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Traces of dipnoan fish document the earliest adaptations of vertebrates to move on land

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A new trackway produced by crawling fishes, which includes imprints of the trunk, snout, tail, body drag traces, and pectoral fins, was discovered in the Lower Devonian (middle–upper Emsian) marginal marine deposits in the Holy Cross Mountains, Poland. The snout imprints are represented by a low-angle variant of the already described *Osculichnus tarnowskae*, which has generally been interpreted as a hunting trace of fishes. However, in this case, it is considered an imprint of a fish's snout, used for anchoring in the sediment during the locomotion of at least partially emerged fish. This compound trackway provides the first evidence of the previously unknown life behaviour and locomotion abilities of dipnoan fishes in the early stage of their evolution and documents a testing land mobility skills of vertebrates, predating by about 10 million years fully terrestrial tetrapods locomotion traces. Similar trackways are produced by extant lungfish during terrestrial locomotion. The trackway co-occurs with a new resting trace produced by a dipnoan fish supporting itself with one or two pairs of fins on the bottom.

Keywords Dipnoans, Locomotion traces, Lower Devonian, Holy Cross Mountains (Poland)

Locomotion traces of the first vertebrates to colonize land are known from few sites, mainly from Europe and one from Australia[1] with the oldest to date coming from the lower Middle Devonian of the Holy Cross Mountains, Poland[2]. Numerous and variable terrestrial locomotory traces of similar age occur on Valentia Island, Ireland[1,3]. This indicates that tetrapods were capable of efficient locomotion on land already at the beginning of the Middle Devonian and suggests that the origins of quadrupedalism should be sought in Lower Devonian formations.

Trackways and resting traces from the upper Lower Devonian (Emsian) marginal marine deposits in the Holy Cross Mountains, Poland, are presented in this paper. This trackway is a compound locomotion trace attributed to dipnoan fishes. The discovery was made possible through new excavation work at the type locality (Fig. 1A-B) for the fish hunting trace *Osculichnus tanowskae*[4] (Fig. 1C-D), as well as at a new (Kopiec) section (Figs. 1A and 2A). Thanks to 3D scanning, the comprehensive view of the trace fossil assemblage, which includes *O. tarnowskae*, has led to a new interpretation of the traces. A comparison with terrestrial locomotion of some recent fishes strengthens the interpretation. For example the mudskipper *Periophthalmus barbarous*[5] and the osteichthian actinopterygian *Cryptotora thamicola*[6] is capable of performing sequential lateral walking. The resting trace, which co-occurs with the Devonian trackway and is attributed to a fish resting on its fins, contributes to a better understanding of the behaviour of the trace maker.

The interpretation of the presented traces was possible thanks to neoichnological experiments using a modern dipnoan fish, *Protopterus*[8]. When crawling, it leaves complex traces that are almost identically reproduced on the surfaces of Lower Devonian sandstones from the Holy Cross Mountains. This inspired us to analyse the entire set of ichnofossils and present conclusions that relate both to the locomotive abilities of dipnoans and to the Early Devonian environment that prevailed over 400 million years ago in the area discussed.

Geological setting

The sections studied (Figs. 1B and 2B) are exposed in small, abandoned sandstone quarries[4] in the villages of Ujazd (50°42′34.1″N; 21°19′26.1″E; Fig. 1A) and Kopiec (50°42'29.106"N, 21°20'42.514"E, Figs. 1A and 2A)

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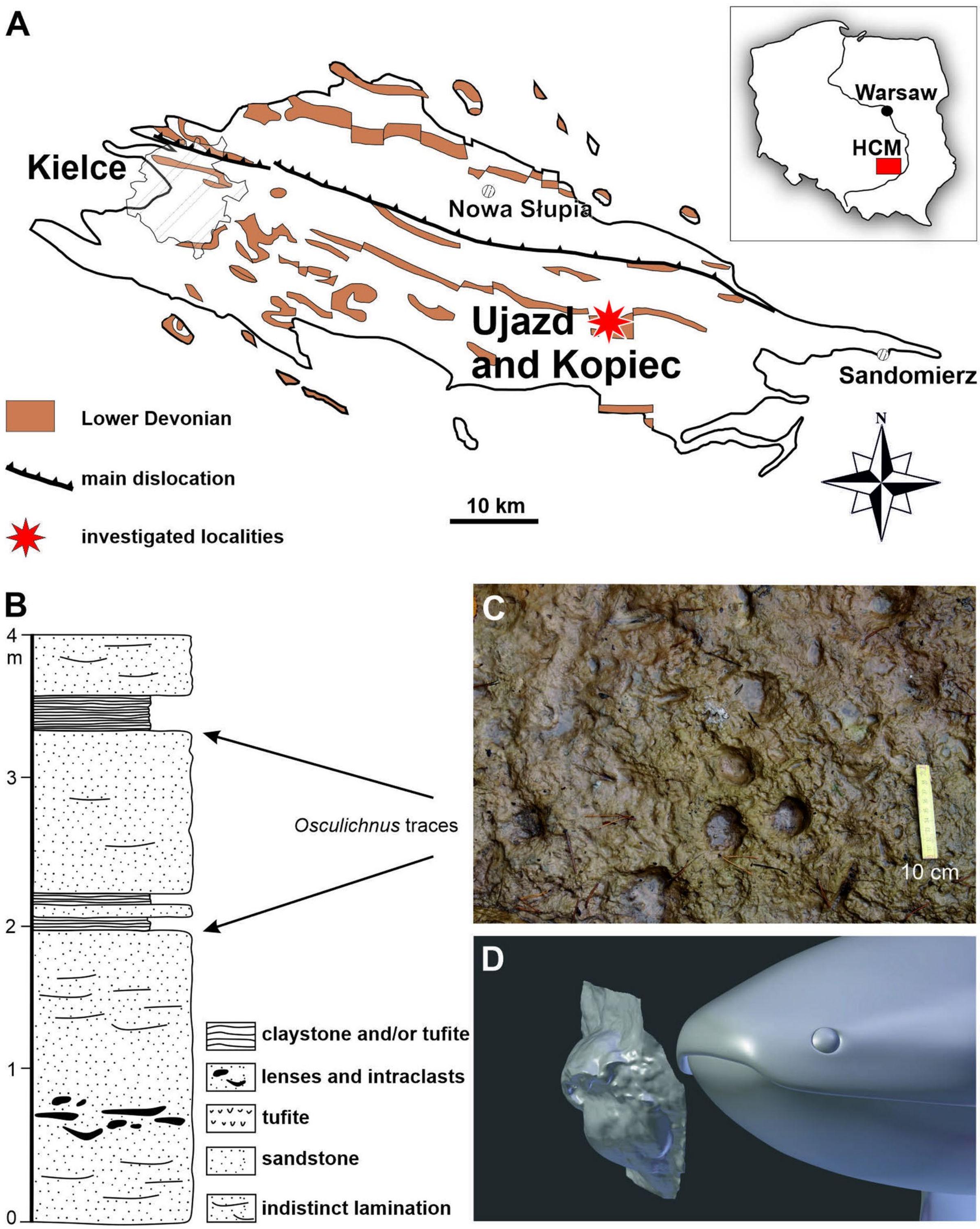

