Devonian climate change, breathing, and the origin of the tetrapod stem group

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Synopsis The diversification of the tetrapod stem group occurred during the late Middle through the Late Devonian, that is from the Givetian to Famennian stages about 385–365 million years ago. The relationships between the known taxa representing this radiation have currently reached a reasonable consensus so that interpretations of the order of appearance of tetrapod characters is possible. The immediate fish relatives of the earliest limbed tetrapods show what is interpreted as a progressive increase in the spiracular chamber and its opening to the outside. Here, this is inferred to be associated with an increased capacity for air-breathing. Lungs are thought to have been present in most early bony fishes, and were most likely ventilated by air-gulping. This could have brought about a facultative capacity for air-breathing, which the tetrapod stem group exploited to the greatest degree. These adaptations are shown not only in freshwater forms but also in estuarine and marginal marine forms. Estimates of oxygen levels during this period suggest that they were unprecedentedly low during the Givetian and Frasnian periods. At the same time, plant diversification was at its most rapid, changing the character of the landscape and contributing, via soils, soluble nutrients, and decaying plant matter, to anoxia in all water systems. The co-occurrence of these global events may explain the evolution of air-breathing adaptations in at least two lobe-finned groups, contributing directly to the rise of the tetrapod stem group. In contrast to recent studies, low atmospheric oxygen is not considered to be a causal factor in the lack of fossils documenting the evolution of Early Carboniferous tetrapods.

Introduction

The diversification of the tetrapod stem group, colloquially known as the "fish–tetrapod transition," occurred during the late Middle through the Late Devonian, that is from the Givetian to Famennian stages about 385–365 million years ago. Over recent years, the picture of the sequence of events and their timing has been augmented by new finds of Devonian tetrapods (Ahlberg 1991a, 1995; Ahlberg et al. 1994; Daeschler et al. 1994; Ahlberg and Clack 1998; Lebedev 2004) and their immediate stem group (Daeschler et al. 2006; Shubin et al. 2006). This has allowed attempts to answer such questions as where and when tetrapods (i.e., limbed vertebrates) evolved, and how and in what order tetrapod characters arose (Clack 2002a, 2005). We also now have somewhat more information about the environments in which they lived (Lebedev 2004; Clack 2006). One question that is often asked but less easily answered is why they began to make the first moves towards terrestrial life. Recent studies have attempted to reconstruct Devonian atmospheric composition,

global temperatures, and continental distribution (Berner 1999, 2006; Scotese 2002; Berner et al. 2003). Combining these with recent assessments of plant cover, the effects of that on sedimentation rates, erosion and the production of soils (Algeo et al. 1995, 2001; Algeo and Scheckler 1998), and taking into account the contemporary invertebrate fauna (Shear and Selden 2001), allows the generation of some new ideas that might explain some of the events that led to the evolution of air-breathing and ultimately land-dwelling tetrapods.

Among the tetrapodomorphs [i.e., stem plus crown group tetrapods (Ahlberg 1991b)] including the early limbed forms, two aspects of their morphology are of particular significance; these are the region of the spiracle and hyoid arch, and the pectoral limb. Furthermore, changes that are seen to these regions among the tetrapodomorphs could be interrelated. The spiracular region is interpreted as intimately associated with air-breathing; the spiracular chamber is known to become enlarged in the tetrapod stem group, and the increasing size and complexity

of the pectoral fin/limb skeleton have been suggested as functioning to support the head and anterior end of the body as the animals partly emerged from the water (Shubin et al. 2004, 2006).

The present article reviews the morphology of the spiracular region and hyoid arch across the transition from basal tetrapodomorph fish to limbed tetrapods to show the apparently increasing capacity of the spiracular chamber and increasing breadth of the spiracular notch among them. It suggests that this could be best explained as an elaboration of an air-breathing mechanism. It then draws together information from the studies of environments, atmospheric composition, soils, sediments, plants, and invertebrates to create a new scenario for the evolution of air-breathing in the tetrapod stem group, and their relatives, the dipnoans, in the Devonian. It finally considers briefly the subsequent evolution of tetrapods in the Carboniferous, during which air-breathing became their major breathing mode.

The tetrapod stem group: members, relationships, and provenances

Recent consenus has suggested that the tetrapodomorph stem group can be partly represented by the following taxa, whose phylogenetic relationships are reasonably well understood: *Eusthenopteron*, *Panderichthys*, *Elpistostege*, *Tiktaalik*, *Elginerpeton*, *Ventastega*, *Acanthostega*, and *Ichthyostega* (Ahlberg and Clack 1998; Ruta et al. 2003; Daeschler et al. 2006). The latter four are limbed tetrapods. *Gogonasus*, according to the most recent analysis, may also belong here, lying between *Eusthenopteron* and *Panderichthys* (Long et al. 2006). Alteratively, it may be more basal as originally considered (P. E. Ahlberg and J. A. Clack, personal observation). Their relationships, postcranial reconstructions and skulls (except for *Elpistostege* and *Elginerpeton*) are shown in Fig. 1.

