Exaptations in the conquest of land by Tetrapoda

Mauro L. Triques[1]
Martin L. Christoffersen[2]

Abstract

Fossil discoveries bridge the transition from fish to land vertebrates ever more closely. Microevolutionary explanations for the origin of terrestrial limbs assume a continuous process of natural selection. Selective pressures, acting slowly and cumulatively on organisms and populations, were supposedly responsible for a gradual evolution from swimming fins of aquatic fish to walking limbs of terrestrial tetrapods. Using a cladistic framework, we argument that digitate fin-lobes were co-opted by evolutionary rapid chance events for walking on land. The monophyly of Tetrapoda, of the subgroup of terrestrial Tetrapoda, and the long time span for gaining ground, are not congruent with an exclusive scenario of gradual and constant selective forces. Punctuated and rapid chance events, acting on previous structures with a long history of stasis for swimming, better explain the rather sudden exaptations of vertebrate limbs for the novel function of walking on land.

Key words: Chance and evolution, cladistic framework, environmental transitions, macroevolution, Sarcopterygii.

Resumo

EXAPTAÇÕES NA CONQUISTA TERRESTRE PELOS TETRAPODA. Descobertas fósseis cada vez mais têm complementado a deficiência de conhecimento sobre a transição entre peixes e vertebrados terrestres. Explicações microevolutivas para a origem dos membros terrestres assumem que houve um processo contínuo de seleção natural. Pressões seletivas, agindo lenta e cumulativamente sobre organismos e populações, foram supostamente responsáveis por uma evolução gradual das nadadeiras de um peixe até os membros locomotores dos tetrápodes terrestres. Embasados pela cladística, argumentamos que nadadeiras lobadas com dedos pré-existentes foram co-optadas por rápidos eventos ao acaso para caminhar em terra. O monofiletismo de Tetrapoda, do subgrupo dos Tetrapoda terrestres, e o longo tempo para a conquista do ambiente terrestre, não são congruentes com um cenário exclusivo de forças seletivas agindo gradual e constantemente. Eventos ao acaso, pontuados e rápidos, agindo sobre estruturas pré-existentes em ambiente aquático por longos períodos de tempo, explicam melhor a súbita co-optação dos membros dos vertebrados para a nova função de caminhar em ambiente terrestre.

Palavras-chave: Acaso e evolução, embasamento cladístico, macro-evolução, Sarcopterygii, transições ambientais.

Introduction

Attaining a terrestrial way of life was one of the most significant events in the history of vertebrates. The transition of vertebrates from water to land is receiving much attention from paleontologists and the press (Ahlberg & Clack, 2006; Pennisi, 2006; Shubin et al., 2006, Ahlberg et al., 2008). However, the adaptive or selective advantage of the transition between life in water and life on land remains difficult to explain (Carroll et al., 2005). This major transition in the history of organism diversity thus is a question of continuing importance and contention (Meyer, 1995). The shortening of the fossil gap from lobed-fish to land tetrapods remains a fascinating segment of vertebrate evolution (Janvier, 2002). More recently, it became clear that the fish-tetrapod transition and the conquest of land represent two quite separate evolutionary steps. All Devonian tetrapod fossils were essentially aquatic, with fish-like gills. They were merely lobe-finned fishes with strange, paddle-like paired fins elongated by new structures, the digits. Even if *Acanthostega*, one of the oldest known tetrapod, had a completely different way of life compared to other sarcopterygians of the time, it yet remained completely aquatic, as it had functional gills (*Ventastega* is the most basal Devonian tetrapod represented by extensive remains, although *Acanthostega* and *Ichthyostega* are still the only Devonian tetrapods known from near-complete skeletons [Ahlberg et al., 2008: 1199]). The transformation of paired fins into limbs does not imply walking or a terrestrial life. Life on land probably appeared later, in the Carboniferous. "The problem actually consists of three parts: origin of limbs with digits, origin of walking, and origin of terrestriality" (Clack, 2002). The possible increased weight-bearing capacity of elpistostegid-like animals suggests that they "walked" in

1 Departamento de Zoologia, Universidade Federal de Minas Gerais, Av. Antônio Carlos, 6627, 31270-901 Belo Horizonte MG, Brasil. triques@mono.icb.ufmg.br

2 Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, 58059-900 João Pessoa PB, Brasil. mlchrist@dse.ufpb.br

the aquatic environment, presenting substrate traction habilities. However, if this represented a new lifestyle, it should be emphasized that the absence of terrestrial animals derived from this group indicates that selection driven evolution toward land possibly was not in course upon these animals, as will be sustained subsequently.