Fig. 1. Location of the investigated outcrops at Ujazd and Kopiec. **A**. Location map in the geological sketch of Holy Cross Mountains (HCM), Central Poland. **B**. Studied section at Ujazd with trace fossil horizons marked. **C**. A photograph of the part of the trace-bearing horizon. **D**. Comparison of 3D reconstruction of the snout with trace fossil in lateral view[4].

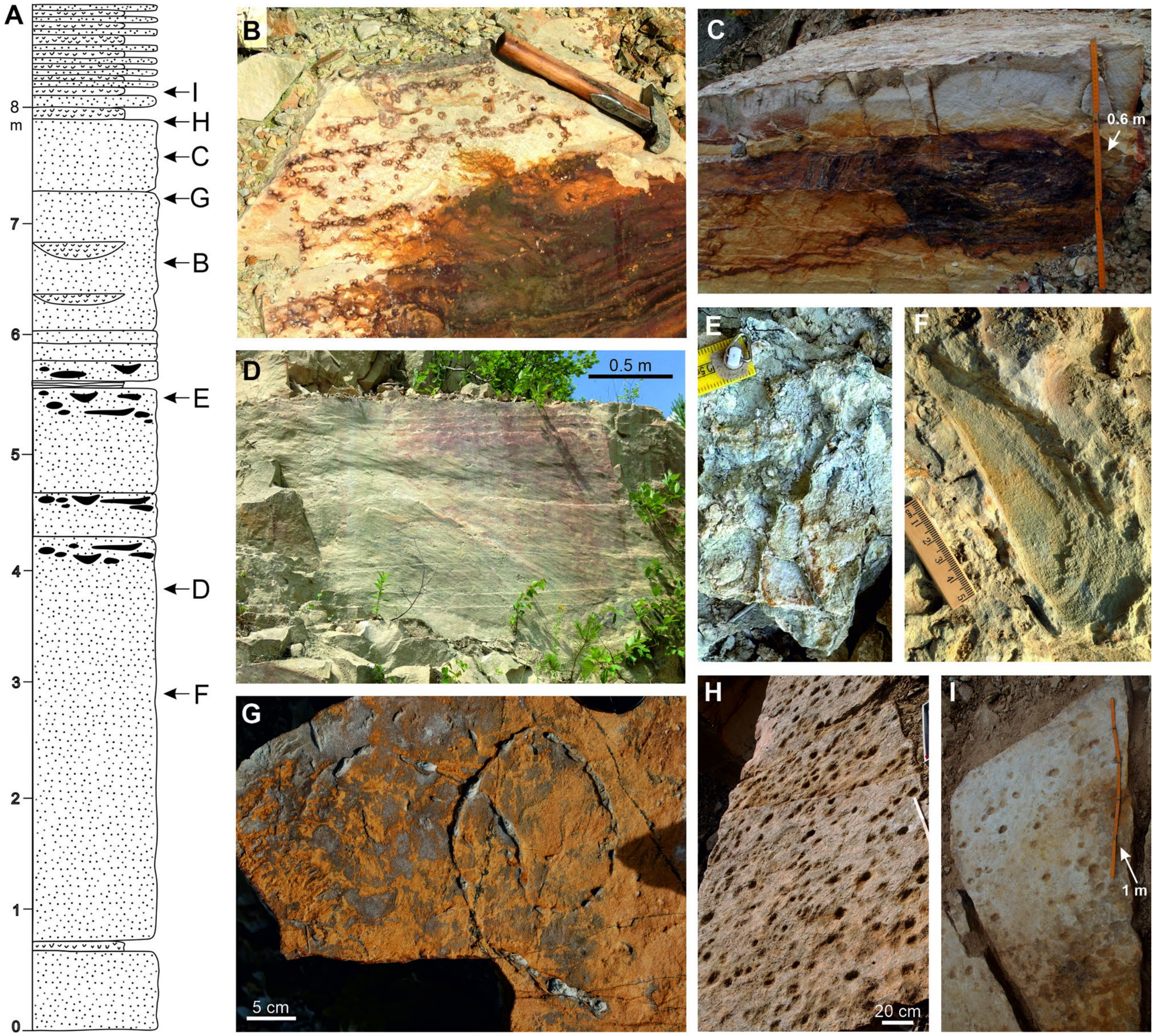

Fig. 2. Details of the section exposed at Kopiec quarry. **A**. Studied section at Kopiec with sedimentological and paleontological phenomena marked with capitals on the profile. **B**. Cross-section of the sandstone block with root traces and paleosol levels visible (specimen in the field). **C**. Cross-section of the sandstone block with an iron-rich paleosol level (specimen in the field). **D**. Thick sandstone bed with cross-stratification (specimen in the field). **E**. Desiccation cracks. **F**. Surface of the sandstone bed with intraclasts containing bones of vertebrates. **G**. Lower surface of the sandstone bed with the trace fossil *Lockeia* (specimen in the field). **H-I**. Upper surface of the sandstone containing numerous trace fossil *Osculichnus*.

near Iwaniska, adjacent to the NW–SE road from Iwaniska to Staszów, in the central part of the Holy Cross Mountains, about 190 km south of Warsaw. The examined material comes from the Lower Devonian (Emsian) siliciclastic deposits of the central part of the Holy Cross Mountains. Trace fossils are preserved in sandstones formed in a marginal marine environment, with numerous manifestations of emersion and settlement by terrestrial vegetation (Fig. 2B-I; Supplementary information 1).

Description

The trackway

Reptanichnus acutori igen. et isp. nov. (Supplementary information 2)

The trackway *Reptanichnus acutori* igen. et isp. nov. is composed of elements showing different morphologies. They include a sinuous or almost straight elongated depression on the upper bedding surface, accompanied by two types of longitudinal, narrow furrows and bilobate pits, which are a variant of the trace fossil *Osculichnus tarnowskae*[4] originally described from the Ujazd section. The elongate depression (Fig. 3A–C) measures 20–30 cm in width, up to 10 cm in depth, and can extend over 1 m in length. The accompanying furrows are either straight or curved, V-shaped, up to 11.5 mm wide, up to 12 mm deep, and up to 70 mm long (Fig. 3A–C). The

