

Early tetrapod evolution

Laurin *et al.*'s recent *TREE* review of early tetrapod evolution¹ focused on the implications of Laurin's² recent cladistic analysis, and pondered developmental changes that could have been involved in the fin–limb transition. Their article raised several issues that deserve comment.

In general, we support Laurin *et al.*'s exploration of node-based taxon definitions, but wonder why they ignored the use of 'total groups'³. A tetrapod total group would include all fossils phylogenetically closer to living tetrapods than to lungfishes and coelacanths. Thus, osteolepiform fishes would be recognized as tetrapods in the broadest sense⁴.

However, this also illustrates one of several problems with nodal definitions that were not discussed in the original article. First, there is a danger that we might be doomed to have higher taxonomic terms only citable *sensu* a specific author for their meaning to be unambiguous. Can fishes be tetrapods? This might seem to be merely a matter of 'badging' and systematists need to be aware that they are only one component of the biological community. In practice, the world at large also has a say about what is, or is not, a tetrapod. Second, a nominate form or subgroup could end up outside the taxon named after it, in contrast to all previous usage. For example, the Anthracosauria (previously allied to the amniotes) now excludes *Anthracosaurus* itself. Third, long-abandoned terms are resurrected with novel content and meaning. Thus, the Stegocephali, formerly an archaic amphibian-grade group of early tetrapods⁵, now includes ourselves(!).

Curiously, the pectoral fins of *Panderichthys*⁶ – probably the most tetrapod-like fish (in the colloquial sense) discovered thus far – are ignored in the discussion of the fin–limb transition. Panderichthiid homologues of humerus, radius and ulna share unique specializations with those of primitive tetrapod limbs. However, the more distal parts of panderichthiid fins do not equate easily with ankles, wrists and digits. In fact, the diversity of outermost skeletal fin and limb patterns indicates profound differences (and thus changes) in the regulation of distal developmental patterning. Therefore, attempts to infer the fate of a fin skeletal axis in the extremities of a tetrapod limb might be entirely misplaced, as suggested by recent developmental research⁷.

Although Laurin's database² is impressively large, unlike those of earlier analyses^{8,9}, it fails to resolve relationships among such primitive taxa as colosteids and *Crassigyrinus*, or *Acanthostega* and *Ichthyostega*. Nonspecialists should be made aware that these tetrapods are anatomically very distinct. Therefore, Laurin's analysis is less informative about evolutionary patterns close to the fish–tetrapod transition than other recent hypotheses, because it cannot discriminate between more primitive and more advanced anatomical conditions at that level of the phylogeny.

Laurin *et al.* do not fully discuss the evolutionary implications of their tree. If, as they conclude, temnospondyls (regarded by many as stem lissamphibians) are separated from lissamphibian ancestry^{10,11}, then a stunning array of features related to hearing, breathing and vocalization in temnospondyls must be evolutionarily convergent with those of lissamphibians (Fig. 1).

It is also noteworthy that all recently published phylogenies, including those of

Laurin *et al.*, imply that the lissamphibian–amniote split must have occurred some 340 million years ago in the early Carboniferous. However, when Laurin's phylogenetic tree is plotted against a stratigraphic column, a huge gap in the fossil record of lissamphibian ancestry becomes apparent. Meanwhile, the vast array of convergent (?) Permo–Carboniferous temnospondyls are, in effect, discarded.

Therefore, we were interested to discover that the lengths of Laurin's² trees increase only minimally when lissamphibians are grafted to various positions within the temnospondyls. These length differences vary from 3.85% when lissamphibians are the sister group of *Apateon* (a Permian temnospondyl genus), to 5.7% when lissamphibians are placed as a sister group to temnospondyls as a whole.

Laurin's challenging hypothesis² requires careful consideration of taxa, characters and methodology. One question is whether such large exercises, using a thin scattering of selected taxa, can ever deliver useful results. In order to encompass the entire lower Tetrapoda, many substantial clades are represented by only a few genera for operational reasons; however, omitted genera also have a significant information content. Smaller, more focused analyses might be a necessary prerequisite to consideration of the 'big picture'.

Laurin *et al.* should not fear that the 'lepospondyl theory' of lissamphibian origin is not generating enough interest. As Colin Patterson put it: 'After all, good morphology lasts forever, whereas today's matrix and the cladograms it yields will soon be superseded'¹².

Michael I. Coates
Marcello Ruta

Dept of Biology, Darwin Building,
University College London,
Gower Street, London,
UK WC1E 6BT
(m.coates@ucl.ac.uk;
m.ruta@ucl.ac.uk)

Andrew R. Milner

Dept of Biology, Birkbeck College,
University of London,
Malet Street, London,
UK WC1E 7HX
(a.milner@biology.bbk.ac.uk)

