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Data Repository Item

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 ichnogeneric 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 Helminthoida has recently been referred to Nereites (Uchman, 1995). None of the material identified as Helminthoida 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 "Helminthoida", 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 fodichnion 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 ethnologies, 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 (*Cosmorhaphe*, *Helminthorhaphe*, *Spirothorhaphe*), uniramur meanders (*Belorhaphe*, *Protopaleodictyon*, *Helicolithus*, *Punctorhaphe*, *Urohelmithoida*, *Dendrodictyon*, *Hormosiroidea*), biramous meanders (*Paleomeandron*, *Desmograpton*, *Oscillorhaphe*, *Protopaleodictyon*), radiating forms (*Tuapseichnium*, "Glockeria" (= *Glockerichnus*), *Lorenzinia*, *Yakutatia*, *Chondrorhaphe*, *Dendrorhaphe*, *Fascicichnium*) irregular forms (*Acanthorhaphe*, *Megagrapton*) regular nets (*Paleodictyon*, including the sub-ichnogenera *Glendonictyum*, *Squamodictyon* and *Ramidictyon*). A simple regularly undulating form such as *Cochlichinus* 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 ichnogenera 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 "Lorenzinia 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 ichnogenera 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, *Cosmorhaphe* has been regarded as a pascichnia by some authors or an agrichnia 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' ichnogenera from the category agrichnia 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 ichnogenus is only classified as an agrichnia (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 pascichnia or agrichnia 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 Cambrian


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 pascichnia) cannot be assessed.
3 Not described or illustrated; assignment not attempted.

2: 1 Cma unit: Niddery Lake Map Area, Selwyn Mountains, Yukon Territory, Canada
Age: early Cambrian


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' Helminthorhaphe 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, Canada

References: Hofmann, Cecile and Lane (1994)
Age: early Cambrian to early Middle Cambrian

Assemblage: "Helminthoidichnites R, Planolites R, hemispherical protrusions C"

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, Canada

References: Hofmann, Cecile and Lane (1994)
Age: early Cambrian to early Middle Cambrian


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 Monomorphicnus 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

References: Hofmann, Cecile and Lane (1994)
Age: early Cambrian to early Middle Cambrian

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

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 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

References: Hofmann, Cecile and Lane (1994)
Age: early Cambrian to early Middle Cambrian


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

References: Hofmann, Cecile and Lane (1994)
Age: early Cambrian to early Middle Cambrian

Assemblage: Didymaulichnus 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

Age: Lower Cambrian


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 Glockericnus (Pickerill, 1982). As illustrated (e.g. Aceñolaza, 1978, Figure 9) Glockericnus 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: Bray Group, Howth Peninsula, eastern Ireland

Age: mid Lower Cambrian
Assemblage: *Arenicolites D, Granularia F(R)*\(^2\), *Planolites R, Skolithos D, Teichichnus F*\(^2\)


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
Assemblage: *Arenicolites D, "Helminthoida" \(^1\) P, Helminthopsis \(^3\) R, "Histioderma" (= Monocraterion) D, Oldhamia F, Palaeophycus R, Planolites R, Protopaleodictyon A(O)*\(^1\)

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 Cambrian\(^1\)
Assemblage: *Chondrites, F Planolites*\(^3\) 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
Age: Middle Cambrian

Assemblage \(^2\): "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 Hantzschel (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 Surlwyk (1982)

Age: Cambrian

Assemblage \(^12\): Gordia \(R\), Helminthopsis \(R\), Planolites \(R\), Protopaleodictyon \(A\), "unnamed horseshoe burrow" \(O(D)\)

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

\(^2\) Assemblage compises 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


Age: Tremadoc

Assemblage \(^2\): Arenicolites \(D\), Chondrites \(F\), Circulichnus \(O(R)\), 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 Hantzschel (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 Circulichnus could represent a local deviation from an otherwise sinuous course.

17: Ribband Group, eastern Ireland


Age: Tremadoc-Arenig

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 Belorhapha 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 Lorenzinia (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 Megagrapton and Paleodictyon to Belorhapha (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 Sublorenzinia 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


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 conspecific 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 Diplorocrat.  

