DICTYODORA FROM THE SILURIAN OF PEEBLESSHIRE, SCOTLAND

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ABSTRACT. The meandering trace fossil *Dictyodora* Weiss, 1884 occurs in deep water greywacke/shale sequences in the Gala Group (lower Silurian) of Thornylee and Grieston Quarries, Galashiels. Two species are recognized; *D. scotica* (M'Coy, 1851) and *D. tenuis* (M'Coy, 1851); the former is distinguished by a more regular meandering form. These traces were originally named *Crossopodia scotica* and *Myrianites tenuis*. It is suggested that *C. scotica* be rejected as the type species of *Crossopodia*.

THORNYLEE QUARRY (Grid ref. NT 4200 3635) (formerly spelt Thornyly, Thorney Lee, Thornielee, Thornilee) is situated on the north bank of the River Tweed, 8 km east of Galashiels and 8 km west of Innerleithen. The quarry is located on a steep slope above a layby on the A72 (Peebles–Galashiels) road. Between the quarry and the road is a dismantled railway with cuttings which provide a 300 m long section through Upper Llandovery greywackes and shales (Gala Group of Lapworth 1870). The first geological description of Thornylee was given by Nicol (1850) who noted some graptolites and abundant 'annelid impressions'.

Grieston Quarry (NT 3130 3618) was also described by Nicol (1850), who noted the abundant graptolite fauna and the trace fossils. More recently the fauna and sediments of this quarry have been described by Toghill and Strachan (1970) and Trewin (1979). The thin greywackes and shales of Grieston also lie within the top of the Gala Group of Lapworth (1870), but are not exactly the same age as those at Thornylee on the basis of the graptolite fauna.

This study stemmed from work on H. A. Nicholson's trace fossil collection in Aberdeen (Benton and Trewin 1978). The following descriptions are based on large collections made at Thornylee and Grieston in April and June, 1977. Comparisons have been made with the type material of M'Coy and Nicholson. Repository abbreviations used are: AUGD, Aberdeen University, Department of Geology and Mineralogy Palaeontology Collection; BMNH, British Museum (Natural History); GSM, Geological Survey Museum, I.G.S., London; HM, Hunterian Museum, Glasgow; SM, Sedgwick Museum, Cambridge.

DEPOSITIONAL ENVIRONMENT AND ASSOCIATED FAUNA

At both localities deep water, interbedded greywacke/shale sequences are exposed in which the coarser lithologies are of turbidite origin. The trace fossils at Thornylee are more abundant in the shale-rich parts of the sequence rather than in association with greywacke beds. There seems to be a greater frequency of meandering traces in the purple rather than the green shales. At Grieston the greywackes are fine-grained and contain abundant ripple-lamination, possibly the results of reworking; other beds are characterized by numerous transported graptolites which produced delicate tool marks on bed bases (Trewin 1979). The greywackes at Thornylee are usually medium grained, graded, and sometimes show tool marks and load casts on the sharp bed bases. Internally, Bouma sequences of structures are frequently seen. The general aspect of the lithofacies is of a low-energy turbidite environment with thin greywacke turbidites and abundant shale.

At both localities graptolites are present but they are much more abundant in the finer grained rocks of Grieston Quarry, where the majority have been transported and deposited in thin turbidites.

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Tail spines of *Ceratiocaris* occur at Grieston, but no other fauna was noted. The ichnofauna dominated by meandering feeding burrows is typical of deep water muds and belongs to Seilacher's *Nereites* facies.

THE ICHNOFAUNA

Introduction. The ichnofauna is dominated by the meandering burrows of two species of *Dictyodora*, which are described below. The small burrow *Caridolites* Etheridge, Woodward and Jones, 1890 is common at both localities. Rare examples of *Nereites* were found at Thornylee and stuffed burrows, cf. *Planolites*, are also present. The meandering traces are described below with more emphasis placed on *Dictyodora scotica* in view of its taxonomic importance. A redescription is given of *Caridolites* and the association with *Nereites* briefly discussed.

Genus DICTYODORA Weiss, 1884

Taxonomic discussion of Dictyodora

Geinitz (1867) founded the species *Dictyodora liebeanum* for a 'plant' from the Culm (Lower Carboniferous) of Gera, East Germany, and Weiss (1884*a*, *b*) proposed the genus *Dictyodora* for this species. He was unable to decide if it was of plant or animal origin.

Zimmermann (1889, 1891) discussed the taxonomic problems associated with German Carboniferous *Dictyodora*, noticing that as with the British examples, different horizontal (bedding parallel) sections had been given distinct names at different times. Zimmermann (1892) gave a detailed account of the type species *D. liebeana*, and considered that the vertical wall contained no infill, but noted longitudinal and oblique streaks. Zimmermann noted that the wall tends to slope inwards towards the top, giving tighter loops than those of the basal burrow, but was puzzled by walls intersecting without disturbance. *D. liebeana* has vertical walls up to 180 mm high and a well-defined over-all cone shape distinguishing it from *D. scotica* and *D. tenuis*. Zimmermann (1892) briefly described a species, *D. hercynica*, which has a looser structure and walls 1-3 cm high, found in the Upper Devonian of the Harz mountains. It has apparently not been figured.

