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First report of fish trace fossils (*Undichna*) from the Middle Devonian Achanarras Limestone, Caithness Flagstone Group

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Abstract

Two newly-discovered specimens of the fish locomotion trace *Undichna* (*U. britannica* and *Undichna* isp.), are described from the Middle Devonian Achanarras Limestone Member (Caithness Flagstone Group, NE Scotland). Fish trace fossils have not previously been reported from the Achanarras Limestone Member, despite decades of study of the unit as a key locality for fish body fossils. The traces comprise discontinuous sinusoidal grooves; one showing multiple parallel incisions, created by the fins of an acanthodian fish swimming close to the substrate. The apparent absence of trace fossils attributable to infaunal or epifaunal benthic organisms suggests that the sediment at the bottom of the lake was relatively inhospitable. The low ichnodiversity of the Achanarras Limestone Member is likely due to low oxygen levels in the depositional environment.

Introduction

The Middle Devonian strata of north and northeast Scotland contain some of the most diverse and completely-preserved Palaeozoic fish fossils in the world (Dineley, 1999), many of which are hosted within lacustrine rhythmites of the Eifelian Achanarras Limestone Member (Lybster Flagstone Formation, Caithness Group). The most fossiliferous site within the member is its type locality, Achanarras Quarry in Caithness (58° 28' 13.2"N, 03° 27' 34.6"W), where 15 fish species are found in abundance, and a total of 13 fish genera have been reported, along with a number of invertebrate taxa (Dineley, 1999; Anderson *et al.*, 2000; Stone, 2005). However, despite the abundance of body fossils, and unlike other Scottish 'Old Red Sandstone' sites (e.g., Pollard and Walker, 1984. Trewin et al., 2012; Shillito and Davies, 2017), there has thus far been a paucity of trace fossils recorded from the locality: only very recently have putative isolated arthropod scratch marks been described from the site (Flannery-Sutherland, 2021). Here we provide the first report of fish trace fossils from the Achanarras Quarry site; two specimens of *Undichna*, a surficial fish swimming trace that is a common ichnological signature of middle and late Palaeozoic lacustrine rhythmites and turbidites (Trewin, 2000, Minter *et al.*, 2016).

Geologic setting

The Caithness Flagstone Group comprises part of the Scottish Middle Old Red Sandstone (ORS), deposited in a variety of lacustrine, fluvial and aeolian settings (Fig. 1, Trewin, 1986; Brown *et al.*, 2019). Middle ORS sedimentation in the far north of Scotland was initially confined to underfilled half-graben basins, in which individual lakes formed; these later coalesced to form a single lake that filled the Orcadian Basin and spanned a width of 2000 km during the Eifelian (Marshall and Fletcher, 2002; Brown *et al.*, 2019).

The Achanarras Limestone Member was deposited within this overfilled-lacustrine setting, forming a stratigraphic marker horizon that now crops out across north-eastern Scotland (Fig. 1, Trewin, 1986; Marshall and Fletcher, 2002). At its type section in Achanarras Quarry, the member comprises a 3.6 metre-thick succession of parallel laminated siltstones, recording background clastic sedimentation from suspension, interspersed with periodic carbonate and organic laminae (Rogers and Astin, 1991; Andrews *et al.*, 2010). Rayner (1963) interpreted repetitions of these laminae as records of seasonal algal blooms that lowered the pH of the lake, promoting carbonate deposition, prior to bloom die-off that supplied an input of organic detritus. Anoxic bottom conditions in the lake are attested to by the preservation of the organic laminae, cubic pyrite pseudomorphs, bitumen and well-preserved fossil fish (Trewin, 1986).

Material

One specimen containing two trace fossils was discovered and collected from talus at the Achanarras Quarry in May 2019 (Figure 2A). The specimen is typical of the overall lithology at the site, comprising alternating dark grey siliciclastic siltstone and pale yellow-grey fine grained carbonate laminae, in couplets which are 1 to 2 mm-thick, aligned plane-parallel and unbioturbated (Figure 2B).

The specimen consists of both a part (32 cm by 17 cm by 1 cm), incised by crescent-shaped grooves in negative epirelief, and a counterpart (33 cm by 17 cm by 1 cm), which is a cast in positive hyporelief (Figure 3). The trace-bearing surface is dark grey micaceous siltstone in both the part and counterpart.

