

1 **The fish swimming trace *Undichna unisulca* from the Silurian of Sweden:**
2 **probably the oldest vertebrate locomotion trace fossil**

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4 The fish swimming trace *Undichna unisulca*

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6 DIRK KNAUST AND NICHOLAS J. MINTER

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8 *Dirk Knaust* [dkna@statoil.com], Statoil ASA, 4035 Stavanger, Norway; *Nicholas J. Minter*,
9 *School of Earth and Environmental Sciences, University of Portsmouth, Portsmouth,*
10 *Hampshire PO1 3QL, UK, nic.minter@port.ac.uk.*

11

12 **Abstract:** The fish swimming trace *Undichna unisulca* is reported from a sandstone block
13 collected from the Upper Silurian (Ludlow) Burgsvik Formation of Gotland, Sweden. It
14 represents the oldest record of a vertebrate trace (apart from coprolites), predating previous
15 finds from the Lower Devonian by at least 10 Ma. A thelodont or acanthodian fish may have
16 produced the sinusoidal trails with the aid of their caudal or anal fins while browsing slowly
17 over the sediment whilst searching for food.

18

19 **Key words:** Trace fossil, *Undichna*, vertebrate, fish, Silurian, Sweden.

1 The body fossil record of vertebrates extends back to the Early Cambrian (Shu 1999; Janvier
2 2015). In contrast, corresponding trace fossils convincingly produced by early vertebrates are
3 very sparse. To date, the oldest fish trails are no older than Early Devonian (Morrissey *et al.*
4 2004; Wisshak *et al.* 2004). Other vertebrate trace fossils, such as tetrapod trackways, only
5 appear later in the Middle Devonian (Lucas 2015). Vertebrate coprolites are reported from at
6 least the Late Ordovician (Hunt *et al.* 2012). Here, we describe an Upper Silurian example of
7 the fish trace fossil *Undichna* Anderson, 1976. Whilst this discovery pushes back the oldest
8 record of a vertebrate trace fossil (apart from coprolites), there is still a significant and
9 perplexing gap from the vertebrate body fossil record. There is no *a priori* reason not to
10 expect fish trace fossils in Ordovician and Cambrian strata. Indeed, trace fossils often
11 predate the oldest body fossils of their producers; for example, presumed euthycarcinoid
12 arthropod trackways (MacNaughton *et al.* 2002) or tetrapod footprints (Lucas 2015).

13 The reasons why there is a huge time gap between the oldest vertebrate body fossils and
14 vertebrate trace fossils can be manifold and not necessarily mutually exclusive: (1)
15 behavioural - traces may have not been produced by these old forms; (2) taphonomic -
16 traces were not formed in suitable environments for preservation; (3) sampling - traces have
17 simply not yet been found in such old strata. Unlike walking, where an animal moves whilst
18 maintaining intimate contact with a substrate that results in a trackway, this is not necessary
19 with swimming and early fish may have adopted a pelagic over a nektobenthic habit.
20 Coupled with this, traces that were produced would need to have been made in suitable
21 environments to facilitate their preservation. Gibert *et al.* (1999) identified four criteria
22 necessary for the preservation of fish trails: (1) absence or scarcity of infaunal burrowers
23 whose bioturbation activity tends to destroy delicate surface traces; (2) very fine-grained
24 sediment with a certain amount of cohesion to allow the production of traces; (3) low-energy
25 conditions to prevent destruction of the traces; and (4) relatively rapid burial with no erosion.
26 The fossil record is generally poorer further back in time due to the amount of rock that has
27 survived (Raup 1972). However, Ordovician examples are known that contain body fossils of

1 fish associated with mixed *Skolithos-Cruziana* Ichnofacies but specifically lack fish trace
2 fossils (Davies & Sansom 2009). Nevertheless, despite their sparse occurrence, vertebrate
3 trace fossils from the Lower Palaeozoic are complementary to the existing record of
4 vertebrate fossils and therefore provide important information about the evolutionary history
5 of this subphylum.

6

7 **Material and Geologic Background**

8 The studied specimen is a sandstone block (25x20x10 cm) from the Late Silurian (Ludlow,
9 Ludfordian Stage) Burgsvik Formation at Hoburgen, the south-westerly tip of the island
10 Gotland in Sweden. It was recently discovered in the trace-fossil collection of the
11 Senckenberg Institute in Frankfurt Main, Germany, and according to its label it was originally
12 collected by Fritz Kaerlein in July 1964 (Fig. 1). The specimen is inventoried at Senckenberg
13 with the number SMF XXX 902.

