

# The new problem of *Chinlestegophis* and the origin of caecilians (Amphibia, Gymnophionomorpha) is highly sensitive to old problems of sampling and character construction

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## Abstract

The description of the small Late Triassic temnospondyl *Chinlestegophis* ushered in a potentially radically new understanding of the origins of the extant amphibian clades. Together with the fragmentary *Rileymillerus*, *Chinlestegophis* was argued to link extant caecilians to Permo-Triassic stereospondyl temnospondyls rather than to frogs and salamanders (and through them to amphibamiform temnospondyls or to brachystelechid and lysorophian “lepospondyls”). We critically review the comparative description of *Chinlestegophis* and phylogenetic analyses of previous studies. Most of the features previously interpreted to be shared by caecilians, *Chinlestegophis* and/or other stereospondyls have different distributions than scored in the analysis. We also find no evidence for an incipient tentacular sulcus in *Chinlestegophis*, and note that its vertebrae, unreduced ribs and dermal shoulder girdle are unlike those of any extant amphibians (nor their likely sister group, Albanerpetidae). Furthermore, the original matrices contain misscores accrued over more than a decade that likewise influence the results. Some features are coded as multiple redundant characters: the double tooththrow of *Chinlestegophis*, other stereospondyls, and caecilians is represented as seven characters. Analysis of the unmodified matrix yields much less resolution than originally reported, and tree topology is altered by a small change to the taxon sample (the addition of Albanerpetidae), limited revisions of irreproducible scores, and ordering the most obviously clinal characters; any one of these changes removes *Chinlestegophis* from Lissamphibia, and confirms it as a stereospondyl.

## Key Words

Amphibia, *Chinlestegophis*, *Funcusvermis*, Gymnophiona, Gymnophionomorpha, Lissamphibia, majority-rule consensus, phylogenetics, phylogeny

## Introduction

Caecilians have a scanty fossil record (Santos et al. 2020; Kligman et al. 2023); the earliest well-supported stem members are *Funcusvermis gilmorei* Kligman et al., 2023 (Late Triassic), and *Eocaecilia micropodia* Jenkins & Walsh, 1993 (Jenkins and Walsh 1993; Early Jurassic).

*Eocaecilia* retains limbs and some cranial bones that are absent in the caecilian crown group (Gymnophiona; see Wake 2020); partial femora were also assigned to *Funcusvermis* and the Early Cretaceous or, more likely, Late Jurassic (Lasseron et al. 2019) *Rubricacaecilia monbaroni* Evans & Sigogneau-Russell, 2001 (Evans and Sigogneau-Russell 2001; Kligman et al. 2023).

Since *Eocaecilia* was named, a more thorough anatomical study (Jenkins et al. 2007) and many phylogenetic analyses confirmed its position along the caecilian stem (Laurin 1998; Vallin and Laurin 2004; Maddin et al. 2012a; Pardo et al. 2017a: fig. S6). However, despite the absence of serious doubts about the status of *Eocaecilia* in the literature (Evans and Sigogneau-Russell 2001; Carroll 2007: 54; Sigurdson and Bolt 2010: 1373; further corroborated by Kligman et al. 2023), Pardo et al. (2017a: abstract) stated: “The position of *Eocaecilia* within tetrapod phylogeny is controversial, as it already acquired the specialized morphology that characterizes modern caecilians by the Jurassic.” That statement is misleading: all phylogenetic analyses that included *Eocaecilia* support its placement as a stem-caecilian; it is the position of caecilians as a group in the context of its ancestry among extinct tetrapods that remained controversial.

To this controversy, Pardo et al. (2017a) added *Chinlestegophis jenkinsi*, which they named and described as a stem-caecilian from the Late Triassic (slightly younger than *Funcusvermis*: Kligman et al. 2023). Their phylogenetic analyses surprisingly appeared to anchor the caecilians (through *Chinlestegophis*) within the stereospondyl temnospondyls, whereas frogs and salamanders (i.e., batrachians) remained in a more common placement as dissorophoid temnospondyls, producing a new and confidently delivered hypothesis of lissamphibian origins. The captivating notion of the problem of amphibian origins and the evolution of specialized caecilian traits having been “solved” with the discovery of *Chinlestegophis* has already permeated popular zoology textbooks (Pough et al. 2022: figs. 9.2 and 9.5).

Although we agree that *Chinlestegophis* presents an interesting mix of characters, we wish to respond to claims Pardo et al. (2017a) made about *Chinlestegophis* that were incompletely tested in that and subsequent studies (Schoch et al. 2020; Serra Silva and Wilkinson 2021; Gee 2022; Kligman et al. 2023). We find in Pardo et al. (2017a), and review and evaluate below: 1) problems with the matrices used, including narrow taxon sampling, errors and oversights in character construction and modification, and incorrect scores within the original data sets underpinning the resulting matrices; 2) a suboptimal methodology, including reliance on a majority-rule consensus tree and incomplete reporting of tree statistics; and 3) qualitative problems with the diagnostic features linking *Chinlestegophis* (and in some cases *Rileymillerus* Bolt & Chatterjee, 2000) to caecilians. Our reanalyses show that *Chinlestegophis* in particular and stereospondyls in general currently cannot be supported as stem-caecilians and should not be treated as such in textbooks or in secondary analyses, such as molecular estimates of divergence times (as previously stated by Santos et al. 2020 and Kligman et al. 2023).

## Scope

Recent works have investigated selected aspects of the work of Pardo et al. (2017a). Marjanović and Laurin (2018) and Serra Silva and Wilkinson (2021) reanalyzed one of the two matrices, finding that the published majority-rule consensus tree was a highly incomplete presentation of the results. Kligman et al. (2023: supplementary information parts 3–4) reevaluated a large number of scores of that matrix, enlarged the taxon sample and discussed the character states that Pardo et al. (2017a) had used to tie caecilians to *Chinlestegophis* and other stereospondyls, focusing on their distribution in stereospondyls. We focus on their distribution in lissamphibians and so-called lepospondyls, experiment with (and discuss) ordering characters, adding taxa and reevaluating a different set of scores, and first of all we reanalyze the other matrix for the first time, both without and with a topological constraint.

## Nomenclature and terminology

Our usage of the clade names Gymnophiona, Amphibia and Lissamphibia follows Wake (2020) and Laurin et al. (2020a, b); temnospondyl nomenclature follows Schoch (2013, 2018), except for the names Temnospondyli, Euskelia and Limnarchia (Yates and Warren 2000). Whenever practicable, we applied the same set of names to all figures. Junior synonyms are shown in parentheses, and names that cannot be applied to a particular tree (because of qualifying clauses or definitions that restrict their applicability to certain phylogenetic contexts) are not shown on that tree. Schoch (2013) gave identical definitions for Stereospondyli and Stereospondylomorpha; it is obvious that that is an accident and that the intended definition for Stereospondyli can be recovered by replacing “most” by “least”. Misspellings of genus and species names in the matrices and figures of Pardo et al. (2017a) are corrected. See Marjanović and Laurin (2019: 13) for the correction of “Albanerpetontidae” to Albanerpetidae.

We use “caecilians” for crown-group caecilians (Gymnophiona: Wake 2020) and their uncontroversial relatives like *Eocaecilia* and *Funcusvermis*. The names Lepospondyli and Microsauria are used here informally for traditional groupings of taxa; the likely para- or polyphyly of these groupings (supported and reviewed by Marjanović and Laurin 2019) is beyond the scope of this work. For simplicity we present these names without quotation marks throughout.

We use “coding” for the process of choosing and defining the characters and their states, and “scoring” for filling in the matrix. Observed morphology is “miscoded” if, for example, it is represented as two redundant characters in the character sample, but “misscored” if the scores (numbers, state symbols) in the matrix are not what they should be according to the existing state definitions.

## Abbreviations

<b>AMNH FARB</b>	Collection of Fossil Amphibians, Reptiles and Birds at the American Museum of Natural History (New York).
<b>app.</b>	appendix (of cited works).
<b>CI</b>	consistency index.
<b>MPT</b>	most parsimonious tree.
<b>MRC</b>	majority-rule consensus.
<b>OTU</b>	operational taxonomic unit (a line in a data matrix).
<b>RC</b>	rescaled consistency index.
<b>RI</b>	retention index.
<b>supp. inf.</b>	supplementary information (of cited works).

## Matrices, methodologies, and missteps

### Matrix history and taxon sampling

Pardo et al. (2017a) analyzed two matrices: a taxonomically broader, unpublished dataset, and an expanded, published matrix focused on the position of *Chinlestegophis* and *Rileymillerus* within temnospondyls. The originally unpublished matrix (see Suppl. material 1 for a NEXUS file), which generated the trees shown in Pardo et al. (2017a: fig. S6), contains 319 characters (27 of them parsimony-uninformative, including five constant ones) and 71 OTUs; it is based on the matrix of Maddin et al. (2012a), with additions of characters and taxa from Huttenlocker et al. (2013) and several new ones. Those earlier matrices are based on that of Anderson et al. (2008a), but subsequently proposed corrections to that matrix (Marjanović and Laurin 2009; Skutschas and Martin 2011; Sigurdson and Green 2011) were neither included in the resulting composite matrix nor addressed in the text by Pardo et al. (2017a) or any of the references therein. Those changes have considerable influence on the resulting tree topology, as exemplified in Fig. 1.

The published matrix (Pardo et al. 2017a: supporting information part D), which generated the trees shown in Pardo et al. (2017a: fig. 2, 3, S7), has 345 characters (23 parsimony-uninformative) and 76 OTUs. It is built on the unpublished matrix by the deletion of most non-temnospondyl taxa and the addition of characters and taxa taken primarily from Schoch (2013)—see Gee (2022) for a thorough discussion of that lineage of matrices.

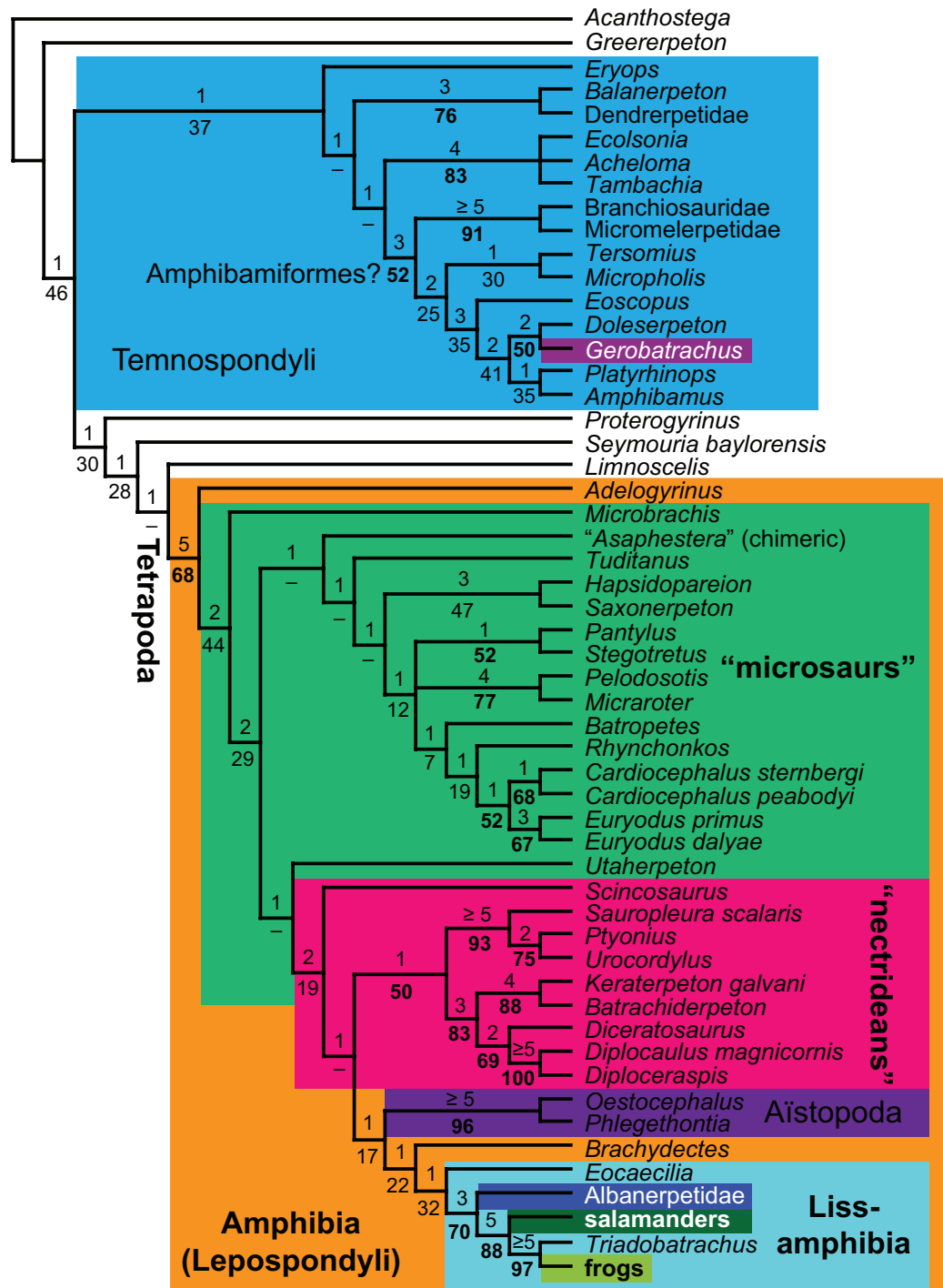
It is, of course, common practice to modify and expand existing data sets, and underlying errors are frequently perpetuated into later generations of matrices when first-hand reassessment of specimens is infeasible, detailed comparison to the literature is deemed too time-consuming, or the full history of characters becomes obscured over time, leading to different meanings of the same character for different taxa that were added or revised at different times (Marjanović and Laurin 2019;

Gee 2021, 2022). In those cases, conservative practice is to accept preexisting descriptions and scores as reliable. However, over many iterations of matrices, substantial errors can and do accumulate—this is a known and pervasive problem with large data matrices that are recycled in consecutive studies (Simões et al. 2017; Laurin and Piñeiro 2018; Marjanović and Laurin 2019; Gee 2021, 2022; Kligman et al. 2023: supp. inf. part 4; and see our Discussion section).

The merging of existing matrices can also generate additional problems related to redundant characters and states. As an example, multiple characters related to the lower jaw in the published matrix of Pardo et al. (2017a) carry redundancy (in particular characters 147, 148, 146, 272, 273, 322, 344; see full evaluation below), and because each is strongly associated with specialized morphologies mainly observed in caecilians, they may, even when correctly scored, generate bias by inflating support for the purported relationship between *Chinlestegophis* and caecilians. Moreover, as characters are merged, moved, modified, and added, it becomes increasingly easy to overlook simple mechanical errors, such as state 26(2) being mentioned neither in the list of state labels within the matrix file nor in the character list despite all three states being scored for numerous taxa in the matrix (Pardo et al. 2017a: SI appendix parts C, D).

Robust analyses also may be thwarted by constraints related to the original taxon sampling of the underlying matrices; in other words, matrices compiled by other authors were (implicitly or explicitly) constructed with the intent to apply them to specific problems, and thus any clade may be densely or sparsely sampled depending on the question that was originally addressed, rather than on questions of later interest. Inserting new taxa may be difficult if additional variation is not easily accommodated without major character revisions, and this may limit which taxa can be speedily added. The matrix of Anderson et al. (2008a) is slightly modified from that of Anderson (2007), which is a merger of a matrix that sampled lepospondyls (Anderson 2001) and a matrix that sampled amphibamiform temnospondyls (Anderson et al. 2008b). As a result, all descendants of the matrix of Anderson et al. (2008a), including the unpublished matrix of Pardo et al. (2017a), sample lepospondyls, amphibamiforms, and very little in between; in the case of Pardo et al. (2017a: fig. S6), other than the amphibamiforms and the added taxa *Chinlestegophis* and *Rileymillerus*, taxa include only seven other temnospondyl OTUs (some composite), the colosteid *Greererpeton*, lepospondyls, the diadectomorph pan-amniote *Limnoscelis*, the seymouriamorph *Seymouria* and the anthracosaur *Proterogyrinus*. The taxon sample is completed by the designated outgroup *Acanthostega*, the earliest well-understood limbed vertebrate.

The more narrowly focused published matrix of Pardo et al. (2017a) omits almost all taxa not sampled by Schoch (2013), retaining only temnospondyls,



**Figure 1.** Strict consensus of the four MPTs obtained by Marjanović & Laurin (2009: electronic supplementary material 2) from their modified version of the matrix of Anderson et al. (2008a) with ordering of clinal characters. Note that contrary to Anderson et al. (2008a), who had found extant amphibians to be diphylectic, with the stem-caecilian *Eocaecilia* among lepospondyls but *Albanerpetidae*, “salamanders”, *Triadobatrachus* and “frogs” among temnospondyls, Lissamphibia is found as a clade (cyan rectangle) and placed among lepospondyls (orange rectangle). The temnospondyl *Gerobatrachus*, interpreted as a member of the batrachian stem by Anderson et al. (2008a), i.e., closest to frogs and salamanders, is marked with a purple rectangle and white font. The names of extant taxa are in boldface; “frogs” and “salamanders” are composites. The application of the name *Amphibamiformes* is unclear due to the absence of *Dissorophus*. Numbers below internodes are bootstrap percentages (in bold if 50 or higher; “–” indicates clades contradicted by the bootstrap tree, always by clades with bootstrap percentages of 40 or less), numbers above internodes are Bremer values. Some or all of the Bremer values shown as “≥ 5” are probably 5 (Marjanović and Laurin 2009). Note that “*Asaphestera*” as used here is a chimera of the amniote *Asaphestera*, the microsauro *Steenerpeton* Mann et al., 2020, and an indeterminate lower jaw; most of the material belongs to *Steenerpeton*, however (Mann et al. 2020). The *Dendrerpetidae* OTU was originally called “*Dendrerpeton*” but is mostly based on its apparently close relative *Dendrysekos*.

lissamphibians, and the same two outgroups as Schoch (2013), *Proterogyrinus* and *Greererpeton*. The stated reason for this drastic omission of taxa, which eliminated all lepospondyls, *Seymouria* and *Limnoscelis*, was to reduce calculation time for the Bayesian analysis (Pardo et al. 2017a: E5394), after analysis of the unpublished matrix suggested that *Chinlestegophis* and lissamphibians nested within Temnospondyli.

In short, Pardo et al. (2017a) first tested the phylogenetic position of *Chinlestegophis* and the similar *Rileymillerus* (Bolt and Chatterjee 2000) “coarsely” by adding them to a matrix that sampled lepospondyls, amphibamiforms, a few other extinct taxa, and lissamphibians. *Chinlestegophis* and *Rileymillerus* were found as temnospondyls close to, but outside, Amphibamiformes (Pardo et al. 2017a: fig. S6). Accepting the result that *Chinlestegophis*, *Rileymillerus* and lissamphibians were temnospondyls, Pardo et al. (2017a) zoomed in by adding them to a matrix that sampled temnospondyls (and temnospondyl-related characters) more broadly, but omitted most other extinct clades. The question of whether caecilians are lepospondyls or stereospondyl temnospondyls was never adequately tested; the unpublished matrix lacks stereospondyls and uses unrevised scores for lepospondyls that were previously criticized (Marjanović and Laurin 2009; Sigurdson and Green 2011; Skutschas and Martin 2011), whereas the published one lacks lepospondyls altogether.

The published matrix further lacks representation of Albanerpetidae (a member or the sister group of Lissamphibia), despite their presence in the unpublished matrix. Daza et al. (2020) added Albanerpetidae (as a composite taxon with new data) back into the published matrix of Pardo et al. (2017a) and analyzed the result with implied weighting. They found caecilians and batrachians as sister taxa, followed by Karauridae as the next more distant relative, then Albanerpetidae, then the branchiosaurid *Apateon* and then the rest of Amphibamiformes. *Chinlestegophis* and *Rileymillerus* instead formed the sister-group of Brachyopoidea within Stereospondyli (Daza et al. 2020: fig. 4E, S14). Clearly, omitting Albanerpetidae had a large effect on the resulting relationships among extinct taxa and extant amphibians.

## Phylogeny inferred from parsimony

The original parsimony analysis of the published matrix yielded 882 shortest trees (Pardo et al. 2017a; and see below). As often occurs, the strict consensus was poorly resolved. To remedy this, Pardo et al. (2017a: fig. S7B) produced a majority-rule consensus (MRC) tree and used it as the basis for comparison with the tree resulting from a Bayesian analysis of the same matrix (their fig. 2C = S7A). Both the MRC and Bayesian trees show batrachians as amphibamiforms, but caecilians as stereospondyls closest to *Chinlestegophis*, and *Rileymillerus* as sister to caecilians + *Chinlestegophis*. However, none of

the 28 nodes that separate caecilians from batrachians + karaurids have 50% or higher bootstrap support, and none (even the basal caecilian node) occurs in 100% of the shortest trees (Pardo et al. 2017a: fig. S7B). We stress that the percentage of MPTs in which a given node occurs, as long as it is not 0 or 100, is not a support measure in a parsimony analysis (e.g., Serra Silva and Wilkinson 2021; Kligman et al. 2023: supp. inf. part 3); all MPTs are equally parsimonious, and therefore equally optimal by the sole criterion the analysis used. Therefore, the MRC tree provides an incomplete picture of the results of any parsimony analysis, even if there is only a single island of MPTs (see below). Indeed, a fully resolved MRC is not even necessarily identical to any MPT (J. Felsenstein, pers. comm. to D. M. 2017).

