

USE OF AN EXPLICIT METHOD FOR DISTINGUISHING EXAPTATIONS FROM ADAPTATIONS AT THE ORIGIN OF TERRESTRIALITY IN TETRAPODA, BASED ON CLADOGRAMS AND SYNAPOMORPHIES

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ABSTRACT – We applied a cladogram-based method for discerning between adaptations and exaptations. We used current definitions and recognition criteria to distinguish between the evolutionary terms adaptation and exaptation. Our cladogram identifies 14 specific exaptations for the conquest of land by vertebrates and one possible adaptation, from a total of 16 features associated with the conquest of the land environment (the remaining feature is related to shallow water environment). Further, it was found that 25% of these features emerged before the Devonian period and may not be correlated to Devonian ecological events as suggested in previous works. The other exaptations emerged abruptly in the Devonian and therefore their correlation with adaptive processes directed towards the conquest of land during this period of the Paleozoic Era is not well grounded. As a whole, the ensemble of exaptations permits to falsify the correlation of terrestriality with adaptive scenarios. On the basis of characters that can be comprehensively scored in fossils and some that can also be studied in living forms we propose that macroevolutionary processes (exaptive and/or genetic drift processes), rather than adaptation may be the main evolutionary factors responsible for the conquest of land by vertebrates. The use of the cladogram-based method utilized herein allowed the development of a new perspective for the analysis of both paleontological and neontological data. Starting with cladograms available in current literature, it is possible to reach different interpretations for the same data in evolutionary terms. The resulting viewpoint is almost opposite to the traditional view of slow, gradual, adaptive (microevolutionary) character evolution, resulting in a macroevolutionary perception of chance events conspicuously involved in evolution. We propose that these results ultimately explain why the many different "evolutionary ecological scenarios" (or simply "adaptive scenarios") never explained the emergence of terrestrial tetrapods satisfactorily.

KEY WORDS: *Adaptationism, Adaptive scenarios, Character effects, Evolutionary process, Macroevolution, Sarcopterygii.*

USO DE MÉTODO EXPLÍCITO PARA DISTINGUIR EXAPTAÇÕES DAS ADAPTAÇÕES NA ORIGEM DA TERRESTRIALIDADE EM TETRAPODA, BASEADO EM CLADOGRAMAS E SINAPOMORFIAS

RESUMO – Aplicamos um método baseado em cladística para discernir entre adaptações e exaptações. Usamos definições correntes e critérios de reconhecimento para distinguir entre os termos evolutivos adaptação e exaptação. Nosso cladograma identifica 14 exaptações específicas para a conquista da terra firme pelos vertebrados e uma possível adaptação, de um total de 16 características associadas à terrestriabilidade (a estrutura remanescente está relacionada ao ambiente de águas rasas). Além disto, foi encontrado que 25% das estruturas surgiram antes do período Devoniano e podem não ter correlação com eventos devonianos, como é normalmente sugerido em trabalhos prévios. As outras exaptações surgiram abruptamente no Devoniano e, portanto, sua correlação com processos adaptativos que direcionaram para a conquista do ambiente terrestre durante este período da Era Paleozóica não está bem fundamentada. Como um todo, o conjunto de exaptações permite falsificar a correlação entre terrestriabilidade e cenários adaptativos. Com base em caracteres que podem ser abrangentemente verificados em fósseis e alguns que também podem ser estudados em formas viventes, nós propomos que processos macroevolutivos em vez de adaptação podem ter sido os principais fatores responsáveis pela conquista do ambiente terrestre pelos vertebrados. O método baseado em cladogramas, utilizado aqui, permitiu o desenvolvimento de uma nova perspectiva para a análise de dados tanto paleontológicos quanto neontológicos. Tomando-se cladogramas disponíveis na literatura corrente é possível atingir interpretações diferentes em termos evolutivos, para os mesmos dados. O ponto de vista resultante é quase oposto à visão tradicional da evolução lenta, gradual e adaptativa dos caracteres (microevolutiva), resultando numa visão macroevolutiva (processos exaptativos e/ou de deriva genética) de eventos ao acaso, conspicuamente envolvida na evolução. Nós propomos que estes resultados, em última análise, explicam a razão dos muitos "cenários ecológico-evolutivos" (ou simplesmente "cenários adaptativos") nunca terem esclarecido satisfatoriamente o surgimento da terrestriabilidade nos tetrápodes.

PALAVRAS-CHAVE: *Adaptacionismo, Cenários adaptativos, Efeitos de caracteres, Macroevolução, Processo evolutivo, Sarcopterygii.*

USO DE UN MÉTODO EXPLÍCITO PARA DISTINGUIR EXAPTACIONES DE ADAPTACIONES EN EL ORIGEN DE "TERRESTRIALIDADE" EN TETRAPODA, BASADO EN CLADOGRAMAS Y SINAPOMORFIAS

RESUMEN – Aplicamos un método basado en cladística para discernir entre adaptaciones y exaptaciones. Utilizamos definiciones actuales y criterios de reconocimiento para distinguir entre los términos evolutivos adaptación y exaptación. Nuestro cladograma identifica 14 exaptaciones específicas para la conquista de la tierra firme por los vertebrados y una posible adaptación, de un total de 16 características asociadas a la terrestriabilidad (la estructura restante se relaciona con el medio ambiente en aguas rasas). Además, se encontró que 25 % de las estructuras surgieron antes del período Devónico y no pueden ser correlacionadas con eventos devonianos, como se sugiere comúnmente en estudios anteriores. Las demás exaptaciones surgieron de modo abrupto en el período Devónico y, por lo tanto, su correlación con procesos adaptativos que direccionaron a la conquista del medio ambiente terrestre durante ese período de la Era Paleozoica no está bien fundamentada. En su totalidad, el conjunto de exaptaciones permite falsificar la correlación entre terrestriabilidad y escenarios de adaptación. Basándose en caracteres que se pueden ser exhaustivamente verificados en fósiles y algunos que también se pueden estudiar en formas de vida, proponemos que los procesos macroevolutivos en lugar de adaptación pueden haber sido los principales factores responsables de la conquista del medio ambiente terrestre por los vertebrados. El uso del método basado en cladogramas, utilizado en este estudio, permitió el desarrollo de una nueva perspectiva para el análisis de datos tanto paleontológicos como neontológicos. Tomando cladogramas disponibles en la literatura actual, es posible lograr diferentes interpretaciones en términos evolutivos para los mismos datos. El punto de vista resultante es casi opuesto a la visión tradicional de la evolución lenta, gradual y adaptativa de los caracteres (microevolutiva), resultando en una visión macroevolutiva (procesos de exaptaciones y/o de deriva genética) de eventos al azar, notablemente involucrada en la

evolución. Proponemos que estos resultados, en última instancia, explican la razón de muchos “escenarios ecológico-evolutivos” (o simplemente “escenarios de adaptación”) nunca han aclarado satisfactoriamente el surgimiento de la terestrialidad en los tetrápodos.

PALABRAS CLAVE: *Adaptacionismo, Escenarios de adaptación, Exaptación, Efectos de caracteres, Proceso evolutivo, Sarcopterygii.*

INTRODUCTION

According to Andrews *et al.* (2002: 498), Gould and Lewontin (1979) have helped highlight many ways in which the standards of evidence that adaptationists have used can lead them to erroneously classify a trait as an adaptation for a proposed function. For example, the genes underlying the trait could have evolved by chance or mutation or the trait could be a spandrel or an adaptation for another function that has been subsequently co-opted or “exapted” to the proposed function, among many other possibilities. An *exaptation* is a pre-existing character or trait that acquires a new beneficial effect without being modified by selection for this effect (Gould & Vrba, 1992) as it will be detailed subsequently. Williams (1966: 12) stated that “a frequent practice is to recognize adaptation in any recognizable benefit arising from the activities of an organism”, that “this is an insufficient basis for postulating adaptation and that it has led to some serious errors”. He further says that “a benefit can be the result of chance instead of design”. Williams (1966) defended the viewpoint that researchers should make an inference of adaptation and function only after demonstrating that all alternative hypotheses of adaptation for a particular effect are highly unlikely as complete explanations for the trait. According to him, demonstrating adaptation carries an onerous burden of proof and the principle of adaptation should be used only as a last resort. It should not be used when less onerous principles are sufficient for a complete explanation. It must be emphasized that these authors did not infer that there is no adaptive evolutionary process, but that other evolutionary processes may occur and that these may be undervalued or underestimated and occasionally may possibly be the main evolutionary process in a given taxon or situation (e.g. Gould, 1997). Darwin (1872 apud Gould 1997) himself stated “I am convinced that natural selection has been the main but not the exclusive means of modification.”

