Zootaxa 3750 (3): 265–276
www.mapress.com/zootaxa/

Editorial

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3750.3.6
http://zoobank.org/urn:lsid:zoobank.org:pub:0B8E53D4-9832-4672-9180-CE979AEBDA76

The salmon, the lungfish (or the coelacanth) and the cow: a revival?

FLÁVIO A. BOCKMANN[1,3], MARCELO R. DE CARVALHO[2] & MURILO DE CARVALHO[2]

[1] *Dept. Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo. Av. dos Bandeirantes 3900, 14040-901 Ribeirão Preto, SP. Brazil. E-mail: fabockmann@ffclrp.usp.br*

[2] *Dept. Zoologia, Instituto de Biociências, Universidade de São Paulo. R. Matão 14, Travessa 14, no. 101, 05508-900 São Paulo, SP. Brazil. E-mails: mrcarvalho@ib.usp.br (MRC); mcarvalho79@gmail.com (MC)*

[3] *Programa de Pós-Graduação em Biologia Comparada, FFCLRP, Universidade de São Paul. Av. dos Bandeirantes 3900, 14040-901 Ribeirão Preto, SP. Brazil.*

In the late 1970s, intense and sometimes acrimonious discussions between the recently established phylogeneticists/cladists and the proponents of the long-standing ‘gradistic’ school of systematics transcended specialized periodicals to reach a significantly wider audience through the journal *Nature* (Halstead, 1978, 1981; Gardiner *et al.*, 1979; Halstead *et al.*, 1979). As is well known, cladistis ‘won’ the debate by showing convincingly that mere similarity or ‘adaptive levels’ were not decisive measures to establish kinship. The essay ‘The salmon, the lungfish and the cow: a reply’ by Gardiner *et al.* (1979) epitomized that debate, deliberating to a wider audience the foundations of the cladistic paradigm, advocating that shared derived characters (homologies) support a sister-group relationship between the lungfish and cow exclusive of the salmon (see also Rosen *et al.*, 1981; Forey *et al.*, 1991).

It is therefore noteworthy that more than 30 years later the pages of the same journal recently featured a contribution in which the foremost conclusion is that the lungfish is ‘the closest living fish relative of tetrapods’ (Amemiya *et al.*, 2013). News that coelacanths and lungfishes are closer to humans and other mammals than they are to any ray-finned fishes, such as the tuna and salmon, and that the closest living ‘fish’ relative of tetrapods is the lungfish, echoed with great fanfare in the international media (*e.g.* Morelle, 2013; Morin, 2013; Wade, 2013; Woolston & Nature Magazine, 2013) obscuring other significant contributions of Amemiya *et al.*'s study. For example, in describing the entire genome of the African coelacanth, they filled an important gap in understanding evolutionary changes (including gene losses) underscoring adaptations to live on land by detecting which gene changes were likely involved in immunity, nitrogen excretion and development of the fins, tail, ear, brain, and olfaction. Amemiya *et al.* (2013) were further able to identify that protein-coding genes in coelacanths are evolving more slowly than those of tetrapods and dipnoans (while having, in contrast, a wide variety of transposable elements that resembles many other vertebrate genomes), and that changes in regulatory elements are closely associated with the transition to a terrestrial environment. Another contribution was to compare whole genomes of related species to uncover thousands of conserved, non-coding regulatory elements. Their findings will certainly provide new directions for research on genomic mechanisms involved in vertebrate evolution.

Nevertheless, the phylogenetic approach of Amemiya *et al.* (2013) has caused us some concern by not recognizing the irreplaceable morphological component (especially paleontological, in the present case) necessary to properly elucidate the phylogeny and evolution of ancient lineages. We concede that some of the blame may be attributed to the media, which frequently distorts or paints with vivid colors topics of scientific research that are more aligned with their business interests, but some tendencies in Amemiya *et al*. (2013) appear to be common in large molecular studies, requiring a critical appraisal.

The first issue is the omission of the overwhelming morphological evidence favoring the lungfish-tetrapod sister-group relationship, even though hundreds of published pages exist just in the ‘cladistic era’ expounding this evidence (*e.g.* Løvtrup, 1977; Miles, 1977; Wiley, 1979; Forey, 1980, 1986; Rosen *et al.*, 1981; Maisey, 1986; Panchen & Smithson, 1987; Benton, 1990; Ahlberg, 1991; Cloutier & Ahlberg, 1996; Janvier, 1996; Zhu *et al.*, 2001, 2009, 2010; Zhu & Yu, 2002; Clack, 2012). This well-known anatomical evidence is barely mentioned in their paper or in its 135 pages of supplementary files. Only two specialized accounts dealing with morphology are

Accepted by M. Ebach: 8 Nov. 2013; published: 19 Dec. 2013

mentioned at all, but these are cited just to support particular assumptions: one for the inferred morphological stasis of coelacanths and one concerning the phylogenetic position of coelacanths and dipnoans (Zhu *et al.*, 2012 and Schultze & Trueb, 1991, respectively). Morphology is clearly not the focus of their study, but ideas about basal sarcopterygian relationships can hardly avoid even a cursory glance at the evolutionary information it provides.

A second point concerns Amemiya *et al.*'s (2013) portrayal of the affinities between coelacanths, lungfishes, and tetrapods as a dilemma still awaiting a better-supported outcome. This may be the case in terms of molecular phylogenetic studies but the morphological evolutionary scenario is more consistent—lungfishes are regularly portrayed as the sister-group of tetrapods. Within the cladistic paradigm, the contrasting hypothesis that *Latimeria*, or Actinistia, is closer to tetrapods than are lungfishes was left implicit by Miles (1975) and Fritzsch (1987), and presented in a more assertive manner by Gorr *et al.* (1991) and Schultze (1986), while Northcutt (1986) suggested that actinistians are the sister group of lungfishes. However, these proposals were abandoned as soon as all putative homologies supporting them were reexamined and reinterpreted and new characters and taxa were incorporated into the analyses, as prescribed by the primer of good cladistic practice (Meyer & Wilson, 1991; Stock & Swofford, 1991; Platt, 1994; Cloutier & Ahlberg, 1996; Platt *et al.*, 2004, and many other references cited here).

Unsolved conflicts on sarcopterygian relationships may exist, no doubt, such as when analyses are built from different sources of characters and employ a distinct taxonomic sampling and methodological perspective. But in phylogenetic studies based on morphology this situation is rare because researchers are constantly reviewing the entire body of available evidence and, when appropriate, reinterpreting homologies and adding new characters and taxa. As a result the most commonly accepted hypothesis is, in general, the latest one to appear, which is also usually the most complete in terms of characters and taxa. On the other hand, conflicts emerge when morphological phylogenies are compared to molecular phylogenies, due to difficulties in reconciling different sources of characters, or even among molecular studies when they are based on different genes. Symptomatically, some molecular analyses suggest that dipnoans are the closest living relatives of land vertebrates (Meyer & Wilson, 1990, 1991; Meyer & Dolven, 1992; Hedges *et al.*, 1993; Brinkmann *et al.*, 2004), others contend that coelacanths are closer to tetrapods (*e.g.* Gorr *et al.*, 1991), whereas others indicate a sister-group relationship between lungfishes and coelacanths (*e.g.* Yokobori *et al.*, 1994; Blair & Hedges, 2005).