Investigating that problem specifically, Serra Silva and Wilkinson (2021) reevaluated the full diversity of MPTs supported by the published matrix of Pardo et al. (2017a), noting in their introductory paragraph that “[d]espite concerns that summarizing MPTs with the majority-rule consensus is potentially misleading [...], some workers still use the majority-rule method as if it were unproblematic (e.g. [...] Pardo et al. 2017[a]).” After briefly describing the reanalysis by Marjanović and Laurin (2018: 57–58; 2019: 144, fig. 30I–K), they demonstrated why the MRC is misleading in the specific case of Pardo et al. (2017a), and why it is important to inspect individual trees when the strict consensus is unsatisfactorily resolved: the 882 trees form islands which are each highly congruent internally, but very different from each other. More than half of the MPTs belong to a single island; therefore, the overall MRC (Pardo et al. 2017a: fig. S7B) is almost entirely identical (Serra Silva and Wilkinson 2021: fig. 2) to the MRC of that one island and fails to represent the MPTs on the other equally parsimonious islands.

Of the other islands, one (figured by Marjanović and Laurin 2019: fig. 30I; Serra Silva and Wilkinson 2021: fig. 3c) agrees with the most popular hypothesis of lissamphibian origins, which is also supported by the previously unpublished matrix of Pardo et al. (2017a: fig. S6): that Lissamphibia (including *Eocaecilia* but excluding *Chinlestegophis* and *Rileymillerus*) nests inside Amphibamiformes, close to *Gerobatrachus* (Atkins et al. 2019; Daza et al. 2020: fig. 4D/S13; Schoch et al. 2020; Kligman et al. 2023). It further differs from the largest island in that the karaurids occupy their usual position as stem-salamanders (corroborated by Jones et al. 2022), not the entirely novel one on the batrachian stem found on the largest island. Moreover, on the stereospondyl side of the tree, *Chinlestegophis* and *Rileymillerus* form the sister-group of Brachyopoidea, rather than being nested in it as on the largest island.

Another island (Marjanović and Laurin 2019: fig. 30K; Serra Silva and Wilkinson 2021: fig. 3b) shows Lissamphibia as the sister-group of *Chinlestegophis* + *Rileymillerus*, together nested within Stereospondyli next to Brachyopoidea. Yet another island (Marjanović and Laurin 2019: fig. 30I; Serra Silva and Wilkinson 2021:

fig. 3a) positions Lissamphibia next to *Gerobatrachus* within Amphibamiformes, and *Chinlestegophis* is nested within the caecilians as the sister-group of *Eocaecilia*, while *Rileymillerus* is placed among the stereospondyls as the sister-group of Brachyopoidea.

In other words, parsimony analysis of the published matrix of Pardo et al. (2017a) supports positions within Amphibamiformes or Stereospondyli equally strongly for *Chinlestegophis*, the undoubted caecilians, and Batrachia (including Karauridae).

## Bayesian inference of phylogeny

With the result of the parsimony analysis of the published matrix wholly inconclusive, an argument can still be made that the topology shown in fig. S7B of Pardo et al. (2017a) should be preferred over the equally parsimonious alternatives because it is congruent with the result of the Bayesian analysis of the same matrix, which is the only result figured in the main paper (Pardo et al. 2017a: figs 2B, C, 3, S7A). However, Bayesian inference as a method of phylogenetic analysis of paleontological matrices has its own sources of error.

The supposed problem of common branch lengths for all characters in previous simulations, pointed out by Goloboff et al. (2017, 2018) and given great weight by Marjanović and Laurin (2019: 98), seems not to be one of them; it was accounted for by the two latest treatments of the question of how best to analyze morphological data (Puttick et al. 2018; Keating et al. 2020) and found to be irrelevant. Yet, those two studies did not simulate any missing data, and the misuse of the MRC to represent the results of parsimony analyses by Puttick et al. (2018) will overestimate the precision but underestimate the accuracy of parsimony, as Keating et al. (2020: fig. 5) demonstrated. Furthermore, the homoplasy distributions in the matrices simulated by Puttick et al. (2018), and probably Keating et al. (2020) as well, do not encompass cases like the matrix of Marjanović and Laurin (2019) at the very least, and evidently not the matrix of Pardo et al. (2017a) either—given the multiple starkly different topologies that it supports as equally parsimonious.

Even more importantly, as paleontological matrices generally do (contrary to the implication by King [2020]), the matrix of Pardo et al. (2017a) contains multiple conflicting signals as well as large amounts of missing data. That combination is known to present a major problem for parametric methods in phylogenetics, including Bayesian inference, whereas parsimony (a non-parametric method) is immune to that particular issue (Simmons 2014; King 2019). Specifically, when character conflict is present (and at least one terminal branch has a positive length), parametric methods give much greater weight to the signal present in characters that are sampled for all taxa than to the signal present in incompletely sampled characters, even if very little information is missing (Simmons 2014; King 2019). Given that there is no reason to assume a correlation

between homoplasy and preservation, we regard this as a flaw of parametric methods for paleontological applications.

We also would like to draw attention to figure 1 of Mongiardino Koch et al. (2021), in which the proportion of quartets in a simulation study that are accurately resolved by undated Bayesian inference (as used by Pardo et al. 2017a) increases when the amount of missing data also increases, or in other words decreases when accurate data are added. Although this startling result is not statistically significant, it seems that undated Bayesian inference was, in that case, right for the wrong reasons, and is likely to be wrong for the same reasons in other circumstances.

Further, by default, parsimony is somewhat less vulnerable than parametric methods to the long-known problem of heterotachy (Crotty et al. 2019, and references therein). That problem was solved, but currently the solution is implemented in only one program, which only performs maximum-likelihood analysis and cannot deal with most features of morphological data (Crotty et al. 2019); a solution remains unavailable for Bayesian inference. On the empirical side, Palci et al. (2019) recovered a plausible topology of total-group snakes when they analyzed their dataset with parsimony, but a highly implausible one, requiring ecologically unmotivated reversals, by Bayesian inference. Thus, we strongly emphasize the conclusion of Marjanović and Laurin (2019: 96–99) that the accuracy of the matrix is much more important than the method of analysis, because no method can compensate for misscoring or miscoding of morphological data, a major issue we document for the matrix published and relied upon by Pardo et al. (2017a).

## Materials and methods

As noted above, Pardo et al. (2017a) performed analyses of two matrices (one published, one unpublished) with similar character samples but different taxon samples. The originally unpublished matrix was kindly shared with us by J. Pardo and A. Huttenlocker, and we publish it here: Suppl. material 1 contains the unaltered matrix in a NEXUS file, with an added PAUP command block that replicates our analyses of it (called a1 and a2 below) when the file is executed in PAUP\*. All of our analyses (Table 1) were run in PAUP\* 4.0a169 (Swofford 2021) for Windows. This includes bootstrap analyses to test the results of selected phylogenetic analyses for robustness; we have relied not only on the bootstrap trees, which we present as figures, but also on the lists of bipartitions in the PAUP\* output (Suppl. material 2: tables S1–S4). The published matrix was modified in Mesquite versions up to 3.70 (Maddison and Maddison 2021). The Kishino/Hasegawa, Templeton and winning-sites tests were employed to assess whether constrained and unconstrained trees resulting from the previously unpublished matrix are significantly different; all three tests are available in PAUP\*.

**Table 1.** Overview of analyses and results presented here.

Analysis	Our figure	Base matrix of Pardo et al. (2017a)	Modifications from Pardo et al. (2017a)	Ordering of clinal characters	inf. char.	Length of MPTs	Topology
–	1	–	n/a	yes	212	1264	Marjanović & Laurin (2009: supplementary figure), matrix modified from Anderson et al. (2008a), clinal characters ordered; LH: Lissamphibia next to <i>Brachydectes</i> (Lysorophia), <i>Gerobatrachus</i> in Amphibamiformes
a1	2	unpublished: SM 1	None	no	292	1450	as in Pardo et al. (2017a: fig. S6B)
a2	3	unpublished: SM 1	constraint de facto for LH	no	292	1454	LH; Lissamphibia contains <i>Gerobatrachus</i> , positions of <i>Chinlestegophis</i> + <i>Rileymillerus</i> as in a1
b	–	published: SM 3	None	no	322	1514	five islands: Lissamphibia, when present, in Amphibamiformes or Stereospondyli; <i>Chinlestegophis</i> in Gymnophionomorpha and/or Stereospondyli; figures in Serra Silva & Wilkinson (2021: fig. 2–4), simplified figures in Marjanović & Laurin (2019: fig. 301–K), only one island figured by Pardo et al. (2017a: fig. S7B)
bootstrap of b	4	published: SM 3	None	no	322	n/a	Diphily of modern amphibians: Karauridae + Batrachia next to <i>Gerobatrachus</i> (43%), caecilians next to <i>Chinlestegophis</i> (52%) in Stereospondyli
c	5	published: SM 3	addition of Albanerpetidae from Daza et al. (2020)	no	329	1565	as in Daza et al. (2020: fig. S14) except for slightly lower resolution; (Albanerpetidae (Karauridae, Lissamphibia) in Amphibamiformes, <i>Chinlestegophis</i> + <i>Rileymillerus</i> in Stereospondyli
d1	6	published: SM 4	None	yes	324	1554	Lissamphibia next to <i>Chinlestegophis</i> + <i>Rileymillerus</i> in Stereospondyli
bootstrap of d1	7	published: SM 4	None	yes	324	n/a	Lissamphibia (46%) next to <i>Chinlestegophis</i> + <i>Rileymillerus</i> (29%); <i>Chinlestegophis</i> as gymnophionomorph not compatible with bootstrap tree (44%)
d2	8	published: SM 4	Albanerpetidae	yes	329	1605	Lissamphibia in Amphibamiformes (closer to <i>Apateon</i> than to <i>Doleserpeton</i> or <i>Gerobatrachus</i> ), <i>Chinlestegophis</i> and <i>Rileymillerus</i> in Stereospondyli
bootstrap of d2	9	published: SM 4	Albanerpetidae	yes	329	n/a	Lissamphibia (52%) next to <i>Chinlestegophis</i> + <i>Rileymillerus</i> (27%); <i>Chinlestegophis</i> as gymnophionomorph not compatible with bootstrap tree (40%)
e1	10–12	published: SM 5	corrections of characters and scores	no	319	1514	seven islands: Lissamphibia either next to <i>Gerobatrachus</i> in Amphibamiformes or next to <i>Chinlestegophis</i> + <i>Rileymillerus</i> in Stereospondyli
e2	13, 14	published: SM 6	corrections of characters and scores	yes	321	1558	Lissamphibia next to <i>Chinlestegophis</i> + <i>Rileymillerus</i> in Stereospondyli
e3	15	published: SM 5	corrections; Albanerpetidae	no	326	1564	(Albanerpetidae (Karauridae, Lissamphibia) in Amphibamiformes, <i>Chinlestegophis</i> + <i>Rileymillerus</i> in Stereospondyli
e4	16, 17	published: SM 6	corrections; Albanerpetidae	yes	326	1601	three islands; Lissamphibia always in Amphibamiformes (closer to <i>Apateon</i> than <i>Doleserpeton</i> or <i>Gerobatrachus</i> ), <i>Chinlestegophis</i> + <i>Rileymillerus</i> in Stereospondyli
bootstrap of e4	18	published: SM 6	corrections; Albanerpetidae	yes	326	n/a	Lissamphibia (77%) in Amphibamiformes (Dissorophoidea: 35%), <i>Chinlestegophis</i> + <i>Rileymillerus</i> in Stereospondyli (34%); <i>Chinlestegophis</i> + <i>Rileymillerus</i> as gymnophionomorphs (15%) or next to Lissamphibia (29%), let alone Lissamphibia in Stereospondyli (10%), not compatible with bootstrap tree

inf. char. = number of parsimony-informative characters; LH = “lepospondyl hypothesis” of lissamphibian origins (*Eocaecilia* closer to *Carrollia* than to *Doleserpeton*); SM = Supplementary material file that contains the matrix and the settings for the analysis in question.

As described below, for some of our analyses of the published matrix, we added Albanerpetidae from Daza et al. (2020, based mainly on *Yaksha* Daza et al., 2020) rather than from Schoch et al. (2020, based on *Celtenham ibericus* McGowan & Evans, 1995, with a few additions from *Shirerpeton* Matsumoto & Evans, 2018). We did not add *Funcusvermis* for any analyses; we consider the effects of adding *Funcusvermis* sufficiently tested by Kligman et al. (2023), who added it to their revision of the matrix of Schoch et al. (2020), which was itself an expansion and slight revision of the published matrix of Pardo et al. (2017a).

### Analyses of the unpublished matrix of Pardo et al. (2017a)

We reanalyzed the originally unpublished matrix (associated with figure S6 of Pardo et al. 2017a) to determine

how many steps are needed to change the results. Two analyses were performed: one (a1) unconstrained, to replicate the original results, and one (a2) constrained to find *Eocaecilia* closer to the lepospondyl *Carrollia* than to the temnospondyl *Doleserpeton*, *de facto* enforcing the “lepospondyl hypothesis” of lissamphibian origins (but not any particular version of it) to enable us to compare the number of necessary extra steps. (The constraint also allows the “polyphyly hypothesis” that was supported by earlier versions of that matrix, most recently Huttenlocker et al. [2013].)

In both analyses, all characters were unordered, and no changes were made to the matrix. The search parameters were as follows: 10,000 random addition sequence replicates (far more than proved necessary) were performed holding one tree at each step, followed by branch swapping using TBR (tree bisection and reconnection) with a reconnection limit of 8 and a limit of 50 million

rearrangements per replicate (which was never hit); steepest descent was not in effect; unlimited automatic increases on the Maxtrees setting; branches collapsed if maximum branch length was 0.

### Analyses of the unmodified previously published matrix

We reanalyzed (analysis b) an unrevised version of the published matrix of Pardo et al. (2017a: supporting information part D; basis for their figures 2, 3 and S7) to verify its replicability and to further inspect the results. We computed consensus trees for each island, rather than for the entire sample of MPTs; unlike Serra Silva and Wilkinson (2021), who computed the MRC of each island, we used the strict consensus. The search settings were as above, except for the use of only 1000 unlimited replicates.

We also present a bootstrap analysis of this matrix (200 bootstrap replicates, each with 500 addition sequence replicates limited to 10 million rearrangements) to enable a better understanding of its support for various hypotheses. Most bootstrap values returned by Pardo et al. (2017a: fig. S7B) were below 50% and not originally published; however, clades supported by moderate bootstrap values (e.g., 45%) may still be better supported than any single alternative.

### Addition of Albanerpetidae to the previously published matrix

Daza et al. (2020: fig. 4E, S14) added Albanerpetidae—as a composite OTU based mainly on *Yaksha*, the new albanerpetid they described—to the published matrix of Pardo et al. (2017a) and analyzed the resulting matrix with implied weighting, using concavity values ( $k$ ) ranging from 10 to 200 in increments of 10. The MRC of the results of all twenty analyses pooled together was presented in Daza et al. (2020: fig. S14); numbers of optimal trees, tree lengths or indices were not published. Although most nodes occur in 100% of the trees (a number that may, however, result from rounding up to the nearest unit in some cases), and although the analysis at  $k = 200$  was practically unweighted (the lower the value of  $k$ , the more strongly are homoplastic characters down-weighted), we ran our single analysis (c) unweighted to be sure which trees the matrix supports at face value. Keating et al. (2020) demonstrated that unweighted parsimony is more accurate than implied-weights parsimony under certain realistic conditions; in addition, a basic assumption of implied weighting—an exponential distribution in which homoplasy-free characters are more common than those with any other number of extra steps—is not likely to be met for this matrix, and the performance of implied weights when that assumption is not met has not been studied (Marjanović and Laurin 2019).

Instead of publishing matrix files, Daza et al. (2020) published only the scores of the albanerpetid OTUs they revised in, or added to, the previously published matrix files they used. They confused the scores they added to the matrix of Pardo et al. (2017a; their reference 22) with the scores of Albanerpetidae they revised in the matrix of Pardo et al. (2017b; their reference 21) and presented these scores for the wrong matrix on pp. 16 and 17 of their supplementary text. The matrix of Pardo et al. (2017a) has 345 characters whereas that of Pardo et al. (2017b) has 370. Unable to add a string of 370 scores to a matrix of 345 characters, we added the string of 345 scores to the matrix of Pardo et al. (2017a) without any changes. The resulting NEXUS file, including a PAUP block that repeats analysis c when executed, is published here as Suppl. material 3. The search settings were as above.

### Ordering continuous characters

In the analyses of both matrices performed by Pardo et al. (2017a), as well as that by Daza et al. (2020), all multistate characters were unordered, even though some represent continuous or meristic morphoclines, which are more appropriately treated as ordered characters (Grand et al. 2013; Rineau et al. 2015, 2018; Marjanović and Laurin 2019; and references therein). Many characters used for phylogenetic analysis represent discretizations of intrinsically continuous variables that represent sizes, shapes and ratios, and the rationale for lumping similar values into a single state to produce discrete states follows the same logic as ordering the resulting states linearly (Wiens 2001). Simulations showed that ordering such states increases resolving power (the ability to recover clades) and reduces the occurrence of erroneous topologies (Grand et al. 2013; Rineau et al. 2015, 2018).

In the process of ordering all such clines in the unmodified published matrix, we discovered (like Kligman et al. 2023: supp. inf. part 4) that state 2 of character 9 is missing from the character list of Pardo et al. (2017a: part C of the supplementary text). In the “charstatelabels” block of the NEXUS file published as part D of the supplementary text, state 2 does occur, but in the matrix it is scored exclusively for *Ichthyophis*. J. Pardo (pers. comm. 2021) explained that state 2, absent from Schoch’s (2013) matrix, was intended to be introduced into the matrix, but this was implemented incompletely and accidentally omitted from the published character list. The states of character 9 (“preorbital region length”) originally were: 0, “less than twice the length of posterior skull table”; 1, “more” (than twice the length); 2, “equal in length”, so that state 2 is a subset of state 0. Gee (2022) and Kligman et al. (2023) noted this, but overlooked the fact that state 2 is scored correctly for *Ichthyophis*; they changed the name of state 2 to “twice as long” but did not rescore *Ichthyophis* or score state 2 for any other taxon. We have instead rescored *Ichthyophis* back to 0 for our ordered analyses, making the character binary.



For characters 3, 26 and 201, the implementation of state 2 as published in part D seems complete even though it is likewise missing from part C in all three cases. Conversely, character 292 has three states in part C, of which state 1 does not occur in the matrix. Characters 301 and 318 have three states in part C as well, of which the matrix lacks state 2.

We performed two parsimony and two bootstrap analyses—without (d1) and with (d2) *Albanerpetidae* as in analyses b and c—ordering the following clinal characters of the published matrix: 67, 75, 110, 143, 145, 158, 163, 170, 182, 187, 191, 201, 205, 209, 213, 214, 221, 226, 229, 242, 243, 262, 264, 266, 269, 271, 273, 279, 298, 300, 302, 304, 327, 328, and 334 (35 ordered out of 345 total characters; 10.1%). We first reordered the states of characters 205, 221, 327 and 328 to allow linear ordering because the original order did not follow the cline: states 0 and 1 of characters 205 and 221 had to be exchanged, as well as states 1 and 2 of characters 327 and 328. The resulting data matrix (and PAUP block) is available as Suppl. material 4.

The search settings were as above. 200 bootstrap replicates were performed, each using 500 random addition sequences. Instead of presenting the bootstrap values on consensus trees, we present the bootstrap trees (including the clades with greater frequencies than their alternatives) with their bootstrap values.

## Evaluation of potential synapomorphies and revisions to the published matrix

Pardo et al. (2017a) suggested various features as synapomorphies of caecilians with either *Chinlestegophis* alone or *Chinlestegophis* and other stereospondyls. Many correspond to characters in the published matrix. Here we evaluate all proposed synapomorphies and explain, where applicable, our revisions of scores in the matrix. We quote and discuss them below in the order in which they appeared in Pardo et al. (2017a). Our intention is not to fully revise the matrix (see Gee 2022), but to demonstrate the strong influence exerted by incorrect scores and compounding errors.

The resulting modified matrix is presented in Suppl. materials 5, 6 and was analyzed (analyses e1–e4: Table 1) using the same parameters applied in our analyses b–d, both without ordering characters (e1, e3; Suppl. material 5) and with the same character ordering used in analysis d (e2, e4; Suppl. material 6), and both without (e1, e2) and with *Albanerpetidae* as in analyses c and d2 (e3, e4). Analysis e4 was bootstrapped using the same parameters as for the bootstraps of analyses b, d1 and d2.

The diagnosis of *Chinlestegophis* states on p. E5389: “A shared feature with stereospondyls and caecilians is opisthotics fused to exoccipitals.” As pointed out by Santos et al. (2020), that feature is universal among lissamphibians except larval and some neotenic

salamanders (e.g., Duellman and Trueb 1994; Jones et al. 2022). It further occurs in the amphibamiform temnospondyl *Doleserpeton* (Sigurdson and Bolt 2010), a few lepospondyls (e.g., Pardo et al. 2015) and some (Maddin et al. 2013; Daza et al. 2020) though apparently not all albanerpetids (Matsumoto and Evans 2018). Among stereospondyls, conversely, it seems to be limited to extremely large and correspondingly unusually highly ossified adults of *Mastodonsaurus giganteus* (Jaeger, 1828) (Kligman et al. 2023: supp. inf. part 3). There is no corresponding character in the published matrix of Pardo et al. (2017a).

