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Tetrapod trackways from the early Middle Devonian period of Poland

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The fossil record of the earliest tetrapods (vertebrates with limbs rather than paired fins) consists of body fossils and trackways. The earliest body fossils of tetrapods date to the Late Devonian period (late Frasnian stage) and are preceded by transitional elpistostegids such as *Panderichthys* and *Tiktaalik* that still have paired fins. Claims of tetrapod trackways predating these body fossils have remained controversial with regard to both age and the identity of the track makers. Here we present well-preserved and securely dated tetrapod tracks from Polish marine tidal flat sediments of early Middle Devonian (Eifelian stage) age that are approximately 18 million years older than the earliest tetrapod body fossils and 10 million years earlier than the oldest elpistostegids. They force a radical reassessment of the timing, ecology and environmental setting of the fish–tetrapod transition, as well as the completeness of the body fossil record.

The last quarter-century has seen a dramatic expansion in the known body fossil record of Devonian tetrapods, the earliest known limbed vertebrates^{1–21}. Equally importantly, the discovery of articulated specimens of elpistostegids, the animals that fall immediately below them in the tetrapod stem group, has greatly enhanced our understanding of the origin of tetrapod morphology^{22–31}. Elpistostegids such as *Panderichthys* and *Tiktaalik* show a tetrapod-like head and body shape combined with the retention of ‘fish’ characters such as paired fins^{23,28,29} and the absence of a sacrum²⁸. Their close similarity to Devonian tetrapods and stable phylogenetic position below the latter in the tetrapod stem group^{23,29,32} provide a morphological outline of the fish–tetrapod transition.

In parallel with this expansion of the morphological data set, the environmental, ecological and temporal contexts of the transition have been reassessed. It has become clear that many of the earliest tetrapods and elpistostegids derive from brackish to marginal marine deposits, and their wide geographical distribution also points to marine tolerance^{13,16,19}. Temporally, the earliest record of tetrapod morphology has been pushed back from the late Famennian (about 360 million years ago) to the late Frasnian (about 375 million years ago)^{3,6,9,33}. Known elpistostegids range from late Givetian to mid-Frasnian (approximately 386 to 380 million years ago), and the Frasnian *Elpistostege* and *Tiktaalik* appear more derived than the Givetian *Panderichthys*^{12,29}, suggesting a good fit between stratigraphy and phylogeny, with tetrapods originating sometime during the mid–late Frasnian. Many recent publications argue that tetrapods evolved from and rapidly replaced the elpistostegids, probably in brackish to freshwater environments, in response to the modification of the terrestrial and water’s edge environment caused by the development of extensive tree-sized land vegetation²¹. However, a few data points have clashed with this consensus picture. Notably, the fragmentary genus *Livoniana*, although Givetian and thus contemporary with *Panderichthys*, is more derived than *Tiktaalik*, judging from its limited preserved anatomy¹².

Supposed trackways of very early tetrapods have been recorded from a number of localities in Europe and Australia^{34–39}. The most securely identified of these, the Genoa River trackways from Australia, are Late Devonian (probably Famennian) in age^{34,37}. Two large trackways from

Valentia Island, Ireland³⁶, have been dated radiometrically to 385 million years ago. At the time of publication this was taken to imply an Eifelian (early Middle Devonian) age³⁹, which clashed with the occurrence of the Late Devonian index fossil (for Laurussia) *Bothriolepis* in the same strata. However, subsequent recalibration of the timescale indicates that 385 million years ago corresponds to the Givetian–Frasnian boundary³³. This is consonant with the biostratigraphy but nevertheless suggests an earlier origin for tetrapods than indicated by the body fossil data.

Our discovery of diagnostic and securely dated tetrapod tracks from the marine Eifelian (early Middle Devonian) of Poland shows that the current consensus based on body fossils is substantially mistaken in both the timescale and, probably, the environmental setting of the fish–tetrapod transition.

The locality

The northern Łysogóry region of the Holy Cross Mountains (Góry Świętokrzyskie) in south-eastern Poland contains an extensive and well-dated sequence of marine Middle Devonian strata (Fig. 1)^{40–45}. In the disused Zachełmie Quarry, the lower part of the Kowala Formation and the upper part of the Wojciechowice Formation are exposed. The trackway horizon lies within the Wojciechowice Formation, some 20 m below the level where a conodont sample showing a characteristic *costatus* Zone assemblage (Eifelian) was taken⁴². The Eifelian age of the formation is also indirectly confirmed by previous biostratigraphic data obtained from the underlying and overlying strata exposed in other sections^{43–45}. It can be securely assigned to the lower–middle Eifelian, corresponding to an age of approximately 395 million years (see Supplementary Information).