D. simplex Seilacher, 1955 from the Lower Cambrian of the Salt Range of Pakistan is a simple, loose structure about 6 mm deep. However, this is a structure built from successive sloping layers and Seilacher proposed that the trace was produced by a worm-like animal travelling through the sediment in an oblique position. There is no basal burrow in Seilacher's reconstruction and the 'vertical wall' is of equal width from top to bottom. We consider that these differences are sufficient to exclude *D. simplex* from the genus *Dictyodora*. No alternative generic assignment is suggested without examination of the original material.

Seilacher (1967, p. 77) figured a *Dictyodora* evolutionary sequence from relatively loosely structured forms in the Lower Palaeozoic to tightly spiralling patterns in the Carboniferous. In grade of organization, *D. tenuis* appears similar to Seilacher's most primitive type (a) and *D. scotica* is slightly more advanced.

Pfeiffer (1959) reviewed previous work on *D. liebeana* and gave good three-dimensional reconstructions of Carboniferous examples. Müller (1962) also described the morphology of German Lower Carboniferous *Dictyodora* in detail with many figures, and Ruchholz (1967) gave further examples from the Harz mountains. Pfeiffer (1968) gave a synonomy list for *D. liebeana* (Geinitz, 1867). Müller (1971) discussed the formation of *Dictyodora* meanders, emphasizing that the trace was a feeding structure formed relatively rapidly, since the basal burrow does not change in diameter in any single specimen and since it maintains a constant depth and does not rise gradually to keep up with sedimentation.

There is thus an extensive, mainly German, literature on *Dictyodora* which establishes the characteristic features of the genus as the meandering basal burrow and the dorsal striated wall. The species *D. scotica*, described below, has previously been given the name *Myrianites tenuis* for sections for the vertical wall and *Crossopodia scotica* for the basal burrow.

The genus *Myrianites* MacLeay, 1839 was established for a meandering track with small leaf-like extensions at the sides. The type species, *M. macleayii* Murchison, 1839 (type specimen: GSM Geol. Soc. Coll. 6824) appears to be a small *Nereites*. Species from Spain described by Delgado (1910) as *Myrianites* are certainly *Dictyodora* but are not described or figured well enough to establish synonomy with the material described here.

M'Coy (1851*a*, *b*) founded the species *M. tenuis* based on specimens of small meandering traces from Grieston Quarry. Nicholson (1978, pp. 42, 43) identified wall sections of *D. scotica* from Thornylee as *M. tenuis*, but the specific name *tenuis* is retained here for M'Coy's original material redescribed below as *D. tenuis*.

M'Coy (1851*a*, *b*) also founded the genus *Crossopodia* for two Silurian trace fossils. *C. lata* from Llandeilo, Wales, is a 2 cm wide trail with clear transverse striations and a 'fringe' which better resembles the *Crossopodia* of modern usage. *C. scotica*, however, is the form redescribed here as *D. scotica* and M'Coy's type (SM A45575a–c) clearly shows the diagnostic features (text-fig. 2). The figure of the type of *C. scotica* in M'Coy 1851*b*, pl. 1D, fig. 15, appears to be a composite of the three specimens SM A45575a–c. Fortunately all are of the same species and A45575a is more suitable as the lectotype showing well all the major features. M'Coy's figure has been reversed in the engraving process. Unfortunately, Häntzschel (1962, p. W189) designated *C. scotica* as the type species of *Crossopodia* and repeated this with a mislabelled figure of '*C. scotia*' (*sic*) in Häntzschel (1975, fig. 34, 2b). This figure is derived from Schimper and Schenk (1879, p. 52, fig. 40) and is clearly not the *C. scotica* of M'Coy (1851*a*, *b*) and Nicholson (1978).

In order to preserve the normally accepted usages of *Crossopodia* and *Dictyodora* we propose that *C. scotica* be rejected as the type species of *Crossopodia*. *C. lata* M'Coy (1851) (type specimen SM A37733) would then become the type species of *Crossopodia*. An application to this effect will be made to the I.C.Z.N. or other appropriate body, when agreement has been achieved on the rules of trace fossil nomenclature. Further revision of the genus *Crossopodia* is required, but is outside the scope of this paper.

Dictyodora scotica (M'Coy, 1851)

