bioclastic calcilutite as a series of 13 parallel and equally spaced (4mm) ridges, each 1mm high, 2mm wide and 10.5mm long, oriented transversely to the trace axis. The areas between the ridges are smoother, flatter and slightly wider. Burrow walls are not preserved.

Remarks - Poor preservation and lack of knowledge of the 3-dimensional structure precludes positive identification even at ichnogeneric level but the specimen does resemble **Plagiogmus** to which it is tentatively referred. The specimen is very similar, both in scale and morphology, to **Steinsfjordichnus brutoni** Whitaker, 1979, which as noted previously, is also best included in **Plagiogmus.**

Ichnogenus **Planolites** Nicholson, 1873

Type species - **Planolites vulgaris** Nicholson and Hinde, 1875, by subsequent designation of Miller (1889, p. 520).

Diagnosis **(emended)** - Unlined, rarely lined, rarely branched, straight to tortuous, smooth to irregularly walled or annulated burrows, circular to elliptical in cross-section, of variable dimensions and configurations; infillings essentially structureless, differing in lithology from host rock (after Pemberton and Frey 1982).

Discussion - Although Alpert (1975, p. 512) was the first to designate a type specimen of **Planolites,** Miller (1889, p. 520) and later Bassler (1915, p. 982) were the first authors to designate the (same) type species. Like **Palaeophycus, Planolites** has been a topic of considerable confusion since its original establishment by Nicholson (1873). Detailed summaries have been presented by Alpert (1975), Benton and Trewin (1978) and more recently Pemberton and Frey (1982). As with **Palaeophycus,** we accept the most useful and workable nomenclatural system as that of Pemberton and Frey (1982) and adopt it herein. Nevertheless, we slightly emend their diagnosis to include lined forms, which, although rare in the Trenton Group are consistent with the overall diagnosis of **Planolites** as originally described by Nicholson (see Benton and Trewin 1978,pp. 5-8).

Planolites is a eurybathic form (Chamberlain 1978b) ranging in age from Late Precambrian-Recent (Häntzschel 1975) and is commonly attributed to the sediment-ingesting activity of vagile deposit feeding vermiform organisms (Alpert 1975, Pemberton and Frey 1982), though several phyla may in fact be responsible.

Planolites beverleyensis Billings, 1862
(Figure 9g)

Diagnosis - Relatively large, smooth, straight to gently curved or undulose cylindrical **Planolites** (after Pemberton and Frey 1982).

Material - 21 specimens and several hundreds observed in the field.

Description - Smooth, straight to slightly curved, horizontal to slightly inclined (up to 20°) regularly cylindrical, unbranched or branched (at varied angles of 20-115°), isolated or cross-cutting burrows. Burrow fill is typically coarser than the host rock but may be finer and of different colour. Burrow fill is typically structureless but rare specimens exhibit thin shale or micritic linings up to 9mm thick which may be composed of a series of concentric laminae, giving the burrows an apparent central core. Specimens are preserved in convex or concave epirelief, convex hyporelief and endorelief in a wide variety of lithologies and vary from 5-20mm in diameter and 2.7-100cm in length.

Remarks - Although the diagnosis proposed by Pemberton and Frey (1982) did not include lined burrows, those observed in the Trenton Group are so rare and are so well mixed within crowded **P. beverleyensis** that the use of another name would obscure the close similarity of the burrows. Arguably, strict adherence to the original definition of **Cylindrichnus** Toots in Howard, 1966, might suggest their inclusion within this ichnogenus. However, the original definition of **Cylindrichnus** encompasses a wide variation in morphology, often overlapping into related forms such as **Asterosoma** von Otto, 1854 and **Rosselia** Dahmer, 1937. Additionally, most authors now adopt an undefined but emended usage of **Cylindrichnus** as vertical or steeply inclined, unbranched concentrically lined structures (e.g. Fürsich 1974b, 1981; McCarthy, 1979). We are therefore hesitant to adopt **Cylindrichnus** as a useful description of these Trenton specimens and include them within **Planolites,** to which they best conform.

Otherwise, the specimens described here exhibit all the attributes of **P. beverleyensis** and are definitively conspecific.

Planolites montanus Richter, 1937
(Figure 9h)

Diagnosis - Relatively small, curved to contorted **Planolites** burrows less than 5mm in diameter (after Pemberton and Frey 1982).

Material - 10 specimens and more than a hundred observed in the field.

Description - Straight to slightly sinuous, smooth, horizontal unbranched and rarely branched (angles of 25-83°), irregularly cylindrical burrows, 1-5mm in diameter and 14-74mm in length. Cross-overs, interpenetration and reburrowed segments are common. Burrow fill is typically structureless but rare examples preserve thin wall linings (0.6mm) and, or, concentric laminae. They occur in a wide variety of lithologies and are preserved mainly in endorelief but also in convex epirelief and concave hyporelief.

Remarks - As the various ichnospecies of **Planolites** are based, according to Pemberton and Frey (1982), on size, curvature and wall sculpture, the Trenton material described here can be confidently assigned to **P. montanus.** Lined and concentrically laminated specimens, otherwise exhibiting the same basic size and morphology as **P. montanus,** are here included within the ichnospecies based on the same reasoning as discussed under **P. beverleyensis.**

Planolites sp.
(Figure 9f)

Material - 57 specimens.

Description - Horizontal, straight to slightly sinuous, unbranched, irregularly cylindrical (where observed) burrows, 3-20mm in diameter and up to 12cm in length. The burrows are most typically preserved in endorelief in calcisiltites and calcilutites, where their coarser fill and rare concentric laminae can be readily observed, and only occasionally in convex and concave epirelief.

Remarks - Their preservation as endorelief and only occasionally as semi-relief structures, and hence the lack of knowledge of the wall characteristics and detailed 3-dimensional geometry precludes ichnospecific assignment. They are certainly larger than **P. montanus** and although extremely similar to **P. beverleyensis** differ in that they are occasionally slightly sinuous.

Ichnogenus **Rhizocorallim**
Zenker, 1836

Type species - **Rhizocorallium jenense** Zenker, 1836,by original monotypy.