“Shared features with brachyopoids and caecilians” were proposed to (p. E5389) “include lacrimal fused to maxilla”. This hypothesis is difficult to evaluate. The maxillopalatine of *Funcusvermis* does not contain the nasolacrimal duct, so there is no evidence that it contains the lacrimal bone (Kligman et al. 2023). In *Chinlestegophis*, a separate lacrimal is absent, and the nasolacrimal duct lies entirely in what would otherwise be called the maxilla (Pardo et al. 2017a); however, the maxilla is dorsoventrally much narrower than expected for a fusion product. (The maxilla is slightly taller in the closely related *Rileymillerus* [Bolt and Chatterjee 2000: fig. 1.3]; however, Kligman et al. [2023: supp. inf. part 3] suggested quite plausibly that the fragmentary supposed nasal of *Rileymillerus* is actually a separate lacrimal.) As a result, fusion of the lacrimal to the maxilla cannot be distinguished from wholesale absence of the lacrimal in the currently known material of *Chinlestegophis*. Similarly, the cause of the absence of a separate lacrimal (loss or fusion) in most brachyopoids and a few other stereospondyls is unknown; even the nasolacrimal canal has not been traced in any of them (see Kligman et al. 2023: supp. inf. part 3 for details). Only in a few gymnophionans, as pointed out by Santos et al. (2020) and discussed by Theska et al. (2018), is ontogenetic fusion of the lacrimal to the maxilla documented (*Hypogeophis rostratus* [Cuvier, 1829]: Müller 2006; *Gegeneophis ramaswamii* Taylor, 1964: Müller et al. 2005; probably *Idiocranium russeli* Parker, 1936: Theska et al. 2018; possibly the “prefrontal” of *Dermophis mexicanus* [Duméril & Bibron, 1841]: Wake and Hanken 1982), although it has generally been hard in gymnophionans to tell the prefrontal, the lacrimal, and even the septomaxilla apart, and it is not clear whether the lacrimal ever forms in most gymnophionans (Theska et al. 2018). It is unclear if the two extant species scored in the matrix, *Epicrionops bicolor* Boulenger, 1883, and *Ichthyophis bannanicus* Yang, 1984, let alone the Early Jurassic *Eocaecilia*, possess(ed) a discrete lacrimal bone during development or not. However, character 21 of the published matrix only describes the presence or absence of the lacrimal, without mentioning the causes of such absence (such as fusion to the maxilla). We interpret this as describing the observed presence or absence of a separate bone in adults and have therefore not changed the scores of these taxa (all “absent”, state 1).

The sentence quoted above continues: “and two small posterior processes (‘horns’) on the occipital exposure of the tabular, just posterior to the otic notch (as in chigutisaurids).” Part B of the supplementary text of Pardo et al. (2017a) expressed some uncertainty about this: “two modest protuberances project from the occipital face of the tabular [of *Chinlestegophis*]. These processes may correspond to a rudimentary tabular horn, but their size and unusual topological relationship to the otic notch makes this homology uncertain. However, it is similar in position to the ‘tabular horn’ of some brachyopoids, particularly *Batrachosuchus* and *Vigilius*” (both of which are brachyopids, not chigutisaurids). Intriguingly, *Batrachosuchus* was scored as lacking “tabular horns” (pointed out by Gee 2022: app. 2.4.2), and see Kligman et al. (2023: supp. inf. part 3) for the doubtful homology of the “tabular horns” of *Chinlestegophis* and any brachyopoids. Later on p. E5390, Pardo et al. (2017a) made clear that tabular “horns” are not known in any caecilians. Indeed, for character 65—“Tabular (horn). Present in some form (0), or entirely absent (1)”—*Eocaecilia* was scored as unknown (?), and *Epicrionops* and *Ichthyophis* were scored as inapplicable (-) because they unambiguously lack tabulars (presence/absence of tabulars is coded by character 239). This means that this character does not hold *Chinlestegophis* and caecilians together in the published matrix. We have kept the scores for the caecilians and only changed the scores of the extant salamanders *Cryptobranchus* and *Hynobius* from unknown to inapplicable because they clearly lack tabulars; this change has no impact on any calculations of relationships.

On the same page, “[s]hared features with *Rileymillerus* and caecilians include the following: orbits small and laterally directed.” Orbit size, not coded in the published matrix, should be quantified before it can be evaluated, but is expected to be convergent among animals that live in darkness. Indeed, the orbits of *Funcusvermis* appear to have been considerably larger than those of other caecilians, *Chinlestegophis* or *Rileymillerus* (Kligman et al. 2023). Orbit location was included as character 26: “Orbit location. Medial, framed by wide jugals laterally (0), or lateral emplacement, framed by very slender jugals (1).” Dilkes (2015) revised the definition of character 26, but focused on the width of the jugal in his modifications. We, instead, interpret the intention of character 26 to be the location of the orbit and suggest rewording this character. Additionally, although three states are scored in the original matrix, only two are given in the character definition. The third state refers to particularly large orbits framed by relatively slender jugals and slender frontals (J. Pardo pers. comm. 2021; Kligman et al. 2023: supp. inf. part 4), but it is scored for batrachians that lack jugals. In order to keep the scores, we have reinterpreted it as referring to the size of the orbit or orbitotemporal fenestra rather than the jugal explicitly. Therefore, like Kligman et al. (2023), we have only changed the score of *Eocaecilia* from 2 to 1. We have further followed Kligman et al. (2023) in changing the scores of two amphibamiforms: *Platyrrhinops* from 2 to 1, *Apateon* from 0 to 2.

“Shared features with caecilians include double tooth row on mandible” is stated in the next sentence of Pardo et al. (2017a). This feature is represented in the published matrix as no less than seven characters: 146, 147, 148, 272, 273, 322 and 344.

Character 146 reads: “Symphyseal teeth. No accessory teeth posterior to symphyseal tusks (0), or a transverse row of such teeth (1).” State 1 is found in some stereospondyl taxa. Despite the absence of symphyseal tusks, state 1 also was scored for *Chinlestegophis*, *Eocaecilia* and the two extant caecilians (Pardo et al. 2017a). We changed the score of *Chinlestegophis* to 0 because the lingual tooththrow of the holotype and the referred specimens is restricted to the coronoids, and the coronoids do not participate in the symphyseal region of this animal (Pardo et al. 2017a: fig. S3, movies S4 and S7). The lingual tooththrow of *Eocaecilia*, *Epicrionops* and *Ichthyophis* does reach all the way to the symphysis, so we retained a score of 1 for those, but caution that this likely duplicates scores for the coronoid dentition characters. (As discussed in Marjanović et al. [2023], we provisionally disagree with Kligman et al. [2023] that this tooththrow is borne on the adsymphysial bone.)

Characters 147 and 148 describe presence/absence of teeth on specific coronoids and are thus redundant with character 272, which describes presence/absence of coronoid teeth in general (Pardo et al. 2017a). Characters 147 and 148 contain potentially important, non-overlapping variation, so we opted to keep that variation over retaining the more general variation captured by character 272, which we have excluded from our analyses. Because it is difficult to identify which coronoid is tooth-bearing in some taxa (i.e., when fewer than three distinguishable coronoids are present), *Doleserpeton* and caecilians in particular, we have, unlike Kligman et al. (2023: supp. inf. part 4), modified the definition of characters 147 and 148 as follows, which allowed us to keep all of the original scores:

- 147. Dentition lingual to distal half of labial tooththrow. Present (0), or absent (1).
- 148. Dentition lingual to mesial half of labial tooththrow. Present (0), or absent (1).

Character 322, “Splenic teeth. Present (0), absent (1)”, was scored 0 exclusively for *Ichthyophis*, *Epicrionops* and the dvinosaurian temnospondyl *Trimerorhachis insignis* Cope, 1878. The scores for the former two refer to the fact that the lingual tooththrow of caecilians has historically been thought to be borne on the splenic (references in Müller 2006; “splenic” was still used in quotation marks by Wilkinson et al. 2021). However, the bone that bears this tooththrow is not in the ventral position of a splenic, but the dorsolingual one of a coronoid, in the three extant caecilians whose development is well enough understood to tell (Müller et al. 2005; Müller 2006; Theska et al. 2018); a splenic has never been positively identified in any caecilian—or

any other lissamphibian. In other words, the scores of 1 for *Triadobatrachus*, *Cryptobranchus*, *Hynobius*, *Ambystoma* and *Leptodactylus* are not correct either; we have followed Gee (2022) in changing the scores of all lissamphibians that were not already scored as unknown to inapplicable (-). Moreover, the existence of teeth (including “denticles”: Gee et al. 2017) on the splenial of any species of *Trimerorhachis* has never been claimed or illustrated in the literature (most recently Milner and Schoch 2013), and D. M. found teeth to be absent there in personal observation of AMNH FARB 4565 (type specimen of *T. insignis*) and AMNH FARB 4572 (referred to the same species). This is not surprising. Only one certain and one possible case of tooth-bearing splenials are known in all of Tetrapodomorpha, if not Gnathostomata, and neither is sampled in any of the matrices we mention here: *Caerorhachis*, in which a “denticle” field extends from the coronoids and the prearticular onto the splenial (Ruta et al. 2002), and the unnamed “Parrsboro jaw”, where the same may or may not be the case (Sookias et al. 2014). In short, we changed the score of *Trimerorhachis* to 1, so that state 0 does not occur in the revised matrix at all; the character is constant and therefore uninformative in a parsimony analysis. Finally, *Chinlestegophis* was scored as unknown; we have corrected this to 1 because Pardo et al. (2017a: fig. S3) depicted the absence of teeth on the splenial.

It is worth mentioning that all three caecilians were correctly scored as lacking splenials in the published matrix of Pardo et al. (2017a: state 2 of character 264). This is contrary to the main text, which erroneously described the pseudodentary as “comprising the dentary, coronoid, splenial, and anterior Meckel’s cartilage” (p. E5391).

Character 344 also appears to target the presence of a lingual row of dentition on the mandible as seen in gymnophionans and taxa like *Chinlestegophis*. The character is defined as: “Dentary marginal dentition. Single row (0), multiple rows (1).” The three caecilian OTUs and *Chinlestegophis*, and no other OTUs, were scored as having multiple rows (1); however, *Chinlestegophis* has only one dentary tooththrow as described and illustrated by Pardo et al. (2017a), and in caecilians, as discussed above, the lingual row of teeth is borne on a coronoid rather than on the dentary. Thus, we rescored those taxa as having a single row of dentary teeth (0), meaning that state 1 does not occur in the revised matrix and this character, too, is uninformative.

Additionally, character 273 is: “Coronoid teeth. Larger than marginal (0), equal to marginal (1), smaller than marginal (2).” State 1 was scored exclusively for the three caecilians, *Chinlestegophis* and the stereospondyl *Benthosuchus*. We rescored *Chinlestegophis* as possessing state 2 because Pardo et al. (2017a: fig. S3) showed that the coronoid teeth are smaller than the marginal teeth.

The next feature listed as shared between *Chinlestegophis* and caecilians is “quadrate completely anterior to ear”, possibly meaning the otic capsules. If so,

this character state—which is not coded in the matrix—is standard among brachystelechid and lysorophian lepospondyls (Maddin et al. 2011; Glienke 2013, 2015; Pardo et al. 2015; Pardo and Anderson 2016) and widespread among lissamphibians as well. For present purposes it is only interesting if caecilians are temnospondyls, which this matrix cannot test.

Next is “broad, parallel-sided parasphenoid cultriform process >20% skull width”. Three characters in the published matrix (112, 114, 343) attempt to capture variation in parasphenoid shape, particularly that of the cultriform process, but “broad” and “parallel-sided” have different distributions. Although the cultriform process of *Chinlestegophis* is even broader than that of *Eocaecilia*, this condition is more or less universal among lissamphibians (references in Marjanović and Laurin 2008: 185–189), occurs prominently in lysorophians (Pardo and Anderson 2016), and also is found in the morphologically most immature dissorophoid temnospondyls (e.g., *Nyranerpeton*: Werneburg 2012).

Character 112 is presented in the character list as having two states: “Cultriform process (width). Base not wider than rest, clearly set off from basal plate (0), or merging continuously into plate (1)” (Pardo et al. 2017a: part C of the supplementary text). In the matrix, however, three states are scored; the first two are as given in the list, and the third (state 2) is called “flaring anteriorly” in the “charstatelabels” block, as in Schoch (2013). We followed Gee (2022) and Kligman et al. (2023) in transferring state 2 to character 343, which originally described whether the cultriform process is “[n]arrow, tapering anteriorly (0)” or “spatulate and parallel-sided (1)”. In other words, character 112 now describes the shape of the caudal end of the cultriform process in two states, and character 343 now describes the shape of the rostral end in three states that form a continuum of widths; character 343 is therefore ordered in our analyses with ordered characters (e2, e4). Our scores for both characters follow those of Gee (2022), which represents an update on Kligman et al. (2023). In addition, we scored *Chinlestegophis* as unknown for character 343; it was reconstructed as having state 1 (Pardo et al. 2017a: fig. 1H) and scored accordingly, but the entire rostral half of the cultriform process appears to be unknown (Pardo et al. 2017a: fig. 1B).

Character 114 is: “Cultriform process (outline). Of similar width throughout (0), or posteriorly expanding abruptly to about twice the width (1).” State 1 was scored only for the two extant caecilian OTUs and for the temnospondyls *Rileymillerus*, *Eryops* and *Onchiodon*. We are not sure if the conditions of those taxa should be considered primarily homologous: the two eryopids have a bulbous expansion near the base of the cultriform process, followed caudally by a constriction and then the basal plate along with its contacts to the pterygoids (Sawin 1941; Boy 1990); *Rileymillerus* has a strongly biconcave cultriform process that gradually expands caudally until it reaches five times its narrowest width where it merges

into the basal plate (Bolt and Chatterjee 2000: fig. 1.2, 2.2); *Epicrionops* and *Ichthyophis* have rostrally pointed cultriform processes that widen rather suddenly at the caudal ends of their contacts with the (maxillo)palatines (Jenkins et al. 2007: fig. 6B, D). But, in any case, *Chinlestegophis* and *Eocaecilia* were correctly scored 0, so (like Gee 2022 and Kligman et al. 2023) we have not modified this character or its scores.

“[O]ccipital condyles extend far beyond posterior edge of skull roof” is the next character state proposed to be shared by *Chinlestegophis* and caecilians (Pardo et al. 2017a: E5390). It is coded in the published matrix as character 137: “Exoccipital condyles. Short and broad base, projecting only with their posterior half behind the rim of the skull table (0), or almost the complete element posterior to level of occipital flange (1)”. State 1 was scored exclusively for most trematosauroids and brachyopoids, *Rileymillerus*, *Chinlestegophis*, *Eocaecilia*, *Cryptobranchus* and *Ambystoma*. However, that state (which appears to be more widespread among stereospondyl and dvinosaurian temnospondyls: Kligman et al. 2023: supp. inf. part 3) can be reached by elongating the condyles, reducing the caudal extent of the skull roof, extending the braincase caudally, or a combination of two or all three factors. The stalked occipital condyles of *Chinlestegophis* (and *Rileymillerus*: Bolt and Chatterjee 2000) are standard for stereospondyls, but are not found in any caecilians; this was beautifully illustrated by Pardo et al. (2017a: fig. 3). Rather, lissamphibians (and albanerpetids: Daza et al. 2020) generally expose large parts of the otic capsules in dorsal view, resulting in the entire occipital condyles lying far beyond the posterior edge of the skull roof. The condyles themselves are weakly elongated in some caecilians and not at all in others, as again shown by Pardo et al. (2017a: fig. 3) and described and illustrated by Jenkins et al. (2007: fig. 1–4, 6). This includes *Eocaecilia*, despite its retention of postparietal and probable tabular bones (Pardo et al. 2017a: fig. 3; Jenkins et al. 2007). Conversely, milder examples of the stereospondyl condition exist in various lepospondyls (Santos et al. 2020, and references therein). Therefore, *Eocaecilia* should not receive the same score as *Chinlestegophis*; we reinterpreted the character as referring to condyle elongation instead of the skull table, limiting state 1 to condyles with a stalked base, and consequently revised the scores of *Eocaecilia*, *Cryptobranchus* and *Ambystoma* to 0.

The last character state proposed to be shared by *Chinlestegophis* and caecilians (Pardo et al. 2017a: E5390) is presence of a “pterygoquadrate”, referring to fusion of the pterygoid and the quadrate bones, as observed in the ontogeny of some extant caecilians (Wake and Hanken 1982; Müller et al. 2005; Müller 2006; Theska et al. 2018: fig. 1c). On the next page, however, *Chinlestegophis* is more cautiously stated to possess, “perhaps, an incipient pterygoquadrate based on the structure of the suspensorium and apparent absence of the quadratojugal.” The full description of the skull (Pardo et al. 2017a: part B of the supplementary text) states the matter in a similarly limited way: “A separate quadrate is not evident in

either side of the skull, but it is likely that the saddle-shaped posterolateral face of the pterygoid represents the articular glenoid, and we hypothesize that this therefore represents a fused pterygoid-quadrate element (pterygoquadrate).” Thus, a pterygoquadrate is not observed in *Chinlestegophis*, and cannot be used to link it to caecilians. The issue is further complicated by *Eocaecilia*, in which the quadrate appears to be fused to the stapes and not to the pterygoid (Jenkins et al. 2007). Additionally, a pterygoquadrate is not universal in Gymnophiona, being absent in non-teresomatans like *Ichthyophis*, *Epicrionops* and *Amazops* (Jenkins et al. 2007: fig. 6B, D; Wilkinson et al. 2021: fig. 3) and the teresomatans *Chikila* (“pterygoid process of the quadrate”, separated from the quadrate by a suture and meeting the maxillopalatine, in Kamei et al. 2012: fig. S2(b)). If the fused pterygoquadrate is not only real in *Chinlestegophis*, but also homologous between *Chinlestegophis* and Teresomata or a subset thereof, it must have been independently lost three successive times in *Eocaecilia*, Rhinatrematidae and Ichthyophiidae, and at least once more in *Chikila*.

The pterygoquadrate may be coded as state 2 of character 318: “Quadrate-maxilla separated by. [sic] Pterygoid (0), small pterygoid and pterygoid process of quadrate (1), by pterygoid process of quadrate only (pterygoid absent) (2).” In agreement with the discussion above, state 2 does not occur in the matrix, which lacks teresomatans.

Pardo et al. (2017a: E5390) also stressed that “[i]n the temporal region, there is a small, round supratemporal that is only loosely articulated to its surrounding calvarial elements. This bone is morphologically and topologically identical to an element identified as the ‘tabular’ in *Eocaecilia*”. As pointed out by Marjanović and Laurin (2019: 151, app. S1: 35), the statement of identity rests entirely on the reconstruction drawing published by Jenkins et al. (2007: fig. 1), which shows almost no uncertainty (by dashed lines, differential shading or any other means), but rather depicts a preferred hypothesis of what an undamaged skull looked like. The text, specimen drawings and photos in Jenkins et al. (2007), further supported by the  $\mu$ CT rendering in Maddin et al. (2012a: fig. 1A), make clear that the morphology and topology of the “?tabular” in the reconstruction are guesses—the presence and independence of the bone are evident, but not its shape or size. In the crushed holotype (Jenkins et al. 2007: fig. 2; Maddin et al. 2012a: fig. 1A), the left “?tabular” is caudally broken, but the right one may well have reached the caudal edge of the skull table (pers. obs. H. M. and D. M.), reopening the possibility that it is, in fact, a tabular and not homologous to the supratemporal of *Chinlestegophis*. Pardo et al. (2017a) actually scored the tabular as present in *Eocaecilia* (state 0 of character 239). However, given the uncertainty surrounding the element, we changed this score to unknown (?), and retained the scores of “unknown” in the tabular-related characters 62, 63 and 65–67. We also followed Gee (2022) and Kligman et al. (2023) in changing the scores of all salamanders to not applicable (-) for the tabular-related character 63, because they clearly lack tabulars, and changed the scores

of all lissamphibians (including *Eocaecilia*) to inapplicable for character 71, which references tabular horns.

The implication later in the same paragraph (Pardo et al. 2017a: E5390) that the real tabular could be part of the *os basale* in *Eocaecilia* is unfounded: there is no reason to think, from their shapes or topological relationships, that the dorsal sides of the *ossa basalia* contain tabulars or any other dermal bones of the skull roof (Jenkins et al. 2007: fig. 2, showing the holotype; compare extant caecilians and their ontogeny: Wake and Hanken 1982; Müller et al. 2005; Müller 2006; Theska et al. 2018).

In their Discussion section, Pardo et al. (2017a: E5393) made a far-reaching claim: “a sulcus associated with the opening of the nasolacrimal duct in the orbit is present in both *Chinlestegophis* and *Eocaecilia* in a similar position to the tentacular sulcus of the basal caecilian *Epicrionops petersi*”, citing Jenkins et al. (2007: fig. 10), which indeed shows the tentacular foramen inside the orbit of the extant *Epicrionops* and a “tentacular sulcus” on the orbital margin of the maxilla of *Eocaecilia*. Evidence of the caecilian tentacle, a body part composed mostly of the nasolacrimal duct and eye musculature and associated with chemosensation in extant caecilians, has not been reported from any vertebrates other than *Gymnophiona* and *Eocaecilia*. In *Chinlestegophis*, the maxilla does not reach the orbit, being excluded by a contact of the prefrontal and the lateral exposure of the palatine (Pardo et al. 2017a: fig. 1, S4). The nasolacrimal duct is housed in the maxilla and meets the orbit in two pores well medial of the skull surface (Pardo et al. 2017a: fig. S4C). Although the sulcus is stated to be in the orbit margin in part F of the supplementary material, it was not reconstructed in fig. 1J, which instead shows an elliptical orbit devoid of any corners; the reconstruction in fig. 1I shows a more angular orbit, fitting the  $\mu$ CT images in fig. 1E–G, but these corners are very wide, obtuse and rounded, offering no evidence of a tentacular sulcus. A nasolacrimal duct that is separated from the surface of the head would not function in sensory reception, and seems unlikely to explain the evolution of the caecilian tentacle. *Funcusvermis* also lacked a tentacular sulcus unless the sulcus had an unusually far dorsal position, i.e., at the dorsoventral midpoint of the rostral orbit margin at minimum (Kligman et al. 2023: fig. 1a, g–i). In any case, no feature relating to the nasolacrimal duct or the shape of the orbit is coded in the published matrix.