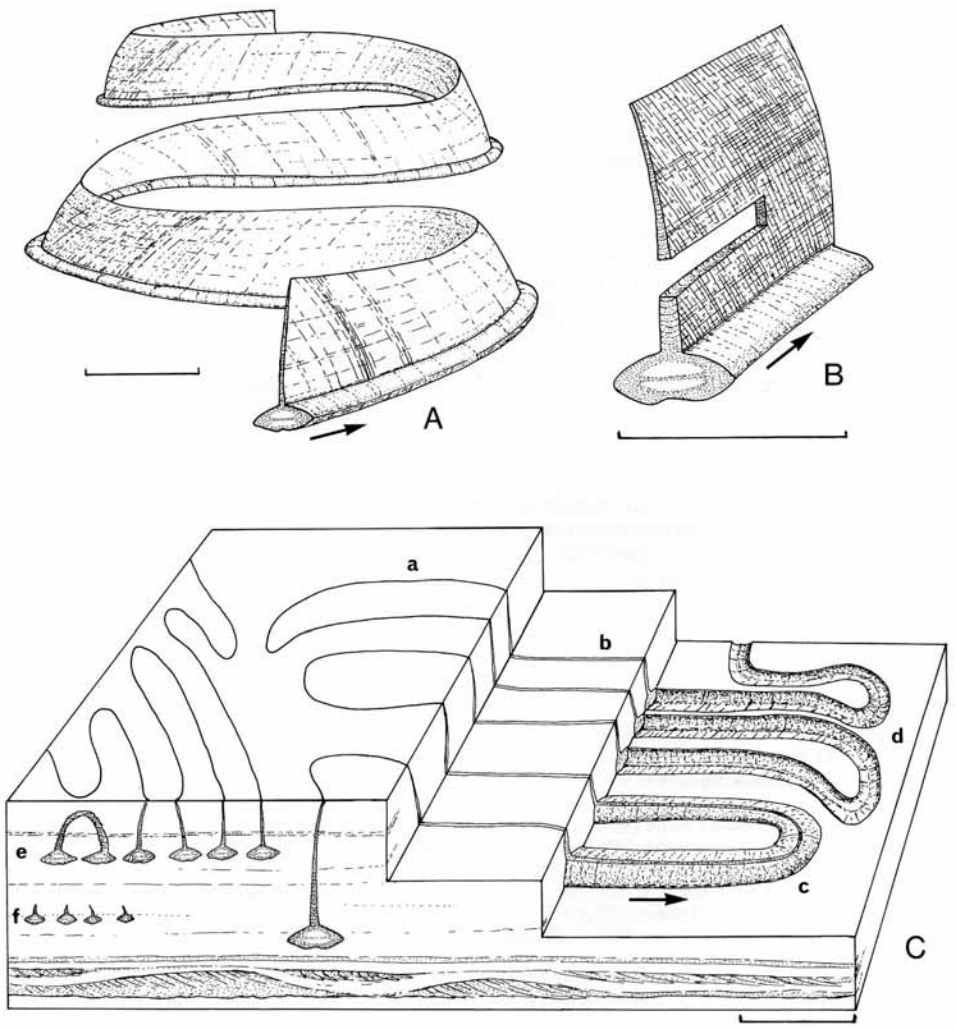
Text-figs. 1, 2, 3

v*1851*a* *Crossopodia scotica* M'Coy, p. 395.
v*1851*b* *Crossopodia scotica* M'Coy; M'Coy, p. 130, pl. 1D, fig. 15.
?1855 *Crossopodia scotica* M'Coy; Harkness, p. 475.
non 1879 *Crossopodia scotica* (M'Coy); Schimper and Schenk, p. 52, fig. 40.
non 1962 *Crossopodia scotia* (M'Coy) (*sic*); Häntzschel, p. W189, fig. 118, 2.
non 1975 *Crossopodia scotia* (M'Coy) (*sic*); Häntzschel, p. W54, fig. 34, 2b.
v1978 *Crossopodia scotica* M'Coy; Nicholson, p. 36, pl. 3, fig. 1, pl. 6.
v1978 *Myrianites tenuis* M'Coy; Nicholson, p. 42, text-fig. 7, *non* pl. 4, fig. 1. [The same specimen as in Benton and Trewin 1978, pl. 2, fig. 2.]
v1978 *Crossopodia scotica* M'Coy; Benton and Trewin, p. 8, pl. 2, fig. 1.

Lectotype. Here designated, SM A45575a, the original of M'Coy (1851*b*, pl. 1D, fig. 15). Gala Group, Upper Llandovery, lower Silurian, Thornylee Quarry, nr. Innerleithen, Peeblesshire, Scotland. Refigured here, text-fig. 2.

Other material. More than two hundred examples from the type locality, a representative selection of which are catalogued as AUGD 10693 to 10710. Also: AUGD 8819, 8820, 10606, 10723, Mus. Coll. 956, 957; BMNH 39451, 58169 (1, 2); GSM 104247, 104249, 104250, RU 2970; HM X871/1–2, X1003/1–7.

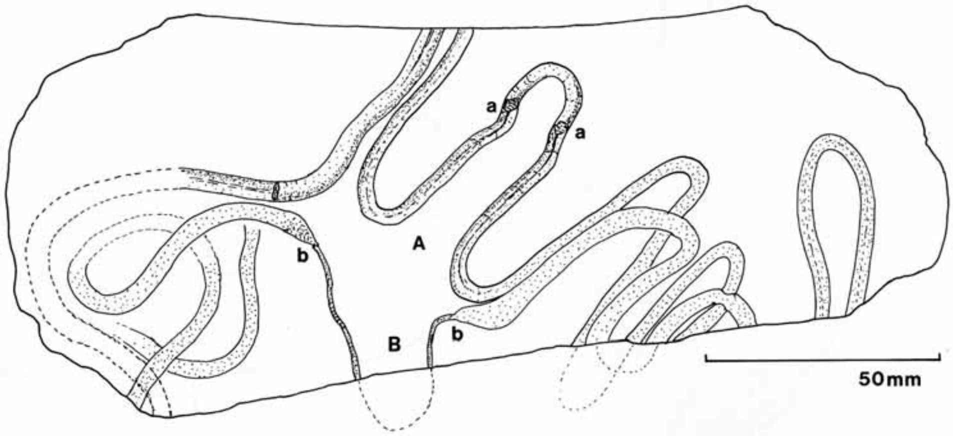
Description. The burrow system illustrated in text-fig. 1 consists of a basal burrow, generally preserved with a lenticular cross section, and having a vertical or inclined longitudinal wall arising from the dorsal mid-line of the basal burrow. The basal burrow varies from 1·5–6 mm wide and up to 3 mm high in slate lithologies, but when developed in fine sand may have a nearly circular cross section due to the small degree of compaction. The wall is up to 13 mm high and tapers upwards from a width of 1–2 mm at the base. The taper is most rapid in small examples. The typical burrow system (text-fig. 3C, D, E) consists of 5–10 parallel meanders each 10–80 mm long



