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Article abstract

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Palichnology of the Lower Devonian Wapske Formation, Perth-Andover-Mount Carleton region, northwestern New Brunswick, eastern Canada

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The Lower Devonian Wapske Formation of the Tobique Group in the Perth-Andover-Mount Carleton region of northwestern New Brunswick forms part of the tectonostratigraphic Tobique Zone. In this region, the formation is 4000 to 9000 m thick and is interpreted as deep-marine turbiditic in origin. Seven sedimentary facies are recognized. These are: conglomerate facies (Facies 1); massive and parallel-laminated sandstone facies (Facies 2); thin- to thick-bedded sandstone with minor mudstone interbeds and/or mud-capped facies (Facies 3); thin-bedded sandstone and mudstone facies (Facies 4); thin-bedded, graded, fine-grained sandstone facies (Facies 5); thin-bedded, fine-grained sandstone and silty mudstone facies (Facies 6); and thin- and medium-bedded siltstone and mudstone facies (Facies 7). These facies are grouped into five facies associations reflecting a deep-marine fan system consisting of distributary channels, depositional lobes, lobe or fan fringes, and interchannel areas associated with a basin plain.

A relatively diverse and well-preserved ichnofauna, consisting of 23 ichnogenera (41 ichnospecies) and three vernacular ichnotaxa, is systematically described, these comprising *Arthraria* Billings, 1872; *Bergaueria* Prantl, 1945; *Chondrites* von Sternberg, 1833; *Cochlichnus* Hitchcock, 1858; *Cosmorhaphe* Fuchs, 1895; *Cruziana* d'Orbigny, 1842; *Dendrotichnium* Häntzschel, 1975; *Didymaulichnus* Young, 1972; *Helminthoida* Schafhäutl, 1851; *Helminthopsis* Heer, 1877; *Hormosiroidea* Schaffer, 1928; *Monomorphichnus* Crimes, 1970; *Neonereites* Seilacher, 1960; *Palaeophycus* Hall, 1847; *Paleodictyon* Meneghini *in* Murchison, 1850; *Phycodes* Richter, 1850; *Protopaleodictyon* Książkiewicz, 1970; *Protovirgularia* M'Coy, 1850; *Rusophycus* Hall, 1852; *Skolithos* Haldeman, 1840; *Taenidium* Heer, 1877; *Uchirites* Macsotay, 1967; *Umfolozia* Savage, 1971; two track forms and indeterminate scratch markings. Their palaeoenvironmental distribution within the sequence correlates well with the interpreted submarine fan complex and compares favourably with other previously documented ichnofaunas from deep-marine fans. Collectively, the ichnofauna of the Wapske Formation is characteristic of Seilacher's (1967) *Nereites* ichnofacies.

La formation de Wapske du Dévonien inférieur du groupe de Tobique dans la région de Perth Andover/mont Carleton du nord-ouest du Nouveau-Brunswick fait partie de la zone tectonostratigraphique de Tobique. Dans cette région, la formation a 4 000 à 9 000 m d'épaisseur et elle est interprétée comme une formation d'origine turbiditique abyssale. On reconnaît sept faciès sédimentaires, notamment : le conglomérat (faciès 1); un faciès de grès laminé massif et parallèle (faciès 2); un faciès de grès en couches épaisses ou minces interstratifié de mudstone en quantité mineure ou couronné de boue (faciès 3); un faciès de mudstone et de grès en couches minces (faciès 4); un faciès de grès à grains fins, profilé, en couches minces (faciès 5); un faciès de mudstone vaseux et de grès à grains fins, en couches minces (faciès 6); et un faciès de mudstone et de microgrès en couches minces et moyennes. Ces faciès sont groupés en cinq associations de faciès correspondant à un système en éventail abyssal constitué de défluents, de lobes sédimentaires, de franges en lobe ou en éventail et de zones inter-canaux associées à une plaine synclinale.

Une ichnofaune relativement diversifiée et bien préservée, constituée de 23 ichnogenres (41 ichnoespèces) et trois *ichnotaxa* courants, est décrite de façon systématique. Ceux-ci comprennent l'*Arthraria* Billings, 1872; le *Bergaueria* Prantl, 1945; les *Chondrites* von Sternberg, 1833; le *Cochlichnus* Hitchcock, 1858; le *Cosmorhaphe* Fuchs, 1895; le *Cruziana* d'Orbigny, 1842; le *Dendrotichnium* Hantzschel, 1975; le *Didymaulichnus* Young, 1972; l'*Helminthoida* Schafhautl, 1851; l'*Helminthopsis* Heer, 1877; l'*Hormosiroidea* Schaffer, 1928; le *Monomorphichnus* Crimes, 1970; le *Neonereites* Seilacher, 1960; le *Palaeophycus* Hall, 1847; le *Palaeodictyon Meneghini* dans Murchison, 1850; le *Phycodes* Richter, 1850; le *Protopaleodictyon* Książkiewicz, 1970; le *Protovirgularia* M'Coy, 1850; le *Rusophycus* Hall, 1852; le *Skolithos* Haldeman, 1840; le *Taenidium* Heer, 1877; l'*Uchirites* Macsotay, 1967; l'*Umfolozia* Savage, 1971; deux formes de pistes et des marques de grattage. Leur répartition paléoenvironnementale à l'intérieur de la séquence correspond bien avec le complexe en éventail sous-marin interprété et elle se compare favorablement avec les autres ichnofaunes des éventails abyssaux documentées auparavant. Collectivement, l'ichnofaune de la formation de Wapske est caractéristique de l'ichnofaciès *Nereites* de Seilacher (1967).

[Traduit par la rédaction]

INTRODUCTION

The study area is located in northwestern New Brunswick, eastern Canada, from Perth-Andover to Mount Carleton, a distance of approximately 93 km, and is part of the tectonostratigraphic Tobique Zone (Fig. 1) (St. Peter, 1978a, 1979; Pickerill, 1986, 1991; Wilson, 1990). In this area, the Lower Devonian (Lochkovian-Pragian) Wapske Formation of the Tobique Group, the subject of this contribution, underlies approximately 205 km^2 and has been estimated by St. Peter (1978a,b, 1979) to be between 4000 and 9000 m in thickness.

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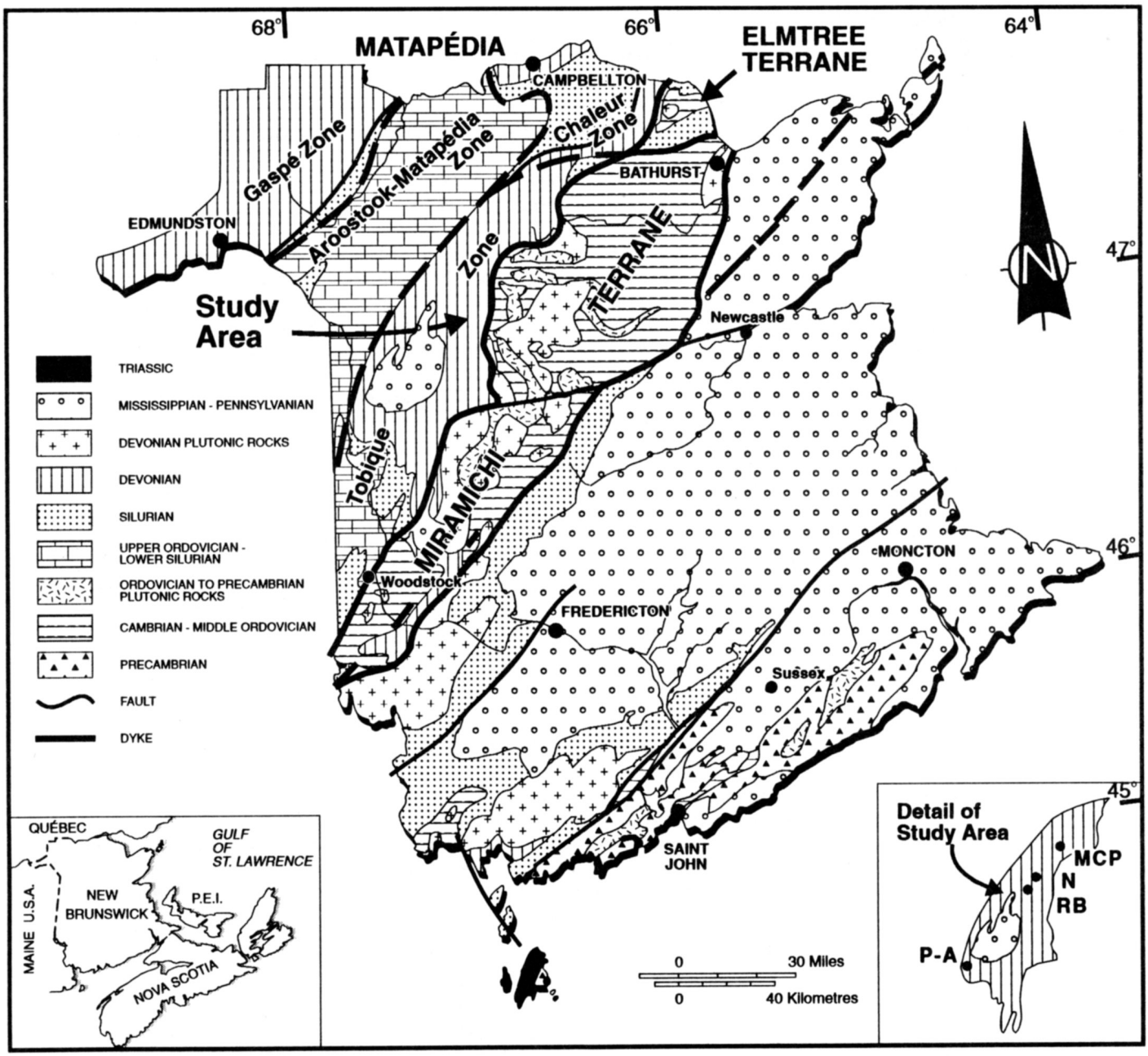


Fig. 1. Generalized tectonostratigraphic map of New Brunswick, eastern Canada, showing location of the study area (modified from Pickerill, 1986; Fyffe and Fricker, 1987; Wilson, 1990). P-A = Perth-Andover; RB = Riley Brook; N = Nictau; MCP = Mount Carleton Park.

Surficial exposure, however, is restricted essentially to roadsides in the Riley Brook, Nictau, Mount Carleton Provincial Park and Perth-Andover districts (Fig. 1). The most common sedimentary lithofacies are grey, greenish grey or green siltstones interbedded with varying proportions of grey, greenish grey and brown, fine- to medium-grained sandstones and mudstones or shales.

Several authors (e.g., St. Peter, 1978b, 1979, 1981, 1982; Skinner, 1982; Irrinki and Crouse, 1986) have proposed a relatively shallow marine, quiet water depositional setting for the Wapske Formation, based essentially on the evidence of its contained faunal communities (see also Boucot and Wilson, 1994). However, an alternative scenario was envisaged by Pickerill (1986, 1991) who, on sedimentological and taphonomic considerations, interpreted the formation as having been deposited below storm wave base in an outer shelf-upper slope depositional environment. In this paper we briefly assess the sedimentology of the Wapske Formation in more detail than in Pickerill (1986, 1991) and, in particular, describe systematically its contained ichnotaxa.

Ichnological research within the adjacent tectonostratigraphic Aroostook-Matapédia Zone has been conducted by Pickerill (1980, 1981, 1987) and Pickerill *et al.* (1987), but essentially on strata of Late Ordovician and Early Silurian age. The ichnology of the Lower Devonian Wapske Formation, until now, remains unstudied, except for a short ichnotaxonomic commentary by Pickerill (1991) and a series of more detailed ichnotaxonomic studies by Han and Pickerill (1994a,b, 1995). Most strata of the Tobique Group in the study area lack body fossils; however, many beds contain relatively well-preserved

and abundant ichnofossils that are considered useful for palaeoenvironmental interpretation, particularly in view of the fact that such previous interpretations of the sequence are at considerable variance. The purpose of this contribution is therefore to describe the ichnofaunas from this region and to comment on their interpreted palaeoenvironmental context.

STRATIGRAPHY AND SEDIMENTOLOGY

The Lower Devonian Tobique Group was originally proposed to comprise a basal Costigan Mountain Formation and a conformably overlying Wapske Formation (St. Peter, 1978b) (Table 1). The constituent lithotypes in these formations are similar, although the relative proportions differ, the Costigan Mountain Formation being dominated by volcanic rocks and the Wapske Formation by siliciclastic strata. Initially, St. Peter (1978b) believed that the contact between these formations was probably isochronous; however, faunal evidence later indicated that the Wapske Formation is locally intercalated and coeval with the Costigan Mountain Formation (St. Peter, 1979, 1981) and thus that the contact should be regarded as diachronous. Faunal evidence, as recently reviewed in Boucot and Wilson (1994), suggests an earliest Lochkovian to latest Pragian age for the Wapske Formation.

Seven sedimentary lithofacies have been recognized in the Wapske Formation in the present study. These lithofacies, individually differentiated on the basis of lithology, bed thickness, sandstone/mudstone ratios, bed geometry and contacts and internal sedimentary structures, are summarized in Table 2. They are very similar to several of the seven submarine fan facies first proposed and described by Mutti and Ricci Lucchi (1972) and subsequently refined by Walker and Mutti (1973) and Ricci Lucchi (1975a,b). Associations of these sedimentary facies are interpreted as representing particular depositional environments present in a deep-water submarine fan system. These lithofacies, their associations and depositional subenvironments will be described separately (Han and Pickerill, in preparation) but are currently available in Han (1995). For brevity, however, the characteristics of these subenvironments, based on our interpretations of individual facies associations, can be summarized as follows.

Mid-fan distributary channels comprise massively bedded,

Table 1. Summary of lithostratigraphy and previously interpreted depositional environments of the Tobique Group. Numbers refer to: 1, Wilson, 1990. 2, Skinner, 1982. 3, Irrinki and Crouse, 1986. 4,5,6 and 7, St. Peter, 1978b, 1979, 1981 and 1982. 8, Pickerill, 1986.

System	Group	Formation	Lithologies	Depositonal Environments
Devonian			Gabbro and granite	
Lower Devonian	Tobique	Wapske	Sedimentary Unit: grey to green, quartzose or argillaceous siltstone and fine- to medium-grained calcareous to non-calcareous, micaceous, quartzose to arkosic, sandstone; minor grey to green shale and slate; Basaltic Unit: green-grey basalt; minor diabase sills and dykes, slate, greywacke and rhyolites; Rhyolitic Unit: pink and grey massive and laminated rhyolite, minor basalt, slate and diabase.	1,3: shallow water marine. 2,4,5,6,7: terrestrial and shallow water marine. 8: outer shelf-upper slope deep water marine.
		Costigan Mountain	Unit 1: pink, red and grey rhyolite, quartz-feldspar porphyry flows, tuffs, and pyroclastic breccia. Unit 2: grey shale, argillite and greywacke; minor diabase, rhyolite and basalt. Unit 3: green-grey basalt flows and tuffs, minor volcanogenic sediments and conglomerate.	1,4,6: terrestrial to shallow water marine.
Silurian	Perham	Chambord Bk.	Grey to pink limestone; red-brown silty limestone.	1,8: shallow marine shelf.
		Hazeldean	Grey to green siltstone and sandstone,minor shale.	1,8: shallow marine shelf.