We argue below that catastrophic exaptations, rather than gradual adaptations, better explain the fish-tetrapod evolutionary events. Our new argument is based on the absence of parallel conquests of land by closely related lineages of sarcopterygian fishes, in spite of the presence of digits (and supposedly some kind of foot) in at least *Acanthostega*, *Crassigyrinus*, *Greererpeton*, *Ichthyostega*, *Pederpes*, and *Whatcheeria* (Ahlberg et al., 2008, suppl. 3: 11), that is, in a number of presumably aquatic Devonian tetrapods. Ahlberg et al. (2008) present a recent and detailed phylogeny of early Tetrapoda. ¨The postcranial elements attributed to *Elginerpeton* show that vertebrates with limbs had originated before the end of the Frasnian¨ (Ahlberg et al., 2008: 1203), indicating that there was a long time for the occurrence of parallel conquest of land by these animals. Further, their cladistic analysis permitted them to conclude that there was a ¨considerable morphological diversification among the earliest tetrapods¨, which at first would suggest the existence of character variation of several features, permitting selection to gradually adapt several of those stem-line animals to life on land. This, in fact, did not occur. Another even older genus, *Tiktaalik*, seems to be at the limit of the Tetrapoda level of evolution, and presents anterior limb features supposedly able to lift the animal to breathe at the surface. We will analyse this taxon subsequently. A cladistic framework is used to arrive at such alternative evolutionary scenarios.

Adaptations, preadaptations, and exaptations

The literature on evolutionary biology frequently includes references to preadaptations. Preadaptation of a structure has been defined as a structure that "can assume a new function without interference with the original function" (Mayr, 1970). It has been suggested that preadaptations are important in the evolution of the skeletal structures of vertebrates (Simpson, 1953; Bock, 1959).

More recently, Gould & Vrba (1982) introduced the term exaptation as an alternative to the concept of adaptation by natural selection. These authors were influenced by the critiques against the adaptationist programme (Williams, 1966, Gould & Lewontin, 1979), and by the historical perspective provided by phylogenetic inference (Harvey, 1996). Exaptation is

a trait evolved for other usages, or with no function at all, that was later coopted for its current function (Gomez-Mestre & Tejedo, 2005). The term has gained general theoretical acceptance, but has rarely been tested empirically, due to practical difficulties in determining the causal origins of traits. Amudson (1996) notes that character evolution may often comprise a mixture of exaptations and secondary adaptations in a nested hierarchy.

Bird feathers are one example of an exaptation. Feathers seem particularly adapted for flight, but they originally evolved for the maintainance of body heat (Gould, 1991). Another example of an exaptation is the evolution of language. Language emerged catastrophically by integrating several sub-faculties, and each of these sub-faculties evolved gradually (Okanova, 2004). Finally, "the order and arrangement of tetrapod limb bones is an exaptation for walking on land; many modifications of shape and musculature are secondary adaptations for terrestrial life" (Gould, 1991). Benton (2005) calculated the time span from *Acanthostega* to the conquest of land to be about 20-30 million years, which is a long time, reinforcing the idea of exaptation of Gould (1991). "Exaptations may not be rare fortuitous accidents, but rather consist in regular occurrences" (Andrews et al., 2002).

Cladistics provides a powerful method for distinguishing exaptation from adaptation. Cladograms indicate whether character traits have predated, accompanied, or followed evolution of particular functions. In adaptation, the modification of a phenotypic feature accompanies or parallels the evolutionary acquisition of a function. In exaptation, on the other hand, the feature originates first, either as a selected or as a chance attribute, and only later is coopted for the function in question (Blackburn, 2002).

Phylogeny of Sarcopterygii

Paleontologists and systematists diagnose some fishes by the presence of fleshy fins, in which the paired appendages form a single proximal skeletal element (Moy-Thomas & Miles, 1971). These fishes are the Sarcopterygii, considered closely related to the Tetrapoda. Cladistic analysis (originally phylogenetic systematics) was formalized by Willi Hennig (1966). Its basic aim is to define evolutionarily natural groups (called monophyletic groups, or clades), on the basis of evolutionary novelties (called apomorphies). These novelties can be found after searches in many taxa, not only the taxa representing the focus of analysis (outgroup method). In the cladistic paradigm, fleshy fins, as well as the presence of a single proximal skeletal element in the paired fins, are

