# Acanthodian fish trace fossils from the Early Devonian of Spitsbergen

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We describe and interpret *Undichna septemsulcata* isp. nov., from the fluvial Old Red Sandstone deposits of the Early Devonian Wood Bay Formation, of Northern Spitsbergen (Svalbard). Its delicate scratch pattern, comprising one unpaired median groove and three pairs of lateral grooves, all with a regular in-phase sinusoidal wave pattern of equal wavelength, allow the reconstruction of the number, position and relative spacing of the fins. The comparatively high-amplitude median groove is attributed to the main propelling action of the tail or caudal fin, the inner pair of the lateral grooves to the action of the pelvic fins, and the low-amplitude outer set of duplicate grooves to bifurcated pectoral fins, respectively. The in-phase geometric pattern is explained by a distance between the unpaired fin (caudal or anal fin) to the pectoral fins corresponding to one wavelength and a position of the pelvic fins half way in between. The direction of movement and the mode of locomotion of the trace maker (a carangiform to ostraciiform type) are deduced. This analysis is leading to an acanthodian (possibly *Diplacanthus*) as the most probable trace maker. By being Pragian or early Emsian (Early Devonian) in age, according to vertebrate and palynomorph biostratigraphy, these specimens are among the world's oldest trace fossils made by a vertebrate.

Key words: Trace fossils, fish trails, *Undichna*, Acanthodii, Old Red Sandstone, Devonian, Spitsbergen, Svalbard.

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## Introduction

Palaeoichnology is the science which deals with fossilized traces of organisms. By deciphering behavioural patterns of extinct life forms it contributes to our knowledge of biological interactions in general and of past ecosystems in particular. Most of the preserved biological activity of metazoans is recorded in Phanerozoic sedimentary rocks by benthic invertebrates restructuring or partly destroying the substrate they lived within or upon. Such palaeoichnological phenomena are a function of organism morphology and behaviour as well as substrate properties.

Sinusoidal, elongate scratch marks found on bedding surfaces are known in the fossil record and are generally assigned to the ichnogenus *Undichna* Anderson, 1976. They are interpreted as traces of swimming fishes, whose fins penetrate the sediment surface. Provided that most ventral fin tips had contact with the bottom surface and if adequately preserved, the scratch marks allow the reconstruction of the number, position and relative spacing of the fins. In addition, deductions can be made on the direction of movement and mode of locomotion of the trace maker.

Fish traces are long known from the fossil record and the ichnogenus *Undichna* was eventually established by Anderson (1976), who erected the first three ichnospecies *U. simplicitas*, *U. bina*, and *U. insolentia*. Some 25 years later, the revision by Trewin (2000) listed 9 ichnospecies and in 2001 Gibert added one more: *Undichna gosiutensis*. This diversity is hardly surprising considering the wealth of known fossil and Recent fish and their considerably different modes of locomotion.

In the present account we describe and interpret a new *Undichna* ichnospecies, which was recently discovered on the Arctic archipelago of Svalbard.

## Geological setting

The Old Red Sandstone of Spitsbergen (Svalbard) is one of a number of well-known Devonian sedimentary basins filled during the Late Silurian to Late Devonian by clastic deposits derived from the rising Caledonides. Located in roughly equatorial latitude (Scotese and McKerrow 1990), this area saw a rapid increase in terrestrial ecosystem complexity by the interaction of land plants, arthropods and vertebrates. On Svalbard, formerly located at the northeastern part of the Old Red Continent, their remains were deposited together with siliciclastic erosional products in a continental molasse basin. Today, these deposits can be studied along a north–south trending zone in central and northern Spitsbergen (Fig. 1).