## Results

See Table 1 for a brief overview of our analyses and their results.

### Analyses of the unpublished matrix of Pardo et al. (2017a)

Our unconstrained analysis (a1; Fig. 2) found 12 MPTs of 1450 steps, as reported in Part G of the supplementary

information of Pardo et al. (2017a); their previously unreported indices are: CI excluding uninformative characters = 0.2668, RI = 0.6532, RC = 0.1815. The resulting strict consensus is identical to that of Pardo et al. (2017a: fig. S6B), with *Chinlestegophis* and *Rileymillerus* positioned as the sister-group to all other amphibamiform temnospondyls including Lissamphibia, which in turn contains *Eocaecilia* and *Gymnophiona*. Of the 319 characters, 292 are parsimony-informative.

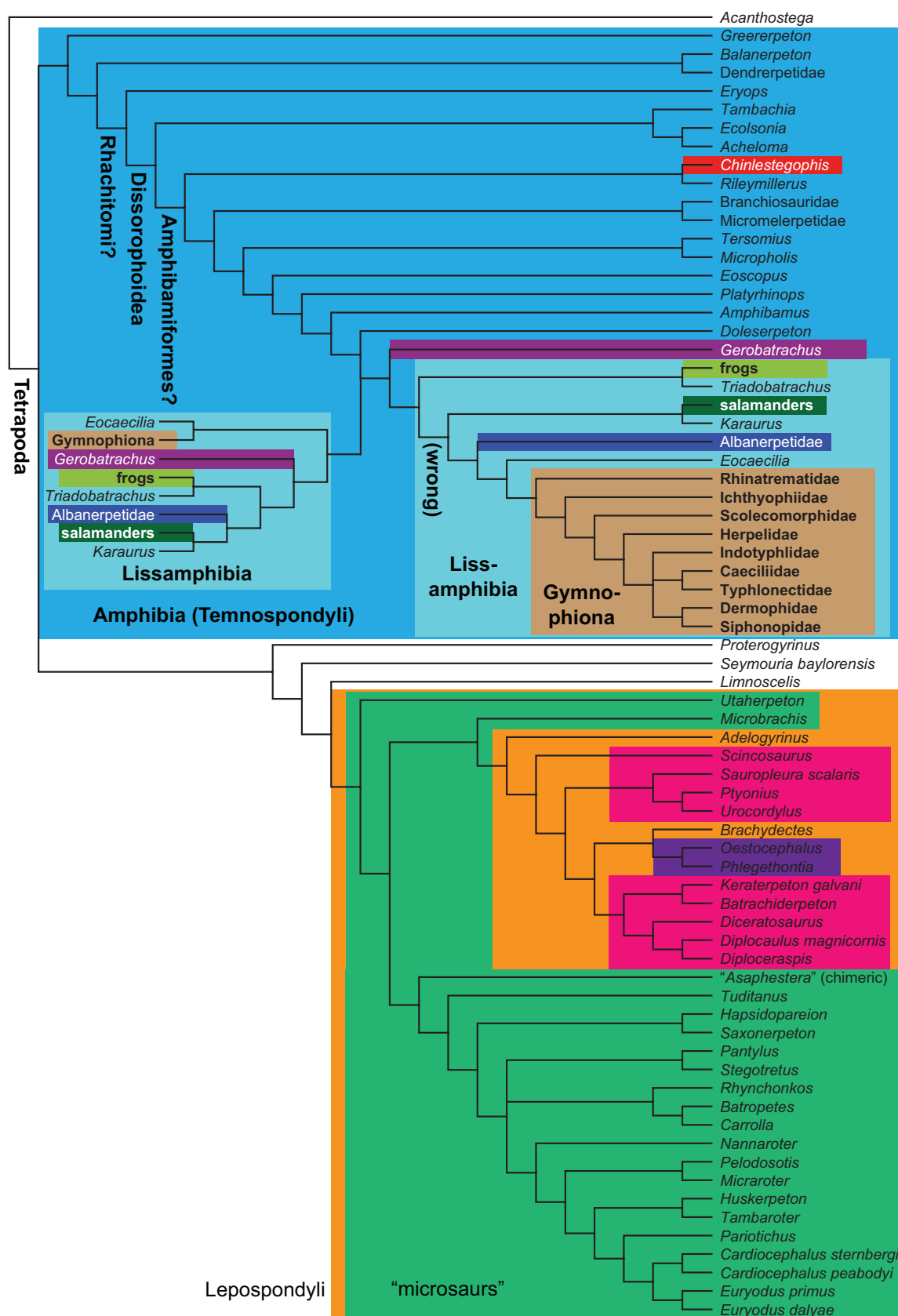
The MPTs form two islands that differ in their resolution of Lissamphibia: (1) *Gerobatrachus* as the sister-group of Lissamphibia, within which “frogs” + *Triadobatrachus* is the sister-group of a clade formed by “salamanders” + *Karaurus* on one side and *Albanerpetidae* + *Eocaecilia* and crown caecilians on the other; (2) crown caecilians + *Eocaecilia* as the sister-group of the other lissamphibians, within which *Gerobatrachus* is the sister-group of a clade formed by “frogs” + *Triadobatrachus* on one side and *Albanerpetidae* + (“salamanders” + *Karaurus*) on the other. Note that only (2) is compatible with phylogenies of extant amphibians based on molecular data (Hime et al. 2020, and references therein).

Constraining *Eocaecilia* to be closer to the lepospondyl *Carrolla* (analysis a2; Fig. 3) than to the temnospondyl *Doleserpeton* produced 48 MPTs of a very similar length (1454 steps) and very similar indices (CI excluding uninformative characters = 0.2661, RI = 0.6519, RC = 0.1807). The positions of *Chinlestegophis* and *Rileymillerus* remain unchanged compared to Pardo et al. (2017a: fig. S6). Although the “lepospondyl hypothesis” is supported in this experiment, Lissamphibia contains *Gerobatrachus*, and it nests far from *Carrolla*, indeed on the other side of the lepospondyl tree—next to the limbless aistopods, followed by the limb-reduced *Brachydectes*, much as in Marjanović and Laurin (2009; Fig. 1) whose matrix has a common ancestor with this one (Anderson et al. 2008a). The strict consensus shows a less well resolved version of the abovementioned topology (2).

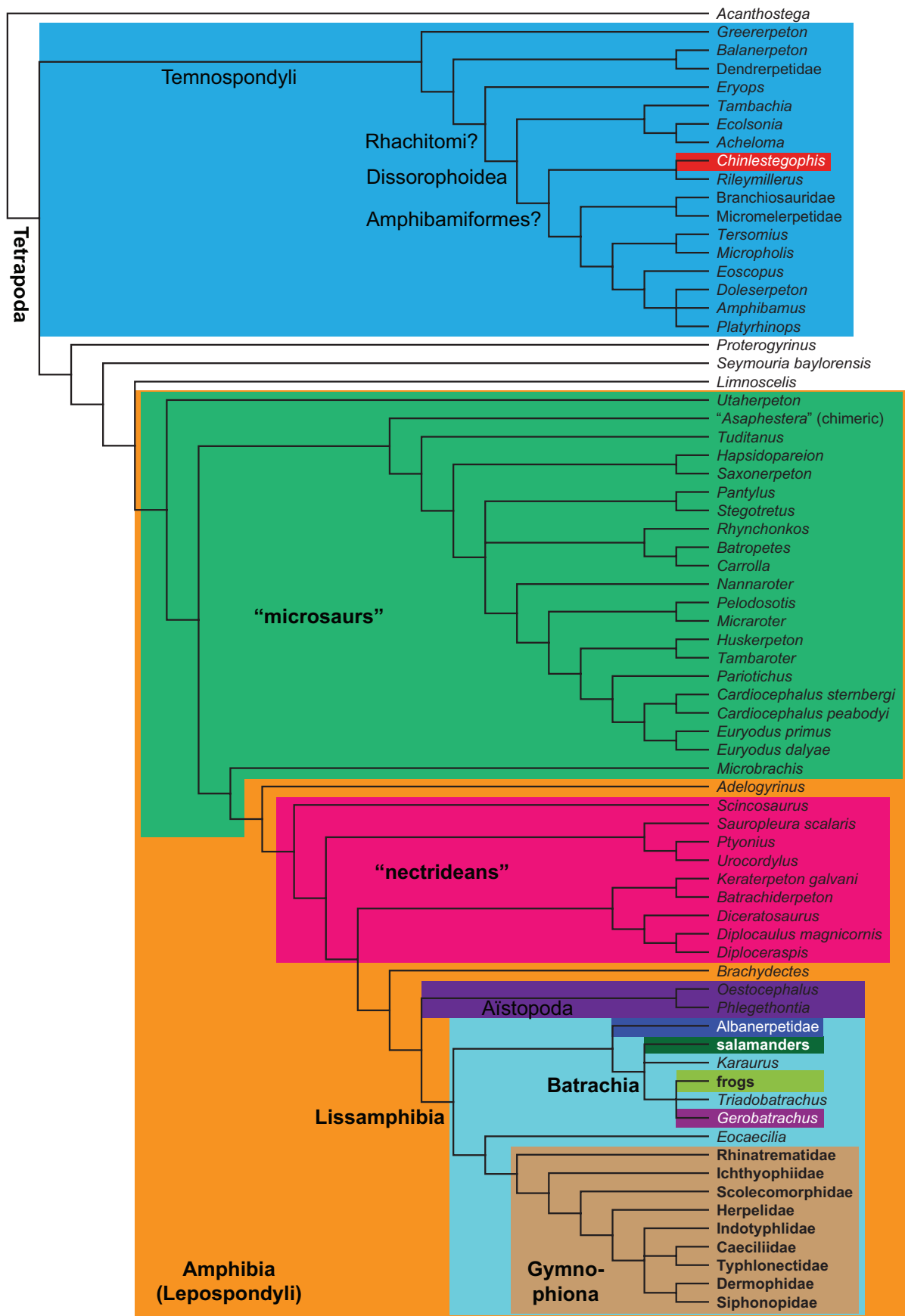
The differences in fit to the matrix between the unconstrained and the constrained trees are not significant (Kishino/Hasegawa test:  $p = 0.6284$ ; Templeton test:  $p = 0.6276$ ; winning-sites test:  $p = 0.7160$ ).

### Analyses of the unmodified previously published matrix

Reanalysis of the published matrix (analysis b) yielded identical results to those of Pardo et al. (2017a), Marjanović and Laurin (2019: fig. 30I–K), Serra Silva and Wilkinson (2021) and Gee (2022), returning 882 MPTs with a length of 1,514 steps, CI excluding uninformative characters = 0.2548, RI = 0.6858, RC = 0.1812. Of the 345 characters, 322 are parsimony-informative. The MPTs are spread across the five islands found and described by Serra Silva and Wilkinson (2021) and above (Matrices, Methodologies, and Missteps: Phylogeny inferred from parsimony).



**Figure 2.** Strict consensus of the 12 MPTs obtained from our analysis a1 (see Table 1), using the unpublished matrix used by Pardo et al. (2017a: fig. S6B). The two islands are represented by the duplication of Lissamphibia and its sister-group (on one island) or member (on the other island) *Gerobatrachus*. The branch marked “(wrong)” contradicts the molecular consensus (Hime et al. 2020). Question marks indicate names with uncertain application given the taxon sample. Colored rectangles and boldface, as well as “*Asaphestera*” and *Dendrerpetidae*, as in Fig. 1; red rectangle for *Chinlestegophis*, brown rectangle for crown-group caecilians (Gymnophiona).



**Figure 3.** Strict consensus of the 48 MPTs obtained from the unpublished matrix used by Pardo et al. (2017a) in an analysis (a2; see Table 1) constrained against the “temnospondyl hypothesis” of lissamphibian origins; a version of the “lepospondyl hypothesis” results. Colors, boldface, “*Asaphestera*” and Dendrerpetidae as in Fig. 2.

The bootstrap tree of analysis b (Fig. 4) shows moderate support for the diphyly of modern amphibians as presented by Pardo et al. (2017a): the three caecilians form the sister-group of the stereospondyl *Chinlestegophis* in 52% of the bootstrap replicates, while the batrachians are found as amphibamiform dissorophoids closest to *Gerobatrachus* in only 43%, and adding any further dissorophoids depresses this value to a maximum of 35%. This latter value is the highest that separates caecilians and batrachians + karaurids; even *Rileymillerus* occurs as the sister-group of *Chinlestegophis* and the caecilians together in only 32%. Most bootstrap values in the rest of the tree, except for the majority of the most highly nested nodes, are even lower.

Inspection of the list of bipartitions in the output of PAUP\* (Suppl. material 2: table S1), including those that are incompatible with the bootstrap tree, shows that Lissamphibia was found in 37% of the bootstrap replicates—support comparable to that for Dissorophoidea including Batrachia (35%), which is shown in the bootstrap tree (Fig. 4). An exclusive clade of all lissamphibians and *Chinlestegophis* occurs in 21% of the replicates and combines with *Rileymillerus* in 20%; all lissamphibians and any or all dissorophoids form an exclusive clade in no more than 16% of the replicates. Stereospondyli excluding *Chinlestegophis* and optionally *Rileymillerus* appears in only 9%, as often as, e.g., an improbable clade of all lissamphibians except *Eocaecilia*. Only 8% group all lissamphibians, *Chinlestegophis* and *Gerobatrachus* exclusively.

### Addition of Albanerpetidae to the previously published matrix

The matrix of Daza et al. (2020: fig. 4E, S14), i.e., the published matrix of Pardo et al. (2017a) with Albanerpetidae added, yielded a single island of 45 MPTs (analysis c; length = 1565 steps, CI excluding uninformative characters = 0.2510, RI = 0.6795, RC = 0.1741). Their strict consensus (Fig. 5) is topologically identical to that of Daza et al. (2020: fig. S14), except for slightly lower resolution: Dissorophidae, Trematopidae, and a node supporting *Edingerella*, *Benthosuchus*, Capitosauroidea and Trematosauroida + Brachyopoidea are unresolved. Interestingly, all nodes marked “95” in the MRC of Daza et al. (2020: fig. S14) are present in the strict consensus of our analysis, whereas a few of those marked “100” are not. Amphibamiformes, including Lissamphibia, is resolved exactly as in Daza et al. (2020: fig. 4E, S14): there is a clade (*Apateon* (Albanerpetidae (Karauridae, Lissamphibia))) which is the sister-group of (*Micropholis* (*Platyrrhinops* (*Amphibamus* (*Doleserpeton*, *Gerobatrachus*)))) within Dissorophoidea. Likewise, *Chinlestegophis* and *Rileymillerus* are positioned as in Daza et al. (2020: fig. S14), as the sister-group to Brachyopoidea within Stereospondyli.

The addition of Albanerpetidae renders seven characters parsimony-informative, so that 329 of the total of 345 now have this status.

### Ordering continuous characters

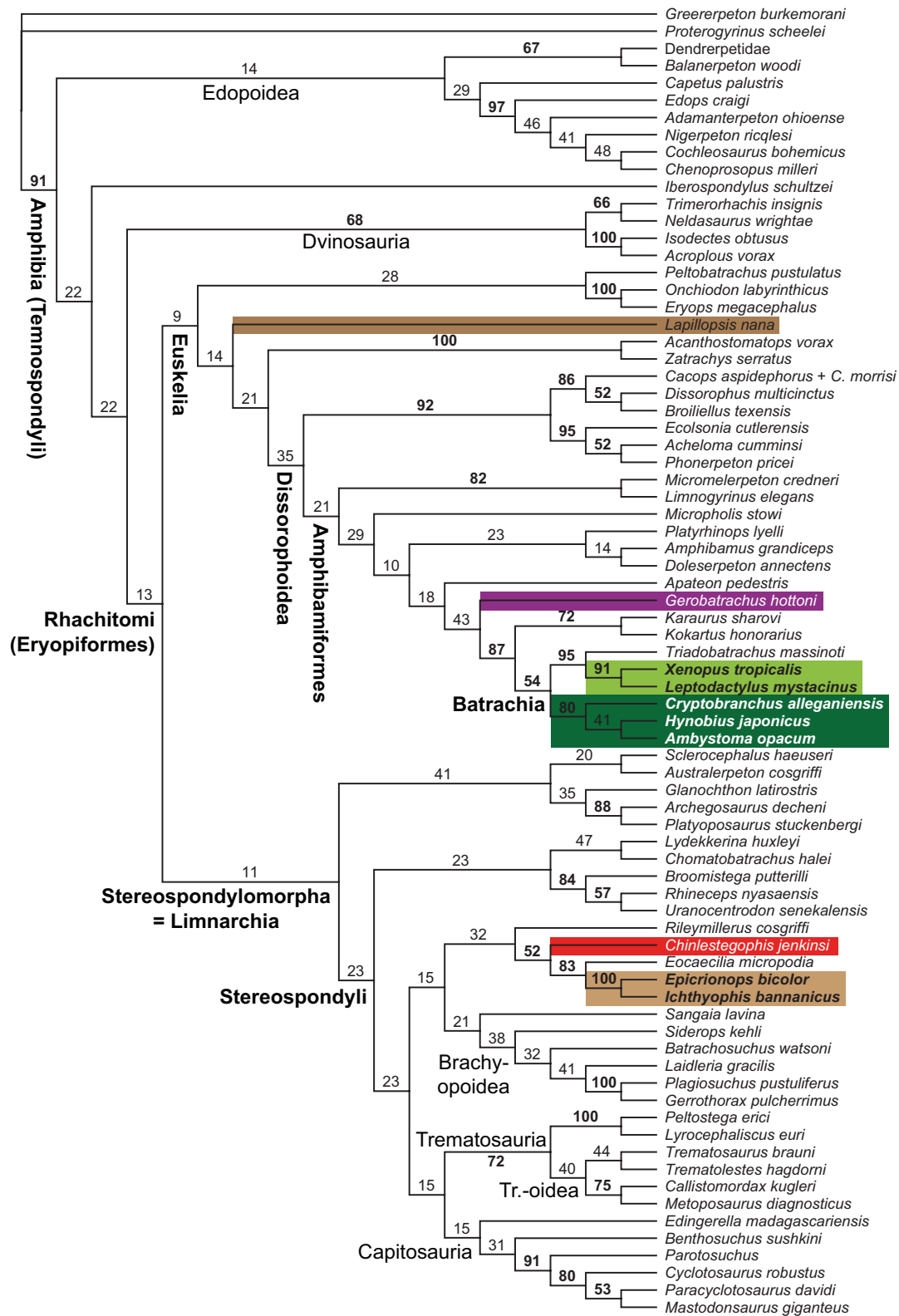
Ordering of clinal characters (analysis d1) in the otherwise unmodified published matrix of Pardo et al. (2017a) rendered two characters parsimony-informative (for a total of 324 of the 345 characters in the matrix) and resulted in three islands of 270 MPTs in total (length = 1554 steps, CI excluding uninformative characters = 0.2508, RI = 0.6885, RC = 0.1777). The strict consensus is well resolved (Fig. 6) and shows Lissamphibia as the sister-group of the clade formed by *Chinlestegophis* and *Rileymillerus*, nested within the brachyopoid stereospondyls.

The bootstrap tree of analysis d1 (Fig. 7) recovers a rather weakly supported (46% frequency) Lissamphibia with the same sister-group, and the *Chinlestegophis*-*Rileymillerus* clade is again less supported (40%). Affinities between the *Chinlestegophis*-*Rileymillerus* clade and Lissamphibia are slightly better supported than with unordered states, but at 29%, this clade is still weak. The position of *Chinlestegophis* as a stem-caecilian, incompatible with the bootstrap tree, occurs with a frequency of 44% (Suppl. material 2: table S2). Lissamphibia is separated from *Doleserpeton* or *Gerobatrachus* by bootstrap values no higher than 30%; an exclusive clade of frogs, salamanders, karaurids and *Gerobatrachus* has 36% support (less if any other dissorophoids are added) and an exclusive Lissamphibia-*Gerobatrachus* clade only 15% (likewise less if other dissorophoids are added; Suppl. material 2: table S2).

