

The Origin(s) of Modern Amphibians: A Commentary

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Anderson (2008) recently reviewed the controversial topic of extant amphibian origins, on which three (groups of) hypotheses exist at the moment. Anderson favors the “polyphyly hypothesis” (PH), which considers the extant amphibians to be polyphyletic with respect to many Paleozoic limbed vertebrates and was most recently supported by the analysis of Anderson et al. (2008). Another is the “temnospondyl hypothesis” (TH—lissamphibians nested within temnospondyls), most recently supported by Ruta and Coates (2007). We prefer the “lepospondyl hypothesis” (LH—lissamphibians nested within “lepospondyls”; most recently supported by Vallin and Laurin 2004 and Marjanović and Laurin 2008a). We would like to clarify important points that were not discussed in Anderson’s review, or for which crucial arguments were left out.

Anderson (2008) argues that most molecular dates favor the PH because they suggest a Devonian or Early Carboniferous diversification of Lissamphibia. This is inaccurate, since the confidence intervals of the dates obtained by Hugall et al. (2007) range from Early Carboniferous to Middle Permian, and our own molecular dating suggests a Permian origin. Indeed, three methods (molecular dating, a paleontological supertree and a confidence interval on the stratigraphic range of Lissamphibia) all hint at a Permian or

(less likely) a Late Carboniferous origin of Lissamphibia (Marjanović and Laurin 2007, 2008b).

Citing Schoch and Milner (2004), Anderson (2008, p. 234) argues that the LH is mainly supported by loss characters, and that this is problematic “given the relative ease that these losses can arise via paedomorphosis, which appears to evolve repeatedly.” This is especially surprising because we count (Supplementary Table 1) about fifty loss characters in the matrix by Anderson et al. (2008)—more than one out of five characters—, including several that describe the loss of bones that ossified late in the ontogeny of branchiosaurids (Schoch 1992) and/or the aistopod *Phlegethontia* (Anderson 2002) and are absent in lissamphibians.

Furthermore, Anderson’s remark amounts to criticizing the use of loss characters simply because they *could* be homoplastic. Yet, Anderson (2008) emphasizes development characters such as digit development and skull ossification order, which are *known* to be homoplastic. For instance, under Anderson’s version of the PH, the similarity between the digit development orders of the branchiosaurid temnospondyl *Apateon* and the urodeles is either convergent, or homologous between these two taxa but reversed in anurans; indeed, Johanson et al. (2007) suggest that the digits of tetrapods are homologous to the “radials” of other sarcopterygians and find the “radials” of the Australian lungfish to develop independently of the rest of the forelimb (pectoral fin), like in urodeles and *Apateon* (and unlike in anurans and amniotes, where the limb chondrifies in a strict proximal-to-distal sequence), strongly suggesting that the urodele-*Apateon* pattern is plesiomorphic—regardless of whether the PH, the TH, or the LH is (closest to) correct. Anderson (2008, p. 242) furthermore mentions that “the pattern of cranial ossification [...] has compared very closely with the sequence of cranial ossification seen in salamanders” (making explicit on the next page that these

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similarities are plesiomorphic); more recently, however, Germain and Laurin (2009) have shown that the ancestral urodele sequence, even though poorly constrained, differed in several respects from that of *Apateon*.

Nonetheless, the suggestion that loss characters are likely to be strongly correlated to each other and homoplastic is serious; and indeed the matrix by Vallin and Laurin (2004) contains a greater proportion of loss characters (Supplementary Table 2) than that by Anderson et al. (2008). Unfortunately, no rigorous test of this possibility exists. The closest workable approximation we are aware of is the skewness test proposed by Huelsenbeck (1991), which measures how well a set of characters is compatible with different numbers of phylogenetic hypotheses: the smaller the g_1 statistic, the fewer trees are compatible with the character set, and the stronger is therefore the coherent phylogenetic signal in that character set. The g_1 of the loss characters is much lower (and thus their phylogenetic signal higher) than that of the others in the matrix of Vallin and Laurin (2004), but higher in that of Anderson et al. (2008), and highly significant in all four partitions (Supplementary Table 3), showing that loss characters are not necessarily strongly correlated to each other, and that they appear to contain a phylogenetic signal.