Eusthenopteron was for a long time the best known of the tetrapodomorph fishes, and has provided
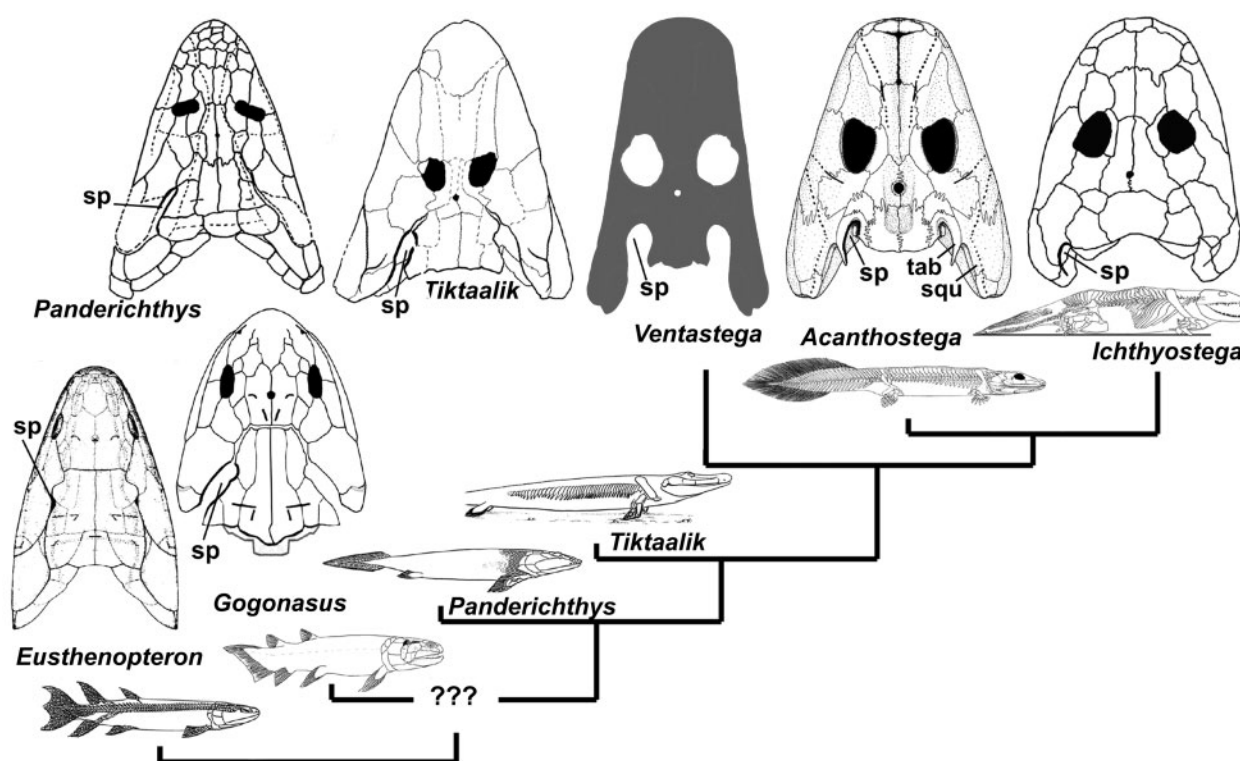
Fig. 1 Illustrated cladogram of stem-group tetrapods, showing body reconstructions and skulls in dorsal view with location of spiracular opening indicated (sp). No postcranial skeleton is available for *Ventastega*. *Eusthenopteron*; dorsal view of skull redrawn from Jarvik (1980), postcranial reconstruction from Jarvik (1980): *Gogonasus*; skull modified from Long (1997) and Long et al. (2006), postcranial reconstruction original based on unpublished illustration courtesy of J. Long and B. Choo (Museum of Victoria); *Panderichthys*, skull from Vorobyeva and Schultze (1991) postcranial reconstruction from Clack (2002a); *Tiktaalik*, skull and postcranium from Daeschler et al. 2006; *Ventastega*, from work in progress by Ahlberg, Clack, Lukševičs and Zupiņš; *Acanthostega*, skull original, postcranium from Ahlberg et al. 2005; *Ichthyostega*, skull original, postcranium from Ahlberg et al. 2005. Illustrations not to scale. tab, tabular; sp, spiracle; squ, squamosal.

a model for a tetrapod "ancestor" since early in the last century. It was described in detail by Jarvik in a series of papers in the 1940s and 1950s, summarized in his book in 1980 (Jarvik 1980). Most of the best material derives from the site of Miguasha, Quebec, Canada, and is Frasnian in age. Environments at this site vary from estuarine though marginal marine to fully marine (Chidiac 1996). *Eusthenopteron* is found throughout the sequence though it is not clear whether it is tied to particular horizons (Parent and Cloutier 1996). It also occurs in some other localites such as Scotland and the Baltic states. Recent phylogenetic studies have placed it as a member of the Tristichopteridae, though not the most basal member (Ahlberg and Johanson 1998). Tristichopterids are found worldwide, with derived members in Gondwanan and Euramerican sediments.

Panderichthys has been known for some years, but details of several key aspects of its morphology have not been described until relatively recently. It was first recognized as closer to tetrapods than to "osteolepiforms" in 1985 (Schultze and Arsenault 1985). Its skull was described in 1991 (Vorobyeva and Schultze 1991), the humerus in 2000 (Vorobyeva 2000), and the pelvic fin and spiracular region in 2005 and 2006 (Boisvert 2005; Brazeau and Ahlberg 2006). Only *P. rhombolepis* is known in any detail. *P. rhombolepis* comes from the Baltic States, in particular Lode in Latvia. Some consider this locality to be latest Givetian, though some estimates place it in the Frasnian. *Panderichthys* definitely occurs in Frasnian deposits in other Latvian localities (P. E. Ahlberg, personal communication). Lode represents a marginal marine environment.

Elpistostege was first described in 1938 from a partial skull roof showing the postparietal shield and interorbital region (Westoll 1938). Even at that early stage, it was recognized as fitting between limbed tetrapods and "osteolepiforms." Further, partial skull material and a section of vertebral column were described in 1985 confirming that position, and it was placed in the Panderichthyidae (Schultze and Arsenault 1985). Like *Eusthenopteron*, it comes from the Frasnian locality of Miguasha, though the known specimens only occur toward the top of the sequence (Parent and Cloutier 1996). Because neither its spiracular anatomy nor its pectoral limb are known, it will not be considered further here, except in the context of its provenance.

Tiktaalik is the most recently described tetrapodomorph, based on a series of excellently preserved material from the Canadian Nunavut Territory. It is represented by at least three nearly complete skulls with postcrania and many lower jaws. The skull roof and pectoral fin have been described in detail, though not the braincase or hyomandibula (Daeschler et al. 2006; Shubin et al. 2006). The locality is Frasnian in age. Work on this taxon, *Panderichthys* and other stem tetrapods, has recently split the "Panderichthyidae" into a series of stem tetrapod taxa rather than a discrete clade. With the inclusion of limbed tetrapods, this group has been named the Elpistostegalia (Ahlberg et al. 2000; Daeschler et al. 2006).

Elginerpeton is the earliest tetrapodomorph that is known to have had limbs, though it is only known from fragments. These consist of several pieces of lower jaw, partial premaxillae, partial scapulocoracoids, partial ilia, part of a femur, and a possible humerus (Ahlberg 1991, 1995, 1998; Shubin et al. 2004). The ilium bears similarities to that of *Ichthyostega*, and is thus inferred to have been associated with similar hind limbs. Because of its fragmentary nature, its anatomy will not be considered further, but it serves to peg the latest date for the appearance of limbs. It comes from the Frasnian of Scat Craig in Scotland (Ahlberg 1991a, 1995, 1998).