TEXT-FIG. 1. Scale bars 10 mm at front faces of figures. Arrows indicate direction of travel of *Dictyodora* organism. A, general morphology of *Dictyodora* meanders showing basal burrow and wall; wall curves inwards at meander bends. B, section of burrow to show features of burrow and wall fill, horizontal striations and curved vertical/oblique striations of wall surface. C, block diagram illustrating different preservational aspects of the burrow in plan and section; *a*, narrow sections at top of wall; *b*, wider sections near base of wall; *c*, convex top of basal burrow with base of wall fill preserved on top; *d*, concave impression of underside of burrow with fill removed, a weak median ridge may be present; *e*, smaller example showing effect of sectioning the inclined wall at meander turn; *f*, juvenile burrow in section. The style of ripples and fine parallel lamination present is also illustrated on the front face of C.

(usually 30–50 mm) and internally measured at basal burrow level as 0–20 mm apart (usually 5–15 mm). Where successive meanders touch, a tight turning circle is present at the meander turn. The meanders may also be irregular and broad as in text-fig. 3A, B. The relevant features of the type specimen are illustrated in text-fig. 2.

The burrow shows various preservational aspects (text-fig. 1C) dependent on the level at which it is sectioned. Sections of the wall appear as meandering lines up to 2 mm wide, occasional sharp turns are seen in sections close to the top of the wall (text-fig. 3E) but nearer the basal burrow the wall displays smooth curves. The wall has a finite thickness and the burrow may break either side of the wall as shown in text-fig. 3B. Sections at the top of the basal burrow show the entire infill with a median ridge marking the base of the wall (text-fig. 1C). Specimens showing the lower surface of the basal burrow display a smooth groove which is sometimes double, with a weak median ridge (text-fig. 1C). The burrow may also split within the burrow fill giving very little relief to the preserved trace. Internally, a distinct pattern is frequently seen in polished or etched cross-sections of the burrow fill resulting from reorientation of platey minerals (text-fig. 1B).