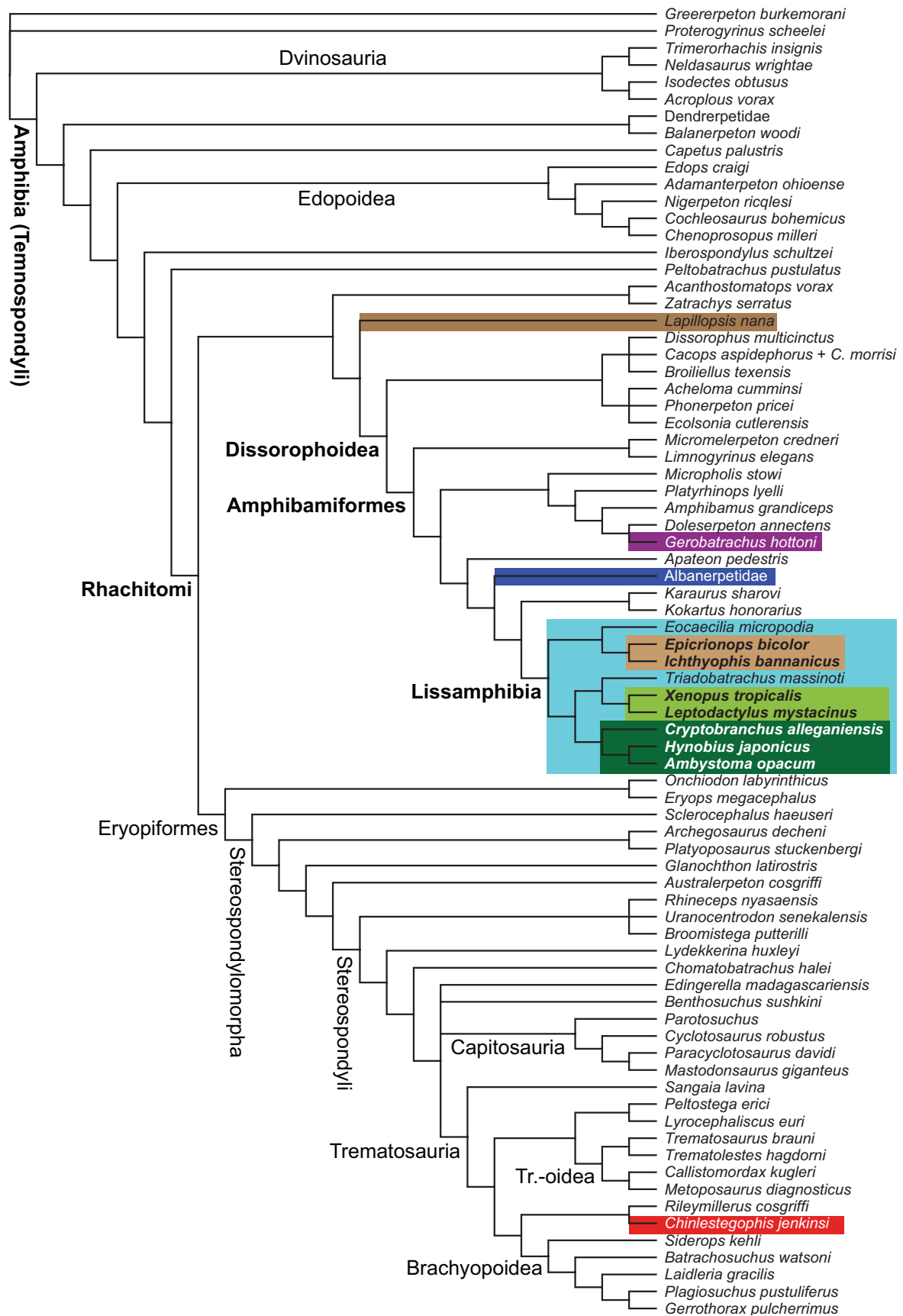
When the clinal characters are ordered and Albanerpetidae is added (analysis d2), 329 characters are parsimony-informative, and the published matrix yields a single island of 30 MPTs (1605 steps, CI excluding uninformative characters = 0.2453, RI = 0.6830, RC = 0.1711). The strict consensus (Fig. 8) shows (*Apateon* (Albanerpetidae (Karauridae, Lissamphibia))) in Amphibamiformes—next to a clade that contains *Doleserpeton* and *Gerobatrachus*—while the *Chinlestegophis*-*Rileymillerus* clade forms the sister-group of the brachyopoid stereospondyls.

Bootstrapping analysis d2 (Fig. 9) shows moderate support for Lissamphibia (52%). Lissamphibia and a clade formed by *Chinlestegophis* and *Rileymillerus* are found as sister groups with low support (27%). Interestingly, both clades together form the sister-group of Dissorophoidea; the support for exclusion from a position close to *Gerobatrachus* or *Doleserpeton* is comparatively high (62%), but the support for exclusion from Trematosauria within Stereospondyli is very low (12%). Noteworthy, on the other hand, is the support (75%) for excluding Karauridae (*Karaurus* and *Kokartus*), universally considered a clade of stem-salamanders (Jones et al. 2022, and references therein), from Batrachia (frogs + salamanders). An exclusive clade of Albanerpetidae, Karauridae and Batrachia has 58% support, moderately contradicting Matsumoto and Evans (2018) and Daza et al. (2020); this may be due to character sampling.





**Figure 4.** Bootstrap tree obtained from the published matrix used by Pardo et al. (2017a) when all characters are unordered (analysis b). The bootstrap tree shows moderate support (52%) for the diphyly of extant amphibians. Colors and boldface as in Fig. 3, bootstrap values  $\geq 50\%$  also in boldface; darker brown rectangle for *Lapillopsis*, a small temnospondyl thought to be a stereospondyl convergent to dissorophoids. The blue rectangle for Temnospondyli is omitted because all OTUs except *Greererpeton* and *Proterogyrinus* are (inferred to be) temnospondyls; the cyan rectangle for Lissamphibia is omitted because the name Lissamphibia does not apply on this tree. Tr.-oidea = Trematosauroida. The Dendrerpetidae OTU was called “*Dendrerpeton acadianum*” by Pardo et al. (2017a) but is mostly based on its apparently close relative *Dendrysekos*. In this and the following figures we have also corrected spelling mistakes in taxon names compared to the matrix and the figures of Pardo et al. (2017a).



**Figure 5.** Strict consensus of the 45 MPTs obtained from the published matrix of Pardo et al. (2017a) with addition of *Albanerpetidae* from Daza et al. (2020); all characters are unordered (analysis c). The resolution differs slightly from Daza et al. (2020: fig. S14) because we used parsimony with equal rather than implied weights. Colors, boldface and *Dendrerpetidae* as in Fig. 3 and 4 here and in all following figures; Tr.-oidea = Trematosauroidae.

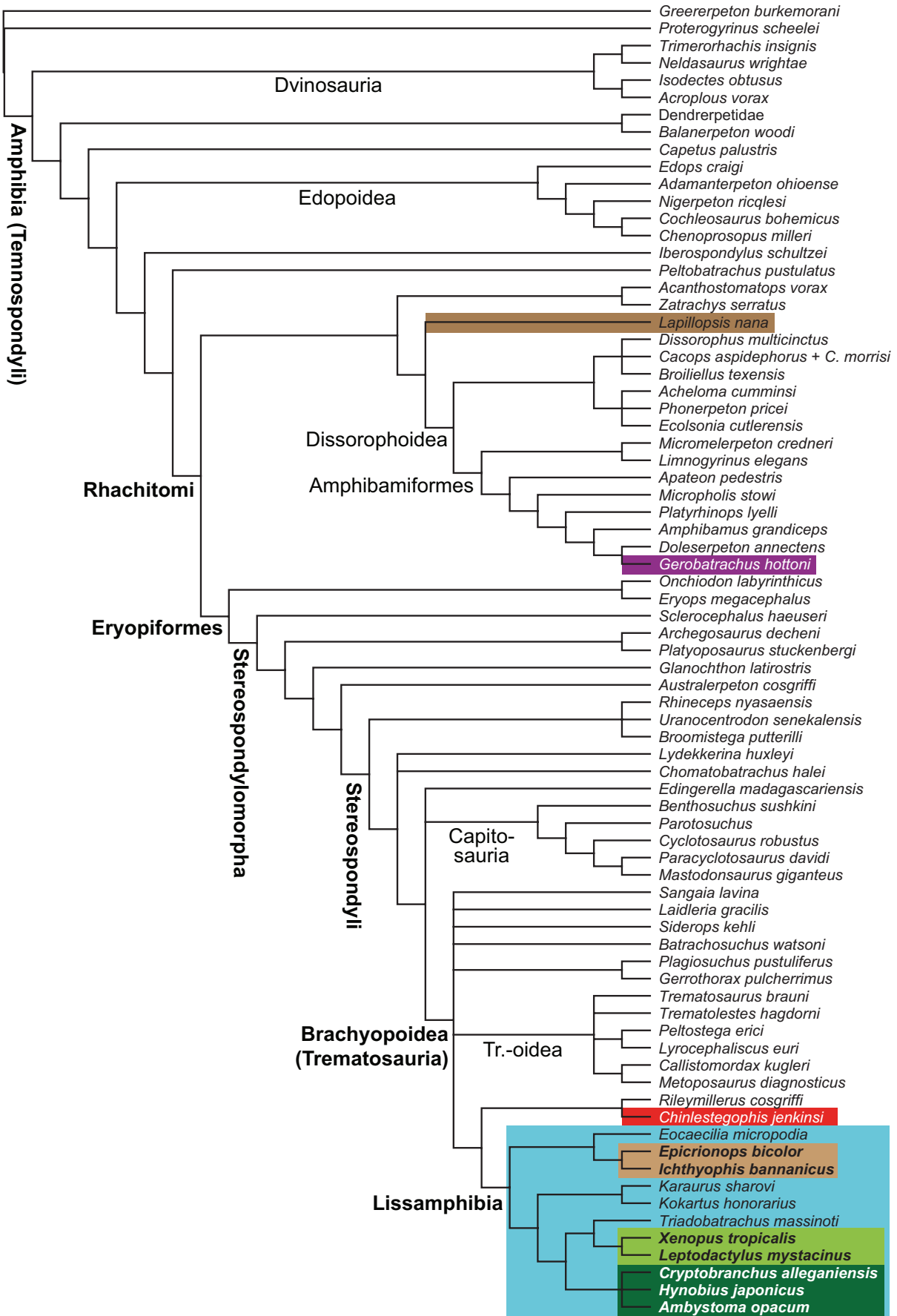
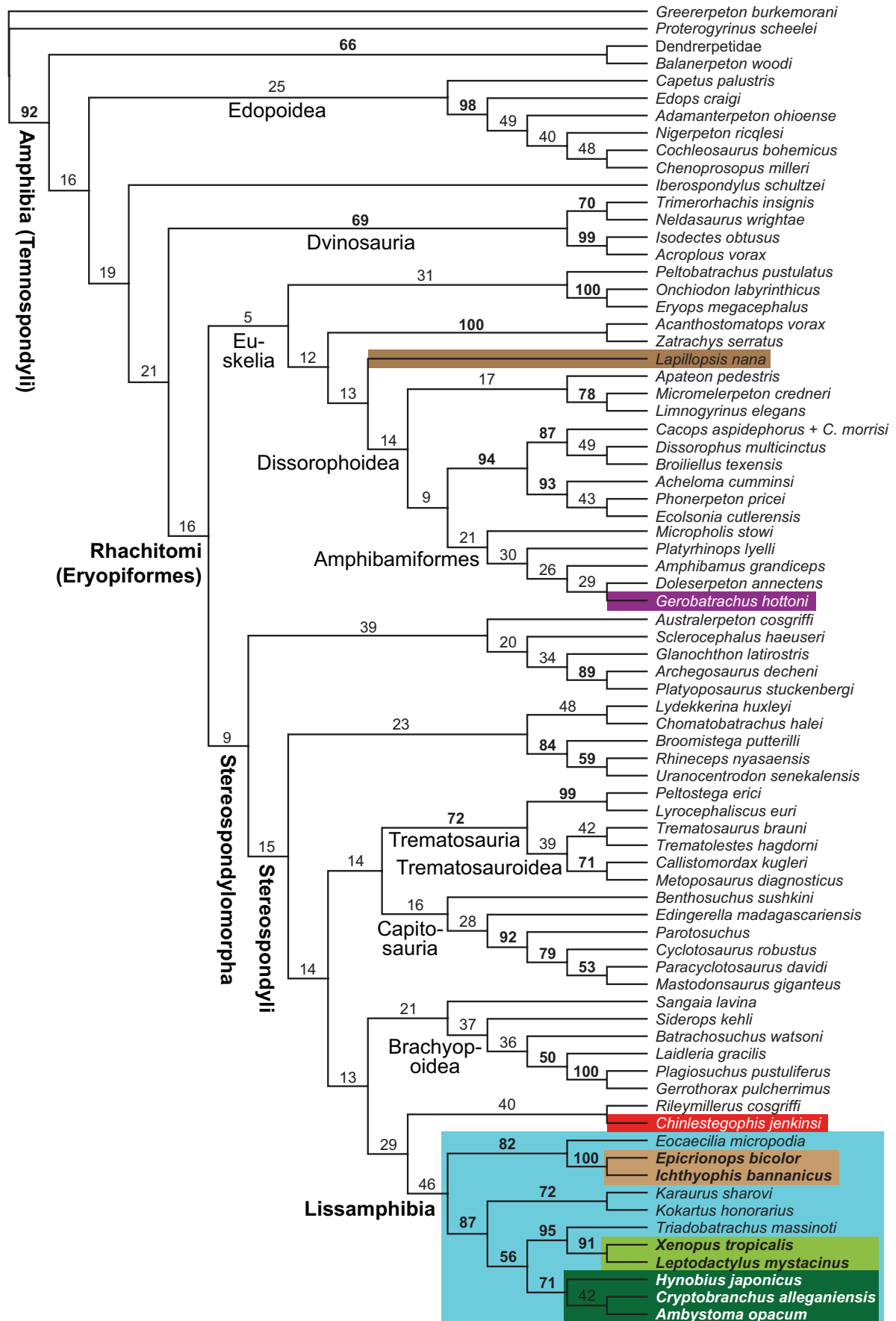


Figure 6. Strict consensus of the 270 MPTs obtained from the published matrix of Pardo et al. (2017a) with clinal characters ordered (analysis d1). Tr.-oidea = Trematosauoidea.



**Figure 7.** Bootstrap tree obtained from the published matrix of Pardo et al. (2017a) with clinal characters ordered (analysis d1). Bootstrap values  $\geq 50\%$  in boldface.

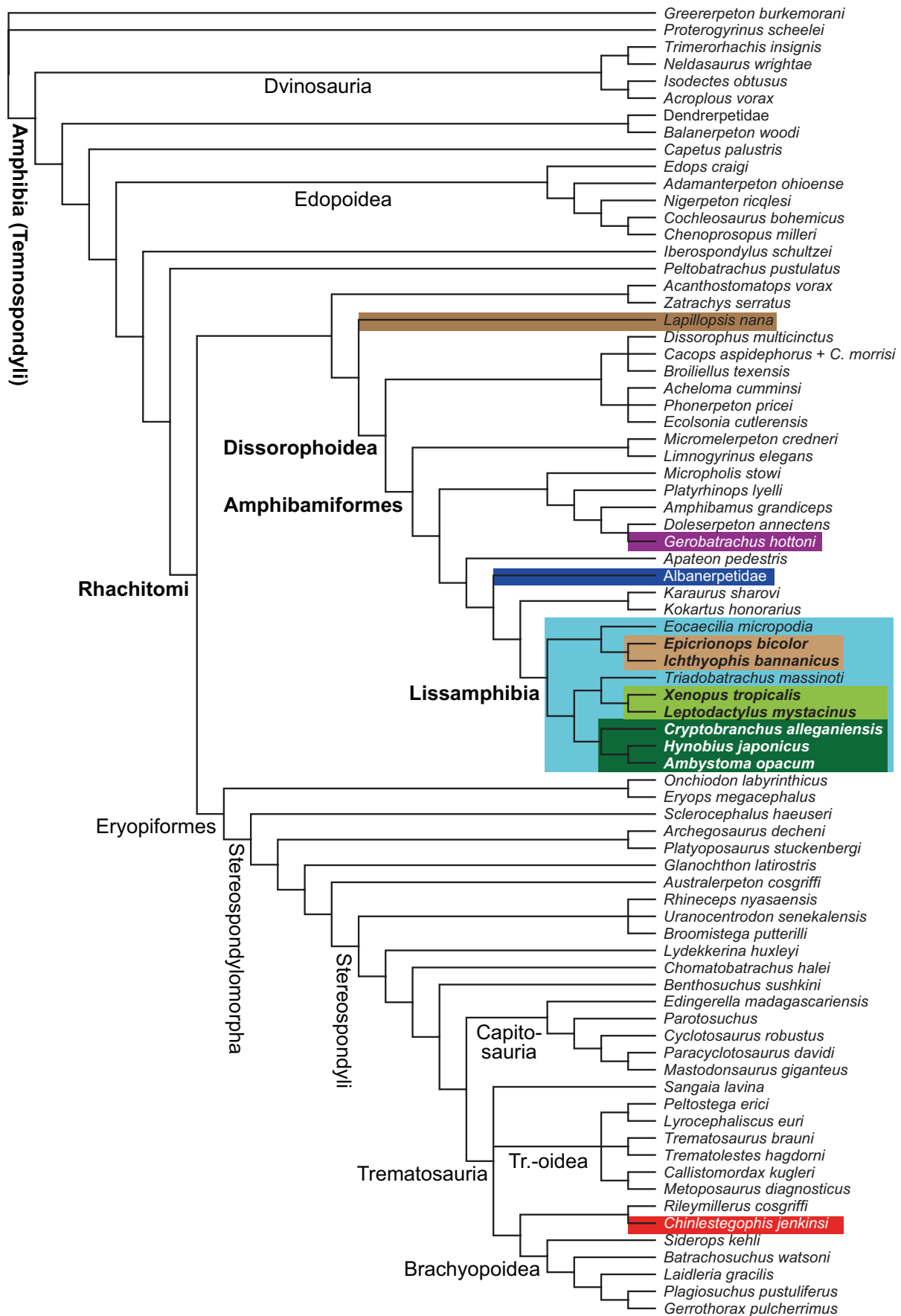
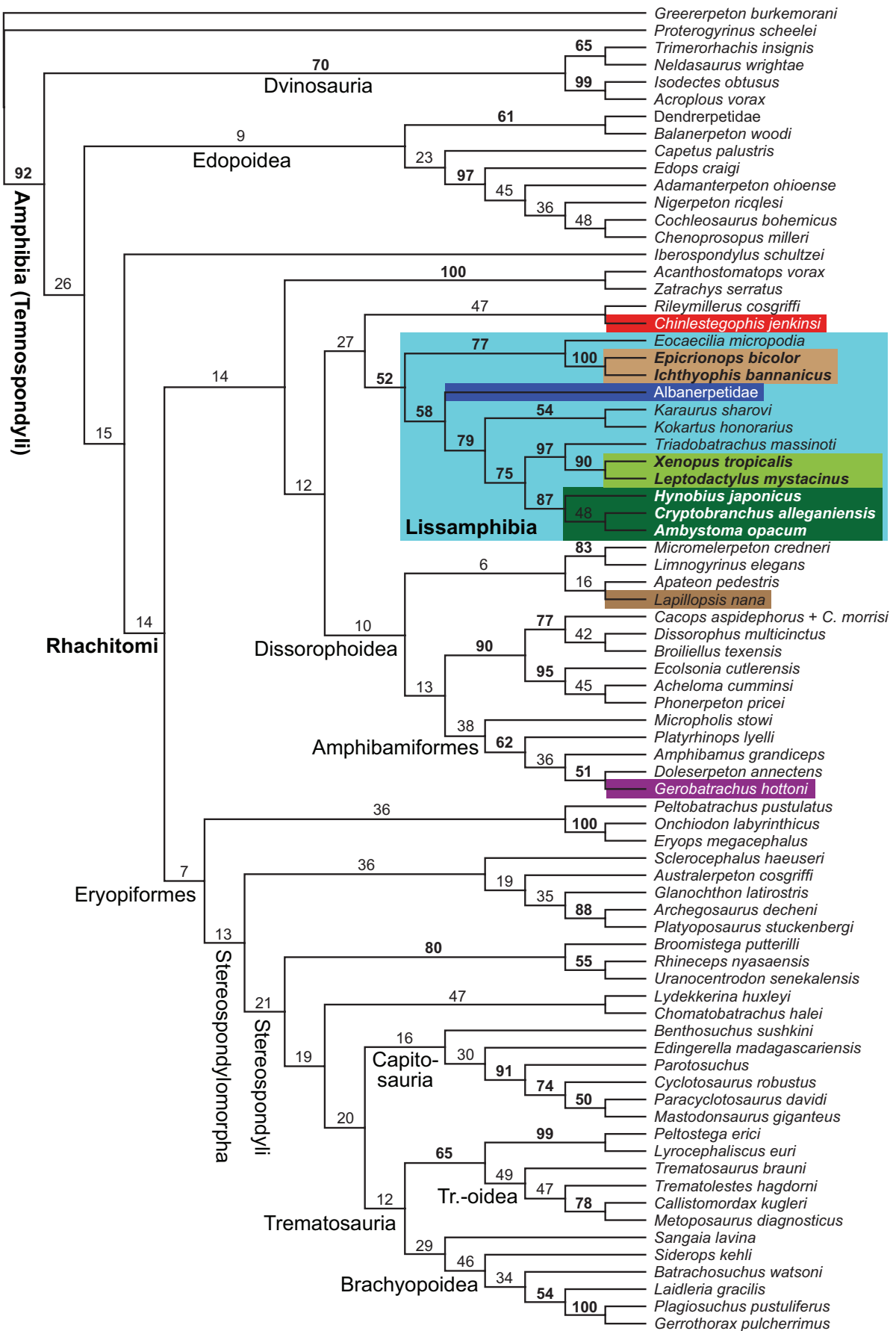


Figure 8. Strict consensus of the 30 MPTs obtained from the published matrix of Pardo et al. (2017a) with clinal characters ordered and Albanerpetidae added (analysis d2).