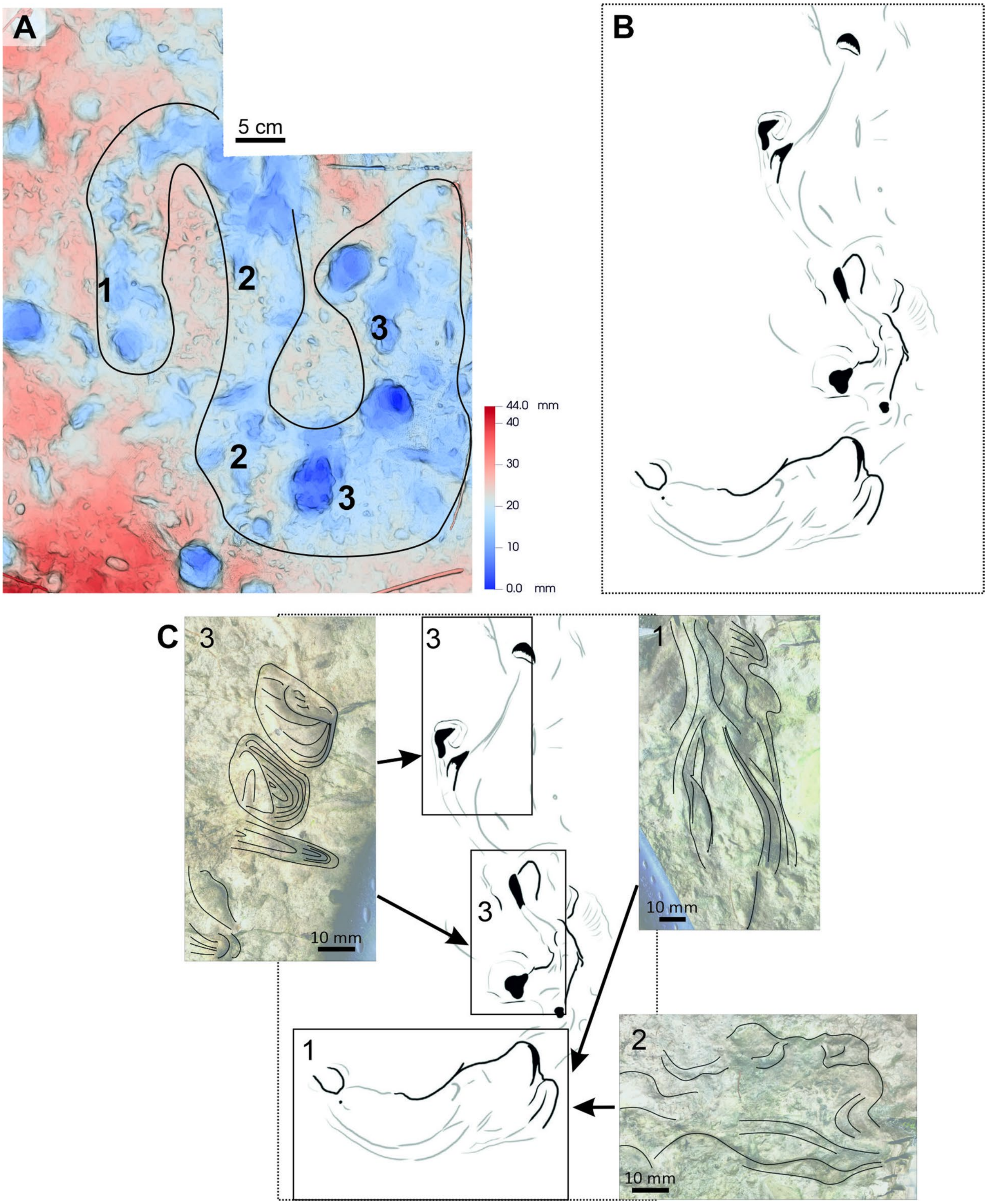

Fig. 3. Upper bedding surface of the sandstone bed containing the holotype of the trackway *Reptanichnus acutori* igen. et isp. nov. (Muz PGI-NRI 1733.II.438). **A**. 3D scan of the trackway with sinusoidal route preserved with different stages of the movement marked with rectangular. **B**. An outline of trace left by extant dipnoan fish[8]. **C**. Particular elements of the trackway containing furrows, shallower (1) and deeper (2) and imprints of mouth (3). All elements compared to the contour of the movement of extant *Protopterus*[8].

furrows gradually or abruptly narrow and shallow towards both ends, eventually disappearing at a distance of 15 mm. The slopes of the furrows exhibit subtle