The Wojciechowice Formation represents a unique episode of restricted, extremely shallow-water carbonate sedimentation within the generally open marine marly carbonate and, subordinately, siliciclastic deposition that prevailed during the Middle Devonian in the northern Holy Cross Mountains. The lower, trackway-containing part of this formation, almost devoid of other fossils, contains abundant laminites with desiccation cracks and raindrop impressions and seems to represent an extremely shallow marine tidal, perhaps lagoonal, environment. The tetrapod trackway assemblage is not only the earliest but by far the richest from the Devonian. What follows is a preliminary

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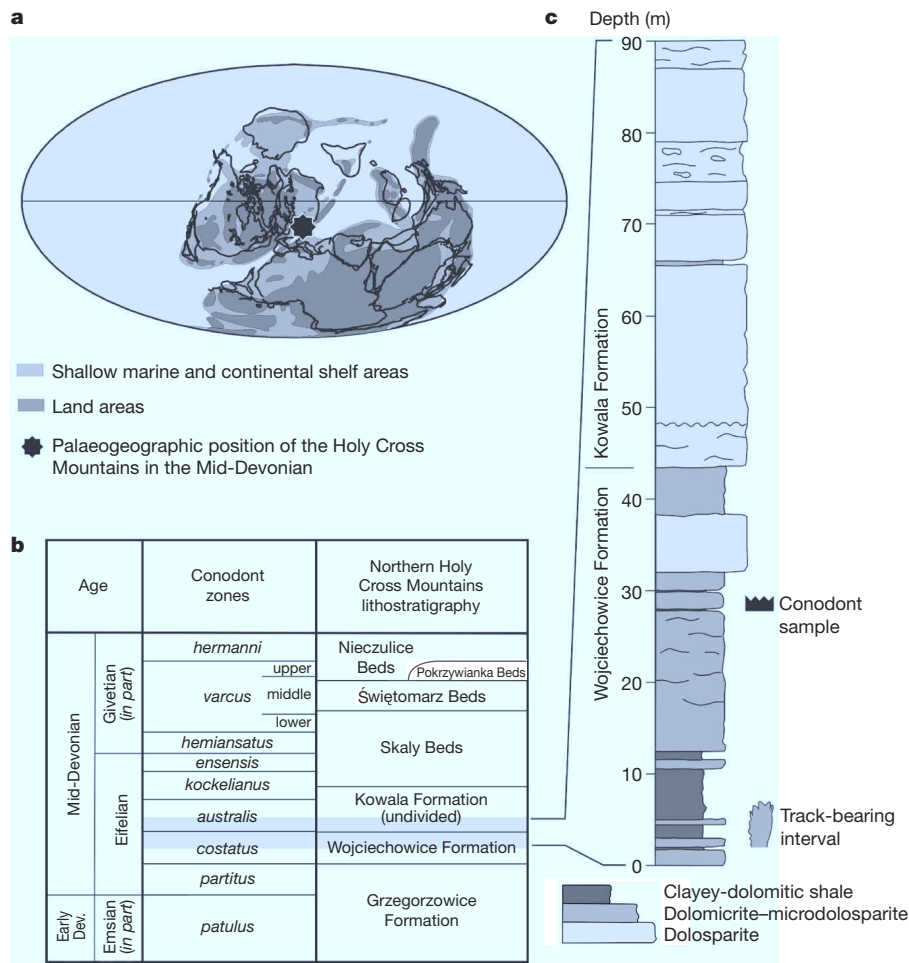


Figure 1 | The locality. **a**, Palaeogeographic position of the Holy Cross Mountains during Middle Devonian (map from ref. 50). **b**, Middle Devonian lithostratigraphy of the northern Holy Cross Mountains. **c**, Zachełmie quarry section showing locations of trackway horizon and *costatus* Zone conodont sample.

description: further study, including ichnotaxonomic description of the trackways, is in progress.