Table 2. Summary of lithofacies of the Wapske Formation and their essential characteristics.

Lithofacies	1	2	3	4	5	6	7
Main lithologies	grey matrix-supported conglomerates	fine- to coarse-grained sandstones without mudstones	fine- to medium-grained sandstones with minor thin mudstone interbeds, typically with mud-top	thinly interbedded fine-grained sandstones & mudstones	graded fine-grained sandstones or siltstone with rare mudstones	grey fine- to very fine-grained sandstones, siltstones & dark grey mudstones	mudstones, siltstones with minor thin sanstone interbeds
Bed thickness	70-340 cm	2->100 cm	2-50 cm	1-20 cm	1-10 cm	0.5-5 cm	1-20 cm
Sand/mud ratio	1:0	1:0	1:0.2	1:0.4	1:0.2	1:1	1:5
Bed geometry	N/A	tabular	tabular or lenticular	tabular	tabular	tabular or lenticular	tabular
Bed base	N/A	sharp	sharp	sharp or erosive	sharp and planar	sharp	sharp
Bouma units	No	Ta, Tb	Tae, abe, a-d	Tabc, bc, b-d, b-e	Ta; rare Tb-e, c-e, de	Tde, Tc-e	Tde, Te
Sedimentary structures	crude parallel-laminated	massive or parallel-laminated	parallel-, cross-laminated, scours, flute casts, mud clasts	parallel-, cross-laminated, flute casts, mud clasts	graded, parallel-, cross-, cross climbing-laminated, flute casts	massive, parallel-laminated	massive, parallel-laminated
Interpreted depositional processes	mass flow, esp. debris flows	high-density turbidity currents	turbidity currents	low-density turbidity currents	high-density gravity & traction flows	low-density turbidity currents & hemipelagic	hemipelagic, pelagic & low-density turbidity currents

matrix-supported conglomerates (Facies 1) that only rarely crop out in the study area. Clasts are dispersed within a muddy or silty matrix.

Mid-fan depositional lobes consist of thin-bedded, fine-grained, graded sandstones or coarse-grained siltstones (Facies 5), in association with thin- to medium-bedded fine-grained sandstones interbedded with mudstones (Facies 4), medium-grained mud-capped sandstones (Facies 3) and rare medium- to thick-bedded, medium-grained, massive and parallel-laminated sandstones (Facies 2). Facies 2 is generally restricted to upper parts of individual sequences in which the thin-bedded, fine-grained sandstone beds are dominant. Thickening and coarsening upward cycles, high sandstone/mudstone ratios and laterally continuous beds are characteristic of this subenvironment.

Outer fan lobes or fan fringes are dominated by thin-bedded sandstones and mudstones (Facies 4) accompanied by mudstones and graded fine-grained sandstones. Beds within these sequences exhibit a thinning and fining upward tendency.

Interchannel deposits consist of thin-bedded (with rare medium-bedded), fine-grained, graded sandstones (Facies 5). Amalgamation of sandstone beds is very common. Interbedded sandstones and mudstones (Facies 4), mudstones (Facies 7), and thinly interbedded sandstones and mudstones (Facies 6) are also present. The sequences show a thinning or minor thickening upward trend.

Basin plain-distal outer fan associations are characterized by laterally continuous thin-bedded mudstones and silty mudstones with thin, fine-grained sandstone interbeds (Facies 7); mud-capped sandstones (Facies 3) may be locally present. No specific cyclical sequences occur.

Within the proposed deep-water submarine fan system, the precise location of the actual feeder channel(s) of the submarine fan(s) cannot be assessed. However, it is likely that the source was located to the east or southeast of the present study area, as most conglomerates (Facies 1) are present there and palaeocurrent indicators such as flutes and cross-lamination suggest a west-northwest direction of turbidity current flow. The rare presence of coarse-grained channelized deposits, and common occurrence of thin- to medium-bedded, laterally continuous sandstones and mudstones suggest that the overall depositional environment was probably that of a mid or outer fan region of a deep-sea fan complex.

PALAEOENVIRONMENTAL DISTRIBUTION OF TRACE FOSSILS

Ichnofaunas in the Wapske Formation are represented by horizontal fodinichnia, pascichnia, agrichnia and fewer repichnia, and were produced by unknown representatives of both deposit- and suspension-feeders (Table 3). The ichnotaxa, comprising 23 ichnogenera, are collectively characteristic of the deep-water *Nereites* ichnofacies of Seilacher (1967) (Fig. 2). The ichnofauna is relatively diverse and abundant with *Helminthopsis* and *Palaeophycus* representing most trace fossils. Graphoglyptids (notably *Paleodictyon*, *Protopaleodictyon*, *Cosmorhaphe*) and pascichnia (such as *Helminthopsis*, *Helminthoida*, *Uchirites*, *Palaeophycus*) dominate the pre-depositional ichnocoenosis. In contrast, fodinichnia (especially *Chondrites*), domichnia (e.g., *Bergaueria*, *Skolithos*) and repichnia (such as *Umfolozia*, *Protovirgularia*, *Cruziana*) typify the post-depositional ichnocoenosis. Collectively, the overall ichnofaunal assemblage of the Wapske Formation is comparable to several of those recorded from other deep-marine fans (see McCann and Pickerill, 1988; Miller, 1991, 1993; Crimes and Crossley, 1991; Crimes *et al.*, 1992; Crimes and Fedonkin, 1994; and references therein). This is consistent with our sedimentological interpretations that suggest that deposition of the formation occurred in a deep-marine environment.

The most important parameters governing the distribution of deep-marine organisms are sediment texture, energy levels, substrate consistency and stability, oxygen levels at or immediately below the sediment-water interface, availability of food, sedimentation rates and frequency of event deposition. The palaeoecological controls over ichnofacies have been extensively discussed (e.g., Crimes, 1970a; Kern and Warme, 1974; Corbo, 1979; Frey and Seilacher, 1980; Pickerill *et al.*, 1984; Bromley *et al.*, 1984; Ekdale, 1985; Fillion and Pickerill, 1990; Uchman,

Table 3. Characteristics of ichnotaxa from the Wapske Formation.

Ichnotaxa	D	S	F	Feeding	Ethology	Toponomy	N	Pre-/Post-
Arthraria antiquata			T	Filter	Fo	CXH	R	?
Bergaueria hemispherica	M	T		?Filter	Cu/Dm	EN	C	Post-
B. aff. *perata*	M	T		?Filter	Cu/Dm	EN	R	Post-
Chondrites furcatus			T	Deposit	Fo	EN	C	Post-
C. targionii			T	Deposit	Fo	EN	R	Post-
Chondrites isp. form A			T	Deposit	Fo	CXH	R	?
Chondrites isp. form B			T	Deposit	Fo	CXH	R	Post-
Cochlichnus anguineus			T	Deposit	Rp	CXH	R	?
Cosmorhaphe fuchsi	T			Deposit	Ps	CXH	R	Pre-
C. sinuosa	T			Deposit	Ps	CXH	C	Pre-
Cruziana problematica	M	T		Deposit	Rp	CXH	C	Pre-
Dendrotichnium haentzscheli	T			Deposit	Fo	CXH	R	?
Didymaulichnus lyelli			T	Deposit	Rp/Ps	CXH	R	?
Helminthoida cf. *labyrinthica*	T			Deposit	Ps	CXH	R	Pre-
H. miocenica	T			Deposit	Ps	CXH	C	Pre-
Helminthopsis abeli	T		M	Deposit	Ps	CXH	A	Pre-
H. cf. *granulata*	T		M	Deposit	Ps	CXH	A	Pre-
H. hieroglyphica	T		M	Deposit	Ps	CXH	R	Pre-
Helminthopsis isp.	T		M	Deposit	Ps	CXH	A	Pre-
Hormosiroidea cf. *beskidensis*			T	?	Rp	CXH	C	?Pre-
Monomorphichnus multilineatus		T		-	Rp/Ps	CXH	R	?Post-
Neonereites biserialis			T	Deposit	Ps	CXH	C	Post-
N. multiserialis	T			Deposit	Ps	CXH	A	Post-
N. uniserialis			T	Deposit	Ps	CXH	C	Post-
Palaeophycus heberti			T	?Filter	Ps	CXH	C	Pre-
P. striatus			T	?Filter	Ps	CXH	C	Pre-
P. tubularis			T	?Filter	Ps	CXH	A	Pre-
Palaeophycus isp.			T	?Filter	Ps	CXH	A	Pre-
Paleodictyon isp.	T	M		Deposit	Ag	CXH	C	Pre-
Phycodes flabellus			T	Deposit	Fo	CXH	C	Post-
P. palmatus			T	Deposit	Fo	CXH	C	Post-
P. aff. *palmatus*			T	Deposit	Fo	CXH/EN	R	Post-
P. pedum			T	Deposit	Fo	CXH	C	Post-
P. templus			T	Deposit	Fo	CXH	A	Post-
Protopaleodictyon incompositum	T	M		Deposit	Ag	CXH/COH	R	Pre-
Protovirgularia dichotoma	T	M		Deposit	Rp/Fo?	CXH	A	?Post-
Rusophycus cf. *carbonarius*		T	M	Deposit	Cu	CXH	R	Pre-
Skolithos linearis	M	T		Filter	Dm	EN	A	Post-
Taenidium serpentinum	M	T		Deposit	Fo/Ps	CXH	R	Post-
Uchirites implexus			T	Deposit	Rp/Ps	CXH	C	Pre-
Umfolozia cf. *sinuosa*		T		?	Rp	NA	R	Post-

Key: D = deep-water preference, S = shallow-water preference, F = facies crossing (T = typical, M = minor); Ethology: Ag = agrichnia, Cu = cubichnia, Dm = domichnia, Fo = fodinichnia, Ps = pascichnia, Rp = repichnia; Toponomy: CXH = convex hyporelief, COH = concave hyporelief, EN = endorelief, NA = not available; N = number of trace fossils (A = abundant (>10), C = common (3-10), R = rare (<3)); Pre-/Post- = pre - and post-depositional origin.

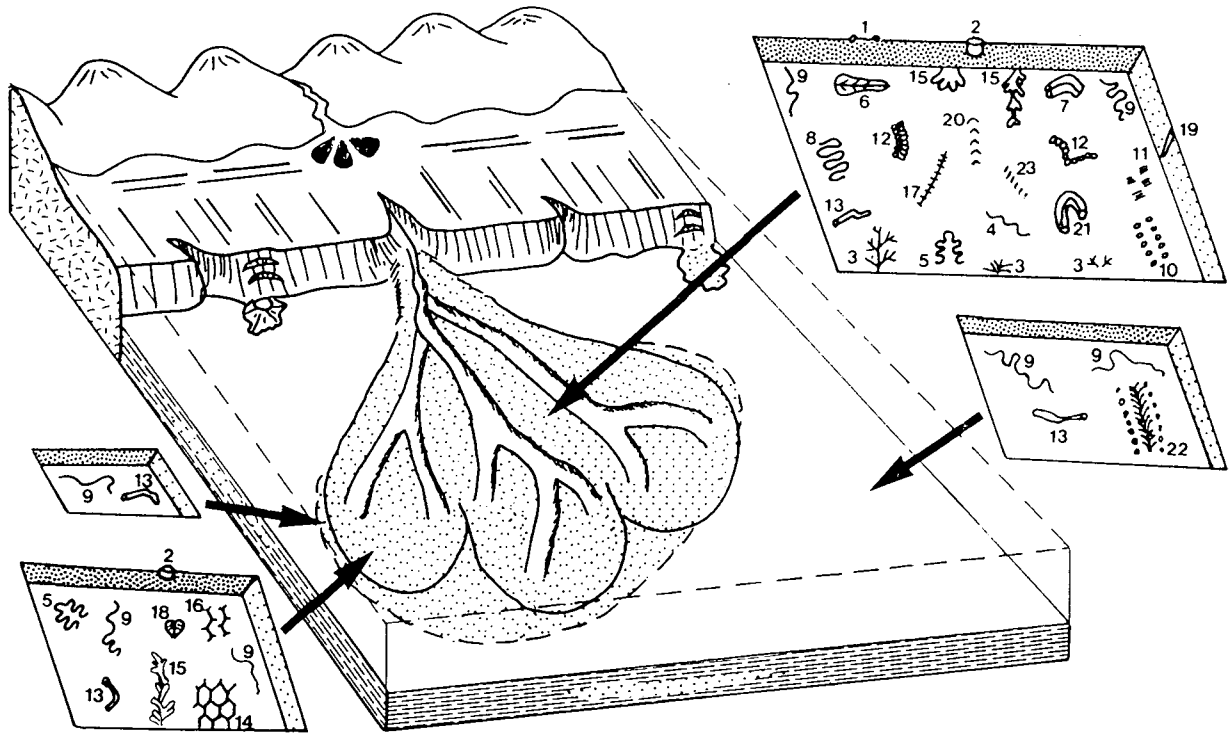


Fig. 2. Schematic representation showing distribution of the common trace fossils within the deep-sea fan of the Wapske Formation (no scale implied). Numbers represent: 1. *Arthraria*, 2. *Bergaueria*, 3. *Chondrites*, 4. *Cochlichnus*, 5. *Cosmorhaphe*, 6. *Cruziana*, 7. *Didymaulichnus*, 8. *Helminthoida*, 9. *Helminthopsis*, 10. *Hormosiroidea*, 11. *Monomorphichnus*, 12. *Neonereites*, 13. *Palaeophycus*, 14. *Paleodictyon*, 15. *Phycodes*, 16. *Protopaleodictyon*, 17. *Protovirgularia*, 18. *Rusophycus*, 19. *Skolithos*, 20. *Taenidium*, 21. *Uchirites*, 22. Track form B, 23. Scratch marks. Note: Track form A, *Dendrotichnium haentzscheli* and *Umfolozia* cf. *sinuosa* are not included as a result of their occurrence in small and isolated exposures that cannot be interpreted in terms of a specific palaeoenvironment (see also Table 4).

1992; Miller, 1993) and will not be repeated here. The palaeoenvironmental distribution of trace fossils in the Wapske Formation has been directed toward the interpreted depositional environments as determined by sedimentological analysis (Table 4) and is summarized below.

The distributary channel facies association is devoid of body fossils, trace fossils and bioturbation. The primary reasons for this are the coarse grain size and high-energy deposition, as well as the absence of shale interbeds precluding possible preservation of interface trace fossils.

The mid-fan depositional lobe facies association possesses a relatively diverse and abundant ichnocoenosis comprising traces produced by both suspension- and deposit-feeders that were responsible for the formation of cubichnia, domichnia, fodinichnia, pascichnia and agrichnia. The most common forms are horizontal agrichnia and pascichnia such as *Cosmorhaphe*, *Helminthopsis*, *Palaeophycus*, *Paleodictyon* and *Protopaleodictyon*, with fewer examples of cubichnia (*Rusophycus*), domichnia (*Bergaueria*) and fodinichnia (*Phycodes*). The relative abundance of agrichnia and pascichnia in the sequences is suggestive of a deep-water regime. The varied ethological groupings and the existence of both deposit- and suspension-feeding ichnofaunas suggest the presence of sufficient nutrient levels and adequate oxygenation both within the water column and at, or slightly below, the sediment-water interface. Most trace fossils are preserved in thinly interbedded, fine-grained sandstone and mudstone lithofacies (Facies 4), whereas associated lithofacies only exhibit *Palaeophycus* and *Helminthopsis*. Therefore, the sandstone and mudstone couplets are, in most examples, important with respect to toponomic preservation of trace fossils. The preservation of fine details in *Palaeophycus striatus*, *Phycodes palmatus* and *Rusophycus* cf. *carbonarius* indicates that the muds were relatively cohesive, as also suggested by the sharp burrow outlines of the associated ichnotaxa (cf. Fillion and Pickerill, 1990).