corrugations or indistinct oblique ribs which incline in the same direction on both sides, or occasionally on only one side of the furrow (Figs. 3, 4A-B and 5). Additionally, there are shallower furrows, measuring 3.5 mm in depth and 10 mm in width, which display a few more distinct

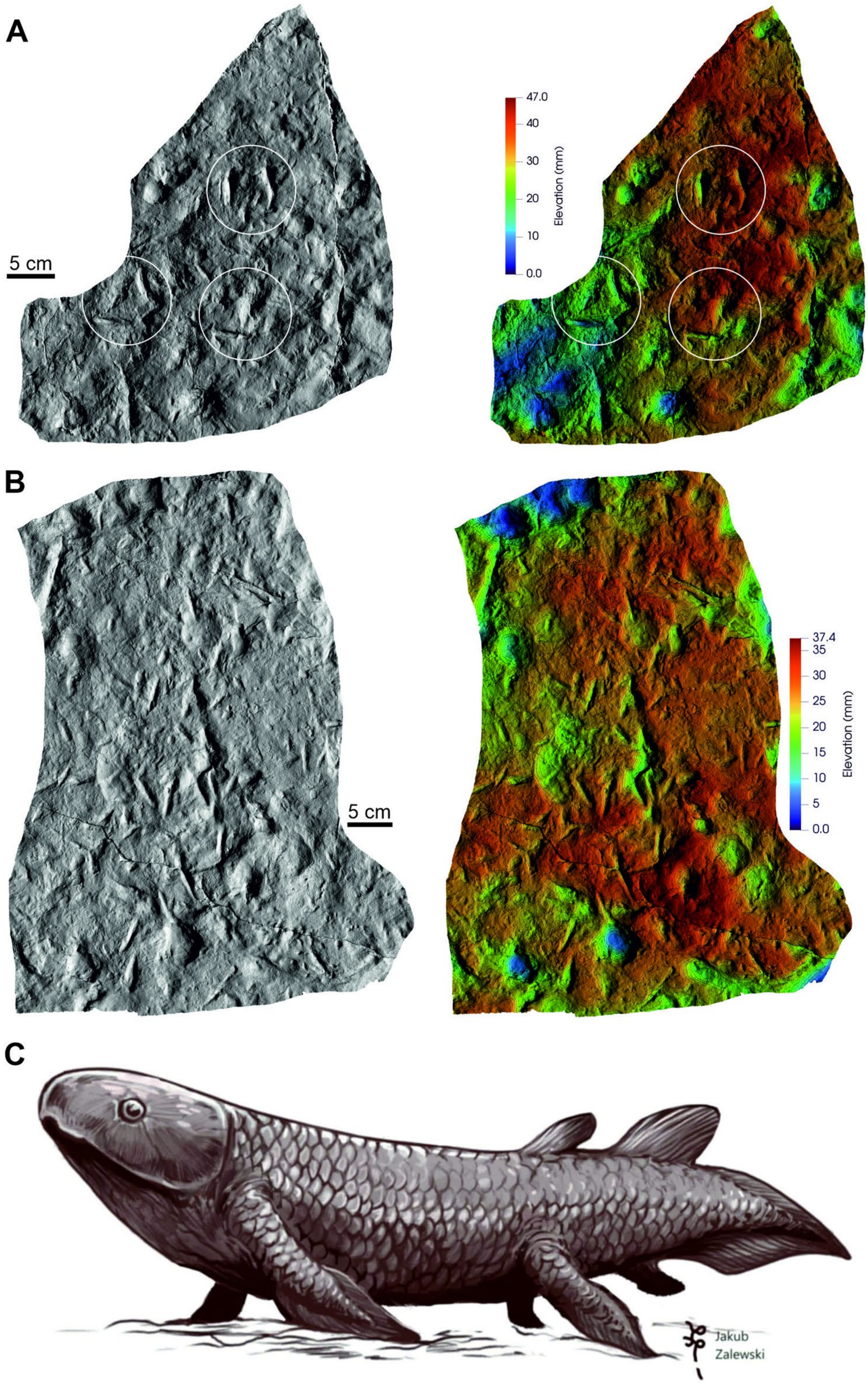

Fig. 4. 3D scans of the upper bedding surfaces with *Broomichnium ujazdensis* isp. nov. (specimens in the field) **A**. Specimen no Muz PGI-NRI 1733.II.442. Three pairs of fins imprints marked with circles. **B**. Specimen no Muz PGI-NRI 1733.II.443. Several pairs of *Broomichnium ujazdensis* isp. nov. arranged linearly. **C**. Reconstruction of how *Broomichnium ujazdensis* isp. nov. were created (drawn by Jakub Zalewski).