Trackways

The footprint fossils comprise numerous trackways of different sizes and characteristics, as well as a large number of isolated prints and a densely trampled surface. The appearance of the prints varies greatly depending on the size of the animal, the condition of the sediment and the pattern of movement. Digit marks are variably present or absent, probably depending on the cohesiveness of the sediment. Some very crisp and detailed prints are almost certainly true prints, whereas others may represent underprints. For a detailed account of the range of print preservations at Zachełmie see Supplementary Information.

Muz. PGI 1728.II.16 (Fig. 2a) has distinct manus ('hand') and pes ('foot') prints of somewhat different size arranged in diagonal stride sequence. The animal is moving in a straight line and is not leaving a body drag. The prints are circular without digit impressions or displacement rims. A single, slightly larger print on the same slab (Fig. 2a) shows a strong posterior displacement rim with digit marks. We interpret this type of isolated print, which is seen frequently at Zachełmie, as an aquatic print where a swimming tetrapod has used a single limb to kick against the substrate. It should not be confused with the larger single prints discussed below, which have been found on small blocks in the quarry scree and may well derive from longer trackways.

Stride length, relative spacing of the prints, and the absence of a body drag demonstrate that Muz. PGI 1728.II.16 is a tetrapod trackway.

Elpistostegids and other tetrapodomorph fishes all have straight 'knees' and 'elbows', and shoulder and hip joints that face posteriorly^{23–26,28}. In early tetrapods, by contrast, the knees and (in particular) elbows of the short, sprawling limbs allow greater flexion, and the shoulder and hip joints face laterally. The relative stride length shows that both fore- and hindlimbs were oriented anterolaterally at the anterior extremity of the movement arc, with the manus and pes placed on the ground well anterior to the respective shoulder and hip joint (Fig. 2b). This would be impossible for an animal with the girdle morphologies documented in *Tiktaalik* and *Panderichthys*^{23–26,28}, and in any case the absence of a sacrum would prevent the fish from lifting its tail clear off the substrate (Fig. 2b). Assuming standard early tetrapod proportions^{8,18,21}, the total length of the track maker was probably in the region of 40–50 cm.

Muz. PGI 1728.II.15 (Fig. 2c), a track made by a slightly smaller animal, is an example of a second trackway type. Its stride pattern is partly ladder-like, suggesting that for a few strides the limbs were moved symmetrically rather than alternately. The strides are short and no distinction between manus and pes prints can be observed, suggesting that only one pair of appendages is represented. If this is a true track, preserving the actual sediment surface impressed by the feet, the animal was pushing itself along using only one pair of limbs. If, on the other hand, it is an undertrack, we cannot rule out the possibility that both pairs of limbs contacted the sediment, but if so the second pair must have carried less weight and made shallower impressions. (An undertrack is the indentation that a foot leaves in sub-surface sediment layers.) It may have been made subaquatically, by an animal using one pair of limbs, but a confident interpretation of this trackway type must await detailed examination of multiple examples.

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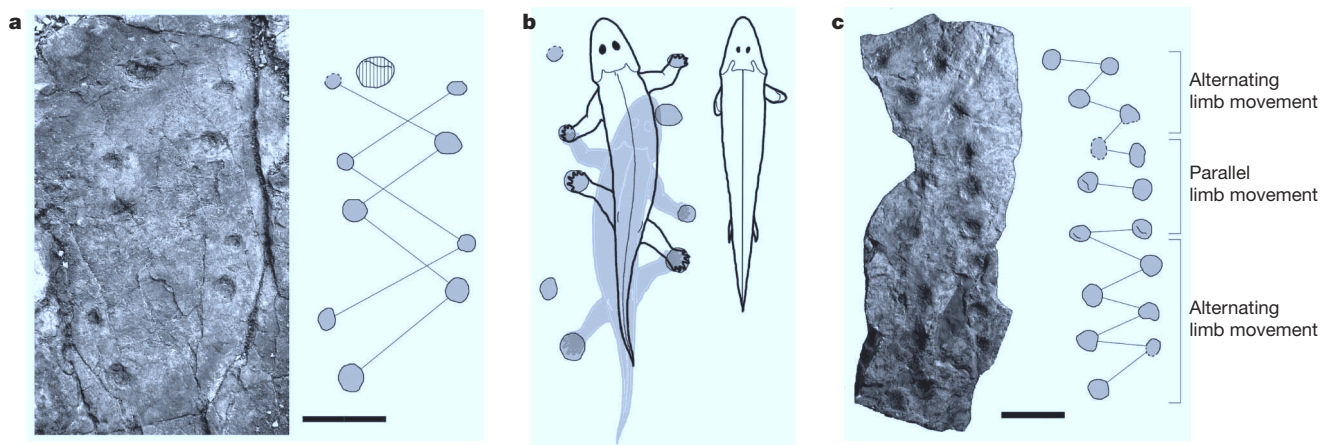