Triques and Christoffersen (2009), using a cladistic framework, argued that environmental scenarios of selective forces are not compatible with the emergence of a single monophyletic vertebrate group gaining ground, having a single kind of paired limbs based on its internal skeleton, and unique feet. Thus, the monophyly of either Sarcopterygii or Tetrapoda lends weak support for a single emergence of a weight supporting feature (either the limb or the foot itself) leading to terrestrial invasion if microevolution (utilized in this paper as evolution based on adaptive processes) is used to elucidate this evolutionary process.

When the environment acts in favor of selection (microevolution) of certain life forms to better explore a particular way of life, clearly the final expression of those given forms can be traced back from different evolutionary lineages. In fact, some of these adaptations have long been used in text-books (e.g. Hildebrand 1982: 17, figs 1 – 5). For example, hydrodynamic vertebrates (considered as animals with fusiform – streamlined – bodies) are notably known to have evolved separately many times. Animals as different in origin as ichthyosaurs, white sharks and their relatives (lamnid sharks together with *Alopias* and *Megachasma*) (e.g. Shirai 1996: 20), dolphins and tuna fish have been used as examples of analogous (as opposed to homologous) evolution of body shape. Indeed, the emergence of hydrodynamic body shape in Teleostei (Actinopterygii) occurred so many times, independently, that probably only a team of specialists could establish an appropriate number of parallel events.

As examples, we can consider the following teleost fishes that independently evolved nearly fusiform bodies: Scombroidei (tuna fish and their relatives, swordfishes, barracuda and their likes), Rachycentridae + Coryphaenidae, Carangidae (possibly with several reversals), Anoplomatidae, Scomberesocidae, Exocetidae, Paralepididae, Belonidae, Mugilidae, Salmonidae, Esocidae, Cetopsidae, *Salminus*, *Acestrorhynchus*, *Oligosarcus*, Hemiodontidae, Chanidae, Albulidae, Megalopidae, Aspidorhynchidae (e.g. Nelson 1994; de Pinna 1998; Weitzman and Malabarba 1998 among many other examples). Further, we can assign separate, independent origins for fusiform body forms also for the chondrichthyans Lamnidae + Alopiidae + Megachasmidae, Carcharhinidae (but possibly with different origins inside this family), *Rhincodon typus* and Cladoselachidae (e.g. Shirai 1996: 20). The sarcopterygian †*Eusthenopteron* (†Osteolepiformes) and the “agnathan” †Anaspida are also roughly fusiform. Even the penguins (Sphenisciformes) are relatively fusiform birds. The occurrence of some more, other less fusiform groups inside the above mentioned suborders and families indicate that microevolution might have occurred in each of these taxa. These in turn could be considered as evolutionary lines under selective forces to better explore a way of life involving high speed as a directing evolutionary factor.

Another example of multiple conquests of an environment is also long known: the return of tetrapods to water — presumably an advantageous way of life under some circumstances — as offshoots from groups very well established on land. This evolutionary trend includes several non-related tetrapod groups (e.g. Pough *et al.* 2007): Ichthyosaurs, Placodontia + Plesiosauria, Crocodylia, Cetacea, Sirenia, etc. In many of these lineages the fossil record has been traced back close to their terrestrial origins, showing progressive adaptations for water dwelling.

A third example of selective pressures acting in favor of adaptation to a new environment seems to be the depressed “fishes” (involving a dorso-ventral compression of the body shape). The squaliform sharks apparently are progressively more depressed, with an initial loss of the anal fin (clade 19 of Shirai 1996: 20, character 84), subsequent flattening of the caudal peduncle and culminating with partially benthonic habits (although some are mid-water active aggressive predators, as *Istiopus brasiliensis*). This trend continues towards a truly depressed body and benthonic habits in Hypnosqualea (De Carvalho 1996: 38, fig. 5). This evolutionary adaptation supposedly is accompanied by a habitat shift in some rays, including the manta rays, which live under the sea surface. Many independent origins for this body shape include the rhenanid placoderms, several independently depressed families (e.g. de Pinna 1998: 289, fig. 1) and genera of siluriform teleost fishes (Chacidae, Aspredinidae, *Loricaria*, *Rineloricaria*, *Lophiosilurus*, *Hemiodontichthys*, *Sturisoma*, etc.), Ogocephalidae, Lophiidae, Batrachoididae, among many others.

On the other hand, a foot appeared a single time in vertebrate evolution and the conquest of land occurred as a single event in the vertebrate group with feet. These single events for feet and for the invasion of land in vertebrates contrasts with the numerous independent acquisitions of streamlined body forms to better inhabit the water column, the many returns to an aquatic environment by land tetrapods, and the many evolutionary experimentations to better fit flat environments (such as shallow waters) by several previously mid-water vertebrate groups. This

corroborates the previous proposition of Triques and Christoffersen (2009) that adaptation to life on land seems unlikely for the vertebrates. Therefore a macroevolutionary instead of a microevolutionary event seems to be involved ("macroevolution" is used in this paper, as non-adaptive evolutionary processes, including exaptation, genetic drift and other possible evolutionary processes; chance events, for short).

Polish marine tidal flat sediments of early Middle Devonian age (Eifelian Stage) are approximately 18 million years older than the earliest tetrapod body fossils and arose at least 10 m. y. earlier than the oldest elpistostegids (†*Elpistostege* + †*Tiktaalik*). In these Polish sediments, fossil trails were found and considered to be produced by tetrapods that, therefore, represent the oldest known tetrapod vestiges. "They force a radical reassessment of the timing, ecology and environmental setting of the fish–tetrapod transition, as well as of the completeness of the body fossil record" (Niedzwiedzki et al. 2010: 43). These tetrapod trackways of 395 m. y. ago indeed corroborate

Triques and Christoffersen's (2009) idea that microevolution does not support the emergence of Tetrapoda nor the current hypotheses of land tetrapod origins. Niedzwiedzki et al. (2010) thus found tetrapod fossil evidence that increases the time of existence of Tetrapoda by 18 m. y. Therefore, there was much more geological time available for the tinkering of tetrapods towards land. An even longer time available makes microevolution less likely as the factor responsible for leading tetrapods onto land. These new findings include trackways of manus and pes prints. Some of these well preserved footprints (Muz. PGI 1728.II.1 and Muz. PGI 1728.II.2) seem to be very close to what is known from †*Acanthostega* and mainly †*Ichthyostega* (Niedzwiedzki et al. 2010: 46).

