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Use of Well-Known Names in Phylogenetic Nomenclature: A Reply to Laurin

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Laurin (2002) recently raised some concerns with my study (Anderson, 2001) that require clarification and merit further discussion. Laurin's criticisms fall into two categories: the monophyly of Lissamphibia (modern amphibians: frogs, salamanders, and caecilians) and my preference for a definition of Tetrapoda other than that of Gauthier et al. (1988), the definition with priority. The latter criticism touches upon several problems with the application of phylogenetic nomenclature to historical names that have arisen due to recent work (Laurin, 1998), which I address here in detail. I illustrate how adoption of the PhyloCode (Cantino and de Queiroz, 2000) resolves my nomenclatural issues. For purposes of clarity, I assume the large-scale tree shape found by Laurin and Reisz (1997), Laurin (1998), Anderson (2001), and Ruta et al. (in press) of (temnospondyls (lepospondyls + amniotes)) to be valid and stable. Thus, the discussion is limited to where lissamphibians root with respect to this topology and what names are appropriate for these clades.

LISSAMPHIBIA?

As Laurin (2002) summarized succinctly, there are three options for the origins of modern amphibians: They are a clade

with origins within Temnospondyli (temnospondyl hypothesis), they are a clade with origins within Lepospondyli (lepospondyl hypothesis), or they are polyphyletic with origins in both Temnospondyli and Lepospondyli (polyphyletic hypothesis). My study, which was an analyses of lepospondyl relationships, only included one lissamphibian, the Jurassic *Eocaecilia* (Jenkins and Walsh, 1993; Carroll, 2000) because caecilians have been cited as closely resembling such "microsaurs" as *Rhynchonkos* (Carroll and Currie, 1975; Carroll, 2000). Therefore, my study was not a test of lissamphibian monophyly (that work is ongoing), as was stated. However, Laurin took exception to a passing comment I made that my analyses suggested the possibility of a polyphyletic Lissamphibia. This comment of mine requires clarification.

I found *Eocaecilia* nested deeply within "microsaurs." Specifically, it was placed as the sister taxon to brachystelechids (node 23 of Anderson, 2001), and they in turn were sister taxa to *Rhynchonkos* (node 22). There are several synapomorphies supporting these relationships (nine and eight unambiguous synapomorphies, respectively; Anderson, 2001) and the more general placement of *Eocaecilia* within Lepospondyli. For example, there is the presence of the odontoid process of the atlas (a lepospondyl

synapomorphy also shared with salamanders), the palatal teeth forming a matching row lingual to the marginal teeth, the elongate vertebral column (a general lepospondyl character further accentuated in "microsaurs" and also shared with salamanders), and specializations of the lower jaw including a long retroarticular process. These characters are not present in frogs, which share other characters uniquely with temnospondyls such as *Dolesempetion* (Bolt, 1969, 1991; Trueb and Cloutier, 1991; Milner, 1993): alary processes on the premaxilla, bicondylar occipital condyles with no odontoid process of the atlas, large otic embayments on the posterior margins of the skull (which may have supported tympanic membranes in dissorophoids), wide rounded interpterygoid vacuities, and a shortened vertebral column.

In addition, Carroll et al. (1999) provided new vertebral developmental evidence to this controversy. They found that in frogs, like temnospondyls (branchiosaurs), the neural arch ossifies first, followed by a delay before the centrum ossifies. This pattern is also present in the tristichopterid sacropterygian *Eusthenopteron* and seems to be primitive for tetrapods (Cote et al., 2002). In contrast, salamanders and lepospondyls such as "microsaurs" (Carroll et al., 1999) and aïstopods (Anderson, 2002, in press) the entire vertebra ossifies simultaneously at an extremely early stage. The pattern of vertebral developmental in frogs would have to reverse to the primitive condition under the lepospondyl hypothesis, which is as parsimonious as the temnospondyl hypothesis (derived developmental pattern arises within lissamphibians and lepospondyls) but is one step less parsimonious than the polyphyletic hypothesis (derived vertebral pattern arises once, within lepospondyls including salamanders and caecilians). Furthermore, the order of divergence necessitated by the polyphyletic hypothesis of (frogs (salamanders + caecilians)) matches the pattern of divergence found by Feller and Hedges (1998), which is the context in which that article was cited.