Diagnosis - U-shaped spreiten burrows, parallel or oblique to bedding plane, limbs more or less parallel and distinct; tube diameter: diameter of spreite 1.5 (after Fürsich 1974c).

Discussion - Two of the three ichnospecies of **Rhizocorallium,** namely **R. irregulare** Mayer, 1954 and **R. uliarense** Firtion, 1958, are clearly the result of deposit-feeding organisms, whilst the third, **R. jenense** Zenker, 1836, is the product of a suspension feeder (Fürsich 1974c). In both cases, the most likely producers have been suggested to be crustaceans or even nymphs of ephemerids (Fürsich 1974c, Fürsich and Mayr 1981) or even possibly annelids (Basan and Scott 1979). The ichnogenus is cosmopolitan, Cambrian-Tertiary in age and although commonly reported in marginal or shallow marine strata (e.g. Hakes 1976; Fürsich 1974c, 1981) has also been reported in deep-water (Crimes 1977, Pickerill **et al.** 1982) and non-marine (Fürsich and Mayr 1981) environments. A full review of its nomenclatural and interpretive history is given in Fürsich (1974c).

?**Rhizocorallium** cf. **R. irregulare**
Mayer, 1954
(Fig. 10, Pickerill and Forbes 1979)

Diagnosis - Long, sinuous, bifurcating or planispiral U-shaped spreiten burrows, in the main horizontal (after Fürsich 1974c).

Material - 5 specimens.

Description - Straight, parallel or slightly oblique to stratification, isolated, U-shaped burrows, with tube diameter (where discernible) 2-3mm, total width 12-15mm and length 60-70mm with irregularly shaped and often discontinuous poorly preserved protrusive spreiten. The burrows are smooth and fill is identical to the enclosing sediment thus making for extremely poor preservation which is in both full relief and concave epirelief.

Remarks - The poor preservation and the extremely small size of the burrows precludes confident assignment to **Rhizocorallium.** However, slightly larger material and with comparable discontinuous or even no spreiten has been recently described by Fürsich and Mayr (1981) from the Miocene of southern Germany. If, indeed, the specimens are true **Rhizocorallium,** then they are conspecific with **R. irregulare** Mayer, 1954, as **R. uliarense** is a 3-dimensional spiral and **R. jenense** is shorter and typically oblique. Several attempts to photograph the specimens proved futile but a schematic figure is reproduced in Pickerill and Forbes (1979, p. 2032, fig. 10).

Ichnogenus **Rosselia** Dahmer, 1937

Type species - **Rosselia socialis** Dahmer, 1937, by original monotypy.

Diagnosis - "Cylindrical pencil-thick burrows, filled with quartzite, dug in the sediment at various distances and orientations. Most are inclined at an angle of 30° or more to bedding. The lower end is not observed; the opening is expanded and filled with imbricated concentric layers of matrix which as a rule are strongly weathered; these structures are clearly distinctive in their appearance" (Dahmer 1937, pp. 532-533 - **trans. litt.**).

Discussion - Dahmer (1937) originally erected **Rosselia** for cone or funnel-shaped burrows with a concentric backfill structure and, as outlined briefly in the discussion of **P. beverleyensis,** there has been considerable confusion regarding its use with respect to the morphologically related forms **Cylindrichnus** Toots in Howard, 1966 and **Asterosoma** von Otto, 1854. **Asterosoma** should only be used for star-shaped, concentrically lined and longitudinally wrinkled burrows and, for example, the specimens figured by Frey and Howard (1970) are not consistent in any sense of the original diagnosis (cf. Häntzschel 1975). Many authors now employ **Cylindrichnus** for vertical or steeply inclined, straight to weakly curved, unbranched **Skolithos**-like structures with multiple layered walls (e.g. Fürsich 1974a, 1981; McCarthy 1979), that is in contradiction to its original and extremely broad diagnosis (see Howard 1966). Strict adherence to this emended usage is to be recommended, because once morphologically similar structures assume a cone or funnel-shape, they should be included within **Rosselia** and **Asterosoma.** Although the three ichnogenera are clearly end members of intergradational burrow systems (e.g. Chamberlain 1971, Fürsich 1974a, McCarthy 1979), providing caution is observed, ichnogeneric assignment should be possible.

Rosselia ranges in age from Lower Cambrian (Seilacher 1955) to Upper Eocene (Książkiewicz 1977) and although most commonly reported from shallow sublittoral environments (Garcia-Ramos 1976, McCarthy 1979, Pemberton et al. 1982) has also been reported in association with deep-water flysch (Książkiewicz 1970, 1977). It may represent the feeding or dwelling burrows of annelids (Chamberlain 1971), crustaceans (Frey 1970) or sea anenomes (Chamberlain and Clark 1973, Książkiewicz 1977).

?**Rosselia** sp.
(Figures 10f, g)

Material - 10 specimens.

Description - Vertical to slightly inclined, funnel-shaped burrows preserved only in concave epirelief on upper surfaces of thinly bedded (20-35mm) calcilutites. Burrow diameter is 4-9mm; depth is up to 9mm. In most examples the filling has been eroded but some exhibit a poorly preserved concentric wall surrounding a central tube up to 3mm in diameter.

Remarks - The material is so poorly preserved even ichnogeneric identification is uncertain. However, its vertical attitude and funnel-like cross-section and its poorly preserved concentric layering and central tube are sufficient to tentatively assign it to **Rosselia** Dahmer, 1937.

Ichnogenus **Rusophycus** Hall, 1852

Type species - **Fucoides biloba** Vanuxem, 1842, first? subsequent designation by Seilacher (1955, p. 110) as **R. bilobatus** (=**R. bilobatum**).

Diagnosis - Shallow to deep, short, posteriorly tapering bilobed resting burrows (cubichnia) of trilobites. Lobes may be smooth or exhibit transverse to oblique scratch marks in various arrangements directed anterolaterally. Coxal, exopodal, spinal, cephalic and pygidial markings may be present (after Osgood 1970, Alpert 1976).