considered apomorphies of the Sarcopterygii, because no other fish or invertebrates closely related to Vertebrata have similar features. Belonging to the Sarcopterygii are the coelacanths (including the living genus *Latimeria*), the lungfishes (including the living genera *Neoceratodus*, *Protopterus* and *Lepidosiren*), an increasing number of fossil taxa, and the Tetrapoda. The humerus in the human arm and the femur in the leg are homologous to the single skeletal element of the paired appendages of Sarcopterygii. Sarcopterygian "fishes" have paired appendages in the form of fins, while Tetrapoda have these same appendages in the form of legs, but their common origin is undisputed. The muscles of our arms and legs are homologous to the flesh present on the original paired fins of the sarcopterygian "fishes" (Clack, 2002; Pough et al., 2005). Consequently, Tetrapoda are considered derived sarcopterygian "fishes".

Tetrapoda and its closest relative (sister group), the Panderichthyidae (= Elpistostegidae), comprise the most derived clade in the phylogeny of the Sarcopterygii. The more recent cladistic analyses (the phylogenies we use herein) agree among each other exactly on this point (e.g. Clack, 2002; Benton, 2005; Ahlberg et al., 2008). We choose Cloutier & Ahlberg's (1996) hypothesis, because it is simpler than others, and relatively recent. However, any of the alternative hypotheses would render essentially the same argument presented herein. In this phylogeny (Cloutier & Ahlberg, 1996) (Fig. 1), Actinistia (= Coelacanthiformes) is the sister group of the other sarcopterygians, called Rhipidistia. This latter clade has apomorphies such as the pelvic girdle with anterior and posterior processes, maxillary bone far from the preopercle bone, and partially septate conus arteriosus. Dipnoi + Porolepiformes (together called Dipnomorpha) is the sister group of the remaining sarcopterygians,

called Tetrapodomorpha. This latter clade in turn has characteristic bones close to the choanae (internal nares). Osteolepiformes is the sister group of Panderichthyidae + Tetrapoda (*Eusthenopteron* is excluded from this presentation for simplicity and clearness). Recent (Clack, 2002; Daeschler et al., 2006; Ahlberg et al., 2008) non-monophyletic interpretations of Panderichthyidae do not change our argument. Dipnoi include the extant lungfishes, which obligatorily breathe atmospheric air and have a relatively basal, non-derived position in most current cladograms. In the cladogram we present in Fig. 1, this taxon is the sister group of Porolepiformes. Whether basal or derived in the accepted cladograms, their position does not change our argument. Central to our reasoning is that Tetrapoda is a derived taxon within Sarcopterygii.

Panderichthyidae and Tetrapoda share the absence of dorsal and anal fins, a depressed head with dorsal eyes, among other apomorphies. Tetrapoda, in turn, has paired fins partially transformed into feet. While this information has been available for some time, there is controversy about the factors that finally led Tetrapoda to conquer the terrestrial environment. Some theories support the idea that there is a constant evolutionary process, working through selective pressures, and leading gradually to the Tetrapoda. This same process in Tetrapoda would produce a transition from an aquatic environment to a terrestrial habitat (Clack, 2002; Pough et al., 2005). Clack (2002) uses the expression "happenstance" for her opinion of "being at the right place at the right time". We will try to demonstrate that catastrophic chance events, not a single directional process, or a single guiding selective pressure, were responsible for the transition.
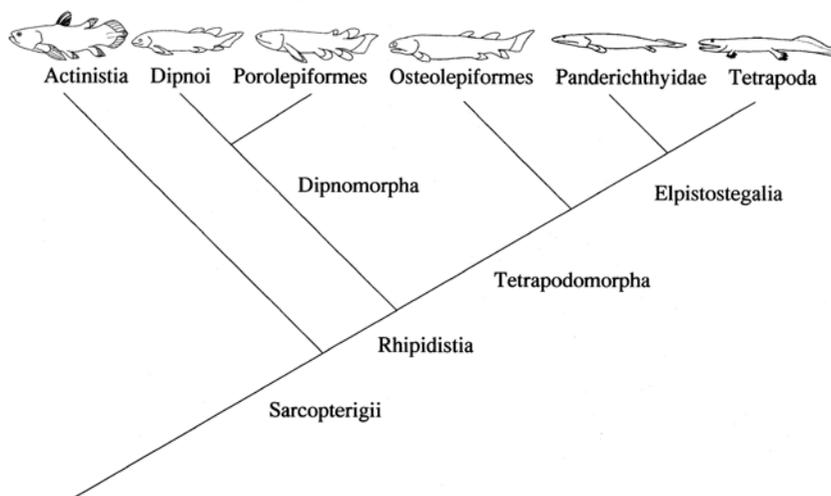

Figure 1. Cladogram of the Sarcopterygians, based on Cloutier & Ahlberg (1996) (Panderichthyidae = Elpistostegidae; Eusthenopteron not included). Illustrations simplified from many sources. Synapomorphies for the inclusive groups are presented in the text. Autapomorphies of the terminal taxa can be found in the included references.