Ichnology

Ichnogenus *Undichna* Anderson, 1976

The ichnogenus *Undichna* comprises individual or multiple, incised, sinusoidal grooves along horizontal bedding surfaces, which maintain a common alignment. Individual grooves can be continuous or discontinuous (i.e., lacking inner or outer parts of their sine curves). Grooves may occur in sets of one to nine, but paired instances are most common, occurring as any combination of 1) parallel pairs, 2) non–parallel pairs which are a) intertwined or b) separate, and 3) unpaired grooves (Anderson 1976, Higgs 1988).

Undichna britannica Higgs, 1988

One of the two identified traces consists of two discontinuous sinusoidal grooves in antiphase (see Figure 3 and 4A), comprised of eight crescent-shaped incisions. The grooves have a wavelength of 140 mm, individual amplitudes of 20 and 35 mm, and are approximately in antiphase. They are 23 cm long and truncated by the edge of the slab. All incisions have gently-dipping slopes on their concave side and steep slopes on their convex side; six incisions have one to three, narrow, shallow, sharp grooves next to their convex edge. Two of these incisions are 50 and 55 mm from the centre-line.

The trace can be identified as the ichnospecies *Undichna britannica* due to the presence of two overlapping antiphase sinusoidal grooves with different amplitudes (Trewin, 2000; Minter and Braddy, 2006). The trace can be clearly distinguished from sinusoidal invertebrate traces such as *Cochlichnus* due to the size of the trace (*Cochlichnus* is typically less than 1 mm wide), the asymmetric nature and non-uniform diameter of the grooves (steeper on the convex side than concave side) and their highly discontinuous nature (Elliott, 1984).

Undichna isp.

A second, incomplete trace on the same slab consists of two crescent shaped grooves (Figure 4A, 5). Whilst it is likely that this trace has a similar origin to the other specimen, its incomplete nature makes it impossible to draw any firm conclusions. As such, this trace is tentatively assigned to *Undichna* isp..

Discussion

Undichna is interpreted as a trace made by fish swimming close to the substrate – the sinusoidal imprints are the marks of fins contacting the sediment surface (Trewin, 2000). *U. britannica* commonly has discontinuous fin imprints on the outer edges of the trace, interpreted as the imprints of pectoral fins (Figure 4B; Trewin, 2000). This trace is thus interpreted as representing the imprints of pectoral, pelvic and anal fins of a fish in lake-bottom sediment (Figure 4C,D).

Where present, the pectoral fin imprints in previously described *U*. *britannica* are present on both sides of the trace (Figure 4B; Trewin, 2000). However, in this specimen, the pectoral fin imprints are only present on one side (Figure 4C). We suggest that this reflects an instance where the tracemaker was swimming at a roll angle, with fins etching the substrate on only one side of the body (Figure 4C).

The combination of one deep imprint and one to three parallel shallower grooves (without sediment ridges) is best explained by a fin spine and adjacent fin membrane of a spiny-finned fish brushing the sediment (Figure 4D). Acanthodians with this fin structure are well represented in the Achanarras fauna and are present throughout the Caithness Group (Newman, 2010; Burrow *et al*., 2020; Newman *et al*., 2020). As such, organisms such as *Diplacanthus*, *Mesacanthus* or *Cheiracanthus* (Dineley, 1999; Newman, 2010) are the most likely candidates for the tracemaker.

Rayner's (1963) interpretation of the seasonal significance of mineralogically different laminae contextualizes when the traces were registered. The traces are recorded between two siltstone laminae – implying that they were contemporaneous with background sedimentation (rather than the summer algal bloom events recorded by the organic and carbonate laminae - see Donovan, 1980; Andrews *et al*., 2010). Their presence refines our understanding of the sedimentation in the lake – they are an instance of a true substrate (Davies and Shillito, 2018) and so the fact that they are recorded implies the fish were swimming close to a substrate that was in stasis (i.e., not undergoing active sediment accrual; also evidenced by the presence of shrinkage cracks - e.g., Rayner, 1963). As such, deposition of siltstone laminae in the Achanarras lake should be envisaged not as continuous siliciclastic sedimentation punctuated by algal bloom events, but discontinuous sedimentation of discrete silt laminae, separated by intervals of stasis (i.e., intermittent deposition that could have been disharmonic with any bloom events). The presence of the traces shows that oxygenated lake bottom-water persisted during some such stasis intervals: indicating that some were independent of those lake overturn events that mixed oxic and anoxic water and actively deposited organic matter (Trewin, 1986). A potential explanation for this is that some intervals of lake bottom oxygenation were instead associated with reduced seasonal supply of anoxia-inducing organic matter.