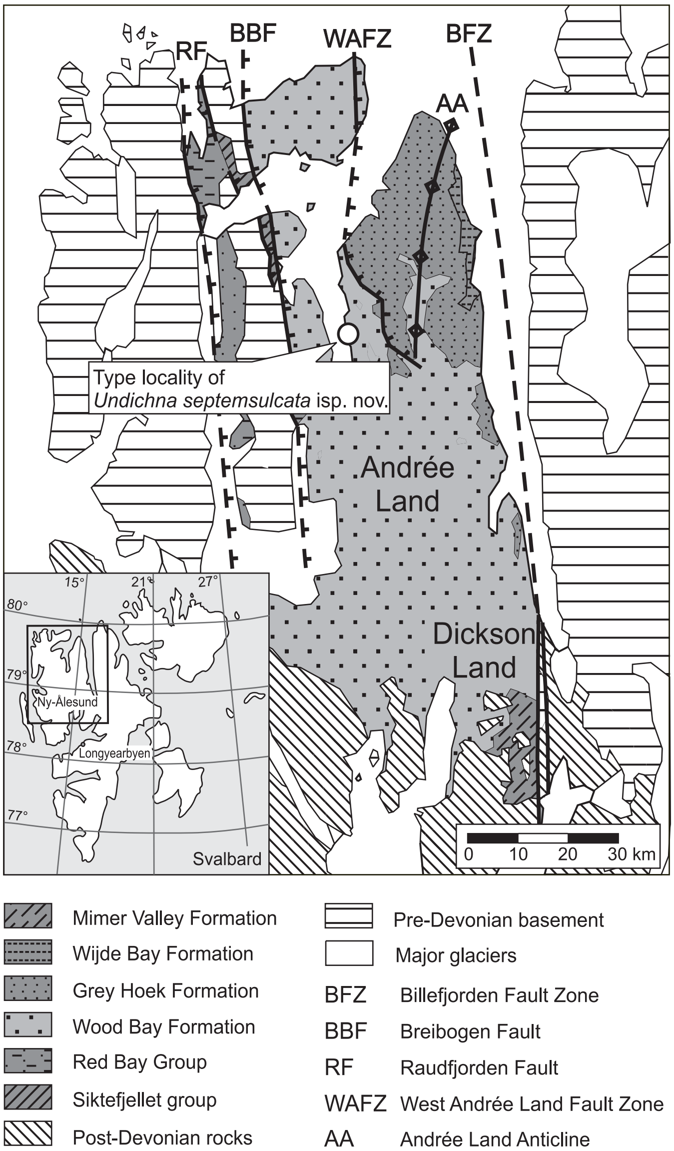


Fig. 1. The structural setting of the Devonian fault graben in NW Svalbard, the distribution of the main Devonian lithostratigraphic units, and the type locality of *Undichna septemsulcata* isp. nov. (modified after Piepjohn and Thiedig 1997 and Harland et al. 1997).

In terms of thickness as well as lateral extent, the Wood Bay Formation accounts for the major part of this sedimentary succession (Friend and Moody-Stuart 1972; Dallmann et al. 2002; Blomeier et al. 2003). It was subdivided by Føyn and Heintz (1943) into three faunal divisions based on vertebrate biostratigraphy: the Kapp Kjeldsen, the Lytka, and the Stjørdalen faunal divisions. Lithostratigraphically, the Wood Bay Formation is subdivided in the Austfjorden-, Dicksonfjorden-, and Verdalen Members (Blomeier et al. 2003), the second one of which yielded the recent *Undichna* finding.

A comprehensive facies model for the Wood Bay Formation was presented by Friend and Moody-Stuart (1972). Based on extensive petrological and sedimentological studies, they suggest three meandering to braided river systems draining from the southwest, south and southeast, respectively, into a northern area of vast clay flats. This model was recently confirmed and refined by Blomeier et al. 2003, who focused on the various sub-environments of this depositional basin.

Since the majority of other occurrences of the ichnogenus *Undichna* have been reported from freshwater settings (Gibert et al. 1999) and only rarely in marine sequences (Gibert 2001), these fluvial bed load and suspended load deposits of a braided to meandering river system, with a large volume of overbank deposition is a typical setting. However, this fact is rather a taphonomic artefact than a real ecologic preference, since by the Devonian, fish capable of producing sinusoidal traces were present in all major aquatic environments.

The trace fossil assemblage encountered in the Wood Bay Formation is dominated by arthropod traces (*Diplichnites*, *Merostomichnites*, *Siskemia*, *Cruziana*, *Svalbardichnus*) besides traces of unknown origin (*Planolites*, *Beaconites*) and is described in detail by Wisshak et al. (2004).