Discussion - If the ichnogenera **Cruziana** and **Rusophycus** are to be retained as distinctive forms, the designations by Miller (1889, p. 138), Bassler (1915, p. 1132), Andrews (1955, p. 230) and Hakes (1976, p. 32) of the type species of **Rusophycus** as **R. clavatus** must be rejected, as Hall's (1852) original material should more correctly be diagnosed as **Cruziana clavata** (Hall), as suggested by Osgood and Drennen (1975). Other authors (e.g. Osgood 1970, Häntzschel 1975, Osgood and Drennen 1975, Alpert 1976) quote **Fucoides biloba** (Vanuxem) as the type, even though Hall (1852) did not designate **R. bilobatus** (=R. bilobatum) as his nomenclatural type. Arguably, his **R. pudicus** (=R. pudicum) could equally be regarded as the type as it was described prior to **R. bilobatus.** To retain some semblance of nomenclatural stability, however, particularly as **R. bilobatum** is more closely representative of typical rusophycids, as originally inferred by Hall himself (1852, p. 23), we accept **F. biloba** Vanuxem, 1842 as the type species.

The morphology, interpretation and detailed taxonomy of **Rusophycus** has been fully discussed by Osgood (1970) and Osgood and Drennen (1975). It ranges in age from Cambrian-Triassic (Crimes 1975, Bromley and Asgaard 1979) and, following Seilacher (1955) and Osgood (1970), was produced by trilobites and is a trace diagnostic of the **Cruziana** ichnofacies of Seilacher (1967).

Rusophycus sp.
(Figure 7h)

Material - 9 specimens.

Description - Variably and generally poorly preserved (in convex hyporelief) posteriorly tapering bilobate traces; maximum length 44mm, maximum width 26mm and a mean length/width ratio of 1.7:1. Depth variable, up to 8mm. Lobes are smooth and outer margins grade imperceptibly into surrounding material.

Remarks - Poor preservation and the absence of detailed scratch markings precludes ichnospecific assignment. They are certainly extremely similar to specimens of **Rusophycus** described from the Trenton Group northeast of Quebec City by Pickerill and Forbes (1979), who noted a close similarity to **R. pudicum.** Sectioning reveals the traces were formed at the sediment-water interface.

Ichnogenus **Scalarituba** Weller, 1899

Type species - **Scalarituba missouriensis** Weller, 1899, by original montypy.

Diagnosis - Mainly horizontal "burrows ...., *subcylindrical in form*, never straight for more than a few centimeters, curving in all directions, and marked by transverse ridges situated at distances of one or two millimeters, ... filled with material similar to that which surrounds them, ... detected by their slightly different color ...." (after Weller 1899, p. 12).

Discussion - **Scalarituba** has been the subject of much nomenclatural controversy since Seilacher and Meischner (1965) first considered it to be a behavioural variant but not strictly synonymous with associated **Nereites** and **Neo-**

nereites traces. Chamberlain (1971), with extremely well-preserved material, demonstrated that for a single specimen, preservation in hyporelief resulted in biserially arranged pustules characteristic of **Neonereites biserialis** whereas preservation in epirelief resulted in a median gallery with lateral lobes characteristic of **S. missouriensis, Nereites** sp. (=**Phyllodocites** view) and **Neonereites uniserialis.** He placed **N. uniserialis** and **N. biserialis** in synonymy with **S. missouriensis** and expanded **Scalarituba** to include a '**Nereites** view' in convex hyporelief and a '**Phyllodocites** view' in concave epirelief. Although this approach has subsequently gained a large following (e.g. Chamberlain 1977, 1978b; Chaplin 1980; Jordan 1981; Larson 1982) several authors have preferred to retain the forms as distinctive ichnogenera, particularly because poorer preserved material than that described by Chamberlain (1971) does not illustrate the morphological overlap and, instead, conforms more closely to individual ichnogenera as originally defined (e.g. Häntzschel 1975; Hakes 1976; Brasier and Hewitt 1979; Pickerill 1980, 1981; Marintsch and Finks 1982). We adopt the latter approach herein.

Scalarituba represents the deposit-feeding activity of a worm-like organism burrowing in the sediment and periodically backfilling its burrow (Weller 1899, Conkin and Conkin 1968). It is a marine but eurybathic form (Crimes 1977) having been reported from a wide spectrum of environments ranging from tidal flat (Conkin and Conkin 1968) to deep-water flysch (Chamberlain 1971, Pickerill 1980). It ranges in age from Ordovician-Permian (Häntzschel 1975).

Scalarituba missouriensis Weller, 1899
(Figure 10c)

Diagnosis - As for ichnogenus

Material - 5 specimens.

Description - Horizontal, sinuous meniscate burrows, that straighten over short distances, preserved in endorelief on upper surfaces of calcilutites. Burrow fill is identical to host material but occasionally meniscae possess coarser bioclastic material. Burrow diameter is 2.5-5mm and is consistent within a single specimen; length is variable, a maximum of 18cm having been observed. Meniscae are irregularly distributed but up to 3 per cm may be observed.

Remarks - The Trenton material can undoubtedly be diagnosed as **S. missouriensis** and is extremely similar to conspecific material described by Pickerill (1981) and by Marintsch and Finks (1982) as **S. missouriensis** var. "meniscate form".

Ichnogenus **Scolicia** de Quatrefages, 1849

Type species - **Scolicia prisca** de Quatrefages, 1849, by original monotypy.

Diagnosis - Concave, top-surface meandering trails broadly U-shaped in section with floor and lateral walls. Most of the floor shows a single or biserially alternating series of laminae, but the edges of the floor are smooth tracks, sometimes consisting of discrete sediment strings. Lateral walls with distinct curved laminae, concave surface anterior and steep (after Smith and Crimes 1983).