Ventastega is a limbed tetrapod known from exquisitely preserved skull and lower jaw material, with partial pectoral and pelvic girdle elements also represented (Ahlberg et al. 1994; Ahlberg and Lukševičs 1998). It bears many resemblances to *Acanthostega* (see subsequently), suggesting the presence of digited limbs, but is more primitive in its lower jaw morphology. It also bears some details of the skull roof in which it resembles *Tiktaalik* rather precisely (Ahlberg et al., manuscript in preparation). It comes from the marginal marine late Famennian Ketleri Formation in Latvia (Lukševičs and Zupiņš 2004).

Acanthostega was first described in 1952 (Jarvik 1952) from two partial skull roofs, but further material was discovered in 1987, forming the basis of detailed descriptions. It is a limbed tetrapod known from many articulated specimens that preserve almost complete vertebral columns and limbs as well as skulls, braincase, and associated stapes, allowing detailed description of its entire skeletal anatomy (Clack 1994, 1998, 2002a, 2002b; Coates and Clack 1991; Coates 1996). The limbs bore eight digits each (Coates and Clack 1990). It comes from Famennian deposits in East Greenland, that may represent abandoned or active river channels (Clack and Neininger 2000). There is no evidence of marine influence in the Greenland Devonian sediments where it was found, though the top of the sequence

is marked by black shale horizons unlike the sandstones in which the fossils are more commonly found (Marshall et al. 1999).

Ichthyostega was the first Devonian tetrapod to be described (Säve-Söderbergh 1932), though detailed descriptions remained scarce until 1996 (Jarvik 1996). Though early reconstructions show it as a terrestrial, quadrupedally locomoting animal (Jarvik 1952, 1955), recent investigations have reinterpreted its anatomy and pointed out some of its unique and unexpected features (Clack et al. 2003; Ahlberg et al. 2005). It comes from the same Famennian sequences as *Acanthostega*, though it is not usually found in the same beds. Most specimens seem to be derived from flood deposits that are not informative about its life environment (Clack and Neininger 2000).

Given the distribution of *Elpistostege*, *Panderichthys* and *Tiktaalik* around the margins of the "Old Red Sandstone" continent (i.e., Laurussia), in inlets and estuaries, it seems likely that this area and this environment was the cradle for the origin of near-tetrapods and probably of tetrapods themselves (Daeschler et al. 2006).

Based on the currently understood relationships of these forms, we can hypothesize an approximate date for the first appearance of limbed tetrapods and their closest stem-group relatives (Fig. 2). The earliest known member of the basal group often called "osteolepidids" is from the late Early Devonian Emsian stage (Janvier 1980). It seems unlikely that more derived tetrapodomorphs occur prior to this date, though without further evidence, that could still be true. However, the more derived tetrapodomorphs from *Eusthenopteron* to *Tiktaalik* are mainly Frasnian with *Panderichthys* and some tristichopterids also known from the Givetian (late Middle Devonian) stage. The earliest limbed tetrapod, *Elginerpeton*, is also Frasnian, though somewhat
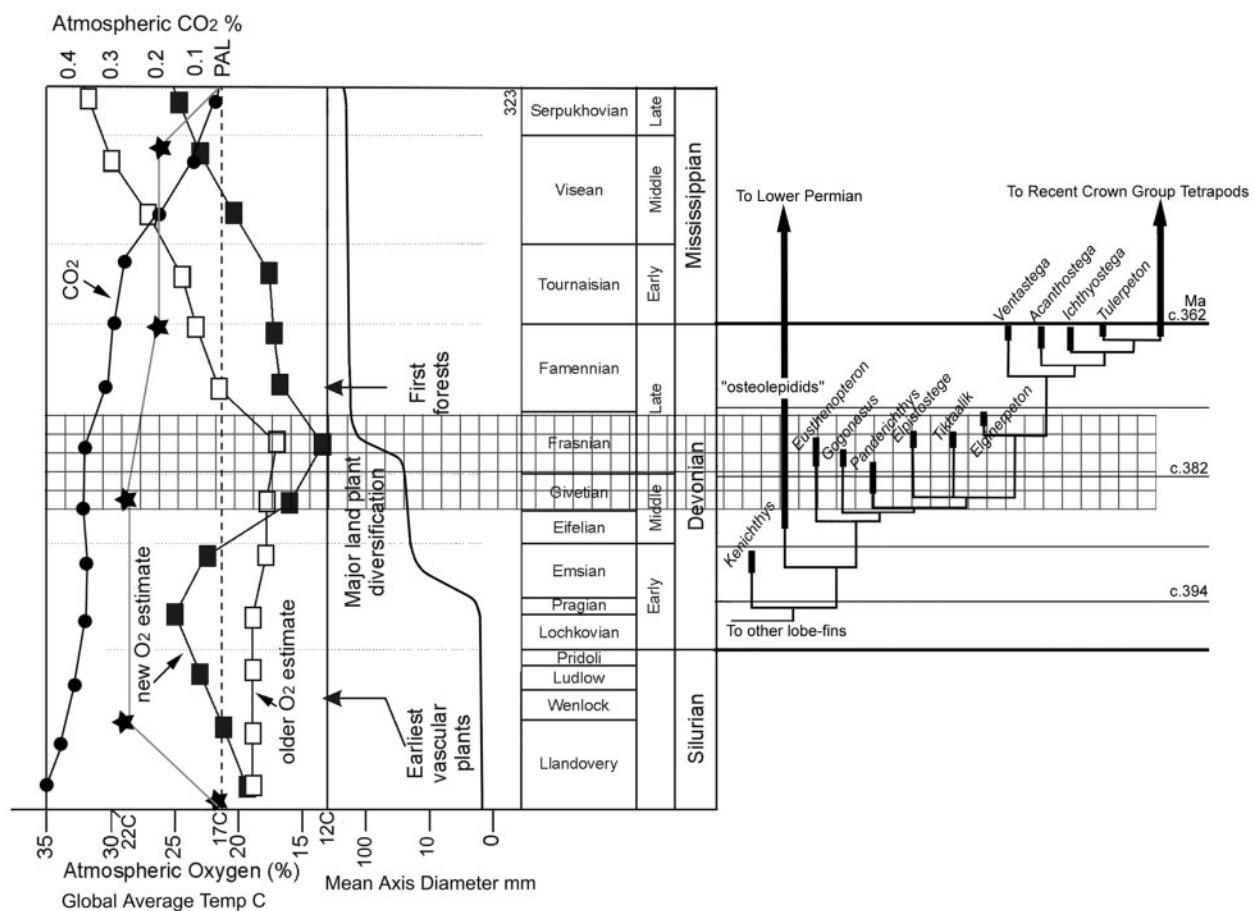