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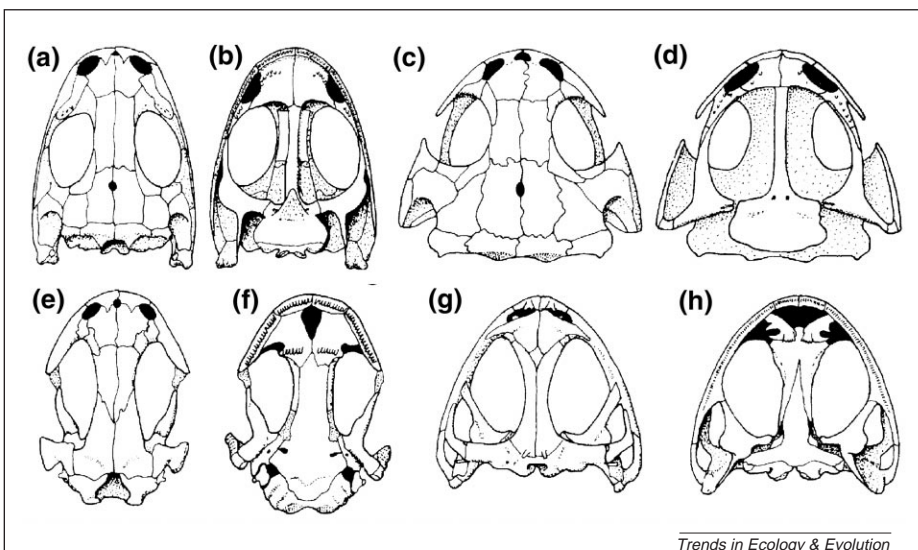


Fig. 1. Skulls of temnospondyls and lissamphibians in dorsal views [(a), (c), (e) and (g)] and palatal views [(b), (d), (f) and (h)]. These show either a remarkable case of evolutionary convergence or a series of uniquely derived and shared cranial specializations (e.g. spade-shaped skulls, broad palatal vacuities, lateral otic notches, tooth reduction, pedicellate teeth, double occipital condyles and circumorbital bone reduction, etc.). (a) and (b) *Dolesempetron*, a temnospondyl; (c) and (d) *Schoenfelderpeton*, a temnospondyl; (e) and (f) *Hynobius*, a lissamphibian; and (g) and (h) *Barbourula*, a lissamphibian. Reproduced, with permission, from Ref. 10.

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Reply from M. Laurin, M. Girondot and A. de Ricqlès

Coates *et al.*'s letter¹, dealing with our recent *TREE* review, shows that some of the points we made deserve to be clarified further.

Coates *et al.*¹ wonder why we 'ignored the use of total groups'. The taxonomy that we used included the first published phylogenetic definitions (referring to 'node-based' taxa and 'total groups'), because such definitions were introduced primarily to provide a system of synonymy and priority above the genus level². This system clarifies the taxonomy (rather than confusing it further) because there is only one valid phylogenetic definition (the first published one) for each taxon name.

We did not discuss the fins of panderichthyids (the closest known relatives of stegocephalians) because their extremities are apparently simplified and unlike those of any other known sarcopterygians³, and thus might represent an autapomorphy of this group.

The lack of resolution between the earliest stegocephalians in one of Laurin's phylogenies⁴ is not surprising. A comparison of recently published phylogenies of stegocephalians^{5,6} shows that we are far from a consensus and that most of the recently published trees are wrong (because only one can be right). More recent studies by Laurin resolve the phylogeny fully^{7,8}.

The array of features related to hearing (otic notch and slender stapes, etc.), which are claimed¹ to be shared between temnospondyls and lissamphibians (actually present only in anurans, among lissamphibians), are known to be homoplastic because the classic phylogeny implies that they have been lost (twice?) by urodeles and apodans. Therefore, these characters do not support the traditional phylogeny. Furthermore, the claimed function of many of

these features in temnospondyls is poorly established⁴.

The large gap in the fossil record of lissamphibians, implied by the phylogeny of Laurin⁴, is not surprising given the extremely poor fossil record of that group (there is a single known specimen in the Triassic, that lasted for about 37 million years)⁹ – this gap is only marginally longer than that implied by the classic phylogeny (about 78 million years instead of 66 million years).

Coates *et al.*¹ report that changing the position of Lissamphibia (to reflect the widely held view that they are temnospondyls) increases the tree length by 3.85% or 5.7%, and they suggest that this increase is minimal. However, a 'winning-sites' test¹⁰ indicates that the trees discussed by Coates *et al.*¹ are statistically worse ($P < 0.001$) than the shortest tree, in which lissamphibians are 'lepospondyls' (note also that a fully resolved tree with 40 terminal taxa possesses 78 branches, each accounting, on average, for only 1.3% of the total length).

For many years, progress in understanding stegocephalian phylogeny was hampered by the fact that small groups were analysed in isolation. Such studies^{11,12} are useful to document the phylogeny within obviously monophyletic groups, but they can neither provide a test of the relationships between these clades nor test the monophyly of these groups.

We agree that morphological descriptions are valuable, but we suggest that one of the most interesting uses of such data is the production of phylogenies, which can be tested as any other hypothesis. We suggest that the next step in this debate is for other scientists to perform phylogenetic analyses designed to test the origin of lissamphibians.

**Michel Laurin
Marc Girondot
Armand de Ricqlès**

Équipe 'Formations squelettiques',
UMR CNRS 8570 'Evolution et adaptation
des systèmes ostéomusculaires', Case
7077, Université Paris 7-Denis Diderot,
2 place Jussieu, F-75251 Paris Cedex 05,
France (laurin@ccr.jussieu.fr;
mgi@ccr.jussieu.fr; ricqlès@ccr.jussieu.fr)

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