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Ethologic structure of Cambrian-Carboniferous trace fossils assemblages from slope and basinal settings

Data for:**Post-Cambrian closure of the deep-water slope-basin taphonomic window**

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CODINGS.**A**, agrichnion; **C**, cubichnion; **D**, domichnion; **F**, fodinichnion; **G**, graphoglyptid; **O**, other; **P**, pascichnion; **R**, repichnion.**NOTES.**

- (1) The diversity of each ichnofaunal assemblage was revised at the ichnogenetic level whenever possible; see comments accompanying each data point. The taxonomy of trace fossils is complex and, for many ichnotaxa, remains controversial at the ichnospecific level. In contrast, the ichnotaxobases used to identify at least the majority of ichnogenera are now well established (largely due to Häntzschel, 1975), although subject to on-going revision. The type material of *Helminthoidea* has recently been referred to *Nereites* (Uchman, 1995). None of the material identified as *Helminthoidea* in the data set conforms to the diagnosis of *Nereites* provided by Orr and Pickerill (1995, p. 396). Distinction of the two ichnotaxa is warranted within this data set; for convenience, the former is referred to as "*Helminthoidea*", herein. Care was taken to ensure that informally named ichnotaxa were not preservational variants, and thus synonyms, of ichnogenera within each assemblage.
- (2) The ethology of each ichnotaxon was identified according to the criteria of Bromley (1990, 1996). Fodinichnia are restricted to trace fossils that combine feeding with semi-stationary behaviour, and pascichnia to structures in which a systematic foraging pattern, involving thigmotactic and/or strophotactic behaviour, is present ('in such it is clear that an animal has exploited a particular area or region of the substrate for food'; Bromley, 1990, p. 167). *Planolites*, for example, has been regarded as a fodinichnion by some authors (e.g. Ekdale et al., 1984, p. 25; Frey and Pemberton, 1985), and as a pascichnion by others (Ekdale, 1985). Herein, *Planolites* conforms to the diagnosis of neither and is regarded as an infaunal repichnion.
- (3) Although ichnotaxa may recur between assemblages their ethology may not be similar. For example, *Nereites* is diagnosed in part by Orr and Pickerill (1995, p. 396) as "straight, irregularly to systematically meandering and, or, spiralling"; it need not therefore display the well-developed strophotactic and/or thigmotactic behaviour characteristic of a pascichnion. The ethology of each ichnotaxon was assessed individually using the illustrations and/or descriptions of the original authors; reference was made to the descriptions provided by Häntzschel (1975) only if neither were provided. This is a major difference from the approach of Orr (2001) in which pascichnia and agrichnia were identified on the basis of the ichnogenus *characteristically* having this ethology.
- (4) For some ichnotaxa an alternative, less favoured, ethology is indicated in parentheses, e.g. D(F), and the reasoning explained in the accompanying text. Where it proved impossible to favour either of two possible ethologies, both are indicated thus: D/F. These situations can arise in several ways. (1) The ichnotaxon combines more than one behaviour, in which case the primary and secondary functions are separated (see also comments by Miller (1998) on what he terms 'complex trace fossils'). (2) In an individual assemblage the ichnogenus accommodates more than one ichnospecies each with its own, different, ethology. (3) Collectively, specimens of an ichnotaxon display more than one behaviour pattern e.g. where a repichnion grades into a pascichnion.

- (5) Graphoglyptids *sensu* Seilacher (1977a) are sub-divided into continuous meanders (*Cosmorhapse**, *Helminthorhapse**, *Spirorhapse**), uniramous meanders (*Belorhapse**, *Protopaleodictyon**, *Helicolithus**, *Punctorhapse*, *Urohelminthoida*, *Dendrotichnium*, *Hormosiroidea**), biramous meanders (*Paleomeandron*, *Desmograpton**, *Oscillorhapse*, *Protopaleodictyon**), radiating forms (*Tuapseichnium*, "Glockeria" (= *Glockerichnus**), *Lorenzina**, *Yakutatia**, *Chondrorhapse*, *Dendrorhapse*, *Fascicichnium*) irregular forms (*Acanthorhapse*, *Megagrapton**) regular nets (*Paleodictyon**, including the sub-ichnogenes *Glenodictyum*, *Squamodictyon* and *Ramidictyon*). A simple regularly undulating form such as *Cochlichnus** is suggested by Seilacher (1977a, p. 296, Figure 3) as the 'prototype' (p. 296) from which graphoglyptids formed by continuous meanders were 'theoretically derived' (caption to Figure 3). Those ichnogenes indicated by * occur within this data set.

Graphoglyptids *sensu* Seilacher (1977a) are three-dimensional, infaunal, open burrow networks that may have functioned as 'traps' or 'mushroom gardens' (see Seilacher, 1977a, p. 331-333, Figure 15); following Bromley (1990) these would be classified as agrichnia herein. The suggestion by Kern (1980, p. 351) to automatically exclude "*Lorenzina* and other stellate traces ... [from the graphoglyptids, as they lack] ... the regularly cylindrical burrows and branching geometries of the other graphoglyptids" is not automatically followed. However, some of the ichnogenes considered graphoglyptids by Seilacher (1977a) have also been used to describe continuous, essentially two-dimensional, bedding parallel, post-depositional, actively-infilled, meandering and/or spiralling trace fossils (which would be classified as pascichnia herein) and post-depositional, actively-infilled, semi-stationary radiating traces (which would be classified as fodinichnia herein) For example, *Cosmorhapse* has been regarded as a pascichnion by some authors or an agrichnion by others, a point illustrated by (Bromley, 1990, p. 167, 171) who cited it as representative of both ethologies.

In the majority of cases identifying the ethology of such 'graphoglyptids' is possible on the basis of their mode of preservation. The majority of open burrow structures are pre-depositional and preserved as secondary casts in positive hyporelief on the sole of the succeeding event bed (Seilacher, 1977a, p. 289-292, Figure 1); the preserved part is therefore a horizontal section through the three-dimensional structure. There are, however, rare exceptions; for example, Kern (1980, p. 349) noted that "fecal strings rarely may be broken and displaced by the sand bearing current before their impressions are cast by sand"; thus, although pre-depositional these were not maintained as open burrow structures. Kern (1980) provides criteria to discriminate pre-depositional and post-depositional structures.

Important criteria used to exclude 'graphoglyptid' ichnogenes from the category agrichnion included (1) evidence for having been actively backfilled, the criterion used by Seilacher (1977a, p. 317) to exclude "painted radial burrows" from graphoglyptids; (2) preservation in other than positive hyporelief on the soles of beds; (3) evidence that in vertical section the outline of the burrow system was complete, i.e. had not been partially exposed and secondarily cast.

An ichnogenes is only classified as an agrichnion (A) if *proven* to have been a pre-depositional open burrow network. If the ethology and/or mode of preservation cannot be proven from the original description and/or illustration(s) the structure is only, or first, classified as a graphoglyptid (G). Most of these will be either a pascichnion or agrichnion and if one alternative is favoured, but considered unproven, P or A is added in parentheses, i.e. G(P). The proportion of agrichnia and pascichnia in the assemblages has therefore probably been under-estimated; this is considered desirable as in the text particular emphasis is placed on the temporal distribution of these ethologies as a causal factor for post-Cambrian closure of the deep-water slope-basin taphonomic window.

1: Blow Me Down Brook Formation, Newfoundland

References: Lindholm and Casey (1989, 1990)

Age: early Cambrian¹

Assemblage: *Gordia* **R**², *Oldhamia* **F**, *Planolites* **R**, "other simple indistinguishable forms" **O**³

¹ Age partly based upon presence of *Oldhamia*.

² Not described or illustrated, so regularity of meandering or spiralling (that might suggest it is a pascichnion) cannot be assessed.

³ Not described or illustrated; assignment not attempted.

2: I Cma unit: Niddy Lake Map Area, Selwyn Mountains, Yukon Territory, Canada ¹

References: Hofmann and Cecile (1981) Hofmann, Cecile and Lane (1994)

Age: early Cambrian²

Assemblage: *Helminthoidichnites*³ **R**, *Helminthorhapse* **R(P)**⁴, *Oldhamia* **F**, *Planolites* **R**, *?Plagiogmus*⁵ **R**

¹ Localities N1, N2, N3, N5, N7, N8, N10, N11, N12 and N14 of Hofmann, Cecile and Lane (1994, Figs. 1B, 2 column 1)

² Age is based on comparison with *Oldhamia*-bearing ichnofaunas of similar age elsewhere and on archaeocyathids and olenellids in overlying units.

³ Referred to *Gordia* by Hofmann and Cecile (1981).

⁴ A similarity to the 'graphoglyptid' *Helminthorhapse* described by Seilacher (1977a) is suggested by Hofmann et al., (1994, p. 773); this is inconsistent with evidence that illustrated example (Hofmann et al., 1994, Figures 3A, 3C) is a post-depositional trace. Does display strophotactic behaviour, but no thigmotactic behaviour; could be interpreted as a poorly developed pascichnion.

⁵ Recovered from a loose block at locality N11; may be from the succeeding Ca unit.

3: Ca unit: Niddery Lake Map Area, Selwyn Mountains, Yukon Territory, Canada¹

References: Hofmann, Cecile and Lane (1994)

Age: early Cambrian to early Middle Cambrian²

Assemblage^{3 4}: ?*Helminthoidichnites* **R**, *Planolites* **R**, hemispherical protrusions **C**⁵

¹ Localities N4, N6, N9 and N13 of Hofmann, Cecile and Lane (1994, Figs. 1B, 2 column 1).

² Age is based on an archaeocyathid from this unit.

³ Hofmann et al. (1994, p. 767) record ?*Tuberculichnus* from the Ca unit; this is not consistent with the appendix to this paper in which a "single specimen" (Hofmann et al., 1994, p. 779) of ?*Tuberculichnus* is recorded from locality BR13 in the British Mountains, Yukon Territory, Canada.

⁴ The example of ? *Plagiogmus* from locality N11 of Hofmann et al. (1994) and assigned to their ICma unit was recovered from a loose block and may have come from the Ca unit.

⁵ These 'have the appearance of bases of *Skolithos*-like tubes', but 'vertical polished sections show a lack of vertical burrowing in the sand above the protrusions ...; they are better regarded as depressions made in the underlying pelite before being filled with sand' (Hofmann et al., 1994, p. 779). Therefore regarded as a cubichnion, not a domichnion.

4: Ca unit: Barn Mountains, Yukon Territory, Canada¹

References: Hofmann, Cecile and Lane (1994)

Age: early Cambrian to early Middle Cambrian²

Assemblage: *Bergaueria* **C**, *Monomorphichnus*³ **F/R**⁴, *Oldhamia* **F**, *Planolites* **R**

¹ Localities BN1 - 10 of Hofmann et al. (1994, Figs. 1C, 2 column 2).

² Age is based on comparison with *Oldhamia*-bearing ichnofaunas of similar age elsewhere.

³ Misspelt *Monomorphichnus* in caption to Table A1 in Appendix of Hofmann et al. (1994).

⁴ Is characterized by a series of long raking imprints produced by the appendages of arthropods (often in Palaeozoic marine strata attributed to trilobites). Has been interpreted as either a feeding trace, and/or locomotion at an angle to a current, e.g. 'swimming-grazing trail' (Häntzschel, 1975, p. W84).

5: western British Mountains, Yukon Territory and State of Alaska, North America^{1 2}

References: Hofmann, Cecile and Lane (1994)

Age: early Cambrian to early Middle Cambrian³

Assemblage: *Cochlichnus* **R**⁴, *Oldhamia* **F**, *Planolites* **R**, *Protopaleodictyon* **R(A)**⁵

¹ Localities BR5 - 9 of Hofmann et al. (1994, Figs. 1D and E, 2 column 3).

² Listed as Neruokpuk Formation in Table A1 in Appendix of Hofmann et al. (1994), but referred to in Fig. 2 column 3 of Hofmann, Cecile and Lane (1994) as the Ca, Cqa, Caq, Clac, and Cac units.

³ Age is based on comparison with *Oldhamia*-bearing ichnofaunas of similar age elsewhere.

⁴ Two specimens illustrated (Hofmann et al., 1994, Figures 5I, J) one in positive, and one in negative relief, but no evidence as to orientation of either; neither specimen shows associated flute, groove casts etc. (or counterparts thereof) that would suggest they were secondary casts of pre-depositional open burrows, although little of each slab is included in the images. There is no evidence to suggest that this is other than a simple repichnion.

⁵ On the basis of the identification by Hofmann et al. (1994, p. 779) who note it to be 'irregular, mesh-like', this would be interpreted as an agrichnion; however, the figured specimen (Hofmann et al., 1994, Figure 5M) could also be interpreted as simply a network of overlapping straight burrows of *Planolites/Palaeophycus* affinity; locally on the right hand side burrows at an angle to each other appear to show cross-cutting, inconsistent with their being co-joined parts of an open burrow structure.