Fig. 2 Graphs of atmospheric oxygen and carbon dioxide levels, global temperatures and plant stem diameters placed on the same time scale as a cladogram showing the occurrences and relationships of the tetrapod stem group. Gridded area highlights the Givetian–Frasnian stages, showing the co-occurrence of lowest oxygen levels, maximum plant diversification, and the diversification of the tetrapod stem group. Graph of oxygen levels from Scott and Glasspool based on Berner (2006); carbon dioxide levels from Berner (2006); global temperatures from Scotese (2002); plant stem diameters from Algeo et al. (1995).

later than the tetrapodomorph fish. Therefore, the origin of the proximate stem tetrapod line is likely to be dated to the Givetian, with a radiation occurring during Frasnian times. The total timespan for this process is about 10 million years.

Gogonasus was initially described by Long (1985), with more details given later (Long 1997). In these papers it was considered to be a basal tetrapodomorph (an "osteolepidid") retaining some primitive features, such as cosmine cover on the scales and skull bones, that are lost in tristichopterids and more crownward tetrapodomorphs. Recent discoveries suggest that its enlarged spiracular cleft and chamber and robust pectoral fin skeleton give it a more crownward position than tristichopterids (Long et al. 2006). It comes from the Australian locality of Gogo Station, and is Frasnian in age. The locality of Gogo represents basin deposits within inter-reef bays and inlets that form part of a reef complex in the north of Western Australia (Long 1988). Thus, *Gogonasus* comes from a fully marine environment.

Work in progress on British "osteolepidids" (R. Wade, University of Cambridge) aims to clarify the relationships of this group, including *Gogonasus*. Early indications are that *Osteolepis* itself, from the Middle Devonian of Caithness in Scotland, has a larger spiracular notch than previously envisaged, potentially similar to that of *Gogonasus* (R. Wade, personal communication). Conclusions regarding that genus must therefore await the completion of her study.

The tetrapod stem group: spiracular and hyoid anatomy and functional morphology

Eusthenopteron exhibits what can be regarded as the plesiomorphic condition for tetrapodomorphs of the spiracular notch and chamber, and of the hyomandibula. In most respects it resembles that of contemporary actinopterygians, such as the Frasnian genus *Mimia* from the Gogo Formation in Australia (Gardiner 1984), and indeed many primitive actinopterygians in which the braincase is known. That is to say, the hyomandibula of *Eusthenopteron* was long, articulating with the braincase at two facets (only a single one in actinopterygians), running down the posterior margin of the palatoquadrate ossification. It had a process (the opercular process) by which it contacted the opercular series that covered the gill chamber and its enclosed branchial arches. Thus, the hyomandibula controlled the operation of the gill system and coordinated

the movements with those of the palate during ventilation and feeding. The spiracular cleft was a narrow slot between the cheek and skull table, at the apex of which lay the spiracular opening. The length of the opening in the associated soft tissue pouch is unknown, and the width of the cleft may have been greater than that which Jarvik reconstructed (P. E. Ahlberg, personal communication). Running up the side of the braincase and ending at the apex of the notch was a groove interpreted as the for the spiracular tract leading from the pharynx to exit at the spiracular opening. Jarvik (1980) interpreted the spiracular chamber as quite extensive in area, broadly open to the pharynx, rather than a narrow tube (p 192, Fig. 134).

The spiracular chamber of *Panderichthys* was expanded to a greater extent than in *Eusthenopteron*, and the hyomandibula was shortened relative to the condition in that fish, lacking the posteroventrally directed ramus that reached to the quadrate in more basal tetrapodomorphs. Instead, the opercular process lay at its distal end, and the bone had little contact with the palatoquadrate ossifications. This arrangement produced a "wider, straighter, and less obstructed" spiracular chamber than in more basal "osteolepiforms" (Brazeau and Ahlberg, 2006, p 320). The opercular series of *Panderichthys* was also reduced in anteroposterior length relative to those genera [compare the reconstruction of the skulls of *Panderichthys* (Vorobyeva and Schultze 1991) and that of *Eusthenopteron* (Jarvik 1980) in lateral view; see also Clack 2005)].

Tiktaalik shows the condition taken one step further. The spiracular notch is broad and rounded at its apex, the chamber is yet further inflated. The hyomandibula reached across the chamber to the palatoquadrate and may have been even shorter than in *Panderichthys* (personal observation), though it is hard to judge from the published figures. The dorsal components of the opercular series have been lost (though the gulars remain), as indeed has the extrascapular series that in other fish link the back of the head to the dorsal part of the shoulder girdle (though the supracleithral bones remain) (Daeschler et al. 2006).

In *Ventastega*, there is a broad and deep spiracular opening in the skull roof, comparable to that in *Tiktaalik* (Lukševičs and Zupiņš, 2004; Ahlberg et al. work in progress).

Acanthostega shows the tetrapod condition in which the proximal end of the hyomandibula (the footplate) has become inserted into the wall of the braincase via the fenestra vestibuli, and is much shortened with a broad and flat distal portion. It is now called a stapes

(Clack 1989, 1994). The spiracular chamber is broadly open to the outside, and in the case of *Acanthostega*, the tabular bone is deeply embayed, inferred to house the opening of the spiracle, though this is separated by a prong-like extension of the lateral margin of the tabular from a second embayment in the more conventional position for a spiracular opening between the tabular and squamosal (Fig. 1). *Acanthostega* is known to have possessed deeply grooved ossified gill bars, that are inferred to have supported functional internal gills, a retained plesiomorphy. Gill-breathing is inferred to have supplemented air-breathing in this as in other tetrapodomorphs (Coates and Clack 1991).