This again corroborates Triques and Christoffersen's (2009) idea that microevolution was not involved in the single origin known for the Tetrapod. If microevolution was the evolutionary process involved, we would expect to encounter a comparatively less developed foot morphology 18 m. y. earlier than in the known tetrapods. If previously to the discovery of these Polish trackways it would be possible to consider 25 million years from the origin of the Tetrapoda to the conquest of land (Benton 2005: 85), after the new findings from Poland (Niedzwiedzki et al. 2010) this gap may reach 35 million years (McGhee Jr 2013: 32, tab.2.2) or up to 41 million years (Benton 2005: 27, box 2.2), depending on where we establish the beginning of Carboniferous — usually identified as the possible date of conquest of land by vertebrates. These very considerable time spans are incongruent for explanations of the origin of land vertebrates based on microevolution and inconsistent with ecological scenarios for the environmental transition towards land. This only strengthens Triques and Christoffersen's (2009) hypothesis that alternative macroevolutionary mechanisms must be sought. This presumed diagonal stride pattern for the Muz. PGI 1728.II.16 fossil sample from Poland (Niedzwiedzki et al. 2010) seems to be in accordance with the peculiar alternating movement of *Latimeria chalumnae* (Coelacanthiformes), as observed from a submersible (Janvier 1996: 74). Thus the walking pattern of entirely aquatic Silurian fishes were similar to the walking pattern of a present land vertebrate. This pattern is also seen in the paired fin movements of living lungfishes (Dipnoi) (Janvier 1996: 74–75). Although *Latimeria* and the lungfishes can move their paired fins like land vertebrates do, they do not walk on the bottom of water bodies and it is possible that fossil species like this one from Poland only "walked" sporadically, not as a usual way of life. Therefore, this trait could be neutral in terms of natural selection.

"Adaptationism is a research strategy that seeks to identify adaptations and the specific selective forces that drove their evolution in past environments. Since the mid-1970s, paleontologist Stephen J.

Gould and geneticist Richard Lewontin have been critical of adaptationism, especially as applied toward understanding human behavior and cognition. Perhaps the most prominent criticism they made was that adaptationist explanations were analogous to Rudyard Kipling's *Just So Stories* (outlandish explanations for questions such as how the elephant got its trunk).

Since storytelling (through the generation of hypotheses and the making of inferences) is an inherent part of science, the criticism refers to the acceptance of stories without sufficient empirical evidence. In particular, Gould, Lewontin, and their colleagues argue that adaptationists often use inappropriate evidentiary standards for identifying adaptations and their functions, and that they often fail to consider alternative hypotheses to adaptation" (Andrews et al. 2002). In response, Blackburn (2002) proposed a way to distinguish exaptation (a pre-existing feature or trait, with a determined function in a taxon, that later in evolution is co-opted for another use - see further explanations below) from adaptation, suggesting the use of cladograms as a framework.

Triques and Christoffersen (2009: 70) indicated, but did not explore, this other argument, reinforcing the proposition of macroevolution rather than microevolution, in the cases of the emergence of a foot, the use of this feature for walking inside water, and finally for walking on land. In adaptation, the modification (that is, an apomorphy, in the cladistic jargon) of a phenotypic feature accompanies or parallels the evolutionary acquisition of a function. In exaptation (apomorphy) originates first, no matter if by positive or neutral selection, and only later is co-opted for the function in question (Blackburn 2002). Here, we combine this idea of Blackburn (2002) and that of Gould (1991) that "order and arrangement of tetrapod limb bone is an exaptation for walking on land" to verify, by an explicit reasoning scheme, if a chance event — macroevolution — or natural selection — microevolution — is the main evolutionary mode for the environmental transition from water to land in vertebrates.

Presently it is admitted that "the origin of the tetrapods must have involved numerous exaptations" (Schoch 2014: 10). The invasion of land is accepted as having been a very unlikely event (McGhee Jr 2013). Yet the overwhelming preponderance of exaptations may strike readers as surprising, given the indiscriminate and preferential use of adaptive scenarios for explaining any and all cases of vertebrate evolution.

METHODS

Blackburn (2002) developed a procedure for discerning adaptation from exaptation. According to him (Blackburn 2002: 507) one crucial difference between adaptation and exaptation lies in the chronological sequence of structural and functional modifications. The timing of evolution of a feature is inferred from its taxonomic distribution (Brooks and McLennan 1991, apud Blackburn 2002: 508). Therefore, plotting apomorphies and independently their functions in the same cladogram reveals possible adaptations when function predates or accompanies the emergence of a structural feature, whereas when the structure originates first and only later takes on the function in question, exaptation is indicated (Blackburn 2002: 508). "That a structure antedated the function it performs, offers a sufficient criterion for recognition of exaptation. However, a function predating or accompanying evolution of a given structure is a necessary but insufficient criterion for recognition of adaptation; therefore, other criteria (such as those discussed by Andrews et al. 2002) must also be brought to bear" (Blackburn 2002: 508). "As a practical matter, phylogenetic analysis is useful chiefly where a robust cladogram can be constructed from taxa that vary in structural and functional features of interest" (Blackburn 2002: 508).

Therefore, it is not the aim of this paper to construct a data matrix to generate a new cladogram, not to optimize, these features in this process. Instead, what we seek is a cladogram inclusive enough for the reader to visualize, in one glance, the broad or main taxa involved, and their associated features, including their functions and effects. Exaptations are said to have effects and adaptations to have functions. The main taxa comprise Actinopterygii, and Sarcopterygii subsets such as Coelacanthiformes, Dipnoi, †Porolepiformes, †Rhizodontida, †Osteolepiformes, †Panderichthyidae, †*Elginerpeton*, †*Ventastega* and other known fossil tetrapod genera considered to be at the tetrapod origin, as well as †Colosteidae, †Crassigyrinidae, †Whatcheeriidae, †Baphetidae and the crown-group Tetrapoda (the group with living representatives). A single published cladogram is not available for this purpose, so we had to combine more than one, following the character optimization from them, except when otherwise noted in the text. A large number of terminals would make this cladogram unworkable because we still had to include features, functions and effects in it, so several terminals had to be withdrawn. We thus chose and simplified some of Benton's (2005) cladograms for this task, as will be detailed subsequently.

Apomorphic features associated with the conquest of the land environment were plotted on the cladogram, as well as their concerned functionalities, independently of one another. From this framework, it will be possible to discern the adaptive from the exaptive apomorphies. Finally, we will discuss if it is appropriate to refer them to evolutionary scenarios or not. It is not the aim of this paper to include exhaustive apomorphies concerning the cladogram. We only include illustrative apomorphies that clearly address questions of the occurrence of adaptations and/or exaptations at the origin of Tetrapoda and in the conquest of land. In other words, we ask at which moment in the evolution of the Sarcopterygii do the Tetrapoda originate and gain ground, and which main evolutionary process, micro- or macroevolution, is involved.

Through the text, we refer to a taxon or taxa that split off more basally in the cladogram as "basal taxa" in relation to a mentioned larger taxon we are dealing with at a given moment in the paper.

Sarcopterygii is here defined as in Benton (2005: 69), including taxa with muscular pectoral and pelvic limbs with substantial limb bones (among other synapomorphies) but we also include the presence of a single skeletal element proximally in each paired fin (called the "stylopod"). However, it should be pointed out that Zhu and Yu (2009) found three or four skeletal elements in basal sarcopterygians taxa (in two genera, so far) and considered as crown group Sarcopterygii the ones with a single element. For the sake of simplicity and clearness, here we consider the occurrence of a single element basally in paired walking appendages as a synapomorphy for Sarcopterygii.

As explained above, we combined and simplified three cladograms from Benton (2005: 68, 80, 98, boxes 3.6 and 4.1), omitting †*Obruchevichthys* (as the sister group of †*Elginerpeton*), †*Metaxygnathus* (the sister group of †*Ventastega*) and the taxa included within Batrachomorpha, Lepospondyli and Reptilomorpha. On the other hand, we included Rhizodontida as the sister group of the remaining tetrapodomorph groups (Figure 1). The cladogram-based method used in this paper is benefitted by a simplified cladogram that at the same time is wide enough in taxonomic perspective to include, in the same figure, all of the studied apomorphies, together with their respective functions and/or effects.