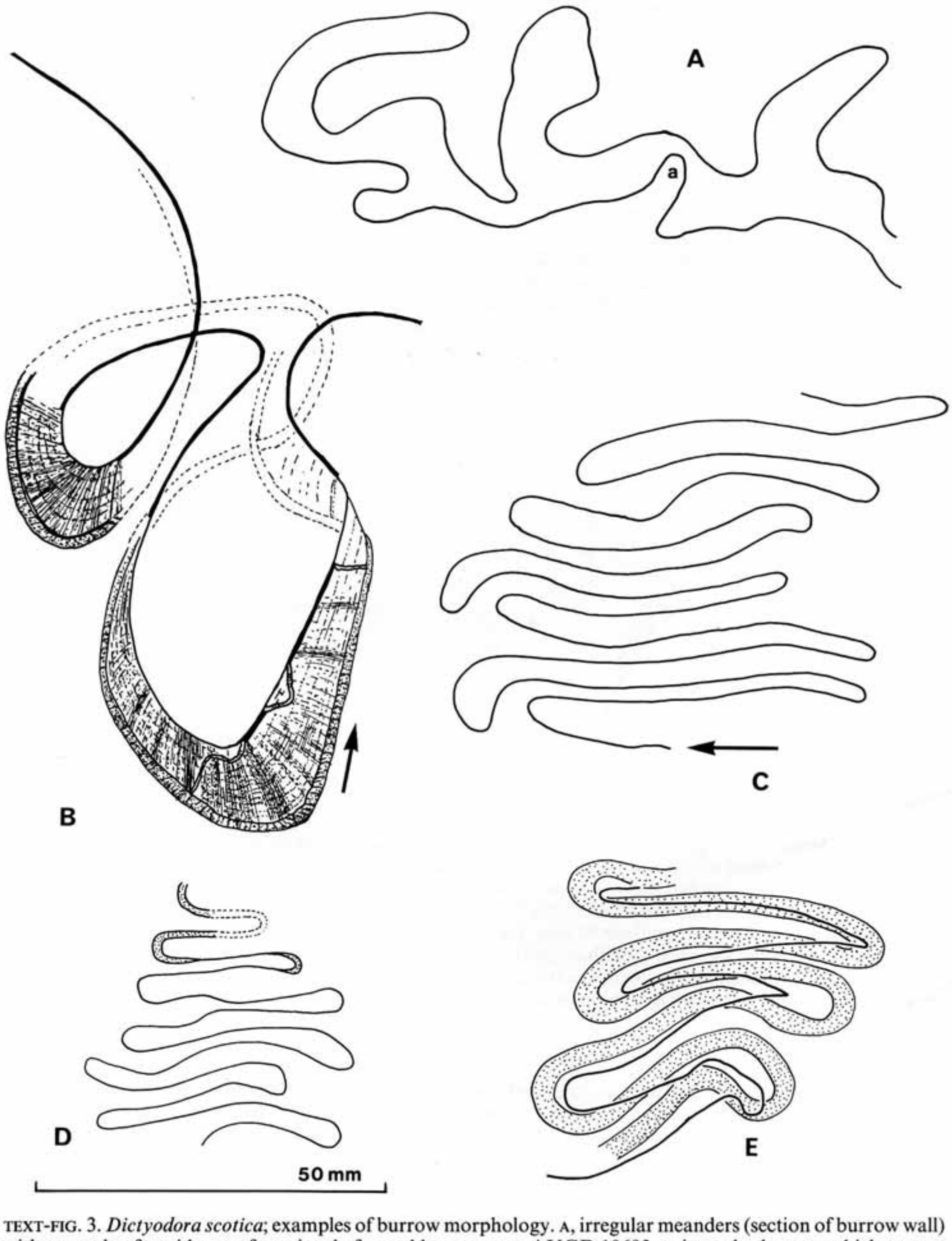


TEXT-FIG. 2. Sketch of lectotype of *Dictyodora scotica*, SM A45575a showing the lower surface of the specimen. Trace A shows the typical meander pattern. Most of the specimen displays the lower surface of the burrow but at *a* the burrow fill is broken out to show a mould of the upper surface of the basal burrow. The wall of A is 5 mm high and is not seen on the top of the slab. Trace B is larger than A and later since it clearly crosses A. At *b* the transition from basal burrow to wall can be seen. The wall passes through the full 8 mm thickness of the slab and is seen on the top of the specimen (not illustrated).

The burrows are indistinct in places due to the presence of several crossing burrows, and fracture irregularities on the surface of the slab which have been omitted for clarity.

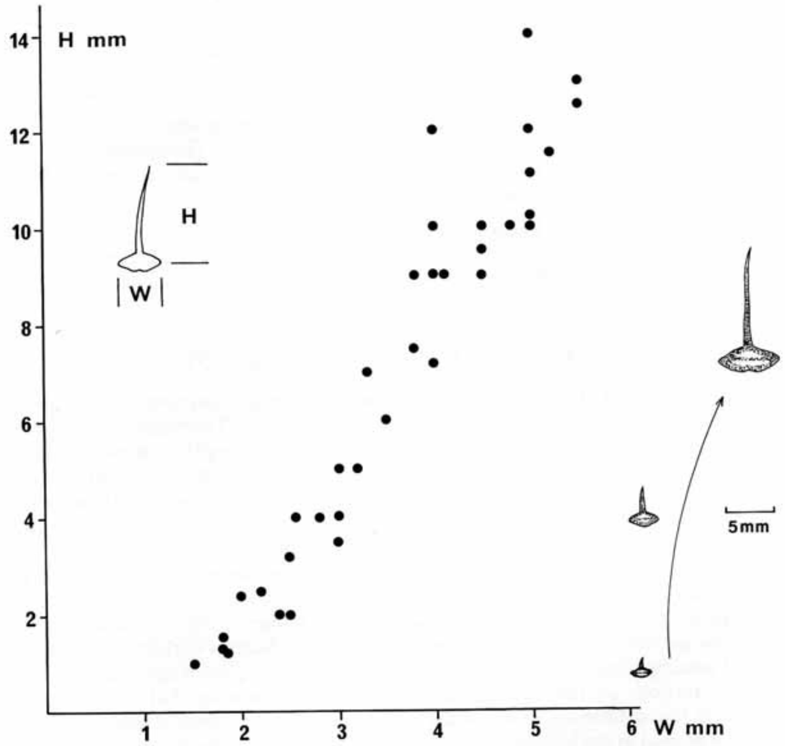
The wall is normally vertical above straight stretches of burrow, but curves inwards at meander bends (text-figs. 1A, C, 3B, E). Fine bedding parallel striations are present on the surface of the wall closely spaced at 4 per mm. A similar bedding parallel banding due to platey mineral orientation occurs within the wall fill, and is not related to sedimentary laminae. Curved vertical/oblique striations are also present on the wall surface normally spaced at 3·5 per mm. Internally the wall may show fine curved structures marked by reoriented platey minerals and resembling backfill within the wall (text-figs. 1B, 3B). Detailed observation of features is difficult in the wall fill but it is likely that the possible backfill structures seen normal to bedding occur between the bedding parallel bands.

The smallest forms recognized have a basal burrow 1.5 mm wide and a wall only 1 mm high, and a full gradation exists up to the larger forms with a progressive increase in wall height relative to burrow width (text-fig. 4). Detailed measurement of the morphology and meander patterns of over 170 specimens using principal components analyses failed to differentiate any groups with significantly different characters, and we consider that all the meandering burrows of this type are growth stages of a single species.



TEXT-FIG. 3. *Dictyodora scotica*; examples of burrow morphology. A, irregular meanders (section of burrow wall) with example of avoidance of previously formed burrow at *a*, AUGD 10693. B, irregular burrow which crosses previously formed burrow; plan view shows wall above basal burrow to be partly broken away, and inward slope of wall at meander curves; thickness of slab 10 mm; AUGD 10697. C, D, typical regular meander forms, hooked ends to meanders seen in C; both on AUGD 10694. E, plan view of basal burrow (stipple) and position of top of wall (solid line); sharp bends present at top of wall become smooth curves at lower levels close to the basal burrow; AUGD 10698. All examples from Thornylee Quarry.

