THE EVOLUTION OF TERRESTRIALITY: A LOOK AT THE FACTORS THAT DROVE TETRAPODS TO MOVE ONTO LAND

INTRODUCTION

The fish-tetrapod transition has been called "the greatest step in vertebrate history" (Long and Gordon, 2004) and even "one of the most significant events in the history of life" (Carroll, 2001). Indeed, the morphological, physiological, and behavioral changes necessary for such a transformation in lifestyle to occur are astounding. The sum of these modifications occurring during the Devonian and Carboniferous led to the eventual filling of the terrestrial realm with vertebrate life, forever altering the structure and ecology of terrestrial communities.

Long and Gordon (2004) cited six critical questions relating to the evolution of tetrapods. These questions aimed to ascertain which sarcopterygian fish were basal to tetrapods, how morphological changes occurred sequentially, and when, where, how, and why these changes took place. Many researchers have described the morphological changes that occurred (Clack, 2002b; Eaton, 1951; Jarvik, 1955; Long and Gordon, 2004; Thomson, 1993), and others have focused specifically on the development of limbs and digits (Clack, 2002b; Coates and Clack, 1990; Coates et al, 2002; Daeschler and Shubin, 1995; Shubin et al, 1997; Shubin et al, 2004). As Long and Gordon (2004) pointed out, the question that is the least well answered is the question of why these modifications occurred. Exactly what factors drove these changes to take place? Many researchers have posited theories over the years attempting to answer this question, and the aim of this paper is to assess these arguments and suggest some possible common causes that could tie many of the proposed causal factors together. However, a brief description of known data pertaining to the time and place of tetrapod origins is first necessary in order to make valid statements regarding possible influential factors.

TIMING OF TETRAPOD ORIGINS

The first tetrapods (defined as vertebrates with paired limbs and digits) appeared during the Late Devonian, and it is now well-accepted that the panderichtyid fish are the sister group to tetrapods (Carroll, 1995; Long and Gordon, 2004). Prior to the past couple of decades, very few Devonian tetrapod taxa were known: mainly *Ichthyostega* and *Acanthostega*, both from the uppermost Famennian. The discovery of possible tetrapod trackways in Australia and Brazil (Bray, 1985; Warren and Wakefield, 1972) stretched the potential range of tetrapods back into the Frasnian, and these speculations were supported by the discovery of *Elginerpeton*, the oldest known stem tetrapod, from the Late Frasnian about 368 million years ago (mya) (Figure 1) (Ahlberg, 1995; Carroll, 1995).

However, it is important not to necessarily equate limbs and digits with terrestriality. Classically, the idea was that limbs developed to enable tetrapods to locomote on land. Jarvik (1955) originally reconstructed *Ichthyostega* in such a way that implied terrestriality, but a recent analysis indicates that *Ichthyostega* was not well-adapted for terrestrial locomotion (Ahlberg et al, 2005). It is now assumed that limbs with digits evolved completely for aquatic adaptation (Ahlberg and Milner, 1994; Ahlberg et al, 2005; Carroll, 1995; Clack, 2002b; Coates and Clack, 1990; Daeschler and Shubin, 1995; Lebedev, 1997). Romer (1958) even pointed this out, differentiating between "the development of limbs giving the *potentiality* of terrestrial existence, and…the utilization of these limbs for life on land." The

