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# What do ossification sequences tell us about the origin of extant amphibians?



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Third preprint posted right about now: <https://www.biorxiv.org/content/10.1101/352609v3>

## Updated abstract

The controversial origin of extant amphibians has been studied using several sources of data and methods, including phylogenetic analyses of morphological data, molecular dating, stratigraphic data, and integration of ossification sequence data, but a consensus has failed to emerge.

We have compiled five datasets to assess the relative support for six competing hypotheses about the origin of extant amphibians:

- a monophyletic origin among temnospondyls (TH, a),
- a monophyletic origin among lepospondyls (LH, b),
- a diphylectic origin among both temnospondyls and lepospondyls (DH1, c),
- a diphylectic origin among temnospondyls alone (DH2, d),
- and two variants of a triphyletic origin, in which frogs & toads (Anura) and salamanders & newts (Urodela) come from different temnospondyl taxa while caecilians (Gymnophiona) come from lepospondyls and are either closer to amniotes (PH1, e) or to anurans and urodeles (PH2, f).

Our datasets comprise ossification sequences of up to 107 terminal taxa and up to eight cranial bones, and up to 65 terminal taxa and up to seven appendicular bones, respectively.

Among extinct taxa, only two or three temnospondyls can be analyzed simultaneously for cranial data, but this is not an insuperable problem because each of the six tested hypotheses implies a different position of temnospondyls and caecilians relative to other sampled taxa.

For appendicular data, more extinct taxa can be analyzed, including two lepospondyls and the finned tetrapodomorph *Eusthenopteron*, in addition to more temnospondyls.

The data are analyzed through maximum likelihood, and the AICc (corrected Akaike Information Criterion) weights of the six hypotheses allow us to assess their relative support.

By an unexpectedly large margin, our analyses of the cranial data support a monophyletic origin among lepospondyls; a monophyletic origin among temnospondyls, the current near-consensus, is a distant second. All other hypotheses are exceedingly unlikely according to our data.

Surprisingly, analysis of the appendicular data supports triphyly of extant amphibians within a clade that unites lepospondyls and temnospondyls (f), contrary to all recent paleontological phylogenies, but this conclusion is not very robust.

## Methods

Phylogenetic analyses of our data (see preprint) show that phylogenetic signal is present (more in cranial than in appendicular ossification sequences), but insufficient (para- or polyphyletic frogs, mammals etc.). Therefore we tested instead how well the data fit each of the trees in the Figure in CoMET (Lee et al. 2006) for Mesquite (Maddison & Maddison 2018).

CoMET cannot handle missing data. This creates a tradeoff between including more taxa vs. more characters in the same analysis. Therefore we ran five different analyses:

- 105 terminal taxa (incl. 2 *Apateon* spp.), 7 cranial characters
- 107 taxa (incl. 2 *Apateon* spp. and *Sclerocephalus*), 6 cranial characters
- 84 taxa (incl. 2 *Apateon* spp. and *Sclerocephalus*), 8 cranial characters
- 62 taxa (incl. 2 *Apateon* spp., *Micromelerpeton*, *Sclerocephalus*, *Archegosaurus*, *Eusthenopteron*, *Microbrachis*, *Hyloplezion*), 7 appendicular characters
- 65 taxa (incl. 2 *Apateon* spp. from 2 localities each, "*Melanerpeton humbergense*", and all the above), 4 appendicular characters

There are not enough cranial data available for any outgroups or any potential lepospondyls (including aïstopods). Nonetheless, in the first two analyses, all six trees in the Figure are distinguishable by the positions of caecilians or *Apateon*.

Caecilians (and aïstopods) do not have an appendicular skeleton; therefore, the trees for TH, DH1, DH2 (a, c, d) become identical in the last two analyses, but they are doubled into variants by alternative positions of *Micromelerpeton* (not shown).