Theories of natural selection, contrary arguments, and exaptations

Among several explanations accounting for the structural modifications of sarcopterygians for life on land, two main adaptive explanations are encountered.

The first explanation relies on the idea that an aquatic environment, susceptible to periodic drying, will select animals that can walk or creep from one drying water body to another. This would permit animals to finally reach the main river. The major criticism to this idea is that such an animal would not suffer continuous pressure to keep on land. Also, adult tetrapods were large animals in the beginning, and would hardly be able to move in this fashion. The African and South American living lungfish (Dipnoi) apparently have followed yet another evolutionary possibility: they estivate through the dry season (Nelson, 1994).

The second explanation proposes selective pressure as occurring inside the water. Rising competition within water would lead juveniles to creep out of the water to avoid predators and competitors. As a consequence, these animals would gain access to an increasing amount of terrestrial invertebrates on land. A possible criticism we see against this explanation is that developed pectoral and pelvic girdles, zygapophyzes, downward directed legs, and onward directed feet, only became functional on land about 20-30 million years after *Acanthostega* and *Ichthyostega* (Benton, 2005). Tetrapoda, in all likelihood, would have become extinct in such a time span if they were to depend exclusively on modifications due to selective pressures to feed on land. If all necessary structures for the conquest of land were appearing slowly through 40 million years or more, and could have been present together in an aquatic animal dozens of millions of years prior to the conquest of land (Benton, 2005), why did the transition to land take such a long time? We believe that all these characters developing in water could not have been the result of selective pressures to conquer land. Non-deleterious characters thus accumulated in aquatic environments by contingent events and by evolutionary tinkering on available structures (Monod, 1971). These structures would have suddenly been coopted for new functions on land, making the complete and rapid conquest of this novel environment finally possible after such a long time.

Other selection scenarios proposed in the literature usually indicate initial pressures towards exploiting very shallow waters; this idea, however, implies the origin of features in water, which are later used on land, which correspond to exaptations, as we have pointed out above. The idea of progressively more terrestrial forms from elpistostegids through *Acanthostega* to *Ichthyostega* may indicate adaptations to shallow waters, but these adaptations originated as exaptations for a terrestrial habitat, not indicating true selective pressures toward land or for life outside of water. The competence for living in shallow waters in part is useful for later terrestrial life, but we interpret these features as exaptations for terrestriality, not as adaptations for life on land. That is why we see no reason to believe that the evolutionary process was driven by selection for the conquest of land.

The main criticism we see against adaptive explanations is historical, that is, cladistic. If selective pressures of any kind (drought, aquatic predators and competitors, absence of predators and competitors on land, and existence of plenty of food in terrestrial environments) were the main forces toward the conquest of land, Tetrapoda would have had several independent origins, that is, the group, as historically defined, would be found to be polyphyletic under cladistic analysis. We would expect a series of fossil "tetrapods" originating from Chondrichthyes, Actinopterygii, and several different phylogenetic lineages of Sarcopterygii leading successfully and independently to land.

For instance, there are living catfishes (Siluriformes, an order of Teleostei, in turn a group of Actinopterygii) in South America (Callichthyidae) and in Africa (Clariidae) that can creep on land, at night, from one small body of water to another. They can somehow "breathe" air. Other actinopterygian air "breathers" are the African and Asian Anabantidae, the South American and African Osteoglossidae, and the South American Electrophoridae (Nelson, 1994). Species of some genera of Gobiidae (Actinopterygii, Perciformes), such as *Boleophthalmus*, *Periophthalmus*, and *Periophthalmodon*, can move along with considerable speed. Also belonging to Gobiidae, *Gillichthys mirabilis* comes to the surface when the water is low in oxygen and gulps air, which is held in the highly vascularized buccopharynx for respiratory exchange. Some species of Bleniidae, tribe Salariini (Actynopterygii, Perciformes) can spend much of their time out of the water (Nelson, 1994). However, these bony fishes (and the cartilaginous chondrichthyans) could never have conquered land, because they did not have some of the major apomorphies of the Sarcopterygii: a single skeletal element positioned proximally on paired and muscular appendages.

