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An enigmatic large discoidal fossil from the Pennsylvanian of County Clare, Ireland

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Abstract

A rare and unusual large solitary discoidal fossil has been discovered on a paving slab quarried from the cyclothems of the Central Clare Group (Kinderscoutian, Pennsylvanian, Carboniferous), western Ireland. The fossil impression consists of a smooth raised inner discoidal area, surrounded by a slightly lower relief outer ring, ca. 130–135 mm in diameter, with eight prominent equidistant ovoid raised nodes towards the outermost margin. The octoradial body plan of this enigmatic specimen suggests a cnidarian connection and, as it is preserved as a positive hyporelief cast, it is tentatively interpreted as the resting trace of a large benthic anemone, which was either partially or fully infaunal. The discoidal fossil is interesting palaeoecologically; it occurs within the well-known Liscannor flagstone, which consists of thinly bedded, fine-grained sandstone that is extensively covered by prominent, sinuous to meandering, horizontal grazing trails attributed to *Psammichnites plummeri*. This sedimentary facies likely represents mouth-bar sedimentation on a delta front of a river-dominated delta. The discoidal impression occurs on a portion of the slab where these trace fossils are relatively scarce. Uncertainty surrounds the classification and interpretation of the disc due to its relatively simple morphological form, coupled with a lack of unequivocally diagnostic features — a problem commonly encountered in studies of discoidal fossils from both the Ediacaran and the Phanerozoic.

Keywords: Carboniferous; Central Clare Group; Liscannor flagstone; cyclothem; discoidal fossil; octoradial symmetry

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1. Introduction

Discoidal, unmineralised fossils preserved as casts in siliciclastic sediments are a conspicuous component of Ediacaran fossil assemblages (e.g., Gehling et al., 2000; MacGabhann, 2007; Hofmann et al., 2008; Gehling and Droser, 2013; Burzynski et al., 2017), with older discs reported from the Cryogenian (e.g., Hofmann et al., 1990; Bertrand-Sarfati et al., 1995; Burzynski et al., 2020). Radial symmetry is a feature of several animal groups, including some of the simplest metazoans. Molecular clock estimates suggest a deep-time origin for crown-group cnidarians at around 700 Ma (Erwin et al., 2011; Van Iten et al., 2016) and there are suggestions that discoidal animal morphologies were present in even older strata (Rasmussen et al., 2002; Bengtson et al., 2007), although the cnidarian affinities of these records have been

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questioned (Grazhdankin and Gerdes, 2007). Ediacaran discs were initially interpreted as pelagic medusae (e.g., Sprigg, 1947, 1949; Glaessner and Wade, 1966; Wade, 1972); however, more recent interpretations have suggested a range of benthic ecologies, such as deposit feeders, grazers and osmotrophs (e.g., Clapham et al., 2003; MacGabhann, 2007; Xiao and Laflamme, 2009; Burzynski and Narbonne, 2015).

Discoidal unmineralised fossils also occur as casts in younger Phanerozoic strata (e.g., Crimes and McIlroy, 1999; Hagadorn et al., 2000), however, their perceived prevalence in palaeocommunities is noticeably diminished and records are more sporadic. This may be a taphonomic artefact, due in part to the requirement for soft-part preservation coupled with the rise in bioturbation and disappearance of matground environments (e.g., Seilacher et al., 2005; Mángano and Buatois, 2014; Gougeon et al., 2018; see also MacGabhann et al., 2019).

This paper describes a rare and unusual large solitary discoidal fossil from the Carboniferous cyclothems of the Central Clare Group (Bashkirian, Pennsylvanian) of County Clare in western Ireland (Fig. 1). The specimen in question was discovered on a paving slab which had been laid at the Cliffs of Moher Visitor Centre, before it was removed for safe keeping from the pathway in 2009. The slab had been sourced locally from one of several quarries producing 'Liscannor flagstone' for paving and cladding purposes. This sedimentary facies features distinctive horizontal sinuous grazing trails attributed to *Psammichnites plummeri*, and it has been commercially quarried from the local area since at least the 19th Century. Despite this long history of extraction, discoidal fossils have not been recorded before from this particular facies. Even though the new Irish Carboniferous discoidal specimen is just a single find, its distinctive morphology warrants morphological description and preliminary evaluation of potential biological affinity and palaeoecology, which are the aims of this contribution.

2. Stratigraphic context of the find

The Carboniferous Shannon Basin in western Ireland was a long-lived intracratonic depocentre, with carbonate sedimentation dominant during the Tournaisian and Viséan (Strogen, 1988; Somerville and Strogen, 1992; Strogen et al., 1996; Sevastopulo and Wyse Jackson, 2009; Murray, 2010). Sedimentary cyclicity is apparent in upper Viséan (Asbian and Brigantian regional substages) strata on the adjacent Burren Platform, which lay north of the Shannon Basin proper (Gallagher et al., 2006). This cyclicity is also observed regionally elsewhere and has been interpreted as glacioeustatically driven, associated with the onset of the Late Paleozoic Ice Age (e.g., Soreghan and Giles, 1999; Wright and Vanstone, 2001; Fielding et al., 2008; Barham et al., 2012).

Carbonate sedimentation ceased during the Serpukhovian and Bashkirian in the Shannon Basin, and this transition is marked by the widespread deposition of organic-rich marine dark shales (Barham et al., 2015; O'Sullivan et al., 2021). These are collectively termed the Clare Shale Formation and are interpreted as representing deep and quiet, anoxic to dysoxic bottom water conditions (Hodson and Lewarne, 1961; Sevastopulo, 2009; Fallon and Murray, 2015).

The Clare Shale Formation is relatively thin in north County Clare and is overlain by the Gull Island Formation, a series of basin-slope siltstones and fine- to very fine-grained sandstones which commonly display high levels of slumping and soft sediment deformation, especially in the lower part of the unit (Rider, 1974;