19: Lévis Formation, Québec, Canada

References: Pickerill and Narbonne (1995)

Age: middle Arenig to earliest Llanvirn

Assemblage: Alcyonidiopsis F(R)3, Chondrites F, Circulichnis O(R)4, Helminthopsis R, Nereites P, Planolites R, Taenidium R, Tomaculum O1, "irregular bioturbate textures that cannot be accorded formal ichnotaxonomic status" O
The Lévis Formation as a whole spans the Middle Cambrian to lower Middle Ordovician interval; studied sections lie within stratigraphic range quoted.

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 Hántzschel (1975).

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

See comments under Data Point 16 for Circulichnis.

Occurs as isolated pellets as well as fill of Alcyonidiopsis; use of Tomaculum, Syncoprus 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), "oblique lamellae" F, "mottled background ichnofabric" O

Has been noted as cf. Ophiomorpha in data set accompanying Orr (2001) as some of the burrows show a structureless core of unpeletted 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 Ordovician
Assemblage: Helminthopsis (? or Dictyodora) R(P), Megagrapton R(A), Nereites P, "arthropod track" R, "bilobed track with median furrow" R, "meandering trail Type A cf. Cosmorhaphe" A

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.

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.

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

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

Recognized as 'meandering cast (convex hyporelief)' by Roberts (1969, p. 231); specimen in Plate I, 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 Ordovician

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 5c) 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 Poitré (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 ichnogeneric level. The curving rays meet medially (see discussion under Data Point 18, Note 2) and the specimen is preserved in positive epi relief, 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 *Cosmorhaphe* (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 *Spiropharpe* 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 Toponomy (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
Age: Upper Ordovician
Assemblage1: Arenicolites D, Cosmorhaphe P2, Granularia F3, Helminthopsis R4, Protopaleodictyon A5, Spirophycus P/A6

1 Arenicolites, Granularia, Protopaleodictyon and Spirophycus were recorded from the lower part of the Puerto de Vega section and *Helminthopsis* and *Cosmorhaphe* 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 fodi nichnion.

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

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 (1977<sup>1</sup>, 1979<sup>2</sup>)

Age: Orдовician


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 cubicichnion or domicichnion (the former is favoured herein). However, as illustrated (Chamberlain, 1977, Figures 2b<sup>1</sup> and 7G<sup>1</sup>), it appears sufficiently distinct to warrant inclusion. Pemberton, Frey and Bromley (1988, p. 870, 888) regard *Mammillichnus* as a valid ichnogenus.

6 The brief descriptions of *Megagrapton* (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**


Age: Upper Ordovician to Early Silurian<sup>1</sup>


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.
Diplichnites.  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.

7. Recorded as "Glockerichus" in Pickerill (1980, Figure 5c) but illustrated with a different specimen; here both are included under Glockerichnus.  "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).

8. 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.

9. Recorded as Muensteria in Pickerill et al. (1987); changed to Taenidium in Pickerill et al. (1988).

10. 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

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. Scalarituba 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

1 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
Age: Telychian Stage, late Llandovery

1 The traces are, unless otherwise stated, preserved in semirelief as positive features on the soles of sandstones and siltstones (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 *Cosmorhaphe*: 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 ‘Glockerida’) 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.
Examples of *Lorenzinia* 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.

Preservation of *Megagrapton* in full relief (“full burrows”; Crimes and Crossley, 1991, p. 52) contrasts with the typical preservation of graphoglyptids, but is not uncommon for *Megagrapton*. 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.

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.

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.

*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).