Occurrence. Dictyodora scotica is common at Thornylee Quarry and scarce at Grieston Quarry. It is probably common in the Llandovery strata of the Southern Uplands since Peach and Horne (1899) mention '*Crossopodia*' and '*Myrianites*' from at least twenty localities in the Galashiels–Hawick region. It also occurs in the Llandovery of Penwhapple Glen, Girvan (Nicholson and Etheridge 1880, pp. 304–318). P. Doughty (pers. comm.) also records *Dictyodora* from the Silurian of Co. Down, Northern Ireland.



TEXT-FIG. 4. *Dictyodora scotica*. Relationship of width of basal burrow W with burrow height H to show range of variation and the relative increase in wall height in the larger examples.

Dictyodora tenuis (M'Coy, 1851)

Text-fig. 5

v*1851*a* *Myrianites tenuis* M'Coy, p. 394.
v*1851*b* *Myrianites tenuis* M'Coy; M'Coy, p. 130, pl. 1D, fig. 13.
v1978 *Myrianites tenuis* M'Coy; Nicholson, pl. 4, fig. 1, *non* text-fig. 7.
v1978 *Myrianites murchisoni* Emmons; Nicholson, p. 43, pl. 5, fig. 1.

Lectotype. Here designated, SM A45579a, the original of M'Coy (1851*b*, pl. 1D, fig. 13). Gala Group, Upper Llandovery, Lower Silurian, Grieston Quarry, nr. Innerleithen, Peeblesshire, Scotland (text-fig. 5A).

Other material. AUGD 9224, 10329, 10607, 10612, and 10711 to 10720 from Grieston Quarry and AUGD 10710 from Thornylee Quarry.

Description. Dictyodora with broad irregular meanders, as in text-fig. 5, which frequently have a secondary sinuosity with a wavelength of 3–15 mm which may develop into meanders with length roughly equal to breadth in larger examples. The basal burrow is from 1·5 to 3 mm wide and the wall has not been observed to exceed 10 mm in height. The wall is 0·2–0·7 mm wide and striated in the same manner as in *D. scotica*. Traces range from tiny 'scribbles' (text-fig. 5E) up to large examples as in text-fig. 5B, D.

Trace endings are observed as in text-fig. 5B where lengths of trace as short as 10 mm occur between inclined circular burrows 3 mm in diameter; other traces can be followed for over 200 mm without interruption.

Discussion. The distinction of *D. tenuis* from *D. scotica* can be made on maximum size and on the meandering pattern, which is more regular and smooth in *D. scotica* compared with the irregular meanders with secondary sinuosity displayed by *D. tenuis*.

In the past specimens displaying sections of the wall have been identified as *Myrianites* and specimens showing the basal burrow as *Crossopodia* or *Nemertites*. The specimens from Grieston called *M. murchisoni* by Nicholson (1978, p. 43, pl. 15, fig. 1) are not synonymous with the American form described by Emmons (1844) and are ascribed here to *D. tenuis*.

Occurrence. Common in the Upper Llandovery (*griestonensis* Zone) of Grieston Quarry, nr. Innerleithen, Peeblesshire, and also present in association with much commoner *D. scotica* at Thornylee Quarry. The form illustrated by Raup and Seilacher (1969, fig. 1a) from the Ordovician of Barrancos, Portugal, appears to be *D. tenuis*.

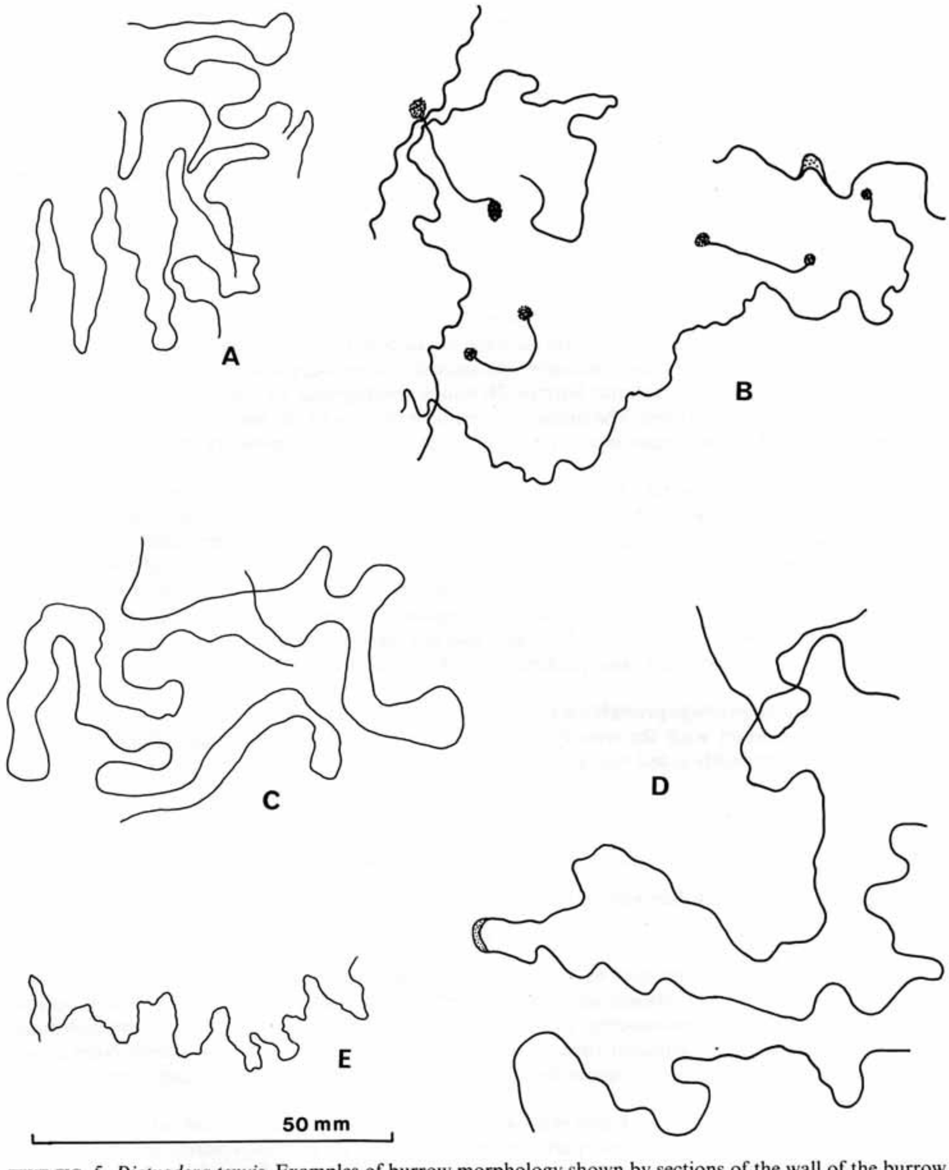
THE *DICTYODORA* ANIMAL AND ITS BEHAVIOUR