# The Svalbard material

During the 2001 geological expedition of the Norwegian Polar Institute, a fine-grained, laminated sandstone slab, housed at the Paleontologisk Museum in Oslo (PMO), and numbered PMO 169.565, being 36 × 78 cm in size, was recovered from the fluvial middle Wood Bay Formation (Dicksonfjorden Member) at Wigdehlpynten (Western Andrée Land, Northern Spitsbergen). On the slab, the underlying layer is partly preserved, with no distinct difference in lithology. Besides low relief groove casts and an array of common arthropod trackways (predominantly the ichnogenera *Merostomichnites* and *Diplichnites*), it displays two rhythmic patterns of sinusoidal scratch marks, preserved in positive hyporelief (Fig. 2). The more prominent of these scratch patterns (Fig. 2B, C) is arranged in a 30 mm wide, straight trail extending 0.5 m across the slab. It consists of one continuous sinusoidal median groove and three pairs of partly discontinuous lateral grooves. Each groove is a sinusoidal wave with a constant wavelength of about 60 mm. All waves are in-phase and their amplitude decreases from 10 mm to 2 mm with increasing distance from the median axis of the trace. The second specimen (Fig. 2D, E) is less well-preserved and in parts heavily obscured by arthropod traces or sediment. Its path extends about one metre across the slab, describing two sharp turns. The trace is in average only 1.5 cm wide and in contrast to the other trace, the inner lateral grooves are rarely visible.

These specimens do not fit any of the nine *Undichna* species listed in the recent revision of this ichnogenus (Trewin 2000), nor the more recently erected species *Undichna gosiutensis* Gibert, 2001. We thus propose a new ichnospecies, *Undichna septemsulcata*, characterized by the paired double groove with very low amplitude and by the in-phase geometric relationship of all seven waves.