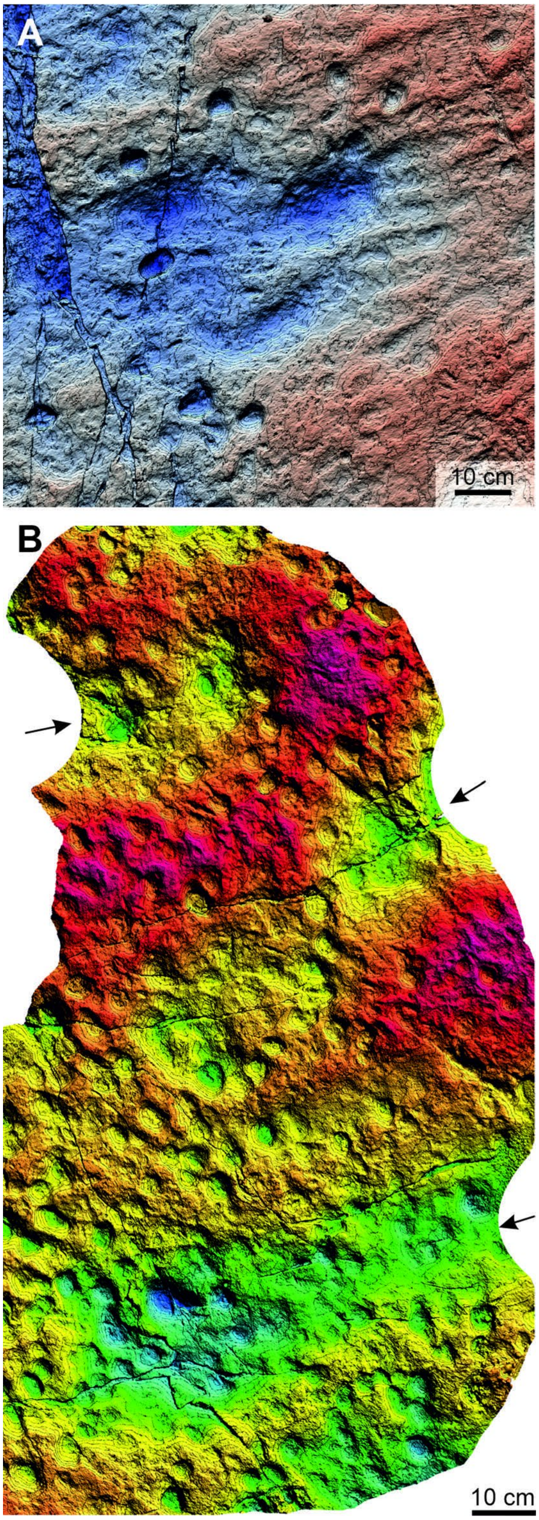

Fig. 5. 3D scans of *Reptanichnus acutori* igen. et isp. nov. (specimens in the field). **A**. Specimen no Muz PGI-NRI 1733.II.444 single depression with few mouth imprints at margins. **B**. Specimen no Muz PGI-NRI 1733.II.445. Three depressions marked with arrows.

oblique ribs, 1–1.5 mm wide, located 2–3 mm apart. These furrows, although short, are generally co-aligned to the overall shape of the depression.

Both the longitudinal sinusoidal depressions and the furrows are associated with *Osculichnus*, though they do not overlap with it. Instead, *Osculichnus* occurs on the both sides (Fig. 3). Originally, *O. tarnowskae* was characterized as an epichnial, generally bilobate shallow pit, up to 20 mm deep, mostly elliptical or crescentic in outline, with a smaller and a larger lobe separated by an undulating furrow. In some specimens, a deeply arcuate line or, more commonly, a trapezoidal depression replaces the line. The surface inside the pit is undulating, with additional wrinkles. Various morphotypes are common[4].

The morphometric parameters of *O. tarnowskae* reveal two statistically significant populations. The first concerns traces with a width of 39–57 mm, and the second with a width of 64–77 mm. The second population does not occur in the trackway and shows no correlation between width and length, whereas the first population demonstrates a correlation between the width of the trace and the width of its narrower lobe. Ten of 185 specimens displaying only one asymmetric lobe were noted[4]. These specimens were formed by a fish tilted to one side—always to the left. This was interpreted as an example of left-handedness in vertebrates. This paper supplements those observations with 26 new cases out of a total of 240, including one exceptional instance of a right tilt. Of the entire set of traces, almost 11% are twisted, of which 97% are twisted to the left.

The resting trace

Broomichnium ujazdensis isp. nov. (Supplementary information 2)

Some of the straight grooves described in the trackway *Reptanichnus acutori* isp. nov. are arranged symmetrically as single pairs, or more rarely, as double pairs, where they are parallel to each other in one pair and angled towards each other in the other (Fig. 4A-C), approximately 3–3.5 cm apart. The angle between the grooves in each pair is about 40°, but they do not touch each other. The converging ends of the grooves are 15 mm apart, while the diverging ends are about 30 mm apart. In three instances, double pairs of grooves were observed (Figs. 5A-B and 6A-B), with one pair consisting of longer grooves (about 3 cm long), facing each other at an angle of about 40° with the converging and diverging ends measuring 15 and 30 mm apart, respectively. The second pair is approximately 35–40 mm apart from the first and consists of grooves that are slightly wider (about 5 mm) and shallower (up to 0.5 cm) than those in the first pair. The two grooves from this second pair are parallel or nearly parallel, spaced up to 10 mm apart. The orientation of all the traces from such double pairs forms a radial arrangement (Fig. 6A, B).