More importantly, morphology provides numerous insights unobtainable in the mega-phylogenomic analysis of Amemiya *et al.* (2013). The mapping of genomic changes associated with the water-to-land transition in vertebrates exemplifies this. Amemiya *et al.* (2013) stated that because *Latimeria chalumnae* is the species with a completely sequenced genome closest to our most recent aquatic ancestor, it provides a unique opportunity to identify genomic changes that were associated with the successful adaptation of vertebrates to the terrestrial environment. Even though lungfishes are considered more closely related to tetrapods than the coelacanth, living lungfish species have huge genomes that are presently computationally cumbersome (Gregory, 2005 and references therein). But Amemiya *et al.* (2013) analyzed few living sarcopterygians—the marine actinistian *Latimeria*, which inhabits relatively deep volcanic slopes (Fricke *et al.*, 2000; Hissmann *et al.*, 2006), the obligatory air-breather *Protopterus*, a dipnoan present in shallow, stagnant continental waters of Africa (Budget, 1901), and two species of frogs (as representatives of basal tetrapods). Clearly, only living species can provide high quality and complete genetic material, but interspersed between them are many extinct lineages displaying distinct morphologies, ecologies, behaviors, and habitats. Although not attainable by direct observation, information on the ecology, habitat, locomotion, respiration, and feeding habits of extinct sarcopterygian fishes may be inferred from an array of anatomical data including body form, axial and appendicular skeletons (form and position of fins), mouth position, size, dentition, jaw suspension, position of eyes, opercular arrangement, gill arches, and hypobranchial apparatus (*e.g.* Thomson, 1969; Clement & Long, 2010). In other words, our understanding of this specific evolutionary transition benefits from knowledge of living sarcopterygians but mostly relies on the detailed morphological study of numerous 'intermediate' fossils. These studies, capably summarized by Clack (2012), reveal the gradual sequence of acquisition of morphological features that aided the transition from water to land, such as the dorsal elongation of the pubis, the development of a 'neck' and a stouter, more imbricated rib cage, specific morphology of zeugo- and autopodia, flattening of the head, among numerous other featured. One could also cite the analogous situation concerning the evolution of the mammalian middle ear, which involved stepwise transformations of the maxillary and hyomandibular arches from stem gnathostomes to basal mammaliaforms, and all superbly revealed not only in ontogeny but also through the discovery and detailed study of many 'intermediate' fossils (*e.g.* Rougier & White, 2006; Meng *et al.*, 2011).

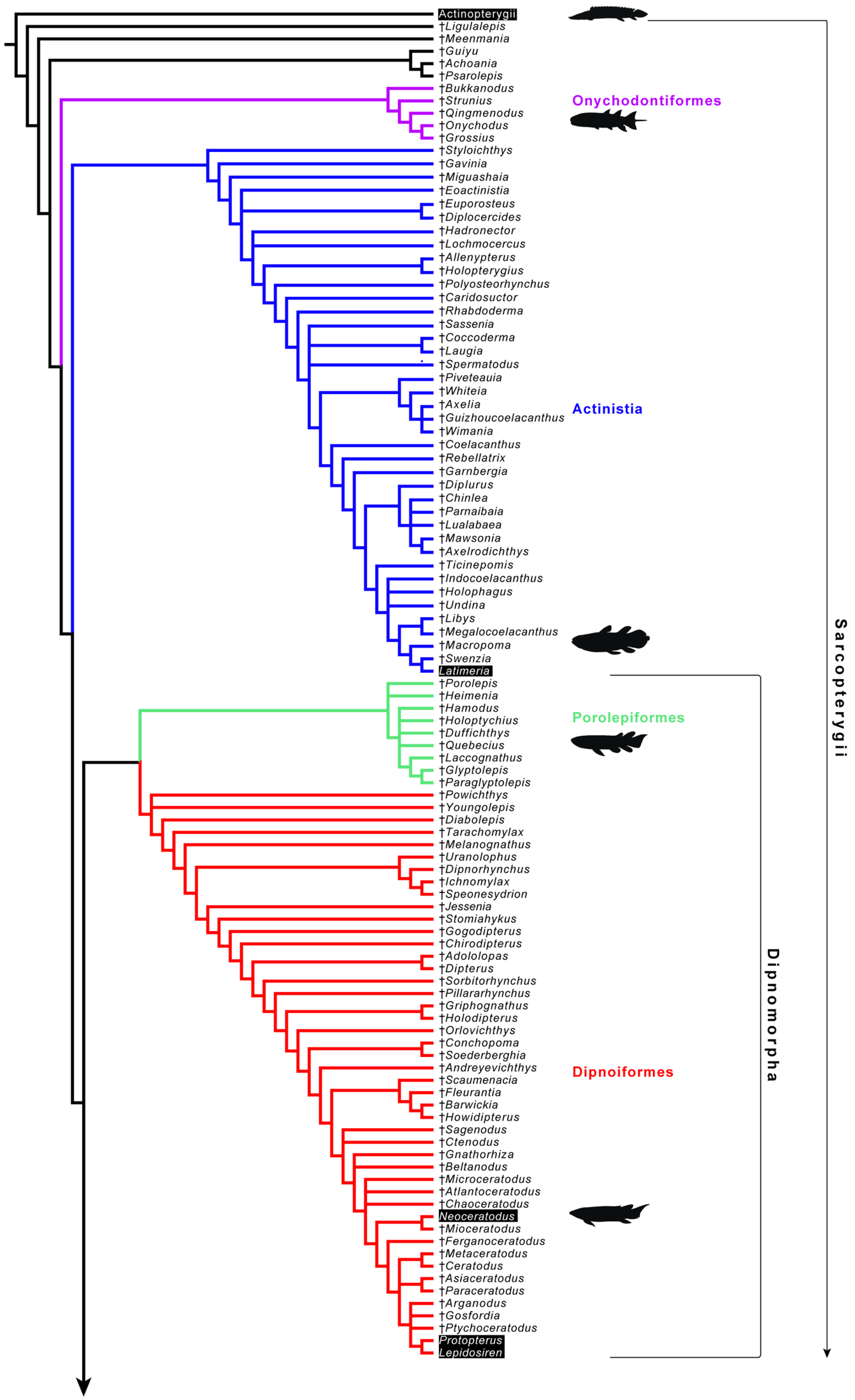

FIGURE 1. (continued on next page)