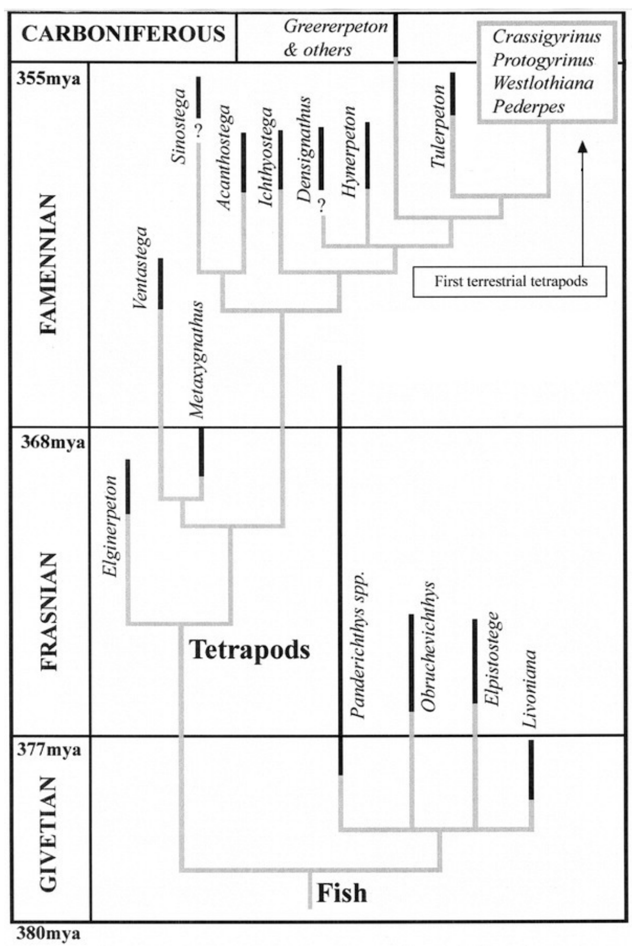

Figure 1. *Stratigraphic appearances and interrelationships of early tetrapods. Adapted from Long and Gordon (2004).*

earliest fully terrestrial tetrapod appears to be *Pederpes* from the Tournaisian about 354 to 344 mya (Figure 1) (Clack, 2002a; Long and Gordon, 2004).

Given the constraints imposed by the fossil record, it appears that the evolution of terrestriality took place in tetrapods between the Frasnian of the Late Devonian and the Tournaisian of the Early Carboniferous some time between 368 and 344 mya. An analysis of the environmental and ecological conditions imposed on creatures during this timeframe can help elucidate the major factors that drove terrestriality in tetrapods.

LOCATION OF TETRAPOD ORIGINS

Before making assertions about these environmental and ecological pressures, it is first necessary to locate where tetrapods were likely evolving. This question of place involves at least two aspects: (1) where *geographically* they were evolving, and (2) where *ecologically* they were evolving, i.e. whether they were evolving in marine or freshwater conditions.

Geographically, the first early tetrapod specimens collected were from the Old Red Sandstone of North America and western Europe (Clack, 2002b; Jarvik, 1955), and the majority of Late Devonian tetrapods have been concentrated in localities on the southern coastal belt of the Euramerican plate, in what is modern-day Scotland, Greenland, eastern North America, and the Baltic states (Clack, 2002b; Daeschler and Shubin, 1995; Milner, 1990). Some authors hypothesized an East Gondwanan origin of tetrapods based on the Australian trackways (Milner, 1993), but the discovery of Frasnian-age panderichthyids and tetrapods in Latvia and Russia offer strong support for a Euramerican origin of tetrapods (Ahlberg, 1995; Clack 2002b; Daeschler and Shubin, 1995). However, it is clear that by the end of the Famennian, tetrapods had achieved a broad geographic distribution in equatorial regions from Euramerica all the way to Australia and even China (Daeschler, 2000; Daeschler, et al, 1994; Long and Gordon, 2004; Milner, 1993; Zhu, et al, 2002).

As for marine versus freshwater considerations, it has traditionally been hypothesized that tetrapods evolved in freshwater conditions and that seasonal drying of these water bodies had driven terrestriality (Clack, 2002b; Gordon and Olson, 1995; Long and Gordon, 2004; Milner, 1990; Thomson, 1993). Some authors have argued that certain factors in freshwater conditions that could have driven terrestriality would have exerted an even stronger influence in marine conditions. For instance, Packard (1974, 1976) argued that anoxia would be even more of a problem in marine habitats than it is in freshwater habitats. However, other authors have argued that the intertidal habitats for early vertebrates proposed by Schultze (1999, quoted in Graham and Lee, 2004; Long and Gordon, 2004) would not have exhibited a strong enough selective force to initiate air breathing or the invasion of land (Graham and Lee, 2004). Most modern amphibians are unable to live in salt water (Clack 2002b), and most amphibian fossils have been discovered in what appear to be freshwater environments (Bendix-Almgreen, et al, 1990; Clack, 2002b; Daeschler, 2000; Long and Gordon, 2004).