The lobe or fan fringe facies association contains the fewest number of ichnotaxa (excepting the distributary channel facies association). *Helminthopsis* and *Palaeophycus* are the only two types of traces found, being produced, respectively, by deposit- and suspension-feeders. Such a low diversity and abundance may not, however, be representative of the original ichnocoenoses, because lobe fringe deposits are not well represented in the sequence or, where present, are typically poorly exposed. Additionally, their component sandstones and/or siltstones are commonly amalgamated, without shale interbeds, thereby suggesting that surface and shallow traces may have been eroded by turbidity currents.

The interchannel facies association exhibits the most diverse and abundant ichnotaxa, comprising 18 ichnogenera and one unnamed form (36 ichnospecies), including vertical domichnia (*Bergaueria* and *Skolithos*), horizontal repichnia (*Cochlichnus*, *Cruziana*, *Didymaulichnus*, *Hormosiroidea*, *Protovirgularia* and scratch marks), fodinichnia (*Chondrites*, *Phycodes*) and pascichnia (*Cosmorhaphe*, *Helminthoida*, *Helminthopsis*, *Neonereites*, *Palaeophycus*, *Uchirites*). The high diversity and abundance of deposit-feeding traces presumably reflects the existence of an abundant nutrient supply and sufficient oxygen levels to support a wide variety of infaunal and

Table 4. Palaeoenvironmental distribution of trace fossils from the Wapske Formation.

Environments	Ichnotaxa
Basin plain-distal outer fan	*Helminthopsis abeli, H.* isp., *Palaeophycus* isp., Track form B
Lobe fringes	*Helminthopsis* isp., *Palaeophycus* isp.
Depositional lobes in mid-fan	*Bergaueria hemispherica, Cosmorhaphe fuchsi, Helminthopsis abeli, H. hieroglyphica, H.* isp., *Palaeophycus striatus, P.* isp., *Paleodictyon* isp., *Phycodes templus, Protopaleodictyon incompositum, Rusophycus* cf. *carbonarius*
Interchannel areas	*Arthraria antiquata, Bergaueria hemispherica, B.* aff. *perata, Chondrites furcatus, C. targionii, C.* isp. form A and B, *Cochlichnus anguineus, Cosmorhaphe fuchsi, C. sinuosa, Cruziana problematica, Didymaulichnus lyelli, Helminthoida* cf. *labyrinthica, H. miocenica, Helminthopsis abeli, H.* cf. *granulata, H. hieroglyphica, H.* isp., *Hormosiroidea* cf. *beskidensis, Monomorphichnus multilineatus, Neonereites biserialis, N. multiserialis, N. uniserialis, Palaeophycus heberti, P. striatus, P. tubularis, P.* isp., *Phycodes flabellus, P. palmatus, P.* aff. *palmatus, P. pedum, P. templus, Protovirgularia dichotoma, Skolithos linearis, Taenidium serpentinum, Uchirites implexus,* scratch marks

Note: *Dendrotichnium haentzscheli, Umfolozia* cf. *sinuosa* and Track form A are not included as a result of their occurrence in small and isolated exposures that cannot be interpreted in terms of a specific palaeoenvironment (see also Fig. 2).

epifaunal benthos. The occurrence of suspension feeders (domichnia) also suggests the existence of bottom currents carrying a continuous supply of suspended nutrients onto the sea floor. The preservation of surficial repichnia may reflect a reduced erosive capacity of turbidity currents and/or less intensive bioturbation by infaunal animals. *Phycodes* and the horizontal repichnia display sharp, and only rarely lined boundaries, thereby indicating a relatively cohesive muddy substrate (cf. Fillion and Pickerill, 1990). Interchannel deposits are characterized by thin-bedded sandstones and mudstones (Facies 4) and thin-bedded, fine-grained, graded sandstones (Facies 5), which provide ideal preservational conditions for the traces. From an environmental aspect, interchannel areas are more stable than channel, fan fringe and depositional lobe areas. In addition to preservational considerations, this could perhaps explain the presence of a presumably abundant and diverse epifauna and infauna. Crimes and Fedonkin (1994) recently concluded that interchannel areas associated with inner fans possessed diverse "shallow-water" trace fossils but fewer "deep-water" ichnotaxa, whereas those in outer fans had diverse "deep-water" trace fossils and a general absence of "shallow-water" trace fossils. Interchannel deposit sequences from the Wapske Formation exhibit mostly facies-crossing forms and more or less equal representatives of typical "shallow" and "deep" water forms.

The basin plain-distal outer fan facies association comprises essentially homogeneous muddy strata with sporadic turbidite sandstone interbeds. Exposed sequences reveal only isolated examples of *Helminthopsis*, *Palaeophycus* and unassigned tracks. The scarcity of ichnotaxa may reflect incomplete preservation of trace fossils because of the lack of turbidite sandstones as a casting medium, or may be a result of the environment being inimical to the support of a benthic population either as a result of low nutrient levels or depressed oxygen supplies at, or within, the upper levels of the surficial substrates.

In a general context, thin-bedded sandstones and siltstones contain considerably more ichnotaxa, both in terms of diversity and abundance, than do the thick-bedded turbidites, similar to analogous Cretaceous turbidites of northern California described by Miller (1993). The submarine fan system of the Wapske Formation appears to have contained sufficient food supplies and oxygen levels to support a widespread population of benthic organisms. However, oxygen levels in sediment below the sediment-water interface were at times presumably sufficiently reduced so that only the producer of *Chondrites* occurred in the sequence (see also Bromley and Ekdale, 1984; Hakes, 1985; Savrda and Bottjer, 1986). Secondary factors, such as mode of preservation and degree of exposure and weathering, also potentially influence the observed ichnocoenoses. In newly exposed outcrops where both talus and weathering processes are relatively minor, detailed examination and sampling of trace fossils was more difficult compared to outcrops with extensively exposed and weathered talus. For example, distributary channel deposits near Nictau Lake and depositional lobe deposits near Perth-Andover revealed no, or only sporadic, trace fossils because of the generally poor exposure and smaller outcrop size, resulting in a deficiency of talus. Secondly, traces are preserved

toponomically as semireliefs and, for optimum preservation, a contrast in lithology between the excavated and casting sediments is required (Fillion and Pickerill, 1990). In the Wapske Formation, both monolithologic sandstones (lobe deposits and portions of lobe fringe deposits) and shales (basin plain deposits) display the fewest number of trace fossils and a realistic scenario of the ichnocoenoses is difficult to reconstruct. However, couplets of thinly interbedded sandstones and mudstones provide an ideal medium for the preservation of trace fossils and the degree of weathering and talus development in these rock types provide ideal conditions for observations of semirelief traces, such as with the lobe fringe and interchannel deposits.

CONCLUSIONS

The main conclusions that can be drawn from this study are:

(1) The Wapske Formation of the Lower Devonian (Lochkovian-Pragian) Tobique Group, located between Perth-Andover and Mount Carleton, northwestern New Brunswick, possesses seven sedimentary lithofacies that can be organized into five facies associations. These facies associations reflect deposition in distributary channels, depositional lobes, lobe or fan fringes, interchannel and basin plain subenvironments in association with a deep-water submarine fan complex.

(2) A relatively diverse and well-preserved ichnofauna is, to varying degrees, present in these various subenvironments. In total these ichnofaunas include 23 ichnogenera (41 ichnospecies) and three vernacular forms. Their palaeoenvironmental distribution, as determined from facies analysis, suggests close comparisons with other ichnofaunas described from deep-water submarine fan systems. The ichnofauna of the Wapske Formation is, collectively, characteristic of Seilacher's (1967) *Nereites* ichnofacies. The main primary controlling factors of the ichnofaunal distribution were food supply, oxygen levels, sediment texture, sedimentation rates and frequency of event deposition.

(3) Secondary factors considered important with respect to trace fossil distributions in the various subenvironments of the Wapske Formation include nature and quality of outcrop, such as weathering characteristics, and amount of talus available for detailed analysis.

SYSTEMATIC ICHNOLOGY

In accordance with common ichnological procedure (Häntzschel, 1975; Pemberton and Frey, 1984; Fillion and Pickerill, 1990), the ichnotaxa in this contribution are described in alphabetical order rather than in any morphological or behavioural classification groupings (e.g., as in Osgood, 1970; Książkiewicz, 1977). This procedure is adopted for ease of reference to a particular ichnotaxon and also because in practice many ichnotaxa may be indicative of more than one behavioural activity. For those ichnotaxa we have previously considered in detail (Han and Pickerill, 1994a,b, 1995), namely *Helminthopsis* ispp., *Phycodes templus* and *Protovirgularia dichotoma*, we only include our previous diagnoses and avoid repetitious descriptions. For completeness, however, each of these ichnotaxa are figured herein. Ichnotaxa described in open nomenclature are described separately.

The preservational styles and essential characteristics of each form are listed in Table 3. Table 4 summarizes the palaeoenvironmental distribution in the sequence. Specimens with prefix TF and TF.F are housed in the Department of Geology, University of New Brunswick, Fredericton, New Brunswick, Canada; the prefix NBMG represents specimens deposited in the Division of Natural Sciences, New Brunswick Museum, Saint John, New Brunswick, Canada.

Ichnogenus *Arthraria* Billings, 1872

Type ichnospecies: *Arthraria antiquata* Billings, 1872

***Arthraria antiquata* Billings, 1872**
Figure 3A

Material: Four specimens (TF9208-23, TF9208-30, TF9210-10, TF112).

Description: Dumb-bell shaped traces preserved in convex hyporelief on 26 to 30 mm thick, grey, parallel-laminated fine-grained sandstone or siltstone. Each consists of a shallow and narrow stem connecting two wider and more deeply impressed terminations which are heart-, kidney-, or arrowhead-shaped. The stems are about 3 to 30 mm long and 2 to 11 mm wide and terminations 4 to 11 mm long and 2 to 11 mm wide. Terminations do not extend upward to form U-shaped tubes and the burrows possess no spreiten.

Remarks: Fillion and Pickerill (1984) reviewed and redefined the monospecific ichnotaxon *Arthraria*, distinguishing it from the morphologically similar, at least in basal expression, *Bifungites* Desio, which, however, has vertical tubes without a spreite, and *Diplocraterion* Torell which has both vertical tubes and a spreite. *Arthraria* is believed to have been produced by a worm or wormlike organism (Fillion and Pickerill, 1990). Terminations of different shapes may occur in this ichnospecies, even within a single specimen. Size of individual specimens may also vary considerably. Thus all reliable specimens of *Arthraria* should be included within *Arthararia antiquata* (Fillion and Pickerill, 1984).

Ichnogenus *Bergaueria* Prantl, 1945

Type ichnospecies: *Bergaueria perata* Prantl, 1945

The ichnotaxonomy of single-entrance, plug-shaped, soft-substrate trace fossils has been reviewed in detail by Pemberton *et al.* (1988). By its much larger diameter/height ratio, *Bergaueria* can be distinguished from *Conichnus* Myannil, *Dolopichnus* Alpert and Moore and *Conostichus* Lesquereux by its lack of a distinct apical disc and wall ornamentation (Pemberton *et al.*, 1988).

Based mainly on characteristics of the distal termination and the presence or absence of wall linings, Pemberton *et al.*

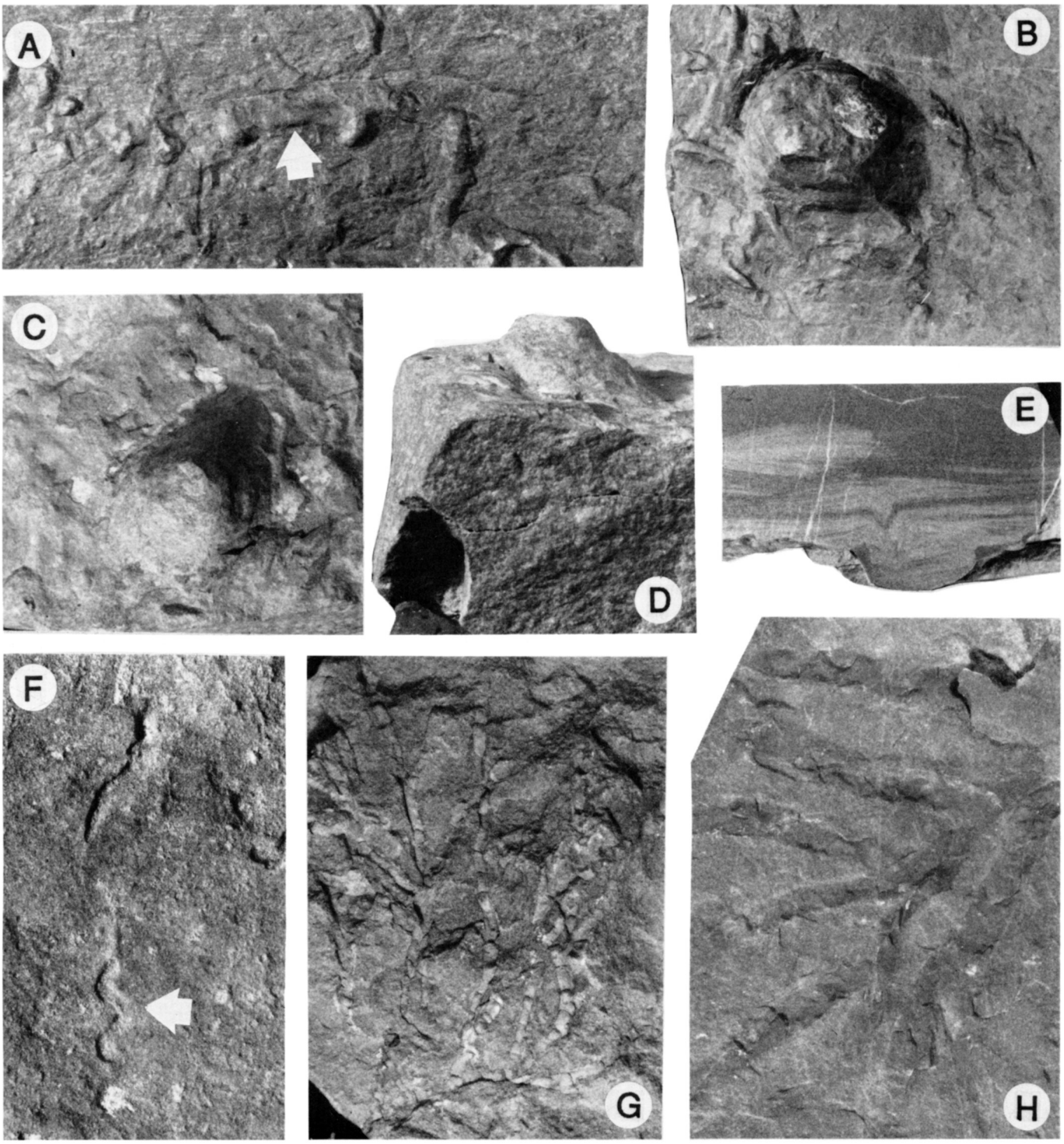


Fig. 3. Trace fossils from the Wapske Formation. (A) *Arthraria antiquata* (TF9208-23) (arrowed), x 1.14. (B) *Bergaueria hemispherica* (TF9209-20), x 0.77. (C, D) *Bergaueria* aff. *perata* (TF 9201-21), x 1.0 (C, top view; D, lateral view). (E) *Bergaueria hemispherica* (TF9208-24), x 0.86 (vertical section showing the V-shaped laminae). (F) *Cochlichnus anguineus* (TF.F118) (arrowed) intergradational with *Helminthopsis* isp., x 1.38. (G) *Chondrites furcatus* (TF.F223), x 0.83. (H) *Chondrites targionii* (TF9307-04), x 0.82. A-F are preserved in convex hyporelief; G and H in endorelief.