6: Okpioyulak Creek area, British Mountains, Yukon Territory, Canada^{1 2}

References: Hofmann, Cecile and Lane (1994)

Age: early Cambrian to early Middle Cambrian³

Assemblage: ?*Helminthoidichnites* **R**, *Oldhamia* **F**, *Planolites* **R**

¹ Localities BR1 - 4 of Hofmann et al. (1994, Figs. 1E, 2 column 4)

² Listed as Neruokpuk Formation in Table A1 in Appendix of Hofmann et al. (1994), but referred to in Fig. 2 column 4 of Hofmann et al. (1994) as the Ca, Cqa, Caq, Clac, and Cac units.

³ age is based on comparison with *Oldhamia*-bearing ichnofaunas of similar age elsewhere.

7: Member B, Grant Land Formation, Tanquary Fjord, Ellesmere Island, Canada^{1 2}

References: Hofmann, Cecile and Lane (1994)

Age: early Cambrian to early Middle Cambrian³

Assemblage: *Didymaulichnus*⁴ **R**, *Oldhamia* **F**, *Planolites* **R**

¹ Localities TQ1 - 3 of Hofmann, Cecile and Lane (1994, Figs. 1F, 2 column 5).

² The Grant Land Formation is a deep-water facies; although the depositional environment of Member B is problematical, a complex submarine fan environment is favoured (Hofmann et al., 1994, p. 771).

³ Age is based on comparison with *Oldhamia*-bearing ichnofaunas of similar age elsewhere.

⁴ Assignment considered questionable by Hofmann et al. (1994, p. 773), but clearly a repichnion.

8: Puncoviscana Formation and coeval strata, northwestern Argentina

References: Aceñolaza and Durand (1973, 1986) Aceñolaza (1978) Aceñolaza and Toselli (1981) Aceñolaza and Miller (1982)

Age: Lower Cambrian¹

Assemblage²: *Cochlichnus* **R**³, *Dimorphichnus* **F/R**⁴, *Diplichnites* **R**, "*Glockeria*" (= *Glockerichnus*)⁵ **F**, *Gordia* **R**⁶, *Helminthopsis*, **R**⁷ *Nereites* **P**⁸, *Oldhamia* **F**, *Planolites* **R**, *Protovirgularia* **R**, *Tasmanadia* **R**, *Torrowangea* **R**⁹

¹ Age is partly defined on the trace fossils: "various forms which can be considered to be of Lower Cambrian age" (Aceñolaza and Miller, 1982, p. 34).

² The interpreted basinal facies is only observed around Salta (see Aceñolaza and Miller, 1982, Figure 1). The ichnogenera listed are recorded from localities 2-4 and 6-7 in Table 1 of Aceñolaza and Miller (1982) which are in the vicinity of Salta. The assemblage therefore differs from that listed in Crimes et al. (1992, p. 70).

³ Orientation of specimen unknown, but no evidence, e.g. flute, groove casts etc. (or counterparts thereof) that would suggest the trace fossil is a secondary cast of a pre-depositional open burrow. Confidently interpreted as a repichnion.

⁴ Is characterized by a series of long raking imprints produced by the appendages of arthropods (often in Palaeozoic marine strata attributed to trilobites). Has been interpreted as either a feeding trace, or locomotion at an angle to a current.

⁵ The name "*Glockeria*" is unavailable, and examples thereof have been referred to *Glockerichnus* (Pickerill, 1982). As illustrated (e.g. Aceñolaza, 1978, Figure 9) *Glockerichnus* may actually represent *Volkichnium*; this does not affect the diversity of the assemblage, and both have the same ethology. The straight unbranched shafts of the burrow system are arranged in a stellate pattern and meet medially, suggesting the presence of a central shaft; this contrasts with the 'central area' being 'completely untouched' that was suggested by Seilacher (1977a, p. 314) to be indicative of 'radiating graphoglyptid' affinity. Secondly, orientation of specimen unknown but there is no evidence, e.g. flute, groove casts etc. (or counterparts thereof) that would suggest the trace fossil is a secondary cast of a pre-depositional open burrow. Confidently interpreted as a fodinichnion.

⁶ *Gordia* from Cachi (Aceñolaza, 1978, Figure 10; locality 3 of Aceñolaza and Miller, 1982) exhibits no well-developed behaviour patterns.

⁷ *Helminthopsis* from Muñano (Aceñolaza, 1978, Figure 11; locality 6 of Aceñolaza and Miller, 1982) exhibits poor strophotactic behaviour, but neither phobotactic nor thigmotactic behaviour, and is not classified as a pascichnion.

⁸ *Nereites* from Campo Quijano (Aceñolaza and Durand, 1973, Figure 2A; Aceñolaza, 1978, Figure 12; Aceñolaza and Durand, 1986, Figure 3F; locality 7 of Aceñolaza and Miller, 1982) exhibits phobotactic and regular strophotactic behaviour, but not thigmotactic behaviour.

⁹ *Torrowangea* is not illustrated by Aceñolaza (1978) or Aceñolaza and Durand (1973, 1986) but the brief description (Aceñolaza, 1978, p. 33-34) is consistent with the diagnosis by Häntzschel (1975, p. W117).

9: Bray Group, Howth Peninsula, eastern Ireland

References: Crimes (1976) Holland (1981, p. 41)

Age: mid Lower Cambrian¹

Assemblage: *Arenicolites* **D**, *Granularia* **F(R)**², *Planolites* **R**, *Skolithos* **D**, *Teichichnus* **F**

¹ Based on an acritarch assemblage from Howth recorded in Holland (1981, p. 45).

² Continuity of burrows (2-5mm wide, up to 5cm long; Crimes, 1976, p. 62) suggests repichnion, but presence of 'frequent branching' (Crimes, 1976, p. 62) favours fodinichnion.

10: Hell's Mouth Grits, St. Tudwal's Peninsula, north Wales

References: Crimes, Garcia Hidalgo and Poire (1992, p. 70)

Age: high Lower Cambrian

Assemblage: *Palaeophycus* **R**, *Phycodes* **F**, *Planolites* **R**

11: Cilan Grits, St. Tudwal's Peninsula, north Wales

References: Crimes, Garcia Hidalgo and Poire (1992, p. 70)

Age: Lower-Middle Cambrian

Assemblage: *Bergaueria* **C**, *Cruziana* **R**, *Planolites* **R**, *Protopaleodictyon* **A(O)**¹

¹ Material not described or illustrated, but *Paleodictyon* from the Ribband Group is (see Data Point 17), and is clearly an agrichnion; thus, this is interpreted to probably have a similar ethology. However, *Protopaleodictyon* is repeatedly used for what are herein considered to be networks of overlapping post-depositional burrows of *Palaeophycus/Planolites* affinity, and an alternative interpretation is possible.

12: Polduff Formation, Cahore Group, south-eastern Ireland

References: Crimes and Crossley (1968, p. 203-204; Figure 7) Crimes, Garcia Hidalgo and Poire (1992, p. 70)

Age: Lower-Middle Cambrian

Assemblage¹: *Arenicolites* **D**, "*Helminthoida*"² **P**, *Helminthopsis*² **R**, "*Histioderma*" (= *Monocraterion*) **D**, *Oldhamia* **F**, *Palaeophycus* **R**, *Planolites* **R**, *Protopaleodictyon* **A(O)**³

¹ Simple line drawings of three ichnotaxa (*Oldhamia*, "*Histioderma*", and 'irregular trails') are illustrated by Crimes and Crossley (1968, Figure 7); the text (Crimes and Crossley, 1968, p. 204) mentions, in addition, 'isolated meandering trails ... that show insufficient morphological detail to allow identification'. The 'irregular trails' are illustrated (Crimes and Crossley, 1968, Plate XA), and appear to be overlapping burrows of *Palaeophycus/Planolites* affinity; both these ichnotaxa were added by Crimes et al. (1992, p. 70). The 'isolated meandering trails' are presumed to be either "*Helminthoida*" or *Helminthopsis*, both of which were added by Crimes, Garcia Hidalgo and Poire (1992, p. 70).

² The illustrations of each (Crimes et al., 1992, Figures 4F and 4G) do not show obvious differences; the example of *Helminthopsis* (Figure 4F), could represent one 'meander bend' of "*Helminthoida*"; the two ichnotaxa are retained, and their ethology distinguished as *Helminthopsis* from the Ribband Group (Data Point 17; Crimes et al., 1992, Figures 5A) shows no systematic meandering.

³ Material not described or illustrated, but *Paleodictyon* from Ribband Group is (see Data Point 17), and is clearly an agrichnion; thus, this interpreted to have a similar ethology. However, *Protopaleodictyon* is repeatedly used for what are herein considered to be networks of overlapping post-depositional burrows of *Palaeophycus/Planolites* affinity, and an alternative interpretation is possible.

13: Copper Mine Range Beds, New South Wales, Australia

References: Webby (1984)

Age: Middle Cambrian¹

Assemblage: *Chondrites*, **F** *Planolites*² **R**

¹ Based upon (a) the overlying Cupala Creek Formation is of Late Cambrian age, and, (b) the absence of volcanic-derived material from the adjacent Early Cambrian Mount Wright Volcanics.

² Although recorded as *Planolites*, the description (Webby, 1984, p. 433) cites the presence of a "wall" "composed of a zone of dark, structureless, shale surrounding a vaguely transversely annulated lighter axial zone"; this is clearly shown in the accompanying figures (Webby, 1984, Figures 4g and 4h). Probably should be referred to *Macaronichnus*; in either case it is considered herein as a repichnion.

14: Goldenville Formation; Meguma Group, Nova Scotia, Canada

References: Pickerill (1992, 1994) Pickerill and Keppie (1981) Pickerill and Williams (1989) Pratt and Waldron (1991)

Age: Middle Cambrian¹

Assemblage²: "*Helminthoida*" **P**, *Helminthoidichnites* **R**, *Palaeophycus* **R**, *Paleodictyon* **A(O)**³, *Planolites* **R**, *Rhizocorallium* **D**, *Rusophycus* **C**, *Skolithos* **D**, *Taenidium* **R**, *Teichichnus* **F**, "enigmatic, unnamed burrow systems" **O/R**⁴

¹ At least as old as Middle Cambrian; at the top of the formation a trilobite faunule is of Middle Cambrian age (Pratt and Waldron, 1991).

² "*Astropolithon*" *hindii* was erected using material from the Meguma Group by Dawson (1878). It is of inorganic origin (Pickerill and Harris, 1979) and is not included here. The diversity of the assemblage is recorded by Pickerill (1992) in an abstract; Pickerill and Keppie (1981) describe and illustrate *Arenicolites*, *Circulichnus* and *Paleodictyon*, the first two of which are from the Halifax Formation (Data Point 16); otherwise, interpretation of the ethologies is based on descriptions by Häntzschel (1975).

³ Clearly a network of irregular (?deformed) to polygonal, (some of which are crudely hexagonal) meshes (Pickerill and Keppie, 1981, Figure 4) preserved in 'convex (= positive) hyporelief' (Pickerill and Keppie, 1981, p. 134), favouring interpretation as agrichnion, although 'whether the system is pre-depositional or post-depositional in origin also remains an enigma' (Pickerill and Keppie, 1981, p. 134-135), hence alternative suggestion.

⁴ The "enigmatic, unnamed burrow systems" are attributed to the activities of mobile deposit-feeding organisms by Pickerill and Williams (1989) but their ethology is difficult to classify.

15: Polkorridoren Group, north Peary Land, Greenland

References: Pickerill, Hurst and Surlyk (1982)

Age: Cambrian

Assemblage¹²: *Gordia* **R**, *Helminthopsis* **R**, *Planolites* **R**, *Protopaleodictyon* **A**³, "unnamed horseshoe burrow" **O(D)**⁴

¹ Only *Protopaleodictyon* is described and illustrated; the ethology of the other ichnogenera is based on descriptions by Häntzschel (1975).

² Assemblage comprises GGU collections 230278 and 230279. Note that an "unnamed horseshoe burrow" also occurs in GGU collections 230195 and 230197, both collected from the Silurian of northern Hall Land, Greenland (locality 4 in Figure 1 of Pickerill et al., 1982). See Data Point 38.

³ Identification as a 'flysch graphoglyptid trace fossil' (Pickerill et al., 1982, Figure 2c, p. 28) supported; 'incomplete and poor preservation' (Pickerill et al., 1982, p. 28), especially former, would be consistent with a pre-depositional origin.

⁴ The ethology of the informal ichnotaxon "unnamed horseshoe burrow" is impossible to assess; the 'horseshoe' shape may suggest an ethology similar to *Arenicolites*, *Diplocraterion* or *Rhizocorallium*.