However, Bray (1985) and Clack (2002b) noted that it is not always easy to distinguish between fluvially-influenced and tidally-influenced sediments. Bray (1985) hypothesized that tetrapods evolved in marginal marine rather than freshwater conditions, arguing that there was less of a salinity gradient between fresh and salt water in the Devonian than there is today. He noted that the density of terrestrial plants at that time was likely less than what we have today, which would allow weathering to occur at a higher rate, thus increasing the dissolved ion concentration in freshwater. Recent fossil finds have included some early tetrapods from possible tidal, lagoonal, marginal marine, and/or brackish water sediments (Carroll, 2001; Clack, 2002b; Daeschler and Shubin, 1995; Janvier, 1996; Long and Gordon, 2004), as well as evidence that many early sarcopterygians dwelt in marine habitats (Clack, 2002b; Thomson, 1993). Some authors have even suggested that the apparent widespread geographic range of early tetrapods (from modern-day North America to Australia and China) could only be a result of dispersal through epicontinental seas (Carroll, 2001; Daeschler, 2000; Thomson, 1993). While the evidence is not necessarily conclusive of either freshwater or marine origins, recent evidence seems to indicate that tetrapods likely arose in marginal marine and possibly lowland freshwater environments, and it is possible that they could have been tolerant of both marine and freshwater conditions, as are many modern vertebrate types (Clack, 2002b; Daeschler and Shubin, 1995).

CONDITIONS OF TERRESTRIAL ECOSYSTEMS

So it appears that tetrapods evolved in some sort of coastal wetland environment around the margins of the Euramerican plate during the Late Devonian. An analysis of terrestrial flora, fauna, climate, and geography at this time could help elucidate some of the factors that would have favored terrestriality in these earliest tetrapods.

The advent of land plants had important evolutionary consequences for terrestrial life. During the Silurian, the first terrestrial plants (mainly lichens, liverworts, and moss-like plants) evolved and were able to grow in habitats near the shore (Kenrick and Crane, 1997). True vascular plants with stomata evolved by the end of the Silurian (Clack, 2002b), and by the end of the Devonian, many other advanced characteristics had already evolved as well, including leaves, roots, sporangia, seeds, and secondary growth allowing plants to have a tree-like habit (Algeo and Scheckler, 1998; Edwards, 1998; Kenrick and Crane, 1997). Frasnian floras were dominated by progymnosperms, including *Archaeopteris* trees with trunks in excess of a meter in diameter (DiMichele and Hook, 1992; Edwards, 1998). At the Frasnian-Famennian boundary, an extinction event occurred that resulted in significant changes to the constituent flora (Clack, 2002b). As the plants recovered during the Famennian, species diversity and structural complexity of floral communities increased; multi-storied forests developed, and different plant groups evolved down distinct ecological lines (Algeo and Scheckler, 1998; DiMichele and Hook, 1992; Kenrick and Crane, 1997). These developing forests generated oxygen as a photosynthetic waste product, thus increasing its abundance in the atmosphere and making the land a much more suitable place for animal life (Bray, 1985; Clack, 2002b).

By the Late Silurian and Early Devonian, there was already a complex terrestrial ecosystem in place, which included arthropod populations. Centipedes, millipedes, arachnids, mites, scorpions, and other terrestrial arthropods were all present by this time (DiMichele and Hook, 1992; Gordon and Olson, 1995; Jeram, et al, 1990; Kenrick and Crane, 1997). They appear to have been mainly predators and detritivores (Kenrick and Crane, 1997), thus establishing themselves as a major link between animals and plants (DiMichele and Hook, 1992). The radiation of these terrestrial invertebrates likely had a strong influence on the later radiation of terrestrial vertebrates.

The classical idea regarding climate in the Late Devonian was that it was a time of warm, arid conditions with only seasonal rainfall (Barrell, 1916; Bendix-Almgreen et al, 1990; Clack 2002b; DiMichele and Hook, 1992; Ewer, 1955; Long and Gordon, 2004; Orton, 1954; Romer, 1945, 1958, 1966; Warburton and Denman, 1961). The red beds in which the early tetrapods were found were thought to be indicative of arid conditions. However, Inger (1957) cited Krynine (1949) as demonstrating that red beds often form in non-drought conditions; thus, red beds in and of themselves are not necessarily indicative of aridity. Romer (1958) responded to Inger's arguments by citing evidence of aridity in these strata other than the red color, including associated evaporites and evidence of subaerial deposition. The consensus today is that at least some areas appear to have been semi-arid with seasonal rainfall, especially those areas that were around the equator (Gordon and Olson, 1995), but it is clear that not all Devonian rocks indicate arid conditions (Clack, 2002b).