(1988) recognized four ichnospecies of *Bergaueria*, namely, *B. perata*, *B. langi* (Hallam), *B. radiata* Alpert and *B. hemispherica* Crimes, Legg, Marcos and Arboleya. Ethological considerations of these have been discussed by Pemberton *et al.* (1988) and Pickerill (1989).

Bergaueria hemispherica **Crimes, Legg, Marcos and Arboleya, 1977**
Figure 3B,E

Material: Five specimens (TF9208-24, TF9208-1-13, TF9209-20, TF.F172, TF.F58).

Description: Vertical, cylindrical to dome-like burrows preserved in convex hyporelief on the soles of 8 to 75 mm thick, grey, parallel- and cross-laminated siltstone and fine-grained sandstone. The burrows have steeply to gently inclined, unornamented outer margins. The basal surfaces are flat or rounded without typical depressions or ridges. Dimensions are variable. Diameter is equal to or generally greater than height. The distal ends are 15 to 28 mm in diameter, the proximal ends 18 to 35 mm, and the heights 8 to 12 mm; the average ratio of diameter/height is between 2.5-1. The burrow-fill is the same as the host rock and no lining is observed in vertical section. However, in one vertically sectioned specimen, the primary parallel laminae are distorted to a V-shape pointing to the burrow base (Fig. 3E), which has not been described previously.

Remarks: *Bergaueria hemispherica* differs from *B. perata* and *B. radiata* by the absence of a central depression and radial ridges and from *B. langi* by the absence of a thick burrow wall (Pemberton *et al.*, 1988).

Bergaueria **aff.** *perata* **Prantl, 1945**
Figure 3C,D

Material: One specimen (TF9201-21).

Description: Hemispherical burrow preserved in convex hyporelief on the sole of a 29 mm thick siltstone. The burrow has a smooth, unornamented, gently inclined outer wall and a flat apical base which has a circular depression. In plan view, the specimen is circular with an upper diameter of 26 mm, a lower diameter of 8.5 mm, and a height of 12 mm. The base of the specimen is flat, symmetric and possesses a small depression, 3 to 3.5 mm in width. The burrow-fill is massive and of the same grain size as the host rock. A thin lining is present.

Remarks: Pickerill (1989) provided an in-depth discussion on this ichnospecies. The present specimen has a flat base with a central depression, but no radial ridges as in *B. perata* to which, however, it is otherwise most comparable. The central depression differentiates it from *B. hemispherica*.

Ichnogenus *Chondrites* von Sternberg, 1833

Type ichnospecies: *Fucoides antiquus* Brongniart, 1828

Chondrites has previously been interpreted as both a feeding and dwelling burrow and probably indicates a systematic search for food by repeated probing of sediment (Vossler and Pemberton, 1988). Previously proposed tracemakers include a variety of endobenthic deposit feeders such as sipunculids (Simpson, 1957), multitentacled organisms (Taylor, 1967), vermiform worms (Osgood, 1970; Howard and Frey, 1984), arthropods (Ekdale, 1977), anthoptiloid sea pens (Bradley, 1981) and nematodes (Bromley and Ekdale, 1984; Howard and Frey, 1984; Swinbanks and Shirayama, 1984).

Ichnospecific classification of *Chondrites* is traditionally based on width of the branches and mode and angle of branching (Książkiewicz, 1977), and has resulted in the description of more than 170 ichnospecies (Chamberlain, 1971), many of which are extremely difficult, if not impossible, to differentiate or may, in fact, be simply ontogenetic variants (Hakes, 1976; Książkiewicz, 1977).

Typically occurring infaunally beneath an oxygen-deficient sea-floor below the sediment-water interface (Bromley and Ekdale, 1984), *Chondrites* has commonly been regarded as an indicator of dysaerobic or even anoxic conditions (Bandel, 1973; Bromley and Ekdale, 1984, 1986). The presence of *Chondrites* alone in a sedimentary unit, its burrow diameter and the degree of branching can all be used to interpret changes in environmental parameters (Hakes, 1985; Savrda and Bottjer, 1986).

Chondrites furcatus **von Sternberg, 1833**
Figure 3G

Material: Three specimens (TF9211-12, TF.F223, TF.F227).

Description: The burrow systems are well-preserved in endorelief within greenish grey, fine-grained, 10 to 15 mm thick, sandstones. The burrows are dendritic, maximum width 95 mm, ramifying symmetrically or asymmetrically at very acute angles, 25° to 55°, commonly 30° to 40°. Mostly they bifurcate, but occasionally trifurcate. There are up to 3 or 4 orders of branching. The interval length of branching is irregular, either long or short. At branching sites no expansion is present. Individual branches are cylindrical, horizontal or inclined, straight or curved, but never bend, wind, cross or interpenetrate. Burrow fill is lighter in colour and finer in grain size than the host rock. The burrow-fill is separated into transverse segments, which are individually 2.5 to 5 mm (commonly 4 mm) long and 2 to 2.5 mm wide. The boundaries of the transverse segments are either straight or meniscate without unique form. There is no change in width along the branches.

Remarks: The present specimens are very similar to *Chondrites* type B of Osgood (1970) and virtually identical to *C. furcatus* of Książkiewicz (1977) and Crimes and Crossley (1991), and, therefore, are considered conspecific. Chamberlain (1977) regarded *C. furcatus* as a junior synonym of *C. recurvus* Brongniart. However, *C. furcatus* differs from *C. recurvus* by the former's more asymmetrical dichotomous branching pattern and the latter's more symmetrical dichotomous branches which are also more regular and outward curving. Additionally, the present specimens do not exhibit the prominent recurvature characteristic of *C. recurvus*. *C. furcatus* differs from *C. targionii* (Brongniart) by its curved branches and narrower branching angles and from *C. intricatus* (Brongniart) by its larger size and predominance of asymmetrical dichotomous branching.

Chondrites targionii (Brongniart, 1828)
Figure 3H

Material: Two specimens (TF9307-04, TF115).

Description: The specimens are well-preserved in endorelief in a greater than 50 mm thick, grey, parallel-laminated, fine-grained sandstone. A maximum of five orders of branching are present, resulting in a straight-branched dendritic pattern up to 127 mm across. The burrow systems are regular, asymmetric and loosely bifurcated. Branches regularly alternately diverge from a "main" stem with branching angles ranging from 30° to 50°. Branches are straight, 2 to 7 mm wide, constant or tapering and 7 to 53 mm long. Burrow fill is black mudstone which is finer in grain size and darker in colour than the host matrix.

Remarks: The present specimens are regarded as *Chondrites targionii*, because they show a dendritic branching pattern, strong or slender, straight, uniformly wide or slightly tapering branches, and angular branching patterns. It differs from *C. furcatus*, *C. intricatus* and *C. recurvus* by its straighter branches, and from *C. intricatus* by its larger size, smaller branching angles, and possession of asymmetrical dichotomous branches. It also differs from *C. succulens* which is characterized by irregular, nodose, curved to tortuous burrows.

Chondrites isp. form A
Figure 4B

Material: One specimen (TF9208-43).

Description: The tiny, tree-like specimen is poorly preserved in convex hyporelief on the surface of a 75 mm thick, grey, parallel-laminated, fine-grained sandstone. It consists of a very small, horizontal to inclined, symmetrically bifurcated branching system, up to 20 mm across and possessing two orders of branching. Branching sites have no swelling and are subangular. Branching angles vary between 30° to 75°. Burrows are slender, straight to slightly wavy, about 1 mm wide and 3 to 6 mm long. Branch width is uniform throughout the whole burrow system.

Remarks: The poor and incomplete preservation of the specimen precludes ichnospecific assignment.

Chondrites isp. form B
Figure 4A

Material: One specimen (TF9211-10).

Description: Fan-shaped burrow system preserved in endorelief within a 20 mm thick, brown, fine-grained sandstone. It consists of a slender, widely spaced, symmetrically dichotomous branching system, 31 mm across. The almost straight branches are 0.5 to 1.2 mm wide and 20 to 50 mm long, with constant width along individual segments. A maximum of two orders of branching are present. Branching junctions are without swellings and diverge with angles varying from 20° to 30°. Burrow-fill is dark grey mudstone.

Remarks: The poorly preserved and incomplete specimen was found only by splitting the sandstone. Its distinctive fan-like branching system with slender branches distinguishes it from the other ichnospecies of *Chondrites* described here.

Ichnogenus *Cochlichnus* Hitchcock, 1858

Type ichnospecies: *Cochlichnus anguineus* Hitchcock, 1858
Cochlichnus anguineus Hitchcock, 1858
Figure 3F

Material: One specimen (TF.F118).

Description: Smooth, unbranched sine-like trail preserved in convex hyporelief on the sole of a 25 mm thick, brown, fine-grained sandstone. The trail, 16 mm long and 1.5 mm wide, exhibits a wavelength of 2 mm and amplitude of 4 mm.

Remarks: *Cochlichnus* is usually regarded as a repichnion (Hitchcock, 1858; Pieńkowski and Westwalewicz-Mogilska, 1986), but true burrows have also been documented (Webby, 1970; Eagar *et al.*, 1985). It is thought to have been produced by nematodes and annelids (Hitchcock, 1858; Seilacher, 1963; Moussa, 1969, 1970; Hakes, 1976). Elliott (1985) demonstrated the geometric nature of the repeated clothoid curves of *Cochlichnus kochi* Ludwig, concluding that this enabled efficient propulsion through watery surface muds of an animal with a hydrostatic skeleton.

The present specimen is directly connected to *Helminthopsis* isp. as a compound specimen (Pickerill, 1994). The regular sine curve changes to an irregularly winding structure presumably as a result of change in the tracemaker's behaviour.

Ichnogenus *Cosmorhaphe* Fuchs, 1895

Type ichnospecies: *Cosmorhaphe sinuosa* Azpeitia Moros, 1933
Cosmorhaphe fuchsi Książkiewicz, 1970
Figure 4C

Material: Three specimens (TF9202-16, TF9208-41, TF9208-1-30).

Description: Smooth, unbranched, composite meanders preserved in convex hyporelief on the soles of 40 to 85 mm thick, grey, massive to parallel-laminated, fine-grained sandstones. The meanders of the first-order are high but wide at the base (wavelength 120 to 250 mm, amplitude 45 to 170 mm, wavelength/amplitude ratio 1.47-2.67). Meanders of the second-order are very variable, deep or shallow, usually not compressed or constricted, regular to irregular (wavelength 25 to 80 mm, amplitude 5 to 35 mm, wavelength/amplitude ratio changeable, most at least larger than 2.5). The structures are continuous, each with almost a constant diameter of between 1 to 15 mm.

Remarks: The absence of compression and constriction of both the first- and second-order meanders characterizes *Cosmorhaphe fuchsi*. There are distinct difference between *C. fuchsi*, whose first- and second-order meanders are not compressed, and *C.*

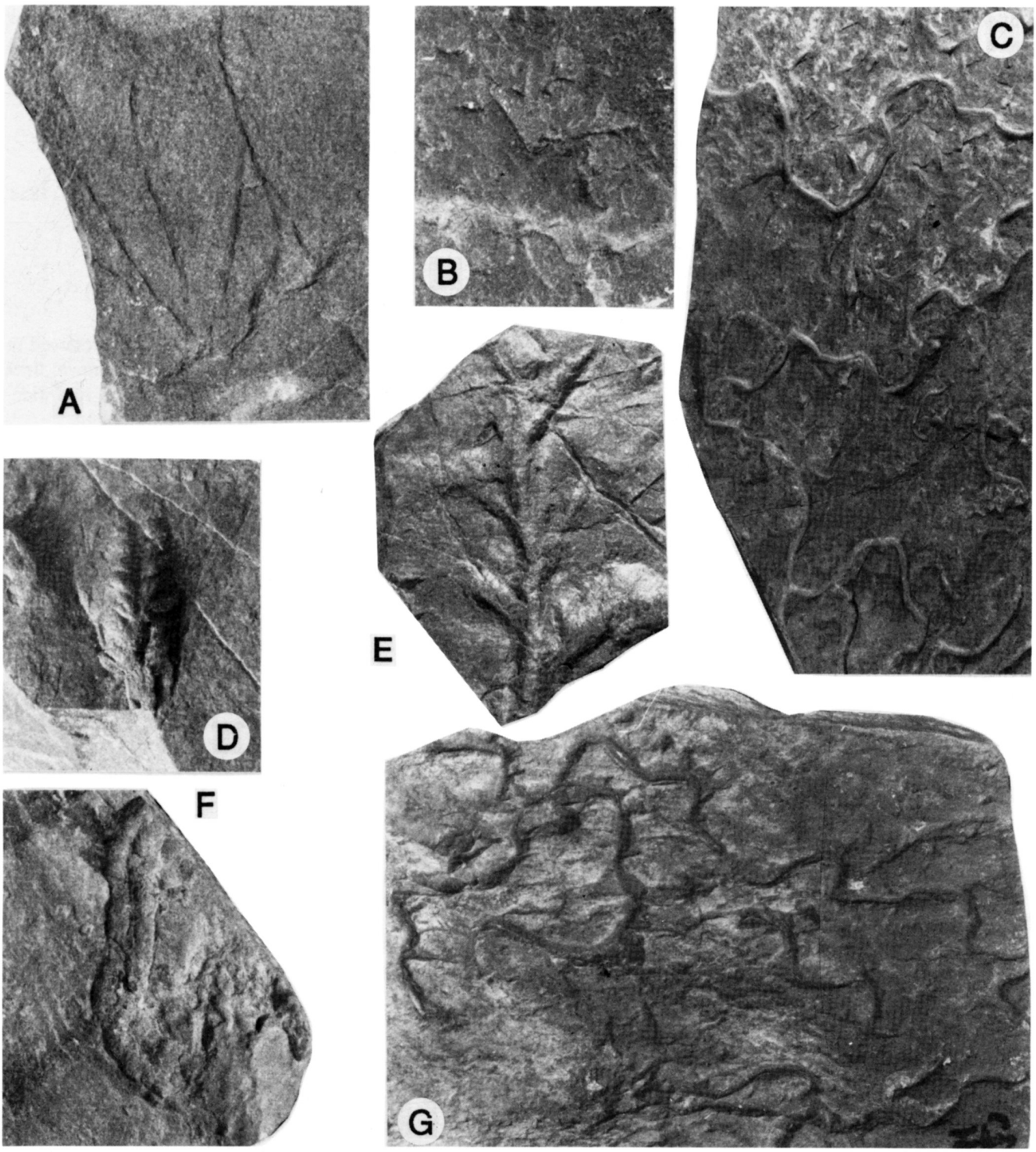


Fig. 4. Trace fossils from the Wapske Formation. (A) *Chondrites* isp. form B (TF9211-10), x 1.12. (B) *Chondrites* isp. form A (TF9208-43), x 1.0. (C) *Cosmorhaphe fuchsi* (TF9208-1-30), x 0.54. (D) *Cruziana problematica* (TF9209-18), x 1.93. (E) *Dendrotichnium haentzscheli* (TF9210-2-11), x 1.0. (F) *Didymaulichnus lyelli* (TF9201-13), x 1.12. (G) *Cosmorhaphe sinuosa* (TF.F142), x 0.74. A is preserved in endorelief; the remainder in convex hyporelief.

sinuosa (Azpeitia Moros), whose first-order meanders are compressed, but whose second-order meanders may or may not be restricted. *Cosmorhaphe* is a distinctive and typically deep-water flysch form that may be pre- or post-depositional in origin (Książkiewicz, 1977). It may be produced by animals which could live both on the sea-bottom or close to it, as indicated by present day *Cosmorhaphe* in the deep sea where it is interpreted as an infaunal burrow system positioned just below the sediment surface (Ekdale and Berger, 1978; Ekdale, 1980a, b). It has been interpreted as a grazing trail (Webby, 1969; Häntzschel,

1975) or a feeding burrow (Seilacher, 1962). Any worm-shaped animal or gastropod without external ornamentation could be responsible for this trace (Książkiewicz, 1977).

