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# Devonian tetrapod trackways and trackmakers; a review of the fossils and footprints

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## Abstract

The earliest tetrapods are known from the Upper Devonian. Their remains are becoming better known from increasing numbers of specimens, localities, environments and ichnofossils. Each of the eight (or possibly nine) genera now represented by skeletal fossils is reviewed in its sedimentological, faunal and stratigraphic context, with an assessment of what might be inferred about the habitus and locomotory capabilities of each. Fossil trackways and their interpretations are then re-examined in the context of the known body forms, and consideration given to the degree of fit between the skeletal fossils, the trackways and their interpretations. The currently known Devonian tetrapods are unlikely to have made any of the known tracks, unless they were produced under water. Neither the skeletal fossils nor the trackways show good evidence of terrestrial locomotion among Devonian tetrapods. When the fossil material and recent phylogenetic analyses are taken in combination, it appears that neither tetrapods nor limbs with digits are likely to have arisen before the Frasnian. This should be borne in mind in palaeoecological studies of these animals. © Elsevier Science B.V. All rights reserved.

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## 1. Introduction

The earliest evidence of the existence of vertebrates with limbs and digits comes from the Upper Devonian period. In the last few years, the available information on anatomy and distribution of animals representing the so-called fish–tetrapod transition has been increased by the discovery of many skeletal fossils representing several new genera (Ahlberg, 1991a, 1995; Ahlberg et al., 1994; Daeschler et al., 1994). Knowledge of previously discovered and named genera has been enhanced

and expanded by full descriptions of both old and new material (Clack, 1989, 1992, 1994a,b, 1997 in press, Coates and Clack, 1990, 1991, 1995; Coates, 1991, 1993, 1994, 1996; Clack and Coates, 1993, 1995; Lebedev and Clack, 1993; Lebedev and Coates, 1995; Jarvik, 1996). Alongside the skeletal evidence is that from trackways, of which new reports have been published recently (Rogers, 1990; Stössel, 1995).

A common assumption has been that the evolution of legs is coupled to the evolution of terrestriality, and that at least some Devonian tetrapods were capable of sustained, limb-supported locomotion on land. A series of scenarios put forward between the 1940's and 1960's (e.g. Westoll, 1943;

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Eaton, 1951; Orton, 1954; Ewer, 1955; Goin and Goin, 1956; Gunter, 1956; Inger, 1957; Romer, 1958; Warburton and Denman, 1961; Schaeffer, 1965), envisaged the first terrestrial excursions by vertebrates to have been made by “rhpidistian” fishes as they were then called (i.e. sarcopterygians like *Eusthenopteron*). The fins of *Sterropterygion* were interpreted to demonstrate the evolution of tetrapod-like limb joints (Rackoff, 1980). Thus “walking” in the sense of terrestrial progression was thought to have preceded legs. It resulted in the earliest tetrapods being envisaged as employing quadrupedal locomotion, exemplified by the often-reproduced image of *Ichthyostega* given by Jarvik in 1980. The existence of trackways made by Devonian tetrapods has been taken as good evidence that they were capable of terrestrial locomotion. Recent work on *Acanthostega* and other Devonian tetrapod genera has put forward the alternative hypothesis that limbs with digits evolved first among tetrapods for use in water, and only later were co-opted for terrestrial use (Coates and Clack, 1990; Gould, 1991). Recent ideas on the origin of tetrapods and limbs have recently been reviewed by a number of authors (Thomson, 1991, 1993; Ahlberg and Milner, 1994; Daeschler and Shubin, 1995).

The time is now ripe to bring together all the available new data on these creatures, to document what is actually known, to review what has been assumed and what can be reliably inferred about the habits and lifestyle of these transitional animals. This paper therefore reexamines the morphology, occurrence and associations of the body fossils and reassesses that from trackways in an attempt to investigate the quality of the fit between these two types of evidence. It considers what kind of tracks might be made by the known tetrapods and their relatives and the likelihood that any of the described tracks were made by any of these animals. Evidence from phylogeny is then brought to bear to give an estimate of the likely time of origin of tetrapods and for the possible origin of terrestriality.

For the purposes of this paper, the vernacular term “tetrapod” is taken to mean members of a monophyletic group defined by a suite of characters of the skull and postcranial skeleton (Godfrey,

1989; Clack and Coates, 1995) which includes the possession of limbs with jointed post-axial endoskeletal elements (digits) clustered around an array of interarticulated carpal or tarsal elements. The relationship of this group to members of a formal clade Tetrapoda is no longer simple, but since it has implications for the link between the appearance of tetrapods, the appearance of limbs and the onset of terrestriality, the arguments are outlined below.

## 2. Review of material

### 2.1. Devonian tetrapod skeletal fossils

The eight (or nine) Devonian tetrapod genera represented by skeletal fossils are documented below. Information on their taphonomic, stratigraphic, faunal and palaeoenvironmental context is combined to make an assessment of the likely palaeoecology and habitus of the animals. In particular the evidence concerning possible locomotory capabilities are considered. The taxa are listed in order of stratigraphical age as far as possible.

#### 2.1.1. *Obruchevichthys* and *Elginerpeton*

Two closely related genera, *Obruchevichthys gracilis* from Latvia (Ahlberg, 1991a; Ahlberg et al., 1994) and *Elginerpeton pancheni* from Scat Craig near Elgin in Scotland (Ahlberg, 1995), both Upper Frasnian in age, constitute the earliest record of tetrapod skeletal fossils (Ahlberg, 1991a). Specimens of *Obruchevichthys* consist of jaw fragments originally considered to be sarcopterygian fishes (Vorobyeva, 1977). They have recently been recognised as tetrapods on the grounds of derived lower jaw characters which they share with other tetrapods.

*Obruchevichthys* occurs in light greenish-grey well consolidated sandstone of the Ogre formation (E. Luksevics, pers. commun., Sorokin, 1981) along with heterostracans such as *Psammosteus* spp., placoderms including *Bothriolepis*, the acanthodian *Devononchus*, the porolepiform *Holoptychius* and dipnoans.

The remains themselves provide little evidence of the habitus of the animals, except that they

were taken for fish remains for many years. They show evidence of lateral line canals, and the coronoid dentition includes large fang pairs, a character usually associated with some sarcopterygian fishes. Taken at face value, the occurrence of *Obruchevichthys* with a typical Upper Devonian fish fauna suggests that the animals were more likely aquatic than terrestrial.

The Scat Craig locality, at which *Elginerpeton* is found, consists of reddish to pale yellow channel sands, with bands of small pebbles, clay clasts and occasional silt lenses. The vertebrate fossils usually occur in association with the pebbles and clay clasts. They are always disarticulated and often highly abraded. The bone-rich bands are probably lag deposits containing reworked and transported material (Ahlberg, 1997 in press). Also occurring at this locality are placoderms including *Bothriolepis*, acanthodians, porolepiforms, a lung-fish and heterostracans, constituting a fairly typical assemblage of Upper Devonian fishes (Ahlberg, 1997 in press).

*Elginerpeton* is represented by upper and lower jaw fragments, skull fragments including a premaxilla, and some limb and girdle elements (Ahlberg, 1995, 1997 in press). The postcranial elements comprise a tibia resembling that of *Ichthyostega*, a short, flattened femur, a humerus, large but incomplete pelvic elements and parts of several shoulder girdles. The lower jaw and premaxilla suggest a large animal with a skull about 400 mm long, flat-headed and rather like *Panderichthys* in shape but even more pointed in the snout. Lateral line organs occur in tubes in the bone, in common with sarcopterygian fishes and other very early tetrapods. The ilium and femur associated with *Elginerpeton* are of massive proportions, comparable in morphology to that of *Ichthyostega*, but much larger and in keeping with the skull material of *Elginerpeton*. The humerus attributed to *Elginerpeton* has a morphology which in most respects falls between that of the sarcopterygian *Panderichthys* and the tetrapod *Acanthostega*, and may belong to a smaller individual than the ilium and femur. The scapulocoracoid, though only partially preserved, resembles that of *Ichthyostega* in particular (Ahlberg, 1997 in press).

Both deep and superficial lateral line neuromasts

occur among modern bony fishes (Webb, 1989), but the ecological significance of the difference remains unknown. The distinction often made by palaeontologists between “fish-like” canals running in tubes through the bone, and “tetrapod-like” canals running in grooves is over-simplified and requires investigation. However, there is a possibility that more superficial neuromasts display a paedomorphic condition. Without further study, the condition of the lateral line canals adds little more evidence to the debate about terrestriality than that the adult animals were predominantly, but not necessarily exclusively, aquatic.

The sheer bulk of the ilium from Scat Craig suggests a very stout hind-limb, one which some may read as evidence that this animal was using hindlimbs for terrestrial propulsion, if not actual support on land. The flattened femur, by contrast, was apparently held in such a way as to make it very unlikely to have supported weight, rather it appears to have functioned as a paddle (Ahlberg, 1997 in press). The hind limb of *Ichthyostega* (see below) was flipper-like, and a morphology of this kind in *Elginerpeton* again suggests an aquatic habitus. If the ilium and femur belong together, a paddle-like femur demonstrates an aquatic animal despite the appearance of the ilium. If the ilium does not belong to the same genus as the femur, humerus, tibia or lower jaw fragments, a case could be made from it for a large terrestrial animal at this locality. However, the size of the animal appears to preclude terrestrial limb-powered locomotion without rather specialised limb morphology for which there is no evidence. No extrinsic evidence suggests a terrestrial origin, though terrestrial remains could have been washed into an aquatic environment.