Discussion - **Scolicia** was erected from the Paleocene flysch of Spain but its original description was inadequate and had no accompanying figure (Smith and Crimes 1983). This led to utter confusion in the literature and the "**Scolicia** group" now comprises extremely variable traces interpreted as the trails of annelids, gastropods, crustaceans, polychaetes, echinoids, holothuroids, Pennatulacea (as reviewed by Bradley 1980) and more recently by Smith and Crimes (1983) as heart urchins. Following Książkiewicz (1977), Crimes et al. (1981) and Smith and Crimes (1983) used **Scolicia** for either shallow burrows or furrows and **Subphyllochorda** for cylindrical backfilled burrows. Although this approach is followed herein we do not agree with the suggestion of Smith and Crimes (1983) that all Palaeozoic forms referred to **Scolicia** should be transferred to other ichnogenera because they cannot possibly be related to heart urchins. Knowledge of the producer of a trace fossil is not taxonomically significant in ichnology (see Fillion and Pickerill 1984). Clearly, a full and detailed taxonomic revision of the ichnogenus is still required and until such a study is undertaken we regard **Scolicia** as a variable and facies transgressive form which ranges in age from Lower Cambrian to Recent (Häntzschel 1975).

Scolicia sp.
(Figure 7c)

Material - 3 specimens and several occurrences on a single bedding plane.

Description - All specimens are preserved on the upper surface of a 5mm thick chert bed in concave epirelief and consists of two parallel furrows, each 4mm wide, separated by a slightly raised central lobe 4-4.5mm wide. The latter is smooth and rounded whereas the furrows exhibit crude transverse striations oriented approximately normal to the central lobe, usually less than 2mm apart. Total depth of the furrows is 1.5 mm. The traces are sinuous, often tens of centimetres in length and never self-crossing.

Remarks - Because of the generally poor preservation of the traces and the unsatisfactory taxonomic status of the ichnogenus, the Trenton material is only identified at the ichnogeneric level. Although we know of no identical analogues, they do resemble specimens of **Scolicia** figured by both Garcia-Ramos (1976) from the Devonian of Spain and Chamberlain (1971) from the Carboniferous of Oklahoma.

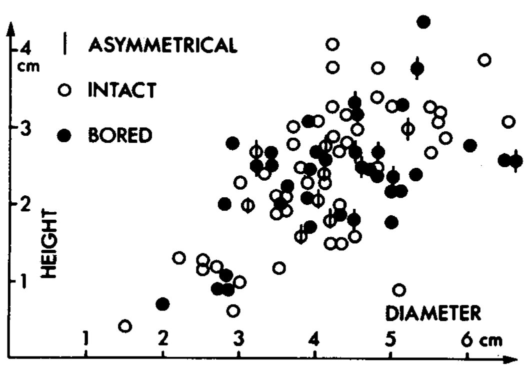

Fig. 12 - Height: Diameter plot of intact and bored, symmetric and asymmetric colonies of the bryozoan Prasopora spp.

Ichnogenus **Skolithos** Haldeman, 1840

Type species - **Fucoides? linearis** Haldeman, 1840, by original montypy.

Diagnosis - Unbranched, vertical or steeply inclined, cylindrical or subcylindrical, lined or unlined burrows, 1-15mm in diameter and a few centimetres to up to a meter in length. Burrow walls distinct or indistinct, smooth to rough, possibly annulated; burrow diameter may vary slightly along its length. Burrow fill structureless (after Alpert 1974).

Discussion - As with several other commonly occurring ichnogenera, **Skolithos** has received considerable discussion and systematic treatment. Alpert (1974) recently published a systematic review, conducted solely on literature research, and suggested that many of the numerous previously published ichnospecies and even ichnogenera such as **Tigillites, Stipsellus** and **Foralites** could confidently be placed within five ichnospecies of **Skolithos.** He later proposed a sixth, **S. bulbus** (Alpert 1975), and more recently Hofmann (1979) erected a new ichnospecies, **S. gyratus.** James (1891), Richter (1920, 1921), Howell (1943) and Osgood (1970) have also extensively discussed the ichnogenus. Undoubtedly, a thorough systematic review still seems necessary, but until this is undertaken we regard Alpert's (1974, 1975) scheme as the most satisfactory.

Skolithos has been reported from a variety of marine environments and is typically found in association with 'high energy' conditions, particularly in nearshore shallow-water conditions but also in deep-water submarine channels and canyons (see Seilacher 1967, Alpert 1974, Crimes 1977, Pickerill 1981 etc.) or even in floodplain and dune environments (e.g. Ratcliffe and Fagerstrom 1980). It constitutes the type ichnogenus of the **Skolithos** ichnofacies of Seilacher (1967) and is generally regarded as the dwelling and feeding burrow of annelids or phoronids (Alpert 1974) and ranges in age from Late Precambrian-Recent (Crimes and Germs 1982).

Skolithos linearis Haldeman, 1840
(Figure 13a)

Diagnosis - Burrows cylindrical to subcylindrical, perfectly straight to slightly curved and inclined, up to a meter in length. Diameter 3-7mm, occasionally up to 12mm. Burrow wall distinct to indistinct, may be annulated (after Alpert 1974, p. 663).

Material - 13 specimens.

Description - Straight, vertical, unbranched burrows 3-5mm in diameter and up to 66mm in length. Burrow fill is typically coarser than host material, rarely finer. Burrow walls are distinct, parallel, apparently smooth and unlined. Preservation is in endorelief.

Remarks - Of the seven existing ichnospecies of **Skolithos,** the Trenton material most closely resembles **S. linearis** Haldeman, 1840 and is diagnosed as such Although they superficially resemble **S. verticalis** (Hall), this ichnospecies is generally shorter and smaller and more commonly inclined and curved (Alpert 1974).

Skolithos sp.
(Figure 10d)

Material - 4 specimens and several occurrences in the field.

Description - Straight, vertical to steeply inclined (up to 60°) burrows 4-10mm in diameter and up to 35mm in length. Burrow fill is finer or identical to the host rock (calcisiltite). Burrow walls are distinct and iregular; some specimens possess a thick calcilutite wall (2-3mm) around an inner tube of 4mm diameter. Preservation is in endorelief.

