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Spencer G. Lucas

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# *Thinopus* and a Critical Review of Devonian Tetrapod Footprints

Spencer G. Lucas

New Mexico Museum of Natural History, Albuquerque, New Mexico, USA

Devonian tetrapod tracks and trackways can be recognized by three criteria: morphology of the manus and pes impressions that matches known Devonian tetrapod skeletal morphology, manus smaller than pes, and the alternating trackway pattern that results from lateral sequence walking in quadrupedal tetrapod locomotion. The first reported Devonian tetrapod track, named *Thinopus antiquus*, from Pennsylvania, is not a tetrapod track and is likely an impression of a fish coprolite(s). A critical review of the published Devonian track record indicates only three can be verified as produced by a tetrapod trackmaker—Genoa River, Australia; Easter Ross, Scotland; and Valentia Island, Ireland. The supposed tetrapod tracks from the Middle Devonian of the Zachelmie quarry, Poland, fail the criteria for identification as Devonian tetrapod tracks. Indeed, no convincing case has been made that the Zachelmie structures are tetrapod tracks. Instead, they are reinterpreted as fish nests/feeding traces (ichnogenus *Piscichnus*). The oldest Devonian tetrapod trackway is Givetian and this is the oldest record of a tetrapod, but the sparse record of Devonian tetrapod tracks is of no other biostratigraphic and little paleobiogeographic significance. Bona fide Devonian tetrapod tracks are from nonmarine facies, so they do not support a marginal marine origin of tetrapods. They indicate lateral sequence walking and pelvic-limb-propelled, fully terrestrial (subaerial) locomotion in freshwater environments by at least some Devonian tetrapods.

**Keywords** *Thinopus*, Tetrapod, Track, Trackway, Lateral sequence walking, Devonian, *Piscichnus*

## INTRODUCTION

The origin of tetrapods—classically, the transition from fish to amphibian—was a Devonian event that has been the focus of much research and discussion for over a century. Aside from character evolution and phylogeny reconstruction, much of the discussion has focused on timing and paleoenvironmental context—when and where did the origin of tetrapods take place? In other words, how old is the oldest Devonian tetrapod fossil? And, did the fish-amphibian transition take place in a marginal marine or a freshwater setting?

Address correspondence to Spencer G. Lucas, New Mexico Museum of Natural History, 1801 Mountain Road N. W., Albuquerque, NM 87104, USA. E-mail: spencer.lucas@state.nm.us

The answers to these questions have mostly been based on the body fossil record of Devonian tetrapods and their closest relatives. This record was long only the fossils of *Ichthyostega* and *Acanthostega* from the Upper Devonian of Greenland (Jarvik, 1996). However, in the last few decades, the body fossil record of Devonian tetrapods has been much augmented by the discovery of new genera of tetrapods (e.g., *Elginerpeton*, *Metaxygnathus*, *Sinostega*, *Hynierpeton*, *Densignathus*, *Tulerpeton*, *Ventastega*) and of their nearest relatives, the “tetrapodomorph fishes” (particularly *Panderichthys*, *Elpistostege*, and *Tiktaalik*) (e.g., Campbell and Bell, 1977; Ahlberg, 1998; Ahlberg et al., 1994, 2008; Lebedev and Clack, 1993; Lebedev and Coates, 1995; Zhu et al., 2002; Shubin et al., 2004; Daeschler et al., 2006). Current understanding thus is of a Devonian tetrapod body fossil record from diverse localities and an important record of the tetrapodomorph fishes that are the closest relatives of tetrapods.

Trace fossils of Devonian tetrapods—their inferred trackways—have also played a role in understanding tetrapod origins (Fig. 1). Initially, this role was mostly in efforts to interpret the locomotion of the earliest tetrapods, well exemplified by the discussion of the supposed tetrapod footprint *Thinopus* reviewed below. However, since the 1970s, several records of inferred Devonian tetrapod trackways have been used to illuminate the timing of tetrapod origins and even aspects of that evolutionary history. Particularly significant in this regard was a recent report of Middle Devonian tetrapod trackways from Poland by Niedźwiedski et al. (2010). This record has been used to both push back the origin of tetrapods and to reassess the paleoenvironmental setting of tetrapod origins.

The first published claim of a Devonian tetrapod footprint was by Marsh (1896), of “footprints” he named *Thinopus antiquus*. This ichnotaxon figured prominently in early discussions of basal tetrapod locomotion, but was later rejected as a tetrapod footprint and essentially forgotten. This, however, was done without a careful re-evaluation of the holotype of *Thinopus*, which is undertaken here. Clack (1997) presented a useful review of the ichnological record of Devonian tetrapods (also see Clack, 2000, 2002, 2012). However, I feel that an even

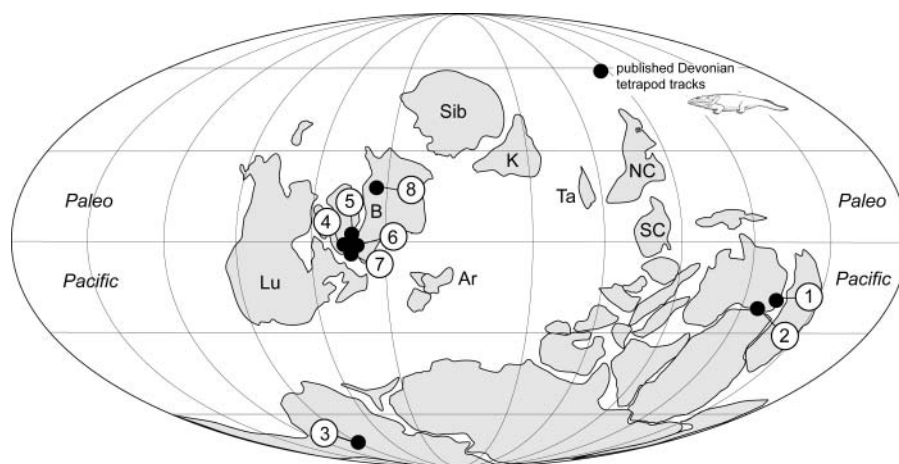


FIG. 1. Map of Devonian continental configuration showing principal tetrapod body fossil localities and localities of putative Devonian tetrapod tracks discussed in the text. Abbreviations are Ar = Avalonia, B = Baltica, K = Kazakstan, Lu = Laurentia, NC = North China, SC = South China, Sib = Siberia, Ta = Tarim. Localities are: 1. Genoa River, Australia; 2. Grampians Range, Australia; 3. Paraná, Brazil; 4. Kap Graah, Greenland; 5. Orkney Islands, Scotland; 6. Easter Ross, Scotland; 7. Valentia Island, Ireland; 8. Zachełmie quarry, Poland.

more critical and current evaluation than she presented is needed. Thus, this paper not only presents a “long lost” reappraisal of *Thinopus*, but also an up-to-date critical review of the Devonian record of tetrapod tracks and trackways and its significance.

## RECOGNITION CRITERIA

Before reviewing the Devonian tetrapod track and trackway record, I identify criteria for the recognition of Devonian trace fossils as tetrapod tracks or trackways. These criteria are implicit in much of the literature on this subject but have not been explicitly articulated.

Assignment of a structure to a Devonian tetrapod must, of course, be informed by the skeletal morphology of Devonian tetrapods. However, what we know about geologically younger tracks and trackways, and what we know about the quadrupedal locomotion of tetrapods, are also important in establishing criteria. These criteria are threefold: (1) track morphology, (2) differentiation of manus and pes, and (3) trackway pattern.

## Footprint Morphology

Single “footprints” attributed to Devonian tetrapods have proven to be highly problematic, as the examples of *Thinopus* and *Notopus* discussed below demonstrate. This is because we lack an extensive Devonian record of tetrapod footprints so that matching such isolated structures to a well-documented range of footprint morphologies and extramorphologies is not possible. In contrast, younger Paleozoic footprint records are extensive, so even isolated footprints can be compared with a well understood range of track morphology and extramorphology (e.g., Haubold, 1971; Voigt, 2005; Fillmore et al., 2010).

The fins of tetrapodomorph fishes all bear endochondral bones partially sheathed in lepidotrichia (Figs. 2 and 3). Furthermore, the proximal portions of the fins were covered with scales. These two features, the scales and lepidotrichia, make it difficult to conceive of any extensive amount of terrestrial locomotion supported by the fins of tetrapodomorph fishes. However, the tetrapod limbs of *Acanthostega* and *Ichthyostega* lack the scales and lepidotrichia (except for a few retained in *Acanthostega*, perhaps to strengthen the foot; Coates, 1996). Instead, they have endochondral phalanges (Figs. 2 and 3).

The skeletal morphology of the limited fossil record of the manus and pes of Devonian tetrapods (Fig. 3) indicates that the manus is short and wide, polydactyl (more than five digits) and has digits that are straight, slightly tapering distally and blunt tipped or pointed. The pes is longer than wide and also polydactyl with digit shapes similar to those of the manus. Typically, Devonian tetrapods are reconstructed with webbed feet, but that webbing is inferential. The inferred limb posture of Devonian tetrapods has been restored as a paddle limb (Ahlgberg et al., 2005) in which the digits face laterally, or a straight limb with forward-directed digits (Jarvik, 1996). Given the lack of an ossified carpus/tarsus in Devonian tetrapods, the skeletal anatomy makes both digit postures possible.

In sum, the footprints of Devonian tetrapods, if well preserved (ideal morphology, no extramorphology) would have a manus wider than long and a pes longer than wide. Both manus and pes would be polydactyl (have more than five digits). The impression of interdigital webbing might be present, and the digits could have been oriented laterally.

## Differentiation of Manus and Pes

Differentiation of the manus and pes is characteristic of tetrapods (Figs. 3 and 4). Indeed, the manus and pes skeletons of

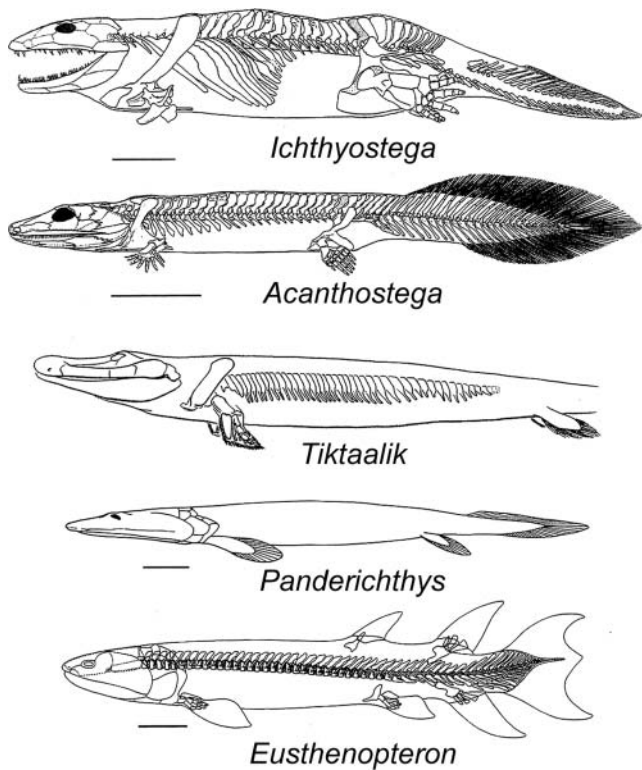


FIG. 2. Lateral views of skeletons and body outlines of selected tetrapodomorph fishes and Devonian tetrapods. Scale bars = 10 cm; note that all of these animals have gleno-acetabular lengths between 19 and 54 cm. After Carroll (2009, fig. 3.1).

early tetrapods, and the pectoral and pelvic fins of their crossopterygian ancestors, differ from each other (Fig. 2). Thus, in Carboniferous-Permian (late Paleozoic) tetrapods, the manus is characteristically smaller than the pes, and it has a different configuration (often is more compact) than the pes (Fig. 4). Very early, differentiation of digit number is seen as well, with a pentadactyl pes and tetradactyl manus common in many late Paleozoic tetrapods (amphibians), mirrored by the well known Carboniferous footprint ichnotaxa *Hylopus*, *Palaeosauropus*, *Batrachichnus*, *Limnopus* and *Matthewichnus* (Haubold, 1971; Fillmore et al., 2010).

Therefore, I expect that we should be able to distinguish the manus and pes in Devonian tetrapod trackways by both size and shape—manus smaller, short and wide, pes larger, longer than wide and manus with the same number or fewer digits than the pes. Nevertheless, this prediction is confounded by the Devonian tetrapodomorph fish body fossil record, which encompasses some animals with larger forefins than hind fins, and a less than clear differentiation of size and shape between the fore feet and hind feet in some Devonian tetrapods (Figs. 2 and 3). Against that are evident Devonian tetrapod trackways (discussed below) that show a size difference between manus and pes impressions. Thus, the balance of data suggest that

there were Devonian tetrapods with a manus smaller than the pes, though other shape differences that might be evident in the track record were likely not present.