16: Halifax Formation, Meguma Group, Nova Scotia, Canada

References: Pickerill (1992) Waldron (1992) Pickerill and Keppie (1981) Pickerill and Williams (1989)

Age: Tremadoc¹

Assemblage²: *Arenicolites* **D**, *Chondrites* **F**, *Circulichnis* **O(R)**³, *Dactyloidites* **F**, *Gordia* **R**, *Helminthopsis* **R**, *Phycodes* **F**, *Planolites* **R**, *Teichichnus* **F**

¹ Graptolites and acritarchs from the Halifax Formation have yielded only Tremadocian ages (Waldron, 1992, p. 1092).

² "*Astropolithon*" *hindii* was erected using material from the Meguma Group by Dawson (1878). It is of inorganic origin (Pickerill and Harris, 1979) and is not included here. The diversity of the assemblage is recorded by Pickerill (1992) in an abstract. Pickerill and Keppie (1981) describe and illustrate *Arenicolites*, *Circulichnus* and *Paleodictyon*, the last of which is from the Goldenville Formation (Data Point 14); otherwise, interpretation of the ethologies is based on descriptions by Häntzschel (1975).

³ Illustrated by Pickerill and Keppie (1981, Figure 3), the ethology of this burrow system is difficult to classify; its circular to elliptical course is inconsistent with a repichnion in which the primary function is interpreted to be locomotion. Pickerill and Keppie (1981, p. 134) describe "*C. montanus* with a burrow of *Helminthopsis*-type leaving the completed ellipse", suggesting *Circulichnis* could represent a local deviation from an otherwise sinuous course.

17: Ribband Group, eastern Ireland

References: Crimes and Crossley (1968) Crimes, Garcia Hidalgo and Poiré (1992) McIlroy (1998/9)

Age: Tremadoc-Arenig

Assemblage: *Belorhapse* **A**¹, *Chondrites* **F**, *Glockerichnus* (= *Bifasciculus* in Crimes and Crossley, 1968) **F**², *Gordia* (= "scribbling grazing traces" in Crimes and Crossley, 1968) **R**, *Helminthopsis* **R**, *Lorenzina* **O**³, *Megagraption* **A**⁴, *Neonereites* **R**⁵, *Palaeophycus* **R**, *Paleodictyon* **A**⁴, *Planolites* **R**, *Sublorenzina*⁶ **F**, *Taenidium* **R**, *Taphrhelminthopsis* **R**, *Teichichnus* **F**, *Tomaculum* **F**⁴, "pellet-filled branching burrows" **A**⁵

¹ Interpretation as a complex three-dimensional trace fossil (see McIlroy, 1998/9, Figure 3) is supported by presence of 'vertical pipes emanating from the apices of the zigzags' of the bedding-parallel basal burrow (McIlroy, 1998/9, p. 104, Figure 2b). Identification of *Belorhapse* as a 'locomotion trail' by Häntzschel (1975, p. W45) is rejected in favour of this example being a 'uniramous graphoglyptid' *sensu* Seilacher (1977a, p. 304). Infill appears to be highly different from host lithology suggesting passive infill of an open structure from the overlying bed, although McIlroy (1998/9, p. 104) notes this difference may have been exacerbated by "dissolution of primary cements (probably carbonate)".

² Regarded as con-specific with material from Skiddaw Group, Lake District (Orr, 1996) and Santon Formation, Isle of Man (Orr and Howe, 1999), former of which is interpreted as a fodinichnion; see Data Point 18, Note 2.

³ The ethology of *Lorenzina* (Crimes et al., 1992, Figure 3F, p. 66) cannot be determined; incomplete and poor preservation of the specimens could indicate poor-quality secondary casting of open structures, rather than their being post-depositional. This might be supported if the specimens were preserved in hyporelief; the orientation of the specimens is not stated.

⁴ Similar preservation of *Megagraption* and *Paleodictyon* to *Belorhapse* (McIlroy, 1998/9, p. 107-108 used to suggest former are also agrichnia, in which case *Paleodictyon* is preserved as a rare example in full relief, rather than a secondary cast in hyporelief on the sole of the succeeding event bed.

⁵ *Neonereites* only forms continuous to sinuous chains; no evidence for systematic meandering; see also notes under Data Point 28.

⁶ *Sublorenzina* is possibly a preservational variant of *Glockerichnus*, but is included herein; a similar ethology is inferred.

⁷ Use of *Tomaculum*, *Syncoprulus* and *Alcyonidiopsis* is confused in the geological literature; see discussion by Orr (1996, 195-196). Classified herein as a fodinichnion as pellets are presumably fecal.

⁸ Material was 'fragmentary' and McIlroy (1998/9, p. 110) considered it 'premature to ascribe it to a named taxon', but noted its 'graphoglyptid-like appearance', hence assignment as an agrichnion.

18: Skiddaw Group, Lake District, England

References: Orr (1996)

Age: Tremadoc to Arenig

Assemblage: *Alcyonidiopsis* **F(R)**¹, *Chondrites* **F**, *Dictyodora* **P**, *Glockerichnus* **F**², *Gordia* **R**, *Ixalichnus* **R**, *Phycodes* **F**, *Planolites* **R**, *Volkichnium* **F**, ?*Gordia*³ **O**⁴, "arthropod repichnion" **R**, "thinly-walled, looping, burrows" **O**⁴ "paired pits" **D**⁵, "overlapping burrows of *Planolites*/*Palaeophycus* affinity" **R**

¹ Combines locomotion and, as burrows are pellet-filled, deposit feeding; latter considered more significant, hence fodinichnion favoured.

² Vertical sectioning of specimens of *Glockerichnus* from the Skiddaw Group (Orr, unpub.) confirms that each ray curves beneath the plane of splitting and continues to a central point, to which it is presumed that a ventral, vertical, shaft was connected; it is thus post-depositional. This contrasts with the argument by Seilacher (1977a, p. 314) that the presence of a 'central area [that] remains completely untouched favours interpretation of forms such as *Glockerichnus* (= '*Glockeria*' *sensu* Seilacher, 1977a) as a 'radiating graphoglyptid'. *Glockerichnus* from the Ribband Group (Data Point 17) is considered con-specific with that from Skiddaw Group (Orr, 1996), and the two are considered fodinichnia.

³ Distinct from *Gordia* (*contra* McIlroy 1998/9, p. 107) but taxonomic status uncertain; recorded as ?*Gordia* aff. *marina* by Orr (1996).

⁴ Both these ichnotaxa form a series of intersecting circles and ellipses. Difficult to classify ethologically as they lack the systematic coverage of an area integral to a pascichnion, but do not conform to a repichnion, in which the primary interpreted function is locomotion.

⁵ Only observed in horizontal cross-section, but occurrence in pairs suggests ethology similar to *Arenicolites* or *Diplocraterion*.

19: Lévis Formation, Québec, Canada

References: Pickerill and Narbonne (1995)

Age: middle Arenig to earliest Llanvirn¹

Assemblage²: *Alcyonidiopsis* **F(R)**³, *Chondrites* **F**, *Circulichnis* **O(R)**⁴, *Helminthopsis* **R**, *Nereites* **P**, *Planolites* **R**, *Taenidium* **R**, *Tomaculum*⁵ **F**, "irregular bioturbate textures that cannot be accorded formal ichnotaxonomic status" **O**

¹ The Lévis Formation as a whole spans the Middle Cambrian to lower Middle Ordovician interval; studied sections lie within stratigraphic range quoted.

² Composition of the assemblage listed, but only *Planolites*, *Alcyonidiopsis* and *Tomaculum* described in detail. Interpretation of the ethologies is based in part on descriptions by Häntzschel (1975).

³ Combines locomotion and, as burrows are pellet-filled, deposit feeding; latter considered significant, hence fodinichnion favoured.

⁴ See comments under Data Point 16 for *Circulichnis*.

⁵ Occurs as isolated pellets as well as fill of *Alcyonidiopsis*; use of *Tomaculum*, *Syncoprulus* and *Alcyonidiopsis* is confused in the geological literature; see discussion by Orr (1996, 195-196). Classified herein as a fodinichnion as pellets are presumably fecal.

20: Blakely Sandstone, western Arkansas, U.S.A.

References: Orr, in press

Age: Middle Ordovician

Assemblage: *Chondrites* **F**, *Palaeophycus* **R**, *Planolites* **R**, *?Teichichnus* **F**, *Alcyonidiopsis* **F(D)**¹, "oblique lamellae" **F**, "mottled background ichnofabric" **O**

¹ Has been noted as cf. *Ophiomorpha* in data set accompanying Orr (2001) as some of the burrows show a structureless core of unpelleted material with a margin of fecal pellets. Other examples are completely infilled by pellets, thus conforming to diagnosis of *Alcyonidiopsis*. Considered to be 'over-splitting' to identify as two ichnotaxa, particularly as most specimens were only observed in vertical sections. Fecal pellets are recurrent and thus deposit feeding considered the primary function.

21: Eastern Trondheimsfjord area, Norway

References: Roberts (1969, 1972, 1984)

Age: Middle-Upper Ordovician¹

Assemblage: *Helminthopsis* (? or *Dictyodora*) **R(P)**², *Megagraption* **R(A)**³, *Nereites* **P**⁴, "arthropod track" **R**, "bilobed track with median furrow"⁵ **R**, "meandering trail Type A cf. *Cosmorhaphé*" **A**⁶

¹ Roberts (1972, p. 235) records the Lower Hovin Group as Lower-Middle Ordovician, and the Upper Hovin Group as Upper Ordovician, in age. Trace fossils were recorded at three localities, one in the uppermost part of the Lower Hovin Group, and two in the ?lower part of the Upper Hovin Group.

² Independent of the taxonomic uncertainty, the figured specimen (Roberts, 1969, Plate II, Figure 1) shows poorly developed strophotactic behaviour and lacks thigmotactic behaviour, hence repichnion favoured over pascichnion. Post-depositional as specimen is preserved along length in both positive and negative relief.

³ The illustrated examples (Roberts, 1969, Plate I, Figures 2 and 3) could represent a series of overlapping burrows of *Planolites/Palaeophycus* affinity. Roberts (1969, p. 232), referring to the specimen in his Plate I, Figure 3, notes 'branches appear to cross at slightly different levels', inconsistent with it being a secondary cast of an open burrow structure. Continuity of trace fossil appears unaffected by what appears to be top left-bottom right trending ridges (?groove casts, as specimen is in hyporelief), which would favour it being post-depositional. Evidence favours repichnion as opposed to agrichnion.

⁴ Illustrated in Roberts (1984 Figures 1-3); high % coverage of area.

⁵ Described in text as "bilobed track with median furrow" (Roberts, 1969, p. 233), but in figure caption to Plate II, Figure 3 as *?Scolicia*.

⁶ Recognized as 'meandering cast (convex hyporelief)' by Roberts (1969, p. 231); specimen in Plate 1, Figure 1 of Roberts (1969) partially 'washed-out' in upper right hand corner.

22: Grog Brook Group, New Brunswick, Canada

References: Pickerill (1980, 1987)

Age: late Middle Ordovician to Late Ordovician¹

Assemblage²: *Asteriacites* **C**, *Asterosoma* **F**, *Belorhaphé* **A**³, *Bifasciculus*⁴ **F**, *Buthotrephis*⁵ **F**, *Cosmorhaphé* **A**⁶, *Fucusopsis*⁷ **R**, "*Glockeria*" (= *Glockerichnus*)⁸ **F**⁸, *Gordia* **R**, *Gyrochorte* **R**, *Helminthopsis* **R**, *Neonereites* **R**, *Nereites* **P**, *Paleodictyon* **A**⁹, *Palaeophycus* **R**, *Planolites* **R**, *Protopaleodictyon* **A**, *Spirodesmos* **O(A)**¹¹, *Spirorhaphé* **G(A)**¹², *Strobilorhaphé* **F**, *Taenidium* **R**

¹ See Malo (1988, p. 905).

² Pickerill (1980) illustrated material from the Grog Brook and Matapedia Groups; each can be distinguished using the figure captions, and details in Pickerill (1987, p. 387).

³ The illustrated specimen (Pickerill, 1980, Figure 5e) is preserved in (positive, at least in part) hyporelief but otherwise shows no information that would assist in interpreting it as having been an open burrow structure; however, interpreted as a graphoglyptid by Pickerill (1980, p. 1270), an interpretation followed herein.

⁴ *Bifasciculus sensu* Crimes and Crossley (1968; see Data Point 17) was referred to *Glockerichnus* by Crimes, Garcia Hidalgo and Poiré (1992, p. 63). *Glockerichnus* also occurs in this assemblage (as "*Glockeria*" in Pickerill, 1980 and *Glockerichnus* in Pickerill, 1987; see note 5), but the illustrated material (*Glockerichnus* Pickerill, 1980, Figure 5c; 1987, Figure 3r; *Bifasciculus* Pickerill, 1980, Figure 3f) are sufficiently distinctive, notably the curvature in the horizontal plane of the individual burrows in *Bifasciculus* to merit distinction at the ichnogenic level. The curving rays meet medially (see discussion under Data Point 18, Note 2) and the specimen is preserved in positive epirelief, both strongly supporting interpretation as a fodinichnion.