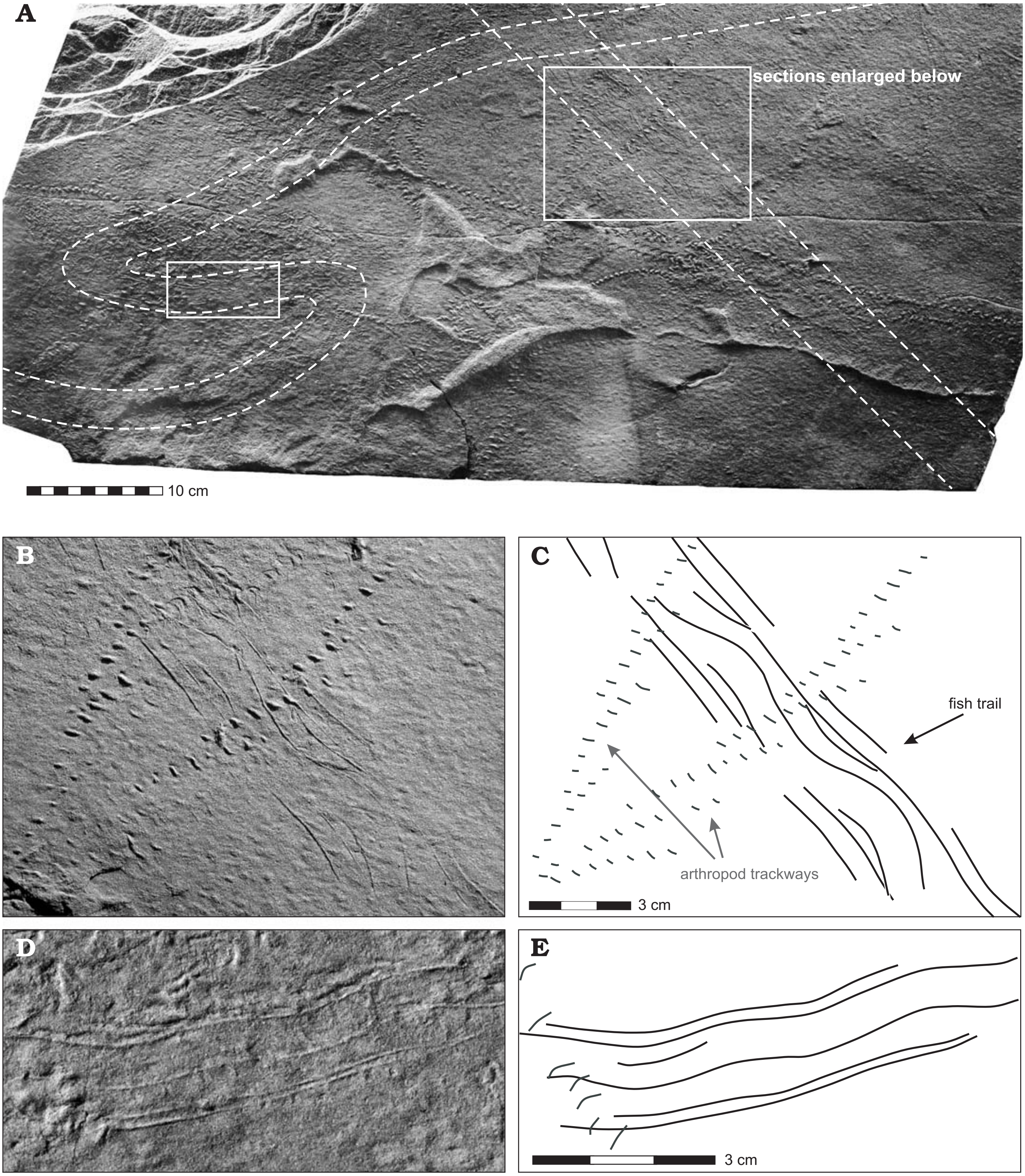


Fig. 2. *Undichna septemsulcata* isp. nov., Early Devonian, Spitsbergen. **A**. Sandstone slab (PMO 169.565) with two specimens of the fish trace *Undichna septemsulcata* isp. nov., and numerous arthropod trackways (ichnogenera: *Merostomichnites, Diplichnites*) preserved as delicate positive hyporelief. **B**, **C**. Enlarged section and line drawing of the holotype specimen of *Undichna septemsulcata* isp. nov., overprinted by two arthropod trackways (*Diplichnites*). **D**, **E**. Enlarged section and line drawing of the second, less well-preserved and narrower specimen.

# Systematic palaeontology

## Ichnogenus *Undichna* Anderson, 1976

*Type species*: *Undichna simplicitas* Anderson, 1976.

*Diagnosis*.—Swimming traces comprising a set of sinusoidal drag marks (incised grooves) with a common wavelength and alignment. Individual drag marks may be continuous, or the troughs/crests may be preferentially absent or preferentially present. There may be up to nine sinusoidal elements in a set; commonly, there are only two, and in some cases just one. Waves occur as (1) parallel pairs, (2) non-parallel pairs which are (a) intertwined or (b) separate, and (3) unpaired waves. These wave types occur in a variety of combinations. The traces are preserved as impressions (and corresponding moulds) on parting surfaces of flaggy rocks (after Higgs 1988; emended from Anderson 1976).

## *Undichna septemsulcata* isp. nov.

Fig. 2.

*Derivation of name*: Latin *septem*, seven, and *sulcus*, a furrow, groove, referring to the characteristic number of groove marks exhibited by well-preserved specimens in "full morphology".

*Type material*: Slab with two traces, the more prominent of which is defined as the holotype (Fig. 2A–C; PMO 169.565).

*Type locality and horizon*: Wigdehlpynten (UTM: 4 79 516 E; 88 14 111 N), West Andrée Land, Northern Spitsbergen, Svalbard. Middle Wood Bay Formation, Dicksonfjorden Member.

*Diagnosis*.—One unpaired median groove and three pairs of lateral grooves, all with a regular in-phase sinusoidal wave pattern of equal wavelength. The lateral grooves have a lower amplitude and may or may not be discontinuous while the continuous median groove has the largest amplitude and does not cross any lateral groove. Differs from all previously described *Undichna* ichnospecies by its outer paired double-groove with a very low amplitude, and by all seven sinusoidal scratch marks being in-phase.