Do the developmental or character data listed above mean anything with respect to monophyly of lissamphibians? No analyses has considered all of these different data simultaneously, let alone combined them with the molecular data cited by Laurin (2002). Despite the strength of the character evidence

of caecilians (and to a lesser extent salamanders) that supports a lepospondyl origin, lissamphibian monophyly within leospondyls is contradicted by anuran character and developmental data. Although Laurin's analyses (Laurin and Reisz, 1997; Laurin, 1998) support the lepospondyl hypothesis, the morphological characters listed above have led most workers to agree that Lissamphibia is nested within Temnospondyli (e.g., Bolt, 1991; Trueb and Cloutier, 1991; Gardiner, 2001). The temnospondyl hypothesis is also supported by the most comprehensive phylogenetic analyses of Paleozoic tetrapods yet attempted (Ruta et al., in press). However, the conflicting data are numerous enough that one new analyses (McGowan, 2002) supported the polyphyletic hypothesis. While my finding of a lepospondyl origin for at least one group of lissamphibians provides superficial support for the lepospondyl hypothesis, I was uncomfortable giving it my full support before incorporating dissorophoids (and less derived temnospondyls) into my analyses. Thus, I made my aside comment acknowledging the conflict in the data and one possible, and tantalizing, outcome. Obviously, this area of research is very contentious and requires further study along multiple lines of evidence.

HISTORICAL NAMES IN PHYLOGENETIC NOMENCLATURE

Laurin's second and more detailed line of criticism deals with my rejection of the definition with priority for Tetrapoda (Gauthier et al., 1988). Elsewhere Laurin and colleagues (Laurin et al., 2000) noted the controversy created by Laurin's (1998) adherence to strict priority of definition with respect to the names Tetrapoda and Anthracosauria and the ramifications of new tree topologies. They incorrectly attributed this controversy to "part of a larger controversy between practitioners of Linnean taxonomy... and practitioners of phylogenetic taxonomy" (Laurin et al., 2000:118). Although Laurin (2002) did not make this contention with respect to my article, my criticisms actually address a controversy within phylogenetic taxonomy over the applicability of the specific definitions of Tetrapoda and Anthracosauria that currently have priority and under what circumstances definitions with priority may be overturned. Disagreements over where

definitions are best placed are not rejections of phylogenetic taxonomy itself (Brochu and Sumrall, 2001). Most of my concerns have been addressed by the publication of the draft of the PhyloCode (Cantino and de Queiroz, 2000). Here, I outline my justifications for rejecting of the definitions with priority for Anthracosauria and Tetrapoda (Gauthier et al., 1988) and demonstrate how the implementation of the PhyloCode would resolve issues that have arisen when inadequately formed definitions are applied to new topologies (e.g., Laurin, 1998). I additionally argue for the PhyloCode, when it is published, to adopt new definitions for Anthracosauria and Tetrapoda that will preserve continuity of widely understood meanings of these taxon names.

Anthracosauria

Although there has been debate over the exact content of "Anthracosauria" (summarized by Panchen, 1970), a near consensus was reached that it included embolomeres (including *Anthracosaurus*), gephyrostegids, and others. Most of the controversy centered on the relative rank of Anthracosauria (Panchen, 1970; Panchen and Smithson, 1988). The anthracosaur concept was initially brought into the phylogenetic paradigm by Panchen and Smithson (1988), who proposed that anthracosaurs were part of a lineage called Reptilomorpha that ultimately led to amniotes. This change in concept involved including a series of Paleozoic stem amniotes within Anthracosauria. Gauthier et al. (1988) further associated amniotes with anthracosaurs by defining Anthracosauria to be a stem taxon including amniotes and all taxa closer to Amniota than Amphibia, but given their taxon sample and tree topology this definition produced a content that was consistent with earlier concepts of Anthracosauria, including that of Panchen and Smithson (1988). However, given the topology of Laurin and Reisz (1997), Laurin (1998), and Anderson (2001), this definition leads to the exclusion of most traditional "anthracosaurs," i.e., embolomeres, gephyrostegids, and even *Anthracosaurus*. This radical departure from the historical use of this name leads to confusion. Consider one of the problems found by Laurin (1998:11) with the definition of "Anthracosauria": "In the new phylogeny all anthracosaurs are more closely re-