During the Devonian, Euramerica (also known as Laurussia), consisting primarily of Laurentia and Baltica, is hypothesized as being in an equatorial position (Clack, 2002b; Daeschler and Shubin, 1995; Daeschler et al, 1994; DiMichele and Hook, 1992; Gordon and Olson, 1995; Scotese and McKerrow, 1990; Thomson, 1993). Gondwana lay southward, with the Iapetus Sea separating the two (Figure 2). While there is not necessarily a consensus as to how much ocean separated the two major continents during the Late Devonian (Daeschler 2000; Dalziel, et al, 1994; Milner, 1993; Thomson, 1993; Van Der Voo, 1988), it is agreed that the Iapetus Sea was in the process of closing up as Gondwana and Laurussia were moving closer, ultimately coming together in the Carboniferous (Clack, 2002b; Gordon and Olson, 1995; Van Der Voo, 1988). This tectonically active region would have had a great effect on the lives of early tetrapods as their habitats were being resized, reshaped, and eventually eliminated.

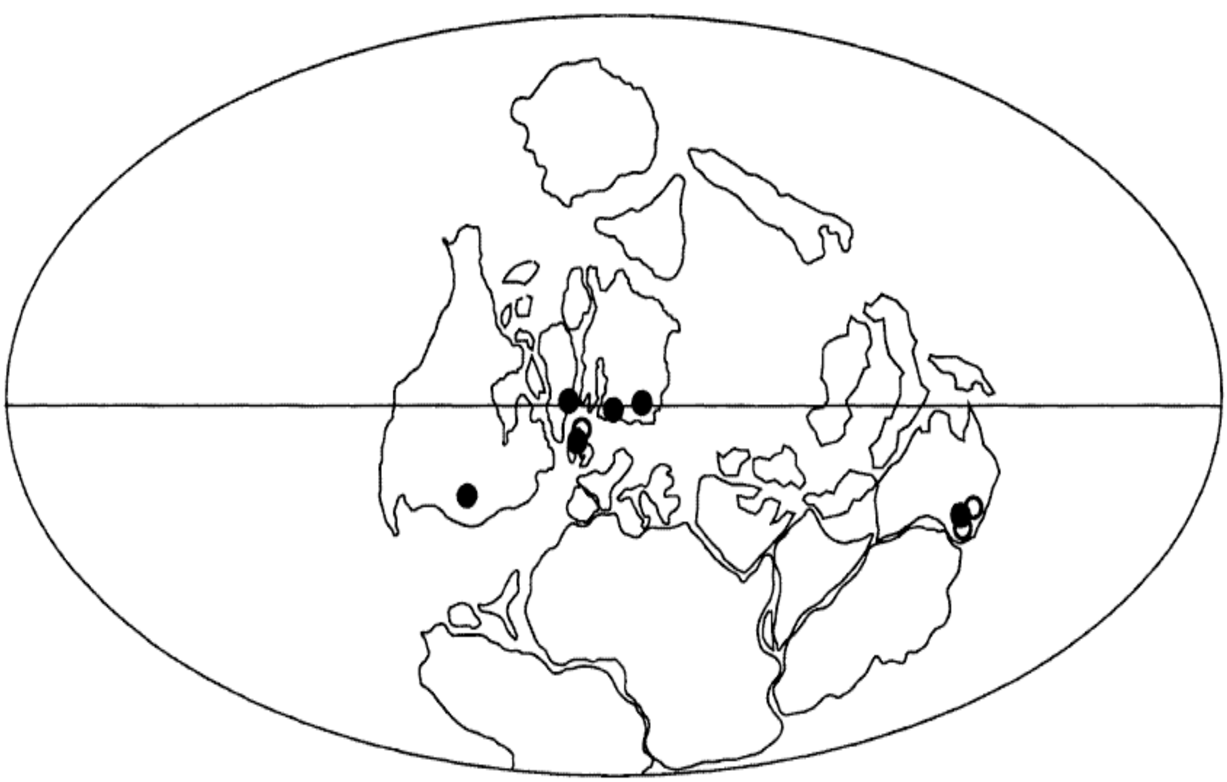

Figure 2. *Late Devonian (Famennian) paleogeographic reconstruction from Scotese and McKerrow (1990) in Daeschler and Shubin (1995). Filled circles indicate tetrapod body fossils, and open circles represent trackways.*

THEORIES ON THE ORIGIN OF TERRESTRIALITY

Over the years, many authors have considered these ecological and environmental factors and posited theories as to why tetrapods evolved into fully terrestrial creatures. Barrell (1916) was one of the earliest to propose that adverse climatic conditions were the driving factor in the origin of terrestriality. He cited the red beds in which early tetrapods had been found as evidence of aridity and hypothesized that shrinking pools of water during the dry season would have pushed amphibious tetrapods out onto land in order to survive. Romer (1945, 1966) advanced this theory, postulating that tetrapods evolved limbs in order to remain in the water. When these small pools dried up, those creatures with the stoutest limbs and most efficient terrestrial locomotion would be more likely to make it to another body of water and survive. He noted that amphibians and crossopterygians lived in the same habitat and argued that amphibians would have an obvious advantage if their habitat evaporated. He proposed that these short treks on land would eventually increase in duration as some amphibians would possibly linger on land to eat. For many years, this was the popular theory, and many authors proposed nuanced versions of this basic idea.