⁵ The dubious ichnogenus *Buthotrephis* is recorded, but does not represent *Chondrites* and is therefore included.

⁶ The illustrated specimen of *Cosmorhaphé* (Pickerill, 1980, Figure 4d) is preserved in positive hyporelief but other than appearing indistinct in parts, shows no information that would assist in interpreting it as having originally been an open burrow structure; however, interpreted as a graphoglyptid by Pickerill (1980, p. 1270), an interpretation followed herein.

⁷ The figured specimen (Pickerill, 1980, right hand side of Figure 4a) is also figured as from the Siegas Formation in Pickerill (1981, Figure 5b), from which it was actually collected (Pickerill *pers. comm.*). The appendix to Pickerill (1980, p. 1270) notes that *Fucusopsis* is 'common' and it therefore probably can be included here.

⁸ The name "*Glockeria*" is unavailable, and examples thereof have been referred to *Glockerichnus* (Pickerill, 1982). Although the illustrated specimen (Pickerill, 1980, Figure 5c) is preserved in hyporelief and recorded as a 'graphoglyptid' by Pickerill (1980, p. 1270), the rays meet in the middle (see discussion under Data Point 18, Note 2); there appears to be a difference in colour between the trace fossil and the sediment, suggesting piping of sediment between superjacent layers. These two pieces of evidence strongly favor it being a post-depositional fodinichnion, not an agrichnion.

⁹ Clearly pre-depositional, the illustrated specimen (Pickerill, 1980, Figure 2f) is preserved in positive hyporelief and its lower half has a partially 'washed out' appearance.

¹⁰ Clearly pre-depositional, the illustrated specimen (Pickerill, 1980, Figure 4b) is incompletely preserved in positive relief on the current-marked sole of a bed.

¹¹ *Spirodesmos* was excluded from graphoglyptids by Seilacher (1977a, p. 302); this specimen has similar toponomy to *Spirorhaphé* which on other criteria is favoured as an agrichnion (see Note 12). The spiralling pattern (Pickerill, 1980, Figure 2d) suggests it may not be a simple repichnion. Pickerill (1980, p. 1270) suggests that the material 'commonly only preserves the initial one or two whorls', which could imply incomplete preservation during secondary casting of a three-dimensional pre-depositional open burrow structure in which the central whorls were a distance above, or less likely, below, the remainder of the structure. The possibility that this is an agrichnion cannot be excluded.

¹² Toponymy (positive hyporelief) consistent with it being a pre-depositional structure, but illustrated specimen (Pickerill, 1980, Figure 2b) shows no other supporting evidence; agrichnion favoured as coiling, including turning loop in the centre, is more complex than would be generated by strophotactic behaviour in a pascichnion.

23: Agüeira Formation, northern Spain

References: Crimes, Marcos and Perez-Estaún (1974)

Age: Upper Ordovician

Assemblage¹: *Arenicolites* **D**, *Cosmorhaphé* **P**², *Granularia* **F**³, *Helminthopsis* **R**⁴, *Protopaleodictyon* **A**⁵, *Spirophycus* **P/A**⁶

¹ *Arenicolites*, *Granularia*, *Protopaleodictyon* and *Spirophycus* were recorded from the lower part of the Puerto de Vega section and *Helminthopsis* and *Cosmorhaphé* from the middle of the Oscos section. Only very brief descriptions of the trace fossils, schematic sketches (Crimes et al., 1974, Figure 2) and no comment on their toponomy are provided.

² Sketch implies behaviour pattern is only slightly more regular than in *Helminthopsis*; poorly regular strophotactic behaviour and no thigmotactic behaviour present; tentatively interpreted as a pascichnion.

³ No mention of a wall structure which would suggest construction primarily as a domichnion; therefore presence of branching favours fodinichnion.

⁴ Sinuous course, lacking strophotactic behaviour, favours repichnion over pascichnion.

⁵ Irregular burrow network, with no indication of overlapping of individual burrows that would suggest a series of overlapping burrows of *Planolites/Palaeophycus* affinity.

⁶ Coiled, horn-like, and based on sketch pre-depositional, but impossible to favour either agrichnion or pascichnion.

24: Hauptquarzit, Germany

References: Benton (1982a)

Age: ?Llandeilo-Caradoc

Assemblage: *Dictyodora* **P**, *Diplocraterion* **D**, *Planolites* **R**, "Caridolites-like scratch-marks" **R**¹

¹ Not illustrated by Benton (1982a) who noted a similarity with *Caridolites* from the Scottish Lower Silurian; identified as a repichnion on this basis.

25: Vinini and Palmetto Formations, Nevada, U.S.A.

References: Chamberlain (1977¹, 1979²)

Age: Ordovician

Assemblage: *Alcyonidiopsis* **F(R)**³, *Chondrites* **F**, *Gordia* **P(R)**⁴, *Mammillichnis*⁵ **C**, *Megagraption* **R(A)**⁶, *Palaeophycus* **R**, *Planolites* **R**, *Scolicia* **R**, *Strobilorhapha* **F**, *Taenidium* **R(P)**⁷, *Teichichnus* **F**, *Tomaculum*⁸ **F**, ["*Zonarites*"⁹], ["boxwork burrows"]¹⁰

¹ Ichnofauna described was matched against Table 1 of Chamberlain (1977) which divides the localities into relatively deep (= "eugeoclinal facies") and shallow (= "miogeoclinal facie"); only the former are used.

² Chamberlain (1979, Figure 2) distinguishes between the Palmetto Formation and tectonically-interleaved Devonian; this allows some additional information to be added. However, in Chamberlain (1979, Figure 3 and Table 2) this distinction is not made and it is unclear which trace fossils are unique to each; information from this figure and table is therefore not used.

³ Combines locomotion and, as burrows are pellet-filled, deposit feeding; latter considered significant, hence fodinichnion favoured, as suggested by Chamberlain (1977, p. 7).

⁴ The specimen illustrated in Figure 3G of Chamberlain (1977) shows regular meandering, unlike either *Gordia* or *Helminthopsis*, and could possibly be regraded as an example of "*Helminthoida*"; Chamberlain (1977, p. 12) identifies it as a pascichnion.

⁵ Noted by Chamberlain (1977, p. 14) as "probably a variant of *Alcyonidiopsis*", which is significantly at odds with his interpretation of it as a cubichnion or domichnion (the former is favoured herein). However, as illustrated (Chamberlain, 1977, Figures 2b' and 7G), it appears sufficiently distinct to warrant inclusion. Pemberton, Frey and Bromley (1988, p. 870, 888) regard *Mammillichnis* as a valid ichnogenus.

⁶ The brief descriptions of *Megagraption* (Chamberlain, 1977, p. 14; 1979, p. 17) indicate that although observed in hyporelief it is interpreted to be an endogenic structure; the illustrated specimens (Chamberlain, 1977 Figures 3H, 4E) show no indication that they are other than overlapping and interpenetrating simple burrows; their intersecting at an angle giving the appearance of a network. Considered more likely to be a simple repichnion than an agrichnion.

⁷ *Taenidium* is considered a pascichnion by Chamberlain (1977, p. 18); only one of the three specimens illustrated (Figure 3F) shows strophotactic behaviour, although this is quite regular.

⁸ Chamberlain (1977) uses *Tomaculum* for the individual pellets within *Alcyonidiopsis*, but also notes their occurrence "as isolated pellets clustered on same surface" (Chamberlain (1977, p. 20), therefore the ichnogenus is included here, as a fodinichnion as the pellets are presumably fecal.

⁹ "*Zonarites*" is described as "similar to *Chondrites*" (Chamberlain (1977, p. 20), and therefore is not included here.

¹⁰ Recorded as present in Figure 2 of Chamberlain (1979, p. 20, as number 4), but not recorded in Table 2 of Chamberlain (1977) and therefore not included here.

26: Matapedia Group, New Brunswick, Canada

References: Pickerill (1980, 1987, 1989) Pickerill, Fyffe and Forbes (1987, 1988)

Age: Upper Ordovician to Early Silurian¹

Assemblage²: *Chondrites* **F**, *Circulichnis* **O(R)**³, *Cochlichnus* **R**⁴, *Compaginatichnus*⁵ **F/R**⁵, *Cruziana* **R**, *Dictyodora* **P**⁶, *Dimorphichnus*⁷ **F/R**⁸, *Diplichnites*⁹ **R**, *Glockerichnus*¹⁰ **F**¹⁰, *Gordia*, **R** "*Helminthoida*" **P**, *Helminthopsis* **R**, *Megagraption* **A**¹¹, *Monocraterion* **D**, *Neonereites* **R**, *Nereites* **P**, *Palaeophycus* **R**, *Phycosiphon* **F**, *Planolites* **R**, *Rusophycus* **C**, *Scolicia* **R**, *Taenidium*¹² **R**, *Tuberculichnus* **F**, *Yakutatia* **A/F**¹³, "arthropod trace" **R**

¹ At Runnymede, the Matapedia Group is Upper Ordovician in age; the Tobique River section is Upper Ordovician to Lower Silurian, based on correlation with Maine; around Matapedia, the sections are unfossiliferous and probably Lower Silurian in age (Pickerill *pers. comm.*).

² Pickerill (1980) illustrated material from the Grog Brook and Matapedia Groups; each can be distinguished using the figure captions.

³ See also comments under Data Point 16 note 3.

- ⁴ There is no evidence that *Cochlichnus* ("preserved in positive convex (?epirelief or hyporelief) semi-relief parallel to stratification" [Pickerill et al., 1987, p. 82, Figure 3c]) is other than a post-depositional trace.
- ⁵ Pickerill, Fyffe and Forbes (1987) record the presence of *Syncoprulus* (= *Alcyonidiopsis*, in Pickerill (1980)); Pickerill (1989) illustrated that at least some examples of this, and *Scalartituba* (Pickerill, 1987), are preservational variants of *Compaginatichnus*. Neither are therefore recorded here, although Pickerill (1989) does not cite the example of *Syncoprulus* figured in Pickerill et al. (1987, Figure 5b) as part of *Compaginatichnus*. This trace fossil appears to combine locomotion (meniscate infill) with feeding (?fecal pellet infill); as with *Alcyonidiopsis* the primary function is interpreted to be feeding, and the secondary locomotion.
- ⁶ Present as two ichnospecies, *D. tenuis* and *D. scotica*, the latter of which exhibits highly systematic behaviour (Pickerill et al., 1987, Figure 3e).
- ⁷ Described in the text as *Dimorphichnus* by Pickerill et al. (1987, p. 83), but the figure cited (Figure 4a) is captioned *Diplichnites*.
- ⁸ Is characterized by a series of long raking imprints produced by the appendages of arthropods (often in Palaeozoic marine strata attributed to trilobites). Has been interpreted as either a feeding trace, or locomotion at an angle to a current.
- ⁹ The same specimen of *Diplichnites* is figured in Pickerill (1980, Figure 3a) and Pickerill (1981, Figure 5f), but recorded as from the Matapedia Group and Siegas Formation, respectively. However, as another specimen is also figured from the Matapedia Group (Pickerill et al., 1988, Figure 2b), the ichnogenus can be included.
- ¹⁰ Recorded as "*Glockeria*" in Pickerill (1980, Figure 5c) but illustrated with a different specimen; here both are included under *Glockericchnus*. "Incomplete stellate trace preserved in negative ?epirelief, parallel to stratification, ... [with] ... burrows which radiate out from a diffuse and poorly-preserved center" (Pickerill et al., 1987, p. 83); there is no evidence that would suggest this is a graphoglyptid rather than a post-depositional fodinichnion; notably the individual shafts or rays ('burrows' of Pickerill et al., 1987, p. 83) apparently coalesce centrally (see Data Point 18, Note 2).
- ¹¹ Clearly a polygonal network (as opposed to a series of overlapping/interpenetrating individual burrows; see for example, Data Point 5, Note 5, Data Point 21, Note 3 and Data Point 25, Note 6). Preserved in negative epirelief, it could represent the counterpart to a secondary cast of an open burrow structure. Pickerill et al. (1988, p. 143) note it represents either this or a surface trace. Confidently identified as an agrichnion.
- ¹² Recorded as *Muensteria* in Pickerill et al. (1987); changed to *Taenidium* in Pickerill et al. (1988).
- ¹³ *Yakutatia* is preserved in positive hyporelief, and "the infill is identical to surrounding host material" (Pickerill et al., 1987, p. 86, Figure 5c), both of which would be consistent with it being a secondary cast of an open burrow structure, i.e. an agrichnion. Otherwise, as a branched structure radiating from a central point (i.e. not produced by continuous locomotion), and although the branches show thigmotactic behaviour, it could be interpreted as a fodinichnion.
- 27: Siegas Formation; northwestern New Brunswick, Canada**
- References: Pickerill (1981)
- Age: early Llandovery
- Assemblage¹: *Chondrites* **F**, *Cochlichnus* **R**², *Diplichnites*³ **R**, *Fucusopsis*⁴ **R**, *Gordia* **R**, *Gyrochorte* **R**, "*Helminthoida*" **P**, *Helminthopsis* **R**, *Neonereites* **R**, *Planolites* **R**, *Protopaleodictyon*⁵ **A**, *Scalartituba*⁶ **R**, *Skolithos* **D**
- ¹ The dubious ichnogenus "*Buthrotrephis*" is not included in this list, although Pickerill (1981, p. 41) distinguished it from *Chondrites*, by the former's non-systematic branching pattern.
- ² Preservation in "convex hyporelief and more rarely in negative epirelief" (Pickerill, 1981, p. 42) (i.e. not positive epirelief) would be consistent with, but, on its own, is considered insufficient to prove, an origin as a secondary cast of an open burrow structure; the alternative, a simple repichnion, is favoured.
- ³ The same specimen of *Diplichnites* is figured in Pickerill (1980, Figure 3a) and Pickerill (1981, Figure 5f), but recorded as from the Matapedia Group and Siegas Formation, respectively. However, as another specimen is also figured from the Siegas Formation (Pickerill, 1981, Figure 2h), the ichnogenus can be included.
- ⁴ The illustrated example is also figured in Pickerill (1980, Figure 4a), but recorded as from the Grog Brook Group. However, it is actually from Siegas Quarry (the Siegas Formation) (Pickerill, *pers. comm.*) and is included here.
- ⁵ The illustrated example of *Protopaleodictyon* (Pickerill, 1981, Figure 5a) occurs on the sole of a current-fluted sandstone and is probably an incompletely preserved *Paleodictyon*. As the latter is not recorded, diversity is unaffected; the two ichnogenera are both unequivocal agrichnia.
- ⁶ *Scalartituba* as figured by Pickerill (1981, Figure 2f) closely resembles material referred to *Compaginatichnus* by Pickerill (1989); the latter ichnogenus is not recorded and diversity thus unaffected; until proven to be one view of *Compaginatichnus* it is retained as a repichnion (see also Data Point 26, note 5).