lated to amniotes than embolomeres." This is extremely confusing because *Anthracosaurus* is an embolomere (Panchen, 1977), and for a number of years there was heated debate over whether "Anthracosauria" and "Embolomeri" were synonymous (Panchen, 1970).

The PhyloCode specifies (Article 11.8) that "a clade whose name is converted from a genus name under a preexisting code, or is derived from the stem of a genus name, should include the type of the genus name." Anthracosauria does not include *Anthracosaurus* in the trees of Laurin and Reisz (1997), Laurin (1998), and Anderson (2001) and should therefore be abandoned given these hypotheses. The PhyloCode continues (Article 11.8), "Therefore, when a name is converted from a preexisting genus name or is a new or converted name derived from the stem of a genus name, the definition of the clade name must use the type species of that genus as an internal specifier." This is the reason Laurin (2001) redefined Anthracosauria to be "the taxon including *Anthracosaurus russelli* and all taxa more closely related to *Anthracosaurus* than to *Rana pipiens*." Given the topology of Laurin (Laurin and Reisz, 1997; Laurin, 1998) and Anderson (2001), Anthracosauria encompass the same taxa as Embolomeri, which was defined by Laurin (1998) as the last common ancestor of *Proterogyrinus* and *Archeria*, and all its descendants. This definition preserves the meaning of Anthracosauria as a higher taxon including embolomeres and would be used should future analyses place another taxon, Seymouriamorpha for example, as sister group to embolomeres exclusive of all other taxa.

Furthermore, the PhyloCode provides mechanisms for the amendment (Article 13) or suppression (Article 15) of definitions with priority if they should contravene long accepted usage and thus create instability in nomenclature. If the PhyloCode were currently in effect, there would have been recourse for amending the situation where a name becomes displaced from its derivative species, preventing the current situation in which two parallel nomenclatures are in use.

Tetrapoda

Since its conception, Tetrapoda has referred to all taxa with digitized manus and pes. It is a widely known taxon easily

recognizable by nonspecialists. Gauthier et al. (1988) defined Tetrapoda as a crown taxon encompassing all organisms descended from the most recent common ancestor of extant amphibians and amniotes. Unlike their definition of Anthracosauria, their definition of Tetrapoda has never been consistent with traditional usage. This definition excludes the vast majority of Paleozoic limbed vertebrates given the topology of Laurin (Laurin and Reisz, 1997; Laurin, 1998) and Anderson (2001).

Gauthier et al. (1988) chose this definition for several reasons. First, they argued that well-known names should be attached only to crown groups, which may explain why they did not use Gaffney's (1979) Neotetrapoda, which as Laurin (2002) pointed out was not proposed as a node-based definition, presumably because of a lack of resolution at that node and because the convention was not developed for another 10 years. Gauthier et al. justified this position by stating that widely known names are used by "most biologists" when speaking of extant taxa and as such are already effectively crown names. Sereno (1998, 1999) disagreed with this assumption. General biology texts written by nonsystematists and nonpaleontologists examined by Sereno showed an evolutionary understanding of taxa not restricted to crown taxa. Additionally, although there is a physiological component to other names such as Aves (Gauthier and de Queiroz, 2001) and Mammalia (Rowe, 1988) that justifies the restriction of those names to the crown, no such component exists for Tetrapoda. The defining feature of tetrapods is based in hard anatomy easily preservable and observable in the fossil record, which is why for all previous uses of Tetrapoda as a taxon name, including that by Gaffney (1979), it included *Ichthyostega* and other fossils.