The meandering burrow of *Dictyodora* resembles the meandering burrows and trails produced by worms and molluscs efficiently utilizing an area as a food source. The tightly packed meanders of *Dictyodora* were probably formed during feeding, and the looser irregular meanders may have been the result of searching for areas rich in food. We assume that the body of the animal occupied the basal burrow, and probably progressed by peristaltic movement. Since individual burrows cannot be traced from small to large size, and considering that the burrows are sometimes seen to end by rising through the sediment it is likely that the animal moved from place to place on or above the sediment surface. Thus the burrows are considered to be produced by short periods of food search and utilization at a constant level within the sediment.

The animal appears to have maintained contact with the surface by means of an organ which was responsible for the production of the striated wall on the dorsal burrow surface; this we term the wall-organ to avoid assumptions implicit in the use of known zoological terms such as 'siphon'. The curved vertical striations on the wall and the fill of the wall indicate that the wall-organ moved regularly through the sediments, maintaining a constant convex-forward edge and followed the movement of the animal in the burrow; thus wall-organ traces occasionally touch or cross each other while the corresponding burrows do not.

The behaviour of animals that form meandering traces has been discussed by several authors. Seilacher (1967) suggested that the *Dictyodora* animal measured its meander length by the length of its body. It maintained contact with a previously formed burrow (thigmotaxis) until its body was straight and then the animal was 'programmed' to make a sharp U-turn (homostrophy) as its tail straightened, and to follow beside the last-formed portion of the burrow. However, this explanation does not satisfactorily explain individual burrows where meander length varies, or the Carboniferous *Dictyodora* where the meanders spiral out from a central point, each meander being longer than its predecessor.

Seilacher based his interpretation on the classic work of Richter (1924, 1928), who studied the Cretaceous/Tertiary *Helminthoida labyrinthica* Heer, 1865 which forms similar meandering feeding traces. Richter's interpretation differs from Seilacher's in one important way: he defined the homostrophic turning stimulus as caused by loss of contact with a former trace and not by tail straightening. The animal followed a former trace and could at times curve in front of previous meander ends (e.g. text-fig. 3C) before turning back when it lost contact with disturbed mud. In text-fig. 3 meander length varies from 30 to 80 mm and was clearly not measured by the body length of the



TEXT-FIG. 5. *Dictyodora tenuis*. Examples of burrow morphology shown by sections of the wall of the burrow. A, small meandering trace with irregular meanders showing secondary sinuosity; part of lectotype SM 45579a. B, parts of typical irregular meanders, together with short lengths of burrow terminated by inclined sections of basal burrow; AUGD 10719. C, D, E, irregular meanders of various sizes to show variation in meander morphology; C, E AUGD 10716; D AUGD 10718. All from Grieston Quarry.

animal. The reactions of the animal while feeding in meanders as listed by Seilacher (1967) and Raup and Seilacher (1969) may be modified to:

(1) Move horizontally keeping within a single stratum of sediment (?controlled by wall-organ length);
(2) Always keep in touch with previously formed burrow while feeding (thigmotaxis);
(3) Never come closer to a previously formed burrow than a particular distance 'd' (phobotaxis);
(4) If contact is lost with a former burrow, make a 180° turn (homostrophy/strophotaxis).

These 'rules' appear to apply reasonably well, and obvious cases of burrow avoidance can be found (text-fig. 3A). Traces made by individuals at different levels in the sediment frequently cross each other, but the basal burrows in such cases are normally at different levels. In the Thornylee examples population density was probably low and thus there was no need for attempting to utilize an area more than once.