#### 2.1.2. *Metaxygnathus*

*Metaxygnathus denticulus* from the Famennian of Australia (Campbell and Bell, 1977) consists of an isolated lower jaw found among plates of the placoderms *Bothriolepis* and *Remigolepis* and a skull of the dipnoan *Soederberghia*, in the Cloghnan Shales near Forbes, New South Wales. It is dated as “most probably late Frasnian or early Famennian”. It was interpreted as tetrapod by Campbell and Bell (1977), and although

Schultze (Schultze and Arsenault, 1985; Schultze, 1987) has disputed this interpretation, more recent studies and discoveries of early tetrapod lower jaws (Ahlberg et al., 1994; Ahlberg, 1995; Ahlberg and Clack, work in progress) have all tended to strengthen the interpretation. The jaw alone offers few clues to the ecology of the animal, except for the presence of lateral line organs, shown by both pores and short stretches of grooving.

### 2.1.3. *Hynerpeton*

*Hynerpeton bassetti* (Daeschler et al., 1994) from the Middle to Upper Famennian of Pennsylvania, USA, is represented by two incomplete left shoulder girdles, plus several fragments including a jugal, scutes and a partial lower jaw. The specimen comes from fine grained, non-marine floodplain deposits representing meandering stream systems. Other components of the fauna include the large osteolepiform *Hyneria lindae*, two undescribed osteolepiforms, basal actinopterygians and the antiarch *Bothriolepis*. The faunal remains occur as undistorted, sometimes articulated, and occasionally abundant specimens.

Like *Ichthyostega* and *Acanthostega*, *Hynerpeton* has the cleithrum integrated with the scapulocoracoid to form a robust unit. It lacks the post-branchial lamina associated with gill-breathing which is found in *Acanthostega*. The subscapular fossa appears to have accommodated extensive musculature to tie the shoulder girdle to the vertebral column, and the shape of the infraglenoid fossa and large infraglenoid buttress suggests the presence of large, powerful muscles for protraction, retraction and elevation of the forelimb. Because the rest of the postcranial skeleton is unknown, it is impossible at present to be sure if these muscles were engaged in swimming or walking on land.

### 2.1.4. *Acanthostega* and *Ichthyostega*

*Acanthostega gunnari* (Jarvik, 1952; Clack, 1989, 1992, 1994a,b, 1997 in press; Coates and Clack, 1990, 1991, 1995; Coates, 1991, 1993, 1994, 1996; Clack and Coates, 1993, 1995) and *Ichthyostega* spp. (Säve-Söderbergh, 1932, 1935; Jarvik, 1952, 1980, 1996; Coates and Clack, 1990) from East Greenland, are the two longest known and best

represented genera of Devonian tetrapod. *Ichthyostegopsis* (Säve-Söderbergh, 1932) may represent a third genus, or may be a junior synonym of *Ichthyostega* (Jarvik 1996). Clack (1988) described part of a palate and dentition which may represent a further unnamed taxon from these deposits.

The fossils derive from two horizons of the East Greenland Famennian, the older Aina Dal and the younger Britta Dal formations. The dating of the sediments is still only coarsely resolved within the Famennian, and is based largely on the vertebrate fauna (Bendix-Almgreen, 1976; Olsen and Larsen, 1993). Olsen and Larsen (1993) place the Devonian – Carboniferous boundary within the Stensiö Bjerg formation, which overlies the Britta Dal.

The deposits of the Devonian of East Greenland have been extensively studied by sedimentologists (e.g. Johansson, 1935; Büttler, 1961; Haller, 1971; Friend et al., 1976, 1983; Nicholson and Friend, 1976). Most recently, the work of Olsen and colleagues (Olsen, 1993, 1994; Olsen and Larsen, 1993) has given a vivid picture of the landscape and conditions of the region during the periods in which we know it was occupied by tetrapods. During Aina Dal formation times, the region was a plain bounded to what is now the south by uplands from which rivers drained to the north and east. The climate was moderately wet, and the rivers formed a permanent, meandering system winding over a floodplain. As the climate became drier towards the end of the interval, the rivers became more ephemeral. Following the Aina Dal formation, the Wiman Bjerg formation represents a period of aridity, when shallow ephemeral playa lakes lay over the basin, and no vertebrate fossils are found. The deposits show evidence of Milankovitch cyclicity (Olsen, 1993, 1994). After this period, the sediments of the Britta Dal were laid in a period of ameliorating climate, when first ephemeral and later more permanent rivers appeared again. These studies also confirm that there was no marine influence in the deposition of the East Greenland Upper Devonian sediments.

The Britta Dal formation has yielded the great majority of specimens of *Acanthostega*. The richest site, on Stensiö Bjerg, represents several burial

events in sediments from a point-bar deposit formed in an active channel in a meandering river system (Bendix-Almgreen et al., 1990). The matrix is a reddish-grey sandy siltstone of mixed grain size and composition. At this site, *Acanthostega* is the only tetrapod taxon to have been recovered, and while much of this material is articulated all the accompanying fish remains are disarticulated (Clack, 1994a). *Holoptychius* scales comprise the majority of non-tetrapod elements, with only two isolated lungfish bones, a small toothplate and a parasphenoid, recovered from this site. Two fragments of ctenacanth shark spines were also found associated with one of the *Acanthostega* skulls. In the Britta Dal Formation generally, both the antiarch *Remigolepis* and the porolepiform *Holoptychius* are common, while *Eusthenodon* and lungfish are occasional constituents of the fauna.

Almost the entire skeleton of *Acanthostega* is now known, based on several partial, articulated skeletons and many disarticulated elements. The animal retains many fish-like characters and is arguably the most primitive known tetrapod. Fish-like characters include grooved gillbars resembling most closely those of fishes, being in some respects more fish-like than those of modern lungfishes (Coates and Clack, 1991), and certainly better ossified. From these, it has been argued that *Acanthostega* possessed internal gills. In addition, it retains a post-branchial lamina on the cleithrum, which again has been interpreted as evidence for a functional internal gill chamber and an operculum formed from soft tissue. No bony opercular bones remain. It retains an anocleithrum in the shoulder girdle. All these could also be interpreted as retained primitive features with no functional significance.

In addition, *Acanthostega* possessed paddle-like limbs each bearing eight digits (Coates, 1996 in press) attached to a poorly ossified carpus or tarsus. Based on this evidence and the form of the wrist, ankle and shoulder joints, the limbs have been judged unlikely to be directly weight-bearing. The vertebrae bore poorly developed zygapophyses, the ribs were short, and the tail bore long, numerous lepidotrichia supported by caudal radials to form a deep tail-fin interpreted most easily as providing a sudden thrust to an aquatic, lurking

predator (Coates, 1994; Clack and Coates, 1995) (Fig. 1A). There is no doubt that *Acanthostega* was an aquatic animal, but arguments could still be made to support its interpretation as secondarily so. These arguments are reviewed elsewhere (Clack and Coates, 1995).

Of the many specimens which exist of *Ichthyostega*, the majority are talus-derived. Very few have been recovered from known parent deposits, and of these, none has been studied in its sedimentological context. Sediments yielding *Ichthyostega* bones vary from coarse red sandstones to very dark reddish-grey, fine-grained and homogenous siltstones. The latter have supplied the most completely articulated material. Specimens collected in 1987 from this type of sediment appear to have derived from a channel fill visible at the top of the Aina Dal formation, but unfortunately inaccessible for collecting directly.

In the Aina Dal formation as a whole, the antiarch *Remigolepis* is the commonest component of the fauna, with porolepiforms (*Holoptychius*), osteolepiforms (*Eusthenodon*) and dipnoans (*Soederberghia*) as additional elements. *Ichthyostega* bones are frequently associated with *Remigolepis* plates and *Holoptychius* scales, so there is no doubt they occurred in the same horizons, but whether they ultimately derived from the same habitats cannot yet be ascertained. Both *Eusthenodon* and *Soederberghia* attained large sizes, suggesting the presence of large water-bodies. The fish constitute a typical Upper Devonian fauna (Bendix-Almgreen, 1976).

*Ichthyostega* is the most widely known Devonian tetrapod, featuring in many text-books, popular works and children's books as the paradigm earliest tetrapod with legs. In these publications, it is almost always reconstructed in a terrestrial pose, with the basis of the reconstruction taken from Jarvik (1980). However, when *Ichthyostega* was first figured by Jarvik (1952) he showed it with relatively small paddle-like hind limbs. It is interesting to note its transmutation over subsequent years into the more stoutly terrestrial animal of popular image, exemplified in the 1980 book. Bjerring (1985) produced a different reconstruction which, like Jarvik (1952), showed the hind-limb