A number of cladistic phylogenies were published for Sarcopterygii, some of which have placed Tetrapoda as the sister group of the remaining sarcopterygians (e.g. Chang 1991 apud Benton, 2005) or one of the basal groups (Romer 1966: 47, fig. 67). On the other hand, whenever †Panderichthyidae, †Elpistostegidae or

†Panderichthyida" are considered in the phylogeny, Tetrapoda appears as the sister group of this last taxon, both emerging as the most derived sarcopterygians in the cladogram. This is central to our discussion of adaptation/exaptation at the origin of the Tetrapoda: the more detailed the cladogram, the more derived are "†Panderichthyidae" + Tetrapoda in the cladogram. Thus, it is not necessary to pick up the most recent or complete cladogram to discuss the features the way we intend to. According to Clack (2012: 98), it is hard to see that opinion will be swayed away from the idea that tetrapods are the descendants of a tetrapodomorph lineage including fish such as †*Tiktaalik*, †*Panderichthys*, †*Eusthenopteron* and †*Osteolepis*. "†Panderichthyidae" is written between quotation marks as it is indeed a paraphyletic group. †*Panderichthys* is more basal in phylogenetic position and the two other genera are closer to Tetrapoda (e.g. Clack 2012: 60, fig. 3.2; Niedzwiedzki et al. 2010: 43), but for the sake of simplicity we did not split these taxa apart. Baphetids (fossil Amphibia) are sometimes indicated between quotation marks to indicate their paraphyletic nature, but some authors found them to be monophyletic (Clack 2012: 329). Baphetidae is usually placed as the sister taxon of the crown group (i.e., directly related to modern tetrapods) or sometimes one-step more removed from this group (e.g. Laurin 2010: 162, fig. 7.1).

These different interpretations will not alter our results, as will be discussed at the appropriate point in the text. The true phylogenetic position of †*Crassigyrinus* still remains disputed (Clack 2012: 287), but most studies place it outside the crown-group Tetrapoda. "†Osteolepiformes" includes a number of taxa that may be progressively closer to Tetrapoda (e.g. Clouthier and Ahlberg 1996: 464, fig. 3) and is placed between quotation marks. "Coelacanthiformes" was preferred over "Actinistia" for being more widespread in popular and undergraduate literature. Onychodontida was omitted for being incompletely known regarding some key characters such as choanae (e.g. Clouthier and Ahlberg 1996: 465); as a possibly rhipidistian group that splitted off basally in group's phylogeny, its absence from the cladogram does not change our reasoning. Actinopterygii is the sister group of Sarcopterygii (e.g. Zhu and Yu 2009; Lauder and Liem 1983, among many others), both groups composing the Osteichthyes.

Concerns on topologies and synapomorphies that support them may rise because we did not implement a cladistic analysis ourselves. Yet these concerns may be clarified considering that the single topology that possibly could invalidate our proposals of exaptations is that one in which the monophyletic terrestrial tetrapods are placed as the sister group of all other sarcopterygians. This would make every synapomorphy we studied here coincide with terrestriality, following the method of Blackburn (2002). However, as Clack (2012:98) stated, there is strong cladistic support for a position of Tetrapoda as derived in a cladogram with "Osteolepiformes" and "Panderichthyidae". In this case, as already detailed above, our proposals of exaptations remain valid. Thus, any other proposal of phylogenetic relationships among terminals that conflicts with the one we are using does not alter the final results we obtained for exaptations.

Whenever new cladograms are published with different topologies and/or character optimizations that may change interpretations of exaptations and/or adaptations, a new analysis based on Blackburn's (2002) method may be done.

RESULTS AND DISCUSSION

Criticisms of "Adaptationism"

Clack (2012: 98) seems to have found the beginning of the focus on evolutionary environmental scenarios (adaptive scenarios) when she refers to the New Synthesis, in which "evolution was seen

in terms of adaptive radiation, with adaptation to certain environments more important than their phylogenetic descent in determining animal forms". It was to be expected, indeed, that most of the following work on tetrapod origin would be focused on an adaptationist reasoning.

Adaptationists seem to correlate Devonian geological and biological events with a progressive development of terrestriality. Clack (2012) summarized many proposals in this sense as well as presented a complete chapter on the "Devonian word". Although without intending to be exhaustive; Andrews et al. (2002) presented a revisionary and critical article on "adaptationism", aimed at evolutionary psychology, but also highlighting exaptation and "an exaptationism program". According to these authors, "adaptationism, as a research strategy, seeks to identify adaptations and to elucidate the specific selection pressures that forged them in an organism's evolutionary past". Although they believe that everyone agrees that organisms have adaptations, they believe that adaptationism as a research strategy has not enjoyed consensus within evolutionary

biology. In the 1970s, it became the target of criticisms by paleontologist Stephen Jay Gould and geneticist Richard Lewontin (e.g. Lewontin 1978, 1979; Gould and Lewontin 1979). Andrews et al (2002: 489), mentioning Williams (1966), consider that perhaps adaptationists use intuitive arguments for how a particular feature must have served a goal responsible for its evolution. Thus, Clack (2002: 99 – 104) was able to identify several scenarios to explain the evolution of limbs with digits, supposedly to be intimately tied to those speculating on the environment of the earliest tetrapods, and, for her, it is difficult to tease the strands apart.

Our view is closer to that of Gould and Vrba (1982: 12) that 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. In this paper, we formally propose this exaptive view for the evolution of the tetrapod limb, elaborating the methodological procedure presented initially in Blackburn (2002).