*Description*.—The holotype trace is 30 mm wide and extends over 0.5 m across the slab. The wavelength ($\lambda$) of all waves is ca. 60 mm, and their amplitudes (A) decrease outward from 10 mm (median groove) and 5–6 mm (inner lateral grooves) to 1–2 mm (outer lateral grooves). All waves are nearly or completely in-phase. The median groove is central or laterally slightly displaced, and does not crosscut any of the lateral grooves. The inner lateral groove occasionally crosscuts the inner one of the outer lateral pair of grooves. Individual grooves are sharply incised and up to 1 mm wide. The width of individual pairs (w) is generally near-constant. In contrast to the median groove, the lateral grooves are intermittent, disappearing in the range of their outer maximum amplitude.

*Remarks*.—Since the preservation of the holotype is excellent, the figured pattern is regarded as fully developed and may be modified by the effect of undertracking as well as by the assumed trace maker swimming at slightly varying elevations above the sediment-water interface. The well-preserved "full morphology" and the significant difference to all (fully or incompletely developed) other ichnospecies of *Undichna* justifies the establishment of a new ichnospecies even though it is based on limited material.

# The reconstruction of the trace maker

Can this undulating pattern reveal the morphology of the trace maker or even the direction of locomotion? In fact, this trace displays records of all major elements a swimming fish needs to propel itself by axial undulation (Fig. 3). The median scratch has the largest amplitude and can be attributed to the main propelling action of the tail or the caudal fin. The inner pair of the lateral scratches records the action of the pelvic fins. The outer set of duplicate scratches has the lowest amplitude and can be attributed to double or bifurcated pectoral fins. This interpretation is based on the observation that amplitudes of undulation in a swimming fish decrease from the rear to the front end, while fin spans increase (Bainbridge 1963). The alternating discontinuity of the lateral fin marks results from a rotatory component in the undulatory motion and is possibly amplified by a preservational phenomenon called undertrack deficiency. The oddity that all waves are in-phase can only be explained if the distance between the unpaired fin (caudal or anal fin) to the pectoral fins corresponds to one wavelength, while the pelvic fins were placed half way in between. Locomotion analyses carried out by Bainbridge (1958) and Videler (1993) found that the wavelength of a tail beat equals about two thirds of the animal length in most modern fish, which would give us a rough estimate of 90 mm for the length of the trace maker. The relationship, noted by Bainbridge (1958), in which fish length is about five times the largest wave amplitude (caudal fin), would give an unrealistic body length of less than one wavelength (ca. 50 mm). This discrepancy, however, is less prominent, if we assume that the unpaired groove has been left by the anal fin (with considerably lower amplitude) and the caudal fin was not in contact with the bottom. The approximate pectoral span of 30 mm is recorded by the width of the trace. The pelvic fins reached about half this span.

The direction of travel (from the lower right to the upper left in Fig. 2) can be deduced from chevron ruffling along the scratch marks and from the crosscutting relationship of the pelvic fin marks occasionally overprinting the pectoral fin marks. From the geometric wave pattern alone, the direction of travel cannot be deduced, since all waves are symmetrical and in phase, producing the same pattern in either direction. The slightly offset median-groove is common in *Undichna* (Trewin 2000). This is probably due to a slight current (from the left to the right in Fig. 2), which is as well reflected in sedimentary structures (low relief groove casts) on the same