This specimen of *U. britannica* is the first definitive fish trace fossil identified from Achanarras Quarry. Rayner (1963) noted arcuate ridges and depressions which she suggested 'might be attributed to the sweeping action of fins', but concluded instead that they were desiccation cracks. Rayner (1963) also tentatively identified 'wavy anastomosing ridges' as burrows, but Trewin (1986) concluded that these were inorganic structures formed by shrinkage cracks. Although not a trace fossil, Trewin (1986, p. 34) figured a continuous drag mark on a bedding surface which he suggested may have been carved by the passive movement of a fish carcass.

Unusually for lacustrine strata of the Scottish ORS, Achanarras Quarry lacks trace fossils of permanently resident arthropod populations (despite the presence of arthropod body fossils: Anderson *et al.,* 2000). In equivalent strata elsewhere in Scotland, *Undichna* specimens are usually found in association with arthropod trackways and burrows, such as in the Port Dubh fish beds on Kerrara and in the Tillywhandland fish bed in Strathmore (Trewin and Davidson, 1996; Trewin *et al.*, 2012). Shallow bilobate scratch marks have recently been reported from Achanarras Quarry, but these are thought to have been made by doomed arthropods swept into a deep lacustrine setting by sediment flows, rather than animals normally resident at the lake bottom (Flannery-Sutherland, 2021). These traces, along with equivalents from younger lacustrine deposits (Buatois and Mangano, 1995; Minter *et al.*, 2016), show that arthropod traces would be expected to be preserved in the fine-grained substrate of the Achanarras Limestone Member, if they were ever present. The fact that they are absent is thus strong circumstantial evidence for a lack of benthic tracemakers in the original depositional environment, most likely due to lake bottom anoxia.

The Devonian marks an increase in the ecological complexity of lacustrine environments (Park & Gierlowski-Kordesch, 2007, Minter *et al.*, 2016). The spatial variation in these evolving ecosystems is well demonstrated by the lacustrine sediments of the ORS. By the Eifelian, lake margins were occupied by a variety of tracemaker organisms (Donovan, 1980), the open water body hosted a wide range of nektonic species recorded as body fossils, and yet lake bottoms remained essentially barren of life (Minter *et al*., 2016). The *Undichna* reported here are rare examples of trace fossils within a Devonian non-marginal lacustrine environment.

Conclusions

- *Undichna* are the first reported vertebrate trace fossils from the Achanarras Limestone Member and record the action of an acanthodian fish swimming close to the lake bottom.
- The trace-bearing surface is a true substrate that marks a hiatus between the deposition of siltstone laminae, attesting to depositional discontinuity within siltstone packages.
- Trace fossil evidence for nektonic life indicates that oxygen was present near the sediment-water interface of the lake in which the member was deposited.
- The trace fossils record the activity of early pioneers during the Devonian expansion of lacustrine ecospace utilization.

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Figure 1 Geological setting of the Achanarras Limestone Member. A) Location of Achanarras Quarry in the mid-Devonian Orcadian Basin, adapted from Trewin and Davidson (1999). B) Stratigraphy of the Caithness Flagstone Group adapted from Rogers and Astin, 1991; and Newman and Dean, 2005 (with permission British Geological Survey © UKRI 2021 http://nora.nerc.ac.uk/id/eprint/11184/1/IR05160.pdf). Dates from Cohen *et al*. 2013.

Figure 2 Sedimentological context of the trace fossils: A) Outcrop at Achanarras Quarry is dominated by talus, in which the trace fossils were discovered. B) Side view of the counterpart of the trace fossil showing sub-mm thick alternations of siltstone and carbonate laminae.

Figure 3 *Undichna* from the Achanarras Limestone Member. Part (left) and counterpart (right), both illuminated by low-angle light from the right.

Figure 4 Detail of the specimen shown in Figure 3. A) Interpretation of the part, showing two discontinuous sinusoidal grooves (1 and 2) with parallel incisions (purple; 3), and outer grooves (4). A second, separate, instance of *Undichna* s shown at (5). B) *Undichna britannica* morphology, redrawn from Trewin, 2000. C) Schematic of a fish swimming at a roll angle of 20˚ producing a discontinuous trace. D) Posterior of *Diplacanthus tenuistriatus* from Achanarras Quarry (adapted from Newman, 2010, Figure 18), showing possible correlation between pelvic fin spines (1), anal fin spine (2) and anal fin membrane (3) and the trace.