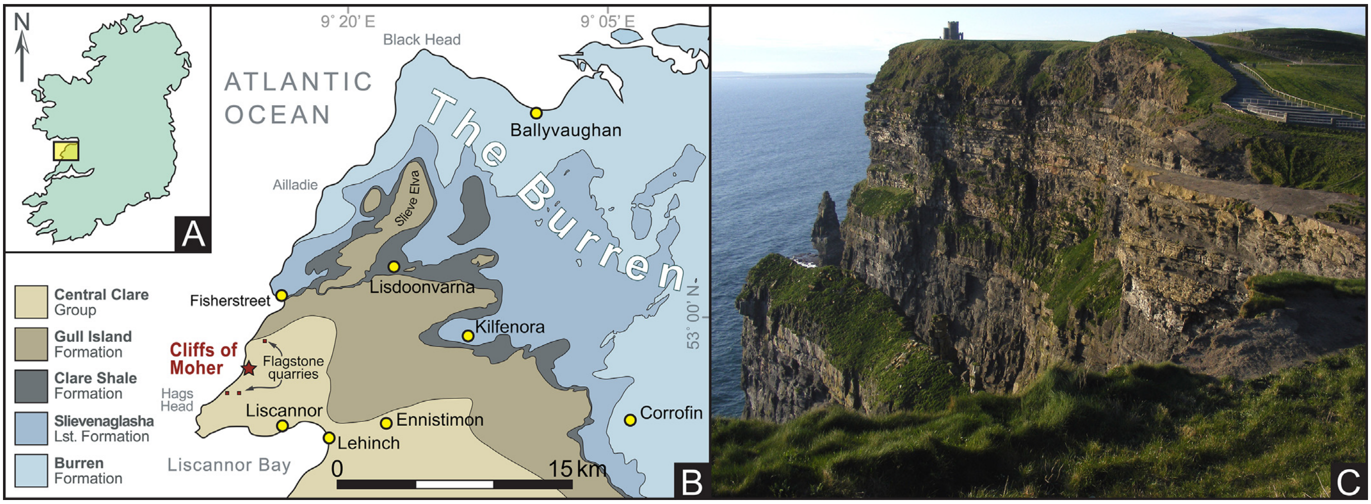

Fig. 1. Geographic location and geological context of the Liscannor fossil disc. (A) Location in western Ireland (highlighted by yellow box) of main geological map compilation in (B). (B) Geological map of Carboniferous strata in north County Clare, also showing location of Cliffs of Moher (red star) and several surrounding flagstone quarries (adapted from MacDermot et al., 2003). **(C)** Field photograph of the Cliffs of Moher with O'Brien's Tower in the background; strata exposed above the main sandstone ledge belong to the Cyclothem II (Kilkee) of the Central Clare Group, below that level the top of Cyclothem I (Tullig) is exposed (see Fig. 2).

Martinsen, 1989; Doyle and Hoey, 2022). The overlying cyclothems of the Central Clare Group reflect subsequent delta progradation into the Shannon Basin. At least five large-scale coarsening-upwards cycles are recognised (I–V), and these are interpreted as reflecting repeated phases of shallowing in what was a fluvial-dominated deltaic system (Rider, 1974; Gill, 1979; Pulham, 1989; Wignall and Best, 2000).

The Liscannor flagstone facies occurs towards the top of the Kilkee Cyclothem (Cyclothem II) in the Central Clare Group, above the strata exposed along the Atlantic coast at the Cliffs of Moher (Fig. 1C), between the *Reticuloceras* aff. *stubblefieldi* (R1b) and *Reticuloceras reticulatum* (R1c) ammonoid marine bands, indicative of a Kinderscoutian age (Fig. 2). This distinct sedimentary facies is generally interpreted as representing mouth-bar sedimentation on a delta front (Wignall and Best, 2000), consisting of thinly-bedded, fine-grained sandstone, which is extensively covered by prominent, sinuous to meandering horizontal grazing trails assigned to *Psammichnites plummeri* (ca. 10–20 mm in width). *Psammichnites* is a backfilled trace fossil representing the feeding activities of a subsurface vagile animal that used a siphon-like device to connect back to the seafloor surface above (Mángano et al., 2002; see also Mángano et al., 2022 for an updated ichnotaxonomic discussion). This ichnogenus has provided key evidence for marine conditions in Carboniferous sedimentary successions elsewhere (e.g., Maples and Suttner, 1990; Mángano et al., 2003; Mángano and Buatois, 2004). In particular, *P. plummeri* has been commonly recorded in marginal marine settings affected by fluvial discharge, most notably deltas and estuaries. Specifically, this ichnospecies is a common component of delta front deposits (including in some cases mouth bars) of late Paleozoic river-dominated deltas (e.g., Eagar et al., 1985; Martino, 1989; Maples and Suttner, 1990; Buckman, 1992; Mángano et al., 2003).