The braincase and ear region of *Ichthyostega* show a unique morphology, in which inflated chambers on either side of the otic region are thought to have enclosed an air-space as part of an underwater hearing organ. The stapes is of a unique shape that is interpreted to have formed much of the ventral wall of the air-filled chamber. The entrance to this chamber, via the spiracular tube passing anterior to the stapes, would have been very narrow to judge from the relative positions of palatal, braincase, and stapedial ossifications. The proximity of the stapedial footplate to the saccular chamber, its position partly within a fenestra, and its ability to pivot about a point below this fenestra, suggest function as an ear. However, the chamber could possibly have been derived from an accessory air-breathing organ. *Ichthyostega* is also known to have retained ossified gill bars, as in *Acanthostega* (Clack et al. 2003).

Function of the spiracular region in other Palaeozoic fishes

There is no evidence that chondrichthyans ever possessed an air-bladder or any air-breathing capacity, and the evidence for other jawed vertebrate (gnathostome) groups is dubious. Most chondrichthyans retain a spiracular opening, but it is in some cases associated with housing a chemosensory organ, in the case of batoids for intake of water during following ventilation, and in other cases its function is unknown (Kardong 1998).

The phylogeny of basal gnathostomes is highly contentious, but there are two entirely extinct groups to be considered: the acanthodians and the placoderms. One study, that has never been repeated, has suggested that in one placoderm (i.e., one specimen of one species), the antiarch *Bothriolepis*, there was an additional pharyngeal pouch that could have acted as a buoyancy device or an accessory air-breathing organ (Denison 1941).

Bothriolepis occurred worldwide during the Frasnian, but the specimen in question came from Miguasha. Even if confirmed, this suggestion cannot necessarily be extended to all placoderms, since *Bothriolepis* is a derived antiarch (Zhu 1996) and antiarchs are not the most primitive placoderms (Goujet 2001). No evidence for a spiracular tract or opening has been suggested for acanthodians, but only the late occurring and specialized *Acanthodes* is known from braincase material (Miles 1973).

Because of its presence in many "primitive" living fishes, an air bladder (a lung or lungs) has for a long time been assumed to be primitive for all osteichthyans (bony vertebrates), with the further assumption that lungs and the swimbladders of actinopterygians are likely homologues (Romer 1962). The evidence for the existence of lungs and the presence of air-breathing in osteichthyans is based on a number of independent lines of evidence.

Recent work has tested the hypothesis that air-breathing in osteichthyans is a primitive feature, based on neurology, embryology, and circulatory systems (Perry et al. 2001). This work suggested that the capacity for air-breathing began with the neural mechanism for control of ventilation, in connection with ventilating in surface waters, these would have been warmer and richer in dissolved oxygen than deeper waters. In that study, air-breathing is considered to have arisen very early in the evolution of bony vertebrates.

In modern actinopterygians, many of the most primitive forms are air-breathing, such as *Polypterus*, gars, and bowfins. In *Polypterus*, the spiracle is known to be used to expel exhaled air, and its operation is controlled by some of the muscles inserting on the hyomandibula (Allis 1922). There have also been suggestions that the spiracle is also used to inhale air (Magid 1966, 1967; Thomson 1969). Despite not being confirmed experimentally (e.g., by Brainerd et al. 1989), this observation has been repeated on a number of occasions (J. A. Clack, personal observation, P. E. Ahlberg, personal communication 2007). The lungs of *Polypterus* share many characters with those of tetrapods.

Many fossil osteichthyans show what is interpreted as a spiracular groove running from the pharynx to the dorsal surface of the skull. It is seen, for example, in the braincase of early fossil actinopterygians such as *Mimia* (Gardiner 1984). A spiracular hole in the skull roof lies in a similar place to that in *Polypterus*. The fossil record of Devonian actinopterygians is poor, and the earliest genus known from articulated material is Givetian. The earliest evidence for a spiracular groove in bony vertebrates occurs in

Youngolepis, a basal dipnomorph from the Lochkovian of China (Chang 1982), and an actinopterygian-like osteichthyan braincase, *Ligulalepis*, from the Emsian of Australia (Basden et al. 2000; Zhu et al. 2005).

No evidence of the spiracular groove is seen in the braincases of early fossil coelacanths, but very few well-preserved Palaeozoic fossil coelacanth braincases have been found (Forey 1998). Even though modern coelacanths possess only an oil-filled swim-bladder, and several fossil forms show swim-bladders with ossified walls, it has been assumed that they too possessed an air-bladder early in their evolutionary history (Thomson 1969). Furthermore, *Latimeria* possesses a pulmonary circulation (Millot et al. 1978), though the spiracular pouch is closed (Forey 1998). A spiracular notch is known in the basal sarcopterygian onychodonts, seen in *Onychodus* from Gogo (Andrews et al. 2006). Dipnoans specialized their air-breathing mechanisms later in the Carboniferous, but they appear to have had some air-breathing capacity early in their history (Long 1993). However, even the earliest dipnoan braincases are highly specialized, and do not resemble those of their sister-group the porolepiforms, that do exhibit a spiracular opening (Jarvik 1980). Among modern dipnoans, only the more derived members (*Protopterus* and *Lepidosiren*) are obligate air-breathers. Dipnoans will be considered further below.

Filling the air-bladder with air in early osteichthyans is assumed to be by means of the primitive mechanism of air-gulping, since internal secretion of gases into the swimbladder is a feature of derived actinopterygians. The occurrence of air-breathing in at least a facultative way is thus an associated inference. Though the spiracular mechanism seen in these animals cannot be unequivocably demonstrated to have been associated with air-breathing, it is here suggested as plausible based on the proximity of the spiracular chamber to the buccal cavity.

Alternative proposals for the function of the spiracular mechanism need to be considered. The primitive condition is probably to have been water-filled, as in chondrichthyans, and to operate either as part of the gill-ventilation system or as an additional sensory device for detecting gas or other chemical concentrations in the water. It implies that primitively, the spiracular tube had an external opening. This may have been the condition in early osteichthyans, or it may have been closed as in more derived actinopterygians. The spiracular pouch, the soft tissue correlate of the spiracular region, is air-filled in tetrapods but is closed by a membrane. At some point in evolutionary history, this region became associated with air-breathing. Thus questions arise as to when this association arose within the clade leading to tetrapods and why, if the enlarged chamber remained water-filled, the chamber and notch increased in dimensions in the more crown-ward tetrapodomorphs. A further question concerns the time of closure of the spiracular opening.