Figure 2 | Trackways. **a**, Muz. PGI 1728.II.16. (Geological Museum of the Polish Geological Institute). Trackway showing manus and pes prints in diagonal stride pattern, presumed direction of travel from bottom to top. A larger print (vertical hatching) may represent a swimming animal moving from top to bottom. **b**, On the left is a generic Devonian tetrapod based on *Ichthyostega* and *Acanthostega* (from ref. 18) fitted to the trackway. On the right, *Tiktaalik* (from ref. 29 with tail reconstructed from *Panderichthys*²³) is

drawn to the same shoulder–hip length. Positions of pectoral fins show approximate maximum ‘stride length’. **c**, Muz. PGI 1728.II.15. Trackway showing alternating diagonal and parallel stride patterns. In **a** and **c**, photographs are on the left, interpretative drawings are on the right. Thin lines linking prints indicate stride pattern. Dotted outlines indicate indistinct margins and wavy lines show the edge of the displacement rim. Scale bars, 10 cm.

Individual prints

A number of large prints, collected from the quarry scree, provide information about the foot morphology in the largest Zachełmie tetrapods. In most instances, the foot is approximately 15 cm wide measured across the junction between sole and toe prints, more than twice the linear dimensions of the best-preserved *Ichthyostega* foot² and suggesting an animal about 2.5 m in length, but the largest print (Muz. PGI 1728.II.5) is 26 cm wide. Three prints, all representing the left pes, will be considered here (Figs 3 and 4); for others see Supplementary Information.

Muz. PGI 1728.II.3 (Fig. 3a) shows a large proximal displacement rim and long curved toe prints. Muz. PGI 1728.II.1 (Fig. 4a) and Muz. PGI 1728.II.2a,b (Fig. 3b) on the other hand have short, triangular toe impressions, as does Muz. PGI 1728.II.5. Their outlines are crisp. Muz. PGI 1728.II.1 has a moderate-sized, low, anterior displacement rim, whereas Muz. PGI 1728.II.2 has only a very small rim along the anterior margin of one of the toe impressions. We infer that the shared morphological features of Muz. PGI 1728.II.1, Muz. PGI 1728.II.2 and Muz. PGI 1728.II.5 reflect the morphology of the foot. By contrast, the large displacement rim of Muz. PGI 1728.II.3 suggests that the foot slipped during the formation of the print; the differences in toe shape between this and the other large prints may thus be an artefact, though a real morphological difference cannot be ruled out.

Muz. PGI 1728.II.1 and Muz. PGI 1728.II.2 both show three large triangular toe impressions, the anteriormost somewhat divergent from the other two. Posterior to these, Muz. PGI 1728.II.1 shows a slender toe that has not left an impression in Muz. PGI 1728.II.2. Anterior to the triangular toes, Muz. PGI 1728.II.1 shows a single slender anteriorly divergent toe whereas Muz. PGI 1728.II.2 shows two similar toes side by side. There are no claws. The tip of each triangular toe shows a small distinct cushion or pad, but there are no separate phalangeal pads, whereas such pads can be discerned faintly on the slender digits.

Comparison of Muz. PGI 1728.II.1 with known early tetrapod limb skeletons^{2,7,8,21}, all of which have short broad feet, indicates that the print includes the ventral surface of the lower leg and knee (Fig. 4a–c). It seems that the ankle was almost flat, as has been argued for *Ichthyostega* and *Acanthostega* on morphological grounds⁸. Supplementary Information 3 and 4 show a three-dimensional surface scan of Muz. PGI 1728.II.1.