28: Llandovery strata, central west Wales

References: Orr (1995)

Age: Llandovery

Assemblage: *Chondrites* **F**, *Dictyodora* **P**, "*Helminthoida*" **P**, *Macaronichnus* **R**, *Neonereites* **R/P**¹, *Nereites* **P**², *Palaeophycus* **R**, *Planolites* **R**, *Protovirgularia* **R**, "braided trace" **P**³⁵ Occurs as both a simple repichnion (*N. uniserialis* Orr, 1995 Figure 6f) but also as a pascichnion displaying excellent thigmotactic behaviour (*N. biserialis* Orr, 1995 Figure 6e).² Various ichnospecies present and majority of examples of each, esp *N. macleayii*, show highly regular strophotactic behaviour that can be combined with excellent thigmotactic behaviour (Orr, 1995 Figures 4a,d, 6a-d); a small minority, notably examples of *N. cambrensis* (e.g. Orr, 1995 Figures 4d-f), lack both.³ Displays excellent thigmotactic behaviour without strophotactic behaviour.**29: Heceta Formation, southeastern Alaska, U.S.A.**

References: Soja (1991)

Age: late Llandovery/early Wenlock to Ludlow

Assemblage: *Chondrites* **F**, *Palaeophycus* **R**, *Planolites* **R****30: Aberystwyth Grits Group, west Wales**

References: Crimes and Crossley (1991) McCann (1989, 1990, 1993)

Age: Telychian Stage, late Llandovery

Assemblage¹: *Asteriacites* **C**, *Bergaueria* **C**, *Chondrites* **F**, *Circulichnis* **O(R)**², *Cochlichnus* **R**³, *Cosmorhapse* **P/A**⁴, *Desmograption* **A/O**⁵, *Glockerichnus* **A(F)**⁶, *Gordia* **R**, *Helicolithus* **O**⁷, *Helminthopsis* **R(P)**⁸, "*Helminthoida*" **P**, *Hormosiroidea* **O(A)**⁹, *Lorenzina* **O**¹⁰, *Megagraption* **A**¹¹, *Monomorphichnus* **F/R**¹², *Neonereites* **R**, *Nereites* **P(R)**¹³, *Palaeophycus* **R**, *Paleodictyon* **A**¹⁴, *Planolites* **R**, *Protopaleodictyon* **A(R)**¹⁵, *Spirorhapse* **G(A)**¹⁶, *Spirophycus* **P**¹⁷, *Subphyllochorda* **R**, *Taphrhelminthopsis* **R**¹ "The traces are, unless otherwise stated, preserved in semirelief as positive features on the soles of sandstones and sitstones (convex hyporelief). Fill is normally of the same sediment as the overlying bed" (Crimes and Crossley, 1991, p. 28). This, however, is, on its own, insufficient to discriminate between pre-depositional open burrows cast on the sole of a succeeding event bed and a post-depositional, bedding parallel, structure.² *Circulichnus*: McCann (1990, 1993) provides no information that can resolve the ethology of this ichnotaxon.³ *Cochlichnus*: McCann (1993, p. 3) also identifies it as in positive hyporelief; alone this is considered insufficient to suggest it is other than a simple repichnion.⁴ *Cosmorhapse*: positive hyporelief, but whether pre-, or post-depositional not determined (McCann, 1993, p. 3-4); if not agrichnion, then systematic behaviour pattern identifies it as a pascichnion.⁵ Its being incompletely preserved in positive hyporelief (McCann, 1989, Figure 2) could suggest it was a secondary cast of an open burrow structure (see Seilacher, 1977a). An unequivocal identification is not possible but, as it lacks systematic strophotactic and thigmotactic behaviour, a grazing trail (pascichnion) can be confidently excluded.⁶ *Glockerichnus* from the Aberystwyth Grits Group is illustrated by Seilacher (1977a, Figure 10a, as '*Glockeria*') as a graphoglyptid and an example, possibly the same example, studied by Crimes and Crossley (1991, p. 35) shows evidence of current erosion, indicating it to be pre-depositional. Preservation in positive hyporelief is further support for it having been an open burrow structure, preserved as a secondary cast. Evidence therefore favours it being an agrichnion, but especially as "rays meet centrally in one specimen", (Crimes and Crossley, 1991, p. 35) the possibility that it is a fodinichnion cannot be rejected (see discussion under Data Point 18, Note 2).⁷ Noted by Crimes and Crossley (1991, p. 47) as 'forming a meandering trace', although it is difficult to support this interpretation on the basis of the specimen illustrated (Crimes and Crossley, 1991, Figure 8k); considered a graphoglyptid by Seilacher (1977a). An interpretation of its ethology is not attempted.⁸ Some examples sketched by Crimes and Crossley (1991, e.g. Figures 5e, h and i) show regular meandering, approaching that of "*Helminthoida*"; Crimes and Crossley (1991, p. 37) note 'a tendency to meander' although the meanders are 'irregular'; note also erection of new ichnospecies *H. regularis* with 'burrows in fairly regular sine curves' (Crimes and Crossley, 1991, p. 38). An alternative interpretation as a pascichnion is possible.⁹ Occurs as two parallel rows of circular protrusions that alternate in position; 'may form part of a looping burrow system' (Crimes and Crossley, 1991, p. 33); considered a graphoglyptid by Seilacher (1977a) but interpretation herein is uncertain.

¹⁰ Examples of *Lorenzina* described by Crimes and Crossley (1991, p. 36) are probably incompletely preserved. This suggests, but alone is insufficient to confirm, that they are pre-depositional.

¹¹ Preservation of *Megagraption* in full relief ("full burrows"; Crimes and Crossley, 1991, p. 52) contrasts with the typical preservation of graphoglyptids, but is not uncommon for *Megagraption*. Specimens illustrated show irregular meshwork; only the two short sub-horizontally directed lengths of burrow in the upper part and lower left hand corner specimen in Figure 11e of Crimes and Crossley (1991), (which might, in any case, not be part of the network) would suggest that the specimens represent a series of overlapping burrows (contrast with Data Point 5, Note 5, Data Point 21, Note 3 and Data Point 25, Note 6 and see also Note 15). Interpreted as an agrichnion.

¹² Is characterized by a series of long raking imprints produced by the appendages of arthropods (often in Palaeozoic marine strata attributed to trilobites). Has been interpreted as either a feeding trace, and/or locomotion at an angle to a current, e.g. 'swimming-grazing trail' (Häntzschel, 1975, p. W84); sketches by Crimes and Crossley (1991, Figures 3f, g) do not favor one ethology over the other.

¹³ Single specimen identified by Crimes and Crossley (1991, Figure 9a) from Locality 12, a 'quarry several km east of Aberystwyth ... exact locality not known'. It resembles material described by Orr (1995) and may not be from the Aberystwyth Grits Group; it exhibits regular strophotactic and excellent thigmotactic behaviour. Single specimen of McCann (1990, Figures 5a, 6) is from the Aberystwyth Grits Group, but its course is straight. There is therefore some uncertainty as to whether *Nereites* from the Aberystwyth Grits Group should be classified as a pascichnion.

¹⁴ Crimes and Crossley (1991) record both *Paleodictyon* and *Squamodictyon*. McCann (1990, 1993) records *Glenodictyon* (= *Paleodictyon sensu* Crimes and Crossley, 1991) and *Squamodictyon* as sub-ichnogenera of the ichnogenus *Paleodictyon*. The latter approach is followed herein. Unequivocal agrichnion.

¹⁵ *Protopaleodictyon* is present as two ichnospecies: *P. incompositum* and *P. submontanum*. The former (Crimes and Crossley, 1991, Figures 10g-i) is unequivocally a burrow network, albeit incomplete; (Crimes and Crossley, 1999, p. 51) note 'these examples might be incomplete *Paleodictyon*'. The individual, straight, burrows branch rather than overlap and terminate where each intersects the other; the angle between any two branches is highly regular within each burrow system. In contrast, although the examples of *P. submontanum* illustrated (Crimes and Crossley, 1991, Figures 10j and k) have a greater tendency to form closed networks this is achieved by considerable overlap of burrows, the individual courses of which are curved to sinuous. The possibility that this ichnospecies represents overlapping burrows of *Planolites/Palaeophycus* affinity cannot be excluded (see also Note 11).

¹⁶ Illustrated examples of *Spirorhaphe* (Crimes and Crossley, 1991 Figures 7a, b, and, possibly, c) are planispirals that maintain fairly constant spacing between successive whorls. This confirms that they represent either an agrichnion or pascichnion; which cannot be proven. Incomplete preservation favours possibility that they represent secondary casts and thus an agrichnion (cf. *Spirophycus*; Note 17).

¹⁷ Examples of *Spirophycus* illustrated (Crimes and Crossley, 1991 Figures 7d-f) are compared to *Spirorhaphe*; however specimen in Figure 7e 'appears to be stuffed with faecal pellets' (Crimes and Crossley, 1991, p. 43) and thus more likely to be a pascichnion. Further, the preserved length of each is continuous (cf. *Spirorhaphe*; Note 16).

31: Gala and Penkill Groups; Southern Uplands, Scotland

References: Benton (1982b)

Age: late Llandovery

Assemblage¹: *Caridolites* **R**, *Chondrites* **F**, *Dictyodora* **P**², *Gordia* **R**, "*Helminthoida*" **P**³, *Megagraption* **A(R)**⁴, *Neonereites* **R**, *Nereites* **P**⁵, *Paleodictyon* **A**⁶, *Planolites* **R**, *Protovirgularia* **R**, *Skolithos* **D**

¹ An extensive survey: 29 localities visited; individual localities contained between 1 and 8 ichnogenera.

² Examples of *Dictyodora* illustrated (Benton, 1982b, Figure 2) display strophotactic and excellent thigmotactic behaviour.

³ Examples of "*Helminthoida*" illustrated (Benton, 1982b, Figures 4b, c) display strophotactic behaviour and maintain constant spacing between successive meanders; appearance superficially similar to horizontal sections through wall structure of *Dictyodora*, but lacks vertical component of latter; very similar to material described (and distinguished similarly) by Orr (1995).

⁴ *Megagraption* is preserved in positive hyporelief (consistent with interpretation as an agrichnion) (Benton, 1982b, p. 79) and illustrated specimen (Benton, 1982b, Figure 8c) includes many examples of true Y-shaped branching (notably at the bottom centre of illustration), consistent with it being a network. Occasionally, however, branches appear to overlap each other; this could arise by juxtaposition of two or more network systems, but, although unlikely, interpretation as a simple repichnion cannot be entirely excluded.