Another possible function for the notch itself is as a site for the origin of the depressor mandibulae or other jaw-operating muscles. However, lower jaw structure in *Panderichthys* and *Tiktaalik* is virtually identical (Ahlberg and Clack 1998; Daeschler et al. 2006). The first changes apparent in tetrapodomorph jaw structure are seen in the dentition, exemplified by that of *Ventastega* (Ahlberg and Clack 1998), whose spiracular notch is comparable in size to that of *Tiktaalik*. Changes to the lower jaw and spiracular regions would appear to be "out of phase" with each other, rather than directly correlated.

A third possibility might be that the spiracular notch, rather than being open to the outside, was closed by a membrane even in basal tetrapodomorphs. The spiracular notch is closed in living sarcopterygian fishes and in extant tetrapods, thus a closed notch is suggested by the "Extant Phylogenetic Bracket" (Witmer 1995). In extant tetrapods, the air-filled spiracular chamber is part of the middle ear cavity, and as such is involved in audition. The spiracular chamber and notch of advanced tetrapodomorphs could therefore have functioned as a primitive ear, in the way that was envisaged for many decades of the last century (Thomson 1966). If that were the case, it implies that the chamber was air-filled and the connection to air-breathing mechanisms is maintained. The Extant Phylogenetic Bracket method, however, is problematical in this context, since neither living sarcopterygian fish nor extant tetrapods provide good models for reconstructing the soft anatomy and physiology of the earliest tetrapods (Clack 2005).

Early fossil bony fish, whether actinoptergyian or sarcopterygian, have been regarded as at least faculative air-breathers, based on the assumed possession of an air-bladder, and most of them exhibit evidence of a spiracular groove and cleft. When and under what circumstances the change from facultative air-gulpers to obligatory air-breathers took place remains to be answered. Based on evidence presented here, it is suggested that a gradually increasing reliance on air-breathing is a feature of the tetrapodomorph clade, but that it is also seen in at least one other sarcopterygian lineage.

Mid-late Devonian atmosphere, climates, and environments

Several recent studies have estimated oxygen, carbon dioxide, and temperature levels through the Late Palaeozoic. Scotese (2002) gave estimates of global temperatures of about 22°C through the early part of the Devonian, dropping to about 19.5°C through the Frasnian and Famennian. This has been associated with glaciation in the southern continents during the latest Famennian. By the mid-Carboniferous temperatures had dropped to a global average of about 17°C, which is about the same as present levels (Fig. 2). His palaeogeographic reconstructions show that Laurussia was situated south of the equator, with coals beginning to form for the first time in latitudes north of the equator. Localities that have yielded Devonian tetrapods and their immediate stem group appear to have been located in areas where the continental climate was arid, but these animals were living along the continental margins, where the climate may have been ameliorated. Certainly, one of the few tetrapod-bearing localities that provides environmental information, Red Hill in Pennsylvania (Famennian), suggests a seasonal wet and dry climate (Cressler 2006). There, the fauna is associated with freshwater lakes and streams.

Estimates of oxygen and carbon dioxide levels have been produced by Berner and colleagues (Berner 1999, 2006; Berner et al. 2003) in recent years. Generally speaking, the levels of CO_2 are estimated to have been higher than present levels throughout the Devonian, dropping from about 0.35% in the Early and Middle Devonian to about 0.3% by the end of the Famennian. Causes for this drop are suggested to be the increased rates of burial of organic carbon and enhanced weathering of silicates. These processes also had an effect on climate cooling (Algeo et al. 2001). Present atmospheric levels of 0.03% were reached by the mid-Carboniferous (late Mississippian) (Fig. 2).

Previous estimates suggested that during the Early and Late Devonian, oxygen levels were somewhat lower than the present 21%, dropping slightly from about 19% to about 17% by the middle of the Frasnian, then rising steadily throughout the Mississippian to reach about 33% by the end of that period (Fig. 2) (Berner 1999; Berner et al. 2003). However, a new model for estimating oxygen levels has been produced that combines and refines previous models; it gives a new estimate for the Devonian. These are based on a GEOCARBSULF model (Berner 2006)). This computer-based model uses factors such as weathering rates of calcium and magnesium silicates and pyrite, organic matter decay,

degree of exposure of coastal lands, and the variability of volcanic rock weathering, to obtain its estimate. In contrast to earlier estimates, the new figures suggest that during the Early Devonian, levels first rose from about 22% to nearer 25%, but then dropped precipitously through most of the rest of the Devonian until the end of the Frasnian, at which point they were as low as 13%. Levels then rose slowly to reach about 16% by the end of the Famennian. They only reached present levels by the mid-Viséan (Fig. 2).

These observations are corroborated by work on fossil charcoals. Depending on circumstances, plant material can only burn at a minimum concentration of atmospheric oxygen, and that at the low concentrations suggested to pertain during the Givetian and Frasnian, wildfires would be very rare. This is reflected in the virtual absence of fossil charcoal from the record in this period, despite its first appearance in the Late Silurian, and its common occurrence that began in the Early Carboniferous (Scott and Glasspool 2006).

If this model is correct, the Middle and Late Devonian was warm and carbon dioxide rich, but with almost continuous relative oxygen deprivation. Even if further work suggest that the earlier estimates are more accurate, oxygen levels would still be relatively low in the Middle and Late Devonian. The Middle and Late Devonian were times of unprecedented change in the appearance of land surfaces across the planet. It saw the expansion of size (both height and average axis diameter), taxonomic and morphological diversity, habitats, and area of ground cover occupied by land plants. This had a profound effect upon the entire global system (Algeo et al. 1995, 2001; Algeo and Scheckler 1998).

Beginning in the late Early Devonian Pragian stage, the average diameter of plant stems increased almost exponentially from less than a centimeter to about 10 cm by the middle of the Emsian. Through the early Middle Devonian values increased slowly until by the mid Givetian, they had reached about 12 cm. Another rapid burst through the Givetian saw them increase further so that by the beginning of the Frasnian, the average diameter of plant stems found in the fossil record had reached more than a meter.