Comparisons

Trackway Muz. PGI 1728.II.16 from Zachełmie is in many ways similar to previously described Devonian tetrapod tracks^{34,36,37}. The trackways from Valentia Island (Ireland) and Tarbat Ness (Scotland), and one of the Genoa River tracks (Australia), all show similar

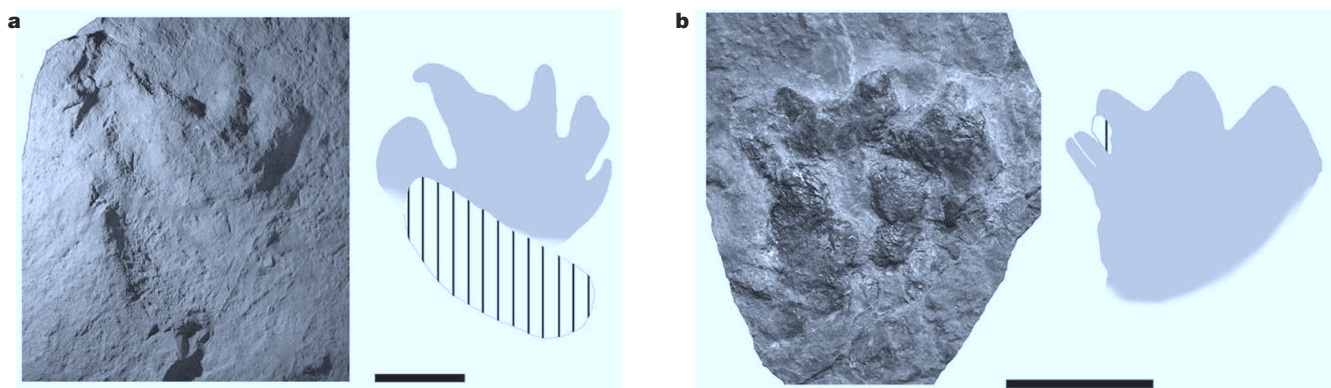


Figure 3 | Footprints. **a**, Muz. PGI 1728.II.3. Probable pes, preserved as natural cast (that is, mirror-imaged). Print with long digit impressions and large displacement rim, probably indicating slippage plus anticlockwise rotation of the foot. **b**, Muz. PGI 1728.II.2. Left pes, preserved as natural cast

(that is, mirror-imaged). Photographs are on the left, interpretative drawings are on the right. In the drawings, grey indicates footprint, and vertical hatching indicates displacement rim. Scale bars, 10 cm.

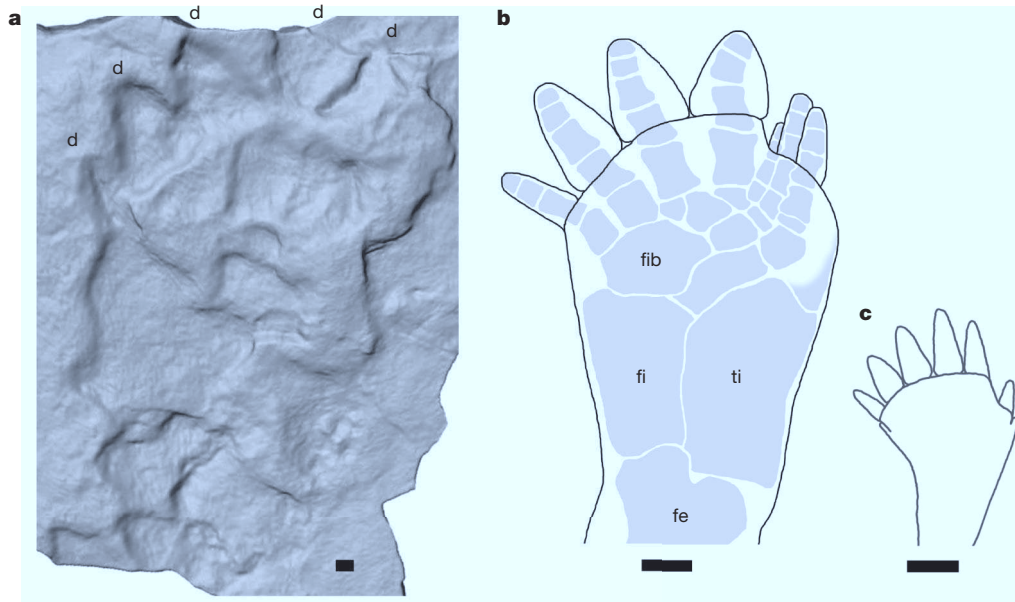


Figure 4 | Foot morphologies. **a**, Laser surface scan of Muz. PGI 1728.II.1, left pes. **b**, Complete articulated left hind limb skeleton of *Ichthyostega*, MGUH f.n. 1349, with reconstructed soft tissue outline. **c**, Left hind limb of *Acanthostega*, reconstructed soft tissue outline based on skeletal