**Figure 9.** Bootstrap tree obtained from the published matrix of Pardo et al. (2017a) with clinal characters ordered and Albanerpetidae added (analysis d2). Bootstrap values  $\geq 50\%$  in boldface. Tr.-oidea = Trematosauroidae.

The list of bipartitions not compatible with the bootstrap tree (Suppl. material 2: table S3) reveals 40% bootstrap support for a clade of *Chinlestegophis* and the three caecilians (slightly more than the 38% without ordering and without Albanerpetidae) and 30% for a clade that includes these four and *Rileymillerus*. *Chinlestegophis* and *Rileymillerus* are excluded from Dissorophoidea + Lissamphibia in 21% of the bootstrap replicates. The support for exclusion of Albanerpetidae from Lissamphibia (17%) is lower than it could be given the 58% for a specific placement in Lissamphibia mentioned above; 12% of the replicates group the caecilians with Albanerpetidae, 6% find all dissorophoids, all batrachians, the karaurids and Albanerpetidae in an exclusive clade.

## Revised published matrix

The matrix including the changes we propose was run both with all characters unordered, as they were in Pardo et al. (2017a), and with the herein proposed characters that form morphological clines ordered; both of these options were used both without and with the addition of Albanerpetidae from Daza et al. (2020). The analysis with all characters unordered and Albanerpetidae excluded (e1) resulted in 1341 MPTs, each with a length of 1514 steps (CI excluding uninformative characters = 0.2535, RI = 0.6849, RC = 0.1801), distributed over seven islands of optimal trees. Of the 344 characters, only 319 are parsimony-informative. In all seven islands, Lissamphibia is recovered and excludes *Chinlestegophis* (as well as *Rileymillerus*). One island (Fig. 10) places (Brachyopoidea (Lissamphibia (*Chinlestegophis*, *Rileymillerus*))) in Stereospondyli, and Karauridae on the batrachian stem; the others recover Lissamphibia next to *Gerobatrachus* in Amphibamiformes while the *Chinlestegophis*-*Rileymillerus* clade remains nested in Stereospondyli next to or inside Brachyopoidea, and Lissamphibia is resolved either as (frogs (karaurids (caecilians, salamanders))) (Fig. 11), contradicting the molecular consensus (Hime et al. 2020), or as (caecilians (frogs (karaurids, salamanders))) (Fig. 12).

The second analysis, using ordered characters (e2), resulted in three islands of 99 MPTs in total (1558 steps; CI excluding parsimony-uninformative characters = 0.2489, RI = 0.6870, RC = 0.1759). 321 characters were parsimony-informative. The well-resolved strict consensus is shown in Figs 13, 14. Lissamphibia is recovered and placed next to a *Rileymillerus* + *Chinlestegophis* clade, which lies next to Plagiosauridae within the brachyopoid stereospondyls; Karauridae lies on the batrachian stem. *Gerobatrachus* remains next to *Doleserpeton* inside a variably resolved Dissorophoidea.

The third and fourth analyses differ from the first and second by the addition of Albanerpetidae (from Daza et al. 2020) as in analysis c. In both, 326 of the 344 characters were parsimony-informative. The unordered analysis e3 yielded 297 MPTs (1564 steps, CI

excluding uninformative characters = 0.2498, RI = 0.6790, RC = 0.1732); PAUP\* groups them as two islands, but these are similar enough that we present the overall strict consensus in Fig. 15. Dissorophoidea including Lissamphibia is resolved as in analysis c; the *Rileymillerus* + *Chinlestegophis* clade is grouped with the poorly resolved brachyopoid stereospondyls.

In the ordered analysis e4, 81 MPTs are recovered (1609 steps, CI without uninformative characters = 0.2434, RI = 0.6817, RC = 0.1695). They all group the *Rileymillerus* + *Chinlestegophis* clade with Brachyopoidea as in analysis e3, while Lissamphibia is nested among the amphibamiform dissorophoids, closer to *Apateon* than to *Gerobatrachus* or *Doleserpeton*. PAUP\* groups the MPTs into three islands depending on how they resolve amphibamiform phylogeny: one island (Fig. 16) has (*Doleserpeton* (*Gerobatrachus* (*Apateon*, Lissamphibia))) inside Amphibamidae, Albanerpetidae on the caecilian stem and Karauridae on the batrachian stem; the other two (Fig. 17) have (*Apateon* (Albanerpetidae (Karauridae, Lissamphibia))) close to but outside Amphibamidae, which contains *Gerobatrachus*; the Early Triassic amphibamiform *Micropholis* is either on the amphibamid or on the lissamphibian side.

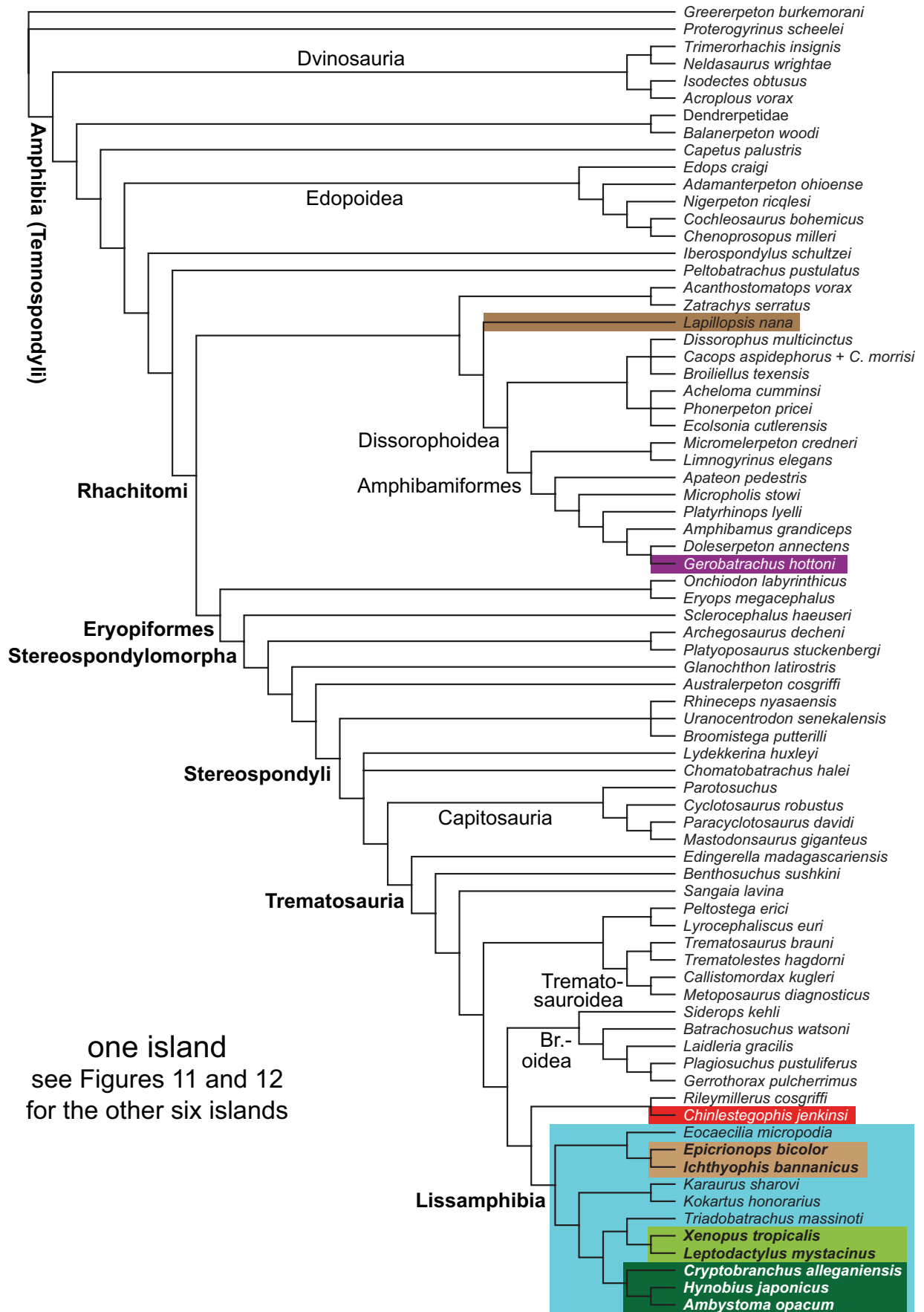
Bootstrapping analysis e4 reveals (Fig. 18) considerable support for Lissamphibia (77%), within which Albanerpetidae (43%) and Karauridae (64%) lie on the batrachian stem but not in Batrachia (75%). Lissamphibia is, with limited support, placed next to *Apateon* (22%) in Dissorophoidea (35%); similar support is recovered for placing *Chinlestegophis* (and *Rileymillerus*) close to brachyopoids including plagiosaurids (27%) in Stereospondyli (34%).

Groupings not compatible with the bootstrap tree (Suppl. material 2: table S4) include *Chinlestegophis* + *Rileymillerus* as gymnophionomorphs (15%) or in an exclusive clade with Lissamphibia (29%); comparable support exists for Lissamphibia without Albanerpetidae (30%) or Lissamphibia without Karauridae or Albanerpetidae (20%), both of which are also incompatible with the bootstrap tree. An exclusive clade of lissamphibians and stereospondyls occurs in only 10% of the bootstrap replicates.

## Discussion

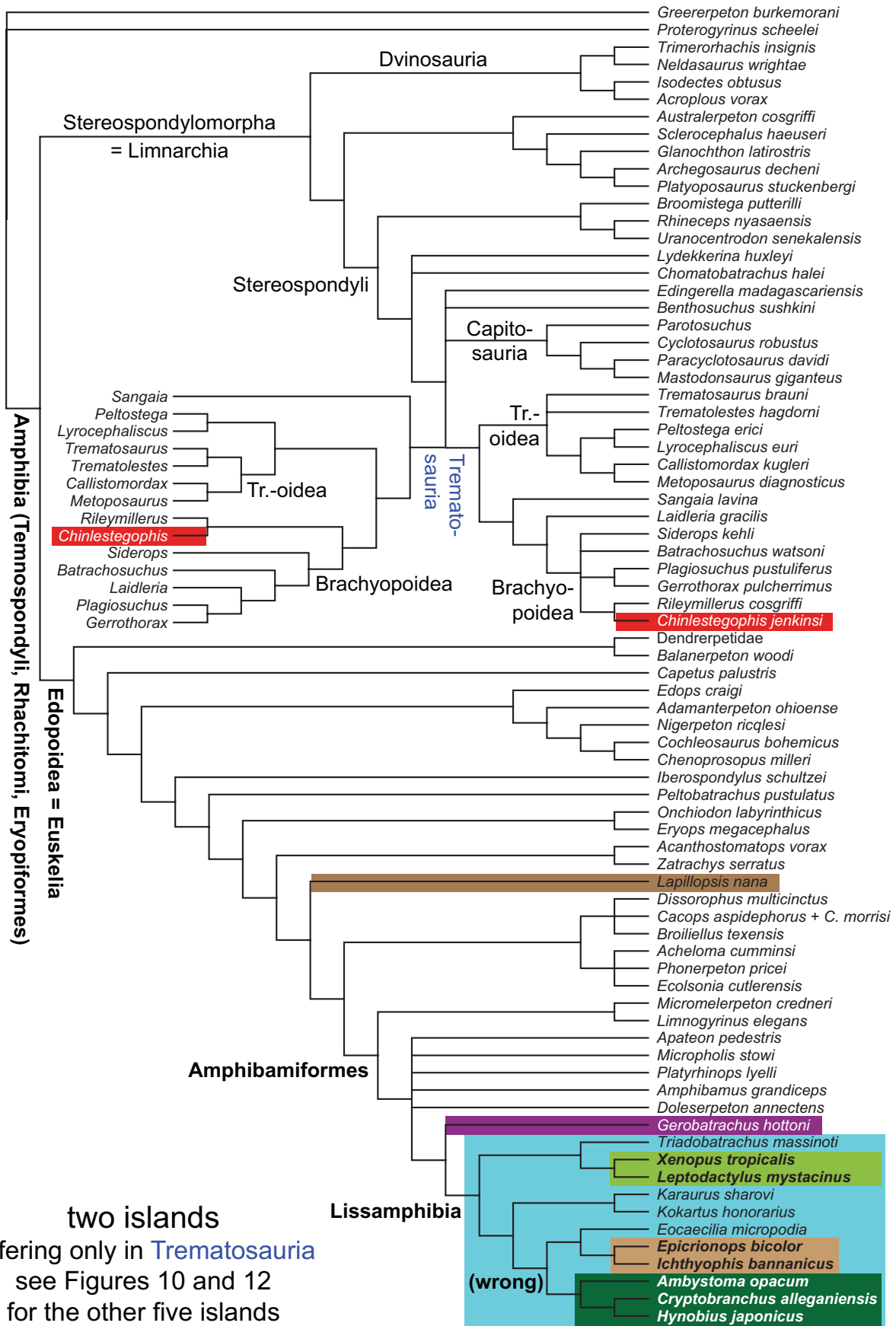
### Support for alternative topologies

Our work corroborates some of the results of the analyses performed by Pardo et al. (2017a), but also highlights weaknesses in the phylogenetic signal that was claimed to support caecilian affinities of *Chinlestegophis*. Indeed, Pardo et al. (2017a: abstract) claimed: “Our results place the taxon confidently within lissamphibians.” On the contrary, our results demonstrate that the affinities of *Chinlestegophis* cannot be ascertained with confidence based on either of the two matrices of Pardo et al. (2017a).

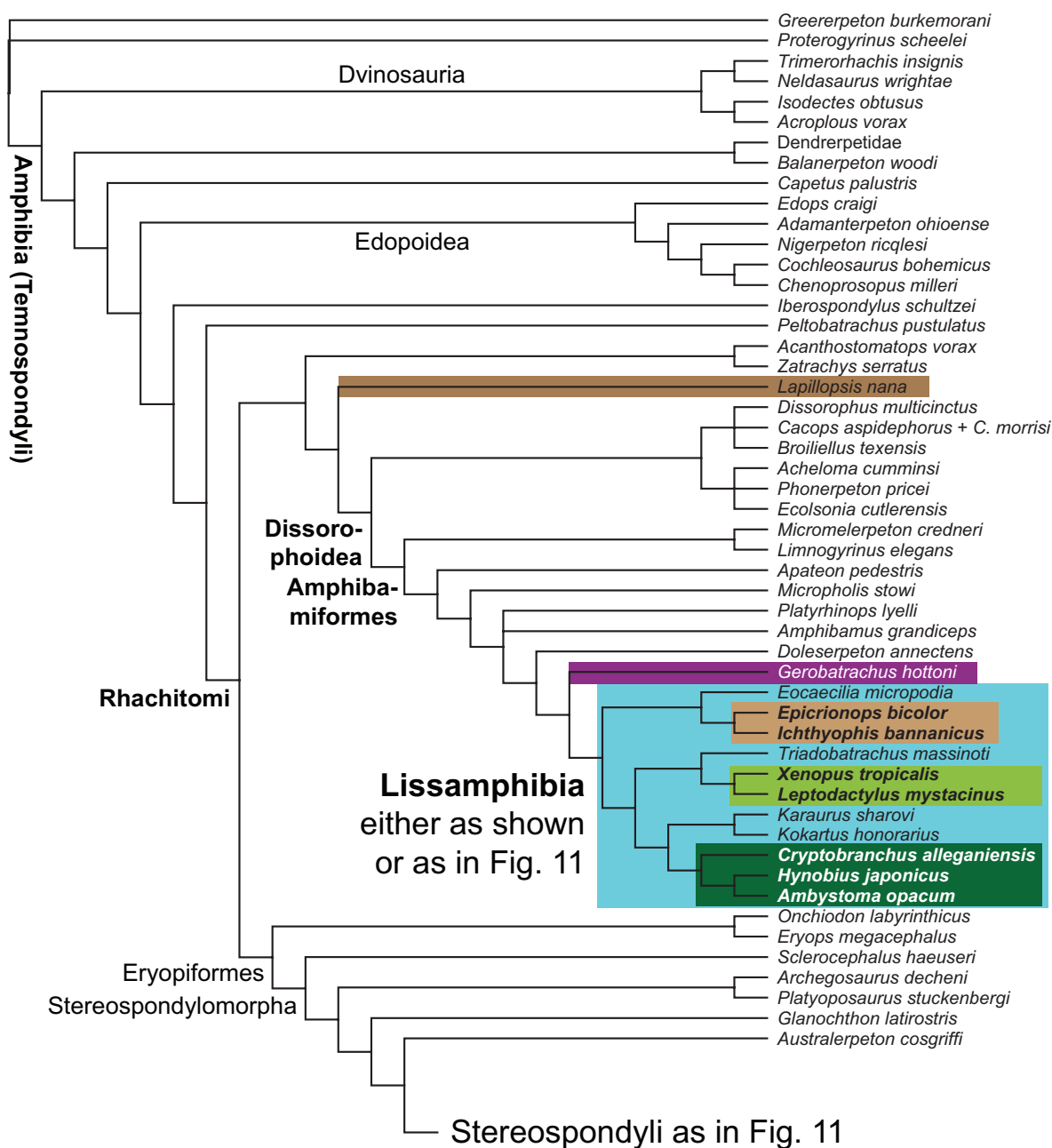


**Figure 10.** Strict consensus tree of some of the 1341 MPTs recovered in analysis e1 (published matrix of Pardo et al. [2017a] after revision, all characters unordered). For the other MPTs, see Figs. 11 and 12. Br.-oidea = Brachyopoidea.





**Figure 11.** Strict consensus of each of two further islands of MPTs from analysis e1. For space reasons, one of the two resolutions of Trematosauria is mirrored and presented without species names. For the other MPTs, see Figs 10, 12. Tr.-oidea = Trematosauroida. The branch marked “(wrong)” contradicts the molecular consensus (Hime et al. 2020).

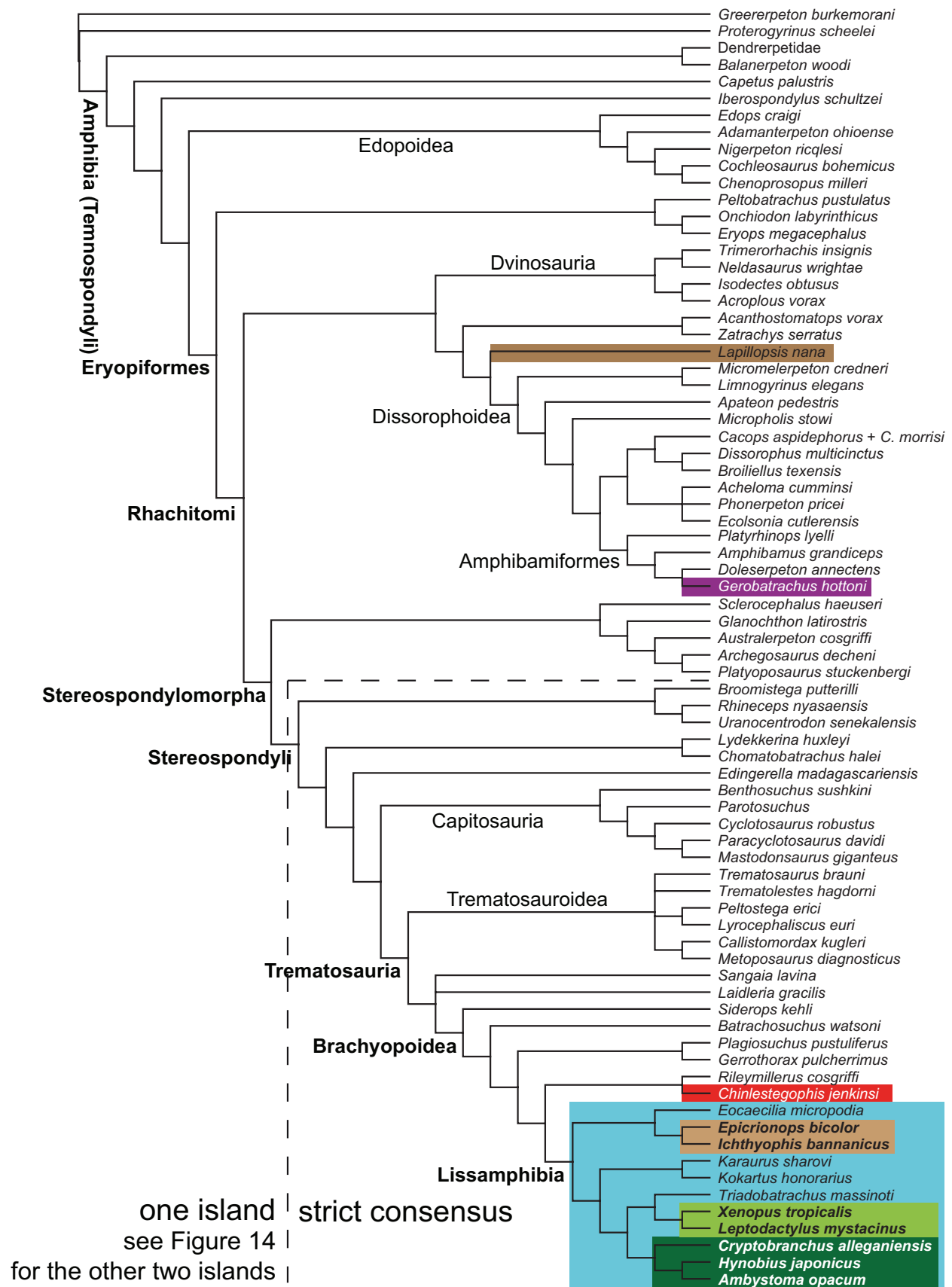


four islands  
 (both combinations of both  
 resolutions of Lissamphibia  
 and Stereospondyli occur)  
 see Figures 10 and 11  
 for the other three islands

**Figure 12.** Strict consensus of each of the remaining four islands of MPTs from analysis e1. Except for Lissamphibia, the part depicted here is identical in all four islands; Lissamphibia is resolved either as shown or as in Fig. 11, Stereospondyli is resolved as in Fig. 11 (with both options shown there for Trematosauria). For the other MPTs, see Figs 10, 11.