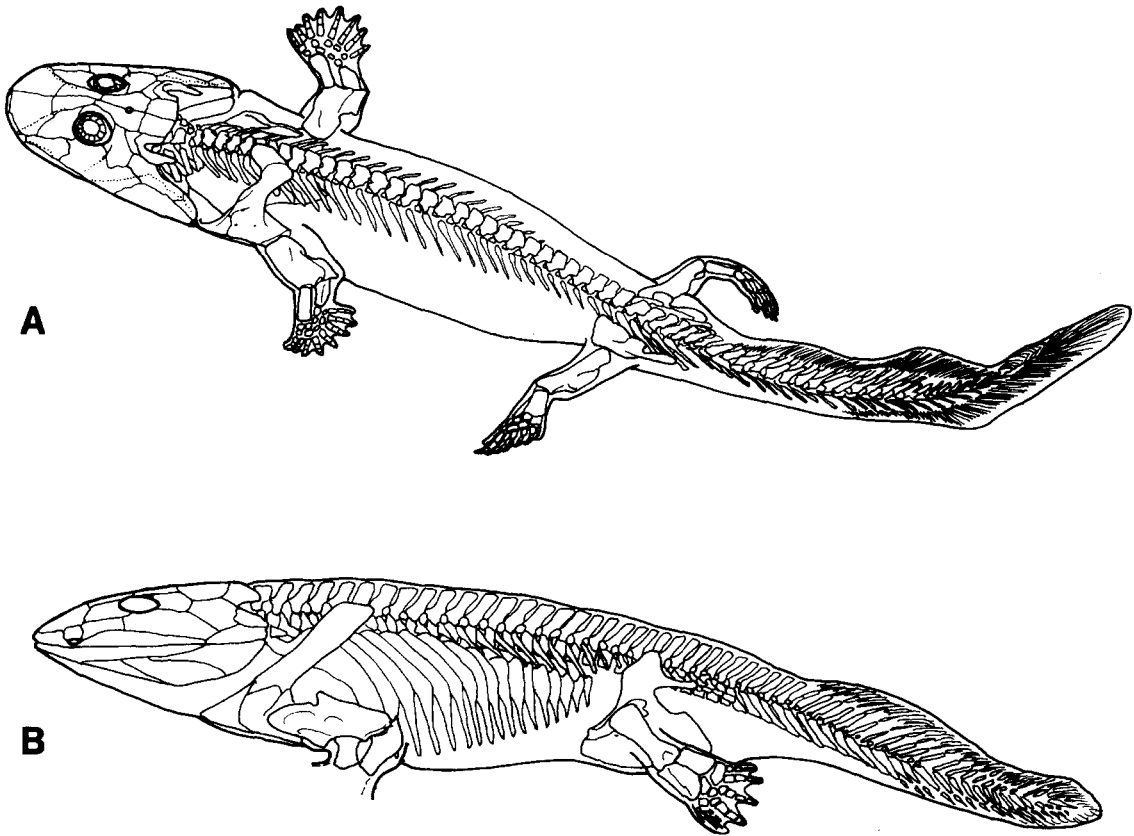


Fig. 1. (A) *Acanthostega gunnari*, skeletal reconstruction after Coates (1996). The majority of *Acanthostega* specimens have a skull length of about 120–150 mm. (B) *Ichthyostega* sp., skeletal reconstruction after Coates and Clack (1995). The majority of *Ichthyostega* specimens have a skull length of about 200–250 mm.

as backwardly directed and paddle-like. This went almost entirely unremarked until the more recent discoveries (Coates and Clack, 1995), which are in accord with Jarvik's original figure and Bjerring's re-interpretation. The following observations are drawn from examination of original material.

The evidence for the stance of *Ichthyostega* is quite scarce. Only one specimen, MGUH A115, shows the head, trunk and fore-limbs in articulation. This specimen is associated with a femur and a tail section, which are considered to belong to the same individual (E. Jarvik, pers. commun., 1990). They were collected at the same time from the same site and horizon, but can no longer be fitted onto the main body of the specimen. The femur is much smaller than other examples, which

are by contrast found in articulation with hindlimbs and tails. However, it is the latter, which lack bodies or heads, that have been used to generate the reconstructions of the hindquarters of the genus.

If the articulated body is used as a guide and the femur accepted as associated, the proportions of *Ichthyostega* are seen to be dramatically different from those conventionally given (Coates and Clack, 1995) (Fig. 1B). The femur is about half the length of the humerus, so that the animal must be reconstructed with massive forequarters and diminutive hind limbs. The hindlimbs are paddle-like, with large, flattened tibia and fibula, a low number of tarsals compared with most other tetrapods and seven digits. Three of the digits form what appears to be the "leading edge" of the

paddle, with the third digit reduced to two tiny phalanges. A further osseous “spur” continues distally the line formed by a ridge on the tibia, contributing to the strengthening of the leading edge of the pes (Coates and Clack, 1990). The overall pattern of the limb most strikingly resembles the pectoral flipper of a dolphin (in particular a river-dolphin). There appears to be no clearly functional ankle (Bjerring, 1985; Coates and Clack, 1990), nor is it obvious that the limb was capable of bending very much at any joint. A full skeletal reconstruction of the hindlimb of *Ichthyostega* has not so far been published, and important details such as the size of the interepipodial space, remain unknown.

The acetabulum into which the femur fitted has a strap of unfinished bone directed anteriorly (Jarvik, 1980, pers. obs.). This form of acetabulum also occurs in *Acanthostega*. It remains unclear what range of movement would have been possible for the hind limb.

What is known of the forelimb is in marked contrast to the hind limb, not only in proportion but in structure. In specimen MGUH f.n. A115, the glenoid appears strongly curved such that about half its articular face was directed posteriorly, and the rest laterally (Jarvik, 1980, pers. obs.). The humerus, based on this specimen, had a maximum forward position of about 90° to the body, though it was probably capable of being pulled back into the animal’s side for swimming. However, a specimen of the scapulocoracoid collected in 1987 (MGUH f.n. 1396) shows a much less strongly curved glenoid. Both specimens may exhibit distortion to some extent.

The elbow is characterised by a dorsally projecting olecranon process on the ulna which would effectively have prevented the elbow from being straightened. Uniquely, the olecranon is forked, the functional implications of which remain uninvestigated. The radius articulated onto a bulbous facet positioned beneath and just proximal to the end of the humerus. The forearm therefore appears to have acted as a vertical pillar on which the horizontally held humerus was supported. The carpus and digits of the forelimb are completely unknown, so that the form of the wrist and number of digits remain a source of speculation.

Reconstructions which show them are entirely conjectural.

One of the most characteristic features of *Ichthyostega* as figured is its barrel-shaped body, girded by massive overlapping ribs. No dorsal view of *Ichthyostega* has been published, but an accurate three-dimensional reconstruction may well demonstrate that this barrel-shaped body could not fit into the given reconstructions of the shoulder girdle. However at least two specimens show that each of the foremost pairs of thoracic ribs overlapped about three or four posterior ones. This structure rules out all but the lowest amplitude bending of the body, rendering sinusoidal locomotion for this animal virtually impossible. It is tempting to speculate that the forelimbs might have moved in parallel rather than in sequence.

Given our current information, an accurate reflection of the body form of *Ichthyostega* should give it a seal-like stance, and indeed the skeleton of the elephant seal seems to provide a close morphological analogue in terms of overall proportions (Coates and Clack, 1995; Coates, 1996). *Ichthyostega* can be imagined as heaving itself up a shelving shore using its powerful forelimbs, dragging its hindquarters and tail behind it.

#### 2.1.5. *Tulerpeton*

*Tulerpeton curtum* (Lebedev, 1984, 1985; Lebedev and Clack, 1993; Lebedev and Coates, 1995) from the Tula region, Central Russia, is dated as Famennian (Alekseyev et al., 1994). The animal is represented by a single block containing essentially complete articulated hind and forelimbs, with parts of the pectoral girdle and ventral squamation. Parts of the premaxilla and vomer were also present in the same block and almost certainly come from the same individual. A partial pelvis, a few centra, rib fragments, four interclavicles and isolated skull bones were discovered at the same site, but they may represent more than one species of tetrapod.

The site, Andreyevka 2, yields many vertebrates, all represented by disarticulated remains (Lebedev and Clack, 1993; Alekseyev et al., 1994). At this locality, *Tulerpeton* is almost unique in its state of completeness. The fauna includes the antiarchs *Remigolepis* and *Bothriolepis*, the osteolepiforms

*Eusthenodon* sp. and an unnamed species, the onychodont *Strunius*, the lungfish *Andreyevichthys* and acanthodians, a few actinopterygians and chondrichthyans. The site also yields numerous species of ostracod, as well as bivalves, serpulids, and remarkably, stromatolites and charophytes. The sediments indicate that the locality was a shallow, warm, epicontinental sea having strongly fluctuating salinity. It appears to have been situated about 200 km from the Old Red Sandstone Continent to its west.

The limbs of *Tulerpeton* appear more “conventionally” tetrapod-like as compared with those of *Acanthostega* and *Ichthyostega*, in that the epipodials are relatively elongated and slender. At first sight, they may be interpreted as representing a more terrestrially adapted animal. However, the large adductor blade on the femur of *Tulerpeton* is consistent with large muscles which pull the hind limb strongly in towards the body. This adductor blade, associated with distally placed muscle insertions, may reflect similarly distally placed muscle insertions seen in some modern primarily aquatic salamanders. There the muscle position seems to be an adaptation for swimming (Coates, 1996, and references therein). The ankle in *Tulerpeton* shows some similarities to those of *Ichthyostega* and *Acanthostega* in that the fibulare supports the bases of two digits, and metapodial elements are not clearly identifiable. The joint may have functioned in a similarly paddle-like manner (Lebedev and Coates, 1995) (Fig. 2).

*Tulerpeton* provides equivocal evidence about its locomotory capabilities, because many of the features one would wish to consider, such as the tail construction, vertebrae and ribs are missing. Although the limbs show some evidence of paddle-like construction, its epipodials are more in keeping with those of more crownward tetrapods.