### Trackway Pattern

It has long been argued that the primitive pattern of tetrapod walking is an alternating gait (lateral sequence walking), in which the manus of one side is placed forward in sync with the pes of the opposite side, followed by the reverse, so the sequence of limb movement is right forelimb-left hind limb-left-forelimb-right hind limb (e.g., Gray, 1939; Schaeffer, 1941; Hildebrand, 1980) (Fig. 4). This pattern is well documented in living lissamphibians and is evident in all Carboniferous and Permian tetrapod trackways (e.g., Haubold, 1984). In contrast, arthropod gaits produce trackways that are characteristically a set of symmetrical marks (tracks) that define a linear or curved trail that may have a median impression (usually a telson drag mark) or no median impression (e.g., Trewin, 1994). *Diplichnites* is a well-known ichnogenus of Paleozoic arthropod walking traces, and includes the large Carboniferous trails of myriapod-like producers (some of which are as large as 28 cm wide: Schneider et al., 2010).

Only under special conditions could a Devonian tetrapod produce such a symmetrical trail, as this would require hopping or trotting. Indeed, a symmetrical gait in Devonian tetrapods seems highly unlikely given its mechanical demands, which include bending of the vertebral column, rotation of the limb girdles and a large amount of rotation and retraction of the limbs (Pridmore, 1995; Pierce et al., 2012, 2013). Ahlberg et al. (2005) suggested that *Ichthyostega* walked with an alternating gait with a rigid trunk elevated above the substrate, or used an “inchworm” motion with vertical flexure of the lumbar region of the vertebral column. In contrast, Pierce et al. (2012, 2013) argued that *Ichthyostega* locomoted like a modern mudskipper, “crutching” on the pectoral appendage. This would have allowed *Ichthyostega* to make symmetrical gait impressions (“a series of bilateral forelimb impressions” Pierce et al., 2012, p. 525) with the pectoral appendage. However, as in the case of the mudskipper (see below), there would also be a body/tail drag impression(s) unless somehow the animal’s hind limbs and abdomen were water supported while it “crutched” on the pectoral appendage. I thus think it was theoretically possible for a Devonian tetrapod to produce a symmetrical trackway (Edwards, 1977), but the circumstances and mechanism both seem unlikely.

Living sarcopterygian fishes, notably the coelacanth *Latimeria*, use an alternating motion of the fins when slow swimming (Fricke et al., 1987; Fricke and Hissmann, 1991). This suggests that the muscular ability to produce an alternating gait was primitive among sarcopterygians and thus was inherited by tetrapods from their ancestors. Roček and Rage (1994) argued that Devonian tetrapod locomotion on land was by

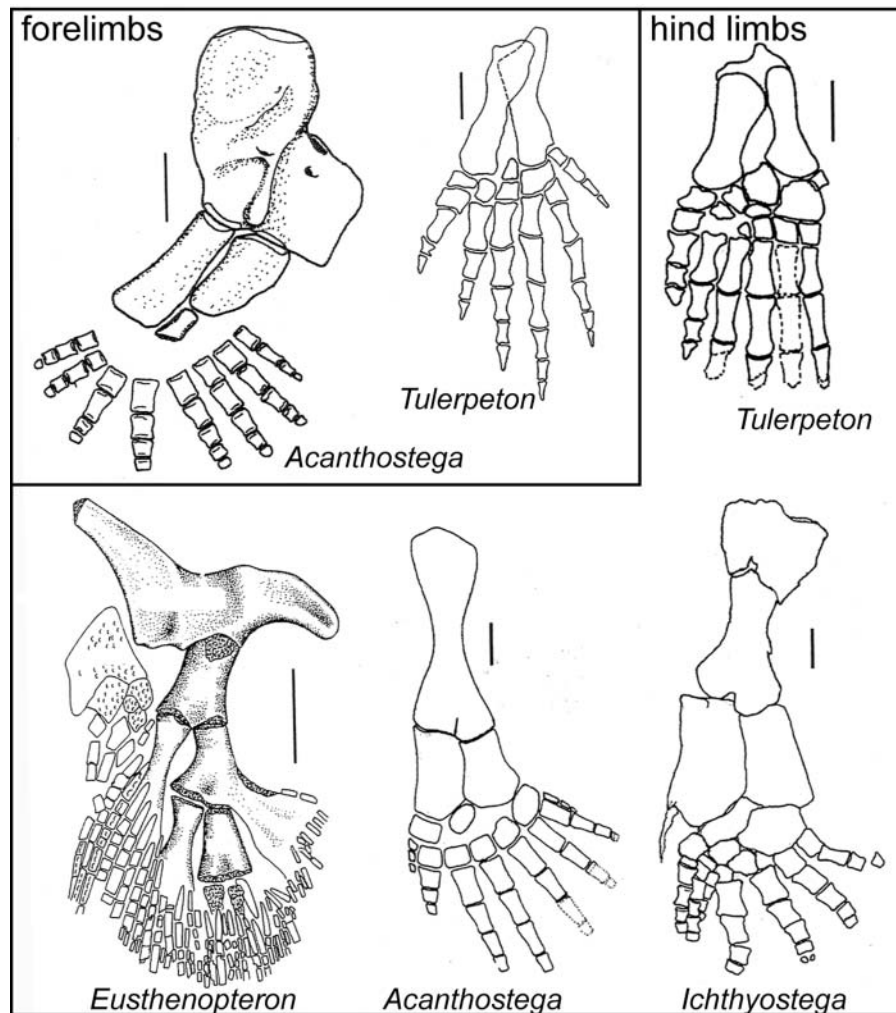


FIG. 3. Selected limb skeletons of a tetrapodomorph fish (*Eusthenopteron*) and Devonian tetrapods (*Acanthostega*, *Ichthyostega*, *Tulerpeton*). Scale bars = 1 cm. After Carroll (2009, figs. 3.9–3.10).

crawling, dragging the ventral part of the body, instead of walking with the body supported by the limbs. They pointed to the heavy ribs and gastralia of *Ichthyostega* as evidence that the animal dragged its abdomen. However, Ahlberg et al. (2005) and Carroll and Holmes (2007) argued that the relatively large and robust limb girdles of *Acanthostega* and *Ichthyostega* indicate that the trunk could be held above the ground.

Indeed, late Paleozoic tracks of amphibians encompass relatively few examples of body dragging (e.g., Haubold, 1971; Voigt, 2005; Lucas et al., 2010; Fillmore et al., 2010). Dragging the body produces tremendous resistance to forward motion and can damage the abdomen—quadrupedal tetrapods habitually avoid doing so—and the footprint record documents this. Thus, a median drag mark is not diagnostic of Devonian tetrapod trackways, though it could be present.

### Walking Fish

Some living fishes locomote on land, the so-called amphibious or walking fishes. They include the mudskippers (Oxudercinae), some catfishes (Clariidae) and the bichir, *Polypterus*. Some other fishes walk subaqueously on the substrate (sea, lake or river bottom), such as batfishes (Ogocephalidae), handfishes (*Brachionichthys*), frogfish (*Antennarius*), some selachians (notably skates) and the African lungfish *Protopterus* (e.g., Helman et al., 1997). Most of the amphibious fishes locomote by using their pectoral appendage—either the fin rays or a pectoral spine—as a “stilt” that is planted in the substrate and used as an anchor around which the body is flexed forward. An exception is the African lungfish *Protopterus*, which does not use such an anchor point. Instead, the lungfish relies on trunk-driven crawling powered by wave-like flexure of the axial musculature (Horner and Jayne, 2014).

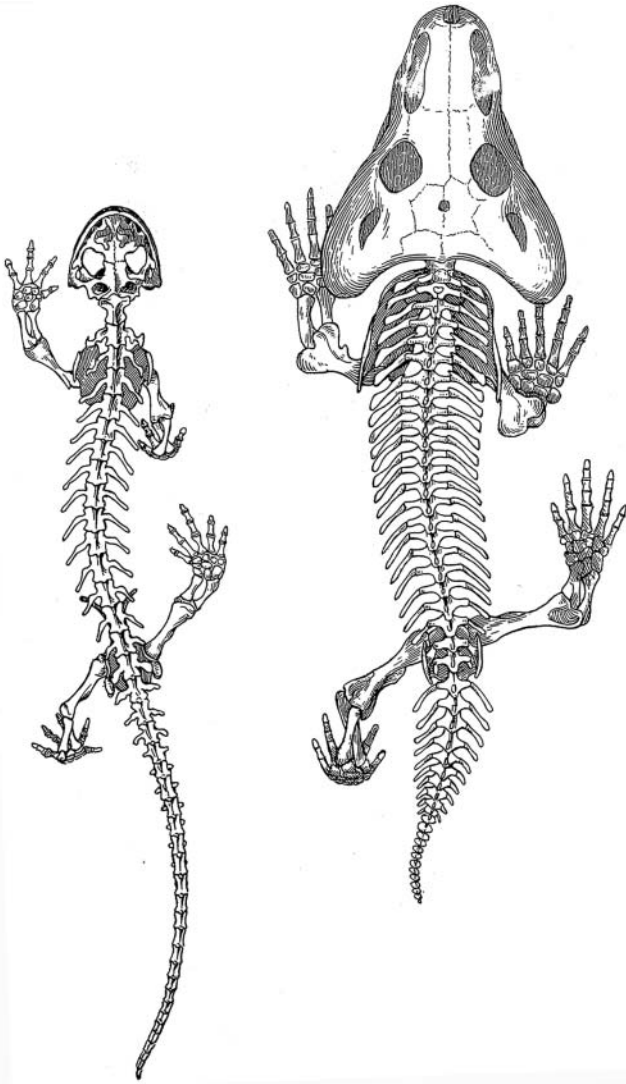


FIG. 4. Dorsal views of skeletons of tetrapods (modern amphibian on left, Permian *Trematops* on right), showing lateral sequence walking and differentiation of manus and pes skeletons characteristic of quadrupedal tetrapods (after Schaeffer, 1941).

There are few data about modern or fossil traces left by amphibious fishes, other than images on the worldwide web or in some publications that give a superficial impression of what such traces look like (e.g., Johnels, 1957; Pace and Gibb, 2009; Kawano and Blob, 2013). I have examined the trace fossil from the Pennsylvanian of Alabama recently described as a “walking fish” trace (Martin, 2014), and it is an underprint of the well-known trace *Undichna*, which represents the sinusoidal impression of one or more fins dragging on the subaqueous substrate (Minter and Braddy, 2006), not a record of a “walking fish.” Nevertheless, despite the absence of an extensive ichnological database, the traces produced by amphibious fishes certainly do not look like a quadrupedal tetrapod trackway. They include the mark of the anchor point and/or drag marks of the body, tail and fins made while the fish pivoted on

the anchor (or crawled without such an anchor). Thus, the locomotion traces of amphibious fishes could not be mistaken for a tetrapod trackway.

Vorobyeva and Kuznetsov (1992) argued that the tetrapodomorph fish *Panderichthys* moved on land by anchoring the pectoral fin, then curving the trunk forward, then anchoring the pelvic fin. This is analogous to locomotion by living catfish that anchor the pectoral spine and then the tail. However, it seems more likely that *Panderichthys* would have anchored the tail, like a catfish. Nevertheless, regardless of the anchor point, terrestrial locomotion by *Panderichthys* would not have produced a trace similar to a tetrapod trackway.

Some living selachians, notably skates, also locomote subaqueously on pelvic fins in an alternating pattern that mimics that of tetrapod walkers (e.g., Pridmore, 1995; Goto et al., 1999; Wilga and Lauder, 2001; Lucifora and Vassallo, 2002). King et al. (2011) analyzed contact locomotion on a subaqueous substrate by the African lungfish *Protopterus annectens* to show that these fishes use their pelvic fins to produce bipedal walking gaits with the body lifted off of the substrate. They thus demonstrated the potential for a lungfish to create a subaqueous trackway with alternating steps of equal-sized footprints (King et al., 2011, fig. 1), and apparently some modern selachians can produce similar trackways subaqueously. However, preservation of such subaqueous tracks seems unlikely. Subaqueous walking by sharks and lungfish has little relevance to the Devonian tetrapod trackway record because the criteria outlined above would eliminate their trackways from consideration as tetrapod produced.

The important conclusion is that no fish leaves a subaerial or a subaqueous trackway that can be mistaken for a quadrupedal tetrapod trackway. The three criteria listed to diagnose Devonian tetrapod tracks/trackways eliminate any terrestrial or subaqueous fish walking trace from consideration.

### An Unlikely Possibility

Let us suppose that the criteria I propose here for the recognition of Devonian tetrapod tracks and trackways do not actually apply, because the foot structure and locomotion of Devonian tetrapods differed fundamentally from those of their Carboniferous-Permian descendants. Such a supposition is implicit in the recognition of some Devonian structures as tetrapod tracks, such as the isolated “footprint” *Thinopus* (does not resemble a tetrapod foot skeleton) or the putative tetrapod tracks from Zachełmie, Poland (mostly symmetrical trackways). This would necessitate that very late in the Devonian and/or very early in the Carboniferous major changes in either tetrapod foot structure or gait (or both) took place. However, both the body fossil and the trace fossil records provide no support for this change. Furthermore, the Devonian tetrapod body fossil and footprint record suggests, as analyzed below, at least different sizes of manus and pes and lateral sequence walking as far back as the Middle Devonian.

**THINOPUS**

The scientific record of Devonian footprint reports begins with Marsh (1896), who published a short article documenting what he identified as Devonian amphibian footprints (Figs. 5 and 6). They consist of a more complete structure that Marsh identified as a left pes impression and a less complete structure that he identified as the posterior end of the left manus impression (Figs. 5A, 6). Marsh stated that the rock containing the “footprints” came from Upper Devonian strata in the town of Pleasant, Warren County, Pennsylvania. Marsh acquired the fossil from Dr. Charles E. Beecher, who identified the stratigraphic horizon as near the top of the “Chemung Formation” in strata that also contain ripple marks, raindrops impression, and mud cracks and that more generally include fossils of both land plants and marine bivalves. Note, however, that “Chemung Formation” is no longer used as a lithostratigraphic unit in Pennsylvania, so the stratigraphic unit the type of *Thinopus* came from is likely the Scherr Formation of Frasnian (Chemungian) age (Harper, 1999).