⁵ Illustrated examples of *Nereites* include material with systematic strophotactic and excellent thigmotactic behaviour (e.g. Benton, 1982b, Figures 6a and, less obviously, 6b); as with material described by Orr (1995; Data Point 28) these behaviour patterns appear to most prevalent in *N. macleayi* (*N. macleayi* of Benton, 1982b; see Orr (1995, p. 277) for discussion of use of these ichnospecific suffixes).

⁶ Unequivocal agrichnion, present as both *Squamodictyon* and *Glenodictyon*; see also Data Point 30, Note 14.

32: unnamed succession at Quidong, southern N.S.W., Australia

References: Webby (1969)

Age: Lower Silurian

Assemblage¹: *Paleodictyon* **A**², ?*Gordia* **R**

¹ Paper is description of certain ichnotaxa and does not give impression of having been a comprehensive study of the ichnofaunal assemblage; implications for diversity of fauna limited.

² Incomplete example of *Paleodictyon* preserved in positive hyporelief in Webby (1969, Plate 10, Figure 8); unequivocal agrichnion.

33: Prague Basin, Czechoslovakia

References: Mikulás (1992)

Age: Llandovery

Assemblage: *Alcyonidiopsis* **F(R)**¹, ?*Arenicolites*² **D**, [*Buthotrephis*³], *Chondrites* **F**, *Circulichnis* **O(R)**⁴, *Neodictyon* **A**⁵, *Planolites* **R**, ?*Rhabdoglyphus* **R**, *Taenidium* **R**

¹ Combines locomotion and, as burrows are pellet-filled, deposit feeding (Mikulás, 1992, p. 222); latter considered significant, hence fodinichnion favoured.

² Mikulás (1992, p. 222) does not exclude possibility that this is *Diplocraterion*; both are examples of domichnia.

³ Referred to *Chondrites*, therefore not included here.

⁴ Mikulás (1992, p. 223) provides no information that can resolve the ethology of this ichnotaxon.

⁵ Mikulás (1992, p. 224) erects this new ichnogenus, but notes their being 'horizontal networks ... consisting of polygonal meshes'. Although 'it is very likely that the specimens belong to pascichnia', this is inconsistent with 'their morphological resemblance to *Paleodictyon* ... and *Protopaleodictyon* ... [and] ... suggests functional similarities'; herein considered an agrichnion. Probably should be accommodated within *Paleodictyon*, but as latter is not recorded, diversity is unaffected.

34: lower part of Wulff Land Formation, Greenland

References: Pickerill and Harland (1988)

Age: early Wenlock

Assemblage: *Chondrites* **F**, *Gordia* **R**, *Helminthopsis* **R**, *Megagraption* **A**¹, *Muensteria*² **P(R)**³, *Neonereites* **R**, *Nereites* **R(P)**⁴, *Paleodictyon* **A**⁵

¹ Preserved incompletely with 'washed-out' appearance in positive hyporelief on the current-marked sole of sandstone bed, suggesting a pre-depositional origin; fill appears similar to matrix; interpreted as an agrichnion.

² = *Taenidium*; see note added in proof by Pickerill and Harland (1988).

³ Described as 'curved to irregularly meandrine' (Pickerill and Harland, 1988, p. 125), the illustrated example (Pickerill and Harland, 1988, Figure 4d) appears to exhibit strophotactic behaviour and maintain constant spacing between successive meanders, suggestive of systematic behavior.

⁴ Described as 'variably and irregularly sinuous to meandering burrows' (Pickerill and Harland, 1988, p. 128), the illustrated example (Pickerill and Harland, 1988, Figure 4e) exhibits no regular strophotactic behaviour and lacks thigmotactic behaviour; interpretation as a repichnion is the favoured alternative.

⁵ Incompletely preserved in positive hyporelief on the sole of a sandstone bed suggesting a pre-depositional origin; fill appears similar to matrix; unequivocal agrichnion.

35: Waterville Formation, Waterville, Maine

References: Orr and Pickerill (1995)

Age: early Silurian

Assemblage¹: *Chondrites* **F**, ?*Dictyodora*² **P**, *Euproopichmus* **R**, *Neonereites* **R**, *Nereites* **P**³, *Protovirgularia* **R**, *Rusophycus* **C**, *Planolites* **R**

¹ Based on a study of museum specimens and fieldwork by PJO.

² No new material of *Dictyodora* was observed by Orr and Pickerill (1995, p. 406) and its occurrence in the assemblage is based on a re-interpretation of Emmons' (1844) original illustrations. If this interpretation is correct the specimens exhibit strophotactic behaviour, maintain a constant spacing between successive meanders and can be interpreted as a pascichnion.

³ Several ichnospecies present of which *N. macleayii* repeatedly, and *N. cambrensis* occasionally, show either strophotactic behavior while maintaining constant spacing between successive meanders (e.g. Orr and Pickerill, 1995, Figures 2C and 4F) or strophotactic and thigmotactic behavior (e.g. Orr and Pickerill, 1995, Figures 4A, 4D and E).

36: ?Cape Phillips Formation, Cornwallis Island, Arctic Canada¹

References: Narbonne (1984)

Age: Ludlow²

Assemblage³: *Chondrites* **F**, *Magaratichnus?* **R**, *?Neonereites* **R**, *Palaeophycus* **R**, *Phycodes* **F**, *Skolithos* **D**, *Teichichnus* **F**

¹ Depositional setting is interpreted as "basin-slope below storm wave base" Narbonne (1984, p. 402) in a very calm, poorly-oxygenated, environment.

² See Narbonne (1984, Figure 2).

³ Ichnofauna present in the upper 10m of this unit was not included as this part of the section was deposited "near storm wave-base along the shelf-slope transition" (Narbonne (1984, p. 402).

37: Cheshires Creek (Cookman Formation) and at Gowan Green; central-western N.S.W., Australia

References: Webby (1969)

Age: Upper Silurian

Assemblage¹: *Cosmorhaphé* **P(A)**², *Granularia* **F/R**³, *Paleodictyon* **A**⁴, "unnamed branching trace" **O**

¹ Assemblage includes specimens with two superimposed orders of meandering, and a single order of meandering (Webby, 1969, Plate 10, Figures 1 and 2, respectively), both assigned to *Cosmorhaphé*. Latter could be referred to "*Helminthoida*".

² Webby (1969, p. 83-84) discusses possible modes of preservation but there is little detail that resolves the ethology of this example of *Cosmorhaphé*. Continuity of specimens (Webby, 1969, Plate 10, Figures 1 and 2) along their length is notable, favoring post-depositional origin as a pascichnion.

³ Text (Webby, 1969, p. 88) makes reference to 'branching' in what are sinuous trails (suggesting continuous locomotion); this discrepancy forms basis for uncertainty re its ethology.

⁴ Incomplete example of *Paleodictyon* from Cheshires Creek (Cookman Formation) preserved in positive hyporelief illustrated in Webby (1969, Plate 10, Figure 4); an unequivocal agrichnion.

38: northern Hall Land, Greenland

References: Pickerill, Hurst and Surlyk (1982)

Age: Silurian

Assemblage¹: *Cochlichnus* **R(G)**², *Planolites* **R**, *Scolicia* **R**, "unnamed horseshoe burrow" **O(D)**³

¹ Assemblage comprises GGU collections 230195 and 230197, both collected from locality 4 in Figure 1 of Pickerill, Hurst and Surlyk (1982). Note that an "unnamed horseshoe burrow" also occurs in GGU collections 230278 and 230279 from the Cambrian Polkorridoren Group, north Peary Land, Greenland (locality 1 in Figure 1 of Pickerill, Hurst and Surlyk, 1982). See Data Point 15.

² No description or illustration of material precludes rejecting it as a graphoglyptid *sensu* Seilacher (1977a), although as no other example of *Cochlichnus* in the data set has been unequivocally identified as such, this is considered the less likely alternative.

³ The ethology of the informal ichnotaxon "unnamed horseshoe burrow" is impossible to assess; the 'horseshoe' shape may suggest an ethology similar to *Arenicolites*, *Diplocraterion* or *Rhizocorallium*.

39: Argentina

References: Aceñolaza (1978)

Age: Silurian-Devonian¹

Assemblage: *Chondrites* **F**, *Cosmorhaphé* **R**², *Dictyodora* **P**³, *Dimorphichnus* **F/R**⁴, *Gordia* **R**, *Paleodictyon*⁵ **A**, *Planolites* **R**, *Scolicia* **R**, *Zoophycos* **F**

¹ Note poor stratigraphic control.

² Although text makes reference to meandering (Aceñolaza, 1978, p. 56), as illustrated (Aceñolaza, 1978, Plate IV, Figure 6), it exhibits no systematic behaviour and is regarded herein as a repichnion. Probably could be referred to *Helminthopsis*; diversity of the assemblage would be unaffected.

³ Specimen figured by Aceñolaza (1978, Plate IV, Figure 8) is interpreted herein as a horizontal cross-section through the 'wall' structure; clearly has vertical component and the overall form is very similar to examples of *D. zimmermani* illustrated by Orr (1996, Figure 4a-c). Exhibits strophotactic behavior and successive meanders maintain constant spacing; the basal burrow itself may even have been thigmotactic (see three-dimensional reconstruction of *Dictyodora* by Benton and Trewin (1980, Text-Figure 1C)).

⁴ Is characterized by a series of long raking imprints produced by the appendages of arthropods (often in Palaeozoic marine strata attributed to trilobites). Has been interpreted as either a feeding trace, or locomotion at an angle to a current.

⁵ Mis-spelt 'Paleocityon' on caption to Plate III of Aceñolaza (1978); preserved in positive hyporelief, locally incomplete, with washed out appearance; unequivocal agrichnion.

40: Nereitenquarzit, Germany

References: Benton (1982a; see Figure 9)

Age: Emisian, Lower Devonian¹

Assemblage²: *Agrichnium* P³, *Chondrites* F, *Lophoctenium* F, *Neonereites* R, *Nereites* P⁴, *Phycosiphon* F, *Protopaleodictyon* A⁵, *Protovirgularia* R, "burrows" O

¹ Dated as Emisian on the basis of tentaculitids and other fossils by Steinback (1974, p. 208, 247).

² Database equals 250 specimens.

³ The ethology of this ichnotaxon is uncertain; as illustrated by Benton (1982a, Figure 5A) it shows excellent thigmotactic behaviour, and towards the right hand side (as a single U-shaped termination) strophotactic behaviour, hence interpretation as a pascichnion. Benton's illustration is based on a specimen illustrated by Pfeiffer (1968); which is not stated, though it is almost certainly the holotype of *A. bruhmi* (Pfeiffer, 1968, Plate III, Figure 5). The ichnotaxon may be a junior synonym of *Nereites*, or as used herein '*Helminthoida*'; until this is clarified it is retained. However, the morphology of this ichnospecies appears to differ from that of *Agrichnium* from the 'Kulm' (Pfeiffer, 1968, Plate III, Figure 4); see data point 45.

⁴ Incomplete specimen illustrated by Pfeiffer (1968, Plate II, Figure 4) shows excellent thigmotactic behaviour; efficient coverage of the surface area can be achieved without strophotactic behaviour (i.e. via plani-spiralling), but orientation of lateral lobes in opposing directions in successive whorls suggests latter is also present.

⁵ Specimen, illustrated as a line drawing (Benton, 1982a, Figure 5K), shows a series of short, straight, shafts that extend from either side of a continuous, zig-zagging, main axis. Most of these shafts are oriented at a constant, acute, angle to the main axis and originate at the point where the main axis changes course. They therefore represent branches of a burrow network, and have not been produced via the overlap of a series of burrows of *Planolites/Palaeophycus* affinity. The overall form is, however, less regular than the example of *Protopaleodictyon* from the Culm of Germany (Data Point 45) illustrated by Benton (1982a, Figure 6S).

41: Wapske Formation (Tobique Group), Riley Brook area, northwestern New Brunswick, Canada

References: Pickerill (1991)

Age: Lower Devonian

Assemblage¹: *Chondrites* F, *Cochlichnus* R(G)¹, *Cosmorhapha* G¹, *Cruziana* R, *Helminthopsis* R, *Neonereites* R, *Palaeophycus* R, *Phycodes* F, *Planolites* R, *Protovirgularia* R, *Skolithos* D, *Taenidium* R, *Umfolozia* R, cf. *Conostichus* D²

¹ Pickerill (1991, p. 120) provides a list of ichnotaxa identified after 'preliminary analysis', but, with exception of *Neonereites*, does not discuss these further. This precludes rejecting *Cochlichnus* as a graphoglyptid *sensu* Seilacher (1977a), although as no other example of *Cochlichnus* in the data set has been unequivocally identified as such, this is considered the less likely alternative. Similarly, it cannot be determined whether is a pascichnion or agrichnion and it is thus simply coded as a graphoglyptid.

