

Points of View

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Tetrapod Phylogeny, Amphibian Origins, and the Definition of the Name Tetrapoda

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The most detailed, computer-generated phylogeny of early amphibians has been published recently (Anderson, 2001). The study was based on an analysis of 182 osteological characters and 49 taxa, including 41 "lepospondyls," 7 other Paleozoic taxa representing other major groups (seymouriamorphs, embolomeres, temnospondyls, etc.), and a single lissamphibian (the oldest known apodan, the Jurassic taxon *Eocacilia*). The publication of this phylogeny is welcome, but several points raised in that paper deserve to be discussed further. Especially problematic are the views Anderson expressed about the polyphyletic origin of extant amphibians and about the application of phylogenetic nomenclature.

TETRAPOD PHYLOGENY

Anderson (2001) found that the lepospondyls are more closely related to amniotes than to seymouriamorphs and embolomeres. This result had been previously reported by the other authors who had done a computer-assisted phylogenetic analysis of the main early stegocephalian taxa (Carroll, 1995; Laurin and Reisz, 1997, 1999; Laurin, 1998; Ahlberg and Clack, 1998; Paton et al., 1999). These results (Figs. 1a, 1b) are clearly incompatible with the more traditional stegocephalian phylogeny (Figs. 1c, 1d) exemplified by Gauthier et al. (1988), Panchen and Smithson (1988), Lombard and Sumida (1992), and Ahlberg and Milner (1994). However, those older studies either were not based on a data matrix (Panchen and Smithson, 1988; Lombard and Sumida, 1992;

Ahlberg and Milner, 1994) or did not include amphibians (Gauthier et al., 1988), thus precluding identification of the dichotomy between amphibians and reptiliomorphs (the clade that includes amniotes and the extinct taxa that are more closely related to amniotes than to lissamphibians). The latest phylogeny (Anderson, 2001) suggests that despite initial skepticism (Coates et al., 2000), the new pattern of stegocephalian relationships appears to be well supported and relatively stable, at least as it pertains to the relationships between major taxa such as Temnospondyli, Embolomeri, Seymouriamorpha, Amniota, and the paraphyletic group informally called lepospondyls (Figs. 1a, 1b).

Origin of Extant Amphibians

This brings us to the more difficult question of amphibian origins. Many authors have considered that extant amphibians (i.e., anurans, urodeles, and apodans) form a clade (Lissamphibia) that excludes all known Paleozoic taxa. The most common opinion (e.g., Gauthier et al., 1988:105; Trueb and Cloutier, 1991; Ahlberg and Milner, 1994) is that this lissamphibian clade is part of Temnospondyli (Figs. 1c, 1d). However, this opinion has never been substantiated by a published data matrix that included lissamphibians, temnospondyls, and other potential relatives of lissamphibians (such as lepospondyls). For instance, the computer-assisted phylogenetic analysis of Trueb and Cloutier (1991) included only