Marsh (1896) presented a simple line drawing of the “footprints” (Fig. 5A), assigning them the name *Thinopus*

*antiquus*, without diagnosis. By Article 12 of the *International Code of Zoological Nomenclature*, this constitutes an indication, so Marsh’s ichnotaxonomic name is available.

**Description**

The holotype and only specimen of *Thinopus antiquus* is YPM 784, which contains a single, complex structure in concave epirelief that I will refer to as the “footprint” for convenience (Fig. 6). The concave mark at the edge of the rock surface identified by Marsh as part of a manus impression contains little information and may not be related to the more complete “footprint.” The rock matrix that contains the traces is a brownish gray sandstone that is generally fine grained but has coarse grains dispersed through it. Maximum length of the “footprint” is 84.3 mm, maximum width is 64 mm and the depth of the concavity is as much as 9 mm.

The “footprint” is deeply concave, with sharp, well-defined margins that slightly overhang (are constricted around) the concavity. The concavity of the “footprint” is readily divided into two long structures that are joined at one edge. These

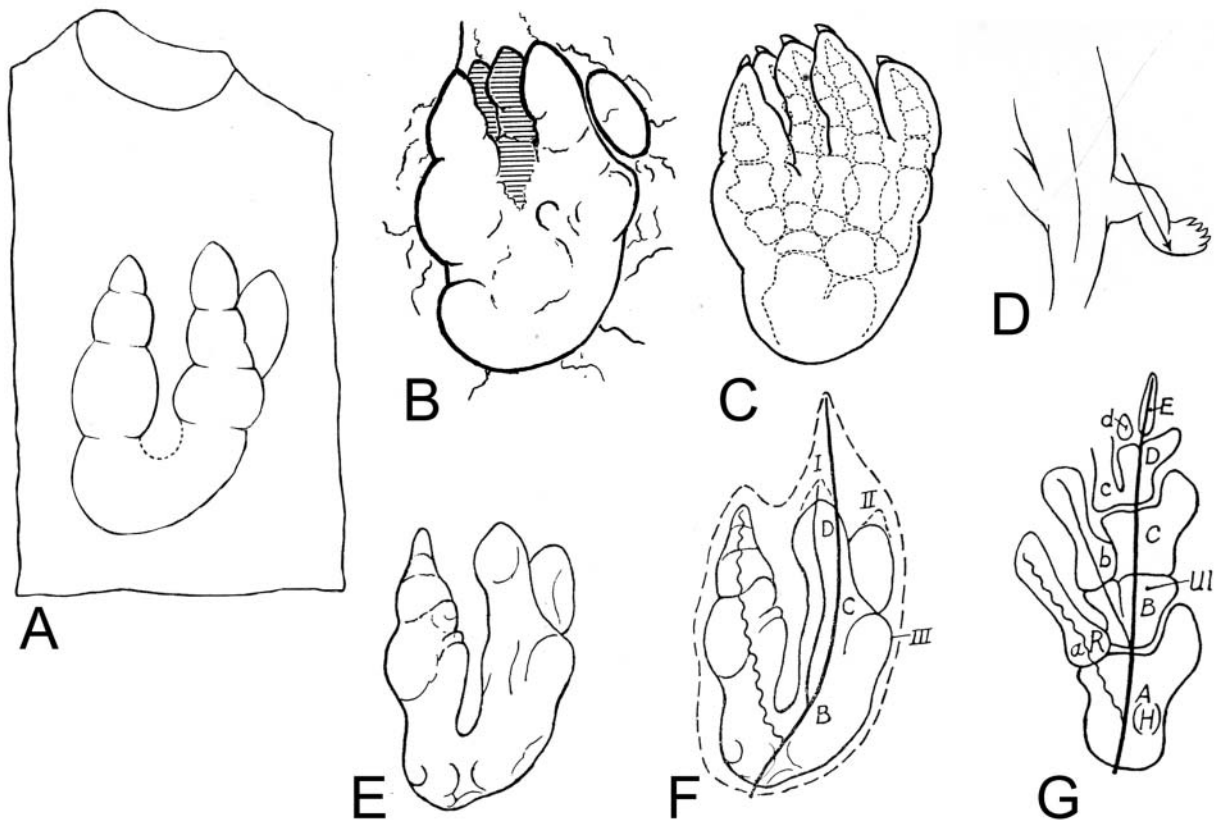


FIG. 5. Published drawings of the holotype of *Thinopus antiquus* (A, B, E), interpretation of that trace (C, D, F) and the proximal fin skeleton of *Eusthenopteron* (G). A, Drawing of the holotype of *T. antiquus* (from Marsh, 1896). B–D, Interpretation of the holotype of *T. antiquus* with five digits (B–C) and right pes with laterally directed digits based on this interpretation (from Morton, 1926). E–G, After Gregory (1951, fig. 11.25), drawing of *Thinopus* “footprint” (E), interpretation of skeletal structure (F) and homologized fin skeleton of *Eusthenopteron* (G). Abbreviations are H = humerus, R = radius, Ul = ulna. For scale, length of “footprint” in A is ~ 84 mm.



FIG. 6. Photograph of YPM 784, the holotype of *Thinopus antiquus*.

have been interpreted as “digits,” which gives the overall impression of a footprint consisting of two or more digits joined at a “heel” and separated by a median sulcus (Fig. 5). One of these “digits” has a very narrowly pointed tip and consists of three bulbous segments separated by marked constrictions. These segments have been interpreted as phalangeal pads (Fig. 5B, E). The other “digit” has a blunter tip and less distinct segments. The two “digits” are joined at one end by a parabolic concavity. To the outside of the blunt-tipped digit there is a distinct concave impression, which has been interpreted as the impression of a third “digit” (Figs. 5B–C, E).

### Discussion

Before the 1930s, *Thinopus* was readily accepted as a Devonian tetrapod footprint and identified as the earliest evidence of amphibians (e.g., Case, 1898; Osborn, 1916; Lull, 1920). Until the discoveries of the ichthyostegalian in Greenland during 1931 (Jarvik, 1996), it was regarded as the oldest fossil evidence of tetrapods. Indeed, *Thinopus* was the basis of

Williston’s (1917) basal tetrapod taxonomic group, which he called the Protopoda.

With regard to its significance, the analyses of Morton (1926) and of Gregory (1951) were particularly significant. Thus, Morton (1926) reconstructed a pentadactyl pes based on the holotype of *Thinopus* (Figs. 5B–C). To do so, he added two crowded central digits on a different plane than the other three digits, and thus argued that the foot had a cupped shape when impressed. He concluded that this pes was oriented during locomotion with the digits facing laterally (outward) (Fig. 5D). Gregory (1951), however, presented a different analysis that identified a manus based on the *Thinopus* holotype that he readily homologized to the fin structure of the crossopterygian fish *Eusthenopteron* (Figs. 5F–G).

Willard (1935) questioned the age of the *Thinopus* type material, stating it is probably Early Mississippian in age based on a personal communication from K. Caster, but did not elaborate. The disappearance of *Thinopus* from the literature of vertebrate ichnology began with Abel (1935, p. 77), who questioned it as a footprint and suggested it is an impression of a fish coprolite. Kuhn (1963, p. 112) listed *Thinopus* as an invertebrate trace fossil without commentary. Häntzschel (1975, p. W188) repeated Abel’s conclusion, listing *Thinopus* with other “unrecognized or unrecognizable genera” of trace fossils. In his comprehensive review of all named tetrapod footprints, Haubold (1971) did not even mention *Thinopus*.

However, although *Thinopus* disappeared from the literature of vertebrate ichnology, it still remained a Devonian tetrapod footprint according to various authors. For example, Pepperell and Grigg (1974), in their identification of laterally-directed digits in a putative amphibian trackway from the Triassic of Australia, referred to Morton’s (1926) interpretation of *Thinopus* indicating laterally directed digits in the earliest tetrapods. Moore (1958, p. 366) listed it in a college geology textbook, and *Thinopus* appeared most recently as a Devonian tetrapod footprint in an encyclopedia of evolutionary biology (Arora, 2003, p. 21).

I agree with Abel (1935) and, by implication, subsequent vertebrate ichnologists who ignored the ichnotaxon, that *Thinopus antiquus* is not a tetrapod footprint. It has too few digits and the wrong digit morphology to meet my criteria for a Devonian tetrapod track. It also lacks the symmetry and any other characteristic morphology of a tetrapod track. The fact that the sides of the structure overhang the concavity (the concavity is constricted at the bedding plane surface) also argues against a footprint, and instead identifies the *Thinopus* structure as the mold of a three-dimensional object with rounded edges.

Abel (1935) proclaimed the holotype of *Thinopus antiquus* a fish coprolite/coprolites, and I concur. It well resembles coprolites, likely made by fish, from the Early Mississippian of Nova Scotia (Mansky et al., 2012, fig. 5). Indeed, I regard *Thinopus* as the earliest ichnotaxonomic name proposed for a fish coprolite (cf. Hunt et al., 2012).



## DEVONIAN TETRAPOD TRACKS AND TRACKWAYS

Some early reports of supposed Devonian tetrapod footprints (e. g., Ami, 1903; Willard, 1935) were shown to be traces left by limulids, ichnogenus *Kouphichnium* (Abel, 1935; Caster, 1938). Here, I review subsequent published records of putative Devonian tetrapod tracks and trackways. To evaluate them, I apply the criteria discussed above. These criteria indicate that few bona fide Devonian tetrapod trackways are known.

### Genoa River, Australia

Warren and Wakefield (1972) published what I regard as a very convincing record of Devonian tetrapod trackways from Upper Devonian strata on the Genoa River in New South Wales, Australia. These are from nonmarine strata of fluvial origin of the Combyingbar Formation of Frasnian age (Young, 2006). Here, two trackways show differentiation of manus and pes sizes, alternating trackway patterns and, in some imprints, evident digit impressions (Fig. 7). One trackway has a clear median drag, and the other lacks a median impression. The estimated gleno-acetabular length of the trackmaker is 22 cm.

Both trackways (see Leonardi, 1987, pl. 11B for the best published photograph) show an alternating pattern and differentiation (by size) of the manus (smaller) and pes (larger) (Fig. 7). The trackway without a median drag impression preserves overstepped, broad and short manus impressions smaller than pes impressions that are longer than wide. Some of the manus and pes impressions have at least five, short and blunt, laterally-directed digit imprints. The other trackway

shows a definite median drag mark and well-separated manus and pes impressions that lack definition.

Clack (1997) drew attention to how different the two trackways are, and argued that no known Devonian tetrapod could have made the tracks unless they were made subaqueously. However, Pridmore (1995) posited that the same kind of animal moving at different speeds produced the two different trackways, and I agree with that assessment. Associated mudcracks suggest the tracks were impressed subaerially (Young, 2006), and this would apparently exclude *Acanthostega* and *Ichthyostega*, so a more likely candidate for trackmaker is a tetrapod similar to *Tulerpeton* (Clack, 1997, p. 241). My conclusion is that the Genoa River trackways meet the diagnostic criteria outlined above, so they are tetrapod trackways made subaerially, in a nonmarine setting.

### Grampians Range, Australia

Warren et al. (1986) described a “tetrapod trackway” from the Grampians Group at Glenisla in the Grampians Range in eastern Australia and attributed it to a tetrapod. This trackway has been assigned an Early Devonian (Turner, 1986; Warren, 1991) or Late Silurian (Gourmanis et al., 2003) age, and is no younger than either of those age assignments (Young, 2006). Milner (1993) accepted this trackway as the oldest record of tetrapods, though he hesitated to conclude that it demonstrated an origin of tetrapods in eastern Australia. Based in part on the Genoa River tracks discussed above, some workers (Panchen, 1977; Janvier, 1977) had argued for an origin of tetrapods in eastern Gondwana. In contrast, Roček and Rage (1994) questioned the trackmaker of the Grampians trackway as a tetrapod and identified it as a “rhipidistian” trackway lacking the median body drag.

However, as noted by Clack (1997), this trackway lacks an alternating pattern and instead has what she referred to as a “ladder” pattern that I would describe as indicative of a symmetrical gait. Furthermore, there is no evident differentiation (based even on size) of manus and pes imprints, and the imprints themselves lack clear definition. Clack (1997) therefore expressed skepticism of attributing this trackway to a tetrapod, and I reject this attribution.

Indeed, Gourmanis et al. (2003) recently attributed the Grampians trackway to an arthropod and identified it as *Diplichnites*. They interpreted the depositional environment of the tracksite as a nonmarine sheetflood on a delta plain. The tracks appear to have been impressed subaerially, in part because there are associated raindrop impressions. George and Blicek (2011), however, regarded the Grampians trackway as tetrapod tracks made in an Early Devonian marine environment, and this was repeated by Schultze (2013). Instead, the Grampians tracks are not tetrapod, were not made in a marine environment and are of Late Silurian age. These arthropod tracks need to disappear from discussions of tetrapod origins.