During the 1950s, a series of papers was published on this topic. Orton (1954) espoused the possibility that limbs may have been a digging adaptation. She cited extant amphibians digging aestivation burrows to stay moist when surrounding conditions got dry rather than dispersing to find another body of water. However, even she noted that there are many burrowing animals that are able to do so without any limbs at all. Ewer (1955) suggested that early tetrapods did not leave the shrinking ponds simply because their habitat was shrinking; rather, he noted that the receding habitat would have greatly increased population pressure, which would have triggered migration if environmental conditions were adequate. Gunter (1956) held to the basic Romer/Ewer theory, but he argued that the tetrapod limb had to be formed prior to these excursions. He emphasized that this was a gradual process, with the limbs first acting as props under water and the tetrapods making very short excursions onto land to escape predators or seek nearby food. The longer terrestrial excursions to escape the drying conditions were the final step of the process towards terrestriality. Goin and Goin (1956) theorized that competition for food was the major driving factor, citing the presence of arthropods in the shallows and on the shore that could have served as an untapped food source for early tetrapods, even though Romer (1958) argued that these food sources were not nearly adequate. In Inger's (1957) paper offering a different climatic interpretation, he noted that the hypothesized aridity would have caused a great desiccation problem for migrating amphibians; a humid climate would have offered more favorable migration conditions for early tetrapods. Warburton and Denman (1961) pointed out that in order to be a successful frog, one first must be a successful tadpole. They postulated that protoamphibians laid their eggs in shallow pools away from competition with larger lungfish and predators. Terrestrial locomotion would have been necessary for these larvae to get back to the water, and they pointed out that in this case, selection would be operating on a large number of individuals. This view was echoed by Gordon and Olson (1995) as well. Thomson (1993) considered the whole pool-drying scenario to be logically inadequate, instead claiming that ecological conditions had to be the driving factor. It was the emergence of wetlands that fostered the origination of terrestrial tetrapods, offering a moist environment with abundant new food sources and protection from predators.

Sayer and Davenport (1991) conducted a study of modern-day amphibious fishes and found that they leave water under a variety of factors. Environmental degradation, including decreased oxygen content, increased temperature, and drastically fluctuating salinity, often causes fishes to evacuate the water. Biotic factors, such as competition for food and space, predation, feeding, and reproduction, can have a large influence as well.

It is clear that a large number of potential factors could have played a role in the evolution of terrestriality, and because of this, the discussion of tetrapod origins has been "unusually-theory laden" (Thomson, 1993). Yet it is important to try and understand what conditions may have driven such an important evolutionary event. By analyzing the available evidence and assessing the validity of the many theories put forth, it may be possible to elucidate a small number of major factors that could have driven this critical occurrence in the history of life.

AN ASSESSMENT AND SYNTHESIS OF THEORIES

Long and Gordon (2004) cited that both evolutionary pushes and pulls likely influenced the evolution of terrestriality. The pushes—the factors that encouraged tetrapods to leave the water—included poor environmental conditions, predators, competitors, diseases, and parasites. The pulls—the factors that encouraged tetrapods to come onto land—included favorable conditions, empty niches, abundant food resources, and a lack of predators, competitors, diseases, and parasites. The influences of all of these factors seem logical, so how can one disentangle them and determine the most important factors? Maybe it is not possible to sort out these factors and give some of them priority over others; they might all have been of equal importance. But if one or two primary causes could be determined that would have amplified the effects of these ecological factors, one could assign primary importance to these causes.

The evolution of plants could have been one of these primary causes. In order for animals to move on to land, it first had to be habitable for them, and, as described earlier, the evolution of land plants drastically altered the composition of the atmosphere and formed the basis of new terrestrial ecosystems. The emergence of coastal wetlands offered an array of habitats previously unseen in earth's history (Thomson, 1993) and encouraged the evolution of terrestriality in arthropods. Despite Romer's (1958) objections that these food sources would not have been adequate, it is probable that even piscivorous fishes would have fed on these new prey items (Clack, 2002b; Goin and Goin, 1956; Thomson, 1993). There were no vertebrate predators on land, so this would basically have been an unexploited niche. Rather than competing with fish in the sea, they could have an untapped source of food on land as long as they could get to it. Yet, in addition to these evolutionary pulls, plants exerted some pushes on tetrapods as well.