Among the three genera for which articulated limb material is available, the relationship between degree of apparent terrestrial adaptation and association with a terrestrial habitat is at first sight inverse (Coates and Clack, 1995). However, carcasses have sometimes been recorded as having been carried long distances out to sea in quiet conditions, the skeletons remaining more or less intact, so that the aquatic, marine conditions pre-

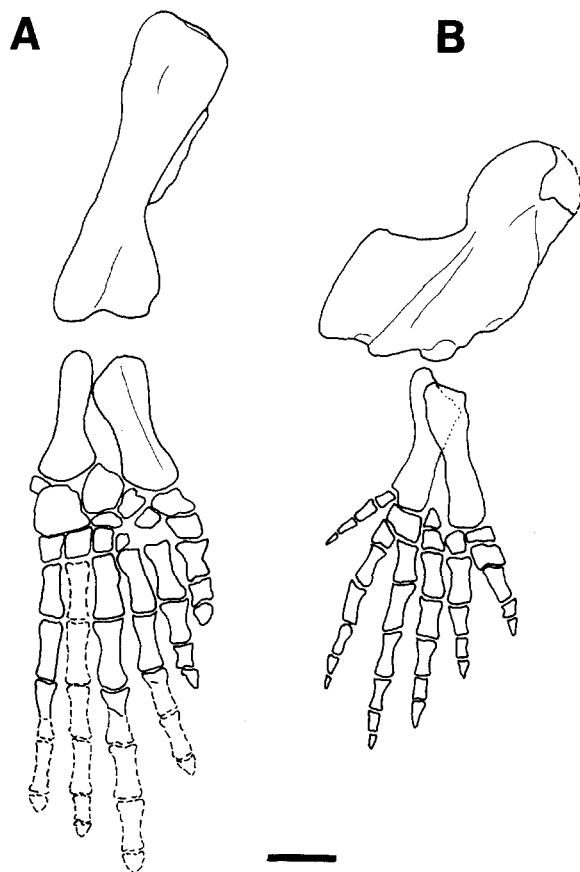


Fig. 2. *Tulerpeton curtum*. (A) Hindlimb. (B) Forelimb. Skeletal reconstructions after Lebedev and Coates (1995). Scale bar 10 mm.

viously envisaged (Lebedev and Clack, 1993) for *Tulerpeton* may be incorrect. Alternatively, remains of other, disarticulated, tetrapods which are also present in the sediments might suggest that populations could have lived on islands in the lagoon.

#### 2.1.6. *Ventastega*

*Ventastega curonica*, a recently recognised and described genus from the Upper Famennian of Latvia (Ahlberg et al., 1994) is known from lower jaws, cheek and palate bones, a clavicle, a partial interclavicle and a partial ilium, though further collecting is yielding more material. The species is represented, like all the vertebrates from the Pavari site, by unworn but isolated bones with good



3-dimensional preservation. The majority of other vertebrate specimens consist of detached plates and head shields of the antiarch *Bothriolepis*. Other species from the site include the porolepiform *Holoptychius*, the osteolepiforms *Cryptolepis* sp. and *Panderichthys bystrowi*, the lungfish *Orlovichthys* together with acanthodians, and a large unnamed eusthenopterid (Ahlberg et al., 1994).

The remains of *Ventastega* provide little evidence of its lifestyle. The lower jaw retains surangular pit-lines like those found in osteolepiform fishes but which are generally absent in tetrapods, including *Acanthostega*. The clavicle is of a form typical of other early tetrapods with an expanded ventral plate and narrow dorsal process. What is preserved of the ilium, the dorsal process, resembles that of *Acanthostega*. A complement of fish genera similar to those associated with most other Devonian tetrapod skeletal fossils form the majority of vertebrates in the deposit.

## 2.2. Trackways

Below follows a review of fossil trackways and footprints which have been attributed to Devonian tetrapods, with a consideration of interpretations which have been given for them. Since the dating of most of these trackway records is disputed, and at best each lies within a broad time range, they are arranged according to date of publication.

### 2.2.1. Genoa River, Australia

The first Devonian tetrapod trackways to be described came from the Genoa River Beds in New South Wales (Warren and Wakefield, 1972). Two trackways were figured and there can be no doubt that both these were made by tetrapods, though they differ from one another in almost all respects. A third track was mentioned but not figured, and its identity is less certain.

The Genoa River Beds were dated as “probably Frasnian” by Warren and Wakefield (1972) based on plant fossils and stratigraphic relationships, though Young (1993) places it firmly in the Famennian. On the same bedding plane there are other trace fossils, some of which Warren and

Wakefield suggest might be invertebrate trails, although they do not give details.

Trackway I of Warren and Wakefield (labelled as II in their Fig. 1) shows sets of overlapping manus and pes impressions arranged alternately along left and right sides of the track. This alternation of right and left footprints is characteristic of tetrapod tracks. The pes overlies the manus print, again characteristic of many tetrapods. In several of the prints, digit impressions can be seen, and the best preserved show at least five, lying on the lateral side of the print (Fig. 3). The animal left no belly or tail-drag.

Coarser sandstone still infills some of the impressions, and careful preparation could reveal a more accurate count of digits. Presence of this infill corroborates the interpretation of these tracks as original footprints rather than underprints or ghost-prints (subsurface impressions formed by compaction of sediment, later revealed by erosion or splitting of strata).

The animal was calculated by Warren and Wakefield to have a glenoacetabular length (effectively the body length minus tail and head) of about 220 mm, and a total length of about 550 mm, but a more recent examination of the tracks by Pridmore suggests two possible alternatives (see below). The best-preserved pes impression is about 35 mm wide and about 5 mm deep and the width across the trackway is about 110 mm.

Trackway II runs parallel to trackway I. In this track, a small manual print alternates with a larger pedal print which clearly shows a drag-mark. Trackway II also shows a sinuous tail or belly-drag down the centre. Manus and pes prints alternate with each other both across and along the track. Separation of the prints across the track is given as 93 mm with about 175 mm between each consecutive pes print; the animal appears to have been smaller than that which made trackway I. Warren (pers. commun., 1994) now recognises that the trail mark lies to the rear of each print, so that the direction of travel is in fact opposite to that shown in the paper.

The third trackway from the Genoa River site is from the same horizon as the first two, but on a loose block. It shows a more ladder-like

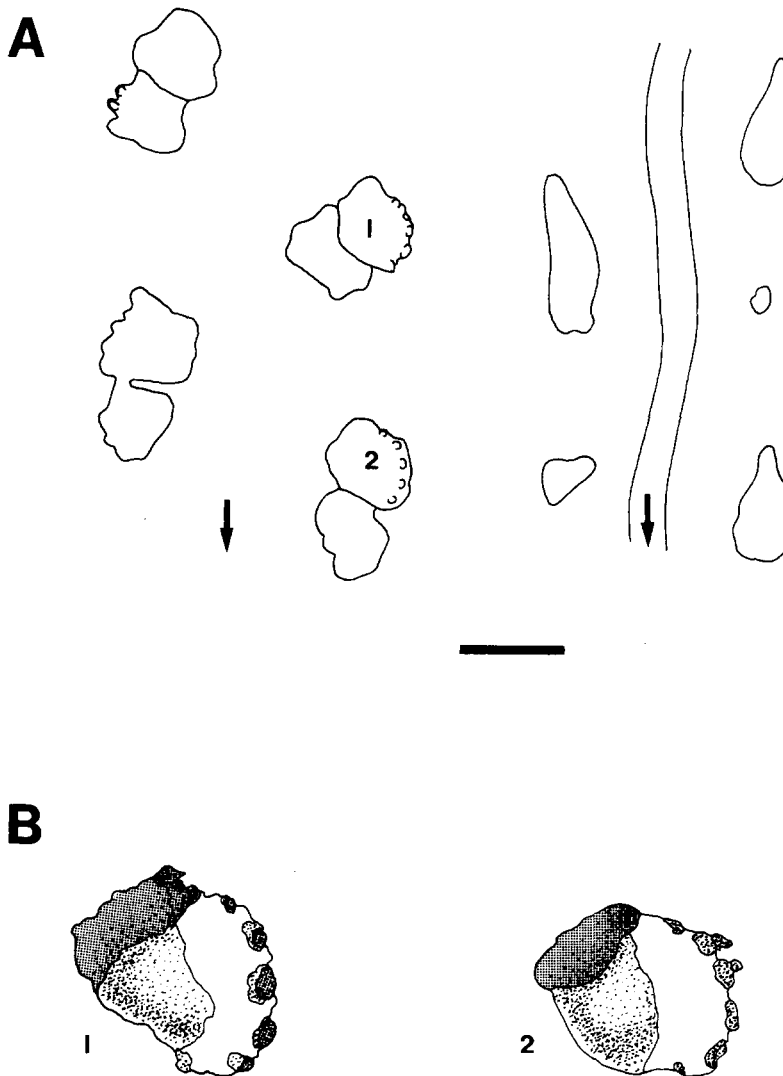


Fig. 3. Genoa River tracks. (A) Two adjacent tracks after Warren and Wakefield (1972). Arrow shows supposed direction of travel. Scale bar 50 mm. (B) Individual pes footprints drawn from the specimens, not to scale. (Scale may be judged Fig. 3A).

trackway, with the individual prints more irregular. Warren and Wakefield assumed it to have been made by a tetrapod.

#### 2.2.2. *Parana, Brazil*

A single, isolated print from the Ponta Grossa Formation of Brazil was interpreted by Leonardi (1983) as the left manus of an amphibian, and its date was given as probably the base of the Upper Devonian.

As an isolated block, there is room for doubt about this print's provenance and thus its date. As a natural cast, there is doubt about the circumstances in which the print was formed. Further doubt has been cast recently on its identity as a footprint. Roček and Rage (1994) have commented on the description of this specimen working from a cast and photographs, and suggest that it is more plausibly interpreted as the resting trace of a starfish. Other interpretations of this specimen

are also possible, and until further material from the same locality comes to light, it should be treated with extreme caution as a record of a Devonian tetrapod. Furthermore, the specimen derives from an apparently marine environment which contains brachiopods (Roček and Rage, 1994). Thus it would normally be considered as subaqueous in origin. This specimen provides no convincing evidence of terrestriality among Devonian tetrapods.