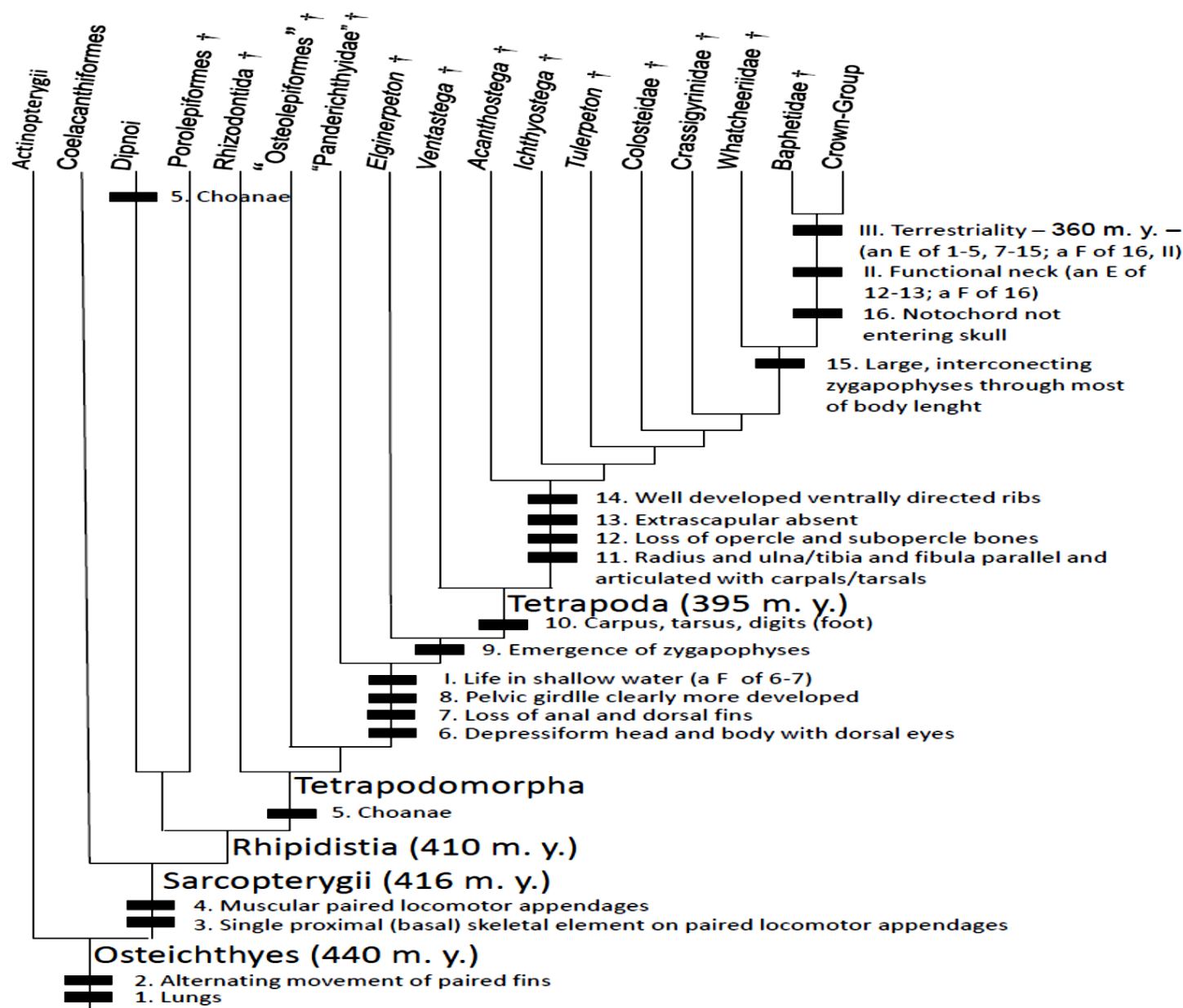


Figure 1. Cladogram of Osteichthyes with selected taxa illustrating the origin of terrestriality in the Tetrapoda. Life styles are numbered with Roman numerals (I – III) and features are numbered with Arabic numerals (1 –16). Hyphen-linked Arabic or Roman numerals in the cladogram merely mean that features emerged at that node in the cladogram, not that they are somehow connected, or ordered in any sense. Functions and Effects of features are indicated in the cladogram by "F" and "E", respectively. Minimum ages are provided for selected taxa and for the advent of

terrestriality, in millions of years ago, in parentheses or between hyphens. Internode depths in cladogram are only meant to accommodate lines for synapomorphies, effects, functions, life styles and taxon names discussed in text; no other meanings should be attributed to internode differences in length. The crown-group includes the monophyletic terrestrial Tetrapoda with living representatives (Batrachomorpha + Reptilomorpha + Lepospondyli). See text for further explanations.

The goal of adaptationism is to determine whether traits are adaptations (Andrews *et al.*, 2002: 493). To classify a trait as an adaptation is to identify its function (Andrews *et al.* 2002: 493). To identify a trait's function is to determine the specific selection pressures (if any) that were at least partially responsible for the evolution of the trait (Andrews *et al.* 2002: 493). Over the years, Gould, Lewontin, and their colleagues have argued that adaptationism is not only a flawed methodology for understanding the outcome of evolution in general, but even for understanding the specific outcome of its core concern, selection (Andrews *et al.* 2002: 493). Their arguments all involve a similar complaint: Adaptationism is built on a view of evolution that overemphasizes the power of selection and under-appreciates the constraints on selection and other evolutionary processes (Andrews *et al.* 2002: 493). They do not deny that selection is responsible for workable design. Gould (1997: 57) acknowledges that natural selection is the only known cause of eminently workable design and that adaptive design must be the product of natural selection.

Nor does Gould deny that natural selection is the primary force responsible for evolutionary change (Gould 1984). Rather, Andrews *et al.* (2002: 493) believe that the point is that factors other than selection can lead an adaptationist to misunderstand the selective processes that gave rise to the trait. We consider that the understanding of the origin of the tetrapods and of the conquest of the terrestrial environment is currently concerned with all these statements: an adaptationist view of the entire evolutionary process, from feet to life on land, is dependent on ecological-evolutionary scenarios, and the related exaptations have been in our view under-appreciated and/or underweighted. The point of disagreement between adaptationists and their critics is centered on the probative value of the evidentiary standards that adaptationists used do classify a trait as an adaptation which are no better than mere consistency between adaptationists hypotheses and evidence for function of a trait (Andrews *et al.* 2002: 493).

Biologists use the term "trait" to refer to aspects of organisms' phenotypes. But the question of what qualifies as a trait is not answered so straightforwardly. A liberal definition would allow a trait to be any aspect of the phenotype that can be discriminated on the basis of any criterion – its causes, its effects, its appearance, and so on (Andrews *et al.* 2002: 490). Behaviors are not traits because they are not constructed from genes or their products. On other words, they may be considered as effects of components of the nervous system interacting with each other (e.g. emotional experience), or effects of the nervous system interacting with the muscular-skeletal system (e.g. behaviors). However, behaviors and psychological processes are like traits in that they produce effects of their own (e.g., the movement of a hand that shapes the environment to create a tool), and these effects are often functional (Andrews *et al.* 2002: 490 – 491). Therefore, the alternate movements of paired fins found in sarcopterygians, as a behavior, may be used to test the selected or exapted nature of their paired fins.

Because all aspects of the organism's phenotype are integrated with one another, organisms are not collections of discrete objects (Gould and Lewontin 1979). Genes often have pleiotropic effects (*i.e.*, a single gene may influence many aspects of the organism's phenotype) and they often interact epistatically with each other *i.e.*, an allele at one locus may influence the phenotypic expression of an allele at another locus). Nevertheless, biologists interested in how an organism's phenotype evolved are forced to

discriminate between aspects of the phenotype (Andrews *et al.* 2002: 490). This issue will be discussed subsequently with regard to the nature of the sarcopterygian lobed fins.

Gould and Vrba (1982) were the first to define and discuss the concept of exaptation (Andrews *et al.* 2002: 491). An *exaptation* is a pre-existing trait (*i.e.*, one that has already evolved) that acquires a new beneficial effect without being modified by selection for this effect (*i.e.* it takes on a new role, but was not designed for it by selection). Because the beneficial effect did not contribute to the trait's evolution, the effect the trait is exapted to is not a function but just an *effect*: Adaptations have functions; exaptations have effects (Gould and Vrba 1982: 6). Subsequently we show how exactly most mechanical features used by tetrapods to live on land appeared long before their use on land and also before any kind of "walking" in water. Indeed, some behavioral features may have appeared before the emergence of the Sarcopterygii. For a trait to have become exapted to a new beneficial effect, it must have been acquired without being phenotypically modified by selection for the effect (Andrews *et al.* 2002: 491). As soft parts become fossilized more rarely, this seems to be the case for most of the above mentioned mechanical features, which represent the major information left for us in the fossil record. On the other hand, any co-opted effect (an exaptation) will probably not arise perfected for its new effect, but will develop secondary adaptations for the new role (Gould and Vrba 1982: 13). In principle, then, primary exaptations and secondary adaptations can be distinguished.

Features

The studied features are presented and discussed below and numbered in Figure 1 as structural features (1 – 16), together with the respective life style features (Roman numerals I –III), followed by their respective functions (F) and effects (E).

Paired appendages (3 – 4, 11, III). Sarcopterygii present muscular paired appendages, which are also provided with an elongated axial skeleton (the lobed paired fins) that, in turn, have a single element contacting the girdles. This combination does not occur in other vertebrates. Whether or not it is possible, or desirable, to split this features into more than a single synapomorphy is a matter of interest both to cladistic analysis and to evolutionary studies. Independently of the final decision (if any) about this, it is still possible to discuss the whole structure here. To elevate the body and support weight on and above land, and yet to walk freely, tetrapods use not only four feet but also skeletal struts directed downwards from the girdles: the four (two pairs of) walking limbs. Each limb has a long internal axial skeleton, which is in fact responsible for elevating the body above ground.

This feature emerged at the origin of the Sarcopterygii and was not used originally for body elevation, as it is possible to verify in *Latimeria* (Coelacanthiformes), *Neoceratodus* (Dipnoi). These taxa are living representatives of basal or relatively basal large subsets of the Sarcopterygii, and present few differences in limb structure with regard to related fossil forms.

Therefore these structures originally had other functions. These very fins are muscular, that is, have intrinsic muscles, not occurring in other vertebrates. These muscles are fundamental for walking (in water or on land) but, as living basal forms do not walk, their original function must have been different. Finally, a single bone connecting limbs to girdles is fundamental for walking. The articulations may be rounded (ball-and-socket type), and the limb

can rotate nearly in any direction; the paired fin-bases of non-sarcopterygian gnathostomes have three or more elements and the articulation is elongated, restricting particular movements necessary for walking. As living basal (in phylogenetic position) sarcopterygian forms do not walk, their original function must have been different. Although these features emerged at the origin of Sarcopterygii — and are thus considered as synapomorphies of this group — they did not evolve for terrestrial walking, as argued above, once terrestriality appeared only in much more recent and derived tetrapods. The parallel radius and ulna/tibia and fibula, articulated respectively with carpals/tarsals make the locomotor appendage stronger and more suitable for walking, but emerged in aquatic forms, such as †*Acanthostega*, and were later eventually exapted in evolution for walking. Therefore, according to Blackburn (2002), all these features (or this character complex) must be considered exaptations for the conquest of land by Tetrapoda. Several exaptations related to the humerus and femur will be treated elsewhere.