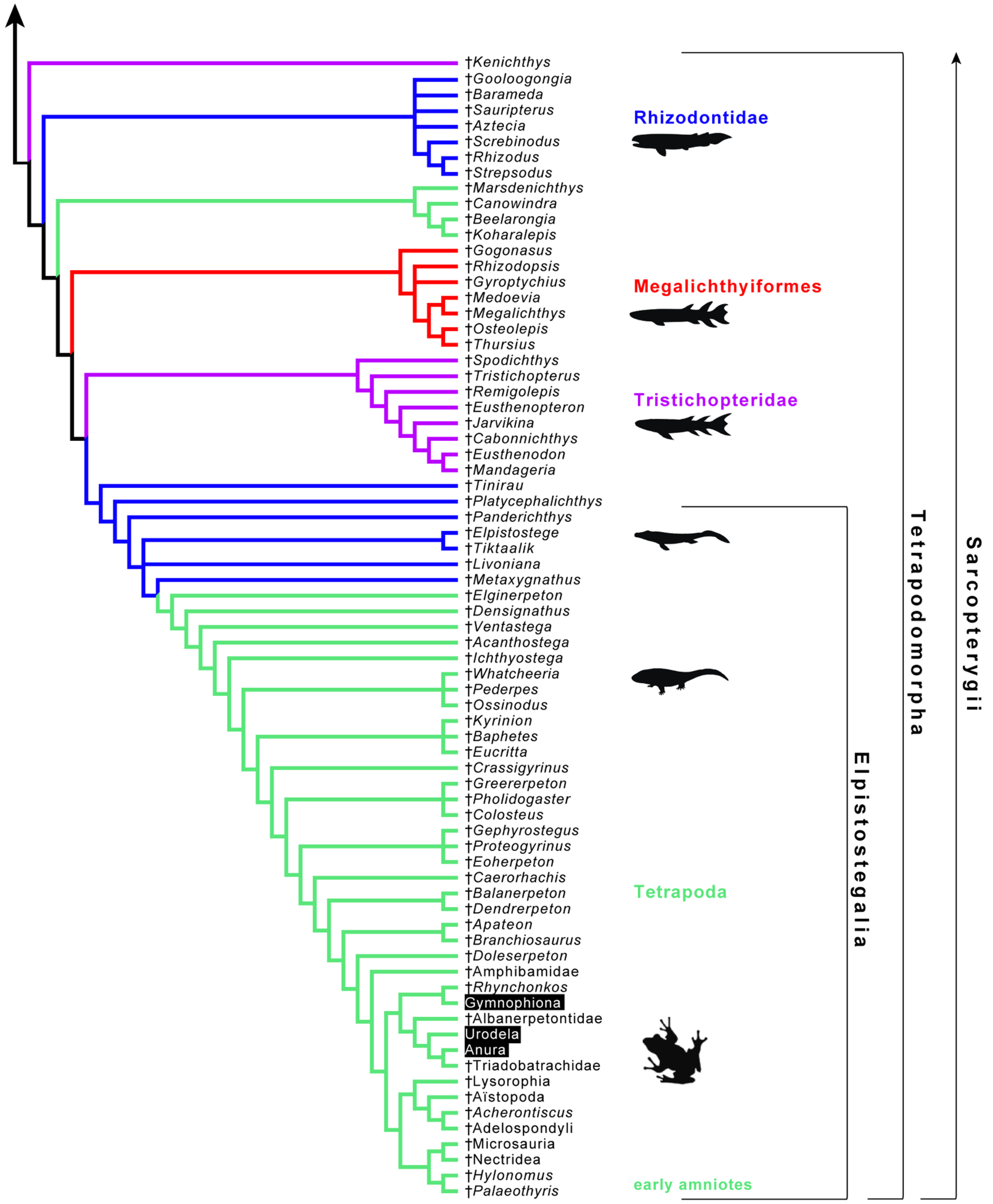

FIGURE 1. Cladogram depicting phylogenetic relationships among basal sarcopterygians. Phylogenetic information was mainly compiled from: Cloutier & Ahlberg (1996) and Zhu *et al.* (2009, 2012) for Sarcopterygii; Zhu *et al.* (2009) for †*Achoania*, †*Ligulalepis*, †*Meenmania*, †*Guiyu*, and †*Psarolepis*; Lu & Zhu (2010) for Onychodontiformes; Friedman (2007b), Dutel *et al.* (2012), and Zhu *et al.* (2012) for Actinistia; Ahlberg (1991), Ahlberg *et al.* (2006), Cione *et al.* (2007), Cavin *et al.* (2007), Friedman (2007a), Agnolin (2010), and Clement & Long (2010) for †*Diabolepis*, †*Powichthys*, †*Youngolepis*, and Dipnoi; Cloutier & Ahlberg (1996) and Clement (2001) for Porolepiformes; Ahlberg *et al.* (2003) and Swartz *et al.* (2012) for Tetrapodomorpha [despite Holland (2013) having proposed important changes in tetrapodomorph phylogeny, his work was not here considered because many dipnoan terminals were lacking]; Holland *et al.* (2007) for Rhizodontidae; Ahlberg *et al.* (2008) for Elpistostegalia; and Carroll (2007) for Tetrapoda. The cladogram was built with the software Mesquite, version 2.75 (Maddison & Maddison, 2011). Names of terminals that have extant members are marked in black.

To demonstrate this point we present in Figure 1 a rather complete summary to genus level of the current state of knowledge of basal sarcopterygian relationships. Represented here are only those fossils that have their positions assigned with some precision; taxa represented only by heavily fragmented specimens were excluded. For the sake of simplification, genera admittedly polyphyletic or whose monophyly is unsubstantiated (*e.g.* the porolepiforms †*Holoptychius* and †*Porolepis*, and the dipnoans †*Chirodipterus* and †*Griphognathus*; see Clement, 2001; Friedman, 2007a; Downs *et al.*, 2013) were represented as single terminals (the inclusion of other species of these genera would add several new branches, substantially increasing the complexity of the tree). Living amphibians were represented by its three orders (Anura, Gymnophiona, and Urodela), despite that only two species of frogs were included by Amemiya *et al.* (2013). Of the 178 terminal taxa of this cladogram (Figure 1), living sarcopterygians (the coelacanth *Latimeria*, the dipnoans *Lepidosiren*, *Neoceratodus*, and *Protopterus*, the lissamphibians Anura, Urodela, and Gymnophiona, and Amniota) represent only a tiny fraction of the mostly extinct cladal diversity of the Sarcopterygii. In a very simplified perspective, the actinistian *Latimeria* is separated from the dipnoan *Protopterus* by more than 46 cladogenetic events, while the oldest common ancestor of Dipnomorpha (Dipnoi + Porolepiformes) is distant from the nearest common ancestor of living amphibians by at least 29 cladal diversification events.

The ability to breathe air is a milestone in the occupation of the terrestrial environment. But while the ability of dipnoans to breath air has been in existence in some capacity since the Middle Devonian (Clement & Long, 2010), mandatory air ventilation, accompanied by a number of physiological and anatomical modifications, as seen in the extant dipnoans *Lepidosiren* and *Protopterus*, is likely to have appeared much later. Based primarily on broader comparisons including fossils, the similarities in air-breathing between Dipnoi and Tetrapoda were, consequently, rejected as synapomorphies and deemed non-homologous (*cf.* Cloutier & Ahlberg, 1996; Zhu *et al*., 2009). In this sense, despite agreeing with the hypothesis based on morphology, strong support for the sister-group relationship between *Protopterus* and tetrapods obtained by Amemiya *et al.*'s (2013) study may have been artificially inflated by molecular homoplasies associated with anatomical and physiological adaptations to their mandatory air-breathing behaviors, a problem that could be minimized with the inclusion of the Australian lungfish *Neoceratodus*, which does not share those modifications to the same degree.

Moreover, some of the most basal members of Actinopterygii—the counterpart of Sarcopterygii, namely *Polypterus*, *Amia*, and *Lepisosteus*—have a bimodal respiration pattern, undergoing facultative air breathing by using their gas bladders as sites for gas exchange in the same way as living sarcopterygian fishes (Magid, 1966, 1967; Johansen *et al.*, 1970; Rahn *et al.*, 1971; Deyst & Liem, 1985; Graham, 1997). Many representatives of basal teleostean lineages, such as juveniles of the elopomorph *Megalops* (Megalopidae), and the osteoglossomorphs *Arapaima* (Arapaimidae), *Heterotis* (Arapaimidae), *Notopterus* (Notopteridae), and *Pantodon* (Pantodontidae), are also obligatory air breathers using highly vascularized and subdivided gas bladders (Babcock, 1951; Dehadrai, 1962; Poll & Nysten, 1962; Schwartz, 1969; Greenwood & Liem, 1984; Merrick & Schmida, 1984; Graham, 1997). Therefore, taking into account that *Latimeria* is understood to comprise highly divergent, water-breathing fishes, these basal, air-breathing actinopterygians would be more suitable candidates for a comparative genomic research program aiming to trace evolutionary changes relevant to the water-to-land transition. Furthermore, it is not unlikely that air breathing and terrestriality may have taken place on more occasions during evolution, as indicated by the large spiracular openings on top of the skull and advanced internal spiracular architecture of †*Gogonasus*, a fish-like tetrapodomorph from the Late Devonian of Australia (Long *et al.*, 2006; Clement & Long, 2010), and by the digit-like radials of †*Sauripterus*, a rhizodontid from the Late Devonian of Pennsylvania (Daeschler & Shubin, 1997).

The lack of a comprehensive phylogenetic framework suitable to support interpretations of genomic structure and its possible implications for the evolution of a given group can lead to erroneous interpretations. In the present case, living coelacanths are repeatedly considered to be morphologically conserved in relation to older actinistians, and hence commonly dubbed 'living fossils', a condition that has been endorsed by their low rates of protein-coding gene evolution (Noonan *et al.*, 2004; Amemiya *et al.*, 2010, 2013). Apart from the fact that low intra-specific molecular diversity does not necessarily imply in a low mutation rate (*cf.* Casane & Laurenti, 2013), the issue is that coelacanths along with lungfishes are the few fish-like survivors of the Sarcopterygii, a Devonian lineage (over 410 million years old) that diversified into more than 32,700 species of living tetrapods (*cf.* Schipper *et al*., 2008; AmphibiaWeb, 2013; Clements *et al.*, 2013; Uetz, 2013) but that possessed, also, a stunning diversity of extinct fish-like forms (Figure 1). Differing from the most typical habitus of coelacanths, which is shared by the well-known *Latimeria*, are actinistians as aberrant as the small sized, tear-drop shaped †*Allenypterus* and the stout and small-sized (about 10 cm long) †*Hadronector*, both from the Early Carboniferous of Montana (Melton, 1969; Lund & Lund, 1984, 1985). The mid-Late Devonian †*Holopterygius* is an eel-like actinistian, with a diphycercal caudal fin (Friedman & Coates, 2006) reminiscent of the extant cusk-eels and brotulas of the order Ophidiiformes, fishes that typically live within confined spaces such as caves and even inside body cavities of echinoderms (*cf.* Nielsen *et al.*, 1999; Nelson, 2006). The recent discovery of the tuna-like †*Rebellatrix divaricerca* from the Lower Triassic of British Columbia, which bears a streamlined body and a deeply forked caudal fin, suggestive of a fast-swimming and active lifestyle (Wendruff & Wilson, 2012), also undermines the ingrained notion that coelacanths are morphologically static over their roughly 410 million years of existence (*cf.* Friedman & Coates, 2006; Wendruff & Wilson, 2012; Casane & Laurenti, 2013). Even within the crown clade Latimeroidei, the differences between head shape, dentition, structure of swim bladder (lung), and several other anatomical structures, as well as in paleohabitats, are striking, such as those exhibited by the Lower Cretaceous marine †*Axelrodichthys* (*e.g.* Maisey, 1986, 1991) and the Triassic freshwater †*Chinlea* (*cf.* Elliott, 1987; Dutel *et al.*, 2012; Casane & Laurenti, 2013).