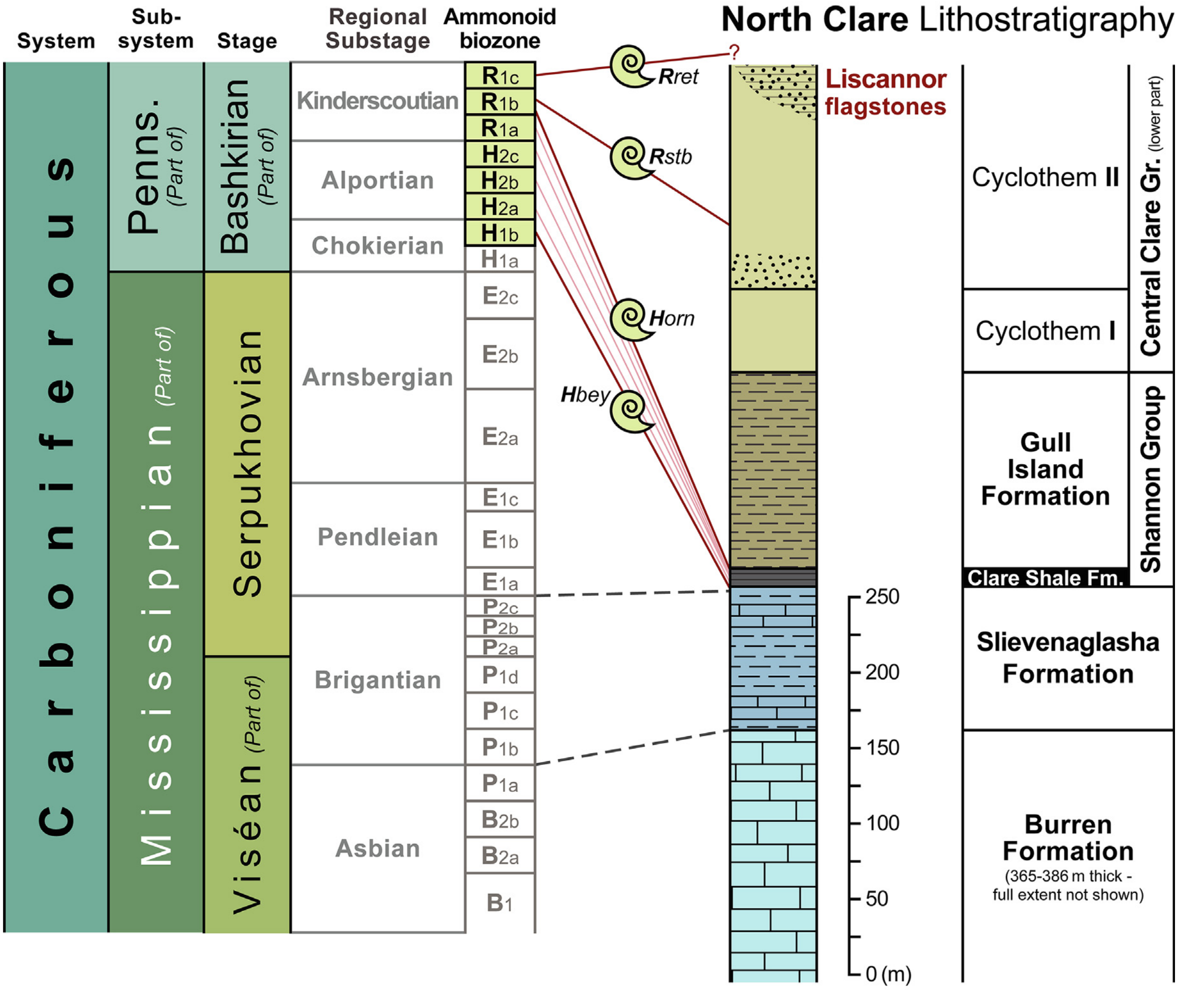

Fig. 2. Carboniferous stratigraphy of north Clare showing Liscannor Flagstone facies occurring in the upper part of Cyclothem II of the Central Clare Group. The Burren and Slievenaglasha formations are both limestone dominant and are biostratigraphically dated (grey dashed lines) using calcareous microfossils (principally foraminiferans) and rugose corals. The overlying Pendleian to Kinderscoutian lithostratigraphy is dated using condensed ammonoid horizons (those relevant to North Clare are shown as red lines). The more significant ammonoid horizons are highlighted in darker red and key species summarised thus: Hbey – *Homoceras beyrichianum*; Horn – *Hudsonoceras ornatum*; Rstb – *Reticuloceras* aff. *stubblefieldi*; Rret – *Reticuloceras reticulatum*. Other abbreviations: Penns. = Pennsylvanian, Gr. = Group. Adapted from Rider (1974), Gallagher et al. (2006), and Sevastopulo (2009). Colour coding of global chronostratigraphic boundaries is that prescribed by the Commission for the Geological Map of the World, Paris.

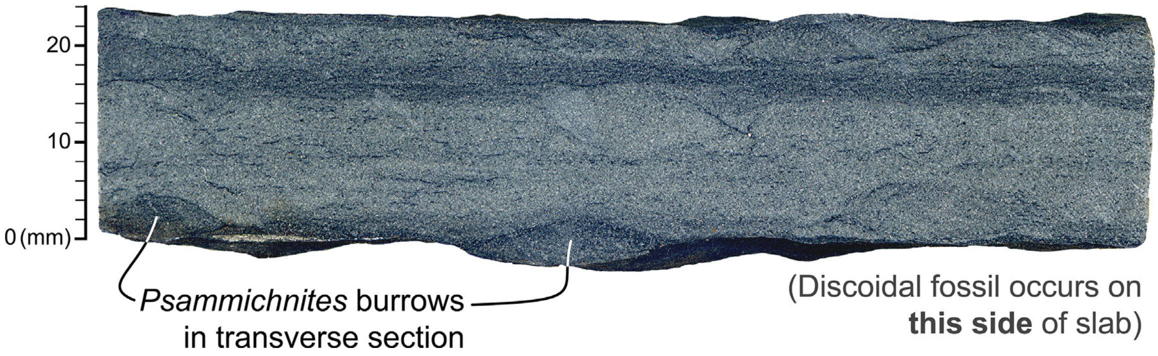

Fig. 3. Section through the discoidal fossil-bearing Liscannor slab showing detail of *Psammichnites plummeri* and (somewhat diffuse) internal lamination.

Liscannor sandstone is typically parallel-laminated, but may also display cross-lamination in the upper parts of beds due to the development of linguoid ripples (Wignall and Best, 2004). Abundant, thin darker laminae, rich in organic debris, also occur. The sedimentary rock hosting the discoidal fossil comprises ∼50% clay matrix, which includes fine-grained chlorite, calcite, biotite, clay minerals and carbonaceous material. Quartz is the dominant framework mineral, and grains commonly display syntaxial overgrowths. Feldspar grains represent a minor component (< 5% of the framework). Compositionally, the sedimentary rock can be classified as a quartzwacke (Pettijohn, 1975). In textural terms, the framework is dominated by relatively coarse-grained silt and fine sand, which is well-mixed and shows no evidence of grading. Thorough bioturbation, represented by *P. plummeri*, most likely obliterated much of the primary sedimentary fabric (Fig. 3).

3. Material and methods

The single discoidal fossil specimen was discovered on a paving stone of Liscannor flagstone measuring 69.5 cm by 53 cm (Fig. 4; see Supplementary data for short film compilation of high-resolution images of the slab illuminated from different directions) from the pathway at the Cliffs of Moher Visitor Centre in County Clare, western Ireland. The paving stones were supplied by two local quarry owners, including the quarry on the Doolin side of the Cliffs of Moher at Lough. A more definitive provenance for the slab with the discoidal impression cannot be established. It should be noted that these local quarries are active and privately owned and are not open to the public. The slab has been curated by the National Museum of Ireland – Natural History (NMING: F34747).

The specimen was subject to visual examination and photography with a Canon EOS 500D (18–55 mm lens), using a variety of high- and low-angle lighting. Approximately 1 cm was trimmed from one edge of the slab using a rock saw, and several polished sections and thin sections were made from the offcut portion for petrographic analysis, but no destructive testing was conducted on the specimen itself due to the rare nature of the find.

4. The enigmatic discoidal structure

The unique fossil specimen is discoidal in overall morphology, approximately circular in shape, with the disc 130–135 mm in diameter (Fig. 5). There is no evidence of mineralisation, nor any discolouration to suggest authigenic mineralisation. The disc margin is defined by a groove, which varies from well-defined and narrow on one side of the disc, to broader and more poorly defined on the other side (Fig. 5B).

The most prominent feature of the disc is a conspicuous inner boss, with ca. 4 mm of relief, about 80 mm in diameter. The surface of this protuberance is smooth and flat, save for an area which has suffered percussive damage. The edge of this feature is sloped, rather than cylindrical, and it is surrounded by a shallow groove where the sloped sides meet the outer area of the disc. The inner boss is not centred with respect to the full disc but is ca. 5 mm closer to the side of the disc on which the marginal groove is well defined. The sloped margin of the inner boss is also steeper on this side of the disc. This slightly offset radial symmetry, coupled with concentric wrinkling towards the outer edge of the boss, suggests some degree of compaction or perhaps partial collapse/deflation of the structure on one side.

The remainder of the disc forms an outer annulus, slightly wider on the side of the disc where the marginal groove is poorly defined as a result of the off-central placement of the inner boss, tapering into the grooves at both inner and outer margins. The surface of this outer annulus is generally smooth with generally negligible relief from the surrounding bedding plane, but is interrupted by eight raised nodes, spaced equiangularly around the disc margin. These nodes are broadly irregular ovoid in shape (some are nearly circular), with long axes approximately half the width of the outer annulus, approximately 15–20 mm, and relief in the order of 2 mm. An obvious 7 cm by 4 cm elliptical depression, ca. 5 mm deep, occurs on the obverse side of the ca. 22 mm thick fine-grained sandstone slab, and it corresponds closely with the position of the inner discoidal area of the fossil on the opposite side.