## Results: AICc weights

(add up to 1, more is better)

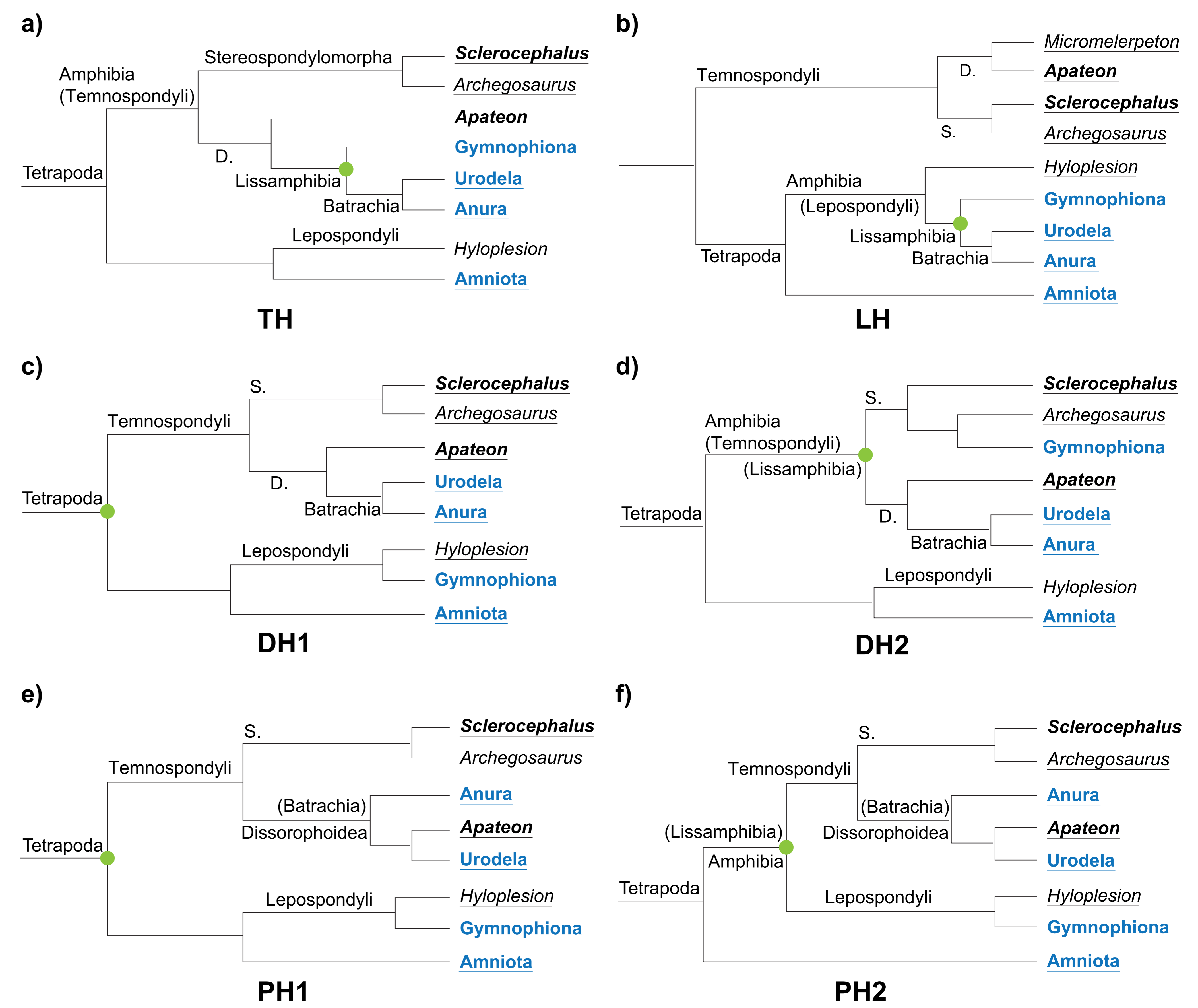
Dataset	Cranial			Appendicular		
	105	107	84	62	65	
Terminal taxa	105	107	84	62	65	
Characters	7	6	8	7	4	
TH (a)	0.1056	0.0114	6.493 E-3			
LH (b)	<b>0.8848</b>	<b>0.9885</b>	<b>0.9935</b>	2.177 E-3	0.21407	LH
DH1 (c)	<b>4.42 E-4</b>	1.738 E-5	6.493 E-3	0.1874	0.05492	TH/DH I
DH2 (d)	6.89 E-4	1.827 E-7	6.493 E-3	<b>3.027 E-4</b>	<b>0.03713</b>	TH/DH II
PH1 (e)	1.792 E-3	1.196 E-7	<b>1.628 E-5</b>	0.01232	0.05653	PH1
PH2 (f)	6.615 E-3	<b>7.143 E-8</b>	<b>1.628 E-5</b>	<b>0.7978</b>	<b>0.63735</b>	PH2