Gauthier et al. (1988) also argued that crown taxa are more stable because the whole creature is available for study (including rarely preserved soft anatomy), making recent taxa more fully known. Lee (1996) and Lee and Spencer (1997) demonstrated that there is no difference in stability in either content or meaning between definitions delimited by crown or extinct taxa. Lack of preservation of soft anatomy does not mean such anatomy was present or absent; its state is simply uncertain. What crown groups do, however, is provide brackets for inference of

soft anatomy in fossils (Witmer, 1997) and as such deserve a name of some sort (Brochu, 1999) but not necessarily the well-known name (Benton, 2000).

Opposition to the crown definition of Tetrapoda is so deep that some would prefer to abandon the name altogether. When presented with the (mistaken) alternatives of a crown-based definition (excluding many "tetrapods" from Tetrapoda) or a total group definition (including many nondigitized "fish" in Tetrapoda), Clack (1997:245) said, "I make a heartfelt plea herein for the term Tetrapoda not to be employed as a formal taxonomic term . . . in order to allow continued use of the vernacular term 'tetrapod' as it is widely understood."

This opposition is presumably because Tetrapoda is easily definable following phylogenetic conventions in such a way as to leave the traditional concept intact. I proposed (Anderson, 2001) a stem-based definition using crown tetrapods and Elpistostegalia as specifiers. However, this definition is not ideal because the discovery of more plesiomorphic forms that might be placed between *Ichthyostega* and Elpistostegalia could exclude an organism with unquestionable digits. Ahlberg and Clack (1998) offered another alternative, an apomorphy-based definition including all taxa with limbs rather than paired fins. Lee (1999) suggested modifying the formulation of the apomorphy-based definition so that it specifies the homology of the apomorphy in question (a modification adopted by the current draft of the PhyloCode; Cantino and de Queiroz, 2000). Following Lee (1999), Tetrapoda would be defined as including organisms derived from the sarcopterygian to have first possessed digits homologous with those in *Homo sapiens*, and all its descendants. This reformulation avoids most of the ambiguities of previous apomorphy-based definitions cited as undesirable by many workers (Bryant, 1994, 1996; Padian et al., 1999; Sereno, 1999). The PhyloCode states clearly (Article 10, Recommendation 10A) that conversion of names from Linnean taxonomy should minimize disruption of current usage. Article 11, Recommendation 11A states that definitions of converted names should attempt to capture the spirit of historical use within the contemporary concept of monophyly. Because the apomorphy-based definition best captures the original

meaning of Tetrapoda (de Queiroz and Gauthier, 1990) and would minimize disruption of current usage (unlike crown or total group definitions), I urge its adoption.

The reason I rejected the definitions with priority for Tetrapoda and Anthracosauria (Anderson, 2001) was not because I adhere to typological taxonomy or because priority of definition is unworkable. I rejected these definitions because they are inappropriate for the taxa in question. They do not capture the spirit of historical use and lead to confusion as a result. Both taxon names are definable in ways that capture historical use, and I hope that these proposed definitions are adopted in some form upon the publication of the PhyloCode. I also hope that biologists who have reservations regarding the PhyloCode will examine these case studies to see how a set of rules is necessary to reduce nomenclatural instability as we move to a phylogenetic concept of taxa. The instability illustrated here is not the fault of phylogenetic nomenclature itself but rather is the result of the period of transition currently underway within classification.

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New Zealand Kauri (*Agathis australis* (D. Don) Lindl., Araucariaceae) Survives Oligocene Drowning

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The drowning of New Zealand's landmasses during the Oligocene period (30 million years ago [MYA]) was a major environmental crisis for the biota of New Zealand. The extent of submergence has been controversial. New Zealand is thought by some to have been reduced to relatively small areas of landmass (Cooper and Cooper, 1995, and references therein; Hickson et al., 2000) and by others to have been completely submerged

(Pole, 1994; Macphail, 1997). Certainly the diversity of some faunal groups appears to have been severely reduced (bottlenecked) during this period (Cooper and Cooper, 1995; Hickson et al., 2000). In contrast, the effect of land reduction on plant diversity has been more difficult to interpret (McGlone et al., 2000; Lee et al., 2001).

A number of extant plant groups first appear in the fossil record in New Zealand