***Cosmorhaphe sinuosa* (Azpeitia Moros, 1933)**
Figure 4G

Material: One specimen (TF.F142).

Description: Smooth, unbranched, composite meanders, 1.8 mm in diameter, preserved in convex hyporelief on the sole of a 25 mm thick, parallel-laminated, fine-grained sandstone. The first-order meanders are narrow and high, 15 to 53 mm in wavelength and 130 mm in amplitude. These are superimposed by second-order meanders which range from 25 to 37 mm in wavelength and 5 to 15 mm in amplitude. The second-order meanders vary in size within the specimen.

Remarks: Seilacher (1977) suggested that *Cosmorhaphe sinuosa* can be distinguished from other related forms by the low amplitude of the secondary meanders and the relatively small burrow diameter. *Cosmorhaphe sinuosa* is related to *C. helminthopsoida* differing only in the latter's less regularly meandering course (Książkiewicz, 1977).

Ichnogenus *Cruziana* d'Orbigny, 1842

Type ichnospecies: *Cruziana rugosa* d'Orbigny, 1842
***Cruziana problematica* (Schindewolf, 1921)**
Figure 4D

Material: Nine specimens (TF9201-22, TF9209-18, TF.F162, TF.F155).

Description: Specimens are moderately or poorly preserved in convex hyporelief on the soles of 20 to 40 mm thick, brown or grey, parallel-laminated, fine-grained sandstones. They are straight or slightly curved, 8 to 26 mm long and 4 to 8 mm wide, and composed of two lobes (symmetrical or slightly asymmetrical), each 1.8 to 3.5 mm wide and 0.1 to 1.5 mm deep, separated by a very shallow median furrow more or less extending the length of the traces. The lobes are characterized by faint or strong, closely spaced transverse or slightly oblique scratch marks which are neither bifid nor bunch together.

Remarks: Lessertisseur (1955) and Osgood (1970) reviewed the origin of *Cruziana*. It is believed that most were produced by trilobites (Seilacher, 1970) though some may have been produced by trilobite-like arthropods, notostracan branchiopods (Bromley and Asgaard, 1979), aglaspidids (Fisher, 1978) or even vertebrates (Shone, 1978, 1979). Typically a shallow-marine form, *Cruziana* has also previously been reported from freshwater (Bromley and Asgaard, 1979) and deep-marine (Pickerill *et al.*, 1987) deposits. *Cruziana problematica* differs from *Didymaulichnus* Young by the presence of scratch marks on each lobe. It is morphologically identical to the ribbon forms of *Isopodichnus* Bornemann, though following Bromley and Asgaard (1979), such forms should be regarded as synonyms of *Cruziana* (cf. Romano and Whyte, 1987; Pickerill and Peel, 1990; Pickerill, 1994; Keighley and Pickerill, 1995a).

Ichnogenus *Dendrotichnium* Häntzschel, 1975

Type ichnospecies: *Dendrotichnium llarenai* (Farrés, 1967)
***Dendrotichnium haentzscheli* (Farrés, 1967)**
Figure 4E

Material: One specimen (TF9210-2-11).

Description: The specimen comprises a smooth, horizontal burrow system preserved in convex hyporelief on the sole of a grey siltstone. The burrow consists of a central main stem and nearly alternately branched lateral appendages. The burrow system covers a width of 32 mm. The straight main stem is 4 mm wide and 63 mm long; the lateral appendages, 3 to 4 mm wide and 12 to 20 mm long, branch out obliquely at angles of 30° to 45° and are constant in width. The burrow-fill is similar in grain size to the host rock.

Remarks: In contrast to truly dendritic burrow systems such as *Chondrites*, the side branches of *Dendrotichnium* may alternate regularly and never show any secondary branches (Seilacher, 1977). Three ichnospecies of *Dendrotichnium* have been described, namely *D. haentzscheli*, *D. llarenai* and *D. alternans* Seilacher. They are differentiated on the basis of appendage branching angles and patterns and nature of the central stem. *Dendrotichnium haentzscheli* differs from *D. llarenai* by the latter's right angled branched appendages and from *D. alternans* by the latter's regularly alternately branched lateral appendages and zigzag meandering main stem. *Dendrotichnium* occurs most commonly in flysch deposits (Seilacher, 1977; Crimes *et al.*, 1981).

Ichnogenus *Didymaulichnus* Young, 1972

Type ichnospecies: *Fraena lyelli* (Rouault, 1850)
***Didymaulichnus lyelli* (Rouault, 1850)**
Figure 4F

Material: One specimen (TF9201-13).

Description: Narrow and elongate, curved, horizontal bilobate convex hyporelief, 7 to 8 mm wide and 53 mm long, preserved on the sole of a maroon siltstone. A distinct median furrow, 0.5 to 1 mm wide, runs the whole length. The symmetrical lobes have no surface ornament. The specimen undulates slightly in the horizontal plane and therefore the lobe margins are not strictly straight but wavy though still clearly defined. The margins of the lobes are steep, without marginal ridges.

Remarks: The smooth lobes in *Didymaulichnus* differentiates it from *Cruziana* which has scratch marks (Young, 1972). It is commonly attributed to gastropods (Glaessner, 1969; Hakes, 1976) or trilobites (Crimes, 1970b; Bradshaw, 1981) and is a facies-crossing form (Young, 1972; Hakes, 1976; Eagar *et al.*, 1985). As the present specimen is characterized by an absence

of oblique scratches, lateral ridges, marginal bevels or alternating step-wise compressed sections, it is assigned to *Didymaulichnus lyelli*.

Ichnogenus *Helminthoida* Schafhäutl, 1851

Type ichnospecies: *Helminthoida labyrinthica* Heer, 1865

Seilacher (1977) erected the ichnogenus *Helminthorhaphe* to include *Helminthoida crassa* Schafhäutl, *H. japonica* Tanaka and a new ichnospecies *H. reflecta*. However, Crimes *et al.*, (1981), Crimes and Anderson (1985) and Crimes and Crossley (1991) argued for retention of *Helminthoida*, their view being accepted, amongst others, by Benton (1982a), McCann and Pickerill (1988), Narbonne and Aitken (1990) as well as herein. *Helminthoida* is still, however, an ichnogenus that exhibits considerable diversity in form and spacing of its meanders (Książkiewicz, 1977) and course, and there is considerable confusion regarding differentiation of several of its ichnospecies. Recently, Crimes and Crossley (1991) provided a detailed study of *Helminthoida* and placed *H. japonica* in synonymy with *H. crassa*. They also suggested that more or less regular and closely spaced parallel meanders arranged in a bow-like forms should be included within *H. crassa*, while lower, less compressed meanders and a totally unbowed form with no spiral development should be regarded as *H. miocenica* Sacco. For those with a distinct tendency to coil they suggested accommodation within *H. labyrinthica*. In our experience, this is a workable scheme and is therefore adopted herein. *Helminthoida* is typically, though not exclusively, a deep-water trace fossil.

Helminthoida cf. *labyrinthica* Heer, 1865
Figure 5B

Material: One specimen (TF.F178).

Description: Burrow is preserved in convex hyporelief on the sole of a 23 mm thick, buff, fine-grained sandstone. The meanders are closely spaced and even partially overlap. The meanders vary in width between 2 to 9 mm (commonly 6 mm); meander height is 35 to 50 mm and intervals between them 0 to 4 mm. The burrow surface is smooth and burrow-fill is similar in grain size to the enclosing sandstone.

Remarks: The present specimen is only partially complete but is tentatively assigned to *H.* cf. *labyrinthica* by the presence of tight meanders and its tendency to coil.

Helminthoida miocenica Sacco, 1886
Figure 5A

Material: Three specimens (TF.F111, TF.F113, TF.F114).

Description: Specimens are preserved in convex hyporelief on the soles of 20 to 27 mm thick, brown, fine-grained sandstones. The meanders are up to 34 mm high while the distance between the arms of the meanders is 5 to 14 mm, giving a ratio of height/width between 2-5. The meanders are parallel to each other without a bow-like form or tendency to coil. Most meanders bulge at their turning sites resulting in a horseshoe-like form. The width of the meanders is between 1 to 2 mm, this remaining constant in individual specimens. The surface of the meanders is smooth.

Remarks: These specimens are very similar to descriptions, and criteria for the recognition, of *H. miocenica* by Książkiewicz (1977) and Crimes and Crossley (1991). The meanders of *H. miocenica* are less regular and tighter than in *H. crassa*. Similar bulging meanders can also be observed in Książkiewicz's (1977, p. 166, figs. 36a,d,e) specimens.

Ichnogenus *Helminthopsis* Heer, 1877

Type ichnospecies: *Helminthopsis magna* Heer, 1877
***Helminthopsis abeli* Książkiewicz, 1977**
Figure 5C

Material: Seven specimens (NBMG 9670 - NBMG 9675, and NBMG 9676 (*partim*)) and more than 50 specimens collected and many more field occurrences.

Emended diagnosis: *Helminthopsis* that is loosely winding or meandering. Meanders irregular and variable in shape, mostly deep, but also shallow, with bell-shaped and, or, horseshoe-shaped segments, but no straight segments or loops. The axes of the meanders are not parallel. Diameter is variable and generally constant within a single specimen (modified from Książkiewicz, 1977).

Description and Remarks: See Han and Pickerill, 1995.

Helminthopsis cf. *granulata* Książkiewicz, 1968
Figure 5D

Material: One specimen (NBMG 9682).

Emended diagnosis: *Helminthopsis* which is variably and irregularly but loosely meandering. Surface is characteristically covered with warts and ridges arranged parallel to its axis (modified from Książkiewicz, 1977).

Description and Remarks: See Han and Pickerill, 1995.

Helminthopsis hieroglyphica Heer *in* Maillard, 1887
Figure 5F

Material: Six specimens (NBMG 9676 (*partim*), NBMG 9677 - NBMG 9681) and more than 44 specimens collected and many more field occurrences.

Diagnosis: *Helminthopsis* in which the windings, normally wide and low, comprise straight segments interspersed with irregularly sinuous and variably developed segments. The tortuous segments may be bell-shaped but not horseshoe-shaped. The full course is commonly, though not exclusively, alternately winding and straight (modified from Książkiewicz, 1977).

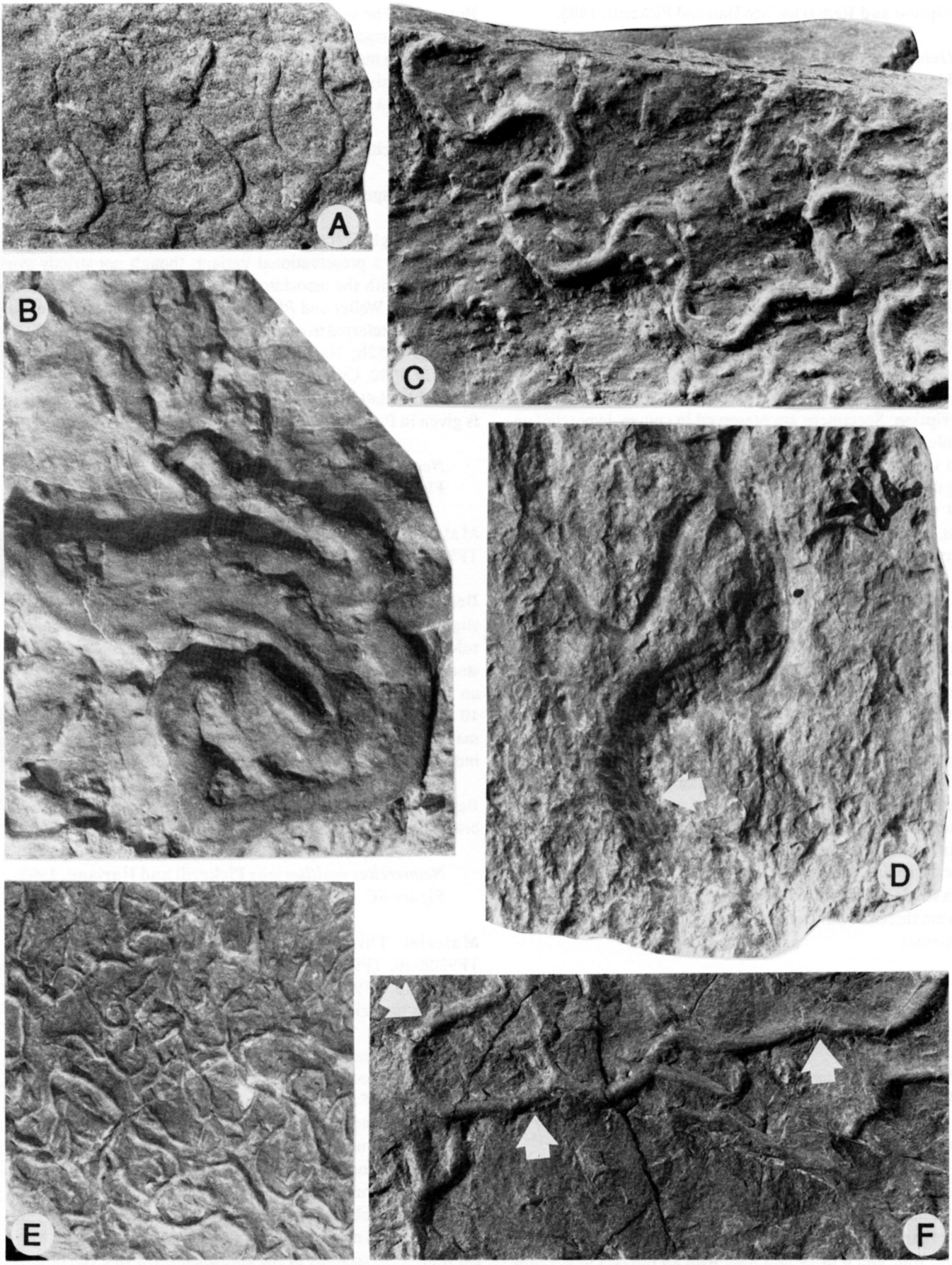


Fig. 5. Trace fossils from the Wapske Formation. (A) *Helminthoida miocenica* (TF.F111), x 1.64. (B) *Helminthoida* cf. *labyrinthica* (TF.F178), x 1.20. (C) *Helminthopsis abeli* (NBMG 9675), x 1.19. (D) *Helminthopsis* cf. *granulata* (NBMG 9682) (arrowed), x 0.91. (E) *Helminthopsis* isp. (NBMG 9683), x 0.51. (F) *Helminthopsis hieroglyphica* (NBMG 9680) (arrowed), x 1.1. All specimens are preserved in convex hyporelief.