First, we stress that the unpublished matrix (our analysis a1, see Table 1; Fig. 2; Pardo et al. 2017a: fig. S6) yielded a commonly recovered Lissamphibia, nested within dissorophoids and optionally containing *Gerobatrachus* but never *Chinlestegophis*. This is important because it suggests that

when a broader sample of extinct tetrapods is included, a more mainstream hypothesis of both lissamphibian ancestry and Paleozoic tetrapod relationships is produced, and the stereospondyls represented in this matrix, *Rileymillerus* and *Chinlestegophis*, are distanced from lissamphibian



**Figure 13.** Strict consensus of all (to the right and below the dashed line) or some (to the left and above the stippled line) of the 99 MPTs recovered in analysis e2 (published matrix of Pardo et al. [2017a] after revision, clinal characters ordered). See Fig. 14 for the remaining MPTs.

origins. Constraining *Eocaecilia* to nest among lepospondyls (analysis a2; Fig. 3) results in only slightly longer trees (4 steps added to the 1450 of the unconstrained trees) that are not significantly different from the unconstrained trees ( $p$  between 0.62 and 0.72 according to the three usual tests) despite conforming to the “lepospondyl hypothesis” of amphibian origins.

All of our remaining analyses focused on the published matrix of Pardo et al. (2017a). Unsurprisingly, we confirmed (analysis b) the results of Marjanović and Laurin (2019: fig. 30I–K), Serra Silva and Wilkinson (2021) and Gee (2022) that Pardo et al. (2017a) found all MPTs that fit this matrix, that the MRC tree they reported is accurate as such, and that the MRC tree is a highly incomplete representation of the MPTs: it is equally parsimonious for Batrachia and Gymnophiona to lie in Stereospondyli or Amphibamiformes, and for them to form Lissamphibia or not, which may or may not contain *Chinlestegophis*. We further contribute the first fully published bootstrap analysis of this matrix (Fig. 4, Suppl. material 2: table S1); contrary to Pardo et al. (2017a: fig. S7B), it supports diphyly of extant amphibians, although the support is not strong (52% for grouping *Chinlestegophis* with the caecilians; 43% for grouping *Gerobatrachus* with the batrachians; only 35% for grouping all dissorophoids with the batrachians to the exclusion of any caecilians).

Pardo et al. (2017a: fig. S7B) found no bootstrap values of 50% or higher on any node that separates caecilians and batrachians. Differences in bootstrap settings may explain why our results differ somewhat from those of Pardo et al. (2017a); we used 200 bootstrap replicates of 500 addition-sequence replicates each, whereas Pardo et al. (2017a) used 1000 bootstrap replicates of 100 addition-sequence replicates each (J. Pardo pers. comm. 2023; the settings were not published).

However, adding Albanerpetidae to the matrix (analysis c; Fig. 5) confirms the result of Daza et al. (2020): Lissamphibia is found in Amphibamiformes in all MPTs, while *Chinlestegophis* is always a stereospondyl. The omission of albanerpetids from the original matrix was clearly a suboptimal choice, given that all studies published since their discovery over half a century ago support close affinities between albanerpetids and lissamphibians, if not a position among lissamphibians (e.g., Estes 1969; Estes and Hoffstetter 1976; Fox and Naylor 1982; McGowan and Evans 1995; Maddin et al. 2013; Daza et al. 2020; Kligman et al. 2023). Even the most unorthodox analysis of albanerpetid affinities that we know of suggested close affinities to batrachians (McGowan 2002).

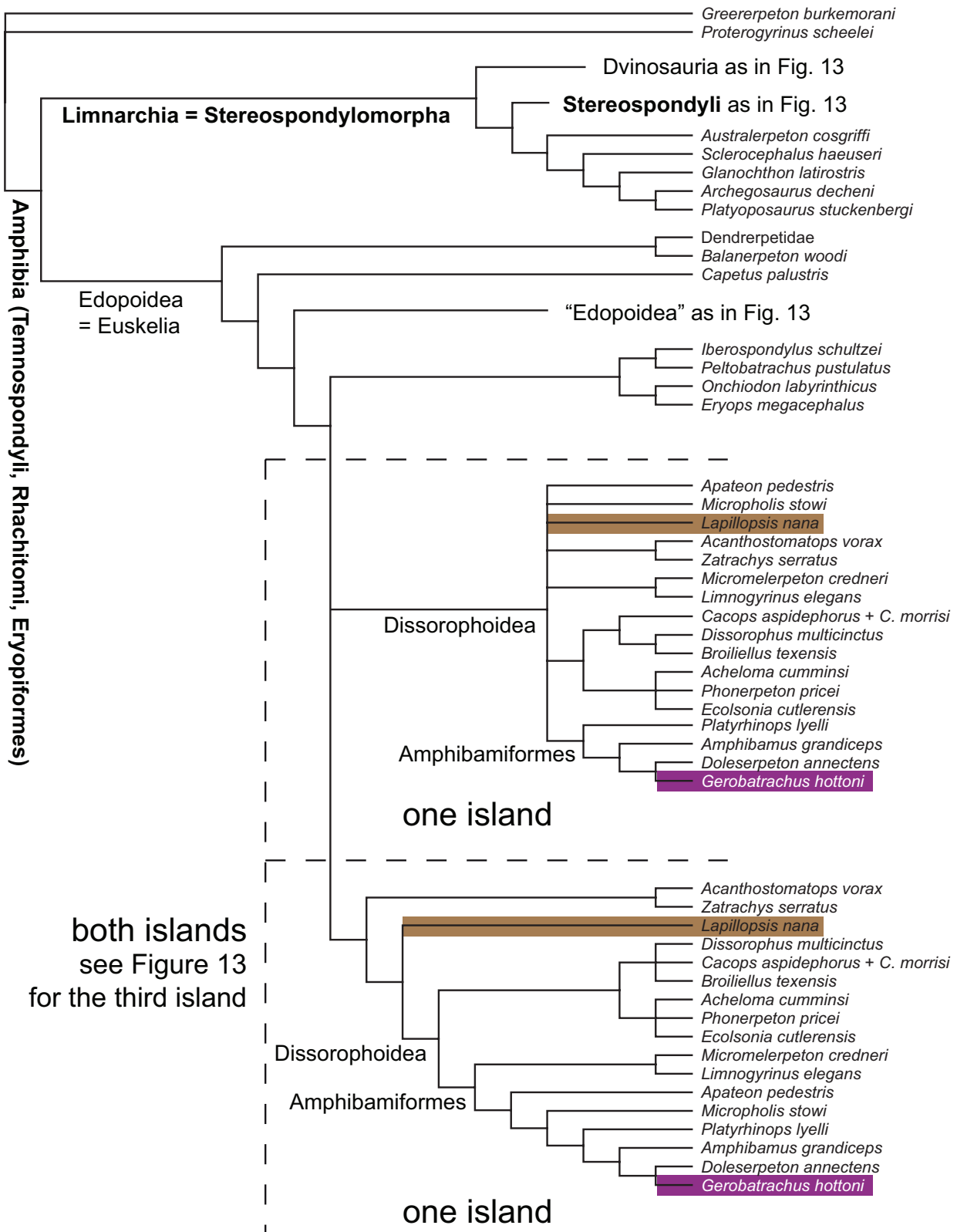
The effect of ordering characters within the original published matrix (i.e., without Albanerpetidae and without corrections other than renumbering the states of some ordered characters) (analysis d1; Fig. 6) was to decrease the number of islands from five to one: Lissamphibia (which has 46% bootstrap support) forms the sister group of the stereospondyls *Chinlestegophis* and

*Rileymillerus*. This arrangement only occurs in 29% of the bootstrap replicates, however (Fig. 7; Suppl. material 2: table S2). Adding Albanerpetidae (analysis d2) moved Lissamphibia into the amphibamiform dissorophoids; *Chinlestegophis* and *Rileymillerus* remained brachyopoid stereospondyls (Fig. 8). Bootstrapping this analysis (Fig. 9; Suppl. material 2: table S3) revealed increased, if still modest, support for Lissamphibia (52%) and weak support for any position of that clade, but comparatively strong support against a position close to *Gerobatrachus* or *Doleserpeton* (62%).

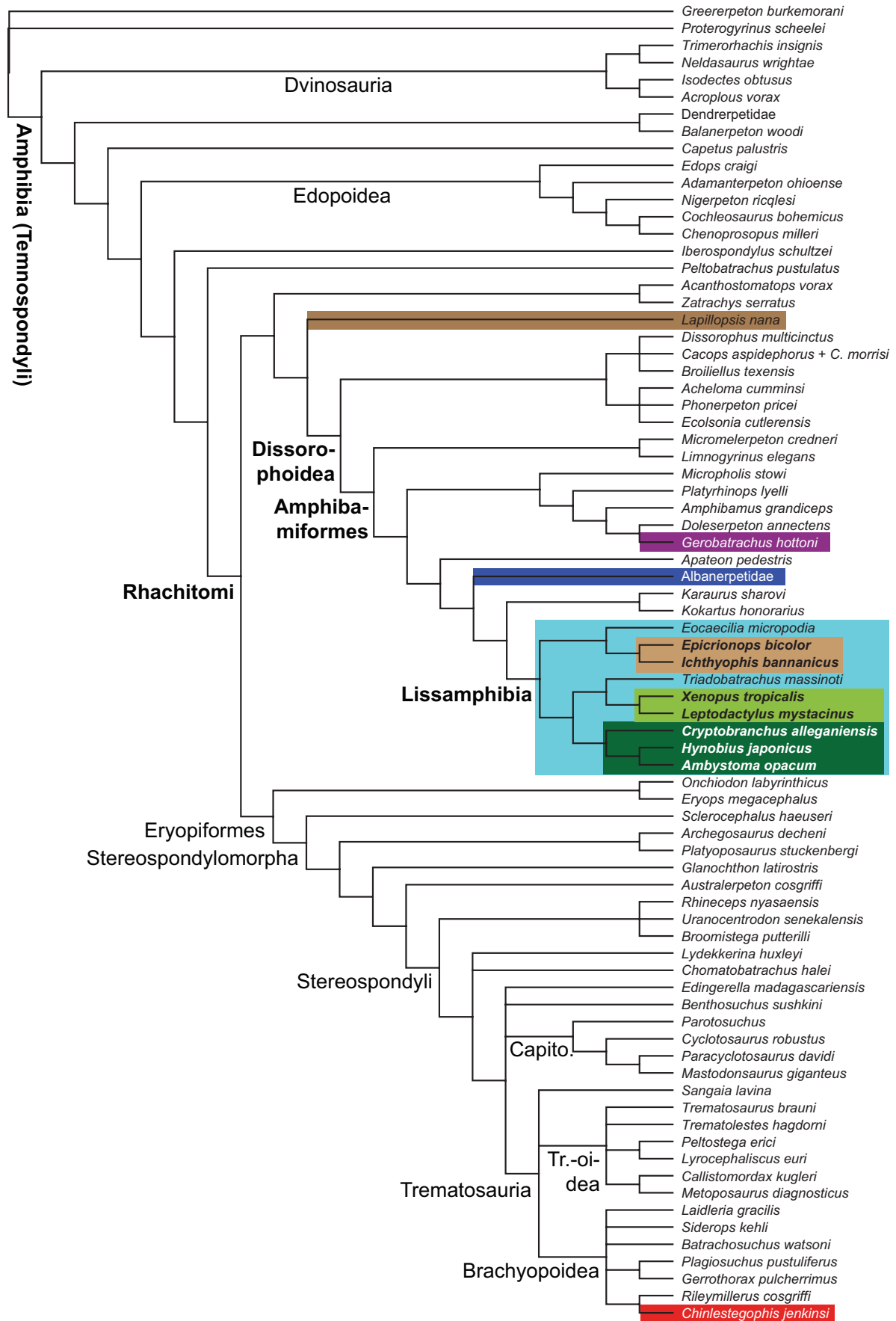
A modest revision of the published matrix, without Albanerpetidae, replicated the basic results of analyses c and d1 as equally parsimonious when all characters were unordered (analysis e1; Figs 10–12). Ordering (analysis e2; Figs 13, 14) restricted Lissamphibia to Stereospondyli as in analysis d1 (unmodified matrix, likewise ordered, likewise without Albanerpetidae). Adding Albanerpetidae without ordering (analysis e3; Fig. 15) essentially replicated analysis c; ordering (analysis e4; Figs 16, 17) introduced variation within Lissamphibia but kept it in the same place as in analysis c—with strong bootstrap support: a lissamphibian-stereospondyl clade is not compatible with the bootstrap tree (Fig. 18) and only occurs in 10% of the replicates (Suppl. material 2: table S4). The 77% support for Lissamphibia (with Albanerpetidae) excluding *Chinlestegophis* (or *Rileymillerus*, *Gerobatrachus* or any other traditional non-member) is worth highlighting.

In all four cases, ordering increased the resolution of the results. We interpret this as an example of ordering bringing out phylogenetic signal in data, congruent with results from simulations and some empirical examples; note that ordering does not automatically increase the net resolution (Marjanović and Laurin 2008, 2019; Grand et al. 2013; Rineau et al. 2015, 2018; and references therein).

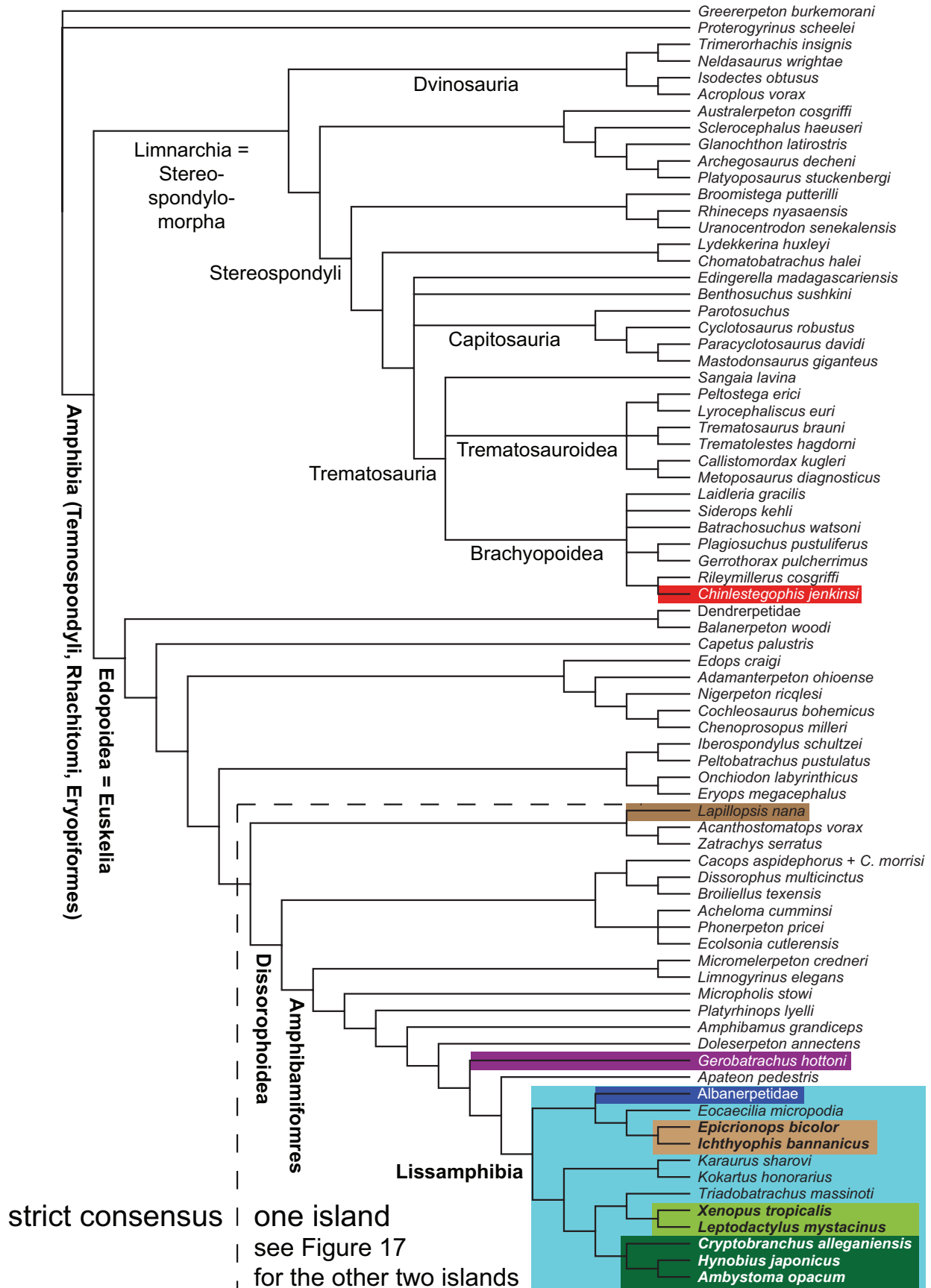
Strikingly, none of the trees from analyses c, d or e (most parsimonious or bootstrap) support affinities between *Chinlestegophis* and caecilians to the exclusion of other lissamphibians. The bootstrap analysis of the original matrix under original conditions (analysis b; Fig. 4, Suppl. material 2: table S1) only weakly supports diphyly of extant amphibians and an exclusive clade of *Chinlestegophis* and the three caecilians (bootstrap frequency of 52%) or an exclusive clade of frogs, salamanders, karaurids and *Gerobatrachus* (frequency of 43%). Our highly restricted revisions to the published matrix (analyses e1, e2; see Gee 2022 for a generally much more thorough revision), as well as the addition of Albanerpetidae to the taxon sample (analysis c) or the combination of both (analyses e3, e4), resulted in an exclusive clade comprising lissamphibians being nested among dissorophoids (analyses c, e1, e3, e4 and its bootstrap analysis), or Lissamphibia as sister to *Chinlestegophis* + *Rileymillerus* within Stereospondyli (analyses e1, e2). The former is the currently most widespread hypothesis on the origin of the extant amphibian clades; the latter is new, but considerably less novel than extant amphibian diphyly as proposed by Pardo et al. (2017a).



**Figure 14.** Strict consensus of the remaining MPTs recovered in analysis e2 (published matrix of Pardo et al. [2017a] after revision, clinal characters ordered). See Fig. 13 for the MPTs not represented here and for the clades shown collapsed here.



**Figure 15.** Strict consensus of the 297 MPTs recovered in analysis e3 (published matrix of Pardo et al. [2017a] after revision, Albanerpetidae added from Daza et al. [2020], all characters unordered). Capito. = Capitosauria; Tr.-oidea = Trematosauroida.



**Figure 16.** Strict consensus of all (to the left and above the stippled line) or some (to the right and below the stippled line) of the 81 MPTs recovered in analysis e4 (published matrix of Pardo et al. [2017a] after revision, Albanerpetidae added from Daza et al. [2020], clinal characters ordered). For the other MPTs, see Fig. 17.

The published matrix of Pardo et al. (2017a) contains some data that suggest affinities between Lissamphibia and the *Chinlestegophis* + *Rileymillerus* clade, always within Stereospondyli, as recovered in analyses b (as one of several equal options), d1 (if only with 29% bootstrap support), e1 (as one of two options) and e2. Although weakly supported, the fact that this result occurred in the original (analyses b, d1) and the revised matrix (analyses e1, 2) suggests that *Chinlestegophis* may contribute important information about amphibian evolution in the context of the “temnospondyl hypothesis”, even if it cannot be supported specifically as a stem-caecilian. More likely, however, it may highlight convergence between the *Chinlestegophis* + *Rileymillerus* clade and lissamphibians in general or caecilians in particular; this is supported to an extent by our bootstrap of analysis e4 (Fig. 18; Suppl. material 2: table S4), where *Chinlestegophis* + *Rileymillerus* were recovered next to Lissamphibia in only 29% and as gymnophionomorphs in only 15% of the bootstrap replicates while a lissamphibian-stereospondyl clade only has 10% bootstrap support (all three groupings are incompatible with the bootstrap tree: Fig. 18), as well as by the bootstrap analysis conducted by Kligman et al. (2023: extended data figure 6), where Lissamphibia excluding *Chinlestegophis* and *Rileymillerus* occurred in 55% of the replicates and Stereospondyli including a *Chinlestegophis* + *Rileymillerus* clade in 57%. Minimally, our results highlight the importance of albanerpetids—sampled in analyses c, d2, e3 and e4—for understanding lissamphibian relationships.

Pardo et al. (2017a) emphasized that the topology they presented was supported by Bayesian inference. As discussed above (Matrices, Methodologies, and Missteps: Bayesian inference of phylogeny), missing data have unpredictable, sometimes very strong, effects on parametric methods of phylogenetics such as Bayesian inference, while the non-parametric method called parsimony is unaffected by this particular issue and therefore safer for paleontological data. Matrix quality remains more important than the method of analysis (Simões et al. 2017; Marjanović and Laurin 2019; Gee 2021, 2022; and references therein).