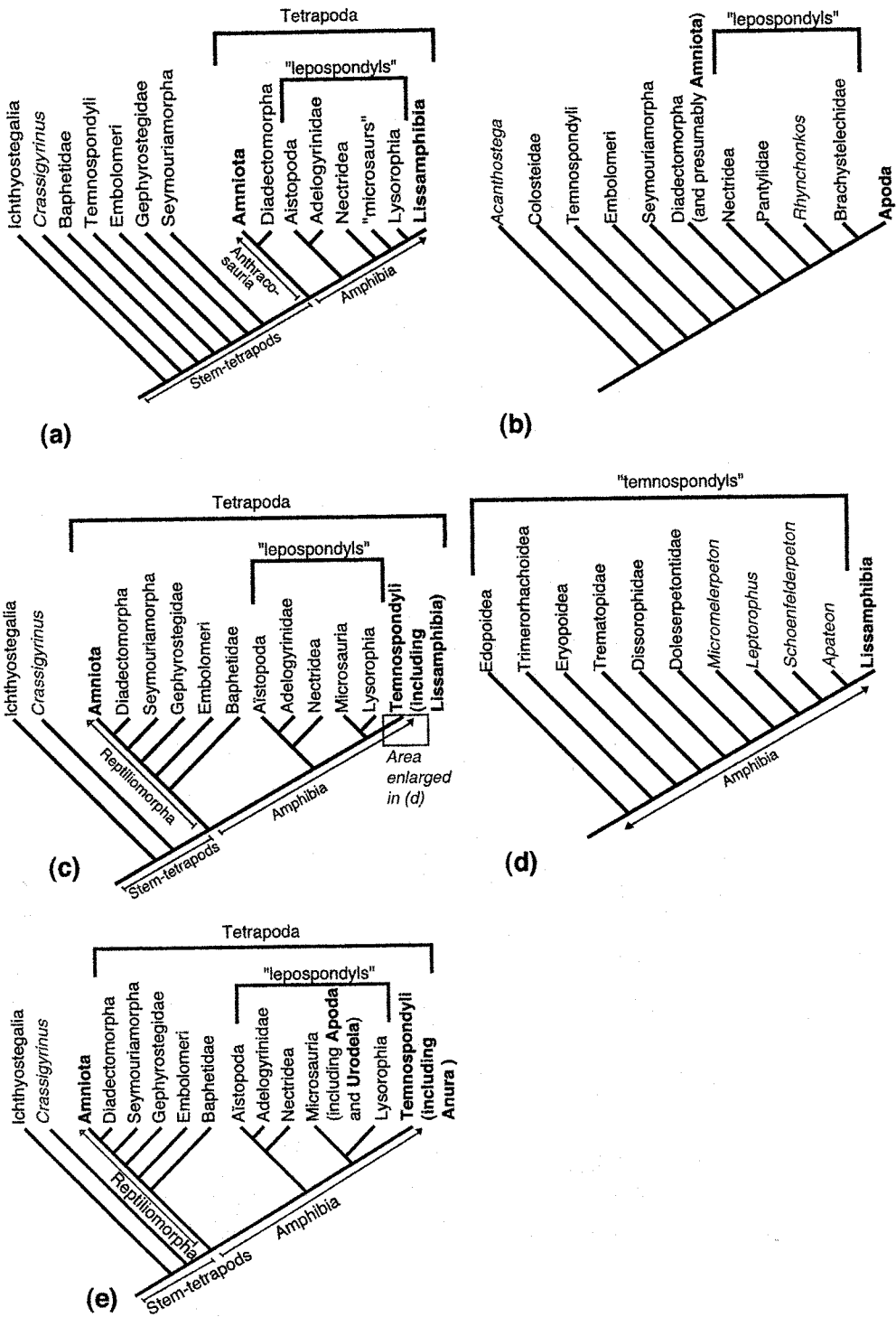


FIGURE 1. Stegocephalian phylogeny. (a) Recent phylogeny, as found in Laurin and Reisz (1997, 1999) and Laurin (1998). Similar variants have been published by Carroll (1995), Ahlberg and Clack (1998), and Paton et al. (1999). (b) Phylogeny of Anderson (2001). (c) Classical stegocephalian phylogeny, as exemplified by Gauthier et al. (1988), Panchen and Smithson (1988), Lombard and Sumida (1992), and Ahlberg and Milner (1994). (d) Phylogeny within temnospondyls, as assessed by Trueb and Cloutier (1991). (e) Polyphyletic origin of extant amphibians, adapted from the sources cited in (c) and Carroll (1988). All phylogenies have been simplified by eliminating some terminal taxa or regrouping them into larger clades.

temnospondyls and lissamphibians (Fig. 1d). A second, recently proposed hypothesis (Fig. 1a) is that Lissamphibia is nested within lepospondyls (Laurin and Reisz, 1997, 1999; Laurin, 1998). The third hypothesis that needs to be considered here is that extant amphibians do not form a monophyletic group unless at least some Paleozoic taxa are also included. This hypothesis has not usually been formulated in a cladistic context (except by the variant presented in Milner, 1993), but a free translation into a cladistic form is shown here (Fig. 1e). Indeed, this approach has been championed by Carroll and some of his former students (Carroll and Currie, 1975; Carroll and Holmes, 1980; Carroll, 1988). According to that hypothesis, apodans and urodeles are derived from lepospondyls, whereas anurans are derived from temnospondyls.