### 2.2.3. *Glen Isla, Grampians, Australia*

Tracks described by Warren et al. (1986) were interpreted as the earliest tetrapod trackway known at the time. This remains the case if both the date and the identity of the trackmaker are as Warren et al. suggest, but there is considerable room for doubt about both.

The trackway was found on a block formerly used as a paving slab in the yard of a homestead at Glen Isla in the Grampians of Australia. Warren et al. (1986) indicate the problems associated with dating this slab, stemming in part from uncertainty about the provenance of the paving slab, and the problems of dating the Grampian sediments in general. Estimates for this have ranged from early Carboniferous in older studies (Talent and Spencer-Jones, 1963), to late Silurian (references in Warren et al., 1986). In more recent analyses (Turner, 1986; Milner, 1993) a Givetian or basal Frasnian date is given. Lower or Middle Devonian seems most likely, but until more evidence as to the origin of the slab is forthcoming, the date must remain questionable.

The trackway consists of a ladder-like, as opposed to an alternating, set of poorly defined prints of differing sizes and variable shape (Fig. 4). There is no evidence of overstepping or differentiation between manus and pes. They occur on a ripple-marked sandstone, and occur mostly as natural casts and therefore as mounds rather than depressions. Warren et al. interpret the sandstone as poorly consolidated. This seems to be based on the lack of definition of the prints, however neither the original prints nor the grain size of the original sediment is available for study. Often, footprints are infilled with coarser sediment as in the Genoa River tracks and as shown in dinosaur track



Fig. 4. Glen Isla tracks. (A) After Warren et al. (1986) Scale bar 100 mm. (B) Redrawn from a fibreglass replica.

formation (Thulborn, 1990). Warren et al. argue that the prints were made subaerially, rather than subaqueously, because “such poorly consolidated sediments are unlikely to preserve tracks made subaqueously”.

If made by a tetrapod, they calculate that the animal was about the same size as that which made the Genoa River trackway (though they do not say which one). A gleno-acetabular length of 290 mm was calculated by Warren et al. (1986) using the factor of  $1.5 \times$  the stride-length, and they calculated a total body-length of about

855 mm using the reconstruction of *Ichthyostega* given by Jarvik (1980). This is rather larger than that given by Warren and Wakefield (1972) for the maker of trackway I (Fig. 5A, B).

Fig. 4A shows the Glen Isla track as figured by Warren et al. (1986) but the lines showing supposed pace angulation have been removed. The alternation of pes and manus prints thus becomes

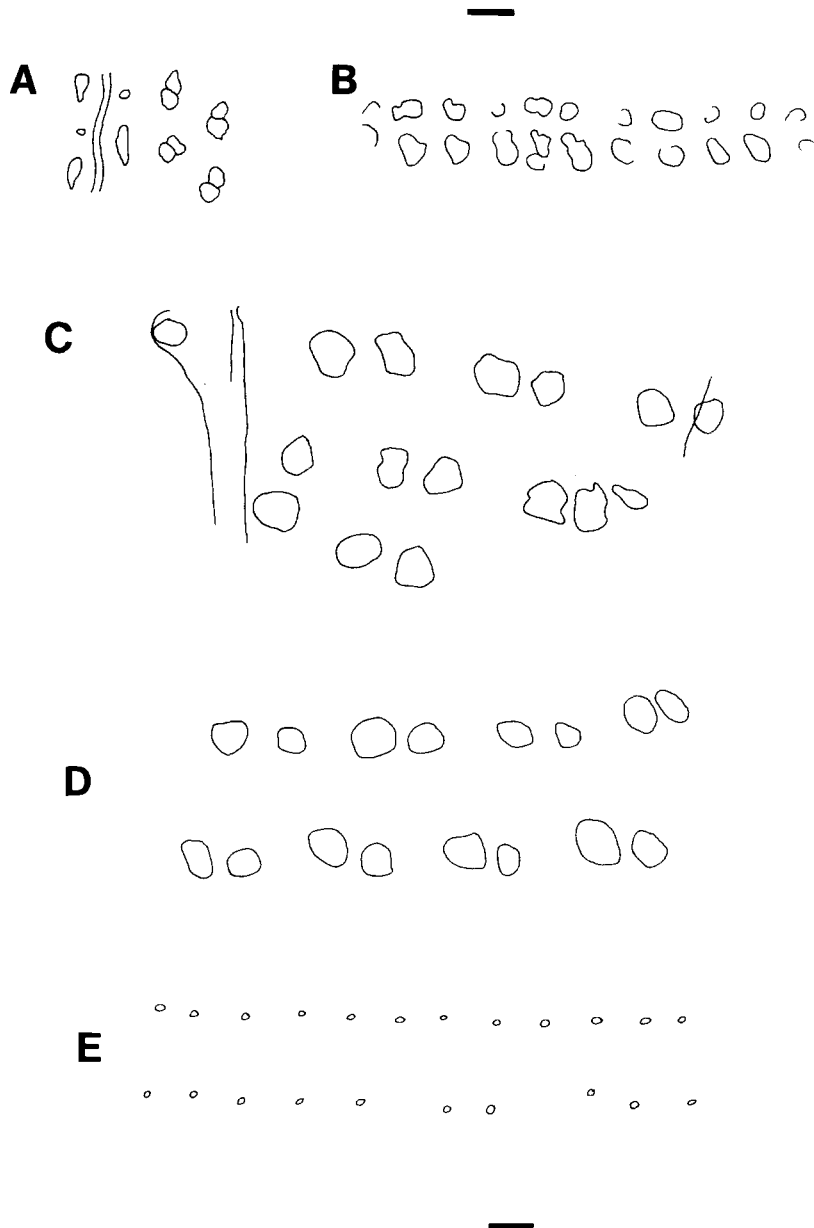


Fig. 5. Trackways drawn to the same scale. (A) Genoa River tracks. (B) Glen Isla tracks. (C) Tarbat Ness tracks after Rogers (1990). (D) Short section of the Valentia Island tracks after Stössel (1995). (E) Short section of one of the Kap Graah tracks after Friend et al. (1976). Scale bar 100 mm.

far less obvious, rather, prints of the left side of the track are on average larger than the right. I have also examined a fibreglass replica of the trackway and Fig. 4B gives further details of the prints from this. Warren et al. figured a peel from the original specimen, so that our figures show right–left reversal.

#### 2.2.4. *Tarbat Ness, Scotland*

Trackways from this locality are interpreted by Rogers (1990) as consisting of one short sequence of alternating footprints in a double parallel row, and an additional three prints presumably from a partial second trackway (Fig. 5C). If considered thus, there is a reasonably convincing case for a sequence of fore and hind-foot imprints, alternating in typical tetrapod fashion for a series of three steps. However, from the same locality, large arthropod tracks are found resembling those described below by Friend et al. (1976), and Rogers does not totally dismiss the possibility that arthropods made both these apparent tetrapod tracks and those from the Grampians. From the diagram in his paper, Rogers gives the size of the individual impressions as about 100 mm in diameter and the majority between 10 and 20 mm deep. Separation between left and right prints is about 320–350 mm.

With respect to the palaeoenvironment, it seems likely, but not certain, that the tracks were subaerial rather than subaqueous. Probable rain marks extend over the surface and into the imprints, thus post-dating them, and a fine mud deposit overlies the bedding plane and drapes the imprints. Rogers concludes that the prints are not underprints, that the mud layer was aeolian, and that the preservation of the prints may have been assisted by the surface having been dampened and then bound by algae or evaporitic cementation. However, he notes that this surface may not be the one which was originally walked upon, since aeolian scour or deposition may have occurred prior to the rain.

Dating for this trackway is uncertain. It lies about 900 m above the highest fossiliferous bed of the Middle Old Red Sandstone, and Rogers seems to imply that a Givetian age is likely. However, as he points out, the Upper Old Red Sandstone of

which this sequence is part ranges between the late Givetian and the Tournaisian.

While this trackway set is reasonably convincing as being left by a Devonian tetrapod, its maker, its environment and its date are all uncertain.

#### 2.2.5. *Valentia Island, Eire*

A trackway recently described by Stössel (1995) from southwest Ireland shows prints in alternating pairs with manus and pes impressions closely associated though not overstepping on each side. The tracks cross a ripple-marked bedding plane, leaving a trail several metres long. The tracks have been almost uniformly distorted by cleavage strain, but Stössel provides diagrams which have corrected for this. No details of the foot impressions are preserved, but smaller prints alternate with larger ones suggesting manus and pes impressions. These occur more or less in pairs on each side, and appear to form an alternate as distinct from opposite pattern (Fig. 5D). The track is therefore reasonably convincing as a tetrapod trackway.

The age of the Valentia Slate Formation in which these tracks are found is difficult to ascertain; Stössel gives the range as somewhere between Eifelian and Famennian. He discusses the circumstances and environment in which the tracks were made, concluding it to be very unlikely that a track would be preserved in fully water-saturated sediment of this grain-size. Furthermore he points out that a swimming animal would most likely produce a more undulating track than this one, and that the sediments in which the tracks were found were produced by flood-accumulations in a non-channelized alluvial plain.

### 2.3. *Other Devonian trackways of uncertain origin*

#### 2.3.1. *Hoy Sandstone, Orkney, Scotland*

In 1974, Sarjeant (1974) reproduced a figure of a trackway, the specimen long since lost, which has sometimes been considered a candidate for a tetrapod track. From the Upper Devonian of the Isle of Hoy (Wilson et al., 1935), it consists of a straight, central groove, flanked on each side by small, regular blobs, approximately alternating on left and right sides, with the blobs sometimes

connected to the central band and sometimes not (Fig. 6).