14 The fine-grained, grey sandstone is calcite-cemented and contains millimetre-size
15 sulphide concretions. Most of its surface is covered with epichnial grooves and punctate
16 imprints. Internally, the sandstone has a massive fabric but the trails are partly infilled with
17 mud, suggesting that it is part of an interbedded sandstone-mudstone facies association. The
18 bedding surface is slightly worn out, probably due to the sample being eroded by breakwater.

19 The Burgsvik Formation with its basal Burgsvik Sandstone Member is Ludfordian (Ludlow,
20 Late Silurian, ca. 424 Ma) in age, based on a robust conodont and graptolite zonation
21 (Jeppsson *et al.* 2006). The Burgsvik Sandstone was deposited on a delta front during a
22 period of regression (Eriksson & Calner 2008). Compared to underlying and overlying
23 strata, the Burgsvik Sandstone is poor in macrofossils but abundant in terrestrial plant
24 material, indicating freshwater influence. Moreover, vertebrate micro-remains of anapsid,
25 thelodont, osteostracan, acanthodian and actinopterygian fish are commonly encountered
26 (Eriksson *et al.* 2009; Bremer & Blom 2015).

1 **Description and Comparison**

2 The surface of the specimen is riddled by numerous epichnial grooves, of which about 15 are
3 most discernible (Figure 1). Given the comparably small sample size, most trails are only
4 partly preserved, or probably were only partly carved into the sediment. The measurable
5 wavelength of the two most complete trails is about 88 and 118 mm and their amplitude
6 about 6 and 16 mm. Penetration depth of the 1-3 (typically 2) mm wide grooves varies from
7 as deep as several millimetres to very shallow and complete disappearance within a trail.
8 Other trails appear interrupted and show needle-like extensions obliquely penetrating the
9 sediment with varying spacing (up to three per centimetre). Such penetrations also occur
10 isolated and scattered on the sediment surface in association with the trails.

11 The described trails comprise a single sinusoidal wave and thus are consistent with
12 *Undichna unisulca* Gibert *et al.*, 1999, the simplest ichnospecies of *Undichna*. The
13 amplitude/wavelength ratio of 0.07 and 0.14 is characteristic for *U. unisulca*, although
14 absolute measurements are rather at the lower limit compared with the type material of this
15 ichnospecies (cf. Gibert *et al.* 1999). Given its simplicity, there is the potential for confusion of
16 *U. unisulca* with other similar trace fossils. Morphological resemblance exists with the grossly
17 similar sinusoidal burrow *Cochlichnus* Hitchcock, 1858; however, the latter is generally an
18 order of magnitude smaller and includes burrows (Gibert *et al.* 1999; Morrissey *et al.* 2004;
19 Minter & Braddy 2006). *Gordia* Emmons, 1844 (and its potential junior synonym *Mermia*;
20 Uchman *et al.* 2009) also appear as minute winding traces on the bedding plane, including
21 cylindrical burrows (Wang *et al.* 2009) and trails. Superficially, *Dictyodora* Weiss, 1884 is a
22 characteristic trace fossil of the Silurian and may appear with trail-like traces on the bedding
23 surface. In contrast to *Undichna* trails on the bedding surface, *Dictyodora* is a meandering (in
24 contrast to sinusoidal) spreite burrow within the bed (e.g. Benton & Trewin 1980; Orr 1996). It
25 is interpreted as the product of a burrowing organism with a “snorkel” projecting a trace on
26 the bedding surface (Seilacher 2007; Pazos *et al.* 2015). *Dictyodora* is mainly known from

1 deep-marine deposits, an environment that contrasts with the marginal-marine setting of the
2 described *Undichna*.

3

4 **Interpretation and Implications**

5 The ichnogenus *Undichna* Anderson, 1976 is a fish swimming trace containing nine
6 ichnospecies, which are common in subaquatic continental and marine environments of
7 Devonian to Pleistocene age (Minter & Braddy 2006). The ichnospecies of *Undichna*
8 comprise varying combinations of sinusoidal trails produced by interactions of the different
9 fins with the substrate while cruising just above the seafloor. These findings support an
10 interpretation of the behaviour of the producer as slow locomotion whilst searching for food.