## Assessment of qualitative arguments

As further support for a close relationship between *Chinlestegophis* and caecilians, Pardo et al. (2017a) proposed a number of features supposedly shared between both taxa, and in some cases with other stereospondyls. Most of them are coded in the matrix in some form. However, our review of these features (Materials and Methods: Evaluation of potential synapomorphies and revisions to the published matrix) finds serious problems in all of them; none supports placing caecilians as the sister taxon of *Chinlestegophis* (or *Chinlestegophis* + *Rileymillerus*), or in stereospondyls in general.

We note several other features, not discussed by Pardo et al. (2017a), by which *Chinlestegophis* resembles other stereospondyls but differs starkly from caecilians. The basicranial articulation in *Chinlestegophis* superficially

resembles that of *Eocaecilia* and Gymnophiona. However, in *Chinlestegophis*, the basicranial joint forms a strong girder, tightly sutured (Pardo et al. 2017a), similar to the condition seen in other stereospondyls. In caecilians, the basicranial joint is instead loosely constructed, with thick cartilage covering the bony joint surfaces of both the *os basale* and the (epi)pterygoid or pterygoquadrate (Maddin et al. 2012b). Furthermore, *Chinlestegophis* has well-developed posttemporal fenestrae, as in brachyopoid stereospondyls, while in lissamphibians and albanerpetids these fenestrae are absent.

What little is known and described of the postcranial skeleton of *Chinlestegophis* (Pardo et al. 2017a: fig. S5) also resembles other stereospondyls but starkly differs from caecilians. The interclavicle of *Chinlestegophis* is a large plate, as usual for stereospondyls; in lissamphibians and albanerpetids, no interclavicle is known. Similarly, the clavicles consist mostly of a large plate and look unremarkable for a stereospondyl in all details of their shape; clavicles are absent in albanerpetids, caecilians (including *Eocaecilia*) and salamanders, and those of frogs are robust curved struts more similar to those of extant amniotes. A few neural arches are preserved in *Chinlestegophis*, but centra are not; this is standard for morphologically immature temnospondyls, but only observable (as presence or absence of ossification) in a very short phase in the ontogeny of frogs and hynobiid salamanders, and not known in caecilians—in *Gegeneophis* and in *Caecilia orientalis* Taylor, 1968, the centra ossify before the neural arches (Müller 2006; Pérez et al. 2009). Indeed, early ossification of the centra (earlier than the neural arches or not long after them), quickly followed by suturing or even fusion to the neural arches, is a synapomorphy of lissamphibians and probably a few amphibamiforms (notably *Doleserpeton* and *Gerobatrachus*) under the “temnospondyl hypothesis”, or of Seymouriamorpha, Chroniosuchia and Tetrapoda under the “lepospondyl hypothesis” (Laurin and Reisz 1997; Danto et al. 2019). Full neurocentral fusion is not found outside these clades (and Albanerpetidae), but is found in all known vertebrae of *Eocaecilia* (Jenkins et al. 2007) and the lone vertebra referred to *Funcusvermis* (Kligman et al. 2023). The ribs of *Chinlestegophis* are, plesiomorphically, longer than three successive vertebrae; they are shorter in amphibamiforms and a few select lepospondyls (Marjanović and Laurin 2008, 2019), and much shorter, about as long as one vertebra, in albanerpetids and all lissamphibians except a few peramorphic salamandrids (Marjanović and Witzmann 2015, and references therein). The only known postcranial similarity to caecilians is body elongation; the massive dermal shoulder girdle does not suggest limb reduction, and indeed the presumed ulna has an unremarkable size.

## Homoplastic rather than stepwise evolution

Interpretations of functional biology and evolutionary trends rely on our perspective of phylogenetic relationships. In the original description of *Chinlestegophis*, once



rest of tree identical to overall strict consensus in Figure 16

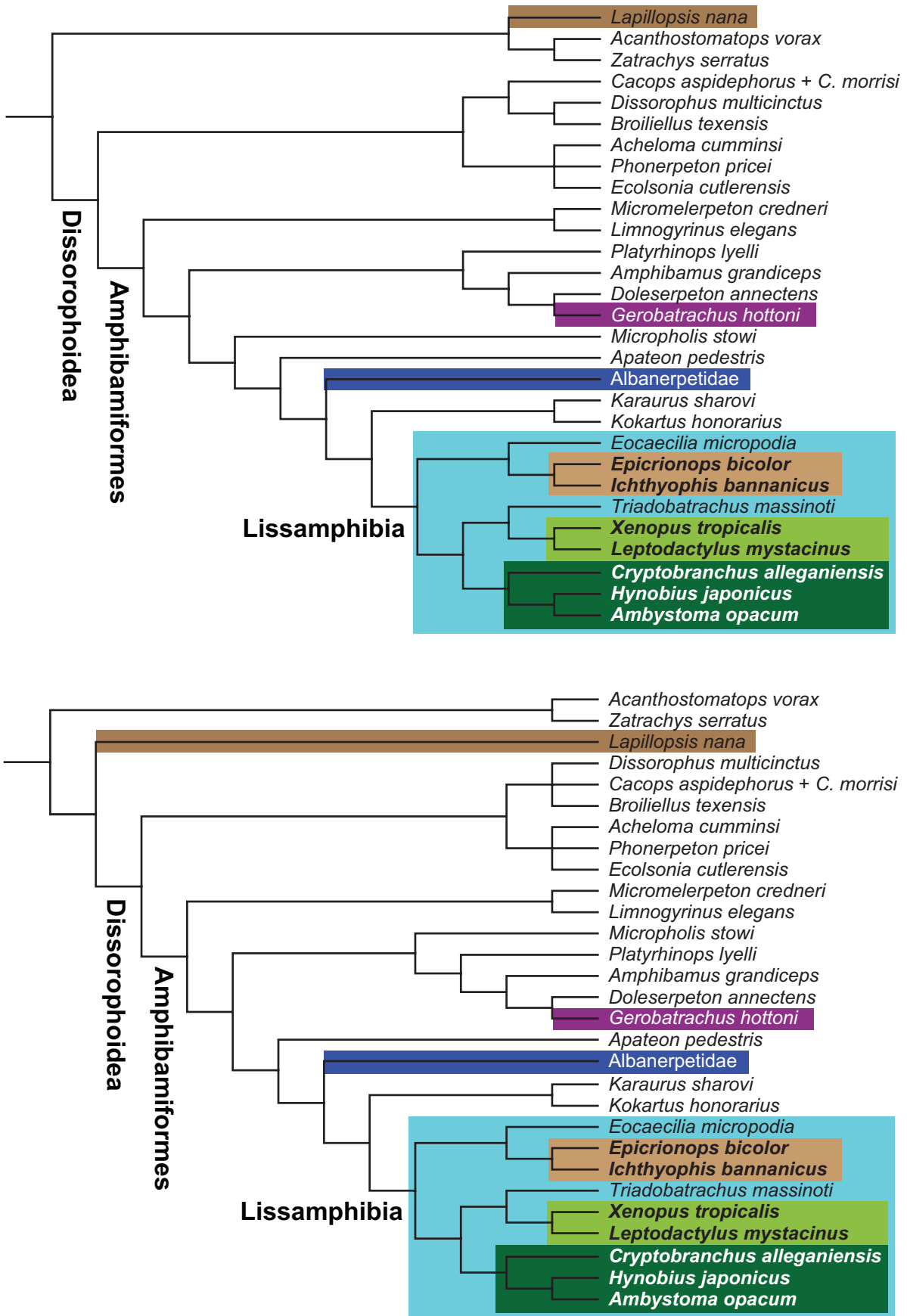
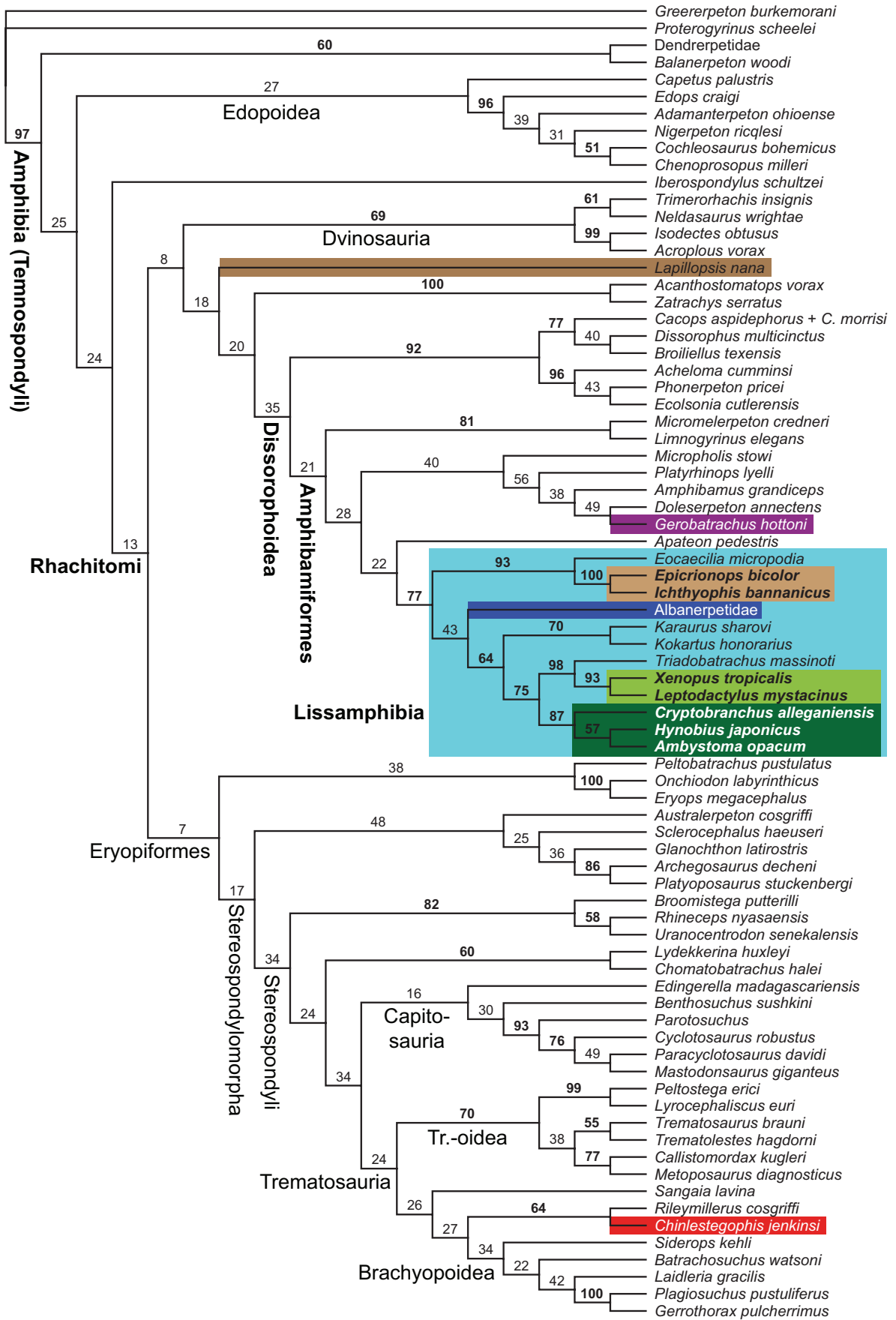


Figure 17. Strict consensus of each of the remaining two islands of MPTs from analysis e4. The remainder of the tree is identical in all three islands and not repeated here; see Fig. 16.



**Figure 18.** Bootstrap tree of analysis e4 (published matrix of Pardo et al. [2017a] after revision, Albanerpetidae added from Daza et al. [2020], clinal characters ordered). Bootstrap values  $\geq 50\%$  in boldface. Tr.-oidea = Trematosauroidae.

a consensus tree was selected and reported, a number of the characteristics used in the matrices and discussed above were used to infer a stepwise evolution of traits toward the specialized fossorial and head-first burrowing lifestyle of caecilians. Those features include fusion of the lacrimal + maxilla and exoccipital + opisthotic (interpreted as stages in the consolidation of the skull), repositioning of the jaw suspension, small and laterally oriented eyes, etc. However, as we demonstrate above, most of those features have a wider distribution across Paleozoic tetrapods or present confounding problems of homoplasy across many disparate clades, extinct and extant.

In particular, we regard as unfortunate the aforementioned removal of all lepospondyls from the unpublished matrix to create the published matrix after the initial recovery of *Chinlestegophis* as a temnospondyl by Pardo et al. (2017a). Potential affinities between lepospondyls and lissamphibians have been controversial for more than two decades (Anderson 2001; Marjanović and Laurin 2008, 2009, 2013, 2019; Laurin et al. 2022; Jansen and Marjanović 2022; Mann et al. 2022; and references therein). Thus, including lepospondyls in tests of the origins of extant amphibians is critical to represent the full range of morphology during the Paleozoic and reveal potential homoplasy. Removing those taxa from analyses could make it more likely that any elongate, fossorial, or burrowing taxa such as *Chinlestegophis* and caecilians be placed together incorrectly in the phylogeny.

Schoch et al. (2020) added three lepospondyls to the published matrix of Pardo et al. (2017a), but they did not add any characters that would help resolve their phylogeny or their relationship to lissamphibians. This was not changed by Kligman et al. (2023), in whose results those three lepospondyls form the sister-group of *Greererpeton* (Kligman et al. 2023: extended data figs 5–7), an Early Carboniferous colosteid that is a more appropriate outgroup than the anthracosaur *Proterogyrinus* that was used as such.

Considering that alternative hypotheses of relationships are equally supported by the published matrix, even without broader taxonomic sampling to include lepospondyls, the proposed stepwise evolution of caecilian features falls apart. Rather than traits linking *Chinlestegophis* and caecilians, those same characteristics appear to represent homoplasy, as shown in trees that place *Chinlestegophis* close to but outside Lissamphibia (our analyses a, d, e2 and some MPTs of b and e1 plus the bootstrap of b) or far away (our analyses c, e3, e4 and some MPTs of b and e1).

## Evolutionary ecology

The grooves for the lateral-line organ identified by Pardo et al. (2017a) on the skull of *Chinlestegophis* indicate an animal that was strictly aquatic for at least part of its adult life. In contrast, there is no evidence of lateral-line grooves or other aquatic features in *Eocaecilia* or the admittedly fragmentary *Funcusvermis*, and among extant caecilians aquatic lifestyles are restricted to larvae

(of those few taxa that have them) and the highly nested clade Typhlonectidae. The inference of an aquatic lifestyle in *Chinlestegophis* is further supported by its poorly ossified vertebral column and probably also by its cranio-caudally elongate plate-like clavicles. Perhaps aquatic vs. terrestrial lifestyles explain why *Chinlestegophis* was able to coexist with caecilians like the slightly older *Funcusvermis*; the wide, flat vertebra referred to the latter lacks a neural spine, interpreted as a fossorial adaptation by Kligman et al. (2023).

## Matrix quality, taxon sampling and character sampling

The discussion above takes at face value both the coding and scoring of the two matrices, and their character and taxon samples, apart from our limited modifications in analyses c, d2 and e; but these issues deserve comments. We have not scrutinized the matrices in full (see Gee 2022 for a cautious but comprehensive treatment of the published matrix of Pardo et al. 2017a), as we wished only to test whether alternative topologies can be equally (or better) supported by the original matrices, and to show the impact of a few scoring changes that were obviously needed. The absence of lepospondyls in the matrix published by Pardo et al. (2017a) prevents us from looking into how many extra steps an origin of lissamphibians among them would imply, compared to an origin among temnospondyls. Similarly, the removal of characters that are variable only among lepospondyls prevents using the published matrix as a starting point for such comparisons; unfortunately, this was not changed by Schoch et al. (2020) or Kligman et al. (2023) despite the former's addition of three lepospondyl OTUs which the latter then retained. The heretofore unpublished precursor matrix remains available for this purpose, but it would need to be updated and greatly enlarged; in its present form, only four extra steps need to be added to the original 1450 to make an odd version of the lepospondyl hypothesis possible.

## Conclusions

Published in one of the most prestigious journals, the description of *Chinlestegophis* (Pardo et al. 2017a) resulted in a new hypothesis about the origins of the extant amphibian clades and a new scenario for the origin of caecilians and their fossorial lifestyle that has attracted attention far beyond that of specialist researchers (Pough et al. 2022). We show that these exciting proposals are poorly supported by the original datasets and the original methods of analysis, as well as by limited revisions to one of the datasets aimed at eliminating the most conspicuous cases of character redundancy and a few questionable anatomical interpretations of *Chinlestegophis* and other taxa. The question of lissamphibian origins

remains unsolved, although our revisions to the matrix reveal further support for Lissamphibia excluding *Chinlestegophis* and any Paleozoic taxa. In any case, we join Kligman et al. (2023) in cautioning against calibrating the divergence of caecilians and batrachians according to the phylogenetic hypothesis of Pardo et al. (2017a), i.e., by using the Late Carboniferous age of certain dissorophoid temnospondyls as the calibration date.

Concerning phylogenetics, we reiterate that the majority-rule consensus is not a useful representation of the result of a parsimony analysis, and that not all issues with Bayesian analysis of matrices with missing data have been solved; but most importantly, matrix quality remains paramount in phylogenetic analysis. This concerns typographic errors, misinterpretations of published literature, redundant characters (in the dataset we revised, the double toothrow in the lower jaw of caecilians was coded as seven characters that an analysis could only treat as independent), characters that represent two or more independently varying features, and inconsistencies in scoring. As previously pointed out (e.g. Marjanović and Laurin 2019; Kligman et al. 2023; and references in both), avoiding, detecting and mitigating these issues is time-consuming but not difficult.

## Acknowledgments

Jason Pardo and Adam Huttenlocker kindly sent us both matrices, and J. Pardo and Ben Kligman discussed certain characters with us. The reviewers Marvalee Wake and Christian Sidor led us to improve the clarity of our writing. D. M.'s understanding of current issues in phylogenetics benefited from a course taught by Tiago Simões and Oksana Vernygora and organized by Transmitting Science.

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## Supplementary material 1

### Mesquite NEXUS file of Pardo et al. (2017a: fig. S6), previously unpublished

Authors: David Marjanović, Hillary C. Maddin, Jennifer C. Olori, Michel Laurin

Data type: nex

Explanation note: We have added a PAUP block that repeats our unconstrained and constrained analyses (a1, a2) if the file is executed in PAUP\*, and a TREES block that contains one tree resulting from each analysis; before conducting the analyses, the PAUP block performs the statistical tests comparing the trees in the TREES block. Otherwise the file remains as provided by J. Pardo and A. Huttenlocker.

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Link: <https://doi.org/10.3897/fr.27.109555.suppl1>

## Supplementary material 2

### Frequencies of bipartitions in our (unrooted) bootstrap analyses

Authors: David Marjanović, Hillary C. Maddin, Jennifer C. Olori, Michel Laurin

Data type: pdf

Explanation note: Tables S1–S4, showing the bootstrap bipartitions corresponding to analyses b, d1, d2 and e4.

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Link: <https://doi.org/10.3897/fr.27.109555.suppl2>

### Supplementary material 3

#### **Mesquite NEXUS file of Pardo et al. (2017a: fig. 2, 3, S7) with the albanerpetid OTU of Daza et al. (2020) added**

Authors: David Marjanović, Hillary C. Maddin, Jennifer C. Olori, Michel Laurin

Data type: nex

Explanation note: No scores are changed, all characters are unordered. We have also added a PAUP block and deleted the CHARSTATELABELS block because Mesquite could not deal with it correctly. If the file is executed in PAUP\*, it repeats our analysis b (without Albanerpetidae), bootstraps it, and repeats analysis c (with Albanerpetidae).

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Link: <https://doi.org/10.3897/fr.27.109555.suppl3>

### Supplementary material 4

#### **Mesquite NEXUS file of Pardo et al. (2017a: fig. 2, 3, S7) with the clinal characters ordered and the albanerpetid OTU of Daza et al. (2020) added**

Authors: David Marjanović, Hillary C. Maddin, Jennifer C. Olori, Michel Laurin

Data type: nex

Explanation note: For characters 205, 221, 327 and 328, the states had to be reordered to allow for linear ordering as described in the text. If executed in PAUP\*, the file repeats our analysis d1 (without Albanerpetidae), bootstraps it, repeats analysis d2 (with Albanerpetidae) and bootstraps it as well.

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Link: <https://doi.org/10.3897/fr.27.109555.suppl4>

### Supplementary material 5

#### **Mesquite NEXUS file of Pardo et al. (2017a: fig. 2, 3, S7) with the modifications to characters and individual scores described in the text and the albanerpetid OTU of Daza et al. (2020) added**

Authors: David Marjanović, Hillary C. Maddin, Jennifer C. Olori, Michel Laurin

Data type: nex

Explanation note: If executed in PAUP\*, the file repeats our analyses e1 (without Albanerpetidae) and e3 (with Albanerpetidae).

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Link: <https://doi.org/10.3897/fr.27.109555.suppl5>

### Supplementary material 6

#### **Mesquite NEXUS file of Pardo et al. (2017a: fig. 2, 3, S7) with the modifications to characters and individual scores described in the text, the albanerpetid OTU of Daza et al. (2020) added and the clinal characters ordered as in Suppl. material 4**

Authors: David Marjanović, Hillary C. Maddin, Jennifer C. Olori, Michel Laurin

Data type: nex

Explanation note: If executed in PAUP\*, the file performs our analyses e2 (without Albanerpetidae) and e4 (with Albanerpetidae) and then bootstraps e4.

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