Description and Remarks: See Han and Pickerill, 1995.

***Helminthopsis* isp.**
Figure 5E

Material: One specimen (NBMG 9683) and 67 specimens collected and over one hundred field occurrences.

Description and Remarks: See Han and Pickerill, 1995.

Ichnogenus *Hormosiroidea* Schaffer, 1928

Type ichnospecies: *Hormosiroidea florentina* Schaffer, 1928
***Hormosiroidea* cf. *beskidensis* (Plička, 1974)**
Figure 6A

Material: Three specimens (TF.F176, TF.F177, TF.F 209).

Description: Specimens are preserved in convex hyporelief on the sole of a ripple-marked, 30 mm thick, buff, parallel-laminated siltstone. They consist of two parallel rows of circular or elongate knobs, each 2 to 7 mm in diameter. Individual rows 10 to 19 mm apart; the interval between successive individual knobs, 3 to 8 mm, is not constant along the length. The knobs are arranged alternately, in pairs, or irregularly.

Remarks: The nomenclature of *Hormosiroidea* (and the morphologically similar ichnotaxon *Saerichnites* Billings) has been discussed by Seilacher (1977) and Crimes and Anderson (1985) and there is little need for further discussion. It is a form that occurs both in deep-water (Seilacher, 1977; Crimes *et al.*, 1981; Crimes and Crossley, 1991) and shallow-water (Frey and Chowns, 1972; Crimes and Anderson, 1985; Walter *et al.*, 1989) marine environments, though mostly in flysch deposits.

Depending on the degree of erosion, *Hormosiroidea* can exhibit considerable morphological variation (Seilacher, 1977). The alternation of knobs in material from the Wapske Formation is not as well developed as in Plička's (1974) specimen of *H. beskidensis*. Additionally, in some parts of the specimens only a single row of burrow knobs is present. The present specimens are therefore only tentatively identified as *Hormosiroidea beskidensis*.

Ichnogenus *Monomorphichnus* Crimes, 1970

Type ichnospecies: *Monomorphichnus bilinearis* Crimes, 1970
***Monomorphichnus multilineatus* Alpert, 1976**
Figure 6B

Material: One specimen (NBMG 9352 (*partim*)).

Description: Trace preserved in convex hyporelief on the sole of a 13 mm thick, parallel-laminated, fine-grained sandstone as three to seven parallel, very low, straight ridges or dig marks, 0.5 mm wide and 6 to 14 mm long with an interval of 0.4 mm between adjacent ridges, forming sets 2 to 3 mm deep and 4 to 6 mm wide. The central ridges are deeper and of the same width as the lateral ones.

Remarks: The sets of multiple ridges in the present specimen suggest the trace was produced by the digging action of an organism with multidigited appendages. The ridges are well-preserved in only one set which, however, permits confident assignment to *Monomorphichnus multilineatus*.

Ichnogenus *Neonereites* Seilacher, 1960

Type ichnospecies: *Neonereites biserialis* Seilacher, 1960

Although Seilacher and Meischner (1965) considered *Neonereites* a preservational variant, though not strictly synonymous, with the associated ichnogenera *Nereites* MacLeay, *Scalarituba* Weller and *Phyllodocites* Geinitz, most recent authors have preferred to retain it as a distinctive ichnotaxon (e.g., Benton, 1982b; Narbonne and Aitken, 1990; Fillion and Pickerill, 1990; Crimes and Crossley, 1991). We follow the opinion of these latter authors, more complete reasoning for which is given in Pickerill (1991).

***Neonereites biserialis* Seilacher, 1960**
Figure 6E

Material: Seven specimens (TF9202-13, TF9206-1-10, TF9208-11, TF9209-10, TF9210-11, TF9210-2-10).

Description: Straight to winding biserial rows of circular to slightly ovate pustules preserved in convex hyporelief on the soles of 23 to 60 mm thick, grey siltstones or fine-grained sandstones. The two rows are closely spaced or slightly separated by an axial groove. Individual traces are up to 115 mm long and 10 to 22 mm wide. Though typically biserial some specimens may have only one or three pustules arranged in places. The individual pustules are 4 to 8 mm in diameter.

Remarks. The predominant arrangement of the pustules biserially permits assignment to *N. biserialis*.

***Neonereites multiserialis* Pickerill and Harland, 1988**
Figure 6C

Material: Thirteen specimens (TF9201-10, TF9201-11, TF9208-10, TF9208-21, TF9209-11, TF9210-10, TF9210-12, TF9210-13, TF9210a-10, TF.F100 (*partim*)) and several occurrences in the field.

Description: Individual specimens comprise three, up to four, rows of interconnected pustules preserved in convex hyporelief on the soles of 12 to 58 mm thick, grey or brown, parallel-laminated siltstones or fine-grained sandstones. The burrows are horizontal, unbranched and longitudinally curved to irregularly sinuous. Individual rows are up to 100 mm long and 11 to 24 mm wide. Pustules are smooth and unornamented, spheroidal to ellipsoidal, variable in size (3 to 6 mm in diameter). Individual pustules may occur discretely or be amalgamated. Vertical transverse sections of the specimen show that the pustules are hemispheres. Burrow-fill is massive and similar to the host rock.

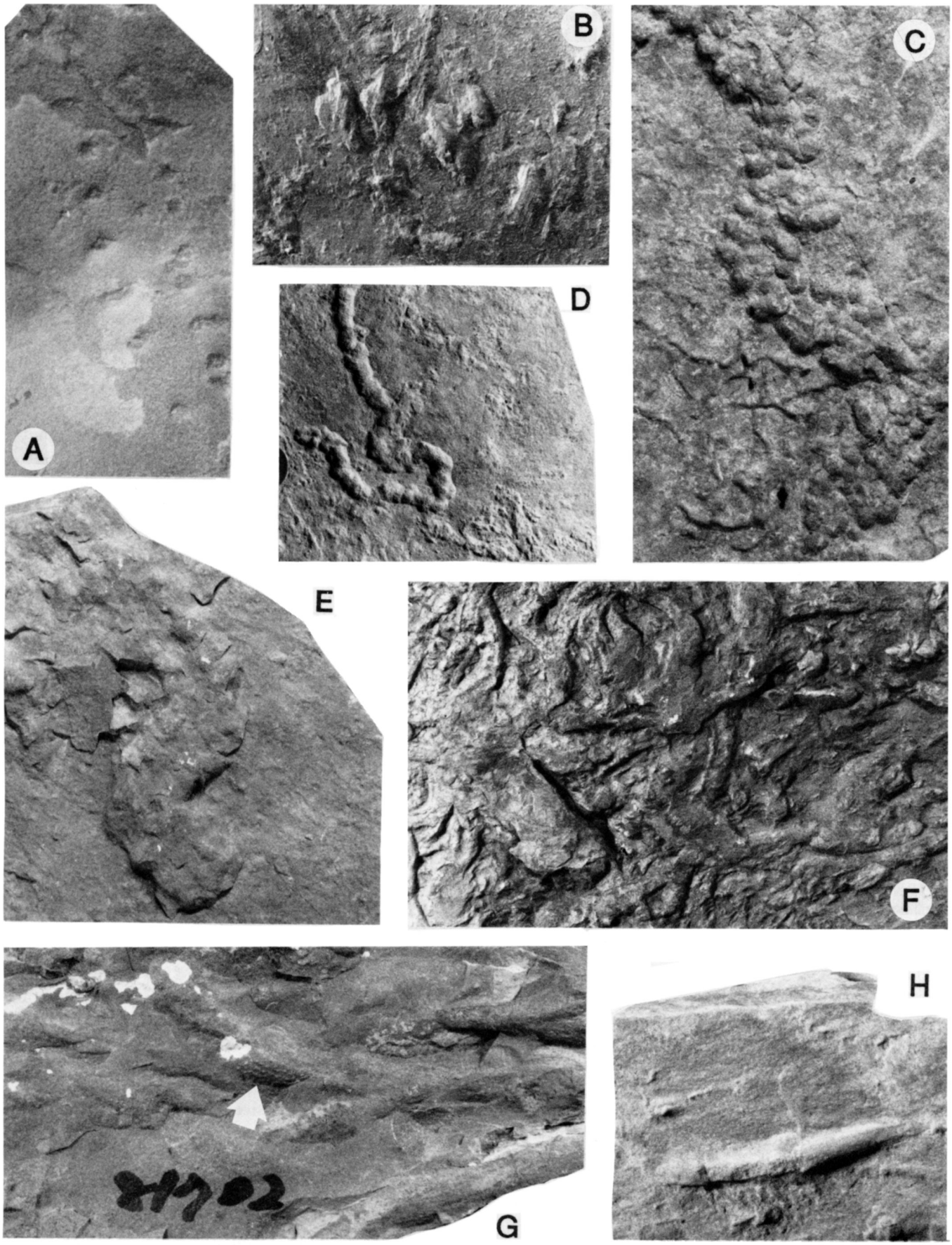


Fig. 6. Trace fossils from the Wapske Formation. (A) *Hormosiroidea* cf. *beskidensis* (TF.F177), x 1.0. (B) *Monomorphichnus multilineatus* (NBMG 9352 (*partim*)), x 1.0. (C) *Neonereites multiserialis* (TF9201-11), x 1.11. (D) *Neonereites uniserialis* (TF.F100), x 1.23. (E) *Neonereites biserialis* (TF9206-1-10), x 1.0. (F) *Palaeophycus heberti* (TF.F225), x 0.84. (G) *Palaeophycus striatus* (arrowed) and *Palaeophycus* isp. (TF.F218), x 1.0. (H) *Palaeophycus tubularis* (TF.F129), x 1.0. All specimens are preserved in convex hyporelief.

Remarks: Pickerill (1991) has discussed this ichnospecies in detail based on material previously collected from the Wapske Formation. Specimens described herein, and more recently collected, support his conclusions.

***Neonereites uniserialis* Seilacher, 1960**
Figure 6D

Material: Three specimens (TF112, TF.F100 (*partim*), TF.F103) and several occurrences in the field.

Description: Curved to irregularly winding, uniserial rows of circular to subcircular pustules preserved in convex hyporelief on the soles of 25 to 30 mm thick, massive or parallel-laminated, siltstones and fine-grained sandstones. Individual rows, up to 730 mm long, are composed of pustules of 2.5 to 3.5 mm diameter typically identical throughout their exposed length. Pustules, however, may be connected with *Helminthopsis* isp. to form a compound specimen. Individual pustules are smooth and closely connected or occasionally mutually overlap.

Remarks: *Neonereites uniserialis* differs from *N. biserialis* and *N. multiserialis* in being uniserial and from *Microspherichnus linearis* Hakes in being preserved in convex hyporelief. The compound (*sensu* Pickerill, 1994) specimen has not been previously described in the literature. Its occurrence possibly suggests that the individual tracemaker could produce different structures reflecting different behavioural patterns (cf. Bromley, 1990).

Ichnogenus *Palaeophycus* Hall, 1847

Type ichnospecies: *Palaeophycus tubularis* Hall, 1847

The nomenclatural history of *Palaeophycus* and the morphologically similar ichnotaxon *Planolites* Nicholson has been recently reviewed by Keighley and Pickerill (1995b). These authors recommended that despite the inherent difficulties, the nomenclatural scheme comprehensively proposed by Pemberton and Frey (1982) is the most workable and, therefore, is that adopted herein (see also Fillion, 1989; Fillion and Pickerill, 1990).

***Palaeophycus heberti* (de Saporta, 1872)**
Figure 6F

Material: Four specimens (TF.F161, TF.F224 (*partim*), TF.F225 (*partim*), TF.F226 (*partim*)) and several occurrences in the field.

Description: Straight to slightly curved, cylindrical to flattened, horizontal, unbranched, smooth-walled, lined burrows, 4 to 11 mm wide and up to 105 mm long, preserved in convex hyporelief on 27 mm thick, greenish grey, buff, cross- to parallel-laminated siltstones and fine-grained sandstones. The well-developed wall-lining is 1 to 2 mm thick and darker in colour than the burrow-fill which is massive and similar to the host rock. Burrow width remains constant though some burrows exhibit collapse and show central furrows and two narrow walls. Burrows overlap or run alongside each other to create false branching.

Remarks. The present specimens are classified as *P. heberti* based on their characteristic thickly lined, unornamented walls which distinguish this ichnospecies from *P. tubularis*. The lack of any external surface ornamentation distinguishes *P. heberti* from all other ichnospecies of *Palaeophycus* (Pemberton and Frey, 1982; Frey and Pemberton, 1991).

***Palaeophycus striatus* Hall, 1852**
Figure 6G

Material: Six specimens (TF9208-1-12, TF9209-19, TF9210-4-10, TF129, TF.F206, TF.F218 (*partim*)) and several field occurrences.

Description: Horizontal to slightly inclined unbranched burrows, straight or slightly sinuous, covered with faint, parallel, longitudinal striae, preserved on the soles and in full relief of 35 to 50 mm thick, greenish grey, grey, buff, parallel-laminated siltstones or fine-grained sandstones. Burrow-fill is massive and similar to the host rock. Longitudinal striae consist of multiple and yet continuously aligned minute circular individual dots. Transverse cross-sections show that the burrows are circular. Burrows are 5 to 19 mm wide and up to 150 mm long. Burrow width is generally constant along the length but may swell or narrow in places, especially where entering an interface.

Remarks: The massive burrow-fill suggests that it has not been sorted or processed by the tracemaker. The continuous and longitudinal parallel striae distinguish *P. striatus* from other striate ichnospecies of *Palaeophycus* (Pemberton and Frey, 1982).

***Palaeophycus tubularis* Hall, 1847**
Figure 6H

Material: Fourteen specimens (TF9201-14, TF9201-19, TF9201-20, TF9202-14, TF9209-19, TF129, TF.F126-TF.F129, TF.F164—TF.F167) and many more occurrences in the field.

Description: The burrows are preserved in convex hyporelief on the soles of, or in endorelief within, 25 to 50 mm thick, buff, brown, grey, parallel- or cross-laminated siltstones and fine-grained sandstones. The burrows are unbranched, straight to slightly curved, horizontal to undulatory, cylindrical, elliptical or flattened, 4 to 12 mm in diameter and up to 120 mm long. Wall-lining, where preserved, is thin; burrow-fill is similar to host rock and typically massive. Burrow surfaces are typically smooth.