diagonal patterns of manus and pes prints without a body drag. These trackways are all demonstrably younger than Zachelmie. More problematic is the Glenisla trackway from Australia, which appears to be no later than Late Silurian³⁸. The known body fossil record of this period includes stem sarcopterygians⁴⁶, but no tetrapodomorph lobe-fins or tetrapods. The trackway is ladder-like, a characteristic that has been used to argue against a tetrapod identity³⁷, but which is shared with some Zachelmie trackways. The best-preserved Zachelmie footprints are quite similar to the pes morphology of *Acanthostega* and, in particular, *Ichthyostega* (Fig. 4b, c). It is possible to reconstruct approximate footprint morphologies for the two latter genera, though with lower precision for *Acanthostega* because the pes skeleton is partly reconstructed.

Implications

The Zachelmie trackways show that very large stem-group tetrapods, exceeding 2 m in length, lived in fully marine intertidal to lagoonal

environments along the south coast of Laurussia during the early Eifelian, some 18 million years before the earliest-known tetrapod body fossils were deposited. This forces us to infer much longer ghost lineages for tetrapods and elpistostegids than the body fossil record suggests (Fig. 5a, b). (Ghost lineages are those that must have existed at a particular time, according to the phylogeny, but which are not represented by fossils at that time.) Until now, the replacement of elpistostegids by tetrapods in the body-fossil record during the mid-late Frasnian has appeared to reflect an evolutionary event, with the elpistostegids as a short-lived 'transitional grade' between fish and tetrapod morphotypes (Fig. 5a). In fact, tetrapods and elpistostegids coexisted for at least 10 million years (Fig. 5b). This implies that the elpistostegid morphology was not a brief transitional stage, but a stable adaptive position in its own right. It is reminiscent of the lengthy coexistence of non-volant but feathered and 'winged' theropod dinosaurs with volant stem-group birds during the Mesozoic.

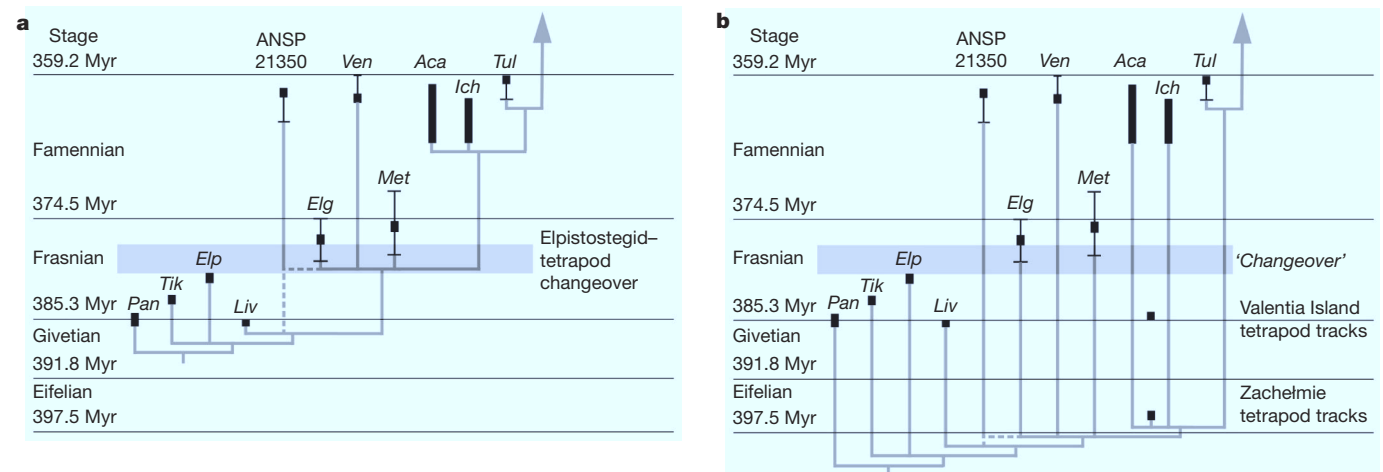


Figure 5 | Phylogenetic implications of tracks. **a**, Phylogeny of selected elpistostegids and stem tetrapods, based on refs 10, 12, 19 and 20, fitted to Devonian stratigraphy. The grey bar indicates replacement of elpistostegids by tetrapods in body fossil record. **b**, Effect of adding the Zachelmie tracks to the phylogeny: the ghost ranges of tetrapods and elpistostegids are greatly extended and the 'changeover' is revealed to be an artefact. *Pan*,