Anderson (2001:182) also subscribes to a polyphyletic origin of extant amphibians, but his results do not warrant this opinion. Indeed, in his phylogeny, the early apodan *Eocaecilia* (the only potential lissamphibian included) is deeply nested within lepospondyls, a result compatible with both the second and third hypotheses above (in which modern amphibians are monophyletic and polyphyletic, respectively) regarding amphibian origins (e.g., Carroll and Currie, 1975; Carroll and Holmes, 1980; Laurin and Reisz, 1997, 1999). Anderson then concludes, "The present hypothesis, which

tentatively suggests an origin of caecilians [apodans] separate from frogs [anurans] (assuming a temnospondyl origin), has received support from molecular (Feller and Hedges, 1998) and developmental (Carroll et al., 1999) studies" (p. 182). However, the molecular phylogeny presented by Feller and Hedges (1998), far from supporting the suggestion by Anderson (2001), is incompatible with it. Indeed, if the phylogeny of Anderson (2001) is accepted, and if anurans truly are temnospondyls, then apodans must necessarily be more closely related to amniotes than to anurans because apodans are lepospondyls, and lepospondyls are more closely related to amniotes than to temnospondyls (Fig. 2a). In contrast, Feller and Hedges (1998) found a monophyletic Lissamphibia (i.e., apodans are more closely related to anurans than to amniotes). Most, if not all other molecular phylogenies (Hedges et al., 1990; Hedges and Maxson, 1993; Hay et al., 1995; Zardoya and Meyer, 2001) show a similar pattern (Fig. 2b). Because Feller and Hedges (1998) did not have an outgroup, they rooted their tree between lissamphibians and amniotes. Thus, rerooting the tree could have rendered it compatible with the suggestion by Anderson (2001) and Carroll (1988) that apodans and anurans are lepospondyls and temnospondyls, respectively. However, Hedges et al. (1990) and Hedges and Maxson (1993) did have an outgroup, and their phylogenies, if correct, show a monophyletic and

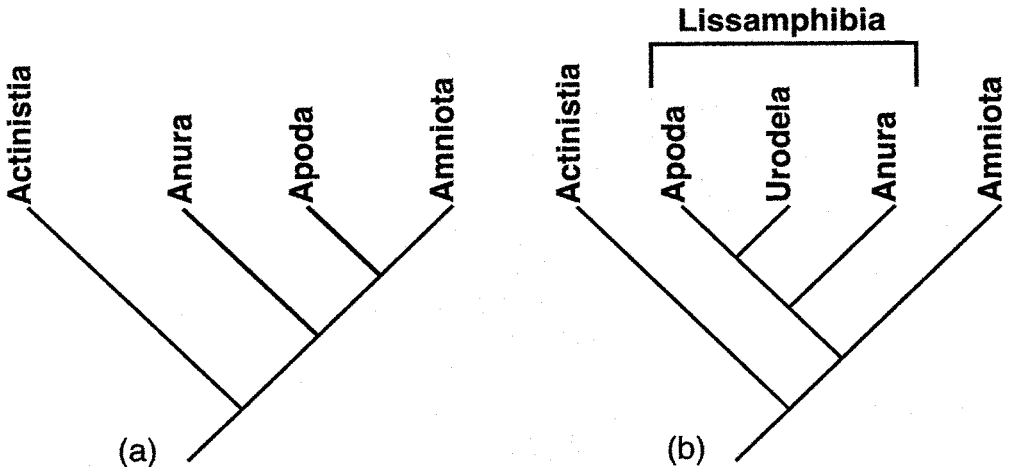


FIGURE 2. Relationships between extant amphibians and amniotes. (a) Phylogeny postulated by Anderson (2001). (b) Phylogeny proposed in various molecular studies (Hedges et al., 1990; Hedges and Maxson, 1993; Hay et al., 1995; Feller and Hedges, 1998; Zardoya and Meyer, 2001).

strongly supported Lissamphibia (Fig. 2b). Thus, the molecular phylogenies are incompatible with the diphyletic or triphyletic origin of extant amphibians suggested by Anderson (2001) and Carroll (1988).