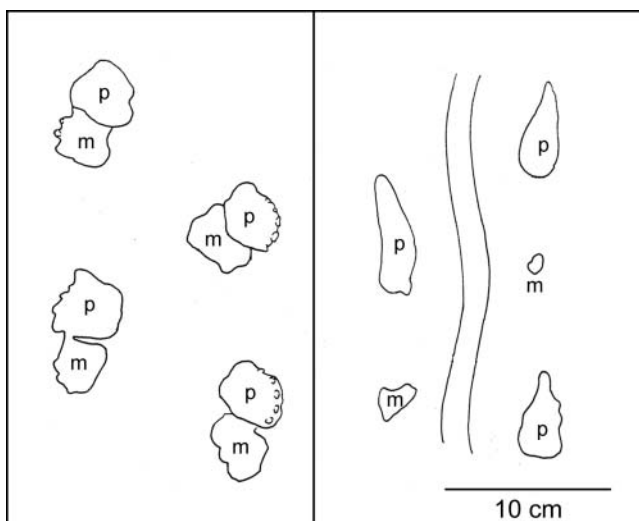


FIG. 7. Drawings of parts of the Genoa River, Australia, tetrapod trackways (after Warren and Wakefield, 1972). The trackway on the left has overstepped manus and pes impressions and appears to show laterally oriented digits. The trackway on the right has a median drag and poorly preserved manus and pes impressions. Abbreviations are: m = manus, p = pes.

## Brazil

Leonardi (1983) described a structure from the Middle (Givetian) or Upper (early Frasnian) Devonian(?) Ponta Gross Formation of Tibagi, Paraná, Brazil that he identified as a single ichthyostegalian? left manus track (also see Leonardi, 1982, 1994) (Fig. 8). The Ponta Gross Formation also yields marine brachiopod fossils as well as invertebrate traces and plant fragments, so the depositional setting of the “track” appears to be shallow marine (Leonardi, 1994, fig. 11a). Leonardi (1983) named the “track” *Notopus petri*, making it the second (after *Thinopus antiquus*) ichnotaxonomic name applied to a supposed Devonian tetrapod track. Milner et al. (1986), Milner (1993) and Stössel (1995) accepted *Notopus* as a Devonian tetrapod track.

Roček and Rage (1994), however, noted that this trace has only four digits that are relatively long and curved, far fewer and morphologically very different from any known polydactyl Devonian tetrapod foot. Therefore, *Notopus* fails my criterion of identifying a Devonian tetrapod track by its morphology, in this case, the shape and number of digits. So, I agree with Roček and Rage that it is not a tetrapod track.

Roček and Rage (1994) re-interpreted *Notopus* as a trace similar to the starfish trace fossil *Asteriacites*, though they hesitated to make a definite ichnotaxonomic reassignment. Indeed, *Notopus* differs from *Asteriacites*, which has thinner, longer and less curved arm impressions and is much smaller, having a diameter less than ~ 32 mm (e.g., Seilacher, 1953; Mikulaš, 1992; Mángano et al., 1999). Therefore, *Notopus* may be an ophiuroid trace fossil, but it is not a synonym of *Asteriacites*.

As an isolated sedimentary structure, the holotype of *Notopus* is, like the isolated holotype of *Thinopus*, difficult to

attribute to a tracemaker with certainty. Clack (1997, p. 237) concluded that “it should be treated with extreme caution as a record of a Devonian tetrapod,” but I go further and simply reject *Notopus* as a Devonian tetrapod footprint.

## Greenland

Friend et al. (1976), fig. 35, pl. 28) illustrated and briefly described two trackways from the Devonian Kap Graah Group in eastern Greenland. These trackways occur on a sandstone surface as two long, curved trails of symmetrically arranged marks without median traces (Fig. 9). Friend et al. (1976, p. 64) suggested that these trackways “might have been made by an early tetrapod” but concluded that “their regularity [meaning their symmetry] and lack of overprinting suggest to us that these tracks were not formed by tetrapods” (pp. 65–66). I concur, and identify these as arthropod trackways of relatively large size, with trail widths up to 20 cm. Friend et al. (1976, p. 66) discussed but rejected an arthropod tracemaker because “no fossil of such large arthropods are known from fresh-water strata of Devonian age.”

However, even larger arthropod trackways assigned to *Diplichnites* are now known from Devonian strata (e.g., Smith et al., 2003; Braddy, 2004). Therefore, I feel confident in identifying the Kap Graah trackways as arthropod made, and they likely are assignable to *Diplichnites*. Instead, Friend et al. (1976) identified the tracemaker as the placoderm fish *Bothriolepis*. They thus envisioned the fish touching the bottom simultaneously and regularly with its pectoral fins while swimming. Given that no such fin traces are known from the fossil record, I regard this interpretation as interesting, ergo fanciful, speculation.

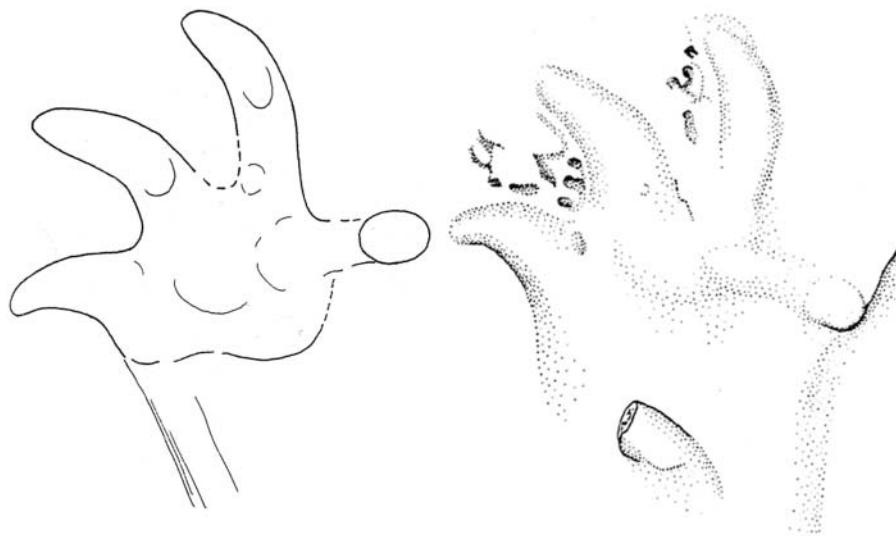


FIG. 8. Two drawings of the holotype of *Notopus petri*, from the Devonian of Brazil. Drawing on left after Leonardi (1983), on right after Roček and Rage (1994). For scale, total width of the “footprint” is about 71 mm.

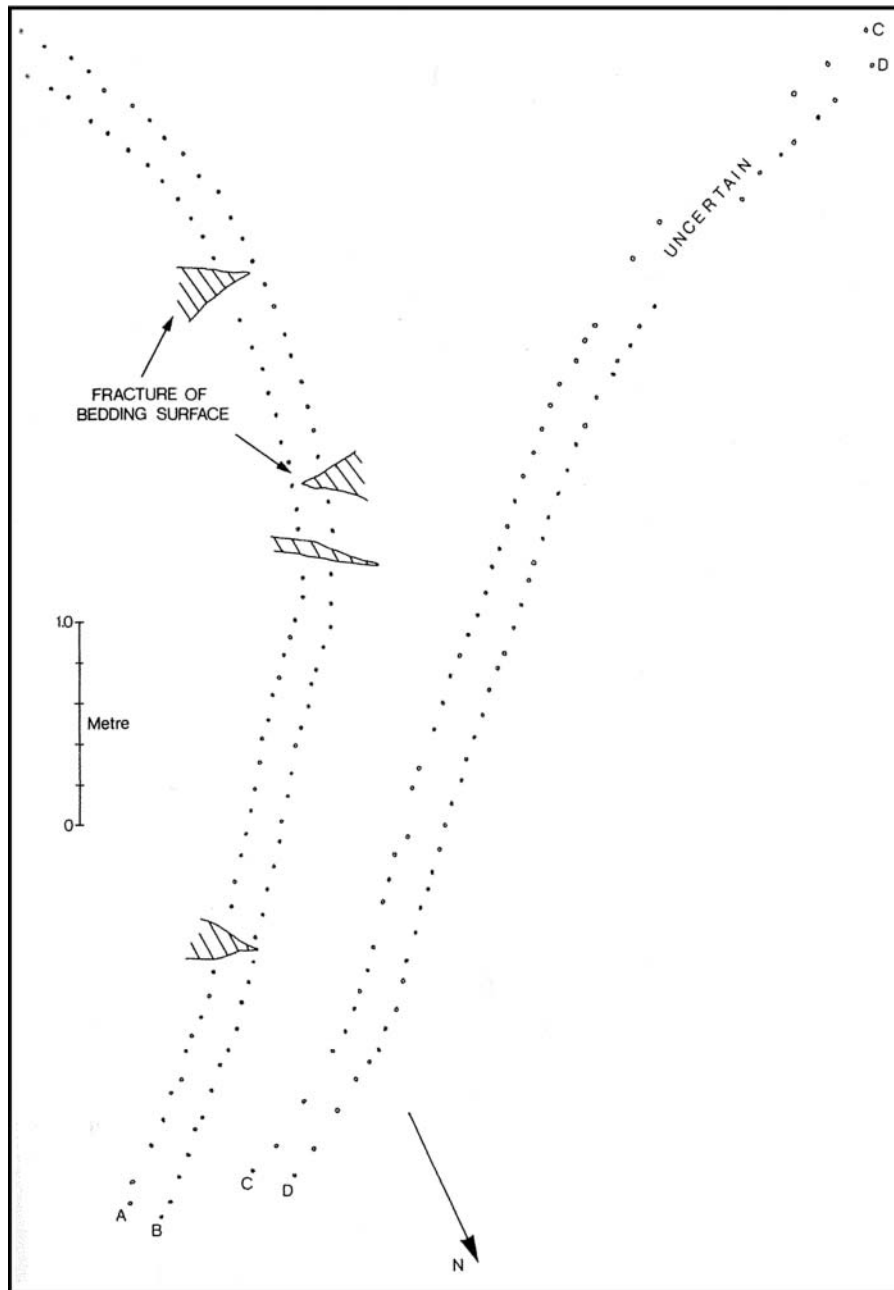


FIG. 9. Arthropod trackways from the Devonian Kap Graah Group in eastern Greenland (after Friend et al., 1979, fig. 35).

### Orkney Islands

Sarjeant (1974, fig. 5) published an earlier illustration from Wilson et al. (1935, fig. 20) of a supposed trackway from the upper part of the Old Red Sandstone on the Isle of Hoy in the Orkney Islands, and Leonardi (1987, pl. 11A) also re-published this illustration (Fig. 10). This trace was either not collected or the original fossil has been lost, according to Sarjeant (1974).

Westoll (1937, p. 32) tentatively suggested the Hoy fossil might be a tetrapod trackway in which the animal completely overstepped. Sarjeant (1974) offered no opinion as to its origin, but Leonardi (1987) identified the Hoy fossil as a trackway left by a rhipidistian fish. Rogers (1990) suggested that it is an arthropod trackway similar to *Siskemia*, but *Siskemia* is quite different, especially in not having an impressed central ridge/furrow (its central pattern is two parallel but separated

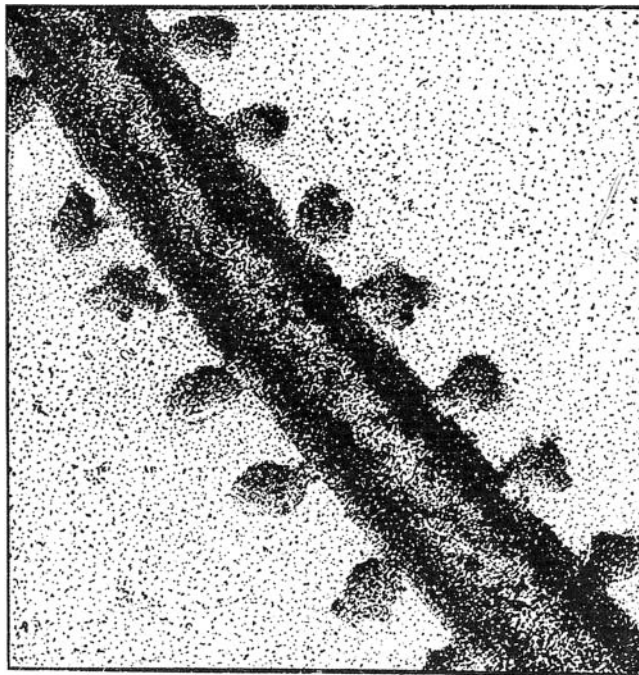


FIG. 10. Supposed trackway (external width  $\sim 3$  cm) from the Devonian of the Orkney Islands (after Leonardi, 1987).

marks) and not showing any connection of the appendage imprints to the central trail (e.g., Walker, 1985, fig. 2; Trewin, 1994, text-fig. 6D; Wisshak et al., 2004, fig. 6B; Davies et al., 2006, fig. 3C–D). Clack (1997, p. 240) regarded the Hoy fossil as a trackway and stated “these tracks might be exactly what one would predict for a very small *Ichthyostega*.”

However, given its symmetry and the connection of lateral projections to a central trail, the Hoy fossil is clearly not a tetrapod trackway, nor is it obviously an arthropod trackway. Indeed, it more resembles a plant, possibly a stem with attached sporangia of a zosterophyll (P. Gensel, personal commun., 2015). Therefore, its identity as a trace fossil is questionable and it cannot be re-examined, so it is of no relevance to the record of Devonian tetrapod tracks.