Discussion

Interpretation of the *Reptanichnus acutori* igen. et isp. nov

The newly discovered trackway is a crucial trace fossil for the analysis presented in this paper. It was produced by a fish moving in extremely shallow water or even across exposed sediment, with at least part of its body emerging. In this state, buoyancy is either reduced or absent, preventing the fish from swimming. Under such conditions, all parts of the body involved in locomotion left different traces (Figs. 3, 4 and 5). The elongated depression was formed by the trunk being dragged across the sediment, partly due to lateral body twists, as reflected in the sinuous stretches, and partly by sliding in straighter stretches. Swimming is excluded because the sinuous pattern characteristic of swimming is absent, unlike in the well documented fish swimming trace *Undichna*. The various ichnospecies of *Undichna* are preserved on bedding surfaces of very fine-grained deposits and display single, paired, or tangled sinusoidal waves. The shape, amplitude, regularity and mutual relationship of these waves reflect the type of fins and manner of swimming of the fish that left them[7].

The longitudinal furrows (Fig. 6A, B), previously interpreted as the invertebrate locomotion trace fossil *Protovirgularia*[4] are here reinterpreted as traces of fins that were raised and lowered, touching the bottom and leaving isolated impressions during the locomotion of the fish. The ribs in some of the furrows may reflect the structure of the fins. The bilobate depressions (low-angle *Osculichnus*) are traces of the snout, which was pushed into the sediment to anchor and create leverage for lifting the body. The fins were used as an auxiliary tool to adjust the movement.

This interpretation of the trackway is supported by observations of the modern West African lungfish *Protopterus annectens*, which leaves characteristic traces when moving on land by rotating its body and supporting itself using its head[8]. The body and fins of primitive fishes rarely leave clear traces on the ground. The exception is when the fish slips during a rotational movement, in which case shallow, sinusoidal traces of the body dragging may appear on soft ground. On sand, due to the lack of cohesion of the substrate, the traces are more irregular and less distinct than on mud. The traces left during pauses in movement do not differ morphologically from those left during continuous movement. As a result, it produces circular headprints that form a left-right alternating series. These imprints are variable and can take the form of single semi-circular indentations or double, more elongated imprints when the fish has its mouth open, with the upper and lower jaws forming separate imprints. The spacing between the imprints is irregular, ranging from 1 to 15 cm, although it is most often around 10 cm[8].

Interpretation of the *Broomichnium ujazdensis* isp. nov

The pairs of furrows were produced by ventral fins of a fish resting on the sediment with its body was raised at low angle enough that only one pair of fins left an impression (Fig. 6C). This corresponds to the behavior of modern lungfish, where the rear part rests on the sediment[9]. A few traces of this type were also found in double pairs. They are imprints of the pectoral and pelvic fins, formed when the entire fish rested on the bottom. It is likely that there are more resting traces, but the recognition of convincing pairs is difficult due to the high density and overlapping of the furrows.

Similar trace fossils are known as *Broomichnium flirii*[10] from late Pleistocene glacial lacustrine sediments. These are characterized by two bilaterally symmetrical two pairs of thin, linear or curved imprints corresponding to the pectoral and pelvic fins, with additional straight imprints in the middle, attributed to the anal fin. They occur either in a series or as solitary traces and have been interpreted as locomotion traces of a bony fish from the family Cottidae, using their pectoral and pelvic fins to "hop" or "crawl[10].