Remarks - Though clearly lacking the characteristics of **S. linearis,** the specimens are not well enough preserved for ichnospecific identification. Similar structures have been figured by Pickerill and Forbes (1979, p. 2033, fig. 116).

Ichnogenus **Teichichnus** Seilacher, 1955

Type species - **Teichichnus rectus,** Seilacher 1955, by original monotypy.

Diagnosis - Long wall-shaped septate structures consisting of a pile of gutter shaped laminae (Seilacher 1955, p. 378 -**trans. litt.**).

Discussion - **Teichichnus** was introduced by Seilacher (1955) to describe a type of spreiten trace fossil formed by a series of long horizontal burrows stacked vertical to bedding. He interpreted the burrow as resulting from continual upward-shift by the producing deposit-feeding organism. Since its original description, it has been shown to intergrade with **Phycodes** (Häntzschel and Reineck 1968, Hofmann 1979), **Thalassinoides, Ophiomorpha** and **Gyrolithes** (Hester and Pryor 1972, Frey **et al.** 1978, Frey and Seilacher 1980), **Rhizocorallium** (Chisholm 1970, Sellwood 1970) and even **Cruziana** (Garcia-Ramos 1976). As such, its producers are probably polyphyletic, though *annelids and arthropods are usually most* favoured (Martinsson 1965, Chisholm 1970, Chamberlain 1977).

It is a strictly marine but eurybathic form, most commonly occurring in shallow subtidal sediments (e.g. Fürsich 1981) but also in association with submarine fans and abyssal environments (Ekdale 1977, Wetzel 1981). It ranges in age from Lower Cambrian-Recent.

Teichichnus rectus Seilacher, 1955
(Figure 10c)

Diagnosis - Straight, unbranched **Teichichnus** with an exclusively retrusive spreite (after Seilacher 1955).

Material - 138 specimens.

Description - Straight, smooth, unbranched burrows, parallel or slightly oblique to stratification possessing retrusive spreiten. Length 8.5-125mm, width 4-35mm and height 14-25mm; individual specimens are consistently deeper than wide, are preserved in full relief and possess a calcilutite or calcisiltite fill of identical grain size to host rock.

Remarks - **T. rectus** is the product of a shallow burrower usually associated with low sedimentation rates (Fürsich 1975, Hakes 1976) *but occasionally* observed in environments subject to rapid deposition (Chisholm 1970). Specimens from the Trenton Group within Quebec City

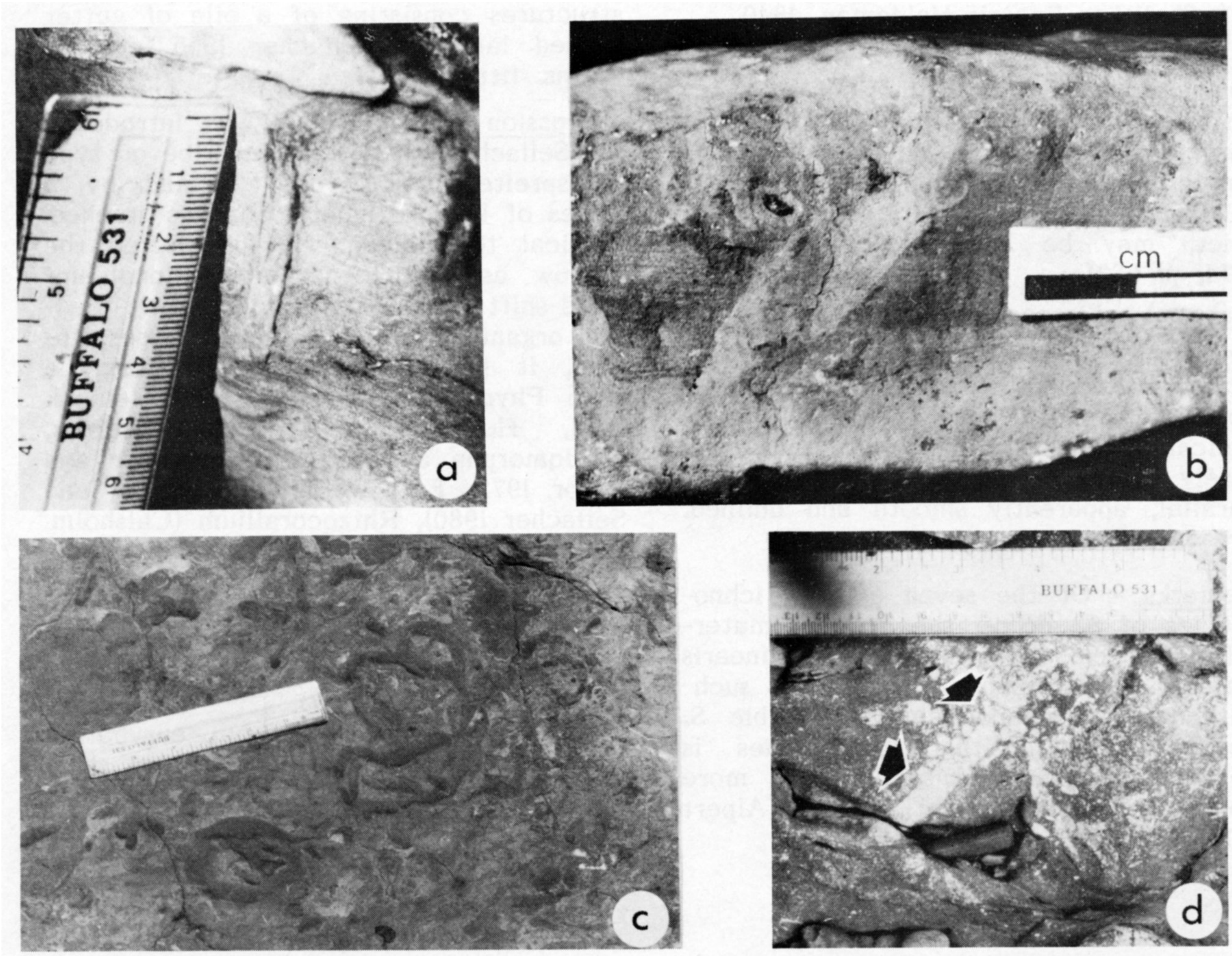

Fig. 13 - a. Skolithos linearis in vertical section, Grondines Member, locality 18. b. 'Oblique burrow' in transverse section, Grondines Member, locality 18. c. 'Loop burrows' on lower bedding surface in convex hyporelief, Grondines Member, locality 21. d. 'Pronged burrows' with typical prongs arrowed, on upper bedding surface, Grondines Member, locality 21.

have also been figured in Pickerill and Forbes (1979, p. 2031, figs. 9c, 9d).