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. *Spirorhaphe*; Note 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

Assemblage 1: *Caridolites* *R*, *Chondrites* *F*, *Dictyodora* *P²*, *Gordia* *R*, *"Helminthoida"* *P³*, *Megagrapton A(R)⁴*, *Neonereites R*, *Nereites P⁵*, *Paleodictyon A⁶*, *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 *Megagrapton* 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. macleayii* (*N. macleayii* of Benton, 1982b; see Orr (1995, p. 277) for discussion of use of these ichnospecific suffixes).
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  
Assemblage: Paleodictyon A², ?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: Aleyoniopsis F(R)¹, ?Arenicolites² D, [Buthotrephs³], Chondrites F, Circulichnis O(R)⁴, Neodictony A⁵, 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 domicnichia.  
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, Megagrapton A¹, Muensteria² P(R)³, Neonereites R, Nereites R(P)⁴, Paleodictyon A⁵  
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  
¹ Based on a study of museum specimens and fieldwork by PJO.
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.

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 Canada**

References: Narbonne (1984)

Age: Ludlow


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

See Narbonne (1984, Figure 2).

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


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 *Cosmorhaphe*. Latter could be referred to "Helminthoida".

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

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.

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


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.

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.

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 *Rhizocrallium*.

39: **Argentina**

References: Aceñolaza (1978)

Age: Silurian-Devonian


Note poor stratigraphic control.
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.

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)).

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.

Mis-spelt 'Paleoctyon' 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 Devonian
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 Neonereites, 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/Paleophycus 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
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

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

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.

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/Paraeophycus* affinity.

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*, *Megagrapton A(R)*, *[Muensteria]*³, *Paraleophycus 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/Paraeophycus* 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: *Arthrophycus F*, *Chondrites F*, *Dictyodora P¹*, *Lophoctenium F(P)²*, *Nereites³ P*, *Phycosiphon F*, *Syncoprulus P⁴*, "annulated burrows" R, "vertical burrow" O⁵

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/F*, *Chondrites F*, *Cylindrichnus D*, *Dictyodora P*, *Laevicyclus C/D*, *Lophoctenium F*, *Megagrapton A/R*, *Neoneites R*, *Nereites P*, *Paleodictyon A*, *Palminichnium R*, *Phycosiphon F*, *Protopaleodictyon A*, *Protovirgularia R*, *Scolicia P*, *Taenidium F*, *Volkichnium F*

1 Data from the Unterkulm and Oberkulm are combined; database of 650 specimens. *Guilielmites* is considered a pseudofossil (see Hantzschel, 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 an 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 Hantzschel (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 fadinichnion, hence the alternative suggestion herein re the ethology of *Agrichnium*. The morphology of this ichnotaxon appears to differ from that of *Agrichnium* 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 *Megagrapton* (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 Drahanská Vrchovina Highlands, eastern Bohemian Massif, Czech Republic

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

Age: Upper Viséan, Lower Carboniferous

Assemblage*: *Arencolites D*, *Chondrites F*, *Cosmorhaphe P*, *Cossropodia P*, *Dictyodora P*, *Granularia F/D*, *Phycosiphon F*, *Phyllococites 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 "Cosmorapha", 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 *Cosmorapha*, 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 granulas"
(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 fodichnion or domicnion, 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.


Age: Upper Mississippian


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 Lophocitenium present represent fodichnium. 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. Belorhaphe 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 an infaunal bedding parallel zig-zag burrow system similar to Belorhaphe. 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 Phyllocodites 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.


Age: Mississippian/Pennsylvanian boundary


1 A questionable occurrence of *Scolicia* is not included.

2 *L. cosmosum* absent (Chamberlain, 1971a, Table 1); the other ichnospieces of *Lophocentrum* 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 ichnospiece 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) 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 *Phyllococites* 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.


Age: Lower Pennsylvanian


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 *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 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 ichnospieces of *Lophocentrum* 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 Toponomy (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

Assemblage\(^1\): Arenicolites\(^2\) D, Chondrites F, Lophocentrum 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, Lophocentrum 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 kurtoctic 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 Toponomy, 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 kurtoctic' (Burton and Link, 1991, Table 1) this is insufficiently regular to be considered a pascichnion.

References.

Chamberlain, C. K. 1971b, Bathymetry and paleoecology of the Ouachita Geosyncline of southeastern Oklahoma as


McCann, T., 1993, A Nereites ichnofacies from the Ordovician-Silurian succession of the Welsh depositional basin, U.K.