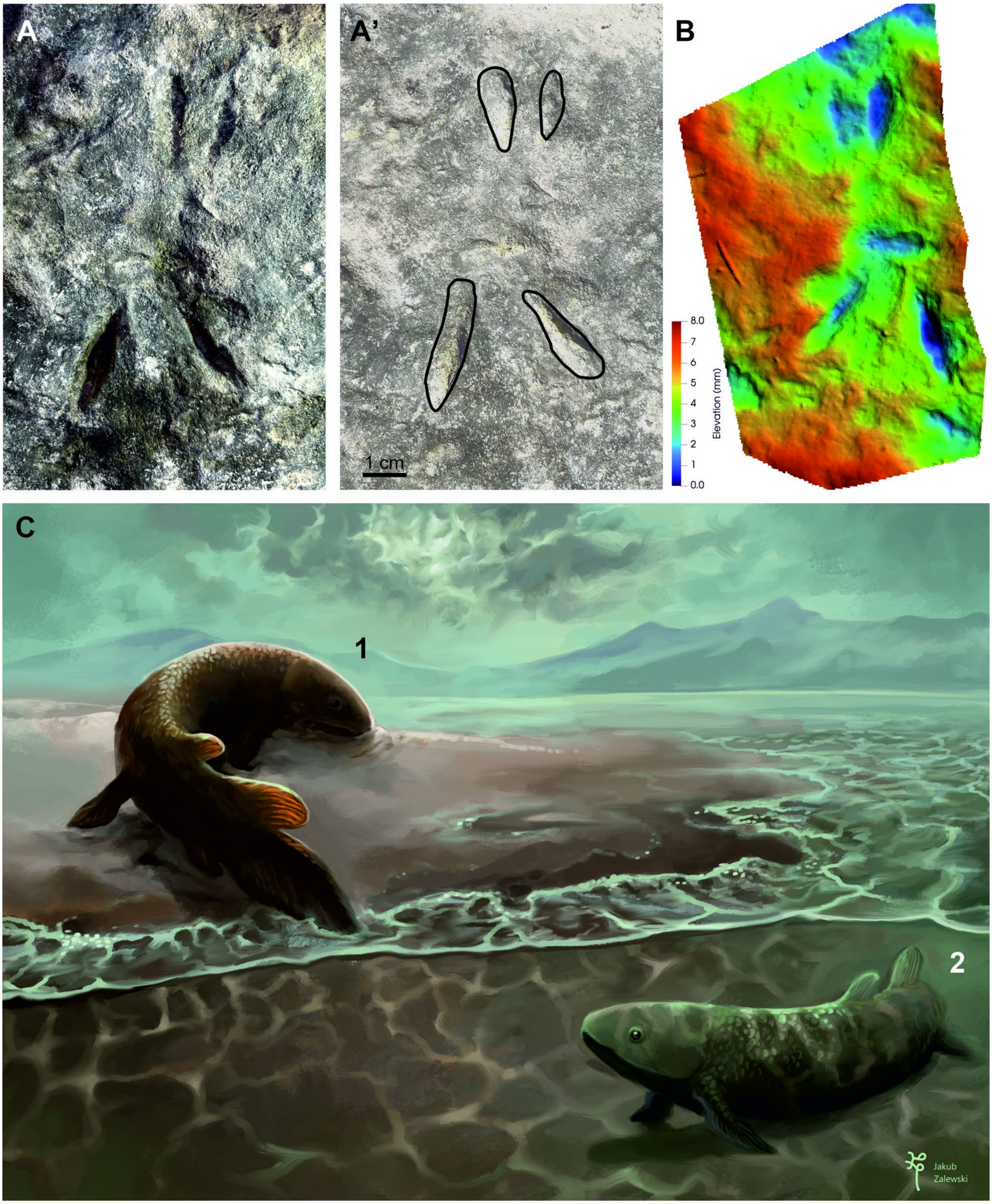

Fig. 6. *Broomichnium ujazdensis* isp. nov. composed of two pairs of fins imprints on the upper bedding surface. **A**. Specimen no Muz PGI-NRI 1733.II.439. Original specimen (protected in the field) with an (A') outline of imprints marked. **B**. 3D scan of the trace. **C**. Reconstruction of how *Reptanichnus acutori* igen. et isp. nov. (1) and *Broomichnium ujazdensis* isp. nov. (2) were created (drawn by Jakub Zalewski).

The trace maker

The identification of the trace maker was discussed already at the stage of the description of the *Osculichnus*[4]. Characteristic features of the imprints that help to identify the trace maker are the trapezoidal outline of the snout in dorsal view, the deep, curved profile of the lower jaw in lateral view, and the presence of a pair of arches in the ventral margin of the upper lip. All of these characteristics match in short-snouted Devonian lungfishes such as *Dipnorhynchus* or *'Chirodipterus' australis*[4]. Since *Osculichnus* is now one of the elements of the described trackway, their production by the same group seems obvious.

Dipnoan fishes have a fascinating evolutionary history that began about 415 million years ago in an aquatic environment. During this time, they made the transition from marine environments to inland waters, where they continue to thrive today[11,12]. At the same time, their anatomical structure has undergone only minor changes, which is why they are sometimes referred to as "living fossils"[11,13]. Some representatives of this taxonomically small group (*Protopterus* and *Lepidosiren*) are capable of surviving in periodically drying water. reservoir. In particular, *Protopterus*[8] can crawl in search of water and, as a last resort, dig a burrow where they enter torpor, awaiting favourable conditions. This ability has been known since the early Triassic, when they first appeared in the fossil record[14]. The fossil record of dipnoan fishes is sparse, particularly from the early stages of their appearance in the Early Devonian. Only a few forms are known from this time: *Melanognathus*[15] *Uranolophus*[16,17] *Jessenia*[18] *Sorbitorhynchus*[19] *Tarachomylax*[20] and *Dipnorhynchus*[21] preserved as more or less complete skull remains. Until the description of the hunting trace fossil *Osculichnus tarnowskae*[4] details of the dipnoans' way of life were inferred primarily from their skeletal remains.

Adaptaions to invasion on land

Adaptations of vertebrates for moving on land are complex and not limited to a single evolutionary lineage, having evolved independently in at least two groups of Devonian vertebrates. The ability to move in very shallow water, where part of the body is emerged and swimming is not efficient, may have been present in early/lower vertebrates[22]. Many fossil fish groups, such as the Late Devonian elpistostegids *Tiktaalik*, *Panderichthys*, and *Elpistostege* adapted to semi-terrestrial environments. Their elongated bodies and eyes positioned on top of their heads helped them to move with a semi-submerged body. Such adaptations suggesting a transition to land were observed in *Tiktaalik*[23–25]. The process of vertebrate terrestrialisation was therefore multi-staged, suggesting that the ability to walk and/or near-walking in very shallow water may have existed even before the appearance of tetrapods. In this context, morphological studies and molecular data on lungfishes show that they are a modern-day sister group to tetrapods[26,27]. These assumptions are strongly supported by the described trackway, which represents the oldest evidence of pre-tetrapod preadaptations and attempts to move in terrestrial or near-terrestrial conditions. By moving towards land, the fishes avoided competition and predation, gaining access to new feeding areas. Feeding was possible during low tide, while non-adapted taxa have had to retreat to the subtidal zone.