If made by a tetrapod, the remarkable feature of this track would be its small size, only about 30 mm across, in comparison with other alleged tetrapod tracks. Of course, tetrapods started life as small animals, and some interpretations for the acquisition of terrestriality would have the juveniles more adventurous in that direction than adults (Warburton and Denman, 1961), so the suggestion of a tetrapod origin for this track has some merit. Westoll (1937) commented on these tracks as plausibly made by a tetrapod.

It is notable that these tracks might be exactly what one could predict for a very small *Ichthyostega* as reconstructed according to the model suggested here. However, without the specimen, or further similar specimens, and without knowledge of the context, it is impossible to be sure what animal or environment this track could represent.

### 2.3.2. Kap Graah, Greenland

In 1976, Friend et al. (1976) described trace fossils in the Kap Graah group sediments of the Frasnian of Central East Greenland. Among these were two sets of tracks found near the Kap Graah peninsula, about 100 m below an horizon known to yield *Bothriolepis*, *Phyllolepis* and *Holoptychius* remains. The tracks consist of approximately opposite pairs of more or less circular impressions, the track width being about 200 mm with about 120–140 mm longitudinally between each print (Fig. 5E).

Friend et al. (1976) review several possibilities for the maker of these tracks. Tetrapods are considered but dismissed because of the lack of evidence

of overprinting or dragging which would be expected from the overlap between manus and pes prints. In addition, tetrapod footprints would normally be expected to lie in alternating pairs rather than opposite pairs. Large arthropod prints are also considered, and they mention the similarity between these prints and some arthropod prints from the Ordovician and Silurian of South Africa. However, they note that the Greenland prints are much larger than could have been made by any known arthropod from the Devonian. Thirdly, they consider the possibility of resting prints made by the pectoral appendages of a placoderm such as *Bothriolepis*. If so, these prints must have been made under water, since this animal could not otherwise have moved, supported solely by its anterior appendages without leaving a tail or body trace. However, since it was not possible to determine the relationship between the prints and mudcracks also present on the bedding plane, there is no extrinsic evidence for this.

## 3. Discussion

### 3.1. Interpretation of the trackways

Interpreting Devonian trackways is an example of the general problem of attributing ichnotaxa to skeletal remains exacerbated by having so little information on the animals themselves. Interpretation of the environment in which the trackways were created is equally problematical without good information about their sedimentological context. Below I consider interpretations of the Devonian trackways in the light of the skeletal anatomy of known Devonian tetrapods, and also consider what kinds of tracks might be predicted for them, to see how close the match might be between the tracks and the animals.

The Genoa River trackways are the most completely convincing as those of Devonian tetrapods, but though they are declared to be “the earliest known terrestrial trackways” evidence for their terrestriality seems to rest solely on the fact that they were made by tetrapods. However, without independent evidence this is open to the charge of circular reasoning, since there is little to suggest



Fig. 6. Hoy track after Sarjeant (1974). Scale bar 10 mm.

that any Devonian tetrapods were capable of terrestrial locomotion. Indeed, of all the known material, these trackways might be seen as the strongest evidence for it. Yet from what is known of Devonian tetrapod body fossils, one could run the circle in reverse and argue that the tracks must both have been made subaqueously, since that is the only way the known animals could have made them. There may be further evidence that this bedding plane formed subaerially, but it was not referred to by Warren and Wakefield (1972).

Many instances are known of tetrapod trackways being successfully preserved from a subaqueous environment (McAllister, 1989). Swimming trackways are known not only from dinosaurs (Coombs, 1980) but from much earlier tetrapods (Sundberg et al., 1990). It is also known from study of dinosaur tracks that prints made below water can in some circumstances be clearer, certainly more deeply impressed, than those made above the waterline (McAllister, 1989; Thulborn, 1990). Experimental work in progress (P.J. Manning, pers. commun., 1996) supports the contention that well-preserved tetrapod tracks may form subaqueously. Devonian tetrapod tracks thus cannot be assumed a priori to have been made by terrestrial animals, without a thorough study of the context, and preferably with some clue about the body form of the animals which might have made them.

Of the Devonian tetrapods whose limbs are preserved, neither *Acanthostega* nor *Ichthyostega* in its more recent guise, is likely to have made tracks like trackway I had it been made subaerially. Both animals would have left belly traces, as in trackway II. However, the sinuous tail or belly-drag mark seen in trackway II, as pointed out above is unlikely for *Ichthyostega*. A terrestrial trackway left by *Ichthyostega* as interpreted here would most likely leave an almost straight belly-drag mark, with any tail-mark likely to be difficult to distinguish from this, and it would have produced larger manus than pes prints. The most likely candidate for trackway I is an animal like *Tulerpeton*, whose home environment is unknown. An *Acanthostega*-like animal could have made a trace like either trackway I or II, walking semi-supported in shallow water.

Notable in trackway I is the fact that the digit impressions are placed laterally, indicating an animal whose manus and pes were directed at right angles to the body. There is therefore no evidence of supination, an action normally associated with directing the epipodial part of the limb and thus the manus or pes forwards to engage the power-stroke in walking. Presumably the humerus correspondingly bore no significant supinator process. The implied action would be more consistent with a paddle-like stroke. I have had the opportunity to examine this trackway first hand, and Fig. 3B gives further details of two of the pes prints. There are impressions of least five digits, but six or more may actually be present.

A recent consideration of these tracks has been given by Pridmore (1995), in a paper dealing with gait in the epaulette shark and other aquatic or semi-aquatic vertebrates. He suggested that the two tracks might have been made by animals moving at different speeds, with trackway I made by a slower-moving animal than trackway II. Both show a symmetrical gait in operation, with each left and right pes or manus print positioned alternately across the track. However in trackway I, the pedal impression lies over and slightly ahead of the manual on the same side, where trackway II shows the manus and pes on each side separated by half a stride length, so that the right pes is positioned opposite the left manus and vice versa. This could be produced either by two animals of differing gleno-acetabular proportions, or by two animals of the same proportions moving at different speeds and gaits.

Pridmore suggests that trackway II might have been made by a faster-moving and thus "trotting" animal, with a girdle separation equivalent to twice the width of the trackway, and thus about 186 mm. Trackway I can be interpreted in several ways. One is as made by a slowly-trotting animal of trunk-length about 85% of that of trackway II (thus 158 mm), less plausibly a longer one of 150% of the length of animal II, or thirdly, by an animal similar in proportion to that of II but using a lateral-sequence walk. Pridmore did not consider the scenario that either or both these tracks might have been made by partially or completely submerged animals. These analyses, with all their

possible interpretations, point up the difficulty of interpreting trackways, especially with such limited knowledge of the animals which made them.

Pridmore (1995) suggested that the most likely aquatic gait for *Acanthostega* would have been a "walking trot", aided by body undulations and the long tail. Because this gait derives directly from the axial motion of swimming in fishes, the neural circuitry to control it was already in place. However he argues that because of the long tail, the centre of mass of the body would have been only slightly forward of the pelvic girdle, which might have enabled the animal to use its tail as a support in the manner of a fifth limb while engaging in the "walking trot" on land. Thus he suggests that because of its adaptations to swimming, it was, ironically, thereby more capable of overland progression. Presumably the track it might have so made would have resembled that of trackway II from the Genoa River.

Unfortunately, a full description of the joint morphology in *Acanthostega*, was not available to Pridmore, but has recently been published (Coates, 1996). The morphology of *Acanthostega* is manifestly that of an aquatic animal, attested by the form of the limb joints and digits, the extensive tail fin, notochordal vertebrae, lack of zygapophyses and short ribs with poorly differentiated sacral rib. Other features, notably the postbranchial lamina, well-ossified hyobranchial apparatus, fish-like dentition, lateral line organs embedded in bone, small naris, large stapes and possibly functional spiracle (Clack and Coates, 1995) (Fig. 1A) suggest that it was permanently so. The limbs are now known to have been ill-suited to bear the weight of the animal during any part of the locomotor cycle.

In *Ichthyostega*, at least the forelimbs appear to have been weight bearing, and thus it was more likely to have been at least occasionally capable of terrestrial excursions. Using the body-form described in Jarvik (1980), Pridmore speculates that *Ichthyostega* was probably an obligate belly-walker on land, given that its tail was too short and its centre of mass too far forward to employ the tail-supported walking trot which he suggests for *Acanthostega*. However, if the body-form of *Ichthyostega* were as suggested here (Fig. 1B),

none of the conventionally described gaits might apply.

While *Acanthostega* is likely to have swum in a sinusoidal manner as suggested by Stössel and Pridmore, *Ichthyostega*, as interpreted above, would have been unable to produce sinusoidal body waves, though its tail might have. Thus, supported in shallow water, it might have been responsible for a track like that in the Valentia Slate. To speculate further, if *Ichthyostega*, propelled itself through shallow water by its forelimbs moving together, it could have made sets of prints in opposite pairs such as those of the Kap Graah, (Friend et al., 1976) but they would have to have been made subaqueously.

Pridmore suggests that for slow progression out of water, the most stable gait for early tetrapods in general would prove to be the lateral-sequence walk, used by modern slow-moving terrestrial quadrupeds. This gait would require an adjustment to the length of axial waves in the body in the change from swimming to walking, with, he maintains, consequent need for rewiring of the neural circuitry. Thus he suggests not only that the acquisition of this gait was gradual, but was likely to have been acquired before the animals ever moved out of shallow water. This picture fits the hypothesis that limbs evolved before walking and terrestriality.