### Northern Scotland

Rogers (1990) documented what he interpreted as a tetrapod trackway from the Upper Old Red Sandstone of Easter Ross in northern Scotland. However, the Devonian age of this tracksite is not certain. According to Rogers (1990) it is  $\sim 900$  m stratigraphically above a marine fossiliferous bed of Givetian age, and could range from Givetian to Tournasian. Clack (1997) also stressed that this tracksite could be Early Carboniferous in age. According to Rogers, the track-bearing stratum is part of an eolian sabkha deposit in a sandstone bed with wind ripple and planar laminations, and therefore the tracks were impressed subaerially.

The tracks form an alternating trackway of three steps in which inferred manus and pes imprints can be differentiated on the basis of size (manus much smaller than pes). Rogers described the manus and pes as of similar size, but on the left side of the trackway the inferred manus impressions are clearly smaller than the pes impressions. The estimated glenoacetabular length of the tetrapod trackmaker is  $\sim 29$  cm. Clack (1997, p. 239) judged this as a “reasonably convincing” tetrapod trackway, and I concur, though its Devonian age remains uncertain.

Incidentally, Rogers (1990) provided a useful review of the history of the supposed tetrapod (“reptilian”) tracks from the Old Red Sandstone first reported by Gordon and Joass (1863). These tracks were never well documented nor can specimens to vouch the report be found, so their identity remains unclear.

### Ireland

Stössel (1995) reported a trackway from the Devonian Valentia Slate Formation on Valentia Island in southwestern Ireland. Subsequently, Williams et al. (1997) published a U-Pb age of  $\sim 385$  Ma for an air-fall tuff that is  $\sim 230$  m stratigraphically above the trackway. On the current ICS timecale, 385 Ma is a Givetian age, so this makes the trackway Middle Devonian, though the biostratigraphy (based on fishes and miospores) of the track-bearing stratigraphic interval is less precise and indicates a Mid-Devonian through Fammenian age (Stössel, 1995). Stössel (1995) provided few data on the environment of deposition of the track-bearing layer, merely stating that it was a nonchannelized sheetflood deposit of alluvial (nonmarine) origin, and he doubted that the tracks were made subaqueously.

At the Valentia Island tracksite, there are 150 tracks without median drag marks in a long, meandering trackway that extends for a course of about 10 m. This trackway shows both size differentiation of manus and pes tracks and an alternating trackway pattern of a quadruped with an estimated glenoacetabular length of 38 cm and a coupling value (coupling value = glenoacetabular distance/length of forelimb + length of hind limb: Peabody, 1959) of 1.2–1.4 (Stössel, 1995). No details of footprint morphology are preserved because of cleavage of the sediments, but Stössel drew attention to the tracks being wider than long, and suggested this indicated a polydactyl trackmaker (it also infers laterally-oriented digits). Clack (1997) accepted the Valentia Island trackway as a tetrapod trackway, and I concur.

### Poland

Niedźwiedzki et al. (2010) reported putative tetrapod trackways from Middle Devonian (middle Eifelian: Narkiewicz and Narkiewicz, 2015), marginal marine strata at the Zachełmie quarry in Poland (Figs. 11 and 12). Acceptance of the

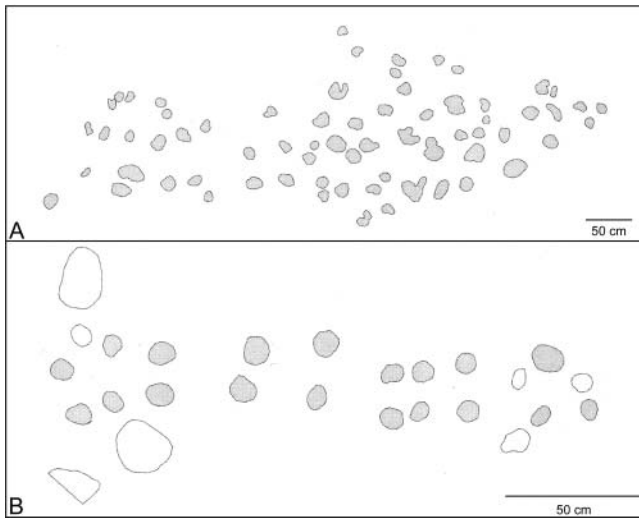


FIG. 11. Two drawings of “tracks” from the Middle Devonian of the Zachełmie quarry in Poland (after Niedźwiedzki et al., 2010, supplementary material). A, Main “track” surface. B, “Trackway” with symmetrical gait.

structures from the Zachełmie quarry as the oldest tetrapod tracks, ergo the oldest record of tetrapods, has been widespread among students of early tetrapod evolution (e.g., Janvier and Clément, 2010; Clack, 2012; Steyer, 2012). Indeed, the Devonian “trackways” from Zachełmie even

appeared in a recent edition of a prominent historical geology textbook (Stanley and Luczaj, 2014, fig. 14.21).

Pushing back the oldest record of tetrapods based on the Zachełmie quarry “tracks” forces the recognition of numerous lengthy ghost lineages (Niedźwiedzki et al., 2010). Furthermore, the Zachełmie quarry “tracks” indicate much larger tetrapods than do other Devonian tetrapod trackways and the tetrapod body fossil record. As Clack (2012) noted, they indicate a trackmaker with a body length of as much as 2.5 m, whereas known body fossils of most Devonian tetrapods and their close relatives among “fishes” are of much smaller animals (e.g., Fig. 2). Indeed, extremely large, “enigmatic” structures at the Zachełmie quarry, as much as 50 cm long, have been interpreted as tetrapod undertracks (Niedźwiedzki et al., 2010, supplementary information, fig. 18B), although no known Paleozoic tetrapod footprint is remotely near that size. Also, the Zachełmie quarry “tracks” are in marginal marine strata (Lagoonal: Narkiewicz et al., 2015), so they are taken to indicate locomotion in a shallow nearshore marine setting by a Devonian tetrapod, and this bears on discussion of the paleo-environment of tetrapod origins.

If we accept the Zachełmie quarry structures as tetrapod tracks, Clack (2012, p. 126) wrote that “we may well have to rethink the whole question of timing, sequence and circumstances of the origin of tetrapods.” However, I believe that what needs a rethink is the identity of the structures in the Zachełmie quarry. Not only did the original publication by

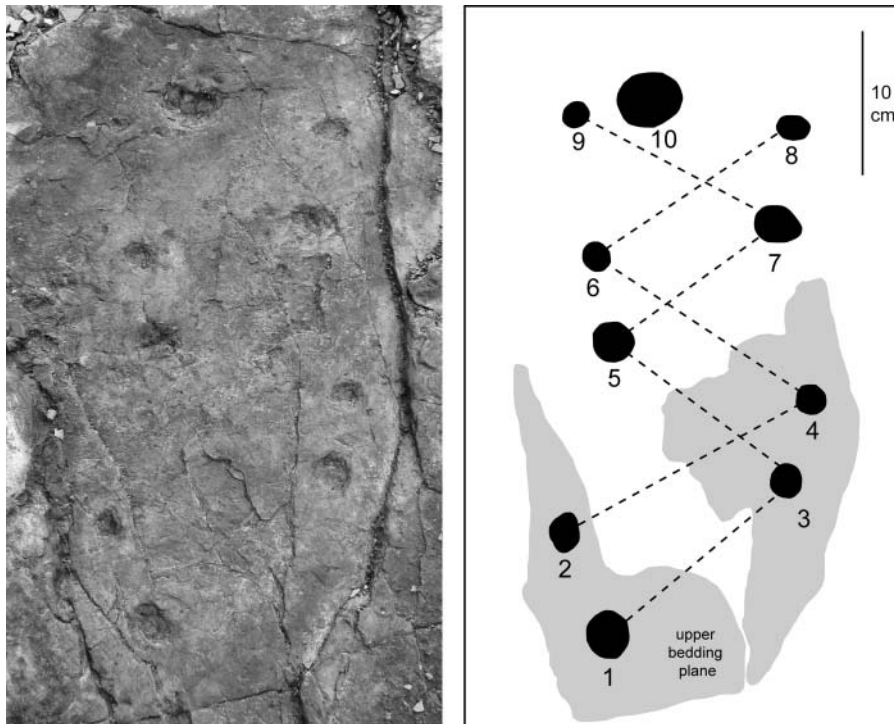


FIG. 12. On left, photograph of “tetrapod trackway” in the Zachełmie quarry of Poland (courtesy of G. Niedźwiedzki) and drawing on right of key features, with “tracks” numbered (after Niedźwiedzki et al., 2010, fig. 2), different bedding surfaces identified.

Niedźwiedzki et al. (2010) fail to make a convincing case that the Zachełmie structures are tetrapod footprints, it failed to consider and evaluate alternative interpretations. Subsequent articles relevant to the Zachełmie structures (e.g., Narkiewicz and Retallack, 2014; Narkiewicz et al., 2015) simply accept them as tetrapod tracks without further evaluation. Therefore, in my judgment, no convincing case has been made that they are tetrapod tracks, and I can make a compelling argument that they are fish-feeding traces/nests.

The “tracks” from the Zachełmie quarry are in a 3.2–3.8 m thick interval of thin-bedded dolomicrites, interpreted as shallow marine/lagoonal sediments (Niedźwiedzki et al., 2010). The “trackways” come from three stratigraphic levels and include 220 so-called “tracks” and nine “trackways.” However, only 20 of the “tracks” are “well enough preserved to contain useful ichnological information” (Niedźwiedzki et al., 2010, supplementary information, p. 6). Significantly, the “main surface” shows no organized “trackways” and no overlapping “tracks” (overprinting), but was interpreted by Niedźwiedzki et al. (2010) as a trampled surface (Fig. 11A).

Most of the “trackways” display what Niedźwiedzki et al. (2010) refer to as a “symmetrical gait” (e.g., Fig. 11B), which would be “ladder trackways” in the terminology of Clack (Niedźwiedzki et al., 2010, fig. 2C; supplementary information, figs. 12 15, 20, 21). These “trackways” show no evidence of manus and pes differentiation or any distinctive morphology of the inferred manus and pes imprints that reflects skeletal morphology.

Thus, the Zachełmie structures do not meet the criteria I have proposed to diagnose Devonian tetrapod tracks and trackways. Furthermore, the so-called symmetrical gait trackways interpreted by Niedźwiedzki et al. (2010) lack any regularity of pattern by which to identify them as trackways (Fig. 11B). Distinguishing manus and pes imprints is also not obvious among the so-called trackways from Zachełmie. The claimed single footprints with digit impressions all look different from each other (Niedźwiedzki et al., 2010, supplementary information, fig. 10). Thus, they have from three to five variably shaped “digit” imprints, so they do not provide clear evidence of a polydactyl trackmaker. The “sole” impressions vary considerably, from short and broad, with a rounded posterior margin, to long with complex shapes. Particularly interesting is a supposed footprint matched by Niedźwiedzki et al. (2010, fig. 4) to an articulated pes skeleton of *Ichthyostega*. This match requires extending the sole impression well out onto the digits, coalescing three digits into one and having a remaining digit wholly within the sole impression. As Schultze (2013, p. 379) put it, “I cannot see the skeletal structure superimposed on [this] one track.”

The only published “trackway” at the Zachełmie quarry that appears to show an alternating trackway pattern and size differentiation of the manus and pes is Muz PGI 1728.II.16 (Geological Museum of the Polish Geological Institute) (Niedźwiedzki et al., 2010, fig. 2a,b) (Fig. 12). This

“trackway” has been interpreted to show 4–5 footfalls in which smaller “manus” impressions precede larger “pes” impressions. Niedźwiedzki et al. (2010, fig. 2b) fit a “generic Devonian tetrapod” to this trackway, but there are serious problems with their interpretation. First, the orientation and spacing of the identified manus-pes pairs varies considerably, so this is an irregular trackway (*sensu* Leonardi, 1987), if it is a trackway. Thus, the tracks on the left side of the “trackway” are angled away from the “trackway” midline, whereas those on the right side are parallel to that midline. Furthermore, at its “beginning” (structures 1–4 in Fig. 12), the “trackway” is much wider than its remaining course. Spacing between “manus-pes pairs” is variable. To explain all of this, the trackmaker would have had to change its bearing and the width of its gait abruptly and to have walked irregularly.

Second, the “tracks” in this “trackway” appear to be on two different bedding planes and have very varied depths, as a clear photograph of them indicates (Fig. 12). They are thus underprints on varied surfaces. Breakage behind one of the “tracks” (number 7 in Figure 12) suggests the presence of another “track” in this location. The relative sizes of the “tracks” also is open to reconsideration. For example, structures 3 and 4 in Figure 12 look nearly the same size, but are drawn by Niedźwiedzki et al. (2010, fig. 2) as of very different sizes. The presence of a very large “track” (number 10 in Figure 12) at the end of the “trackway” also merits explanation.