The molecular data cannot test directly whether extant amphibians are temnospondyls, lepospondyls, or both, but do clearly suggest that they cannot be descendants of both of these Paleozoic groups unless temnospondyls and lepospondyls form a clade that excludes amniotes. Therefore, the finding that lepospondyls are more closely related to amniotes than to temnospondyls seems to rule out a polyphyletic origin of extant amphibians.

PHYLOGENETIC NOMENCLATURE

Anderson (2001:171) states: "... I do not adhere to the principle of priority of explicit phylogenetic definition advocated by Laurin when applied to historically laden names. Instead I follow de Queiroz and Gauthier (1990, 1992, 1994), who advocate following the first use of a name with a specific clade, which in this case (Tetrapoda) would be Gaffney (1979) ... Furthermore, although never explicitly stated, Gaffney's Neotetrapoda is clearly a crown taxon and thus takes priority over a crown-based definition of Tetrapoda." This statement is an attempt to justify his use of a traditional meaning of the name Tetrapoda, which, following Ahlberg and Clack (1998), Anderson defines as "a stem taxon comprising all taxa crownward of *Elpistostegalia*" (Anderson [2001:171]). These statements are problematical in three respects, as shown below.

First, Anderson (2001) gives me undue credit for having suggested a principle of priority of phylogenetic definitions of taxon names. Although I have tried to follow this principle in my work (e.g., Laurin and Reisz, 1997, 1999; Laurin, 1998), I am not one of the original proponents of this principle; those authors are de Queiroz and Gauthier (1990, 1992, 1994). Therefore, it is particularly puzzling that Anderson (2001) cites them as not following this principle and that he suggests that I use a principle of priority different from that of de Queiroz and Gauthier.

Second, the principle of priority proposed by de Queiroz and Gauthier (1990, 1992, 1994) does not appear to support Anderson's (2001) opinion that the concept of Tetrapoda

or Neotetrapoda proposed by Gaffney (1979) constitutes a valid phylogenetic definition. Indeed, de Queiroz and Gauthier (1990, 1992, 1994) did not recognize a name on a cladogram (as found in Gaffney, 1979) or other implicit references to a clade as a valid phylogenetic definition. Several passages in those articles tackle this issue. For instance, de Queiroz and Gauthier (1990:309) stated, "Thus, an evolutionary ostensive definition, hereafter referred to as a phylogenetic definition, consists of pointing to a clade, that is, to an ancestor and its descendants." The authors then explain that this can be accomplished in three ways, corresponding to the node-based, stem-based, and apomorphy-based definitions. Gaffney (1979) did not explicitly define the names Tetrapoda or Neotetrapoda.

Third, Anderson's (2001:171) statement that "Gaffney's Neotetrapoda is clearly a crown taxon and thus takes priority over a crown-based definition of Tetrapoda" is problematic because it is far from obvious (or certain) that Gaffney's concept of Neotetrapoda was crown-based. Anderson's (2001) opinion may stem from the observation that on Gaffney's (1979) Figure 2, Neotetrapoda coincides with a crown-group. However, Gaffney's (1979) Figure 1b shows an unresolved polytomy at the base of Neotetrapoda, which suggests that Gaffney's (1979) concept of Neotetrapoda was closer to a definition that used all the taxa stemming from the polytomy ("*Temnospondyli*," *Lissamphibia*, *Lepospondyli*, "*Anthracosauria*," and *Amniota*) as specifiers. Thus, if lepospondyls were the first group to diverge, they would still be part of Neotetrapoda, but Neotetrapoda would not correspond with a crown-group. Therefore, the name Neotetrapoda was not defined (or intended) as a crown-group, although some phylogenies can make this clade correspond to a crown-group (if *Lepospondyli* and *Lissamphibia* formed a clade that was the sister-group of the remaining taxa, for example). This interpretation is confirmed by Gaffney's statement (1979:95) that "Neotetrapoda are monophyletic and consist of an unresolved multichotomy tested by characters 12-16." All the taxa included by Gaffney (1979) in Neotetrapoda possessed these characters, so Neotetrapoda was closer to an apomorphy-based taxon than to a crown-based taxon. However, the statement