Figure 1

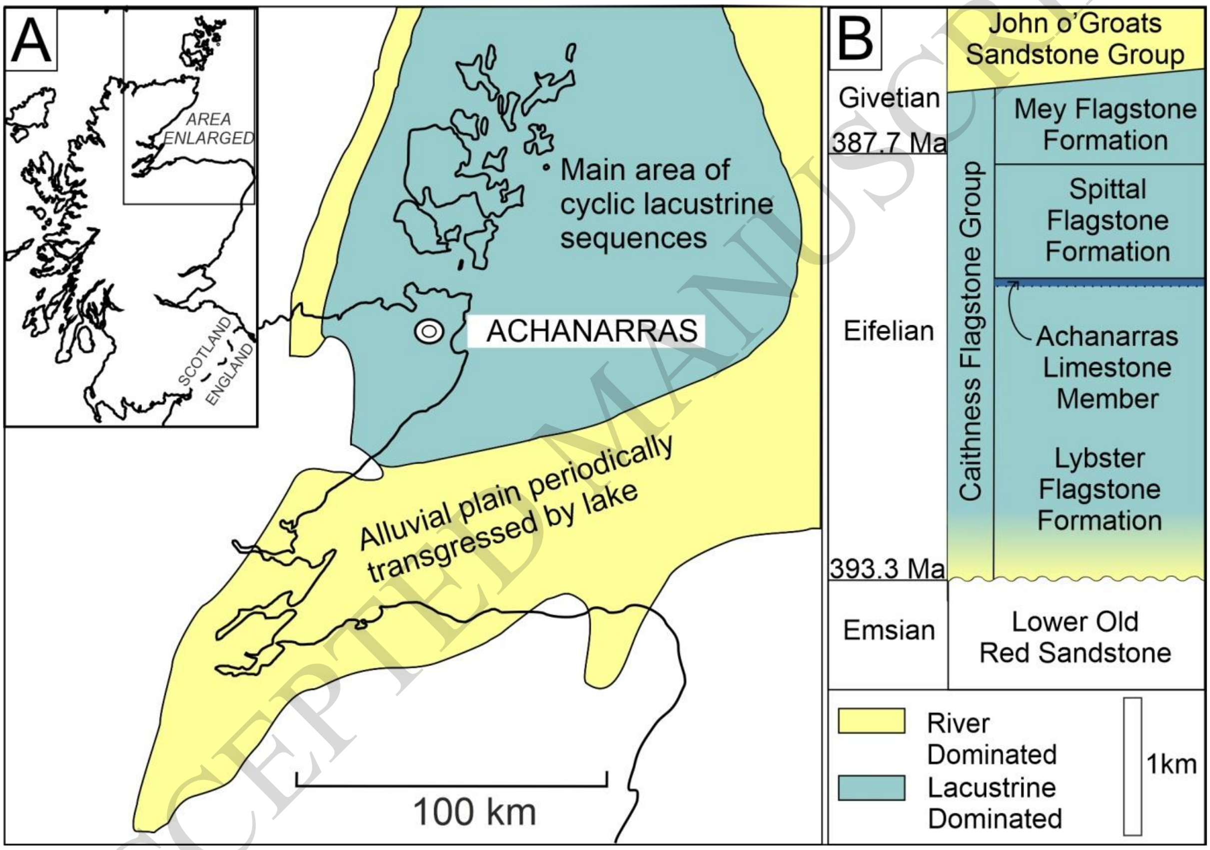
A
AREA
ENLARGED
SCOTLAND
ENGLAND
Main area of
cyclic lacustrine
sequences
ACHANARRAS
Alluvial plain periodically
transgressed by lake
100 km
B
John o'Groats
Sandstone Group
Givetian
387.7 Ma
Mey Flagstone
Formation
Spittal
Flagstone
Formation
Eifelian
Caithness Flagstone Group
Achanarras
Limestone
Member
Lybster
Flagstone
Formation
393.3 Ma
Emsian
Lower Old
Red Sandstone
River
Dominated
Lacustrine
Dominated
1km

Figure 2

Figure 3

Figure 4