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RECOMMENDATION

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lennifer Olori and two anonymous

Correspondence:

r.asher@zoo.cam.ac.uk

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The origins of Lissamphibia

Robert | Asher¹

¹ Department of Zoology, University of Cambridge - Cambridge, UK

A recommendation of

Laurin M, Lapauze O, and Marjanović D (2019). What do ossification sequences tell us about the origin of extant amphibians? bioRxiv 352609, ver. 4 peer-reviewed by PCI Paleo. DOI: 10.1101/352609

Among living vertebrates, there is broad consensus that living tetrapods consist of amphibians and amniotes. Crown clade Lissamphibia contains frogs (Anura), salamanders (Urodela) and caecilians (Gymnophiona); Amniota contains Sauropsida (reptiles including birds) and Synapsida (mammals). Within Lissamphibia, most studies place frogs and salamanders in a clade together to the exclusion of caecilians (see Pyron and Wiens, 2011). Among fossils, there are a number of amphibian and amphibian-like taxa generally placed in Temnospondyli and Lepospondyli. In contrast to the tree of living tetrapods, affinities of these fossils to some or all of the three extant lissamphibian groups have proven to be much harder to resolve. For example, temnospondyls might be stem tetrapods and lissamphibians a derived group of lepospondyls; alternatively, temnospondyls might be closer to the clade of frogs and salamanders, and lepospondyls to caecilians (compare Laurin et al., 2019, fig. 1d vs. 1f).

Here, in order to assess which of these and other mutually exclusive topologies is optimal, Laurin et al. (2019) extract phylogenetic information from developmental sequences, in particular ossification. Several major differences in ossification are known to distinguish vertebrate clades. For example, due to their short intrauterine development and need to climb from the reproductive tract into the pouch, marsupial mammals famously accelerate ossification of their facial skeleton and forelimb; in contrast to placentals, newborn marsupials can climb, smell and suck before they have much in the way of lungs, kidneys, or hindlimbs (Smith, 2001).

Divergences among living and fossil amphibian groups are likely pre-Triassic (San Mauro, 2010; Pyron, 2011), much older than a Jurassic split between marsupials and placentals (Tarver et al., 2016), and the quality of the fossil record generally decreases with ever-older divergences. Nonetheless, there are a number of well-preserved examples of "amphibian"-grade tetrapods representing distinct ontogenetic stages (Schoch, 2003, 2004; Schoch and Witzmann, 2009; Olori, 2013; Werneburg, 2018; among others), all amenable to analysis of ossification sequences.

Putting together a phylogenetic dataset based on ossification sequences is not trivial; sequences are not static features apparent on individual specimens. Rather, one needs multiple specimens representing



discrete developmental stages for each taxon to be compared, meaning that sequences are usually available for only a few characters. Laurin et al. (2019) have nonetheless put together the most exhaustive matrix of tetrapod sequences so far, with taxon coverage ranging from 62 genera for appendicular characters to 107 for one of their cranial datasets, each sampling between 4-8 characters (Laurin et al., 2019, table 1). The small number of characters means that simply applying an optimality criterion (such as parsimony) is unlikely to resolve most nodes; treespace is too flat to be able to offer optimal peaks up which a search algorithm might climb. However, Laurin et al. (2019) were able to test each of the main competing hypotheses, defined a priori as a branching topology, given their ossification sequence dataset and a likelihood optimality criterion. Their most consistent result comes from their cranial ossification sequences and supports their "LH", or lepospondyl hypothesis (Laurin et al., 2019, fig. 1d). That is, relative to extinct, "amphibian"-grade taxa, Lissamphibia is monophyletic and nested within lepospondyls.

Compared to mammals and birds (including dinosaurs), crown amphibian branches of the Tree of Life are exceptionally old. Each lissamphibian clade likely had diverged during Permian times (Marjanović and Laurin, 2008) and the crown group itself may even date to the Carboniferous (Pyron, 2011). In contrast to mammoths and moas, no ancient DNA or collagen sequences are going to be available from >300 million-year-old fossils like the lepospondyl *Hyloplesion* (Olori, 2013), although recently published methods for incorporating genomic signal from extant taxa (Beck and Baillie, 2018; Asher et al., 2019) into studies of fossils could also be applied to these ancient divergences among amphibian-grade tetrapods. Ossification sequences represent another important, additional source of data with which to test the conclusion of Laurin et al. (2019) that monophyletic Lissamphibians shared a common ancestor with lepospondyls, among other hypotheses.

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Appendix

Reviews by Jennifer Olori and two anonymous reviewers, DOI: 10.24072/pci.paleo.100002.