(Gaffney, 1979:98) that "*Crassigyrinus* . . . has a cheek with bone proportions more rhipidistian-like than occurs in *Ichthyostega*, but its lateral line system is in grooves not canals, a good neotetrapod (see below) character" is more suggestive of a stem-based concept of Neotetrapoda. That is, because the presence of a single character suggesting that *Crassigyrinus* was closer to temnospondyls, lepospondyls, and so forth than to *Ichthyostega*, Gaffney seems to have considered *Crassigyrinus* a neotetrapod on that basis. This impression is at least partly confirmed by his statement, "The Neotetrapoda is the group of tetrapods which are the sister group of *Ichthyostega* . . ." (Gaffney, 1979:102). Finally, despite the reference to characters in the discussion of Neotetrapoda, this name does not correspond to an apomorphy-based definition in the modern sense of the word either, because Gaffney (1979) referred to four (rather than just one) apomorphies. Gaffney (1979) may have meant to define Neotetrapod on the basis of the first ancestor that possessed all four characters, but he did not state this explicitly. Thus, Gaffney's (1979) concept of Neotetrapoda is not clearly crown-based, stem-based, or apomorphy-based, but that is not surprising because his paper was published before a formal distinction was made between these three kinds of taxonomic definitions. Given the uncertainty about to which ancestor (and its descendants) Gaffney's definition of Neotetrapoda applies (i.e., it is not even clear whether this concept was node-based, stem-based, or apomorphy-based), it seems best to consider that Gaffney's definition does not have priority, as I already suggested (Laurin, 1998:9).

The current draft of the PHYLOCODE (Cantino and de Queiroz, <http://www.ohiou.edu/phylocode/preface.html>) does not consider as established any of the definitions published before this code becomes effective, but the purpose of the above discussion is to show that Gaffney's concept of Neotetrapoda would not qualify as an established phylogenetic definition of this name. The definition of Tetrapoda that Anderson (2001) follows and that was formulated by Ahlberg and Clack (1998) is not valid according to the principles of synonymy and priority proposed by de Queiroz and Gauthier (1990, 1992, 1994) because

Tetrapoda was already defined by Gauthier et al. (1989). Anderson can use whatever definition of Tetrapoda and Neotetrapoda he wants because the principles of synonymy, homonymy, and priority of phylogenetic nomenclature are currently not compulsory, but his claim that his usage of these terms follows the proposals of de Queiroz and Gauthier (1990, 1992, 1994) is dubious.

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Fragmentary Taxa, Missing Data, and Ambiguity: Mistaken Assumptions and Conclusions

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It is unclear under what circumstances incomplete taxa will be problematic in phylogenetic analyses, and whether such potential problems are outweighed by the benefits of their inclusion. In Gauthier et al. (1988), the potential importance and uniqueness of fossil taxa despite their fragmentary nature was emphasized, and a total evidence approach (Kluge, 1989; Eernisse and Kluge, 1993) was advocated (see also Doyle and Donoghue, 1987). Later papers explicated analytical problems associated with missing data from incomplete fossil taxa in combined analyses (e.g., Crepet and Nixon, 1989a,b; Nixon and Wheeler, 1992; Novacek, 1992; Wilkinson, 1995a; Wiens, 1998). Many systematists are now reluctant to include fragmentary taxa because of perceived

problems associated with missing data, especially the relationship between missing data and ambiguity of results. Recently, some have suggested that, because of missing data associated with fossils, the positive effects of total evidence versus the potentially negative effects of missing data must be weighed (e.g., Nixon, 1996; Grande and Bemis, 1998; O'Leary, 2000).

Despite all the papers mentioned above, and despite the now popular buzzwords "missing data," it remains to be clarified whether commonly made generalizations about missing data hold true. Certainly, the assertion that adding incomplete taxa *necessarily* increases the number of primary trees or overall ambiguity is simplistic because many studies belie this assumption (e.g.,