Remarks: These morphologically simple burrows are assigned to *P. tubularis* despite the fact that the burrow linings are difficult to detect. Thin wall-linings are easily removed by weathering, commonly resulting in seemingly unlined burrows, which, nevertheless, should be assigned to this ichnospecies.

Palaeophycus isp.
Figure 6G

Material: Three specimens (TF124, TF9208-42, TF.F218 (*partim*)) and numerous specimens collected and observed in the field.

Description: Cylindrical to ellipsoidal, seemingly unlined or thinly lined, horizontal to inclined burrows, preserved in convex hyporelief on the soles of, or endorelief within, siltstones and fine- to medium-grained sandstones. The straight to slightly curved burrows are 1 to 8 mm in width and variable in length. Burrow-fill is massive and similar to the host rock.

Remarks: Poor and incomplete preservation, as well as lack of knowledge of the three-dimensional character of the specimens, precludes ichnospecific assignment.

Ichnogenus *Paleodictyon* Meneghini *in* Murchison, 1850

Type ichnospecies: *Paleodictyon strozzi* Meneghini *in* Murchison, 1850
Paleodictyon isp.
Figure 7A

Material: Three specimens (TF9208-1-14, TF9208-1-16, TF9208-1-17).

Description: String-sized networks preserved in convex hyporelief on the soles of 26 to 60 mm thick, grey, parallel-laminated, fine-grained sandstones. The poorly preserved specimens consist of irregular or regular polygons. Though no complete horizontal meshes are present, hexagonal meshes can be inferred. Individual polygons are, diagonally, approximately 25 to 45 mm in diameter and of the same shape. Strings are cylindrical to subcylindrical and vary in thickness from 2 to 3 mm depending on height. Strings are characteristically straight and smooth; course change in strings is typically sharp and no vertical outlets are observed.

Remarks: Classification of *Paleodictyon* at the ichnospecific level is still plagued by different authors adopting different criteria (McCann and Pickerill, 1988; Pickerill, 1990; Crimes and Crossley, 1991). Mesh size, regularity, and thickness of string diameter (Książkiewicz, 1970, 1977) or only mesh shape (Seilacher, 1977) have been considered important in the distinction of ichnospecies. The main problem with each of these schemes is the complete gradation between different net sizes, string diameters and, indeed, net shapes (Crimes and Crossley, 1991). Therefore, a taxonomic revision of the ichnogenus is still warranted (McCann and Pickerill, 1988; Pickerill, 1990; Crimes and Crossley, 1991). The generally incomplete preservation of the material described herein precludes ichnospecific assignment.

Ichnogenus *Phycodes* Richter, 1850

Type ichnospecies: *Phycodes circinatus* Richter, 1853
***Phycodes flabellus* Miller and Dyer, 1878**
Figure 7E

Material: Three specimens (TF9207-10, TF.F185, TF.F186).

Description: The burrow systems are preserved in convex hyporelief on the soles of 18 to 28 mm thick, grey, parallel-laminated siltstones and fine-grained sandstones. The specimens are 30 to 40 mm long, 10 to 25 mm wide and 2 to 5 mm deep. The proximal branches are initially parallel and then project out at very acute angles in a flabellate or broomlike fashion. The entire systems are composed of 3 to 7 branches which are 2 to 5 mm wide. The branches are close to each other, straight to slightly curved. The burrows are faintly annulated and some portions are smooth or covered with small dots. The proximal portion of the burrows consists of a few tunnels. Burrow-fill is similar to the host rock and massive.

Remarks: Osgood (1970) discussed this ichnospecies in detail. It is difficult to generalize on an absolutely distinctive pattern for *Phycodes flabellus*, because the ichnospecies exhibits much variation in overall shape. *P. flabellus* differs from the morphologically similar *P. circinatus* Richter by its lack of a spreite, and the presence of a more shallow, flabellate burrow network.

***Phycodes palmatus* (Hall, 1852)**
Figure 7H

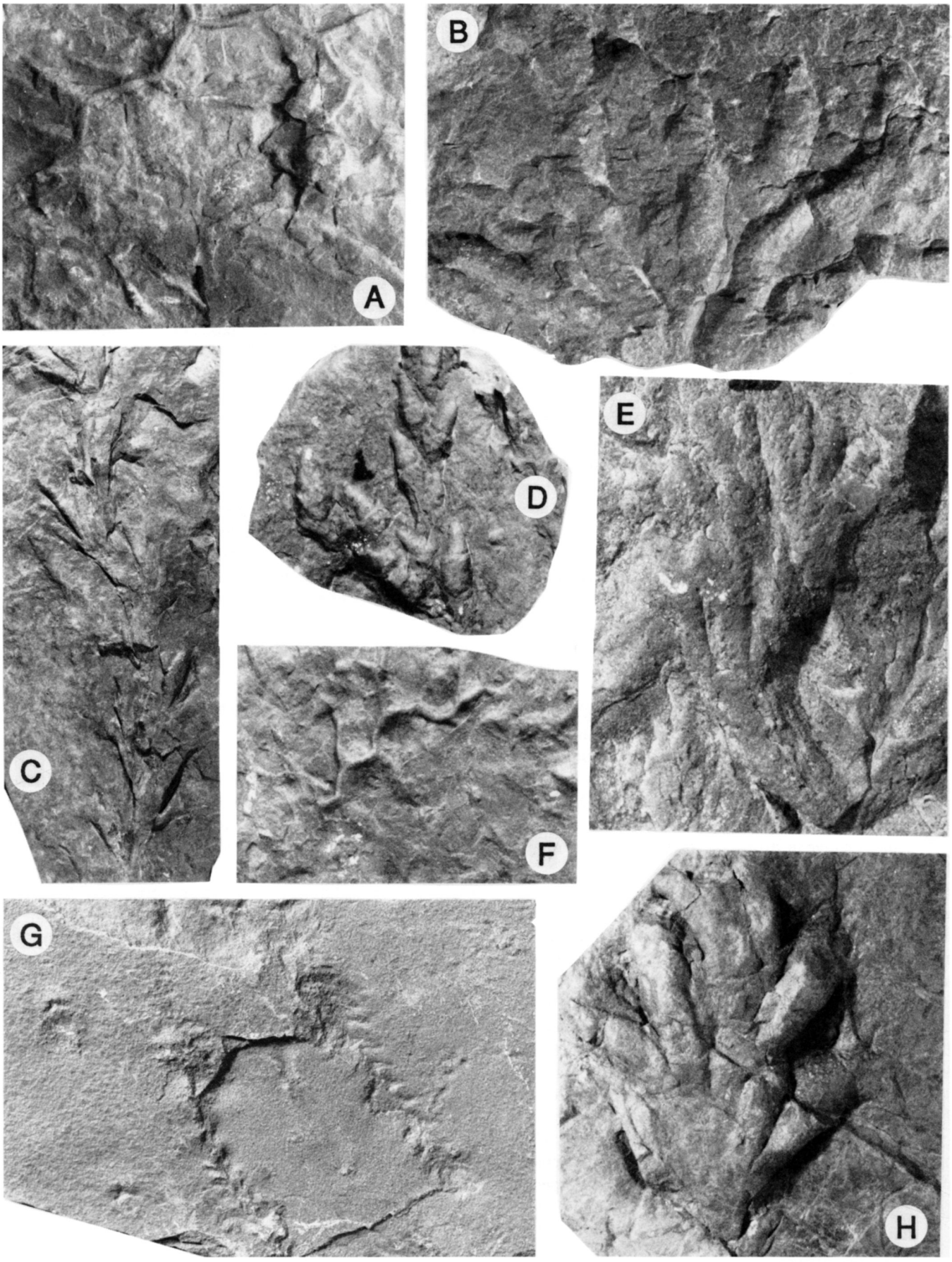
Material: Five specimens (TF9208-21, TF9208-22, TF9210-13, TF9306-5, TF128).

Description: The burrow systems are preserved as horizontal palmate structures, 40 to 55 mm in overall width, on the soles of 28 to 60 mm thick, grey, parallel-laminated siltstones and fine-grained sandstones or interlayered sandstones and mudstones. Each consists of a smooth proximal burrow, from which project, at acute angles, two to seven burrows, each 7 to 10 mm in diameter and 20 to 55 mm long. The branches, straight or very slightly curved, are close to or depart slightly from each other. Burrow surfaces may be covered by minute tubercles.

Remarks. Specimens described here closely resemble Hall's (1852) syntypes and, accordingly, are assigned to *P. palmatus*. Although a spreite is not present, the palmate branching pattern is clearly obvious.

***Phycodes* aff. *palmatus* (Hall, 1852)**
Figure 7B

Material: Seven specimens (TF9209-16, TF9209-22, TF9209-24, TF9209-25, TF.F187, TF.F204).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Description: Horizontal burrow systems preserved in convex hyporelief on the soles of 11 to 45 mm thick, grey, argillaceous siltstones and fine-grained sandstones. The overall pattern of the burrows is thicket-shaped. The systems, 40 to 100 mm wide and 40 to 80 mm long, consist of 5 to 8 individual cylindrical branches that project outward from a centre. The proximal portions are not well-preserved or even absent. The branches, smooth, straight or slightly or strongly curved, are 35 to 65 mm in length and 5.5 to 7 mm in width which is constant or slightly tapers distally. The elongate branches are closely spaced proximally and widely spaced distally, between 1 and 22 mm apart (mostly 10 mm apart).

Remarks. The present specimens differ from typical *P. palmatus* by individual branches being more widely spaced, elongate, strongly curved and lacking a spreite. However, the overall pattern is similar to *P. palmatus*; therefore, the specimens are assigned to *P.* aff. *palmatus*.

***Phycodes pedum* Seilacher, 1955**
Figure 7D

Material: Three specimens (TF9210-14, TF102, TF.F191).

Description: Burrow systems preserved in convex hyporelief or full relief on the soles of 19 to 28 mm thick, grey siltstones and fine-grained sandstones. The burrows consist of a straight row of short, corn-like branches which are of similar size and arranged in a zigzag fashion or closely spaced and bundled in a fan-shape, with branches projecting in a similar direction. No central stem is present. The cylindrical to subcylindrical branches alternately emerge or branch out from the inner side of previous branches at angle of 50° to 70° and form a zigzag shape. The surfaces of the branches are transversely ringed with one rounded to subrounded shallow, narrow furrow which cuts the branches into two equal-length parts. The branches, 9 to 11 mm long and 5 to 6 mm wide at midlength, taper gradually outward and form sharp terminations. The distal parts of the branches are less deeply impressed than the proximal parts. The incomplete specimens have lengths of 46 to 65 mm and widths of 8 to 16 mm. Burrow-fill is the same as the host rock. No sickle-like gallery is observed. Cross-cutting reveals that the individual branches are almost on the same plane and mud-lined.

Remarks: *Phycodes pedum* was originally described by Seilacher (1955) as a semicircular form; however, meandering and more or less straight and looping forms have each been subsequently described (Crimes *et al.*, 1977; Bryant and Pickerill, 1990). The minor branches normally all occur on the same side of the main burrow but specimens with one or more on the opposite side to the remainder (Crimes *et al.*, 1977) and even alternating dextral and sinistral branches (Bryant and Pickerill, 1990) have been reported. In the latter case, the branching fashion is similar to that found in the ichnogenus *Treptichnus* Miller which is probably closely related to *Phycodes pedum* (Banks, 1970).

***Phycodes templus* Han and Pickerill, 1994**
Figure 7C

Material: Eight specimens (NBMG 9202 - NBMG 9209) and other collected specimens.

Diagnosis: *Phycodes* possessing two or, more typically, several horizontally interconnected broomlike or flabellate bundles that collectively form an inverted pagoda-like structure.

Description and Remarks: See Han and Pickerill, 1994a.

Ichnogenus *Protopaleodictyon* Książkiewicz, 1970

Type ichnospecies: *Protopaleodictyon incompositum* Książkiewicz, 1970

***Protopaleodictyon incompositum* Książkiewicz, 1970**
Figure 7F

Material: One specimen (TF9208-1-15).

Description: Burrow system preserved in convex hyporelief on the sole of a 60 mm thick, grey, parallel-laminated, fine-grained sandstone. The burrow system consists of wide first-order meanders and sinuous second-order meanders with apical appendages. The first-order meanders are only partially preserved. The appendages are of variable length, 3 to 15 mm, and are positioned on the apices of the second-order meanders and never form a mesh; only one appendix branches from the apex on the convex side of the meanders. The second-order meander have a wavelength of 7 to 16 mm and amplitude of 2 to 3 mm. The strings, 1.5 to 2 mm wide, are smooth.

Remarks: Similar to *Paleodictyon*, there is still no general agreement as to which characters constitute a distinctive ichnospecies of *Protopaleodictyon* (Pickerill, 1981; Pickerill *et al.*, 1982). Seilacher (1977) utilized the number of branches/undulations and the presence of first- and second-order meanders, while Książkiewicz (1977) employed the regularity and spacing of the first-order meanders, and the size and thickness of the strings. Książkiewicz's (1977) scheme is that adopted herein in view of the obvious variability exhibited in the specimens figured by him. The ichnogenus has been ascribed to a burrowing deposit feeder, possibly an infaunal annelid (Tanaka, 1971; Kern, 1980; Pickerill, 1981).

The specimen from the Wapske Formation rarely shows first-order meanders, but the second-order meanders, typically with apical appendages, differentiates it from *Cosmorhaphe*. *P. incompositum* is distinguished from the morphologically similar ichnospecies *P. minutum* Książkiewicz by its larger size and

Fig. 7. Trace fossils from the Wapske Formation. (A) *Paleodictyon* isp. (TF9208-1-17), x 0.68. (B) *Phycodes* aff. *palmatus* (TF9209-22), x 1.22. (C) *Phycodes templus* (NBMG 9202), x 0.60. (D) *Phycodes pedum* (TF102), x 1.06. (E) *Phycodes flabellus* (TF.F186), x 2.28. (F) *Protopaleodictyon incompositum* (TF9208-1-15), x 1.0. (G) *Protovirgularia dichotoma* (NBMG9348 (right one) and NBMG 9349 (left one), x 0.82. (H) *Phycodes palmatus* (TF9208-21), x 1.22. All specimens are preserved in convex hyporelief.

from *P. submontanum* (Azpeitia Moros) by its more regular meander pattern of the first-order meanders and also by the latter's much longer appendages and a more pronounced tendency toward formation of networks.

Ichnogenus *Protovirgularia* M'Coy, 1850

Type ichnospecies: *Protovirgularia dichotoma* M'Coy, 1850
***Protovirgularia dichotoma* M'Coy, 1850**
Figure 7G

Material: Nineteen specimens (NBMG 9334 - NBMG 9352).

Emended diagnosis: Unbranched, keel-like trail, typically, but not universally, with a median ridge or furrow from where paired, lateral, wedge-shaped appendages, commonly only a few millimetres in length, and of even or variable spacing, originate. Lateral appendages may be normal or at an acute angle to the median ridge or furrow (modified after Volk, 1961; Benton, 1982a).