In addition to the discoidal fossil, the Liscannor slab (NMING: F34747) also displays a dense, monospecific

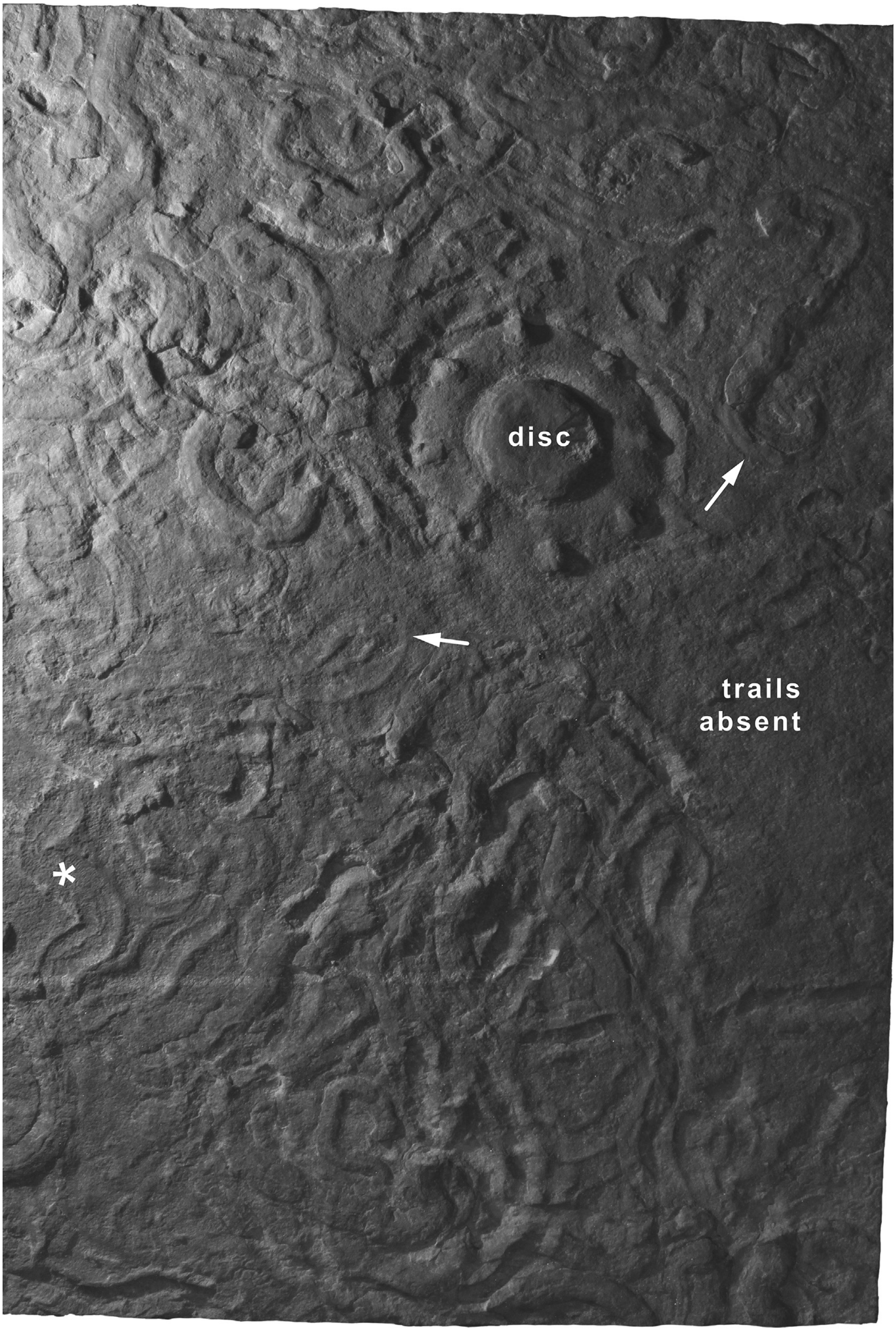

Fig. 4. View of complete Liscannor sandstone slab showing position of the discoidal fossil (labelled in white as disc) surrounded by numerous *Psammichnites plummeri*. Note that in certain areas, close to the discoidal impression itself, the trails are noticeably absent or reduced in concentration. In a few instances (marked with white arrows), *P. plummeri* appear to turn away (perhaps) from the larger disc structure. Fine menisci present at the top of *P. plummeri* towards the left side of the slab (as viewed, one specimen is indicated with a white asterisk) are preserved in negative hyporelief indicating that this slab surface is the base of the bed. Slab measures 69.5 cm by 53 cm. A short film compilation of several images of the slab, illuminated from different angles and without labelling, is available in Supplementary data.