The essay by Amemiya *et al.* (2013) may also highlight a broader issue at the very core of systematics. Recent technological developments have prompted the advancement of phylogenetic hypotheses based on whole genomes, most of which have been featured in leading scientific journals (*e.g.* Merchant *et al.*, 2007; Hackett *et al.*, 2008; Putnam *et al.*, 2008; Faircloth *et al.*, 2013). It is of course true that these mega-genomic approaches are highly promising and exciting for evolutionary biology (see Eisen & Fraser, 2003). However, as currently conducted, these studies may unintentionally reinforce an undesired conflict centered on the nature of the data employed (morphology *vs*. molecules). This antagonism is apparent in the repeated exclusion of morphological data and literature—molecular phylogenies are commonly identical to known morphological hypotheses but are repackaged as ‘new’ and portrayed as innovative simply because they are built from matrices of thousands of characters that decipher entire genomes. Phylogenomics is thereby perceived as a Rosetta stone for solving outstanding evolutionary questions, supposedly untangling conflicts between different phylogenetic hypotheses based on molecules or on so-called ‘traditional’ morphology (*e.g.* Delsuc *et al.*, 2005, 2006; Hackett *et al.*, 2008; Amemiya *et al.*, 2013; Faircloth *et al.*, 2013).

While it is true that these macro-genomic initiatives potentially clarify controversies between phylogenies derived from different sections of the genome, this reasoning does not apply to all phylogenetic hypotheses generated from morphological characters. That is because the phenotype is only a partial expression of the genome, shaped by the evolution of developmental and ecological interactions. Despite this fact, complex morphological phylogenies are frequently presented as only one hypothesis among many. This is exemplified by the treatment given to the monumental work of Livezey & Zusi (2006, 2007) on the higher-level phylogeny of Aves in the phylogenomic study by Hackett *et al.* (2008), which gave it the same importance as the molecular phylogeny of Sibley & Ahlquist (1990), an influential but outdated work, and Peters *et al.*’s (1931–1979) ‘Check-list of Birds of the World’, whose classification was entirely phenetic. Another example of this lack of due credit is the molecular phylogenetic study of archosaurs by Xia *et al.* (2003), who fail to acknowledge the overwhelming morphological evidence in support of the close relationship between birds and crocodiles (*e.g.* Gauthier *et al.*, 1988a, b; Kemp, 1988; Benton, 1990; Patterson *et al*., 1993), maintaining an unrealistic uncertainty about the issue.

Combining mega-genomic data and morphology, or simply understanding the relative contribution of both kinds of data within their specific contexts, can generate a clearer picture of major events in evolution. Evolutionary scenarios, even those founded on massive genetic evidence, are incomplete without the interpretation of specific morphological transformations. The effort to establish a functional correspondence between complex gene networks and phenotypes is still in its infancy, so to choose a molecular phylogeny over a morphological one based simply on the number of characters (base-pairs) and the appeal of technology is inappropriate. Furthermore, the increasingly more common trend of selectively sorting those anatomical features that corroborate a ‘true’ molecular phylogeny (*e.g.* Jiménez-Guri *et al.*, 2007; Amemiya *et al.*, 2013) is epistemologically questionable (see critique in Assis & Carvalho, 2010).

One issue at the heart of the original ‘salmon-lungfish-cow’ debate (Gardiner *et al.*, 1979) concerned the importance then given to the fossil record in explicating deep phylogenetic divergences. At the time, the fossil record was departing center stage to become just one more source of information for phylogenetic reconstruction, with a greater significance being given to comparative morphology of extant organisms (see Rosen *et al.*, 1981).

Cladistics rose to prominence, to some extent, as a reform of paleontology (Nelson, 2004). Reflecting further on that debate in *Nature*, and with Amemiya *et al*. (2013) in hand, it may appear that the privileged data set that was previously 'set in stone' has now switched to the genome—in other words, *genomics as the new fossil record* (D. Williams, pers. comm.). Even though we praise the significant contributions advanced by Amemiya *et al.* (2013), we hope to see more studies that are truly integrative, such as in the sense envisioned by Eisen & Fraser (2003), or that place the very important contributions of morphology into proper context. Exemplary integrative studies involving developmental biology, anatomy, paleontology, molecular biology and biogeography have surfaced in recent years with remarkable overall achievements (*e.g.* Kuratani *et al.*, 2012; Hirasawa *et al.*, 2013). Whereas the progress to genomics put forth by Amemiya *et al.* (2013) is not in dispute, the impact their study may have on the evolution of basal tetrapods and the terrestrialization of vertebrates is still premature if the numerous 'intermediate' fossils and relevant morphological transformations are not taken into account.

Acknowledgements

We thank David Williams for insightful comments that improved the manuscript. The Fundação de Amparo à Pesquisa do Estado de São Paulo, State of São Paulo Government (FAPESP; Proc. No. 2009/54931-0, 2012/21159–5 to FAB; Proc. No. 2010/51193-5, 2012/02349-8, 2012/09877-0, 2012/05391-5 to MRC; Proc. No. 2012/05152-0 to MC) and Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazilian Federal Government (CNPq; 309752/2010-8 to FAB, 304615/2011-0 to MRC) are acknowledged for funding the authors.

Literature cited

Agnolin, F. (2010) A new species of the genus *Atlantoceratodus* (Dipnoiformes: Ceratodontoidei) from the Uppermost Cretaceous of Patagonia and a brief overview of fossil dipnoans from the Cretaceous and Paleogene of South America. *Brazilian Geographical Journal: Geosciences and Humanities Research Medium*, 1, 162–210.

Ahlberg, P.E. (1991) A re-examination of sarcopterygian interrelationships, with special reference to the Porolepiformes. *Zoological Journal of the Linnean Society*, 103, 241–287.
http://dx.doi.org/10.1111/j.1096-3642.1991.tb00905.x

Ahlberg, P.E., Lukševičs, E. & Mark-Kurik, E. (2003) A near-tetrapod from the Baltic Middle Devonian. *Paleontology*, 43, 533–548.
http://dx.doi.org/10.1111/j.0031-0239.2000.00138.x

Ahlberg, P.E., Smith, M.M. & Johanson, Z. (2006) Developmental plasticity and disparity in early dipnoan (lungfish) dentitions. *Evolution and Development*, 8, 331–349.
http://dx.doi.org/10.1111/j.1525-142x.2006.00106.x

Ahlberg, P.E., Clack, J.A., Luksevics, E., Blom, H. & Zupins, I. (2008) *Ventastega curonica* and the origin of tetrapod morphology. *Nature*, 453, 1199–1204.
http://dx.doi.org/10.1038/nature06991