Though the co-occurrence of lowered oxygen levels with increased plant size and diversity might appear counterintuitive, given that plants produce oxygen as a waste-product, it is nevertheless an established fact that oxygen actually inhibits photosynthesis. The lowered oxygen levels may have been

a key factor in promoting plant growth during that period.

During that time, plants pushed inland from restricted marginal habitats to occupy wide tracts of land surface. In doing so, they coincidentally created more and different habitats for terrestrial organisms, and the increase in size and diversity of air-breathing arthropods occurred during this period. Givetian terrestrial arthropods included trigonotarbids, centipedes, spiders and amblypygids, scorpions, pseudoscorpions, arthropleurids, and archaeognaths (Shear and Selden 2001).

Much of the increase in plant density was contributed by the the progymnosperm *Archaeopteris* (Algeo et al. 2001). This plant arose in the Givetian, and dominated the land surface until about the mid-Famennian, when it began its slow decline, followed by extinction in the Carboniferous. At its peak, it reached heights of 30 m, with trunk diameters of 1.5 m. Other plants that contributed to this expansion were tree lycopods such as *Lepidodendropis* and *Cyclostigma*. Cladoxylalean ferns such as *Pseudosporochnus* and the zygopterid fern *Rhacophyton* were also substantial plants that occupied wetland habitats. All these plants produced complex root systems, but particularly in the progymnosperms they were massive and deep, disturbing the land surface and creating deep soils for the first time. Additionally, these plants shed leaves and branches (DiMichele and Hook 1992) creating surface litter that was home to detritivores, bacteria, and fungi. *Pseudosporochnus* from the Eifelian of Belgium and *Wattiezia* from the Givetian of New York State are some of the first plants known to have had abscission layers at the bases of their leaves, and the leaves were shed as these tree-like forms grew (Berry and Fairon-Demaret 2002; Stein et al. 2007). The Famennian saw the initiation of the first forests with a structure analagous to modern ones.

These developments changed the face of the land surface and the production of soils. They influenced erosion from land surfaces, slowing the rates of run-off as well as changing its character and content. Acidic products of plant decomposition and solutes from the soil leached into the water, meaning that lakes and rivers received increasing quantities of carbon-based compounds and soluble nutrients that encouraged the growth of algae (Algeo et al. 2001), and importantly for water-dwelling vertebrates, used much of the dissolved oxygen in the water.

Algeo et al. (2001) suggested that there is a strong link between these events in the evolution of plants and the concurrent conditions in the marine realm. The Givetian through Famennian is known as a time of major biotic crisis exemplified by the Frasnian/Famennian extinction event. However, this is only one of several crises evident among marine organisms during that time. The geological record is marked by a series of black shale horizons initiated in the Givetian that represent anoxic events in marine waters. The last of these, known as the "Hangenburg event," occurred at the end of the Famennian. Algeo et al. (2001) suggested, in what they described as the "Devonian plant hypothesis," that this was directly related to the increase in plant cover seen during that time. They suggest that "elevated river-borne nutrient fluxes may have promoted eutrophication of semi-restricted epicontinental seas" and could have "stimulated algal blooms," with this high marine productivity resulting in the black shales. The shales represent "intense anoxia on an intercontinental scale" (Algeo et al. 2001, p 221, 233). They also link this with the fate of the contemporary stromatoporoid and tabulate coral reefs that "declined rapidly through the mid-late Frasnian."

Not only marine and marginal marine regions would have been affected, but also the rivers and lakes whose waters flowed into them, and which must also have been becoming increasingly eutrophic and anoxic. The scenario proposed suggests that conditions in all these environments were profoundly affected by low dissolved oxygen concentrations, and also casts doubt on the suggestion that "oxygen is rarely in short supply in the seas" (Thomson 1969, p 110).

All this, according to the latest estimates by Berner (2006), took place at a time of unprecedently low atmospheric oxygen concentration. Given that oxygen is very much less soluble in water than it is in air, it would mean that waters, whether freshwater, brackish, or fully marine, would have experienced a double crisis for the animals living in it. Any animal that could exploit the higher, though still low, concentrations in the air compared to that in the water, would have been at an advantage.

The origin of air-breathing in bony vertebrates

Figure 2 places superimposed graphs of Devonian atmosphere, climate, and plant growth on the same time-scale as the evolution of the tetrapod stem group, and shows the coincidence of timing of the origin of the proximate tetrapod stem group, especially those with enlarged spiracular notches and chambers, with the lowest concentrations of oxygen and the greatest expansion of plant size and diversity.

Though coincidence is not necessarily evidence of correlation, it is tempting to suggest that these events were indeed related, and that enlargement of the spiracular notch and chamber in tetrapodomorphs is related to the evolution of air-breathing mechanisms, and resulted from the double challenge that aquatic animals faced during that period.

The dipnoans present an interesting parallel case to that of the tetrapodomorphs, in their acquisiton of air-breathing adaptations from the Middle Devonian onwards. Among the earliest dipnoans, *Dipterus* is known from the Middle Devonian of Caithness in Scotland. Though it may not possess a cranial rib (contra Ahlberg and Trewin 1995; P. E. Ahlberg, personal communication 2007) it does appear to possess palatal adaptations including a tongue pad similar to that in modern dipnoans, and associated with air-breathing (den Blaauwen et al. 2005). The Caithness sequences in which *Dipterus* is found represent cyclical filling and drying of a seasonal lake, with occasional marine incursions (Marshall et al. 1996). *Dipterus* occurs throughout the sequence, and "probably had the greatest tolerance of adverse (low oxygen) conditions" (Trewin 1986, p 44). Notably, some of these sequences also contain *Osteolepis*. Whereas Early Devonian dipnoans do not show adaptations for air-breathing (den Blaauwen et al. 2005), those from the Late Devonian onwards show other air-breathing skeletal correlates including cranial ribs, and the localities in which they are found, apart from the fully marine ones, often yield tetrapod fossils as well. The Gogo dipnoans seem to be exceptional among Late Devonian forms in not exhibiting overt air-breathing structures.

Potentially, then, the increased size of the spiracular notch among osteolepidids, and the onset of air-breathing specialization of dipnoans, which both occurred in the Eifelian/Givetian, may correlate with the gradual decline of oxygen levels through the Middle Devonian, and initiated trends that continued in their respective lineages as oxygen levels continued to decline throughout the Late Devonian.