Panderichthys; *Tik*, *Tiktaalik*; *Elp*, *Elpistostege*; *Liv*, *Livoniana*; *Elg*, *Elginerpeton*; *Ven*, *Ventastega*; *Met*, *Metaxygnathus*; *Aca*, *Acanthostega*; *Ich*, *Ichthyostega*; *Tul*, *Tulerpeton*. ANSP 21350 is an unnamed humerus described in ref 17. The bars are approximate measures of the uncertainty of dating. These are not statistical error bars but an attempt to reflect ongoing debate.

The Wojciechowiec Formation represents a tidal flat environment or a lagoon in a broad shallow carbonate basin with little terrigenous input. This suggests that the origin of tetrapods occurred, not in the vegetated margins or surrounding seasonal 'flooded forest' environments of rivers, as has frequently been argued, but in the marine intertidal and/or lagoonal zone. Such a scenario has considerable explanatory power. The intertidal environment provides a ready food source of stranded marine animals on a twice-daily basis, in the immediate vicinity of the sea, and would thus have allowed marine ancestors of tetrapods gradually to acquire terrestrial competence while accessing a new and essentially untouched resource. The mid-Devonian riverine environment by contrast would probably not have provided any such reliable and easily captured terrestrial food source. Recent hypotheses about non-marine tetrapod origins have accordingly focused on other perceived benefits of limb-driven locomotion, either on land or in shallow water, relegating terrestrial feeding to a later stage of tetrapod evolution even though both dentition and sutural morphology indicate changes in feeding mechanics at the origin of tetrapods^{10,21,47}. Under the intertidal hypothesis, these somewhat counterintuitive arguments become unnecessary.

The replacement of elpistostegids by tetrapods in the body fossil record of the mid-late Frasnian raises two questions: why do both groups have such long initial ghost ranges (a minimum of 10 and 18 million years, respectively), and why do the elpistostegids appear before tetrapods in the body fossil record in a manner that neatly simulates a stratophylogenetic fit (Fig. 5)? The first question is answered in part by the observation that the Wojciechowiec Formation is almost devoid of body fossils; this environment was evidently not conducive to the preservation of skeletons. Contemporary vertebrate body fossil faunas, known mainly from the Baltic States and Scotland, come from rather different environments. The Baltic shallow marine strata are dominated by sandy terrigenous sediments⁴⁸ and the Scottish fossil assemblages derive from a succession of lakes within the Orcadian basin⁴⁹. The absence of tetrapods in these deposits may simply be a matter of environmental preference. The false stratophylogenetic succession from elpistostegids to tetrapods is more of a puzzle. If their first appearance as body fossils reflects the time when they first colonized environments with preservation potential, as seems likely, the elpistostegids evidently arrived in advance of the tetrapods. The reason was presumably ecological but cannot be determined at present.

The discovery of the Zachełmie footprints substantially changes the context for future research on the origin of tetrapods. Intertidal laminites of Middle and Early Devonian age should be examined systematically for tetrapod tracks, and we should search for tetrapod and elpistostegid body fossils in associated marginal marine strata. For the present the timing of the fish-tetrapod transition is best regarded as uncertain, though it clearly pre-dates the early Eifelian; an Early Devonian date seems most likely, but even earlier potential tetrapod ichnofossils such as the Silurian Glenisla track should not be dismissed out of hand.

METHODS SUMMARY

The tracks were photographed in low-angle light to bring out the details, and were sometimes also highlighted with pigments. Tracks that could not be collected from the quarry were cast *in situ* using silicone rubber, and these silicone peels were then used as moulds to produce Jesmonite plaster replicas of the original surfaces. Surface scanning of Muz. PGI 1728.II.1 was performed in the Museum and Institute of Zoology of Polish Academy of Sciences using a three-dimensional Minolta VI-9i laser scanner. The movies of this scan, presented in Supplementary Information 7 and 8, were rendered using the rendering software package Rhino with the animation plug-in Bongo, both published by McNeel.

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