If the meandering burrows are formed during feeding then the question arises of how feeding was accomplished. The wall-organ could have been a food collector at the surface, with the animal protected in its burrow, or the animal could have fed by sediment ingestion at burrow level leaving the wall-organ to perform a respiratory function. The second of these suggestions seems most favourable since the basal burrow has a definite burrow fill which corresponds to the sediment type at basal burrow rather than surface level. The apparently passive motion of the wall-organ does not accord with a function as a feeding organ, and it is more likely to have had a respiratory function and to have controlled burrow depth.

In laminated sediment the fill of the wall roughly matches the characteristics of the immediately adjacent sediment, with only slight downward movement of sediment during filling occasionally seen in thin section. Thus the wall-organ does not seem to have had a significant sediment transport function. No annulation of the burrow fill is seen and the constant fine spacing of the striations formed by the wall-organ would seem to indicate a slow regular movement through the sediment. The wall-organ may have been ciliated to facilitate its progress through the sediment. The striations and structured fill of the wall indicate that the organ was not merely dragged through the sediment but that the thin wall of sediment was packed in both horizontal and vertical increments by the wall-organ.

The *Dictyodora* animal was probably a worm or shell-less mollusc which fed by sediment ingestion and maintained contact with the over-lying water by means of the wall-organ which controlled burrow depth and possibly aided respiration.

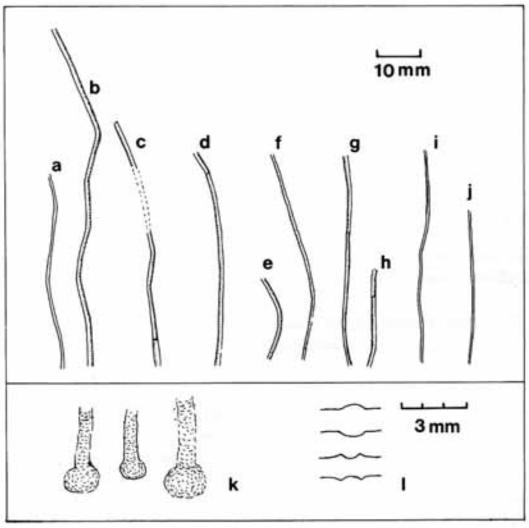
OTHER TRACES PRESENT

Caridolites wilsoni Etheridge, Woodward and Jones, 1890

Text-figs. 6, 7

The name *Caridolites wilsoni* was first mentioned in Nicholson (1873) and a brief description appeared in Etheridge, Woodward and Jones (1890), which must rank as the type description. Nicholson's original (1872) manuscript with a description and figure of *C. wilsoni* has been published recently together with a discussion (Benton and Trewin 1978, p. 10, pl. 3) in which Nicholson's interpretation that the trace was made by the tail spines of shoals of swimming *Ceratiocaris* is rejected.

The traces are generally about 1 mm wide and may consist of a slight central ridge bounded by hollows or a single ridge, or the counterpart of either. The traces are generally nearly straight for from 10–50 mm before disappearing or turning fairly sharply on a new course. Typical examples are shown in text-fig. 6*a–j* and typical profiles in text-fig. 6*l*. In cross section the traces are seen to be burrows with a vertical depth of up to 5 mm and consist of a basal tunnel with a narrower vertical extension (text-fig. 6*k*). These traces thus resemble minute *Dictyodora* without the meanders. *Caridolites* frequently covers bedding surfaces with a confusion of burrows as in text-fig. 7.



TEXT-FIG. 6. *Caridolites wilsoni*. *a–j*, typical burrow traces as seen on bedding surfaces; *a–c*, AUGD 10675; *d–f*, AUGD 10748; *i*, *j*, AUGD 7055, Grieston Quarry; *g*, *h*, AUGD 10723, Thornylee Quarry. *k*, typical vertical cross sections of burrows. *l*, profiles of surface expressions of the burrows.

TEXT-FIG. 7. *Caridolites wilsoni*. Bedding surface covered with typical examples, × 1, AUGD 10674, Grieston Quarry.

Caridolites is abundant at both Grieston and Thornylee and is frequently associated with both *D. scotica* and *D. tenuis*. It seems possible that *Caridolites* represents the activities of juvenile *Dictyodora* animals which had not developed sufficiently to meander. Certainly the observed size ranges of the traces fit this possibility.

Genus NEREITES MacLeay, 1839

Nereites is rare in the Thornylee–Grieston assemblage, with only two clear examples of this surface trace seen. Sediment surface texture was probably not suited to preservation of surface trails and most were probably removed by turbidity currents. The slaty muds and silts generally do not split at the top surfaces of beds. The common association of *Nereites* surface traces in sequences with *Dictyodora* burrows of similar width raises the speculation that *Nereites* could be a surface trace of the *Dictyodora* animal moving from one feeding spot to another.

CONCLUSIONS

The deep water ichnofauna of the greywacke/shale turbidite facies of the Llandovery in southern Scotland is dominated by two species of *Dictyodora*. The small burrow *Caridolites* is probably the juvenile burrow of the '*Dictyodora*' animal. *Nereites* is also present but rare, probably owing to original sediment texture and preservation.

Crossopodia scotica is shown to be a *Dictyodora*, and it is suggested that it should be rejected as the type species of *Crossopodia*, being replaced by *C. lata*.

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