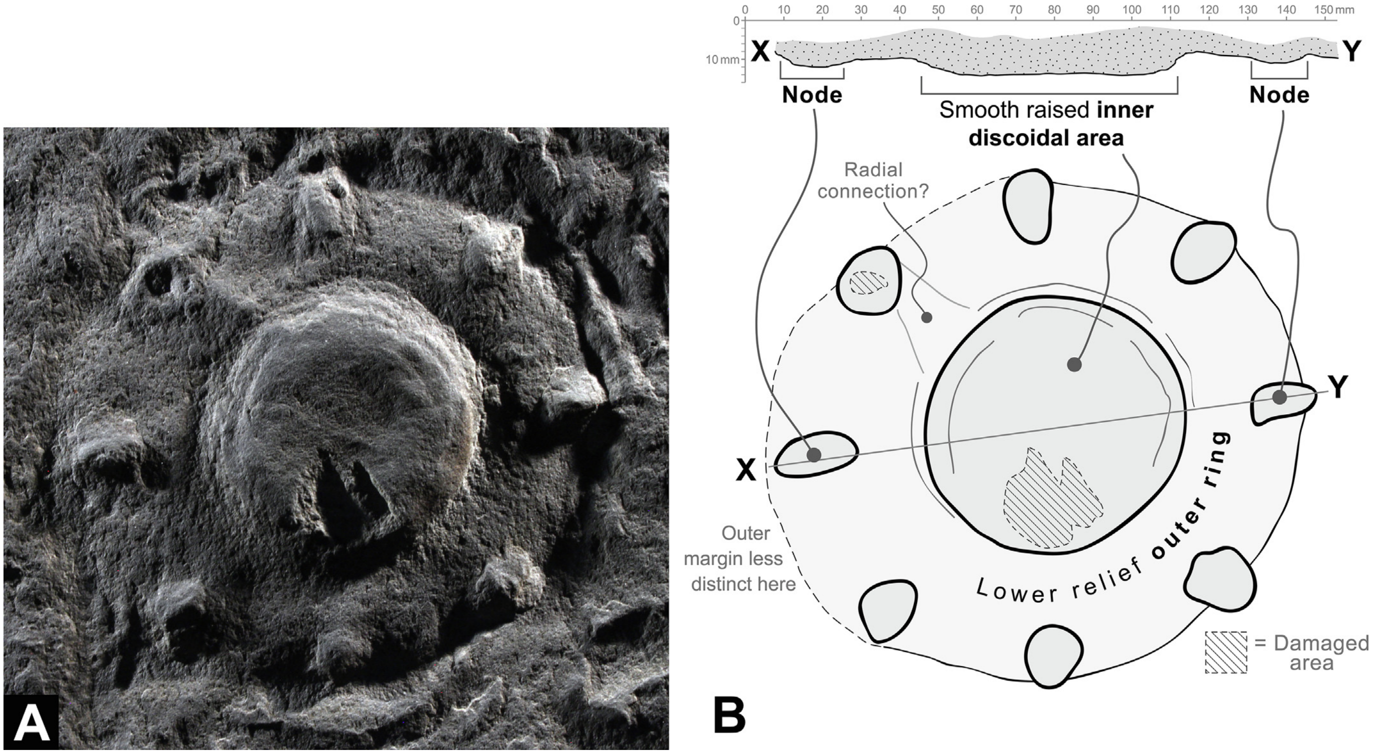

Fig. 5. Detailed morphology of the fossil disc (specimen NMING: F34747) on the slab of Liscannor flagstone. (A) Detailed photograph of the discoidal fossil, with strong oblique lighting to highlight relief of fine detail on the specimen. (B) Outline sketch interpretation of discoidal fossil in (A). A topographic profile (X-Y) taken across the surface of the specimen is shown at the top of the image and was drawn using a contour gauge. Horizontal and vertical scales are the same and horizontal scale is applicable to both plan and profile views.

association of *Psammichnites plummeri*, with traces preserved as semireliefs and full reliefs at the bed boundary, recording a variety of morphologies, including negative and positive reliefs (Fig. 4; see also Supplementary data). A delicate, tightly laminated backfill is only locally well preserved. Interestingly, *P. plummeri* is scarce or absent in a discrete zone immediately adjacent to the larger discoidal impression.

5. Discussion

5.1. The question of orientation: top or base?

Way-up was not recorded when the slab was initially extracted during quarrying, and no bedforms (e.g., ripples) are present to help decipher polarity of the bed. Attempts to identify grading in polished sections (Fig. 3) have proven inconclusive. Despite this, several critical observations strongly suggest that the Liscannor disc is preserved at a bed sole:

- The marginal groove is reminiscent of similar features in other unmineralised discoidal fossils and ichnofossils preserved in positive hyporelief, including paropsonemids, where it has been related to post-mortem shrinkage of a carcass in situ (MacGabhann, 2012).
- The depression on the obverse side of the slab above the central boss may have been produced due to sediment collapse and downward advection under the force of gravity, following decay of the buried or partially infaunal organism.
- *Psammichnites* is typically preserved in a wide variety of morphologies on bed surfaces within the Liscannor flagstones, both as negative (concave) hyporeliefs displaying an axial structure or as full reliefs displaying the delicate, crenulated backfill (Fig. 4). The presence of a dorsal axial structure in negative semireliefs suggests that the slab surface bearing the discoidal impression is the base of a bed.

Based on all features observed, the most parsimonious interpretation is that preservation of the disc is in convex relief at the bed base and the animal was probably present at the time of entombment.

5.2. Discoidal body fossil or trace fossil?

Interpretation of the Liscannor disc as a positive hyporelief impression then raises the further question of whether the specimen should be considered as a trace fossil (representing either domichnia or cubichnia) or as a body fossil. This fundamental difference in interpretation is also mirrored in broader evaluations of discoidal fossils: in rocks of Ediacaran age, unmineralised discoidal positive hyporelief casts are typically considered as body fossils, whereas in Phanerozoic strata plug-shaped and discoidal structures are often described as either domichnia (displaying lining suggestive of permanent burrows) or cubichnia (transient resting structures) produced by actiniarians (cf. Pemberton et al., 1988). The hypothesis that an organism was present and decayed in situ post-burial may suggest that the specimen is a direct cast of the lower surface of an organism, and so should be considered as a body fossil. Evidence for active movement of the organism (horizontally or vertically) in the sediment is admittedly lacking. However, the presence of the discoidal specimen as a positive hyporelief cast on a heavily bioturbated interfacial surface of Liscannor sandstone (Fig. 4) suggests that the animal responsible for producing the impression may itself have been at least partially infaunal in life. This would imply that the organism was able to burrow into (most likely using features of its hydrostatic skeleton) and live at least partially within the sediment. Whether these biogenic structures were permanent domiciles (i.e., domichnia) or temporary resting traces (i.e., cubichnia) is difficult to assess based on a single specimen.

Moreover, in the case of other Phanerozoic discoidal traces, the physical presence of an organism on burial has not previously been regarded as sufficient grounds to reject a trace fossil interpretation. For example, both Arai and McGugan (1968) and Alpert (1973) noted slump structures above *Bergaueria* specimens, interpreting these as indicating a body decayed in situ post burial, and still considered the specimens to be trace fossils.

The consensus definition of a trace fossil by Bertling et al. (2006, p. 266) specifies: “a morphologically recurrent structure resulting from the life activity of an individual organism (or homotypic organisms) modifying the substrate”.

Given the rarity of the find, it cannot be stated with any confidence that the Liscannor disc is a morphologically recurrent structure. However, it does appear to have been created through active modification of the substrate; and while this may have preserved a shape mimicking some surficial anatomical elements of the original organism, no unequivocally distinct body parts are preserved.

Relatively large diameter (ca. 20–40 mm) vertical plug-shaped burrows have also recently been observed in Liscannor flagstone facies (Fig. 6). These are also quite rare in terms of occurrence; however, their scale, shape and form are similar to several reported anemone burrows elsewhere, for example *Conichnus* described from Cambrian strata by Mata et al. (2012, figs. 7, 10). However, the animal responsible for producing the Liscannor disc would have been clearly too large to have been the maker of these particular vertical burrows. Aside from the overlying sediment depression feature, there is no evidence of the disc structure on the opposite side of the slab (which is ca. 22 mm thick), suggesting either negligible vertical continuation (i.e., implying the inability to escape moving upwards) or erosion of the upper part of the structure due to the dynamics of sedimentation in a mouth bar setting.

5.3. *Biological affinity of the maker of the discoidal impression*

The prominent raised central boss of the Liscannor disc (Fig. 5) is reminiscent of discoidal holdfasts of some Ediacaran-aged frondose arboreomorph taxa (e.g., Laflamme et al., 2018), as well as some isolated Ediacaran discoidal fossils interpreted as likely holdfasts (e.g., Burzynski et al., 2017). In such cases, the central boss is interpreted as the attachment point of the stem, and is regarded as less compressible than the outer area of the disc. The potential presence of an overlying stem in the Liscannor disc cannot be definitively rejected; however, the surface of the depression on the obverse side of the slab is generally smooth and lacks any structures indicative of the former presence or removal of a stem (e.g., see Tarhan et al., 2010).