In the past, most arguments about the origin of limbs and walking have concentrated on the morphology of the osteolepiform fin as a precursor to the tetrapod limb, and have cast osteolepiforms in the role of the first vertebrates to engage in overland excursions (Westoll, 1943; Eaton, 1951; Gunter, 1956; Goin and Goin, 1956; Romer, 1958; Schaeffer, 1965). An exception to this was the speculation by Inger (1957) that the tetrapod limb was first developed as a fossorial device used in digging aestivation burrows. However, it is not clear from the context whether this was envisaged as an aquatic or a terrestrial activity.

These speculations, coming in a flurry during the mid-nineteen-fifties and early nineteen-sixties, were put forward at a time when only *Ichthyostega* was known of the Devonian tetrapods, panderichthyids were represented only by some lower jaw fragments (Gross, 1941; Vorobyeva, 1962), and a



partial skull roof of (at the time) uncertain affinities (Westoll, 1938). Perhaps most significantly, the locomotory capabilities of *Latimeria* were unknown. We are often presented, in museum displays, children's books and textbooks, with a picture of *Eusthenopteron* setting out across a barren landscape in search of another pool (Romer, 1958 and references therein). This may be an appropriate place to consider the potential of this and other sarcopterygian fishes to make terrestrial trackways, and what kind if any they may have produced.

Given the morphology of *Eusthenopteron*, the above scenario may be viewed as unlikely. With its deep symmetrical tail and dorsal, anal and pelvic fins set towards the rear, *Eusthenopteron* has a body form associated with "unsteady swimming" (Webb, 1982), providing rapid acceleration and swift turning (Fig. 7A). In cluttered environments, flexible paired fins may assist with braking (Webb, 1982). Similar body forms are found in both porolepiforms and some early lungfish (Ahlberg, 1992), and the shape is often associated with aquatic ambush predators. With this form, *Eusthenopteron* surely played the role of a "Palaeozoic pike".

*Panderichthys*, whose skull and body are dorso-ventrally flattened, makes a better candidate for a shallow water dweller (Fig. 7B, C), and Vorobyeva and Kuznetzov (1992) suggested a means by which it might have moved on land. They envisaged it moving, belly remaining on the ground, by lateral undulations of the body with the paired fins playing only an anchoring role, activated singly in sequence (Pridmore's diagonal sequence walk). Pridmore (1995) points out a number of difficulties which this would produce for a fish such as *Panderichthys*, such as the resulting zig-zag course which it would be forced to take, and the requirement for complex neural development it would perhaps entail. Any other mode of progression however would result in periods of instability, and it is difficult to envisage *Panderichthys* using any of them. Despite a relationship to tetrapods which is apparently closer than that of *Eusthenopteron*, with its somewhat plate-like radius and more distal fin elements (Vorobyeva and Kuznetzov, 1992), the forelimb skeleton of *Panderichthys* is in

some ways less tetrapod-like than that of *Eusthenopteron*. With the rather flattened body profile and relatively small paired fins of *Panderichthys*, none of the known Devonian trackways can be attributed to it or to its close relatives.

The dubiousness of speculating of the mode of action of fossil fish limbs is made manifest by recent studies of the coelacanth *Latimeria*. While this fish has the characteristic lobed fin of its osteolepiform and tetrapod relatives (Millot and Anthony, 1958), it does not employ them in any form of "bottom-walking", as it might have been suspected of doing based on their construction. Although it sometimes employs them in a lateral sequence as envisaged for an early tetrapod, they are used exclusively in swimming (Fricke et al., 1987).

Until recently, speculations on the advent of terrestrialisation assumed that it was achieved first by a "fish", such that the first tetrapods were more or less fully capable of land locomotion by the time the limb evolved. Since the discovery of *Acanthostega* and multi-digitated limbs, a different scenario has been espoused by several early tetrapod workers, in which tetrapods remained primitively aquatic, developing limbs for some alternative activity before they were used for "walking". This has received some support in recent reviews and has been accepted by a number of other authors (e.g. Daeschler and Shubin, 1995) while others (e.g. Ahlberg and Milner, 1994) appear less convinced. If it is accepted, the origin of terrestriality has not only been "pushed up" the stratigraphical table but also up the phylogenetic stem, and we must look for the first evidence of overland excursions among tetrapods, not among fishes.

### 3.2. Evidence from phylogeny

It may be possible to infer a time-frame for the evolution of limbs with the development of a well founded phylogeny. Discoveries of potential tetrapod tracks and theories of how and when limbs might have evolved may then be tested against it.

It should be noted at this point that there is currently a debate concerning the definition of the taxon Tetrapoda. This is part of a wider debate

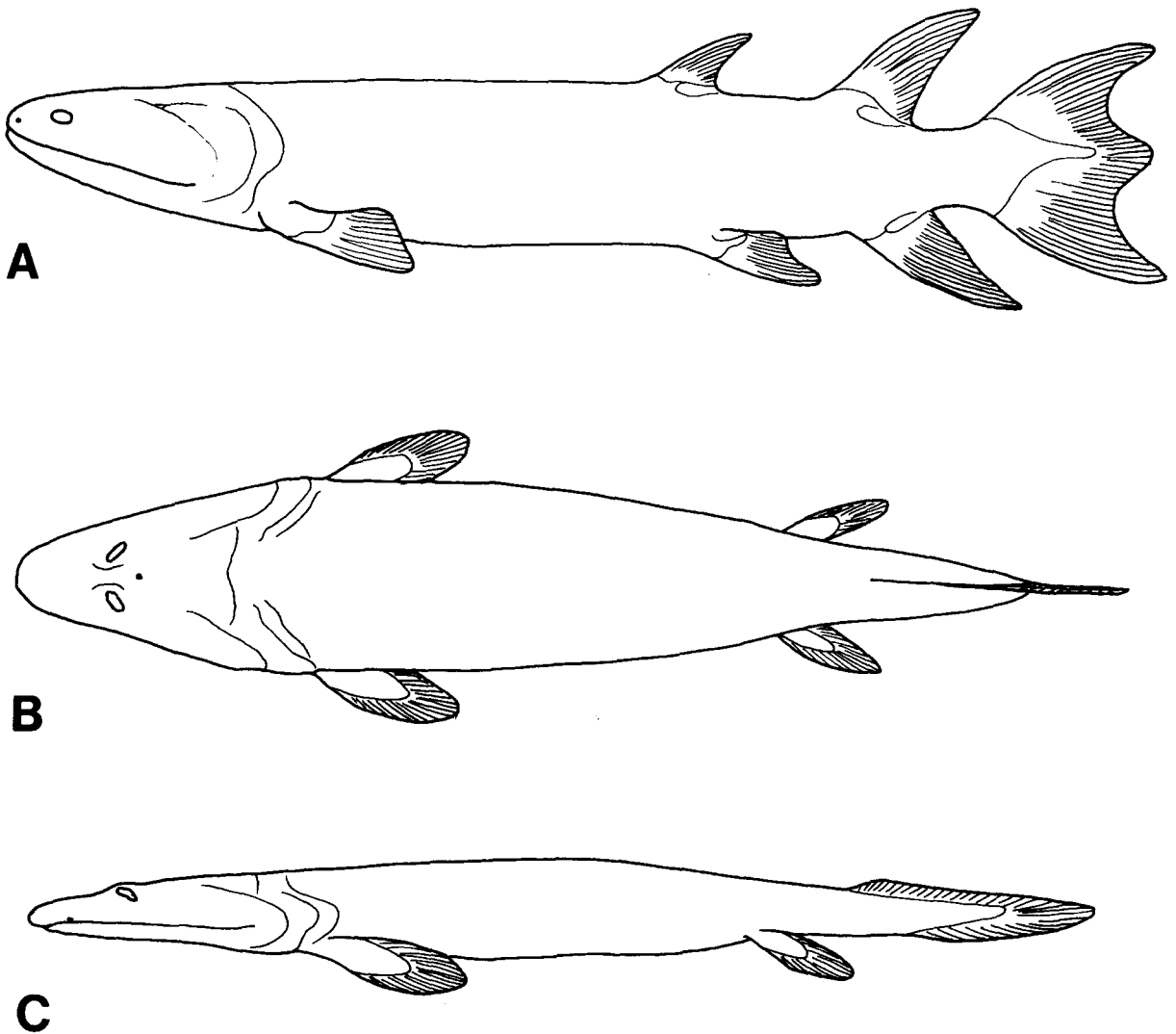


Fig. 7. (A) *Eusthenopteron foordi* body form in lateral view after Jarvik (1980). *Eusthenopteron* specimens vary in size up to a maximum of about 400 mm total length. (B) *Panderichthys rhombolepis* body form in dorsal view. (C) Lateral view, after Vorobyeva and Schultze (1991). The majority of *Panderichthys* specimens have a skull length of about 300 mm.

dealing with the definition of phylogenetic groups, but it has implications for the debate about limbs and terrestriality, so should be mentioned here.

Many recent papers (e.g. Rowe, 1988; Gauthier et al., 1989; de Queiroz and Gauthier, 1992; Rowe and Gauthier, 1992) have suggested that a phylogenetic, or node-based, definition, is more rigorous than one which employs a "key-character", with both a "crown-group" definition (Norell and

Novacek, 1992; Altangerel et al., 1993; Norell et al., 1993; Lebedev and Coates, 1995) and a "total-group" definition (Patterson, 1993; Coates, 1996) having its adherents. In the case of the Tetrapoda, the crown-group would encompass the clade containing all the modern representatives, namely the Amphibia and the Amniota, plus any fossil taxa falling above that node uniting them in the cladogram. In this case, Tetrapoda would

exclude any fossil taxon which falls outside this grouping, independent of the possession of any key character such as limbs with digits. It has been stressed elsewhere (Clack and Coates, 1995) that as a key character, “limbs with digits” is unsatisfactory since it can be broken down into many separate characters. The “total-group” concept is an alternative to the “crown-group” concept for defining monophyletic clades by a node-based criterion. The “total-group” includes the crown-group plus all the taxa between it and its nearest living relatives, i.e. the stem group. In the case of Tetrapoda, that includes many animals which clearly do not have limbs with digits.