Foot: carpals, metacarpals/tarsals, metatarsals and digits (10, III). The lanceolate paired locomotor appendages present in Dipnoi, Porolepiformes and Actinistia (= Coelacanthiformes) (e.g. Clack 2012: 53, fig. 2.14) are probably less effective than the roundish paired fins of actinopterygians in terms of maneuverability. This is because the water foil area is progressively smaller — tapering towards the distal tip — and would benefit from a distal rounded expansion in terms of use both as a paddle and/or as a water foil to direct forward movement of the body. The distal change to a rounded "foot" was attained in water forms such as †*Acanthostega*, maybe by selective forces, for use underwater as foils or paddles about 395 m. y. ago (Niedzwiedzki et al. 2010: 43). The emergence of a feature with one function that is later co-opted for another function is enough to characterize it as an exaptation. This reasoning can be used to infer the exaptive nature of feet for terrestriality.

Pelvic girdle (8, III). Developed girdles are necessary for walking and the pectoral-fin girdle is already well developed in non-sarcopterygian fishes (e.g. Weitzman 1962, among many others) but the pelvic girdle remained undeveloped to the level of basal tetrapodomorphs (e.g. SHUBIN et al. 2014: 898, fig. 5) and recently it was shown that a developed pelvic girdle may be a synapomorphy for †*Elpistostegalia* ("†*Panderichthyida*") together with more derived sarcopterygians, including Tetrapoda (Shubin et al., 2014). The developed pelvic girdle is an exaptation for terrestriality, as it emerged in aquatic forms, such as †*Tiktaalik* and †*Acanthostega*, indeed in all stem "†*Elpistostegalia*". Furthermore, although Clack (2012: 438) states that adaptation of the sacral region for terrestriality (that is to say, weight bearing and transmission of limb propulsion to the vertebral column) can be seen as a gradual process, with the earliest tetrapods having little in the way of a firm connection between the girdle and the vertebral column, the statement itself shows the emergence of the feature as an exaptation for terrestriality.

Only much later in the cladogram was this structure finally adapted to function in terrestrial environments. This allows the interpretation that the earliest tetrapods had little in the way of a firm connection between girdle and vertebral column, as Clack (2012: 438) stated. †*Tiktaalik* already had a large pelvic girdle (Shubin et al., 2014), corroborating Clack's statement, itself. The whole structure only became functional on land a long time later (several steps or nodes later in the cladogram). Therefore, according to Blackburn (2002), a developed pelvic girdle must be considered as an exaptation for the conquest of land by Tetrapoda.

Column rigidity (9, 15, III). It has long been recognized that some bones may confer additional strength to the column and this may be the case of teleost inter-muscular bones, the epineurals and epipleurals (e.g. Weitzman 1962). Certainly this is the case of interlocking zygapophyses of powerful swimmers such as tunas (e.g.

Bond 1996: 73), of Tetrapoda (e.g. Romer and Parsons, 1977: 162) including †*Whatcheeria* (†*Watcheeriidae*) (Clack: 2002: 202, fig. 7.6; 2012: 274, fig. 7.7), †*Pederpes* (†*Watcheeriidae*) (Clack 2012: 271, fig. 7.5), and of the expanded ribs of †*Tiktaalik* (Shubin et al. 2014: 898, fig. 6), †*Ichthyostega* (e.g. Benton 2005: 81, fig. 4.5d), †*Eryops* (Amphibia, Temnospondyli) (e.g. Benton 2005: 100, fig. 4.17a) and possibly many others. The interlocking of zygapophyses (as well as presumably the expanded ribs and the not-interlocking intermuscular bones of teleosts) prevents excessive rotation of vertebrae on each other (Bond 1996: 73) and is obviously useful not only for terrestrial tetrapods, but also for species with completely different life styles such as tunas. Therefore, interlocking zygapophyses may have been useful for the clearly fully aquatic colosteids (Clack 2012: 281), as well as the presumably aquatic watcheeriids, which had paddle-shaped limbs (Clack 2002: 202 – 203).

Because limbs are not paddle-shaped in †*Pederpes* (Clack 2012: 274), a possibly non-monophyletic nature of the family is indicated (Clack 2012: 270). Thus, adaptively correlating the evolution of interlocking pre- and post-zygapophyses to the conquest of the terrestrial habitat is not possible and the same can be stated for the expanded interlocking ribs. Following the method of Blackburn (2002), it is realized that interlocking zygapophyses emerged prior to the conquest of land by Tetrapoda and must be considered an exaptation for terrestriality in Tetrapoda.

Lungs (1, III). Some authors consider the presence of lungs as a synapomorphy for Osteichthyes (e.g. Pough et al. 2005). We follow them in this regard, but the following statements of Romer (1966: 33) are noteworthy in this regard: In some specimens of antiarchs (†*Placodermi*), traces of soft internal structures have been preserved and of great interest are distinct traces of a pair of large sacs connected with the floor of the pharynx. These can be interpreted only as lungs, according to Romer (1966). Such structure, Romer believes, were present in early bony fishes of all sorts, but they are absent in sharks and have been thought to be a relatively late development in fishes. The evidence from the antiarchs suggests, however, that they may have arisen at a much lower stage in vertebrate evolution than had been suspected (Romer 1966: 33). Benton (2005: 58) also states that one specimen of †*Bothriolepis* (†*Placodermi*) shows possible evidence for lungs preserved inside the dorsal armour... and it may have been able to survive stagnant ponds by breathing air. Therefore, following Blackburn (2002), lungs must be considered an exaptation for the conquest of land by Tetrapoda.

Choanae (5, III). These are the paired internal openings for the entering of air to the lungs. According to Janvier (2004) they are homologous to the posterior nostrils present on each side of snout in coelacanth and teleosts, which have independently migrated downward and finally reached the inner side of mouth in Dipnoi and Tetrapodomorpha. They thus must be considered exaptations for the conquest of land by Tetrapoda (Blackburn 2002). Additionally, Clack (2012: 90 – 191) states that the external nostril of †*Acanthostega* is small enough to suggest that it was not used for the intake of air in breathing, being used as in basal fishlike species, reinforcing the proposition that this feature was an exaptation for terrestriality. Clack (2012: 388) considers that the external nostril may have been enlarged rapidly in the Carboniferous forms. Therefore, the use for respiratory purposes of the internal nostril (the choana, obviously connected to the external one) should be interpreted as an exaptation for terrestriality, instead of an adaptation.

Alternating movement of paired locomotor appendages (2, III). The emergence of lungs in Osteichthyes and its derivative swimming bladder in teleosts conferred these animals with buoyancy and, therefore, with the need to stabilize the body during slow movements (because in this situation, the paired fins do not work so well as hydrofoils). Thus the need for alternate movement of paired

fins may be explained. Considering the lung-less or bladder-less chimaeras and manta rays as good out-groups to ordinate the character direction, the plesiomorphic condition would be the coordinated movements of paired fins up and down (e.g. Lagler et al. 1962: 191, fig. 6.2.d), both in ordinary movements or foraging. Therefore, the observed behavioral of alternating paired fins in non-walking sarcopterygians is herein considered only a by-product of the emergence of the lungs/gas bladder. That is, a buoyancy organ cancels body density relative to water.