Amemiya, C.T., Alföldi, J., Lee, A.P., Fan, S., Philippe, H., MacCallum, I., Braasch, I., Manousaki, T., Schneider, I., Rohner, N., Organ, C., Chalopin, D., Smith, J.J., Robinson, M., Dorrington, R.A., Gerdol, M., Aken, B., Biscotti, M.A., Barucca, M., Baurain, D., Berlin, A.M., Blatch, G.L., Buonocore, F., Burmester, T., Campbell, M.S., Canapa, A., Cannon, J.P., Christoffels, A., De Moro, G., Edkins, A.L., Fan, L., Fausto, A.M., Feiner, N., Forconi, M., Gamieldien, J., Gnerre, S., Gnirke, A., Goldstone, J.V., Haerty, W., Hahn, M.E., Hesse, U., Hoffmann, S., Johnson, J., Karchner, S.I., Kuraku, S., Lara, M., Levin, J.Z. Litman, G.W., Mauceli, E., Miyake, T., Gail Mueller, M., Nelson, D.R., Nitsche, A., Olmo, E., Ota, T., Pallavicini, A., Panji, S., Picone, B., Ponting, C.P., Prohaska, S.J., Przybylski, D., Saha, N.R., Ravi, V., Ribeiro, F.J., Sauka-Spengler, T., Scapigliati, G., Searle, S.M.J., Sharpe, T., Simakov, O., Stadler, P.F., Stegeman, J.J., Sumiyama, K., Tabbaa, D., Tafer, H., Turner-Maier, J., van Heusden, P., White, S., Williams, L., Yandell, M., Brinkmann, H., Volff, J.-N., Tabin, C.J., Shubin, N., Schartl, M., Jaffe, D.B., Postlethwait, J.H., Venkatesh, B., Di Palma, F., Lander, E.S., Meyer, A. & Lindblad-Toh, K. (2013) The African coelacanth genome provides insights into tetrapod evolution. *Nature*, 496, 311–316. [suppl.]
http://dx.doi.org/10.1038/nature12027

Amemiya, C.T., Powers, T.P., Prohaska, S.J., Grimwood, J., Schmutz, J., Dickson, M., Miyake, T., Schoenborn, M.A., Myers, R.M., Ruddle, F.H. & Stadler, P.F. (2010) Complete HOX cluster characterization of the coelacanth provides further evidence for slow evolution of its genome. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 3623–3627.
http://dx.doi.org/10.1073/pnas.0914312107

AmphibiaWeb (2013) *AmphibiaWeb: Information on Amphibian Biology and Conservation*. University of California, Berkeley. Available from: http://amphibiaweb.org/ (accessed 30 September, 2013)

Assis, L.C.S. & Carvalho, M.R. de (2010) Key innovations: further remarks on the importance of morphology in elucidating systematic relationships and adaptive radiations. *Evolutionary Biology*, 37, 247–254. http://dx.doi.org/10.1007/s11692-010-9098-z

Babcock, L.L. (1951) *The Tarpon: A Description of the Fish With Some Hints on Its Capture*. 5th Ed. Printed by author, Buffalo, NY, 157 pp.

Benton, M.J. (1990) Phylogeny of the major tetrapod groups: morphological data and divergence dates. *Journal of Molecular Evolution*, 30, 409–424. http://dx.doi.org/10.1007/bf02101113

Blair, J.E. & Hedges, S.B. (2005) Molecular phylogeny and divergence times of deuterostome animals. *Molecular Biology and Evolution*, 22, 2275–2284. http://dx.doi.org/10.1093/molbev/msi225

Brinkmann, H., Venkatesh, B., Brenner, S. & Meyer, A. (2004) Nuclear protein-coding genes support lungfish and not the coelacanth as the closest living relatives of land vertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 4900–4905. http://dx.doi.org/10.1073/pnas.0400609101

Budgett, J.S. (1901) On the breeding-habits of some West-African fishes, with an account of the external features in development of *Protopterus annectens*, and a description of the larva of *Polypterus lapradei*. *Transactions of the Zoological Society of London*, 16, 115–136. http://dx.doi.org/10.1111/j.1096-3642.1901.tb00028.x

Carroll, R.L. (2007) The Palaeozoic ancestry of salamanders, frogs and caecilians. *Zoological Journal of the Linnean Society*, 150 (Suppl. 1), 1–140. http://dx.doi.org/10.1111/j.1096-3642.2007.00246.x

Casane, D. & Laurenti, P. (2013) Why coelacanths are not living 'fossils'. A review of molecular and morphological data. *BioEssays*, 35, 332–338. http://dx.doi.org/10.1002/bies.201200145

Cavin, L., Suteethorn, V., Buffetaut, E. & Tong, H. (2007) A new Thai Mesozoic lungfish (Sarcopterygii, Dipnoi) with an insight into pos-Paleozoic dipnoan evolution. *Zoological Journal of the Linnean Society*, 149, 141–177. http://dx.doi.org/10.1111/j.1096-3642.2007.00238.x

Cione, A.L., Gouiric, S., Goin, F. & Poiré, D. (2007) *Atlantoceratodus*, a new genus of lungfish from the upper Cretaceous of South America and Africa. *Revista del Museo de La Plata*, 10, 1–12.

Clack, J.A. (2012) *Gaining Ground: the Origin and Evolution of Tetrapods*. 2nd edition. Indiana University Press, Bloomington, 523 pp.

Clement, A.M. & Long, J.A. (2010) Air-breathing adaptation in a marine Devonian lungfish. *Biological Letters*, 6, 509–512. http://dx.doi.org/10.1098/rsbl.2009.1033

Clement, G. (2001) Evidence for lack of choanae in the Porolepiformes. *Journal of Vertebrate Paleontology*, 21, 795–802. http://dx.doi.org/10.1671/0272-4634(2001)021[0795:efloci]2.0.co;2

Clements, J.F., Schulenberg, T.S., Iliff, M.J., Sullivan, B.L., Wood, C.L. & Roberson, D. (2013) *The eBird/Clements Checklist of Birds of the World: Version 6.8*. Cornell University, Ithaca. Available from: http://www.birds.cornell.edu/clementschecklist/download/ (accessed 30 September 2013)

Cloutier, R. & Ahlberg, P.A. (1996) Morphology, characters, and the interrelationships of basal sarcopterygians. *In*: Stiassny, M.L.J., Parenti, L.R., Johnson, G.D. (Eds.), *Interrelationships of Fishes*. Academic Press, New York, pp. 445–479.

Daeschler, E.B. & Shubin, N.H. (1997) Fish with fingers? *Nature*, 391, 133. http://dx.doi.org/10.1038/34317

Dehadrai, P.V. (1962) Respiratory function of the swimbladder of *Notopterus* (Lacépède). *Proceeding of the Zoological Society of London*, 139, 341–357. http://dx.doi.org/10.1111/j.1469-7998.1962.tb01834.x

Delsuc, F., Brinkmann, H. & Philippe, H. (2005) Phylogenomics and the reconstruction of the tree of life. *Nature Revues, Genetics*, 6, 361–375. http://dx.doi.org/10.1038/nrg1603

Delsuc, F., Brinkmann, H., Chourrout, D. & Philippe, H. (2006) Tunicates and not cephalochordates are the closest living relatives of vertebrates. *Nature*, 439, 965–968. http://dx.doi.org/10.1038/nature04336

Deyst, K.A. & Liem, K.F. (1985) The muscular basis of aerial ventilation of the primitive lung of *Amia calva*. *Respiration Physiology*, 59, 213–223. http://dx.doi.org/10.1016/0034-5687(85)90008-8

Downs, J.P., Daeschler, E.B., Jenkins, Jr., F.A. & Shubin, N.H. (2013) *Holoptychius bergmanni* sp. nov. (Sarcopterygii, Porolepiformes) from the Upper Devonian of Nunavut, Canada, and a review of *Holoptychius* taxonomy. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 162, 47–59. http://dx.doi.org/10.1635/053.162.0104

Dutel, H., Maisey, J.G., Schwimmer, D.R., Janvier, P., Herbin, M. & Clément, G. (2012) The giant Cretaceous coelacanth (Actinistia, Sarcopterygii) *Megalocoelacanthus dobiei* Schwimmer, Stewart & Williams, 1994, and its bearing on Latimerioidei interrelationships. *PLoS ONE*, 7 (11), e49911. http://dx.doi.org/10.1371/journal.pone.0049911

Eisen, J.A. & Fraser, C.M. (2003) Phylogenomics: intersection of evolution and genomics. *Science*, 300, 1706–1707. http://dx.doi.org/10.1126/science.1086292

Elliott, D.K. (1987) A new specimen of *Chinlea sorenseni* from the Chinle Formation, Dolores River, Colorado. *Journal of the Arizona-Nevada Academy of Science*, 22, 47–52.