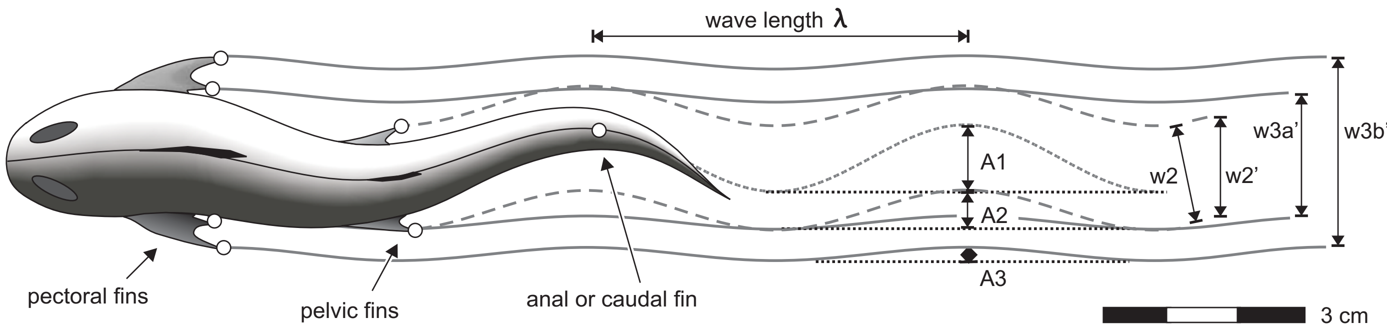


Fig. 3. Idealised trackway of *Undichna septemsulcata* isp. nov. with the geometric properties (A1, A2, A3 = amplitudes of groove waves; w2 = width of paired grooves; w2', w3a', w3b' = apparent width of paired grooves; λ = wavelength) and the proposed trace maker: an acanthodian with bifurcated and spined pectoral fins, spined pelvic fins and a spined caudal or anal fin.

sandstone slab. This slight current, however, does not bias the interpretation of the geometric pattern.

In addition to these morphological details, the mode of locomotion and the flexibility of the fish's body can be deduced from the wave pattern. The extremely low amplitude of the pectoral fins and the moderate amplitude of the unpaired fin indicate a carangiform (fish with tapering tails of medium length; similar to the salmon and most other pelagic fish) to even ostraciiform (fish with relatively rigid bodies and short tails exhibiting very little bending) type of caudal propulsion (Gray 1968).

Bringing all these observations together, and keeping known vertebrate fauna of the Wood Bay Formation in mind (e.g., Blieck et al. 1987; Janvier 1998; Harland 1997), consisting of osteostracans, heterostracans, thelodonts, placoderms, acanthodians and crossopterygians, we can envisage an acanthodian as the most probable trace maker. These early gnathostome fishes experienced their heyday during the Devonian and correspond in size, assumed body flexibility, as well as appendage number, proportions and spacing to the maker of the analysed trace. Additionally, their fossil remains in form of isolated scales or spines of *Nostolepis*, *Onchus*, *Gomphonchus*, and *Xylacanthus*, were reported from the Wood Bay Formation (Harland 1997). In order to have produced the external, double-parallel grooves, the acanthodian travelling above the sediment-water interface and slightly ploughing through it must have had a double pectoral fin spine or two extremely closely positioned pairs of pectoral fins, perhaps with spines. Any significant distance along the body axis between the two pairs would have resulted in a shift in phase, precluding the formation of the equidistant, parallel character of the grooves. As a model candidate for such a trace maker, we propose an acanthodian reminiscent of *Diplacanthus*, whose characteristic features are two rigid spines in each pectoral fin, as well as spined pelvic fins and a spined anal fin. Even though, the earliest *Diplacanthus* known from the fossil record is Eifelian (Benton 1993), and no unequivocal fossil remains are known from the Wood Bay Formation, excluding *Diplacanthus* on these grounds would be based on negative evidence.

# Evolutionary and stratigraphical implications

Another important message is the stratigraphic age of *Undichna septemsulcata*. Coming from the middle part of the Wood Bay Formation, it is Pragian or early Emsian in age according to vertebrate and palynomorph biostratigraphy (Allen 1967; Blieck et al. 1987). It is thus not only older than the bulk of the described *Undichna* specimens, which are recorded from Upper Carboniferous and Lower Permian strata, but it is among the oldest complex vertebrate traces known (together with one short specimen of a simple *Undichna unisulca* from the Lochkovian (Early Devonian) of Scotland figured by Trewin and Davidson (1996), and noted by Trewin 2000). However, there still remains a gap between the oldest vertebrate body fossil record (Ordovician or even older) and the vertebrate trace fossil record (Lower Devonian). Future discoveries could close this gap and contribute to our knowledge of the evolution of vertebrate axial undulatory locomotion.

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