11 The late Ludlow Lau Event caused large extinctions of fish faunas with significant
12 ecological reorganizations, during which an acanthodian-dominated pre-event fauna was
13 replaced by a thelodont-dominated post-event fauna (Eriksson *et al.* 2009). The described
14 *Undichna* specimen from the Burgsvik Formation falls within timing of the thelodont-
15 dominated post-event fauna, and the caudal or anal fin of such a fish could have caused *U.*
16 *unisulca* (Figure 2). Nevertheless, the rather dense occurrence of the grooves and their
17 partly interrupted appearance, together with the occurrence of spine-like imprints also
18 suggest acanthodians (spiny sharks) as possible producers; although there are no parallel
19 grooves that would be predicted from the multiple fins and fin rays of an acanthodian as in *U.*
20 *septemsulcata* (Wisshak *et al.* 2004).

21 Morrissey *et al.* (2004) report the hitherto oldest *Undichna unisulca* from the Lochkovian
22 (Early Devonian) of Wales, and Wisshak *et al.* (2004) describe *U. septemsulcata* from the
23 Pragian or Early Emsian (Early Devonian) of Svalbard. Older reports of supposed fish trails
24 remain controversial because of their poor preservation and uncertain age. Gouramanis *et al.*
25 (2003) describe and figure a questionable fish trace from the Silurian fluvio-deltaic Major
26 Mitchell Sandstone (Grampians Group) of Victoria, Australia. The material consists of a

1 series of five curved ridges interpreted as half of a trace being made by the fins of a fish
2 (Gouramanis *et al.* 2003); but they could equally conceivably be produced by an arthropod.
3 The Major Mitchell Sandstone also has a controversial age range from Late Ordovician to
4 Upper Silurian (Ludlow) (Welch *et al.* 2011).

5 Other Early Palaeozoic vertebrate traces include those reported by McNamara (2014),
6 who describes a possible tetrapod trackway from the Tumblagooda Sandstone of Western
7 Australia, the age of which remains uncertain between Late Ordovician and Early Silurian
8 (Kettanah *et al.* 2015). This find would considerably predate the oldest record of tetrapod
9 footprints from the Middle Devonian (Givetian) (Lucas 2015), but it does not fulfil the
10 recognition criteria of tetrapod tracks and trackways and probably results from the activity of
11 an arthropod (Minter *et al.* 2016). Evidence of early vertebrate burrowing remains scattered
12 and does not seem to be older than Late Devonian (reviewed in Storm *et al.* 2010).
13 Morphological transition of such burrows with arthropod burrows, in addition to a reduced
14 size, may be challenging in their distinction from invertebrate burrows. Vertebrate coprolites
15 are also considered trace fossils and convincing forms range back at least to the Late
16 Ordovician (Aldridge *et al.* 2006; Hunt *et al.* 2012), and thus indeed have a fossil record
17 predating the Silurian fish trails from Gotland.

18

19 **Conclusions**

20 Vertebrate trace fossils complement the body-fossil record, may predate them, and bear
21 important information about the behaviour of their trace makers. The reported *Undichna*
22 *unisulca* from the Upper Silurian of Sweden represents the oldest unequivocal fish trace
23 fossil hitherto known, and the oldest vertebrate trace fossil, apart from vertebrate coprolites.
24 It predates the so far oldest record of *Undichna* from the Lower Devonian of Wales
25 (Morrissey *et al.* 2004) by at least 10 Ma. Articulated vertebrate fossils are rare in the Lower
26 Palaeozoic (Friedman & Sallan 2012), and thus trace fossils such as *Undichna* provide

1 important clues to the functional morphology and behaviour of such old vertebrates. Further
2 search will show if more Silurian or even older vertebrate trace fossils emerge.

3

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7

8 **Figure Caption**

9 *Fig. 1. Undichna unisulca*, fish swimming trails preserved on top of a sandstone bed and
10 collected in 1964 from the Upper Silurian (Ludlow) Burgsvik Sandstone of Gotland, Sweden.
11 Palaeontological collection of the Senckenberg Institute in Frankfurt Main, Germany (SMF
12 XXX 902). **A**, Overview of sample with numerous grooves, many of them with a sinusoidal
13 course. Scale bars in millimetres and centimetres. **B**, Line drawing of A, highlighting the most
14 pronounced trails, of which the numbered trails (1 and 2) were measured (see text). The
15 trails in the lower left corner (a and b) are shown in cross section in D. **C**, Detail of A,
16 showing crossing of different trails. **D**, Cross section of trails labelled a and b in B, showing
17 their wedge-shaped pinching out and thus proving their nature as trail instead of burrow (e.g.
18 *Dictyodora*). Scale bars in millimetres and centimetres. Image courtesy of Gunnar Riedel
19 (Frankfurt).

20

21 *Fig. 2. Thelodont producing Undichna unisulca* with its caudal fin (modified after Wilson &
22 Märss 2012).