The case of *Gogonasus* with its enlarged spiracular notch and robust pectoral fin skeleton, while inhabiting a fully marine environment, remains to be explained. Further work may suggest that these features are more widely spread among osteolepidids than was previously recognized, and originated in the Middle Devonian with *Osteolepis*. Additionally, work on the sedimentology of the Gogo sequences has shown that the environment was subject to fluctuations in oxygen levels, and that at least three anoxic

events are recorded (Becker et al. 1993; K. Trinajstic pers. comm 2007; Trinajstic et al. 2007).

Though other sarcopterygian and possibly even actinopterygian groups may have exploited air-borne oxygen to a degree, it seems to have been the tetrapodomorphs that were able, for some reason, to adapt to its use more extensively. One possible reason is that in shallow waters, their robust endochondral fin skeletons allowed them to support their heads out of water to gulp air, and the parallel elaboration of the spiracular mechanism with the increase in size and complexity of the pectoral limb is compelling. A second possible factor may be connected with the evolution of the choana, or internal nostril, which is a tetrapodomorph synapomorphy. The relationship of this structure to air-breathing is not immediately obvious, as the external naris remained small even in the earliest limbed tetrapods, and the nasal capsules were most likely primarily olfactory. Appearance of the choana may at least have provided an "exaptation" for narial breathing in later tetrapods.

The origin of limbed tetrapods, based on the evidence of *Elginerpeton*, can be dated to no later than the late Frasnian, coinciding with the end of the second phase of expansion among Devonian plants. Breathing air, and with limbs more fully capable of support, these animals could explore the vegetation-choked anoxic waters of rivers and lakes whose banks were now home to a wide variety of terrestrial arthropods. Though the late Frasnian and Famennian record of terrestrial arthropods is surprisingly poor, those groups present in the Givetian are known to have been present in the Famennian. The next radiation of tetrapods is known from the Famennian, subsequent to the Frasnian/Famennian extinction, though their relationship to the Frasnian genera is not simple. *Ventastega*, one of the later forms, is the most primitive, whereas *Elginerpeton* shares some features with the specialized tetrapod *Ichthyostega*. None of them is known from Carboniferous deposits, and the relationship between them and later forms is unclear. They may have been victims of an end-Famennian mass extinction.

Subsequent events: the early Carboniferous

After the end of the Devonian, the fossil record of tetrapods as well as of tetrapodomorph fish, is famously lacking, such that the next 15–20 million years is represented by very few examples and has been designated "Romer's Gap" (Coates and Clack 1995). For limbed tetrapods, and depending on when

the interval is taken to end, the record consists of a single articulated specimen, *Pederpes* from the Tournaisian of Scotland (Clack 2002c) fragmentary or isolated elements from the Tournaisian of Horton Bluff in Canada (Clack and Carroll 2000), and the early Viséan of Australia (Warren and Turner 2003). Given a slightly less conservative upper bound, it also includes two other articulated skeletons, the small amniote-like *Casineria* (Paton et al. 1999) and the aïstopod *Lethiscus* (Wellstead 1982), a limbless snake-analogue from slightly later in the Viséan of Scotland.

The end of Romer's Gap is marked by the terrrestrial assemblage of plants, arthropods and tetrapods from the Viséan locality of East Kirkton in Scotland. In this one locality are represented the earliest known members of most of the major groups that dominated the rest of the Carboniferous: temnospondyls, anthracosaurs, baphetids, aïstopods, and amniotes and/or microsaurs (Clack 2002a). To judge from their limb structure and degree of their skeletal ossification, there seems no doubt that they were mainly, if not entirely, terrestrial. Most of the articulated material is small, but isolated elements show that there were contemporarily large or very large tetrapods living in the same area. It is clear that during the interval represented by Romer's Gap, a great deal of morphological and phyletic evolution had taken place, producing tetrapods of a wide range of sizes, skull construction, body forms and habits, all of which features are in complete contrast to those found among the tetrapods of the Devonian. They had become adapted to deal with living on land and breathing air and were exploiting the new niches and environments that the terrestrial biome had produced, but lack of material prevents understanding of how any of this came about (Clack 2002a).

A recent study has investigated the existence of Romer's Gap, and compared the record of fossil tetrapods (called "stegocephalians" in that study, a term essentially synonymous with "large primitive tetrapod") with that of arthropods (Ward et al. 2006). Ward et al. (2006) inferred, from the near absence of fossil record for both of these groups, that their absence was "real," rather than a result of collection bias, and suggested a possible reason for it. They drew attention to the study by Berner (2006), which estimated lower atmospheric oxygen levels during the Early Carboniferous than previous studies had found. Their hypothesis was that both arthropods and tetrapods were essentially constrained to remain in the water during this period because the oxygen concentration in the atmosphere was too low to allow them to exploit the terrestrial environment.

At first sight, this seems an attractive idea, based as it is on two independent lines of evidence to suggest that the gap was not an artefact of preservation, and that the same conditions caused the lack of both groups. However, there are some problems with the basic premise. First, if atmospheric oxygen was low, as for the Middle and Late Devonian, then that in the water would have been correspondingly lower. One might almost expect this factor to have driven the animals out of the water, rather than confined them to it. Secondly, as far as tetrapods are concerned, the assemblage at East Kirkton and elsewhere shows that major events in their evolution took place during this interval, including origins of the modern lineages that consitute the tetrapod crown group.

There is one possible influence that low oxgyen concentration might have had upon tetrapod evolution. One of the earliest Carboniferous tetrapods known is *Casineria*. No small tetrapods are known from the Devonian, but during Romer's Gap tetrapods evolved into a number of small terrestrial forms like *Casineria*, and the pentadactyl limb first appeared. Evolution of small size might have been one of the possible responses to low atmospheric oxgyen, by exploiting the advantages of a favorable surface to volume ratio for an animal that retained some dependence on cutaneous gas exchange. Miniaturization seems to have been a major process in the evolution of both amniotes and the small "lepospondyl" groups that also appeared in the Early Carboniferous. The reason for Romer's Gap in terms of tetrapod evolution seems more likely to be accounted for by the lack of suitable continental sequences for that period.

Acknowledgments

whose stringent criticism of an earlier draft and whose valuable suggestions have contributed greatly to this article. Three anonymous referees and the editor, Hal Heatwole, also helped to improve the article.

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