Yet, we do have derived Sarcopterygii (the Panderichthyidae, also called Elpistostegidae) with these apomorphies, and also with lungs, choanae, a partially divided conus arteriosus, absence of dorsal and anal fins, and presence of anterior and posterior skeletal processes in the pelvic girdles. Even so, the panderichthyids still

do not have the skeletal structure of feet, the defining feature of Tetrapoda, and did not conquer land.

No matter how strong the selective forces may have been for leaving water, or for invading land, there was no conquest of the terrestrial environment until a useful array of structures for this transition was present. All the aquatic, tetrapod-like organisms, each of them supposedly under the continuing pressure of selective forces, were probably unable to rise independently to land, because of the lack of other necessary structures for life on land, such as developed, fully functional zygapophyses. Although *Ichthyostega* already had zygapophyses, these were not well developed, or completely effective for terrestrial locomotion. If selective forces were the main reason to gain land, we could have expected a second, independent origin of terrestrial tetrapods arising at least from *Ichthyostega*.

Tiktaalik is a sarcopterygian genus phylogenetically very close to the Tetrapoda (Ahlberg et al., 2008). It presents the conjunction of dorsoventrally compressed head and body, dorsally placed eyes, and mobile head (as the shoulder girdle is not connected to it). These features are congruent with the hypotheses of locomotion on the water bottom, along the water margins, or close to the water surface (Shubin et al., 2006: 768). This environment is the same as that where remains of *Tiktaalik* were found. The genus presents several features necessary for life on the ground: (1) a pectoral fin in the form of an articulated, weight-bearing, downward directed foot; (2) muscles able to elevate the body upwards; (3) a head free from the pectoral girdle, allowing the development of a neck; (4) bones of the opercular series absent; (5) presence of lungs; and (6) partially overlapping ribs, with a function similar to the terrestrial vertebrate zygapophyzes (Daeschler et al., 2006; Shubin et al., 2006). The Tetrapoda only attained a weight-supportive capacity of its pectoral fins (forelimbs) about 10 million years, or more, later. An evolutionary process based on selective pressures to leave the water and to gain ground apparently could have been more effective in the *Tiktaalik* lineage than in the *Acanthostega* lineage (Tetrapoda), because an articulated weight-bearing pectoral fin was already present. However, there are no terrestrial vertebrates, living or fossil, known to have originated from the *Tiktaalik* lineage. This demonstrates that there was no gradual evolutionary process toward the conquest of land. Therefore, the conquest of the terrestrial environment by vertebrates appears to have represented a chance event.

Only Tetrapoda (Batrachomorpha and Reptilomorpha), among so many possibilities of adaptive radiations onto land, remains monophyletic for life out of water. Batrachomorpha includes the living amphibians, such as salamanders and toads, and several relatively terrestrial fossil forms, such as the famous *Eryops* and the even more terrestrial *Cacops* and its relatives. Reptilomorpha includes several fossil forms progressively more terrestrial, including the Amniota, the animals with a shell and other protective membranes surrounding their eggs. These animals are popularly known as reptiles, mammals and birds. Batrachomorpha + Reptilomorpha (unnamed in Pough et al., 2005) is a monophyletic group and the ancestral species of this clade were alone among vertebrates in conquering the terrestrial environment.

With more and better fossil specimens being presently discovered and described for the critical fish-tetrapod transition (Clack, 2006), it has become untenable to overlook that the critical features for the conquest of land had emerged previously in aquatic animals.

Conclusions

Arguments supporting the occurrence of selective forces on particular features can be tested with an historical framework for evaluating the timing of key innovations in the scenario of a progressive evolutionary radiation into terrestrial environments. If selective forces were the main evolutionary processes shaping the conquest of land, we would expect independent lineages, such as Chondrichthyes, several fossil and extant Actinopterygii, Dipnoi, *Ichthyostega*, *Tiktaalik*, and other fish-like animals, to have evolved in parallel for a terrestrial mode of life. This has not been the case.

The historical constraints of a cladogram indicate the temporal order of emergence of apomorphies, and show that important features for life on land appeared in the ancestral aquatic environment of vertebrates. The monophyly of terrestrial tetrapods (Batrachomorpha + Reptilomorpha) corroborates the hypothesis that catastrophic ruptures of previous evolutionary equilibria for life in water, and exaptations for entirely new functions on land, rather than uniform selective forces, were the main evolutionary forces acting in the conquest of a terrestrial way of life. "The future of research on the 'fish-tetrapod' transition looks bright" (Clack, 2006). Macroevolution is becoming respectable again, with more evolutionary data becoming available for its support.

Acknowledgements

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