Blue: best; green: 2<sup>nd</sup> best; red: worst.

The analysis with 84 taxa and 8 cranial characters lacks caecilians, so cannot distinguish between TH, DH1 and DH2 or between PH1 and PH2.

TH/DH I: *Micromelerpeton* close to *Apateon* (often found, but likely due to convergent paedomorphosis); TH/DH II: *Micromelerpeton* as basal dissorophoid (mainstream).

DH2 (d), proposed only in 2017 (Pardo et al.), always 2<sup>nd</sup> or 3<sup>rd</sup> worst with cranial data, always worst with appendicular.



**Bold:** cranial data; **underlined:** appendicular data. **Blue:** extant. **Green dot:** last common ancestor of all extant amphibians. **D.:** Dissorophoidea; **S.:** Stereospondylomorpha. *Hyloplezion* always also stands in for its sister-group *Microbrachis*; "*Melanerpeton humbergense* (not shown, appendicular only) is always the sister-group of *Apateon*"; see text for *Micromelerpeton* except in b).

**a) Temnospondyl hypothesis:** lissamphibians as dissorophoid temnospondyls. Currently mainstream.

**b) Lepospondyl hypothesis:** lissamphibians nested among at least some "lepospondyls", temnospondyls are stem-tetrapodomorphs. So far found only by ML & varying coauthors (latest & largest: Marjanović & Laurin 2019) and Pawley (2006).

**c) Diphyly hypothesis 1:** frogs & salamanders (Batrachia) as in a), caecilians as lepospondyls. Currently abandoned; most famously found by Anderson et al. (2008).

**d) Diphyly hypothesis 2:** batrachians as in a), caecilians as stereospondyl temnospondyls. Found by Pardo et al. (2017) in their Bayesian analysis, and as one of four equally most parsimonious results, using a dataset that contained only batrachians, caecilians and temnospondyls.

**e) Polyphyly hypothesis 1:** salamanders (crown group: *Urodela*) next to *Apateon* and "*M. humbergense*", frogs (crown group: *Anura*) elsewhere in Dissorophoidea, caecilians (crown group: *Gymnophiona*) as lepospondyls like in c). Never found in a phylogenetic analysis; argued for most recently and in the greatest detail by Carroll (2007).

**f) Polyphyly hypothesis 2:** like e), but temno- and lepospondyls as sister-groups to the exclusion of Amniota. Never explicitly proposed, but implied in papers e.g. by Carroll from the 1970s through early '90s (before an amniote-lepospondyl clade became consensus).

## Discussion

The cranial ossification sequences contain a strong phylogenetic signal that supports the lepospondyl hypothesis (d) much more robustly than expected. Cranial ossification sequence data should be added to future phylogenetic analyses.

The appendicular ossification sequences, on the other hand, show the same distribution as preaxial polarity in limb development. This may be an ecological signal (although a phylogenetic signal is present): all sampled taxa that use(d) the developing limbs for locomotion underwater – salamanders (plesiomorphically), temnospondyls, *Microbrachis* + *Hyloplezion* – belong to the "amphibian clade" in polyphyly hypothesis 2 (f), so that tree is favored by these data. In a larger taxon sample, preaxial polarity is plesiomorphic (see preprint and e.g. Marjanović & Laurin 2019).

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