Therefore the necessity arises for equilibrium through slow moving. If the fins moved disorderly, the body would move astatically in the water. Another way to illustrate the situation: A man in a canoe will use paddles alternately in order to go evenly straight ahead (if one is more used than the other, the direction of the movement turns — if both paddles are used at the same time, the movement ahead is of the stop-and-go kind, not constantly ahead, so that the alternating method of moving in a canoe is the most even possible, the same working for aquatic vertebrates). The same is necessary for a fish or fish-like animal using paired fins to move (using the caudal fin for fast swimming usually implies another kind of use of the paired fins or appendages — as water foils). In fact, even actinopterygians alternate the position of pectoral fins, when they move slowly. We consider this movement simply a by-product of the emergence of the lungs/gas bladder. Obviously, occasionally any of the living paired-limbed animals can use their paired limbs together in the same direction at the same time, like humans during breast-stroke swimming or jumping in a basketball game, galloping mammals or even as a permanent way to run, as kangaroos do, but we consider the original movement as being the alternating one, as explained above.

Therefore, the trackways of *manus* and *pes* prints found in Poland by Niedzwiedzki et al. (2010) was predictably of the alternating pattern, as encountered by these authors. They move in the very same way as teleost ogocephalid batfishes (actinopterygian fishes) do (the paired fins move independently in a diagonal sequence gait according to Rade (2013) and not as an adaptation for walking previously to the conquest of land. Thus, the “dog-like” movements of paired fins of *Latimeria*, *Lepidosiren* (Dipnoi) (e.g. Janvier 1996: 74) and the trackways from Poland are here considered as homologous to the alternating movements of actinopterygians in slow maneuvering and may be an osteichthyian feature, or even a more ancient behavior. Therefore, the alternating movement of paired appendages is considered an exaptation for the conquest of land, following the method initially proposed by Blackburn (2002).

Functional neck (II, 12 – 13, 16, III). The neck is advantageous for land vertebrates as it permits the head to rotate, making it easier to feed and to seek around without affecting locomotion (Hildebrand 1982: 57). The development of a functional neck apparently occurred through several distinct steps. The loss of opercular bones permitted an up and down bending of the head more freely, an advantage that is unknown for aquatic vertebrates, which are benefitted by suction (and/or other kinds of uses of the prehensile jaws [e.g. Lauder and Liem 1983: 158 – 159]) alternative to *stricto sensu* biting. A disconnection of the pectoral girdle relative to head is necessary to free the head from the body. It is not easy to discuss favorable terms of evolutionary advantages for this condition, as a functional neck was not yet developed at this moment in the evolution of the Tetrapoda. The notochord was inserted inside the skull, preventing a free movement of the head. Finally, but not less important, was the withdrawal of the notochord from inside the skull, again to free the head from the body. According to Clack (2012: 207) “the notochord is bendable, but springs naturally back to a straight line unless muscular effort is exerted.

The earliest tetrapods probably had little control over the attitude of the head and probably had to expend considerable energy to move it sideways or up and down”. Therefore, to make the neck a functional feature in the way land tetrapods use it, all of these conditions should be present at the same time, but the cladogram shows that they appeared successively and independently in evolution (in any case, the withdraw of the notochord from the skull was a much later occurrence). According to the cladogram presented herein, only the withdrawal of the notochord from the skull occurred together with a functional neck and selective forces can only be suggested at this moment, from the perspective of the method of Blackburn (2002). In case a more basal position is preferred for the baphetids (e.g. Laurin 2010: 162, fig. 7.1), the reasoning continues to be the same and indeed in this case a selectionist explanation is reinforced as the same feature would be emerging independently twice. It is worth noting that in †*Tikkaalik*, the opercular series of bones appear to be completely missing, and the same may be the case for the extra-scapular series (Clack 2012: 196). That is, they may be a synapomorphy for the Tetrapoda plus some more basal taxa than those indicated in Figure 1.

Depressiform head and body (6, I). A body form flattened from top to bottom is usually called “depressed” (e.g. Lagler et al. 1962: 53) and, less often, “depressiform” (Bond 1996: 17). Such are the cases of skates and their relatives, angel sharks, toad fish, angler fishes, batfishes as well as manta rays, for example. Such a body form suits the fish for life on the bottom, for living under the water surface, and for flight-like swimming above the bottom. “†Panderichthyidae” or “†Elpistostegidae” (possibly a paraphyletic assemblage of taxa progressively closer to Tetrapoda) and basal tetrapods are depressiform, with dorsal eyes, and likely lived on the shore or edge of lakes and/or rivers, avoiding deep areas because of the need to breath air into their lungs. In the cladogram it is possible to regard this body form as selected for life in shallow waters, being likely an adaptation instead of an exaptation for this kind of habitat, following Blackburn’s (2002) method. The depressiform shape of the skull can hardly be correlated with selective pressures for gaining ground, because amongst the taxa known from even the earliest part of the Carboniferous (such as †*Pederpes* and †*Whatcheeria*), we find skulls deeper than broad, or conspicuously deep in †*Crassigyrinus* (†*Crassigyrinidae*) (Clack 2012: 388).

Loss of anal and dorsal fins (7, I, III). Dorsal and anal fins are median appendages usually regarded as horizontally directed for fast movements in water. For a bottom living species, the absence of one or both of these fins may not be too disadvantageous if the life style is ambush-like. Supposedly, species living in very shallow waters could benefit from the absence of these fins by reducing drag from both the surface of the both bottom and of the water surface. This may have been the case of panderichthyids and basal tetrapods, being adaptive instead of exaptive after the use of Blackburn’s (2002) method. On the other hand, the absence of these median fins should be considered exaptations for terrestriality, following Blackburn’s (2002) method. These exaptations have the effect of diminishing water loss by evaporation on dry land because, in this environment, flaps would permit a better evaporative effect through the thin air.

Ribs developed and ventrally directed (14). Because Carboniferous lungfishes possess long and curved ribs, almost enclosing the trunk and yet use buccal pumping for air intake, it appears that the ribs were more likely to have been involved in locomotion (Clack 2012: 429). These characters of ribs appeared in the cladogram much before terrestriality and Blackburn’s (2002) procedure indicates the exaptive nature of these novelties.

Life Style

The "functions" of features (or "effects" of exaptations) seem to be better referred to as "life styles" in two of three cases, in the following text. That is, life styles represent the way the animals live or use their herein studied anatomical attributes or features to deal with their environment. Therefore, the life style is assumed to exist as a function (or effect) of particular features. Thus, in Figure 1, life styles are indicated with Roman numerals (I – III) in opposition to features, which are enumerated (1 through 16). Functions and Effects of features are indicated in the cladogram by "F" and "E", respectively.

Life in shallow waters (I, a Function of 6 – 7). Apparently, several tetrapodomorph representatives underwent a trend toward a role as ambush predators in shallow waters (Clack, 2012: 84 – 85), maybe correlated to the actinopterygian prey diversification through the Devonian. †*Elpistostege* (†"Panderichthyidae"), †*Tiktaalik* (†"Panderichthyidae") and †*Panderichthys* (†"Panderichthyidae") come from estuarine localities (Daeschler et al. 2006); †*Panderichthys*, †*Obruchevichthys* (†Elginerpetonidae: †Ichthyostegalia) and †*Ventastega* (†Ichthyostegalia) findings are interpreted as marginal localities at the edge of a large marine basin (e.g. Luksevics and Zupins 2004). Clack (2012: 185) considers that many basal tetrapods, such as †*Tulerpeton* (†Tulerpetonidae: †Ichthyostegalia), †*Ventastega*, †*Hynierpeton* (†Ichthyostegalia: †Ichthyostegalia), †*Densignathus* (†Ichthyostegalia), †*Metaxygnathus* (†Ichthyostegalia), †*Sinostega* (†Ichthyostegalia), and †*Jakubsonia* (†Ichthyostegalia) lived at the water margins of lakes, deltas or coasts. Depressiform body shape and loss of the dorsal and anal fins emerged together with this life style and may be considered possible adaptations for it.