Third, the trackmaker reconstructed by Niedźwiedzki et al. (2010, fig. 2) to fit Muz PGI 1728.II.16 has a very short coupling value of 0.9. This is much less than coupling values for Devonian tetrapods known from skeletal material, such as *Acanthostega* (coupling value of 1.5), and less than the coupling value estimated from bona fide Devonian tetrapod trackways (see above). The reason for this is that the “trackway” Muz PGI 1728.II.16 is very wide relative to the calculated gleno-acetabular distance, so that the inferred trackmaker must have had an extremely long set of limbs or a very wide body to have made it. In other words, it would have had exactly the reverse of the body proportions seen in early tetrapods and in the tetrapodomorph fishes, all of which are characterized by relatively long bodies and relatively short limbs/fins (Fig. 2). My conclusion is that Muz PGI 1728.II.16 comes closest among the Zachełmie quarry structures to looking like a tetrapod trackway, but is not convincingly a trackway left by a walking animal.

The supposed tracks and trackways from the Zachełmie quarry do not meet the criteria diagnostic of Devonian tetrapod tracks/trackways. Given that failure, let me offer a very different interpretation of the Zachełmie “trackways,” namely that they are not tetrapod footprints and are more likely fish feeding traces/nests. Fish feeding traces/nests made by both chondrichthyans and osteichthyans are well documented in modern shallow marine and freshwater settings (e.g., Cook, 1971; Howard et al., 1977; Gregory et al., 1979; Pearson et al., 2007; Barber, 2013 and references cited therein). These are

mostly shallow, circular to subcircular depressions that fishes excavate in sediment while feeding (searching for buried benthic prey), or in which to lay eggs or hide (Fig. 13).

Feibel (1987) described fossil fish feeding traces/nests from the Pleistocene of East Africa, coining the ichnogenic name *Piscichnus* for shallow, circular, dish-shaped structures. However, not all such structures made by fish are shallow and dish shaped. Some are relatively deep and cylindrical, for example those made by hydraulic jetting by some rays (Gregory et al., 1979). Therefore, Gregory (1991) distinguished two ichnospecies of *Piscichnus*, *P. brownii* Feibel, 1987 for shallow structures and *P. waitemata* Gregory, 1991 for deeper, cylindrical structures. *Piscichnus* is thus a well-known, subvertical, plug-shaped, and unbranched burrow structure (Knaust, 2012). In the vernacular, it encompasses what are called fish nests, fish feeding traces and fish breeding pits.

Fossil traces as old as Devonian have been identified as fish feeding traces/nests, many of which are assigned to *Piscichnus* (e.g., Gregory, 1991; Carroll and Trewin, 1995; Martinell et al., 2001; Kotake and Nara, 2002; Kotake, 2007; Kirkham and Evans, 2008; Joeckel, 2008; Belvedere et al., 2011; Knaust et al., 2012), and there were many Devonian fishes, including osteichthyans and chondrichthyans, who are candidates for tracemakers of such feeding traces/nests (e.g., Long, 1993). *Piscichnus* is considered a typical ichnofossil of the *Skolithos* ichnofacies, which is often present in shallow marine settings with high levels of wave or current energy (MacEachern et al., 2007). It is characteristic of marine estuaries and subtidal lagoons in association with *Thalassinoides*, *Skolithos* and other invertebrate burrows (Gingras et al., 2012; Knaust et al., 2012)

Instead of tetrapod tracks, the Zachełmie structures well match an aggregation of *Piscichnus* much like that interpreted in the Cretaceous of Spain by Martinell et al. (2001) and the Eocene of Italy by Belvedere et al. (2011). The arguments to identify the Zachełmie structures as fish nests/feeding traces and reassigning them to *Piscichnus* are:



FIG. 13. Modern fish feeding traces/nests in Shepody Bay, Canada (courtesy of Murray Gingras). Note the similarity to the Devonian Zachełmie structures.

1. The Zachełmie structures are circular, sub-circular or somewhat irregular in outline and shallow to cylindrical in cross section. They well match the morphology of *Piscichnus* (e.g., Feibel, 1987, fig. 2; Gregory, 1991, fig. 8; Martinell et al., 2001, fig. 3; Kirkham and Evans, 2008, fig. 10; Belvedere et al., 2011, figs. 2, 4). They also closely resemble modern fish feeding traces/nests (e.g., Howard et al., 1977, fig. 2; Feibel, 1987, fig. 3; Pearson et al., 2007, fig. 2) (Fig. 13). Based on morphology, the Zachełmie structures can be assigned to *P. brownii*.
2. The pattern of the Zachełmie structures, particularly on the “main surface” (Fig. 11A), is of nonoverlapping and, in places, regularly spaced, even locally aligned, pits. This kind of pattern—no overlap, regular spacing and alignment—is often seen in modern and fossil fish feeding traces/nests (e.g., Feibel, 1987, figs. 2.2, 3.2; Gregory, 1991, fig. 8A; Martinell et al., 2001, figs. 2–4; Pearson et al., 2007, fig. 5; Kirkham and Evans, 2008, Figs. 10, 12; Belvedere et al., 2011, fig. 4). In particular, the lack of overprinting of the Zachełmie structures (though Niedźwiedzki et al., 2010, supplementary information, fig. 22 may show some overprinting) suggests they are not tracks. Most of the Zachełmie structures are of similar size, a feature characteristic of aggregations of modern fish feeding traces/nests. Indeed, Martinell et al. (2001) re-interpreted a trace-fossil locality in the Cretaceous of Spain, originally identified as a trampled surface of dinosaur tracks, as fish nests (*Piscichnus*). The mapped distributions of portions of that surface are strikingly similar to the pattern of traces on the main surface at the Zachełmie quarry (compare Figure 11A to parts of Martinell et al., 2001, fig. 4).
3. The irregular-shaped Zachełmie structures illustrated by Niedźwiedzki et al. (2010, fig. 4, supplementary information, fig. 10) as tracks with digit impressions are well matched by both modern and fossil fish feeding traces/nests (e.g., Martinell et al., 2001, fig. 3D; Pearson et al., 2007, fig. 2; Belvedere et al., 2011, fig. 5). These irregularities at the margin of the trace are caused by the digging of the fish to produce the dish-shaped structure, and are usually the imprints of the fish’s fins or mouth. The structure illustrated by Niedźwiedzki et al. (2010, fig. 4) to match the pes skeleton of *Ichthyostega* should be compared to broken up fish fecal material associated with nests on a beach in Canada illustrated by Pearson et al. (2007, fig. 7A). The irregularities of the Zachełmie structure, instead of being digit imprints, well resemble the broken up fish fecal matter.
4. Niedźwiedzki et al. (2010, supplementary information, fig. 13B–F) also identified the asymmetry of some of the Zachełmie structures as reflecting the presence of displacement rims behind tracks. Instead, this asymmetry is readily seen as a result of a fish digging a pit and pushing/dropping sediment on one side, as is evident in modern and fossil feeding traces/nests (e.g., Howard et al., 1977, figs. 1–2;

- Feibel, 1987, fig. 2.1; Martinell et al., 2001, fig. 10; Pearson et al., 2007, fig. 2).
5. The cross section of one of the Zachełmie structures illustrated by Niedzwiedzki et al. (2010, supplementary information, fig. 19) shows a clearly-defined, plug-shaped filling of a shallow, dish-like structure. Such fillings are characteristic of modern and fossil fish feeding traces/nests when they are seen in cross section filled by sediment (e.g., Howard et al., 1977, figs. 3–4; Gregory 1991, figs. 6–7).
  6. Narkiewicz et al. (2015) concluded that the Zachełmie structures were made subaqueously, as are fish nests/feeding traces.
  7. A shallow marine, lagoonal setting, such as that interpreted for the Zachełmie quarry structures, is the environment where *Piscichnus* is common and characteristic (Gingras et al., 2012; Knaust et al., 2012). Traces associated with the Zachełmie structures represent a low diversity ichnoassemblage dominated by horizontal burrows assigned to *Balanoglossites* and *Spongiomorpha* as well as cf. *Skolithos* that Niedzwiedzki et al. (2014) interpreted as an impoverished *Cruziana* ichnofacies. *Piscichnus* is commonly found in the *Skolithos* ichnofacies, which is characteristic of sandy substrates, so in a carbonate-mud substrate an impoverished *Cruziana* ichnofacies, indicative of shallow, agitated waters, is a likely facies association for *Piscichnus* (cf. Belvedere et al., 2011).

Re-interpreting the Zachełmie structures as *Piscichnus* instead of tetrapod tracks is well supported by their morphology, distribution and facies association. Furthermore, the original case for interpreting them as tetrapod tracks failed to meet the diagnostic criteria outlined here. The conclusion that an undiscovered lineage of surprisingly large Middle Devonian tetrapods lived in and around a shallow marine lagoon based on the Zachełmie quarry structures (Niedzwiedzki et al., 2010; Narkiewicz and Retallack, 2014; Narkiewicz et al., 2015) should be abandoned.

## DISCUSSION

This review of the record of supposed Devonian tetrapod tracks/trackways indicates that only three records meet the criteria by which such trackways should be distinguished—Genoa River in Australia, Easter Ross in Scotland, and Valentia Island in Ireland. What, then, does the Devonian tetrapod track record tell us of utility to understanding tetrapod origins? Here, I answer this question by focusing on four areas in which this record is potentially important: biostratigraphy, biogeography, paleoecology and locomotion.

### Biostratigraphy

As Lucas (2007, p. 8) concluded, the Devonian tetrapod footprint record “lacks abundance, diversity and any sort of

index taxa that would be of use in biostratigraphy.” He went on to note that “the stratigraphically lowest occurrence of tetrapod tracks may be viewed as a valuable biostratigraphic datum that helps to define the oldest record of tetrapods.” Indeed, the tetrapod trackways from Valentia Island in Ireland are no younger than Givetian, so this is the oldest record of tetrapods. The oldest Devonian tetrapod trackway thus provides an important datum that places tetrapod origins during the Middle Devonian, or earlier.

### Paleobiogeography

Tetrapod tracks of Middle Devonian age are known from Ireland, and Late Devonian tetrapod tracks are known from Scotland and Australia. The Irish record is the oldest tetrapod record, so on face value it could indicate an origin of tetrapods in Euramerica. However, given how sparse the Devonian tetrapod footprint record is, this conclusion should be viewed with great caution. Too few Devonian tetrapod trackways are known to provide a reliable basis for paleobiogeographic interpretation.

### Paleoecology

The paleoenvironment of tetrapod origins has been debated—marine or nonmarine, dry or wet—for about a century (e.g., Retallack, 2011; George and Blicek, 2011; Clack, 2012; Schultze, 2013). Clack (2000, p. 100) argued that environments are difficult to infer from trackways, and concluded that “one cannot place much weight on the trackways as evidence of the habitus of the earliest tetrapods.”

However, all tracksites are subject to sedimentological interpretation, and the tracks themselves, and other associated trace fossils, are often important clues to interpreting the paleoenvironment of any tracksite. Such interpretations indicate that the three bona fide Devonian tetrapod tracksites were formed in nonmarine environments. They thus provide no support for tetrapod origins in a marine or marginal marine setting, though that is not totally excluded by such a meager track record. Most important is elimination of the Polish “tracks” from the Devonian tetrapod track record, as they are from a marginal marine paleoenvironment and thus provided apparent (but erroneous) prima facie evidence of locomotion in a shallow marine setting by Devonian tetrapods.

### Locomotion

The tetrapodomorph fishes, notably *Panderichthys* and *Tiktaalik*, are seen as the sister taxon to tetrapods. However, *Panderichthys* has robust pectoral fins, much larger than its hind fins, quite different from the larger pelvic limbs of tetrapods (Shubin et al., 2006; Swartz, 2012) and the recently described pelvic and hind limb elements of *Tiktaalik* (Shubin et al., 2014). *Tiktaalik* thus appears to help bridge the gap between



the locomotory apparatus of fully terrestrial tetrapods, driven by hind limb propulsion, and that of many of their nearest relatives, driven by forelimb propulsion (e.g., Boisvert, 2005; Boisvert et al., 2008; Pierce et al., 2013). The Devonian tetrapod track record suggests this evolutionary gap had already been bridged by the Middle Devonian.

It has long been believed that while walking, the earliest tetrapods had forward-pointing digits (e.g., Romer and Byrne, 1931; Romer and Price, 1940; Gregory and Raven, 1941; Schaeffer, 1941). Morton (1926) dissented, but Schaeffer (1941) argued that his reconstruction of laterally facing digits was based on one footprint (the holotype of *Thinopus antiquus*) and contradicted by a wealth of other footprint evidence. However, one set of tracks at the Genoa River tracksite (Fig. 7) suggests laterally oriented digits during terrestrial locomotion.

The transition from fins to limbs is widely regarded to have taken place in the aquatic realm. In other words, Devonian tetrapods are regarded as primarily aquatic (e.g., Coates and Ruta, 2007; Clack, 2012). Indeed, Coates and Clack (1995) argued that the limbs of *Ichthyostega* and *Acanthostega* were relatively inflexible paddles that were unlikely to have left the kinds of Devonian trackways that I attribute to tetrapods. This may in part explain the rarity of Devonian tetrapod footprints—most Devonian tetrapods spent little or no time walking on land.

The bona fide Devonian tetrapod footprints indicate an alternating pattern of limb supported locomotion with a larger hind foot than forefoot. This is the characteristic pattern of quadrupedal locomotion of post-Devonian tetrapods. The Devonian tetrapod track record thus indicates such locomotion was possible at least some of the time by some Devonian tetrapods. Body fossils of these Devonian tetrapods await discovery.