² Ethological interpretation follows Pemberton et al. (1988, p. 872)

42: Rheinisches Schiefergebirge, Germany

References: Franke and Paul (1980)

Age: Famennian, Upper Devonian

Assemblage¹: *Chondrites* F, *Helminthopsis* R², "*Helminthoida*" P², ?*Nereites* P², *Paleodictyon* A³, "spreiten-burrows of uncertain affinity" D⁴

¹ Franke and Paul (1980, p. 240) suggest that the composition of the assemblage is partly toponomically-controlled.

² Ichnotaxa illustrated as line drawings by Franke and Paul (1980, Figure 3); their distinction of 'irregular meanders' and 'regular meanders' (p. 239) is retained to identify the ethology of each of these ichnotaxa; however, Figure 3 no. 4 shows two cross-cutting burrow systems; this, and the general morphology of each, resemble the wall structure of *Dictyodora* in horizontal cross-section. This remains to be confirmed.

³ No information on the toponomy of the specimens is provided, but line drawings of them (Franke and Paul, 1980, Figures 3.8 and 3.9) indicate they represent a network with polygonal meshes, not a series of overlapping burrows of *Planolites/Palaeophycus* affinity.

⁴ Interpretation as a domichnion based on the presence of spreiten and a tendency to occur as pairs of silt-filled tubes (Franke and Paul, 1980, p. 239); paired nature suggests two limbs of a U-shaped burrow and lithological distinction from matrix suggests passive infill of an open structure.

43: Devonian strata, Nevada, U.S.A.

References: Chamberlain (1977, 1979)

Age: Devonian

Assemblage: *Alcyonidiopsis* (= *Syncoprulus*) **F(R)**¹, *Chondrites* **F**, *Gordia* **R**, *Megagraption* **A(R)**, [*Muensteria*]³, *Palaeophycus* **R**, *Planolites* **R**, [*Scalarituba*]⁴, *Taenidium* **R**

¹ Combines locomotion and, as burrows are pellet-filled, deposit feeding; latter considered significant, hence fodinichnion favoured, as suggested by Chamberlain (1977, p. 7).

² The highly schematic illustration (e.g. in Figure 3 of Chamberlain, 1979) shows a series of burrows in hyporelief. Part of this series (left hand side) shows true branching and the possible development of a polygonal pattern supporting interpretation as a burrow network, and thus a possible agrichnion. This network appears to be superimposed on a second, similar, structure; this could arise via juxtaposition, or short vertical separation, of two separate networks. However, the upper of the two networks appears to merge with the lower in the bottom right hand corner of the illustration, and an origin as a series of overlapping burrows of *Planolites/Palaeophycus* affinity, although considered less likely, cannot be excluded. See also Data Point 45, note 4.

³ Recorded as present in Devonian strata tectonically interleaved with the Palmetto Formation in Chamberlain (1979, Figure 2, as no. 13). Given its similarity, except in size, to *Taenidium* which was recorded previously (Chamberlain, 1977) it is not included here.

⁴ *Scalarituba* is recorded from locality T17 (Chamberlain, 1977, Table 1) which was noted as D? (= Devonian?). However, the locality is listed in the text as the Palmetto Formation (i.e. Ordovician in age), and the example illustrated is from the Palmetto Formation. This ichnogenus is therefore not included.

44: east coast of Menorca

References: Orr, Benton and Trewin (1996)

Age: Lower Carboniferous

Assemblage: *Arthropycus* **F**, *Chondrites* **F**, *Dictyodora* **P**¹, *Lophoctenium* **F(P)**², *Nereites*³ **P**, *Phycosiphon* **F**, *Syncoprulus* **P**⁴, "annulated burrows" **R**, "vertical burrow" **O**⁵

¹ Often displays excellent thigmotactic behaviour, usually in a planispiral (i.e. without strophotactic behaviour).

² Includes, as *L. cosmosum*, forms that represent continuous locomotion (producing meniscate infill) accompanied by excellent thigmotactic behaviour (e.g. Orr et al., 1996, Figures 8E and F); the other ichnospecies of *Lophoctenium* present represent fodinichnia. See also Data Point 47, Note 4.

³ *Neonereites* is also present but is *exclusively* a preservational variant of *Nereites*, and is therefore not included; specimens of *Nereites* can show excellent strophotactic and thigmotactic behaviour (Orr et al., 1996, p. 245).

⁴ *Syncoprulus* (or *Alcyonidiopsis*) combines locomotion and, as burrows are pellet-filled, deposit feeding; often sinuous (e.g. Orr et al., 1996, Figure 9D) it can also display strophotactic and highly developed thigmotactic behaviour (e.g. Orr et al., 1996, Figure 9E), hence interpretation as P, not F(R).

⁵ No ethological interpretation of this morphologically simple structure is attempted.

45: Culm, Germany

References: Benton (1982a; see Figures 6 and 9)

Age: Lower Carboniferous¹

Assemblage: *Agrichnium* P/F², *Chondrites* F, *Cylindrichnus* D, *Dictyodora* P, *Laevicyclus* C/D³, *Lophoctenium* F, *Megagraption* A/R⁴, *Neonereites* R, *Nereites* P, *Paleodictyon*⁵ A, *Palmichnium* R, *Phycosiphon* F, *Protopalaeodictyon* A⁶, *Protovirgularia* R, *Scolicia*⁷ P, *Taenidium* F, *Volkichnium* F

¹ Data from the Unterkulm and Oberkulm are combined; database of 650 specimens. *Guilielmites* is considered a pseudofossil (see Häntzschel, W175) and is therefore not included.

² The ethology of this ichnotaxon is uncertain; as illustrated by Benton (1982a, Figure 6A) it shows excellent thigmotactic behaviour, although strophotactic behaviour is not obvious. Benton's illustration is based on a specimen illustrated by Pfeiffer (1968); which is not stated, though it is almost certainly part of the specimen of *A. fimbriatum* illustrated in Pfeiffer (1968, Plate III, Figure 4) and Häntzschel (1975, Figure 22). In apparently possessing a central axis, and its overall pinnate form, it bears a superficial resemblance to supposed examples of "*Oldhamia*" from the Ordovician of Barrancos, Portugal (see, for example, Seilacher, 1974; Figure 2; 1977b, Figure 4); original material is figured but not described by Delgado (1910, Plate XXXVIII, Figure 1). Although this taxonomy, to my knowledge, has never been formalized, the Barrancos material represents a fodinichnion, hence the alternative suggestion herein re the ethology of *Agrichnium*. The morphology of this ichnotaxon appears to differ from that of *Agrichnum* from the Nereitenquarzit, Germany (Pfeiffer, 1968, Plate III, Figure 5); see Data Point 40, note 3.

³ Benton (1982a, p. 123) notes this ichnotaxon 'may represent the top of' the vertical/sub-vertical burrows of *Cylindrichnus*, hence alternative suggestion as regards ethology; if confirmed, diversity of the assemblage should reduce by one.

⁴ While the upper part of the illustration of *Megagraption* (Benton, 1982a, Figure 6R) clearly shows a network structure, this is continuous with a similar network in the lower part of the figure, part of which underlies (as illustrated; specimen orientation unknown) the former. The possibility that the material represents a series of overlapping burrows of *Planolites/Palaeophycus* affinity cannot be excluded. See also Data Point 43, note 2.

⁵ As *Glenodictyon*; a clearly defined polygonal network (Benton, 1982a, Figure 6O).

⁶ A network with incomplete polygonal meshes, not a series of overlapping burrows of *Planolites/Palaeophycus* affinity. Could represent incompletely preserved *Paleodictyon*, in which case diversity of assemblage should reduce by one.

⁷ As illustrated by Pfeiffer (1968, Plate VIII, Figure 7) could represent an epirelief view of the basal burrow of *Dictyodora*; note the central groove/ridge, and compare with Orr (1995, Figures 3c and d; 1996, Figure 4d). Displays regular strophotactic behaviour and, towards the right hand side of the figure, thigmotactic behaviour.

46: Myslejovice Formation, southeastern part of the Dražanská Vrchovina Highlands, eastern Bohemian Massif, Czech Republic

References: Lang, Pek and Zapletal (1979) Pek and Zapletal (1990)

Age: Upper Viséan, Lower Carboniferous

Assemblage¹: *Arenicolites* D, *Chondrites* F, *Cosmorhapse*² P, *Crossopodia*³ P, *Dictyodora* P⁴, *Gramularia* F/D⁵, *Phycosiphon* F, *Phyllocytes*⁶ P, *Planolites* R, *Rhizocorallium* D

¹ Also includes four informal ichnotaxa for which brief descriptions are provided (Lang et al., 1979, p. 86), which are not included here.

² Spelt incorrectly, as "*Cosmoraphe*", on p. 83 and 84 of Lang et al. (1979) who observe (p. 84; see also text-figure 5) "a medial structure oriented parallelly (sic.) to the outside margin", suggestive of the wall structure in an epirelief view of the basal burrow of *Dictyodora*; compare with Orr (1995, Figures 3c and d; 1996, Figure 4d). However, Lang et al. (1979, p. 83) observed 'second order meanders', a diagnostic feature of *Cosmorhapse*, although these are not obvious in the accompanying figures (Lang et al., 1979 Plate VI, Figure 1, text-figure 5). No evidence that it is a graphoglyptid *sensu* Seilacher (1977a). Appears to vary in the extent of its relief, and surface of splitting lacks any evidence that it is a bed sole (Lang et al., 1979 Plate VI, Figure 1); presumably an epirelief view which given presence of strophotactic behaviour, albeit poorly developed, favours pascichnion rather than agrichnion.

³ Contrary to Lang et al. (1979, p. 84) who claimed 'trace without median furrow', a medial structure appears to be present (Lang et al., 1979 Plate VI, Figure 2), and resembles the wall structure in an epirelief view of the basal burrow of *Dictyodora*; compare with Orr (1995, Figures 3c and d; 1996, Figure 4d). Can display strophotactic behaviour and constant spacing between successive meanders (Lang et al., 1979 Plate VII, Figure 2), hence interpreted as a pascichnion.

⁴ Unequivocal examples of *Dictyodora* (Lang et al., 1979 Plate VIII, Figures 3 and 4) observed as horizontal structures through the wall structure exhibit spiralling and strophotactic behaviour while maintaining a constant spacing apart; the basal burrow itself may even have been thigmotactic (see three-dimensional reconstruction of *Dictyodora* by Benton and Trewin (1980, Text-Figure 1C)).

⁵ The example in Plate VII Figure 1 of Lang et al. (1979) apparently shows a series of branches radiating from a common origin; other examples are less obvious (Lang et al., 1979 Plate VII Figures 2 and 3) or show what appears to be branches extending from a continuous, bedding parallel, burrow (Lang et al., 1979 Plate VIII, Figure 2); "surface is covered by fine granules"

(presumably pellets) (Lang et al., 1979, p. 65 and 80). It is not clear if these infill the interior or are a wall lining, and, thus, a fodinichnion or domichnion, respectively.

⁶ No lateral lobes are present: Lang et al. (1979, p. 66 and 81) suggest that this is toponomic; possibly = *Taenidium*; displays regular strophotactic behaviour with constant spacing between successive meanders (Lang et al., 1979 Plate VIII, Figure 1).

47: Stanley and Jackfork Groups (central Ouachitas), Ouachita Mtns., Oklahoma, U.S.A.

References: Chamberlain (1971a, 1971b, 1978)

Age: Upper Mississippian

Assemblage: *Asterichnus* **F**, *Biformites* **F**, *Chondrites* **F**, "*Helminthoida*"¹ **P**, *Helminthopsis*² **P**³, *Lophoctenium* **F(P)**⁴, *Paleodictyon*² **A**⁵, *Phycosiphon* **F**, *Saerichnites*⁶ **A**⁷, *Scalarituba* (= *Nereites*)⁸ **R**⁹, *Spirophycus*² **A**¹⁰, *Sustergichnus* **R**, *Taenidium* **R**, *Mammilichnis* **C(F)**¹¹, ?*Scolicia* **R**, cf. *Belorhappe*⁶ **A**⁷, "annulated mantle burrows"⁶ **O**¹²

¹ Addition in Chamberlain (1971b, Table 2).

² Chamberlain (1971a, Table 2) states that *Helminthopsis* (mis-spelt as Helmenthiopsis), *Paleodictyon* and *Spirophycus* are "endogenic; scour cast hyporelief"; see also comments on p. 231 on *Spirophycus*; although all are regarded by Chamberlain as pascichnia (the ethology agrichnia was defined subsequently: Ekdale et al., 1984) they are differentiated from *Scalarituba* and *Sustergichnus*.