There are thus major problems with node-based definitions for use in a paper such as this. One mode excludes many fossil taxa which indisputably have limbs with digits, including all of those with which this paper is concerned. Strict application would not only forbid the use of the term “Tetrapoda” for the animals discussed here, but logically also places an embargo on calling them “tetrapods”. The whole-group definition would admit to the Tetrapoda many animals that would be colloquially known as “fish”. The problem arises in my opinion, not with the node-based concept itself, but with the logical difficulty of applying to a node-based group, a name whose origins are etymologically founded upon a “key-character” definition. Furthermore, each mode of node-based definition seems equally defensible and each has its proponents and detractors. This demonstrates that both the “key-character” and “node-based” definitions are equally volatile. Whichever of the rigorous, defensible and equally valid phylogenetic definitions of the group Tetrapoda may be supported, the result will be counterintuitive in respect of some animals. I make a heartfelt plea herein for the term Tetrapoda not to be employed as a formal taxonomic term if this is to be the result, in order to allow continued use of the vernacular term “tetrapod” as it is widely understood. Readers should bear in mind these arguments and views while this paper continues to refer to the Devonian animals in question as “tetrapods”.

Nevertheless, one benefit of this debate is that it not only completely divorces arguments about

the origin of “Tetrapoda” from the origin of limbs, but also the origin of limbs from the onset of terrestriality. Assuming more intermediate forms are eventually discovered, it may become increasingly difficult to define what constitutes a limb and correspondingly difficult to make functional assumptions about limbs.

Phylogenies put forward in recent years have implications for the time of origin of the tetrapod lineage which further reflect on the timing of the origin of limbs. Most recent analyses (e.g. Maisey, 1986; Ahlberg, 1991b, 1996, in press; Vorobyeva and Schultze, 1991; Cloutier and Ahlberg, 1995) place tetrapods in the conventional sense together with the family Panderichthyidae (or *Elpistostegalia*) as its sister-group, within a clade which also contains the lobe-finned fish groups *Osteolepiformes* and *Rhizodontiformes*. A second clade of lobe-finned fishes containing *Dipnoi* (lungfishes) and *Porolepiformes* is widely recognised as the sister-group of that assemblage (Fig. 8).

Accepting this phylogeny implies that tetrapods (defined by limbs with digits) cannot have arisen before the split between these two great lobe-finned clades, which current estimates place in the Lower Devonian. Even in those phylogenies which place osteolepiforms in a closer relationship to porolepiforms than to lungfish (e.g. Schultze, 1987) the implications for the timing of the origin of tetrapods are the same. Granted that the osteolepiform clade and its intra-relationships are not well understood at present, it nevertheless seems unlikely that any member of the tetrapod stem lineage had arisen before the Lower Devonian. Indeed, no members of any currently recognised sarcopterygian group are found before this time. This contrasts with early dates for the origin of tetrapods suggested in some recent analyses (Milner, 1993; Jarvik, 1996). Phylogenetic considerations argue against an early date, rendering unlikely any claims for tetrapod tracks in the Upper Silurian, and even more so the proposal that by this stage tetrapods were walking on land.

Tetrapods are also unlikely to have arisen before the split between osteolepiforms and the clade containing panderichthyids (Ahlberg et al., 1996). *Osteolepiformes* are first known from the basal

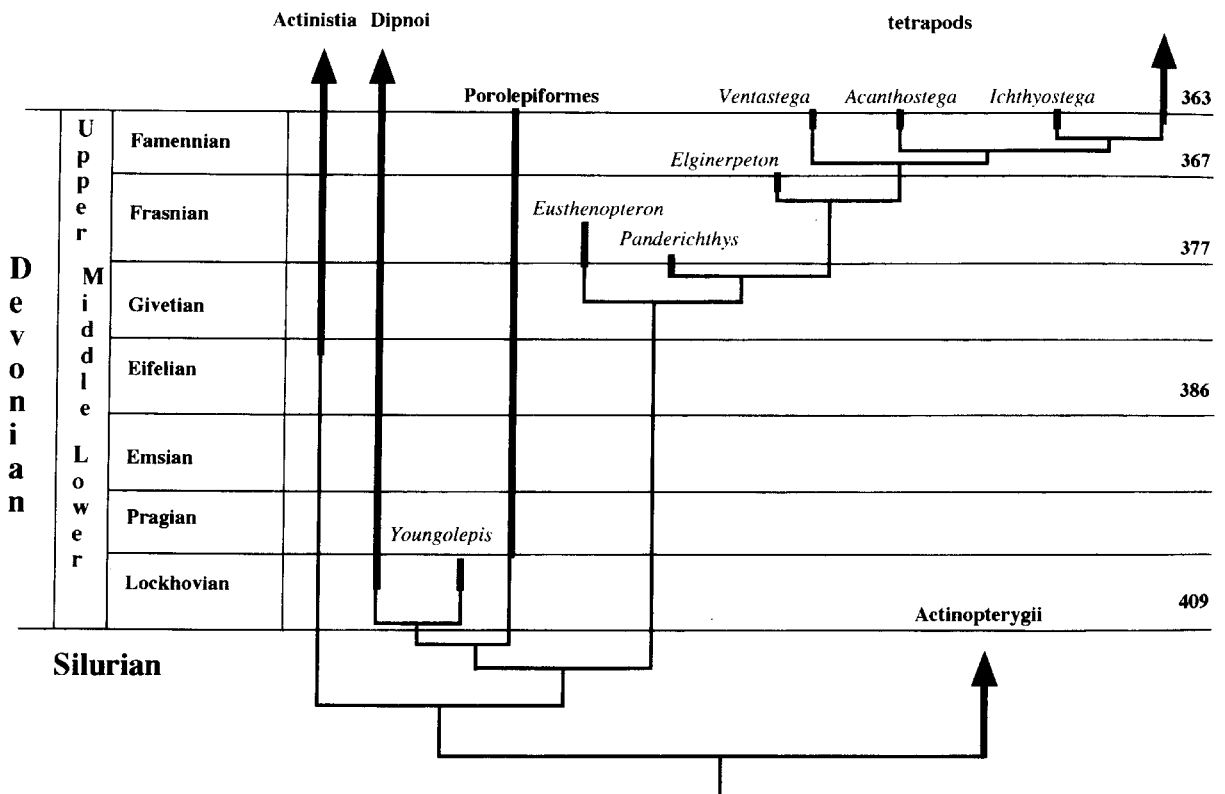


Fig. 8. Phylogeny of sarcopterygians superimposed on a timescale, data from Ahlberg et al. (1996).

Eifelian (*Thursius macrolepidotus*, Saxon, 1967), while panderichthyids are not known before the Upper Givetian (Mark-Kurik, 1993). Thus a date as late as the Frasnian for the origin of tetrapods is not unreasonable, though perhaps we might accept that the split between these groups occurred earlier than our current first record of them and suggest a Givetian date for the event.

Other evidence from recent finds of tetrapod-like fishes or fish-like tetrapods is in accordance with this. *Elginerpeton* and *Obruchevichthys* (Ahlberg, 1995) straddle the gap between the panderichthyid-tetrapod node and the earliest known appearance of digits (*Acanthostega* and *Ichthyostega*), and are dated as Upper Frasnian. Ahlberg (1995) proposed a Lower–Middle Frasnian date for the origin of limbs and digits, and suggested that the panderichthyid–tetrapod split occurred somewhat earlier than this. There is however no evidence that either fish-like tetrapods

such as *Acanthostega*, nor tetrapod-like fish such as *Panderichthys* existed before the upper part of the Middle Devonian. Claims for terrestrial tetrapod tracks dated earlier than this should be treated with informed scepticism.

Presumptions of terrestriality among Devonian tetrapods seem to run very deeply in the collective psyche, in descriptions of both trackways and assessment of the habits of the animals. As a coda to this review, I give a couple of quotations to illustrate this. Shear (1991), in a review of the development of terrestrial ecosystems, states that the skeletons of the earliest tetrapods “were already quite modern” (see discussion in Coates and Clack, 1995). It is not clear what he meant by this, and although full descriptions of neither *Acanthostega* nor *Ichthyostega* were available, the subliminal message seems to be that they were fully terrestrial. In another review considering the pressures which animals, both invertebrate and

vertebrate, might have been under to force them into terrestriality, McNamara and Selden (1993) end with a paragraph on *Acanthostega* and *Ichthyostega*. They accept that the limbs of both were paddle-like, and cite descriptions by Coates and Clack, but then in the same paragraph go on to conclude that “these well-developed legs... were superbly equipped for life on land”. This may reflect editorial input, but the inconsistency is clear. The interpretation of the Genoa River tracks (Warren and Wakefield, 1972) is another example of implicit assumption of terrestrial locomotion by these early forms.

Until very recently there was little enough evidence of any kind about Devonian tetrapods, but now that more and more is coming to light it is time to re-examine old assumptions. One aim of this paper is to demonstrate what the available evidence actually consists of, and to try to give an objective view of its current status. Taken at face value, the fossil record of Devonian tetrapods gives little evidence for the existence of terrestrial locomotion among them, and assumptions that some of them must have been capable of it is open to serious challenge.

#### 4. Abbreviations used in text

MGUH—Geological Museum, University of Copenhagen F.n.—field number

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