Eoporpita has both a central boss and lobes, but specimens from Canada (Burzynski et al., 2017) demonstrate the lobes to be an internal structure extending from the central boss. Specimens assigned to *Eoporpita* from Ukraine (Dzik and Martyshyn, 2017) have quite different lobes, emanating from the margin of the outer disc; these serve to increase the surface area (and stabilisation capacity) of the basal support structure (like tree roots). This is clearly not the case with the Liscannor disc — it is difficult to reconcile how the eight nodes would have served to stabilize the discoidal structure, or indeed a vertical stem structure above this. Perhaps more significantly, *Eoporpita* lobes do not display the conspicuous octoradial symmetry of the Liscannor disc. The Ediacaran taxon *Eoandromeda* does have octoradial symmetry (Zhu et al., 2008), but has a very different morphology. In any case, the > 200 million year gap separating these Ediacaran-aged discoidal forms and the Carboniferous Liscannor specimen makes any suggestion of a direct biological relationship highly unlikely; any perceived similarities may be merely be analogous and a reflection of the relatively simple morphologies concerned.

Several groups of organisms are known to have discoidal fossil morphologies in the Phanerozoic and they commonly prove difficult to unequivocally classify (e.g., MacGabhann et al., 2007; Kirkland et al., 2016; Lieberman et al., 2017). Proposed cnidarian affinities for these structures feature prominently in interpretations, and include scyphozoan and hydrozoan medusae, cubozoans and porpitids (‘chondrophorines’). These pelagic groups have been identified in strata ranging from the Cambrian to the Jurassic, generally as shoreline strandings in Konservat-Lagerstätten settings (see Young and Hagadorn, 2010, 2020). An extensive list of fossil occurrences is tabulated in Young and Hagadorn (2010). How-

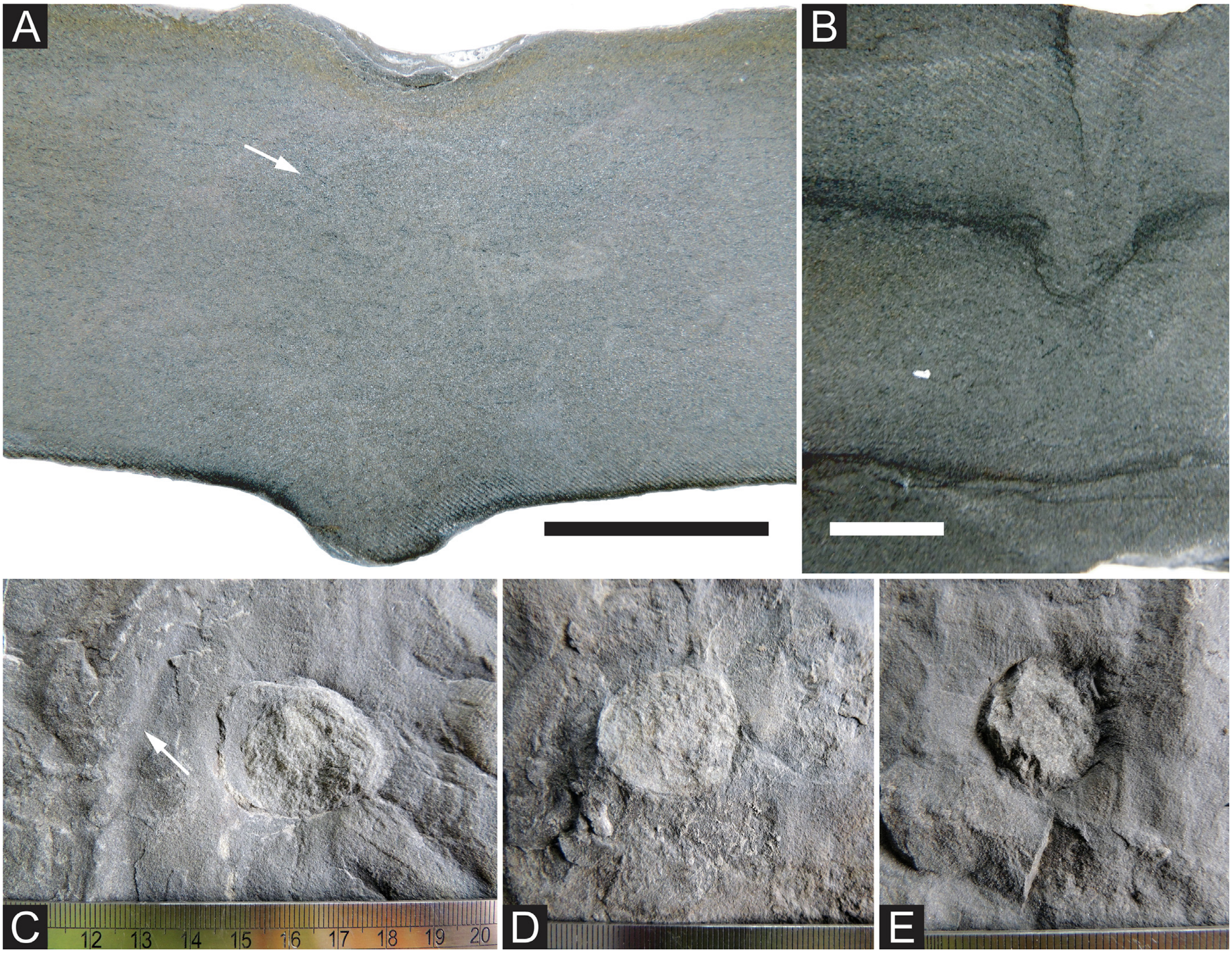

Fig. 6. Relatively large (2–4 cm) diameter vertical plug-shaped burrows from Liscannor sandstone facies, possibly ascribable to the activities of burrowing anemones. These specimens were photographed in a working quarry located farther south from the probable source of the Liscannor disc, exposing broadly the same stratigraphical level. (A) Cross-sectional view of sandstone slab showing domed positive hyporelief impression on bed sole, with corresponding sunken negative epirelief depression on bed top; the boundary between burrow and host matrix is diffuse and indistinct; however, downward deflected laminae are evident (white arrow); black scale bar is 3 cm. (B) Cross-sectional view of another specimen showing vertical burrow penetrating two sandstone beds; note more sharply defined conical internal fill in comparison to (A); white scale bar is 1 cm. (C) Large diameter vertical burrow on bed top; note more sharply defined boundary with surrounding matrix and also the presence of an adjacent horizontal trail (white arrow). (D) Same vertical burrow as (C) photographed on underside of bed — this burrow crosses into the underlying horizon. (E) Bed top view of large diameter vertical burrow. Scale at bottom of photographs (C–E) is in mm divisions.

ever, evidence for periodic emergence has not previously been recorded in Liscannor sandstone facies (e.g., Wignall and Best, 2004; Sevastopulo, 2009) making interpretation of the discoidal fossil as a medusan shoreline stranding problematic.

An alternative non-biomineralising animal group responsible for producing discoidal fossils in Cambrian to Devonian strata is the paropsonemids. Representatives from this enigmatic group have been variously determined as scyphozoan medusae, benthic actiniarians, or porpitid hydrozoans (e.g., Scrutton, 1979; Stanley, 1986); however, they are clearly triploblastic in nature and not radially symmetric. They have also been interpreted as lophophorate-grade organisms (Sun and Hou, 1987; Dzik et al., 1997), but are best considered as stem-group deuterostomes (Friend, 1995; Caron et al., 2010; MacGabhann and Murray, 2010; MacGabhann, 2012; Hagadorn and Allmon, 2019; MacGabhann et al., 2019).