³ Illustrated examples of *Helminthopsis* (Chamberlain, 1971a, Text Figure 8K, Plate 32 Figure 6), except for that in Plate 32 Figure 11, display regular strophotactic behaviour and maintain constant spacing between successive meanders; Chamberlain (1971a, p. 238, caption to Text-Figure 8) notes "regularity almost sufficient to be referred to *Helminthoida*" (diversity of this assemblage would then reduce by one). There is some suggestion in Text Figure 8K of Chamberlain (1971a; see also Chamberlain and Basan, 1978, Figure 10) of a narrow median structure running the length of the burrow system, resembling the wall structure in an epirelief view of the basal burrow of *Dictyodora* (compare with Orr, 1995, Figures 3c and d; 1996, Figure 4d) and possibly passage of the basal burrow into the wall structure along the length of the burrow in the top left hand corner of Text Figure 8K. Although *Helminthopsis* is apparently preserved as a "scour cast hyporelief" (see Note 2), the specimen in Chamberlain, 1971a Plate 32, Figure 6, p. 241 caption to Plate 32) is a "full relief endogene". Interpreted as a pascichnion as opposed to an agrichnion.

⁴ Includes, as *L. cosmosum*, forms that represent continuous locomotion (producing meniscate infill) accompanied by excellent thigmotactic behaviour (e.g. Chamberlain, 1971a, Plate 32, Figure 9); the other ichnospecies of *Lophoctenium* present represent fodinichnia. See also Data Point 44, Note 2.

⁵ Three ichnospecies of *Paleodictyon* defined (as *Paleodictyon* and *Squamodictyon*; Chamberlain, 1971a, p. 228) of which one (that illustrated in Plate 31 figure 5) is recorded from the Stanley Group in Table 1 of Chamberlain (1971a). Locality 138 from which the specimen illustrated was recovered (Chamberlain, 1971a, caption to Plate 31, Figure 5) is recorded as the Atoka Formation (Chamberlain, 1971a, Appendix 1). This does not preclude similar material occurring in the Stanley Group, but see Data Point 48, Note 3. The specimen shows an incomplete, clearly defined, burrow network. Unequivocal agrichnion; see also note 2.

⁶ Additions in Chamberlain and Basan (1978, Stop 5a).

⁷ Chamberlain (1978, Table 2) records the preservation of *Saerichnites* as 'epigenic scour-cast hyporelief', and cf. *Belorhappe* as 'endogenic scour-cast hyporelief', consistent with interpretation of latter as a graphoglyptid by Seilacher (1977a). Chamberlain (1978, Figure 4) and Chamberlain and Basan (1978, Figures 10 and 11) show two possible reconstructions of *Saerichnites*, in one of which it acts as vertical outlets to a infaunal bedding parallel zig-zag burrow system similar to *Belorhappe*. Both are therefore interpreted as agrichnia; if the two ichnotaxa are preservational variants of the same open burrow system then the diversity of the assemblage should reduce by one.

⁸ *Neonereites* and *Phyllodocites* are also present but at least in part are preservational variants of *Scalarituba* (= *Nereites*) and are not included.

⁹ Chamberlain (1971a, p. 229) notes that these forms have 'irregular meanders and were 'not as strict (as early Palaeozoic *Nereites*) in their horizontal or lateral control'; they are interpreted as repichnia, not pascichnia.

¹⁰ Toponomy (see Note 2) and morphology of specimen illustrated (Chamberlain, 1971a, Plate 32, Figure 1), including local incompleteness along length and fill similar to overlying bed support interpretation as an infaunal open burrow system cast by a subsequent event-bed. Specimen illustrated is from the Atoka Formation, but the same ichnospecies is identified in the Stanley Group (Chamberlain, 1971a, Table 1).

¹¹ "exact nature of this form difficult to determine" (Chamberlain, 1971a, p. 238), but interpretation as "made by an animal resting or hiding" or "juveniles or 'egg cases' deposited in the sediment", is favoured over "peculiar preservation of the upper end of an animal working the sediment for food or packing it with fecal pellets".

¹² Not described or illustrated; ethological interpretation not attempted.

48: John's Valley Shale (central Ouachitas), Ouachita Mtns., Oklahoma, U.S.A.

References: Chamberlain (1971a, 1971b, 1978)

Age: @ Mississippian/Pennsylvanian boundary

Assemblage¹: *Chondrites* **F**, *Lophoctenium* **F**², *Paleodictyon*³ **A**, *Phycosiphon* **F**, *Scalarituba* (= *Nereites*)⁴ **R**⁵, *Sustergichmus* **R**, *Taenidium* **R**¹ A questionable occurrence of ?*Scolicia* is not included.² *L. cosmosum* absent (Chamberlain, 1971a, Table 1); the other ichnospecies of *Lophoctenium* present represent fodinichnia. See also Data Point 47, Note 4.³ Chamberlain (1971a, Table 1) does *not* record *Paleodictyon* from the John's Valley Shale; however, the figure caption to Plate 32 Figures 6 and 7 identifies these specimens as from his locality 1 which in the Appendix (p. 243) is listed as from this lithostratigraphical unit, and in his Text-Figure 1 is located (about 10 miles west of Talihina) south of the Ti Valley Fault which separates the "central Ouachitas" from the more northerly "frontal Ouachitas" (Chamberlain, 1971a, Text-Figure 2). This conclusion is possibly supported by reference to Stop 6 of Chamberlain and Basan (1978, p. 52) in which *Paleodictyon* (possibly more than one ichnospecies thereof; see Chamberlain and Basan, 1978, Figure 11) occurs in the John's Valley Shale. Stop 6 is south of the Ti Valley Fault (Chamberlain and Basan, 1978, Figure 6) and thus would be, by reference to Chamberlain (1971a), in the "central Ouachitas" although the locality itself is labelled by Chamberlain and Basan (1978, p. 52) as in the "frontal Ouachitas". The stratigraphical column of the region (by Briggs and Roeder, 1975 Figure 3, (note: in Chamberlain, 1978)) identifies the John's Valley Shale (as the John's Valley Formation) in the stratigraphical succession of the central Ouachitas only; the accompanying text, however, (op cit., p. 5) refers to the 'Johns Valley Shale' and 'Johns Valley Formation in the frontal Ouachitas'. Independent of the exact tectono-stratigraphic setting of this lithostratigraphic unit it clearly contains *Paleodictyon* which probably should be included here. Material clearly represents an agrichnion.³ *Neonereites* and *Phyllocytes* are also present but at least in part are preservational variants of *Scalarituba* (= *Nereites*) and are not included.⁴ Chamberlain (1971a, p. 229) notes that these forms have 'irregular meanders and were 'not as strict (as early Palaeozoic *Nereites*) in their horizontal or lateral control'; they are interpreted as repichnia, not pascichnia.**49: Atoka Formation (central and frontal Ouachitas¹), Ouachita Mtns., Oklahoma, U.S.A.**

References: Chamberlain (1971a, 1971b, 1978)

Age: Lower Pennsylvanian

Assemblage: *Asterichnus* **F**, ?*Biformites* **R**, *Chondrites* **F**, *Conostichus* **C**, *Helminthopsis*² **P**³, *Laevicyclus*⁴ **O**, *Lophoctenium* **F(P)**⁵, *Mammilichnis* **C(F)**⁶, *Paleodictyon*^{2,7} **A**⁸, *Parahaentzschelinia* **F**, *Phycosiphon* **F**, *Scalarituba* (= *Nereites*)⁹ **R**¹⁰, *Scolicia* **R**, *Spirophycus*² **A**¹¹, *Stelloglyphus* **F/O**¹², *Sustergichmus* **R**, *Taenidium* **R**, cf. *Belorhaphé*⁴ **A**¹ Chamberlain (1971b, p. 34) interprets the Atoka Formation in the frontal Ouachitas as a slope environment, partly on the basis of the trace fossil assemblage. Lithologically, it is very similar to the Atoka Formation in the central Ouachitas (see Chamberlain, 1971b, Table 1).² Chamberlain (1971a, Table 2) states that *Helminthopsis* (mis-spelt as Helmenthiopsis), *Paleodictyon* and *Spirophycus* are "endogenic; scour cast hyporelief"; see also comments on p. 231 on *Spirophycus*; although all are regarded by Chamberlain as pascichnia (the ethology agrichnia was defined subsequently: Ekdale et al., 1984) they are differentiated from *Scalarituba* and *Sustergichmus*.³ Illustrated examples of *Helminthopsis* (Chamberlain, 1971a, Text Figure 8K, Plate 32 Figure 6), except for that in Plate 32 Figure 11, display regular strophotactic behaviour and maintain constant spacing between successive meanders; Chamberlain (1971a, p. 238, caption to Text-Figure 8) notes "regularity almost sufficient to be referred to *Helminthoida*" (diversity of this assemblage would be unaffected). There is some suggestion in Text Figure 8K of Chamberlain (1971a; see also Chamberlain and Basan, 1978, Figure 10) of a narrow median structure running the length of the burrow system, resembling the wall structure in an epirelief view of the basal burrow of *Dictyodora* (compare with Orr, 1995, Figures 3c and d; 1996, Figure 4d) and possibly passage of the basal burrow into the wall structure along the length of the burrow in the top left hand corner of Text Figure 8K. Although *Helminthopsis* is apparently preserved as "scour cast hyporelief" (see Note 2), the specimen in Chamberlain, 1971a Plate 32, Figure 6, p. 241 caption to Plate 32) is a "full relief endogene". Interpreted as a pascichnion as opposed to agrichnion.⁴ Additions in Chamberlain and Basan (1978, Stop 7).⁵ Includes, as *L. cosmosum*, forms that represent continuous locomotion (producing meniscate infill) accompanied by excellent thigmotactic behaviour (e.g. Chamberlain, 1971a, Plate 32, Figure 9); the other ichnospecies of *Lophoctenium* present represent fodinichnia.

⁶ "exact nature of this form difficult to determine" (Chamberlain, 1971a, p. 238), but interpretation as "made by an animal resting or hiding" or "juveniles or 'egg cases' deposited in the sediment", is favoured over "peculiar preservation of the upper end of an animal working the sediment for food or packing it with fecal pellets".

⁷ Chamberlain (1971a and b) records *Squamodictyon* as a separate ichnogenus; it occurs in the Atoka Formation from the 'Frontal Ouachitas' and is, herein, included under *Paleodictyon*. The two ichnospecies of *Paleodictyon* identified by Chamberlain (1971a) occur in the Atoka Formation from both the 'Frontal' and 'Central Ouachitas'.

⁸ Material from Atoka Formation shows an incomplete, clearly defined, burrow network, especially specimen in Chamberlain (1971a, Plate 31, Figure 5). Unequivocal agrichnion; see also note 2.

⁹ *Neonereites* and *Phyllodocites* are also present but at least in part are preservational variants of *Scalarituba* (= *Nereites*) and are not included.

¹⁰ Chamberlain (1971a, p. 229) comments that these forms have 'irregular meanders and were 'not as strict (as early Palaeozoic *Nereites*) in their horizontal or lateral control'; they are interpreted as repichnia, not pascichnia.

¹¹ Toponymy (see Note 2) and morphology of the specimen illustrated from the Atoka Formation (Chamberlain, 1971a, Plate 32, Figure 1), including local incompleteness along length and fill similar to overlying bed support interpretation as infaunal open burrow system cast by a subsequent event-bed.

¹² *Stelloglyphus* is interpreted as either 'a feeding pattern' or 'the attempt of a small animal escaping through freshly deposited sand' (Chamberlain, 1971a, p. 241), hence interpretation as either a fodinichnion or fugichnia (latter included within Other, herein).

50: Wood River Formation, south-central Idaho, U.S.A.

References: Burton and Link (1991)

Age: Upper Pennsylvanian to Lower Permian

Assemblage¹: *Arenicolites*² **D**, *Chondrites* **F**, *Lophoctenium* **F**, *Phycosiphon* **R**³, *Phyllodocites* **O**⁴, *Spirophycus* **R**⁵, *Taenidium* **R**, *Zoophycos* **F**

¹ Burton and Link (1991, p. 295) sub-divide the assemblage into pascichnia (*Phycosiphon*, *Phyllodocites*, *Spirophycus* and *Taenidium*) and fodinichnia (*Chondrites*, *Lophoctenium* and *Zoophycos*).

² Rare and does not occur associated with the other trace fossils.

³ As illustrated (Burton and Link, 1991, Figure 7f) appears to be 'sinuous to kurtotic meandering traces' (Burton and Link, 1991, Table 1), but insufficiently regular to be considered as a pascichnion.

⁴ Ethology difficult to determine from illustration (Burton and Link, 1991, Figure 7h) and description: 'Parallel, subcylindrical, occasionally branching traces flanking faint median spreite' (Burton and Link, 1991, Table 1). Material assigned to *Phyllodocites* often similar to *Nereites*; not in this case, and also not a pascichnion.

⁵ Toponymy, particularly preservation within "Te and minor Td" intervals of turbidites and 'continuous backfill lighter in color than rock matrix' (Burton and Link, 1991, Table 1) implies it does not represent an agrichnion. Although 'meandering, sinuous to kurtotic' (Burton and Link, 1991, Table 1) this is insufficiently regular to be considered a pascichnion.

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