Teichichnus sp.
(Figure 10h)

Material - 12 specimens.

Description - All specimens preserved in full relief on upper bedding plane surfaces as elongate, unbranched, straight endoreliefs with parallel sides and rounded terminations. Length 50-105mm, width 11-20mm and depth, where observed, 16-21mm. Plan views exhibit bidirectional spreite concave towards the centre of the burrow; transverse sections indicate spreite are concave-up and retrusive.

Remarks - The total character of this form is not fully preserved and not clearly understood, but the absence of a tube clearly distinguishes them from the similar **Polarichnus** Narbonne (in Narbonne et al. 1979). They most closely accord to **Teichichnus** Seilacher, 1955 and are diagnosed as such but only at ichnogeneric level.

Ichnogenus **Trichichnus** Frey, 1970

Type species - **Trichichnus linearis** Frey, 1970, by original designation.

Diagnosis - Branched or unbranched, hairlike, cylindrical, straight to sinuous burrows distinctly 1mm in diameter, oriented at various angles with respect to bedding. Burrow walls distinct, commonly lined with diagenetic minerals (after Frey 1970).

Discussion - Frey (1970) interpreted **Trichichnus** as the feeding and dwelling burrow of a minute deposit-feeding vermiform or crustacean-like organism, and since its original formulation remains a monospecific form, even though it has been reported from strata of Tremadoc-Recent age (Wetzel 1981, Fillion and Pickerill 1982). It is strictly marine but eurybathic, having been reported from shallow (Frey 1970, 1975; Pickerill and Forbes 1979) and less commonly deep-water (Kennedy 1975) environments.

Trichichnus sp.
(Figure 10a)

Material - 15 specimens and several occurrences recorded in the field.

Description - Unbranched, straight to slightly curved, thin cylindrical burrows less than 1mm in diameter and up to 30mm long. Commonly vertical but may be inclined and rarely horizontal. Burrow walls distinct and fill is typically coarser than enclosing material but may be finer. Preservation is in full relief.

Remarks - The Trenton material is only identified at ichnogeneric level as specimens lack the diagenetic wall linings diagnostic of **T. linearis** (see Frey 1970, p. 22), thus suggesting that the producing organism was not required to reinforce its burrow. Pickerill and Forbes (1979, p. 2031, fig. 9e) have also figured identical material from the Trenton Group at Pont Rouge (see Fig. 1).

Ichnogenus **Trypanites** Mägdefrau, 1932

Type species - **Trypanites weisei** Mägdefrau, 1932, by original monotypy.

Diagnosis - Simple, unbranched borings in hard substrates, non-parallel to the surface with a single opening to the surface (after Bromley 1972).

Discussion - As recently noted by Bradshaw (1980), Mägdefrau (1932) named **Trypanites weisei,** the type species, for slender more or less straight-sided and long (up to 4cm) but very narrow (1mm) vertical borings in the Middle Triassic Muschelkalk hardgrounds. At a later date, however, Bromley (1972) expanded **Trypanites** to include all single-entrance pouch-shaped borings (e.g. **Teredolites, Gastrochaenolites**) resulting from the activities of a variety of organisms but excluding acrothoracican cirripeds. The expanded definition has generally been accepted apart from the inclusion by Bromley (1972) of **Vermiforichnus** Cameron, 1969, which is still adopted by many authors (e.g. Pickerill 1976, Elias 1976, Hofmann 1979) as a useful descriptor of unbranched horizontal or subhorizontal cylindrical borings. In this paper we also exclude borings more closely akin to **Vermiforichnus** and adopt **Trypanites** as originally defined by Mägdefrau (1932).

Trypanites ranges in age from Lower Cambrian (James **et al.** 1977) to Recent (Kobluk **et al.** 1978) and is commonly attributed to the activities of polychaetes, sipunculids, phoronids and thoracican cirripeds of which the sipunculids (Pemberton **et al.** 1980) or polychaetes (Kobluk and Nemcsok 1982) are most favoured. It constitutes the type of the recently defined **Trypanites** ichnofacies of Frey and Seilacher (1980).

Trypanites weisei Mägdefrau, 1932
(Figures 11b, c)

Diagnosis - More or less straight and vertical **Trypanites,** diameter **ca.** 1mm and reaching over 4cm in length (after Bromley 1972).

Material - 97 specimens and several hundred recordings in the field.

Description - All borings are preserved in colonies of the calcareous red alga **Solenopora compacta** or the bryozoans

Prasopora spp. and **Diplotrypa** spp. Diameter is 0.1-3mm and length up to 17mm; they are straight to gently curved, parallel sided with clearly defined unlined walls and typically possess a micrite fill. In **Prasopora,** walls of the borings are smooth provided they parallel zoecia but as soon as they turn they become ragged.

Remarks - Restriction of the borings to **Solenopora, Prasopora** and **Diplotrypa** suggests host specificity as a result of larval selectivity of the producing sipunculids or polychaetes probably as a result of the availability of the large surface area substrates afforded by these genera. As all the examined colonies do not show any reaction to the borings we also conclude that individual colonies were dead prior to boring activity. In a recent study of comparable material from the Middle Ordovician of Ontario, Kobluk and Nemcsok (1982) suggested that the producing ?polychaetes preferred large and asymmetrical **Prasopora** colonies. However, our data (Fig. 12) suggest that populations of bored and intact colonies thoroughly overlap and symmetrical and asymmetrical colonies were bored indiscriminately.