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## REFERENCES

- Abel, O. 1935. Vorzeitliche Lebensspuren. Gustav Fischer, Jena, 644 p.
- Ahlberg, P. 1998. Postcranial stem tetrapod remains from the Devonian of Scat Craig, Morayshire, Scotland. *Zoological Journal of the Linnean Society*, 122:99–141.
- Ahlberg, P. E., Clack, J. A., and Blom, H. 2005. The axial skeleton of the Devonian tetrapod *Ichthyostega*. *Nature*, 437:137–140.
- Ahlberg, P. E., Lukševičs, E., and Lebedev, O. 1994. The first tetrapod finds from the Devonian (Upper Fammenian) of Latvia. *Philosophical Transactions of the Royal Society of London*, B343:303–328.
- Ahlberg, P. E., Clack, J. A., Lukševičs, E., Blom, H., and Zupins, I. 2008. *Ventastega curonica* and the origin of tetrapod morphology. *Nature*, 453:1199–1204.
- Ami, H. M. 1903. Description of tracks from the fine-grained siliceous mudstones of the Knoydart Formation (Eo-Devonian) of Antigonish County, Nova Scotia. *Proceedings and Transactions of the Nova Scotian Institute of Science*, 10:330–332.
- Arora, R. 2003. Encyclopaedia of Evolutionary Biology. Anmol Publications, New Delhi, 1742 p.
- Barber, I. 2013. The evolutionary ecology of nest construction: Insight from recent fish studies. *Avian Biology Research*, 6:83–98.
- Belvedere, M., Franceschi, M., Morsilli, M., Zoccarato, P. L., and Mietto, P. 2011. Fish feeding traces from Middle Eocene limestones (Gargano Promontory, Apulia, southern Italy). *Palaios*, 26:693–699.
- Boisvert, C. A. 2005. The pelvic fin and girdle of *Panderichthys* and the origin of tetrapod locomotion. *Nature*, 438:1145–1147.
- Boisvert, C. A., Mark-Kurik, E., and Ahlberg, P. E. 2008. The pectoral fin of *Panderichthys* and the origin of digits. *Nature*, 456:636–638.
- Braddy, S. J. 2004. Ichnological evidence for the arthropod invasion of land. *Fossils and Strata*, 51:136–140.
- Campbell, K. S. W., and Bell, M. W. 1977. A primitive amphibian from the Late Devonian of New South Wales. *Alcheringa*, 1:369–381.
- Carroll, R. 2009. The Rise of Amphibians: 365 Million Years of Evolution. The Johns Hopkins University Press, Baltimore, 360 p.
- Carroll, R. L., and Holmes, R. B. 2007. Evolution of the appendicular skeleton of amphibians. In Hall, B. K. (ed.). *Fins into Limbs: Evolution, Development, and Transformation*. University of Chicago Press, Chicago, pp. 185–224.
- Carroll, S., and Trewin, N. H. 1995. *Cornulaticchnus*: A new trace fossil from the Old Red Sandstone of Orkney. *Scottish Journal of Geology*, 31:37–41.
- Case, E. C. 1898. Studies for students. The development and geological relation of the vertebrates. *Journal of Geology*, 6:500–523.
- Caster, K. E. 1938. A restudy of the tracks of *Paramphibius*. *Journal of Paleontology*, 12:3–60.
- Clack, J. A. 1997. Devonian tetrapod trackways and trackmakers; A review of the fossils and footprints. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 130:277–250.
- Clack, J. A. 2000. The origin of tetrapods. In Heatwole, H., and Carroll, R. L. (eds.). *Amphibian Biology Volume 4 Palaeontology*. Beatty & Sons, Surrey, pp. 980–1029.
- Clack, J. A. 2002. *Gaining Ground: The Origin and Evolution of Tetrapods*. Indiana University Press, Bloomfield, IN, 369 p.
- Clack, J. A. 2012. *Gaining Ground: The Origin and Evolution of Tetrapods*, 2nd ed. Indiana University Press, Bloomfield, IN, 523 p.
- Coates, M. I. 1996. The Devonian tetrapod *Acanthostega gunnari* Jarvik: Postcranial anatomy, basal tetrapod relationships and patterns of skeletal evolution. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 87:363–421.
- Coates, M. I., and Clack, J. A. 1995. Romer's gap: Tetrapod origins and terrestriality. *Bulletin du Muséum National d'Histoire Naturelle Series 4*, 17:373–388.
- Coates, M. I., and Ruta, M. 2007. Skeletal changes in the transition from fins to limbs. In Hall, B. K. (ed.). *Fins into Limbs: Evolution, Development, and Transformation*. University of Chicago Press, Chicago, pp. 15–37.
- Cook, D. O. 1971. Depressions in shallow marine sediment made by benthic fish. *Journal of Sedimentary Petrology*, 41:577–578.
- Daeschler, E. B., Shubin, N. H., and Jenkins, F. A., Jr. 2006. A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature*, 440:757–763.

- Davies, N. S., Sanson, I. J., and Turner, P. 2006. Trace fossils and paleoenvironments of a Late Silurian marginal-marine/alluvial system: The Ringerike Group (Lower Old Red Sandstone), Oslo Region, Norway. *Palaios*, 21:46–62.
- Edwards, J. L. 1977. The evolution of terrestrial locomotion. In Hecht, M. K., Goody, P. C., and Hecht, B. M. (eds.). *Major Patterns in Vertebrate Evolution*. Plenum Press, New York, pp. 553–577.
- Feibel, C. S. 1987. Fossil fish nests from the Koobi Fora Formation (Plio-Pleistocene) of northern Kenya. *Journal of Paleontology*, 61:130–134.
- Fillmore, D. L., Lucas, S. G., and Simpson, E. L. 2012. Ichnology of the Mississippian Mauch Chunk Formation, eastern Pennsylvania. *New Mexico Museum of Natural History and Science Bulletin*, 54:1–136.
- Fricke, H., and Hissmann, K. 1991. Locomotion, fin coordination and body form of the living coelacanth *Latimeria chalumnae*. *Environmental Biology of Fishes*, 43:329–356.
- Fricke, H., Reinecke, O., Hofer, H., and Nachtigall, W. 1987. Locomotion of the coelacanth *Latimeria chalumnae* in its natural environment. *Nature*, 329:331–333.
- Friend, P. F., Alexander-Marrack, P. D., Nicholson, J., and Yeats, A. K. 1976. Devonian sediments of East Greenland II. Sedimentary structures and fossils. *Meddelelser om Grønland*, 206(2):1–91.
- George, D., and Blicek, A. 2011. Rise of the earliest tetrapods: An Early Devonian origin from a marine environment. *PLoS ONE*, 6(7):e22136.
- Gingras, M. K., MacEachern, J. A., Dashtgard, S. E., Zneveveld, J.-P., Schongut, J., Ranger, M. J., and Pemberton, S. G. 2012. Estuaries. In Knaust, D., and Bromley, R. G. (eds.). *Trace Fossils as Indicators of Sedimentary Environments*. Elsevier Developments in Sedimentology, Amsterdam, 64, pp. 463–505.
- Gordon, G., and Joass, J. M. 1863. On the relations of the Ross-shire sandstones containing reptilian footprints. *Quarterly Journal of the Geological Society of London*, 19:506–509.
- Goto, T., Nishida, K., and Nakaya, K. 1999. Internal morphology and function of paired fins in the epaulette shark, *Hemiscyllium ocellatum*. *Ichthyological Research*, 46:281–287.
- Gourmanis, C., Webb, J. A., and Warren, A. A. 2003. Fluviodeltaic sedimentology and ichnology of part of the Silurian Grampians Group, western Victoria. *Australian Journal of Earth Sciences*, 50:811–825.
- Gray, J. 1939. Aspects of animal locomotion. *Proceedings of the Royal Society of London Series B Biological Sciences*, 128:28–62.
- Gregory, M. R. 1991. New trace fossils from the Miocene of Northland, New Zealand: *Rorschachichnus amoeba* and *Piscichnus waitemata*. *Ichnos*, 1:195–205.
- Gregory, M. R., Balance, P. F., Gibson, G. W., and Ayling, A. M. 1979. On how some rays (Elasmobranchia) excavate feeding depressions by jetting water. *Journal of Sedimentary Petrology*, 49:1125–1130.
- Gregory, W. K. 1951. *Evolution Emerging*, 2 volumes. The MacMillan Company, New York, 1013 p.
- Gregory, W. K., and Raven, H. C. 1941. Studies on the origin and early evolution of paired fins and limbs. *Annals of the New York Academy of Sciences*, 42:273–360.
- Häntzschel, W. 1975. Trace Fossils and Problematica. Treatise on Invertebrate Paleontology Part W, Supplement 1, 2nd ed., 269 p.
- Harper, J. A. 1999. Chapter 7 Devonian. In Shultz, C. H. (ed.). *The Geology of Pennsylvania*. Pennsylvania Geological Survey, Harrisburg, pp. 109–127.
- Haubold, H. 1971. Ichnia Amphibiorum et Reptiliorum Fossilium. *Handbuch der Palaoherpétologie*, 18:1–124.
- Haubold, H. 1984. *Saurierfährten*. A. Ziemsen Verlag, Wittenberg-Lutherstadt, 231 p.
- Hildebrand, M. 1980. The adaptive significance of tetrapod gait selection. *The American Zoologist*, 20:255–267.
- Horner, A. M., and Jayne, B. C. 2014. Lungfish axial muscle function and the vertebrate water to land transition. *PLoS ONE*, 9(5):e96516.
- Howard, J. D., Mayou, T. V., and Heard, R. W. 1977. Biogenic sedimentary structures formed by rays. *Journal of Sedimentary Petrology*, 47:339–346.
- Hunt, A. P., Lucas, S. G., Milàn, J., and Spielmann, J. A. 2012. Vertebrate coprolite studies: Status and prospectus. *New Mexico Museum of Natural History and Science Bulletin*, 57:5–24.
- Janvier, P. 1977. Vertébrés dévoniens de deux nouveaux gisements du Moyen-Orient. Le problème des relations intercontinentales au Paléozoïque moyen vu à la lumière de la paléobiogéographie des rhipidiens ostéolepiformes et des premiers tétrapodes. *Annales de la Société Géologique du Nord*, 47:373–382.
- Janvier, P., and Clément, G. 2010. Muddy tetrapod origins. *Nature*, 463:40–41.
- Jarvik, E. 1996. The Devonian tetrapod *Ichthyostega*. *Fossils and Strata*, 40:1–213.
- Joeckel, R. M. 2008. Enigmatic structures in an Upper Pennsylvanian (Kasimovian) marine limestone. *Palaios*, 23:833–847.
- Johnels, A. G. 1957. The mode of terrestrial locomotion in *Clarias*. *Oikos*, 8:122–129.
- Kawano, S. M., and Blob, R. W. 2013. Propulsive forces of mudskipper fins and salamander limbs during terrestrial locomotion: Implications for the invasion of land. *Integrative and Comparative Biology*, 2013:1–12.
- King, H. M., Shubin, N. H., Coates, M. I., and Hale, M. E. 2011. Behavioral evidence for the evolution of walking and bounding before terrestriality in sarcopterygian fishes. *Proceedings of the National Academy of Sciences*, 108:21146–21151.
- Kirkham, A., and Evans, G. 2008. Giant burrows in the Quaternary limestones of Futaysi Island and Al Dabb'iyah, Abu Dhabi Emirate. *Palaeoecology, Palaeoclimatology, Palaeoecology*, 270:324–331.
- Knaust, D. 2012. Trace-fossil systematics. In Knaust, D., and Bromley, R. G. (eds.). *Trace Fossils as Indicators of Sedimentary Environments*. Elsevier Developments in Sedimentology, Amsterdam, 64, pp. 79–101.
- Knaust, D., Curran, H. A., and Dronov, A. V. 2012. Shallow-marine carbonates. In Knaust, D., and Bromley, R. G. (eds.), *Trace Fossils as Indicators of Sedimentary Environments*. Elsevier Developments in Sedimentology, Amsterdam, 64, pp. 705–750.
- Kotake, N. 2007. *Macaronichnus* isp. associated with *Piscichnus waitemata* in the Miocene of Yonanguni-jima Island, southwest Japan. In Miller, W. (ed.), *Trace Fossils: Concepts, Problems, Prospects*. Elsevier, Amsterdam, pp. 492–501.
- Kotake, N., and Nara, M. 2002. The ichnofossil *Piscichnus waitemata*: Biogenic sedimentary structure produced by the foraging behavior using water jet. *The Journal of the Geological Society of Japan*, 108:1–2.
- Kuhn, O. 1963. Ichnia tetrapodorum. *Fossilium Catalogus*, 101:1–176.
- Lebedev, O. A., and Clack, J. A. 1993. Upper Devonian tetrapods from Andreyevka, Tula Region, Russia. *Palaontology*, 36:721–734.
- Lebedev, O. A., and Coates, M. I. 1995. The postcranial skeleton of the Devonian tetrapod *Tulerpeton curtum* Lebedev. *Zoological Journal of the Linnean Society*, 114:307–348.
- Leonardi, G. 1982. Descorbeta de pegada de um anfíbio devoniano no Paraná. *Ciências da Terra*, 5:36–37.
- Leonardi, G. 1983. *Notopus petri* nov. gen. nov. sp.: un empreinte d'amphibien du Devonien au Paraná (Bresil). *Geobios*, 16:233–239.
- Leonardi, G. (Ed.) 1987. Glossary and Manual of Tetrapod Footprint Palaeoichnology. República Federativa do Brasil, Ministério de Minas e Energia, Departamento Nacional da Produção Mineral, Brasília, 75 p.
- Leonardi, G. 1994. Annotated Atlas of South America Tetrapod Footprints (Devonian to Holocene). República Federativa do Brasil, Ministério de Minas e Energia, Secretaria de Minas e Metalurgia, Companhia de Pesquisa de Recursos Minerais, Brasília, 247 p.
- Li, Z. X., Powell, C. McA., and Trench, A. 1993. Palaeozoic global reconstructions. In Long, J. A. (ed.). *Palaeozoic Vertebrate Biostratigraphy and Biogeography*. The Johns Hopkins University Press, Baltimore, pp. 25–53.
- Long, J. A. 1993. Morphological characteristics of Palaeozoic vertebrates used in biostratigraphy. In Long, J. A. (ed.). *Palaeozoic Vertebrate Biostratigraphy and Biogeography*. The Johns Hopkins University Press, Baltimore, pp. 3–24.
- Lucas, S. G. 2007. Tetrapod footprint biostratigraphy and biochronology. *Ichnos*, 14:5–38.