Terrestriality (III, an Effect of 1 – 5, 7 – 15; I – II, a Function of 16). Walking with limbs, breathing air and feeding on land is herein summarized as "terrestriality", to differentiate this life style from the crawling and foraging on land, but not truly walking and certainly not-breathing of some teleost fishes such as *Periophthalmus* (Actinopterygii). Walking (in opposition to crawling), in terrestrial vertebrates is accomplished with the use of columnar paired walking appendages. These have intrinsic musculature, capable of alternating movements, and not only feet with digits, which, in turn, are also essential at least in non-specialized forms. It is necessary to highlight the need of columnar appendages because many researchers seem to neglect the need of this feature for the feet to be able to step on dry land. This differentiates walking from crawling (possible for non-sarcopterygian vertebrates). It is noteworthy that columnar (strut-like) paired walking appendages could emerge in Sarcopterygii by means of a single proximal element because its emergence in the taxon is relatively ancient, and because of its parallel position in relation to the more distal radius and ulna/tibia and fibula.

Furthermore, the columnar paired appendages could not be used for walking if its connection with girdles were not somehow rounded, that is, if there was more than a single proximal skeletal element on each of the paired walking appendages. If elongated, this connection would limit limb movement to the extent that walking could hardly be achieved. The lobe-fins, by contrast, attach their paired fins by a single radial to the shoulder girdle and form the main axis of the fin by stringing the rest of the radials in a chain growing outward from the body and having a narrow, flexible base that allows it to rotate as well as be raised and lowered (Clack 2002: 17). Clearly, this character complex (muscular columnar appendage with a single proximal skeletal element and two subsequent elements) arose a single time, around 416 m. y. ago, in the beginning of Devonian (Zhu and Yu 2009). Therefore, walking appendages arose prior to all the Devonian geological alterations about 56 m. y. before the conquest of land, if we consider the boundary of

Devonian/Carboniferous as the beginning of terrestriality: a much too long a time to expect microevolution to be responsible for this "task".

Although air breathing could occur without internal nares or choanae, this feature diminished moisture loss to the environment to an extent that permitted the free conquest of land and full terrestriality. However, choanae emerged at about the time of origin of the Rhipidistia, not at the time of the origin of terrestriality. Zygopophyses are of fundamental importance to avoid the vertebral column from collapsing during dry land walking, but emerged prior to terrestriality. The loss of dorsal and anal fins is advantageous for a land vertebrate because these structures represent widened surfaces whose moistness would harm the animal because of unwanted water loss as well as possible damaging during walks through the woods. However, these losses emerged before the emergence of feet and much earlier than terrestriality.

Finally, but often neglected, is the need for a functional neck for feeding, as foraging may be the more striking advantage for a land vertebrate in comparison to aquatic forms. The closer relatives of terrestrial vertebrates were large predatory aquatic animals that had little to fear in their environment and reproduction apparently continued in water. Simply staying outside of the water, walking around, has no benefit without feeding, as reproduction could be achieved on land by other means (and in fact continued in water for a long time, apparently). The functional neck was discussed in detail above. Finally, the shallow water habitat that apparently was the ecological niche of "†Elpistostegidae" and the first tetrapods benefitted with the emergence of terrestriality because it is at first easier to colonize ground from shallow water than from deep water. Thus adaptation to shallow or marginal waters is better interpreted as an exaptation for terrestriality.

Because fourteen of the fifteen studied features needed for terrestriality emerged along osteichthyan evolution much earlier than terrestriality, it became very clear that they are exaptations for the conquest of land by vertebrates, after the use of Blackburn's (2002) insight.

Clack (2012: 138) considers that the origin of tetrapods lies on a three-part issue: origin of limbs with digits, origin of walking, and origin of terrestriality. However, we consider that the focus on the foot (the feature that supports the digits) is linked to the idea of microevolution and lacks deepness to explain the whole problem, which is perceived only by analyzing the paired walking appendages in their entirety, as muscular struts with articulated distal bases (the feet), as was discussed in detail previously in text, as well as all the other fundamental features needed on land, as shown in Figure 1 and discussed in detail in the text.

When the focus is reduced to the suggested three parts, it gives credit to microevolution as the process involved, when in fact it is not. Indeed, the "limbs with digits" arose abruptly (as far as the paleontological record permits us to say) for aquatic locomotion and is clearly part of a macroevolutionary process, being an exaptation. Furthermore, Clack (2012: 138) states that the plethora of reasons for why modern fish leave the water demonstrates how difficult it would be to cite any one as the main stimulus for the tetrapods to have done so. We consider this reasoning as misleading, because these animals do not present columnar, strut-like, paired, walking appendages and many other features for real locomotion and terrestriality, namely features 1, 3 – 5, 7 – 16, II, exactly because there was no microevolutionary process working towards land. The process represents, rather, a unique, chance, macroevolutionary event.

The number of fossil features known currently, as well as those not fossilized, but somehow represented in living forms is large. It is not the aim of this paper to make an exhaustive

exploration of these features. However, even if literally all the features we did not study could be shown by the method of Blackburn (2002) to be adaptations for terrestriality, all these processes should still be interpreted as basically chance, macroevolutionary events. Without the previous emergence of the exaptations we presented herein, the final adaptive part of the emergence of terrestriality could not have happened.

CONCLUSION

We used a cladogram for plotting and organizing the emergence of synapomorphies and, independently, their functions and/or effects. For the features accessible to us and subjected to the applied method, we have been able to clearly discriminate exaptations for terrestriality and to consistently point out a possible single adaptation, in our analysis, for life on the ground.

Our results corroborate Gould's (1991) idea of feet as representing an exaptation for terrestriality as well as Triques and Christoffersen's (2009) proposal that the conquest of land by Tetrapoda should be mainly regarded as a chance event attributed to exaptations and Clack's (2002: 2) affirmation that much of the evolutionary changes leading to the ground occurred because of happenstance — being at the right place at the right time — rather than being the result of a directed process. That is, 13 of 15 studied anatomical features (all but depressed body and withdrawal of the notochord from the skull) and two behavioral features (life in shallow waters and alternating movement of paired fins) were exapted to terrestriality, instead of adapted to it. Thus, adaptationist hypotheses regarding terrestriality for the vertebrates should be carefully reconsidered, avoiding mere consistency and always using a cladistic or phylogenetic framework for their foundation.

Therefore, arguments derived from ecological adaptive scenarios (for example, increasing or decreasing O₂, CO₂ and other similar considerations), may be fundamental in a microevolutionary perspective, but are not needed for macroevolutionary reasoning. In a sense, ecological adaptive scenarios seem to be misleading because they only make sense in a microevolutionary context and create a tautology that misdirects a researcher's understanding of evolution. Clearly, the presence of land plants and arthropods prior to vertebrate progress towards land were necessary, but these events had already occurred much earlier, since Silurian times. Therefore it is difficult to connect them to the evolutionary process used predominantly by vertebrates for gaining ground.

The major significance of the concept of exaptation, when applied to the transition of vertebrates from water to land with the method of Blackburn (2002), is that it permits us conclude with clearness and discernment that terrestriality in vertebrates probably did not occur as the major result of adaptations to environmental conditions in the geological framework. Rather, terrestriality became possible after the independent evolution of a set of apomorphies that originated through geologic time but were unrelated to terrestrial or aquatic environmental variations. In other words, these apomorphies appeared by chance in relation to the terrestrial environment. Finally, when this particular set of apomorphies became sufficient for the successful conquest of land, a major transition to a new environment became possible, with a single adaptation for land (or with adaptations being numerically and qualitatively much more restricted for this transition than previously suspected).

Without the concept of exaptation, reasoning becomes restricted to the straitjacket of adaptation, failing to be convincingly justified even among evolutionary adaptationists. Such explanatory failings can now be convincingly attributed to the fact that the evolutionary process involved was not adaptive, but preponderantly exaptive. "Being at the right place at the right time", as perceptively

noted by Clack (2002), was fundamental for a single lineage of vertebrates to successfully walk and forage on land, dozens of millions of years after the necessary traits had evolved in water for entirely different reasons than for living on land.

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