The conspicuous octoradial symmetry of the Liscannor disc, due to the presence of eight prominent raised nodes towards the outer margin (Fig. 5), is not a feature of known paropsonemid groups, and none of the characteristic features of the paropsonemids (MacGabhann, 2012) are present. Despite the comparable size, an interpretation as a member of that particular clade is discounted. There is thus no requirement to extend the range of paropsonemids into the Carboniferous. The octoradial symmetry of the Liscannor disc does, however, suggest possible affinities with either the ctenophores or cnidarians.

Ctenophore symmetry is a function of a biradial body plan, with each 'hemisphere' hosting four distinctive ctene rows or 'comb plates' (Martindale, 1986; Martindale and Henry, 1998). The main body axis of the ctenophore is organised with a mouth at one end and an apical sensory organ at the opposite end (Pang and Martindale, 2008). The aboral view of the living ctenophore *Pleurobrachia pileus* presented by Manuel (2009, see fig. 5E) clearly displays all of these features: a combination of biradial and octoradial symmetry with a centrally placed apical sensory organ. It is superficially similar in some respects to the Liscannor disc, particularly with regards to the arrangement of the eight comb structures around the outer margin. A ctenophore interpretation is, however, not favoured here as there is clearly no evidence for either an apical sensory organ or a mouth in the centre of the Liscannor specimen. Due to their soft, delicate, gelatinous bodies, ctenophores are very rare as fossils (e.g., Conway Morris and Collins, 1996; Dunn et al., 2015). Additionally, the vast majority of ctenophores are pelagic which would not readily fit with the inferred sedimentological and taphonomic setting of the Liscannor fossil specimen (see discussion in subsection 5.4). Interestingly, living benthic and semi-benthic ctenophores are known, but they tend to lose their characteristic ciliary comb rows (Whelan et al., 2017).

The general morphology of the Liscannor disc is similar to Cnidaria bauplans, and octoradial symmetry (Fig. 5) is viewed as an important feature of several cnidarian groups (e.g., Park et al., 2011; Dzik et al., 2017). Octocoral polyps (class Anthozoa, subclass Octocorallia) very clearly display this feature: they possess eight tentacles, arranged radially, but they are exclusively colonial (Bayer, 1973). The colonial mode of life for the octocoral group precludes it as a candidate for accommodating the maker of the Liscannor disc, which was clearly a large solitary organism, considerably larger than the typical size of octocoral polyps (e.g., Baker et al., 2015; Rossi et al., 2018). Scyphomedusans are also known to display regular octoradiate bell symmetry (Holst, 2012); however, a jellyfish interpretation is discounted for similar reasons as the ctenophores (above): their pelagic lifestyle and soft-bodied construction make them unlikely candidates for preservation.

Benthic anemones (class Anthozoa, order Actiniaria; Rodríguez et al., 2014) provide an alternative and perhaps more suitable analogue for interpreting the Liscannor specimen. They are solitary, can grow relatively large, have muscular hydrostatic skeletons and several extant forms are known to actively burrow (e.g., Ansell and Trueman, 1968; Mangum, 1970; Sassaman and Mangum, 1972).

Actiniarians typically display hexaradial symmetry; however, they (along with several representatives from the broader subclass Zooantharia) transiently display eight first cycle mesenteries during their larval stages (the 'Edwardsia stage'; Malakhov, 2016; see also Finnerty et al., 2004; Manuel, 2009). One anemone group, the family Edwardsiidae, retains eight mesenteries into adulthood; these small anemones are quite elongate (vermiform), they lack a pedal disc, and they are infaunal in habit (Daly et al., 2002; Bocharova and Kozevich, 2011; Izumi et al., 2018). A second (non-actiniarian) anthozoan group, the ceriantharians, also lives benthically as solitary anemones and live infaunally in tubes (Stampar et al., 2016).

Solitary benthic cnidarians have been proposed as trace-makers of discoidal fossils, in particular partially infaunal anemones (actiniarians) which produced plug-shaped burrows (e.g., Arai and McGugan, 1968; Alpert, 1973; Orłowski and Radwański, 1986; Pemberton and Jones, 1988; Pemberton et al., 1988; Pemberton and Magwood, 1990). The ichnogenus *Bergaueria* is a common and particularly well-known example of an actiniarian burrow, and it ranges from the Cambrian to Holocene. *Bergaueria radiata* Alpert, 1973 is particularly pertinent to discussion about the general morphology of the Liscannor disc. The base of this ichnospecies displays eight to ten 'lobes' or radial ridges that emanate from the centre of the disc. *B. radiata* varies in diameter from 19 mm to 35 mm in the type material (Alpert, 1973), which again is considerably smaller than the Liscannor specimen; however, size per se is not considered a strong ichnotaxobase (Bertling et al., 2006). Most importantly, the radial ornamentation of *B. radiata* differs significantly from the marginal nodes of the Liscannor disc which displays diverse axial orientation. *Bergaueria sucta* is the only ichnospecies of *Bergaueria* that displays a conspicuously flat discoidal morphology (Seilacher, 1990; Hofmann et al., 2012), and in this respect, it is more relevant to the Liscannor specimen. *B. sucta* characteristically displays laterally repeated crescent-shaped impressions on the disc, which are interpreted as evidence of lateral movement by an actinarian or ceriantharian cnidarian (e.g., Seilacher, 1990; Seilacher et al., 2005; de Gibert et al., 2011; Hofmann et al., 2012). No evidence of lateral movement, however, is evident in the Irish specimen, which is also significantly larger than the size range of *B. sucta*.

Dense concentrations of anemone burrows (*Bergaueria perata*, but recorded as *Alpertia sanctacrucensis* in its original description) were described by Orłowski and Radwański (1986) from Devonian tempestites in the Holy Cross Mountains of Poland (see Pemberton et al., 1988 for ichnotaxonomic revision). These ichnofossils range in diameter from ca. 11–26.5 mm and their smaller size, general morphology and the inferred gregarious nature of the original burrow-makers are all quite distinct from the Liscannor disc. However, certain aspects of the inferred taphonomic history of the Polish burrows are comparable to the Irish specimen: the Devonian anemones were rapidly buried by episodic and pulsed sedimentation, which caused them to contract their bodies markedly. Following death and decay of the anemone, sediment infill of the resulting void space led to casting and preservation of only the lower parts of the anemone burrow (see fig. 2 of Orłowski and Radwański, 1986). Gibson et al. (2018) ran decay experiments on recent sea anemones and found that the internal musculature, particularly around the pedal disc was least susceptible to decay; however, the tentacles (at the opposite end) were the most labile, which would support the proposed taphonomic model of Orłowski and Radwański (1986).