Matrices of various sizes support the various hypotheses on lissamphibian origins. Anderson (2008, p. 234), citing Schoch and Milner (2004), criticizes the “limited number of taxa analyzed” by LH proponents. There is a trade-off between quantity and quality in a data matrix for a given time investment, and quality is as important as quantity for reaching accurate phylogenetic results. Even small matrices are sometimes not coded carefully enough. We recently showed that 35% of the cells of the first matrix that supported the PH, that by McGowan (2002), were problematic (Marjanović and Laurin 2008a); with only the original taxa included, our modified version supports the TH, while adding *Gerobatrachus* and the “lepospondyl” *Brachydeutes* results in the LH.

Until recently, few studies supported the LH, but two recent dissertations which contain large phylogenetic analyses bolster it (Pawley 2006, p. 239 and appendix 16; Germain 2008a). Pawley (2006) built upon the data matrix by Ruta et al. (2003), which originally supported the TH; Germain (2008a) merely took the matrix by Ruta and Coates (2007), which likewise originally supported the TH, did not change its taxon or character sampling (except for fusing four correlated characters), and improved the accuracy of the scoring. Although Germain (2008a) found the LH to be only one step more parsimonious than the TH, continuation of his work by David Marjanović (supplemented by the fusion of further correlated characters and the addition of information published in or after 2007) has

so far increased the difference to eight steps. Incidentally, the LH is no longer supported only by Michel Laurin and his students; neither of us knew of Pawley’s dissertation till 2 years after the defense.

As with that by McGowan (2002), we find much to disagree with in the matrix of Anderson et al. (2008). Our rescoring and/or recoding of 39 characters and all but five taxa (and ordering of 38 of the multistate characters for reasons explained by Marjanović and Laurin 2008a, p. 163, partially overlapping with the set of rescored characters) supports the LH, with the lysorophian *Brachydeutes* as the sister-group of Lissamphibia; the bootstrap and Bremer values for a “lepospondyl”-lissamphibian clade (Amphibia) which excludes all temnospondyls are high. Again as with the matrix by McGowan (2002), our changes range from the correction of probable typographic errors (like the alleged lack of a cleithrum in *Triadobatrachus* and “frogs” in character 193, or the alleged absence of a caudolateral flange or corner on the pterygoid that constricts the subtemporal fenestra in *Seymouria* and *Limnoscelis* in character 120) to disagreements of interpretation; for example, having compared all described temnospondyl tarsi, we are not convinced that an *os basale commune* (character 207) is present in *Gerobatrachus* (Marjanović and Laurin 2008a, pp. 168–169), and although strong cases for tooth pedicely (character 99) in closely related temnospondyls have been made, we do not think the published evidence establishes whether *Gerobatrachus* shares this feature (Marjanović and Laurin 2008a, p. 179), so we had to score these two characters as unknown in *Gerobatrachus*. See the Electronic Supplementary Material for more information about the cells that were rescored, the supporting references, the methods, the resulting topology, the support values, and the modified matrix.

Furthermore, possibly pedicellate teeth have now been described in an aistopod (Germain 2008b) and may be present in another (Carroll 1998, Fig. 4B). In addition, Milner (1980, p. 392) calls the teeth of the nectridean *Scincosaurus* “pedicellate [...] without a line of abscission”; to the best of our knowledge, the teeth of *Scincosaurus* have never been mentioned in the literature before or since (most notably not by Bossy and Milner 1998). Further research will be necessary to determine if pedicely is much more widespread than previously thought.

For all these reasons, we conclude that the polyphyly hypothesis is less likely than suggested by Anderson (2008), and that the lepospondyl hypothesis seems to be at least as well supported as the temnospondyl hypothesis.

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