Faircloth, B.C., Sorenson, L., Santini, F. & Alfaro, M.E. (2013) A phylogenomic perspective on the radiation of ray-finned fishes based upon targeted sequencing of ultraconserved elements (UCEs). *PLoS ONE*, 8, e65923. http://dx.doi.org/10.1371/journal.pone.0065923

Forey, P.L. (1980) *Latimeria*: a paradoxical fish. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, 208, 369–384. http://dx.doi.org/10.1098/rspb.1980.0056

Forey, P.L. (1986) Relationships of lungfishes. *Journal of Morphology*, 190 (Suppl. 1), 75–91. http://dx.doi.org/10.1002/jmor.1051900408

Forey, P.L., Gardiner, B.G. & Patterson, C. (1991) The lungfish, the coelacanth, and the cow revisited. *In*: Schultze, H.-P. & Trueb, L. (Eds.), *Origins of the Higher Groups of Tetrapods, Controversy and Consensus*. Cornell University Press, Ithaca, pp. 145–172.

Fricke, H., Hissmann, K., Schauer, J., Erdmann, M., Moosa, M.K. & Plante, R. (2000) Biogeography of the Indonesian coelacanths. *Nature*, 403, 39. http://dx.doi.org/10.1038/47400

Friedman, M. (2007a) The interrelationships of Devonian lungfishes (Sarcopterygii: Dipnoi) as inferred from neurocranial evidence and new data from the genus *Soederberghia* Lehman, 1959. *Zoological Journal of the Linnean Society*, 151, 115–171. http://dx.doi.org/10.1111/j.1096-3642.2007.00320.x

Friedman, M. (2007b) *Styloichthys* as the oldest coelacanth: implications for early osteichthyan interrelationships. *Journal of Systematic Palaeontology*, 5, 289–343. http://dx.doi.org/10.1017/s1477201907002052

Friedman, M. & Coates, M.I. (2006) A newly recognized fossil coelacanth highlights the early morphological diversification of the clade. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, 273, 245–250. http://dx.doi.org/10.1098/rspb.2005.3316

Fritzsch, B. (1987) Inner ear of the coelacanth fish *Latimeria* has tetrapod affinities. *Nature*, 327, 153–154. http://dx.doi.org/10.1038/327153a0

Gardiner, B., Janvier, P., Patterson, C., Forey, P.L., Greenwood, P.H., Miles, R.S. & Jefferies, R.P.S. (1979) The salmon, the lungfish, the cow: a reply. *Nature*, 277, 175–176. http://dx.doi.org/10.1038/277175b0

Gauthier, J.A., Kluge, A.G. & Rowe, T. (1988a) Amniote phylogeny and the importance of fossils. *Cladistics*, 4, 105–209. http://dx.doi.org/10.1111/j.1096-0031.1988.tb00514.x

Gauthier, J.A., Kluge, A.G. & Rowe, T. (1988b) The early evolution of the Amniota. *In*: Benton, M.J. (Ed.), *The Phylogeny and Classification of the Tetrapods, Vol. 1. Amphibians, Reptiles, Birds.* The Systematics Association Special Volume Series, no. 35A. Oxford University Press, New York, pp. 103–155.

Gorr, T., Kleinschmidt, T. & Fricke, H. (1991) Close tetrapod relationships of the coelacanth *Latimeria* indicated by haemoglobin sequences. *Nature*, 351, 394−397. http://dx.doi.org/10.1038/351394a0

Graham, J.B. (1997) *Air-Breathing Fishes: Evolution, Diversity, and Adaptation*. Academic Press, San Diego, 299 pp.

Greenwood, P.H. & Liem, K.F. (1984) Aspiratory respiration in *Arapaima gigas* (Teleostei, Osteoglossomorpha): a reappraisal. *Journal of Zoology*, 203, 411−425. http://dx.doi.org/10.1111/j.1469-7998.1984.tb02341.x

Gregory, T.R. (2005) Genome size evolution in animals. *In*: Gregory, T.R. (Ed.), *The Evolution of the Genome*. Elsevier, San Diego, pp. 3–87. http://dx.doi.org/10.1016/b978-012301463-4/50003-6

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Andrew Cox, W., Han, K.-L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W., Witt, C.C. & Yuri, T. (2008) A phylogenomic study of birds reveals their evolutionary history. *Science*, 320, 1763–1768. http://dx.doi.org/10.1126/science.1157704

Halstead, L.B. (1978) Cladistic revolution – can it make the grade? *Nature*, 276, 759–760. http://dx.doi.org/10.1038/276759a0

Halstead, L.B. (1981) Halstead's defense against irrelevance. *Nature*, 292, 403–404. http://dx.doi.org/10.1038/292403b0

Halstead, L.B., White, E.I. & MacIntire, G.T. (1979) L. B. Halstead and colleagues reply. *Nature*, 277, 176. http://dx.doi.org/10.1038/277176a0

Hedges, S.B., Hass, C.A. & Maxson, L.R. (1993) Relations of fish and tetrapods. *Nature*, 363, 501–502. http://dx.doi.org/10.1038/363501b0

Hirasawa, T., Nagashima, H. & Kuratani, S. (2013) The endoskeletal origin of the turtle carapace. *Nature Communications*, 2107. http://dx.doi.org/10.1038/ncomms3107

Hissmann, K., Fricke, H., Schauer, J., Ribbink, A.J., Roberts, M., Sink, K. & Heemstra, P. (2006) The South African coelacanths – an account of what is known after three submersible expeditions. *South African Journal of Science*, 102, 491–500.

Holland, T. (2013) Pectoral girdle and fin anatomy of *Gogonasus andrewsae* Long, 1985: implications for tetrapodomorph limb evolution. *Journal of Morphology*, 274, 147–164.
http://dx.doi.org/10.1002/jmor.20078

Holland, T., Warren, A., Johanson, Z., Long, J., Parker, K. & Garvey, J. (2007) A new species of *Barameda* (Rhizodontida) and heterochrony in the rhizodontid pectoral fin. *Journal of Vertebrate Paleontology*, 27, 295–315.
http://dx.doi.org/10.1671/0272-4634(2007)27[295:ansobr]2.0.co;2

Janvier, P. (1996) *Early Vertebrates*. Oxford University Press, New York, 393 pp.

Jiménez-Guri, E., Philippe, H., Okamura, B. & Holland, P.W.H. (2007) *Buddenbrockia* is a cnidarian worm. *Science*, 317, 116–118.
http://dx.doi.org/10.1126/science.1142024

Johansen, K., Hanson, D. & Lenfant, C. (1970) Respiration in a primitive air breather, *Amia calva*. *Respiration Physiology*, 9, 162–174.
http://dx.doi.org/10.1016/0034-5687(70)90068-x

Kemp, T.S. (1988) Haemothermia or Archosauria? The interrelationships of mammals, birds and crocodiles. *Zoological Journal of the Linnean Society*, 92, 67–104.
http://dx.doi.org/10.1111/j.1096-3642.1988.tb01527.x

Kuratani, S., Adachi, N., Wada, N., Oisi, Y., Sugahara, F. (2012) Developmental and evolutionary significance of the mandibular arch and prechordal/premandibular cranium in vertebrates: revising the heterotopy scenario of gnathostome jaw evolution. *Journal of Anatomy, Zoological Science*, 22, 1–15.
http://dx.doi.org/10.1111/j.1469-7580.2012.01505.x

Livezey, B.C. & Zusi, R.L. (2006) Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy: I. Methods and characters. *Bulletin of the Carnegie Museum of Natural History*, 37, 1–556.
http://dx.doi.org/10.1111/j.1096-3642.2006.00293.x

Livezey, B.C. & Zusi, R.L. (2007) Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. II. Analysis and discussion. *Zoological Journal of the Linnean Society*, 149, 1–95.
http://dx.doi.org/10.1111/j.1096-3642.2006.00293.x

Long, J.A., Young, G.C., Holland, T., Senden, T.J. & Fitzgerald, E.M.G. (2006) An exceptional Devonian fish from Australia sheds light on tetrapod origins. *Nature*, 444, 199–202.
http://dx.doi.org/10.1038/nature05243

Løvtrup, S. (1977) *The Phylogeny of Vertebrata*. John Wiley & Sons, London, 330 pp.