The evolution of deciduousness in plants could have played a crucial role. Not only would mass senescing of leaves have enhanced the terrestrial ecosystem by enriching soil development (an evolutionary pull), it also likely caused anoxia in near-shore waters (Algeo and Scheckler, 1998; Clack, 2002b). As the plant matter decayed in the water, oxygen levels in the water would have decreased. This situation could have encouraged air breathing in some fish (Sayer and Davenport, 1991), which was a requisite step in the transition to life on land. Certainly, of course, the fish could have merely come up to the surface to breathe air and survived that way, but as Sayer and Davenport (1991) pointed out, many modern-day fish do leave anoxic waters.

The evolution of land plants clearly played a critical role in the evolution of terrestriality. They enhanced the terrestrial ecosystem and offered wide open niches, abundant invertebrate food resources, protection from predators, and an oxygen-rich atmosphere as opposed to anoxic waters. However, aside from the anoxia in the water, all of these would be considered evolutionary pulls rather than pushes. There had to have been some factors in their aquatic environment that made a move onto land—and all of the requisite changes—beneficial. The tectonic activity occurring in and around the Iapetus Sea at this time could have enhanced the effects of many various evolutionary pushes.

As discussed previously, early tetrapod evolution appears to have been concentrated along the southern coast of Euramerica during the Late Devonian. During this time, Euramerica and Gondwana were converging, eventually forming Pangaea during the Permo-Carboniferous. This closing of the Iapetus Sea would have affected aquatic tetrapods living in this region in several ways. As the continents came together, the major direct effect would have been habitat loss, and this could happen in several ways. The convergence of continents would decrease the amount of coastlines and lower global sea level (Clack 2002b). The arrangement of the continents also led to a short period of global cooling and glaciation during the Famennian in Gondwana (Algeo and Scheckler, 1998; Johnson, et al, 1985; Van Der Voo, 1988). The uptake of water by glaciers would have lowered sea level as well. For tetrapods living in coastal habitats, these compounding factors would have led to a great decline in available habitat. As the amount of habitat decreased, previously separated populations of animals would be brought together into more of a confined space. In such a situation, the competition would be very intense. This recalls Ewer's (1955) emphasis on the importance of population pressure, as well as Goin and Goin's (1956) focus on competition, in tetrapod evolution. Clack (2002b) also noted that when previously separated populations are forced to share a common environment, the biodiversity would actually decrease, while distribution of the remaining species would increase. This intense competition would have been a strong evolutionary push for tetrapods to find another suitable habitat.

When Inger (1957) was contesting the interpretation of red beds as indicative of an arid climate, he argued that discerning the stimulus that pushed terrestriality is dependent on one's climatic interpretation. And it is clear that there is not consensus about the climate in which early tetrapods evolved. But at the heart of Romer's classic scenario of tetrapods escaping drying pools is the loss of habitat. It has been suggested here that tectonic activity and its effects could have caused the habitat of early tetrapods to be lost; thus, an arid climate need not necessarily be a critical component in theories of the evolution of terrestriality.

CONCLUSION

The evolution of terrestrial tetrapods has certainly sparked much discussion over the years, and deservedly so, for a rich terrestrial vertebrate fauna of about 360 million years is contingent on this event. During the Late Devonian, the first tetrapods made their way onto land. As their habitat was shrinking and causing fierce intra- and interspecific competition for resources in the shallows, a new habitat with abundant resources had been brought about by plants in the terrestrial realm. The filling of these new niches available on land forever changed the course of life on earth.

To understand the full breadth of evolution, it is crucial to try and understand these landmark events in the history of life on this planet. The origin of new species depends on a complex combination of environmental conditions, ecological factors, and chance. The environmental conditions of the Late Devonian certainly made life difficult for aquatic organisms, as evidenced by the mass extinction event in the marine community (DiMichele and Hook, 1992; Johnson, et al, 1985; Long and Gordon, 2004); but had the opportunity for the colonization of land never been presented by the changes brought about by plants, the early aquatic tetrapods may have never survived long excursions in the terrestrial realm. The chance coincidence of increasingly poor quality and decreasingly abundant aquatic habitats, an emerging high quality terrestrial ecosystem, and the acquiring of morphological adaptations by the first tetrapods set the stage for one of the most important steps in the history of animal life.

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