Description and Remarks. See Han and Pickerill, 1994b.

Ichnogenus *Rusophycus* Hall, 1852

Type ichnospecies: *Rusophycus clavatus* Hall, 1852
***Rusophycus* cf. *carbonarius* Dawson, 1864**
Figure 8A

Material: One specimen (TF9208-1-34).

Description: Small, bilobate bean-like lobes preserved in convex hyporelief on the sole of a 55 mm thick, grey, parallel-laminated, fine-grained sandstone. The lobes taper very slightly anteriorly. Maximum width is 10 mm, near the mid-length, and tapers to only 2.5 mm. Maximum length is 17 mm, giving a length/width ratio 1.7. The median longitudinal furrow is shallow and narrow, being deepest near the mid-length of the lobes. Surface of the lobes possess very poorly preserved transverse scratch marks, each 1 mm in width.

Remarks: The ichnotaxonomy of small cruzianids and rusophycids has recently been reviewed by Keighley and Pickerill (1995a). Although poorly preserved, the specimen described herein closely resembles *R. carbonarius* and is tentatively identified as such.

Ichnogenus *Skolithos* Haldeman, 1840

Type ichnospecies: *Fucoides? linearis* Haldeman, 1840
***Skolithos linearis* Haldeman, 1840**
Figure 8C

Material: Four specimens (TF9210-4-11, TF9302-01, TF122, TF.F203).

Description: Straight, vertical to slightly inclined, unbranched, cylindrical burrows, 3 to 7.5 mm in diameter and of uncertain length, preserved in endorelief within 20 to 40 mm thick, grey, parallel-laminated siltstones or fine-grained sandstones. Burrow walls are either sharp and smooth or indistinct. The burrow-fill is massive and may be finer or coarser in grain size and darker or lighter in colour than the surrounding matrix.

Remarks: Although Alpert's (1974, 1975) nomenclatural scheme for the main ichnospecies of *Skolithos* is still regarded as the most satisfactory (Fillion and Pickerill, 1990), its taxonomy is still in need of revision. With respect to this scheme, specimens from the Wapske Formation are identical to *S. linearis* and are identified accordingly.

Ichnogenus *Taenidium* Heer, 1877

Type ichnospecies: *Taenidium serpentinum* Heer, 1877
***Taenidium serpentinum* Heer, 1877**
Figure 8B

Material: Two specimens (TF.F206, TF.F235).

Description: Unlined, or very thinly mudstone lined, cylindrical serpentiform burrows, possessing a well-spaced arcuate meniscate backfill and preserved in convex hyporelief on the soles of 45 and 75 mm thick, grey, brown, parallel-laminated, fine-grained sandstones. The burrows are straight or slightly curved, unbranched, 4 mm wide and 100 mm long. Terminations are obscure. The outer surfaces are wavy or slightly annulated. The faint annulations appear to correspond to the menisci of the fills. In places where the grey mudstone has been removed by weathering, the inner surfaces are obviously annulated by menisci which are 4 mm wide and 3.5 to 4 mm long.

Remarks: The ichnotaxonomy of simple, unbranched meniscate burrows has been reviewed by D'Alessandro and Bromley (1987) and more recently by Keighley and Pickerill (1994). With respect to these revisions the material described herein can confidently be assigned to *T. serpentinum*. *T. cameronensis* (Brady) differs by possessing intermeniscate segments distinctly longer than wide, *T. satanassi* D'Alessandro and Bromley possesses only weakly arcuate menisci and an obviously pelleted fill (see D'Alessandro and Bromley, 1987) and *T. barretti* (Bradshaw) possesses deeply arcuate or hemispherical, tightly packed menisci.

Ichnogenus *Uchirites* Macsotay, 1967

Type ichnospecies: *Uchirites triangularis* Macsotay, 1967
***Uchirites implexus* Rindsberg, 1994**
Figure 8D

Material: Seven specimens (TF9201-15, TF9201-16, TF9207-11, TF9208-24, TF.F182, TF.F183).

Description: Straight, curved or meandering, triangular, horizontal structures, preserved in convex hyporelief on the soles of 24 to 45 mm thick, grey, brown or orange, parallel- and cross-laminated siltstones and fine-grained sandstones. Specimens possess a single median crest on the lower (ventral) surface and

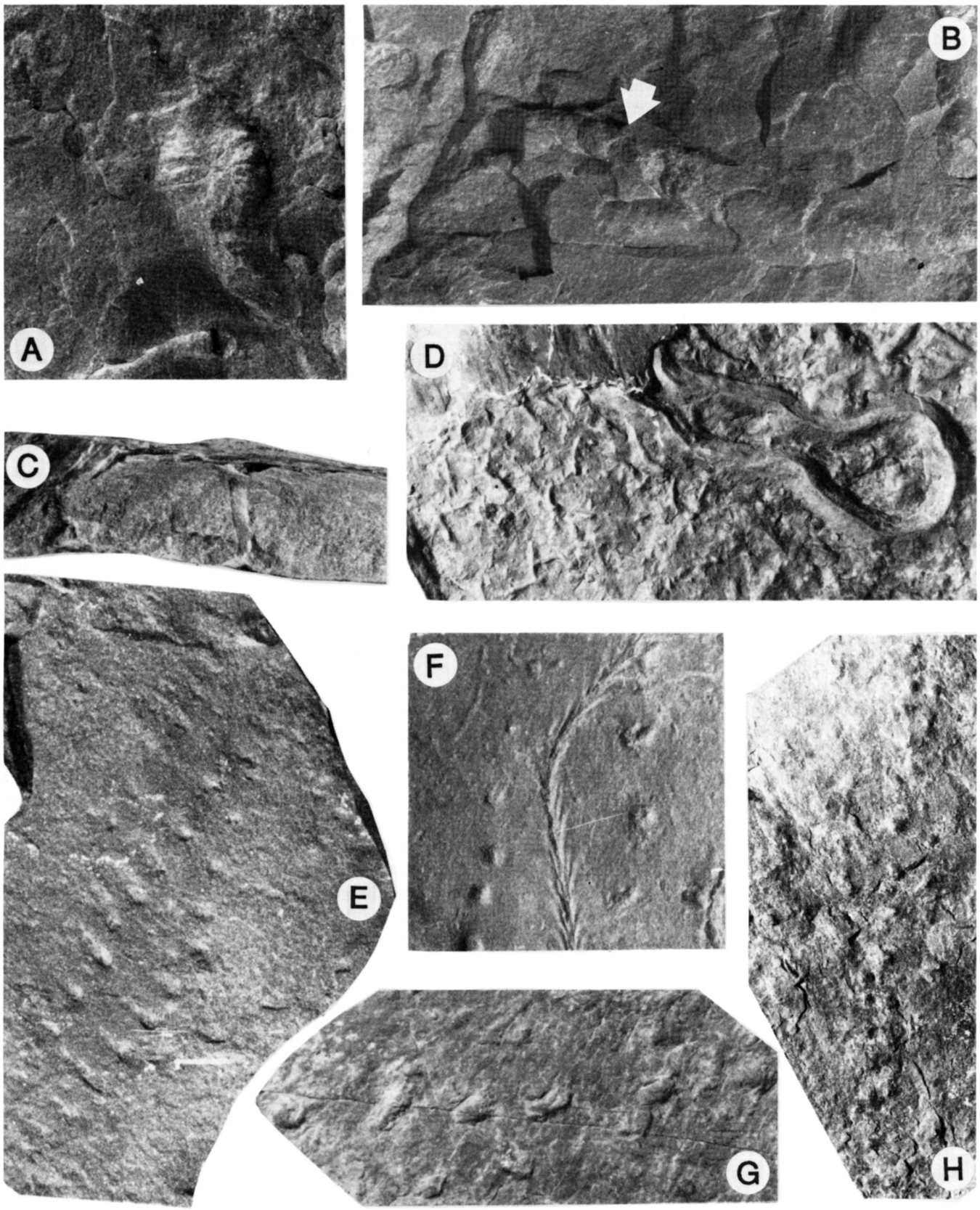

Fig. 8. Trace fossils from the Wapske Formation. (A) *Rusophycus* cf. *carbonarius* (TF9208-1-34), x 2.0. (B) *Taenidium serpentinum* (TF.F206) (arrowed), x 1.63. (C) *Skolithos linearis* (TF9302-01), x 1.13. (D) *Uchirites implexus* (TF.F183), x 0.46. (E) *Umfolozia* cf. *sinuosa* (TF.F235), x 1.61. (F) Track form B (TF9203-11), x 1.11. (G) Scratch marks (TF.F194), x 1.11. (H) Track form A (TF.F210), x 0.97. C is preserved in endorelief; E in concave relief; remainder in convex hyporelief.

paired, lateral, smooth marginal flanks. The crests, 1.5 to 2 mm wide, are typically axial but may be slightly disposed to one side probably as a result of compaction. Structures are 57 to 320 mm in length and 12 to 15 mm in width which is constant in single examples. In two specimens, terminations are composed of oval-shaped bulges that lack both the median crest and the inclined lateral lobes but are wider and higher than the main portion of the structures. In one specimen, the median crest terminates 10 mm before the bulging termination. The fill is similar to or slightly coarser than the surrounding host rock but does not disturb the horizontal laminae in and above the unlined structures.

Remarks: Rindsberg (1994) has recently reviewed the ichnotaxonomy of *Uchirites* and, in so doing, formulated the ichnospecies *U. implexus*. The present material differs only from his types in the absence of delicate lateral striations, though we regard the absence of these in the Wapske Formation material as preservational. Otherwise, the material is identical and is therefore considered conspecific.

Ichnogenus *Umfolozia* Savage, 1971

Type ichnospecies: *Umfolozia sinuosa* Savage, 1971
***Umfolozia* cf. *sinuosa* Savage, 1971**
Figure 8E

Material: Two specimens (TF.F235, TF.F237).

Description: Simple trackways preserved in concave relief, respectively, on the surfaces of 29 and 80 mm thick, grey, parallel-laminated, fine-grained sandstone and siltstone. The trackways, 55 to 90 mm long and 8 to 12 mm wide, consist of two, more or less parallel, straight rows of imprints. Individual imprints, 0.5 to 1 mm wide and up to 4 mm long, are arranged approximately in cycles of five and are circular or tadpole-shaped, having a circular deep impression and an elongate shallow or deep tail. The paired imprints are 4 to 9 mm apart and successive imprints are separated by a distance of 3 to 9 mm. Individual imprints are transverse or oblique to the axial line, oriented at angles of 40° to 50°. The tails in both rows of trackways are oriented toward the same direction.

Remarks: The significant characteristic of *Umfolozia*, a trackway suggested by Savage (1971) and Anderson (1981) to have been produced by peracarid crustaceans, is the repetitive nature of the tracks comprising five pairs of appendages and the presence or otherwise of a sinuous series of small oval telson marks (Anderson, 1981). The present samples have a diagnostic track cycle of five, though this is not completely developed along their entire length. Additionally, there are no longitudinal drag lines or drag marks. Nevertheless, we tentatively regard the material as *U. sinuosa*.

Track form A
Figure 8H

Material: One specimen (TF.F210).

Description: Trackway preserved in convex hyporelief on the surface of a greenish grey siltstone. The straight trackway consists of two parallel rows or series of circular impressions. It is 120 mm long and 5 to 6 mm wide, individual impressions being 1 mm in diameter and usually 5 to 6 mm apart in successive rows, rarely 4 mm apart. The impressions occur commonly in pairs, more rarely dispersed. The area between the two rows is undisturbed.

Remarks: Morphologically, this trackway is similar to examples of *Hormosiroidea beskidensis*. However, the latter is much larger in size and possesses vertical outlets arranged alternately. The trackway was probably produced by an arthropod-like, bilaterally symmetrical animal.

Track form B
Figure 8F

Material: One specimen (TF9203-11).

Description: Preserved in convex hyporelief on the sole of a 32 mm thick, grey, fine-grained sandstone. The trace is composed of two contrasting morphologies, an axial feather-like form and two lateral parallel rows of paired foot or claw imprints appearing as small circular knobs. The whole trace is 62 mm long and 28 mm wide.

The slightly curved axial feather-like trail consists of a 'stem' and lateral fine 'filaments'. The 'stem' is 0.5 to 1.0 mm wide. The fine 'filaments' propagate from the 'stem' and form a V-shape with angles of 16° to 22° and individual arms are 0.5 mm wide and 8 to 10 mm long. The 'stem' may be formed by overlapping 'filaments'. The axial trail is 4 to 5 mm wide. The 'filaments' have no branches.

The two rows of foot or claw imprints on each side of the axial trail are roughly parallel and symmetrical. The foot imprints are clear and distinct, circular, large or small, unifid or bifid, and 2 to 4 mm in diameter with intervals of 4 to 9 mm, up to 11 mm, in a successive row. The distance between rows of imprints and the axial trail is between 5 and 12 mm. The central trail is slightly curved while the lateral rows of imprints remain virtually straight.

Remarks: The axial part of this trackway is similar to both '*Chloephycus*' Miller and Dyer (Osgood, 1970, pl. 80, figs. 1, 6) and inorganic groove moulds and chevron marks (Dżułyński and Walton, 1965, p. 88, fig. 61; p. 100, figs. 68B, C). The present specimen, however, is believed to be biogenic in origin based on the following observations:

(1) The central feather-like marks are curved, unlike typical '*Chloephycus*' or inorganic groove markings;

(2) On the same slab, another poorly preserved specimen shows similar feather-like features in which the V-angles point in an opposite direction to the described specimen;

(3) The feather-like marks are flanked by two rows of tracks which are more or less parallel and possess scratches;

(4) Other scratch marks occur on the same stratification surface.

Given a biogenic origin, this trackway does invite com-

parison with several previously described ichnotaxa. For example, *Protovirgularia* M'Coy is an ichnotaxon that only has the central feather-like parts. *Protichnites* Owen has two rows of bifid or trifid imprints which flank the median double straight trails and *Mesichnium* Gilmore has two parallel rows of footprints with a median row of suboval regularly spaced depressions.

Imprints of this type were probably made by an unknown bilaterally symmetrical arthropod which had vertical appendages resulting in the central feather-like drag marks, and paired feet leaving lateral rows of scratch marks. Assignment to previously described ichnotaxa is, however, considered unwise pending discovery of additional or more informative material.

Scratch marks
Figure 8G

Material: One specimen (TF.F194).

Description: A series of imprints are preserved in convex hyporelief on the surface of a 33 mm thick, grey, fine-grained sandstone. The imprints consist of rectangular impressions, individually 3 mm wide and 5 to 7 mm long, with a shallow, short furrow on their lower portions. Individual impressions are parallel to each other but all align at 30° to 35° with the presumed axis of movement. The specimen is 96 mm long and 5 to 6 mm wide, having intervals between successive imprints of 5 to 10 mm.

Remarks: Mikuláš (1992) established the ichnogenus *Interruptida* for similar surface traces interrupted in regular intervals and, indeed, the description, dimensions and illustration of *Interruptida* indet. B (Mikuláš, 1992, pl. 13, fig. 5) are similar to the present specimen. However, without more material we are reluctant to accept Mikuláš's (*ibid.*) taxonomic decision, as such examples could conceivably represent taphonomic variants of previously established ichnotaxa. As such we retain the specimen in open nomenclature.

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