Handedness of early dipnoans

The presence of fish snout traces pushed into the sediment, coordinated with the body twisting to the left, was already reported[4] as evidence of an almost exclusive left-handedness phenomenon based on ten trace fossils from the Ujazd section. These observations were later supplemented by an additional 26 traces from the Ujazd and Kopiec sections. The merged dataset of 35 left-turning traces appears to be statistically significant and may represent the earliest known instance of handedness among vertebrates.

Asymmetries in whole-body actions, particularly those with a right-sided predominance, are common across various vertebrate groups, including amphibians, reptiles, birds, and mammals. Existing literature[28] on the evolution of lateralization in vertebrates—the preference of one side of the body over the other—provides information on humans and marine mammals but lacks detailed data on fishes. This right-sided preference[28] primarily controlled by the left hemisphere of the brain, may have originated in early vertebrates, possibly including fishes, even before the development of limbs. However, data from the studied sections suggest that the process of handedness in early vertebrates was more complex and that later right-handedness was not present from the outset.

Overall significance

The surfaces containing the described trace fossils are exceptionally well-preserved because they were covered by tuffite. This coverage prevented further bioturbation, which might have obliterated the traces left by fishes. As a result, the traces have been conserved, and the surfaces represent a form of "true substrate"[29] capturing the original sediment-water or sediment-air interface and recording a period of stasis before subsequent deposition.

The significance of the presented trackway *Reptanichnus acutori* igen. et isp. nov. lies in its documentation of both the locomotory abilities of fishes as well as their preadaptation to terrestrial conditions. It also presents the oldest known evidence of vertebrate movement in the transition between sea and land. Furthermore, it is relevant to the ongoing discussion regarding the interpretation of early tetrapod traces, such as those from Zachełmie[2]. The suggested possibility that these traces originated from fishes[8,30] appears less likely in light of the evidence presented in this paper, as the morphology and development of these traces differ from the Middle Devonian material[2,31].

A neoichnological experiment showing that the tracks left by crawling *Protopterus* resemble those of tetrapods[8] in light of our observations, demonstrated the identical behaviour of this creature on land to that of its Devonian ancestors.

The pattern of tetrapod footprints is different from those of moving fishes primarily through the presence (someplace only subtle) of fingers imprints and regular alignment. However, the additional structures left by the fins and thorax are absent.

An important characteristic of the traces left by the crawling dipnoans is the absence of a clear body midline, which is often present in quadruped traces. Additionally, the trackways of early fishes can display irregular distances between head imprints, although they may become more regular when the animal moved continuously in a single direction. In a palaeontological context, such traces—featuring alternating, evenly spaced, rounded impressions—can be mistaken for those of early tetrapods, particularly in the absence of distinct digit imprints.

Some trace fossils record various behaviours of the trace-maker, with a classic example being the tellinacean bivalve trace fossil *Hillichnus lobosensis*[32] whose morphological elements reflect locomotion, feeding, and ventilation. The described trackway exhibits different morphological elements that are genetically related, although only locomotion is inferred. Nevertheless, different parts of fish's body played distinct roles during locomotion. Therefore, it can also be considered as compound trace fossil, which should be classified under a single ichnotaxonomic name. It further represents an example of structural and developmental complexity[33].

The described trackway *Reptanichnus acutori* igen. et isp. nov. suggests that *Osculichnus* is not necessarily a hunting trace when it forms a part of the trackway. Such trackways can be difficult to recognize if their remaining elements are less distinct. However, *Osculichnus* occurring outside of trackways can still be considered a hunting trace, as demonstrated by examples of younger, Late Devonian trace fossils from China[4,7].

Conclusions

1. A new trackway *Reptanichnus acutori* igen. et isp. nov. produced by a partly emerged dipnoan fish in the sediment is described. It includes traces of the trunk, fins and snout anchoring in the sediment for body leverage. The fins were used as auxiliary tools to adjust movement, leaving characteristic furrows.
2. There are also single or double pairs of furrows (*Broomichnium ujazdensis* isp. nov.), interpreted as traces left by the fish resting on its fins in the sediment.
3. The described trackway *Reptanichnus acutori* igen. et isp. nov. represents the oldest known evidence of vertebrate locomotion in a semi-terrestrial environment, documenting preadaptation to the invasion on land. It also reveals the anatomical capabilities of a sister group independent of the true tetrapod lineage.
4. The oldest presumed evidence of handedness within vertebrates is documented, indicating a preference for left-handedness. This suggests that left-handedness preceded the assumed right-handed preference, at least in lower/early vertebrates.

Methods

About 30 m^2 and about 15 m^2 surfaces with several dozen documented trace fossils are available in situ in the Ujazd and Kopiec sections, respectively. Initially, some partially exposed sandstone bed surfaces bearing trace fossils were excavated, cleaned of debris cover, and washed. Most of the well-preserved fossils were photographed in the field, scanned with a 3D scanner, cast with silicone rubber and protected in situ for further investigation. All casts and original specimens were deposited in the collection of the Geological Museum of the Polish Geological Institute—National Research Institute under numbers Muz. PGI-NRI 1733.II. Casts have been measured and scanned using a 3D scanner eviXscan Loupe + and were then analysed using the BLENDER 2.6 program. 3D scans were made using a hand-held scanner (ZScannerTM 800 h with XYZ resolution 50 mm).

Data availability

All data generated or analysed during this study are included in this article [and its supplementary information files] in the manuscript.

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Author contributions
All authors participated in fieldwork, documentation of fossils and geological phenomena, and their interpretations. P.S. conceived the project and, together with K.G., processed the 3D data and interpretation of the presented material. Environmental interpretations were developed by K.G. P.S. and A.U. prepared the final version of the manuscript, which was accepted by all the authors.

Declarations

Competing interests
The authors declare no competing interests.

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