Lu, J. & Zhu, M. (2010) An onychodont fish (Osteichthyes, Sarcopterygii) from the Early Devonian of China, and the evolution of the Onychodontiformes. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, 277, 293–299.
http://dx.doi.org/10.1098/rspb.2009.0708

Lund, R. & Lund, W. (1984) New genera and species of coelacanths from the Bear Gulch limestone (Lower Carboniferous) of Montana (U.S.A.). *Geobios*, 17, 237–244.
http://dx.doi.org/10.1016/s0016-6995(84)80145-x

Lund, R. & Lund, W.L. (1985) Coelacanths from the Bear Gulch Limestone (Namurian) of Montana and the evolution of the Coelacanthiformes. *Bulletin of Carnegie Museum of Natural History*, 25, 1–74.

Maddison, W.P. & Maddison, D.R. (2011) *Mesquite: a Modular System for Evolutionary Analysis*. Version 2.75. Available from: http://mesquiteproject.org (accessed 18 November 2013)

Magid, A.M.A. (1966) Breathing and functions of the spiracles in *Polypterus senegalus*. *Animal Behaviour*, 14, 530–533.
http://dx.doi.org/10.1016/s0003-3472(66)80055-6

Magid, A.M.A. (1967) Respiration of air by the primitive fish *Polypterus senegalus*. *Nature*, 215, 1096–1097.

Maisey, J.G. (1986) Coelacanths from the Lower Cretaceous of Brazil. *American Museum Novitates*, no. 2866, 1–30.

Maisey, J.G. (1991) *Santana Fossils, an Illustrated Atlas* (Ed.), TFH Publications, Neptune City, 456 pp.

Melton, Jr., W.G. (1969) A new dorypterid fish from central Montana. *Northwest Science*, 43, 196–206.

Meng, J., Wang, Y & Li, C. (2011) Transitional mammalian middle ear from a new Cretaceous Jehol eutriconodont. *Nature*, 472, 181–185.
http://dx.doi.org/10.1038/nature09921

Merchant, S.S., Prochnik, S.E., Vallon, O., Harris, E.H., Karpowicz, S.J., Witman, G.B., Terry, A., Salamov, A., Fritz-Laylin, L.K., Maréchal-Drouard, L., Marshall, W.F., Qu, L.-H., Nelson, D.R., Sanderfoot, A.A., Spalding, M.H., Kapitonov, V.V., Ren, Q., Ferris, P., Lindquist, E., Shapiro, H., Lucas, S.M., Grimwood, J., Schmutz, J., *Chlamydomonas* Annotation Team, JGI Annotation Team, Grigoriev, I.V., Rokhsar, D.S. & Grossman, A.R. (2007) The *Chlamydomonas* genome reveals the evolution of key animal and plant functions. *Nature*, 318, 245–251.

Merrick, J.R & Schmida, G.E. (1984) *Australian Freshwater Fishes: Biology and Management.* Griffin Press, Netley, Australia, 409 pp.

Meyer, A. & Dolven, S.I. (1992) Molecules, fossils, and the origin of tetrapods. *Journal of Molecular Evolution*, 35, 102–113.
http://dx.doi.org/10.1007/bf00183221

Meyer, A. & Wilson, A.C. (1990) Origin of tetrapods inferred from their mitochondrial DNA affiliation to lungfish. *Journal of Molecular Evolution*, 31, 359–364.
http://dx.doi.org/10.1007/bf02106050

Meyer, A. & Wilson, A.C. (1991) Coelacanth's relationships. *Nature*, 353, 219.
http://dx.doi.org/10.1038/353219a0

Miles, R.S. (1975) The relationships of the Dipnoi. *Colloques Internationaux du Centre National de la Recherche Scientifique*, 218, 133–148.
http://dx.doi.org/10.1016/0031-0182(79)90162-7

Miles, R.S. (1977) Dipnoan (lungfish) skulls and the relationships of the group: a study based on a new species from the Devonian of Australia. *Zoological Journal of the Linnean Society*, 61, 1–328.
http://dx.doi.org/10.1111/j.1096-3642.1977.tb01031.x

Morelle, R. (2013) 'Living fossil' coelacanth genome sequenced. Available from: http://www.bbc.co.uk/news/science-environment-22184556 (accessed 18 November 2013)

Morin, H. (2013) Le cœlacanthe n'est pas un "fossile vivant" Available from: http://www.lemonde.fr/sciences/article/2013/04/19/le-coelacanthe-eclaire-la-sortie-des-eaux-de-nos-ancetres_3162086_1650684.html (accessed 18 November 2013)

Nelson, G. (2004) Cladistics: its arrested development. *In*: Williams, D.M. & Forey, P.L. (Eds.), *Milestones in Systematics*. The Systematics Association Special Volume Series, no. 67. CRC Press, Boca Raton, pp. 127–147.

Nelson, J.S. (2006) *Fishes of the World. Fourth Edition*. John Wiley & Sons, Inc., Hoboken, New Jersey, 601 pp.

Nielsen, J.G., Cohen, D.M., Markle, D.F. & Robins, C.R. (1999) *Ophidiiform Fishes of the World (Order Ophidiiformes). An Annotated and Illustrated Catalogue of Pearlfishes, Cusk-eels, Brotulas and Other Ophidiiform Fishes Known to Date*. FAO, Rome, 178 pp. [FAO Fisheries Synopsis No. 125, Vol. 18]

Noonan, J.P., Grimwood, J., Danke, J., Schmutz, J., Dickson, M., Amemiya, C.T. & Myers, R.M. (2004) Coelacanth genome sequence reveals the evolutionary history of vertebrate genes. *Genome Research*, 14, 2397–2405.
http://dx.doi.org/10.1101/gr.2972804

Northcutt, R.G. (1986) Lungfish neural characters and their bearing on sarcopterygian phylogeny. *Journal of Morphology*, 190 (Suppl. 1), 277–297.
http://dx.doi.org/10.1002/jmor.1051900418

Panchen, A.L. & Smithson, T.R. (1987) Character diagnosis, fossils, and the origin of tetrapods. *Biological Reviews*, 62, 341–438.
http://dx.doi.org/10.1111/j.1469-185x.1987.tb01635.x

Patterson, C., Williams, D.M. & Humphries, C.J. (1993) Congruence between molecular and morphological phylogenies. *Annual Review of Ecology and Systematics*, 24, 153–188.
http://dx.doi.org/10.1146/annurev.ecolsys.24.1.153

Peters, J.L. *et al.* (Eds.) (1931–1979) *Check-list of Birds of the World, Vols. I to XV.* Museum of Comparative Anatomy, Cambridge, 6372 pp.

Platt, C. (1994) Hair cells in the lagenar otolith organ of the coelacanth are unlike those in amphibians. *Journal of Morphology*, 220, 381.

Platt, C., Jørgensen, J.M. & Popper, A.N. (2004) The inner ear of the lungfish *Protopterus*. *The Journal of Comparative Neurology*, 471, 277–288.
http://dx.doi.org/10.1002/cne.20038

Poll, M. & Nysten, M. (1962) Vessie natatoire pulmonoïde et pneumatisation des vertèbres chez *Pantodon buchholzi* Peters. *Bulletin des Séances*, *Académie royale des Sciences d'Outre-Mer*, 8, 434–454.