- Lucas, S. G., Fillmore, D. L., and Simpson, E. L. 2010. The Mississippian tetrapod footprint ichnogenus *Palaeosauropus*: Extramorphological variation and ichnotaxonomy. *Ichnos*, 17:177–186.
- Lucifora, L. O., and Vassallo, A. I. 2002. Walking in skates (Chondrichthyes, Rajidae): Anatomy, behavior and analogies to tetrapod locomotion. *Biological Journal of the Linnean Society*, 77:35–41.
- Lull, R. S. 1920. Organic Evolution. The MacMillan Company, New York, 488 p.
- MacEachern, J. A., Pemberton, S. G., Gingras, M. K., and Bann, K. L. 2007. The ichnofacies paradigm: A fifty-year retrospective. In Miller, W. (ed.). Trace Fossils: Concepts, Problems, Prospects. Elsevier, Amsterdam, pp. 52–77.
- Mángano, M. G., Buatois, L. A., West, R. R., and Maples, C. G. 1999. The origin and paleoecologic significance of the trace fossil *Asteriacites* in the Pennsylvanian of Kansas and Missouri. *Lethaia*, 32:17–30.
- Mansky, C. F., Lucas, S. G., Spielmann, J. A., and Hunt, A. P. 2012. Mississippian bromalites from Blue Beach, Nova Scotia, Canada. *New Mexico Museum of Natural History and Science Bulletin*, 57:161–170.
- Marsh, O. C. 1896. Amphibian footprints from the Devonian. *American Journal of Science*, 152:374–375.
- Martin, A. J. 2014. Trace fossil of a walking fish from the Pottsville Formation (Late Carboniferous) of Alabama. *Geological Society of America, Abstracts with Programs*, 46(3):86.
- Martinell, J., De Gibert, J. M., Doménech, R., Ekdale, A. A., and Steen, P. P. 2001. Cretaceous ray traces?: Alternative interpretation for the alleged dinosaur tracks of La Posa, Isona, NE Spain. *Palaios*, 16:409–416.
- Mikuláš, R. 1992. The ichnogenus *Asteriacites*: Paleoenvironmental trends. *Vestník Českého Geologického ústavu*, 67:423–433.
- Milner, A. R. 1993. Biogeography of Palaeozoic tetrapods. In Long, J. A. (ed.). Palaeozoic Vertebrate Biostratigraphy and Biogeography. The Johns Hopkins University Press, Baltimore, pp. 324–353.
- Milner, A. R., Smithson, T. R., Milner, A. C., Coates, M. I., and Rolfe, W. D. I. 1986. The search for early tetrapods. *Modern Geology*, 10:1–28.
- Minter, N. K., and Braddy, S. J. 2006. The fish and amphibian swimming traces *Undichna* and *Lunichnium*, with examples from the Lower Permian of New Mexico, USA. *Palaeontology*, 49:1123–1142.
- Moore, R. C. 1958. Introduction to Historical Geology, 2nd ed. McGraw-Hill, Boston, 582 p.
- Morton, D. J. 1926. Notes on the footprint of *Thinopus antiquus*. *American Journal of Science*, 12(5):409–414.
- Narkiewicz, K., and Narkiewicz, M. 2015. The age of the oldest tetrapod tracks from Zachełmie, Poland. *Lethaia*, 48:10–12.
- Narkiewicz, M., and Retallack, G. J. 2014. Dolomitic paleosols in the lagoonal tetrapod track-bearing succession of the Holy Cross Mountains (Middle Devonian, Poland). *Sedimentary Geology*, 299:74–87.
- Narkiewicz, M., Grabowski, J., Narkiewicz, K., Niedźwiedzki, G., Retallack, G. J., Szrek, P., and De Vleeschouwer, D. 2015. Palaeoenvironments of the Eifelian dolomites with earliest tetrapod trackways (Holy Cross Mountains, Poland). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 420:173–192.
- Niedźwiedzki, G., Narkiewicz, M., and Szrek, P. 2014. Middle Devonian invertebrate trace fossils from the marginal marine carbonates of the Zachełmie tetrapod tracksite, Holy Cross Mountains, Poland. *Bulletin of Geosciences*, 89:593–606.
- Niedźwiedzki, G., Szrek, P., Narkiewicz, K., Narkiewicz, M., and Ahlberg, P. E. 2010. Tetrapod trackways from the early Middle Devonian period of Poland. *Nature*, 463:43–48.
- Osborn, H. F. 1916. The origin and evolution of life on earth. *The Scientific Monthly*, 3:601–614.
- Pace, C. M., and Gibb, A. C. 2009. Mudskipper pectoral fin kinematics in aquatic and terrestrial environments. *The Journal of Experimental Biology*, 212:2279–2286.
- Panchen, A. L. 1977. Geographical and ecological distribution of the earliest tetrapods. In Hecht, M. K., Goody, P. C., and Hecht, B. M. (eds.). Major Patterns in Vertebrate Evolution. Plenum, New York, pp. 728–738.
- Peabody, F. E. 1959. Trackways of living and fossil salamanders. *University of California Publications in Zoology*, 63:1–72.
- Pearson, N. J., Gingras, M. K., Armitage, I. A., and Pemberton, S. G. 2007. Significance of Atlantic sturgeon feeding excavations, Mary's Point, Bay of Fundy, New Brunswick, Canada. *Palaios*, 22:457–464.
- Pepperell, J., and Grigg, G. 1974. A labyrinthodont trackway from the Mid-Triassic near Sydney, New South Wales. *Proceedings of the Linnean Society of New South Wales*, 99:54–56.
- Pierce, S. E., Clack, J. A., and Hutchinson, J. R. 2012. Three-dimensional limb joint mobility in the early tetrapod *Ichthyostega*. *Nature*, 486:523–526.
- Pierce, S. E., Hutchinson, J. R., and Clack, J. A. 2013. Historical perspectives on the evolution of tetrapodomorph movement. *Integrative and Comparative Biology*, 53:209–223.
- Pridmore, P. A. 1995. Submerged walking in the epaulette shark *Hemiscyllium ocellatum* (Hemiscyllidae) and its implications for locomotion in rhipidistian fishes and early tetrapods. *Zoology: Analysis of Complex Systems*, 98:278–297.
- Retallack, G. J. 2011. Woodland hypothesis for Devonian tetrapod evolution. *Journal of Geology*, 119:235–258.
- Roček, Z., and Rage, J.-C. 1994. The presumed amphibian footprint *Notopus petri* from the Devonian: A probable starfish trace fossil. *Lethaia*, 27:241–244.
- Rogers, D. A. 1990. Probable tetrapod tracks rediscovered in the Devonian of N Scotland. *Journal of the Geological Society, London*, 147:746–748.
- Romer, A. S., and Byrne, F. 1931. The pes of *Diadectes*: Notes on the primitive tetrapod limb. *Paleobiologica*, 4:25–48.
- Romer, A. S., and Price, L. I. 1940. Review of the Pelycosauria. Geological Society of America Special Paper, 28, 538 p.
- Sarjeant, W. A. S. 1974. A history and bibliography of the study of fossil vertebrate footprints in the British Isles. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 16:265–378.
- Schaeffer, B. 1941. The morphological and functional evolution of the tarsus in amphibians and reptiles. *Bulletin of the American Museum of Natural History*, 78:395–472.
- Schultze, H.-P. 2013. The paleoenvironment at the transition from piscine to tetrapod sarcopterygians. *New Mexico Museum of Natural History and Science Bulletin*, 60:373–397.
- Seilacher, A. 1953. Studien zur Palichnologie II. Die fossilen Ruhespuren (Cubichnia). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 98:87–124.
- Shubin, N. H., Daeschler, E. B., and Coates, M. I. 2004. The early evolution of the tetrapod humerus. *Science*, 304:90–93.
- Shubin, N. H., Daeschler, E. B., and Jenkins, F. A., Jr. 2006. The pectoral fin of *Tiktaalik roseae* and the origin of the tetrapod limb. *Nature*, 440:764–771.
- Shubin, N. H., Daeschler, E. B., and Jenkins, F. A., Jr. 2014. Pelvic girdle and fin of *Tiktaalik roseae*. *Proceedings of the National Academy of Science*, 111:893–899.
- Smith, A., Braddy, S. J., Marriot, B., and Briggs, D. E. G. 2003. Arthropod trackways from the Early Devonian of South Wales: A functional analysis of producers and their behavior. *Geological Magazine*, 140:63–72.
- Stanley, S. D., and Luczaj, J. A. 2014. Earth System History, 4th ed. W. H. Freeman, New York, 587 p.
- Steyer, S. 2012. Earth Before the Dinosaurs. Indiana University Press, Bloomington, IN, 182 p.
- Stossel, I. 1995. The discovery of a new Devonian tetrapod trackway in SW Ireland. *Journal of the Geological Society of London*, 152:407–413.
- Swartz, B. 2012. A marine stem-tetrapod from the Devonian of western North America. *PLoS ONE*, 7(3):e33683.
- Trewin, N. H. 1994. A draft system for the identification and description of arthropod trackways. *Palaeontology*, 37:811–823.
- Turner, S. 1986. Vertebrate faunas of the Silverband Formation, Grampians, western Victoria. *Proceedings of the Royal Society of Victoria*, 98:53–62.
- Voigt, S. 2005. Die Tetrapodenichnofauna des kontinentalen Oberkarbon und Perm im Thüringer Wald-Ichnotaxonomie, Paläoökologie und Biostratigraphie. Göttingen, Cuvillier Verlag, 179 p.

- Vorobyeva, E., and Kuznetsov, A. 1992. The locomotor apparatus of *Panderichthys rhombolepis* (Gross), a supplement to the problem of the fish-tetrapod transition. In Mark-Kurik, E. (ed.). *Fossil Fishes as Living Animals*. Academy of Sciences of Estonia, Tallinn, pp. 131–140.
- Walker, E. F. 1985. Arthropod ichnofauna of the Old Red Sandstone at Dunure and Montrose, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Science*, 76:287–297.
- Warren, A. 1991. Australian fossil amphibians. In Vicker-Rich, P., Monaghan, J. M., Baird, R. F., and Rich, T. H. (eds.). *Vertebrate Palaeontology of Australasia*. Pioneer Design, Melbourne, pp. 569–590.
- Warren, A. A., Jupp, R., and Bolton, B. 1986. Earliest tetrapod trackway. *Alcheringa*, 10:183–186.
- Warren, A. W., and Wakefield, N. A. 1972. Trackways of tetrapod vertebrates from the Upper Devonian of Victoria, Australia. *Nature*, 238:469–470.
- Westoll, T. S. 1937. The Old Red Sandstone fishes of the north of Scotland, particularly of Orkney and Shetland. *Proceedings of the Geologists Association*, 48:13–45.
- Wilga, C. D., and Luader, G. V. 2001. Functional morphology of the pectoral fins in bamboo sharks, *Chiloscyllium plagiosum*: Benthic vs. pelagic station-holding. *Journal of Morphology*, 249:195–209.
- Willard, B. 1935. Chemung tracks and trails from Pennsylvania. *Journal of Paleontology*, 9:43–56.
- Williams, E. A., Sergeev, S. A., Stössel, I., and Ford, M. 1997. An Eifelian U-Pb zircon date for the Enagh Tuff Bed from the Old Red Sandstone of the Munster Basin in NW Iveragh, SW Ireland. *Journal of The Geological Society, London*, 154:189–193.
- Williston, S. W. 1917. The phylogeny and classification of reptiles. *Journal of Geology*, 25:411–421.
- Wilson, G. V., Edwards, W., Knox, J., Jones, R. C. B., and Stephens, J. V. 1935. The geology of the Orkneys. *Memoir Geological Survey Great Britain*, 205 p.
- Wisshak, M., Volohonsky, E., Seilacher, A., and Freiwald, A. 2004. A trace fossil assemblage from fluvial Old Red deposits (Wood Bay Formation; Lower to Middle Devonian) of NW-Spitsbergen, Svalbard. *Lethaia*, 37:149–163.
- Young, G. C. 2006. Biostratigraphic and biogeographic context for tetrapod origins during the Devonian: Australian evidence. *Alcheringa Special Issue*, 1:409–428.
- Zhu, M., Ahlberg, P. E., Zhao, W., and Jia, L. 2002. First Devonian tetrapod from Asia. *Nature*, 420:760–761.