Ichnogenus **Vermiforichnus** Cameron, 1969

Type species - **Vermiforichnus clarkei** Cameron, 1969, by monotypy.

Diagnosis - Unbranched, horizontal or subhorizontal, straight to slightly curved, rarely irregular hooked or coiled, non-intersecting borings (after Cameron 1969a, b).

Discussion - Although Bromley (1972) included **Vermiforichnus** within **Trypanites,** we regard it as a useful descriptor of horizontal or subhorizontal unbranched borings, as discussed under the description of **Trypanites** in this paper. The borings have been reported in a wide variety of hosts (Cameron 1969a, b) and range in age from Middle Ordovician-Permian (Kobluk **et al.** 1978). Cameron (1969a, b) has demonstrated that at least some **Vermiforichnus** were produced by spionid polychaetes and Pickerill (1976) has demonstrated at least a single example of its host and size specificity.

Vermiforichnus clarkei Cameron, 1969 (Figures 11a, d)

Diagnosis - As for ichnogenus.

Material - 3 specimens.

Description - (i) A single boring preserved in endorelief in a pygidium of the isotelinid **Isotelus gigas,** 4.5mm long and 1-1.3mm wide with slightly expanded terminations. The boring is smooth, slightly sinuous and is filled with calcisiltite (Fig. 11a). (ii) A single boring preserved in endorelief on an undetermined branching bryozoan, 11mm long and 2mm wide. The boring is smooth, straight with rounded terminations and is filled with partially dolomitized sparite. (iii) Numerous smaller unbranched borings preserved in endorelief surrounding the right eye of **Isotelus gigas,** 0.09-0.16mm wide and 0.6-1mm long. The borings are straight to slightly sinuous, crowded but non-intersecting (Fig. 11d).

Remarks - Despite the small number of specimens, the variability exhibited by the borings of **V. clarkei** in the Trenton Group suggests that different groups of organisms were responsible for its production. Type (iii) borings differ from those of **Talpina pungens** Quenstedt, 1849 in being parallel and not oblique to the surface (see Voigt and Soule 1973).

Ichnogenus **Zoophycos** Massalongo, 1855

Type species - **Zoophycos caputmedusae** Massalongo, 1855, by subsequent designation of Andrews (1955, p. 262).

Diagnosis - Variably shaped spreiten structures comprised of numerous small protrusive more or less U- or J-shaped burrows of variable length and orientation. Spreite tabular or arranged in helicoid spirals giving an overall outline of circular, elliptical or lobate shape; central vertical tunnel or marginal tube may be present (after Frey 1970, Häntzschel 1975, Wetzel and Werner 1981).

Discussion - The ichnogenus **Zoophycos** has been plagued with excessive taxonomic splitting, different species, many of which are probably synonymous, being created merely on the whorl shape and the width and manner of branching of the rays (Frey, 1970, Häntzschel 1975, Książkiewicz 1977). Furthermore, there is still disagreement on the type species, because following the designation of the type as **Z. camputmedusae** by Andrews (1955, p. 262), Häntzschel (1962, p. 220), Taylor (1967, p. 4) and Plička (1968, p. 840) respectively designated **Fucoides brianteus, Zoophycos laminatus** and **Fucoides circinatus.** Häntzschel (1962), however, noted his designation only by an asterisk, and although still adopted as the type by several recent authors (e.g. Marintsch and Finks 1982) we regard such a designation as invalid by rule of priority. The original illustration of **Fucoides circinatus** by Brongniart (1828, p. 83) is too schematic to ascertain its true nature and **Zoophycos laminatus** is a **nomen nudum.** Until resolved, therefore, we accept Andrews' (1955) designation of the nomenclatural type as **Z. caputmedusae** by rule of priority.

Although there is still no general agreement on its origin, **Zoophycos** has been commonly attributed to the deposit-feeding activity of polychaetes (Bischoff 1968) and sipunculids (Wetzel and Werner 1981), to the imprints of prostomia of sabellids (Plička 1970) and even the feeding activity of umbellulids (Pennatulaceids) (Bradley 1973). Though considerable environmental significance has been attached to the ichnogenus, particularly regarding bathymetry, it is now realized to be a eurybathic form ranging in age from Ordovician-Quaternary and is typical of fine-grained substrates characterized by low sedimentation rates (for reviews see Frey 1970, Kennedy 1970, Simpson 1970, Chamberlain 1971, Osgood and Szmuc 1972, Bradley 1973, Häntzschel 1975, Ekdale 1977, Książkiewicz 1977, Wetzel and Werner 1981, Marintsch and Finks 1982).

Zoophycos sp.
(Figure 10b)

Material - 1 specimen.

Description - Horizontal arcuate burrow 7.5cm in width and preserved in epirelief, possessing disturbed backfilled coarse spreiten which are straight to moderately curved, composed of bioclastic material, ca. 3-6mm wide and separated by furrows up to 10mm wide. A J-shaped tube, 6.5mm wide and filled with bioclastic material bounds the burrow and gives it its particular outline.

Remarks - Because of the poor preservation identification at the ichnospecific level is uncertain, but the structure clearly has a J-form (**sensu** Wetzel and Werner 1981) in which only one side of the spreite is bounded by a tube, and is therefore regarded as **Zoophycos.** It resembles parts of **Zoophycos insignis** as illustrated by Ksiazkiewicz (1977, pl. 10, figs. 1, 7, text-fig. 16) but otherwise we are unaware of any comparable form.

MISCELLANEOUS TRACES

In addition to the morphologically distinctive forms recognized from the Trenton Group several forms are present which, because of their poor preservation, morphological variability and sufficient differences in configuration to already established ichnogenera, or combinations thereof, are not formally diagnosed. Four broad categories may be recognized:

(i) 'Loop burrows' (Fig. 13c) - Irregularly meandering and winding, subcylindrical, unlined horseshoe or more commonly loop-shaped burrows, 4-11mm wide and up to 28cm long, preserved in convex hyporelief on the soles of calcilutites. Burrow fill is coarser than enclosing sediment. Although looped, the burrows never intersect; rather they go under or over previous pathways. They are obviously the product of an unknown deposit feeder and resemble **Lumbricaria** as figured by Gutschick and Rodriguez (1977, p. 206, pl. 1a-c).