Putnam, N.H., Butts, T., Ferrier, D.E.K., Furlong, R.F., Hellsten, U., Kawashima, T., Robinson-Rechavi, M., Shoguchi, E., Terry, A., Yu, J.-K., Benito-Gutiérrez, È., Dubchak, I., Garcia-Fernàndez, J., Gibson-Brown, J.J., Grigoriev, I.V., Horton, A.C., de Jong, P.J., Jurka, J., Kapitonov, V.V., Kohara, Y., Kuroki, Y., Lindquist, E., Lucas, S., Osoegawa, K., Pennacchio, L.A., Salamov, A.A., Satou, Y., Sauka-Spengler, T., Schmutz, J., Shin-I, T., Toyoda, A., Bronner-Fraser, M., Fujiyama, A., Holland, L.Z., Holland, P.W.H., Satoh, N. & Rokhsar, D.S. (2008) The amphioxus genome and the evolution of the chordate karyotype. *Nature*, 453, 1064–1072.
http://dx.doi.org/10.1038/nature06967

Rahn, H., Rahn, K.B., Howell, B.J., Gans, C. & Tenney, S.M. (1971) Air breathing of the garfish *(Lepisosteus osseus*). *Respiration Physiology*, 11, 285–307.
http://dx.doi.org/10.1016/0034-5687(71)90003-x

Rosen, D.E., Forey, P.L., Gardiner, B.G. & Patterson, C. (1981) Lungfishes tetrapods, paleontology and plesiomorphy. *Bulletin of American Museum of Natural History*, 167, 159–276.
http://dx.doi.org/10.2307/2413259

Rougier, G.W. & White, J.R. (2006) Major changes in the ear region and basicranium of early mammals. *In*: Carrano, M.T., Gaudin, T.J., Blob, R.W. & Wible, J.R. (Eds.), *Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles: a Volume Honoring James Allen Hopson*. University of Chicago Press, Chicago, pp. 269–311.

Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A.S.L., Stuart, S.N., Temple, H.J., Baillie, J., Boitani, L., Lacher, Jr., T.E., Mittermeier, R.A., Smith, A.T., Absolon, D., Aguiar, J.M., Amori, G., Bakkour, N., Baldi, R., Berridge, R.J., Bielby, J., Black, P.A., Blanc, J.J., Brooks, T.M., Burton, J.A., Butynski, T.M., Catullo, G., Chapman, R., Cokeliss, Z., Collen, B., Conroy, J., Cooke, J.G., Fonseca, G.A.B., Derocher, A.E., Dublin, H.T.,

Duckworth, J.W., Emmons, L., Emslie, R.H., Festa-Bianchet, M., Foster, M., Foster, S., Garshelis, D.L., Gates, C., Gimenez-Dixon, M., Gonzalez, S., Gonzalez-Maya, J.F., Good, T.C., Hammerson, G., Hammond, P.S., Happold, D., Happold, M., Hare, J., Harris, R.B., Hawkins, C.E., Haywood, M., Heaney, L.R., Hedges, S., Helgen, K.M., Hilton-Taylor, C., Hussain, S.A., Ishii, N., Jefferson, T.A., Jenkins, R.K.B., Johnston, C.H., Keith, M., Kingdon, J., Knox, D.H., Kovacs, K.M., Langhammer, P., Leus, K., Lewison, R., Lichtenstein, G., Lowry, L.F., Macavoy, Z., Mace, G.M., Mallon, D.P., Masi, M., McKnight, M.W., Medellín, R.A., Medici, P., Mills, G., Moehlman, P.D., Molur, S., Mora, A., Nowell, K., Oates, J.F., Olech, W., Oliver, W.R.L., Oprea, M., Patterson, B.D., Perrin, W.F., Polidoro, B.A., Pollock, C., Powel, A., Protas, Y., Racey, P., Ragle, J., Ramani, P., Rathbun, G., Reeves, R.R., Reilly, S.B., Reynolds III, J.E., Rondinini, C., Rosell-Ambal, R.C., Rulli, M., Rylands, A.B., Savini, S., Schank, C.J., Sechrest, W., Self-Sullivan, C., Shoemaker, A., Sillero-Zubiri, C., De Silva, N., Smith, D.E., Srinivasulu, C., Stephenson, P.J., van Strien, N., Talukdar, B.K., Taylor, B.L, Timmins, R., Tirira, D.G., Tognelli, M.F., Tsytsulina, K., Veiga, L.M., Vié, J.-C., Williamson, E.A., Wyatt, S.A., Xie, Y. & Young, B.E. (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science*, 322, 225–230.
http://dx.doi.org/10.1126/science.1165115

Schultze H.-P. (1986) Dipnoans as sarcopterygians. *Journal of Morphology*, 190 (Suppl. 1), 39–74.
http://dx.doi.org/10.1002/jmor.1051900407

Schultze, H.-P. & Trueb, L. (1991) *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. Cornell University Press, Ithaca, 724 pp.

Schwartz, E. (1969) Luftatmung bei *Pantodon buchholzi* und ihre Beziehung zur Kiemenatmung. *Zeitschrift für vergleichende Physiologie*, 65, 324–330.
http://dx.doi.org/10.1007/bf00298136

Sibley, C.G. & Ahlquist, J.E. (1990) *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. Yale University Press, New Haven, 976 pp.

Stock, D.W. & Swofford, D.L. (1991) Coelacanth's relationships. *Nature*, 353, 217–218.
http://dx.doi.org/10.1038/353217a0

Swartz, B. (2012) A marine stem-tetrapod from the Devonian of Western North America. *PLoS ONE*, 7, e33683.
http://dx.doi.org/10.1371/journal.pone.0033683

Thomson, K.S. (1969) The biology of the lobe-finned fishes. *Biological Review*, 44, 91–154.
http://dx.doi.org/10.1111/j.1469-185x.1969.tb00823.x

Uetz, P. (2013) *The Reptile Database*. Available from: http://www.reptile-database.org/ (accessed 30 September 2013)

Wade, N. (2013) Fish's DNA may explain how fins turned to feet. Available from: http://www.nytimes.com/2013/04/18/science/coelacanth-dna-may-tell-how-fish-learned-to-walk.html?_r=0 (accessed 18 November 2013)

Wendruff, A.J. & Wilson, M.V.H. (2012) A fork-tailed coelacanth, *Rebellatrix divaricerca*, gen. et sp. nov. (Actinistia, Rebellatricidae, fam. nov.), from the Lower Triassic of Western Canada. *Journal of Vertebrate Paleontology*, 32, 499–511.
http://dx.doi.org/10.1080/02724634.2012.657317

Wiley, E.O. (1979) Ventral gill arch muscles and the interrelationships of gnathostomes, with a new classification of the Vertebrata. *Zoological Journal of the Linnean Society*, 67, 149–179.
http://dx.doi.org/10.1111/j.1096-3642.1979.tb01110.x

Woolston, C. & Nature Magazine (2013) 'Coelacanth' genome unlocked. Available from: http://www.scientificamerican.com/article.cfm?id=slow-evolving-lobe-finned-coelacanth-genome-unlocked (accessed 18 November 2013)

Xia, X., Xie, Z. & Kjer, K.M. (2003) 18S ribosomal RNA and tetrapod phylogeny. *Systematic Biology*, 52, 283–295.

Yokobori, S., Hasegawa, M., Ueda, T., Okada, N., Nishikawa, K. & Watanabe, K. (1994) Relationship among coelacanths, lungfishes, and tetrapods: a phylogenetic analysis based on mitochondrial cytochrome oxidase I gene sequences. *Journal of Molecular Evolution*, 38, 602–609.
http://dx.doi.org/10.1007/bf00175880

Zhu, M., Wang, W. & Yu, X. (2010) *Meemannia eos*, a basal sarcopterygian fish from the Lower Devonian of China – expanded description and significance. *In*: Elliott, D.K., Maisey, J.G., Yu, X. & Miao, D. (Eds.), *Morphology, Phylogeny and Paleobiogeography of Fossil Fishes*, Munchen, Verlag Dr. Friedrich Pfeil, pp. 199–214.

Zhu, M. & Yu, X. (2002) A primitive fish close to the common ancestor of tetrapods and lungfish. *Nature*, 418, 767–770.
http://dx.doi.org/10.1038/nature00871

Zhu, M., Yu, X. & Ahlberg, P. (2001) A primitive sarcopterygian fish with an eyestalk. *Nature*, 410, 81–84.
http://dx.doi.org/10.1038/35065078

Zhu, M., Yu, X., Lu, J., Qiao, T., Zhao, W. & Jia, L. (2012) Earliest known coelacanth skull extends the range of anatomically modern coelacanths to the Early Devonian. *Nature Communications*, 772.
http://dx.doi.org/10.1038/ncomms1764

Zhu, M., Zhao, W., Jia, L., Lu, J., Qiao, T. & Qu, Q. (2009) The oldest articulated osteichthyan reveals mosaic gnathostome characters. *Nature*, 458, 469–474.
http://dx.doi.org/10.1038/nature07855