Buckman (1992) recorded *Bergaueria perata* from the Viséan-aged Mullaghmore Sandstone Formation in northwest Ireland. This clastic unit is interpreted as the result of a regional lowstand (e.g., Graham, 2017; Anders et al., 2022). Like the Liscannor disc, the Mullaghmore *B. perata* co-occurs in the same unit in the formation with paschichnia such as *P. plummeri* and other cubichnia with a conical shape tentatively assigned to *Conostichus* (Buckman, 1992). However, these *B. perata* reach only 35 mm in width, and display faint concentric laminae and radial ornamentation, quite distinct from the Liscannor disc's larger size and generally smooth surface. The Liscannor disc is morphologically distinct from other reported Carboniferous cnidarian trace or body fossils. For example, Lech (1986, 2009) described *Palaeoanemone marcusi*, an elongate burrowing actiniarian anemone from the Carboniferous Leoncito Formation of Argentina. The aboral end of this taxon is simply described as rounded, and it is considerably smaller in diameter than the Irish specimen.

A range of cnidarian taxa have been recorded from the Middle Pennsylvanian (Moscovian) Francis Creek Shale Member of the Mazon Creek Lagerstätte in Illinois (Foster, 1979; Sroka, 1997; Clements et al., 2019). They dominate what has been termed the 'Essex Fauna', and the closest comparable discoidal form from that assemblage is *Octomedusa piekorum*, which may represent either a coronate scyphozoan or a narcomedusan hydrozoan (Young and Hagadorn, 2010). This fossil medusa has eight tentacles and displays prominent octoradial symmetry (Johnson and Richardson, 1968). Its octagonal outline is typically scalloped, with a cruciform mouth evident in the middle of the bell, and it is also considerably smaller than the Irish discoidal specimen (bell diameter ranges from ca. 3–21 mm). Plotnick et al. (in press) recently redescribed *Essexella asherae* as an infaunal or semi-infaunal actinian anemone from the Mazon Creek Lagerstätte and suggested that it might be a producer of *Conostichus*. Specimens of *E. asherae* preserved vertically (i.e., displaying the oral or aboral ends; see 'Taphonomic Variant IV' of Plotnick et al., in press, fig. 8) are discoidal in form, with distinction between an inner and outer discoidal area sometimes apparent; however, this taxon displays hexamerous symmetry and is smaller than the Liscannor disc.

The scyphomedusan *Prothysanostoma eleanorae*, preserved as carbon films in the Upper Pennsylvanian Wea Shale of Iowa, also displays octoradial symmetry (eight arms and 16 lappets around the margin of the bell; Ossian, 1973). This reflects an underlying tetraradial body plan, but it clearly lacks the arrangement of nodes in the Liscannor disc.

Precise interpretation of the anatomy of the organism responsible for creating the Liscannor disc is difficult: its most conspicuous morphological element is the eight raised nodes towards the outer periphery of the disc (Fig. 5). These must reflect morphological features on one side of an anemone-like organism; however, the precise function of these structures remains speculative — they might reflect (internal) mesenteries, or they could be related to reproduction (gonads). The latter structures are, however, typically carried internally in living anemones. If the Liscannor disc is, in fact, a medusan body fossil, these could be sensory structures connected with the nervous system (e.g., rhopalium), or perhaps tentacular structures, as interpreted for similar node-like features in the Cambrian pentaradial medusozoan *Hanagyroia orientalis* Wang et al., 2020. Unlike *H. orientalis*, though, there is no clear evidence for either a mouth or anus in the Irish specimen, suggesting that the discoidal impression may in fact reflect features on the aboral surface of the organism — in the case of a benthic actinian-ceriantheid anemone this could reflect morphological features of the pedal or basal disc.

The relatively simple morphology and paucity of additional key diagnostic features precludes a more precise assignment of the Liscannor disc. Similar limitations have commonly led to uncertainty in classification of both Neoproterozoic and Phanerozoic discoidal fossils elsewhere (e.g., MacGabhann, 2007).

5.4. Palaeoecological considerations

Ross et al. (2013) interpreted the sheeted and well-bedded nature of Liscannor sedimentary facies as a reflection of pulsed depositional cycles in the mouth bar of a prograding river in flood. Bioturbation took place in the quieter intervals between successive flood events. As *Psammichnites* prominently features in the Liscannor deposits, marine conditions presumably prevailed, at least during the periods of low fluvial discharge. The close association of the discoidal fossil and *P. plummeri* on the Liscannor slab also requires consideration in terms of potential palaeoecologic relationships. The relatively pristine surface of the larger disc (Figs. 4, 5), with no bioturbation overprint by *P. plummeri* suggests either:

1. avoidance of the larger sessile animal by the active grazers (i.e., co-existence and ecological interaction as members of the same colonisation window),
2. a later colonisation of the substrate by the larger discoidal animal, crosscutting and obliterating the previous bioturbated fabric (i.e., two successive events not recording ecological interaction), or
3. merely serendipitous preservation: intense bioturbation by the *P. plummeri* producer would normally obliterate other plug-shaped impressions, with the studied specimen being by chance the only one preserved.

In scenario 2 above, if the larger discoidal animal moved downwards in the sediment sometime after the *P. plummeri* producers (thus enhancing its preservation potential), it would be reasonable to expect examples of this ichnofossil elsewhere in Liscannor flagstone; however, to-date, this has not proven the case. Close inspection of the area around the discoidal fossil reveals that more than half of the immediate adjacent region around the perimeter is essentially non-bioturbated. A small area of the slab is conspicuously unbioturbated (Fig. 4), but the rest of the surface is profusely bioturbated with common overcrossing *Psammichnites* trails. Two meandering trails (white arrows in Fig. 4) turn away from the larger disc; although no direct contact and inflexion is recorded, there is close proximity suggesting avoidance. Other trails approach more closely to the discoidal structure without disturbing it.

Based on this available evidence, the co-existence of the discoidal organism and *P. plummeri* seems plausible; however, the possibility of a subsequent colonisation by the former cannot be fully discarded.

6. Conclusions

A novel type of discoidal fossil is described from Pennsylvanian cyclothem facies in County Clare, Ireland. It is not clear precisely what organism was responsible for making the impression, but the octoradial symmetry tentatively suggests some form of cnidarian, possibly a very large diameter anemone. Vertical burrows observed elsewhere in Liscannor flagstone facies (Fig. 6) suggest that other anemones may possibly have been present during and immediately after sediment deposition; however, these plug-shaped structures are much too small to have been created by the organism responsible for the Liscannor disc, and they are also much simpler in terms of morphology.

This find is important for a number of reasons: the Liscannor disc is morphologically very distinct, but additionally large discoidal fossil impressions are uncommon in Carboniferous strata. Moreover, due to the relatively simple morphology, it remains unclear how this enigmatic Carboniferous fossil should be classified. It could readily be interpreted as an anemone dwelling trace (domichnia), principally on the basis of the sedimentological, ichnological and taphonomic context of the find. Alternatively, it could equally be considered the direct impression of the underside of the organism and, thus, a body fossil. Similar conflicting approaches are routinely taken in the interpretation of discoidal fossils from both the Ediacaran and the Phanerozoic, and this matter admittedly requires urgent clarification.

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Supplementary data

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