(ii) 'Oblique burrows' (Fig. 13b) - Straight, unbranched, inclined (30-50°) cylindrical burrows preserved in endorelief, 4-9mm in diameter and downward tapering to a rounded or pointed termination. Length 20-35mm, walls distinct and regular, lined or more commonly unlined, with a structureless burrow fill of identical grain size to enclosing material. We were initially tempted to include these structures within **Obliquus** Marintsch and Finks, 1982; however, this ichnogenus is consistently lined, inclined at 45° or less and upper portions may approach the horizontal and lower portions the vertical. Furthermore, there are difficulties in distinguishing this recently formed ichnogenus from **Cylindrichnus** as originally defined (Toots in Howard 1966) and inclined specimens of **Palaeophycus.**

(iii) 'Pronged burrows' (Fig. 13d) - Straight, unbranched, elongate burrows preserved in epirelief on the upper surfaces of calcilutites, 4-8mm wide, up to 9cm long. Burrow fill is typically structureless calcilutite but occasionally poorly preserved spreite can be discerned. Irregular prongs up to 4mm in width and length project from the burrows (Fig. 13d). Similar unnamed material has been figured by Ward and Lewis (1975, p. 884, fig. 2) and Pickerill and Forbes (1979, p. 2033, fig. 11a). The presence of a spreite in some specimens suggests the burrows were produced by deposit-feeding organisms and their overall morphology suggests they are akin to teichichnids.

(iv) 'Bryozoan borings' (Figs. 11e, f) - Delicate pinnate or net-like systems of tear-drop shaped zooecial pits, each 0.3-0.5mm in length, 0.07-0.1mm in width, rarely adjoined and more commonly separated by stolomate impressions up to 1mm long and 0.02mm wide preserved in two pygidia of **Isotelus gigas.** Similar borings or etching traces have been figured by Bromley and Surlyk (1973, p. 362, fig. 14c), Warme (1975, p. 201, fig. 11-14), Pickerill and Forbes (1979, p. 2033, fig. 11g) and Hofmann (1979, p. 57, pl. 22) and all have been interpreted as bryozoan in origin.

CONCLUSIONS

As outlined previously, sediments of the Trenton Group were deposited initially in lagoons followed in turn by offshore "bar", shallow and, finally, deeper offshore shelf environments. Trace fossils in each of these environments may be summarized as follows (see also Fig. 6):

Lagoon - **Arenicolites** sp., **Chondrites** type A, **Chondrites** type B, **Clematischnia** sp., **Helminthopsis hieroglyphica, Helminthopsis** sp., **Palaeophycus tubularis, Palaeophycus** sp., **Planolites beverleyensis, Planolites montanus, Planolites** sp., **Scalarituba missouriensis, Skolithos linearis, Skolithos** sp., **Teichichnus rectus,** ?**Teichichnus** sp., **Trichichnus** sp., **Trypanites weisei** and oblique burrows.

"Bar" - ?**Calycraterion** sp., **Chondrites** type A, **Chondrites** type B, **Chondrites** spp., **Circulichnis montanus, Cruziana problematica, Helminthopsis** sp., **Palaeophycus tubularis,** ?**Plagiogmus, Planolites beverleyensis, Skolithos linearis,** ?**Skolithos** sp. and **Trypanites weisei.**

Shallow shelf - **Arenicolites** sp., **Chondrites** Type A, **Chondrites** type B, **Chondrites** spp., **Cruziana problematica, Furculosus carpathicus, Helminthopsis hieroglyphica, Helminthopsis** sp., **Palaeophycus tubularis, Planolites beverleyensis, P. montanus, Planolites** sp., ?**Rhizocorallium** cf. **R. irregulare,** ?**Rosselia, Rusophycus** sp., ?**Scalarituba missouriensis, Skolithos linearis, Skolithos** sp., **Teichichnus** sp., **Trichichnus** sp., **Trypanites weisei** and **Zoophycos** sp.

Offshore shelf - **Arenicolites** sp., **Chondrites** type B, **Chondrites** spp., **Clem-**

atischnia sp., ?Conostichnus, Cruziana sp. cf. Diplichnites sp., Helminthopsis sp., Oichnus paraboloides, Palaeophycus tubularis, Palaeophycus sp., Planolites beverleyensis, P. montanus, Planolites sp., ?Rosselia, Rusophycus sp., Scalarituba missouriensis, Scolicia sp., Skolithos linearis, Skolithos sp., Teichichnus rectus, Teichichnus sp., Trypanites weisei, Vermiforichnus clarkei and informally diagnosed loop, oblique and pronged burrows and bryozoan borings.

Although there is some obvious variation in the abundance of traces in different environments (Fig. 6), this is believed to reflect preservational and other hazards such as nature and quality of outcrop, burrow density, toponomic or diagenetic preservation, grain size and sediment stability as discussed more fully by Fillion **et al.** (1984). The entire assemblage, irespective of environment of deposition, can best be equated with the **Cruziana** ichnofacies of Seilacher (1967), which is characterized by a mixed association of vertical, inclined and particularly horizontal deposit-feeding but also filter feeding traces. The abundant borings, more characteristic of the recently formulated **Trypanites** ichnofacies of Frey and Seilacher (1980), are no cause for concern as their presence merely reflects the availability of abundant hard substrates, in this case essentially in the form of the bryozoans **Prasopora** spp. and **Diplotrypa** spp., the red alga **Solenopora compacta** and the isotelenid trilobite **Isotelus gigas.**

Finally, and as discussed more fully by Fillion **et al.** (1984), the most significant environmental parameter governing the production, nature and preservation of the trace fossils was substrate and its overall characteristics, which in turn reflected the prevailing hydrodynamic regime and depositional rate. Substrate not only provided a primary control but also directly influenced diagenetic affects which both enhanced and masked specific traces depending on their original character.

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